



# Theoretical plurality, the extended evolutionary synthesis, and archaeology

Anna Marie Prentiss<sup>a,1</sup>

Edited by Dolores R. Piperno, Smithsonian Institution, Washington, DC, and approved November 18, 2020 (received for review April 29, 2020)

**The study of cultural evolution now includes multiple theoretical frameworks. Despite common influence from Darwinian evolutionary theory, there is considerable diversity. Thus, we recognize those most influenced by the tenets of the Modern Synthesis (evolutionary archaeology, cultural transmission theory, and human behavioral ecology) and those most aligned more closely with concepts emerging in the Extended Evolutionary Synthesis (cultural macroevolution and evolutionary cognitive archaeology). There has been substantial debate between adherents of these schools of thought as to their appropriateness and priority for addressing the fundamentals of cultural evolution. I argue that theoretical diversity is necessary to address research questions arising from a complex archaeological record. Concepts associated with the Extended Evolutionary Synthesis may offer unique insights into the cultural evolutionary process.**

archaeology | cultural evolution | Modern Synthesis | Extended Evolutionary Synthesis

The study of cultural evolution has itself evolved and diversified over the past 150 y. In this paper, I examine the diversity in Darwinian-inspired cultural evolutionary models as applied in archaeology in order to make recommendations for how we make critical advances in the twenty-first century. I use the term cultural evolution to imply the processes of change (descent with modification) in the widest panoply of cultural phenomena inclusive of artifact traits, socioeconomic strategies, and social and ideological traditions. Cultural evolution may lead to human adaptations (in Darwinian evolutionary frameworks, this means improved ability to survive and have viable offspring within an environmental context), but it might be neutral to human adaptation or even maladaptive (1–3). This broad definition permits me to explore theoretical approaches to phenomena as diverse as the evolution of technologies, subsistence and the domestication process, sociopolitical structures, and the cognitive scaffolding of culture. None should be off limits to archaeological analysis.

Anthropologists of the mid-20th century were the first to develop a truly Darwinian approach to cultural evolution by reference to tenets of the Modern Synthesis (MS) (1) using an approach now widely

recognized as cultural transmission theory (CTT) (2). Ecologists meanwhile rethought their *modus operandi* during the 1950s and 1960s, combining microeconomics with concepts from the MS to create evolutionary ecology (EE) and its human-focused variant, human behavioral ecology (HBE) (3). Models drawn from EE quickly became influential in anthropology and archaeology as an approach to explaining change in economic, reproductive, and social behavior in time and space (4). Archaeologists developed their own MS-inspired approach to material cultural evolution widely identified as evolutionary archaeology (EA) or selectionism (5). Recognition that sociocultural evolution is a complex and diverse process led to development of macro-EA (6) and calls for embedding of cultural evolution within the emerging Extended Evolutionary Synthesis (EES) (7, 8). Finally, advances in the cognitive sciences and Darwinian thought have recently led to the establishment of evolutionary cognitive archaeology (9), which has yet to find a clear theoretical home (10).

The fundamental problem facing evolutionary research in archaeology today concerns its ability to engage with the complexity of the cultural evolutionary process. Zeder (11) argues that the frameworks of

<sup>a</sup>Department of Anthropology, University of Montana, Missoula, MT 59812

Author contributions: A.M.P. designed research, performed research, and wrote the paper.

The author declares no competing interest.

This article is a PNAS Direct Submission.

Published under the [PNAS license](#).

<sup>1</sup>Email: [anna.prentiss@umontana.edu](mailto:anna.prentiss@umontana.edu).

Published January 5, 2021.

the most prominent MS-aligned approaches (EA and HBE) are incomplete as the former avoids consideration of the human decision making, while the latter affords nearly complete explanatory priority to the same process. Rosenberg (12), Spencer (13), Prentiss and Chatters (14), and Zeder (8) criticize these frameworks for avoidance of complex multiscalar process across diverse time spans. Piperno (15), Smith (16, 17), and Zeder (8, 18) point to inadequate consideration of biocultural process as associated with niche construction, coevolution, ecological inheritance, developmental plasticity, and epigenetics. Laue and Wright (19) along with Kandler and Crema (20) demonstrate that population-associated factors in the evolutionary process are far more complex than originally imagined by simple neo-Darwinian models. Clearly, we are challenged to engage in more advanced approaches to evolutionary analysis in archaeology, and the substantive nature of these critiques indicates that diversifying our study of cultural evolution is not merely a politically progressive call for diversity and plurality as raised by one reviewer.

I argue that evolutionary research in archaeology benefits from a theoretical plurality that includes engagement with the EES. To make this case, I briefly review the history of cultural evolutionary studies, and then, I provide a more detailed review of contemporary theoretical approaches. I divide the latter review into theoretical frameworks influenced by the MS and those most closely aligned with the EES. Following Garofoli (21), I embed evolutionary cognitive archaeology into the latter group. This discussion provides me with the grounds for gauging our ability pursue a diverse array of advanced cultural evolutionary studies with the archaeological record. I close by noting that both evolutionist and humanist scholars working in historicist frameworks will benefit from consideration of EES concepts.

### A Theoretical Timeline

Cultural evolutionary thinking had its beginnings in the ruminations of early to mid-19th-century scholars. Early thinkers on organic evolution typically assumed that cultural evolution was a simple outgrowth of biological change, whether associated with inherent drives toward gaining a better fit to the environment (22), coping with catastrophes (23, 24), or reactions to sudden environmental change (25). Darwin drew influences from a diverse array of scholars spanning Charles Lyell to Thomas Malthus in developing his critical argument that evolution resulted from a process of natural selection acting on blindly inherited variation in populations. Darwin's theory of evolution (26, 27) negated teleological assumptions and has been termed original Darwinism (28).

Darwin's model was not agreeable to all scholars of the time. Chambers (29) had made the case for gradual progression toward an ultimate goal of perfection. Spencer (30) followed Chambers in promoting a teleological framework analogically based upon ontogenic development (31) that connected biological and sociocultural evolution within the same progressivist framework (32). Spencer's conception of a single unilineal path, or as termed by Gould (33), the "ladder of progress," would be influential well into the 20th century. Neoevolutionary thought (34) during the mid-20th century owed more to Spencer (than Darwin) given its emphasis on general evolution through universal cultural stages (35). As an extension of neoevolution, processual archaeology designed explanations for change as the solving of ecological problems leading to the major cultural transitions (36). Childe (37) also pursued cultural evolution, although his work was most

influenced by another progressivist, Karl Marx, who maintained quite a different political agenda from that of Spencer.

Darwinian ideas were not entirely lost upon archaeologists. As noted by Riede (38), Scandinavian archaeologists of the late 19th century were highly influenced by Darwinian thought. Hildebrandt (39, 40) and Montelius (41) recognized alignments between archaeology and paleontology. Each argued for a typological approach to artifacts that was analogical to paleontologist's use of species and directed toward the goal of defining cultural evolutionary lineages (42). The typological approach became the standard in archaeology even while paleontology lost its influence on evolutionary biology during the first decades of the 20th century due to the rise of genetics research and the eventual emergence of the MS (1), whose framework is also known as neo-Darwinism. Under the influence of Boasian relativism (43) and the humanities (38), early 20th-century culture-historical archaeologists dropped their interest in evolutionary thinking. Mid-20th-century culture historians remained wary of engaging in consideration of evolutionary ideas given concerns with both neoevolution and neo-Darwinian evolutionary theory (5, 44, 45).

