Niche construction, co-evolution and biodiversity[☆]

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ARTICLE DATA

ABSTRACT

Many organisms modulate the availability of resources to other species, in the process changing the selection to which they and other organisms are exposed (niche construction). Niche construction drives co-evolutionary episodes, and builds connectance between the biotic components of ecosystems. Organisms have significant non-trophic impacts on ecosystem structure, function, and biodiversity. Based on a review of the most recent literature, we propose measures that could be employed to manage environments and enhance conservation efforts.

Niche-construction theory is a fledgling branch of evolutionary biology that places emphasis on the capacity of organisms to modify natural selection in their environment and thereby act as co-directors of their own, and other species' evolution. Niche construction can be characterised as "the process whereby organisms, through their metabolism, their activities and their choices, modify their own and/or each other's niches" (Odling-Smee et al., 2003, p. 419). Niche construction revolves around the same concept as "ecosystem engineering", a term introduced to ecology by Jones et al. (1994, 1997) to describe the modification, maintenance and/or creation of habitats by organisms. Ecosystem engineering has been the topic of many recent publications in the ecological literature (Wright and Jones, 2006). The term "niche construction", on the other hand, is adopted by evolutionary biologists, who are mainly interested in the evolutionary consequences of ecosystem engineering and the coevolution between organisms and their environment. Here we treat "niche construction" and "ecosystem engineering" as synonyms.

One of the most famous examples of an organism modifying its environment is the beaver building dams. When beavers build dams, they affect a great deal more than the probability that genes for dam-building will spread: they modify nutrient cycling and decomposition dynamics, modify the structure and dynamics of the riparian zone, influence the character of water and materials transported downstream, and ultimately influence plant and community composition and diversity (Naiman et al., 1988; Wright et al., 2002). In doing so, they indirectly modify the pattern and strength of selection acting on a host of beaver traits, and similarly modify selection acting on thousands of other species (Odling-Smee et al., 2003). Niche construction is thus both an important source of co-evolutionary interactions and a major form of connectance between biota.

In fact, niche construction is all around us: we owe our oxygen-rich atmosphere to niche-constructing cyanobacteria that started to harvest light and release oxygen approximately 3.6 billion years ago (Stal, 2000); villages along the Indian coast are protected from destructive tsunami waves by niche

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constructing mangroves (Danielsen et al., 2005), and the soil-perturbing activities of earthworms greatly improve soil fertility (Satchell, 1983). Other examples of niche construction include animals manufacturing nests, burrows, webs and pupal cases, plants changing levels of atmospheric gases and modifying nutrient cycles, fungi decomposing of organic matter and bacteria fixing nutrients (Wcislo, 1989; Jones et al., 1994, 1997; Odling-Smee et al., 2003). These, and myriad other cases, exemplify the huge range of temporal and spatial scales across which niche construction occurs (Hastings et al., 2007), and the many ways in which it affects our everyday lives.

Here we suggest that this new evolutionary viewpoint, which highlights the significance of living organisms in shaping local environments and ecosystems, as well as the greater connectance between species that such non-trophic interactions generate, may be of considerable value to economists and conservationists, not just biologists.

1.   How does niche construction theory differ from standard evolutionary theory?

Standard evolutionary theory treats niche construction as an (extended) phenotype (Dawkins, 1982) resulting from selection, but not as a cause of evolutionary change. Thus, within evolutionary biology and ecology textbooks one can find extensive theories describing how selection shapes organisms' capacity to modify environmental states and construct artefacts, but little theory concerned with the effects of niche construction on subsequent natural selection. Conversely, advocates of the niche-construction perspective maintain that it is both accurate and useful to regard niche construction as a major evolutionary process in its own right (Odling-Smee et al., 2003; Laland and Sterelny, 2006). The niche-construction perspective was introduced to evolutionary biology back in the 1980s (Lewontin, 1982, 1983). Although still controversial (Laland et al., 2004; Laland and Sterelny, 2006), it has recently gathered momentum (Odling-Smee, 1988, 1996; Odling-Smee et al., 2003; Laland et al., 1996, 1999; Lewontin, 2000; Oyama et al., 2001; Sterelny, 2003, 2007; Boni and Feldman, 2005; Donohue, 2005; Corenblit et al., 2008; Erwin, 2008; Lehmann, 2008).

