

Niche Construction Theory and Archaeology

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Abstract Niche construction theory (NCT) is a relatively new development within evolutionary biology, but one that has important implications for many adjacent fields of research, including the human sciences. Here, we present a broad overview of NCT and discuss its application to archaeology. We begin by laying out the basic arguments of NCT, including a historical overview, focusing on how it affects understanding of human behavior and evolution. We then consider how NCT can be used to inform empirical research and how it might profitably be applied in archaeology, using as a case study the origins of agriculture. We suggest that the unrivaled potency of human niche construction, compared with that of other species, means that archaeologists need not be mere consumers of biological insights but can become important contributors to evolutionary theory.

Keywords Agriculture · Archaeology · Human evolution · Niche construction · Plant domestication

The Niche Construction Perspective within Evolutionary Biology

Niche construction theory (NCT) is a fledgling branch of evolutionary biology that places emphasis on the capacity of organisms to modify natural selection in their environment and thereby act as co-directors of their own, and other species', evolution. It is best regarded as an alternative means of thinking about evolutionary problems rather than as a discrete field of evolutionary enquiry. In the same way that advocates of the gene's-eye perspective (Williams 1966; Dawkins 1976) argued that

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their alternative means of conceptualizing evolutionary issues paid dividends relative to analysis at the individual level, so advocates of the niche construction perspective maintain there is considerable accuracy and utility in their alternative viewpoint (Odling-Smee *et al.* 2003; Laland and Sterelny 2006).

Niche construction is “the process whereby organisms, through their metabolism, their activities and their choices, modify their own and/or each other's niches” (Odling-Smee *et al.* 2003, p. 419). Examples of niche construction include animals manufacturing nests, burrows, webs, and pupal cases; plants changing levels of atmospheric gases and modifying nutrient cycles; fungi decomposing organic matter; and bacteria fixing nutrients (Wcislo 1989; Jones *et al.* 1994, 1997; Odling-Smee *et al.* 2003).

The niche construction perspective was first introduced to evolutionary biology through a series of seminal essays in the 1980s by Harvard evolutionary biologist Richard Lewontin (1982, 1983). Lewontin pointed out that contemporary evolutionary theory implicitly assumes that natural selection pressures in environments are decoupled from the adaptations of the organisms for which they select. Therefore, with some exceptions—for example, those that involve frequency-dependent selection or habitat selection—standard theory treats sources of natural selection in environments and adaptations in organisms as independent of each other or, as Lewontin (1983, p. 276) put it, “the environment ‘poses the problem’; the organisms ‘posit solutions,’ of which the best is finally ‘chosen.’” What this classical approach overlooks is that the selective environments of organisms are themselves partly built by the niche construction activities of organisms. To again quote Lewontin (1983, p. 280), “organisms do not adapt to their environments; they construct them out of the bits and pieces of the external world.” Some selection pressures are not independent of the activities of organisms. Instead, they must be regarded as participants in a system of feedbacks between natural selection pressures in environments and the characteristics of organisms. That organisms in general, and humans in particular, modify their environment is no more news for archaeologists than it is for biologists. However, the full ramifications of this platitude, in terms of various forms of feedback that stem from niche construction, are rarely fully appreciated.

Standard evolutionary theory treats niche construction as phenotypic, or extended phenotypic (Dawkins 1990), consequences of prior selection, not as a cause of evolutionary change. (An “extended phenotype” is an adaptation that is the product of genes expressed outside of the body of the organism that carries them—for example, a bird's nest or a spider's web.) As a result, there exists extensive theory within evolutionary biology and evolutionary ecology concerning how selection shapes the capacity of organisms to modify environmental states and construct artifacts, but little theory is concerned with how niche construction modifies natural selection (particularly at loci other than those expressed in the niche construction), nor has there been much consideration of the evolutionary ramifications of this capability.

For niche construction enthusiasts, the conventional perspective subtly downplays the active role that organisms play in the evolutionary process as co-causes and co-directors of their own evolution and that of other species. The conceptual leap that niche construction theorists embrace is to regard niche construction as an evolutionary process in its own right. In other words, niche construction is viewed

as an initiator of evolutionary change rather than merely the end product of earlier selection. Although this position remains controversial (Laland *et al.* 2005; Laland and Sterelny 2006), there is now extensive evidence that niche construction is evolutionarily consequential.

In recent years, NCT has gathered momentum, largely through the development of formal population genetics theory, which has demonstrated that niche construction strongly affects evolutionary outcomes (Odling-Smee 1988; Laland *et al.* 1996, 1999; Odling-Smee *et al.* 1996, 2003; Lewontin 2000; Oyama *et al.* 2001; Sterelny 2003, 2007; Boni and Feldman 2005; Donohue 2005; Lehmann 2008). Some organism-driven changes in environments persist as a legacy to modify selection on subsequent generations, which Odling-Smee (1988) called an “ecological inheritance.” Population-genetic models reveal that this ecological inheritance generates unusual evolutionary dynamics (Laland *et al.* 1996, 1999, 2000, 2001; Silver and Di Paolo 2006). Populations evolving in response to features of the environment modified by their ancestors exhibit momentum effects (continuing to evolve in the same direction after selection has stopped or reversed—a lag effect), inertia effects (no noticeable evolutionary response to selection for a number of generations—another kind of lag effect), and opposite and sudden catastrophic responses to selection. Niche-constructing traits can drive themselves to fixation by generating disequilibrium between niche-constructing alleles and alleles whose fitness depends on resources modified by niche construction (Silver and Di Paolo 2006). Costly niche-constructing traits can be favored because of the benefits of the niche construction that will accrue to distant descendants (Lehmann 2008); this is because evolutionary fitness ultimately depends not on number of offspring, or even grand-offspring, but on the long-term genetic legacy of alleles or genotypes.

