

# RETHINKING ADAPTATION

## *the niche-construction perspective*

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**ABSTRACT** Niche construction refers to the capacity of organisms to construct, modify, and select important components of their local environments, such as nests, burrows, pupal cases, chemicals, and nutrients. A small but increasing number of evolutionary biologists regard niche construction as an evolutionary process in its own right, rather than as a mere product of natural selection. Through niche construction organisms not only influence the nature of their world, but also in part determine the selection pressures to which they and their descendants are exposed, and they do so in a non-random manner. Mathematical population genetics analyses have revealed that niche construction is likely to be evolutionarily consequential because of the feedback that it generates in the evolutionary process. A parallel movement has emerged in ecosystem ecology, where researchers stress the utility of regarding organisms as ecosystem engineers, who partly control energy and matter flows. From the niche construction standpoint, the evolving complementary match between organisms and environments is the product of reciprocal interacting processes of natural selection and niche construction. This essay reviews the arguments put forward in favor of the niche-construction perspective.

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CLASSICALLY, ADAPTATION HAS BEEN REGARDED as a process by which natural selection, stemming from an external environment, gradually molds organisms to be well suited to their environments (Godfrey-Smith 1998). Despite recognition that processes independent of organisms often change the world to which populations adapt (Van Valen 1973), with notable exceptions addressed below, the changes that organisms themselves bring about in their environments are rarely considered in evolutionary analyses. Yet all living creatures, through their metabolism, their activities, and their choices, partly create and partly destroy their own niches, on scales ranging from the extremely local to the global. To varying degrees, organisms choose habitats and resources; construct aspects of their environments, such as nests, holes, burrows, webs, pupil cases, and a chemical milieu, and destroy other components; and frequently choose, protect, and provision nursery environments for their offspring (Lewontin 1983; Odling-Smee 1988). These processes of environmental selection and modification are known as *niche construction* (Odling-Smee 1988).

Recently, a small number of evolutionary biologists have sought a reconceptualization of the process of adaptation by placing emphasis on niche construction (Gray 1988; Griffiths and Gray 1994; Laland, Odling-Smee, and Feldman, 1996, 1999; Lewontin 1982, 1983; Odling-Smee 1988; Odling-Smee, Laland, and Feldman, 1996; Oyama, Griffiths, and Gray 2001). These researchers treat niche construction as an evolutionary process in its own right, rather than as a mere product of natural selection. Through niche construction, organisms not only shape the nature of their world, but also in part determine the selection pressures to which they and their descendants are exposed. They thereby generate feedback in evolution. As a consequence, there are two routes to the fit between organisms and their environments: (1) organisms may, as a result of natural selection, evolve characteristics that render them well-suited to their environments; or (2) niche-constructing organisms may change their environments to suit their current characteristics.

In many instances, the changes brought about in the local environment through the niche construction of an organism will also be experienced by the organism's offspring or other descendants. Thus generations of organisms not only acquire genes from their ancestors but also an *ecological inheritance*, that is, a legacy of a sub-set of natural selection pressures that have been modified by the niche construction of their genetic or ecological ancestors (Odling-Smee 1988). Thus the niche-construction perspective incorporates two kinds of descent (genetic and ecological inheritance), and two kinds of modifying process (natural selection and niche construction) each of which is potentially capable of generating a complementary match between organism and environment. This conceptualization is portrayed in Figure 1.

The conventional way of thinking about niche construction asserts that niche construction is no more than an adaptation. The match between organism and environment is treated as a consequence of natural selection, as it is natural selec-

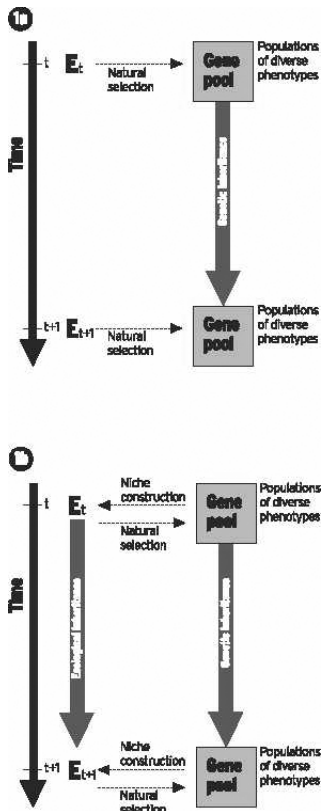


FIGURE 1

- a. Standard evolutionary perspective: Populations of organisms transmit genes from one generation to the next, under the direction of natural selection.
- b. Niche-construction perspective: Phenotypes modify their local environments (E) through niche construction. Each generation inherits both genes and a legacy of modified selection pressures (ecological inheritance) from ancestral organisms.

