Ecosystem Engineers

Advanced article

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Ecosystem engineers, or more precisely *physical ecosystem engineers*, are organisms that change the abiotic environment by physically altering structure. As a consequence they often, but not invariably, have effects on other biota and their interactions, and on ecosystem processes. The physical ecosystem engineering concept interconnects a number of important ecological and evolutionary concepts and is particularly relevant to environmental management.

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Introduction

Ecologists have long been aware that organisms can physically modify the nonliving environment via their presence or activities, thereby affecting the availability of abiotic resources and conditions on which they and other organisms depend (Buchman *et al*., 2007). Some specialized areas of ecology and other disciplines had emphasized some aspects of this phenomenon (e.g. marine sediment bioturbation, mammalian soil disturbance, zoogeomorphology). Nevertheless, formal recognition and study of the general process of organismally induced, structurally mediated abiotic change, along with its many consequences was not historically central to ecological science, as evidenced by its omission from ecological textbooks. The *ecosystem engineering* concept (Jones *et al*., 1994, 1997) was introduced to draw attention to the ubiquity and importance of this process and its consequences, to provide an integrative general framework, to lay out a question-based research agenda and to give it a name. The concept was developed to encompass a variety of superficially disparate and oft-ignored ecological phenomena not addressed by the historical focus of ecology on trophic relations (i.e. predation, resource competition, food webs, energy flow, nutrient cycling and the like).

What is an Ecosystem Engineer?

Trees cast shade, moderate temperature extremes and reduce the impact of rain and wind. Beaver-built dams reduce upstream water velocity and increase sedimentation. Coral reefs attenuate wave action and increase the three-dimensional structure of the seafloor. Trees, beaver and reef-forming corals – together with a myriad of other organisms – share the common characteristic of changing physical structure within the environment. These structural changes then affect abiotic resources and abiotic environmental conditions that may be critical for other organisms and even themselves (**Figure 1**). Such organisms were called *physical ecosystem engineers* by Jones *et al*. (1994, 1997). They originally defined ecosystem engineers as *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. The direct provision of resources by an organism to other species, in the form of living or dead tissues is not engineering*.

Abiotic environmental change is caused by the physical structure of organisms (*autogenic engineering*, see later) or by organisms changing the physical structure of living and nonliving materials (*allogenic engineering*, see later). These abiotic changes can then affect biota, including the engineer (**Figure 1**). Biotic influences encompass organisms, populations, communities, ecosystems and landscapes and can be integrated by thinking of physical ecosystem engineering as the creation, modification, maintenance and destruction of habitats.

The terms *ecosystem engineering* and *physical ecosystem engineering* are often used interchangeably, although ecosystem engineering was intended as a more general concept encompassing not only the physical modification of the environment by organisms but also chemical analogues that have not yet received substantial conceptual development (see Jones *et al*., 1994).

The physical ecosystem engineering concept addresses the combined influence of two coupled direct interactions (Jones and Gutiérrez, 2007). The first is the way organisms change the abiotic environment – *the physical ecosystem engineering process*. The second is how these abiotic changes affect biota – *ecosystem engineering consequence* (**Figure 1**). The physical ecosystem engineering process is defined as: *Organismally caused, structurally mediated changes in the distribution, abundance and composition of energy and materials in the abiotic environment arising independent or irrespective of changes due to assimilation and dissimilation* (Jones and Gutiérrez, 2007). This distinguishes physical ecosystem engineering from purely abiotic

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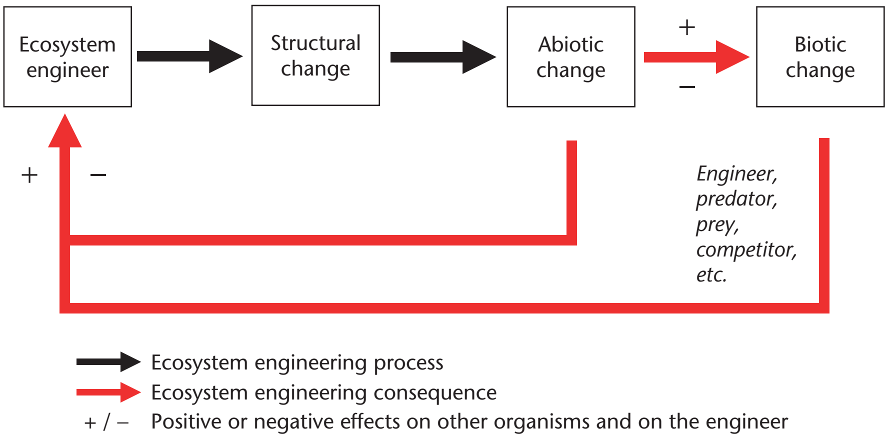