Campbell (46) made the case for using tenets from the MS to understand the cultural process. Campbell asserted that sociocultural evolution can be understood as a Darwinian process, there is a relationship between sociocultural and genetic evolution, natural selection remains the dominant force in evolution, and natural selection acts on cultural variation. While archaeologists of the 1960s and 1970s continued to pursue research dominated by culture-historical and processualist frameworks, a small number of sociocultural anthropologists, psychologists, and biologists advanced the study of sociocultural evolution-defining processes of cultural transmission (47, 48), gene-culture relationships (49–51), and culture as phenotypic plasticity (52, 53).

EE developed well outside of anthropology as a framework designed to provide microeconomic understandings of animal behavior, reproduction, and community structure (3). However, anthropologists and archaeologists soon co-opted the models of EE to address economic aspects of human foraging behavior, sociality, and reproduction (4, 54). Archaeologists defined their own neo-Darwinian evolutionary model during the late 1970s and 1980s, borrowing directly from the MS with a particular focus on artifacts (5, 35, 55). Macro-EA drew heavily on the revised Darwinian theory developed in paleobiology (56–58) to favor an evolutionary approach that could be inclusive of material culture but also more ephemeral concepts such as resource management strategies (14) and political systems (12, 13). Macroevolutionary thought and developments in the evolution of human cognition (9, 10) have since become essential components to the developing EES, particularly as manifested in discussions of niche construction theory (NCT) and major biocultural transitions (59, 60).

### Evolutionary Approaches in Archaeology Aligned with the MS

EA, CTT, and HBE owe their theoretical allegiance most closely to the MS. Their innovative uses of evolutionary theory and creative methodological frameworks have played significant roles in our understanding of the cultural evolutionary process.

Dunnell (35, 55) initiated EA with a focus on defining a theoretical model for archaeology as a natural science of human evolution drawing from the most fundamental tenets of the MS. Dunnell's vision of the archaeological research process, often termed selectionism, requires several components. First, Dunnell

views the archaeological record as an extension of the human phenotype along the lines of Dawkins (61). The archaeological record is thus a continuous population of variants described by Dunnell (55) as the “hard parts” of the human behavioral phenotype and by Leonard and Jones (62) as the material expression of behavioral variation. Second, the approach to change maintains an exclusive emphasis on descent with modification requiring quantitative documentation of differential persistence of cultural variation (35, 63). Third, explanation requires an understanding of sorting mechanisms, specifically the effects of selection and drift. An important caveat here is the assumption that details of the transmission mechanism (cultural vs. biological) are unimportant as long as there is variation on which selection and drift can work (5, 64). Traits likely to be impacted by selection are defined by engineering studies focused on function (55, 62, 65, 66). Drift is associated with stylistic traits lacking potential to affect reproductive fitness (67–69).

EA forced us to confront the problem of studying the cultural evolutionary process using the archaeological record. It attempted to solve the problem by simply placing descent with modification in artifacts as simply another form of general evolution as framed within the caveats of the MS. However, this is not without its problems, and thus, three substantive critiques affect the viability of this original formulation as a natural science of human evolution. First, while evolutionary archaeologists have periodically defended themselves against charges of reductionism (5, 64), the critique remains important. Spencer (13) notes that the MS (and thus, selectionism) is an incomplete model of evolutionary process given its inability to grasp the complexities of inheritance and selection on sociocultural systems structured on multiple scales. Spencer’s critique is in line with a long-standing critique of reductionism in evolutionary biology (31, 56–58). Second, selectionist archaeology is subject to the sociobiological critique. In his early writing, Dunnell (35) sought to distance EA from sociobiology but only in its most extreme form, that of genetic determination. By downplaying cultural transmission as a parallel evolutionary process (5, 64, 70), evolutionary archaeologists must assume that while cultural transmission is responsible for short-term variation, long-term descent with modification is selection driven and thus, by definition, tied to genetic fitness. This is, in effect, the “genes plus culture” hypothesis of sociobiology argued to be an unlikely model of cultural evolution by Boyd and Richerson (2). Third, Zeder’s (11) criticism that EA ignores the human decision maker and associated cultural transmission process remains a serious concern. Multiple theoretical and empirical works in CTT demonstrate that the strict natural selection is not an exclusive requirement for directional trends in cultural variants (2, 71).

The fundamentals of CTT developed in the decade before the appearance of Dunnell’s early papers in EA (46, 49, 72). This early work established cultural evolution as a process of cultural inheritance paralleling that of biological evolution. Natural selection was recognized to have a role in the cultural process but was not necessarily the primary causal factor for descent with modification. Subsequent refinements have led to an integrated set of processes collectively labeled gene culture coevolution (49, 50, 73), CTT (47), dual-inheritance theory (2), or more generically, cultural microevolution (74, 75). They include specifications for transmission pathways, sources of variation in the transmission process, culturally based selection factors (bias mechanisms), cultural drift, natural selection, and migration process (74). While fundamentally based in the MS, CTT departs from EA in

emphasizing culturally specific evolutionary process: in particular, the Lamarckian nature of cultural inheritance and its overwhelming impact on descent with modification. An important consequence is that cultural transmission theorists develop explicit models in order to explore the differential effects of so-called cultural selection vs. natural selection. Group selection (76) emerges as essential to the evolutionary process (77).

The influence of CTT is particularly obvious in archaeology (78), although it has also had impacts in sociocultural anthropology (71, 79). Empirical studies are far too diverse to catalog here, although there are some clear trends. Early empirical work favored direct testing of predictions of specific transmission models for the evolution of technologies (80). The adoption of cladistics and related approaches in material culture studies has revolutionized our understanding of how technologies evolve in varied conditions. Most specifically, the longstanding position that culture is too blended to evolve in a branching pattern has been laid to rest (81). Studies demonstrate that technologies evolve via cultural transmission processes in diverse ways dependent upon the nature of the technology, learning strategies, gender relations, marriage practices, intergroup interactions, and ecological context. Thus, we recognize remarkably different inheritance systems within and between different social contexts (71). Population dynamics also appear to play a critical role in the processes of cultural transmission (20).

CTT largely avoids the sociobiological critique given recognition that cultural inheritance is a substantially independent process to biological inheritance. The reductionist critique is also avoided for the most part, as cultural transmission is recognized to operate between group (population) and individual levels (2). CTT avoids the Zeder (11) critique regarding the active role of decision makers in the cultural evolutionary process. Given its strengths, it is perhaps not surprising that CTT eventually has become influential among evolutionary archaeologists (78). Richerson and Boyd (82) note that CTT could be subject to the adaptationist critique (83). The microevolutionary models of CTT do depend upon the assumption that many cultural traditions are adaptive, although certainly not all as exemplified by maladaptive runaway processes (2). Phylogenetics research has demonstrated that cultural transmission does play a significant role in the formation of adaptive cultural lineages (71, 84). Yet, recent fitness landscape modeling suggests that mildly deleterious traits may persist for long time spans in low-density human populations and with potential to evolve further in social conditions favoring high information dimensionality (19). This raises the possibility of macroevolutionary phenomena not well captured by CTT alone.

An alternate approach to cultural evolution reduces the roles of both cultural transmission and natural selection to background in order to focus on adaptive behavior. EE recognizes that the evolutionary process as described by the MS has led to organisms adapted to thrive in their respective environments. We can gain an understanding of those adaptations by modeling economically optimal choices and testing those models with field research (4). The challenge comes with using models of synchronic behavior to explain diachronic patterns. This is accomplished by assuming that change is a by-product of countless adaptive decisions and subsequent actions (85). Put differently, what anthropologists call culture change is in effect the unfolding of phenotypic plasticity (4, 86).

