

MINI- REVIEW

Minireviews provides an opportunity to summarize existing knowledge of selected ecological areas, with special emphasis on current topics where rapid and significant advances are occurring. Reviews should be concise and not too wide-ranging. All key references should be cited. A summary is required.

Characterizing ecosystem-level consequences of biological invasions: the role of ecosystem engineers

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Invasions by exotic species represent both threats to ecosystems as well as opportunities to learn more about them. Among the invaders that will have the largest impacts are those that directly modify ecosystems and thus have cascading effects for resident biota. Exotics can affect ecosystems by altering system-level flows, availability, or quality of nutrients, food, and physical resources (e.g. living space, water, heat or light). The invader-mediated control of physical resources, typically achieved through the modification of habitats, has received limited attention in invasion biology. This reflects a general trend in ecology, and only recently has the concept of ecosystem engineering been developed to account for the role of species that shape habitats.

Plants and animals in terrestrial and aquatic systems can both create and destroy structure. When introduced into ecosystems, these exotic engineers cause physical state changes with effects that ramify throughout the system. Although the consequences of these modifications are varied and complex, insight gained from general ecological principles offers an opportunity to predict what invaders will do upon their integration into systems. Examples from the literature suggest that introduced ecosystem engineers that increase habitat complexity or heterogeneity tend to cause abundances and/or species richness to rise, while those that decrease complexity tend to have the reverse effect. In assessing such patterns, however, it is critical to also consider spatial scales and the life habits of resident organisms. In addition to providing predictive power, recognition of engineering as a major means by which invasive species affect ecosystems provides a unifying theme for invasion biology and offers a chance to consider more fully the general role of species in ecosystems.

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A biological invasion is fundamentally a natural process, representing the arrival of a species into a location in which it did not exist in historical time (Carlton

1979). However, the rates, routes, and manners with which species now traverse the globe are wholly unprecedented (Elton 1958, Williamson 1996, Vitousek et

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al. 1997). In order to address the scale and impacts of this anthropogenic mixing of biotas, as well as offer an opportunity for basic biological insight, invasion biology has become a rapidly developing discipline with broad ecological and conservation implications (Elton 1958, Vermeij 1996, Williamson 1996, Carlton 1999).

A primary focus of invasion biology is assessing the impacts of invaders (Williamson 1996, Parker et al. 1999, Ruiz et al. 1999). Negative interactions between exotics and natives are among the most commonly considered consequences of invasion. Exotic species can be parasites or pathogens, often transmitted to natives via other species of invaders. For example, the introduction of the rinderpest virus into sub-Saharan Africa, transmitted through domestic cattle, decimated native ungulates (Dobson and Crawley 1994, McCallum and Dobson 1995). Exotics also can compete with natives for resources such as food or space. Examples of successful invasive competitors include snails (Race 1982, Brenchley and Carlton 1983, Byers 2000), squirrels (Okubo et al. 1989), and lizards (Petren and Case 1998). Direct consumption of natives by exotics is among the most familiar of invader impacts. Notorious exotic predators include the comb jelly *Mnemiopsis leidyi* in the Black Sea (Oguz et al. 2001), the brown tree snake (*Boiga irregularis*) in Guam (Savidge 1987), the carnivorous snail *Euglandina rosea* on Pacific islands (Cowie 1992), and filter-feeding clams in aquatic systems (Kimmerer et al. 1994, Vander Zanden et al. 1999). Exotics can have genetic effects through hybridization or altering gene flow of native species, and at larger spatio-temporal scales they homogenize biotas across biogeographic realms and alter evolutionary pathways (Carroll and Dingle 1996, Williamson 1996, Cox 1999). Invaders also can benefit natives. They can serve as food resources for resident biota (Carlton 1979, Singer et al. 1993, Reusch 1998, Crooks 2002), or facilitate natives through indirect or commensal relationships (Posey 1988, Crooks 1998a).

One of the most dramatic invader effects is the alteration of ecosystems, where an ecosystem is defined as the spatially-explicit association of abiotic and biotic elements within which there is a flow of resources, such as nutrients, biomass, or energy (Tansley 1935, Odum 1972, Golley 1993, Carpenter and Turner 1998, Dickinson and Murphy 1998). A variety of schemes have been developed to categorize ecosystem-level effects of invaders (Macdonald et al. 1989, Vitousek 1990, Williamson 1996, Gordon 1998, Parker et al. 1999), and it is often considered that there are three primary ways in which exotics can affect ecosystems (Vitousek 1990). First, exotics can differ from natives in their use of resources (typically considered to be nutrients), thus affecting resource availability for other species. For example, the introduction of the nitrogen-fixing plant *Myrica faya* on the lava flows of Hawai'i has allowed the growth of vegetation on nitrogen-poor sediments

(Vitousek et al. 1987). Second, exotics can alter the flow of energy or biomass by changing food webs, such as introducing a top predator into ecosystems (e.g. Savidge 1987). Third, exotics can affect disturbance regimes, such as the familiar examples of increased erosion attributed to introduced herbivores such as goats, sheep, and rabbits (Coblentz 1978, Chapuis et al. 1994).

Another fundamental means by which invaders have ecosystem-level effects is to change the physical structure of the ecosystem itself (Bertness 1984, Simberloff 1991, Schmitz et al. 1997, Crooks and Khim 1999). This is not readily accounted for in current considerations of invader impacts, however, and even in the literature of general ecology habitat modification received little attention until the recent development of the concept of ecosystem engineering (Jones et al. 1994, 1997b). A consideration of ecosystem engineering in the context of biological invasions offers valuable perspectives on exotic species impacts and a chance to further examine the general role of species that modify habitats. In this review, I will 1) characterize potential effects of exotic engineers on the physical environment, 2) provide some examples of how the physical alteration of ecosystems affects other biota, 3) identify patterns in community-level responses to invader-induced changes in habitat complexity, and 4) discuss how the recognition of engineering and habitat modification affects the classification of invaders' ecosystem-level effects.

Ecosystem engineering

Ecosystem engineering, a term introduced by Jones et al. (1994, 1997b), is defined as the indirect or direct control of resource availability mediated by an organism's ability to cause physical state changes in abiotic or biotic materials. Although there has been some debate regarding the semantics of "engineering" (Power 1997, Jones et al. 1997a), the physical alteration of habitats is clearly an important, yet not fully considered, effect of organisms (Brown 1995, Alper 1998, Bruno and Bertness 2001). Ecosystem engineering is in essence the creation, destruction, or modification of habitats. Physical resources that may be affected by ecosystem engineers are varied and include living space or "habitat", light, humidity, sediment, heat, water, and physical materials. For example, coral reefs directly provide living space, and also modulate abiotic forces such as currents that in turn affect resource supply to other organisms.

Jones et al. (1994, 1997b) distinguish between autogenic engineering, where organisms themselves are part of the engineered habitats (e.g. trees in a forest), and allogenic engineering, where organisms transform other living or non-living materials from one physical state to

another (e.g. dam creation by beavers). For example, trees autogenically engineer systems by creating structure in the form of a forest, and beavers allogically engineer systems by removing trees to create dams. A pathogen that directly altered the stand structure of trees also would be considered an allogenic engineer, whereas a disease agent that killed beavers would not because it has no direct effect on physical structure. Also, it is important to note that many organisms can autogenically and allogically engineer simultaneously (e.g. corals).

Abiotic and biotic effects of exotic engineers

Many examples of invaders that affect the physical nature of ecosystems can be found in the literature. These species span a number of taxa in both aquatic and terrestrial ecosystems (Table 1). This physical alteration of ecosystems typically has cascading effects on many other biota, although these biotic consequences are less well characterized because it is typically easier to measure the effects on physical ecosystem properties than to assess the many and variable ways in which species may respond to these changes. In this section, I will provide some examples of invader effects on physical ecosystem resources, and characterize some of the potential biotic effects of these ecosystem alterations. Community-level effects will be considered further in the following section.

Some of the most familiar exotic engineers are introduced, landscape-altering plants in terrestrial systems. Tamarisk, or salt cedar (*Tamarix* spp.), is a deep-rooted plant with high rates of evapotranspiration. In the arid southwestern U.S., these invaders can lower the local water table and cease water flows and seeps, thus impacting native plants and animals depending on this resource (Vitousek 1986, Randall 1993). Ice plant (*Mesembryanthemum crystallinum*) is another troublesome invader that forms dense monocultures on a variety of soil types (such as sand). This species concentrates salts at the sediment surface, to the detriment of competing plant species (Vivrette and Muller 1977, Vitousek 1986). Melaleuca, the paper bark tree (*Melaleuca quinquenervia*), is an aggressive invader of the sawgrass prairies of the Everglades. This large tree alters the architectural characteristics of the vegetation, essentially creating forests where none existed before (Ewel 1986). Australian pines (*Casuarina equisetifolia*), which also have created forests on some of Florida's formerly treeless coastlines, have had ecosystem effects that include increased erosion rates resulting from exclusion of native soil stabilizers (Schmitz et al. 1997). In addition, fallen pines can physically impede sea turtle nesting (Office of Technology Assessment 1993), although standing trees can block city lights and thus

promote nesting on some pine-infested beaches (Salmon et al. 1995). Another important engineering effect of invasive terrestrial plants, especially grasses, is the alteration of fire regimes (D'Antonio and Vitousek 1992). The change in the frequency and intensity of fires often appears to promote the further expansion of exotics at the expense of natives.

