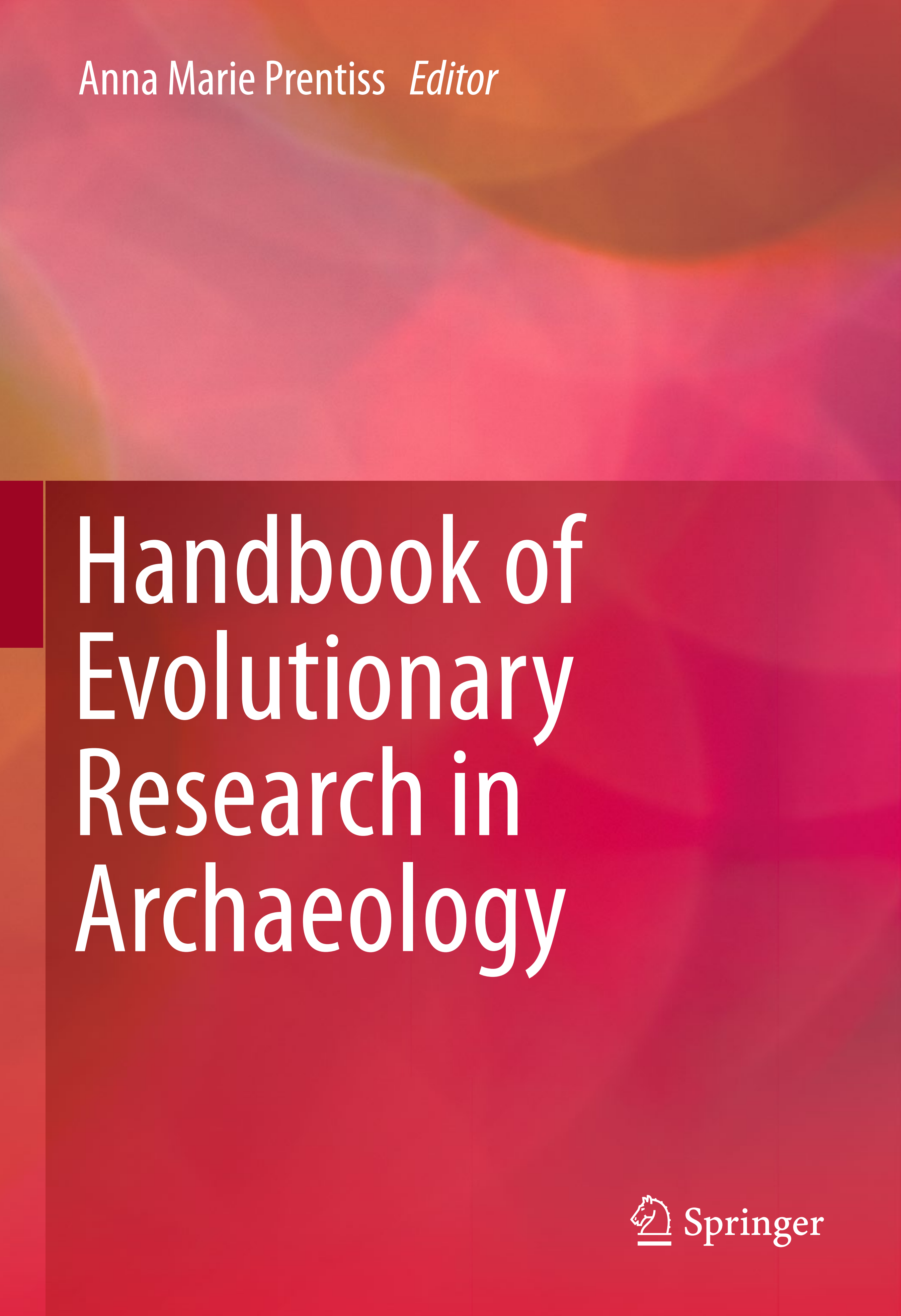

Anna Marie Prentiss *Editor*

Handbook of Evolutionary Research in Archaeology

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Chapter 1
Introduction

Anna Marie Prentiss

Introduction

Evolutionary archaeology has developed from a marginal discussion to a mainstream focus in modern archaeology. Archaeologists have become widely aware that the rigorous procedures developed in the guise of evolutionary research can provide significant insight into a host of phenomena including technological change, migration, subsistence adaptation, demography, sociality, and cognition on long and short scales (Lycett 2015). This handbook is designed as a guide to current research trends, insights, and contributions of evolutionary research in archaeology. The theoretical focus in all chapters is Darwinian evolution process inclusive of perspectives broadly derived from the modern evolutionary synthesis (Huxley 1942) and the emerging extended evolutionary synthesis (Laland et al. 2015). Contributions to the book are not about neoevolution and other social science paradigms more influenced by the writing of Spencer (1857; e.g. Harris (1979); White (1959)). Given the focus on archaeology, the book also excludes specific coverage of evolutionary psychology though issues of cultural transmission and cognitive archaeology at times take us into psychological realms. Finally, this is not specifically a book about paleoanthropology though the models of evolutionary archaeology, human ecology, and evolutionary cognitive archaeology offer a wide range of contributions to our understanding of human bio-cultural evolution.

Evolutionary research in archaeology is now a vast endeavor driven by scholars throughout the globe integrating theoretical concepts spanning evolutionary biology to the various cultural sciences (Mesoudi 2011; Mesoudi et al. 2006). The diversity of evolutionary research in archaeology thus poses a significant challenge for explicating its contributions within a single book. I accomplish this by drawing organizational concepts from the work of Niles Eldredge (1985), who, in his book, *Unfinished Synthesis*, argued that evolutionary process can be understood within dual genealogical and ecological frameworks, both hierarchically structured and implicating evolutionary and ecological process on multiple scales. Entities within the genealogical or evolutionary hierarchy span genes to species to monophyletic taxa implicating processes of evolution acting across time measured on scales of single to thousands of generations or, put differently, as microevolution and macroevolution. It is, thus, within the genealogical hierarchy that we monitor evolutionary change through time. However, Eldredge argues that the process of evolution cannot unfold without activity in the adjoining ecological hierarchy as it is here, with its organisms, avatars, and ecosystems, that energy is exchanged,

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reproduction accomplished, and the process of natural selection actually played out. Thus, the effects of economic, social, and reproductive decision-making among living entities in their ecological surroundings are essential to understanding the wider evolutionary process.

Cultural evolution can also be understood within evolutionary and ecological frameworks. Evolutionary anthropologists established the cultural evolution can be understood to act as an inheritance system operating in parallel to biological inheritance (Boyd and Richerson 1985). This dual inheritance framework permits us to recognize a cultural microevolutionary process with a wide array of potential impacts on the development of cultural concepts and their subsequent evolution over shorter and longer time spans. In the shorter term, cultural inheritance is recognized as a complex process of transmission by imitation, teaching, and experimentation regarding cultural characters that vary with the accumulation of errors, modifications, and innovations. Over longer or macroevolutionary spans, cultural evolution can be understood as a product of accumulated microevolution (O'Brien and Lyman 2000), a result punctuated change on higher integrated scales (Prentiss et al. 2009), or the effect of more complex neutral and nearly neutral processes (Kandler and Crema, this volume; Kandler and Shennan 2013; Laue and Wright, this volume). Boyd and Richerson (1992a, b) recognize that cultural inheritance affects ecological (and reproductive) decision-making. Simultaneously, ecological/reproductive decisions have long- and short-term impacts on the persistence of human populations and their associated cultural traditions (Richerson and Boyd 2005). Consequently it is highly appropriate that we study human ecology within evolutionary frameworks. Finally, given the central importance of human cognition to short- and long-term cultural evolutionary process (Abramiuk 2012), evolutionary cognitive research remains a critical concern to an integrated evolutionary approach to archaeology.

The *Handbook of Evolutionary Research in Archaeology* is thus organized around four major themes: cultural microevolution, cultural macroevolution, human ecology, and evolutionary cognitive archaeology. In the following, Chap. 1 introduces each theme and provides a short history of research and a review of associated critical theoretical and methodological milestones. I close with a short review of book contents by subject matter and author.

Research Themes

Cultural Microevolution

Our understanding of evolutionary process on any scale depends upon our knowledge of microevolutionary process as it is here that change occurs and variants persist on an intergenerational basis. The most widely influential model of microevolution derives from the Darwinian synthesis of the mid-twentieth century in which Darwin's (1859) naturalism was combined with genetics (Huxley 1942). Synthetic Darwinism embodied a number of distinct conclusions regarding the structure of the evolutionary process. These included an emphasis on population thinking such that change was reflected in changes in character frequencies. Given this assumption, species were not "real" in an empirical sense (Brooks 2011). Evolutionary process was understood to be an undirected process (thus, non-Lamarckian) that combined exclusively genetic inheritance with sorting mechanisms consisting of natural selection and drift. Put differently, inheritance was viewed as logically independent or "blind" to the effects of selection or drift processes. Evolution was thus assumed to be a gradual process by which organisms with high fitness would outcompete those with lower fitness within an ecological context. This could be visualized as exclusive occupancy of optimal fitness space held as long as not outcompeted by another variant (Brooks 2011).

Anthropologists have been interested in cultural evolution since the era of the social Darwinists (Morgan 1877; Spencer 1857; Tylor 1871). However, it was not until the 1960s that anthropologists and evolutionary biologists took their first forays into serious consideration of cultural evolution from a Darwinian standpoint. An important early paper was Campbell's (1965) "Variation and Selective Retention in Sociocultural Systems." Campbell made four critical arguments that (1) sociocultural evolution is a process of descent with modification and can thus be examined from a Darwinian perspective; (2) evolution is a genetic and cultural process; (3) natural selection is the ultimate force in cultural and biological evolution; and (4) natural selection has direct impacts on cultural variants. As noted by Richerson and Boyd (2000), these arguments were highly influential and shortly led to a number of important papers. Collectively these contributions suggested that it would be possible to use formal models from evolutionary biology to explore nuances of cultural evolutionary process, particularly cultural transmission (Cavalli-Sforza and Feldman 1973, 1981; Ruyle 1973), and if so, then scholars would also be able to model culture as a fitness-enhancing system (Durham 1976). Durham (1976) introduced the concept of cultural selection, suggesting that if cultural variants offered benefits to biological fitness, then selective retention of those traits might be best understood within the synthetic Darwinian framework. Durham (1976, p. 115) called this process "coevolution" and pointed to cultural evolution as a logically separate but complimentary process to biological evolution.

Lumsden and Wilson (1981) took gene-culture coevolution a step further in their explication of its linkages to sociobiological process. Adherents to sociobiology had argued that behavior could be explained as optimal choices for enhancing fitness in particular settings (Krebs and Davies 1981; Wilson 1975). Critiques of this position focused on the nature of cultural behavior as not inherited biologically and thus inappropriate for sociobiological modeling. But Alexander (1979) and Irons (1979) argued that even cultural behavior could be viewed as phenotypic plasticity and thus still fitness enhancing and subject to effects of selection. Yet, this argument still suffered from its inability to adequately explain the diversity of culture using fitness optimality arguments. Lumsden and Wilson (1981, pp. 343–344) argued that while traditional sociobiology could not adequately account for transitional relationships between genes and cultures, coevolution could make that jump via what they called epigenesis or the rules for development of behavior as proscribed by "gene ensembles inherited by single organisms." Persistence of cultural variants within this framework was thus substantially dependent upon genetic fitness resulting from behavior stimulated by acceptance of those variants.

Boyd and Richerson (1985) note that a wide variety of scholars made similar arguments regarding relationships between genes and culture during this period (e.g., Alexander 1979; Baldwin and Baldwin 1981; Boehm 1978; Harris 1979; Plotkin and Odling-Smee 1981) that ultimately amounted to four substantially sociobiological hypotheses: (1) the "pure environment" hypothesis asserts that different behaviors among different groups is the result of optimal decision-making by individuals as structured by the inherited genetic traits and not culture (cf. Alexander 1979); (2) the environment plus culture hypothesis states that inherited cultural variants can have fitness-enhancing effects along with optimal behavior as explicated under the pure environment hypothesis (cf. Durham 1978, 1979); (3) the pure genes hypothesis holds at its ultimate extreme that cultural differences between human populations are best explained by genetic differentiation (cf. Lumsden and Wilson 1981); and (4) the genes plus culture hypothesis asserts that while cultural inheritance is an important force, its impact is generally short term such that decisions to accept or reject particular cultural variants are still most strongly impacted by population genetics (cf. Lumsden and Wilson 1981). Boyd and Richerson (1985, pp. 170–171) point out that these hypotheses are important in that they provide a biologically oriented standard by which other models of cultural evolution must be compared. However, they argue that there is good reason to believe that none are correct given that the impacts of human decision-making outside of culturally inherited tools to solve complex problems are probably quite minimal and there are many examples of cultural traditions persisting despite environmental change.

Boyd and Richerson's (1985) and Richerson and Boyd's (2005) highly influential dual inheritance theory was a critical outcome of the sociobiology and gene-culture coevolution discussions in the late 1970s and early 1980s. Dual inheritance theory was developed as set of formal models specifying culture as information that was acquired through either imitation or teaching/learning.

Boyd and Richerson sought to overcome challenges of the sociobiological models as well as contra-sociobiological perspectives of other anthropologists, for example, Sahlins (1976) who asserted that genetics and adaptation to environmental contexts could be ignored in theorizing culture and culture change. The outcome was recognition of culture as an inheritance system that included explicit mechanisms by which diversity was introduced over time leading to the possibility of divergent cultural traditions. Boyd and Richerson developed explicit models that included guided variation or the effects of learning from a teacher and bias mechanisms that specified the means by which individuals might preferentially favor one cultural variant over another. The latter included direct bias or the results of evaluations of options, frequency-dependent bias or the effects of chooses that which is most common or rare within a social network, and, finally, indirect biases, those that derive from modeling on an index trait (e.g., prestige) that leads to acceptance of additional traits without question. Boyd and Richerson's work firmly established the study of cultural transmission in the social and biological sciences leading to a wide variety of new studies in and out of archaeology (e.g., Bettinger and Eerkens 1999; Eerkens and Lipo 2007; Kandler and Crema, this volume; McElreath et al. 2003; O'Brien 2008; Richerson et al. 2001; Soltis et al. 1995; Stark et al. 2008; Walsh et al. Chaps. 2 and 3, this volume). Theories of cultural transmission were also an important antecedent to the so-called cultural virus theory, which borrowed equally from Dawkins' (1976) concept of the selfish gene imagining cultural entities ("memes") engaging much like genes in strategies to self-replicate (Blackmore 1999; Cullen 1996). Despite the importance of cultural transmission theory to early evolutionary anthropologists, it was curiously unimportant in early evolutionary archaeology.

During the 1970s and through the 1980s, Robert Dunnell published a series of papers promoting what eventually became known as evolutionary archaeology. Dunnell (1980) offered a number of critiques of archaeological (and by extension, anthropological) theory focusing in particular on problems of essentialism and uses of "common sense" in anthropological interpretation. Dunnell's fundamental concern was that in pursuit of the goals of processual archaeology that involved interpretation of sites in order to reconstruct the functioning of cultural systems, scholars effectively reified the present thus biasing any hope of understanding change. Further, they introduced explanatory bias clouded by ethnocentric assumptions by relying implicitly on so-called common sense arguments derived from Western culture. To Dunnell, this left archaeologists in the position of seeking explanations for change between invalid cultural constructions without reference to defensible theoretical concepts. Interestingly, the post-processual theorists of the 1980s posed some of the same critiques but answered them with a push to move away from science toward Marxian-inspired interpretivist archaeology (Hodder 1985; Shanks and Tilley 1987). Dunnell took the opposite tact promoting an empirically based archaeology that relied heavily on the synthetic evolutionary model. Dunnell's (1980, 1982, 1989) conception of an evolutionary archaeology aligned archaeology with paleontology in the sense that archaeologists cannot direct monitor cultural change at the level of information as proposed, for example, by Boyd and Richerson just as paleontologists could not study evolution as change in gene frequencies. Rather, archaeologists were faced with variation in material culture (artifacts and features), which evidently changed over time but not in the same way as biological species. Indeed, this issue had been a long-standing concern to archaeologists effectively preventing culture history era scholars from adopting synthetic Darwinism at much earlier dates (e.g., Brew 1946; Willey 1966). The study of artifacts with a particular focus on classification became a central concern to early evolutionary archaeology (e.g., Dunnell 1989, 1995; Ramenofsky and Steffen 1998), and this along with a concern for change over extremely long time spans helps to explain its limited engagement with cultural transmission theory (Cochrane 2009).

To create a truly Darwinian scientific archaeology, Dunnell argued that artifacts represent the hard parts of the human phenotype much like fossils and that change was not qualitative but quantitative as characters were added and replaced (Dunnell 1989). If artifacts reflected the evolution of the human phenotype, then it positioned archaeology as another evolutionary science (Goodale et al. this volume). Next, Dunnell needed a way to understand the evolutionary process from a material cultural standpoint. Drawing from the basic tenets of the synthetic model, Dunnell (1989) and colleagues (e.g., Rindos 1989) made the critical argument that, despite the well-recognized fact that cultural transmission is rather Lamarckian in structure (e.g., Boyd and Richerson 1985), when viewed in the long term, cultural variation is still undirected or blind to future developments. This view permitted early evolutionary archaeologists to thus avoid issues of cultural transmission process and to focus on sorting mechanisms of cultural variation (however acquired). Early papers emphasized the importance of natural selection as the dominant force in material cultural evolution (O'Brien and Holland 1990). Fitness was a thorny problem given the challenges of explaining artifact change with a biological model but was resolved as potential for replicative success (Leonard and Jones 1987) or, later, acquisitive fitness (Chatters 2009). Although Dunnell (1980) had initially recognized the possibility of complex macroevolutionary processes in cultural lineages, evolutionary archaeology in effect hardened around a somewhat narrow interpretation of the synthetic model that generally assumed a process of microevolutionary gradualism as the primary pattern and process of cultural evolution (O'Brien and Lyman 2000).

While natural selection was the subject of such attention that 1990s evolutionary archaeology also came to be known as "selectionism," evolutionary archaeologists did not focus exclusively on selection-driven evolutionary trends. Extending back to some of Dunnell's early writing (e.g., 1978), scholars also recognized the importance of drift processes, expected to be associated with artifact style, for example. It was generally assumed that in the absence of adaptive forces, cultural entities would vary due to rates of innovation and "cultural drift" (Shennan 2002). In an important early paper, Neiman (1995) demonstrated that neutral innovation and cultural drift would create patterns in the frequencies of ceramic types resembling what archaeologists call "battleship curves." The issue of neutrality in the cultural evolutionary process remains important as indicated by the frequency of recent papers concerned with the topic (e.g., Acerbi and Bentley 2014; Brantingham and Perreault 2010; Crema et al. 2014; Kandler and Shennan 2013). Advanced quantitative techniques are now being applied to test hypotheses about cultural transmission and neutrality in the archaeological record (Kandler and Crema, this volume). Important outcomes to date from this research suggest that tests of neutrality and transmission process using archaeological data should be designed to recognize the effects of equifinality as in some cases multiple transmission histories may give rise to common patterns.

Cultural Macroevolution

Macroevolution developed as the study of evolution at the species level, which for organic evolution means primary data come from fossil record (Eldredge 1989; Stanley 1998). This contrasts with neontology with its focus on extant organisms. Simpson (1944) made use of the term macroevolution in his overview of paleontological contributions in reference to evolutionary trends, patterns, and rates, drawing from Goldschmidt (1940), to make a distinction between changes within species and that above the level of species. However Simpson's use of the term macroevolution was apparently not in recognition of macroevolution process as distinct from that of microevolution. Rather, to Simpson the term was a practical necessity given different sources of data where microevolution focused on genetic changes across limited numbers of generations and macroevolution emphasizing evolution on scales of species, genera, families, and orders (Stanley 1998). Macroevolution as a distinct area of study faced two major challenges. First, it is hard to do given necessary reliance on fossils. An overarching bias against evolutionary research using fossils had been set in motion by Darwin himself (1859) who sought to defend his position that species were in constant and very gradual state of change by noting that the spotty fossil record of the mid-nineteenth century and its implications for a punctuated process could not possibly be valid for anything other than a marker of the fact that evolution had occurred and that it indeed had significant time depth. A century later, assumptions of an insufficient fossil record still relegated paleontology to the study of geological time and explication of the history of animal and plant life (Gould 1995). Then, the development of evolutionary genetics (Dobzhansky 1937; Wright 1931) strongly reinforced the assumption that evolutionary process played out on microevolutionary scales. Thus, the second challenge for macroevolution was the assumption that there was no such thing as macroevolutionary process, only microevolution stretched out to long time scales (Eldredge 1999). Yet even Darwin had titled his epic tome "On the Origin of *Species*..." (Italics mine) implying that such biological entities might be real and that they could evolve in a process as described by Darwin and, later, the scholars of evolutionary genetics. One potential pathway out of this paradox was the study of speciation (e.g., Mayr 1942; Lewis 1962) with its implication that species were stable entities and that the bulk of evolution occurred during their emergence (Stanley 1998). A "hardened" synthetic evolutionary biology was ultimately not generally receptive to species as real entities (Eldredge 1995), and it eventually fell back to paleontologists (at least to a substantial degree) to make the case. Thus, the publication of Eldredge and Gould's (1972; Gould and Eldredge 1977) arguments for a process of punctuated equilibria acting on species and higher scales ushered in a substantial debate in evolutionary biology that in part resulted in the establishment of the field of paleobiology and its primary focus on macroevolutionary process (Gould 1995). Discussions in paleobiology regarding punctuated equilibria (Gould 2002), multi-level selection (Eldredge 1985; Stanley 1998), and heterochrony (Gould 1977) would help set the stage for today's considerations of the extended evolutionary synthesis, though recognizing that primary contributions are also coming from wider evolutionary biology (Laland et al. 2015).

While the term macroevolution was rarely used, earliest writings in evolutionary archaeology invoked macroevolutionary issues. Dunnell (1980) noted that the pattern of evolution regarding cultural entities could be gradualist or punctuated depending upon scale. Inter-individual genetic change would necessarily be gradual, while change on the scale of species would appear punctuated. Applied to culture Dunnell (1980) pointed to findings of culture history archaeologists that archaeological phases seemed to reflect punctuated change and periods of stasis. However, he also cautioned that such inferences could also be by-products of applied analytical methods. Implicit within Dunnell's argument was an apparent assumption that culture could be measured on different scales with selection favoring traits inherited on both individual and group scales. In the latter case, the implication was that some cultural codes were too complex for any single individual to carry (Dunnell 1980, 1996). If this is the case, then we can only presume that Dunnell was referring to integrated cultural entities more complex than simple rules for making artifacts. It also implied that the cultural evolution could be a hierarchical process with the possibility of change on one scale overriding that of another much as described by Eldredge (1985) in his hierarchical model.

By 1989 however, Dunnell seemed to have little interest in pursuit of evolution on more complex scales beyond artifacts as markers of the human phenotype (Dunnell 1989). Dunnell's positions were substantially reinforced in O'Brien and Lyman's (2000) lengthy review of method and theory in evolutionary archaeology. While still generally avoiding mention of macroevolution by name, these scholars were clearly concerned with macroevolutionary issues as exemplified by their detailed consideration of relationships between archaeology and paleobiology. Ultimately however, their position remained entrenched in the fundamental tenets of the synthetic evolutionary model emphasizing undirected variation and gradual change in the composition of populations over time as impacted by selection and drift. While their focus remained on artifacts, the authors did, however, note the importance for evolutionary archaeology of studying change on all scales. Thus, as exemplified by the work of other scholars (e.g., Braund 1987; Jones et al. 1995; Leonard and Jones 1987; Neff 1992), evolutionary archaeology retained the possibility of inclusiveness in evolutionary analysis within a framework best defined as organismic macroevolution (Prentiss et al. 2009; c.f. Eldredge 1989).

Taxic macroevolution developed within paleobiology as the study of evolutionary forces operating on evolutionary entities at scales above the organism, for example, species and genera (Eldredge

1989; Gould 2002; Jablonski 1999; Stanley 1998). Central to taxic macroevolution was the concept of species selection in which selective forces acted at the level of species as evolutionary individuals. While debated during the 1970s through 1990s (reviewed in Gould 2002), concepts of multi-scalar evolution would eventually become essential to the extended Darwinian synthesis (Brooks 2011; Laland et al. 2015; Müller 2017). This kind of thinking was highly influential on a group of archaeologists during the 1990s seeking a way to move beyond the artifact-centered approach of the evolutionary archaeologists. Prior to this time, scholars had proposed cultural macroevolutionary models (Diener 1974; Diener et al. 1980; Marks and Staski 1988). However, these had generally suffered from poor integration of cultural microevolutionary and macroevolutionary thought. This was particularly evident in Marks and Staski's culture as species approach (see also Pagel and Mace 2004), critiqued for ignoring the cultural evolutionary process on lower scales (e.g., inter-individual cultural transmission) (Boyd et al. 1997; Prentiss et al. 2009).

Rosenberg (1994) provided the first model that could best be linked to taxic macroevolution in recognizing evolutionary process on scales of integrated cultures, termed *baupläne* by Rosenberg. The *bauplan* concept was useful to Rosenberg as it was originally developed in morphometrics to describe a structural design (Seilacher 1970), not a specific evolving entity. Thus, we might envision the "rodent *bauplan*" while recognizing that it was not the *bauplan* specifically that was evolving in contrast to say a particular species of mouse or rat. Regardless, to Rosenberg it was those structural elements within a culture that could be inherited and, thus, evolve in a punctuated manner through periodic crises that could trigger the breakdown and recrystallization of cultural structures. These cultural crises acted something like species selection as, for example, in Vrba's (1985) turnover pulse hypothesis that relied upon periodic ecological crises to eliminate some species and favor others. Thus, Rosenberg's vision of cultural macroevolution relied heavily on the assumption that while lower scale evolution was continuously present, it was the higher scale forces that had the most lasting impacts. Spencer (1990, 1997, 2009; Spender and Redmond 2001) developed a model that recognized selection-driven trends (e.g., McShea 1994) from lower levels leading to newly emergent forms of higher-level integration. For example, decisions made between persons or factions promoting new forms of social organization could be rewarded socially and biologically, thus feeding a growth process leading to new forms of organization. Spencer (1997, 2009) provides the example of the emergent Monte Alban chiefdom "extrapolating" its sociopolitical strategy onto the wider region and thus giving rise to a state-like organization. Spencer's approach was equally influenced by action theory as exemplified by the so-called Michigan school of social evolution (e.g., Marcus 2008; Marcus and Flannery 1996) that recognized a critical role for individual self-interested actors and factions as essential to the emergence of new social strategies. While "intent" was excluded as epiphenomena to evolutionary archaeologists (O'Brien and Lyman 2000), it retained a role to action theorists even when enveloped within a Darwinian-influenced framework.

Prentiss and Chatters (2003), Chatters (2009), Prentiss (2009), and Chatters and Prentiss (2005) offered a third approach to cultural macroevolution that recognized what they termed resource management strategies (RMS) or the integrated logic of human economic organization as evolutionary entities. Recognizing that an entire RMS with its potentially many parts, spanning technology to hunting and gathering tactics and seasonal scheduling, could not be easily transmitted between persons, they suggested that the structural logic of such a complex entity could be transmitted and thus subject to evolutionary forces. Borrowing from Mayr's (1942) model for speciation via reproductive isolation, they argued that local groups socially or physically isolated from dominant regional strategies, while operating under productive resource conditions, offered the best opportunities for rapid evolutionary change. Their model left open the possibility that isolated groups could drift into new forms of organization, for example, by scheduling mishaps and consequent organizational shifts versus simple selection-driven changes as resource structure and demographic conditions changed. Finally, they proposed that regional ecological change could have severe impacts on the survival and further evolution of RMS such that during environmental transitions entire strategies could be driven extinct during short-lived periods resembling Vrba's (1985) turnover pulses. Prentiss and Chatters' arguments regarding the evolution of hunter-gatherer and horticulturalist economic organization are similar to those of Barton et al. (2007), Bettinger and Baumhoff (1982), and Foley and Lahr (2011).

The first decades of evolutionary archaeology were generally long on rhetorical argument and short on empirical tests. A fundamental question lingered and that was whether culture could actually evolve via descent with modification in a branching fashion similar to biological lineages. Evolution by branching is central to a Darwinian understanding of the evolutionary process and is best demonstrated by phylogenetic study designed to determine evolutionary relationships between taxa typically defined as clades (Straffon 2016). Moore (1994) had published a scathing critique of cladistic thought in archaeology and anthropology favoring a model based on the concept of ethnogenesis suggesting that culture change was metaphorically more akin to a braided stream due to blending and borrowing of cultural traits. Moore's argument was influential to those outside of the evolutionary archaeology community who sometimes reified his position with similar statements (e.g., Sassaman 2011). None of these scholars, however, marshaled data to demonstrate whether or not the critique was accurate. Evolutionary archaeology held a long-standing interest in defining artifact lineages and seeking selectionist explanations for particular trends (O'Brien and Lyman 2000). Indeed, it could be argued that this endeavor is essential to creating archaeological histories regardless of explanatory apparatus. Thus, culture historians relied intensively on seriations to not only place artifacts in time space sequences but also to define ancestor descendent relationships (Lyman et al. 1997).

Anthropologists and archaeologists developed an increasingly serious interest in defining phylogenies during the 1980s and 1990s while focusing on two problems: defining lines of inheritance to earliest ancestors to develop an understanding of geographic expansion and cultural change and distributional studies focused on explanation of adaptive diversity (O'Brien and Lyman 2003). Examples of these studies include Kirch and Green's (1987) research into Polynesia adaptations and dispersals; Renfrew's (1987, 1992, 2000) studies of culture, language, and DNA distributions; and various studies into African population movements and cultural adaptations (e.g., Holden and Mace 1997, 1999; Mace and Pagel 1994). Of particular significance for evolutionary archaeology was for some an exploration of phylogenetic modeling using cladistics (Straffon, this volume). Cladistics was developed in biology as a formal means of defining ancestral relationships under the assumption that evolutionary lines eventually split with descendants retaining some ancestral traits while also acquiring new or "derived" traits (Hennig 1966). In theory the most recent descendants within a given phylogeny would also have the greatest frequency of derived traits (Mayr 1969), and thus, all things equal, the "trees" generated by cladistics should represent some underlying historical pattern that could be explained using evolutionary theory (O'Brien and Lyman 2003). But phylogenies generated by cladistics or phenetic techniques that replicate cladistic outcomes (e.g., neighbor joining and NeighborNet networks) are complicated by the possibility that not all relationships between taxa developed from simple branching. In some cases, results are clouded by borrowing and blending effects that are identified as reticulations as might be typical of ethnogenesis per Moore (1994) and earlier concerns by Kroeber (1948). Fortunately, there are quantitative techniques that permit assessment of the degree to which cladistic outcomes are impacted by reticulations, and this provides the opportunity to test the hypothesis that cultural evolution occurs via descent with modification.

A wide range of phylogenetic studies directly addressed the problem of vertical versus oblique and horizontal inheritance initially demonstrating that the issue was one of quantitative variability. Descent with modification was recognizable along with the variable effects of blending in multiple artifact lineages including projectile points (O'Brien et al. 2001), weavings (Tehrani and Collard 2009), skateboards (Prentiss et al. 2011), basketry (Jordan and Shennan 2009), pottery (Cochrane and Lipo 2010), and Lower Paleolithic hand axes (Lycett 2007). Mace and Holden (2005) argued that the phylogenetic approach could be expanded to study the evolution of a wider range of phenomena including complex cultural adaptations. Consequently, scholars demonstrated descent with modification had also occurred in complex technological traditions including ritual features (Cochrane 2015), house architecture (Jordan 2015; Jordan and O'Neill 2010), Neolithic plant economies (Coward et al. 2008), and hunter-gatherer resource management strategies (Prentiss et al. 2014a, b, 2015). An outcome of the latter studies was confirmation of the cultural macroevolutionary contention that higher-scale entities can be measured and shown to evolve via descent with modification. Bayesian phylogenetic analysis is now increasing our ability to directly address macroevolutionary questions regarding cultural branching on higher scales along with variation in rates of evolution (Gjesfjeld and Jordan, this volume).

Cladistic analysis has been very effective at demonstrating the pattern of evolution with multiple data sets reflecting on phenomena of multiple scales. However, explanation remains a matter requiring explicit attention to theoretical concerns. A number of cultural evolutionary scholars have promoted the use of fitness landscapes to envision shifts between adaptive strategies whether optimal means of projectile point manufacture (Mesoudi and O'Brien 2008a, b) or wider adaptive strategies (Bettinger 2015). The fitness landscape concept was originated by geneticist Sewell Wright (1932) who used simple drawings to depict a hypothetical topographic landscape to depict a range of theoretical fitness possibilities (Z axis) for genetic combinations (X and Y axes). Higher "peaks" on the landscape meant higher potential fitness, while low peaks and troughs in between reflected lower fitness options. Evolution was envisioned as a process by which characters shifted between peaks due to the effects of genetic drift and natural selection. While Wright's ideas have been extensively discussed and debated (e.g., Arnold et al. 2001; Boyd and Richerson 1992a; Calcott 2008; Gavrilets 2003; Kaplan 2008; Kauffman and Levin 1987; Pigliucci 2008), they remain important to scholars in evolutionary biology, paleobiology, and evolutionary archaeology. Evolutionary archaeologists have used fitness landscapes as metaphors for microevolutionary process in reference to projectile point manufacture (Mesoudi and O'Brien 2008a, b) and macroevolutionary process regarding stasis (Prentiss 2009; Prentiss and Lenert 2009) and rapid change (Bettinger 2009; Chatters 2009; Kuhn 2006; Spencer 2009). Challenges remain however, as archaeologists have generally relied upon fitness landscape concepts that are little changed from Wright's original models, whereas much is changing in evolutionary biology. Future research will be necessary to develop a more sophisticated approach for cultural evolution drawing from more complex landscape metaphors as associated with nearly neutral models and dynamic, three-dimensional, and holey fitness landscapes (e.g., Kauffman and Weinberger 1989; Gavrilets 2004; Gravner et al. 2007). Such models may offer significant potential for tackling challenging cultural macroevolutionary and paleoanthropological challenges including extremely long-lived technologies in the Paleolithic (e.g., hand axes, Mousterian tool complexes, Upper Paleolithic blade production systems) and major cultural transitions such as the origins of agriculture (Laue and Wright, this volume).

Human Ecology

Anthropologists and archaeologists have had a long-standing interest in human ecological relationships. This has led to a variety of productive research ventures and alternative theoretical perspectives, not all of which were in line with Darwinian thinking. Neoevolution (Sahlins 1960; Service 1962; White 1959) and cultural ecology (Steward 1955) were significant theoretical advances over simple environmental determinism and historical particularism of the late nineteenth and early twentieth centuries. Each directed scholars toward consideration of cultural adaptations within environmental contexts. Yet each suffered significant flaws. As argued by Smith (1991; Smith and Winterhalder 1992), neoevolutionism's primary flaw was typological essentialism, the requirement that a tremendous array of variation be collapsed into "types" such as "bands" and "chiefdoms." Neoevolution, with its theoretical base in Spencer's (1857) brand of evolutionary thinking (Dunnell 1980), was very influential on archaeological theorizing during the 1960s and later as, for example, is evident in the writing of early processual archaeologists (e.g., Binford 1962, 1968). Debates over the use of neoevolutionary terminology continue in anthropological archaeology (e.g., Pauketat 2007). Cultural ecology led to a wide range of studies focused on systemic relationships between local environments and aspects of culture (e.g., Lee 1979; Rappaport 1968). The primary problem with cultural ecology was its reliance on functionalist explanations involving circular logic such that outcome (e.g., benefits to a population) would explain origin. Typically on weak theoretical grounds, such explanations were also not well validated empirically (Smith 1991). Piddocke's (1965) work on the Kwakiutl potlatch is a particularly good example of the functionalist approach. Harris' (1979) cultural materialism was a theoretical descendent of cultural ecology and neoevolution and suffered from the same challenges, in particular, insufficient capacity to define and integrate critical concepts (compare to explanatory structure of synthetic Darwinism) and inability to generate adequate testable propositions, thus leading to nothing much better than "loose plausibility arguments" and "an extreme polemical tone in anthropological theorizing" (Smith 1991, p. 7).

Problems with neoevolution and cultural ecology inevitably led to a strong theoretical response both in sociocultural anthropology and archaeology. Despite the array of important and insightful studies generated within the cultural ecology framework, many sociocultural anthropologists left the fold during the 1970s to focus on non-ecological issues associated with belief systems, symbolism, and Marxian criticism (e.g., Sahlins 1976). A similar trend was initiated in the 1980s in archaeology leading to the so-called post-processual rebellion against Lewis Binford and the processualists (e.g., Hodder 1985). A chief criticism of the latter scholars was that cultural ecology and neoevolutionism left little place for individual agency given their focus on systemic relationships. Their solution was to relinquish interest in ecology in favor of culture-centered understandings. However, as seen with evolutionary archaeology, there was really no need to drop evolution or ecology when Darwinism offered a powerful framework that recognized and indeed relied upon concepts of individual agency as a core element in the structure of explanation. Evolutionary biology was meanwhile already substantially down the road in developing a Darwinian ecological approach to economic, reproductive, and social behavior.

While much ecological research prior to the 1960s had been substantially descriptive, a few mathematically inclined ecologists explored models concerned with competition, predation, and population dynamics (Winterhalder and Smith 1992). This set the stage for the first recognized studies in evolutionary ecology by David Lack (e.g., 1954) and Robert MacArthur (e.g., 1958, 1960). Critically, these scholars wed natural selection thinking from the Darwinian synthesis with the interests of ecologists in thinking about predation strategies, population regulation, community structure, and competitive relationships (Winterhalder and Smith 1992). This was in many ways revolutionary as it opened doors to study of many topics that had long challenged ecologists and simultaneously led to new subfields including island biogeography (MacArthur and Wilson 1967), foraging theory (MacArthur and Pianka 1966), and reproductive ecology (Orians 1969). By the 1970s, the field of evolutionary ecology was formalized by the appearance of multiple textbooks (e.g., Emlen 1973; Pianka 1974; Roughgarden 1979Winterhalder and Smith 1992). In the late 1970s, an initially small group of anthropological scholars recognized the advantages of evolutionary ecology for addressing questions of variability in human behavior in its ecological context (e.g., Smith and Winterhalder 1992; Winterhalder and Smith 1981). Evolutionary ecology offered a comprehensive approach to understanding diversity while avoiding problems of environmental determinism, normative types, functionalism, and culture exclusiveness inherent in other approaches. It permitted linkage to the well-developed tenets of synthetic Darwinism, and it required formal hypothesis testing (Richerson 1977).

Evolutionary ecology (EE) is a diverse field with many subareas. The variant most widely in use by anthropologists and archaeologists is human behavioral ecology (HBE) given a focus on human decision-making and adaptive behavior. Within HBE, anthropological scholars pursue in particular foraging theory, reproductive ecology, and socioecology. While details of individual models vary, all have certain aspects in common. First, models in EE are explicitly formulated within a synthetic Darwinian framework assuming that behavior is part of the human phenotype. Natural selection is assumed to act on phenotypes thus favoring the preservation of certain phenotypes and their associated genotypes. As noted by Kelly (1995), this raises two positions on the evolutionary process in reference to adaptive behavior. The "strong sociobiological thesis" recognizes a strong link between behavior and genetic variation, thus arguing that if behavior is genetically controlled and permits significant reproductive success, then that behavior will become more common. This view immediately encounters the well-debated problem that variability in human behavior is not determined by genetics. This then takes us to the "weak sociobiological thesis" that human behavior results from decision-making that could impact reproductive success measured as inclusive fitness (Kelly 1995). As recognized by cultural microevolutionary scholars (e.g., Boyd and Richerson 1985), this does not mean that natural selection does not affect persistence of cultural characters and their associated human behaviors. Ultimately, HBE proponents favor the weak thesis and assume that behavior comes about via a complex relationship between individual learning and cultural and genetic inheritance, the critical factor being that, however inherited, behavior has impacts on fitness. This naturally leads to the second common characteristic of models in EE, the assumption of methodological individualism (Smith and Winterhalder 1992). Synthetic Darwinism recognizes the effects of selection on variation in phenotypes within population expressed over an intergenerational basic. This requires that analysts be concerned with variability whether expressed with genetic, cultural, or behavioral data. Hypotheses within HBE are then constructed around adaptive decision-making by individuals whether associated with food getting, land use, population regulation, or social cooperation (Cannon and Broughton 2010; Kelly 1995). Third, EE and HBE hypotheses are therefore structured as formal models incorporating optimization assumptions associated with some currency, calories, for example, as a proxy for reproductive fitness in foraging theory (Kelly 1995; but see Bamforth 2002). Optimality has come under criticism as unrealistic for cultural bearing species (Joseph 2000) and as another example of "Panglossian" storytelling (Gould and Lewontin 1979). However, EE/HBE proponents respond that optimality assumptions are simply hypotheses that when tested provide insight as to actual behavioral decision-making that might permit refinement and further research (Cannon and Broughton 2010; see also Gremillion, this volume; Nagaoka, this volume). Finally, in developing optimality models, EE/HBE scholars often rely on assumptions of rationality and universal environmental knowledge by individual actors. This has generated substantial discussion (Cannon and Broughton 2010). As with optimization, rationality has been critiqued as inappropriate given complexities of cultural and cultural inheritance, and yet empirical testing has repeatedly supported the fact that people often do act in economically rational ways (Winterhalder and Smith 2000). Several responses have been proposed to concerns over knowledge assumptions. The first is that cultural inheritance provides "rules of thumb" that often act as proxies for universal knowledge (Boyd and Richerson 1992b). Second, not all models derived from HBE assume universal knowledge as associated with colonization scenarios (Kelly 1999). Third, as noted by Cannon and Broughton (2010), economists have increasingly adjusted their cost-benefit models (the logic of which typically influences those of HBE) to reflect knowledge derived from previous experience.

Evolutionary ecology has been enthusiastically integrated into archaeological research agendas (Bird and O'Connell 2006; Codding and Bird 2015) focusing on a variety of questions that include hominin evolution (e.g., O'Connell et al. 1999), hunter-gatherer subsistence and mobility behavior (e.g., Grayson and Delpech 1998; Kelly 1999; Nagaoka 2005; Stiner et al. 1999), forager-farmer transitions (Kennett and Winterhalder 2006 [and papers therein]), food production (e.g., Barlow 2002; Gremillion 1996), technological decision-making (e.g., Beck et al. 2002; Borrazzo 2012; Clarkson et al. 2015; Goodale et al. 2008; Goodale and Andrefsky 2015 [and papers therein], Kuhn 1994; Messineo and Barros 2015; Surovell 2009), and socioecology (e.g., Bettinger 2015; Eerkens 2013; Hildebrandt and McGuire 2002; Zeanah 2004). Archaeologists interested in using models from evolutionary ecology for explanation of diachronic process have needed to come to terms with the challenge of working with effectively "space-like" models for "time-like" process (e.g., Leonard 1998). Archaeologists are not able to monitor the decision-making of the individual actor and typically cope with measuring decision-making resulting from many events. This does not preclude archaeology from the use of such models given that the record could reflect the cumulative impact many decision-making events. Simple models can thus be very useful for understanding persistent behavioral phenomena. However, this raises an additional concern regarding the appropriate currency used in model construction. Simple models may indeed offer powerful explanations, but they may also be wrong given the possibility of inappropriate assumptions. Debates over Middle Holocene hunting behavior in California illustrate this issue very effectively. The expanded role for mid to large game in hunter-gatherer subsistence economies has been explained as costly signaling by men (Hildebrandt and McGuire 2002) implicating social prestige as a currency. In contrast, a counter hypothesis suggests that cooler and wetter conditions (and thus, better forage production and more game) made hunting a calorically less costly option thus leading to increased frequency of hunting decisions and successful outcomes (Broughton and Bayham 2003; see also Winterhalder 2004). Within the theoretical and methodological framework of evolutionary ecology, resolution of such debates does not depend entirely upon rhetorical flourish or theoretical logic but empirical testing.

An important constraint on human behavior comes with the relationship between resource productivity and demography. The models of Boserup (1965) and Malthus (1976) have been equally influential in EE/HBE theorizing and research. Boserup's (1965) position regarding population pressure and intensification was influential on thinking about subsistence intensification among, for example, hunter-gatherers (e.g., Broughton 1994; Janetski 1997; Morgan 2015). Malthusian models are increasingly important for understanding subsistence, technology, reproduction, and social decision-making (Lee 1993; Puleston et al. 2014; Winterhalder et al. 2015; Wood 1998). Theoretical models offer explicit predictions for optimal decisions and potential outcomes in Malthusian population cycles defined by Puleston et al. (2014) as copial, transitional, and Malthusian. Limited archaeological research has focused on testing these predictions with some success (e.g., Prentiss et al. 2014a, b).

Archaeological applications of EE/HBE logic in explanations for major subsistence and settlement change, in particular, the forager-farmer transition, have recently been challenged by proponents of niche construction theory (NCT) a component of the extended evolutionary synthesis (Smith 2015; Zeder 2016, 2017). Niche construction theory asserts that organisms create changes in their environments that alter ecological interactions and consequently affect evolutionary process. A major implication is that through niche alteration and/or engineering, a coevolutionary process is initiated between the organisms inhabiting a constructed niche (Odling-Smee et al. 1996; Kuijt and Prentiss 2009; Laland and O'Brien 2010; Zeder 2017). When applied to the origins of agriculture, it predicts in that human niche constructing activities could have created contexts favoring increased local biomass and thus a wider resource base that in turn would favor rapidly expanding landscape alteration by human groups and rapid change in the nature and scale of human cooperative activities (Zeder 2016, 2017). This is in substantial contrast with models drawn from human behavioral ecology, which predict domestication as an incidental by-product of expanding diet breadth in the context of demographic packing or climate-induced ecological change reducing access to highest-ranked resources and associated with social changes that include increased inter-group competitive behavior (Zeder 2016). This has led to substantial debate (Gremillion et al. 2014; Zeder 2016), but given that precepts drawn from HBE may be useful for predicting and understanding incidences of niche construction, it is likely that aspects of each will prove not incompatible (Mohlenhoff and Codding 2017).

Evolutionary Cognitive Archaeology

Archaeologists have long been interested in the evolution of human cognition, and this interest has played a significant role in the development of approaches to measuring variation in human behavior. Over the past 150 or so years, the sophistication with which archaeologists have come to approach human behavior, material culture, and human cognition has undergone radical change. Today, the recently developed field of evolutionary cognitive archaeology (ECA) has become aligned with the related fields of paleoneurology, primatology, and evolutionary psychology. However, getting to today's level of discourse and ongoing research has taken considerable time beginning with early concerns about the meaning of artifact typology and progressing through initial theories of the mind as related to artifact manufacture and finally to recent debates concerning the extended mind and its implications for the meaning artifacts as related to the evolution of cognition.

Debates over the uses of archaeological typology exemplify early concerns regarding the manufacture and meaning of artifacts. While nineteenth-century typologies were often designed to show human progress (Daniel 2013), some early archaeological scholars explored concepts that would later be considered in cognitive archaeology, for example, the lithic reduction systems of Holmes (1894). The debate between Ford (1954) and Spaulding (1960) over the nature of archaeological typology exemplifies concerns over our ability as archaeologists to measure human intent and thought processes. Ford favored artifact types as measures of human organization, whereas Spaulding felt that typologies could be reflections of decisions made by their creators and thus indicators of thought processes as, for example, mental templates. The idea that artifacts could reflect mental images or templates strongly influenced the research and writing of Bordes (1968), who eventually debated Binford (1973) regarding the meaning of Mousterian artifact variation. Curiously, despite their differences of opinion regarding the ultimate cause of differences at the assemblage scale, Binford favoring functional variation and Bordes arguing for ethnic distinctions, neither questioned the underlying tenets of the typology as reflecting mental templates. Simultaneous to these discussions, archaeologists had also introduced the "generative concept" emphasizing the mental rule book underlying the development of certain material items (e.g., Breuil 1952; Leroi-Gourhan 1965, 1972). The concept of *chaîne opératoire* or operational sequence was developed to explicate the organization of toolmaking, in effect providing insight into the syntax of artifact manufacture. *Chaîne opératoire* has been widely used within various areas of archaeological research from lithic technology (Geneste 1985) to evolutionary archaeology (Jordan 2015). Abramiuk (this volume) notes that *chaîne opératoire* was foundational to the development of evolutionary cognitive archaeology as it has provided a means by which archaeologists could begin to explore the logic behind decision-making at specific stages of manufacture but also the structural logic behind the production system overall.

By the 1970s, archaeologists interested in cognition had begun to recognize that their research could be enhanced by reference to a cognition research well outside of archaeology. Wynn (1979) explored the manufacture of Acheulian stone tools in light of Piaget's development model and thus demonstrated that archaeological understanding of major classes of tools could be significantly enhanced by formal use of cognitive theory. This in turn had important impacts on how the ECA developed during the 1980s and 1990s. This approach to understanding artifacts in light of their evolved cognitive capabilities would be termed the internalist approach by Garofoli (this volume) and the conditional approach by Abramiuk (2012). Abramiuk (this volume) explains that using this approach, cognitive capabilities can be defined within a framework that links actions within cognitive capabilities as defined by conditioning arguments. Garofoli (this volume) notes that this approach recognizes that artifacts develop from computational mechanisms in the human brain, thus the "internalist" label. The conditional or internalist approach received wide attention during the 1990s with the publication of significant books including works by Renfrew and Zubrow (1994), Donald (1991), and Mithen (1996). These works, especially Renfrew and Zubrow, sought to expand our understanding of how people thought and consequently how that impacted human technology. The works by Donald and Mithen expanded cognitive archaeology explicitly into evolutionary discussions proposing hypotheses for human bio-cultural evolution.

Donald (1991) set the stage for the theoretical expansion of ECA by making the case that the mind might be understood as exiting beyond our physical selves. Thus, to him, stages of cognitive evolution were also cultural stages. In just over a decade, central discussions in ECA began to focus on the extended mind (DeMarrais et al. 2004) with its focus on the extension of cognition into a variety of material media. The reaction against the older “internalist” approach drew from new thinking that rejected the idea that material objects were merely by-products of operationalized codes in our minds while omitting the opportunity for the mind to also engage in intentional construction of its cultural surroundings (Garofoli, this volume). Two branches developed from this line of thinking known as material engagement theory (MET) (Malafouris 2013) and the related, radical enactive cognitive archaeology (RECA) (Garofoli 2018). As noted by Abramiuk (this volume), MET depends upon an ontological assumption that the mind constitutes a whole simultaneously inclusive of the body, the physical world, and actions undertaken therein. RECA takes these perspectives one further step in linking cognitive acts to coupling of an agent with the surrounding world and thus permitting the material world a role in imagination and the scaffolding of new representations (Garofoli 2015, 2018, this volume). Thus, there is the fuel for an emerging debate between proponents of internalist/conditional approaches to ECA and that of MET/RECA. Abramiuk (this volume) argues that both can be criticized with the conditional approach focusing too strongly on abstract qualities over ecological conditions associated with evolutionary process and MET suffering from challenges to theoretical validity, epistemological rigor, and methodological difficulty (in defining data for formal tests). Abramiuk and Garofoli are optimistic that a young ECA will resolve some of these challenges and continue to offer significant contributions to evolutionary research in archaeology particularly given theoretical linkages to concepts associated with the extended evolutionary synthesis including plasticity and exaptation. The potential for significant contributions is well illustrated by the debates over the evolution of “art” from the Paleolithic (Straffon, this volume).

Organization of the Handbook

Evolutionary research in archaeology has a great history and a grand future. This handbook is designed to introduce the reader to major research directions and contributions within the four major themes. In doing so, it provides opportunities for a range of scholars, many early to mid-career, to address the state of the art in the field and, in so doing, define future directions. The handbook is divided into four sections associated with the previously discussed logical divisions to scholarly endeavors in the field. The microevolution section begins with an introduction to the basic concepts underlying the bio-cultural evolutionary process (Walsh et al. Chap. 2) and continues with a focus on innovation and cultural transmission (Walsh et al. Chap. 3), selection (Goodale, this volume) and neutral models (Kandler and Crema). Macroevolution chapters outline major metaphors, models, debates, and future directions (Prentiss and Laue), landscapes and nearly neutral models (Laue and Wright), phylogenetics (Straffon, Chap. 8; Gjesfjeld and Jordan), and macroevolution and social change (Spencer). The human ecology section includes chapters exploring basic concepts (Prentiss), key tenets of optimal foraging theory (Nagaoka, Gremillion), socioecology with special reference to signaling theory (Quinn), ecological demographic theory (Puleston and Winterhalder), and niche construction theory (Riede). Evolutionary cognitive archaeology chapters cover introductory concepts (Abramiuk), radical enactive cognitive archaeology (Garofilo), and ECA’s contributions to the study of art (Straffon, Chap. 20).

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Part I
Microevolution

Chapter 2
Introduction to Cultural Microevolutionary Research in Anthropology and Archaeology

Matthew J. Walsh, Anna Marie Prentiss, and Felix Riede

Introduction

Evolutionary perspectives in anthropology and archaeology have come a long way since Binford (1962, p. 224) observed that archaeologists could "be among the best qualified to study and directly test hypotheses concerning the process of evolutionary change, particularly processes of change that are relatively slow, or hypotheses that postulate temporal-processual priorities as regards total cultural systems." Over the last few decades, scholars concerned with the evolution of culture—although by no means only anthropologists and archaeologists—have weighed in with numerous insights on the relationships between biological and cultural evolutionary processes in general and the cultural evolutionary process in particular. Here we offer an overview of biological microevolution processes and discuss how these are approximated in evolutionary studies of material culture in archaeology and cultural anthropology. The goal is to clarify common terms and definitions and to explore microevolutionary processes as they are used in sociocultural perspective. We hope to provide a foundation from which to better understand these concepts and their applications to method and theory in cultural evolution as further developed throughout this section.

The recognition of cultural developments as the consequence of complex and diverse histories as opposed to rungs on a teleological, stage-oriented step ladder out of the darkness of prehistory into the light of civilization is a critically important note in the history of anthropological evolutionary thinking, as is the revelation that cultural evolution can at least be understood through the larger framework of Darwinian evolution and associated forces and processes (Boyd and Richerson 1985; Richerson and Boyd 2005, 2010; Mesoudi et al. 2006). Despite early efforts by pioneering archaeologists in the nineteenth and early twentieth century to link evolutionary theory as then understood with observations of culture change (see Riede 2010), it is only in the last four decades

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or so that the field of evolutionary anthropology and archaeology has begun to emerge in a coherent fashion. To date, anthropological evolutionary theory has far eclipsed the earlier presumptions and ideas as to the nature of cultural evolution, such as those espoused by Lewis Henry Morgan (1877) and Herbert Spencer, for example (see Tehrani 2010). Over the last few decades, the field has also developed well beyond the neoevolutionary concepts of mid-twentieth-century thinkers such as Julian Steward (1955), Leslie White (1949, 1959), and other early contributions to the subject as, for example, presented in Sahlins and Service (1960). But, as O'Brien and Lyman (1998, p. 132) point out for evolutionary studies in archaeology, "the words evolution, selection, adaptation, and drift appear regularly in evolution-based studies, but in delving into both the biological as well as the archaeological literature, one soon gets the feeling that there is considerable diversity of opinion," and this holds true even in self-proclaimed Darwinian theoretical contexts. Likewise, other evolutionary terms such as variation, mutation, inheritance, and transmission are often brought to bear in discussions of cultural change without clarifying their meaning in regard to cultural phenomena.

When it comes to studying the evolution of material culture in general and in the past in particular, microscale perspectives can be tricky to tease out of the archaeological record. Even at the scale of the single artifact, feature, or assemblage, we are generally left only with the option of saying something about macroscale contexts rather than their microscale components (see Gould and Eldredge 1986; O'Brien and Lyman 2000, p. 130). There are two main reasons for this. First, it is nearly impossible to archaeologically discern, much less track, descent with modification between *individuals* as opposed to such changes occurring in *populations*. For the latter, ethnographers are perhaps the closest to being able to achieve this, as they have the opportunity to observe the interactions of their informants at the scale of individuals. To a degree, the combination of ethnographic, ethnohistoric, and detailed material culture study can bridge the inferential divides between these different scales of observation, as Jordan's (2015) recent attempt has demonstrated for one Siberian group. Yet, for most archaeologists, such records are not available, and judicious ethnographic analogues have to be combined with theoretical and perhaps mathematical models and a close reading of the archaeological record in order to strengthen inferences about general transmission modes (Tehrani and Riede 2008).

Archaeologists cannot directly observe the individual interactions and behaviors that result in the archaeological record. We can certainly infer as to what may likely have taken place (e.g., by drawing insights from ethno-archaeological analogy or from behavioral studies, sensu O'Connell 1995) or through diligent fieldwork under conditions of extremely favorable preservation (e.g., Assaf et al. 2016; Donahue and Fischer 2015; Högberg 2008). Indeed, this latter approach has recently been placed in a cultural evolutionary and life-history perspective framed within niche construction theory; Riede et al. (2018) have argued that play objects take on a critical role in the cognitive niche of maturing individuals in relation to innovation later in life. This study tried to unpack the microevolutionary mechanism that generates novelty—creativity—rather than framing it strictly analogous to mutation, i.e., as effectively random. Still, microevolutionary processes are most commonly inferred with reference to mathematical and/or ethnographic models. Even when instances of teaching and learning can be excavated and identified with some degree of confidence, linking these up with the bulk of the archaeological record, which represents time-averaged and usually poorly constrained population-level patterns of cultural macroevolution, relies on inferences.

Yet, archaeologists have long been wary of the fact that getting at the singular instances or events that make up units (or moments) of change is tenuous, as is also supported by recent formal modeling that has cultural evolutionary inferences in mind (Porčić 2015; Premo 2014). This was one of the major issues at the heart of the processual movement and the development of middle-range theory (e.g., Binford 1977, 1981, 2001). Conversely, the time depth that archaeology can provide is tailor-made for producing macroscale discussions about change over time in the past, but it also makes getting at the details of interchange extremely problematic.

Second, and related, cultural processes of selection, adaptation, drift, and mutation—while acting on individuals—only become discernable in broad, retrospective view. They are observable as processes only when we see them as patterns at the population scale. Here, we must explicitly understand that microevolution is generally reserved for those processes of change over time within a species, while macroevolution represents "change at larger, more inclusive scales in the taxonomic hierarchy" (O'Brien and Lyman 2000, p. 302). There are certainly more mundane but fundamental reasons as well: a third, less-broad critique could be definitional—that we tend to dwell on and define our evolutionary concepts strictly in their biological contexts, repeatedly attempting to force the square block of biological process into the round space that is culture change. Social scientists concerned with evolution have long recognized this problem also but rarely have attempts been made to operationalize solutions. In the last few decades, evolutionary anthropologists have taken strides toward addressing these, and other, critical issues in the investigation of human evolution (Boyd and Richerson 1985; Cavalli-Sforza and Feldman 1981; Jordan 2015; Lipo et al. 2006; O'Brien and Lyman 2002; Prentiss et al. 2009; Richerson and Boyd 2005; Shennan 2002, 2009). This chapter aims to (1) harmonize efforts in cultural anthropology and archaeology that have contributed to building the synthetic evolutionary framework from which to view and investigate cultural change over time at the microscale and (2) outline some of the theoretical and methodological tools utilized to explore microevolution in studies of culture. Structured more or less chronologically, we begin by reviewing early attempts at capturing cultural microevolution and by reflecting on how microevolutionary dynamics play out in the context of cultural phylogenetics and human behavioral ecology studies. We then discuss issues of study design: the selection of traits to be analyzed and the thorny issue of reconciling micro- and macroevolutionary *scales* of analysis. Thereafter, we reflect on the various *mechanisms* impacting on microevolutionary patterns and seek to provide cultural counterparts to the mechanism active in the biological domain. According to Mesoudi et al.'s (2006) classification of cultural evolutionary studies, archaeology belongs firmly to the macroevolutionary branch (Fig. 2.1); archaeological data are simply not well-suited to the study of microevolutionary patterns. By the same token, this chapter ultimately provides more questions than answers but also offers a challenge to future cultural evolutionary studies that through a judicious combination of approaches may well be better able to bridge the gap between cultural evolution at the smallest and the largest of scales.

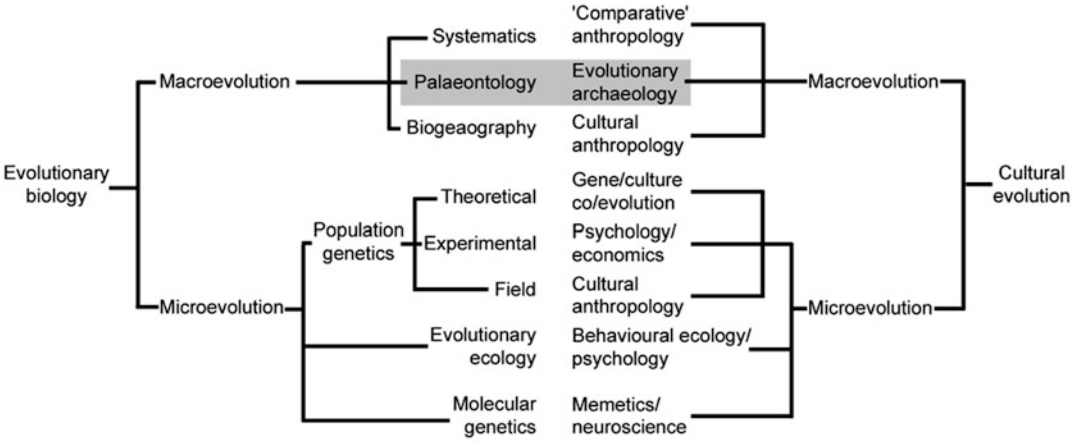

Fig. 2.1 Mesoudi et al. (2006) place archaeology on the macroevolutionary branch of the field of cultural evolution. Drawing on methods and insights from the sister clade may allow us to bridge this bifurcation

Cultural Evolution Evolves

Reviews of the history of evolutionary studies in anthropology and archaeology adequately cover developments in the field to date as they relate to macroevolutionary processes (e.g., see reviews in Barton and Clark 1997; Dunnell 1978, 1986, p. 166; Hodder 2012; Johnson 2010; Lyman 2008; Lyman and O'Brien 1997; O'Brien 1996; Prentiss et al. 2009; Shennan 2008; Trigger 2006). The challenge of this chapter is to illuminate some of the implications of *micro*scale processes of change on culture and in particular on cultural evolution by descent with modification. Considering evolution as what Dunnell (1980, p. 37) so aptly defined as "the differential persistence of variability," this is perhaps more difficult than it sounds. This is because getting at persistent variability requires a temporal aspect in order to see persistence and a population aspect in order to observe variability, which necessitates viewing diversity across multiple spatial and temporal scales. Methodologically, evolutionary research in anthropology and archaeology has swung from early foci on the development of diversity among societies or essential "types" (e.g., Sahlins and Service 1960) to studying changes in material culture traditions by way of seriation studies (Lyman and O'Brien 2006; O'Brien and Lyman 2002) to applications of evolutionary ecology and optimal behavior modeling (see, e.g., Bettinger 2009; Broughton and O'Connell 1999; Cronk 1991; Nettle et al. 2013; Winterhalder and Smith 1981; see also Davies et al. 2012 for broad applications in nonhuman ecology) to a growing contemporary range of phylogenetic applications to studies of material culture (see reviews in Straffon, Chap. 8, this volume; Jordan and Gjesfeld, this volume), as well as even more inclusive views of how cultural phenomena can be studied from an evolutionary perspective (e.g., Kandler and Crema, this volume; Mesoudi et al. 2006; Riede, this volume).

Seriation

As a method of developing lineal evolutionary histories of cultural materials, systematic uses of seriation can offer valuable insights into population-scale developmental trajectories. But the understandings they provide are patently macroevolutionary in scope, as observed in the conceptual definition of taxonomic types that usually have "relatively long temporal (and broad spatial) distributions" (Dunnell 1986, p. 173). However, as Lyman and O'Brien (2006) demonstrate, seriation methods can still be a useful classificatory exercise, for example, as a tool in establishing taxonomies for cladistics analyses. Lipo and Eerkens (2008) provide an excellent example of the utility of seriation in systematically developing culture history chronologies in time and across space. Given an accurate understanding of known material chronologies, seriation can even provide a near microscale perspective on character trait evolution (e.g., Dethlefsen and Deetz 1966).

Human Behavioral Ecology

One analytical framework that comes close to operationalizing processes at the scale of the individual is human behavioral ecology (HBE)/evolutionary ecology and the application of optimal foraging theory and attendant models. HBE is unconcerned with the nature of transmission whether genetic or cultural. Rather, it concerns itself with the overall adaptiveness of behavior and thus decisions made by individuals in response to contextual—most often ecological—circumstances. These studies attempt to predict the decision-making behaviors of *individuals* in specific contexts, thus modeling individual behavioral adaptation under environmental constraints to determine if and how individuals adapt behaviorally to various circumstances and conditions (HBE and OFT, respectively; see Bettinger 2009; Chaps. 11, 12, 13, 14, 15, 16, 17, 18, and 19, this volume; Winterhalder 1981; Winterhalder and Smith 1981 and references therein; and review in Shennan 2008, pp. 82–87).

Phylogenetics

Since Mace and Pagel (1994) suggested that a phylogenetic approach to cross-cultural comparative studies could potentially provide a systematic, statistical framework from which to investigate patterns of hierarchical descent, cultural evolution has increasingly been illustrated through the application of cladistics or tree-based models. Cladistic analyses hypothesize the relational histories of changing trait states within species or groups from a common ancestor. As these models are concerned with identifying the points of divergence over time from earlier ancestral states, they are an exceptional heuristic for thinking about evolutionary relationships of descent within and between units of culture. Applied phylogenetics methods in anthropological studies have become increasingly common, particularly in tracing the development of material culture traditions. For example, Buchanan and Collard (2007), Darwent and O'Brien (2006), Lycett (2009), O'Brien et al. (2001, 2014), Prentiss et al. (2015), and Riede (2008), among others, have utilized cladistic methods to investigate change over time in lithic projectile and core traditions in various temporal and spatial aspects of prehistory. Others have applied phylogenetic methods to studies of, e.g., pottery (Cochrane 2008; Collard and Shennan 2000), historic cutlery (Riede 2009a), clothing, and textile traditions (Buckley 2012; Jordan 2009; Matthews et al. 2011; Tehrani and Collard 2009), and to design elements in various forms of material construction and craft traditions (Jordan 2015; Jordan and Mace 2006; Jordan and O'Neill 2010; Jordan and Shennan 2005, 2009; Marwick 2012; O'Neill 2013; Tehrani and Collard 2013).

While continuing to prove useful to archaeological hypothesis testing to date, phylogenetics explicitly addresses processes of change at the *macro*scale. Thus, microevolutionary studies in the cultural sciences remain somewhat elusive. However, the application of network analyses in conjunction with tree-thinking logic has been used to infer microscale instances of social information transmission within traditions, thus coming close to modeling within-population change over time (e.g., Prentiss et al. 2011; Riede 2008; Jordan 2015). Similarly, recent applications of Bayesian phylogenetic methods have proved effective for identifying some aspects of microscale change, such as frequency rates of change (Atkinson et al. 2008; Pagel et al. 2007) and estimating instances of ancestral state change (Fortunato et al. 2006). Thus far, the most successful applications of Bayesian phylogenetic methods have been undertaken in language-related studies (e.g., Gray and Atkinson 2003; Gray and Jordan 2000; Greenhill and Gray 2005), as the transmission and spread of language have proven to be a close cultural proxy of gene flow since language is a steady delimiter of cultural groups as they have migrated throughout history. However, further applications of a variety of phylogenetics methods appear promising and could theoretically be applied to a wide range of cultural data on diverse cultural traditions, for example, in tracing language descent relationships in broad regional contexts (Gray et al. 2007).

Cultural Microevolution: A Problem of Commensurability

Relatively early in the rocky process of commensuration between Darwinian evolutionary theory and the anthropological sciences, Robert Dunnell (1980, p. 37) observed that "evolutionary biology cannot… be applied unamended and uncritically to cultural phenomena." Dunnell realized that the accepted modes of biological evolution, though clearly at least somewhat analogous to those of cultural evolution, were not the same, but could, if modified and critically applied, “provide the elements of a suitable explanatory structure” for cultural change by way of selection and descent with modification. Dunnell was not the first to point this out, as E.B. Tylor’s (1881, p. 20) observation illustrates:

> On the whole it appears that wherever there are found elaborate arts, abstruse knowledge, complex institutions, these are the results of gradual development from an earlier, simpler, and ruder state of life. No stage of civilization comes into existence spontaneously, but grows or is developed out of the stage before it.

Not much later, the Swedish archaeologist Oscar Montelius linked the typological method directly to the principles of Darwinian evolution as then understood (Montelius 1884, 1899) and actually developed a formal method aimed at tracking patterns of descent with modification (Montelius 1903; see also Riede 2006, 2010). Clearly then, descent with modification of technologies as well as whole cultural systems was a subject of concern to earlier social scientists. However, early qualitative reflections on the subject aside, it was not until the mid-twentieth century that systematic evolutionary thinking began to take hold in anthropology and archaeology in particular.

In 1965, Campbell (1965, p. 26) dissected earlier arguments on sociocultural evolution and processes of variation, selection and retention. He argued that identifying an “analogy between natural selection in biological evolution and the selective propagation of cultural forms” was not only applicable to cultural studies but relevant to the interpretation that culture does in fact evolve through histories of descent from previous forms and as a result of selection pressures. The following year, F.T. Cloak, Jr., presented a brief but insightful discussion of cultural microevolution as it was (and still often is) compared to processes of Darwinian evolution in the biological sciences. Cloak noted that a major deficiency in the utility of using Darwinian evolutionary terms in relation to culture was (and is) that scholars often “have failed to use the proper analogues … they have related the wrong biological concepts to the cultural concepts they wish to explicate” (Cloak 1966, p. 7). Cloak observed that the use of cultures as analogous to species breaks down in Kroeber’s (1948, p. 260) traditional “Tree of Culture” schema (Fig. 2.2) because cultures, unlike plants and animals, can potentially continue to exchange traits after they have become speciated or rather widely separated through processes akin to speciation through genetic mutation and drift. In this sense culture evolves unlike a biological entity since biological reproduction is not necessary for cultural inheritance processes to take place. However, the crisscrossing branching pattern in Kroeber’s “Tree of Culture” remains relevant to this day to cultural evolutionary heuristics, as it illustrates remarkably well the combinations of branches, reticulations, and complex interconnectedness evident between disparate cultural phenomena. A further criticism leveled by Cloak lay in the “functionalist” approach to culture in which a single given culture was viewed as directly analogous to a single organism. This, he

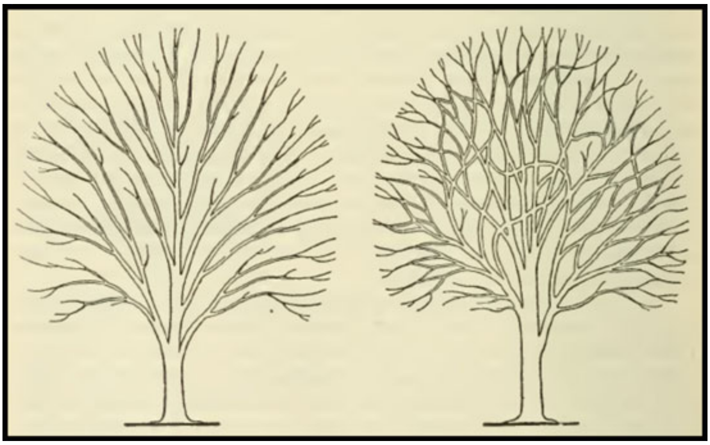

Fig. 2.2 Kroeber’s “Tree of Culture” diagram (1948, p. 260). The “Tree of Life” on the left represents the bifurcating phylogeny of biological organisms. The “Tree of Knowledge” (i.e., culture) on the right represents the braided-stream model (Moore 1994) of weaving and intersecting branches of cultural traditions and their interrelationships

noted, ignored the phylogenetic relationships between cultures—the coherence and congruence within and between cultures that results from the historical contingencies inherent in cultural contact and subsequent change (an issue that has come to be known as "Galton's problem" [Naroll 1965]). As previously observed, this is actually illuminated by the reticulations in Kroeber's more bush-like tree.

Somewhat ironically, Kroeber (1948, pp. 260–261) recognized the importance of this same historicity in his "Tree of Culture" schematic (Fig. 2.2), stating that the branching patterns were meant to illustrate not only how cultures diverge but that reticulations also showed how "it syncretizes and anastomoses too . . . a ramification of such coalescences, assimilations, or acculturations" that are the indelible marks of the historic relationships between cultural traditions. It is these dynamics inherent in cultural lineages that emphasize the importance of recognizing historical contexts as much as possible when hypothesizing about patterns of cultural change. At any rate, contemporary computational methods are able to explicitly integrate potential blending and reticulations (e.g., Bryant et al. 2005).

Cloak went on to present a series of analogies commonly used to juxtapose biological evolutionary concepts with those observed in cultural evolution, namely:

Biological	Cultural
Populations of organisms	Populations of culture bearers
Phenotypic traits	Cultural traits
Gene flow	Diffusion
Natural selection	Natural selection
Biological fixing	Cultural fixing
. . .	Cultural selection

Simply put, Cloak made distinctions between (1) populations of organisms and populations of culture bearers; (2) phenotypic traits and cultural traits; (3) gene flow and diffusion—the ways in which traits move between populations; (4) natural selection and natural selection in biological and in cultural contexts, respectively; (5) fixing processes of introduced traits in receptor populations, biological and cultural "fixing through chance"; and finally (6) not an analogy, but a process that Cloak proposed has no clearly delimited biological analog,[1] cultural selection.

The following discussion treats with each of these somewhat irregular analogues in light of over half a century of further research into processes of cultural evolution, particularly taking into account the extended discussions into the validity of analogies between genetic/biological and cultural/social-learning evolutionary transmission processes (e.g., Claidière and André 2012; Daly 1982; Durham 1982; Durham et al. 1997; Mesoudi et al. 2006; Weingart et al. 1997; see also various chapters, this volume).

Populations: Scale and Commensurable Units of Analysis

At the most general population scale is (1) the individual (the smallest population possible); (2) a given population of closely or relatively closely genetically related individuals; and (3) larger and increasingly unrelated populations that differ from other populations in some distinguishable way

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[1] It should be noted that the field of epigenetics has identified instances where cultural phenomena and sociocultural environmental circumstances precipitate change at the genetic level (e.g., Jablonka and Lamb 2005). Thus, growing evidence indicates that cultural selection has at least some measurable biological consequences.

(e.g., “organisms, species, kingdoms” à la Eldredge 1985, p. 93). In genetics, a population is a straightforward metric—it is made up of interbreeding organisms. In anthropology and archaeology, it is cultural traits which serve as proxies for the behaviors of our informants and the artifacts and assemblages that they create. Each of these can be seen as a single unit of analysis and thus assessed from a microscale perspective, but at any scale that moves beyond the individual, we quickly reach a macroevolutionary imperative that makes discerning between what we define as “micro” and “macro” problematic depending on the overall scale of analysis itself—e.g., localized, regional, or global. The importance of scale becomes most acute when attempting to assess cultures or subgroups within cultures as individual units—e.g., as “organisms” rather than “taxa.” Explicitly in cultural evolution studies, we make generalities based on the scale of our analyses (Binford 1965, p. 203). Because cultural phenomena are prone to such inimitability given high variability in the quality of fidelity of transmitted information between individuals and across time, we can designate commensurable cultural units only so long as we focus on tracing the evolution of cultural traits themselves rather than attempting to trace the “cultural evolution” of populations to which traits are allocated. Cultures, *as such*, do not evolve. What evolves are the ideas and associated behaviors that combine to make identifiable sets of cultural traits empirically observable in specific societies through shared behaviors and practices. It is these behavioral *recipes*—evident as they are in *communities of practice*—that make up what we call “culture” and that evince change over time (cf. Riede 2011). Thus, when it comes to microevolutionary processes of culture change, the size of a population is not as important as the demographic makeup of the population and its pre-existing historical contexts and epistemology that may impose significant effects on how introduced changes are manifest, received, and dealt with. Thus, if we are to say anything about *micro*scale cultural evolution, we must focus on transmission processes that result from mutation, selection (both natural and cultural), gene flow, migration, and drift. Luckily, transmission is something that we *can* observe in anthropology and in the archaeological record, e.g., by way of inferring instances of pedagogy by way of proxies (agent-based modeling has made significant contributions to advancing the accuracy of behavioral computer simulations; see Laue and Wright, this volume).

In any individual, biological ontogeny begins with a pretty straightforward transmission of genetic data from two individuals to a single host individual (or individuals in the case of twins, etc.). Cultural exchange is generally not so straightforward. Even at its closest approximation, for example, vertical transmission of information between parent and offspring, cultural transmission is a complex process. It depends on the nature of the information, its contextual usefulness in the long term (is it adaptive or perceived as in some way fitness enhancing?), as well as the social values in place that may encourage or discourage creativity or innovation or, conversely, that call for conservativism or conformity to the status quo and, of course, any number of existing sociocultural norms that put pressure on the selection of ideas. In cultural evolutionary processes, the transmission of ideas happens at the interindividual level but plays out on the community and population levels. Ultimately, it is vital to appreciate the existing historical, environmental, and social contexts into which cultural traits are introduced in a given population. Thus, within this scenario, we may consider any given cultural unit as a dynamic community of practice or member thereof and prone to change through diverse vectors and dynamically at different relative demographics. Cultural drift, for example, can allow for isolated populations to become increasingly unique over time—effectively micropopulations in a macroscale scenario. In cultural evolutionary processes, transmission isolating mechanisms (TRIMS, Durham 1992, p. 333) precipitate cultural drift in similar fashion to how biogeographical isolation leads to genetic drift in populations of biological organisms (see Chap. 3, this volume).

Traits

In biological terms, a phenotypic trait is one that is expressed as a result of variations in allele frequencies. It is an empirically observable, measurable expression of genes (i.e., variant(s) of alleles), for example, those that determine hair or eye color or that cause diastema or any other observable genetic variation in an individual. A cultural trait is similar in that it could be any number of expressed variants of cultural concepts thus reflected in behavior or material culture. Anthropologists (and archaeologists in particular) have long used "cultural traits" as units of analysis for defining what is and is not a specific culture, feature of a particular culture, or otherwise some variant of a specific cultural phenomenon (Moylan et al. 2006; O'Brien et al. 2010; Pocklington 2006). This is because identifying cultural characteristics as "traits" is useful for quantifying the similarities and differences observed between social groups and the diverse expressions of their material culture. Here, the distinction between phenotypic traits and cultural traits becomes blurred. This is because cultural traits are themselves non-biological phenotypic traits. In many cases they can be observed in quite similar ways. Just as we may observe someone possessing brown hair due to their inheritance of genes that code for brown hair, so too we may observe that this same person is wearing their brown hair made up in a French braid—itself a heritable cultural trait, the knowledge of which was culturally transmitted, probably through social learning (e.g., Mace 2005, p. 2).

But, generally speaking, defining any particular cultural trait necessitates an explicitly synchronic perspective that regards the trait in question to be either present or absent in any given group at the moment of observation. This is not to say that variation cannot be taken into account. Indeed, accounting for change is one of the main purposes of the exercise of identifying cultural traits, and this is accomplished by establishing the rate and frequency of trait changes over time within what can be deemed a coherent cultural unit. The set(s) of cultural traits that anthropologists use to define any given cultural group are necessarily subjective. One can easily discern basic culture traits of a given society quite quickly based on extant ethnographic and archaeological literature, and nowadays detailed information can be rendered relatively quickly using digital resources like the Electronic Human Relations Area Files (eHRAF) (http://ehrafworldcultures.yale.edu/ehrafe/), D-PLACE (Kirby et al. 2016), (https://d-place.org/home), and EnvCalc2.1 (Binford and Johnson 2014), (http://ajohnson.sites.truman.edu/data-and-program/) and language databases such as Ethnologue (Grimes 2002; Lewis et al. 2016) (http://www.ethnologue.com/19/) and Glottolog (Hammarström et al. 2017) (http://glottolog.org/).

For instance, ethnographically the nineteenth- to mid-twentieth-century Netsilik Inuit (Balikci 1970, 1984; Rasmussen 1931) of the central Canadian Arctic could be categorized by 14 general cultural traits (e.g., small band-level groups, mixed subsistence, Inuit-Inupiaq language, animistic cosmology, etc.). While arguably more or less accurate, these traits are such gross generalizations that they tell us very little about actual Netsilik culture. As traits, these do not even approach—much less scratch the surface of—what was representative of Netsilik culture at the time of ethnographic encounters (Balikci 1970; Rasmussen 1931). While taking into account basics of cosmology and social structure, the trait list remains purely phenotypic in what it describes of the culture in question, missing entirely the "nonempirical character" of culture (Osgood 1951). Thus, these "cultural traits" no more define the Netsilik culturally than the allele frequency that generates blue eyes defining a blue-eyed individual's biology. Yet, identifying these traits does help us delineate the Netsilik from say the Araweté of Amazonian Brazil (Viveiros de Castro 1992), with whom they have in common only the presence of a generally animistic worldview, a shamanic tradition, and recognition of various taboos, although each of these manifests so remarkably different between the two as to be arguably incongruent at all but the most generic scale. Steward (1955) recognized that the difference lies in "secondary" versus "core" cultural traits, with core traits being the true delimiters of cultural relatedness (a fundamental discussion of the operationalization of a similar concept of prototypical cultural "core" traditions is drafted in Boyd et al. (1997), although this breaks considerably from

Steward's concept of the cultural core being the suite of technological adaptations to the particular ecological niche, how a society adapts to the specific environment in which they live; rather, Boyd et al. imagine "core traditions" as the conservative features of the specific culture in question in a relative sense—the equivalent of a cultural genotype rather than the phenotypical traits that empirically define it and make it discernable from any other culture).

In evolutionary studies in cross-cultural anthropology and archaeology, trait determination is extremely important, because it sets out the units of analysis to be studied. This is imperative for identifying microevolution since it changes in the frequency or sometimes simply the presence or absence of traits themselves that allow us to observe processes of evolution in both biology and culture. In cultural studies, appropriate traits must be determined, collated, and assessed based on the hypothesis being tested. Ideally, it is best that many are considered. This is because the frequency of some traits changes over time at different rates and for different reasons, while other may persist for so long as to show little or no observable change (see Nunn et al. 2010). This should be taken into account when determining any cultural traits as units of analysis (Dunnell 1986; O'Brien et al. 2010). Material culture traits tend to be categorized by explicit details of artifacts or assemblages—presence or absence of morphological features, design elements, probable or known use—functions, materials, etc. (e.g., Andrefsky 2008) but may also encompass manufacturing techniques, stages of curation, and even conceptual-symbolic considerations (e.g., Haidle 2009), all of which are to some degree culturally determined.

Dunnell's early concept of style vs function as dichotomous and incommensurate units of analysis did not take into account that stylistic features and forms can serve symbolic functions that significantly do directly affect the Darwinian fitness of the population in which they occur and that, further, function does not always get reflected as we assume it should. For example, task-specific efficacy of a particular morphology or material (i.e., functional advantages) often does not play as big a role in material culture being passed to the next generation as one might think. In the Final Palaeolithic of northern Europe, for instance, lithic projectile points should be conforming to certain ballistic parameters in relation to the target prey animals (Friis-Hansen 1990). Yet, analyses of the shape variation among different techno-complexes in this period show that such functional considerations were not consistently heeded (Dev and Riede 2012; Riede 2009b), suggesting that functional differences were not discernable or that transmission processes overrode any such concerns. Due to its learning efficiency, the imitative copying of certain practices or materials can and does occur entirely independent of function (Gergely and Csirba 2006). Failing (or refusing) to recognize this, Dunnell (1978, p. 197) ultimately suggested that style could not explain cultural evolution from a rigorous evolutionary framework. However, we clearly see in the archaeological record numerous instances where nonfunctional features of a cultural system evolve through descent with modification and maladaptive traits regularly emerge and persist in human traditions (see Bettinger et al. 1996).

Ultimately, cultural traits *are* analogous to phenotypic traits in that they are observable features of our species expressed through materials, appearances, behaviors, and practices, all resulting from diverse responses to the natural and sociocultural environment experienced by previous generations.

Modes of Transmission: Gene Flow and Diffusion

In biology, gene flow at the microscale takes a simple trajectory: with very few exceptions in the Animal Kingdom, at least parents pass genes on to their offspring at a balanced ratio, half from the biological mother and half from the biological father. Replication errors and mutations may cause significant differences between the genetic makeups of individual offspring as compared to that of parents, but the overall process of genetic inheritance remains quite steady. Recent studies into epigenetics show that developmental stresses and dramatic life changes actually make things a bit more complicated at the level of alleles and in the determination of what genes become switched on and off in an individual as they develop, but at its most basic, the process remains pretty straightforward (Jablonka and Lamb 2005). At the population scale, gene flow gets more complicated and describes the frequencies of traits moving between sample populations, not individuals, though individuals are the vectors of trait movements within the population as a whole. Over time, as individuals reproduce, interbreeding between populations causes the frequency of certain traits to become more or less prevalent, ultimately altering the gene pool of each population. Generally speaking, this leads to variation in the gene pool between the populations in question (but, see the section on fixation below, as genetic diversity does not prevail in all cases of gene migration).

Diffusion is said to occur as introduced variants spread throughout a population, effectively fanning out through the community over generations. Where diffusion is somehow hindered by geophysical isolation, allopatric (or geographic) speciation occurs (Eldredge and Gould 1972; see also, e.g., Mayr 1942, 1963). In different pockets of isolated populations, genetic drift may take place further altering a particular population in unique ways. These same phenomena happen in human culture, as populations can become separated by physical barriers such as mountain ranges, rivers, oceans, and the like. Both gene and information flow can also be stifled by populations simply not interacting for reasons such as differences in language that may hinder communication, conflicting ideologies, or cultural norms—aspects of culture are themselves often barriers to information transmission, and "ecological, psychological, linguistic, and cultural" aspects can all be highly effective *transmission isolating mechanisms*, or "TRIMS" for short (Durham 1982, p. 292; 1992, p. 333). As Boyd and Richerson (1985, p. 9) point out, a cultural mechanism akin to genetic drift can occur when, in small populations, "chance variations in which cultural variants are observed and remembered may cause substantial changes in frequency from time to time . . . rarely performed variants may be lost entirely" simply by not being observed from one generation to the next. Often, the more relatively isolated a group becomes, the more likely processes such as cultural mutation, drift, or inertia will alter the developing culture as it evolves in place (Richerson and Boyd 2005; to be clear, by definition cultural inertia tends to "keep the population the same from one time period to the next," but in the context of isolate populations, it is proposed to affect stasis over the long term even acting to maintain the slightest inevitable changes introduced into the otherwise static system through cultural mutation [e.g., innovation] and drift. In these instances, inertia actually acts to legitimize and perpetuate introduced cultural variants, at least once they have been introduced—see discussion on "fixation" below).

To a certain extent, cultural transmission is much more complex because it need not rely on individual-to-individual modes of contact to initiate or propagate even at the microscale. A single individual can simultaneously communicate ideas to multiple observers at once, thus potentially planting ideas or impressions in the minds of those around them—a process referred to as one-to-many cultural transmission (e.g., Shennan 2002, p. 49). However, at the macroscale, processes of information flow and diffusion empirically appear quite similar to their biological antecedents, if not spreading at a potentially much greater rate and degree. Unlike genes, which require generations across which to spread, ideas (the alleles of culture) often travel fast, change frequently, and can even quite dynamically alter the diffusion of biological information by biasing individuals toward or against interacting with others. While similar in concept, cultural diffusion is thus far more fluid than gene flow, with the potential even to dramatically influence its trajectory.

Modes of Selection: Natural Selection in Nature and on Culture

Conway Zirkle (1941) has traced the concept of natural selection, so intrinsically attributed to Charles Darwin in contemporary reckoning, well beyond Darwin or even Alfred Wallace (1870), and past recognized influences from Thomas Malthus' *An Essay on the Principle of Population* (1798) among others, all the way back to the Greek philosopher Empedocles (c. 400 B.C.). Clearly, concepts synonymous with Darwinian natural selection have been around for a long time. As Zirkle chronicles so well, Darwin was quite open about his influences, although it is generally accepted that he came to his conclusions predominantly on his own. It was often after the fact that others pointed out to Darwin similarities to his explanations that others had earlier developed but not so widely circulated, for example, W.C. Wells' 1813 paper speculating a principle of natural selection at work on human skin pigmentation (see Wade 2010) or Patrick Matthew's 1831 treatise on macroevolutionary processes of natural selection in relation to tree cultivation (see Weale 2015). That there had been numerous earlier observations of natural selection *as such* does not detract from the importance of Darwinian evolutionary theory as we know it. Rather, these observations reinforce our scientific understanding of descent with modification as a result of natural selection as an empirical, testable, and supported theory of change over time in living organisms in relation to the environments in which they develop.

Darwin's (1859, p. 5) own description of natural selection:

> as many more individuals of each species are born than can possibly survive; and as, consequently, there is a frequent recurrent struggle for existence, it follows that any being, if it varies however slightly in any manner profitable to itself, under the complex and sometimes varying conditions of life, will have a better chance of surviving, and thus be *naturally selected*,

addressed (at least initially) more the ultimate effects of environmental adaptation over time in organisms rather than the mechanisms driving it. Principally, Darwin's concept suggested that natural selection represent the *process* (Darwin's "principle") whereby slight variations accumulate in species over time, adapting them to the environments in which they live. The elegance of this observation is such that—even with the vast expansion of knowledge in regard to evolutionary thinking that has developed out of the last century and a half of research on the subject—contemporary understandings of processes of natural selection do not fundamentally stray far from Darwin's (and Wallace's) original concept. In general, research since has expanded and refined—rather than amended—the theory. It is far beyond the auspices of this chapter to rehash the well-established theory of natural selection as it stands in the biological sciences (see Goodale, this volume). Thus, we take for granted the accepted general definition of natural selection as a process in which organisms that possess variants of (genetic) traits and that facilitate survival and thus reproductive fitness in their host environment tend to pass on those traits to their offspring, imparting an enhanced (at least to some degree) survivability; this in turn over time can be observed as population diversity and distribution at the macroscale. Of particular relevance to anthropology, this same process of course works on humans and influences their behaviors and can therefore be applied to observed diversity and change in cultural traditions such as material culture. In addition to natural selection affecting change over time in cultural phenomena, culture is also subject to cultural selection that significantly influences variability (e.g., Durham 1982, p. 297): a process in which individuals and populations that possess variants of (cultural) traits and that persist and diffuse in their host environment tend to pass on those traits to their descendants and others, imparting an altered (at least to some degree) survivability; this in turn over time can be observed as population diversity and distribution of cultural variants at the macroscale—what Mace and Pagel (2004) so eloquently refer to as "the cultural wealth of nations."

As pointed out widely elsewhere, natural selection and cultural selection are not justly comparable processes (e.g., Ames 1996, p. 115; Durham 1991; Graves-Brown 1996, p. 170; O'Brien and Holland 1990, 1992; Richerson and Boyd 2005; Shennan 2002; among many others). However, it has become clear that each affects the other in dynamic fashion. Laland et al. (2013, p. 68) observe that "natural selection fashions highly specific cultural capabilities in particular species... according to their ecology and life-history." Similarly, cultural selection or more specifically the behavioral variants that emerge by natural selection that are then retained and develop further variation due to cultural constraints, transmission biases, or inertia (such as those leading to the development of agriculture, sensu Rindos [1980]) alter the natural environment and thus have potentially wide-ranging effects on subsequent "natural" selection processes. The feedback loop between natural and cultural selection processes has been of increasing interest in the evolutionary social sciences, particularly under the auspices of niche construction, or triple-inheritance theory of gene-culture-ecology dynamics (sensu Odling-Smee et al. 2003; see Riede, this volume). Up until the last few decades, failing to recognize the symbiosis between these forces has been perhaps the most common failure in evolutionary culture theory and in its relation to contemporary concepts in evolutionary biology (see Lyman and O'Brien 1997 for a review). Natural selection is, of course, a significant force at work on cultural selection. More accurately, natural selection is foundational regarding "the natural selection of behavior" that finds expression in culture (Skinner 1981). As an expression of human behaviors in response to experienced circumstances, cultural selection is a flexible variant of natural selection—a hierarchically dependent variable of much broader natural selection. As Bettinger et al. (1996, p. 150) note, cultural selection, as such, is ultimately the result of "natural selection acting in the long run to produce decision rules that in turn vicariously select cultural variants." Cultural selection is in fact an aspect of natural selection in which culture itself in a broad sense is the fitness-enhancing adaptation.

Fixing Through Chance: Mutation, Drift, Adaptation, and Persistence

Durham (1990, p. 191) proposes that "*coincidence* (i.e. similarity by accident or chance), *analogy* (similarity by convergence or independent invention), *homology* (similarity by descent), and . . . *synology* (similarity by diffusion)" create similarities (or seeming similarities) between cultures. He contends that analogy, homology, and possibly coincidence function in culture more-or-less similarly as they do in biology. However, in culture, all of these processes rely on some form of social transmission of cultural information fundamentally separated from sexual reproductive transfer of genetic information (not taking into account the subsequent parent-offspring relationship that plays a dramatic role in the transmission of cultural information). As information (genetic, cultural, or otherwise) is transmitted between individuals and populations, it is not enough that it emerges and is passed on from a single individual to another—for descent with modification to occur, the unit of information must be transmitted at a broader scale; the products of mutation and drift (i.e., variation) must persist to some degree in a given population; the information has to stick. This occurs through a process known as fixation.

Initially, novel traits must emerge. The issue of true novelty, innovation, and creativity has often been sidestepped by evolutionary archaeologists. The simple solution has been to treat novelty as strictly analogous to mutation and hence to let novel traits emerge by chance only. While fortuitous errors surely do and did occur in the past, this is mostly likely a poor concept for innovation. In a recent attempt to tackle this issue, Riede et al. (2018) suggest that the provisioning of youngsters to play things during childhood—extended in *Homo sapiens* well beyond the duration of other great apes and hominids—primes innovation within the given constraints of a broad cultural evolutionary lineage. The argument is that once reproductive concerns kick in, the costs of experimenting with novel raw materials and combinations of different components are not favored given the risk of failure. During play, however, such constraints are absent, allowing individuals to freely toy with objects and materials and their combinations and uses. As children mature cognitively and physically, they become more likely to be able to hit on genuine innovations making adolescence the sweet spot for creativity. At the same time, the making of scaled toys of functional objects (sleds, carts, bows, etc.) by adults allows them to explore the mechanical affordances and other properties of such objects without incurring the time, energy, and material costs of building a full-scale version. In this approach, the inter-generational niche construction dynamics become critical in seeing innovations not as random but not as the work of some lone genius either (see also Riede, this volume, on further examples of such niche construction processes).

In genetics, fixation occurs when a new allele (variant of a particular gene) appears (i.e., mutation) and it gets passed to the next generation. Conversely, if it doesn't get passed on, it is simply lost. If it does continue to be passed on—inherited from one generation to the next—*and* is passed on in the population *and* eventually replaces the other variant(s) of the same gene, it is said to be "fixed" in the population. Thus, one allele replaces other alleles of the same gene and eventually becomes the only remaining variant of that gene in the population. The fixed variant is then permanent in the population until another mutation occurs, potentially causing this series of events to repeat. Generally, this process is based on random mutation and the subsequent vicissitudes of contextual selection pressures, making the chances of any particular variant becoming lost or fixed quite difficult to predict—seemingly a product of chance (Hartl and Glark 2006; Kimura and Ohta 1969; see also Koerper and Stickel 1980 for an early treatment of drift and fixation processes in cultural phenomena).

In terms of culture, a trait could be said to become fixed through similar processes, but the chances of certain variants being perpetuated are not as subject to change once they have been introduced. In cultural systems, once a new variant shows up (e.g., through the cultural equivalents of mutation, an accidental invention and innovation, or as the result of guided variation; see Walsh et al., Chap. 3, this volume), its fixation potential is subject to both natural selection *and* cultural selection—social-learning, providing an adaptive advantage to local conditions (i.e., imparting enhanced fitness on those choosing to adopt the new variant over those that choose not to), transmission biases, etc. can all contribute to whether a cultural variant is retained and transmitted through the population over time and to what extent. Furthermore, conservative forces such as pedagogy may cause a variant to be selected over others and cultural inertia could effectively "fix" an introduced variant into the existing cultural system (e.g., Neiman 1995).

Neff and Larson (1997) point out that, in evolutionary archaeological theory, adaptation studies focus on deducing how selection processes (e.g., natural selection) lead to diversity. They propose that adaptation "is a key component of a strategy for understanding the living world as the product of natural selection coupled with chance, historical constraints, and developmental constraints" (Neff and Larson 1997, p. 78). In the case of fixation, it is the cultural equivalences of mutation that introduce variability (just as mutation does in biological systems), but individual proclivities, existing cultural norms, the perceived value of the introduced phenomenon within the population in question, and the potential for cultural inertia are significant deciding factors as to what cultural variants become fixed and lost or reach equilibrium (Neiman 1995). In both biological and cultural contexts (Table 2.1), whether or not particular variations persist in a given population—Dunnell's (1980, p. 272) "differential persistence of variability"—is thus the very lens through which we can even begin to observe patterns of descent with modification.

Cultural Selection

Finally, Cloak (1966, p. 10) submitted that "the true biological analogue for cultural diffusion . . . would have to be a sort of *selective* gene flow." "Selective" in this sense is indicative of a flow of information that is purposely directed, assumedly as a result of human intentionality (see Mesoudi et al. 2006, p. 372). This suggests that cultural information can evolve in accordance with the Lamarckian evolutionary process of acquisition of acquired traits or directed variation (e.g., Jablonka and Lamb 1995). In general, biological evolutionary models have not taken such processes very seriously until relatively recently. However, Boyd and Richerson's (1985) dual-inheritance model—which takes into account that biological and cultural systems coevolve in dynamic fashion—has gained significant support in the last few decades across anthropology and archaeology. Added to this, recent research in the fields of epigenetics and niche construction (or triple-inheritance theory) posits inter-dynamics between biological, cultural, and environmental factors in the development of individual organisms.

Table 2.1 Biological processes of evolution and examples of their cultural variants

Biological	Cultural
Mutation "Any heritable change . . . brought about by an alteration in the genetic material. Includes gene conversion, deletion, duplication, insertion and so forth"	Random (but see Riede et al. 2018) change to any aspect of the cultural system as a result of, for example: Invention Innovation Creativity/idiosyncratic variability Accidental variation
Drift (genetic) "Evolutionary change over generations due to random events in small populations . . . operates unless overcome by strong selective forces"	As above, inventions, innovations, idiosyncratic variability, and change as a result of accidents occurring in populations isolated as a result of allopatric separation or resulting from any number of other reproductive isolating mechanism (RIMS) and/or (cultural) transmission isolating mechanisms (TRIMS)
Adaptation "Adjustment to environmental demands through the long-term process of natural selection acting on genotypes"	Adaptation Niche construction (although niche construction theory (NCT) attempts to address the relationships between environments and the organisms that inhabit them, not focused simply on adaptation as such, but rather on the dynamic interplay between organisms and the environment over the long term [see Riede, this volume])
Persistence (The result of fitness/reproductive success) Fitness: "Lifetime reproductive success of an individual... It can be seen as the extent to which an individual successfully passes on its genes to the next generation. It has two components: Survival (viability) and reproductive success (fecundity). Variation in fitness is the major driving force in biological evolution"	Fixation; in cultural this might result from: Cultural inertia Acculturation Conservative transmission biases Pedagogy

Evolutionary biology term definitions taken from M. Tevfik Dorak's online glossary (http://www.dorak.info/evolution/glossary.html)

As a means for evaluating holistic and dynamic selection processes in cultural contexts, such as the acquisition of acquired traits or the horizontal transmission of ideas from one individual to many, cultural selection may have a metaphorical correspondence to epigenetic and constructed environment-induced selection pressures (e.g., niche construction; see Riede, this volume). Understanding selection processes and constraints in general—regardless of whether we designate them as exclusively "natural" or "cultural"—is key to more accurately understand the interplay between humans and their surroundings and vice versa. To distance cultural selection too far from natural selection is to ignore that Darwin's own concept of natural selection was rather plastic and accounted for the "preservation of favourable [*sic*] variations and the rejection of injurious variations" regardless of the overall driving forces involved. Darwin was rather vague as to the specific nature of natural selection forces and certainly did not count out the possibility of human behaviors playing a role in selection pressure. To Darwin, forces at work in producing selection pressures could derive from any number of causes, from natural predator-prey relationships to human proclivities (e.g., domestication), to geophysical constraints such as may be encountered in insular, or otherwise isolated environments, and more (Darwin 1859, p. 81). Thinking about cultural evolution implicitly as variation in the frequency of behaviors from one generation to the next within a society, it is easy to conclude that cultural evolution is driven by natural forces and entirely accountable within the framework of Darwinian evolution by natural selection. One can also remain open-minded to the empirical reality that cultural change in this way appears—and may well be—more dynamic than its biological simile due to the extra-reproductive modes of transmission that are possible thanks to culture.

Cultures evolve in more diverse ways than do biological systems. They can also evolve rapidly in some of their aspects and often along seemingly inexplicable paths. This is why the rate and tempo of cultural evolution is often noted to occur rapidly relative to genetic changes in communities of noncultural biological organisms (although clearly some organisms—such as bacteria and viruses—can and do sometimes evolve very quickly). The combination of purely natural (environmental, circumstantial) and cultural selection pressures is generally much more dynamic, and cultural transmission is of course not limited to the vertical pathway that constrains gene flow. However, not all features of a culture evolve fast and certainly not all the time. Cultural change is not necessarily an inherent property but one that emerges under specific historical conditions (e.g., under conditions favoring enhanced sharing and spread of innovations). Relative to absolute time, the actual and potential speed of evolutionary change depends entirely on "generation length" or the number of replications that a given cultural trait undergoes during a given unit of time (e.g., Fletcher 1996; Jordan and O'Neill 2010). As the expression of human behaviors, themselves, subject to numerous selection and transmission altering forces—from environmental and geophysical to social to idiosyncratic and beyond—cultural traditions clearly change by way of descent with modification over time, founded at the level of single organisms, i.e., human beings interacting with their surroundings. Ultimately, instances of cultural change occur as the result of interactions between individuals (just like changes in allele frequencies passed between or occurring between parents and offspring), and such microscale processes happen constantly in regard to the transmission of cultural variants within and between populations. Yet, it is the *expression* of cultural variants at the population scale that makes any form of descent actually observable. So, while we can theorize about microscale processes in anthropological and archaeological studies, we must operationalize them at the macroscale if we are to say anything relevant about cultural evolution as a process rather than as an isolated incident of change.

In population genetics, it is widely recognized that neutral or nearly neutral mutations—those that have little or no effect on fitness and are therefore weakly or seemingly not at all selected for—predominate at the molecular level (see Wakeley 2010, pp. 123–125). Kimura (1968) calculated that within finite populations of complex organisms, neutral or nearly neutral mutations actually occur at a much higher rate than they do modeled simply as responses to natural selection pressures. Thus, neutral mutations can arise and diffuse within a population relatively rapidly without having any direct impact on the community in question. When fitness is more-or-less equal between differing genotypes (i.e., none of the existing genotypes provides a distinct adaptive advantage under given conditions), there is "weak" or "nearly neutral" selection (Hartl and Clark 2006, pp. 248–251; Ohta 1973). In principle, this same phenomenon is observable in the archaeological record (Kandler and Crema, this volume; Laue and Wright, this volume). In regard to culture, Durham (1982, p. 307) observed that "some cultural variability has little or no impact on the adaptiveness of its carriers." In fact, many attributes of culture have no discernable consequence when it comes to fitness—at least not which can be observed. In cultural evolutionary studies, just as in evolutionary biology, this concept is known as the *neutral* or *nearly neutral model* evolutionary model that accounts for changes in cultural systems that have "little or no impact on human survival and reproduction" (Durham 1982, p. 308). Even in early evolutionary archaeology studies, neutral cultural traits were recognized in the material record, especially when the appearance of new variants of design or morphology appear and disappear rapidly. For example, Dunnell's "stylistic" traits could be seen as neutral in that accordingly their "frequencies in a population are not directly accountable in terms of selection . . . their behavior should be more adequately accommodated by stochastic processes" (Dunnell 1978, p. 199). At the very least, "stylistic" traits as Dunnell conceived them fit the nearly neutral model. As it turns out, in both organisms and cultural phenomena, ephemeral changes resulting from random mutation and drift are more commonly drivers of diversity than have often been theorized (see Laue and Wright, this volume).

In cultural studies, we may be able to more appropriately understand cultural selection as a form of synecdoche with Darwinian natural selection processes—in fact as an intrinsic part of those processes—without dwelling too dogmatically on the constraints imposed by biological imperatives such as the "reductionist argument that focuses solely on human reproductive success" (O'Brien and Holland 1990). Ultimately, culturally selected traits are still subject to natural selection pressures *and* subsequent cultural selection pressures over the long term. The false dichotomy between nature and culture in which culture remained somehow outside of nature has only recently been dismantled. Culture is subject to both Darwinian *and* non-Darwinian selection and evolutionary trajectories (e.g., Lamarckian accumulation of acquired traits [Jablonka and Lamb 2005]). While modes of selection pressure may theoretically appear different between adapting to the natural environment and adapting to, for instance, the social environment, the ultimate broad effects of selection pressures are the same between biological and cultural systems. Changes over time, driven by the natural *and* social environment *and* by chance *and* purposefully directed, still fall within the natural domain, because behaviors themselves are responses to selection pressures (e.g., see Riede, this volume).

Synthesis

The chapters in this section of the handbook illustrate that evolutionary archaeology has developed a significant degree of theoretical and methodological sophistication during recent years. In closing we offer two critical points. First, the archaeological study of cultural microevolution remains as difficult as it remains critical and is providing significant new insights. Scholars are developing increasingly sophisticated models referencing the effects of plasticity, selective context, learning and innovation, transmission bias, and neutral and nearly neutral processes. Walsh et al. (Chap. 3, this volume) argue that the processes by which cultural variations emerge and are transmitted are complex and affected by a variety of factors inclusive of (but not limited to) population density and interaction parameters, cultural constraints on creativity, the nature of cultural entities (e.g., simple artifacts versus more complex cultural configurations), and modes of learning and communication. Goodale (this volume) reflects on the importance of selective context and the impacts of short-term processes on the unfolding of long-term (macroevolutionary) trends. Kandler and Crema illustrate the challenges faced by archaeologists seeking to identify directionally biased cultural transmission and neutral processes in the archaeological record. They offer sophisticated mathematical approaches to initiating the process of testing alternative hypotheses. Second, contributors make it clear that there is no firm boundary between cultural microevolution and macroevolution, at least as measured with archaeological data. Compare, for example, discussions in Kandler and Crema (microevolution section, this volume) versus those of Laue and Wright (macroevolution section, this volume). These two chapters provide a vivid argument as to the necessity that we gain nuanced understanding of both bottom-up and top-down cultural processes. As we do that, we recognize that knowledge derived from studies on different scales is essential to creatively imagine the cultural evolutionary process in general.

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Chapter 3
Cultural Transmission and Innovation in Archaeology

Matthew J. Walsh, Felix Riede, and Sean O'Neill

Introduction

Homo sapiens are reliant on material culture as a vital component of their adaptive toolbox more than any other hominid extant or extinct. High-fidelity cultural transmission is said to be the key to the long-term maintenance of these material culture traditions, yet we are left to infer and extrapolate the various modes of learning and teaching of ancient hominins from quantitative, cognitive, ethnographic, or archaeological models (e.g., Fogarty et al. 2011; Gärdenfors and Högberg 2015). Some workers have emphasized that effective social learning and the habitual use of much material culture may be a rather recent element in human evolution (Shea 2017; Corbey et al. 2016). Be that as it may, modes of high-fidelity transmission certainly reduce the costs of learning the many routines and the many forms of knowledge critical for any member of a given human society to function saliently. In the absence of such transmission, the persistence of the kinds of material culture traditions identified in the archaeological record would almost certainly be impossible. Yet, at the level of microevolution, a major paradox remains: if individuals growing up within such traditions merely learn their material culture routines from close relatives of the previous generations, how do genuine innovations emerge in the first place? In order to move toward potential solutions and to stimulate further research, this chapter seeks to review both aspects of cultural transmission and of innovation, the dual forces that (1) introduce variability into the cultural pool of ideas and actions on which selection can act and that (2) channel the bulk of learning along fairly constrained pathways circumscribed by tradition and chosen due to their low cost and high efficacy.

Different modes of social learning have been proposed as generators of innovations. One of these modes, intentional teaching, has received much attention as an evolved feature of uniquely human social learning that strengthens fidelity in cultural transmission while keeping costs low when learning

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complex, cognitively opaque skills such as the making of multicomponent tools, weaving, or similarly intricate techno-behaviors (d'Errico and Banks 2015; Gärdenfors and Högberg 2015, 2017; Haidle 2012; Kline 2015; Tehrani and Riede 2008). Unsurprisingly, cross-cultural research underlines that teaching is particularly emphasized in economic and cultural domains associated with high values (Kline et al. 2013). In addition, studies in cultural psychology indicate that different modes of teaching may lead to correspondingly different degrees of innovation among older children and young adults. Interestingly, some studies have also demonstrated that those differing degrees of creative flexibility can be transferred to other domains of activity beyond that originally taught (Greenfield 2004). Hence, intentional teaching can be thought of as a scaffolding that at once facilitates fast and efficient learning of norms and routines while also inculcating the potential for creative problem-solving within—and to perhaps a more limited degree across—the material culture domains in question (Lombard 2015). Similar scaffolding may be present in other primates (Musgrave et al. 2016) but is seen to lead to cumulative cultural evolution in humans when coupled flexibly with alternative social learning strategies (Dean et al. 2014). As important as learning modes and trajectories are, the acquisition of a certain skill through learning is one thing, innovating another. At present, no consensus on the role, on the mechanism, or on the drivers of innovation exists. In this chapter, we attempt to provide a view of innovation in relation to cultural transmission in the hope of sketching out productive avenues for future research.

First Things First: What Is "Culture"?

There are myriad definitions of culture, but here we offer a focused brief. Richerson and Boyd (1984), p. 430 define culture as "information acquired by imitating or learning from other individuals and able to affect an individual's phenotype, usually behavior." Further, this information must be shared within some scale of a population. As Cavalli-Sforza and Feldman (1981, p. 10) put it: "The feature common to all . . . 'cultural entities' is that they are capable of being transmitted culturally from one individual to another." Thus, culture is specifically something transmitted from individual to individual. It is "a system for the inheritance of acquired variation" that is directly altered by individual interactions at the *microscale*, that is to say, the observable on-the-ground interactions between individuals, within a group (e.g., Pagel and Mace 2004).

Yet, in archaeology, we rarely get a glimpse of individual (i.e., microscale) interactions without making some significant inferences as to what information transactions were probably taking place in the past. These inferences are based on the often incomplete material culture proxies that we have at hand. Certainly, we may infer from archaeological features or materials the activities that likely occurred at a given site, but we can rarely be absolutely certain of the specific personal interactions that may have accompanied any given instance in the past.

The fact is we will never be able to eavesdrop into the casual conversations or 'artist's shoptalk' that perhaps took place during the making of the first cave paintings at Lascaux or Chauvet (e.g., Clottes and Lewis-Williams 1998; Lewis-Williams 2004; Mithen 1998). We will never know the technical instructions given by one toolmaker to another as they prepped stone tools for butchering horses 400,000 years ago at Schöningen (Haidle 2009; Thieme 1997; Voormolen 2008). But maximal reconstruction is important, because aggregate cultural traditions that were consistently maintained over multigenerational time spans gave rise to cultural change over the long term at the macroscale, between populations. Indeed, under rare conditions of preservation and using detailed analytical techniques, instruction and learning can be made plain in the archaeological material even deep into the past (e.g., Fischer 1990; Högberg 1999; Grimm 2000; Milne 2005; see also Chap. 2).

As it relates to the archaeological record, Bettinger (2009, p. 275) notes of microscale evolutionary change that it "is relatively fast, but much of it is random, and therefore offsetting, over the long periods of macroevolution, at which scale change proceeds more slowly...small-scale events and processes are critical in generating the needed variation, but their individual outcomes are unpredictable and essentially random, depending so much on myriad historically contingent events". At the microscale, culture change is prone to appear random and unpredictable (because it is largely dependent on chance probabilities and the proclivities of individuals) simply because we cannot observe interpersonal interactions and their innumerable consequences directly. Yet, the changes that actually occur are essentially sources of variation, itself a product of historical contingency. In this sense what we see as the evolution of culture, regardless of scale, is a combination of chance, scaffolding, individual proclivities and vagaries, and historical circumstances.

Viewing cultures as complex assemblages of traits that are more or less coherently associated with one another can be modelled on population genetics, where any given population consists of individuals with genetic sequences that show much similarity but also differences. These are structured spatially and change over time as processes such as mutation, drift, and selection affect them. In the long run, these processes lead to changes that generate significant population subdivisions, which can then be captured using tree-building, phylogenetic methods. Substituting genes for traits, cultural dynamics in space and time can be understood in a like fashion (O'Brien et al. 2008; Shennan 2002). Yet, in this model, innovations are closely modelled on mutations and seen as little more than random. While the function of mutations and innovations in population-scale models is identical—and while it is appropriate to black box innovations as variation generators at that scale—this view adds little to our understanding of innovation per se.

Defining Cultural Transmission

If we view culture as a sum of phenotypic traits transmitted and shared between individuals, then the ways through which culture is transmitted become extremely important if we are to understand how culture manifests itself through processes of descent with modification over time and across space.

Cultural transmission is the movement of ideas—or cohesive sets of ideas—the recipes for stringing together thoughts and conceptualizing actions as well as the knowledge of the necessary materials needed to accomplish specific tasks, their whereabouts, and affordances. In archaeology, we have many models for imagining and describing these processes, e.g., *chaîne opératoire* or "operational sequences" as originally described by Leroi-Gourhan (1964, 1993; see also Riede 2006, 2011), what Prentiss and Chatters (2003) designate *resource management strategies*, or what Schiffer and Skibo (1987) refer to as *recipes for action* in regard to the manufacture of technology (but these can also indicate cognitive *recipes for action*). Similarly, Mesoudi and O'Brien (2008, p. 70) describe "recipes" of hierarchically structured behavioral knowledge that correspondingly set together "functionally interlinked behaviors" (i.e., cultural traits) that aid the accurate retention of information during learning (e.g., effectively easing vertical cultural transmission from one generation to the next). At the microgeographic scale, transmission explicitly refers to the interchange of information from one individual to another. More specifically, as a process of descent—it describes the passing of ideas temporally from one generation to another, most commonly between rather closely related individuals within a given population. As ideas move from one individual to another, these recipes for action may accurately retain information, lose portions of it, and become modified to varying degrees, remaining either intact, relatively so, or becoming erroneous in relation to the original source material. The level of fidelity depends on a staggering array of circumstances the depth of which often remains inscrutable. Generally, the simpler the information being transmitted, the more likely it is to be transmitted with high fidelity and, hence, to remain intact across multiple transmission events.

The actual dissemination of ideas happens in numerous ways and through diverse trajectories, from hands-on instruction to secondhand imitation and copying. Here, we understand that the transmission of ideas is subject to selective forces at both the individual and group level (Boyd and Richerson 1982, 1985; Richerson and Boyd 1984). To avoid guesswork and the loss of fidelity of information it often entails, cultural practices have unavoidably led to the development of complex communication strategies such as social learning, pedagogy, apprenticeship, systems of writing, and manifold media channels, and all of these have become hallmarks of the ways through which humans pass information between individuals at every scale.

Many societies, especially those that are politically complex and hierarchical, have also developed strong norms, where conformity in social behaviors and material culture also become linked to political conformity. Studies have shown that cultural transmission strategies appear to direct information from individual to individual with at least as much fidelity as generally attributed to biological inheritance systems (e.g., Boyd and Richerson 1985; Shennan 2002). However, in culture the tempo of transmission is often much faster and does not necessarily require biological relatedness through sexual reproduction—although the two are often aligned in traditional societies, making kinship a major factor in transmission trajectories (MacDonald 1998).

Synchronic Studies of Innovation in the Past Century

Innovation theory in the social sciences owes much of its foundation to economist Joseph Schumpeter's (1934) observation that innovation is an historical process—part of long cycles of change and continuity driven by past circumstances and dependent upon contemporaneous conditions. This goes along with the recognition that for something to be an "innovation" *as such*, it must not only happen but also successfully spread. To Schumpeter, for such diffusion to take place, the innovation must not only be reasonably replicable but its replication must also be deemed as advantageous by adapters ("entrepreneurs"; this school of innovation theory is studied more at business schools than in academe). Entrepreneurs make specific choices over others, because innovation is part, parcel, and process of the market economy. For social scientists, this means that identifying and classifying innovation also requires considerable recognition of the historical, economic, social, environmental, technological, and any other contexts at play in any observable instance of cultural change. Elements of Schumpeter's economic innovation model may be useful for archaeologists because it takes into account the diachronic perspective necessary to understand processes of change as historically contingent. However, Schumpeter's model of innovation diffusions may limit our understanding of the material record as it ignores the behavioral and life history aspects of innovation, focusing on the economics of individual entrepreneurial decision-making rather than innovation, diffusion, and adaptation as processes contingent on the given social and natural environment into which technologies and ideas are engaged (and which are often actually generated by phenomena such as copying errors and freewheeling tinkering). Indeed, in societies where one cannot make a living through innovation and where the costs of extensive trial-and-error exploration potentially represent significant burdens, innovative behavior—the search for novel solutions to problems, where potential future improvements need to be balanced against the immediate risks of failure—is not immediately incentivized or encouraged in any way. Hence, the Western ideal of the "inventive genius" is likely to be misleading when trying to understand microscale innovation in the traditional societies of the recent and deep past.

Rogers (2005, p. 12) defines innovation as "an idea, practice, or object that is perceived as new by an individual or other unit of adoption... if an idea seems new to an individual, it is an innovation." Again, this notion is most applicable to postindustrial revolution modes of thought, based on conscious striving for innovation, within a highly specialized civilization where leisure time and/or direct economic support from other sectors of society has allowed such a focus. It is entirely possible that practitioners were not so conscious of innovations before the modern era and that concatenated innovations normally took place so gradually over the *longue dureé* that they were not actually consciously noted by individuals within a given generation.

Others put a premium on a kind of hardwired *urge to create*. More in line with interpretational modes of thinking, Mithen (1998, p. 7) describes innovation not as the earliest stage in ontogenesis but as an inevitability of human creativity and imagination—a driver of change beyond function or even symbolism: "a universal human trait that is almost limitless." Interestingly, he elsewhere proposes that technological innovation was rare in human prehistory up until around 50,000 years ago, due to a general disability of earlier human ancestors "to integrate their knowledge of tool making with that of the natural world"—a literal inability to cognitively connect tool making with an understanding of the surrounding environment (Mithen 1997, p. 71; see also Shennan 2001, p. 15). However, attributing innovation to some innate creativity precludes a full understanding of it. In this sense, Mithen's view would provide a complementary argument for innovation as a form of random and constant "cultural mutation," which is a by-product of a proclivity all humans possess to a greater or lesser but at any rate innate degree.

Significantly, innovations are not evenly distributed across the human career, and unlike biological mutations, they often clump in time and space—through a form of temporal-spatial "punctuated equilibrium"—so, something else must be going on (for an insightful illustration of the dynamics of innovation in the form of word proliferation in small lexical populations, see, e.g., Greenhill et al. 2018). Specifically with regard to material culture, Riede et al. (2018) have recently drawn attention to the importance of including life-history perspectives and the material culture provided to children as part of their ontogenetic niche in our understanding of innovation. In this model, children and adolescents are free to play—that is, to experiment—with objects, object combinations, and their material and mechanical affordances until the onset of reproduction when experimentation becomes an activity that is predicted to be too costly. Hence, there emerges a trajectory of physical and cognitive development leading up to a "sweet spot" of innovation likelihood in late childhood and adolescence. Playful experimentation with objects here provides the counterpart to imitative learning. In this context, it is also important to understand that the material culture given to youngsters as part of a niche construction process (see Riede, Chap. 17) both facilitates innovation specific to the technologies at hand and also constrains it to these very same domains. In this way, innovation occurs in and further diversifies existing material culture traditions.

In archaeological parlance, the term "innovation" is generally used to describe the process or result of novel change to an existing form, where the new form appears to persist in place of the latter. But the connotation also brings with it a level of functional adaptivity, as the new trait has been "selected." As mentioned above, from an empirical perspective, we may not actually *see* innovation happening. We see the material consequences of the adoption of innovations at the macroscale (i.e., Binford 1962). However, Girard (1990, p. 7) points out: "'Innovation', from the Latin *innovare*, *innovatio*, should signify renewal, rejuvenation from inside, rather than novelty." By this definition, innovations do not indicate a "Eureka!" moment of invention or transmogrification but rather the occurrences of alteration from a previously static form to any other, often only very slightly altered, state. In this sense, innovation is not the emergence of something new so much as it is a process of diversification of something that already exists, through an often subtle process of descent with modification: basically, *phylogenesis* in action. Indeed, detailed studies of innovation in recent periods show the painstaking and often error-ridden process that is more akin to the novel combining of existing materials and technologies rather than some completely new idea or item suddenly emerging. Such processes can be documented empirically (see Ziman 2000) and simulated in the laboratory (Mesoudi et al. 2016). This is telling from an evolutionary perspective, since it places innovation not as we often think of it in archaeological contexts as the act itself of introducing a hitherto unknown and subsequently useful change—but as the events of trait accumulation and recombination, phyletic gradualism in real time, emerging as a result of human behaviors, proclivities, and historical happenstance. Here, innovations facilitate, perhaps even catalyze, instances of cultural cladogenesis, much like biological adaptations in living organisms (Allen 1989; Gould and Eldredge 1977) over the long term. Ultimately, as a process, innovation is a driver of cultural variation that can be dependent on decision-making and information transmission (Shennan 1989), but it can also arise by a serendipitous accident or as a result of copying error—leading to what theoretical biologist Stuart Kauffman called “the adjacent possible.”

Diachronic Analysis of Innovation: The Archaeologists Weigh-In

Innovation has been defined in different contexts for different disciplines. Understanding the history of archaeological investigations into long-term processes of innovation is necessary toward developing a more rigorous archaeological theory on the subject as well as in developing methods for identifying it as a quantifiable phenomenon. Over the last few decades, some discussions of innovation in evolutionary anthropology and archaeology have even skirted defining the term at all, presumably since the concept has already received so much theoretical attention. However, there exists no clear consensus as to the exact parameters of innovation, per se. One major thread of contention has been the difference between *invention* and *innovation*, about which most evolutionary anthropologists now seem to agree, as being the difference between the emergence of what can be identified as a wholly new phenomenon (i.e., invention) on the one hand and a novel modification of something already in existence that proves adaptive and diffuses through a population by processes of selection (i.e., innovation), on the other.

A review of archaeological theory relating to innovation over the last 30 years, taking Van der Leeuw and Torrence’s (1989) compilation *What’s New?* A Closer Look at the Process of Innovation as a starting point and moving forward to current research on the subject, provides a selection of the different ways in which the term has come to describe both processes and products of specific types of change (e.g., Reader and Laland 2003) and sheds light on the variety of ways in which the concept has been most recently applied to discussions of the emergence of changes in material culture traditions and associated behaviors. Earlier works on the subject of innovation are comprehensively reviewed and summarized elsewhere, for instance, in Barnett (1953), Van der Leeuw (1989), and O’Brien and Shennan (2010).

In the introduction to their edited volume on the subject, Torrence and Van der Leeuw (1989) suggest that “[i]nnovation exists by virtue of an extant tradition to which it contributes something new”. Rather than redefining innovation, they suggest that innovation represents the discernible material result of risk-taking in technological change, a process visible in the archaeological record as the result of choices and events that in some cases might be reasonably inferred. Bargatzky (1989) further suggests that innovation is “something which affects the overall performance of a sociocultural system at a certain time and which did not exercise this influence before—be it an idea, an object, an attribute of an object, or just a new interrelationship between objects . . . when innovation takes place, there is a readjustment of the system’s elements and interrelationships, leading to a new system”.

But rather than simply ‘define’ innovation and to add depth to traditional business studies of innovation, Layton (1989) turns to the ethnoarchaeological record to discuss innovators. Focusing on a community-scale analysis, he observes a case study from a small French farming village. Here, at the local scale, innovations are rarely the idiosyncrasies of individuals for very long, quickly altering at the community level the scope of change and the trajectory of future decision-making. He suggests that the diffusion of innovation is driven largely by content-based bias (see below) based on the perceived efficacy of a given technique or technology when it has been observed to be successfully or otherwise advantageous by neighbors. Another important take-home message from Layton’s detailed study is that innovations can spread slowly, that there can be active resistance, and that not everybody in a given population adopts novel technologies in their own lifetime.

On another tack, Van der Leeuw (1989) offers a broad review of earlier innovation literature drawing on his own personal experience in craftwork, emphasizing that for an innovation to be defined as such, it must be perceived of as being worth the risk: that innovation involves the perception (and ultimately the acceptance) of risk. He contends that, as a conscious creative act, innovation is mediated by one's ability to assess the possibilities and outcomes of success, failure, and the possible consequences of both, based on one's previous knowledge or experience. For archaeologists, this is exceptionally difficult to infer since we cannot know the exact level of a priori information or understanding (as well as a posteriori expectations) that an individual in the past may have had. Ultimately, as others have observed, an understanding of the situational and historical contexts of a given event of innovation is necessary when attempting to model the complexities of such changes.

Wiessner (1997) situates the effects of innovation as a marker (along with increased variability over time) of individual or group expression. She describes how 'isochrestic' variation in material culture (that which is not afforded meaning) and 'style' (that which is given meaning) can be identified in the material record, thus placing the recognition of innovation as a proxy for changing social identities or economic status, for example (see Sackett 1982, 1986). In the past quarter-century, many archaeologists have sought a more systematic, comprehensive model for understanding patterns of innovation at the population level. A large number have turned to evolutionary theory to provide coherent explanations of pattern and process, in some cases with spectacular results. Shennan (2001) suggests again that innovation in relation to cultural evolutionary processes acts in similar fashion to genetic mutation in biological evolution—that it introduces variability. He also provides a model and formulas for testing how innovations diffuse mutation as in variable demographic contexts (see "Methods" section below). O'Brien and Shennan (2010, p. 3) emphasize the utility and the limitations of the "straightforward definition: something new and different," noting that innovation as a process is considerably more complex in terms of cultural evolution. This is because the spread of innovations introduces variation in existing systems, and as innovations represent changes to those systems, they offer a primary example of descent with modification in units of culture. Further identifying innovation with evolutionary processes, Ariew (2010, p. 22) argues that "innovations are appropriately explained by natural selection," while inventions are not, since processes of natural selection do not invent novel things, they alter already existing ones. Thus, natural selection leads to innovation—i.e., changes to existing forms. Thus, he calls for the development of more rigorous inferential logic in evolutionary anthropological studies and suggests that "a line between the explanation of innovation and that of invention" be more clearly established (Ariew 2010, p. 32).

Furthermore, Henrich (2010, p. 99) describes innovations as those inventions—"useful or adaptive novelties"—that are spread through a population. O'Brien and Bentley (2010, p. 311) propose that invention *and* innovation are "the key components of cultural transmission" as well as integral to complex technological systems (CTSs). Further situating innovation into the cultural evolutionary paradigm, Roux (2013, p. 313) observes that "according to the Darwinian approach, the social mechanisms underlying the spreading of innovative traits are twofold: either these traits become prevalent through a process of 'natural selection'... or through a process of copy..." While not a definition of innovation, Roux's observation brings us neatly to the subject of innovation's relationship to cultural transmission, as the diffusion of innovations as variants of units of culture relies on how they become spread through a population. Along these lines, Ellen and Fischer (2013) argue that innovation is but one microscale aspect of cultural transmission—that it is relational to learning and thought processes and the ways in which we communicate ideas between individuals. They state that "in studying cultural transmission we have to explore and attempt to synthesize hypotheses and data over a series of levels... the micro-level, applying to bodily and cognitive aspects of processes of learning and innovation and to interpersonal interaction" (Ellen and Fischer 2013, p. 3).

How Cultural Transmission Works: The Channels

In their seminal work on the subject, the late Luigi Luca Cavalli-Sforza and his long-term collaborator Marc Feldman (1981) characterize cultural transmission as occurring in three basic modes: "vertical," "oblique," and "horizontal." They set out a now well-established model in which vertical transmission represents the transmission of cultural traits from parents to offspring; oblique transmission describes information passed down to the younger generation from non-parental members of the *older* generation (e.g., grandparents, aunts, uncles, etc.); and horizontal transmission describes processes where information is transmitted between members of the offspring generation—i.e., information exchange between peers. Others have embellished these concepts further (e.g., Boyd and Richerson 2005; Shennan 2002), observing processes such as "random forces" affecting transmission of culture traits, cultural mutation and drift, and decision-making forces such as various transmission biases and effects such as cultural inertia, guided variation, and processes of natural and guided selection forces that dynamically inform how cultural information persists, changes, and gets around (Boyd and Richerson 2005, p. 69).

Transmission biases describe forces that lead to some cultural variants to be adopted rather than others (Richerson and Boyd 2005, p. 68) and can result in innovations getting introduced into cultural systems. Biases can regulate the rate of introduction of alternative cultural traits. Below, we provide an overview—drawing from a variety of sources—of the numerous forces and processes associated with cultural evolution (Table 3.1).

More on Innovation in Evolutionary Archaeological Contexts

Now that we have reintroduced the basic concept of innovation above, it is important to try to unpack the theoretical history of this term as it relates specifically to evolutionary studies in archaeology. Key to observing innovation in the archaeological record is temporality. A diachronic perspective allows for the identification of earlier forms and their modified later states (Shennan 2006). As Van der Leeuw (1990, p. 92) points out, identifying innovation in the archaeological record is a critical exercise in recognizing context—looking back in time in the hopes of "finding the *conditions of occurrence* of new phenomena... the *context* of the emergence of the present...." Thus, in archaeology at least, innovation is defined by the context of adaptation: when later versions of an observably earlier phenomenon that has undergone alteration (the accumulation of newly derived traits) appear to provide an adaptive advantage and persist in a given niche, we can consider them to be "innovations."

