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Niche Construction Theory: A Practical Guide for Ecologists

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## NICHE CONSTRUCTION THEORY: A PRACTICAL GUIDE FOR ECOLOGISTS

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## KEYWORDS

niche construction, ecological inheritance, ecosystem engineering, eco-evolutionary feedbacks, ecosystem ecology

## ABSTRACT

*Niche construction theory (NCT) explicitly recognizes environmental modification by organisms (“niche construction”) and their legacy over time (“ecological inheritance”) to be evolutionary processes in their own right. Here we illustrate how niche construction theory provides useful conceptual tools and theoretical insights for integrating ecosystem ecology and evolutionary theory. We begin by briefly describing NCT, and illustrating how it differs from conventional evolutionary approaches. We then distinguish between two aspects of niche construction—environment alteration and subsequent evolution in response to constructed environments—equating the first of these with “ecosystem engineering.” We describe some of the ecological and evolutionary impacts on ecosystems of niche construction, ecosystem engineering, and ecological inheritance, and illustrate how these processes trigger ecological and evolutionary feedbacks and leave detectable ecological signatures that are open to investigation. Finally, we provide a practical guide to how NCT could be deployed by ecologists and evolutionary biologists to explore eco-evolutionary dynamics. We suggest that, by highlighting the ecological and evolutionary ramifications of changes that organisms bring about in ecosystems, NCT helps link ecosystem ecology to evolutionary biology, potentially leading to a deeper understanding of how ecosystems change over time.*

## INTRODUCTION

**E**COLOGY has long been portrayed as a discipline separated by the different ways in which its two principal subfields, population-community and ecosystem ecology, relate to evolution (Ehrlich 1986; O’Neill et al. 1986; Jones and Lawton 1995; Likens 1995; Loreau 2010; Schoener 2011). Why?

A primary concern of many ecologists is to understand how energy and matter flow through organisms and their environments. In contrast, evolutionary biologists are principally concerned with information: that is, with the acquisition and inheritance across generations of algorithmic information by organisms (Chaitin 1987), primarily in the form of the heritable DNA sequences that underpin their adaptations. Standard evolutionary theory (henceforth SET) permits evolutionary ecologists to integrate population-community ecology and evolutionary biology (Whitham et al. 2006; Rowntree et al. 2011), but at the price of restricting population-community ecology largely to biota (O’Neill et al. 1986). SET recognizes abiota as sources of natural selection, but rarely considers the converse relationship, where organisms modify abiotic components in environments, to be ecologically consequential or evolutionarily generative. As ecosystems necessarily include abiota, evolutionary ecologists frequently “edit out” abiota from commu-

nities, and focus on the interactions of phenotypes in different species (for instance, in food webs). This means that many forms of environmental modification by organisms are left out of coevolutionary analyses, and partly accounts for the prevailing division between population-community ecology and ecosystem ecology. As a result: “The disciplinary links between ecosystem science and evolutionary biology are among the weakest in the biological sciences” (Matthews et al. 2011:690).

The need to overcome this weakness is now becoming urgent, particularly with increasing recognition that evolution and ecology can happen at the same pace (Kingsolver et al. 2001; Hairston et al. 2005; Ellner et al. 2011) and must shape each other (Palkovacs and Hendry 2010). Schoener (2011) describes “The Newest Synthesis” as “the emerging field of eco-evolutionary dynamics, whose major precept is that both directions of effect—ecology to evolution and evolution to ecology—are substantial” (Schoener 2011:426). A primary goal of this new field is to elucidate the consequences of bidirectional eco-evo interactions and “eco-evolutionary feedbacks” in ecosystems (Post and Palkovacs 2009).

The aim of this article is to illustrate how niche construction theory provides useful theoretical insights and practical tools that contribute to the integration of ecosystem ecology and evolutionary theory. The niche-

construction perspective explicitly recognizes environmental modification by organisms (“niche construction”), and its legacy over time (“ecological inheritance”), to be *evolutionary processes*: that is, they cause evolutionary change by acting as sources of modified selection, as well as of modified phenotypes (Lewontin 1983; Odling-Smee et al. 2003). This stance can be contrasted with the more tacit recognition of organisms’ environmental impacts in standard accounts. The extension has produced a body of conceptual and formal theory, known as “niche construction theory” (henceforth NCT), which explores the ecological and evolutionary ramifications of niche construction. NCT has begun to be used as a vehicle for integrating ecosystem ecology and evolution (Erwin 2008; Kylafis and Loreau 2008; Krakauer et al. 2009; Post and Palkovacs 2009; Loreau 2010; Van Dyken and Wade 2012). We begin by summarizing these findings.

NCT is derived from insights that were first introduced to evolutionary biology in the 1980s by Richard Lewontin (1982, 1983, 2000). Niche construction refers to the modification of both biotic and abiotic components in environments via trophic interactions and the informed (i.e., based on genetic or acquired information) physical “work” of organisms. It includes the metabolic, physiological, and behavioral activities of organisms, as well as their choices. For example, many species of animals manufacture nests, burrows, holes, webs, and pupal cases; algae and plants change levels of atmospheric redox states and influence energy and matter flows by modifying nutrient cycles; fungi and bacteria decompose organic matter; and bacteria also fix nutrients and excrete compounds that alter environments. Niche-constructing species include several categories of species recognized in the ecological literature, including ecosystem engineers (i.e., species that modify their environments via nontrophic interactions), keystone species (i.e., rare species with large effects on communities and ecosystems disproportionate to their abundance, often via predation), dominant species (common species with large effects on communities and ecosystems, often via competition), and foundation and facultative species (i.e., habitat-creating species;

Wright et al. 2002). For simplicity, we refer to all such activities as ecosystem engineering, although some of these activities are excluded from more strict definitions of this term. Ecological inheritance refers to legacies of change, in both biota and abiota, bequeathed by niche-constructing organisms to subsequent populations, which modify selection pressures on descendant organisms (Odling-Smee et al. 2003); this can be regarded as a second general inheritance system in evolution.

NCT has generated a body of conceptual and formal theory that explores the ramifications of niche construction for evolutionary biology (Odling-Smee 1988; Laland et al. 1996, 1999; Odling-Smee et al. 2003; Laland and Sterelny 2006; Silver and DiPaolo 2006; Lehmann 2008; Van Dyken and Wade 2012), and for related disciplines (Boni and Feldman 2005; Laland et al. 2010; Kendal et al. 2011), including ecology (Erwin 2008; Kylafis and Loreau 2008; Krakauer et al. 2009; Post and Palkovacs 2009; Loreau 2010), and the Earth sciences (Corenblit et al. 2009, 2011). Insights from mathematical evolutionary theory, summarized in Table 1, provide unambiguous evidence that niche construction is of considerable ecological and evolutionary importance.

The significance of niche construction for evolution is threefold. First, niche construction can influence spatial and temporal patterns in the strength and direction of selection acting on the constructors themselves (Odling-Smee et al. 1996, 2003). By modifying their own environments, and by legating modified selection pressures to their descendents via ecological inheritance, populations can influence the direction and the rate of their evolution; for instance, generating time-lagged responses to selection (Laland et al. 1999). Second, niche construction can increase the abundance of individuals within species by increasing fecundity and/or extending the longevity of individuals. By influencing population structure, it may thus decrease the significance of drift and potentially increase the longevity of species, independent of any direct selection. Third, through ecological spillovers that occur in the process of modifying their own niches, organisms can also

TABLE 1  
*Twelve insights from niche construction theory*

Finding	References
Niche construction can:	
1. Fix genes or phenotypes that would, under standard evolutionary theory, be deleterious; support stable polymorphisms where none are expected and eliminate polymorphisms that without niche construction would be stable.	Laland et al. 1996, 1999, 2001; Kerr et al. 1999; Creanza et al. 2012
2. Affect evolutionary rates, both speeding up and slowing down responses to selection under different conditions.	Laland et al. 1996, 1999, 2001; Silver and Di Paolo 2006
3. Cause evolutionary time lags, generate momentum, inertia, and autocatalytic effects. Interactions with evolving environments can produce catastrophic responses to selection, as well as cyclical dynamics.	Laland et al. 1996, 1999, 2001; Kerr et al. 1999
4. Drive niche-constructing traits to fixation by creating statistical associations with recipient traits.	Silver and Di Paolo 2006; Rendell et al. 2011
5. Influence the dynamics, competition, and diversity of meta-populations.	Hui et al. 2004; Borenstein et al. 2006
6. Be favored, even when currently costly, because of the benefits that will accrue to distant descendants.	Lehmann 2007, 2008
7. Allow the persistence of organisms in currently inhospitable environmental conditions that would otherwise lead to their extinction; facilitate range expansion.	Kylafis and Loreau 2008
8. Regulate environmental states, keeping essential parameters within tolerable ranges.	Laland et al. 1996, 1999; Kylafis and Loreau 2008
9. Facilitate the evolution of cooperative behavior.	Lehmann 2007, 2008; Van Dyken and Wade 2012
10. Drive coevolutionary events, both exacerbate and ameliorate competition, and affect the likelihood of coexistence.	Krakauer et al. 2009; Kylafis and Loreau 2011
11. Affect carrying capacities, species diversity and robustness, and macroevolutionary trends.	Krakauer et al. 2009
12. Affect long-term fitness (not just the number of offspring or grand-offspring) by contributing to the long-term legacy of alleles, genotypes, or phenotypes within a population.	McNamara and Houston 2006; Lehmann 2007; Palmer and Feldman 2012

change the niches of other species in an ecosystem. Where these spillovers are effectively coupled to other species they can lead to coevolution. Thus, niche construction has the potential to percolate through ecosystems and precipitate multiple evolutionary and coevolutionary events. In NCT, it is possible for *one:many*, *many:one*, and *many:many* relationships to occur between niche-constructing populations and other populations that coevolve as a result of the niche construction. Beavers provide a *one:many* example because beaver dams alter the environments of many populations (Naiman et al. 1988), while the soil environment coconstructed by earthworms, arthropods, plants, and bacteria, among others, is a *many:many* case. By drawing attention to the many important consequences that flow from time-lagged effects,

byproducts, acquired characters, and collective activity in ecosystems, the broader conceptualization offered by NCT compared to SET potentially allows it to make useful contributions to ecosystem ecology. The principal differences between SET and NCT are summarized in Table 2.

