

Cultural Niche Construction: An Introduction

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Abstract Niche construction is the process whereby organisms, through their activities and choices, modify their own and each other's niches. By transforming natural-selection pressures, niche construction generates feedback in evolution at various different levels. Niche-constructing species play important ecological roles by creating habitats and resources used by other species and thereby affecting the flow of energy and matter through ecosystems—a process often referred to as “ecosystem engineering.” An important emphasis of niche construction theory (NCT) is that acquired characters play an evolutionary role through transforming selective environments. This is particularly relevant to human evolution, where our species has engaged in extensive environmental modification through cultural practices. Humans can construct developmental environments that feed back to affect how individuals learn and develop and the diseases to which they are exposed. Here we provide an introduction to NCT and illustrate some of its more important implications for the human sciences.

Keywords Cultural inheritance · Cultural niche construction · Eco-evolutionary dynamics · Ecological inheritance · Legacy effects · Niche construction

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The organism influences its own evolution, by being both the object of natural selection and the creator of the conditions of that selection (Levins and Lewontin 1985, p. 106).

The conventional view of evolution is that species, through the action of natural selection, have come to exhibit those characteristics that best enable them to survive and reproduce in their environments. Although environmental change may trigger bouts of selection, from the standard evolutionary perspective it is always changes in organisms, rather than changes in environments, that are held responsible for generating the organism–environment match that is commonly described as “adaptation.” Organisms are generally perceived as being molded by selection to become better suited to their environments (Fig. 1a). Under this perspective, “adaptation is always asymmetrical; organisms adapt to their environment, never vice versa” (Williams 1992, p. 484).

The niche-construction perspective in evolutionary biology, as encapsulated in the above quote from Levins and Lewontin (1985), contrasts with the conventional perspective by placing emphasis on the capacity of organisms to modify environmental states. Thus, “Organisms do not adapt to their environments; they construct them out of the bits and pieces of the external world” (Lewontin 1983, p. 280). In so doing, organisms co-direct their own evolution, often but not exclusively in a manner that suits their genotypes, in the process modifying patterns of selection acting back on themselves as well as on other species that inhabit their environment (Fig. 1b). Early advocates of related arguments include Conrad Waddington (1959) and Herbert Simon (1983).

This emphasis on the modification of habitat and resources by organisms is shared by ecologists who

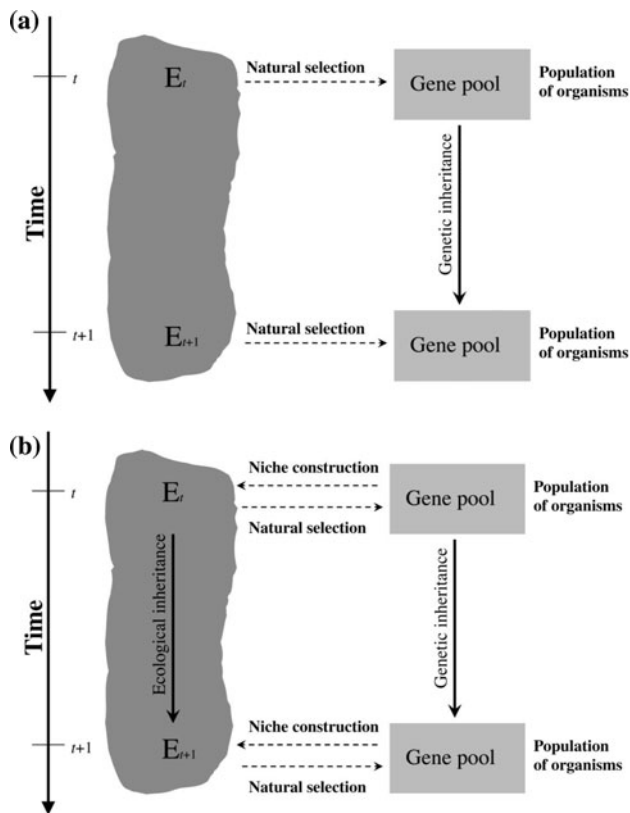


Fig. 1 Two views of evolution. Under the conventional perspective (a), niche construction is recognized as a product of natural selection but not as an evolutionary process. Inheritance is primarily genetic. Under the niche-construction perspective (b), niche construction is recognized as an evolutionary process. Here, ecological inheritance plays a parallel role to genetic inheritance

emphasize the significance of “ecosystem engineering,” by which organisms modulate flows of energy and matter through environments (e.g., Jones et al. 1994, 1997; Jones and Lawton 1995; Cuddington et al. 2007; Cuddington 2012, this issue). Such engineering activity can have significant impacts on community structure, composition, and diversity. Young beavers, for example, inherit from their parents not only a local environment comprising a dam, a lake, and a lodge but also an altered community of microorganisms, plants, and animals (Naiman et al. 1988; Wright et al. 2002). In this vein, Martinsen et al. (1998) found that the browsing of cottonwood trees by beavers stimulates elevated levels of defensive chemicals in the resprout growth and that these chemicals in turn are sequestered and used by leaf beetles for their own defense. Conversely, other invertebrates are driven out by the chemicals.