Otherwise, potential changes in the material culture record are generally discounted as the background *noise* of past human behaviors and manufacturing mistakes (e.g., Van der Leeuw 1989, p. 301). In most cases for much of human history—at least up until the modern age in which innovation is as much a buzzword as a sought-after process of change—technological innovation was probably the result of accidental change or, at best, the result of stopgap measures that happened to prove more efficient or effective than the technologies that preceded them (but see Riede et al. 2018). Such novel changes—for whatever reason they occurred—without adoption and propagation (i.e., diffusion) are not innovations per se, when it comes to what we can identify in the archaeological record unless we are able to observe *descent* of one form to that of another. Thus, a theory of evolution is indeed essential for a material culture concept of innovation as adaptation. However, while innovative change may be adaptive in a specific context, their persistence over generations through inertia may prove maladaptive if those contexts change. Ultimately, certain innovations may not only be useless or ineffective (just like neutral or nearly neutral mutations; see Laue and Wright, Chap. 7, this volume)—they could prove downright disastrous from a fitness perspective. Also, the environmental or social

Table 3.1 Matrix of terms and definitions describing cultural evolutionary forces and processes, adapted from Richerson and Boyd (2005), Jordan (2015), and O'Neill (2015)

Random forces	*Cultural mutation*	Variation "due to random individual-level processes, such as misremembering" a stage of a process, as in a cultural recipe for action (Richerson and Boyd 2005, p. 69). Invention and innovation reflect processes of mutation in culture (e.g., Read et al. 2009; Shennan 2001). Note, however, that the provisioning of young learners with "qualifier toys" (Lancy 2017) can prime innovation through familiarizing learners with the mechanical and material properties of especially complex technologies whose proper function is an emergent property of its components, and where it is not obvious precisely which modifications may lead to a functional improvement (Riede et al. 2018). This priming makes such "cultural mutations" nonrandom
	Cultural drift	Change guided by random anomalies occurring in small or isolated populations (Richerson and Boyd 2005, p. 69)
	Cultural inertia[a]	The feedback loop of cultural traits within a specific culture that influences or directs the frequency of new or existing traits conservatively: what Richerson and Boyd (2005), p. 68 describe as "the process that tends to keep the population the same from one time period to the next." In common terms cultural inertia represents maintenance of the status quo, often the result of conservative modes of transmission that tend to reject change: e.g., frequency-based bias founded on the imitation of the most commonly observed behaviors (see below) or the building up—through pedagogy—of very specific sets of ideas and ways of doing things, e.g., cultural "scaffolding" (Tehrani and Riede 2008) or normative pressures
Decision-making forces	*Guided variation*	"Nonrandom changes in cultural variants by individuals that are subsequently transmitted. This force results from transformations during social learning, of the learning, invention, or adaptive modification of cultural variants" (Richerson and Boyd 2005, p. 69). Basically, this is Lamarckian cultural evolution: when a trait is deemed beneficial, it may be differentially (i.e., purposely) passed on to other individuals within the population
	Biased transmission: content-based (or direct) bias	"Individuals are more likely to learn or remember some cultural variant based on their content" (Richerson and Boyd 2005, p. 69)
	Biased transmission: frequency-based bias	"The use of the commonness or rarity of a cultural variant as a basis for choice" (Richerson and Boyd 2005), p. 69. Shennan (1989), p. 337 describes this as "the tendency, which may or may not exist in any particular case, for individuals to imitate the more common, or the less common, of two different versions of a behaviour pattern precisely because it is more common, or less common"
	Biased transmission: model-based bias (a form of indirect bias)	Choice of trait based on the observable attributes of the individuals who exhibit the trait (Richerson and Boyd 2005), p. 69. Shennan (1989), p. 337 points out that indirect bias "can be a sensible strategy for individuals to follow: imitating all the characteristics of individuals who appear to be locally successful . . . ." This is also referred to as "prestige-based" bias (see also "pedagogy" below)
Natural selection		"Changes in the cultural composition of a population caused by the effects of holding one cultural variant rather than others. The *natural selection* of cultural variants can occur at individual or group levels" (Richerson and Boyd 2005, p. 69)
Cultural selection		"Processes of cultural selection can . . . change through time not as a result of natural selection affecting people's survival and reproductive success but as a result of conscious and unconscious decision-making based on a variety of criteria" (Shennan 2002, p. 35)

(continued)

Table 3.1 (continued)

Social learning		In broad terms, a way in which information is acquired . . . *the mechanism of cultural inheritance* (Shennan 2002, p. 38)
	Cultural inheritance	The regeneration of phenotypic traits and processes through the direct or indirect transmission of information between entities (Avital and Jablonka 2000, p. 54). How cultural traits get passed down from generation to generation
	Cultural transmission	Generally defined as analogous to biological transmission. Generically, the movement of cultural traits from one place to another; at the microscale, from one individual to another. Describes ways in which information passes from one entity to another leading to descent with modification of cultural traits. The different ways in which cultural traits get passed between individuals and diffuse through and between populations
	Pedagogy	The capacity to learn and transfer information through guidance in a tutor-to-pupil format, as well as the act of doing so. Tehrani and Riede (2008), p. 319 describe it as a "correction mechanism" within social learning—a form of "relevance-guided transmission" in which a teacher uses cues (e.g., approval/disapproval) to guide specifically targeted behaviors and actions in order to maintain transmission fidelity of conventional/desired traits
	Propagation	Mainly microscale evolution of material culture traits *within* defined populations (Jordan 2015, p. 61)
Additional terms	*Cultural coherence*	Macroscale evolution of material culture traits *across* ethnolinguistic populations (Jordan 2015, p. 61). Describes how, within a single cultural tradition, processes of descent with modification make patterns of cultural transmission between groups clear
	Historical congruence	Macroscale evolution of material culture traits *across* ethnolinguistic populations (Jordan 2015, p. 61). Describes how different cultural traditions travel together in space and time; when linked, historical congruence of cultural traits represents the presence of empirically identifiable cultural cores or distinct sets of shared, derived traits that can be observed to be the same or very similar between groups, generally as a consequence of historical processes and contingencies

[a] While not technically "random," cultural inertia is subject to any number of stochastic forces interacting in such complex ways as to make it probabilistically random

contexts in which a given technology functions can change over time, sometimes turning a once adaptive feature into a feature that either has no or negative selective consequences (see Table 3.2).

This holds true not only in natural environmental contexts but also within the social environment. Girard (1990) even suggests that at times perpetuating novelty or change has been perceived as confounding and even downright dangerous. Perhaps it is for similar reasons that early hominin technologies like Acheulean handaxes remained in such more or less consistent form for over a million years (Shennan 2001, p. 15). Creativity is a risky business. Could it be that the mere ability to recognize (and accept) innovation when it occurs, be a hallmark of human cognitive abilities? From a Darwinian evolutionary perspective, innovation can be observed at both the micro- and macroscales as a catalyst of variation—a necessity for *descent with modification* to occur. Read et al. (2009, p. 43) state that:

> By coupling innovation (in the form of mutation in the genetic material transmitted) with differential reproductive success, Darwinian evolution connects patterning expressed at the level of the individual (novel traits) with patterning expressed at the aggregate level of a population (frequency of traits).

The same can be said of innovation of cultural phenomena, i.e., novel traits arising at the individual scale, whether by accident or creativity scaffolded within the strongly modified ontogenetic niches

Table 3.2 The difference between adaptive behavior and adaptations

	Is the behavior adaptive? *Adaptive behavior* is functional behavior that increments reproductive success		
Is the behavior an adaptation? An *adaptation* is a character favored by natural selection for its effectiveness in a particular role		Yes	No
	Yes	*Current adaptation* A current adaptation is an adaptation that has remained adaptive because of continuity in the selective environment	*Past adaptation* A past adaptation is an adaptation that is no longer adaptive because of a change in the selective environment
	No	*Exaptation* An exaptation is a character that now enhances fitness but was not built by natural selection for its current role	*Dysfunctional by-product* A dysfunctional by-product is a character that neither enhances fitness nor was built by natural selection

Adapted from Laland and Brown (2002, p. 133)

of human society, can only really be observed archaeologically beyond the level of “accident” or “creativity” when they are expressed more widely at some variation of a population scale.

For archaeologists, innovation is an important feature of cultural evolutionary processes, particularly technological innovations, since modifications to existing technologies that prove adaptive in a given context (i.e., niche) can be observed in the archaeological record in their temporal, spatial, and environmental contexts, allowing us to infer circumstances of their emergence and persistence. Richerson and Boyd (2005, p. 69) point out that the spread of innovations is usually the result of the diffusion of ideas that come with interpersonal contact between individuals: innovations spread in and between populations as individuals observe the use of new things among their neighbors, adopting hybrid forms and taking them into practice, especially when they are perceived as being more utilitarian than previous approaches or are consistently linked to individuals or groups that are otherwise successful (see also Rogers 2005, p. 11). Thus, recognizing innovation can provide insights into decision-making in processes such as tool manufacture or shelter construction in the past, as particular novel modifications to existing technologies may or may not have been innovative under differing circumstances. So, innovation is all about context. For example, in stone tool production, if manufacturing blades adequately provides *all* the necessary and effective implements required in a given subsistence context, then creating a biface (although the manufacture methods may be technically more multifaceted) is not necessarily innovative, unless the biface proves useful in some other way *and* biface manufacture gets passed on to successive generations (Fitzhugh and Trusler 2009). One person’s microblade may be another person’s waste, the circumstances in which innovations actually arise as the result of novel change can tell us a great deal about very specific conditions leading to *descent with modification* of material culture and the traditions they reflect.

Enemies of Innovation

Innovation as it appears as a feature of material culture evolution, like biological evolution, is not a teleological progress-oriented process (Ariew 2010; Dunnell 1980). Indeed, the ability of humans to foresee the efficacy of their experimentations with material culture is likely very limited (Mesoudi 2008). Cultural evolution is a contextual process driven by a multiplicity of historical and environmental circumstances and myriad possibilities, including everything from random chance to guided-variation to environmental factors, and beyond (Layton 1989). In nonhuman animals, the emergence of novel behaviors and especially of those behaviors involving some form of material culture appear strongly clued to the affordances of those objects and environmental cues (see Reader and Laland 2003). Much remains to be learned about animal innovations, but it is quite possible that much human innovation is structurally not so different from that of other great apes, for instance.

So, an innovation need not only prove adaptive at some point in the long term. In fact, it is probably imperative that this occur in the short term before the change in question faces greater probability of being discarded from the social or technological system (see Chatters 2009; Prentiss et al. 2009; Zeder 2009); it must also prove heritable in a broad sense. We differentiate between modified versions of things as one-offs on the one hand and others that prove for some reason heritable. Simply changing from one thing into another is not an example of innovation that can be observed in the archaeological record. At any given time, there usually is extensive variation in material culture at various scales (e.g., Bettinger and Eerkens 1999; Eerkens and Lipo 2005). It is only when selected variants get consistently passed on—diffusion to some degree must occur for innovation to be identifiable—that we can hope to identify "true" innovations. It is important to keep this in mind as we move toward macroevolutionary discussions of *descent with modification* (see chapters in the "Macroevolution" section, this volume).

Here, it is necessary to bring up an antithetical process to innovation, as we introduce examples of how information (and innovation) gets transmitted from generation to generation. As a mechanism for limiting the loss of fidelity of cultural information, pedagogy is the enemy of innovation (Tehrani and Riede 2008), although different pedagogical approaches also facilitate experimentation in different ways and to different degrees (see Briggs 1991). Arnold (2012, p. 276) observes that learning "the latitude for innovation" in complex craft systems is a significant part of the learning and apprenticeship period and depends on what is being taught or manufactured: "freedom to innovate is greater for purely ornamental objects than for economically functional objects," although given the salience of ornaments as social signals, this difference may also signify the variable functions that any single object can reference, i.e., their mechanical affordance as well as their value as a costly signal, a signal of group membership, status, or the like. In addition, we see great variance diachronically and cross-culturally to what degree conformity is valued also in the ornamental components of craft production.

Imitation itself inadvertently does not lead to innovation given poor enough imitation skills and some luck, but it is still a limiting mechanism since the idea behind imitation—in theory—is to successfully copy as closely (with as little copying error) as possible that which is being imitated. Learning by trial and error or self-teaching may be the best breeding ground for innovation, but these innovations are still subjected to going through the bottleneck of forms of social learning for any given change to get passed into common usage. Low copying fidelity is likely to result in deterioration of function or even loss of technological/cultural know-how rather than an accumulation of positive change (Henrick 2004; Mesoudi and O'Brien 2008). Because of this, innovation relies heavily on individual creativity (idiosyncratic variability), social learning, cultural flexibility, and chance. This notion of cultural flexibility has generally flown under the radar of cultural transmission studies, yet it is an extremely important factor when it comes to cultural descent with modification, because if the conditions are not amenable to accepting change in the status quo of any given cultural phenomenon, any innovation introduced (or attempted to be introduced) into the system is likely to be stifled and the individual(s) attempting to introduce it may even face negative consequences (e.g., Girard 1990; Rogers 2005; Schumpeter 2008, p. 132). In other words, the corollary of accepting the very premise for the evident prevalence of and evolved predisposition of *Homo sapiens* to pedagogy (Csibra and Gergely 2011), namely, that this highly efficient form of transmission minimizes the costs of learning while ensuring maximum fidelity, implies that innovative behavior is inherently risky and costly.

Innovation potentially reintroduces the Lamarckian concept of inheritance of acquired characteristics back into a predominantly neo-Darwinian epistemology (Daly 1982, p. 402). Simply put, the phenomenon of culture allows for the inheritance of acquired characteristics from one generation to the next. Choosing to adopt any particular modification to an existing system (social, technological, or otherwise) may necessitate a significant conscious or subconscious cost-benefit understanding of the uncertainties and potential consequences of that decision (e.g., Henrich 2010). But such risk-takers are essential for cultural change—particularly when it comes to innovation. As O'Brien and Shennan (2010, p. 11) put it, the more "loners," the more innovation, while the more conformists, the less innovation.

Innovation is perhaps the most difficult cultural evolutionary feature to juxtapose as an analogue to biological processes because it can be random *or* directed. Through diffusion, innovation is the macroscale expression of microscale creativity and happenstance under selective pressures and—at least in prehistory—was often likely exaptation, where a trait or group of traits evolved as an adaptation in one environment survived to function in a completely different way in an altered adaptive environment (e.g., Gould and Vrba 1982; Laland and Brown 2002). As an overall process, the closest analogy may be made with niche construction (Kuijt and Prentiss 2009, p. 264), in that innovation is a cumulative process dependent on adaptation to any number of given environmental circumstances and even triggers. Thus, to identify and attempt to understand innovation in the archaeological record, we must establish as comprehensive a context as possible for viewing the phenomenon at hand, whether it be a change in a complex material technology (e.g., Eldredge 2009; Mason 2009) or even within an existing cosmology (e.g., Steadman and Palmer 1995). For innovation studies in archaeology—as with so many aspects of archaeological interpretation—context is everything.

Innovation and Cultural Transmission in Archaeological Contexts: Three Cases Comparing Micro- with Macroscale Processes

Researchers applying cultural transmission theory inhabit what Stephen Shennan has characterized, possibly somewhat ironically, as "a broad church," with diverse and often seemingly only partially overlapping interests. One way to distinguish their concerns is to consider what cultural tradition is of primary interest to them and at what scale they are inclined to work at, both spatially and temporally. For example, language phylogenies are often used to test hypotheses about the history of populations, often over vast supra-regional expanses—explicitly macro in scale. Meanwhile, a study of a material culture tradition may be made in a more limited geographical area as a starting point but then throw light on their congruence with social traditions and languages at *that* specific social scale. Conversely, an interest in the history of a social tradition could be the primary goal, even if language and aspects of material culture are the starting point. However, when we attempt to synthesize these approaches with the "diffusion of innovations" school (e.g., propagated by Rogers and focusing primarily on industrial or postindustrial societies), the picture becomes even more complicated.

A possible key to reconciling the schools and forging a new synthesis is to identify common interests and viable methodological approaches that will serve in effective analyses and better-informed research, at any scale. Furthermore, studies that seek to empirically identify emergent patterns in the transition from the microscale to macroscale cultural processes would be seen to be of benefit to all. Because there are some aspects of cultural transmission that can be understood only by direct, synchronic, behavioral observation of social actions, individual agency or intent (as with participant observation of on-the-ground social learning processes on the part of social anthropologists or the recording of recent memories of these processes), and others that are best apprehended by archaeology (tracking the development of material culture products across widely distributed populations across geographic space and over generations through patterns of decent with modification), a seamless integration of both of these approaches is most effective when brought to bear in a single case study. Innovative practices can be analyzed by unpacking individual, agent-based activities, with a specific focus in time and place (methodological individualism, which sees societies built up from the sum total of the individual actions of rational, self-interested actors at the

Fig. 3.1 Investigating the dynamics of innovation

microscale). On the other hand, the patterns and processes of cultural change and continuity can be observed on the population level, over generations (population dynamics which determine long-term patterns of cultural evolution at the macroscale). Workers have emphasized specific zones of this wide spectrum, but actually most archaeological data warrants scrutiny of their implications across all scales (Fig. 3.1).

Workers currently applying cultural transmission theory in ethnoarchaeological fieldwork-based empirical studies offer a more explicit rendering of the emergent patterns involved in moving from the micro- to the macroscale. These inform studies in both the cultural transmission *and* the diffusion of innovations schools. The following first two cases involve primarily material culture traditions, with implications for both social traditions and language, and both focus on emergent patterns of cultural transmission as the scales are steadily increased; the third case analyzes social traditions over a relatively vast scale in time and space and suggests that material culture studies could potentially follow.

Case 1: "They Do It Over There, But We Don't Do It Here" (Bowie, D. 1981 Fashion. *Scary Monsters*)—How TRIMS Can Ring-Fence Coherence at the Microscale Analysis of Cultural Transmission

Enduring lineages of socially learned material cultural traditions are frequently recognized by archaeologists, with some traditions spanning many thousands of years. It is maintained here that these large-scale patterns are an aggregate result of individual, agent-based behaviors. This means that the cumulative effects of specific dynamics of social learning and innovation at the "microscale," meaning between individuals *within* populations (e.g., *who* is doing the learning, from *whom* they decide to learn, *what* they are interested in learning, *when* they want to learn it, and *why*), will have a cumulative effect and generate the emergent patterns of cultural transmission that can then occur *between* populations (the latter being the "macroscale" of analysis, specifically dealt with in Chap. 20 of this book). Population thinking in general has provided a useful framework for understanding both these scales of analysis.

Durham held that a clear distinction between cultures could be created not only by geographic isolation and subsequent independent development alone but also by other TRIMS (*transmission isolating mechanisms*) within the cultures themselves (Durham 1992; examined in Tehrani and Collard 2002, 2013). Analogous to RIMS (*reproductive isolating mechanisms*) in biological speciation theory, TRIMS are any mechanisms that inhibit relations between different populations or different cultures within the same populations (see Tehrani and Collard 2013) and could be based on any range of ecological, psychological, linguistic, religious, or other cultural factors that clearly define in-group/out-group relations. Populations can be separated over time by ecological divisions, as happens with divergent patterns of migration or gradual geologic change; however many ideological TRIMS can be propagated rapidly through social learning and grow or decline in relative frequencies, depending upon historical contingency. Xenophobia, racism, religious intolerance, nationalism, and other socially learned forms of community solidarity or divisive social alienation and anomie (where closed, "imagined communities" are modelled by establishing "others" who are not a part of the "in-group"; see Anderson 1983) all can cut off the flow of cultural transmission between groups. The result of this is that cultural traits are clustered in such a way as to maintain specific combinations of cultural traits which are more like separate species branching away from each other, than gene pools within biological populations. In these situations, patterns of cultural evolution could be amenable to phylogenetic analysis. These kinds of branching splits do not require geographic isolation, and it is reasonable to assume that they actually could occur between groups that are co-resident in the same population in the same geographic place (Collard et al. 2008; Tehrani and Collard 2013). A growing number of empirical cases have indeed demonstrated the strong coherence of material culture traditions at the microscale, or within populations, for an interesting variety of reasons. When there are coherent branching patterns between co-resident groups, as opposed to merely a "blur," it is possible to then reconstruct which groups have been closer to each other in terms of descent with modification, supporting inferences about their mutual histories together without written records and even without surviving oral histories.

In an explicit test of the presence of postulated in-group/out-group transmission isolating mechanisms (TRIMS), Tehrani and Collard (2013) hypothesized that patterns of craft diversity between tribal populations in southwestern Iran would exhibit greater branching (phylogenetic) structure than patterns of craft diversity between clans belonging to one of the tribes, where more blending (ethnogenetic) patterns were predicted to be observed. According to Durham (1990, 1992) TRIMS can take the form of ecological boundaries and mutually unintelligible languages. However, in this case, based on ethnographic knowledge, the primary TRIMS predicted to create alienation between tribes, but at the same time more in-group coherence within the tribes, were (a) constant warfare between the tribes and (b) strictly observed endogamous marriage practices, which both would have constrained the movement of people, and ideas, between tribal populations.

In Tehrani and Collard (2013), patterns of textile diversity between four tribes were sampled during ethnographic fieldwork and from a published work based on an extensive museum collection. Secondly, designs for five clan groups within *one* of the tribes represented in the dataset, the Bakhtiari, were also collected. Phylogenetic tests on the respective databases found a significant phylogenetic signal in the inter-tribal data, but not in the intra-tribe data.

Therefore, this test supported the TRIMS hypothesis: that each tribal unit within itself was possessed of more culturally coherent entities in contrast to each other, because of strong in-group/out-group affiliations. This supported the hypothesis that endogamous marriage practices and warfare at the tribal level (the macroscale, between populations), as opposed to the smaller clan units within the single tribe, which were not aggressive with each other and could intermarry (the microscale, within one tribal group), constrained cultural transmission between the larger groups. While aspects of ecology, language, social customs, xenophobic ideology, and phenomena such as warfare can structure TRIMS, this work suggests that it is also possible that material culture itself can function as a TRIM among contemporaneous communities, in an ongoing reciprocal relationship with specific forms of human behavior. People can more easily reinforce in-group/out-group distinctions, for example, if they wear visibly different clothing and carry other material appurtenances that clearly distinguish their self-identity. Furthermore, entire man-made architectural habitats can function to keep social groups apart, but the results described here indicate that ideological (and powerfully symbolic) aspects of smaller-scale, portable material culture traditions might also function in similar, if more subtle, ways.

Tehrani and Collard (2013) caution that these patterns of cultural evolution and the specific mechanisms that may underpin them are applicable to this historically contingent situation only and do not equate to a universal rule valid across differing patterns of the evolution of culture at different social scales of analysis. However, to date there has been very little research done which actually compares and attempts to connect patterns generated at the different scales of analysis, and this particular study moves research further in this direction by examining a material culture lineage across populations but also comparing the same traditions within groups embedded in a single population in the study. The work suggests that similar studies could be done elsewhere.

Since this research uniquely compared cultural evolution patterns of the same material culture tradition at both the microscale and the macroscale, it begs a further question. If more borrowing and blending of material culture traits can occur at the microscale, and branching patterns are more likely to emerge at the macroscale in an extended cultural milieu—in some cases, at least—then is it possible some extreme views taken in the ethnogenesis versus phylogenesis debate actually are formed by biases based on specific researcher's experience in anthropology or archaeology, the actual social scale they habitually study at (e.g., archaeologists who study diachronic processes vs. social anthropologists who may spend 18 months garnering a highly detailed, synchronic snapshot of one small society through participant observation within that group)? It is relatively rare for workers to span both scales, as in this specific case.

Case 2: Building Scale—Tracing Cultural Transmission

Over three extended fieldwork seasons, Jordan (2015, p. 150–184, 213–216) sought to understand the propagation of Khanty hunting ski design traits, initially at 29 basecamp sites along rivers within the Iugan River basin, south of the Ob River in northwestern Siberia, a subregion with an area of approx. 40,000 k^2. These wide skis function more as snowshoes in the wilderness, and not downhill or cross-country skis, as in the West; they are designed for hunting in remote areas and enable people to safely cross extended, shoulder-height banks of snow in pursuit of prey. Across these basecamps Jordan (2015) interviewed the makers and owners of the 50 skis in his sample, specifically enquiring about the social learning processes involved in making the complex equipment (via *indirect bias*; all men and women, who worked together to make the skis in specialized roles, learned primarily by watching their fathers and mothers). However, Jordan (2015) explains that the functional qualities of these skis were under constant, intense scrutiny by their individual owners out in the field throughout the hunting season. This is because any lack of high-performance of the skis, or abrupt structural failure in deep snow in obscure places, could put the hunter's life at risk or at the very least cause days-long setbacks to food procurement. Here there was observed a constant two-stage learning process between the generations: while there was a strong vertical transmission of design methods from parents to children, there was also a degree of personal tinkering (guided variation) involved in the ongoing maintenance and design development of the skis. These new modifications may or may not be passed on to others by way of vertical, oblique, or horizontal routes of transmission, but if they were, they could become an inherited part of the tradition.

In studying the skis themselves, Jordan (2015) also compiled a database of the observed presence and absence of 41 material culture traits for the 50 skis which he then analyzed by way of both network and phylogenetic methods. These returned strong signals of coherence in this tradition, within this subregion. This was attributed to the strong functional requirements for the skis; however there was greater variation tracked in the more recently introduced cloth ski covers used to keep snow off of the hunter's boots.

Jordan (2015) also consulted ethnographic literature from over a century before his fieldwork (e.g., Martin 1897), in order to provide a form of baseline data on the historical design of skis in the area, for comparison with the contemporary database. Here he found wider variation in the design, and a second different design, one with an upward-protruding narrow platform or "fin" carved from the same block of wood as the body of the ski, included to support the feet and raise them above the level of the skis, keeping them more free from the accumulations of snow passing over the ski. This second design appeared to have gone "extinct" by the early part of the twentieth century, once affordable cloth for making the protective ski covers was available for the easier-to-handle contemporary design.

Jordan (2015) then further extended the geographical range of the ski study twice more at a roughly exponential rate (which could be expressed as 10^3), firstly to a much wider region encompassing five more major Khanty groups across adjacent river basins, and ultimately from this area across all of Siberia to the Far East. For further historical baseline reference, he consulted Levin and Popatov (1961) in order to understand wider baseline historical developments.

Again, employing network and phylogenetic analyses to the wider Khanty regional groups, there was significantly more variation found between ski designs from these six major groups, including the first group examined from the Iugan River basin. This is a similar finding to Tehrani and Collard (above), in that the canalized coherence of groups in smaller areas creates a strong contrast when compared with groups in adjacent areas. However, in this particular case, Jordan (2015, p. 176) attributes these variations to the restrictions of physical geography as TRIMS (*transmission isolating mechanisms*; see case study above), as opposed to warfare or marriage practices, that it is the isolation between the different river basins that has led to the respective specific canalization/coherence of traditions in each separate basin area and this isolation also may have impacted the patterns of other cultural traditions, such as the noted significant variation in Khanty dialects.

Through a similar analysis of ski design at the all-Siberian scale, the combination of traits for all contemporary skis in the database displayed wider variation still, but all were clustered more closely together than with the second, “archaic” design, which appears to have gone extinct everywhere with the arrival of affordable cloth. Jordan (2015) explains this development in terms of “trade-offs”; the contemporary ski design was easier to manage than the archaic design, the archaic design being more difficult to master, but the latter was traditionally quieter and much more effective in approaching prey. However, once the contemporary design was enhanced with protective cloth covers (which rendered it quiet as well), the contemporary design was selected for very rapidly because it was easier to use *and* now equally as silent.

Here it has been possible to describe and better explain a process of relatively rapid cultural change across a vast continent by beginning with careful observations of micro-processes of cultural transmission in one subregion alone and then increasing the scale of analysis on a systematic basis.

Both of the above cases demonstrate how patterns of cultural transmission and the diffusion of innovations can best be apprehended by thinking on a constant, multi-scalar spatial and temporal basis. Researchers working with the macroscale often cannot directly address the microscale and vice versa. Tehrani and Collard (2013) and Jordan (2015) drive home the benefits of seeking to understand emerging patterns across the scales. The following case extends the brief to further cultural traditions, and an even larger geographical range.

Case 3: Do Cultural Traditions Marry Well?

As mentioned above, patterns of macroscale language evolution are generally used as the basic lattice for historical reconstruction and congruence studies, where different cultural traditions can be mapped on to each other to see if there are congruent parallels between them (e.g., language and the evolution of architecture; see Jordan and Mace 2006; Jordan and O’Neill 2010). However, it is possible that language and material culture traditions can be demonstrably impacted by other discernible suites of tradition, such as social customs (Jordan and Mace 2006), and it is proposed here that these can be analyzed even at the grandest possible scales of cultural evolution.

Fortunato and Mace (2009), building further on work published by Fortunato et al. (2006), wanted to trace the relationship between the evolution of wealth transfers at marriage on the one hand and marriage systems on the other, in Indo-European societies across all of Eurasia. Building on the findings of other scholars, they had predicted that bride wealth (wealth transferred from the groom or his kin to the bride's kin) and dowry (wealth transferred from the bride's kin to the bride) should be correlated with polygynous vs. monogamous marriage, respectively.

This hypothesis is based on a functional explanation provided by behavioral ecology (addressing one of Tinbergen's "why" questions, 1963), which focuses on the survival value of behaviors in relation to the environment (the human social environment included). In parental investment theory, necessarily limited resources for provisioning children's future will be allocated to maximize the parents' own reproductive success. Because men invest less in gametes than women, they are likely to deliver more grandchildren for the investing parents in polygynous societies. This would predict an emphasis on investment in male children (therefore the payment of bride wealth). However—in societies where polygyny is not allowed, the difference in reproductive success is more balanced. Fortunato and Mace (2009) found that in Indo-European societies that observed monogamy, changes in wealth transfer practices were correlated with changes in marriage systems.

The case suggests the possibility that, along with language trees, trees based on the evolution of social traditions themselves could be a viable starting framework to work with in reconstructing population histories, and historical congruence with material culture traditions could be pursued in the future. This particular case deals with binary relationships of social traditions involved; however overall, "...one important use of phylogeny is to make manageable the overwhelming complexity of populations and cultures" (Boyd et al. 1997). A phylogeny of social traditions which compares different social groups would have to include many more variables in order to stand on its own as a language tree does. But the promise of further integrating analyses of data on language, social customs/traditions, and material culture suggests further fruitful work with congruence studies that can be done.

Final Thoughts

Throughout human prehistory, there have been both inventions and innovations that have literally changed the ways in which our species has evolved. Likewise, the ways and degrees to which information has passed from generation to generation have varied in both mode and scale. Thus, observing the cultural transmission of new and novel ways of doing things is really a question of establishing context. That said, identifying invention, innovation, and indeed their transmission over time and across populations is often difficult to tease out of the archaeological record with any level of certainty. Add to this the fact that long periods of technological conservatism are the norm rather than the exception throughout the vast majority of the human story, and the challenge becomes greater. Where we can recognize novel inventions and innovations of existing traditions in prehistory—as during major transitions such as the emergence of the Neolithic, the Upper Paleolithic, and the Middle-Late Stone Age, moving back in time—each is hallmarked by a new set of adaptations that in the specific contexts of their place and time, changed the game board completely. But of course, we can only observe such major shifts in retrospect and only when provided with enough context of what came before and after to recognize their significance. This need for context is because where changes are visible in the archaeological record, they are likely often the results of very complex processes and compounding contingent scenarios that are difficult to illuminate clearly and even more difficult to model comprehensively.

Cultural adaptations, as seen from the point-of-view of *la longue durée*, are the results of life histories at various scales: interactions between individuals, communities, populations, and the environments in which they live. Furthermore, we must factor in adaptation as being very often punctuated by regional cataclysms or other dramatic and often rapid environmental changes to preexisting conditions, driving natural selection of cultural variants. Even individual proclivities and happenstance can cause changes within a cultural system and over time become the "normal" way of doing things. This complexity is what makes the evolutionary study of cultural transmission and technological innovation so fascinating—and why it continues to generate new insights. Simply put, there is still a lot for us to try to understand.

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Chapter 4
Natural Selection, Material Culture, and Archaeology

Nathan Goodale

Introduction

A Darwinian approach to evolution is to understand that natural selection is the mechanism that operates to change biological populations over time. Charles Darwin wrote that natural selection is the “preservation of favourable variations, and the rejection of injurious variations” (1859). Darwin also recognized that for natural selection to produce change over time, some variations would be favored over others. Favored variations (or traits) were most likely selected through reproduction that was or was not passed on to future generations. Moving toward the perspective of natural selection in archaeology today, the concept is applied to human behavior and material culture that are the products of that behavior, recognizing that some behaviors may have greater payoffs than others. In other words, behaviors become metaphor for biological traits when acted out in a social setting, and some behaviors will be selected over others because they have an impact on fitness. The purpose of this chapter is to introduce the reader to the concept of natural selection and its implication that when behavior is examined as a trait, we recognize that it may have consequences for reproductive success. We can then set up hypotheses to test in the archaeological record by examining the materials that are the by-product of human behavior.

The Theory of Natural Selection

Within an evolutionary paradigm, natural selection operates on the individual, but the result is encountered at the population level (see Walsh et al., Chap. 2, this volume). Most individual organisms have unique genetics that constitute their genotype. In conjunction with the organisms’ environment, their genotype helps to define the phenotype, or the outward expression of that individual. The phenotype is where selection operates, but the genetic code is what is transmitted from parent to offspring. It is important to note that not all genetic code is evident in the phenotype as an outward expression. A phenotypic expression will be present if a dominant trait is inherited from only one parent. However, for there to be a phenotypic expression for a recessive trait, that trait must be inherited from both parents. Thus, if a recessive trait is only inherited from one parent, it will not be

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expressed phenotypically and therefore will not come under selection, regardless if it is advantageous or injurious. In other words, it will not impact the fitness of the individual carrying the recessive trait. The fitness of an individual is predicated by their success in producing offspring that survive to produce offspring themselves. This is often referred to as individual somatic interests (Herzog and Goodale, this volume). The most successful individuals in perusing mates and producing offspring will have the highest fitness. They will also be the most likely individuals to contribute the most genetic information down the generational line. Subsequently, the genetic composition of a population will change from generation to generation, thus representing the evolutionary process.

It is important to understand that even if a phenotype is expressed, only some traits are likely to be under selection. It is possible to distinguish between those that are under selection, deemed functional traits, and those that are not under selection, deemed adaptively neutral. The frequency of a functionally advantageous trait that is under selection will increase steadily in the population to some ceiling, while an adaptively neutral trait will be the subject of random drift from generation to generation. An adaptively neutral trait will eventually become fixed at the ceiling or disappear among the population (O'Brien and Holland 1990; see also Kandler and Crema, this volume; Laue and Wright, this volume). The frequency of neutral traits in a population is due to random drift, whereas the frequency of functional traits is due to natural selection. Context plays an important role in determining if a trait is functional or neutral and a trait that is under selection in one circumstance may be neutral in another.

Endler (1992, p. 221) suggests that there are three conditions that must be at play in order to recognize the action of natural selection:

> … the population has (*a*) variation among individuals in some attribute or trait (phenotypic variation); (*b*) a consistent relationship between that trait and mating ability, fertilizing ability, fertility, fecundity, and/or survivorship (fitness variation); and (*c*) a consistent relationship, for that trait, between parents and their offspring, which is at least partially independent of common environment effects (inheritance).

Fitness variation *b* is the important variable to understand among the three. Drift is recognized when the conditions *a* and *c* are met while *b* is not.

This is best understood with a well-known example. Male peacocks are an interesting case because the selective advantage for males to bear long trains is not immediately obvious. The trains are not light and can have variable ornamental size/condition that makes male peacocks more likely to suffer from predation than their female counterparts. The trains are expensive metabolically to produce, and not all male peacocks are able to provide the energy investment toward the growth and maintenance of their train. Therefore, Endler's condition *a* is met with phenotypic variation in peacock trains. Hale et al. (2009) demonstrate that male peacocks with well-endowed trains tend to get more mates than those with more modest trains. Males with trains that were longer and more ornamental also tended to produce more fit offspring (Hale et al. 2009) satisfying Endler's condition *b* where the condition of the train influences mating ability and signals survivorship. Offspring genetically inherit the ability to grow a train, and it is a signal of inheritance, satisfying Endler's condition *c*. We can then conclude that natural selection has shaped this relationship. The peacock train is, by definition, a functional adaptation shaped by natural selection that impacts male fitness. If by chance, Endler's condition *b* was not a factor, and male peacocks with trains that were shorter and less ornamental found mates in the same frequency and fitness levels as those with longer and more ornamental trains, then the male peacock train would be subject to drift, not natural selection.

Natural Selection and Studies of Evolution in Archaeology

Although natural selection and the relationship to biological features are well understood, its influence on human behavior is highly debated. The discussion concerns genetics, and the link to human behavior has been rigorously debated for a half century. While the level of genetic contribution to

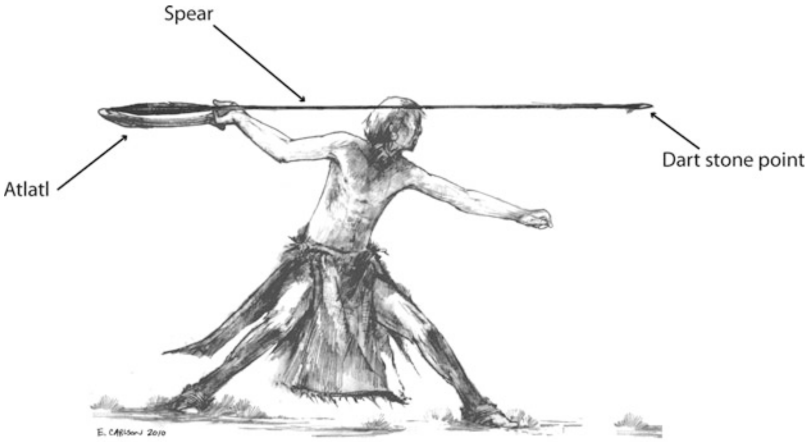

Fig. 4.1 An atlatl and components of the technology. Credit Eric S. Carlson

human behavior is debated, for example, nature vs. nurture, what is clearly evident is that behavior is part of the human phenotype and thus susceptible to natural selection because behavior can have fitness consequences. In the 1970s, archaeologists initiated the argument that human behavior is subject to natural selection and also the products of that behavior including material culture (e.g., Dunnell 1978a, b). The argument suggested that technology contributes to our fitness, and therefore, natural selection relates to the material products of behavior as part of the human phenotype (Leonard and Jones 1987). The link here is that since natural selection acts on phenotypes and phenotypes have fitness consequences, then by definition natural selection acts on material culture as well.

Endler's (1992) argument concerning natural selection in a biological system may be restated for material culture to include (1) variation exists in human-produced technology, (2) that certain variants of technology or components of technology impact fitness, and (3) inheritance occurs through information exchange as information is passed between teachers and pupils. In light of considerations regarding peacock trains, we can also consider Endler's (1992) argument in more detail using an archaeological example of the transition from the atlatl and dart technology to the bow and arrow among North American hunter-gatherers.

Archaeological evidence suggests that before approximately 9000 years ago, the hand-propelled spear or javelin was replaced by the spear-thrower, called an atlatl (e.g., Hughes 1998). The atlatl extends the arm and can substantially expand the range by which a spear can be used (Fig. 4.1). Atlatl technology is comprised of three components including (1) the atlatl, (2) the dart (a long wood spear), and (3) the dart point (typically a stone projectile tip). Over the more than 7000 years during which this technology was in use, the morphologies of these components varied across geographic regions. At approximately 2000 years ago, the bow and arrow was invented and replaced the atlatl and dart throughout much of North America. This replacement was relatively rapid likely representing that this new technology offered considerable advantage to hunters and thus increased fitness. How does Endler's (1992) model fit with the transition from dart to arrow? Understanding phenotypic variation and impacts to fitness is a useful starting point.

For natural selection to affect the evolution of a technological system, there must be variation in the technology that can complete the same task, and some variants may be more efficient at accomplishing the same task than others. Variation may exist within or between technologies, and this can include morphological (size, shape) or raw material variants and/or different combinations of all of those variants for composite technologies.

Atlatls come in multiple forms, for example, some are single units, and others are composite in construction. Some designs make use of weights, often called banner stones, some have formal grips,

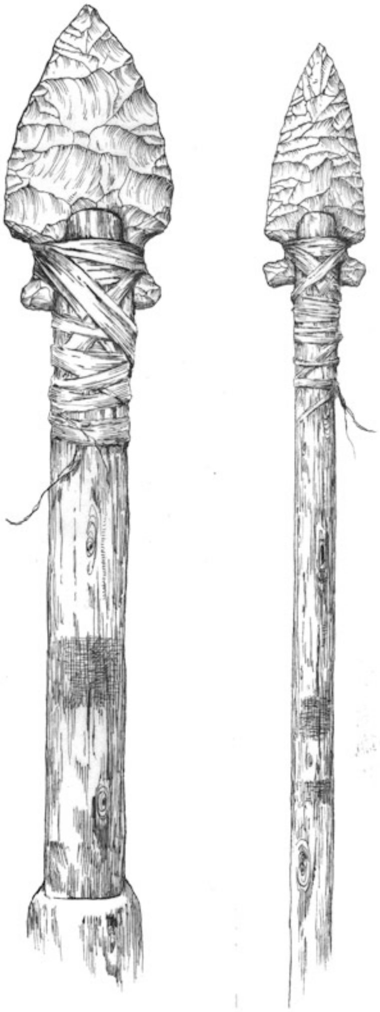

Fig. 4.2 Distinction in morphology of Besant dart technology (left) and Avonlea arrow technology (right). Credit Eric S. Carlson

and raw materials can be highly diverse. The associated dart points also vary substantially given the different approaches to the use of raw material and preferences for form and size.

Natural selection can be said to be acting if any of these variants increase the fitness of the producer/consumer.

The variation between the atlatl/dart and bow and arrow technologies is a difference in propulsive force and accuracy. Natural selection here is potentially operating on both the totality of components comprising each technology and, within each technology, on variations within individual components over time. Natural selection likely operated on variation within the components of the bow and arrow and changes in that technology after it was introduced on the bow size and form, arrow shaft form, and point size and form (e.g., Fig. 4.2). The bow and arrow carried an advantage over the atlatl and dart and undoubtedly led to increased fitness of the producer/consumer, and just as likely more successful variants would refine the technology and be adopted over time.

Archaeologists argue that just like biological traits, cultural traits can also be functional or neutral. Neutral traits are designated as stylistic, and their role is context-specific at any given time (Dunnell 1978a, b; Kandler and Crema, this volume; Laue and Wright, this volume). On the other hand, just as in biology, functional traits do not always enhance fitness. In this case, some traits may be transmitted via teacher-student learning along generational lines because they are attached to other traits under selection. Endler's argument only requires that some variants affect fitness and the two propulsion technologies largely represent functional traits. However, there are decorative traits in the individual components of each that could be considered stylistic. It could be argued that some functional traits of these technologies do impact fitness where natural selection could be operating to positively or negatively reproduce those traits. This could include optimal projectile point size, bow or string material, or arrow composition, anything that could optimize hunting. This also assumes that hunting in the given population is an activity that, if successful, increases an individual reproductive success.

It is also worthwhile to examine the fitness advantages that the bow and arrow may have for the producer/consumer over the atlatl and dart. The bow and arrow had the same selective advantage over the atlatl/dart that the atlatl/dart had over the javelin. That selective advantage includes increased propulsion distance allowing a hunter to launch a dart from a greater distance from the prey which decreases the likelihood of the prey discovering the hunter and running away. The bow and arrow had the included advantages of greater arrow speed and greater precision and accuracy. The rapid replacement of the atlatl and dart by the bow and arrow across a large part of the North American continent was likely due to natural selection operating on technological decision-making through increasing a hunter's efficiency. At the same time, this assumes that hunting was an activity that, if successful, increased a hunter reproductive success.

Inheritance in technological reproduction is the part of applying natural selection to cultural systems that has been the most contentious and the main reason why it has been used to reject the application of Darwinian principles to explain artifact variation through human behavior. The rationale for the rejection of inheritance in artifact variation is that artifacts do not reproduce like biological organisms. The idea here is that artifacts cannot inherit anything. However, evolutionary archaeologists argue that the teaching-learning process where cultural information is passed between persons is analogous to the biological inheritance process (Boyd and Richerson 1985; Walsh et al., Chap. 2, this volume). While the latter is better understood, archaeologists have argued that the former operates in a similar but less tangible and more complicated way. Where biological transmission occurs from parent to offspring, cultural transmission (or learned behavior) can occur as vertical transmission between parent and offspring, through oblique transmission between learners and relatives or other more experienced members of the social unit, or through horizontal pathways via peer-to-peer transmission. Variation in material culture production can also be a by-product of how much and the mode of instruction given in the teaching-learning process. For example, projectile points may exhibit little variation if there is a positive impact on reproductive success that creates uniform morphologies of the most successful types of points. The mode or intensity of instruction in the cultural transmission process could also relate to the prestige a person may obtain based on some behavioral variant (Quinn, this volume).

The concept of cultural transmission has been used on an intuitive basis in the form of a culture contact and diffusion model where invention of new technologies is more often a result of diffusion rather than independent invention. The concept of cultural transmission was more introduced in the evolutionary anthropology of the 1970s and then formally developed in the 1980s (Boyd and Richerson 1985; Cavalli-Sforza and Feldman 1981; Dunnell 1978a, b). From this perspective, similarity in form, especially for traits that equate to style, normally indicates a degree of contact and transmission. Anthropologists and other behavioral scientists do not have a strong definition for what actually constitutes transmitted cultural information. Simply stated, in cultural transmission, we do not have the exact equivalent to the gene. What makes studying cultural transmission even more complicated is that the packages are stored and reproduced in different ways, often to generate opportunities for the producers/consumers that can impact reproductive success. One approach that archaeologists employ is through morphometric analyses and the notion that artifact physical form and similarities/differences between artifacts convey how closely they are related. Goodale et al. (2015)

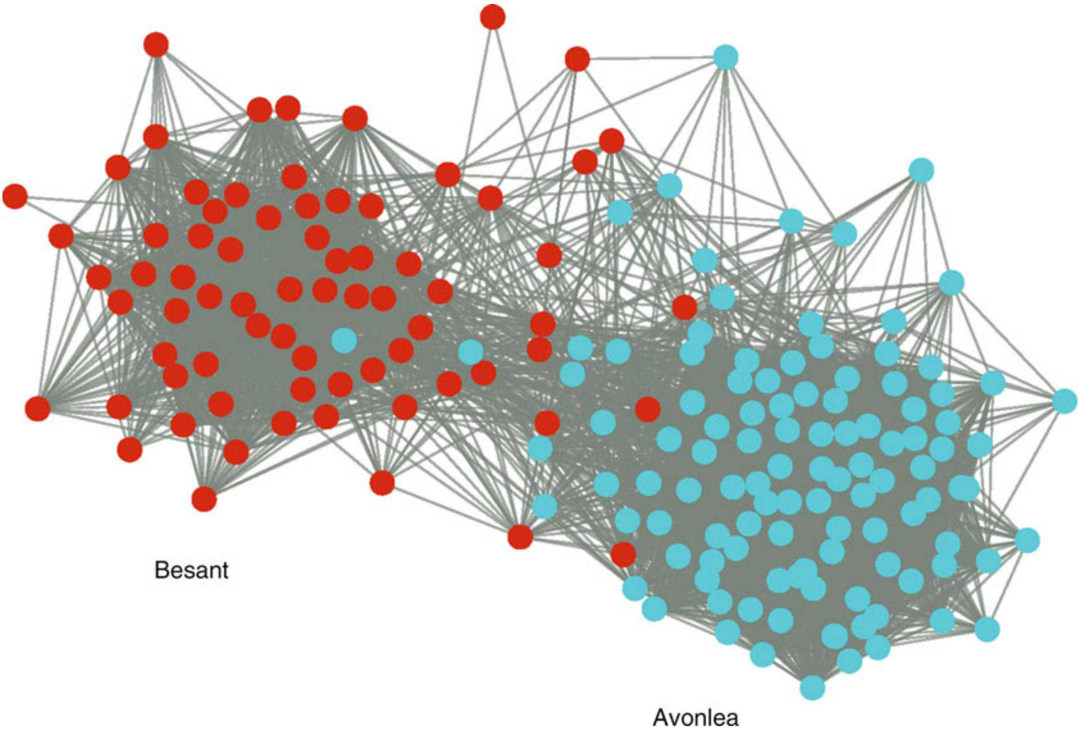

Fig. 4.3 The dart to arrow transition graphed by technology where Besant dart points and Avonlea arrow points

applied this approach to a group of projectile points from the early Neolithic site of Dhra', Jordan. They argue that similarity in artifact form relates to both the form of transmission and the knapping kit used in production.

Goodale et al. (2011) utilize a similar approach for the transition from dart (Besant) to arrow (Avonlea) points in the northern Plains of North America. Using network analysis, they graphically display the relationship of morphology between dart and arrow points (Fig. 4.3). Lines are called degrees that connect nodes which represent the artifacts that are most similar in morphology. It is clear that the network of dart and arrow points is partitioned into two sub-networks, which mostly align with the cultural units, or what archaeologists call *types* previously labeled Besant and Avonlea projectile point traditions. The blue nodes represent Avonlea projectile points, likely used within a bow and arrow technology, while the red nodes represent Besant dart points, likely used within an atlatl composite technology. The results suggest that these dart and arrow points are quite distinct in morphology. There are clearly two sub-networks in this technological system of making stone tips for points that represent a larger network of technological decision-making (Herzog and Goodale, this volume). What is interesting is that the two sub-networks are connected by some of the artifacts used in the analysis. Those artifacts that connect the sub-networks may be experiments or otherwise had traits that natural selection operated on. There are other ways to model the relationships between similar morphologies that suggest a degree of relatedness, for example, cladistics (e.g., O'Brien and Lyman 2001, 2003; Straffon, Chap. 8, this volume). While approaches such as these have provided results, the interesting and potentially problematic aspect to using morphology to talk about relatedness is that in biology, morphology or morphometrics has been completely replaced with the modern mapping of genetics. We still do not have the cultural equivalent of the gene.

When examining the relationship between natural selection and material culture, it is difficult to understand how materiality impacts reproductive success. Material culture such as projectile points does not genetically reproduce, so the question becomes as follows: Can projectile points have reproductive success? The literal answer is no, but the argument is that artifacts may enhance the reproductive success of their producers/consumers depending on the nature of the enterprise and the performance of the items in question. This implicates the notion of replicative success of cultural materials manufactured by humans or those cultural units that have differential persistence across time and space (Leonard and Jones 1987). Replicative success refers to a circumstance when a social group is given a set of alternative forms some will be chosen to be produced and/or consumed (used) more often than others. Replicative success also means that the most commonly chosen forms will be made known to others in the social unit through cultural transmission at the expense of the forms that have less impact on fitness. Replicative success is a concept that allows us to operationalize natural selection in archaeology by considering frequency of technological items, the degree of technological diversity, and the potential causes of that variation.

In Endler's (1992) model, change in a trait that does not enhance fitness will be due to drift, and change in a trait that does enhance fitness will be due to natural selection. Under these parameters, both functional and stylistic traits can have replicative success where functional traits are under natural selection and stylistic traits are subject to drift (Dunnell 1978b). Often artifacts or the tools people used in the past were likely comprised of both functional and stylistic traits. The problem is in understanding which traits are functional and which are stylistic. Experimental archaeology, where artifacts are reproduced and then used in practice, is a possible way to understand which traits are functional and which are stylistic. An experimental archaeologist could replicate projectile points with the same morphology as dart and arrow points. Then they could be hafted and then tested for their relative performance and success rates. To take another technological example, pottery vessels could be replicated and performance tested. The issue with experimental archaeology is that we may garner information about a technology's performance, but we will, however, never be able to recreate the social setting of the past and the impact of those artifacts on actual reproductive fitness in those contexts.

In terms of Endler's argument, a functional trait should remain in use until something better comes along. The archaeological record allows us to understand that functional traits can be adopted and used for a long period of time. This is why evolution via natural selection is perhaps one of the most powerful theoretical perspectives for interpreting the archaeological record because it allows for a depth of time to be a significant factor. However, functional traits may come and go over time, as the producers/users' needs change. The stone end scraper is a technology used in many cultural contexts for long periods of time to scrap the membrane from animal hides. Scraping tools first were adopted hundreds of thousands of years ago. Their frequencies have fluctuated through time, which makes their temporal frequency follow a multimodal distribution. In most cases, end scrapers persisted in roughly the same form (a steep edge perpendicular to a flat surface) until the appearance of metal tools. This is a very functional tool, and there is not much about an un-hafted end scraper that could be considered stylistic (but see Arthur 2018). On the other hand, traits that are stylistic tend to have a unimodal temporal frequency through time. After a stylistic trait comes into being, it gains popularity, rises to a peak, then fades, and eventually disappears. In addition, styles rarely return in the same form which provides the basis of seriation chronology building in archaeology. Unimodal distributions of stylistic traits and the fact that they rarely reoccur in exactly the same form make stylistic traits especially useful for chronology building (Goodale et al. 2011).

Generally, functional traits that have an impact on fitness to the producers/users tend to spread rapidly once they are invented or introduced. The bow and arrow was adopted relatively quickly, meaning that it offered significant advantages to its users over the atlatl and dart. From this example, distinguishing between a functional trait and a stylistic trait may seem easy. However, this example was chosen because it is fairly easy to illustrate. As argued by Goodale et al. (2011), many technological histories offer much more complex scenarios in which style and function are less easily separated. Consequently it may be hard to discern which traits affect fitness. Thus multiple lines of evidence are required to tease apart functional and stylistic traits and to explore their relationships in wider archaeological context.

Signaling and Natural Selection

Archaeologists are used to thinking about questions like as follows: Why did one technological trait replace another? In such cases, experimental archaeology can help us understand the answers to that question through performance-based studies. The degree to which one technological trait brought greater efficiency to food procurement could have enhanced the survival of its producers/users. Because of this relationship, one technological trait could have a likely impact on fitness over another technological trait. It is also likely that a combination of traits in the technological system could be under selection such as the physical tools, the technique of the archer, and the knowledge passed on through cultural transmission required to effectively use and reproduce the components of the system. None of this seems too big of an assumption, despite the fact that we probably cannot demonstrate that early adopters of this technology achieved enhanced reproductive success relative to those that may have held on to the alternative technology (e.g., Bamforth 2002). It may also be suspected, but not easily demonstrated, that the speed with which the shift from darts to arrows occurred was accentuated by some additional process, like conformist or prestige-based cultural transmission (added prestige incentive to have replicative success above survival fitness). And yet there are many other changes in material culture for which appeals to improvements in design and increased efficiency do not appear to be satisfactory solutions.

Binford (1962) argued that artifact function is just as much a part of the social and ideological contexts as it is related to a functional performance. Many efforts in archaeology to explain the social and ideological roles of artifacts have drawn largely from an anthropological perspective of function attributable to Emile Durkheim. With this perspective one might ask the question: How is social integration maintained through the social and ideological roles of artifacts? An evolutionary perspective helps to answer this question. Some artifact production systems are extremely time-consuming and also costly in terms of materials. Their manufacture thus may defy practical logic, thus fitting Veblen's (1899) notion of "conspicuous consumption." Such seeming waste may seem irrational if it does not evidently favor fitness. But if we recognize that the peacock's plumage serves to attract more or higher-quality mates, we also recognize that a similar consequence can happen with those who possess more elaborate technology. Neiman (1997) effectively argues this for the case of Mayan stone monuments (Neiman 1997). Groups of artifacts or types illustrate very nicely the temporal patterns of artificial clades, that is, a group of individuals such as organisms or projectile points that are related by descent (Lyman and O'Brien 2000). Sometimes artifact clades can be long-lived, reach high frequencies, and be widely distributed in time and space, while other artifact clades do not persist and disappear relatively quickly. The reasons for this dichotomy can be complex but in some way or another likely link with natural selection and the fitness consequences of the artifact clade. It is also important that natural selection is taken into account with great time depth when considering the impact on fitness that artifacts can have on humans when looking at evolutionary process over long time spans (see Chap. 6).

Even with the interesting phenomenon that technological clades can come and go in popularity through time and space, and those clades can have an impact on individual fitness, there are interesting analogies to the biological world. Connecting back to the peacock's elaborate plumage example, to explain why the male peacock makes such sizeable investments, biologists make arguments that sexual selection and costly signaling can account for peacock fitness, and individual fitness is advertised by the elaborate plumage (Hale et al. 2009). The case could be made that the male peacock uses its plumage to both attract the female and also convey its relative comparison to other male peacocks. If it turns out that the signal is honest and the peacock's plumage does correlate with other reproductively fit characteristics, discerning females that select males with elaborate plumage as mates will in turn have greater reproductive success. Where time becomes important is in the circumstance that the behavior is passed on generation to generation, and it impacts female peacock mate choice selection reinforcing male's investments in their plumage.

Humans are very sensitive to signals (see Quinn, this volume), and signals shape the way we interact and perceive the world around us. Signals reach us in a multitude of ways from language all the way to all of our senses (aural, visual, tactile, and olfactory). As an extension to this, our behavior is tied to our material culture, and because of that relationship, our phenotype is also enhanced by material culture. We use material signals as references for group membership to denote objects and activities where signals are associated with individuals or social groups that mark them as distinct from other social groups. Material culture allows for considerable occasions to construct signals, some of which might include the quality and quantity of raw materials used in production, the skill of the producer (s), and the relationship to how many producers versus consumers there are in the population (see Herzog and Goodale, this volume). Personal identity or group membership can be directly tied to the variant of choice (such as the type of raw material selected) to the manipulation of traits (specific combination of raw materials) that the producer/consumer makes. The replicative success of an artifact variant will wax and wane through time but is likely to be linked to the signaling of the most successful variants.

Artifact tool production and use is an interesting case study for signal construction. Tool use can appear early in a human life, actual tool production probably much later. Tool use is likely practiced and enhanced by imitation and through play with peers, parents, and other members of the social unit (Fig. 4.4). Signals can reproduce normative cultural content and reinforce affinities between people (promote social solidarity). On the other hand, signals can show the distinctiveness of the producer/user. In other circumstances, signals can convey some measure of the user's dominance or relative prestige over others. Certain individuals may be dominant because they have the family fitness that can use certain material culture because it is expensive (monetarily or, e.g., expensive in terms of the energy needed to procure raw materials). The link here with natural selection is that cultural materials inherently send signals from the producers and users to the rest of the social unit. That signal can be very much like the peacock's plumage with the potential to convey information regarding individual or even family fitness levels. In mate selection, if the signals have an honest and positive correlation to other aspects of reproductive success, material culture can increase individual reproductive success.

Fig. 4.4 Hunter-gatherer camp with hypothetical situation of children mimicking adult tool use. Credit Eric S. Carlson

Conclusions

This chapter has attempted to provide simple examples of how natural selection operates on biological variation, human behavior, and its by-products especially focused on the production and use of material culture. In making this argument, the emphasis was made that behavioral variation and fitness have a formal relationship. In the recent literature, critiques have been made about the relationship where functional traits are linked to fitness variation (e.g., Bamforth 2002; Eldridge 2009). There is the basic underlying assumption that some technological variants have implications for the reproductive success of their producers/users. There still seems to be an objection to the notion that artifacts have a direct influence on fitness. Perhaps this is because such a relationship fails to account for human agency as part of the process relating tool performance to greater reproductive success? This is not to deny the influence of human agency but instead to make explicit that the variation among artifacts yields differences in efficiencies and that variation influences energy capture and output, two critical variables in maintaining or increasing reproductive success. There is a fundamental relationship between the artifacts and the variable strategies and techniques for using technology. What is complex is the proportion that each contributes to the efficiency of tool production/use. Realizing the relationship between technology and fitness does allow us to construct plausible arguments built on performance studies, considering the modes by which cultural transmission takes place.

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Chapter 5
Analysing Cultural Frequency Data: Neutral Theory and Beyond

Anne Kandler and Enrico R. Crema

Introduction

The question of how humans use social information has been subject of a large amount of empirical and theoretical research in a variety of scientific disciplines (e.g. Coultas 2004; Mesoudi and O'Brien 2008; Kirby et al. 2008; Caldwell and Millen 2009; Henrich 2001; Bentley et al. 2004; Baum et al. 2004; Rendell et al. 2010; McElreath et al. 2008; Morgan et al. 2012). But in order to answer this question directly one would need fine-grained individual-level data detailing who learns from whom. However, outside of controlled experimental conditions, large longitudinal data sets of this kind are difficult to obtain (but see Henrich and Broesch 2011; Beheim et al. 2014), especially so in archaeological contexts. The archaeological record documents the frequencies of different cultural variants in sparse samples taken from the whole population for a single or multiple time intervals. As these frequency data often present the only direct empirical information about past cultural traditions and the forces affecting them (Shennan 2011), researchers have attempted to use the population-level patterns to infer processes of cultural transmission that may underlie them. But given the large number of transmission processes that have been identified in the literature (e.g. Laland 2004) and the sparseness of the archaeological record this represents a challenging task, especially as it is far from obvious whether the observed frequency data contain a strong signature about the underlying transmission processes.

Early approaches based on the pioneering work of Neiman (1995) addressed this challenge by using principles and methods derived from the neutral theory of molecular evolution (see, e.g., Shennan 2011; Eerkens and Lipo 2005; Lycett 2015, for comprehensive reviews, but see Chap. 7 in this volume for an alternative approach). Using mostly ceramic assemblages researchers tested whether the observed frequency distributions at particular points in time could be distinguished from the ones that may emerge under the hypothesis of unbiased transmission, i.e. in a situation where cultural variants are chosen at random for reproduction. In other words, this research attempted to establish whether observed data sets are consistent with neutral evolution. In the first part of this chapter we briefly

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summarise cultural neutral theory and evaluate what consistency or inconsistency between observed empirical patterns and neutral expectations, derived from commonly used statistical tests, can tell us.

In the second part we focus on the generative inference approach, recently developed in population genetics (e.g. Veeramah et al. 2011; Eriksson et al. 2012; Posth et al. 2016; Ray et al. 2009) which goes beyond the hypothesis testing framework. This approach simultaneously evaluates the consistency of a number of cultural transmission processes with the available data while also accounting for demographic and cultural properties of the system considered. In this way we can analyse the challenge of inferring underlying processes of cultural transmission from sparse population-level frequency data in more depth, in particular we can identify equifinal transmission processes (cf. Cochrane 2009; Premo 2010; Crema 2018; Kandler and Powell 2018), i.e. processes that are able to generate very similar population-level patterns, and therefore investigate how much information about underlying transmission processes can be extracted from sparse archaeological data.

Readers interested in running the simulation models presented in this chapter can install the dedicated R package (which can be found on https://github.com/ercrema/HERAChp.KandlerCrema and https://doi.org/10.5281/zenodo.1422010) and follow the vignette for reproducing the analysis presented here.

Neutral Theory

Introduced prominently by Kimura (1968, 1983) the neutral theory of molecular evolution claims, unlike the Darwinian theory of evolution by natural selection, that the overwhelming majority of evolutionary changes at the molecular level are not caused by natural selection acting on advantageous mutants but by random fixation of selectively equivalent or nearly equivalent mutants through the cumulative effects of sampling drift due to finite population size and mutation processes (Kimura 1991). Importantly, the relatively simple assumptions of neutral theory enabled the development of a large body of mathematical theories to treat molecular evolution and variation in quantitative terms. In part the success of neutral theory is rooted in the fact that these mathematical theories generate strong predictions that can be tested against data.

Subsequently other scientific disciplines started exploring the applicability of neutral evolution. Building on the foundational ideas, neutral theory in ecology, most prominently expressed in Hubbel's unified neutral theory of biodiversity and biogeography (Hubbell 2001), seeks to capture the influence of speciation, extinction, dispersal, and ecological drift on diversity and the relative species abundance under the assumption that all species are demographically alike on a per capita basis (Volkov et al. 2003). In particular, neutral theory implies that niche differences are not needed to explain biodiversity patterns. As in the population genetics case the assumption of neutrality allowed for the development of a tractable theory for testing hypotheses about community assembly rules (Volkov et al. 2003). In both fields the hypothesis of neutral evolution generated huge controversies which ultimately advanced our understanding about the evolutionary process.

Also in archaeology neutral theory has been used to analyse the composition of cultural assemblages. But already prior to that a lot of research had been dedicated to distinguishing "functional" from "stylistic" aspects of artefact traditions and to identifying the forces acting on them as they change through time (e.g. Binford 1963; Wiessner 1983). These discussions took a new direction when Dunnell (1978) proposed that "stylistic" aspects of artefacts could be defined as "those not under selection". Subsequently, Neiman (1995) used the framework of molecular neutral theory to introduce the idea that observed temporal changes in cultural assemblages can be explained by random processes involved in the neutral theory and the factors that affect these processes, such as effective population size or innovation rate. In particular, this model assumed that artefacts (or cultural variants in general) are chosen to be replicated according to their relative frequency, and new variants not previously seen in the populations are introduced by a process resembling random mutation (i.e. innovation). In finite populations this copying process is affected by sampling error, and consequently at each iteration we expect some changes in the frequency of the variants. After multiple iterations frequencies will drift away from their original values, particularly when population size is small. If no variants are introduced via innovation, this iterative process will eventually lead a given variant to either go extinct or to fixate. However when innovations are introduced, this unbiased transmission process alone can replicate the rise and fall in the popularity of cultural variants over time as well as their disappearance. Neiman (1995) applied this theory to a data set recording the frequencies of selectively neutral stylistic elements in Woodland ceramics over time and showed that the patterns of within- and between-assemblage diversity in those stylistic elements could be explained by a hypothesis of unbiased and inter-group transmission. Following this pioneering work neutral theory has been applied to a number of archaeological case studies (e.g. Bentley et al. 2004; Shennan and Wilkinson 2001; Lipo 2001; Kohler et al. 2004; Eerkens and Lipo 2005; Schauer 2008; Steele et al. 2010).

In the following we provide some mathematical details on modelling neutral evolution (section "Mathematical Formulation: Wright–Fisher Model"), commonly used statistical tests for detecting departures from neutrality in cultural data (section "Detecting Departures from Neutrality") and their applications to archaeology (section "Application to Archaeology") as well as a discussion of how consistency or inconsistency between neutral expectations and data may be interpreted (section "Interpreting the Test Results").

Mathematical Formulation: Wright–Fisher Model

Neutral theory in cultural evolution has been mainly modelled using the Wright–Fisher infinitely many allele model (see, e.g., Ewens 2004, for a review of the mathematical properties). This model assumes that the composition of the population of cultural variants at time t is derived by sampling with replacement from the population of variants at time $t-1$ resulting in non-overlapping generations. In more detail, the population of cultural variants at time $t-1$ can be described by the abundances $[m_1, m_2, \ldots, m_{k_{t-1}}]$ of all k_{t-1} variants present at this time. It holds $\sum_{i=1}^{k_{t-1}} m_i = N$ where N denotes the temporally constant population size. In order to generate the population of cultural variants at time step t, N copying events are carried out. In each of these copying events a variant i is randomly chosen from the population at time $t-1$, i.e. with probability

$$\pi_i = \frac{m_i}{N}(1-\mu), \tag{5.1}$$

and a new instance of variant i is produced. Consequently a new population of cultural variants with the abundances $[n_1, n_2, \ldots, n_{k_t}]$ is generated. The term m_i/N (we later refer to it as p_i) describes the relative frequency of variant i in the population, i.e. Eq. (5.1) means that a variant is chosen to be reproduced proportional to its relative frequency and therefore the transmission process is denoted as unbiased. The variable μ stands for the innovation rate, meaning that with probability μ a new cultural variant, not currently or previously seen in the population, is introduced in each copying event. Repeating this process for many time steps will generate the rise and fall in the popularity of cultural variants over time, similar to diachronic patterns in type frequency observed by cultural historians (see Fig. 5.1).

Importantly, if the innovation rate μ is larger than 0, then every cultural variant will eventually go extinct. It may take a long time but it will happen with probability 1. This implies that variant frequencies will never stabilise over time but after sufficiently many time steps the cultural system will reach a stationary state where some aspects of system do not change anymore (see Box 5.1 for mathematical details). For instance, at steady state the expected level of cultural diversity at the

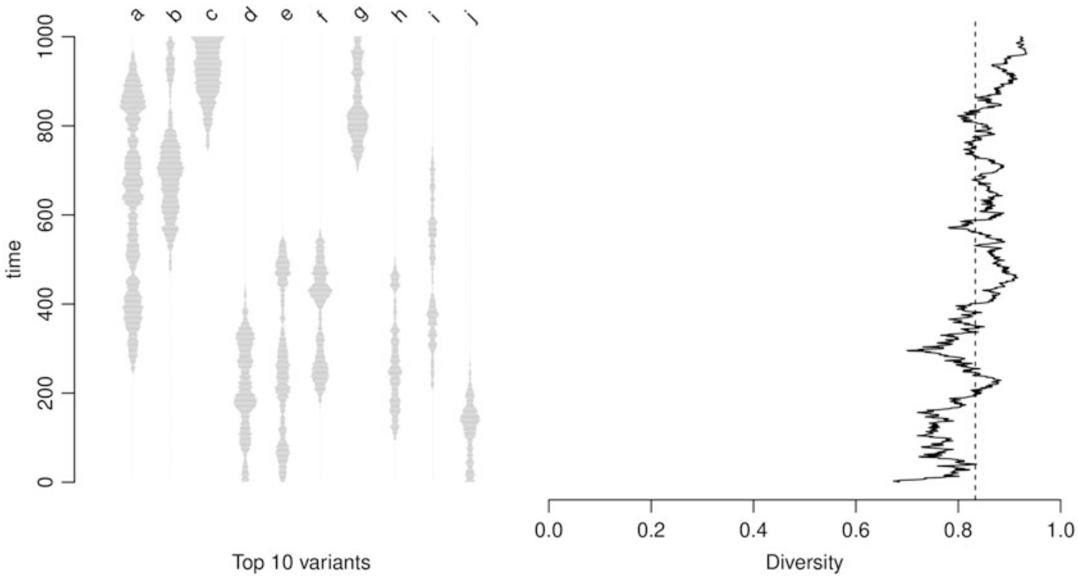


Fig. 5.1 Left figure: battleship curve of the ten most common variants across 1000 time steps obtained from a simulation run of unbiased transmission with $N = 500$ and $\mu = 0.005$. Right figure: corresponding time-series of the level of cultural diversity calculated by $1 - \sum_{i=1}^{k_t} p_i^2(t)$ (solid line) where k stands for the number of variants present and neutral prediction according to Eq. (5.4) (dashed line). It is obvious that the time series fluctuates around the neutral prediction

population level or the expected number of different cultural variants in a sample of size n (with $n << N$) can be derived under the assumption of neutrality (see Eqs. (5.4) and (5.6) in Box 5.1 and Fig. 5.1).

Box 5.1: Mathematical Details of the Wright–Fisher Model

The properties of the infinite allele Wright–Fisher model are well-understood and we summarise here only some of the characteristics (see, e.g., Ewens 2004, for more details). The probability that the population of cultural variants with abundances $[m_1, m_2, \ldots]$ at time $t-1$ is transformed into a population with abundances $[n_0, n_1, n_2, \ldots]$ at time t (where n_0 describes the abundance of all innovations in this time step) is given by

$$P(X_0(t) = n_0, X_1(t) = n_1, \ldots | X_1(t-1) = m_1, \ldots) = \frac{N!}{\prod_i m_i!} \prod_i \pi_i^{n_i} \tag{5.2}$$

with $\pi_0 = \mu$, $\pi_i = (m_i/N)(1-\mu)$, and $\sum_i m_i = \sum_i n_i = N$. The state space of the Markov process defined by these transition probabilities can be extremely large making the derivation of population-level properties of this stochastic process almost intractable. But as the neutrality assumption implies that all variants are considered identical, the time evolution of a single variant can be described by a two-variant formulation

$$P(X_i(t) = n_i | X_i(t-1) = m_i) = \binom{N}{n_i} \pi_i^{n_i} (1-\pi_i)^{N-n_i}. \tag{5.3}$$

(continued)

Box 5.1 (continued)

Importantly, for $\mu > 0$ Eq. (5.2) suggests that the extinction of any variant is inevitable over time and consequently there does not exist a non-trivial stationary distribution for the variant frequencies. Nevertheless, it has been shown that some stationary properties of a cultural system evolving through neutral evolution can be determined. At steady state, it holds that the level of cultural homogeneity (defined as the probability that two instances randomly drawn from the population are of the same variant) at the population level can be approximated by

$$F \approx \frac{1}{1+\theta} \quad \text{with } \theta = 2N\mu. \tag{5.4}$$

The corresponding level of cultural diversity is given by $1 - F$. Further, for random samples of known size n (with $n << N$) the probability that k different variants are observed is given by

$$P(K = k) = \frac{|S_n^k|\theta^k}{S_n(\theta)} \tag{5.5}$$

where $S_n(\theta) = \prod_{i=0}^{n-1}(\theta + i)$ and $|S_n^k|$ is the absolute value of a Stirling number of the first kind. Derived from the expression above, the expected value of the number of observed variants in a sample of size n has the form

$$\mathbf{E}\{K\} = \sum_{i=0}^{n-1} \frac{\theta}{\theta + i}. \tag{5.6}$$

If precisely k variants are observed in the sample, the probability of an assemblage $[n_1, \ldots, n_k]$ of cultural variants is given by

$$P([n_1, \ldots, n_k]|k, n) = \frac{n!}{|S_n^k|k!n_1 n_2 \cdot \ldots \cdot n_k} \tag{5.7}$$

which is known as Ewens sampling distribution (Ewens 1972). Further, the probability that a variants with only one instance are observed in a sample of size n and k variants is

$$P(A_1 = a|k, n) = \sum_{j=a}^{k-1} (-1)^{j-a} \frac{|S_{k-1}^n|}{a!(j-a)!|S_k^n|} \tag{5.8}$$

which is approximately Poisson distributed with mean $|S_{k-1}^n|/|S_k^n|$ (Ewens 2004).

Archaeological applications of the Wright–Fisher model have mainly focused on two issues: inference of temporal changes in the values of the population size N (or effective population size) or the innovation rate μ from the observed frequency distribution of variants when there is no departure from neutrality assumed; and inference of non-neutrality (i.e., the existence of processes other than unbiased transmission) at a given location. In the following we focus on the latter application and discuss three approaches to detect departures from neutrality. Before delving into this statistical aspect we briefly mention an alternative framework for modelling neutral evolution that allows for overlapping generations but is only rarely used in archaeological studies.

Moran Model

The classical Wright–Fisher model described above assumes non-overlapping generations, i.e. after one time step the whole population of cultural variants is assumed to "die" and to be replaced by an offspring generation. This assumption is often at odds with reality. The model by Moran (1958) allows for overlapping generation, i.e. there is variation in the individual life spans of the instances of a variant. In more detail, the Moran model assumes that in each time step only one instance of the cultural variants is chosen at random to reproduce (whereby the reproduction/copying process is only faithful with probability $1 - \mu$ and, as above, with probability μ an entirely new variant is introduced). After reproduction one instance (excluding the new offspring instance) is chosen to "die". This model is an example of birth and death models which are studied extensively in the stochastic process literature. As with the Wright–Fisher model for $\mu > 0$ there is no concept of stationarity of the frequency of any cultural variant. However, the stationary distribution of variant configurations (and related results similar to the ones shown in Box 1) can be found (see, e.g., Ewens 2004).

Detecting Departures from Neutrality

An advantage of developing a mathematical framework of neutral theory is that it allows for the derivation of expectations about the values of certain statistics such as the expected number of distinct variants in a sample of size n which then can be compared to observed data. If those theoretical expectation and empirical patterns coincide, we can conclude that the hypothesis of neutral evolution is consistent with the data. In the following we briefly review three different approaches commonly used in cultural evolution literature for detecting departures from neutrality.

Ewens Sampling Distribution

One of the earliest approaches for testing the neutral hypothesis has been based on the cultural homogeneity index, defined analogously to its genetic counterpart as the probability that two randomly drawn cultural variants are of the same type. The Ewens-Watterson test of homozygosity (Ewens 1972; Watterson 1977, 1978) evaluates the empirical homogeneity statistic

$$f = \sum_{i=1}^{k} p_i^2 \tag{5.9}$$

where p_i denotes the relative frequency of variant i. To determine how small or large f has to be so that the hypothesis of neutrality is rejected, its expectation under neutrality or more precisely its neutral distribution has to be calculated. To do so, Watterson (1978) suggested an approximate procedure which randomly draws samples from Ewens sampling distribution (5.7) given the observed sample size n and the number k of different variants present in this sample and determines the corresponding homogeneity statistic. In this way reliable statistical estimates can be made of various significance level points. Thus the homozygosity test was designed to test against processes that lead to significantly lower or higher levels of diversity than predicted under neutrality.

In contrast, Slatkin's test (Slatkin 1994, 1996) does not employ the concept of homozygosity, and relies only upon the "shape" of Ewens sampling distribution. It evaluates the empirical sample against all possible configurations $[n_1, \ldots, n_k]$ for given n and k drawn from distribution (5.7) and therefore makes fewer assumptions about the characteristics of the distribution that may indicate the presence of selective forces.

Both tests have been applied by archaeologists, mainly to analyse the composition of ceramic assemblages. The homozygosity test was explicitly or implicitly used by, e.g., Lipo (2001), Shennan and Wilkinson (2001) and Kohler et al. (2004). The Slatkin's exact test was used by, e.g., Steele et al. (2010), Premo and Scholnick (2011) and Bortolini (2014).

Progeny Distribution

Taking a different view, Bentley and colleagues (e.g. Bentley et al. 2004; Hahn and Bentley 2003; Herzog et al. 2004) used the Wright–Fisher model to explore the properties of the neutral progeny distribution. The progeny distribution records the frequencies of cultural variants which produce k new variants over a fixed period of time (We note that this distribution naturally accounts for the problem of time-averaging.). Through simulation techniques (e.g. Bentley et al. 2004; Hahn and Bentley 2003; Premo 2014) they concluded that the neutral progeny distribution takes the form of a power law. The exponent, $\alpha(N, \mu)$, of this power law has been fitted as a function that depends on innovation rate μ and total population size N. Consequently, they hypothesised that testing whether an empirical progeny distribution describe a power law with an exponent similar to the 'neutral' exponent α for given N and μ allows for conclusion about the consistency between data and neutral evolution. This method has been applied to data sets describing the choice of baby names in the US, US patents and their citations or Neolithic pottery motifs and provided support for the neutral hypothesis in all cases (Bentley et al. 2004; Hahn and Bentley 2003).

However, we note that results of this analysis have to be interpreted cautiously as their accuracy depends on the completeness of the data set considered. To illustrate this O'Dwyer and Kandler (2017) used an overlapping generations model commonly applied in ecology and derived an analytical representation of the neutral progeny distribution. In agreement with the earlier work, it was shown that neutral theory generates a power-law progeny distribution but with a constant exponent of 3/2 (i.e. the power-law exponent does not depend on innovation rate or population size). The power law is followed by an exponential cut-off, whereby the onset of this cut-off depends on the innovation rate: the larger the rate, the earlier is the onset. The analytical representation of the progeny distribution allowed for maximum-likelihood estimations of the model parameter and therefore provided a direct way of parameterising neutral models using cultural data, and of subsequently evaluating the consistency between observed data and the neutral hypothesis (The code of the framework can be downloaded from https://github.com/odwyer-lab/neutral_progeny_distribution). Importantly, this study established that analyses based on only the most popular variants, as is often the case in studies of cultural evolution, can provide misleading evidence for neutral evolution. If the data set is incomplete, i.e. if it does not include rare variants, then consistency of neutral theory with the empirical patterns can be inferred even in situations where selection processes are acting in the population. While the analysis of a complete data set recording boys and girls first names in Southern Australia revealed a mismatch between neutral theory and empirical data, the analysis of the same data set but with all names possessing abundances of less than five in the considered time interval removed showed consistency between neutral theory and empirical data (O'Dwyer and Kandler 2017). This result points to the crucial importance of rare variants for evaluating processes of cultural evolution based on aggregated population-level data in the form of progeny distributions.

Turn-Over Rates

Focusing on the temporal dynamic of cultural change, Bentley et al. (2007) analysed the turn-over behaviour in top lists by determining the number of new variants to enter the list of the y most popular/frequent variants in the population relative to the previously sampled interval (see ElBahrawy et al. 2017, for an alternative definition). Based on simulations of the Wright–Fisher model they estimated that under neutral evolution the average number of turn-overs for a top-list of length y (denoted as z_y) is given by

$$z_y \approx y\sqrt{\mu}. \tag{5.10}$$

The turn-over rate seems to be approximately proportional to the list length and largely independent of the underlying population size. These theoretical predictions have been compared to estimations of turnover-rates for the Billboard Top 200 Pop Chart, various top lists for US baby names, dog breeds (Bentley et al. 2007) and cryptocurrencies (ElBahrawy et al. 2017) and a good coincidence has been obtained.

A subsequent study by Evans and Giometto (2011) revealed that this relationship can be more accurately described by

$$z_y = A \cdot y^x \tag{5.11}$$

where the coefficient A depends on N. If it holds $N\mu > 0.15y$, then the exponent x assumes the value of 0.86 under neutrality (Acerbi and Bentley 2014) and thus empirical estimates of x can be used to identify instances where the observed turn-over profile deviates from the patterns expected under neutrality. Acerbi and Bentley (2014) explored this idea and examined the shape of the turn-over profile and estimates of x under three alternative biased transmission processes (neutral evolution, negative and positive frequency-dependent selection). They concluded that in some situations the estimate of x is indicative of the underlying process of cultural transmission.

In general, however, the turn-over rate approach has limited applicability for archaeological data, and there are currently no known applications. The coefficient x can be estimated by regression based techniques but these estimates are sensitive to the number of data points available to calculate the turn-over rate. To illustrate this point Fig. 5.2 shows the interquartile range, i.e. the range between the 25th and 75th percentile, of the estimated values of x from simulation data generated under neutral model with fixed values for μ and N, but different number of time steps from which turn-over rates were calculated. The graphs show that with increasing number of time steps the variance in the estimates of x becomes smaller. Data sets with less than 40 times-steps—as typically encountered in archaeology—are likely to yield estimates of x that strongly diverge from the theoretical expectations (displayed as dashed line in Fig. 5.2) even when the underlying process is neutral evolution.

Alternative Approaches

Stronger tests of departure from neutrality than testing the goodness of fit between empirical and theoretical frequency distributions have been developed mainly in population genetics and ecology. These tests often involve the analysis of the temporal dynamic of change. For example, it has been shown that neutral theories in ecology have had less success in predicting the dynamics of biodiversity, from decadal-scale species abundance fluctuations to geological ages of species (Leigh 2007; Wang et al. 2013; Chisholm and O'Dwyer 2014; O'Dwyer et al. 2015).

Similarly, recent work in cultural evolution has pointed to the importance of analysing temporal patterns of change as opposed to static measures of cultural diversity (e.g. McElreath et al. 2005; Hoppitt et al. 2010; Kandler et al. 2017; Kandler and Shennan 2013; Sindi and Dale 2016). For example, Sindi and Dale (2016) analysed the patterns of frequency change, in particular, the kurtosis of the distribution of changes over time, of stable words in the Google Ngram database. Interestingly, this approach identified words under selection: kurtosis values close to zero signalled neutrality while deviations from zero were indicative of selection. Approaching this problem from a different

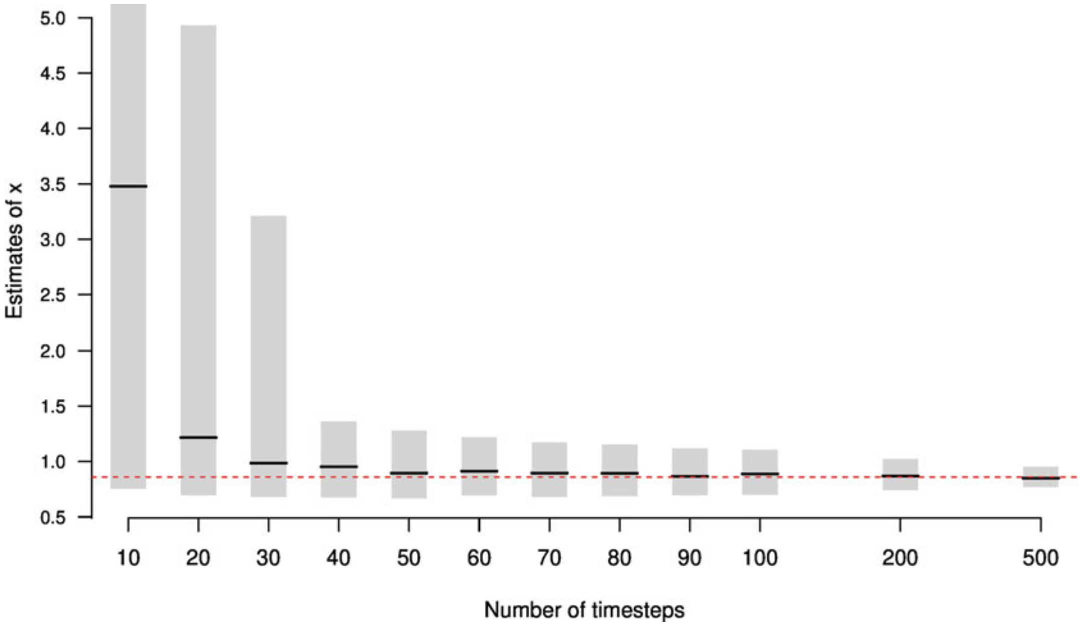


Fig. 5.2 Interquartile ranges of estimates of x based on different numbers of time steps. The exponent x and the coefficient A in Eq. (5.11) are estimated by fitting a linear model to $ln(z_y)$ using $ln(y)$ as predictor variable. The coefficient of the predictor represents an estimate of x and the intercept the estimate of A. The response variable z_y is however the *average* turn-over rate, which will fluctuate considerable for smaller number of time steps. The grey areas show the interquartile range of the estimated values of x obtained from 1000 simulations of unbiased cultural transmission with $N = 500$ and $\mu = 0.01$ but different number of recorded time steps. The red dashed line illustrates the theoretical expectation of x equivalent to 0.86

angle, Steele et al. (2010) showed, using the example of Hittite ceramic bowl types, that the neutral hypothesis was not rejected on the basis of the frequency distribution. However, examination of the characteristics of the bowl types revealed a correlation between those characteristics and their abundance ranking which indicated clear departure from the neutral hypothesis (which assumes functional equivalence and therefore predicts the absence of such a correlation). Brantingham and Perreault (2010) analysed the same data set and extended the use of the Price equation to the analysis of selective and stochastic forces operating on multiple artefact types within an assemblage. Based on this approach they concluded that selection is a dominant process driving the frequency evolution of the different bowl types within the assemblage and that stochastic forces played little or no role.

Application to Archaeology

Archaeological applications of the methods described above have been primarily focused on ceramic assemblages (but see Bortolini 2014; Scholnick 2010, for exceptions). Most of these case studies rest on the comparison between expected and observed homogeneity index derived from Ewens sampling distribution (e.g. Neiman 1995; Shennan and Wilkinson 2001; Lipo 2001; Kohler et al. 2004; Schauer 2008; Steele et al. 2010; Premo and Scholnick 2011; Bortolini 2014; Scholnick 2010).

Methods based on the progeny distribution have been applied only to the Merzbach assemblage mentioned above, yielding contrasting results (Bentley et al. 2004). While Shennan and Wilkinson's original study (Shennan and Wilkinson 2001) suggested the rejection of the neutral model on the grounds of a level of cultural diversity lower than that expected under neutrality, Bentley et al. (2004) argued that this might be the case for earlier phases but not for the later ones where the observed pattern have a good fit with the expected neutral progeny distribution (Bentley and Shennan 2003).

As mentioned earlier, we are unaware of any application of the turn-over rates based method, most likely because its strict requirement of frequency data recorded across a relatively larger number of time points for accurate estimates of turn-over rates (cf. Fig. 5.2).

The limited number of time points and phases is only one of the many issues challenging the application of these methods to archaeological assemblages. Premo (2014), for example, explored the problem of time-averaging and showed how methods based on diversity indices have an inflation of type I error with increasing duration (hence magnitude of time-averaging) of archaeological phases. This is simply due to the fact that with increasing duration more variants with shorter life spans are likely to be included, effectively increasing the observed number of variants and cultural diversity of the assemblage. Premo (2014) noted that progeny distributions are more robust to the effect of time-averaging.

Another key issue in the applications of these methods is the exact definition of what constitutes a cultural variant. All the methods summarised above require count data, but counts of what? In some domains such as baby names or dog breeds this is arguably a straightforward exercise (though one may argue whether *Cliff* and *Clifford* should be regarded as instances of the same variant or two distinct ones), but in other contexts this is less so. Some decorative traits in pottery design might be affected by substantially high levels of inter-observer variability in defining what constitutes the unit of transmission (or replicator), potentially biasing the inferential enterprise. This issue is also linked to the extent by which the units of transmission can be assumed to be discrete entities rather than continuous ones. While the extent of the problem is, again, likely to vary case by case, theoretical models have shown that in presence of strong cognitive attractors, discrete replicator approximation can be effective even if the unit of transmission is continuous (Henrich and Boyd 2002). It is worth pointing out that the question of what constitute a cultural trait is also epistemological in nature, and can be described as a classification issue (see also Lipo et al. 1997; Pocklington and Best 1997; O'Brien et al. 2010).

Lastly, in many contexts changes in the frequency of specific variants may be strongly affected by the mode of production and extent of unevenness in productivity. For example, an assemblage of *n* ceramic bowl produced by only two potters engaged in serial production may exhibit a different pattern of cultural variation than an assemblage of the same size but produced by, e.g., ten potters. While these issues of cultural growth *vs* cultural reproduction have been discussed from a philosophical standpoint (see, e.g., Ramsey and De Block 2017), their potential inferential challenges, particularly in production economies, have yet to be explored adequately.

Interpreting the Test Results

At a first glance, the assumptions of neutral theory are often at odds with the vast stores of knowledge archaeologist and anthropologists have accumulated for social systems. Humans are generally not thought of as making decisions at random. Neutrality would imply that individuals do not possess any preferences for existing cultural variants nor does the adoption of a particular cultural variant provide an evolutionary advantage over the adoption of a different variant. Additionally neutral evolution assumes that each cultural variant evolves independently. While these inherent assumptions are likely to be violated (for detailed discussions see, e.g., Neiman 1995; Shennan and Wilkinson 2001; Steele et al. 2010), it has been shown that population-level patterns of various observed episodes of cultural change resemble the ones expected under neutrality (see, e.g., Bentley et al. (2004); Hahn and Bentley (2003); Neiman (1995); Bentley et al. (2007) and section "Application to Archaeology"). In other

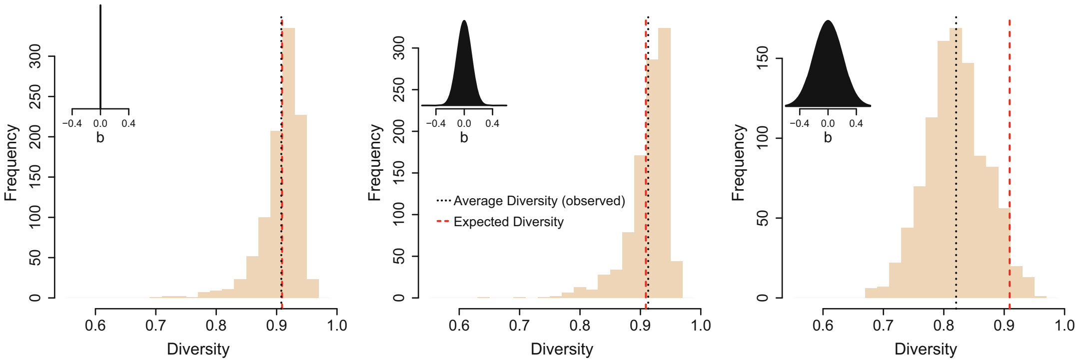


Fig. 5.3 Distribution of the level of cultural diversity for increasing levels of heterogeneity in individual preferences after 1000 time-steps with $N = 500$ and $\mu = 0.01$. We assumed that individuals can have different propensities for frequency-dependent transmission, i.e. individuals can possess different b values (see Eq. (5.12)), but kept the mean propensity of the population at zero which would imply unbiased transmission. Left figure: all individuals use unbiased transmission (i.e. $b = 0$); centre figure: individual propensities at each time step are drawn from a normal distribution with mean 0 and standard deviation 0.1 (see inset); right figure: same situation as in the central figure but with standard deviation increased to 0.2 (see inset). The black dashed lines represent the mean level of cultural diversity across all simulations and the red dashed lines the neutral predictions $1 - F$ (see Eq. (5.4)). If the deviations of the propensities from zero are not too large (central figure), then the resulting population-level patterns are consistent with neutral theory (cf. left figure and dashed red line). If, however, the deviations get larger (right figure), then the population-level patterns deviate from neutral expectations and consequently there is no guarantee that a population expressing heterogeneous preferences will exhibit a population-level signal of neutrality

words, we are confronted with a situation where we *know* that individuals possess heterogeneous preferences for choosing one cultural variant over another, however, the resulting population-level patterns may still be consistent with neutrality.

So what does consistency between population-level predictions of the neutral theory and empirical data tell us? It has been suggested that if each individual act of choosing one cultural variant rather than another has a different motivation, the emerging population-level patterns will be that there are no directional selective forces affecting what is copied, and therefore population-level patterns of cultural change should be consistent with neutral theory (e.g. Shennan 2011). While this is plausible at least for narrow distributions of individual preferences (but see Fig. 5.3 which shows that there is no guarantee for a population-level signal of neutrality if individual preferences are very heterogeneous) we need to be careful with the "reverse" argument that the presence of collective selective forces or systematic biases in the transmission process will produce patterns that deviate from neutral expectations, which in turn would make neutral theory a suitable cultural null hypothesis (see, e.g., Richerson and Boyd 2008). Although this interpretation is very appealing we discuss two potential problems in the following (for discussions in the ecological context see, e.g., Gotelli and McGill 2006; Rosindell et al. 2012).

Link Between Population-Level Patterns and Individual-Level Processes

On the one hand, the cultural evolution literature has identified a large number of selective cultural transmission processes (e.g. Cavalli-Sforza and Feldman 1981; Boyd and Richerson 1985; Laland 2004). Henrich and McElreath (2003) categorised these selective biases into two broad groups: content biases and context biases. While content biases refer to differential copying or replication of a cultural trait due to outward features it displays (e.g. a cultural variant provides a functional benefit compared to other alternatives), context biases do not refer directly to physical features of cultural variants but the social or material context in which they are used (e.g. a cultural variant is copied due to its high frequency in the population; Lycett 2015). On the other hand, archaeological data sets usually record frequencies of different variants of cultural artefacts in a sample taken from a population of often unknown size at a single or several time points and therefore possess a sparse nature. Consequently, we face a scenario where there are many transmission hypotheses that could potentially explain the observed (sparse) data and we should not a priori expect a unique relationship between underlying processes of cultural transmission and population-level frequency patterns. In other words, we need to account for the problem of equifinality, i.e. situations where various individual-level processes can result in very similar population-level characteristics (e.g. von Bertalanffy 1969; Premo 2010). The problem is even worsened in populations of small sizes where the effects of random drift are magnified potentially obscuring any signatures of selective processes in the data. More generally random drift and innovation are not exclusive to neutral theory and hence expected differences in population-level patterns are rooted in the specifics of the underlying cultural transmission process.

Kandler et al. (2017) started examining this problem theoretically by developing a simulation framework aimed at exploring the level of distinguishability of processes of cultural transmission from population-level statistics. To do so they generated the probability distributions for a number of statistics such as the level of cultural diversity conditioned on different transmission processes. Those distributions describe the possible range of values of the statistics that can be assumed under the same environmental conditions. Therefore the area of overlap between these distributions indicates to what degree the two corresponding transmission processes can be distinguished based on the statistic (without knowledge of an empirical estimate). At one extreme, no overlap suggests that the processes can be reliably distinguished (as they result in distinct values of the statistic); at the other, complete overlap suggests that they cannot be distinguished as they result in almost similar values of the statistic (see also Crema et al. 2014, and their use of confusion matrices to assess the extent of equifinality). Further, they calculated the probability that an empirical estimate of a particular statistics could have been generated by a transmission process x as opposed to another process y. The analysis revealed that different processes of cultural transmission (vertical, oblique, horizontal and unbiased transmission as well as their frequency-dependent versions) will result in very similar population-level patterns, especially if those patterns describe the cultural composition of a population at a single point in time. In other words, neutral evolution is likely not distinguishable from alternative transmission processes based on, e.g., the observed level of cultural diversity as measured by Eq. (5.9). However, the temporal dynamic of cultural change, as, e.g., measured by the time a variant stays the most common variant, can retain a stronger signature of the underlying transmission processes than a “snapshot” of the relative frequencies of the variants at a given point in time. These results suggest that even when outcomes are similar in terms of cultural composition, they can differ substantially in temporal dynamics: similar distributions of cultural variants at a specific point in time can be reached through substantially different processes. Therefore attempts to infer processes of cultural transmission from population-level data should be based on measures of the temporal dynamic of cultural change.

But it is often not possible to increase the temporal resolution of archaeological data sets to the level that would be needed to reliably distinguish between a number of cultural transmission processes. Therefore the consistency between empirical data and neutral evolution (i.e. unbiased transmission) needs to be interpreted carefully as other cultural transmission hypotheses may be equally consistent.

Equilibrium Assumption

Most of the approaches mentioned in section “Detecting Departures from Neutrality” for detecting departures from neutral theory rest on the equilibrium assumptions, i.e. the predictions only hold for cultural systems at steady state. This implies that the observed frequency data was generated from a system where, among others, population size, innovation rate, and transmission process (unbiased transmission in the case of neutral evolution) were constant for a sufficiently long amount of time so that observed summary statistics are approximately constant over time and the initial conditions of the system play a minimal or no role. If this is not the case, e.g. because the population has recently undergone or is undergoing an expansion event or bottleneck, then those predictions are likely to be violated even if the population evolves neutrally. For example, in the situation of a bottleneck where the population size has decreased from N_1 to N_2 the level of cultural diversity "moves" from one steady state conditioned on N_1 to another steady state conditioned on N_2. However, this process takes time and any level of diversity observed in this transition period will not match the neutral prediction for neither N_1 nor N_2 (see also Rorabaugh 2014, for an extensive discussion of the effect of population bottleneck with regard to continuous neutral traits).

Figure 5.4 illustrates another potential source for non-equilibrium dynamics. Based on Wright–Fisher simulations with temporally constant population size N and innovation rate μ we show in panel (a) the level of cultural diversity as determined by $1 - f_t = 1 - \sum_{i=1}^{k_t} p_i^2(t)$ at each time step. The grey lines show the time course of the diversity level for a single simulation and the red-shaded area indicates the 95% prediction interval of the simulation output. The solid red line represents the corresponding average level of diversity at each time step and the dashed black line the neutral expectation $1 - F$ (see Eq. (5.4)). It is obvious that both, theoretical and simulation results match very closely.

In panel (b) we show the same results for a situation where the underlying process of cultural transmission changes for a brief time period (indicated by the blue shaded area) from unbiased transmission to negative frequency-dependent transmission. Negative frequency-dependent transmission is defined as the disproportional support for rare variants and is known to increase cultural diversity,

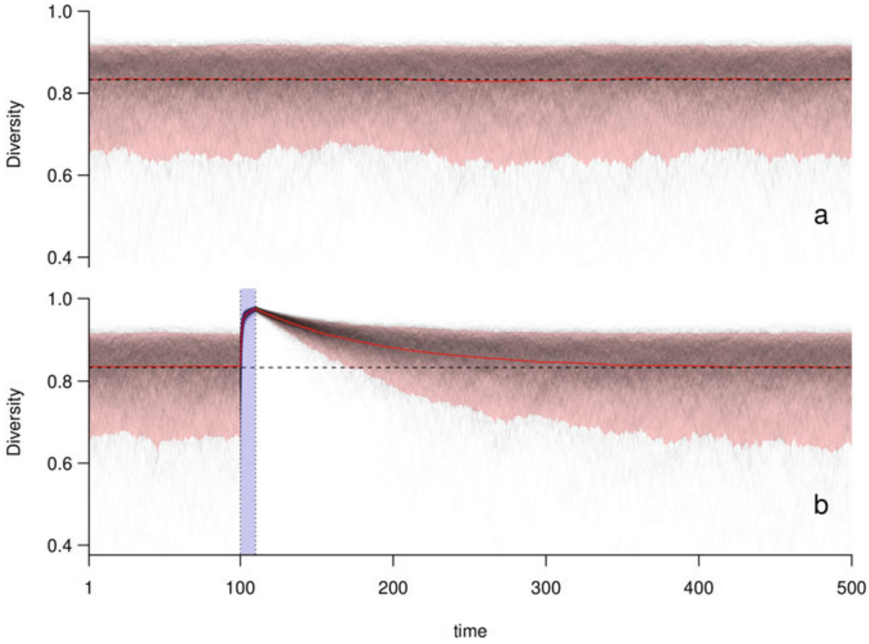


Fig. 5.4 Time series of the level of diversity under (**a**) equilibrium and (**b**) non-equilibrium regimes. In both figures the thin grey lines show the time series for individual simulation runs, the solid red lines the average diversity values, the red shaded area the 95% prediction interval out of 1000 simulations, and the black dashed lines the neutral expectation $1 - F$ (see Eq. (5.4)). The blue region in (**b**) highlights the interval where the transmission process temporarily changed to negative frequency-dependent transmission as described by Eq. (5.12) with $b = 0.5$

in particular to result in more even frequency distributions (Boyd and Richerson 1985). In modelling terms, this means that the probability that a variant i is chosen to be copied is changed from unbiased transmission expressed by Eq. (5.1)

$$\pi_i = \frac{m_i}{N}(1 - \mu)$$

to negative frequency-dependent transmission expressed by

$$\pi_i = \frac{\left(\frac{m_i}{N}\right)^{1-b}}{\sum_{j=1}^{k} \left(\frac{m_j}{N}\right)^{1-b}}(1 - \mu) \quad \text{with } b > 0 \tag{5.12}$$

for a short time period. The term m_i/N represents the relative frequency of variant i in the population, μ the innovation rate, k the number of different variants present in the population and the coefficient b controls the strength of the frequency-dependent transmission ($b = 0$ results in unbiased transmission, $b < 0$ in positive frequency-dependent transmission and $b > 0$ in negative frequency-dependent transmission). We set $b = 0.5$ in our example. It is obvious that the level of diversity quickly reacts to the change in transmission process and increases. But after transmission returns to its unbiased way it takes time until the level of diversity reaches its equilibrium level again (see red solid line in panel (b) which needs several hundred time steps to reach the neutral expectation shown by the black dashed line). As in the situation of changing population size, if the level of diversity is measured in this transitional period, then the hypothesis of neutral evolution will be rejected as the empirical estimate does not coincide with the neutral expectation. Consequently, non-equilibrium dynamics may be entirely responsible for the discrepancy between empirical observations and theoretical expectations. In this context, Crema et al. (2016) argued that the steady state assumption should be a hypothesis to be tested, rather than simply held a priori.

Summarising, we need to be careful with interpreting the consistency (or inconsistency) of archaeological data with theoretical neutral expectations as evidence for the absence (or presence) of selective forces. While it is likely that selective processes of cultural transmission generate population-level patterns similar to the ones expected under neutrality, especially in the light of sparse data, deviations between data and neutral theory can be entirely caused by non-equilibrium dynamics resulting from, e.g., temporal changes in population size. Additionally, the observed composition of the archaeological record may be the product of the accumulation of variants from various time points what also can produce a discrepancy with neutral theory (Premo 2014; Madsen 2012; Perreault 2018). Given these problems, Richerson and Boyd (2008) suggested to fit all plausible cultural transmission hypotheses to the data and see which, if any particular one, fits best. In the next section we describe a modelling framework which follows this suggestion and has the potential to address some of issues discussed in this section.

Inferring Alternative Processes of Cultural Transmission

If our aim is to uncover the specifics of the cultural transmission process from population-level frequency data, then we should analyse the temporal dynamic of cultural change. Further, it would be desirable to develop a modelling framework that simultaneously evaluates the consistency of a number of transmission hypotheses with the available data while also accounting for demographic and cultural properties of the system considered.

The general problem we are facing—the inference of underlying evolutionary processes from population-level data—is of course not unique to archaeology. In fact, other scientific fields have successfully overcome similar problems, in particular population genetics, which aims to understand the evolutionary mechanisms that produced the allele frequency distributions observed both now and in the past. Recent work has focused on developing efficient generative inference frameworks, which allowed for the statistical testing of increasingly realistic and complex evolutionary hypotheses (e.g. Veeramah et al. 2011; Eriksson et al. 2012; Posth et al. 2016; Ray et al. 2009).

Archaeology and more generally cultural evolution have adopted this modelling paradigm and generative inference frameworks enjoy increasing popularity (e.g. Crema et al. 2014, 2016; Kandler and Laland 2013; Kandler and Shennan 2015; Porčić and Nikolić 2016; Edinborough et al. 2015; Kovacevic et al. 2015; Rubio-Campillo 2016; Thouzeau et al. 2017). They have been applied to questions as diverse as the inference of processes of cultural transmission (e.g. Crema et al. 2014, 2016; Kandler and Shennan 2015) and the estimation of growth rates and population sizes from cultural frequency data (e.g. Porčić and Nikolić 2016), the investigation of the evolution of combat (Rubio-Campillo 2016) or of the coevolution between genes and languages at a regional scale (e.g. Thouzeau et al. 2017).

In this section we briefly introduce the idea of generative inference frameworks (for a detailed discussion see, e.g., Kandler and Powell 2018) and illustrate the applicability of this approach to archaeological data. Thereby we assume that the data provide a description of the dynamic of cultural change by recording the composition of samples of cultural variants (usually drawn from populations of unknown size) at several points in time.

Generative Inference Framework

The generative inference procedure consists of two main steps. The first step comprises the development of a generative model to produce pseudo-data, in our case population-level frequencies of different variants at different points in time conditioned on an assumed cultural transmission process. The second step uses Bayesian techniques such as approximate Bayesian computation to statistically compare theoretical predictions and empirical observations and to derive conclusions about which (mixtures of) transmission processes are consistent with the observable frequency data (and which are not). The outcome of this approach is not only the identification of the most likely underlying transmission process given the empirical data but a description of the breadth of processes that could have produced the these data equally well which in turn can be interpreted as an informal measure of the level of equifinality (Kandler and Powell 2018).

In more detail, the **generative model** is aimed at capturing the main cultural and demographic dynamics of the cultural system considered. Importantly, the model produces data of the same type as the observed data but conditioned on the assumed cultural transmission process. Thereby different transmission processes are expressed by different model parameterisations; the model parameters are denoted by $\theta = (\theta_1, \dots, \theta_s)$ in the following. In other words, the generative model establishes an explicit causal relationship between the assumed processes of cultural transmission defined by θ and observable population-level patterns of cultural change. There are no restrictions on the type of generative model used. Models ranging from systems of partial differential equations to agent-based simulations have been applied successfully.

As the generative model generates frequency distributions at different points in time it can be designed as a non-equilibrium framework where some of the issues mentioned in section "Equilibrium Assumption" are accounted for. In other words, starting from an initial condition we are interested in the frequencies of the cultural variants at a specific time point and not necessarily at steady state. Naturally this also allows for the incorporation of temporally changing model parameters such as population size and innovation rate. Consequently, the risk of misinterpreting non-equilibrium dynamics as evidence for the presence or absence of particular cultural transmission processes can be reduced but this modelling choice requires relatively accurate knowledge about the time points at which the observed frequencies are recorded.

Summarising, the generative model produces pseudo-data of the same type as the observed data conditioned on a specific hypothesis of cultural transmission which is parameterised by the values of the model parameters $\theta = (\theta_1, \ldots, \theta_s)$. **Statistical comparisons** then determine which of the cultural transmission processes considered in the generative model could produce pseudo-data similar to the observed data. For that one would ideally determine the likelihood function of the generative model. However, in many cases the likelihood functions cannot be determined easily. **Approximate Bayesian computation (ABC)** (Beaumont et al. 2002; Pritchard et al. 1999) was developed to circumvent this difficulty. In the following we briefly describe the ABC procedure in its simplest form, the rejection algorithm, but note that many extensions have been published (e.g. Beaumont et al. 2002; Blum and François 2010; Marjoram et al. 2003; Toni et al. 2009).

Given observed data D, the ABC approach approximates the joint posterior distribution of the model parameters θ, denoted by $P(\theta|D)$. It does this through repeatedly simulating data $D^\star$ under a generative model with parameter values drawn from their prior distributions $P(\theta)$. These prior distributions describe the possible values the parameter can assume or summarise all prior knowledge researchers may have. Retaining those parameter sets that generate data $D^\star$ sufficiently "close" to the observed data D, and rejecting the rest, results in a random sample from the distribution $P(\theta|d(D, D^\star) \leq \varepsilon)$, where $d(\cdot, \cdot)$ is a distance metric between the observed and simulated data, and ε is a tolerance level determining the approximation to the true posterior $P(\theta|D)$. In situation where the observed data D is high-dimensional it may become a challenge to determine how the distance between empirical and theoretical data should be calculated. Here often summary statistics S (such as the level of cultural diversity) are used which implies that not the distribution $P(\theta|d(D, D^\star) \leq \varepsilon)$ but $P(\theta|d(S, S^\star) \leq \varepsilon)$ is sampled. The choice of appropriate summary statistics is not straightforward and can have crucial consequences on the inference accuracy (the choice of summary statistics is currently an active area of statistical research, e.g., Harrison and Baker 2017). However, those problems are evaded if the distance is calculated based on the 'raw' data D and $D^\star$, in our case by calculating the euclidean distance between the observed and theoretical frequencies.

The output of any ABC procedure is the joint posterior distribution of the model parameters $\theta = (\theta_1, \ldots, \theta_s)$ (and derived from that the marginal posterior distributions for each individual parameter), indicating the range of the parameter space that is able to produce frequency data within a given tolerance level ε of the observed data, and consequently the transmission that is consistent with the data. Therefore the widths of these distributions may provide an informal measure of the level of equifinality. If the posterior distributions are narrow (compared to their corresponding prior distributions), then only a small region of the parameter space is consistent with the data and therefore a large number of transmission processes are not able to produce the observed frequency changes. In this case the data carries a relatively strong signature of the underlying processes of cultural transmission. In contrast, if the distributions are wide, a large region of the parameter space is consistent with the data and therefore many processes of cultural transmission are able to generate very similar population-level frequency patterns (Kandler and Powell 2018).

In practice, performing ABC analyses has been made relatively straightforward by the release of software such as *DIY-ABC* (Cornuet et al. 2008), *ABCtoolbox* (Wegmann et al. 2010), and *R* packages such as *abc* (Csilléry et al. 2012), *abctools* (Nunes and Prangle 2015) and *EasyABC* (Jabot et al. 2013).

Cautionary Notes

One of the main advantages of the generative inference approach described above is that it allows for the statistical evaluation of complex cultural and demographic scenarios. Nevertheless the interpretation of the analysis results has to be done cautiously; it is, after all, an analysis based on an underlying model of cultural change. If this model does not capture the main cultural and demographic processes contributing to the observed temporal frequency changes, the inferences obtained will likely be misleading.

The ABC procedure *always* outputs a joint posterior distribution of the inferred model parameter. But as mentioned before this distribution only approximates the 'true' distribution if the achieved error level ε, i.e. the distance between theoretical and empirical data, is close to zero. If the obtained ε is large and cannot be improved upon the inferred parameter spaces are likely not meaningful and should not be interpreted. This situation may point to an inadequacy of the model, and therefore the assumed processes of cultural transmission, to explain the data. The explanatory value of the obtained posterior distribution can be further investigated by posterior predictive checks (Gelman et al. 2013, see Crema et al. 2016 for an archaeological application). In our situation, these checks consist of sampling values of the model parameters from the joint posterior distribution, inserting these into the generative model and producing theoretical frequencies at the required time points. Repeating this procedure generated theoretical expectations of the frequency ranges for each individual variant based on the joint posterior distribution. The comparison of the observed frequencies of each variant with these frequency ranges allowed the explanatory power of the derived posterior distribution to be assessed. If observations are outside the theoretical expectations, then the inferred cultural transmission processes cannot replicate all aspects of the dynamic of cultural change, indicating a mismatch between theory and data. Additionally, crossvalidation tests or coverage plots have been developed to further investigate the accuracy of the results of the ABC analysis (Csillléry et al. 2012; Prangle et al. 2014; van der Vaart et al. 2015).

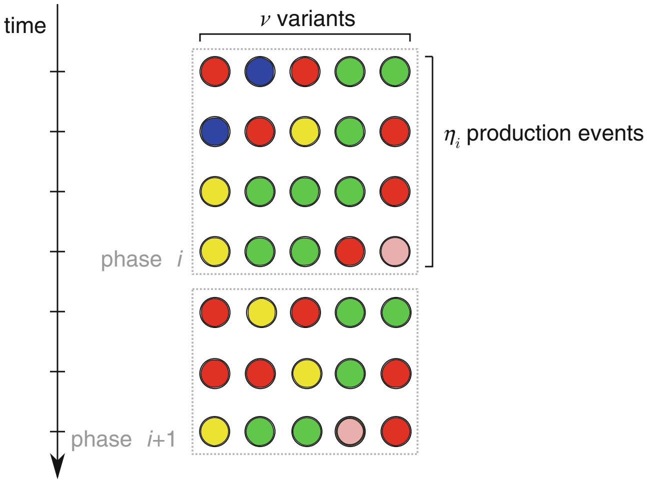
A common criticism of the ABC method focuses on the choice of prior distributions which may only be "guessed based upon the subjective opinion of the investigators" (Templeton 2010). This argument is connected to classical objections of Bayesian approaches (Beaumont et al. 2010). The prior distribution represents prior beliefs about the distribution of the parameters and should if possible be defined based on known properties of the system studied (e.g. the duration of archaeological phases, the hypothesised number of social learners, etc.) but may for practical applications necessitate an educated guess (Sunnåker et al. 2013). While informative priors can influence the widths of the posterior distributions, uninformative and flat priors can still yield reasonable parameter estimates. However, Bayes factors (for model comparisons) are highly sensitive to the prior distribution of parameters (Sunnåker et al. 2013).

As already mentioned, the accuracy of the inference depends partly on the way the distance between theoretical and empirical data is calculated. Calculating the difference based on an insufficient summary statistics S instead of the full data D results in discarding likely useful information and the posterior distribution will not be equal to that computed with the full data (Csilléry et al. 2010). Therefore, if possible, inferences should be based on the full data and if this is not possible the summary statistic (or a set of) needs to be carefully chosen (see Csilléry et al. 2010, for a review of strategies of how to do so).

Example

In the following we demonstrate how such an inference framework can be constructed and used by summarising the analysis of an archaeological data set describing the culture of the first farmers in

Fig. 5.5 In each time step, ν variants are generated (For the sake of simplicity we kept ν constant in each time step, however, this assumption is relaxed in the non-equilibrium versions of the model described below.) and the population-level frequencies of the different variants (indicated by different colours) at the end of each phase i describe the accumulation of all η_i production events. It holds $N_i = \nu\eta_i$



Central Europe in the valley of the Merzbach stream in western Germany, the so-called Linearbandkeramik (LBK) culture, from ca. 5300 to 4850 cal. B.C. (see Crema et al. 2016, for the complete analysis). The data set records the frequencies of 36 types of pottery vessels in eight different phases. The aim of this study was to explore whether observed frequency changes in different types of pottery between the different phases are consistent with a specific hypothesis about the underlying cultural transmission process, in particular unbiased transmission and frequency-dependent transmission, under the assumptions that (1) the cultural system producing those frequencies is at equilibrium and (2) certain aspects of the system change over time.

First, we developed the generative model. As mentioned above, the model had to generate frequency changes of the different cultural variants between two successive phase conditioned on a specific process of cultural transmission but also reflect the essential features of the way the frequencies have been generated. Crucially this model had to take into account that the observed frequencies in phase i describe the composition of a sample of size n_i but not of the population of unknown size. Any evolutionary process, however, acts on the whole population and not only on the sample and consequently processes of cultural transmission need to be modelled on the population-level. To do so we assumed that the population size N_i can be determined from the sample size through the relation $N_i = n_i/r$ with $0 < r < 1$. The variable r describes the expected fraction of the population that has been sampled. We further assumed that the N_i cultural variants are the result of the accumulation of η_i production events of ν_t variants throughout phase i (see Fig. 5.5). In other words, it holds $N_i = \sum_{t=t_i}^{t_i+\eta_i-1} \nu_t$.

The composition of the ν_t variants in each production event is determined by the assumed process of cultural transmission which guides the decision to add an instance of a certain variant based on the available social information. Here social information consists of a sampling pool, composed of the cultural variants of the last w production events. In detail, an instance of variant j, $j = 1, \dots, k$ is chosen to be added to the population according to the probability

$$\pi_j = \frac{{p_j}^{1-b}}{\sum_{l=1}^{k} {p_l}^{1-b}}(1-\mu) \tag{5.13}$$

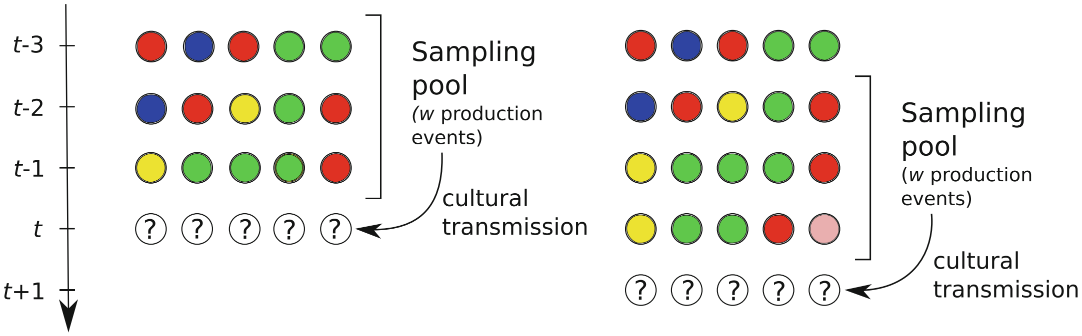


Fig. 5.6 Scheme of the transmission dynamic. In each production event ν instances of cultural variants are produced and the probability with which one of the existing variants is produced is given by Eq. (5.13). For instance, in the left figure any of the five instances at time t turns red with probability $\frac{(5/15)^{1-b}}{(5/15)^{1-b}+(2/15)^{1-b}+(6/15)^{1-b}+(2/15)^{1-b}}(1-\mu)$. With probability μ an entirely new variant is introduced (see the pink variant at time $t+1$ in the right figure)

where p_i describes the relative frequency of variant i in the sampling pool, the parameter b controls the strength of frequency-dependent transmission, and μ stands for the innovation rate (see Fig. 5.6). Importantly, setting $b = 0$ reduces Eq. (5.13) to unbiased transmission (cf. Eq. (5.1)).

This process is repeated until η_i production events have produced in total N_i instances of cultural variants. In this way we have generated a theoretical population of variants conditioned on a specific process of cultural transmission (parameterised by the value of parameters b, μ, and w) given by Eq. (5.13). In order to create data that can be compared to the observed data we lastly drew n_i variants randomly from this population. Summarising, we developed a model that, based on certain cultural and demographic assumptions, can describe the dynamic of cultural change conditioned on a specific process of cultural transmission. Further, this model is flexible enough to replicate equilibrium and non-equilibrium systems. In order to explore the consequences of these modelling choices we analysed the following three versions of the model (see Crema et al. 2016, for details).

Equilibrium Condition To generate data for a system at equilibrium we repeated the above described dynamic sufficiently long (starting from an arbitrary initial condition) under constant parameter values, i.e. $\theta = [\mu, b, \nu, r, w]$ did not change over time. This means that both, the process of cultural transmission and the number of variants ν generated in each production event were kept constant. After this burn-in period, we generated populations of sizes N_i for all seven consecutive phases i and randomly sampled from these populations n_i instances of cultural variants. If the observed data was generated by a process of unbiased transmission (i.e. $b = 0$), the posterior distribution of b should be centred around 0.

Variable Population Condition We relaxed the assumption that the number of cultural variants generated in each production events is constant over time but still assumed that the process of cultural transmission is the same throughout all phases. Therefore the main differences to the equilibrium version are that (1) ν is time-dependent, and hence its value can change at each production event; and (2) the model is no longer initialised through a burn-in phase. Instead the initial sampling pool is derived from the observed frequencies at the end of phase $i-1$ using the Dirichlet distribution approach (Gelman et al. 2013).

Variable Population-Transmission Process Condition We allowed both, the number of cultural variants produced per production event and the cultural transmission process to vary over time. For this we applied the same routine described in the variable population size condition but considered each phase separately. Thus we generated a sampling pool at the beginning of each phase i (following the Dirichlet approach and using the observed frequencies at the end of phase $i-1$), let η_i production events occur to generate a population of cultural variants at the end of phase i conditioned on the cultural transmission process defined by the parameters b_i, μ_i, and w_i and drew a random sample of size n_i.

Now to infer which cultural transmission hypotheses are consistent with observed data we applied the ABC rejection procedure. For each version of the model we determined the parameter values which were able to generate variant frequencies "close" to the observed ones. As distance measure we used the euclidean distance between theoretical and observed frequencies. In detail, we sampled parameter combinations from prior distributions of b, μ, w, r, and ν, executed the simulation model, and measured the euclidean distance ε between the obtained theoretical data and observed data. From the pool of s iterations of this procedure a proportion α, representing the lowest values of the error level ε, are retained and the parameter values associated with these were assessed. We set $s = 10^7$ and $\alpha = 2 \times 10^{-5}$ for all three versions of the model. Sample codes of the simulation model, the ABC framework, and the data set can be downloaded at https://github.com/ercrema/CulturalTransmissionModel.

The output of this inference procedure is the joint posterior distribution of the inferred parameters $\theta = [b, \mu, w, r, \nu]$. This distribution reveals which parameter values, and therefore which processes (amongst the models considered in the generative model) could replicate the observed samples.

From the range of the corresponding marginal distributions we concluded that the strength of frequency-dependent transmission b was by far the most informative parameter, pointing to a relationship between processes of cultural transmission and observable patterns of cultural change. The posterior distributions of the other model parameters covered in all cases nearly the same range as their respective prior distributions indicating that the data is not informative about those parameters.

The 95% highest posterior density interval (HPDI) of the posterior distribution of b for all three model versions are shown in Fig. 5.7. But before exploring the differences between the versions we take a closer look at the distributions. The HPDIs describe the parameter ranges that could have generated the observed frequencies. In all cases we *cannot* infer a single transmission processes (such as unbiased transmission) as the sole candidate for explaining the data. We instead observed an equifinal situation: a range of values of b (and therefore frequency-dependent transmission of various strengths) are consistent with the data. The median values (indicated by the black horizontal lines) point to the most likely process but nevertheless all other values of b within HDPI have produced frequency data with a similar error tolerance ε.

In the equilibrium version, the median value of the distribution of b is 0.028 which would suggest the presence of some degree of weak negative frequency-dependent transmission, albeit the HPDI covers a range between −0.005 and 0.102 (see Fig. 5.7). The variable population version appeared to show a stronger support of negative frequency-dependent transmission, with the entire 95% HPDI (0.015–0.134) larger than zero and a median value of 0.066. To further analyse the data we performed a posterior predictive check of the equilibrium and the variable population versions where both versions showed a relatively poor performance with a considerable number of observations outside their expected frequency ranges. This suggested that neither equilibrium conditions nor a changing number of copying events can explain the observed data.

In the variable population-transmission process version the posterior distributions of b for the individual phases suggest fluctuations (although the 95% HPDI of b is not sufficiently narrow to fully dismiss competing models), with earlier stages showing stronger support for negative frequency-dependent transmission and intermediate phases for a positive frequency-dependent transmission (see Fig. 5.7). The posterior predictive check of the variable population-transmission mode version showed a clear improvement with the 95% range of the model prediction including all observed frequencies except three variant types suggesting a change in the process of cultural transmission between successive phases. Consequently, this kind of analysis may also reveal individual variants which are "special" in the sense that they do not follow the general dynamic of the system and

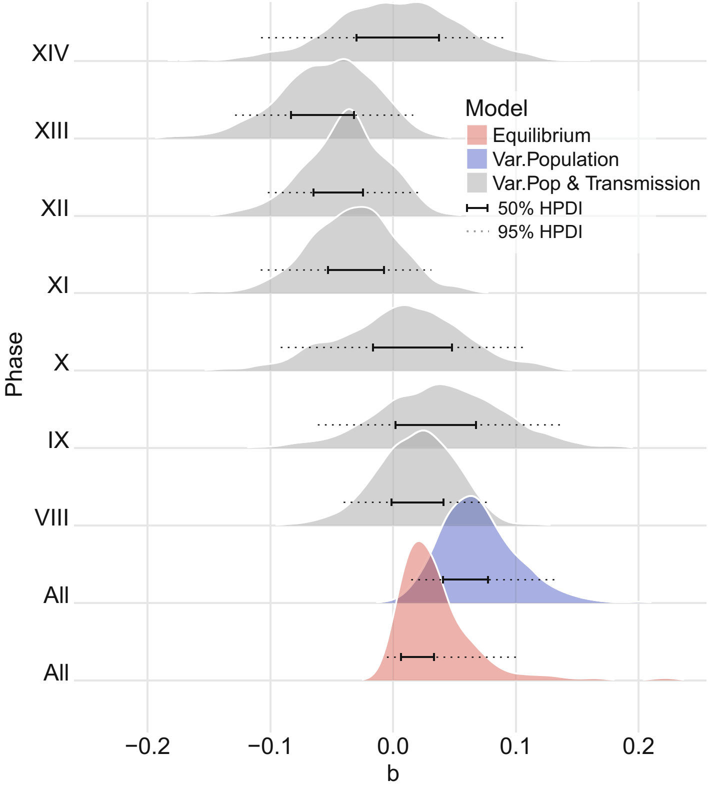


Fig. 5.7 Marginal posterior distributions of the strength of frequency-dependent transmission *b* for the equilibrium (across all phases), variable population (across all phases), and variable population-transmission (per individual phase) version of the generative model

potentially are selected for or against by other forms of cultural transmission such as content biased transmission.

Summarising, our attempts at inferring patterns of cultural transmission in the Merzbach assemblage revealed a cultural system that is unlikely to be in equilibrium conditions. Instead our results hinted at the possibility of shifts between negative and positive frequency-dependent transmission. But crucially the widths of the obtained posterior distributions showed that there exist limits to the inference of underlying processes from cultural transmission from the observed population-level frequency data.

Discussion and Conclusion

Neutral theory has been central to applying quantitative evolutionary thinking to archaeology. It suggests that temporal changes in cultural assemblages can be explained by a process of unbiased transmission, random drift, and innovation and the mathematical frameworks developed in population genetics provided means to analyse the patterns of assemblage variation by exploring their consistency (or inconsistency) with neutral expectations. In other words, these frameworks present a way of testing whether observed population-level data describing the frequencies of various cultural variants can be explained by the process of unbiased transmission. Archaeological applications of neutral theory have mainly focused on ceramic assemblages and the comparison between expected and observed levels of cultural diversity (e.g. Neiman 1995; Shennan and Wilkinson 2001; Lipo 2001; Kohler et al.

2004; Schauer 2008; Steele et al. 2010; Premo and Scholnick 2011). Most of these studies concluded consistency between neutral theory and the observed assemblages.

But the assumption of unbiased transmission is often at odds with what archaeologist and anthropologists know about social systems. So what can we learn from the consistency of between neutral theory and empirical data? It is worth mentioning that consistency has not been interpreted as evidence that all individuals adopt cultural variants at random. Consistency does mean that no selective processes have to be invoked in order to explain the observed population-level frequency patterns making neutral theory the most parsimonious mechanism to account for the commonly observed life cycles of artefact attributes, such as decoration patterns: initial appearance, rise and decline in popularity followed by eventual extinction. But we argue in this chapter that we need to be careful with interpreting the consistency (or inconsistency) of archaeological data with theoretical neutral expectations as evidence for the absence (or presence) of selective force in the population. While neutral theory does very well in replicating population-level frequency patterns, many alternative processes of cultural transmission may do so, too, making the pattern-matching approach a fairly weak approach for inferring underlying transmission processes (see, e.g., Gotelli and McGill 2006; Rosindell et al. 2012, for discussions of this in the ecological context). Now one may argue that this is not a problem of neutral theory but of the (sparse) data, or the test statistics used. In fact, stronger tests of departures from neutrality, e.g. involving analyses of the temporal dynamic of cultural change, have proven more powerful in distinguishing between neutral evolution and selective forces (e.g. Sindi and Dale 2016). But in archaeological applications it is unlikely to easily improve the temporal and/or spatial resolution of the data and therefore the pattern-process issue has to be accounted for.

Here we advocated the use of a generative inference approach as one possibility to go beyond the hypothesis testing approach. At the heart of this framework is a generative model, which captures the main cultural and demographic properties of the system considered. These models establish a causal link between model parameters controlling the strengths of underlying evolutionary processes and observable population-level patterns; in our case between parameters controlling the strengths and nature of the cultural transmission processes considered and population-level frequencies of cultural variants. Bayesian inference techniques, such as ABC, can then evaluate whether a specific process of cultural transmission is able to produce frequency patterns consistent with the observed ones. The main advantage of this approach that it allows for relatively complex, potentially non-equilibrium generative models which may include all information researches may have about the system considered (e.g. time-averaging processes, changes in population size, precise time points of observations). This comes at the cost that the statistical comparison is computationally very intensive, however, modern-day computing equipment (especially the use of high-performance clusters) can overcome this obstacle.

The outcome of this inference approach are posterior distributions of the model parameters, specifying the transmission processes, that are consistent with the observed frequency data. While there are a number of important factors, potentially influencing the accuracy of the analysis, to consider (see, e.g., Kandler and Powell 2018, for more details), the widths of the posterior distributions may be indicative of the amount of information about the underlying transmission processes contained in the data. Narrow posterior distributions indicate that the data carries a relatively strong signature of these processes, while wider distributions suggest that the data is largely uninformative or that the models considered do not provide an adequate description of the cultural system. Therefore this approach does not only allow for the identification of the most likely underlying learning process given the empirical data but for a description of the breadth of processes that could have produced these data equally well, providing an informal measure of equifinality.

Applications of this framework to archaeological data have shown that researchers should not expect to be able to infer a single cultural transmission process that solely can explain the data. Different transmission processes will be consistent with the data. And it is one of the strengths of mathematical modelling approaches to archaeological data to help us understand these limits to inferring underlying transmission processes from population-level frequency data and therefore to identify which kinds of questions can be answered with which kinds of data. The value of the analyses similar to the one described in section "Application to Archaeology" lies in the exclusion of transmission processes that could not have produced the observed data and therefore in a reduction of the pool of potential hypotheses. Subsequently, different lines of evidence may be used to reduce this pool even further.

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Part II
Macroevolution

Chapter 6
Cultural Macroevolution

Anna Marie Prentiss and Cheyenne L. Laue

Introduction

As detailed in Chaps. 2–5 (this volume), the study of cultural microevolution is focused on innovation, error, transmission, neutral factors, and selection studied on inter-generational bases. Cultural macroevolution adds further insights with concerns for patterns and rates of evolution, impacts of diverse evolutionary forces, and interactions between organic and cultural evolution, as expressed over multi-generational time periods. The extended evolutionary synthesis provides a useful framework for considering theoretical aspects of cultural macroevolution given emphases on plasticity, contingency, evolution of development (evo-devo), hierarchical evolutionary process (multilevel selection), and stasis, cladogenesis, and emergence (Laland et al. 2015; Pigliucci 2009; Zeder 2017). Thus, macroevolutionary archaeology, like that of paleobiology, permits us to address complex multi-scalar evolutionary process over long time spans. We accomplish this via developing models and conducting tests of macroevolutionary hypotheses.

Cultural macroevolutionary research permits the development of explicit hypotheses about evolutionary process concerning evolutionary entities identified on multiple scales across long time spans. Fundamental research in cultural macroevolution has addressed the problem of evolutionary scale or what actually evolves (Boyd et al. 1997; Jordan and Shennan 2009; Jordan 2015; Prentiss et al. 2009, 2017); whether cultural evolution occurs in a branching or blending process (O'Brien and Lyman 2003; Tehrani and Collard 2002); variability in the rates of evolution (Bentley and O'Brien 2011); fitness landscapes and cultural macroevolutionary process (Bettinger 2009; Spencer 2009); and demographic and ecological factors conditioning variability in tempo and mode of cultural innovation and extinction (Collard et al. 2016; Henrich 2004a). Outcomes of these studies have been applied in a variety of contexts to enhance our understanding of particular cultural evolutionary sequences (e.g., Barton et al. 2007; Jordan 2015; Prentiss et al. 2014, 2015, 2017; Prentiss and Walsh 2016; Spencer 2013; Zeder 2009, 2017). Yet, it is clear from theoretical advances shared between evolutionary biology and archaeology (Fuentes 2017; Zeder 2017) that we still have much to learn. Relationships between micro- and macroevolution require more study into the effects of plasticity, ecological inheritance, and niche construction (Riede, this volume). Advanced fitness landscape theory and nearly neutral modeling (Laue and Wright, this volume) have yet to be effectively integrated into archaeological research.

