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Ecosystem Engineering across Environmental Gradients: Implications for Conservation and Management

CAITLIN MULLAN CRAIN AND MARK D. BERTNESS

Ecosystem engineers are organisms whose presence or activity alters their physical surroundings or changes the flow of resources, thereby creating or modifying habitats. Because ecosystem engineers affect communities through environmentally mediated interactions, their impact and importance are likely to shift across environmental stress gradients. We hypothesize that in extreme physical environments, ecosystem engineers that ameliorate physical stress are essential for ecosystem function, whereas in physically benign environments where competitor and consumer pressure is typically high, engineers support ecosystem processes by providing competitor- or predator-free space. Important ecosystem engineers alleviate limiting abiotic and biotic stresses, expanding distributional limits for numerous species, and often form the foundation for community development. Because managing important engineers can protect numerous associated species and functions, we advocate using these organisms as conservation targets, harnessing the benefits of ecosystem engineers in various environments. Developing a predictive understanding of engineering across environmental gradients is important for furthering our conceptual understanding of ecosystem structure and function, and could aid in directing limited management resources to critical ecosystem engineers.

Keywords: stress gradients, ecosystem engineers, conservation, associational defenses, environmental stress model

Ecosystem engineers can have inordinately large effects on associated communities through environmentally mediated interactions. An ecosystem engineer is an organism whose presence or activity alters its physical surroundings or changes the flow of resources, thereby creating or modifying habitats and influencing all associated species (Jones et al. 1994, 1997). For example, a beaver creates ponds and wetlands where there were previously running streams. A tree shades the understory and drops leaf litter, which lowers soil temperatures, changes pH, and forms a physical barrier to seedling emergence. Marsh grass dampens wave energy, promoting sediment deposition and peat accretion; provides binding substrate for benthic invertebrates; and aerates the sediment through loss of oxygen in its rooting zone. These are a few of the myriad examples of changes organisms make in the abiotic environment, and in all cases, a suite of other species are affected by these physical alterations.

A major criticism of the ecosystem engineering concept is that all organisms engineer their environments to some degree, and such a ubiquitous process is thus trivial to understanding ecological communities (Reichman and Seabloom 2002a, 2002b, Wilby 2002). However, as with all common processes, the challenge is to determine when, where, and which organisms engineer habitats with important outcomes for community and ecosystem processes. Developing this predictive understanding for ecosystem engineering would benefit the concept and its applicability substantially. We argue that important ecosystem engineers are those that provide limiting resources or reduce constraining variables, and these limiting resources and variables change consistently with background environmental conditions. While all ecosystem engineering will have both positive and negative local effects on organisms, important engineers will significantly influence ecosystem functions of interest. Finally, because maintenance of ecosystem function is a top conservation priority (Balvanera et al. 2001), identifying which types of engineers maintain or influence ecosystem functions of interest in varying environments provides a wise target for conservation attention.

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Here we review the current scientific understanding of the role ecosystem engineers play across environmental stress gradients. We explore how species interactions and the role of engineers shift across gradients in physical stress, present a general model of what types of engineers are expected to have large effects in different environments, and review research performed on ecosystem engineers in habitats that vary in environmental stress. We use these insights to suggest where ecosystem engineers are most important as conservation targets and which engineers will be most important in contributing to various ecosystem functions across environmental gradients.

Environmental stress gradients

Environmental stress gradients have a long history of utility to ecologists, despite some controversy over terminology. The concept of environmental stress has opponents (Korner 2003), as it is relative, depending on the organism and the range of environments considered. Environmental stress can be quantified using survival rates (Menge and Sutherland 1987), biomass (Grime 1989), or resource availability (Wilson and Tilman 1993), but generally the biology of the organism and environmental factors are sufficient to provide an intuitive basis for experimental study (i.e., exposure to air for marine-derived organisms). In spite of the debate over terminology, the value of analyzing community patterns across environmental gradients is undeniable and has led to substantial ecological advances.

