

Organisms as ecosystem engineers

Clive G. Jones, John H. Lawton and Moshe Shachak

Jones, C. G., Lawton, J. H. and Shachak, M. 1994. Organisms as ecosystem engineers. – *Oikos* 69: 373–386.

Ecosystem engineers are organisms that directly or indirectly modulate the availability of resources to other species, by causing physical state changes in biotic or abiotic materials. In so doing they modify, maintain and create habitats. Autogenic engineers (e.g. corals, or trees) change the environment via their own physical structures (i.e. their living and dead tissues). Allogenic engineers (e.g. woodpeckers, beavers) change the environment by transforming living or non-living materials from one physical state to another, via mechanical or other means. The direct provision of resources to other species, in the form of living or dead tissues is not engineering. Organisms act as engineers when they modulate the supply of a resource or resources other than themselves. We recognise and define five types of engineering and provide examples. Humans are allogenic engineers par excellence, and also mimic the behaviour of autogenic engineers, for example by constructing glasshouses. We explore related concepts including the notions of extended phenotypes and keystone species. Some (but not all) products of ecosystem engineering are extended phenotypes. Many (perhaps most) impacts of keystone species include not only trophic effects, but also engineers and engineering. Engineers differ in their impacts. The biggest effects are attributable to species with large per capita impacts, living at high densities, over large areas for a long time, giving rise to structures that persist for millennia and that modulate many resource flows (e.g. mima mounds created by fossorial rodents). The ephemeral nests constructed by small, passerine birds lie at the opposite end of this continuum. We provide a tentative research agenda for an exploration of the phenomenon of organisms as ecosystem engineers, and suggest that all habitats on earth support, and are influenced by, ecosystem engineers.

Jones, C. G., *Inst. of Ecosystem Studies (IES), Box AB, Millbrook, NY 12545, USA.* – J. H. Lawton, *NERC Centre for Population Biology, Imperial College, Silwood Park, Ascot, Berks, UK, SL5 7PY, and IES.* – M. Shachak, *Mitrani Center for Desert Ecology, Blaustein Inst. for Desert Research, Ben-Gurion Univ. of the Negev, Sede Boqer 84900, Israel, and IES.*

Interactions between organisms are a major determinant of the distribution and abundance of species. Ecology textbooks (e.g. Ricklefs 1984, Krebs 1985, Begon et al. 1990) summarise these important interactions as intra- and inter-specific competition for abiotic and biotic resources, predation, parasitism and mutualism. Conspicuously lacking from the list of key processes in most text books is the role that many organisms play in the creation, modification and maintenance of habitats. These activities do not involve direct trophic interactions between species, but they are nevertheless important and

common. The ecological literature is rich in examples of habitat modification by organisms, some of which have been extensively studied (e.g. Thayer 1979, Naiman et al. 1988). However, in general, population and community ecology have neither defined nor systematically identified and studied the role of organisms in the creation and maintenance of habitats. There is not even a word, or words, in common use to describe the process. We will call the process *Ecosystem Engineering* and the organisms responsible *Ecosystem Engineers*.

Beaver (*Castor canadensis*) are familiar examples of

Accepted 21 September 1993

Copyright © OIKOS 1994

ISSN 0030-1299

Printed in Denmark – all rights reserved

organisms acting as ecosystem engineers. By cutting trees and using them to construct dams they alter hydrology, creating wetlands that may persist for centuries. "These activities retain sediments and organic matter in the channel, ... modify nutrient cycling and decomposition dynamics, modify the structure and dynamics of the riparian zone, influence the character of water and materials transported downstream, and ultimately influence plant and animal community composition and diversity" (Naiman et al. 1988).

However, beaver are by no means the only ecosystem engineers. As we will show, a vast array of species have effects that are fundamentally similar, albeit often on more modest spatial and temporal scales. Yet there is no common language to describe what ecosystem engineers do, no formal structure to model their effects, and no general theory round which to organise understanding of the process. Examples, which are developed more formally below (for others, see Table 1), include not only beaver and their dams but also gophers, ants and termites that move soil, woodpeckers that drill holes, alligators that make wallows, rock-eating snails, trees, corals, seagrass beds and *Sphagnum* blanket bogs.

The purposes of this article are fourfold: (i) to define and to give examples of ecosystem engineering by organisms; (ii) to develop a conceptual framework that explains and classifies its effects; (iii) to show how organismal engineering differs from related concepts (e.g. 'keystone species' Paine 1969, Krebs 1985); (iv) and to identify questions for further work on organisms as ecosystem engineers. First we define what we mean by an ecosystem engineer, before providing examples and a conceptual framework for what is, and is not, ecosystem engineering.

Definitions

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

The direct provision of resources by an organism to other species, in the form of living or dead tissues is not engineering. Rather, it is the stuff of most contemporary ecological research, for example plant-herbivore or predator-prey interactions, food web studies and decomposition processes.

Autogenic engineers change the environment via their own physical structures, i.e. their living and dead tissues. *Allogenic engineers* change the environment by transforming living or non-living materials from one physical state to another, via mechanical or other means.

Armed with these definitions we can now proceed to consider some detailed examples. We are not, at this juncture, concerned with the magnitude or scale of the

impacts of engineers on communities and ecosystems. We are interested solely in discovering properties that all engineers have in common. We address the scale and magnitude of their effects later.

Classification of organisms as engineers

Table 1 summarises examples of organisms as ecosystem engineers. The table is illustrative, not exhaustive. Additional examples are discussed at greater length in the text.

All the examples of which we are aware can be assigned to one of five possible cases (Fig. 1), or to a combination of two or more of these cases. As in many other areas of ecology, the diversity of biological processes means that precise pigeon-holing is sometimes difficult. The boundaries between types of engineering are occasionally fuzzy and, in the real world, separating engineering from other ecological processes may also be difficult, simply because these non-trophic interactions always co-occur with trophic interactions. We discuss some difficult cases as we proceed. The majority of examples are, however, easy to classify. The legend to Fig. 1 explains the conventional notation used to describe them. For clarity, it is easiest to introduce the arguments using beaver and their dams.

Beaver conform to case 4 in Fig. 1. That is they are allogenic engineers, taking materials in the environment (in this case trees, but in the more general case it can be any living or non-living material), and turning them (engineering them) from physical state 1 (living trees) into physical state 2 (dead trees in a beaver dam). This act of engineering then creates a pond, and it is the pond which has profound effects on a whole series of resource-flows used by other organisms. The critical step in this process is the transformation of trees from state 1 (living) to state 2 (a dam). This transformation modulates the supply of other resources, particularly water, but also sediments, nutrients etc. A critical characteristic of ecosystem engineering is that it must change the availability (quality, quantity, distribution) of resources utilised by other taxa, excluding the biomass provided directly by the population of allogenic engineers. Engineering is not the direct provision of resources in the form of meat, fruits, leaves, or corpses. Beaver are not the direct providers of water, in the way that prey are a direct resource for predators, or leaves are food for caterpillars.

Now consider the autogenic equivalents of beaver (Fig. 1, case 3). Simple examples are the growth of a forest or a coral reef. Trees and corals are direct sources of food and living space for numerous organisms, but the production of branches, leaves or living coral tissue does not constitute engineering. Rather, it conforms to case 1 in Fig. 1 (the direct provision of resources). However, the development of the forest or the reef results in physical structures which do change the environment and modulate the distribution and abundance of other resources.

Table 1. Examples of organisms acting as ecosystem engineers. Classification according to Fig. 1. Additional examples are discussed in the text.