Research in EE has led to the development of a number of different frameworks designed to provide insight into topics relevant to the human group including foraging, social relations

(especially altruism and cooperation), reproduction, and demography (87). HBE (the wing of EE focused on *Homo sapiens*) has made significant inroads into several major discussions in cultural evolution emphasizing subsistence intensification (88), origins of agriculture (89), and social inequality (90). A commonality in these arguments is the assumption that fundamentals of population and resource relationships affect human decisions. Intensification is most typically framed in light of the diet breadth model as a process by which populations increase returns per unit of land at the cost of working harder (91, 92). A by-product of sustained intensification may be enhanced focus on plant resources that could lead toward manipulation of those plants and the onset of domestication and cultivation (93). Intensification may also be associated with social change as population resource imbalances could change a group's social calculus favoring greater control of territory, protection of resources, and establishment of rules associated with wealth and status differentiation (69, 94, 95). Despite these contributions, evolutionary ecologists have had to address a withering array of criticisms.

Cultural transmission theorists have recognized alignments with evolutionary ecological theory as both recognize that human decisions may have economic and reproductive consequences (96). However, as with selectionism, EE has faced accusations of sociobiology and adaptationism. Kelly (97) notes that evolutionary ecologists settled on a "weak sociobiological thesis" recognizing that while behavior can affect genetic fitness, it is not determined by genetics. Adaptationism, as expressed in the optimality assumptions inherent in the models of EE, is generally defended as the default prior to empirical testing (85). In theory, such hypotheses could be rejected in favor of less well-adapted solutions, although typically, weak model performance leads to a rethinking of fundamental assumptions and development of alternative adaptive scenarios. Marwick (98) offers a solution to the problem of optimality by suggesting that there may be multiple optima given shifting conditions. Critiques that are even more penetrating have focused on neo-Darwinian assumptions and the impact of NCT. Selectionists argue that EE underplays the role of natural selection operating on undirected variation over long time spans (99). Responses (100) assert that phenotypic plasticity may allow populations of organisms to bypass the effects of selection and at least partially moot the issue of undirected variation. Smith (16, 17) points out that the theoretical foundations of EE are not in neo-Darwinism but rather, in microeconomics and that optimization assumptions built into formal models are often unsupported and perhaps even untestable with archaeological data. He proposes NCT as a more theoretically based and empirically supported approach to subsistence change. Alternatively, supporters of EE see formal microeconomic models as useful for gaining insight into daily decisions (101): for example, regarding patch management (102).

### Theoretical Frameworks Aligned with the EES

The EES offers a number of advantages to cultural evolutionists. First, from the standpoint of EES-inspired thinking, evolutionary targets are diverse, and thus change spans multiple levels from genes to larger entities (8). In cultural frameworks, this means basic artifact traits to organizing principles associated with complexly integrated systems functioning on population scales (6). Second, evolution is often characterized by punctuated equilibria (8, 73). Third, the evolutionary process is reciprocal, whereby organisms shape and are shaped by their developmental environments (15). This process of niche construction implicates the

importance of acquired characteristics and inherited socio-ecological systems (59). Fourth, the directionality of evolution is affected by inherent phenotypic bias (73). For culture, this means technological and organizational change may occur through developmental constraints and phenotypic plasticity (8, 15, 103). Finally, while still requiring further research, relationships between the evolution of cognition and cultural variation benefit from EES alignments (21). Cultural evolution is thus a complex aspect of general evolution affected by genetic, cultural, and ecological inheritance with associated feedback loops and human biocultural plasticity.

Multiscalar evolution and punctuated equilibria have been central concerns to macroevolutionary research in paleobiology (104, 105). Given a focus on material evidence expressed on diverse scales over lengthy periods, it is logical that archaeologists would develop a concern with cultural macroevolution. Selectionists have long recognized the nature of archaeology as a macroevolutionary pursuit (5, 35). Selectionists recognized ethnographic variation in human organization but eschewed (as essentialist) inferential identification of organizational forms in the archaeological record (5). Consequently, they favored an analytical focus on defining paradigmatic classes as a tactic for measuring artifact variation, which when plotted against time, would allow them to identify predominant evolutionary forces acting on their associated human groups. This MS-aligned approach thus precluded evolutionary study of human organization outside of artifact design and led to counterarguments favoring a taxic cultural macroevolution (in contrast to the organismic form favored by EA) (12–14, 106). The challenge faced by the latter scholars was identifying evolutionary units that could be transmitted by microevolution but manifested on higher population scales as organizational entities. This problem was solved by reference to the hierarchy of cultural units by Boyd et al. (107) that identified progressively integrated sets of information often identified as ephemeral entities, packages, cores, and species (71, 84). While a conception of cultural species has been consistently rejected, packages and cores have proven useful concepts for identifying and measuring variability in the integrated logic of human organization (71).

There have been significant empirical contributions to cultural macroevolution. Some of these have examined the evolution of artifacts including Acheulean hand axes (108), Middle Stone Age core technologies (109), and Paleoindian projectile points (110). Others have explored the evolution of more complex cultural entities including Paleo-Inuit lithic technological strategies (111), Neolithic subsistence economies (112), sociopolitical organizations (113, 114), and other cultural configurations (115–119). There has also been significant research concerning macroevolutionary processes associated with cultural diversity (120–123).

The combination of modeling and empirical research can lead to insights into multiscalar relationships that are virtually impossible to study on purely microevolutionary scales. An emerging theoretical insight is that cultural macroevolutionary processes may be quite different from those of microevolution as has been recognized in paleobiology (104). Drawing from work on advanced fitness landscapes by Gavrillets (124), Laue and Wright (19) argue, for example, that when giant networks of equivalent fitness emerge, entities may traverse entire fitness spaces, thus making classic peak shifting [expected in microevolutionary models (125)] largely obsolete in some scenarios. This line of thought is potentially revolutionary when we consider its implications for complex phenomena such as the origins of agriculture. Advanced

fitness landscape models suggest that even during what appears to be stasis, evolutionary process is still productive in the sense of accumulating variation that might be fuel for rapid change later as would be expected by the punctuated equilibria model.

The process of domestication has emerged as a critical issue in the debate over the acceptance of EES concepts in the biocultural evolutionary process (8, 15). NCT (126) has become central to an EES understanding of the domestication process (8, 15–17, 127–130). Zeder (130) outlines three critical theoretical constructs underlying the niche construction process. First, niche construction requires coevolution as the niche must be made up of at least two species, the niche constructor and one other. Coevolution is manifested in three pathways to domestication: ecosystem engineering, plant or animal colonization or invasion of anthropogenic habitats, and direct human breeding. The domestication process is thereby impacted by the degree to which these relationships are sustained, the potential for domestication in the species involved, and genetic variation in those populations including the potential effects of phenotypic plasticity and epigenetics (15). Second, ecological inheritance is essential as changes initiated by a niche constructor survive past the life of that individual or population, thus creating the selective context acting on the next generation. Ecological inheritance is facilitated by persistence of external (landscapes) and internal (epigenetic and genetic) systems, cultural traditions as embodied by the concept of traditional ecological knowledge, and cognitive changes (59). Third, cooperation is essential for human niche constructors in order to provide payoffs for active participants while blocking or punishing freeloaders. Cooperation is manifested in the creation of social boundaries, defended territories, and via establishment and reinforcement of cultural norms (131).