Similarly, Lill and Marquis (2003) describe how *Pseudotelphusa* caterpillars build leaf shelters by binding leaves into leaf ties using silk, providing a habitat that is colonized by many other insects. Through clever experiments, they established that removal of leaf ties

significantly decreased the mean species richness of leaf-chewing insects, whereas trees with artificial ties exhibited increased species richness of caterpillars, sawflies, and beetles. Lill and Marquis concluded that the engineering of leaf shelters was the principal mode of the caterpillars’ effect on their environment.

This niche construction can generate long-term effects on ecosystems (Cuddington 2012, this issue; Odling-Smee and Laland 2012, this issue). For instance, Hastings et al. (2007) describe how beaver dams deteriorate in the absence of beaver activity but that this leads to beaver meadows that can persist for nearly a century and are rarely converted back to the original riparian vegetation. “Ecological inheritance” refers to legacies of change, in both biota and abiota, bequeathed by niche-constructing organisms to subsequently evolving populations, often in the form of modified natural-selection pressures on descendent organisms (Odling-Smee et al. 2003) and can be regarded as a second general inheritance system in evolution (Fig. 1).

More generally, living organisms interact, indirectly, via engineered abiotic components, creating “engineering webs,” which affect the stability of ecosystems (Jones et al. 1994) as well as drive “eco-evolutionary feedbacks” (Post and Palkovacs 2009). The field of “eco-evolutionary dynamics” emphasizes that ecological and evolutionary changes are intimately linked and may often occur on the same time scales (Pelletier et al. 2009; Post and Palkovacs 2009; Loreau 2010). Many of the ecological processes that trigger evolutionary episodes depend on niche construction and ecological inheritance (Odling-Smee 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; Odling-Smee and Laland 2012, this issue; Odling-Smee and Turner 2012, this issue). This is relevant to conservation and biodiversity goals because the anthropogenic environmental changes precipitated by humans (e.g., habitat degradation, deforestation, industrial and urban development, agricultural practices, livestock grazing, and pesticide use) are primarily examples of human niche construction/ecosystem engineering, which destroys the engineering control webs that underlie ecosystems (Boogert et al. 2006; see also Schielke et al. 2012, this issue).

This process of niche construction provides a second evolutionary route to establishing the adaptive fit, or match, between organism and environment. From the niche-construction perspective, such matches need not be treated as products of a one-way process, exclusively involving the responses of organisms to environmentally imposed

problems. Instead, they should be thought of as the dynamical products of a two-way process involving organisms both responding to “problems” posed by their environments and solving some of those problems, as well as setting themselves some new problems by changing their environments through niche construction (Lewontin 1983, 2000; Odling-Smee 1988; Odling-Smee and Turner 2012, this issue).

This is not meant to imply that niche construction theory (NCT) always anticipates a perfect synergy between the features of an organism and the factors in its selective environment. It does not. In criticizing static adaptive-landscape concepts prevalent in evolutionary biology, the father of NCT, Richard Lewontin (1983), described the evolution of a population as resembling an individual walking on a trampoline. Each change in the organism, as with each step, inevitably deforms the selective landscape. Like Lewontin, we argue here that this metaphor is an apt characterization not only of evolution but also of development. All living organisms construct aspects of their world, and in doing so they do not just respond to environments by being driven to higher levels of fitness through selection. They also fashion new agendas, changing the environment in which they and others about them grow, develop, and learn, frequently in ways that re-script the pattern of natural selection acting back on their population as well as on other species that cohabit their niche.

Of course, evolutionary biologists are well aware that organisms modify environments. The difference between the niche-construction perspective and conventional evolutionary perspectives is far more subtle than the recognition, or failure to recognize, organism-mediated environmental change. The developmental biologist Patrick Bateson (1988, p. 191) captures nicely the point we are making:

Many biologists (including myself) have unthinkingly accepted the Darwinian image of selection, with nature picking those organisms that fitted best into the environments in which they lived. The picture of an external hand doing all of the work is so vivid that it is easy to treat organisms as if they were entirely passive in the evolutionary process. That is not, of course, to suggest that any biologist would deny that organisms, and animals especially, are active. But the notion of “selection pressure” does subtly downplay the organisms’ part in the process of change... When developmental issues are recoupled to questions about evolution, it becomes much easier to perceive how an organism’s behaviour can initiate and direct lines of evolution.