tion that has left organisms with adaptations to change factors in their world. Niche construction and natural selection are not regarded as parallel, interactive processes contributing to the synergic match between organisms and environments, but rather the former is treated as a product of the latter. However, we argue that niche construction is best regarded not only as an evolutionary product but also an evolutionary process. Niche-constructing traits are more than just adaptations, because they play the additional role of modifying natural selection pressures, frequently in a directed manner, and in doing so they change the evolutionary dynamic. According to the niche-construction perspective, the changes to the evolutionary process brought about by niche construction and ecological inheritance are sufficiently important and occur sufficiently frequently to warrant an overhaul in evolutionary thinking.

The argument that niche construction can be disregarded because it is partly a product of natural selection makes no more sense than the proposition that natural selection can be disregarded because it is partly a product of niche construction. Because organisms' prior niche-constructing activity would account for at least part of the selective environment that fosters further niche construction, one cannot assume that the ultimate cause of niche construction is the environment itself (Godfrey-Smith 1998). Ultimately, such recursions would regress back to the beginning of life.

Some aspects of population biology and related disciplines are concerned with the evolutionary consequences of the modifications that organisms bring about in their own and in other populations' selective environments. These include frequency-dependent selection (including evolutionary stable strategy or ESS models), density-dependent selection, habitat selection, co-evolution, maternal inheritance, and indirect genetic effects. Each captures some restricted features of niche construction, and although none can be described as providing a satisfactory general theory of the role of niche construction in evolution, all at least inadvertently encourage the view that niche construction is likely to be evolutionarily consequential. In some respects, these more conventional approaches even converge on the niche-construction perspective. For instance, the widely acknowledged pervasiveness of frequency-dependent selection, the well-known repercussions of active choice in habitat and sexual selection, the evidence for unusual evolutionary dynamics with additional inheritance systems (Mousseau and Fox 1998), and the finding that indirect genetic effects can exert strong influences on the rate and direction of evolution (Wolf, Brodie, and Wade 2000), all attest to the likely importance of niche construction in evolution.

The conventional view of adaptation enjoys the advantage of being relatively simple, and hence the added complexity of treating niche construction as a process must reap dividends to become accepted. In this essay, we suggest that the niche-construction perspective is a more accurate portrayal of the evolutionary process than the standard view and is likely to be of considerable utility in providing new insights, testable hypotheses, and facts. Treating niche construction as a process is likely to enhance the understanding of evolutionary phenomena.

The extent to which niche construction can be regarded as a significant process in evolutionary and ecological systems is dependent upon its prevalence and impact. While there is widespread acknowledgment that some species, such as the beaver (*Castor fiber*), should be regarded as important to ecosystem functioning, it is not clear whether such species should be regarded as special cases or as the more visible examples of a general process. In fact, a closer look at the taxonomic breadth of niche construction reveals that it is far from restricted to the complex artifacts of vertebrates, but encompasses a wide array of processes found in every major group of organisms.

The evolutionary significance of niche construction hangs on the fact that organisms regularly modify both biotic and abiotic sources of natural selection

in their environments, thereby generating forms of feedback in evolution that are rarely considered in evolutionary analyses (Laland, Odling-Smee, and Feldman 1996; Odling-Smee, Laland, and Feldman 1996). However, recent mathematical analyses using population genetics models have revealed that feedback from niche construction can make a considerable difference to the evolutionary process and can generate unusual evolutionary dynamics (Laland, Odling-Smee, and Feldman 1996, 1999, 2001). Mathematical models of maternal inheritance and indirect genetic effects are drawing parallel conclusions (Mousseau and Fox 1998; Wolf, Brodie, and Wade 2000; Wolf et al. 1998). This body of theory suggests that niche construction changes the nature of the evolutionary process. (The findings of these analyses are described later.)

