

Particularism and the retreat from theory in the archaeology of agricultural origins

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The introduction of new analytic methods and expansion of research into previously untapped regions have greatly increased the scale and resolution of data relevant to the origins of agriculture (OA). As a result, the recognition of varied historical pathways to agriculture and the continuum of management strategies have complicated the search for general explanations for the transition to food production. In this environment, higher-level theoretical frameworks are sometimes rejected on the grounds that they force conclusions that are incompatible with real-world variability. Some of those who take this position argue instead that OA should be explained in terms of local and historically contingent factors. This retreat from theory in favor of particularism is based on the faulty beliefs that complex phenomena such as agricultural origins demand equally complex explanations and that explanation is possible in the absence of theoretically based assumptions. The same scholars who are suspicious of generalization are reluctant to embrace evolutionary approaches to human behavior on the grounds that they are ahistorical, overly simplistic, and dismissive of agency and intent. We argue that these criticisms are misplaced and explain why a coherent theory of human behavior that acknowledges its evolutionary history is essential to advancing understanding of OA. Continued progress depends on the integration of human behavior and culture into the emerging synthesis of evolutionary developmental biology that informs contemporary research into plant and animal domestication.

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Over the last decade there has been a major expansion of knowledge regarding the timing and socioecological context of plant domestication and emerging agricultural systems. This wealth of data is due in large part to methodological innovations (e.g., in genetics and paleogenomics, in the analysis of plant micro- and macroremains and biological residues, and in the physical and biogeochemical analyses of anthropogenic sediments), re-excavations of some important archaeological sites, and the expansion of archaeological research into regions whose record of agricultural origins has been until recently poorly known [such as New Guinea (1, 2), lowland areas of Mesoamerica and northern South America (3–7), and northern and southern China (8–13)]. These research activities have enriched both the scale and resolution of the data relevant to agricultural origins worldwide. One result of this welcome enhancement of the empirical record is wider acknowledgment of the variability in the historical pathways taken by emerging food production systems across space and time. The dichotomy between foraging and food production has been discarded in favor of a continuum of landscape, plant, and animal management strategies that sometimes resist classification. However, for some scholars (2, 14), the richly detailed records of change seem to have dampened the appeal of general explanations for the transition to agriculture.

This trend, coupled with the critical stance toward hypothetico-deductive science currently influential in archaeological thought (15), has motivated many archaeologists to favor interpretive modes of explanation. In origins of agriculture (OA) research, one result of this changing climate has been a proliferation of historical narratives that highlight local events and processes and downplay general principles. Although we recognize the value of empirical rigor, we argue that the progress of OA research is significantly hampered by the denial of explanations derived from a systematic program of theoretically driven hypothesis testing. We also reject assertions that evolutionary theory is teleological, needlessly reductionist, ahistorical, and therefore irrelevant to understanding human behavior. Without a coherent theory of human behavior, arguments about agricultural origins must rely on assumptions that are often intuitive, unstated, and largely implicit. Coupled with the increasing emphasis on human exceptionalism, the erosion of scientific method is troubling because it creates a rift between researchers in biology and archaeology whose collaboration is essential to advancing understanding of OA. To address these weaknesses, we contend that evolutionary theory (broadly construed to include cultural as well as biological processes) must play a central role in OA research.

In arguing for the systematic use of theory as a tool for the advancement of knowledge, we are not making the claim that evolutionary theory is the only possible realm from which to choose. However, neo-Darwinism has withstood repeated challenges to its core elements, having earned status as an overarching framework for explaining the diversity of life. For this reason, evolutionary theory is central to understanding the root causes of human behavior and indeed culture itself (16). An even stronger case for the evolutionary perspective on human behavior can be made now that the distinctive features of cultural transmission and evolution are becoming more fully incorporated into the synthesis (e.g., refs. 17–20).

We divide our discussion of these issues into three sections. The first elaborates upon some of the weaknesses of particularism in OA research. Next, we sharpen the focus to respond to critiques of evolutionary approaches to human behavior [particularly the research program of human behavioral ecology (HBE) and one of its tools, optimal foraging theory (OFT)]. We argue that recent calls to abandon HBE or OFT are misguided,

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and we explain why the particularist alternatives might provide more explanatory depth and power when situated within a program of behavioral ecology. Finally, we assess the prospects for a synthetic evolutionary research program for the study of domestication and agriculture.

Limitations of Particularism in OA Research and the Need for Theory

The research trend that we critique in this paper shares several characteristics with the approach labeled historical particularism by historians of anthropology (21). Most closely associated with Franz Boas and his students, historical particularism emphasized the collection and compilation of ethnographic data without the distorting effects of theory. Boas and his adherents, weary of unsubstantiated theorizing unsupported by rigorous fieldwork, viewed theory as an obstacle to scientific investigation. Generalizations about culture were suspect because exceptions to them could always be found. Any reliable generalizations would be derived inductively from large bodies of data. Similar recommendations and concerns have been voiced in the OA literature (14, 22–24), with the important difference that current expressions of particularism, rather than disavowing theory, embed it in arguments without explicit acknowledgment or relegate it to a minor role that prioritizes empirically based inference.

We argue that the retreat from theory and the embrace of particularism are not only unwarranted but also counterproductive. Particularistic approaches that reject generalization fail to treat inductive inferences as hypotheses to be tested and substitute appeals to agency for a consistent theory of human behavior. These strategies are problematic for reasons we detail below.

Particularistic Approaches Reject General Principles in the Mistaken Belief That They Imply Universal Causes and Ignore History. In the current climate, it is not surprising that some OA researchers call for a more particularistic approach to understanding why human groups became involved in plant cultivation and animal husbandry. Among the reasons given for rejecting generalizations about causality is that contradictory cases can be answered only by adding qualifiers (ref. 2, p. S380). Some investigators conflate universal explanations (i.e., “prime movers” like environmental change, population pressure, or divine inspiration), which imply that all transitions to agriculture conform to the same causal sequence, with the principles and assumptions of HBE, which do not

(23). The result is a rejection of both universal causation and general principles in favor of “frameworks of explanation that pay close and careful attention to existing relevant archaeological information, that are scaled at the regional level, and that focus on the complex interplay of a range of different environmental and social pre-conditions, prompts, and factors of various kinds” (ref. 23, p. 681).

