The Implications of Niche Construction and Ecosystem Engineering for Conservation Biology

NEELTJE J. BOOGERT, DAVID M. PATERSON, AND KEVIN N. LALAND

Although strategies to conserve biodiversity (e.g., the establishment of reserves and the management of flagship, umbrella, indicator, and keystone species) are valuable, they entail practical and conceptual difficulties. A focus on niche construction and ecosystem engineering, however, could provide new insights and methods for conservation biology. Many organisms modulate the availability of resources to other species by causing state changes in biotic or abiotic materials (ecosystem engineering), in the process frequently changing the selection to which the ecosystem engineers and other organisms are exposed (niche construction). We describe growing evidence that organisms have significant nontrophic impacts on ecosystem structure, function, and biodiversity, and outline established means of identifying key species involved in niche construction. On the basis of this engineering perspective, we propose a number of measures that could be employed to enhance conservation efforts.

Keywords: niche construction, ecosystem engineering, conservation strategies, keystone species, biodiversity

Through their metabolism and behavior, organisms modify their environments, frequently changing the selection pressures to which they and other organisms are exposed. This process is known as "niche construction" (Odling-Smee FJ 1988), a term that refers to all of the impacts, positive and negative, that organisms have on their selective environments. The role of cyanobacteria in the creation of Earth's oxygen-rich atmosphere, the soil-perturbing activities of earthworms, and the dam building of beavers exemplify the huge range of temporal and spatial scales across which niche construction occurs. Moreover, niche construction is ubiquitous, as illustrated by the large number of examples, encompassing hundreds of thousands of species, in *Niche Construction,* a monograph by Odling-Smee and colleagues (2003).

Advocates of the niche construction perspective stress the role of organisms as drivers of evolutionary and ecological dynamics (Odling-Smee et al. 2003). An increasing number of biologists view niche construction as an important evolutionary process (Day et al. 2003), and acknowledge that each generation of organisms inherits both genes and a legacy of modified selection pressures from the ancestral generation. Meffe and Carroll (1997a) have emphasized that conservation biologists should take an evolutionary perspective. Here we suggest that this new evolutionary view, which highlights the significance of the activities of living organisms in shaping local environments and ecosystems, as well as the greater connectance between species that such nontrophic interactions generate, has considerable potential value to conservationists.

A focus on organisms' modification of environments is also central to the concept of ecosystem engineering, which was introduced to ecology by Jones and colleagues (1994, 1997; see the special section "Organisms as Ecosystem Engineers" in the March 2006 edition of *BioScience*). ("Ecosystem engineering" and "niche construction" can be considered synonyms, although "ecosystem engineering" is mainly used in ecology, whereas "niche construction" is the term adopted by evolutionary biologists.) Jones and colleagues (1994) drew attention to a lack of ecological research effort dedicated to organisms that modulate the availability of resources and habitat to other species by causing physical state changes in biotic or

---

Neeltje J. Boogert is a doctoral candidate in the Department of Biology, McGill University, 1205 Avenue Docteur Penfield, Montreal, Quebec H3A 1B1, Canada. David M. Paterson is a professor of coastal ecology at Gatty Marine Laboratory, St. Andrews University, St. Andrews, Fife KY16 8LB, United Kingdom. Kevin N. Laland (e-mail: knl1@st-andrews.ac.uk) is a professor of biology in the School of Biology, St. Andrews University, St. Andrews, Fife KY16 9TS, United Kingdom.

abiotic materials. They argued that ecosystem engineers can regulate energy flows, mass flows, and trophic patterns in ecosystems to generate an "engineering web," a web of connectance comprising the engineering interactions of diverse species, which regulates ecosystem functioning in conjunction with the well-studied webs of trophic interactions (Wilby 2002). Moreover, ecosystem engineers can control flows of energy and materials among trophically interconnected organisms without being part of those flows. The laws of conservation of mass and energy and the stoichiometry used in understanding the trophic dynamics of food webs cannot be used to predict ecosystem engineering, which presents a challenge to ecologists. For instance, the amounts of mass and energy and the elemental stoichiometry of the beaver do not equal the mass, energy, and stoichiometry of the dam or the water it holds (Jones et al. 1997).

Jones and colleagues (1997) envisaged some utility for an ecosystem-engineering approach to conservation, particularly if it is possible to predict which species will be important ecosystem engineers in which ecosystems (see also Crain and Bertness 2006, Wright and Jones 2006). Similarly, Odling-Smee and colleagues (2003) state, "Conservation efforts may be most effective if they ensure the survival of the key engineers in an ecosystem" (p. 384). These suggestions raise three questions: (1) What conservation strategies are currently being implemented? (2) To what extent are they effective? (3) Could biodiversity be preserved by taking key engineers and their products into account?

The need for new approaches is apparent. In spite of extensive conservation efforts and many acknowledged successes, the world's flora and fauna are disappearing at ever increasing rates (Myers 1997, Pimm 1998). The objective of this article is to assess whether and how a focus on niche construction and ecosystem engineering could provide new insights and methods for conservation biology (see also Crooks 2002). We begin by presenting a concise overview and assessment of traditional conservation strategies, namely, the establishment of protected areas, the protection of surrogate species, and the protection of keystone species. We dwell on the distinction between keystone species and key ecosystem engineers, and the divergent conservation measures that a focus on each suggests. We go on to describe research demonstrating the importance of key engineers to ecosystem structure, function, and biodiversity, and consider how this new perspective might affect conservation.