As on land, exotic plants in aquatic systems can be important habitat modifiers. For example, two introduced vascular plants, the Atlantic cordgrass *Spartina alterniflora* and the Japanese eelgrass *Zostera japonica*, are encroaching upon unvegetated tidal flats on the North American Pacific coast, a biologically rich habitat that is feeding grounds for fish and migratory shorebirds. The introduced cordgrass can grow lower in the intertidal than native cordgrass (*Spartina foliosa*) (Callaway and Josselyn 1992), whereas Japanese eelgrass is able to live higher in the intertidal than native eelgrass (*Zostera marina*) (Posey 1988). Within Connecticut brackish and salt marshes, the creation of dense litter layers associated with an invasive reed (*Phragmites australis*) have altered the density and distribution of many macrofaunal taxa (Talley and Levin 2001). In freshwater systems, invasive plants are well-known and often-cursed habitat modifiers. Species such as hydrilla (*Hydrilla verticillata*), Eurasian water milfoil (*Myriophyllum spicatum*), and water hyacinth (*Eichhornia crassipes*) are invasive weeds capable of creating thick beds that limit water movement and light penetration, but they also offer refuge for some small animals (Schmitz et al. 1993, 1997).

Exotic animals often are considered agents of disturbance that destroy physical structure (Table 1). For example, the rooting of pigs (*Sus scrofa*) has marked ecosystem-level effects, including thinned forest floors, altered soil chemistry, and increased leaching (Bratton 1975, Singer et al. 1984). Introduced herbivores on islands, such as sheep, goats, and rabbits, can destroy autogenic engineers (i.e. vegetation), with resultant effects on sediment stability and erosion (Coblentz 1978, van Vuren and Coblentz 1987, North et al. 1994). The feeding activities of the notorious gypsy moth (*Lymantria dispar*) have had devastating effects on North American forests (Liebhold et al. 1996). Consequences of the invasion include altered canopy structure, increased growth of understory plants, and changed availability of bird nesting sites (Thurber et al. 1994, Fajvan and Wood 1996, Bell and Whitmore 1997). In marine systems, the periwinkle *Littorina littorea*, a grazing snail that bulldozes sediments and inhibits plants and algae, has markedly shaped invaded intertidal habitats (Bertness 1984, 1999). Although the engineering effects of animals often are associated with trophic activities, feeding per se is not essential for engineering (Jones et al. 1994). This is illustrated by the effects of Sphaerotid isopods (Rotramel 1975, Carlton and Ruckelshaus 1997). *Sphaeroma terebrans* burrows into

Table 1. Exotic ecosystem engineers and examples of their physical and biological effects

Species	Effects on physical resources	Effects on resident biota	Location	Reference
Plants				
Tank bromeliads (e.g., <i>Billbergia pyramidalis</i>)	Traps water	Creates aquatic habitat (phytotelmata) for <i>Aedes</i> spp. Mosquitoes	Florida	O'Meara et al. 1995
Blue gum (<i>Eucalyptus globulus</i>)	Increases shade and accumulation of litter; alters fire regime, creates structure	Decreases abundance and diversity of soil Collembola and aquatic invertebrates compared to native forests; provides raptor nesting sites	California, South America, Europe	Robles and Chapin 1995, Abelho and Graca 1996, Sousa et al. 1997, 2000, Rottenborn 2000
Australian pines (<i>Casuarina equisetifolia</i>)	Creates forests on treeless coastlines; increased litter production promotes erosion by excluding soil stabilizers	Blocking of city lights promotes sea turtle nesting; falling trees inhibit nesting; increases nesting success of Oystercatchers; decreases rodent density; decreases understory	Florida	Mazzotti et al. 1981, Toland 1992, Office of Technology Assessment 1993, Salmon et al. 1995, Schmitz et al. 1997, Gordon 1998
Brazilian pepper (<i>Schinus terebinthifolius</i>)	Forms dense, monospecific stands that depress fire intensity and spread; increases local soil elevation	Decreases avian abundance and diversity	Florida	Curnutt 1989, Schmitz et al. 1997, Gordon 1998
Broomsedge (<i>Andropogon virginicus</i>)	Low transpiration during winter allows soils to become saturated with water, increasing landslides; increases fire frequency	Altered fire regime inhibits native plants	Hawai'i	Mueller-Dombois 1973, Smith 1989, Randall 1996
Salt cedar (<i>Tamarix</i> spp.)	Decreases channel width by stabilization; ceases water flows and deepens water table by high transpiration rates	Inhibits native plants and animals by elimination of surface water	Southwest United States	Graf 1978, Vitousek 1986, Randall 1993, 1996
Black wattle (<i>Acacia mearnsii</i>)	Intercepts rainfall; easy uprooting increases erosion; creates dense canopy	Thick vegetation inhibits dragonflies	South Africa	Macdonald and Cooper 1995, Versfeld and van Wilgen 1986, Kinvig and Samways 2000
Cheatgrass (<i>Bromus tectorum</i>)	Replaces shrubs and perennial grasses; increases fire frequency; provision of nest sites	Increased fire frequency inhibits native plants; facilitates shorebird nesting	North America	D'Antonio and Vitousek 1992, Pampush and Anthony 1993, Knapp 1996
Catclaw mimosa (<i>Mimosa pigra</i>)	Converts wide range of plant structural types into homogeneous shrubland; accumulates sediment	Alters abundance and diversity of native plants, birds, amphibians, and mammals	Australia, Florida	Braithwaite et al. 1989, Lonsdale et al. 1990, Gordon 1998
Marram grass (<i>Ammophila arenaria</i>)	Alters dune geomorphology by creation of dense stands which trap sand, leading to large foredunes	Promotes growth of tall shrubs	North America, New Zealand, Australia	Weidemann 1984, Barbour and Johnson 1988, Mack and D'Antonio 1998
Cordgrass (<i>Spartina anglica</i> , <i>S. alterniflora</i>)	Colonizes unvegetated mud flats; increases sedimentation	Increases invertebrate density and diversity compared to mudflats	Great Britain, United States, Australia	Elton 1958, Callaway and Josselyn 1992, Hedge and Kriwoken 2000
Red mangrove (<i>Rhizophora mangle</i>)	Creates dense mangal habitat	Reduces habitat suitability for some endemic birds	Hawaii	Simberloff 1990, Allen 1998
Water hyacinth (<i>Eichhornia crassipes</i>)	Forms plant cover on open water; clogs waterways; increases anoxia; lowers water level	Creates invertebrate habitat and predation refuge for fish; Inhibits hunting of raptors	Lake Victoria, Florida	O'Hara 1967, Sykes 1987, Schmitz et al. 1993, Ogutu-Ohwayo 1999

Table 1. (Continued)

Species	Effects on physical resources	Effects on resident biota	Location	Reference
Fungi				
Dutch elm disease (<i>Ceratocytis ulmi</i>)	Canopy gaps created by dead elms (<i>Ulmus</i> spp.) create microclimates; dead trees contribute to coarse woody debris in streams; decreases availability of cavity nest sites	Alters growth of shrubs; changes bird density and diversity	North America, Europe	Elton 1958, Osborne 1983, Osborne, 1985, Hanula 1996, Peterken and Mountford 1998
Animals				
Australian isopod (<i>Sphaeroma quoyanum</i>)	Burrows into mud banks of salt marshes	Increases loss of marsh plants; burrows may facilitate some small infauna	Pacific Coast of North America	Carlton 1979, Talley et al. 2001
Zebra mussels (<i>Dreissena polymorpha</i>)	Filters water column and increases light penetration; creates shell beds	Shells provide habitat for macrofauna; increased light penetration increases macrophyte growth	Lakes and rivers of North America, Europe	Skubinna et al. 1995, Ricciardi et al. 1997, Strayer 1999, Strayer et al. 1999, Vander Zanden et al. 1999
Japanese mussel (<i>Musculista senhousia</i>)	Creates byssal mats on intertidal and subtidal soft sediments	Dense mats inhibit eelgrass and native clams while facilitating many small invertebrates	United States, Australia, New Zealand	Creese et al. 1997, Crooks 1998a, b, 2001, Reusch and Williams 1998, Crooks and Khim 1999
Serpulid tube worm (<i>Ficopomatus enigmaticus</i>)	Creates reefs on muddy bottoms; source of carbonate sediment	Increases abundance of benthic species such as crabs, snails, and amphipods	Italy, United States, South America	Carlton 1979, Bianchi and Morri 1996, Schwindt and Iribarne 2000
Carp (<i>Cyprinus carpio</i>), goldfish (<i>Carassius auratus</i>)	Destroys submerged vegetation; increases turbidity	Turbidity and nutrient loads alters planktonic standing stocks	North America, Australia	Richardson et al. 1995, King et al. 1997, Robertson et al. 1997, Lougheed et al. 1998
Nutria (<i>Myocastor coypus</i>)	Digs into banks; tramples and grazes wetland and aquatic plants	Decreases habitat available for native wildlife	Europe, North America	de Vos et al. 1956, Usher 1986, Nyman et al. 1993, Gosling et al. 1988
Water buffalo (<i>Bubalus bubalis</i>)	Soil disruption by creation of wallows, trails, and hoof prints	Promotes plant invasion; alters abundance and diversity of animals	Australia	Friend and Taylor 1984, Russell-Smith and Bowman 1992, Cowie and Werner 1993
Sheep (<i>Ovis aires</i>), goats (<i>Capra hircus</i>)	Generalist herbivores that overgraze vegetation and increase erosion	Affects birds, reptiles, and other wildlife	Islands worldwide	Coblentz 1978, van Vuren and Coblentz 1987
Gypsy moth (<i>Lymantria dispar</i>)	Alters canopy structure of forests; alters availability of nest sites	Increases growth of understory plants; affects nesting birds	United States	Thurber et al. 1994, Fajvan and Wood 1996, Bell and Whitmore 1997
Balsam woolly adelgid (<i>Adelges piceae</i>)	Destroys balsam-fir and spruce-fir forests	Alters bird diversity, including facilitation of exotic birds	Eastern United States	Alsop and Laughlin 1991, Rabenold et al. 1998

the prop roots of mangroves, and *S. quoyanum* burrows into salt marsh mud banks, but because they are suspension feeders, they do so primarily to create living space and not to gain direct access to food. Both species, which are presumed to be exotic in the United States, are suggested to cause loss of vegetated wetland habitat through bioerosion (Carlton and Ruckelshaus 1997, Talley et al. 2001).

