Integrating Ecology and Evolution: Niche Construction and Ecological Engineering

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Abstract Ecology and evolution remain poorly integrated despite their obvious mutual relevance. Such integration poses serious challenges: evolutionary biologists' and ecologists' conceptualizations of the organic world—and the models and theories based upon them—are conceptually incompatible. Work on organism-environment interaction by both evolutionary theorists (niche construction theory) and ecologists (ecosystem engineering theory) has begun to bridge the gap separating the two conceptual frameworks, but the integration achieved has so far been limited. An emerging extension of niche construction theory—*ecological niche construction*—now promises to achieve a richer integration of evolutionary and ecological conceptual frameworks. This work raises broader philosophical problems about how to choose and combine idealized models of complex phenomena, which can be addressed with the aid of ideas developed by biologists (such as Richard Levins) and philosophers (such as Sandra Mitchell) on the goals and strategies of model-building in the complex sciences. The result is an opening up of new pathways for conceptual change, empirical investigation, and reconsideration of the familiar that has only just begun. Ecological niche construction combines with new developments in evolutionary developmental biology to reveal the need for a deep transformation of the conceptual framework of evolution and the emergence of an integrative biology re-uniting development, evolution and ecology.

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1 Ecology and Evolution

The importance of integrating ecological and evolutionary thinking has been discussed for decades now (Hutchinson 1965; Levins 1966), yet this “newest synthesis” (Schoener 2011) remains more notional than real. The Modern Synthesis of the 1930s and 1940s succeeded in integrating genetics with Darwinian evolutionary theory in a framework that combined intuitive appeal with mathematical rigor, generating simple models that could be elaborated to fit increasingly complex evolutionary scenarios (Mayr and Provine 1998). The complexities of organismal development and of organisms’ ecological relationships to their environments were for the most part put aside in the construction and early elaboration of that first synthesis, as inessential to the main story of genetic replication, assortment, and selection. Criticism of both of these omissions became prominent in the 1960s and 1970s (Levins 1968; Gould 1977; Lewontin 1978; Gould and Lewontin 1979). Positive work integrating evolutionary biology with developmental biology has recently moved forward rapidly in the wake of progress in the understanding of genetic regulatory mechanisms and their role in development (Hall 1992; Gilbert et al. 1996; Carroll 2005; Laubichler and Maienschein 2007). Ecology and evolution, however, remain poorly integrated at a theoretical level despite their obvious mutual relevance.

The separate treatment of ecological and evolutionary change was justified, originally, by the presumption that these two kinds of processes take place over time scales so disparate that there is no possibility of significant interaction between them (Slobodkin 1961). According to this presumption, the evolutionary environments that ecosystems constitute are usually stable over evolutionary timescales: the short-term ecological fluctuations that disturb this underlying stability are too ephemeral to have any important effect on evolution. Evolutionary change, on the other hand, is seen as too slow to matter to ecology. Critics of the presumption of separated time-scales have shown it to be false on both counts: evolutionary processes can be both sensitive enough to be influenced by ecological processes and rapid enough to influence them (Thompson 1998; Palumbi 2001; Hairston et al. 2005; Caroll et al. 2007; Pelletier et al. 2009). But there is a more general point to consider. The stability or mutability of ecosystems is itself a complex matter, affected by evolved characteristics of member organisms and perhaps by evolved ecosystem qualities, as well as by ongoing evolutionary processes at various levels. And the tempo of evolution is itself importantly affected by ecosystem functioning—by the stability or change occurring within the ecosystem, and by causal interactions among its component parts. To the extent that the presumption of markedly different evolutionary and ecological time-scales holds, this may itself be an outcome of eco-evolutionary interactions rather than a barrier to them. Understanding those interactions is thus inescapably important for both fields of inquiry.

Another way to think about the disjuncture between ecology and evolution is to see it as an outcome of differences in theoretical perspective. Evolutionary biologists and ecologists conceptualize the world differently enough that the relevance of ecological knowledge to evolutionary questions (and vice versa) is often not easy to see. More problematically, the basic simplifying assumptions with which they work may yield conceptual systems that cannot easily be combined. If this is the case there is clearly work to do: if evolutionists' and ecologists' conceptualizations—and the models and theories based upon them—are really in substantial tension with one another, it is worth investigating why that is, and exploring what to think about it. A central question concerns the best way to bridge the gap separating the two conceptual frameworks. Is it possible, and desirable, to unify the divergent frameworks? Or can the two fields of study be brought into illuminating interaction without such unification? This paper begins by exploring the conceptual disconnection between ecology and evolution, and its implications for thinking about the role of eco-evolutionary interaction in explaining change and stability in both ecological and evolutionary contexts. Sections 2 and 3 provide overviews of ideas about organism-environment interaction that take steps, from both sides, toward bridging the gap between the two fields: *niche construction* and *ecosystem engineering*. Sections 4 and 5 outline an emerging extension of niche construction theory—*ecological niche construction*—that is now beginning to achieve a richer integration of evolutionary and ecological conceptual frameworks. Sections 6 and 7 examine more closely the challenges posed by such an integration and how they may be met, in light of work by biologists and philosophers on the broader issue of how best to choose and combine idealized models of complex phenomena.