Protected areas

Between 1962 and 2003, worldwide protected areas—established for the conservation of ecosystems, natural habitats, and viable populations of species—increased approximately tenfold, amounting to 18.8 million square kilometers, or 11.5% of global land area, in 2003. However, high numbers and large areas do not necessarily reflect achievement of conservation objectives (Chape et al. 2004). The statistics are skewed by the location of many protected areas in remote, infertile, and low-diversity landscapes, while other highly threatened but economically important regions remain poorly protected (see, e.g., Pressey et al. 2002, Rouget et al. 2003, Chape et al. 2004). In addition, because of political, economic, and sociological factors (Meffe and Carroll 1997b), protected areas may be too small or isolated (or both) to prevent further decline of the populations under protection. There are no marine protected areas in international waters (63% of the world's ocean area; Boersma and Parrish 1999, Chape et al. 2004), and some nominally protected areas may never be properly protected owing to lack of funding (Chape et al. 2004). The strategy of focusing conservation efforts on regions representing biodiversity hotspots has recently come under fire as well: There is an alarming lack of overlap between hotspots identified using different criteria, and the emphasis on hotspots means that many other important ecosystems are neglected (Odling-Smee L 2005).

Surrogate species

The Endangered Species Act of 1973 aims to conserve endangered and threatened species of fish, wildlife, and plants and the ecosystems on which these species depend. Yet confronted with limited resources for burgeoning conservation needs and the impossibility of keeping pace with the individual needs of increasing numbers of endangered and threatened species, lawmakers have proposed shortcuts whereby the protection of a single species is designed indirectly to protect the regional biota (Simberloff 1998). These "surrogate species" can be broadly categorized into three classes (Andelman and Fagan 2000): (1) flagships, charismatic species that attract public support; (2) umbrellas, species requiring such large areas of habitat that their protection might protect other species; and (3) biodiversity indicators, taxa whose presence may indicate high species richness. Although these schemes are attractive tools in theory, their effectiveness has been questioned (Simberloff 1998, Andelman and Fagan 2000). Flagship species may be effective at attracting funds, but their habitat requirements do not necessarily correlate with those of other species, their conservation can itself be expensive, and regions without charismatic species may remain unprotected (Simberloff 1998).

The lack of empirical evidence for the usefulness of umbrella species for conservation planning has led to the development and implementation of three criteria for selection: (1) rarity, (2) sensitivity to human disturbance, and (3) mean percentage of co-occurring species. These criteria produced divergent rankings in assessments of species' potential to serve as umbrellas for their taxonomic group (Fleishman et al. 2000). In addition, the comprehensive databases necessary for establishing mean percentages of co-occurring species, for example, are rarely available (Fleishman et al. 2000, Betrus et al. 2005). Finally, Simberloff (1998) has pointed out that single-species management of an indicator species is a self-contradiction, because artificially improving the indicator species' status would logically result in its losing its function as an indicator. In summary, the surrogate-species approach has encountered a number of practical problems.

Keystone species

Simberloff (1998) suggested that single-species management might be more effective when directed toward "keystone species," originally defined by Paine (1969) as species of high trophic status whose activities disproportionately affect the patterns of species occurrence, distribution, and density in the species' community. The term "keystone species" enjoyed great popularity among ecologists and was applied to increasing numbers of species at many trophic levels. This development led Mills and colleagues (1993) to warn of the dangers inherent in shaping conservation strategies around this concept, as it lacked a clear operational definition. In an attempt to meet these concerns, ecologists at a United Nations–sponsored workshop proposed this definition: "A keystone species is a species whose impacts on its community or ecosystem are large, and much larger than would be expected from its abundance" (Power and Mills 1995, p. 184). To define the strength of the effect of a species on a community or ecosystem trait, Power and colleagues (1996) developed the measure of community importance (CI), which is the change in a community or ecosystem trait per unit change in the abundance of the species. In mathematical terms,

$$CI = [\delta(\text{trait})/\delta p]\ [1/(\text{trait})],$$

where p stands for the proportional abundance of the species whose abundance is experimentally modified. It was suggested that the CI index could be used to measure keystone effects on community traits such as productivity, nutrient cycling, species richness, and the abundance of functional groups or dominant species (Power et al. 1996).

However, ecologists' attempts to apply this index encountered operational difficulties. For example, prairie dogs greatly affect the structure and function of prairie ecosystems and meet Power and colleagues' (1996) definition of keystone species. However, prairie dog abundance was found to vary considerably, leaving CI strongly dependent on choice of abundance level and scale of analysis (Kotliar 2000). Davic (2003) pointed out that implementation of the CI index would be impractical for an applied research program, as it requires quantification of the total biomass of all the other species in a community to determine the keystone species' proportional abundance. Davic (2003) advocated returning to a food-web focus.

In summary, the strategy of prioritizing the protection of the keystone species in an ecosystem has encountered difficulties, and there seems to be little consensus as to how this strategy should be implemented.