We agree that no single cause explains all instances of transition from foraging to food production (25–27); this observation is true but trivial. An explanation that claims universal validity loses its universality when exceptions are found to exist. However, its remaining components—variables, processes, and assumptions—often remain relevant at a more modest level of generality. The fatal flaw in the prime mover arguments is not that they rely on overarching laws or assumptions, but rather that they are applied at an inappropriate scale. Following the same logic, the optimization assumptions used heuristically in many HBE models should not be confused with a claim that economic optimization explains all transitions to agriculture (ref. 23, p. 682).

We agree that multiple broad-scale and local factors are involved in any agricultural transition (25, 26). However, this is a commonsense observation about the world, not a template for explanation (ref. 23, p. 681). In fact, complex phenomena such as OA must be simplified to be understood. A theoretical framework is needed to guide this process to ensure that explanations are not fashioned from a hodgepodge of factors and variables selected at the discretion of the researcher. For this reason, we advocate an approach to understanding OA that examines theoretical assumptions before interpreting data. Such assumptions always exist, acknowledged or not. Brought to the forefront, they serve to anchor observations to bodies of knowledge that have withstood repeated testing. Such high-level bodies of general theory inform middle- and lower-level theories that in turn generate testable hypotheses (16, 28). The explanatory relevance of broadly applicable principles does not conflict with the observation that domestication of any plant or animal is a particular, local, and historically contingent process. If it did, evolutionary theory could not be said to explain the diversity of life without implying that all evolutionary lineages follow the same path.

To be clear, we applaud the attention being paid to accurate reconstructions of the trajectory and context of agricultural transitions at regional and local scales. Detail-oriented analysis of observations and data yield rich

historical accounts of OA (see, for example, refs. 25 and 29–32). However, to the extent that they purport to engage in explanation, such accounts often rely on inductions that are expected to stand on the strength of available evidence alone. Although we recognize that the prioritization of data is often intentional and explicitly stated (e.g., ref. 33), we disagree that it is a good idea to abandon the iterative process of hypothesis testing, revision, and retesting that drives incremental advances in scientific understanding.

Particularistic Explanations Lack a General Theory for the Evolution of Human Behavior Yet Rely on a General Theory of Evolution for All Other Organisms.

There is little disagreement that change in the frequency of attributes in populations of humans, animals and plants under domestication is inherently coevolutionary. Understanding this process requires a general theory that links change in one population to change in another. Certainly, humans possess a unique mode of inheritance and an unusual degree of behavioral flexibility. However, cultural inheritance and the mechanics of human learning that enable it are constrained (at least, in the long run) by processes that constrain the evolution of other organisms. Far from being an obstacle to evolutionary analysis, human uniqueness offers one of the most important justifications for using it.

By not interpreting human behavior as a product of natural selection, particularistic approaches miss the opportunity to explore commonalities in human behavior that enable comparative analysis of agricultural origins in starkly different contexts. Nothing about an evolutionary perspective suggests that natural selection generates a predetermined template for human behavior, nor does it claim to explain everything that humans do. Human social learning has its own distinctive processes that influence patterns of behavior at the population level. However, human abilities (including the capacity for communication, learning, and choice—all components of cultural inheritance) are products of natural selection, and human culture is a function of those abilities (16, 34–36). Because agriculture has been adopted (or inherited) by nearly all human groups and because it was invented separately by many, the process will be understood best by looking at change in the history of human adaptation as a function of attributes shared by all humans, rather than looking at novel attributes unique to a few.

Because they lack a general theory for human behavior, particularistic approaches

rely on diverse and often conflicted principles to account for the decision-making behavior of human agents. In some cases, they retain the rational-actor optimization logic of HBE (e.g., that people will act in their own best interest with regards to survival-related utility); in other cases, they rely on creative or arbitrary combinations of a “bounded rationality” (sensu refs. 37 and 38) drawn opportunistically from ethnographic or contemporary observations; still others seem to gather principles of behavior from social theory (39, 40). Such principles are seldom made explicit; in some cases they are revealed by references to undefined or vaguely conceptualized properties or goals [e.g., “resource-rich,” “intensification of resource manipulation,” “rich array of plant and animal species,” “enrichment,” “stable and sustainable,” “stress,” etc. (23)]. Such terms betray embedded assumptions about the ecological situations that humans prefer and presumably strive for. Consistent theory that illustrates how and why these organizing principles emerge in the first place is essential for explaining the outcomes of diverse motivations in the distant past, particularly when these outcomes are visible today only in the aggregate records of archaeology and population biology.

Researchers who reject general theories of human behavior and cultural evolution as overly deterministic sometimes invoke human agency as an alternative causal mechanism. Agency is a contested term in archaeology, and the OA literature seems to have adopted one sense of it to the exclusion of others. Advocates use the common reading of agency (refs. 15 and 41, p. 67) to illustrate how individual choice and creativity explain cultural change, including the transition to agriculture (ref. 29, p. 44). Although we acknowledge the role of human creativity and innovation in OA, we are not convinced that appeals to agency have much explanatory power, simply because they sidestep the problem of identifying the evolutionary basis of the beliefs and preferences that guide human action (42). In contrast, HBE generates hypotheses about why humans behave the way they do and evaluates whether or not these hypotheses about agency explain the material remains of those behaviors. We agree that human agency is a critical component of evolutionary change, but we do not see it as having an equally important role in the scientific explanation of change.

Another problem with explanation by agency is that it often implies that decision makers have complete information about the long-term consequences of their actions. This feat would require far more involved data

analysis than the simple arithmetic required to find optimal solutions to foraging problems (for example) and is even farther removed from the practical heuristics (e.g., rules of thumb, tacit or explicit learning, rational calculation, etc.) that people actually use to make those decisions. By contrast, simple agency in foraging models is one of individual decision making, but does not imply (and does not require) long-term teleological self-determination.

The Evolutionary Approach Is a Robust, Flexible, and Practical Avenue for an Incrementally Better Understanding of Human Behavior and Cultural Change

Whereas evolutionary biologists seldom have to confront the question of human exceptionalism, the issue is a central one in anthropology and archaeology. The application of evolutionary theory to human behavior has been criticized for excessive adaptationism, reductionism, positivism, and materialism (e.g., refs. 43 and 44). These criticisms have been taken up by many advocates of interpretive archaeology, who question the exclusive claim of science to the production of useful knowledge (many examples appear in ref. 45; see also ref. 24).