There is also increasing recognition that niche construction has important, and hitherto neglected, implications for ecology (Gurney and Lawton 1996; Jones, Lawton, and Shachak 1994, 1997; Laland, Odling-Smee, and Feldman 1999; Odling-Smee 1988; Shachak and Jones 1995; Turner 2000). A parallel movement has emerged in ecosystem ecology, where ecologists have noted that the niche construction of organisms, described as ecosystem engineering, partly controls the flows of energy and matter through ecosystems and may play vital roles in ecosystem stability and resilience (Jones, Lawton, and Shachak 1994, 1997).

## EMPIRICAL EVIDENCE

### *Perturbation and Relocation*

Laland, Odling-Smee, and Feldman (2000) define two means by which organisms can change both their local environments and the selection pressures to which they are exposed. *Perturbation* refers to instances where organisms actively change components of their environments at specified locations and times, and pertains to the causal impact that organisms may have upon their world. For example, organisms secrete chemicals, deplete resources and construct artifacts. *Relocation* refers to cases in which organisms actively move in space, sometimes choosing the time when they do so. In the process they expose themselves to alternative habitats, with different environmental factors. In practice, most cases of niche construction are likely to involve some degree of both perturbation and relocation, but the distinction is a useful and logical way to organize and categorize data.

### *Perturbatory Niche Construction*

The fact that perturbatory niche construction occurs may be of no surprise, but the number and range of species that modify their selective environment to a significant degree is astonishing. An obvious example is the photosynthesis of many bacteria, algae, and the 260,000 extant species of plants, which has drastically altered the chemical composition of the atmosphere (Holland 1995). Micro-

organisms make numerous other large-scale contributions to the biosphere. For instance, marine phytoplankton scatter and absorb light in the upper layers of water columns, enhance the warming of surface waters, initiate the development of thermoclines, and play an important role in nitrogen fixation (Capone et al. 1997; Jones, Lawton, and Shachak 1994). Marine phytoplankton and zooplankton contribute significantly to the global carbon cycle by acting as biological organic carbon pumps in subtropical oceans, and by affecting the exchange of O<sub>2</sub> and CO<sub>2</sub> between those oceans and the atmosphere (Doney 1997; Emerson et al. 1997). Microorganisms, including both bacteria and protists, also build large microbial mats in shallow sea—and have done so for billions of years (Reid et al. 2000).

Forests contribute to the hydrological cycle, through the retention and evapotranspiration of water, and by doing so they may affect their own weather (Holling 1992; Shukla, Nobre, and Sellers 1990). Other kinds of plants, for instance, species of bog-forming sphagnum mosses, can also profoundly affect local hydrology (Jones, Lawton, and Shachak 1994; Tansley 1949). Niche construction by marine plants may take forms not observed on land, but it too can have significant consequences. One example is the formation of kelp forests, which benefit from, and modify, the actions of waves near shorelines, and by so doing create relatively protected three-dimensional submerged habitats for many other species. For instance, they provide nursery grounds for lobsters (Barnes and Hughes 1999).

Perturbatory niche construction is most visible in animals. For instance, there are 9,500 known species of ants and 2,000 known species of termites (Isoptera), almost all building some kind of nest (Hölldobler and Wilson 1994; Pearce 1997). There are more than 9,000 species of birds, the vast majority of which construct nests (Forshaw 1998), and probably as many species of fish that do the same, as well as construct elaborate spawning sites and bowers (Paxton and Eschmeyer 1998). There are 20,000 species of solitary bees, with immensely varied nests, and many social bees construct nests too (Gullan and Cranston 1994). There are more than 7,000 species of Caddis fly (Trichoptera), with the great majority as larvae using their silk, vegetation, and stones to build fixed or portable shelters, or even to construct foraging tools, thereby defending themselves and exploiting their habitats in novel ways (Gullan and Cranston 1994; Hansell 1984). Moreover, there are 140,000 described species of butterflies and moths, most of which construct a pupal cocoon (Gullan and Cranston 1994). Of the 34,000 or more species of spider, almost all construct a silk shelter or sac to enclose and protect their eggs; those that do not, spin webs, dig burrows, or make nests (Preston-Mafham and Preston-Mafham 1996).