Figure 1 General pathways of physical ecosystem engineering.

forces causing structural change; reflects the requirement for abiotic change to arise via structural change (i.e. physical state changes, Jones *et al*., 1994, 1997) and distinguishes the engineering process from abiotic changes caused by the universal processes of organismal uptake and release of materials and energy. Physical ecosystem engineering consequence is defined as: *Influence arising from engineer control on abiotic factors that occurs independent or irrespective of use of or impact of these abiotic factors on the engineer or the participation by the engineer in biotic interactions, despite the fact that all these can affect the engineer and its engineering activities* (Jones and Gutiérrez, 2007). This helps distinguish engineering effects on biota and their interactions from any other influence of the engineer via other types of ecological interactions, such as abiotic resource uptake and direct resource competition; role as predator, prey, pollinator or disperser. (It is worth noting here that direct resource competition can sometimes be viewed as the result of ecosystem engineering, e.g. tree shading of understory saplings is traditionally viewed as direct resource competition even though it can be described as an ecosystem engineering process where the structure of the canopy trees absorbs *and* reflects light affecting the understory light environment as well as other abiotic variables relevant to understory plants, such as temperature and soil moisture. When tree shade provides habitat for shade-tolerant understory herbs, it is clearly engineering, not direct resource competition.) It also recognizes that engineering effects will be context dependent on the degree of abiotic change caused by the engineering process and the degree of abiotic limitation, constraint or enablement experienced by species, and highlights the potential importance of engineering feedbacks to the engineer and effects of other biotic interactions on engineering activities.

Types of Ecosystem Engineering

Ecosystem engineers physically modify the environment in two basic ways (Jones *et al*., 1994, 1997). *Autogenic engineers* (**Figure 2a–c**) change the environment via their own physical structure (i.e. their living and dead tissues, such as a tree casting shade). In contrast, *allogenic engineers* (**Figure 2d–f**) change the environment by transforming living or nonliving materials from one physical state to another via mechanical or other means, and the engineer is not necessarily part of the permanent physical ecosystem structure (e.g. dam-building beaver). Animals, plants and microorganisms can be both autogenic and allogenic engineers (Jones *et al*., 1994, 1997). Examples of autogenic engineering include tree shade effects on understory microclimate, litter effects on soil heat transfer, wave attenuation by sea grasses, and refuges created by coral reefs. Examples of allogenic engineering include burrow excavation by mammals, mound building by ants and termites, creation of tree holes by woodpeckers, and rock weathering by tree root growth. It is important to realize that many organisms can simultaneously autogenically and allogenically engineer the environment (e.g. trees cast shade autogenically while making soil macropores allogenically).

Effects of Ecosystem Engineers

The impacts that engineers have on other organisms vary from the trivial to substantial, and can be positive or negative. An engineer can increase the growth and survival of one species while decreasing that of another species. Engineers can likewise have positive and negative community-level impacts. For example, while dam-building beaver make habitats for a very large number of species, the conversion of a stream to a beaver pond also has negative effects on many stream organisms (Jones *et al*., 1997).