Some archaeologists who do embrace evolutionary concepts in their OA research remain uncomfortable with their application to human behavior. Particularly heavy criticism has been leveled at evolutionary ecology (EE), defined as the “study of evolution and adaptive design in ecological context” (ref. 46, p. 3), especially the subdiscipline of HBE and its optimal foraging models. These critiques target either the basic assumptions of EE (many of which are shared by other evolutionary approaches) or elements of HBE or OFT specifically (14, 22, 23). Although the objections are numerous, they commonly revolve around the following themes: (i) explanations based on evolution by natural selection are “covering law” explanations that fail to account for the particular historical circumstances of their social and biological contexts; (ii) simple models are inappropriate for complex phenomena; (iii) the use of multiple simplifying models is compromised when one or more models fail to explain or predict the phenomena at hand; (iv) models do not explain human subsistence (or any other) behavior; (v) explanatory, predictive models deny human agency and are therefore dehumanizing; and (vi) some models do not account for environmental change and are therefore inappropriate for historical or evolutionary analysis. We find these critiques unwarranted and explain our reasoning below.

The Study of Evolution Is a Historical Science. Evolutionary theory is not covering law science (ref. 23, p. 681). It is a scientific approach to history (47) that views change as both cause and consequence of the immediate and long-term fitness implications of inherited and acquired variation. Although focused on the processes of change, nothing about these processes, or the analysis of them, is deterministic, teleological, or scripted. The context and consequences of one case might be completely different from the next (i.e., both historical and particular), but the foundations of evolutionary analysis are unifying. At the same time, it is flexible enough to deal with the hyper-variability of human behavior, which, for a variety of evolutionarily sound reasons, evolves and diversifies rapidly (48). In part, this flexibility comes from the application of a wide range of models that isolate specific aspects of behavioral and evolutionary phenomena.

Simple Models of Complex Phenomena Are Useful Even When They Fail.

Recent reactions to the use of OFT’s simplifying models in hunter-gatherer and OA research (14, 49, 50) take their cue from older critiques in biology and ecology (e.g., refs. 51 and 52) but differ on the issue of culture. For many social science scholars, models that isolate specific aspects of individual behavior in a *ceteris paribus* world (53) are impractical because (i) the *ceteris paribus* world doesn’t exist, and (ii) individuals perform in a complex, indivisible milieu that can be understood only in its holistic totality. For many, the practice of methodological isolation and analytical simplification has “reduced human actors to disemboweled humans who no longer have cultural anchors” (ref. 54, p. 59). They complain that evolutionary models isolate individuals from populations and remove both from the thing that binds them, which is culture.

Reservations about heuristic models are welcome (indeed these reservations and the resulting critiques may lead to better models); outright rejection of them is not. Unfortunately, and in many cases, rejection of simple, heuristic models is based on an idealized (but often unstated and unsupported) view of how the world works and on the complaint that too many people take the modeled predictions as fact, with or without empirical backing (14). Such critiques mistakenly conclude that the optimization assumptions used heuristically in many HBE models constitute a claim that optimal resource use explains all transitions to agriculture (ref. 23, p. 682).

The use of simple models (like those used in OFT) does not imply that the predictions of the models must be true. All things being equal (in the *ceteris paribus* world), the models should explain the behavior of organisms foraging optimally to maximize reproductive success. In the absence of data, the modeled predictions are simply that, and if the assumptions are correct, the predictions simply ought to be true. When data do exist but do not fit the model, either all things are not equal (e.g., the assumptions are incorrect), the model is inappropriately applied (e.g., the scale or resolution of the behaviors does not match those of the resulting data and/or the currency of the model is inappropriate), or the organism simply doesn't conform to expectation. Observations of the final type can also be productive by leading to further hypothesis testing built on related versions of EE developed specifically to explain the proliferation and persistence of suboptimal or maladaptive behavior (17, 55–58).

The criticism that HBE models sometimes fail to yield accurate predictions when tested misses the point that the exploration of the model's vulnerability can itself be a source of insight. Models are productive means for "eliminating problematic answers and identifying and pursuing more promising ones" (ref. 59, p. 171). In other words, failure is an option. For example, when empirical tests of the diet breadth model (DBM) failed to show a good fit of data to model predictions for agricultural transitions in the eastern United States, the findings led to a better grasp of the variables and tradeoffs (such as travel and processing costs) that most influenced subsistence strategies (e.g., refs. 60 and 61). Piperno and Pearsall (62) also discussed how OFT models, whose predictions conformed to Neotropical empirical data on the emergence of food production, were unlikely to address subsequent agricultural intensification satisfactorily, which evoked other explanations. Others (63–65) have investigated the failure of simple foraging models such as the DBM to capture important influences on agricultural decision making, such as yield variability and labor investment. These studies counter claims that applications of OFT demand idealistic purism or seek perfection in model/data fit (14, 50).

Simple, well-used models of OFT like the DBM (66) outline the logic of individual, time-sensitive decisions, and, because individuals make decisions in different contexts, the model anticipates behavioral variation. The extent of this variation in time and space is exactly what we find interesting, and relevant

to OA research. Aggregate patterns of individual behavior are what we see in the archives of the past. Therefore, the study of the past requires evaluation of models against data aggregated over different scales. The DBM is one model that makes this procedure possible. It is not the only model, and there is no reason to expect it to explain all data on all scales of time or space. However, in combination with related models, it is a very powerful analytical tool.

A Challenge to One Model Does Not Negate the Others.

One critique of the evolutionary program is that it shifts arbitrarily between models that isolate and address different aspects of phenomena staged at different scales of time, space, or number (e.g., ref. 67). The observation is fair, but the critique is not. Indeed, what makes EE so versatile is that it draws from a "family of models" to address the tradeoffs between generality, realism, and precision inherent to any approach to scientific inquiry (68–70). The important point here is that we draw on models rooted in a unified body of theory, even if some of the models fail to explain the existing data, or if the models explain the data on different scales or levels of analysis.

Models of EE Often Generate Accurate Predictions of Human Subsistence Behavior, Including OA.

As previously noted, OFT is one class of models with a reasonable purchase in the explanatory realm, and one that has provided a number of insights for biologists and archaeologists. A review of the past few years of biological literature finds persistent employment of OFT models, with empirical data often showing good fits with their predictions in a variety of organisms (e.g., refs. 71–74). OFT applications in human research also continue apace with valuable insights on varied topics (e.g., refs. 75–78).

