



SYMPOSIUM

Functional Groups of Ecosystem Engineers: A Proposed Classification with Comments on Current Issues

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Synopsis Ecologists have long known that certain organisms fundamentally modify, create, or define habitats by altering the habitat’s physical properties. In the past 15 years, these processes have been formally defined as “ecosystem engineering”, reflecting a growing consensus that environmental structuring by organisms represents a fundamental class of ecological interactions occurring in most, if not all, ecosystems. Yet, the precise definition and scope of ecosystem engineering remains debated, as one should expect given the complexity, enormity, and variability of ecological systems. Here I briefly comment on a few specific current points of contention in the ecosystem engineering concept. I then suggest that ecosystem engineering can be profitably subdivided into four narrower functional categories reflecting four broad mechanisms by which ecosystem engineering occurs: structural engineers, bioturbators, chemical engineers, and light engineers. Finally, I suggest some conceptual model frameworks that could apply broadly within these functional groups.

The ecosystem engineering concept

Scientists have long known that some organisms fundamentally structure ecosystems, just as trees create forests, grasses create prairies, and oysters create oyster reefs (reviewed in Buchman et al. 2007). Long before the advent of modern ecology, Darwin (1842) knew that atolls were formed by coral colonies, Darwin (1881) and Shaler (1892) knew that soils were structured and created by earthworms and other invertebrates, and Morgan (1868) knew that stream geomorphology was dramatically altered by beaver dams. However, the idea that physical modification by organisms is a widespread, fundamental class of ecological interactions did not coalesce until 1994, when Jones, Lawton, and Shachak first proposed the ecosystem engineering concept. In so doing, they initiated a period of progress and controversy, and of thinking seriously about the myriad physical ways in which organisms influence habitats.

Jones et al. (1994) 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 authors explicitly excluded trophic interactions in the form of provision or consumption of tissue. From this foundational paper, the ecosystem engineering concept has blossomed—it is now cited in well over 100 publication per year, and has eclipsed citations for the related keystone species concept since 2004 (based on citation frequencies in Thomson’s Science Citation Index). Clearly, the concept is gaining broad acceptance, and many scientists are at least invoking it as a context for their work. Unsurprisingly, however, ecologists continue to differ on the spirit, definition, and utility of ecosystem engineering. Here, I comment on some current points of contention and offer a new way of

categorizing engineers based on the mechanisms by which they exert influence on ecosystems.

Current issues in ecosystem engineering

Several early objections to ecosystem engineering—that it is an unhelpful buzzword (Power 1997a, 1997b), a restatement of the keystone species concept (Wright and Jones 2006), and so broad as to be useless (Reichman and Seabloom 2002a, 2002b) have been thoroughly addressed elsewhere (Jones et al. 1997a, 1997b; Wright and Jones 2006; Jones and Gutiérrez 2007). Two issues, however, continuously recur in the literature and in my own interactions with colleagues, meriting some brief comments here.

Nearly everyone agrees that engineering is only worthwhile if it can move beyond “just-so” stories to expand our understanding of ecological processes. Not everyone is convinced that this is happening. As one participant pointed out during this symposium, one could delete all occurrences of the term “ecosystem engineering” from many papers without losing any information. The issue of utility has been discussed extensively elsewhere (Wright and Jones 2006), but for the skeptical reader two points bear repeating: (1) ecosystem engineering allows us to treat organisms’ effects on the environment as a coherent suite of interactions, rather than a collection of unrelated case studies. This promotes integrative and comparative studies, which is unarguably a step forward. (2) The ongoing development of engineering models is evidence that the concept is indeed advancing our theoretical understanding of ecological systems, even if explicit tests of models are not yet widespread (Cuddington et al. 2009; Cuddington and Hastings 2007; Wilson 2007b).

