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Ecosystem engineering, experiment, and evolution

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Abstract This paper argues that philosophers should pay more attention to the idea of ecosystem engineering and to the scientific literature surrounding it. *Ecosystem engineering* is a broad but clearly delimited concept that is less subject to many of the "it encompasses too much" criticisms that philosophers have directed at *niche construction*. The limitations placed on the idea of ecosystem engineering point the way to a narrower idea of niche construction. Moreover, experimental studies in the ecosystem engineering literature provide detailed accounts of particular empirical situations in which we cannot neglect the O term in $dE/dt = g\ (O, E)$, which helps us get beyond verbal arguments and simple models purporting to show that niche construction must not be ignored as a factor in evolution. Finally, this literature demonstrates that while ecosystem engineering studies may not require us to embrace a new evolutionary process, as niche construction advocates have claimed, they do teach us that the myriad abiotic factors concealed by the abstract term 'environment' are often controlled in large part by organisms.

Keywords Ecosystem engineering · Niche construction · Evolution · Causal factors · Experiment

Introduction

What does it take to be "a new factor in evolution," as Baldwin (1896) put it at the at the end of the nineteenth century? How do we assess the importance of putative causal factors in evolution? Biologists and philosophers have shown that experimental approaches can determine the significance of particular factors, for

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example constraints on variation, in local cases (Brakefield 2006; Pearce 2011). Demonstrating the importance of a factor like constraints in a local context is the first step toward broader "new factor" claims: there is at least one situation in which the factor must be considered. Although there is no magic number of cases beyond which the importance of some factor is automatically established, it does seem that with each subsequent case, other biologists will experience more pressure to pay attention to the factor in question in their own studies. As Maclaurin and Sterelny (2008, 80) suggest, local assessments "allow us to make some progress in answering global questions piecemeal." This empirical approach assumes that "is an important factor in evolution" means "played an important role in evolutionary history" rather than "must always be part of our abstract representation of the evolutionary process." It is normally only the latter that matters to philosophers and theorists; however, understanding the evolutionary process requires understanding how it works in concrete situations. Thus, to establish something as an important factor in evolution, one must move beyond verbal arguments and mathematical models to assess the actual contribution of the factor in specific cases. I will argue in this paper that ecosystem engineering—not only niche construction—deserves more attention from philosophers, since a variety of empirical case studies have begun to establish it as a major factor in evolution.

Niche construction is a putative "new factor" that has received a great deal of attention from a vocal subset of evolutionary biologists, social scientists, and philosophers in recent years. First presented in 1988 and made more widely known in the late 1990s, the idea of niche construction stems from Richard Lewontin's famous claim: "Organisms do not experience environments passively; they create and define the environment in which they live." In other words, "the environments of organisms are made by the organisms themselves as a consequence of their own life activities" (Lewontin 1978, 215, 1983, 280; cf. Levins and Lewontin 1985, 65–106).[1] Lewontin claimed that traditional evolutionary biologists understood changes in the environment to be independent of the activities of organisms, and argued in contrast that each was a function of the other. He represented this difference with two pairs of differential equations (Lewontin 1983, 282; Levins and Lewontin 1985, 104–105):

Traditional View: $\mathrm{d}O/\mathrm{d}t = \mathrm{f}\,(O, E)$; $\mathrm{d}E/\mathrm{d}t = \mathbf{g}\ (\boldsymbol{E})$
Lewontin's View: $\mathrm{d}O/\mathrm{d}t = \mathrm{f}\,(O, E)$; $\mathrm{d}E/\mathrm{d}t = \mathbf{g}\ (\boldsymbol{O}, \boldsymbol{E})$

These equations were the inspiration for Odling-Smee's essay "Niche-Constructing Phenotypes" (1988) and the more widely available article "Niche Construction," the latter of which argued that niche construction "generates a form of feedback in evolution that is not yet fully appreciated by contemporary evolutionary theory" (Odling-Smee et al. 1996, 641). The idea became more widely known in philosophy of biology and in the social sciences with the publication of "Niche Construction, Biological Evolution, and Cultural Change" in *Behavioral and Brain Sciences*, an article by Odling-Smee and colleagues that featured responses from biologists, cognitive scientists, anthropologists, psychologists, and

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[1] For a critical discussion of Lewontin's position, see Godfrey-Smith (2001).

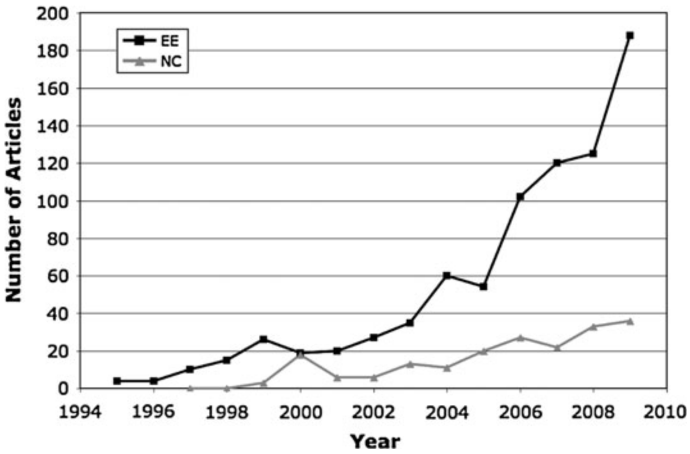

Fig. 1 Articles on ecosystem engineering (EE) and niche construction (NC). Data from Thomson Reuters ISI Web of Knowledge, http://www.isiwebofknowledge.com/ (accessed 3 May 2010). Compiled using 'Topic' searches on "ecosystem engineer*" and "niche construct*" for each year from first appearance in a major journal through 2009. Initial publications were Jones et al. (1994) and Odling-Smee et al. (1996). The NC spike in 2000 is due to Laland et al. (2000), each of the replies to which was counted as an individual article

several philosophers including Peter Godfrey-Smith (Laland et al. 2000). Niche construction was subsequently discussed at length in the journal *Biology & Philosophy* in roundtable reviews of Richard Dawkins's *The Extended Phenotype* (1982) and Odling-Smee et al.'s *Niche Construction* (2003), exposing the philosophy of biology community as a whole to the details of the position (Laland 2004; Dawkins 2004; Okasha 2005; Griffiths 2005; Sterelny 2005; Laland et al. 2005).

The idea of ecosystem engineering, in contrast, has been almost completely ignored by philosophers.[2] Ironically, however, it appears to have been much more influential in peer-reviewed science journals than that of niche construction, as Fig. 1 suggests.[3] One reason philosophers have paid less attention to ecosystem engineering may be that almost all articles on the topic have appeared in ecology journals, with few publications in general biology or evolutionary biology journals (but see Jablonski 2008). Articles on niche construction, however, tend to appear in evolutionary biology, behavioral science, philosophy, or general biology journals, although some studies do appear in ecology journals (data from Thomson ISI Web

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[2] Although it is mentioned in several papers by Sterelny (2001, 333, 2005, 23), he follows Odling-Smee and colleagues in neglecting important differences between the concepts of niche construction and ecosystem engineering.

