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Genes, Culture, and Agriculture

An Example of Human Niche Construction

by Michael J. O'Brien and Kevin N. Laland

Theory and empirical data from a variety of disciplines strongly imply that recent human history involves extensive gene-culture coevolution, much of it as a direct result of human agricultural practices. Here we draw on niche-construction theory (NCT) and gene-culture coevolutionary theory (GCT) to propose a broad theoretical framework (NCT-GCT) with which archaeologists and anthropologists can explore coevolutionary dynamics. Humans are enormously potent niche constructors, and understanding how niche construction regulates ecosystem dynamics is central to understanding the impact of human populations on their ecological and developmental environments. We use as primary examples the evolution of dairying by Neolithic groups in Europe and Africa and the rise of the "sickle-cell allele" among certain agricultural groups in West Africa and suggest that these examples are broadly representative of much of human recent history. Although the core aspects of these case studies are familiar, we lay out the examples with a specific NCT-GCT focus, which allows us to highlight how archaeology, when coupled with genetic research, can play an important role in better understanding human history. Finally, we suggest that the NCT-GCT perspective is likely to be of widespread general utility because it inherently promotes consideratiwon of the active agency of humans, and other organisms, in modifying their ecological and developmental niches and naturally draws attention to the various forms of feedback that flow from human activities at multiple levels, in multiple populations, and across multiple species.

Genes, Niches, and Agriculture

Perhaps no topic has received more attention in anthropology than the origins of agriculture—what Kareiva et al. (2007:1866) single out as perhaps "the single most important feature of the human domination of our planet" and Bleed (2006:8) calls "one of anthropology's most enduring challenges." With respect to the "what, when, and where" questions (B. D. Smith 2007*b*) of agriculture, it is now recognized that there were multiple core areas of plant domestication—anywhere between seven and 10, depending on who is doing the counting (e.g., B. D. Smith 1998; Vavilov 1992; Zeder et al. 2006). Agriculture also includes the domestication of animals for any number of purposes: as sources of food, especially meat and milk; as sources of products such as hides and wool; and for the protection, work, and even companionship they offer (Shipman 2010). Animals, like plants, exhibit highly localized areas of domestication (Zeder et al. 2006).

The logistical questions of what, when, and where lead to more complex questions concerning the appearance of agriculture, including why people began to domesticate plants and animals in the first place (O'Brien and Wilson 1988; Richerson, Boyd, and Bettinger 2001; Rindos 1984; Rowley-Conwy and Layton 2011; Zeder 2012). How did they cope with the unintended by-products of entering the agricultural niche, including high labor costs, high rates of failure, in some cases no clear economic incentive, and above all, more than occasional ill effects on health? Are these effects strictly phenotypic, meaning that they can be reversed through such things as dietary change, or are some of them genetic, meaning that selection, through agriculture, has reached beyond the phenotype to modify selection and leave its mark on the human genome? We agree with Zeder (2006*b*) that the history of domestication and agricultural origins comprises complex regional puzzles shaped in unique ways by dynamic macro- and microforces, including climate change, opportunities, and constraints at the sociopolitical level, resource availability, and population levels.

Our approach to handling these factors is based in niche-construction theory (NCT), a young branch of evolutionary biology that places emphasis on the capacity of organisms to modify natural selection in their environment and thereby act as codirectors of their own evolution as well as that of others. Although it had its origin in population genetics, NCT has become a multidisciplinary movement, involving evolutionary biologists, ecologists, psychologists, anthropologists,

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archaeologists, computer scientists, philosophers, and others (Kendal, Tehrani, and Odling-Smee 2011). Our approach also incorporates gene-culture coevolutionary theory (GCT), which explores how cultural and genetic processes interact over evolutionary time. Anthropologists have long known the power that culture exerts in shaping the human condition, but it is becoming increasingly clear that the interactions of genes and culture—literally, their coevolution—offer a faster and stronger mode of human evolution than either by itself (Ehrlich 2000; Ihara 2011; Laland 2008; Laland, Odling-Smee, and Myles 2010; Rendell, Fogarty, and Laland 2011; Richerson and Boyd 2005; Richerson, Boyd, and Henrich 2010).

In our view, nowhere has gene-culture coevolution happened faster than within agricultural societies. We propose that the NCT-GCT approach to the evolution and development of agriculture provides numerous opportunities to link the findings of human genetics with those of anthropologists and archaeologists and to generate novel hypotheses about human evolution (Gerbault et al. 2011; Itan et al. 2009; Laland and O'Brien 2010; Laland, Odling-Smee, and Myles 2010; Richerson, Boyd, and Henrich 2010). We begin with a discussion of NCT and how it can be used to structure empirical research in anthropology and archaeology. As humans are enormously potent niche constructors, understanding how niche construction regulates ecosystem dynamics is central to understanding the impact of human populations on their environments. We then briefly discuss GCT, outlining some of the tenets that guide its application, before considering how NCT and GCT can be used to better understand human behavior and evolution in the agricultural niche. We use as primary examples the evolution of dairying by Neolithic groups in Europe and Africa and the rise of the (*HbS*) allele—the so-called sickle-cell allele—among certain agricultural groups in West Africa. These examples will be familiar to many researchers, but here we lay them out in detail with a specific NCT-GCT focus. We argue that the case studies are, in fact, broadly representative of much of human recent history and that the NCT-GCT perspective is likely to be of widespread general utility in analyzing key aspects of that history. Finally, we consider some of the results of agricultural niche construction that are mainstream components of the modern human condition.

Niche Construction

The ecological niche concept was one of the significant developments in twentieth-century biology (Chase and Leibold 2003). In comparison to earlier uses, "the niche" is no longer viewed as a preset recess in the environment but rather as a relativistic concept, defined in part by the organism at its center. The modern niche concept is associated with a species, rather than a place, and specifies a "multidimensional hyperspace" of environmental factors acting on the organism (Hutchinson 1957). This is explicit recognition of the fact that organisms specify which environmental factors are significant components of their world. Organisms do more than passively make their living in that hyperspace. They modify their niches, and/or those of other organisms, through their metabolism, activities, and choices (Laland et al. 2011; Lewontin 1983; Odling-Smee, Laland, and Feldman 2003). Examples of niche construction include animals manufacturing nests, burrows, and webs and provisioning those sites for their offspring; plants changing levels of atmospheric gases and modifying nutrient cycles; fungi decomposing and/or storing organic matter; and bacteria fixing nutrients.

Ecologists and evolutionary biologists have long recognized the complex interplay of animal behavior and the physical environment, with Mayr (1973:388) claiming that behavior is "perhaps the strongest selection pressure operating in the animal kingdom." Despite this recognition, it is difficult to escape the feeling that standard evolutionary theory treats the interplay as unidirectional, where "adaptation is always asymmetrical; organisms adapt to their environment, never vice versa" (Williams 1992:484). Thus, with some exceptions, standard theory holds that "the environment 'poses the problem'; the organisms 'posit solutions,' of which the best is finally 'chosen'" (Lewontin 1983:276). This standard theory is fine as far as it goes, but it fails to emphasize the fact that the selective environments of organisms are themselves partially built by the niche-construction activities of organisms. Thus, "organisms do not adapt to their environments; they construct them out of the bits and pieces of the external world" (Lewontin 1983:280). That organisms in general, and humans in particular, modify their environment is no more news for anthropologists than it is for biologists, but 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 typically treats niche construction as phenotypic, or extended phenotypic (Dawkins 1982), 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, a spider's web, or a caddis fly larvae's house (Dawkins 1982). 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 there is little theory concerned with how niche construction feeds back subsequently to modify natural selection, particularly selection acting at loci other than those expressed in the niche construction.

In archaeology, the notion of the extended phenotype has been applied to features such as ceramic vessels, stone tools, and wattle-and-daub houses (O'Brien and Holland 1995), but strictly speaking, such artifacts are not true extended phenotypes, given that they are not biological adaptations (O'Brien and Holland 1992). To the extent that such artifacts can be characterized as functional products of a selective process, it is cultural selection, not natural selection, that is responsible. This statement, however, overlooks the feedback effects of human artifacts on natural selection (Odling-Smee 2007, 2010). One such feedback effect, for example, is our ability to control temperature by manufacturing clothes and building shelters, which has damped selection favoring anatomical and physiological responses to temperature extremes and fluctuations and allowed us to inhabit colder areas of the world (Laland, Kendal, and Brown 2007). More significant to our discussion here, the crops and animals that humans domesticate have substantially modified selection on alleles expressed in the ability of humans to process novel diets and to resist inadvertently produced disease. Nor is this feedback from cultural processes restricted to the genetic level, given that pots, houses, crops, and myriad other cultural products also transform the human developmental niche (Sterelny 2009, 2011), altering learning environments and shaping local traditions.

An important insight from NCT is that acquired characters play an evolutionary role through transforming selective environments. For example, mathematical models suggest that niche construction resulting from human cultural processes is likely to be even more potent than gene-based niche construction, and they establish that cultural niche construction could plausibly modify selection on human genes and drive evolutionary events (Laland, Odling-Smee, and Feldman 2001; Rendell, Fogarty, and Laland 2011). The relative potency of cultural niche construction stems from the capacity for rapid rates of change through cultural transmission, a point to which we return below. There is now little doubt that human cultural niche construction has codirected human evolution (Laland, Odling-Smee, and Myles 2010). Over the past 50,000 years, humans have spread from Africa around the globe, experienced an ice age, witnessed rapid increases in population densities, domesticated hundreds of species of plants and animals, and, by keeping animals, experienced a new proximity to animal pathogens (Stringer and Andrews 2005). Each of these events represents a major transformation in human selection pressures, recognized through substantive genetic change in human populations (Laland, Odling-Smee, and Myles 2010), and virtually all have been self-imposed.

Another key concept within NCT is that some organism-driven changes in environments persist as a legacy to modify selection on subsequent generations—referred to as "ecological inheritance" (Odling-Smee 1988) or "ontogenetic inheritance" (West, King, and Arberg 1988). Ecological inheritance does not depend on the presence of environmental "replicators" but merely on intergenerational persistence (often through repeated acts of construction) of whatever physical—or, in the case of humans, cultural—changes are caused by ancestral organisms in the local selective environments of their descendants (Odling-Smee 2010). Thus, ecological inheritance more closely resembles the inheritance of land or other property than it does the inheritance of genes (Laland 2004; Shennan 2011). Population-genetic models demonstrate that this ecological inheritance can generate unusual evolutionary dynamics (Borenstein, Kendal, and Feldman 2006; Ihara and Feldman 2004; Laland, Odling-Smee, and Feldman 2000, 2001; Silver and Di Paolo 2006). Importantly, costly niche-constructing traits can be favored because of the benefits of the niche construction that will accrue to distant descendants (Lehmann 2008). Thus, evolutionary fitness ultimately depends not on the number of offspring, or even of grand-offspring, but on the long-term genetic legacy of alleles or genotypes within a population.

Niche-constructing traits can drive themselves to fixation by generating statistical associations between niche-constructing alleles and those whose fitness depends on resources modified by niche construction. Of particular significance here is the observation, from related theoretical analyses, that the same runaway process can occur even if the niche-constructing trait is a cultural practice, such as the planting of a crop (Rendell, Fogarty, and Laland 2011). Here, costly cultural practices propagate themselves through inadvertently generating selection for local genotypes with which they are statistically associated and subsequently hitchhiking to high prevalence in the process.

A focus on organisms' modification of environments is also central to the concept of "ecosystem engineering" (Jones, Lawton, and Shachak 1994). 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 certainly is not news to anthropologists, who have long had an ecological perspective when it comes to humans and their interactions with natural and cultural environments (e.g., Steward 1955), and, with global warming and the like taking center stage today, we seriously doubt that it's news to anyone else. Nonetheless, academicians and politicians alike tend to overlook both the role that engineering control webs play in affecting the stability and productivity of ecosystems and the consequences of human activities that destroy those webs of connectivity.

How does NCT differ from the conventional view of coevolution, which in standard form models aspects of niche construction and its consequences? Models of the coevolution of two or more species implicitly or explicitly take account of the fact that niche-constructing activities of one population can affect selection on another. 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. In contrast, NCT treats environmental modification as an evolutionary process. Certainly niche construction is frequently influenced by prior selection, but it is, at most, only partly determined by genes. NCT places emphasis on environmental influences and on other inherited information and materials that together shape the developing organism and fashion how it interacts with the world. This is particularly relevant to human coevolutionary dynamics. There are no genes for domesticating dogs, manufacturing cheese, or cultivating cassava (using "genes for" in the sense of Williams [1966] 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.

Human activities have imposed selection on mice, houseflies, or mosquitoes, but it is not because we are their competitors or predators, or even because we are linked in an elaborate food chain. Such coevolutionary episodes are probably driven by nontrophic and indirect interactions between species—that is, by the engineering web and not by the food web. Like those coevolutionary episodes precipitated by acquired characters—through learning and culture—these indirect coevolutionary events are not well described and indeed are virtually ignored by current evolutionary theory. They do, however, resonate with anthropologists, as we discuss below. The important general point here is that theoretical frameworks channel thinking, encouraging researchers to embrace certain processes and explanations and to neglect others (Laland et al. 2011). 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 (Kendal, Tehrani, and Odling-Smee 2011; Laland and Sterelny 2006).

Gene-Culture Coevolution

Gene-culture coevolution is a branch of theoretical population genetics that incorporates cultural traits into models of the transmission of genes from one generation to the next (Boyd and Richerson 1985; Cavalli-Sforza and Feldman 1981; Feldman and Laland 1996; Laland, Odling-Smee, and Myles 2010; Richerson and Boyd 2005; Richerson, Boyd, and Henrich 2010). The two inheritance systems cannot always be treated independently because (*a*) what an individual learns may depend on his or her genotype expressed throughout development and (*b*) selection acting on the genetic system may be generated or modified by the spread of a cultural trait. Anthropologists rarely consider that an individual's genotype may affect which cultural traits he or she acquires, but this should not be regarded as contentious, particularly with regard to agriculture, food production, and dietary habits. Below we discuss several examples, from consuming dairy products and starchy food to drinking alcohol, where there is strong empirical evidence that genotype affects acquired behavior. "Culture" is treated as information—for example, knowledge, beliefs, and skills—that is capable of affecting the behavior of individuals and which they acquire from other individuals through any of a number of social-learning pathways, including teaching and imitation (Richerson and Boyd 2005).

Gene-culture theorists model cultural transmission as a Darwinian process in which there is selective retention of favorable cultural variants, with concomitant effects on biological fitness, recognizing that other, nonselective processes such as mutation (invention, innovation), spread (diffusion), and drift (random change) play significant roles as well (Bentley, Hahn, and Shennan 2004; Shennan 2002). Other animals exhibit social learning, but it is the fact that human culture evolves quickly and is cumulative (Enquist, Ghirlanda, and Eriksson 2011) that makes it an exceptional case. By this we mean that one generation does things in a certain way, and the next generation, instead of starting from scratch, does them in more or less the same way, except that perhaps it adds a modification or improvement. The succeeding generation then learns the modified version, which then persists across generations until further changes are made (Tennie, Call, and Tomasello 2009). Human cultural transmission is thus characterized by the so-called ratchet effect, in which modifications and improvements stay in the population until further changes ratchet things up again (Tomasello, Kruger, and Ratner 1993), although there is nothing inevitable about progress and no guarantee that any "improvements" will be fitness enhancing.

As we discuss in the next section, culturally derived selection pressures can be stronger than noncultural ones. There are at least two reasons for this. First, there is highly reliable transmission of cultural information between individuals. Although reliability differs among kinds of traits, culturally modified selective environments can produce unusually strong natural selection that is directionally consistent over time (Bersaglieri et al. 2004). Second, cultural innovations typically spread more quickly than genetic mutations because social learning usually operates at a much faster rate than does biological evolution (Feldman and Laland 1996). If cultural practices modify selection on human genes, the more individuals exhibiting a trait, the greater the intensity of selection will be on a gene (Laland, Odling-Smee, and Myles 2010). The rapid spread of a particular cultural practice often leads to maximum intensity of selection on the advantageous genetic variant or variants. Gene-culture coevolutionary models repeatedly demonstrate more rapid responses to selection than conventional population-genetic models. This helps explain the argument that culture has accelerated human evolution (Hawks et al. 2007), although a number of other factors undoubtedly played significant roles, including the larger populations that have been facilitated by agriculture (Cochran and Harpending 2009). Moreover, under different circumstances, culture can also slow down genetic change (Feldman and Laland 1996).

Those who study gene-culture interactions are not trying to model how entire cultures change over time but rather to explore some of the general properties of gene-culture coevolution and to predict patterns of change in certain specific traits (Laland and Brown 2006). Examples include investigations of the evolution of altruism and cooperation (Boyd and Richerson 1985; Gintis 2003), the coevolution of female-biased infanticide and sex-ratio-distorter genes (Kumm, Laland, and Feldman 1994), and the evolution of handedness (Laland 2008). The study of gene-culture coevolution has associated with it a formal discipline and a progressive theoretical research program, and we would be among the first to admit that formal gene-culture models are technical and mathematical and often difficult to appreciate. Our concern here, however, is not with mathematical modeling but rather with the degree of fit between expectations derived from GCT and select aspects of the empirical record as they pertain to the agricultural niche. Moreover, it is widely recognized among its practitioners that an empirical science of gene-culture coevolution is desirable (Laland and Brown 2011; Richerson and Boyd 2005), to which even those with little knowledge of mathematics can contribute.