The traditional evolutionary picture divides the world into two parts: a population of organisms (whose relevant features are typically taken to be defined by their genes) and their environment. What is to be explained is change (or sometimes stability) in the genetic constitution of the organisms in a population. The organisms of each generation inherit their genes from their parents (perhaps slightly modified by mutation and recombination); the environment then selects among them, determining how many offspring each genetic variant contributes to the next generation. These processes, iterated, result in evolutionary change over time. In the traditional version of this picture, as it appears in the simple population genetics models central to evolutionary theory, the environment is taken to be unchanging (in which case it may be represented simply in the form of fixed fitness values assigned to the various genotypes) or as changing only as a result of causes that are independent of the organisms that inhabit it. A new and important revision to this evolutionary picture[1] has recently become widely accepted, however; it adds to the picture an explicit recognition that organisms affect their environments as well as being affected by them (Lewontin 1978, 1982, 1983, 2000; Dawkins 1982; Laland et al. 1999; Odling-Smee et al. 1996, 2003). This modified evolutionary picture differs from the traditional one in more important ways than is initially obvious; the differences will be explored in the next section. The point here is simply

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[1] Though one with deep historical roots: see Lewontin (1978), Godfrey-Smith (1996), and Pearce (2010).

that, despite its important innovations, even this enriched picture leaves in place the basic conceptual division between organism and environment that it inherits from the traditional picture.

The traditional and revised evolutionary pictures can be contrasted with equally-simple pictures from two different fields of ecological theory: population ecology and ecosystem ecology. Like population genetics (and evolutionary theory more broadly), population ecology begins by partitioning the world into population and environment.[2] But where the evolutionary theorist sees a population whose members have properties that vary within each generation and can change between generations, the population ecologist sees a collection of interchangeable individuals, whose common and unchanging features play out against the background of a (possibly changing) environment to produce, and explain, the properties and dynamics characterizing the population as a whole. Like evolutionary theory, population ecology has developed models that begin to take account of the two-way causal interplay between organisms and their environments; as in the evolutionary case, these revisions have far-reaching implications but leave the basic conceptual architecture of the picture in place.

The traditional ecosystem ecology picture is quite different from the others considered so far. Instead of beginning with the organism-environment division, it begins by dividing the part of the world falling within the ecosystem of interest into multiple interconnected functional components, both biotic and abiotic, whose interactions are understood in terms of flows of energy and materials. Parts of the world external to the ecosystem appear as sources and sinks for these resources. What is to be explained here is change or stability of features of the ecosystem structure. Though the factors external to the ecosystem are often referred to as “the environment,” nothing in this picture corresponds closely to the “organism-environment” division of the evolutionary and population ecology pictures, since there is no single focal population of organisms relative to which “the environment” can be defined. Many of the most important components of any organism’s local environment are other organisms, including members of its own population and of other local populations, and every organism is a part of many other organisms’ environments. There is also nothing in this picture that corresponds easily to the genetically-defined individuals and populations of evolutionary models: what matters for ecosystem ecology is the functional role that the organisms play, not their genetic constitution. Finally, in sharp contrast to the simple structure of the evolutionary models, in which the fundamental division is into elements “internal” to the organism and those “external” to it, ecosystem ecology pictures natural systems as composed of many interacting elements, linked in hierarchically-structured webs of causal connection.

There are thus two conceptual gaps to be considered, presenting rather different sorts of challenges to the would-be synthesizer. The gap between evolutionary

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[2] Population genetics and population ecology individuate populations somewhat differently, but this contrast is not important here.

genetics and population ecology is the result of idealizations that leave out different aspects of the relationship between population and environment: the two frameworks parse the world in roughly the same way, but they take different perspectives on the elements that result. As others have noted (Levins 1966; Shavit and Griesemer 2011), the factors that each of these two frameworks treats as variable, the other treats as fixed. The gap separating both of these frameworks from ecosystem ecology appears to pose a much more serious obstacle to the achievement of any substantial integration of ecology and evolution, representing as it does the divide between two fundamentally different representations of the causal structure of the organic world.

2 Niche Construction Theory

Niche construction theory (NCT) was first formulated as a revision of evolutionary theory, one of several different theoretical developments in the mid-to-late twentieth century that began to explore the variety of ways in which organisms interact with their selective environments—others included co-evolution theory (Janzen 1966) and extended phenotype theory (Dawkins 1982, 2004). As Sects. 4 and 5 will show, however, a broader application of the core idea of NCT can now help integrate the conceptual frameworks of evolutionary biology and ecosystem ecology.

Niche construction theory, as initially formulated, made a point about evolution. By modifying their own environments—in diverse ways—organisms modify some of the selective pressures that their environments exert upon them, and thus create reciprocal relationships between their own genetic characteristics and features of their environments. These relationships can affect the course of evolution in certain distinctive ways that are characteristic of causal feedback structures, such as producing rapid evolutionary change (and environmental change) via positive feedback, or ensuring evolutionary (and environmental) stability via negative feedback (Robertson 1991). They can thus, for example, change the tempo of evolutionary change—causing evolutionary time-lags, generating momentum and inertia effects, or precipitating episodes of abrupt evolutionary change. They can also change the equilibrium states of the population—creating conditions that lead to the fixation of genes that would otherwise be deleterious, supporting stable polymorphisms where none would otherwise be expected, eliminating polymorphisms that would otherwise be stable, or influencing the population's linkage disequilibrium (Laland et al. 1996, 1999, 2001a, b; Odling-Smee et al. 2003). Two simple examples illustrate some of these effects. The modern earthworm, despite its terrestrial habitat, retains many features that were important for the survival of its freshwater-dwelling aquatic ancestors. This evolutionary stability is maintained by the interaction between earthworms and their environment: by tunnelling, moving materials in and out of the soil surrounding their tunnels, and secreting mucus to coat tunnel walls, earthworms create an environment to which their quasi-aquatic physiology is well suited (Turner 2000). On the other hand, orb-weaving spiders create environments radically different from those experienced by their non-weaving ancestors: environments containing spider webs. Consequently, orb-weaving spiders have evolved a battery of morphological and behavioural features, fitting them for life in this special kind of environment.

Niche construction consists of two separate causal “steps” or sub-processes: the sub-process by which the organisms of a population modify their environment, and the sub-process by which the modified environment subsequently exerts modified natural selection on a population (Post and Palkovacs 2009).