Originally, physical gradients were useful for establishing correlative patterns between physical variables and biological communities (Stephenson and Stephenson 1949, Whittaker and Niering 1975). These correlations were then helpful for generating testable hypotheses concerning biotic patterns across these gradients, and aided in developing a more sophisticated understanding, in which the role of biotic interactions as well as physical gradients became widely recognized (Connell 1961, Paine 1966, Dayton 1971). In 1987, Menge and Sutherland synthesized a wide range of environmental and experimental studies to develop the environmental stress model, predicting where competition and predation would be important relative to environmental stress (Menge and Sutherland 1987). The model predicts that under high recruitment, as environmental stress varies from low to high, the most important community-driving variable will shift from predation to competition to abiotic stress (figure 1). Mobile predators are expected to be more susceptible to environmental stress than more basal species, leading to a shift in importance from predation to competition as stress increases at the benign end of the gradient. This model was modified to include positive interactions (Bruno and Bertness 2001, Bruno et al. 2003), defined as species associations that result in a net fitness increase of one or both species through a variety of mechanisms. The model predicts that positive interactions will significantly affect community structure in stressful environments, because of the habitat-ameliorating effects of organisms (Bertness and Callaway 1994), and in benign environments where predators are important, because of associational defenses (Hay 1986, Stachowicz and Hay 1999).

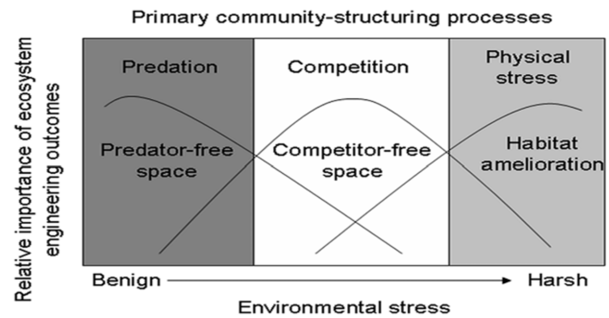

Figure 1. Relative importance of various types of ecosystem engineering across an environmental stress gradient. Shaded boxes indicate dominant community-structuring processes predicted by the Menge-Sutherland environmental stress model. Ecosystem engineers that influence and alleviate the predominancy of these driving factors will be the most important in structuring community processes in varying environments.

The role of ecosystem engineers across stress gradients has been explicitly addressed only rarely (Wright and Jones 2004, Crain and Bertness 2005). However, many species interactions that have previously been investigated actually work through engineering mechanisms, making an analysis of engineering across physical gradients possible. For instance, the positive effects of fiddler crabs on *Spartina alterniflora* productivity (Bertness 1984a) result from burrow formation (a physical modification) that brings oxygen into the soil and reduces the amount of toxic sulfide accumulation, which otherwise stunts plant growth. Experimental evidence such as this, in addition to combining theoretical understanding of species interactions across stress gradients with knowledge of specific engineering mechanisms, enables a unified predictive understanding of where and why ecosystem engineers have large community impacts.

Ecosystem engineers and environmental gradients

Because interactions between ecosystem engineers and ecological communities depend integrally on the modification of physical conditions, we hypothesize that the impact (direction or nature of interactions) and importance (interaction strength and community consequences) of engineers will vary predictably along gradients of physical stress. The engineers with the greatest positive impacts on the community, and therefore with the most importance as conservation targets, will be those that modify the limiting resources or constraining variables in the system (these are broadly defined to include limitations ranging from nutrients to environmental factors or excess predation pressure; figure 1, table 1). For example, in physically harsh habitats, slight alterations in physical parameters could create hospitable habitats for organisms that would otherwise be unable to tolerate limiting physical conditions. On the other hand, in more benign phys-

Table 1. Predicted mechanisms and outcomes of important ecosystem engineers in environments under varying levels of stress.

Environmental stress	Important engineering mechanisms	Engineering impact (community outcome)	Importance of engineer
Extreme	Stress amelioration	Increased population, diversity, abundance, ecosystem functioning	Essential
Intermediate	Competitor refuge	Increased biodiversity, ecosystem functioning	Improves and stabilizes ecosystem function
Benign	Predator refuge	Increased biodiversity, ecosystem functioning	Improves and stabilizes ecosystem function

ical habitats, slight modifications to the physical environment may be irrelevant or may even reduce suitable habitat for other species. In fact, negative outcomes of ecosystem engineers on the local community are predicted to increase in more benign physical environments (Crain and Bertness 2005), as physical modifications in these environments are more likely to interfere with suitable habitat for other species. However, engineers that offer refuge from competitors or predators, while increasing habitat heterogeneity in these relatively benign physical environments, may be key to retaining biodiversity and proper ecosystem functioning. Because the relative importance of community-limiting processes has been explored across environmental stress gradients (Menge and Sutherland 1987, Bruno et al. 2003), we can now apply the concept of ecosystem engineering to identify which organisms are capable of alleviating these limitations and therefore have major community impacts (figure 1).

