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POSITIVE AND NEGATIVE EFFECTS OF ORGANISMS AS PHYSICAL ECOSYSTEM ENGINEERS

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Abstract. Physical ecosystem engineers are organisms that directly or indirectly control the availability of resources to other organisms by causing physical state changes in biotic or abiotic materials. Physical ecosystem engineering by organisms is the physical modification, maintenance, or creation of habitats. Ecological effects of engineers on many other species occur in virtually all ecosystems because the physical state changes directly create nonfood resources such as living space, directly control abiotic resources, and indirectly modulate abiotic forces that, in turn, affect resource use by other organisms. Trophic interactions and resource competition do not constitute engineering. Engineering can have significant or trivial effects on other species, may involve the physical structure of an organism (like a tree) or structures made by an organism (like a beaver dam), and can, but does not invariably, have feedback effects on the engineer. We argue that engineering has both negative and positive effects on species richness and abundances at small scales, but the net effects are probably positive at larger scales encompassing engineered and nonengineered environments in ecological and evolutionary space and time. Models of the population dynamics of engineers suggest that the engineer/habitat equilibrium is often, but not always, locally stable and may show long-term cycles, with potential ramifications for community and ecosystem stability. As yet, data adequate to parameterize such a model do not exist for any engineer species. Because engineers control flows of energy and materials but do not have to participate in these flows, energy, mass, and stoichiometry do not appear to be useful in predicting which engineers will have big effects. Empirical observations suggest some potential generalizations about which species will be important engineers in which ecosystems. We point out some of the obvious, and not so obvious, ways in which engineering and trophic relations interact, and we call for greater research on physical ecosystem engineers, their impacts, and their interface with trophic relations.

Key words: *cascades, coupled trophic and engineering; community stability; ecosystem engineers; ecosystem function; feedbacks; habitat formation and destruction; population dynamics; positive and negative effects; species diversity.*

WHAT IS THE ECOLOGICAL ROLE OF A TREE IN A FOREST?

What does a tree do in a forest? Of course the living and dead tissues are eaten by many animals and microorganisms, and the tree competes with other plants for light, water, and nutrients. But a tree does much more than provide food and directly compete for resources. The branch, bark, root, and living and dead leaf surfaces make shelter, resting locations, and living space. Small ponds full of organisms form where throughfall gets channelled into crotches (Kitching 1971, 1983), and the soil cavities that form as roots grow provide animals with places to live and cache food (Foster 1988, Vander Wall 1990). The leaves and

branches cast shade, reduce the impact of rain and wind, moderate temperature extremes, and increase humidity for organisms in the understory and the soil (Holling 1992, Callaway and Walker 1997). Root growth aerates the soil, alters its texture, and affects the infiltration rate of water (Bouma and Anderson 1973, Tisdall and Oades 1982, Smiles 1988, Juma 1993). Dead leaves fall to the forest floor altering rain-drop impact, drainage, and heat and gas exchange in the soil habitat, and make barriers or protection for seeds, seedlings, animals, and microbes (Facelli and Pickett 1991, Callaway and Walker 1997). The trunk, branches, and leaves can fall into forest streams creating debris dams and ponds for species to live in (Likens and Bilby 1982, Hedin et al. 1988). The roots can bind around rocks, stabilizing the substrate and ameliorating hurricane impacts on other species (Basnet et al. 1992). If the tree falls, the downed trunk, branches,

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and resulting tip-up soil pit and mound create habitats for numerous organisms (Collins and Pickett 1982, Peterson and Pickett 1990, Peterson et al. 1990).

WHAT SHOULD WE CALL THESE EFFECTS?

It is probable that more species are affected by these things that a tree does than directly use the tree for food or compete with it for light, water, and nutrient resources. And yet, these diverse ecological effects are not trophic. Nor is the tree in the forest unique. Most plants have similar effects, and many animals and microorganisms cause ecologically significant physical changes in their environments (Jones et al. 1994). A woodpecker or rot fungus may make holes in the tree that are then used by other species (Kitching 1971, Bradshaw and Holzapfel 1985, 1992, Daily et al. 1993), and a beaver may come along and cut down the tree, making a dam and pond in which hundreds of species live (Pollock et al. 1995).

If these effects are not trophic, what are they? Despite their diversity, all of them involve changes from one physical state or condition to another in the tree (e.g., a tree without crotch ponds to a tree with them) or its local environment (e.g., a stream without a debris dam to a dam and pond). These physical state changes are caused by the tree itself or by an organism, like the woodpecker, fungus, or beaver, that changes the physical state of the tree (e.g., a tree without holes to a tree with holes) or the local environment (e.g., a stream without a beaver dam to a tree dam and a pond). In all of these cases the physical state changes can have both positive and negative ecological consequences for other species that live in the old or the new environment that is created. This is because these other species depend on resources whose availability is directly or indirectly controlled by these physical state changes.

Examples of species that benefit from these changes include mosquito species that breed exclusively in water-filled tree holes (Kitching 1971, Bradshaw and Holzapfel 1985), stream organisms that live in ponds behind debris or beaver dams (Likens and Bilby 1982, Pollock et al. 1995), and plant species that are susceptible to the effects of hurricanes in the forest, and that in part, are dependent upon the protection conferred by the stabilizing effects of tree roots binding around rocks (Basnet et al. 1992). But not all species benefit from such physical state changes. Negative effects are also common, for example, terrestrial organisms flooded out behind a debris or beaver dam, or grassland plants and animals excluded by succession to forest (a similar balance between positive and negative effects is discussed by Callaway and Walker [1997]).

We have called these processes "physical ecosystem engineering" and the organisms responsible "physical ecosystem engineers" (Jones et al. 1994, Lawton and Jones 1995). A tremendous diversity of examples can be found in the literature (see Viles 1988, Meadows

and Meadows 1991, Wilson and Agnew 1992, Jones et al. 1994, Butler 1995, Jones and Lawton 1995, Flecker 1996), including many effects caused by *Homo sapiens*, a physical ecosystem engineer par excellence (see Jones et al. 1994). We have argued that physical ecosystem engineering by organisms plays a major role in determining the structure and functioning of most ecosystems, and we have yet to find an ecosystem in which physical ecosystem engineering by organisms does not play some role, even in such hostile environments as Arctic ice (Buynitskiy 1968, Arrigo et al. 1991). Here, we refine the concept of engineering, distinguishing it from trophic relations and competitive interactions. We explore the probable net effects of physical ecosystem engineers on species diversity and abundances, and upon population, community, and ecosystem stability. We also ask whether there are ways to predict which species will be important physical engineers, and which ecosystems will be the most affected by them. Lastly, we explore ways in which physical engineering and trophic interactions can be integrated.

WHAT IS ECOSYSTEM ENGINEERING?