Genes and Culture in the Agricultural Niche

Not all NCT involves cultural niche construction, while very little GCT has explicitly modeled constructed environmental resources. Hence, a suitable theoretical framework for our purposes necessarily draws on both bodies of theory. Because it extends and builds on traditional dual-inheritance (genetic and cultural) models of cultural evolution that have provided significant insights into human behavior, NCT is sometimes referred to as "triple-inheritance theory" (genetic, cultural, and ecological inheritance; e.g., Day et al. 2003; Odling-Smee, Laland, and Feldman 2003), although Odling-Smee (2007, 2010) has recently argued that this terminology is unnecessary. Regardless, we would argue that attempts to understand how genes and culture coevolve frequently benefit from the concept of niche construction, with its emphasis on environmental impacts and their feedbacks. This would appear especially true with respect to agriculture, given its roots in a uniquely potent and cumulative knowledge base (Bleed 2006; Laland and O'Brien 2010; Rowley-Conwy and Layton 2011; B. D. Smith 2007*a*, 2009, 2011*b*). To niche-construction theorists, there is an expectation that gene-culture coevolution has been a general feature of human evolution, but there is every reason to assume that the last 10,000–12,000 years—the time period of visible signs of ever more sophisticated interactions with plants and animals—witnessed unparalleled niche construction and may have driven equally unparalleled selection on human genes (Laland, Odling-Smee, and Myles 2010).

Among the most familiar examples of agricultural niche construction are the geographic distribution of two alleles—one providing an ability to tolerate lactose and the other providing protection against the deadly disease malaria. In the following discussion, we treat them in detail, moving back and forth between the two in order to emphasize various aspects of gene-culture interaction and to show how that interaction is key to human niche construction and, more generally, to our understanding of agriculture. Central to our discussion are the origin and spread of the two traits and the effects that the spread had on the evolution of specific agricultural niches outside their centers of origin.

Most Westerners are surprised to learn that the majority of adults in the world are physically incapable of ingesting fresh, unprocessed milk without getting sick. Even more surprising is the fact that it was not until 1965 that biomedical researchers recognized that systematic variation exists in milk-digestion physiology (Cuatrecasas, Lockwood, and Caldwell 1965). We commonly think of milk as a superfood that promotes strong bones and offers numerous other benefits, including "strong families," as ads from the California Milk Processor Board proclaim. When celebrities such as Sheryl Crow, Brooke Shields, and Beyoncé sport milk mustaches and pose the question "Got milk?" we naturally answer yes. But for the vast majority of the world's adult population, the answer is no. Milk is a "nutritional bonanza" (Wooding 2007: 8) of fat, proteins, carbohydrates, vitamins, calcium, and even water, but only if it can be digested. Milk contains the disaccharide sugar lactose, which is the primary osmotic regulator of milk synthesis and as such is typically the least variable macrocomponent of milk. In humans, lactose comprises about 7% of the milk yield on a mass basis and in goats and cattle a little less than 5%. In modern U.S. cattle, which produce about 70 pounds (31.8 kg) of milk per day, this translates into roughly 3.4 pounds (1.54 kg) of lactose per animal (M. Waldron, personal communication).

For complete digestion, lactose must be broken down into the two monosaccharides from which it was synthesized, glucose and galactose. Most babies naturally produce the enzyme lactase (also known as lactase-phlorizin hydrolase, or LPH) so that they can take advantage of the nutrients in mother's milk, but for most of the world's population, lactase production shuts down in the postweaning years. Drinking milk after that leads to a battery of symptoms, including diarrhea, cramping, gas, nausea, and vomiting. For most modern populations, with access to medical care if needed, this is not much of a problem, but for those without access, untreated diarrhea, especially in juveniles, can be fatal.

Simoons (1970) and McCracken (1971) first noticed a pattern in the geographic distribution of lactose tolerance, usually referred to as lactase persistence (LP): populations that show high percentages of LP—those in northern Europe, for example, where rates can exceed 95% (Ingram et al. 2009; Itan et al. 2010)—also exhibit a history of cattle dairying that goes back at least several millennia. As Simoons (1981:29) put it, "with the beginning of dairying . . . significant changes occurred in the diets of many human groups. In some of these, moreover, there may have been a selective advantage for those aberrant individuals who experienced high levels of intestinal lactase through life." That advantage would have occurred in situations where milk was, or could be, an important part of the diet, where the group was under dietary stress, and where its members did not process all of their milk into low-lactose products such as cheese, yogurt, and kumis. Under these conditions, "such aberrant individuals would drink more milk, would benefit more nutritionally as a result, and would enjoy increased prospects of survival, well-being, and of bearing progeny and supporting them" (Simoons 1981:29). Several lines of evidence support this classic hypothesis of gene-culture coevolution (Gerbault et al. 2011; Myles et al. 2005; Ulijaszek and Strickland 1993).

Various kinds of modeling have helped us understand both how LP alleles might have arisen and how they could have spread within the agricultural niche. Feldman and Cavalli-Sforza (1989) constructed a mathematical model in which LP was controlled by a single gene, with one allele resulting in lactose tolerance and the other in lactose intolerance. This is the situation in the genome of northern Europeans with LP, where a single nucleotide polymorphism located 13.9 kilobases upstream of the lactase (*LCT*) gene has been shown to be responsible for lactose tolerance (Enattah et al. 2002). Feldman and Cavalli-Sforza's model showed that whether or not the LP allele achieved high frequency depended on the probability of the offspring of milk drinkers becoming milk drinkers themselves. In other words, milk drinking had to be not just a learned tradition but a reliably learned tradition (see Aoki 1996). If that probability was high, then a significant fitness advantage to LP individuals resulted in a high frequency of LP within a few hundred generations. Conversely, if a significant proportion of the offspring of milk drinkers did not drink milk themselves, then unrealistically strong selection for LP was needed for the allele to spread. We return to the issue of the spread of LP throughout Europe when we bring in archaeological perspectives on the agricultural niche.

If we had no knowledge of the timing of cattle domestication and dairying and were simply presented with the information that some groups across the world became milk drinkers, intuitively we might think that LP led to dairying instead of the other way around. Certainly in anthropology there is a long history of viewing adaptation as a process that leads from the development of genes "for" something to humans actually using the genes for whatever was intended. Here, however, the use of formal phylogenetic comparative methods has produced indisputable evidence of niche construction, in which culture acted as a selective pressure and the human genome responded (Gerbault et al. 2011; Holden and Mace 1997; Mace 2009). There is no doubt that dairy farming came first, and only subsequently were alleles for adult lactase persistence favored. The LP allele was absent in ancient DNA extracted from early Neolithic Europeans, suggesting that it was absent or at low frequency 7,000–8,000 years ago (Burger et al. 2007).

How strong was the cultural selection? Based on a study of a Scandinavian population, Bersaglieri et al. (2004:1111) estimated that the coefficient of selection associated with carrying at least one copy of the LP allele to be between 0.09 and 0.19—"among the strongest yet seen for any gene in the genome." Tishkoff and colleagues (2006) made similar estimates. This should squelch any notion that culture is at best a weak evolutionary process. Rather, it can be the instigator of dramatic selective sweeps—positive directional selection in which a new genetic variant increases in frequency and quickly fixes in a population. Cultural practices can also generate selection acting on other species, most obviously the domesticates. Beja-Pereira et al. (2003) established that the increasing frequency of lactose tolerance and the spread of dairying also affected geographical variation in milk-protein genes in European cattle breeds, which covary with present-day patterns of lactose tolerance in human populations.

Cultural practices can strike more than once on the same trait. Even granting the selective strength of cultural activities, one might be tempted to think that a trait such as LP would occur only once and that its wide distribution would be a result of diffusion, say, by herders moving and taking their herds with them. At one time, genetic analysis made this appear likely, but recent work (Enattah et al. 2002, 2008; Gerbault et al. 2011; Ingram et al. 2007; Itan et al. 2009; Mulcare et al. 2004; Nagy et al. 2011; Tishkoff et al. 2006) has shown that the situation is much more complicated. For example, the polymorphism found in northern European populations, where there is an extremely high correlation between LP and dairying (Enattah et al. 2002), does not show up at all, or only rarely, in sub-Saharan groups that exhibit high percentages of LP (Mulcare et al. 2004). In Africa, there is evidence of at least three evolutionary convergences with respect to LP and cattle (Ingram et al. 2007; Tishkoff et al. 2006). Further, Enattah et al. (2008) note that the age estimate they derived for an LP allele among Arabian Peninsula populations—4,095 ± 2,045 years old—suggests that the introduction of that particular LP variant might be associated with the domestication of the Arabian camel more than 6,000 years ago. In summary, alleles for postweaning lactase production had multiple origins—perhaps as many as four (three in Africa and one in Europe)—and involved different animals. Human construction of a dairying niche led to genetic change in multiple species.

Analyzing the Agricultural Niche

In the case of lactase persistence in northern Europe and parts of sub-Saharan Africa, cultural influences favored milk drinking and precipitated a rapid genetic sweep as manifest in the rise in the frequency of the LP allele. Culture was able to effect that sweep because of the interplay of behaviors between humans and cattle—animals that are fairly easily tamed and can be milked. Archaeology can help fill in temporal gaps with respect to the development and spread of dairying, but before we turn to that discussion, we take a brief look at where an instance of gene-culture evolution such as LP might fit in the broad category of niche construction. Specifically, we ask how general are the kinds of processes that led to LP and whether similar bouts of niche construction may have played a central role in recent human history. To address that issue requires some simple conceptual tools that help illustrate the general patterns, one of which is a two-by-two classification (fig. 1) that employs two sets of dimensions—one that tracks whether an organism initiates or counteracts a change in the selective environment and the other that tracks whether the organism physically transforms the novel selective environment or moves away from a less suitable environment and into one that it views as being more suitable (Odling-Smee, Laland, and Feldman 2003).

Inceptive niche construction applies to cases in which organisms initiate change in any environmental factor, through either perturbation of their surroundings (cell 1 in fig. 1) or opportunistic dispersal into a new location (cell 2). Earthworms are classic "perturbers," burrowing through the soil, dragging in organic materials, excreting casts, which serve as a basis for microbial activity, and thereby changing both the structure and chemistry of soils (Lee 1985). As a result of the accumulated effects of past generations of earthworm niche construction, present generations inhabit radically altered environments and are exposed to changing sets of selection pressures, although some aspects of earthworm niche construction also counteract changing features of the environment, such as hydrology (Odling-Smee, Laland, and Feldman 1996). Similarly, humans clear forests for agricultural fields, turn their herds out onto ungrazed grasslands, tether their animals, and build corrals and pens. All these activities and myriad others can have dramatic effects on the environment, and a subset have knock-on consequences for the evolution of the constructor or of other populations that share its local environment. Overgrazing by cattle, for example, stunts or kills vegetation, which can lead not only to soil erosion but also to health-related problems for the animals. Cows having inadequate pasture do not have a chance to gain weight after calves are weaned. In northern climates, this makes them hard to winter and may reduce the health and vigor of cows and calves at calving. Also, cows in poor body condition do not cycle as soon after calving, which can result in delayed breeding. This can result in long calving seasons and poor weaning weights on calves (Rayburn 2000). At the same time, contributions of cattle dung can lead to enrichment of grasslands, especially through the quick release of potassium (Rodríguez et al. 2001). Grazing is an interesting phenomenon from the standpoint of inceptive niche construction because it was only within the last 10,000 years or so that humans were involved—in essence, humans exposed themselves to a novel selective environment as dramatically as moving to a new location.[1] Although humans did not "invent" grazing, their activities have dramatically increased the scale of grazing, frequently with major, long-lasting effects on local ecology.

Humans have also modified selection acting on themselves—for example, by dispersing out of Africa into new environments with different climatic regimes, inadvertently favoring genes expressed in skin pigmentation as well as heat-shock and salt-retention genes, all of which show signatures of recent selection (Gleibermann 1973; Williamson et al. 2007). Another example is provided by the movements of Polynesians, who during their settlement of the Pacific experienced long open-ocean voyages, which subjected them to cold stress and starvation. There may have been strong se-

	PERTURBATION	RELOCATION
INCEPTIVE	1. Organisms initiate a change in their selective environment by physically modifying their surroundings. *e.g., Emission of detritus.*	2. Organisms expose themselves to a novel selective environment by moving to or growing into a new place. *e.g., Invasion of a new habitat.*
COUNTERACTIVE	3. Organisms counteract a prior change in the environment by physically modifying their surroundings. *e.g., Thermo-regulation of nests.*	4. Organisms respond to a change in the environment by moving to or growing into a more suitable place. *e.g., Seasonal migration.*

Figure 1. Four categories of niche construction (reproduced from Odling-Smee, Laland, and Feldman 2003, table 2.1). Niche construction may be inceptive or counteractive and may occur through perturbation of the environment or through relocation in space.

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[1] Keep in mind that humans were late to the scene in terms of coevolutionary interactions with cattle and the physical environment. Conversely, cattle had constructed their own niches over millions of years, which led to extensive genetic as well as phenotypic differentiation (Beja-Pereira et al. 2003; Bradley and Magee 2006; Wiener, Burton, and Williams 2004).

lection for energetic efficiency (Helgason et al. 2007), which would explain why a type 2 diabetes–associated allele that is thought to lead to a "thrifty metabolism" shows a signature of strong positive selection in present-day Polynesians, as predicted by the thrifty-gene hypothesis (Myles et al. 2007; Neel 1962). These are all examples of inceptive relocation (cell 2).

As opposed to inceptive niche construction, 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 environmental factors. Counteractive niche construction is therefore conservative or stabilizing, and it functions to protect organisms from shifts in factors away from states to which they have been adapted. Restoring overgrazed grasslands is an example of counteractive niche construction, as is building shelters for animals in the face of cooling annual temperature (cell 3). If herders moved to a new area to escape deteriorating climate, we would refer to that as counteractive-relocation niche construction (cell 4).

If we think back to our example of LP, we see that it encompasses several of the cells shown in figure 1. It clearly is a case of inceptive niche construction caused by perturbation, the initiation of cattle herding. Humans then exposed themselves to a novel selective environment, defined in large part by cattle herds and the protein offered by milk. This opportunistic expansion of the dairying niche into new regions throughout Europe and Africa is an example of cell 2 in figure 1. More important, however, than pigeonholing various niche-construction processes is understanding the ability of humans, because of their information-accumulating abilities, to quickly assess situations and to make adjustments in their cultural practices to take advantage of the opportunities that a new niche can afford. Construction of a dairying niche itself created opportunities, for example, by allowing humans to disperse into areas that without dairying would be uninhabitable or by providing the raw materials for the emergence of technologies for processed dairy products.

But, of course, this is not always the case, as is illustrated by the classic example provided by Kwa-speaking agricultural groups of West Africa, who for at least several millennia have cleared forests to create fields in which to plant crops (Posnansky 1969). Tree removal had the unintended consequence of increasing the amount of standing water after heavy rainfalls, which led to a rapid increase in mosquitoes such as *Anopheles gambiae*, which need sunlit pools in which to breed effectively (Livingstone 1958). Anopheline mosquitoes are vectors for the protozoan *Plasmodium falciparum.* Bites from infected mosquitoes transfer the parasite into the human bloodstream, where it quickly makes its way to the liver and invades hepatocytes. The parasite emerges from the liver after 1–3 weeks and invades the red blood cells. The cells usually rupture within 72 hours, releasing both new invasive parasites and free hemoglobin into the bloodstream (Evans and Wellems 2002). Today, there are several hundred million clinical cases of malaria worldwide and roughly 800,000 deaths each year (Kappe et al. 2010), the majority of them in sub-Saharan Africa. With respect to the Kwa, this is a classic case of ecological inheritance, with generations of descendants being affected by the upstream activities of their forest-clearing ancestors many generations before.[2]

But similar to what occurred with Neolithic dairying, this culturally induced disruption of the ecosystem had recursive effects on the human genotype. The effect that is of interest here concerns hemoglobin, the protein that transports oxygen from the lungs to the rest of the body, where it releases the oxygen for cell use. Many different types of hemoglobin (*Hb*) exist, one of the more common of which is (*HbA*). A variant form is (*HbS*), where there is a variation in the beta polypeptide chain, which results in the polymerization of the hemoglobin, causing some red blood cells to become stiff and take on a sickle shape. This sickling provides some protection against malaria because sickled cells are recognized by the spleen as they flow through and are removed, thus flushing the parasite with them. The recursive effect on humans is that the variant (*HbS*) form confers heightened protection against malaria in heterozygotes. Decades of yam cultivation intensified natural selection on the human hemoglobin (*HbS*) allele, causing it to increase in frequency.[3] The fact that neighboring Kwa-speakers with different agricultural practices do not show the same increase in (*HbS*) supports the conclusion that culture—clearing fields for yam cultivation—is driving human genetic evolution (Durham 1991).

The protection, however, comes at a premium. Sickled red blood cells, because they are stiff, block small blood vessels on their way through. This is not particularly problematic for those in the heterozygous state (*HbA/HbS*), but for anyone who exhibits the homozygous recessive condition (*HbS/HbS*), known as sickle-cell disease, the chances of morbidity and mortality increase significantly, especially for children younger than 16 months (Aidoo et al. 2002). Numerous drugs and

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[2] The cell-sickling mutation apparently arose in at least three different areas in Africa and in the Indus Valley (Green et al. 2006; Stuart and Nagel 2004). With respect to the timing of the mutation in Africa, Modiano et al. (2008) suggest a "quick but costly" genetic adaptation that occurred some 25 generations ago.