Central to the EES is the argument that phenotypic bias will constrain the direction of the evolutionary process (73). Evolution of development, or “evo-devo,” has existed in evolutionary biology since the 1980s (132). Evo-devo research demonstrates that phenotypic variation in populations depend upon both genetic variation and developmental systems (133). As noted by Laland et al. (73), gene regulatory systems affect amount, type, timing, and locations of gene products. Genetic regulation has the effect of providing developmental constraints and also opportunities for novel adaptive evolution by connecting or disconnecting diverse phenotypic units. Thus, convergent evolution may be a product of common selective regimes, but it may also be an effect of channeled morphological constraints. Yet, new evolutionary lineages could potentially emerge from changes in gene regulation. Adaptive evolution may be enhanced by the potential of a phenotype to adapt to multiple environments through plastic expression of physiological, morphological, and/or behavioral traits (8). In theory, variation linked to phenotypic plasticity or accommodation could be stabilized and refined by selection leading to genetic accommodation (73).

These ideas have implications for how we understand the cultural evolutionary process. The evolution of lithic tool traditions provides a good beginning example. As argued by Charbonneau (103), variation in stone tools is a consequence of application of techniques to create products reflecting knapper goals and error variability. Given functional constraints on form, change may be a slow and gradual process with high potential for convergent evolution (134). Yet, given our propensity for behavioral plasticity, there is also the capacity to adjust forms to fit altered needs without changing the basic instructions for manufacture. Thus, knappers may alter forms, sizes, and use sequences to fit

immediate contingencies as, for example, might be required under different transport situations and resource configurations (135, 136). Logically, selection (or selection-like cultural processes) could refine varied forms developed in this behavioral plasticity scenario into lineage-like histories.

The models considered thus far have focused only limited interest on cognitive evolution, and this would seem to be a significant oversight. MS-inspired models assume an implicit cognitive model termed the internalist view that asserts a parallel evolutionary process between biology and culture that leads to an expanding ability to provide meaning to material items, thus resulting in “modern” cognitive abilities or architecture (21, 137). Critiques of the MS framework include, not surprisingly, concerns with humans as mere replicators of codes (whether cultural or biological) who, lacking agency, encounter artifacts as mere epiphenomena of the mind (21, 138). Expanded to a wider field, cultural constructs are thus no more than accommodations for adaptive needs. The embodied and extended view thus argues that cognitive evolution is not limited to the brain but occurs as an extended process uniting the mind with the surrounding socio-material environment scaffolded by core emotions and material relationships (10, 21, 139). Taking this logic a step further, the radical enactive cognition (REC) model eliminates representation from cognition in favor of a direct alignment between mind and object (21). This phenomenological framework moves evolutionary cognition theory far from MS frameworks and potentially beyond evolutionary thinking. However, Garofoli (21) [see also Fuentes (140), Riede (59), and Riede et al. (141)] ties REC to a version of the EES in which artifacts play a greater role in structuring social relations, views of reality, and consequently, cognitive function. This model combines culture, cognition, and environment such that cognition coevolves with its cultural and ecological niche. Abramiuk (10) argues that this framework provides for a perpetual feedback loop leading to further cognitive and cultural developments. He is, therefore, concerned that is not clear how historical processes (e.g., natural selection) contribute. The REC model makes better sense when embedded within an NCT standpoint that recognizes the importance of historical process (142). This in turn may permit a perspective on cognitive evolution that also considers a wider role for spandrels and exaptations (143, 144).

## Concluding Thoughts

I have made the case for theoretical plurality in an archaeology that is capable of engaging with the advanced concepts implied by the EES. In so doing, I have referenced a wide range of case studies employing different theoretical approaches to cultural evolution and human adaptation. Yet, I want to return to a concern raised by one peer reviewer, who asked whether most archaeologists would have a reasonable ability to identify complex processes described by advanced evolutionary models. I address this question in two ways. First, can we study complex evolutionary questions with typical archaeological data? I think the answer is yes, although we must find realistic matches between the nature of the record, our research problems, and analytical procedures. Second, can evolutionary thinking contribute to wider discussions involving other disciplinary frameworks? I answer this also in the affirmative, recognizing that when we cross theoretical boundaries, we may be forced to rethink long-held assumptions.

Evolutionary analysis considered most broadly provides us with a wide range of frameworks and methodological approaches that permit us to answer a diverse range of questions about

human cultural diversity and history (87). I have explored relationships between demography, subsistence, and social change in village-scale settlements using theoretical models drawn from HBE including foraging theory, demographic ecology, and socioecology (145). CTT is very useful in helping us to understand intergenerational change in cultural practices as with the evolution of house architecture and tool-making traditions within and between communities (84, 146). EES-aligned frameworks (e.g., punctuated equilibria, evo-devo, exaptation, niche construction, and ecological inheritance) are critical for the study of cultural change across long timescales where data might span lithic scatters to urban centers (111, 118, 119, 147). EES concepts such as developmental plasticity and reciprocal evolution are also essential in the study of the domestication process (8, 15), as for example, with our current study of canids in the interior Pacific Northwest.

Clearly, advanced evolutionary analysis is possible with routine archaeological data. Yet, theory in archaeology remains somewhat Balkanized (148) with a strong contingent favoring historicist approaches emphasizing human agency. Agency theory in archaeology as embodied in what is often termed historical processualist theory (HPT) (149–153) seeks to reconstruct human history as genealogies of cultural practice. A major implication of this framework is that change is continuous and gradual, unfolding across different independent scales, constrained by previous history and social context, and lacking convergence with other histories (114). This scenario is similar to elements in the MS including transmission/inheritance between individuals leading to population variation, effects of phenotypic constraints, and long-

term outcomes resembling organismic macroevolution. Natural selection is essential in the MS but not always critical for envisioning the formation of cultural lineages whether associated with HPT (151) or CTT (2).

Frameworks aligned with the EES offer potentially revolutionary conceptions of cultural variation and history that should be of utility to historicists and evolutionists in archaeology. First, the EES anticipates diverse means by which variation develops in cultural traditions by expecting evolutionary potential to derive from the fundamentals of cultural transmission and also plasticity and evo-devo (154). Second, the EES provides theoretical constructs to address unique (to some, unintended) outcomes via cultural exaptation and sociocultural epistasis (143). Third, the EES provides equally powerful frameworks for envisioning directional and sometimes convergent historical trajectories by multiscale trends (115), niche construction and ecological inheritance (127), and differential cooperation (8). Fourth, the EES encourages us to engage in simulation modeling in order to imagine long-term dynamics not easily envisioned on ethnographic timescales (19). Engagement with such productive theory should favor innovative collaborations across the discipline

**Data Availability.** There are no data underlying this work.

### Acknowledgments

I thank PNAS Associate Editor Dolores R. Piperno for inviting me to write this paper. I thank Cheyenne Laue, Matthew Walsh, Felix Riede, and two anonymous peer reviewers for their very helpful comments on the manuscript.