Keystone species versus key ecosystem engineers

Many ecosystem engineers (e.g., beavers, elephants, woodpeckers) have also been described as putative keystone species (Mills et al. 1993, Power et al. 1996, Primack 1998). However, "keystone species" and "ecosystem engineers" are not synonyms (Jones et al. 1997). Jones and colleagues (1994) thought it unlikely that a keystone species would exert its effects entirely trophically, and argued that many so-called keystone species influence ecosystems primarily through their engineering. Whereas Jones and colleagues (1994) use the term "keystone engineers" to further differentiate keystone species from important ecosystem engineers and avoid confusion, we adopt instead the term "key (ecosystem) engineers." The distinction between the concepts of keystone species and ecosystem engineers is vital here, since the latter is not merely a subset of the former, and the distinction points to different conservation-related ways of managing ecosystems. Jones and colleagues (1997) identify several factors that potentially scale up the impact of engineering, including per capita lifetime activity of individual engineering organisms, density of the engineering population, length of time a population persists in the same place, durability of the engineered construct in the environment, number and type of resource flows that are modulated by the engineering, and number of other species utilizing those flows. It is immediately apparent that such factors differ markedly from the aforementioned criteria employed to identify keystone species. Means of quantifying engineering effects are described elsewhere (Jones et al. 1994, 1997, Shachak and Jones 1995, Odling-Smee et al. 2003).

Ecological cascades illustrate the distinction between keystone species and key engineer. In the Bay of Fundy, Canada, estuarine sediments are dominated by benthic diatoms that produce carbohydrate exudates. These secretions bind the sand and stabilize its movement, which causes a physical state change in the environment that allows other species to colonize the area (figure 1; Daborn et al. 1993, Jones et al. 1997). An amphipod (*Corophium volutator*) that grazes on the diatoms affects soil stability; where these amphipods are abundant, sand stabilization by diatoms is reduced. In turn, migratory sandpipers (*Calidris pusilla*) feed on the amphipods (figure 2). With the appearance of these birds, amphipod numbers decline, promoting restabilization of the habitat by diatoms. Jones and colleagues (1997) point out that the sandpiper might be seen as the keystone species in the system, since it meets keystone definitions, and variation in its abundance has great knock-on effects on the ecosystem. However, these effects transpire only because of the engineering activities of the diatoms, which are the key ecosystem engineers. Conservation efforts to counteract sediment erosion would be misguided if directed solely at the keystone predators. Sandpiper presence does not guarantee diatom activity, whereas only engineering by diatoms results in sand stabilization, and thereby ecosystem stabilization. Moreover, diatoms are abundant, and thus do not qualify as keystone species.

Jones and colleagues (1994, 1997) described a similar coupled engineering and trophic cascade for sea otters, urchins, and kelp. Kelp forests dampen waves, create understory conditions favorable for species adapted to low light intensity, are substratum for numerous sessile animals and algae, and provide habitat for mobile pelagic and benthic organisms (Steneck et al. 2002). At midlatitudes, herbivory by sea urchins

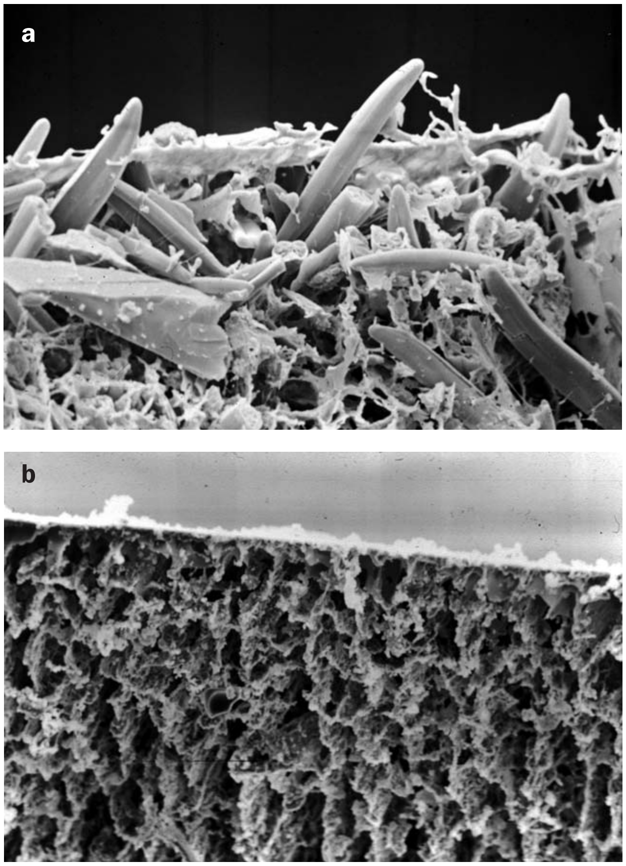

Figure 1. Mudflat sediment with (a) and without (b) benthic diatoms. The diatoms, which excrete extracellular polymeric substances (weblike white filaments) that bind the sediment to enhance soil cohesion (Daborn et al. 1993), can be regarded as key ecosystem engineers. Photographs: David Paterson.

(*Strongylocentrotus* spp.) is the most common and important agent of kelp deforestation (Steneck et al. 2002). Sea urchins are, in turn, an important food for sea otters (*Enhydra lutris*). Estes and Palmisano (1974) showed that a dense population of sea otters greatly reduced sea urchin numbers, and the resultant release from grazing pressure permitted a significant increase in kelp-bed size and associated communities, in comparison with the island group where sea otters were absent. Hence, while the sea otter is traditionally regarded as the keystone species in kelp forest ecosystems in the Northern Hemisphere (Estes and Palmisano 1974, Jessup et al. 2004), it is the engineering by kelp that provides the foundations for the ecosystem as a whole (Jones et al. 1994, 1997). Whereas other apex predators, such as lobsters and sheephead, may fulfill the functional role of the sea otter (Dayton et al. 1998, Steneck et al. 2002), there seems to be no such substitute for kelp engineering. Kelp forest management would be most effective if the ultimate focus were on kelp rather than on conservation of the sea otter as "sentinel of marine ecosystem health" (Jessup et al. 2004).