A particularly important and well-studied example of subsistence change associated with OA and one that has been a focus of OFT applications is the "broad spectrum revolution" (BSR) (79). The BSR describes the expansion of human diets and the intensification of plant and animal exploitation that preceded agricultural beginnings in many parts of the world. Investigations of the BSR with OFT typically use the diet breadth model (DBM) and have shown a good fit of model predictions with empirical data from archaeological sites in southwest Asia, the Neotropics, and elsewhere (e.g., refs. 6, 62, and 80–87). Research shows that dietary shifts from higher- to lower-ranked plant and animal resources, or a more even dependence

on small-sized dietary items, occurred as a result of climate- and/or human-driven factors, depending on the region involved. Examples include terminal Pleistocene faunal extinctions and vegetational change (Neotropics) and increasing human demographic pressure leading to resource depression (southwest Asia). It is important to reiterate (88) that ethnographic datasets on foraging efficiency from around the world support the ranking of general categories of resources such as small and large game according to their energetic return rates (net energy obtained per unit time spent). Although exceptions occur, most plant foods and small and medium-sized mammals are ranked lower than most large game, and nuts and seeds are often the lowest-ranked of all (80, 88). It would be counterproductive for investigations of cultural developments through time, such as agricultural origins, to ignore those associations.

The collective archaeological data clearly underline how dietary diversification and intensification of plant use by foragers and incipient farmers probably occurred in an environmental milieu of shifting energetic return rates. Arguments that DBM predictions for the BSR are frequently invalidated by the archaeological data (14) are difficult to reconcile with the results of these studies. As a number of scholars have pointed out, the DBM is particularly suited for studying major directional changes in subsistence through time because of its ability to make robust, qualitative predictions of prey choice and dietary diversity. Using the model does not require that every past or present resource ranking set be in perfect order with respect to the general category of resource, package size, and the energetic return rates of individual items.

Ecological Models Accommodate Human Agency.

Rejection of models like the DBM in favor of explanation by agency echoes a long-standing debate in evolutionary biology over the levels of causation (89–93). In behavioral science, ultimate explanations view behavior as a product of natural selection (cultural and biological) whereas proximate explanations attempt to understand how individuals identify challenges, make decisions, and initiate action (this being the realm of agency). The former have been caricatured as evolutionary "why" questions whereas the latter have been equated with questions of "how." Many see the conflation of these issues as a general challenge to evolutionary theory (93) whereas others recognize that both are important to understanding the structure

of biological, cultural, and socio-ecological change (42, 92).

HBE models, specifically the contingency models such as the DBM, seek ultimate explanations by identifying optimal solutions to immediate problems. They assume that organisms possess an evolved general capacity to achieve these optimal solutions, at least on average. Although it is true that models like the DBM rest heavily on ultimate rather than proximate explanation, this trait is no reason to reject them. Indeed, users of the model regularly acknowledge that it is silent about proximate causes while recognizing that many such causes exist. Both proximate and ultimate causes shape evolution, and the study of evolution must be able to identify where and when the feedbacks between “hows” and “whys” are reciprocal (92). The HBE modeling format makes this step possible by being agnostic about proximate causes, and testing hypotheses premised on ultimate causation. This agnosticism does not deny human agency but notes that agency, practice, and habitus (for example) are ultimately constrained by natural selection, at least over time. Because the models are not absolute covering-law statements, they can accommodate feedbacks between proximate and ultimate causes when, for example, natural selection (the ultimate cause) shapes the way people make decisions (the proximate cause), and those decisions further shape the environment of selection.

Whether or not the domestication of plants, animals, people, or landscapes entails morphological, genetic, or associational change, by design (i.e., “agency”) or by accident, abruptly or gradually, understanding the process on the human side of things requires an archaeology that tracks change in human behavior. Archaeological data typically say little about individuals but speak volumes about individuals in aggregate. HBE provides the theoretical foundation for understanding aggregate patterns as the product of individual decisions. Indeed, archaeological data are best viewed as the products of traits most common across a population of individuals; change in the spatial and temporal patterns of archaeological data reflects change in the distribution or frequency of traits within and among populations, through space and time.

Ecological Models Accommodate Environmental Change. Some critics of OFT suggest that it assumes an unchanging environment (refs. 14 and 50, p. 257). They argue that OFT models do not account for change in the environment of selection that creates domestic plants and animals and suggest that they should be discarded in favor of

explanations drawn from niche construction theory (NCT) (94). NCT highlights the multiple kinds of feedback that flow to the niche constructor and to other populations whose environments its niche-constructing activity influences (e.g., ref. 95). In doing so, NCT makes it possible to better characterize the ecological context in which optimality must be assessed. That hunter-gatherers did (and do) modify landscapes and resources for calculated gain is inarguable (96–98); however, the extent and scope of this practice are a matter of considerable debate (49). In the case of domestication and agriculture, landscape modification has long been recognized as an important phenomenon (99–101). However, we do not agree with the contention that OFT models cannot accommodate dynamic environments and argue that EE is well-positioned to support and complement NCT.

Although environmental stasis might be necessary to some aspects of model building (e.g., the contingency of the DBM assumes a static prey ranking), the simple models of foraging theory are equally applicable to dynamic environments (102–104). For example, the decision contingency of the DBM (66) is based on the marginal rate of return established by two important inputs: encounter rate (a function of prey abundance) and postencounter return rate (a function of prey value offset by the costs of acquiring and processing it). Data for the latter define the ranking of different prey, which is fixed until either the size (or total nutritional value) of the prey changes, or the energetics of capturing and processing it do. Thus, for each decision contingency there might be a different prey ranking, and, if so, the “optimal” diet in that instance may be different from during the previous instance. The standard logic of the DBM is that lower-ranked prey enter the diet as the abundance of higher-ranked prey declines; increasing abundance of lower-ranked prey has only a minimal effect on the decision to include them in the diet (105, 106). However, environmental modification may affect more than just absolute abundance and rates of encounter: change in the distribution of taxa also affects postencounter return rates that, in turn, affect the ranking of different prey taxa. Harvesting and replanting can raise the density of plants within a patch, which can alter the ranking of the resource (by reducing the costs of collecting the seeds) and boost its dietary importance (which may have been constrained initially by scarcity) (107). In other cases, selective, intensive harvests may reduce the body size of the average individual prey, again affecting the prey ranking and therefore the optimal decision.