In the following sections, we first distinguish between the environment-altering and subsequent evolutionary aspects of niche construction; we then consider how these effects can be detected by ecologists and paleoecologists and used to comprehend eco-evolutionary dynamics.

#### NICHE CONSTRUCTION THEORY AND ECOSYSTEM-LEVEL ECOLOGY

Post and Palkovacs (2009) distinguish between two aspects of niche construction:

TABLE 2  
*Comparing standard evolutionary theory and niche construction theory*

Standard Evolutionary Theory	Niche Construction Theory
<b>Focus:</b> Organismic evolution in response to environments.	<b>Focus:</b> The coevolution of organisms and environments.
<b>Causation:</b> Primarily unidirectional, with autonomous selective environments shaping organisms. Reciprocal causation is recognized in some "special cases" where the source of selection is biotic (e.g., sexual selection, predator-prey coevolution).	<b>Causation:</b> Primarily reciprocal, with selective environments shaping organisms, and organisms shaping selective environments, either relative to themselves or other organisms.
<b>Niche construction:</b> Organisms acknowledged to change environmental states, but this is treated as the product of natural selection and rarely as an evolutionary process in its own right. Focus is restricted to adaptations expressed outside the bodies of the organisms (e.g., extended phenotypes).	<b>Niche construction:</b> Treated as an evolutionary process in its own right. Focus is not exclusively on adaptations, but includes changes in environments caused by the byproducts of organisms (e.g., detritus), acquired characters (e.g., learned), or the collective metabolism or behaviors of multiple individuals/species.
<b>Inheritance:</b> Primarily genetic, although maternal, epigenetic, cytoplasmic, and cultural inheritances recognized as "special cases."	<b>Inheritance:</b> Genetic and ecological inheritance (i.e., legacies of selection pressures previously modified by niche construction). Genetic and ecological inheritance interact to form "niche inheritance." Maternal, epigenetic, cytoplasmic, and cultural inheritances can be examples.
<b>Organism-environment complementarity (adaptation):</b> The product of natural selection.	<b>Organism-environment complementarity (adaptation):</b> The match between organism and environment results from dynamic interactions between niche construction and natural selection.

environment alteration and the subsequent evolution of population(s) in an ecosystem in response to natural selection pressures previously altered by the niche constructor(s). Although environmental alteration may commonly lead to subsequent evolution, some acts of niche construction are dissipated, swamped, or counteracted by other processes, such that their ecological and/or evolutionary ramifications are trivial and, in principle, ecologically and evolutionarily negligible cases of niche construction need not coincide (Post and Palkovacs 2009). This means that the ecological consequences of niche construction may sometimes usefully be studied without considering evolutionary ramifications and vice versa.

#### THE ENVIRONMENT-ALTERING ASPECT OF NICHE CONSTRUCTION

The environment-altering aspect of niche construction is similar to *ecosystem engineering* in ecology (Jones et al. 1994, 1997; Wright and Jones 2006; Cuddington et al. 2007; see

Glossary). Jones et al. (1997) describe *allogenic engineers* that modify environments by mechanically changing materials from one form to another (e.g., nest-building wasps) and *autogenic engineers* that modify environments by changing themselves (e.g., trees that provide living space for insects, birds, and mammals, or windbreaks). Researchers have proposed various classes of ecosystem engineering, including structural engineers, bioturbators and bioconsolidators, chemical engineers, light engineers, and wind attenuators (Berke 2010; Jones et al. 2010). Although to some ecologists the term ecosystem engineering is restricted to nontrophic effects, it is important to recognize that important environmental alterations can also occur through trophic interactions, which is why we consider them here.

Jones et al. (1994, 1997) and Cuddington et al. (2007) drew attention to the paucity of ecological research dedicated to studying organisms that modulate the availability of resources and habitats in ecosystems. Many species influence energy flows, mass flows, and trophic

## Glossary

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**Algorithmic information:** Structural and functional “know-how” carried by organisms typically, but not exclusively, in their genomes (Chaitin 1987).

**Byproducts:** Phenotypic effects that evolve as a consequence of selection on some other character, rather than being an adaptation directly favored by selection for its current role.

**Eco-evolutionary dynamics:** Interactions between ecology and evolution occurring on overlapping time scales (Pelletier et al. 2009). The recognition that evolution can happen at the pace of ecology means that ecological changes can directly shape evolution and vice versa.

**Ecological inheritance:** The inheritance, via an external environment, of one or more natural selection pressures previously modified by niche-constructing organisms (Odling-Smee et al. 2003). Ecological inheritance typically depends on organisms bequeathing altered selective environments to their descendants, but other organisms, including unrelated conspecifics and members of other species that share the same ecosystem may also be affected by this legacy. Where an act of niche construction leads to a change in the species composition of the local ecological community, this too is regarded as an aspect of the ecological inheritance.

**Ecosystem engineering:** The creation, destruction, or modification of habitats and/or modulation of the availability of resources to other species by organisms (Jones et al. 1994). Ecosystem engineering can be equated with the environment-altering component of niche construction, although some definitions of ecosystem engineering are more restrictive.

**EMGAs (environmentally mediated genotypic associations):** Indirect but specific connections between distinct genotypes mediated either by biotic or abiotic environmental components in the external environment (Odling-Smee et al. 2003). EMGAs may either associate different genes in a single population or they may associate different genes in different populations.

**Engineering webs:** Webs of connectance in ecosystems, caused by species influencing energy and mass flows, and creating habitat and other resources for other species (Jones et al. 1994, 1997). Engineering webs contribute to the stability and dynamics of ecosystems, alongside webs of trophic interactions. Ecosystem engineers may influence and control energy and matter flows without themselves being part of those flows.

**Extended phenotypes:** Phenotypic characters expressed outside the body of the organism (Dawkins 1982). Although byproducts are sometimes characterized as extended phenotypes, Dawkins is explicit in stating that this is “not profitable,” and restricts use of the term to adaptations. Thus, extended phenotypes correspond to that subset of niche-constructing activities that are biological adaptations.

**Niche construction:** The process whereby organisms, through their metabolism, their activities, and their choices, modify their own and/or each other’s niches (Odling-Smee et al. 2003). Niche construction may result in changes in one or more natural selection pressures in the external environment of populations. Niche-constructing organisms may either alter the natural selection pressures of their own population, of other populations, or of both. Niche construction may occur through physical perturbation of the environment or through relocation to a new environment. Niche construction may have both positive and negative effects on the constructor’s fitness.

**Niche inheritance:** Combinations of genetic inheritance and ecological inheritance that descendant organisms inherit from ancestral organisms.

**Time lags:** Delayed evolutionary response of characters exposed to selection pressures modified by niche construction. These time lags are generated by ecological inheritance that affects availability of a resource for multiple descendant generations, and can be orders of magnitude larger than the number of generations of niche constructing affecting that resource. Time lags may generate unusual evolutionary dynamics, including momentum, inertia, and autocatalytic effects, as well as opposite and catastrophic responses to selection.

patterns in ecosystems nontrophically by generating *engineering webs* based on mosaics of connectivity among different species. Although the ecological consequences of niche construction should be the same as those of ecosystem engineering, NCT focuses primarily on those environment-altering activities of organisms that modify natural selection in ways that affect the evolution of population(s) (e.g., Loreau 2010).

As a discipline, evolutionary biology has focused overwhelmingly on the passage of genetic information via DNA, although there is increasing recognition that a broader notion of heredity may be required (Bonduriansky and Day 2009; Danchin et al. 2011; Bonduriansky 2012). In contrast, ecosystem ecologists are concerned with the flux and flow of energy and materials. If researchers are to bridge these disciplines, they require a framework capable of reconciling these differences. With this in mind, we define an ecological variable,  $R$ , representing any resource or condition that is both a potential source of selection for a recipient population, and is modifiable by at least one niche-constructing population (Laland et al. 1996, 1999). An increase in  $R$  can have either positive (e.g.,  $R = \text{prey}$ ) or negative (e.g.,  $R = \text{predator}$ ) consequences for the fitness of organisms in the recipient population. Here we differentiate between three broad categories of resource/condition that have different properties, and respond to niche construction in different ways (Figure 1).  $R$  could represent an abiotic component of the environment (e.g., water, sediment), or a biotic component (e.g., another organism), or an artifact or other construct built by an organism (e.g., a spider's web).