Organism	Habitat	Activity	Impact	Refs.
Case 2 (allogenic)				
American alligators, <i>Alligator mississippiensis</i>	Everglades National Park	create wallows	retain water in droughts; provide refuges for fish, fish-eating birds, etc.	Finlayson & Moser (1991)
Rabbits, <i>Oryctolagus cuniculus</i> , badgers, <i>Meles meles</i>	Europe	dig extensive burrows (rabbit warrens, badger setts)	burrows occupied by other species, e.g. fox, <i>Vulpes vulpes</i> , and by many invertebrates	Southern (1964); Neal & Roper (1991)
Case 3 (autogenic)				
Marine phytoplankton	Gulf of Maine	blooms of phytoplankton particles scatter and absorb light in upper layers of water column	enhance warming of surface waters that may initiate development of thermocline	Townsend et al. (1992)
Microalgae in sea ice	Antarctica	scatter and absorb light within ice and underlying seawater; reduce strength of ice	enhance melting and break up of ice	Bynitskiy (1986); Arrigo et al. (1991)
Freshwater phytoplankton	Lake St. George, Ontario	intercept light in upper water column; small algal spp. more effective than large spp.	light interception leads to shallower mixing depth, lower metalimnetic temperatures and lower heat content of water column	Mazumder et al. (1990)
Cyanobacteria and other nonvascular plants	desert and semi-desert soils	exude mucilaginous organic compounds	glue the organisms, organic matter and soil particles together to form a microphytic crust; change infiltration, percolation, retention and evaporation of water; reduce soil erosion; affect seedling emergence	West (1990)
Bog moss, <i>Sphagnum</i> spp.	Northern and western Britain	build 'blanket' and 'raised' bogs via accumulated peat	major changes in hydrology, pH, and topography	Tansley (1949)
Submerged macrophytes	freshwater lakes, ponds and rivers	grow to create weed beds	attenuate light; steepen vertical temperature gradient; retard flow; enhance sedimentation; oxygenate rhizosphere	Carpenter & Lodge (1986)
Forest trees (broad-leaved and coniferous)	Hubbard Brook Experimental Forest, New Hampshire	shed branches and trunks into streams	create debris dams; alter morphology and stability of stream channels, storage and transport of dissolved organic matter and sediments; different tree species may create dams which differ in persistence	Likens & Bilby (1982); Hedin et al. (1988)
Higher plants	ubiquitous	dead leaves etc. accumulate as litter	alter microenvironment of soil; change surface structure, affecting drainage, and transfer of heat and gasses; act as physical barrier for seeds and seedlings; numerous impacts on structure and composition of plant communities	Facelli & Pickett (1991)
Terrestrial plants in 29 families, with >1,500 species	ubiquitous	grow structures (modified leaves, leaf axils etc.) that impound water	create small aquatic habitats, supporting a highly specialised insect fauna	Fish (1983)
Case 4 (allogenic)				
Marine meiofauna (protozoa and representatives of many invertebrate phyla)	ubiquitous	biodeposition, bioturbation, porewater circulation, and faecal pellet production	change physical, chemical and biological properties of sediments; change direction and magnitude of nutrient fluxes; increase oxygenation of sediments	Reichelt (1991)
Marine burrowing macrofauna	ubiquitous	burrow into and redistribute sediments; bioturbation; burrow ventilation	create dynamic sediment mosaics; actively transport solutes into burrows; increase oxygenation of sediments; stimulate microflora; increase decomposition rates	Anderson & Kristensen (1991); de Wilde (1991); Meadows & Meadows (1991b)

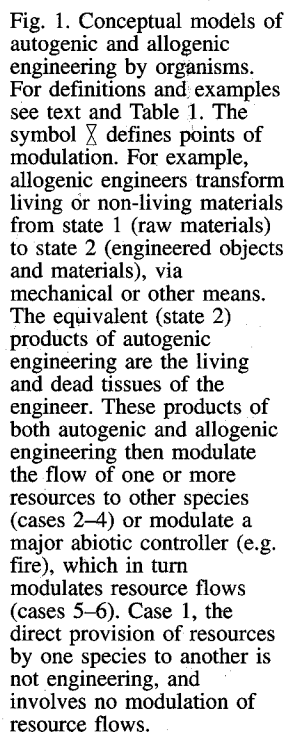
(cont.)

Tab. 1. (cont.)

Organism	Habitat	Activity	Impact	Refs.
Marine zooplankton	ubiquitous	filter living, dead organic and inorganic (e.g. clay) particles, and concentrate into faecal pellets	sinking faecal pellets important in vertical transport and exchange of elements and organic compounds in oceans	Dunbar & Berger (1981); Wallace et al. (1981); Fowler & Knauer (1986)
Fiddler crab, <i>Uca pugnax</i>	New England salt marsh	dig burrows	increase soil drainage and oxidation-reduction potential; increase decomposition rates; increase primary production at intermediate tidal heights	Bertness (1985)
European periwinkle, <i>Littorina littorea</i>	New England rocky beach	bulldoze sediments from hard substrates	prevent sediment accumulation and hence growth and establishment of algal canopy; algae are case 3 engineers and further increase sedimentation rates; faunal composition markedly different with and without snails	Bertness (1984a)
Snails, <i>Euchondrus</i> spp.	Negev desert	eat endolithic lichens and the rock they grow in	increase rate of nitrogen cycling, soil formation and rock erosion	Shachak et al. (1987); Jones & Shachak (1990)
Bagworm caterpillars, <i>Penestoglossa</i> sp.	Golden Gate Highlands, South Africa	eat endolithic lichens and construct larval shelters ('bags') from quartz crystals	small increase in erosion rate, nutrient cycling and soil formation	Wessels & Wessels (1991)
Mound-building termites, Isoptera	widespread in tropics and subtropics	mound and subterranean gallery construction; redistribution of soil particles	change mineral and organic composition of soils; alter hydrology and drainage	Wood & Sands (1978); Lal (1991)
Ants, Formicidae	ubiquitous	nest and subterranean gallery construction; redistribution of soil particles	change local structure and composition of soils; alter 'above nest' vegetation; produce microsite enrichment	Elmes (1991)
Earthworms, Lumbricidae, Megascolecidae	ubiquitous	burrowing, mixing and casting	change mineral and organic composition of soils; affect nutrient cycling; alter hydrology and drainage; affect plant population dynamics and community composition	Lal (1991); Thompson et al. (1993)
Blind mole rats, <i>Spalax ehrenbergi</i>	Israel	digging and tunnelling	move large quantities of soil; increase aeration; create distinctive ecosystem	Heth (1991)
Mole rats, Bathyergidae (several genera)	South African lowland fynbos	digging and tunnelling	create impressive, cratered landscapes, with effects on soil formation, plant productivity and species composition	Richardson et al. (in press)
Prairie dogs, <i>Cynomys</i> spp.	North American short and mixed grass prairie	continual intense disruption by burrowing, creating soil mounds	change physical and chemical properties of soil persisting for 100–1000s of years	Whicker & Detling (1988)
Pocket gophers, <i>Geomys bursarius</i>	North American grasslands and arid shrublands	construct tunnels and move soil to surface mounds	alter patterns and rates of soil development, nutrient availability and microtopography; change plant demography, diversity and primary productivity; affect behaviour and abundance of other herbivores	Huntly & Inouye (1988); Moloney et al. (1992)
Indian crested porcupine, <i>Hystrix indica</i>	Negev desert	digging for food	dig up to 2–3 holes m ⁻² ; diggings accumulate organic matter, runoff water; create favourable sites for seed germination	Yair & Rutin (1981); Gutterman (1982)
Elephants, <i>Loxodonta africana</i>	East African woodland and savannah	physical disturbance and destruction of trees and shrubs	widespread vegetation changes; alteration of fire regime; effects on food supply and population dynamics of other animals; ultimately changes in soil formation, riparian zones, and biogeochemical cycling	Naiman (1988)

(cont.)

