

## CAUTION: NICHE CONSTRUCTION AHEAD<sup>1</sup>

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This fall, I watched as my neighbors waged war on moles (to be fair, it was the wife's mother and aunt, who became known as the "mole patrol"). It seems the moles were suspected as weapons-of-grass-destruction and were deemed to be dangerous to the way of life of free lawns everywhere. The mole patrol roamed the lawn each evening, pouring all manner of organic and inorganic chemical warfare into the burrows of the unsuspecting moles, setting up conventional implements of physical torture in mole runs, and finally chasing moving tunnels with sharp sticks. To my knowledge, no single mole succumbed to this police action, though I did notice that some crossed borders into a more protective sovereignty and dug up my yard. Not really caring about some dirt mounds in my yard, I found myself instead thinking about the selective forces faced by suburban moles and how their actions modified the microhabitat in which they lived. I did not realize it then, but the moles and the mole patrol they brought down upon themselves through their burrowing behavior are examples of niche construction, wherein organisms modify their surroundings and in doing so, alter patterns of selection. The extended phenotype of the moles—the mole-hills they created—altered the action of potential predators (the mole patrol). In so doing, the moles indirectly affected the soil environment by causing a variety of chemical cocktails to be poured into the ground. Finally, they relocated to a new and less-challenging selective environment by moving into my yard.

As defined by Odling-Smee, Laland, and Feldman, niche construction occurs "when an organism modifies the feature-factor relationship between itself and its environment by actively changing one or more of the factors in its environment" (p. 41). The authors cast a broad net that encompasses such a diversity of biological phenomena that it is hard to imagine a subdiscipline of biology that would not be touched by this concept. As summarized in a lengthy chapter on the evidence for niche construction, virtually all beings, live or dead, fit this broad criterion. Any living organism alters its environment, whether it be as simple and passive as a plant altering the wavelengths of light experienced by itself and others through reflection off of and transmission through its leaves, or as dramatic as the pond habitat created by beavers when they dam a stream. A predator that moves to a new foraging locality when food becomes scarce constructs its niche by relocating and thereby changing the selection it experiences. The mere act of respiration alters the mixture of gases experienced by other organisms in the community. Ironically,

death may be an equally important form of niche construction in this framework in that an organism, by dying, alters the nutrient composition of the place that it falls. This return of ashes-to-ashes and dust-to-dust alters the selective environment for those around the corpse and thereby constitutes niche construction. Even branches and leaves falling from trees becomes a form of niche construction by generating fuel for wildfires.

Few ecologists or evolutionary biologists would be surprised to learn that organisms interact with their environment in ways that change both the environment and the organism's perception of it. What, then, is the importance of defining a new concept to encompass all such actions? Odling-Smee, Laland, and Feldman claim that this action of niche construction is a fundamentally different and hitherto unappreciated force in evolution and ecology—a selective force of tantamount importance to natural selection. They argue that the "Darwinian algorithm" of variation, heritability, and differential reproduction fails to consider how organisms may modify selection that is experienced now and in future generations. Niche construction is portrayed as an alternative to standard evolutionary theory, one that brings the feedback between evolutionary product and process into play in an explicit way. Unfortunately, the authors' hard sell for the novelty, breadth, and significance of their flagship concept results in a diminished impact for the elements of their theory that are potentially unique and groundbreaking.

The core buzzword of niche construction is *feedback*. Natural selection is depicted as resulting from inanimate and abiotic features of the environment, features that are not changed during the evolution of a population. This version of the Darwinian algorithm was characterized by Lewontin (1983) as a pair of differential equations describing change of an organism (*O*) and the environment (*E*) over time (*t*):  $dO/dt = f(O, E)$  and  $dE/dt = g(E)$ . The key point of these equations is that, while change in organisms depends on features of both the organism and the environment, environmental change is not viewed as being influenced by the organism. Lewontin noted that the second equation should really reflect the fact that organisms change environments, too:  $dE/dt = g(O, E)$ ; such changes in environments may carry forward through time forming a sort of ecological inheritance. This pair of equations then becomes the framework for both the verbal and mathematical models that build the theory of niche construction.

It should be immediately apparent that the differential equations above are extremely general, and this fact allows niche construction to be applied to any situation in which an organism affects change in the environment or the selective nature of the environment. Odling-Smee, Laland, and Feldman spend a large part of their book supporting their con-

<sup>1</sup> *Niche Construction: The Neglected Process in Evolution*. F. John Odling-Smee, Kevin N. Laland, and Marcus W. Feldman. 2003. Princeton University Press, Princeton, NJ. 468 pp. PB \$39.50, ISBN 0-691-04437-6; HB \$75.00, ISBN 0-691-04438-4.

tention that niche construction is a fundamental aspect of all organisms. The authors categorize niche construction into a two-by-two system that distinguishes physical changes to the environment (perturbation) from movement of organisms to experience new environments (relocation). Either of these sorts of change may create new environmental conditions (inceptive) or may alter existing ones (counteractive). Within this broad scheme there is something for everyone. The authors offer examples of niche construction by every major group of extant organisms, from the decomposition of archaeabacteria, to allelopathy in plants, to social learning in animals, including humans. The result is a rich compendium of the diverse ways that organisms alter the environmental context in which they, or their descendants, experience selection. Readers cannot help but be persuaded that what the authors call niche construction is virtually universal.