[3] Figure 1 strictly shows only that the term 'ecosystem engineering' is cited more commonly than 'niche construction', and not that the former concept is more often employed. However, given that the original ecosystem engineering papers are more frequently cited than the original niche construction papers (see below), and the fact that the literatures are to some extent divided along disciplinary lines, I believe it suggests that the idea of ecosystem engineering has been more influential than that of niche construction. Synonymous uses of the two terms are more common in the niche construction literature than in the ecosystem engineering literature.

of Knowledge). Since philosophers of biology have traditionally been more interested in evolutionary biology and cultural evolution than in ecology and organismal biology, this disciplinary separation is likely partly responsible for their neglect of ecosystem engineering.

In this paper, I will argue that this neglect is a mistake. Philosophers should address the ecosystem engineering literature for several reasons. First, it provides a clearly delimited but broad concept, *ecosystem engineering*, that is less subject to many of the "it encompasses too much" criticisms that philosophers have directed at the concept of niche construction. The limitations placed on the idea of ecosystem engineering point the way to a more useful definition of niche construction. Second, experimental studies in the ecosystem engineering literature provide detailed accounts of particular empirical situations in which we cannot neglect the O term in $dE/dt = g\ (O, E)$, which helps us get beyond verbal arguments and simple models purporting to show that niche construction must not be ignored as a factor in evolution. Finally, this literature demonstrates that while ecosystem engineering studies may not require us to embrace a new evolutionary process, as niche construction advocates have claimed, they do teach us that the myriad abiotic factors concealed by the abstract term 'environment' are often controlled in large part by organisms. Even if the role of these engineering organisms can be neglected when we focus on a particular evolving population, this role is essential to understanding the complexity of environments at ecological, microevolutionary, and macroevolutionary timescales.

In the first part of the paper, I will discuss various existing definitions of 'ecosystem engineering' and 'niche construction', arguing that the narrower idea of ecosystem engineering should replace the more general idea of niche construction, and suggesting that the term 'niche construction' could be restricted to cases in which there is feedback from the results of ecosystem engineering to the engineering organism(s). Some but not all products of niche construction in this narrower sense are best treated as extended phenotypes. In the second part, I will present several case studies of structural ecosystem engineering, showing how the role of organism-produced physical structures in ecological communities can be experimentally isolated. Classic ecological experimental design provides an elegant means by which the importance of ecosystem engineering can be assessed in local cases. Finally, in the third part of the paper, I will argue that even if ecosystem engineering, i.e., the effects of organisms on their physical environments, can often be ignored in studies of particular evolving populations, it nevertheless gives us a richer understanding of what controls abiotic environmental factors. These factors are not independent of organisms, and even if ecosystem engineering is not itself an evolutionary process, it has played an integral role in what Dewey (1898, 339) once called "the evolution of environments."

Ecosystem engineering and niche construction

The ideas of ecosystem engineering and niche construction, each often discussed, are only infrequently contrasted. In this section, I present a working distinction between the two that is designed to be useful to scientists: ecosystem engineering is the physical modification of the environment by an organism or population, whereas niche construction is ecosystem engineering that feeds back directly on the engineer(s). Although this involves several adjustments to the idea of niche construction as currently employed, it captures current work in the area as well as highlighting one of the original thoughts behind the idea—that an organism can construct its own niche.

The concept of ecosystem engineering was first presented by Clive Jones and colleagues in "Organisms as Ecosystem Engineers." They provided the following definition:

> Ecosystem engineers are organisms that directly or indirectly modulate the availability of resources (other than themselves) to other species, by causing physical state changes in biotic or abiotic materials. In so doing, they modify, maintain and/or create habitats. (Jones et al. 1994, 374)

It is important to notice the limitations they place on the concept: only physical and not biological interactions are included. That is, Jones et al. (1994, 374) explicitly exclude "direct provision of resources by an organism to other species, in the form of living or dead tissues." Thus the concept as originally defined is quite broad, although it is restricted to non-trophic interactions. This paper has been cited over a thousand times, according to the Thomson Reuters ISI Web of Knowledge, primarily in ecology, marine biology, and soil biology journals. Its citation record suggests that the concept of ecosystem engineering has been useful to a wide array of empirically inclined biologists.

A few years later, Odling-Smee and colleagues published "Niche Construction," and defined the title concept as follows: Organisms, through their metabolism, their activities, and their choices, define, partly create, and partly destroy their own niches. We refer to these phenomena as 'niche construction' (Odling-Smee et al. 1996, 641).[4] This definition makes niche construction broader than ecosystem engineering in one sense, but narrower in another: it is broader because trophic effects are included, and narrower because it is restricted to the construction of organisms' own niches. This paper has been cited about a hundred times, according to the Thomson Reuters ISI Web of Knowledge, mainly in evolutionary biology, philosophy, and behavioral science journals. The contrast between the citation records of the original papers on ecosystem engineering and niche construction indicates that not only is the former more popular among scientists, it is also more closely tied to empirical approaches.[5]

By the end of the decade, Odling-Smee and colleagues were already equating the two concepts, despite their distinct definitions: "There is increasing recognition that

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[4] As mentioned above, Odling-Smee had previously published "Niche-Constructing Phenotypes" (1988), but since it was a book chapter rather than a journal article it had much less influence.

[5] As of June 6, 2010, Odling-Smee et al. (1996) has 786 citations listed on Google Scholar, versus 1,462 for Jones et al. (1994). The reason for this 1:2 ratio (versus 1:10 for ISI) is unclear, but it may be because niche construction is referenced in book chapters or journal articles that do not appear in the Thomson Reuters ISI Web of Knowledge database (e.g., Sterelny 2001). Hence, this discrepancy may indicate that niche construction has been more popular outside the scientific community than within it.

all organisms modify their environments, a process that we call 'niche construction' but is elsewhere described as 'ecosystem engineering'" (Laland et al. 1999, 10242; cf. Odling-Smee et al. 2003, 6). To complicate matters further, both groups also modified their respective definitions in the 2000s. As Sarah Berke (2010) has emphasized, Jones and colleagues now exclude all assimilatory and dissimilatory processes from *ecosystem engineering*: i.e., neither eating nor defecating nor taking up water from soil counts as engineering according to the modified definition (Wright and Jones 2006, 205; Gutiérrez and Jones 2006, 227; Jones and Gutiérrez 2007). While Jones et al. have narrowed their definition, Odling-Smee and colleagues have broadened theirs. They now define the concept as follows: "*Niche construction* occurs when an organism modifies the feature-factor relationship between itself and its environment by actively changing one or more of the factors in its environment" (Odling-Smee et al. 2003, 41).[6] This seems similar to the definition in Odling-Smee et al. (1996), but they expand it in their elaboration: "When they construct niches, individual organisms may modify a natural selection pressure in their own selective environment, or they may modify a natural selection pressure in the environments of one or more other populations, or both" (Ibid., 42). Niche construction, on this broader definition, can thus involve the modification of one's own niche or the modification of niches of other organisms.