Effects on species richness at the patch scale

At the scale of the engineered environment (i.e. an engineered patch), there is no a priori rationale for assuming that the total number of other species that can live in the new, engineered habitat should be more, less or the same as

Figure 2 Autogenic (a, b, c) and allogenic (d, e, f) ecosystem engineering. (a) Secondary oak (*Quercus rubra*) forest near Millbrook, NY, USA (changes microclimate; affects soil biogeochemistry and understory species). (b) Smooth cordgrass, *Spartina alterniflora*, in a tidal marsh in the La Plata estuary near Playa Peninos, Uruguay (attenuates storm surges, increases sedimentation and retains organic matter; affects biogeochemistry and creates protected habitat for other species). (c) Reefs of tube-building polychaetes, *Ficopomatus enigmaticus*, an exotic species in Mar Chiquita coastal lagoon, Argentina (reef in foreground is *c.* 3 m across. Alters hydrodynamics, increases sedimentation; provides shelter for many invertebrates). (d) Riparian forest area transformed by the dam building activity of beaver, *Castor canadensis*, in Tierra del Fuego, Chile, where it is an exotic species (alters hydrology, sedimentation, light levels; affects biogeochemistry and species habitats). (e) Mound of leaf-cutting ant, *Atta sexdens*, in the 'blanqueal' area near Fray Bentos, Uruguay (brings saline soil at depth to surface, eliminating most vegetation on mound). (f) The Southwestern Atlantic burrowing crab, *Neohelice* (*Chasmagnathus*) *granulata*, in Mar Chiquita coastal lagoon, Argentina (buries litter in excavation mounds; prevents litter export as a nutrient subsidy to adjacent estuary). Photo credits: (a) Jorge Gutiérrez, (b) Cesar Fagúndez, (c) Martín Bruschetti, (d) and (e) Clive Jones and (f) Pablo Ribeiro, all reproduced with permission.

the number of species that disappear when the old habitat is eliminated. Accordingly, there is no expected or observed general pattern at the patch scale; species richness can be increased, decreased or not changed by ecosystem engineering (Wright and Jones, 2004). Nevertheless, the effect of an ecosystem engineer on patch-scale species richness along a gradient of primary productivity can be predicted. Wright and Jones (2004) developed a simple conceptual model that predicts the patch level effects of ecosystem engineers on species richness based on how habitat modification caused by engineers affects primary productivity, assuming a hump-shaped relationship between primary productivity and species richness. Confirming the predictions of the conceptual model using data from many different studies, they observed a significant negative relationship between primary productivity and the engineering effect on species richness when ecosystem engineers increased primary productivity and a positive relationship when engineers decreased primary productivity (albeit a weak relationship due to a limited number of studies at high primary productivity).

Effects on species richness at the landscape scale

At sufficiently large scales, encompassing unmodified habitats, engineered habitats and areas at different stages of recovery from prior engineering (i.e. the landscape scale), the net effect of engineering will almost inevitably be to enhance species richness via a net increase in habitat diversity (Jones *et al.*, 1997). Many studies have now shown that ecosystem engineers increase landscape-scale species richness by creating new habitats and enabling the persistence of species that would otherwise be excluded from the environment. For example, beaver increases the number of herbaceous plant species in riparian zones by at least 33% by creating wetlands (Wright *et al.*, 2002). Similarly, leaf-tying caterpillars on white oak increase the richness of herbivorous insects by up to 38% by making shelters (Lill and Marquis, 2003).

Effects on biogeochemical processes as an illustration of ecosystem effects

Ecosystem engineers can affect biogeochemical processes by changing the availability of resources (e.g. carbon, nutrients) for microbes or by changing abiotic conditions that affect microbial process rates (e.g. soil moisture or temperature). Physical ecosystem engineers can create biogeochemical hot and cold spots in soils and sediments (Gutiérrez and Jones, 2006). They do so by physically influencing the flows of materials or the transfer of heat. Engineering mechanisms that affect material flow include changes in fluid dynamic properties caused by physical structures (e.g. wind attenuation by trees), active fluid pumping (e.g. burrow irrigation by aquatic invertebrates) and active material transport (e.g. litter burial by anecic earthworms). Engineering mechanisms influencing heat transfer include physical alteration of heat transfer properties (e.g. soil insulation by plant litter), direct heat transfer (e.g. transfer of metabolic heat in ant and termite nests) and convective forcing (e.g. aquatic invertebrates that irrigate their burrows with overlying warmer or cooler water). The consequences of physical ecosystem engineering for biogeochemical processes can be predicted by considering the abiotic resources or conditions that limit or promote a biogeochemical reaction, and the effect of physical ecosystem engineering on these resources or conditions via the control they exert on material flows and heat transfer (Gutiérrez and Jones, 2006).