We further subdivide  $R$  into physical

energy and matter resources, henceforth labeled  $R_p$ , and semantic informational resources—e.g., “know-how” or algorithmic information, such as is encoded by genes, or is acquired through learning (Chaitin 1987), labeled  $R_i$  (Figure 1). Abiots are usually physical energy and matter resources only (exclusively  $R_p$ ), while biota always carry both physical  $R_p$  and algorithmic informational  $R_i$  resources. All organisms carry  $R_i$  (i.e., genetic information) in their genomes in addition to the  $R_p$  in their bodies, while animals also carry  $R_i$  (i.e., acquired knowledge) in their brains. Artifacts primarily carry  $R_p$ , but it is possible for them to carry  $R_i$  too as, for instance, in human artifacts such as computers or books. These distinctions are significant since the differences between different kinds of  $R$  potentially lead to different ecological responses to niche construction.

#### SIGNATURES OF NICHE CONSTRUCTION/ ECOSYSTEM ENGINEERING

Let us assume that  $R$  is modified by niche construction, such that  $R$  becomes  $R + \Delta R$ , where  $\Delta R$  could be positive or negative. Then  $\Delta R$  is a potential “ecological signature” of niche construction (ecosystem engineering), and offers a useful way to measure the ecological change caused by organisms. Detection and quantification of the impact of niche construction on an ecosystem therefore requires that  $\Delta R$  must be differentiated from all other potential sources of change in  $R$ , including those resulting from abiotic (physical or chemical) processes or from other biota not of focal interest. This is the usual

	<b>R</b> <i>(Any resource that can be modified by niche construction)</i>	
	<i>R<sub>p</sub> (Physical resources in the form of energy and matter. These are ecological resources.)</i>	<i>R<sub>i</sub> (Informational or algorithmic resources in the form of genetic or acquired knowledge. These are evolutionary resources<sup>§</sup>.)</i>
<b>Abiota</b>	Present	Absent <sup>§</sup>
<b>Biota</b>	Present	Present
<b>Artifacts</b>	Present	Sometimes

FIGURE 1. TYPES OF RESOURCE SUBJECT TO NICHE CONSTRUCTION

§ If the  $R_i$  in other organisms can be modified by the separate  $R_i$  in niche-constructing organisms (e.g., genetic manipulation by parasites), then the  $R_i$  in other organisms becomes an ecological resource for the niche constructors. § Some organisms superimpose “signals,” such as scent marks, on abiota. If they do that, abiota may carry  $R_i$  as well as  $R_p$ . However, in that case, abiota are probably better described as  $R_i$ -carrying “quasi-artifacts” rather than as abiota.

strategy of researchers who study NCT, ecosystem engineering, and eco-evolutionary feedbacks (Jones et al. 1994, 1997; Odling-Smee et al. 2003; Cuddington et al. 2007; Post and Palkovacs 2009), with a variety of observational, correlational, and experimental methods (for details see Jones and Lawton 1995; Odling-Smee et al. 2003; Hairston et al. 2005; Ellner et al. 2011). These include experimental manipulation of the presence, abundance, or potency of niche construction, common gardening experiments, selection experiments and experimental evolution, and often involve breaking a complex system down into component parts, which involve single-species or species-pair effects.

As the niche-constructing activities of many animals are shaped by the knowledge

that they carry in their genomes or brains, the  $\Delta R$  ecological signatures left by niche construction should reflect this information to the extent that an ecological signature of niche construction might stand out relative to changes in  $R$  resulting from other external processes. Below we spell out how abiota, biota, and artifacts potentially offer different signatures of prior niche construction.

#### Abiota

As abiota carry only physical resources ( $R_p$ ), niche-constructing organisms are only able to change abiota physically or chemically. However, there are often clear signatures of prior niche construction ( $\Delta R_p$ ) left in abiota; for example, in sedi-

ments, soils, oceans, and rocks (e.g., Erwin 2008). Unlike other causes of change in abiota, changes due to niche-construction must be due to the information ( $R_i$ ) in those organisms. Abiotic resources that have been affected by multiple generations of niche construction may have been driven far from thermodynamic equilibrium by the prior nonrandom work of organisms, and may therefore occupy states that could not occur, or would be highly unlikely to occur, on a “dead planet.” Examples include soil states changed by niche-constructing invertebrates, ocean states changed by Ediacaran organisms, and sediment or rock states changed by burrowing organisms (Odling-Smee et al. 2003; Erwin 2008; Erwin and Tweedt 2012). Even when it is due to byproducts, for instance, by their metabolism or their detritus, any alteration to an abiotic ecosystem component caused by niche construction will ultimately still be shaped by genetic information. It may therefore be nonrandom and should frequently stand out relative to any change caused by nonliving agents by virtue of its improbability (for instance, elevated rates of nutrient flux or improbable chemical composition). Such signatures may well be produced by multiple individuals, perhaps emanating from multiple species, and possibly detectable over periods of time substantially longer than the lifetimes of the constructors. The temporal and spatial patterns associated with the signature often covary with the density and duration of the constructor population(s) and the magnitude of their individual effects (Jones et al. 1994, 1997), and may be characterized by long-term trends in accumulation, depletion, or transformation of resources over time. Such patterns are also likely to represent an extremely broad range of scales.

### Biota

The biotic components of ecosystems differ from abiota in potentially being able to respond to prior niche construction by reciprocating with further niche construction of their own. Niche-constructing organisms can change biota in two ways: either by modifying the physical ( $R_p$ ) or informational ( $R_i$ ) states of other organisms (Figure 1). Niche-constructing organisms modify the physical

states of other organisms in ways long-studied by ecologists, for example, by provisioning or protecting other organisms (e.g., offspring), supplying them with nutrients (e.g., mutualism), eating them (e.g., prey), or competing with them (e.g., for light). At the population level, a niche-constructing population should therefore leave an ecological signature of its prior activities in biota ( $\Delta R_p$ ). It might modify the demographics of another population (e.g., the impact of guppies on algal growth), or its population structure (e.g., the impact of guppy predators on guppy size distributions), or its distribution across an environment (e.g., the impact of alewife populations on zooplankton communities in different lakes), or one of its engineering functions in an ecosystem (Post and Palkovacs 2009).

An ecological signature in a recipient population could also show signs of feedback to the original niche-constructing population in the form of a modified biotic resource, generating another ( $\Delta R_p$  and probably  $\Delta R_i$ ) ecological signature in the original niche constructors. This could result in demographic signatures among populations in ecosystems, potentially mediated by changes in intermediate abiotic ecosystem components, even in the absence of any genetic coevolution. Such interactions contribute to many of the phenomena that are routinely studied by ecologists (for example, trophic relations, community assemblies, energy/matter flows in ecosystems, and “engineering webs”). NCT predicts that these phenomena should depend on the niche-constructing activities of organisms far more often than has previously been recognized (except by those ecologists who study ecosystem engineering); it is therefore important that niche-constructing effects be quantified.

Niche-constructing organisms may also change the information ( $R_i$ ) carried by other organisms. For instance, horizontal gene transfer can occur in bacteria while a parasite, such as a virus or an insect, may affect the genome of its host by inserting a hostile “message” into its host’s genome. In animals, including invertebrates, useful acquired knowledge is often transmitted through social learning from conspecifics and heterospecifics (Galef and Laland 2005; Leadbeater and Chittka 2007).

Flack et al. (2006) describe how aggressive policing by dominant pigtail macaques creates a “social niche,” stabilizing and integrating macaque societies. Similarly, Oh and Badyaev (2010) describe how male house finches actively seek or create social environments with properties that enhance their attractiveness or conspicuousness to females (see also Cornwallis and Uller 2010). One of the strongest  $\Delta R_i$  impacts of human niche construction is the selective modification of other species, both intentional (e.g., domestication) and unintentional (e.g., evolution in response to human activities such as urbanization; Palkovacs et al. 2012). In such cases, “transmitting” organisms leave a  $\Delta R_i$  signature in the “receiving” organisms.

### Artifacts

Niche-constructing organisms may also modify selection by building artifacts, including nests, burrows, webs, mounds, and dams, all the way up to the houses, cars, factories, and computers of contemporary humans. We include in this category constructed resources such as crop fields, hedgerows, terraces, canals, artificial lakes, forest clearings, and so forth (Kendal et al. 2011). Artifacts are usually physical abiotic resources, but can be biotic resources (e.g., crop fields, ant gardens) and are often underpinned by information stored in the genome or brains of the constructor, as though they were “intelligently designed.”