The key—and indeed subtle—distinction between the two perspectives is that one views niche construction as a *cause* of evolutionary change as opposed to an *effect* of a

prior cause (namely, natural selection). Niche construction, then, is a process rather than merely a product. Organisms and environments are treated by NCT as engaged in reciprocally caused relationships (Laland and Sterelny 2006; Laland et al. 2011) that are negotiated over both ontogenetic and phylogenetic timescales, entwined in, to coin a very apt phrase from developmental systems theory, “cycles of contingency” (Oyama et al. 2001). Moreover, as Bateson intimates, niche construction is a developmental process, and the niche-construction perspective in evolutionary biology is all about exploring the evolutionary ramifications of coupling this particular developmental process with natural selection.

The switch from treating niche construction as a cause rather than an effect cannot be dismissed as little more than a relabeling of already well-defined evolutionary phenomena. Conceptual frameworks channel scientific thinking and direct research agendas. This inadvertent “channeling” process is emphasized by Bickerton (2009, p. 36), who describes some of the conceptual barriers to his developing a novel theory of language evolution that draws on NCT: “What makes interdisciplinary work so hard is that any academic discipline acts like a straightjacket, forcing you to look only in certain directions, blocking other perspectives from view... The process [of devising his new theory] was speeded up by my encounter with niche construction theory, which made sense of a lot of things that baffled me.”

In putting together this special issue of *Biological Theory*, we hope to provide other researchers, particularly those in the human sciences, with a conceptual framework based around NCT as well as a series of illustrations of how it can be used. We are convinced that NCT provides tools for thought by drawing attention to certain important phenomena that are often neglected and encouraging researchers to address established problems with a different mindset. Phenomena that NCT encourages us to remember (see Odling-Smee et al. 2003, for elaboration) include the following:

- There is selective feedback from niche construction to genes in the constructor other than those expressed in niche construction.
- Niche-constructed effects can persist and act as modified sources of selection for longer than the lifetime of their constructors (ecological inheritance).
- By-products can play an evolutionary role by modifying selection pressures through niche construction.
- Acquired characters can play an evolutionary role by modifying selection pressures through niche construction.
- Evolutionary causality does not always start in the environment.

- Niche construction can drive (diffuse and direct) coevolutionary events.
- Niche construction can modify developmental environments.
- Adaptation (adaptive complementarity) results from two processes (selection and construction), not one.

The value of the niche-construction perspective is that it discourages the kind of “subtle downplaying” that concerns Bateson (1988; see above) and makes the kind of progress heralded by Bickerton (2009) marginally more probable (Laland and Sterelny 2006). Two examples can be found in Smith’s and Collard et al.’s contributions to this issue. Smith’s (2012, this issue) cultural niche-construction model of initial domestication presents a fresh alternative to optimal-foraging-theory accounts of the origins of agriculture and supersedes it in explanatory power. Likewise Collard et al. (2012, this issue) apply NCT to ethnographic data to explore the causes of cross-cultural variation in the diversity of subsistence toolkits. They find that the data fit well with predictions from NCT, unlike the fit with both the established “risk” and “population-size” hypotheses.

Other successes include a suite of novel theoretical and empirical findings (e.g., Laland et al. 1996, 1999, 2001; Odling-Smee et al. 2003; Ihara and Feldman 2004; Flack et al. 2006; Silver and Di Paolo 2006; Erwin 2008; Kylafis and Loreau 2008, 2011; Lehmann 2008; Krakauer et al. 2009; Post and Palkovacs 2009; Corenblit et al. 2011; Kendal et al. 2011; Rowley-Conwy and Layton 2011). One important finding has been that niche-constructing traits can drive themselves to fixation by generating disequilibrium between niche-constructing alleles and those alleles whose fitness depends on resources modified by niche construction (Silver and Di Paolo 2006). The same runaway process can occur even if the niche-constructing trait is a cultural practice, such as the planting of a crop (Rendell et al. 2011c). 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. More generally, gene–culture models have shown that cultural processes can also affect the rate of change of allelic frequencies in response to selection (Boyd and Richerson 1985; Feldman and Cavalli-Sforza 1989; Laland et al. 2001).

Niche Construction Theory as a Conceptual Framework for the Human Sciences

Most of the authors of the articles in this issue investigate some of the repercussions of this niche-construction perspective for the human sciences. We suggest that a focus