EE offers a systematic way to evaluate the motivations for niche-construction activities such as landscape management and its intensification. In fact, applications of behavioral ecological models in archaeology often highlight the active role of humans in shaping their habitats (62, 80, 97, 108). Assertions to the contrary (50) neglect a substantial amount of literature on the subject. Critically, HBE permits an evaluation of the overall return rates associated with resource acquisition, which must include the costs of investing in land management as well as the returns of a managed landscape. EE (including HBE and OFT) can be useful for understanding the evolution of landscape management practices and other forms of niche construction and for evaluating the relationship between land, labor, and resource productivity.

We see a problem with using NCT as a “single unifying approach for integrating consideration of human and non-human modification of ecosystems” (ref. 50, p. 265) because it does not systematically address how or why humans alter their resource-acquisition patterns. There is little doubt that intensive human activity modifies ecosystems in diverse ways that nonetheless follow a limited set of pathways (50). However, a more intriguing question is why altered ecosystems engender or permit novel behavioral strategies in some cases but not others. Indeed, if hunter-gatherer landscape modification (including intentional enhancement of resource abundance) is a common feature of hunter-gatherer adaptive systems, why do so few cases generate the environment of selection that yields domestic plants and animals? Clearly, more is at work than the pervasiveness of niche construction: insights from NCT require the evolutionary logic of human decision making in tandem with a tighter consideration of the interactions between multiple taxa in novel settings to explain the origins of agriculture. Without a theory of organismal behavior, such as HBE, the alternatives imply either (*i*) that humans invented agriculture and its long-term consequences knowingly (as some advocates of human agency would have us believe), or (*ii*) that agriculture emerged almost randomly as a function of dynamic feedbacks between genes, environment, and the interactions between them (according to the strict version of NCT).

Integration of Evolutionary Frameworks

Evolutionary theory as applied to archaeological questions such as OA remains diverse, as expected for a relatively new but maturing field. However, the various approaches share

a commitment to evolutionary explanation even though they emphasize different processes, questions, and types of causation. EE (inclusive of HBE and OFT) (61, 64, 109), niche construction theory (19, 26), and models of cultural transmission and gene-culture coevolution (19, 110–112) all have the potential to link empirical findings to a well-established body of knowledge, but they target different implications of selection. OFT predicts how organisms might mobilize evolved decision-making mechanisms to maximize utility in the face of conflicting needs; niche construction theory asks how environmental engineering sets up pathways of ecological inheritance that affect the fitness of the organism and its descendants; cultural transmission theory asks how patterns of social learning peculiar to our species generate patterns of descent and divergence in cultural lineages.

Debates over the relative utility of these approaches have been helpful in distinguishing between fundamental incommensurabilities and superficial differences, thereby moving us closer to synthesis. We agree with Bettinger and Richerson that “Darwinian theory accommodates a virtually limitless range of interesting, fruitful projects. It is perhaps this diversity that causes us sometimes to forget the basic commonalities that unite the Darwinian enterprise” (ref. 112, p. 222). To declare that any of these theoretical perspectives is fatally flawed (14, 45) closes the door on potentially productive alliances among them.

For example, we believe that NCT can continue to move forward by joining forces with other evolutionary programs. Complementarity between NCT and EE has already been illustrated in case studies of New World hunter-gatherers and agriculturalists (108). Broughton et al. (ref. 108, p. 371) note that EE “focuses on how behavioral adjustments to changing socio-ecological conditions create novel selective pressures that in turn drive other changes in morphology and behavior” and therefore “draws on the same evolutionary logic that underlies niche construction theory.” Others (e.g., ref. 113) illustrate how NCT-based hypotheses can explain technological change across the transition to agriculture. O’Brien and Laland (19) make a strong case that gene-culture coevolution theory and NCT strengthen and support explanations of adaptive complexes related to agriculture, such as adult lactose tolerance and persistence of sickle-cell disease.

Conclusions

We believe strongly that the most significant archaeological contributions to our under-

standing of domestication will be those that acknowledge that humans are subject to the forces of evolution. We find little justification for the argument that, of all species, only *Homo sapiens* is capable of transcending these forces. We also advocate the use of theoretical frameworks that serve to link testable hypotheses to ultimate explanations for human behavior. However, we also wish to make it clear that, in doing so, we are not advocating any approach that ignores the distinctiveness of cultural evolution or the great behavioral plasticity that characterizes human interactions with the natural world. Nor are we in favor of glossing over historical particulars in the interests of advancing general theories of change.

Calls to purge OA research of HBE or OFT fail to distinguish between levels of theory and their respective epistemological roles. In OA research, certain core elements of Darwinian evolutionary theory (as advanced and amended by the neo-Darwinian

synthesis and, more recently, evolutionary and ecological developmental biology) have earned the status of basic assumptions. The reality of evolution by natural selection is such a core idea, arguably the most important one for OA research. It unifies approaches that use different analytic tools and methods and target different kinds of questions.

The research programs that cluster under the umbrella of evolutionary theory have generated, and continue to generate, testable hypotheses that contribute to our understanding of OA. Of these, HBE and OFT have a longstanding record of productivity, and, more recently, models of cultural inheritance have begun to show considerable promise. Although there is no way of predicting which evolutionary perspectives will prove most useful in the long run, one thing is certain: a retreat from theory in favor of particularism will ensure that none of them achieve their full potential.