Yet this inclusiveness is precisely what weakens the power of the idea. In an attempt to create a mantle so broad, organismal influences on the environment with profoundly different evolutionary impacts are lumped together. For example, Dawkins (2004), in an exchange loosely focused on his extended phenotype framework, favors a division between niche construction and what he calls “niche changing.” This latter term distinguishes changes in the environment that are simply “a byproduct of the organism’s way of life” (Dawkins 2004, p. 378) from active engineering of the environment more akin to Dawkins’s concept of extended phenotypes (Dawkins 1982). Niche changing might include general environmental effects such as the increase in soil nutrients resulting from large ungulates defecating or the oxygenation of the early earth’s atmosphere by the first photosynthesizers.

What’s the harm in lumping niche construction and niche changing? The answer is covariance. If evolution is a statistical process, covariance is surely its engine. The fundamental aspect of inheritance, genetic or cultural, is phenotypic covariance across generations. The translation of genetic information to phenotypic variation (the genotype-phenotype map) reduces to covariance between genes and phenotype. Selection itself, the fundamental adaptive force in the Darwinian algorithm, is simply a covariance between phenotypes and fitness (Price 1970). As Dawkins (2004) so acutely points out, some forms of niche construction (*sensu* Odling-Smee, Laland, and Feldman) have this engine, whereas others lack it. The problem is that the presence or absence of differing forms of covariances generate different kinds of dynamics—combining them under a single label obfuscates the differences and does little to build new understandings of how feedback loops can alter evolution.

At one end of the spectrum, respiration by plants may increase oxygen in the environment, thereby creating a new selective environment for subsequent generations of animals, but given the biochemistry of photosynthesis, there is little chance that a causal covariance exists between the production or lack of production of oxygen and any aspect of plant genomes. The feedback does not exist to explain respiration of oxygen as an adaptation of plants, or even as an evolved selection pressure on other species. Conversely, when a dung beetle constructs a tunnel and brood ball of dung to rear offspring, covariances are possible between genetic differences among adult dung beetles and their niche construction

efforts, as well as between the details of the constructed niche and their effects on the next generation of beetles. Such covariances are fundamental to generating the feedback across generations that makes niche construction a compelling evolutionary phenomenon within a gene pool. In other cases, covariances exist among features of different species, such as between variation in a parasite’s infectivity and its host’s fitness. Evolutionary response by hosts might further generate covariances between host phenotype and pathogen fitness, completing feedback whereby pathogens influence the selection pressure that subsequent generations of pathogens experience. Most readers will recognize this process as reciprocal selection leading to antagonistic coevolution, though it fits cleanly into the rubric that defines niche construction. It seems unlikely that we will better understand each of these qualitatively different phenomena by combining them into a single category that masks the differences in their patterns, dynamics, and outcomes.

Existing theoretical frameworks in ecology and evolution encompass much of what the authors seek to capture in niche construction, though clearly not under a single unified banner. In chapter 3 of *Niche Construction*, the authors briefly review some of the prior conceptualizations of the feedback between organism and environment. Each of these approaches was developed for a different sort of biological scenario with specific rules, yet all would be subsumed under a common theory of niche construction. It is difficult to see how a single model or framework can productively unify density-dependent ecological processes, reciprocal coevolution between species, cultural inheritance of nongenetic phenotypes, and indirect genetic effects between relatives within a population.

In the act of spinning the novelty of their own theory, the authors misrepresent some of the alternative approaches to feedback. Two common themes arise in their treatments that are exemplified in their explanation of indirect genetic effects (IGEs). Odling-Smee, Laland and Feldman argue that alternative theories treat environmental modification as a result of selection, not part of the process. IGEs, the authors claim, are viewed “solely as ‘effects’ or products of prior natural selection and not part of a process of environmental modification” (p. 128). On the contrary, IGEs only exist because individuals modify the phenotypes of conspecifics they interact with. In the case of maternal effects, the genes expressed in mothers are expected to alter the phenotype and fitness of offspring that have a finite probability of sharing the same genes that cause the modification. Surely this qualifies as a process of modification of the selective environment that a gene experiences. In more general cases, selection resulting from conspecifics is often described as social selection, one of the few relevant concepts I found conspicuously absent from the general discussion in *Niche Construction*.