Odling-Smee *et al.* (2003) authored the first book on the topic—*Niche Construction: The Neglected Process in Evolution*—which summarized the empirical and theoretical findings and presented methods for investigating niche construction. Numerous empirical studies followed (*e.g.*, Donohue 2005; Flack *et al.* 2006), and interest in the topic has blossomed into a multidisciplinary movement, involving evolutionary biologists, ecologists, psychologists, anthropologists, archaeologists, computer scientists, philosophers, and others.

NCT stresses that, in modifying their own world, organisms frequently modify the environments of other organisms that share those environments. The role of cyanobacteria in the creation of Earth's oxygen-rich atmosphere, the soil-perturbing activities of earthworms, and the dam building of beavers exemplify the huge range of temporal and spatial scales across which niche construction occurs. Such examples bring out the dependencies of co-evolution on nontrophic as well as trophic interactions. When beavers build dams, they affect considerably more than the probability that genes for dam building will spread. They also modify nutrient cycling and decomposition dynamics, modify the structure and dynamics of the riparian zone, influence the character of water and materials transported downstream, and ultimately influence plant and community composition and diversity (Naiman *et al.* 1988). In doing so, they indirectly modify the pattern and strength of selection acting on a host of beaver traits and similarly modify selection acting on thousands of other species (Odling-Smee *et al.* 2003). Niche construction is both an important source of co-evolutionary interactions and a major form of connectivity between biota.

A focus on organisms' modification of environments is also central to the concept of "ecosystem engineering," which was introduced to ecology by Jones *et al.* (1994, 1997). Here, "ecosystem engineering" and "niche construction" are considered synonyms, although the phrase "ecosystem engineering" is used mainly in ecology, whereas "niche construction" is the term adopted by evolutionary biologists. Jones *et al.* (1994) drew attention to a lack of ecological research effort dedicated to organisms that modulate the availability of resources and habitat to other species by causing physical state changes in biotic or abiotic materials. From an archaeological standpoint, one might argue that in part, this lack of effort reflects the misguided tendency of some ecologists to factor out humans rather than view their activities as embedded in ecosystems and therefore valid foci of research. However, Jones and his collaborators point out that many species of ecosystem engineers can regulate energy flows, mass flows, and trophic patterns in ecosystems to generate an "engineering web"—a mosaic of connectivity comprising the engineering interactions of diverse species, which regulates ecosystem functioning in conjunction with the well-studied webs of trophic interactions (Wilby 2002). Moreover, ecosystem engineers can control flows of energy and materials among trophically interconnected organisms without being part of those flows.

This connectivity that occurs through niche construction does not involve only biota. When niche-constructing organisms cause physical state changes in abiotic compartments, the compartments may become evolutionarily significant to other species, as they confer modified selection pressures to other populations (Odling-Smee *et al.* 2003). Two populations may be connected through one or more abiotic compartments, even without any direct contact between them (Jones *et al.* 1997; Odling-Smee *et al.* 2003). From the niche construction perspective, the connectivity in ecosystems is massively increased compared with, say, food webs.

This insight has important implications for understanding, managing, and conserving ecosystems. Satisfactory comprehension of the properties and dynamics of ecosystems requires recognizing that organisms do considerably more in ecosystems than compete with each other, eat, and be eaten (trophic interactions). Organisms also produce, modify, and destroy habitat and resources for other living creatures, in the process driving co-evolutionary dynamics. Such niche construction plays a key role in regulating hydrological, nutrient, and element (*e.g.*, carbon) cycling (Odling-Smee *et al.* 2003). As humans are enormously potent niche constructors—Smith (2007b, p. 188) refers to them as "the ultimate niche constructing species"—understanding how niche construction regulates ecosystem dynamics is central to understanding the impact of human populations on their environments—a topic we take up in a later section.

Categories of Niche Construction

Odling-Smee *et al.* (2003) introduce two binary categories of niche construction, which are relevant to our consideration of the application of NCT to archaeology (Table 1). First, they recognize two ways that organisms can change the selection pressures to which they are exposed: *perturbation* and *relocation*. Perturbation occurs if organisms actively modify one or more factors in their environments at

Table 1 Examples of the Four Categories of Niche Construction

	Perturbation	Relocation
Inceptive	Organisms initiate a change in their selective environment by physically modifying their surroundings, <i>e.g.</i> , emission of detritus	Organisms expose themselves to a novel selective environment by moving to or growing into a new place, <i>e.g.</i> , invasion of a new habitat
Counteractive	Organisms counteract a prior change in the environment by physically modifying their surroundings, <i>e.g.</i> , thermoregulation of nests	Organisms respond to a change in the environment by moving to or growing into a more suitable place, <i>e.g.</i> , seasonal migration

Niche construction may be inceptive or counteractive and may occur through perturbation of the environment or through relocation in space. Reproduced from Odling-Smee *et al.* (2003) Table 2.1

specified locations and times, by physically changing them. For example, organisms secrete chemicals, exploit resources, and construct artifacts. Relocation refers to cases in which organisms actively move in space, choosing not only the direction and/or the distance in space through which they travel but sometimes the time when they travel. In the process, relocating organisms expose themselves to alternative habitats, at different times, and thus to different environmental factors.