Relative to the first of these sub-process, several different kinds of niche construction can be distinguished (Odling-Smee et al. 2003). Though cases such as earthworms’ tunnels and spiders’ webs are the most obvious, very diverse interactions between organisms and their environments can play the distinctive evolutionary role that characterizes niche construction. For example, organisms can affect their evolutionary environments by *perturbation* (by physically changing some properties of the world around them—building structures, consuming resources, or producing waste, for example) or by *relocation* (changing which parts of the world they interact with, by moving or growing into a new location where they confront different environmental properties). Either of these kinds of niche construction can be *inceptive* (producing novel changes in the effective environment) or *counteractive* (responding to externally-produced change in ways that override or limit its effects). Niche construction processes can also vary in their plasticity: *obligate* processes of niche construction are those that organisms cannot avoid (waste-production is an obvious example) while *facultative* niche construction processes are possible but not necessary for the organism. Thirdly, niche-construction processes can be classified according to their current selective effects or their selective histories. *Positive* niche construction enhances the current fitness of the niche-constructing organisms, while *negative* niche construction reduces it. *Historically-selected* niche-construction has been selected for in the history of the population, while *adventitious* niche construction has not been selected for (adventitious niche-construction is often a side-effect of features or processes that are themselves the result of selection, metabolism, for instance). Facultative niche construction is often historically-selected—the building of structures such as beaver-dams and spider-webs are paradigm cases here. Historically-selected niche-construction, in turn, will of course often be positive in its current effect, but in changing environments this is by no means guaranteed.

The second sub-process of niche construction, the exertion of modified natural selection on a population, is contingent on the capacity of the first sub-process to generate an *ecological inheritance* for a recipient population. The defining characteristic of niche construction is thus not the modification of environments *per se*, but the modification of natural selection pressures in environments, combined with the subsequent transmission of modified natural selection pressures from niche-constructing populations to recipient populations, via ecological inheritances, in ecosystems (Odling-Smee 1988; Odling-Smee et al. 2003).

For an ecological inheritance to become evolutionarily consequential it is then also necessary for whatever selection pressures have been modified by the prior niche construction to persist in their modified form in the environment, and therefore in the ecological inheritance of a recipient population, for long enough to cause an evolutionary response in the recipient population. However, in practice that is not a demanding requirement. The persistence of a modified selection pressure in a given environment over a period of generations in an evolving recipient population can be achieved in a variety of ways. For instance, it can be achieved by the sheer physical endurance of an environmental change caused by prior niche construction. The long term persistence of some changes in soils caused by earthworm niche-construction is an example. Conversely, it can also be achieved by highly transitory modifications of environments, through the constant repetition of the "same" niche-constructing acts by a series of generations of a niche-constructing population, often simply as a function of the "same" genes being inherited by successive generations of that niche-constructing population. Webs—repeatedly constructed and repaired by orb web spiders, generation after generation—are one example (Odling-Smee et al. 2003; Odling-Smee 2010). Therefore, it is not only possible but frequently inevitable for features of environments that are produced or maintained by niche-constructing organisms to be reliably passed on to descendent organisms, in the form of ecological inheritances. When that happens, an evolutionarily significant feedback path is likely to be completed. An ecological inheritance may then enable the prior niche-constructing activities of a population to influence the subsequent development of individual organisms in a population within each generation, and the subsequent evolution of a population between generations.

Thus the main differences distinguishing niche construction theory (NCT) from standard evolutionary theory (SET) are twofold: a changed picture of the causal relationship between organisms and their environments, and a changed conception of inheritance in evolution. First, natural selection, combined with niche construction, results in *reciprocal causation*, both in development and in evolution (Laland et al. 2011). Causal influences flow from environments to organisms, as described by SET, but also return from organisms to environments, as described by NCT. Second, because niche construction cannot be evolutionarily consequential until it generates an ecological inheritance, NCT is a dual-inheritance theory of evolution. It necessarily depends on genetic inheritance, as per SET, and ecological inheritance, as per NCT. (Instances of ecological inheritance are more diverse than those of genetic inheritance in their fidelity, in the classes of organisms that they link, and in the time-spans that they involve, but this difference does not obviate their importance as channels of inheritance.) NCT thus introduces one further novel concept, *niche inheritance*. Niche inheritance in evolution is constituted by interrelated genetic inheritance and ecological inheritance processes. It is not just genetic inheritance, but rather niche inheritance, that allows descendent organisms to inherit viable "start-up" niches from their parents (Odling-Smee 2010).

These differences between NCT and SET also give NCT a new focus: SET is about the evolution of organisms; NCT is about the evolution of organisms *together with* those changes in environments that are caused by the evolution of organisms. Hence NCT sees evolution in the same way that Richard Lewontin once articulated so succinctly: "Organism and environment coevolve, each as a function of the other" (Lewontin 1983, 282).

Last, insofar as genes are involved in both of NCT's two sub-processes (they are not always[3]) they can be connected by different feedback paths. The simplest form of niche construction is one in which the genes responsible for a niche-constructing trait are also the recipient genes that are affected by the changed selection pressures that, via their phenotypes, they themselves induced. Instances of this sort constitute a special case of niche construction, similar to what Richard Dawkins (1982, 2004) has called the "extended phenotype." Recognizing the independence of the two niche-construction sub-processes, however, allows us to take account of more complex reciprocal interactions between organisms and their environments, in which the modified environment exerts new selective pressures on genes other than those responsible for the niche construction (Post and Palkovacs 2009). This possibility can be represented in two-locus population genetics models (Laland et al. 1996; Odling-Smee et al. 2003). The state of some resource R in the environment is dependent on the niche-constructing activity associated with genes at the first locus. The state of R, in turn, influences the pattern and strength of selection acting on the second locus. Niche construction results in a changed environment, and this may affect the course of subsequent evolution for the niche-constructing population in many different ways. Thus beavers are adapted by evolution in numerous ways—morphological, physiological and behavioural—both to create and to thrive in environments containing lodges, dams, and the kinds of ponds and modified woodlands that beaver-dams produce; oaks are similarly adapted in many ways both to create and to thrive in environments containing frequent low-intensity fires. In both cases, the adaptations that fit the niche-constructing organisms to their modified environments extend far beyond the traits involved in the niche-construction itself. The genes involved in producing the niche-constructing traits thus help to create a modified environment that bestows selective benefits on the many other genes involved in producing traits that are adaptive in the modified environment.