Physically stressful habitats are defined by the harsh physical conditions present, often limiting the ability for organisms to inhabit the system. In these types of environments, the importance of positive interactions between organisms has been recognized (Bertness and Callaway 1994, Bruno et al. 2003). These positive interactions almost always take place through engineering means, as the presence or activities of one species ameliorate environmental conditions and other organisms benefit from this amelioration (Bertness 1984a, Fogel et al. 2004). For example, in semiarid environments where vegetation is limited by dry soils, nurse plants that shade soils and trap moisture are of key importance in maintaining a vegetative community (Aguiar and Sala 1994). In salt marshes, the dominant plant cover is dependent on engineering by salt-tolerant fugitive species that shade the sediment, reducing evaporation and soil salinities, so that dominant plants can tolerate abiotic conditions (Shumway and Bertness 1994). The most important engineers in physically prohibitive environments are those whose presence or activities alleviate environmental limitations and effectively support an ecosystem and its concomitant functions.

In more benign physical environments, the environment no longer inhibits species occupancy, and instead biotic interactions (competition and predation) are constraining variables that drive community structure (Menge and Sutherland 1987). In these environments, engineers that offer competitor- or predator-free space, or change the availability of limiting competitive resources, become most important in maintaining biodiversity and ecosystem function. For example, in systems characterized by competitive dominance, competitor-free space is critical for biodiversity maintenance and can be provided by engineers that create open space by removing competitive dominants such as pathogens or predators (Burdon and Chilvers 1977, Lubchenco 1978), or by engineers that physically generate disturbance (Flecker and Taylor 2004). Competitive refuge can also be provided by organisms that generate alternative habitats where dominant competitors are absent, as do corals that form reefs where sponges that are competitively excluded from mangroves can persist in the absence of dominant competitors (Wulff 2005). In addition, engineers that alter the availability of limiting resources—for example, nitrogen-fixing bacteria, intertidal mussels that deposit nutrient-rich pseudofeces (Bertness 1984b), or sea grasses that slow water and increase sediment deposition (Thomas et al. 2000)—can change competitive hierarchies and therefore can be highly influential in competitively driven environments.

On the other hand, in ecosystems dominated by predation pressure, engineers that offer predator-free space, through associational defenses or predator refuges, are essential for maintaining species diversity. For example, polychaetes in Argentinian mudflats gain refuge from soft-sediment predators by occupying dead bivalve shells (Gutiérrez et al. 2003), leaf-tying insects provide refuge for larval development of more than 70 other herbivorous insect species (Lill and Marquis 2003), and dense vegetation structure reduces herbivore efficiency in late-successional salt marshes (figure 2; van de Koppel et al. 1996).

As a result of both physical and biotic stress amelioration, ecosystem engineers can expand species distributions across environmental gradients. Classic studies of species distribution across environmental gradients focused on the physical parameters defining a species range, or niche (Grinnell 1917, Elton 1927). Later studies uncovered the role biotic interactions can play in limiting an organism's occurrence because of competitive displacement or consumer pressure, and thus the concept of the realized niche as a subset of the organism's fundamental niche was developed (Gause 1934, Hutchinson 1957, Connell 1961). In contrast, through habitat modification, ecosystem engineers can increase the extent of suitable habitat for a species, expanding occupancy into physically harsh environments and relieving biotic limitation in more benign environments, leading to the paradox wherein the realized niche is apparently larger than the fundamental niche (figure 3; Bruno et al. 2003). In evolutionary theory, the