#### *Relocatory Niche Construction*

There are also countless examples of relocational niche construction. For example, algae and plants may initiate or perpetuate ecological successions through fortuitous dispersal caused by independent agents in their environ-

ments, but many species of animals may subsequently follow in their wake non-fortuitously by actively relocating. Animals also frequently select habitats, nesting sites, and developmental environments for their offspring (e.g., birds and spiders; see Attenborough 1998; Forshaw 1998; Turnbull 1964). Many colonies of ants are concentrated beneath rocks or in the bark of decaying stumps and logs, as these locations warm in the sun faster than soil (Hölldobler and Wilson 1994). Through such movements, organisms import and export nutrients to and from local environments, playing vital roles in the dynamics of resource flow through ecosystems (Jones, Lawton, and Shachak 1994, 1997). Most animals of the oceanic plankton and cyanobacteria show a diurnal pattern of vertical movements, in response to changes in light intensity and temperature (Capone et al. 1997; McFarland 1987). Annual or seasonal migrators include the European swallows (Hirundinidae) and swifts (Apodidae), who migrate to Africa and return each spring (Nowak 1991), and plains zebras (*Equus burchelli*), wildebeest (*Connochaetes taurinus*), and Thompson's gazelles (*Gazella thomsoni*), who travel across the African plains, following the rains (McFarland 1987).

#### *Evolutionary Responses to Prior Niche Construction*

When organisms construct niches, they also change the pattern of selection acting on other traits in their own and in other populations (Odling-Smee, Laland, and Feldman 1996). Odling-Smee, Laland, and Feldman (in press) have documented extensive evidence for evolutionary responses to selection generated by niche construction. For instance, consider cases where there has been selection for anatomical and behavioral adaptations that allow organisms to carry out their niche construction with greater efficiency. Many animals that dig burrows or build nests exhibit characters that appear to be anatomical or behavioral adaptations to their ancestors' perturbational niche construction. Thus, many burrowing frogs, and reptiles such as pipesnakes, wormsnakes, worm-lizards and caecilians, have evolved well-developed and specialized limbs, hardened snouts and skulls, reduced eyesight or limbs, and specialized sensory organs (Cogger 1998). Similarly, spiders have evolved responses to the threat of predation on the web, or for communication on the web (Preston-Mafham and Preston-Mafham 1996), which logically could not have evolved without the repetitive construction of webs by many previous generations of spiders (Odling-Smee, Laland, and Feldman 1996).

In other instances, selection appears to have favored further niche-constructing behavior, resulting in an elaboration of the constructed resource. For example, in many spiders (e.g., Segestriidae), the construction of a burrow has established selection pressures favoring the evolution of a number of extensions to the simple burrow structure, transforming it into an effective foraging tool, and enhancing its security. Most tube web spiders spin a series of trip-lines that radiate out from their burrows, and if an insect touches one the spider rushes out and grabs it (Henschel 1995). Comparative studies by Crook (1963) and Schnell

(1973) have led to the construction of phylogenies for weaverbirds, based on nest structure. Such studies provide compelling evidence that relatively simple nest construction preceded, and set up, the selection pressures favoring nest elaborations, such as a roof to protect chicks from rain (Hansell 1984). Further support for this theory is provided by the evolution of specific latrine sites positioned apart from the nest sites of numerous species, such as blind mole-rats, lemmings, and rats. Species without latrines, such as deer mice (*Peromyscus spp.*), are forced to make several nests each year as soiled nests must be abandoned when excretory products build up to noxious levels (Nowak 1991).

A third class of responses to prior perturbatory niche construction are adaptations for regulating the constructed resource. Consider temperature regulation. Ants function poorly below 20°C but can survive in temperate zones by regulating the temperature of their nests (Hölldobler and Wilson 1994). They plug entrances to their nests at night or in the cold and adjust the height or slope of the mound to optimize intake of heat from the sun. The plugging of nest entrances is also characteristic of many burrowing mammals in arid or cold regions (Nowak 1991).

Further evidence for anatomical and behavioral traits that are evolutionary responses to prior niche construction, including modified courtship, mating and parental behavior, can be found in Odling-Smee, Laland, and Feldman (in press). Living organisms exhibit an enormous amount of niche construction, and the products, resources, and habitats that those organisms construct frequently constitute fundamental components of their worlds and those of other species. Niche construction has modified selection pressures on the constructing organisms and has generated selection for further characteristics.