- 1 J. S. Huxley, *Evolution, the Modern Synthesis* (Allen and Unwin, London, United Kingdom, 1942).
- 2 R. Boyd, P. J. Richerson, *Culture and the Evolutionary Process* (University of Chicago Press, Chicago, IL, 1985).
- 3 B. Winterhalder, E. A. Smith, "Evolutionary ecology and the social sciences" in *Evolutionary Ecology and Human Behavior*, B. Winterhalder, E. A. Smith, Eds. (Aldine de Gruyter, New York, NY, 1992), pp. 1–24.
- 4 E. A. Smith, B. Winterhalder, *Evolutionary Ecology and Human Behavior* (Aldine de Gruyter, New York, NY, 1992).
- 5 M. J. O'Brien, R. L. Lyman, *Applying Evolutionary Archaeology: A Systematic Approach* (Kluwer Academic, New York, NY, 2000).
- 6 A. M. Prentiss, I. Kuijt, J. C. Chatters, *Macroevolution in Human Prehistory: Evolutionary Theory and Processual Archaeology* (Springer, New York, NY, 2009).
- 7 A. M. Prentiss, C. L. Laue, "Cultural macroevolution" in *Handbook of Evolutionary Research in Archaeology*, A. M. Prentiss, Ed. (Springer, New York, NY, 2019), pp. 111–126.
- 8 M. A. Zeder, Domestication as a model system for the extended evolutionary synthesis. *Interface Focus* **7**, 20160133 (2017).
- 9 M. A. Abramiuk, *The Foundations of Cognitive Archaeology* (The MIT Press, Cambridge, MA, 2010).
- 10 M. A. Abramiuk, "A brief overview of evolutionary cognitive archaeology" in *Handbook of Evolutionary Research in Archaeology*, A. M. Prentiss, Ed. (Springer, New York, NY, 2019), pp. 361–378.
- 11 M. A. Zeder, "Evolutionary biology and the emergence of agriculture: The value of co-opted models of evolution in the study of culture change" in *Macroevolution in Human Prehistory: Evolutionary Theory and Processual Archaeology*, A. M. Prentiss, I. Kuijt, J. C. Chatters, Eds. (Springer, New York, NY, 2009), pp. 157–212.
- 12 M. Rosenberg, Pattern, process, and hierarchy in the evolution of culture. *J. Anthropol. Archaeol.* **13**, 307–340 (1994).
- 13 C. S. Spencer, Evolutionary approaches in archaeology. *J. Archaeol. Res.* **5**, 209–264 (1997).
- 14 W. C. Prentiss, J. C. Chatters, Cultural diversification and decimation in the prehistoric record. *Curr. Anthropol.* **44**, 33–58 (2003).
- 15 D. R. Piperno, Assessing elements of an extended evolutionary synthesis for plant domestication and agricultural origin research. *Proc. Natl. Acad. Sci. U.S.A.* **114**, 6429–6437 (2017).
- 16 B. D. Smith, A comparison of niche construction theory and diet breadth models as explanatory frameworks for the initial domestication of plants and animals. *J. Archaeol. Res.* **23**, 215–262 (2015).
- 17 B. Smith, Neo-Darwinism, niche construction theory, and the initial domestication of plants and animals. *Evol. Ecol.* **30**, 307–324 (2015).
- 18 M. A. Zeder, Domestication as a model system for niche construction theory. *Evol. Ecol.* **30**, 325–348 (2016).
- 19 C. L. Laue, A. H. Wright, "Landscape revolutions for cultural evolution: Integrating advanced fitness landscapes into the study of cultural change" in *Handbook of Evolutionary Research in Archaeology*, A. M. Prentiss, Ed. (Springer, New York, NY, 2019), pp. 127–148.
- 20 A. Kandler, E. R. Crema, "Analyzing cultural frequency data: Neutral theory and beyond" in *Handbook of Evolutionary Research in Archaeology*, A. M. Prentiss, Ed. (Springer, New York, NY, 2019), pp. 83–108.
- 21 D. Garofoli, "Embodied cognition and the archaeology of mind: A radical reassessment" in *Handbook of Evolutionary Research in Archaeology*, A. M. Prentiss, Ed. (Springer, New York, NY, 2019), pp. 379–406.
- 22 J.-B. Lamarck, *Philosophie Zoologique, ou Exposition des Considérations relatives à l'histoire naturelle des Animaux* (MacMillan, London, United Kingdom, 1809).
- 23 L. Agassiz, "Essay on classification" in *Contributions to the Natural History of the United States* (Little, Brown, and Co., Boston, MA, 1857), vol. 1, pp. 3–136.
- 24 G. Cuvier, *Essay on the History of the Earth* (William Blackwood, Edinburgh, Scotland, 1813).
- 25 I. S. H. Geoffroy, *Principes de Philosophie Zoologique discutés en Mars* (Pichan, Paris, France, 1830).