Physical structure also can be created by invasive animals. In terrestrial systems, exotic (as well as native) fauna rarely autogenically engineer, although they can create structures via allogenic engineering. Introduced fire ants (*Solenopsis invicta*) can form large mounds (Tschinkel 1993), and introduced beavers create dams that alter water flow (Lizarrdale et al. 1996). Unlike animals on land, introduced animals in aquatic systems can be dominant structural agents. For example, the introduced tube-dwelling polychaete worm *Ficopomatus enigmaticus* forms masses of carbonate tubes in estuaries (Bianchi and Morri 1996, Schwindt and Iribarne 2000), and its first reports in San Francisco Bay prompted reports of "coral reefs" in the system (Carlton 1979). Zebra mussels (*Dreissena polymorpha*), in addition to altering food chains by filtering plankton from the water (Vander Zanden et al. 1999), also have physical effects that include increased water clarity and creation of dense shell beds that harbor relatively high densities of other small invertebrates (Nalepa and Schloesser 1993, Stewart and Haynes 1994, Skubinna et al. 1995, Ricciardi et al. 1997).

Invasive pathogens also can allogenicly engineer ecosystems (Thomas et al. 1999). The killing of elms by Dutch Elm Disease, caused by the fungus *Ceratocytis ulmi*, affects forest structure by changing the amount of standing material and creating canopy gaps that alter microclimates. Chestnut Blight, caused by the Asian fungus *Cryphonectria parasitica*, also has led to alterations of forest habitats wrought by the ecological extinction of American chestnut (*Castanea dentata*) on the U.S. East Coast. The oomycete *Phytophthora cinnamomi*, introduced into *Eucalyptus marginata* forests of Western Australia, also has resulted in widespread forest destruction (von Broembsen 1989). In addition to contributing to the removal of structure, plant pathogens that leave dead or diseased standing trees can provide living space for other organisms (Gilbert and Hubbell 1996). In marine systems, introduced protistan pathogens (*Haplosporidium nelsoni* and *Perkinsus marinus*) have played a role in the decline of the Virginia oyster (*Crassostrea virginica*), a formerly abundant species that was important in filtering bay water and providing structure in the form of oyster reefs (Ruiz et al. 1999).

In heavily invaded systems, there often are complex relationships between invasive ecosystem modifiers. This is exemplified by the well-chronicled invasion of the fire weed (*Myrica faya*) in Hawai'i. This plant, and its associated nitrogen-fixing bacteria, has directly affected

biogeochemical cycling within invaded ecosystems (Vitousek et al. 1997). However, other significant effects have resulted primarily from its physical modification of habitats. These include creation of structure on bare lava flows, shading, and litter production (Walker and Vitousek 1991, Adler et al. 1998). The increased high-quality litter produced by the plant has promoted the invasion of exotic earthworms (Aplet 1990). Although this facilitation of worms through the production of leaf litter appears to be primarily a trophic response (and thus not the result of engineering), the worms themselves are soil-bioturbating engineers. Furthermore, an introduced leaf hopper (*Sophonia rufofascia*) has had effects that have somewhat counteracted those of *Myrica*, as the grazing of this herbivorous insect has caused diebacks of the plant invader (Adler et al. 1998).

Introduced non-engineers that interact with native engineers can have large, indirect effects on the physical nature of ecosystems. Diseases of herbivores are good examples of this interaction (Dobson and Crawley 1994). The spread of anthrax in African impala resulted in decreased grazing pressure and the subsequent appearance of even-aged, homogenous stands of *Acacia tortilis*. Similar homogenization of tree stands also has been reported after the outbreak of rinderpest in African mammals (McCallum and Dobson 1995) and myxomatosis in invasive rabbit (*Oryctolagus cuniculus*) populations in England (Dobson and Crawley 1994). Introduced predators can affect engineers as well. In the United Kingdom, the invasion of an earthworm predator, the large New Zealand flatworm (*Artiosthia trianguata*), has led to concern about the loss of native, soil-engineering earthworms (Blackshaw and Stewart 1992).

Community-level responses to engineer-induced alterations of habitat complexity

An important question with regard to exotic engineers, and with invasive species in general, is whether they will have predictable effects upon integration into foreign ecosystems. This is a broad issue that deserves much more explicit attention, although it is possible to approach the question in general terms. One likely consequence of physically altering habitats is changing the abundance and diversity of structural elements in ecosystems, thus affecting habitat complexity (and/or habitat heterogeneity; see McCoy and Bell 1991, Turner et al. 1999, Beck 2000 for further discussion). In the literature of general ecology, there is a well-developed body of evidence suggesting a positive relationship between habitat complexity and biotic diversity and abundance. This has been observed on a variety of scales for plants and animals on land (MacArthur and MacArthur 1961,

Murdoch et al. 1972, Denno and Roderick 1991) and in the water (Krecker 1939, Stoner and Lewis 1985, Dean and Connell 1987). This relationship can be used to examine the community-level effects of exotics that modify habitat complexity.

The literature offers examples of a variety of studies that have compared diversity and/or abundance in areas where habitat complexity differed as a result of invader activity (Table 2). Although complexity was not quantified in these studies, it was possible to qualitatively identify habitats that could be considered relatively complex. A habitat was considered complex if it had either a higher density or a greater diversity of structural elements than the habitat to which it was being compared. For example, an area with vegetation would be considered more complex than bare soils, and a mixed forest would be considered more complex than a monoculture.

Increasing habitat complexity typically resulted from the invasion of autogenically-engineering plants or animals, and this often resulted in elevated biotic densities and/or diversities. For example, zebra mussels, which create dense beds on cobbles, had more individuals and species than the bare cobbles alone (Stewart and Haynes 1994). Similarly, mixed-age stands of hybrid poplars had higher bird abundances and species richness than structurally simple row crops (Hanowski et al. 1997). Allo-genic engineering also can result in increased habitat complexity, such as pig rooting in freshwater marshes, which increased the number of soil microhabitats and enhanced plant species richness (Arrington et al. 1999).

In contrast, decreased complexity typically arose when structure-destroying animals (i.e. allogenic engineers) invaded ecosystems. This often resulted in lowered densities and species richness (Table 2). For example, locations with sheep or rabbits can have lower vertebrate diversities or densities than locations with none or few of these exotic herbivores (van Vuren and Coblenz 1987, North et al. 1994). In addition, invasive autogenic engineers can decrease complexity of habitats by replacing more heterogeneous native species or assemblages. Hybrid poplar plantations had lower avian abundances and diversity than heterogeneous native forest and shrub (Hanowski et al. 1997), and exotic willows decreased macrofaunal density and species richness when compared to structurally more complex eucalyptus (Read and Barmuta 1999).

Although many cases fit with the general pattern of increased diversity and/or abundance with increased habitat complexity, some exceptions were found (Table 2). These highlight the complex relationships between the physical environment and species-specific habitat requirements. For example, beds of Japanese oysters in the Mediterranean were found to have decreased macrofaunal densities compared to oyster-free sediments, even though these beds are structurally much more complex than the bare substrate. However, living oysters biode-

posit organic-rich materials that lead to decreased oxygen levels, representing a potential mechanism for the observed decline in larger invertebrates (Castel et al. 1989). Also, dung beetle density and diversity were lower in structurally-complex thickets of introduced mesquite. This was suggested to result from thickets impeding beetle flying, search success, and dung rolling abilities, as well as limiting the diversity of native dung-producers within the thickets (Steenkamp and Chown 1996).

The importance of considering the life habits of resident biota was clearly expressed by Bertness (1984) in his work on the invasive snail *Littorina littorea*, which is capable of bulldozing and grazing intertidal shores. Since *Littorina* in essence created rocky shore at the expense of mud habitats, soft-sediment species did poorly while hard-sediment species fared well in *Littorina*-affected habitats. This illustrates an important cautionary note. Although it is tempting to characterize species like plants or macroalgae as habitat creators and grazing snails as habitat destroyers, in fact they both create one habitat type at the expense of another (i.e. unvegetated substrate to vegetated substrate or vice versa). This has direct implications for considering the effects of exotic ecosystem engineers on other biota (Jones et al. 1997b). Species able to live in the invader-modified habitat type would be expected to benefit from the ecosystem engineering, while those living in the unmodified habitat might be inhibited. Although this appears obvious, the bulk of the attention is usually focused on the latter, detrimental type of impact.

Biotic responses to ecosystem engineers also will depend at least partially on spatial scale. For example, *Musculista senhousia* is a mytilid mussel that forms structurally complex byssal mats on the surface of intertidal and subtidal soft sediments (Creese et al. 1997, Crooks 1998a, b, Crooks and Khim 1999). Descriptive studies and manipulative experiments demonstrate that the direction of the response to this habitat modification depends on the size of associated biota. Small invertebrates typically live within the mussel mat matrix at higher abundances than in mat-free sediments (Crooks 1998a). However, beds of these suspension-feeding mussels can inhibit larger, native, suspension-feeding clams living in the same depth horizon, probably through competition for both space and food (Crooks 2001). The creation of dense mussel mats has similar effects on native eelgrass (*Zostera marina*), and can inhibit the vegetative propagation of this plant (Reusch and Williams 1998). The mussel is also typically patchily distributed, resulting in a mosaic of mat and no-mat areas that will likely increase diversity at the landscape level. Such effects highlight potential positive effects of invaders, which have been underemphasized in ecology (Bertness and Callaway 1994, Jones et al. 1997b, Bruno and Bertness 2001), but suggest that they probably come at a cost that depends on scale and the life habits of resident biota.