I propose that the original definition of ecosystem engineering as physical modification of the environment be retained, and that niche construction be redefined as ecosystem engineering that has a direct impact on the engineer. The narrowing of the idea of niche construction has been suggested previously. Virtually every philosopher who has written about niche construction has argued that Odling-Smee et al. would be better off with a narrower concept (Godfrey-Smith 2000, 154; Sterelny 2001, 333, 2005, 24). Okasha (2005, 2) puts the point as follows:

> […] the distinction between organisms' activities which alter the niche of those self-same organisms, and activities which alter the niche of *other* organisms, seems highly pertinent from an evolutionary point of view; but activities of both types fall under the rubric of niche-construction as defined by [Odling-Smee et al. (2003)].

As pointed out above, the 1996 definition of niche construction was narrower in precisely this way, and only included organisms' alteration of their own niches.[7] Despite this, Odling-Smee and colleagues reassert their broadened definition in a response to Okasha, arguing that niche construction by an organism "might generate feedback in the form of a modified natural selection pressure" for that same organism, but that it might also "affect selection acting on other organisms in its own population, on other populations of the same species, on other species, on descendent populations of the same or different species, and so forth" (Laland et al. 2005, 40).

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[6] Odling Smee et al. (2003) follow Bock (1980) in decomposing organism and environment into features and factors, respectively.

[7] See Odling-Smee et al. (1996, 641). Thus the statement by Laland et al. (2005, 41) that "throughout our studies on niche construction we have been consistent in utilizing the broad definition" is false.

I suggest that we go further than Okasha: the term ‘niche construction’ should be restricted to those cases in which an organism or population alters physical aspects of its own environment.[8] For example, *Sphagnum* mosses alter the pH of the soil in which they grow. This activity is ecosystem engineering; however, it is also niche construction, since the pH modification not only affects other organisms, but feeds back to the mosses themselves (Breemen 1995). Many cases of ecosystem engineering will also be cases of niche construction (though not all—think of rays disturbing sediments as they feed). Hence, it is often a question of focus: if we are interested in the effects of the activity on the engineering organism, we are investigating niche construction; if we are interested in its effects on other organisms we are studying ecosystem engineering more broadly. Physical modification of the environment is meant also to encompass physical effects of trophic activities, e.g., the results of the activities of the detritivorous fish mentioned below. Therefore, I modify the niche construction idea in two ways. First, like ecosystem engineering, it includes only modifications of the physical environment, making it a specific type of ecosystem engineering. Second, it includes only modifications of the organism or population’s *own* physical environment, excluding other ecosystem engineering effects. This latter point brings it closer to the original conception as described in Odling-Smee et al. (1996). I will discuss each of these proposed changes in turn.

(1) Why make niche construction a kind of ecosystem engineering? The biological interactions of organisms are already addressed by traditional approaches to ecology and evolution. Niche construction in the broad sense of Odling-Smee et al. (2003)—the large rectangle in Fig. 2—encompasses all interactions between organisms and their environments. Given the thermodynamic constraints on organisms, they must “live at their environments’ expense, and they can do that only by acting on and perturbing their environments” (Odling-Smee et al. 2003, 170). Since all organisms are constantly exporting entropy into their surroundings just by existing, they are constantly engaging in niche construction. However, what distinguishes empirical studies of ecosystem engineering and niche construction from previous work is the focus on biotic control of abiotic factors, with ramifications for other organisms and/or the engineer.

It does not seem fruitful to count predation as a kind of niche construction, despite its notable effects on prey and predator: the claim that predation is important in ecology and evolution is not groundbreaking. Modifications of the physical environment, on the other hand, can result in indirect effects that are not often noted or studied, i.e., indirect biotic-biotic interactions mediated by abiotic factors. Thus, it seems best to narrow the term ‘niche construction’ so that it includes only physical interactions with the environment, keeping in mind that ‘physical interactions’ includes the physical effects of trophic activities: i.e., physical effects of prey removal count, but food web changes do not.

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[8] I am using ‘environment’ here to mean the external environment in Robert Brandon’s sense, for even if niche construction that modifies physical aspects of an organism or population’s ecological or selective environment is more relevant to evolution, all modifications of the latter two environments depend on modifications of the external environment (see Brandon 1990, 47–49, 2001). It is difficult to separate these different types of modifications a priori.

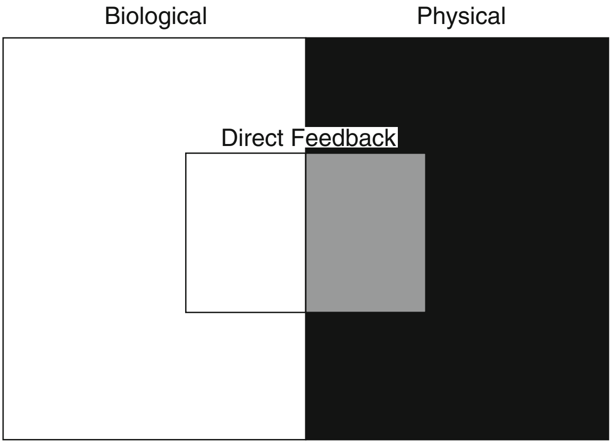

Fig. 2 Scope of definitions of 'niche construction' and 'ecosystem engineering'. The entire large rectangle represents all interactions between a given focal organism and its environment, with white indicating biological interactions and *gray* + *black* indicating physical interactions. The small rectangle (*white* + *gray*) represents those modifications of the environment (physical or biological) that feed back on the modifier. I count the *right-hand side* of the large rectangle (*gray* + *black*) as ecosystem engineering, and the *gray portion* as niche construction. Odling-Smee et al. (2003) count the entire *large rectangle* as niche construction, and Okasha (2005) counts the entire *small rectangle* as niche construction

It might be argued that ecosystem engineering, of which niche construction is to be made a species, is itself too broad a concept. After all, organisms also modify their *physical* environment just by existing, and this may trivialize the idea of ecosystem engineering (Reichman and Seabloom 2002, 44). However, the Jones et al. (1994) definition avoids triviality by including only physical effects that modulate resource flows. Since not all effects are physical, and not all physical effects modulate resource flows, the concept is not as general as it seems (Wilby 2002). Moreover, even if ecosystem engineering is ubiquitous, it is not always important. Given some physical effect, "whether or not there will be biotic consequence will depend upon the degree of abiotic change (magnitude and direction) *and* the sensitivity of the biota or their interactions to this abiotic variable" (Jones and Gutiérrez 2007, 13). Jones and colleagues suggest that ecosystem engineering usually need only be considered "when the temporal and spatial scales of engineering effects differ from the temporal and spatial scales of direct organismal interactions" (Hastings et al. 2007, 154; cf. Jones et al. 1994, 381–382). Thus the concept of ecosystem engineering is broad, but it is restricted enough to be useful, unlike the even broader concept of niche construction presented in Odling-Smee et al. (2003).