Feedbacks to the engineer

Feedbacks occur when physical environmental modification by the engineer positively or negatively affects the engineer (Jones *et al.*, 1997) via two possible pathways (**Figure 1**). Feedbacks are fundamentally important to engineer population dynamics and abiotic environmental dynamics. Engineering feedbacks have direct consequences for the fitness of the engineer and is the process underlying many – perhaps most – examples of niche construction (Odling-Smee *et al.*, 2003, see section Niche construction later). Positive engineering feedbacks can also increase the population growth rates of exotic species that engineer their environment compared to exotic species that are not engineers (Cuddington and Hastings, 2004).

Ecosystem Engineering and Environmental Management

Ecosystem engineering processes are very relevant to many pressing environmental problems and management concerns. Humans are physical ecosystem engineers *par excellence* and many of the adverse effects of humans on the environment arise because of the unintended consequences of our activities as physical ecosystem engineers (e.g. dam building, dredging, harbor building or ploughing; Jones *et al.*, 1994). In a world of increasing population density and resource use, the management of our engineering impacts could be improved by viewing them from an ecosystem engineering perspective (Rosemond and Anderson, 2003). We can use our rapidly growing knowledge of nature's engineers to help understand, predict and manage human ecosystem engineering impacts, including using engineering species to help conserve and restore habitats. For example, ecosystem engineers are often the cause of a transition between a degraded and a restored abiotic state (or vice versa), and their explicit incorporation into restoration frameworks can lead to enhanced restoration success while simultaneously reducing human cost and effort (Byers *et al.*, 2006).

The ecosystem engineering concept is also helpful in understanding species invasions. For example, ecosystem engineers can create habitat for exotic species. Badano *et al.* (2007) found that cushion plants ameliorate environmental conditions in stressful, high Andean ecosystems, facilitating invasion by exotic forbs. In addition, we now know that ecosystem engineering is often the reason why some exotic species have large impacts on native communities and ecosystems (see review in Crooks, 2002). The ability of some exotic species to engineer the environments they invade such that they enhance their own performance (positive feedbacks) may be a major influence on their invasion success and rate of spread (Crooks, 2002). Exotic species that modify their environment can have significantly faster population growth rates in suboptimal habitats than species that do not modify their environment (Cuddington and Hastings, 2004).

The ecosystem engineering concept is also central to biodiversity conservation and land-use change. Species diversity often depends on habitat created by a particular species of ecosystem engineer. Overexploiting or eradicating such engineers may have dramatic, negative consequences for biodiversity (Coleman and Williams, 2002). Ecosystem engineers are often removed or impacted by human activities with limited recognition of their important engineering contributions. For example, trees are removed when converting forests to agriculture despite their key engineering roles in maintaining soil fertility and preventing soil erosion. The rapid soil degradation and soil loss that then can occur is often unforeseen by landowners. Conversely, trees are sometimes planted in naturally unforested areas (e.g. grasslands, shrublands, sand dunes) for shade, or aesthetics, or perhaps to increase carbon sequestration and mitigate climate change. However, this can negatively impact local biodiversity when the trees create a new physical habitat.

In general, ecosystem engineers affect a variety of environmental processes and variables of management concern – hydrology, erosion, microclimate, biodiversity and nutrient cycling and retention – suggesting many potential benefits of integrating the concept into environmental management.