on niche construction has important implications for the relationship among genetic evolution, development, and cultural processes. One implication is that niche-constructing organisms can no longer be treated as merely “vehicles” for their genes (Dawkins 1976) because they also modify selection pressures in their own and in other species’ environments. In the process, they can introduce feedback to both ontogenetic and evolutionary processes. Alongside others (e.g., Gottlieb 1998, 2000, 2002; Oyama et al. 2001; Odling-Smee et al. 2003; Bickerton 2009; Layton 2010; Plotkin 2010; Kendal et al. 2011), we suggest (Laland et al. 2000; Laland and O’Brien 2010; O’Brien and Laland 2012) that this active, constructive conception of the role of organisms in evolution, and indeed in ontogeny, fits well with conceptualizations of human agency that are widespread within the human sciences (VanPool and VanPool 2003). Of course, social scientists do not need to be told that humans build their world, nor that in the process they devise learning environments not only for their offspring but potentially for any conspecific. Indeed, Kendal (2012, this issue) draws attention to four independent theories developed by sociologists, cognitive scientists, and sociocultural anthropologists (situated learning, activity theory, practice theory, and distributed cognition) that all emphasize the reciprocal interplay between the construction of the sociocultural environment and human development. However, social scientists may be less conscious of the fact that other organisms do the same and may, we believe, feel more comfortable with a conceptualization of evolution that, while fully in accord with the modern synthetic theory, nonetheless has an emphasis that aligns with their own thinking.

A second implication is that there is no requirement for niche construction to result directly from genetic variation in order for it to modify natural selection. Humans can and do modify their environments mainly through cultural processes, and it is this reliance on culture that lends human niche construction a special potency (Smith 2007; Kendal et al. 2011; O’Brien and Laland 2012). We stress, however, that humans are far from unique in engaging in niche construction, as some of the architects of the modern synthetic theory originally claimed (Simpson 1949; Dobzhansky 1955). Niche construction is a very general process, exhibited by *all* living organisms (Odling-Smee et al. 2003), and species do not require advanced intellect or sophisticated technology to change their world (Jones et al. 1994, 1997; Odling-Smee et al. 2003; Cuddington et al. 2007).

The general replacement of a single role for phenotypes in evolution (as gene-carrying vehicles) by the dual role (also encompassing environmental modification and regulation) envisaged by NCT removes from cultural processes any claim to a unique status with respect to their capacity

to transform natural-selection pressures. Nonetheless, cultural processes provide a particularly powerful engine for human niche construction. Moreover, this dual role for phenotypes in evolution does imply that a complete understanding of the relationship between human genes and cultural processes must acknowledge not only genetic and cultural inheritance but also take account of the legacy of modified selection pressures in environments (Laland et al. 2000; Odling-Smee et al. 2003; Laland and O'Brien 2010; see Odling-Smee and Laland 2012, this issue, for a discussion of the relationship between ecological and cultural inheritance). Again, it is readily apparent that contemporary humans are born into a massively constructed world, with an ecological inheritance that includes houses, hospitals, farms, factories, computers, satellites, and the World Wide Web. Niche construction and ecological inheritance are thus likely to be at least as consequential for developmental processes as they are now known to be in human evolution (Laland et al. 2010; Richerson et al. 2010; Kendal 2012, this issue).

For those of us comfortable with describing human cultural change as “cultural evolution” (e.g., Cavalli-Sforza and Feldman 1981; Boyd and Richerson 1985; Mesoudi 2011), the feedback from niche construction can be seen as co-directing two evolutionary processes through modifying selection—biological and cultural evolution. For those of us willing to regard human learning as operating through a process of selective retention of acquired variants (Skinner 1981; Plotkin 1994, 2010), niche construction may even be seen as co-directing a third selective process—individual learning (Plotkin and Odling-Smee 1981; Laland 2004). However, recognition of the significance of niche construction to developmental and cultural processes does not require any commitment to evolutionary epistemology, and the niche-construction perspective is broad enough to encompass those who regard learning and cultural change as only weakly analogous to biological evolution.

The Multiple Processes Responsible for Niche Construction

Following Odling-Smee et al. (2003), here we consider more closely the set of processes through which humans can acquire the information that is expressed in niche construction. Humans can acquire relevant knowledge through a set of information-acquisition processes operating in three different domains: population genetic, ontogenetic, and cultural (Fig. 2). In various combinations, these are the primary processes that supply *all* organisms with the knowledge that organizes their behavior, but humans are unusual in being heavily reliant on all three.

Every species is informed by naturally selected genes, and many animals are also informed by complex, information-acquiring ontogenetic processes such as learning or the immune system, but humans, and arguably a few other species (depending on how culture is defined), are also informed by cultural processes.

The three domains are distinct but interconnected (Odling-Smee et al. 2003), with each interacting with, but not completely determined by, the others (Fig. 3). That is, learning is informed by, but not fully specified by, genetic information, and cultural transmission may be informed by, but again, not completely specified by, both genetic and developmental processes. Genes may affect information gain at the ontogenetic level, which in turn influences information acquisition in the cultural domain. In addition, ontogenetic processes—particularly learning—may be affected by cultural processes, whereas population-genetic processes may be affected by both ontogenetic processes and cultural processes when humans modify environments, generating selective feedback to each process.