A more substantial point of contention is whether ecosystem engineering should have a process- or outcome-based definition. So far, most definitions have focused on the physical processes by which organisms affect the environment, rather than on ecosystem-level effects per se [this is a major point of distinction between engineers and keystone species; see Wright and Jones (2006) and Jones and Gutiérrez (2007)]. Some have argued that ignoring outcomes will render the concept applicable to any organism on earth, rendering it meaningless (Reichman and Seabloom 2002a, 2002b; Wilson 2007a). Wilson (2007a) goes even further, breaking with previous definitions to suggest that engineering be limited to cases in which it can be shown to feed back positively on the organism’s per-capita growth rate.

The reply to such arguments has been three-fold: (1) a process-based definition is preferable to an outcome-based definition because it eliminates the burden of demonstrating ecological significance (which has been a sticking point for the keystone species concept) (Davic 2003; Mills et al. 1993; Wright and Jones 2006; Jones and Gutiérrez 2007); (2) most organisms probably can be considered ecosystem engineers to some degree, and this is a strength of the concept—it applies broadly to many organisms in many habitats; and (3) ecologists are good at distinguishing between the interesting and the trivial, so a process-based definition that can technically be applied to some trivial situations is simply not problematic (Jones and Gutiérrez 2007).

The argument, however, is as much about issues of scale as about process versus outcome—is ecosystem engineering *only* interesting if its effects are widespread, or *can it be interesting* at a broad range of spatial scales, from lone organisms to whole ecosystems? I agree with those who argue that a process-based, scale-independent definition is desirable. In such a framework, individual-based models exploring engineering feed-backs on fitness, individual behavior, or population dynamics of a single species can coexist with models exploring engineering effects on multiple populations, energy transfer, or other components of ecosystem function; this breadth is a major strength of the concept. At the same time, it would be myopic to focus on process to the exclusion of outcomes. The engineering concept would collapse to pure niche construction (*sensu* Odling-Smee 2003) if widespread effects never occurred, and most definitions do make some reference to outcomes (e.g., “modulat[ing] the availability of resources to other organisms”) (Jones et al. 1997b). Consideration of outcomes can be particularly helpful in grey areas when deciding whether or not the engineering concept applies.

Gray areas: to what extent should assimilation/dissimilation be excluded from engineering?

Ecosystem engineering was originally developed as a counterpoint to traditional flux-based models, to account for physically mediated interactions between organism and environment that were ignored by other theoretical frameworks. While the concept has always excluded trophic interactions (the direct consumption or provision of tissue), some recent work has gone further to explicitly exclude all endogenous assimilatory and dissimilatory processes (Jones et al. 2006; Byers 2007; Jones and Gutiérrez 2007). This proscription appears to conflict with the

many publications that cite assimilatory and dissimilatory processes as ecosystem engineering, such as sediment-binding mucous exuded by microorganisms or oxygen consumption by plants (Jones et al. 1994, 1997a, 1997b; Caraco et al. 2006; Volkenborn et al. 2007). There appears to be particular confusion in regard to organism-driven chemical changes in environments such as soils and bodies of water. Nearly everyone agrees that many types of chemical changes rightly constitute ecosystem engineering, yet some authors have argued that chemical changes specifically arising from physiological processes of assimilation or dissimilation are entirely distinct from ecosystem engineering (Jones et al. 2006; Byers 2007; Jones and Gutiérrez 2007). These authors have contributed careful, cogent arguments to the issue, but additional discussion is still needed to resolve apparent conflicts and reach a robust consensus.

The exclusion of trophic interactions unarguably makes sense, as trophic interactions are already described by a vast body of theory. By extension, it may seem logical to exclude all assimilatory and dissimilatory processes. However, wholly excluding assimilation and dissimilation might force us to exclude processes that have been considered engineering in the past. For example, excluding defecation would exclude many effects of earthworms on soils—although earthworms undeniably have mechanical effects, their defecation plays a major role in consolidating soils and creating topsoil (Lavelle 2002). By the same token, lugworms are major bioturbators of marine sediments: they defecate on the surface after feeding on subsurface sediments, thus mixing sediments and substantially altering early diagenesis. Their defecation also buries smaller infauna, alters geochemical cues at the surface, and influences larval settlement (Marinelli and Woodin 2002). There is widespread agreement that such processes constitute ecosystem engineering (Jones et al. 1994; Gutiérrez and Jones 2006; Berke et al. 2010), yet they clearly also involve assimilation and dissimilation.