### MATHEMATICAL MODELS OF NICHE CONSTRUCTION

The evolutionary significance of niche construction hangs on the fact that organisms regularly modify both biotic and abiotic sources of natural selection in their environments, thereby generating a form of feedback in evolution that is rarely considered in evolutionary analyses. Recent theoretical population genetics models have revealed that feedback from niche construction can make a considerable difference to the evolutionary process. Laland, Odling-Smee, and Feldman (1996, 1999, 2001) have explored the dynamics of the joint evolution of environment-altering, niche-constructing traits in organisms and other traits (called *recipient traits*) whose fitness depends on feedback from natural selection in environments that can be altered by niche construction. The findings are consistent with those of related theoretical analyses, such as analyses of feedback in evolution, maternal inheritance, indirect genetic effects, and gene-culture co-evolutionary models with uniparental transmission of a dichotomous trait (Feldman and Cavalli-Sforza 1976; Kirkpatrick and Lande 1989; Mousseau and Fox 1998; Robertson 1991; Wolf, Brodie, and Wade 2000; Wolf et al. 1998).



The analyses suggest that the effects of niche construction can override external sources of selection to create new evolutionary trajectories, which leads to the fixation of otherwise deleterious alleles, the support of stable equilibria where none are expected, and the elimination of what would otherwise be stable polymorphisms. Even small amounts of niche construction, or niche construction that only weakly affects resource dynamics, can significantly alter both ecological and evolutionary patterns. This is because traits whose fitness depends on alterable sources of selection co-evolve with traits that alter sources of selection. This results in evolutionary dynamics for both traits that are very different from what would occur if each trait had evolved in isolation.

Frequently, the evolution of the recipient trait depends on the frequency of the niche-constructing trait over several generations, as is the case when there is an ecological inheritance. Theoretical population genetic analyses have established that processes that carry over from past generations can change the evolutionary dynamic in a number of ways, generating time lags in response to selection of the recipient trait, momentum effects (populations continuing to evolve in the same direction after selection has stopped or reversed), inertia effects (no noticeable evolutionary response to selection for a number of generations), opposite responses to selection, and sudden catastrophic responses to selection (Feldman and Cavalli-Sforza 1976; Kirkpatrick and Lande 1989; Laland, Odling-Smee, and Feldman 1996, 1999, 2001; Robertson 1991; Wolf, Brodie, and Wade 2000; Wolf et al. 1998). Moreover, as niche-constructing organisms modify the environments of other species, the feedback to the niche constructors may be indirect, and operate via any number of ecological components in the local ecosystem, including even abiotic components that are not normally incorporated in evolutionary models (Laland, Odling-Smee, and Feldman 1999).

Consider a situation in which the amount of a resource in the environment of a population depends upon the frequencies of alleles underlying the niche-constructing activities over many generations. This would be the case for a population of earthworms, whose soil processing or burrow-lining behavior over multiple generations affects the amount of topsoil, and soil nutrients. The amount of this constructed resource in turn feeds back to influence selection on alleles that influence aspects of the earthworm phenotype affected by soil conditions, such as the structure of the epidermis or the amount of mucous secreted. Laland, Odling-Smee, and Feldman (1996) found that under such conditions a time lag is generated between the change in frequency of alleles at the first locus, and the response to the frequency-dependent selection at the second locus. The time lag can be considerably larger than the number of prior niche-constructing generations.

This time lag creates an evolutionary momentum. When selection at the genetic loci influencing niche construction stops or reverses, the amount of the resource in the environment continues to accumulate for a number of genera-

tions. Hence, alleles at loci whose selection is affected by the amount of the resource will continue to change frequencies in the original direction, despite selection favoring the alternate allele. This has two consequences. First, assuming it takes an evolving population many generations to change its own selection pressures, it may not be able to do so fast enough to prevent the genetic variation upon which its eventual response relies from being lost. In this instance, the population will continue to evolve in the same direction despite the change or reversal in the selection pressure. Second, once a population reaches a stable equilibrium, it takes a greater period of time, or unusually strong selection, for the population to move away from it (evolutionary inertia). The findings of such analyses are in accordance with Lewontin's (1983) original intuition that niche construction does change the dynamic of the evolutionary process in fundamental ways.