Although the most familiar artifacts (nests, mounds) are “extended phenotypes” (Dawkins 1982), this concept is of limited utility here as it is restricted to niche-constructing *adaptations*, yet artifacts can sometimes be built by the *byproducts* of organisms. Examples include the dead coral substrate and sand of coral reefs, which are constructed by interactions among multiple species over long periods of time, and the paths and routes created by habitual animals. Moreover, particularly in the case of those manufactured by humans, artifacts built through the expression of acquired knowledge may still be informed and structured, even if they are not themselves biological adaptations. For instance, human buildings are not biological adaptations and, accordingly, a sim-

ple adaptation-byproduct dichotomy would imply that they are byproducts. However, humans and other animals possess some very general, knowledge-gaining adaptations, such as the ability to learn, which allow them to acquire and store information in their brains, to communicate this information to others, and in humans to build on that shared knowledge base cumulatively (for instance, through technological advance). This means that some artifacts may possess a designed property in spite of the fact that they are not adaptations. This property should shape the ( $\Delta R_p$ ) ecological signatures found in artifacts, and potentially facilitate their recognition. Finally, artifacts may sometimes include ( $\Delta R_i$ ) signs or signals such as the “advertising signals” in a bowerbird’s bower (Madden et al. 2012).

### CORRELATES OF SIGNATURES OF NICHE CONSTRUCTION

If a new niche-constructing activity evolves, it should start to generate a signature immediately, although probably only locally at first. Conversely, if a niche-constructing activity changes, or if the niche-constructing population goes extinct, then the signature it previously generated should dissipate from that time on. However, niche-constructed effects might be expected to accumulate over time, before they become detectable, either because the per-capita impact of a single act of niche construction is very small or because low-impact effects are dissipated, counteracted, or swamped by other processes. However, in searching for the covariation between putative niche-constructing acts and putative ecological effects, we note that this relationship may be time-lagged (Laland et al. 1996, 1999; Jones et al. 2010). Analyses of such time lags have been based on genetic models, but similar time lags occur in demographic and ecological models (Ihara and Feldman 2004; Jones et al. 2010), partly because structure formation and decay and biotic responses to structural and abiotic change are rarely instantaneous (Jones et al. 2010), although the dynamics of gene-frequency change may also contribute to time lags (Laland et al. 1996).

### Abiota

It should be possible to detect associations between specific niche-constructing populations and specific ecological signatures in abiota. It may even also be possible to detect traces of such associations in remains of extinct populations, the “ghosts” of ancient niche constructors, still capable of affecting contemporary ecological and evolutionary processes (Odling-Smee et al. 2003). For instance, bog-forming *Sphagnum* mosses produce peat that can persist for hundreds or thousands of years after the death of the living moss (van Breemen 1995), while the plants of the Carboniferous produced the fossil fuels that with human help are constructing the modern climate of Earth. These kinds of traces are particularly likely to be found in abiota, which commonly persist for a longer time than the populations that gave rise to them. Even if the information ( $R_i$ ) expressed by an extinct niche-constructing population is now gone, it may still be possible to retrieve a proxy for it from a functionally equivalent contemporary population, thereby allowing its original biological functionality to be inferred. For example, the individual organisms responsible for the oxygenation of the atmosphere are extinct, but many contemporary organisms exhibit photosynthesis, suggesting parallel characteristics in the original oxygenators. Features related to the prevalence or density of extinct or ancestral organisms, the signatures of their niche-constructing activity, may still be recoverable in contemporary oceans, sediments, or in the atmosphere (for examples see Erwin 2008; Corenblit et al. 2011).

### Biota

Ecological associations between niche-constructing and recipient biota typically involve ongoing interactions between currently living organisms, corresponding to familiar ecological relationships, such as predator-prey, host-parasite, mutualisms, or competition for a shared resource. However, NCT draws attention to the possibility that such interactions may also be mediated by any number of abiotic or biotic intermediate ecosystem components.

Moreover, the density of a recipient population may covary with the density of a constructor population  $n$  time steps ago, if their interaction occurs via a resource, manufactured by the constructor population that takes time to accumulate, or is gradually depleted through niche construction (Laland et al. 1999). Indirect associations increase the likelihood that the effects are time-lagged. Although these observations might make species' associations appear complicated, in practice, it need not make the job of the ecologist or evolutionary biologist any more difficult, and may often make it easier since established procedures and methods can address the problem and render systems more predictable (Jones and Lawton 1995; Odling-Smee et al. 2003). The key to progress is to break down complicated pathways into tractable component pieces (e.g., Post and Palkovacs 2009; see the section entitled Methods of Implementation).

Ecological associations should typically occur in the presence of the species expressing the genetic or acquired knowledge responsible for the niche construction, although this association may be time-lagged and may fade or disappear when the relevant niche-constructing population disappears. It follows that ecological signatures of the novel appearance, the ongoing presence, or the subsequent disappearance of niche constructors may affect inference about the structure, function, and regulation of ecosystems. Here NCT can offer some useful predictions—for instance, concerning when invasions occur and how they should change ecosystem functioning when they do occur (e.g., see Odling-Smee et al. 2003; Loreau 2010).

Reciprocal acts of niche construction by recipient biota may be repeated many times, so the knock-on consequences of a single type of niche construction could cascade through many compartments of an ecosystem. Such causal chains, or cascades, resulting from niche construction may include evolutionary as well as ecological responses and trigger eco-evolutionary dynamics (Pelletier et al. 2009; Post and Palkovacs 2009; Loreau 2010).

### Artifacts

Ecological signatures left in artifacts by niche construction may be very different from those left in other kinds of abiota, since they often comprise the entire artifact and may possess a designed quality. This should be reflected in particularly strong associations between the expressed information ( $R_i$ ) and the signature ( $\Delta R_p$ ), particularly in extended phenotypes such as nests, webs, and mounds. They should also clearly demonstrate their roles in contributing to the fitness of their constructors. Artifacts are also often highly organized, one consequence of which is that they may spontaneously dissipate or be deconstructed by other organisms, leaving only transitory ecological signatures unless they are constantly repaired and/or reconstructed. Moreover, since artifacts are often difficult and costly to construct and maintain, they, or their component parts, will frequently be valuable to other organisms and may require defending. Artifacts can also feed back to the constructor population to modify the latter's developmental environment. A good example is provided by Leca et al. (2010) who describe how piles of stone tools left by macaques shape the learning of tool-using traditions in these monkeys.

### THE EVOLUTIONARY CONSEQUENCES OF PRIOR NICHE CONSTRUCTION

We now turn to the second major aspect of niche construction, namely, the subsequent evolution of populations due to natural selection modified by organisms. Note the niche-constructing population that causes the ecological change does not necessarily have to be the same as the recipient population(s) whose subsequent evolution is affected by the selection that has been modified by that particular ecological change (Odling-Smee et al. 2003; Post and Palkovacs 2009). This means that niche construction can potentially trigger both "diffuse coevolution" (Strauss and Irwin 2004), and coupled coevolutionary dynamics. Below, we consider what it takes to convert an ( $\Delta R$ ) ecological signature into an evolutionarily significant modified natural selection pressure for one or more populations, and then review the principal alternative

eco-evolutionary paths in ecosystems described by NCT.

### FROM ECOLOGICAL SIGNATURES TO MODIFIED SELECTION

To affect evolution, any change in any ecological variable caused by niche construction ( $\Delta R$ ) must translate into at least one modified natural selection pressure for at least one population in an ecosystem. It cannot do that unless the ecological signature caused by the niche construction becomes a component in the ecological inheritance of at least one population. There would be no evolutionary consequences if the ecological changes caused by NCT dissipated too rapidly, or if they were swamped by other processes or by other agents, or if there were a constraint on the rate of evolution such as the absence of genetic variation. In such cases, niche construction would have only ecological consequences. Niche construction may have evolutionary consequences that are not easily detectable. For example, the evolutionary consequences of counteractive niche construction may be stabilizing, and they may be difficult to detect until the "constructor" disappears from an ecosystem.

In practice, the criteria necessary for an ecological signature of niche construction to be evolutionarily consequential are easily satisfied. Jones et al. (1994, 1997) describe the principal ecological factors that scale up the impact of "engineering" species in ecosystems: "(1) lifetime per capita activity of individual engineering organisms; (2) population density; (3) the local and regional spatial distribution of the population; (4) the length of time the population has been at a site; (5) the type and formation of the constructs, artifacts, or impacts, and their durability in the absence of the engineers; and (6) the number and types of resources that are directly or indirectly controlled, the ways these resources are controlled, and the number of other organisms that depend on these resources" (Jones et al. 1997:1952). All of these ecological factors should also make any ( $\Delta R$ ) change caused by the niche con-

struction more likely to translate into an evolutionarily significant, modified natural selection pressure for at least one population in an ecosystem. The higher the value of each of these six variables, the more ecologically potent the niche construction should be and the more likely it is that this will subsequently translate into evolutionarily significant ecological inheritance for at least one population in an ecosystem. It is not necessary for all six of the above variables to be high simultaneously. Some organisms, such as beavers, are potent niche constructors because they produce large, durable effects (Moore 2006). Others, such as photosynthesizing cyanobacteria whose individual impacts on their environments are tiny, can have a vast impact if they are present in sufficiently high densities over sufficiently large areas for sufficient time and may affect vast numbers of species (Odling-Smee 2010).