The concepts of keystone species and key ecosystem engineer are not identical, nor is the latter subsumed within the former. Conservation efforts guided by the keystone species concept alone could lose sight of the importance of ecosystem engineers' activities for ecosystem structure and function. It is true that in many ecosystems species of high trophic status impose, through predation, direct regulatory effects that are independent of engineering activity at lower trophic levels, but the current view of keystone species risks confounding such influences with cases in which the predators' influence is solely indirect, brought about through its effects on the frequency of engineers. Preservation of the apex predators of trophic cascades may be necessary for conserving ecosystems, but it is not sufficient, as key ecosystem engineers may be providing the structural and functional foundations of ecosystems (Crain and Bertness 2006).

Ecosystem engineers and ecosystems

In recent years the number of studies explicitly addressing ecosystem engineers and their nontrophic impacts on ecosystems has been growing, with many revealing the effects of ecosystem engineering on biodiversity (see Wright and Jones 2006 for a recent overview). For example, the selective removal of a detritivorous fish (*Prochilodus mariae*) from a stream in the Andean foothills resulted in the rapid accretion of sediments and significant changes in the composition of algal and invertebrate assemblages (Flecker 1996). Through their modification of habitat structure and resource availability, sediment-processing fish were shown to be key to structuring biotic communities. Overexploitation of *Prochilodus* fisheries in South America may have broad consequences that are manifested throughout Andean stream ecosystems (Flecker 1996).

Exotic species represent one of the leading threats to biodiversity (Vitousek et al. 1997, Godfray and Crawley 1998, Chapin et al. 2000), but they also provide opportunities to learn more about the ecological effects of adding engineering species to ecosystems (Crooks 2002). For example, observations and enclosure experiments demonstrate that the Australasian isopod *Sphaeroma quoyanum* exacerbates California salt marsh erosion through its burrowing and filter feeding, with losses exceeding 100 centimeters of marsh edge per year (Talley et al. 2001). Littoral soft-sediment habitats and fringing salt marshes may have been changed into hard-substrate environments in southern New England by the invasion of the European periwinkle (*Littorina littorea*), as suggested by the rapid accumulation of soft-sediment organisms observed in areas from which this herbivorous snail was experimentally removed (Bertness 1984). The introduced mussel *Musculista senhousia* represents a serious problem for native eelgrass (*Zostera marina*) habitat restoration because it negatively affects rhizome elongation rates, probably through spatial interference from the mussels' byssal mats, and thereby impedes population growth of this clonal eelgrass (Reusch and Williams 1998).

*Figure 2. Semipalmated sandpipers (***Calidris pusilla L.***) feeding on an amphipod* **Corophium volutator** *in the Bay of Fundy. Each bird is estimated to consume more than 10,000* **Corophium** *per day, sufficient to result in a decline in* **Corophium** *activity. As* **Corophium** *graze diatoms, the sandpipers' feeding is correlated with enhanced sediment stability (Daborn et al. 1993). Photograph: David Paterson.*

Although exotic species are often considered agents of disturbance that destroy physical structure (Crooks 2002), their effects may depend on whether these invaders are key engineers, or on the impact they have on such engineers. Furthermore, introductions may not necessarily be detrimental to native organisms. Indeed, it has been shown that habitat modification by exotics may benefit the resident fauna. A case in point is the introduced mussel *M. senhousia,* which was subject to studies (Crooks and Khim 1999) that experimentally examined the relationship between (a) the ecosystem effects of the physical structure of mussel mats created by these invading mussels and (b) the mussels' biological activities. Artificial mussel mats were shown to increase species richness and macrofaunal density, whereas the influence of mussel shells and living mussels was less pronounced (Crooks and Khim 1999). Sedimentary and faunal changes caused by the introduced seagrass *Zostera japonica* were similar to those associated with native seagrass. Moreover, local faunal richness and abundance within both naturally invaded and transplanted *Z. japonica* patches were higher than in adjacent unvegetated control areas, and no negative effects of *Z. japonica* on resident species were observed (Posey 1988).

Jones and colleagues (1997) hypothesized that at a scale encompassing unmodified or "virgin" habitats, engineered habitats, and degraded areas abandoned by engineers, the net effect of ecosystem engineering should be to enhance species richness via a net increase in habitat diversity. Recent studies provide support for this hypothesis. For example, natural sites with and without beavers (*Castor canadensis*) exhibit low overlap in species composition. By increasing habitat heterogeneity, beavers increased herbaceous plant species numbers by more than 33% (Wright et al. 2002).

Another example is provided by *Pseudotelphusa* caterpillars, which build leaf shelters by using silk to bind pairs of leaves together, creating a habitat that a succession of leaf-tying and non-leaf-tying species can colonize (Lill and Marquis 2003). Lill and Marquis (2003) quantified the relative impact of engineering versus nonengineering effects of *Pseudotelphusa* on insect herbivores occupying white oak saplings by removing leaf ties from some saplings and constructing artificial leaf ties on others, and adding a single caterpillar to some artificial ties. Removal of leaf ties significantly decreased the mean species richness of leaf-chewing insects. In addition, trees with artificial ties exhibited increased species richness of leaf-tying caterpillars, sawflies, and beetles. No significant differences were found between the artificial tie treatments with and without caterpillars, implying that the engineering of leaf shelters was the principal mode of the caterpillars' effect on their environment, superseding effects from trophic interactions (Lill and Marquis 2003).