Excluding all assimilation and dissimilation would also force us to exclude physiologically derived chemical gradients, such as oxygen gradients arising from the respiration of aquatic plants and microbes, or nutrient and hydrological gradients arising near plant roots. For example, aquatic vegetation creates strong and predictable oxygen gradients, and Caraco et al. (2006) have argued strongly that such structuring should be considered ecosystem engineering. However, these gradients are the direct result of oxygen consumption in respiration and release from photosynthesis.

By the same token, excluding physiologically derived chemical gradients would force us to exclude dead zones, in which bacterial decomposition of phytoplankton blooms creates an oxygen-depleted region of the water column that persists for days to months or even years in a single location. Many marine ecologists would agree that dead zones constitute physical structuring of the habitat by organisms, and thus rightly belong to ecosystem engineering. This is an example in which our understanding of ecosystem-level effects can inform whether or not a process can profitably be included in engineering. Few would argue that a single decomposing planktoner is an ecosystem engineer. However, a spatially extensive population of microbes acting on dying plankton to create a spatially and temporally persistent dead zone “feels” like ecosystem engineering in the original sense—the direct or indirect modification of abiotic resources by organisms (Jones et al. 1994)—and engineering models linking populations of plankton to, for example, populations of fish and crustaceans via their effects on oxygen saturation might indeed be useful.

With regard to hydrological gradients near plant roots, Gutiérrez and Jones (2006) have argued that hydrological gradients can be included in ecosystem engineering, provided that plants take water in passively. In their view, xylem is dead tissue through which water moves due to physical forces not requiring energy, rendering the uptake “independent or irrespective” of the plant’s assimilation of water. Thus, the logic seems to be that chemical engineering can arise from passive transport through physical structures even if it leads to assimilation, but not through physiological processes requiring ATP which lead to assimilation. However, water transport is fundamentally a process of assimilation whether it occurs actively or passively, and a plant lacking xylem would certainly perish from dehydration. If the crux of the matter is active versus passive transport, then we would have to reconsider burrow irrigation and, for that matter, beaver dams, which are undeniably the result of active behavioral processes. Why should passivity be required at the cellular level but not at the organismal level? It is not clear that distinguishing active versus passive processes will be useful to ecosystem engineering theory. Both active and passive assimilation/dissimilation can lead to chemical changes in the environment; thus, any models linking engineer populations to chemical gradients and thence to other organisms should apply to a broad range of chemical gradients, not only passively induced ones, and they should enhance our

understanding of ecosystem function beyond what flux-based models alone can provide.

Defining ecosystem engineering as “independent or irrespective” of assimilation and dissimulation can lead to contradictory interpretations. Assimilation and dissimulation undeniably play a role in constructing the physical matrix of an ecosystem. If the benchmark is utility—can engineering deepen our understanding?—then surely engineering can enrich our understanding of many such processes. I would advocate for a return to the original definition of ecosystem engineering, placing emphasis on modulating the availability of resources (as in Jones et al. 1994). When assimilatory and dissimilatory processes alter the availability of non-tissue resources to other organisms, I suggest that they should be included under the umbrella of ecosystem engineering.

A functional classification of ecosystem engineers

The true utility of ecosystem engineering will be the applicability of its theoretical contributions, which are so far quite promising. Models for generalized engineers have explored a variety of issues, such as population dynamics when environmental modification is required for survival, and community interactions when modification affects interaction coefficients. (Cuddington and Hastings 2007; Wilson 2007b; Cuddington et al. 2009). A challenge to modeling, however, is that ecosystem engineering encompasses enormously diverse systems, spanning all habitats and all major phyla of the world. Subdividing the concept is clearly necessary, and several categorization schemes for ecosystem engineers already exist. Jones et al. (1994) originally distinguished between autogenic engineers, which directly create habitat (e.g., trees) and allogenic engineers, which engineer through their effects on habitat that they do not directly occupy (e.g., beavers). More recently, Cuddington et al. (2009) differentiated between obligate and non-obligate engineers, an important distinction for population dynamic models and evolutionary models of engineering. While both of these schemas are reasonable and are useful for many questions, it is striking that no existing classification scheme attempts to break down the enormous functional diversity of ecosystem engineers—that is, the diverse mechanisms and pathways through which engineers influence ecosystems. Such a classification scheme would advance the field by opening the door for new classes of models which explicitly incorporate the environmental effects of