Table 2. Examples of community-level responses to exotic-induced increases or decreases in habitat complexity. Responses are in terms of increased (+), decreased (–), or equal (0) total density and species richness in the exotic-engineered habitat vs a reference habitat. Data are from quantitative descriptive or experimental field studies in aquatic and terrestrial systems. na = not assessed in the study.

Exotic engineer	Habitats compared	Community examined	Density	Diversity	Comments	Reference
Invader increases complexity						
Japanese oyster (<i>Crassostrea gigas</i>)	Oyster reefs vs bare sediments	Intertidal meiofauna	+	na	Oyster shells create structure on bare mudflats	Castel et al. 1989
		Intertidal macrofauna	–	na	Macrofaunal responses attributed to low sediment O ₂	
Zebra mussel (<i>Dreissena polymorpha</i>)	Mussel beds vs bare cobbles	Subtidal macrofauna	+	+	Mussel shells create structure on bare rock	Stewart and Haynes 1994
	Mussel beds vs artificial rocks	Subtidal macrofauna	+	+		Horvath et al. 1999
Japanese mussel (<i>Musculista senhousia</i>)	Mussel mats vs bare sediments	Mudflat macrofauna	+	+	Mussel shells and byssus create structure on bare mudflats	Crooks 1998a, Crooks and Khim 1999
Japanese eelgrass (<i>Zostera japonica</i>)	Macrophyte beds vs bare sediments	Mudflat macrofauna	+	+	Eelgrass creates structure on bare mudflats	Posey 1988
Hydrilla (<i>Hydrilla verticillata</i>)	Macrophyte beds vs bare sediments	Subtidal macrofauna	+	na	Hydrilla forms dense beds in shallow waters	Posey et al. 1993
Mesquite (<i>Prosopis glandulosa</i>)	Thickets vs undisturbed savanna	Dung beetles	–	–	Mesquite forms dense stands	Steenkamp and Chown 1996
Paper-bark tree (<i>Melaleuca quinquenervia</i>)	Melaleuca forests vs native sawgrass wetland	Wildlife	na	+	Melaleuca trees increase structure; Moderate Melaleuca coverage has highest diversity	O'Hare and Dalrymple 1997
Spruce (<i>Picea</i>)	Mixed pine (<i>Pinus</i>) and spruce forest vs spruce forest	Birds	na	+	Pine and spruce forest more heterogeneous than spruce monoculture	Gjerde and Sætersdal 1997
Pigs (<i>Sus scrofa</i>)	Pig-rooted wetland plots vs unrooted plots	Broadleaf marsh plants (% cover)	–	+	Pig rooting increases microhabitat diversity	Arrington et al. 1999
		Wet prairie marsh plants (% cover)	0	+		Arrington et al. 1999
Hybrid poplars (<i>Populus</i>)	Poplar forest vs row crops	Birds	+	+	Row crops are structurally simple relative to poplar forests	Hanowski et al. 1997
Invader decreases complexity						
Hybrid poplars (<i>Populus</i>)	Poplar forest vs native forest/shrub	Birds	–	–	Poplar forests are more homogeneous than native vegetation	Hanowski et al. 1997
Sheep (<i>Ovis aries</i>)	Grazed plots vs lightly grazed plots	Birds	na	–	Grazing decreases structural complexity of vegetation	van Vuren and Coblenz 1987
Rabbits (<i>Oryctolagus cuniculus</i>)	Islands before eradication vs islands after eradication	Reptiles	–	0	Grazing decreases structural complexity of vegetation	North et al. 1994
Periwinkle snail (<i>Littorina littorea</i>)	Grazed rocks vs ungrazed rocks	Soft-sediment fauna	–	–	Grazing decreases structural complexity of vegetation	Bertness 1984
		Hard-substrate fauna	+	+		
Willow (<i>Salix</i> spp.)	River habitats next to willows vs river habitats next to Eucalyptus during summer low flows	Riparian macrofauna	–	–	Willows decrease microhabitat diversity; Effects also related to factors such as shading and water flow	Read and Barmuta 1999

It is clear that addressing engineering by exotics and all its attendant effects is complicated and more refinement is needed. However, these examples (Table 2) suggest that further studies aimed at specifically addressing the relationship between invader-modified habitat complexity and the response of resident species are needed. This relationship may prove to be one of the most predictable effects of invaders, and might be related to the preadaptation of organisms to take advantage of structure in ecosystems, whether it be native, exotic, or even artificial (e.g. man-made reefs and fish aggregating devices; Carlisle et al. 1964, Crowder and Cooper 1982).

Effects of invaders on ecosystem-level properties

Given that some of the biological consequences of engineering (such as provision of living space) are not readily accounted for by current classifications of invader impacts (Macdonald et al. 1989, Vitousek 1990, Williamson 1996, Parker et al. 1999), a new framework for classifying ecosystem-level effects should be considered. This framework, which is based on Vitousek (1990), recognizes three principal effects of exotics on ecosystems: the alteration of the flow, availability or quality of 1) nutrient resources within biogeochemical cycles, 2) trophic resources within food webs, and 3) physical resources such as living space, sediment, light, or water. This classification readily accounts for ecosystem engineering, which represents one proximate mechanism by which any of these ecosystem-level resources (and particularly physical resources) can be affected. Other mechanisms include virtually any interaction between one organism and another organism or the physical environment, including predation, herbivory, competition, and novel use of resources. In general, by focusing on the resources on which other species depend, this framework attempts to directly link invader activities to impacts on other biota.

First, exotics can affect the availability and flow of nutrients by altering biogeochemical cycling. This can occur when an invader directly participates in the biogeochemical cycle itself, such as the invasion of the symbiotic nitrogen-fixer, *Myrica faya*, onto bare lava flows in Hawai'i. The *Myrica* invasion is an example of an exotic that utilizes resources differently than natives, and alterations of nutrient cycling have often been phrased in these terms (Vitousek 1990, Parker et al. 1999). However, the unique use of resources does not relate only to nutrient cycling, because alterations of food webs or habitats also can involve the novel use and subsequent control of a wide variety of resources. In addition to fundamentally differing from natives in their ability to acquire or use nutrients, exotics also may directly affect availability of nutrients by swamp-

ing ecosystems with their sheer numbers (Williamson 1996). For example, biodeposition by invasive bivalves can directly affect benthic-pelagic coupling and the downward flux of organic matter (Crooks and Khim 1999), even though native, but far less abundant, suspension feeders also biodeposit materials. Ecosystem engineering also is a mechanism by which nutrient cycling can be affected. For example, the presence of mussel shells can decrease water flow and cause passive deposition of organic matter, as opposed to the active biodeposition of materials by the living organisms (Crooks and Khim 1999). Invaders also can affect nutrient flows indirectly, mediated by an interspecific interaction with an important biotic element of the biogeochemical cycle. On a sub-Antarctic island, for example, predation by the introduced house mouse (*Mus musculus*) on a detritivorous moth (*Pringleophaga marioni*) can substantially decrease litter decomposition rates (Crafford 1990, Cushman 1995)

Second, invasive species can affect the flow of energy through food webs. Whereas biogeochemical cycling typically has an abiotic component in the flow, food webs are solely biotic interrelationships. Williamson (1996) suggests that these trophic alterations not be considered as ecosystem-level effects because 1) ecosystems are typically defined as the assemblage of both living organisms and the physical and chemical environment, and 2) exotics rarely have trophic effects that spread beyond the species directly affected (with the exotic eating the native, or vice versa). However, the triggering of trophic cascades by predators, of which there are an increasing number of examples (e.g. Hurlbert et al. 1972, Kitchell et al. 1997, Crooks and Soulé 1999, Pace et al. 1999), can lead to broad consequences and alterations in energy flow that seem appropriately addressed at the ecosystem level. For example, predation by an introduced mysid (*Mysis relicta*) on zooplankton in a Montana lake has led to subsequent declines in planktivorous fish and piscivorous birds (Spencer et al. 1991, 1999), and water filtration by invasive zebra mussels can result in direct alterations of Great Lakes food webs (Vander Zanden et al. 1999). As with alterations of nutrient cycling, ecosystem engineering can affect food webs. For example, the predation refuge afforded to species taking advantage of engineered habitats might affect food webs without the invader actually participating in the trophic flow itself.

Third, invasive species can affect the availability or quality of physical resources in the ecosystem. These types of physical resources, including living space or "habitat," physical materials, sediment, light, or water often characterize the nature of the ecosystems itself (Grimm 1995, Jones et al. 1997b). As discussed earlier, ecosystem engineering represents the primary means by which physical resources are directly controlled. Ecosystem engineers also can have indirect effects on physical resources by affecting the ability of other

species to regulate resource flows or availability. For example, increased water clarity caused by filtration by invasive bivalves (e.g. zebra mussels and *Corbicula fluminea*) can allow the growth of submerged aquatic vegetation (another engineer), which in turn affects resources such as living space and the flow of water (Phelps 1994, Strayer et al. 1999). Also, non-engineers can indirectly affect physical resources, such as the herbivore diseases discussed above.