[3] Although we concentrate exclusively on (*HbS*), extensive evidence for genome-shaping interactions can be found in the geographic and ethnic distributions of other families of traits such as blood-group antigens, thalassemias, red-cell membrane molecules, human lymphocyte antigen classes, cytokines (Evans and Wellems 2002), and especially low-activity alleles of the (*G6PD*) gene, which is responsible for production of an enzyme that protects against oxidative stress. Ganczakowski et al. (1995) demonstrate that the geographical distribution of low-activity (*G6PD*) alleles is consistent with the action of selection for malarial resistance. Tishkoff et al. (2001) estimate that one mutation of the (*G6PD*) gene, the (A−) allele, arose prior to West African clearing of forests for yam plots, perhaps as a result of an increase in human population density in the Sahara and northeastern Africa, especially around lakes. This could have allowed for the spread of mosquito-borne pathogens and increased the importance of malaria as a selective agent.

treatments have reduced mortality worldwide (Kappe et al. 2010), but malaria is still a deadly threat.[4]

As shown in cell 4 in figure 1, 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, the organisms expose themselves to alternative habitats, at different times and thus to different environmental factors. But cell 4 oversimplifies things. What about instances where organisms are not free to locate on their own terms? For example, between roughly the years 1550 and 1820 some 12 million descendants of yam cultivators "emigrated" from West Africa as a result of the slave trade, which carried them first to the West Indies and then on to either mainland North America or South America (Lovejoy 1989). These people carried with them an inheritance—(*HbS*) and/or (*HbA*) alleles—to the New World, where it provided them the same selective advantage from malaria that it had in Africa. With the eradication of malaria in portions of the Western Hemisphere by the mid-twentieth century—a cultural practice—one might predict that in terms of fitness, heterozygous (*HbS/HbA*) and homozygous dominant (*HbA/HbA*) individuals (the latter of whom carry no resistance to malaria) would be equivalent, and that over time the (*HbS*) allele would decrease in relative frequency, perhaps eventually disappearing from the population. We see this phenomenon in the West Indies, where some 3 centuries ago Dutch settlers imported slaves from West Africa to the island of Curaçao and neighboring mainland South America. Whereas the mainland was in large part swampy and infested with malaria-carrying mosquitoes, the mountainous island of Curaçao has always been free of malaria. Jonxis (1965) reported that by the mid-1960s, the frequency of (*HbS*) was only 6.5% on Curaçao but 18.5% on the mainland—clear evidence of relaxed selection on (*HbS/HbA*) individuals and selection against (*HbS*) homozygotes.

This prediction—that in, say, the United States, the heterozygous condition would be equally as fit as the homozygous dominant condition—would hold true if certain aspects of the niche as relocated to the New World had stayed the same as in Africa, but they did not. In terms of ecological inheritance, (*HbS/HbA*) heterozygotes do well in most physical environments, but they do not do well in high-altitude areas. Flying in unpressurized aircraft, mountain hiking, and visiting high-altitude cities can cause severe problems for individuals who under normal circumstances—residing at lower altitudes—would have no problems coping with a slight amount of sickling of red blood cells (Godwin and Embury 1981; Kark et al. 1987). Relocation, then, can be a powerful component of human niche construction—a point clearly demonstrated in the work of Modiano et al. (2008) on the timing of the (*HbS*) mutation.

An interesting twist to the Kwa story comes with the possibility that yams may actually provide some relief from the symptoms of sickle-cell disease. Some foods—horseradish, cassava, corn, sweet potatoes, and, yes, yams—contain cyanogenic glucosides, or natural plant compounds, that interact with bacteria in the large intestine and aid the body in producing a type of hemoglobin that can effectively carry oxygen through blood cells, possibly leading to less pain (Agbai 1986; Houston 1973). We suggest that it would be too much of a coincidence—not to mention an irony—for a population to just happen to have chosen by chance a crop that alleviates the symptoms of the disease that its planting inadvertently promotes! Far more plausible is the hypothesis that these agriculturists originally planted other crops and subsequently switched to yams once their medicinal properties had been discovered.[5] If our suspicions are proved correct, then an instance of inceptive perturbation (planting crops that led to prevalent sickle-cell disease) has elicited a further act of counteractive niche construction (switching to growing yams, which alleviates sickle-cell disease). We suspect such causal chains following acts of inceptive niche construction to be a regular pattern; indeed, crops such as cassava, corn, and sweet potato may plausibly have been cultivated because they too had medicinal effects.

In practice, most cases of human niche construction are likely to involve both perturbation and relocation. For example, we would expect that most humans choose their house locations with some care. Similarly, every time humans move, they necessarily alter the habitats from which they moved by depriving them of their presence. This could have significant consequences for plants and animals left behind, especially

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[4] Space restrictions force us to bypass detailed discussion of a fascinating subject, niche construction from both the eyes of an anopheline mosquito and those of a *Plasmodium* parasite. *Plasmodia* are incredibly powerful and efficient niche constructors (Coluzzi 1999; Evans and Wellems 2002). Here is how Kappe et al. (2010:863) describe the efficiency: "After invasion, the parasite begins a remarkable process of remodeling that converts the terminally differentiated erythrocyte, which lacks a nucleus and machinery for functions such as protein trafficking, into a niche in which the parasite obtains nutrients and hides from host protective mechanisms." But the parasite also has to be able to exit the erythrocyte (red blood cell), and here is one locale where new drugs might nail it (Yeoh et al. 2007). In the face of constant threats, the parasite needs ongoing, up-to-the-minute feedback relative to how its adaptive strategies are playing out both within its host (weakened hosts are fine, but dead hosts are not of much use) and within the epidemiological environment (Mackinnon and Marsh 2010). There literally is an all-out arms race to see which side can outgain the other. For thousands of years, the *Plasmodia* have been winning round after round, but now there is a new cultural factor involved in human-mosquito-parasite niche construction: the Gates Foundation. Bill and Melinda Gates's challenge to the scientific community in 2007 was, don't just control malaria, eradicate it (Enserink 2010). Given the depth of their commitment and the extent of their resources, we wouldn't bet against eventual eradication. Certainly from a niche-construction standpoint, it will be fascinating to see how the parasite reacts to new, stepped-up assaults on its existence.

[5] In Alice Walker's (1990:263–264) *The Color Purple*, the narrator quotes from a letter her sister had written from Africa around 1930: "The Olinka have been eating yams to prevent malaria and to control chronic blood diseases for thousands and thousands of years. Left without a sufficient supply of yams, the people—what's left of them—are sickening and dying at an alarming rate."

those that had developed mutualistic or commensal relationships with humans. Similarly, new locations are altered as the result of a move into them. Moreover, as relocation is likely to result in the modification of multiple selection pressures, it subsequently may result in new trade-offs being made in response to the fitness effects associated with each selection pressure at the new location. Alteration of life histories may follow (Odling-Smee, Laland, and Feldman 2003, chap. 9), and it is those histories that are of paramount interest to social scientists. Perturbation and relocation can also work together through resource depression. Broughton, Cannon, and Bartlelink (2010) suggest that niche construction might affect patterns of movement through resource depression, thereby influencing human population's rate of colonization. We have suggested that, other factors being equal, the greater the sophistication of the population's niche construction, the faster one might expect such colonization to occur (Laland and O'Brien 2010). Equally, cultural niche construction can lead to demographic expansion, thereby promoting dispersal. A good example is provided by Itan et al.'s (2009) observation that the spread of LP in Europe is associated with demographic success. Although it obviously is possible for organisms to disperse without using cultural knowledge, in practice, most recent human dispersal is likely to have been heavily reliant on culturally transmitted information and skills.

Moreover, as the study by Rendell, Fogarty, and Laland (2011) demonstrates, perturbational niche construction can drive its own spread through generating statistical associations between niche-constructing cultural practices and the biological traits that such practices favor. Indeed, that study was inspired by the Kwa case, with yam cultivation being the cultural practice and the (*HbS*) allele the gene variant favored by culturally instigated selection. If Rendell and colleagues' analysis is correct, then agricultural practices such as planting crops not only spread, despite the fact they promoted disease, but may even have spread because they did so, allowing the practice to hitchhike through association. Even without dispersal, the theory predicts that regions of crop-planting (*HbS*) carriers would gradually grow in space. Were individuals to move away from disease-ridden regions but retain their crop-cultivating culture, as seems highly plausible, then perturbational and relocational niche construction would have worked together to propagate the agricultural-disease complex.

Note also that in our examples thus far, we have concentrated on the effect of human cultural practices on the selection of human genes, but such practices will drive selection on other species too. We have already mentioned the case of selection on dairy cattle (Beja-Pereira et al. 2003), and similar effects are found in a host of domesticated animals and plants. They might also be expected in commensal and parasitic species, from rats and mice to houseflies. Disease vectors, too, have evolved in response to cultural practices—for example, *Plasmodium falciparum* and *Anopheles* species have evolved resistance to the eradication treatments of chloroquine and DDT, respectively. An interesting case concerns the coevolution of the body louse (*Pediculus h. humanus*) and humans' use of clothing. Kittler, Kayser, and Stoneking (2003) proposed that head and body lice differentiated when humans adopted frequent use of clothing, and they used a molecular-clock analysis of louse mtDNA to place this differentiation in Africa around 72,000 years ago. Recent research by Toups et al. (2011) suggests that the differentiation occurred by at least 83,000 and possibly as early as 170,000 years ago. These results suggest that clothing was a surprisingly recent innovation and that its use initiated a speciation event in the louse. The general point here is that human cultural practices construct niches, affecting the biological evolution and developmental experiences not only of humans but of many other organisms as well.

Constructing Life Histories of Agricultural Niches

Archaeological evidence is an important contributor to our understanding of life histories and the trade-offs made in the face of new selection pressures. With respect to our understanding of the agricultural niche defined in part by cattle domestication, dairying, and the rise of LP, isotope ratios from lipids extracted from broken ceramic vessels show the presence of milk fats in northwestern Anatolia (roughly modern-day Turkey) around 7,000–8,000 years ago (Evershed et al. 2008). These early dates contrast markedly with those from central and southeastern Anatolia, where milk use started more than a millennium later (Evershed et al. 2008). Milk use has been documented in Romania sometime before 7,000 years ago (Craig et al. 2005*a*, 2005*b*) and in Britain between 4,000 and 6,000 years ago (Copley et al. 2003, 2005), the result of northward movement of people or knowledge (see below).

The key word here is milk "use" because it is unclear in some cases whether milk itself was being consumed or whether it was being processed into cheese or other milk products that are significantly lower in lactose. Experimental evidence (Dudd and Evershed 1998) indicates that raw-milk lipids absorbed by ceramic containers are rapidly destroyed by burial (as opposed to processed milk lipids), so it is fairly safe to conclude that at least some milk was being converted into milk products by Neolithic farmers in northwestern Anatolia.[6] In addition to making milk easier to digest, processing raw milk into milk products provides a means of storing surplus milk (Evershed et al. 2008). Of course, one has to know how to process milk into products—an acquired knowl-

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[6] The same applies to mare's milk, lipids from which have been identified in pottery from Kazakhstan dating about 5,500 years ago (Outram et al. 2009).

edge that itself is a key component of the agricultural niche.[7] Here again is an illustration of long-term consequences of niche construction: keeping cattle for their milk, together with the spread of *LP*, created the developmental niche that scaffolded the invention of various processed-milk products and their associated technologies. This feedback from acts of cultural niche construction to the developmental environment is an important general feature of human niche construction that merits further attention (Sterelny 2009, 2011).

In terms of the timing of milk production, Neolithic farmers began domesticating cattle, goats, and sheep between 10,000 and 11,000 years ago in Anatolia, western Iran, and northern Mesopotamia (Helmer et al. 2005; Peters, von den Dreisch, and Helmer 2005; Troy et al. 2001; Zeder and Hesse 2000). Like Itan et al. (2009), we suspect that few individuals at that time were lactose tolerant. In fact, selection would not have favored LP, or only weakly so, because it was frequently damped by alternative activities of the niche constructors, who killed and ate the cattle that would otherwise have been "sources" of selection. The transition from a perspective that emphasized meat on the hoof to one that emphasized milk in the bank was not an overnight phenomenon, and neither was domestication (McCorriston et al. 2012). We tend to treat domestication as an either/or state, meaning either something is or is not domesticated, but there is a huge amount of gray area in between—more so in animals than in plants and more so in some animals than in others. Selective pressures on animals undergoing domestication focus on behavioral changes, some of which may leave physiological or morphological markers—for example, tooth-size reduction and juvenilization of the skull—whereas others might not. Such markers can be considered signatures of cultural niche construction. Of all the behavioral traits that make certain animals attractive candidates for domestication—what Bleed and Matsui (2010:367) refer to as "domesticate fitness" (e.g., tolerance for penning or selective breeding)—possession of a less wary and aggressive nature leads the list (Zeder 2006*a*; see also Shipman 2010). Certainly early Neolithic peoples living in and near the Fertile Crescent were unable to turn wild sheep, goats, and cattle into unwary creatures overnight, but by the same token, herds of "wild" animals living in proximity to early camps were used to having humans on the landscape. It may have been only a small widening of the early Neolithic niche to accommodate a few captured animals, which then could have (inadvertently) been selectively bred for desired attributes.

The timing of the transition from domestic animals as simply "primary" producers of products to be consumed to "secondary" producers of products such as wool, traction, and milk (Sherratt 1983) is open to question.[8] Some researchers argue that once animals were domesticated, the potential benefits of these products would have been exploited rapidly, whereas others argue that it would have occurred much later. The work of Evershed et al. (2008) indicates that there might have been as little as 500–1,000 years between the time of domestication and the production of milk products in northwestern Anatolia. By 7,500 years ago, the agricultural niche moved beyond northwestern Hungary and southwestern Slovakia and into central and northwestern Europe as a result of expansion of what archaeologists refer to as the LBK culture (Whittle 1996).

One question concerns the nature of the Neolithic niche expansion: Was it demic or diffusion, meaning was it a movement of people or a transmission of ideas? Certainly the speed of the wave suggests demic expansion (Cavalli-Sforza, Piazza, and Menozzi 1994)—Fort, Jana, and Humet (2004) and Pinhasi, Fort, and Ammerman (2005) indicate a rate of 0.6–1.3 km per year—and DNA studies support that conclusion. Itan et al. (2009) used computer simulation to model the spread of LP, dairying, and other subsistence practices across Europe and western Asia. They inferred that the coevolution of European LP and dairying originated in a region between the northern Balkans and central Europe sometime between about 6,250 and 8,700 years ago. They proposed that after cattle herding and dairying became increasingly important components of southeastern European Neolithic culture, natural selection began acting on a few LP individuals in Neolithic cultures of the northern Balkans. After the initial slow increase of LP frequency in those populations and the onset of the LBK culture around 7,500 years ago, LP frequencies rose more rapidly in a gene-culture coevolutionary process and on the wave front of a demographic expansion into central and north-central Europe that brought along cattle (Edwards et al. 2007). This led to the establishment of highly developed cattle-based (as well as goat-based) dairying economies during the central European middle Neolithic around 6,500 years ago.

Although DNA indicates a demic spread, it also indicates that the demographic processes were anything but straightforward (Gerbault et al. 2011). Four recent studies highlight what we know of the emerging picture. First, the work of Haak et al. (2005) on mitochondrial DNA from Neolithic skeletons from Germany, Austria, and Hungary shows that the contribution of the first European farmers to modern

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[7] Milk is host to a variety of microorganisms—*Streptococcus*, *Lactobacillus*, *Bacillus*, yeasts, and molds—and each plays a role in converting milk into milk products such as yogurt by breaking down lactose into lactic acid, which sours the milk and coagulates the milk protein, allowing yeast and mold to proliferate and reduce the acid. The fermented milk product can then be safely stored because it is still acidic enough to kill harmful microorganisms. Alternatively, cheese is made by adding the digestive enzyme rennet to acidified milk, coagulating it to the point that solids can be set aside and stored. Cheese making possibly was discovered by accident when milk was stored in a container made from the stomach of an animal, which still contained rennet. The heat from the sun turned the milk sour, and the rennet turned the milk into curds and whey (Ridgwell and Ridgway 1986).

[8] Vigne and Helmer (2007) propose replacing the term "primary products" with "final products" and the term "secondary products" with "antemortem (life-time) products."

European female lineages was negligible. Instead of Neolithic farmers overrunning and swamping the gene pools of Mesolithic peoples, perhaps small pioneer groups carried farming into Europe and, once the agricultural methods had taken hold, the surrounding hunter-gatherers not only adopted the new LBK culture but incorporated the immigrants as well, in the process swamping the genetic contribution of the immigrants. Second, Itan et al. (2009) found no evidence that the positively selected LP allele in early dairying groups increased the unlinked genetic contribution to the modern European gene pool by people living in regions where LP-dairying coevolution started. They suggest that the main reason for this is likely to have been the relatively high rates of intrademic gene flow between dairying and nondairying farmers and similarly high rates of interdemic gene flow between neighboring demes. There may also have been successive migrations, which had a homogenizing effect on LP allele frequencies. Third, Bramanti et al. (2009) demonstrated a genetic discontinuity between Mesolithic hunter-gatherers and early Neolithic farmers around 7,500 years ago, supporting the notion of migrating farmers. Fourth, simulations by Gerbault et al. (2011) demonstrate that selection on LP was unlikely to have been consistent across time and space and that the role of demography in its spread cannot be ignored. Specifically with respect to niche construction, they suggest that, based on the absence of hunters-gatherers in Europe today, it is logical to assume that niche modification by farmers, perhaps tied to density-dependent competition (Currat and Excoffier 2004), had a direct effect on hunter-gatherers, ultimately resulting in their disappearance.[9]

Causal Graphs and Construction Chains

Having presented the LP and (*HbS*) examples in depth, we now consider the more general lessons that might be learned from such case studies. To this end, we begin by summarizing in graphical form the key processes underlying each example.