engineers and their subsequent effects on other organisms.

I propose that ecosystem engineers naturally fall into four functional classes, each of which can be associated with its own suite of models (Table 1, Figure 1). These classes are not mutually exclusive, given that many engineers affect ecosystems through multiple pathways simultaneously, as discussed below. These proposed categories are largely independent of previous categorization schemes—most of them encompasses autogenic and allogenic engineers (which are themselves not mutually exclusive), as well as obligate and non-obligate engineers. This is not meant to supersede or replace previous classifications, and the examples of engineering that I describe below are generally not new. I merely suggest a new way of organizing our knowledge by accounting for functional similarities between broad classes of engineers and pointing out potentially useful new ways to model them. This schema has grown from my perspective as a marine ecologist, but should largely apply to terrestrial systems as well.

Structural engineers

Structural engineers are perhaps the most obvious class—these are organisms that create or modify structural elements of the habitat. Reef-builders, tube-builders, macroalgae, seagrasses, and mangroves are all marine structural engineers. Terrestrial structural engineers are equally obvious—most plants, mound-building insects, and beavers, for example (note that these examples include both autogenic and allogenic engineers). Structures in marine habitats play myriad well-documented roles, providing living space for other organisms and refugia from predation, increasing heterogeneity, altering hydrodynamic regimes, and altering deposition of sediments and larvae (Chamberlain and Graus 1975; Eckman et al. 1981; Woodin 1981; Eckman 1983; Twilley et al. 1996; Moberg and Folke 1999; Schwindt and Iribarne 2000; Dubois et al. 2002; Burnaford 2004; Boström et al. 2006; Crain and Bertness 2006). Structural engineers generally enhance diversity and richness (although not necessarily of native species, in the case of non-native structural engineers; see Heiman 2005 and current issue), although any blanket statement will likely be false in some contexts. Such effects have demonstrably occurred over large swaths of geologic time, despite extensive evolutionary turnover in the species responsible (Kidwell and Jablonski 1983; Marenco and Bottjer 2007; Erwin 2008; Jablonski 2008). Because structural engineers operate through similar

Table 1 Summary of proposed functional classes of ecosystem engineer

Class of engineer	Ecosystem effects	Marine and aquatic examples	Terrestrial examples
Structural Engineers	Create living space	Corals	Most plants
	Reduce disturbance	Bivalves	Mound-building insects
	Alter hydrodynamics	Tube-building invertebrates	Beavers
	Alter sedimentation	Seagrasses and aquatic Plants	
	Alter diversity / richness (usually enhance)	Mangroves Macroalgae	
Bioturbators	Enhance disturbance	Burrowing infauna (polychaetes, bivalves, crustaceans, echinoderms, nemertean, fish)	Burrowing vertebrates (e.g., fossorial rodents, mammals, lizards)
	Mix Sediment		
	Alter biogeochemistry		
Light engineers	Alter light intensity, penetration, scatter	Zooplankton Phytoplankton	Overlaps with structural engineers; anything casting shade, most plants
	Alter turbidity	Filterers (e.g., bivalves, ascidians)	
Chemical engineers	Create biogeochemical gradients (physically or physiologically)	Microbes	Most plants
		Seagrasses and aquatic plants	Mycorrhizal fungi
		Macroalgae	Nutrient vectors, e.g., seabirds and bears
		Many burrowers, e.g., lugworms	

Examples of ecosystem-level effects, marine organisms, and terrestrial organisms are not exhaustive.

processes and have similar types of effects, models pertaining to one structural engineer will likely be relevant for many others (Figure 1).