In existing characterizations of the ecosystem-level role of exotics (Vitousek 1990), engineering appears most closely related to the effects of invaders that modify disturbance regimes (e.g. soil-stabilizing plants) or that are agents of disturbance themselves (e.g. pigs) (Mack and D'Antonio 1998). Indeed, disturbance is a critical factor in ecosystems, and the concepts of biogenic alteration of disturbance regimes and engineering are quite similar. In general, however, ecosystem engineering appears more inclusive as it readily accounts for provision of resources such as living space and encompasses the addition, removal, or modification of physical structure, while disturbance deals primarily with structural damage or removal (Sousa 1984, 2001, Pickett et al. 1989). Ecosystem engineering also provides unifying themes across aquatic and terrestrial systems by de-emphasizing the often considered roles of plants as dominant structural elements in ecosystems and animals as agents of disturbance.

Conclusions

A principal goal of examining biological invaders is to develop ecological principles that apply generally (Lewin 1987, Vitousek 1990), and continued study of invasive habitat modifiers will contribute to a better understanding of the role of engineers in ecosystems. Useful approaches will include comparing invaded and non-invaded habitats, and examining the role of invasive engineers within both its invaded and native ranges. It also will be of interest to examine whether native and exotic species respond differently to exotic engineers. There is already some evidence that invasive habitat modifiers can facilitate further invasions (Veblen et al. 1992, Cammell et al. 1996), leading to an "invasion meltdown" (Simberloff and Von Holle 1999).

Efforts aimed at investigating ecosystem engineering will benefit from identifying and quantifying resources affected, including developing and utilizing biologically meaningful metrics of habitat structure (Morse et al. 1985, McCoy and Bell 1991, Beck 2000). Once effects on these resources are quantified, it will be possible to more directly relate engineering to impacts on other species. At larger scales, it will be valuable to consider the role of engineers and engineered patches in landscapes (Jones et al. 1997b), and test models assessing the importance of engineering in relation to varying

amounts of other factors, including environmental stress, competition, predation, and recruitment (Wilson and Agnew 1992, Bertness and Callaway 1994, Bruno 2000, Bruno and Bertness 2001).

In broader terms, the creation of a framework with which to view the potential ecosystem-level effects of invaders should lend insight the general role of species in ecosystems (Vitousek 1990, Chapin et al. 1997). Considering ecosystem-level effects in terms of mediating the flow or availability of nutrient, trophic, and physical resources should apply for all species, although natives and exotics may differ in their ability to exert biological control over ecosystem processes.

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References

- Abelho, M. and Graca, M. A. S. 1996. Effects of eucalyptus afforestation on leaf litter dynamics and macroinvertebrate community structure of streams in central Portugal. – *Hydrobiologia* 324: 195–204.
- Adler, P. B., D'Antonio, C. M. and Tunison, J. T. 1998. Understorey succession following a dieback of *Myrica faya* in Hawai'i Volcanoes National Park. – *Pac. Sci.* 52: 69–78.
- Allen, J. A. 1998. Mangroves as alien species: The case of Hawai'i. – *Global Ecol. Biogeogr.* 7: 61–71.
- Alper, J. 1998. Ecosystem engineers shape habitats for other species. – *Science* 280: 1195–1196.
- Alsop, F. J. and Laughlin, T. F. 1991. Changes in the spruce-fir avifauna of Mt. Guyot, Tennessee, 1967–1985. – *J. Tennessee Acad. Sci.* 66: 207–209.
- Aplet, G. H. 1990. Alteration of earthworm community biomass by the alien *Myrica faya* in Hawaii (USA). – *Oecologia* 82: 414–416.
- Arrington, D. A., Toth, L. A. and Koebel, J. W., Jr 1999. Effects of rooting by feral hogs *Sus scrofa* L. on the structure of a floodplain vegetation assemblage. – *Wetlands* 9: 535–544.
- Barbour, M. and Johnson, A. F. 1988. Beach and dune. – In: Barbour, M. and Major, J. (eds), *Terrestrial vegetation of California*. California Native Plant Society Special Publication No. 9. California Native Plant Society, pp. 223–261.
- Beck, M. W. 2000. Separating the elements of habitat structure: independent effects of habitat complexity and structural components on rocky intertidal gastropods. – *J. Exp. Mar. Biol. Ecol.* 249: 29–49.
- Bell, J. L. and Whitmore, R. C. 1997. Eastern towhee numbers increase following defoliation by gypsy moths. – *Auk* 114: 708–716.
- Bertness, M. D. 1984. Habitat and community modification by an introduced herbivorous snail. – *Ecology* 65: 370–381.
- Bertness, M. D. 1999. *The ecology of Atlantic shorelines*. – Sinauer Associates Inc.
- Bertness, M. D. and Callaway, R. 1994. Positive interactions in communities. – *Trends Ecol. Evol.* 9: 191–193.

- Bianchi, C. N. and Morri, C. 1996. Ficopomatus 'reefs' in the Po River delta (northern Adriatic): their constructional dynamics, biology, and influences on the brackish-water biota. – *Mar. Ecol.* 17: 51–66.
- Blackshaw, R. P. and Stewart, V. I. 1992. *Artioposthia triangulata* Dendy 1894, a predatory terrestrial planarian and its potential impact on lumbricid earthworms. – *Agr. Zool. Rev.* 5: 201–219.
- Braithwaite, R. W., Lonsdale, W. M. and Estbergs, J. A. 1989. Alien vegetation and native biota in tropical Australia: the impacts of *Mimosa pigra*. – *Biol. Conserv.* 48: 189–210.
- Bratton, S. P. 1975. The effect of the European wild boar, *Sus scrofa*, on Gray Beech Forest in the Great Smoky Mountains. – *Ecology* 56: 1356–1366.
- Brenchley, G. A. and Carlton, J. T. 1983. Competitive displacement of native mud snails by introduced periwinkles in the New England intertidal zone. – *Biol. Bull.* 165: 543–558.
- Brown, J. H. 1995. Organisms as engineers: a useful framework for studying effects on ecosystems? – *Trends Ecol. Evol.* 10: 51–52.
- Bruno, J. F. 2000. Facilitation of cobble beach plant communities through habitat modification by *Spartina alterniflora*. – *Ecology* 81: 1179–1192.
- Bruno, J. F. and Bertness, M. D. 2001. Habitat modification and facilitation in benthic marine communities. – In: Bertness, M. D., Gaines, S. D. and Hay, M. E. (eds), *Marine community ecology*. Sinauer Associates Inc, pp. 201–218.
- Byers, J. E. 2000. Competition between two estuarine snails: implications for invasions of exotic species. – *Ecology* 81: 1225–1239.
- Callaway, J. C. and Josselyn, M. N. 1992. The introduction and spread of smooth cordgrass (*Spartina alterniflora*) in south San Francisco Bay. – *Estuaries* 15: 218–226.
- Cammell, M. E., Way, M. J. and Paiva, M. R. 1996. Diversity and structure of ant communities associated with oak, pine, eucalyptus, and arable habitats in Portugal. – *Insect Soc.* 43: 37–46.
- Carlisle, J. G. Jr., Turner, C. H. and Ebert, E. E. 1964. Artificial habitat in the marine environment. – California Department of Fish and Game, Fish Bulletin 124.
- Carlton, J. T. 1979. History, biogeography, and ecology of the introduced marine and estuarine invertebrates of the Pacific coast of North America. – Ph.D. thesis, Univ. of California, Davis.
- Carlton, J. T. 1999. A journal of biological invasions. – *Biol. Invasions* 1: 1.
- Carlton, J. T. and Ruckelshaus, M. H. 1997. Nonindigenous marine invertebrates and algae. – In: Schmitz, D. C., Simberloff, D. and Brown, T. C. (eds), *Strangers in paradise*. Island Press, pp. 187–201.
- Carpenter, S. R. and Turner, M. G. 1998. At last: a journal devoted to ecosystem science. – *Ecosystems* 1: 1–5.
- Carroll, S. P. and Dingle, H. 1996. The biology of post-invasion events. – *Biol. Conserv.* 78: 207–214.
- Castel, J., Labourg, P. J., Escaravage, V. et al. 1989. Influence of seagrass beds and oyster parks on the abundance and biomass patterns of meio- and macrobenthos in tidal flats. – *Estuar. Coast. Shelf Sci.* 28: 71–85.
- Chapin, F. S. III, Walker, B. H., Hobbs, R. J. et al. 1997. Biotic control over the functioning of ecosystems. – *Science* 277: 500–504.
- Chapuis, J. L., Boussès, P. and Barnaud, G. 1994. Alien mammals, impact and management in the French subantarctic islands. – *Biol. Conserv.* 67: 97–104.
- Coblentz, B. E. 1978. The effects of feral goats (*Capra hircus*) on island ecosystems. – *Biol. Conserv.* 13: 279–286.
- Cowie, I. D. and Werner, P. A. 1993. Alien plant species invasive in Kakadu National Park, tropical Northern Australia. – *Biol. Conserv.* 63: 127–135.
- Cowie, R. H. 1992. Evolution and extinction of Partulidae, endemic Pacific island snails. – *Philos. Trans. R. Soc. Lond. B Biol. Sci.* 335: 167–191.
- Cox, G. W. 1999. Alien species in North America and Hawaii. – Island Press.
- Crafford, J. E. 1990. The role of feral house mice in ecosystem functioning on Marion Island. – In: Kerry, K. R. and Hempel, G. (eds), *Antarctic ecosystems: ecological change and conservation*. Springer-Verlag, pp. 359–364.
- Creese, R., Hooker, S., DeLuca, S. and Wharton, W. 1997. Ecology and environmental impact of *Musculista senhousia* (Mollusca: Bivalvia: Mytilidae) in Tamaki Estuary, Auckland, New Zealand. – *N. Z. J. Mar. Freshwat. Res.* 31: 225–236.
- Crooks, J. A. 1998a. Habitat alteration and community-level effects of an exotic mussel, *Musculista senhousia*. – *Mar. Ecol. Prog. Ser.* 162: 137–152.
- Crooks, J. A. 1998b. The effects of the introduced mussel, *Musculista senhousia*, and other anthropogenic agents on benthic ecosystems of Mission Bay, San Diego. – Ph.D. thesis. Scripps Inst. Oceanogr, Univ. of California San Diego.
- Crooks, J. A. 2001. Assessing invader effects within changing ecosystems: historical and experimental perspectives on the role of an exotic mussel in an urbanized lagoon. – *Biol. Invasions* 3: 23–36.
- Crooks, J. A. 2002. Predators of the invasive mussel, *Musculista senhousia*. – *Pac. Sci.* 56: 49–56.
- Crooks, J. A. and Khim, H. S. 1999. Architectural vs. biological effects of a habitat-altering, exotic mussel, *Musculista senhousia*. – *J. Exp. Mar. Biol. Ecol.* 240: 53–75.
- Crooks, K. R. and Soulé, M. E. 1999. Mesopredator release and avifaunal extinctions in a fragmented system. – *Nature* 400: 563–566.
- Crowder, L. B. and Cooper, W. E. 1982. Habitat structural complexity and the interaction between bluegills and their prey. – *Ecology* 63: 1802–1813.
- Curnutt, J. L. 1989. Breeding bird use of a mature stand of Brazilian pepper. – *Florida Ornithol. Soc.* 17: 53–76.
- Cushman, J. H. 1995. Ecosystem-level consequences of species additions and deletions on islands. – In: Vitousek, P. M., Loope, L. L., Adersen, H. and Madsen, K. (eds), *Islands: biological diversity and ecosystem function*. Springer-Verlag, pp. 135–147.
- D'Antonio, C. M. and Vitousek, P. M. 1992. Biological invasions by exotic grasses, the grass/fire cycle, and global change. – *Annu. Rev. Ecol. Syst.* 23: 63–87.
- de Vos, A., Manville, R. H. and Van Gelder, R. G. 1956. Introduced mammals and their influence on native biota. – *Zoologica* 41: 163–194.
- Dean, R. L. and Connell, J. H. 1987. Marine invertebrates in an algal succession. III. Mechanisms linking habitat complexity with diversity. – *J. Exp. Mar. Biol. Ecol.* 109: 249–273.
- Denno, R. F. and Roderick, G. K. 1991. Influence of patch size, vegetation texture, and host plant architecture on the diversity, abundance, and life history styles of sap-feeding herbivores. – In: Bell, S. S., McCoy, E. D. and Mushinsky, H. R. (eds), *Habitat structure: the physical arrangement of objects in space*. Chapman and Hall, pp. 169–196.
- Dickinson, G. and Murphy, K. 1998. *Ecosystems. A functional approach*. – Routledge.
- Dobson, A. and Crawley, M. 1994. Pathogens and the structure of plant communities. – *Trends Ecol. Evol.* 9: 393–397.
- Elton, C. S. 1958. *The ecology of invasions by animals and plants*. – John Wiley and Sons.
- Ewel, J. J. 1986. Invasibility: lessons from South Florida. – In: Mooney, H. A. and Drake, J. A. (eds), *Ecology of biological invasions of North America and Hawaii*. Springer-Verlag, pp. 215–230.
- Fajvan, M. A. and Wood, J. M. 1996. Stand structure and development after gypsy moth defoliation in the Appalachian Plateau. – *For. Ecol. Manage.* 89: 79–88.