Figure 2 illustrates various means by which a human population could respond to its own cultural niche-constructing activities. Route 1 (fig. 2*A*) comprises an entirely cultural response to a change in an environment brought about by earlier cultural niche construction. For example, suppose humans change their environment through an agricultural practice that inadvertently promotes the spread of a disease, such as in the case of the Kwa. However, imagine that, unlike the Kwa, the population responds through devising new technology to alleviate the problem, such as medical treatment or changed agricultural practices. Provided the response is sufficiently effective to counteract the environmental change, the route should be confined to the cultural level alone and should have no effect on human genetics. Here, human niche-constructing activities have modified the developmental environment, triggering further bouts of learning that are expressed in further cultural niche construction. The initial cultural niche-constructing episode has not modified selection on human genes because the problem was dealt with at the cultural level. Although there is nothing inevitable about the capacity of human populations to construct solutions to self-imposed problems, their capacity for culture renders human niche construction uniquely potent and fast acting. Human populations regularly clean up after themselves, constantly devising technology that addresses problems caused by the previous act of cultural niche construction, in the process frequently triggering new problems. For example, agriculture can lead to food excesses, which trigger new challenges to store and preserve food, which in turn lead to new challenges associated with defending the food, pest control, trade, population growth, and so forth. In such cases, the alleviating technology damps selection on human genes.

Analyses of the human genome have revealed hundreds of genes showing statistical signatures of recent positive selection (Voight et al. 2006; Wang et al. 2006), suggesting much more human evolutionary change, and more rapid change, than traditionally thought. This change in perspective on evolutionary rates opens up the possibility that humans could realistically have evolved solutions to problems self-imposed over the last few millennia. This is illustrated by route 2 (fig. 2*B*), which applies whenever human cultural processes fail to express a sufficiently effective response to an environmental change, resulting in modified natural selection. Returning to the Kwa example, here agricultural practices increased the amount of standing water present, creating improved breeding grounds for mosquitoes and increasing the prevalence of malaria, generating selection for the (*HbS*) allele that, in the heterozygous condition, confers protection against malaria. Similarly, route 2 captures the major causal link in the dairy-farming example, with a cultural practice triggering a genetic response.

Finally, sickle-cell disease in our agricultural population modifies its developmental niche to trigger further learning, leading to technological innovations such as the planting and consumption of crops that alleviate the symptoms of anemia, including yams (route 3, fig. 2*C*). Here, cultural niche construction (crop planting) inadvertently led to the spread of genes that confer resistance to one disease (malaria) but promote another one (sickle-cell anemia). In turn, the spread of (*HbS*) created a new developmental niche, scaffolding the learning of the medicinal properties of crops such as yams and promoting a change in cultivation. In the case of dairy farming, the spread of LP likely promoted the exploitation of processed dairy products and scaffolded a long series of other innovations, from chocolate bars to milking machines.

We can illustrate the causal texture of acts of cultural niche

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[9] The paper by Gerbault et al. (2011) is an excellent example of how simulation studies of demographic processes can figure prominently in discussions of human niche construction (see also Gerbault et al. 2009). It is also an excellent example of convergent thinking, as it appeared in print well after our initial draft went in for review. We tailored some of our presentation here to complement rather than overlap their excellent discussion.

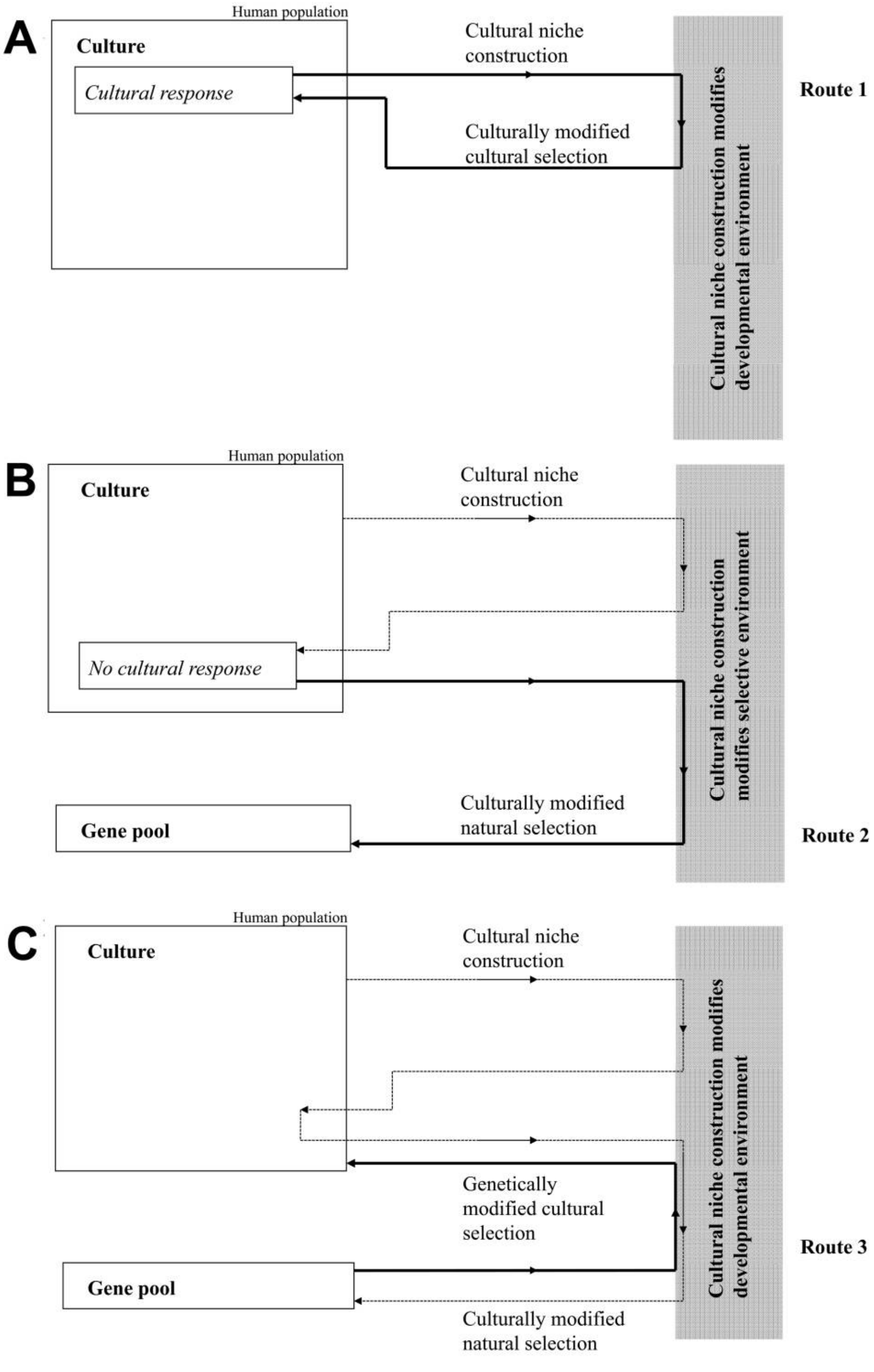

Figure 2. Three routes to feedback from cultural niche construction (based on Odling-Smee, Laland, and Feldman 2003, fig. 6.3): (*A*) cultural processes modify the environment but are responded to through further cultural niche construction; (*B*) a failure to respond at the cultural level triggers a genetic response to cultural niche construction; and (*C*) a changed genetic constitution within the population modifies the developmental environment, triggering further innovation and cultural learning.

construction by introducing the concept of "construction chain," which we define as a summary of the immediate and downstream consequences of an act of niche construction and their consequences for other processes, operating at other levels and in other species. Figure 3 presents construction chains for (*A*) the dairy farming and LP and (*B*) the Kwa yam-cultivating examples. White boxes represent a human cultural activity, and shaded boxes signify the genetic signature of prior niche construction, either in humans or in other species inhabiting the constructed niche. Arrows signify a causal influence, through the construction of either an ecological niche that triggered a genetic response or a developmental niche that scaffolded an episode of learning or innovation. Causal influences can be seen to flow from culture to genes and back to culture, in a bidirectional pattern, with resultant effects on population growth and dispersal. Note that although figures 2 and 3 are purely conceptual tools, it would be possible to extend the applied logic to analytical tools. For instance, causal influences can be estimated and quantified using causal graph theory (Shipley 2000).

Also of considerable interest to archaeologists is the possibility of extending the construction chains backward in time to derive the causal influences that led to the origins of agriculture. Here, we envisage that the challenge for our ancestors was how best to damp out variability in the availability of food. We would not expect humans to engage in costly

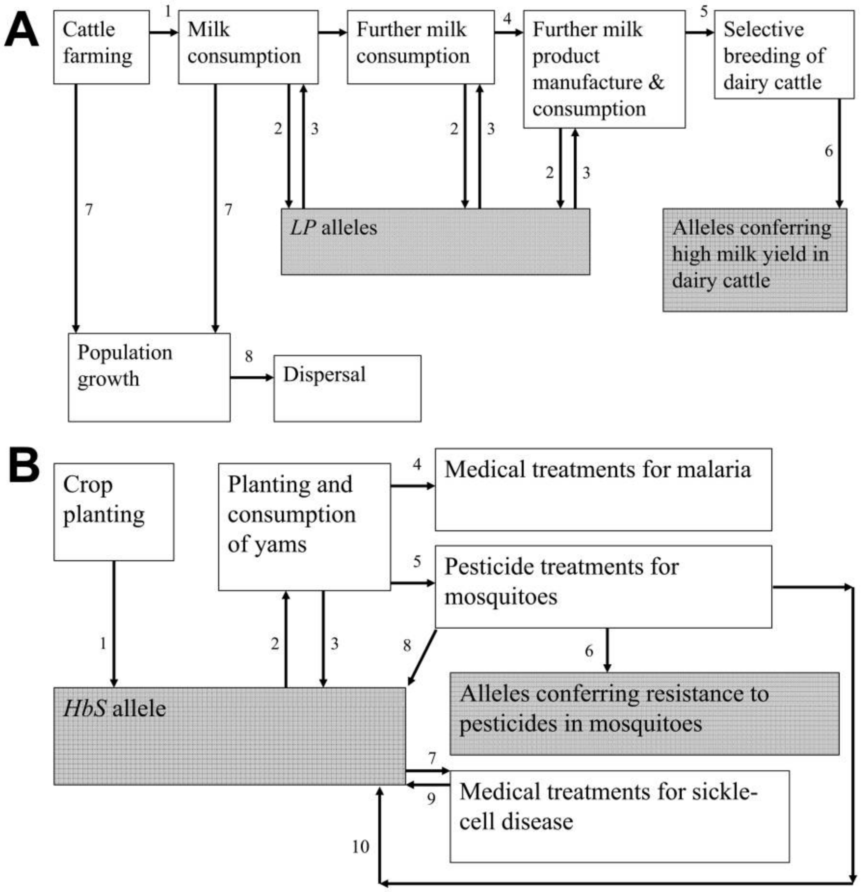

Figure 3. Construction chains, depicting the chain of causal influences following a cultural niche-constructing practice for (*A*) dairy farming and (*B*) crop planting. Cultural processes are shown in white boxes, and genetic change is shown in shaded boxes. In panel *A*, the domestication of cattle triggers (1) milk consumption, which (2) favors the spread of lactase persistence (LP), (3) promoting further milk consumption, which (4) elicits further milk-product manufacture and consumption, which (5) leads to selective breeding of cattle, which (6) selects for alleles conferring high milk yield in dairy cattle. In addition, cattle farming and dairy-product consumption (7) lead to population growth, which (8) triggers dispersal into new environments. In panel *B*, crop planting (1) inadvertently promotes the spread of malaria, leading to selection for (*HbS*), and the resulting incidence of sickle-cell disease (2) favors the planting of yams and other crops with medicinal benefits, which (3) further promotes the spread of (*HbS*) and (4) scaffolds the development and/or application of medical treatments for malaria, as well as (5) pesticide treatments for mosquitoes, which (6) generates selection for alleles conferring resistance to pesticides in mosquitoes. The spread of sickle cell (7) scaffolds the development and/or application of medical treatments for sickle-cell disease. Pesticide treatment of mosquitoes (8), medical treatment for sufferers of sickle-cell disease (9), and malaria victims (10) affect the intensity of selection on the *HbS* allele.

and labor-intensive forms of food production if alternative capturable or gatherable wild food were available (Bleed and Matsui 2010; Rowley-Conwy and Layton 2011). Like many others before us (e.g., Barlow 2002), we anticipate that agriculture should be promoted by conditions where 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 (Laland and O'Brien 2010; Zeder 2012); indeed, we find compelling B. D. Smith's (2007*a*, 2007*b*, 2011) evidence that this has occurred. From an NCT perspective, such observations do not conflict as much as they might appear to. We might well expect that in a rich environment, human population growth will frequently be followed by resource depression (Broughton, Cannon, and Bartelink 2010), thereby raising the economic value of investment in agriculture. The important point is that environments are not fixed as rich or poor; rather, they are dynamic variables, vulnerable to change as a result of the activity of potent niche constructors. This reasoning leads to the testable prediction that 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 (Laland and O'Brien 2010).

The Agricultural Niche in Broader Perspective

We have treated the LP and (*HbS*) examples in depth, drawing on the extensive empirical and theoretical insights that have been amassed by literally hundreds of researchers from many disciplines in order to reconstruct the various causal influences and patterns of feedback involved. They illustrate the kind of interdisciplinary research program likely to be required if we are to fully understand a challenging problem such as the origins of agriculture. We would like to believe that NCT and GCT combine to provide a compelling conceptual evolutionary framework within which such cases can be understood. Whereas it is easy to defend our use of the LP and (*HbS*) examples, given that no other cases of gene-culture coevolution are as well researched, we understand that the skeptical reader will want to know to what extent these examples are representative of recent human history.

It is here that recent analyses of the human genome identifying genes subject to selection over the last 10,000 years or so have the potential to revolutionize thinking within archaeology and anthropology (Nielsen et al. 2007; Sabeti et al. 2007; Voight et al. 2006; Wang et al. 2006; Williamson et al. 2007). Many hundreds of such genes have now been identified, and in most cases the time depth of the selective sweep would seem to be sufficiently shallow to render highly plausible the suggestion that human cultural activities triggered the response to selection. These data strongly suggest that the LP and (*HbS*) examples are not exceptions but rather are representative of a very general pattern of gene-culture coevolution over the last 20,000 years. For example, Laland, Odling-Smee, and Myles (2010) collate 27 separate genes thought to have been subject to recent selection and for which the inferred cultural selection pressure is a change in diet associated with the advent of agriculture (see also Perry et al. 2007; Pickrell et al. 2009). LP is the most familiar of these, but the list also includes genes expressed in the metabolism of carbohydrates, starch, proteins, lipids, phosphates, plant secondary compounds and alcohol, as well as in jaw-muscle fiber and tooth-enamel thickness. They also collate a further 30 cases of genes that provide some immunity from, or resistance to, disease or pathogens thought to have been promoted by agriculture or other farming practices. Once again, (*HbS*) is the most familiar example, but it is likely to be representative of a broader category.

There are also several other categories of genes, expressed in energy metabolism, heat or cold tolerance, skeletal development, the nervous system, brain function, the externally visible phenotype, and more, that are documented to have been subject to recent selection and for which the inferred selection pathway is a cultural practice (Laland, Odling-Smee, and Myles 2010). Such genetic analyses are not foolproof, and each example will need to be followed up with detailed empirical research before gene-culture coevolution can be proven. However, the data are sufficiently tantalizing to suggest that there are likely to be rich pickings here for anthropologists and archaeologists interested in investigating such gene-culture interactions, where the NCT-GCT framework may well prove widely applicable.

The reader might also ask in what way the NCT-GCT approach supersedes previous treatments of these cases (e.g., Durham 1991). Our emphasis on the generality of the interacting processes, and the representativeness of these examples as manifestations of the kinds of dynamical interplay between gene and culture that truly characterizes recent human history, is one kind of answer that we could give to such a question. However, it is not the only point that we would choose to make.

A second advantage of the NCT-GCT framework is that human niche construction is not viewed as the isolated product of our unique capacity for culture (Kendal, Tehrani, and Odling-Smee 2011). Rather, it is placed in a general evolutionary framework that recognizes that all organisms modify and construct their environments, albeit to greater and lesser degrees, and that human niche construction is unusual only for its heavy reliance on culture. We can make sense of human activities as inceptive or counteractive niche construction or as generating perturbational and relocational patterns, with the benefit of drawing on the broad and rapidly growing body of formal and conceptual theory on niche construction as a source of ideas, hypotheses, and methods (Odling-Smee, Laland, and Feldman 2003).

A third benefit of the NCT-GCT framework is that it promotes consideration of the active agency of humans, and other organisms, in modifying their ecological and developmental niches and naturally draws attention to the various forms of feedback that flow from human activities, at multiple levels, in multiple populations, and across multiple species. At the same time, the evolutionary framework automatically considers the biological fitness consequences of acts of perturbation and relocation, thereby leading researchers directly to consider the demographic consequences of human cultural activities and their impact of dispersal. The spirit of interactionism is implicit in previous treatments (e.g., Durham 1991), but by making interactionism explicit (Godfrey-Smith 1996), the NCT-GCT perspective is heuristically valuable because it draws our attention to a range of phenomena that are both important and easy to overlook using standard perspectives (Laland and Sterelny 2006).

Niche construction represents a classic example of human minds and human environments engaging in a long-standing, intimate exchange of information, leaving each beautifully fashioned in the other's image. The concept is especially useful when studying humans because it encourages us to think beyond climate, instability, and external environments as causes of evolutionary events and to quantify and incorporate human activities as active variables in driving both environmental change and human evolution. Anthropologists and archaeologists are, of course, conscious of the fact that humans can cause changes in their immediate environments, although the full ramifications of these changes relative to the triggering of recent evolutionary episodes in both humans and other species that inhabit our world, and feedback to the developmental niche, have only recently become clear.