### ECOSYSTEM ENGINEERING

The niche-construction perspective could shed light on several problems that have hitherto been considered within the domain of ecology. Jones and colleagues (1994, 1997) point to several ecosystem phenomena that cannot be understood exclusively in terms of energy and matter flows only, and they stress the critical role played by the creation of physical structures and other modifications of their environments by organisms that partly control the distribution of resources for other species. Niche construction of organisms establishes "engineering webs," or control webs, in both communities and ecosystems. Such webs are not well explained by conventional ecological theory, largely because "ecosystem engineers" are not necessarily part of the flows or cycles they control. To give an example, it is generally assumed that trophic relations must conform to the principles of mass flow and conservation of energy (i.e., the mass consumed minus the wastes produced times the growth efficiency equals the mass gained by the consumer). But the amount of mass or energy put into a beaver (minus its wastes and the energy it uses to build its dam) does not equal the mass of the dam or the water it holds, nor the magnitude of the varied ecosystem effects that flow from dam construction. Jones, Lawton, and Shachak (1997) posit that a focus on niche construction helps to understand how engineering webs achieve their control and to predict which organisms are likely to have the biggest effect on an ecosystem. Moreover, Gurney and Lawton (1996) have demonstrated theoretically that the efficacy with which an engineering population degrades a virgin habitat not only determines whether there will be no engineers, a stable population of engineers, or population cycles in the frequency of engineering, but also the extent of virgin and degraded habitat.

Evolutionary phenomena associated with niche construction complement and add to these observations. For instance, organisms can pump abiota into physical states that the abiota could never reach on a dead planet, and these modified abi-

otic components of ecosystems may later become the source of modified natural selection pressures acting on other species. This has a number of implications for ecosystems. First, when they engineer, niche-constructing organisms frequently influence their own evolution by modifying their own selective environments, often indirectly via biotic and even abiotic components, or chains of such components. Second, niche-constructing organisms may also influence the evolution of other populations, again often indirectly via intermediary abiotic components. Third, organisms can create new niches for themselves, for example through technological innovation or relocation to a novel environment, which again will influence the dynamics of their ecosystems. Fourth, where the co-evolution of populations occurs indirectly, via the impact of niche-constructing organisms on intermediate abiotic ecosystem components, the intensity of selection on the biotic sink population will not necessarily be proportional to the number of individuals or frequency of genotypes in the biotic source population. Since the dynamics of the intermediate abiotic component may be qualitatively different from either the frequency changes in the genes that underlie the niche construction, or the number of niche-constructing organisms in the first population, this indirect feedback between species may generate some interesting, as-yet-unexplored behavior in co-evolutionary systems, differing from the dynamics associated with established coevolutionary models (Futuyma and Slatkin 1983).

Hitherto it has not been easy to apply evolutionary theory to ecosystems, because of the presence of non-evolving abiotia in ecosystems. This obstacle has been largely responsible for preventing the full integration of ecosystem ecology and population-community ecology, or of ecosystem ecology and standard evolutionary theory (Odling-Smee 1988; O'Neill et al. 1986). By adding the process of niche construction to the established process of natural selection, the niche-construction perspective enables the incorporation of both abiotic environmental components and interactions between biota and abiotia into evolutionary models, such that evolutionary control webs begin to emerge. Unlike standard evolutionary theory, this approach is equally applicable to both population-community ecology and ecosystem-level ecology, which may eventually make it easier to reconcile these two ecological sub-disciplines under the rubric of an extended evolutionary theory that includes niche construction (Odling-Smee, Laland, and Feldman, 2003).

### TESTING NICHE CONSTRUCTION THEORY

If niche construction is going to pay its way scientifically, it must stimulate useful empirical work. Hypotheses concerning the evolutionary role of niche construction can be tested through laboratory and field experiments, and theoretical studies. (See Jones, Lawton, and Shachak [1997]; Laland, Odling-Smee, and Feldman [1996, 1999, 2000]; Odling-Smee [1988]; Odling-Smee, Laland, and Feldman [2003].)

*Consequences of Canceling or Enhancing a Population's Capacity for Niche Construction*

One fairly straightforward experimental design that allows researchers to assess the evolutionary consequences of niche construction is to contrast, over several generations, experimental populations of niche-constructing organisms with otherwise identical populations for which the impact of their niche construction is experimentally negated (Odling-Smee 1988). Control conditions—for instance, without the subject organism—may be required in order to establish the nature and magnitude of the niche-constructed changes in the experimental environment. This information can then be exploited in the experimental condition, in order to cancel out the effects of niche construction. A further experimental condition, highlighting the effects of niche construction, could involve experimentally enhancing (instead of negating) the effects of niche construction on the environment. Jones, Lawton, and Shachak (1997) have proposed a virtually identical method with which to investigate experimentally the effects of ecosystem engineering using virgin, engineered, and degraded habitats.