3 Ecosystem Engineering

The effects of niche construction modify selection pressures not only for the niche-constructing organisms, but for other organisms as well. Beaver ponds, forest fires, spider webs, and the modified soil structure that earthworms produce, all have important selective consequences for many organisms other than their creators. This wider effect of niche construction connects it with a set of ideas that have been developed to address issues in ecology.

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[3] In humans, for example, niche construction is typically cultural; it depends primarily on acquired cultural traits, and not directly on inherited human genes (see Laland et al. 2001b, 2010; Odling-Smee and Laland 2012).

In ecosystem ecology, the concept of *ecosystem engineering* (EE) was introduced to make a point about ecological structure: that in modifying their own surroundings organisms change ecosystem features in ways that have effects on other organisms as well; that the features of ecosystems that are affected may be either biotic or abiotic; and that these processes have certain kinds of ecological consequences (Jones et al. 1994, 1997; Moore 2006; Cuddington et al. 2007; Cuddington et al. 2009). Types of ecosystem engineers can be distinguished according to the nature of their effects. Berke (2010) distinguishes four main categories. *Structural engineers* change or create relatively durable structural features of their surroundings: beaver dams, termite mounds, coral reefs, and the woody parts of plants are all examples of this sort of engineering. Structural engineers often reduce disturbance and increase the heterogeneity of their surroundings. *Bioturbators* such as burrowers and excavators disturb and mix materials in their surroundings, often producing an increase in uniformity. *Chemical engineers* modify the chemistry of soil, water, or air through processes such as respiration or photosynthesis, or by moving or depositing materials. *Light engineers* alter the local patterns of light transmission, changing the intensity of light in nearby locations by casting shade or causing light scattering, for example. All of these kinds of ecosystem engineering can be either *allogenic* or *autogenic*, i.e., they can take the form either of effects organisms have on their (external) surroundings, or of aspects of the organisms' own growth and development (Jones et al. 1994). The structural engineering carried out by beavers and termites, for example, is allogenic, while that carried out by trees or giant kelp is autogenic. In either case, ecosystem engineers have effects on ecosystem functioning that may be important for other organisms as well as for themselves. Importantly, ecosystem engineering is defined so as to exclude competitive and trophic interactions, since the ecological roles of these are already accounted for in existing models and theories.

4 Ecological Niche Construction

Many—perhaps all—instances of ecosystem engineering are also instances of the first sub-process of niche construction,[4] and it is easy to see that the two theoretical frameworks can be extended to reveal a further important relationship between them. Both frameworks emphasize the importance of the processes by which organisms modify their environments. Niche construction theory, as originally articulated, focuses on the evolutionary effects these processes have on the organisms that initiate them, while the ecosystem engineering perspective

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[4] Though the reverse is not the case, since niche-constructing activities that are part of the trophic web would not normally be regarded as ecosystem engineering, and relocational niche construction would also normally be excluded. For a different view of the relationship between ecosystem engineering and niche construction see Pearce (2011).

focuses on their ecological effects on local ecosystems and on other organisms within it. But it is obvious that these basic insights can be brought together to show the possibility—indeed the inevitability—of *organisms' modifying their environments in ways that have effects on ecosystem functioning that in turn affect the evolution of other members of the ecosystem*. Niche construction theorists have thus begun to focus more closely on cases of niche construction in which the two sub-processes of niche construction involve different populations of organisms, so that the genes responsible for the modification of the environment and the genes subject to modified selection pressure as a result are found in organisms belonging to different populations (usually of different species) (Barker 2008; Post and Palkovacs 2009; Laland et al. 2009; Laland and Boogert 2010). Ecologists working with models of ecological engineering processes have meanwhile begun to consider the evolutionary effects of those processes (Moore 2006; Erwin 2008). The result is an emerging framework that some ecologists have called *ecological niche construction* (Loreau and Kylafis 2008). This new framework promises insights into the relationship between evolution and ecology, including a new approach to thinking about the evolution of ecosystems (Odling-Smee et al. 2013). At a different level of analysis, it provides an illuminating example for thinking about the challenges and importance of the integration of different theoretical and conceptual systems in the sciences.

Consider a simple model of ecological niche construction. The first sub-process of niche construction modifies some R, a resource or feature of the local environment that plays a role in natural selection for some population. R may be abiotic (e.g. topsoil, or a water hole), biotic (e.g. another population of organisms), or artifactual (e.g. a beaver dam or termite mound).[5] We can represent the change produced in R by δR, so that the outcome of the first process of niche construction is a new $\mathbf{R}' = [\mathbf{R} + \boldsymbol{\delta}\mathbf{R}]$. Niche construction leaves different *δR ecological signatures* of change in different kinds of R. Typical δR signatures of prior niche construction in abiota include geo-chemical and thermodynamic effects (often simply by-products of biotic processes or activities). In biota, typical δR signatures are ecological (e.g. demographic changes in other populations). In artifacts, typical δR signatures include the features often identified with "design."

Distinguishing the two sub-processes of niche-construction, and their effects, allows us to enrich the very simple original picture of niche construction, and its role in evolution, with which we began (Post and Palkovacs 2009). Environment-altering populations and the recipient populations whose evolution is affected need not be identical, and various kinds of causal pathways linking them are possible. A niche-constructing population can act directly on a recipient population, or indirectly via intermediate biota or abiota. There can be (and often are) both one:many

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[5] This division is not an exclusive one, since artifacts are usually composed of abiotic and occasionally of biotic components. But artifacts as such have a distinctive role to play as environmental resources for organisms, as is indicated by their typical δR signatures.

and many:one relationships between environment-altering populations and recipient populations in ecosystems.