- 26 C. Darwin, *On the Origin of Species by Means of Natural Selection or the Preservation of Favored Races in the Struggle for Life* (Murray, London, United Kingdom, 1859).
- 27 A. R. Wallace, *Contributions to the Theory of Natural Selection* (MacMillan, London, United Kingdom, 1870).
- 28 D. R. Brooks, The extended synthesis: Something old, something new. *Evolution* (N. Y.) **4**, 3–7 (2011).
- 29 R. Chambers, *Vestiges of the Natural History of Creation* (John Churchill, London, United Kingdom, 1844).
- 30 H. Spencer, Progress: Its law and cause. *Westminster Rev.* **67**, 244–267 (1857).
- 31 E. Mayr, *The Growth of Biological Thought* (Belknap Press, Cambridge, MA, 1982).
- 32 M. Candea, "Severed roots: Evolutionism, diffusionism and (structural-) functionalism" in *Schools and Styles of Anthropological Theory*, M. Candea, Ed. (Routledge, London, United Kingdom, 2018), pp. 18–59.
- 33 S. J. Gould, *Wonderful Life: The Burgess Shale and the Nature of History* (W. W. Norton and Company, New York, NY, 1989).
- 34 L. A. White, *The Science of Culture: A Study of Man and Civilization* (Grove Press, New York, NY, 1949).
- 35 R. C. Dunnell, "Evolutionary theory and archaeology" in *Advances in Archaeological Method and Theory*, M. B. Schiffer, Ed. (Academic Press, New York, NY, 1980), pp. 35–99.
- 36 L. R. Binford, "Post-Pleistocene adaptations" in *New Perspectives in Archaeology*, S. R. Binford, L. R. Binford, Eds. (Aldine de Gruyter, New York, NY, 1968), pp. 313–341.
- 37 V. G. Childe, *Man Makes Himself* (Watts, London, United Kingdom, 1936).
- 38 F. Riede, Why isn't archaeology (more) Darwinian? A historical perspective. *J. Evol. Psychol.* **8**, 183–204 (2010).
- 39 H. Hildebrandt, *Den vetenskapliga fornsforskningen, hennes uppgift, behof och rätt* (L. Norman, Stockholm, Sweden, 1873).
- 40 H. Hildebrandt, *De förhistoriska folken i Europa. En handbok i jämförande fornunskap* (Jos. Seligmann & Co. Förlag, Stockholm, Sweden, 1880).
- 41 G. O. A. Montelius, Den förhistoriska fornsforskarens metod och material. *Antikvarisk Tidskrift för Sverige* **3**, 1–28 (1884).
- 42 R. L. Lyman, M. J. O'Brien, "Seriation and cladistics: The difference between anagenetic and cladogenetic evolution" in *Mapping Our Ancestors: Phylogenetic Approaches in Anthropology and Prehistory*, C. P. Lipo, M. J. O'Brien, M. Collard, S. Shennan, Eds. (Aldine Transaction, New Brunswick, NJ, 2006), pp. 65–88.
- 43 D. Cole, *Franz Boas: The Early Years, 1858-1906* (Douglas and McIntyre, Vancouver, Canada, 1999).
- 44 W. G. Haag, "The status of evolutionary theory in American archeology" in *Evolution and Anthropology: A Centennial Appraisal*, B. J. Meggars, Ed. (The Anthropological Society of Washington DC, Washington, DC, 1959), pp. 90–105.
- 45 G. R. Willey, Review of evolution and culture. *Am. Antiq.* **26**, 441–443 (1961).
- 46 D. T. Campbell, "Variation and selective retention in socio-cultural evolution" in *Social Change in Developing Areas*, H. R. Barrington, G. I. Blanksten, R. W. Mack, Eds. (Schenkman, Cambridge, MA, 1965), pp. 19–49.
- 47 L. Cavalli-Sforza, M. W. Feldman, Models for cultural inheritance. I. Group mean and within group variation. *Theor. Popul. Biol.* **4**, 42–55 (1973).
- 48 L. L. Cavalli-Sforza, M. W. Feldman, *Cultural Transmission and Evolution: A Quantitative Approach* (Princeton University Press, Princeton, NJ, 1981).
- 49 W. H. Durham, The adaptive significance of cultural behavior. *Hum. Ecol.* **4**, 89–121 (1976).
- 50 W. H. Durham, *Coevolution: Genes, Culture, and Human Diversity* (Stanford University Press, Stanford, CA, 1991).
- 51 C. J. Lumsden, E. O. Wilson, *Genes, Mind, and Culture: The Coevolutionary Process* (Harvard University Press, Cambridge, MA, 1981).
- 52 R. D. Alexander, "Evolution and culture" in *Evolutionary Biology and Human Social Behavior: An Anthropological Perspective*, N. A. Chagnon, W. Irons, Eds. (Duxbury, North Scituate, MA, 1979), pp. 39–59.
- 53 W. Irons, "Natural selection, adaptation, and human social behavior" in *Evolutionary Biology and Human Social Behavior: An Anthropological Perspective*, N. A. Chagnon, W. Irons, Eds. (Duxbury, North Scituate, MA, 1979), pp. 4–39.
- 54 B. Winterhalder, E. A. Smith, Eds., *Hunter-Gatherer Foraging Strategies: Ethnographic and Archaeological Analyses* (University of Chicago Press, Chicago, IL, 1981).
- 55 R. C. Dunnell, "Aspects of the application of evolutionary theory in archaeology" in *Archaeological Thought in America*, C. C. Lamberg-Karlovsky, Ed. (Cambridge University Press, Cambridge, United Kingdom, 1989), pp. 35–49.
- 56 N. Eldredge, *Unfinished Synthesis: Biological Hierarchies and Modern Evolutionary Thought* (Oxford University Press, New York, NY, 1985).
- 57 N. Eldredge, *Macroevolutionary Dynamics: Species, Niches, and Adaptive Peaks* (McGraw Hill, New York, NY, 1989).
- 58 S. J. Gould, *The Structure of Evolutionary Theory* (Belknap Press of Harvard University Press, Cambridge, MA, 2002).
- 59 F. Riede, "Niche construction theory and human biocultural evolution" in *Handbook of Evolutionary Research in Archaeology*, A. M. Prentiss, Ed. (Springer, New York, NY, 2019), pp. 337–360.
- 60 M. A. Zeder, Why evolutionary biology needs anthropology: Evaluating core assumptions of the extended evolutionary synthesis. *Evol. Anthropol.* **27**, 267–284 (2018).
- 61 R. Dawkins, *The Extended Phenotype: The Long Reach of the Gene* (Oxford University Press, Oxford, United Kingdom, 1990).
- 62 R. D. Leonard, G. T. Jones, Elements of an inclusive evolutionary model for archaeology. *J. Anthropol. Archaeol.* **6**, 199–219 (1987).
- 63 M. J. O'Brien, T. D. Holland, "Variation, selection, and the archaeological record" in *Advances in Archaeological Method and Theory*, M. B. Schiffer, Ed. (University of Arizona Press, Tucson, AZ, 1990), pp. 31–79.
- 64 M. J. O'Brien, "Evolutionary archaeology: An introduction" in *Evolutionary Archaeology Theory and Application*, M. J. O'Brien, Ed. (University of Utah Press, Salt Lake City, UT, 1996), pp. 1–15.
- 65 R. C. Dunnell, "What is it that actually evolves?" in *Evolutionary Archaeology: Methodological Issues*, P. A. Teltser, Ed. (University of Arizona Press, Tucson, AZ, 1995), pp. 33–50.
- 66 M. J. O'Brien, R. L. Lyman, "Style, function, and transmission: An introduction" in *Style, Function, Transmission: Evolutionary Archaeological Perspectives*, M. J. O'Brien, R. L. Lyman, Eds. (University of Utah Press, Salt Lake City, UT, 2003), pp. 1–32.
- 67 R. C. Dunnell, Style and function: A fundamental dichotomy. *Am. Antiq.* **43**, 192–202 (1978).
- 68 F. D. Neiman, Stylistic variation in evolutionary perspective: Inferences from decorative diversity and inter-assemblage distance in Illinois woodland ceramic assemblages. *Am. Antiq.* **60**, 7–36 (1995).
- 69 A. M. Prentiss, H. S. Cail, L. M. Smith, At the Malthusian ceiling: Subsistence and inequality at Bridge River, British Columbia. *J. Anthropol. Archaeol.* **33**, 34–48 (2014).
- 70 M. J. O'Brien, T. D. Holland, "The nature and premise of selection-based archaeology" in *Evolutionary Archaeology: Methodological Issues*, P. A. Teltser, Ed. (University of Arizona Press, Tucson, AZ, 1995), pp. 175–200.
- 71 P. Jordan, *Technology as Human Social Tradition* (University of California Press, Berkeley, CA, 2015).
- 72 E. E. Ruyle, Genetic and cultural pools: Some suggestions for a unified theory of biocultural evolution. *Hum. Ecol.* **1**, 201–215 (1973).
- 73 K. N. Laland et al., The extended evolutionary synthesis: Its structure, assumptions and predictions. *Proc. Biol. Sci.* **282**, 20151019 (2015).
- 74 A. Mesoudi, *Cultural Evolution: How Darwinian Theory Can Explain Human Culture & Synthesize the Social Sciences* (University of Chicago Press, Chicago, IL, 2011).
- 75 A. Mesoudi, A. Whiten, K. N. Laland, Towards a unified science of cultural evolution. *Behav. Brain Sci.* **29**, 329–347 (2006).
- 76 V. C. Wynne-Edwards, *Animal Dispersion in Relation to Social Behavior* (Oliver and Boyd, Edinburgh, Scotland, 1962).
- 77 R. L. Bettinger, "Cultural transmission and archaeology" in *Cultural Transmission and Archaeology: Issues and Case Studies*, M. J. O'Brien, Ed. (SAA Press, Washington, DC, 2008), pp. 1–9.
- 78 M. J. O'Brien, Ed., *Cultural Transmission and Archaeology: Issues and Case Studies* (SAA Press, Washington, DC, 2008).