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In this chapter we review basic concepts and contributions in cultural macroevolution and follow with introductions to the extended evolutionary synthesis and recent advances in empirical macroevolutionary research. We also include a section on advanced fitness landscapes and nearly neutral modeling as a preface to the chapter by Laue and Wright (this volume) on this topic. Theory is only useful if it helps us to better understand our empirical material, and we argue that advanced concepts emerging in macroevolutionary archaeology have that potential. Thus, in closing we provide several brief examples of empirical concerns that could benefit from explicit macroevolutionary attention.

Cultural Macroevolution

As discussed in Chap. 1 (this volume), evolutionary biologists and paleobiologists make a distinction between microevolution and macroevolution on the grounds that the former is defined by the study inter-generational evolutionary process on the scale of genes, organisms, and populations, while the latter is concerned with evolutionary process on the scale of species and higher phylogenetic units across long time spans (Eldredge 1989; Stanley 1998). Eldredge (1989) draws a distinction between organismic macroevolution or the study of phenotypic and genotypic change in populations of various scales within their environmental context over long time spans and taxic macroevolution, the study of evolutionary dynamics among species and monophyletic taxa. Inherent in the latter endeavor are research emphases on defining the phylogenetic pattern of evolution (Eldredge and Cracraft 1980) and understanding the dynamics of long-term evolutionary process (Eldredge 1989; Gould 2002; Stanley 1998). Significant outcomes of this agenda in paleobiology have included recognition of ecological and genealogical hierarchies (Eldredge 1985), species selection and sorting (Stanley 1998), driven and passive trends (McShea 1994), contingency and genealogical turnover (Gould 1989; Vrba 1985), heterochrony (Gould 1977), and punctuated equilibria encompassing stasis and cladogenesis (Eldredge and Gould 1972; Gould and Eldredge 1977). The significance of these findings is reflected in the degree to which these same concepts are reflected with today's extended evolutionary synthesis (Brooks and Agosta 2012; Laland et al. 2015; Pigliucci 2009).

Archaeology, like paleobiology, draws much of its primary data from the material record of the past. Thus, by its very nature archaeological research is effectively macroevolutionary. The early decades of evolutionary archaeology focused attention on the evolutionary fundamentals of synthetic Darwinism, in effect seeking to establish archaeology as an evolutionary science focused on the persistence of cultural characters in their social and environmental contexts. While occasionally hinting at the possibility of evolutionary dynamics on higher scales than basic artifact traits (e.g., Dunnell 1980; Leonard and Jones 1987; Neff 1992), the architects of evolutionary archaeology tied their emerging field of study to organismic macroevolution (Mesoudi 2011; Prentiss et al. 2009). This focus on explanation of long-term process with microevolutionary models seemed to preclude archaeology as a taxic macroevolutionary science (e.g., O'Brien and Lyman 2000). Yet, evolutionary scholars still raised the possibility that cultural elements could be configured in complexly integrated "packages" and "cores" (Boyd et al. 1997) suggesting that evolutionary dynamics could act on multiple scales. Other scholars offered the argument that the nature of evolutionary process could also vary with scale (Prentiss and Chatters 2003; Rosenberg 1994; Spencer 1997, this volume). Combined, these studies raised the possibility that culture could also be studied as a taxic macroevolutionary process. If so, it opens a range of questions about cultural macroevolution as multi-scalar (Mace and Holden 2005), manifesting patterns and processes of stasis and cladogenesis (Prentiss and Lenert 2009; O'Brien and Lyman 2003) and affected by historical contingency and genealogical turnover (Chatters and Prentiss 2005; Prentiss et al. 2014). Given this situation it would appear that cultural macroevolution is well positioned to contribute to the emerging extended evolutionary synthesis (EES) (e.g., Fuentes 2017; Zeder 2017). In turn, the EES provides a strong comprehensive theoretical basis for framing the range of cultural macroevolutionary research endeavors in archaeology.

The Extended Synthesis: Implications for Cultural Macroevolution

In order to appreciate the extent to which an EES could potentially inform the study of cultural evolution (and vice versa), it is helpful to summarize the tenants of the modern synthesis (MS), which remains the dominant theoretical paradigm in both cultural and biological evolution. The MS is often defined as an integration of neo-Darwinism (e.g., Darwinian theory minus Lamarckism), Mendel's theory of genetic heredity, and the population scale thinking introduced through work on statistical genetics by early-century theorists such as Haldane, Wright, and Fisher. The MS perspective holds that random changes in gene frequencies worked on by drift, gene flow, and (especially) natural selection result in evolutionary change that is inherently gradual as individuals inherit genetic variation and are the sole targets of selection. Central to the MS paradigm are the ideas that genetic changes precede and direct phenotypic changes, that both individual adaptation and taxonomic diversity are entirely the result of selection modifying individuals to better fit their environment, and that macroscale evolutionary change is the result of accumulated microscale (individual or species-level) changes considered over long time spans (Pigliucci 2007).

Despite the continued resonance of this perspective, and the ability of MS ideas to explain microscale changes and the results of these changes within species or populations, many theorists have begun to recognize the inability of the MS to adequately explain evolution on larger time scales or the degree to which evolution is often guided by factors outside of natural selection. Growing recognition of the often-punctuated nature of large-scale evolutionary change (Gould and Eldredge 1977), the importance of coevolution, niche construction (Laland et al. 2000), and contingency events (Oyama et al. 2003), as well as the likely prevalence of multiple forms of inheritance and levels of selection, has led many scholars to call for a "rethink" of the dominant evolutionary paradigm (Brooks 2011; Laland et al. 2014, 2015).

While biologists have been at the forefront of this movement, scholars with an interest in cultural evolution have recently joined as well, using knowledge of human-environment interactions as an entrada into discussions of an EES (Fuentes 2017; Zeder 2017). Indeed, research on the process of niche construction by human groups has been pivotal in integrating EES thinking with current cultural evolutionary theory. While the idea that human evolutionary success has been driven by the technological modification of inhabited ecologies is now canonical, EES-driven research further suggests that evolving socio-natural systems have emergent properties and that evolution is best studied as a co-constructive process in which humans, ecologies, and technologies all play pivotal, agentive roles. Examples of niche construction in the cultural literature include the initial domestication of plants and animals in the Near East (Kuijt and Prentiss 2009; Zeder 2017), the interaction between crop types and sickle cell disease (O'Brien and Laland 2012), and the relationship between dairying and the ability to metabolize lactase (O'Brien and Laland 2012). Zeder (2017) contends that this process enables the development of coevolutionary relationships and a series of "reciprocal niche-constructing activities" suggesting that cause and effect are patterned by feedback between interacting components of an evolving system.

The idea of reciprocal causation further highlights the degree to which organismal development is seen as a primary source of evolutionary change in the EES, indicating that natural selection may be only one of many factors influencing the process of adaptation (Laland et al. 2011). From this perspective evolving entities not only influence the environments they inhabit but are acted upon as well. According to Laland et al. (2014, p. 162), "Organisms are constructed in development, not simply 'programmed' to develop by genes. Living things do not evolve to fit into preexisting environments, but co-construct and coevolve with their environments, in the process changing the structure of ecosystems." Critical to the EES is the assumption that such developmental changes to the phenotype may persist in evolving populations and ultimately become heritable (Jablonka and Lamb 2014). The examples derived from NCT and noted above demonstrate how cultural and ecological factors may interact to induce biological changes as selection eventually works to increase the frequency of genotypes of individuals who have acquired favorable phenotypic changes. However, the EES also holds that there are important non-genetic inheritance systems as well and that "evolutionarily relevant information" (Fuentes 2017, p. S15) is often transferred outside of the confines of DNA (Danchin et al. 2011). In other words, inheritance under the EES is "inclusive," and selection is seen to operate not only on the individual and the genes it carries (as in the MS) but also on larger groups (Jablonka and Lamb 2014). Thus, according to EES, thought, behavioral, cultural, symbolic, and ecological inheritance may all play critical roles in evolution, and while natural selection may act on individuals in certain cases, both natural and cultural selection may favor phenotypic variants that promote the success of entire social or family groups.

The transmission of non-genetic information and alternative mechanisms of selection are particularly well-theorized in the social sciences, with a deep literature on both social learning and cultural transmission that now spans decades (Cavalli-Sforza and Feldman 1981; Flinn 1997; Richerson and Boyd 2005). The inheritance of behavioral or symbolic information results from the imitation or instruction of individuals by others within a group (e.g., social learning) with a number of culturally mediated transmission styles and biases that may prefer particular individuals or traits as models or teachers. Relevant to an EES extension, social learning has been shown to be adaptive only in particular environmental conditions (Kameda and Nakanishi 2002; Nakahashi 2007; Richerson and Boyd 2000) and to have coevolved with human biology potentially facilitating the evolution of human characteristics such as cooperation, altruism, and cultural conformity (Boyd and Richerson 2009; Henrich and Boyd 1998; Henrich and McElreath 2003). Research on cultural transmission and social learning has also demonstrated that social learning nearly assures the prevalence of cultural conformity and that critical outcomes of the norms facilitated by conformism—specifically the reluctance to adopt novel traits and between-group differentiation—likely facilitate group selection as well (Uyenoyama and Feldman 1980; Henrich 2004b).

Culture thus perfectly represents the drivers and constraints inherent in developmental bias, which refers to the idea that "some variant trajectories are more probable than others" (Arthur 2002, p. 1). Developmental constraint may restrict evolution to particular forms or pathways, effectively reducing variation and channeling the flow of change toward particular functions or forms (Oyama et al. 2003). In the context of culture, we note the prevalence of common social institutions, practices, and objects, which often arise spontaneously in different places and result in locally adaptive variations on more globally common themes (e.g., marriage and inheritance, feasting and competitive generosity, food procurement, and processing strategies). Such constraints represent likely pathways of cultural change given conditions at a particular moment in time (i.e., it is impossible to invent a car without first working through the creation of components such the wheel, metallurgy, internal combustion, and so on). Developmental plasticity on the other hand, a key driver of change, refers to the ability of an organism to respond rapidly to shifts in environmental conditions, often resulting in a great deal of variability within species as individual phenotypes are altered as a response to ecological changes (Moczek et al. 2011). Despite group-stable norms and the prevalence of conformity, culture also enables a great degree of plasticity as well, giving rise to a diverse array of skills, technologies, and practices, many of which have enabled responses to environmental shifts that are far more rapid than those allowed by biological evolution. It is further clear that some cultural forms (or characteristics of particular cultural traits) are more "plastic" than others; in other words some cultural forms are more "phenotypically" malleable, allowing adjustments and improvisations based on shifts in social or natural conditions (e.g., good example here), while others are less prone to modification.

With the EES concepts described above, we can begin to sketch out a picture of stability and change over long time spans, moving from alterations in individual traits to major cultural diversifications. Research on cultural microevolution has shown that cultural variation is often introduced either randomly (e.g., errors in transmission or copy events) or through guided processes (e.g., trial-and-error experimentation) and that culturally selective biases or drift works to increase or decrease the frequencies of variants (Richerson and Boyd 2005). The fact that cultural forms may be altered, selected, and discarded numerous times during a biological generation means that cultural evolution has the potential to be very rapid. However, the selective retention of highly adaptive traits as well as the tendency for conformity evidenced through shared cultural norms, values, and practices means that culture is inherently constant as well. The EES demonstrates how plasticity and various forms of selection operating at multiple levels can work together in complex ways and how these two evolutionary dynamics may result in temporally fluctuating rates of evolutionary change over long time scales. For example, plasticity may result not only in the rapid acquisition of variation but in evolvability (the propensity of a population to generate adaptive variation) and accommodation (the modification and/or stabilization of initially plastic traits by selection) as well (Badyaev 2009; Pigliucci 2008). This means that individual traits may cycle through phases of plasticity and selection depending on the stability of the socio-natural conditions of the organisms possessing them.

To begin at the microscale, small randomly introduced changes accumulate within the lineages of single cultural traits. Because these variants are often effectively neutral, they may largely escape the winnowing effects of selection leading to population drift over time (Bentley et al. 2004) and potentially to periods of apparent stasis in the material record. Variation acquired through guided efforts at improving plastic traits may tend toward beneficial change; however, as individuals actively work at niche construction or the improvement of existing technologies (Mesoudi 2011), these variants may be rapidly selected at the individual level or, as the EES predicts that environmentally induced phenotypic changes often occur in multiple individuals, at the level of the group as well. These periods of selection may appear in the material record as rapid increases in a particular variant, while periods after these rapid increases may appear static as conformity or other forms of selection hold constant relative frequencies. Critical to the EES, these evolutionary changes may result from biological, cultural, and ecological inheritance (or combinations of these) and may be driven by both organismal development and selection with feedback between the environment and the individual resulting in an evolutionary process throughout the lifetime of individuals (Day and Bondurianski 2011).

In the case of environmental shifts or other contingency events, we begin to see the potential for more macroscale processes emerging. Notably, the MS predicts that parallel evolution is the result of convergence and that variability between taxa is the result of differences in selective environments. According to the EES, however, developmental processes play a major role in macroscale evolutionary processes as feedback between organisms and their environments works to constantly shift the shape of the evolutionary landscape. Plasticity, in particular, may have major implications for macroevolution by enabling the expansion of groups into novel habitat, and the ability of organisms with highly plastic traits to adapt to new conditions is shown to be critical to the expansion of biological species into new territories and the possibility of subsequent speciation (Pfennig et al. 2010). It is possible that many of the culturally mediated colonization events evidenced in human prehistory were also facilitated by plasticity in cultural or technological traits that could be rapidly honed and adapted to fit new ecological opportunities and constraints (e.g., the transition to agricultural production described by Zeder 2017). Indeed, the EES predicts that major diversifications, including the processes of adaptive radiation—the rapid differentiation of subgroups from an ancestral population—are all facilitated by constructive developmental (particularly plasticity) rather than by the working of selection alone.

Research in Cultural Macroevolution

Archaeological research into cultural macroevolutionary process is now highly varied and includes basic hypothesis development and testing, advanced fitness landscape modeling, and interdisciplinary research linking cultural evolution to organic human evolution. In the following section we review the array of basic cultural macroevolutionary research problems and associated empirical research endeavors. These include the pattern of evolution, multi-scalar nature of cultural evolution, and geographic, demographic, and ecological factors affecting the cultural evolutionary process. Next, we go beyond research into basic macroevolutionary problems to an exploration of the potential contributions of advanced fitness landscape and nearly neutral theory. Such models allow potential insight into variability in evolutionary process on drastically different temporal scales across different geographic spaces. We propose that future research should focus on testing predictions drawn from EES (particularly associated with concepts of emergence, punctuated equilibria, and plasticity) along with advanced fitness landscape and nearly neutral theory given the potential of such models for deciphering long vexing problems in cultural evolution.

Fundamental Research Problems

An initial critical problem for cultural macroevolutionary research has been establishing that evolution as a Darwinian branching process across long time spans had even occurred (Borgerhoff Mulder et al. 2006). An entrenched perspective from social anthropology and social theoretical archaeology favored culture change as ethnogenesis, graphically portrayed as either a braided stream (Moore 1994) or a tree with tangled branches (Kroeber 1948). Paleobiologists have also expressed concerns regarding the validity of cultural evolution (e.g., Gould 1996). Eldredge (2000) and Tëmkin and Eldredge (2007) are most specifically critical in his documentation of the potential for extensive reticulations in the evolutionary trees for musical instruments. Yet, Eldredge (2009) also recognizes parallels between material cultural and organic evolution. As documented by Rivero (2006), scholars have been interested in defining historical lineages of languages and manuscript traditions extending back to the sixteenth century. However, it was not until the latter twentieth and early twenty-first centuries that scholars interested in language and sociocultural phenomena began to employ cladistics to formally examined evolutionary histories (e.g., Gray and Jordan 2000; Holden 2002; Holden and Mace 2003; Jordan and O'Neill 2010). Archaeological researchers also contributed to these discussions (e.g., Collard et al. 2006 [and chapters therein]; Jordan and Shennan 2003; O'Brien et al. 2001; O'Brien and Lyman 2003). An important outcome of this research was the recognition that the question of ethnogenesis versus descent with modification was not a qualitative issue but one of variation best understood using quantitative research approaches. Descent with modification was strongly evident in some lineages, for example, Iranian textiles (Tehrani 2011), while blending and borrowing better characterized others, as, for example, with Lapita pottery in western Oceania (Cochrane and Lipo 2010).

A second critical problem for cultural macroevolution has been the scale of evolutionary process. In 1995, Dunnell argued that selection could target cultural entities or "individuals" on multiple scales. Boyd et al. (1997) formalized this idea by proposing four scales on which cultural evolution could occur: (1) as species or complexly integrated entities not sharing the same characters with others; (2) as cores or hierarchical systems with limited capacity to exchange information with others; (3) as packages or coherent units existing within wider populations; and finally (4) populations of highly ephemeral entities. Critical to these models was the recognition that phylogenetic histories featuring a significant degree of evolutionary branching would be evident on the scales of species, cores, and packages, while evolutionary process for ephemeral entities would be characterized by such a high degree of blending and borrowing that descent with modification would not be recognizable. These ideas gained substantial traction in the cultural macroevolutionary literature (e.g., Prentiss et al. 2009 [and chapters therein]) but until relatively recently were rarely tested. Regardless, a substantial corpus of phylogenetic studies (Straffon, Chap. 8, this volume; Gjesfjeld and Jordan, this volume) provided direct evidence for evolution at multiple scales. Descent with modification was shown to have occurred with North American projectile points (O'Brien et al. 2001, 2014; Prentiss et al. 2016), Lower and Middle Paleolithic hand axes and Levallois cores (Lycett 2007, 2009), weaving traditions (Mattews et al. 2011; Tehrani 2011; Tehrani and Collard 2002), Polynesian bark cloth (Larsen 2011), skateboard decks (Prentiss et al. 2011, 2016), bronze statues (Marwick 2012), and Upper Paleolithic Venus figurines (Tripp 2016), among other things. Similarly, strong results were obtained for more complex technologies, for example, Polynesian ritual architecture (Cochrane 2015), Salish plank houses (Jordan and Mace 2008), traditional California earth lodges (Jordan and Shennan 2009), and Thule houses (Prentiss et al. 2017). Finally, strong signals for descent with modification were demonstrated by a variety of cultural traditions not directly measured as characters on specific artifact or feature classes. These include folk traditions (Ross and Atkinson 2016), stories (Tehrani 2013), Neolithic subsistence strategies (Coward et al. 2008), and North American Arctic and Pacific Northwest resource management strategies and village organization (Prentiss et al. 2014, 2015; Prentiss and Walsh 2016). The fact that evolution by branching can be demonstrated in these cases suggests that cultural evolution at a minimum acts on the scale of Boyd et al.'s (1997) populations of coherent units or packages. Evolution by branching in complex entities is suggestive of evolution on the scale of cores. Jordan's research on Salish, Californian, and Siberian technological traditions has demonstrated that the evolution of some technologies correlated with the evolution of others along with other traditions such as language in a limited number of cases (Jordan 2015; Jordan and Mace 2008; Jordan and Shennan 2009) raising the possibility of evolution on the scale of cores given the coevolution of multiple cultural traditions within single groups. Shennan et al. (2015) demonstrated evidence for evolution on the scale of packages with reference to Neolithic personal adornment and pottery. Prentiss et al. (2017) used archaeological data from Thule Inuit sites the North American Arctic to also test hypotheses about the scale of evolution. Their findings indicated that evolutionary processes for stone tool and house architecture were very similar in branching structure but also in correlations with passage of time since the earliest taxon and two ecological variables. All things considered, it suggested to the authors that these entities evolved as minimally as packages but likely also as components of cores. Evolutionary trees for harpoons in contrast had a weak branching structure and were heavily affected by reticulations, suggesting cultural evolution was operating at best on packages but likely also collections of ephemeral entities. Thus, Prentiss et al. (2017) drew similar conclusions to Jordan (2015) that cultural evolutionary process varies in scale and process depending upon what is evolving and its local social and ecological context.

Macroevolutionary research provides the opportunity to address evolutionary questions that require evidence from long time spans. Paleobiologists have taken significant advantage of the fossil record to test macroevolutionary hypotheses concerning an array of topics including speciation and extinction rates, large-scale evolutionary trends, global turnovers, causes of diversity, and evolutionary process on variable time scales (Eldredge 1989; Gavrilets 2004; Gould 2002; Stanley 1998; Vrba 1985). Similarly archaeologists in recent years have also begun to explicitly address an array of cultural macroevolutionary problems within the realms of explaining long-term temporal trends and understanding variability in cultural diversity. Long-term trend research has focused on factors favoring emergence of complex higher scale cultural entities (Prentiss et al. 2014; Prentiss and Walsh 2016), exploration of passive versus selectively driven trends (Spencer and Redmond 2001), social and ecological conditions affecting macroevolutionary trends (Prentiss et al. 2015, 2017; Roux 2013), long-term effects of trait biases (Acerbi and Bentley 2014; Crema et al. 2014), and variability in rates of evolution (Bentley and O'Brien 2011; Kashtan et al. 2007; O'Brien and Bentley 2011). While macroevolutionary research into factors promoting or reducing cultural diversity have highlighted subjects as diverse as memory (Bentley et al. 2014), ecological context (Mace and Jordan 2011), and capacity for social constructions (Plotkin 2011), by far the greatest attention has focused on relationships between diversity and demography.

To simplify a complex discussion, the argument has been made that demography plays a major role in that higher numbers and/or density of persons increases the chance that innovations will emerge and spread while lower density reduces innovation rates and also increases that likelihood that there will be critical losses and information holders die without passing on their knowledge (Henrich 2004a; Powell et al. 2009; Shennan 2001). Counterarguments suggest that diversity is more strongly impacted by ecological context (Nettle 2009), environmental variability (Collard et al. 2016), and social interactions (Andersson and Read 2016). However, the debate is not easily settled given variability in approaches to measuring diversity, assumptions about the nature of the underlying cultural process, and definitions of population size (Andersson and Read 2016; Premo 2016). A critical area that has not yet been adequately explored is the nature of the evolutionary process on drastically different time scales, and for that we need to consider advances in fitness landscape theory and its implications for diversity in cultural macroevolution (Laue and Wright, this volume).

Landscape Models

The chapters in this section address issues of cultural evolution on the macroscale. Tying this work to the rich existing literature on microscale cultural change, we highlight the importance of continued efforts toward developing theory and methods that allow archaeologists to theorize cultural change across diverse evolutionary scales. This is a difficult task with many of the quantitative tools commonly employed in archaeological research, where statistics have been developed to examine small changes to individual artifact traits allowing the typological classification of cultural variants, the quantification of variation, and examination of patterns of cultural descent (Jordan and Mace 2005; Lipo et al. 1997; Shennan 2011). Ongoing research has enabled researchers to link artifact variation seen in the record with larger dynamics such as environmental fluctuations, group contact, and migration (Eerkins and Lipo 2007; Lycett and von Cramon-Taubadel 2008; McElreath 2004). Population genetics and statistics developed for the study of continuous cultural traits have enabled archaeologists to examine patterns of cultural transmission, shifts in the spatial and temporal distribution of artifacts, and changes in population statistics such as group size and dispersal (Eerkens and Lipo 2005; Neiman 1995; Premo 2016; Shennan et al. 2015). These approaches have allowed archaeologists to extrapolate mesoscale evolutionary changes that emerge from micro-level variation using powerful quantitative methods developing data from field-based research and modeling. While these have been influential methods contributing broadly to the archaeological literature, recent research suggests that data acquired across multiple time periods may decrease the statistical power of some of these approaches (Madsen 2012; Premo 2014). The movement toward an EES asks us to consider the possibility that some (or even much) evolutionary change is emergent and not the result of accumulated microscale variation as previous models assume.

Here we suggest that in some cases recent advances in fitness landscape models may provide archaeologists with a powerful tool for examining microscale changes, larger macroscale patterns, and the connections between them (Arnold et al. 2001). Traditional fitness landscapes based on early work in population genetics have been widely employed in archaeological studies as metaphors for cultural change (Bettinger 2009; Kuhn 2006; Prentiss and Lenert 2009; Spencer 2009; Wright 1932). Such landscapes, based on a “rugged” topography similar to the peaks and valleys of a mountain range, have provided archaeologists with a set of unique metaphors such as “hill climbing” and “peak shifting” that allow extrapolation of the interaction between cultural characteristics and the larger processes such as adaptation and group differentiation. Population dynamics on these landscapes are driven by analogues of biological evolutionary processes such as selection and drift with the movement of populations across the space arising from cultural change.

These landscapes have been extremely influential in the past several decades in archaeology, particularly as they have facilitated theory building in macroscale cultural evolution. Most importantly, these landscapes have been used to generate the prediction that evolving populations may become trapped on high fitness peaks and that movement between high fitness cultural strategies likely involves intervening movement through a low-fitness, maladaptive valley. New research, however, shows that many of the assumptions of traditional fitness landscapes may be inaccurate, with some scholars claiming that explanations generated from these landscapes may be misleading (Gavrilets 2004). Specifically, the low-dimensional simplicity (explained in greater detail in Chap. 7, this volume) that makes them appealing as a modeling tool also gives rise to a set of inherent dynamics that may not adequately encapsulate realistic evolutionary processes (Pigliucci and Kaplan 2006). Recent advances in fitness landscape research indicate that highly multidimensional landscapes are likely pervasive in most realistic evolutionary scenarios (although we note that this has yet to be tested in the case of culture). These landscapes reveal alternative topographies and patterns of movement not possible on traditional landscapes, including large neutral pathways between peaks that allow populations traversing the space to move between adaptive strategies without moving through low-fitness valleys (Gavrilets 1997, 2003). This indicates that populations may experience large-scale shifts driven by drift rather by selection, without also experiencing an inherent period of decreased adaptation or group fitness.

These landscapes also highlight the ways in which microscale changes, which are often fitness-neutral, may drive macroscale evolutionary dynamics. For example, the “holey” landscapes of Gavrilets (1997, 2003) demonstrate that speciation and extinction may both occur extremely rapidly, entirely as the result of neutral changes. Huynen et al. (1996) show that evolution on multidimensional landscapes gives rise to punctuated equilibria, where long periods of stasis defined by neutral drift are disrupted by the rapid movement of a population toward a highly optimal area of the landscape space. Complex landscapes may also combine properties of neutrality and ruggedness (Huynen et al. 1996). On such landscapes drifting populations may rapidly “converge” on high fitness areas, ultimately working to spread high fitness variants through the population and enabling for future generations immediate access to the higher fitness area. Other landscape research has described the degree to which neutral and nearly neutral changes may facilitate later adaptive transitions in populations and the ways in which neutral drift may dramatically increase overall population-level variation over long time spans (Van Nimwegen et al. 1997; Vassilev et al. 2000).

While there is a great deal of work to be done in terms of integrating these alternative landscape models into archaeology, the benefits of doing so may be profound. Research using these models in biology has produced results that show the complex integration between shifts in individual genotypes and the dynamics that drive processes such as species divergences and other major macroscale events such as extinction and stasis (Gavrilets 2003). For scholars of cultural change, these landscapes may provide a methodology for extrapolating the microscale changes in artifact types, the mainstay of archaeological data, to major transitions in human prehistory. Many new fitness landscapes emphasize the importance of approximately neutral mutational error, as well as how such errors when combined with population size may drive large-scale evolutionary dynamics (Barnett 1998; Derrida and Peliti 1991). Based on their ability to model evolutionary dynamics across scales, these landscapes may prove useful in resolving ongoing debates surrounding major evolutionary transitions in human prehistory, such as the roles of demography and cultural transmission (Andersson and Read 2016; Henrich 2004a). Laue and Wright (this volume) provide an example of how such a solution might be developed.

Discussion

Cultural macroevolutionary theory clearly offers strong linkages to the wider discussion broadly defined by the extended evolutionary synthesis. Consequently, it significantly expands our ability to develop new understandings of many evolutionary issues in archaeology. Discussions concerning long-lived technologies such as Acheulian hand axes and Levallois technology (e.g., Lycett 2007, 2009) come readily to mind. However, archaeologists have long debated the major cultural transitions in prehistory typically posing simple prime mover or microevolutionary (organismic macroevolutionary and behavioral ecological) explanations. The origins of agriculture are a particularly vivid example wherein as argued by Zeder (2017) advanced evolutionary concepts offer the potential to significantly enhance our understandings. Innovations in cultural macroevolutionary theory tied to the use of advanced fitness landscape models and updated thoughts on the use of nearly neutral models (Laue and Wright, this volume) offer opportunities for us to gain an even greater understanding, for example, better theorizing developments in the Near Eastern Epipaleolithic (Zeder 2009) and the East Asian Upper Paleolithic (Barton et al. 2007). Another important opportunity concerns the effects of migration of human groups into new landscapes and the complex cultural dynamics that unfold under those geographically isolated contexts. Paleo-Inuit and Neo-Inuit expansions across the North American arctic (Prentiss et al. 2015, 2017) are particularly good examples where archaeological understanding could be enhanced by consideration of the effects of plasticity versus selection on tempo and mode of cultural change. Archaeologists will continue to work toward solving the methodological challenges that come with the use of the new theoretical concepts. Phylogenetic modeling will to play a role in this process. Straffon (Chap. 8, this volume) introduces fundamental concepts and contributions of phylogenetic analysis with a focus on cladogenetic procedures and phenetic approaches such as Neighbor-joining and NeighborNet networks that replicate cladogenetic outcomes. Gjefjeld and Jordan (this volume) introduce Bayesian approaches to phylogenetic analysis and provide an illustration of potential insights into cultural evolution as a branching and blending process among Plains Village groups on the Great Plains of North America. Finally, theories of social evolution are strongly enhanced when expanded in light of cultural macroevolutionary theory (Spencer, this volume).

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Chapter 7

Landscape Revolutions for Cultural Evolution: Integrating Advanced Fitness Landscapes into the Study of Cultural Change

Cheyenne L. Laue and Alden H. Wright

Introduction

In 1932 Sewall Wright introduced the idea of the fitness landscape at the Sixth International Congress of Genetics. His landscapes, presented at the conference as a series of drawings, were visual metaphors—tools to help his biologist colleagues conceptualize the mathematics underlying his new theory of evolutionary dynamics in small populations. In their most basic form, Wright's landscapes diagrammed the mutational paths between genotypes and demonstrated the increase in dimensions necessary to depict a complete set of all possible gene combinations in a simple example where a maximum of five genetic variants (allelomorphs) were considered (Fig. 7.1). Wright then proposed reducing this complexity to a simple illustration where the movements of populations driven by drift and selection could be visualized in a two-dimensional geographic space (Figs. 7.2 and 7.3). On these fitness landscapes, the combination of all possible genetic variants represents genotype space along the X and Y axes, while the fitness assessed to each variant genotype represented the height of the landscape on the Z axis. The landscapes depicted were what we refer to today as rugged (following Kauffman and Levin 1987) as fitness differences between genotypes gave rise to highly topographically variable terrain.

Wright's drawings, however, not only staked out this theoretical geography, but they also demonstrated the process of movement along the landscapes as small, subdivided populations interacted through migration and were moved across the landscape by a combination of drift and selection. Selection, Wright proposed, should move populations to the top of fitness peaks and hold them there, even if the landscape contained significantly higher peaks. The evolutionary problem then was one of "peak shifting"—how might populations stuck on a peak move to alternative, often higher peaks without risking extinction traversing the low-lying valleys in between? According to Wright and his now (in)famous shifting balance theory, movement across these rugged landscapes is a dynamic, complex interaction between the evolutionary processes of selection, drift, and migration with small populations evolving and speciating (i.e., diverging) more rapidly than those with larger effective size.

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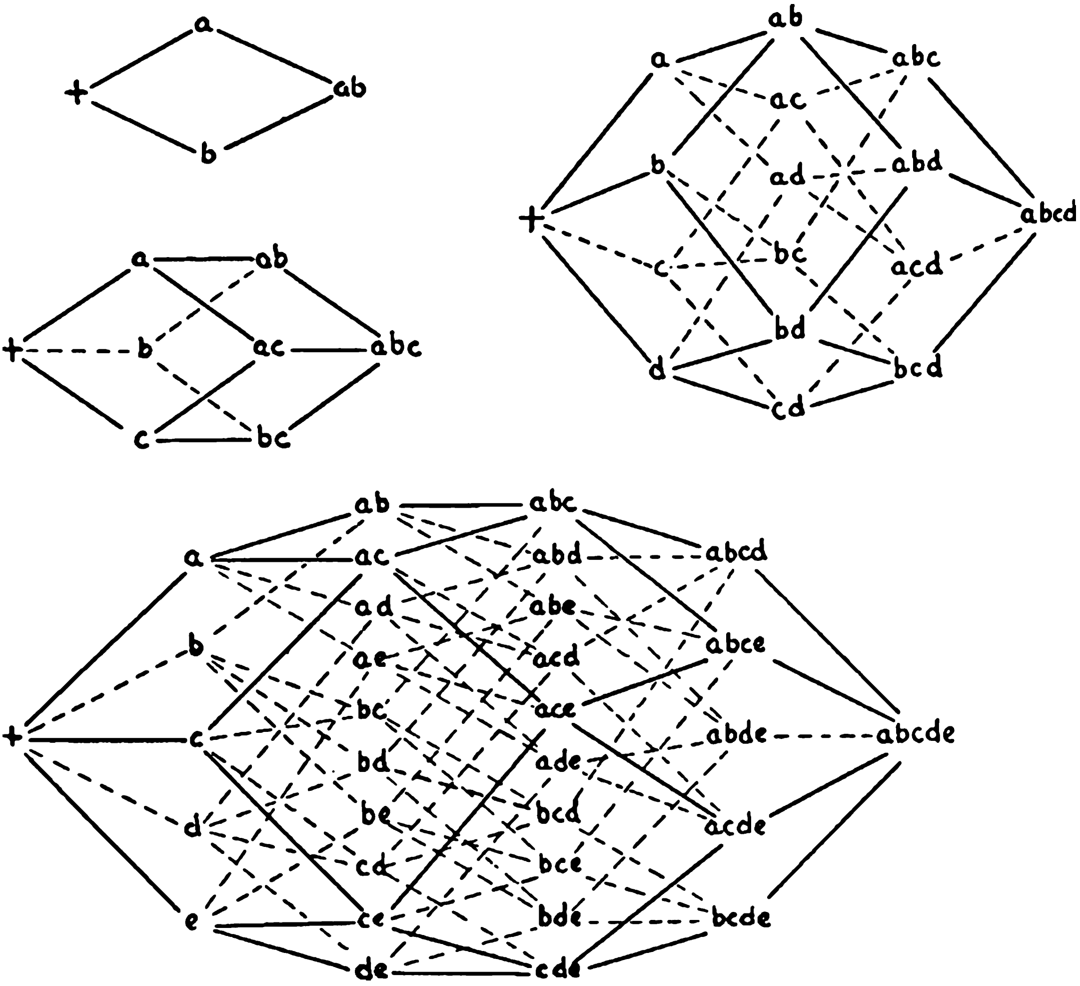

Fig. 7.1 Wright's (1932) depictions of two to five paired allelomorphs

Despite widespread criticism of the theoretical paradigm they were developed to explain, 70 years later Wright's images of evolutionary change have permeated the study of complex systems in disciplines from biology to economics and have held a sustained place in the study of cultural evolution. During this time, fitness landscapes have been used and interpreted in a wide variety of ways; they are variably employed as metaphors and images for illustrating evolutionary processes as well as powerful theoretical models that allow the generation of hypotheses and the subsequent derivation of explanations for evolutionary changes seen in the past.[1] However, as recent critics of fitness landscapes note, models and metaphors are quite methodologically distinct, as are the tools and techniques that help us explain something versus merely describe it. Indeed, some theorists now contend that landscapes as metaphors are the least productive application of landscape theory and in fact landscapes used in this way may mislead us in many situations (see Gavrilets 2004). This

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[1] Much less frequently they represent real data linked to a formal set of mathematics or equations; although with the rise in gene sequencing data, empirical fitness landscapes are becoming increasingly common (De Visser and Krug 2014; Poelwijk et al. 2007).

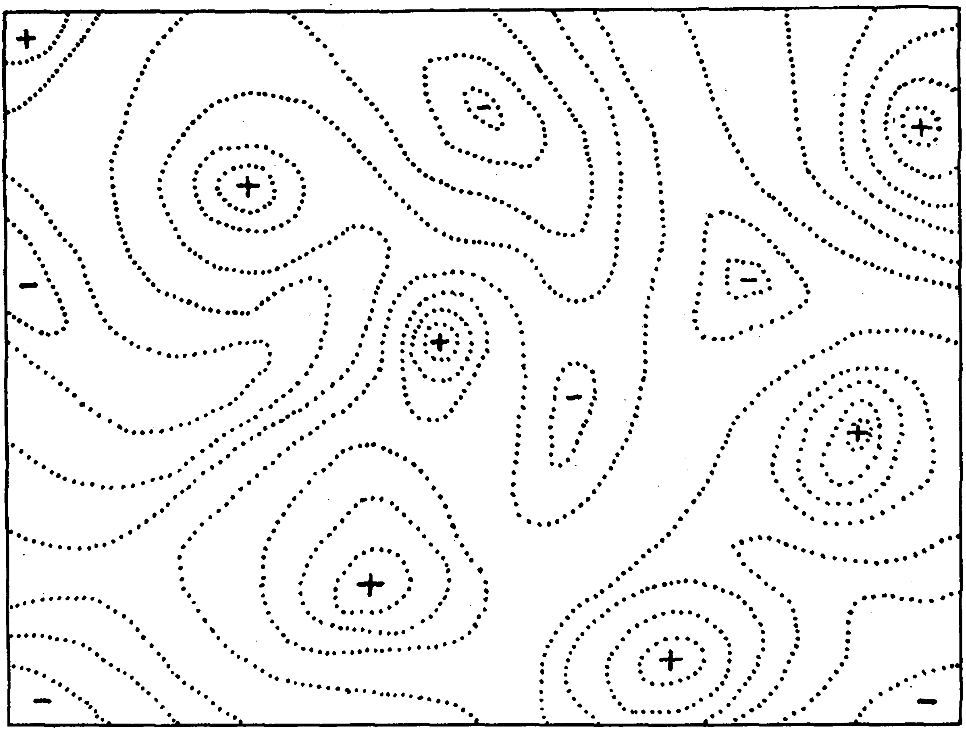

Fig. 7.2 Wright's (1932) diagrammatic representation of the field of gene combinations in two dimensions. Dotted lines represent contours with respect to adaptiveness

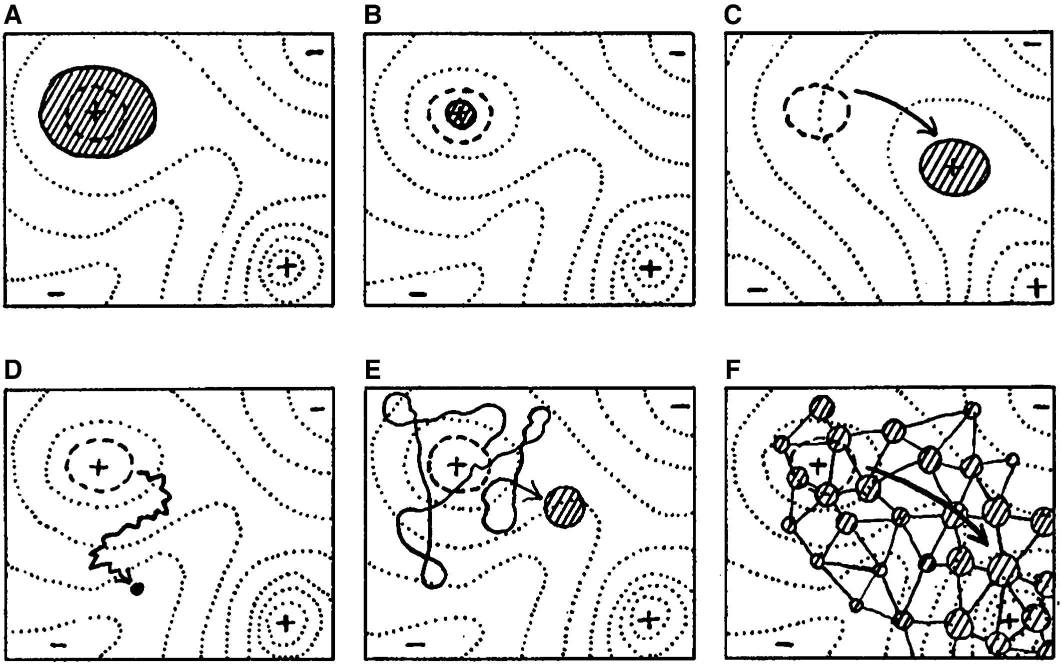

Fig. 7.3 Wright's (1932) diagrams showing gene combinations occupied by a population under various evolutionary scenarios. (**a**) Increased mutation or reduced selection 4NU, 4NS very large. (**b**) Increased selection or reduced mutation 4NU, 4NS very large. (**c**) Quantitative change of environment 4NU, 4NS very large. (**d**) Close inbreeding 4NU, 4NS very small. (**e**) Slight inbreeding 4NU, 4NS medium. (**f**) Division into local races 4 nm medium

is the crux of the recently proposed "landscape revolution," which claims that traditional landscape images are in need of renovation, replacement, or even abandonment (Calcott 2008; Kaplan 2008; Plutynski 2008). According to proponents of this position, inaccurate landscape metaphors often obscure the processes they seek to reveal and in some cases may even create false explanations when researchers "reverse the relationship between imagery and reality . . . projecting the simplicity of [landscapes] onto their predictions of how the real world works" (Pigliucci and Kaplan 2006, p. 178). For those already familiar with the mountainous geography of the landscapes originally drawn by Wright and commonly employed since, this is likely intuitive—a static landscape comprised of permanent, rugged peaks and low-lying valleys depicts certain evolutionary dynamics well and others not at all. Indeed, decades of research since Wright have revealed the existence of fitness landscapes capable of modeling numerous complex evolutionary scenarios including spatial variation (Lewontin 1978), temporal variation (Richter 2014), the evolution of diversity as a response to the underlying complexity of the fitness landscape itself (Niklas 2004), and the role that interactions between traits plays in evolutionary dynamics (Kauffman 1993, 1995; Kauffman and Levin 1987; Kauffman and Weinberger 1989). In particular, recent approaches to studying highly multidimensional landscapes have led to important insights regarding the role of nonselective evolution in the process of adaptation (Gavrilets 1997, 2004).

Here we join the above-cited scholars in proposing that the landscape metaphors commonly used in the study of cultural evolution are in need of renovation. Indeed, a survey of applications of fitness landscapes in the cultural evolutionary literature indicates that many cultural evolutionists still rely on Wright's original images, despite decades of both theoretical and methodological advancement. Here we provide examples of major advances in fitness landscape research and examine some of the potential theoretical implications of those advances for the study of cultural change. Despite the fact that the implications of these advances discussed are theoretical in nature, we hope scholars will see the research presented here as a platform for integrating these advancements into quantitative fitness landscape models of cultural change.

Before turning to examples of major advances in fitness landscape research and examining the potential implications of those advances as metaphors or models for cultural change, we give a brief introduction of some of the fundamental modeling concepts that underlie fitness landscape theory and a survey of the literature applying landscapes to the study of cultural evolution.

Landscape Fundamentals

All landscapes models share three basic properties: a set of configurations, a way of measuring the evolutionary distance between configurations, and a function for determining how adapted configurations are relative to each other. Together these properties give rise to the topographical structure of the landscape as well as the evolutionary dynamics that can occur on the landscape space.

Configurations On landscapes developed to depict biological evolution, the configuration is a set of all possible genotypes or phenotypes evolving in a particular environment,[2] where genotypes are

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[2] Each type of landscape is privy to a unique set of theoretical and methodological issues (for an exhaustive review, see Kaplan 2008). While detailing all of these is outside the purview of this paper, we note that the types of landscapes most often relied upon by cultural evolutionists, phenotypic adaptive and phenotypic fitness landscapes, are no exception. In the case of adaptive landscapes, the assumption is made that mean population fitness can be mapped onto frequencies (rather than distributions) of traits within a population (Kaplan 2008, p. 628), ignoring the fact that major evolutionary movement on landscapes, guided by selection, is dependent on the differential reproductive success of the individuals traversing it. For this reason, adaptive landscapes should be viewed as descriptive, rather than explanatory of the

the genetic structures of individuals and phenotypes are the physical characteristics that interact with the environment. Landscapes may then be either genotypic (where non-fitness axes represent combinations of alleles or loci) or phenotypic (where non-fitness axes represent morphological traits). In either case fitness is mapped directly to the phenotypic or genotypic configurations under consideration allowing a direct representation of their adaptive implications.

Here it is helpful to differentiate between fitness and adaptive landscapes as well, as the two terms are often used interchangeably but refer to very different landscape structures based on the set of underlying configurations. Specifically, fitness landscapes map individual genotypes or phenotypes against a measurement of relative adaptiveness or fitness with populations represented as clouds or clusters of points, and adaptive landscapes map genotypic or phenotypic frequencies against the fitness mean for an entire population, which is then represented as a single point.

Neighborhood, Distance, Nearness Together with the configuration set, the distance metric used to describe the possible relationships between configurations gives rise to the topographical surface of the landscape. Each point in space, as noted above, represents a distinct genotype or phenotype (or the average frequency of either in a population). The accessibility (nearness) of one genotype or phenotype from another is simply the number of mutations necessary for the offspring of individuals to move from the space occupied by their parents to another space on the landscape. Using bit strings comprised of 0’s and 1’s as an example of genotypic alleles or phenotypic traits, it is relatively obvious that it only takes one mutation (one transition of a 0 to a 1) to move an individual from the genotype space 0001 to the genotype space 0011 but two steps to move the same individual to the genotype space 0111. Thus, the individual with genotype 0001 is a “one-step neighbor” to individual 0011 and is closer on the landscape to the individual with genotype 0011 than it is to individual 0111.

Fitness Assignment When the landscape is constructed, each configuration on the space is assigned a numerical fitness value,[3] which demonstrates the degree to which configurations are optimal or adaptive, relative to each other. These fitness assignments give rise to the shape of the landscape, including the presence and height of any peaks, the depth of valleys, and the width of plateaus or other fitness neutral spaces. In the simplest case, all configurations share the same fitness, and the landscape is completely flat and entirely “fitness neutral” as no configuration provides an adaptive advantage or disadvantage over any other. In most cases, however, some configurations are more

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evolutionary process, and scholars of cultural evolution should use appropriate terminology to reflect this. In the case of fitness landscapes, there are often problems of accurate representation, for example, there is an inherent inability to meaningfully situate individual, discrete genotypes along a continuous axis, a problem that has now been widely commented on in the literature (Calcott 2008). There is also the issue of constructing a fitness function that provides a meaningful quantification of adaptive success with often limited knowledge of the genotype and population structure necessary to map genotypes to individual fitness values (in the case of genotypic fitness landscapes) or genotypes to phenotypes to fitness values (in the case of phenotypic fitness landscapes) (Pigliucci 2012; Pigliucci and Kaplan 2006, p. 185).

[3] Fitnesses on non-flat landscapes are assigned in a number of ways, including completely randomly, manually, or based on more complex functions. While an exhaustive account of all of these is impossible here we provide an example of landscape correlation in order to demonstrate the degree to which the process of fitness assignment impacts the topographical structure of the landscape. Uncorrelated fitness landscapes result from the random assignment of fitnesses to configurations on the space. In other words, on an uncorrelated landscape knowing the fitness of one configuration will reveal nothing about the fitness of its one-step neighbors. For example, on the well-studied NK landscape model evolutionary relationships between configurations depend on the interaction between traits (epistasis). The NK model has two parameters, N and K, where N is the number of traits and K is the number of interactions between traits and the K parameter determines the ruggedness of the fitness landscape. The $K = N-1$ landscape is an example of an entirely uncorrelated landscape space that is extremely rugged, with numerous peaks that are low and steep. The $K = 0$ landscape is highly correlated and knowing the fitness of one configuration does provide some information about the fitness of each of its one-step neighbors. On this landscape, the surface is smooth and there is a single, high peak with gradually increasing sides.

or less advantageous, and when this is the case, more complex topography begins to emerge. On low-dimensional landscapes, adaptive peaks and low-fitness valleys develop as a result of fitness differences between configuration, while on highly multidimensional spaces, the landscape (which can best be visualized as a hypercube) is punctuated by networks of fitness neutral configurations (Gavrilets 2003). In all cases, fitness assignments determine both the lowest and highest points on the landscape, including the presence of locally and globally optimal peaks on rugged landscapes, and the width of low-fitness holes in multidimensional spaces.

Evolution on Fitness Landscapes Once fitness values are assigned, they are then used to determine the probability that an individual configuration will be replicated in the next generation. New generations are created as the fitness of existing configurations (the parent generation) are fed to a stochastic selection algorithm that determines the likelihood that they will reproduce based on their fitness relative to other fitnesses in the population. The configurations of the offspring generation are then mutated with a pre-defined probability known as the mutation rate, and this new generation is then established on the landscape space (e.g., a parent configuration 0001 is mutated to 0011, and the offspring "point" is now located on the later configuration).

In natural populations, random drift and selection interact in complex ways to drive large-scale evolutionary patterns. Selection as noted above determines the replication rate of individuals based on their fitness; drift on the other hand is the intervening hand of random chance that allows some individuals to survive and reproduce despite the fact that they are less fit than others in the same population. Along with the shape of the fitness landscape, drift, selection, and mutation determine the patterns of movement that occur on the fitness landscape. In the case of an entirely neutral, flat landscape, drift determines the fate of new mutations; as offspring are produced with mutation, they are sampled entirely randomly for reproduction in the next generation, and the population moves across the space in a "random walk" fashion. As the fitness effects of mutations become increasingly non-neutral, however, the landscape becomes increasingly rugged, and new mutations are more frequently located up or downhill from the population. In this case selection will begin to favor the reproduction of individuals possessing higher-fitness configurations, including offspring with mutations that provide an adaptive advantage relative to existing individuals. Under the pressure of selection, populations will tend to move upward over time as less fit individuals are winnowed, with both the size of the population and the selective advantage of new mutations determining the effectiveness of selection and the rapidity with which populations ascend peaks. Here we note that for populations evolving on rugged landscapes, the process of evolution is likely to slow toward the top of adaptive peaks due to the fact that most new mutations will be downhill (and thus deleterious) relative to configurations already present in the population.

Finally, we note that while the fitness effects of variants may appear to result in a landscape geography that is stable, a great deal of research has demonstrated the inherently fluid nature of landscape space (Lewontin 1978). Topographical shifts on fitness landscapes occur due to environmental changes (Grefenstette 1999; Richter 2009; Wilke et al. 2001) or to coevolution, the process whereby evolving entities deform the landscape topography for other organisms or entities populating it (Kauffman and Johnson 1991). On rugged landscapes, either of these factors might change the locations of peaks as the fitnesses of configurations are adjusted to new conditions. Based on these dynamics, populations that occupied peaks prior to such changes may suddenly find themselves in low-fitness valleys, or vice versa, and the meaning of neutrality may shift as well, with previously neutral configurations becoming either adaptive or maladaptive.

Fitness and Adaptive Landscapes in Cultural Evolution

What do these parameters and dynamics mean for the study of cultural change? To begin it is important to distinguish between ideas of biological and cultural fitness and selection. Biological fitness, as used in fitness landscape theory, indicates the degree to which a physical entity or organism is adapted to its environment and thus is able to survive and reproduce. Fitness in cultural evolutionary research can be used to indicate the degree to which elements of culture or technology impact human survivability and reproduction (e.g., there may be cultural selection for technologies that enhance biological fitness). Cultural selection may also work on the level of artifacts themselves; in other words, a group of people crafting stone tools may select the best examples as templates for future copying, thereby increasing the frequencies of particular characteristics. Finally, cultural selection may act directly on human biology, increasing the frequencies of certain culturally valued biological characteristics in human populations (for a review of these concepts see Shennan 2009). The appropriate usage of selection and fitness in cultural evolutionary studies thus depends greatly on the context. Fitness landscape-based research that is macroevolutionary in nature (see examples below) tends to define fitness and selection in terms of the implications of cultural and technological packages on the survival or persistence of cultural groups. Microevolutionary research, on the other hand, often uses fitness as a way of thinking about the differential reproduction of particular characteristics within a certain artifact or cultural type, with selection acting directly on the objects in question to increase or decrease their frequencies.

Peaks on the landscapes employed in cultural evolutionary theory are variably tied to both cultural strategies—complete packages that enable groups to meet needs of shelter, mobility, and subsistence—and to the adaptive advantages that individual artifacts provide. Indeed, peaks may be thought of as “felicitous evolutionary solutions” (Bettinger 2009, p. 279) to sociocultural problems allowing human groups to better adapt to or survive in their cultural and natural environments (Richerson and Boyd 1992). As noted above, the rugged landscape images composed of peaks and valleys remain critical in cultural applications of fitness landscapes, and the problem of “peak shifting”, as introduced by Wright, is still of enormous importance to cultural evolutionists. Indeed, Wright’s shifting balance theory is still widely employed alongside these images and has been a formative theoretical perspective in the study of cultural diversification and change, particularly that occurring in human prehistory. Peaks and valleys in this context are highly meaningful metaphors for the process of adaptation when population sizes were fragile and when technological failure was potentially catastrophic for small, isolated groups. Microevolution in these depictions can be visualized as movement up and around peaks, as cultural groups fine-tune aspects of their social, economic, or political practices, or refine single technologies to better meet group needs. Peak shifts—movements across valleys of less fit strategies to other more adaptive strategies—represent changes in technology use or shifts in optimal combinations of technologies, skills, and cultural practices. These shifts imply alterations in the interactions between people and the landscapes that they inhabit and have important implications for the larger cultural packages in question, including social and economic organization, technological repertoires, mobility, and resource acquisition (see Prentiss and Lenert 2009 for discussion).

Fitness landscapes in cultural evolutionary theory are predominantly used to explain macroevolutionary processes (but see Mesoudi 2011) and tend to orient around broad themes of cultural divergence and large-scale transitions. In fact, a survey of the literature indicates that landscapes are often employed in explanations of major cultural diversification and that they are particularly useful in describing the pace and potential directionality of such change. For example, Prentiss and Lenert (2009) draw on fitness landscapes in order to explain transitions between socioeconomic strategies in the prehistoric arctic, and both Spencer (2009) and Flannery and Marcus (2000) use landscape theory to think through primary state formation occurring in chiefdoms. While Prentiss and Spencer both utilize the concept of peak shifting to aid in their explanations of the process of these large-scale cultural transitions, Flannery and Marcus draw from Wright's ideas of subpopulation isolation and communication to help explain the tempo of cultural change observed in the case of Olmec Meso-America. Bettinger (2009) similarly uses landscapes to help explain the rapid cultural change experienced by humans during the Holocene, noting that increasingly rapid cultural transmission possibly resulted in the establishment of multiple, local optimal solutions to cultural problems. In this volume, Spencer extends use of the fitness landscape metaphor to explain the transition from autonomous villages to chiefdoms and further notes that peak shifts involve both quantitative and discontinuous qualitative cultural changes. Further, such explanations of rapid transition are often extended to the potential directionality of cultural evolution. For example, Bettinger (2015) used landscapes to theorize the persistence and intensification of hunter-gatherer strategies in the precontact Great Basin, Kuhn (2006) to describe the trajectory of Middle Paleolithic technological evolution, and Lombard and Parsons (2011) to explain the disruption of bow-and-arrow usage in Upper Paleolithic Africa.

However, fitness landscapes are not only used to theorize obvious or rapid cultural evolution but to explain periods of stasis and the ways in which such times of little or no change integrate with larger evolutionary dynamics revealed over long time spans. Prentiss and Lenert (2009) discuss the idea that evolutionary stasis can be extrapolated from the archaeological record and interpret the transition from Pre-Dorset forager strategies to Dorset collecting in the Canadian Arctic in terms of Wright's shifting balance theory. Chatters (2009) similarly notes evidence for long periods of stasis in the archaeological record and suggests that cultural continuity often emerges as a strategy for remaining on top of local adaptive peaks. Both Chatters (2009) and Bettinger (2015) look at the often punctuated nature of cultural stasis—what Bettinger describes as periods of "change-stasis-change"—and the authors provide explanations of these periods in the context of demography and isolation and cultural transmission, respectively.

Finally, fitness landscapes are sometimes employed in order to depict the adaptive value that a particular technology provides a cultural group. For example, Lansing and Kremer (1993) use landscapes to examine the complex systems composed of water temples, agricultural production, and religious activity in rural Bali and propose that water temples represent adaptive solutions to the problem of managing irrigation for rural Balinese farmers. Similarly Mesoudi and O'Brien (2008a, b) and Mesoudi (2011) constructed fitness landscapes for the simulated innovation of projectile points and examined the role that underlying fitness functions played in the innovation of new technological forms. Marwick (2013) uses a landscape containing multiple optima to help explain shifts in stone tool technology based on ecological conditions and resource proximity. While such microevolutionary models are rare, they provide valuable insight into the differences between fitness and adaptive landscapes, as they are employed in the context of cultural evolution.

Neutral Networks and Landscape Exploration

In most cases, fitness landscapes are assumed to represent the complete set of all possible configurations possible in a particular evolutionary scenario. Depending on the number of traits and variants of those traits that must be represented to achieve this, the number of configurations on realistic landscapes can be extremely large and with increases in the number of configurations comes an increase in the number of dimensions required to accurately represent them. In the context of a configuration space that is sequence-based, as described in the section on configurations above, dimensionality can be defined as the length of the sequences present on the landscape. Despite the absence of a multidimensional representation in his original images, the highly multidimensional nature of realistic fitness landscapes did not escape Wright. Indeed, he believed that the comprehensibility of his landscape metaphor depended on "some enormous simplification" (Wright 1988,

p. 117) most notably the reduction of the multidimensional configuration space he determined to be a realistic representation of the genotype he was modeling to the three dimensions of his classic rugged configuration space. However, although Wright noted that his models were simplifications, he incorrectly assumed that the reduction in dimensionality would not impact the dynamics he described (Pigliucci and Kaplan 2006). This turns out not to be the case, and research continues to demonstrate that the dynamics of evolution in high dimensions are often fundamentally different from those occurring in low-dimensional spaces (Gavrilets 1997; Pigliucci 2012).

While there are numerous evolutionary implications of increasing the number of dimensions on a fitness landscape, here we highlight the emergence of configurations with identical functions and fitness, a property called redundancy (Vassilev et al. 2000). Redundancy results naturally from the process of mapping configurations to fitness values when there are large numbers of configurations present on the landscape. This is due to the fact that there are a limited number of fitness values that are both realistic and that result in discernable differences in configuration function, while there may be significantly more configurations that those fitness values must be mapped to (Gavrilets 1999). The result of this is that multiple configurations are assigned identical (or practically identical) fitness values with the level of redundancy increasing along with the number of configurations added and, quite intuitively therefore, along with increases in the dimensionality of the landscape. Redundancy results in neutrality due to the presence of configurations with the same fitness effect. In other words as redundancy increases, there are an increasing number of evolutionary movements that evolving organisms can take that do not result in significant changes to their fitness. This implies potentially large regions of the landscape where evolutionary movements do not result in fitness changes (Derrida and Peliti 1991) due to the fact that one-step neighbors have equal fitness and similar functions or phenotypes, despite differences in their underlying configuration. This is consistent with the neutral theory of evolution (Freese and Yoshida 1965; Kimura 1968), which states that most genetic diversity level is the result of neutral mutations that produce no effect on the fitness of the organisms in which they occur. Based on this, the neutral theory predicts that most genotypic evolutionary change should be the result of genetic drift, rather than selection (Hughes 2007).

Recent work using theoretical fitness landscapes demonstrates the importance of neutrality in producing long-term macroevolutionary patterns. In order to illustrate the impact of neutrality on evolutionary dynamics, Gavrilets (1997, 2004) (see also Gravner et al. 2007) uses a simplified landscape of two fitnesses, viable and inviable, and assigns these fitnesses randomly to configurations on the space. Gavrilets shows that there is a critical threshold (i.e., the percolation threshold) above which the emergence of a large network of viable configurations (i.e., a giant component) is extremely probable. Percolation specifically describes the probability that there is a connected path across a space of interest (typically a graph or fitness landscape), while a giant component in the context of fitness landscapes is mathematically defined in relation to the size of other connected components. Gavrilets shows that this is complexly related to both the probability of viability for each configuration and to the dimensionality of landscape; assuming a branching process defined by a Poisson distribution, Gavrilets shows that for a Poisson mean greater than 1, the probability of a giant component scales inversely with the number of dimensions. This means that as dimensionality increases, lower probabilities of viability for each configuration will result in the percolation of a giant component across the landscape. In other words, when these conditions are met, increasing the dimensions of a landscape nearly assures the emergence of large networks of configurations with identical fitnesses (i.e., they are all viable and the path connecting them is entirely neutral). Critically, when giant components are present on the landscape, a random (neutral) walk beginning at any viable point is highly likely to lead evolving entities across the entire landscape space. According to Gavrilets, this indicates that populations are extremely likely to traverse the entire landscape via neutral networks, rendering the classic problem of peak shifting largely obsolete.

Both biological and artificial evolution models have largely supported Gavrilets conclusions regarding the pervasiveness of neutral networks on realistic fitness landscapes and the degree to which populations may undergo large evolutionary changes through neutral one-step mutations. Schuster et al. (1994) found that RNA sequence space contains extensive neutral networks and noted that finding novel configurations from neutral mutation and small amounts of selection should be relatively common. Building from this, Huynen et al. (1996) described the prevalence of neutral networks and the "high diversity phenotypic neighborhoods" that lay along them. He noted that the implication of neutral networks is "perpetual innovation" (Huynen et al. 1996, p. 166), whereby organisms evolving through neutral mutation are incredibly likely to be constantly evolving novel, high-fitness configurations through neutral mutation with an innovation rate that is defined by the number of novel configurations that are accessible with each new mutation. Similarly, Andreas Wagner (2011) recently showed the existence of vast neutral networks of genotype configuration corresponding to the same phenotype in biological metabolic and regulatory networks. Wagner confirmed that these networks contained connected components that tended to percolate through genotype space, making them spatially proximate to most other genotypes on the landscape. He demonstrated the neutral property of these landscapes via random walks and found that these walks typically traverse configurations that are very far from their point of origin.

The implications of this research for theorizing evolutionary change are profound. First, these results highlight that in complex evolutionary scenarios, the number of configurations and thus the number of dimensions on the landscape is likely to be quite large. As shown above, increasing dimensionality is very likely to result in an increase in the number of neutral changes that are possible when evolving entities move across the landscape space. Archaeologists using fitness landscapes as aids for the study of cultural change should thus be aware that the complexity of the evolutionary scenario being described (e.g., all possible characteristics of a Clovis point vs. those of a digging stick), including any interactions between the configurations present on the landscape, should help the careful theorist construct the appropriate model or metaphor. Second, cultural evolutionists should be aware that a great deal of cultural change (particularly in more complex evolutionary scenarios) may occur entirely outside of the influence of selection. This indicates that explanations of major shifts in patterns of artifact use or manufacture seen in the archaeological record need not always be explained by mechanisms of culturally biased selection. Indeed, the property of perpetual innovation describes how large quantities of cultural diversity may manifest solely from the accumulation of minor, fitness neutral changes, particularly over long periods of time.

Neutrality, Stasis, Potentiation

While the fitness landscape research described above illustrates how neutral evolution may lead to rapid exploration of the fitness landscape, often resulting in the acquisition of novel configurations, one of the most compelling insights of recent advances in landscape research is the idea that phases of neutral evolution are potentiating of later periods of adaptive change. Such periods of neutral drift on fitness landscapes are often referred to as "metastable episodes" and may appear largely static as populations move across large portions of the landscape space without accruing visible changes in fitness or phenotype (Adami 1995; Barnett 1998; Elena et al. 1996; Fontana and Schuster 1998; Newman and Engelhardt 1998; Van Nimwegen et al. 1997). Some scholars claim that such metastable periods are generic on evolutionary landscapes, particularly those containing neutral networks (Barnett 1998). Even though these long, apparently stable phases may visually seem to lack change, however, they are actually highly productive periods of time (Vassilev et al. 2000, p. 255) that often have surprising evolutionary outcomes.

The fact that most variants fixed during drift have been shown to be very slightly deleterious, rather than entirely neutral (Ohta 1992), suggests that periods of stasis should be brief as they may be expected to result in the inevitable degradation of mean group fitness (Lande 1994). However,

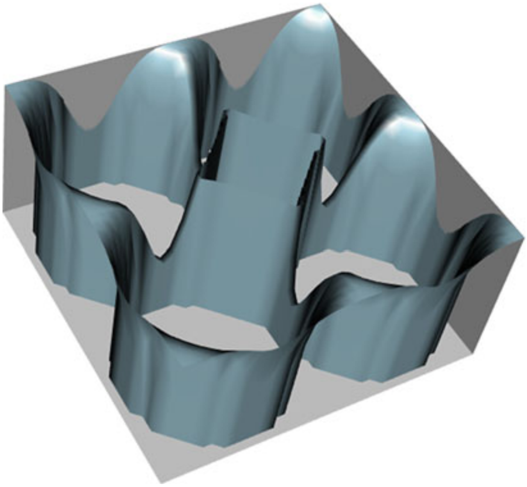

Fig. 7.4 A holey adaptive landscape formed by genotypes within a narrow fitness band. Evolution along a holey landscape is nearly neutral

recent research has resulted in the discovery of an entire class of weakly beneficial mutations and the corresponding idea that the degrading effects of drift are often corrected for across long time spans (Stephan 1996). These results suggest that populations may drift for very long periods of time without suffering severe fitness losses as novel, higher-fitness configurations are discovered accidentally or through two critical processes—potentiation and compensation. According to Lynch and Walsh (2007, p. 70), the accumulation of slightly deleterious variants during drift, while immediately detrimental to population fitness, can ultimately "provide a potential setting for secondary adaptive changes," and Huynen et al. (1996) found that evolution on fitness landscapes was often best described by punctuated equilibria, with long periods of stasis corresponding to neutral drift followed by significant fitness increases resulting from the discovery of beneficial mutations (see also Elena et al. (1996)). Research in experimental biology has since validated this claim through the discovery of neutral and slightly deleterious mutations whose interactions with the organisms in question are "potentiating" of future beneficial mutations (Blount et al. 2012). Further, research has also revealed how long periods of neutral drift may increase the probability of mutations with beneficial effects, a process known as "compensatory evolution" (Hartl and Taubes 1996; Stephan 1996). Phases of stasis, defined by neutral drift, may thus be both prolonged and common and extremely important to large-scale evolutionary patterns and outcomes that emerge only over long periods of time (Barnett 1998).

One such outcome of neutral and nearly neutral evolution, according to Gavrilets (1997, 2010), is the process of population divergence or speciation. Again, Gavrilets demonstrates how the discovery of novel phenotypes through neutral evolution may occur as populations drift along interconnected neutral networks of "viable" configurations, which are punctuated randomly by inviable, low-fitness "holes" (Fig. 7.4). A population that evolves into an inviable hole faces impending extinction, according to Gavrilets, while populations that move to the other side of a hole vis a vis their original position have split from the lineage defining their parent population and have become a distinct species. Gavrilets (1997, p. 309) demonstrates that not only *can* such divergences occur via the accumulation of small neutral mutations but that if a population can avoid extinction long enough, speciation is "an inevitable consequence" of evolution on high-dimensional holey landscapes as populations traverse large portions of the fitness landscape.

While Gavrilets simplified landscapes reveal critical properties and outcome of stasis and neutral drift, other evolutionary landscapes help us visualize how selection and drift might interact in some circumstances. Huynen et al. (1996) note that in some cases, landscapes demonstrate the property of "neutrality within ruggedness," exhibiting spaces that are defined by both peaks and valleys and pervasive neutral networks. Figure 7.5 depicts the relationship between a rugged landscape and neutral

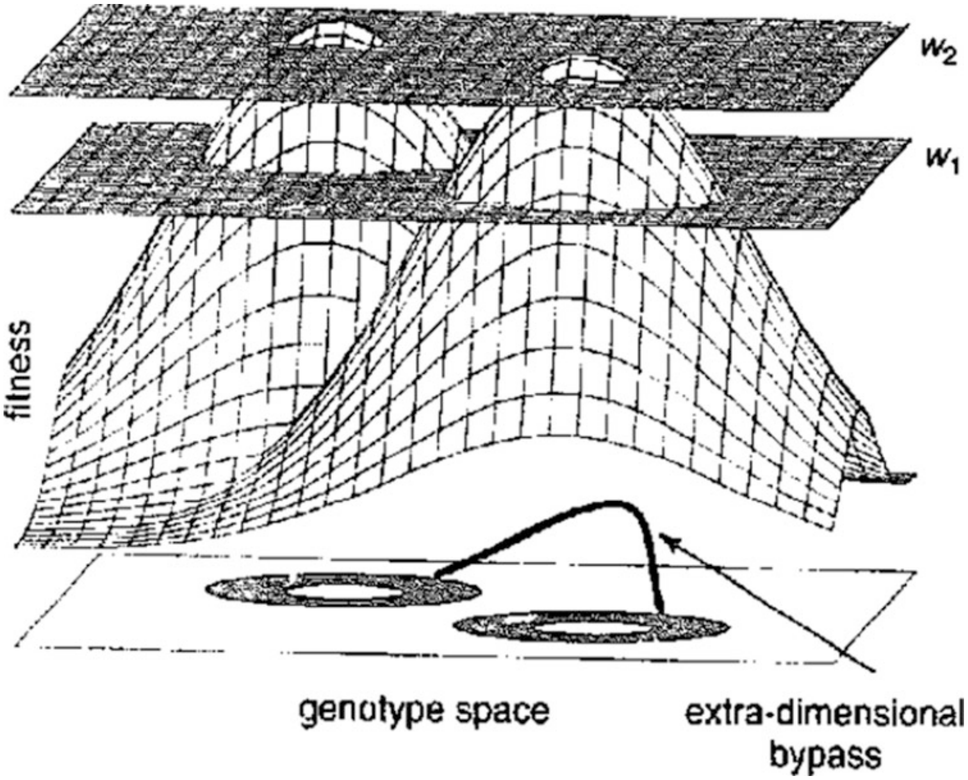

Fig. 7.5 The relationship between a rugged adaptive landscape and a holey adaptive landscape (Gavrilets 1997, p. 311)

plateaus, as one example of how different evolutionary dynamics may be represented on a single space. On the landscapes described by Huynen et al., contact regions between networks of higher and lower fitness may occur, enabling populations to transition to networks of higher fitness at these points of contact or "convergence." When convergence on a contact region between the occupied network and one of higher fitness occurs, Huynen et al. show that selection acts rapidly to "amplify" members of the population around the point of contact, facilitating the fixation of the variant and thereby allowing the next generation of the entire meta-population to access the network of higher-fitness mutations. According to Huynen et al., on a reasonable time scale, there is no limit to the number of configurations that can be accessed via the neutral network indicating that prolonged neutral evolution can result in the evolution of any possible adaptive change.

Similarly, Derrida and Peliti (1991) show that the combined effects of mutation and previous selection events may fracture populations into small subgroups that share a recent common ancestor on the neutral space of the fitness landscape. These subdivided groups continue to undergo the process of drift, compensatory evolution, and subdivision, spreading out along a single neutral network until, by chance, a highly beneficial mutation enters the population. These beneficial mutations, under the right demographic conditions, provide the opportunity for the entire population to transition to a new neutral network of higher fitness than the one currently occupied (Barnett 1998). Van Nimwegen et al. (1999) also demonstrate how the presence of highly interconnected regions of the space where networks of different fitness levels connect facilitates transitions between networks of higher and lower fitness (Fig. 7.6). Large populations, according to the authors, are more likely to converge on these highly interconnected areas than they are to move stochastically across the space due to the fact

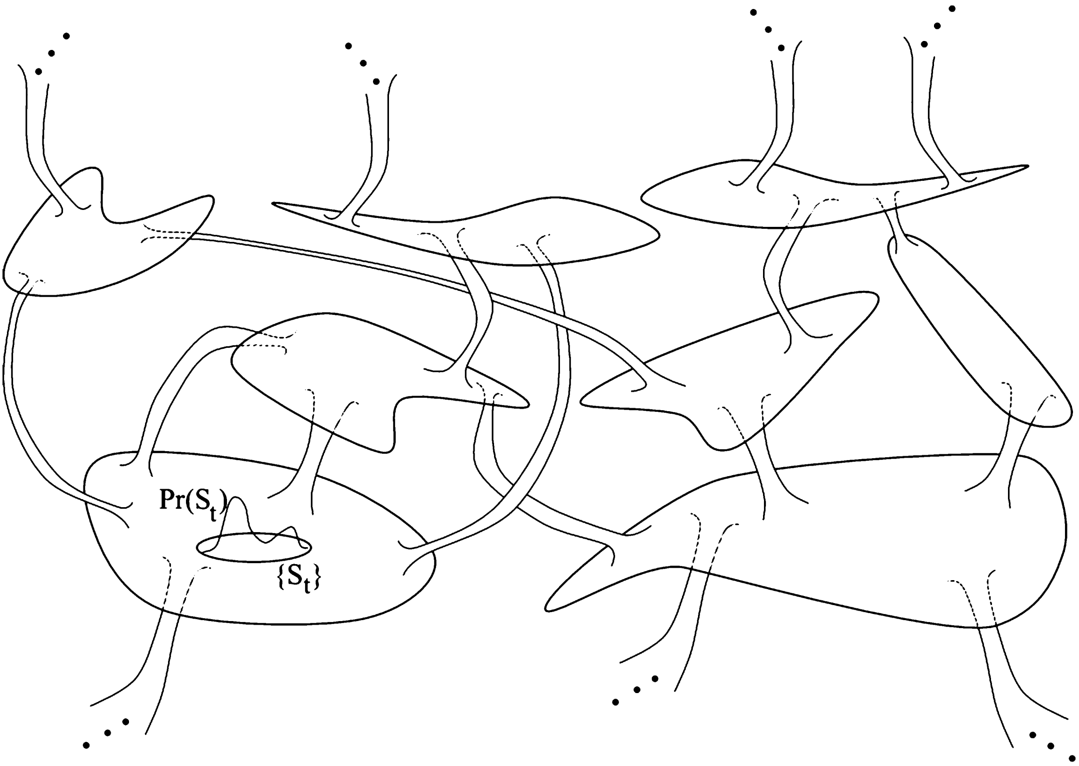

Fig. 7.6 Subbasin and portal architecture underlying macroevolutionary dynamics. A population diffuses in subbasins (large sets) until a portal (tube) to a higher-fitness subbasin is found (from Crutchfield and van Nimwegen 2002, p. 5)

that selection, rather than drift, dominates their evolutionary dynamics, while small populations may encounter, or miss, these contact regions as the result of chance.

Finally, we highlight that despite the emphasis placed on selection in traditional evolutionary theory, landscape-based research continues to reveal the limitations of selection in complex evolutionary scenarios and suggests that we must look beyond this one factor in robust explanations of cultural change. Kauffman and Levin (1987) extensively modeled the interactions between complexity and selection in artificial environments and found that selection is often inefficient at increasing mean population fitness and that it is largely incapable of maintaining populations on adaptive peaks when those peaks are connected by a series of one-step mutations (see Pigliucci and Kaplan (2006) for discussion) indicating that neutral drift, rather than selection, may be the evolutionary "default." Indeed, some theorists contend that populations located next to landscape peaks are highly unlikely to climb at all (Moran 2007; see Plutynski 2008 for discussion) and that, even in cases when they do, the probability of Wrightian style peak shifting is still incredibly small (Gavrilets 2004). Moreover, many of these theorists claim that small populations are far more likely to go extinct than they are to cross a valley and climb a new peak (Coyne and Orr 2004; Gavrilets 2004). Strathmann (1978) linked the probability of a successful climb to the level of evolutionary complexity attained by the organism involved; generalist (less complex) species he thought would be more likely to evolve toward unoccupied peaks than specialists, who would be unable to attain the rapid, adaptive diversification necessary to do so. Other research has shown that in some situations, selection actually leads to a "survival of the flattest" rather than a survival of the fittest effect, where the most mutationally robust, rather than the fittest, variants within a population are retained for future generations (Wilke et al. 2001; Zaman et al. 2012).

These results indicate not only that selection is often surprisingly ineffective at producing uphill, progressive evolutionary change but that traditional ideas regarding the predictability of selection-driven population movement on landscapes are likely inaccurate in most situations. Research on pNK landscapes, which combine neutral and non-neutral spaces, shows that under certain circumstances "reluctant" adaptive walks (movement to a neighboring square with the least fitness gain of all available beneficial moves) and random adaptive walks (movement to the next randomly chosen square), while often immediately *less optimal*, produce long-term payoffs that are often greater than those provided by "greedy" adaptive walks (movement to the neighboring square with the largest fitness gain) (Nowak and Krug 2015; Valente 2014). This indicates precisely the opposite of what we might expect—that organisms that move slowly and risk making less-optimal short-term decisions may actually fare evolutionarily better in the long term, perhaps because their long, slow walks allow exploration of larger portions of the landscape space, thereby opening up access to previously unavailable peaks.

Conclusion: Applying Landscape Revolutions to Cultural Change

What are the implications of all of these new fitness landscapes for the study of cultural change? To begin, we assert that ongoing landscape-based research has fundamentally called into question the pervasiveness of the most commonly used fitness landscape model in evolutionary anthropology—the landscape of peaks and valleys first proposed by Wright. Based on this we must also begin to question the peak-shifting "problem" as the quintessential evolutionary conundrum that cultural evolutionists attempt to solve and to imagine many scenarios in which cultural change cannot be placed on a landscape defined by a rugged topography. Indeed, while explaining evolution via hill climbing and peak shifting holds particular appeal in cultural evolutionary theory, as selection is deemed critical in sculpting major adaptive changes, new landscape research demonstrates the power of neutral evolution to bring about these beneficial shifts as well.

Here we note that the neutral theory has been an important component of research on cultural evolution for more than two decades. However, following from early controversies on stylistic vs. functional cultural traits (Dunnell 1980), the majority of the work on cultural change has continued to highlight the roles of biological and cultural selection in increasing the frequencies of adaptive cultural variants and influencing macroscale patterns in the human social groups. Indeed, the neutral theory has been employed entirely as a null model, and most cultural evolutionists still tend to see selection as the defining force in the production of adaptive cultural forms (Bentley 2008; Bentley et al. 2004, 2007; Lycett 2008; Shennan 2001; Steele et al. 2010).

While fitness landscape modeling has not been a part of all of this research, the metaphor of evolutionary ruggedness has certainly permeated disciplinary expectations. If we return to Gavrilets claim that inappropriate landscape metaphors are capable of misleading us into envisioning the process of evolution in incorrect ways, we begin to see how incorporating fitness landscapes that contain neutral spaces into our landscape toolkit can greatly expand the expectations that we are able to generate and the conclusions that we are capable of drawing from our cultural data. For example, the presence of large connected neutral networks and neutral ridges between peaks provides evolving populations with evolutionary paths not available on the rugged topographies typically imagined. In the context of cultural change, peak shifting and hill climbing cease to be the sole paths to novel, adaptive cultural innovations as cultural groups may feasibly move between peaks solely through the accumulation of neutral variants and the process of random drift. The property of perpetual innovation, now documented in a great deal of landscape research, demonstrates that through the continual discovery of new and often higher-fitness configurations neutral evolution may have critical implications for large-scale patterns of change.

How might we expect this to happen in cultural populations? The process of mutation in cultural models is analogous to that of random innovations (Neiman 1995) or small errors introduced during the processes of manufacture or the cultural transmission of knowledge and skills (Eerkens and Lipo 2005). Because these changes are not purposeful, their effects on the technologies or cultural forms in question are modeled as being entirely random, with the neutral hypothesis stating that many or most of these changes should have little or no effect on the functionality or desirability of the objects or practices in which they occur. This situation seems entirely plausible as individuals make and use technologies in different ways and transmit information regarding cultural knowledge, skills, customs, and beliefs that is subject to small often unnoticeable errors (Cavalli-Sforza and Feldman 1981). Rather than disregarding these theoretically neutral differences as trivial, however, the landscape theory discussed above asks us to consider how such small changes might accumulate in populations over time to drive larger patterns of stasis and change. Based on this we might consider the implications of placing small cultural populations on a landscape of large interconnected neutral networks that allow rapid transitions between dimensions, rather than envisioning their evolution on traditional rugged landscapes. On such a landscape, each small, neutral technological change represents the shift of individuals or populations (depending on the type of landscape) to an alternate space on the landscape with no loss or gain in fitness.

Given that small populations are likely to encounter points of contact with higher-fitness networks only by chance during the process of drift (Huynen et al. 1996), it is easy to envision extended periods of cultural stasis during which a single technological variant dominates and variation emerges only because of the types of errors in perception, skill, or memory noted above. While Gavrilets notes that speciation (what in cultural terms we might envision as ethnogenesis or major cultural diversification) is inevitable if evolving populations drift across the landscape for sufficient periods of time, he also notes that the space on the landscape between extinction and divergence is very slight (often as small as one mutational error). Thus, it is only through chance that small populations go extinct, or persist and diversify, and on landscapes defined by neutral networks, either of these outcomes can be determined through very small, randomly introduced errors alone.

Here we note that the extinction of small human groups in the past must certainly have been the norm, and recent research has shown that cultural fidelity (which would work to reduce error) has major implications for the retention of adaptive technologies and the survival of the groups relying on them (Andersson 2013; Andersson and Törnberg 2016). Poor fidelity in these small populations would have certainly resulted in the accumulation of tiny errors in cultural information and the technologies such information encoded, potentially causing the deterioration of cultural and technological fitness over time. Indeed, the loss of beneficial technologies in small prehistoric populations and the resulting population fragility that ensues have been documented in multiple instances (Henrich 2004; Lombard and Parsons 2011; Prentiss et al. 2015). However, in the event that the same small groups were fortunate enough to survive long enough, they would inevitably have been the beneficiaries of lucky technological moments as well—an encounter with another group possessing a better version of a currently used technology or an individual within the group creating an adaptive modification in order to solve a cultural problem, both of which would have provided “compensatory” sources of change. As noted above, such compensatory evolution corrects for the degradation of fitness experienced by populations over prolonged periods.

Although rare, some of these lucky moments certainly resulted in the creation of entirely novel, highly adaptive technologies as well. In these situations, the coalescence of many small random events would bring a population to a “point of contact” between the network they currently occupied and one that allowed access to a higher-fitness dimension on the landscape. These cultural or technological innovations might then have spread rapidly between subdivided populations (again, there is evidence for the rapid transmission of highly adaptive technologies among closely related prehistoric populations (Boyd et al. 2011; Smith 2001)), and selection would act to "amplify" communicating populations to the same point of network contact, effectively transitioning them all to the new landscape dimension and future evolution on the same new neutral network. It is possible that these innovations might have dramatically altered the resource management strategies (Prentiss and Lenert 2009) of the groups in question, shifting entire cultural and technological packages as a result. In this case, we can envision these evolutionary moments in light of Gavrilets speciation theory and see how prolonged periods of stasis, driven only by neutral drift, might cause entire populations to rapidly acquire novel technologies and to shift entire cultural strategies as a result.

There are numerous examples from the cultural evolutionary literature documenting not only the presence of punctuated equilibria in cultural evolution (Barton et al. 2007; Prentiss and Lenert 2009) but also the degree to which prolonged periods of stasis often had unpredictable outcomes, including extinction or cultural stagnation, cultural diversification, and the rapid innovation, adoption, and spread of novel and highly adaptive new technologies (Henrich 2004; Prentiss and Chatters 2003). For example, the case of agricultural origins in the Near East shows how the accumulation of small-scale changes over a long period of time may work to bring about major evolutionary transitions. In this case, the Epipaleolithic has been shown to be a period of small but varied cultural innovations that when viewed from a certain temporal perspective appears largely random. However, these small innovative changes eventually came together to facilitate the advent and spread of agriculture during the Holocene, an obviously profound shift in the entire cultural strategies of the groups that adopted an agricultural lifestyle (Zeder 2009a, b). Similarly, the transition between the Middle and Upper Paleolithic provides compelling evidence for the degree to which periods of stasis, rather than being stagnant, are often highly productive periods of time that are potentiating later episodes of rapid, innovative change (Hovers and Belfer-Cohen 2006). In this case, the prolonged use of major tool traditions during the extensive periods of both the Lower and Middle Paleolithic results in the rapid explosion of technological and cultural change that characterizes the beginning of behavioral modernity seen in the archaeological record around 50 KYA (Ambrose 2001; Petraglia et al. 2003). In both of these cases, the application of neutral fitness landscape theory provides a way of envisioning how this might occur and challenges our prevailing assumptions regarding the nature of cultural stasis as unproductive and stagnant.

The landscapes introduced above also question the straightforward relationship between human behavior, selection, and evolutionary progress that remains, despite our best efforts, a pervasive part of the narrative on human cultural and technological change. These "myths of innovation" (Watts and Gilbert 2014) and the models that have followed from them (Broughton and Cannon 2010; Henrich and Gil-White 2001; Kennett and Winterhalder 2006) posit human beings as hyper-rational, fundamentally creative and innovative, or inherently optimizing beings. While these models are typically purposeful simplifications of complex socio-natural situations, the idea of humans as rational optimizers has had an obvious impact on cultural evolutionary theory as we tend to view cultural strategies or technological packages as potentially optimal solutions to adaptive problems (Bettinger 2015; Boyd and Richerson 1985; Boyd and Richerson 1987; Boyd and Richerson 1995; Smith and Winterhalder 1992). In cases where theorists note that specific instances of human behavior may be sub-optimal, the conclusion is often drawn that such behaviors are selectively retained due to their interaction with other fitness-enhancing processes, such as social learning (Richerson and Boyd 1992). Further, the application of traditional rugged landscape imagery to such scenarios provides us with a vision of hill-climbing cultural groups that are able to see the contours of the adaptive landscape they are traversing and to use their unique human knowledge of adaptive peaks and valleys to hone future adaptive moves, thereby guiding the process of evolution in a beneficial direction (see Bettinger 2015 and Mesoudi 2008 for opposing perspectives on the role of foresight in evolution).

Indeed, research on the evolution of artificial populations has largely shown that our expectations of population optimization on rugged landscapes are likely entirely misguided, as the height and length of adaptive walks are complexly related to the interaction between the landscape properties and the characteristics of the organisms populating it (Nowak and Krug 2015). More simply, on rugged fitness landscapes, where the traits in question interact (a realistic assumption for the evolution of cultural and technological package with multiple integrated traits or components), the evolution of populations is constrained by the very complexity of those interactions, with highly interactive landscapes tending to permanently trap populations on sub-optimal fitness peaks (Valente 2014). Research on niche construction (see Riede this volume) further indicates the inherently complex interactions that underlie the process of adaptation, and work by Caiado et al. (2016) highlights the degree to which social processes may fundamentally change the shape of the landscape. Even more realistically, according to Gavrilets (2003), rugged landscapes provide us no accurate information about the process of macroevolution at all, including the major innovations or cultural diversifications typically described using peaks shifts. Rather they are solely a way of reasoning through the process of microevolution, and based on this they might give us a great deal of insight into the process of refinement within a single trait or technology, but nothing else. Given the increasing momentum in cultural evolutionary research to integrate understandings of micro- and macroevolutionary processes (Walsh et al. Chap. 2 and Prentiss Chap. 1, both this volume), a theory of fitness landscapes that allows us to do so should be particularly appealing.

New landscape imagery provides examples of evolution that are random and drift dominated yet highly productive, with populations that take long, slow, non-optimal evolutionary paths often experiencing the most productive high-fitness outcomes. This is a particularly timely discussion in light of increasing archaeological evidence for the nondirectional nature of cultural evolution in some contexts. For example, there is now consensus for the abandonment of bow-and-arrow technology at Howiesons Poort (Lombard and Parsons 2011) and for the abandonment of agriculture in many portions of precontact North America (Bettinger 2015). There is also growing acknowledgment for the lack of Mousterian “progress” toward Upper Paleolithic complexes (Kuhn 2006) as well as evidence that the transition from Middle to Upper Stone Age complexes in Africa did not follow a liner, progressive path. Similarly, Arctic Small Tool tradition of the North American Arctic provides an example of nonprogressive losses and gains in Pre-Dorset tool types (ca. 4000–2500 cal. B.P.) that do not in any way predict the comparatively rapid evolution of Dorset socioeconomic strategies and toolkits at later points in time (Prentiss et al. 2015).

Indeed, the ideas that cultural evolution is sometimes nonprogressive and that immediate non-optimal decisions are incapable of predicting later evolutionary developments have been growing among evolutionary anthropologists (Ambrose 1998; Brown et al. 2012; Lombard 2012; McBrearty and Brooks 2000; Tryon and Faith 2013). Likewise is the notion that evolutionary dynamics such as mutation (e.g., innovation and error), drift, selection, and population size are complexly intertwined and thus not easy to either measure or directly predict. Further, while a great deal of evolutionary work on culture does highlight culturally selective biases, many researchers acknowledge that the interaction between neutrality and selection is most likely complex and that both neutral drift and selection may potentially play important roles in cultural evolution (Bentley 2008; Bentley et al. 2004; Brantingham and Perreault 2010). Cultural evolutionary research is thus poised to consider many of the critical topics currently advanced by fitness landscape theory, and the inclusion of these alternative landscape dynamics and topographies could serve as useful tools and visual aids for this purpose. Further, while the implications described in this paper are at this point largely theoretical in nature and involve the use of advanced fitness landscapes as metaphors or visualizations for thinking through complex evolutionary scenarios, we hope this paper provides a catalyst for quantitative applications as well. In particular, we see the integration of neutral and nearly neutral spaces on the fitness landscapes used to model cultural microevolution as an especially reasonable addition to the existing literature. Such spaces would allow integration of neutral (or nearly neutral) microscale changes seen in archaeological contexts, providing the researcher with the ability to explain both periods of stasis within tool technologies or traditions and long-term selective trends. Research using the plethora of data surrounding the Acheulean tool industry might prove particularly useful for such a project as existing models include nuanced discussions of neutrality, fitness, and selection (Lycett 2008).

In conclusion, we note that the examples drawn from this paper are but a small sampling of a very deep literature spanning the decades since Wright's original work. While representing only a brief introduction to the topic, this paper will hopefully be a source of encouragement to scholars of cultural change to consider the "landscape revolutions" described above in ongoing work. In particular, we feel that consideration of recent advances in landscape theory may have major implications for the ways in which evolutionary anthropologists theorize stasis, cultural divergence, and macroevolution, the role of neutral evolution in facilitating the process of innovation, and the complex interactions between selection, drift, and human behavior in determining large-scale patterns of cultural change.

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Chapter 8
The Uses of Cultural Phylogenetics in Archaeology

Larissa Mendoza Straffon

Introduction

Studies on the processes of cultural transmission and cultural evolution have been at the center of archaeological research and debate for the first two decades of the twenty-first century (García Rivero 2016; Lipo et al. 2006; Mace and Jordan 2011; Richerson and Christiansen 2013; Shennan 2009; Whithen et al. 2011). During this time, the methods of cultural phylogenetics have gradually become established as the standard method for describing and analyzing these processes (Mace et al. 2005) and have consequently found numerous applications in historical linguistics, social science, anthropology, and archaeology (Levinson and Gray 2012; Mace and Jordan 2011; Mesoudi 2011).

Despite the success of these methods' applications and the increasing presence of phylogenetic analyses in archaeological research, many of the key concepts of phylogenetics and their purpose in studies of material culture may seem somewhat intricate to many archaeologists, especially those unacquainted with the jargon of evolutionary science. This chapter will first introduce some basic concepts of phylogenetics, focusing on those which are relevant for understating its uses in cultural studies. The second section will review some of the most fruitful applications of phylogenetics in archaeology and discuss the types of research questions that can be addressed with these methods. In the final section, I lay out some of the most recurrent challenges of using cultural phylogenetics in archaeological research and look into how researchers are rising up to them.

Basic Concepts in Phylogenetics

In biology and paleontology, phylogenies are family trees generated by real or hypothesized ancestor-descendant relations between species or groups of species, based on shared morphological traits, genes, or proteins. In these fields, phylogenetic methods aim at reconstructing evolutionary histories by tracing lineages back to a most recent common ancestor (Sterelny and Griffiths 2012). Phylogenies are usually represented as branching tree diagrams, called cladograms, where a single branch is constituted by a last common ancestor (the node or branching point) and all its descendant lineages, which in conjunction are called a *clade*. The working assumption is that the more traits two or more

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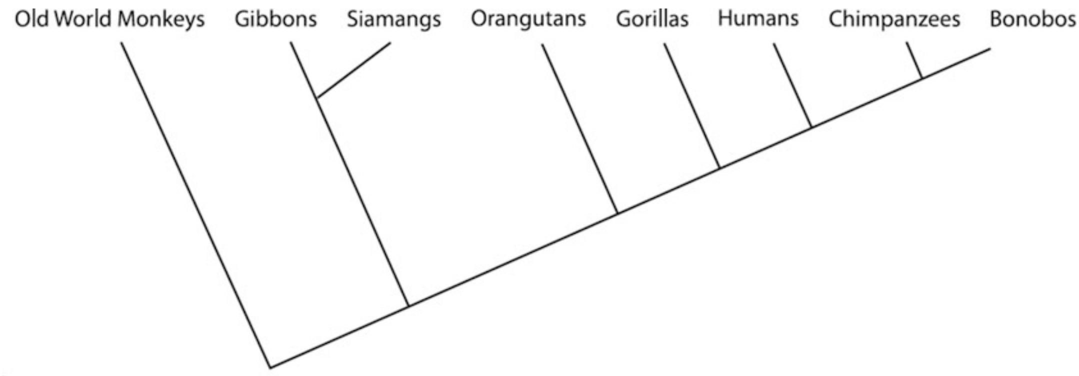

Fig. 8.1 Fragment of the phylogenetic tree of primates (After Shoshani et al. 1996)

species share, the more closely related they are to each other through a recent ancestor than to any species outside their clade. The members of a clade are therefore united by shared traits inherited from the same ancestral species; such traits are called synapomorphies or, more commonly, homologies, whereas those that evolve independently are known as homoplasies (Meisel 2010; Tëmkin 2016). Among extant primates, for instance, chimpanzees, bonobos (*Pan*), and humans (*Homo*) form a clade, having shared a common ancestor with each other more recently than with any other great ape (Fig. 8.1). Two examples of the many homologies of the *Pan-Homo* clade are high encephalization and delayed puberty (Shoshani et al. 1996).[1]

The criterion of similarity between species or taxa is determined by the comparison of their characters, which are the attributes of form, structure, or composition that distinguish each of them. For example, comparable characters for primate species may be genetic, such as the location of a particular gene on a chromosome (Chen and Li 2001), morphological, such as the shape and size of the skull and teeth (Shoshani et al. 1996), or even behavioral, like diet or group size (MacLean et al. 2012). The variants of those characters' expressions among species, called character states (e.g., absent/present, long/short, large/small), help determine relatedness. The result of the character states analysis results in a diagram. The most common is the phylogenetic tree or cladogram, represented by branching lines that group taxa by shared descent, i.e., the phylogeny of a group. Phylogenetic trees, then, trace vertical evolutionary processes like divergence, branching episodes, convergence, continuity, or extinction, but other diagrams, such as networks, help visualize reticulate or horizontal processes as well, like hybridization, recombination, fusion, and horizontal gene transfer (Morrison 2016; Tëmkin 2016). Thus, the most common representations of phylogenetic trees are branching cladograms and reticulate networks, which can be portrayed in many different styles (Fig. 8.2).

In broad lines, phylogenetic analysis proceeds by selecting the study group, determining the evolutionary relevant characters, and comparing these across the entities in the study group (Marwick 2012). The character states are first integrated in a data matrix, and then an out-group is distinguished for comparison (Maddison et al. 1984; Buchanan and Collard 2007). The latter may be a close relative of the study group, generally a species that diverged earlier (Holden and Shennan 2005). Looking at the character states of the out-group helps the researcher infer the ancestral states of the last common ancestor. Then, if any character states are found in the study group but not in the out-group, parsimony

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[1] Note that clades are hierarchically nested, i.e., each clade is included within a larger cluster. For example, chimpanzees and bonobos constitute a clade because they shared a common ancestor most recently. At the same time, these two cluster with humans in another clade, since all three show greater similarity with each other than with gorillas, and again gorillas form a clade with humans, chimpanzees, and bonobos because these four are more similar to one another than to orangutans and so on (Nickels and Nelson 2005).

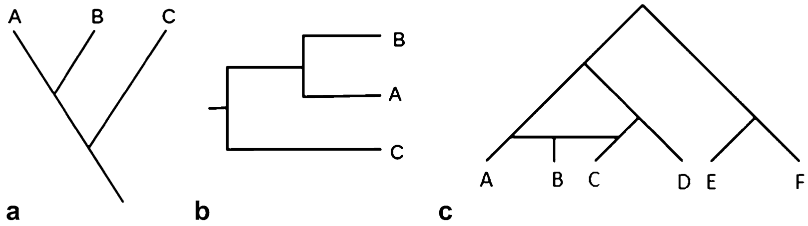

Fig. 8.2 Basic cladograms. (**a**) and (**b**) are identical but drawn in different styles and orientations. (**a**) cladogram with diagonal branches. (**b**) cladogram with rectangular branches. (**c**) simplified network cladogram

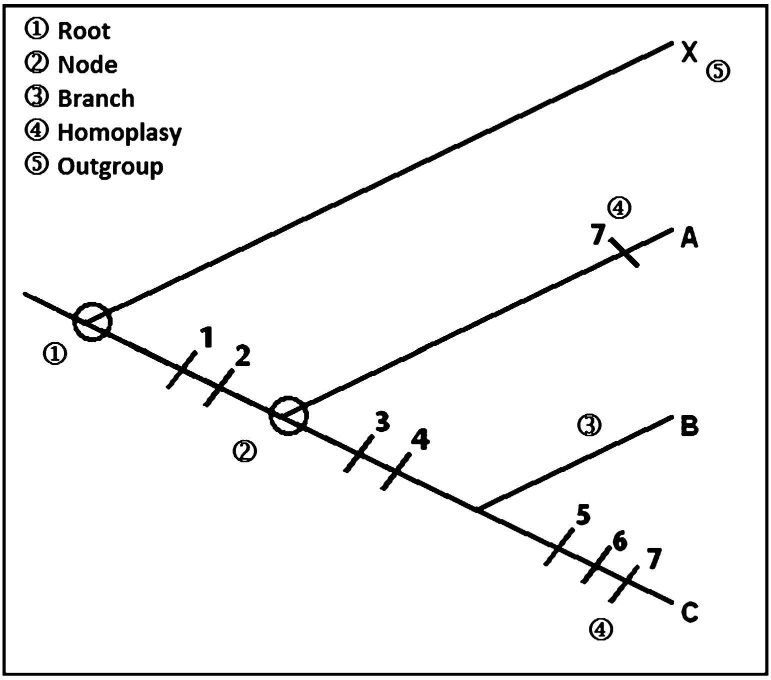

Fig. 8.3 Example of a cladogram with the character state matrix from which it was generated. Taxon B and C form a clade to the exclusion of A based on the shared possession of the character states for characters 3 and 4. Taxa A, B, and C form another clade based on the similar character states for characters 1 and 2. Taxon C is the most derived taxon, with derived characters states for characters 5, 6, and 7. Character 7 is a homoplasy, in a derived state in taxa A and C, even though these do not share a most recent common ancestor. In an alternative, equally parsimonious cladogram, taxa A and C form a clade to the exclusion of taxon B (After Buchanan and Collard 2007)

	1	2	3	4	5	6	7
A	1	1	0	0	0	0	1
B	1	1	1	1	0	0	0
C	1	1	1	1	1	1	1
X	0	0	0	0	0	0	0

dictates that those evolved only in the former and were not inherited from the latter (Buchanan and Collard 2007). The resulting cladogram will trace how the study group relates and deviates from the out-group, revealing the evolutionary relationships between them (O'Brien and Lyman 2003) (Fig. 8.3). This way, by tracing common descent on the basis of character comparison (identifying shared ancestral characters vs. shared derived characters evolved in a clade), phylogenetic methods allow researchers to carry out quantitative assessments of the degree of relatedness between species, as well as to infer the traits of extinct species, and to identify the timing and location of significant evolutionary changes (MacLean et al. 2012).

Since different character state matrices generate different cladograms, it is frequent to obtain several classificatory proposals of how the entities in the study group relate to one another. To choose among alternatives, cladistics methods generally apply the principle of parsimony (García Rivero 2016). This means that when there are different possible explanations, the simplest one will be adopted as the most probable, and because in evolution stasis is more common than change, when selecting among different phylogenetic trees, the one requiring the least evolutionary steps will be preferred (Eldredge 1989; Gould 2002; Mayr and Ashlock 1991). To carry out the analysis, phylogenetic approaches implement a number of computational tools and packages to generate character state matrices and cladograms; some widely used programs are PAUP* (Swofford 2000), Mesquite (Maddison and Maddison 2007), and TNT (Goloboff et al. 2008)—specifically for phylogenetic analysis, and R (Paradis 2011)—a statistical computing program.[2]

Since phylogenetic classification and analysis trace common descent and variation from an ancestral form, phylogenetics may very well be used to infer the histories of cultural traits, as long as these undergo the evolutionary processes of drift/selection, transmission, and modification (Levinson and Gray 2012; Mesoudi 2011; O'Brien et al. 2001; Tëmkin 2016; Whiten et al. 2011). In this sense, cultural evolution refers to the emergence and change of cultural forms by means of descent with modification, and, just like in biology, cultural phylogenetics aims at understanding cultural evolution through relations of relatedness by reconstructing the "genealogical" relations of artifacts and artifact traditions (Currie 2013).

Applications in Archaeology

The emergence, diffusion, and diversification of artifacts over time and in space (traditions) usually leave a distinctive trace in the material record (Whiten et al. 2011). It is the analysis of those traces which makes it possible for archaeologists to find or infer patterns to reconstruct and explain the paths of cultural evolution (Mesoudi and O'Brien 2009). Phylogenetic methods in archaeology are precisely meant to reveal the course and channels of cultural change.

Evidently, the study of cultural evolution is not new to our field. The notion that social phenomena such as the emergence and dispersal of populations and artifacts may be revealed by tracing back links among different cultural practices has a deep history in the human and social sciences (Richerson and Christiansen 2013; Walsh et al. Chap. 2 this volume). In archaeology, plotting artifact genealogies goes back to the early establishment of the discipline in the nineteenth century (Lipo et al. 2006; García Rivero 2016). A standard method of this kind is the creation of archaeological typologies, which are classifications of artifacts divided in types and sub-types "based upon a consideration of qualitative, quantitative, morphological, technological and functional attributes" (Bahn 1992, p. 519). Like phylogenetic methods, typologies also aim at organizing artifacts in discrete groups in order to better understand their histories; however, making typologies and phylogenies are fundamentally different processes. Typologies are descriptive, based on the overall similarity of an artifact or one of its attributes (e.g., decoration, shape), but there is no necessary element of hierarchy or succession. Therefore typologies are often limited to establishing likeness. Artifact phylogenies, on the other hand, hone in on those homologous attributes (characters) that have been potentially transmitted and modified over time. These, in turn, can then be compared and analyzed quantitatively allowing researchers to infer degrees of relatedness between entities, to identify divergence events, and ultimately to reconstruct patterns of cultural evolution (García Rivero 2016; O'Brien and Lyman 2003). In brief, we could say that in a typology, the predetermined category of the *type* determines

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[2] Each of these has an explanatory website and free online tutorials. For a comprehensive list of Phylogeny programs, see: http://evolution.genetics.washington.edu/phylip/software.html.

the attributes that the artifact should present, but in a phylogeny, it is the attributes which determine whether a type belongs or not to a set (see O'Brien et al. 2001).

So, the appeal of phylogenetic methods in archaeology is that it allows researchers to systematically build theoretically sound maps and classifications of relatedness to track culturally transmitted information across space and through time (Lipo et al. 2006). The first momentous examples of the use of archaeological cladistics are found in the seminal work on Paleoindian stone tool technologies by Michael O'Brien and his collaborators, which really set the foundations for the current state of the field (O'Brien and Lyman 2003; O'Brien et al. 2001, 2002). Since then, the methods of cultural phylogenetics have been applied in archaeology to a growing variety of regions and materials, such as Native Californian baskets (Jordan and Shennan 2003); Middle Paleolithic technology (Lycett 2007, 2011); pottery from Fiji (Cochrane 2008), the European Neolithic (Collard and Shennan 2000), and the North American Southwest (Harmon et al. 2006); Turkmen carpets (Tehrani and Collard 2002) and Iranian textiles (Matthews et al. 2011); symbolic items from the Iberian Neolithic (García Rivero and O'Brien 2014); Northern European Mesolithic bone points (Riede 2008); houses from the American Great Plains (Gjesfjeld and Jordan, Chap. 9 this volume); musical instruments like brass cornets (Eldredge 2000) and the Baltic psaltery (Tëmkin and Eldredge 2007; Veloz et al. 2012); and artistic traditions from Thailand (Marwick 2012) and the European Upper Paleolithic (Tripp 2016), just to mention a few.[3]

Not only has the scope of regions and artifacts diversified, but also the aims of research have found many more applications. García Rivero (2016) has divided phylogenetic studies in archaeology in three categories: (1) those that examine the geographical distribution and cultural development of artifacts or traditions by tracking transmission and descent back to a common ancestor or prototype, for example, studies which explain the causes and rates of change in material culture traditions (Tehrani and Collard 2002) and help make inferences about the factors that shaped the traits of artifacts (Mace and Pagel 1994; Mesoudi and O'Brien 2005). (2) Those that create nested groups of artifacts, or clades, to track them geographically or temporally. Here we find works that construct artifact lineages (O'Brien et al. 2001) and those that establish the chronological arrangement of cultural traditions by identifying splitting events in a branch (Gray and Atkinson 2003; Holden and Shennan 2005). In archaeology, like in linguistics, phylogenetic methods can also add to the chronological arrangement of cultural traditions (Gray and Atkinson 2003; Holden and Shennan 2005). For example, by temporally situating a splitting event, a branch, or node in a tree or network diagram, researchers can relatively date traits or specimens whose ages remain unknown. (3) Comparative studies that aim at understanding models of descent to explain the distribution of functionally adaptive traits by, for instance, testing the coevolution of characters or testing competing hypotheses. The patterns of relatedness that emerge from artifact cladograms can then be used to test alternative explanations about the distribution and configuration of material culture across regions and periods (O'Brien and Lyman 2005).

In fact, this latter application, as a strategy to test different scenarios of cultural change, may be one of the most important contributions of cultural phylogenetics to archaeological analyses (Houkes 2011). Like in biology, the comparative method based on formal analogy alone cannot inform researchers about the nature of the similarities and differences between cultural traditions, that is, whether these are rooted in kinship, resulted of parallelism or convergence, or were transmitted horizontally through borrowing.[4] However, phylogenetic methods actually address that issue directly and are therefore able to produce sequences of classification based not only on appearance but on historical hypotheses (García Rivero 2016).

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[3] For more thorough and detailed reviews of relevant contributions of cultural phylogenetics in archaeological research, see García Rivero 2016; Mace et al. 2005; Renfrew and Forster, 2006; Lipo et al. 2006; O'Brien 2008; Shennan 2009.

[4] What is known as Galton's problem.

A good example of how cladistic methods can be used to test competing archaeological scenarios is a recent study by Allison Tripp (2016) on one of the most fascinating and challenging group of artifacts from the European Upper Paleolithic, the so-called Venus figurines. Over 50 such figures have been found from France in the West, to Siberia in the East, and Italy in the South. They are made from materials as diverse as sandstone, bone, clay, ivory, and amber, and in their majority dated to the Gravettian period (*c.* 30,000–20,000 BP), although there are specimens known from before and after. In spite of their wide geographic and temporal span, there has been a tendency to lump these figurines together as a single category, based on some general stylistic similarities, for example, the fact that many (although not all) are small portable statuettes depicting nude females with exaggerated breasts and buttocks. Some researchers have supported this classification, arguing that the figurines comprise a cohesive group determined by their shared core features, such as those mentioned before (Leroi-Gourhan 1968). The opposing view is that the Venuses should cluster in groups according to their regional and chronological distribution and, therefore, despite their apparent similarity, might represent independent regional cultural traditions (Gamble 1982; Gvozdover 1989). The first model supports horizontal cultural transmission patterns (blending), whereas the second implies vertical transmission (branching). Higher similarity between figures from clusters of sites/regions would support horizontal transmission and blending, while higher differences between groups would support branching. To test these opposing views, Tripp suggested a cladistics analysis focusing on multiple variables at the individual artifact level, i.e., specific characters across the set (Fig. 8.4). After selecting only complete full-bodied specimens for study and the earlier Aurignacian Hohle Fels Venus as an out-group, Tipp examined the character state matrix of the sample. The result ultimately supported the second hypothesis that the figurines do not form a cohesive group but rather comprise regional groups generated by vertical information flow. The artifact cladogram revealed, for example, that the Russian figurines (Gagarino, Avdeevo, Kostenki) cluster together to the exclusion of other regions, indicating a definite regional tradition (Fig. 8.5). This paper illustrates well how phylogenetic methods can help us test and contrast specific archaeological hypotheses and demonstrates that traditional archaeological models will not always hold up to a phylogenetic analysis.

Challenges and Prospects

As we have seen, the analogies between biological and cultural evolution seem enough to justify the use of phylogenetic methods in archaeology. But the processes of biological and cultural evolution also differ in many ways. On the one hand, both organisms and artifacts can be distilled into characters that lend themselves to a phylogenetic approach. On the other hand, the concepts that guide the methods of cladistics in biology are relatively well understood and defined, whereas that is not always the case in culture studies. For instance, it is not at all clear what the equivalent of a cultural homology, and therefore the study unit of cultural change, should be (Tëmkin 2016). Furthermore, because cultural evolution draws on design elements, it includes much higher rates of horizontal transfer, novelty, hybridization, and borrowing than its genetic counterpart. For this reason, its effects can occur much faster and are not limited to continuity or extinction but can involve the reintroduction of lost traits and reversibility to previous states (Eldredge 2000; Meisel 2010; Walsh et al. Chap. 3 this volume). Finally, cultural evolution does not only operate by the Darwinian mechanism of descent with modification but also in Lamarckian fashion, through the inheritance of traits acquired through use or disuse during (operational) life (Gould 1996). These differences have spurred debates on whether methods designed to study genetic evolution may be viable to analyze the various and complex modes of cultural evolution and to what extent (Mace and Holden 2005; Lipo et al. 2006; Tëmkin and Eldredge 2007).

Head	
1. Facial features	(0) absent, (1) present
2. Orientation	(0) forward, (1) downward
3. Proportion	(0) miniature, (1) normal, (2) enlarged
4. Head shape (profile)	(0) round, (1) intermediate, (2) club, (3) pointed, (4) flat
5. Head shape (frontal)	(0) round, (1) intermediate, (2) club, (3) pointed, (4) flat
Torso	
6. Proportion	(0) miniature, (1) normal, (2) enlarged
7. Belly button	(0) absent, (1) present
Arms and hands	
8. Completeness	(0) complete, (1) hand absent, (2) hand + forearm absent
9. Proportion	(0) miniature, (1) normal, (2) enlarged
10. Arm position	(0) absent, (1) at sides, (2) above breaste, (3) below breasts, (4) on abdomen, (5) on hips, (6) away form body,
11. Fingers	(0) absent, (1) present
Legs and feet	
12. Completeness	(0) complete, (1) feet absent, (2) feet + lower leg absent
13. Apart	(0) absent, (1)^knees, (2)ˇkness, (3) at knees
14. Proportion	(0) miniature, (1) normal, (2) enlarged
15. Realism	(0) normol, (1) abstract
16. Knees turn inward	(0) absent, (1) present
17. Puncture in place of feet	(0) absent, (1) present
18. Tocs	(0) absent, (1) present
Sexual features	
19. Breasts	(0) elongated, (1) intermediate, (2) round
20. Belly	(0) absent, (1) pronounced
21. Hips	(0) narrow, (1) broad
22. Pubic triangle	(0) absent, (1) present
23. Vulva	(0) absent, (1) present
24. Buttock shape (profile)	(0) absent, (1) flat, (2) shelf, (3) intermediate, (4) round
25. Buttock shape (rear)	(0) absent, (1) flat, (2) heart, (3) intermediate, (4) round
Decorations	
26. Head (type)	(0) absent, (1) incision, (2) hat, (3) puncture, (4) hair
27. Torso (front) (type)	(0) absent, (1) incision, (2) rope, (3) puncture
28. Torso (back) (type)	(0) absent, (1) incision, (2) rope, (3) puncture
29. Arms	(0) absent, (1) present
30. Legs	(0) absent, (1) present

Fig. 8.4 Character list of Gravettian Venus figurines (After Tripp 2016, reproduced with permission)

One of the main challenges of applying cultural phylogenetics in archaeology is that although artifact phylogenies do reflect transmission histories, they remain somewhat arbitrary because in absence of an hereditary mechanism equivalent to DNA, there is no necessary congruence in similarity across characters, for example, knowing the overall form of an artifact, e.g. a nail, does not allow us to predict confidently the form of its parts, e.g. round or flat head, or the material it will be made of e.g. steel or brass (Nickels and Nelson 2005). So, phylogenies could be built upon any of these characters.

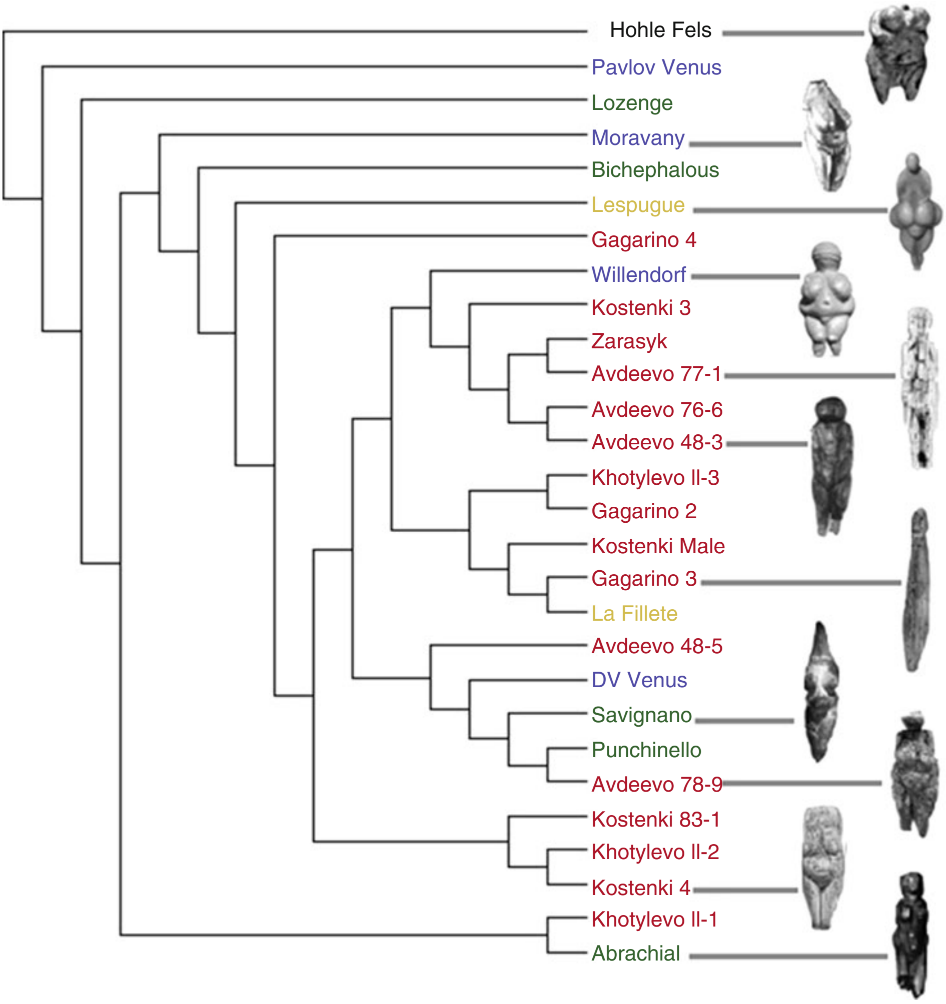

Fig. 8.5 Cladogram of Gravettian Venus figurines suggesting a Russian cluster. (After Tripp 2016, reproduced with permission)

This means that as archaeologists increasingly look to phylogenetics for interpreting the patterns by which cultural traits evolve, their success will partially depend on the accuracy of the cladograms they use in their interpretations (Houkes 2011). For that reason, it is particularly important for cultural evolution researchers to justify their selection criteria, to use all the information available to them to reconstruct the most factual cultural phylogenies and explanations of cultural change.

Again, due to the lack of an equivalent to the genomic component in biological evolution, some of the most common methodological issues in cultural phylogenetics have to do with deciding on the units and scale of analysis, such as the material set (artifact, tradition, culture), the attributes or characters with more information potential, and the interpretation of transmission mechanisms. To identify and select the appropriate units of transmission to be studied, for example, researchers can be aided by using ethnographic data and results of replication experiments (Eren et al. 2016; Mace and Jordan 2011; Mesoudi and O'Brien 2008; Schillinger et al. 2015). Similarly, choosing relevant artifact characters for analysis can be supported by examining different find resolutions (e.g., locale, site, region), which at the same time allows to better identify and test hypotheses of vertical vs. horizontal transmission (Prentiss et al. 2016). Finally, discussions on the nature and form of information transmission and of how to account for the role of the environment in cultural evolution may benefit from incorporating research on social learning and pedagogy, which can throw light on the mechanisms underlying cultural transmission (Knappett 2016; Tehrani and Riede 2008).

Researchers have also been taking important steps toward further formalizing cultural evolution studies in archaeology, for example, by adapting computational and mathematical models to match the specific and unique processes of cultural transmission, such as borrowing and horizontal transfer (Gray et al. 2007; Shennan 2009; Whiten et al. 2011), fine-tuning statistical methods to identify coherent evolution histories, such as Bayesian analyses (Crema et al. 2014; Gjesfjeld and Jordan, this volume; Matthews et al. 2011), using robust statistics measures and performing goodness of fit tests between cladograms and datasets (Marwick 2012), and developing a strong quantitative body of theory to link statistical variation in artifactual traits to account for different sources of transmission and variation (Lycett 2015, 2016; Mace and Holden 2005; Mace and Jordan 2011).

In sum, the biggest challenge to cultural phylogenetics remains that, despite the methodological compatibility with biological phylogenetics, many of the concepts and mechanisms of the latter cannot be applied to cultural evolution. But, by looking at the actual processes and mechanisms of social learning, cultural transmission, and imitation, by comparing attributes and rates of change across different spacial and temporal scales, and by developing methods and theories specific to cultural evolution, archaeologists have been steadily figuring out the different constraints and biases that influence and change cultural traits in different ways, illuminating paths of selection and reproduction that may be particular to material culture. This emerges as the biggest prospect for the immediate future of the field.

Conclusion

As I have reviewed in this chapter, over the past two decades, phylogenetic methods have been successfully employed in archaeology to trace cultural prototypes and their variations, to identify cultural clusters, to examine the distribution of functional traits, and to test ideas about the temporal and geographical spans of cultural forms and transmission mechanisms. So, the use of phylogenetics in archaeology represents a fertile field that allows researchers to generate new historical hypotheses based on the analysis of shared characters, to test them through statistical principles with quantifiable confidence levels, and use them to reconstruct evolutionary relations among material culture sets.

Cultural phylogenetics, then, contributes to archaeological research minimally in four ways: (1) as an aid in the classification of artifacts by measuring the relatedness of particular traits; (2) by testing hypotheses about cultural relatedness; (3) in the absence of a complete record, it can inform about the sequence of changes in cultural forms and the characters of missing types; and (4) it can provide a sound basis for the interpretation and explanation of archaeological phenomena. Through these four aspects, phylogenetics provides archaeology with an important tool to reflect on how the diversity and similarity of cultural traits have evolved throughout human history.

All in all, it is worth exploring the potential that the phylogenetic methods have for formulating new questions about archaeological materials and for testing established hypotheses that explain patterns of cultural origin, development, and loss. Currently, researchers like the ones mentioned in this chapter and many of the contributors of this volume strive to find ways of achieving more accurate artifact phylogenies and a more sophisticated evolutionary framework able to reveal and account for population-level mechanisms of cultural change. Like in biology, the study of cultural evolution does not end with the creation of cultural phylogenies but is a crucial first step toward understanding the processes that underlie it.

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Chapter 9
Contributions of Bayesian Phylogenetics to Exploring Patterns of Macroevolution in Archaeological Data

Erik Gjesfjeld and Peter Jordan

Introduction

Charles Darwin, in his "B" notebook on the transmutation of species, now famously wrote "I think" directly above a sketch that visualizes evolutionary relationships as a network of interconnected branches or tree (Barrett 2009). This simple tree sketch, drawn nearly 20 years before *On the Origin of Species* (Darwin 1859) was published, has now become a powerful metaphor in understanding the evolutionary history of organisms. Since Darwin, the methods for constructing trees have changed dramatically, but the overall goal of phylogenetic methods remains the same, to represent evolutionary relationships between taxa.

The application of phylogenetic methods in archaeology relies on the perspective that material culture participates in a system of inheritance and transformation (sensu Boyd and Richerson 1985) and that material culture diversity results from historical processes of cultural change. Broadly, phylogenetic inference provides a methodological framework to reconstruct the dynamics of cultural macroevolution, which emphasizes cultural change over longer time scales and between cultural traditions and artifact *lineages* (see Chapter 6, this volume). Phylogenetic methods are often most helpful as a basis for classification, to reconstruct historical relationships in the absence of complete data and/or to examine traits shared between entities due to their common ancestry (Boyd et al. 1997). We stress that phylogenetic inference emphasizes a macroevolutionary perspective which is a related but alternative perspective to microevolutionary models of social learning and cultural transmission. This is not to suggest that cultural transmission processes are not an important part of shaping the archaeological record but rather an acknowledgement that cultural phylogenies are often better suited to examine broader historical changes between and across artifact *lineages* (see Box 9.1 Glossary for definition). This includes variability in the tempo of artifact change, temporal periods of divergence between artifact *lineages*, and the dynamic relationship between the emergence and loss of artifact traditions.

We argue here that recent advancements in phylogenetic methods provide substantial added value to archaeological research by permitting the exploration of unique macroevolutionary phenomena.

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We demonstrate the potential of model-based inference by providing a worked case study that applies Bayesian phylogenetics to the archaeological record of the Great Plains. Through this example we guide the reader through key components of the analysis including data acquisition, model selection, and archaeological interpretation. Our goal is to demonstrate how a Bayesian approach can help to illuminate poorly understood patterns of material culture diversity and aid in refining interpretations of the archaeological record and the complexities of material culture evolution.

Box 9.1: Glossary for Definition

Bayes Factor: The ratio between marginal likelihoods from different models. These are commonly used to evaluate whether there is evidence to favor one model over another (Drummond and Bouckaert 2015).

Bayesian Skyline Coalescent Prior: Prior distribution on tree shape that links the divergence times of artifact lineages from the same population. The process broadly works by merging characters through time from most recent to least recent by estimating population sizes at each coalescent interval. For additional details, consult Drummond et al. (2005).

Burn-in: Initial part of the Markov chain Monte Carlo when it is approaching the sampling distribution from its starting point (BEASTdoc Glossary 2018).

Clock Model: A model setting based on the assumptions of a molecular clock. A strict clock model assumes constant but stochastic change across branches of the phylogeny. A relaxed clock allows the rate of change to vary across lineages, or among different parts of the phylogeny (BEASTdoc Glossary 2018).

Characters/Character States: Characters are a set of mutually exclusive attributes that can be used to categorize the variation of an artifact assemblage (O'Brien and Lyman 2003). The choice of characters in a phylogenetic analysis is often based on which traits of the artifact are expected to change most over time as a result of vertical transmission (O'Brien et al. 2002). Each character can take a range of values which are known as character states so that every artifact is defined by at least one character state in each class of characters.

Gamma Rate Categories: Number of discrete divisions that are used to approximate the gamma distribution of rates with the mean of each category used to represent all the rates falling in the category (Yang 1994).

Homoplasy: Character states that cannot be shown to be homologous or shared by a set of artifacts that is present in their common ancestor (O'Brien and Lyman 2003).

Lineage: A sequence of artifacts that are thought to have direct descent from a particular ancestor or ancestral group (O'Brien and Lyman 2003).

Marginal Likelihood: Also referred to as model evidence, this is the likelihood of the data integrated over all parameter configurations.

Markov Chain Monte Carlo: Stochastic algorithm for drawing samples from a posterior distribution. Often used to search the space of possible trees in order to identify trees with the highest likelihoods, which go on to form the posterior distribution (BEASTdoc Glossary 2018).

Maximum Likelihood: The highest probability of the observed data given the model of evolution (i.e., the tree, the rate of change, the gamma shape, etc.) (BEASTdoc Glossary 2018).

Mk Model: A model of character state change developed by Lewis (2001) and Pagel (1994) that assumes the transition among characters states follows a random Markov process where the probability of change from one state to another depends only on the current state (Harmon 2018). The model also assumes that every state is equally likely to change to any other states and is therefore similar to the Jukes-Cantor model for sequence evolution (Harmon 2018).

(continued)

Box 9.1 (continued)

Monophyletic: A complete set of taxa that is descended from a common ancestor (O'Brien and Lyman 2003).

Parameters: Numerical characteristics that specify the properties of a mathematical model or distribution (Everitt and Skrondal 2010). In phylogenetics, parameter values often aim to describe the rate of change or substitution in character states.

Parsimony: The scientific principle of choosing from among competing hypotheses the one that explains the data most simply (O'Brien and Lyman 2003).

Path Sampling: Path sampling (via the stepping stone algorithm Baele et al. (2012)) is a technique to estimate the marginal likelihood by running MCMC chains at different "temperatures" (Drummond and Bouckaert 2015). Bayes factors can be calculated from these techniques in order to compare different models.

Prior: The prior probability distribution, which represents your prior assumptions about the different model parameter values before analyzing the data. The prior combined with the likelihood yields the posterior (BEASTdoc Glossary 2018).

Posterior: The posterior probability distribution, which represents the probability distribution over the parameter state space given the data under the chosen model of evolution (BEASTdoc Glossary 2018).

Rate Heterogeneity: Variability in the rates of change among character states among lineages. Constant rate models assume no rate heterogeneity across character states, whereas variable rate models often use a gamma distribution to model differences in rates between lineages (Skinner 2010).

Tip Dates: Temporal date specified for each individual unit of analysis (i.e., house style).

Topology: The arrangement of taxa (such as artifact classes or house styles) on a phylogenetic tree (O'Brien and Lyman 2003).

Yule Tree Prior: A prior parameter that describes the net rate of origination and assumes a constant rate of lineage emergence for each branch in the tree (Bouckaert et al. 2014).

Model-Based Approaches to Phylogenetic Inference

Over the last 25 years, computational biology has witnessed remarkable advancements in the statistical methods used to infer phylogenies. The initial and continuing driving force behind many of these new approaches is the rapid accumulation of large-scale genetic data. The emergence of new "molecular" approaches has perpetuated a misconception that model-based phylogenetic inference is only applicable to genetic data, even though these approaches can be equally applied to sequence data, morphological data, or cultural data.

The most significant difference of "molecular" phylogenetic methods is the use of an explicit mathematical model of how biological or cultural traits change over time. Previously, the reconstruction of evolutionary relationships primarily relied on cladistic methods (Hennig and Davis 1999; O'Brien and Lyman 2003). These methods were often advertised as "model-free" (Harmon et al. 2006) as the principle of *parsimony* is used to infer how traits change over time. *Parsimony* advocates that nature favors simplicity and that trees with the fewest number of changes are the trees that best represent the evolutionary relationships between taxa (Straffon 2016). When presented with a range of phylogenetic hypotheses, *parsimony* acts as the optimality criterion for selecting among the different trees (García Rivero 2016). The reality is that minimizing the changes in *character states* (i.e., *parsimony*) may not technically be a model of character change, but it is still a very strong assumption about how *character states* evolve through time (Swofford et al. 1996).

Starting in the 1990s, Bayesian phylogenetic methods were introduced into evolutionary biology and since their introduction have become an influential tool for inferring the evolutionary history of genomic sequences (Yang and Rannala 1997; Huelsenbeck et al. 2001). The popularity of Bayesian methods can be attributed to two factors: the development of powerful models of data analysis and the availability of user-friendly computer programs to apply these models (Nascimento et al. 2017). Broadly, Bayesian phylogenetic inference builds from *maximum likelihood* estimation where the data is treated as a fixed observation and the analysis aims to find values of model *parameters* that best explain the data (see Greenhill and Gray 2009 for an extended discussion of likelihood calculations).

Current models of how *character states* change vary from simple to increasing complex depending on the number or model *parameters*. One of the simplest DNA models of change is the Jukes-Cantor model (Harmon 2018), which assumes equal rates of change across *character states* and therefore has only one *parameter*. More complex DNA models, such as the generalized time-reversible (GTR) model, has up to 12 *parameters* which specify different frequencies and rates of change across DNA sites. In a traditional statistical sense, model-based approaches can be viewed as parametric models of character evolution, where we assume that we have a general understanding of the distribution of *character states* (Lukhtanov 2010).

One of the most commonly leveled criticisms against a model-based approach is that models of character evolution developed in the biological sciences are inappropriate for understanding change in artifacts, cultural traits, or languages. As highlighted by Greenhill and Gray (2009, p. 6), this criticism represents a misunderstanding of model-based inference. The application of a seemingly simple model of change does not invalidate the methodology of model-based inference, but rather emphasizes the balance between finding a model with *parameters* that capture the process of change. For example, Greenhill and Gray (2009, p. 6) highlight a biological model that assumes symmetrical change, where the rate of a trait arising is the same as the rate of a trait being loss. However, the symmetrical change assumption may not be appropriate for linguistic data as once a cognate word has arisen, it is much more likely for it to be lost than for that same cognate word to arise in another language. In this situation, model *parameters* can be modified based on our expectations such as adding a second *parameter* so that there is one rate for the origination of a new cognate and one rate for the loss of a cognate. We may even want a more flexible model where each *character* (or artifact trait) is given an inherent rate of change so that some traits may arise or be lost more rapidly, whereas other traits may be more resistant to change (Greenhill and Gray 2009).

Drawing on the success of Bayesian approaches in biology and linguistic anthropology, we argue here that these methods can provide three contributions to improving our understanding of macroevolutionary patterns in archaeological data.