In practice, researchers may choose to focus on the ecological impacts of niche construction, or on its evolutionary consequences in organisms, either in phenotypes (how have target traits changed with or without niche construction?), or at a genetic level (how have target alleles or genotypes changed in frequency in populations with or without niche construction?). Obviously, the feasibility of evolutionary experimentation depends very much on the generation span of the organism concerned, and experiments that focus on changes in gene frequencies may be restricted to comparatively short-lived organisms.

*Evolution of Recipient Traits and Prior Evolution of Niche-Constructing Traits*

For any clade of organisms, it should be possible to establish those phenotypic characters (recipient traits) that might have been selected as a consequence of feedback from prior niche-constructing traits. Pertinent characters could be measured in closely related organisms that do and do not exhibit this niche construction. Such comparisons could determine if the recipient character changes correlate with niche-constructing activity, and whether the characters are derived. At the very least, these studies could establish that the niche-constructing trait preceded the evolution of the recipient trait, and they might determine to what extent the niche-constructing trait is necessary for the evolution of the recipient trait (Laland, Odling-Smee, and Feldman 2000).

*Patterns of Response to Selection and the Capacity for Niche Construction*

Many niche-constructing behavior patterns have evolved that allow regulation of the environment in such a way as to buffer against particular natural selection pressures. As a consequence, potent niche constructors should be more resistant to genetic evolution in response to autonomously changing environments than

less able niche constructors (Laland, Odling-Smee, and Feldman 2000). For instance, if we assume that primate niche construction is more flexible than that of other mammals, or that vertebrates have a more extensive niche-constructing capability than invertebrates, a number of hypotheses follow. First, consider Vrba's (1992) hypothesis of "turnover pulses." We would expect advanced niche constructors such as primates, including hominids, to show a weaker evolutionary response to fluctuating climates than other mammals. Similarly, we would expect vertebrates to exhibit less of a response to fluctuating climates than invertebrates. Second, consider Bergmann's and Allen's rules (Gaston, Blackburn, and Spicer 1998). These rules suggest that populations in warmer climates will be smaller bodied and have bigger extremities than those in cooler climates. Again we would expect sophisticated niche constructors to show less correspondence to these rules than other animals, since they will be better able to regulate temperature through niche construction. Third, it should be possible to reverse the inference, and to use the fossil record to infer something about the niche-constructing capabilities of animals. The greater the organism's phenotypic (as opposed to extended phenotypic) response to environmental change, the more restricted its capacity for niche construction is likely to have been.

#### *Detecting Niche Construction in the Wild*

Perhaps the commonest method for detecting natural selection in the wild is to investigate whether there is a correlation across a geographical region between the trait of interest in an organism and the suspected environmental factor thought to be the source of selection favoring the trait (Endler 1986). Failure to detect such a relationship is generally interpreted as consistent with the null hypothesis that this environmental factor exerts no selection on the trait (Endler 1986). However, there is another evolutionary explanation, which is that the organism can afford poor structural adaptation of the trait to the environment because it compensates through niche construction. Earthworms are a good example. Earthworms have kidneys suited to living in freshwater, yet they are terrestrial, and live in soil (Turner 2000). Only because of their niche-constructing activities (described above) can they do this. One straightforward procedure for investigating such phenomena would be, first, to search for a correlation between some organismal structure with environmental factors. If no relationship is found, then investigate whether the organism exhibits niche construction that might compensate for poor adaptation of the structural trait and investigate whether there is evidence for an organism-driven modification of the selective environment. If so, search for evidence for evolutionary feedback in the form of structural or functional adaptations to the constructed environment. We predict that weak or absent correlations between structural traits and environmental factors that might otherwise be expected to be sources of selection will commonly be found to arise when organisms construct niches in a manner that counteracts or circumvents this selection.

## CONCLUSION

There is now considerable evidence that niche construction is widespread across all taxonomic groups of organisms and that it regularly modifies selection pressures. Theoretical models have demonstrated that the feedback from niche construction will almost certainly bring about important changes in the evolutionary process. However, the niche-construction perspective is not merely a more accurate portrayal of evolution. A major benefit provided by the explicit introduction of niche construction into evolutionary theory is that it is likely to generate new hypotheses and stimulate new empirical work. It is fruitful to regard the dynamic complementary match between organisms and environments as a product of reciprocal interacting processes of natural selection and niche construction.

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