- Friend, G. R. and Taylor, J. A. 1984. Ground surface features attributable to feral buffalo, *Bubalus bubalis*. II. Their relationship to the abundance of small animal species. – Aust. Wildl. Res. 11: 311–323.
- Gilbert, G. S. and Hubbell, S. P. 1996. Plant diseases and the conservation of tropical forests. – Bioscience 46: 98–106.
- Gjerde, I. and Sætersdal, M. 1997. Effects on avian diversity of introducing spruce *Picea* spp. plantations in the native pine *Pinus sylvestris* forests of western Norway. – Biol. Conserv. 79: 241–250.
- Golley, F. B. 1993. A history of the ecosystem concept in ecology. – Yale University Press.
- Gordon, D. R. 1998. Effects of invasive, non-indigenous plant species on ecosystem processes: lessons from Florida. – Ecol. Appl. 8: 975–989.
- Gosling, L. M., Baker, S. J. and Clarke, C. N. 1988. An attempt to remove coypus (*Myocastor coypus*) from a wetland habitat in East Anglia. – J. Appl. Ecol. 25: 49–62.
- Graf, W. L. 1978. Fluvial adjustments to the spread of tamarisk in the Colorado River Plateau region. – Geol. Soc. Am. Bull. 89: 1491–1501.
- Grimm, N. B. 1995. Why link species and ecosystems? A perspective from ecosystem ecology. – In: Jones, C. G. and Lawton, J. H. (eds), Linking species and ecosystems. Chapman and Hall, pp. 5–15.
- Hanowski, J. M., Niemi, G. J. and Christian, D. C. 1997. Influence of within-plantation heterogeneity and surrounding landscape composition on avian communities in hybrid poplar plantations. – Conserv. Biol. 11: 936–944.
- Hanula, J. L. 1996. Relationship of wood-feeding insects and coarse woody debris. – In: McMinn, J. W. (ed.), Biodiversity and coarse woody debris in Southern forests. United States Dept. Agric., pp. 55–81.
- Hedge, P. and Kriwoken, L. K. 2000. Evidence for effects of *Spartina anglica* invasion on benthic macrofauna in Little Swanport Estuary, Tasmania. – Austral. Ecol. 25: 150–159.
- Horvath, T. G., Martin, K. M. and Lamberti, G. A. 1999. Effect of zebra mussels, *Dreissena polymorpha*, on macroinvertebrates in a lake-outlet stream. – Am. Midl. Nat. 142: 340–347.
- Hurlbert, S. H., Zedler, J. and Fairbanks, D. 1972. Ecosystem alteration by mosquitofish (*Gambusia affinis*) predation. – Science 175: 639–641.
- Jones, C. G., Lawton, J. H. and Shachak, M. 1994. Organisms as ecosystem engineers. – Oikos 689: 373–386.
- Jones, C. G., Lawton, J. H. and Shachak, M. 1997a. Ecosystem engineering by animals: why semantics matters. – Trends Ecol. Evol. 12: 275.
- Jones, C. G., Lawton, J. H. and Shachak, M. 1997b. Positive and negative effects of organisms as physical ecosystem engineers. – Ecology 78: 1946–1957.
- Kimmerer, W. J., Gartside, E. and Orsi, J. J. 1994. Predation by an introduced clam as the likely cause of substantial declines in zooplankton of San Francisco Bay. – Mar. Ecol. Prog. Ser. 113: 81–93.
- King, A. J., Robertson, A. I. and Healey, M. R. 1997. Experimental manipulations of the biomass of introduced carp (*Cyprinus carpio*) in billabongs. I. Impacts on water column properties. – Mar. Freshwat. Res. 48: 435–443.
- Kinzig, R. G. and Samways, M. J. 2000. Conserving dragonflies (Odonata) along streams running through commercial forestry. – Odonatologica 29: 195–208.
- Kitchell, J. F., Schindler, D. E., Ogutu-Ohwayo, R. and Reinthal, P. N. 1997. The Nile perch in Lake Victoria: interactions between predation and fisheries. – Ecol. Appl. 7: 653–664.
- Knapp, P. A. 1996. Cheatgrass (*Bromus tectorum* L.) dominance in the Great Basin Desert. – Global Environ. Change 6: 37–52.
- Krecker, F. H. 1939. Animal population of submerged aquatic plants. – Ecology 20: 553–562.
- Lewin, R. 1987. Ecological invasions offer opportunities. – Science 238: 752–753.
- Liebholt, A. M., Macdonald, W. L., Bergdahl, D. and Masstro, V. C. 1996. Invasion by exotic forest pests: a threat to forest ecosystems. – Forest Sci. Monogr. 30: 1–49.
- Lizarrdale, M. S., Deferrari, G. A., Alvarez, S. E. and Escobar, J. M. 1996. Effects of beaver (*Castor canadensis*) on the nutrient dynamics of the Southern Beech forest of Tierra del Fuego (Argentina). – Ecologia Austral. 6: 101–105.
- Lonsdale, W. M., Miller, I. L. and Forno, I. W. 1990. The biology of Australian weeds. 20. *Mimosa pigra*. – Plant Prot. Q. 4: 119–131.
- Lougheed, V. L., Crosbie, B. and Chow-Fraser, P. 1998. Predictions on the effect of common carp (*Cyprinus carpio*) exclusion on water quality, zooplankton, and submergent macrophytes in a Great Lakes wetland. – Can. J. Fish. Aquat. Sci. 55: 1189–1197.
- MacArthur, R. H. and MacArthur, J. W. 1961. On bird species diversity. – Ecology 42: 594–598.
- Macdonald, I. A. W. and Cooper, J. 1995. Insular lessons for global biodiversity conservation with particular reference to alien invasions. – In: Vitousek, P. M., Loope, L. L., Adersen, H. and Madsen, K. (eds), Islands: biological diversity and ecosystem function. Springer-Verlag, pp. 189–203.
- Macdonald, I. A. W., Loope, L. L., Usher, M. B. and Hamann, O. 1989. Wildlife conservation and the invasion of nature reserves by introduced species: a global perspective. – In: Drake, J. A., Mooney, H. A., di Castri, F. et al. (eds), Biological invasions: a global perspective. John Wiley and Sons, pp. 215–255.
- Mack, M. C. and D'Antonio, C. M. 1998. Impacts of biological invasions on disturbance regimes. – Trends Ecol. Evol. 13: 195–198.
- Mazzotti, F. J., Ostrenko, W. and Smith, A. T. 1981. Effects of the exotic plants *Melaleuca quinquenervia* and *Casuarina equisetifolia* on small mammal populations in the eastern Florida Everglades. – Fla. Sci. 44: 65–71.
- McCallum, H. and Dobson, A. 1995. Detecting disease and parasite threats to endangered species and ecosystems. – Trends Ecol. Evol. 10: 190–194.
- McCoy, E. D. and Bell, S. S. 1991. Habitat structure: the evolution and diversification of a complex topic. – In: McCoy, E. D. and Bell, S. S. (eds), Habitat structure: the physical arrangement of objects in space. Chapman and Hall, pp. 427–430.
- Morse, D. R., Lawton, J. H., Dodson, M. M. and Williamson, M. H. 1985. Fractal dimension of vegetation and the distribution of arthropod body lengths. – Nature 314: 731–733.
- Mueller-Dombois, D. 1973. A non-adapted vegetation interferes with water removal in a tropical rain forest area in Hawaii. – Trop. Ecol. 14: 1–18.
- Murdoch, W. W., Evans, F. C. and Peterson, C. H. 1972. Diversity and pattern in plants and insects. – Ecology 53: 819–828.
- Nalepa, T. F. and Schloesser, S. W. 1993. Zebra mussels. Biology, impacts, and control. – Lewis Publishers.
- North, S. G., Bullock, D. J. and Dulloo, M. E. 1994. Changes in the vegetation and reptile populations on Round Island, Mauritius, following eradication of rabbits. – Biol. Conserv. 67: 21–28.
- Nyman, J. A., Chabreck, R. H. and Kinler, N. W. 1993. Some effects of herbivory and 30 years of weir management on emergent vegetation in brackish marsh. – Wetlands 13: 165–175.
- Odum, E. P. 1972. Ecosystem theory in relation to man. – In: Wiens, J. A. (ed.), Ecosystem structure and function. Oregon State University Press, pp. 11–24.
- Office of Technology Assessment 1993. Harmful non-indigenous species in the United States, OTA-f-565 – United States Government Printing Office.