- *Mosaic evolution*: Mosaic evolution can be defined as the process of independent changes in different portions of the phenotype (Stanley 1979). The concept highlights that different organism traits can evolve at different rates as opposed to the assumption that organism traits evolve as an integrated whole (Prentiss et al. 2016). Characterizing mosaic evolution requires the ability to quantify and visualize variability in the rates that artifact *lineages* (or *characters*) are evolving. As highlighted above, a model-based approach allows us to relax the assumption that change occurs at a constant rate or that the fewest number of changes is the correct model of change. Instead, we are able to investigate how rates of change may vary (or not vary) across artifact *lineages* and traits. This quantification of *rate heterogeneity* is a valuable step toward disentangling patterns of "mosaic evolution" that are likely prevalent within many cultural contexts (Prentiss et al. 2016).
- *Divergence times*: Model-based approaches also allow for the integration of temporal information in order to time calibrate our trees. In contrast to linguistic and anthropological data, archaeologists often have fairly robust knowledge of when particular changes occurred in the archaeological record. Model-based methods allow us to integrate this valuable information into our analysis by

either assigning *tip dates* to artifact *lineages* or constraining specific nodes in the tree to make sure divergence events occurred during specific time frames.

- *Rates of diversification*: Recent advancements in quantitative paleontology provide a set of Bayesian model-based tools to explore changing rates of diversification through time. These approaches provide new insights into old archaeological questions about how variability in rates of origination and extinction influence patterns of artifact diversity (Lyman and O'Brien 2000). We argue here that by inferring rates of artifact diversification over time, we can shift our expectations beyond tracing the diversity of artifact *lineages* through time and closer toward a more comprehensive understanding of the unique macroevolutionary patterns found in cultural data.

Application of Bayesian Phylogenetic Methods to Archaeological Evidence

Despite the potential of Bayesian phylogenetic methods, their application to archaeological data can seem daunting. Our goal is to provide a worked example of a Bayesian approach that will help facilitate the application of these methods to additional archaeological datasets. We will demonstrate the implementation and interpretation of our framework by working through key stages in the research process: (1) defining research questions, (2) data acquisition and classification, (3) model selection, (4) tree-building, (5) modeling macroevolutionary patterns, and (6) archaeological interpretation.

All of the phylogenetic analysis performed in this chapter uses the freely available BEAST2 program (Bouckaert et al. 2014) with additional help from packages available in the R statistical environment (R Core Team 2017). The data and code used here are available for download at GitHub and Zenodo (Gjesfjeld 2018). The files in the repositories contain all the necessary files in order to replicate this analysis along with a help file that provides supplementary details on performing the phylogenetic analysis.

Defining Research Questions

The Great Plains of North America is a geographic area consisting of roughly 25% of the United States and represents the largest cultural area of American Indians. Early archaeological and ethnographic research in the Great Plains often emphasized the shared characteristics between cultural groups such as the importance of large game hunting (Lowie 1954). The features of Great Plains groups served as a basis for the stereotypical image of American Indians as heavily reliant on the horse, living in skin tipis, wearing feather headdresses, and hunting bison (Wood 1998). One obvious exception to this is the Plains Village period, which is broadly defined as groups that engaged in a small-village, semi-horticultural way of life beginning around 900 AD and ending after European contact. The emergence and continuity of traditions during this period are of primary interest to this project as we broadly aim to address the question of whether the similarities between Plains Village cultural groups developed due to recent shared ancestry or through independent convergence.

Our decision to focus on the archaeology of the Plains Village period does not stem from any previous affiliation or strong knowledge about the archaeology of the region but rather an interest into defining and resolving questions about cultural continuity, blending, and divergence. We believe that the questions faced by Great Plains archaeologists are common to many archaeological contexts, and we therefore aim to demonstrate how a phylogenetic approach can provide insights into disentangling the historical relationships between archaeological traditions.

Table 9.1 Major periods and cultural traditions in three Plains subareas (redrawn from original in Lehmer 1971, p. 30)

<table>
<tr><th rowspan="2">Major Periods</th><th colspan="3">Subareas</th></tr>
<tr><th>Northestern Plains</th><th>Central Plains</th><th>Middle Missouri</th></tr>
<tr><td>Equestrian</td><td>Horse Tribes
1720 AD</td><td colspan="2">Disorganized Coalescent
Coalescent Tradition</td></tr>
<tr><td>Plains Village</td><td>900 AD</td><td>Central Plains Tradition</td><td>Middle Missouri Tradition</td></tr>
<tr><td>Plains Woodland</td><td>500 BC</td><td colspan="2">Plains Woodland Complexes</td></tr>
<tr><td>Foraging</td><td colspan="3">Foraging Complexes
6000 BC</td></tr>
<tr><td>Paleo-Indian</td><td colspan="3">Early Hunting Complexes</td></tr>
</table>

The Plains Village period is viewed as a geographical and cultural intermediate between the nomadic groups present in the Northwestern Plains and the fixed settlement populations of the Eastern Woodlands. The emergence of this lifestyle appears in various geographic subareas including the Central Plains (southeastern Nebraska and Eastern Kansas) (Wedel 2001) and the Middle Missouri (southeastern South Dakota and west-central North Dakota) (Wood 2001). The origins of the Central Plains and Middle Missouri cultural traditions are largely considered unknown and subject to debate (Wood 2001, p. 190; Wedel 2001, p. 183) but are often viewed as independent from each other with similar horticultural practices arising through connections with neighboring populations to the south and east.

The later tradition of the Plains Village period is referred to as the Coalescent, beginning around 1400 AD and centering around the Missouri River in central South Dakota. As highlighted by Krause (2001), the origins of the Coalescent are considered a product of immigration from the Central Plains geographic subarea, which brought their cultural practices north to the Middle Missouri geographic subarea. Here, Central Plains populations are believed to have resettled abandoned or at least sparsely settled areas that were previously associated with the Middle Missouri tradition. Post-European contact variants of the Coalescent tradition are identified as an amalgamation of Central Plains and Middle Missouri traditions (Table 9.1).

Based on this archaeological background, we can develop a set of initial expectations for what we would expect from our phylogenetic analysis.

Expectation 1: No shared ancestry between the Central Plains tradition and the Middle Missouri tradition as current archaeological evidence suggests that these are traditions with independent origins from each other. The phylogenetic expectation is that distinct or *monophyletic* clades for each tradition will be apparent in the tree *topology* (Fig. 9.1).

Expectation 2: Partial shared ancestry between the Central Plains tradition and the Coalescent tradition as the origins of the Coalescent are viewed as a product of immigration from the Central Plains region. The phylogenetic expectation is that artifact traditions associated with sites from the Central Plains will group within clades that also contain artifact traditions from Coalescent sites (Fig. 9.1).

Our expectations are intentionally presented as broad hypotheses about the historical relationships between Plains Village cultural traditions. We want to emphasize that tree *topologies* from either cladistics or model-based frameworks should not be used as confirmatory tests of cultural transmission but rather as exploratory hypotheses of the heritable continuity between our units of analysis. If our tree *topology* mirrors our simple archaeological expectations, we could argue that our phylogenetic model is a potentially useful proxy for the culture history of the Plains Village period. If it becomes

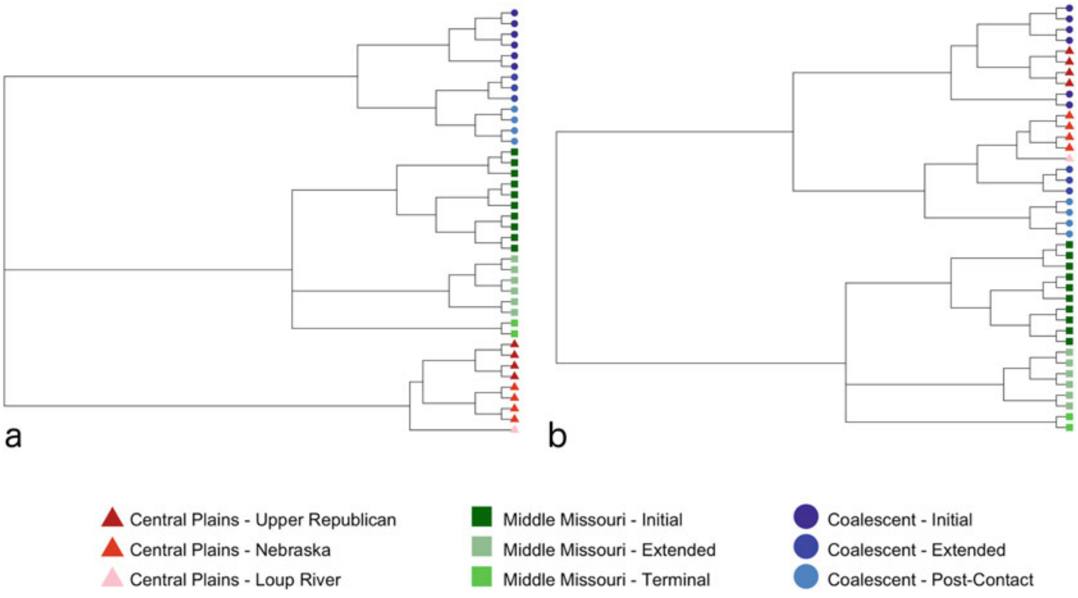

Fig. 9.1 Hypothetical tree topologies for expectations of shared ancestry between Plains Village traditions. Tree on left is suggestive of the first expectation of no shared ancestry between traditions indicated by deep branch lengths between monophyletic clades that are associated with each cultural tradition. The tree topology on the right suggests partial shared ancestry between the Central Plains and the Coalescent traditions as the clades contain sites that are associated with both traditions

apparent that our phylogenetic model clearly does not fit with our previous archaeological knowledge, we should critically evaluate whether our phylogenetic assumptions and/or our archaeological data are appropriate to evaluate questions about the cultural continuity between Plains Village traditions.

Data Acquisition and Classification

One of the most significant challenges in applying phylogenetic analysis to archaeological data is the construction of taxa (O'Brien et al. 2002). In biology, the most common forms of taxa construction use the species concept, despite many debates surrounding the definition of a species. In archaeology, defining artifact *lineages* based on the species concept is problematic at best, so we use our own paradigmatic classification scheme which defines each artifact or feature on a series of unordered and unweighted *character states* (O'Brien et al. 2002; Prentiss et al. 2014). We used house feature data from 30 archaeological sites associated with specific Plains Village traditions. Seven *characters* with between three and eight *character states* were used to categorize each house style (see Table 9.2). Each house style was recorded as a series of binary variables based on the presence or absence of each *character state.* The raw data can be accessed in the online data repository associated with this volume (Gjesfjeld 2018). The choice of *characters* to be included is based on expectations as to which parts of house would change most over time and thus would create the strongest phylogenetic signal (see O'Brien et al. 2002 for an extended discussion about choosing *characters* for analysis).

It is important to note that the characters used in this analysis are assumed to be independent. This assumption of character independence is a necessary but often incorrect assumption when

Table 9.2 *Characters* and *character states* used to classify house features

Character *Character state*	
I. Interior posthole pattern	V. Entrance direction
1. Circular	1. North
2. Square/rectangular	2. Northeast
3. Linear	3. East
4. Double linear	4. Southeast
	5. South
II. Number of central postholes	6. Southwest
1. Two	7. West
2. Four	8. Northwest
3. More than five	
	VI. Number of hearths
III. Exterior posthole pattern	1. 0
1. Circular	2. 1
2. Square	3. 2 or more
3. Rectangular	
	VII. Estimated size of house (sq. ft.)
IV. Number of exterior postholes	1. 0–250
1. Less than ten	2. 251–500
2. 11–20	3. 501–750
3. 21–30	4. 751–1000
4. 31–40	5. 1001–1250
5. 41–50	6. 1251–1500
6. 51–60	7. 1501–1750
7. 61–70	8. 1751–2000
8. 71–80	
9. 81–90	
10. Over 91	

evaluating morphological (or technological) characters as these traits often strongly interact with each other (Harmon 2018). If traits are thought to be non-independent, it can no longer be assumed that the phylogeny is a direct measure of phylogenetic signal and may in fact represent functional relationships between *characters*. This does not undermine the construction of the tree topology but may alter the inference of shared ancestry between taxa. The statistical determination of character independence is a topic outside of the scope of this chapter but has been widely discussed and should be considered in any phylogenetic analysis. Depending on the structure of the data used, helpful methods include testing for the correlated evolution of different characters (Dunn et al. 2011) or assessing the nonrandom association of character states across various characters (i.e., linkage disequilibrium).

The taxa (i.e., house styles) used in this analysis (Table 9.3) were chosen to represent a range of time periods, cultural phases, and geographic regions (similar to Prentiss et al. 2014). The house styles used in this analysis by no means represent a comprehensive list of house styles associated with Plains Village traditions and variants. In this respect, we view this study as a preliminary demonstration of how to apply Bayesian phylogenetic inference with future studies needing to consult with specialists in Great Plains archaeology to identify additional sites and samples for analysis.

Table 9.3 List of archaeological sites where house styles were chosen from along with literature reference

Central Plains tradition		Middle Missouri tradition	
Upper Republican phase		*Initial Middle Missouri variant*	
Red willow	Grange (1980)	Dodd	Lehmer (1954)
Owens	Wedel (1933)	Breeden	Brown (1974)
Holdredge	Wedel (1934)	Swanson	Hurt (1951)
Mowry bluff	Wood (1969)	Langdeau	Caldwell and Jensen (1969)
Nebraska phase		Pretty head	Caldwell and Jensen (1969)
Theodore Davis	Gradwohl (1969)	Jiggs Thompson	Caldwell and Jensen (1969)
Patterson	Bozell and Ludwickson (1994)	Mitchell	Alex (1973)
Little Pawnee Creek	Bozell and Ludwickson (1994)	*Extended Middle Missouri variant*	
Loup River phase		Thomas Riggs	Hurt (1953)
Sweetwater	Champe (1936)	Cannonball	Griffin (1984)
Coalescent tradition		Bendish	Theissen (1976)
Initial variant		Fire Heart Creek	Lehmer (1966)
Black Partizan	Caldwell (1966)	*Terminal variant*	
Arzberger	Spaulding (1956)	Huff	Howard (1962)
Crow Creek	Kivett and Jensen (1976)	Shermer	Sperry and Bass (1968)
Talking crow	Smith (1977)		
Extended variant			
Demery	Woolworth and Wood (1964)		
Over’s La Roche	Hoffman (1968)		
Molstad	Hoffman (1967)		
Post-contact			
Big village	O’Shea and Ludwickson (1992)		
Like a fishhook	Smith (1972)		

Model Selection

All scientific models aim to find the balance between being too simple and too complex. One of the advantages of a model-based phylogenetic framework is the ability to evaluate a range of different models and select the model that best fits our data. This explicit testing between models of change is perhaps one of the most significant differences from cladistics where it is assumed that the best-fitting model is the one with the fewest changes.

Choosing the Model Family

The archaeological data used in this case study is structured as a set of binary *character states* (see Table 9.2) that summarize the morphology of each house feature. Based on literature from biological systematics, we implemented the *Mk model* (Lewis 2001) in our analysis of Plains Village house features for a number of reasons. First, in the estimation of phylogeny from discrete morphological data, the *Mk model* assumes that no *character state* is predetermined as ancestral or dependent, which is in contrast to a *parsimony* framework that encourages the user to select an ancestral form or outgroup. Second, the *Mk model* allows *characters* to change freely back and forth between two states, and this probability of change is symmetrical (Lewis 2001, p. 916; Harmon et al. 2006, p. 217). Third, a *character* can change state at any instance in time, which is a valid assumption for any scenario where change at the day-to-day or even year-to-year scale is unknown (Harmon et al. 2006). Finally, the *Mk model* does not favor any broad trend of evolutionary change and therefore provides equal weight to either gradual or punctuated change. The *Mk model*, like most phylogenetic models, is not an exact specification of how characteristics change but rather a broader set of assumptions given what we know about our data. In some instances, such as DNA nucleotide substitutions, model assumptions may be highly specified given our existing knowledge. In cultural contexts, where we know less about *character state* changes, it may be beneficial to implement a broad model of change so that we can explore a wide range of *parameter* values. The *Mk model* is implemented in BEAST2 by installing the additional morph-model (MM) package.

The *Mk model* has also demonstrated greater accuracy in tree reconstruction than *parsimony* methods (O'Reilly et al. 2016; Wright and Hillis 2014). In two independent studies, phylogenies produced using likelihood models were considered more accurate in recovering a tree *topology* from simulated morphological data. Model-based approaches also demonstrated less error in analyses that used fewer *characters* and realistic values of *homoplasy*. However, O'Reilly et al. (2016) do suggest that while *parsimony* methods were less accurate than likelihood methods, they did achieve higher levels or precision (i.e., higher consistency in the number of nodes reconstructed across a range of tree *topologies*).

Specifying Model Settings

A model-based framework also strongly encourages the researcher to specify model settings in order to improve the fit of our model to the data. The first setting to adjust is the number of *gamma rate categories*. The number of *gamma rate categories* aims to encompass the amount of variation in the rates of change between different *characters*. For example, a gamma category count of one would suggest there is no variability in rates of change between *characters* (i.e., all house style traits change at approximately the same rate), whereas a value of four would indicate higher variability in rates. Broadly, you can imagine that with four rate categories, we are suggesting that each house style *character* is able to change at one of four different speeds such as very slow, slow, medium, and fast (Greenhill and Gray 2009).

We can also investigate how the branches of the tree (not just the traits) vary in their rates of change, referred to as the *clock model*. A strict clock assumes that there is no variation in rates of change across branches. A relaxed clock assumes variation across branches is autocorrelated, so that neighboring branches are more similar in their rates of change than branches that are further apart from each other.

Finally, as this is a Bayesian framework, we can also consider different *priors* on the underlying process that generates the tree (Drummond and Bouckaert 2015). Here, we consider two *priors*. The first is a pure-birth *Yule process* which starts with one lineage and then splits into two *lineages* after some amount of time, similar to a traditional bifurcating tree. The second is a *Coalescent Bayesian Skyline prior* (Drummond et al. 2005) which moves backward in time merging *characters* together according to a random process that assumes each *character state* is equally likely to have been passed from one generation to the next.

Adjusting model settings is most easily accomplished in BEAST2 by loading the morphological data (as a nexus file) into the BEAUTi interface. The user is then able to select the *Mk model* under the Site Model tab and adjust the clock model settings, Bayesian prior settings, tip dates, and MCMC settings. After the necessary settings are chosen, BEAUTi will create an XML control file, which will be imported in BEAST, with the preferred configuration of model settings. The nexus and XML control files associated with this analysis can be found in the repositories highlighted above.

Table 9.4 Results of model selection presenting the top six models (out of 16) including their *parameter* settings, *marginal likelihoods*, and *Bayes factors*

γ rate categories	Clock	Prior	Marginal likelihood	Bayes factor
4	Strict	Coalescent Bayes skyline	−582	–
2	Strict	Coalescent Bayes skyline	−583	2
3	Relax	Coalescent Bayes skyline	−583	2
4	Relax	Coalescent Bayes skyline	−583	2
2	Relax	Coalescent Bayes skyline	−585	6
3	Relax	Yule	−586	8

Choosing the Best-Fitting Model

We created 16 different models based on our three different settings. This included proposing between one and four different *gamma rate categories* (1, 2, 3, 4), two different *clock models* (strict, relaxed), and two different tree *priors* (*Yule* and *Coalescent Bayesian Skyline*). To choose the best-fitting model, we implemented a *path sampling* procedure in BEAST2 (Suchard et al. 2001), which can be implemented through the additional BEAST2 path sampling app (see Bouckaert 2014 for additional details). Broadly, path sampling calculates the *marginal likelihood* of each model by comparing *posterior* likelihoods across a range of "temperatures." The highest *marginal likelihood* value indicates the best-fitting model given our data. Results of the model selection procedure reveal that the best-fitting model of character evolution for Plains Village houses is a strict clock with four *gamma rate categories* and a *Coalescent Bayesian Skyline prior*. However, it is important to note that three other models demonstrate nearly the same strength of evidence based on *Bayes factor* (Kass and Raftery 1995) comparisons (see Table 9.4).

Tree-Building

Perhaps the most significant difference of a Bayesian phylogenetic approach to other approaches is that there is no attempt to maximize or minimize some aspect of the tree, such as finding the tree(s) with the highest likelihood or the tree(s) with the minimum number of changes. Bayesian approaches sample the entire space of all possible trees. In this regard, the workhorse of many Bayesian analyses relies on the implementation of a *Markov chain Monte Carlo (MCMC)* (Nascimento et al. 2017). The goal of the *MCMC* is to search through the range of possible trees and identify which trees best fit our data given the model and our *priors*.

The search process starts with an initial tree and random values for the number of *parameters* in the model. After initialization, a neighboring tree (one that has a similar likelihood score) is proposed, and if the newly proposed tree has a higher *posterior* probability than the initial or current tree, the *MCMC* algorithm will accept the new tree (Yang and Rannala 2012, p. 310). The *MCMC* search will proceed to explore the space of all possible trees and if run long enough will provide a representative sample of the most probable trees. The general expectation is that trees with higher *posterior* probabilities, meaning a better fit of the data to the model, will be visited more often by the *MCMC* algorithm. By simply counting the frequency by which each tree is visited, we can get an estimate of the *posterior* probabilities for the tress (Yang and Rannala 2012, p. 310).

Based on the results of our model selection procedure, we can build our tree based on the best-fitting model specifications. In our case, these are four *gamma rate categories*, a strict clock, and a *Coalescent Bayesian Skyline prior*. Using BEAST2, we sample the entire space of possible trees using the *MCMC* chains to identify which trees best fit our data given our model and our *priors*. We

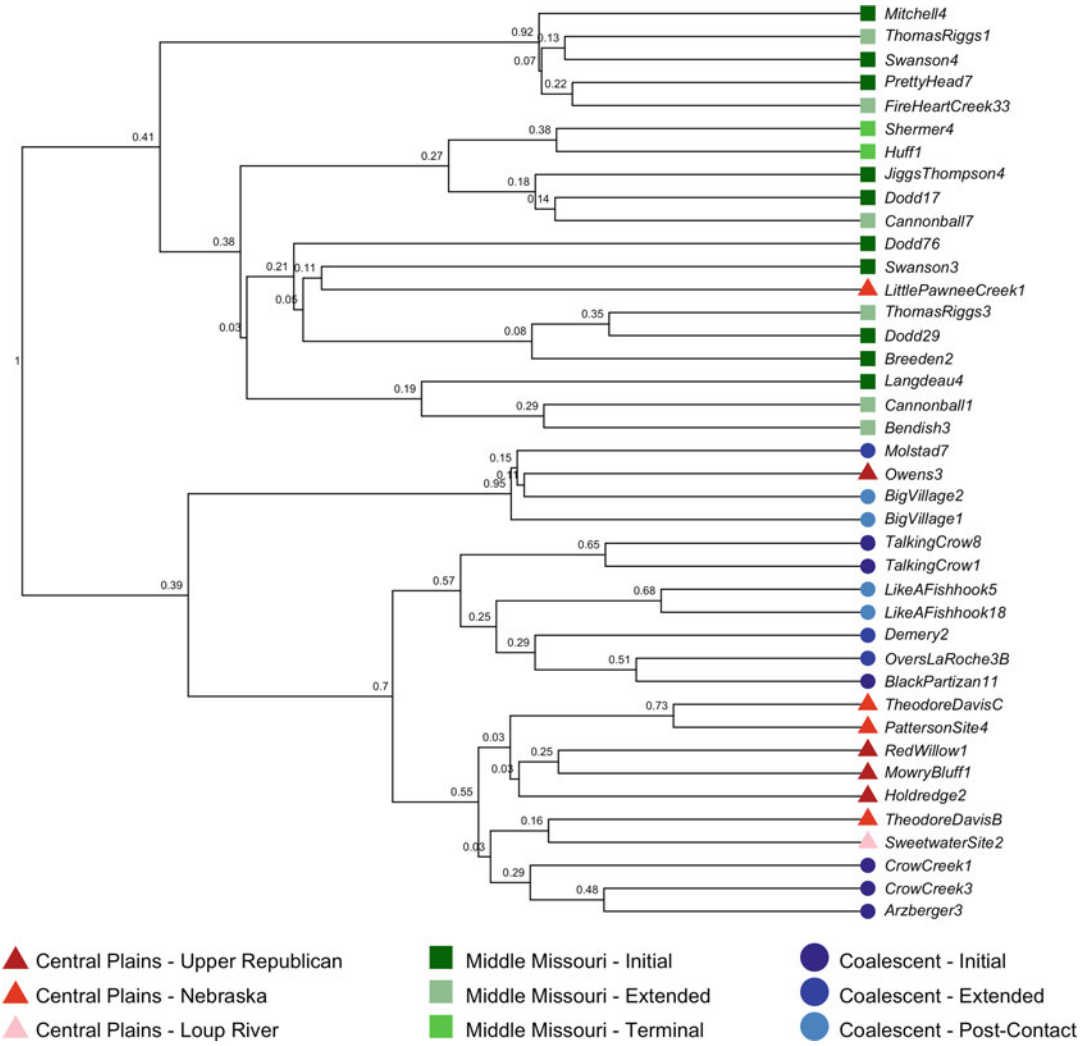

Fig. 9.2 Maximum clade credibility tree with *posterior* probabilities as the node labels and branch lengths that are proportional to the amount of change in each branch. Tip labels correspond to Plains Village tradition and variant/phase categories

summarize post-*burn in* trees sampled by the *MCMC* algorithm into a single tree *topology*, known as the maximum clade credibility tree (Fig. 9.2). The maximum clade credibility tree can be created by reading the full sample of trees into the TreeAnnotator program associated with the BEAST2 package. Once the maximum clade credibility tree is produced, this file can be read into the R statistical environment (R Core Team 2017) using the phyloch package (Heibl 2008). The plotting and visualization of trees, including those provided here, can be done with R packages such as ape (Paradis et al. 2004), phytools (Revell 2012), and phangorn (Schliep et al. 2017). Additional packages in R can also perform a wide range of tasks including diversification analysis, tree simulations, trait evolution, and ancestral state reconstruction to name only a few.

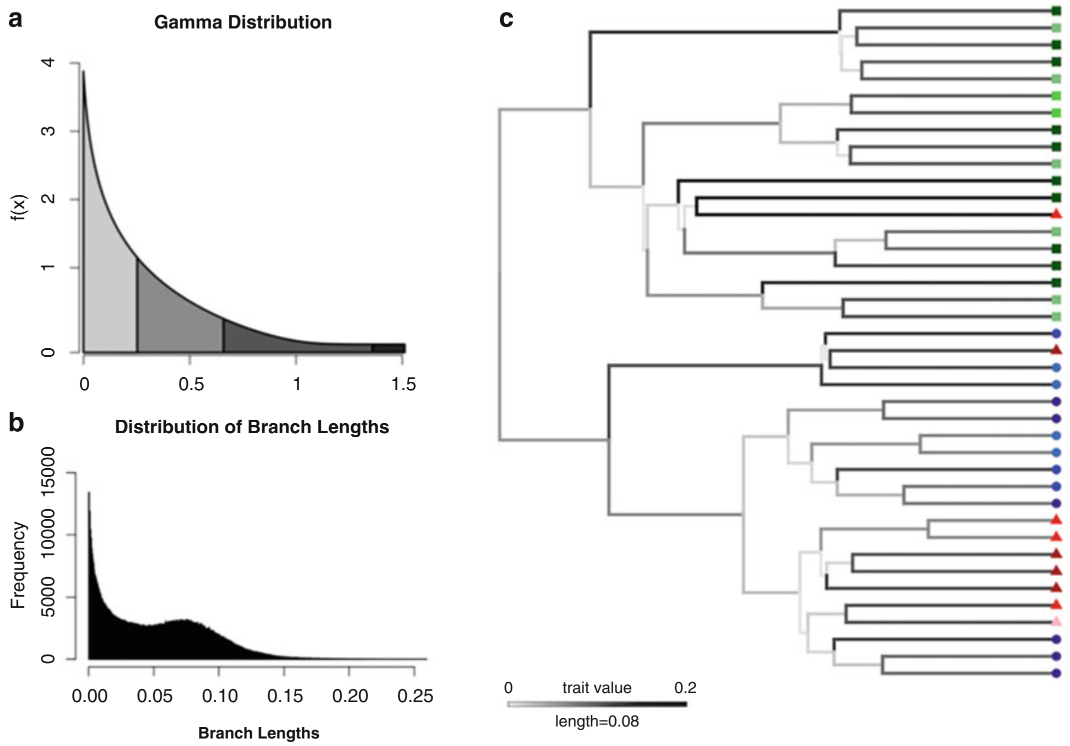

Fig. 9.3 Examples of three different methods to examine the variation of rates across our tree including (**a**) the distribution of *gamma rate categories* for a gamma shape of 0.95 following Yang (1994), (**b**) a histogram of branch lengths across all trees in the *posterior* distribution, and (**c**) a rate of substitution for each branch lengths plotted across the tree with darker branches indicating a branch with a higher rate of character state changes (i.e., substitutions) and lighter branches indicating a slower rate of character changes

Modeling Macroevolutionary Patterns

In addition to more accurate tree-building, Bayesian methods provide additional benefits to modeling patterns of cultural macroevolution. Here we focus on three features that provide insights into the variability of rates, divergence times, and patterns of diversification.

Mosaic Evolution

One of the most significant advantages of a model-based approach is being able to more fully understand variation in rates of change across the tree (*rate heterogeneity*). This is particularly important for interpreting material culture phylogenies where the units of analysis (such as artifact traditions) are known to be an assemblage of many units or *characters*. Furthermore, change across these different units is not likely to be constant with some traits changing more or less quickly than others, often referred to as mosaic evolution (Prentiss et al. 2016). Model-based approaches allow researchers to relax assumptions of constant change by using rate variation to their benefit. Broadly, *characters* that change quickly are used to resolve more recently derived *lineages* and more slowly evolving *characters* to resolve deeper divergences in the tree (Wright and Hillis 2014).

Here, we demonstrate three ways to explore rate differences between taxa (i.e., house styles). The first is to identify the variability of rates, which is achieved by examining the shape of the gamma distribution that is estimated from our Bayesian analysis. The mean gamma shape estimate from our analysis of house styles is 0.95, which produces a skewed, long-tailed distribution, which suggests our data consists of a majority of slow rates but also a few more quickly evolving artifact *lineages* (see Fig. 9.3a). Our model selection results reinforce this notion by indicating that best-fitting division of our gamma distribution is into four rate categories, so that most of our *lineages* are evolving slowly, but a few are evolving much more quickly. We can also plot all the branch lengths from the trees that were sampled by the *MCMC* and view the distribution of substitution rates. We can see in Fig. 9.3b that a majority of our branch lengths have fairly small amounts of change, but we do have some branches that demonstrate longer branch lengths and therefore greater rates of change. Finally, we can map substitution rates from our Bayesian analysis onto each branch of our maximum clade credibility tree to visually examine which branches of the tree may be changing fast or slow in relation to other branches (see Fig. 9.3c). Plotting trait values onto tree topologies is most easily accomplished using the functions associated with phytools (Revell 2012).

Divergence Time Estimates (Time Calibration)

One of the most potentially informative aspects of model-based phylogenetic inference is its ability to estimate times of divergence. Early applications of divergence time estimation typically used a strict clock where change was assumed to be constant. In more recent approaches, where we fully expect *rate heterogeneity* across the tree, calculating divergence time estimates requires supplemental dating information. In general, the branch lengths of a tree created from a model-based framework are proportional to the amount of change in that branch, typically expressed as the rate of substitution (Greenhill and Gray 2009). In order to time calibrate our phylogeny, we need to add calibration points. In other words, we need to place age ranges on certain nodes of the tree, which in turn allows certain branches of the tree to either change faster or slower than others depending on the date estimate. When chronological information of artifact *lineages* is known precisely, then divergence time estimates may not provide increased resolution. However, in cases were little chronological information is available, as is common with languages or cultural traits, divergence time estimates can provide intriguing insights into the evolutionary histories of populations (Gray and Atkinson 2003; Gray and Jordan 2000).

In this example, we used a combination of existing radiocarbon dates and generally accepted Plains Village age ranges to time calibrate our maximum clade credibility tree. We constrained divergence points for house features associated with the Central Plains to 1050–1250 AD, Middle Missouri to 1000–1300 AD, and Coalescent to 1300–1600 AD. Each house feature used in the analysis was also given a mean date of occupation based on chronological data from Johnson (2007), O'Shea and Ludwickson (1992), Smith (1972), and Wedel (2001). The resulting time-calibrated tree can be seen in Fig. 9.4. This tree was also produced using BEAST2 (Bouckaert et al. 2014) with tip dates added to the dataset through the tip dates option in BEAUTi. The range of ages associated with each monophyletic clade was incorporated into the analysis by adjusting the shape of the log normal distribution in the prior section of the BEAUTi.

Diversification Rates (Origination and Extinction)

The goals of cultural macroevolution find strong parallels with research themes in evolutionary paleobiology such as measures of taxonomic diversity, rates of taxonomic change, the quality of preservation, and stratigraphy (Foote 2000). The parallels are undoubtedly influenced by similar limitations of the fossil and archaeological records, such as sampling and preservation biases.

One of the more significant advancements in paleontology is the ability to estimate diversification rates from occurrence data, which at a minimum is a set of two dates for the first and last appearance

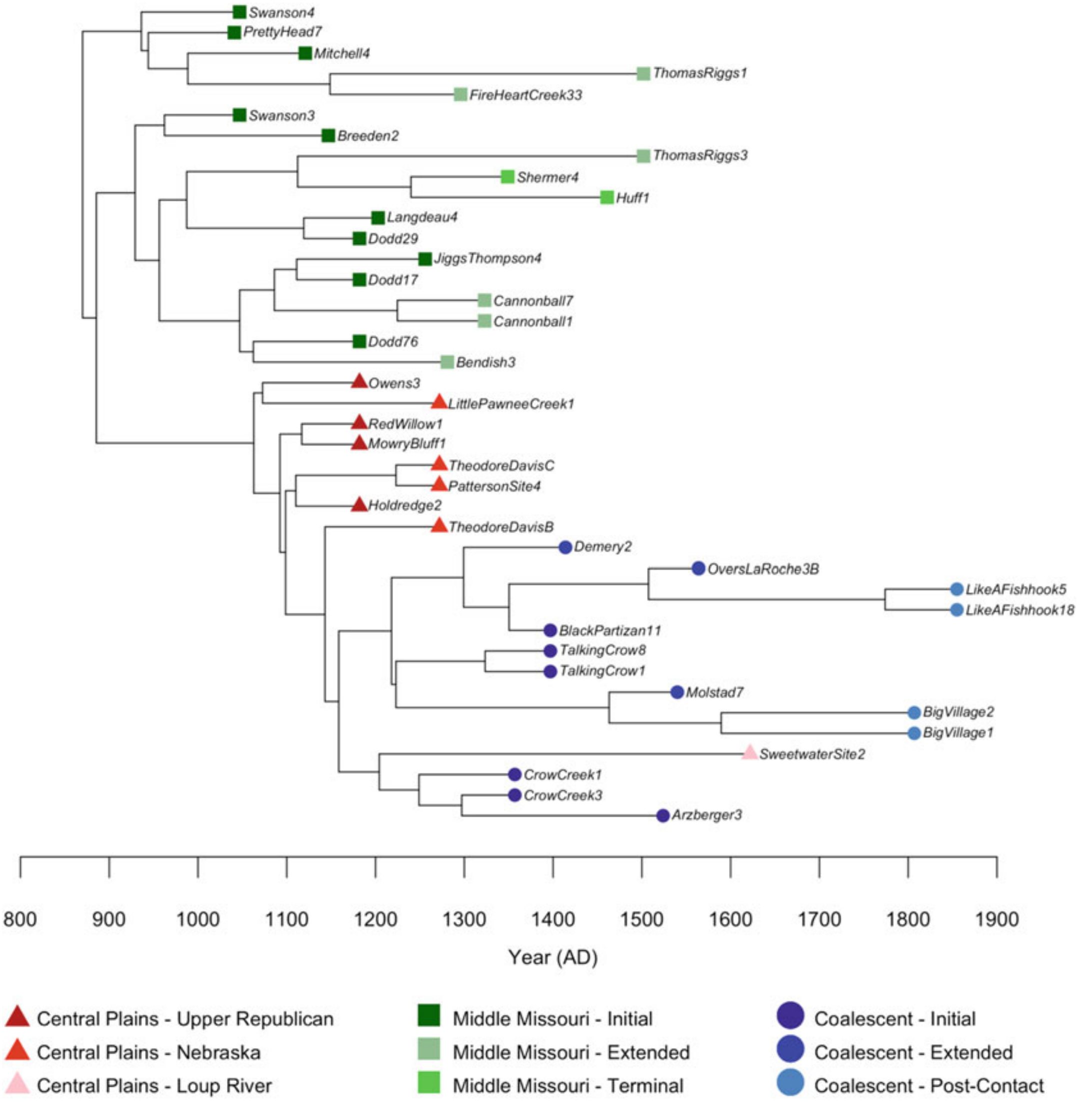

Fig. 9.4 Time-calibrated maximum clade credibility tree

of a *lineage* (or only one date if a *lineage* is extant). Given that the times of first and last appearance in the fossil record are unlikely to reflect true origination or extinction events, refinements have been made to estimate rates of diversification from incomplete data (Foote 2001; Foote and Raup 1996). Recently, paleontological methods have implemented Bayesian inference to model the dynamics of origination and extinction from incomplete occurrence data (Silvestro et al. 2014). We argue here that these methods provide an intriguing set of tools for archaeologists as they minimize phylogenetic assumptions such as the contemporaneity of taxa and a constant rate of extinction over evolutionary history. For an example of these emerging paleontological methods applied to modern technological data, see Gjesfjeld et al. (2016).

Here, we applied a Bayesian approach to estimating diversification rates (Fig. 9.5) from occurrence data as outlined by Silvestro et al. (2014). This approach uses the program PyRate, which is implemented in python with code and tutorials freely available (Silvestro 2018). Once again, temporal

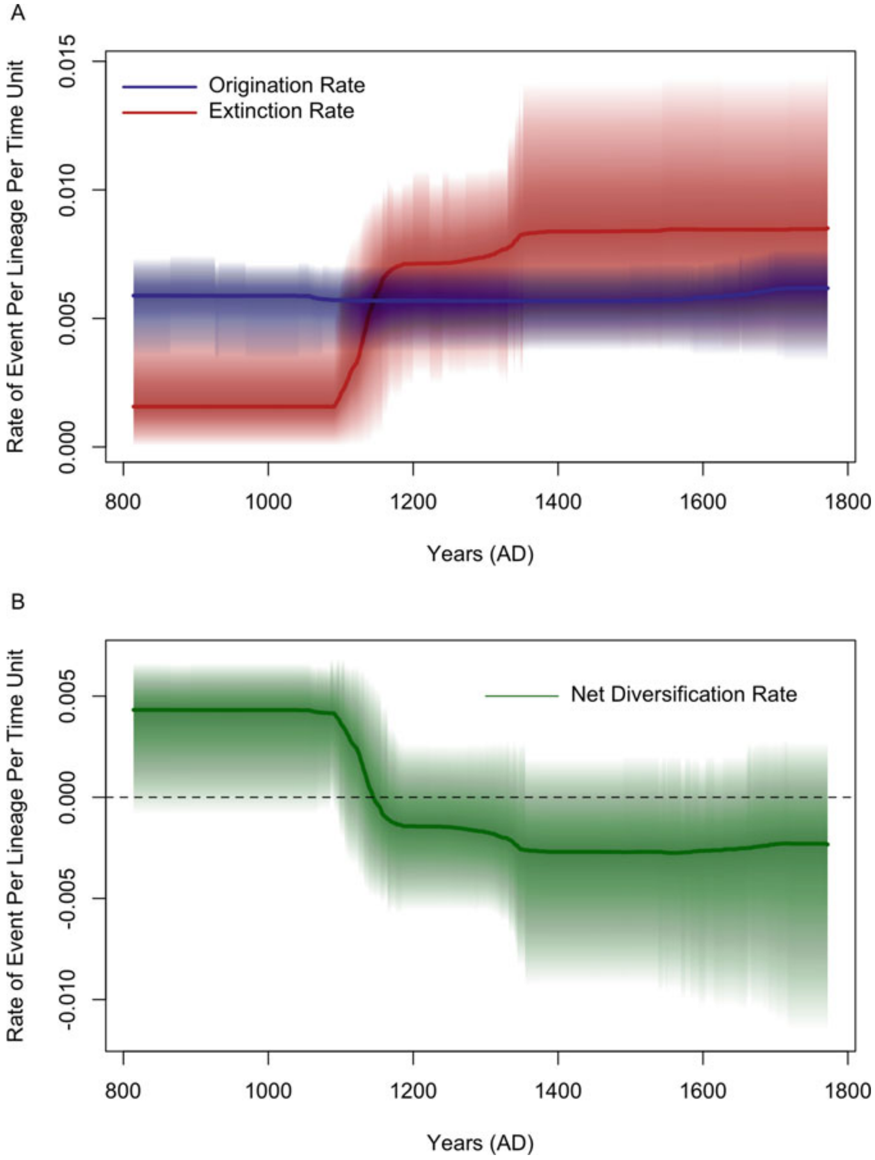

Fig. 9.5 Origination and extinction rates (**a**) of house styles across all three Plains Village traditions (Central Plains, Middle Missouri, and Coalescent). Net diversification rate (**b**) is calculated by subtracting the extinction rate from the origination rate with the dotted line indicating a net diversification of zero. If the net diversification rate is above this line, then diversity is increasing, whereas values below this line suggest diversity in house styles is decreasing. Shaded areas represent the 95% highest *posterior* density

data was derived from a combination of radiocarbon dates and established cultural chronologies so that each house style could be assigned an estimated date of first and last appearance (or age range). If radiocarbon dates could be tied to a specific house structure, then these dates were used; otherwise dates were aggregated for each cultural variant. It should be noted that many of the radiocarbon dates used in this work were compiled and calibrated by the Plains Village Dating project with the results published as an excellent monograph by Johnson (2007).

Archaeological Interpretations

The Bayesian frameworks highlighted above provide various pieces of evidence with which to evaluate our archaeological expectations and build archaeological interpretations. Evidence produced includes (1) a maximum clade credibility tree that hypothesizes the evolutionary relationships between house styles, (2) *posterior* probabilities that can indicate support for the *topology* of the tree, (3) insights into how fast or slow each house style is changing in relation to other house styles in the analysis, (4) estimates for the time in which each house style (or cultural tradition) last shared a common ancestor, and (5) the overall rate of house style diversification based on occurrence data. We believe that the additional pieces of evidence that result from our Bayesian approaches help to not only evaluate our existing expectations but also build hypotheses about patterns of cultural macroevolution.

Our first expectation posited limited shared ancestry between the Central Plains tradition and the Middle Missouri tradition. With the possible exception of the house style associated with Little Pawnee Creek, house styles associated with the Middle Missouri tradition demonstrate a nearly complete *monophyletic clade* and a clear divergence from house styles associated with the Central Plains and Coalescent traditions. This lends support to theories that view the ancestral history of Middle Missouri populations as strongly different from their neighbors to the north and south (Wood 2001). This phylogenetic result is an encouraging "proof of method" as significant differences in Middle Missouri house shape and size have been well-chronicled in Great Plains archaeology (Lehmer 1971).

We can draw from our additional pieces of evidence to suggest that the lack of shared ancestry between Middle Missouri and Central Plains traditions is not due to a more recent, rapid evolution of house styles in either tradition. Overall, we see rates of *character state* change (or substitution rate) remain low across the tree (Fig. 9.2b, c) with only a few sites demonstrating higher rates of change (Dodd, Swanson, Little Pawnee Creek). These observed rates of change are on average slightly slower then rates of linguistic evolution (Greenhill et al. 2010) but still firmly within the range of variability. This suggests that the differences in house style morphology are more likely due to longer independent origins rather than more recent origins with rapid independent adaptation to different social and environmental circumstances.

The second expectation highlighted in this work is the potential for shared ancestry between the Central Plains tradition and the Coalescent tradition. The MCCT tree that results from our Bayesian analysis suggests that house styles from the Central Plains are more closely related to house styles from the Coalescent than they are to the Middle Missouri. However, two distinct clades in the bottom half of the tree generally divide house styles associated with the Coalescent tradition and house styles associated with the Central Plains tradition. Perhaps the most intriguing is that the three Coalescent house styles (Crow Creek House 1, Crow Creek House 3, Arzberger House 3) that are most closely related to Central Plains house styles all are associated with the Initial Coalescent variant. This would suggest that fairly substantial differences exist between house styles associated with the Initial Coalescent and those associated with later Extended and Post-Contact house styles like those from Big Village and Like-A-Fishhook village. It is important to note that good archaeological data for the diversity of house styles during the Post-Contact variant is hard to come by as some villages were extremely large, but most were likely much smaller and scattered around the landscape (Lehmer 2001).

The broader macroevolutionary pattern that can be extracted from our suite of Bayesian analyses is that changes in Plains Village house styles are generally regular over time, but some time periods and house styles show higher rates of change. Our estimation of diversification rates (Fig. 9.5) based on occurrence data demonstrates a strong rise in the extinction rate between 1100 and 1250 AD, which suggests a decrease in house style diversity over this time period. This can also be identified in the time-calibrated tree which highlights numerous divergence events during this time frame and a clear expectation of Central Plains and Coalescent divergence.

Undoubtedly, the quality and resolution of house style dates plays a significant role in creating this pattern, but the results do demonstrate that the rate of house style loss is not constant through time.

These results suggest that the strongest influence on the diversity of house styles is not the innovation of new house styles but rather the disappearance of previous house styles. This may indicate that the cultural evolution of Plains Village traditions is not indicative of gradual change but rather a complex series of punctuated events (such as village abandonments).

In summary, through the application of our Bayesian framework, we are able to collaborate existing archaeological perspectives that the Middle Missouri and Central Plains traditions do not appear to share a recent common ancestor and any similarities are more likely due to independent convergence. In addition, the emergence of the Coalescent tradition appears to be more heavily influenced by the Central Plains tradition than the Middle Missouri tradition. Potential new insights that are gained through our approach include the acknowledgment of a fairly stable origination of new house styles through time but a period of increased divergence and loss of house style *lineages* between 1150 and 1300 AD.

The Future of Model-Based Phylogenetics in Archaeology

Phylogenetic inference is an undeniably powerful set of tools with which infer macroevolutionary patterns, but it does not come without challenges. Some concerns are conceptual in nature, in that artifact lineages are impacted by many different cultural transmission processes that can obscure our attempts to reconstruct evolutionary relationships. Other concerns are methodological, such as inherent assumptions about the non-independence of characters or a branching pattern of evolutionary change. Here, we suggest that for the effective use of model-based phylogenetics using archaeological data, we must continue to not only refine our models of evolutionary change but also our expectations for the archaeological questions we are able to answer.

For example, previous applications of phylogenetic inference using archaeological data often sought to infer microevolutionary processes from macroevolutionary patterns. One of the most common, and perhaps incorrect, expectations was that tree topologies could provide insights into cultural transmission processes such as the degree of vertical transmission or horizontal transmission. Broadly, the degree of transmission was evaluated by interpreting the consistency or retention index (RI) provided in a cladistic analysis. The RI examines the relationship between the fraction of possible *homoplasy* in the tree divided by the maximum possible value of *homoplasy* with values closest to zero indicating complete *homoplasy* and values closer to one indicating no *homoplasy* (Tripp 2016). The predominant view is that higher RI values indicate a stronger fit of the data to bifurcating tree model with a related assumption of greater vertical transmission, whereas lower RI values indicated higher amounts of horizontal transmission. Based on research from Crema et al. (2014) and Nunn et al. (2010), we view high RI values as potentially indicative of vertical transmission but also view interpretations of horizontal transmission from low RI values with skepticism due to numerous confounding effects. Future application of either cladistic or model-based phylogenetic inference needs to rely on not a single tree metric but rather responsible use of a range of various tests and metrics to evaluate the relationship between data and tree topology (Marwick 2012).

Given what we know about the dynamics of cultural evolution, we have reason to believe that our models of technological change are overly simplistic. However, we view an explicit modeling approach that requires exposing our assumptions about evolutionary change as an opportunity to continually refine and test models of macroevolution. One of the distinct advantages of a model-based approach is to select and adjust model *parameters* to better fit our data. The process of finding the best-fitting model not only improves confidence in our phylogenetic inference but also allows us to explore the variability of our data. For simplicity, we chose to compare the fit between models within the same general family (the *Mk model*) with various combinations of initial model settings. However, there is nothing to limit us from exploring a wider range of model families that may align more closely to assumptions we have about our data. If we look at the Bayesian approach as applied in linguistics, we see the comparison of numerous models of *character* change including the continuous-time Markov chain (CTMC) model, the covarion model, and the stochastic Dollo model. The Dollo model, for example, is based on a model of *character* evolution where once a feature is lost, it can never be regained. Depending on the data, the Dollo model may at times perform poorly, whereas the covarion or CTMC model may perform better (Bouckaert and Robbeets 2017).

In evolutionary biology, the ability to infer macroevolutionary patterns has been greatly facilitated in recent years by emerging computer programs such as PyRate (Silvestro et al. 2014), which was used above to estimate diversification rates from occurrence data. This program has a similar goal of estimating rates of diversification but does so based on occurrence data and not on a tree *topology* produced from a paradigmatic classification of artifact traits. Furthermore, PyRate removes any strict assumptions about the underlying model of evolutionary change or the "tree-likeness" of the data. We view these new Bayesian tools as holding incredible potential for modeling emergent macroevolutionary patterns without imposing potentially difficult and unwarranted assumptions about material culture change.

Conclusions

We have demonstrated a working example of how Bayesian phylogenetics can be used to study macroevolutionary patterns in archaeological data. Through this case study, we emphasized that Bayesian approaches can facilitate new questions and understandings about the tempo of change in artifacts, time periods of cultural divergences, and the unique macroevolutionary dynamics of material culture. Our Bayesian approach was applied to a dataset of 40 house styles that were associated with the Central Plains, Middle Missouri, and Coalescent traditions of the Great Plains Village period. We highlight that our phylogenetic analysis broadly agreed with our archaeological expectations for the relationship between these traditions but also provided new insights into the variability of changes between house styles and the importance of village abandonment between 1100 and 1250 AD in shaping the diversity of house styles in the archaeological record. We believe that this is one of the first examples of a thoroughly Bayesian approach to an explicitly archaeological data set, and we hope that by sharing this worked example, other researchers will be encouraged to follow a similar approach.

Despite the limited use of model-based phylogenetics in archaeology to date, we believe that the methodological approach taken here can provide a new generation of insights into the dynamic patterns of macroevolution. We see that model-based approaches to phylogenetic inference as important in operationalizing our interests in macroevolutionary patterns as they provide a robust framework for testing different models of *character* change and estimating rates of diversification from our tree *topologies*. As we continue to develop more informed models of cultural change, we are optimistic that model-based phylogenetics may help to illuminate novel evolutionary patterns that we are not yet aware of. Ultimately, we aim to more fully integrate phylogenetic analyses with the wealth of archaeological and ethnohistorical data that we already have to achieve a fuller and more holistic understanding of how macroevolutionary processes have contributed to cultural diversity and change.

Data Sharing Statement The data and help files supporting the results of the book chapter are available in repositories at Zenodo (DOI: https://doi.org/10.5281/zenodo.1443276) and GitHub (https://github.com/erikgjes/Bayes_Phylogenies).

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Chapter 10
Cultural Macroevolution and Social Change

Charles S. Spencer

Introduction

In this chapter I discuss the macroevolutionist approach to the study of sociopolitical transformations, paying particular attention to how this perspective can help us identify the key manifestations of major social change in the archaeological record. Building upon the framework discussed in Prentiss et al. (2009a), I add some ideas from recent research in evolutionary archaeology as well as from evolutionary biology and even a bit of physics. I then apply this modified macroevolutionist framework to archaeologically documented trajectories of social change. But first, I will review the historical background of the research problem at hand.

Background: The Research Problem and the Debate

If you drive across the Río Grande into Mexico and keep heading south, you will eventually arrive in the Valley of Oaxaca, the Zapotec homeland, perched a mile above sea level amidst the peaks and ridges of the Sierra Madre del Sur. The archaeological record here is bountiful and has attracted several generations of researchers, whose discoveries add up to a thrilling tale of cultural evolution (Flannery and Marcus 1983a; Marcus and Flannery 1996). The evidence is reported in numerous publications but can also be seen, firsthand, in the archaeological sites themselves. Consider just two landmarks on this evolutionary path. The first is Guilá Naquitz (Fig. 10.1), a small cave in the thorn forest above the town of Mitla, in the eastern or Tlacolula subvalley of the Oaxaca Valley. Guilá Naquitz is one of several sites that seasonally nomadic hunter-gatherers occupied during the Archaic Period in Oaxaca (ca. 8000–2000 B.C.). The cave floor of Guilá Naquitz measured about 9 m by 4 m. Excavations directed by Kent Flannery indicated that the cave was occasionally occupied during the dry season (November–April) by a microband of perhaps 4–6 people, who exploited the agave or century plant (*Agave* spp.), hunted deer, peccary, and cottontail rabbit and cultivated early forms of domesticated maize and squash (Flannery 1986; Marcus and Flannery 1996, pp. 54–57; Piperno and Flannery 2001; Smith 1997). During the wet season (May–October), the Guilá Naquitz occupants probably aggregated with other microbands at a macroband site such as Gheo-Shih, an open-air camp

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Fig. 10.1 Guilá Naquitz cave, a hunter-gatherer camp of the Archaic period (8000–2000 B.C.), in the eastern branch of the Oaxaca Valley, Mexico

site covering 1.5 ha in the alluvial zone of the Río Mitla, a prime habitat for mesquite trees whose nutritious pods were ready for harvest between July and September. Gheo-Shih not only was the largest site of its time but also has produced the only evidence (so far) of Archaic Period public architecture in Oaxaca, consisting of two parallel lines of boulders, 20 m long and 7 m apart. The 140-m^2 enclosure between the boulders had been kept relatively clean, even though artifacts were abundant on either side of the enclosure. To the excavators, this feature "most resembled a cleared dance ground, like the ones laid out by some Indians of North America at their macroband camps" (Marcus and Flannery 1996, p. 59).

Now let us leap forward in time to 100 B.C. At this point, human habitation in Oaxaca was stunningly different. The largest occupation was Monte Albán (Fig. 10.2), a city of 15,000 that sprawled across 440 ha on a hilltop overlooking the junction of the three radiating subvalleys (Etla-Central, Tlacolula, and Ocotlán-Zimatlán) that comprise the entire Oaxaca Valley (Blanton 1978; Blanton et al. 1982; Kowalewski et al. 1989). Survey archaeologists have determined that Monte Albán was one of 745 habitation sites in the Valley by 100 B.C., the temporal division between the Late Monte Albán I phase (300–100 B.C.) and the Monte Albán II phase (100 B.C.–A.D. 200). These sites were permanent, year-round settlements, home to agriculturalists whose diet emphasized domesticated maize, beans, chiles, and squash. By the Monte Albán II phase, a diverse array of some two dozen public/institutional buildings had been constructed in and around Monte Albán's Main Plaza, which measured 300 m by 200 m and was laid out by leveling rock outcrops and filling deep crevices, a massive construction effort (Acosta 1965, pp. 817–824). These public buildings included several multiroom temples, an I-shaped masonry ballcourt, an arrowhead-shaped structure

Fig. 10.2 The ancient city of Monte Albán; by the Monte Albán II phase (100 B.C.–A.D. 200) numerous public/institutional buildings had been constructed around the city's Main Plaza

(Building J) with carved "conquest slabs," and a number of altars or adoratories (Flannery 1983, pp. 103–104). Excavations at other sites in the Oaxaca Valley have recovered the remains of royal palaces and multiroom temples dating to the Late Monte Albán I and Monte Albán II phases (Flannery and Marcus 1976, 1983b, c, d; Redmond and Spencer 2013, 2017; Spencer and Redmond 2004a). The quantity and diversity of institutional buildings at this time are viewed as evidence of an administration that was both centralized and internally specialized—in short, a state form of government (Flannery and Marcus 1976; Spencer and Redmond 2004b; Wright 1977). Also, for both the Late Monte Albán I and Monte Albán II phases, one can detect a four-tier regional settlement hierarchy based on site size, another trait considered to be diagnostic of state organization (Flannery and Marcus 1983b, p. 82; Marcus and Flannery 1996, p. 162; Spencer and Redmond 2004b; Wright and Johnson 1975). Furthermore, there is archaeological evidence that Monte Albán had expanded its political domain far outside the Oaxaca Valley by this time, to include regions that lay up to 100 km distant from Monte Albán, such as the Sola Valley and the Cañada de Cuicatlán (Balkansky 2002; Spencer and Redmond 1997, 2001a). This evidence, dating to the Late Monte Albán I and Monte Albán II phases, is consistent with contemporaneous inscriptions of conquest on Building J, in Monte Albán's Main Plaza (Caso 1947; Marcus 1976, 1980). In sum, by 2000 years ago, the Monte Albán polity was a centralized, internally specialized state whose domain included not only the surrounding Oaxaca Valley but also some territories that lay well beyond a day's round-trip travel from the capital city. It has been argued that Monte Albán was the earliest state to emerge in Mesoamerica and that its successful strategy of territorial conquest was a key factor in the emergence of state organization here (Spencer 2003; Spencer and Redmond 2004b).

What lies between Guilá Naquitz and Monte Albán is not merely time or the conspicuous growth in human population, but rather a profound change in how society was *organized*. Multiple generations of Zapotec speakers were the actors in this process of increasing social and political complexity

(Flannery and Marcus 1983a), which can reasonably be considered an example of Darwinian social evolution, i.e., descent with modification mediated by selection or "what worked better than what" (Eldredge 1995, p. 34). Yet, we should also bear in mind that Darwin's framework (Darwin 1859), strictly speaking, can account for inter-generational persistence (or lack thereof) but harbors no necessary expectation of increasing complexity over the long term (Spencer 1997). In our Oaxaca case, it is significant that we observe not just change but directional and progressive change, from small and simple to big and complex. And therein lies the intrigue, which only deepens when one realizes that broadly similar—though completely independent—trajectories of major social change have been documented by archaeologists in at least five other parts of the world: coastal Peru, Egypt, Mesopotamia, the Indus Valley, and northern China (Flannery and Marcus 2012; Service 1975; Spencer 2010). These are cases where complex human societies, including those managed by state governments, emerged from simpler antecedent societies in a pristine fashion, without the assistance of organizational "blueprints" gleaned through contact with other preexisting complex societies (Spencer 2014). The question they pose for the researcher is perhaps the most fundamental and significant in all of anthropology: how and why did social change lead in certain cases to profound transformations of human society?

Taking note of the similarities exhibited by such widely separated developmental trajectories, researchers have wondered whether they could be analyzed from a comparative perspective and eventually understood as variant manifestations of some general, underlying evolutionary process—or, alternatively, whether each trajectory should be analyzed on its own terms, as a unique phenomenon best understood from a strictly historical viewpoint. This debate was already underway in the early years of anthropology. In *Ancient Society*, Lewis H. Morgan (1877) embraced the comparative, generalizing approach and proposed his Savagery/Barbarism/Civilization scheme of progressive evolutionary development, in which the primary organizing principle was a series of technological innovations, accompanied by social and political developments. His assessment of the available evidence led him to conclude: "Progress has been found to be substantially the same in kind in tribes and nations inhabiting different and even disconnected continents, while in the same status, with deviations from uniformity in particular instances produced by special causes" (Morgan 1877, p. 18). Edward B. Tylor also saw an overall direction in human history from simple to complex: "not a history of a course of degeneration, or even of equal oscillations to and fro, but of a movement which, in spite of frequent stops and relapses, has on the whole been forward" (Tylor 1870, p. 193, cited in Carneiro 2003, p. 28).

Shortly after, Franz Boas took a critical stance in *The Limitations of the Comparative Method of Anthropology*: "we must consider all the ingenious attempts at the construction of a grand system of the evolution of society as of very doubtful value, unless at the same time proof is given that the same phenomena could not develop by any other method. Until this is done, the presumption is always in favor of a variety of courses which historical growth may have taken" (Boas 1896, p. 905). As an alternative, Boas offered the "historical method," the objective of which would be to record "the histories of the cultures of diverse tribes" (Boas 1896, p. 907). Although Boas is credited with fathering the *historical particularist* school of anthropology (e.g., Harris 1968), it is not as widely recognized that he gave himself some cover on the issue of comparative analysis and generalizing theory: "When we have cleared up the history of a single culture and understand the effects of environment and the psychological conditions that are reflected in it we have made a step forward, as we can then investigate in how far the same causes or other causes were at work in the development of other cultures. Thus by comparing histories of growth general laws may be found" (Boas 1896, p. 907). But more strident views were expressed by other advocates of the historicist approach: "The theory of cultural evolution, to my mind, the most inane, sterile, and pernicious theory ever conceived in the history of science (a cheap toy for the amusement of big children), is duly disparaged . . . All the practical investigator can hope for, at least for the present, is to study each cultural phenomenon as exactly as possible in its geographical distribution, its historical development, and its relation or association with other kindred ideas" (Laufer 1918, pp. 90–91).

Although evolutionism fell out of favor in early twentieth century anthropology, it was making a comeback by mid-century, nurtured by archaeologist V. Gordon Childe and ethnologist Leslie White. In 1936, Childe published *Man Makes Himself*, in which he made the case for "an analogy between organic evolution and progress in culture. Natural history traces the emergence of new species each better adapted for survival, and more fitted to obtain food and shelter, and so to multiply. Human history reveals man creating new industries and new economies than have furthered the increase of the species and thereby vindicated its enhanced fitness" (Childe 1983, p. 12). Childe presented a scheme that saw all cultures evolving through a series of general developmental stages, from food-gathering societies through a Neolithic revolution to village farming societies, and then through an urban revolution to civilization (Childe 1950, 1951, 1983). White advocated the study of cultural evolution and proposed that the evolution of more complex forms of culture will be associated with major increases in the energy harnessed by the evolving social system (White 1949, 1959)—what some have called "White's Law" (Carneiro 2003, p. 192).

The evolutionist approach gained support from archaeologists and ethnologists over the ensuing decades (Carneiro 1970, 1981; Flannery 1972; Flannery and Marcus 1983a; Fried 1967; Sanders and Price 1968; Service 1962, 1975; Steward 1949, 1955). Yet, such efforts have drawn criticism from some researchers (Feinman and Neitzel 1984; McGuire 1983; Upham 1987; Yoffee 1979, 1993, 2005). Feinman and Neitzel (1984) aimed to assess stage-like schemes like Service's (1962) Band/Tribe/Chiefdom/State model or Fried's (1967) Egalitarian Society/Ranked Society/Stratified Society/State framework by analyzing a sample of 63 New World societies from the ethnographic and ethnohistoric literature. They selected their sample to represent just the Tribe/Chiefdom (or Egalitarian/Ranked) portion (the "middle range") of the Service or Fried schemes (Feinman and Neitzel 1984, pp. 45–46). After studying the patterns of covariation among leadership functions, social differentiation, political complexity (number of administrative levels), and population sizes of the major community and the polity as a whole, they concluded: "The continuous distribution of each examined attribute and the complexities of the relationships among them indicate that serious inadequacies characterize the typological approach to societal diversity" (Feinman and Neitzel 1984, p. 72). At the same time, they also acknowledged the essentially synchronic nature of their cross-cultural analysis, noting that "Synchronic studies can only demonstrate correlations and cannot reveal the historical or causal processes responsible for societal variation . . . Long-term processual studies are necessary" (Feinman and Neitzel 1984, p. 78).

In a paper on the chiefdom concept (Spencer 1987), I concurred with Feinman and Neitzel's call for more diachronic studies: "the essential evolutionary issue here seems to be whether the overall tempo of cultural evolution is always gradual and continuous or whether times of continuous change have been punctuated on occasion by periods of very rapid, transformational change. A stage-wise approach to cultural evolution would imply, for instance, that the transition from egalitarian society to chiefdom and from chiefdom to state in any particular developmental sequence ought to be more punctuational in character than the processes of growth and/or decline within the chiefly *Bauplan* . . . Questions concerning the tempo and mode of cultural evolution will be best approached, I think, through the diachronic examination of specific cultural system trajectories" (Spencer 1987, p. 381). My use of the term *Bauplan* (Mayr 1982, p. 468) was based on an analogy between cultural and biological evolution and particularly upon the recognition by biologists that "a relatively meager number of fundamental patterns underlie a great animal diversity" (Frazetta 1975, p. 237). As Prentiss et al. (2009b) have more recently pointed out, *Bauplan* (*Bauplane*, pl.) is a German term that can be translated as "ground plan" or "engineering design" and is used "to define a basic organizational structure for entire monophyletic clades" (Prentiss et al. 2009b, p. 10). A similar analogy between biological and social evolution was drawn by Flannery (1995, p. 4): "In both fields, scholars have defined *stages of evolution*, mutually-agreed upon units which allow researchers to discuss common problems." He suggested that the biological-evolutionary sequence of bony fishes, amphibians, reptiles, birds, and mammals is analogous to such social-evolutionary sequences as bands, tribes, chiefdoms, and states—or, in his phrasing, band societies, autonomous village societies, rank societies, and archaic states.

I contend that we can distinguish between the chiefdom and state *Bauplane* as follows: a chiefdom is a regional polity consisting of a number of villages under the rule of a paramount chief, whose administrative authority is centralized but not internally specialized; by contrast, a state has an administration that is both centralized and internally specialized, which allows the state to effectively delegate partial authority to specialized administrators and thus integrate a much larger territory and population than a chiefdom (Wright 1977; Spencer 1990). I have argued that the lack of internal administrative specialization in a chiefdom inhibits its ability to delegate partial authority, and this, in turn, places a limit on the size of the political territory it can integrate; that limit may lie in the vicinity of about 1-day round-trip from the chiefly center, which would be a radius of roughly 25 km for pedestrian travel (Spencer 1987, 1990). I join others in postulating that chiefdom organization is a necessary precursor of the state in any evolutionary trajectory (e.g., Carneiro 1981; Flannery 1995; Earle 1987; Wright 1977); before a regional administration can be both centralized and internally specialized, it must first be centralized (Spencer 1990). The potentially larger size of the nascent state would be expected to give it a selective advantage over smaller polities in most competitive situations; consequently, over the long term, a directional trend will be imparted to cultural evolution (Carneiro 1992; Kosse 1994). This does not mean, however, that the evolution of the state is inevitable. Both chiefdoms and states are dynamic entities and are capable of exhibiting considerable variation while adhering to the basic design of their respective *Bauplane*. For example, chiefdoms are especially prone to recurring cycles of political growth, signaled by an increase on the power and resources controlled by the central chiefly authority, followed by decline (Anderson 1994, 1996; Menzies and Haller 2012; Redmond et al. 1999). The growth part of this cycle is ultimately limited by the aforementioned territorial constraints on effective political-economic management that result from the centralized but not internally specialized nature of chiefly decision-making.

Whether we should expect the emergence of new sociopolitical *Bauplane* to come about gradually or punctuationally was the focus of Spencer (1990), in which I used archaeological data as well as diachronic ethnohistoric data to analyze the tempo and mode of several cases of early state formation, some of which were successful over the long term while others were not. For example, in Tonga between A.D. 950 and A.D. 1610 there were two attempts by the paramount chief of the time to establish the centralized and internally specialized administration characteristic of state organization (Wright 1977). In both cases, central authority was shared with just one new administrative official, who soon usurped the chiefly leadership. A more successful attempt at state formation occurred in Hawai'i toward the end of the sixteenth century A.D., when Umi-a-Liloa brought the entire Big Island under unified control for the first time, dividing it into six administrative districts that were run by appointed lesser chiefs and promoting widespread specialization of religious, political, and economic roles. This early state was short-lived, however. Upon Umi's death, he was succeeded by his eldest son who was not as adept at rulership, and the administrative system built by Umi soon disintegrated. The next episode of state formation in Hawai'i took place in the nineteenth century and enjoyed longer-lasting success: Kamehameha I's access to European firearms and political advice helped him overcome opposition and establish his authority over not only the entire Big Island but also over most of the other large islands of the chain as well (Kirch 2010).

Turning to two archaeological cases of early state formation, Teotihuacan and Monte Albán, I highlighted these contextual differences: (1) surrounding the Oaxaca Valley were a series of lightly populated but fertile canyons and valleys that were tempting prey for a Monte Albán leadership that chose interregional conquest as a way to advance its political-economic agenda, but had to develop state institutions in order to carry out this expansionist strategy successfully; and (2) Teotihuacan's rise to political dominance in the Basin of Mexico was surely aided by the volcanic eruption leading to the abandonment of Cuicuilco, its greatest competitor in the period just prior to its dramatic ascendance. Yet, these differences notwithstanding, I concluded: "in both cases, state emergence involved a process of internal differentiation of central authority that came about at a relatively rapid pace. These archaeological cases, like the ethnohistorical ones discussed earlier, are consistent with a transformationalist view of state development, which suggests that we should look with renewed interest at the stepwise frameworks of neoevolutionism" (Spencer 1990, p. 23).

It is fair to say that this suggestion was not widely followed and the evolutionist approach has been subjected to continuing criticism for, among other things, being excessively "top-down" in its focus on leadership and administration while ignoring other dimensions of cultural variability (Blanton and Fargher 2008; Blanton et al. 1996; Feinman 2012) and using a flawed comparative method that neglects the unique histories of different societies (Pauketat 2007, 2010; Yoffee 2005). Criticizing the chiefdom concept in particular, Pauketat (2010, p. 168) argued that scholars should "dispense with those naïve, delusional constructs derived from ethnographic readings of 'documentary history' that, by projecting a societal analogy derived from one time or place onto another in the distant past, block the way forward." His preferred "historical-processual" method (Pauketat 2000, 2001a, b) emphasizes the study of "traditions" as "continuous and historically contingent enactments or embodiments of . . . attitudes, agendas, and dispositions" (Pauketat 2000, p. 115), an approach that brings to mind the culture history school in American archaeology (Willey and Sabloff 1974). In response, I would point out that a focus on each trajectory as unique will inevitably preclude the recognition of broadly shared patterns and processes.

Meanwhile, other archaeologists have been engaged in comparative analyses (Drennan and Peterson 2006, 2012; Smith 2012), some of which have lent support to the evolutionist position. For example, utilizing data in the electronic Human Relations Area Files Collection of Archaeology, Peregrine et al. (2004) applied a Guttman Scale analysis to test for universal patterns in cultural evolution. They examined a dataset of 15 variables coded for 8 regional evolutionary sequences (Yellow River Valley, Indus River Valley, Nile River Valley, Mesopotamia, West Africa, Highland Peru, Lowland Mesoamerica, and Highland Mesoamerica). The analytical results led them to conclude: "there are universal patterns in cultural evolution. Cultural traits evolve in regular ways and some traits appear to co-evolve in punctuated evolutionary events that may parallel the typologies through which anthropologists frequently classify the cultures of the world" (Peregrine et al. 2004, p. 149). There is little doubt that the debate between the historicist and evolutionist views of social change—a fundamental tension that dates back to the earliest years of anthropology—is still with us. To move forward, it is more important than ever for evolutionists to present their ideas in ways that are not only theoretically grounded but also verifiable with empirical data, a goal toward which I will take some steps in the next section.

Microevolutionary Variation and Macroevolutionary Transformations

Underlying the various contributions in Prentiss et al. (2009a), I suggest, was an assumption of intellectual consilience between evolutionary anthropology and evolutionary biology (sensu Wilson 1998). In the volume's introduction the editors noted: "microevolutionary and macroevolutionary processes combine to produce evolution in the long term. This is an inclusive view of the evolutionary process that is at odds with programs that exclude action at higher levels of cultural organization" (Prentiss et al. 2009b, p. 11). The interplay between microevolution and macroevolution is a concern for contemporary biologists as well (Arnold et al. 2001; Cooney et al. 2017; Reznick and Ricklefs 2009; see also Chap. 1 by Prentiss in this volume). Moreover, the cultural-macroevolutionist perspective is consistent with recent investigations in evolutionary biology that are attributing increasing importance to convergence—when unrelated species pursue similar adaptive solutions to similar problems—in shaping the world's array of evolutionary outcomes (Conway Morris 2003; Losos 2017; McGhee 2011). The growing interest in convergence represents a noteworthy change from previous views that emphasized historical contingency and the quirky unpredictability of evolution (e.g., Gould 1989; Gould and Lewontin 1979). Theorists of cultural evolution also recognize convergence as a key feature of cultural evolution: “out of the hundreds of possible ways that human societies could be organized, certain types of organization work so well that they show up over and over again throughout the world” (Flannery 1995, p. 21).

The macroevolutionary perspective is based on an explicit recognition of the “scalar hierarchy” of cultural organization—comprising the individual, household, village, region, and macroregion—a framework that invites the researcher to conceive of long-term change as the product of evolutionary mechanisms that operate on multiple organizational levels (Crumley 1995; Spencer 1997). Accordingly, a major research focus is the emergence of more inclusive forms of political organization (Crumley 1995). One example of this approach is the mechanism that Flannery (1972) termed *promotion*, through which centralized leadership appears on a higher level than had previously been the case, such as when a village headman becomes a regional paramount chief, or when a paramount chief becomes a state ruler whose domain includes more than one region. I have suggested that promotion, and the more inclusive control hierarchy it signals, are the products of *extrapolation*, defined as: “an extension or projection of the internal model of authority from one social unit to others on the same level of the scalar hierarchy” (Spencer 1997, p. 239). In the context of autonomous villages, an extrapolation attempt would involve a village headman attempting to extend his internal (villagewide) authority to other villages, which, if successful, can lead to the emergence of a centralized regional polity: the chiefdom (Spencer 1994). Another example would be when the chiefly leadership of one of several regional chiefdoms uses successful military force to expand the range of its intrapolity authority, linking the previously autonomous chiefdoms into a more inclusive state (Spencer 1998, 2010).

Whether such an extrapolation effort ultimately succeeds will of course be determined by selection: the newly created chiefdom (or state) must be able to deal with competitors and other challenges in order to reproduce itself and persist over the long term. Furthermore, as I have noted, “the act of extrapolation itself changes the relative impact of selection among levels of the scalar hierarchy” (Spencer 1997, p. 239). In the case of autonomous villages, selection on the inter-family and inter-village levels will tend to be stronger than selection on the multivillage (or regional) level. But, if the leadership of one of these villages embarks upon an extrapolation strategy, with the aim of extending its internal (intravillage) authority to other villages and establishing a regional chiefdom, this will increase the relative impact of selection on the multivillage level; the survival of the more inclusive social unit depends on withstanding challenges to its persistence. In analogous fashion, when the leadership of a chiefdom seeks to extrapolate its centralized regional authority to link other regional chiefdoms into a nascent state, there is a consequent increase in the relative importance of selection on the level of that new multiregional polity. This viewpoint is compatible with the ongoing resurgence of interest in multilevel selection models in biology, which recognize the crucial role played by shifts in the scale of selection to more inclusive levels as a key driver of macroevolutionary change (Wilson and Wilson 2007).

The transition from chiefdom to state, I would argue, can be conceptualized as a shift from one peak to another on an adaptive landscape; the chiefdom and state in this framework are seen as stable but also dynamic forms, capable of continuous microevolutionary variation around the adaptive peaks (Spencer 2009; see also Chap. 7 by Laue and Wright in this volume). We can expand this visualization to include the transition from autonomous village society to chiefdom (Fig. 10.3). A shift from one adaptive peak to another will involve not only quantitative but also discontinuous, qualitative change (Spencer 2009). Moreover, we should expect substantial energy costs to be involved in such a shift, in line with “White’s Law” (White 1959). An attempted transition from autonomous village to chiefdom, for example, will have a greater chance of success if the emergent centralized (though nonbureaucratic) regional authority is reinforced through the simultaneous appearance of changes in sanctification of authority, institutionalized social differentiation, and novel forms of prestige-good exchange and elite-directed warfare (Johnson 1982; Spencer 1987). Since additional resources will be needed to meet the costs of these institutional changes, the transition will be unlikely to succeed unless

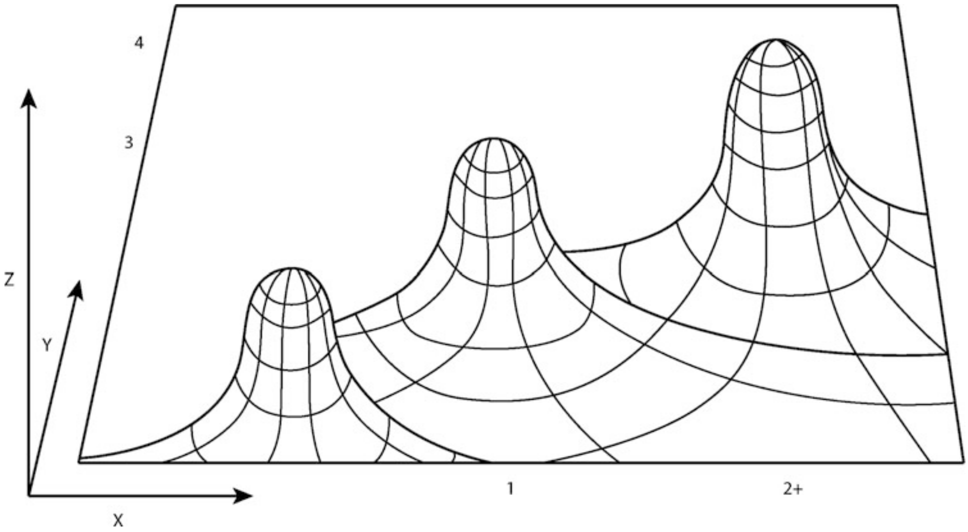


Fig. 10.3 Model of the macroevolutionary transition from autonomous village (tribal) society (*left*), to chiefdom (*middle*), to primary state (*right*), as depicted by a triple-peaked adaptive landscape. X = polity size, expressed in days of round-trip pedestrian travel from the first-tier center to the farthest edge; Y = administrative complexity, expressed in tiers in the polity's regional settlement hierarchy; Z = relative adaptedness

the emergent chiefly leadership can harness additional forms of energy. Infrastructural development aimed at generating increased surplus production (e.g., irrigation or other forms of agricultural intensification) can be an important strategy for meeting such energy needs (Spencer 1993; Spencer et al. 1994).

Parallel considerations also apply to the transition from chiefdom to state. My territorial expansion model of primary state formation attributes the emergence of bureaucracy to the novel administrative adjustments that need to be made when a regional chiefdom attempts to expand its political-economic territory to distant territories, those lying more than a day's round-trip travel from the political capital of the expanding polity (Spencer 1998). In order for such a strategy to enjoy long-term success, the expanding polity will have to develop the capacity to delegate partial authority to specialized military and civil administrators who can be dispatched to carry out the conquest or annexation and the long-term management of the target territories. Financing these developments obviously presents a challenge, but the effective mobilization of resources in the form of tribute will do much to defray the costs (Spencer 1982, 1990, 1998).

I also hypothesize that these transitions—from autonomous village to chiefdom or from chiefdom to state—will be more likely to persist if the strategic adjustments take place both rapidly and extensively; in short, we should expect a successful macroevolutionary transformation to be a more punctuational process than microevolutionary change (Spencer 1990, 1998). An analogous conclusion was reached by Cooney et al. (2017) in their recent study of the macroevolutionary dynamics of avian evolution. They conducted a global analysis of bill morphology in more than 2000 species of birds and found that after initial diversification the rates of bill evolution have been comparatively stable over time within and between clades. On rare occasions, however, they do observe major discontinuities in phenotypes that emerge in the context of rapid increases in evolutionary rate in a single clade, sometimes resulting in the establishment of new clades with novel morphological features. They conclude: "macroevolutionary processes underlying global-scale adaptive radiations support Darwinian and Simpsonian ideas of microevolution within adaptive zones and accelerated evolution between distinct adaptive peaks" (Cooney et al. 2017, p. 344).

How tempo and mode work together to generate major directional change has been explored by McShea (1994), who offered a useful distinction between *passive* and *driven* evolutionary trends, the latter of which are instrumental in macroevolutionary processes. McShea considered simulation studies as well as paleontological data pertaining to evolutionary trends and concluded: "the significance of the passive-driven distinction lies in the independence among hierarchical levels implied by the passive mechanism" (McShea 1994, p. 1761). In the case of a passive trend, there is a lack of correlation between adaptive fitness on different levels of the evolving system; selection processes are operating independently on each level. The converse of this, of course, is that "driven evolutionary trends should be associated with interdependent relationships among the hierarchical levels of evolving systems," a proposition with important implications for the study of cultural macroevolution (Spencer and Redmond 2001b, p. 201). When we examine an archaeological sequence, we would expect a macroevolutionary transformation—involving a shift from one major adaptive peak (*Bauplan*) to another—to be associated with *concordant changes on multiple levels of the system's scalar hierarchy*. The emergence of a chiefdom from antecedent autonomous villages, or the state from the preexisting chiefdoms, should be associated with concurrent changes on the level of the individual, household, community, and region, the evidence of which we would expect to observe in the archaeological record.

For instance, if we examine chiefdom emergence as a driven trend in a cultural sequence, we should expect to find evidence of political centralization and social differentiation evolving hand-in-hand (Johnson 1982); the appearance of a settlement hierarchy focused on a single large regional settlement ought to be accompanied by evidence of increased social inequality between communities and residential units. In analogous fashion, when a chiefdom transforms itself into a state by extending its political authority over previously independent chiefdoms, certain administrative changes will be necessary for this strategy to succeed, most notably the development of internal specialization of central authority (i.e., bureaucratization) and the concomitant capacity to delegate partial authority to military and civil subordinates who can be sent to manage the initial conquest and long-term control of distant territories (Spencer 1990, 1998, 2010). Thus, we would expect to find evidence of a concurrence between the appearance of an internally specialized administration and the expansion of political control to distant regions, with profound consequences for the inhabitants not only of the annexed regions but also the core area of the expanding polity. This would include evidence of the state's capacity to delegate authority and engage in direct intervention down to the local level—what Flannery (1972) called "linearization."

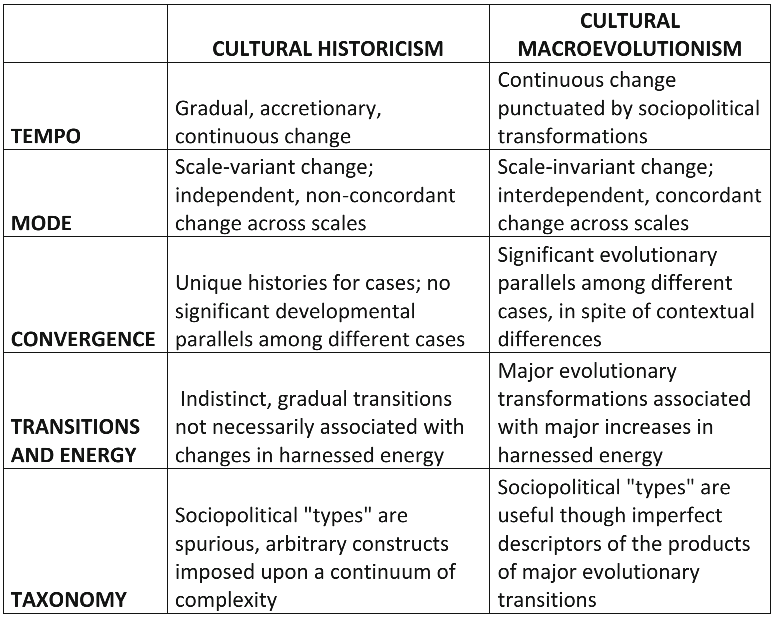
These expectations regarding driven evolutionary trends are consistent with an even more general view of change, the *Renormalization Group Theory* (*RGT*) of physicist Kenneth Wilson (1971a, b, 1979, 1983). Wilson originally applied RGT to phase transitions in physical systems, such as the transition between liquid and solid states, but his ideas are thought to be applicable to a broad range of phenomena (Kadanoff 2013). I suggest we draw an analogy between the tribe/chiefdom or chiefdom/state transitions and Wilson's phase transitions and then apply elements of RGT to the study of cultural macroevolution. In doing so, I will be assuming that the main value of any analogy lies in its heuristic utility: "finding new ways of thinking about old problems, finding linkages between what had previously looked like unconnected factors of lines of evidence, finding novel ways to bring data to bear on ideas" (Spencer 2009, p. 140). Analogy can help us generate the hypotheses or expectations with which we test theories against the empirical record. A key expectation of RGT is that, when an evolving system crosses the critical point of a major phase transition, it will exhibit *scale invariance*, that is, the transitioning system will show *self-similarity* at all scales of measurement, expressed as coordinated, directional variation on multiple scales or levels of organization (Altenberger and Dahler 2002). Applying this insight to cultural evolution, I suggest, leads to the expectation that *macroevolutionary transformations will be linked to a high degree of multiscalar concordance of microevolutionary variation.* This expectation of RGT is consistent with McShea's (1994) view that driven evolutionary trends are a consequence of interdependent selection among the various levels of a system's scalar hierarchy. The combination of McShea's and Wilson's perspectives strengthens the theoretical foundations—and shows the way for an empirical test—of cultural macroevolutionism.

Empirical Assessment of Cultural Macroevolutionism

In this section I assess the utility of cultural macroevolutionism by applying it to the empirical record of transformational social change. As a guidepost for the discussion, I offer a summary of the key expectations of the macroevolutionist framework and also, by way of comparison, the corresponding expectations from the culture-historicist perspective in terms of tempo, mode, convergence, transitions, energy mobilization, and sociopolitical taxonomy (Fig. 10.4).

While recognizing the considerable historical and contextual variation exhibited by cultures on a global scale, the macroevolutionist perspective would nonetheless expect us to observe *convergent patterns* in the long-term record of major social transformations, while the historicist perspective would not. In Spencer (2010), I addressed the convergence issue by carrying out a comparative assessment of what I called the territorial-expansion model of primary state formation, which argued that bureaucratization was required for the success of long-distance expansion that, in turn, would have generated the revenues necessary to finance the administrative transformation (Spencer 1998). I examined six major cases of first-generation state formation: Oaxaca, Peru, Egypt, Mesopotamia, the Indus Valley, and China. In each of the six cases, the first appearance of state institutions was contemporaneous with the first signs of long-distance territorial expansion of state control (often through aggression) to places much more than a 1-day round-trip from the capital, in line with the territorial-expansion model.

In Oaxaca, a four-tier regional settlement hierarchy (an indicator of state organization) appeared for the first time in the core area of the Monte Albán polity in the Late Monte Albán I phase (300–100 B.C.), contemporaneous with the earliest evidence of Monte Albán's conquest of the Cañada de



	CULTURAL HISTORICISM	CULTURAL MACROEVOLUTIONISM
TEMPO	Gradual, accretionary, continuous change	Continuous change punctuated by sociopolitical transformations
MODE	Scale-variant change; independent, non-concordant change across scales	Scale-invariant change; interdependent, concordant change across scales
CONVERGENCE	Unique histories for cases; no significant developmental parallels among different cases	Significant evolutionary parallels among different cases, in spite of contextual differences
TRANSITIONS AND ENERGY	Indistinct, gradual transitions not necessarily associated with changes in harnessed energy	Major evolutionary transformations associated with major increases in harnessed energy
TAXONOMY	Sociopolitical "types" are spurious, arbitrary constructs imposed upon a continuum of complexity	Sociopolitical "types" are useful though imperfect descriptors of the products of major evolutionary transitions

Fig. 10.4 Differing empirical expectations for cultural historicism versus cultural macroevolutionism

Cuicatlán, a separate region lying some 80 km north of Monte Albán and more than 40 km across mountain ridges from the northernmost end of the Oaxaca Valley (Spencer and Redmond 1997, 2001a). In Peru, there is evidence that an outpost of the early Gallinazo state was established at Huaca Prieta, located 80 km north of the state capital at the Gallinazo Group in the Virú Valley. A series of recently obtained radiocarbon dates place the Virú-Gallinazo presence at Huaca Prieta in the first century B.C, concurrent with the very early years of the Gallinazo state (Millaire 2010; Millaire et al. 2016). In Egypt, Hierakonpolis emerged as an urban center and a state capital around 3400–3200 B.C.; at the same time, it expanded its control over much of Upper Egypt, to places like Naqada and Abydos, 80 km and 140 km away (Bard 1994; Hoffman et al. 1986). In Mesopotamia, the site of Uruk (or Warka) emerged around 3500 B.C., with large and diverse temples and administrative buildings. There is evidence of Uruk outposts in the Susiana plain, some 250 km away, and even farther to the north (Algaze 1993, 2004; Johnson 1973). In the Indus Valley, the site of Mohenjo-daro emerged around 2500 B.C. as a state capital with diverse public buildings; this development was associated with evidence of the establishment of outposts as far as 400 km away, in the Kutch and Gujarat regions (Kenoyer 1991, 2008; Lawler 2008). China's first state was probably the Erlitou state, whose capital was the site of Erlitou, which grew by 1700 B.C. to urban proportions, with impressive institutional buildings, including at least two large palaces and specialized temple structures. There is contemporaneous evidence of Erlitou expansion to places as distant as Donglongshan, 250 km away (Liu 1996; Liu and Chen 2003). In each of these cases, the emergence of the state was concurrent with the expansion of its political-economic territory to areas that lay well beyond a day's round-trip from the home region. Moreover, the pattern of territorial growth in each case was notably asymmetric, probably because of variable relationships of acquiescence and resistance between the expanding polity and its neighbors (Spencer 2010).

The comprehensive comparative analysis by Flannery and Marcus (2012) also noted numerous evolutionary parallels among different cultural sequences from an array of regions around the world. And convergent patterning was discovered in the cross-cultural analysis carried out by Turchin et al. (2017), who concluded that "different characteristics of social complexity are highly predictable across different world regions. These results suggest that key aspects of social organization are functionally related and do indeed coevolve in predictable ways" (Turchin et al. 2017, p. E414).

There are salient differences between the expectations of the culture-historicist and macroevolutionist frameworks regarding the *tempo* and *mode* of major social change within a given developmental trajectory. From the culture-historicist framework, one would tend to view the development of increasing complexity as a continuously ramifying process; emphasis would be placed on the enormous amount of cultural variability and the alleged futility of trying to pigeonhole it into broad categories. By contrast, the macroevolutionist perspective would acknowledge this abundant variability but would tend to view cultural descent as a process characterized by periods of relative stability or gradual change that are punctuated by relatively rapid episodes of transformational, stepwise change, leading to new cultural forms that are both quantitatively and qualitatively more complex. We can evaluate the two alternative frameworks by examining how well their expectations match the empirical record of major social change. I now turn to two archaeological sequences of major social change; the first pertains to chiefdom formation in Venezuela, which occurred around A.D. 500–600; the second focuses on primary state formation in Oaxaca, Mexico, which took place around 300 B.C.

The Venezuelan research was conducted by Elsa Redmond and me in a study area that overlapped portions of the Andean piedmont and adjacent llanos (or savanna grasslands) in the state of Barinas (Redmond and Spencer 2007; Spencer and Redmond 2014). We documented cultural developments over some eight centuries of occupation, divided into two phases that are relevant to the problem of chiefdom formation. The first was Early Gaván phase (A.D. 300–550), during which there were three small occupations (3–5 ha each) with no earthen mounds, which we concluded were consistent with an uncentralized regional polity. The next period was the Late Gaván phase (A.D. 550–1000), which had 34 habitation sites of widely varying size and two drained-field agricultural sites (Fig. 10.5).

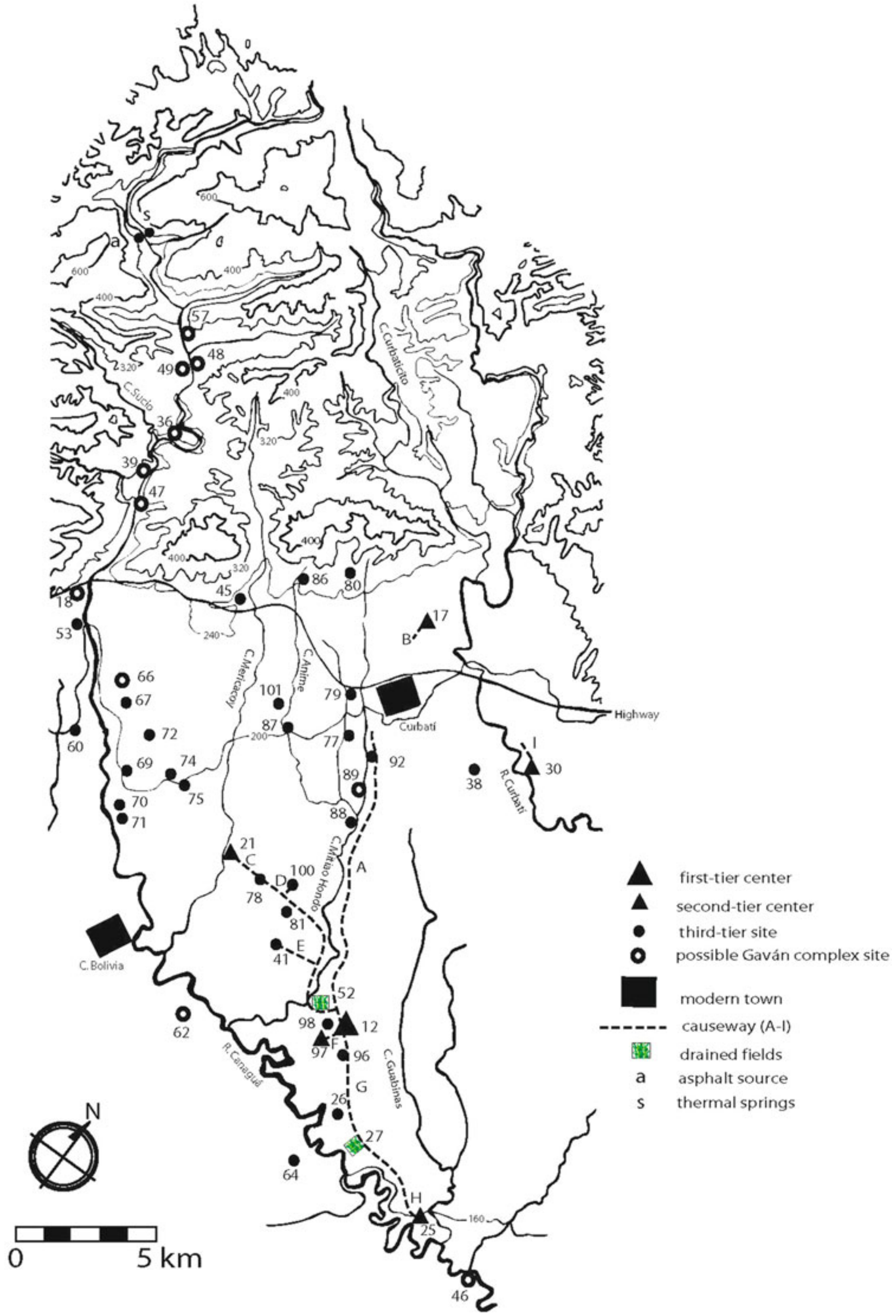


Fig. 10.5 Settlements of the Late Gaván phase (A.D. 550–1000), Barinas, Venezuela; adapted from Spencer and Redmond (2015, Fig. 2)

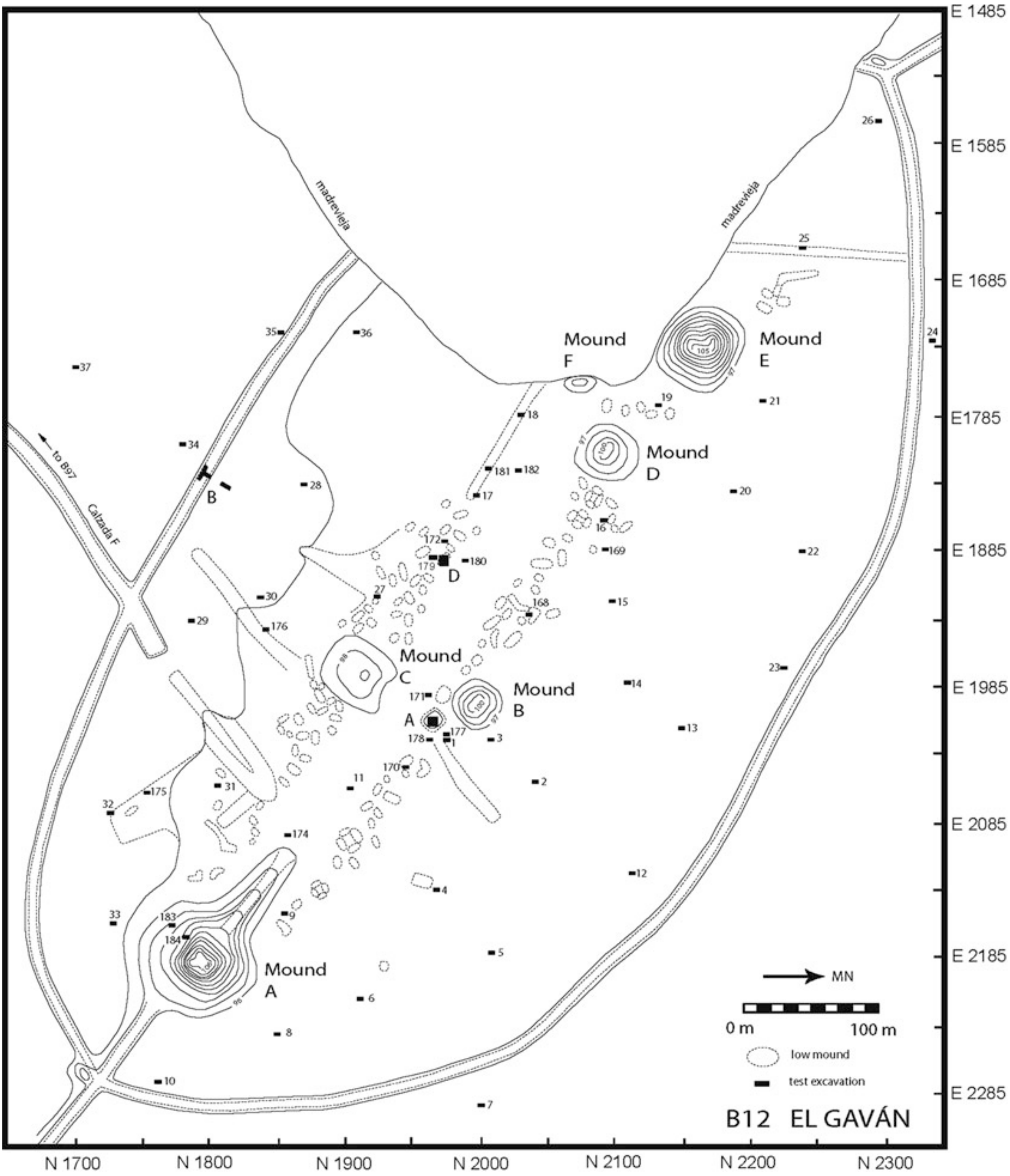


Fig. 10.6 Map of the Gaván site (B12), showing locations of the two major mounds (A and E), house mounds, causeways (*calzadas*), the circumscribing earthwork, test pits, and block excavations; adapted from Spencer and Redmond (2015, Fig. 3)

A histogram of Late Gaván site sizes revealed a bimodal distribution: B12 covered an estimated 33 ha and was much larger than the others, which ranged in size from 0.5 to 9.4 ha (Redmond and Spencer 2007, Table 5.2, Fig. 5.2). B12 also had the largest earthen mounds in the El Gaván region; two mounds, measuring 10 m and 12 m in height, faced each other from opposite ends of an avenue or elongated plaza 500 m long (Fig. 10.6). At B12 we also recorded four other mounds 1–4 m in height and 130 other mounds 1 m or less high. Only the two largest mounds show signs of having been public/institutional in function; the other mounds seem to have supported residences (Spencer and Redmond 1998). All the mounds at B12 lie within an oval earthwork that circumscribes the site (Fig. 10.6). B12's large size and impressive mounds would appear to reflect a centralized regional political organization; at the same time, the low quantity and diversity noted in B12's public architecture (just two large mounds) would be consistent with chiefdom organization (Spencer 1987). To draw a contrast, the internally specialized administration of the state is typically associated with much more diversity in public architecture at its political capital than we see at B12 (Flannery and Marcus 1976; Spencer 1990).

Our field program at B12 included the horizontal excavation of two Late Gaván housemounds, Area A and Area D, lying on opposite sides of the site's central avenue (Fig. 10.5). In Area A, atop a 1-m-high housemound, we exposed a pattern of postmolds that defined a house covering about 28 m^2. On the Area D housemound, which was about half as high as the Area A housemound, we excavated the postmolds of a house measuring just 17 m^2. We inferred that the Area A house was of higher social status, an interpretation that was supported by the higher relative frequency of status-related artifacts, such as elaborate pottery and imported chert, found with the Area A house (Spencer and Redmond 2014, pp. 352–355). In short, Areas A and D show social status differentiation on the household level in Late Gaván times.

We also detected evidence of status differences on the individual level in the Late Gaván phase. Burial 6 was an adult who had been interred within the Area A housemound and beneath the floor of the Area A house. Burial 6 was accompanied by three ceramic vessels (Spencer and Redmond 2014, pp. 267–275). By contrast, Burial 5 was an adult buried beneath the floor of a house that was not upon a housemound at a separate, smaller site; Burial 5 had no funerary accompaniments (Spencer and Redmond 2014, pp. 562–563).

We have argued that the two sectors of housemounds at B12, divided by the central avenue, represented two exogamous moieties, i.e., two components of the village that intermarried (Spencer and Redmond 2015). We found evidence that this bilateral pattern existed in the earliest occupation of B12, when it covered no more than 5 hectares. Using data from our test-pit program, we analyzed the distribution of imported chert over time, and we found that the two moieties (which we labeled A and D) showed no evidence of social status differences in the Early Gaván phase. By contrast, a clear difference had developed by the Late Gaván phase (Fig. 10.7). Thus, we observe status differentiation on the moiety level at this time, just as we saw on the household and individual levels.

A parallel shift toward increasing differentiation also took place on the regional level. The three sites of the Early Gaván phase, all lacking mounded architecture and ranging from 3 ha to 5 ha in size, were succeeded by the 34 habitation sites of the Late Gaván phase, ranging from less than 1 ha to 33 ha in size. Our regional survey located five other sites that we interpret as possible second-tier settlements in the El Gaván region (B97, B21, B25, B17, and B30); these sites vary in size from 4.6 to 9.4 ha and have two to four mounds that reach 2–6 m in height. A third settlement tier is represented by the remaining 28 sites, which range in size between less than 1 ha up to almost 5 ha and had no mounds detectable by surface survey (Redmond and Spencer 2007, Table 5.2). But, whether we interpret the regional settlement hierarchy as having two or three tiers, the Late Gaván settlement system would be consistent with chiefdom political organization (Redmond and Spencer 2007, pp. 323–324; Spencer and Redmond 1992, 1998, 2014, pp. 754–755).

B12 was linked by a *calzada* (earthen causeway) network to four and perhaps all five of the proposed second-tier sites, as well as to many of the smaller sites (Fig. 10.5). Three inter-site *calzadas* approached B12 from the northwest, southeast, and southwest (Fig. 10.6). We have estimated that the *calzada* network would have linked together some two-thirds of the total population of the El Gaván regional chiefdom (Spencer and Redmond 1998, p. 107). It is significant, we think, that the two drained-field agricultural sites we recorded (B27, B52) were both located alongside *calzadas* (Fig. 10.5). The results of our survey and excavation at one of them (B27) revealed that maize was the primary crop, which we suspect was cultivated by farmers who lived at the nearby village of

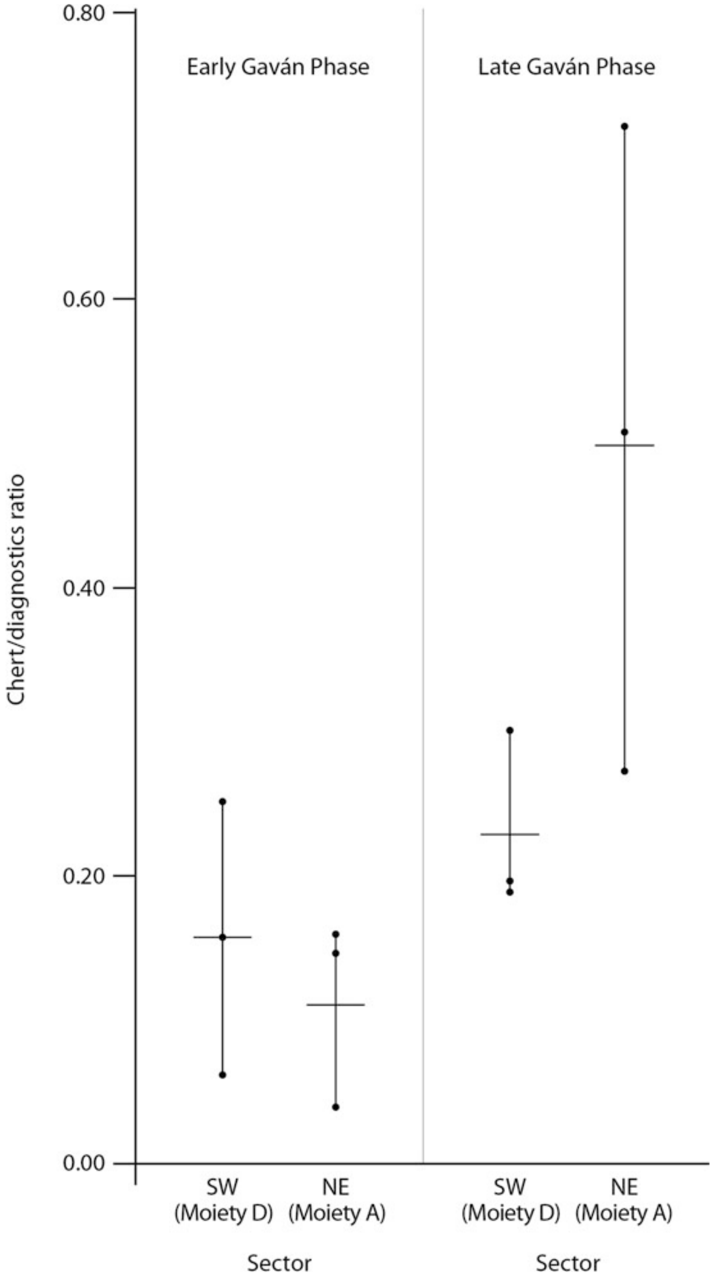


Fig. 10.7 Sample distributions of the ratio of chert fragments to total ceramic diagnostics for the Early Gaván phase and the Late Gaván phase; horizontal bars indicate sample averages; adapted from Spencer and Redmond (2015, Fig. 16)

B26 (Spencer et al. 1994). We have calculated that the B27 fields were capable of substantial surplus production well beyond the needs of these local cultivators. Such surplus was probably transported along the *calzada* network to B12, where the regional chiefly leadership would have coordinated its mobilization, storage, and utilization (Spencer et al. 1994). Based on the extent of the regional *calzada* network and the associated pattern of settlement, we estimated that the El Gaván regional chiefdom extended over a territory of approximately 290 km^2 in the Late Gaván phase (Redmond et al. 1999, p. 117). We have concluded that all of the Late Gaván habitation sites would have lain within a 1-day round-trip by foot from the regional center of B12, a distance compatible with the centralized but not internally specialized nature of chiefdom political organization (Spencer and Redmond 2014, p. 761).

Where did the first inhabitants of our study region come from? The earliest sedentary agricultural villages known in Venezuela were established around 2000 B.C. in the Parmana area in the middle Orinoco (Roosevelt 1980). The number and size of villages in Parmana grew between 2000 B.C. and A.D. 100, according to Roosevelt's data. But, there is no evidence of a settlement hierarchy in Parmana until A.D. 1100, which is much later than we saw for Barinas. We have proposed that, as population grew after 1000 B.C., some people emigrated from the middle Orinoco and founded new daughter villages, a process that repeated itself successively, moving in a westward direction, higher and higher upstream (Spencer and Redmond 2014, p. 789). By about A.D. 300, the demographic expansion reached the foot of the Venezuelan Andes. At this point, the good alluvial land was increasingly restricted; moreover, it has been established that there were people already living in the Andes by this time (Tarble 1977; Wagner 1967, 1972, 1973a, b). So, it would appear that conditions of environmental and social circumscription were both developing (Spencer and Redmond 2014, p. 790). As Carneiro (1981, 1998) has argued, such a context is favorable for the formation of chiefdoms, and that is what we observe in our study region around A.D. 550. After chiefdoms first emerged here, we hypothesize that a chain reaction of chiefdom formation set in, eventually reaching the Parmana area by A.D. 1100 (Spencer and Redmond 2014, p. 791).

What can we conclude about the tempo and mode of chiefdom formation in Venezuela? Although our data are not as complete as we would like, especially for the pre-A.D. 550 time period, I can offer a provisional assessment. First, consider the tempo of change. I suggest that one rough measure of political centralization in a society is the maximum number of villages integrated within the regional polity. If we combine the Parmana and Barinas data and graph this measure over time, we see a punctuational increase in the number of villages within a given region around A.D. 550 (Fig. 10.8). This graph, of course, can be considered a reflection not only of population growth but also of organizational change; regional integration among separate villages was undoubtedly much weaker before A.D. 550 than after, when a clear regional settlement hierarchy existed. It is reasonable to conclude that the tempo of social change in the El Gaván region around A.D. 550 was markedly punctuational. As far as the mode of change is concerned, I have discussed the appearance around A.D. 550 of inequality on multiple scales, including the community, moiety, household, and individual levels. Moreover, there is tangible evidence (the drained fields and causeway system) that this multiscalar social transformation was associated with a substantial increase in the energy-mobilizing potential of the regional political system.

Now let us shift our attention to the early Zapotec state, which emerged around 300 B.C. in the Oaxaca Valley. Earlier I referred to Zapotec state formation as one of several examples of convergent evolution in the world at large. In this section I focus on the tempo and mode of change in the Oaxaca case, i.e., whether early state formation here was a punctuational process and whether it involved concurrent major changes on multiple scales or levels of cultural organization.

Archaeologists have suspected for some time that a profound change occurred around 300 B.C. in the way that the Monte Albán polity interacted with other polities. One way to detect this is through certain changes in the carved inscriptions at Monte Albán. In the Early Monte Albán I phase (from 500 B.C., when the site was founded, to 300 B.C.), there were just three public buildings at Monte Albán, and one of them (Building L) had a display of stones carved with what are thought to be the likenesses of sacrificed captives taken through inter-polity raiding, a form of warfare that is highly characteristic of chiefdoms; raiding involves looting and the seizure of captives but not the taking and holding of distant territory (Flannery and Marcus 1983c; Marcus 1974, 1976; Redmond and Spencer 2006). At this time, there were no more than 2–3 tiers in the regional settlement hierarchy, consistent with chiefdom organization (Spencer and Redmond 2001b, 2003, 2004b). But, around 300 B.C. Monte Albán switched to a very different way of interacting with other polities: a shift from raiding to conquest (Redmond and Spencer 2006). We can see glyphic evidence of this shift if we compare

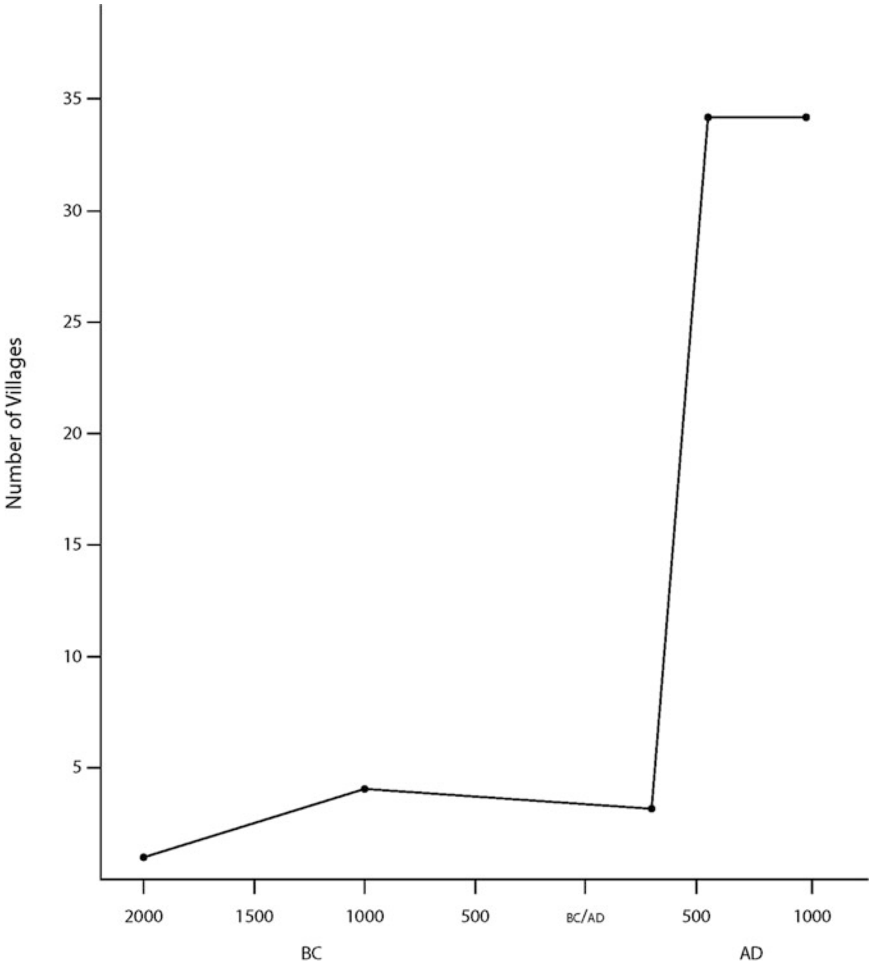


Fig. 10.8 Change over time in the estimated number of villages in a regional polity, documenting the transition from autonomous village (tribal) society to chiefdom in Venezuela around A.D. 550

Building L with Building J, which was built in the Monte Albán II phase (and perhaps as early as the Late Monte Albán I phase) and has more than 40 stone slabs with inscriptions that were interpreted by Alfonso Caso (1947) as signifying territorial conquest; the inscriptions include place names to specify the regions that were subjugated.

Following up on Caso's pioneering work, Marcus (1976, 1980) sought to identify the actual places to which the conquest inscriptions might be referring. She noted certain similarities between the toponyms (place-name glyphs) on the Building J conquest slabs and the toponyms that appeared (with Spanish glosses) in the Codex Mendoza, a sixteenth-century Aztec document containing a list of places that were paying tribute to the Aztec (Marcus 1976, 1980). One of these tributary places in the Codex Mendoza was Cuicatlán, the toponym of which depicted a face with a flowery speech scroll ("place of song"), and Marcus proposed that a certain Building J conquest slab with a similar speech scroll was referring to a conquest of Cuicatlán by Monte Albán (Marcus 1980, p. 59). As she commented, "such a correlation between a 16th-century Aztec codex and Zapotec glyphs of Period II implies some 1500 years of place-name continuity. Hence, my suggestion is no more than a hypothesis" (Marcus 1980, p. 56).

To test this hypothesis, Redmond and I carried out a multistage field project in the Cañada that included regional survey, intensive site mapping plus controlled surface collecting, and extensive excavation (Redmond 1983; Spencer 1982, 2007; Redmond and Spencer 2006; Spencer and Redmond 1997, 2001a). We concluded that the data provided compelling support for the hypothesis that the Cañada was conquered by the Monte Albán state at the end of the Cañada's Perdido phase (750–300 B.C.) and remained in a subordinate status until the end of the Cañada's Lomas phase (300 B.C.–A.D. 200). The absolute dates assigned to these phases are supported by a series of radiocarbon dates (Spencer and Redmond 2001a).

A dramatic disruption occurred in the Cañada's settlement patterns around 300 B.C. All the pre-300 B.C. sites were abandoned, and new settlements were founded on nearby slopes and ridges (Redmond 1983, p. 83; Spencer and Redmond 1997, p. 600). In the central and southern Cañada, the 11 Perdido phase sites were succeeded by 14 Lomas phase sites, none larger than 5 ha, with a total occupied area of 27 ha, a decline from the situation in the Perdido phase, when the central and southern Cañada had 36 ha of occupation (Spencer 1982, p. 234; Spencer and Redmond 1997, pp. 599–600). A different pattern was observed at the northern end of the Cañada in the Quiotepec locality, where the single small (1.5 ha) Perdido phase site was succeeded by a massive 45-ha complex of seven Lomas phase sites that surrounded the natural pass leading into the Cañada from the Tehuacán Valley to the north. We have argued that these seven Quiotepec sites (some of which showed evidence of fortifications) constituted a military frontier installation, strategically positioned to monitor movement through the northern frontier of the Cañada (Redmond 1983, pp. 9–120; Spencer and Redmond 1997, p. 601). We observed that the Quiotepec locality also marked the northern limit of a distinctive Lomas phase pottery that showed stylistic similarities to contemporaneous pottery at Monte Albán, some 100 km to the south (Redmond 1983, p. 86; Spencer and Redmond 1997, p. 601).

At the southern end of the Cañada, the 2.25-ha Perdido phase village of Llano Perdido on the high alluvium was burned to the ground and completely abandoned; a new Lomas phase settlement (Loma de La Coyotera) was then established on an adjacent ridge (Spencer and Redmond 1997, pp. 505–506, Fig. 9.1). The 3-ha Lomas phase village was not much larger than Llano Perdido, but it differed from the earlier site in several ways. The basic residential unit changed from the Perdido phase pattern of large multifamily compounds to a pattern in Lomas phase of separate nuclear family households, each on its own residential terrace (Spencer 1982, pp. 231–234; Spencer and Redmond 1997, pp. 507–510). The latter resembles the typical household unit that has been reported for the Valley Zapotec (Blanton 1978; Flannery and Marcus 2005). We have proposed that the conquering Zapotec broke up the traditional Cuicatec multifamily compounds in order to disrupt interfamilial ties, which could have strengthened their hold over the subjugated locals (Spencer and Redmond 1997, p. 602).

Associated with the Lomas phase community was an extensive irrigation facility, evidenced by a canal scar and a dozen aqueducts that carried the canal over gullies; our excavation in the largest of these aqueducts dated its construction to the Lomas phase (Spencer and Redmond 1997, pp. 525–529). We were able to trace the canal scar down to the high alluvium, where the earlier Perdido phase village had been located. Since we also found surface evidence of canal irrigation at other Lomas phase sites in the central and southern Cañada, we think it likely that much or all of the 740 ha of high alluvium in the Cañada was brought under cultivation during the Lomas phase. Along with the 997 ha of low alluvium—which could have been farmed with diversionary dam and/or floodwater irrigation techniques—the introduction of canal irrigation to the high alluvium would have greatly increased the overall agricultural potential of the Canãda. It is important to note that the Cañada lies in a severe rain shadow, although it does receive substantial runoff from precipitation in the surrounding mountains; all successful farming in the region today depends on some form of irrigation. Redmond (1983, pp. 123–126) calculated that the Lomas phase population in the central and southern Cañada (i.e., south of the Quiotepec frontier) was well below the carrying capacity of just the low alluvium in both Perdido and Lomas phase times. So we suspect that the evident expansion of agricultural production onto the high alluvium in Lomas phase was primarily a response to tribute demands.

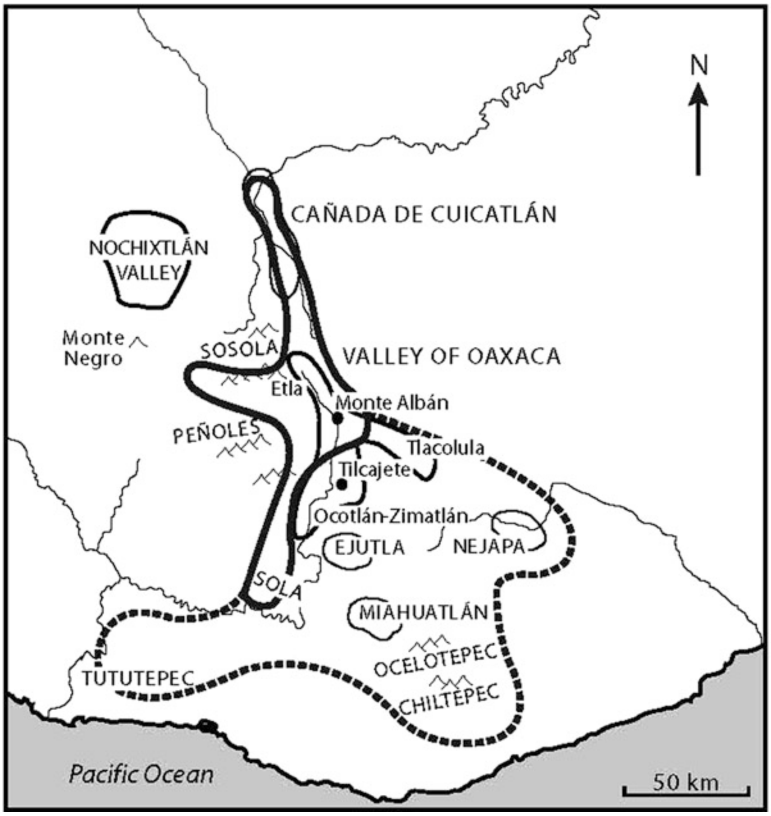


Fig. 10.9 Proposed territorial extent of the Monte Albán state; solid bold line shows territory during the Late Monte Albán I phase (300–100 B.C.); dashed bold line shows territory added in the Monte Albán II phase (100 B.C.–A.D. 200); adapted from Spencer (2010, Fig. 4)

A two-phase process of territorial expansion by Monte Albán (Fig. 10.9) would be consistent with our research in the Cañada and with the work of researchers in other regions of Oaxaca (Balkansky 2002; Finsten 1996; Sherman et al. 2010; Spencer et al. 2008). In the first phase of this expansion, from 300 to 100 B.C. (Late Monte Albán I phase), Monte Albán extended its domain to the north, west, and southwest. Areas to the east and south—including the eastern (Tlacolula) and southern (Ocotlán-Zimatlán) subvalleys and other areas outside the Valley proper—appear to have resisted successfully for a while (Spencer and Redmond 2001b, 2003; Spencer et al. 2008). Then, in the second phase of Zapotec expansion, from 100 B.C. to A.D. 200 (the Monte Albán II phase), Monte Albán extended its control eastward and southward to annex the eastern and southern subvalleys and beyond, bringing its total political territory to perhaps as much as 20,000 km^2 (Marcus and Flannery 1996, pp. 206–207, Fig. 242).

In the Oaxaca Valley, there were significant changes in settlement patterns between the Early Monte Albán I phase and the Late Monte Albán I phase within the Etla-Central subvalley, the core area of the Monte Albán polity (Spencer and Redmond 2001b, Figs. 4, 5). Notably, the Late Monte Albán I phase witnessed the first appearance of a four-tier settlement-size hierarchy (an indicator of state organization) in the Etla-Central subvalley, with the top tier occupied by Monte Albán itself (Spencer and Redmond 2001b, 2003, 2004b). Another change in the Etla-Central subvalley was detected through a linear regression analysis of archaeological population (dependent variable) against potential population (independent variable), conducted by Spencer and Redmond (2001b) with data reported by Nicholas (1989). The regression analysis revealed the following: for the Early Monte Albán I phase, the R^2 value was 0.081 and the significance value was 0.056; for the Late Monte Albán I phase, the R^2 value was 0.158 and the significance value was 0.002, a much stronger significance level than for the Early Monte Albán I phase (Spencer and Redmond 2001b). This outcome reflects

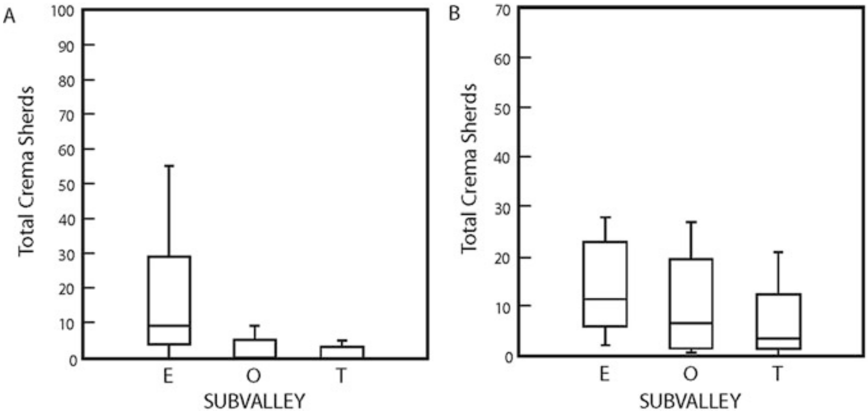


Fig. 10.10 Distribution of cream ware (Crema) sherds among archaeological sites in the Etla-Central (E), Ocotlán-Zimatlán (O), and Tlacolula (T) subvalleys of the Oaxaca Valley. (**a**) Distribution of sherds of 10 Late Monte Albán I Crema types among 48 sites listed as Late Monte Albán I "central places" by Kowalewski et al. (1989, Table 6.4), of which 22 were in Etla-Central, 12 in Ocotlán-Zimatlán, 14 in Tlacolula. (**b**) Distribution of sherds of 9 Monte Albán II Crema types among 40 sites listed as Monte Albán II "central places" by Kowalewski et al. (1989, Table 7.4), of which 20 were in Etla-Central, 8 in Ocotlán-Zimatlán, 12 in Tlacolula. Ceramic data from Kowalewski et al. (1989, Appendix VI). Adapted from Spencer (2010, Fig. 3)

a shift in village location between the Early Monte Albán I phase and the Late Monte Albán I phase: after 300 B.C., villages were located so that the distribution of population more closely matched the distribution of agricultural resources (expressed in the regression analysis as potential population). Such a settlement shift would have enhanced the overall agricultural efficiency of the core area dominated by Monte Albán, allowing for the more effective mobilization of agricultural surplus to support the state's growing administration and burgeoning capital city. I conclude that by Late Monte Albán I times the nascent Monte Albán state had developed the capacity to intervene significantly into local-level decision-making regarding settlement location in the Etla-Central subvalley.

By the Monte Albán II phase (100 B.C.–A.D. 200), Monte Albán had evidently succeeded in bringing the southern (Ocotlán-Zimatlán) and eastern (Tlacolula) subvalleys under its control; the entire Oaxaca Valley showed a clear four-tier site-size hierarchy with Monte Albán at the top (Marcus and Flannery 1996, pp. 172–175). This political unification was reflected in the changing distribution of cream ware (or Crema) pottery, made from a distinctive clay whose source was near Monte Albán (Minc et al. 2007). Compare the distribution of Crema wares among the three subvalleys of the Oaxaca Valley in the Late Monte Albán Late I phase (Fig. 10.10a, left), with the distribution of Crema wares in the Monte Albán II phase (Fig. 10.10b, right). In Late Monte Albán I, the Etla-Central subvalley had statistically significant higher amounts than the Ocotlán-Zimatlán and Tlacolula subvalleys (Kruskal-Wallis statistic $= 17.954$; $P < 0.001$), probably because the political independence of the latter two subvalleys blocked the free exchange of Crema pottery. However, by the Monte Albán II phase, there was no statistically significant difference in the valley-wide distribution of the Crema wares (Kruskal-Wallis statistic $= 4.829$; $P = 0.089$), probably because all three subvalleys of the Oaxaca Valley were incorporated into the Monte Albán state by that time.

Major changes also occurred after the Early Monte Albán I phase in the architectural ground plans of individual sites. Most prominently, between 300 B.C. and A.D. 200 (the Late Monte Albán I and Monte Albán II phases, inclusive), many new institutional buildings were constructed on Monte Albán's main plaza (Fig. 10.11). They were highly diverse in morphology and likely function, including several kinds of temples, secular public buildings, a royal palace, a formal ballcourt—by my count, a total of approximately two dozen in all, representing an enormous increase from the three public/institutional buildings of the Early Monte Albán I phase (Acosta 1965; Flannery and

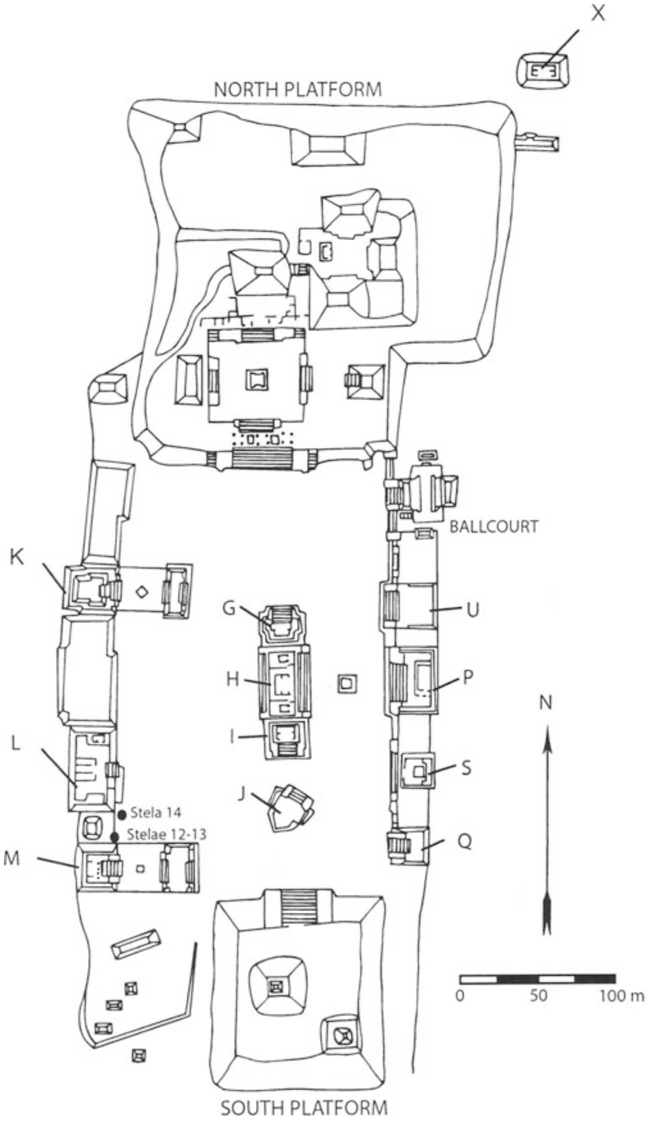


Fig. 10.11 Main Plaza of Monte Albán; major buildings are identified by upper-case letters (redrawn from Flannery 1983, Fig. 412)

Marcus 1976; Marcus and Flannery 1996). The specific functions of all these buildings have not yet been determined, but it is reasonable to posit that the great increase in the diversity of religious and secular institutional architecture here reflects a comparable diversification of central authority and administrative personnel by the Monte Albán II phase. Unfortunately, construction activities after A.D. 200 at Monte Albán have made it difficult for archaeologists to document with precision the institutional architecture of Late Monte Albán I times. But useful information has resulted from recent fieldwork at the El Palenque site near San Martín Tilcajete, a Late Monte Albán I site located some 25 km south of Monte Albán in the Ocotlán-Zimatlán subvalley. Excavations at El Palenque exposed a palace complex that covered some 2790 m^2 on the plaza's north side, as well as a 5000-m^2-temple precinct on the plaza's east side, both securely dated by radiocarbon analysis to the Late Monte Albán I phase (Fig. 10.12; Redmond and Spencer 2013, 2017; Spencer and Redmond, 2004a, b).