(2) Why include only those effects that feed back on the organism or population itself? There are two reasons. First, this limitation highlights the difference between two different kinds of feedback: (A) physical modifications affect the modifier directly; (B) physical modifications affect other organisms, and changes to these other organisms affect the modifier. In Case A, a physical environmental variable is changed, affecting the engineer, whereas in Case B, the physical variable affects

other organisms, changing a biotic variable that in turn affects the engineer. My definition counts Case A as niche construction, but not Case B. Both are cases of ecosystem engineering, but only Case A involves direct feedback to the engineer.

Second, niche construction in this narrow sense is of evolutionary interest insofar as it offers a way for a population to adapt to an environment via behavioral rather than morphological or physiological changes.[9] As Mary Jane West-Eberhard (2003, 180) notes, behavioral traits are often plastic and thus the first to change when an organism is faced with a new environment. Genetic changes linked to morphological or physiological traits may then follow, depending on the nature and results of the new behavior, but these changes would be much less drastic than those expected given no behavioral change. Take, for example, Darwin's favorite case: "Earthworms must be considered as terrestrial animals, though they are still in one sense semi-aquatic, like the other members of the great class of annelids to which they belong" (Darwin 1881, 12). As Odling-Smee et al. (2003, 11–12) point out,

> Because these originally aquatic creatures are able to solve their water- and salt-balance problems through tunneling, exuding mucus, eliminating calcite, and dragging leaf litter below ground, that is, through their niche construction, earthworms have retained the ancestral freshwater kidneys (or nephridia) and have evolved few of the structural adaptations one would expect to see in an animal living on land.

Earthworms have thus constructed for themselves something approximating a freshwater niche in a terrestrial environment. The idea of niche construction applies most naturally to such cases, which is why some proponents of niche construction employ a narrower definition (Laland and Sterelny 2006). These worms are, of course, ecosystem engineers that affect a whole variety of other organisms through their activities; but when we focus on how earthworm activities affect earthworms, we are focusing on niche construction.

Dawkins (2004, 379) has argued that positive results of niche construction in the narrow sense can be viewed as "a special case of the extended phenotype." Dawkins (1982, 196) coined the term 'extended phenotype' to refer to the "*extended* phenotypic effects" of genes, "effects which need not be expressed at the level of any particular vehicle." When we think of extended phenotypes, however, we tend to think only of birds' nests, beavers' dams, and spiders' webs. Though Dawkins did highlight such artifacts, he also thought that genes in one organism could be selected 'for' a behavior in another: for example, "a reed warbler's limbs [can] work for a cuckoo's genes" (Ibid., 233). Thus, according to Dawkins, the results of niche construction can be viewed as extended phenotypes, even though not all extended phenotypes are the result of niche construction. Treating the results of niche construction as extended phenotypes may seem to exclude those cases in which several species jointly modify their surroundings in ways that are adaptive for each of them; but in Dawkins's view, such phenotypes can be manipulated "by

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[9] This second reason is not general, for there are many cases of niche construction, especially in plants, that do not involve behavior: e.g., Dawson (1998).

genes from distantly related individuals, individuals of different species, even different kingdoms" (Ibid., 208).

However, despite Dawkins's claim that niche construction is the special case, there are many results of niche construction that cannot be seen as extended phenotypes.[10] For something to count as an extended phenotype it has to be an adaptation "for the benefit of replicators," i.e., there must be a causal connection between replicator-variants and phenotype-variants that advantages those replicators associated with certain phenotypes (Dawkins 2004, 379). Since in many cases of niche construction this is not explicitly assessed (and such assessment is difficult at the best of times), the result of niche construction, even when positive, is usually only a *putative* extended phenotype. For example, although ecosystem engineering by *Sphagnum* mosses is niche construction, i.e., it alters its environment such that the growth of other plants is suppressed and its own growth is promoted, it is difficult to sort out which properties of *Sphagnum*-modified soil are true extended phenotypes, and which are byproducts (Breemen 1995). Moreover, some engineering activities will have measurable effects on the engineer, but not measurable fitness effects; i.e., they will be fitness-neutral.[11] This turns Dawkins's original claim on its head, and suggests that only some results of niche construction are extended phenotypes strictly speaking.

This leaves us with two nested concepts:

Ecosystem engineering: *modification of the physical environment by organisms*

- Includes physical consequences of trophic activities
- Importance depends upon the direction and magnitude of the modifications, and on the sensitivity of the affected organisms
- Must usually be considered when its effects exceed the spatial and temporal scales of direct organismic interactions

Niche construction: *ecosystem engineering with results feeding back to the engineer(s)*

- Fitness effects of feedback can be positive, negative, or neutral
- Evolutionary importance depends on whether fitness effects can be identified
- Can result in extended phenotypes in some cases

In retaining the existing definition of ecosystem engineering and narrowing the existing definition of niche construction, I have attempted to capture the respective approaches of case studies that employ the two different concepts. For instance, some of the most cited niche construction studies describe how trees with traits that promote environment-altering fires—a form of niche construction—also have fast-growing seedlings that reproduce at an early age, ensuring that they compete well in

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[10] Sterelny (2005, 29–31) argues that there is a deeper problem. Because niche construction is the modification of *environments* and extended phenotypes are parts of *organisms*, it is unclear how one can result in the other.

[11] This is an important difference between my account and that of Erwin (2008, 304). Erwin does not require that niche construction affect the fitness of the constructing organisms, does not indicate that only *physical* modification counts as ecosystem engineering, and does not treat the two concepts as nested.

the environment they have created (Schwilk and Ackerly 2001; Schwilk 2003; Ne'eman et al. 2004). This is a classic case of ecosystem engineering feeding back on the engineer with evolutionary consequences, and thus of niche construction in my sense. Ecosystem engineering studies, in contrast, normally look at how the environment-modifying activities of one species affect a variety of other organisms. For example, the detritivorous fish *Prochilodus mariae* substantially reduces the amount of sediment in streams, dramatically altering community structure through its engineering activities (Flecker 1996). The distinction made above between niche construction and ecosystem engineering thus corresponds to two distinct types of case study.

Ecosystem engineering and experiment

The *Prochilodus* case raises a problem, however. How do we know that it is the engineering activities of the fish that are affecting algal and invertebrate assemblages, rather than its trophic activities? In this section of the paper, I will explore how ecologists have attempted to address this problem, demonstrating that certain kinds of experimental design can prove the importance of ecosystem engineering in particular cases. As I will discuss in the final section, these local experiments make up part of the case for the importance of ecosystem engineering in evolution.

Berke (2010) has provided a useful functional classification of different kinds of ecosystem engineers: *structural engineers*—e.g., reef-builders, forest-builders—create structures; *bioturbators*—e.g., burrowers, excavators—disturb or transport sediment; *chemical engineers*—e.g., water-modifiers, soil-modifiers—alter environmental chemistry; and *light engineers*—e.g., filter-feeders, shade-casters—modify different aspects of light. I will focus on structural engineers.