- 79 M. T. Stark, B. J. Bowser, L. Home, *Cultural Transmission and Material Culture: Breaking Down Boundaries* (University of Arizona Press, Tucson, AZ, 2008).
- 80 R. L. Bettinger, J. Eerkens, Point typologies, cultural transmission, and the spread of bow and arrow technology in the prehistoric great basin. *Am. Antiq.* **64**, 231–242 (1999).
- 81 A. M. Prentiss, Introduction to this special issue on evolution of material culture. *Evolution* (N. Y.) **4**, 374–378 (2011).
- 82 P. J. Richerson, R. Boyd, *Not by Genes Alone: How Culture Transformed Human Evolution* (University of Chicago Press, Chicago, IL, 2005).
- 83 S. J. Gould, R. C. Lewontin, The spandrels of San Marco and the Panglossian paradigm: A critique of the adaptationist programme. *Proc. R. Soc. Lond. B Biol. Sci.* **205**, 581–598 (1979).
- 84 A. M. Prentiss, M. J. Walsh, T. A. Foor, Evolution of early Thule material culture: Cultural transmission and terrestrial ecology. *Hum. Ecol.* **46**, 633–650 (2017).
- 85 M. D. Cannon, J. M. Broughton, “Evolutionary ecology and archaeology: An introduction” in *Evolutionary Ecology and Archaeology: Applications to Problems in Human Evolution and Prehistory*, J. M. Broughton, M. D. Cannon, Eds. (University of Utah Press, Salt Lake City, UT, 2010), pp. 1–12.
- 86 A. Grafen, “Natural selection, kin selection, and group selection” in *Behavioural Ecology: An Evolutionary Approach*, J. R. Krebs, N. N. Davies, Eds. (Sinauer Associates, 1984), pp. 62–84.
- 87 A. M. Prentiss, “Human ecology” in *Handbook of Evolutionary Research in Archaeology*, A. M. Prentiss, Ed. (Springer, New York, NY, 2019), pp. 217–230.
- 88 C. Morgan, Is it intensification yet? Current archaeological perspectives on the evolution of hunter-gatherer economics. *J. Archaeol. Res.* **23**, 163–213 (2015).
- 89 D. J. Kennett, B. Winterhalder, Eds., *Behavioral Ecology and the Transition to Agriculture* (University of California Press, Berkeley, CA, 2006).
- 90 S. M. Mattison, E. A. Smith, M. K. Shenk, E. E. Cochrane, The evolution of inequality. *Evol. Anthropol.* **25**, 184–199 (2016).
- 91 E. Boserup, *The Conditions of Agricultural Growth: The Economics of Agrarian Change under Population Pressure* (Aldine, Chicago, IL, 1965).
- 92 J. M. Broughton, Late Holocene resource intensification in the Sacramento River valley: The vertebrate evidence. *J. Archaeol. Sci.* **21**, 501–514 (1994).
- 93 K. Gremillion, Seed processing and the origins of food production in eastern North America. *Am. Antiq.* **69**, 215–233 (2004).
- 94 J. L. Boone, “Competition, conflict, and the evolution of social hierarchies” in *Evolutionary Ecology and Human Behavior*, E. A. Smith, B. Winterhalder, Eds. (Aldine de Gruyter, Chicago, IL, 1992), pp. 301–338.
- 95 M. Borgerhoff Mulder et al., Intergenerational wealth transmission and the dynamics of inequality in small-scale societies. *Science* **326**, 682–688 (2009).
- 96 P. J. Richerson, R. Boyd, “Cultural inheritance and evolutionary” in *Ecology Evolutionary Ecology and Human Behavior*, B. Winterhalder, E. A. Smith, Eds. (Aldine Transaction, Chicago, IL, 1992), pp. 61–94.
- 97 R. L. Kelly, *The Foraging Spectrum: Diversity in Hunter-Gatherer Lifeways* (Smithsonian Institution Press, Washington, DC, 1995).
- 98 B. Marwick, Multiple optima in hoabinhian flaked stone artefact palaeoeconomics and palaeoecology at two archaeological sites in northwest Thailand. *J. Anthropol. Archaeol.* **32**, 553–564 (2013).
- 99 R. D. Leonard, Comment on “Is it evolution yet? A critique of evolutionary archaeology” by J. L. Boone and E. A. Smith. *Curr. Anthropol.* **39**, S162–S163 (1998).
- 100 J. L. Boone, E. A. Smith, Is it evolution yet? A critique of evolutionary archaeology. *Curr. Anthropol.* **39**, S141–S173 (1998).
- 101 M. C. Stiner, S. L. Kuhn, Are we missing the “sweet spot” between optimality and niche construction in archaeology? *J. Anthropol. Archaeol.* **44**, 177–184 (2016).
- 102 K. A. Mohlenhoff, B. F. Codding, When does it pay to invest in a patch? The evolution of intentional niche construction. *Evol. Anthropol.* **26**, 218–227 (2017).
- 103 M. Charbonneau, “Technical constraints on the convergent evolution of technologies” in *Convergent Evolution in Stone Tool Technology*, M. J. O’Brien, B. Buchanan, M. I. Eren, Eds. (The MIT Press, Cambridge, MA, 2018), pp. 73–90.
- 104 N. Eldredge, S. J. Gould, “Punctuated equilibria: An alternative to phyletic gradualism” in *Models in Paleobiology*, T. J. M. Schopf, Ed. (Freeman, Cooper, San Francisco, CA, 1972), pp. 82–115.
- 105 S. M. Stanley, A theory of evolution above the species level. *Proc. Natl. Acad. Sci. U.S.A.* **72**, 646–650 (1975).
- 106 R. Mace, C. J. Holden, A phylogenetic approach to cultural evolution. *Trends Ecol. Evol.* **20**, 116–121 (2005).
- 107 R. Boyd, M. Borgerhoff Mulder, W. H. Durham, P. J. Richerson, “Are cultural phylogenies possible?” in *Human by Nature: Between Biology and the Social Sciences*, P. Weingart, S. D. Mitchell, P. J. Richerson, S. Maasen, Eds. (Lawrence Erlbaum Associates, Mahwah, NJ, 1997), pp. 355–384.
- 108 S. J. Lycett, Understanding ancient hominin dispersals using artefactual data: A phylogenetic analysis of Acheulean handaxes. *PLoS One* **4**, e7404 (2009).
- 109 S. J. Lycett, Are Victoria west cores “proto-Levallois?” A phylogenetic assessment. *J. Hum. Evol.* **56**, 175–191 (2009).
- 110 M. J. O’Brien, J. Darwent, R. L. Lyman, Cladistics is useful for reconstructing archaeological phylogenies: Palaeoindian points from the southeastern United States. *J. Archaeol. Sci.* **28**, 1115–1136 (2001).
- 111 A. M. Prentiss, M. J. Walsh, T. A. Foor, K. D. Barnett, Cultural macroevolution among high latitude hunter-gatherers: A phylogenetic study of the arctic small tool tradition. *J. Archaeol. Sci.* **59**, 64–79 (2015).
- 112 F. Coward et al., The spread of Neolithic plant economies from the near east to northwest Europe: A phylogenetic analysis. *J. Archaeol. Sci.* **35**, 42–56 (2008).
- 113 C. S. Spencer, “Testing the morphogenesis model of state formation: The Zapotec case” in *Macroevolution in Human Prehistory: Evolutionary Theory and Processual Archaeology*, A. M. Prentiss, I. Kuijt, J. C. Chatters, Eds. (Springer, New York, NY, 2009), pp. 133–155.
- 114 C. S. Spencer, *Cultural Macroevolution and Social Change, Handbook of Evolutionary Research in Archaeology*, A. M. Prentiss, Ed. (Springer, New York, NY, 2019), pp. 183–216.
- 115 C. S. Spencer, E. M. Redmond, Multilevel selection and political evolution in the valley of Oaxaca 500–100 B.C. *J. Anthropol. Archaeol.* **20**, 195–229 (2001).
- 116 L. Barton, P. J. Brantingham, D. Ji, Late Pleistocene climate change and paleolithic cultural evolution in northern China: Implications from the last glacial maximum. *Develop. in Quat. Sci.* **9**, 105–128 (2007).
- 117 R. A. Foley, M. M. Lahr, The evolution of the diversity of cultures. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* **366**, 1080–1089 (2011).
- 118 A. M. Prentiss, J. C. Chatters, M. J. Walsh, R. R. Skelton, Cultural macroevolution in the Pacific Northwest: A phylogenetic test of the diversification and decimation model. *J. Archaeol. Sci.* **41**, 29–43 (2014).
- 119 A. M. Prentiss, M. J. Walsh, “Was there a Neolithic ‘(R)evolution’ in North America’s Pacific Northwest region? Exploring alternative models of socio-economic and political change” in *The Origins of Food Production*, N. Sans, Ed. (World Heritage Papers HEADS 6, UNESCO, Paris, France, 2016), pp. 276–291.
- 120 M. Collard, A. Ruttle, B. Buchanan, M. J. O’Brien, Population size and cultural evolution in nonindustrial food-producing societies. *PLoS One* **8**, e72628 (2013).
- 121 J. Henrich, Demography and cultural evolution: Why adaptive cultural processes produced maladaptive cultural losses in Tasmania. *Am. Antiq.* **69**, 197–218 (2004).
- 122 S. Shennan, Demography and cultural innovation: A model and its implications for the emergence of modern culture. *Camb. Archaeol. J.* **11**, 5–16 (2001).
- 123 E. Gjesfeld et al., A quantitative workflow for modeling diversification in material culture. *PLoS One* **15**, e0227579 (2020).
- 124 S. Gavrillets, Evolution and speciation on holey adaptive landscapes. *Trends Ecol. Evol.* **12**, 307–312 (1997).
- 125 S. Wright, “The roles of mutation, inbreeding, crossbreeding, and selection in evolution” in *The Sixth International Congress of Genetics*, D. F. Jones, Ed. (Brooklyn Botanic Garden, Brooklyn, NY, 1932), vol. 1, pp. 356–366.
- 126 T. C. Scott-Phillips, K. N. Laland, D. M. Shuker, T. E. Dickins, S.A. West, The niche construction perspective: A critical appraisal. *Evolution* **68**, 1231–1243 (2013).
- 127 N. L. Boivin et al., Ecological consequences of human niche construction: Examining long-term anthropogenic shaping of global species distributions. *Proc. Natl. Acad. Sci. U.S.A.* **113**, 6388–6396 (2016).
- 128 K. J. Gremillion, L. Barton, D. R. Piperno, Particularism and the retreat from theory in the archaeology of agricultural origins. *Proc. Natl. Acad. Sci. U.S.A.* **111**, 6171–6177 (2014).
- 129 D. R. Piperno, A. J. Ranere, R. Dickau, F. Aceituno, Niche construction and optimal foraging theory in neotropical agricultural origins: A re-evaluation in consideration of the empirical evidence. *J. Archaeol. Sci.* **78**, 214–226 (2017).
- 130 M. A. Zeder, Domestication as a model system for niche construction theory. *Evol. Ecol.* **30**, 325–348 (2015).