Certain conditions must be met if the first niche-construction sub-process is to give rise to the second. There are no evolutionary consequences of niche construction if the δR ecological changes caused by organisms are too variable, or if they dissipate too rapidly. To influence evolution, a population's niche construction must generate an ecological inheritance: i.e., it must reliably cause a δR change that modifies at least one natural selection pressure for at least one recipient population (itself or another) in an ecosystem, and that persists for a sufficient span of time as measured in generations of the recipient population for selection to be effective.

Ecologists have identified factors that scale up the consequences of ecosystem engineering in ecosystems (Jones et al. 1994, 1997; Hastings et al. 2007). Since the possible consequences include evolutionary ones, the same factors also enhance the evolutionary role of niche construction. They include factors associated with the nature of the niche-constructing population (the lifetime per-capita niche-constructing activity of individual members of the population, the density of the population, and the length of time that it persists in the same place), factors associated with the nature of the δR modifications the population produces (the durability of the modifications in the relevant environmental context, and the number and types of flows of resources (materials and energy) that they modulate), and factors associated with the ecological role of the modifications (how many other species utilise those flows).

The simple one-population picture of niche-construction showed how genes involved in producing a niche-constructing trait and genes involved in producing traits that are advantageous in the resulting modified environment can come to be associated within a population. The genes that contribute to making oaks prone to experiencing frequent fires are associated with the genes that contribute to making them good at surviving fires. The broader conception of niche construction reveals that such *environmentally-mediated gene-associations* (EMGAs) may cross the boundaries between populations or species within an ecosystem. EMGAs can connect *any* environment-altering phenotypic traits (expressed by any genotypes, in any niche-constructing population) to *any* recipient genotypes (in any recipient populations) via *any* modified natural selection pressures in the niches of the recipient populations (Odling-Smee et al. 2003, 2013).

The linked evolutionary processes that produce trans-species EMGAs can bring about a close coordination between the traits of two closely-associated species to produce impressive instances of co-evolved mutualism between the two species. In these cases, there are often several different niche-construction pathways connecting the two species. In the case of the mutualistic relationship between acacia ants and swollen-thorn acacias in Central America (Janzen 1966), for example, the acacias provide ants with shelter in the form of enlarged hollow thorn-like stipules, and food in the form of nectar and specialized detachable leaf-tip structures (Beltian bodies) rich in fats and proteins. The ants, in turn, protect the trees from herbivore damage (attacking both insects and vertebrates that come in contact with the trees) and from competition (cutting away other nearby plants).

Less obvious, but probably much more common, are EMGAs involving a larger number of species linked by looser but more complex webs of niche-construction. Consider, for example, the web of interrelationships involved in a meadow community, in which numerous species affect each other's environments, but each species' niche-construction affects a different subset of the others in the community, and some effects are felt only indirectly through the activity of a mediating species. The evolution of such webs may produce "facilitation networks" that play important roles both in maintaining the stability of ecosystems (Verdú and Valiente-Banuet 2008; see also Bruno et al. 2003) and in enabling assemblages of introduced organisms to succeed in invading established ecosystems (Simberloff and von Holle 1999; O'Dowd et al. 2003; Simberloff 2006; Lindroth and Madritch 2009).

5 Ecosystem Evolution

Ecosystem evolution occurs when evolutionary change in a population or populations of organisms brings about change to ecosystem properties. Ecologist Michel Loreau distinguishes three ways that such change can come about: classical individual-level selective evolution, evolution involving organism-environment feedback, or ecosystem-level selection (Loreau 2010). The first type of ecosystem evolution is represented well by standard evolutionary theory. It comes about when evolutionary changes in one or more populations within an ecosystem, brought about by simple individual-level selection, result in changes to ecosystem properties. Thus, for example, evolutionary changes in the ability of particular species of plants or decomposers to compete for resources can modify nutrient-cycle functioning in the ecosystem as a whole. Here the ecosystem-level changes are no more than side-effects of organismal evolution. This type of ecosystem evolution is possible whenever at least one population that plays a significant role in the ecosystem undergoes evolutionary change, though whether ecosystem evolution actually occurs depends on the particular traits that are evolving, and their contribution to the organisms' ecological role.

The second type of ecosystem evolution is represented well by niche construction theory. It occurs when there is feedback between the two kinds of change involved in the first type of ecosystem evolution: the evolutionary changes at the organism level, and the ecosystem-level changes that these bring about. The results may ramify far beyond the populations that are most directly involved in starting the process, and can also involve environmentally-mediated coevolutionary interactions linking two or more species.[6] In the most complex cases, Loreau points out, this type of ecosystem evolution involves diffuse coevolution among many interacting

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[6] Loreau notes that the first type of ecosystem evolution can also involve coevolution between species, but extended coevolutionary networks usually depend on the links provided by niche construction, as in the second type of ecosystem evolution.

populations, together with associated changes in the ecosystem processes that they affect—changes that in turn modulate the coevolutionary selection pressures acting on the populations. In addition to the conditions required for the occurrence of ecosystem evolution of the first type, this second type requires long-lasting interactions between populations and their environments; where coevolution is involved, it also requires long-lasting interactions between different populations. Models suggest that ecosystem evolution of this type is capable of giving rise to tightly integrated networks of interdependent populations, linked both directly and through abiotic resources via the two sub-processes of niche-construction (Loreau 2010).