The second dichotomous category of niche construction focuses on whether organisms initiate or respond to a change in an environmental factor, such as a conventional resource or condition. Odling-Smee *et al.* (2003) describe as *inceptive* niche construction all cases in which organisms initiate changes in any factor, through either perturbation or relocation. Organisms express inceptive niche construction when by their activities they generate a change in the environment to which they are exposed. Conversely, if an environmental factor is already changing, or has changed, organisms may oppose or cancel out that change, a process labeled *counteractive* niche construction. They thereby restore a match between their previously evolved features and their environment's factors. Counteractive niche construction is therefore conservative or stabilizing, and it generally functions to protect organisms from shifts in factors away from states to which they have been adapted.

Human Niche Construction

From the above, it is apparent that niche construction is an extremely general process and that humans are far from alone in their capacity to modify the environment in significant ways. Nonetheless, human niche construction may be uniquely potent. In the last 100,000 years, humans have dispersed from East Africa around the globe and exhibited massive population growth. This success story would not have been possible without their ability to modify environments to compensate for different climatic regimes and other challenges—manufacturing clothes and shelters, controlling fire, devising agricultural practices, and domesticating livestock. The basis for human success as a species is the inordinately high capacity for learning that its members possess. The significance of acquired characters to evolutionary

processes becomes amplified with stable transgenerational culture (Laland and Brown 2006), creating what anthropologists and archaeologists refer to as “traditions”—patterned ways of doing things that exist in identifiable form over extended periods of time (e.g., Rouse 1939; Willey 1945). There is every reason to suspect that the ability to amass and pass on considerable bodies of information was extremely important to hominin evolution (Boyd and Richerson 1985; Richerson and Boyd 2005). It certainly has made humans effective niche constructors (Laland and Brown 2006).

The capacity for technology and culture is clearly a critical factor underlying the potency of human niche construction—the point Hardesty (1972) was making when he stated that culture is the human ecological niche. Agriculture, for example, was not independently invented by each farmer, nor is its presence an unlearned maturational outcome of human gene expression. The argument that human cultural niche construction has been a co-director of recent human evolution is essentially the conclusion reached by the geneticists analyzing the human genome, who observe that many genes subject to recent selective sweeps are responses to cultural activities (e.g., Voight *et al.* 2006; Wang *et al.* 2006). This perspective is supported by some well-researched cases of gene–culture co-evolution. For instance, there are several examples of culturally induced genetic responses to human agriculture (Odling-Smee *et al.* 2003), the best known being the co-evolution of the gene for lactose absorption and dairy farming (Durham 1991). There is now compelling theoretical and empirical evidence that dairy farming spread prior to the allele for lactose absorption, generating a selection pressure favoring this gene in some human pastoralist societies (Feldman and Cavalli-Sforza 1989; Holden and Mace 1997; Burger *et al.* 2007).

Another example is provided by a population of Kwa-speaking yam cultivators in West Africa (Durham 1991). These people cut clearings in forests to grow crops, with a cascade of consequences. The clearings increased the amount of standing water, which provided better breeding grounds for mosquitoes and increased the prevalence of malaria. This, in turn, modified natural selection pressures in favor of an increase in the frequency of the sickle-cell (*HbS*) allele because, in the heterozygous condition, the (*HbS*) allele confers protection against malaria. The fact that other Kwa speakers, whose agricultural practices are different, do not show the same increase in the (*HbS*) allele frequency supports the conclusion that cultural practices can drive genetic evolution (Durham 1991). It is not just yam cultivation that generates this pattern of selection: modern Asian tire manufacturing is having the same effect, with mosquitoes infesting pools of rainwater that collect in tires stored outside, and tire export contributing to the spread of malaria and dengue (Hawley *et al.* 1987).

These examples are, of course, very familiar to archaeologists, and one might ask what NCT brings to the discussion that is new here. The answer is the perspective, now well supported with hard data, that the lactose and sickle-cell examples, far from being special cases, are rather manifestations of a general pattern (Laland *et al.* 2010). Recent analyses of human genetic variation reveal that hundreds of genes have been subject to recent positive selection, often in response to human niche-constructing activities. The lactose absorption allele (*LCT*) is just one of several genes (e.g., *MAN2A1*, *SI*, *SLC27A4*, *PPARD*, and *SLC25A20*) now thought to have been selected over recent millennia in response to culturally generated changes in

diet. Another extremely compelling example of a human culture-initiated selective sweep concerns the evolution of the human amylase gene (Perry *et al.* 2007). Starch consumption is a feature of agricultural societies and hunter–gatherers in arid environments, whereas other hunter–gatherers and some pastoralists consume much less starch. This behavioral variation raises the possibility that different selective pressures have acted on amylase, the enzyme responsible for starch hydrolysis. Consistent with this hypothesis, Perry *et al.* found that copy number of the salivary amylase gene (*AMY1*) is positively correlated with salivary amylase protein level and that individuals from populations with high-starch diets have, on average, more *AMY1* copies than those with traditionally low-starch diets. Higher *AMY1* copy numbers and protein levels are thought to improve the digestion of starchy foods and may buffer against the fitness-reducing effects of intestinal disease.