The NCT-GCT framework we endorse has broad applicability, including to timeframes and populations that long precede the advent of agriculture, given that humans and their ancestors have been constructing niches for millions of years (Bickerton 2009; Kennett and Winterhalder 2006; Odling-Smee, Laland, and Feldman 2003). Agriculture, because of the central role it has played in the last 10,000 years of human evolution, is an excellent vehicle for examining some of the components of niche construction, especially the positive and negative effects that human actions have with respect to such seemingly disparate variables as social organization and general health. Anthropologists have long held that the development of civilizations is impossible without agriculture. That fact seems unassailable. No civilizations, however defined, have existed without the kind of food base provided by agriculture. It also is well established that plant and animal domestication preceded the population growth and nucleation that accompanied the rise of civilizations in both the Old and New Worlds. Agriculture was accompanied by greater degrees of sedentism and increased population growth, and its adoption typically led to its expansion into new territories through a combination of demic expansion and diffusion (M. E. Smith 2009). The agricultural niches of some of these farming societies expanded, and they evolved into larger and more complex social systems characterized by urban centers and class inequalities. For some, the niche continued to expand, allowing the new way of life to expand beyond its zones of origin through such mechanisms as conquest and trade. In the process, human agricultural practices also created new niches for cats, dogs, rats, mice, houseflies, bedbugs, rhododendrons, weeds, microbes, and a host of other commensal species, each triggering construction chains, frequently with feedback that shaped subsequent cultural practices. In time, through cultural practices ranging from selective breeding, to artificial hybridization, to the induction of mutation through bombardment with gamma rays, humans started to transform the genomes of agricultural crops directly.

Food processing, in a variety of guises, is a very important form of human niche construction, which is likely to have strongly affected the evolution of human genes, particularly those associated with digestion and metabolism, and triggered recursive interactions among culture, environment, and biology. Wollstonecroft (2011:145), for example, points out that

> without innovations such as soaking, fragmentation, chopping, slicing, grating, grinding, fermentation and thermal processing such as roasting, steaming, boiling and baking, the dietary diversity that humans enjoy today would not be possible. . . . Many (wild and domesticated) plants that are of importance in the human diet, particularly the pulses and cereals such as rice (*Oryza* spp.) and wheat (*Triticum* spp.), cannot be properly digested when eaten raw. Legumes, for example, are highly nutritious high-protein low Glycaemic Index (GI) foods but contain mildly toxic and anti-nutritional substances that are difficult for humans to digest, unless they are first detoxified by soaking and cooking (Hultin and Milner 1978). Likewise, many of the carbohydrates in root and seed foods, such as insulin and starch, require heating to change them into digestible forms.

In addition, complex processing techniques, such as combining plant or animal ingredients into composite foods, can generate greater nutrition than the sum of the raw materials. Food storage and preservation technologies are equally important. In all such cases, human cultural knowledge has affected the availability, diversity, and nutrition of foods for human populations, transforming their developmental and ecological niches.

Cohen (1989) underscores the point that despite the "benefits" agriculture offers, no clear evidence exists that the evolution of civilization has reduced the risk of resource failure and starvation as successfully as one might believe. Any such belief fails to take account of the dynamic, constantly changing world that humans partly engineer themselves through their niche-constructing activities. Lewontin (1983) described evolution as like "walking on a trampoline." Every act of niche construction potentially modifies the selective environment of the constructor and builds new developmental niches in the process. Agricultural peoples may have more advanced knowledge of storage and transportation than hunter-gatherers, and it is clear that agricultural groups do not face some of the severe fluctuations in natural resources that nonagricultural groups do, but the strategies that sedentary and civilized populations use to reduce or eliminate food crises generate costs and risks as well as benefits, precisely because they modify niches. In fact, the advantages may oftentimes be outweighed by such factors as the greater vulnerability that domesticated crops display toward climatic fluctuations or other natural hazards, a vulnerability that is then exacerbated by the specialized nature or narrow focus of many agricultural systems (Cohen 1989; Rowley-Conwy and Layton 2011). Such challenges are exacerbated by the fact that the feedback from any act of niche construction may operate via any number of compartments, both biotic and abiotic, in the local environment, leading to consequences for the constructors that may be considerably delayed in time (Laland and Brown 2006; Laland, Odling-Smee, and Feldman 2001; Riel-Salvatore 2010).

Certainly health, at least in many parts of the world, was dramatically affected by the onset of agriculture (Cohen and Armelagos 1984; Cohen and Crane-Kramer 2007), with a wealth of new data being provided by the European module of the Global History of Health Project (GHHP). One key finding is that the health of many Europeans began to decline markedly about 3,000 years ago, after agriculture became widely adopted in Europe and during the rise of the Greek and Roman civilizations (Gibbons 2009). The aforementioned excess of genes expressed in immunity and resistance to disease that have been subject to recent selective sweeps is a potential signature of this fallout from the widespread deployment of agricultural practices and the increase in density and exposure to zoonoses that such practices afforded. Similarly, researchers document shrinking stature and growing numbers of skeletal lesions from leprosy and tuberculosis—zoonotic diseases caused by living close to livestock and other humans in settlements where waste accumulated (Armelagos and Harper 2005; Pearce-Duvet 2006). Also, the frequency of dental cavities and enamel hypoplasia—incomplete formation of the enamel that is usually transmitted as an X-linked or autosomal dominant trait—also increased as people switched to a grain-based diet with fewer nutrients and more sugars. To this can be added inherited pathological deficiencies such as genetic anemias (e.g., sicklemia and thalassemia; Durham 1991; Holland and O'Brien 1997; Walker et al. 2009).

Once again, there are rich opportunities to tie such archaeological and anthropological data to human genetic data, thereby developing a deeper understanding of the causal pathways involved. Further, simply because food is available does not ensure that people will necessarily receive it. The GHHP found, for example, that Europeans became shorter over time, with males shrinking an average of 7 cm between about 2,300 years ago and 400 years ago—a sure sign that children who were not members of elite families were eating less nutritious food or suffering from disease (Gibbons 2009). Such observations are suggestive of feedback from agricultural practices to the developmental niche, ranging from effects on childhood growth to reorganizations in societal structure, all of which are open for exploration using the aforementioned tools.

What about the modern agricultural niche? Are things much different today? In fact, one can see the niche construction of yam cultivators almost exactly mirrored in that of modern Asian tire factories, where mosquitoes infest the pools of rainwater that collect in tires stored outside, and tire export contributes to the spread of malaria and dengue (Hawley et al. 1987). Plausibly, agriculture typically provides modern humans with a fairly stable and reliable subsistence, although this is far from guaranteed, with crop failure, storage failure, and so forth. Moreover, there still are niche-constructing behaviors that have what seemingly are positive effects but that, under changes in the niche, can have negative effects. Take diet, for example. In most Western countries, diet-related chronic diseases represent the largest single cause of morbidity and mortality (Cordain et al. 2005). Although we frequently attempt to identify a single dietary element as the cause of chronic disease, an overwhelming amount of evidence indicates that virtually all so-called diseases of civilization have multiple and complex dietary and genetic causes. Heart disease, for instance, does not arise simply from excessive saturated fat in the diet but rather from a complex interaction of multiple foods that are part of our ecological inheritance from our Neolithic forebears—dairy products, cereals, sugars, fatty meats, and salt. These foods, in turn, adversely influence proximate nutritional factors—glycemic load, fatty-acid composition, acid-base balance, sodium-potassium ratio, and fiber content—all of which underlie or exacerbate virtually the entire spectrum of chronic diseases of civilization. Dietary changes since the agricultural revolution have likely triggered extensive selection on human genes expressed in metabolism, but such selection is likely to be ongoing and only partially compensatory for the ill effects of the diseases concerned. The ultimate factor underlying diseases of civilization remains "the collision of our ancient genome with the new conditions of life in affluent nations, including the nutritional qualities of recently introduced foods" (Cordain et al. 2005), although our genomes may not be quite as ancient as Cordain and colleagues envisage. In other words, the agricultural niche developed so recently in terms of evolutionary time, not to mention its exponential growth rate and almost limitless cultural changes that it created, that even allowing for rapid genetic change, the human genome cannot keep up.

We humans have the unique advantage, afforded by our culture, of responding to such self-generated challenges through further cultural niche construction (route 1 in fig. 2). For example, we can develop medical treatments for heart disease. Virtually all other species, somewhat tragically, do not possess this luxury and are forced to respond to human cultural activities largely through biological evolution or go extinct (route 2 in fig. 2). As a consequence, the actions of humans relative to agricultural production can have dire consequences for the engineering web, some of which may take decades to surface. The effects of environmental perturbation today are on a scale that no Neolithic cattle herder or yam producer could have imagined. Kwa-speaking cultivators in West Africa may have aided in the spread of malaria by hand-clearing forests, but they did not deforest, overgraze, or overcultivate some 320 million hectares, or 25%, of the already fragile sub-Saharan African farmland, as has occurred over the last few decades (Moorhead 2009). Nor were they responsible for fertilizer runoffs that contribute excessive nutrients to aquatic ecosystems, which results in algal blooms and anoxia, which then leads to fish kills and other losses of biodiversity and poisons water sources. The potency of human agricultural niche construction is difficult to underestimate because of the rapidity at which the control webs that underlie ecosystems can be destroyed (Laland and Boogert 2010). Due recognition of the existence of such control webs, and the manner in which human cultural practices undermine them, is vital if the agricultural revolution is not to precipitate the destruction of countless other species' niches.

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Comments

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In this paper, O'Brien and Laland suggest that the integration of niche-construction theory (NCT) with gene-culture coevolutionary theory (GCT) can provide a broadly applicable approach with which archaeologists can explore evolutionary dynamics, in general, and "better understand human behavior and evolution in the agricultural niche," in particular. We are in broad agreement with the authors on the heuristic utility of the niche-construction approach and agree that the phenomenon of niche construction has likely played a fundamental role throughout human evolution and prehistory and that past human activities represent a potent cause of evolution. However, we recognize evolutionary ecology (EE) as an essential theoretical complement to effectively operationalize NCT logic in archaeological contexts, and we note that archaeological applications of EE have long encompassed the basic tenets of NCT to the extent that they view evolution as a continuous, cumulative, iterative process in which humans play a role in shaping their own selective environments. Both approaches, though, clearly have something to offer the other (Broughton, Cannon, and Bartelink 2010).

For example, more explicit use of the theoretical tools of NCT and GCT that O'Brien and Laland clearly articulate—especially the framework that it provides for considering the evolutionary roles of genetic, cultural, and facultative proximate mechanisms—can only result in further advancement of the EE approach in archaeology, which has largely ignored such issues thus far. There are two reasons, in particular, why unpacking the black box of the phenotypic gambit (Grafen 1984) could be productive.

For one, both evolutionary ecologists working in biological disciplines (Owens 2006) and archaeologists operating under different Darwinian approaches (e.g., evolutionary archaeology, dual-inheritance theory; Eerkens and Lipo 2005; Henrich 2004; Lipo et al. 2006; Mesoudi and O'Brien 2009) have begun to explore how the details of the mechanisms of inheritance can have substantial effects on evolutionary outcomes. Mismatches between EE-derived predictions and the empirical record that might potentially result from such issues could be fruitfully explored using the framework of NCT and GCT.

Second, greater consideration of such issues might also serve to strengthen the links between EE and these other Darwinian approaches in archaeology, which have traditionally placed more emphasis on the role that cultural transmission can play in the evolution and expression of the human phenotype. Because practitioners of all Darwinian approaches in archaeology share the goal of understanding the human past through the application of evolutionary logic and scientific methods, such integration of approaches, including the niche-construction perspective advocated by O'Brien and Laland, can only serve to strengthen the general Darwinian enterprise (see also Bentley, Lipo, and Maschner 2008; Cannon and Broughton 2010; Mesoudi and O'Brien 2009; Neff 2000).

At the same time, the modeling tools of EE have much to offer to advocates of the use of NCT in archaeology, and it can be argued further that EE is an effective vehicle through which to apply NCT to the archaeological record (see Broughton, Cannon, and Bartelink 2010 for detailed case studies). This is because there is, in fact, nothing in NCT-GCT, in and of itself, that allows us to predict and understand the initial variation in human behavior that ultimately becomes an explicit source of further coevolutionary dynamics within this approach. One could say that, in the framework outlined by O'Brien and Laland, human behavior is afforded the position, at least initially, of being a normative input variable. In the specific examples they discuss, for instance, the causative chains begin with "cattle farming" and "crop planting." Certainly, the authors effectively link a rich cascade of further behavioral and genetic changes to the niche-constructing factors influenced by these set behaviors, but it should be clear that the NCT approach that they advocate is silent on the socioecological factors that might influence the degree to which any group of people, past or present, should farm cattle or grow crops in the first place. By contrast, these are just the sorts of questions that EE models explicitly address, and EE models have now been successfully applied in archaeological contexts of domestication and agricultural origins the world over (e.g., Alvard and Kuznar 2010; Barlow 2002; Bird and O'Connell 2006; Broughton and Cannon 2010; Kennett and Winterhalder 2006). More explicit use of formal EE models and of EE-inspired methods can only result in further advancement of the NCT approach the authors advocate here.

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The emergence of the niche-construction perspective is among the most important advances in evolutionary theory in the last century. O'Brien and Laland have produced an important contribution, adding substantively to the growing body of niche-construction literature. Their efforts using specific examples of lactase persistence and West African sickle-cell patterns in the context of human agricultural practices and processes are decidedly in the right direction. They emphasize the need for focus on interactions between multiple evolutionary forces, the coevolution and mutual mutability between organisms and their environments, and the fact that humans are agents in their own evolution. O'Brien and Laland tackle the supremacy of natural selection as the only prominent evolutionary process, bring ecosystem engineering to the fore, and highlight how approaches focusing on niche construction and gene-culture coevolution can improve our understanding of human evolution.

However, given that we are in the midst of monumental changes across the biological and social sciences, the article could have gone farther in integrating emergent evolutionary theory, developmental perspectives, and anthropological knowledge. Despite the overall usefulness and clarity of the article, O'Brien and Laland fall prey to the lure of the "gene" and "optimality-striving" metaphors. They fail to consider that cultural evolution might not always be analogous to neo-Darwinian processes and thus underplay the potential benefits from increased engagement with a broader anthropology (e.g., Marks 2012).

Throughout the article, use of simple notions of "gene" and "trait" obfuscate what we know about the range of phenotypes and epigenetic effects even in single "gene" scenarios (e.g., Beutler 2001; Nagel 2005). This is understandable in one sense; the authors are trying to link easily modeled allele-trait outcomes with human histories and behavior. However, this approach underrepresents the evolutionary impact of the complex intertwined nature of physiological, genomic, and epigenetic systems. While there are some nods to development in the article, the reliance on relatively uncomplicated "genotype" to "phenotype" metaphors runs the risk of missing significant components in the very processes they are proposing. "Gene" and "culture" are really placeholders for much more nuanced and complex, but extremely important, elements—it is worth acknowledging this, even if it makes the analyses and explanations more difficult.

O'Brien and Laland do not engage the multiple modes of inheritance work of Jablonka and Lamb (2005; see also Jablonka and Raz 2009). Including epigenetic, behavioral, and symbolic modes of inheritance, in addition to genetic inheritance, as part of a niche-construction system makes their argument more robust. O'Brien and Laland note genetic and ecological inheritances, and their "cultural" inheritance can be seen as combining behavioral and symbolic facets, but this argument is not made explicit, and much that is entailed in human symbolic reality is not incorporated. Significant aspects of human action and inheritance are not always, or even necessarily, best understood in the context of optimal returns or fitness trade-offs.

Social, political, and symbolic histories and contexts affect and structure the evolutionarily relevant actions people undertake and experience (e.g., Dressler, Oths, and Gravlee 2005; Fuentes 2012; Gravlee 2009; Ingold 2011; Odden 2010), and this process can be integrated into the niche-construction approach (e.g., Lansing and Fox 2011; Lipatov, Brown, and Feldman 2011). This article would benefit by including a more complicated view of human agency, seeing physiological and symbolic systems as existing in significantly entangled manners (Fuentes 2009; Ingold 2007; Lansing and Fox 2011). Humans have agency in more ways than just ecological engineering; social engineering and political/economic perceptions count as factors as well. For example, Andrea Wiley's (2004, 2011) work on milk, which combines the physiological, the political, and the behavioral, alongside ecological, could have been incorporated here. The authors could go beyond stating that "the niche construction of yam cultivators [is] almost exactly mirrored in that of modern Asian tire factories, where mosquitoes infest the pools of rainwater that collect in tires stored outside, and tire export contributes to the spread of malaria and dengue" and actually consider how politics, economics, and social histories, not just basic ecological interfaces, can be niche constructive factors. Figure 3 moves in this direction (as does fig. 2*C* in Laland et al. 2011), but a more representative diagram would involve increased interfaces for mutual modification between ecological, physiological, symbolic, behavioral, and species boundaries.

I admit that the expanded approach I suggest is quite difficult, but it is the next step in advancing niche construction/gene-cultural evolution past mainstream human behavioral ecology and other traditional neo-Darwinian approaches. The continual returning to "genes" and "culture" as shorthand for genomic and epigenetic factors interfacing with the physiological, behavioral, and experiential facets of being human is insufficient. It is time to fully engage the complexity at play and the possibility that the processes of niche construction and genomic-behavioral evolution are much more elaborate than we currently imagine.