Organism	Habitat	Activity	Impact	Refs.
Case 5 (autogenic) and case 6 (allogenic) (examples combining elements of both)				
Crustose coralline algae, <i>Porolithon</i> , <i>Lithophyllum</i>	coral reefs	overgrow and cement together detritus on outer algal ridge of barrier reef	break force of water and protect corals against major wave action; effect via own bodies (case 5) and secretion of 'cement' (case 6)	Anderson (1992)
Ribbed mussels, <i>Geukensia demissa</i>	Rhode Island <i>Spartina</i> salt marsh	secrete byssal threads, and form dense mussel beds	on marsh edge, dense beds of mussels (case 5) and byssal threads (case 6) bind and protect sediments and prevent physical erosion and disturbance, e.g. by storms	Bertness (1984b)



This modulation constitutes autogenic engineering. Trees alter hydrology, nutrient cycles and soil stability, as well as humidity, temperature, windspeed and light levels (see Holling 1992); corals modulate current speeds, siltation rates and so on. It is obvious, but surprisingly rarely explicitly stated, that numerous inhabitants of the habitats so created are dependent upon the physical conditions modulated by the autogenic engineers, and upon resource flows which they influence but do not directly provide; without the engineers, most of these other organisms would disappear.

One further example may help to clarify the distinction between case 1 and case 3. The growth of seagrass beds modulates ocean currents, which in turn may alter sedimentation rates and hence food supplies for other organisms with substantial effects upon their performance (e.g. growth and survival in the clam *Mercenaria mercenaria* (Irlandi and Peterson 1991)). The direct provision of food or living space by seagrasses (case 1) is not critical for *Mercenaria* but the clam's survival is nonetheless dependent upon these plants.

It could be argued that the growth of tree-trunks, branches, reefs or similar substantial biological structures (case 1, Fig. 1) itself constitutes ecosystem engineering. Inclusion or exclusion is a matter of choice. We have chosen to exclude it (whether it is the provision of food or of 'architecture' (Southwood et al. 1979 and Lawton 1983)) when the structures are considered solely and directly as resources, because this differs in kind from the remaining cases in Fig. 1. To qualify for our definition of an ecosystem engineer, an organism must modulate the supply of other resources for other species, rather than be the direct provider of resources. The growth of biological structures is thus a necessary but not a sufficient requirement for autogenic engineering.

We can illustrate our arguments further by considering the simplest kind of allogenic engineering (case 2, Fig. 1). Various organisms make holes in tree trunks and branches, some quickly (woodpeckers), others more slowly (rot fungi). They transform wood without holes into wood with holes, and indirectly provide resources for other creatures, nesting and roosting cavities for birds and bats for instance. The holes are the resource, not the organisms that make them. Notice that if some of the holes fill up with water (Kitching 1983), the little ponds so created are examples of case 4, and are conceptually identical to beaver dams.

Inevitably there are some grey areas in this classification and at the risk of being pedantic it is worthwhile considering just one. The natural hollows and cavities formed at branch junctions and root bases as the tree grows, and which may subsequently fill up with water ('pans' sensu Kitching (1983)) are not the same as rot- or woodpecker-holes and they do not belong in case 4; rather they conform to case 3 (trees are now autogenic engineers because their biomass gives rise to water-filled hollows). Numerous examples of these 'phytotelmata' are summarised by Fish (1983) (Table 1).

It is not universally the case that plants are allogenic and animals are autogenic engineers. Enhanced rates of physical and chemical weathering of rocks into soil by algae or higher plants (Bloom 1978) constitute allogenic engineering (case 4). Plants may act either as autogenic or as allogenic engineers, and provide some of the most complex cases of ecosystem engineering, to which we now turn.

Autogenic (case 5) and allogenic (case 6) engineering are at the extremes of continua that merge with cases 3 and 4 respectively. Cases 5 and 6 have the common property that autogenic or allogenic engineers interact with, and modulate powerful abiotic forces, for instance fires or hurricanes. Examples in cases 5 and 6 are distinguished from cases 3 and 4 by the extreme magnitude of the processes modulated by the engineers, and by the fact that these major abiotic forces are themselves fundamental modulators of the distribution and abundance of resources.

Fire provides a particularly interesting case. It is logical, albeit unconventional, to regard the production of combustible living and dead biomass as autogenic engineering (case 5). Different species of plants produce different qualities and quantities of living and dead fuel, modulating the magnitude, intensity and duration of fire and, in turn, profoundly altering the supply of resources for many other species (Christensen 1985). High grassland productivity in Serengeti-Mara in the 1960s markedly increased the incidence of fire, resulting in conversion of savannah woodland to an alternative state – grassland – which is now maintained by elephants (Dublin et al. 1990). The effects of elephants as allogenic engineers are summarised in Table 1.

Plants also act as allogenic engineers (case 6). In Puerto Rico *Dacryodes excelsa* trees are able to withstand hurricanes because their extensive roots and root grafts bind and stabilise bedrock and superficial rocks; this species therefore dominates tropical mountain forests where hurricanes are common (Basnet et al. 1992).

Difficult cases: Pollinators, gall formers and cows

The richness of biological processes means that a completely satisfactory, comprehensive yet exclusive definition of ecosystem engineering may be impossible to achieve, although numerous examples are easy to classify (Table 1). Given the diversity of species interactions in nature, efforts to classify many other ecological phenomena suffer similar problems 'at the margin'.

Pollinators and gall-formers present an interesting challenge for our definition of engineering. Both have profound effects on the growth of plant tissue; in so doing, pollinators modulate the supply of resources for seed predators, and gall-formers create structures that are used not only by themselves for shelter and food, but also by inquilines (e.g. Askew 1975). Both types of interaction conform broadly to case 2 (Fig. 1). However, we do not find it helpful to regard pollinators as engineers, not least since self-pollination is case 1 and not engineering.

But it is possible to regard gall-formers as engineers for inquilines; they physically modify plant-tissues, and create new habitats and resources for other organisms. The distinction between pollinators and gall-formers is, however, a fine one.

Our definition of engineering also embraces other, unexpected ecological phenomena, for example dung masses produced by large herbivores. Cows turn grass into cow pats, which are then colonised by a rich community of invertebrates, dependent upon the pats for food and shelter (Mohr 1943). The physical structure and environment provided by the droppings is at least as important to its inhabitants as the concentration of food resources (Elton 1966). It does not stretch the definition of engineering too far to regard cows as allogenic engineers, turning grass into cow pats (case 2). We would be the first to admit, however, that it is an unconventional perspective. Similar remarks apply to faecal pellet production by oceanic zooplankton (Table 1). For these and other borderline cases, the common sense way to view the issue is to ask whether understanding the ecological interactions is enhanced by recognising the engineering dimension.

Human analogues

The parallels between ecological and human engineers are, not surprisingly, very close. Humans are tool-using organisms that specialise in engineering. While human engineering often has intent or purpose, it is probably true to say that the major reason why humans have such adverse effects on the environment is because of the unintended consequences of our activities as engineers. Indeed people are now the primary agents of environmental change in most areas of the world (Naiman 1988, Likens 1992). Many human activities, from dam-building and skyscraper construction to forest clearance and the dredging and canalization of water courses, conform exactly to cases in Fig. 1, in which humans are allogenic engineers, altering the physical environment and modifying the flow of resources to other species.