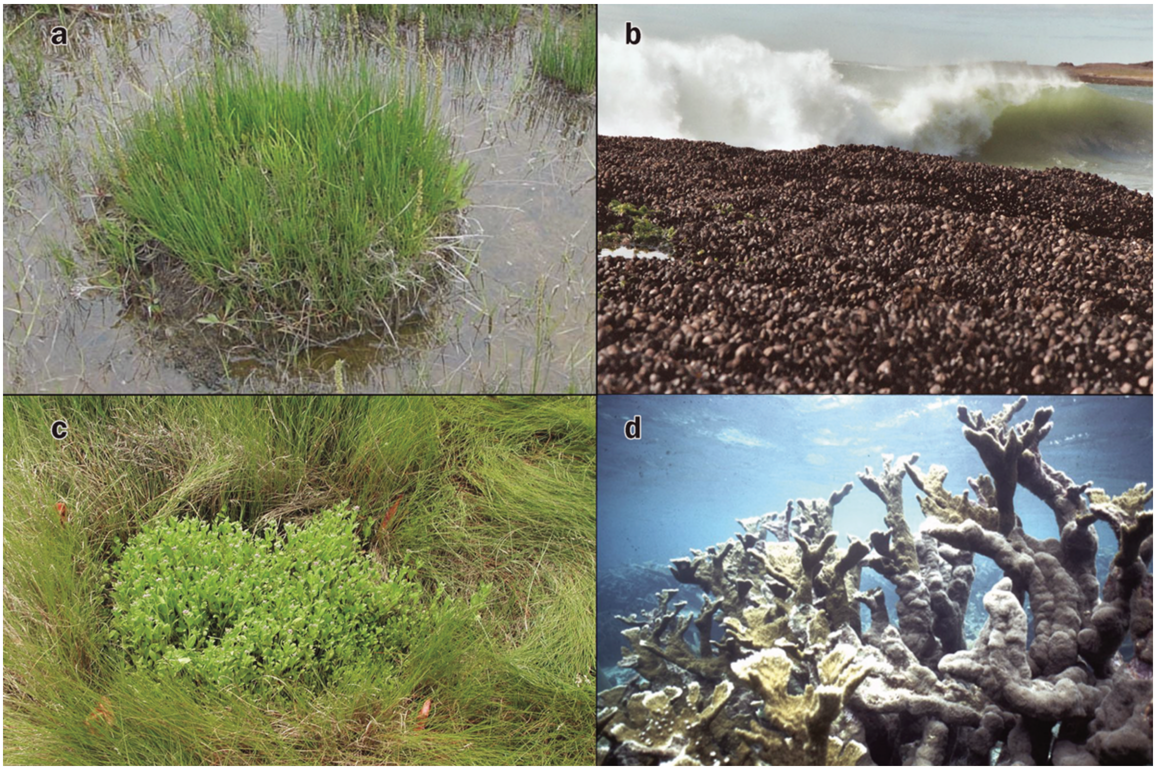

Figure 2. Important ecosystem engineers and the types of resources they provide vary with background environmental variables. In harsh environments, stress-ameliorating engineers enable species to persist that would otherwise be limited by physiological stress: for example, (a) the hummock-forming **Triglochin maritimum** *maintains high plant diversity in waterlogged salt marsh pannes, and (b) mussel beds provide a habitat that permits higher invertebrate diversity on exceedingly dry Patagonian shores. In more benign physical environments, ecosystem engineers maintain species diversity and ecosystem function by alleviating stressors, as when (c) mammals open space in competitively dominant matrix grasses and enable fugitive seedlings to persist, and (d) reef corals create physical structures in which numerous fish species find refuge from predators. Photographs: Caitlin Mullan Crain (a, b, and c) and Mark D. Bertness (d).*

independently derived concept of niche construction could be considered ecosystem engineering in an evolutionary context (Odling-Smee et al. 1996, Laland et al. 2004), emphasizing the role ecosystem engineers play in supplying habitat free of the physical or biotic stresses that typically limit species ranges. As evidenced in the examples below, ecosystem engineers can extend a species range across environmental gradients to physical environments the species would otherwise be unable to inhabit. This expansion of the realized niche due to ecosystem engineering must be incorporated into stress gradient models to improve understanding of species distribution patterns.