We first need to formally define what we mean by engineering (the definition that follows is modified slightly from Jones et al. [1994], further clarifying the concept and should be read in consultation with Fig. 1). "Physical ecosystem engineers are organisms that directly or indirectly control the availability of resources to other organisms by causing physical state changes in biotic or abiotic materials. Physical ecosystem engineering by organisms is the physical modification, maintenance, or creation of habitats. The ecological effects of engineering on other species occur because the physical state changes directly or indirectly control resources used by these other species."

Living space and engineering

It is debatable whether or not the direct provision of living space by the structure of an organism (e.g., leaf, bark, root surfaces of a tree), and quantitative changes in the amount of living space as an organism grows (e.g., a bigger tree) should be considered physical engineering. In our original paper (Jones et al. 1994), we said that inclusion or exclusion was a matter of choice, and elected to exclude these processes in our subsequent discussion. We now include these processes in physical engineering. The changes in living space via branch growth of a tree has more in common with the creation of living space in soil cavities caused by root growth, which is engineering, than with the consumption of tree tissues, which is not engineering.

Engineering vs. other processes

The definition of engineering can be sharpened by contrasting it with other important ecological processes. Clearly, the utilization of the living or dead tissues

PHYSICAL STATE 1	PHYSICAL STATE 2	EXAMPLES OF CONTROLS ON RESOURCE AVAILABILITY TO OTHER ORGANISMS		
		CREATION OF RESOURCES	CONTROL OVER ABIOTIC RESOURCES	MODULATION OF ABIOTIC FORCES
a. TREE growth	TREE WITH CROTCH POND	Living Space	Water Capture Sediment Capture Nutrient Capture	
<i>autogenic</i>				
b. TREE	TREE WITH HOLES	Living Space Caching Space		
<i>allogenic</i>				
WOODPECKER OR ROT FUNGUS feeding				
c. SOIL	SOIL WITH CAVITIES	Living Space Caching Space	Water Infiltration Soil Texture Aeration	
<i>allogenic</i>				
TREE root growth				
d. PLANT COVER AND SOIL	UNDERSTORY AND SOIL	Shaded Habitat	Water Input Nutrient Input	Rain Impact Wind Impact Relative Humidity Temperature
<i>allogenic</i>				
TREE growth and leaf production				
e. SOIL	SOIL WITH LEAF LITTER LAYER	Living Space	Physical Barrier Water Drainage Soil Erosion Gas Exchange	Rainsplash Impact Heat Exchange
<i>autogenic and allogenic</i>				
TREE leaf abscission				
f. LOOSE ROCK AND SOIL	STABLE SUBSTRATE		Soil Erosion	Hurricane Impact
<i>autogenic and allogenic</i>				
TREE root growth binding				
g. FOREST STREAM	STREAM WITH DEBRIS DAM AND POND	Living Space	Water Retention Sediment Retention Nutrient Retention Oxygenation	
<i>autogenic and allogenic</i>				
TREE leaf, branch abscission				

of one organism as food by a consumer or decomposer, or the direct uptake and utilization of an abiotic resource (light, water, nutrients) by an organism is not engineering. While trophic or competitive interactions can lead to the physical engineering of habitats, they do not inevitably do so; nor are they necessary for engineering to occur. When a beaver cuts down the tree to make the dam it does not have to eat any part of the tree in order for the dam and resulting pond to have an effect. And while disturbance (Pickett and White 1985) and engineering can often have similar effects, not all engineering is disturbance (e.g., tree growth) and not all disturbance is engineering (e.g., a hurricane). Many "keystone species" (Mills et al. 1993, Menge et al. 1994) are engineers (e.g., beavers), but others (e.g., sea otters) are not; some engineering has big effects on other species (e.g., beaver dams), while other impacts may be relatively trivial (e.g., a cow hoofprint).

We suspect that one reason ecology has placed little emphasis on physical ecosystem engineering as an important general phenomenon is because of the bewildering apparent variety of ways in which organisms engineer habitats. By comparison, trophic or competitive effects seem relatively straightforward. While the devil is in the, as yet, poorly understood details, engineering is a very simple concept with relatively few key features.

Who does the engineering?

Understanding who the engineer is and what is engineered is critical for predicting how other ecological processes will influence the impact of an engineer. Ecosystem engineers bring about physical state changes in two basic ways. Autogenic physical engineers directly transform the environment via endogenous processes (e.g., tree growth, development) that alter the structure of the engineer, and the engineer remains as part of the engineered environment. Good examples of autogenic engineering by plants are summarized elsewhere in this Special Feature (Bertness and Leonard 1997, Callaway and Walker 1997, Hacker and Gaines 1997). In contrast, allogenic engineers change the environment by transforming living or nonliving materials from one physical state to another, and the engineer is not necessarily part of the permanent physical ecosystem structure (e.g., beavers). Both animals and plants can

be both autogenic and allogenic engineers (Jones et al. 1994). There are many examples of animals acting as autogenic engineers (corals, for instance), and plants as allogenic engineers (e.g., tree canopies affect the understory that does not contain the tree engineer). Trees often have mixed autogenic and allogenic engineering impacts (see Fig. 1).

Feedbacks to engineers

Feedbacks occur when the physical state change directly affects the engineer either positively or negatively. Jones et al. (1994) referred to positive feedbacks as "extended phenotype engineering," because the engineered habitat has direct consequences for the fitness of the engineer (Dawkins 1982). For example, beavers build dams and then use ponds as a place to live, avoid predators, and cache food (positive effects). In the longer term, the level of the beaver pond may extend into habitats that can no longer be effectively engineered, and beavers will lose a habitat, abandoning the area (negative effects) (Johnston and Naiman 1990, Hartman 1994).

However, physical engineering does not necessarily have a feedback effect on the engineer. For example, the formation of a debris dam by tree branches might have no significant beneficial or adverse consequences for the tree. Such "accidental engineering" (see Jones et al. 1994) may have profound effects on other taxa, but has no effect on the organism responsible for the physical transformation of the habitat. There is an important difference here between the variable fitness consequences of physical ecosystem engineering, and eating, being eaten, or competing for resources, which always have direct consequences for the fitness of the participants.

Direct and indirect control

Physical engineering controls the availability of resources to other species either directly or indirectly. Tree crotch ponds and beaver dams directly control water availability. On the other hand, tree roots that bind around rocks and ameliorate the impact of hurricanes on other species exert indirect control. The resources used by other species that are controlled or modulated by the engineer can be energy, materials, space, food organisms, or combinations of these resources.