Construction of nesting boxes for birds and hives for bees are examples of case 2. Ploughing by farmers and the construction of dams and reservoirs by water engineers provide examples of case 4. Building harbours and sea walls to reduce storm damage from waves are examples of case 6. Humans mimic autogenic effects, using tools to construct glasshouses and build air conditioning plants (mimicking case 3), and by bulldozing fire breaks to counteract fire (mimicking case 5). We classify human engineering activities as heavy or light, construction, civil, heating, plumbing, and air-conditioning to name but a few. Organisms do all these jobs, and from a functional perspective we see no fundamental difference between human and non-human engineering.

Related concepts

The idea that some organisms alter the physical structure of their environment, with impacts on their own and other populations is not new. But earlier work either focuses on particular species and habitats and lacks generality, or takes a more general view but fails clearly to define ecological engineering, or to distinguish it from other processes. For example, in an important set of reviews dealing with animal influences on ecosystem dynamics, co-ordinated by Naiman (1988), engineering and direct trophic effects are interwoven. Within this series of papers, Huntly and Inouye (1988) explicitly describe pocket gophers *Geomys bursarius* as "soil engineers" because of their role as earth-movers. Gophers are, indeed, excellent examples of allogenic (case 4) engineers (Table 1).

Ecologists in general have paid surprisingly little attention to how environments are created and maintained; most appear content to follow Andrewartha and Birch (1954) in recognising "a place to live" and "weather" as two of the four essential features of species' environments, without formally considering the role of engineering in habitat modification, creation and maintenance.

Bioturbators

In marine benthic environments the activities of large burrowing animals are known to play a dominant role in determining the physical structure of sediments, altering habitat suitability for other species (Rhoads and Young 1970, Thayer 1979, Lopez and Levinton 1987, Meadows and Meadows 1991a, see also Table 1). Rhoads and Young (1970) called the process 'trophic amensalism' when large deposit feeders create unstable sediments, restricting the presence of suspension feeders and attachment by sessile epifauna. The term amensalism is reasonable, because the effect is asymmetrical and is a form of competitive exclusion (Lawton and Hassell 1981), but the mechanism is not trophic and clearly differs from normal exploitation competition for food. 'Trophic amensalism' is actually another good example of case 4 allogenic engineering brought about by bioturbation of sediments.

Patch dynamics

Numerous studies recognise the importance of patches of bare or different substrates in otherwise closed communities (e.g. Dayton 1971, Wiens 1976, Paine 1979, Pickett and White 1985). Patches may be created by physical disturbance (waves, fire, landslips) or by the activities of organisms (grazing, predation or engineering), or by interactions between engineering, trophic and physical processes. For some applications of patch dynamic theory the way in which patches are created may be less important than their existence. In general, however, we believe that it is desirable to recognise engineering as one of several distinct ways in which patches are created and maintained, particularly since the factors that control patch formation by engineers are often different from those controlling patch formation by abiotic forces.

Animal and plant artifacts

In their *Theory of Environment* Andrewartha and Birch (1984) define a framework for examining all the processes that impinge upon a single species population. This target species occupies the centrum of a web of directly and indirectly acting components, and Andrewartha and Birch point out that a link in the web may be another living organism or its artifact or residue. The Theory of Environment therefore clearly allows for engineering, without explicitly identifying it as a defined modifier in the web, or as a process worthy of study in its own right.

Meadows and Meadows (1991a) and Meadows (1991) review the environmental impacts of animal burrows and burrowing animals, and Hansell (1993) the ecological consequences of animal burrows and nests. Many of these artifacts (e.g. meiofaunal burrows, megapode nests, termite mounds and mole rat colonies) have landscape level effects, and serve to concentrate and redistribute resources for other species – that is they are classic examples of ecological engineering (Table 1).

Meadows (1991) points out that there are “underlying similarities between the impact of [burrowing] animals from different terrestrial and aquatic habitats on environmental change and modification.” He provides a formal system to quantify the impacts of burrowing, distinguishing between animals with large per capita but geographically restricted effects (e.g. badgers) and those species with small per capita effects that nevertheless, because of their abundance and distribution, have impacts on entire landscapes (e.g. earthworms). Hansell (1993) recognises that the “services and substances of the builders create a new range of habitat niches which can be exploited by a wide variety of specialists” and suggests that “the presence of nest builders and burrowers can ... significantly contribute to species diversity in habitats.” The examples provided by both authors all conform to either case 2 (other species use the nests and burrows) or case 4 (species respond to changes in distribution and abundance of resources). Their work therefore differs from ours only in its more restricted focus.

Extended phenotypes

The importance of animal artifacts is also recognised by Dawkins (1982), as an example of species' extended phenotypes. Dawkins writes (p.200): “A beaver dam is built close to the lodge, but the effect of the dam may be to flood an area thousands of square meters in extent. As to the advantage of the pond from the beaver's point of view, the best guess seems to be that it increases the distance the beaver can travel by water, which is safer than travelling by land, and easier for transporting wood. ... If this interpretation is right the lake may be regarded as a huge extended phenotype.” Dawkins recognises other products of animal engineering as extensions of species' phenotypes and hence subject to natural selection, including caddis-fly cases, termite mounds and birds' nests.

He also points out that not every example of what we are now calling allogenic engineering can be regarded as an extended phenotype, because impacts on the environment are of no consequence to the engineer's fitness and hence are not subject to natural selection. A good example would be water-filled footprints made by an ungulate. The distinction between engineering that is subject to natural selection (because it is an extended phenotype) and engineering that is not ('accidental' engineering) appears to be unimportant in terms of its shorter-term ecological consequences; all types of engineering modify and modulate resource flows for other organisms. But there may be interesting longer-term differences, particularly in the nature of the feed-back loops that operate on 'extended phenotype' versus 'accidental' forms of engineered artifacts. We return to this point later.

Keystone species

Keystone species (Paine 1969, Krebs 1985, Daily et al. 1993) play a critical role in determining community structure. By definition, removal of keystone species causes massive changes in species composition and other ecosystem attributes. The critical links are usually regarded as trophic and therefore within the realm of traditional ecological thinking. For example, removing top predators has a cascading effect throughout the foodweb, altering species composition and hence physical structure and nutrient cycling at lower levels (Estes and Palmisano 1974, Carpenter et al. 1987).

But critical effects frequently involve engineering, for example via disturbance (e.g. bioturbators (Thayer (1979), above; case 4). In the frequently cited example of sea-otters *Enhydra lutris*, removal of otters leads to an increase in sea urchins (*Strongylocentrotus* sp.) and hence to the disappearance of kelp beds, which in turn changes wave action and siltation rates, with profound consequences for other inshore flora and fauna (Estes and Palmisano 1974). Kelp are autogenic engineers (case 3); removal of kelp by urchins is, amongst other things, allogenic engineering (case 4). In other words, in this familiar example, the species traditionally regarded as the keystone (sea otter) has major effects because it changes the impact of one engineer (urchin) on another (kelp), with knock-on effects on other species in the web of interactions. The equally well known impact of kangaroo rats (*Dipodomys* spp.) on desert vegetation occurs because the rodents not only eat seeds but also cause considerable physical disturbance. By burrowing and moving large quantities of soil they create many shallow pits and little mounds, which facilitate decomposition and the establishment of annual plants (case 4 engineering) (Brown and Heske 1990).

Direct effects of keystone species via their role as engineers have recently been reported by Daily et al. (1993). Red-naped sapsuckers *Sphyrapicus nuchalis* (a type of woodpecker) act as keystone species in two ways in Colorado subalpine meadows. Their nesting holes

drilled in aspens, *Populus tremuloides*, are essential nesting sites for two species of swallows (case 2); the swallows are missing from the community in the absence of sapsuckers. Feeding holes drilled by the sapsuckers in willows, *Salix* spp., also make sap flows available to several birds, mammals and insects (directly changing the distribution and abundance of this resource for other species – and therefore again conforming to case 2).