The Late Monte Albán I palace complex and temple precinct at El Palenque represent major institutional changes from the previous Early Monte Albán I occupation at El Mogote, which lies

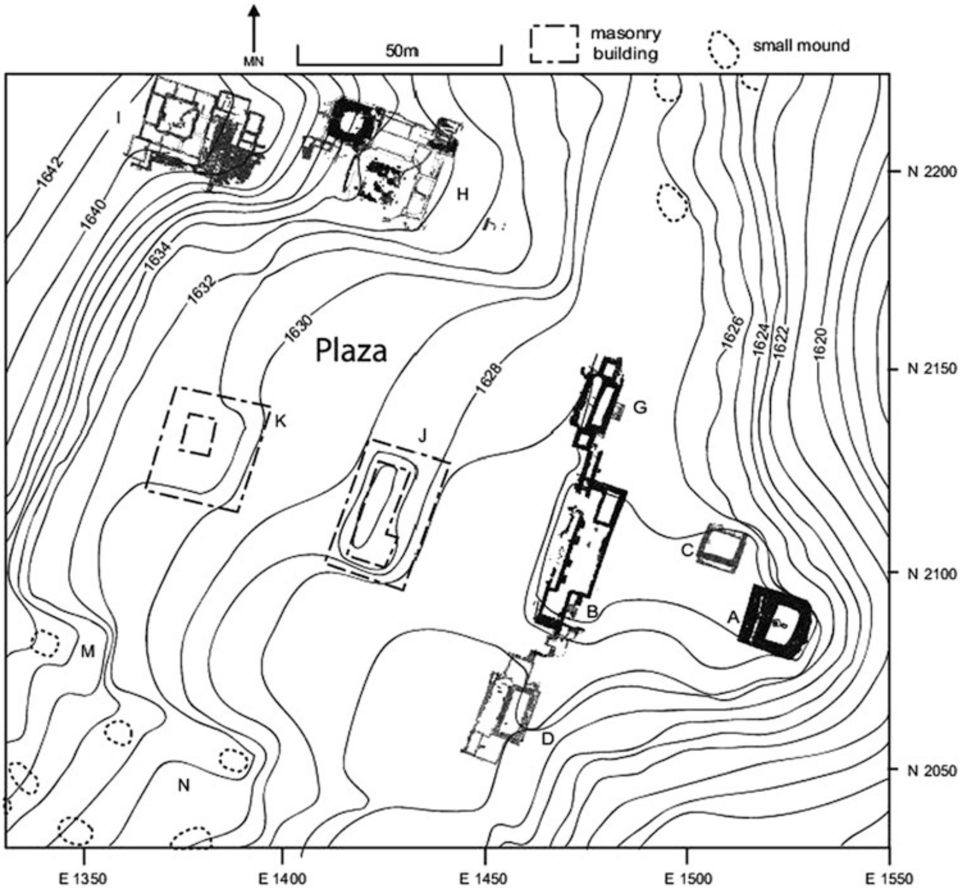


Fig. 10.12 Plaza of El Palenque showing major buildings dating to the Late Monte Albán I phase (300–100 B.C.), including the palace complex on the plaza's north side and the temple precinct on the plaza's east side (redrawn from Redmond and Spencer 2017, Fig. 3)

across a gulley and less than 1 km to the east (Redmond and Spencer 2017, Fig. 1). Atop a 4-m-high mound on the north side of El Mogote's plaza, we excavated the masonry foundations of a high-status residence that consisted of four rooms arranged around a patio, along with 1–2 small ancillary structures, all dating to the Early Monte Albán I phase (Redmond and Spencer 2017, Fig. S1). By contrast, at the Late Monte Albán I palace complex at El Palenque, we exposed the masonry foundations of a 256-m^2 residence (Structure 7) that had 8 rooms surrounding a patio, along with the masonry foundations of 11 additional structures; the entire 2790-m^2 complex sprawled across two levels connected by a grand masonry staircase and extended along the entire northern side of the El Palenque plaza (Redmond and Spencer 2017, Figs. 3–4).

On the east side of El Mogote's plaza, we excavated the masonry foundations of a one-room temple dating to the Early Monte Albán I phase (Redmond and Spencer 2008, Fig. 4). At El Palenque, by contrast, the Late Monte Albán I temple precinct consisted of five masonry structures; three of them were multiroom temples and two were specialized priests' residences (Redmond and Spencer 2013). We also conducted limited excavations elsewhere in the plaza area of El Palenque that yielded Late Monte Albán I dates for several other institutional buildings, among them a possible ballcourt (Mounds K and J) in the middle of the plaza (Fig. 10.12). Based on the data from our horizontal excavations, the smaller-scale excavations, and the intensive survey at El Palenque, I estimate there were 18 public/institutional buildings in and around the plaza during the Late Monte Albán I phase. By comparison, I estimate that the El Mogote had no more than 2–3 public/institutional buildings during the Early Monte Albán I phase, analogous to the situation on the Main Plaza of Monte Albán during the same phase (Flannery and Marcus 1983c).

We have argued that, during the Late Monte Albán I phase, El Palenque was the political capital of an independent state whose territory included all or most of the Ocotlán-Zimatlán subvalley; as such, it succeeded the nearby El Mogote site that was the probable capital of a chiefdom during the Early Monte Albán I phase and perhaps earlier as well (Redmond and Spencer 2006; Spencer and Redmond 2001b, 2003). In the very early years of the Monte Albán II phase, El Palenque was evidently burned and completely abandoned (Redmond and Spencer 2013, 2017; Spencer and Redmond 2001b, 2004a). A new site (Cerro Tilcajete) was founded on a hilltop 1 km to the north (Elson 2007; Spencer et al. 2008, Fig. 2). Based on the results of a surface survey and her extensive excavations, Elson (2007) concluded that Cerro Tilcajete served as a secondary administrative center of the Monte Albán state during the Monte Albán II phase.

Although the evidence at El Palenque of institutional architecture was recovered at the likely capital of an independent state in Ocotlán-Zimatlán and not at Monte Albán itself, we hypothesize that the latter site must have had a similarly diverse array of public/institutional buildings by the Late Monte Albán I phase, a hypothesis that future excavators will hopefully be able to test (Spencer 2003; Spencer and Redmond 2004b). In the meantime, we can use our data from El Palenque as a proxy estimate for the number of public/institutional buildings at the first-tier center of an independent polity during the Late Monte Albán I phase. I suggest that, for the purposes of comparative analysis, such an estimate may serve as a relative measure of the degree of internal specialization in a polity's central administration. We can use this measure to assess administrative complexity at different points of time in a single regional trajectory or to compare different regional polities. Accordingly, I have generated estimates for a series of Valley of Oaxaca phases that bracket the time of state formation, drawing on information in Acosta (1965), Elson (2007), Flannery (1983), Flannery and Marcus (1976, 1983c, 2015), Marcus and Flannery (2004), Redmond and Spencer (2013, 2017), and Spencer and Redmond (2004a, b). Note that the relevant first-tier site is San José Mogote for the phases prior to the Early Monte Albán I phase. El Palenque can serve as a proxy first-tier site for the Late Monte Albán I phase, while Monte Albán itself, of course, is the first-tier site for the remaining phases. While bearing in mind the very approximate nature of these measures, we can graph them against time and can gain an appreciation of the overall tempo of change here (Fig. 10.13). As the graph indicates, around 300 B.C. (the onset of the Late Monte Albán I phase) there was a dramatic, punctuational increase in the number of public/institutional buildings at the first-tier center, most likely a reflection of a corresponding increase in the degree of institutional specialization or differentiation in the political/religious administrative organization that used these buildings, which is a key indicator of state formation. And, as pointed out earlier, this development was contemporaneous with the appearance of a four-tier regional settlement hierarchy and also the annexation through conquest of distant territories, both of which are also characteristic features of state organization (Spencer and Redmond 2004b).

In addition, a growing body of data indicates that significant changes were occurring around 300 B.C. in household-level organization. Based on his excavations in a residential area at Monte Albán, Winter (1974) proposed that the typical household unit shifted from a single rectangular house in the Early Monte Albán I phase to an L-shaped construction composed of two rectangular units in the Late Monte Albán I phase. More recently, Lacey Carpenter (2017) has been conducting a program of horizontal excavations in domestic contexts at both El Mogote and El Palenque. Her initial findings reveal intriguing shifts in household ground plans between the Early Monte Albán I phase and the Late Monte Albán I phase. Carpenter's ongoing research promises to contribute substantially to our understanding of this important transition.

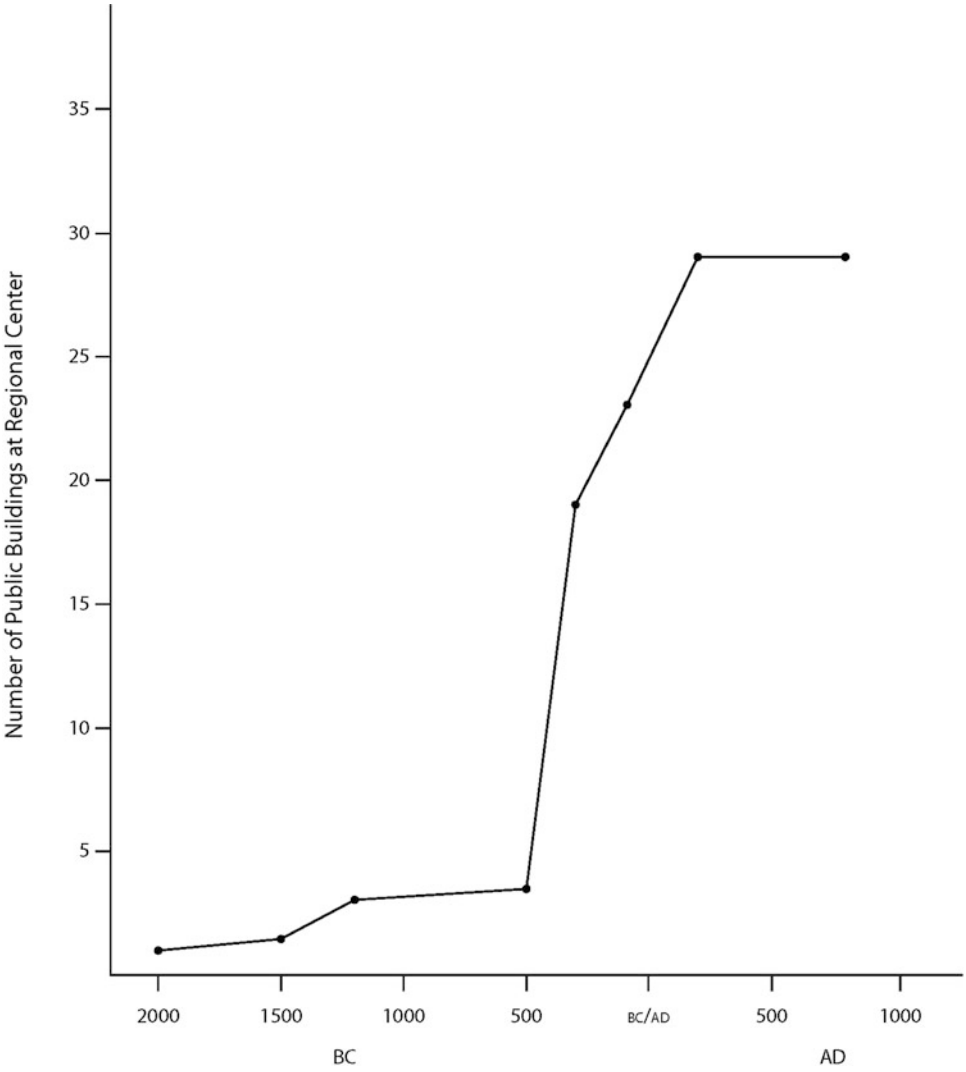


Fig. 10.13 Change over time in the estimated number of public/institutional buildings in a regional polity's first-tier center, documenting the transition from chiefdom to state in Oaxaca around 300 B.C.

To sum up the data on state emergence in Oaxaca, I conclude that the tempo of change was punctuational while the mode of change was multiscalar and transformational. Between the Early Monte Albán I phase and the Late Monte Albán I phase, major changes occurred simultaneously on multiple scales of system organization: on the interregional level (the shift from raiding to conquest), on the regional level (more complex settlement patterns), on the community level (the emergence of new suprahousehold political and religious institutions), and probably on the household level as well. Moreover, this multiscalar transformation was accompanied by a substantial increase in energy mobilized by the Monte Albán polity, which it accomplished not only through successful interregional conquests and consequent tribute exaction but also through a settlement shift within the nascent state's core area that brought the distribution of the agricultural labor force more efficiently into line with the distribution of agricultural resources.

Conclusion

Recalling the contrasting empirical expectations for cultural historicism versus cultural macroevolutionism (Fig. 10.4), I submit that the data on chiefdom formation in Venezuela and the data on state formation in Oaxaca are consistent with the macroevolutionist framework. In both cases, major social transformations came about punctuationally, involved concordant changes across multiple organizational levels of the system, and were associated with major increases in mobilized energy. I have also noted comparative analyses that found evidence of convergent patterning among several independent cases of state formation. While I recognize that the long-standing dispute between the historicist and macroevolutionist perspectives can hardly be resolved in a single paper, I conclude that cultural macroevolutionism is still very much on the anthropological table and worthy of further investigation and debate. Hopefully more archaeological trajectories will soon be subjected to detailed diachronic assessments of tempo, mode, sociopolitical complexity, energy mobilization, and convergence, with the goal of facilitating comparative analyses among evolutionary trajectories and the testing of competing theories about long-term social change.

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Part III
Human Ecology

Chapter 11
Human Ecology

Anna Marie Prentiss

Introduction

Archaeologists study human ecology in a wide range of contexts asking an equally diverse range of questions. This chapter provides a short overview of major research directions pursued by archaeologists within an evolutionary ecological framework. As outlined in Chap. 1 (this volume), evolutionary ecology (EE) is a Neo-Darwinian approach to understanding diverse phenomena spanning reproductive decisions and population regulation to predation and competition. Drawing from this body of method and theory, human behavioral ecology (HBE) developed as the specific study of human behavior in an evolutionary framework. Research in HBE has addressed many topics, some including reproduction and population regulation, foraging behavior, and social relationships (signaling, territoriality, and cooperation). Assumptions of HBE models are reviewed in Chap. 1 (this volume) and considered in greater depth in individual chapters within this section. But briefly, models in HBE work on the assumption that behavior has economic implications and thus also reproductive fitness implications. Behavior is assumed to be a by-product of decision-making drawing from some combination of learning and genetic and behavioral inheritance (Kelly 1995; Smith and Winterhalder 1992). Consequently, scholars working within HBE frameworks develop decision-making models based in assumption of methodological individualism (Smith 1991; Smith and Winterhalder 1992). Models are typically structured in microeconomic frameworks based in optimality assumptions recognizing that such assumptions are to be tested and refined (Bettinger et al. 2015; Cannon and Broughton 2010). Optimality assumptions are based in the idea of economic rationality and environmental knowledge. The HBE research process is structurally hypothetico-deductive, depending heavily on outcomes of precisely structured empirical research for advancement of knowledge (Kelly 1995; Smith and Winterhalder 1992).

Archaeologists have benefited substantially from development and testing models based in the logical of evolutionary ecology (Bird and O'Connell 2006; Codding and Bird 2015). HBE scholars in archaeology have studied foraging and food production behavior, land use/mobility, tool production/use and raw material transport, socio-ecological relationships, and demographic ecology. Archaeologists face challenges making use of space-like models based in methodological individualism given the inherent challenge of tracing individual behavior in the archaeological record. Archaeologists typically must assume that the archaeological record is accumulated from

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many decision-making events. Testing models from HBE thus requires the assumption that adaptive behaviors will persist over time and thus leave an identifiable signature in the archaeological record. Taking this one step further, this presents the possibility of explaining processing of stability and change in aspects of culture and behavior by use of economic optimization models from HBE. However, given the intense focus on formal testing, the option remains open that simple optimization models will fail either by virtue of problems with embedded specific assumptions or via wider issues with evolutionary process. The most credible critique today of HBE-inspired models comes from niche construction theory asserting that a number of fundamentals structuring, for example, foraging theory, are too simplistic in light of advanced evolutionary thinking that is coming from the extended evolutionary synthesis in the form of niche construction theory (NCT) (Zeder 2017).

Despite critiques, it is clear that human behavioral ecology (and related models) has made substantial contributions to archaeological research. In this chapter, I outline the major areas of contributions within four major themes. First, I consider contributions of foraging theory with a focus on diet breadth, patch choice and use, central place foraging, and food storage. This permits me to explore subsistence intensification and origins of food production drawing in particular upon HBE perspectives. Second, I consider aspects of socio-ecology with a particular emphasis on signaling, territoriality, and cooperation research. There is an emerging debate over the role of HBE-inspired cooperation theory in explanations of sociopolitical complexity (e.g., Carballo 2013) and while this is not yet well-enough developed to warrant a stand-alone chapter, I consider it here. Third, I introduce the basics of ecological demography with a focus on implications of Boserupian and Malthusian models. I follow with a focus on the predictions of Malthusian modeling and its implications for our understanding of demography, subsistence, storage, and social behavior, thinking in particular about conditions favoring competitiveness. Finally, I offer a brief introduction to niche construction theory reflecting again upon the origins of agriculture debate and the potential of NCT to offer wider understanding of global human-linked phenomena.

Foraging Theory

Foraging theory (also known as optimal foraging theory) developed in biology to provide evolutionary explanations of foraging behavior across the animal kingdom (MacArthur and Pianka 1966). Foraging theory was first broadly introduced to archaeology by Winterhalder and Smith (1981), and it has become a prominent area of research in recent decades, for many scholars substantially replacing Binford's (1977, 1981) middle-range theory approaches to understand subsistence and mobility decision-making (Bettinger et al. 2015). Foraging theory, as applied in anthropology and archaeology, asserts that human decision-makers will seek to maximize net energy return on activities associated with prey choice or diet breadth, choice of foraging places and timing, field processing and transport, and food storage (Bettinger et al. 2015). As the models associated with these topics are considered in greater depth in individual chapters within this section, I focus here on basic definitions, major contributions, and some debates.

For archaeologists, the diet breadth model (also known as the fine-grained prey choice model) is probably the most widely used HBE approach to understanding subsistence behavior among hunter-gatherers and has been discussed extensively in other texts (Bettinger 2009; Bettinger et al. 2015; Kelly 1995). The model recognizes that hunting and gathering people need to make choices as to which prey to pursue when in a field context as affected by the costs of encounter rates and total handling time (handling includes pursuit once a prey item is encountered). The model asserts that prey items will be chosen in reverse order of prey rank (ranking based on caloric return per unit handling time) until search and handling times are approximately equivalent. Thus, a forager would evaluate the relative payoffs for prey packages always choosing the higher-ranked items and excluding the others as long as search and handling conditions remain about the same. The diet breadth model has been prominent in discussions of hunter-gatherer subsistence intensification, particularly where associated with the problem of declining access to highest-ranked resources, a process often called resource depression (e.g., Basgall 1987; Broughton 1994, 2002; Fisher and Valentine 2013; Janetski 1997; Nagaoka 2005; Munro and Atici 2009). This has led to a wider discussion of the meaning of intensification and the recognition that the term can have multiple meanings and implications whether associated with a maladaptive broadening of the diet under conditions of resource depression or a narrowing of the diet made possible by technological innovations (Chatters 1989, 1995; Morgan 2015). The diet breadth model has also been central to discussions and debates regarding the so-called forager-farmer transition (Kennett and Winterhalder 2006). Essentially, proponents argue that intensification of plants leading to farming can be understood in light of predictions drawn from the diet breadth model suggesting that early food production can be viewed as a greater investment in handling costs favoring a diet focused on low trophic scale items such as maize (Barlow 2002; Gremillion 1996; Gremillion et al. 2014). Niche construction theorists argue that the process of domestication of plants and animals and adoption of agrarian lifestyles is too complex to be explained via simple cost-benefit models, thereby implicating the complex dynamics of niche construction and macroevolutionary process (Smith 2015; Zeder 2016, 2017). Responses to the NCT critique assert that models from HBE are still important for developing an understanding of the economic logic behind decisions to engage in niche construction (Mohlenhoff and Codding 2017).

Another approach to understanding foraging behavior concerns questions of decision-making regarding choice of places to acquire food and how long to stay in those places. The patch choice model is structured much like that of diet breadth and is designed to predict the optimal range of ranked foraging patches (patches are bounded spaces containing a particular set of prey [Smith 1991]). This model also has similar implications to that of the diet breadth model in that, as patch productivity rises, foragers might become more selective in choice of patches, thus reducing inter-patch travel. The inverse would be expected given declining inter-patch productivity (Bettinger et al. 2015). These predictions are reflected in studies of shifts in hunting and gathering behavior under conditions of resource depression. Drawing data from the Keatley Creek site from interior British Columbia, Prentiss et al. (2007) documented that as access to salmon declined, occupants not only diversified their diet but likely added new and more distant patches to summer food-gathering trips. The marginal value theorem (Charnov 1976; Venkataraman et al. 2017) allows researchers to predict optimal time spent in a specific patch assuming that the forager will choose to depart when the net return drops below the net rate of return for the entire environment. The marginal value theorem (MVT) has proven useful in a number of ways, in particular thinking about human colonization and colonization rates in new environments. For example, Kelly (1995) draws on the MVT to model Clovis land-use decisions from which he projects different options for colonization rates in the Americas. The ideal free distribution (IFD) (Fretwell and Lucas 1969) is yet another model that can provide insight into decision-making regarding choices of living spaces as affected by the range of options and associated demographic pressures. At its simplest level, the model assumes that populations will fill most productive habitat first before accepting less productive habitat. The model has been used to address a variety of research questions concerning colonization in various parts of the world (e.g., Kennett 2005; Kennett et al. 2006; O'Connell and Allen 2012). A variant of the IFD known as the despotic ideal free distribution (DIFD) models the process by which packing and associated social competition pushes populations to choose loss of autonomy to avoid being pressed into extremely marginal habitats (e.g., Giovas and Fitzpatrick 2014; Kennett et al. 2009).

Central place foraging (CPF) models (Orians and Pearson 1979) offer the opportunity to model optimal choices for field processing and transport of resources. In brief, CPF models predict that foragers faced with transport costs for acquired food or other items such as tool-making material will seek to optimize net return by raising the net utility of the item or items in reference to costs of transport (Bettinger 2009; Bettinger et al. 2015). Imagine a hunter-gatherer faced with transporting a collection of coconuts. Given thick rinds and hard inner hulls, the cost of transporting them to consumers is quite high. However, if the consumers are very close by then, it might be most cost efficient to just transport the unprocessed nuts. As anticipated travel distances get longer, it makes better economic sense to remove thick rinds and possibly the inner shells and, thus, to carry exclusively edible material. In the latter case, the trade-off between higher field labor and reduced transport cost is worth it given the high caloric return on the increased quantity of transported nut meat. A similar argument could be made for decisions regarding prey choice given variation in anticipated prey transport (Bayham 1986). CPF models have proven useful in many contexts associated with subsistence behavior inclusive of plants (Barlow and Metcalf 1996), animals (Cannon 2003), or both (Zeanah 2004). Given their applicability to technological decision-making, Beck et al. (2002) developed an influential central place foraging model to explain differential field processing decisions for Paleoarchaic period quarrying and tool transport finding that more distant quarries from base camps contained greater late-stage reduction debris, thus confirming investment in field processing. Other scholars have relied on similar cost-benefit logic to model optimal decision-making with regard to lithic procurement (Borrazzo 2012; Garvey 2015), design of toolkits (Elston and Brantingham 2002; Kuhn 1994; Surovell 2009), tool maintenance strategies (Clarkson et al. 2015), and lithic core reduction techniques (Goodale et al. 2008).

As noted by Bettinger et al. (2015), there has been little attention to the costs and benefits of different approaches to food storage. Tushingham and Bettinger (2013) presented the “front-back” model to consider costs and payoffs for decisions as whether to invest in front-loaded meaning costs up front to get a food source into storage versus back-loaded where costs incurred after storage. Thus, a resource like salmon can be stored but only after significant effort in smoking and/or drying. In contrast, nuts like acorns can be immediately stored but require substantial work in the form of milling, leaching, and cooking before they are edible. In the latter case, while the back-loaded model is more costly in total handling time, it is also less risky for groups exploring storage option as the process of getting nuts into storage costs little, and thus little is lost if storage caches are raided or otherwise lost. The model provides an explanation for why acorn caching emerged long before salmon storage among residentially mobile hunter-gatherers in California (Tushingham and Bettinger 2013).

Evolutionary Ecology of Social Relations

Social cooperation has been an area of significant concern to human behavioral ecologists in anthropology and archaeology. Human beings are social animals thus requiring decisions regarding many aspects of cooperation with one another. Fundamentally, cooperation often requires altruism. As noted by Bettinger et al. (2015), p. 194, altruistic behaviors are those “in which an individual sacrifices self-interest (compromises personal genetic fitness) to further the interest (genetic fitness) of other individuals . . . ” This is, of course, a problem for frameworks that assert the importance of individual fitness maximization. Consequently a substantial amount of attention has been placed on developing theoretical understanding of the evolution of altruism among populations of genus *Homo* and to consider its implications for the evolution of culture. Explanations for the evolution of altruism have been diverse including the original group selection model of Wynn-Edwards (1962), the inclusive fitness and kin selection model of Hamilton (1964), various models concerned with implications of the prisoner’s dilemma and related models (e.g., Chadefoux and Helbing 2010; Hauert and Doebell 2004; Helbing and Yu 2009; Koella 2000; Smaldino and Schank 2012; Smaldino et al. 2013), punishment and cultural transmission (e.g., Boyd and Richerson 1985, 1992; Boyd et al. 2003; Guzman et al. 2007; Henrich and Boyd 2001), and recent reconsiderations of group selection under the guise of multilevel selection frameworks (e.g., Bowles 2006; Nowak et al. 2010; Wilson 2012; Wilson and Hölldobler 2005). Typical research in human behavioral ecology is less concerned with the evolutionary origins of the capacity for altruism than it is with understanding variability in fitness-enhancing decisions within human societies already including significant degrees of cooperation and thus altruism. Cooperation strategies are diverse and can include managing group size, sharing, signaling, territorial management, defense, and reproduction (e.g., Bettinger et al. 2015; Boone 1992; Borgerhoff Mulder 1992; Hawkes 1992; Kelly 1995; Smith 1991). Testing social cooperation models with archaeological data can be challenging, and consequently not all areas of HBE-inspired cooperation research have been strongly represented in archaeology. Here I focus on three areas that have been prominent or show significant promise for future research: sharing and signaling, land tenure, and emergence of social inequality.

The question of sharing has drawn considerable attention and debate. A simple model from game theory, the prisoner's dilemma, predicts that in a single play of the game, defecting (not sharing) is always the best option. However, an important study showed that when played across multiple iterations, tit for tat (cooperation in the first round and then repeat of the other player's action in all subsequent rounds) offered a consistently better payoff (Axelrod 1984; Axelrod and Hamilton 1981). Subsequent research demonstrates that outcomes of sharing games vary substantially with assumptions and conditions (Hawkes 1992). Smaldino et al. (2013), for example, demonstrate that over very long time spans, harsh conditions will favor populations of reciprocating cooperators over populations of those who do not reciprocate. Other studies implicate the effects of spatial relationships (Koella 2000), movement patterns (Smaldino and Schank 2012), and wealth accumulation (Chadefaux and Helbing 2010) on persistence of groups of cooperators. An important potential lesson from some of this research is that cooperation decisions are contingent upon a variety of social, geographic, and ecological conditions. It should be no surprise then that anthropologists have recognized multiple contexts whereby the structure of cooperation with regard to sharing of goods varies. Thus, we encounter sharing models including kin selection, tolerated theft, simple reciprocity, cooperative acquisition, mutualism, and signaling (Bettinger et al. 2015; Hawkes 1992; Kelly 1995; Winterhalder 1986).

Signaling theory has garnered attention due to its potential ability to explain behaviors that seem to be otherwise wasteful or expensive in reference to economic payoffs (Quinn this volume). Hawkes' influential (1992) paper raised the possibility that males might engage in economically risky behavior (hunting) in order to signal prowess and gain mating opportunities. While this has led to some debate (Bettinger et al. (2015), the argument was highly influential. The debate over Middle Holocene hunting in California and the Great Basin by those favoring a similar (to Hawkes' argument) signaling hypothesis (Hildebrandt and McGuire 2002) and those favoring a diet breadth model (Broughton and Bayham 2003) is an illustrative example (Winterhalder 2004).

Human groups have highly diverse approaches to sharing access to land (Kelly 1995). As with sharing particular goods, decisions regarding access to land may also have fitness implications and thus can be modeled in cost-benefit terms. Such models may be very useful as hypotheses for archaeologists seeking to understand and explain the structure of ancient land tenure systems. Dyson-Hudson and Smith (1978) published a very important model in which they predicted variation in territoriality among hunter-gatherers on the basis on resource density and predictability. Among other things, the model predicts stable territories when resources are both dense and predictable. In contrast, group dispersion and mobility are associated with low density and predictability resources. Predictions of the model have been partially confirmed in the Great Basin (Thomas 1981) and likely hold in other regions, for example, the Northwest Coast and Fraser-Columbia Plateau where indigenous groups also defended formal territories associated with localities for annual harvest of salmon, sea mammals, clams, and root crops (cf. Lepofsky et al. 2005, 2015; Lyons and Ritchie 2017) not unlike agriculturalists. However, the Dyson-Hudson and Smith model also opens the possibility of other land tenure systems, for example, social boundary defense and passive territories (Kelly 1995). Such models help us to better understand decision-making by groups whose resource structures may be more variable in spatiotemporal terms, thus often increasing variability between groups and promoting the possibility of alternative strategies. Such variable land tenure strategies might have characterized many groups during the Middle Holocene when resources fluctuated seasonally and varied spatially (cf. Habu 2001).

The emergence of wealth-based inequality has been of significant interest to social anthropologists and archaeologists working within human behavioral ecology frameworks. A variety of models have been developed to explore key issues in the evolution of inequality. These can be collectively reviewed as those concerned with conditions versus actions. From the standpoint of conditions, a variety of research projects point to three critical factors associated with emergent wealth-based inequality: resource defensibility, transmittable wealth, and population pressure (Mattison et al. 2016). Ethnographic studies strongly back up these conclusions (Borgerhoff Mulder et al. 2009; Smith et al. 2010), and archaeological research increasingly offers similar support (Kohler et al. 2017; Prentiss et al. 2012, 2014). Eerkens (2013) and Bettinger (2015) point to shifts in the control of goods as precursors to inequality. Their argument is the nonkin free riders are costly, and under some conditions, it is worthwhile engaging in strategies to prevent free riding that might include privatizing certain resources, restricting cooperating groups, and introducing punishment for free riders making the latter inherently more expensive. Several models focus on adaptive strategies that result in inequality. Smith and Choi (2007) develop a model termed managerial mutualism linking inequality to decisions made to permit managers greater control of resource decision-making in contexts of complex information loads. Boone (1992) argues that patron-client relationships can develop when there is emerging differentiation in access to critical subsistence items. Prentiss et al. (2007) argued for a process similar to Boone’s (1992) model regarding the development of inequality at the Keatley Creek site in British Columbia. Boone (1998) added that signaling could be advantageous even when costly to establish cooperating groups under competitive conditions. Kennett et al. (2009) develop a DIFD model to explain how control of space played a critical role in emergent inequality in the Northern Channel Islands of southern California.

Ecological Demography

Demography has been an implicit and explicit factor in the development of models in human ecology. Decision models in optimal foraging theory are typically dependent upon variation in access to critical resources. Optimal diet breadth can be affected by demographic packing and dispersal. Likewise, field butchering decisions are dependent upon anticipated transport distance and that may be affected by search costs associated with most-desired resources which may be overharvested if population sizes become out of balance with local resource structures. Choices of which patches to use and how long to stay may also be impacted by local demographics. Models of social inequality typically also have a demographic component concerning population needs and access to critical resources. While the effects of demographic variability are not the specific goal of the latter models, they are clearly important and thus worthy of study. Scholars in demographic ecology have developed an array of models to explore the interactions between resource variability, food harvest, processing, and storage, demography, and social cooperation and competition (e.g., Lande 1993; Lee 1986, 1993; Lee et al. 2009; Lee and Tuljapurkar 2008; Puleston and Tuljapurkar 2008; Puleston and Winterhalder this volume; Puleston et al. 2014; Winterhalder et al. 2015; Wood 1998). This work offers a range of explicit predictions that may be used to hypothesize a variety of trajectories of demographic, economic, sociopolitical change in the near and remote human past (e.g., French 2016; Holopainen and Helama 2009; Kirch et al. 2012; Morrison 1994; Prentiss et al. 2014). I introduce the basics of the Boserupian and Malthusian approaches to demographic ecology as they are relevant to archaeology.

Boserup’s (1965) model concerned with the impact of population growth on agricultural intensification has been extraordinarily influential. In brief, she argued that by viewing steady population growth as the independent variable, it was possible to anticipate the need to intensify production of crops by virtue of expanding cropping frequency or some other process elevating production. In the short term, this meant reducing relative per capita income associated with higher labor costs, while in the longer term, it meant innovation would be rewarded (Lee 1986). Thus, in the larger picture, subsistence intensification and technological evolution could come about in a largely maladaptive process driven by steadily rising population. This model influenced processual archaeologists in a substantial way encouraging them to think about the forager-farmer transition and the emergence of complex society as outcomes of population pressure (Cohen 1977, 1981) and packing (Binford 1968, 2001). The model was also influential to foraging theorists seeking to understand diet changes and variation in food handling decisions in contexts of rising populations and local resource depression. Broughton (1994) documented expanding choice of lower-ranked prey over time in the Sacramento River Valley, thus a hunter-gatherer version of intensification in Boserup's (1965) sense. However, increased ratios of limbs to axial skeletal parts also reflected the possibility of extensification (Boserup 1965), assuming investment in field butchery for prey acquired at greater distances or use of a wider landscape, another costly strategy driven by local (to villages) resource depression. This fit a wider pattern of intensification and extensification in California as documented by other scholars (Basgall 1987; Beaton 1991). Intensification and resource depression has been recognized in many other contexts (e.g., Butler and Campbell 2004; Fisher and Valentine 2013; Janetski 1997; Nagaoka 2005). Subsistence intensification, however, has also come to be recognized as an adaptive process in cases where technological innovations enhance harvest such that higher energy returns can be had with reduced labor investment (Morgan 2015). Net and storage technologies in the Pacific Northwest have been suggested as examples (Chatters 1989, 1995; Prentiss et al. 2005). The logic of Boserup's model has also influenced recent theorizing of population growth and cooperation and the development of ritual traditions and social inequality (Stanish 2017).

The Malthusian demographic model asserts that population growth is not necessarily an independent variable but rather a by-product of low population demands relative to technology and food resources (Lee 1986; Malthus 1976; Puleston and Winterhalder this volume). This has the implication that population dynamics may fluctuate over time depending upon resource conditions, technological enhancements, and even sociopolitical factors (Lee 1986; Wood 1998). Recent modeling by Puleston et al. (2014) has defined several stages that well illustrates the Malthusian cycle. The copial period is a period of slow growth following the establishment of a settlement in a new context. This is followed by a shorter transition phase where food shortages increase mortality and reduce fertility and a subsequent Malthusian phase where there can be a true demographic crisis in maintaining a population. An outcome of this and other modeling (Lee et al. 2009; Lee and Tuljapurkar 2008; Puleston and Tuljapurkar 2008) is the recognition that loss of very young and old during these events can lessen crisis conditions though if human losses extend into productive age adults, the process can be catastrophic. Other implications concern the effects of investments in storage (Angourakis et al. 2015: Winterhalder et al. 2015) and ecosystem vulnerability (Kirch 2007). Archaeological exploration of the predictions of Malthusian models have demonstrated its utility for better understanding subsistence intensification (Kirch et al. 2012), investment in storage (Kuijt 2015; Prentiss, Foor, and Hampton 2018), development of social inequality (Prentiss et al. 2014), and settlement abandonments (Holopainen and Helama 2009). Social inequality can be a by-product of social competitiveness linked to differential food storage arising during a transitional or full Malthusian period (Winterhalder et al. 2015; see also Boone 1998; Hegmon 1991).

Niche Construction Theory

Niche construction theory (NCT) developed from discussions during the 1970s and 1980s concerning the influence of organisms on their environment (e.g., Lewontin 1970a, b), the concept of extended phenotype (Dawkins 1982), and, as applied to human beings, conceptions of dual inheritance (Boyd and Richerson 1985) creating parallel evolutionary cultural trajectories with the potential for impacts on organic evolution. Formalized in a series of papers by Odling-Smee and colleagues (Odling-Smee 1988, 1995; Odling-Smee et al. 2003), NCT recognized that organisms can play a significant role in affecting their selective environments with *Homo sapiens* being the ultimate niche constructor. Riede (this volume) details a range of means by which the human niche has been created with significant evolutionary impacts. Particularly dramatic examples include use of fire as a tool for modifying landscapes, shaping tools, and preparing food; domestication of animals and plants; and cognitive niche construction. Domestication as niche construction has become the center of an extensive debate over the domestication process and the origins of agriculture. Smith (2015) and Zeder (2016, 2017) argue that agriculture is best understood as the by-product of a niche construction process by human groups making conscious decisions to enhance productivity and reliability of subsistence resources. Aligning their arguments with the emerging concepts of an extended evolutionary synthesis, they argue that agricultural origins are better understood as more than the effects of cost-benefit decision-making as argued by foraging theorists (e.g., Gremillion 1996). However, Stiner and Kuhn (2016) point out that both models may offer insight, cost-benefit decision-making explaining daily decisions and NCT placing outcomes of those decisions across longer time spans in a more inclusive evolutionary framework. Mohlenhoff and Codding (2017) view niche construction as a form of patch investment with such decisions contingent upon considerations of net economic benefits. If NCT offers novel insights into a major human process such as domestication and the "Neolithic Revolution," then NCT may also hold the potential to help us understand contemporary human impacts on global climate and perhaps to begin modeling realistic means by which we might lessen the predicted adverse effects. This is reflected in the active discussions surrounding NCT and conceptions of the Anthropocene (Riede this volume).

Discussion

Archaeological research in evolutionary ecology remains diverse and essential to our wider interests in human bio-cultural evolution. Chapters in this section of the book illustrate the vibrancy of this research agenda and its important contributions and ongoing debates. Nagaoka and Gremillion review the important contributions of foraging theory to understanding the economic logic and potential fitness consequences of foraging decisions and associated behavior. As noted by Gremillion, these models have important implications for our understanding of wider processes, for example, domestication and the development of food production. There are also economic and reproductive impacts from an array of behaviors widely classified as signaling (Quinn, this volume). On a wider scale, the interactions between resource conditions, foraging and food production behavior, and social and reproductive behavior clearly impact demography as reviewed by Puleston and Winterhalder. Additional nuance to human ecology and the debate over aspects of the cultural evolutionary process is enhanced by considerations of the effects of human niche construction as reviewed by Riede.

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Chapter 12
Human Behavioral Ecology and Zooarchaeology

Lisa Nagaoka

Introduction

Human behavioral ecology has contributed to zooarchaeological research for about 40 years (Anderson 1981; Bayham 1979). Most archaeologists were first exposed to HBE models, in particular foraging theory, through the anthropological and ethnoarchaeological literature (Hames and Vickers 1982; Hawkes et al. 1982; O'Connell and Hawkes 1981, 1984; O'Connell et al. 1988, 1990; Smith 1991; Smith and Winterhalder 1992; Winterhalder and Smith 1981). While the ethnoarchaeological literature, in particular, examined archaeologically relevant topics, such as butchery and transport practices, zooarchaeological applications of the HBE models were not as common. Given the differences in the datasets, zooarchaeologists had to adapt the models to archaeological contexts and develop measures to be used with faunal samples.

Jack Broughton's (1994a, b, 1997, 1999) analyses of the faunal remains from the Emeryville Shellmound were the first comprehensive bodies of work that demonstrated how HBE models could be applied to zooarchaeological datasets. He used the three main HBE models (prey choice, patch use, and central place) to develop expectations about diet breadth, foraging efficiency, patch use, and transport that were evaluated using relatively simple zooarchaeological measures. Since then, HBE has been used to study human subsistence in a variety of archaeological contexts and across different types of faunal material (Alvarez 2014; Emery 2007; Faith 2007; Fisher and Valentine 2013; Giovas et al. 2016; Jones 2004; Morrison and Hunt 2007; Neme and Gil 2008; Otaola et al. 2015; Starkovich 2014; Thomas 2007; Whitaker 2010). Numerous reviews of archaeological applications of HBE models also have been published (Bird and O'Connell 2006; Broughton and Cannon 2010; Broughton and O'Connell 1999; Codding and Bird 2015; Grayson and Cannon 1999; Jones and Hurley 2017; Lupo 2007; Winterhalder and Smith 2000; Wolverton and Nagaoka 2018). Many of these reviews examine both ethnoarchaeological and zooarchaeological applications and contributions. This chapter focuses on zooarchaeological studies specifically because the methodology and datasets employed are distinctive from those in ethnographic or ethnoarchaeological studies. I review the foraging theory models typically used in zooarchaeological studies and then discuss the zooarchaeological measures developed and used to evaluate hypotheses generated by these models.

While HBE research has become more established in zooarchaeology, it still faces challenges that are more epistemological and ontological. Zooarchaeological and ethnoarchaeological HBE

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may appear to have similar goals, but the two differ significantly in the nature of their datasets. Thus, a challenge for zooarchaeologists is evaluating the relevance of ethnoarchaeological studies for study of archaeological contexts. Also, HBE approaches are often faced with the criticism that the interpretations they develop do not meet the expectations of an anthropological archaeology. Both of these challenges are reviewed in this chapter.

HBE Models

When examining how fauna were exploited by human predators in the past, zooarchaeologists generally use three foraging theory models: prey choice, patch use, and central place foraging. The most commonly used model is the prey choice model, which addresses the question of which prey foragers should try to exploit (Charnov and Orians 1973; MacArthur and Pianka 1966; Pulliam 1974; Schoener 1971). Two variables related to prey choice that are typically examined are diet breadth and foraging efficiency. Diet breadth is the number of prey types exploited. A narrow diet breadth would be reflected by just a few prey types in the diet, while foragers with a broad diet breadth would exploit a large number of prey types. To determine diet breadth, prey are ranked based on their net returns, the gains of exploiting the prey relative to the costs. Net returns only incorporate post-encounter return rates, and search time is not included because it is assumed that foragers are searching for all prey in the diet breadth simultaneously. Once encountered, the net returns of a prey type include the costs of pursuing, capturing, processing, and consuming the prey. Diet breadth should expand down the rank order of prey until a point of diminishing returns when the next lower-ranked prey type has lower net returns than the mean net returns across all prey types. The encounter rates of high-ranked prey affect diet breadth. When high-ranked prey are abundant and encounter rates are high, diet breadth should be narrower than when they are scarce (Pyke et al. 1977).

Differences in diet breadth are sometimes used to characterize a subsistence strategy as generalized or specialized (Alvarez 2014). For example, the overkill model hypothesizes that early peoples in North America hunted Pleistocene megafauna to extinction (Martin 1973). If so, then the prey choice model provides a means for testing a logical extension of this argument. Diet is expected to be narrow or specialized because high-ranked prey types would have been abundant and the average net return rate would have been high enough to exclude small fauna from the diet (Waguespack and Surovell 2003). However, zooarchaeological analyses indicate that diet was much broader or more generalized than expected and varied across regions (Byers and Ugan 2005; Cannon and Meltzer 2004, 2008).

In addition to diet breadth, foraging efficiency, the net returns per unit time, can also be documented using the prey choice model (Smith 1979, 1991, pp. 185–191; Broughton 1999). Predators are expected to have greater foraging efficiency if they can obtain significant net returns in shorter amounts of time. Like diet breadth, foraging efficiency is affected by the encounter rates of high-ranked prey. When high-ranked prey are common on the landscape, they are encountered frequently and thus comprise a large portion of the diet resulting in higher foraging efficiency.

Declines in foraging efficiency are often linked to resource depression or the decline in prey encounter rates as a result of foraging behavior (Charnov 1976). Depression can occur from direct harvesting that reduces population numbers (exploitation depression), from an increase in anti-predator behaviors (behavioral depression), and from predator avoidance behaviors (microhabitat depression) (Charnov et al. 1976; Wolverton et al. 2012). However, there are other explanations beyond predator-prey interactions that can explain a shift in the proportion of high- versus low-ranked prey. More efficient technology can decrease handling costs of prey (e.g., guns versus spears, motorized vehicles versus horses), which can increase the net returns of that prey (Madsen and Schmitt 1998; Grayson and Cannon 1999; Jones 2006). Thus, what may appear to be a shift away from high-ranked prey could actually be an increase in the net returns and rank of a lower-ranked prey. Mass capture technology can aggregate the returns of single prey items while reducing the overall handling costs such that the net returns per foraging bout increases for that prey type (Jones 2006; Lupo and Schmitt 2002; Madsen and Schmitt 1998). In addition to technological improvements, environmental change can also impact foraging efficiency by creating more or less favorable habitats, which affects population abundances, encounter rates, and foraging efficiency (Ugan 2005; Wolverton 2005).

Patch choice and use models address the question of which patches should be exploited and how much time should be spent foraging in each patch (Smith 1991, pp. 246–256). The prey choice model assumes random prey encounter rates, which would require prey to be randomly distributed across the landscape. If prey are spatially clustered, then there is also travel time incurred between these prey distributions that is not accounted for in search costs of the prey choice model. MacArthur and Pianka (1966) argued that the prey choice model should be applied to each patch or cluster of prey types separately. Which patches a forager chooses to search in is then modeled similarly to prey choice. Patches are ranked based on the net returns gained from each patch. Patches are added to the foraging suite until the net returns for the next available patch is less than the average net returns across all patches. Net returns include the cost of traveling between patches.

The marginal value theorem (MVT) was developed to address an issue that the patch choice model does not (Charnov 1976). Specifically, it models the time that a forager should harvest resources within a patch given the net returns of that patch and for all patches and the travel costs between patches. In addition, it incorporates resource depression within the model (Charnov et al. 1976). As foragers hunt prey in a patch, they cause a decline in the encounter rates of that prey. Foragers should remain in a patch until the declining net returns reach the average net returns for all patches. Because the MVT develops expectations of foraging time, it is often described as a time allocation model.

Both the prey and patch models were developed to consider predators that consume their prey at the point of capture. But some foragers, such as humans, transport resources back to a central location. Central place foraging models were designed to encompass the additional travel costs of transporting prey back to a home base for consumption (Orians and Pearson 1979; Cannon 2003). Distance and prey loading are important factors in this type of foraging. Distance to prey should increase as prey abundances first decline around the central place (Hamilton and Watt 1970). Over time, the depletion zone should expand with the rate of expansion which will be related to population density. As distance increases, foragers have to make choices about what they carry back to the central place (Schoener 1979). The prey load, or the amount that a forager can carry, also affects these choices. For humans, distance and prey loading have been used to study field processing patterns. If a prey item is too large to be transported whole, then it must be butchered into manageable packages. The costs associated with this are considered handling costs that should vary little across individuals (Cannon 2003). In contrast, butchering a carcass to maximize the delivery rate or prey load is considered a processing cost, which will vary with distance and prey encounter rates. If the distance to the central place is far, then a carcass may be field processed beyond creating transportable packages to discard the lower return parts and maximize the load. If prey encounter rates are low, then more of a carcass may be transported.

Overall, these models have been useful for providing conceptual frameworks that are logically consistent, embedded within evolution and ecology, and generate empirically testable hypotheses. Although the models may appear to provide a monolithic unicausal explanation, the reality is that this structure brings alternative explanations out into the open to be evaluated equally. The goal is not to demonstrate that resource depression occurred but to evaluate the causes for change in diet breadth, foraging efficiency, or carcass exploitation. For example, declines in foraging efficiency are hypothesized to be the result of resource depression. But the pattern could also be caused by environmental change impacting faunal abundances or technological innovations that reduce handling costs or allow for mass capture. Any study on resource depression would have to evaluate these known alternative explanations and rule them out to conclude that resource depression had occurred. So instead of research that focuses on finding data to support an explanation, HBE research is set up to evaluate multiple explanations for how human-prey interactions changed over time and differed across space.

Developing HBE Methodologies for Zooarchaeological Data

Applying HBE models to zooarchaeological contexts can be challenging. The models were developed by evolutionary ecologists who were able to directly observe the behavior of organisms and estimate the costs and benefits of their behavior using the currency of kilocalories. Thus, it should be no surprise then that these models were first used in anthropological and ethnoarchaeological studies on modern hunter-gatherers (Hames and Vickers 1982; Hawkes et al. 1982; O'Connell and Hawkes 1981, 1984; O'Connell et al. 1988, 1990; Smith and Winterhalder 1992; Winterhalder and Smith 1981). These studies illustrated the logic and explanatory power of the models for understanding human subsistence practices. But unlike research conducted on contemporary peoples, zooarchaeologists cannot directly observe costs/benefits in terms of kilocalories per hour. Instead, the zooarchaeological record consists of samples of skeletal remains of organisms accumulated over long time spans by populations rather than individuals (Lyman 2003a; Otaola et al. 2015; Wolverton et al. 2015). Thus, for these models to be applied using the archaeological record, researchers had to modify them for archaeological contexts and develop zooarchaeological measures. These measures are reviewed for six variables commonly used in zooarchaeological HBE studies (Table 12.1).

Foraging Efficiency

Measuring foraging efficiency ecologically and anthropologically entails documenting the net caloric returns per unit time (kcal/h) and determining prey ranks (Smith 1979, 1991, pp. 186–188). Developing an archaeological measure that focuses on net caloric returns requires making numerous assumptions or a significant investment in actualistic studies to determine nutritional value, pursuit

Table 12.1 HBE models used and patterns and explanations evaluated in zooarchaeological research along with some key references

Models	Patterns	Explanations	Key references
Prey choice	Foraging efficiency	Resource depression	Charnov et al. (1976), Broughton (1994a, b)
		Environmental change	Nagaoka (2002), Wolverton (2005)
		Technological innovations	Butler (2001)
		Mass capture	Madsen and Schmitt (1998), Jones (2006)
		Sustainability	Butler and Campbell (2004), Lyman (2003b)
		Taphonomic factors	Lyman (1994a, b)
	Diet breadth	Sampling issues	Grayson (1984), Lyman (2008)
Patch choice	Patch number		MacArthur and Pianka (1966)
Patch use (MVT)	Residence time	Resource depression	Charnov (1976), Nagaoka (2002)
		Environmental change	Jones (2009)
		Technological innovations	Smith (1991)
	Intensification	Resource depression	Nagaoka (2005, 2006)
Central place	Prey load	Transport distance	Broughton (1999), Cannon (2003), Nagaoka (2005, 2006)

costs, and handling costs of prey types. Fortunately, Bayham (1979) developed a uniquely archaeological measure to document changing foraging efficiency using zooarchaeological data. The index uses two taxa that represented high- and low-ranked prey. Body size has been shown to correlate with net returns such that large-bodied prey can provide higher net returns than small-bodied ones (Broughton et al. 2010; Jones 2004; Simms 1987; Ugan and Bright 2001). The taxa used in the index have to be common and present across all samples, whether spatial or temporal, because that means the two taxa were in the diet breadth across all samples. The prey choice model assumes that foragers will take whatever they encounter as long as it is within the diet breadth; thus, the proportion in the index requires a similar assumption that the proportion reflects the abundance of these taxa on the landscape. A high proportion of the large-bodied taxon indicates that encounter rates were high and the taxon was likely abundant in the environment. When high-ranked prey are abundant, the index and thus foraging efficiency are high. Lower index values indicate a greater proportion of the small prey type and thus lower foraging efficiency. These faunal indices may appear to oversimplify a complex process by using two taxa. But as a zooarchaeological measure of foraging efficiency, it is elegant in its simplicity and can be combined with multiple other lines of evidence (Broughton 1997; Munro 2004; Ugan 2005; Wolverton et al. 2008). It should be noted that faunal indices are becoming a more commonly used measure outside of HBE research. Indices have been used extensively in the American Southwest (Badenhorst and Driver 2009; Dean 2001, 2007a, b; Driver and Woiderski 2008; Potter 1995; Quirt-Booth and Cruz-Uribe 1997; Reynolds 2012; Schollmeyer and Driver 2013; Szuter 1991) and can be traced back to Bayham's (1979) research.

While there is ethnographic evidence that body size generally correlates with prey rank, there are also cases where the relationship does not hold. As mentioned above, prey obtained through mass capture techniques will have higher net returns than expected given their size. And extremely large taxa can have lower net returns given high handling costs. Thus, researchers have used other criteria for determining prey rank. Prey mobility and predator defense have been used to differentiate prey ranks (Stiner et al. 2000; Munro 2004). In this case, the two prey types, tortoises and hares, were of similar body sizes, and it was assumed that tortoises (slow prey that becomes immobile in its shell) would have lower pursuit costs and thus higher post-encounter returns than the quicker more agile hares. Alternatively, instead of using faunal indices, evenness measures have also been used to document foraging efficiency (Jones 2004; Nagaoka 2001). Evenness is used to examine changes in the proportions of all prey in the diet. If high-ranked prey are initially abundant and then decline over time, the relative abundance of each taxon should become more evenly distributed.

Many studies demonstrate that over time, a decline in a faunal index or an increase in evenness is caused by resource depression, either through a decrease in the population abundance of the large taxon or a decrease in its availability due to behavioral changes (Allen 2002; Alvarez 2014; Broughton 1999; Butler 2000; Cannon 2000; Giovas et al. 2016; Janetski 1997; Morrison and Hunt 2007; Nagaoka 2002). As discussed above, a decline in foraging efficiency can be caused by other processes besides resource depression. Faunal index values can be affected by anything that can lead to changes in the specimen counts for the small taxon and/or the large one. Thus, there are several alternative explanations besides hunting pressure that could cause a decline in a faunal index that also need to be evaluated. Environmental factors can impact population abundances of the large taxon or the small taxon or both (Byers and Broughton 2004; Jones 2009; Wolverton 2005). Technological innovations can improve handling costs for either taxon (Butler 2001; Smith 1991). And taphonomic factors could lead to differential preservation or fragmentation of either taxon used in the index (Lyman 1994a). All of these potential explanations for a change in the index values should be evaluated.

Diet Breadth

A decrease in foraging efficiency can lead to an increase in diet breadth but only if the average net returns decline such that the returns for the next low-ranked prey type become greater than the declining average (Pyke et al. 1977; Stephens and Krebs 1986). Archaeologically, diet breadth is measured using the number of taxa (NTAXA) represented in the sample. However, this measure has one significant drawback. It is known to correlate positively with sample size (Grayson 1984; Lyman 2008). The larger the sample of faunal remains, the greater the number of taxa identified. Thus, sometimes it is difficult to determine whether a change in NTAXA is due to shifts in diet breadth or sample size. However, if there are enough samples to compare, the relationship between NTAXA and sample size can be used to determine whether or not a shift over time in NTAXA relates to a change in diet breadth or is an effect of sample size. In particular, the slope of the regression line for NTAXA and sample size describes the rate at which taxa are added with an increase in sample size (Grayson and Delpech 1998, 2001; Nagaoka 2002). Thus, if one sample of assemblages has a regression line with a greater slope or a larger y-intercept, then it is adding taxa at a higher rate than the sample of assemblages with a lower slope or y-intercept, which suggests that diet breadth is wider. Like foraging efficiency, other explanations besides resource depression can lead to an expansion of the diet breadth, such as shifting environments or differential preservation or recovery, and they should all be assessed. Given that diet breadth may or may not increase with declines in foraging efficiency, and given the issues with NTAXA as a measure, diet breadth tends to be used as a supplementary indicator of changing subsistence.

Patch Choice and Residence Time

Studying changes in patch choice archaeologically is not common. Much of this stems from the challenge of defining patches and identifying which prey types should be found in each patch (Lupo 2007). Patches should consist of mutually exclusive sets of fauna such that any prey type within a patch has an equal chance of being encountered but prey types from other patches should not be encountered. Some fauna have broad habitats, and for extirpated or extinct fauna, environmental and behavioral reconstructions are required. When patches have been identified in studies, they are often broad habitat descriptions, such as terrestrial versus marine (Cannon and Meltzer 2004; Jones 2009; Nagaoka 2002; Wolverton et al. 2015). These broadly defined patches likely characterize most of the foraging universe, leaving little room for the addition of new patches. Thus, patch choice is not often used to examine if patches were added or removed from the foraging radius.

A more common use of patch models in zooarchaeological research is to examine shifts in patch residence times (Broughton 1994a, b, 1997, 2002; Jones 2009; Nagaoka 2002). Faunal indices and relative abundance data are used to demonstrate that foragers increase/decrease the amount of time they spend in one patch versus others. Relative abundance of prey types of each patch are often used to document shifts in the amount of time spent in each patch. For example, in my research in southern New Zealand, I documented an increase in the time allocated to the offshore fishing patch that corresponded to a decline in foraging efficiency within the two terrestrial hunting patches (Nagaoka 2002). The inland and coastal patches both had large-bodied, high-ranked fauna that declined in abundance over time. As this occurred, offshore fishing of a large seasonal fish species became an important part of the subsistence. As with foraging efficiency, shifts in patch residence time could be explained by other processes besides resource depression. For example, Jones (2009) documented changes in the proportion of riverine, grassland, and forest taxa exploited to show that foragers spent increasingly more time in the grassland patch. Instead of resource depression of resources within the riverine or forest patches, this shift in patch use was linked to changing environmental conditions that favored expansion of the grasslands.

Intensification

Patch residence time can also be used to study intensification. Intensification can be described generally as the process in which foragers put more time into extracting resources of increasingly lower returns (Morgan 2015). Thus, declines in foraging efficiency would lead to conditions in which intensification should occur. In zooarchaeology, intensification commonly refers to how intensively individual carcasses are used. A prey carcass is comprised of meat, marrow, and grease, each of which provides different nutritional returns (Binford 1978). When should foragers intensify their use of individual carcasses and put more effort into harvesting the lower-ranked resources from a carcass?

To address this question, we can use the MVT and apply it to the prey item or carcass as the patch. The question becomes, how much time should a forager spend harvesting resources from a carcass? Zooarchaeologists commonly study the butchery and transport of carcass parts. Theoretically, when foraging efficiency is low (e.g., under conditions of resource depression and/or environmental constraint), foragers should transport as much of the carcass as possible back to their campsites or villages. A separate factor, however, is the impact of transport distance. A forager may focus on transporting only high-value carcass parts not because lower-value parts are not needed but because transport distance requires them to maximize the load (see the next section). One way to address this concern is to study how the transported carcass parts are used at the home base. The resources that are typically examined archaeologically are the within-bone nutrients of marrow and grease. Marrow is found mainly in long bones and can be obtained by breaking into the marrow cavities of bones. The process is relatively simple, and a significant amount of marrow can be extracted depending on the size of the animal and the skeletal element. In contrast, grease extraction entails breaking bones into smaller pieces to maximize the surface area exposed and then boiling them to remove the grease. Thus, it is a more time-consuming and lower return process.

When a carcass is treated as a patch, then the amount of time a forager spends in marrow and grease extraction should be affected by the net returns of other carcasses because marrow and grease are relatively low-ranked resources. When the productivity of other patches is high, foragers should spend less time extracting marrow and grease. If other higher-ranked resources decline in terms of encounter rates and/or other patches decline in terms of average net returns, then time invested in marrow and grease extraction may increase.

Marrow and grease extraction can be documented by using bone fragmentation measures commonly used in zooarchaeological studies. Often, fragmentation is used to measure both marrow and grease. However, since marrow and grease extractions are different processes that likely have different net returns, they should be measured independently when possible (Lyman 1994b; Wolverton 2002; Nagaoka 2005, 2006). Marrow extraction only requires that the shafts be broken to access the marrow cavity. Thus, the proportion of broken shafts indicates that marrow may have been accessed, but marrow was definitely not extracted from whole bones. The measure of “% whole” documents this latter condition. It uses the percentage of the total minimal number of elements (MNE) for each long bone that is whole. For grease extraction, since smaller bone fragments can make the process more efficient, the ratio of the number of identified specimens (NISP) to the MNE measures the number of fragments per skeletal element (NISP/MNE). If carcass exploitation intensifies, there should be a decrease in % whole and an increase in the NISP/MNE. Since both of these measures rely on bone breakage, the impact of taphonomic processes on the assemblage must be evaluated (Nagaoka et al. 2008).

Prey Loading or Delivery Rate

A significant portion of early HBE applications in archaeology focused on carcass field processing and transport (Bartram 1993; Bartram and Marean 1999; Lupo 2001; O'Connell et al. 1988, 1990; O'Connell and Marshall 1989). Binford's (1978, 1981) research, in particular, is credited with using ethnoarchaeological studies to understand how to interpret the zooarchaeological record. He was specifically interested in how skeletal element representation was being used to weigh in on the hunting versus scavenging debate in early hominid research. Even though Binford's ethnoarchaeological research was not directly derived from HBE models, his concept of element "economic utility" is analogous to net returns. Binford argued that each portion of a carcass then has its own nutritional value based on the amount of meat, marrow, and grease associated with it. Higher-value portions were more likely to be transported back to the home base than lower-value ones.

In HBE research, central place foraging models can be used to generate similar expectations about carcass transport patterns. It is often difficult to know exactly how carcasses may have been butchered. However, the butchery process can be differentiated into two steps (Cannon 2003). Butchery required to cut a carcass up into transportable units (e.g., hind limb, rib cage, etc.) is part of the handling costs and should be fairly constant for a prey type. Additional field processing costs are incurred to maximize the prey load and will vary depending on the transport distance to the central place and the prey encounter rates. When transport distance is low, and high-ranked prey are abundant, transporting mainly portions with high nutritional value may be the appropriate strategy. Time could be better spent transporting the choice cuts to the home base and then hunting for more prey than investing more time into maximizing the prey load. If distance increases but encounter rates remain constant, then a carcass may be processed to remove the low-return portions or riders to maximize the load. When prey encounter rates decline, then each carcass becomes more valuable, and there is incentive to extract more out of each carcass. Thus, the carcass may be field processed more extensively, perhaps even to the point of removing and discarding bone tissue at the butchery site (Bartram 1993).

To measure these changes in processing, the nutritional value of each portion of a carcass needs to be determined. Binford (1978) established a methodology for quantifying the value of carcass portion called utility indices. Each skeletal element is associated with a nutritional value derived from actualistic research (Metcalfe and Jones 1988). Utility indices have been generated for a broad range of species (see Lyman 2012, Table 1). If the utility for the species of interest has not been developed, then a proxy species must be used. Binford used utility curves to evaluate the butchery and transport strategy for an individual faunal sample. However, this method is difficult to use for examining temporal patterns. Broughton (1999) developed the mean utility measure, which simplifies Binford's calculations and summarizes the average utility or returns represented in a sample. To calculate the mean utility of a sample, the utility value of an element is multiplied by the MNE for that element, and then the values for all elements are then summed and divided by the total MNE for the sample. When a greater number of high-value elements are represented, the mean utility is high. In contrast, when lower-value elements are more common, mean utility will be lower. Thus, mean utility can be used to evaluate over time whether foragers are selecting and transporting higher utility elements or if the transport strategy is much broader with a diverse range of elements selected.

While mean utility can provide insight into whether high- or low-return elements were transported, other measures are required to evaluate whether increased field processing has occurred. One method is to compare the frequency of individual skeletal elements, especially high- and low-value elements, that may have been transported together. For example, to demonstrate an increase in field processing of moas, I compared the frequency of cervical vertebrae and ossified tracheal rings of moa across time (Nagaoka 2005). There was a significant decrease in tracheal rings compared to the cervical vertebrae over time, suggesting that tracheal rings were discarded when the internal organs were removed in the field, while the necks were transported with the rest of the carcass.

Since these analyses rely on skeletal element representation, the impact of various taphonomic factors on element abundance has to be evaluated (Lyman 1994a). Differential preservation can be assessed by comparing bone density patterns with skeletal element frequency (Lyman 1984, 1992). Differential fragmentation and identification can also impact element representation. Some elements can only be identified from larger fragments. Thus, if fragmentation rates change across time, this can impact the identifiability and representation of those elements in assemblages. This can be assessed by comparing the NISP/MNE for those elements across samples. For example, if the relative abundance of a high-utility element declines while fragmentation rate increases, then a decline in the mean utility may be reflecting differential fragmentation rather than differential transport.

Summary

The challenge of applying HBE models to the zooarchaeological record has been to develop measures using faunal data to evaluate hypotheses generated by the models. Some, like faunal indices, were developed for use in HBE models. Others were common ecological or zooarchaeological measures such as evenness, richness (NTAXA), or fragmentation (NISP/MNE). HBE practitioners have explored, developed, and evaluated different methodologies to suit the type of faunal data (e.g., invertebrates vs. vertebrates) or contexts (foraging vs. food production, etc.) that comprise their samples. Just as important as the measures is the practice of evaluating alternative explanations, particularly taphonomic processes that affect the composition of the faunal data. These steps have made the application of HBE models uniquely zooarchaeological.

Ethnoarchaeological vs. Zooarchaeological

Generally, there have been two approaches to HBE in faunal research—ethnoarchaeological and zooarchaeological. Ethnoarchaeological research has a much longer history and has provided important insights into how human subsistence practices produce the zooarchaeological record (Bartram and Marean 1999; Binford 1978, 1981; Bird and Bliege Bird 2000; Hudson 1993; Lupo 1994, 1995, 2001; Lupo and O'Connell 2002; Lupo et al. 2013; O'Connell et al. 1988; O'Connell and Marshall 1989; Yellen 1991). Unlike research in other archaeological areas, ethnoarchaeological and zooarchaeological HBE research on human subsistence has been less particularistic, leading to more studies building a common knowledge base (O'Connell 1995). The shared theoretical framework means that both groups of researchers are interested in similar processes and expectations under the models. Where they differ is in the scale of research, which then requires differences in methodology, specifically variables and measures that are appropriate for data at the two different scales. From a zooarchaeological perspective, ethnoarchaeological research is useful when it provides insight into processes that impact outcomes. But it can be less useful when the research describes complexities at a finer resolution than the zooarchaeological record and does not provide guidance on how to apply findings to zooarchaeological contexts.

The issue of scale is important to consider when trying to apply ethnoarchaeological findings to zooarchaeological datasets. Ethnoarchaeological research occurs at a different temporal and spatial scale than zooarchaeological research (Table 12.2). Which of the variables and processes that have been identified ethnographically are archaeologically relevant? And if they are relevant, how should they be handled analytically? The faunal assemblages that zooarchaeologists study are often

Table 12.2 Differences between ethnoarchaeological and zooarchaeological HBE research

	Ethnoarchaeology	Zooarchaeology
Observable	Human behavior	Bone specimens
Currency	Energy (kcal)	Bone counts
Temporal scale	Hour, day	Decade, century, millennium
Spatial scale	Individual, household	Excavation layer, unit, site

aggregations across time, space, and demographic factors (Lyman 2003a; Otaola et al. 2015). They are amalgams of decades if not centuries of resource exploitation. To use a garbology analogy, zooarchaeological data are analogous to the data that would be generated from studying a city landfill, while anthropological and ethnoarchaeological data are like the data that could be gathered through observations of individuals' refuse behavior. With the latter, we can understand variability across a variety of demographic, economic, social, and geographic variables at a specific moment in time. But with the landfill data, our understanding is likely limited to patterns at the scale of the city over years. Thus, for zooarchaeologists, the challenge is to determine which of the patterns and processes documented by the fine-scale ethnoarchaeological data are relevant for analyzing zooarchaeological datasets.

In some cases, ethnoarchaeological findings can be easily integrated into existing models. For example, Bartram (1993) documented extensive field processing among the Kua, such that skeletal elements were removed and only the meat was dried and transported to the home base. Thus, in some cases, few faunal remains may be returned back to the home base, creating an absence of evidence in the zooarchaeological record of how carcasses were utilized. As a cautionary tale, this research could be used as an example of how taphonomic processes can remove skeletal elements from the archaeological record. But this case study may also provide an extreme end of field processing decisions. When encounter rates for high-ranked prey are low and transport distances are high, there is an incentive to field process to maximize the prey load (Cannon 2003). The significant amount of time spent processing the carcass at the butchery site suggests that time was better spent extracting resources out of carcass than expediently processing the carcass and going out to hunt again. The importance of "missing elements" is easier to understand when the data are evaluated across time or space rather than as a single sample. Instead of seeing just an absence of skeletal elements in one sample, looking across samples allows zooarchaeologists to understand how one or another sample fits into a larger context. Ethnoarchaeological research into transport and butchery patterns has been particularly easy to integrate into zooarchaeological studies because both use skeletal element abundances as their data.

For some ethnoarchaeological research, zooarchaeologists have to assess whether the findings are archaeologically relevant. For example, ethnoarchaeological research has identified a number of factors that can affect transport decisions besides transport distance including prey size, the size of the carrying party, transport method, and processing time (Bartram 1993; Bird and Bliege-Bird 1997; Metcalfe and Barlow 1992; O'Connell et al. 1988, 1990; O'Connell and Marshall 1989). Zooarchaeologists have to evaluate which of these factors are likely to be strong candidates for alternative explanations, which ones may be supplemental, which ones can be dismissed, and which can be measured archaeologically. For example, O'Connell et al. (1988) documented that larger carrying parties could transport more of a carcass back to the central place. Given that zooarchaeologists commonly have data aggregated across numerous foraging bouts spanning decades or centuries rather than data from individual foraging bouts, we may only be able to track a change in the average carrying party size over time. But can average carrying party size be measured in the archaeological record? Whether this can be measureable or not, is there any evidence that party size is a significant factor, more so than other factors? Unfortunately, little guidance is provided in the ethnoarchaeological literature on how to handle these issues archaeologically. Thus, zooarchaeologists choose what variables are important to focus on and determine what is measureable in the archaeological record. In this instance, I would argue that transport distance is probably more important than carrying party size. The central place models emphasize that with increasing distance, there should be an increase in prey load. Thus, average carrying party size should covary with average distance. Also because a carcass is finite, there should be a ceiling for the number of people needed to maximize the prey load no matter the distance.

There are cases when it is even more difficult to assess the archaeological utility of ethnoarchaeological research. This can be illustrated by discussions about the validity of using body size as a proxy for prey rank (Bird and O'Connell 2006; Lupo 2007). There are several well-documented issues with the relationship between body size and prey rank. As discussed above, extremely large species tend to have significant handling costs and lower net returns given their size. And prey obtained by mass capture techniques can have lower handling costs such that its net returns may be greater than predicted by its individual size. In these situations, body size is not argued to be a poor proxy for prey. Instead, it is expected that zooarchaeologists evaluate whether either of them is likely to affect prey ranks in their samples.

In contrast, one discussion has pitted body size against prey mobility as a better proxy for prey ranks. The debate on the importance of prey mobility is split along ethnoarchaeological and zooarchaeological lines. Bird et al. (2009) studied Martu hunting in which they demonstrated that there are more failed hunts for some highly mobile taxa, which can lead to higher pursuit costs. The result is that post-encounter return rates and thus prey ranks may correlate more closely with prey mobility than prey body size. Bird et al. conclude that body size is "often an inappropriate proxy for prey ranks" (Bird et al. 2009, p. 3). In contrast, zooarchaeologists continue to support the use of body size as a proxy for prey rank. Broughton et al. (2011) have provided an extensive evaluation of the relationship indicating that in many cases, large game provides higher net returns and thus would be higher-ranked than small game. Ugan and Simms (2012) question the Martu analysis and how net returns were calculated in the ethnoarchaeological study. Time spent tracking an animal was included with pursuit time rather than search time. Thus, they argue that post-encounter return rates were inflated for some mobile prey. They note that including tracking time differentially increases the costs of larger-bodied fauna because they tend to have much larger foraging radii. Thus, prey mobility really relates to the size of a prey's home range, which should fall under search costs, rather than under predator evasion strategies within pursuit costs (e.g., fast/slow) as Bird et al. determined.

So why the difference in perspectives between ethnoarchaeologists and zooarchaeologists? It is likely that some ethnoarchaeologists consider their research to be zooarchaeological and that translating their findings is not necessary. But the differences in the nature of the data and the scale of the research must be acknowledged. Thus, zooarchaeologists have to determine if the patterns seen in ethnoarchaeological data are contributing to a general pattern that can be seen archaeologically, or are they noise at an archaeological scale? Broughton et al.'s (2011) review makes a strong case that the relationship between body size and post-encounter return generally holds across many contexts and at an archaeologically relevant scale. In contrast, even though Bird et al.'s (2009) data show that the ranks of one or two taxa are significantly altered when prey mobility is used, mobility still correlates with prey size (Figure 6b, Table 2). Given this, it would appear that prey mobility in the Martu study is tracking fine-scale variability that may not be appropriate for time- and space-aggregated zooarchaeological datasets.

Even if prey mobility can be identified as an appropriate proxy, then the next question would be how can prey ranks based on prey mobility be determined zooarchaeologically? Unlike body size which can be estimated based on average species weight, prey mobility is more challenging to measure for archaeological contexts. In the Martu study, the costs associated with prey mobility, particularly the tracking costs, were influenced by several variables such as the extent of home range, speed, and predator evasion strategies. Prey mobility was rated on a 5-point scale based only on prey speed relative to hunters as well as the need for capture technology. But the size of the home range was also important, particularly for hunt failure, since the prey with high hunt failure rates were also ones that had large enough ranges such that they may not be encountered even after tracking. Thus, archaeological prey ranks could be estimated based on any one of these variables or a combination of each of them. Some of these variables would require assumptions about prey behavior or hunting capabilities. It is likely that, as in the Martu study, prey mobility would be ordinal categories with faster prey as low-ranked and slow prey as high-ranked.

To extend this hypothetical situation further, if prey mobility can be used to rank taxa, then how will this affect the index as a measure of foraging efficiency? In Bird et al.'s (2009, Table 2) Martu dataset, two commonly hunted taxa, the hill kangaroo and the skink, vary significantly in prey ranks and net returns depending on whether tracking time is included or not. The hill kangaroo is the largest species (21 kg) in the diet, while the skink is only 300 grams. When tracking is not included in the net return calculations, the hill kangaroo is second ranked with an average return rate of 58,973 kcal/h, while skinks are third ranked with almost 1/3 of the net returns of kangaroos (21,188 kcal/h). When tracking time is included, skinks become the taxon with the highest net returns of all fauna (20,403 kcal/h), while hill kangaroos drop to fifth with net returns of only 3844 kcal/h. In a faunal index based on prey mobility net return rates then, skinks would be the high-ranked prey and kangaroo the lower-ranked prey:

$$\text{skinks}/\left(\text{skinks} + \text{hill kangaroos}\right).$$

A decline in the faunal index should still reflect a decrease in foraging efficiency with the less mobile, high-ranked skinks comprising a smaller portion of the diet. However, evaluating whether resource depression was reflected in the index would be more challenging. Hill kangaroos, as a larger-bodied species, have a lower reproductive rate than skinks and will likely experience greater declines in population abundances with continued harvest pressure. If resource depression occurred, especially exploitation depression, then hill kangaroo populations would decline at a greater rate than skinks, and the faunal index will likely increase rather than decrease. Thus, the index using prey mobility to determine prey ranks may be able to document changes in foraging efficiency. But the measure could no longer be directly linked to resource depression of the large-bodied prey type when those prey types are no longer considered high-ranked. Thus, another measure would be needed to evaluate the cause of the change in prey choice.

Ethnoarchaeological research has played an important role in the development of zooarchaeological HBE studies. Both are unified by a common conceptual framework, which has made it easier to incorporate ethnoarchaeological findings into faunal studies. However, the difference in the scale at which each operates makes each approach distinct. The results of ethnoarchaeological studies more closely resemble anthropological studies because both are conducted at a much finer temporal and spatial scale than what is recorded in the archaeological record. As a result, the challenge for zooarchaeologists is figuring out how ethnoarchaeological findings can be incorporated methodologically. Unfortunately, the work of evaluating how to use these findings in archaeological contexts often falls upon zooarchaeologists. In this sense, zooarchaeologists are consumers of ethnoarchaeological research rather than ethnoarchaeologists being providers of new zooarchaeological methodology. This is an important distinction because when the latter is assumed without consideration of zooarchaeological needs, then ethnoarchaeological research aligns with criticisms identifying the role of ethnoarchaeology as deconstructionist or "obnoxious spectator" rather than as a means for bridging the divide between the past and the present (Simms 1992).

Anthropological vs. Ecological

Another area where HBE practitioners diverge is when anthropological interpretive goals conflict with ecological (or scientific) ones. Criticisms of evolutionary ecological models in archaeology highlight the perspective that anthropological interpretations are missing from these studies. HBE models have been criticized for being environmentally deterministic and for not incorporating individual intentions and motivations (Boone and Smith 1998). However, these models were never intended to delve into this area of human behavior. Instead, they are designed to study humans as simply another living organism interacting as a predator in an ecological community. Thus, the focus is not on what makes humans unique but what we have in common with other organisms. This is not to say that "culture" is unimportant, only that the models were developed to study organisms from an ecological perspective. While other organisms may or may not have a rich internal life, ecologists do not study how their subjects feel or think. So HBE models provide a specific way of looking at human behavior, an ecological or evolutionary one.

Generally, HBE studies in zooarchaeology assume natural selection is the driving mechanism for the foraging choices that humans make. However, two other processes, sexual selection and niche construction, have recently come to the fore. Both focus on behavior that is more in line with anthropological interpretations. Research using these processes have become opportunities to explore aspects of humanity from an evolutionary perspective that foraging theory does not. However, even within both of these areas, there is conflict between the ecological focus and the anthropological expectations within archaeology.

An area of research that explores sexual selection as the explanatory mechanism is costly signaling. Costly signaling is one aspect of signaling theory research that focuses on how organisms convey messages to others that ultimately impacts their fitness (Cronk 2005; Hasson 1997, Zahavi 1975). Sexual selection becomes the mechanism for determining the fitness of a behavior when signals impact mating success. Organisms can signal their fitness to potential mates through mating behavior and morphological features such as antlers or plumage. These signals become costly when they are disadvantageous from the perspective of natural selection. For example, they may require a significant input of energy (e.g., large morphological features such as antlers) or may hinder predator avoidance or evasion (e.g., brightly colored plumage). In ethnographic HBE studies, costly signaling is typically used to explain differential fitness of hunters based on their ability to hunt and capture game. Hunters can "show off" by pursuing large game that can be shared with others, signaling their value as a mate (Bliege Bird et al. 2001; Hawkes 1991; Smith et al. 2003). The cost of this behavior is that the forager may ignore resources that would have been within the diet breadth using an energy-maximizing approach to pursue prey that are higher in social prestige. Thus, there is a trade-off of greater net returns for enhanced access to mates.

Since costly signaling related to hunting strategies involves prey abundances, it would seem a natural topic for zooarchaeological researchers to study. One example of costly signaling research using zooarchaeological data resulted in a debate about the validity of the research. Hildebrandt and McGuire (2002, 2003, McGuire and Hildebrandt 2005) used an increase in the artiodactyl index to argue that deer hunting increased because of costly signaling. This research was critiqued by Codding and Jones (2007) for not adequately addressing the conceptual and empirical issues with this area of research. They agree that being a good hunter may confer fitness based on sexual selection, but the problem is differentiating good hunters from lesser hunters archaeologically. They question whether the artiodactyl index can reflect evidence of greater hunting of prestige-prey than should be expected by an energy-maximizing strategy. Codding and Jones also critique how Hildebrandt and McGuire simplify costly signaling to an evolutionarily stable strategy that consists only of honest signals with uniformly positive evolutionary outcomes. Signaling is a diverse strategy with honest and dishonest signaling that result in both positive and negative fitness outcomes depending on the context. Thus, archaeologically, signaling was conceptualized in a progressive manner (of course the strategy should be used; it is advantageous) rather than evaluated for its advantage or disadvantage as a driver of hunting behavior. McGuire et al. (2007) responded to Codding and Jones' critiques as "no can do" archaeology because they interpret the criticisms to state that costly signaling is outside the realm of what archaeology can know.

These two perspectives on costly signaling research diverge because of their differing perspectives on empirical rigor and archaeological interpretations. HBE has been a way to provide empirical expectations or hypotheses about the zooarchaeological record. Although resource depression has become a common explanation, it is often based on multiple lines of evidence that support resource depression and rule out other explanations. Codding and Jones are advocating for this type of approach in zooarchaeology. An increase in a faunal index value could be caused by costly signaling practices, but it could also be caused by other factors, such as environmental conditions or technological innovations, which improve the encounter rates for the large-bodied taxon or decrease them for the smaller-bodied taxon (Broughton and Bayham 2003). All of the potential explanations should be evaluated before claiming that a particular explanation is the cause (see Grimstead 2010; Whitaker and Carpenter 2012). In contrast, McGuire et al. are less concerned with the empirical rigor of their analyses and the validity of the faunal index for measuring costly signaling. Instead, they favor a more complete anthropological study of the past, which can be provided by a costly signaling interpretation. Codding and Jones criticize this approach as creating "just so" stories that advocate for an interpretation rather than empirically evaluating the many possible interpretations. One could argue that McGuire et al. relax their expectations about empirical rigor normally found in HBE zooarchaeological studies to prioritize the more anthropological interpretation.

Another example of this trade-off between scientific rigor and anthropological interpretation can be seen in research involving niche construction. In the evolutionary biology literature, niche construction theory (NCT) is used to understand how environmental engineering by organisms impacts the fitness of those organisms (Odling-Smee et al. 1996). The classic example is beavers who modify their environment, creating their own niches and thus enhancing their evolutionary success. The utility of NCT as a distinct evolutionary process is still being debated within evolutionary biology. Many evolutionary biologists argue that NCT is unnecessary because much of what is proposed under NCT can be explained using established mechanisms (Scott-Phillips et al. 2014). However, applying NCT to archaeological contexts seems an obvious research avenue to pursue given that humans can be characterized as the consummate environmental engineers (Smith 2007). In archaeological contexts, NCT has been introduced as a framework to explain important cultural developments such as the origins of domestication and agriculture (Broughton et al. 2010; O'Brien and Laland 2012; Smith 2007, 2015; Stiner and Kuhn 2016; Zeder 2016, see also Riede, this volume).

There have been two approaches that archaeologists have used NCT to explain the past. In one approach, humans are inherently different from other organisms simply by the degree to which we modify the environment to suit our needs and improve our situation (Smith 2015; Zeder 2016). NCT is thus used to portray humans as actively modifying their environment to their selective advantage in contrast to being at the mercy of the environment as under natural selection. In this sense, NCT is directional, a chosen path that is always beneficial. However, this approach to NCT has been critiqued for being tautological (Codding and Bird 2015). For example, NCT is argued to be oppositional to foraging theory in the archaeological literature because it is more appropriate to prioritize humans as different or exceptional rather than treat humans as any other rate-maximizing organism (Smith 2007; Zeder 2016). NCT is not just argued to be appropriate in some conditions but held to be the better explanation than foraging theory in any context. However, in contrast to foraging theory, NCT proponents have not developed the means to measure and evaluate niche construction. Instead, NCT is presented simply as the starting point and the end point, the question and the answer.

The alternative approach to niche construction treats humans as other organisms and environmental engineering as just another strategy that may or may not be intentional or have selective benefits

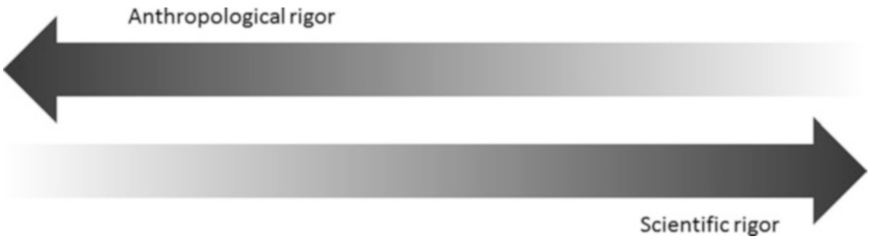

Fig. 12.1 The relationship between the expectations of anthropological and scientific rigor

(Laland and O'Brien 2010; Broughton et al. 2010; Codding and Bird 2015). Thus niche construction is not directional and can result in either positive or negative impact on an organism. Some researchers argue that niche construction is not oppositional to foraging theory models but can be incorporated into these models through established processes such as resource depression (Broughton et al. 2010). Resource depression qualifies as niche construction because humans are modifying the environment and the availability of resources. In this approach, researchers generated expectations across multiple lines of evidence and used zooarchaeological data to evaluate these hypotheses, concluding that the human-altered environment led to increased time allocated to agriculture.

These contrasting perspectives on costly signaling and niche construction reflect not just differences in how HBE models are applied or whether they are seen as valuable for understanding subsistence change. They reflect a conflict embedded within the structure of processual archaeology. When laying out the New Archaeology, Binford (1962) argued that archaeology should have two goals. It should be less particularistic and unstructured (i.e., more scientific) and should also strive to contribute specifically to anthropological theory. Processual archaeologists have long assumed that we can achieve both the anthropological and scientific goals within archaeology, even though critics such as Dunnell (1980, 1989) have argued that achieving both is difficult if not impossible. The differences in perspective relate to how we perceive the relationship between the anthropological and scientific goals. We often assume that both goals are positively correlated and measured on a similar scale so that if we are more anthropological, then we are more scientific. However, this only works if the anthropological goal is prioritized. Few would agree with the statement that if we are more scientific, then we are more anthropological. Thus, I argue that the anthropological and scientific goals and standards are measured on two different scales that are inversely related to one another (Fig. 12.1). Under this model, archaeologists have to make a choice between prioritizing the anthropological or the scientific. In the diagram, the far right side would represent more scientific, less anthropological archaeological research. HBE research falls on this side of the diagram where humans are studied as an organism for which ecological and evolutionary processes are important for explaining human actions. On the far left side would be more humanistic research such as post-processual archaeology that does not claim to pursue a scientific goal. Anthropological archaeology occupies the wide range in the middle. We could see these as different approaches to archaeological research, each of which provides different products. However, the anthropological goal is often prioritized in a way that devalues the research on the scientific end of the spectrum.

The anthropological is paramount in processual archaeology. We envision archaeology as an anthropological sub-discipline that studies human cultures, societies, or the human past. The mantra of "archaeology is anthropology" makes it clear that the anthropological goal should be prioritized (Willey and Phillips 1958, p. 2) and determines what archaeologists consider "good" research. Job announcements for academic positions in the United States often describe their ideal candidate as an "anthropological archaeologist." The major funding agency in the United States, the National Science Foundation, funds research that "furthers anthropologically relevant archaeological knowledge" (National Science Foundation Archaeology and Archaeometry program page: https://www.nsf.gov/funding/pgm_summ.jsp?pims_id=11690). "Scientific" may be implied, but anthropological is explicit.

The impact of the anthropological goal on archaeology is also evident when contrasting introductory archaeology textbooks to those in paleontology or paleobiology. The first section of most archaeological textbooks discusses how archaeology fits within anthropology or how archaeology uses an anthropological approach (Renfrew and Bahn 2010; Thomas and Kelly 2006; Sutton and Yohe II 2008; see also Lyman 2010). A textbook with direct roots to the New Archaeology defines archaeology as "the study of human societies that emphasizes the interaction between human behavior and artifacts" (Rathje and Schiffer 1980, p. 390). This definition has morphed into archaeology as "the study of the human past," sometimes qualified with "through analysis material culture." Thus, our definition focuses on human societies or the human past as what we study. We study people just like anthropologists. The emphasis on archaeology as a sub-discipline of anthropology suggests we simply do anthropology of the past. In contrast, paleontology textbooks do not discuss the discipline's relationship to geology or evolutionary biology. Paleontology is not set up as ecology of the past. Instead, paleontology is presented as its own discipline, one with its own unique dataset—fossils (Foote and Miller 2007; Prothero 2003; Tattersall 2010). Paleontologists study fossils to understand the evolution of organisms and use its own set of methodologies to contribute a different product and perspective on those ecological and evolutionary processes (Lyman 2007). Archaeology could prioritize the archaeological record as a unique dataset that can be used to generate a different kind of product through empirically rigorous analyses, but the interpretations produced are unlikely to look anthropological (Dunnell 1971).

While processual archaeology appears to be a unified approach, the reality is that the methodology and products vary depending on whether researchers prioritize the anthropological versus the scientific (or in the case of HBE, ecological) and by how much each is prioritized. The costly signaling debate provides an example of this. For the archaeologists accused of producing the "just so story," identifying specific measures to differentiate costly signaling from other explanations is not as important as demonstrating the validity of the costly signaling interpretation. The "no can do" archaeologists would rather see an empirically rigorous analysis than paleoethnographies or "stories." Each side is using different standards to measure the quality of the archaeological output. The difference is that the archaeologists prioritizing empiricism have no qualms about giving up the anthropological goal. But those focusing on the anthropological insist that their argument is empirically sound, thus achieving both goals. The niche construction research also illustrates how the different approaches manifest themselves in archaeological research. Broughton et al. (2010) use multiple lines of evidence to evaluate expectations generated from NCT and foraging theory models about when domestication might have a selective advantage. Smith (2015) and Zeder (2016) generated an anthropological narrative on domestication by using data to support the claim that niche construction occurred. The former focuses on the empirical evaluation of hypotheses, while the latter emphasizes empirical support for the anthropological interpretation. The products for these different approaches vary markedly. It is likely that "appeal" or "preference" will determine which approach a zooarchaeologist will follow rather than the strength of any argument. Thus, critiquing the different approaches typically does not alter researchers' views. However, when researchers argue that they are serving both anthropological and scientific goals, it is often based on the assumption that the two goals are correlated rather than following scientific standards that would be recognized by other disciplines.

The recent debate on the origins of agriculture provides another example of this conflict between the scientific and anthropological goals (Gremillion et al. 2014a, b, c; Mohlenhoff et al. 2015; Smith 2014; Zeder 2014, 2015). In this debate, niche construction theory was argued to be a better explanatory model rather than a different approach to HBE in understanding the origins of agriculture (Smith 2014; Zeder 2014, 2015). NCT is a more anthropological-friendly approach because it focuses on humans as unique environmental engineers and it has a more relaxed interpretation of scientific rigor that includes analogic reasoning, an advocacy rather than evaluative analytical structure, and the use of plausibility to determine validity (Smith 2015). Since the HBE researchers are not focused on similar anthropological interpretations, their critique focused on the evaluation of scientific rigor. They found the use of analogy and limited empirical analysis of alternative explanations as less scientifically rigorous than HBE analyses. But the NCT proponents countered that the HBE results were not "compelling" (Smith 2014). Dunnell (1989, pp. 36–42) has argued that these types of debates between researchers arise because "reason-giving" associated with anthropological interpretations is conflated with or treated as equivalent to "scientific cause." An example of reason-giving is providing evidence to support a particular interpretation. In contrast, to evaluate scientific cause, data are produced to evaluate all possible interpretations. This difference in approaches suggests that anthropological and scientific goals are assumed to be autocorrelated within anthropological archaeology but are often two separate goals within HBE research.

The challenge for HBE research is how to persist in a context dominated by anthropological archaeology in which anthropological and scientific goals are both seen as equally achievable and the anthropological goal is deeply embedded within the psyche of Americanist archaeology (Lyman 2007). HBE research, in contrast, often focuses on the scientific rather than the anthropological goal. Most HBE studies approach humans as biological organisms rather than as cultural beings. Thus the archaeological product may look more ecological than anthropological. Indeed, some HBE researchers may be more likely to describe themselves as paleoecologists rather than anthropologists. HBE and anthropological archaeology could be valued as different approaches to the archaeological record. However, anthropological archaeology is the dominant perspective and often the gatekeepers for determining what good archaeology looks like. Thus, HBE studies are critiqued for being environmentally deterministic and not incorporating humans' capacity to make their own choices (Zeder 2016). The implication is that "good archaeology" rather than "good anthropological archaeology" provides anthropological interpretations in which humans are dynamic actors and the products are paleoethnographies. HBE researchers would argue that "good HBE research" prioritizes scientific rigor over generating paleoethnographies by focusing on the empirical expectations of the models and evaluating interpretations through multiple lines of evidence. In many ways, anthropological archaeology is antithetical to HBE.

The impact of this anthropological focus in archaeology will likely have only a few outcomes for HBE zooarchaeological research. It is likely that HBE research will continue to be deconstructed by anthropological archaeologists as being not anthropological enough. Since anthropological archaeology is the dominant paradigm in North American archaeology, this perspective can have long-term impacts on funding and publications. Alternatively, HBE researchers could relax their scientific standards to develop interpretations that are more anthropological. However, this approach will likely be criticized by other HBE archaeologists. The ideal outcome, however, would be for HBE to simply be recognized as a different approach to archaeology, one that prioritizes a narrow definition of scientific rigor and makes no claims of being anthropological. In this way, HBE would be analogous to post-processual archaeology, an approach that is ontologically different from anthropological archaeology so not held to the same standards or an approach that more closely aligns with history than anthropology (Cruz Berrocal 2013). But the challenge for HBE research is not just cutting ties to the anthropological goal but also advocating for a different perspective of what scientific research looks like.

Conclusions

HBE models have proven to be useful for understanding certain aspects of human subsistence change using zooarchaeological data. Researchers have applied these models across different types of faunal data, taxa, and archaeological contexts. While zooarchaeological HBE research has gained significant insights from anthropological and ethnoarchaeological studies, the success of this approach in faunal studies is linked to the development of its own set of archaeological expectations and methodologies for its unique zooarchaeological datasets. Researchers are exploring other areas of human subsistence such as the relationship between HBE models and niche construction, which could be useful in integrating the study on the origins of agriculture using both plant and animal remains. However, as long as HBE is considered an approach within processual archaeology, the challenge will be advocating for its unique product as an alternative to the anthropological interpretations for which it is ill-suited to generate.

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Chapter 13
Human Behavioral Ecology and Plant Resources in Archaeological Research

Kristen J. Gremillion

Once associated primarily with simple foraging models that analyze food choice using economic efficiency as a proxy for fitness, human behavioral ecology (HBE) in archaeology has expanded well beyond its original parameters. However, applications of optimal foraging theory (whose models often figure prominently in HBE) to understand the archaeobotanical record of plant use remain outnumbered by those that target hunting behavior and zooarchaeology (Jones and Hurley 2017). The reasons for this pattern are partly historical but also signal some specific methodological challenges that are peculiar to plant resources. Despite these challenges, HBE models have been used successfully to gain insights into changes in plant foraging, including the labor inputs involved in modifying plant communities to increase production. While simple models remain useful because of their generality, modifications to make them more realistic have been successful in advancing knowledge of how and why subsistence changes. These efforts have spawned fruitful examinations of the economic consequences of central place foraging and food storage (Bettinger et al. 1997; Gremillion 2002a; Price 2016; Rhode 1990; Barlow and Metcalfe 1996), gendered division of labor (Zeanah 2004; Elston and Zeanah 2002; Elston et al. 2014), colonization of landscapes (Winterhalder et al. 2010), and the costs of agricultural production (Barlow 2006).

The results obtained have encouraged more complex modeling efforts, some of which take the principle of economic optimization that is central to many HBE models and apply it to predict the behavior of virtual agents tasked with achieving multiple goals at once (Kohler et al. 2012). Increasing attention is being given to the dynamic relationship between human populations and the plant populations that sustain them. Although the current fashion for niche construction theory has brought this issue into the limelight, human behavioral ecologists have long recognized that population interactions of predators and prey influence resource abundance and shift economic preferences. The most vocal critics of optimal foraging theory tend to ignore this literature, as well as more recent efforts to incorporate anthropogenic effects into traditional optimal foraging approaches. Far from being the excessively reductionistic, mechanistic, and dehumanizing discipline characterized by critics, HBE is becoming increasingly holistic. In archaeology, HBE provides a theoretical framework that relates the general process of natural selection (and parallel cultural mechanisms) to human behavior in specific ecological settings. HBE's formal models further structure inquiry by specifying assumptions and systematically comparing the archaeological record with predictions based on natural

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selection theory. In recognizing that humans as well as plants and other animals are the products of evolutionary processes, HBE is well positioned to contribute to the ongoing effort to explain the origins of agriculture.

This chapter reviews the application of HBE to the study of plant foraging and domestication through archaeology. I first outline the initial appearance of HBE and its models in archaeological subsistence studies. Then I discuss some of the methodological issues that relate specifically to plant resources, particularly the difficulties involved in testing model-derived hypotheses against archaeological data. I proceed with a tour through applications of simple HBE models to plant use, including the prey choice model's predictions and the role of resource depression in broad-spectrum foraging; the implications of central place foraging and storage; and the economics of plant domestication and food production. I then discuss efforts within HBE to introduce greater realism into modeling efforts by using techniques such as simulation to examine the interaction of multiple variables across time.

Evolutionary Ecology, Behavioral Ecology, and Models

Evolutionary ecology has been defined as the study of "evolution and adaptive design in ecological context" (Winterhalder and Smith 1992, p. 3). One of its subfields, behavioral ecology, is devoted to behavior and its consequences for fitness under varying environmental conditions. One of the underlying assumptions of HBE is that the human lineage has evolved to rely upon a highly flexible phenotype capable of quickly adjusting to changing conditions (Winterhalder and Smith 1992, 2000; Codding and Bird 2015). The cognitive mechanisms that support this adaptation have been shaped by natural selection in ways that promoted survival in diverse contexts. Using these assumptions, HBE predicts solutions to challenges such as finding food and successfully raising children. Formal models in HBE employ phenotypically measurable proxies for fitness, such as foraging efficiency, to compare the adaptedness of behavioral options under different environmental conditions (Codding and Bird 2015; Bird and O'Connell 2006).

In archaeology, modeled outcomes are generally compared to behavior as inferred from the material record. One of the earliest and most frequently used models, the diet breadth or prey choice model (PCM), still plays an important role in HBE studies of subsistence and diet. However, the PCM emphasizes generality at the expense of realism and precision (Winterhalder 2002) and makes a number of assumptions that fit poorly with human behavior. HBE archaeologists have addressed this issue by constructing more complex models that account for the costs of central place foraging, the discounting effects of delayed returns, and other phenomena that violate the assumptions of simpler models.

The proliferation of terminology in HBE has created some confusion among archaeologists regarding what the approach actually includes. First, HBE is a broad field that encompasses both ethnographic and archaeological methodologies (Codding and Bird 2015). It is not limited to studies of diet breath, or indeed subsistence more generally, but is flexible enough to analyze any behavior set that affects fitness. In archaeology, HBE research is often congruent with the application of formal models, but this ingredient is not essential to the approach. Models do provide a structured format for creating hypotheses through deductive inference, such that if the model's assumptions are true, the hypotheses deduced from it must also be true. Negative tests indicate a mismatch between model and real world. Finding out whether that mismatch is the result of a violated assumption, a poorly estimated environmental parameter, or an inappropriate currency permits ongoing refinement of models to improve their predictive accuracy (Winterhalder 2002). Many models used in HBE are based on optimization—solving the problem of how to meet competing demands at the lowest possible cost. Unlike maximization, optimization recognizes constraints like fixed environmental parameters, limitations on available time, and costs of lost opportunity. The PCM, for instance, predicts the optimal roster of prey items which, if pursued whenever encountered, will maximize energetic efficiency of the food quest under the constraints specified (e.g., prey population size, distance traveled, and the like) (Winterhalder and Smith 1992).

One common misconception about evolutionary approaches to human behavior is that they require that fitness-enhancing behaviors be perpetuated through genetic inheritance. This notion is not only false; it should be easily recognized as inconsistent with the modern understanding of how evolution works. Phenotypic plasticity and epigenetic inheritance are widely recognized in evolutionary biology as processes that mediate gene expression (Piperno 2017). Given this understanding, the notion that HBE endorses genetic determinism is far wide of the mark. Instead, HBE generally remains agnostic about the means of transmission of variant behaviors, which may be primarily cultural and unconstrained by biological relatedness (Winterhalder and Smith 1992). Transmission mechanisms and their dynamics are being investigated theoretically and empirically by other evolutionary researchers (Borgerhoff Mulder et al. 2006; Eerkens and Lipo 2007; Bettinger 2008; Kolodny 2018).

HBE and Archaeological Subsistence Studies

It is not surprising that human behavioral ecology entered the repertoire of archaeologists during the era when processualism was near its peak. At the same time archaeologists were seeking scientific legitimacy by explicitly employing hypothesis testing and empirical rigor, systems ecology was on the rise (Harris 1968). Americanist archaeology in particular became preoccupied with Julian Steward's cultural core, which structures relationships between human groups and the natural environment (Steward 1955). Research took a distinct turn toward analyzing subsistence behavior as one element of larger adaptive cultural systems. Process was in; description, taxonomy, and even history were out. Cultural evolution provided a framework for understanding human adaptations. Processual archaeology found inspiration in the transformational cultural evolution of Leslie White, in which cultural progress tracked the increasing ability to control and capture energy (White 1949, 1959). Subsistence patterns were expected to evolve accordingly, from hunting and gathering to horticulture, to pastoralism and agriculture, in step with transformations in social organization, religious beliefs, and economic exchange.

But in this, processualism had left Darwinian evolution behind. Robert Dunnell (1980) pointed this out in a compelling essay and advocated instead for a revival of natural selection theory and its application to cultural variation (see also Chap. 1, this volume). Dunnell's evolutionary archaeology saw artifacts as fossils whose correct interpretation would reveal differential replication of advantageous variants over time. However, evolutionary archaeology's mission was to identify time-transgressive evolutionary processes such as selection and drift in the artifactual record. In this, it took its methodological cues from paleontology rather than ecology. Some archaeologists sought a more systematic framework for linking behavior to natural selection theory. They found it in the emerging field of behavioral ecology, which enlisted a set of simple formal models that could predict optimal behavior in specific environmental settings (Winterhalder 1981; Bettinger 1980). Many archaeologists were intrigued by the possibilities of formal modeling to identify optimal strategies of food acquisition—that is, strategies that balance trade-offs in the most advantageous way. For example, the prey choice model derives the optimal solution to the contingent choice faced by a hunter: whether to pursue a prey item or continue searching for something better. The trade-off here is that in an environment of scarcity, broad diets are more efficient energetically than narrow ones because the cost of searching for profitable but rare items erodes the benefit of specialization.

Behavioral ecology models were first embraced by zooarchaeologists and applied to the analysis of changing hunting patterns (see also Chap. 12, this volume). The logic of the prey choice model was compelling; it could explain, for example, why depression of preferred game populations would lead to expansion of the diet to include smaller animals and plants with relatively low rates of return. There were some notable successes in understanding the evolutionary logic behind changes in zooarchaeological assemblages (Broughton 1994b; Stiner 2001). However, few researchers attempted similar studies with plant resources (for an exception, see Barlow and Metcalfe (1996)). Some regarded the strategy of modeling suspect, concerned about a loss of empirical rigor. Others rejected such applications of evolutionary theory on grounds of human exceptionalism (Smith 1983). However, even for researchers open to evolutionary explanation and convinced of the usefulness of models, applying them to plant resources presented some unique challenges.

HBE and Plant Resources: Methodological Issues

Because HBE models were initially developed in reference to predators in search of mobile prey, the simplifying assumptions they make are usually more applicable to hunting than to plant foraging (Gremillion 2014). For example, unlike most vertebrate prey, plant foods often require extensive pre-consumption processing. Uncertainty about processing methods complicates the estimation of return rates, which can differ significantly depending on the technology available. Delayed returns related to storage or agricultural production are additional complications that pertain more often to plant than to animal resources. And whereas vertebrate assemblages often provide the opportunity to estimate the amounts of food they represent, macrobotanical remains are often too fragmented to reliably extrapolate from in this way.

Plants and the Prey Choice Model

One of the earliest, simplest, and most widely discussed HBE models is the prey choice model (PCM), which predicts the optimal roster of prey items a forager ought to pursue on encounter (see also Chap. 12, this volume). Optimal in this case is defined as the resource set that provides the best average rate of return while foraging. This average represents an optimum, not a maximum, because of the trade-off that exists between the time spent searching for prey (a function of prey abundance) and time spent handling it (pursuing, capturing, and processing). Under the assumptions of the PCM, handling time increases compared to search time as the most highly ranked resources become less abundant. Foraging efficiency declines in this case because common but low-ranked prey are being passed up as increasing time is spent searching for food. Addition of items to the diet in rank order of their profitability reduces mounting search costs while also lowering the average rate of return, reaching an optimum at which either expansion or contraction of diet breadth would lower rates of return (Bird and O'Connell 2006; Winterhalder and Goland 1997; Bettinger 1991).

The PCM is not complex mathematically, although it requires some work to estimate realistic parameters. It is fairly robust, meaning that is relatively insensitive to violations of its assumptions. Random encounter of prey items might fit some hunting forays, but plants are likely to be sought in known locations. Encounters are therefore more likely to be predicted based on previous knowledge of resource abundance and acted on accordingly, rather than experienced directly by the forager. Other concerns arise in the case of mass resources, animals or plants of small body size that occur in concentrations. Mass resources violate the assumptions of sequential encounter of prey, mutual exclusivity of search and handling, and consistent response to prey types (Madsen and Schmitt 1998). A stand of seed-producing grasses, unlike an individual animal, does not have a consistent profitability ranking because the density of individual plants varies. In a sense, this prey item is more like a patch because it declines in quality under predation (and can rise in rank as a result of labor input) (Winterhalder and Goland 1997).

Estimating Return Rates and Evaluating Archaeological Tests

The nature of archaeological data makes it difficult to complete one of the key tasks that makes models useful: finding out why the model failed to accurately predict behavior (Winterhalder 2002). A poor fit can potentially be traced to violated assumptions, inaccurate estimates of environmental parameters, an inappropriate currency (e.g., energy) or goal (e.g., maximization of efficiency under constraints), or a failure to account for the effects of improved technology on return rates. Discovering the source of the discrepancy is handicapped by the inability to observe behavior directly, or to accurately determine the structure of plant and animal communities using environmental proxies.

Application of HBE to paleoethnobotanical data has lagged behind similar work in zooarchaeology. One reason for this pattern is the difficulty of accurately reconstructing plant use from material remains. In part, this situation reflects the fragmentary nature of the archaeobotanical record and the difficulty of estimating food quantity or subsistence importance from plant remains (Gremillion 2014). For animal resources, especially mammals, body size can in some situations be an appropriate proxy for the return rate of a prey type (although not in the case of mass resources; see discussion above) (Broughton 1994a, b; Grayson and Cannon 1999). This method obviates the need for detailed calculations of energy content and procurement costs for each prey type in order to predict optimal diet breadth. Researchers have also developed ratios of large- to small-bodied prey and of fast-moving to slow-moving animals in order to assess diet optimization (Stiner et al. 2000).

There is no such simple solution for plants in part because the unit of capture is not always congruent with an individual in the biological sense. Compared to vertebrates, there is much more variation between plants in anatomical and chemical characteristics that have nutritional significance. Costs and benefits must be derived experimentally or from ethnographic data for each taxon (Grayson and Cannon 1999), sometimes from published data on related taxa rather than the species in question. Plant foraging often occurs as foraging within a patch (like mass resources more generally), in which the rate of return declines as resources are harvested. Also contributing to the difficulty of estimating return rates of plant resources is that their handling costs may vary widely depending on the technology available for post-harvest processing. A dramatic example is the hickory nut of North America, which is nutrient-rich but requires laborious removal of the inedible mesocarp (shell). With waterproof vessels, bulk crushing and boiling of the nuts is possible, greatly reducing processing effort. Hickory nuts can consequently be near the top of a ranked list of resources or near the bottom, depending on technology (Gremillion 2002).

Production Cycles and Delayed Returns

When food is not consumed immediately on collection, and returns are delayed by caching or storage, there may be some loss over time due to spoilage and predation. For this reason, return rates while foraging may be different than what they are at the point of consumption (Bettinger 2009; Tucker 2002). This departure from simple models like the PCM is more likely to be an issue for plant foods than most animal foods. However, the costs of such losses can be estimated and incorporated into return rates. It is more difficult to account for the risk that a cache will not be needed at all, which may be the case with highly flexible economies with fluid settlement patterns. These situations favor back-loaded resources, which are relatively cheap to collect and store so that the expensive processing required can be deferred until the need is certain. The front-back-loaded model addresses this complication by separating storage costs from culinary costs (Bettinger 2009) (see discussion below).

Delayed returns also characterize agricultural production even when storage is not involved; like foods that are costly to process, crops require the investment of labor "up front," introducing some risk of loss that is not accounted for in the PCM or other simple, general models that assume immediate consumption. The delay between planting and eating and its attendant risks may significantly discount the energetic payoff from foods that are produced rather than collected (Tucker 2002).

Applications of Simple Foraging Models to Plant Resource Use

HBE researchers have taken up the challenge of applying simple models to foraging systems in which both plants and animals play important roles. Much of the pioneering work in the behavioral ecology of plant resource use was done in the context of hunter-gatherer research in the western USA, particularly the Great Basin (Madsen 1993; Jones and Madsen 1989; Grayson 2000; Grayson and Cannon 1999; Elston and Zeanah 2002). Here, plant resources were crucial components of stable long-term subsistence adaptations (Fowler and Rhode 2011). Researchers attended to the energetics of harvesting plant resources such as small seeds, which were dietarily important despite their high processing costs and low returns relative to hunting (Simms 1987; Barlow and Metcalfe 1996).

A similar logic may underlie other archaeological examples of diet diversification, such as the transition that took place in the Near East and elsewhere across the Late Pleistocene-Early Holocene boundary (Stiner 2001). Because this shift preceded the domestication and cultivation of plants, and because grass seeds and other small grains tend to have relatively low return rates, broad-spectrum foraging offers a potential explanation for the initial use of cereal grains and weedy annual seed producers. This is the link between resource depression and initial domestication of plants that some researchers have dismissed as untenable, maintaining instead that the coevolutionary trajectory of plant domestication is an ongoing ecological process that emerges from human niche constructing tendencies (Smith 2009, 2016). While true, this interpretation does not explicitly address the economic logic of the decisions to plant, tend, and replant that must have initiated the process. Beyond the domestication question, HBE researchers have introduced greater realism to the original suite of relatively simple HBE models by modifying some of their assumptions to better accord with observed human behavior. For example, central place foraging models consider the costs of round-trip travel (Gremillion 2002a; Zeanah 2004) and the discounting of delayed returns when consumables are stored for future use (Tucker 2006). Other studies have taken the simple models of HBE and modified them to account for delayed returns and the labor investments that drive food production (Bettinger 2009; Tushingham and Bettinger 2013).

Diet Breadth and Resource Depression

The PCM is particularly useful for helping with explanations for the expansion of diet breadth because it specifies the economic consequences of being a specialist or a generalist under different environmental conditions. The simplicity and elegance of the model have been attractive to researchers attempting to understand the causes of subsistence change, particularly the transition from reliance on a few high-quality resources to a more diversified subsistence base (Gremillion 2014). This so-called broad-spectrum revolution (Flannery 1969) matched the predictions of the prey choice model in intriguing ways (Stiner et al. 2000). It offers a causal mechanism behind the frequently observed shift from focused hunting of large game to the more diversified diets of the Pleistocene. In PCM terms, resource depression (here used to mean a decline in abundance whether caused by human predation or some other factor) made specialization on a limited number of high-value game animals too costly an option. Whether due to population growth and circumscription or climate change, the phenomenon of resource depression (in which declining abundance of top-ranked resources erodes foraging efficiency) predicted by the prey choice model was a potential evolutionary explanation for the broad-spectrum foraging that emerged during the Early Holocene.

Stiner and her colleagues recognized early on the potential of the PCM to help explain the broad-spectrum revolution of the Mediterranean Basin (Stiner 2001; Stiner et al. 2000). She conducted an analysis of zooarchaeological data from multiple components across the region dating to the Late Pleistocene and early Holocene (Stiner et al. 2000). Stiner observed that applications of the PCM were often flawed by reliance on Linnean taxonomic categories to define types of prey, which do not adequately distinguish between small prey that are difficult to catch and those that are easy targets. By making these distinctions, Stiner was able to identify diet breadth expansion to include lower-ranking prey in the zooarchaeological record—in other words, confirmation that the broad-spectrum foraging transition was indeed a real phenomenon and one that seemed to match the predictions of the PCM.

Zeder (2012) dismisses Stiner's findings in this study on the grounds that her interpretations of patterning in the zooarchaeological data were inappropriately "dictated" by the assumption that broad-spectrum foraging is invariably caused by resource depression. More importantly, Zeder refers to numerous examples of broad-spectrum foraging in a context of resource abundance that "defy optimal foraging predictions and call for the consideration of alternative approaches to the explanation of subsistence change in human history" (Zeder 2012, p. 7). This conclusion betrays a fundamental misunderstanding about the use of HBE models: that if its predictions fail, the model itself should be discarded. In fact, the HBE approach offers a systematic way to probe causality by testing model assumptions and reexamining environmental parameters. It forces researchers to quantify "resource abundance" and "resource scarcity" in ways that make hypotheses about resource depression or anything else more amenable to testing.

While many researchers have found that the application of the PCM to cases of expanding diet breadth succeeds in clarifying the link between natural selection theory and subsistence behavior, others remain skeptical on theoretical grounds. Critiques claim that HBE in general, and optimization models in particular, are fundamentally wrong-headed because they ignore human agency and narrowly constrain explanations to conform to the model's assumptions (Zeder 2009, 2012; Smith 2006, 2009, 2011, 2015). Such critics argue that the application of HBE models to initial plant domestication is flawed because they ignore niche construction, the process by which organisms (humans in this case) modify the environment in ways that affect their own fitness and that of their offspring. Archaeologists who work with HBE models have been unimpressed with the critique on theoretical grounds, citing the critics' misunderstanding of the logic of modeling and the stance of HBE with respect to agency and niche construction (Gremillion et al. 2014; Stiner and Kuhn 2016; Codding and Bird 2015). In fact, HBE has no difficulty incorporating niche construction effects into its analyses (see discussion below under Niche Construction and HBE in Origins of Agriculture Research).

Central Place Foraging

One point at which the PCM lacks realism in the human case is the assumption that the optimal forager should maximize the rate of return *while foraging*. In the interests of simplicity, the PCM does not consider the costs that may accrue outside of the search for and capture of prey. In the human case, particularly for groups with high residential stability, foragers typically remain tethered to a central place that is situated near multiple resource patches to which community members must travel to obtain food. Once acquired, the bulk of food collected is generally carried back to the central place for consumption. The costs of round-trip travel are taken into account by the central place foraging (CPF) model, initially formulated by Orians and Pearson (1979). These costs have implications for food choice because travel can significantly alter the ranking of resources. In addition, CPF places constraints on the quantity that can be collected during a foraging trip (Bettinger et al. 1997; Barlow and Metcalfe 1996).

Jones and Madsen (1989) introduced the concept of maximum transport distance (MTD), the maximum distance at which the amount of energy expended and the amount obtained are equal. The constraints of human biology set limits on the weight and volume of material that can be transported using simple carrying tools such as baskets. Because of this constraint, the relevant currency is not the average rate of return while foraging, but rather rate at which energy can be transported to the central place. Jones and Madsen explored the performance of the CPF model and found that plant foods that offer modest return rates but are energy-dense have a greater MTD than alternatives that have higher rates of return but represent poor-quality loads. Thus, resource rankings should vary considerably with distance from the central place, with some dropping out of the diet entirely as their MTDs are exceeded. The effects of the load size constraint are particularly marked in the case of grasshoppers, which are cheap to procure locally and can yield a whopping 272,649 kcal/h, but have an MTD of 301 km. Beyond that distance, the poor quality of a basketload of grasshoppers boosts the relative ranking of small seeds (such as bulrush and tansy mustard) that have much lower return rates. Rhode (1990) observed that the MTDs calculated by Jones and Madsen are in many cases much greater than actually observed ethnographically and archaeologically, suggesting that other constraints are operating, such as the quality of locally available resources. When profitable alternatives are available nearby, the opportunity costs of ignoring them can be high enough to encourage foragers to abandon distant resources well before travel costs exceed caloric returns. While this critique makes an important point about marginal valuation as a decision criterion, the CPF model as applied by Jones and Madsen takes a step toward greater realism as compared to the simple PCM.

Despite its shortcomings, the Jones and Madsen CPF model inspired other researchers to seek further refinements. Metcalfe and Barlow (1992) followed up by asking how processing at the collection site can improve the value of a load by reducing the quantity of inedible material included in it. They analyze the trade-off between the increased utility of the load and the added costs of processing to remove waste. Their analysis shows that greater distances demand a greater investment in processing to maximize the rate at which energy can be delivered. For example, pinyon seeds can be profitably collected as entire cones when very close to camp, but as distance increases, further processing is required to counter the costs of travel and transport. This model of field processing is important because of its implications for the archaeological record, which may contain little evidence of plants that are typically processed far away from the central location where material evidence has accumulated. Recently, Price (2016) further refined the model by recognizing that the costs of labor at home and in the field are not always equivalent because processing at home faces competition from a larger array of alternatives (introducing greater opportunity costs).

Travel costs also are central to David Zeanah's marginal value model (Zeanah 2017). This project takes up the question posed by Gremillion (2004) for eastern Kentucky: given the low return rates from small seeds (precursors to domesticates), why were they incorporated into human diets at all? This outcome diverges from what the PCM predicts for an environment in which higher-quality resources are abundant. Gremillion suggests that seasonal scarcity of food during the cold season calls for reconsideration of resource rankings; stored seeds rise to the top when alternatives are in short supply, and expensive processing can be carried out when opportunity costs are low because other activities are curtailed. Zeanah incorporates travel costs and marginal valuation into his model in order to show that hickory nuts, despite their high rate of return, can be costly to harvest during years of low yields. Low yields occur periodically but unpredictably because hickory produces masts, superabundant but periodic annual crops that exceed the demands of predators (Gardner 1997). In non-masting years, hickory trees are both less productive (thus more quickly exhausted) and more widely scattered than in masting years. Zeanah compares return rates for a nearby patch of goosefoot (also known as chenopod, a weedy annual producing edible seed that was domesticated in the central USA by ca. 4000 BC) with those of hickory nuts at varying distances from a home base. This model more accurately mimics the perspective of a forager, who is more likely to be sensitive to what the next unit of labor will yield, than the PCM, which is based on average rates of return. With these adjustments, it is apparent that despite their nutrient density, in years of low production, the costs of traveling between diminished patches becomes prohibitive. In such situations, harvesting a nearby dense patch of seed crops is more efficient. Zeanah's analysis establishes that a broad diet including small seeds does not necessarily indicate a sacrifice of efficiency in order to extend food availability through storage. It demonstrates how the structure provided by HBE models offers a systematic way to explore alternative hypotheses when models fail to perform as expected.

Storage and Delayed Returns

When foragers return their harvests to a central place, they often do so with the intention of storing them in whole or in part for future use. Collection for storage requires a different economic calculus than collecting for immediate use. Because of the delay, there is a greater likelihood of loss (to predation or spoilage), and where storage practice varies interannually and mobility is high, there is also a chance that the stored food will not be used. If that probability is large, foragers should choose resources that are back-loaded (i.e., their costs of collecting for storage are low relative to culinary costs) (Bettinger 2009). Such resources can be collected cheaply, and culinary costs are not incurred until (and unless) the stored food is needed. In contrast, front-loaded resources (for which storage costs are high relative to culinary costs) are a poor choice when future use is unpredictable or unlikely. Failing to consider this factor can result in puzzling divergences from the predictions of the PCM, like the reliance on acorns in California predating economies based on storage of salmon. Salmon offers better returns overall, but it is too heavily front-loaded to be compatible with high mobility and the absence of permanent storage facilities (Tushingham and Bettinger 2013).

The economics of storage and central place foraging have also informed explorations of gendered division of labor. HBE models as applied in archaeology usually make the simplifying assumption that a generic individual makes decisions based on economic payoff, an assumption that perhaps justified when little is known about the distribution of tasks within past communities. However, the fact that collecting plant foods is usually women's work ethnographically worldwide supports consideration of plant foraging in the context of specifically female constraints. Zeanah (2004) assumed that women and men in the Carson Desert of western Nevada, USA, foraged separately based on ethnographic evidence and the prevalence of female-sourced, seed-rich coprolites in caves that indicate foraging in nearby marshes. However, reconstruction of the local environment indicates that pursuit of these small seeds would have been a poor choice economically when other more productive patches were present. Zeanah explores a number of possible reasons for the mismatch that relate to the concerns and constraints of female foragers that were probably different from those of males. Women's foraging was likely biased by concern for provisioning children and the constraints child care may have placed on long-distance foraging. Women's plant collecting could be relied upon, whereas male hunting had a highly variable success rate. For males, the value of big game hunting was enhanced beyond its caloric value because success in this endeavor conferred prestige. To incorporate these variables, Zeanah employs a central place foraging model that takes into account the contrasting and sometimes conflicting goals of women and men. His argument is too complex to recount here, but it convincingly synthesizes modeled predictions, archaeological evidence, and ethnographic data in an effort to explain settlement patterns as representing a compromise that allowed both women and men access to the patches most productive for them.

Gendered division of labor also means that women and men face different opportunity costs. When deciding what resources to collect for storage, women must consider how these activities preclude attention to child care. Whelan et al. (2013) suggest that women living on the western slopes of the Sierra Nevada mountains in California chose to store acorns rather than gray pine seeds despite their lower rate of return because acorns are strongly back-loaded. Acorns could therefore be collected efficiently and transported for processing at the base camp, easing the conflict between mobility and caring for children.

Plant Domestication and Optimization of Production

It is not surprising that HBE and its models attracted the attention of a number of researchers interested primarily in the transition from foraging to food production. In principle, decisions about what resources to use are agnostic with respect to whether the resources in question are domesticated or not. Handling costs for crops include the labor investments in clearing, planting, soil amendments, and other agricultural tasks. William Keegan (1986) first grappled with the task of adjusting optimization models to better capture the economic costs and benefits of food production. He reasoned that garden preparation costs, like search costs in the PCM, are a characteristic of the diet as a whole and can play a similar in an optimization analysis of production. In this version of the PCM, “garden breadth” (the variety of crops planted) should expand as the costs of labor mount because of declining soil fertility. Although Keegan compared the modeled outcomes to ethnographic rather than archaeological data, archaeologists took up the challenge of including the management of plant resources in studies of subsistence optimization. Early efforts along these lines used linear programming to identify optimal combinations of food resources under specific demographic and environmental conditions (Keene 1981; Reidhead 1976; Gardner 1992). More recently, methods and concepts from HBE have informed attempts to explain the adoption or intensification of food production (Gremillion 1998, 2004; Diehl 1997; Diehl and Waters 2006; Piperno and Pearsall 1998; Piperno et al. 2017; Barlow 2002, 2006). In 2006, an entire book was published (Kennett and Winterhalder 2006) that showcases applications of HBE to the analysis of food production.

The promotion of NCT as an alternative to HBE, and the belief that the two are fundamentally opposed, seems to depend on a failure to recognize that evolutionary questions often require a division of labor (Gremillion 2009). Because HBE is focused on the economic logic of human decisions, it is not well equipped to analyze the selective forces at work across generations during the process of domestication. That process is best understood as a form of mutualistic coevolution, a natural consequence of animals feeding on plants and dispersing their propagules. Rindos (1984) became famous for pointing out that such relationships are not unique to humans and are understandable as an outcome of natural selection. Framed in this way, domestication is not an economic decision, but rather an evolutionary process. While this observation is correct (and ripe for dissemination at the time of its publication), this insight does not imply that the economic logic of human decisions is irrelevant to initial domestication. In fact, the microeconomic models of HBE are extremely useful for understanding this logic as it relates to habitat disturbance, seed saving and planting, residential mobility, and other behaviors that comprise “primary mechanics” (Stiner and Kuhn 2016). They are poorly suited to understanding the “compounding mechanics” of larger-scale emergent phenomena that operate across generations, a task better performed by analyzing feedback between human alteration of the environment and selection in plant and human populations (the framework provided by NCT).

Resource Depression and the Eastern Agricultural Complex

Gremillion (1996, 1998, 2002a, b, 2004) has used the PCM as a platform from which to examine the rise of seed crop cultivation in eastern North America. In the uplands along the western slope of the Appalachians in eastern Kentucky, rock-shelters with excellent conditions for organic preservation have yielded collections of plant remains from the Archaic (8000–1000 BC) and Woodland (1000 BC to AD 400) periods. Paleoethnobotanical research has indicated that storage and consumption of small starchy and oily seeds, many of which show morphological signs of domestication, intensified after ca. 1000 BC. This change seems puzzling in an environment in which hickory, oak, chestnut, butternut, and walnut trees were common and in some cases locally abundant. All produce potentially high yields of edible seeds (nuts), although they do so by masting at irregular intervals. In comparison to these nuts, which can be quite profitable, seeds seem like an inefficient choice for an optimal diet. Analyses of models using realistic environmental and demographic parameters confirmed that cultivation of small seed crops in a habitat with abundant mast would have been inefficient (Gremillion 2002).

Estimates based on average yields of different tree types fail to account for interannual variation, which was high due to the masting adaptation. This pattern required a flexible strategy that could shift between types as conditions changed. It is plausible that only in particularly poor masting years across all species would seed crops have been an appropriate choice, as Zeanah (2017) has noted. Gremillion (2004) also considered the costs of processing plant foods and the impact of technology on their return rates, concluding that whereas some nuts could offer high return rates with improved technology, the profitability of small seeds was consistently constrained by the time-consuming tasks of winnowing, pounding, and cooking. One insight to emerge from this analysis is that stored seeds would have had a much higher rank during the winter, when other foods were scarce, especially in years when mast yields were low. Small seeds are relatively cheap to harvest and need not have interfered with collection of other foods; processing could have been postponed until winter or spring, when energy was scarce and time was freed from many competing activities (Gremillion 2004).

While Gremillion did not see evidence of population density at levels that would suggest resource depression, she did not conduct a formal test. Smith also claims that there is no evidence of “population packing” associated with sites yielding evidence of early domesticated plants, citing the distance between known sites likely to have been contemporaneous (Smith and Yarnell 2009). Weitzel and Codding (2016) test this component of Smith’s argument by using archaeological data to estimate demographic trends across time in the midcontinent of the USA. Based primarily upon radiocarbon dates, their reconstruction of the population history of eastern North America shows correlations between periods of relatively high population and the initial appearance of domesticates. This finding challenges Smith’s generalization that initial plant domestication is not associated with resource depression in the context of population growth. Additional studies of this kind will be needed to assess whether the historical record of subsistence change supports the resource depression to domestication scenario in particular cases. It does clearly illustrate, however, why claims about resource depression must be evaluated empirically and quantitatively rather than asserted as guesswork or excluded on theoretical grounds.

Fremont Agriculture and Marginal Valuation

A second example of application of optimization models to explain incorporation of domesticates into subsistence is Barlow’s study of Fremont maize farming (Barlow 2002, 2006). This research takes into account the diminishing returns over time that are characteristic of agriculture, a factor that is likely to influence decisions about whether to continue investing or switch to an alternative food source. Decision-making “at the margin” thus has potential for explaining the great spatial variability in the economic importance of maize agriculture within a mixed foraging-farming economy. Barlow approaches the question of why the prehistoric Fremont populations of the Great Basin, USA, maintained a flexible and varied strategy of maize production by estimating return rates for different levels of investment. Because maize yields follow a diminishing returns curve over time (i.e., the rate of increase in yield falls off as more labor is invested), after some period of time, farming should be abandoned in favor of more profitable alternatives. Intensive agriculture is so costly due to the heavy investment in labor it requires that it would have paid off only rarely. However, low to moderate investments in maize cultivation would have made economic sense, but only if game and highly ranked wild plant foods became scarce. These results indicate that maize farming is not a single resource type because rates of return vary depending upon labor costs. The combined predictions of the DBM and the diminishing returns curve for agricultural investment help to make sense of the variability in Fremont agriculture. Barlow's use of models in this study argues against the idea that agriculture is either so highly productive that it will outrank foraging for wild foods or so unproductive that it should be adopted only in the most dire shortages. Fremont populations chose a flexible strategy that allowed for casual maize farming as an occasional supplement to reduced availability of preferred wild foods.

Production Strategies

Some HBE-oriented archaeologists have investigated specific aspects of the practice of plant cultivation from an optimization perspective. In fact, the earliest attempt at optimization modeling of food production (Keegan 1986) investigated whether ethnographically documented garden "patches" of the Machiguenga were populated with an optimal set of plant resources. Observing that the return rates available from garden patches greatly exceeded those available from alternatives such as fishing and hunting, he proposes that protein constraints limit the utility of maximizing the rate of overall energy capture. Availability of protein within the energetically optimal diets varies seasonally, requiring adjustments to meet nutritional requirements. Keegan's argument is notable for its conceptualization of the garden as a patch and its efforts to consider multiple relevant variables, including marginal valuation, travel costs, and seasonal variability. Since that time, many researchers have had success in more systematically investigating how models perform under modified assumptions, currencies, and goals.

For example, Gremillion (2002a) compared rates of return available from garden plots with different soil characteristics in eastern Kentucky. This study used a simulation approach to compare energetic returns from alternative garden locations at varying distances from a central place. Her conclusion is that cultivation of alluvial soils at some distance from the storage location could pay off energetically despite the added travel costs because the fertile soils allowed for delivery of higher-quality packages. In comparison, the lower yields available from an upland plot with less fertile soils could be compensated by the reduction or elimination of travel costs. Though it did not settle the question of where garden plots were actually located, this study demonstrated that optimal locations for food production need not be limited to a single option.

Foster (2003, 2010) also used optimization principles in conjunction with simulation as a method for explaining decisions about field location among the Creek (Muskogee) people of southeastern North America during the historic period. His dynamic optimization model of a single historical village's farmland showed that fields were abandoned well before the marginal value theorem predicts they should have been on the basis of diminishing returns over time. Foster concludes that the strategy of field rotation practiced by the villagers of Cussetuh, though not optimal with respect to energy capture, minimized the risk of a serious food shortage. Risk minimization may under some conditions have more profound fitness consequences than energetic efficiency, as when variance in subsistence outcomes and energy requirements are both high (Winterhalder and Goland 1997; Winterhalder et al. 1999).

Dominguez (2002) examined labor inputs into water capture and conservation techniques in the Pueblo IV period of the northern US Southwest. Using hydrologic data, he was able to show that gridded plots were an efficient and reliable technique for increasing moisture. On this basis he argues that the shared technological attributes of Pueblo water management converged on an optimal solution to the problem of producing maize in an arid environment.

Summary

Although the appropriateness of the PCM and other simple HBE models for studying the origins of food production has not gone unchallenged, researchers persist in applying them to this research domain. Models such as the PCM are particularly useful for specifying the economic consequences of different subsistence options (usually measured in terms of efficiency, or kcal per unit time spent). They also provide a justification for using efficiency measures as a proxy for fitness. They were not originally designed with cultural animals in mind, but their simplicity and generality allow for broad application and permit modest adjustments to introduce variables (such as round-trip travel costs) that are likely to have been important to human foragers and farmers. Researchers have also tried to move beyond relatively simple models of optimal food choice to better understand the process of subsistence change. These newer approaches pose questions about how and why plant food production developed and changed over time, often employing dynamic models that can simulate outcomes under different conditions by manipulating multiple variables.

Beyond Optimization: New Directions

The optimization approach and reliance on simple models derived from foraging theory have clearly yielded benefits in the improved understanding of the energetics of plant subsistence (Gremillion 2014; Gremillion and Piperno 2009; Gremillion et al. 2014). However, these simple optimization models are not well suited to address causal questions about the process of plant domestication and long-term trends to agricultural intensification. In the following section, I focus on two elements missing from traditional HBE models: the effects of anthropogenic environmental modification on resource characteristics and future selection pressures (niche construction) and the simultaneous manipulation of multiple variables across time in agent-based models.

Niche Construction and HBE in Origins of Agriculture Research

The application of HBE models to agricultural subsistence has been challenged on the grounds that they do not consider niche construction (see also Chaps. 11 and 17, this volume). Niche construction is the process by which organisms modify their own niches and those of other organisms in ways that affect their fitness and that of their offspring (Odling-Smee et al. 1996; Odling-Smee et al. 2003). However, the claim that NCT is incompatible with HBE (Smith 2014) betrays a misunderstanding of the flexibility of optimal foraging models. These models fail to acknowledge niche construction, not because they require the assumption that humans passively react to environments over which they have no control, but because they were not designed to model the feedback between predator and prey populations. Even before the term "niche construction" had entered the literature, a number of researchers had employed HBE models to better understand the economic implications of interactions between human predators and their prey. Winterhalder and Goland (1993, 1997) explored the PCM as a framework for understanding the adoption of small-seeded annuals in eastern North America and their subsequent domestication. They use it to frame their discussion of the varying economic implications of reliance on plant resources depending on their quality (profitability) and density (abundance). This structured analysis shows how reliance on an abundant but low-ranked plant resource is likely to spur population growth, stimulating attempts to intensify production and thereby fueling domestication.