A final example is seaside arrowgrass (*Triglochin maritima*), which facilitates plant diversity in salt marshes. By creating elevated rings, maintained structurally by its rhizomes, *T. maritima* supports both a greater abundance of species and the growth of species not present in the adjacent substratum (Fogel et al. 2004). Experimental analysis revealed that the primary mechanism underlying enhanced plant species diversity was the physical increase in height afforded by the *T. maritima* rings, which increased reductive potentials and habitat heterogeneity and reduced salinity for neighboring plants (Fogel et al. 2004).

These studies illustrate two important points. First, they show the impacts that ecosystem engineers can have on ecosystem structure, function, and biodiversity, and demonstrate that these impacts are explicitly nontrophic in character (in contrast to most keystone species' effects). Second, the experimental methods adopted point to several means of identifying key engineering species in ecosystems, such as removing or adding the engineering species, comparing naturally occurring sites with and without the engineer, and manipulating the environment to mimic engineering effects in the absence of the engineer.

As more studies are conducted, general characteristics of key engineering species are starting to emerge (Jones et al. 1997). Many groups of organisms have already been recognized for their engineering roles, and these are now reasonably well documented (Jones et al. 1994, 1997, Odling-Smee et al. 2003, Hansell 2004). Notably, conservation of key ecosystem engineers can coincide with conservation of "critical habitat" (a signature component of the Endangered Species Act), as exemplified by the aforementioned studies on kelp, seagrass, and arrowgrass. However, the critical habitat approach omits the numerous nonvegetative ecosystem engineers, such as diatoms, beavers, and leaf-tying caterpillars, that are key to the structure and functioning of their respective ecosystems.

Although the burgeoning research on ecosystem engineering is promising, it is clear that even if a particular species is a proven key engineer under some circumstances, it may not be under other circumstances (Crain and Bertness 2006). The phenomenon of behavior varying according to the specific circumstances in which an organism finds itself is well established (Krebs and Davies 1997). The extent to which context dependency (also known as "functional plasticity"; Biles et al. 2003, Paterson 2005) applies to key ecosystem engineers remains to be established. However, there are grounds for being optimistic about the possibility of identifying fundamental engineering roles in ecosystems, even if the specific species involved may differ from one context to the next. Meffe and Carroll (1997b) stress that ecosystems are dynamic and nonequilibrial, and therefore changing species composition must be a part of conservation. To the extent that ecosystems are truly regulated by engineering webs (Jones et al. 1997), however, the same ecosystem structure may be maintained in the face of changing species composition, provided that the *activity* of the key engineers is preserved. Odling-Smee and colleagues (2003) refer to "benign invasions," in which the species composition changes but the species that invades is one that expresses niche-constructing activities similar to those of the replaced species (see below).

Evolution and niche construction

Meffe and Carroll (1997a) stressed that answers to conservation problems must be developed within an evolutionary framework. Standard evolutionary theory describes a single way to establish an adaptive match between organisms and their environment: natural selection acting on genetic variability. However, natural selection can work only on the genetic resource base available, and if genetic diversity is reduced by population decline and extinction, evolutionary responses to anthropogenic threats are hindered (Myers 1997). Thus, from the standard evolutionary perspective, the prospects for natural preservation of biodiversity become increasingly bleak with further species loss.

The niche construction perspective stresses a second route to the complementarity between organisms and their environments (Odling-Smee et al. 2003). Not only do organisms evolve characteristics that suit their environments, they can also change their environments to suit themselves, through niche construction. Whereas the inheritance of genes is a one-way process from parents to offspring, niche construction by one organism can modify selection pressures acting on many other organisms (Odling-Smee FJ 1988). Moreover, this connectance through niche construction does not involve only biota. When niche-constructing organisms cause physical state changes in abiotic compartments, these abiotic compartments may become evolutionarily significant to other species, as they confer modified selection pressures to other populations (Odling-Smee et al. 2003). Two populations may be connected through one or more abiotic compartments, even without any direct contact between them (Jones et al. 1997, Odling-Smee et al. 2003). From the niche construction perspective, the connectivity in ecosystems is massively increased compared with, say, food webs.

Perhaps the first example of critical niche construction concerns the development of the early atmosphere on Earth. The first fossil evidence of life is preserved in rock as laminated structures, known as stromatolites, that emerged 3.6 billion years ago (Reid et al. 2003) through the niche-constructing activities of microbial mats (figure 3). The evolutionary trajectory of the microbial biofilms was subjected to quite different pressures once a substratum was stabilized. Microbes stabilized at the substratum surface harvested light in a manner that led to the oxygenation of Earth's atmosphere (Stal 2000). This example illustrates how niche construction can dramatically affect evolutionary as well as ecological processes.

If ecosystems are threaded by engineering control webs, then the disappearance of key niche constructors may lead to abrupt and significant changes in the selection pressures created by them and acting on other populations. Recipient populations may have become dependent on niche-constructed resources to the extent that they are unable to cope with the loss, and adaptation through genetic inheritance may be too slow to counteract environmental modifications, leading to further decline. This highlights the importance of preserving species that construct or maintain habitat and resources for other species.

Figure 3. (a) A stromatolite. (b) Stromatolites* in situ. *Stromatolites are layered structures formed by bacterial colonies, dated as early as 3.6 billion years ago. Bacterial niche construction harvested light in a way that led to the oxygenation of Earth's atmosphere (Stal 2000). Photographs: David Paterson.