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FIG. 1. Examples of physical ecosystem engineering involving a tree in a forest. Physical ecosystem engineering requires a change in physical state (physical state 1 to physical state 2) that then controls the availability of resources to other organisms. Control may be direct, via the creation of habitat and control over the supply of abiotic resources, and/or indirect, by modulation of abiotic forces that, in turn, affect resource use by other organisms. With autogenic engineering (a), the engineer is a part of the new physical state (via tree growth in this example). With allogenic engineering (b–d) the new physical state is caused by the engineer (X), but the engineer is not part of the new physical state. In examples e–g, both autogenic and allogenic engineering are involved because the tree not only creates a new physical state for parts of the environment in which it does not occur, but also becomes a part of the new environment. The processes involved in engineering (e.g., growth, feeding, etc.) are shown in the boxes using lowercase type.

NET EFFECTS OF ENGINEERS

Impacts of engineers on species diversity and abundances

At first sight it might appear that engineering will have mostly positive effects on other species. After all, if engineers make habitat, other species will now have a place to live (see Hacker and Gaines 1997, for an excellent example). In practice, the impacts that engineers have on species' abundances and richness vary from trivial to enormous, and they are not necessarily positive. It is certainly true that beavers make habitats for a very large number of species. But, it is also true that the conversion of a stream to a beaver pond must also have negative effects on many organisms, including aquatic species. First, a section of stream has been eliminated. Second, the upstream dam and pond may decrease the availability of downstream resources, via reduced water, oxygen, or nutrients, adversely affecting many organisms living downstream. Third, the changes in the riparian habitat that result from the felling of trees will have negative effects on the species that live there, even though it will create new habitat for other species. It is probable that in many cases the effects of the transformation of the habitat will be sufficient to entirely eliminate some species from the environs of the beaver pond, and to make others much rarer. Only some species will benefit from the changes.

From the perspective of the locale in which engineering takes place, we see no a priori rationale for assuming that the total number of other species that can now live in the new habitat should be more, less, or the same as the number of species that disappear when the old habitat is eliminated. Nor is there any reason to suppose that species able to live in both engineered and unmodified habitat will necessarily be commoner or rarer as a result of the engineer's activities; some will benefit, others will not. The answer will depend on the magnitude and types of changes that occur, the resources that are controlled, the number of species in the habitat that depend on these resources, and the extent to which these resources are adequate to support persistence in the new habitat. Whether or not it will be possible to predict such impacts in the future remains to be seen.

On the other hand, if our temporal and spatial scale encompasses more than the time and place that is engineered, we see a different picture. At the landscape level, beaver dams result in a net increase in the number of habitat types, space, and resources for other species, because what was once a valley with a stream and a riparian zone is now a valley with unmodified stream and riparian habitat, a pond, new type of riparian habitat, modified downstream habitats, and sites with abandoned and collapsed beaver dams supporting their own distinctive flora and fauna. If we watch the valley over time, as beavers come and go, we will certainly see a

more dynamic landscape with greater rates of change in habitats, resources, and organisms compared to the adjacent valley where beavers never came. Hence, at sufficiently large scales, encompassing unmodified habitats, engineered habitats, and areas abandoned by engineers, the net effect of engineering will almost inevitably be to enhance regional species richness via a net increase in habitat diversity.

A similar sort of scale dependency of positive and negative effects must have existed as engineers evolved. In a given habitat, the evolution of an engineer may have destroyed some niches, but at the same time created new ecological opportunities to be filled by new species. For example, the evolution and increasing importance in marine environments of mobile, benthic bioturbators from the Devonian onwards appear to have created a highly unfavorable environment for sessile suspension feeders, which are now largely confined to hard substrates (Thayer 1979); on the other hand, taxa able to survive the disturbance created by these "biological bulldozers," swimming particle feeders for example, may have benefitted. In general, we suggest that the net effect of the evolution of physical ecosystem engineers, across a mosaic of habitats, will be to increase species richness. Today we have sediment environments that contain bioturbators and the organisms that thrive because of them, as well as sediments and hard substrates without bioturbators, containing different organisms. No doubt many species have been dragged along through evolution in the wake of engineers, while others were lost by the wayside. What happened to the species that depended on the putatively massive soil, sediment, and rock engineering effects of dinosaurs?

Our tentative suggestion that physical ecosystem engineering by organisms on a global scale has a net positive effect on total species richness would benefit from more critical evaluation. Estimating how big the effects are, where they are the greatest, how the net positive effects arise from the balance of habitat addition and elimination, and how these have changed in evolutionary time are major research challenges of the future.

Impacts of engineers on population, community, and ecosystem stability

Gurney and Lawton (1996) have recently formulated variations on a simple, very general differential equation model in Lotka-Volterra form for the population dynamics of ecosystem engineers. In this family of models, the engineers (allogenic or autogenic) must physically modify virgin habitat in order to survive, that is, they are extended phenotype engineers. In the simplest case, individual engineers work alone; in a second version of the model they must collaborate to successfully physically modify the habitat. A key feature of both versions of the model is that engineered

habitat decays and eventually becomes unsuitable for occupation by the engineering population. A recovery period is necessary before degraded habitat returns to the virgin state, and again becomes suitable for recolonization and reuse by engineers. A third version of the model explores the population dynamic consequences of the distribution of residence times of habitat in a degraded state. One interesting result to emerge from this exercise is that no single population of ecosystem engineers has been sufficiently well studied to completely parameterize any version of the model. Examples of the essential features (the necessity of habitat modification for survival, cooperative and noncooperative engineering, habitat decay, and the recovery of degraded habitat) are all well documented in the literature (see Gurney and Lawton [1996] for a review), but have not been adequately quantified for any single species of engineer.

The model seeks to predict the dynamics and stability of the population of engineers, and of the three habitat states (virgin, engineered, and degraded). It makes no attempt to predict the dynamics of other species that are either dependent upon virgin habitat (and therefore suffer from the impacts of the engineer), or require engineered or degraded habitat (and therefore benefit from the presence of the engineer). The broad consequences for other organisms are, however, implicit in the dynamics of these three habitat states, although time delays and trophic and interspecific competitive interactions could greatly complicate the general picture, and have not yet been studied in detail. (Wilson and Nisbet's [1997] model in this Special Feature is formulated in the same spirit as Gurney and Lawton's model, but does not require the creation of engineered habitat for the survival of the engineer. Rather, it focuses on the role of engineering in creating sheltered settlement or germination sites for young individuals of the engineer or other species.)

Although Gurney and Lawton's models are a minimalist caricature of the dynamics of a population of physical ecosystem engineers, they make some simple and interesting predictions amenable to field testing. For instance, where the engineers do not co-operate to any significant degree, and where the distribution of residence times of habitat in the degraded state is wide (very variable rates of recovery at different points in the landscape), the engineer/habitat equilibrium is always locally stable, and simulations suggest that it is also globally stable. We think this will be a very general result, implying that in the absence of severe abiotic environmental disturbance, many engineers create very stable and predictable conditions for those species that are dependent upon them for habitat, and presumably, a concomitant degree of stability in ecosystem processes.