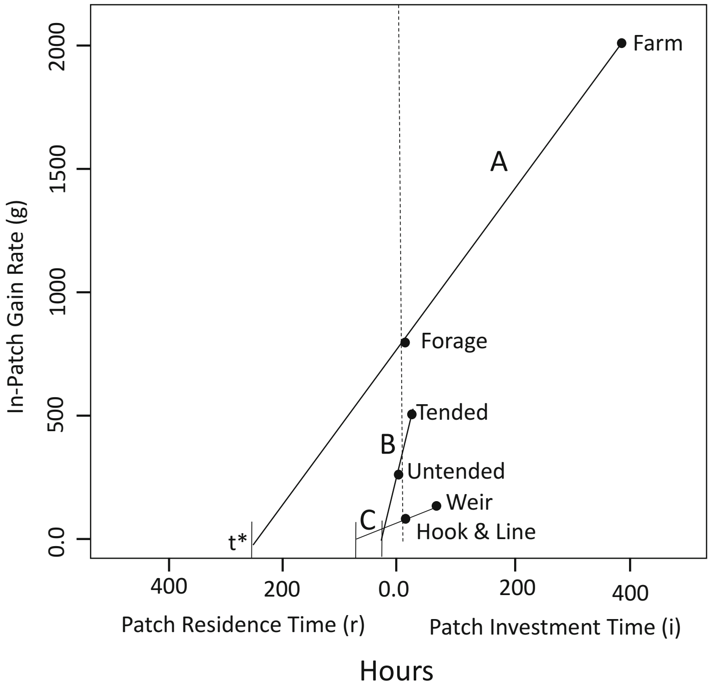

Fig. 13.1 Graphical illustration of the optimal patch investment model applied to three different subsistence activities. Line A shows that investment in maize farming in the Great Basin of western North America would have offered superior return rates compared to foraging, but only after 248 h spent harvesting. This critical threshold for maize farming (t*) is considerably higher than the one for burning acorn groves in California (Line B) or constructing a fishing weir on the Northwest Coast (Line C). Redrawn from Mohlenhoff and Codding (2017, p. 221, Figure 2)

More recently, niche construction was quickly recognized by HBE archaeologists as the process driving resource depression. Broughton et al. (2010) documented a relationship between resource depression and the intensification of agriculture in the Mimbres region of southern New Mexico. Increasing reliance on maize there corresponds to a decline in foraging efficiency documented by zooarchaeological data. Here the application of HBE makes sense of a correlation between bone chemistry, settlement, and technology that might otherwise go unexplained.

Mohlenhoff and Codding (2017) demonstrate one way in which these two important theoretical and methodological tools can be applied together to a problem. They conceptualize incipient food production as a decision to invest labor in a resource patch (by tending, weeding, soil amendments, and possibly planting). Using several case studies, they show how optimal investment in a patch varies with the time spent in it. Investment is only worthwhile when time spent harvesting the patch is sufficient to offset its cost, further discounted by uncertainty about the future yields of the improved patch. For example, controlled burning of acorn groves is a low-cost activity that pays for itself after about an hour of foraging. In contrast, even the most rudimentary type of maize production in the Great Basin Desert would exceed returns from foraging only after 248 h spent harvesting (Fig. 13.1).

Agent-Based Models

The relatively simple models typically employed to investigate foraging decisions (e.g., the PCM and models of central place foraging) are analogous to snapshots; they attempt to identify the key variables driving subsistence choice at a given moment in time. A series of such “snapshots” can help to determine whether change has occurred as well as its magnitude and direction. However, a different approach is required to assess the dynamics of a system over time. One way to effectively model process is by using simulation, which sacrifices generality in favor of greater realism and precision

(Levins 1966). Simulations are time transgressive and able to capture not only the results of static strategies at different points in time but also aspects of the process itself such as rates of change and cycling.

Agent-based models (ABMs) hold particular appeal for researchers studying subsistence transitions because they predict the behavior of decision-makers in the context of the complex system of which they are a part (Cegielski and Rogers 2016). ABMs are based on simulation rather than mathematically derived solutions to optimization problems (Winterhalder and Kennett 2006). Often they use optimization principles to determine how virtual agents make decisions under changing conditions. The computational models employed in ABM, once constructed, can be easily manipulated to assess optimal outcomes under different conditions.

Because of their scale of analysis at the system level, ABMs take into account multiple variables and therefore do not restrict themselves to the plant component of subsistence. They can be very useful for modeling the costs and payoffs of food production under realistic environmental conditions that fluctuate over time. A notable example is the Village Ecodynamics Model used to investigate patterns of population aggregation and dispersal in the Mesa Verde area of the northern US Southwest. Agents representing households were set the virtual task of acquiring sufficient supplies of firewood, game, and maize under different demographic and environmental conditions. The failure of the original model to accurately predict human population sizes led investigators to reevaluate the model inputs. By omitting domestic turkeys as a potential resource, the model had greatly underestimated the ability of the study area to support human communities (Varien et al. 2007; Kohler et al. 2008; Kohler 2010; Kohler et al. 2012).

It is not difficult to envision how HBE models might be embedded within ABMs to address specific decision points within a larger, system-level analysis. Like the agents of the Village Ecodynamics Model, the virtual foragers of the PCM operate under particular decision rules. These rules, predicted from evolutionary theory, can then be integrated into an agent-based model of a larger dynamic system. An example of such an approach appears in Morrison and Allen (2017). This study explores the relationship between life histories of molluscan prey, human foraging efficiency, and resource depression over time using an ABM. Within the model, resource rankings and prey choice are derived in the manner of the PCM but are integrated into a more complex simulation that also includes human and mollusc population dynamics and the life histories and growth patterns of multiple molluscan taxa. Similar efforts might be productively applied to other sessile resources, such as plants.

Conclusions

Archaeologists who specialize in analysis of plant remains and origins of agriculture have been relatively slow to adopt the models of HBE as analytic tools. However, microeconomic models such as the PCM offer a framework for linking behavior to natural selection by using proxy measures (such as efficiency). They encourage researchers to be explicit about their assumptions. Models require metrics such as yields (energy per unit land) and return rates (energy per unit time spent) that may challenge impressionistic assessments of resource values and costs. The structure afforded by HBE also facilitates the research process by directing the evaluation of models that fail to replicate real-world outcomes. Microeconomic models are not well suited to investigating how evolutionary processes, such as plant domestication, unfold over time, but they can help in identifying the decision criteria that initiate and maintain those processes. A broad HBE perspective does not limit itself to modeling as a method, or even to a particular set of models. As the study of adaptive design of human behavior in ecological context, HBE will continue to play a key role in the search for evolutionary explanations of human-plant interaction.

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Chapter 14

Costly Signaling Theory in Archaeology

Colin P. Quinn

Introduction

Our ability to signal contributes significantly to what it means to be human. As social primates, humans have evolved to live in groups. Among our many biocultural adaptations to living in groups, we have developed a tremendous capacity for complex verbal and nonverbal communication. These different forms of communication have allowed us to share information with others, including people with whom we have had no previous interactions. More than any other species, we use material culture to convey and gather information—*signal*—to both compete and better facilitate cooperation with others.

The evolution of the capacity for nonverbal signaling is an important part of our evolutionary heritage. The earliest known evidence for humans using material culture to signal can be traced back to the use of ochre and other pigments as far back as 300,000 years ago (Kuhn 2014). By 75,000 years ago, there is evidence of objects being intentionally manufactured, such as the perforated shell beads and ochre from Blombos Cave, with the primary purpose of sending messages (d'Errico et al. 2005; Henshilwood et al. 2009, 2011). It is likely, however, that the underlying capacity for these material signals evolved much earlier. The use of signs to index information can be directly linked to the origins of language (Knight and Lewis 2017), which would necessarily predate the investment in material signals. Recent discoveries of personal adornment items and art associated with Neanderthals suggest that the underlying capacity for signaling may have predated the emergence of anatomically modern humans (see Finlayson et al. 2012; Radovčić et al. 2015; Rodríguez-Vidal et al. 2014).

In order to better understand how we evolved our incredible ability to signal, as well as the roles signaling has had in shaping our societies, archaeologists have increasingly turned to signaling theory (Bliege Bird and Smith 2005). One subset of signaling theoretical applications that has received increased attention in the past decade is costly signaling theory. Originally developed in biology, costly signaling theory (CST) provides an evolutionary explanation for why people engage in seemingly wasteful behaviors and invest in extravagant material displays. Due to the unique opportunities and limitations in the archaeological record, archaeologists employing CST have transformed the initial theory into a new approach. Archaeologists have broadened CST's focus on individual reproductive fitness to community-scale phenomena, such as the creation, maintenance, and subversion of social hierarchy. However, some applications have been critiqued as just-so-stories (see Codding and

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Jones 2007), with a lack of scientific rigor, ambiguity over potential archaeological correlates, and a lack of awareness of the limitations of the theoretical approach. While CST has great potential within a broader evolutionary framework to the human past, archaeologists must continue to refine both the theoretical framework and the analytical methods used to study costly signaling in the archaeological record.

In this chapter, I present an overview of the current state of costly signaling theory research in archaeology. First, I trace its theoretical origins and history of adoption into anthropological archaeology. Second, I highlight key issues that archaeologists have been wrestling with in order to make CST applicable to the past. Third, I discuss the breadth of uses of CST in the recent archaeological literature. Fourth and finally, I present an analytical framework that can make CST more rigorous, and hopefully impactful, in the future. By situating archaeological applications of CST within a broader evolutionary framework focused on human interaction, information exchange, and material culture, signaling will likely continue to grow in importance within investigations of the human past.

What is Costly Signaling Theory?

CST is a theoretical approach designed to explain seemingly wasteful behavior. CST is premised on the following basic elements (drawing on Bliege Bird and Smith 2005; Boone 1998; Johnstone 1997; Smith 2010; Wright 2017, p. 548):

1. There is variation between individuals in a particular trait (e.g., genes, wealth) (Kantner and Vaughn 2012).
2. Individuals signal information to others (personal qualities) and interpret signals from others to help gauge their potential as ally, foe, or mate.
3. The underlying information being signaled is not immediately obvious to others (Glatz and Plourde 2011; Smith 2010).
4. Signals impose a cost on the signaler above and beyond the energetic costs of staying alive and reproducing. Resources that are dedicated to the signal must be able to be put toward other ends, such as survival and reproduction.
5. Signals must have an audience and must provoke a response from the recipients. Recipients of signals use signaled information about personal qualities to determine who to interact with and how they should interact. Both successful signalers and recipients can benefit from the decisions and actions taken by the recipient (Galle 2010).
6. The cost of signaling information should be substantial enough to either ensure honesty (that the signaler really has the quality being signaled) or to pose a significant debt on those attempting to fake the signal (partially honest signaling—see Kane and Zollman 2015). Cheating with costly signals is not a sustainable long-term strategy, as a cheated audience will no longer associate the signal with the underlying information (Neiman 1997; Quinn 2015).
7. Because both the signaler and recipient benefit from the exchange of information, there is long-term evolutionary stability selecting for the capacity for signaling. Honest costly signals ultimately save time and energy for all involved by reducing the need to find out the underlying qualities directly (e.g., ability to provide as a mate) (Gintis et al. 2001; Safi 2015). However, honesty is not a requirement of costly signals in biology or human behavior (see Higham 2014; Wandsnider 2015).
8. The signal that is used to communicate underlying information may change without changing the nature information being exchanged. Runaway signaling, where costs are exponentially increased with minimal increase in benefit, is not an evolutionary stable strategy (Gintis et al. 2001). As such, there is an upper limit on the scale of any one signal. When signals lose effectiveness, individuals may create new, different signals.

While all signals convey information, certain types of signaling provide additional benefits. Hawkes and Bliege Bird (2002) distinguish altruistic signaling from more wasteful signals. Altruistic signals, such as hunters sharing meat or throwing feasts, benefit signal recipients in more than one way. In addition to information, the audience receives other gains (e.g., additional calories) that wasteful signals (e.g., peacock tails, conspicuous leisure) do not convey (Hawkes and Bliege Bird 2002, p. 64–65).

Rather than wasting resources, costly signalers receive a social benefit as a return. While the social benefit may not match the resources put in, in some cases the return may exceed what was originally signaled (e.g., using a costly signal to secure an ally that may provide assistance in times of life and death). As such, signals—even costly ones—should not necessarily be seen as wasteful. CST provides a selective mechanism, rooted in human biology, for the capacity to send and receive signals. Archaeological applications of CST, however, have gone further. Archaeologists have used CST to explore what is signaled, how it is signaled, and why it is signaled in past cultural contexts. Before exploring some of these applications, it is necessary to trace the adoption of CST into anthropological archaeology to better understand its present uses and future potential.

Origins

There are three primary bodies of theory that form the pillars of modern applications of costly signaling theory in archaeology: (1) costly signaling in biology, (2) human behavioral ecology, and (3) non-evolutionary approaches to conspicuous consumption and the use of material culture to communicate information. Separately, each of these theoretical frameworks has advantages and disadvantages for identifying and interpreting signaling behavior in the archaeological record. When combined, they provide an opportunity for a theoretical synthesis that can explain the evolution of human capacity for signaling while taking into account diversity and contradictions within human signaling strategies across time and space.

Costly Signaling and Biology

The most direct theoretical lineage of costly signaling theory in anthropological archaeology can be traced back to biological approaches to animal signaling. In animal studies, costly signaling has been defined as something that increases the fitness of an individual by altering the behavior of recipients of the signal (Dawkins and Krebs 1978; Hasson 1994; Krebs and Dawkins 1984; Maynard Smith and Harper 1995). Fitness, in this context, is an individual's ability to have their genes represented in subsequent generations through both direct fitness (e.g., their offspring that survive to reproduce) and indirect fitness (e.g., genetic material shared with kin) (Bettinger 1991; Hamilton 1964).

Biological approaches to costly signaling are rooted in the concept of the handicap principle (Cronk 2005; Grafen 1990; Higham 2014; Wandsnider 2015; Zahavi 1975; Zahavi and Zahavi 1997). The handicap principle, originally formulated by Zahavi (1975), seeks to explain why animals engage in costly physical displays and invest in seemingly inefficient biological structures. Grafen (1990) expanded on the work by Zahavi to propose a series of models, including costly signaling, that sought to define that the benefits of these handicaps actually outweighed their costs for those who were able to shoulder them. The classic example of costly signaling in animals is a peacock's tail. Peacocks' large, colorful, and highly visible tails require a significant investment of calories to create and maintain while making them more susceptible to predation. Costly signaling approaches suggest that there are benefits to both peacocks via competition for mates and peahens to select mates that are able to shoulder significant parasite loads and the caloric demands to grow full tails. That peacocks' tails evolved and are maintained through natural and sexual selection suggests that the benefits outweigh the costs of these seemingly wasteful physical traits.

Biological applications of costly signaling have contributed to archaeological studies in several ways. First, they established that costly signaling can be an evolutionary stable strategy. While on the surface an action or characteristic might seem like a waste of resources, individuals actually receive benefits. Individuals that have the resources to invest in costly signals reap benefits in the form of increased reproductive fitness. If there is a genetic component to the signal, such as a physical characteristic like a peacock's tail or the cognitive capacity for symbolic behavior, then over time the strategy of individuals that signal will spread throughout the population.

Second, biological applications of costly signaling have emphasized that the honesty of a signal is of critical importance. In biological cases, the underlying quality that is being signaled (e.g., quality as a mate) is hidden and not immediately obvious to others. The cost of signaling is supposed to be high enough that individuals that do not have the underlying quality cannot produce the signal. Signals do not need to be truly honest, where if it is present it is guaranteed the individual has the underlying quality and where it is absent the individual lacks that quality (see Higham 2014; Wandsnider 2015). Instead, signals can be honest even when they index a scalar quality, where signals with a high cost will soon expose the dishonest signaler. Biological signals can also be honest and not costly (Grose 2011; Maynard Smith and Harper 2003; Searcy and Nowicki 2005). This has led some biologists to note that a cost "handicap" is not necessary for honest signaling that confers benefits on both the signaler and the recipient (Grose 2011; Számadó 2011, 2012).

Third, biological applications of costly signaling have demonstrated that signaling is a social process. Each signaling episode involves both a signaler and one or more recipients. While the costs are incurred by the signaler, benefits extend to both the signalers and the recipients. Signalers are able to attract other individuals to interact with them, while the recipients of signals are able to make more informed decisions about which individuals to interact with if they can accurately interpret them. Highly visible signals expand the potential audience and increase the benefit returned to the signaler.

Translating theoretical approaches from biology to anthropology and anthropological archaeology has historically been difficult (see Prentiss 2011). Costly signaling is no different. Biologists have critiqued the translation between the handicap principle and costly signaling in anthropology and other social sciences (see Grose 2011; Számadó 2012). These critiques note in the decades since Zahavi and Grafen, biologists have tested, revised, and added more nuance to animal signaling. Social scientists have relied on the original formulations even though the approaches in more recent animal signaling literature are often more in line with observations from social contexts (e.g., that a signal is costly is insufficient for demonstrating its role as a costly signal). As will be discussed below, archaeologists have made changes to adapt costly signaling to address anthropological questions with the particulars of the archaeological record. The end result is that costly signaling in archaeology is distinct from biological and economic approaches, though problems of empirical testing remain.

Costly Signaling and Anthropological Archaeology

Costly signaling theory became adopted into anthropology through human behavioral ecology. Human behavioral ecology is the study of evolutionary ecology of human behavior, focusing on the recursive relationship between human behavior and our species' evolutionary history (Cronk 1991; Herzog and Goodale, this volume; Prentiss, this volume Chaps. 1 and 11). Human behavior ecology approaches, compared with other similar approaches such as evolutionary psychology and dual-inheritance models, focus on subsistence and reproductive strategies (Nagaoka, this volume; Smith 2000; Winterhalder and Smith 2000). This approach often uses simple models, such as optimal foraging theory, to identify both when people optimize their resource and, more importantly, when people do not. Deviations from expected behaviors as predicted through these simple models are often a window into cultural values and taboos as well as individual agency (Gremillion, this volume). Additional explanatory models are needed to help explain when people do not optimize subsistence efficiency and resilience. This is where CST has fit into human behavioral ecology: CST provides an explanation for seemingly wasteful behaviors that must have an impact on reproductive fitness in order to be evolutionarily stable and persistent in human societies.

Early applications of costly signaling in anthropology were discussed under the handicap principle or show-off hypothesis. Hawkes (1990, 1991, 1993) examined how hunting behavior, especially for men, is influenced by the desire to show off skills and attract potential allies and mates. Examining torch fishing on Ifaluk atoll, Sosis (2000) found mixed support for the hypothesis that torch fishing is a costly signal of a man's work ethic, which followed work by Hawkes as well as Smith and Bliege Bird (2000) on Meriam turtle hunters. Boone (1998) modified the work by Zahavi and Grafen to explore how costly signaling in the form of altruism, what Boone calls magnanimity, evolved. From the start, these early adopters of costly signaling principles in anthropology distinguished between different types of signaling (e.g., altruistic vs. non-altruistic; mate selection vs. prestige).

CST received expanded attention in anthropology following the 2005 publication of a case for its potential explanatory value by Bliege Bird and Smith in *Current Anthropology*. Bliege Bird and Smith (2005) successfully situated signaling behavior as part of a wider suite of social activities and strategic interactions, making the case that behavioral ecological approaches and social theoretical approaches to conspicuous consumption, status, and communication can be integrated into a single approach they call signaling theory. This work drew heavily upon their previous research on Meriam turtle hunting (Bliege Bird et al. 2002; Smith and Bliege Bird 2000), as well as a wide range of case studies such as yam growing in Papua New Guinea and costly religious rituals (Boone 1998, 2000; Henrich 2007, 2009; Sosis 2003; Sosis and Alcorta 2003; Sosis and Bressler 2003).

The first application of CST in archaeology, and a key example in Bliege Bird and Smith (2005), was Neiman's (1997) examination of monumentality in Mesoamerica. Neiman developed a Darwinian theory of wasteful advertising, built on the work by Zahavi and Grafen, which sought to explain the spatial and temporal pattern of the Maya collapse. During the Maya collapse, an ecological disaster impacted the persistence of monumental architecture by spurring migration and increasing population density and audience sizes for signals. Neiman's work both introduced concepts of CST into anthropological archaeology and highlighted the need for quantitative approaches to identifying signaling in archaeological contexts.

Over the past two decades, archaeological applications have expanded beyond monumentality (e.g., Čučković 2017; O'Driscoll 2017; Wright 2017) to include major debates about big game hunting (e.g., Codding and Jones 2007; Fisher 2015; Hildebrandt and McGuire 2002; McGuire and Hildebrandt 2005; McGuire et al. 2007), religious behavior (e.g., Kantner and Vaughn 2012; Munson et al. 2014), trade and exchange (e.g., Quinn 2006a), collective action (e.g., Carballo 2013), art (e.g., Gittins and Pettitt 2017; Hodgson 2017), and material culture signaling (e.g., Neff 2014; Pierce 2017; Plourde 2008; Quinn 2015).

Non-evolutionary Approaches to Signaling

Costly signaling theory is not the only approach for exploring how actions and material culture convey social information (Cronk 2005). Since the 1970s, the communication of social information through material culture, often discussed under the concept of *style*, has been a central part of anthropological archaeological systematics (Sackett 1982, 1985; Wiessner 1983, 1985; Wobst 1977). As anthropologists, archaeologists consider the roles that artifacts and behaviors in the past may have played in promoting social cohesion and/or competition (Binford 1962; Goodale et al. 2011, p. 432). Researchers from diverse theoretical backgrounds continue to explore how actions and material culture convey social information and affect human decision-making (e.g., Appadurai 1986; DeMarrais and Earle 2017; Hodder 2012; Ingold 2013; Keane 2003).

Prior to the introduction of CST into anthropological archaeology, archaeologists used concepts such as conspicuous consumption (Veblen 1994), gift giving (Mauss 1924), and feasting (e.g., Hayden 2014) to explain seemingly wasteful behavior in the past. For each of these concepts, their importance is social: individuals use conspicuous consumption, gift giving, and feasting to create social capital or debt that could be transformed into political authority or power. These theoretical approaches, which were developed outside of a strictly Darwinian framework (but in some cases were operationalized in social evolutionary frameworks of processual archaeology), have been more widely applied than those from behavioral ecology. CST provides a complementary perspective that provides an evolutionary mechanism for how social information exchange and debt creation through seemingly wasteful behavior could first emerge and be maintained in humans.

The broader familiarity with concepts of conspicuous consumption, gift giving, feasting, and social information exchange have helped prime the field for the introduction and adoption of CST. Consequently, there is an opportunity for a broader synthesis that combines the theoretical insights of evolutionary approaches with social theoretical approaches to human behavior and group living to emerge. Galle (2010, p. 20) laments that biases against evolutionary approaches, which are often characterized as deterministic, reductionist, and devoid of individual agency, have made such a synthesis difficult. However, by recognizing the complementary nature of CST and agency theoretical approaches to material culture, decision-making, and the creation of identities, Galle (2010) provides an example of how such a broader synthesis would work in practice.

Yet many members of the anthropological archaeology community remain skeptical that CST, a concept rooted in evolutionary biology, can adequately explain social behavior (see Blanton 2016). While there continue to be valid concerns about several aspects of the theoretical approach and its utility to explain behavior in the archaeological record, the rapid expansion of CST in archaeology over the past two decades speaks to its broader appeal. In order for interpretations rooted in CST to become more broadly accepted within the field of anthropological archaeology, researchers must address several lingering issues.

Key Issues with CST and Archaeology

There are several issues in archaeological applications of CST that are the topic of ongoing debate, theory-building, and modeling. The strongest criticism of CST in archaeology has been that it is too often proposed as a "just-so-story"—an underdeveloped theoretical approach with an underdeveloped suite of predictive and testable models to be able to identify when costly signaling is and is not occurring (Codding and Jones 2007; Quinn 2015). I highlight five key issues that illustrate the dynamic nature of this theoretical approach and the need for CST proponents to continue to develop testable models of costly signaling in the past.

Challenging the Biological Dimensions of CST

Adapting theories from biology to explain the social lives and history of humans has been an issue that anthropologists have wrestled with for over a century. From the earliest proponents of Darwinian concepts to social evolution, the relationship between biological and social theory has been complicated. Recently, archaeologists employing evolutionary theory have more critically examined how models from biology are adopted into the discipline (e.g., Goodale and Andrefsky Jr. 2015; Prentiss 2011, this volume, Chap. 1; Prentiss et al. 2011). There are two aspects of how CST was first developed that must be modified for anthropological archaeology: individual selection and reproductive fitness.

In biology, CST individual organisms are the signalers and recipients of signals. Humans live in multi-scalar social systems, where collections of individuals (e.g., households, villages, polities) have the ability to make decisions (have agency) that may or may not reflect the choices of individuals within those collective social units. In several cases of signaling, such as large monuments (e.g., Neiman 1997), the signaler is not always a single individual. Roscoe (2009) has argued that signaling co-occurs at the individual and group levels. Using an example from contact-era New Guinea, he argues that while individuals seek authority through within-group signaling, the same signaling events, such as feasting, performances, and large-scale architecture, are used by villages to communicate with other villages (Wandsnider 2015, p. 72–73). Glatz and Plourde (2011) also hint at polities being capable of contesting territory through costly monumental architecture. Going forward, archaeologists will have to confront how group-level signaling might work, especially as it relates to broader concepts of who is incurring the costs and reaping the benefits of signaling.

Signaling in biology is also firmly rooted in the idea that the individuals that are capable of incurring the cost of signaling receive a return in increased quantity and quality of mates (Hasson 1994; Maynard Smith and Harper 1995). In biological and ethnographic contexts, it may be possible to monitor if the most active signalers actually have a higher reproductive fitness (see Smith 2004). In archaeological contexts, it is difficult, if not impossible, to measure individual reproductive fitness to see if it was increased by signaling. Madsen et al. (1999), building on Dunnell's (1989) discussion of the role of waste in cultural elaboration, suggest that fitness can be conceptualized as a statistical summary of real-world interactions of individual fitness (Madsen et al. 1999, p. 258).

Human signaling can provide returns in social prestige, an alternative to reproductive or inclusive fitness (see Hamilton 1964). While the ultimate benefit of added social capital is to be able to differentially survive and reproduce (e.g., social networks to buffer against subsistence failures), the proximate benefit of signaling may not result in that ultimate benefit. This added layer of benefit between signal and reproductive fitness means that signaling cannot simply be explained by counting the number of offspring that reach reproductive age. As a result, we must ask (1) can we measure reproductive fitness in the archaeological record, (2) can we link signaling behavior to specific reproductive fitness outcomes, and (3) does it really matter? Kantner (2010), p. 234–235) argues that while, according to human behavioral ecology, humans optimize utility, culture impacts what we actually seek to optimize. Rather than focusing on a single index of fitness, archaeologists have the opportunity to explore what attributes, resources, and relationships are the most important in a particular cultural context (see Madsen et al. 1999). As an evolutionary stable strategy, the capacity signaling—on average—has become widespread through its impact on individual reproductive fitness. The more socially dynamic aspects of signaling, such as how signals mediate social relationships, are more accessible through the archaeological record and more interesting to most anthropological archaeologists than reproductive fitness measures.

Costly and Non-costly Signals

One of the most important aspects in identifying costly signals in the archaeological record is to be able to distinguish costly and non-costly signals. To this end, many applications of CST situate costly signaling more broadly as part of "signaling theory" (e.g., Bliege Bird and Smith 2005). Previously, I have distinguished costly signals and non-costly signals based on how they relate to reproductive

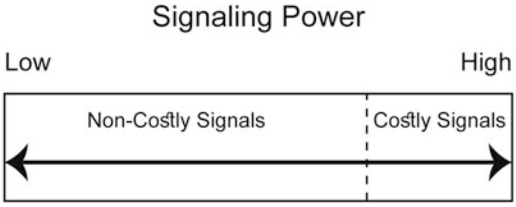

Fig. 14.1 Representation of the continuum of signaling power and the relationship between costly and non-costly signals (after Quinn 2015: Fig. 11.1)

fitness (Quinn 2015). Costly signals are more directly related to reproductive fitness than others, and some signals do not impact reproductive fitness at all. The power of a signal varies along a continuum based on how significant they are in broadcasting and enhancing reproductive fitness (Fig. 14.1). Non-costly signals convey social information, such as age, gender, and group membership, but this information does not directly factor in reproductive fitness. This may be because (1) there is no cost incurred by signaling, (2) there is minimal variation between individuals in the information being signaled, or (3) the signaled information is not received by an audience.

There is a point along the signaling power continuum where people treat signals differently. Below a particular threshold, non-costly signals are broadcast and received that convey information but do not raise or lower the social standing or opportunities for increased reproductive fitness for the signaler significantly. Above that threshold, costly signals are restricted to a smaller portion of society and actively impact the social standing and/or the biological fitness of both the signaler and recipients of the signal.

Whether a signal is costly and provides a social or biological benefit is dependent on its context. Each geographic, temporal, environmental, cultural, and sociopolitical context will have different information that is important to signal. A costly signal that enhances reproductive fitness in one context may neither be costly nor provide a positive return in another context. For example, the ability to hunt is an important skill to signal to others in most hunting and gathering societies. The ability to hunt, however, is not something that is actively signaled today in the streets of New York City. Instead, expensive cars, designer clothes, and the newest technologies signal key fitness attributes in the modern United States: wealth and access to resources. In state-level societies, where there is more segmentation within society (counter culture groups, subcultures, etc.), we should expect signals to vary widely depending on the identities of the signaler and desired audience. As a result, there are many communities within the modern United States where costly signaling through expensive cars, designer clothes, and the newest technologies may be considered gauche and repulsive. In these communities, costly signaling often takes other forms, such as investing time and money in community service or gaining eclectic knowledge.

Socio-ecological variation impacts the cost, information, and necessity of signals. The ecological differences among environments affect the predictability of access to resources, ability to restrict access to resources, and the ability to amass surplus resources. Archaeologists have long recognized that environmental predictability and uncertain access to key economic resources significantly impact cooperation and competition among communities (e.g., Halstead and O'Shea 1989; Winterhalder et al. 1999). As with other socioeconomic strategies, such as food sharing, warfare, and feasting, we should expect the nature of costly signaling to vary across different ecological and environmental contexts. In a case study comparing Rapa Nui and Rapa Iti, DiNapoli et al. (2017) argue that costly signaling may explain the divergent histories of communal investment in large-scale construction projects. People living on Rapa Nui invested in the construction of stone statues (*moai*) and large ritual monuments (*abu*), while people on Rapa Iti constructed fortifications amidst evidence of intergroup conflict (DiNapoli et al. 2017, p. 208). DiNapoli et al. predict that signaling should increase in contexts where key resources are more evenly distributed, as it is only through costly signals that groups can stand out from each other. Where there is heterogeneity in resources, the information about differences in competitive ability should be readily apparent in the access to uneven resources. They also predict that the investment into monumental signals should covary with the quality and availability of key resources. DiNapoli et al. suggest that communities on Rapa Nua invested in monumental ritual architecture and statuary as a way of signaling competitive ability in part because agricultural land was not easily controllable, unlike on Rapa Iti. This example highlights how environmental variability can impact socioeconomic strategies such as costly signaling.

The materials or behaviors available to signal an underlying characteristic will also vary across time and space. The signaling power of any object, monument, or behavior is socially mediated. Consequently, there are no universal criteria for distinguishing costly from non-costly signals. Instead, archaeologists must examine the broader social contexts in which signaling behaviors or materials were deployed and allow for the same signals to gain or lose their social power as costly signals (Quinn 2015).

The consequences for archaeologists are clear. There are no types of objects, raw materials, or behaviors that are inherently costly signals. Archaeologists must demonstrate, and not assume, that something is a costly signal based on characteristics of the object; its context of manufacture, use, and deposition; as well as the broader social context. Archaeologists employing CST must allow for signals to gain or lose signaling power and for signals to be either costly or non-costly. This requires an analytical approach that considers the characteristics of the signal, the signaler, the audience, and the broader social context in which signaling occurred. An example of such a framework is described below.

Costly Material and Behavioral Signals

There are two significant differences between costly behaviors and costly material signals that archaeologists must consider: honesty and archaeological visibility. Archaeologists must take into account these differences when developing models of costly signaling in the past.

Behavioral signals are more honest and more difficult to fake than material signals. In biology, costly signals such as peacocks' tails are honest signals that the individual has the caloric resources and can withstand a high parasite load to grow a large tail. In ethnographic contexts, such as torch fishing and turtle hunting, other individuals witness the behaviors, ensuring that the individual must have had the skill to complete the task. Material culture represents an additional layer between signal and the underlying attribute being signaled that decreases a material culture's signaling power. For example, a bear tooth pendant may indicate that the wearer killed a bear. However, they may have also taken it off a dead carcass, been given it as a gift, or stolen it. The uncertainty on whether the individual who possesses an object incurred the full costs of its production or acquisition diminishes the benefits observers assign to the signaler.

Behaviors are also more difficult to observe in the archaeological record. The material record encourages archaeologists to focus on objects. The physical characteristics, their production, use wear, and deposition are much more accessible to archaeologists than the full suite of behaviors in the past, some of which may not produce material traces that can be identified in the archaeological record. For example, Smith and Bliege Bird (2000) have identified turtle hunting as a form of costly signaling among the Meriam Islanders. Hunters dive for turtles as they swim, requiring strength, ability to control their breath, and knowledge of turtle behavior. Hunting turtles at their nesting sites would be much less costly. Indeed, 90% of turtles eaten during the year are taken when they are vulnerable on land (Codding and Jones 2007, p. 354). In an archaeological trash deposit full of turtle bones, it would be impossible to determine if, and in what proportion, hunters took the easy or hard way. Additionally, a collection of turtle shells would make a great material signal of an individual's hunting prowess. The Meriam, however, toss the turtle shells after they are processed. The lack of a curated material signal of the costly behavior does not diminish the hunt's signaling power for those who witness it. We cannot assume that every costly signaling behavior will be materialized in the archaeological record. The challenges of identifying costly signaling behaviors in the past are expanded in the next section.

Finding Costly Signals in the Archaeological Record

The most important debate to date about the visibility of costly signaling in the archaeological record occurred in *American Antiquity* in the 2000s. McGuire and Hildebrandt (Hildebrandt and McGuire 2002, 2003; McGuire and Hildebrandt 2005) published a series of studies about hunting practices in the Great Basin and California, arguing that communities were hunting bigger game for prestige. The prestige hunting hypothesis cast as CST by McGuire and Hildebrandt (McGuire and Hildebrandt 2005; McGuire et al. 2007) predicts that an increase in group size or frequency of social aggregations will spur individuals to target larger game to receive a social benefit for showing off their hunting skill (Codding et al. 2010, p. 56). The hypothesized archaeological signature of this process is that the relative abundance of large taxa in faunal assemblages will increase, leading to an increase in acquisition costs as hunters have to travel increasingly longer distances to find big game.

In response, Codding and Jones (2007; Jones and Codding 2010) challenged how McGuire and Hildebrandt applied costly signaling theory. Rather than expecting the relative portion of large taxa to increase when costly signaling in hunting was occurring, Codding and Jones suggest that prestige hunting may actually lead to an overall decrease in the archaeological abundance of large prey as only those able to incur the costs of procurement could take large game. Codding and Jones suggest that costly signaling hunting behavior would be difficult, if not impossible, to identify in the archaeological record. Codding and Jones draw attention to ethnographic examples of costly hunting behaviors (e.g., Bliege Bird and Smith 2005; Bliege Bird et al. 2001; Smith and Bliege Bird 2000; Smith et al. 2003; Sosis 2000). Ethnographic studies show that while costly signaling does occur, these events are rare and do not contribute significantly to the diets of communities. Only a few individuals engage in these high-risk hunting strategies and, even then, only rarely (Codding and Jones 2007, p. 350). As a result, costly hunting behaviors contribute very little to faunal assemblages in ethnographic contexts. Codding and Jones argue that any material traces of costly signaling hunting behaviors in the past would be overwhelmed by non-prestige-based provisioning activity (Codding and Jones 2007, p. 354). Instead of prestige hunting, environmental shifts that benefited large game populations may have led to a higher encounter rate (Byers and Broughton 2004; Codding et al. 2010). Based on the difficulty of identifying costly signaling in archaeological assemblages, Codding and Jones suggested restraint in extolling CST's value in archaeology until more work to model CST in archaeological contexts was completed, lest it become a "just-so-story" with no predictive or explanatory power.

In the subsequent years, several archaeologists have developed models for how to identify the material signatures of costly signaling in the archaeological record. Returning to prestige hunting in California and the Great Basin, Codding et al. (2010, p. 56) suggest that looking at butchery and transport patterns could be used to demonstrate whether (1) the increase in large taxa in faunal assemblages is due to an increased encounter rate or (2) that hunters continued to target large game despite an increase in acquisition costs. The incorporation of this additional line of evidence provides a more robust assessment of the costs associated with hunting that are needed before assessing whether hunters gained prestige from hunting large game.

Galle (2010, p. 27–30) provides a template for the archaeological expectations of costly signaling in a study on material culture in eighteenth-century Chesapeake-enslaved communities. Plantations diversified and towns and cities grew throughout the eighteenth century, and Galle predicts that the use of costly imported goods—such as metal buttons and refined ceramics—should have increased as the opportunities for slaves to interact with nonkin and strangers on a regular basis grew. Galle then proposes an abundance index that can be used to compare the distribution of imported goods across houses and between plantations. In her discussion of the origins of prestige goods, Plourde (2008) uses distance from source as a proxy for raw material acquisitions cost. Other archaeologists have also suggested that peculiar distributions and frequencies of artifacts in assemblages that cannot be explained by the function of objects may indicate costly signaling (e.g., Goodale et al. 2011). By combining testable hypotheses with quantitative measures designed to evaluate signaling strategies, Galle demonstrates how archaeologists can identify costly signaling in the archaeological record.

How Costly Signals Change Over Time

The diachronic dynamics of costly signals remain undertheorized. Most work has examined how costly signaling would first emerge (e.g., Plourde 2008). Much less work has focused on how signals change. In one example, Wright (2017) suggests that once Eurasian Steppe pastoral communities began using monuments as costly signals, new forms of monumentality replaced the early stone burial mounds to also serve as signals. For Wright, change in the medium of signaling is not symptomatic of a collapse of socioeconomic networks; instead they were replacements within an already established social strategy that monumental sites are effective signals (Wright 2017, p. 561). Elsewhere, I have argued that the signaling power of material culture items will necessarily drop over time as they become more easily available to individuals who did not incur the cost of their acquisition or production (Quinn 2015). In such a situation, it is not that medium of costly signaling *can* change over time; it is that it *must* change if they are to continue to be honest signals.

Any changes in socio-environmental contexts will impact the costs and benefits of signaling. As DiNapoli et al. (2017) have highlighted, there is a strong link between signaling strategies and the environment. In the uncertain and risky environment of Rapa Nui, signaling took the form of communal monument construction that emphasized cooperation (DiNapoli et al. 2017). As a consequence, less risky and unpredictable environments should diminish the payoff of communal signaling. As environments change, the types of signaling, as well as their costs and benefits, will likewise change. For hunting strategies, environmental changes often impact encounter rates of different types of game and therefore change the cost of acquiring big game. Changes in population density, inter-community conflict and alliances, marriage patterns, and technological systems—to name only a few factors—will also change the payoffs of different signaling strategies. Costly signals must therefore be studied as part of broader socio-environmental evolutionary trajectories. More work is needed to develop predictable models for how costly signaling should change over time.

The challenges and potential solutions to these key issues in archaeological applications of CST are best seen in the diversity of case studies in which it has been employed.

Current Applications of Costly Signaling Theory in Archaeology

The applications of CST in anthropological archaeology can be broadly divided into those that focus on costly signaling behaviors and those that focus on costly signaling materials. Costly signaling behaviors represent an intersection of cooperative and competitive actions. Signaling promotes increased, and more informed, interaction between the signaler and the signal recipients. At the same time, signaling is meant to allow certain individuals to increase their reproductive fitness often at the expense of competitors for mates. The tension between cooperation and competition in signaling strategies is a central aspect of most archaeological investigations of costly signaling behaviors.

One of the first applications of costly signaling in anthropological archaeology is in prey choice and big game hunting. Thanks to optimal foraging theory and prey choice models, archaeologists have had a long history of successfully evaluating hunting strategies. Foraging models make it possible for archaeologists to use deviation from predictions to be able to more systematically assess the social, cultural, and ecological contexts in which subsistence decisions are made (Bird and O'Connell 2012; Bird et al. 2013). Hunting strategies that target prey with either low returns or very high risks may be the product of hunting for prestige. As described above, McGuire and Hildebrandt have been at the forefront on these applications in anthropological archaeology (see Hildebrandt and McGuire 2002; McGuire and Hildebrandt 2005; McGuire et al. 2007), though their work has not gone without critique (see Broughton and Bayham 2003; Broughton et al. 2011; Byers and Broughton 2004; Codding and Jones 2007; Grimstead 2010; Hockett 2005; Fisher 2015; Morgan 2015; Simms et al. 2014). Speth (2010) uses CST to explain why human ancestors spent so much time and effort pursuing big and potentially dangerous prey when they could easily and more reliably acquire the requisite calories and protein by pursing a less risky hunting and gathering strategy. O'Connell et al. (2002) argue that the scavenging of big game during the Plio-Pleistocene is less consistent with provisioning and more consistent with a hypothesis of competitive male displays. Bird et al. (2009) have argued that the costs of big game hunting, in particular frequent failed searches and pursuits, are often underestimated within optimal foraging models. Lupo and Schmitt (2016) emphasize that the social rewards associated with big game hunting are usually limited to only a few select individuals. These works continue to highlight the roles of hunting beyond meeting basic subsistence needs.

A second collection of works on costly signaling behavior has focused on religion, ritual practice, and religious pilgrimage. The potential for religious behavior to be costly signals was first explored in depth by Sosis (2000); Sosis and Bressler 2003). In particular, the costs of practicing religion are often undertaken in highly visible contexts to promote intragroup cooperation (Munson et al. 2014). In one archaeological example, Kantner and Vaughn (2012) developed a model of religious adherence as a costly signal. Kantner and Vaughn postulate that (1) the strength of adherence to a religious system is an underlying attribute that is not easily visible; (2) devotees benefit from reliable information about who is, and who is not, committed to the religion; and (3) devotees benefit from broadcasting their adherence but that these signals would be ideal if they were not able to be faked by non-devotees (Kantner and Vaughn 2012, p. 69). Using case studies from Chaco Canyon and Nasca, Kantner and Vaughn argue that devotees can signal their commitment by undertaking costly pilgrimages to religious centers. Picking up and bringing back material culture objects, such as ceramics, can provide pilgrims a way to signal their devotion and for the audience back home to make better informed decisions about them. These costly signaling activities display a commitment to prosocial beliefs that would foster greater cooperation within the group and could confer prestige on those who coordinated them (Blanton 2016; Blanton and Fargher 2013; Carballo 2013; DeMarrais and Earle 2017).

Feasting is a third type of behavior that researchers suggest could be an example of costly signaling (see Ames 2010; Boone 1998, 2000; Nolan and Howard 2010). For several decades archaeologists have considered feasting as a possible mechanism to promote intergroup cooperation as well as status-driven competition between individuals, lineages, and polities (see Bray 2003; Hayden 1995, 2014; Hayden and Villeneuve 2011). Individuals throwing a feast take on the costs of providing food to others, and in return they receive a benefit of increased reputation and prestige. Only individuals with the ability to procure enough resources for a feast, such as through food production prowess or wealth, can signal—which ensures its honesty as a costly signal. Nolan and Howard (2010) suggest that a model of ceremonial subsistence in the Hopewell based on concepts of costly signaling may explain the rise and fall of Woodland period cultural elaboration in the Ohio River Valley. Ames (2010) suggests that costly signaling feasting behaviors, such as Northwest Coast potlatches, may have contributed to the creation of inequality.

Monumentality and mortuary practices, which combine material and behavioral aspects of CST, continue to be an important topic for employing costly signaling in archaeology (see Neiman 1997; Church 2012). Wandsnider (2013, 2015) has explored the roles of monumental civic architecture and signaling within and between Hellenistic Greek and Greco-Roman cities. O'Driscoll (2017) has argued that highly fortified defensive hillforts in Ireland were constructed as costly signals to convey the power and strength of a community to others. Looking at monuments constructed away from population centers, Glatz and Plourde (2011) argue that landscape monuments of Late Bronze Age Anatolia were used as costly signals to contest territorial boundaries. Wright's (2017) recent work on late prehistoric burial mounds in the Eurasian Steppe has explored signaling in pastoral communities. Silvestri et al. (2017) suggest that plant remains in Middle Bronze Age funerary contexts in Central Italy are evidence of costly signaling through the consumption of valuable food resources. Watson and Phelps (2016) use mortuary practices in early irrigation communities in the US Southwest to identify atypical burials. Watson and Phelps interpret atypical burials as representing acts of violence on the body at, or after, the death of the individual and argue that these practices—what they call "perimortem signaling"—are a form of costly signaling stemming from socialized violence. In one of the more classic examples of monumental architecture that has proven difficult to explain, several authors have explored the significance of *moai* from the Easter Islands (Rapa Nui and Rapa Iti) as costly signals of island communities' competitive ability to cooperate and defend its limited resources (DiNapoli et al. 2017; Graves and Ladefoged 1995; Hunt and Lipo 2011).

Material culture signaling has been explored in a wide range of artifact categories. Adornment items, such as beads, pendants, and buttons, are one of the more obvious artifact classes that signals information (see Galle 2010; Kuhn 2014; Quinn 2006b). Ceramics, which often vary in quality of production and decoration, are effective signals of identity, status, and interregional connections (see Galle 2010; Neff 2014). Groundstone artifacts made of rare stone such as turquoise have high acquisition and production costs (see Kantner 2010). Pipes, the most elaborate of which are often used in important social events, can communicate the status of their users (see Blanton 2016; Bollwerk 2016). More broadly, artifacts classified as "prestige goods," due to their scarcity or difficulty to produce, acquire, and maintain, have also been discussed as potential costly signals (see Ames 2010; Kantner 2010; Plourde 2008; Quinn 2006a). Even chipped stone tools, which are normally studied for their insight into prehistoric technological and economic organization, communicate information in a variety of contexts, from hafting styles, to blade caches, to ritual bloodletting (see Pierce 2017; Quinn 2015; Waguespack et al. 2009).

The diversity of applications of CST in the past decade indicates that the theoretical approach is growing in appeal across the globe. However, the challenges described above remain. While many archaeologists are beginning to use CST to develop testable predictions for costly signaling that can be evaluated in the archaeological record, some continue to use it as a post hoc explanation of a material record that contains perceived, rather than demonstrated, wasteful behavior. Additional modeling is necessary to harness the explanatory power of costly signaling in the archaeological record. In the next section, I provide a generalized framework for assessing material culture signaling power in its cultural context.

A General Framework for Assessing Material Culture Signaling

The signaling power of objects varies across time and space. This general framework serves as an analytical tool for archaeologists to assess the signaling power of material culture. This framework has previously been tailored to the study of lithics (see Quinn 2015, p. 207–212), though this more general version can be adjusted to assess the signaling power of any material culture category. This framework is based on the following premises:

1. The underlying attributes that impact reproductive fitness vary based on the social and environmental setting (e.g., hunting prowess in foraging communities vs. amassing wealth in state-level societies).

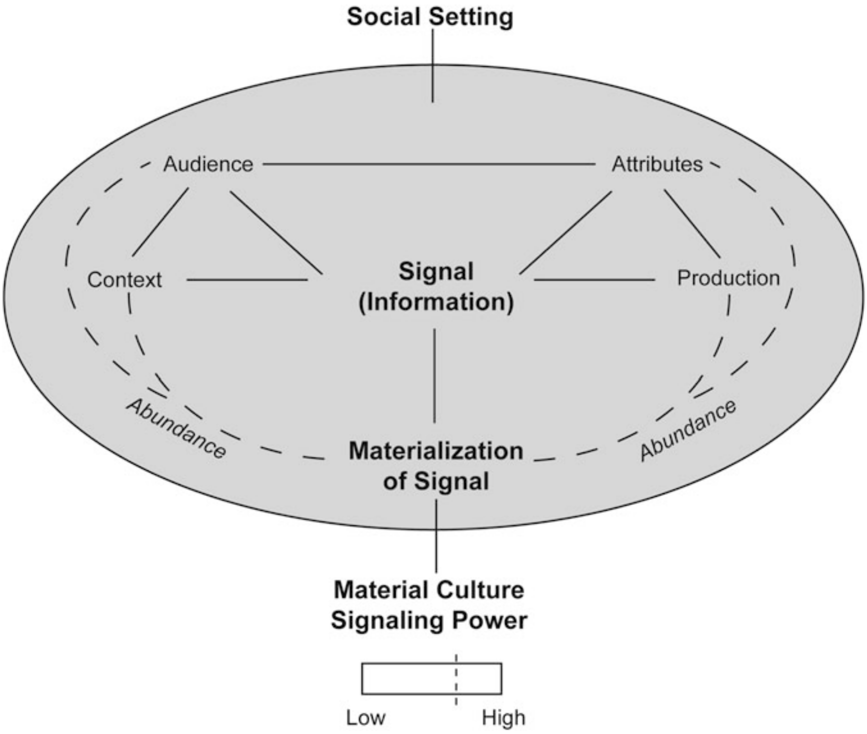

Fig. 14.2 A general framework for studying costly signaling behavior with material culture (after Quinn 2015: Fig. 11.2)

2. The costs of signals are the product of the physical attributes of the object and the social, economic, and technological systems that influence its procurement, production, distribution, and use.
3. The visibility of the signal is a product of its physical characteristics and the audiences that can see it in the situations where it is displayed.
4. The signaling power of an object is dynamic and subject to constant negotiation.
5. Signals will decrease in power the longer they stay in circulation, especially if they are able to be transferred easily between people.

With this framework, archaeologists can begin to quantify the relevant variables to provide a more empirical perspective on costly and non-costly signaling in the archaeological record.

There are several first-order variables that impact the signaling power of material culture: (1) the audience of the signal, (2) the contexts of use and discard of the signal, (3) the physical attributes of the signal, and (4) how the signal is procured, produced, and distributed (Fig. 14.2). These first-order variables are interrelated. As an example, consider the raw material of an object, which can be considered a second-order variable. The raw material an object is made of is a physical attribute of the signal, but it also impacts how the signal is acquired—such as being locally available or only available through long-distance exchange—and its visibility. There are several second-order variables that can serve as potentially quantifiable lines of evidence of the costs and benefits of the signals (Table 14.1). The costliest signals will be difficult to produce or acquire, made of exotic or very rare raw materials, highly visible, and used in social contexts with large audiences.

Costly material signals should rarely enter the archaeological record through loss, as their immense social value would lead people to search and recover them (see Schiffer 1987). The intentional

Table 14.1 Variables which archaeologists can study within the generalized framework in order to identify and explain material culture based costly signaling behavior in the past (after Quinn 2015: Table 11.1)

First-order variables	Second-order variables
Artifact attributes	Size
	Color
	Sheen
	Raw material (distance to source; distribution/access)
Production	Skill level required
	Time to manufacture
	Producer/consumer relationship
	Cost of maintenance
Audience	Relationship between signaler and recipient
	Population size/density
	Visibility of material culture
Context	Use context (daily life; ritual/event)
	Deposition context (caches, graves, votive offerings; loss; discard)

deposition of costly signals—such as in graves, ritual caches, and other votive deposits—would provide additional benefits to the signaler by demonstrating to audiences that they are able to withstand the loss of a valuable signal.

The abundance of material signals in circulation will significantly impact the overall signaling power of material culture. As objects become more common, it is more likely that individuals who do not have the underlying attribute being signaled could come to possess the signal. As audiences encountered these non-honest signalers, the link between the material signal and the underlying attribute would be weakened. The signaling power of all objects, even those possessed by honest signalers, would be lowered. At a certain point, the increasingly abundant objects would no longer be effective costly signals. We would expect the individuals who have the underlying attribute would find a new form of material signal (e.g., conspicuous destruction of the objects or a new type of object) to replace the original costly signal that is no longer honest. The feedback between the abundance of materialized signals and the variables that contribute to the signaling power of an object produces a tension that can lead to rapid changes in signaling strategies.

The approach outlined here begins with archaeologists assessing the information and attributes that most directly impact reproductive fitness in the particular socio-ecological setting. Next, archaeologists use second-order lines of evidence to reconstruct the first-order variables of audience, context of use and discard, physical attributes of the material, and procurement, production, and distribution system. This assessment allows archaeologists to reconstruct (1) how costly a signal is, (2) how visible a signal is, and (3) how well the signal indexes the underlying information being conveyed. Following this initial assessment, archaeologists must look to see how abundant an object is in the archaeological record to assess how well the object would work as an honest costly signal.

This general framework can help archaeologists produce testable hypotheses about signaling strategies in the archaeological record. For example, costly material signals should be rare enough that not everyone can adequately signal. People will seek out costly signals, and even fake costly signals, which over time will lead to an increase in the signal. Finally, signals should be abandoned when audiences determine they no longer accurately display the underlying information being signaled. Future work modeling the spatial-temporal dynamics of costly signaling will provide additional ways to measure signaling power, assess change in signaling over time, and distinguish costly and non-costly signals in the archaeological record.

Conclusion

CST represents a dynamic frontier in evolutionary approaches to the archaeological record. While archaeologists from many theoretical backgrounds have recognized that humans use material culture to convey information, CST provides a unique way of understanding (1) how this capacity first evolved, (2) how signaling fosters both cooperation and competition, and (3) how signals change over time. The global appeal of CST, perhaps best represented in a recent special issue of *World Archaeology* edited by James Conolly (2017), continues to grow. However, there remain significant issues that require additional theoretical models and analytical methods to resolve before CST can reach its potential as an archaeological theoretical framework. In order to explain human behavior through its material consequences, archaeologists must develop theoretical models to frame research questions and identify the data necessary to answer them (Codding and Bird 2015, p. 9). The continued development of CST will require additional conceptual models as well as new case studies. By considering how costly behavioral and material signals mediate social relationships, archaeologists can better understand how individuals influenced the organization and evolution of social, economic, and political systems in the past.

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Chapter 15
Human Behavioral Ecology and Technological Decision-Making

Nicole M. Herzog and Nathan Goodale

Introduction to Human Behavioral Ecology as a Theoretical Framework

Within the HBE framework, optimal foraging theory (Emlen 1966; MacArthur and Pianka 1966) is the most common lens through which archaeologists work. The classic model, termed "encounter-contingent prey choice" or "diet-breadth" model, was developed by evolutionary biologists (Stephens and Krebs 1986; Pyke et al. 1977; Charnov 1976a) to identify which types of prey one would expect to be included in the diet. In this subsistence-based model, the individual forager's goal is to maximize net rate of energy intake given the set of resources available. Foraging decisions are distilled into simple yes/no choices that depend upon the profitability of the object at hand vs. the assumed net rate of return achieved by passing up the resource to continue the search for something else. The profitability of a given resource is calculated by quantifying its energetic content (kcals) and then dividing that by the amount of time spent handling (i.e., harvesting, butchering, grinding, cooking) the resource to convert it into an edible product. The expectation is that a forager should decide to pursue a resource when encountered if the profitability of that resource is greater than the anticipated net rate of foraging return per unit foraging time.

The prey choice model can be expanded to examine patchily distributed resources as well (MacArthur and Pianka 1966). Within the "patch choice" model, the decision variable becomes, should one enter a patch, and if so, how long should one stay. Thereby, patches themselves enter and fall from the diet based on the average return across all available patches. In a given patch, profitabilities will fall based on time spent in exploitation, a phenomenon formally modeled by the marginal value theorem (MVT; Charnov 1976b). MVT describes the amount of time a forager should spend in a particular patch before moving to another. The decision for a forager is how much of the resource to take and how long to stay in each patch. Trade-offs are made between time spent in the patch and time spent traveling between patches. In accordance, "One would expect a forager's patch-leaving behavior to reflect a balance between the diminishing returns of patch gain and the value of the forager's options elsewhere" (Stephens 2008, p. 475). MVT predicts behavior based on diminishing returns, a common occurrence in natural systems, something humans are cognitively aware of, and

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a concept which has proven to be an invaluable tool in the study of human decision-making across many aspects of behavior both past and present (Bettinger and Grote 2016).

While the optimal foraging model, MVT, and others center on subsistence, these same models have been recast by archaeologists to focus on a broad range of subsistence-related problems such as central place foraging (e.g., Metcalfe and Barlow 1992), the origins and spread of agriculture (e.g., Barlow 2002; Kennett and Winterhalder 2006), and the sexual division of labor (e.g., Elston and Zeanah 2002). Archaeologists have used these models to explore problems in prehistory for the past four decades, leading to a comprehensive body of literature (for reviews see Broughton and O'Connell 1999; Bird and O'Connell 2006; Codding and Bird, 2015). Here, we turn to a set of optimality models that focus specifically on the procurement, manufacture, and use of primitive technologies. Using the same cost/benefit logic of the optimal foraging tradition, these models explore variables related to tool manufacture and use including raw material extraction, transport and processing, tool construction and maintenance, and use and service life. The models are also useful in explaining technological changes from simple/expedient to complex/costlier tools.

Constraints on Technological Decision-Making and Design

Variation in technological systems involves complicated interactions between human decision-making with relationship to raw material availability, raw material quality, and the ratio of producers to consumers (Goodale et al. 2008). Tool categories that make up technological systems are often considered to be systematic, meaning close to uniform in size, shape, weight, or any other functional attributes, or unsystematic, meaning highly variable (Bleed 2001; Brantingham et al. 2000), but can usually be described along a continuum of uniformity (Shott 1996). The use of technology incorporates both the procurement of resources, which may be modeled within an HBE framework (Surovell 2009), and the relative skill (Bleed 2008) of the producers, which may be better understood through evolutionary frameworks such as dual inheritance theory (Chap. 3; Boyd and Richerson 1985; Shennan 2002). For example, there is an interesting debate surrounding the maintenance of complex technologies and whether they are driven by imitation or are the result of adaptive change in response to subsistence shifts (Henrich 2004; Read 2006). However, here, we concentrate on HBE frameworks and begin with the fundamental principle of optimality in technological decision-making.

Technological systems are composed of design features that have the potential to be converted into individual reproductive success, and thus, natural selection can have the consequence of optimizing design features. When portions of technological systems are under selection because they optimize somatic interests (increase access to resources), technology can contribute to an individual's reproductive success (Krebs and Davies 1997; Smith and Winterhalder 1992). In circumstances where resource access is competitive and there is variation in the strategies to solve for a particular goal, natural selection should favor the strategy that solves the problem with a least-cost path over other strategies that may be available (Foley 1985). The reason for natural selection to favor the least cost decision is that humans have limited energetic budgets. Those individuals that can save energy while at the same time solve particular problems that optimize their somatic interests can convert energetic surpluses into other endeavors that also increase reproductive success (Kaplan et al. 2000). Based on this argument, one might draw the conclusion that humans are designed to optimally adapt to their environment because of technological decision-making. Alternatively, the conclusion to be drawn from this line of reasoning is that natural selection tends toward the optimal solution given a range of available solutions present in the environment (Foley 1985; Smith and Winterhalder 1992). There is also contingency from their evolutionary history as decision-making occurs through time (Prentiss and Clarke 2008).

Human decision-making can be described as behavior that is behaviorally and cognitively flexible or plastic (Flinn 2005). Plasticity allows humans to respond to fluctuating social and ecological selection pressures. Over time, technological decision-making will tend toward optimizing the net return rate in relation to the energy invested. Concurrently, humans are aware of diminishing returns that may be associated with particular decisions in problem-solving. This allows humans to adjust investments according to optimal return rates (Kaplan and Lancaster 2000; Smith 2000).

The degree of optimization is dependent on the selection pressures associated with a particular resource (Foley 1985) and the technology used to procure the resource. When a resource has a high impact on fitness (high contribution toward reproductive or other somatic interests), individuals who focus attention on procuring that resource can achieve greater fitness (Hames 1992; Winterhalder 1983) and are also likely to invest in the technology used to procure the resource. If the opportunity exists to increase fitness through procuring a resource, optimal strategies will outcompete other strategies. Alternatively, if a resource has low impact on fitness, optimization may not occur, but it is more likely that satisfactory solutions for obtaining resources with low selective pressures will be viable and variation in the ways of completing a task will be tolerated. Winterhalder (1983) provides a model demonstrating the circumstances that would favor decisions to invest an additional unit of time and energy into a specific activity (conditions of limited energy) or to cause limited resources into other activities (conditions of limited time).

For human populations that rely on technology for access to food or other interests, the nature and access of technology impacts reproductive success. Raw materials used to create technology, in many cases, approximate a zero-sum game. In other words, when one individual accesses raw materials used to make technology, it represents a loss for other individuals in a population. When raw materials are proportionally high compared to a hypothetical population, the depletion of raw materials may be inconsequential to everyone. Therefore, access to raw materials to produce technology may have low fitness consequences, as there is likely little competition in procurement. When available raw materials for producing technology are proportionally low compared to demand, competition in procuring those resources will likely be high.

Under optimality reasoning, one would conclude that when use of raw materials to produce technology is highly competitive, strategies for converting the raw materials into usable technology will be constrained with the likely solution (or solutions) being those that are most economical given the range of possible solutions present. An outcome could be that only a few individuals might specialize in production from a limited resource, with others opting to consume the other resource types that are available (Nakahashi and Feldman 2014). If a resource is quickly being depleted, individuals may obtain a better payoff by redirecting their time and energy into other goals that increase fitness or other interests. Reasons for this are that when there are constraints on resource availability, not everyone can effectively engage in a specific economic pursuit (i.e., technological production), and the range of strategies employed may be more broad. On the other hand, when raw materials are under low selection pressure, access to them is unlikely to have a negative impact on other people using the raw materials. In this case, more people will be likely to act as both producers and consumers (engaged in producing technology as well as using the products).

Modeling Technological Variation: Raw Material Availability, Quality, and Ratio of Producers to Consumers

Variability in technology is a likely result of human decision-making in relation to raw material availability, quality, and the ratio of producers to consumers. Investments in technology vary both spatially and temporally (e.g., Beck et al. 2002; Bleed 2008; Prentiss et al. 2015; Surovell 2009), and the links between raw material availability (Beck et al. 2002; Kuhn 1996) and quality (Andrefsky

1994; Brantingham et al. 2000; Kuhn 1996; Surovell 2009) on the constraints of technological design and conformity have been made in a number of studies. More specifically, Surovell (2009) provides a mathematical model to examine the differing transport costs of lithic cores and tool blanks within Paleoindian contexts of North America. Following Kuhn (1996), the model as Surovell (2009) presents it is applicable as a general model of decision-making with regard to the question of when to transport cores versus tool blanks. Raw material availability can be modeled in HBE terms as the kcal/hour expended to procure and transport the resource. This takes into account the distance one has to travel to procure the raw materials and package size/weight that has to be carried (Beck et al. 2002). Goodale et al. (2008) model variation in technology as increasing at the square root of availability. Where variation increases drastically with changes in low availability, the slope becomes less extreme as availability approaches maximum (total availability equates to easy access and travel time/distance is short). This is similar to Surovell's (2009) model which is tested explicitly against the archaeological records of a number of Paleoindian sites in North America.

Raw material quality relates to the composition of the resource and also how easily it is converted/manipulated to be used as technology. As one may imagine, raw material quality could be described in a number of ways depending on the material's composition. For stone to be converted into technology, one might describe quality as the homogeneity, percent impurities, crystal size, or anything that relates to the fracture mechanics of the material. In other technological instances, such as ceramic production, quality might relate to clay grain size and mineralogical make up as well as what temper needed to be added to produce vessels that function as intended by the maker.

Goodale et al. (2008) present a graphical model to illustrate the relationship between raw material availability, quality, and the ratio of producers to consumers (Fig. 15.1). The model was developed for examining variation in stone tool core reduction strategies but is more widely applicable across technological systems (Goodale and Andrefsky 2015). Goodale et al. (2008) model variation in technology as it relates to quality as a decaying exponential. Here, variation (v) is proportional to the ratio of producers to consumers (μ), the square root of availability (a), and the base of the natural logarithms ($e \approx 2.718$), to the negative power of α times quality (q).

$$v\,(a, q, \mu) \propto \mu\sqrt{a}\, e^{-\alpha q} \tag{15.1}$$

From this perspective, variation in technology is highest when the quality of raw materials is lowest, and variation in technology is lowest when raw material quality is highest. There is the further expectation that at low quality, variation increases rapidly but when quality increases, variation does not change nearly as rapidly. In reality, this simplified relationship is probably much more complicated and based on a number of variables that would be difficult to model in mathematical terms. However, as a main goal of HBE is to generate predictive models to provide a set of expected outcomes under circumstances of optimization, not every case may meet all predictions. In this circumstance, the link between technological variation and the ratio of producers to consumers may be more complicated than a simple linear relationship (as the ratio of producers to consumers approaches 1:1, variation will constantly increase).

General models that attempt to ask questions regarding the ratio of producers to consumers in a given cultural and geographic context can help test hypotheses about the nature of human behavior and lithic technological organization (Bleed 2008; Goodale et al. 2008, 2015; Prentiss et al. 2015). While many of these models have yet to be applied to other technologies and their constraints, the variables within are at the core of the debate around the rise of social transitions such as craft specialization (Costin 1991). As demonstrated above, the constraints on technological decision-making and resulting diversity of outcomes are complexly related with raw material, the number of people engaged in technological decision-making, and selective pressures (or lack thereof). Future applications will no

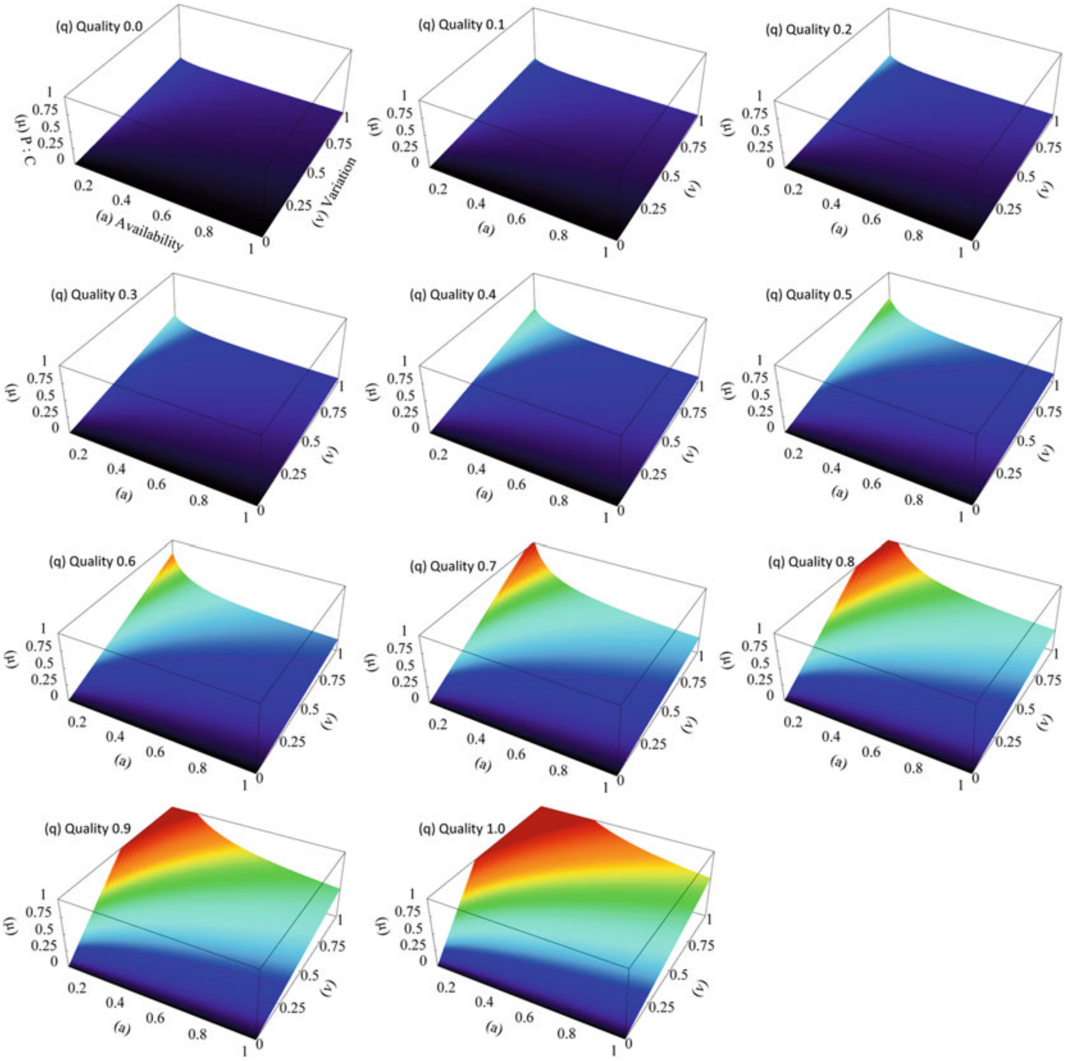


Fig. 15.1 Graphic model of Eq. (15.1) representing the relationship between raw material availability, technological variation, and the ratio of producers to consumers sequentially scaled to increase in raw material quality (Goodale et al. 2008). The mathematical relationships for availability, ratio of producers to consumers, and technological variation are along the X, Y, and Z axes and raw material quality changes in increments of 0.1 (on a scale of 0, lowest quality, and 1, highest quality)

doubt tackle these complicated problems, and the developed set of models outlined here will serve as a sound foundation in addressing the questions of what to produce and how. We now turn to the questions: when and why do people invest in technology?

Constraints on Technological Investment

In an early ethnographic application of the prey choice model among living hunter gatherers, Hawkes and O'Connell (1992) noted that shifts in the amount of time dedicated to search (looking for a resource) vs. handling (pursuit of identified resource, collection, and preparation for consumption) have implications for subsistence transitions. As diets become more broad, rate maximization is constrained because search time has already been greatly reduced, leaving only costs associated with handling to vary. Under these conditions they note, "innovations that increase handling efficiency [tools/technology] will have their greatest effect. In fact, investments in handling improvements will be the *only* way to achieve higher food-acquisition rates." (Hawkes and O'Connell 1992, p. 64). If increased investments in search offer no better returns, populations may tend toward sedentism, at which point we should expect "technological intensification" to follow.

Archaeologists have also noted the links between increasing sedentism and increasingly specialized toolkits (for a review see Morgan, 2014). Drawing on these observations, models of technological innovation aim to provide a mathematical framework from which to evaluate how and why certain technologies evolve. Much like the prey choice model, technological investment models are contingent on optimization; does an investment now provide a higher benefit than forgoing such investment in favor of the existing toolkit? This of course depends on the continued success of the current set of tools and also the structure of the resources available. If conditions change such that the current strategy no longer provides adequate return, an investment in an alternative strategy may provide a higher return despite high initial costs. It should be noted that while expensive technology does make the process of food procurement more efficient, this efficiency should not be confused with improved subsistence efficiency—on the contrary, intensification, as it relates to technological refinement, is often associated with *declines* in overall subsistence efficiency (Bird and O'Connell 2006, p. 153).

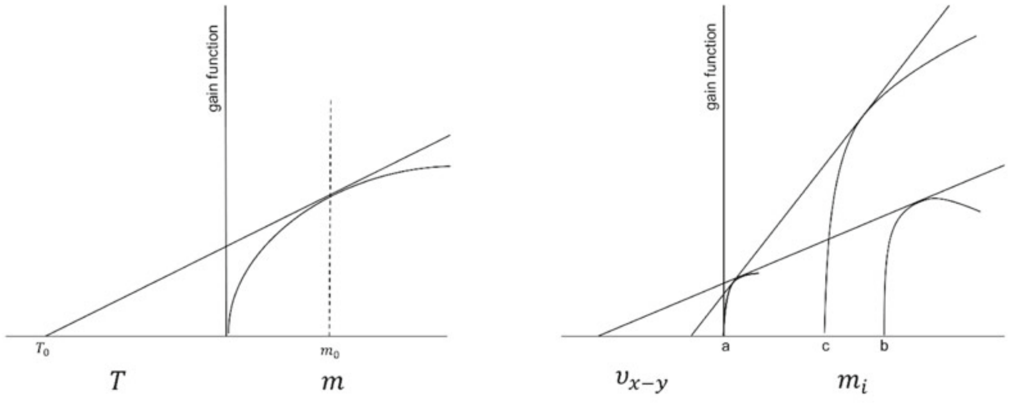
Efforts to evaluate these processes from an optimization approach have been common, but an explicit use of the theoretical framework of HBE less so. One early application of an explicitly HBE technological investment model to an archaeological dataset was published in 2002 (Bright et al. 2002). This paper examines various technological forms (milling stones, ceramic, and flaked stone tools) as they relate to the archaeofaunal record of the late prehistoric era in Little Boulder Basin, north-central Great Basin. A formal treatment of the model was presented in a theoretically driven companion piece published the following year (Ugan et al. 2003). We begin our review of technological investment models with this and a second set of HBE tech models (Bettinger et al. 2006; Bettinger et al. 2015) and then examine subsequent iterations and applications.

Two Theory-Driven Technological Investment Models

Investment as the Decision: When to Invest and When to Stay Simple

In the 2003 piece titled, "When is Technology worth the Trouble", Ugan et al. (2003) outline several technological investment models that articulate the relationship between handling time as a function of time invested in tool manufacture. Here we focus on the variant applied by Bright et al. (2002); it builds on the classic prey model by replacing the yes/no food pursuit decision variable with a yes/no decision regarding investment in a given technology. The model defines the following problem: in order to improve the profitability of a specific resource, a forager must expend some energy improving the processing tools available to handle that resource; when should the forager decide to invest energy in the manufacture and maintenance of processing tools?

The goal of the model is to predict the optimal amount of time to invest in tool manufacture as a product of three variables (see Box 15.1): (1) total time spent in search, (2) encounters with resources, and (3) base handling times for resources (the more handling time a resource requires, the more time should be invested in developing and maintaining associated processing technologies). The currency stipulated in the model is return rate measured as kcals/time.



The Ugan et al. (2003) model predicts the optimal time investment in a given technology.

$f'(m) = \frac{f(m)}{m+T}$	gain function
m	time invested in manufacturing technology
m_0	point at which gains are maximized over time spent

The Bettinger et al. (2006) curve-estimate model predicts the critical use threshold for determining when to switch to a different technology.

$f_i(m_i)$	gain function
m_i	time invested in manufacturing technology
v_{x-y}	critical threshold for switching
a—c	marginal gains curve for three technologies

Box 15.1 Graphical representations of the Ugan et al. (2003) and Bettinger et al. (2006) technological investment models

Like all models, the Ugan et al. (2003) model makes several assumptions regarding past behavior. The first is a time allocation problem in that time invested in tool manufacture cannot also be used to complete an alternate activity. The second assumption is that each unit of time spent in manufacture decreases handling times by an equal amount. Marginal gains per time invested in tool manufacture/maintenance follow a diminishing returns curve akin to those established in patch choice models and Charnovs's (1976a, b) MVT. Finally, the authors assume that the goal of tool manufacture is to maximize net rate of energetic gain.

In an application of the model to single-occupation surface sites located in the north-central Great Basin, Bright et al. (2002) analyzed 250 radiocarbon-dated hearth features for food remnants indicative of prey choice. Contents of hearths were sorted into four categories representative of overall predicted profitabilities. Faunal remains (using numbers of identified bone specimens [NISP]) were considered high, medium, or low profitability. Floral components, such as seeds, were placed in the lowest profitability category, below even low-profitability mammals (see Herzog and Lawlor, 2016 and Chap. 13 for alternative arguments regarding the profitability of "seeds"). Categorical determinations (high, medium, and low profitability) were based on experimental data calculating the amount of time necessary to butcher and/or prepare each food type.

To evaluate the relationships between changing encounter rates and investment in technology, the authors compared the proportion of faunal and floral elements identified in associated hearths to the degree of differential investment observed in three tool types: milling stones, ceramics, and chipped stone tools. They hypothesize that (1) where seeds (and other low-profitability resources) make up only a small portion of the diet, milling stones should be made from locally available material and show no investment, such as shaping; (2) as lower-profitability resources become more common (using hearth size as a proxy), investment in milling stones and the presence of milling stones made from nonlocal materials should increase; (3) since lower-profitability resources (seeds) appear more common in the record later in time, we should see more time-intensive ceramic technology later in time co-occurring with the increasing use of these foods; (4) as the contribution of low-profitability items increases, so too should investments in ceramic types which are more expensive; and (5) a reduced emphasis on large-game hunting should be accompanied by a shift away from costly chipped stone tools. An alternate possibility not considered by the authors is that the use of technology changed the relative ranking of resources such as seeds, elevating their place in the diet.

Results were mixed, though they largely supported the authors' hypotheses. Milling stones made from exotic stone remained uncommon despite measurable increases in seed consumption. However, the number of milling stones did increase with the appearance of small-sized hearths. Specialized and expansive ceramic technologies also tracked the appearance and then increased reliance on small seeds. Likewise, as evidence for consistent large-game hunting decreased, so too did the appearance of formal, bifacial chipped stone tools. Together, these data indicate that the relationship between handling time and technological investment is linked; therefore, the model should be effective at predicting when and where technological investment and subsequent dietary shifts (see Chap. 13) may be expected. Results highlight the role of handling time as a driver in technological investment.

Bettinger et al. (2006) note several conceptual issues with the model. One such issue centers on the measurement of costs over time. The model stipulates that investment in the tool is represented by a one-to-one gain in profitabilities. However, the relationship between investment in the tool and its impact on caloric return is likely not so simple. For example, initial investment costs are often steep, while parallel improvements in profitabilities are not possible until a threshold of investment has been reached. The model assumes that all technologies are on the same gain curve and require that marginal gains are always steeper for cheap rather than costly technologies. This assumption precludes comparing different gain curves for emergent, and therefore fundamentally different, technologies. Noting these issues, and building on the premise of technological investment as a handling innovation, a subsequent set of technological investment models proposed by Bettinger et al. (2006, 2015) aimed to expand the scope of the Ugan et al. (2003) approach.

Multi-Type Technological Investment: How Long to Stay in a Given Technological Category

The Ugan et al. (2003) model is able to capture the trade-offs involved in replacing less costly versions of one category of technology with more advanced, and hence costlier, versions of the same type of technology. Building on this, an alternative set of technological investment models was proposed by Bettinger, Winterhalder, and McElreath (2006). In this paper the authors lay out two models of technological intensification derived from the MVT (Charnov 1976a, b) and Metcalfe and Barlow's (1992) field processing and transport model.

Both models assume different categories of technology have unique cost-benefit curves, and thus examine investment decisions within a category, and also shifts to new, and costlier, types of technology. Where the Ugan et al. model is limited to intensification within a technological type, the Bettinger et al. models draw attention to emergent technologies and the conditions that may lead to dramatic changes in technological organization. They argue that costlier technologies can outperform less costly ones if profitabilities for a particular technology are maximized over the use-life of the tool (measured as cumulative time in use) in addition to the time spent in manufacture. Rather than assuming a single, continuous function as representative of all technological investment (both within and between tool types), the Bettinger et al. approach predicts investments in different tool types using separate functions for each tool category. Bettinger et al. differentiate between technological categories (a related set of forms) and classes (all known categories of artifacts used in a particular subsistence pursuit).

Here we focus on the curve-estimate model proposed by Bettinger et al. (2006). Much like the Ugan et al. model, this model builds on MVT and patch choice models. Unlike the Ugan et al. model, the curve-estimate model focuses on the amount of time that must be dedicated to handling before it becomes optimal to switch to a new strategy. Therefore, the model aims to predict the critical use time, defined as the amount of time spent in post-pursuit handling in which low-cost technologies produce the same profitabilities as high-cost technologies, as the primary variable of interest. At the critical use-time, it becomes optimal to switch from one tool category to another despite high up-front costs for development.

Variables in the model include (see Box 15.1) (1) time spent in handling (excluding time spent in tool manufacture), (2) time spent manufacturing a specific tool, and (3) the possible kcals procured as a function of the time required to manufacture. In the tradition of many other HBE models, the primary currency of the models is profitability (kcals/time). Assumptions within the curve-estimate model are that base energetic costs (kcal/h) for searching and handling (including pursuit and tool manufacture) are constant across technological categories. The model also assumes that there are no external constraints on energy or time. And, as with the Ugan et al. model, the Bettinger et al. model assumes that intensification within a tool category does not impact use-life.

An application of this model to the same data used by Ugan et al. demonstrates that by generating independent function curves, the critical times necessary for technological switching (i.e., investment in more expensive categories results in lower thresholds for switching) can be predicted. Importantly, these predictions provide a conceptual framework from which to distinguish endogenous/emergent vs. diffusion-driven technological change.

Similar to the Ugan et al. model, the Bettinger et al. models are also limited in some aspects. First, to produce multiple independent gain functions requires data on the cost of manufacture for each class of tool within a given category for each category of interest—data which is, at present, limited. Neither model considers the possibility of tool degradation or limitations on the duration of artifacts' use-life as continued investment eventually "spends" the tool. Finally, the model cannot account for transitions back to less costly and/or less efficient tool categories or types because reductions in alternate arenas are not additive assumptions. Despite these limitations, each model clearly outlines both theoretical and methodological pathways to examine technological intensification in the archaeological record.

Novel Applications of Technological Variation and Investment Models

The utility of models grounded in HBE is their simplicity and flexibility. The Ugan et al. (2003) and Bettinger et al. (2006) and Goodale et al. (2008) models provide a theoretical framework for expanded and novel investigations of technological investment. Here, we outline several novel applications and derivations borne from these basic models and from the MVT, generally.

Millingstones and Seed Intensification

Buonasera (2015), for example, adapted the Bettinger et al. point-estimate model to examine the costs and benefits of manufacturing expedient milling tools. Using experimental methods, she tested the profitabilities achieved using milling stones representing four stages of technological investment (expedient, prepared surface—minor shaping, prepared surface—moderate shaping, and metate). She then used these profitabilities to estimate the minimum use-times necessary to predict investment in minor millingstone modification. Her results demonstrated that profitabilities for seed processing (*Achnatherum hymenoides*, Indian ricegrass) did increase as level of investment increased and that the costs in manufacture (measured in units of time) were offset by the increase in profitability. Moreover, her results demonstrate that thresholds for investment in expedient milling tools (no clear evidence of exterior shaping) are rather low, indicating that investment in surface improvement should come earlier than previously assumed. Results also highlight the importance of material type in determining whether to invest in tool improvements—with some material types better suited to millingstone production than others.

Another derivation of the millingstone investment problem was taken on by Stevens and McElreath (2015). Building on both an early model of tool use-life (Ammerman and Feldman 1974) and the Bettinger et al. (2006) models, they introduce a formal technological investment model specifically designed to investigate the conditions under which multi-use tools can outperform specialized tools and vice versa. Their explicit aim was to track the decision to use one tool over another when individual tools are employed in multiple tasks. The authors use the model to explore the transition from shaped milling stones to mortar and pestle milling technology in northcentral California where archaeobotanical data suggest that by approximately 4500 BP, the acorn (*Quercus* spp.) had replaced other wild foods as a dietary staple (Wohlgemuth 1996). Coincident with increased reliance on acorn, formal pestles and mortars make an appearance in the archaeological record with their emergence and prominence in assemblages growing alongside previously existing basin-shaped millingslab implements (Basgall 1987; Glassow 1996). Stevens and McElreath (2015) tackle the problem of the transition to the mortar with a simple question, "when are two tools better than one?" Results demonstrate that decisions to invest in more expensive tools hinge not only on the ability to recoup the initial costs and the total time in use but also on the likelihood that the tool will be used repeatedly over time (see Chap. 13). No matter the improvement in efficiency, expensive technology cannot get off the ground unless there is some certainty that the item will be used repeatedly.

Flaked Stone Tools and Use-Life

Tool manufacture, like food procurement in a patch, involves a trade-off between continuing to use an increasingly ineffective tool/patch and stopping and/or leaving to create or find a better alternative. Combining raw material costs, utility (or lifespan), and production effort, Kuhn and Miller (2015) treat stone tools themselves as patches in an application of MVT to tool manufacture and use. In this model, authors consider the cost of switching between artifacts, calculating the optimal point at which to abandon one tool and invest in producing or procuring a new one. Citing reduced opportunity costs, time to manufacture is converted to energy, and energy alone is used as the currency. While the authors note that different families of artifacts may exhibit different decay curves, as in the Bettinger et al. (2006) approach, they settle on a treatment that places all flaked stone artifacts on the same utility curve following the Ugan et al. (2003) model.

The model predicts the optimum number of uses for any particular tool, and the predictions it generates are generally in line with those from the MVT itself. Increased costs raise the optimal number of uses; the more quickly the tool is spent, the earlier it is abandoned, and the optimal point at which to abandon a tool declines as average returns increase. The authors use these predictions to examine patterns in Paleoindian spear point use-wear and retouch through time and propose two hypotheses to explain the apparent shift in discard time to later in an artifact's use-life. The first is that decreased access to source material as a function of population size drove users to hang on to existing tools for longer periods of time. Alternately, decreases in average return rates may have pushed the longer use of artifacts before discard. Here, the model provides a framework from which to begin to understand observed transitions, and hypotheses generated may be pursued further using additional lines of evidence.

Ceramics and Mobility

The advent and proliferation of pottery are widely viewed as a technological response to resource scarcity and dietary broadening. As noted above (Hawkes and O'Connell 1992), where diets are broad, investment in technology may be one of the *only* ways to achieve higher food-acquisition rates. Ceramics serve this purpose by reducing the handling costs associated with low-ranked foods such as seeds, shellfish, and bones. However, ceramics themselves are time consuming to make, difficult to transport, and susceptible to breakage.

To better understand the conditions under which groups of mobile hunter-gatherers and herders may have invested time and labor into producing pottery, Sturm et al. (2016) apply a derivation of the Ugan et al. and Bettinger et al. models to a series of hypothetical scenarios in which pottery may be adopted in contexts of high residential mobility. These test cases allow the authors to generate expectations about spatial patterns in pottery distribution, namely, that the decision to invest is complex and that expectations for use—duration of utility and anticipated cooking needs—largely constrain outcomes. Authors also note that for some forms of technological investment, social or political returns (if possible to operationalize) may be a more appropriate currency than energetic utility. Though the model has yet to be applied to existing assemblages, the authors note its utility as a heuristic for interpreting the relationships between the appearance, abundance, and distribution of pottery under variable ecological and social conditions.

Landscape Modification and Associated Technologies

Applications of the technological investment models outlined above investigate patterns in the manufacture and modification of material culture. However, in an innovative adaptation of the models, researchers Mohlenhoff and Codding (2017) use the theoretical framework of the Bettinger et al. (2006) model to examine intentional ecological niche construction. They argue that landscape modification can itself be viewed as a handling innovation, similar to the use and manufacture of any type of material tool. As such, they note that the forces/activities used to accomplish landscape modification can and do require some cost to innovate and maintain. Here, in order to invest in a given patch (i.e., modify by some technological means—fire, tillage, etc.), the marginal gains within that patch must be higher than the costs of investment. If true, the continued modification of particular patches can result in intentional niche construction—a process through which local environments are purposefully modified by inhabitants (Mohlenhoff and Codding 2017).

The authors apply the model to a series of case studies, spanning less to more costly forms of patch investment: tending acorn groves with fire, constructing fishing weirs, and adopting maize agriculture. Using both ethnographic and archaeological data to estimate the economic returns for each activity, they are able to demonstrate that investment in less costly forms of patch management/construction such as use of fire should be ubiquitous across human societies, as is the case (Scherjon et al. 2015). However, costlier forms of niche construction such as investment in active agriculture may have only proliferated under certain environmental and socio-ecological circumstances, thus predicting the mixed expression of more intense technological investment for higher-cost forms of patch investment.

Conclusion

Critiques of the EE/HBE approach center on the perceived determinism of the models, their simplicity, violations of the underlying assumptions, and whether one should assume that there is a direct link between the observed phenotype and the adaptive demands that shaped it (a problem also known as the "phenotypic gambit") (Sterelny 2013). Applications of EE/HBE models centered on technological design and investment are not immune to these criticisms. Many include simplified assumptions and are unidirectional; most require positive gains for increased investment, however marginal, but do not and cannot account for nonoptimal investment and/or retrogression, i.e., transitions from complex to simple technology over time (as seen in Sahul and South Africa (Jones 1977; Sealy 2016)). However, the applications described here underscore that their use can and does provide a framework for interpreting patterns in the archaeological record.

Many of the phenomena described in this chapter have been investigated using alternative frameworks that explicitly address the role of culture (see Chaps 2, 3, 4, 6, and 10). Rather than revisit these methods, our goal in this chapter is to outline basic optimality models, review recent archaeological applications in light of technological decision-making and investment, and highlight both the strengths and weaknesses of the approach. To emphasize a point made by Kuhn and Miller (2015), these models do not predict that actors *will* act optimally; rather they provide a description of what that optimal behavior *ought* to look like. When the observed behavior (or in this case, material record) does not appear "optimal," as predicted by the model, this too provides an opportunity to re-evaluate and redefine model assumptions. As outlined by Sterelny (2004), this type of failure can reveal underappreciated features of local ecology or sociology, help identify unanticipated or unexpected costs, and force us to identify limits on adaptive design.

We contend that tech investment models grounded in HBE remain an underutilized tool in addressing issues of technological innovation, diffusion, and refinement. Not only can these models provide predictive power regarding the appearance of highly specialized tools, but more simply, they can be used to explain variation in archaeological assemblages generally. Because many plant and animal foods require some degree of tool-assisted processing, the models can also shed light on other dimensions of subsistence including dietary transitions and landscape modification. Filling in gaps regarding foraging behavior remains a significant area of study in archaeological research, and because physical remains of past diets are often poorly preserved and difficult to detect, technological investment models provide an additional avenue of investigation into the spatial and temporal aspects of diet breadth as well as the strategies employed by past consumers.

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Chapter 16
Demography, Environment, and Human Behavior

Cedric Puleston and Bruce Winterhalder

Introduction

Archaeology's broad engagement with the long-term evolution of human subsistence systems and social forms hinges upon poorly understood relationships among environment, demography, production, and society. Specific examples are conveniently phrased as questions. How long will it take for a colonizing human population to fill a previously unoccupied habitat and what factors determine this duration? At what point in its growth trajectory will a natural fertility population's economic status and its demographic health be greatest, and how does that compare to its situation near equilibrium, when it has stopped growing? At what phase of growth would it make the most sense for a commanding oligarchy to invest a subject population's output into the construction of monumental architecture, and would it be wiser to extract tribute in the form of goods or as labor? Does the presence of food storage structures indicate a population better buffered against variability in food supply and thus famine? How should we assess which theory provides the better explanation of human (pre)history: the demographic pessimism of Malthus or the technological optimism of Boserup? Put somewhat differently, what is the relationship among population, economic intensification, and economic surplus? These questions and more like them routinely engage archaeologists.

Here we consider such questions from the perspective of demography and population ecology. The questions pivot on births and deaths and their linkages via human behavior to environment, technology, and labor. Because they involve complex, dynamic interactions, the effects of these linkages—and answers to the questions like those posed just above—can be difficult to predict from intuition alone. Although the political economists Malthus, Ricardo, and others were pursuing such issues in the eighteenth century, as have others since, we will argue in this chapter that they remain potent. They endure despite scientific progress because of their importance. Most importantly, current analytical modeling tools provide new and promising insight into these old problems.

These tools come from the fields of demography and ecology. Demography is the study of population processes in which the rates of birth and death interact to describe how one generation gives rise to another. Demography is closely bound up with environment and modes of life: how people acquire food and material goods, pay tribute and taxes, construct homes and communities, find partners and raise children, age, and die. The relationships often are reciprocal; environment, production, and society affecting rates of birth and death narrowly and evolutionary change more

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broadly. To varying degree, each of these factors leaves imprints via human behavior on the archaeological record. Having information about the ecology and demography of population allows us to mobilize analytical models (Winterhalder 2002) capable of making predictions about the behavior of individuals and the systems in which they reside. We can then evaluate the predictions against the empirical record gained by archaeologists.

We use models, unconsciously or consciously, whenever we formulate research questions, choose methods, or analyze and interpret results; archaeologists do so as well (Kohler and van der Leeuw 2007, p. 4). Whether explicitly acknowledged or not, we impose a model whenever we try to explain the impact of natural, sexual, and cultural selection (Brown and Richerson 2014) on economic organization and intensification, surplus, social evolution, or the formation and persistence or disappearance of societies. Our approach attempts to make such models as explicit as possible. In doing so we make the claim that demography is of little use to evolutionary archaeology unless it is treated in the context of population ecology, with populations understood to be dynamic and interdependent with their environment. Secondarily, this is a claim about the necessity to archaeological research of explicit analytical models.

We begin in Section "Demography, Population, and Environment Since Malthus" with a brief summary of the major steps from Malthus to contemporary approaches. In Section "Modeling Demography and Work in Environmental Context," we describe the state of the art for modeling the linkages between demography and human behavior, focusing on one promising and well-vetted approach. Section "Space-Limited Insights and Their Archaeological Significance" is divided into subsections addressing the applications of this approach to questions with archaeological implications. In Section "From Simulation Models to Evolutionary Archaeology," we describe several recent cases in which archaeologists have integrated these methods into their own work, and in Section "Concluding Thoughts," we summarize.

Demography, Population, and Environment Since Malthus

The demographic arguments of Robert Thomas Malthus (2003 [1798]) are well known, largely for three reasons: they were presented as semiquantitative model, they were embedded in a wealth of data, and the relationship portrayed between geometric potential for population growth and arithmetic development of agricultural production—and the misery this mismatch foretold for the poor—was consequential for social policy. But Malthus recognized that the problems he was addressing were about much more than demography. His argument included an economic element focused on the growing dominance in Europe of markets for labor and food. As population grew, a larger workforce competing for limited jobs would depress wages, while at the same time, growing demand for food in limited supply would push up its price. Although less explicitly modeled, this economic dynamic was as unrelentingly hard on human welfare as the demographic one.

Malthus sometimes is criticized for neglecting ecology, particularly the agroecological base of subsistence. Indeed his early and most widely known writings say little about the role of environment. Nonetheless, Malthus' later diaries of his travels through continental Europe, Scandinavia, and the British Isles show him to be an engaged and acute observer of weather, seasonality, soils, crops, agricultural techniques and yields, and the welfare of the laboring populations engaged in subsistence production. The biographer Mayhew describes these records as Malthus' environmental economics (Mayhew 2014, p. 103–127). Here too Malthus was seeking dynamic understanding, a model by which to work, as he and the economist David Ricardo popularized the concept of the declining marginal returns to agriculture. They were among the first to emphasize that, as production increased, lands of lower and lower suitability came under cultivation and average output consequently declined, substantiating his conviction that agricultural yields could not keep pace with population potential.

The dynamics of a system like the one Malthus described often are fit to a logistic equation, in which the growth rate of the population is a function of how close it is to its carrying capacity. Carrying capacity is defined as the maximum number of individuals that can be sustained in an environment under a particular form of production, often denoted by the letter K. Expressed as an intuition in Malthus, the relationship was formalized by Pierre François Verhulst in 1838 and is often put in the form

$$\frac{\mathrm{d}N}{\mathrm{d}t} = rN_t\left(1 - \frac{N_t}{K}\right),$$

in which N_t is the population size at time t and r is the maximum rate of growth. In prose, the rate of change in the growth of a population of size N with respect to time ($\mathrm{d}N/\mathrm{d}t$) is a function of its maximum rate of growth (r) times its size (N_t) discounted toward zero by proximity to its carrying capacity, K. This saturating function yields an S-shaped population trajectory. While it can be quite useful in the study of chemical reactions and bacterial growth, it is less useful in the study of complex social organisms with the potential to manipulate fertility and modify their environments, like humans.

The logistic has another serious shortcoming: it is entirely phenomenological. By this we mean that it may capture the *pattern* of increase typically for simple populations in laboratory conditions, but it provides little insight into the *mechanisms* that underlie density-dependent growth. That's because key terms like r and K are meaningful only to the degree that they can be translated into observable variables like births, deaths, and the efficiency and sustainability of subsistence production. Without such translation it is difficult to test and interpret the logistic model.

Work in the 1920s by mathematicians Alfred Lotka and Vito Volterra on commercial fisheries was a major advance on the logistic. Instead of fixed values for r and K, they developed models that envisioned each as a variable: the predator or consuming population grew or declined at a rate depending on the density of its prey; the prey, in turn, grew or declined depending on the intensity of its exploitation. Their models and those that followed generate much more complex and potentially realistic interactions, including population booms and crashes, stable cycles, time lags, and differing degrees of persistence and stability. Readers will find an excellent account of these early models in Hutchinson (1978).

Hunter-gatherers are predators on populations of terrestrial game, fowl, fishes, and plants. Their subsistence effectiveness depends on the selective harvesting of the animal and vegetable foods they encounter. Building on Lotka and Volterra, Winterhalder and students (1988; see also Freeman and Anderies 2012; Szulga 2012) modeled a forager population that grew or declined in size as a function of its foraging efficiency. The human foragers in the analysis are linked via an optimal diet selection model to an environment of animal and plant populations with densities that increase or decrease as a function of whether or not they are exploited upon encounter. The model builds toward greater ecological realism by incorporating biological situated variables such as prey density and kilocalorie value and the time required for pursuit and harvesting of resource species. It allows prediction of how diet is affected by changes in consumption needs, climate, or other impacts on prey density or technological developments affecting harvesting efficiency. Implications for conservation biology and sustainability (Winterhalder and Lu 1997) and domestication (Winterhalder and Goland 1997) follow.

With the advent of cultivation and agriculture, humans began extensively to modify their landscape and to undertake direct reproductive and population management of the resources critical to their economy. In an agricultural scenario, the fixed carrying capacity envisioned by Verhulst or the predator-prey dynamics of Lotka and Volterra are no longer suitable. Mathematical biologist Joel Cohen (1995) cataloged long-standing attempts to estimate the Earth's carrying capacity, coming to the conclusion that we are no closer to consensus today than in Malthus' time, for sound reasons. Human carrying capacity is a conditional and changing property, a function of environment, technology, economy, labor, and consumption, all of which vary over time and space. Similar problems plague archaeological attempts to set prehistoric carrying capacities at regional or local scales (Glassow 1978). Even Malthus allowed for slow, linear changes in food availability, fostered by technological developments but handicapped by the declining marginal productivity of the wastelands being opened up to cultivation.

Attention to behavioral and technological innovations that increase food supply is at the core of work by the development economist Ester Boserup (1965). Boserup often is cited as the antidote to the dismal vision of Malthus, of a world dominated by overpopulation and unavoidable hunger. In her 1965 book, *The Conditions of Agricultural Growth*, Boserup focused on relationships between labor, production techniques, and agroecological yields. Low-density populations are well served by extensive systems of shifting cultivation; systems generally are characterized by high yields to labor but low yields per unit of land due to long fallows. Boserup argued that as population density increases, fallow is progressively shortened or even eliminated. This increases the workload of the farmers who must seek higher yields from the same or perhaps even declining amounts of land. The extra human labor goes into soil amendments and the mulching, weeding, and like efforts required as a substitute for the natural regenerative capacity of the system under less intense or less frequent use.

Contrary to Malthus, Boserup describes a model of agricultural intensification in which yield per unit area increases through innovations prompted by increasing human population density. At low densities, farmers can avoid extra work through fallowing, with its extensive demands on land; however, as density increases, they take the option of employing technological innovations and harder work to coax more food from the increasingly limited land available. Boserup's examples emphasize fallow-based intensification, but the analysis is more generally applicable to other forms of technology substitution.

Although it has been remarkably productive (e.g., Morgan 2014), Boserup's model has limitations. It is developed in informal conceptual terms, and some of its elements are, like those of Verhulst, phenomenological and thus difficult to ground in empirical observation. For instance, the Boserup model assumes but does not explain population growth, and it does not describe the mechanisms by which increasing population density spurs intensification or innovation. Supporting evidence has been mixed (compare Kristinsson and Júlíusson 2016; Pacheco-Cobos et al. 2015), although to be fair, no more mixed than that for the Malthusian approach. Nonetheless, Boserup is critical because her analysis gives redress to factors neglected in Malthus, especially to the potential for innovations that escape the confining arithmetic increase that Malthus allowed for agricultural productivity. As a consequence, her approach better fits to historical evidence in which changing methods, such as shortening or lengthening fallow, allow yields to match population, whether it is growing or declining in density.

In 1998 demographic anthropologist James Wood (1998; see also Lee 1986) proposed a model that linked demography and preindustrial economics, to some degree synthesizing Malthus and Boserup. Wood focused on the marginal agricultural productivity of labor, the yield in food per unit of labor for the last worker added to the system. If resources required to produce food are limited, as a population increases in size, ultimately its marginal productivity must fall. The number of mouths to feed increases but each new pair of hands provides less and less additional food. Eventually the system approaches a stable equilibrium defined by the density-dependent effects of "well-being" on rates of fertility and survival. Wood (1998, p. 110) concluded that "left to itself, a preindustrial system of production will tend toward a state in which the average individual is in just good enough condition to replace himself or herself demographically."

By means of this brief historical summary—written from an explicitly "presentist" point of view (Stocking 1968)—we mean to observe that writers since the late eighteenth century have recognized the importance of understanding the causal mechanisms linking environment, demography, production, and society. There is intellectual continuity to this research tradition, from Malthus to present; there also are recent and important changes: (a) we are moving from loosely conceptualized models stated in prose to more formal mathematical conceptualization, susceptible to more disciplined analysis; (b) we have improved our ability to represent the mutual interactions among multiple variables; and (c) we today are more attentive to the possibility that both Malthus and Boserup may be correct, the importance of their respective insights varying with the time and situation, incumbent upon us to appraise.

Modeling Demography and Work in Environmental Context

We divide recent developments in the modeling of ancient populations into two categories: (1) agent-based and (2) analytical models. Agent-based models are based in computer simulation; analytical models are equation-based and may or may not entail simulation. We describe each category briefly.

Agent-based models, exemplified by the work of archaeologist Timothy Kohler, track simulated individuals who follow a set of behavioral rules and interact in a virtual environment. The Village Ecodynamics Project (reviewed in Kohler et al. 2012) uses agent-based models to study the Pueblo people of the American Southwest, creating rules regarding demography, maize agriculture, trade, social organization, and site abandonment in an ecologically realistic environment that suffers droughts and floods and in which animal populations responded to hunting pressure. The modeling efforts provide insight into population trends and the settlement patterns observed in the archaeological record; they also have been applied to questions regarding the emergence of social stratification and cooperation. Kohler and colleagues argue that modeling is an important supplement to traditional archaeological methods:

> [A]s modellers we begin with processes and use computation to reveal the patterns that emerge through time and space. Working in this way … resolves many of the problems associated with intuition and ethnographic analogy, important as these strategies may remain (Kohler et al. 2012, p. 40).

In another example, Tkachenko et al. (2017) develop an agent-based model parameterized to hunter-gatherers and applied to an analysis of the migration from Beringia into the Americas. Lake (2014) reviews the use of agent-based models in archaeology.

Analytical population models typically begin by defining the population's growth rate as a function of one or more environmental variables, for instance, the dynamics of a renewable resource or changes in climate. This equation-based approach can yield mathematical solutions or approximations amenable to determination of key properties like equilibrium conditions and their stability, a major advantage. For instance, the economists Brander and Taylor (1998) model the rise and fall of Easter Island's population in response to the human rate of forest destruction, an exercise that inspired a generation of responses. Roman et al. (2017) formulate a model of the Classic Maya in which the population may allocate labor resources among swidden, rain-fed intensive agriculture, and monument construction. Each of these three occupations is tracked separately. The authors conclude that drought most likely played only a minor role in the depopulation of Maya urban centers. Purely analytical approaches tend to focus on techniques that may be difficult for the mathematically uninitiated to parse. Nonetheless, significant progress in analytical models that speak to archaeological questions have come from the fields of economics, population biology, and theoretical ecology (e.g., Anderies 2000; Kögel and Prskawetz 2001; review in Nagase and Uehara 2011).

Inspired by intellectual traditions emerging from Malthus and Boserup, and building on Wood (1998), theoretical population biologist Shripad Tuljapurkar and members of his lab at Stanford have created an explicit analytical model of the basic relationships between human demography, population, work, and agroecological environment (Lee and Tuljapurkar 2008; Puleston and Tuljapurkar 2008; Lee et al. 2009; our Fig. 16.1). We follow this analytical research tradition, based in mathematical solutions, approximations, and simulation, for the remainder of the chapter.

Tuljapurkar's "food-limited demography" approach refines Wood's concept of well-being with a more concrete mathematical relationship, the "food ratio," or E. E is defined as the kilocalories

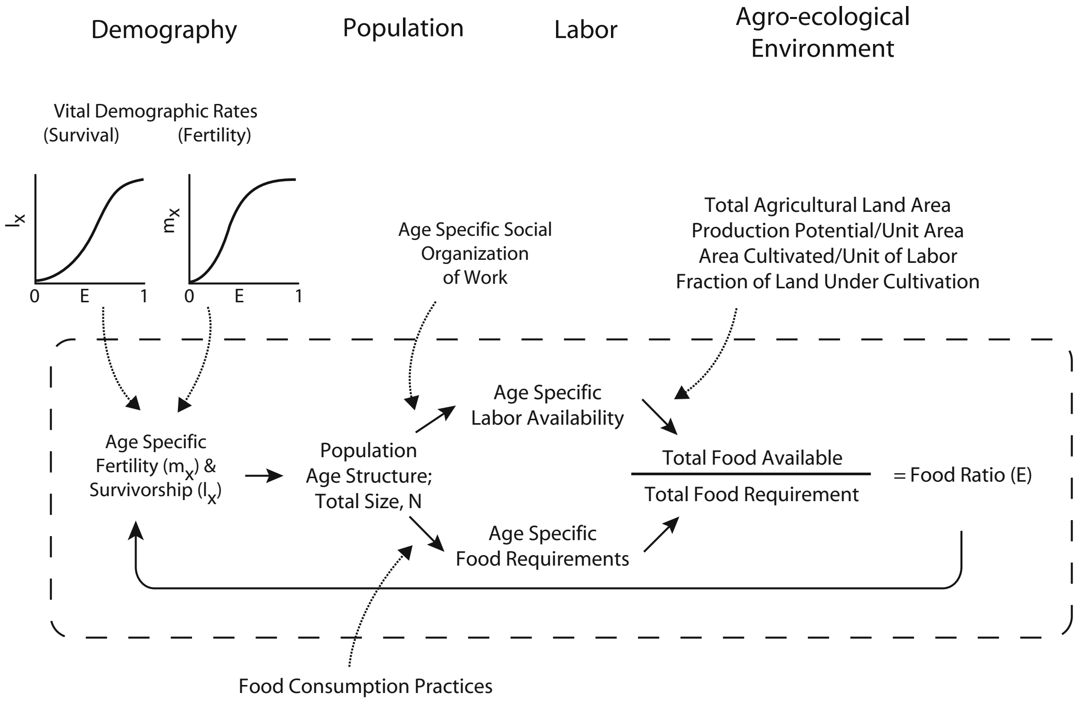

Fig. 16.1 The space-limited population ecology model. Core components of the model and their causal connections (solid arrows) are shown within the dashed line rectangle. Demographic, biosocial, and agroecological factors determining the form and parameter values assigned to those core components are shown around the circumference, with dotted arrows indicating their point of action. We provide a step-by-step description of one iteration through the core components in the text; a more complete description of the mathematical and programming details can be found in Puleston et al. (2014) and references therein

available to individuals in a population as a fraction of the kilocalories required to keep their fertility and survival at levels undiminished by hunger. If the food ratio is 1, then there is exactly enough food to avoid the demographic effects of kilocalorie shortfalls. If $E < 1$, then the population growth rate is diminished due to corresponding decreases in fertility and increasing mortality. If $E > 1$, the population has food kilocalories in excess of need, but the excess does not affect vital rates; births and deaths and thus the growth rate are unaffected. The model relies on specific functions parameterized from studies of famine to delineate the effect of hunger ($E < 1$) on vital rates (Box 16.1).

Box 16.1: A Model of Food- and Space-Limited Population Growth

Population dynamics hinge on the balance of food production and consumption. Production is calculated from a function tracking the fraction of available land in actual cultivation (called F, unitless and ranging from 0 to 1), which is multiplied by the product of total arable land (A_m, in ha) and the yield (Y, in kcal/ha/day). F is usually expressed as a saturating exponential function of the form

$$F = 1 - e^{-\frac{HkN\phi}{A_m}}$$

(continued)

Box 16.1 (continued)

where H is the number of hours an individual of the most productive working age devotes to agriculture and k is the conversion from worker-hours to area cultivated (ha/worker-hour). Note that this expression of H is in terms of working-aged individuals, regardless of sex or other designation. If there is a division of labor, then H would be multiplied by the fraction of individuals engaged in agriculture. N is the total agricultural population size. The variable ϕ is the average age-weighted labor contribution, relative to the most productive age class. It is also weighted by the age structure of the population to provide a measure similar to the dependency ratio but reflecting a producer ratio instead. It can be expressed as the dot product of the vector of relative worker productivity by age ($\boldsymbol{\phi}$, ranging from 0 to 1) and the population structure vector ($\mathbf{u}$, whose elements sum to 1): $\phi = <\boldsymbol{\phi},\mathbf{u}>$. The product $N\phi$ represents the number of equivalent high-quality workers in the population, and the ratio in the exponent within F represents the maximum area the population could farm with the labor available to it, as a fraction of the total arable area. These elements allow the calculation of total production, in kcal/day:

$$\text{Production} = Y A_m F.$$

The amount of food necessary to avoid hunger and maximize fertility and survival also depends on the age structure of the population:

$$\text{Baseline consumption} = J N \rho,$$

where J is the calories required to feed the most energetic age class without diminishing vital rates and ρ is the age- and structure-weighted relative need. Similar to ϕ, but representing the caloric needs of a typical individual in the population, $\rho = <\boldsymbol{\rho},\mathbf{u}>$, where $\boldsymbol{\rho}$ is a vector of age-specific caloric need, as a fraction of the neediest class. This variable ranges from 0 to 1.

The food ratio is the ratio of realized production to baseline consumption, where "baseline" refers to the case where there is no reduction in demographic rates due to hunger:

$$E = \frac{Y A_m F}{J N \rho}.$$

The population in the following year can be calculated from the current one through the effect of E on the age-specific rates of fertility ($m_x(E)$) and survival ($p_x(E)$), where x represents the annual age class. In practical terms this is easiest done through software that allows the construction of a population projection matrix. R code to do these calculations was written by the Winterhalder lab and is available at github.com/puleston/spacelim.

Once the equilibrium food ratio has been determined (or approximated), it can be used to calculate the equilibrium population size:

$$\widehat{N}_m = \frac{A_m}{\left(Hk\widehat{\phi}\right)\log\left(\frac{\widehat{E}_m}{\widehat{E}}\right)},$$

where $\widehat{\phi}$ is the value of ϕ, the worker ratio, determined using the equilibrium population structure, and $\widehat{E}_m = YHk\widehat{\phi}/J\widehat{\rho}$, representing the theoretical maximum of the food ratio, given equilibrium population structure. Here $\widehat{\rho}$ is the value of ρ, the consumption ratio, calculated from the equilibrium population structure. The equilibrium population structure $\widehat{\mathbf{u}}$ is determined from the equilibrium food ratio and the responsiveness of fertility and survival rates to hunger.

The first paper in the Tuljapurkar series describes and interprets the basic food-limited case in which a population may expand into infinite space. The second examines the dynamics of a food-limited population within a finite or space-limited agricultural landscape, and the third analyzes the effects on the model of environmental stochasticity. The series is parameterized to represent the dryland sweet potato field system on the Kohala Peninsula of Hawai'i Island (USA) in the time before European contact (Kirch et al. 2012). Subsequent analyses usually have taken these parameters as defaults, generally representative of demographic and agroecological conditions in prehistory, while adjusting them selectively to explore new questions. The reader should consult the original papers for further technical details.

In application the space-limited approach to preindustrial agricultural population ecology is employed as an iterative computer-based simulation, each cycle representing an annual time step. The core feedback loop is represented within the dashed line in Fig. 16.1. A description of the model's dynamics can begin with the population's total size, N, and its age structure, the latter indexed in 1-year increments. Knowing the parameter values of the age-specific food requirements, the program calculates a total food requirement. At the same time, using assumptions about the age-specific social organization of work, it calculates age-specific labor availability and its total. The total food available, the comestible agricultural output, is calculated using information about labor and the agroecological environment of production. This calculation is based on the total area cultivated by the labor available and the production potential per unit area. The total food requirement relative to total food available completes calculation of the food ratio, E.

Moving around to the left side of Fig. 16.1, E then determines age-specific fertilities and mortality rates achieved by the population's subsistence efforts, updating with new births and deaths the age-specific groups that comprise the total population, N. The general shapes of the relationships between survival and fertility and food availability for $E \leq 1$ are shown in the upper left of Fig. 16.1.

The space-limited model tracks age structure, but it does not track sex for purposes of work, consumption, births, or mortality. Following the practices of single-sex demography, we adjust by allowing only half of the fertile age classes to give birth. Because the model calculates age-specific birth and death rates, it does allow us to track several standard measures of population welfare, such as food availability, total fertility rate, average life span, and survival to a particular age (Fig. 3 in Puleston et al. 2014).

The simulation allows us to represent socio-cultural determinants of subsistence work by specifying what fraction of the available labor by age group is engaged in agriculture. In the agroecological environment component, the model uses a conversion from labor (in hours per day) into an area of land cultivated. This can be made conditional on the technologies available, the environment, and the method and nature of cultivation employed. Assuming labor is applied at its maximum efficiency, this determines the greatest cultivable area. Total food production, based on potential yields per unit area of land, can be set to represent environmental features such as climate and soils.

In the space-limited case that we describe here, land is finite (total agricultural land area). As more of it gets put into use, the efficiency of production decreases as a consequence of competitive inefficiencies. This is calculated using the fraction of land under cultivation. While the population is small, each new farmer has little trouble finding and utilizing an accessible, salubrious, contiguous, and unoccupied plot. But, as the landscape begins to fill up, this becomes more difficult. In terms adopted by Wood (1998), this captures the declining marginal productivity of labor. However, we might also reach back further to Malthus and Ricardo and take it to represent the declining marginal productivity of land. In Box 16.1 we provide a more formal, mathematical description of this and other model elements.

Set upon a course of population growth, this system ultimately achieves a stable equilibrium at which births and deaths balance and population ceases to grow. At this equilibrium an additional individual cannot provide food sufficient to meet her/his needs. The food ratio at which this occurs cannot be derived analytically, but it can be approximated (Eq. (6) in Puleston and Tuljapurkar 2008) or determined numerically. Using the native Hawaiian population parameters mentioned earlier, found in Lee and Tuljapurkar (2008), the equilibrium food ratio, or $\hat{E}$, is 0.67. Given fertility and survival rates reasonable for a preindustrial agricultural population, and food distributed proportional to need, at the Malthusian equilibrium, individuals would be subsisting on a diet of 67% of the kilocalories they would need for maximal fertility and survival. Once the equilibrium food ratio has been determined, it can be used to find the equilibrium population size. This maximum sustainable population depends on the cultivable area available, its productivity under agriculture, and assumptions about labor. This dependence on context makes it a *variable*; unlike carrying capacity (K), it is not stated a priori.

The various components of the food-limited approach are amenable to modification; versatility is one of its virtues. Considered in terms of our earlier history, it links demography, in the form of statements about fertility and mortality, to population dynamics over time, in the form of size, density, and age structure, and finally, to agroecology, represented by environmental potential of land as realized through social organization of labor, food production, and consumption. The interactions of these parameters and variables are represented in quantitative terms and may be modeled as a time series. Importantly, many of the parameters and variables we have described are empirically observable and measureable, not abstractions. The approach has been used to examine population growth trajectories, their phases and timing (Puleston et al. 2014), the potential for agricultural taxation in prehistoric states and its impact on the welfare of the farming population (Puleston and Tuljapurkar 2008; Winterhalder and Puleston 2018), and the risk-minimizing utility of storage facilities in a variable environment (Winterhalder et al. 2015). Extensions to more fully bring Boserupian processes into the model are possible. The availability of enhanced mathematical methods such as Leslie matrices and computational programing resources such as MATLAB® allow us to simulate the outcome of multiple interacting variables. Malthus knew of their mutual significance, but he must scarcely have imagined possibilities for their dynamic synthesis.

Space-Limited Insights and Their Archaeological Significance

Properties of a Population Growth Trajectory

An important result of this approach is more detailed and realistic insight into the growth trajectories of founding populations or those recovering from a significant population decline. The founder case, for instance, might be a small group of Polynesian voyaging canoes with a mixed-sex crew landing on an unoccupied island. We would like to know how long it takes for the population to fill the agricultural space available to it and its experience as it increases in size and approaches and then reaches zero net growth. The space-limited approach is well suited to this type of investigation. In Fig. 16.2 we assume an egalitarian population in a constant environment large enough and sufficiently productive to allow a larger population than the initial number of settlers. No migrants arrive after the founders and the age-specific allocation of work is fixed, as are agroecological methods and technology. We of course could elect to vary any of these fixed conditions to explore model predictions more broadly. For the moment, however, we choose to make the simplifying ceteris paribus assumption (keeping all else constant, see Boyer 1995) in order to focus on the underlying patterns.

Having landed in a salubrious environment with 1000 ha of arable land available, the earliest colonizers ($N = 20$) are able easily to meet their subsistence needs. Their vital rates are not diminished by food shortfalls or the effects of hunger. This period of growth, when $E \geq 1$, we call the *copial* phase (Fig. 16.2, white phase bar labeled (c)). As measured by infant mortality, life expectancy, and the absence of hunger, quality of life is high. Total food production is limited by the size of the labor pool, but the population is capable of covering its consumption and producing a surplus, food in

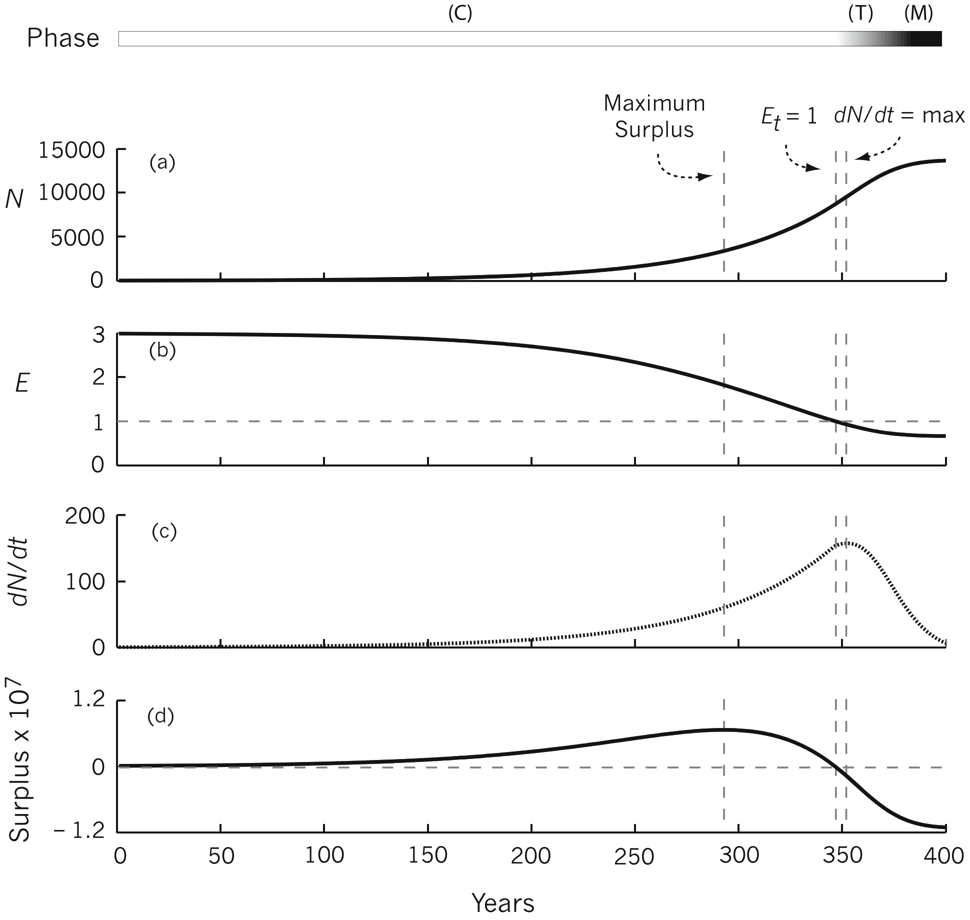

Fig. 16.2 The space-limited population growth trajectory. The simulation begins with a founding population of $N = 20$ occupying a frontier with 1000 ha of arable land. Panel (**a**) shows the population growth time series, N; (**b**) shows the value of the food ratio, E, the variable determining vital rates; (**c**) shows the instantaneous rate of change in N as a function of time, i.e., whether growth is accelerating or decelerating; and, (**d**) depicts the capacity of the population to produce a surplus, given constant work effort. The copial (C, white), transitional (T, increasing gray), and Malthusian (M, black) phases of the trajectory are demarcated at the top. Not depicted: the Malthusian phase would continue indefinitely unless behavior changed or the system was disturbed in some manner. Further details in the text

excess of the amount needed to avoid hunger. The general condition is one of abundance, even as key variables are changing.

As the population moves through the copial phase, the food ratio (panel b) remains >1 although it is dropping continuously as the population expands. E first falls below 1 in year 347, signaling the initiation of shortfalls. The copial phase founding population grows in total size very slowly for almost half of the 400-year series shown, then at a more rapidly accelerating pace until year 352. Year 352 marks the inflection point in curve (a) and the last increment of positive acceleration in the rate of change (c). There is a 5-year lag between the onset of hunger and deceleration of growth due to age structure effects.

The *transition* phase (Fig. 16.2, T) begins with the first experience of hunger in year 347. The food ratio has dropped below 1 and the growth rate begins to decline. The transition phase typically passes quickly, and the drop in quality of life measures is remarkably abrupt (Puleston et al. 2014). From abundance, it takes on only two to three generations for the population to reach an experience of hunger so severe that life spans of 45 years under copial conditions have fallen to 30 years by the transition's end. The number of live births to a woman who lives through her childbearing years falls by more than half. The transition ends with growth rate stabilized at an effective value of zero.

The third and final phase of the population trajectory is the *Malthusian* phase (M). The population is at or very near its equilibrium size of 13,509; food availability is two-thirds of that which would sustain optimal vital rates ($\hat{E} = 0.67$). Without some external perturbation or changes in environment or the population's behavior, this state would continue indefinitely. The Malthusian population is generally larger than predicted by a simple conversion of potential calories to people because such calculations typically assume everyone in the population is fully fed ($\hat{E} = 1$) and the level of food required sometimes is not adjusted for subadult age classes.

Our last panel (d) traces surplus production under the assumption of constant agricultural work effort, set to 5 h/day for all working-age individuals, over the full period of growth. We recognize that constant effort may be counterfactual if Chayanov (1977) is correct that peasants expend only as much subsistence effort as is needed to adequately supply their households. Nonetheless, it is useful as a modeling assumption for revealing key dynamics and potentials. As it expands, population begins to produce more food than it consumes. This surplus peaks at year 293 and drops to zero at year 347, when E falls below 1. It becomes negative thereafter. A counterintuitive result of the model is that a population's potential to generate a surplus with modest effort, not entailing a reduction in demographic welfare, is at its maximum when the population is quite small, only 25% of its ultimate size (3382 of 13,509) and nearly a century before it reaches its maximum size.

Some of the more interesting and robust results of this approach regard the timing of these phases (Fig. 16.2, Phase bar). Under a wide range of starting assumptions, the copial phase (C) lasts about 350 years, meaning that some 14 generations live and grow free of hunger-driven reductions in vital rates. The dramatic impact of the transition phase (T) suggests that founding populations are at risk of an endogenously generated crisis beginning approximately 350 years after their arrival. A population that has spent many generations in a state of sufficiency, if not plenty, is forced suddenly to confront serious shortfalls.

These patterns are quite different from those predicted by the phenomenological Verhulst-style, logistic approach. In the Verhulst conceptualization, a founding population would experience a continuously increasing "pressure" from the moment it arrives, a pressure set ultimately by an assigned carrying capacity (K). For a population starting from zero, the inflection point in the S-shaped growth curve is predetermined to be midway from the initiation to the conclusion of its growth; this also is the point of maximal sustainable yield (Winterhalder et al. 1988). K is not easily tied to specific properties of demography, work, or environment, making case-specific empirical assessment and interpretation difficult. By contrast, in the space-limited approach, the more significant demographic events occur late in the growth period; they are not gradual, but are disruptively abrupt; and they are not predetermined by an a priori parameter like K, but are emergent from observable properties of vital rates, labor, and the environment of agroecological production.

We predict that a small agricultural population arriving in a geographically circumscribed area of anything but the meanest agroecological potential should be able to grow at maximum rates for approximately 350 years. This will be followed by approximately 50 years of difficult transition to a replacement growth rate and equilibrium. This 400-year span is robust across wide ranges of the size of the founding population and the area of available for agriculture (Puleston et al. 2014). The prehistoric settlement of Pacific islands represents an ideal situation in which to assess this pattern and timing; the results are encouraging. Researchers have found evidence in multiple locations of a crisis or transition, occurring approximately 400 years after initial settlement. Archaeologist Pat Kirch describes three separate studies of early Hawaiian populations that are consistent with the pattern of Fig. 16.2 (2012, pp. 164–168). In agreement with the early work of archaeologist Bob Hommon (1976), Kirch finds that the richer agricultural regions were occupied first, and they become fully utilized within about 400 years. At this point settlement and land use patterns shift to less productive and more labor-intensive agricultural zones. Referring to growth trajectories that began about 1100 AD Kirch writes:

> The transition to the second phase of Hawaiian demographic history may have occurred rapidly. By approximately 1500, high-density levels had been achieved over all the best agricultural lands. Marginal leeward slopes in areas like Kahikinui, and Kohala on Hawai'i Island were already being converted into vast rain-fed agricultural field systems. The rate of population growth began to fall dramatically until it leveled off, closer to a steady replacement rate. (Kirch 2012, p. 169)

Likewise, Rapa Nui (Easter Island) was probably settled at about 1200 AD (Hunt and Lipo 2008) and saw rapid expansion in land use, as evidenced by the summed probability densities of obsidian hydration-dated material, until between 1600 and1700 AD (Stevenson et al. 2015). After 1600 the population appears to halt its expansion into more marginal areas and even begins to abandon them, shifting its efforts to make more intensive use of productive lands. The pattern suggests that the behaviors regarding settlement and land use that were dominant for the first 400 years were fairly quickly replaced in the century following. Opportunities to observe founding population and their subsequent growth with closely documented archaeological evidence are rare, and examples such as these increase our confidence in the dynamics and parameter values of the space-limited model.

Population in an Unpredictably Variable Environment

Various features of human subsistence behavior likely are adaptations to reduce the hazards of food shortfalls caused by stochastic variability in environmental factors affecting subsistence production. An example is central place food sharing by hunter-gatherers (Jaeggi and Gurven 2013); another is dispersion by an agricultural household of small field plots over an agricultural landscape in order to minimize the likelihood that localized environmental insults like a hailstorm can affect all of them at once (Goland 1993). Such behaviors can be quite effective in mitigating unpredictable food shortfalls (Winterhalder 1990), but they can also be unavailable or fail. We can investigate the consequences of such failure for population welfare by modifying the space-limited model to incorporate stochastic yields. We change the parameter potential production/unit area (Fig. 16.1) from a fixed value to one randomly drawn at each iteration of the model from a distribution of possible values. The average yield is kept the same. The resulting simulations suggest that environmental variability can have profound and sometimes counterintuitive effects on human population dynamics and welfare (Table 16.1).

These patterns emerge (Table 16.1; Fig. 16.3). If environmental productivity is stochastic instead of constant, mean long-run population size declines even though mean long-run yield remains unchanged. The magnitude of this decline is a function of the magnitude of the environmental variation. At the same time, long-term average food availability, measured by the food ratio, E, actually *increases* with a fluctuating food supply. Average measures of welfare such as life span also improve. At first encounter these results appear paradoxical; how can the affliction of randomly fluctuating harvests improve a population's average welfare? The explanation lies in the interactional dynamics of environment and demography. We assume for illustration that environmental yield varies according to a symmetrical distribution, production shortfalls of a particular degree having the same odds as surfeits of that degree. If this is the case, the demographic response generally is *not* symmetrical due to differential response rates of mortality and fertility in the face of shortfall and abundance. Population size can fall quickly but it recovers only slowly.

With the population at equilibrium, any food shortfall is the equivalent of famine; it suppresses reproduction and elevates mortality, perhaps strikingly. A decline in total population pushes it back toward and perhaps well into the copial phase where food is abundant and welfare high. Once the shortfall has abated, renewed growth starts moving the population back toward equilibrium, but recovery occurs at its usual slow pace (Fig. 16.2a). The return of Malthusian conditions may be

Table 16.1 The effects of storage. The table summarizes the results of multiple iterations of the space-limited model under various assumptions regarding the ability of the population to store surplus food, and presence of obligatory set-asides (e.g., seed or tribute) in the face of yield variability

Condition	Storage	E	N	Frac $E > 1$	e_0 (years)	Death rate	Granary (kcal/year)
Baseline (non-stochastic)	No	0.67	13,509	0.00	30.0	0.033	–
Stochastic CV = 0.3; no set-aside	No	0.85 (0.31)	10,565 (0.10)	0.26	35.3 (0.34)	0.033(0.83)	–
	Yes	0.87 (0.34)	11,208 (0.11)	0.29	35.4 (0.34)	0.033 (0.85)	6.11×10^8 (2.32)
Stochastic CV = 0.3; 22% set-aside	No	1.06 (0.43)	6058 (0.25)	0.50	37.9 (0.31)	0.033(1.28)	–
	Yes	1.11 (0.49)	7970 (0.16)	0.51	37.8 (0.32)	0.033 (1.25)	1.46×10^9 (1.48)

Notes: "set-aside" refers to any food produced but not available for consumption, including that stored as seed and that given as tribute. "Frac $E > 1$" is the fraction of years in which production exceeds need. e_0 is life expectancy at birth. Death rate is the number of annual deaths divided by the size of the population at the start of that year. Numbers in parentheses are standard deviations.