- Ogutu-Ohwayo, R. 1999. Nile perch in Lake Victoria: balancing the costs and benefits of aliens. – In: Sandlund, O. T., Schei, P. J. and Viken, A. (eds), *Invasive species and biodiversity management*. Kluwer, pp. 47–63.
- Oguz, T., Ducklow, H. W., Purcell, J. E. and Malanotte-Rizoli, P. 2001. Modeling the response of top-down control exerted by gelatinous carnivores on the Black Sea pelagic food web. – *J. Geophys. Res. C. Oceans* 106: 4543–4564.
- O'Hara, J. 1967. Invertebrates found in water hyacinth mats. – *Fla. Sci.* 30: 73–80.
- O'Hare, N. K. and Dalrymple, G. H. 1997. Wildlife in southern Everglades wetlands invaded by *Melaleuca* (*Melaleuca quinquenervia*). – *Bull. Florida Mus. Nat. Hist.* 41: 1–68.
- Okubo, A., Maini, P. K., Williamson, M. H. and Murray, J. D. 1989. On the spatial spread of the grey squirrel in Britain. – *Proc. R. Soc. Lond. B Biol. Sci.* 238: 113–125.
- O'Meara, G. F., Evans, L. F. Jr., Gettman, A. D. and Patteson, A. W. 1995. Exotic tank bromeliads harboring immature *Aedes albopictus* and *Aedes bahamensis* (Diptera: Culicidae) in Florida. – *J. Vector Ecol.* 20: 216–224.
- Osborne, P. 1983. The influence of Dutch elm disease on bird population trends. – *Bird Study* 30: 27–38.
- Osborne, P. 1985. Some effects of Dutch elm disease on the birds of a Dorset dairy farm. – *J. Appl. Ecol.* 22: 681–691.
- Pace, M. L., Cole, J. J., Carpenter, S. R. and Kitchell, J. F. 1999. Trophic cascades revealed in diverse ecosystems. – *Trends Ecol. Evol.* 14: 483–488.
- Pampush, G. J. and Anthony, R. G. 1993. Nest success, habitat utilization and nest-site selection of long-billed curlews in the Columbia Basin, Oregon. – *Condor* 95: 957–967.
- Parker, I. M., Simberloff, D., Lonsdale, W. M. et al. 1999. Impact: toward a framework for understanding the ecological effects of invaders. – *Biol. Invasions* 1: 3–19.
- Peterken, G. F. and Mountford, E. P. 1998. Long-term change in an unmanaged population of wych elm subjected to Dutch elm disease. – *J. Ecol.* 86: 205–218.
- Petren, K. and Case, T. J. 1998. Habitat structure determines competition intensity and invasion success in gecko lizards. – *Proc. Natl. Acad. Sci.* 95: 11739–11744.
- Phelps, H. L. 1994. The Asiatic clam (*Corbicula fluminea*) invasion and system-level ecological change in the Potomac River Estuary near Washington, D.C. – *Estuaries* 17: 614–621.
- Pickett, S. T. A., Kolasa, J., Armesto, J. J. and Collins, S. L. 1989. The ecological concept of disturbance and its expression at various hierarchical levels. – *Oikos* 54: 129–136.
- Posey, M. H. 1988. Community changes associated with the spread of an introduced seagrass, *Zostera japonica*. – *Ecology* 69: 974–983.
- Posey, M. H., Wigand, C. and Stevenson, J. C. 1993. Effects of an introduced aquatic plant, *Hydrilla verticillata*, on benthic communities in the upper Chesapeake Bay. – *Estuar. Coast. Shelf Sci.* 37: 539–555.
- Power, M. E. 1997. Estimating impacts of a dominant detritivore in a neotropical stream. – *Trends Ecol. Evol.* 12: 47–49.
- Rabenold, K. N., Fauth, P. T., Goodner, B. W. et al. 1998. Response of avian communities to disturbance by an exotic insect in spruce-fir forests of the southern Appalachians. – *Conserv. Biol.* 12: 177–189.
- Race, M. S. 1982. Competitive displacement and predation between introduced and native mud snails. – *Oecologia* 54: 337–347.
- Randall, J. M. 1993. Exotic weeds in North American and Hawaiian natural areas: The Nature Conservancy's plan of attack. – In: McKnight, B. (ed.), *Biological pollution: the control and impact of invasive exotic species*. Indiana Academy of Sciences, pp. 159–172.
- Randall, J. M. 1996. Weed control for the preservation of biological diversity. – *Weed Technol.* 10: 370–383.
- Read, M. G. and Barmuta, L. A. 1999. Comparisons of benthic communities adjacent to riparian native eucalypt and introduced willow vegetation. – *Freshwater Biol.* 42: 359–374.
- Reusch, T. B. H. 1998. Native predators contribute to invasion resistance to the non-indigenous bivalve *Musculista senhousia* in southern California, USA. – *Mar. Ecol. Prog. Ser.* 170: 159–168.
- Reusch, T. B. H. and Williams, S. L. 1998. Variable responses of native eelgrass *Zostera marina* to a non-indigenous bivalve *Musculista senhousia*. – *Oecologia* 113: 428–441.
- Ricciardi, A., Whoriskey, F. G. and Rasmussen, J. B. 1997. The role of the zebra mussel (*Dreissena polymorpha*) in structuring macroinvertebrate communities on hard substrata. – *Can. J. Fish. Aquat. Sci.* 54: 2596–2608.
- Richardson, M. J., Whoriskey, F. G. and Roy, L. H. 1995. Turbidity generation and biological impacts of an exotic fish *Carassius auratus*, introduced into shallow seasonally anoxic ponds. – *J. Fish Biol.* 47: 576–585.
- Robertson, A. I., Healey, M. R. and King, A. J. 1997. Experimental manipulations of the biomass of introduced carp (*Cyprinus carpio*) in billabongs. II. Impacts on benthic properties and processes. – *Mar. Freshwat. Res.* 48: 445–454.
- Robles, M. and Chapin, F. S., III. 1995. Comparison of the influence of two exotic species on ecosystem processes in the Berkeley hills. – *Madroño* 42: 349–357.
- Rotramel, G. 1975. Filter-feeding by the marine boring isopod *Sphaeroma quoyanum* H. Milne Edwards, 1849 (Isopoda: Sphaeromatidae). – *Crustaceana* 28: 247–256.
- Rottenborn, S. C. 2000. Nest-site selection and reproductive success of urban Red-shouldered Hawks in central California. – *J. Raptor Res.* 34: 18–25.
- Ruiz, G. M., Fofonoff, P., Hines, A. H. and Grosholz, E. D. 1999. Nonindigenous species as stressors in estuarine and marine communities: assessing impacts and interactions. – *Limnol. Oceanogr.* 44: 950–972.
- Russell-Smith, J. and Bowman, D. J. M. S. 1992. Conservation of monsoon rain forest isolates in Northern Territory, Australia. – *Biol. Conserv.* 59: 51–63.
- Salmon, M., Reiners, R., Lavin, C. and Wyneken, J. 1995. Behavior of loggerhead sea turtles on an urban beach. I. Correlates of nest placement. – *J. Herpetol.* 29: 560–567.
- Savidge, J. A. 1987. Extinction of an island forest avifauna by an introduced snake. – *Ecology* 68: 660–668.
- Schmitz, D. C., Schardt, J. D., Leslie, A. J. et al. 1993. The ecological impact and management history of three invasive alien aquatic species in Florida. – In: McKnight, B. N. (ed.), *Biological pollution: the control and impact of invasive exotic species*. Indiana Academy of Sciences, pp. 173–194.
- Schmitz, D. C., Simberloff, D., Hoffstetter, R. H. et al. 1997. The ecological impact of nonindigenous plants. – In: Simberloff, D., Schmitz, D. C. and Brown, T. C. (eds), *Strangers in paradise*. Island Press, pp. 39–61.
- Schwindt, E. and Iribarne, O. O. 2000. Settlement sites, survival and effects on benthos of an introduced reef-building polychaete in a SW Atlantic coastal lagoon. – *Bull. Mar. Sci.* 67: 73–82.
- Simberloff, D. 1990. Reconstructing the ambiguous: can island ecosystems be restored? – In: Towns, D. R., Daugherty, C. H. and Atkinson, I. A. E. (eds), *Ecological restoration of New Zealand Islands*. Conservation Sciences Publication No 2, Department of Conservation, Wellington., pp. 37–51.
- Simberloff, D. 1991. Keystone species and community effects of biological introductions. – In: Ginzburg, L. R. (ed.), *Assessing ecological risks of biotechnology*. Butterworth-Heinemann, pp. 1–19.
- Simberloff, D. and Von Holle, B. 1999. Positive interactions of nonindigenous species: invasional meltdown. – *Biol. Invasions* 1: 21–32.
- Singer, F. J., Swank, W. T. and Clebsch, E. E. C. 1984. Effects of wild pig rooting in a deciduous forest. – *J. Wildl. Manage.* 48: 464–473.