Bioturbators

Burrowers were among the first ecosystem engineers to be recognized, more than a century before the term was coined (Darwin 1881). The important roles that burrowing and excavating organisms (primarily allogenic engineers) play in the geophysical environment and in community dynamics are well established. Burrowing infauna such as polychaetes, crustaceans, bivalves, and echinoderms are important agents of sediment transport and porewater flux (Aller et al. 2001; Wetthey et al. 2008). Excavating organisms such as crabs, bottom-feeding fish, rays, walrus, and Gray whales similarly disturb and transport sediment, creating biological and physical changes that persist for periods of days to months (Reidenauer and Thistle 1981; VanBlaricom 1982; Oliver and Slattery 1985; Klaus et al. 1990). Whereas structural engineers stabilize sediment, reduce disturbance and typically enhance local diversity, bioturbators mix and transport sediments, increase disturbance, and typically reduce local diversity (reviewed Volkenborn and Reise 2006, 2007; DeWitt 2009; Berke et al. 2010), but effects are variable and context-dependent (VanBlaricom 1982; Volkenborn and Reise 2007). Partitioning

bioturbators into burrowing and excavating subclasses might prove useful—e.g., lugworms versus stingrays—particularly if models for one are not applicable to the other, but as a first approximation it seems reasonable to suppose that excavating and burrowing models will at least be more relevant to each other than to any other type of engineer.

Terrestrial analogues to marine bioturbators are readily apparent: burrowing soil invertebrates such as earthworms, ants and termites (Lavelle et al. 2007; Straube et al. 2009), burrowing vertebrates such as prairie dogs, gophers, gopher tortoises, some lizards, and birds (Reichman and Seabloom 2002b; Van Nimwegen et al. 2008), and a plethora of vertebrates that excavate shallow holes for foraging or nesting, such as porcupines, skunks, canids, and bears (Gutterman et al. 1990; Tardiff and Stanford 1998).

Chemical engineers

Many organisms alter the chemical matrix of their environment through physical or physiological activities, and many authors have suggested that ecosystem engineering encompasses such processes (Jones et al. 1994, 2006; Caraco et al. 2006; Wright and Jones 2006; Volkenborn et al. 2007). Biogenic chemical gradients are common in aquatic, marine, and terrestrial habitats: respiration by corals and photosynthesis and respiration by zooxanthellae induce