In an experiment well known to marine ecologists, Sarah Woodin (1978) employed an ingenious method to demonstrate the importance of ecosystem engineering in a particular case. She was interested in refuges from ecological disturbance, and focused on tube dwellings constructed by the marine polychaete worm *Diopatra cuprea*. As the French naturalist Louis Augustin Guillaume Bosc first described in the early 1800s, *D. cuprea*

> […] lives in a cartilaginous tube sunken four to five decimeters [40–50 cm] into the sand and extending two to three centimeters above its surface, [built] by means of bits of wood, shell fragments, and other foreign bodies held together by a very strong silk. (Bosc 1801, 1:143)[12]

The portion of the tube below the sediment–water interface is actually formed via a secreted mucus that hardens and forms a tube around the animal as it moves through the substrate, whereas the shorter section of tube above the interface is built in the way Bosc describes: i.e., the worm uses the same mucus to glue various particles

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[12] Bosc referred to the species in question as *Nereis cuprea*, and mentioned that the tube-worms were common in Charleston Harbor, South Carolina.

and objects to the tube edges, extending its dwelling a short distance above the substrate (Myers 1972, 351).

Woodin wanted to know whether portions of the seabed with high densities of *Diopatra* served as refuges for other organisms, and suspected that the presence of *Diopatra* tubes might reduce substrate disturbance. In her first set of experiments, she took samples each month for one year from areas with 0, 1, or 6 living *Diopatra*. Areas with high *Diopatra* density were almost always characterized by a higher diversity and abundance of other organisms, in particular other smaller polychaete worms. Woodin hypothesized that the large tubes of *Diopatra* prevented excavation and predation by blue crabs and horseshoe crabs, thus allowing smaller polychaetes with smaller and less robust tubes (e.g., *Spio pettiboneae*) to persist. In a later study, she confirmed one aspect of this theory through crab removal experiments, which cancelled the effect of *Diopatra* density (Woodin 1981).

However, she needed to test whether the effect was truly caused by the ecosystem engineering activities of *Diopatra*. Were the tube structures themselves behind the effect? To this end, Woodin created artificial areas of high *Diopatra* density using plastic straws wedged onto wooden stakes inserted into the substrate. Areas with (a) six artificial tubes, (b) five artificial tubes and one *Diopatra* tube, (c) six *Diopatra* tubes, and (d) no tubes of any kind were compared after 5 months. There were significant differences between plots with no tubes and each of the other plots, but no significant differences between any of the other plots. As she concluded, this meant that

> […] the apparent effect of the density of *Diopatra* on the infauna is a tube effect, not a worm effect. The effect on the infauna was the same regardless of whether the structures were real *Diopatra* tubes, plastic straws of approximately the same dimensions, or a mixture of the 2. (Woodin 1978, 282)

Thus, *Diopatra cuprea* is a structural ecosystem engineer, in Berke's terminology. Its tubes, at high densities, prevent bulldozing, excavation, and predation by crabs and have a dramatic influence on community structure.[13]

Just as trophic activities determine food webs, engineering activities cascade through what Jones et al. (1997, 1952) call an "engineering web," i.e., a set of organisms causally linked via the effects of their ecosystem engineering. Once an engineering effect is isolated, ecologists can investigate these details. For instance, not all physical effects of *Diopatra* tube density are as important as disturbance prevention. A few years later, Mark Luckenbach (1986) demonstrated that tube-bed-induced flow alterations are not responsible for lower erosion thresholds in areas of high tube density. Ironically, however, it may be the engineering activities of organisms present in higher numbers due to the structural effects of *Diopatra* tubes that lead to reduced surface sediment stability: tube density reduces the effect of one set of bioturbators (crabs), which in turn increases the numbers of another set of bioturbators (smaller polychaetes). The structure of these kinds of engineering webs

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[13] There are also, of course, organisms that live on the tubes themselves (Bell and Coen 1982a, b; Bell 1985).

may be just as important to community stability as that of food webs (Manne and Pimm 1996).

It is also possible to determine which structural aspect of the organism or population is the difference-maker, which can have important consequences for the viability of interventions in conservation biology. For example, the Asian mussel *Musculista senhousia* is invasive in California (Crooks 2002). *M. senhousia*, like many bivalve species, attaches to the substrate via a set of threads called the 'byssus'. The mechanical properties of byssal threads vary significantly between different bivalve species, but the material from which they are made is relatively tough and stretchy (Pearce and LaBarbera 2009a, b). *Musculista* lives almost completely buried in the substrate, and wraps itself with its byssal threads to form a kind of nest or cocoon (Morton 1974, 19–20).[14] Since the mussel lives in dense populations, especially when invasive, these cocoons combine to form a tangled 'mat' of byssal threads. It is this mat that makes *Musculista* an important structural ecosystem engineer.

Jeffrey Crooks (1998) quantified the effects of these mats on invaded environments in Mission Bay, California. He sampled areas with and without *Musculista* mats, measuring the diversity and abundance of other organisms as well as sediment composition and shear strength. The mats created patches approximately 2 cm higher than the surrounding substrate. These patches contained significantly higher percentages of silts, clays, and organic matter than areas without mats, and were more resistant to shear forces. Moreover, they boasted a significantly greater diversity and abundance of other organisms (e.g., the tiny tube-building crustacean *Leptochelia dubia*). The mat areas also contained a significantly higher percentage of surface feeders and a significantly lower percentage of sub-surface feeders. Crooks (1998) then attempted to isolate the physical contribution of the mat structure by clearing several areas of seabed and placing artificial mat-mimics on some but not others. After 2 weeks, mat-mimic plots had significantly more crustaceans and similar significant effects on surface versus sub-surface feeders compared to control areas, although the diversity and abundance of other organisms was not significantly different.

So far, the approach parallels Woodin's. However, in a later study Crooks and Khim (1999) performed a similar experiment at the same site, but with five area-types to further isolate the relevant variables: (a) mat-mimics and mussel-mimics; (b) mat-mimics and live mussels; (c) no mats and mussel-mimics; (d) no mats and live mussels; (e) neither mats nor mussels. None of the areas contained natural mussel mats, and each area was sampled after three and 6 weeks. Woodin had wanted to distinguish between a tube-effect and a worm-effect; Crooks and Khim here attempted to distinguish between a mat-effect, a shell-effect, and a mussel-effect. They discovered that the effect of *Musculista* beds on sediment and community composition is primarily a mat-effect. Areas with mat-mimics, like areas with natural mats in the previous study, contained sediments with a significantly higher percentage of silts, clays, and organic matter than control areas,

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[14] Strangely, W.H. Benson, the original describer of this species (as *Modiola senhousia*), does not even mention the byssal cocoon (Cantor 1842, 489).

whereas areas without mat-mimics did not. Mat-mimic effects on community composition were also more pronounced than the effects of living mussels, and diversity and abundance were significantly increased in mat-mimic areas but not in mussel areas. Only a few species were significantly affected by living mussels, whereas many groups were affected by mat-mimics. Overall, mat-mimic area sediments and communities were quite similar to those of natural *Musculista* patches, whereas mussel and mussel-mimic area communities showed only a few similarities to those patches.