More generally, the transition to novel food sources with the advent of agriculture and the colonization of new habitats seems to have been a major source of selection on human genes (Richards *et al.* 2003; Voight *et al.* 2006; Wang *et al.* 2006). Several genes related to the metabolism of protein, carbohydrates, lipids, and phosphates show signals of recent selection. There is also evidence for diet-related selection on the thickness of human teeth enamel (Kelley and Swanson 2008) and bitter-taste receptors (Soranzo *et al.* 2005), and the promoter regions of many nutrition-related genes have experienced positive selection during human evolution (Haygood *et al.* 2007).

The sickle-cell (*HbS*) allele is equally representative of (a) many human alleles expressed in immunity; (b) resistance to disease and pathogen response thought to have been favored by human agriculture, farming, domestication of animals, and aggregation; and (c) the subsequent exposure to new pathogens this human cultural niche construction brought about (*e.g.*, *CD58*, *APOBEC3F*, *CD72*, *FCRL2*, *TSLP*, *RAG1*, and *RAG2*; Laland *et al.* 2010). Malaria became a major health problem only after the development of farming—a human cultural niche-constructing practice—yet several additional genes appear to have been favored by selection because they provide resistance to malaria. These include *G6PD*, *TNFSF5*, and alleles coding for hemoglobin C and Duffy blood groups (Balter 2005; Wang *et al.* 2006). There is also evidence that genes have been selected because they confer resistance to other modern diseases, including AIDS, smallpox (*CCR5*), and hypertension (*AGT* and *CYP3A*; Balter 2005). In all these cases, human modifications of the environment triggered or modified selection on human genes. Moreover, human niche construction has likely affected evolutionary rates too, sometimes speeding them up and sometimes slowing them down (Hawks *et al.* 2007; Cochran and Harpending 2009; Laland *et al.* 2010).

One major difference between NCT and conventional evolutionary theory—of considerable salience in discussions of human evolution—is that niche construction provides a non-Lamarckian route by which acquired characteristics can influence the selection on genes. Whereas the information acquired by individuals through ontogenetic processes clearly cannot be directly (genetically) inherited, processes such as learning can nonetheless still be of considerable importance to subsequent generations because learned knowledge can guide niche construction in ways that modify natural selection acting on future generations. This route is considerably enhanced by social learning, which allows animals to learn from each other.

Hundreds of species of mammals, birds, and fishes are now known to learn socially (Zentall and Galef 1988; Heyes and Galef 1996), allowing novel learned traits to sweep through populations and exposing individuals to novel selection pressures. This process is further amplified with stable transgenerational culture, and it is now widely believed that such characters were probably important to hominin evolution (Cavalli-Sforza and Feldman 1981; Richerson and Boyd 2005).

Theoretical analyses exploring the evolutionary ramifications of human cultural niche construction show it to be potent. Laland *et al.* (2001) found that cultural niche construction could overwhelm, or reverse, natural selection, accelerate the rate at which a favored gene spreads, initiate novel evolutionary events, and trigger hominin speciation. They concluded that, because cultural processes typically operate faster than natural selection, cultural niche construction probably has more profound consequences than gene-based niche construction.

Gene–culture co-evolution may even be the dominant form of evolutionary adaptation for our species (Laland *et al.* 2010). Moreover, it also has driven co-evolutionary interactions with other species, including domesticated animals and plants, commensal species adapted to human-constructed environments (*e.g.*, rats, mice, and insects), and microbes (Boni and Feldman 2005; Smith 2007a, b). Previous studies of the ecological impact of niche construction reveal that organisms can transform ecosystems not just by outcompeting and directly consuming other species but also by constructing and destroying habitat and resources used by other species (Jones *et al.* 1994, 1997; Odling-Smee *et al.* 2003), a point germane to our own species. After all, there currently is great concern that human activities are precipitating a major global extinction (Wilson 1992), but few environmentalists believe that this tragedy is brought about exclusively through our predatory behavior. Siberian tigers, golden lion tamarins, checkerspot butterflies, and millions of other endangered species are vulnerable not primarily because we eat them or their predators but because of our habitat degradation, deforestation, industrial and urban development, agricultural practices, livestock grazing, pesticide use, and so forth—that is, our niche construction. Such activities destroy the (engineering) control webs that underlie ecosystems.

Niche Construction and Co-evolution

Such considerations naturally raise the question of in what way NCT differs from the conventional view of co-evolution (*e.g.*, Ehrlich and Raven 1964). It is true that in the ecology and evolution literature, there is a considerable body of formal theory that models aspects of niche construction and its consequences. Ecological models of competition through resource depletion and evolutionary models of habitat selection are two of the more obvious examples. In these and other bodies of theory (reviewed by Odling-Smee *et al.* 2003), there is recognition of the feedback between organismic activity and the environment. Some of this theory includes niche construction as a process in its own right, although this is rarely acknowledged in conceptual or verbal accounts. Yet, while the basic insight that feedback between niche-constructing organisms and their environments occurs, and that it can have profound effects on evolutionary dynamics, is hardly novel, it is often obscured in

the evolutionary biology literature as a whole. Ecologists and evolutionary biologists have occasionally included niche construction within the framework of standard evolutionary theory, but only on a piecemeal basis. While these models may provide a satisfactory theoretical foundation for other subjects, even collectively they do not constitute a comprehensive formal theory of niche construction, because some important features—for example, positive effects on environmental states—have largely been ignored.