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Natural selection is the main driving force in evolution. It shapes patterns of diversity by preventing heritable traits from being transmitted from one generation to the next "purely" randomly. Niche-construction theory (NCT) is concerned with the interactions of different inheritance processes: ecological, cultural, and genetic. NCT therefore places organisms at the center of their own evolution. This happens in cases where organisms regulate ecosystem dynamics, thereby modifying selective feedbacks, which then they—and their offspring—will consequently be subject to. Using mathematical models of transmission of heritable traits, NCT has proven useful in investigating how genetic and cultural traits can coevolve and drive themselves to fixation (Silver and Di Paolo 2006). They also provide a theoretically and statistically robust framework for investigating sociocultural associations (Lipatov, Brown, and Feldman 2011).

We, as a species, are very potent niche constructors. Hunter-gatherers, for example, choose the stage when plants are to be gathered from wild fields, or which animal is better to be killed off in a wild population, in order to ensure long-term productivity (Rowley-Conwy and Layton 2011). A recent constellation of innovations that highlight how we have strongly modified our selective environment is farming, that is, plant and animal domestication. Farming enabled humans to increase the carrying capacity of their environment, leading to larger population densities. This itself is likely to have triggered increases in the accumulation of cultural complexity (Powell, Shennan, and Thomas 2009). Farming also led to genetic adaptations, including those related to dietary changes (Luca, Perry, and Di Rienzo 2010) or immunity challenges such as zoonoses (Barnes et al. 2011; Jones et al. 2008). In those cases, a particular type of niche construction can occur, where genetic adaptation is associated with cultural innovation, a process also called gene-culture coevolution.

O'Brien and Laland take two examples of gene-culture coevolution to emphasize the importance of human niche-construction ability in our recent evolution. The first example is the coevolution of lactase-persistence-associated alleles and dairying; the second is the coevolution of an allele responsible for sickle-cell anemia and yam cultivation. The authors place these two examples into a general niche-construction framework whereby organisms either instigate or work against a change in their selective environment—what the authors call inceptive versus counteractive niche construction, respectively. Inceptive and counteractive niche construction can equally be associated with two types of responses: either organisms use this new environment to their own benefit or they leave this environment for a more suitable one (what the authors call perturbation versus relocation, respectively).

The two examples O'Brien and Laland go through emphasize how interdisciplinary approaches can bring evolutionary debates forward. Both examples put together information from archaeology, anthropology, and genetics to draw an understanding of evolutionary processes. Information from various fields of research has been accumulated, and it is obvious that the answers to evolution-related questions cannot come from a single discipline, but require various bodies of specialists to collaborate. In this way, NCT is a good example of how future research should be conducted. While interdisciplinary approaches can make analysis more complex by increasing the number of parameters considered, they also have the potential to provide a more precise picture of a system under study.

While both O'Brien and Laland's examples of gene-culture coevolution appear indicative of inceptive niche construction with perturbation, the authors highlight how the choice of herding cattle and cultivating yams could also involve relocation and counteraction. According to the authors, it is likely that most cases of human niche-construction processes involve one or more of the categories within the general framework described above. If these four categories do not help us to posit meaningful evolutionary questions, then appreciating how useful the niche-construction framework may be is not straightforward. Equally, it has been suggested that niche construction is likely to occur in structured environments (Hui, Zizhen, and Yue 2004; Silver and Di Paolo 2006). Homogenous environments seem quite rare, in which case niche construction happens all the time, everywhere. This questions how useful a phenomenon that occurs in every situation is for understanding the evolution of a system.

Disentangling the effects of various factors is not an easy task. Computer simulations coupled with approximate Bayesian computation (ABC; Bertorelle, Benazzo, and Mona 2010) techniques represent one of the most promising approaches for combining multiple sources of information and test scenarios, that is, hypotheses (Fagundes et al. 2007; Ray et al. 2009). The important addition of ABC techniques to niche-construction approaches would introduce model fitting based on descriptions of observed data. This approach enables (i) assessing what are the parameters that affect most observed outcomes and (ii) identifying equally likely scenarios or assessing their relative probabilities.

That humans are potent niche constructors is beyond doubt, as O'Brien and Laland make clear. What is questionable is the extent to which NCT is a necessary explanatory component of any human evolutionary model. For example, would an NCT approach provide much deeper understanding on the extinction of Neanderthals than what we already know about how modern humans, as a very competitive species, have outcompeted them?

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O'Brien and Laland's article is part of an increasing trend to integrate evolutionary thinking into all areas of anthropology. While health systems probably best illustrate gene-culture coevolution (GCC) and niche construction, I suspect that other examples will lead to similarly important anthropological insights. The emphasis on GCC helps to return culture back to the center of evolutionary anthropology, in step with recent movements in biology to focus strongly on epigenetic factors that interact with genetic instructions to create phenotypes. Like genes and culture, genetic and epigenetic systems in other organisms coevolve. Welcome to the twenty-first century, where biological simplicity has given way to a new complex appreciation for phenotypes, including the full suite of human behaviors.

My position here is simple: I strongly endorse the O'Brien and Laland viewpoint, but will go even further in making explicit the centrality of niche construction to all of anthropology, and emphasizing that this consists of the coevolution of human genes and cultural variants, along with the coevolution of genes and extra somatic features of other organisms, all wrapped up into packages that evolve through vertical transmission. The idea that traits can evolve through community-level selection is a controversial but fascinating topic in biology (e.g., Dethlefsen, McFall-Ngai, and Relman 2007; Swenson, Wilson, and Elias 2000).

O'Brien and Laland present an integrated framework that consists of niche-construction theory (NCT) and gene-culture coevolution theory (GCT). They illustrate its explanatory potential by examining the spread of two cultural innovations—agriculture and animal farming. In O'Brien and Laland's view, these practices spread because of (*a*) complex bidirectional relationships between built environments and changes in the gene frequencies of humans and other organisms and (*b*) group-level vertical transmission of these packages coupled with ever increasing amplification of coevolving cultural and genetic traits. In other words, O'Brien and Laland propose that "packages" of multiple causes and effects are passed from one generation to the next through ecological, social, and genetic-inheritance mechanisms giving rise to ever-increasing complex group-level phenomena. Because different gene-culture complexes compete for space and resources, and group-level vertical transmission is typical, this may result in group-level selection. I would prefer to call the outcome of this process "gene-culture evolutionary niches" (GCEN). Like chromosomes, GCENs have subcomponents that change at different rates or that reach fixation. GCENs may be heritable conglomerates that create selective pressures acting on individuals and social groups.

Consider two examples presented by O'Brien and Laland. Cattle farming links humans and many other organisms and creates new environments of subsequent adaptation for all. Cattle are the main food staple; they change the landscape of plants and are themselves niches for micro- and macroparasites. O'Brien and Laland focus on milk production and consumption aspects of cattle farming, their effects on LP allele frequencies, the expression of lactose tolerance, and changes in the gene frequencies of cattle through selection for high yields of milk. Human cultural innovation then ratchets up the arms race once again, forcing a new round of adaptation and counterresponse.

Crop planting also produces complex niches. Deforestation creates swamps, swamps become breeding grounds for mosquitoes, and mosquitoes become breeding reservoirs for *Falciparum* pathogens. The crop-planting niche unleashes a cascade of effects that change the biology of the organisms within it—gene frequencies in humans (*HbS* alleles), mosquitoes (breeding site preference alleles), and *Falciparum* (resistance to human immune defense alleles). But things might be even more interesting. In the early pre-*HbS* genetic adaptation stages of the crop-planting niche, *Falciparum* species may have caused high prevalence rates of malaria-related morbidity. In order to emerge and spread, humans may have added to the crop-planting niche new or amplified norms such as "care for the sick when possible, and elicit help from others when ill." These types of prosocial tendencies might have coevolved with crop-planting and malarial parasites, such that initial niches are even more complex than was once thought.

Niche contstruction is to me a critical framework for exploring the human evolutionary trajectory of exceptionally complex human diversity. Whereas shifts to crop-planting and cattle farming provide well-studied examples of this process, similar gene-culture and niche construction probably began long before. When our hominin ancestors first shifted to hunting prey, they may have experienced greatly increased exposure to zoonotic diseases from prey and pets. This may have led to cultural solutions such as bathing and distant defecation, prosocial care of the sick, and cooking. These provide new adaptive landscapes for plethoras of human pathogens and parasites (see Wrangham 2009).

In summary, although agriculture and animal domestication are critical examples, the introduction to GCEN, in my view, is critical for integrating the social and biological sciences into a larger and more complete understanding of life on our planet.

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O'Brien and Laland point out that human culture is exceptional in its cumulative nature. This is often characterized by the ratchet effect, highlighting that high-fidelity social transmission can underpin the accumulation of trait modifications. They also note that the developmental niche-construction processes underlying cultural evolution are understudied. I agree that the evolutionary consequences of culturally constructed learning environments are indeed understudied and that attention to this area may provide a fresh assessment of cumulative cultural evolution.

An important focus of cumulative cultural evolution research is in assessing individual cognitive prerequisites that facilitate high-fidelity cultural transmission and the adoption of adaptive innovations (Ehn and Laland 2012). However, it is also important to consider the role of developmental niche construction and the ecological inheritance of learning environments, including forms of symbolic representation and material culture, on cumulative cultural evolution (Cole 1995; Sterelny 2012; Wheeler and Clark 2009).

Culturally derived scaffolding for learning can have a direct effect on the differential adoption and retention of cultural traits (cultural selection). For instance, pedagogical traditions in apprenticeships, including traditional patterns of intervention, correction, and collaboration may influence the fidelity of transmission and the potential for cumulative cultural evolution (Gergely and Csibra 2006; Tehrani and Reide 2008; Tennie, Call, and Tomasello 2009).

There is also the potential for cumulative cultural evolutionary dynamics to be shaped by forms of symbolic representation. Mathematical history provides particularly obvious examples, where invention of new notation systems, for instance Hindu-Arabic in place of Roman numerals or Feynman diagrams in quantum mechanics, dramatically altered the evolvability of research fields (Gauvain 1998).

Thus, for the cumulative cultural evolution of many traits, high-fidelity social transmission and the potential for invention may be critically affected by culturally constructed learning environments (Tennie, Call, and Tomasello 2009). Furthermore, a complete account of cognition required for cumulative cultural evolution may often be reliant on its extension beyond the mind of the individual and on its distributed nature across people and artefacts (Donald 2000; Hutchins 1995, 2008). Without accounting explicitly for the role of developmental niche construction and the ecological inheritance of learning environments, there can be an over- or misattribution of cognitive facility to the mind in order to explain the cumulative cultural evolution of skills such as computational tasks (Hutchins 1995).

O'Brien and Laland provide a detailed account of potential gene-culture coevolutionary pathways affecting the cumulative cultural evolution of farming technologies and medicinal practices. A key process in these dynamics is likely to be the niche construction of inherited learning environments, which themselves can be subject to cultural selection and affected by ecological and genetic evolutionary dynamics of human, crop, livestock, and pathogen populations. Thus, the simple ratchet analogy hides complex mechanisms that can result in cumulative cultural evolution of knowledge and beliefs (Tennie, Call, and Tomasello 2009).

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O'Brien and Laland advocate niche-construction theory and gene-culture coevolutionary theory as a broad theoretical framework useful to archaeology and anthropology. I would like to press this claim further and to argue that niche-construction theory offers a route toward encompassing the social and biological sciences in a single theoretical framework.

Durkheim argued that the social sciences study the emergent properties of social systems. In his statistical study of suicide (Durkheim 1952 [1897]), he proposed that the sociological dimension of suicide was to be found in the correlation between suicide rates and the relative coherence of society. Lansing (2003:185) points out Durkheim's remarkable prescience in anticipating the development of complex systems theory, arguing that the concept of fitness landscape developed by Sewell-Wright arose from the work of pioneers in statistics such as Durkheim. Lansing's study of Balinese water temple networks as complex adaptive systems found that, although local communities do not consciously attempt to create an optimal pattern of staggered cropping schedules for entire watersheds, the actual patterns closely resemble computer simulations of the optimal solution. Global control of terrace ecology emerges as local actors strike a balance between opposing constraints (Lansing 2003:199). Giddens's (1984:35) description of "structuration," the long-term process through which agents are bound together in a social network, is entirely compatible with this approach (cf. Kendal, forthcoming). O'Brien and Laland point out that "ecological inheritance more closely resembles the inheritance of land or other property than it does the inheritance of genes."

Durkheim used an analogy taken from Darwin to challenge his contemporary Tarde's account of the diffusion of innovations as a simple transmission chain, writing: "Darwin says that in a small area, opened to immigration, and where, consequently, the conflict of individuals must be acute, there is always to be seen a very great diversity in the species inhabiting it" (Durkheim 1933 [1893]:266; see also Layton 2010). When rural communities expand, Durkheim argued, they come into competition for resources. The success of innovations was determined by this social process (Durkheim 1933 [1893]: 266). Animal populations adapted to competition by finding specialized ecological niches, while human communities responded by adapting specialized economies: some developed wine production, some wheat, some industrial products. A similar tendency has been documented in many ethnographic studies of forager-farmer interaction (e.g., Blackburn 1982; Junker 1996; Turnbull 1965).

O'Brien and Laland touch on the problem of intentionality versus unintended consequences in cultural selection. In the spirit of Boyd and Richerson (1985), I think it would be useful to take this issue further. The case studies in the O'Brien and Laland paper suggest several possible processes of gene-culture coevolution that can be mathematically modeled (Jeremy Kendal [personal communication] recommends Odling-Smee, Laland, and Feldman 2003):

1. A new cultural practice creates a niche that changes the selection pressure on genes, which, over a period of thousands of years, increases the frequency of alleles that provide a more effective adaptation to the new niche.

2. A new cultural practice creates a niche that changes the selection pressure on genes, which is buffered by the introduction of further innovative cultural practices.

Itan et al. (2009) note that it is very likely the prehistoric dairy-based economies of the Mediterranean processed milk into yogurt and cheese, thus breaking down the lactose content before consumption. Most of the Mediterranean consequently lies outside the area where positive selection for the allele for lactase persistence was taking place. O'Brien and Laland cite the case of the Kwa concentrating on cultivating crops that alleviate the effects of sickling. They suggest "it would be too much of a coincidence—not to mention an irony—for a population to just happen to have chosen by chance a crop that alleviates the symptoms of the disease." Yet there are in fact two possibilities: (i) The Kwa recognize that yams have a beneficial effect on health and deliberately favor their cultivation. (ii) Those Kwa who happen by chance to favor yam cultivation have greater reproductive success than those who don't, and the trait is transmitted through what Bourdieu termed "habitus": the practices and values that members of a community have absorbed in a largely unreflective way as they grow up and which guide their social strategies (Bourdieu 1977 [1972]:76–77), thus coming over time to outcompete alternative agricultural practices.

The critical factor here will surely be the length of time that it takes for the beneficial effects of the new practice to become apparent. If the causal relationship can be perceived within one generation (e.g., milk processing), then deliberate cultural selection is plausible. The evolution of the allele for lactase persistence over thousands of years is very unlikely to have been apparent to members of the population experiencing it. The preferential cultivation of crops probably lies between these extremes. Allen (1989) showed that, in an unpredictable pursuit such as marine fishing, the most effective strategy emerged if the population of fishermen was made up of two types, *stochasts*, who behaved in an apparently random manner, and *cartesians*, who behaved rationally in light of the incomplete information available to them.

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O'Brien and Laland propose that the exceptional capacity of humans to modify their own environment (niche construction), in conjunction with their ability to transmit information and resources across generations (gene-culture evolution), has been a potent force in shaping the modern human genome. This niche-construction gene-culture view of evolution (termed NCGC here) differs from the more conventional view of evolution where the organism adapts to its predetermined environment, in that it focuses on the evolution (both genetic and cultural) of a behavior that alters the environment in ways that generate genetic changes in other traits. Examples given are lactose tolerance in response to the dairying culture and sickle-cell anemia in response to cropping practices that cause higher densities of malaria-carrying mosquitoes. They argue that the human genome harbors many examples of culture-driven selection that result from its recent adaptation from a nomadic lifestyle in the African savannah to the many diverse habitats that it currently occupies.

This framework may have much to offer the study of human disease. NCGC brings to the fore the notion that disease is essentially the outcome of a mismatch between environment and genome. In humans, this mismatch has been brought about by self-induced change in habitat or culture, but this has occurred so fast that the genome has not always been able to keep up. Obvious examples are the high rate of type 2 diabetes among the indigenous people of Australia and skin cancer among their European colonists. Where the genome has kept up, it is assumed to have done so through "selective sweeps," in which mutations with large favorable effects in the new environment rise rapidly to fixation, carrying with them chunks of the surrounding genome (haplotypes). Many candidate adaptive genes have been discovered in this way. But adaptation to new environments may not always proceed in this fashion: instead, multiple advantageous mutations, each with small effect, may arise but only reach intermediate frequencies due to concomitant fitness costs (Pritchard, Pickrell, and Coop 2010). Under such balancing selection, one expects to find clines in frequencies of adaptive mutations across environmental selection gradients (Coop et al. 2010; Novembre and Di Rienzo 2009; Pritchard, Pickrell, and Coop 2010). An excellent example of this is the global geographic correlation between malaria transmission intensity and the frequency of the sickle gene found on a global scale (Piel et al. 2010) and also on a local scale across an altitude gradient in Tanzania (Enevold et al. 2007). In recent years, this same principle has been applied to genome-wide discovery of new genes involved in adaptation to high altitude, temperature, and dietary types (Hancock et al. 2008, 2010*a*, 2010*b*, 2011). If NCGC is as important as O'Brien and Laland say, this "environmental correlation" approach (Coop et al. 2010), which particularly exploits niche-specific adaptations across diverse environments, may be valuable for further unraveling of the genetic basis of human disease.