These studies by Crooks and Woodin demonstrate that it is possible, in local cases, to isolate the influence of physical structures created by ecosystem engineers on both abiotic factors and other organisms. In the cases they assessed, this influence was very important: both *Diopatra* tubes and *Musculista* mats had strong effects on community composition, and these effects were not due to the organisms themselves. Crooks and Khim (1999) were even able to test which of two structural effects, that of the mats and that of the shells, was more important, and compared both of these to the effect of the living mussels. All of these experiments also suggest further work to discover exactly why the physical structures produced by these ecosystem engineers have the influence they do. With experiments on other species that produce similar structures, it may be possible to generalize about the influence of such structures on ecological communities.

Local experiments avoid debates about the importance of ecosystem engineering or niche construction in evolutionary history more generally, and simply prove its importance at relatively small temporal and spatial scales. However, such experiments are quite rare – it is not that the Woodin and Crooks examples are the most prominent; they are the some of the only systematic evaluations of structural ecosystem engineering that use physical models, though there have also been a few studies of the influence of artificial reefs and plants (e.g., Bell and Hicks 1991; Gratwicke and Speight 2005).[15] These sorts of case studies complement paleontological evidence for ecosystem engineering (Kidwell and Jablonski 1983; Canfield 2005; Parras and Casadío 2006; Erwin 2008). Experiments on modern populations, evidence of past ecosystem engineering, and mathematical models of ecosystem engineering processes (see Cuddington et al. 2009 and references therein) together make a strong case for the importance of ecosystem engineering in evolution.

Ecosystem engineering, environment, and evolution

But are the above experiments really relevant to evolution? Okasha (2005, 4) claims that restricting niche construction to activities that feed back to the constructing population or organism results in a concept of evolutionary but not ecological significance. He also implies that ecosystem engineering is conversely of ecological but not evolutionary significance. There is something to these claims: it is easy to

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[15] There are also several other studies of polychaete tube effects that employ mimics: Dauer et al. (1982) Eckman and Nowell (1984), Eckman (1985), and Callaway (2003). One study even uses vial caps to mimic dead barnacles (Dean 1981).

see how niche construction can shape the evolution of a population of constructors, and how ecosystem engineering can have cascading effects in ecosystems. However, as I shall argue in this final section, ecosystem engineering is important to evolution when such engineering activities structure and control important aspects of the abiotic environment.

That ecosystem engineering that feeds back directly to the engineer—niche construction—has evolutionary significance is uncontroversial. As mentioned above, niche-constructing behavior can provide an alternative route to adaptation, as in the case of earthworms. However, niche construction in the narrow sense, unlike niche construction in the broad sense of Odling-Smee et al. (2003), is not a process equal in importance to the process of natural selection. Imagine two scenarios: (1) a population adapts to its environment because of selection for morphological or physiological changes that increase fitness; (2) a population adapts to its environment because of selection for niche construction resulting in beneficial environmental changes. That is, the organism can change to fit the environment, or the organism can change the environment. However, selection is acting on the organism (or the genes) in both these scenarios; it is just that in the second case, the changes to the organism result in changes to the environment. Nevertheless, the selective history of a group is often incomplete without a discussion of niche construction, although it will be more or less important depending on the case.

The relevance of ecosystem engineering more generally to evolution is clear when the results of engineering affect another population of organisms, and changes to this population in turn affect the engineer. The dynamics of this indirect feedback, always a possibility in cases of ecosystem engineering, are likely different than those in niche construction cases. For example, ecosystem engineering by *Diopatra* produces tube structures that prevent disturbance by crabs. This engineering creates refuges for smaller polychaetes. If these other organisms, affected by the engineering activities of *Diopatra*, in turn affect the fitness of *Diopatra* in some way, this would be an evolutionary impact.

However, many of the effects of ecosystem engineering are byproducts or ‘mere effects’ from the point of view of the engineering population. Ecosystem engineers are important: they control many of the abiotic factors—forces, topography, stability, chemistry, light—that make up the environments of other organisms. When *Musculista* builds its byssal mats, it provides refuges for other organisms, alters flow regimes, increases sediment stability and composition, etc. But must we take the ecosystem engineering of *Musculista* into account when studying an evolving population of organisms affected by the mats? In one sense no: what matters is the external selection pressures on the affected organism; we need only know the abiotic factors associated with the selection pressure. In another sense yes: *Musculista* mats partly control abiotic factors, and thus affect selection pressures.

I believe the best way to approach this apparent contradiction is to see the activities of ecosystem engineers as adding a layer of causal complexity to what we blithely term the ‘environment’ of an organism or population (Pearce 2010b). As Donald Canfield (2005) relates, the evolution (~2.7 billion years ago) of cyanobacteria that produced oxygen as a waste product led to an increase in atmospheric oxygen levels throughout the Proterozoic Eon. This increase created an external selection pressure that led to the evolution (or radiation) of organisms with an oxygen-based metabolism. However, to study the evolution of aerobic respiration, one does not need to address the ecosystem engineering activities of cyanobacteria except incidentally. What matters is atmospheric oxygen levels, i.e., the abiotic factor partly controlled by cyanobacteria.[16] This example shows that focused evolutionary studies do not necessarily have to take ecosystem engineering into account, even if that engineering has drastic effects. However, to understand the causal factors operating in evolutionary history, it is necessary to understand not only the relation between selection pressures and populations, but also the sources of those selection pressures. Paying attention to ecosystem engineering helps us to understand changes in selection pressures at multiple timescales (Erwin 2008).

Systematic changes in selection pressures due to ecosystem engineering can have an important effect on evolutionary dynamics. Consider the case of the small tube-dwelling polychaete *Spio*, which seems to benefit from the refuge created by the engineering activities of *Diopatra*. The selection pressures on *Spio* can be divided into several kinds: (1) biological pressures like predation; (2) pressures due to the ecosystem engineering activities of *Diopatra*, crab species, etc.; (3) pressures due to the niche construction activities of *Spio*; (4) other abiotic pressures. As we learn more about the sources of the pressures in (4), they may be recategorized as (2). Understanding where the different selection pressures on *Spio* come from can help us understand why they vary in systematic ways. Thus, even though only the relevant abiotic factor matters when thinking about the abstract role of selection in the evolutionary process, the changes that lead to changing selection pressures almost always matter in the consideration of concrete evolutionary cases.

The indirect relation between ecosystem engineering and evolution is likely the reason why there have not been experiments attempting to explicitly link the two. After all, there are plenty of experiments linking ecosystem engineering to changes in the physical environment, and even more experiments linking changes in the physical environment to the evolution of new traits. Thus, an experiment connecting ecosystem engineering and evolution, even if it presented a positive result, might simply be seen as redundant.

Ecosystem engineering is the most recent step in a series of complications of what counts as part of an organism's circumstances or environment, as I have shown elsewhere Pearce (2010a, b). Jean-Baptiste Lamarck and the author of the *Vestiges of the Natural History of Creation* talked primarily of abiotic factors like light, fluid *milieu*, and climate. Charles Lyell added other organisms; Herbert Spencer added social forces. The most recent step, however, is perhaps the most radical. Rather than treating the environment as a set of unrelated factors, ecosystem engineering points out that different parts of the environment can affect one another—in particular, biotic factors are not independent of abiotic factors. At the outset of this paper, I commented that ecosystem engineering experiments focus on particular empirical situations in which we cannot neglect the O term in $\mathrm{d}E/\mathrm{d}t = \mathrm{g}\,(O, E)$.