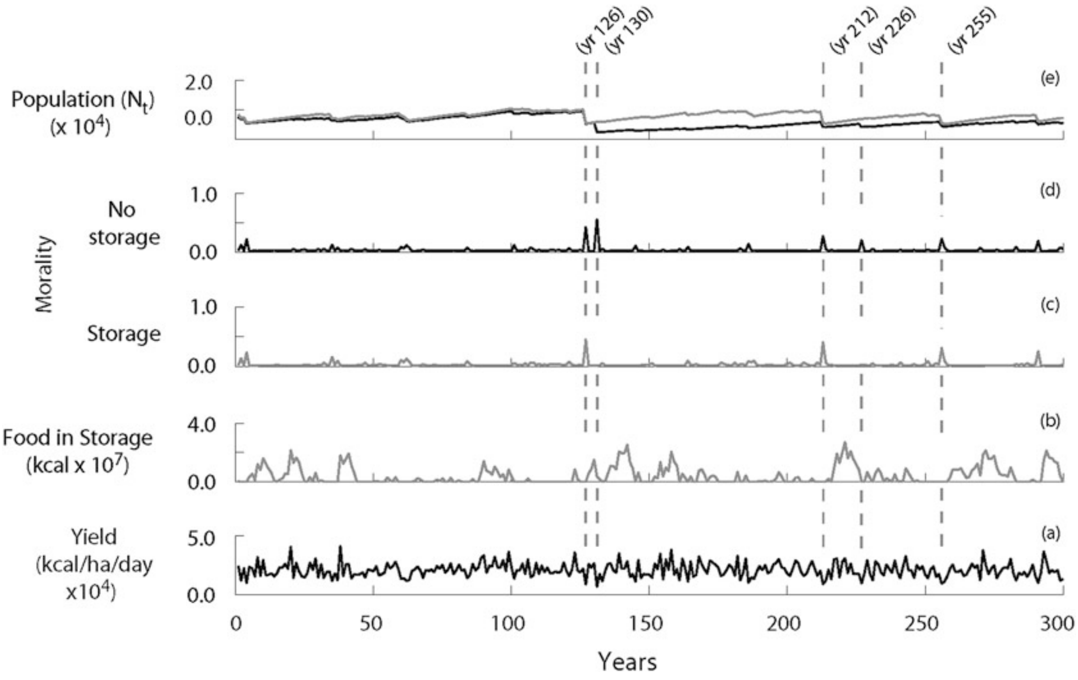

Fig. 16.3 A time series of near-equilibrium population dynamics given unpredictable variability in yields, for populations that do or do not practice inter-annual food storage. To represent environmental variability, yields (production potential/unit area; Fig. 16.1) are drawn randomly from a symmetrical gamma distribution with a mean yield of 21,000 kcal/ha/day and a CV of 0.3 (panel **a**). Panel (**b**) shows the amount of food in storage, a function of whether or not the preceding several years' harvests provided a normal surplus. The spikes in panels **c** (storage) and **d** (no storage) indicate the magnitude of famine-induced mortality associated with years of particularly low agricultural yields. Finally, panel **e** traces the population history of the food-storing group (gray) and the group not storing food (black). The years and events highlighted by vertical dashed lines are described in the text; more detailed interpretation and mathematical and programming details can be found in Winterhalder et al. (2015)

many years in the future. Periodic famines are punctuated events that suppress population size and result in higher welfare for the majority of copial, non-famine years. Even moderate environmental stochasticity, such as a yield coefficient of variation of 0.2, is enough to regularly drive a population from Malthusian back into copial phase conditions. Of course, a year or two of serious famine is a disaster for those experiencing it, but it may be followed by generations of relative prosperity for the survivors. This dynamic inverts normal sensibilities. Benign environments, continuously salubrious one year to the next, may be the most continuously ruthless in imposing the miseries of Malthusian conditions.

Inter-annual storage of surplus in early agricultural societies is thought to have offered preindustrial populations a degree of risk-minimizing control over food availability in variable environments (Halstead and O'Shea 1989). While this may be the case in some contexts, the benefits to a population living near or at its Malthusian equilibrium can be fickle. In a further modification to the stochastic version of the space-limited model, we allow the population to store excess food in years of high production and to withdraw food from those stores to help meet needs in years of production shortfall. This can stabilize the total food available (Fig. 16.1) and thus elevate the average size of the population and its average well-being (Winterhalder et al. 2015). The magnitude of these effects increases with increasing variability in yields.

The general result gives support to the idea that storage is adaptive, but examination of the specifics reveals important qualifications. For instance, if several years of mediocre yields or shortfalls cluster together, there may be no excess of food with which to replenish depleted stores; granaries sometimes are empty, offering no protection. Further, the observed improvement in well-being from storage may result not from the availability of a buffer against famine but as a consequence of famines being *more severe*. The coincidence of an unusually large population, its size enhanced by years of successful use of storage, and a particularly severe shortfall exposes the population to fewer but more deadly famines. The shortfall will be especially acute if harvests immediately prior to the famine have not filled the granaries. Severe mortality spikes can reset the population far into the earliest reaches of the copial phase, in which for a long period food again will be plentiful and welfare high. Storage can abet the paradox that we observed earlier. It may improve the long-run subsistence and demographic welfare of a population not by consistently preventing crises but by ensuring that the rare crisis, when it occurs, is more deadly.

We summarize in Table 16.1 by comparing demographic properties of our baseline scenario at Malthusian equilibrium (see Fig. 16.2) with those derived from the last 300 years of ten 700-year simulations with stochastic yields. We focus on a sample period late in the simulation in order to get past effects of initial conditions and to approximate the same time frame as the enduring Malthusian equilibrium of the non-stochastic case. Our comparisons set the yield coefficient of variation (CV) at 0.3, with and without a fixed set-aside for seed and/or taxes. Stochasticity and, independently, storage increase the average food ratio (E). Stochasticity and set-asides both reduce average population size (N), whereas storage independently has a positive effect. The average food ratio (E) and, indeed, the fraction of years the population experiences an adequate food supply (Frac $E > 1$) is elevated by stochasticity and, independently, by set-asides and storage. The average risk of death in each of the scenarios is the same, although variability is not. While overall mortality remains constant, that risk can be more or less concentrated in time as a function of famine frequency and severity.

Figure 16.3 illustrates a single of the 300-year time series, chosen to illustrate the impact of storage on system dynamics. The distribution of randomly drawn (independent and identically distributed) agroecological yields is depicted in panel (a). Panel (b) shows the amount of food held in storage at the point of inter-annual carry-over, just prior to a new harvest. With unpredictable yield variability, granaries often are empty or hold only small reserves; years of ample storage tend to occur in clusters of approximately 10 years duration. Panels (c) and (d) record population mortality with and without storage, respectively, and panel (e) traces the size of the resulting populations, with storage (gray) and without (black).

In these three centuries of simulation, there were 5 years of particularly bad agricultural yields (years 126, 130, 212, 226, 255). Crop failures in years 130 and 226 follow periods in which stored foods have accumulated, the reserves successfully buffering the production shortfall, thus eliminating for the provident the mortality spike affecting the population without storage. However, bad harvests in years 126, 212, and 255 follow on mediocre yields which have left the granaries empty or nearly so; the provident suffer as well. Perhaps ironically, the mortality spike actually is greater for the food-storing population in years 212 and 255. Being larger size, the food-storing population actually is more susceptible when the famine occurs. From the start of the time series through the famine in year 126, the two populations track one another closely in size. However, the non-storing population has the bad luck to suffer a second mortality spike in year 130, and, growth being slow, it remains smaller through the last 170 years despite the greater impact on the food-storing group of poor yields years 212 and 255. This time series reinforces generalizations we described earlier, and it demonstrates how chance events in unlikely combinations impart unique histories to population dynamics.

Modeling Sociocultural Determinants of Vital Rates

So far we have modeled a natural fertility and mortality population, one not exercising voluntary control over vital rates. The impacts food shortfalls are experienced through what Malthus would call “positive” checks, those acting after an increase has resulted in exposure to disease, malnutrition, or hunger. Positive checks generally are characterized as physiological. It is possible, however, that early societies developed sociocultural norms and practices affecting fertility and survival by age. Delay of marriage or fertility exposure would be an example. Malthus would call this a “preventive” check, one acting *before* fertility is limited by hunger. We can represent preventive checks in the space-limited model by altering the curves (see Fig. 16.1) representing the *elasticities* of fertility and survival relative to food availability. An elasticity is a measure of the sensitivity of one variable to another, weighted to convey a proportional response. An elasticity of 1, for example, means that a 10% increase in a particular parameter (or variable) results in a 10% increase in the variable of interest; an elasticity of 0.5 means the same 10% parameter increase yields a 5% increase in the response variable. Elasticities may be negative, indicating an antagonistic response.

The elasticities of age-specific fertility and survival adopted in the resource-limited model could be formed so that they affect fertility at levels of subsistence production well above the experience of hunger, that is, at $E > 1$. For instance, with refinement such a scenario could be used to model demographic transitions. We, however, continue to focus on responses after E falls below 1. If the elasticity of the fertility response is increased to represent volitional suppression of fertility in hard times, there of course is no change in the copial phase of growth. But as soon as the population enters the transition phase, realized fertility begins to fall more quickly than it would in the default scenario, in which fertility remains unconstrained. This leads to a number of changes at equilibrium. The population is smaller and it is less hungry, suffers less infant mortality, and has a longer life expectancy. We could in fact make the elasticities of fertility large enough that the population equilibrates almost immediately after crossing into the transition phase, coming to equilibrium with only a limited impact on diet.

Puleston et al. (2017) included such a scenario in simulations of the maximum population on Rapa Nui (Easter Island) before European contact. Rapa Nui is an iconic (Diamond 2005) and contested (Hunt and Lipo 2009; Mulrooney et al. 2010) example of societal collapse due to unrestrained ecological exploitation. This debate makes it critical to understand the size and demographic circumstances of the Island’s population over time. Puleston and his co-authors find that, with near-perfect fertility control and egalitarian subsistence, the maximum island population size is reduced by an average of 37%, relative to a population without such control. The simulations show that infanticide, documented in some populations as a response to scarcity of resources (Smith and Smith 1994), has an almost identical demographic signature to fertility control acting before conception. In effect, it would be difficult to distinguish these mechanisms for fertility control from population data.

Population equilibrium is achieved by the convergence of birth and death rates. While we usually imagine sociocultural controls as targeting fertility, it is worth considering how behavioral responses to hunger might affect age-specific rates of morality across the life span. Food can be withheld as well as foregone. Ethnographic accounts of contemporary nonindustrial populations suggest that exiling, abandonment, or killing of the elderly in situations that include resource shortages is mentioned in 20–30% of societies examined (Foner 1993), although details understandably are scarce. Lacking good data, we nonetheless can use our food-limited model to examine the population dynamics of socially induced mortality. It comes as a relief to your authors that the long-term, population welfare benefits of systematic geronticide are minimal, particularly when weighed against the potential social and personal costs (Puleston and Tuljapurkar 2008). Geronticide has no effect on the equilibrium experience of hunger, it generates a very small decrease in equilibrium population size, and it results in a small reduction in the average age of the population, as older individuals are supplanted at equilibrium by younger ones. This of course is a largely hypothetical exercise, but it reveals that fertility control will be much more effective as a long-term population control measure than will geronticide.

Surplus, Taxation, and Sociopolitical Hierarchy

The space-limited model also can be modified to address issues arising in the study of social evolution, such as the origins of social differentiation and political stratification. As an example, we focus on the impact on agrarian producers of taxes extracted by political authorities (Winterhalder and Puleston 2018). We use "tax" as a gloss for any form of taking of goods or labor, such as tallage, tribute, or corvée, and, for simplicity, we focus on net loss incurred by producers after any return to them through redistribution. What is taxed disappears from the system being analyzed, whatever benefits it may provide to the offstage apparatus of the state.

Theories about the origins of political hierarchy often incorporate the concept of surplus, the definition and nature of which has spurred impassioned debate (e.g., Pearson 1957; Harris 1959, current review in Morehart and de Lucia 2015). From a dynamic population ecology perspective, the focus of these debates on the ways in which surplus is extracted and its political uses once available to a polity is incomplete. It misses essential parts of a dynamic system. Agrarian producers provide the work, but they necessarily are consumers, their labor capacity is not uniform, and they come with families and households of old and young of both sexes who are products of cross-generational patterns of population growth and replacement. Adaptations of the space-limited model help us to take account of these features while also defining in more precise terms the relationship between the extraction of goods and/or labor, the impacts on the agricultural class, and, ultimately, the consequences for the dependent political class.

We define the normal surplus as production of food in excess of an operational conception of need, corresponding in our model with production in excess of that required to make at least $E = 1$. This only can occur in the initial copial phase of growth or in subsequent repetitions of the copial phase induced perhaps by environmental variability. To produce a normal surplus, the agricultural population may be required to expend extra labor effort, but they do not otherwise suffer a diminished quality of life as measured by food sufficiency or demographic indicators. As we noted above, the copial surplus can be significant with modest effort; it is maximized when the producer population is still relatively small, about 25% of its equilibrium size and between 250 and 300 years into its growth (Winterhalder and Puleston 2018). At this point the marginal agricultural productivity of labor is high, and the total consumption requirement of the worker population is relatively low.

Although the peak of this normal surplus is fairly broad and thus prolonged (Fig. 16.2d), an excess of food above $E = 1$ is ephemeral. The agrarian population is well fed and thus continues to grow toward its Malthusian equilibrium. As the marginal productivity of labor falls while the population's consumption requirements climb, the normal surplus is extinguished.

The normal surplus may nonetheless be an overlooked but important element in social evolution. Allen (1997), for instance, downplays the importance of population in the development of the Upper Egyptian state because its realm was underpopulated at the time. Our modeling suggests the contrary possibility. Relative underpopulation may have been key in providing a significant normal surplus which could be taxed without severe impacts on the welfare of the agrarian population (discussion in Winterhalder and Puleston 2018), surplus that was critical in underwriting state development.

At the Malthusian equilibrium, elite resource extraction has different characteristics than in the copial phase. For this reason we avoid in this circumstance the word surplus. In a constant Malthusian situation, taxation causes the producer population to be smaller, as fewer resources are available to feed it. The demographic state of well-being at equilibrium and particularly its poor measures of demographic welfare remain unchanged (Puleston and Tuljapurkar 2008). Taxation reduces stable population size but it does not affect an already poor quality of life.

Under Malthusian conditions there exists an intermediate optimum at which the total tax that can be collected from an agrarian population is maximized. We explain with reference to Fig. 16.4. The two x-axes depict the inverse relationship between a per capita tax rate, from zero to 6000 kcal/person/day, and the associated equilibrium population density. If taxes are zero, we recover the population of 13,509, its full equilibrium size (see Fig. 16.2); as taxes remove ever greater amounts of production, the agrarian population becomes less and less able to feed itself, and its numbers necessarily must diminish. Focusing on equilibrium outcomes, the product of the size of the population and the per capita rate of taxation generates a parabolic-like curve of total tax collected. Given our baseline parameter values, this curve peaks at a population of 4507, a tax rate of 2119 kcal/individual/day, and it generates an elite income of 9,550,000 kcal/day.

Allowing for producer consumption and population dynamics brings to light a trade-off neglected in debates about the political economy of state origins: elites cannot have both a large income from their agrarian producers and a large population of them. Further, the parabolic shape of this equilibrium relationship indicates that any level of total tax collected other than the maximum can be produced by two combinations of tax rate and population size. For reasons that we detail in Winterhalder and Puleston (2018), low rates at larger population sizes (solid line) are stable to small temporary perturbations of agrarian population size or accidents of over/under tax collection. High rates at smaller population sizes are unstable (dashed line) to these possibilities. At high rates of taxation (dashed line), perturbations that diminish the number of producers without a concomitant reduction in the total tax being collected set the agrarian population on a course to extirpation; a perturbation that induces an increase in its size sets it on a path to the corresponding stable equilibrium. Considering these stability properties, we generally would expect to find a population subject to a fixed total tax on the left, or low rate/high numbers, portion of the curve.

The equilibrium size of the agrarian population drops dramatically as the rate, and thus total tax, increases. At the point of maximum elite income, the agrarian population is only 33% (4507/13,509) of its untaxed size. Likewise, if a ruler were to impose a total burden $>9.55 \times 10^6$ kcal/day, the agricultural population cannot both pay their tax burden and feed themselves and their families at a level that allows replacement. Agrarian collapse would follow. Traditional political ecology approaches to agrarian revenue generation have suggested that a state that maximized its agrarian population would simultaneously be maximizing its potential income in the form of taxes. But this conclusion applies neither to the potential of a normal surplus during the copial phase, nor to the potential for exploitation through taxes collected near or at a Malthusian equilibrium among producers. Even the tax-collecting despots of antiquity were subject to the dynamics of demography and population ecology.

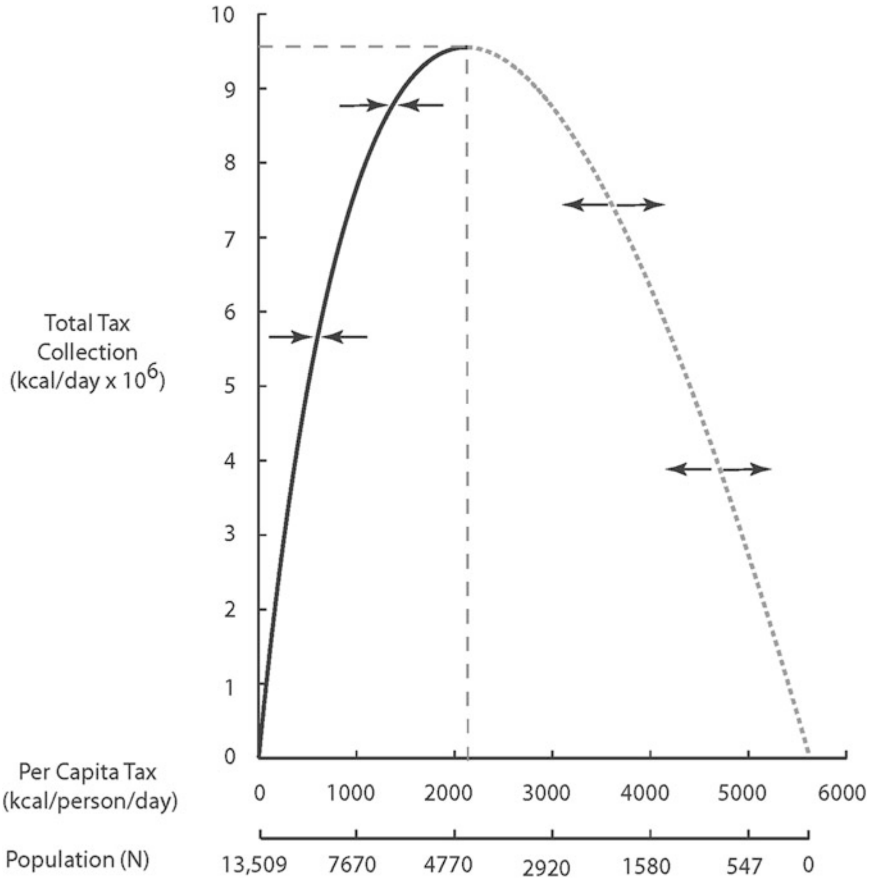

Fig. 16.4 Total tax collection as a function of per capita tax rate and population size at equilibrium. Note that the double x-axes run in opposite directions and that the population axis is not on a linear scale, a result of the nonlinear relationship between tax rate and population. Total tax collection is given by combinations of *N* times the per capita tax rate. The solid black arc on the left side of the arc represents stable equilibrium combinations, whereas dashed line arc on the right side represents unstable combinations. The arrows indicate the direction of population change if a small perturbation were to displace the population from either of the equilibria. Discussion in the text; full mathematical and related details in Winterhalder and Puleston (2018)

The space-limited approach also suggests that the form in which obligations are met will be important. Extraction of surplus or taxes could take the form of agrarian produce, as discussed above, or the ruling class could require contributions in the form of labor. A labor obligation might entail craft production for elites or maintenance of religious monuments. We model a labor obligation as removing some fraction of the time devoted to sustenance production of the individual without altering consumption requirements. Model dynamics indicate that exploitation in the form of goods and labor has quite different impacts on the welfare of the producers. This difference depends on where the population is in its growth trajectory (Fig. 16.5).

Early in the population's growth, unused land is abundant, there is little or no inefficiency due to competition, and the marginal productivity of labor is high. Consequently, it is relatively easy to produce food in abundance, without impacts on demographic welfare. As the population approaches equilibrium, these conditions invert. Little open land remains available, inefficiencies due to crowding are increasing, the marginal productivity of labor is low, and food is scarce. As a result of these contrasts, when the population is small, labor is valuable, but calories are easily produced and just as

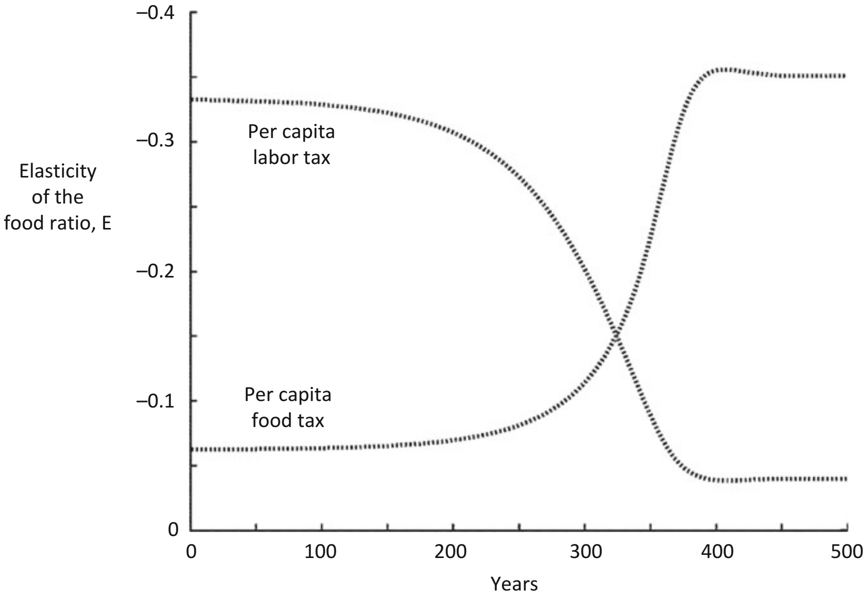

Fig. 16.5 Impact of per capita labor and food taxation on the food ratio (*E*) over the course of population growth. The y-axis values show the relative, negative effect of either form of taxation, measured as the elasticity of its impact on *E*. The relative severity of taxation inverts as a consequence of population growth. Taxation in agrarian produce is less onerous to small and growing populations; taxation in labor is less onerous to populations approaching their Malthusian equilibrium. Further discussion in the text; mathematical and related details in Winterhalder and Puleston (2018)

easily given up. Conversely, when it is large, calories are precious but labor is redundant and costly to feed. We depict this inversion of impacts with elasticities (defined above) in Fig. 16.5. The y-axis values are negative because any degree of increase in taxation imposes some burden, reducing *E*. Nonetheless, the burden is greater for taxation in labor than in produce at low population densities, early in growth, and it inverts late in that growth.

If the persistence and competitive success of prehistoric states depends on the efficiency of their resource generation and the forbearance of their agrarian-producing population, we would predict greater likelihood of success for those that adopt tax policies consistent with this outcome. It also suggests that states requiring labor for armies or the construction of public works or state monuments will be able to call upon that labor with diminished impact on the agrarian production if it is in the late stages of a growth trajectory. This casts doubt, for instance, on the hypothesis that the Maya collapse that ended the Classic Period was precipitated by an irrational choice of leadership to deflect labor from agriculture into the building of monuments (e.g., Culbert 1988).

Rulers and their administrators in pre-modern states faced a variety of choices in the design of their policies for collecting surplus or imposing taxes. The choices they made had population ecology consequences, some of them quite difficult to discern, for their revenue-generating success and the size, persistence, and welfare of the agrarian populations upon which they depended. To cite one additional insight from space-limited modeling, we probably can take as a given that state authorities faced pressures to generate greater and greater revenues. A dramatic example comes from Gutiérrez (2013, p. 158): "I estimate that over these thirty-six years of Aztec domination, the tribute requirement for the Tlapa province increased by 947 percent ...." Some success in meeting such demands, at some risk, potentially could result from fine-tuning the tax burden (Fig. 16.4). It would help to correctly assess the form of contribution—goods or labor—with the least impact on the producers (Fig. 16.5).

Winterhalder and Puleston (2018, their Figs. 3 and 5) show that the opportunities for enhancing state income by reducing producer consumption (food consumption practices, Fig. 16.1) or increasing producer labor time (age-specific social organization of work) are limited and subject to decreasing margins. By contrast, innovations that increase yield without extra labor (production potential/unit area) provide a near-linear increase in the potential for income (elasticity ≈ 1), if they can be developed in a continuous fashion. Territorial expansion that increases access to arable land (total agricultural land area) offers a direct proportional increase in revenue potential (elasticity $= 1$). This may be a reason that territorial expansion is such a regular feature of early polities (Spencer 2010; also this volume).

Better Integrating Boserup into Our Models

Malthus emphasized the power of environmental and economic circumstances to impede population growth, dwelling on the human misery this entailed. Boserup, in contrast, emphasized the power of population growth to provoke changes in agroecological practices and economy that lessened or circumvented altogether such impedance to growth, mitigating the associated impacts on demographic welfare. Malthus was writing before Darwin and trying to explain why things don't change much if at all, whereas Boserup was writing long after Darwin and attempting to account for observations of rapid, historical developments in agricultural practices. Viewed as competing theories for much of the last half century, the current trend is to accept that they are complementary and should be combined. It is evident that an evolutionary anthropology needs both selection pressure for adaptive change coupled to models showing why and how it might occur and with what effectiveness.

Contemporary accounts synthesizing Malthus and Boserup commonly take a narrative form. For instance, Kristinsson and Júlíusson (2016) argue that with increasing cultural complexity, human societies become more readily adaptable. As a result they concurrently undergo a shift from Malthusian to Boserupian regimes of population response. Four archaeological case studies—Göbekli Tepe, Tiwanaku, Iceland, and Rapa Nui—are mustered in support of their observation that processes of agroecological intensification replace those of Malthusian determinism. Examples of more mathematically based Boserupian models can be found in Lee (1988) and Cohen (1995). These models constitute thought experiments designed to probe gaps between our understanding of resource limitation and recent trends in human super-exponential growth. Such models are necessary because, as we have emphasized, reliable *intuitive* assessment of population ecology dynamics can be quite difficult.

As an indication of future directions, we point to the integrative potential of the space-limited model depicted in Fig. 16.1. Broadly speaking, the left side of the schematic holds the elements, demography and population, central to Malthus, whereas the right holds the elements—labor, the agroecological environment, and yields—central to Boserup. To make use of this observation and formally incorporate Boserup into the space-limited model, we could, for instance, place a portion (%) of the total agricultural land area into fallow and create a function to diminish the fallow portion as a function of the food energy ratio (E). The output of this function would measure intensification. Two parameters of the present model, production potential/unit area and cultivated/unit of labor, would be reformulated as variables, the first as an increasing and the second as a decreasing marginal function of some form. While simple enough to state, each of these changes would require detailed empirical investigations and analytical judgments to implement. For instance, at what point in a population growth trajectory do we expect our extensive farmers would feel compelled to shorten fallow? What marginal increases in yield arise from this effort, and how quickly can new methods of intensification be developed and implemented? Innovation modeling focused on the development of new cultural traits (Creanza et al. 2017, p. 7783) could come into play in these efforts.

As such questions indicate, devising a population ecology model is as much a process of research as is interpreting and then assessing its output against evidence. But, even assuming these questions settled, the coding done, and the model poised to run, we would hesitate to predict the outcome with confidence. Our experience with the significantly simpler model of Fig. 16.1 has impressed upon us the difficulty of correctly anticipating from intuition the dynamic behavior of population ecology systems. Surprises are among the good reasons for using models.

From Simulation Models to Evolutionary Archaeology

The methods described here were applied first to the islands in the Pacific. This is not accidental. Islands have been used to better understand demographic, environmental, and evolutionary processes since Darwin and Wallace (Darwin 1989 [1839]; Wallace 1998 [1881]). Archaeologist Pat Kirch, among others, has argued that islands represent wonderful natural experiments in cultural evolution. "[In] the Pacific, history has given us an unparalleled opportunity to compare what literally hundreds of societies have wrought, at times in highly similar environments, at times in strikingly different ones" (2000, p. 324; see also Vitousek 2004). Many of these groups spread quite quickly from a single parent culture, sharing language, foods, ideas about religion, social organization, and farming until time, distance, ecological context, and biological and cultural evolutionary processes caused their development to diverge. This history and diversity facilitates the comparative analyses essential to understanding evolutionary change.

The island of Hawai'i, for example, has been well characterized ecologically, and, although many questions remain, we have some record of what life was like before the arrival of Europeans. Hawai'i is small enough that it was at times ruled by a single individual but large enough to support a complex society. The archaeology of Hawai'i provides insight into the timing of colonization, the pattern of agricultural extensification and intensification, and the history of sociopolitical developments on the island (Kirch 2010). In the areas that have been studied most carefully, there was a single dominant form of food production, a subsistence base relying on unirrigated sweet potatoes, which can be modeled as a function of local soil and climate variables.

Ladefoged et al. (2008) applied space-limited modeling ideas to the question of variance in population growth rates and food production as a function of land quality across a highly subdivided landscape on the Kohala Peninsula on Hawai'i. They find that the region was not subdivided to maximize quality of life for the inhabitants, but instead to optimize surplus production and reduce its variability under the direction of local chiefs who were themselves subordinate to more powerful chiefs. In the same region, Kirch et al. (2012) tested the predictions of food-limited demography against data on residential patterns and land use across time and space. The study concludes that although the archaeological data are coarse with respect to chronology, the pattern supports the space-limited model's predictions of exponential growth followed by a rapid transition to equilibrium in the core areas. Populations in more marginal areas may still have been expanding at the time of European contact.

The space-limited demographic model also has been applied to Rapa Nui (Easter Island). Some researchers have argued Rapa Nui underwent a collapse before the first contact with Europeans (e.g., Diamond 2005), whereas others have argued that a population decline occurred only after contact (e.g., Rainbird 2002). Stevenson et al. (2015) have examined the chronological pattern of obsidian hydration-dated material at three sites on the island, assuming the probability density of these artifacts across time was indicative of intensity of human occupation and use. The food-limited demographic model was parameterized for the island and then run under different combinations of assumptions. The results suggest that although there is evidence for a precontact decline in land use and, by extension, in population, the pattern varied across the landscape. Land use intensity declined earliest in the poorer agricultural regions but was maintained at high levels in better soils until after European contact. Rather than a straightforward example of "ecocide," the data describe a population that faced an ecological crisis and adapted its behavior to the changing context. They abandoned agriculture where sustainable returns were too small to justify their use and intensified where marginal returns allowed it.

More recently modeling was used to estimate the maximum sustainable population on Rapa Nui. Puleston et al. (2017) combined a carefully parameterized food-production model with the demographic model. Under reasonable assumptions regarding agricultural productivity, the maximum population size clusters around 17,500 individuals, lending support to the idea that the island's population had in fact declined significantly by the time observers made careful estimates, decades after regular contact with Europeans.

In an independent line of inquiry, this one in a continental context, Anna Prentiss and colleagues have pursued evidence of population ecology interactions at the Bridge River Village site in British Columbia. Bridge River was occupied by a fisher-forager population from about 1800 B.P. to 100 B.P., with at least one long period of abandonment. Prentiss et al. (2014) find evidence in support of reductions in quality of life at the village level synchronized with regional and local declines in salmon populations. In a detailed study of the stratigraphy of a single house, Prentiss et al. (2018) examine predictions made regarding the relationship between food storage and population trajectories. The evidence suggests that the local population goes through the phases described in Puleston et al. (2014) and that the use of storage pits conforms to the predictions of Winterhalder et al. (2015). The population appears to have increased over time to a peak density with evidence of a plentiful food supply during this growth phase. Fish and deer were processed in the village, indicating that they were acquired nearby and transported home whole. In the next phase of occupation, the population appears to be much diminished, fish and deer are more likely to be acquired at a distance sufficient that they were processed in the field, storage pits become more common, and dogs are being used as a managed food resource. It is unclear whether the peak of population was sustained through active population control (i.e., a Malthusian preventive check), but the later phase has signs of a classical resource-limited population afflicted by the unhappy constraints of Malthus's positive checks.

Concluding Thoughts

Population is a common factor in the wide-ranging renaissance of research traditions in evolutionary anthropology (Creanza et al. 2017; papers in this volume). Like surplus, population has a high-profile role in archaeologists' attempts to explain the major socioeconomic transformations of human history, from the origins of agriculture (Cohen 1977) to the development of states (Carneiro 1970). And, like surplus, the use of population causation in these contexts has provoked intense debates for almost as long (Cowgill 1975; Vaesen et al. 2016).

In these debates population growth generally has been assumed to be of the form modeled by Verhulst, a continuous and unidirectional phenomenon of increase. Carried into archaeological discourse, population has functioned as a slowly increasing pressure, one that eventually catalyzes the particular transformation of interest. We argue that it will be necessary for archaeologists to revisit the old debates with insights more firmly grounded in the dynamics of population ecology. The space-limited model shows us that population sometimes is not what it has seemed. Normal surplus is greatest when population size is small; food storage can make famines worse; a salubrious environment threatens population welfare to a greater degree than an unstable one; a state cannot have both a large agrarian population and a large income from it. Evolutionary archaeology requires a well-developed understanding of the mechanisms giving rise to such observations. It necessarily will be based in developing approaches that integrate into formal models—space-limited and those arising from other approaches—the insights and variables featured in both of Malthus and Boserup.

Data Sharing Statement The data sets (R code) generated and/or analyzed during the current study are available at github.com/puleston/spacelim.

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Chapter 17

Niche Construction Theory and Human Biocultural Evolution

Felix Riede

Introduction

Niche construction can be minimally defined as the process whereby organisms modify—deliberately or inadvertently—their own and other organisms' selective environment to such a degree that it changes the selection pressures acting on present and future generations of said organism or organisms. The genealogy of niche construction theory (NCT) is conventionally traced back to the arguments of Richard Lewontin (1970, 1978, 1983) who suggested that in contrast to traditional, strictly asymmetrical views of adaptation positing that "organisms adapt to their environments, never vice versa" (Williams 1992, p. 484), organisms in fact can and do have a significant and (critically) often selectively relevant influence on their environments. At this time, new quantitative models for capturing the evolutionary interactions between cultures and genes, so-called dual-inheritance or gene-culture co-evolutionary models, were also emerging (Cavalli-Sforza and Feldman 1973a, b; Feldman and Cavalli-Sforza 1975, 1976; Cavalli-Sforza and Feldman 1981). While Lewontin himself was not really taken by the idea of applying evolutionary models to culture change (Fracchia and Lewontin 2005), the respective insights from natural history and formal modelling were combined by Oxford ecologist John Odling-Smee (1988, 1995) in the 1980s and early 1990s into initial arguments for the importance of what he labelled niche construction. Odling-Smee stressed that from this point of view, adaptation can be the result of two processes:

1. Environment > selection > adapted organism
2. Organism > niche construction > modified environment

The eventual result of both pathways is a fit between organism and environment—adaptation—yet the process differs in important ways. Niche-constructing behaviours can act in many ways and lead to different outcomes that can both counteract selection pressures generated by the external environment and initiate more active niche changes such as range expansions (Laland and Brown 2006).

Sometimes known as a triple-inheritance model, the emergence of NCT can be seen in the context of approaches that developed from evolutionary biology in the latter part of the twentieth century and which were broadly aimed at addressing and explaining, with varying degrees of success, human behaviour and cultural evolution—sociobiology, memetics, behavioural ecology and gene-culture

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co-evolutionary theory (see Laland and Brown 2011, for an extended discussion of these different approaches). Throughout the 1990s and early in the current millennium, NCT was being investigated extensively through, in particular, quantitative modelling. The influential behavioural scientist Kevin Laland from St. Andrews University (UK) and computational biologist Marcus Feldman from Stanford University (USA) joined forces with Odling-Smee, and in 2003, the landmark monograph on NCT appeared, marshalling considerable theoretical and empirical support for the relevance of such behaviours as an important evolutionary process (Odling-Smee et al. 2003).

Humans are far from the only organism that persistently modify their environs leaving landscape-scale signatures (Corenblit et al. 2008; Corenblit et al. 2007; Erwin 2008). Yet, together with colleagues from philosophy (Sterelny 2007, 2011), ecology (Laland et al. 1999; Odling-Smee et al. 2013; Boogert et al. 2006; Laland and Boogert 2010; Matthews et al. 2014), developmental biology (Laland et al. 2008; Flynn et al. 2013) and, eventually, archaeology (Shennan 2006; Laland and O'Brien 2010; O'Brien and Laland 2012), an argument in favour of an extended evolutionary synthesis (EES) relevant first and foremost to human biocultural evolution has been made (Laland et al. 2015; Uller and Helanterä 2017; Müller 2017; see also http://extendedevolutionarysynthesis.com/). This EES focuses on two key concepts: *constructive development* and *reciprocal causation*. Both are aspects of niche construction where the actions *on the environment* (at varying scales) *by individual organisms* modify the developmental and/or selective processes acting on their offspring, themselves and/or other organisms.

Despite the evident productivity of NCT, it is far from accepted in all corners of biology or related disciplines. Critical attitudes range from outright and at times rather aggressive rejection (e.g. Gupta et al. 2017b; Futuyma 2017) to more productive dialogues (e.g. Scott-Phillips et al. 2014). These critiques maintain that evolutionary dynamics can be more parsimoniously explained by standard evolutionary theory and that NCT is no more than a highest-order perspective providing no specific ways to be measured and evaluated and hence offering no explanatory power beyond existing models. The supporters of NCT usually counter such attacks with generally measured responses and the intention to clarify misunderstandings or diverging views (Feldman et al. 2017; Mesoudi et al. 2013; Laland et al. 2000; Laland and Sterelny 2006). These efforts are not always crowned with success and consensus (Gupta et al. 2017a), but for those studying human biocultural evolution, the main attraction of NCT remains: organisms—in our case humans and their behaviours—are given a critical role in the evolutionary process, and the evolutionary process is seen as more than genetic change in individual organisms. Three aspects are particularly pertinent:

- First, the notion of *agency* that has had a major influence on archaeology over the last few decades but is generally linked to theoretical approaches antagonistic to evolutionary ones can be readily integrated (Smith 2013; Shennan 2004; VanPool and VanPool 2003; Riede 2005a).
- Second, many archaeological features—huts and houses, hearths, corrals, hunting stands, irrigation canals, farming terraces and the like; Oswalt (1976) calls them *facilities*—are constructed collectively and have lifetimes beyond those of their makers. They effectively become parts of the environment for subsequent generations who were not part of the initial erection of these facilities. These features can only be poorly captured by traditional dual-inheritance models, which focus more on knowledge and material culture clearly linked to individuals and more or less readily tractable pathways of social information transmission. The longevity of these installations and environmental modifications is termed ecological inheritance, which in NCT complements the domains of cultural and genetic inheritance. Environmental archaeologists can identify these signatures of past actions on the environment and often reasonably demonstrate that they have had ecological legacies of selective relevance (Szabó 2010; Butzer 1982; Dincauze 2000; Normand et al. 2017; Kluiving 2015)—even if those consequences are intended or unintended or positive or negative in the short or long run (Dincauze 1993).

- Third, traditional evolutionary approaches as well as cultural evolutionary models such as dual-inheritance theory are rarely if ever concerned with the environmental outcomes of cultural processes. The unit of interest is the organism. For those also genuinely interested in the changes of the environment that are brought about by humans but are selectively relevant for both humans and other species, NCT offers the necessary scope. It is not essential to invoke NCT in every case study. Many cultural evolutionary processes can be understood in less holistic terms. Yet, when the selective feedforward potential of modified environments is also of concern, these inherited environments need to be formally accounted for in our models. Furthermore, as I argue towards the end of the chapter, this focus on the environment articulates archaeology with contemporary concerns about human impacts on ecosystems at a global scale and the emergence of the Anthropocene (Fox et al. 2017; Boggs 2016; Kluiving 2015; Smith and Zeder 2013).

Independently of the emergence of NCT, environmental archaeologists have argued that their discipline offers “a holistic view of past ecosystems and their workings, a view which is valuable both within archaeology and to other disciplines” (O’Connor 1998, p. 5). In the sense that environmental archaeology is the study of human palaeoecology, coupling this record to explicit models for how such behaviours change over time, the role of individual and collective agency and their role in a broader evolutionary process are not only conceptually attractive but also useful for generating specific hypotheses (Riede 2012).

In the following, I begin with outlining the terminology used to conceptualize and describe the elements specific to ecological inheritance and niche construction. I outline the kinds of processes that can be seen as niche construction. I will then use this terminology and processual taxonomy in an initial discussion of an iconic non-human example of niche constructor, the beaver, to further outline the basic tenets of NCT. I then move quickly on to how humans are part of wider niche construction processes and to how humans have constructed their own niche. In this, I selectively focus on the themes of fire use, changing human-animal and human-plant relations (extinction and domestication) and cognitive niche construction. I draw on chronologically disparate examples to stress the evolutionary importance of many of these behaviours and how they have acted on hominins from the deep past to the present. My final examples link NCT to the notion of the Anthropocene that reflects the now pervasive nature of humanly induced ecosystem impacts on scales that range from local to global. In this context, NCT provides an evolutionary backdrop to how we have ended in this situation where one species has a near-comprehensive ecological legacy rife with unintended consequences but also offers hope for how evolutionarily informed actions can help us deal with these quandaries in the present and future.

The Terminology and Taxonomy of Ecological Inheritance and Niche Construction

Anthropologists have long appreciated that material culture constitutes an “extra-somatic means of adaptation” (Binford 1962, p. 218). This notion, going back to White (1959), presaged Dawkins’ (1982) famous discussion of the extended phenotype, which then has again been adapted to anthropological concerns within the emerging evolutionary archaeological paradigm of the 1990s (e.g. O’Brien and Holland 1992, 1995). While it then became quickly apparent that the extended phenotype approach with its strong focus on genotypic selection as a driver of change also in the phenotypic extensions was not as well-suited to understanding cultural change as gene-culture co-evolutionary/dual-inheritance models, it has become equally clear that the actions of organisms on the environment that form such extended phenotypes critically modify those organisms’ physiological niche parameters (Turner 2000). Importantly, if and when these phenotypic extensions affect not only

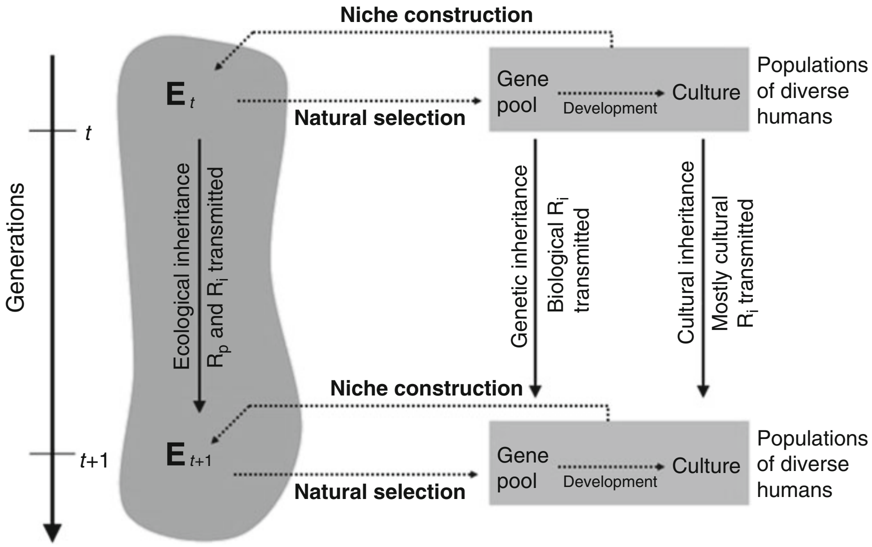

Fig. 17.1 The three domains of inheritance of niche construction theory: genetic, cultural and ecological with the respective resources (R_p, R_i) that are transferred. Redrawn and adapted from Odling-Smee (2007)

Table 17.1 A taxonomy of physical and semantic or informational resources that are transmitted or persist as part of ecological inheritance

Transmission channel	Resource transmitted: R_i | Rp	Type of inheritance
Internal environment	R_i: semantic resources	• Genetic inheritance • Epigenetic inheritance
	R_p: physical resources	• Cytoplasmic inheritance
External environment	R_i: semantic resources	• Cultural transmission, knowledge, know-how
	Rp: physical resources	• Inheritance of altered environs ranging from clothing to landscapes

Adapted from Odling-Smee (2007)

the organism of origin and leave selection-modifying legacies over considerable periods and across generations, they become ecologically inherited (Fig. 17.1): “Ecological inheritance does not depend on the presence of environmental ‘replicators’ but merely on intergenerational persistence (often through repeated acts of construction) of whatever physical—or, in the case of humans, cultural—changes are caused by ancestral organisms in the local selective environments of their descendants” (O’Brien and Laland 2012, p. 436).

Within the domain of ecological inheritance, different kinds of resources can be passed on or persist from generation to generation (Table 17.1). Physical resources (R_p) are literally modified components of the environment—caches, huts, houses, fields and so on. Semantic or informational resources (R_i) are more difficult to capture archaeologically but would cover what is today often referred to as traditional ecological knowledge (TEK; Berkes et al. 2000; Inglis 1993) about the environment and its instantiations. This is at times codified not only in stories and legends (Sugiyama and Sugiyama 2009) but also in art and other artefacts (Barton et al. 1994; Mithen 1991). This is knowledge—counter to Odling-Smee (2007) not strictly identical, in my view, with the kind of knowledge primarily captured by cultural inheritance studies—that plays a critical part in how human communities act in and on the environment. This collectively held knowledge about the environment and about how to modify has evolutionary consequences and often leaves archaeologically visible signatures (Rockman 2009).

Table 17.2 A basic categorization of niche-constructing behaviours

	Perturbation	Relocation
Inceptive	Organisms initiate a change in their selective environment by physically modifying their surroundings	Organisms expose themselves to a novel selective environment by moving to or growing into a new place
Counteractive	Organisms counteract a prior change in the environment by physically modifying their surroundings	Organisms respond to a change in the environment by moving to or growing into a more suitable place

Adapted from Laland and O'Brien (2010)

Table 17.3 Examples of niche-constructing behaviours by humans and affecting humans classified according to the NCT resource and process taxonomies

NC behaviours	R_p/R_i	Effects	NC categories	References
Non-human animals affecting the human niche				
Beaver (*Castor fiber*) damming	Physical	Creates long-lasting lake habitats and patches of open landscape, attracting human settlement	Inceptive, perturbational, later counteractive	Coles (2006), Wright et al. (2002), Brown et al. (2017)
Humans affecting their own niche				
Caching	Physical and semantic	Changes the distribution of critical resources in the landscape	Initially inceptive, later counteractive, perturbational	Potts (1994), Riede (2005b)
Way-marking	Physical and semantic	Creates long-lasting pathways through a landscape	Inceptive, perturbational	Rockman and Steele (2003), Pasda (2004), Odgaard (2007)
Humans affecting their own and other organisms' niches				
Plant domestication	Physical and semantic	Changes genetics and morphology of plant species and creates the agricultural niche	Inceptive, perturbational	Coward et al. (2008), Smith (2007), Terrell et al. (2003), Rindos (1984), Zeder (2017)
Animal domestication	Physical and semantic	Changes genetics and morphology of animal species and creates the pastoral niche	Inceptive, perturbational	Bleed (2006), Zeder (2017)
Expansion into new habitats	Physical and semantic	Introduces foreign species (including humans) into new habitats, often with genetic effects for many species	Relocational, may be inceptive or counteractive	Kirch (1997), Bellwood (2005), Kennett et al. (2006)
Fire management	Physical and semantic	Clears patches of landscape for new growth and animal feed	Perturbational	Mellars (1976), Bird et al. (2008); also see Bond and Keeley (2005), Schwilk (2003) and Verdú et al. (2007)
Art and play objects	Physical and semantic	Assists in the transmission of ecological information; territorial markers	Inceptive	Mithen (1991), Barton et al. (1994), Riede et al. (2018)

The process of niche construction has been classified into the four basic categories of perturbation and relocation effectively reflecting whether the behaviour in question involves movement into novel environments or not and inceptive versus counteractive behaviours reflecting whether the behaviour in question creates novel selection pressures or whether it modulates and buffers existing ones (Table 17.2). Numerous phenomena observed in the archaeological record can be classified according to these simple resource and process taxonomies (Table 17.3). Such novel ways of describing often well-known phenomena facilitate comparison between phenomena and allow an articulation with specific methods that have already been applied within NCT studies.

The Beaver as Ecosystem Engineer and Niche Constructor

Beavers (*Castor fiber*) are widely acknowledged as a so-called ecosystem engineer, a species whose activities demonstrably impact its surrounding environment, as was in fact already noted by pioneering anthropologist Lewis Henry Morgan (1868) in a monograph dedicated to this fascinating animal and its effect on surrounding environs. Beavers constitute also a much-used example within the NCT literature. As a beaver fells trees to make its home, it modifies the adjacent ecosystem, potentially opening the shoreline to new plants and exposure to sunlight, even altering erosional processes that may affect the surrounding environments (Wright et al. 2002; Naiman et al. 1986; Puttock et al. 2017). The reason I use the beaver as example here is that Richard Dawkins (1982) famously used this creature to explicate his notion of the extended phenotype, where the underlying alleles for dam-building evolve in essentially the same way as any other aspects of the beaver genotype, i.e. via natural selection. This view arguably fails to fully appreciate the extent of ecological and hence selective consequences of beaver dam-building. Importantly, the dam-building beavers' offspring are born into a world that already has a dam. Consequently, the dam can no longer be adequately seen as merely an extension of the original beavers' geno- and phenotypes—especially once individuals belonging to that generation pass away—but rather also as part of the new beaver generation's environment, an ecological inheritance of primarily R_p with selective and perhaps also developmental repercussions. Over generations, this niche construction behaviour changes from inceptive to counteractive, and a feedback loop develops in which the environment or niche is changed through an organism's activities, which in turn alters those very activities, in turn altering the environment and so on (Fig. 17.2).

Beaver dams are *facilities*, constructions with effects on the environment and a longevity well beyond the generation of organisms that initially built them. For the beaver cups born in the dam, it is the environment, and it has significant selective effects. It is no big leap from beaver dams the human constructions such as huts, houses and irrigation canals. But there is more: the actions of beavers have also long since attracted humans to those very same habitats (Coles 2006). Indeed, Tolksdorf et al. (2017) have recently demonstrated the close cohabitation of Late Palaeolithic foragers and beavers in the same habitat, and Brown et al. (2017) have further compiled faunal evidence as well as indications

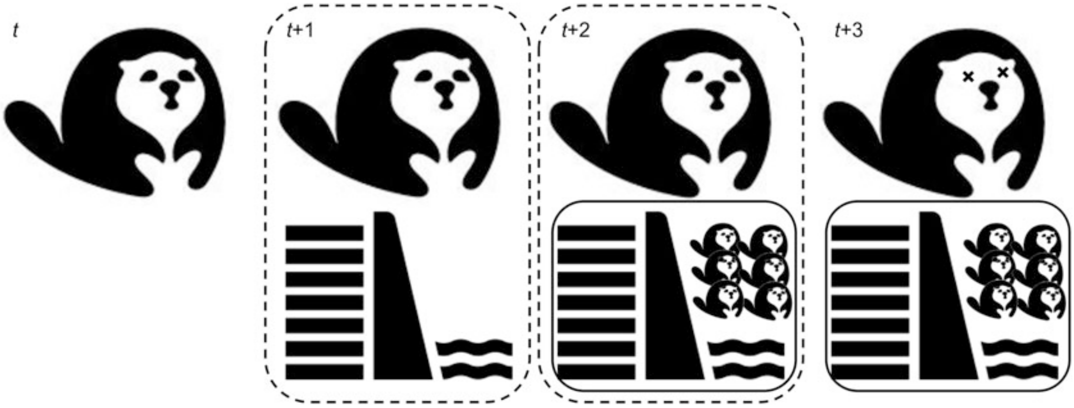

Fig. 17.2 A schematic of how a regular phenotype at t becomes an extended phenotype in $t + 1$ and then transforms into the constructed niche of a new generation of beaver pups at $t + 2$ born into the phenotypic extension of the previous generation. At $t + 3$, the original niche-constructing individual is dead—the current individuals and their offspring hence live in a niche containing many selectively significant elements that are ecological inherited. Dashed lines mark the extend of the extended phenotype; solid lines mark the constructed niche. Beaver individuals at $t + n$ will continually and further modify this constructed niche, and the distinction between any given individual's extended phenotype and their and other individuals' inherited niche cannot be drawn precisely

from Late Palaeolithic (Magdalenian) art that suggest a strong attraction of humans—in Paleoarctic Europe at least—to beaver-modified habitats. Humans learned that these beaver-created habitats offered opportunities for increased hunting success of both beavers and other animals. Within the NCT terminology, then, beavers are the primary niche constructors in this example, affecting both their own niche and that of *Homo sapiens*. Both species have their own trajectories of *genetic inheritance*. At the same time, the ecological knowledge and the know-how used to manufacture the relevant tools for hunting are part of the *ecological* (R_i) and *cultural inheritance* of these Late Palaeolithic groups. Their ecological footprint and hence the *ecological inheritance* (R_p) at the landscape scale were still ephemeral at this time, although their ability to modify landscapes may hitherto, as Brown et al. (2017) point out, been underestimated.

Indeed, the Magdalenian niche contained other constructed R_p elements: They erected tents, made fireplaces and flooring (e.g. Jöris and Terberger 2001), lighted fires that affected their surroundings (Bos and Janssen 1996) and domesticated dogs (Pionnier-Capitan et al. 2011; Musil 2000; Larson et al. 2012). They also furnished the ontogenetic niches of their offspring with play objects (e.g. Langley 2018; Nowell 2015) that are argued to have had effects on their cognitive development (Riede et al. 2018). I will return to some of these examples and facets of niche construction below. Before moving on, however, note that in the long run the niche construction balance between *Homo sapiens* and *Castor fiber* in Europe shifted very much in favour of the former and eventually led to the extirpation of the beaver from many regions (Coles 2006)—a common effect on animals of human niche construction behaviour (e.g. Sandom et al. 2014).

Constructing Niches Through Fire

Hominins are associated with fire since at least 1.5 million years ago (Gowlett 2016). While the chronology of the transition from serendipitous to habitual fire use is disputed (Parker et al. 2016; Shimelmitz et al. 2014; Gowlett and Wrangham 2013), the impact of fire on hominin lifeways and selection has received considerable attention. Based on evidence from a wide range of disciplines, Wrangham (2009) has suggested that the ability to heat-treat foodstuff was essential for allowing Middle Pleistocene hominins to disable toxins and unlock much increased calories of a wide range of foodstuffs. This suggestion interacts well with both the earlier “expensive tissue hypothesis” (Aiello and Wheeler 1995) that addressed the energetic trade-off between guts and brains in the *Homo* linage and the notion that campfires also served as critical foci of social life and knowledge transmission (Wiessner 2014; Stiner and Kuhn 2016). The habitual use of fire sometime after 500,000 years ago (Shimelmitz et al. 2014) almost certainly facilitated the large-scale and successful expansion of the hominin range around this time, especially into higher latitudes (Hosfield 2016).

But as alluded to above, the use of fire by hominins also left landscape-scale imprints that also modified selective pressures. While such impacts are ephemeral in the Pleistocene (Daniau et al. 2010), evidence from the early Holocene onwards points to intentional fires as a major means of modifying landscapes from well before the beginning of agriculture. Such modifications were aimed at creating landscapes more favourable for desired plant (Moore 2000) and animal species (Mellars 1976), and their consequences are visible in ecological proxy records (e.g. Olsson et al. 2010; Innes et al. 2013). The impact of human fire regimes has also been studied extensively outside of Europe. Australia, in particular, has yielded remarkable evidence not just for the intentional use of fire—known as fire-stick farming—but its landscape-scale consequences. In a detailed series of studies, Hill et al. (1999) and Bird et al. (2005, 2008, 2016) have documented how Australian Aborigines deploy fire as part of their hunting strategy and, using remote sensing as well as traditional ecological census methods, how this changes the community structure of vegetation cover at the regional scale. Importantly, the latter effect is incidental to the hunters’ original intention to ease their prey harvest.

Yet, it is precisely these incidental effects that have the greatest ecological and evolutionary effects on flora and fauna that is now evidently adapted to such fire regimes (Codding et al. 2014; Pyne 1991). The results are subtly but effectively "domesticated landscapes" (Terrell et al. 2003, p. 323) or constructed niches that are common amongst many traditional societies the world over. In contrast to the beaver example above, fire-stick farming is an example of niche construction by small-scale human foraging groups where they are in the ecological driving seat.

Changing Relations Between Animals, Plant and Humans

Prior to the global spread of *Homo sapiens* to even the most remote corners of the earth, faunal and floral communities looked quite different, in large part because the presence of very large animals (megafauna) has significant effects on both predators and plants (Malhi et al. 2016; Sandom et al. 2013). There is considerable controversy about the impacts or otherwise of humans on individual species and in particular regions such as the Americas (e.g. Grayson and Meltzer 2003, 2004; Fiedel and Haynes 2004; Johnson et al. 2013; Lima-Ribeiro and Felizola Diniz-Filho 2013). Seen across regions, however, it seems likely that the arrival and continued presence of humans in especially naïve ecosystems had dramatic consequences for first the larger animals and that these effects then trickled through trophic hierarchies to also affect organisms at lower levels (Sandom et al. 2014; Bakker et al. 2016). Such impacts can readily be seen in a niche construction light, where the impact of humans on the selective pressures acting on specific organisms entails marked changes in ecosystem composition and function. It is also a strong case demonstrating the unintended perturbational consequences of such niche impacts.

In reverse, it has long been appreciated that the beginning of animal and plant domestication in the period between ca. 20,000 and 10,000 BP constitutes a major inflection in human biocultural evolution. While some see this as a revolution—classically, Gordon Childe (1936) coined the Marxist-inspired label of the "Neolithic Revolution" in his for contemporary eyes anachronistically but otherwise aptly titled monograph *Man Makes Himself*—it is now considered the model case for human niche construction that recursively impacts a wide range of other species as well as the human niche constructors themselves (Watkins 2017; Sterelny and Watkins 2015; Zeder 2016, 2017). Melinda Zeder (2006; also Zeder et al. 2006) has provided lucid discussions of the intersections between the genetic, behavioural, morphological and material dimensions of the domestication process. Different species of animals and plants respond differently and at different speeds to human interventions; also, the different components of domestication—behavioural adjustments, alterations in the geno- and phenotypes of the target species and the emergence of particular material trappings associated with domestication—should not be seen to proceed in a lockstep fashion. Genetic change, the benchmark of domestication, is merely the endpoint of what is best thought of as a continuum of processes. Archaeology can provide insights into the (conscious or unconscious) manipulations of the behaviour, distribution and breeding patterns of candidate domesticates long before genetic change actually took place and became dominant in the target population. The demographic success of the niche-constructing population itself, here *Homo sapiens*, is also reflected in a range of archaeological proxies, such as range expansion, increases in the number and/or size of sites or the number of ^{14}C dates in a given period (Chamberlain 2006; Riede 2009a).

The first animal domestication began well before the Neolithic. Wolves came into close association with humans in the Late Pleistocene, close enough to lead to commensal, symbiotic and eventually domestication relations, possibly in several locations around the globe (Thalmann et al. 2013; Larson et al. 2012; Savolainen et al. 2004; Savolainen et al. 2002; Vila et al. 1997; Pang et al. 2009). There is considerable controversy about the timing and exact process, however, as genetic evidence conflicts with regard to a single (Europe or Southeast Asia) versus multiple (Europe and Southeast Asia) domestication centres as well as its timing (>100,000 years BP vs. <20,000 years BP). Independently of the precise when and where of dog domestication, the intimate and long co-evolutionary relation between *Canis* and *Homo* has altered not only dog genetics and physical appearance but also their vocalizations and cognitive abilities. Dogs can serve as sources of warmth, comfort and food, and they can carry loads and aid in hunting. Taming and keeping dogs are costly but also usually provide tremendous benefits to their users (Koster 2008; Lupo 2017). It is here at the intersection between everyday decision-making processes and their long-term consequences on both the niche constructor and their subject—in the words of Stiner and Kuhn (2016, p. 177) "the 'sweet spot' between optimality theory and niche construction theory"—that we can understand dog domestication.

It is likely that humans engaged with such experimentation repeatedly and at different times. In Europe, fossil evidence supports incipient but perhaps curtailed domestication attempts in the early Upper Palaeolithic (Germonpré et al. 2009, 2012; Ovodov et al. 2011), followed by a more sustained and successful domestication in the Late and Final Palaeolithic (e.g. Grote 1994; Napierala and Uerpmann 2012; Musil 2000; Street 2002). This latter domestication had further implications for range expansion and economic strategies for Late and Final Palaeolithic hunter-gatherers. The recolonization of the northern European lowlands in the early part of the Late Glacial, for instance, was dependent on foragers being able to efficiently exploit reindeer. The so-called Hamburgian culture is associated with this initial colonization pulse, although much circumstantial evidence suggests that this was ultimately a failed expansion attempt (Riede and Pedersen 2018; Riede 2007, 2009b, 2014). Later on, the region was again colonized by specialized reindeer hunters, this time of the Ahrensburgian culture, where there is evidence of dogs. The coupling of this repeated emergence of specialized reindeer hunting and the use of domestic dogs has been the subject of a detailed NCT-driven analysis. By applying the tools of cultural phylogenetics (Gray et al. 2010; O'Brien et al. 2008) and the comparative method (Freckleton et al. 2002; Mace and Pagel 1994), Riede (2010, 2011) has analysed the correlation between reindeer specialization and dog use as well as the order of emergence. This analysis consists of two steps: first, lithic artefacts are used for deriving explicit hypotheses for the historical relationships amongst Final Palaeolithic communities of flint-working practice in the form of phylogenies, and then, the presence/absence of reindeer and dogs as seen in the faunal evidence is plotted on these phylogenies—all within a Bayesian statistical framework.

The results of this analysis support the hypothesis that the emergence of successful reindeer-specialized adaptations in the absence of dogs is very unlikely and, hence, that the adaptive strategy of the Hamburgian culture was inherently unviable. Conversely, the domestication and use of dogs as transport and hunting aids strongly facilitated the range expansion and reindeer-hunting specialization. In NCT terms, the construction of the dogs' niche by Final Palaeolithic humans through their interactions and the material trappings of dog keeping (Bleed 2006; see also Guagnin et al. 2018) led to a selective feedback loop on both *Canis* and those human populations using dogs: They grew and expanded suggesting modified selection pressures and an improved fit between Late Pleistocene environs and these hunter-gatherers. The statistical support for these niche construction pathways was weak, however, reflecting the relatively ephemeral niche modification enacted by these small groups. Using other methods, the niche-constructing behaviours of prehistoric foragers can be assessed (e.g. Riel-Salvatore 2010; Riel-Salvatore and Negrino 2018), yet the application of phylogenetic methods allows for a stricter control of the historical relatedness amongst the units of analysis, when it comes to seeking correlations amongst traits. Accounting for this relatedness is a fundamental issue in cross-cultural analysis and can be tackled via such comparative methods (see Chap. 9, this volume).

A major inflection in the ability of *Homo sapiens* to affect their environment occurs with the emergence of fully agricultural and pastoral economies: the Neolithic (Rowley-Conwy and Layton 2011). Niche construction theory offers explanations for increasing patch and resource investments (Mohlenhoff and Codding 2017; Zeanah 2017), and, as already alluded to above, Zeder (2016, 2017) has described how the domestication of plants and animals themselves in the Levant and elsewhere (e.g. Allaby et al. 2017) can be understood—at the scale of path-dependent macroevolution—as a niche construction process. Indeed, the ever-greater resolution in our assessments of past human-animal and human-plant relations afforded by new field data and applications such as stable isotope analyses provides detailed insights into dependencies and management practices already well before fully agricultural economies were in place. Maring and Riede (2019), for instance, argue that the complex hunter-gatherer-fishers of the Late Mesolithic in southern Scandinavia had close relations with wild boar somewhere on the trajectory towards domestication. Radiocarbon dating demonstrates that the wild boar specimens in question substantially predate the arrival of agriculture in the region; an osteological assessment does not indicate full domestication; their isotopic values, however, clearly indicate a marine diet otherwise only observed in clearly domesticated pigs from much later prehistoric contexts (e.g. Jones and Mulville 2018; Jones and Mulville 2016) or contemporaneous and clearly domesticated dogs (Fischer et al. 2007). This analysis, using tools specifically designed to elicit information on two specific domains of change associated with domestication (diet/behaviour and skeletal morphology), has revealed how behavioural changes preceded morphological and presumably genetic changes along the domestication continuum, although the latter will need to be demonstrated using ancient DNA approaches. While other explanations for this pattern are possible (cf. Chamberlain et al. 2005) and low sample size only allows for preliminary conclusions, the notion of important land and resource management that had environmentally mediated selective effects on other organisms is fully in line with other evidence (e.g. for fishing facilities, forest manipulation) from this period.

In addition to such largely discovery-driven approaches drawing on new archaeometric techniques, O'Brien and Laland (2012) underline, using causal graph methods, the important point that the major changes in range and genetic composition of both humans and domesticates in the Neolithic often took pathways that included major environmental modifications, rather than arising directly from some individual actions or through cultural transmission trajectories adequately modelled as traditions.

In addition to animals and their products being available in a stable fashion within such economies, Johannsen (2007) has also pointed towards the use of animals as "machines" that transforms the human and domesticate niches, all of which leaves clear traces in the genetic and archaeological (osteological, material, landscape) records. O'Brien and Bentley (2015) have further supplemented this discussion of Neolithic agriculture with detailed arguments about the role of food storage as a crucial element in this constructed niche. Building on these insights about causal pathways from cultural behaviour impacting the environment to modified selective and developmental niche construction, Johannsen (2010) and Sterelny and Watkins (2015) also outline how these developments would have quite fundamentally impacted the cognitive environments of individuals living in these societies: the niches into which Neolithic individuals were born and raised were furnished with different and more manifold artefacts and humanly modified landscapes (e.g. monuments) that facilitated different ways of conceptualizing the world. In turn, these conceptualizations then produce new forms of material culture and behaviour, establishing ever more firmly the feedback between the built environment, new technologies and new forms of sociality.

Most recently, the toolbox for studying the changing human-environment relations associated with the origins of agriculture is expanded to include distribution modelling. Developed in ecology to interrogate the precise causal effects of topographic and climatic factors on the spatial component of a given organism, these powerful tools facilitate detailed studies of adaptation (e.g. Guisan et al. 2017) also in palaeobiological settings (Svenning et al. 2011; Brewer et al. 2012). Distribution models have seen some early application in palaeoanthropology (Franklin et al. 2015) and in modelling some key agricultural species in different parts of the world (d'Alpoim Guedes et al. 2016). Whitford (2018) has recently presented a significant extension of the method by using archaeological taxa—different Neolithic cultures—as basic units of analyses. He showed how spatially the unmodified ecological setting interacted with the niche-constructed subsistence practices of early framers moving out of the Mediterranean and into the continental ecotones in northern Greece and Bulgaria. It is noteworthy that distribution modelling tools are generally freely available and are experiencing rapid development allowing code-sharing and replicability (e.g. Kass et al. 2018), which is also becoming an increasing issue in computational and indeed general archaeology (Marwick et al. 2017; Marwick 2017). The input data required for distribution models—principally climate model data, topographic information and distribution information for the taxa of interest—is often quite readily available in archaeological cases, signalling an exciting future for this suite of methods as a key approach in capturing past human adaptation and niche construction dynamics.

Cognitive Niche Construction

Experimental primate studies show that provisioning with tools changes the neuronal architecture as behaviours integrate objects (Iriki and Sakura 2008). Iriki and Taoka (2012) have argued that this plasticity opens up for a form of developmental niche construction, where the furnishing of early-life niches in hominin evolution is decisive in how neuronal structures develop, and that over time such feedback relations lead to lasting modifications in brain structure. The importance of object provisioning for developing problem-solving skills but also for simply mastering the many material culture-related skills in human communities is supported by computational modelling (Kerr 2007; Kerr and Feldman 2003), by developmental psychological studies and by ethnographic investigations of social learning (Kline 2015; Kline et al. 2013).

It has been argued that *Homo sapiens* is uniquely evolved to learn but also to be receptive to pedagogical interventions (Gärdenfors and Högberg 2015; Csibra and Gergely 2011). The role of object provisioning, however, has only been integrated into this line of thinking recently. Riede et al. (2018) have argued against a background of existing psychological and primatological studies that object provisioning and object play—covering both R_p and R_i—have important modifying influences on the ability of individuals to become competent but also to innovate within certain technological domains. This is particularly relevant with regard to technologies that are cognitively opaque, i.e. whose functional properties emerge only in the non-obvious interaction between its different parts. Put simply, if you are given a miniature bow from early on in life, you are not only more likely to become a proficient bowyer but also to be able to see how this technology can be improved—also under the strict cost-benefit calculations of life-history trade-offs in traditional societies. We see this as a form of inceptive developmental niche construction. The model and its predictions are borne out in a range of archaeological examples—from Arctic prehistory to the invention of the wheel and from the Magdalenian to the Middle Stone Age—where the presence of play objects and object play correlates with increased rates of innovation also in full-scale adult technologies.

So, the different cultural components of human-constructed niches arguably have a direct effect on development, which later on would often have selective effects also. But it is not only these objects but also, as already alluded to above, the built environment that shapes cognitive evolution. Like nests, clothing, papooses, tents, huts and buildings serve as buffers between the external unmodified environment and the immediate niche parameters. Clothing, for instance, has made a crucial difference for anatomically modern humans moving into higher latitudes (e.g. Collard et al. 2016; Gilligan 2010) but has also provided novel selection environments and evolutionary opportunities for facultative human parasites: human clothing is the unintentionally constructed niche of the human body louse (Kittler et al. 2003). But buildings can do more still. Being often long-lasting, they reflect more obviously ecological inheritances; they also impact on how humans experience and think about the world. This is especially pertinent to religious buildings that are designed to leave strong cognitive signatures (Jessen 2012; Bulbulia 2008). Unlike in primate studies, however, it is impossible to easily verify the impact of such niche furnishings on neuronal structures. Future studies employing brain imaging techniques, for instance, may be able to substantiate the actual causal (developmental and neuronal) pathways for this form of cognitive niche construction. These uncertainties notwithstanding, NCT strongly supports the notion—the hypothesis—that the environment you are born into and grow up in at once limits and facilitates the further development of ideas, behaviours and material culture—not only in deep time but also in the present (Johannsen 2010; Sterelny 2007).

Constructing Niches from the Pleistocene to the Anthropocene

Niche construction theory has developed out of earlier models of gene-culture co-evolution and provides a terminology, conceptual framework and suite of methods to study the ways in which lasting modifications of the external environment create intended or unintended developmental and/or selective legacies in generations of organisms subsequent to the ones that initiated such modifications. There is no denying that NCT is a higher-order model for evolutionary process whose explanatory ambition equally aims at large-scale patterns and processes. The corollary of this is that many other approaches such as those employing optimal foraging theory or dual-inheritance theory can be nested within it. Not all workers agree on such nesting (see Gremillion et al. 2014 versus Zeder 2014), but reconciliation is, following Stiner and Kuhn (2016), possible with optimality theory and niche construction perspectives providing complimentary insights at different scales (see Chap. 13, this volume). NCT is, I argue, particularly attractive to human scientists because it rests on the realization that humans especially have a degree of influence—agency—when it comes to shaping the environs and hence the selective pressures under which they come. NCT is furthermore particularly attractive to archaeologists given that the temporal dimension of such niche modifications is a critical factor in the model; NCT articulates well with environmental archaeology (Riede 2012), with behavioural ecology (Stiner and Kuhn 2016) as well as with more agentive approaches (Riede 2005a). This integrative capacity of NCT also comes into play in recent suggestions that anthropology more broadly—that is, including ethnography and social anthropology, which are traditionally difficult to reconcile with any form of evolutionary thinking—can be brought under the wing of evolutionary approaches (Fuentes 2009, 2016).

The literature on NCT and its archaeological applications is growing. Methodological diversity is a strength for any body of theory; a palette of different methodological approaches ranging from the descriptive to the strictly quantitative—including causal graphing, the comparative method using artefact phylogenetics, and modelling—has been brought to bear in this field. Empirical data range from quite traditional archaeological observations and typo-technological analyses to large-scale palaeogenetics. An important next step is that some or all of these methods are applied across multiple data sets and case studies. This would make the effects of different niche construction behaviours and their efficacy and effects more directly comparable and would lead towards the establishment of a standard methodological toolkit associated with this theoretical framework. My recommendation is that, in particular, cultural phylogenetics and distribution modelling are explored further within an NCT framework. The former offers the prospect of controlling for historical relatedness amongst the archaeological operational units of analysis and captures temporally unfolding processes well. The latter's strength rests in its spatial explicitness.

NCT posits that many organisms and above all humans modify their niche parameters so that developmental and selective processes are significantly altered. In parallel with the emergence and formalization of NCT, the idea of the Anthropocene was proposed (Crutzen and Stoermer 2000). The term Anthropocene was intended to signal that humans had collectively matched or surpassed natural forces in shaping biotic and abiotic dynamics on earth. Since its initial proposal, the term has engendered lively debate across the natural and human sciences: some reject it outright; others embrace it as a useful scientific or political concept (e.g. Malhi 2017; Finney and Edwards 2016; Swanson 2016; Carey 2016). Its reality *or* utility aside, there is also considerable debate about when the Anthropocene started—candidate dates range from the period of Late Pleistocene megafauna extinctions some 50,000–40,000 years ago at one extreme to the period of nuclear bomb explosions and the emergence of mass-produced and mass-consumed plastic around AD 1950 at the other (Zalasiewicz et al. 2015, 2017; Waters et al. 2016; Walker et al. 2015; Lewis and Maslin 2015). Numerous commentators stress that defining a late onset of the Anthropocene (i.e. AD 1950 or similar) ignores the long process that has brought humans in this position in the first place (Foley et al. 2013; Braje and Erlandson 2013). Indeed, plant and animal domestication (Braje and Erlandson 2013; Smith and Zeder 2013) and fire use and forest clearance (Glikson 2013; Ruddiman 2013)—the primary examples of human niche construction sketched out above—have also been put forward as either markers for the onset of the Anthropocene or as major milestones on the way towards it. Yet, NCT can also inform conservation and management practices in these novel ecosystems (Boogert et al. 2006; Laland et al. 2014; Laland and Boogert 2010). Returning to the Eurasian beaver, for instance, reintroductions of this species have been quite successful (Nolet and Rosell 1998) and now assist in land management in important ways (Puttock et al. 2017). Informed by NCT, this rewilding strategy—in its own right a deliberate, theory-driven attempt at contemporary niche construction based on scientifically derived predictions of the ensuing selective consequences—could restore many ecosystem services that *prior* human niche construction has disrupted (Ellis et al. 2016; Ellis 2015).

Both NCT and the notion of the Anthropocene remain contested in their own rights. With their intellectual origins in evolutionary and ecological theory on the one hand and political geology on the other, both address the ways in which humans in particular have modified and continue to modify their own and other organisms' niche parameters. It is being increasingly argued that the two concepts can be productively coupled in the sense that NCT provides a process-oriented, evolutionarily, ecologically and socially grounded mechanism for understanding the unfolding of the Anthropocene (Boggs 2016; Smith and Zeder 2013; Ellis 2015; Fox et al. 2017). Indeed, better articulating the idea of the Anthropocene with NCT also offers the potential for deriving action-oriented insights regarding the current socioecological crisis that are informed by biocultural evolutionary theory (Carroll et al. 2017; Ellis et al. 2016; Brewer et al. 2017; Brewer and Riede 2018, see also https://evolution-institute.org/). The jury is still out as to whether these two ideas stand the test of time and of scientific usefulness; both notions, however, seem to be doing a great deal of useful, integrative and interdisciplinary work in the present.

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Part IV
Evolutionary Cognitive Archaeology

Chapter 18

A Brief Overview of Evolutionary Cognitive Archaeology

Marc A. Abramiuk

Introduction: The Two Objectives of Evolutionary Cognitive Archaeology

Evolutionary cognitive archaeology (ECA) makes primary use of archaeological data to study the evolution of mind, also referred to as cognitive evolution, within the human lineage. As a particular subfield of cognitive archaeology, which more generally examines *how* and *what* people thought in the past, ECA is primarily concerned with making cognitive inferences based on material remains. A secondary objective that concerns ECA is determining how cognitive evolution unfolded, which amounts to identifying the mechanisms that are involved in cognitive evolution. Both of these objectives will be discussed—in the first half and second half of this chapter, respectively.

It is worth noting that the primary objective of ECA, namely, inferring cognition from material remains, need not depend on the secondary objective of ascertaining what mechanisms were involved in cognitive change over time. This is to say that one can agree that cognition has changed throughout our lineage and can draw inferences regarding what and how our conspecifics were thinking, without necessarily agreeing on how the changes to cognition manifested. This is a fortunate state of affairs, as scientists can largely work independently on both objectives without relying on the other and, in so doing, advance both fields of inquiry. At the same time, there is much to be gained from cross-disciplinary research between those who reconstruct cognition in the past and those who attempt to understand the processes responsible for cognitive change.

A Brief History of the Methods Used in ECA and the Cognitive Inferences Made

It could be argued that archaeologists from the start were compelled to make inferences about cognition in the past—at first implicitly and, only later, explicitly. In the earliest studies, archaeologists became involved in speculating about the mind in the past using distinctive terminology, such as “mental images” or “mental templates,” “syntax,” and “decisions.” Eventually, inferences concerning past people’s cognitive capabilities and thought processes, concepts recognizable to archaeologists

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and cognitive scientists alike, began to be formulated. Today, inferential research into cognitive capabilities and ways of thought persists but is overlaid by inquiries into the origins of representation, art, mathematics, science, and other forms of expressions and systems of thought. Whatever the aspects of cognition being inferred, it is clear that the development of cognitive inferences in ECA is tied to four main methodological approaches in ECA. In what follows, cognitive inferences and the methods to which they are unreservedly bound will be discussed.

The Typological Approach: Inferring Functional Meanings, Mental Images, and Mental Templates

It has been pointedly argued that typological classification, the activity involving grouping artifacts (into *types*) based on shared attributes (to form *typologies*), is largely for the benefit of the archaeologist in order to organize archaeological material (Ford 1954). The result of synthesizing the archaeological material in this way helps archaeologists communicate with other specialists about the material, as well as helps archaeologists answer particular research questions using the material. However, in the early development of typologies, attributing cognitive meanings to artifact types was commonplace. Archaeologists in many cases assumed that the types being formed were those of which the manufacturers or utilizers of the artifacts would have been cognizant.

Functional Meanings

The three-age system (Thomsen 1848; Worsaae 1849), a chronological typology which has been refined over the years and continues to form the basis for studying early human evolution, exemplifies how a typology can play a role in cognitive inference. While the three-age system's main purpose has been to help archaeologists determine the ages of artifacts and thereby classify them, it implicitly necessitates that archaeologists attempt to identify the functions of the artifacts. In the nineteenth century, this often amounted to naming the artifacts according to their presumed uses. Examples include providing artifacts with such names as axes, knives, spearheads, and chisels, among others. Early archaeologists, therefore, indulged in little cognitive archaeological inference beyond that of naming the artifacts, but, in so doing, they were attributing functional meanings to the artifacts. Moreover, by assuming how artifacts were used, archaeologists were effectively suggesting that they were somehow attuned to how people in the past cognitively categorized the artifacts.

With some obvious exceptions, the names of many types have withstood scrutiny and have persisted. In ideal cases where there is other evidence to support the terminological usage, functional terms are mostly understood only to approximate the artifacts' original functions. In less optimal cases where the only guide to the artifacts' functions is that artifacts *look like* they served particular functions, these terms are seen as arbitrary placeholders. The method of arbitrary assignment, however, has been losing traction. As archaeologists are improving the techniques they use to analyze residues on artifacts, they are providing more compelling insight into the functions the artifacts served (e.g., Lombard 2004). As this research continues, so will the ability to attribute functional meanings to artifacts more accurately.

Mental Images or Templates

By the mid-twentieth century, archaeologists had been paying more attention to aesthetics and attributing complex meanings to morphological types. Types based on aesthetic characteristics were seen as having emic significance that could be uncovered by the archaeologist through "... a process of discovery of combinations of attributes favored by the makers..." (Spaulding 1953, p. 305; cf. Ford 1954). That morphological types were beginning to be seen as reflecting the aesthetic senses of the makers and, therefore, more explicitly viewed as windows into the minds of people in the past is quite clear by the 1960s (e.g., Spaulding 1960, p. 76); this is particularly obvious with the introduction of the term "mental template" (Deetz and Dethlefsen 1965) to refer to an ideal socially learned pattern. This shift toward cognitive concerns is keenly exemplified in how archaeologists began interpreting Lower and Middle Paleolithic stone tools (Bordes 1968). During the 1960s some archaeologists were arguing that Paleolithic people must have had predetermined "mental images" (Bordes 1968, pp. 27, 137) in order to manufacture certain artifacts. Accordingly, morphological types were effectively manifestations of conceptions imagined by the manufacturers (1968, p. 137). Variations, on the other hand, were deemed mistakes made by the makers or modifications made in the face of unanticipated circumstances (Débenath and Dibble 1994, p. 6) (e.g., identifying imperfections in the source rock that could result in affecting the final forms of the artifacts).

It was these early speculations concerning the nature of both functional and morphological types to which the seeds of ECA can be traced. The typologies that archaeologists formed were effectively seen as recapitulations of the functional meanings and morphological mental images that early people had maintained. Indeed, Bordes would suggest that there was an evolutionary sequence to the rise of such mental phenomena. Bordes (1968, pp. 45, 137) believed that toolmakers were generally preoccupied with functional meanings, such as sharp edges, throughout the Lower Paleolithic. It was only at the end of the Lower Paleolithic and the onset of the Middle Paleolithic that attention was being paid to morphology and when mental images of shapes began to develop.

In addition to postulating that the final artifact form could be preconceived, late Middle Paleolithic and Upper Paleolithic people were also deemed capable of maintaining conceptions of geometric shapes, such as triangles and ellipses (Bordes 1968, p. 137). Thus, Bordes was not only suggesting a late cognitive stage in which the currency of thought consisted of mental images, but he was postulating the precise forms that these mental images took. Bordes' more specific claim concerning Paleolithic familiarity with ideal geometric forms was believed to be evidenced by the standardized shapes of later Acheulean handaxes and Solutrean laurel leaf points.

According to Bordes (1968, p. 136), not only was conceptualizing geometric images demonstrated in the chipped stone assemblages by the end of the Lower Paleolithic, but typological distinctions in chipped stone assemblages were seen as cultural differences. This latter point meant that mental images, reflected in the types distinguished by archaeologists, could vary between contemporaneously living peoples. Although propensity for generating mental imagery was deemed to be cognitively universal by the end of the Lower Paleolithic, the kinds of mental images were seen to be culturally inculcated. A case in point is the presence of Acheulean handaxes only in Africa, Western and Southern Asia, and parts of Western Europe, which Bordes attributed to the existence of a culturally distinctive mental image. While the mental image of the handaxe would have figured prominently in the minds of people in the aforementioned locations, it would have had practically no cognitive traction in the rest of the Old World, demonstrated by the lack of handaxes in much of Asia and Eastern Europe.

Generative Concepts

Such views concerning mental images or templates soon began to be overtaken by the work of those who interpreted images or templates as having a generative basis. Here, "generative concept" refers to a mental composite of rules or instructions that would have been responsible for motivating certain cultural expressions (e.g., painted images). Some of the earliest research into generative concepts can be traced to Henri Breuil (1952) and later to André Leroi-Gourhan (1965, 1972). Both Breuil and

Leroi-Gourhan relied on generative concepts to explain the meaning of the Upper Paleolithic images of animals as well as other figures painted on the walls of caves in the Franco-Cantabrian region. Postulating that mental images were responsible in this instance would have been superfluous, as the images that would have been in the mind were clearly painted on the cave walls. The purpose for these researchers, therefore, had less to do with postulating images in the mind and more to do with revealing generative concepts in the form of rules or norms that motivated the creation of these images.

For Breuil (1952), these generative concepts comprised the people's religious beliefs, and for Leroi-Gourhan (1965, 1972) they were the structural underpinnings of the human mind. Breuil asserted that the people of the Upper Paleolithic who painted the images maintained a belief in sympathetic magic—the belief that one can appeal to the supernatural to assist in some real-life event. For Upper Paleolithic people, appeals could be manifested through painting images of the event. For people who relied on hunting as their main means of subsistence, such events would have maintained a universal theme, namely, the need for abundant fauna and success in the hunt. In contrast to Breuil, Leroi-Gourhan believed that generative concepts were binary oppositions in need of reconciliation. Leroi-Gourhan, in this case, asserted that the painted images embodied the universal opposition between male and female and that their composition in the cave allowed for their resolution. This would be much like the recounting of a myth which acts to neutralize the mixed and sometimes antithetical motives of its protagonists (Lévi-Strauss 1981, p. 87).

The Chaîne Opératoire Approach: Inferring Syntactic Aptitude and Decisions

If the seeds of cognitive inferential research in ECA can be traced to archaeologists' penchant for forming typologies, then surely the roots of cognitive inferential research lie in the method of lithic analysis introduced by the French archaeologist Leroi-Gourhan (1993 [1964]) known as *chaîne opératoire* (translated as "operational sequence"). Leroi-Gourhan described *chaîne opératoire* as the sequential organization of actions involved in toolmaking and other activities "... by means of a 'syntax' that imparts both fixity and flexibility to the series of operations" (1993 [1964], p. 114). As an analytical method, its main use has been to understand the process of lithic reduction by organizing it into a series of activity stages leading to the artifact's manufacture (see Geneste 1985). However, the method in its broadest interpretation extends well beyond the initial lithic reduction process to include the procurement of the raw material to manufacture the stone tool, as well as the maintenance (e.g., resharpening) and final discard of the artifact. Beyond lithics, the method has been advocated extensively in archaeology to analyze sequentially the manufacture of other artifact types (e.g., Godon 2010), and its use has even been adopted and promoted in ethnographic work (Lemonnier 1976, 1992). It should be noted too that the method of *chaîne opératoire* appears to postdate a nearly identical method that had first come into fashion in the United States through the work of William H. Holmes (1894) at the end of the nineteenth century referred to as *reduction sequence* (Shott 2003). Nonetheless, it would be *chaîne opératoire* that would have a more direct role to play in the history of ECA even if only in name.

Syntactic Aptitude: Relating the Whole Operational Sequence to its Parts

With the initial use of *chaîne opératoire*, a significant step toward the modern study of cognitive evolution was taken. Leroi-Gourhan believed that operational sequences are products of learning and that, in time, operational sequences become automatic, subconscious behaviors (White 1993, p. xviii). Operational sequences are culturally derived and conditioned; acquiring these operational sequences, it was believed, would have been similar to how an individual learns a language from infancy. Indeed, Leroi-Gourhan elaborated further to suggest that an operational sequence has a syntax that provides a certain amount of structure to the order of operations just like the syntax of a language does for words in a sentence; moreover, he proposed that both syntaxes come from the same stock aptitude. Because of this proposed common cognitive origin, syntactic characteristics, such as flexibility and rigidity, which are observed in operational sequences, could be used to infer similar or analogous syntactic characteristics in the development of language (Leroi-Gourhan 1993 [1964], pp. 114–115).

Leroi-Gourhan envisaged operational sequences as means for gaining insight into the nature of the mind as it relates to linguistic capability, but he also recognized that operational sequences and, by implication, linguistic capability evolved. He observed, for example, that the “syntactic” complexity of operational sequences increased through time, which indicated to him that the capacity for language was developing, albeit at a nonconstant rate (White 1993, p. xix). From the time humans shared a common ancestor with apes, operational sequences were extremely rigid and slow to change, indicating to Leroi-Gourhan that language too was evolving excruciatingly slowly. After our genus emerged, the rate of linguistic evolution was believed to have increased gradually until the last 50,000 years when it suddenly surged (Leroi-Gourhan 1993 [1964], pp. 114–115) in step with the increased syntactic fluidity observed among operational sequences.

Based on discoveries in Europe, figurative representation also proliferated rather suddenly in the last 50,000 years. For Leroi-Gourhan, this cultural “renaissance” indicated the formation of yet another cognitive ability in addition to forming sentences and operational sequences, which he believed arose from the same syntactic aptitude upon which language and technics are based. With the rise of figurative representation, memories and observations could be recorded externally and began to be expressed on a variety of media. Moreover, like operational sequences, figurative representations began to be analyzed in such a way that they too could be used to index syntactic fluidity and, by implication, the development of the linguistic mind.

Decisions: Analyzing the Individual Stages in the Operational Sequence

The method of analyzing archaeological data in terms of operational sequences led archaeologists by the 1980s to consider analyzing each step in its own right (in addition to how the steps relate to the entire operational sequence). The removal of the syntactic connotation in *chaîne opératoire*, which was responsible for holding operational sequences together, naturally permitted their deconstruction. In so doing, different ways of interpreting operational sequences began to emerge, which led to different analytical emphases. Examining each technical decision that was made in the course of each stage of the operational sequence began to overshadow envisioning operational sequences as entire compositions held together by syntactic rules.

The new way of looking at *chaîne opératoire* sought to reveal to the archaeologist each decision that led to each stage in the operational sequence. Ancient toolmakers’ technical decisions were revealed through jointly studying the by-products as well as end products of toolmaking and reconstructing (through analytical activities such as refitting) the techniques and knowledge that would have been involved in each step of the life cycle of the tool. For certain archaeologists, what was inferred from each step is that technical decisions are based on making use of two bodies of knowledge for making tools, *connaissance* and *savoir faire* (Pelegrin 1990; Boëda 1995; Chazan 1997). Although both *connaissance* and *savoir faire* are believed to be discernable beginning as early as the Lower Paleolithic (Hallos 2005; Stout and Khreisheh 2015, p. 869), these proposed knowledge sets become more clearly pronounced by the Middle Paleolithic (Boëda 1995; Chazan 1997).

Connaissance constitutes what can most accurately be described as the declarative knowledge that pertains to the toolmaking task. This is knowledge of facts concerning the manufacturing process—for example, knowing that there are correct and incorrect ways to knap or that applying percussive force from one angle is more effective for removing a flake than applying it from another angle. *Savoir faire* can most accurately be described as procedural knowledge, or the *know-how* needed to make tools as well as the requisite motor skills. Some writers often simply refer to *savoir faire* as skill (Chazan 1997, p. 733), but that *savoir faire* also involves procedural knowledge is quite clear. The procedural knowledge in this case would be the knowledge of how each knapping step unfolds and leads to the next step. Defined in these ways, decision-making can be fundamentally seen as a dialog between *connaissance* and *savoir faire*. *Knowing how* to do a technical act will be guided in part by declarative knowledge, but selecting the declarative knowledge relevant for a particular task will also depend on the state of one's *savoir faire*.

To summarize, one of the major goals of *chaîne opératoire* was to consider all the steps involved in achieving the final artifact form. As an approach, *chaîne opératoire* offered more opportunities to study aspects of cognition that were involved throughout the life cycle of a tool's manufacture, use, and eventual discard. Initially, *chaîne opératoire* was used to postulate the evolution of syntactic aptitude believed to underlie language, technics, and representation. However, since this time, it has facilitated the archaeologist in examining the decisions that are made throughout a specific technical act. By reconstructing the decision-making process, for example, analysts of *chaîne opératoire* have come to infer two sets of knowledge that are seen to be relied upon throughout a given technical act: *connaissance* and *savoir faire*.

The Conditional Approach: Inferring Cognitive Capabilities and Thought Processes

By the end of the 1960s, inquiries about how cognitive capabilities and thought processes evolved began to rise to prominence, overlaying those inquiries concerned with mental images, knowledge, and decisions. With *chaîne opératoire* and the related notion of reduction sequence in the analytical repertoires of European and North American archaeologists, respectively, archaeologists on both sides of the Atlantic were in a position to make the next conceptual move to form a truly explicit archaeological study of cognitive evolution. To take the final step in this direction, however, models from cognitive science were needed to allow the archaeologist to piece together the implications of tool assemblage characteristics and the related operational sequences for the development of the mind.

Although archaeologists throughout the 1960s and 1970s understood the implications of their research for understanding the evolution of mind (e.g., Bordes 1968; Leroi-Gourhan 1993 [1964]), they were working largely independently of cognitive scientists. By the end of the 1970s, archaeologists began to realize that to explain material cultural changes (or lack thereof), as well as to make contributions regarding the development of the mind, they would need to become familiar with cognitive scientific models and empirical research. Short of this kind of cross-disciplinary research, their findings would not translate in ways relatable to cognitive scientists. Cognitive scientists were just beginning to appreciate the implications of studying archaeological remains to glean insight into the topic of cognitive evolution (e.g., Holloway Jr 1969). In the end, it would be these researchers' explicit concern with cognitive evolution together with archaeologists' amenability with becoming steeped in cognitive scientific theory (see Wynn 2017) that would motivate modern ECA.

The earliest explorers of this new wave of evolutionary cognitive archaeological research were Sue T. Parker and Kathleen R. Gibson (1979) and Thomas Wynn (1979), but it would be the latter's work that would more directly address cognitive evolution by analyzing a specific collection of artifacts. Wynn would attempt to account for the cognitive development of Acheulean toolmakers by examining their tools from Isimila Prehistoric Site located in Tanzania. Using Piaget's cognitive development model, Wynn surmised that spatial organizational capability of Acheulean toolmakers differed little from that of modern human adults, as gauged by the knapping techniques used to manufacture their tools. Since the tools could be dated to approximately 300,000 years ago, it suggested that by this time the intelligence of the hominins responsible for making the tools, as judged by their spatial organizational capability, was well established; furthermore, it was concluded that the cultural developments that multiply after this time were likely not the result of increased intelligence. That spatial organizational capability might not be an accurate index for intelligence is something that Wynn (2017) has questioned subsequently; however, the fact that spatial organizational capability could be inferred through deducing what would have been necessary to manufacture ancient tools represents a watershed moment in ECA.

More specifically, Wynn looked at the spatial organizational capability involved in relating a whole to its parts in Euclidean space. Wynn believed that evidence of this capability was recognizable in the retouches that were added to the tool after the core had been generally shaped. By examining a particular stage in the operational sequence of Acheulean toolmaking, Wynn was able to make a claim about cognitive capability. Not only was this one of the earliest attempts by an archaeologist to meet halfway with cognitive scientists to infer cognitive capabilities, thereby enhancing our understanding of cognitive evolution, but it would set a precedent for how ECA would be analytically practiced. Abramiuk (2012) has referred to this analytical approach as the "conditional approach." The conditional approach is a characteristic way certain cognitive archaeologists set up an argument for reasoning about cognitive capabilities, and it has proven extremely useful. As the name implies, it consists of inferring cognitive capabilities through a framework of argumentation using conditional statements.

Reasoning about conditional statements can be found in the way that we reason about many things in everyday life. It is not unique to cognitive archaeology or even to scientific practice in general. However, insofar as the conditional approach relates to cognitive archaeology, the conditions about which one is reasoning specifically concern the relations between particular behaviors and cognitive capabilities. The conditional approach has been known to be used in the modus ponens case, such that if there is particular behavior evidenced, an associated cognitive capability is proposed as its catalyst. In entirely separate cases, it is also common to find the modus tollens version used by cognitive archaeologists. This latter form, for example, can be used to argue that the absence of evidence of a particular behavior implies the absence of a particular cognitive capability (Abramiuk 2012, pp. 148–150).

The conditional approach has been exploited extensively by cognitive archaeologists in general and serves as a means of inferring not only cognitive capabilities but thought processes. This became clear in the publication of *The Ancient Mind: Elements of Cognitive Archaeology* (1994), edited by Colin Renfrew and Ezra B. W. Zubrow, in which it was argued that thought processes can be inferred through what can most accurately be described as a conditional approach. By thought process what is meant is any complex cognitive task that applies to a particular real-world circumstance. A thought process can be assumed to involve certain fundamental functioning cognitive capabilities, e.g., perception, long-term and short-term memory, and reasoning, among others; nevertheless, they clearly differ, particularly as thought processes depend on cognitive capabilities. Examples of thought processes include such tasks as planning, measuring, designing, as well as others.

Inferring cognitive capabilities through the conditional approach was crucial to the advancement of cognitive archaeology, but so too was inferring thought processes through the conditional approach. Not only is examining thought processes a more accessible endeavor for a nonspecialist unfamiliar with cognitive scientific terminology, but it addresses more pragmatically how humans think while they engage in the world. Although focusing on thought processes overlooks the finer elements of cognition, it allows for practical thinking to be teased from the archaeological record. As a result, both cognitive capabilities and thought processes continue to feature prominently as research objectives in evolutionary cognitive archaeological discourse.

The Materiality Approach: Inferring Cognitive Scaffolds

The term "materiality approach," borrowed from DeMarrais et al. (2004, p. 2), is used here to encompass a few related programs for illuminating the mind in the past that are all based on the premise that the mind is inextricably linked in varying degrees to our cultural and, more broadly, material surroundings (Abramiuk 2012, pp. 17–19, 105, 110). Two programs that take on a more forceful position that emphasize the active role of the material world on our minds are material engagement theory (MET) and radical embodied cognitive archaeology (RECA) (see Chap. 19). At the philosophical core of these programs is the view that the mind is embodied, extended, and enacted (EEE). The practitioners of these programs are committed to the idea that mind, body, and surroundings, cultural or otherwise, comprise a unity (Knappett 2005; Malafouris 2004, 2013; Garofoli 2018). Among the advantages of the EEE view of the mind is its ontological perspective, which is monistic. Therefore, it avoids capitulating to Cartesian dualism which the proponents of MET and RECA believe is inherent in much of ECA—an example being the tendency for archaeologists to analytically treat mind frames as *internal* and behavior or material culture as *external*. It also avoids envisioning only humans as agents when agency, it is argued, can be found in the actions and objects with which humans engage.

Through its anti-dualist ontological commitment, advocates of MET argue that they can provide some insight into how certain watershed events, such as the advent of art, initially may have been spawned. A representational and, hence, dualistic explanation would have it that works of art are the products of mental images. One such compelling "representationalist" theory on the origins of art suggests that some of the earliest works of art were reproductions of mental images, in large part determined by the way early painters' brains were hardwired (Lewis-Williams 2004). These mental images, or so-called entoptic images, would have been triggered as the painter first entered an altered state of consciousness (Lewis-Williams and Dowson 1988). As the painter progressed toward unconsciousness, his or her mental images would have become more complex (e.g., visions of animals and hybrids) and clearly would have incorporated knowledge of one's local environment.

In contrast to suggesting that mental images or internal representations form the bases of the earliest art images, MET offers an alternative explanation. MET proponents advocate an enactive view of the mind in which meaning emerges in rudimentary stages beginning with the act of mark-making and culminating eventually in the creation of an image. In other words, the image is built up in a stepwise fashion based on each prior mark, but with no prior complete image or gestalt in mind.

Choosing a Heideggerian manner of describing what is seen as culture's effects on the mind, MET tells us, for example, that stone tools can be "brought forth" through the action of knapping (Malafouris 2013, p. 172–173) and that images and associated cognitive representations can be "brought forth" through mark-making (Malafouris 2013, p. 204). As an example, Malafouris (2013, p. 204) contends that mark-making, such as that evidenced at Blombos Cave as early as 100,000 years ago, functioned as the necessary cognitive scaffolding needed to allow for the development of detailed images (e.g., those painted at Chauvet-Pont-d'Arc Cave and other Franco-Cantabrian caves) and the accompanying representational thoughts. In other words, mark-making would have incrementally afforded the ability to form images over time. The image, in turn, would have acted as a freeing device or device for the "liberation of sight" which would have enabled human perception to be aware of itself, allowing the human to reflect on his or her thoughts.

In RECA, language acquisition has similarly been described in a phenomenological manner. Accordingly, language capability was "brought forth" through artifacts such as body adornments, creating the social contexts for the exchange of vocalizations (Garofoli 2018, p. 17). The repetitiveness of certain vocalizations in particular instances would have resulted in vocalizations being used to refer to concrete things, as well as to abstract concepts which would have found themselves tied to perceptual invariances observed in the course of social interactions (2018, p. 18).

The view that culture acts as cognitive scaffolding adds another dimension of cognition that can be explored by evolutionary cognitive archaeologists. The materiality approach advocated in MET and RECA suggests that each engagement with culture, such as a strike to a lithic core, would have functioned as scaffolding for conceiving and simultaneously guiding the next action. Furthermore, when all such engagements are taken together in relation to a particular context, they can potentially serve as platforms for certain cognitive developments and innovations to take place, such as image making and language acquisition. Like *chaîne opératoire*, the materiality approach proponed in MET and RECA looks at examining cognition dynamically rather than statically, but it does so more seamlessly as well as holistically by incorporating human, material culture, and action into the cognitive process.

Identifying the Mechanisms that Are Involved in Cognitive Evolution

As was discussed above, a number of approaches for inferring mind frames have been adopted over time in ECA. The goal consequently for most evolutionary cognitive archaeologists has been to reconstruct different aspects of cognition (e.g., mental templates, decisions, cognitive capabilities, among others). In the course of these inquiries, the main mechanism by which the different aspects of cognition would have evolved was assumed. Taken from biological evolution and adapted to account for the evolution of "mental faculties," this mechanism was natural selection (Darwin 1888, pp. 127–129).

To briefly summarize the role of natural selection in cognitive evolution, which has enjoyed substantial longevity, one must highlight the role of culture and its relationship to these so-called mental faculties (or what today may be termed cognitive capabilities) and the local environment. According to Darwin, culture is seen as a means of adapting to a specific environment (1888, p. 127). Humans, unlike many other species that are forced to adapt to their environment directly through advantageous physiological traits, use their mental faculties to create culture. The mental faculties that would have aided in inventing and propagating the specific cultural means to adapt to one's environment are variable, and certain advantageous variations would have been inherited. This is to say that natural selection acts on mental faculties through culture. Those mental faculties that are responsible for the creation or adept utilization of cultural items, such as tools or even art (see Mendoza Straffon 2016), and that permit those individuals to succeed in having viable offspring are passed on.

At the same time, Darwin (1888, p. 54) believed that changing mental faculties leads to changes in the properties of the brain—size being the most often cited.[1] This view continues to carry on in much of ECA.[2] Following Santiago Ramón y Cajal's (1894) and Camillo Golgi's (1898)

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[1] It is similarly clear that Darwin (1888, p. 54) had a well-formed notion that relative brain size (to body size) could serve as a metric for comparing cognitive capabilities among different species—what we would refer to today as encephalization quotient.

[2] Darwin believed that it was mental (or cognitive) changes that drive changes to the neural substrate rather than the reverse. Whereas the brain was seen as an anchor point for the mind—and therefore a useful index for understanding the mind—the mind was something not entirely neurophysiological but also extrasomatic (Darwin 1888, pp. 54–55). This is exemplified in his belief that the reason for the smaller brain sizes in domestic rabbits in relation to wild rabbits is their confinement which restricts their "intellect, instincts, senses, and voluntary movements" (p. 55). This extrasomatic view is further anecdotally implied in Darwin's recognition that even though the cerebral ganglia are proportionally larger than those of other insects, he still wonders how such impressive mental powers of ants can fit on "the quarter of a pin's head" (p. 54). His proposal that it is through culture that the natural selection of mental faculties is actualized in cognitive evolution largely explains the leading role of the mind (or cognition) and the role of the brain as an evolutionary by-product, albeit an important one.

breakthrough studies on neuronal functioning and Donald Hebb's (1949) pioneering research on how the synapses of neurons are strengthened through persistent stimulation, Darwin's proposed role for natural selection in cognitive evolution received the neurophysiological backing that was hitherto lacking. This research suggested a link between cognitive processes, such as learning, and neural growth. More specifically what was inferred was that cognitive tasks, such as forming associations, could potentially build or change the metabolic character of neural tissue. As a result, the notion that certain cognitive capabilities could have fostered cultural developments and proficiencies to the extent that these developments and proficiencies could have improved reproductive success and left a neurological imprint seemed entirely plausible. Moreover, the proposal that the properties of the brain, such as size, could provide at least some insight into certain basic cognitive capabilities seemed equally reasonable.

It was not until the last half of the twentieth century that other mechanisms integral to biological evolution—genetic drift, migration, and mutation—were also deemed feasible for explaining how cognition evolves. Mutations of course would suggest that sudden brain alterations could instigate mental changes (e.g., Klein 1992, 2008; Zhang 2003), the reverse of what Darwin envisioned as the mechanism for cognitive evolution. Nevertheless, natural selection continues to play a central role in our understanding of cognitive evolution even in the case of mutations which, of course, require natural selection to perpetuate them.

How Culture and Nature Relate in Cognitive Evolution

With this said, questions persist regarding the relationships between culture, cognition, and natural selection. Darwin (1888, p. 127) in agreement with Wallace (1864, p.158) believed that culture—a product of cognition—affords such advantages to human fitness that human physiology could remain relatively unchanged despite a changing environment. In the Darwinian view, culture is seen as the means through which cognition is expressed and through which fitness can be gauged as humans interact and engage with their local environment. Here, though, the primacy of nature over culture is clear. Cognition evolves so long as the cognitive traits of individuals contribute or perpetuate a cultural repertoire for increasing reproductive success. This view that natural selection is a determining force in congnitive evolution, together with developments in genetics and the rise of the modern evolutionary synthesis (Huxley 1942), has inspired certain interpretations of the relationship between natural selection and culture in cognitive evolution. One of the more extreme interpretations that advocates the primacy of nature as Darwin did, albeit at the expense of internalizing culture—a move that is at odds with Darwin's extrasomatic view of culture—can be found in evolutionary psychology.

Evolutionary Psychology and the Primacy of Nature

Evolutionary psychology is a subfield that explores how psychological traits in the human species can be interpreted as adaptations to ancient environmental conditions. Evolutionary psychology embraces a gradualistic view of cognitive evolution in which adaptation and the resulting effects on cognition through natural selection occur extremely slowly, a consequence of a "stable" environment. This environment, it is asserted, existed throughout most of the Pleistocene. At the end of the Pleistocene and the subsequent Holocene, the environment changed too rapidly for cognitive evolution to unfold via natural selection. Thus, the modern human mind for all intents and purposes exists as a relic of the Early to Late Pleistocene, equipped with innate modules programmed to succeed in Eastern Africa in what is generally taken to be a savanna-like environment. In short, the psychological traits of humans are seen as well-hewn problem-solving traits that were naturally selected and as a result have become hardwired in the human brain.

The roots of evolutionary psychology can be traced to Fodor's (1983) two-tiered model of the mind, which envisioned human perception as a cognitive module that was separated from a central general-purpose module that dealt with conceptual information—a design that was seen as optimal for processing information efficiently. After Fodor, more modules dealing with conceptual information were postulated (see Tooby and Cosmides 1992). These were domain-specific modules, each of which would have evolved to solve a particular problem upon which our lineage's survival depended in the distant past.

There are, however, several problems with a massively modular Darwinian model. We now know that the Pleistocene environment was not as stable as was earlier surmised, that the rate of response to selection is faster than we previously thought among many animals including humans, that culture can actually accelerate this rate in certain cases, and that evidence points to a mind that has evolved with multiple domain-general mechanisms (Bolhuis et al. 2011) rather than one that has evolved though immensely domain-specific ones (Mithen 1996). Despite these seemingly contradictory findings and their respective implications for the nature of cognition, the notion that some cognitive capabilities, such as certain aspects of perception (Abramiuk 2012, p. 104), are largely innate and evolved through natural selection is an idea that cannot be easily dismissed.

Cognitive Evolution: Darwinian or Non-Darwinian?

As discussed above, a Darwinian framework is one that grants natural selection, but also reproduction and inheritance, key roles in the evolution of cognition, as well as the evolution of culture by implication (Darwin 1888, pp. 144–145). Culture effectively functions as an interface through which humans interact and engage with the environment. As an interface, culture has potentially a significant role to play in cognitive evolution provided that culture allows the individual to chart a successful course through the natural historical processes at work. Still, as was mentioned above, the sense is that culture succeeds only if nature permits it, thereby granting culture an indirect facilitative role, but not a direct active role in cognitive evolution.

That culture also has a direct active role in cognitive evolution, however, is a notion that, in recent decades, has begun to feature prominently in research (Boivin 2008; Donald 1991; Renfrew 1998, 2001, 2007). Accordingly, there are now models that have the potential to include or focus almost entirely on the non-biological ways in which cognitive capabilities may emerge. Some of these models find themselves in opposition to a Darwinian framework (e.g., Malafouris 2016, Knappett 2016, Chap. 19). In these non-Darwinian conceptions—MET and RECA being particularly useful examples—cultural products or acts are not expressions of certain cognitive capabilities at work; nor are they means through which humans adapt and potentially succeed in a particular niche. Rather, cultural objects and actions function as cognitive scaffolds that directly support the unfolding of still more cultural and cognitive developments. Accordingly, mind and culture can be seen to be locked in a perpetual feedback loop that mutually reinforce each other, or more accurately described as double aspects of the same material basis progressing together (Abramiuk 2012, pp. 17–18).

This more direct active role that culture is proposed to play in cognitive evolution relates to another distinguishing characteristic of MET and RECA. That is the diminishment of the role that natural historical processes, such as natural selection, play in cognitive evolution (cf. Garofoli 2016) by placing an overriding emphasis on the recursive and entangled relationship that exists between cognition and culture. Although in MET, it is asserted that natural historical processes responsible for biological evolution have some role to play in cognitive evolution (Malafouris 2016), no satisfactory formulation of how they relate to cognition and material engagement, while addressing the ontological concerns of MET and RECA, has been proposed to date. As Malafouris (2016, p. 301) freely admits, quoting Varela et al. (1993 [1991], p. 195), "Part of the difficulty in moving beyond the adaptationist

[Darwinian] framework is to determine what to do after we abandon the idea of natural selection as the main explanation, so that every structure, mechanism, trait, or disposition cannot be explained away by its contribution to survival value" (brackets mine).

In the absence of a satisfactory account of how natural historical processes, cognition, and material engagement can be unified, the effect is that of circumventing natural historical processes altogether in cognitive evolution. Effectively, cognitive evolution is reduced to proposed sequences of material engagements. Considerations of natural selection, reproduction, and inheritance are bypassed, and the circuitous route by which cognitive changes unfold is noticeably simplified.

Circumventing natural historical processes is also a characteristic of cultural transmission (Cavalli-Sforza and Feldman 1981; Boyd and Richerson 1982), which is a crucial process that plays out in the dual-inheritance model of cultural evolution (Boyd and Richerson 1985; Durham 1991). Although cultural transmission does not directly address cognitive development, the notion that natural historical processes can effectively be bypassed is one that is shared with MET and RECA. In the dual-inheritance (or gene-culture coevolution (Feldman and Laland 1996)) model, cultural change interacts with biological evolution, but cultural change can manifest sui generis through the mechanism of social learning (Boyd and Richerson 1985; Flinn 1997; Heinrich 2001; Heinrich and Boyd 1998; Shennan 2002, pp. 60–62). With regard to the interaction between biological and cultural evolution, certain cultural expressions can increase biological fitness; by the same token, certain cultural expressions can be filtered out due to genetic and, by implication, cultural drift. However, this does not preclude the possibility that cultural traits can be passed on and evolve largely independently of the natural historical processes and mechanisms that are entailed in biological evolution (see Chaps. 2, 3, 4, and 5, this volume).[3]

But are there such biological evolutionary shortcuts in *cognitive evolution*? If so, how and why did these shortcuts arise when they did? More importantly, where does this leave the natural historical processes that have been presumed to play such an important role in cognitive evolution? These questions that deserve to be treated in depth are unfortunately beyond the scope of this chapter. What can be said is that if there are such shortcuts, then there are limits on the kinds of cognitive developments for which they can account. The fact that brain expansion and brain organization seem to reach a stage that only begins to compare to that of modern humans at the end of the Pleistocene (Weaver 2005) suggests that it is improbable that natural selection was utterly bypassed. By this time, our lineage's entwinement with culture had been secured for at least 2.8 million years. Cultural expression had become pervasive and well established, and therefore so presumably would have the recursive relation between culture and cognition that MET and RECA advocate as being so central to cognitive evolution. Yet, neurophysiology continued to change and indeed continues to change (Evans et al. 2005). It could be argued that there is no relation between the continued neurophysiological changes and cognitive changes—a case of exaptation perhaps—but until such evidence is produced, natural historical processes cannot be entirely discounted in any account of cognitive evolution. Accepting that there is at least some relation between neurophysiological change and cognitive change and that natural historical processes were continuing to contribute to these changes, the real question for archaeologists concerns cognitive relatability. In other words, how far back can one go to find

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[3] These simpler proposals for addressing certain cultural developments do not directly depend on biological evolutionary or cognitive evolutionary explanations. Recall that Leroi-Gourhan hypothesized that during the Upper Paleolithic, increased fluidity of an underlying syntactic aptitude was responsible for both improved linguistic communication and increased technic complexity; however, Jelinek (1977, p. 15) has suggested that increased complexity during the Upper Paleolithic might have been driven by a shift in pedagogical practices. Lower Paleolithic assemblages largely appear to be the products of rote behavior with minimal innovation. As a result, the techniques involved in their manufacture were likely passed on through demonstration and imitation. Variability in the assemblages does not appear to increase significantly until the end of the Middle Paleolithic, which may be explained by a less directly guided form of passing on knowledge, such as that provided by verbal instruction.

humans that one would have been able to relate to? For epistemological reasons, this question is crucial, as it pertains to the limitations of the approaches that cognitive archaeologists use to infer mind frames in the past (Abramiuk 2012, 2015).

This being said, MET and RECA have an important role to play in ECA. That is that they provide a check on the circuity through which *cognitive functioning* is understood to unfold. In scientific research, it is not unheard of to have more than one credible explanation for a given set of data. In ECA as an example, there are a number of ways for plausibly explaining how people in the past manufactured tools. Whereas some evolutionary cognitive archaeologists are of the perspective that intermediate or final artifact form was dictated by intentional states in the form of mental templates relating to morphology (e.g., Pelegrin 1993; Schick and Toth 1994) or to function (e.g., Machin et al. 2007; Mitchell 1996), it has been alternatively argued that artifact form could be understood to be the result of engaging with the rock and the affordances it provides (Malafouris 2013, pp. 172–173; Chap. 19). Insofar as the latter explanation is concerned, MET and RECA provide ECA with a minimalistic account of cognitive functioning that relies on the scaffolding capacities presumed to be inherent in material engagements. In so doing, MET and RECA force archaeologists to reevaluate more complicated understandings of human cognition that rely on potentially superfluous notions, such as representations, that we might be able to do without (cf. Lewis-Williams and Dowson 1988).

With the rise of MET and RECA, ECA has become a much more critical field in the past couple of decades, a situation that the author feels is beneficial as it motivates the practitioner to seek more evidence to support an explanation or, as the case may be, to offer an alternative explanation for a given set of cultural remains. In Chap. 19 (this volume), for instance, Garofoli lays out an argument against an internalist view of cognition which he sees as unnecessarily complicated and pervasive in traditional ECA. He then goes on to present three alternative, externalist models, namely, the distributed approach, MET, and finally RECA for which he advocates. Focusing on the inseparable, continuously unfolding dynamic between culture and cognition and therefore the ratcheting effect that culture has on cognition, Garofoli proposes that the agenda of RECA is to trace the emergence of scaffolded minds. Such a proposal obviates the need for a toolmaker to maintain a mental image or representation of a final product. The knapper of an Acheulean handaxe, Garofoli argues, does not try to manufacture what he envisions—an assumption that is sometimes made in traditional ECA research; rather, the knapper is attuned to the invariant relationship between the knapping activity and the step-by-step emergence of a crafted handaxe. It is from this direct perception-action that identity associated with the handaxe can emerge without succumbing to the idea that identity is a representation—a meaning that is attached to the handaxe—a view that is seen as ontologically problematic.

Insofar as it offers a critical assessment, Chap. 20 (this volume) goes further than Chap. 19 by questioning whether certain cognitive explanations—in this case, cognitive enhancement—are even appropriate in accounting for certain cultural developments. Mendoza Straffon begins by providing three models that can be used to account for the rise of visual art at the onset of the Upper Paleolithic. The three models that she uses to explain the rise of art are sexual selection, social bonding, and cognitive enhancement. She then conceives of the empirical results that would be expected from each of the models and tests these results against what is actually observed in the archaeological record. The conclusion that Mendoza Straffon draws is that no particular model can fully account for all instances of the beginning of visual art. She does suggest, however, that each of these models may be able to explain certain instances of the emergence of visual art on a case-by-case basis. That a sudden cognitive enhancement resulted in the rise of visual art, however, is ruled out. This agrees with a gradualist interpretation of the rise of art (e.g., McBrearty and Brooks 2000) and is more generally compatible with how a growing number of archaeologists have come to reinterpret the Upper Paleolithic—not as a sudden “revolution” but as a phenomenon that was foreshadowed tens of thousands of years earlier in Africa and the Southwestern Asia.

Summary and Conclusion

The earliest forays into ECA explored those characteristics of the ancient mind that could be elicited through archaeologists' penchant for forming typologies. For many archaeologists, typologies, in addition to serving as means of synthesizing archaeological data, continue to be seen in some sense as recapitulations of instantaneous, imagined functions and forms that guided people in the manufacture of tools and other forms of material culture in the past. ECA subsequently added *chaîne opératoire* to its methodological toolkit. Initially, c*haîne opératoire* provided a diachronic framework for gleaning insight into syntactic aptitude by examining the composition of operational sequences. Operational sequences have since been analyzed by breaking them down into steps, the objective being to infer the technical decisions involved in each step. This progression set the stage for the development of the conditional approach, in which artifacts are seen to be the products of particular behaviors dependent on certain cognitive capabilities or thought processes. In more recent years, the materiality approach has been utilized in ECA. The variant of materiality approach advocated by MET and RECA is motivated by ontological concerns in which cultural objects and actions are seen as scaffolds in a continuously unfolding cognitive developmental process.

The diversity of interests currently being researched in ECA demands that the various approaches summarized above be implemented. Due to their respective limitations, these methods can complement each other. Whereas a typological approach can glean insight into instances of thought along functional and formal dimensions, *chaîne opératoire* can be more useful in eliciting the sequence of decisions that accompany a behavior such as the manufacturing of a tool. The conditional approach, on the other hand, is useful for reconstructing the requisite cognitive capabilities and thought processes that are indicated by material remains. MET and RECA can complement the conditional approach by treating culture and cognition together as the unit of analysis, an ontologically motivated position from which certain cultural developments, such as tool- and mark-making, can be seen to have arisen.

For almost a century and a half, the main mechanism deemed responsible for the evolution of cognition has been natural selection. Under the influence of natural selection, culture has been seen as the means by which cognition is expressed and the body, the substrate through which cognition unfolds and evolves. Subsequent research has proposed that other mechanisms, such as mutation, are implicated in cognitive evolution (Klein 1992, 2008). More recently, it has been suggested by proponents of MET that culture and cognition can work together recursively, thereby bypassing the natural historical processes that otherwise would have been responsible for cognitive change. With these alternative ways of thinking about the mechanisms responsible for cognitive change, ECA has entered a more critical phase in apprehending how the human mind has changed through time and, as a result, how one interprets cultural remains. Both Chaps. 19 and 20 are examples of this new phase. They both pose challenges to understanding cognitive evolution and the traces cognitively evolving people are purported to have left behind.

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Chapter 19

Embodied Cognition and the Archaeology of Mind: A Radical Reassessment

Duilio Garofoli

Introduction: The Internalist View

Evolutionary cognitive archaeology (ECA) is a relatively recent field that attempts at reconstructing the properties of past cognitive systems from the material remains identified within the archaeological record of ancient hominins. During its first era, this discipline was deeply influenced by cognitivist accounts about the evolution of the mind, and in particular evolutionary psychology (Barkow et al. 1992; Buss 2012; Cosmides and Tooby 2013). According to this view, natural selection designs the mind as a series of computational systems, which use internally specified and brain-bound mental representations to identify and appropriately respond to adaptive problems (e.g., environmental, socio-demographic, or nutritional; Tooby and Cosmides 1992; Symons 1992; Barrett et al. 2014, p. 2; Delton and Sell 2014). In particular, mental representations encode knowledge about the world, which is deployed to filter and decode relevant perceptual input and turn it in the most appropriate behavioral output (Hurley 2001; Tooby and Cosmides 2005; Miłkowski 2013; cf. Malafouris 2013, pp. 25–29). Cognitive evolution is therefore seen as the incremental addition of new computational systems coupled with the enhancement of older ones (e.g., Mithen 1996, 2014; Carruthers 2006). At the same time, culture, including artifacts, institutions, traditions, and systems of values, is conceived as information stored within evolved neurocognitive systems, which is transmitted downstream through social learning, made concrete through a set of goal-oriented operations, and ultimately selected for its adaptive value (e.g., Mesoudi et al. 2006; Mesoudi 2011; Richerson and Boyd 2005). This view implies that culture evolves with approximately the same mechanisms as biological systems. Indeed, cultural traits are distributed along patterns of variation, transmitted to offspring, selected for their effects on fitness, subject to drift, and thus ultimately understandable through the concepts and methods of Darwinian evolutionary theory (see Goodale and Prentiss and Laue, this volume for review). Accordingly, some scholars consider cognition and culture as separate and yet complementary systems, which coevolve following a dual inheritance logic (after Boyd and Richerson 1985). Within this framework, biological selection operating on cognitive functions and neural substrates is paralleled by cultural selection acting on artifacts and other practices, while these dimensions mutually influence each other. Grounded in this background, ECA initially focused on the

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identification of artifacts within the archaeological record, which could mark the selection of such representational and computational mechanisms. Conversely, this discipline attempted to identify the appearance of the "algorithms" responsible for bringing these artifacts into being (e.g., Mithen 1994; see Mendoza Straffon and Abramiuk this volume for review). For example, the emergence of progressively more sophisticated utilitarian tools in human prehistory was associated to the selection of internal visuospatial algorithms, possibly specific to toolmaking and technical intelligence (Wynn 2000; Silverman 2002; see German and Barrett 2005 for a more general perspective).[1] A crucial part of this program in ECA implied identifying the time in prehistory when humans became "what they are today", namely, they acquired the condition of behavioral and cognitive modernity (Mellars and Stringer 1989; Conard 2010; Shea 2011). In evolutionary psychology terms, this program required finding out the archaeological evidence for the acquisition of the algorithms and representations universally shared by ethnographic human populations. Consequently, scholars have been grappling with defining appropriate categories of artifacts that could constitute the hallmark of modernity (McBrearty and Brooks 2000; Wadley 2001; Henshilwood and Marean 2003; see also Shea 2011, for discussion). With this respect, the aforementioned utilitarian behaviors did not appear as particularly promising for capturing this concept, since archaic hominins showed capable of quite sophisticated pragmatic behaviors (Mania and Mania 2005). For example, the miraculously preserved wooden spears excavated at Schöningen, Germany, and associated with *Homo heidelbergensis* at ca 320 ka in the Lower Paleolithic (Thieme 1997) support the existence of ambushing tactics and coordinated social maneuvers, which add upon the already complex operations required for carving the spears out of a tree shaft (Thieme 2005; Haidle 2009). Nevertheless, while these hominins were undoubtedly characterized by a level of sophistication in technical abilities comparable to that of early modern humans, for some scholars they lacked a uniquely modern cognitive ability, which marked their difference with modern humans—symbolism (Chase and Dibble 1987; Henshilwood and Marean 2003; d'Errico et al. 2005, p. 4; Nowell 2010; Pettitt 2011; Barham 2013, p. 347).

A common line of argument in ECA maintains that symbolism is the outcome of a quite derivate evolutionary process. Specifically, natural selection provided hominins with the ultimate capacity for internally representing and ascribing meaning to material items, thereby leading to the evolution of the "modern" cognitive architecture (e.g., Mithen 1996; Henshilwood and Dubreuil 2009, 2011). This architecture is considered to explain the origin of quintessential examples of "symbolic artifacts," such as bodily painting and ornamentation currently bound to early modern human Middle Stone Age contexts in Africa (Henshilwood et al. 2004; Bouzouggar et al. 2007; d'Errico et al. 2005; d'Errico and Vanhaeren 2007; Vanhaeren et al. 2013).[2] In sum, this "internalist" view in ECA depicts cognitive evolution as a series of updates within a symbolic code bound to the brain, which culminates in the ability to build material representations of brain-bound representations, namely, a form of "outer" symbolism (see also Abramiuk this volume). During the latest decades, internalist ECA reached center stage in the cognitive evolution debate and currently keeps motivating, at least indirectly, the search for modernity in contemporary archaeological research.

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[1] A similar mechanism can explain, for example, the shift from the Oldowan single-edged cutting tools to the grossly symmetric Acheulean industry at ca 1.4 ma and lately to the coherently symmetric ones of the Late Acheulean at ca 600 ka (see Wynn 2002, for review). Specifically, the combination of an adaptive problem (e.g., butchering animals) and some utilitarian reasons (e.g., maximizing cutting efficiency) selected for the ability to first process bidimensional symmetry and then appreciate the tridimensional coherence between the two sides of a handaxe. This augmentation was based on the addition of mental representations for symmetry and the computational bases for mentally rotating and comparing the two faces of the artifact in an increasingly more accurate way (Silverman 2002).

[2] Nevertheless, some researchers contend that the same categories of artifacts appear also in late Neanderthal Middle Paleolithic sites in Europe, thus showing that cognitive and behavioral modernity are not bound to hominins' physical anatomy (d'Errico 2003; Zilhão 2007; Peresani et al. 2011; Radovčić et al. 2015).

Problems with Internalism

During the last 15 years, criticism arose about the core assumptions with the internalist paradigm in ECA. Firstly, skeptics argued that this view has deterministic implications, because on the one hand internal functions are considered inevitably coupled with specific behavioral outcomes (Tallis 2011). On the other, such functions are entirely shaped through a mechanism of random mutation and passive selection (e.g., Dawkins 1982, quoted by Riede, this volume). Specifically, spontaneous events of mutational enhancement alter the internal computational machinery, by providing a pool of possible algorithms/representations and resulting behaviors. Subsequently, natural selection eliminates the maladaptive cognitive-behavioral packages, thereby creating the modern cognitive architecture provided with the complete set of modern behaviors. This mechanism allows explaining the alleged existence of cultural universals, which at least in their general form are supposed to characterize all contemporary human cultures (e.g., Buss 1994; Atran 1998; Boyer 2001).

This account, currently known as the neo-Darwinian view of cognitive evolution (Ingold and Palsson 2013), encountered resistance at the empirical level, since several scholars argued that both ethnographic and experimental evidence do not confirm the existence of such cultural and cognitive universals, nor do they mark the presence of an inflexible relation between cognition and behavior (Buller 2005; Everett 2005). At the same time, from a theoretical point of view, this view faces the problem of agency, because it reduces humans to mere replicators of internal codes (Ingold 2007) and artifacts to epiphenomena of the mind (Malafouris 2016; Iliopoulos and Garofoli 2016). No room is left within this conception for intentionality, development, and the active construction of the human lifeworld.

Similarly, the internalist view faces problems in explaining the evolution of hominin sociality. Evolutionary changes are indeed confined within an isolated mind, which at the same time coexists with a series of many other individuals and objects. Far from being based on actual relations between people and things, hominin sociality is thus reduced to the juxtaposition of many independent codes (Di Paolo and De Jaegher 2017, p. 94), which are stabilized by natural selection over time through the elimination of unfitting ones, until a sustainable equilibrium is reached. Secondly, the internalist view appears as a contemporary version of Cartesian dualism, according to which mental representations stand as a mental substance divorced from the physical world (Thompson and Cosmelli 2011; Malafouris 2013, chap. 2). These representations are considered to have content, in that they are “about” the world or the body in a truth-conditional way, namely, they provide true descriptions of reality (Evans et al. 1982, pp. 226–227). Natural selection can alter these representational contents, in order to accommodate adaptive needs (e.g., Delton and Sell 2014).

Nevertheless, representationalism is confronted with serious metaphysical problems that threaten its validity. A fundamental issue lies in the fact that it is unclear how changes in the physiological state of neurons that are in *structural correlation* with the external world can become *about* it (i.e., acquire representational content). Indeed, such a structural coupling per se does not generate aboutness, unless we assume that either content is an irreducible property of the world to which neurons get connected (e.g., Chalmers 2010), or there exists a homuncular system within organisms’ brains that decodes stimuli through an interpretive code (call this the “Hard Problem of Content” after Hutto and Myin 2013, 2017, 2018). Furthermore, two additional but related issues affect mental representations, respectively, the problem of substance and origin (Zahidi and Myin 2016). According to the former, if mental representations are supposed to exert actual changes on the brain-body-world physical system, then they require a plausible and realist ontological characterization (i.e., what representations really are; see also Hutto and Myin 2017, Chap. 2). According to the latter, it is necessary to explain the derivation of such representations (i.e., where they come from; see Zahidi and Myin 2016) and, in particular, how content can be inscribed in the brain more than it could be in any other aspect of the material world (i.e., why only neurons can host content).

In light of these problems, during the last decade, a growing minority of scholars in ECA has urged for abandoning the internalist view, by arguing against the idea that material culture, behavioral practices, institutions, and social interactions are just passive by-products of an internally evolved symbolic code. Inspired by the embodied and extended cognition movement in cognitive science (e.g., Menary 2007; Clark 2008; Robbins and Aydede 2009; Rowlands 2010; Shapiro 2014), these scholars contended that the aforementioned elements in fact actively constitute and shape social systems and even cognitive processes. Consequently, they advocated a relational conception of cognitive evolution, based upon the long-term transformation of integrated systems of brains, bodies, and culture. Within the next section, I will illustrate this critique more in depth by focusing upon two of the most relevant relational models in ECA, namely, the distributed approach (Gamble et al. 2011, 2014; Gowlett et al. 2012) and the theory of material engagement/enactive signification (Malafouris 2013; Iliopoulos 2016b).

The Embodied and Extended Turn

Let us introduce the embodied and extended turn by focusing upon the recently proposed distributed approach in ECA. Such an approach is grounded in the social brain hypothesis and accordingly argues that hominin encephalization is primarily explained by social reasons (Aiello and Dunbar 1993; Dunbar 1998a, 2003). In its broader formulation, this hypothesis supports the existence of a positive feedback loop between brain size and cognitive-social complexity (Barton and Dunbar 1997; Dunbar 2003, 2007). Evolutionary drivers led hominins to living together in large groups in order to address the metabolic costs of a large brain. As a consequence, natural selection fostered the cognitive abilities that were able to maintain the social complexity required to support the expansion of such an expensive neural tissue. However, in contrast with the internalist view, cognitive functions did not evolve as merely contained within the head, for this would have imposed on them an unbearable computational burden. Rather, they were extended through their hybridization with behavioral practices, artifacts, and other social forms, which were scaffolded around a core of emotions and material affordances (Dunbar et al. 2010; Gamble et al. 2011; Gowlett et al. 2012). In line with the well-known hypothesis of extended cognition (e.g., Clark 2008), the making of artifacts thus appears as a relational process that taps into other people’s cognitive operations. Indeed, artifact makers can adopt the activity, knowledge, and emotional reactions of social partners as a part of their computations, thus avoiding the necessity to internally conceptualize and individually figure out all the aspects of crafting. Similarly, within the domain of social cognition, material culture and embodied practices scaffold the understanding of others, because they obviate the need to represent and compute social concepts and relationships only within the mind. In addition, social complexity, namely, the organization that a society can take, is not passively dictated by an evolved internal code. In contrast, artifacts and social practices have agency in shaping and constraining hominins’ interaction (Knappett 2002; Gosden 2005; Verbeek 2005; Hodder 2012). Indeed, they segregate and unite, contain and alienate, emphasize meanings, and offer social affordances, so as to deeply transform the social world (Gamble 2010). Thus, by combining their ability in extending cognition with their social agency, these practices allow reconfiguring the connection between people, thereby broadening the range of the social space, and taming its complexity. As a consequence, they allow group size to scale up in a way that would be unfeasible with the internal mind only (Coward 2016). In synthesis, the distributed approach can be visualized as a system at equilibrium, in which hominins extend their social cognition through a series of different social forms, which they use to stabilize the complexity of large groups under adaptive pressure (Fig. 19.1).