This is the case with co-evolutionary theory. Models of the co-evolution of two or more species implicitly or explicitly take account of the fact that the niche construction of one population can affect the selection on another. This is another well-explored area of evolutionary biology and includes models of competitive, predator–prey, host–parasite, plant–herbivore, and mutualistic interactions (e.g., Futuyma and Slatkin 1983; Thompson 1994; Heesterbeek and Roberts 1995; Abrams and Matsuda 1996; Marrow *et al.* 1996; Gavrilets 1997). Organisms creating or transforming environmental states, in the process modifying selection acting on other organisms, can drive co-evolutionary dynamics too. In all such models, selection is frequency dependent, with the fitness of each genotype in one species depending on the allele, genotype, or individual frequencies in the other. Yet, such theory is hardly satisfactory from a niche construction perspective, given that it recognizes the consequences of niche-constructing activity for other species without formally acknowledging the organism as part cause of evolutionary change. The conventional solution describes niche-constructing activity as no more than the *product* of prior selection, with co-evolution characterized as reciprocal bouts of selection. The organism is not viewed as initiating evolutionary change; rather, selection on one species triggers reciprocal selection on the other. Accordingly, niche construction is no more recognized here than in single-species' evolution.

In contrast, NCT explicitly treats the intervening environmental modification as an evolutionary process. Certainly, that process of niche construction will frequently be strongly influenced by prior selection. However, niche construction is, at most, only partly determined by genes, and NCT places emphasis on the other environmental influences, and on other inherited information and materials, that shape the developing organism and fashion how it interacts with the world.

This is particularly relevant to human co-evolutionary dynamics. There are no genes for domesticating dogs, manufacturing cheese, or cultivating rice (using “genes for” in the sense of Williams (1966) and Dawkins (1976) to mean alleles specifically selected for that function), and these activities, while frequently adaptive (increasing fitness in the present), are not adaptations (traits directly fashioned by natural selection). If such niche-constructing activities have precipitated evolutionary responses in dogs, cattle, rice, or humans, then selection is the consequence and not the cause.

Nor if human activities have imposed selection on mice, houseflies, or mosquitoes is it because we are their competitors or predators, or even because we are linked in an elaborate food chain. Such co-evolutionary episodes are probably driven by nontrophic and indirect interactions between species—that is, by the engineering web (Jones *et al.* 1994) and not by the food web. Like those co-evolutionary episodes precipitated by acquired characters—through learning and culture—these indirect co-evolutionary events are not well described (and indeed are

virtually ignored) by current evolutionary theory. They do, however, resonate with archaeologists, as we discuss below.

The important point here is that theoretical frameworks channel thinking, encouraging researchers to embrace certain processes and explanations and to neglect others. NCT is heuristically valuable precisely because it draws our attention to a range of phenomena that are both important and easy to overlook using only standard perspectives (Laland and Sterelny 2006). Because it extends and builds on traditional dual inheritance (genetic and cultural) models of cultural evolution that have provided significant insights into human behavior (*e.g.*, Cavalli-Sforza and Feldman 1981; Boyd and Richerson 1985; Durham 1991), NCT is sometimes referred to as “triple-inheritance theory” (genetic, cultural, and ecological inheritance; *e.g.*, Odling-Smee *et al.* 1996, 2003; Laland *et al.* 1999, 2000, 2001; Day *et al.* 2003; Shennan 2006).

Empirical Methods for Studying Niche Construction

Odling-Smee *et al.* (2003, p. 282) acknowledge that “if niche construction is going to pay its way as a scientific construct it must stimulate useful empirical work.” Accordingly, they devoted three chapters of their monograph to cataloging empirical methods. Rather than detail such methods here, we refer the reader to that source and content ourselves with making three points.

First, NCT offers an alternative means of thinking about problems and, as a result, frequently brings with it a suite of novel hypotheses and explanations. This fertility is apparent in the numerous applications of NCT within countless disciplines. In essence, NCT is of value because it draws attention to the active agency of the organism as a source of ecological and evolutionary change. Accordingly, rather than slipping into the assumption that the external environment (*e.g.*, climate change) triggers an evolutionary or cultural response, NCT enthusiasts are from the outset inclined to consider those additional hypotheses stressing self-constructed (and other organism-constructed) conditions that instigate change. In this respect, NCT can be viewed as more in accord with the perspective of most archaeologists, who are highly attuned to the active agency of their subjects, than standard evolutionary theory (*e.g.*, Dobres 2000; Dobres and Robb 2000; VanPool and VanPool 2003).

Second, NCT offers a variety of methods for testing niche construction hypotheses (Odling-Smee *et al.* 2003). One of the more pertinent here is using the comparative method to detect the dependence of the evolution of recipient traits on the prior evolution of niche-constructing traits (see also Broughton *et al.*, this volume). In principle, for any clade of organisms, it should be possible to determine, using established comparative statistical methods (Harvey and Pagel 1991), those phenotypic characters (recipient traits) that might have been selected as a consequence of feedback from prior niche-constructing traits. Pertinent characters could be measured in closely related organisms that do and do not exhibit this niche construction, or in different populations of the same species. It would then be possible to use statistical methods to determine if the recipient character changes correlate with niche-constructing activity and whether the characters are derived. At

the very least, this would establish that the niche-constructing trait preceded the evolution of the recipient trait and may determine to what extent the niche-constructing trait is necessary for the evolution of the recipient trait. Such methods can also be used to determine whether changes in a selected recipient character correlate with a particular niche-constructing activity, whether the niche-constructing activity is typically ancestral to the recipient character, and whether the recipient character in question is derived. There should be a significant relationship between the pertinent environmental state and the recipient character only when the niche-constructing activity is also present. The same logic applies at the cultural level, and the same methods can be applied to hominins or to contemporary human populations, where they may shed light on the relationship between different kinds of cultural niche construction and their different consequences.