However, many niche constructors, particularly some vertebrates, are flexible organisms endowed with considerable phenotypic plasticity. They are often capable of developing novel solutions to problems, including creating suitable habitats and other resources for themselves (through learning, for instance; Reader and Laland 2003). Some niche-constructing species may be less prone to extinctions by virtue of their ability to counteract environmental change, a capability that Odling-Smee and colleagues (2003) call "counteractive" niche construction, and which they document as extremely prevalent. Moreover, new methods of niche construction by incumbent species may buffer dependent downstream populations from otherwise harmful external changes and sustain relatively stable circumstances for their ongoing evolution. Furthermore, even if a key niche-constructing species is permanently removed, all may not be lost. Niche construction reasoning led Odling-Smee and colleagues (2003) to make a series of predictions about invasions and species replacements. They predicted that when a species is removed from an ecosystem, the most likely species to invade will be one that carries genes allowing it to tolerate or benefit from the niche-constructing activities of "upstream" biota. In a subset of cases referred to as "benign invasions," the substitute will also carry genes that cause it to niche-construct in ways that generate an ecosystem service similar to that provided by its predecessor (Odling-Smee et al. 2003). Here the invader and the original incumbent are members of the same engineering guild. An example of such replacement is provided by a long-term experimental study on a Chihuahuan Desert ecosystem in the United States (Ernest and Brown 2001). Nineteen years after kangaroo rats (*Dipodomys merriami*) were removed, an alien species of pocket mouse (*Chaetodipus baileyi*) colonized the ecosystem, compensating almost completely for the original incumbent in terms of energy use (Ernest and Brown 2001). Conversely, if a species invades and replaces an incumbent, and performs a different kind of niche construction, then it is characterized as a malign invader (Odling-Smee et al. 2003), in the sense that it is likely to contribute to perturbation or destruction of the ecosystem to some degree. All downstream biota may be affected by the invasion, even if they are connected only via abiotic components.

Naturally, such functional redundancy in key engineers cannot be guaranteed, and it is not known what proportion of invasions are benign. In view of possible time lags between extinction and natural substitution (Ernest and Brown 2001), human introduction of replacement niche-constructing species may be necessary. However, the current record on voluntarily or accidentally introduced species negatively affecting the native flora and fauna calls for precautionary research before such a method is implemented (e.g., Myers 1997, Vitousek et al. 1997, Godfray and Crawley 1998, Chapin et al. 2000, Crooks 2002).

Any unforeseen negative consequences of introducing species may be avoided by replenishing the niche constructors' effects on the environment, rather than the organisms themselves. According to Odling-Smee and colleagues (2003), "It is plausible that the most effective means to preserve ecosystems is not to focus on saving particular species, even the most important engineers, but rather to concentrate on preserving their engineering effects, some of which may be abiotic" (p. 384). Examples have already been provided of the kinds of procedures that could be undertaken to preserve engineering effects, including artificially created leaf ties otherwise produced by caterpillars (Lill and Marquis 2003), artificial mussel mats (Crooks and Khim 1999), and artificially raised mud mimicking the elevated rhizome rings of arrowgrass (Fogel et al. 2004). These experimental results show real potential for the artificial imitation of ecosystem engineering effects. Naturally, it remains to be seen whether such manipulations can be successful and cost-effective at scales relevant to conservation goals, and a great deal of additional research is required to assess the applicability of this method. However, the aforementioned studies' findings are sufficiently encouraging to warrant pursuit of this strategy.

Conclusions and a tentative strategy for implementation

It is now over a decade since Jones and colleagues (1994) drew attention to ecosystem engineering, raising the possibility of using "keystone engineers" as a conservation measure alongside other established approaches. The intervening years have witnessed a number of developments that greatly enhance the plausibility of this suggestion:

- Ecosystem engineering by a wide variety of organisms is now better established and better understood, further enhanced by complementary research into niche construction.
- Methods for the identification of key ecosystem engineers and niche constructors have been established and found to be effective.
- The distinction between key engineers/niche constructors and keystone species has been clarified. While keystone predators may have regulatory effects on ecosystems, key engineers uniquely create habitat and resources that support a multitude of other species in ecosystems.
- There is evidence for the existence of functional engineering roles that can be fulfilled by alternative species. This raises the possibility that ecosystems may be conserved through the preservation of functional engineering roles rather than particular species.
- There is evidence that there may be utility in preserving or reproducing the engineering effects, rather than the organisms themselves.

This review is mainly a discussion of the principles of niche construction and ecosystem engineering and a summary of the evidence showing that an organism can have a disproportionate effect, through the construction of habitat and resources, on the ecology and evolution of other species. While we maintain that this is of direct relevance to conservation biology, it is a long way from providing clear, practical recommendations for conservationists and managers. However, every new approach must start somewhere. Below we provide a tentative sketch of a possible implementation strategy for conserving ecosystem engineers key to the structure and functioning of their threatened ecosystem.