An additional factor that facilitates the conversion of an ecological signature of niche construction into a modified natural selection pressure is genetic inheritance. Insofar as most organisms in a niche-constructing population share the same genes, and insofar as these genes predispose them to niche construct in the same way, generation after generation, the collective consequences of their niche construction are likely to accumulate over time to the point where the ( $\Delta R$ ) ecological signatures they generate do become modified natural selection pressures on the population, which may cause further evolution of that or other populations in an ecosystem.

#### ALTERNATIVE ECO-EVOLUTIONARY FEEDBACK PATHS

Figure 2 describes the principal alternative eco-evolutionary feedback paths connecting the environment-altering and selection-pressure-modifying aspects of niche construction.

The simplest path (1) corresponds to that emphasized in Dawkins's extended phenotype. A genotype in a population expresses an environment-altering adaptation, for instance, the "houses" built by caddisfly larvae (Dawkins 1982). This extended phenotype then modifies a natural selection pressure that

feeds back exclusively to that genotype in the bearer responsible for building the extended phenotype and subsequently affects its fitness. Path (1) is described by SET and NCT in the same way. Path (2) is the path modeled in the earliest niche construction models (Laland et al. 1996, 1999) as well as some other modeling frameworks (Bailey 2012). Genotype(s) in a niche-constructing population express an environment-altering trait, which modifies an ecological variable. The ( $\Delta R$ ) signature of change becomes a modified natural selection pressure for the same population. Unlike path (1), however, the modified selection in this case does not solely feed back to the allele(s) or genotype(s) responsible for the environment-altering trait(s); rather it (also) affects the fitness of different allele(s) or genotype(s) in the same population. For example, the beaver dam modifies selection on genes expressed in beaver browsing or exposure to parasites. Path (2) can be supported by environment-altering byproducts as well as adaptations.

Path (3) is similar to path (2), except that the organisms affected by modified natural selection are no longer in the same population as the organisms responsible for modifying the natural selection. For instance, beaver dam building and browsing modify selection acting on genes expressed in the production of defensive chemicals by *Populus* trees (Martinsen et al. 1998). Note that path (3) can also represent environment-altering traits that are either adaptations (e.g., dam building) or byproducts (e.g., excretion). This "diffuse coevolution" is more accurately described as "feed-forward" than "feedback," and may be direct or indirect. The latter would happen if an environment-altering population causes a change in the availability of an abiotic resource, such as water or light, that indirectly affects a different recipient population. Path (3) might also work via intermediate biota that could serve as no more than a catalyst for a subsequent evolutionary change in a recipient population. For instance, an intermediate population might respond to a niche-constructing population with a demographic change, without itself evolving further. This might, nevertheless, translate into a modified

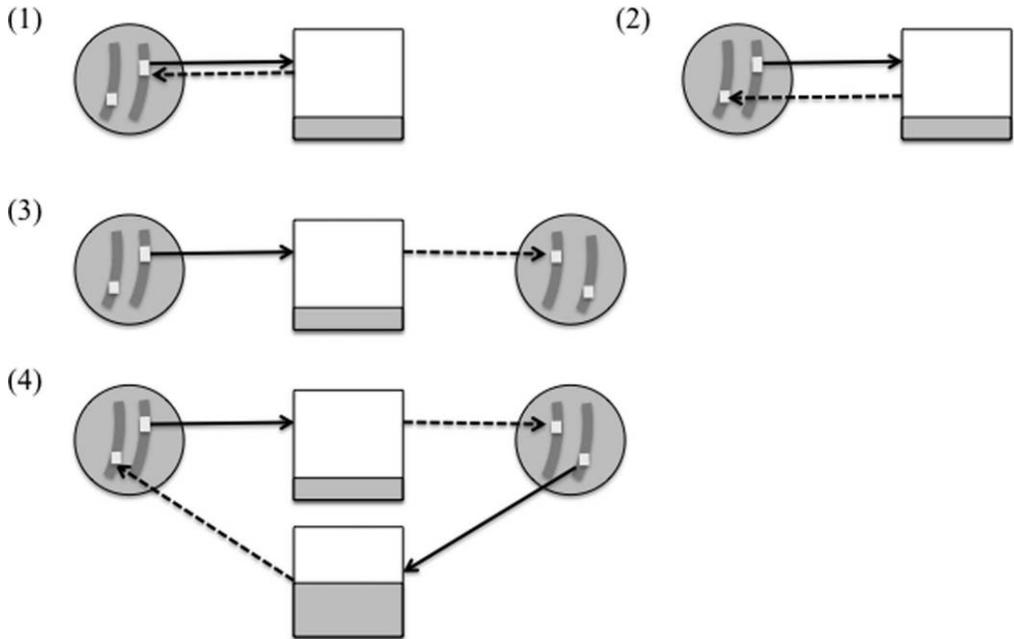


FIGURE 2. ECO-EVOLUTIONARY FEEDBACK PATHS

Alternative eco-evolutionary feedback paths that connect the environment-altering and selection pressure-modifying aspects of niche construction. Here shaded circles represent biota, white squares represent abiotic compartments in ecosystems, and shaded sections in white squares represent the  $\Delta R$  signature of niche construction that has modified the state of the abiota. The grey lines represent chromosomes, with the small white sections specific genes. Continuous arrows represent niche construction, and dashed lines natural selection. Path (1): A genotype in a population expresses an environment-altering trait that builds an extended phenotype, which modifies a natural selection pressure that feeds back exclusively to the genotype responsible for building the extended phenotype. Path (2): A genotype in a niche-constructing population expresses an environment-altering trait that modifies an ecological variable, thereby generating a modified natural selection pressure for the same niche-constructing population, but here affecting the fitness of different genotypes from those responsible for the niche construction. Path (3): Similar to path (2), except that the organisms affected by modified selection are no longer in the same population as the organisms responsible for modifying selection. Here the niche construction of the first population drives ecological change and coevolutionary episodes in the second population. Path (4): Resembles path (3), but with the additional property that the coevolution of two or more populations is facilitated via an additional feedback path. Here the second population modifies another abiotic resource through its own niche construction, which modifies selection acting back on the original population.

natural selection pressure for a third population that subsequently evolves further. Post and Palkovacs (2009) give contemporary examples, while Erwin (2008) discusses several cases of ancient niche construction, including sediment perturbation and the persistence of shell beds in marine ecosystems throughout the Phanerozoic, as well as their possible macroevolutionary consequences in deep time extending as far back as the Cambrian. Erwin and Tweedt (2012) discuss the role of such ecolog-

ical spillovers in influencing redox gradients and other aspects of the Cambrian Explosion.

Path (4) resembles path (3) but with the additional property that it promotes the coevolution of two or more populations via an additional feedback path or paths. If a recipient population responds to modified selection induced by niche construction, by itself becoming an environment-changing niche-constructing population that subsequently modifies selection on the original

niche-constructing population, then the two populations may coevolve. Once again, the feedback paths that connect coevolving niche-constructing populations to each other could be either direct or indirect. If they are indirect (path 4), particularly if the coevolution involves modified intermediate biota such as a mineral nutrient or soil pH, then the different physical dynamics of the abiotic change induced by niche construction may need to be taken into account. A possible example is provided by Goddard (2008) who shows experimentally how niche construction by the yeast *Saccharomyces cerevisiae* allows it to outcompete other species. This species eventually dominates in fruit niches where it is naturally initially rare, by modifying the environment through fermentation (the Crabtree effect) in ways that extend beyond ethanol production. NCT also describes more complicated patterns of connection between environmental alteration and selection-pressure modification. There can be *one:many*, *many:one*, or *many:many* relationships between environment-altering populations and subsequently evolving recipient populations via paths 3 and 4. All of these more complicated consequences of niche construction may also occur on multiple different scales in space and time (Loreau 2010).

#### THE ROLE OF BYPRODUCTS

A primary benefit of our broad conceptualization of niche construction is that it highlights the important roles that niche-constructing byproducts may play in ecosystems. This is significant because such roles are often unintuitive and easy to dismiss. It is far more apparent that the beaver dam may drive coevolutionary episodes than beaver dung may, yet the latter is a very real possibility. Numerous examples have been documented of seemingly inconsequential and inadvertent acts by organisms whose aggregate activity generates an important ecological signature. For example, consider *Euchondrus* snails whose consumption of endolithic lichens inadvertently generates tonnes of soil, thereby playing a vital role in fertilizing desert ecosystems (Jones and Shachak 1990).