The methods can be applied even if one of the traits is gene-based in order to explore gene–culture co-evolution, using genetic signatures of cultural niche construction (see below). In addition, such methods can be deployed to test specific predictions. For instance, Laland *et al.* (2001) propose that patterns of response to selection may depend on the capacity for niche construction. Many counteractive niche-constructing behaviors regulate the environment in such a way as to buffer against particular natural selection pressures. As a consequence, potent niche constructors should be more resistant to genetic evolution in autonomously changing environments than less-able niche constructors. An example of the application of this reasoning is given in the next section.

Third, Odling-Smee *et al.* (2003) describe different types of feedback from cultural niche construction and suggest how each might generate a different detectable signature. They use this notion of signature to illustrate methods that can be employed to detect significant evolutionary ramifications of human cultural niche construction. Many such signatures are familiar to archaeologists—for example, fishhooks, harpoons, and nets are obviously signatures of fishing activity. However, signatures of niche construction also include genes that have been favored in populations as a result of selection modified by cultural practices. For example, the high frequency of the lactose absorption gene *LTP*, the hemoglobin *HbS* allele, and the *G6PD* gene in particular populations are all signatures of prior cultural niche-constructing activities, namely, dairy farming, yam cultivation, and fava cultivation, respectively (Odling-Smee *et al.* 2003). Many potential signature genes have recently been identified in analyses of the human genome, seemingly favored over recent millennia because of human cultural practices (Voight *et al.* 2006; Wang *et al.* 2006; Laland *et al.* 2010). The hemoglobin *HbS* and *G6PD* alleles are interesting because agricultural practices have intensified selection of them by inadvertently affecting the prevalence of malaria. More generally, from gene frequencies, we can draw inferences about ancestral human activities, given that human modifications of the environment triggered or modified selection on human genes.

Using Niche Construction within Archaeology

In considering how NCT might be applied within archaeology, we make a general point that is germane to the human sciences as a whole: Despite the

vibrancy of various subfields of evolution applied to human behavior and society, many social scientists look askance at evolutionary accounts of human behavior. They remain interested in human behavior, society, and culture but not in genes, genetic change, and gene's-eye-view reasoning. For many, adaptationist accounts of humanity, derived from standard evolutionary theory, for example, in evolutionary psychology, are regarded as simplified to the point of distortion. Social scientists typically view humans as active, constructive agents rather than as passive recipients of selection. We agree.

Niche construction advocates (*e.g.*, Odling-Smee *et al.* 2003; Laland *et al.* 2008) argue that, in part, this reflects a problem within evolutionary biology itself: Neo-Darwinism, for all its many virtues and despite its considerable successes, fails to recognize a fundamental cause of evolutionary change, “niche construction,” by which organisms modify environmental states, and consequently selection pressures, thereby acting as co-directors of their own and other species' evolution. Although evolutionary biologists, sociobiologists, and evolutionary psychologists are rarely genetic determinists, they consciously or unconsciously make the assumption that niche construction is fully explained by prior natural selection and therefore has no independent causal significance within evolutionary biology. This unidirectionality of cause and effect is well recognized by philosophers of biology; for instance, Harvard philosopher Peter Godfrey-Smith (1998) characterizes evolutionary biology as “externalist” rather than “interactionist.”

Some earlier arguments in evolutionary archaeology (*e.g.*, Dunnell 1980; O'Brien and Holland 1990, 1992) took a similar stance. It was the exclusion of human agency from the equation that led some archaeologists (*e.g.*, Watson 1986) to question the usefulness of evolutionary archaeology for answering nontrivial questions about the past, echoing concerns expressed by early advocates of niche construction (Lewontin 1982, 1983). The incorporation of niche construction as both a cause and a product of evolution potentially enhances the explanatory power of evolutionary theory for the social sciences and provides what ultimately will prove to be a more satisfactory evolutionary framework for understanding human behavior, more in accord with current thinking within archaeology (Shennan 2006).

A good general illustration of the potential of the niche construction framework to provide novel forms of inquiry related to human evolution concerns the spate of arguments explaining evolutionary and historical events with climate change (*e.g.*, Richerson *et al.* 2001; Burroughs 2005). Without denying that climate is a potent source of selection, we are concerned that such arguments frequently give little consideration to the alternative possibility of human-induced changes in environmental conditions. Granted, in recent history, climate change may have triggered overexploitation and degradation, prompting the development of new technologies (see Riel-Salvatore, this volume), but niche construction can be inceptive too. The development of new technology that allowed more efficient capture or processing of prey may have led to overexploitation of local resources. The development of new forms of travel, communication, and transportation of goods may have fostered intergroup interaction. Inceptive niche construction is a potent agent of change.

Although archaeologists are, of course, conscious of the fact that humans can cause changes in their environments, these remain underexplored, and the full

ramifications, including the triggering of recent evolutionary episodes in both humans and other species that inhabit our worlds, have only recently become clear (Laland *et al.* 2010). After all, if archaeologists from another planet visited in the future and endeavored to reconstruct the history of the extinct human race, would they conclude that climate change led to the invention of the motor car or of CO₂-emitting factories? NCT is of utility because it encourages us to think beyond climate, instability, and an external environment as causes of evolutionary events and to quantify and incorporate human activities as active variables in driving both environmental change and human evolution.