The third type of ecosystem evolution is the most demanding, and indeed Loreau suggests that it may not occur naturally in a pure form. This is the evolution of ecosystem properties by ecosystem-level selection. Loreau argues that selection at the ecosystem level is best understood on the model of trait-group selection as articulated by Sober and Wilson (1998).[7] In trait-group selection, the fitness of each individual organism is determined in part by the kind of group that it belongs to, which in turn is determined by the nature of the organisms that constitute the group and the interactions among them. Thus, for example, an individual organism belonging to a group containing many altruists is fitter than one that is identical to the first except in belonging to a group dominated by selfish individuals; this is true whether the organism itself is selfish or altruistic. Other successful kinds of groups may be composed of particular combinations of individual-level types, such as the different functional castes in social insect colonies. Group-level selection thus favors individuals that belong to groups composed of the best combinations of individual-level types, and so acts to perpetuate such groups. Conflicts between the selective forces at the individual and group levels are common—the classic example is in the case of altruism, which is selected against at the individual level but may be selected for at the group level—and the overall fitness of an individual is determined jointly by the selective forces acting upon it at all levels of selection.

In ecosystem-level selection, then, the fitness of each individual is determined in part by the kind of ecosystem it belongs to, which in turn is determined by the nature of the organisms and abiota that constitute the ecosystem, and the interactions among them. Ecosystem-level selection favors individuals that belong to ecosystems composed of the best combinations of individual-level types, and so acts to perpetuate such ecosystems. Conflicts between the selective forces at the individual and ecosystem levels, like other inter-level conflicts, are expected to be common. This type of ecosystem evolution can occur only when quite stringent conditions are met. It requires that all the conditions for the second type of ecosystem evolution with coevolution be met, but also that interactions between different species, and between organisms and abiota, be strongly localized so that competition between members of the same evolutionary population that are

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[7] For an approach to ecosystem evolution that treats ecosystems directly as units of selection, see Swenson et al. (2000) and Goodnight (2000).

members of different local ecosystems can occur. Loreau notes, however, that recent research suggests that this condition may be met more often than has been supposed: most nutrient cycling turns out to be very localized, for example.

6 Evolution and Ecology, Revisited

Far from being separated by their disparate timescales, ecology and evolution are tightly linked through the reciprocal causal relationships connecting organisms to both biotic and abiotic components of their local environments. As Loreau puts it, "It is the web of interactions at the heart of an ecosystem that maintains both species and ecosystems as they are, or (more exactly) as they are evolving." (Loreau et al. 2004, 327). As we noted at the outset of this paper, failure to take account of these links leads both evolutionists and ecologists to ways of conceptualizing the systems they study that can be limiting or actively misleading, and that are also difficult to combine with one another.

It is worth looking more closely at these conceptual frameworks, now that we have a larger context against which to consider them. We've seen already that one of the key features of each framework is the set of simplifying idealizations that it makes: which properties and causal relationships it represents, and which it omits as inessential. Classical evolutionary theory treats the environment as causally *self-contained* (usually simply as static, but possibly as changing via processes that are independent of the evolving population), and usually as *simple* in the sense that its causal structure need not be represented; a population's environment can thus often be represented by a single parameter. The structural complexity of the environment and the causal patterns that follow from that complexity are thus made invisible. The organisms themselves are then treated as passive recipients of the selective pressures exerted by the environment; their active role in responding to and changing features of the environment are omitted from the picture. Abiota, and the causal links connecting them to the biota, are commonly not represented at all in evolutionary models, on the presumption that they simply act as the invariant background against which the phenomena of interest appear. When feedback effects between organisms and their environments must be represented, they are often captured in the form of, for example, simple density-dependent selection; the changing biotic and abiotic components of the environment, and the effects upon them that the organisms produce, appear only in the form of the function linking a trait's fitness to the population density of the organisms under selection.

The central models of population ecology, on the other hand, treat populations of organisms as homogeneous, and so as lacking any internal structure that depends on variation among members of the population—the causal implications of such variation are therefore omitted from the picture. Populations are represented as changing only with respect to population-level properties such as population size or rate of increase; evolutionary changes in the nature of the individuals composing the populations—and the causes and effects of such changes—are not registered.

Ecosystem ecology, as we have already noted, begins with a parsing of the world very different from the organism-environment division shared by evolutionary biology and population ecology. The ecosystem is conceived as comprising both biotic and abiotic components, linked by complex causal relationships that include many reciprocal relationships and the feedback effects that these make possible. These distinctive features of the causal structure of ecosystems are not accidental, but follow from more basic causal considerations. The factors involved in ecological relationships are conceived not simply as properties (which could vary *ad lib*) but as stocks and flows of materials and energy within the ecosystem, and so as subject to conservation principles. From this fundamental presumption there follow three further key features of the conceptual framework. First, changes taking place within ecosystems are taken to be constrained by conservation principles within the limits set by the flow of materials and energy across the ecosystem boundaries. Second, ecosystems are therefore characterized by interdependent—often reciprocal—causal relationships among their components, since any local change in a stock or flow of energy or material must be matched by a corresponding change elsewhere in the system. Third, because the life processes of the organisms within the ecosystem depend on the energy and materials that thus cycle through the system, the components of an ecosystem are understood as bound together in a web of functional interdependencies mediated by the flow of these resources. Organisms are seen therefore as active contributors to the web of functional relationships that enable them to survive. Like population ecology, however, the basic models of ecosystem ecology treat populations as homogeneous and evolutionarily static; indeed they may go further and treat organisms only in terms of their ecological roles such as decomposers or top predators rather than as single-species populations.