Typically, evolutionary biologists assume that if a niche-constructing activity gener-

ates evolutionary feedback to the constructor, then it must be an adaptation. In fact, recent theory suggests that this need not be the case and niche-constructed byproducts can be consequential for the constructor's evolution. This occurs when byproducts precipitate bouts of selection in their own population by inducing selection on other traits in the same population and hitchhiking to fixation on the back of this selection they generate (Silver and Di Paolo 2006; Rendell et al. 2011). In this instance, spatial structure (local dispersal and mating) may give rise to statistical associations between niche-constructing traits and any genotypes favored in the constructed environments. Drawing on an important distinction made by philosopher Elliot Sober (1984), here there is *selection of* the niche-constructing trait, but not *selection for* it, and only the latter meets the definition of an adaptation (Williams 1966; Sober 1984). Nonetheless, in such hitchhiking cases, there remains evolutionarily consequential feedback to a niche-constructing population stemming directly from its niche-constructing activities.

#### THE ROLE OF ACQUIRED CHARACTERS

All of the aforementioned paths through which niche construction acts to trigger evolutionary episodes remain relevant even if the niche construction is the expression of learned knowledge. This point is of particular relevance for understanding human anthropogenic change within ecosystems; clearly it is acquired knowledge that underpins urbanization, deforestation, agricultural practices, and the majority of major human impacts on the environment. Such processes undoubtedly precipitate evolutionary episodes in humans and other species. It would be unwise for researchers to assume that human-modified selective environments can be treated as equivalent to such independent sources of selection as arise from geological or climatic change since there may be selective feedback to the constructing population of a form that influences its constructing behavior—for instance, a dairy-farming niche created the conditions that favored the spread of alleles facilitating adult lactase persistence, but the consumption of dairy products is more likely in individuals

with the lactose tolerant genotype (Gerbault et al. 2011). Similarly, deforestation for crop planting has apparently inadvertently promoted insect-propagated diseases (such as malaria) in many human populations, generating selection for resistant alleles (Durham 1991; Laland et al. 2010) and triggering further human niche construction, such as the widespread use of chemical insecticides. Hence, anthropogenic change leads to the type of eco-evolutionary dynamics recognized by ecologists, but underpinned by cultural learning.

#### SPATIAL STRUCTURE

The significance of niche construction for the evolution of recipient populations is further enhanced by spatial structure. Spatially explicit niche-constructing models have revealed hitherto unrecognized forms of dynamical feedback in ecosystems. For instance, niche-constructing traits, even if costly, can drive themselves to fixation through spatially enhanced statistical association with genotypes that they inadvertently favor (Silver and Di Paolo 2006). Rather than passively hitchhiking, these traits may actively create the conditions that promote their own spread by association with recipient traits. Such dynamics not only increase the amount of niche-constructing activity across a population, driving increases in the magnitude of the niche construction, but have also been shown, under more restricted conditions, to trigger a secondary hitchhiking process in which genetic variation at other loci that promote the potency of the niche-constructing behavior can also be favored (Rendell et al. 2011). Local spatial effects are also likely to be important in cases in which a population promotes its own range expansion through niche construction (Kylafis and Loreau 2008). An important aspect of spatial structure is its ability to promote simultaneous genetic and ecological diversification if the strength (or nature) of feedbacks differs from patch to patch (Habets et al. 2006). This perspective is important because it has the potential to link eco-evolutionary feedbacks to the process of adaptive radiation, which is usually attributed to an environmental template and the

importance of preexisting “empty niches” (Schluter 2000; Gavrillets and Losos 2009; Tebbich et al. 2010). Although the recent literature on adaptive radiations has emphasized lineage diversification without any necessary ecological changes, trophic novelty is a critical aspect of adaptive radiation (Martin and Wainwright 2011). Rather than lineages simply diversifying to “fill” available niches, niches themselves may be diversifying (Erwin 2005), a process that Losos (2010) termed “self-propagating adaptive radiation.” This process of differential niche construction and subsequent evolutionary diversification has been demonstrated in several microbial laboratory systems (Rainey and Travisano 1998; Habets et al. 2006) and appears to underlie the divergence between landlocked and anadromous alewife populations (Palkovacs and Post 2008; Schielke et al. 2012). What remains to be explored both empirically and through theoretical studies is the extent to which niche construction can drive the acquisition of new resources sufficiently to enable adaptive radiation.

#### TEMPORAL DYNAMICS

Temporal dynamics are likely to be equally important here, since engineering occurs over a broad range of temporal scales (Hastings et al. 2007) and many niche-constructing activities accumulate over time, sometimes even “deep time” (Erwin 2008). Formal theory suggests that time-lagged effects stemming from ecological inheritance can generate rich evolutionary dynamics (e.g., momentum effects, inertia, or catastrophic responses; Laland et al. 1996, 1999). They also raise some fundamental questions for biologists, such as how fitness is measured in natural populations of organisms. If niche-constructing organisms can influence patterns of selection not just on the current and offspring generations, but for many descendant populations, then an accurate estimate of fitness would require consideration of the costs and benefits of niche construction over multiple generations (e.g., McNamara and Houston 2006; Lehmann 2008). Under such circumstances, it may be better to replace conventional fitness proxies (such as repro-

ductive success) with estimates of genotype-specific intrinsic growth rates (McNamara and Houston 2006) or survivability (Palmer and Feldman 2012). It may be unwise to ignore such temporal dynamics since the fitness of niche-constructing genotypes is a dynamical property of resource concentrations, and hence may change over ecological timespans. Moreover, niche-constructing traits that might be considered too costly to evolve just on the basis of the number of offspring can be favored because of the benefits that accrue to more distant descendants (Lehmann 2008; Palmer and Feldman 2012). These theoretical dynamics potentially shed light on time-lagged effects observed in ecosystems (Hastings et al. 2007; Jones et al. 2010). Finally, the observation that there can be delayed feedback is also relevant to our earlier point that byproducts may be evolutionarily consequential. Byproducts can trigger time-lagged evolutionary events in descendant populations of the same species, but this selective feedback may occur too late to greatly influence the selection of the niche-constructing trait.

#### EMGAS AND ENGINEERING CONTROL WEBS

Jones et al. (1994, 1997) describe webs of connectance in ecosystems caused by species influencing energy and mass flows and creating habitat and other resources for other species. The same engineering processes are potentially indirect sources of selection originating from niche-constructing populations and acting on recipient populations and may underlie webs of diffuse and direct coevolution. We describe such indirect evolutionary interactions as *environmentally mediated genotypic associations* or EMGAs (Odling-Smee et al. 2003). EMGAs are “[i]ndirect but specific connections between distinct genotypes mediated either by biotic or abiotic environmental components in the external environment” (Odling-Smee et al. 2003:419). The key feature of EMGAs is that they map sources of selection stemming from one population’s genes onto genotypes in another population that evolve in response to those modified sources. Figure 3a illustrates a single EMGA in an ecosystem. A niche-constructing phenotype, influenced

by a genotype in a population of earthworms, causes an ecological change in an abiotic ecosystem component, the soil. Subsequently, that change in the soil translates into an evolutionarily significant, modified natural selection pressure in the ecological inheritance of a population of plants. The soil mediates an indirect connection between whatever genotype is underpinning the niche-constructing activities of the earthworms and an evolutionarily responsive genotype in the plants. A more complicated eco-evolutionary chain is shown in Figure 3b, based on an example studied by Palkovacs et al. (2009). Here predators differentially prey on two guppy populations (i and ii), generating different prey size distributions, which trigger different patterns of excretion and consequently affect nutrient cycling rates, leading to differential patterns of algal growth, which potentially feed back to affect selection on the guppies through exploitation of carotenoids. This sequence of EMGAs creates a causal chain through the guppies’ ecosystem.

In any real ecosystem, vast numbers of EMGAs must connect multiple environment-altering populations to multiple recipient populations, directly and indirectly, through both biotic and abiotic environmental components in rich networks. We imagine that such networks will frequently resemble engineering webs, although they need not be identical. Figure 3c illustrates a miniature model ecosystem comprising both evolving populations and intermediate abiota. These ecosystem compartments are connected by many EMGAs. If the abiota were to be edited out, then Figure 3c would reduce to a conventional community of populations, such as a food web (Figure 3d). However, it is important to note that Figure 3d may sometimes be a poor model of ecosystem dynamics because it omits the evolutionarily significant changes in intermediate abiota caused by niche-constructing organisms that are also responsible for driving ecological and evolutionary changes in ecosystems. Their inclusion, while it increases complexity, creates the linkages between population-community and ecosystem processes and would be justified if it increased predictability.