The shape of the Paleolithic, namely, the emergence of innovations observed in the archaeological record over time, reflects the different means employed in this structuration process, by privileging

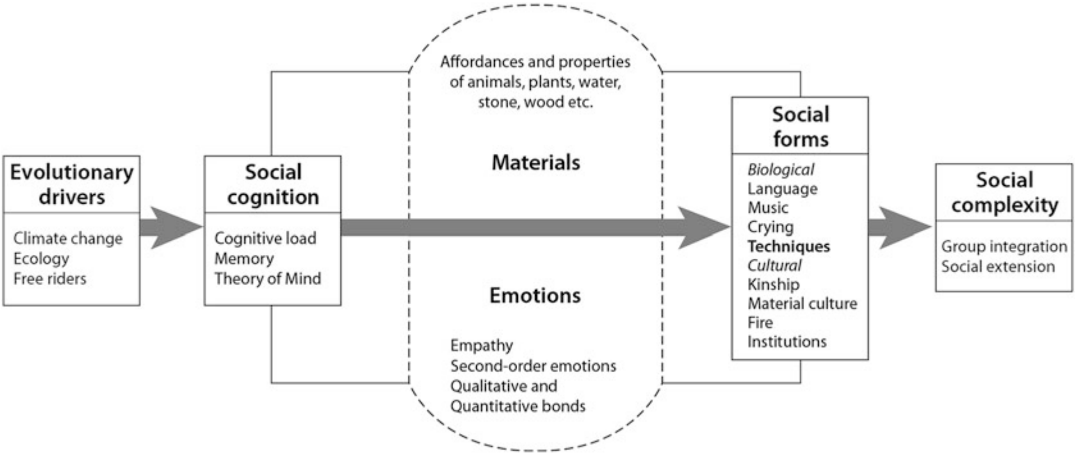

Fig. 19.1 Cognitive evolution mechanism according to the distributed approach (Gamble et al. 2011). Ecological and social problems lead groups to scale up and raise their social complexity, thereby placing adaptive pressure on the socio-cognitive abilities required to accommodate these changes. Since the computational burden of handling such complexities cannot be sustained by internal cognitive resources only, these functions, as well as the structure of social systems, are extended through a set of social forms (e.g., language, institutions, and material culture), which are built around a core of material and emotional affordances (dashed box in the center). These extended cognitive functions evolve in order to stabilize increasing social complexities under selective pressure. Reproduced with permission from Gamble et al. (2011)

in some cases the evolution of internal functions, in others that of immaterial practices (such as language, music, or dance), while in further ones amplifying material culture (Gamble 2010; Gamble et al. 2011).[3] This differential negotiation of societal structures characterizes the entire hominin evolutionary history and obviates the need to think about a single event of mutational enhancement that led to the evolution of a symbolic cognitive package for the stabilization and expansion of the social sphere (Mithen 1996; Mellars 2005; Klein 2008). Symbolism, in fact, is only one of the many ways in which hominins exploited material things and emotions to shape their own sociality, and thus it assumes no privileged role, nor does it mark the advent of a “modern mind” (Gamble 2010, p. 30).

The theory of material engagement (Renfrew 2004; DeMarrais et al. 2004; Knappett 2005; Malafouris 2004, 2013; Overmann and Wynn in press) adds a further step to the distributed approach, by contending that artifacts do not simply participate to the cognitive process. Rather, similarly to the way they actively shape the social world, artifacts profoundly transform the mind, by creating new ways of conceptualizing reality (Malafouris 2010b). Such a transformative process is particularly evident within the theory of enactive signification, according to which the material engagement with artifacts leads to the discovery of new meanings for signs that is accompanied by parallel cognitive restructuring (Malafouris 2007, 2008; Iliopoulos 2016b). This theory is grounded in Peirce’s (1931–1936) semiotic account and accordingly advocates a continuous transformation of meaning along three categories of signs, namely, icons, indexes, and symbols. Within this basic triad, the link of a sign to its object is, respectively, interpreted through criteria of physical resemblance (icons), contiguity or factorality (indexes), and conventional and arbitrary agreement (symbols). As a consequence, far from being the latest update of a modern mind, symbolism developed on top of more basic categories of signs as the result of the relational engagement with artifacts and social agents (Iliopoulos 2015).

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[3] The lags observed in the archaeological record between increases in brain size, inferred population growth, and innovation spurts can be explained by the selective amplification of internal cognitive abilities or external practices that do not leave archaeological traces (unlike material culture; see Gamble et al. 2011).

Following the example elegantly discussed by Froese (2019), the handprints made with pigments on cave walls not only allowed Upper Paleolithic hominins to discover the expressive affordances offered by such media but also to co-perceive their own presence through this material action. The pigments, indeed, exposed the causal coupling between the handprint and the body and led to interpreting this signs as indexes of their makers. At the same time, this action led users to discover that colors can create icons of things, namely, figures that look like real things and yet differ from them. Over time, further explorations of the material properties of pigments and bodily affordances invited humans to produce negative shapes by, for example, spraying the color with their mouths onto hands placed on cave walls. This action in turn led to discovering the concept of outline and then the possibility of creating icons that are not necessarily coupled with the body of their makers, thus discovering figurative drawing. Simultaneously, these lines attracted the attention of other people and created social reactions, leading their makers to wonder about the social meanings of such drawings. This ultimately could have allowed the creation of abstract patterns, whose meanings could exist only within a mental dimension, thereby scaffolding the acquisition of symbolism. The case study of Upper Paleolithic cave painting therefore shows that materiality bootstrapped the emergence of symbolism along a developmental trajectory (see also Hodgson and Pettitt 2018), where a semiotic metamorphosis (in this case, from indexes to icons and ultimately to symbols) is accompanied by a change in the perception of affordances, conceptual categories (e.g., the outline), and the cognitive processes necessary to process such a shared mental dimension (e.g., meta-representation and theory of mind, see below for further discussion).

This enactive transformation is driven by a deep integration of the properties of material culture with the plasticity of the brain (i.e., metaplasticity; Malafouris 2010a, b; Garofoli 2016; Roberts 2016). Indeed, the material engagement with artifacts restructures the connectivity of the brain, thereby fostering new ways of perceiving the world and exploiting material culture and ultimately initiating a positive feedback loop (see below for further discussion). As a consequence, this approach sharply departs from the internalist view, in that it assumes that the mind does not evolve as a complete package, which restitutes a fixed material and social world. Rather, mind and world emerge as a result of their mutual entwinement, thus being co-constructed (Malafouris 2016).

Overall, the distributed approach and the theory of enactive signification share a sense of distributed agency, whereby humans, respectively, structure their own lifeworld and mind through the opportunities (but also the constraints) presented by artifacts and more in general cultural practices. Given the existence of the aforementioned problems with the internalist and neo-Darwinian view, the critique advanced by such embodied and extended models in ECA is therefore as welcome as crucial. However, as I illustrate within the next sections, there exist fundamental problems within the current formulation of these models, which threaten their reformatory enterprise.

Aims

Within this chapter, I analyze the aforementioned families of embodied and extended cognition models in ECA, namely, the distributed approach defended by supporters of the social brain hypothesis and the enactive signification associated with the theory of material engagement. I argue that these models, although leaning toward the idea that the mind is not merely contained within the head, fail to break with the internalist tradition. In claiming that the mind is extended, they still admit the existence of prior conceptual representations that are combined with pieces of material reality. Thus, they conceive cognitive extension as the flooding of conceptual resources from the internal mind to the outer world, which results in the inclusion of artifacts and the relational structures they create within the internal computational architecture. Nevertheless, the a priori representational and conceptual bases that expand upon the world remain affected by the very metaphysical problems mentioned for the evolution of fully internal architectures, such as the problems of substance and origin. I argue that the failure of these models in disengaging from the conceptual apparatus of representationalism seriously jeopardizes their revolutionary scope toward the Cartesian mind. In fact, by maintaining residual forms of representational apriorism, these "conservative embodied" proposals cannot effectively differentiate themselves from the internalist/Cartesian tradition they intend to criticize (Hutto and Myin 2013, Chaps. 1–2; Hutto 2005).[4] Most significantly, I illustrate how they can even be assimilated with some amended versions of the internalist view, thus risking to appear as mere "correctives" within this paradigm. The reform advocated by embodied and extended cognition in ECA in fact requires a more thorough break with such a tradition.

In the positive part of this chapter, I suggest that this rupture can be performed by drawing upon the Radical Enactive and embodied account of Cognition (REC; Hutto and Myin 2013, 2017, 2018). According to this view, basic cognitive acts such as perceiving, recognizing, and imagining are conceived in anti-representational terms. Namely, they are the product of the direct coupling of an agent with the structure of the world and the reenactment of such relational states, given the organism's developmental and evolutionary history. In contrast, representations emerge as the result of shared cultural practices, as exemplified by language and narratives.

Drawing upon these principles, I RECtify the conservative embodied views, by depriving them from residual representationalism while maintaining their embodied and extended lean to cognition (see Hutto and Myin 2017, p. 52). Accordingly, I argue that artifacts do not combine with internal representations in order to provide extended computations, as assumed by these conservative models. Rather, they create structures for the direct perception and imaginative reenactment of the world and scaffold the construction of linguistic representations over the long time. To this goal, I adopt the example of the Acheulean handaxe, by focusing on its pragmatic and social aspects concerning its technical realization, as well as its alleged semiotic value as a communicative sign.[5] Overall, this case study allows laying down guidelines for a radical enactive cognitive archaeology. Ultimately, I discuss the advantages and costs of going radical over investing in the current conservative embodied accounts in ECA.

The Distributed Approach and the Acheulean Handaxe: Residual Internalism

In order to understand where residual internalism lies within the distributed approach, let us consider the case of Acheulean toolmaking mentioned by Gamble (2010). Against an internalist and symbolic view, Gamble proposes that Acheulean handaxes were not the passive by-product of the evolution of internal mechanisms for the appreciation and tridimensional manipulation of symmetry (Wynn, 2002, for review) nor could they be reduced only to the personal satisfaction or disappointment associated with the realization of the finished product by an individual agent. Although individual mechanisms remain crucial, handaxes were in fact also the outcome of social and emotional interactions with other group members (see also Gamble et al. 2014). They indeed contributed to the formation of extended cognitive functions and actively restructured hominin society through their material properties.

Specifically, handaxes could have created an epistemic structure at the social level, which could have been exploited for the making of the artifact. Knappers could indeed adjust and modify their

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[4] Following Hutto and Myin (2013), the conservative aspect of such models in embodied cognitive science is restricted to their acceptance of representationalism.

[5] This case study is particularly valuable in this context, because it is incidentally discussed by the vast majority of the conservative embodied models hereby taken into account, although with different emphasis.

decision-making process and performance by relying upon the actions and indications of others rather than on mental representations. The emotions of other people could be further adopted as an external basis for assessing one's own performance, thus bypassing the need to evolve internal criteria of evaluation. At the same time, the importance of these tools could have led to the formation of progressively more structured "workshops" and teaching-learning contexts (cf. Sterelny 2012). In this way, the artifacts established durable relations between social members and allowed an agent to constantly monitor individual abilities and social relevance without the need to keep them in memory as mentalistic constructs. Similarly, by instantiating centers of attraction of cognitive and emotional mechanisms, handaxes constituted by themselves the motivation for social interaction.

However, the relational conception advocated by the distributed approach is still subject to Cartesian pitfalls. Indeed, the behavioral contingencies created by handaxes are analyzed and computed by (or get integrated with) a priori evolved cognitive mechanisms and in particular the representational bases for theory of mind (see "social cognition" in Fig. 19.1). For instance, let us consider the case of an agent who needs to assess which companion of hers best knows how to craft a handaxe. Within the internalist approach, this agent observes her companions' performance and builds a mental ranking of all the relevant abilities in stone knapping (e.g., dexterity, aesthetic sensibility, effectiveness, etc.). Subsequently, she could infer from this list which results better capture who the "best knapper" is. However, rather than adopting this mentalistic strategy, the agent can simply compare the knappers' finished artifacts to one another. The conformation of the handaxes, indeed, offers a direct way to assess "online" the performance of the others and become part of a wide computation. Nevertheless, this computation implies that the agent uses this material basis to conclude who the knapper that best *knows* how to knap is. Accordingly, the material basis would be in any case the starting point for an inference that connects one's behavioral performance to his or her *knowledge* of the procedure. This process is mediated by theory of mind, namely, the ability to infer other people's mental contents *as such* (Hutto 2011). This ability implies the use of mental state terms such as "know" or "believe," which define propositional attitudes toward a particular content (e.g., I know X; you know Y) and meta-representations, which mediates the embedment of propositions within one another (e.g., I know that → you know Y; see Pylyshyn 1978; Doherty 2009, Chaps. 2–3).

Partisans of the distributed approach conceive the architecture for theory of mind as constituted by sub-personal (meta)-representations independent from natural language, which allegedly evolved as early as with *Homo erectus* at ca 1.4 ma (Dunbar 1998b, 2003, 2009; Gamble et al. 2011; Cole 2015). However, in the absence of language, it is unclear what these (meta)-representational abilities are and how they could be innately specified within the brain. They appear indeed as disembodied entities a priori inscribed in the organism by natural selection while remaining their content, substance, and origin unclear (cf. Hutto 2008a, b). Accordingly, within the distributed approach such internal representations get integrated with external vehicles by forming various sets of possible extended algorithms. As it becomes clear from Gamble's (2010, p. 27) words (emphasis added):

> People did not arrive in Australia because they first thought of symbolic sandy beaches and convinced themselves that was sufficient reason to move. They arrived because they had first accomplished the cognitive task of *manipulating symbols in conjunction with the external world*, which then allowed them to achieve the task of extending their social worlds, and coincidentally in this instance, their geographical extent.

However, these extended algorithms depend on the nature and constraints of the internal representations specified within the brain. Thus, the role of artifacts within this approach is limited to amplifying internal functions through their material properties by extending their computational basis (e.g., Wilson 1994; Wilson and Clark 2009). The distributed approach in this way accepts the existence of representational primitives, provided that they can be integrated with external vehicles, and cognition not only symbolically realized within the head. Furthermore, these substrates can still evolve through mechanisms of mutational enhancement and biological selection acting on the representational bases for theory of mind. Accordingly, the evolution of these representational primitives is still deemed as an a priori condition for the emergence of particular cultural innovations within the archaeological record. Thus, this view remains grounded in internalist tenets, which face the metaphysical difficulties introduced earlier. Furthermore, insofar as cognitive extension is conceptualized as the mere amplification of internal and fixed representations, this approach would still lack a genuine developmental perspective. In order to fulfill this lacuna, it is necessary to shift from the idea that artifacts amplify internal cognitive processes to the conception that they actively create new ones.

Enactive Signification and Internalist Pitfalls

Material engagement theory and in particular the enactive signification account perform the aforementioned conceptual shift by contending that artifacts have cognitive agency and accordingly scaffold the emergence of new classes of signs and conceptual categories (Malafouris 2007, 2013, Chap. 5; Iliopoulos 2016b).[6] Within this section, I will illustrate the principles of such a semiotic and cognitive transformation by relying upon the recently proposed interpretation of handaxes as signs. Indeed, some scholars contend that the coherent tridimensional symmetry of late Acheulean handaxes (see Footnote 1) cannot be explained by mere utilitarian reasons. Rather, *Homo heidelbergensis* populations deliberately produced this shape in order to transmit meanings to other people, thus turning these artifacts into signs. According to some proposals, the handaxes' form had communicative implications, and in particular they might be used for aesthetic purposes (Hodgson 2008; Machin 2009) and in particular as indexes of individual ability for sexual selection (Kohn and Mithen 1999; but see Nowell and Chang 2009, for a counterargument). In contrast, an alternative proposal contends that handaxes were employed to signify identity (Pope et al. 2006; Shipton 2013). The alleged existence of stylistic traditions of handaxe shapes in the Lower and Middle Paleolithic indeed suggests that style could have been used as a marker of membership within a particular group. In any case, this interpretation remains quite controversial at the empirical level, for the presence of coherent symmetry in the Lower and Middle Paleolithic could have been overestimated (McNabb 2013; Cole 2015). Nevertheless, the semiotic interpretation of handaxes provides an effective model for achieving the theoretical objectives of the current section, namely, highlighting the problems of residual internalism with the theory of enactive signification.

This theory disagrees with the internalist view, in that it assumes that handaxes do not receive their meaning through the arbitrary and conventional imposition of an abstraction (i.e., identity) to the artifact, as in the case of symbols (e.g., Cole 2015; cf. Quinn this volume, for a view of semantic transmission of meaning through material culture). In contrast, in order for handaxes to signify something, their meaning needs to be enacted at the conjoint of materiality, the body, and the mind. In order to illustrate this process, we can apply the analogous analysis of enactive transformation of meaning provided by Iliopoulos (2016a) on Middle Stone Age ochre pigments (Watts 2009; Marean et al. 2007) to the current case study with handaxes and the concept of identity (cf. Iliopoulos 2016b, p. 116). This approach allows understanding how indexical signs emerge from brain-body-world complexes and further ground the rise of full symbolism.

To start, we can assume that handaxes were initially produced as tools for pragmatic use. Over time, the teaching and learning of handaxe-making within local contexts unintentionally biased these artifacts to acquiring some particular stylistic form. Subsequently, the particular features of the handaxe and the physical presence of their makers (associated with a sense of ownership of the

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[6] Malafouris' formulation of the theory of enactive signification and more in general Material Engagement seems committed to anti-representationalism, thus being compatible with the radical enactive perspective advocated in this paper. Nevertheless, some specific aspects of his (2013) approach hinge on some more conservative embodied models, and these will be the target of the current critique.

artifacts), both lying in preexisting phenomenal domains, were projected into a third one, namely, the enactive or "blended" space (Fauconnier 1997; Fauconnier and Turner 2002). The stylistic features of handaxes therefore acted as material anchors for the projection of ownership by group members, so that these elements were blended within a concept of identity (Hutchins 2005). Thus, the handaxe is eventually turned into a sign, which "stands for" its meaning, even though not in a symbolic way. Indeed, the concept of identity is warranted by the physical contiguity and causal derivation of group membership and style (the so-called indexical ground) and not by arbitrary convention, thereby representing a Peircean index (Iliopoulos 2016b).

From this level, such an indexical sign could then be exploited to signify, for example, ownership of a particular territory or item. In this case, the concept of ownership capitalizes upon the indexical meaning of handaxes, namely, the fact that they stand for identity. Consequently, an internally specified concept of ownership is now blended upon this indexical relation on the basis of a conventional and arbitrary agreement among the sign's users, whereby the hanging of a handaxe on a tree, for example, can be used to communicate normative rules (e.g., do not trespass). This eventually leads to the emergence of a symbolic usage for handaxes.

However, if the previous characterization is accurate, then the theory of enactive signification is still bound to a form of representational apriorism and computationalism, albeit more moderate than the standard internalist one. Indeed, there exist two main problems with the current formulation of this theory. The first concerns the fact that it postulates the existence of a sub-personal architecture for the processing of signs. By relying on Sonesson's (2006, 2010) approach in semiotics, it claims that a sign acquires its meaning when a sign function ascribes some content to its expression, so as to make the sign "standing for" a specific meaning. This happens independently of whether the sign is an icon, an index, or a symbol. In other terms, the mere existence of a semiotic ground between the stylistic features of a handaxe and the recurrent presence of individuals belonging to a group (see Fig. 19.2 above) does not per se make the handaxe a sign (i.e., an index of identity). In contrast, the handaxe becomes an index only when the system analyzes the two elements of the semiotic ground and binds them to a concept of identity through the sign function (Iliopoulos 2016a). However, this operation seems to be realized through an inferential process, in which some premises are evaluated (i.e., there exist an indexical ground in the world and a concept of identity) and conclusions are drawn (i.e., the indexical ground can be plausibly categorized as an instance of identity). According to Malafouris (2013, p. 114), indeed, a core aspect of the theory of enactive signification is that artifacts create opportunities for *abductive thinking* (which is also inherent to the concept of "abductive index," see Iliopoulos 2016b, p. 116), thereby leading to the discovery of new categories of signs, concepts, and relations (e.g., the concept of index emerges from this blending process), and ultimately restructure cognition itself.

Nevertheless, it is worth noting that the premises and conclusions manipulated within abductive reasoning are propositional states of the mind that correspond to states of the world in a truth-conditional way, namely, they are contentful mental representations. These representations in turn are used to ascribe contentful meaning to handaxes and ultimately create external representations. The reliance of the process of signification upon an inferential architecture creates a daunting problem for the theory of enactive signification. Such an architecture indeed seems to be sub-personally realized through a language of thought, namely, a language-like system characterized by syntax and grammar, which nonetheless is "spoken" by neurons (Davies 1998; Fodor 2008). Accordingly, our brain would be provided with a set of disembodied representations that processes and displays into consciousness the meaning of reality, thereby reintroducing a Cartesian view of the mind.[7]

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[7] Alternatively, one could assume that these propositions are actually mediated by a natural language. Nevertheless, this would suggest that all Peircean signs are realized through language, a position that backfires against Malafouris (2013, p. 135) and Iliopoulos' (2015) critique against the centrality of language in material signification.

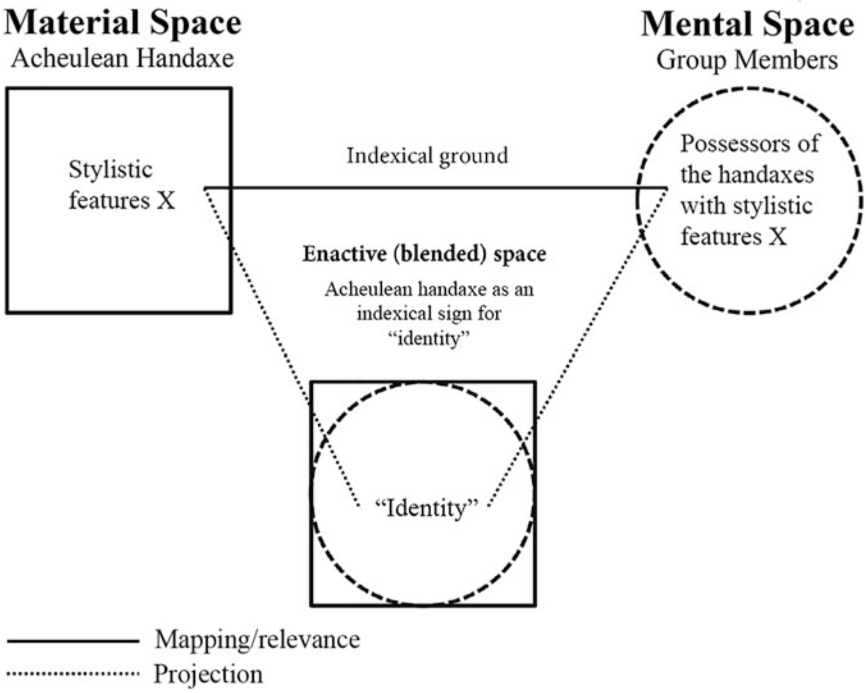

Fig. 19.2 Diagram of the blending process for the concept of identity from the indexical ground created by the recurring association of handaxes' stylistic features and the presence of the same individuals (group members). The stylistic features X of a local tradition of handaxes occupy the material space (above, left). A viewer understands that the handaxes are owned by the members of a certain group, and this happens within her mental space (above, right). The physical contiguity between the X-shaped handaxes and the presence of some group members embodies the indexical ground. A concept of identity allegedly emerges out of the blending of the two aforementioned elements. Redrawn from Iliopoulos (2016a)

Related to the previous point, the second problem with the theory of enactive signification lies in the fact that the conceptual blending involved in the formation of a sign, although assisted by the material world, still requires a priori conceptual representations. Indeed, the contiguity between the stylistic features of a handaxe and the presence of group members scaffolds the inferential processes described above, by providing affordances for the blending of the concept of identity. However, this concept needs to be internally specified within the mind, before it can be applied to the iconic ground, thereby positing again the question about its origin. At the same time, this assumption raises a well-known problem with conceptual categorization in the standard internalist view. In order to categorize the indexical ground within a concept of identity, and consequently form the indexical sign, the brain needs to select precisely that concept among a library of possible conceptual categories it stores. However, it seems that the only way to perform this task would lie in assuming that the internal concept of identity "knows" in advance which aspects of reality it can categorize. To concretize through an analogy, this means that the indexical ground existing in the world displays a label on itself. The brain in turn picks up that label and searches within a library of conceptual representations the corresponding label exposed on the internal concept of identity (Fig. 19.3).

However, this computation is possible only because the concept of identity is innately provided with all the appropriate conditions for matching some particular aspects of the world, including the iconic ground (i.e., the two labels are there since the beginning). Without such an a priori specification, this computational task would in fact be intractable, because there would be no way to reconnect the

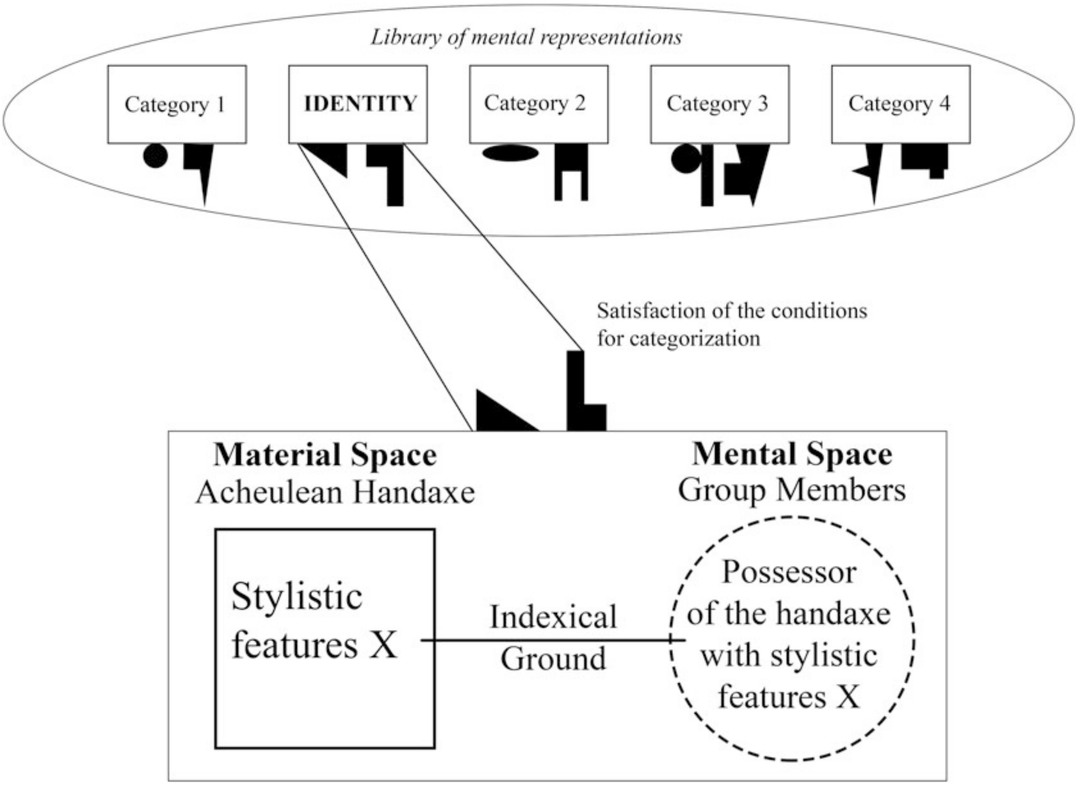

Fig. 19.3 Computational architecture for the categorization of the iconic ground within the concept of identity. The brain needs to select the appropriate concept that matches the indexical ground from a library of mental representations, in order to categorize it as an instance of identity. Aligning the target state (below) with the appropriate concept within the library (above) requires the existence of appropriate labels on both the iconic ground and the identity concept. This in turn implies that the indexical ground displays a label that can be reconnected to the complimentary one on the concept of identity. As a consequence, the computational process requires that the relationship between the identity concept and its target states is hardwired within the system and thus innately specified within the brain. Without this prior specification, it would be unclear how the iconic ground could be categorized in any conceptual category, since each of the categories within the library would have no instruction for matching their targets

iconic ground to any concept appearing within the library (cf. Robbins 2014, 2017, for an example of this problem concerning analogical reasoning).[8]

Overall, the theory of enactive signification maintains elements of representational apriorism in both the sub-personal (propositional) architecture and the a priori meanings used to construct signs, thereby remaining bound to the internalist paradigm. However, this theory departs from standard internalism because it accepts the existence of more general and flexible brain-bound functions, such as those for the creation of "signs," as opposed to full-fledged symbols.

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[8] In alternative, one could argue that the blending process creates a completely new concept of identity out of the iconic ground. Accordingly, the brain creates the mental representation "identity" in the same fashion of an abstract word, namely, by selecting a label and using it to define a set of conditions for the belonging of instances of identity to such a category. This strategy implies that the brain can establish the content of words by itself and without an intersubjective dimension of reference. Nevertheless, the possibility of realizing a private language independent from a social dimension currently faces daunting philosophical problems (Hutto 2008b; Wittgenstein 1953).

Conservative Embodiment Assimilated

Within the previous sections, we have seen that the conservative embodied approaches succeed in opposing the deterministic leans at the basis of the neo-Darwinian view of cognitive evolution while failing to completely disengage from the Cartesian conception of the mind. This residual representational apriorism risks to hamper the whole critique moved toward the internalist view in ECA, by fostering a series of possible counterarguments. A particularly insidious line of response implies reducing conservative embodiment to a peculiar version of the internalist paradigm.

Proponents of the internalist view could indeed renounce deterministic leans and concede that humans did not evolve algorithms and representations that bring into being specific artifact templates, social organizations, and symbolic meanings. They could add that in fact few evolutionary psychologists currently support this deterministic view of cognitive evolution (i.e., the *real* neo-Darwinian account) and that the relational approaches actually have built a straw position on this matter (Kurzban 2010). In contrast, humans were bestowed by natural selection with a series of internal representations, which they creatively combined in order to craft artifacts capable of solving highly demanding environmental and social issues (Carruthers 2006, Chap. 5). Human agency is therefore maintained in the flexible combination and creative use of mental representations. A sense of agency persists also in the idea that human cognitive functions and cultural outcomes do not passively adapt to a fixed external environment, as per the neo-Darwinian view. In contrast, they transform the environment itself, introduce new sources of pressure, and offer further opportunities for natural selection to shape cognition and culture. Accordingly, humans actively shape their own evolutionary dynamics, a conception that overlaps with some formulations of niche construction theory (Odling-Smee 2007) and consequently oppose strict neo-Darwinian interpretations (see Riede and Prentiss and Laue this volume for review). In addition, internalists can contend that evolved cognitive substrates need not be divorced from materiality but could hybridize with aspects of it. Accordingly, natural selection would still shape cognitive functions in response to evolutionary drivers as per the internalist view, but it would now do this by operating upon “wide algorithms.” Namely, it would act on composite structures formed by internal cognitive substrates subject to random mutation and genetic inheritance and cultural practices transmitted through social learning to further generations.

The resulting conception is nearly the same as the one illustrated in Fig. 19.1 for the distributed approach, consequently showing that the internalist view can accommodate the critique about cognitive extension. At the same time, even the mechanism of cognitive and semiotic transformation advocated by the theory of enactive signification could be assimilated within the idea of “extended selectionism,” inasmuch as this transformation relies upon internally specified functions for the creative production of new meanings.

A parallel point can be made in ECA for the definition and causal origin of the “modern mind” and its relation to the appearance of “behaviorally modern” artifacts within the archaeological record of ancient hominins. Supporters of the internalist view can concede that a symbolic internal architecture is in fact unnecessary for defining the concept of modern cognition. In fact, the conceptual primitives and propositional vehicles introduced earlier are quite sufficient signatures for the modern mind. Such minimal representations and functions could still be subject to mechanisms of biological selection, as in the standard internalist view, albeit in a non-deterministic way. Accordingly, these cognitive bricks could have been created by some mutational events incurring at some point in human prehistory and adopted to build the innovations characterizing the Upper Paleolithic and analogous techno-complexes (e.g., the Australian case of rock art). Thus, cognitive modernity could lie in the flexibility and types of transformations afforded by these foundational bricks (e.g., a sign function), rather than in specific algorithms that restitute modern artifacts (e.g., a cognitive package for symbolism). Overall, it appears that each of the objections raised by the relational models can be reconciled with an emended version of the internalist view.

Radicalizing ECA

The conservative embodied and extended approaches introduced earlier risk to foster an "evolutionary psychology v. 2.0," which accommodates the relational critique, while maintaining the deeply problematic assumptions with representationalism. In order to remain connected to a naturalistic framework and avoid the pitfalls of dualism, the Radical Enactive and embodied account of Cognition (REC) urges for abandoning the idea that minds manipulate brain-bound and sub-personal representations about the world. In contrast, cognitive activities such as perceiving, recognizing, imagining, and simulating—what REC defines the "basic mind"—need to be conceived in non-representational way (Hutto and Myin 2013). In other terms, they are the result of the direct coupling of the organism with the external world, given its developmental and evolutionary history. REC allies with the ecological approach to cognition (Gibson 2015 [1979]) and accordingly assumes that the world is provided with deep structure, which offers information *for* the perception of affordances and the understanding of meaning (van Dijk et al. 2015). Given the structural relationship existing between the brain, the body, and the environment, the various aspects of reality invariantly react to the action an organism performs on it. By operating in the environment, the organism creates some variations in sensorimotor contingencies and exploits them to enact the perceptual meaning of reality (Hutto and Myin 2013, Chap. 2; cf. Brooks 1991; O'Regan and Noë 2001; Noë 2004). Accordingly, rather than a computer that processes and makes sense of meaningless stimuli through hardwired symbols, as per the internalist view (Barrett et al. 2014, p. 2; Tooby and Cosmides 2005), the mind is better conceived as a resonating system. To concretize, we can imagine it as a sort of radar emitting waves that propagate into reality on the basis of the embodied movement of the organism. Such waves hit objects and their reciprocal structural relations, thereby bringing forth their meaning (see Gibson 1966, p. 5, and Raja 2017 on the concept of resonance). At the same time, the impact with objects modulates the internal frequency of the wave and sets the whole brain-body-world frequency (a dynamic system) on a certain signal. If the agent leaves a hypothetical room wherein she was situated and then comes back again, her mode of interaction with the previous objects in the room becomes the same as before, with the brain resonating with the same objects with the same frequency. Thus the agent *recognizes* what she saw earlier (cf. Robbins 2006). Similarly, *imaginative reenactment* implies putting oneself in the same relational status with objects one had in the past, although this time without an actual connection with external structures (Hutto 2015). Consequently, given that the reenacting wave now lacks any external structure of resonance, the phenomenological result implies having a fading and less vivid experience of the object. In sum, for REC there is no image of the world that is mentally represented by the brain and displayed to consciousness during perception (Myin and O'Regan 2009), no snapshot of an event that is picked up from a memory deposit and compared to reality in recognition (Robbins 2014; Gibson 2015 [1979], p. 238), nor is there any internal picture that is selected from a library and displayed into the theater of consciousness during reimaging (Thompson 2007, Chap. 10; Gibson 2015 [1979], pp. 243–244). On the contrary, all these aspects of basic cognition imply a relational connection between agents and the material world, and they do not tap internal representations (Hutto and Myin 2017, Chaps. 8–9).

Nevertheless, REC accepts the existence of representations, insofar as their content is conventionally created within a cultural dimension. In particular, words and propositions within a natural language acquire their content through a conventional agreement, which establishes the truth of their reference, thereby counting as genuine representations (Hutto and Myin 2013, Chap. 7.4). At the same time, language is not conceived as an ostensive tool that serves to simply communicate internally specified meanings but rather brings forth new ways of cognitively processing reality (Garfield et al. 2001; Gauker 2003). Indeed, language restructures human cognition by allowing cognitive agents to think in propositional terms and use such propositions for meta-representation (Hutto 2008a, b; Fenici 2012; Fenici and Garofoli 2017). For example, some linguistic beings could build hypothetical models of reality based on if-then inferences or understand other people's actions in terms of mental reasons (i.e., theory of mind). Human children are situated in cognitive niches culturally constructed and inherited from the elders, and thus they get accustomed to such linguistic practices, which become an integral part of their cognitive architecture and are in turn bequeathed to further generations (see discussion in Fenici and Garofoli 2017; Zahidi and Myin 2016; cf. Stotz 2014; Sterelny 2012; Menary and Gillett 2016 for a general analysis of extended cognitive niche construction and inheritance). Accordingly, REC defines this culturally acquired representational thinking and the resulting cognitive opportunities it carries within as the "scaffolded mind." This conception of niche construction differs from the one usually adopted by conservative accounts. Within these proposals, natural selection operates upon a series of biological substrates affecting mental representations, which are causally responsible for or merely coupled to the production of cultural practices. These in turn modify the environment, by shaping the human niche, create new selective pressures, and restart the cycle (e.g., Odling-Smee 2007, see Riede's Fig. 17.1 in this volume). Development is seen as a modulation process, which flexibly alters the cognitive and cultural outcomes of biology in relation to the environment (Laland et al. 2014), while culture stands as semantic information that is transmitted downstream across generations through social learning (Richerson and Boyd 2005; see Prentiss and Laue, this volume for review). Despite the role of agency in influencing natural selection, this approach still maintains that (1) the organism is divorced from the world; (2) culture is epiphenomenal, neutral, or merely instrumental to the mind; and (3) cognition and culture are the result of natural selection operating on these parallel channels (see Ihde and Malafouris in press for critique). In contrast, the radical enactive account in cognitive archaeology (RECA) attempts at eliminating such residual conservative elements by assuming a combination of enactive and post-phrenological theories in cognitive science. Specifically, by endorsing material engagement theory, it argues that artifacts bring forth new material and social affordances, which in turn lead to the acquisition of novel ways of making sense of reality and thus restructure cognitive functions (Malafouris 2010a, b; Roberts 2016; Ihde and Malafouris in press). At the neurobiological level, this transformative process is accounted for through the recently proposed theory of neural reuse (Anderson 2010, 2014), according to which brain regions are not functionally determined by natural selection in a way similar to the tools of a Swiss Army knife, as contended by evolutionary psychologists (e.g., Cosmides and Tooby 1994). In contrast, they are deployed and redeployed in a vast amount of cognitive tasks and dynamically brought together in order to construct new cognitive functions in relation to the degrees of freedom offered by their structural constraints (Anderson 2007a, b). Lying at the conjoint of these two accounts, RECA therefore conceives cognitive evolution as a long-term developmental process, whereby humans actively construct their own minds and lifeworld through artifacts and cultural activities.

However, this focus on creative agency and plasticity does not imply completely ignoring biological selection in cognitive evolution but rather rethinking the way it works, a problem that has been unfortunately underestimated by "materiality approaches" in ECA (see Abramiuk this volume for critique). Instead of acting on single functional traits, linking internal representations to cultural outcomes, selection alters some constraints within the plasticity of the brain and ultimately affects the whole relational entanglement between neurons and materiality that defines cognition (Garofoli 2016). New neural affordances can thus resonate with the world and allow humans to create further material affordances while reconceiving old ones. As a consequence, the unidirectional arrow that connects environment to biology, biology to culture, and culture back to a modified version of the environment in Riede's Fig. 17.1 (this volume, after Odling-Smee 2007) needs to be radically reconceived. For RECA, biology and culture are not separate channels subject to specific mechanisms of selection nor can the environment be in any way decoupled from them. Given the radical mediation of human experience through technology (Ihde 1990, 2002, 2009), and the participation of the material world to cognitive and even neurobiological mechanisms (Anderson 2014, Chaps. 5–6; Malafouris 2010a, b; Mareschal et al. 2007, Chap. 10), RECA conceives the modified ecological niche as simultaneously

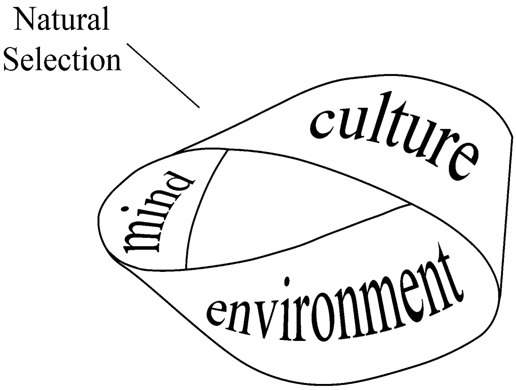

Fig. 19.4 Integrated system of mind, culture, and modified environment illustrated as a Möbius strip. This non-orientable figure (down right) is characterized by no actual distinction between the external and internal surface, so that by moving on the former an agent would find herself on the latter and vice versa without ever crossing an edge. The Möbius strip captures the ontological continuity of mind, culture, and environment and their dynamic shift into one another. Natural selection (top left) is considered to act on such a continuous loop rather than on separated interacting channels

cultural and cognitive. Furthermore, the cultural alterations of the niche are no longer meant as semantic information residing within the individual and transmitted downstream across time like a form of linguistic knowledge. Rather, through their cultural activity, humans construct and bequeath their niche in the shape of a "landscape of affordances," which they learn to navigate and exploit (Rietveld and Kiverstein 2014; Rietveld et al. 2018). The new generations do not simply inherit semantic information from the elders, but are rather guided through this landscape of affordances, which they reenact and transform through the embodied interaction with others (e.g., De Jaegher and Di Paolo 2007; Laroche and Kaddouch 2014). Overall, instead of a series of juxtaposed channels, the dynamics of cognitive evolution are better depicted as a Möbius strip, according to which culture, modified environments, and mind conflate into one another and their distinction persists only in the eye of the observer (Fig. 19.4).

In evolutionary cognitive archaeology, RECA aims at identifying the material conditions for the transformation of these cognitive systems within the archaeological record of ancient hominins while placing particular emphasis on the emergence of scaffolded minds and their integration with basic ones.[9] This radical program renounces the traditional goal in ECA of linking cultural innovations to specific events of mutational enhancement and environmental change occurring at specific evolutionary times (see Mendoza Straffon, Chap. 20, this volume for review of the cognitive enhancement approach). On the contrary, it considers mutational events as necessary conditions for cognitive transformation that happened along trajectories of human becoming (Garofoli 2016). In reconstructing these trajectories, RECA employs a minimalistic agenda because, after denying in principle the existence of sub-personal representations, it wishes to establish to what extent is possible to explain the archaeological record of ancient hominins without invoking linguistic practices (*a la*

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[9] It is worth noting that radical enactive approaches in cognitive archaeology do not exclusively apply to the study of cognitive transformations in early human prehistory but extend also to more recent contexts. Specifically, a significant part of material engagement theory, which can be made compatible with RECA, has been formulated through examples of semiotic and cognitive transformations in Mycenaean and near eastern cultures (e.g., Malafouris 2012, 2013, Chap. 5), as well as used in the context of art history (Woodward 2019) and ethnography (Walls in press). The higher preservation of this material record indeed allows a better reconstruction of trajectories of cognitive changes scaffolded by artifacts than the Paleolithic record. Accordingly, the radical account stands as a general epistemological framework for the human cognitive becoming.

Chemero 2009; see Garofoli 2017a for further discussion). Overall, RECA welcomes Abramiuk's (this volume) epistemological critique by attempting to reconcile conditional approaches in ECA to the concept of long-term development defended by "materiality approaches" and ultimately to the process of natural selection.

A crucial aspect of this enterprise lies in showing that even sophisticated practices, such as early body adornment (Garofoli 2015, 2017b), can be grounded in structures of embodied relations created by artifacts. In this way, agents can make sense of them by relying on the properties of the basic mind only (e.g., direct perception, recognition, and imaginative reenactment) and without necessarily recurring to language and the imposition of representational meaning on objects (contra d'Errico et al. 2005; Henshilwood and Dubreuil 2009, 2011; see Quinn this volume; cf. Garofoli 2015 for a similar critique about spear-making). In contrast, RECA is interested in understanding how these embodied relations could have brought forth representational practices over the long-term. With these concepts in mind, within the next section, I proceed to RECtify the analyses of handaxes introduced earlier for the distributed approach and the theory of enactive signification, and I highlight the similarities and differences between RECA and these conservative embodied models.

The Acheulean Handaxe RECtified

RECA agrees with the distributed approach that handaxes are not the passive by-product of internal algorithms and pre-specified social contexts, but are constitutive of cognition and actively structure the social world. In both the programs, handaxes created behavioral relations that act as a proxy for judging the performance of a knapper. However, the two programs differ from each other in the way hominins make sense of such relational structures. Within the distributed approach, the meaning of these relationships is understood through a priori existing meta-representations and mental state concepts underlying theory of mind (Barham 2010; Gamble 2010; Gamble et al. 2011; Cole 2015). The adoption of such representational primitives in processing materially scaffolded actions creates what we have defined as "wide computations" (e.g., Wilson 1994), which are used to make sense of other people's conduct. These functions remain grounded in evolutionary psychology mechanisms of selection.

In contrast, for RECA, within these intersubjective engagements, the embodied activity performed with and through the handaxe is already significant of the intentionality of action (Garofoli 2018). Indeed, it creates a structure that can be exploited as information for the direct perception and reenactment of meaning. Thus, there is no need to display the shape of a finished artifact to the internal theory of mind in order to *know* that the knapper has a good *knowledge* of the knapping procedure. In contrast, the proficiency of a knapper lies in the invariant relationship between the knapping activity and the emergence of finely crafted handaxes. Agents, therefore, can directly assess one's performance from this set of embodied relations, without the need to process it through metaphysically problematic representational primitives, such as brain-bound meta-representations and mental state concepts (e.g., knowledge; cf. Hutto 2011; Gallagher 2008 ;Fenici 2015).

A similar argument can be made in order to explain the use of standardized handaxe templates in signifying identity concepts (e.g., within *Homo heidelbergensis* contexts, see Pope et al. 2006; Hodgson 2008; Shipton 2013). RECA agrees with the idea of semiotic and cognitive transformation generally proposed by the theory of enactive signification. However, it contends that artifacts need not stand for their meanings, nor do they necessarily acquire such meanings through an inferential logic (i.e., they are not necessarily *about* something in a contentful way). On the contrary, some categories of artifacts can directly embody their meaning, by virtue of their material properties and contextual relations (Hutto 2008b, pp. 54–56). Thus, RECA opposes the traditional view in semiotics according

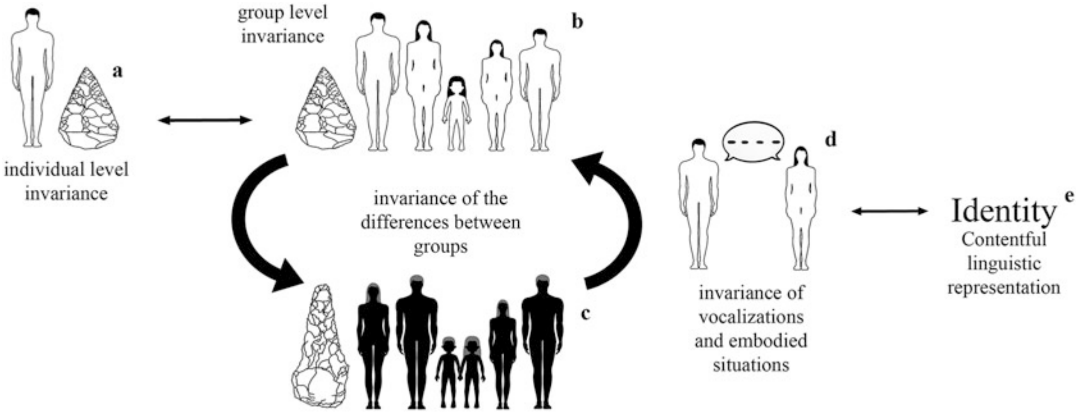

Fig. 19.5 Schematic illustration of the emergence of the contentful concept of identity from a basic (contentless) level of embodied engagement with handaxes and their makers. (**a**) The repeated causal coupling of an agent with a specific handaxe style (drop shaped) creates an invariant relationship at the individual level. (**b**) The handaxe style is transmitted to other group members and establishes an invariant relationship between style and the members of such a group (individuals in white). (**c**) A different (pointed) handaxe style is invariantly associated with the members of another group (individuals in black). Agents can learn to directly perceive the identity of the groups by contrasting the different style-membership relationships (i.e., perception of the invariance of the differences between groups). (**d**) Agents can start accompanying each of these embodied situations with vocalizations, thus gradually establishing an invariant pattern between specific vocalizations and sensorimotor features. (**e**) The contentful concept of identity is socially defined by grounding its content in the previous embodied relations

to which artifacts can act as signs only when referential content is separated from artifacts' expression (Sonesson 2006, 2010).[10]

The inferential production of significative artifacts remains a viable option, but it cannot any longer be based on sub-personal representations and propositions, given the metaphysical problems introduced earlier. In contrast, the inferential strategy needs to be REConceived in terms of an actual linguistic construction. In line with the radical enactive principles of culturally scaffolded mind, this implies creating a language-based "stand for" function and then using it to ascribe declarative concepts to artifacts. Accordingly, rather than a distinction between icons, indexes, and symbols as per the computational logic of sign, object, and interpretant delineated by Peirce, RECA divides signs in contentless (directly perceivable) and contentful (inferentially and language-based) ones. Such a division is transversal to the Peircean classification, so that some categories of signs such as indexes can be either contentless or contentful.

Contextualized to our case study, the regular creation of a particular form for Acheulean handaxes, defined by a set of group-specific habits, establishes a behavioral norm. This contingency creates a reliable association between the members of a certain group and the shape of a tool, thereby instantiating an extended visual icon for these individuals (Fig. 19.5). Consequently, identity is directly perceivable within the collection of bodily and artefactual features that characterizes the visual icon of the members of a specific group. It lies in the structured relations between the observers, the shape of the artifact, and its recurrent association to the body of particular individuals. And it emerges in comparison to the bodily icon of other agents that are not showing the same artifact. The meaning of the handaxe as an index of identity is therefore understandable from this cluster of sensorimotor contingencies (Garofoli 2018). Or, adopting our radio-wave metaphor, the brain

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[10] See Garofoli and Iliopoulos (in press) for a detailed discussion about the differences between the theory of enactive signification and RECA.

becomes progressively attuned to more sophisticated aspects of the world, such as the recurrence of artifact shapes and hominin bodies. Recognizing and imaging this situated concept of identity imply reenacting the same relationship, respectively, in the presence or absence of the external material scaffold.

Furthermore, RECA rejects the conservative embodied idea that abstract concepts, abductive inferences, signs functions, propositions, and meta-representations are brain-bound representational primitives. In contrast, these cognitive properties emerge as linguistic constructs from a culturally scaffolded process. For example, within intersubjective contexts, the material engagement with handaxes can be initially accompanied by the use of prosodical vocalizations, in order to emphasize particular embodied actions (cf. Mithen 2005 on Neanderthals). Later, the invariance of vocalizations and embodied situations can lead to the formation of words referring to such specific contingencies. The accumulation of many of these tokens in turn leads to the progressive development of linguistic propositions that describe states in the world and can be used to communicate empirical aspects of the making of a handaxe and reinforce its use in marking identity. The very abstract concept of identity can emerge as a language-based abstraction, whose content is grounded in embodied situations (Barsalou et al. 2008). Furthermore, propositional strategies can allow exploring the reasons behind actions, by inventing language-based meta-representations (e.g., the linguistic expression "I know that you know"). The human niche therefore changes over time by integrating a landscape of affordances for direct perception and imagining with narrative practices, and accordingly the mind turns into a hybrid of basic and representational processes. In sum, RECtified handaxes offer an example of how representational and propositional thinking is the outcome of cultural engagement with artifacts and other hominins and not its premise, as maintained by the conservative models.

Concluding Discussion

I started this chapter by illustrating the core assumptions behind the internalist view in evolutionary cognitive archaeology and the critique advanced by the relational conservative embodied models. However, I argued that the internalist view can accommodate the relational objections by renouncing deterministic and epiphenomenalist leans and assuming a constructivist perspective. Within this emended version, internal representations, instead of been numerous, specific, and completely internal to the mind, are few and more general and can extend themselves into material reality, thereby widening their computational basis. However, these representations are still subject to the metaphysical problems of content, substance, and origin (see the *Introduction*) and maintain a Cartesian view of the mind. After this assimilation process, rather than a sharply different paradigm from the internalist view, the conservative embodied critique restitutes a milder version of it.

In contrast, I have argued that such remaining problems can be overcome only through a radical reassessment of embodied and extended principles in evolutionary cognitive archaeology, which implies abandoning even minimal forms of representational apriorism. Through the example of RECtified Acheulean handaxes, I have shown that material engagement need not be conceived as the amplification of internal representations. In contrast, we need to see it as a process of resonance to deeper properties of reality brought forth by artifacts, which constitutes the roots for the construction of representational thinking. This move not only allows escaping the aforementioned metaphysical issues, but it also sets aside residual ideas about an evolved modern human nature resurfacing within the more conservative approaches. Insofar as cognitive functions are thoroughly relational and fully constituted through cultural and material reality, the idea of a complete and modern mind becomes difficult to defend, for there is no more fixed component where to anchor the concept of “intrinsic human nature.”[11]

Overall, the handaxe case study offers a gist of how the radical enactive agenda proceeds in evolutionary cognitive archaeology. In its negative part, the radical critique argues against the conservative account by showing that it (1) incurs unbearable metaphysical costs by assuming that handaxes are coupled to deeply problematic representational primitives, (2) lacks a genuine developmental perspective, and (3) fails the (empirical) criteria of minimalism at the core of conditional and realist accounts in evolutionary cognitive archaeology (see Abramiuk this volume, 2012, pp. 30–33; Garofoli 2017a). In relation to the third point, radical analyses of Acheulean contexts have indeed shown that a priori representations are not necessary cognitive conditions to explain a set of Acheulean artifacts that include and go beyond handaxes. In contrast, the abilities of basic minds are quite sufficient to account for these artifacts, thereby disconnecting the conservative explanations from the archaeological record (see Garofoli 2015). Thus, there exist metaphysical, developmental, and empirical reasons to consider the radical account superior to the conservative one. Conversely, in its positive part, the core of the radical enactive program lies in identifying different trajectories of integration of basic and scaffolded minds, by pinpointing the conditions for such a cognitive metamorphosis within the archaeological record. Accordingly, the handaxe case study discussed in this paper sets forth a content-relaxed, developmentally plausible, and minimalistic proposal for the long-term emergence of identity concepts and meta-representations, which needs to be assessed for its plausibility through contextualization with additional trajectories of cognitive/cultural transformation (Garofoli 2017a).

Nevertheless, the critique advanced by RECA implies relevant costs. On the one hand, RECA’s metaphysical discourse engages with the ambitious task of eliminating internalist concepts that are currently deeply entrenched within cognitive science. Among these, it stands out the idea that theory of mind is a sub-personal and innately specified ability present in all human beings, which currently exert great impact in developmental and comparative psychology (e.g., Baron-Cohen 1995; Leslie et al. 2005; Onishi and Baillargeon 2005; Krupenye et al. 2016; Buttelmann et al. 2017). The radical enactive program accordingly presupposes that this basic tenet need be renounced and argues for a language-based construction of theory of mind abilities. On the other hand, this radical program pursues its aims without allying with its cousin, namely, the conservative embodied approach. Although RECA agrees with some aspects of this critique, it urges for a more substantial revolution in the way of criticizing the internalist view. Accordingly, it invites us to deeply rethink theories that are currently on the rise in ECA and more general in cognitive science and archaeology. In particular, as shown by the distributed approach, the application of the extended cognition paradigm to cognitive evolution is in its earliest steps and has shown promising in explaining the scaling up of groups beyond the computational limits of the human brain (Coward 2016). At the same time, Peircean approaches have only recently reached a deeper and more analytic form within ECA (e.g., Preucel 2007). After a decade of imperfect multidisciplinary overlapping between archaeology, cognitive science, and semiotics, the latest years have seen a more thorough application of Peircean semiotics to the study of cognitive and semiotic transformation in human evolution (Malafouris 2013, Chap. 5; Iliopoulos 2016b). This integration helped undermine the idea of a clear-cut emergence of symbolic thinking intrinsic to the standard internalist view. Similarly, the application of niche construction theory in interpreting archaeological changes have invited scholars to abandon narrow neo-Darwinian accounts to cultural and cognitive evolution (see Prentiss and Laue and Prentiss this volume). Nevertheless, although these new theories undoubtedly have powerful epistemological reasons to their favor, their

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[11] See Hutto and Myin (2013) on the difference between the conservative idea of “extended cognition” and the radical one of “extensive” cognition.

reliance on representationalist models motivates RECA's skepticism. Indeed, no epistemological advantage can compensate the risk of maintaining positions that are incompatible with naturalism, reintroduce mysterious mental entities, and foster dualistic views about the relationship between the mind, the body, and the world. Thus, the reasons for RECA's worries remain valid and justify steering away from internalism and fully going radical.

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Chapter 20
Evolution and the Origins of Visual Art: An Archaeological Perspective

Larissa Mendoza Straffon

Introduction

The history of the first discoveries, identification, recognition, and scholarly reception of Palaeolithic art may be one of the most exciting and dramatic tales in the annals of archaeology. The story begins in the late nineteenth century, with the recurrent find of small figurines and carved images in French prehistoric sites, such as La Madeleine. These finds of so-called Ice Age portable art pieces were followed by the discovery of the spectacular painted cave of Altamira, Spain, in 1879 by Sanz de Sautuola. Initially thought to be a fake, Altamira was dismissed by the academic community. It would take 14 years and consequent discoveries of painted caves to convince scholars of Altamira's authenticity, and finally, in 1902 the cave was recognized as a true 'masterpiece' of prehistory, leading to a re-evaluation of cave paintings as humankind's 'first art' (Bahn and Vertut 1997; Cartailhac and Breuil 1903; Conkey 1987; Grand 1967; Lewis-Williams 2002; Pfeiffer 1982).

During the twentieth century, the corpus of European Palaeolithic art became increasingly more abundant, impressive, and ancient. Moreover, since the beginning of this century, finds from African and Middle Eastern sites have forced archaeologists to reconsider not only the initial age of visual art (from 25,000 to 100,000 years ago) but also the location of its emergence (from Europe to Africa) and even the kinds of artefacts that may be considered as art (from paintings to beads). Despite these recent and radical changes spurred by the material record, most archaeological explanations for art's origins have remained fundamentally the same since the first part of the twentieth century. The focus remains on the content of the artworks (e.g. symbolism, information, ritual, etc.), while pleasure, emotion, expression, and religion are still invoked as the prime motives for visual art-making, just as they were over a century ago. As an alternative to these archaeological narratives, evolutionary scholars have developed what have now become some of the most influential hypotheses about the origins of art. These approaches rely on behavioural and biological science and are at the centre of topical debates on the evolution of human cognition and behaviour; however they have seldom been assessed in view of the archaeological evidence of early visual art. The aim of this chapter is precisely to carry out such an evaluation in order to show that the collaboration between evolutionary thinking and archaeology can eventually lead to a better understanding of the emergence human culture, as a whole, and of art in particular.

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The study of visual art from an evolutionary point of view has a long history which can be traced back to Darwin's *The Descent of Man*, where he discussed the evolution of the mental powers and the aesthetic preferences of humans, as a whole and in regard to art (2004) [1879]. Since then, scholars have attempted to account for the place of art in human biology, and vice versa, to explain art-making as a biological phenomenon (Alland 1977; Huxley 1966; Morris 1962). Thanks to anthropological data from across the globe, we know that some sort of visual art is present in every known human culture and is therefore considered a 'universal' human behaviour that involves a propensity to make and/or mark objects with visual patterns or properties (Dissanayake 2010). Two main lines of thinking address the species-wide presence of visual art. The first suggests that visual art may have evolved not because it had a value in itself but because it was coupled to adaptive traits, that is, by 'piggybacking', for instance, on general intelligence, or as a side-effect of visual and perceptual biases (De Smedt and De Cruz 2012; Verpooten and Nelissen 2010), being retained only because it was pleasurable (Pinker 1997). The second view maintains that art most likely had a genuine 'adaptive value' throughout human evolution, meaning that it was shaped by natural selection because it somehow contributed towards the survival and reproduction (i.e. fitness) of the individuals that displayed it and may even be considered a human adaptation (Dissanayake 1980).

On this chapter, I will focus primarily on the second view, as it has generated the most interest in the academic community. Scholars working from this perspective have often started out by asking what art evolved for. There has been no shortage of proposals to answer that question,[1] but three main themes have prevailed: sexual selection, social bonding, and cognitive enhancement. These three hypotheses, in their different versions, are frequently cited in the literature on art's origins and have been the subject of many debates (Fig. 20.1). Most supporters and detractors of these models have based their arguments on the internal logic of the hypotheses or on mere affinity, but they have rarely evaluated them according to their compatibility with archaeological data. After a quick review of the archaeological record, we will see how the scenarios derived from these three hypotheses stand against the material evidence.

Identifying Pleistocene Visual Art

The Pleistocene is the name of the geological era spanning from 2.5 million years ago up to 12,000 years ago by the end of the last Ice Age, which marks the beginning of the following geological epoch, the Holocene. It is in the Pleistocene where we find the earliest evidence for the emergence of both the human lineage and visual art. Therefore we will here use the term 'Pleistocene art' to refer to the oldest examples of visual art on record (Nowell 2006). We will define visual art as objects or patterns made, modified, and displayed to engage attention through the manipulation of visual qualities like colour, shape, texture, brightness, etc., as well as the processes involved in their production (Mendoza Straffon 2014).

Archaeologists, however, often struggle to identify art objects among other traces of past human activity from the remote past. Most researchers have traditionally related art objects to qualities that amount to 'beauty', like symmetry, balance, and elegance (Currie 2011). However, an aesthetic element is not sufficient to define art (van Damme 2008), and by the same token, the 'aesthetic' is not limited to beauty. Rather, aesthetic features include all perceptible, attention-grabbing, visually arresting properties, whose effects need not be pleasing. Despite that, artefacts which have been

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[1] Dissanayake identified at least nine of these proposals (2007), each suggesting that art evolved for some specific purpose: pattern recognition, mental problem-solving, adaptive decision-making, increasing mating opportunities, supporting religious behaviour, providing fictional scenarios for action-planning, social manipulation, social cohesion, and cognitive enhancement.

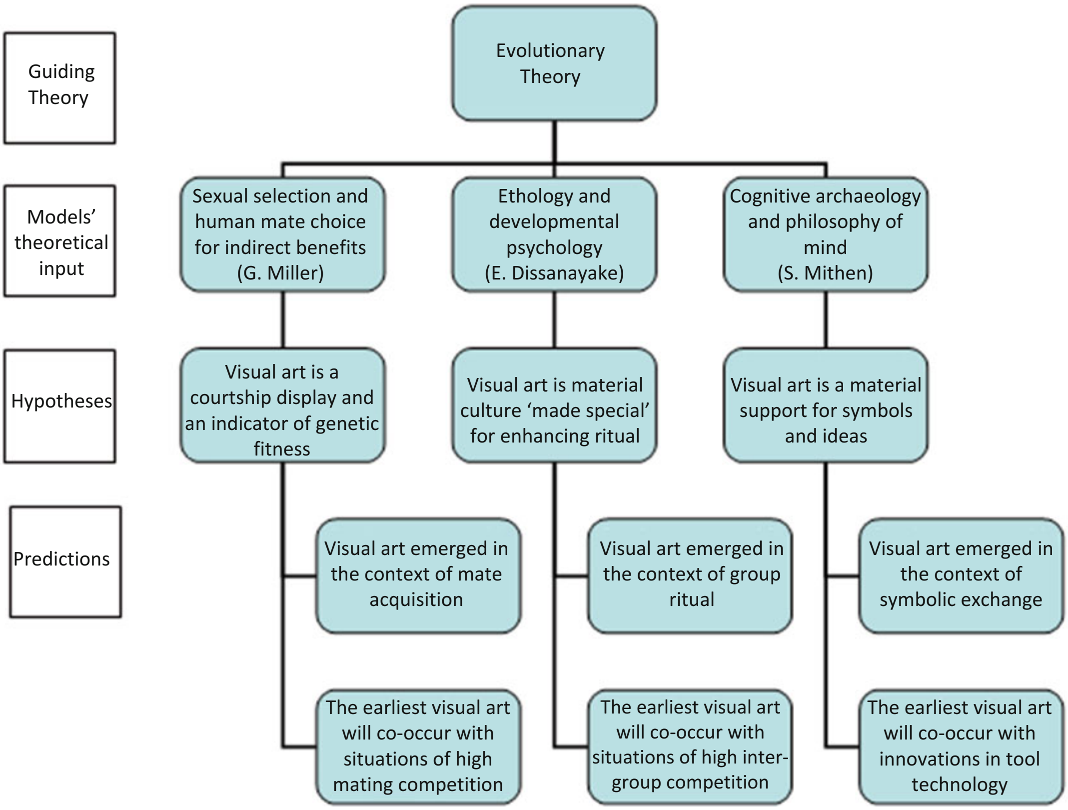

Fig. 20.1 Theoretical scheme of the three hypotheses for the origins of art examined here

produced to comply with gratifying aesthetic properties are more easily identified as artworks by cultural outsiders (Davies 2000). In the end, we classify visual art by analogy to what we historically know to be art (Moro Abadía and González Morales 2010).

Another criterion often used is 'non-function', that is, whenever an artefact does not seem to have any other function other than aesthetic or symbolic, it is often categorized as an artwork (Chase 1991; D'Errico and Villa 1997). However, it is difficult to say with any certainty whether an item has had a utilitarian function or not. Furthermore, neither the aesthetic nor the symbolic are exclusive properties of art, so they do not offer an answer to the question of how to distinguish art from non-art. Perhaps we had rather remind ourselves that visual artworks not only are aesthetic and symbolic but also are powerful communicative tools made to be displayed and perceived and that this may actually be their ultimate function (Mendoza Straffon 2014). Therefore, display will be an important criterion for identifying visual art. That is, when display can be inferred as a primary function of aesthetic or symbolic artefacts, then we may categorize them as visual art.

Finally, conceiving of visual art as part of a cultural system implies that it should appear as a recurrent practice in the archaeological record, and not only as an accumulation of isolated or 'one-off' cases. Cultural traits are typically socially shared, persistent, and variable in a population (van Schaik & Pradhan 2003). Therefore, continuity and/or recurrence in a constrained chrono-geographical span is used as an inclusion criterion. As a result, the present survey of Pleistocene visual art includes forms occurring at more than one site within the same time range and within a particular geographic region; forms that occur at more than one archaeological level in one site (suggesting transmission of cultural behaviour over time); and forms that are quantitatively significant at any given site or period (suggesting that they were used and/or produced by several individuals, i.e. culturally shared behaviour). Overall, the corpus includes evidence related to activities such as the colouring and painting of surfaces, personal and artefact ornamentation by various techniques, and the inferred intentional transformation of materials towards decoration or representation.

Visual Art Before Homo sapiens

The existing literature on prehistoric art often discusses a handful of artefacts as potential 'firsts' of visual art forms. Three of the most prominent examples are the Makapansgat pebble, the Berekhat Ram figurine, and the Tan Tan statuette. These objects apparently show intervention by hominins and are said to represent 'the earliest example of some kind of aesthetic sense, or at least evidence for recognition of a likeness' (Bahn and Vertut 1997, p. 23). The Makapansgat pebble, which resembles a human face, was found in the context of a 3-million-year-old site belonging to *Australopithecus*. The Berekhat Ram statuette was recovered in Israel and estimated to be 250–280,000 years of age and is made of volcanic tuff that was artificially enhanced apparently to make it look like a female figure, which incidentally resembles an Upper Palaeolithic 'Venus' (D'Errico and Nowell 2000). The Tan Tan figurine is an anthropomorphic quartzite fragment found in a 400,000-year-old site in Morocco. Like the previous piece, this one also seems to have been partly shaped through human intervention and further has some minuscule traces of red pigment (Bednarik 2003). Although these alleged cases of early art-like objects cannot be readily dismissed (Bahn and Vertut 1997; D'Errico and Nowell 2000), the lack of academic consensus surrounding their significance rather renders them as archaeological oddities. A recent interesting addition to this list of finds is the incised shell of Trinil, Indonesia. Originally excavated in the nineteenth century and rediscovered a few years ago in a Dutch museum depot, this shell was in the archaeological collection of Eugène Dubois, who dug the *Homo erectus* specimen known as Java Man. The surface of the shell bears a fine geometrical pattern whose meaning or intentionality remains unknown but which shows that by half a million years ago, members of the *Homo* lineage were already inclined to modifying objects through pattern-making (Joordens et al. 2015). But even if these artefacts represented an early aesthetic or formal recognition sense, as far as we can tell, they did not seem to constitute a systematic cultural practice nor do they seem as yet to be directly related to the development visual art in the late Pleistocene (Davis 1993).

The case for Neanderthal art seems more promising. There are a number of incised pieces of bone from Neanderthal contexts which have long been claimed to be of a symbolic nature. One of the best known comes from the German site of Bilzingsleben and bears some parallel markings (Mania and Mania 1998). However, the origins of these pieces have remained debatable (Mithen 1996), as it proves difficult to determine whether the incisions were made intentionally or as a by-product of other actions, such as sharpening cutting tools or defleshing the bone (Davis 1993).

Much more recently, a series of new findings have thrown light on Neanderthal behaviours that may be interpreted as 'artistic'. The earliest of these is an architectural feature deep inside the French Cave of Bruniquel. It is made of stalagmites arranged in circles and has been dated to 175,000 years BP. The structure could not have been used for habitation, so the assumption is that it had a symbolic function (Jaubert et al. 2016). At two Spanish sites, researchers reported the presence of shells in Neanderthal occupation layers, dated to ca. 50,000 BP. At Cueva de los Aviones, four *Glycymeris insubrica* shells were found, and at Cueva Antón, another shell of *Pecten maximus* with pigment remains has been recovered. The authors suggest that these shells may have been used as personal ornaments (Zilhão et al. 2010). Finally, the recent dating of three rock art sites in Spain yielded ages of over 60,000 years for various painted motifs. Because these dates pertain to a period when seemingly *Homo sapiens* had not yet entered Europe, they indicate that the paintings must have been made by Neanderthals (Hoffmann et al. 2018). Although it may be too early to fully appreciate the implications of these recent discoveries, they will definitely force researchers to reconsider much of what is known about the evolution of hominin cultures and of the origins of visual art. We must note, however, that even if these finds show that different *Homo* species developed artistic practices, each would have done so in response to their own particular social and environmental circumstances. That is, the evolution of art, like that of any other type of material culture, cannot be traced as a single, continuous line from *Homo erectus* to modern humans. For the same reason, we should not simply assume that the motivation behind art-making behaviours should be the same for all hominin populations. Hopefully, future research will focus on reconstructing and understanding the particular contexts in which Neanderthals, or any other species, may have created art.[2]

'Modern' Art

I reiterate that the focus of this chapter will be on (purported) *Homo sapiens* contexts. Unlike the previous examples, our species has produced artworks of sufficient quantity and quality to leave a clearer, more recurrent, identifiable trace in the archaeological record, which can help us place art practice in its context and therefore test hypotheses about the emergence of art.

According to the chronological order in which they first appear in the archaeological record and the amount of labour investment that they entail (time and effort), I have grouped Pleistocene visual art forms into five groups: pigments, personal ornaments, incised objects, carved figures, and painting. Evidently, these five categories are an oversimplification, and there is some overlap among them. For example, there is ochre on ornaments, there are engravings on ochre, some carved figures seem to have been used as pendants, and cave art usually includes a combination of techniques such as engraving, finger tracing, and painting. Furthermore, we must assume that there were several other art forms which have been lost to archaeology, such as sand drawings, designs on wood, fibres or leather, and body art. Many researchers in fact agree that the human body surely must have been the first canvas (Donald 1991; Schildkrout 2004; Turner 2012). Ethnographic examples of body art include several techniques applied to the skin, teeth, and hair, like shaping, cutting, piercing, scarifying, tattooing, branding, and painting. We could also include here hairstyles and clothing (Gilligan 2010). Traces of these practices naturally disappear with the decomposition of the human body and organic matter; however, some indirect evidence can be used to infer them, like the presence of ochre pigments.[3]

In sum, the following survey offers a general overview of the earliest examples of such objects, which may be compressed in five categories: (1) pigments, (2) personal ornaments, (3) incised objects, (4) carved and sculpted figures, and (5) painting. The classification somewhat reflects the chronological sequence in which the various art forms appear in the record and, to some extent, correlate with an increase in technical and organizational complexity.

Ochre Pigments

Ochre is a generic term that encompasses several naturally occurring minerals with high contents of iron oxides that produce a range of hues of yellow, brown, orange, and red. Typical ochre minerals

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[2] For a complete review of all purported art objects of Neanderthal origin, see: David (2017), Langley et al. (2008), Roebroeks (2008), and Zilhão (2007).

[3] Body art (e.g. tattoos, scarification, painting) and the use of garments can also be inferred from figurative art. For example, the 'Venus' figurines have proven a valuable source of information about Palaeolithic female hairstyles, headgear, and garments and of possible body art patterns (Soffer et al. 2000). Rock art from the European Palaeolithic has also provided some clues about the use of complex clothing and hats (Gilligan 2010).

like limonite or hematite can be rubbed directly on surfaces to apply colour or be crushed to produce powders of reddish hues that can then be used as pigment (Henshilwood et al. 2011). Other naturally occurring minerals which may be used for pigment production include, among others, gypsum and kaolin (white) and charcoal and manganese dioxide (black). The archaeological evidence of pigment use is ambiguous in that we often only find ochre as a raw material or traces of its processing, and most of the time, its final purpose has to be inferred by the researcher (D'Errico et al. 2012).

Evidence from various sites, most notably Kapthurin in Kenya (Barham 2002; McBrearty and Brooks 2000) and Twin Rivers in Zambia (Barham 1998, 2002), includes the accumulation of large quantities of ochre minerals (e.g. limonite, hematite, specularite), some of which show traces of intentional abrasion, indicating that they may have been scraped and rubbed onto surfaces to obtain yellow and reddish colouration (Barham 1998, 2002). Conservatively, the dates from these sites indicate that by 270,000 years BP, African hominins already 'had incorporated color into their lives' (Barham 2002). Since the origins of our species may go as far back as 300,000 BP (Hublin et al. 2017), this would mean that from very early on, our ancestors were interested in these minerals and their properties (Barham 1998).

The best example of early ochre exploitation by *Homo sapiens* comes from the South African site of Pinnacle Point (Marean et al. 2007; McBrearty and Stringer 2000), where archaeologists found an accumulation of over 50 pieces of red ochre, a dozen of which showed traces of use (grinding and scraping), dated to 164,000 BP (Marean et al. 2007). There is much more evidence of ochre extraction in South Africa during the Late Pleistocene. Ochre use is recorded at the sites of Klasies River and Howiesons Poort going back to 100,000 and 80,000 years BP, respectively. The archaeological material from Border Cave includes hematite 'pencils' older than 100,000 years, and Blombos Cave has a record of ochre exploitation spanning multiple stratigraphic layers dated from 100 to 75,000 years ago (McBrearty and Brooks 2000; Watts 2009).[4]

At Blombos Cave, two recent finds have revealed the sorts of activities and materials involved in ochre processing and its use. The first is an ochre-processing workshop that includes two toolkits used for producing and storing an ochre mixture. The toolkits consist of two abalone shell containers, a stone cobble, probably used as a hammerstone, mineral residues from grindstones, crushed bones whose marrow could be used as a pigment binder, charcoal, and red ochre. This find has been dated to ca. 100,000 years BP and is the best evidence that in the MSA, humans were purposively exploiting ochre for pigment extraction (Henshilwood et al. 2011). The second find, highly relevant to the discussion of visual art's origins, is a stone flake displaying a cross-hatched pattern drawn with a red ochre crayon some 73,000 years ago (Henshilwood et al. 2018). Even though this piece is only a fragment of what must have been a larger design, its significance is huge not only because it demonstrates that the Blombos humans were in fact using ochre pigments to depict visual signs for decoration or communication (and not only for 'practical' purposes), but also it pushes back the origins of drawing as a technique by 30-odd thousand years. That drawing had been practiced by early modern humans was somewhat implied by the previous finds of hematite 'pencils' mentioned above, but the Blombos drawing finally shows with certainty how and what for these ochre instruments were used.

There are other early examples of ochre extraction and use outside Africa. In the site of Qafzeh Cave, in Israel, several lumps of red ochre with traces of scraping have been recovered from stratigraphic layers dated to 92,000 BP. These pieces were transported to the site from outward locations where intense red-hued minerals (hematite) could be found, indicating the purposive

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[4] The sites mentioned here only include the earliest samples of ochre exploitation but the actual record is much more extensive. For a general overview, see Watts (1999).

selection of and preference for particular raw materials. There also is a possible association of ochre occurrence with human burials and marine shells at this site (Bar-Yosef Mayer et al. 2009; Hovers et al. 2003).

In Europe, the use of ochre minerals is well documented in the Neanderthal archaeological record of the Middle Palaeolithic, particularly towards the end of that period, between 60 and 40,000 BP (D'Errico et al. 2008, 2010; Soressi and D'Errico 2007; Roebroeks et al. 2012; Zilhão et al. 2010). Iron oxides producing orange, yellow, and red were exploited, although in low quantities. The most common colour mineral used among these hominins was manganese dioxide, which produces a black pigment (D'Errico et al. 2008). However, the differences in ochre use between the Middle and Early Upper Palaeolithic are both quantitative and qualitative. In the latter, not only is the frequency of ochre exploitation much higher, but also the preference for the colour red is quite marked (Watts 1999, 2009). Furthermore, especially from the Gravettian onwards, red ochre is often found in burials (Riel-Salvatore and Gravel-Miguel 2013; Martínez González and Mendoza Straffon 2017).[5] This suggests that red ochre might have played a much more important role in the lives and beliefs of modern humans.

Whether ochre use qualifies as evidence of human visual art behaviour has been hotly debated among archaeologists. Ochre can have many different utilitarian applications that would not necessarily involve any artistic intentions (Wadley 2005). For example, the minerals may have been used to treat and preserve animal hides (Dubreuil and Grosman 2009); mixed with resins and wax to produce an effective adhesive (Wadley 2005); consumed for their antiseptic, astringent, and deodorizing qualities (Velo 1984, 1986); or used as 'sunblock' (Ellis et al. 1997). There is no need, however, to divorce the utilitarian from the artistic. Ethnographic data show that pigments may be used in both practical and symbolic contexts and that these are not mutually exclusive (McBrearty and Stringer 2007). So, it is rather likely that throughout early prehistory, pigments were used for practical reasons as well as for personal and artefact ornamentation and in ritual.

It is however significant that in sites attributed to *Homo sapiens*, highly red-coloured minerals were recurrently targeted and preferred over blacks or whites, which points to an intentional selection that would not be expected if pigment use had been strictly utilitarian (McBrearty and Stringer 2007; Watts 1999). The aesthetic use of red ochre is also suggested by the fact that Pleistocene ornaments (beads and pendants) often show traces of ochre, meaning that they were either purposefully coloured or they acquired it by contact with coloured surfaces (e.g. skin, hair, garments). Finally, the recent find of a red pigment drawing at Blombos Cave shows that ochres were at times used to depict visual signs on hard surfaces and opens up the possibility that they may have been used in a properly artistic manner.

In sum, ochre use seems to be an ancient human practice. Moreover, in both Africa and Europe, the appearance of modern *H. sapiens* is accompanied by an increase in the frequency and quantity of red ochre exploitation. So, even if by itself it remains ambiguous as evidence for visual artistic behaviour, the habitual occurrence of red ochre minerals (for pigment production) may be considered an archaeological marker of our species (Watts 2009).

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[5] The association of red ochre and human burial is also observed in one of the earliest known archaeological sites in Australia, Lake Mungo, dated around 60–40,000 BP, where a modern human skeleton covered in red ochre pigment was found (Bowler et al. 2003; Klein and Edgar 2002, p. 248; Stringer 1999). It is notable that the source of the ochre was about 200 km away from the burial site, which implies that the material was specifically sought after and transported a long distance (Klein and Edgar 2002, p. 249).

Personal Ornaments

Archaeologists usually include in this category those small objects that were seemingly used for suspension or attachment (Kuhn and Stiner 2007b), such as beads, pendants, and 'charms' which could have been used to decorate garments or utensils, or as jewellery (White 1992). We can divide personal ornaments in the two subcategories of modified and manufactured ornaments.

Modified Ornaments

These include natural items that have been selected and frequently, though not always, modified presumably for display. These often entail collected materials, such as shells, stones, or animal teeth, that have been slightly altered to fulfil a new function, for instance, by polishing, perforating, or stringing them. The amount of labour applied is not considerable, although the modification process might still have required special knowledge and skills (Tátá et al. 2014). Even though such materials are often called beads or pendants, implying their use as jewellery, they could have equally been sewn to pieces of clothing or attached to personal items like bags, baskets, or domestic utensils (White 1992).

Since the discovery of a collection of shells dating from 75,000 BP at the site of Blombos Cave in South Africa in the early 2000s (Henshilwood et al. 2004), the number of shell bead finds and their ages have only increased. The evidence now indicates that by 100,000 years ago, at the latest, humans were using modified marine shells for display purposes, likely as personal ornaments. So far, the oldest of these early beads come from the Levant. In the 1930s, excavations at the cave site of Skhul in Mount Carmel, Israel, exposed a rich archaeological context dated between 100 and 135,000 BP. It included the buried remains of ten (modern human) individuals, lithic artefacts, and a few seashells, two of which were perforated and probably used as beads (Vanhaeren et al. 2006). At the nearby site of Qafzeh Cave (92,000 BP), ten marine bivalve shells were found, most of which have perforations, traces of use wear, and signs of stringing, and some of them also bear red ochre stains (Bar-Yosef Mayer et al. 2009). Seashell beads were also retrieved at the sites of Ksar Akil in Lebanon and Üçağizli Cave in Turkey, dating back between 41 and 43,000 BP (Kuhn et al. 2001).

In Africa, small marine shells probably used as ornaments have been found in several Pleistocene sites, from North to South. In Morocco, they have been recovered at Smuggler's Cave (108,000 BP), at Pigeons Cave (82,500 BP), at Rhafas Cave (80–70,000 BP), and at Ifri n'Ammar (83,000 years BP) (Balter 2011; D'Errico et al. 2009). The 13 seashells (*Nassarius gibbosulus*) from Pigeons Cave were transported some 40 km and show intentional perforations and signs of wear, and one bears red pigment residues (Bouzouggar et al. 2007). Finally, the collection from the Musée de l'Homme in Paris included a *Nassarius* shell from the site of Oued Djebbana, in Algeria, with an estimated age of 90,000 BP (Vanhaeren et al. 2006). In South Africa, a rich collection of Pleistocene shell beads has been recovered at Blombos Cave. A total of 68 *Nassarius* shells are dated to ca. 75,000 BP. Microscopic and experimental analysis has indicated that these shells were probably pierced with a bone point, and some show traces of stringing and wear. Most of the shells were found in groups, indicating that each group might have constituted single beadwork items (Vanhaeren et al. 2013). The shells form Blombos illustrate that these objects were being used for display, probably as ornaments. Elsewhere in South Africa, Border Cave yielded a perforated *Conus* shell associated with a human burial, dated to 76,000 BP (Vanhaeren et al. 2013). Although the production of shell beads in sub-Saharan Africa apparently came to a halt after 70,000 BP, the evidence suggests that by 100,000 years ago, the use of personal ornamentation was a common practice in Africa and the Levant (Bouzouggar et al. 2007).

In Europe, personal ornaments do not appear very frequently until the Early Upper Palaeolithic, at the time related to the spread of modern humans into this region. Throughout the Aurignacian

(45–28,000 BP), there are abundant modified ornaments made often from marine shells like small gastropods (including *Nassarius*) and from mammal teeth, as well as a wide range of other materials, such as freshwater, terrestrial and even fossil shells, fish vertebrae, animal bone, minerals, crystals, and amber (Álvarez Fernández and Jöris 2008; Kuhn and Stiner 2007b; White 2007). Clearly, eye-catching lustrous (and often exotic) raw materials were selected to be modified into ornaments (Álvarez Fernández and Jöris 2008; White 1993). The use of modified natural objects as ornaments continued during the whole of the Upper Palaeolithic, but along these, manufactured beads also became common.

Manufactured Ornaments

In contrast to the previous type, manufactured ornaments have gone through a more elaborated and exhaustive production process, where the raw material has been collected, worked (sometimes extensively), and shaped into the final artefact.[6] This process entails a greater investment of labour and skill, as well as good knowledge of the qualities of the raw material and the tools and techniques to modify it. These kinds of personal ornaments made from scratch appear in the archaeological record later in time than the modified sort and similarly could have been used as body decoration, to adorn artefacts, or even as garment closures or buttons (Gilligan 2010; White 1992).

The oldest manufactured ornaments in Africa are ostrich eggshell beads created by cutting and shaping 'blanks' of ostrich eggshell, which were then perforated and reduced to round discs. At Border Cave, South Africa, 14 of these beads were found in layers pertaining to 44–41,000 BP (D'Errico et al. 2012). At Enkapune Ya Muto rock shelter in Kenya, 25 ostrich eggshell beads in different stages of the production process were excavated in a layer dated to around 41,000 BP, revealing the laborious manufacturing method (Ambrose 1998a). At times, the beads were further modified by heating, to turn them dark (D'Errico et al. 2012), or by applying ochre (Ambrose *pers. comm.*). Nowadays, ostrich eggshell beads play an important role in the exchange economy of the contemporary! Kung San peoples of the Kalahari (Wiessner 1983). This suggests a function for the Pleistocene examples and presents the possibility of some cultural continuity in the region (D'Errico et al. 2012; Deacon 1992).

In Europe, there is a high occurrence of manufactured beads from the Early Upper Palaeolithic onwards. The most common raw material used in this region was mammoth ivory, but other materials like bone, antler, minerals, limestone, and amber were also habitual (Álvarez Fernández and Jöris 2008). The fabrication process of ivory beads has been well-studied and reveals that these ornaments were often semi-mass produced using standard shapes, some of which show regional patterning (White 1993). Ivory pendants could be created individually by carving and scraping a piece of ivory into shape, but more commonly beads were produced in series. This process involved preparing an ivory rod, dividing it in segments by thinning to produce preforms or blanks, perforating each preform, and then smoothing and polishing each blank into the final form (White 1989) (Fig. 20.2).

Greater variation in form is to be expected in beads produced from scratch, as the makers are not as constrained by the natural form of the raw material as in the case of modified natural objects like shells or teeth. The fact that some forms, materials, and production techniques were localized even within regions (Kölbl 2009) indicates that the knowledge involved in bead-making was socially transmitted and, as reproduction experiments have revealed, required considerable time and skill (White 1989). The modern reproduction of Palaeolithic beads reveals on the one hand a labour-intensive sequence, but on the other, it shows that people were maximizing production by using techniques that allowed the creation of several beads from a single piece of raw material, reducing

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[6] White has used the term 'purposely fabricated beads' (1989), for what I have called 'manufactured ornaments'.

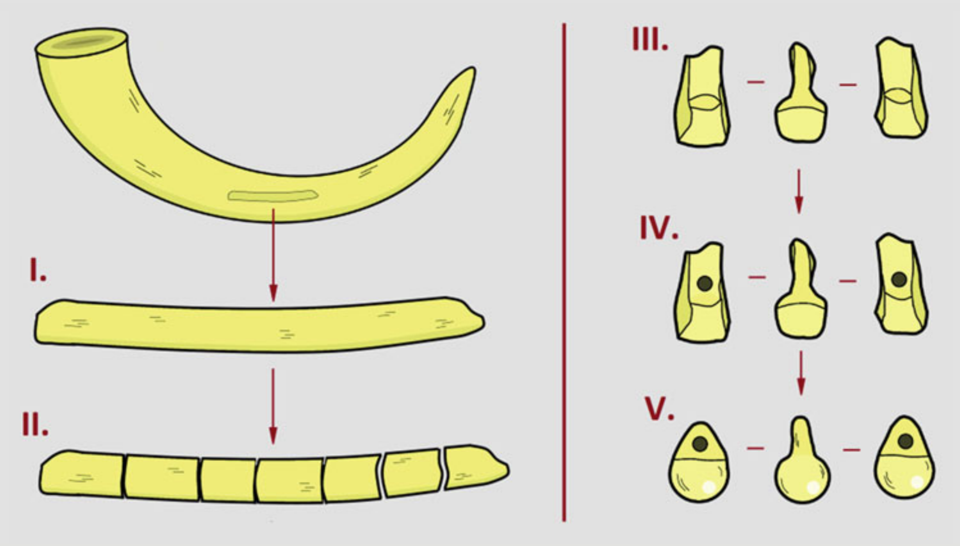

Fig. 20.2 Production process of Aurignacian mammoth ivory beads (after White 1989)

waste and time investment. This, along with the remarkable standardization of Aurignacian beads, hints at the ancient specialization of craft (White 1989, 1993).

The use of these artefacts as personal ornaments during the Early Upper Palaeolithic is supported by the fact that manufactured beads have often been found in burials (Riel-Salvatore and Gravel-Miguel 2013; Martínez González and Mendoza Straffon 2017). In the funerary sample from the Palaeolithic, manufactured beads are commonly found in the graves of adults and infants, and often near the head, neck, torso, and arms, suggesting these were most probably attached to headgear and items of clothing worn in daily life (Riel-Salvatore and Gravel-Miguel 2013). The possibility that both adults and children were frequently buried with their everyday ornaments supports the idea that these items had strong personal connotations of individual identity (Coe 2003; Kölbl 2009; Kuhn and Stiner 2007a, b; Vanhaeren 2005; White 1993; Zilhão 2007).

Incised Objects

This category includes all objects showing traces of intentionally made designs, generally by incision or engraving, on various materials. These patterns may not have required much effort to make, but probably great dexterity and precision were needed to create a discernible design on a surface (Henshilwood and D'Errico 2011; White 1996).

The earliest examples of this category come from various Middle Stone Age sites in Africa (Cain 2006; Henshilwood and D'Errico 2011). Most notably, in Blombos Cave, a collection of over a dozen engraved pieces of ochre dated between 100 and 75,000 years ago has been recovered (Henshilwood et al. 2009; Henshilwood and D'Errico 2011), as well as several bone fragments incised with linear patterns (D'Errico et al. 2001; Henshilwood et al. 2002). A few pieces portray clearly organized geometrical arrangements. The best-known example is the rectangular piece of reddish-brown siltstone which bears a double chevron design, recovered from a layer dated between 78 and 74,000 BP. Closer examination has shown that the piece was faceted and ground in preparation for the engraving (Henshilwood et al. 2009), indicating that the incising involved more than a spontaneous action. In Namibia, notched fragments of ostrich eggshell have been recovered from the basal strata at Apollo 11, dating back to at least 83,000 years ago (Wilkins 2010). Another remarkable collection of incised ostrich eggshell pieces, of no less than 270 fragments, comes from the rock shelter of Diepkloof in South Africa, dated to around 60,000 years BP (Texier et al. 2010). These pieces show deeply engraved, well-arranged linear motifs. The incised eggshell fragments have been interpreted as the probable remains of ostrich egg water containers, like the ones used by contemporary San hunter-gatherers to collect and store water (Henshilwood and D'Errico 2011; Texier et al. 2010).

The archaeological assemblages of the European Early Upper Palaeolithic typically include incised objects such as engraved pieces of bone, ivory, and stone which have generally been classified as mobiliary or portable art (White 2003). Some of the earliest examples from the Aurignacian show linear patterns, dot arrangements, crosses, and some schematic motifs (Mellars 1996; Zilhão 2007); for instance, the bone and ivory shafts engraved with parallel and criss-crossed lines from Vogelherd, Germany, and Mladeč, Czech Republic, and the bone fragments engraved with linear motifs from Arcy-sur-Cure in France (Mellars 1996). Later engraved pieces, from the Gravettian, Solutrean, and Magdalenian periods, frequently feature figurative motifs as well, particularly animal figures and some humans. Engraved motifs are also a common component of European rock art. Cave and open-air rock art sites generally include numerous instances of linear, geometric, or representational patterns engraved on rock (Bahn and Vertut 1997).

Carved and Sculpted Objects

The production of carved or sculpted two- and three-dimensional objects involves a greater amount of work and expertise than the art forms that have been discussed so far. It requires a good knowledge of the base material, appropriate—perhaps specialized—tools, and, in the case of figurative motifs, artistic skill and an understanding of artistic conventions to properly depict the desired subject.

Carved figures are still absent from the archaeological record of Late Pleistocene Africa. The Eurasian Upper Palaeolithic, in contrast, includes several impressive examples of such items. The German region of Swabia has yielded what so far is the earliest tradition of figurative art, consisting of over 40 figurines carved in mammoth ivory, found across various Aurignacian sites dated between 40 and 30,000 BP (Conard 2003; Porr 2010).[7] The caves of Hohle Fels, Geissenklösterle, Vogelherd, and Höhlenstein-Stadel, among others, contained dozens of figures depicting Pleistocene fauna (mammoth, horse, bison, lion, bear, water fowl) and a few anthropomorphic and therianthropic (human-animal) representations (Cook 2013).

The oldest of these carved figures so far is a female 'Venus' figurine from the basal Aurignacian layers at Hohle Fels, estimated to be some 40,000 years of age. The small figure is just 6 × 3.5 cm and shows a female body with exaggerated sexual features; it has a loop for a head which shows use wear, indicating that it was suspended and presumably carried or worn as an ornament or charm (Conard 2009). Its body is marked with grooves, and the right arm has some linear marks that could suggest a body art design (Cook 2013). But probably, the most notable of the Swabian carvings is the *Löwenmensch*, or Lion Man, from Höhlenstein-Stadel, which depicts a standing character with human and feline features (Fig. 20.3a). The body is very anthropomorphic, but the head, hands, and feet are clearly catlike. Like the Hohle Fels Venus, the Lion Man's upper left arm bears a linear design that could be depicting body art. The figure, dated ca. 35,000 BP, measures 31.1 cm in height and was carved on a single mammoth tusk. Replication experiments have indicated that it would have taken up to 400 h of meticulous work to create it (Cook 2013). To some scholars, this figure denotes the

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[7] Remains of what seems to be an ivory anthropomorphic figurine have been recovered at the Russian site of Kostenki. The possible human head has been dated to 42–45,000 BP (Anikovich et al. 2007; Cook 2013, p. 56), which would make it the oldest example of figurative representation yet found. However, identification is uncertain due to the worn condition of the piece.

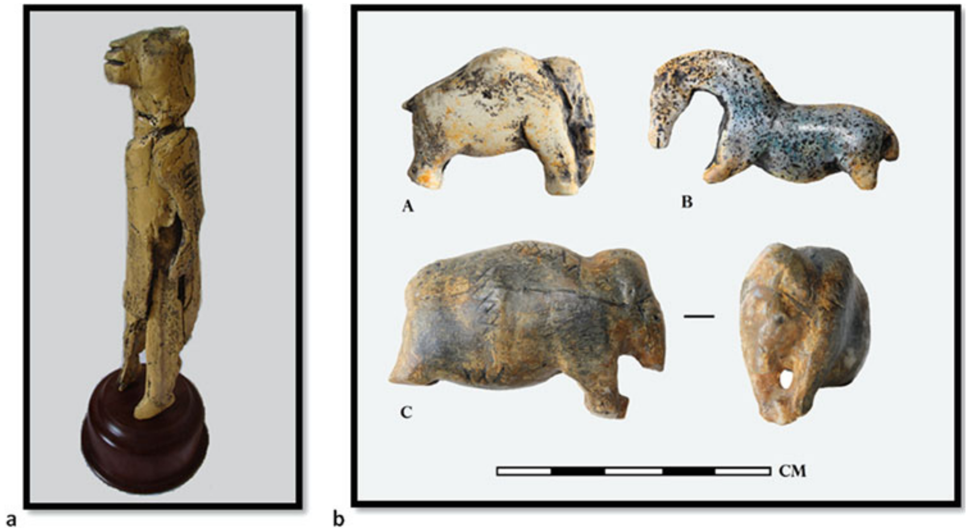

Fig. 20.3 Mammoth ivory figurines from Swabia, Germany (reproductions). (**a**) Lion Man from Höhlenstein-Stadel. (**b**) (A) Hohle Fels mammoth. (B) Hohle Fels horse. (C) Vogelherd mammoth

emergence of truly modern abstract thought, where the fusion of unrelated concepts (animal-human) gives way to a novel idea (Mithen 2007; Wynn et al. 2009). To others, the blending of animal and human properties supports interpretations of shamanic beliefs and practices among Pleistocene hunter-gatherers (Conard 2003; Dowson and Porr 2001; Lewis-Williams 2002). It is remarkable that at the nearby site of Hohle Fels, a second much smaller Lion Man figurine, of just a couple of centimetres in size, was found, indicating that the Aurignacian population of Swabia may be seen as a cultural unity who shared a common system of artistic conventions and most likely of customs and beliefs (Conard 2003; Conard 2003; Porr 2010).

Other remarkable ivory figurines from the Swabian cave sites include small but very detailed representations of a mammoth and a horse from Vogelherd, with an estimated date of 35,000 BP (Cook 2013). All of the carved figures from Swabia show tremendous craftsmanship and dedication, and although each is unique and seems to reflect individual choices and idiosyncrasies, as a whole, they constitute the earliest figurative art tradition in Europe (Porr 2010) (Fig. 20.3b).

After 30,000 BP, figurines and other carved objects become more common in the European Palaeolithic record. Generally grouped under the category of ‘portable’ art, examples include figurative sculptures and decorated tools (e.g. batons, awls, shafts, spear-throwers) carved in ivory, bone, antler, horn, stone, and various minerals (Cook 2013). Perhaps the best-known group of Palaeolithic sculptures are the female statuettes commonly known as ‘Venuses’, which have been found throughout a vast extension of the Eurasian continent. In their majority, these female statuettes pertain to the archaeological period known as Gravettian (28–23,000 BP), although female figures continue to be found up until the end of the Pleistocene (Cook 2013). The stereotypical ‘Venus’ figurine (e.g. Willendorf) is a small female representation, naked or scarcely clothed, with accentuated breasts, hips, thighs, and buttocks and contrastingly minimized upper limbs and facial features (Fig. 20.4). In actuality the term is (mis)used to denote any female figurine from the European Palaeolithic, underestimating their variability and thus giving the wrong impression that they comprise a cohesive group of artefacts similar in appearance and function (White 2003). Some of them, however, show clear regional and temporal variations, which perhaps would allow for more specific interpretations (Gamble 1982).

Fig. 20.4 Venus of Willendorf at the natural history museum in Vienna

Painting

Here I refer specifically to the practice of painting on large surfaces, such as rocks and walls, otherwise known as rock painting or rock art. Rock painting traditions like those from Palaeolithic Europe and Australia are probably the most complex and labour-intensive form of Pleistocene visual art. Wall painting requires not only time and skill but also a large amount of social and natural knowledge (Conkey 1993).

As with the previous category, early Pleistocene examples of wall painting are lacking from the African continent. The earliest known piece of a painted rock surface in Africa is the figurative image of an animal (eland?) on a slab found in the Apollo 11 Cave in Namibia, dated to 27–25,000 years BP (Wendt 1976), although some authors speculate it might be as old as 40,000 years (Masson 2006). It has been suggested that some rock art traditions from Australia (e.g. the Bradshaw paintings at Ubirr and the petroglyphs at Dampier) might also extend as far back as 40,000 years or more (Clarkson et al. 2017; Morell 1995; White 2003). Currently, the earliest dates of rock painting from outside Europe come from the Indonesian Island of Sulawesi, where a hand stencil and an animal figure have been dated to 39.9 and 35.4 thousand years ago, respectively (Aubert et al. 2014). This art is then at least as old as its European counterpart and makes it highly possible that earlier dates will be reported for Australia and the Pacific in the near future.

In Europe, the most renowned of early painted sites is Chauvet Cave, in France, due to its impressively realistic painted panels depicting numerous animals (cave lion, bear, horse, woolly rhino, bison, and mammoth, among others) and because its discovery in 1994 changed the standard view of the development of figurative art in the Palaeolithic. Until then, cave art from the Solutrean and Magdalenian periods, represented by sites like Lascaux and Altamira, had been considered the pinnacle of Palaeolithic painting (Fig. 20.5). But Chauvet yielded Aurignacian dates, going as far back as 32,000 BP, indicating that figurative rock art was not only much older but also quite magnificent from very early on (Clottes and Arnold 2003). By now, it seems that figurative painting may have been a usual practice during the Aurignacian. The site of Fumane Cave in Italy has yielded rock fragments that seem to have detached from the cave ceiling and bear ochre and some simple schematic paintings dated to 35–32,000 BP (Broglio et al. 2006). Another roof collapse with traces of paint depicting a zoomorphic figure and an engraving of a vulva at the site of Abri Castanet, in France, has recently given a date of ca. 36,000 BP (White et al. 2012). Also, a recent dating project covering several well-known painted caves in Spain, including Altamira, El Castillo, and Tito Bustillo, has yielded dates going back to the Aurignacian in all of the sites (40–34,000 BP), suggesting that the caves were

Fig. 20.5 Reproduction of Lascaux panel at the National museum of natural history in Paris

visited throughout the Upper Palaeolithic for artistic motives (Pike et al. 2012). Similarly, the Spanish site of Altxerri B, in the Basque country, includes painted motifs of various animals (feline, bear, horse) and has been dated to 34–30,000 BP (González-Sainz et al. 2013). These results support the suggestion that painting practices have a deep temporality in Europe (Jöris and Street 2008).

As in the case of carved and sculpted objects, instances of rock painting become more common in Europe after 30,000 years. Wall painting practices seem to have peaked towards the Magdalenian period (18,000–10,000 BP), during the coldest phases of the last Glacial era, when most painted caves clustered around the Périgord region in France and the Spanish area of Cantabria. Although at the moment few examples from other regions are known (e.g. Kapova Cave in Russia and Coliboaia Cave in Romania), it is probable that other Palaeolithic painted sites are still to be discovered. The improvement of dating methods and the increasing sample of dated caves also may start clarifying the development of rock painting traditions in the European Pleistocene.

Summary

This brief overview of the development of visual art forms over the Pleistocene allows us to make some very general inferences. First, the earliest traces of possible visual art activities are found in the form of ochre extraction, processing, and use in marking and probably decorating artefacts and the human body. This is followed by the simple modification of materials and later by the crafting of beads, and finally, there is the systematic production of visual art objects and traditions. Nonetheless, this development is not assumed to have happened in strict linear chronological succession. The various visual art forms and techniques frequently appear, disappear, and reappear in the archaeological record, and ‘simple’ forms usually co-occur with more ‘complex’ ones. From an archaeological perspective, the apparent trend in the development of visual art—from simple to more complex forms—has been recurrently attributed to the enhancement of human cognitive capacities over the Pleistocene (e.g. Mithen 1996; Coolidge and Wynn 2009). However, the increasing diversification of visual art forms, media, and techniques may also be interpreted in terms of increasing technological and social sophistication.

We will now see whether the three most cited evolutionary hypotheses on the origins of art can explain the evidence presented above. To reiterate, these are the sexual selection hypothesis, the social bonding hypothesis, and the cognitive enhancement hypothesis.

The Sexual Selection Hypothesis

In his *On the Origin of Species*, not only did Charles Darwin present his famous thesis on natural selection, but he also introduced the principle of sexual selection to explain those armaments and ornaments used in courtship displays (2006) [1859]. He further elaborated on the evolutionary effects of sexual behaviour in *The Descent of Man*, from 1871.[8] In broad lines, he argued that whereas success in natural selection depended on the survival of individuals in relation to the conditions of life, in sexual selection success was measured by the reproductive advantage of certain individuals over others of the same sex and sort in relation to the propagation of the species (Darwin 2004 [1879]; Taylor 1996). That means that while the environment and competition for resources are major factors of natural selection, sexual selection is mainly driven by intraspecies competition over mates and mating opportunities (Andersson 1994). Since females have a higher investment on reproduction and offspring care, they will tend to be the choosier sex, whereas the males will compete among themselves for mating opportunities (Trivers 1972). Hence, the most common mating strategies in the animal world involve male-male competition and female choice (Geary et al. 2004), although these two do not exhaust the mechanisms of sexual selection (Andersson and Iwasa 1996). Mate preference is however of special interest because it seems to correlate with the evolution of 'ornaments' and extravagant traits which are often difficult to explain through natural selection (Kokko et al. 2003).

In the classical example of the peacock, the large, colourful, eye-spotted feathers of its long, heavy tail incur a huge energetic investment that, while attractive to the peahens, makes the male bird less agile and more noticeable to predators. However, if the tail is correlated to the general physical condition of the male, it will be more elaborate among strong, healthy individuals and therefore will be preferred by the peahens as high-quality mates. In this way, the peacock's tail serves as a 'costly signal' or indicator of general genetic quality (see Quinn, this volume; Zahavi 1975). The sexual selection hypothesis for the origins of art suggests that, like the peacock's tail, art behaviour in humans may have evolved through mate choice as a fitness indicator for courtship purposes (Dutton 2009; Miller 2000; Grammer et al. 2003; Taylor 1996; Zahavi and Zahavi 1997).

One of the major proposants of this hypothesis is the evolutionary psychologist Geoffrey Miller (2000), according to whom the mental and physical abilities required for art-making (e.g. creativity, concentration, coordination, dexterity, etc.) correlate with the general condition of the individual and thus serve as a cue of genetic fitness; therefore people, especially women, would have evolved a preference for art. In this view, works of art constitute material extensions of a person's genetic makeup; they are 'extended phenotypes' or out-of-body manifestations of the individual's self, much like a spider's web, a bird's nest, or a beaver's dam (Miller 2000). In consequence, this hypothesis sees early visual art essentially as an individual activity whose resulting products were kept by the maker for all to see and judge. Positive valuations of visual art displays would then bring reproductive as well as social success to the artist (Miller 2001). In short, this hypothesis states that art is a uniquely human behavioural trait that evolved through mate choice to serve a courtship function by signalling the artist's fitness, attracting mates, and outcompeting rivals (Miller 1999, 2000, 2001).

Also, this hypothesis assumes that women are more selective in their mating choices and males are more motivated to produce competitive fitness displays, like visual art; therefore it would predict that an intensification of visual art production in the archaeological record should correlate with periods of increased male-male competition and greater female choosiness, for example, in periods of abundance of resources, when there are more fit males who can afford complex courtship displays and females

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[8] Darwin is often quoted as the first researcher to have drawn a link between sexual selection and the arts, but he actually dedicated few paragraphs to this issue and his opinions concerned mostly the occurrence of song and music, e.g.: 'I conclude that musical notes and rhythm were first acquired by the male or female progenitors of mankind for the sake of charming the opposite sex' (2006, p. 638 [1859], footnote 39).

can afford to exercise mating preferences (Geary et al. 2004, Miller 1999). So, the scenario to test is whether the increased production of visual art correlates archaeologically with periods of high resource availability.

Although the evidence on this issue is not vast, particularly for the earliest sites, we can draw some conclusions based on the available data. Several of the African sites with early presence of visual art (e.g. Blombos Cave, Sibudu, Klasies River) have yielded evidence of the types of resources being exploited. Unfortunately, the information is not detailed enough to get a clear picture of the complete range and frequency of the species extracted. However, some trends can be observed. At Blombos Cave, for example, the phases contemporaneous with the finds of ochre pigment production and shell bead use from 75,000 BP indicate that diet was broad and included both mammals and shellfish. At the time, this coastal site was surrounded by forest, which means that humans could make optimal use of both terrestrial and marine resources (Dusseldorp 2012; Langejans et al. 2012). The period when the earliest evidence of visual art becomes visible was a time of high climatic variation. But, by occupying locations near different sources of food (coast-forest), humans could have maximized their access to supplies. It then seems that the time and location of early visual art production is correlated with potentially high resource availability.[9]

In the European Upper Palaeolithic, personal ornaments would not be a good indicator to quantify variations in visual art production over time, since these are present in large quantities throughout the whole period. Instead, archaeologist Michael Barton et al. (1994) have used carved figures and rock art as a measure of artistic output during the Upper Palaeolithic. They observed that in the climatic downturn episode leading up to the Last Glacial Maximum (27–21,000 BP), when mean temperature deteriorated and glaciers advanced continuously, there was comparatively little figurative art production. In contrast, during the Last Glacial Maximum itself (21–13,000 BP), visual art became abundant, only to wean again at the beginning of the Holocene. Visual art seems to have flourished during the Aurignacian and Gravettian periods (40–28,000 BP), but it would seem that a decrease in art production during the downturn episode could be related to harsh climate change and a decline in available resources. The Last Glacial Maximum, on the other hand, may correlate with the stabilization of the new cold conditions, where despite the low temperatures, there was great availability of faunal resources to be exploited, especially of large grazing herbivores (Gamble 1998; Guthrie and van Kolfschoten 2000).

So, although the data available in relation to resource availability and art production may be sketchy, it seems to support the scenario that an intensification of visual art would correlate with periods of greater resource availability. This would be in accordance with a sexual selection hypothesis which would predict that in prosperous circumstances, females would have more choice of high-fitness partners, becoming choosier and thus prompting male-male competition resulting in an increase of courtship displays, including visual art manifestations.

Despite the seeming correspondence between this scenario and the archaeological record, there are a few caveats. First and foremost, the match could only be corroborated if artworks were made predominantly by men, under the assumption of male fitness display and female mate choice. However, there is no way of saying with any certainty whether the archaeological examples of early art were made only by men. Actually, some evidence would point to the contrary. For example, some of the earliest personal ornaments found in Europe often come from the graves of women and children (Einwögerer et al. 2006; Formicola 2007; Martínez González and Mendoza Straffon 2017), which weakens the hypothesis that personal ornaments were being produced by males for courtship purposes. Furthermore, ethnographically, women play a prominent role in art production in small-scale societies.

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[9] That the early production of visual art in Africa may have been correlated to propitious circumstances that allowed for abundant resource exploitation is further supported by the fact that art declined after 70,000 BP, when it is thought that conditions took a turn for the worse as consequence of the Toba volcanic eruption (Ambrose 1998b; Burroughs 2009).

Second, the correspondence between a rise in visual art production and high resource availability during the Pleistocene could have an alternative explanation. For instance, in periods of scarcity, the decrease of food resources could imply a similar decrease in raw material access for art-making. Third, this hypothesis suggests that visual artworks act as 'extended phenotypes' made to show off personal skill and creativity, in which case, we should expect the earliest examples of visual art to show a great deal of internal variation. But in fact, the increasing corpus of early body ornaments show a low degree of internal variation and a high level of standardization and formal redundancy instead (Kuhn and Stiner 2007a), suggesting that even when the production and use of early Pleistocene beads were personal, their makers were probably following established social conventions regarding the use of specific materials and natural forms, and not their own individual choices, resources, or skills.

The sexual selection hypothesis argues that visual art is a unique human adaptation that evolved to help solve the ancestral problem of finding and keeping a fit partner. In this courtship scenario, visual art is conceived as an indicator of individual quality to guide mate choice. The assessment of this model in view of the archaeological record shows that the Pleistocene data does seem to coincide with some of its predictions, but alternative explanations cannot be discarded. Furthermore, the fundamental premise that art production and display must have been predominantly male is difficult to test archaeologically but is not supported by either ethnography or the Palaeolithic burial record. Finally, the earliest instances of visual art contradict the idea that art was made on the basis of individualistic qualities and motives.

The Social Cohesion Hypothesis

The social cohesion hypothesis suggests that visual art was selected due to its capacity to bring individuals together by reinforcing social bonds (Boyd 2005; Coe 2003; Dissanayake 1992). One of the main proponents of this hypothesis and a pioneer in the field of art and evolution is Ellen Dissanayake. She has suggested that art-making is a universal innate human behaviour, meaning that any normally developed individual of our species will have a natural predisposition towards making art. But to have persisted as it did, she argues, art must have served an important function that throughout human evolution somehow contributed to the survival and reproductive success of the individuals that presented it. To find out what this function may have been, she has looked for the common element to all the arts, concluding that it is a sense of 'specialness' (Dissanayake 1980), which she called 'making special' (Dissanayake 1992, 2000) and more recently 'artification' (Dissanayake 2008, 2009, 2010). This refers to the act of transforming something ordinary (e.g. an activity or object) into something extraordinary by treating or making it in a special manner. To her, this universal tendency towards artification has been moulded by natural selection, constituting a true human adaptation (Dissanayake 1992).

According to Dissanayake the process of artification is achieved through the five operations of formalization, repetition, exaggeration, elaboration, and manipulation of expectation (Dissanayake 2007). For instance, bodily movements when repeated and exaggerated become dance; speech, patterned and embellished, becomes poetry; song emerges from elaborated, amplified vocalizations; and in visual art, regular objects and surfaces are made special by emphasizing their shape, pattern, texture, and colour (Dissanayake 2008). She further argues that the roots of these five basic operations are already present in the communications between carer and baby (Dissanayake 2000, 2010) and are further developed during childhood in play (Dissanayake 2010).[10] Furthermore, carer-baby interaction and play generate the release of the pleasurable prosocial hormone oxytocin, reinforcing social bonds (Dissanayake 2010) and generating an emotional response that is also found in the aesthetic response to the arts (Dissanayake 2000). Thus, in Dissanayake's view, the ontogeny of art is mostly innate and intensely developed in early infancy and childhood; hence it becomes later co-opted in normalized adult artistic behaviour (Dissanayake 2010).

Dissanayake understands the arts as a derived category of human ritualized behaviours that in several aspects overlap with play and ritual but which involve a particular aesthetic dimension. Ethologists like Huxley (1966) had noted that human ritualized activities have a strong self-rewarding component which is also highlighted in artistic behaviour (Morris 1962). For Dissanayake, as the cognitive capacities of hominins increased with encephalization, individuals would have become progressively concerned with vital life-changing and life-threatening situations (e.g. birth, death, puberty, marriages, seasons, hunts, migrations, etc.), causing uncertainty and stress. Ceremonies, she argues, were developed in hominin evolution as a communal strategy to cope with the anxiety and uncertainty generated by those situations, and because artistic behaviours were innately pleasurable, they were eventually co-opted in ritual ceremony (Dissanayake 1992). So, in her view, the arts coevolved with ritual ceremony, acquiring adaptive value and social function by providing psychological relief and promoting social cohesion, which can potentially enhance the survival of individuals and groups (Dissanayake 2000).

The hypothesis that visual art evolved in collective ritual contexts, selected for the adaptive function of reducing stress under uncertainty while promoting intra-group social cohesion, predicts that art will be most prominent in the context of communal rituals and ceremonies. Therefore, a noticeable increase of visual art should correlate with an increase in communal ceremonial activities and signs of emerging group identity. Because Dissanayake argues that groups whose individual members had the tendency to make things special would have had more unifying ritual ceremonies and would have survived better than individuals and groups that did not (Dissanayake 1992), the hypothesis would also expect artistic behaviour to be under strong selective pressure of environmental stress and intensive group-group competition. Let us now see how this prediction stands against the archaeological data.

Unambiguous evidence for ritual and ceremonial activity is difficult to identify in the material record and is often a point of debate in archaeological interpretation (Ross and Davidson 2006). It is clear that not all ceremonies leave a trace, but by analogy some remains are interpreted as evidence of ceremonial behaviour. From ethnographical and historical data, it is known that rituals and ceremonies may take place on a daily basis, and in a domestic environment, for example, the keeping of a home altar, morning prayers, or collective dining. But the types of ceremonies that Dissanayake actually refers to (e.g. public gatherings with lavish displays of visual and other arts) are special-purpose activities that generally require distinctive preparations and a determined time and place setting (Rappaport 1971).

Watts (2002, 2009) has argued that the notable intensification of red ochre exploitation in the record of the African Pleistocene indicates habitual collective ritual. But the presence of ochre as evidence of ritual is ambiguous. An increase in pigment use, even if used for body painting, need not imply that humans were carrying out the kind of communal ceremonies that Watts and Dissanayake seem to have in mind. For instance, body painting could have been an everyday, non-ceremonial (although highly symbolic) custom, as it is today among the Namibian Himba women whose hair and bodies are permanently covered in a mix of butter and red ochre. Also, many African Middle Stone Age ochre finds come from contexts with traces of multiple activities. They have often been found alongside

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[10] For Dissanayake, play is very similar to art in various aspects. Both are 'removed' from reality, carried out in special contexts with special rules, both are pleasurable and encourage novelty and creativity, and both develop innately. In fact, in her earlier work, she suggested that art may have evolved from play (1980).

stone tools and food remains that indicate the sites were likely base camps where people carried out day-to-day subsistence activities rather than special ceremonial ones, for example, at Pinnacle Point (Marean et al. 2007) and Blombos Cave (Henshilwood and D'Errico 2011).[11] Naturally, the fact that the ochre has been found in these locations does not preclude its use in other places; it is still possible that the ochre was processed in these domestic locations and the pigments obtained were applied and/or displayed elsewhere. But in fact, it is not until the Upper Palaeolithic in Europe that we observe better-defined traces of the ceremonial use of space. For instance, the painted caves of France and Spain do not show signs of having been used as permanent habitation, indicating that they were reserved for the special purpose of painting and associated activities, which probably included some ceremonial displays (Conkey 1993).

Regarding identity, the Pleistocene shell bead finds from Middle Stone Age sites like Blombos Cave in South Africa and Pigeons Cave in Morocco have been interpreted as indicators of group cohesion and identity (Wadley 2007). However, these items seem to be too standardized over time and space to signal group differences (Kuhn and Stiner 2007a). Many of the beads from different sites are made of the same marine snail family (*Nassarius*) and show similar perforation and modification patterns. Objects that are meant to tell groups apart from one another should be easily identified as distinct.[12] Like linguistic dialects, which clearly signal specific group affiliations, material social markers should show relative regional and temporal stylistic variability (Wobst 1977). Instead, the formal redundancy and stylistic consistency of these earliest ornaments might relate to individual within-group social identity in the African Middle Stone Age before 75,000 BP (Kuhn and Stiner 2007b). Again, it is in the record of the European Upper Palaeolithic, especially from the late Aurignacian onwards, where we clearly see regional stylistic variations in material culture (like tool types and personal ornaments) that might speak of interaction between distinct groups (Gamble 1998; Vanhaeren and D'Errico 2006). The idea that the earliest signs of visual art might correspond to emerging group identity is thus not well supported by the art record of the African Middle Stone Age up to 75,000 BP but might apply to the evidence of the European Upper Palaeolithic particularly after 30,000 BP.

As previously discussed, the living conditions in Africa around 100–75,000 BP seem to have been relatively favourable for modern humans, with small populations benefiting from diverse productive environments. Under such circumstances, group-group competition is not generally expected to act as an important selective pressure. At the same time, because bands in a rich and stable environment are relatively self-sufficient and scattered, cooperation between groups and across large distances is weak (Ambrose 2010). In the absence of intensive intergroup competition or cooperation, group identity would remain underdeveloped, and markers of group affiliation would be unnecessary (Wobst 1977; Wiessner 1983). Hence, the conditions of precariousness and group-group competition expected by Dissanayake's model are also not met by the African MSA before 75,000 BP. The archaeological predictions deduced from the social cohesion hypothesis are, in conclusion, not entirely consistent with the earliest record of visual art in the African Pleistocene. Nevertheless, some of the circumstances assumed by it seem to apply well to the conditions of the European Upper Palaeolithic. So, this model may potentially explain not the origins of visual art but the emergence of collective art forms, like cave art, and regional art styles of art and ornamentation during the Early Upper Palaeolithic.

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[11] With the exception of a recent find of 100,000-year-old ochre-processing toolkits at Blombos Cave, which have been interpreted as evidence of an ochre-processing workshop (Henshilwood et al. 2011)

[12] Nonetheless, we cannot discard the possibility that it was how these items were displayed by separate groups which made them different (as jewellery, sewn on clothing, as part of a headdress, etc.).

The Cognitive Adaptation Hypothesis

There is no one cognitive hypothesis for the origins of visual art. In fact, any model which proposes that visual art evolved as a direct result or side-effect of a mental capacity, either general intelligence (Mithen 1996), language (Mithen 2005), memory capacity and abstraction (Coolidge and Wynn 2005), or theory of mind (Henshilwood and Dubreuil 2011), may be considered a cognitive hypothesis. However, there is an underlying idea common to most of them, which is that visual art and other so-called complex behaviours (i.e. typical modern human practices such as ritual, trade, and material culture diversity) were the result of a mental change, or cognitive transition, detached from anatomical evolution. In addition, they often argue that visual art became adaptive by allowing people to express, discuss, exchange, and expand concepts and ideas through symbols (Donald 1991; Mithen 1996; Smith 2005; Tooby and Cosmides 2001). These two premises will constitute the focus of this section.

In the early decades of the 1900s, prehistorians had started to systematically record and describe hundreds of examples of ‘portable’ and cave art found all over Europe, known to have originated in a remote Ice Age. In the first instance, these artworks were thought to have been produced ‘for their own sake’ and by an ‘artistic impulse’ that drove Palaeolithic artists to embellish their environment and to depict elements from their surroundings that were important to them, hence the recurrence of primaeval naturalistic themes (Breuil 1974). Inspired by a growing ethnographic record, scholars later began to link prehistoric art to ‘primitive’ ceremonies, rituals, and religious practices like ‘picture magic’ (Bégouen 1929). Hunting and fertility magic then became the standard explanation for the beginning of visual art and remained popular well into the second half of the century (Grand 1967). By the 1950s, a large corpus of Palaeolithic portable art and cave paintings had accumulated, and archaeology had adopted an array of interpretive perspectives that encouraged researchers to start offering explanations in terms of the meanings of artefacts. As a result, Palaeolithic visual art was seen as a coded system whose interpretation could give us a glimpse into the social life and ideology of prehistoric peoples (Levine 1957).

Since the 1960s, under influence of the cognitive revolution in psychology and linguistics (Baars 1986), some influential archaeologists, like the French prehistorian André Leroi-Gourhan (1993) [1964], adopted a view of cognition in which the mind’s function is to create and process symbols that are themselves generated in the brain to represent knowledge or reality (Sperber 1975). In this perspective, symbolic representation is seen as ‘the principal cognitive signature of humans and the main phenomenon whose arrival on the scene has to be accounted for in any scenario of human evolution’ (Donald 1993). This has had a profound effect on the archaeological study of early art. Whereas previous approaches had generally understood art as a noncognitive or affective activity, the cognitive perspective established the processes of art-making and art perception as mental activities originating in the brain and as part and parcel of symbolic thought (Gardner 1987).

Because in the cognitive approach symbolic representation takes pride of place, cognitive hypotheses on the origins of art tend to focus on figurative or representational art which, as reviewed above, only makes it appearance in the European Early Upper Palaeolithic. For this reason, explaining the origins of art has often been part of the greater scheme of explaining the so-called creative explosion, which includes the seemingly abrupt changes observed in the archaeological record of the European Middle to Upper Palaeolithic (Pfeiffer 1982). These include a sudden burst of objects and traits typical to modern humans, such as the production of specialized tools (e.g. harpoons, knives, awls, nets), the use of various raw materials (e.g. bone, wood, antler, ivory), the structured use of space, the exploitation of a wide array of resources for food (e.g. plants, seeds, small animals, aquatic resources), burials with grave goods, exchange, personal ornaments, and visual art.[13] To proponents of cognitive hypotheses, the emergence of these practices is best explained by an enhancement in human

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[13] For a full list of Upper Palaeolithic innovations, see Bar-Yosef (2002, 2007).

neural capacity that allowed the populations of the Upper Palaeolithic to create and exploit culture at a rate never before reached by any other hominin group (Coolidge and Wynn 2009; Klein and Edgar 2002; Mithen 1996).

In brief, the cognitive adaptation hypothesis discussed here suggests that there is a lag between the emergence of anatomical and cognitive modernity (Mithen 2007). That is, whereas the fossil record shows that by 100,000 years BP there already were populations that probably looked much like present-day people, the archaeological evidence for typical modern human behaviours like ritual, symbolic thinking, and art-making does not appear until much later (Klein and Edgar 2002). This is taken to mean that the transition towards 'mental modernity' must have occurred later (Coolidge and Wynn 2009; Donald 1993; Klein and Edgar 2002; Mithen 2007). From this perspective, the earliest examples of visual art, such as the Blombos Cave material, constitute mere 'flashes' of modernity that lack continuity, whereas the emergence of representational art seems sudden and rapidly cumulative (Mithen 2005, 2007).

The relatively abrupt transition towards mental modernity proposed by this hypothesis would be manifested in the archaeological record as greater technological diversity (e.g. more artefact types, use of various new raw materials, and an increase of composite and specialized tools) and cultural complexity (e.g. evidence for religious ritual and art) than in previous periods. Accordingly, the first visual art should appear in tandem with novel tool types and materials and greater artefact variation. Consequently, the scenario to test is whether the earliest evidence of visual art co-occurs with an increase of technological innovation and diversity.

The patchy character of the data available for the African MSA sites with art makes it difficult to assess this scenario. It seems that in most instances, these sites do present a wider variety of artefacts than sites with no art, but this is not always the case. For example, in one of the earliest occurrences of shell beads, Grotte de Pigeons (ca. 82,000 BP), the ornaments were found alongside typical Middle Palaeolithic artefacts (Bouzouggar et al. 2007). However, in sites like Klasies River Mouth and Blombos Cave, different forms of visual art (pigment use, personal ornaments, and engraved objects) coexist with innovative stone tool types (e.g. blades, bladelets, microliths, bone tools), carefully made in fine-grained raw materials (Henshilwood and Dubreuil 2011; Wadley 2001). The latter sites also have provided evidence that their inhabitants had a broader dietary niche and a formal division of space at camps, with separate habitation and work areas, suggesting 'symbolically organized behaviour' (Wadley 2001).

For its part, the archaeological composition of the Aurignacian (45–30,000 BP), which is the earliest phase of the Upper Palaeolithic in Europe and the period when the first figurative art appears, is actually not that different from the previous Mousterian, except for the art (Roebroeks 2008). Both records show the same low typological diversity (Davies 2001) and a similar scope of resource exploitation (Bar-Yosef 2004). The real 'cultural explosion' in fact seems to happen much later, around 30–28,000 BC, at the beginning of the Gravettian. In this phase indeed all of the 'markers' of modernity appear together, but that is some 10–5000 years after the first examples of representational art.

In fact, the archaeological record seems to contradict the very idea of a sudden cognitive transition. The sites from Pleistocene Africa indicate that many of the traits used to identify modern behaviour (e.g. artefact diversity, specialized tool types, the use of organic raw materials, personal ornaments, exchange networks, etc.) show a mosaiclike pattern of incidence and often did not co-occur. So, it is more probable that the transition was not swift but rather a piecemeal gradual development (Henshilwood and Marean 2003; McBrearty and Brooks 2000). So, whereas the co-occurrence of visual art with technological innovation and variability and other 'modern' behaviours may indeed indicate changes in the ways Pleistocene populations lived and interacted, these do not always require a cognitive explanation. At times, such changes can be equally or better explained in terms of social contacts (Gamble 1998; Marwick 2003; Wobst 1977), demography (Kuhn and Stiner 2007b; Powell et al. 2009), or cooperation strategies (Gärdenfors 2004; Mendoza Straffon 2016a), for example.

Finally, as we have seen, the presence or absence of visual art does not prescribe the presence or absence of novel materials or complex technologies during either the African MSA or the Early Upper Palaeolithic, disproving the key prediction of a cognitive hypothesis.

Conclusion

The way scholars deal with early prehistoric art has been profoundly transformed over the past few decades. Once a term reserved exclusively for the enticing images of Europe's Palaeolithic cave paintings, Pleistocene *art* now includes geometric designs before regarded as 'doodles' and items like beads and pendants, previously categorized as trinkets for 'mere' decoration (Moro Abadía and González Morales 2010). More importantly, recent finds have now demonstrated without a doubt that visual art did not emerge in a single sudden event and that its different forms did not appear simultaneously. Rather, it looks like visual art developed over a long time, generating great formal variation—some of which has unquestionably been lost to time.

The three hypotheses that I have discussed in this chapter mainly attend to the question of what art is for and hypothesize answers by looking at some of visual art's effects, each focusing on different aspects of art's current functions. The sexual selection hypothesis 'reverse-engineers' from art's influence in mate choice behaviour; the social cohesion hypothesis builds upon art's emotional power to bond individuals; and the cognitive adaptation hypotheses reflect on the informational symbolic operations involved in art-making. Given that visual art is known to often fulfil sexual, social, or symbolic functions, how are we to asses which hypothesis, if any, can best inform us about the circumstances in which visual art originated? I have aimed to show that one useful strategy is to weigh them against the archaeological record (Henshilwood and Marean 2003).

Once compared to the evidence from archaeology, it becomes clear that some key issues are left unanswered by all three hypotheses, namely, the timing of visual art's appearance and the expansion and diversity of visual art forms. The sexual selection and social cohesion hypotheses actually remain relatively mute on these important issues, perhaps because they are more concerned with assessing whether art, as a whole, has any adaptive value than with its specific path of development. In this sense, we could say that these models are hypotheses of the ancestral functions of art, and not of its origins as such, but function and cause of origin do not always coincide in evolution (Gould and Lewontin 1979). Perhaps, asking what art was selected for is not the right research question to find out about visual art's emergence. Instead, we might ask questions about the specific contexts and conditions that allowed for visual art to be selected and bloom as a social practice.

The cognitive hypothesis for its part predicts that the development of art should mirror the evolution of cognition, from simple to complex. Although at first glance, the archaeological record of visual art may indeed seem to go from the simple processing and use of ochre, to the production of ornaments, to the creation of complex figurative art, in closer detail it becomes evident that this development did not happen in strict linear succession. The various visual art forms and techniques frequently appear, disappear, and reappear across time and geography, and 'simple' forms usually coexist with more 'complex' ones. The trend is not one of complexification but of diversification of forms, media, and techniques which can be better interpreted in terms of increasing technological specialization. That is, the 'progression' of visual art forms may actually represent growing labour investment in visual art, indicating that visual art production became a progressively important practice to which more and more time, effort, knowledge, skill, and people were allocated over time (see Herzog and Goodale, this volume). In other words, over the course of the Pleistocene, visual art forms likely became more frequent, complex, and specialized, by way of cultural scaffolding processes through which existing types and practices occasionally allowed for novel forms (Mendoza Straffon 2016a).

In conclusion, future research on the origins of visual art, from either an evolutionary or archaeological perspective, needs fine-tuning. Researchers should become more specific about what it is that they want to address, be it the emergence of a specific art form or technique (e.g. carving, painting), a content style (e.g. figurative, schematic), or a behavioural pattern (e.g. mate choice, sociality). Also, studies should narrow down on traceable aspects of the development and production of art forms over time, such as conventions, techniques, materials, styles, distribution, etc., and try to relate those to other aspects of the archaeological record. For instance, network analyses (Knappett 2013; Marwick 2003), cultural transmission studies (Walsh et al., Chaps. 2 and 3, this volume), and phylogenetic approaches to material culture and archaeology (Mendoza Straffon 2016b) may offer interesting, fresh perspectives with potential application to the early record of visual art.

Finally, visual art constitutes a highly versatile form of material culture which may indeed be used to attract mates, to bind social groups, to explain and exchange ideas, to evoke emotions, and to obtain and display social prestige, among other things. Despite this, it is often said that art does not seem to serve any purpose in human survival and evolution (Pinker 1997). It is for this very reason that researchers are both puzzled and fascinated by its evolution. However, it may simply be that we got it wrong. It may be that visual art has in fact played an important role throughout human evolution, as a fundamental communication technology that has helped shape our societies and minds (Kuhn and Stiner 2007a; Quinn, this volume; Mendoza Straffon 2016a). Finding out more about that very role may be the way forward.

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