Some Related (and Sometimes Confounded) Concepts

Niche construction

Niche construction is an evolutionary concept. It refers to the 'activities, choices and metabolic processes of organisms through which they define, choose, modify and partly create their own niches by affecting the selective forces acting on them (Odling-Smee *et al*., 2003). Niche construction includes organismal activities that constitute physical ecosystem engineering, but is not limited to engineering. Engineering activities such as dam building by beaver, burrow digging by mammals, path creation by ungulates or sediment reworking by aquatic invertebrates may well affect the fitness of the organisms responsible for physical environmental modification. If these activities are subject to natural selection, then they constitute niche construction. However, while niche construction and ecosystem engineering could be construed as synonymous to some extent, the concepts differ in three important ways. First, physical environmental modification – the defining feature of physical ecosystem engineering – is not a requisite for niche construction. The niche construction concept encompasses any organismal activity that leads to ecological inheritance (i.e. a modified functional relationship between organisms and their environment as a consequence of activities of either its genetic or ecological ancestors; Odling-Smee *et al*., 2003). Nonengineering examples of niche construction include the effects of habitat choice or resource consumption by organisms on the fitness of their descendants, which occur irrespective of any engineering activity of the organism in question (e.g. effects of oviposition site choices made by female insects on the selection pressures affecting their descendants; effects of the grazing history of an area on the subsequent generations of herbivores; see Odling-Smee *et al*., 2003). Second, whereas it is clearly recognized that ecosystem engineering can have evolutionary consequences for the engineer and other species (Jones *et al*., 1994), the engineering concept primarily focuses on ecological consequence. Third, niche construction refers only to effects on the niche constructor, whereas ecosystem engineering addresses ecological effects on both the engineer and on other species and ecological processes.

Keystone species

Keystone species are those having a large effect on a community that is disproportionate to their biomass or abundance (Power *et al*., 1996). Top predators are archetype examples (i.e. keystone predators). Their relative abundance is usually low but their removal often has important cascading effects throughout the food web (e.g. Power *et al*., 1996). Such cascading community effects can also be caused by a low abundance or biomass of ecosystem engineers (such as a pair of beaver) because they create essential habitat for other species and thereby determine community and trophic web structure (i.e. keystone engineers; Jones *et al*., 1994). Although many engineers may be keystone species, other engineers can be abundant with large biomass and have large effects (e.g. trees creating forest climate and affecting many species; see section Foundation species later). Many engineers have small or limited effects on other species, irrespective of their abundance (e.g. burrows and nests occupied only by the builder).

There are two important distinctions between the ecosystem engineering concept and the keystone species concept. First, ecosystem engineering encompasses any physical influence of organisms on the abiotic environment irrespective of whether or not the engineer is abundant or has large effects. Indeed, the concept seeks to predict the relationships between abundance, *per capita* engineering activities and effects, rather than classifying organisms based on the abundance or biomass disproportionality of their effects, as in the keystone species concept.

Second, the keystone species concept does not depend upon the underlying mechanism causing the effect (i.e. there can be keystone predators, pollinators, mutualists, competitors or engineers), whereas ecosystem engineering is defined by the mechanism of interaction.

Foundation species

Foundation species (sensu Dayton, 1972) are dominant species whose structural or functional attributes define much of the structure of a community by creating locally stable conditions for other species, and by modulating and stabilizing fundamental ecosystem processes. They include dominant tree species in forests, bed-forming algae and aquatic macrophytes (e.g. kelp, seagrass), reef-forming corals and bivalves that aggregate into beds and reefs (e.g. mussels, oysters). The foundation species concept often, but not invariably, overlaps with ecosystem engineering because many of the environmental effects of foundation species occur via engineering mechanisms (e.g. tree shading, wave attenuation by seagrasses or provision of shelter and colonizable substrate by bivalve shell aggregations). However, foundation species also affect their environment and associated communities via the uptake and release of materials and energy (e.g. tree evapotranspiration, nutrient uptake by seagrasses, or bivalve biodeposition). In addition, a foundation species is, by definition, a dominant organism while, as noted earlier, the ecosystem engineering concept encompasses any physical influence of organisms on the environment irrespective of the abundance or dominance of the engineer.

Facilitation

Facilitation describes species interactions that benefit at least one of the participants and cause harm to neither (Stachowicz, 2001). A variety of such positive interactions are mediated by ecosystem engineering mechanisms, including positive effects of trees on understory plants by reducing thermal, water or nutrient stress via shading (i.e. nurse plants), or the provision of living space to other species by reef-forming corals. However, facilitation includes interactions such as pollination, seed dispersal, trophic comensalism, and nutritional symbioses (Stachowicz, 2001) that do not involve any physical modification of the environment and, thus, are not ecosystem engineering. Moreover, not all ecosystem engineering results in facilitation. As noted in section Effects of ecosystem engineers earlier, engineers can also have negative effects on other organisms (Jones *et al.*, 1997).

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