Niche construction theory in its original form took several important steps toward bridging the gaps separating the simple conceptual frameworks of evolutionary theory, population ecology, and ecosystem ecology. Its most important contribution was to clarify the implications of the fact, already emphasized by Lewontin and Levins, that both populations and their environments are subject to change, that each is capable of causing change in the other, and that this gives rise to a form of ecological inheritance. From this initial step, which brings together elements of the evolutionary and population ecology pictures, several steps toward the ecosystem ecology picture also follow: that organisms and their environments are in reciprocal causal relationships capable of generating feedback effects; that organisms figure as agents of change rather than merely as passive objects of selection; and that organisms and their local environments must be considered as integrated systems that evolve together. The extended form of niche construction theory that results from unifying it with the insights of ecosystem engineering theory, and recognizing explicitly that the two subprocesses of niche construction may involve different populations, goes much further toward accommodating the key elements of the ecosystem ecology picture. It offers ways of representing and taking account, in an evolutionary context, of the causal links among biotic and abiotic ecosystem components and the complex networks of reciprocal relationships and interdependencies that these create. It provides means of representing the flows of energy and materials through the ecosystem and the crucial constraints that result from them, and reveals the nested hierarchical structure that results from the interplay of ecological relationships at different scales. Perhaps above all, it moves decisively away from treating "the environment" of an evolving population either as a mere background or as an object.

7 Strategies of Idealization

We have seen that the simple ideal models that have been central to evolutionary and ecological theory are unable to capture the complex interrelations between ecology and evolution, and noted some moves toward the enriched models that are needed to bridge the gap between the two theoretical frameworks and to enable both disciplines to develop adequate understanding of the multi-layered interplay between organisms and their environments. But the general observation that more complex and inclusive models are needed gives little guidance about how to develop such models, and about the specific desiderata and constraints that must be considered in choosing a modeling strategy.

Simplifying idealizations are, of course, an essential part of science. The complexities of the world must be tamed by models that omit or simplify many features of the real systems they represent, partly just to make the models tractable enough to work with, but also to enable them to uncover the deeper patterns of similarity that underlie the diversity of particular cases (McMullin 1985; Wimsatt 1987; Weisberg 2007). Idealization is thus an essential means to achieving both generality and explanatory power. But choices among idealizing strategies must always be made. In an influential paper, Richard Levins (1966) argued that, given the practical constraints to which both observation and computation are subject, the idealized models that scientists use must make tradeoffs among three desirable features: precision, generality, and realism.[8] The inevitability of such tradeoffs means that it is insufficient to point out that the basic models of evolutionary theory, population ecology and ecosystem ecology variously oversimplify the systems they represent, and to seek to bridge the gaps that separate these frameworks by reinstating the complexities that they put aside. This response will merely result in models so complex as to be unusable. To evaluate a proposed bridging strategy (and indeed to be sure whether one is really required at all), it is necessary instead to assess the strengths and the failings of the current combination of strategies. What problems should we be aiming to correct? What capacities should we be aiming to preserve?

Niche construction theorists have suggested that several important types of error can result from the simplifying idealizations employed in evolutionary biology and

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[8] For further discussion of such tradeoffs, see Orzack and Sober (1993), Odenbaugh (2003), Orzack (2005), Justus (2005), Weisberg (2006), and Matthewson and Weisberg (2009).

ecology, and from the theoretical disconnection between the two fields of research that these idealizations foster (Odling-Smee et al. 2003; Laland et al. 2009, 2011). In broad terms, the standard models' reliance on idealization strategies that treat either populations or their environments as fixed makes it impossible to see the feedback loops connecting ecological and evolutionary processes, and so to expect the effects that are typical of causal structures involving feedback (such as otherwise unexpected stabilization or runaway change). Recent and more sophisticated models in both population genetics and population ecology do treat both populations and their environments as variable, and some even build in reciprocal relations between the two (e.g. Laland et al. 1999; Krakauer et al. 2009). But without a means of representing the functional relations among both biotic and abiotic ecosystem components in their relationship to evolutionary change, the more serious gap remains.[9] The conceptual disconnection between evolution and ecosystem ecology continues to make it difficult to take full account of two obvious and important facts: that in real-world natural contexts—as opposed to the simplified contexts provided by lab experiments and computer simulations—evolution always takes place within ecosystems subject to constraints set by the conservation of materials and energy, and ecological change always involves species capable both of developmentally plastic responses to environmental change and of evolutionary responses over the longer term (Loreau 2010).

The historical tendency to overlook these structural connections between ecological and evolutionary processes has been consequential. In an era in which an effective understanding of the effects of human interactions with our own environments is of vital practical importance, some of the most serious environmental and evolutionary "surprises" of recent decades[10] involve predictive failures that appear to stem from exactly this sort of conceptual blind spot. Such cases include the rapid evolution of resistant strains of weeds, pests, and especially pathogens (Spellberg et al. 2008; Choffnes et al. 2010); the effects of both the spread of invasive introduced species (plants, animals and pathogens) (Elton 1958; Mooney and Cleland 2001; Facon et al. 2006; Carroll 2011) and the removal of major niche-constructors or "keystone" species (Rosell et al. 2005; Estes et al. 2011); and the effects of human interventions affecting abiota such as the stocks and flows of carbon, water, and topsoil.

The general problem of how to integrate models that represent different aspects of the same system, and that employ incompatible idealizations to do so, is of course a common one in science. Sandra Mitchell (2002, 2003) has distinguished three ways in which such integration can be achieved. In the simplest case, the models simply capture different and independent causes contributing to the system's behavior; they can initially be handled separately in the interests of tractability,

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[9] Pearce draws a similar conclusion at the end of his (2011).