The recognition of networks of EMGAs has potentially important implications for understanding ecosystem dynamics. In practice, the feedback and feed-forward ramifications of niche-constructing activities are likely to go well beyond isolated “eco-evo” links and produce interwoven causal chains that thread ecosystems. The immediate drivers of evolutionary

changes in recipient populations are the ecological changes caused by environment-altering populations, but the preceding cause of evolutionary changes in recipient populations may well be the prior evolution of niche-constructing populations and, therefore, of the niche-constructing traits that cause the ecological changes in the first place. Thus, EMGAs

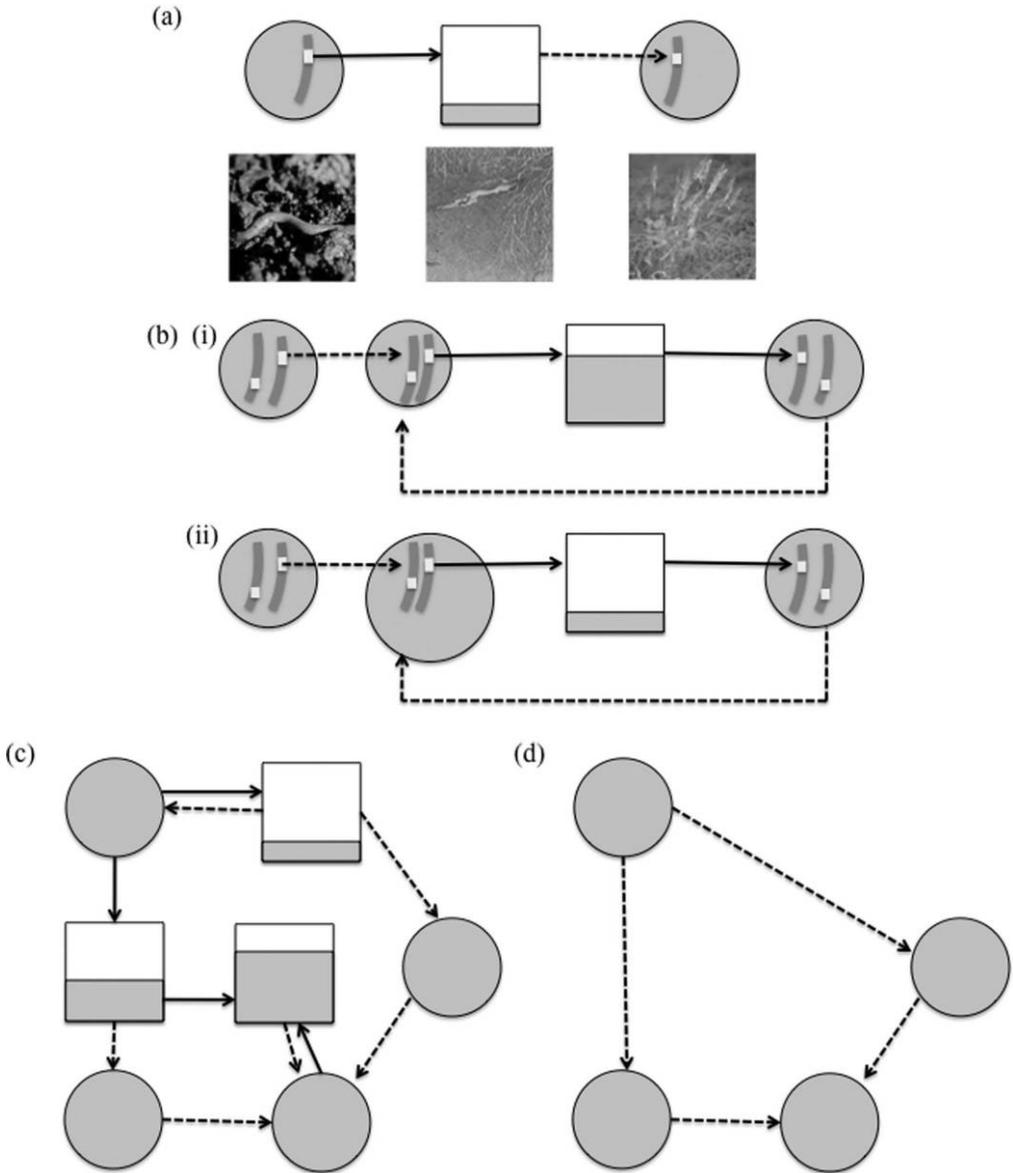


FIGURE 3

connect the prior evolution (“evo”) of genotypes in niche-constructing populations to the subsequent evolution of genotypes in recipient populations via the modification of either biotic (e.g., their phenotypes) or abiotic (e.g., soil chemistry) intermediate ecosystem (“eco”) components. In other words, EMGAs are not just “eco-evo” links in ecosystems, but rather “evo-eco-evo” links.

This argument can be extended further and, in some instances, the cause of selection for the initial evolutionary event in an “evo-eco-evo” link is the prior niche construction of an earlier population, while there may be further downstream ecological or evolutionary consequences of a given act of niche construction. In this manner, causal chains underpinning ecosystem dynamics can potentially be traced, as illustrated by Post and Palkovacs (2009). It is clear that such interactions will influence and to some degree “control” (Jones et al. 1997) ecosystem dynamics. However, it will also be apparent that “ecosystem evolution” need not resemble the simulated dynamics of the same system reduced to its biotic components, as in classical model ecosystems (e.g., May 1973), since such models omit EMGAs mediated by abiota and hence many important drivers of coevolutionary episodes in ecosystems. The inclusion of these additional connections could potentially greatly affect the stability of model eco-

systems. Thus, a full understanding of ecosystem dynamics will require incorporating food webs and engineering webs into dynamical systems that simultaneously consider trophic and competitive interactions alongside ecosystem engineering and niche construction.

While, in theory, any such “evo-eco-evo” causal chain might be traced back ad infinitum, in practice it is useful to assume that some event initiated a particular eco-evolutionary cascade. This might start with a change in the environment, which precipitates an evolutionary response in a focal population, but this is not the only possibility; the initiating event may best be characterized as an act of niche construction. For example, behavioral plasticity in a population of animal niche constructors may generate an innovation that propagates through the population via learning (for instance, birds learning to peck open milk bottles or monkeys discovering new food sources). In such cases, where presumably there is comparatively little advantage to considering the prior evolution of the population responsible for the niche construction, it makes sense to view the causal chain as triggered by an ecological rather than an evolutionary episode (in this case, a learned behavior).

This is particularly apparent in the case

FIGURE 3. FEED-FORWARD AND FEEDBACK PROCESSES IN ECOSYSTEMS

(a) Two populations connected indirectly by an EMGA. A genotype in a worm population expresses an environment-altering phenotype that modifies the soil. The ( $\Delta R$ ) ecological change in the soil modifies a selection pressure for a plant population. The recipient plants respond with genotypic evolutionary changes. The biota, worms, and plants are symbolized by shaded circles, and the intermediate abiotic environmental component, the soil, is symbolized by the square in the middle. The square is partitioned into shaded and white components, the former representing the ( $\Delta R$ ) ecological change in the soil caused by the earthworms’ niche construction, while the latter represents the extent to which the soil’s state is due to other agents. In principle, these components are measurable. (b) This figure symbolizes the guppy system described by Palkovacs et al. (2009). Differential predation in (i) and (ii) by two predator populations (the first shaded circle) lead to different size distributions in two guppy populations (the second circle), leading to differences in rates of excretion in the two populations (niche construction) leaving different ( $\Delta R$ ) signatures (shaded section of white square) affecting nitrogen cycling in the local environments (white square), affecting algal growth (the third circle), and feeding back to affect selection on the guppy populations. (c) An EMGA based “eco-evolutionary network” in a miniature model of an ecosystem. (d) The same ecosystem reduced to a food web, in a conventional population-community approach. Again, shaded circles represent biota, white squares represent abiotic compartments in ecosystems, and shaded sections in white squares represents the  $\Delta R$  signature of niche construction that has modified the state of the abiota. Ecosystem dynamics may be affected by engineering processes and their knock-on consequences, such that sometimes (c) cannot safely be reduced to (d).

of anthropogenic change where, for instance, deforestation or agricultural practices are obviously not triggered by evolution of “tree-chopping” or “crop-planting genes,” but nonetheless can initiate eco-evolutionary events in an ecosystem (Laland et al. 2010). Although we see utility in considering gene networks operating across multiple species in ecosystems (Whitham et al. 2006), such examples serve to emphasize that the interplay between ecological and evolutionary processes cannot always be reduced to the genetic level and, sometimes, such as where acquired characteristics underpin niche construction, a more appropriate focus may be on “environmentally mediated *phenotypic* associations.” One advantage of a niche-construction perspective is that it emphasizes the value of thinking of phenotypes as being reconstructed in each generation by different developmental resources (genetic and nongenetic), rather than as expression of genetically encoded information only. The focus of some methods (e.g., community genetics) on heritable phenotypic variation to the exclusion of nonheritable variation (e.g., plasticity, epigenetics, population structure) may miss many interesting eco-evolutionary processes (Uller 2008; Ellner et al. 2011; Palkovacs et al. 2012).

#### METHODS OF IMPLEMENTATION

The sheer complexity of engineering webs and the challenge of tracing evo-eco-evo causal chains through ecosystems appears to be a daunting ordeal for the ecologist. In reality, the practical study of ecology and evolution is not changed by this perspective, as standard methods regularly and successfully deployed by ecologists and evolutionary biologists can be combined to good effect. What is different is the focus of investigation, which moves from the study of the ecological impact or evolutionary response in a single taxon to the investigation of eco-evolutionary systems, pathways, or networks. This requires that researchers go beyond the normal practice of evolutionary biology and ask, “What causes the selection pressures leading to a specific evolutionary response?” rather than treating those selection pressures as a starting point. It also requires

researchers to go beyond the normal practice of ecosystem ecology and ask, “What evolutionary ramifications follow from species’ ecological impacts on biota and abiota?”