It is theoretically possible (though we think it will be uncommon in practice) for a keystone species to exert its effects entirely trophically, without also acting as an engineer, or without changing the engineering role of other species in the web. On the other hand, many engineers are keystone species even though they play relatively minor roles in community food webs.

Krebs concludes his textbook review of keystone species as follows: "Keystone species may be relatively rare in natural communities, or they may be common but not recognised (our emphasis). At present, few terrestrial communities are believed to be organised by keystone species, but in aquatic communities keystone species may be common". We believe that such views probably reflect a consensus among ecologists. They persist because we have failed to recognize the role of ecosystem engineers as keystone species. It is trite, but true, that a forest is a forest because it has trees, which not only provide food and living space but which also autogenically engineer the forest climate, and modulate the flows of many other resources to forest inhabitants, both above- and below-ground. Many single species of trees in temperate or boreal forests (with low tree-species richness) are both keystone species and significant ecosystem engineers.

Our views are very close to Holling's (1992) *Extended Keystone Hypothesis*, in which he argues that "all terrestrial ecosystems are controlled and organised by a small set of key plant, animal, and abiotic processes that structure the landscape at different scales." We would add two points. First a critical, but not exclusive controlling mechanism is some form of engineering; and second, we believe that keystone engineers occur in virtually all habitats on earth, not just terrestrial ones.

'Top down' vs 'bottom up', asymmetrical and indirect effects

Traditional population models focus on reciprocally coupled pairs of interactions, interspecific competition (-/-), enemy-victim (-/+) and so on (Williamson 1972). Highly asymmetrical competitive interactions (amensalism; 0/-) are common, possibly the norm, in some situations (Lawton and Hassell 1981). Enemy-victim interactions may also be asymmetrical (donor-controlled; 0/+), that is prey abundance controls predator abundance, but not vice versa (Lawton 1989, Hawkins 1992), with a growing debate in ecology about the relative importance of such 'bottom up' vs 'top down' effects (Hunter and Price

1992). Ecological engineering adds enormously to the catalogue of important, highly asymmetrical species interactions, because engineers impact upon many taxa (positively or negatively), but there may often be no direct, reciprocal effects of the impacted species upon the population of engineers.

One example will suffice. Beaver beneficially influence the abundances of aquatic biota, but not vice versa; that is they have massive 'bottom up' effects (o/+) that benefit numerous other aquatic organisms. Their activities are also detrimental to terrestrial species living upstream (and perhaps downstream) from the dam (o/-) just as bioturbators exclude sessile epifauna requiring stable substrates (see above). Generally we expect both the positive and negative effects of engineers to be highly asymmetrical.

This is not to say that there cannot be any feedbacks from organisms in the engineered habitat, back to the engineer. Undoubtedly there are, although feedback pathways are probably often rather long, indirect, and frequently slow. They remain virtually unstudied. For some engineers, it is difficult to imagine any reciprocal effects. For instance, the insect inhabitants of abandoned birds' nests (e.g. some tineid moths in the genus *Monopis* and staphylinid beetles in the genus *Microglotta* (Walsh and Dobb 1954, Emmet 1979)) probably never encounter the builder. Gophers, in contrast, engineer soil and change vegetation composition, biomass and productivity (Table 1); in turn, grasshopper populations become more abundant in the vicinity of gopher mounds (Huntly and Inouye 1988). Two feedbacks may operate on gophers. The first is reasonably well documented, positive and relatively direct, via plants that are food for gophers; soil disturbance favours the plant species that gophers prefer to eat. Second, it is at least conceivable, but untested, (D. Tilman, pers. comm.) that grasshoppers compete with gophers for food, providing a longer, negative feed-back loop on gopher numbers.

We predict that if feed-backs exist at all between engineers and the organisms they affect, they will characteristically be indirect, involving several intermediate processes and species.

Spatial and temporal scales

The impact of an ecological engineer depends upon the spatial and temporal scale of its actions. Water filled woodpecker holes and beaver dams may both be examples of case 4 engineering, but there is not much doubt about which is the more significant ecological phenomenon. Six factors scale the impact of engineers. They are:

- (i) Life time per capita activity of individual organisms.
- (ii) Population density.
- (iii) The spatial distribution, both locally and regionally, of the population.

- (iv) The length of time the population has been present at a site.
- (v) The durability of constructs, artifacts and impacts in the absence of the original engineer.
- (vi) The number and types of resource flows that are modulated by the constructs and artifacts, and the number of other species dependent upon these flows.

Thus, the most obvious ecological engineering is attributable to species with large per capita effects, living at high densities, over large areas for a long time, giving rise to structures that persist for millennia and which affect many resource flows – for instance mima mounds created by fossorial rodents, including gophers (Cox and Gakahu 1985, 1986, Cox et al. 1987, Naiman 1988). Autogenic engineers may also have massive effects; as Holling (1992) succinctly states: “To a degree, ... the boreal forest ‘makes its own weather’ and the animals living therein are exposed to more moderate and slower variation in temperature and moisture than they would otherwise be.” Boreal forest trees have large per capita effects on hydrology and climatic regimes, occur at high densities over large areas, and live for decades. But their impacts as autogenic engineers may have a relatively short memory if the forest is logged.

Organisms with small individual impacts can also have huge ecological effects, providing that they occur at sufficiently high densities over large areas, for sufficient periods of time. Burrowing meiofauna and bogforming *Sphagnum* mosses (Table 1) are good examples. Accumulated *Sphagnum* peat may persist for hundreds to thousands of years after the death of the living moss.

Ecological engineers may also enhance and speed up large scale physical processes, including geological erosion and weathering (Yair and Rutin 1981, Krumbein and Dyer 1985, Hoskin et al. 1986). Examples of rock-eating snails and caterpillars are listed in Table 1. Worldwide, but especially in the tropics, heavily undercut coastal cliffs of sedimentary rock are apparently being eroded by tides and storms. In fact the process is greatly accelerated by two groups of engineers, both with low per capita effects, but very abundant. Cyanobacteria (*Hyella* spp.) bore the rock and are food for chitons which rasp away the rock to reach them, apparently speeding up coastal erosion by an order of magnitude or more (Krumbein and Dyer 1985). Similarly, organisms whose shells, body parts and dead tissues help form sedimentary rocks, coal and soil (e.g. molluscs, diatoms and many higher plants) create structures whose effects on ecosystems persist for eons.

Engineering impacts are often greatest when the resource flows that are modulated are utilised by many other species, or when the engineer modulates abiotic forces that affect many other species. Not surprisingly, engineering that effects soils, sediments, rocks, hydrology, fire and hurricanes provides some of the most striking examples.

We know of very few field manipulation experiments

designed to quantify the impact of ecosystem engineers by removing or adding species. Studies by Bertness (1984a,b, 1985) are excellent examples of manipulative experiments on both allogenic (cases 4 and 6) and autogenic (case 5) engineers (Table 1). A recent study by Hall et al. (1993) shows the potential power of field manipulations for disentangling per capita impacts from population impacts (although in the present context it is not ideal because predation and disturbance [case 4 engineering] effects are confounded). Edible crabs (*Cancer pagurus*) hunting for prey dig pits in shallow subtidal areas of the west coast of Scotland. The pits are conspicuous features of the seabed topography, yet exclusion of crabs from areas of the sea bed for twelve months failed to reveal any landscape-level effects of crab pits, either on substrate structure and composition (particle sizes, organic carbon etc.) or faunal diversity, composition and abundance. Crabs appear not to be abundant enough to significantly alter community structure, either by predation or by engineering, despite large and visually conspicuous individual impacts. This example contrasts markedly with the substantial effects of fiddler crabs (*Uca pugnax*) on productivity, decomposition, oxygenation and drainage in a New England salt marsh, revealed by experimental removal of crabs (Bertness 1985) (Table 1).