- Identify the target ecosystem and set conservation goals.
- Determine the key engineers in the target ecosystem. In some cases these will already be established, or at least plausible candidates will have been identified. However, in many instances further research into ecosystem engineering will be required.
- Conduct pilot studies to assess the effectiveness of the following alternative measures: (a) enhancing key engineers' current activity by supplementing their numbers with introduced members of the same species, (b) enhancing key engineers' current activity by providing them with the resources necessary for population growth, (c) enhancing key engineers' current activity by supplementing the ecosystem with introduced members of the same engineering guild (i.e., a different species that engineers in the same manner), (d) artificially manufacturing and introducing the engineered products of the key engineers, and (e) counteracting negative effects and facilitating positive influences of both abiotic and biotic factors that may affect key engineers through trophic or nontrophic links. (Here we assume that the key engineers are indigenous to the ecosystem. In the case of malign invading engineers, equivalent steps that reduce their impact could be investigated.)
- Implement on a small scale the most successful engineering strategy or combination of strategies, monitoring, and assessment.
- Implement the successful engineering strategy on a large scale.

We recognize that these suggestions are crude, but hope that our article will act as a stimulus for others with greater expertise in conservation to flesh them out or, alternatively, to develop new practical biodiversity conservation strategies based on principles of niche construction and ecosystem engineering, which could complement, rather than replace, the conservation strategies traditionally implemented.

Acknowledgments

We are grateful to Will Cresswell, John Odling-Smee, Simon Reader, and three anonymous reviewers for helpful comments on earlier drafts of this manuscript. David Paterson acknowledges funding from the MarBEF European Union Network of Excellence (contract no. 505446) on Biodiversity and Ecosystem Functioning in developing this research area.

References cited

Andelman SJ, Fagan WF. 2000. Umbrellas and flagships: Efficient conservation surrogates or expensive mistakes? Proceedings of the National Academy of Sciences 97: 5954–5959.

Bertness MD. 1984. Habitat and community modification by an introduced herbivorous snail. Ecology 65: 370–381.

Betrus CJ, Fleishman E, Blair RB. 2005. Cross-taxonomic potential and spatial transferability of an umbrella species index. Journal of Environmental Management 74: 79–87.

Biles CL, Paterson DM, Ford R. 2003.The importance of bioturbation as an ecosystem function in marine sediments. Pages 99–105 in Raffaelli D, Solan M, Paterson DM, Buck AL, Pomfret JR, eds. Coastal Zone Topics 5: The Estuaries and Coasts of North-east Scotland. Aberdeen (United Kingdom): Estuarine Coastal Sciences Association.

Boersma PD, Parrish JK. 1999. Limiting abuse: Marine protected areas, a limited solution. Ecological Economics 31: 287–304.

Chape SP, Coates D, Spalding M, Vierros M. 2004. The extent of the world's protected areas. Pages 25–31 in Mulongoy KJ, Chape SP, eds. Protected Areas and Biodiversity: An Overview of Key Issues. Montreal (Canada): Convention on Biological Diversity Secretariat.

Chapin FS III, et al. 2000. Consequences of changing biodiversity. Nature 405: 234–242.

Crain CM, Bertness MD. 2006. Ecosystem engineering across environmental gradients: Implications for conservation and management. BioScience 56: 211–218.

Crooks JA. 2002. Characterizing ecosystem-level consequences of biological invasions: The role of ecosystem engineers. Oikos 97: 153–166.

Crooks JA, Khim HS. 1999. Architectural vs. biological effects of a habitat-altering, exotic mussel, *Musculista senhousia.* Journal of Experimental Marine Biology and Ecology 240: 53–75.

Daborn GR, et al. 1993. An ecological cascade effect: Migratory birds affect stability of intertidal sediments. Limnology and Oceanography 38: 225–231.

Davic RD. 2003. Linking keystone species and functional groups: A new operational definition of the keystone species concept. Conservation Ecology 7 (1): Response 11. (10 May 2006; *www.consecol.org/vol7/iss1/resp11*)

Day RL, Laland KN, Odling-Smee FJ. 2003. Rethinking adaptation: The niche-construction perspective. Perspectives in Biology and Medicine 46: 80–95.

Dayton PK, Tegner MJ, Edwards PB, Riser KL. 1998. Sliding baselines, ghosts, and reduced expectations in kelp forest communities. Ecological Applications 8: 309–322.

Ernest SKM, Brown JH. 2001. Delayed compensation for missing keystone species by colonization. Science 292: 101–104.

Estes JA, Palmisano JF. 1974. Sea otters: Their role in structuring nearshore communities. Science 85: 1058–1060.

Flecker AS. 1996. Ecosystem engineering by a dominant detritivore in a diverse tropical stream. Ecology 77: 1845–1854.

Fleishman E, Murphy DD, Brussard PF. 2000. A new method for selection of umbrella species for conservation planning. Ecological Applications 10: 569–579.

Fogel BN, Crain CM, Bertness MD. 2004. Community level engineering effects of *Triglochin maritima* (seaside arrowgrass) in a salt marsh in northern New England, USA. Journal of Ecology 92: 589–597.

Godfray HCJ, Crawley MJ. 1998. Introductions. Pages 39–65 in Sutherland WJ, ed. Conservation Science and Action. Oxford (United Kingdom): Blackwell Science.

Hansell MH. 2004. Animal Architecture. Oxford (United Kingdom): Oxford Animal Biology Series.

Jessup DA, Miller M, Ames J, Harris M, Kreuder C, Conrad PA, Mazet JAK. 2004. Southern sea otter as a sentinel of marine ecosystem health. EcoHealth 1: 239–245.

Jones CG, Lawton JH, Shachak M. 1994. Organisms as ecosystem engineers. Oikos 69: 373–386.

———. 1997. Positive and negative effects of organisms as physical ecosystem engineers. Ecology 78: 1946–1957.

Kotliar NB. 2000. Application of the new keystone-species concept to prairie dogs: How well does it work? Conservation Biology 14: 1715–1721.