The NCGC concept of feedback by the organism into its environment, thus altering its genetic destiny, will resonate with infectious-disease ecologists. Pathogens, like humans, are consummate niche constructors. Understanding host-pathogen interactions centers on how the pathogen modifies its host environment, and how that leads to the specific genetic adaptations that allow the pathogen to exploit and survive its host. Pathogens greatly alter their environment by evoking immune responses: this imposes selection pressure on the pathogen to circumvent (e.g., by changing epitopes), subvert (e.g., by damping the immune response), and avoid (e.g., by hiding in different tissues) the immune system. They also spoil their own environment by destroying their resources, for example, red blood cells. Outside the host, pathogens change the environment of future pathogen generations by leaving behind immune hosts, analogous to the "ecological" inheritance of NCGC. There exists a large amount of theory in disease transmission dynamics, in-host dynamics, and the evolution of pathogen strategies to deal with self-induced changes in their host environment (e.g., the evolution of antigenic variability, virulence, host exploitation, manipulation of host behavior), all of which feature feedback between self-induced changes to the pathogen's environment and its onward transmission and evolution. There may be much benefit to closer dialogue between pathogen evolutionary ecologists and NCGC theorists.

A more heuristic example of where NCGC might inform disease research stems from its distinction between the ways in which the organism alters its environment, namely, whether the behavior is inceptive or counteractive, and whether it perturbs the existing environment or involves relocation to a new one. Did populations with lower frequencies of the sickle gene end up living in areas of low malaria transmission intensity out of choice, or were they selected that way (the conventional view; Enevold et al. 2007)? Has the practice of circumcision driven population differences in resistance to sexually transmitted diseases? Can the burden of noninfectious disease be largely eliminated by managing diet and lifestyle? Given the web of interactions in the vertebrate immune system, how should pathogens evolve? By focusing on environmental modification as the primary driver of evolution, NCGC may stimulate new ways of thinking about the ultimate causes of disease, thus potentially leading to better ways to cure and avoid it.

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> *By the use of our hands, we bring into being within the realm of Nature a second nature for ourselves.*
> (Cicero, *De Natura Deorum* II 60)

In "Genes, Culture, and Agriculture: An Example of Human Niche Construction," Michael O'Brien and Kevin Laland reaffirm that few, if any, topics in anthropology have received more attention than the origins of agriculture. It would seem that part of the attraction to making sense of agriculture—the broader intellectual problématique, really—lies in the interaction between humans, their environment, their culture, and the element of agency that exists between these components. Certainly, the theme of culture, nature, and human agency is, in a historical sense, not unique (Cassirer 1961 [1942])—however, O'Brien and Laland's argument that archaeology is uniquely posed to demonstrate humanity's making a "second nature" is particularly compelling.

"Genes, Culture, and Agriculture" would seem to remind us that a theoretical framework is useful to archaeology to solve an interesting problem or question. Indeed, O'Brien and Laland's article isn't so much an argument toward a specifically new model of archaeological knowledge or theory; rather, they remind us that the parts of their rhetoric are scattered across a truly interdisciplinary scientific literature. To this end, they draw on two primary theoretical models, niche-construction theory (NCT) and gene-culture coevolutionary theory (GCT), that, when combined, neatly explain "major transformation[s] in human selection pressures, recognized through substantive genetic change in human populations . . . , and virtually all have been self-imposed." "There is now little doubt that human cultural niche construction has codirected human evolution" (drawing also from Laland, Odling-Smee, and Myles 2010).

In brief, NCT associates the concept of the niche with a species, rather than a specific geographical place, and specifies a "multidimensional hyperspace" of factors, where their space is modified through many factors, including their own agency (Laland and Sterelny 2006; Lewontin 1983). O'Brien and Laland take this relatively recent theoretical schema in biology and combine it with GCT, a branch of theoretical population genetics that assumes cultural traits as being integral in the differential transmission of genes (Richerson, Boyd, and Henrich 2010).

One might ask, What do NCT and GCT have to offer archaeology that other theories or models don't, particularly in terms of the question of agriculture? Why this explanatory schema as opposed to any of the others? What makes this so uniquely compelling? In short, O'Brien and Laland argue that the dual approach of NCT and GCT contain a certain seamlessness in rhetoric and archaeological evidence that could maintain widespread utility, as seen in O'Brien and Laland's examples of dairying by Neolithic groups in Europe and Africa with the rise of the sickle-cell allele among certain agricultural groups in West Africa.

On a more subtle level, however, it would seem as though O'Brien and Laland are offering a disciplinary gesture toward archaeology's legitimacy on the grander stage of NCT and GCT. In moving theory and explanation of biology and culture beyond simply the catch-all of the "Modern Synthesis," many disciplines, like biology, ecology, and genetics, have sought to explore other "dimensions" of evolution, including cultural or symbolic ones (Jablonka and Lamb 2005). Rather than see culture as something "tacked on" as an afterthought of sorts, there are specific efforts to map culture into a specific explanatory schema. What O'Brien and Laland successfully illustrate is that archaeology has a particularly useful depth of data—the deep history and temporal sequences that other disciplines simply don't have. Archaeology's useful examples through process and material culture—the examples of dairying by Neolithic groups and research surrounding other agricultural examples—offer archaeology a place in the broader conversation of niche-construction theory and gene-culture coevolutionary theory (Kendal, Tehrani, and Odling-Smee 2011).

One could see O'Brien and Laland's article as a compelling summary of specific archaeological examples toward niche-construction theory and gene-culture coevolutionary theory, which, in short, it is. However, the real strength of their rhetoric lies not only in the commitment to specific evolutionary theories or models, but in its exploration of the historical depth that speaks to the themes of nature and culture. One sees the historical depth behind Cicero's comment that humanity remakes nature into a second nature for itself. This article serves as a gloss on a thematic text, so to speak—a reaffirmation of the historical context and timelessness of this theme.

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Several interesting questions come into focus when O'Brien and Laland's discussion of niche-construction theory (NCT) and gene-culture coevolutionary theory (GCT) is considered in a broader context. Providing a welcome addition to the recent literature heralding the coalescence of a new human niche-construction (HNCT) paradigm in the study of past and present-day patterns of human-environmental interaction, their article is paradigmatic in both meanings of the term (Kuhn 1962) in that they provide empirical case studies for emulation, while also outlining the theoretical foundation of their NCT-GCT perspective.

The newly emerging HNCT paradigm to which the O'Brien-Laland article contributes offers a refreshing alternative to the long-established human behavioral ecology–optimal foraging (HBE-OFT) paradigm first proposed in the mid-1970s (Winterhalder and Smith 2000). While HNCT and HBE trace their origins respectively to NCT (NCT→HNCT) and behavioral ecology (BE→HBE), NCT is a much more recently emerged and robust perspective (Odling-Smee, Laland, and Feldman 1996, 2003), and the initial application of HNCT in anthropology dates to the middle of the last decade (B. D. Smith 2007*a*).

From its inception, HBE has invested heavily in optimal foraging theory models in an effort to understand hunter-gatherer decision making regarding resource selection and land use (Winterhalder and Smith 2000:51). As a result, HBE and OFT have frequently been viewed as synonymous. As a general area of inquiry in biology, however, behavioral ecology has always encompassed a much broader range of perspectives than OFT (BE $\gg$ OFT), and optimizing models have steadily declined in popularity in biology in recent years, even as OFT perspectives have continued to dominate HBE. A more deliberate definitional decoupling of HBE and OFT over the next decade, which is already underway as HBE practitioners extend their search for appropriate models beyond optimization, should allow for the appropriate inclusion under the general HBE heading of newer perspectives such as HNCT and GCT and smooth the shift away from optimization models to more up-to-date and empirically supported perspectives within the general family of HBE approaches to human-environmental interaction. To add another acronym to the equation, the rich record of ethnobiological studies of traditional ecological knowledge practices and systems (TEK) reflects a long history of HNCT analysis under another label (TEK = HNCT; B. D. Smith 2011*a*, 2012).

Under the general heading of HBE, different perspectives (including OFT, HNCT, TEK, and GCT) can offer a variety of sources for the formulation of alternative hypotheses to account for various aspects of human interaction with ecosystems, and the relative strength of such competing proposed explanations can then be empirically tested with available relevant data. O'Brien and Laland emphasize that their NCT-GCT approach draws attention "to a range of phenomena that are both important and easy to overlook using standard perspectives," that it promotes "consideration of the active agency of humans . . . in modifying their ecological and developmental niches," and that it generates "novel hypotheses about human evolution," which can then be evaluated by determining "the degree of fit between expectations . . . and select aspects of the empirical record." A key point here is that while theoretical perspectives like NCT or OFT are the font of specific hypotheses, the relative explanatory value of hypotheses once generated is determined not by the currency or popularity of the parent perspective or paradigm, but by the extent to which such hypotheses are supported by available information. To this I would add that, given the limited amount of relevant information that is usually available in the archaeological record, it is important to compare the relative strength of a number of alternative hypotheses, rather than narrowly focusing on a solitary favored explanation, which has long been a hallmark of OFT studies (B. D. Smith 2006, 2012).

O'Brien and Laland's quite brief discussion of agricultural origins provides a good example of the importance of weighing the relative strength of alternative explanations rather than considering a single scenario in isolation. They offer a "testable prediction that where agriculture originates in otherwise rich zones, we should witness signs of population growth and resource depression." This prediction—that the initial domestication of plants and animals was in response to human population growth and resource depression—somewhat surprisingly conforms to the general OFT characterization of initial domestication, and contrary to NCT, appears to embrace OFT's outmoded concept of unidirectional adaptation. In contrast, a recently proposed alternative explanatory framework based on NCT, TRM, and central place provisioning (CPP; B. D. Smith 2012) predicts that initial domestication occurred in the context of resource-rich environments in the absence of human population pressure or resource depression. When the relative strength of these two competing explanations is measured in those centers of domestication where considerable archaeological and environmental information is available (e.g., eastern North America, east Asia, and the Near East), there is no indication of resource depression or population growth, and the NCT-based explanation provides a much better fit with currently available evidence (Smith and Yarnell 2009; Zeder 2012; Zeder and Smith 2009).

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I endorse the general theoretical stance developed in this paper: hominins have engineered their physical, biological, and social environments, thus transforming the selective forces acting on our lineage. Hominin evolution can be understood only by understanding the ways in which hominins have both responded to and changed hominin environments. O'Brien and Laland are also right to identify culture as mediating the interplay between lineage and environment. Hominins are potent agents of environmental change in part because we are cooperative primates: like ants and termites, we change our world through the power of collective action. But we are potent because we are rich in informational resources; we learn from others in ways that allow us to transmit to the next generation a modified version of the informational resources we inherit from the previous generation. Cooperation and information powered niche construction is a world-changing combination. Hominin genomes did indeed change as a downstream consequence of culturally mediated niche construction.

Thus, I have no complaints about the framework; indeed, I have used it myself (Sterelny 2003, 2012). But I have a few cautions about the application of the framework to the specific examples. A minor caution is about selection for lactose tolerance. The selective dynamic here is less transparent than the paper suggests, for as O'Brien and Laland note, milk products can be transformed into low-lactose forms (cheese, yogurt). These low-lactose forms are independently useful, since they can be stored longer and transported more readily than milk. Moreover, some version of this technology must have been available early in the histories of dairying; otherwise, dairying would have offered little to predominantly lactose-intolerant populations. Early, lactose-intolerant farming populations exploited dairy resources through these low-lactose forms. What then drove the selective sweep to high levels of tolerance? Perhaps change was mediated by young children drinking milk, enabling mothers to wean earlier. This route to a lactose-tolerant population might be especially effective if there were developmental plasticity in the mechanisms that switch off infants' production of lactase: if milk drinking acted as a mechanism that kept lactase flowing. But how would we use the theory of gene-culture coevolution to test this conjecture?

This minor reservation leads to my more general caution. O'Brien and Laland elegantly and convincingly synthesize the insights of niche construction and gene-culture coevolution in their articulation of the evolutionary dynamics of malaria resistance and lactose tolerance. But this synthesis depends on two special features of these cases. In both cases, the gene-to-phenotype relationship is short, direct, and specific. The relevant traits seem to be under genetic control, in a strong and simple sense: there really do seem to be genes for tolerance and resistance. Second, human populations are structured in ways that allow O'Brien and Laland to use comparative methods: to compare dairying populations with populations with little historical exposure to milk products; to compare populations exposed to the threat of malaria with those that were not. Evolutionary anthropology's problems are typically less tractable. Consider, for example, the origins and expansion of clothing and its relation to body hair, body shape, fat distribution, and the like. Even if the genotype-phenotype map of these traits were simple, the human lineage is not conveniently structured into clothed and naked subpopulations. Moreover, we do not have much handle on the extent and variability of clothing over time (for bold attempts, see Gilligan 2007; Kittler, Kayser, and Stoneking 2003; Toups et al. 2011). It is surely true that the elaboration of clothing has left marks on human genomes and bodies, but identifying them may be very difficult. When our focus changes to behavioral and cognitive traits, the problems of marrying population genetics to niche-construction theory are even greater. Consider, for example, the role of teaching in human cumulative culture. It is very likely an evolutionary response to, and engine of, niche construction. But the genotype-phenotype map is likely to be very complex indeed, and the population history of teaching is obscured.

Of course, O'Brien and Laland should start with the simplest cases. Where else would one start? But I doubt whether these simpler cases will be much of a model for getting genetics to talk to archaeology in these more complex ones, with less cooperative genetics and less-well-preserved population structure.

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This is an important paper: it expands on previous gene-culture niche-construction arguments and introduces new scientific information that strengthens the gene-culture coevolutionary argument; in addition, it presents two highly useful new schematic models (fig. 3) of the evolutionary consequences of cultural niche construction and human interactions with other organisms. While I recognize that O'Brien and Laland were striving for simplicity in these models, my comments highlight several critical variables that have been omitted, which I believe are necessary for the models to work.

In the case of dairying, O'Brien and Laland only briefly allude to the role of microorganisms (combinations of yeasts, bacteria, and fungi) in the manufacturing of secondary products from milk. Yet the practice of harnessing microorganisms to create milk products, for example, fermentation by natural lactic acids, is in itself a developmental niche, one that provides an effective alternative to LP alleles because it transforms milk into forms that can be digested by people who are lactose intolerant. Natural lactic acid bacteria thus represent a third set of participants (in addition to humans and cattle), situated between steps 4–6 in the dairy-farming construction model (fig. 3*A*).

I am not convinced by the proposed sequence of events of the yam crop planting construction chain (fig. 3*B*), particularly the idea that yam agriculture developed because yams were substituted for other crops only after the discovery of their beneficial antimalarial properties. Aside from the likelihood that the medicinal properties of yams were probably known long before agriculture began in West Africa, this scenario overlooks people-plant interactions that facilitated the cultivation of these root crops in the first place. It also overlooks genetic change(s) in yams themselves, many of which doubtlessly resulted from human selection and cropping practices and, in turn, eventually influenced the selection and crop-planting practices of Kwa-speaking yam farmers, and subsequently the rise of the *HbS* allele.

It was not O'Brien and Laland's aim to discuss the timing and processes by which African yams were domesticated, nor is it mine. (In fact, the taxonomic status of the indigenous West African domesticate species [the white Guinea yam, *Dioscorea rotundata* Poir, and yellow Guinea yam, *Dioscorea cayenensis* Lam.] remain in question; in the case of *D. rotundata*, for example, genetic studies have been hampered by the nonexistence of a diploid wild relative and various levels of ploidy, attributed to events that occurred thousands of years ago, such as hybridization, retrogression, and infraspecific variation (Mignouna et al. 2002). Nevertheless, the relationship between yam genetics and human cultural practices is highly relevant here. Therefore, I propose an amended yam-planting construction chain that links yam genes, the inherent botanical characteristics of yams, and human selection through culinary and husbandry practices.

In this amended scenario: (i) prior to agriculture in this region, West African hunter-gathers recognized the food (and possibly medicinal) potential of the wild ancestor(s) of edible yams; through their harvesting and consumption of wild yams, these groups developed significant ecological, culinary, and technological expertise on this plant; (ii) the increasing cultural and economic importance of yams led to a developmental niche, consisting of specialized food-processing techniques and precise selection, planting, and cultivation practices aimed at enhancing specific sensory (taste, texture) qualities and improving tuber productivity, for example, larger tuber size and/or changes to plant morphology that made the tubers easier to uproot; (iii) over time, human-induced genetic change (domestication) of yams occurred with the rise and spread of alleles for particular physiochemical qualities (affecting tuber taste, texture) and morphological characteristics that promote tuber productivity (see above); (iv) conferred with these preferred culinary qualities (which varied among different ethnic groups according to their traditional culinary preferences) and greater productivity over their wild counterparts, the advantages of the domesticated yams motivated people to consume them more frequently, to plant greater numbers and devote larger areas of land to their production; (v) ethically distinct farming and culinary practices evolved, resulting in the specific varieties of yams being produced by specific ethnic groups; in the case of Kwa-speaking yam farmers, their distinct planting practices created more areas of water pooling, increased mosquito breeding, and an increased prevalence of malaria and; (vi) continuing increases in yam consumption for medicinal as well as culinary benefits; among Kwa-speaking farmers, there was a rise and spread of the *HbS* allele, which confers resistance to malaria and also promotes sickle-cell anemia.

Support for this proposed scenario can be inferred from the apparent time depth of the white Guinea yam genome (Mignouna et al. 2002), probable antiquity of human-yam interactions in East Africa, and obvious interdependence of people's culinary knowledge, dietary choices, farming practices, and crop biodiversity, and the associations between particular ethnic groups and specific yam varieties (Ayensu and Coursey 1972; Baco, Biaou, and Lescure 2007; Brydon 1981; Coursey and Coursey 1971; Digbeu et al. 2009).