As a case study with which to illustrate such reasoning, we consider the rise of agriculture, which we define as the end mode of the plant domestication process. Considerable work within archaeology has focused on the origins of agriculture, particularly the “what, when, and where” questions (Smith 2007a, b). It is now well recognized that there were multiple origins, or “core areas,” of plant domestication—anywhere between seven and ten, depending on who is doing the counting (Smith 1998; Richerson *et al.* 2001; Zeder *et al.* 2006). This naturally raises the question as to what factors were central to its appearance. Classical arguments identify such factors as environmental change (*e.g.*, Childe 1936; Wright 1977), population growth/pressure (*e.g.*, Boserup 1965, 1981; Cohen 1977), a cultural/technological plateau being reached that made humans “ready” for domestication (*e.g.*, Braidwood 1960), and even the need to appease the gods after harvests of wild plants (*e.g.*, Heiser 1990). Barlow’s (2002) model of prehistoric agricultural production concluded that it is likely to be economical to practice intensive agriculture only when rates of encounter with high return wild resources are low. Yet, Smith (2007b, p. 196) has recently noted a frequent “rich resource zone” context for domestication of plants and animals worldwide.

On the surface, particularly from a conventional perspective, such *prima facie* conflicting conclusions are confusing, given that researchers have been tempted to assume that some external resource or condition favors domestication (Smith 2007a, b). However, the empirical pattern is messy, and many of the data do not fit with the theoretical expectation. There is an alternative, however. Instead of searching for a prime mover for plant domestication, we can focus attention, at least initially, on the co-evolutionary interactions that exist between humans and plants (*e.g.*, Rindos 1980, 1984; O’Brien 1987; O’Brien and Wilson 1988). More specifically, we can treat plant domestication by humans as a special case or as a subset of all cases of co-evolved mutualism between animals and plants. Animal and plant populations co-evolve as selection occurs for those phenotypic variants that increase the fitness of both populations.

What is different here is that natural selection and cultural selection are both involved when the animal population is human. Whereas, as noted above, there has been human genetic change in response to changes in diet precipitated by human agricultural practices, the co-evolutionary dynamic is not well captured by standard evolutionary theory because the cultural processes that underlie domestication are not viewed as co-evolutionary. Rather, such activities are portrayed as background conditions to evolutionary episodes in the domesticates. In contrast, NCT recognizes such practices to be examples of cultural niche construction and portrays them as genuinely co-evolutionarily causal, both through their triggering evolutionary

episodes in the domesticates and because of the feedback to human genetic evolution. Cultural niche-constructing processes that contribute to plant domestication include selective collecting of reproductive propagules; transporting and storing of propagules; firing of grasslands, either intentionally or accidentally; cutting of trees; incidental tilling; and creating organically rich dump heaps, all of which are potent forms of niche construction.

Plants that are involved may undergo a series of phenotypic changes such as a general increase in size, an increase in the size of propagules, loss of delayed seed germination, simultaneous ripening of the seed crop, and so on. These changes occur as interaction with human agents increases the fitness of the plant community, which, in turn, increases the yield of the plant community. Increasing yield in turn generates selection favoring those cultural traits that maintain or increase productivity of the plants. This reinforcing mutualistic relation between plant and human populations is one process by which plant domestication, and human co-adaptation, evolves. More generally, NCT offers archaeology, and the human sciences in general, an evolutionary framework devoid of a single Aristotelian “prime mover.”

As important as co-evolutionary relationships are, mutualism is, as we noted earlier, only the beginning of the story. For one thing, it lacks resolution for specific geographic areas (Flannery 1986), and it says little about why some plant-using groups “crossed the Rubicon into systematic agriculture” (Bellwood 2005, p. 25), which brought with it high labor costs, high rates of failure and, in some cases, no clear economic incentive. There is a world of difference between what Rindos (1980, 1984) refers to as “incidental” and “specialized” domestication and agricultural domestication. All hunter–gatherers modify their environments to some degree, but few ever become agriculturists. Perhaps, on occasion, some of them kept a few domesticated animals or tended small gardens, but they certainly were not agriculturists. What conditions, then, led to agriculture?

Here is where a niche construction perspective begins to pay dividends, as noted by Bleed (2006) and Smith (2007a, b), by providing a biologically and culturally informed, yet general, evolutionary framework suited to the kind of cost–benefit analyses carried out by archaeologists. When animals engage in niche construction, they do not just build structures, they regulate them to damp out variability in environmental conditions (counteractive niche construction), as documented extensively by Odling-Smee *et al.* (2003), with the result that niche construction can preserve the adaptiveness of behavior. Although humans' ability to engage in counteractive niche construction is massively amplified by their capacity for culture, it is an extremely general phenomenon. Like the acorn-storing squirrel or the wasp that cools her nest with droplets of water, our ancestors ensured the availability of food by tracking game and storing food, and they controlled temperature by manufacturing clothes and building fires and shelters. Such niche construction may change environments, but it actually functions to negate a modified or fluctuating selection pressure.