Each individual inherits genetic information from its ancestors, and this is the most fundamental source of information that underpins niche construction. However, some factors in the environment can potentially change many times within the typical lifespan of the animal concerned, and the natural selection of genetic variation in populations cannot furnish individual organisms with specific adaptations for each of these environmental contingencies. What it can do, however, is select for supplementary processes that permit characteristics of the phenotype to adjust on a within-lifetime basis. These are unusual products of selection, however, because they function to accumulate further information relative to the local environments of individuals. For example, specialized information-acquiring subsystems, such as the immune system in vertebrates, or brain-based learning in

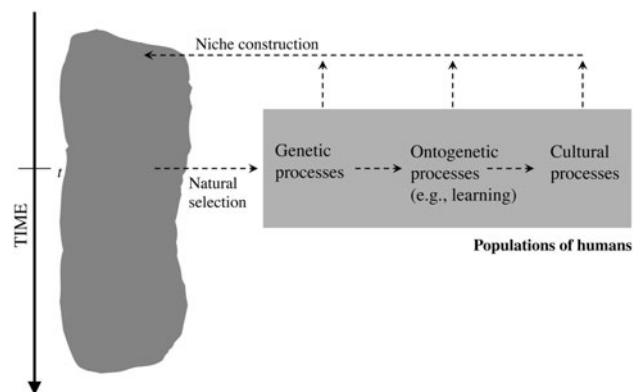


Fig. 2 Diagram showing three domains of information acquisition—genetic, ontogenetic, and cultural. Organisms, especially humans, use all three to generate information that feeds back into niche construction

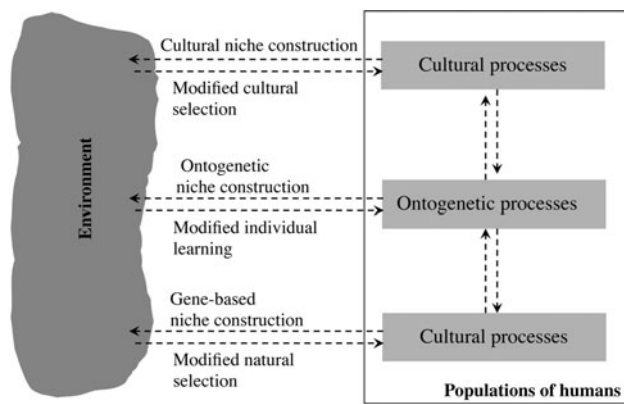


Fig. 3 Interconnectedness of the three domains of information acquisition and their roles in niche construction

animals, are capable of additional, individual-based, information acquisition. These secondary sources of information are complementary to the first; for instance, individual learning allows organisms to fine-tune their behaviors relative to variable environments.

Ontogenetic processes such as learning and the immune response can also be regarded as operating in a manner loosely analogous to the Darwinian algorithm. In each case variants (behavior patterns or antibodies) are produced, their utility is evaluated (e.g., their performance at generating pleasure or avoiding pain, or binding to antigens, is assessed by some kind of system that natural selection has previously selected), and those variants that are most effective are retained, whereas the others are selected out. However, these ontogenetic information-gaining processes are not strictly Darwinian. For example, they rely on evolved aptitudes that generate positive and negative sensations for behavioral patterns that are broadly adaptive and maladaptive, respectively. Those associations and patterns of behavior that animals do learn critically depend on which stimuli are reinforcing under the influence of species-typical motivational and perceptual processes that are informed by their genes (Plotkin and Odling-Smee 1981).

Moreover, whereas the variants that occur during genetic evolution—mutations—are random (or at least blind relative to natural selection), those acquired through ontogenetic processes are not. They are “smart variants” (Laland et al. 2000). During learning, animals typically demonstrate inherited a priori biases in their associations and patterns of behavior that are likely to be adaptive (Garcia et al. 1966; Seligman 1970). These biases influence the behavior of each individual, the associations it forms, the antibodies it generates, and the developmental pathways it takes, usually in the direction of being functional and adaptive.

Because the information-acquisition entity for these ontogenetic processes is no longer an evolving population

but rather each individual organism in a population, the adaptive knowledge acquired cannot be inherited by successive generations. Nonetheless, processes such as learning can still be of considerable importance to subsequent generations because learned knowledge can guide niche construction, the consequences of which can be inherited through ecological inheritance. In this respect, learning provides a second source of semantic information that can be expressed in niche construction.

This highlights one of the major differences that niche construction makes to the evolutionary process: acquired characteristics can play a role in evolution through their influence on the selective environment, in other words through niche construction (Fig. 3). The Galapagos woodpecker finch’s use of tools illustrates this point nicely (Tebich et al. 2001). These birds create a woodpecker-like niche by learning to use a tool such as a cactus spine to peck for insects under bark. One can think of this behavior as the consequence of an internal selective process operating at the ontogenetic level, in individuals, rather than at the genetic level, in populations. Like countless other species, this finch has apparently exploited the more general and flexible adaptation of learning to develop the skills it needs to grub in environments reliably containing cactus spines and similar implements. By modifying natural-selection pressures, this behavior seemingly created a stable selection pressure favoring a bill able to manipulate tools rather than the sharp, pointed bill and long tongue characteristic of more typical woodpeckers, and it may have created selection pressures favoring enhanced learning capabilities as well. A few species, including some vertebrates, have evolved a capacity to learn from other individuals, and this can lead to behavioral traditions (Fragaszy and Perry 2003; Fragaszy 2012, this issue). In humans this ability is facilitated by a further set of processes (e.g., language and teaching) that collectively underlie cultural processes.