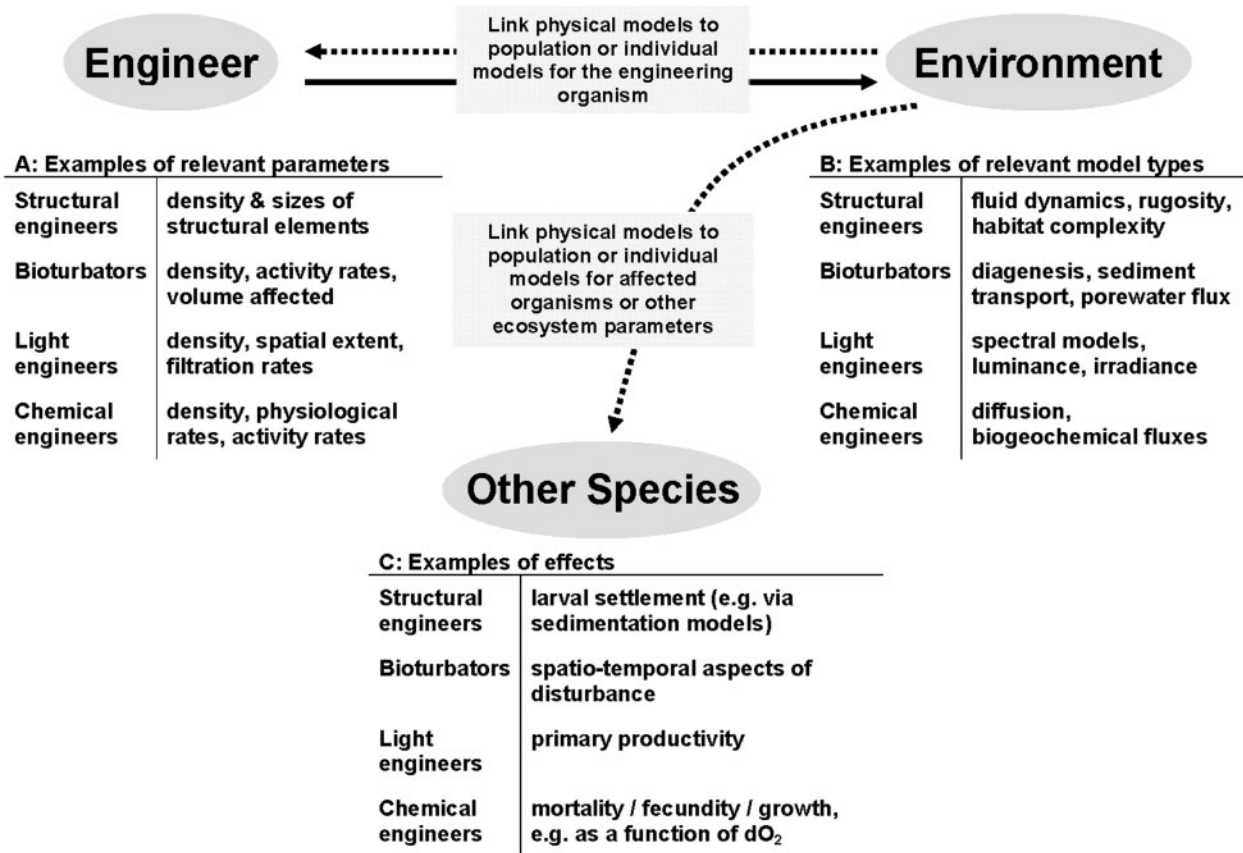


Fig. 1 A conceptual roadmap for ecosystem engineering models based on linking engineer populations to other species via their physical effects. Physical models would likely apply broadly within a class of engineer, but would not apply across classes. Examples are given of (A) population-level parameters relevant to physical models; (B) physical models applicable to each engineering class; and (C) potential effects of physical processes on populations affected by different classes of ecosystem engineers. Historically, ecosystem engineering models have included feedbacks from the environment to the engineer and/or to other systems, but not necessarily to both. Thus, these effects are shown with dotted lines to emphasize that models need not incorporate all three linkages.

microgradients in oxygen near reefs (Shashar et al. 1993), microbial decomposition of phytoplankton blooms creates oxygen dead zones that may persist over large areas for scales of months to years (Rabalais et al. 2002), and sea grasses create nutrient gradients in sediments just as terrestrial plants create nutrient gradients in soils. These examples reflect physiological mechanisms (and clearly include assimilation/dissimilation), but chemical gradients can be induced through physical mechanisms as well. For example, burrowing marine infauna pump oxygen-rich water through their burrows, extending the oxygenated layer deep into the sediment and increasing the local redox potential (Aller et al. 2001). Physical processes driving chemical gradients are clearly included in ecosystem engineering—indeed, irrigation of burrows was one of Jones et al.’s (1994) first examples of engineering—and I have argued that physiological mechanisms should also be included.

Many chemical engineers are also structural engineers or bioturbators. The most obvious terrestrial examples of chemical engineers are plants, which in addition to being structural engineers drive gradients in soil nutrients and moisture (Ehrensfield 2003). Mycorrhizal fungi also alter soil chemistry (Marschner and Dell 1994), as do burrowing animals that tend fungal colonies in underground chambers. Nutrient vectors such as seabirds and bears also arguably act as chemical engineers by controlling the availability of marine-based nutrients in terrestrial soils, with consequences for terrestrial plant communities (Anderson and Polis 1999; Hilderbrand et al. 1999; Maron et al. 2006).