Another extremely poorly researched problem is the way in which the persistence of the products or effects of engineering influence population, community and ecosystem processes. If engineers make long-lived artifacts, then their effects will usually, also, be long lived. But ephemeral products can also have long-term impacts. For example, faecal pellets produced by marine zooplankton (Table 1) decompose relatively quickly, but not before they have sunk into the deep ocean, removing nutrients from surface waters for millennia.

A useful thought experiment is to consider taking the engineers away and imagining the consequences. In many cases their impacts are ephemeral, operating on timescales shorter than, or similar to, the lifetime of the organism itself (e.g. the nests of small passerine birds). But in other cases, the engineers leave monuments with impacts that extend many lifetimes beyond their own – mima mounds, termite nests, buffalo wallows, beaver dams, peat, sedimentary rocks and so on. These persistent effects must greatly slow down rates of ecological change, and impose considerable buffering and inertia on many ecological systems and processes. Rates of decay, the ‘half-lives’ of the products of ecological engineers, and their contributions to population, community and ecosystem stability, resistance and resilience (Pimm 1984) deserve much more attention from theoretical and experimental ecologists.

Evolutionary effects

Earlier, we distinguished between engineered artifacts subject to natural selection as extended phenotypes, and 'the rest' – by-products of some other activity that are not themselves directly subject to selection; water-filled ungulate hoof prints were given as an example. Extended phenotype engineering, by definition, creates structures or effects that directly influence individual fitness (or colony fitness in social insects), for instance a beaver dam, woodpecker hole or termite mound. But the evolutionary effects of extended phenotype engineering, other 'accidental' engineering, and of organisms in the engineered habitat upon the engineer are far from straightforward, and generally unstudied. For example, the extended phenotype may be subject to selection from the physical environment, implying no biotic feedbacks. Or it may be subject to selection from polyphagous predators (e.g. nest-robbing snakes) that are in no way dependent upon the engineered habitat for their existence. On the other hand, engineering might generate habitats with species populations that, ultimately, feed back positively or negatively upon the engineers, via predation, disease, competition, or the invasion of additional species of engineers.

Some engineering undoubtedly has had evolutionary effects on other organisms. One of the best documented examples in the fossil record is a decline, from the Devonian onwards, in the diversity of immobile suspension feeders living on soft marine substrata, as mobile taxa diversified (Thayer 1979). Thayer attributes these major changes in the structure of marine benthic communities to the evolution of 'biological bulldozers' – bioturbators or engineers – that disturb sediments (see above), fouling, overturning and burying immobile suspension feeders, which are now largely confined to hard substrates. Thayer also speculates that by increasing the turnover rate of nutrients in sediments of continental shelves, bulldozers may have contributed to the Mesozoic diversification of phytoplankton (coccoliths, diatoms and dinoflagellates) and, via trophic linkage, to diversification of zooplankton (radiolaria and foraminifera).

An intriguing, but rarely considered problem is the degree to which engineering by other taxa might similarly have changed major patterns in the radiation and extinction of earth's biota. To the extent that engineers shape and modify most, possibly all, habitats on earth (see below), and given the trite but true observation that all organisms are adapted to their environment, engineering in some form or other must have driven, or contributed to, the evolution of myriads of species. But the extent to which major patterns of evolution might have been different if some types of ecological engineering had not evolved, or had taken a different form, is almost entirely unknown.

Questions

We finish with a haphazard list of open questions.

Are there any ecosystems on earth that have not been physically engineered by one or more organisms to a significant degree? A cautious, preliminary answer is no, there are not. We initially thought that it would be difficult to identify evidence of ecosystem engineering by biota in the open waters of oceans or large lakes, or in snow fields and ice packs, for instance. But the examples in Table 1 show that this prediction was wrong. We currently cannot identify any habitat on earth that is not engineered in some way by one or more species.

How many species (or what proportion of species) in various communities have a clearly defined and measurable impact as engineers? Is it 10%, 1% or 0.1%? What are the relative frequencies of the five classes of engineering identified in Fig. 1, say in terms of the numbers of species acting as engineers? Cases 5 and 6 are presumably rather rare; but how much rarer are they than the others types of engineering? Is the predominance of examples involving burrowing animals in case 4 real (we could easily have included still more examples) or is it because this form of engineering is particularly easy to see?

Are the most physically structured ecosystems (or subsystems, e.g. soil or sediments) the ones in which engineers are most important? How much of the structure have they created and modified?

How many other species are impacted by engineers in any ecosystem? What happens to species richness if we remove or add engineers? How much of the effects of keystone species are due to engineering versus trophic effects? Earlier, we speculated that few keystone effects are purely trophic; is this hypothesis correct? How do engineering and trophic relations interact?

Should conservationists and nature reserve managers pay more attention to the role of ecological engineers in maintaining ecosystem integrity, or do managers largely know which the important species are, without having put a name to the idea, or without having recognising the common themes identified in this paper?

How should we model engineering? The biological details in each case will be complicated, and there are at least five kinds of engineering; but there are also several sorts of interspecific competition, various ways of being a herbivore and a rich catalogue of enemy-victim interactions, none of which has stopped theoreticians from developing appropriate families of relatively simple models to understand and to predict the dynamics of such interactions. There is, in principle, no reason why we cannot write down the equation:

$$d\text{mayfly}/d\text{beaver} = F(x, y, z),$$

where mayfly populations respond to changes in beaver numbers on long time-scales, and where the response is influenced by various key variables, including feedbacks

to beaver from other components in the engineered habitat. Interesting theoretical questions centre on the generation time of the engineer, the half-life of whatever it is that is engineered, the rate of restoration of non-engineered habitat, the generation times of impacted species, and their various interactions. There are intriguing problems of nested time-scales, delayed responses, donor-control, long chains of indirect interactions and so on, that might usefully be explored using relatively simple models.

Extending these arguments, there is no reason in principle why processes driven by engineering should not be coupled to the rich diversity of trophic linkages to create not simply descriptions and models of foodwebs (e.g. Pimm et al. 1991), but of *interaction webs*, that more accurately reflect interactions in communities and ecosystems. The conceptual framework brought together by Carpenter (1988) under the title of 'complex interactions' should clearly embrace engineering as one component.

Intriguingly, once the need to define and study interaction webs is recognised, it also becomes apparent that ecological engineering as we have defined it is only part of the picture. We have focused on physical state changes wrought on biotic and abiotic materials by organisms. But physical engineering is not the only form of ecosystem engineering that organisms carry out. Chemical and transport engineering are two obvious other forms that we consider will conceptually fit into the same general classification scheme. For brevity, we have not examined them here.

Last, but by no means least, what new insights will the concept of engineering bring to ecology? This review attempts to define and classify the phenomenon. But definition and classification are merely a small beginning, not an end. Are there major patterns in the distribution and abundance of organisms that might be explained, at least in part, by ecosystem engineering? What are they? What predictions might we make that would not have been made without the conceptual framework provided here, or something akin to it? We do not, currently, know the answers to these questions. But if the notion of organisms as ecosystem engineers results simply in an accumulation of 'just-so' stories, it will not have been particularly useful.

Acknowledgements – This work was supported by the Mary Flagler Cary Charitable Trust, the US–Israel Binational Science Foundation, and the NERC Centre for Population Biology, UK. Numerous colleagues have allowed us to sharpen and refine our ideas about engineering by discussing problems with them, and have generously provided us with examples and references; to all of them we express our sincere thanks. Contribution to the programme of the Institute of Ecosystem Studies. Publication 171 from the Mitrani Center.