The necessary conditions for unstable limit cycles in the abundances of engineers and habitat are either:

(1) highly cooperative engineers exploiting short-lived, slowly recovering habitat; or (2) habitat where the distribution of recovery times from a degraded state varies very little (i.e., the variance in recovery time is small relative to the mean recovery time). Possible examples of populations of engineers that cycle are beavers (in the absence of human persecution) (see, for example, Hartman 1994), and *Dendroctonus* bark beetles that periodically erupt and kill pine-tree hosts over huge areas (Raffa and Berryman 1987), with massive knock-on effects for many other species, both via the generation of large quantities of dead timber, and the modulation of many other ecosystem resources.

Obvious extensions of these simple models are to couple them explicitly to the dynamics of nonengineering species that either require unmodified habitat to survive, or require engineered or degraded habitat. If these nonengineering species interact among themselves (as competitors or predators and prey), and/or interact with the engineer as competitors, predators, or via shared enemies, it is not at all clear to us whether the net effects will be positive or negative, and how the outcome might vary over plausible parameter space. We will return to the issue of coupling the population dynamics of engineers and nonengineers later. A second, major variant will be to develop models of engineering with explicit, spatial structure (Gurney and Lawton 1996), with obvious implications both for the stability of the interactions, and for local and regional species richness.

WHICH SPECIES WILL BE IMPORTANT PHYSICAL ENGINEERS?

As other contributors to this Special Feature point out (e.g., Callaway and Walker 1997), when pairwise trophic interactions are embedded in a complex food web, counterintuitive positive outcomes, such as increases in the density of prey or an inferior competitor, can occur for many reasons (see Yodzis 1988, Pimm 1991, Miller 1994, Menge 1995). These indirect effects and higher order interactions are now reasonably well understood, at least in principle. In many ways, trying to predict a priori which species will be important physical engineers is at least as, if not more, difficult as trying to predict the outcomes of these types of pairwise trophic interactions, or which species is a "keystone" predator (Mills et al. 1993, Menge et al. 1994) or a "strong" trophic interactor (Power 1995).

While many species cause physical state changes in the environment, not all of the changes have important (positive or negative) ecological consequences; some engineers have trivial effects, just as some trophic interactions have trivial population dynamic consequences and some interspecific competitive interactions are feeble. For example, a beaver pond has a much bigger and longer lasting effect than the small pond formed in an animal hoofprint. It would be very useful

to be able to predict which species will be important ecosystem engineers.

Key factors scaling engineering impact

We have previously identified six factors that scale the impact of engineers (Jones et al. 1994) and they are worth reiterating here: (1) lifetime per capita activity of the individual engineering organisms; (2) population density; (3) the local and regional spatial distribution of the population; (4) the length of time the population has been at a site; (5) the type and formation rate of the constructs, artifacts, or impacts, and their durability in the absence of the engineers; and (6) the number and types of resources that are directly or indirectly controlled, the ways these resources are controlled, and the number of other organisms that depend on these resources. Factors 1–5 could be readily measured for many physical engineer species. Getting a handle on factor 6 is much more difficult, but lies at the heart of understanding the impact. Removing or adding the engineer species, comparing naturally occurring sites with and without the engineer, and artificially manipulating the environment to mimic the effects in the absence of the engineer could be useful in many, but not all situations. Field manipulation experiments to understand the effects of ecosystem engineers are still uncommon (Bertness and Leonard 1997); good examples are provided by Bertness (1984a, b, 1985), Flecker (1996), Callaway and Walker (1997), and Hacker and Gaines (1997).

Engineering, mass flow, and the conservation of energy

In trophic interactions, being a part of the direct flow of energy and materials is at least a necessary precondition for membership in a food web. Since the laws of thermodynamics prevent energy or matter from being in more than one place or organism at the same time, one organism must gain benefits (positive) from trophic relations at the expense of another (negative). With physical engineering, however, it is hard to see what preconditions define membership of an “engineering web” (in the sense of Martinez [1995]). We can also say that the sorts of principles used in understanding trophic dynamics in food web and ecosystem theory do not appear to be of much value in understanding engineering. Trophic relations must conform to the principles of mass flow and conservation of energy. The mass consumed minus the wastes produced times the growth efficiency equals the mass gained by the consumer. Engineering does not conform to this principle. The amount of mass or energy put into a beaver (minus its wastes and the energy it uses to build the dam) does not equal the mass of the dam or the water it holds, nor the magnitude of the many and varied ecosystem effects that flow from the construction of the dam. Trophic relationships must also con-

form to stoichiometric requirements. A predator has the elemental composition of its prey minus the elemental composition of its wastes. The elemental ratios of the materials in a beaver dam, or of the organisms in the pond, bear no relationship to the elemental stoichiometry of the beaver. Perhaps the fundamental reason why energy, mass, and stoichiometry appear to be of little value in understanding engineering is that engineers do not have to be a part of the energy and material flows among the trophically connected organisms they affect. They are controllers of these flows, not participants in the flows.

Engineering and the idiosyncrasies of species

We also see another stumbling block to prediction that pervades much of ecology, not just engineering. The propensity of beavers to build dams is a peculiarity of this species and does not seem to us to be predictable a priori. Nevertheless, it is the key design feature of this engineer. Once it is recognized, existing knowledge about hydrology, sedimentology, and stream and pond ecology can go a long way toward telling us what will happen if the beaver starts to build. And we could probably predict many of the effects if we discovered a very different taxon that also built dams (e.g., humans). For some species, as with the beaver, there may be no substitute for starting with natural history and behavior in order to discover the key design feature and thereby understand the potential engineering impact. While it is likely that every engineer species will have at least some unique attributes and impacts, many will share common features. Trees are a good case in point. It should be feasible to measure many of the key structural attributes that determine the engineering impact of trees in forests. Comparison of these attributes among tree species in different ecosystems could lead to valuable insights and generalizations. The same may be true for the common features found among burrowing animals (Meadows and Meadows 1991, Hansell 1993, Butler 1995), and so on.

WHERE WILL PHYSICAL ENGINEERING BE THE MOST IMPORTANT?

We have argued that engineers are found in all ecosystems (Jones et al. 1994). While this contention has yet to be tested, it is nevertheless very likely that engineering is more important in some ecosystems than others. Being able to predict the types of ecosystems in which engineers play the most critical roles is both fundamentally interesting and of considerable pragmatic value in conservation and management. While we certainly do not have anything approaching a definitive answer, our surveys of the literature and some of the points raised earlier provide some postulated nonexclusive generalizations that are amenable to testing via surveys and comparative or experimental stud-

ies. Some generalizations are obvious, while others are not.

The dominant organisms are relatively massive and persistent structures

The mere presence of such physical structures, their continual growth and replacement, and their persistence over long periods of time (including evolutionary time) should lead to systems in which many other species are dependent upon both the autogenic creation of surface area for living space and the autogenic and allogenic modulation of resources controlled by these structures. Forests, *Sphagnum* bogs, and coral reefs are obvious examples. It seems likely that most forests will have many qualitatively similar engineering effects. However, it also seems reasonable to expect that engineering effects would be bigger in a Redwood or Pacific old-growth Douglas-fir forest than in an early-successional or second-growth forest, because of the size and persistence, ecological and perhaps evolutionary, of these huge trees.