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[16] Indirect feedback is also involved in this case, however. The engineering activities of cyanobacteria eventually led to an explosion of aerobic organisms, some of which in turn competed with or predated on cyanobacteria.

However, this equation applies most naturally to niche construction cases, taking O as a particular organism or population and E as the environment of that organism. When it comes to the effects of ecosystem engineering on *other* organisms, however, we must ironically return to what Lewontin called the traditional view: $dE/dt = g(E)$. It is just that other organisms and their various engineering activities are a part of E; E has a dynamic and complex structure that we cannot ignore if we want to understand evolutionary history.

Conclusion

Even if ecosystem engineering is not a process on par with natural selection in terms of its importance for evolution, it is still often essential to understanding ecological relationships and evolutionary history. Ecosystem engineering occurs when an organism modifies its physical environment. Niche construction is best seen as a particular kind of ecosystem engineering—the special case in which the effects of engineering feed back on the engineer. Philosophers have focused on the special case and neglected studies of ecosystem engineering. I have shown that experiments can demonstrate the importance of ecosystem engineering in particular cases, with each experiment adding a bit more evidence for its general importance. And even though ecosystem engineering need not be considered in all evolutionary studies, it is often a key source of changes in selection pressures. Abiotic factors may apply selection pressures directly, but these pressures are also partly controlled by other organisms.

This paper also shows that philosophers' exclusive focus on certain parts of biology—e.g., evolutionary biology rather than ecology or organismal biology—can systematically bias their understanding of biological concepts. Someone reading the *Biology & Philosophy* roundtable review of Odling-Smee et al.'s *Niche Construction* (2003), for example, would have no idea that there existed a conceptually distinct approach within ecology whose originating paper had been cited over a thousand times, ten times as often as the corresponding niche construction papers. This is of course partly the fault of the book's authors, who consistently describe ecosystem engineering as "a synonym for niche construction" (Odling-Smee et al. 2003, 379). Nevertheless, philosophers of biology, in their focus on modeling and evolution, can sometimes miss out on the unique perspectives of experimental approaches.

At the end of the nineteenth century, Dewey (1898, 438) sketched the idea of ecosystem engineering:

> Every living form is dynamically, not simply statically, adapted to its environment. I mean by this [that] it subjects conditions about it to its own needs. This is the very meaning of 'adjustment'; it does not mean that the life-form passively accepts or submits to the conditions just as they are, but that it functionally subordinates these natural circumstances to its own food needs.

Although the process of adaptation or adjustment normally involves changes to both organisms and their circumstances, the relation between organism and environment is not symmetrical. Each affects the other, albeit in very different ways. But when contemplating an entangled bank, one must not forget the importance of Darwin's "worms crawling through the damp earth," for without these worms neither earth nor bank would exist (Darwin 1859, 489).

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References

Baldwin JM (1896) A new factor in evolution. Am Nat 30:441–451, 536–553

Bell SS (1985) Habitat complexity of polychaete tube-caps: influence of architecture on dynamics of a meioepibenthic assemblage. J Mar Res 43:647–671

Bell SS, Coen LD (1982a) Investigations on epibenthic meiofauna. I. Abundances on and repopulation of the tube-caps of *Diopatra cuprea* (Polychaeta: Onuphidae) in a subtropical system. Mar Biol 67:303–309

Bell SS, Coen LD (1982b) Investigations on epibenthic meiofauna. II. Influence of microhabitat and macroalgae on abundance of small invertebrates on *Diopatra cuprea* (Bosc) (Polychaeta: Onuphidae) tube-caps in Virginia. J Exp Mar Biol Ecol 61:175–188

Bell SS, Hicks GRF (1991) Marine landscapes and faunal recruitment: a field test with seagrasses and copepods. Mar Ecol Prog Ser 73:61–68

Berke SK (2010) Functional groups of ecosystem engineers: a proposed classification with comments on current issues. Integr Comp Biol 50:147–157

Bock WJ (1980) The definition and recognition of biological adaptation. Am Zool 20:217–227

Bosc LAG (1801) Histoire naturelle des vers, contenant leur description et leur moeurs; avec figures dessinées d'après nature. Deterville, Paris

Brakefield PM (2006) Evo-devo and constraints on selection. Trends Ecol Evol 21:362–368

Brandon RN (1990) Adaptation and environment. Princeton University Press, Princeton, NJ

Brandon RN (2001) Organism and environment revisited. In: Singh RS, Krimbas CB, Paul DB, Beatty J (eds) Thinking about evolution. Cambridge University Press, Cambridge, pp 336–352

Breemen Nv (1995) How *Sphagnum* bogs down other plants. Trends Ecol Evol 10:270–275

Callaway R (2003) Long-term effects of imitation polychaete tubes on benthic fauna: they anchor *Mytilus edulis* (L.) banks. J Exp Mar Biol Ecol 283:115–132

Canfield DE (2005) The early history of atmospheric oxygen: homage to Robert M. Garrels. Annu Rev Earth Planet Sci 33:1–36

Cantor T (1842) General features of Chusan, with remarks on the flora and fauna of that Island. Ann Mag Nat Hist 9:265–278, 361–370, 481–493

Crooks JA (1998) Habitat alteration and community-level effects of an exotic mussel, *Musculista senhousia*. Mar Ecol Prog Ser 162:137–152

Crooks JA (2002) Characterizing ecosystem-level consequences of biological invasions: the role of ecosystem engineers. Oikos 97:153–166

Crooks JA, Khim HS (1999) Architectural versus biological effects of a habitat-altering, exotic mussel, *Musculista senhousia*. J Exp Mar Biol Ecol 240:53–75

Cuddington K, Wilson WG, Hastings A (2009) Ecosystem engineers: feedback and population dynamics. Am Nat 173:488–498

Darwin C (1859) On the origin of species by means of natural selection, or the preservation of favoured races in the struggle for life. John Murray, London

Darwin C (1881) The formation of vegetable mould, through the action of worms, with observations on their habits. John Murray, London

Dauer DM, Tourtellotte GH, Ewing RM (1982) Benthic studies of the lower Chesapeake Bay. 2. Oyster shells and artificial worm tubes–the role of refuges in structuring benthic communities of the lower Chesapeake Bay. Int Rev Gesamten Hydrobiol 67:661–677

Dawkins R (1982) The extended phenotype: the gene as the unit of selection. Oxford University Press, Oxford

Dawkins R (2004) Extended phenotype–but not too extended. A reply to Laland, Turner and Jablonka. Biol Philos 19:377–396

Dawson TE (1998) Fog in the California redwood forest: ecosystem inputs and use by plants. Oecologia 117:476–485

Dean TA (1981) Structural aspects of sessile invertebrates as organizing forces in an estuarine fouling community. J Exp Mar Biol Ecol 53:163–180

Dewey J (1898) Evolution and ethics. Monist 8:321–341

Eckman JE (1985) Flow disruption by an animal-tube mimic affects sediment bacterial-colonization. J Mar Res 43:419–435