Krebs JR, Davies NB, eds. 1997. Behavioural Ecology: An Evolutionary Approach. Oxford (United Kingdom): Blackwell Science.

Lill JT, Marquis RJ. 2003. Ecosystem engineering by caterpillars increases insect herbivore diversity on white oak. Ecology 84: 682–690.

Meffe GK, Carroll CR. 1997a. What is conservation biology? Pages 3–27 in Meffe GK, Carroll CR, eds. Principles of Conservation Biology. Sunderland (MA): Sinauer.

———. 1997b. Conservation reserves in heterogeneous landscapes. Pages 305–343 in Meffe GK, Carroll CR, eds. Principles of Conservation Biology. Sunderland (MA): Sinauer.

Mills LS, Soulé ME, Doak DF. 1993. The keystone-species concept in ecology and conservation. BioScience 43: 219–224.

Myers N. 1997. Global biodiversity II: Losses and threats. Pages 123–158 in Meffe GK, Carroll CR, eds. Principles of Conservation Biology. Sunderland (MA): Sinauer.

Odling-Smee FJ. 1988. Niche-constructing phenotypes. Pages 73–132 in Plotkin HC, ed. The Role of Behavior in Evolution. Cambridge (MA): MIT Press.

Odling-Smee FJ, Laland KN, Feldman MW. 2003. Niche Construction: The Neglected Process in Evolution. Princeton (NJ): Princeton University Press.

Odling-Smee L. 2005. Dollars and sense. Nature 437: 614–616.

Paine RT. 1969. The *Pisaster–Tegula* interaction: Prey patches, predator food preference, and intertidal community structure. Ecology 50: 950–961.

Paterson DM. 2005. Biodiversity and functioning of freshwater and marine ecosystems. In Barthlott W, Linsenmair KE, Porembski S, eds. Biodiversity: Structure and Function.. Encyclopedia of Life Support Systems (EOLSS). Oxford (United Kingdom): EOLSS.

Pimm SL. 1998. Extinction. Pages 20–38 in Sutherland WJ, ed. Conservation Science and Action. Oxford (United Kingdom): Blackwell Science.

Posey MH. 1988. Community changes associated with the spread of an introduced seagrass, *Zostera japonica.* Ecology 69: 974–983.

Power ME, Mills LS. 1995. The keystone cops meet in Hilo. Trends in Ecology and Evolution 10: 182–184.

Power ME, Tilman D, Estes JA, Menge BA, Bond WJ, Mills LS, Daily G, Castilla JC, Lubchenco J, Paine RT. 1996. Challenges in the quest for keystones. BioScience 46: 609–620.

Pressey RL, Whish GL, Barrett TW, Watts ME. 2002. Effectiveness of protected areas in north-eastern New South Wales: Recent trends in six measures. Biological Conservation 106: 57–69.

Primack RB. 1998. Essentials of Conservation Biology. Sunderland (MA): Sinauer.

Reader SM, Laland KN, eds. 2003. Animal Innovation. Oxford (United Kingdom): Oxford University Press.

Reid P, Dupraz CD, Visscher PT, Sumner DY. 2003. Microbial processes forming marine stromatolites. Pages 103–118 in Krumbein WE, Paterson DM, Zavarzin GA, eds. Fossil and Recent Biofilms: A Natural History of Life on Earth. London: Kluwer Academic.

Reusch TBH, Williams SL. 1998. Variable responses of native eelgrass *Zostera marina* to a non-indigenous bivalve *Musculista senhousia.* Oecologia 113: 428–441.

Rouget M, Richardson DM, Cowling RM. 2003. The current configuration of protected areas in the Cape Floristic Region, South Africa—reservation bias and representation of biodiversity patterns and processes. Biological Conservation 112: 129–145.

Shachak M, Jones CG. 1995. Ecological flow chains and ecological systems: Concepts for linking species and ecosystem perspectives. Pages 280–294 in Jones CG, Lawton JH, eds. Linking Species and Ecosystems. New York: Springer-Verlag.

Simberloff D. 1998. Flagships, umbrellas, and keystones: Is single-species management passé in the landscape era? Biological Conservation 83: 247–257.

Stal LJ. 2000. Cyanobacterial mats and stromatolites. Pages 61–120 in Whitton BA, Potts M, eds. The Ecology of Cyanobacteria: Their Diversity in Time and Space. London: Kluwer Academic.

Steneck RS, Graham MH, Bourque BJ, Corbett D, Erlandson JM, Estes JA, Tegner MJ. 2002. Kelp forest ecosystems: Biodiversity, stability, resilience and future. Environmental Conservation 29: 436–459.

Talley TS, Crooks JA, Levin LA. 2001. Habitat utilization and alteration by the invasive burrowing isopod, *Sphaeroma quoyanum,* in California salt marshes. Marine Biology 138: 561–573.

Vitousek PM, Mooney HA, Lubchenco J, Melillo JM. 1997. Human domination of Earth's ecosystems. Science 277: 494–499.

Wilby A. 2002. Ecosystem engineering: A trivialized concept? Trends in Ecology and Evolution 17: 307.

Wright JP, Jones CG. 2006. The concept of organisms as ecosystem engineers ten years on: Progress, limitations, and challenges. BioScience 56: 203–210.

Wright JP, Jones CG, Flecker AS. 2002. An ecosystem engineer, the beaver, increases species richness at the landscape scale. Oecologia 132: 96–101.