References

- Anderson, F. O. and Kristensen, E. 1991. Effects of burrowing macrofauna on organic matter decomposition in coastal marine sediments. – Symp. zool. Soc. Lond. 63: 69–88.
- Anderson, R. A. 1992. Diversity of eukaryotic algae. – Biodiv. Conserv. 1: 267–292.
- Andrewartha, H. G. and Birch, L. C. 1954. The distribution and abundance of animals. – University of Chicago Press, Chicago.
- and Birch, L. C. 1984. The ecological web. More on the distribution and abundance of Animals. – University of Chicago Press, Chicago.
- Arrigo, K. R., Sullivan, C. W. and Kremer, J. N. 1991. A bio-optical model of Antarctic sea ice. – J. Geophys. Res. 96 C6: 10581–10592.
- Askew, R. R. 1975. The organisation of chalcid-dominated parasitoid communities centred upon endophytic hosts. – In: Price, P. W. (ed.), Evolutionary strategies of parasitic insects and mites. Plenum, New York, pp. 130–153.
- Basnet, K., Likens, G. E., Scatena, F. N. and Lugo, A. E. 1992. Hurricane Hugo: damage to a tropical rain forest in Puerto Rico. – J. Trop. Ecol. 8: 47–55.
- Begon, M., Harper, J. L. and Townsend, C. R. 1990. Ecology. Individuals, populations and communities, Second ed. – Blackwell Scientific, Boston.
- 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.
- Bloom, A. L. 1978. Geomorphology. – Prentice Hall, New York.
- Brown, J. H. and Heske, E. J. 1990. Control of a desert-grassland transition by a keystone rodent guild. – Science 250: 1705–1707.
- Buynitskiy, V. K. 1968. The influence of microalgae on the structure and strength of Antarctic sea ice. – Oceanology 8: 771–776.
- Carpenter, S. R. (ed.). 1988. Complex interactions in lake communities. – Springer, New York.
- and Lodge, D. M. 1986. Effects of submerged macrophytes on ecosystem processes. – Aquat. Bot. 26: 341–370.
- , Kitchell, J. F., Hodgson, J. R., Cochran, P. A., Elser, J. J., Elser, M. M., Lodge, D. M., Kretchmer, D., He, X. and von Ende, C. N. 1987. Regulation of lake primary productivity by food web structure. – Ecology 68: 1863–1876.
- Christensen, N. L. 1985. Shrubland fire regimes and their evolutionary consequences. – In: Pickett, S. T. A. and White, P. S. (eds), The ecology of natural disturbance and patch dynamics. Academic Press, Orlando, FL, pp. 85–100.
- Cox, G. W. and Gakahu, C. G. 1985. Mima mound microtopography and vegetation pattern in Kenyan savannas. – J. Trop. Ecol. 1: 23–36.
- and Gakahu, C. G. 1986. A latitudinal test of the fossorial rodent hypothesis of Mima mound origin. – Z. Geomorphologie 30: 485–501.
- , Lovegrove, B. G. and Siegfried, W. R. 1987. The small stone content of mima-like mounds in the South African Cape region. – Catena 14: 165–176.
- Daily, G. C., Ehrlich, P. R. and Haddad, N. M. 1993. Double keystone bird in a keystone species complex. – PNAS 90: 592–594.
- Dawkins, R. 1982. The extended phenotype. – Oxford University Press, Oxford.
- Dayton, P. K. 1971. Competition, disturbance, and community organisation: the provision and subsequent utilization of space in a rocky intertidal community. – Ecol. Monogr. 41: 351–389.
- Dublin, H. T., Sinclair, A. R. E. and McGlade, J. 1990. Ele-

