

# Chapter 6

## Cultural Macroevolution



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### 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 as 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 examine 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 (Matthews 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; Gavrillets 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 (Eerkins 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 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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