A more troubling confusion about IGEs and alternative frameworks, however, reflects back on the importance of distinguishing subsets of niche construction. The authors suggest that all cases of ecological inheritance will generate IGEs. This is only true if (1) appropriate patterns of covariance exist between interacting individuals and the phenotypes they modify, and (2) interactions are between members of a single interbreeding population. The authors “see no reason why indirect genetic effects should be restricted to within-

species interactions" (p. 128). The reason, again, is that covariances have fundamentally different evolutionary consequences when they occur within a gene pool versus among gene pools. The influence that IGEs have on evolutionary dynamics occurs because of feedback within a genome. Comparable phenotypic manipulation occurs between members of different species (e.g., when an insect eats a toxic plant and sequesters toxins for its own defense), but analogous covariances between genotype, phenotype, and fitness do not result. Are such interspecific interactions evolutionarily interesting? Absolutely. But they are not homologous in dynamics and covariance structure to interactions within populations.

Despite these difficulties, *Niche Construction* does succeed in offering some exciting new possibilities. I found myself particularly captivated by the contrasts between the effects of niche construction in the short term versus long term. Actions of individuals in one generation might be felt by other members of the same generation, the next generation, or many generations into the future. The authors develop a relatively simple model of resource availability, in which the effect of niche construction might carry across generations with different temporal weightings (e.g., the most recent generation has a proportionally stronger effect than prior ones). Not surprisingly, great differences in time lags result in terms of the response to selection. The possibility exists that these sorts of carryover effects could generate evolutionary response long after the active niche construction and resulting selection has ceased. Whether such a multigenerational gap between modification of the environment and selection response forms the kind of self-directing feedback fundamental to the theory of niche construction, depends again on covariances. In this case they must be maintained across the generations that span original niche construction and the eventual response to selection.

Another intriguing manifestation of niche construction is what the authors refer to as environmentally mediated genotypic associations (EMGAs). In interacting communities of organisms, genomes are expected to influence each other through a variety of direct and indirect pathways. Some interactions will occur through direct biotic links, such as when a predator eats a prey, whereas others are likely to be mediated through an intermediate abiotic factor, such as the way in which some mound-building termites alter the thermal and hydric microhabitats available to other species. This approach of following genotypic connections across species boundaries and through networks of ecological association presents some promise for uniting evolutionary genetic and ecological models of coevolutionary interactions. Once again, the dynamics will be very different if the EMGAs maintain covariances across species than if they do not.

The authors work hard to convince the reader that niche construction is a new "extended theory of evolution" that is a "co-contributor, with natural selection, to the evolutionary process itself" (p. 370). This argument is based on the somewhat disingenuous contention that evolutionary biologists view natural selection as an abiotic entity that is not influenced or changed by living organisms, and that "adaptation is conventionally seen as a process by which natural selection shapes organisms to fit pre-established environ-

mental 'templates'" (Laland et al. 2004). This straw man is weakened by the long list of similar ideas that the authors themselves describe, from frequency-dependent selection, to coevolution, to cultural inheritance, to maternal effects. Each of these ideas (and many others) points to a general appreciation that selection is a dynamic process that changes as organisms evolve and interact with their environments. The basic tenets of niche construction can be traced back at least as far as Fisher (1930). The oft-misunderstood fundamental theorem apparently included the assumption that growing populations are expected to degrade their environments so that the positive effects of genetic increases in fitness combine with negative feedback on environmental variation for fitness (Frank and Slatkin 1992). The net result in Fisher's view was that selection for increased fitness would not lead to any observable change in population mean fitness because evolving organisms modify their environments. The more active sense of engineering an organism's own selection was captured early on by Mayr's (1963) notion that behavior leads the evolution of morphology, ecology, and species differences. Through behavioral plasticity, organisms might shift niches, change diets, and move to new habitats, thereby changing selection so that "other adaptations to the new niche. . . are acquired secondarily" (Mayr 1963, p. 604). The basic premise that organisms interact with selection through a dual-direction causal arrow is not particularly novel or earth-shattering.

Nonetheless, *Niche Construction* is a thought-provoking volume. It is a book that should be read widely and thought about deeply. The book is a treasure-trove of natural history factoids, from bacteria to humans, that emphasize the ways in which organisms modify their environment. These observations form the basis of a perspective that seeks to define common connections between fields as disparate as population genetics, community ecology, and human behavior. In each of these applications, there are some exciting ideas that will inevitably lead to new theory and empirical explorations. I believe that existing theoretical frameworks cover most of the ground described here in a more focused and more effective way, but that is not to say there is not a lot to learn by taking a walk with these authors. *Niche Construction* is surely more than a molehill, but something less than the mountain that the authors portray.

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