Plant cover is extensive

As with the forest examples above, the presence of plants affects physical structure and, hence, ecosystem functioning. An early-successional habitat with shrubs and young trees, a grassland, a kelp forest and a sea-grass prairie are all plant-engineered environments. We might expect that early-successional forest, with shrub and saplings, has more engineering than the grassland it invaded, because the plants are bigger. It is not true, however, that size alone will determine the importance of plant engineering in an ecosystem. Many deserts are sparse in cover by higher plants. Instead, the soil is extensively covered by dominant microphytic communities of blue-green algae, cyanobacteria, and fungi that are barely visible to the naked eye (West 1990, Zaady and Shachak 1994). These organisms certainly cannot be construed as massive structures. Nevertheless, these communities have potent engineering effects because they secrete polysaccharides that bind the soil. This controls stability, erosion, runoff, and site availability for germination by higher plants (West 1990, Zaady and Shachak 1994). The same situation exists with diatom carbohydrate secretions that bind sandy sediments (Daborn et al. 1993).

Animals build or destroy massive, persistent, abiotic structures

Beavers, gophers, pack rats, mole rats, alligators, some termite species, tilefish, and corals all build large structures above or below ground that can have ecosystem-level effects and that may last for long periods of time, even centuries or more (Jones et al. 1994, Butler 1995). Animals can also destroy abiotic structures on a massive scale. Puffin burrowing on the island of Grassholm (UK) between 1898 and 1928 was so

great that the entire soil surface of the island more or less completely eroded into the sea (Furness 1991). Many of these species have restricted geographical ranges, and their effects on the ecosystem are often species specific (e.g., beavers). In this sense their engineering effects on ecosystems are somewhat idiosyncratic and unpredictable.

Large animals are abundant

Large animals such as elephants, bison, other ungulates, whales, etc. tend to have large per capita engineering effects on the ecosystems they occupy (e.g., Naiman 1988, see Butler 1995). While many of these effects may be more species specific than others (e.g., elephants tend to knock down more trees than wildebeest), many of the effects of trampling, tearing, pawing, etc., may be quite similar across ecosystems. Most of these animals occurs in herds at high densities, which must lead to additive impacts on their ecosystems, at the very least.

Abiotic substrates are amenable to biogeomorphic action

There are many habitats that may or may not fit any of the above categories, but nevertheless are extensively engineered. A tremendous diversity of small and large animals dig, burrow, or otherwise disturb soils and sediments (Meadows and Meadows 1991, Jones et al. 1994, Butler 1995). In one sense, the ecosystem effects of these animals arise because these substrates are soft enough for organisms to act on. We do not expect much animal digging in hard granite rocks! On the other hand, there are many rock environments where the substrate is not too hard to prevent animal erosion (e.g., Bloom 1978, Krumbein and Dyer 1985, Shachak et al. 1987). In fact, animals are so adept at digging, scraping, burrowing, boring, and even chemically eroding these substrates (Butler 1995), that we doubt whether there are many ecosystems in which these types of activities do not play a key role. Plant roots and chemical exudates from lichens likewise have marked engineering effects on soils, sediments, and rocks (Bloom 1978, Krumbein and Dyer 1985, Jones et al. 1994).

The ecosystem has persistent structure

The magnitude of the effects of physical ecosystem engineering depends on the persistence of physical structures (a tree, a dam, a mound, etc.) created by organisms. So ecosystems that do not have a high degree of physical structuring (either the organisms or what they make), such as the pelagic zones of the waters of the earth, seem unlikely to be dominated by engineering effects. Living planktonic organisms do physically modify the environment, however, for instance by contributing to the formation of a thermocline (Mazumder et al. 1990, Townsend et al. 1992). Fur-

thermore, the effluvia of pelagic organisms, their carapaces and feces (marine and lake "snow" [Silver et al. 1995]), can have surprisingly large effects on the functioning of the entire ecosystem, and some of these effects constitute physical engineering. Nevertheless, we should expect the relative contribution of engineering to ecosystem functioning to be less in these relatively unstructured environments than in many other ecosystems.

Many abiotic resources are integrated

Organisms that engineer rivers, streams, soils, and sediments tend to have large ecosystem-level effects (e.g., beavers, earthworms, benthic bioturbators; Naiman et al. 1988, Lal 1991, Thompson et al. 1993, Levinton 1995, Butler 1995, Pollock et al. 1995). The most likely reason is that water, soil, and sediments integrate many resources (living space, nutrients, prey, etc.) within one locale, thus modifying them has big effects. Water, in particular, tends to move readily from place to place carrying nutrients, sediments, oxygen, etc., all of which are key resources for many species.

Environments are extreme

It might be expected that strong abiotic forces in extreme environments (e.g., hurricanes, wave action, heat, and drought) would diminish the importance of engineering, or at least make it more difficult to detect. This does not seem to be the case; indeed, as pointed out elsewhere in this Special Feature, positive interactions in general are often important in harsh environments (Bertness and Leonard 1997, Hacker and Gaines 1997). Examples involving physical ecosystem engineers include *Dacryodes excelsa* trees in Puerto Rican forests, which resist hurricanes because their roots bind around rocks (Basnet et al. 1992), and crustose and coralline algae on the outer margins of coral reefs, which resist tropical storms (Anderson 1992). The Negev Desert, Israel, contains engineers in the form of rock-eating snails (Shachak et al. 1987, Jones and Shachak 1990), burrowing desert isopods (Shachak and Jones 1995), and digging porcupines (Yair and Rutin 1981, Gutterman 1982), as well as the microphytic crust communities previously mentioned; the engineering of soil and rock by each of these species has very large effects on desert productivity and species diversity. In fact, one could argue that natural selection might particularly favor the evolution of extended phenotype engineers in extreme environments, as a means of enhancing survival, with obvious consequences for cohabiting, but nonengineering taxa.

ENGINEERING MEETS TROPHIC ECOLOGY

So far we have emphasized the distinction between engineering and trophic interactions. There is certainly heuristic value in this, since it serves to highlight engineering as an ecological phenomenon worthy of

study. But if we are ever going to understand nature in all its complexity, we will need to integrate engineering and trophic ecology (Jones and Lawton 1995), as touched on in our concluding remarks on modeling engineering. At its most fundamental and simplest, the connection between engineering and trophic ecology lies in the recognition that the creation of physical structure by organisms controls the distribution and abundance of resources for other species. There are a number of obvious, and not so obvious, ways in which engineering and trophic relations interact that can be deduced from real-world examples.