Any eco-evolutionary system underpinned by niche construction can be viewed as a chain of component links that either comprise the environment-altering (ecosystem engineering) aspect of niche construction (or its downstream consequences) or a subsequent evolutionary response to prior niche construction (Odling-Smee et al. 2003). The study of eco-evolutionary dynamics will require researchers to utilize the methods of both ecology and evolutionary biology. The key to progress is to break down complicated pathways in eco-evolutionary networks into tractable component pieces (e.g., Post and Palkovacs 2009), subject each to analysis and then reconstruct the network, including the strength of interactions and how they vary over time to gain a systems-level understanding. Sophisticated techniques to study network structure and dynamics have been developed via statistical mechanics and applied to a wide variety of problems, from social dynamics revealed by internet traffic to the dynamics of power grids and food webs (Newman 2010).

The guppy system studied by Palkovacs et al. (2009) serves as a useful example (Figure 3b). The first link in the chain is differential predation on two guppy populations. This environment-altering aspect of niche construction by the guppy predators leaves an ecological signature in the form of different size distributions in two guppy populations. Characterizing this link is, at least in principle, straightforward: it requires that the predators be identified, the intensity of predation measured, and the guppy size distributions sampled and quantified. Ideally, statistical analyses would link the intensity of predation to the resulting prey distributions. It is, of course, possible that there has been an evolutionary response to this predation in the guppies with, for instance, more intense predation favoring smaller adult guppy sizes, alternative trophic morphology, or dietary preferences. This is highly plausible

given the evidence for rapid evolution in guppies (Reznik et al. 1997) and in many other species in which the response to selection has been measured (Endler 1986; Kingsolver et al. 2001; Ellner et al. 2011). Again, this can be investigated using standard procedures (Endler 1986).

The second link in the chain is the differential excretion by the two populations and its impact on nitrogen (N) and phosphorus (P) levels in the water. This second environment-altering component of niche construction stems from the guppies and leaves an ecological signature in two abiotic environmental components: the local aquatic N and P levels. Palkovacs et al. (2009) were able to demonstrate this link experimentally with a mesocosm experiment. The results showed that high-predation guppy populations contributed approximately double the amount of N and P to the total nutrient pool via excretion compared to low-predation populations. In this way, differential excretion was identified as a correlate of the signature of niche construction (modified N and P). Under conditions of equal biomass, a population dominated by smaller individuals (the high-predation population) is expected to drive higher nutrient fluxes than a population dominated by larger individuals (low predation; Hall et al. 2007).

The third link in the chain connects the excretion-mediated nutrient fluxes to algal growth in the streams. This link could be demonstrated in the field by correlating measures of guppy excretion rates (or, more realistically, estimates of these based on assays of population densities as a function of size) with rates of algal growth. It could also be demonstrated experimentally, either under controlled conditions in the laboratory or micro-/mesocosms or in the field, by canceling or enhancing the environment-altering behavior (excretion) or mimicking its niche-constructed effects (Odling-Smee et al. 2003). Relevant experimental manipulations include: canceling or enhancing the niche constructors' current activity by removing individuals and/or supplementing their numbers with introduced members of the same species (e.g., decreasing/increasing guppy numbers or manipulating size distributions);

canceling or enhancing niche constructors' current activity by removal and/or providing them with the resources necessary for population growth (e.g., removing prey or feeding the guppies); canceling or enhancing niche constructors' current activity by removing from or supplementing the ecosystem with introduced members of the same guild (i.e., removing or adding a different species that engineers in the same manner, such as another small fish with similar impact on nutrient flux); artificially removing or manufacturing and introducing the products of the niche constructors (e.g., chemically extracting or adding N and P to mimic the effects of excretion); and counteracting negative effects and facilitating positive influences of both abiotic and biotic factors that may affect niche constructors through trophic or nontrophic links (e.g., interfering with the predation regimes). In all cases, the effects of these manipulations on algal growth could be monitored.

The final link in this chain could be to test a hypothesized feedback to trait evolution by connecting changes in algal biomass to guppy color patterns by demonstrating a response to (natural or sexual) selection in this character through sensitivity to the amount of algae-derived carotenoids available in the environment, again through standard procedures for detecting selection (Endler 1986). As this example demonstrates, testing links in eco-evolutionary chains of causality requires working at a variety of scales—from the whole-ecosystem scale to the small-scale experiment. Small-scale experiments are needed to isolate trait change as the driver of ecological change and can be useful for running selection experiments under controlled conditions. However, to show that trait-driven ecosystem dynamics and feedback effects are occurring also requires simultaneous studies at the whole-ecosystem scale, where such dynamics play out in nature.

In practice, the above procedures are likely to be complicated by many additional challenges, including the aforementioned spatial effects, time-lagged responses and other convoluted temporal dynamics, slow responses to selection in long-lived species, and so forth. Nonetheless, this example illustrates the tractability of tracing at least some

causal pathways via eco-evolutionary feedbacks and feed-forwards. Researchers can potentially go beyond merely identifying causal influences to quantifying their magnitude and duration. Other procedures that can be deployed include experimental manipulation of the potency of niche construction, common gardening experiments, selection experiments, and experimental evolution. Where relevant data are available, statistical approaches such as structural equation modeling and causal graphs can help to isolate or confirm putative causal influences and/or reject causal hypotheses that are inconsistent with the data (Pearl 2000; Shipley 2000). Once competing causal hypotheses are translated into statistical models, researchers can assess the evidence for each by standard statistical analyses or comparing competing hypotheses by using information theoretic or Bayesian criteria. The same methods allow the magnitude of causal influences to be quantified and niche-constructing effects on variables to be distinguished from other processes. With time-series data, the duration of niche-constructing effects and the rate of response to selection can also be quantified.

Ecosystems are threaded by a bewildering array of EMGAs, so a primary concern for researchers is how to constrain the system to a manageable size. This amounts to deciding which acts of niche construction and which responses to selection are too weak, transient, or trivial to merit inclusion and, conversely, which are too important to ignore. In many instances, likely or plausible key niche-constructing processes can be identified a priori by taking account of the factors described in the section entitled *From Ecological Signatures to Modified Selection* that scale up the impact of niche construction, supplemented by a knowledge of the basic biology of the species (Jones et al. 1994, 1997). Ideally, however, researchers would go beyond identifying a plausible key niche-constructing process to actually demonstrating its importance through data collection and statistical analysis or experimental manipulations and estimating its magnitude and duration. Likewise, in principle, putatively unimportant processes can be confirmed to be so through the same procedures.

The starting point for an investigation need not be the first link in the chain, as researchers can potentially work backward as well as forward in identifying causal influences (Odling-Smee et al. 2003). We envisage that the signatures of niche construction highlighted in the sections *Niche Construction Theory* and *Ecosystem-Level Ecology* and *The Evolutionary Consequences of Prior Niche Construction* might frequently be the starting points for analysis, triggering investigations of their downstream consequences for other ecosystem compartments or, alternatively, exploration of the causes of the niche construction.

The boundary of the system, in terms of where the eco-evolutionary causal chain or web should start or stop, is a decision for researchers, given the nature of their research interests and the resources available to them. In principle, systems could range in scale from short-term responses in isolated eco-evolutionary links to analysis of long-term patterns of change in entire ecosystems. In the latter case, we note increasing reference to “ecosystem evolution” within the ecological literature (e.g., Loreau et al. 2004), and point out that, to the extent that ecosystems comprise not just biota but also abiota, the integrated changes in entire ecosystems over evolutionary scales must be mediated by niche construction. Related to this point, given that much niche construction is stabilizing in effect, by counteracting prior changes in the environment (Odling-Smee et al. 2003), it follows that the absence of changes in entire ecosystems over evolutionary scales in spite of evolutionary changes in composite species must be mediated by niche construction.

Thus far we have said little about genes, yet our definition of EMGAs places emphasis on indirect associations between potentially distant genotypes. Increasingly, researchers are pointing out the plausibility of community or ecosystem genetics, and experimental and statistical tools are now available to identify the genes underlying a niche-constructing output or a phenotype that responds to selection (Whitham et al. 2006). Although we welcome and indeed encourage such developments, we also stress that the tracing of causality through

mapping eco-evolutionary processes in ecosystems can be done entirely at the phenotypic level. Indeed, in instances where acquired characters underpin the focal niche construction, which includes most anthropogenic change, analysis at the genetic level would be misplaced. As a starting point, a reasonable focus may be on “environmentally mediated phenotypic associations,” with isolating EMGAs a long-term objective.

There is increasing evidence that eco-evolutionary feedbacks play important roles in the dynamics of many ecosystems (Hairston et al. 2005; Pelletier et al. 2009; Post and Palkovacs 2009), with important implications for conservation and biodiversity (Boogert et al.

2006; Crain and Bertness 2006). Niche construction is a core component of such dynamics since it connects ecological to evolutionary processes. We hope that the conceptual tools that we have presented here will be of practical use to ecologists, leading to a deeper understanding of how ecosystems change over time and resist change.

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