[10] Earlier events that have recently been given new and radically-different explanations are also relevant here: see for example work on the role of introduced species in facilitating European colonialism (Crosby 2004; Piper and Sandlos 2007).

generality, and explanatory power, and their outputs can then be combined additively to achieve a more realistic complete picture. This approach to the integration of disparate models by using *mechanical rules* to combine the causes that they variously represent is suitable for cases in which the causes really are independent of one another—classical mechanics offers standard examples of this sort, in which separate forces can be modeled separately and then combined additively. Because of the reciprocal relationship between evolutionary and ecological processes, however, this approach is quite inadequate for dealing with their interaction. In Levins's terms, it achieves generality and precision (preserving the broad scope and mathematical rigor of the various separate models) by sacrificing realism (it fails signally to capture the real causal structure of the organism-environment relationship). The second possibility is to seek *local theoretical unification* within the limits set by the particular pragmatic constraints of the case in question, producing a single model that represents multiple aspects of the system in combination. At its best, this approach can strike a distinctive and useful compromise[11] among various epistemic goals, achieving a high level of generality and realism though at the cost of precision. Here we find models that can be used to frame and test hypotheses about large-scale patterns in ecological evolution and evolutionary ecology, but that are too simple to be capable of giving precise predictions about particular complex situations. For that task, the best approach is Mitchell's third option, *explanatory concrete integration*. This approach combines the various component models piecemeal, in ways that are tailored to and supported by detailed information about the particular circumstances of the case at hand. At its best it achieves very high levels of realism and precision, but at the cost of low generality: the detailed and realistic models of particular complex systems that it produces cannot be applied beyond the bounds of those systems.

Successfully integrating ecology and evolution requires both broader theoretical unification and fine-grained explanatory integration in concrete cases. A good deal of excellent work of the latter sort has been done: the studies that have uncovered the complex interactions between evolutionary and ecological processes underlying the environmental "surprises" noted earlier provide many examples of this sort. What is still barely begun is the sort of conceptual and theoretical synthesis that can help uncover the broad patterns of ecological/evolutionary interaction: precisely the sort of synthesis provided by niche construction theory. Several recent studies give some indication of the kind of work such a synthesis can support. Erwin (2005, 2008; see also Crespi 2004) investigates of the role of niche construction in macroevolution and the evolution of diversity, arguing that some niche-constructing processes produce environmental effects that endure through geologic time, modifying evolutionary trajectories for many species simultaneously over extended periods. Such effects, he argues, may have played an essential role in driving major evolutionary transitions and recoveries from mass extinctions. Two teams explore the interaction between niche construction and regulation or control. Krakauer et al. (2009) show

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[11] Levins (1966) particularly emphasized the virtues of this balance of desiderata.

that positive niche construction results in selection favoring adaptations that make it possible for organisms to monopolize the benefits of their niche-constructing activities, with important implications for the evolution of development, life-cycle patterns, behavioral plasticity, and sociality. McDonald-Gibson et al. (2008), on the other hand, show that interacting negative niche construction processes can coevolve to produce ecosystem-level "rein-control" systems capable of regulating key resources, with important implications for the evolution of ecosystem-level stability and functional integration. Sterelny (2003, 2011) and others (Kerr 2007; Smith 2007; Jablonka 2011; Kendal et al. 2011; Rendell et al. 2011; Van Dyken and Wade 2012a, b) continue to explore the interactions between human genetic and cultural evolution as mediated by niche construction, with models suggesting that niche construction may have played a central role in the evolution of modern human cognitive capacities, behavior patterns, and social systems. Instances like these begin to show how the niche construction perspective can be extended to help researchers in a wide range of contexts investigate the complex interplay between evolving populations and evolving ecosystems.

8 Conclusion

The Modern Synthesis unified key elements of early-twentieth-century theories of evolution and inheritance to yield a set of ideal models of great generality and precision, but lacking contact with the complexities of life outside the fly-bottle—in particular with what was known about how organisms develop and how they interact with their environments. The decision to ignore these aspects of the biological world, and their implications for both heredity and evolution, was justified by theoretical principles essential to the Synthesis: the *Central Dogma* asserting that information flowed only from genes to phenotypes and never in the reverse direction (so that development, including environmental effects, was irrelevant to evolution and heredity) and the *principle of separated time scales* for evolutionary and ecological processes, implying that ecology and evolution could not interact in any very important way. Since the 1970s, however, researchers in many areas of biology have contributed to an increasingly thoroughgoing reconstruction of the life sciences that both elaborates the mathematical models of the Modern Synthesis and integrates them with the flood of information that has been generated over the last decades about the complex realities of genome function and developmental processes in diverse organisms. The result is what many now see as a sea-change in biology: the rise of a new *integrative biology* that differs from the biology of the Modern Synthesis in its core concepts and assumptions, but also in its methods and in the institutional structures that can best help it to thrive (Wake 2001, 2004, 2008; Rose and Oakley 2007; Schwenk et al. 2009). Where the Modern Synthesis fostered specialization and work with mathematical models and fruit flies, integrative biology calls for transdisciplinary work incorporating the strengths of complex computer simulations as well as analytical models, diverse organisms outside as well as inside the laboratory, and contributions from relevant research in adjacent fields including the physical sciences (for understanding genome functioning at the physical level) and the social sciences (for understanding some aspects of human development).

Some characterizations of integrative biology emphasize the importance of ecology as well as development (Wainwright and Reilly 1994; Wake 2004), but the integration of ecological with evolutionary understanding has lagged behind the integration of evolution and development, and its importance has not yet been as widely appreciated. We have seen reason to believe, however, that it is just as consequential for our understanding of evolution and heredity, and that it is urgently needed for our understanding of human impacts on both ecological and evolutionary processes at the global scale.

Like the integration of evolution and development, work at the interface of ecology and evolution has been moved forward partly by purely conceptual work, partly by new empirical results, and partly by a reassessment of the importance of what everybody has known all along. Niche construction theory and ecosystem engineering offered perspectives on organism-environment interaction that now take on a new importance as they have begun to be combined as ecological niche construction, and as empirical results increasingly challenge the assumption of separated ecological and evolutionary time scales. The result is an opening up of new pathways for conceptual change, empirical investigation, and reconsideration of the familiar that has only just begun. Niche construction theorists have been arguing for decades that attention to the "neglected process in evolution" (Laland et al. 1996; Odling-Smee et al. 2003; Laland et al. 2011) reveals the need for a deep transformation of the conceptual framework of evolution. Steps toward an integrative biology that links development, evolution, and ecology seem to confirm that assessment, and indeed to reveal new horizons for transformation beyond the classical bounds of evolution.

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