Cultural change can also be regarded as loosely Darwinian in character in the sense that cultural variants are generated by individuals and as a result of social learning are culturally selected through their differential adoption (Plotkin and Odling-Smee 1981; Dennett 1995; Simonton 1999; O’Brien and Shennan 2010). Cultural processes, as with biological evolution, may accumulate functional solutions to problems posed by the environment (Mesoudi 2011). Most of the time, cultural processes can be regarded as a shortcut to acquiring adaptive information, as individuals rapidly learn or are shown what to eat, where to live, or how to avoid danger by doing what other, more-knowledgeable individuals do (Henrich 2004; Rendell et al. 2010). Experienced others such as parents are a reservoir of smart variants, allowing naive individuals to shortcut the many iterations of ontogenetic selection necessary to learn

for themselves behavioral patterns appropriate to their environment and thus leapfrog to the functional and already-tested solutions established by others (Mesoudi 2008).

Cultural and biological evolution differ in important respects too, and many of the same caveats that pertain to the ontogenetic level apply again at the cultural level (Mesoudi et al. 2004, 2006). For instance, humans do not typically create or adopt cultural variants at random; rather, past phylogenetic and developmental aptitudes, including past asocial and social learning as well as aspects of the social context, inform these creative and selective processes. Human social learning, like that in other animals, is guided by adaptive social learning strategies, including conforming to the majority behavior and payoff-based copying (Boyd and Richerson 1985; Henrich and McElreath 2003; Laland 2004; Rendell et al. 2010; Rendell et al. 2011a, b).

Much of human niche construction is guided by socially learned knowledge and cultural inheritance, but the transmission and acquisition of this knowledge is itself dependent on pre-existing information acquired through genetic evolution, complex ontogenetic processes, or prior social learning (O'Brien and Laland 2012). As a result, niche construction that is based on either learned or culturally transmitted information may be expressed “intentionally” relative to a specific goal, such as planting a crop or constructing terraces. Other components of cultural processes, such as fads and fashions, are less clearly directed and may be subject to so many complex and frequency-dependent selective processes that their evolution is unpredictable and more difficult to describe quantitatively (Bentley et al. 2011).

The Multiple Forms of Feedback from Niche Construction

Niche construction modifies selection not only at the genetic level but at the ontogenetic and cultural levels as well (Fig. 3), with consequences that not only feed back to the constructor population but also modify selection for other organisms. Human niche construction, through modification of the environment, creates artifacts and other ecologically inherited resources that not only act as sources of biological selection on human genes (Laland et al. 2010) but also facilitate learning and mediate cultural traditions. For example, the construction of villages, towns, and cities creates new health hazards associated with large-scale human aggregation, such as the spread of epidemics (Diamond 1997). Humans may respond to this novel selection pressure either through cultural evolution (represented in Fig. 3 as “modified cultural selection”)—

constructing hospitals and developing medicines and vaccines or, at the ontogenetic level, developing antibodies that confer some immunity—or through biological evolution, with the selection of resistant genotypes. As cultural niche construction typically offers a more immediate solution to new challenges, we expect that it will usually favor further counteractive cultural niche construction rather than genetic change (Odling-Smee et al. 2003). Collard et al. (2012, this issue) provide an example of this cultural damping of natural selection, showing that farmers are less affected by macroscale environmental variables than are hunter–gatherers. Likewise, Fogarty and Feldman (2012, this issue) describe how the spread of beliefs about son and marriage-type preferences constructs a cultural niche that feeds back to distort the adult sex ratio and the perceived value of daughters.

However, where a culturally transmitted response is not possible, perhaps because the population lacks the requisite knowledge or technology, then a genetic response may occur (represented in Fig. 3 as “modified natural selection”). A familiar example is the Kwa-speaking yam cultivators of West Africa whose niche construction, in the form of agricultural activities, created breeding grounds for malaria-carrying mosquitoes, which generated a culturally modified selection pressure favoring the sickle-cell (*HbS*) allele (Durham 1991; O'Brien and Laland 2012). Other human populations responded to the threat of disease at the cultural level, for example, through eradication treatments (e.g., DDT and chloroquine) for disease vectors such as *Plasmodium falciparum* and *Anopheles* spp., thereby damping selection for resistance on themselves but intensifying selection for treatment resistance in the vectors.