Examples: Ecosystem engineers across gradients

While the mechanisms and outcomes of ecosystem engineering across physical gradients have rarely been explicitly and experimentally examined, examples of shifting species interactions through engineering pathways that occur across physical gradients can be found in the scientific literature. The importance of various types of engineers in varying physical environments is apparent at local, regional, and biogeographic scales, as outlined below, and these examples point to the generality of these patterns and their utility to conservation.

Local gradients. Small-scale, steep environmental gradients have been extensively studied because species distribution patterns are relatively easy to visualize and manipulate at these local scales. Particularly popular experimental gradients include intertidal shorelines, and studies in these ecosystems have driven scientific understanding of the shifting importance of community parameters across gradients of physical stress.

Across elevation gradients in rocky shore intertidal settings, physical stress for marine-derived occupants increases at higher intertidal elevations, where increasing exposure to air increases desiccation stress. Lower intertidal elevations are increasingly structured by competitive interactions among species or by heavy predation pressure from mobile subtidal predators that forage in the low intertidal zone at high tide (Connell 1961, Dayton 1971, Menge 1976, Bertness 1989). Experimental manipulations on rocky shores have provided consistent evidence that habitat amelioration by conspecifics

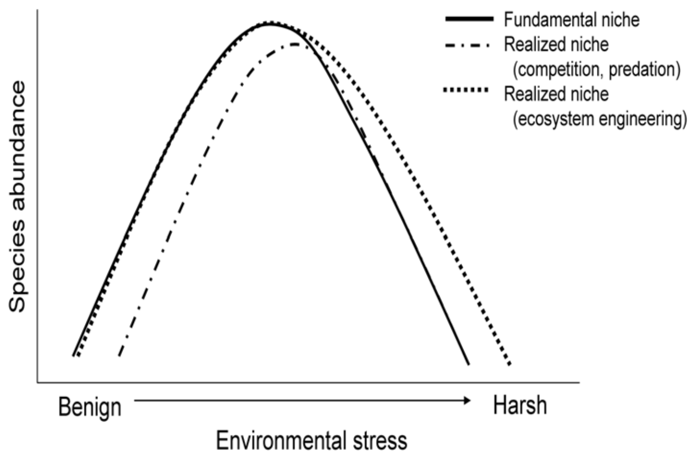

Figure 3. Hypothetical species abundance, indicating the species niche across an environmental stress gradient. The fundamental niche is the space occupied by a species based on physical and biotic predictors alone, in the absence of species interactions, while the realized niche in the traditional sense is expected to be reduced in size as a result of competition and predation on the benign end of a stress gradient. In contrast, the realized niche based on positive outcomes of ecosystem engineering can be enlarged to include species range expansions into areas not predicted on the basis of the physical requirements of the fundamental niche alone.

or by other engineering intertidal species extends the upper species borders, thus expanding the fundamental and realized niche (Bertness and Leonard 1997). For instance, the upper limit of barnacle and mussel cover, and of herbivorous and predatory snail populations, is extended by the habitat-ameliorating effects of the brown algae *Ascophyllum nodosum* (Bertness et al. 1999). *Ascophyllum* shades the substrate and retains moisture during low tide, substantially lowering rock temperatures and alleviating desiccation stress. In the absence of *Ascophyllum,* these highest intertidal elevations become uninhabitable by many marine organisms. At the lower *Ascophyllum* border, the obligate dependence of marine invertebrates on *Ascophyllum* for canopy cover breaks down (Bertness et al. 1999). Many more organisms are capable of tolerating the physical conditions at lower tidal elevations, and here competition for space determines species assemblages. In these habitats, ice disturbance or predation that opens space becomes important for maintaining species diversity. Predation and herbivory also become intense in these habitats, and the community becomes dependent on predation refuges to colonize and establish. Predator or herbivore refuge can be found in cracks or crevices in the rock (Connell 1961, Bertness et al. 2002), or can be established by engineering organisms that create sufficient surface heterogeneity to reduce feeding rates; for example, barnacle cover enables fucoid and mussel development as snail feeding rates are reduced (Menge 1976). Without the benefit of engineers in high-predation environments, secondary succession can be exceedingly slow, as organisms cannot establish (Lubchenco 1980). Thus, across the intertidal stress gradient, engineering of greatest significance switches from habitat amelioration in high intertidal zones to competitor or predator refuge providers in lower intertidal zones.