Direct consumption of engineers

Herbivores that graze grasses, eat algae, or defoliate trees, and pathogens or bark beetles that kill plants obviously have impacts that go well beyond the direct impact of consumption on the resource. The same is true for predators of animal engineers. In essence, the interaction is fairly straightforward. If you know what the engineer does to other species in the habitat, the effects of removing or reducing the density of the engineer should be relatively easy to figure out, at least in comparison to some of the other examples we discuss below.

Competition between engineers

Plant engineers can compete with each other for abiotic resources, with the success of one species affecting the performance of the other. The consequences of these competitive outcomes for other species in the ecosystem that do not feed upon the two competing engineers will therefore depend on the species-specific and nonspecific effects that the two engineers have on the environment. Knowing exactly which species engineers what features with what consequences may not be easy. On the other hand, once this is known, working out the consequences of changes in the relative abundance of these two engineers ought to be relatively straightforward.

Coupled engineering and trophic cascades

Sandy shorelines in the Bay of Fundy are subject to wave action that constantly changes the physical structure. Diatoms that dominate in certain areas produce carbohydrate exudates. These chemical secretions cause a physical state change in the environment by binding the sand, stabilizing its movement. The diatoms are auto- and allogenic engineers, and this presumably has important effects on both the diatoms and all the other organisms that live in this habitat. Amphipods are the dominant grazers of diatoms in these environments. Where amphipods are abundant, stabilization is reduced. Sandpipers, the dominant predators on the amphipods, reduce amphipod grazing and hence promote restabilization of the habitat by diatoms (Daborn et al. 1993). We will call this a "coupled engi-

neering and trophic cascade.” The reason why sandpiper distribution and abundance have such a large effect is not simply because they eat many amphipods. Rather, it is because the engineer has big effects, and the engineer is part of a food web. Some might call the sandpiper a keystone species or a keystone predator, but it is important to recognize that the effects of sandpipers only occur because the diatoms are engineers.

As we have pointed out previously (Jones et al. 1994), a very similar coupling of engineering and trophic cascades occurs with sea otters, urchins, and kelp forests on the Pacific coast of the United States (Estes and Palmisano 1974, Estes 1995). Otters eat urchins, urchins eat kelp, and kelp are auto- and allogenic engineers. Kelp reduce impacts of waves and currents, maintain water clarity, and prevent sediment movement, providing a habitat for numerous species that do not feed on kelp. The otter can be considered a keystone predator, but only because it eats urchins, which destroy the kelp engineers. We suspect that coupled engineering and trophic cascades will be very common. Recognition that the effects arise because engineers often belong to food webs that exist in the engineered habitat is crucial to predicting the impacts on species that occur in the habitat but do not necessarily belong in the food web.

Multiple engineers and coupled and uncoupled trophic interactions

Coupling between trophic and engineering interactions does not require all engineers to be a part of the same food web, however. The Negev Desert example of autogenic and allogenic engineering by the microphytic crust (West 1990, Zaady and Shachak 1994) discussed earlier illustrates this point particularly clearly. The physical state changes caused by the crust have a major influence on, among other things, the availability of germination sites for the seeds of annuals, which are the major food source for both native grazing species and livestock (Boeken and Shachak 1994). These large herbivores do not feed on the microphytic crust. Most of these animals are hooved, and when they graze on the annuals they disturb the adjacent crust. The small-scale pits and mounds caused by hooves (accidental allogenic engineering) trap seeds of annuals and runoff water, creating an ideal environment for seed germination and growth. Here the animal engineers destroy the effects of the microbial physical engineers, increasing the production of annuals, a positive feedback from their engineering activities.

However, the small soil pits and mounds that are occupied by the annuals are highly dependent on the runoff water that comes as overland flow. The amount of runoff is controlled by the microphytic crust, because the polysaccharide secretions of these organisms form a surface that is more or less impermeable to water infiltration, generating runoff into the pits and mounds.

As a consequence, the productivity of annuals, and hence food for large grazers in this desert, depends on there being enough crusted soil to generate sufficient runoff. If grazing becomes too intense, the destruction of the crust-engineered environment has a negative impact on productivity. This is not just a short-term effect of overgrazing the annuals, but a much longer term effect on ecosystem productivity. After overgrazing, productivity only recovers once the slow-growing crust organisms re-engineer the habitat.

In this example, we have one physical engineer (the microphytic crust community) that is not part of the annual plant–ungulate food web, but that nevertheless prevents annuals from getting established (few cracks in the soil in which to germinate, little moisture infiltrating). Paradoxically, this first engineer also facilitates the growth of annual plants (via runoff) once a second physical engineer (hooved mammals) creates suitable habitat (pits and mounds). This second engineer, in a different food web from the microphytic crust, also negatively impacts the crust (via disturbance from hooves). While this example is very complex, we suspect that nature will be full of similar, or even more complex examples. It is our job to figure them out.

CONCLUDING REMARKS

Compared with the huge efforts that ecologists have devoted to the study of trophic interactions among species, interspecific competition, species diversity, and ecosystem fluxes, engineering is a very poor relative. To start to reverse this imbalance, we need empirical data from comparative and experimental studies, models, and conceptual integration of the phenomenon we call physical ecosystem engineering. We need to know which attributes of species are relevant to engineering, and which are not relevant, and which attributes are general, and which are not. We need to understand which species or functional types exert what types of controls on what type of resource flows, in which ecosystems. Until we have as good a conceptual and empirical understanding of engineering as we do of trophic relations, integrating these two aspects of ecology, or even distinguishing engineering from trophic effects in real ecosystems, will be difficult.

One thing, at least, should by now be clear. Ecologists interested in the significance of positive interactions in ecosystems cannot ignore engineering. Not all effects of engineers are positive—within the ambit of the physically altered locality there may be as many species that suffer from the resulting changes in resource flows and habitat structure as benefit. But at regional or landscape scales, among a mosaic of engineered and nonengineered habitat, the overall impacts of engineering are most likely to enhance species richness. Similar remarks probably apply to the effects of engineers over evolutionary time.

It is also important to realize that engineers and

“keystone species” are not synonymous. Many engineers have small, difficult-to-detect effects; only some have dramatic effects, but where they do, understanding how the engineers modify and modulate resource flows for other species, and create and maintain entire habitats, are among the most significant and poorly researched questions in ecology.