Light engineers

Light penetration is widely recognized as an important physical property of habitats in both marine and terrestrial systems. Many ecosystem engineers modulate light penetration—for example, Jones et al.

(1997b) refer to shaded habitat as one result of allo-genic engineering by trees, and Jones et al. (1994) describe phytoplankton and micro-algae that scatter and absorb light as ecosystem engineers. In marine systems, organisms such as phytoplankton, zooplankton, and filter feeders alter the turbidity, intensity, scattering, and penetration of light, thereby controlling the depth at which photosynthesis can occur, and in turn limiting the primary productivity of benthic and pelagic habitats and influencing predation for many organisms (Abrahams and Kattenfeld 1997; Hartman and Abrahams 2000). In modifying light, plankton and filter feeders are analogous to those terrestrial organisms that cast shade, most if not all of which are structural engineers. In terrestrial systems, then, light engineering entirely overlaps with structural engineering, while in marine systems light is largely controlled by organisms that do not create structure (or, in the case of filtering bivalves, the structure is unrelated to modification of light). Thus, a distinct category for light engineering is clearly necessary in marine systems, although it is arguably not necessary in terrestrial systems, if all light modulation in terrestrial systems can be treated within the context of structural engineering.

The light engineering category again raises the assimilation/dissimilation issue. If we exclude assimilation, then we must accept Byers' (2007) argument that bivalves are ecosystem engineers when they filter sediments, but not when they filter phytoplankton, because filtering phytoplankton is a trophic interaction. Such splitting of hairs seems unhelpful—first, models for bivalves' clearance of sediment are nearly identical to models for bivalves' clearance of phytoplankton, so no purpose can be served by including one case but not the other. Second, some bivalves may well feed on the microbial coatings of particles of sediment that they filter—should that prevent them from being considered ecosystem engineers? Surely not. In both cases, bivalves' activities alter the penetration of light in the water column, modulating its availability to other organisms. This satisfies the classic definition of ecosystem engineering, as Jones et al. (1994) recognized. This again emphasizes my point that we should be careful before blanket exclusion of all assimilation and dissimilation processes from the engineering concept.

Discussion

I have chosen to focus on process-based classifications rather than on outcome-based classifications for several reasons: (1) I agree that the ecosystem

engineering concept is epistemologically process-oriented; (2) the ecosystem engineers I know of seem to fall naturally into these categories; and (3) outcome categories would be so numerous as to be cumbersome. For example, infaunal polychaetes can affect flow, particle deposition, habitat heterogeneity, local abundance, local richness, local community composition, frequency of disturbance, mixing of sediments, and the depth of oxygen penetration (Berke et al. 2010). We have quickly framed at least nine different categories without even broaching the fact that infaunal polychaetes encompass structure-builders and bioturbators, which operate through entirely different mechanisms. Outcome-based categories would thus be prone to infinite expansion as the myriad ways in which engineers affect the environment become better known. Process-based categories are altogether more manageable, and have the added advantage that organisms within a category are likely to have broadly similar ecosystem-level effects, allowing for models that are generally applicable to entire engineering categories.

How might these categories aid efforts in modeling? One approach might be to couple individual or population-level models for the engineer to physical models for the processes it influences, and then link the physical model to populations of other species (Fig. 1). For example, marine structural engineers influence fluid dynamics. Fluid dynamic models can use information about the size and density of emergent structures to make predictions about a variety of physical parameters, including the sedimentation rates of particles and larvae (Eckman 1990; Gross et al. 1992; Eckman et al. 1994; Vogel 1994). Fluid dynamic models could thus provide a bridge between populations of a structural engineer and recruitment of other species. Such a framework should be broadly applicable within the structural engineering category.

As another example, consider oxygen gradients. Physiological models for respiration and photosynthesis can predict consumption and absorption of oxygen. Physical diffusion models using diffusion kernels can predict the movement of chemicals in space and time and population models, e.g., for fisheries, could predict mortality risk as a function of oxygen saturation. Chemical-diffusion models could thus provide a bridge from a population of submerged aquatic plants to associated fishery species and, with modification, that model framework should be broadly applicable within the chemical engineering category.