Landscape-scale gradients. Large, landscape-scale gradients over a few hundred meters to kilometers may have more diffuse spatial organization, but are nonetheless structured by varying species interactions. The interactions of marsh plants across estuarine salinity gradients provide particularly good evidence for the shifting role of engineering species across landscape-scale gradients in physical stress.

In coastal tidal marshes, the degree of salinity and sulfide stress for marsh macrophytes decreases with increasing distance from the coast. Plant community structure has been shown to vary across this large-scale environmental stress gradient (Odum 1988), and recent experimental studies have investigated how engineering plants influence patterns in the distribution of associated plant species (Crain et al. 2004). In transplant studies across estuarine salinity gradients into vegetated and unvegetated patches, transplants and seedlings in salt marshes survive longer when growing within the marsh matrix. This is because the dominant marsh grasses ameliorate physical stresses by reducing evaporation and salinity and increasing soil oxygen (Bertness et al. 1992). By contrast, in lower-salinity, oligohaline marshes, transplants and seedlings grow better in unvegetated patches because of competitive release, easily reaching four times the biomass of vegetated areas (Crain et al. 2004). Herbivorous small mammals open bare space in the dominant vegetative matrix and therefore create competitive refuge for competitively inferior plants, most likely promoting the high species diversity characteristic of low-salinity marshes. Across the estuarine salinity gradient, engineering organisms promote marsh functions through varying means: alleviation of physical stress in the salt marsh and provision of space in the oligohaline marsh.

Also across the estuarine salinity gradient, the mechanisms and outcomes of engineering by hummock-forming marsh plants shift dramatically (Fogel et al. 2004, Crain and Bertness 2005). Hummock formation is a characteristic growth form some wetland plants exhibit in response to waterlogging, in which they create raised root mounds to escape waterlogging stress. The impact of hummock engineering was recently examined experimentally in salt marsh pannes (waterlogged areas of low vegetative cover) where *Triglochin maritimum* creates raised rings, and in tidal freshwater marshes where *Carex stricta* forms large, regularly spaced tussocks separated by unvegetated soil buried in *C. stricta* wrack. In both of these habitats, the spatial distribution of marsh vegetation is limited almost exclusively to the tops of hummocks. Despite this similar spatial patterning, hummock manipulations and transplants of common wetland plants showed that the mechanisms and impacts of the engineer varied dramatically in the two environments. In salt marshes, *T. maritimum* hummocks caused the substrate to be less waterlogged, to have higher oxygen content and less salinity, and thus to promote higher species diversity and abundance than the background marsh. In contrast, species distribution in the tidal freshwater marsh was driven by negative impacts of tussock formation and wrack deposition into the intertussock spaces that prevented plant colonization. Once the tussocks were established, herbivory by small mammals was concentrated in intertussock spaces where mammals could move easily along runways protected by wrack cover, and raised tussocks thus provided an herbivore refuge for plants. In estuarine marshes, engineering by *T. maritimum* ameliorated harsh physical conditions and enabled the development of a salt marsh community on hummocks, whereas engineering by *C. stricta* created unfavorable plant conditions in intertussock spaces while providing a spatial refuge from herbivores on the raised tussocks. *Triglochin maritimum* is essential for marsh population by a number of species in the salt marsh, while *C. stricta* provides herbivore refuge and thus enables maximum species diversity in the fresh marsh.

Biogeographic gradients. Large-scale variation in climate and in associated physical and biotic variables leads to shifts in community properties such as species diversity and intensity of biotic interactions. These patterns have been explored as latitudinal patterns of diversity and predation.