Even better studied is the coevolution of dairy farming and autosomal dominant alleles for adult lactose absorption, where several lines of evidence now support the hypothesis that dairy farming created the selection pressures that favored these alleles in pastoralist populations (Simoons 1970; Durham 1991; Holden and Mace 1997; Myles et al. 2005; Burger et al. 2007). Through a combination of responding to challenges by means of (further) cultural niche construction and/or evolving genetic responses—often rapidly (e.g., Hawks et al. 2007; Laland et al. 2010)—humans typically maintain broadly adaptive behavior despite dramatic self-induced changes in their environment (Laland and Brown 2006; Bolhuis et al. 2011; O'Brien and Laland 2012).

Cultural niche construction can also generate selection on other species, most obviously domesticates. Beja-Pereira et al. (2003) established that the spread of dairying affected geographical variation in milk-protein genes in European cattle breeds, which covary with present-day patterns of lactose tolerance (Gerbault et al. 2011). Such coevolutionary, or diffuse coevolutionary, events highlight

the fact, emphasized by Post and Palkovacs (2009) and Schielke et al. (2012, this issue), that niche-constructing organisms are not isolated from other evolving populations and that their activities frequently trigger eco-evolutionary feedbacks, or feed-forwards, in ecosystems (Fig. 4). Post and Palkovacs (2009) describe how it is possible to trace causal chains through ecosystems, comprising sequential bouts of natural selection and niche construction that ripple through environments. For examples, see the predator–guppy–algae system (Post and Palkovacs 2009) depicted in Fig. 4 or the niche differentiation (a potential speciation event) driven by alternative patterns of alewife foraging, which impacts on prey community structure and modifies selection on alewife foraging traits (Schielke et al. 2012, this issue). Being able to trace such causal influences is increasingly a goal of ecologists as they seek to integrate understanding of ecological and evolutionary interactions (Post and Palkovacs 2009; Schielke et al. 2012, this issue). There is a deeper understanding of ecosystems that stems from this holistic perspective.

An important aspect of the alewife system discussed by Schielke et al. is the fact that human cultural niche construction—here the damming of rivers—is responsible for generating landlocked fish populations, with their alternative foraging habits. In other words, anthropogenic activity has triggered a cascade of ecological and evolutionary events. Many social scientists are interested in such consequences of human activity. Indeed, social scientists frequently have essentially the same objective as ecologists: they, too, often wish to trace causal influences through ecosystems, but with the focus on human niche construction and the ecological or evolutionary episodes this anthropogenic change precipitates. An illustration of such a

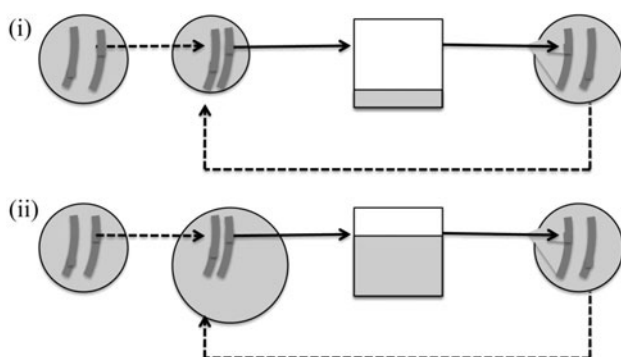


Fig. 4 Example of eco-evolutionary feedbacks showing the guppy system described by Palkovacs et al. (2009). Differential predation in (i) and (ii) by two predator populations (the left-hand circles) lead to different size distributions in the two guppy populations (second circles), leading to differences in the rates of excretion in the two populations (niche construction), leaving different signatures (shaded sections of squares) affecting nitrogen cycling in the local environments (squares), affecting algal growth (the third circle), and feeding back to affect selection on the guppy populations

causal construction chain, taken from O'Brien and Laland (2012) is shown in Fig. 5, which captures some of the most important ramifications of human crop (here yam) planting, as described above. Causal influences can be seen to flow from culture to genes and back to culture, in a bi-directional pattern, with resultant effects on population growth and dispersal. Note that although Figs. 4 and 5 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 (Shiple 2000).