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LITERATURE CITED

- Anderson, R. A. 1992. Diversity of eukaryotic algae. *Biodiversity and Conservation* **1**:267–292.
- Arrigo, K. R., C. W. Sullivan, and J. N. Kremer. 1991. A bio-optical model of Antarctic sea ice. *Journal of Geophysical Research* **96** C6:10581–10592.
- Basnet, K., G. E. Likens, F. N. Scatena, and A. E. Lugo. 1992. Hurricane Hugo: damage to a tropical rain forest in Puerto Rico. *Journal of Tropical Ecology* **8**:47–55.
- Bertness, M. D. 1984a. Habitat and community modification by an introduced herbivorous snail. *Ecology* **65**:370–381.
- . 1984b. Ribbed mussels and *Spartina alterniflora* production in a New England salt marsh. *Ecology* **65**:1794–1807.
- . 1985. Fiddler crab regulation of *Spartina alterniflora* production on a New England salt marsh. *Ecology* **66**:1042–1055.
- Bertness, M. D., and G. H. Leonard. 1997. The role of positive interactions in communities: lessons from intertidal habitats. *Ecology* **78**:1976–1989.
- Bloom, A. L. 1978. *Geomorphology*. Prentice Hall, Englewood Cliffs, New Jersey, USA.
- Boeken, B., and M. Shachak. 1994. Desert plant communities in human made patches—implications for management. *Ecological Applications* **4**:702–716.
- Bouma, J., and J. L. Anderson. 1973. Relationships between soil structure characteristics and hydraulic conductivity. Pages 77–105 in M. Steely, R. C. Dinauer, and J. M. Hach, editors. *Field soil water regime*. Soil Science Society of America Special Publication Number 5. Soil Science Society of America, Madison, Wisconsin, USA.
- Bradshaw, W. E., and C. M. Holzapfel. 1985. The distribution and abundance of treehole mosquitoes in eastern North America: perspectives from north Florida. Pages 3–23 in L. P. Lounibos, J. R. Rey, and J. H. Frank, editors. *Ecology of mosquitoes: proceedings of a workshop*. Florida Medical Entomology Laboratory, Vero Beach, Florida, USA.
- Bradshaw, W. E., and C. M. Holzapfel. 1992. Resource limitation, habitat segregation, and species interactions of British tree-hole mosquitoes in nature. *Oecologia* **90**:227–237.
- Butler, D. R. 1995. *Zoogeomorphology: animals as geomorphic agents*. Cambridge University Press, New York, New York, USA.
- Buynitskiy, V. K. 1968. The influence of microalgae on the structure and strength of Antarctic sea ice. *Oceanology* **8**:771–776.
- Callaway, R. M., and L. R. Walker. 1997. Competition and facilitation: a synthetic approach to interactions in plant communities. *Ecology* **78**:1958–1965.
- Collins, B. S., and S. T. A. Pickett. 1982. Vegetation composition and relation to environment in an Allegheny hardwoods forest. *American Midland Naturalist* **108**:117–123.
- Daborn, G. R., C. L. Amos, M. Brylinsky, H. Christian, G. Drapeau, R. W. Faas, J. Grant, B. Long, D. M. Paterson, G. M. E. Perillo, and M. C. Piccolo. 1993. An ecological cascade effect: migratory birds affect stability of intertidal sediments. *Limnology and Oceanography* **38**:225–231.
- Daily, G. C., P. R. Ehrlich, and N. M. Haddad. 1993. Double keystone bird in a keystone species complex. *Proceedings of the National Academy of Sciences (USA)* **90**:592–594.
- Dawkins, R. 1982. *The extended phenotype*. Oxford University Press, Oxford, England.
- Estes, J. A. 1995. Top-level carnivores and ecosystem effects: questions and approaches. Pages 151–158 in C. G. Jones and J. H. Lawton, editors. *Linking species and ecosystems*. Chapman and Hall, New York, New York, USA.
- Estes, J. A., and J. F. Palmisano. 1974. Sea-otters: their role in structuring nearshore communities. *Science* **185**:1058–1060.
- Facelli, J. M., and S. T. A. Pickett. 1991. Plant litter: its dynamics and effects on plant community structure. *Botanical Review* **57**:1–32.
- Flecker, A. S. 1996. Ecosystem engineering by a dominant detritivore in a diverse tropical stream. *Ecology* **77**:1845–1854.
- Foster, R. C. 1988. Microenvironments of soil microorganisms. *Biology and Fertility of Soils* **6**:189–203.
- Furness, R. W. 1991. The occurrence of burrow-nesting among birds and its influence on soil fertility and stability. *Symposium of the Zoological Society of London* **63**:53–67.
- Gurney, W. S. C., and J. H. Lawton. 1996. The population dynamics of ecosystem engineers. *Oikos* **76**:273–283.
- Gutterman, Y. 1982. Observations on the feeding habits of the Indian crested porcupine (*Hystrix indica*) and the distribution of some hemicryptophytes and geophytes in the Negev desert highlands. *Journal of Arid Environments* **5**:261–268.
- Hacker, S. D., and S. D. Gaines. 1997. Some implications of direct positive interactions for community species diversity. *Ecology* **78**:1990–2003.
- Hansell, M. H. 1993. The ecological impact of animal nests and burrows. *Functional Ecology* **7**:5–12.
- Hartman, G. 1994. Long-term population development of a reintroduced beaver (*Castor fiber*) population in Sweden. *Conservation Biology* **8**:713–717.
- Hedin, L. O., M. S. Mayer, and G. E. Likens. 1988. The effect of deforestation on organic debris dams. *Proceedings of the International Association for Theoretical and Applied Limnology* **23**:1135–1141.
- Holling, C. S. 1992. Cross-scale morphology, geometry, and dynamics of ecosystems. *Ecological Monographs* **62**:447–502.
- Johnston, C. A., and R. J. Naiman. 1990. Aquatic patch creation in relation to beaver population trends. *Ecology* **71**:1617–1621.
- Jones, C. G., and J. H. Lawton, editors. 1995. *Linking species and ecosystems*. Chapman and Hall, New York, New York, USA.
- Jones, C. G., J. H. Lawton, and M. Shachak. 1994. Organisms as ecosystem engineers. *Oikos* **69**:373–386.
- Jones, C. G., and M. Shachak. 1990. Fertilization of the desert soil by rock-eating snails. *Nature* **346**:839–841.
- Juma, N. G. 1993. Interrelationships between soil structure/texture, soil biota/soil organic matter and crop production. *Geoderma* **57**:3–30.
- Kitching, R. L. 1971. An ecological study of water-filled tree-holes and their position in the woodland ecosystem. *Journal of Animal Ecology* **40**:281–302.