- 1 Denham TP, et al. (2003) Origins of agriculture at Kuk Swamp in the highlands of New Guinea. *Science* 301(5630):189–193.
- 2 Denham T (2011) Early agriculture and plant domestication in New Guinea and island Southeast Asia. *Curr Anthropol* 52(Suppl 4): S379–S395.
- 3 Piperno DR, Ranere AJ, Holst I, Iriarte J, Dickau R (2009) Starch grain and phytolith evidence for early ninth millennium B.P. maize from the Central Balsas River Valley, Mexico. *Proc Natl Acad Sci USA* 106(13):5019–5024.
- 4 Dillehay TD, Rossen J, Andres TC, Williams DE (2007) Preceramic adoption of peanut, squash, and cotton in northern Peru. *Science* 316(5833):1890–1893.
- 5 Iriarte J (2007) New perspectives on plant domestication and the development of agriculture in the new world. *Rethinking Agriculture: Archaeological and Ethnoarchaeological Perspectives*, eds Denham T, Iriarte J, Vrydaghs L (Left Coast Press, Walnut Creek, CA), pp 167–188.
- 6 Piperno DR (2011) The origins of plant cultivation and domestication in the New World tropics: Patterns, process, and new developments. *Curr Anthropol* 52(Suppl 4):S453–S469.
- 7 Iriarte J (2009) Narrowing the gap exploring the diversity of early food-production economies in the Americas. *Curr Anthropol* 50(5): 677–680.
- 8 Barton L, et al. (2009) Agricultural origins and the isotopic identity of domestication in northern China. *Proc Natl Acad Sci USA* 106(14): 5523–5528.
- 9 Zhao Z (2011) New archaeobotanic data for the study of the origins of agriculture in China. *Curr Anthropol* 52(Suppl 4): S295–S306.
- 10 Fuller DQ, Harvey E, Qin L (2007) Presumed domestication? Evidence for wild rice cultivation and domestication in the fifth millennium BC of the Lower Yangtze region. *Antiquity* 81:316–331.
- 11 Fuller DQ, et al. (2009) The domestication process and domestication rate in rice: Spikelet bases from the Lower Yangtze. *Science* 323(5921):1607–1610.
- 12 Bettinger RL, Barton L, Morgan C (2010) The origins of food production in North China: A different kind of agricultural revolution. *Evol Anthropol* 19(1):9–21.
- 13 Bettinger RL, et al. (2010) The transition to agriculture at Dadiwan, People’s Republic of China. *Curr Anthropol* 51(5):703–714.
- 14 Zeder MA (2012) The Broad Spectrum Revolution at 40: Resource diversity, intensification, and an alternative to optimal foraging explanations. *J Anthropol Archaeol* 31:241–264.
- 15 Hegmon M (2003) Setting theoretical egos aside: Issues and theory in North American archaeology. *Am Antiq* 68:213–243.
- 16 Ellen R (2010) Theories in anthropology and “anthropological theory”. *J R Anthropol Inst* 16:387–404.
- 17 Boyd R, Richerson PJ (1985) *Culture and the Evolutionary Process* (Univ of Chicago Press, Chicago).
- 18 Mesoudi A, Whiten A, Laland KN (2006) Towards a unified science of cultural evolution. *Behav Brain Sci* 29(4):329–347, discussion 347–383.
- 19 O’Brien MJ, Laland KN (2012) Genes, culture, and agriculture: An example of human niche construction. *Curr Anthropol* 53:434–470.
- 20 Richerson PJ, Boyd R, Henrich J (2010) Colloquium paper: Gene-culture coevolution in the age of genomics. *Proc Natl Acad Sci USA* 107(Suppl 2):8985–8992.
- 21 Harris M (1968) *The Rise of Anthropological Theory* (Thomas Crowell, New York).
- 22 Smith BD (2009) Core conceptual flaws in human behavioral ecology. *Commun Integr Biol* 6:533–534.
- 23 Zeder MA, Smith BD (2009) A conversation on agricultural origins: Talking past each other in a crowded room. *Curr Anthropol* 50:681–691.
- 24 Vrydaghs L, Denham T (2007) Rethinking agriculture: Introductory thoughts. *Rethinking Agriculture: Archaeological and Ethnoarchaeological Perspectives*, eds Denham T, Iriarte J, Vrydaghs L (Left Coast Press, Walnut Creek, CA), pp 1–15.
- 25 Zeder MA (2006) Central questions in the domestication of plants and animals. *Evol Anthropol* 15:105–117.
- 26 Smith BD (2007) Niche construction and the behavioral context of plant and animal domestication. *Evol Anthropol* 16:188–199.
- 27 Smith BD (2001) Documenting plant domestication: The consilience of biological and archaeological approaches. *Proc Natl Acad Sci USA* 98(4):1324–1326.
- 28 Ketelaar T (2003) The evaluation of competing approaches within human evolutionary psychology. *Evolutionary Psychology: Alternative Approaches*, eds Scher SJ, Rauscher F (Kluwer, Boston), pp 31–54.
- 29 Zeder MA (2008) The Neolithic macro-(r)evolution: Macroevolutionary theory and the study of culture change. *J Archaeol Res* 17(1):1–63.
- 30 Zeder MA (2008) Domestication and early agriculture in the Mediterranean Basin: Origins, diffusion, and impact. *Proc Natl Acad Sci USA* 105(33):11597–11604.
- 31 Bar-Yosef O (2011) Climatic fluctuations and early farming in West and East Asia. *Curr Anthropol* 52(Suppl 4):S175–S193.
- 32 Belfer-Cohen A, Goring-Morris AN (2011) Becoming farmers: The inside story. *Curr Anthropol* 52(Suppl 4):S209–S220.
- 33 Belfer-Cohen A, Goring-Morris AN (2009) For the first time. *Curr Anthropol* 50:669–671.
- 34 Flinn M (1997) Culture and the evolution of social learning. *Evol Hum Behav* 18:23–67.
- 35 Henrich J, McElreath R (2003) The evolution of cultural evolution. *Evol Anthropol* 12:123–135.
- 36 Nettle D (2009) Beyond nature versus culture: Cultural variation as an evolved characteristic. *J R Anthropol Inst* 15:223–240.
- 37 Jones BD (1999) Bounded rationality. *Annu Rev Polit Sci* 2:297–321.