Examples of shifts in engineering impacts across large-scale biogeographic gradients again come from the rocky intertidal. We recently investigated community patterns in one of the most stressful intertidal environments ever described, Patagonia, Argentina (Bertness et al. 2006). Here, the dessication stress from unrelenting winds is intense, with evaporation rates more than an order of magnitude greater than those of temperate North American coasts (Bertness et al. 2006). In this system, intertidal organisms are rarely found outside the protective habitats of two stress-alleviating ecosystem engineers: the mussel *Perumytilus purpuratus* and the coralline algae *Corallina officinalis.* These foundation species (Dayton 1972) are dominant engineers that create a three-dimensional habitat with less than a fifth of the evaporative stress of the outside environment and that harbor a high diversity of interstitial organisms. When bare space is opened artificially in this system, secondary succession is remarkably slow, and the persistent bare areas mean that nearly all ecosystem functions are eliminated with removal of the engineers. In contrast, temperate rocky shorelines in North America are far less extreme. Shorelines in Washington State are also dominated by mussel beds, but when space is created within these beds, ephemeral algae and subordinate competitors opportunistically exploit the limited resource (Paine and Levin 1981). In this system, space-opening predators on the mussel (particularly the keystone species *Pisaster*) are important engineers for maintenance of intertidal species diversity. Across the biogeographic gradient in physical stress, important engineers shift from habitat ameliorators to species that provide competitor-free space.

Ecosystem engineers and conservation

Within a variety of environmental backgrounds, engineers can be identified that have numerous positive impacts on communities and ecosystems. These positive engineering outcomes make ecosystem engineers particularly useful conservation targets, since through managing a single species, we can influence entire communities. As we have indicated, which ecosystem engineers are important will depend on the background environment, the limiting variables, and the ecosystem functions of interest. In more benign environments, ecosystem engineers will tend to increase species coexistence and biodiversity or to retain specific ecosystem functions. In stressful environments, physical modifications can effectively create new habitat and enable the establishment of organisms that would otherwise be unable to persist. In these harsh physical environments, ecosystem engineers are of critical importance, as they are essential to any population of the habitat. Therefore, across environmental stress gradients, engineers can be identified that protect specific ecosystem properties.

In most habitats, regardless of environmental stress, ecosystem engineers provide the template for all other ecosystem processes, making these engineers essential to conservation. Within any environmental regime, most ecosystems are hierarchically organized, with ecosystem engineers generating the habitat structure. These engineers can also be considered foundation species—dominant, sessile organisms that transform two-dimensional to three-dimensional structure and provide habitat for many associated organisms (*sensu* Dayton 1972). The engineers shelter community members from physical stress or consumer pressure, depending on the background environment. All other physical and biological processes commonly investigated, such as competition, predation, and stress tolerance, lead to spatial and temporal distribution and abundance patterns across the engineered landscape (Bruno et al. 2003). This engineering template has received relatively less ecological attention than the processes generating spatial and temporal patterns of organisms within engineered landscapes. The ubiquity of essential engineering features must be recognized, particularly since the organisms in many communities, especially those in physically and biologically stressful habitats, could not live in their native communities without the habitat provided by ecosystem engineers.

The critical role of ecosystem engineers in the structure and function of natural communities has enormous implications for conservation biology. While traditional conservation efforts have focused on charismatic species, the species that are the most critical in retaining community and ecosystem integrity and function are the ecosystem engineers that provide stress amelioration and associational defenses, and these should be the primary target of conservation efforts. Engineers and their biotic feedbacks set the stage for communities and ecosystems to perform the services, be they biodiversity maintenance or specific ecosystem functions, that humans depend on. The value of conserving ecosystem engineers that serve as foundation species has been advocated elsewhere (Bruno et al. 2003), but protecting other significant engineers that control resource flow or habitat heterogeneity in any environmental setting can aid in achieving a variety of conservation goals, including the protection of species, habitat, or ecosystem functions. By developing a predictive understanding of which engineers are important in which types of environments, we can better recognize the essential engineers that can serve as important conservation targets.

Conclusions

To increase the value of the ecosystem engineering concept in ecology and conservation biology, ecologists need to examine when, where, and how ecosystem engineers play critical roles in ecosystem structure and function. Here we have argued that most natural communities are hierarchically structured, with habitat-modifying ecosystem engineers providing the physical template of communities, and that the habitat-ameliorating function of engineers shifts from providing refuge from consumers or competitors in physically benign habitats to providing refuge from limiting physical conditions in physically stressful habitats. Over the next century, the single largest challenge facing ecology will be whether it has developed into a sufficiently predictive science to be a valuable tool in conserving and restoring damaged ecosystems at local, regional, and global spatial scales. Ecosystem engineering can develop into a more rigorous, predictive concept in order to help meet this challenge.

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