Reply

We thank all of those who commented on our article. Each response offers numerous excellent points, and here we attempt to address as many of them as possible. We are delighted with the overwhelmingly positive response and are tempted to interpret this as a sign that niche-construction theory (NCT), suitably combined with gene-culture coevolution (GCC) and other established features of behavioral and evolutionary ecology, has the potential to become a central component of the toolbox used in the human sciences.

We agree with Broughton and Cannon that the NCT-GCC framework can usefully be complemented by the thinking, models, and methods of evolutionary (and behavioral) ecology and that these potentially have considerable utility in predicting where and what niche-constructing behavior will occur. We also agree that it is likely to matter what the processes underlying niche construction are, that different processes will elicit different ecological and evolutionary outcomes, and that building process-specific evolutionary models is a useful way forward. However, we stress that NCT is not entirely silent on where, and under what conditions, niche construction will be favored. Although the bulk of NCT has explored the evolutionary consequences of niche construction, we can point to several analyses that investigate its evolution. Indeed, one important message of NCT is that consequences and evolution frequently cannot be studied independently, given that the niche-constructing trait coevolves with a recipient character whose fitness is modified by the constructed environment (Kylafis and Loreau 2008; Laland, Odling-Smee, and Feldman 1996, 1999, 2001; Lehmann 2007, 2008; Rendell et al. 2010; Silver and Di Paolo 2006).

Fuentes endorses our approach but is concerned that we are overly wedded to a genetic metaphor for culture, overly reliant on optimality thinking, and fail to consider that cultural evolution might not be analogous to neo-Darwinian processes. We agree that population-genetic and phylogenetic styles of modeling cultural processes, which frequently treat cultural evolution as changes in trait frequency, may not adequately capture some important aspects of culture, such as the roles of institutions, but we contest the assertion that we—and for that matter others (e.g., Boyd and Richerson, Feldman, Henrich) who model culture—are wedded to optimality thinking and have failed to consider the differences between cultural evolution and neo-Darwinian processes. GCC theories explicitly incorporate countless alternatives to conventional biological evolutionary models, including the centrality of learning rules such as conformity- or payoff-biased copying and, as we underscore in this paper, the importance of complicated multigenerational legacies such as ecological inheritance. These refinements are incorporated as explicit recognition of the differences between biological and cultural evolution, and it is a distortion to imply that cultural evolutionists are mindlessly applying biological theory to culture.

If there is a difference in perspective here, it is between those who are content to describe the world and those who wish to go further and analyze it through mathematical modeling or experimentation. The latter inevitably requires simplification to bring insight. Simply substituting a complex model for a complex world does not aid our understanding, and experiments rapidly become cumbersome and intractable unless nonfocal processes are held constant. The NCT-GCC approach is an overarching conceptual framework that both draws attention to the kinds of processes and feedbacks that might be operating in any specific system and describes generalities across systems. Such a framework can embrace complexity because its function is largely descriptive. However, researchers can, and should, do more than this. Both NCT and GCC, like cultural evolution models, have been used to address more specific issues—the evolutionary consequences of ecological inheritance, the coevolution of milk use and alleles for adult lactase persistence, the circumstances under which conformity is favored by selection—and simplification is vital if an analytical exercise is to be useful.

At this level, alternative processes and feedback can be incorporated only by leaving out other processes. Nonetheless, analyses such as these are of great value because, unlike the overarching framework, they can generate compelling answers to the kinds of issues listed above. It is precisely because our minds cannot juggle how multiple interacting variables will play out that constructing a model is often useful. We would like to believe that there is a middle ground to be found here between an entirely descriptive holism, or the destructive negativity of some critics of cultural evolution modeling (e.g., Marks 2012), and the unthinking and inflexible application of biological metaphors to culture.

Gerbault questions how useful a phenomenon that occurs in every situation is for understanding the evolution of a system. All organisms niche-construct, albeit to greater and lesser degrees, and with consequences that range from the entirely negligible to the globally important. Nonetheless, it would be a mistake to dismiss niche construction just because it is universal. After all, natural selection is a universal feature of living organisms too, and we do not disregard it. Equally, growth, development, and metabolism are all worthy topics of study despite being characteristic of all life. The important point is this: as both the potency and the consequences (be they evolutionary, ecological, or social) of niche construction vary dramatically from species to species, and from case to case, it is interesting and important to isolate where niche construction affects the dynamics.

More generally, we have three answers to the question of how NCT is useful to human scientists:

1. NCT has heuristic value in drawing attention to the active agency of humans as a source of environmental and social change as well as to the evolutionary, ecological, and social ramifications of human niche construction. By foregrounding niche construction, NCT reduces the likelihood that it will be neglected (Laland and Sterelny 2006).

2. NCT offers conceptual tools for understanding human-science phenomena. These range from the overarching conceptual framework depicted in our article and elsewhere, to established ways of categorizing and organizing cases of niche construction (perturbation vs. relocation, inceptive vs. counteractive, positive vs. negative), to a variety of experimental and theoretical methods for establishing where niche construction is consequential and quantifying its impact (Odling-Smee, Laland, and Feldman 2003).

3. NCT offers theoretically and empirically derived insights into the dynamics of evolving systems under the influence of niche construction. It is now well established that niche construction can affect evolutionary rates, change evolutionary equilibria, preserve genetic and phenotypic variation, generate time lags in response to selection (with associated momentum, inertia, catastrophic, and cyclical effects), drive niche-constructing traits to fixation in a runaway process, propagate costly traits that have a selective disadvantage in the current generation, allow the persistence of organisms in currently inhospitable conditions, affect carrying capacities, and more (Kerr et al. 1999; Krakauer, Page, and Erwin 2009; Kylafis and Loreau 2008; Laland, Odling-Smee, and Feldman 1996, 1999, 2001; Lehmann 2007, 2008; Rendell et al. 2010; Silver and Di Paolo 2006). Scientists working in the human realm can draw from these established findings to better understand the complex dynamics of their own study systems.

We (re)emphasize that NCT is no panacea for difficult theoretical and methodological issues. Put bluntly, it will not "magic up" answers to challenging and often long-standing puzzles. Nonetheless, its careful application, combined with a detailed understanding of the system at hand, potentially sheds light on a range of phenomena of interest to scientists. Who knows, perhaps this includes even the demise of the Neanderthals.

Hurtado, like Fuentes, Layton, and others, emphasizes the potential of NCT to provide an integrated theoretical framework for the social and biological sciences. We agree and see this as an exciting possibility. We also see considerable utility in Hurtado's argument that humans inherit not just genes and resources but evolutionary niches, which resonates with similar arguments stemming from NCT itself (Odling-Smee 2010). We also agree with the suggestion that human cultural niche-constructing activities, such as crop planting, could plausibly precipitate the propagation of norms such as caring for the sick, a suggestion consistent with Fuentes's lobby for an expanded framework.

Hurtado fleetingly mentions the possibility of group-level processes underlying, or following from, human cultural niche construction, a possibility that we feel merits careful consideration. It is important to distinguish between group selection and group niche construction. One disadvantage of the conventional evolutionary perspective is that natural selection and niche construction are typically wrapped together as cause and effect of the same process, leading researchers to automatically assume that group-level niche construction results from group selection (or vice versa). In fact, these are two logically distinct processes and need not cooccur, although they might. The changes that organisms bring about in their environments are often products of the activities of multiple individuals from multiple species. Think, for example, of sediment bioturbators or the accumulation of shell beds (Erwin 2008). The enriched soil processed by earthworms is not a lattice of independent extended phenotypes but rather the interwoven collective product of multiple earthworm activities (as well as of those of many other soil inhabitants), stemming from their by-products as much as from their adaptations.

Here there is group-level niche construction in the sense that environmental change is best described as the outcome of activities of populations rather than of individuals. However, whether there is also group selection depends on whether those collective activities are organized into well-bounded groups and whether those groups are differentially effective in their collective products. The same holds for humans. Clearly, humans exhibit widespread and extensive group-level niche construction. Although it is an important possibility that this may support group selection, this is best regarded as an empirical issue ripe for further investigation rather than as a given.

We agree with Kendal's point about culturally derived scaffolding of learning environments being important to the adoption and retention of cultural traits and norms. Cultural evolution and GCC theory model trait propagation as occurring through imitation, and we agree this is a reasonable and effective approximation. However, as Kendal emphasizes, reality is more complex and often comprises the advertent and inadvertent construction of learning environments by experienced individuals. This not only ups the probability that the naive will learn, it also reinforces the stability of traditions (Sterelny 2012). We also agree with Kendal that cumulative culture is critically dependent on high-fidelity information transmission (Dean et al. 2012; Lewis and Laland 2012) and that this high fidelity can be enhanced through the manufacture of culturally constructed learning environments. This developmental niche construction is an important and understudied phenomenon that merits further attention.

We appreciate Layton's thoughtful contribution, which notes links between NCT and compatible approaches within the social sciences. We think it likely that the reciprocal causation that characterizes NCT is also found in many distinct academic domains (Laland et al. 2011) and believe there is value in drawing attention to these connections. Of particular interest here is Layton's (2010) characterization of Durkheim's position as evocative of three types of coevolution in biology: interspecies, gene-culture, and organism-environment. We are no authorities on Durkheim, but we find Layton's analysis exciting, given that all three components are central to our NCT-GCC framework. We agree that it would be worthwhile pursuing these parallels because, if they hold, they offer a means of analyzing the social environment, which can appear somewhat nebulous in terms of constituent processes.

Layton and Wollstonecroft both propose alternative yam-construction chains to the one we depict. We welcome these alternative hypotheses and agree that they are plausible. In principle, with good data, it should be possible to sort among the various scenarios. Although we have done our best to reconstruct the history of the crop-planting and dairy-farming cases, our primary objective was less to shed light on these case studies and more to use them as illustrations of a general approach with associated methods. We would like nothing more than for other researchers to start using this perspective and will be content if that leads to a deeper understanding that eventually rejects aspects of the specific accounts we propose. The important point here is that NCT-GCC offers rich opportunities for fruitful analysis.

We agree with Mackinnon and Hurtado that the NCT-GCC framework may have much to offer the study of human disease and concur that niche construction is likely to be bidirectional. Indeed, there already exist formal NCT models of this reciprocal relationship (Boni and Feldman 2005). We particularly appreciate the array of questions Mackinnon raises as potentially fruitfully addressed by NCT-GCC and agree that there are exciting opportunities here afforded by closer attention to the human-induced causes of disease. We emphasize two of her points. First, it remains commonplace for researchers to think of disease and human activities as alternative sources of selection on the human genome, but this manner of thinking may be counterproductive. Human cultural activities frequently create opportunities for disease vectors to generate a culturally induced selection pressure. Whereas not all human diseases fit into this category, we submit that the majority may well do so and that there may be benefits to disease researchers to investigate this interaction. Second, it follows that we expect statistical associations to be observed between human activities and both disease incidence and resistance allele frequencies, across human populations. That is, we predict that environmental correlations observed between human allele frequencies and features of the environment will frequently be conditionally dependent on the prior existence of human cultural activities that construct those environmental features.

Pyne makes three important points. First, she suggests, and we affirm, that there is a central place for archaeology "on the grander stage" of this newly developing evolutionary perspective. The Synthetic Theory of the 1940s and 50s, despite its title, actually made core assumptions that either sidelined or severely constrained many adjacent disciplines, including ecology, developmental biology, and much of the human sciences (Laland et al. 2011; Odling-Smee, Laland, and Feldman 2003). By explicitly recognizing the active agency of organisms in modifying developmental and ecological environments, together with (1) the feedbacks that flow from these activities, (2) the relevance of developmental processes to the construction of variants subject to selection, and (3) the overlapping temporal and spatial scales by which ecological and evolutionary processes operate, NCT sets the scene for a broader evolutionary synthesis to which adjacent disciplines can contribute significantly. As our examples highlight, when it comes to understanding recent human evolution, archaeological data are not only relevant but absolutely central. Now that it is apparent that culture has shaped the human genome, and in significant ways, there is a need for a major cross-disciplinary effort to integrate theory and empirical data and build a deeper understanding of human evolution (Laland, Odling-Smee, and Myles 2010). This turns archaeologists from consumers of to contributors to evolutionary theory (Laland and O'Brien 2010).

Second, archaeology has a particularly useful depth of data. Evolutionary and coevolutionary events take place at temporal scales that range from millions of years down to shorter than hundreds. The tradition of assuming that biological evolution is too slow to be relevant to much of archaeology, or that human evolution stopped some 100,000 years ago, must now be rejected. Archaeological data are needed to reconstruct human history and to sort among various alternative accounts of change in human phenotypes, including biological evolutionary change, GCC, and cultural and/or ecological change.

Third, NCT-GCC offers a powerful set of tools for exploring this historical depth. One widely acknowledged contribution of NCT to evolutionary thinking is that it has drawn attention to some complexities in the temporal dimension of evolutionary dynamics. Evolutionary change cannot be understood solely as selection in the present, as it must incorporate legacies of modified environmental states bequeathed by ancestral generations that channeled and directed the action of selection. These historical legacies affect rates of change, equilibria reached, and how fitness is measured; they generate unusual evolutionary dynamics; and they can explain the evolution of costly characters. These complexities amplify the challenges associated with understanding human evolution, but they bring with them a deeper understanding that renders hitherto mysterious patterns of change potentially interpretable.

We agree with much of Smith's analysis of the historical coupling of HBE and OFT. Nonetheless, we would not want to juxtapose NCT-GCC with HBE as competing alternatives. We see NCT as compatible with, indeed broadening the remit of, HBE (Laland and Brown 2006; Laland, Kendal, and Brown

2007; Zeder 2012). Although neither GCC nor NCT is reliant on OFT, and both emphasize how evolving systems can reach suboptimal equilibria, we nonetheless foresee utility to optimality methods as a heuristic for generating and testing plausible hypotheses. However, we part company with optimality purists who refuse to conceive of suboptimal equilibria and, like Smith, would encourage evolutionary anthropologists to incorporate hypotheses derived from NCT. Indeed, some human behavioral ecologists are already beginning to do this (E. A. Smith 2011).

Further, like OFT, NCT potentially offers a range of hypotheses for a given phenomenon rather than a single core prediction. Hence, we would prefer to cast Smith's and our alternative accounts of the initial origins of domestication as competing NCT-derived hypotheses and regard this plurality as a manifestation of the rich and healthy generativeness of the NCT perspective. Here, too, we emphasize, as we did in response to Layton's and Wollstonecroft's alternative accounts of crop planting, that we are at greater pains to advocate the general utility of the NCT-GCC framework than of our specific predictions about the origins of domestication.

Sterelny cautions that many cases of gene-culture coevolution are likely to prove more complex than the examples we highlight. Specifically, he suggests that even the dairy-farming case is more convoluted than our portrayal suggests. We make two points. First, there is good comparative evidence that in populations with a history of consuming dairy products transformed into low-lactose processed forms (e.g., cheese and yogurt), there are modest increases in lactose tolerance relative to populations with no history of dairy farming (Durham 1991; Ulijaszek and Strickland 1993). This suggests that consuming processed dairy products partially, but not completely, ameliorated the selection for LP alleles. Second, if, as Sterelny hypothesizes, milk drinking acts as a developmentally plastic mechanism to retain lactase into adulthood, then in those genetically lactose-intolerant contemporary populations that consume dairy products, we should see early weaning, associated fitness benefits, and elevated levels of adult tolerance in individuals lacking the persistence genotype. Behavioral and genetic variation is present here, as it is in many GCC scenarios, to sort between alternative hypotheses.

With respect to Sterelny's more general concern, Laland, Odling-Smee, and Myles (2010) catalog alleles at over a hundred human genetic loci for which there is both evidence of recent selection and reason to think that cultural practices were the source of that selection. They suggest that each of these is best regarded as a hypothesis and that a lot of hard work is necessary to confirm any one as a bona fide case of GCC. If dairy farming–lactose persistence is any guide, then many tens of empirical and theoretical studies, carried out by many hundreds of researchers in diverse disciplines, are necessary to nail down a given case. These studies include anthropological and demographic studies of the covariation between cultural practices and human phenotypes, detection of a variety of statistical signatures of recent selection by geneticists, analysis of ancient DNA to determine whether ancestral populations possessed putatively adaptive alleles, statistical estimation from genetic data of the magnitude of selection pressures, biochemical analyses, analyses of genetic variation in animals (and plants) that have coevolved with humans, and mathematical models of GCC processes using population-genetic and phylogenetic methods. In other words, even if only a small fraction of the cases highlighted by Laland, Odling-Smee, and Myles (2010) prove amenable to analysis, there is plenty to keep a large number of people, including archaeologists, busy for a very long time.

Moreover, the complexity of the genotype to phenotype translation is not necessarily an insurmountable barrier to analysis. Our understanding of human genetics increases at breakneck speed, and researchers will soon be in a position to explore gene-culture interactions with precise knowledge of the genetic architecture of the focal trait (how many loci, with how many alleles, their distribution across populations, the magnitude of each loci's effect, and so on). This detailed knowledge may render simple single-locus or infinite-allele analytical models anachronistic, but it does not preclude the deployment of simulation approaches such as those Gerbault advocates. The logic of the exercise is unchanged, even if the details differ. Moreover, as Sterelny points out, researchers consistently devise imaginative means of deriving clues to our evolutionary history, including related to the origins of wearing clothes and teaching (e.g., Fogarty, Strimling, and Laland 2011; Toups et al. 2011). Accordingly, we have every reason to be optimistic that plenty of good work can and will be done using the NCT-GCC framework.

—Michael J. O'Brien and Kevin N. Laland

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