- 38 Simon HA (1947) *Administrative Behavior* (Macmillan, New York).
- 39 Hodder I (1990) *The Domestication of Europe: Structure and Contingency in Neolithic Societies* (B. Blackwell, Oxford).
- 40 Cauvin J (2000) *The Birth of the Gods and the Origins of Agriculture*, trans Watkins T (Cambridge Univ Press, Cambridge, UK).
- 41 Gardner A (2011) Action and structure in interpretive archaeologies. *Evolutionary and Interpretive Archaeologies: A Dialogue*, eds Cochran EE, Gardner A (Left Coast Press, Walnut Creek, CA), pp 63–82.
- 42 Smith EA (2013) Agency and adaptation. *Annu Rev Anthropol* 42:103–120.
- 43 Ingold T (2000) *The Perception of the Environment: Essays in Livelihood, Dwelling and Skill* (Routledge, London).
- 44 Joseph S (2000) Anthropological evolutionary ecology: A critique. *J Ecol Anthropol* 4:6–30.
- 45 Cochran EE, Gardner A, eds (2011) *Evolutionary and Interpretive Archaeologies: A Dialogue* (Left Coast Press, Walnut Creek, CA).
- 46 Winterhalder B, Smith EA (1992) Evolutionary ecology and the social sciences. *Evolutionary Ecology and Human Behavior*, eds Smith EA, Winterhalder B (Aldine de Gruyter, New York), pp 3–24.
- 47 Nitecki MH, Nitecki DV (1992) *History and Evolution* (State Univ of New York Press, Albany, NY).
- 48 Richerson PJ, Boyd R (1997) Built for speed, not for comfort: Darwinian theory and human culture. *Philosophica* 60:13–43.
- 49 Lightfoot KG, Cuthrell RQ, Striplen CJ, Hylkema MG (2013) Rethinking the study of landscape management practices among hunter-gatherers in North America. *Am Antiq* 78(2):285–301.
- 50 Smith BD (2011) A cultural niche construction theory of initial domestication. *Biol Theory* 6:260–271.
- 51 Gray RD (1987) Faith and foraging: A critique of the “paradigm argument from design”. *Foraging Behavior*, eds Kamil AC, Krebs JR, Pulliam HR (Plenum, New York), pp 69–140.
- 52 Pierce GJ, Ollason JG (1987) Eight reasons why optimal foraging theory is a complete waste of time. *Oikos* 49:111–118.
- 53 Boyer P (1995) *Ceteris paribus* (all else being equal). *How Things Are: A Science Tool-Kit for the Mind*, eds Brockman J, Matson K (William Morrow, New York), pp 169–175.
- 54 Yengoyan AA (2004) *Anthropological History and the Study of Hunters and Gatherers: Cultural and Non-Cultural Hunter-Gatherers in History, Archaeology and Anthropology*, ed Barnard A, Berg, New York), pp 57–66.
- 55 Henrich J (2002) Decision making, cultural transmission, and adaptation in economic anthropology. *Theory in Economic Anthropology*, ed Ensminger J (Alta Mira, Walnut Creek, CA), pp 251–295.
- 56 Henrich J (2004) Demography and cultural evolution: How adaptive cultural processes can produce maladaptive losses—the Tasmanian case. *Am Antiq* 69(2):197–214.
- 57 McElreath R (2004) Social learning and the maintenance of cultural variation: An evolutionary model and data from East Africa. *Am Anthropol* 106(2):308–321.
- 58 Richerson PJ, Boyd R (2005) *Not by Genes Alone: How Culture Transformed Human Evolution* (Univ of Chicago Press, Chicago).
- 59 Bird D, O’Connell JF (2006) Behavioral ecology and archaeology. *J Archaeol Res* 14:143–188.
- 60 Gremillion KJ (2004) Seed processing and the origins of food production in eastern North America. *Am Antiq* 69:215–234.
- 61 Gremillion KJ (1998) Changing roles of wild and cultivated plant resources among early farmers of Eastern Kentucky. *Southeastern Archaeol* 17:140–157.
- 62 Piperno DR, Pearsall DM (1998) *The Origins of Agriculture in the Lowland Neotropics* (Academic, San Diego).
- 63 Barlow KR (2006) A formal model for predicting agriculture among the Fremont. *Behavioral Ecology and the Transition to Agriculture*, eds Kennett DJ, Winterhalder B (Univ of California Press, Berkeley, CA), pp 87–102.
- 64 Marston JM (2011) Archaeological markers of agricultural risk management. *J Anthropol Archaeol* 30:190–205.
- 65 Foster HT II (2003) Dynamic optimization of horticulture among the Muscogee Creek Indians of the southeastern United States. *J Anthropol Archaeol* 22:411–424.
- 66 MacArthur RH, Pianka ER (1966) On optimal use of a patchy environment. *Am Nat* 100:603–609.
- 67 Smith BD (2006) Human behavioral ecology and the transition to food production. *Behavioral Ecology and the Transition to Agriculture*, eds Kennett DJ, Winterhalder B (Univ of California Press, Berkeley, CA), pp 289–303.
- 68 Levins R (1966) The strategy of model-building in population biology. *Am Sci* 54:421–431.
- 69 Richerson PJ, Boyd R (1987) Simple models of complex phenomena: The case of cultural evolution. *The Latest on the Best: Essays on Evolution and Optimality*, ed Dupre J (MIT Press, Cambridge, MA), pp 27–52.
- 70 Winterhalder B (2002) Models. *Darwin and Archaeology: A Handbook of Key Concepts*, eds Hart JP, Terrell JE (Bergin and Garvey, Westport, CT), pp 201–224.
- 71 Catania KC (2012) Evolution of brains and behavior for optimal foraging: A tale of two predators. *Proc Natl Acad Sci USA* 109(Suppl 1):10701–10708.
- 72 Lai Y, Chen J-H, Lee L-L (2011) Prey selection of shell-invading leech as predicted by optimal foraging theory with consumption success incorporated into estimation of prey profitability. *Funct Ecol* 25:147–157.
- 73 Danial-Valcroze T, Lesage V, Giard J, Michaud R (2011) Optimal foraging theory predicts diving and feeding strategies of the largest marine predator. *Behav Ecol* 22:880–888.
- 74 Sayers K, Norconk MA, Conklin-Brittain NL (2010) Optimal foraging on the roof of the world: Himalayan langurs and the classical prey model. *Am J Phys Anthropol* 141(3):337–357.
- 75 Levi T, Lu F, Tu DS, Mangel M (2011) The behaviour and diet breadth of central-place foragers: An application of human hunters and Neotropical game management. *Evol Ecol Res* 13:171–185.
- 76 Lupo KD, Fancher JM, Schmitt DN (2012) The taphonomy of resource intensification: Zooarchaeological implications of resource scarcity among Bofi and Aka forest foragers. *J Archaeol Method Theory* 20:420–447.
- 77 Dwairy M, Dowell AC, Stahl J-C (2011) The application of foraging theory to the information searching behaviour of general practitioners. *BMC Fam Pract* 12:90–98.