Figure 1 provides an overview of this conceptual approach, and provides some examples of the kinds of population parameters, physical models, and ecosystem effects that might be feasible for each class of engineer. Clearly, these heuristic examples are meant only to give a sense of the general types of models that might emerge, and are far from exhaustive.

Issues for further consideration

Pelagic mixers

Current work is revealing the importance of pelagic mixing by organisms swimming through the water column, generating turbulence, and transporting packets of fluid (Kunze et al. 2006; Katija and Dabiri 2009; Breitbart et al. in this issue). Such activities may be conceptually analogous to bioturbation, but in a fluid environment rather than in a sediment environment. However, sediment models are very different from fluid dynamic models, so a separate category may prove necessary.

Thermal modifiers

It is difficult to separate light from temperature, particularly in terrestrial and inter-tidal habitats. Thermal changes are well-known consequences of shading by plants and macroalgae. As Dianna Padilla discusses in this issue, invasive oysters change the color of the substratum from dark to light and thereby altering the thermal environment. Heat transfer in soils can also be affected by organisms, with biogeochemical consequences (Gutiérrez and Jones 2006). If the mechanisms of thermal modification differ across systems, then different models will likely be needed for each class of engineer, in which case thermal change would best be treated within the proposed classes. A separate category for thermal engineering would only be helpful if a single type of thermal model can be applied across all engineering classes.

Threshold effects and context dependency

The engineering literature has long acknowledged that ecosystem effects are likely to be context-dependent and/or density-dependent (Flecker et al. 1999; Jones and Gutiérrez 2007, Berke 2010). Recent theoretical work has explored density dependence as it relates to the population dynamics of ecosystem engineers (Cuddington et al. 2009), but relatively few studies have experimentally evaluated the density threshold needed to affect ecosystem function (but see Woodin 1978; Flecker et al. 1999), or the ecological contexts that cause an engineer to switch from having weak effects to having

strong ones, or vice versa. The topic remains ripe for further theoretical and experimental explorations.

The big picture

The world is changing. In oceans with warmer and more variable temperatures, lower salinity, lower pH, larger and more frequent dead zones, and altered food webs, what can we learn from ecosystem engineering? Ecosystem engineers are often most appreciated when things go wrong—when they invade non-native habitat (e.g., reef-building polychaetes in estuaries), or when their absence leads to collapse of an ecosystem (e.g., oysters in the Chesapeake Bay). As climatic change proceeds, range shifts and local extinctions can be expected to intensify. Ideally, the ecosystem engineering concept would help quantify the ecosystem services that are most critical and most in need of conservation as these changes progress (see also Byers et al. 2006). If ecosystem engineering models yield insight into questions such as “How will this system function differently if X populations crash?” or “What would this habitat look like if Y invades?”, then we will be farther along the path to making smart decisions about conservation.

The promise of ecosystem engineering is quintessentially integrative. Until now, integration has been primarily horizontal, across species, and habitats. Ecosystem engineering, however, also provides a framework for integrating across ecological and evolutionary timescales, e.g., by comparing clades of engineers over geologic time, or drawing comparisons between neogene and paleogene assemblages. At evolutionary scales, of course, ecosystem engineering is intimately related to niche construction and the extended phenotype concepts, both topics that have commanded considerable theoretical attention in their own right (Dawkins and Dennett 1999; Odling-Smee 2003, Laland and Sterelny 2006), and explicit comparisons between the concepts will undoubtedly continue to prove fruitful [for an extended discussion of niche construction and ecosystem engineering, see Pearce (2010)]. Finally, ecosystem engineering has untapped potential for integrating from genes to ecosystems—if an organism is the unification of complex systems from genes to cells, tissues, and the physiology thereof, then an ecosystem is the unification of complex systems from populations to environmental physics and climate. Ultimately, the success of the concept of ecosystem engineering will be measured not only in the models it contributes, but in the links it helps forge between diverse corners of biology.

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