- phants and fire as causes of multiple stable states in the Serengeti-Mara woodlands. – *J. Anim. Ecol.* 1990: 1147–1164.
- Dunbar, R. B. and Berger, W. H. 1981. Fecal pellet flux to modern bottom sediment of Santa Barbara Basin (California) based on sediment trapping. – *Geol. Soc. Amer. Bull.* pt.1 92: 212–218.
- Elmes, G. W. 1991. Ant colonies and environmental disturbance. – *Symp. zool. Soc. Lond.* 63: 1–13.
- Elton, C. S. 1966. The pattern of animal communities. – Methuen, London.
- Emmet, A. M. (ed.). 1979. A field guide to the smaller British Lepidoptera. – British Entomological and Natural History Society, London.
- Estes, J. A. and Palmisano, J. F. 1974. Sea-otters: their role in structuring nearshore communities. – *Science* 185: 1058–1060.
- Facelli, J. M. and Pickett, S. T. A. 1991. Plant litter: its dynamics and effects on plant community structure. – *Bot. Rev.* 57: 1–32.
- Finlayson, M. and Moser, M. (eds.). 1991. Wetlands. – International Waterfowl and Wetlands Research Bureau, Oxford.
- Fish, D. 1983. Phytotelmata: flora and fauna. – In: Frank, J. H. and Lounibos, L. P. (eds), *Phytotelmata: terrestrial plants as hosts for aquatic insect communities*. Plexus, Medford, NJ, pp. 1–27.
- Fowler, S. W. and Knauer, G. A. 1986. Role of large particles in the transport of elements and organic compounds through the oceanic water column. – *Prog. Oceanog.* 16: 147–194.
- Gutterman, Y. 1982. Observations on the feeding habits of the Indian crested porcupine (*Hystrix indica*) and the distribution of some hemiepiphytes and geophytes in the Negev desert highlands. – *J. Arid. Env.* 5: 261–268.
- Hall, S. J., Robertson, M. R., Basford, D. J. and Fryer, R. 1993. Pitdigging by the crab *Cancer pagurus*: a test for long-term, large-scale effects on infaunal community structure. – *J. Anim. Ecol.* 62: 59–66.
- Hansell, M. H. 1993. The ecological impact of animal nests and burrows. – *Funct. Ecol.* 7: 5–12.
- Hawkins, B. A. 1992. Parasitoid-host food webs and donor control. – *Oikos* 65: 159–162.
- Hedin, L. O., Mayer, M. S. and Likens, G. E. 1988. The effect of deforestation on organic debris dams. – *Verh. Internat. Verein. Limnol.* 23: 1135–1141.
- Heth, G. 1991. The environmental impact of subterranean mole rats (*Spalax ehrenbergi*) and their burrows. – *Symp. zool. Soc. Lond.* 63: 265–280.
- Holling, C. S. 1992. Cross-scale morphology, geometry, and dynamics of ecosystems. – *Ecol. Monogr.* 62: 447–502.
- Hoskin, C. M., Reed, J. K. and Mook, D. H. 1986. Production and off-bank transport of carbonate sediment, Black Rock, southwest Little Bahama Bank. – *Mar. Geol.* 73: 125–144.
- Hunter, M. D. and Price, P. W. 1992. Playing chutes and ladders: heterogeneity and the relative roles of bottom-up and top-down forces in natural communities. – *Ecology* 73: 724–732.
- Huntly, N. and Inouye, R. 1988. Pocket gophers in ecosystems: patterns and mechanisms. – *BioScience* 38: 786–793.
- Irlandi, E. A. and Peterson, C. H. 1991. Modification of animal habitat by large plants: mechanisms by which seagrasses influence clam growth. – *Oecologia* 87: 307–318.
- Jones, C. G. and Shachak, M. 1990. Fertilization of the desert soil by rock-eating snails. – *Nature* 346: 839–841.
- Kitching, R. L. 1983. Community structure in water-filled tree-holes in Europe and Australia – comparisons and speculations. – In: Frank, J. K. and Lounibos, L. P. (eds), *Phytotelmata: terrestrial plants as hosts for aquatic insect communities*. Plexus, Medford, NJ, pp. 205–222.
- Krebs, C. J. 1985. *Ecology. The experimental analysis of distribution and abundance*, Third ed. – Harper and Row, New York.
- Krumbein, W. E. and Dyer, B. D. 1985. This planet is alive – weathering and biology, a multi-faceted problem. – In: Drever, J. I. (ed.), *The chemistry of weathering*. D.Reidel Publishing Co., pp. 143–160.
- Lal, R. 1991. Soil conservation and biodiversity. – In: Hawksworth, D. L. (ed.), *The biodiversity of microorganisms and invertebrates: its role in sustainable agriculture*. CAB International, Wallingford, pp. 89–103.
- Lawton, J. H. 1983. Plant architecture and the diversity of phytophagous insects. – *Ann. Rev. Ent.* 28: 23–39.
- 1989. Food webs. – In: Cherrett, J. M. (ed.), *Ecological concepts*. Blackwell Scientific Publications, Oxford, pp. 43–78.
- and Hassell, M. P. 1981. Asymmetrical competition in insects. – *Nature* 289: 793–795.
- Likens, G. E. 1992. The ecosystem approach: its use and abuse. – Ecology Institute, Oldendorf/Luhe.
- and Bilby, R. E. 1982. Development, maintenance, and role of organic-debris dams in New England streams. – In: Swanson, F. J., Janda, R. J., Dunne, T. and Swanson, D. N. (eds), *Sediment budgets and routing in forest drainage basins*. USDA Forest Service General Technical Report PNW141. USDA Forest Service, Pacific Northwest Forest and Range Experimental Station, pp. 122–128.
- Lopez, G. R. and Levinton, J. S. 1987. Ecology of deposit-feeding animals in marine sediments. – *Quart. Rev. Biol.* 62: 235–260.
- Mazumder, A., Taylor, W. D., McQueen, D. J. and Lean, D. R. S. 1990. Effects of fish and plankton on lake temperature and mixing depth. – *Science* 247: 312–315.
- Meadows, P. S. 1991. The environmental impact of burrows and burrowing animals – conclusions and a model. – *Symp. zool. Soc. Lond.* 63: 327–338.
- and Meadows, A. (eds), 1991a. *The environmental impact of burrowing animals and animal burrows*. – Clarendon Press, Oxford.
- and Meadows, A. 1991b. The geotechnical and geochemical implications of bioturbation in marine sedimentary ecosystems. – *Symp. zool. Soc. Lond.* 63: 157–181.
- Mohr, C. O. 1943. Cattle droppings as ecological units. – *Ecol. Monogr.* 13: 276–298.
- Moloney, K. A., Levin, S. A., Chiariello, N. R. and Buttel, L. 1992. Pattern and scale in a serpentine grassland. – *Theoret. Pop. Biol.* 41: 257–276.
- Naiman, R. J. 1988. Animal influences on ecosystem dynamics. – *BioScience* 38: 750–752.
- , Johnston, C. A. and Kelley, J. C. 1988. Alteration of North American streams by beaver. – *BioScience* 38: 753–762.
- Neal, E. G. and Roper, T. J. 1991. The environmental impact of badgers (*Meles meles*) and their sets. – *Symp. zool. Soc. Lond.* 63: 89–106.
- Paine, R. T. 1969. A note on trophic complexity and community stability. – *Am. Nat.* 103: 91–93.
- 1979. Disaster, catastrophe, and local persistence of the sea palm *Postelia palmaeformis*. – *Science* 205: 685–687.
- Pickett, S. T. A. and White, P. S. (eds), 1985. *The ecology of natural disturbance and patch dynamics*. – Academic Press, Orlando.
- Pimm, S. L. 1984. The complexity and stability of ecosystems. – *Nature* 307: 321–326.
- , Lawton, J. H. and Cohen, J. E. 1991. Food web patterns and their consequences. – *Nature* 350: 669–674.
- Reichelt, A. C. 1991. Environmental effects of meiofaunal burrowing. – *Symp. zool. Soc. Lond.* 63: 33–52.
- Rhoads, D. C. and Young, D. G. 1970. The influence of deposit-feeding organisms on sediment stability and community trophic structure. – *J. Mar. Res.* 28: 150–178.
- Richardson, D. M., Cowling, R. M., Bond, W. J., Stock, W. D. and Davis, G. W. in press. Links between biodiversity and ecosystem function: evidence from the Cape Floristic Region. – In: Davis, G. W. and Richardson, D. M. (eds),

- Biodiversity and ecosystem function in Mediterranean-type ecosystems. Springer-Verlag, Heidelberg.
- Ricklefs, R. E. 1984. *Ecology*, Second ed. – Chiron Press, New York.
- Shachak, M., Jones, C. G. and Granot, Y. 1987. Herbivory in rocks and the weathering of a desert. – *Science* 236: 1098–1099.
- Southern, H. N. (ed.). 1964. *The handbook of British mammals*, First ed. – Blackwell Scientific, Oxford.
- Southwood, T. R. E., Brown, V. K. and Reader, P. M. 1979. The relationship of plant and insect diversities in succession. – *Biol. J. Linn. Soc.* 12: 327–348.
- Tansley, A. G. 1949. *Britain's green mantle*. – George Allen and Unwin, London.
- Thayer, C. W. 1979. Biological bulldozers and the evolution of marine benthic communities. – *Science* 203: 458–461.
- Thompson, L., Thomas, C. D., Radley, J. M. A., Williamson, S. and Lawton, J. H. 1993. The effect of earthworms and snails in a simple plant community. – *Oecologia* 95: 171–178.
- Townsend, D. W., Keller, M. D., Sieracki, M. E. and Ackleson, S. G. 1992. Spring phytoplankton blooms in the absence of vertical water column stratification. – *Nature* 360: 59–62.
- Wallace, G. T., Jr., Mahoney, O. M., Dulmage, R., Storti, F. and Dudek, N. 1981. First-order removal of particulate aluminium in oceanic surface water. – *Nature* 293: 729–731.
- Walsh, G. B. and Dibb, J. R. (eds.). 1954. *A coleopterist's handbook*. – The Amateur Entomologists' Society, London.
- Wessels, D. C. J. and Wessels, L.-A. 1991. Erosion of biogenically weathered Clarens sandstone by lichenophagous bagworm larvae (Lepidoptera; Psychidae). – *Lichenol.* 23: 283–291.
- West, N. E. 1990. Structure and function of microphytic soil crusts in wildland ecosystems of arid to semi-arid regions. – *Adv. Ecol. Res.* 20: 180–223.
- Whicker, A. D. and Detling, J. K. 1988. Ecological consequences of prairie dog disturbances. – *BioScience* 38: 778–785.
- Wiens, J. A. 1976. Population responses to patchy environments. – *Annu. Rev. Ecol. Syst.* 7: 81–120.
- de Wilde, A. W. J. 1991. Interactions in burrowing communities and their effects on the structure of marine ecosystems. – *Symp. zool. Soc. Lond.* 63: 107–117.
- Williamson, M. 1972. *The analysis of biological populations*. – Edward Arnold, London.
- Wood, T. G. and Sands, W. A. 1978. The role of termites in ecosystems. – In: Brian, M. V. (ed.), *Production ecology of ants and termites*. Cambridge University Press, Cambridge, pp. 245–292.
- Yair, A. and Rutin, J. 1981. Some aspects of the regional variation in the amount of available sediment produced by isopods and porcupines, northern Negev, Israel. – *Earth Surf. Proc. Land.* 6: 221–234.