- Singer, M. C., Thomas, C. D. and Parmesan, C. 1993. Rapid human-induced evolution of insect-host associations. – *Nature* 366: 681–683.
- Skubinna, J. P., Coon, T. G. and Batterson, T. R. 1995. Increased abundance and depth of submersed macrophytes in response to decreased turbidity in Saginaw Bay, Lake Huron. – *J. Great Lakes Res.* 21: 476–488.
- Smith, C. W. 1989. Non-native plants. – In: Stone, C. P. and Scott, J. M. (eds), *Conservation biology in Hawaii*. University of Hawaii Press, pp. 60–69.
- Sousa, J. P., Vingada, J. V., Barrocas, H. and da Gama, M. M. 1997. Effects of introduced exotic tree species on Collembola communities: the importance of management techniques. – *Pedobiologia* 41: 145–153.
- Sousa, J. P., da Gamma, M. M., Ferreira, C. and Barrocas, H. 2000. Effect of eucalyptus plantations on Collembola communities in Portugal: a review. – *Belgian J. Entomol.* 2: 187–201.
- Sousa, W. P. 1984. The role of disturbance in natural communities. – *Annu. Rev. Ecol. Syst.* 15: 353–391.
- Sousa, W. P. 2001. Natural disturbance and the dynamics of marine benthic communities. – In: Bertness, M. D., Gaines, S. D. and Hay, M. E. (eds), *Marine community ecology*. Sinauer Associates Inc, pp. 85–130.
- Spencer, C. N., McClelland, B. R. and Stanford, J. A. 1991. Shrimp stocking, salmon collapse, and eagle displacement. – *Bioscience* 41: 14–21.
- Spencer, C. N., Potter, D. S., Bukatis, R. T. and Stanford, J. A. 1999. Impact of predation by *Mysis relicta* on zooplankton in Flathead Lake, Montana, USA. – *J. Plank. Res.* 21: 51–64.
- Steenkamp, H. E. and Chown, S. L. 1996. Influence of dense stands of an exotic tree, *Prosopis glandulosa* Benson, on a savanna dung beetle (Coleoptera: Scarabaeinae) assemblage in southern Africa. – *Biol. Conserv.* 78: 305–311.
- Stewart, T. W. and Haynes, J. M. 1994. Benthic macroinvertebrate communities of southwestern Lake Ontario following invasion of *Dreissena*. – *J. Great Lakes Res.* 20: 479–493.
- Stoner, A. W. and Lewis, F. G. III 1985. The influence of quantitative and qualitative aspects of habitat complexity in tropical seagrass meadows. – *J. Exp. Mar. Biol. Ecol.* 94: 19–40.
- Strayer, D. L. 1999. Effects of alien species on freshwater mollusks in North America. – *J. N. Am. Benthol. Soc.* 18: 74–98.
- Strayer, D. L., Caraco, N. F., Cole, J. J., Findlay, S. and Pace, M. L. 1999. Transformation of freshwater ecosystems by bivalves. – *Bioscience* 49: 19–27.
- Sykes, P. W. Jr 1987. The feeding habits of the snail kite in Florida, USA. – *Colonial Waterbirds* 10: 84–92.
- Talley, T. S. and Levin, L. A. 2001. Modification of sediments and macrofauna by an invasive marsh plant. – *Biol. Inv.* 3: 51–68.
- Talley, T. S., Crooks, J. A. and Levin, L. A. 2001. Habitat utilization and alteration by the burrowing isopod *Sphaeroma quoyanum* in California salt marshes. – *Mar. Biol.* 138: 561–573.
- Tansley, A. G. 1935. The use and abuse of vegetational concepts and terms. – *Ecology* 16: 284–307.
- Thomas, F., Poulin, R. and de Meeüs, T. 1999. Parasites and ecosystem engineering: what role could they play? – *Oikos* 84: 167–171.
- Thurber, D. K., McClain, W. R. and Whitmore, R. C. 1994. Indirect effects of gypsy moth defoliation on nest predation. – *J. Wildl. Manage.* 58: 493–500.
- Toland, B. 1992. Use of forested spoil islands by nesting American oystercatchers in southeast Florida. – *J. Field Ornithol.* 63: 155–158.
- Tschinkel, W. R. 1993. The fire ant (*Solenopsis invicta*): still unvanquished. – In: McKnight, B. (ed.), *Biological pollution: the control and impact of invasive exotic species*. Indiana Academy of Sciences, pp. 121–136.
- Turner, S. J., Thrush, S. F., Hewitt, J. E. et al. 1999. Fishing impacts and the degradation or loss of habitat structure. – *Fish. Manage. Ecol.* 6: 401–420.
- Usher, M. B. 1986. Invasibility and wildlife conservation: invasive species on nature reserves. – *Philos. Trans. R. Soc. Lond. B* 314: 695–710.
- van Vuren, D. and Coblenz, B. E. 1987. Some ecological effects of feral sheep on Santa Cruz Island, California, USA. – *Biol. Conserv.* 41: 253–268.
- Vander Zanden, M. J., Casselman, J. M. and Rasmussen, J. B. 1999. Stable isotope evidence for the food web consequences of species invasions in lakes. – *Nature* 401: 464–467.
- Veblen, T. T., Mermoz, M., Martin, C. and Kitzberger, T. 1992. Ecological impacts of introduced animals in Nahuel Huapi National Park, Argentina. – *Conserv. Biol.* 6: 71–83.
- Vermeij, G. J. 1996. An agenda for invasion biology. – *Biol. Conserv.* 78: 3–9.
- Versfeld, D. B. and van Wilgen, B. W. 1986. Impact of woody aliens on ecosystem properties. – In: Macdonald, I. A. W., Kruger, F. J. and Ferrar, A. A. (eds), *The ecology and management of biological invasions in Southern Africa*. Oxford University Press, pp. 239–246.
- Vitousek, P. M. 1986. Biological invasions and ecosystem properties: can species make a difference? – In: Mooney, H. A. and Drake, J. A. (eds), *Ecology of biological invasions of North America and Hawaii*. Springer-Verlag, pp. 163–176.
- Vitousek, P. M. 1990. Biological invasions and ecosystem processes: towards an integration of population biology and ecosystem studies. – *Oikos* 57: 7–13.
- Vitousek, P. M., Walker, L. R., Whiteaker, L. D. et al. 1987. Biological invasion by *Myrica faya* alters ecosystem development in Hawaii. – *Science* 238: 802–804.
- Vitousek, P. M., D'Antonio, C. M., Loope, L. L. et al. 1997. Introduced species: a significant component of human-caused global change. – *N. Z. J. Ecol.* 21: 1–16.
- Vivrette, N. J. and Muller, C. H. 1977. Mechanism of invasion and dominance of coastal grassland by *Mesembryanthemum crystallinum*. – *Ecol. Monogr.* 47: 301–318.
- von Broembsen, S. L. 1989. Invasions of natural ecosystems by plant pathogens. – In: Drake, J. A., Mooney, H. A., di Castri, F. et al. (eds), *Biological invasions: a global perspective*. John Wiley and Sons, pp. 77–83.
- Walker, L. R. and Vitousek, P. M. 1991. An invader alters germination and growth of a native dominant tree in Hawaii (USA). – *Ecology* 72: 1449–1455.
- Weidemann, A. M. 1984. The ecology of Pacific Northwest coastal sand dunes: a community profile. – United States Fish and Wildlife Service Biological Report 84/04.
- Williamson, M. 1996. *Biological invasions*. – Chapman and Hall.
- Wilson, J. B. and Agnew, A. D. Q. 1992. Positive-feedback switches in plant communities. – *Adv. Ecol. Res.* 23: 263–336.