Humans, and other animals, can also construct social niches. For example, Flack et al. (2006) deploy network theory to quantify how “policing” (intervening in disputes) by dominant pigtail macaques creates a social niche, stabilizing and integrating macaque societies. Without this policing, societies rapidly fragment. Once again, there is feedback from this social niche construction, potentially at a number of levels. For example, Fragaszy (2012, this issue) and Kendal (2012, this issue) describe how capuchin monkeys and humans, respectively, create learning environments for youngsters, often by advertently or inadvertently transforming the environment in a manner that scaffolds learning in others and channels it toward established traditions (see Caporael et al., forthcoming, on scaffolding in biological and cultural development and cognition generally). From Fragaszy’s paper, we learn how the discarded nutshells or stone hammers, or spilt traces of

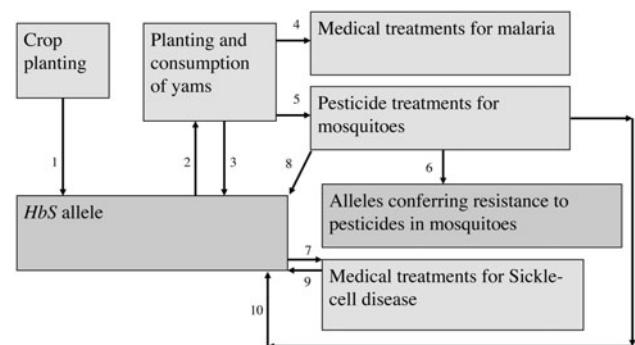


Fig. 5 Construction chain depicting the causal influences following a cultural niche-constructing practice, here the planting of yams in West Africa. Planting, which involves deforestation, (1) inadvertently promotes the spread of malaria by leaving standing pools of water, leading to selection for the hemoglobin (*HbS*) allele. 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. Reproduced from O'Brien and Laland (2012)

drinks consumed in particular locations, can act to facilitate acquisition of stone use in young monkeys and thereby support traditions even without direct observation of the behavior.

Social transmission maintained through inadvertent, or less commonly advertent, modification of the local environment is surprisingly common. It is known to underlie pine-cone opening in black rats (Terkel 1996), milk-bottle opening in various birds (Sherry and Galef 1984), the learning of food sites through pheromone trails in ants (Denny et al. 2001), mate-choice copying in egg-dumping fishes (Goldschmidt et al. 1993), and food-preference learning through excretory products in rats (Laland and Plotkin 1991, 1993). Odling-Smee and Turner (2012, this issue) even challenge us to conceive of termite mounds as exhibiting properties akin to human culture because of their legacy effects. For Odling-Smee and Turner, a key point is that adaptation is a two-way process, with the fit between organism and environment resulting from a combination of natural selection and niche construction. They argue that this has important implications for those academic fields—here architecture—that have drawn inspiration from nature through biomimetic reasoning.

Conclusions

We hope that the view of NCT sketched above, and depicted in Fig. 3, provides a useful conceptual framework for those social scientists who are evolution friendly but dissatisfied with overly adaptationist and gene-centered approaches. To portray humans as mere gene-carrying vehicles seriously underplays their role in the evolutionary process. Humans are massive constructors of selective and developmental environments, and an accurate depiction of this role calls for the recognition of niche construction as an evolutionary cause, not simply an effect of prior selection. In humans, this is incontestable: learning in a culturally constructed environment is widely recognized as playing pervasive roles within several aspects of the social sciences (Kendal 2012, this issue). One advantage of the niche-construction perspective is that it encourages the tracing of causal influences through ecosystems rather than treating each bout of selection separately, such that the full ramifications of anthropogenic activity can be better understood. A second advantage is that it emphasizes how the adaptive complementarity of organism and environment are the product of two reciprocal causes—selection and niche construction (Laland and Sterelny 2006; Laland et al. 2011).

It is important to recognize that different types of information, including genetic, individually learned, and

cultural, are expressed in human niche construction. Moreover, the environmental change that results feeds back again to the constructor population, as modified sources of natural selection and modified developmental and cultural environments. Human cultural niche construction is also a cause of changed developmental environments and sources of modified selection to a multitude of other species that inhabit the human niche.

In putting together this special issue of *Biological Theory* on the topic of cultural niche construction, we sought to provide the reader with the background to understand the complex multiple-level, multiple-species interactions that are frequently either causes or consequences of human cultural niche construction. For that reason, we have invited contributions from ecologists (Cuddington, Schielke et al.) that, through their emphases on ecosystem engineering, legacy effects, and eco-evolutionary dynamics, draw attention to the important roles that niche construction and ecological inheritance play in nature. With the recognition that other organisms leave ecological legacies, it then becomes a moot point to understand how ecological and cultural inheritance relate to each other, a challenge taken up by Odling-Smee and Laland. The articles by Fragaszy and Kendal illustrate how both capuchin monkeys and humans construct developmental environments that structure the learning environments of youngsters, thereby contributing to the stability of traditions. Each of the last four articles provides an illustration of the utility of NCT as a means to understand aspects of human behavior and society, ranging from the diversity of subsistence toolkits (Collard et al.), to the origins of plant and animal domestication (Smith), to the changing sex ratio in China (Fogarty and Feldman), to human architecture (Odling-Smee and Turner).

We believe this set of articles collectively paints a coherent picture of human niche construction as a major source of functionality in the world as well as a major driver of ecological and evolutionary dynamics. As we point out elsewhere (O'Brien and Laland 2012), human 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.

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