- . 1983. Community structure in water-filled treeholes in Europe and Australia—comparisons and speculations. Pages 205–222 in J. K. Frank and L. P. Lounibos, editors. *Phytotelmata: terrestrial plants as hosts for aquatic insect communities*. Plexus, Medford, New Jersey, USA.
- Krumbein, W. E., and B. D. Dyer. 1985. This planet is alive—weathering and biology, a multi-faceted problem. Pages 143–160 in J. I. Drever, editor. *The chemistry of weathering*. D. Reidel, Dordrecht, The Netherlands.
- Lal, R. 1991. Soil conservation and biodiversity. Pages 89–103 in D. L. Hawksworth, editor. *The biodiversity of microorganisms and invertebrates: its role in sustainable agriculture*. CAB International, Wallingford, England.
- Lawton, J. H., and C. G. Jones. 1995. Linking species and ecosystems: organisms as ecosystem engineers. Pages 141–150 in C. G. Jones and J. H. Lawton, editors. *Linking species and ecosystems*. Chapman and Hall, New York, New York, USA.
- Levinton, J. 1995. Bioturbators as ecosystem engineers: control of the sediment fabric, inter-individual interactions, and material fluxes. Pages 29–36 in C. G. Jones and J. H. Lawton, editors. *Linking species and ecosystems*. Chapman and Hall, New York, New York, USA.
- Likens, G. E., and R. E. Bilby. 1982. Development, maintenance, and role of organic-debris dams in New England streams. Pages 122–128 in F. J. Swanson, R. J. Janda, T. Dunne, and D. N. Swanston, editors. *Sediment budgets and routing in forest drainage basins*. USDA Forest Service General Technical Report **PNW-141**.
- Martinez, N. D. 1995. Unifying ecological subdisciplines with ecosystem food webs. Pages 166–175 in C. G. Jones and J. H. Lawton, editors. *Linking species and ecosystems*. Chapman and Hall, New York, New York, USA.
- Mazumder, A., W. D. Taylor, D. J. McQueen, and D. R. S. Lean. 1990. Effects of fish and plankton on lake temperature and mixing depth. *Science* **247**:312–315.
- Meadows, P. S., and A. Meadows, editors. 1991. *The environmental impact of burrowing animals and animal burrows*. Clarendon, Oxford, England.
- Menge, B. A. 1995. Indirect effects in marine rocky intertidal interaction webs: patterns and importance. *Ecological Monographs* **65**:21–74.
- Menge, B. A., E. L. Berlow, C. A. Blanchette, S. A. Navarrete, and S. B. Yamada. 1994. The keystone species concept: variation in interaction strength in a rocky intertidal habitat. *Ecological Monographs* **64**:249–286.
- Miller, T. E. 1994. Direct and indirect species interactions in an early old-field plant community. *American Naturalist* **143**:1007–1025.
- Mills, L. S. M., M. E. Soulé, and D. F. Doak. 1993. The keystone-species concept in ecology and conservation. *BioScience* **43**:219–224.
- Naiman, R. J. 1988. Animal influences on ecosystem dynamics. *BioScience* **38**:750–752.
- Naiman, R. J., C. A. Johnston, and J. C. Kelley. 1988. Alteration of North American streams by beaver. *BioScience* **38**:753–762.
- Peterson, C. J., W. P. Carson, B. C. McCarthy, and S. T. A. Pickett. 1990. Microsite variation and soil dynamics within newly created treefall pits and mounds. *Oikos* **58**:39–46.
- Peterson, C. J., and S. T. A. Pickett. 1990. Microsite and elevational influences on early forest regeneration after catastrophic windthrow. *Journal of Vegetation Science* **1**:657–662.
- Pickett, S. T. A., and P. S. White, editors. 1985. *The ecology of natural disturbance and patch dynamics*. Academic Press, Orlando, Florida, USA.
- Pimm, S. L. 1991. *The balance of nature?* University of Chicago Press, Chicago, Illinois, USA.
- Pollock, M. M., R. J. Naiman, H. E. Erickson, C. A. Johnston, J. Pastor, and G. Pinay. 1995. Beaver as engineers: influences on biotic and abiotic characteristics of drainage basins. Pages 117–126 in C. G. Jones and J. H. Lawton, editors. *Linking species and ecosystems*. Chapman and Hall, New York, New York, USA.
- Power, M. E. 1995. Floods, food chains, and ecosystem processes in rivers. Pages 52–60 in C. G. Jones and J. H. Lawton, editors. *Linking species and ecosystems*. Chapman and Hall, New York, New York, USA.
- Raffa, K. F., and A. A. Berryman. 1987. Interacting selective pressures in conifer-bark beetle systems: a basis for reciprocal adaptations? *American Naturalist* **129**:234–262.
- Shachak, M., and C. G. Jones. 1995. Ecological flow chains and ecological systems: concepts for linking species and ecosystem perspectives. Pages 280–294 in C. G. Jones and J. H. Lawton, editors. *Linking species and ecosystems*. Chapman and Hall, New York, New York, USA.
- Shachak, M., C. G. Jones, and Y. Granot. 1987. Herbivory in rocks and the weathering of a desert. *Science* **236**:1098–1099.
- Silver, M. W., S. L. Coale, D. K. Steinberg, and C. H. Pilska. 1995. Marine snow: what it is and how it affects ecosystem function. Pages 45–51 in C. G. Jones and J. H. Lawton, editors. *Linking species and ecosystems*. Chapman and Hall, New York, New York, USA.
- Smiles, D. E. 1988. Aspects of the physical environment of soil organisms. *Biology and Fertility of Soils* **6**:204–215.
- Thayer, C. W. 1979. Biological bulldozers and the evolution of marine benthic communities. *Science* **203**:458–461.
- Thompson, L., C. D. Thomas, J. M. A. Radley, S. Williamson, and J. H. Lawton. 1993. The effect of earthworms and snails in a simple plant community. *Oecologia* **95**:171–178.
- Tisdall, J. M., and J. M. Oades. 1982. Organic matter and water-stable aggregates in soils. *Journal of Soil Science* **33**:141–163.
- Townsend, D. W., M. D. Keller, M. E. Sieracki, and S. G. Ackleson. 1992. Spring phytoplankton blooms in the absence of vertical water column stratification. *Nature* **360**:59–62.
- Vander Wall, S. B. 1990. *Food hoarding in animals*. University of Chicago Press, Chicago, Illinois, USA.
- Viles, H. A., editor. 1988. *Biogeomorphology*. Basil Blackwell, Oxford, UK.
- West, N. E. 1990. Structure and function of microphytic soil crusts in wildland ecosystems of arid to semi-arid regions. *Advances in Ecological Research* **20**:180–223.
- Wilson, J. B., and A. D. Q. Agnew. 1992. Positive-feedback switches in plant communities. *Advances in Ecological Research* **23**:263–336.
- Wilson, W. G., and R. M. Nisbet. 1997. Cooperation and competition along smooth environmental gradients. *Ecology* **78**:2004–2017.
- Yair, A., and J. Rutin. 1981. Some aspects of the regional variation in the amount of available sediment produced by isopods and porcupines, northern Negev, Israel. *Earth Surface Processes and Landforms* **6**:221–234.
- Yodzis, P. 1988. The indeterminacy of ecological interactions as perceived through perturbation experiments. *Ecology* **69**:508–515.
- Zaady, E., and M. Shachak. 1994. Microphytic soil crust and ecosystem leakage in the Negev Desert. *American Journal of Botany* **81**:109.