Eckman JE, Nowell ARM (1984) Boundary skin friction and sediment transport about an animal-tube mimic. Sedimentology 31:851–862

Erwin DH (2008) Macroevolution of ecosystem engineering, niche construction and diversity. Trends Ecol Evol 23:304–310

Flecker AS (1996) Ecosystem engineering by a dominant detritivore in a diverse tropical stream. Ecology 77:1845–1854

Godfrey-Smith P (2000) Niche construction in biological and philosophical theories. Behav Brain Sci 23:153–154

Godfrey-Smith P (2001) Organism, environment, and dialectics. In: Singh RS, Krimbas CB, Paul DB, Beatty J (eds) Thinking about evolution: historical, philosophical, and political perspectives. Cambridge University Press, Cambridge, pp 253–266

Gratwicke B, Speight MR (2005) Effects of habitat complexity on Caribbean marine fish assemblages. Mar Ecol Prog Ser 292:301–310

Griffiths PE (2005) Review of 'Niche Construction'. Biol Philos 20:11–20

Gutiérrez JL, Jones CG (2006) Physical ecosystem engineers as agents of biogeochemical heterogeneity. Bioscience 56:227–236

Hastings A, Byers JE, Crooks JA, Cuddington K, Jones CG, Lambrinos JG, Talley TS, Wilson WG (2007) Ecosystem engineering in space and time. Ecol Lett 10:153–164

Jablonski D (2008) Biotic interactions and macroevolution: extensions and mismatches across scales and levels. Evolution 62:715–739

Jones CG, Gutiérrez JL (2007) On the purpose, meaning, and usage of the physical ecosystem engineering concept. In: Cuddington K, Byers JE, Wilson WG, Hastings A (eds) Ecosystem engineers: from plants to protists. Amsterdam, Elsevier, pp 3–24

Jones CG, Lawton JH, Shachak M (1994) Organisms as ecosystem engineers. Oikos 69:373–386

Jones CG, Lawton JH, Shachak M (1997) Positive and negative effects of organisms as ecosystem engineers. Ecology 78:1946–1957

Kidwell SM, Jablonski D (1983) Taphonomic feedback: ecological consequences of shell accumulation. In: Tevesz MJS, McCall PL (eds) Biotic interactions in recent and fossil benthic communities. Plenum, New York, pp 195–248

Laland KN (2004) Extending the extended phenotype. Biol Philos 19:313–325

Laland KN, Sterelny K (2006) Seven reasons (not) to neglect niche construction. Evolution 60:1751–1762

Laland KN, Odling-Smee FJ, Feldman MW (1999) Evolutionary consequences of niche construction and their implications for ecology. Proc Natl Acad Sci USA 96:10242–10247

Laland KN, Odling-Smee FJ, Feldman MW (2000) Niche construction, biological evolution, and cultural change. Behav Brain Sci 23:131–175

Laland KN, Odling-Smee FJ, Feldman MW (2005) On the breadth and significance of niche construction: a reply to Griffiths, Okasha and Sterelny. Biol Philos 20:37–55

Levins R, Lewontin RC (1985) The dialectical biologist. Harvard University Press, Cambridge

Lewontin RC (1978) Adaptation. Sci Am 239:213–230

Lewontin RC (1983) Gene, organism and environment. In: Bendall DS (ed) Evolution from molecules to men. Cambridge University Press, Cambridge, pp 273–285

Luckenbach MW (1986) Sediment stability around animal tubes: the roles of hydrodynamic processes and biotic activity. Limnol Oceanogr 31:779–787

Maclaurin J, Sterelny K (2008) What is biodiversity?. University of Chicago Press, Chicago

Manne L, Pimm SL (1996) Engineered food webs. Curr Biol 6:29–31

Morton B (1974) Some Aspects of the biology, population dynamics, and functional morphology of *Musculista senhausia* Benson (Bivalvia, Mytilidae). Pac Sci 28:19–33

Myers AC (1972) Tube-worm-sediment relationships of *Diopatra cuprea* (Polychaeta: Onuphidae). Mar Biol 17:350–356

Ne'eman G, Goubitz S, Nathan R (2004) Reproductive traits of *Pinus halepensis* in the light of fire–a critical review. Plant Ecol 171:69–79

Odling-Smee FJ (1988) Niche-constructing phenotypes. In: Plotkin HC (ed) The role of behavior in evolution. MIT Press, Cambridge, MA, pp 73–132

Odling-Smee FJ, Laland KN, Feldman MW (1996) Niche construction. Am Nat 147:641–648

Odling-Smee FJ, Laland KN, Feldman MW (2003) Niche construction: the neglected process in evolution. Princeton University Press, Princeton

Okasha S (2005) On niche construction and extended evolutionary theory. Biol Philos 20:1–10

Parras A, Casadío S (2006) The oyster Crassostrea? hatcheri (Ortmann, 1897), a physical ecosystem engineer from the upper Oligocene–lower Miocene of Patagonia, southern Argentina. Palaios 21:168–186

Pearce T (2010a) 'A great complication of circumstances'–Darwin and the economy of nature. J Hist Biol 43:493–528

Pearce T (2010b) From 'circumstances' to 'environment'–Herbert Spencer and the origins of the idea of organism-environment interaction. Stud Hist Philos Biol Biomed Sci 41:241–252

Pearce T (2011) Evolution and constraints on variation: variant specification and range of assessment. Philos Sci 78

Pearce T, LaBarbera M (2009a) A comparative study of the mechanical properties of Mytilid byssal threads. J Exp Biol 212:1442–1448

Pearce T, LaBarbera M (2009b) Biomechanics of byssal threads outside the Mytilidae: *Atrina rigida* and *Ctenoides mitis*. J Exp Biol 212:1449–1454

Reichman OJ, Seabloom EW (2002) The role of pocket gophers as subterranean ecosystem engineers. Trends Ecol Evol 17:44–49

Schwilk DW (2003) Flammability is a niche construction trait: canopy architecture affects fire intensity. Am Nat 162:725–733

Schwilk DW, Ackerly DD (2001) Flammability and serotiny as strategies: correlated evolution in pines. Oikos 94:326–336

Sterelny K (2001) Niche construction, developmental systems, and the extended replicator. In: Oyama S, Griffiths PE, Gray RD (eds) Cycles of contingency: developmental systems and evolution. MIT Press, Cambridge, pp 333–349

Sterelny K (2005) Made by each other: organisms and their environment. Biol Philos 20:21–36

West-Eberhard MJ (2003) Developmental plasticity and evolution. Oxford University Press, Oxford

Wilby A (2002) Ecosystem engineering: a trivialized concept? Trends Ecol Evol 17:307

Woodin SA (1978) Refuges, disturbance, and community structure: a marine soft-bottom example. Ecology 59:274–284

Woodin SA (1981) Disturbance and community structure in a shallow water sand flat. Ecology 62:1052–1066

Wright JP, Jones CG (2006) The concept of organisms as ecosystem engineers ten years on: progress, limitations, and challenges. Bioscience 56:203–209