- 78 Robinson ME, McKillop HI (2013) Ancient Maya wood selection and forest exploitation: A view from the Paynes Creek salt works, Belize. *J Archaeol Sci* 10:3584–3595.
- 79 Flannery KV (1969) Origins and ecological effects of early domestication in Iran and the Near East. *The Domestication and Exploitation of Plants and Animals*, eds Ucko PJ, Dimbleby GW (Aldine, Chicago), pp 73–100.
- 80 Piperno DR (2006) The origins of plant cultivation and domestication in the Neotropics: A behavioral ecological perspective. *Behavioral Ecology and the Transition to Agriculture*, eds Kennett D, Winterhalder B (Univ of California Press, Berkeley, CA), pp 137–166.
- 81 Stiner MC, Munro ND, Surovell TA (2000) The tortoise and the hare: Small game use, the broad spectrum revolution, and Paleolithic demography. *Curr Anthropol* 41(1):39–79.
- 82 Stiner MC, Munro DN (2002) Approaches to prehistoric diet breadth, demography, and prey ranking systems in time and space. *J Archaeol Method Theory* 9:181–214.
- 83 Jones EL (2009) Climate change, patch choice, and intensification at Pont d’Ambon (Dordogne, France) during the Younger Dryas. *Quat Res* 72:371–376.
- 84 Munro ND (2009) Epipaleolithic subsistence intensification in the southern Levant: The faunal evidence. *Integrating Approaches to the Study of Paleolithic Subsistence*, eds Hublin J-J, Richards MJ (Springer, The Hague), pp 141–155.
- 85 Munro ND (2009) Integrating inter- and intra-site analyses of Epipaleolithic faunal assemblages from Israel. *Before Farming: Archaeol Anthropol Hunter-Gatherers*. 2009(1):4.
- 86 Stutz AJ, Munro ND, Bar-Oz G (2009) Increasing the resolution of the Broad Spectrum Revolution in the Southern Levantine Epipaleolithic (19–12 ka). *J Hum Evol* 56(3):294–306.
- 87 Starkovich BM, Stiner MC (2010) Upper Palaeolithic animal exploitation at Klissoura Cave 1 in southern Greece: Dietary trends and mammal taphonomy. *Eurasian Prehistory* 7:107–132.
- 88 Ugan A, Simms S (2012) On prey mobility, prey rank, and foraging goals. *Am Antiq* 77(1):179–185.
- 89 Mayr E (1961) Cause and effect in biology. *Science* 134(3489):1501–1506.
- 90 Tinbergen N (1963) On aims and methods of ethology. *Z Tierpsychol* 20:410–433.
- 91 West-Eberhard MJ (2003) *Developmental Plasticity and Evolution* (Oxford Univ Press, Oxford).
- 92 Laland KN, Sterelny K, Odling-Smee J, Hoppitt W, Uller T (2011) Cause and effect in biology revisited: Is Mayr’s proximate-ultimate dichotomy still useful? *Science* 334(6062):1512–1516.
- 93 Scott-Phillips TC, Dickens TE, West SA (2011) Evolutionary theory and the ultimate-proximate distinction in the human behavioral sciences. *Perspect Psychol Sci* 6:38–47.
- 94 Odling-Smee J, Laland KN, Feldman W (2003) *Niche Construction* (Princeton Univ Press, Princeton).
- 95 Odling-Smee J, Laland KN (2011) Ecological inheritance and cultural inheritance: What are they and how do they differ? *Biol Theory* 6(3):220–230.
- 96 Anderson MK (2005) *Tending the Wild: Native American knowledge and the management of California’s natural resources* (Univ of California Press, Berkeley, CA).
- 97 Blegie Bird R, Bird DW, Codding BF, Parker CH, Jones JH (2008) The “fire stick farming” hypothesis: Australian Aboriginal foraging strategies, biodiversity, and anthropogenic fire mosaics. *Proc Natl Acad Sci USA* 105(39):14796–14801.
- 98 Smith BD (2007) Behavior: The ultimate ecosystem engineers. *Science* 315(5820):1797–1798.
- 99 Anderson E (1952) *Plants, Man, and Life* (Univ of California Press, Berkeley, CA).
- 100 Anderson E (1956) Man as a maker of new plants and new plant communities. *Man’s Role in Changing the Face of the Earth*, ed Thomas WL (Univ of Chicago Press, Chicago), pp 763–777.
- 101 Lewis HT (1972) The role of fire in the domestication of plants and animals in Southwest Asia: A hypothesis. *Man (Lond)* 7(2):195–222.
- 102 Belovsky GE (1988) An optimal foraging-based model of hunter-gatherer population dynamics. *J Anthropol Archaeol* 7(4):329–372.
- 103 Winterhalder B (1986) Diet choice, risk, and food sharing in a stochastic environment. *J Anthropol Archaeol* 5:369–392.
- 104 Winterhalder B, et al. (1988) The populations ecology of Hunter-Gatherers and their prey. *J Anthropol Archaeol* 7:289–328.
- 105 Pyke GH, Pulliam HR, Charnov EL (1977) Optimal foraging: A selective review of theory and tests. *Q Rev Biol* 52:137–154.
- 106 Winterhalder B (1981) Optimal foraging strategies and hunter-gatherer research in anthropology: Theory and methods. *Hunter-Gatherer Foraging Strategies: Ethnographic and Archeological Analyses*, eds Winterhalder B, Smith EA (Univ of Chicago Press, Chicago), pp 13–35.
- 107 Winterhalder B, Goland C (1997) An evolutionary ecology perspective on diet choice, risk, and plant domestication. *People, Plants, and Landscapes: Studies in Paleoethnobotany*, ed Gremillion KJ (Univ of Alabama Press, Tuscaloosa, AL), pp 123–160.
- 108 Broughton JM, Cannon MD, Bartelink EJ (2010) Evolutionary ecology, resource depression, and niche construction theory: Applications to central California hunter-gatherers and Mimbres-Mogollon agriculturalists. *J Archaeol Method Theory* 17:371–421.
- 109 Bettinger RL (2006) Agriculture, archaeology, and human behavioral ecology. *Behavioral Ecology and the Transition to Agriculture*, eds Kennett DJ, Winterhalder B (Univ of California Press, Berkeley, CA), pp 304–322.
- 110 Richerson PJ, Boyd R, Bettinger RL (2001) Was agriculture impossible during the Pleistocene but mandatory during the Holocene? A climate change hypothesis. *Am Antiq* 66:387–412.
- 111 Coward F, Shennan S, Colledge S, Conolly J, Collard M (2008) The spread of Neolithic plant economies from the Near East to northwest Europe: A phylogenetic analysis. *J Archaeol Sci* 35:42–56.
- 112 Bettinger RL, Richerson PJ (1996) The state of evolutionary archaeology: Evolutionary correctness, or the search for common ground. *Darwinian Archaeologies*, ed Maschner HDG (Plenum, New York), pp 221–231.
- 113 Collard M, Buchanan B, Ruttle A, O’Brien MJ (2011) Niche construction and the toolkits of hunter-gatherers and food producers. *Biol Theory* 6:251–259.