- 131 C. Stanish, *The Evolution of Human Co-operation: Ritual and Social Complexity in Stateless Societies* (Cambridge University Press, Cambridge, United Kingdom, 2017).
- 132 M. Pigliucci, An extended synthesis for evolutionary biology. *Ann. N. Y. Acad. Sci.* **1168**, 218–228 (2009).
- 133 G. B. Müller, Why an extended evolutionary synthesis is necessary. *Interface Focus* **7**, 20170015 (2017).
- 134 G. R. McGhee, “Limits on the possible forms of stone tools: A perspective from convergent biological evolution” in *Convergent Evolution in Stone Tool Technology*, M. J. O’Brien, B. Buchanan, M. I. Eren, Eds. (The MIT Press, Cambridge, MA, 2018), pp. 23–46.
- 135 N. M. Herzog, N. Goodale, “Human behavioral ecology and technological decision-making” in *Handbook of Evolutionary Research in Archaeology*, A. M. Prentiss, Ed. (Springer, New York, NY, 2019), pp. 311–336.
- 136 M. J. Shott, History written in stone: Evolutionary analysis of stone tools in archeology. *Evolution (N. Y.)* **4**, 435–445 (2011).
- 137 S. Mithen, *The Prehistory of the Mind: A Search for the Origins of Art, Religion, and Science* (Thames and Hudson, London, United Kingdom, 1996).
- 138 L. Malafouris, “On human becoming and incompleteness: A material engagement approach to the study of embodiment in evolution and culture” in *Embodiment in Evolution and Culture*, G. Etzelmüller, C. Tewes, Eds. (Mohr Siebeck, 2016), pp. 289–305.
- 139 C. Gamble, J. Gowlett, R. Dunbar, The social brain and the shape of the paleolithic. *Camb. Archaeol. J.* **21**, 115–136 (2011).
- 140 A. Fuentes, Human niche, human behaviour, human nature. *Interface Focus* **7**, 20160136 (2017).
- 141 F. Riede, N. N. Johannsen, A. Högberg, A. Nowell, M. Lombard, The role of play objects and object play in human cognitive evolution and innovation. *Evol. Anthropol.* **27**, 46–59 (2018).
- 142 K. N. Laland, M. J. O’Brien, Niche construction theory and archaeology. *J. Archaeol. Method Theory* **17**, 303–332 (2010).
- 143 M. J. Brown, M. W. Feldman, Sociocultural epistasis and cultural exaptation in footbinding, marriage form, and religious practices in early 20<sup>th</sup>-century Taiwan. *Proc. Natl. Acad. Sci. U.S.A.* **106**, 22139–22144 (2009).
- 144 S. J. Gould, “More things in heaven and earth” in *Alas Poor Darwin: Arguments against Evolutionary Psychology*, H. Rose, S. Rose, Eds. (Harmony Books, 2000), pp. 101–126.
- 145 A. M. Prentiss et al., Malthusian cycles among semi-sedentary fisher-hunter-gatherers: The socio-economic and demographic history of housepit 54, Bridge River site, British Columbia. *J. Anthropol. Archaeol.* **59**, 101181 (2020).
- 146 A. M. Prentiss, M. J. Walsh, T. A. Foor, A. Hampton, E. Ryan, Evolutionary household archaeology: Inter-generational cultural transmission at housepit 54, Bridge River site, British Columbia. *J. Archaeol. Sci.* **124**, 105260 (2020).
- 147 I. Kuijt, A. M. Prentiss, “Niche construction, macroevolution and the late Epipaleolithic of the near east” in *Macroevolution in Human Prehistory: Evolutionary Theory and Processual Archaeology*, A. M. Prentiss, I. Kuijt, J. Chatters, Eds. (Springer, New York, NY, 2009), pp. 253–274.
- 148 C. Perreault, *The Quality of the Archaeological Record* (University of Chicago Press, Chicago, IL, 2019).
- 149 J. C. Barrett, “Agency, the duality of structure, and the problem of the archaeological record” in *Archaeological Theory Today*, I. Hodder, Ed. (Polity Press, Cambridge, United Kingdom, 2001), pp. 141–164.
- 150 M.-A. Dobres, J. E. Robb, “Agency in archaeology: Paradigm or platitude” in *Agency in Archaeology*, M.-A. Dobres, J. E. Robb, Eds. (Routledge, London, United Kingdom, 2000), pp. 3–18.
- 151 T. R. Pauketat, Practice and history in archaeology: An emerging paradigm. *Anthropol. Theory* **1**, 73–98 (2001).
- 152 J. Robb, Beyond agency. *World Archaeol.* **42**, 493–520 (2010).
- 153 J. Robb, T. R. Pauketat, “From moments to millennia: Theorizing scale and change in human history” in *Big Histories, Human Lives: Tackling Problems of Scale in Archaeology*, J. Robb, T. R. Pauketat, Eds. (School for Advanced Research Press, Santa Fe, NM, 2013), pp. 3–34.
- 154 J. S. Robert, Taking old ideas seriously: Evolution, development, and human behavior. *New Ideas Psychol.* **26**, 387–404 (2008).