With respect to the origins of agriculture, the challenge for our ancestors was how best to damp out variability in the availability of food, such that they could survive in a variable and changing world. Here, we note that squirrels do not store acorns in the spring—or at least, store far fewer than in the autumn—

because it would be an unnecessary waste of energy. Similarly, we would not expect humans to engage in potentially intensive forms of food production if alternatives, in the form of readily caught or gathered wild food, are freely available. There is nothing particularly perceptive about this observation; clearly, many other people share this intuition (e.g., Reed 1977). Accordingly, the conclusions of Barlow (2002) analysis are probably a manifestation of a more general rule, along the lines of *engage in costly niche construction only when you need to*. Exactly the same logic applies in other domains. A recent evolutionary ecology model of a plant–soil–nutrient ecosystem in which plants were able to expand their range by manufacturing soil nutrients found that investing in this form of niche construction paid off only in comparatively poor soils, resulting in plants partially regulating soil–nutrient content (Kylafis and Loreau 2008).

Assuming an incipient knowledge base for domestication is present and (in the case of domesticated plants) the soil is sufficiently fertile to grow crops, agriculture should evolve when the availability or productivity of wild resources is low. However, it does not follow from this that agriculture would never be expected to occur in a rich environment. There needs to be only one key limiting resource to undermine bounteous other commodities and render investing in resource production potentially economical. More to the point here, in a rich environment, we might well expect human population growth, frequently followed by resource depression, particularly given the potency of human exploitation of the natural world, raising the economic value of investment in agriculture. Environments are not fixed as rich or poor; they are dynamic variables, vulnerable to change as a result of the activity of potent niche constructors. Of course, it is easy for us to tell such stories, but this reasoning leads to testable hypotheses—for instance, where agriculture originates in otherwise rich zones, we should witness signs of population growth and resource depression, but not where it originates in poor zones. Such hypotheses could be tested statistically, using the methods described above.

Another potential means of cashing in on NCT logic is by focusing on the two alternative forms of niche construction: perturbation and relocation. Such consideration could also be used as a vehicle to explore why populations didn't domesticate plants (e.g., Pryor 1986), or at least didn't do it intensively. For populations that are constantly on the move (that is, “relocators”), there are severe constraints on what species, if any, can be domesticated (Bleed, this volume). Conversely, sedentary existence, which demands considerable “perturbation,” also imposes constraints on what species can be domesticated. In principle, which species of domesticates will and will not be found should be to some extent predictable, given knowledge of the relocatory or perturbatory lifestyle of the population (O'Brien and Wilson 1988). Again, there would be opportunities to test such hypotheses statistically.

Such reasoning leads to further predictions regarding colonization, based on Laland *et al.* (2001). As others have noted, niche construction could affect patterns of movement through resource depression, thereby influencing human population's rate of colonization (Cannon 2000; Broughton 2002; Broughton *et al.*, this volume). Drawing on the logic spelled out in the preceding section, other factors being equal, the greater the sophistication of a population's niche construction, the faster one might expect the colonization to occur. Humans should colonize faster

than other mammals. More culturally sophisticated hominins should colonize faster than less culturally sophisticated hominins. Were such patterns to be confirmed, it might be possible to reverse this inference and to draw conclusions about the potency of a population's niche construction on the basis of its rate of colonization.

Concluding Remarks

Much though we would like to see archaeologists using niche construction, we would not like this to be an alternative form of “just-so” evolutionary storytelling, nor would we feel comfortable if NCT were so open and vague that it could explain any conceivable dataset. To be useful, it must encourage rigorous science. What is it, then, that NCT has to offer? First, it offers a broad, biologically and culturally informed conceptual framework suited to the human sciences—one that recognizes the active agency of humans as part causes of their own development, history, and evolution. Second, it recognizes niche construction as an evolutionary process and ecological inheritance as a second general legacy that organisms inherit from their ancestors, thereby providing researchers with additional explanatory mechanisms. Such mechanisms are particularly relevant to archaeologists, given that human niche construction is frequently a manifestation of acquired characters and human ecological inheritance includes a rich material culture. There is little opportunity to recognize these facts, nor dwell on their significance, using standard evolutionary theory. Third, the niche construction perspective offers a new, highly fertile way of thinking about problems and brings with it a suite of novel hypotheses, both directly from an emphasis on the agency of the organism and indirectly by suggesting general patterns and rules. Finally, the niche construction perspective also brings with it a suite of novel methods, some of which are described above.

As of yet, the developing interest of archaeologists in niche construction may seem akin to a tiny ripple within the field of archaeology as a whole. However, enthusiasts can take encouragement from the knowledge that they are part of a much bigger, multidisciplinary initiative that includes social science fields such as philosophy (*e.g.*, Sterelny 2003; Bardone and Magnani 2007; Barker 2008), primatology (*e.g.*, Fragaszy and Visalberghi 2001; Fragaszy and Perry 2003; Flack *et al.* 2006; Iriki and Sakura 2008), psychology (*e.g.*, Mameli 2001; Mesoudi 2008), evolutionary anthropology (*e.g.*, Laland and Brown 2006) and demography (*e.g.*, Ihara and Feldman 2004; Kendal *et al.* 2005; Borenstein *et al.* 2006). In any one discipline, the impact of NCT may still yet be modest, but across them collectively, it is starting to become a powerful force for change. Archaeology, because of its ability to track thousands upon thousands of years of human niche construction, is well suited to be a major contributor to NCT. The great evolutionary ecologist Robert May said recently in a talk, “all good ideas in science start off as heresy and end up as dogma.” There may be some way to go before niche construction becomes dogma, but at least it is no longer heresy.

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