There is now extensive evidence from both theoretical and empirical studies that niche construction is evolutionarily consequential. Moreover, population genetic models reveal that niche construction generates unusual evolutionary dynamics (Laland et al., 1996, 1999, 2001; Silver and Di Paolo, 2006), such as momentum effects (populations continue to evolve in the same direction after selection has stopped or reversed), inertia effects (no noticeable evolutionary response to selection for a number of generations), as well as opposite and sudden catastrophic responses to selection. Niche-constructing traits can drive themselves to fixation by generating disequilibrium between niche-constructing alleles and alleles whose fitness depends on resources modified by niche construction (Silver and Di Paolo, 2006). Costly niche-constructing traits can be favoured because of the benefits that will accrue to distant descendants (Lehmann, 2008). Niche construction allows the persistence of organisms in inhospitable environmental condi-

tions that would otherwise lead to their extinction (Kylafis and Loreau, 2008).

2.   Niche construction and conservation

The importance of niche construction/ecosystem engineering for ecosystem functioning and biodiversity has been pointed out by several authors. Jones et al. (1994) argued that ecosystem engineers can regulate energy and mass flows, as well as trophic patterns, without necessarily being part of those flows/patterns. These interactions form an "engineering web" that, together with the well-established trophic interactions, regulates ecosystem functioning (Jones et al., 1994). Odling-Smee and colleagues also emphasized the great increase in connectivity within ecosystems from a niche-construction perspective; when organisms modify their abiotic environment, these physical state changes may modify the selection on other populations that rely on the same abiotic compartments. Multiple populations may thus be connected and affecting each other in evolutionarily significant ways through one or more abiotic compartments, without any direct contact (Jones et al., 1997; Odling-Smee et al., 2003). In fact, niche constructers can enable other species to live in otherwise physically stressful environments by providing critical resources such as moisture, shade, favourable soil chemistry and refuges (Crain and Bertness, 2006). To quote Crain and Bertness (2006, p. 216): "In most habitats [...] ecosystem engineers provide the template for all other ecosystem processes, making these engineers essential to conservation."

Here we argue that efforts to understand and conserve ecosystem functioning and biodiversity will be facilitated by taking niche construction into account. The properties and dynamics of ecosystems will never be satisfactorily comprehended until it is recognized that organisms do considerably more than compete with each other, eat and be eaten (i.e. engage in trophic interactions). Organisms also produce, modify and destroy habitat and resources for other living creatures, in the process regulating hydrological, nutrient and element (e.g. carbon) cycling and driving coevolutionary dynamics (Odling-Smee et al., 2003). As humans are enormously potent niche constructors, understanding how niche construction regulates ecosystem dynamics and affects selection pressures on other species is central to understanding our impact on the environment.

3.   Empirical evidence

Although the concepts of niche construction and ecosystem engineering are relatively new, researchers quickly realized that the importance of engineering organisms for ecosystem functioning and biodiversity could provide novel insights for conservation efforts. Crain and Bertness (2006) and Boogert et al. (2006) review the empirical evidence for a link between niche construction/ecosystem engineering and biodiversity. One of the clearest illustrations is provided by the engineering effects of *Pseudotelphusa* caterpillars. These caterpillars use silk to bind pairs of leaves together into leaf shelters. Leaf shelters, in turn, provide habitat for a variety of both leaf tying and non-leaf-tying species. Lill and Marquis (2003) compared the engineering effects of these

leaf-tying caterpillars to their trophic effects on insect herbivores occupying white oak saplings, by removing leaf ties from some white oak saplings and constructing artificial leaf ties on others. They found that removal of leaf ties significantly decreased species richness of leaf-chewing insects, whereas trees with artificial ties contained more species of leaf-tying caterpillars, sawflies, and beetles. Furthermore, artificial tie-treatments to which a single caterpillar was added did not differ from artificial tie-treatments without caterpillars, indicating that the caterpillars' effect on species richness was a result of their leaf shelter building-activities, not their trophic interactions (Lill and Marquis, 2003).

In a similar vein, Pringle (2008) recently provided unequivocal evidence that elephants are the creators of lizard habitat. He counted far more lizards (Lygodactylus keniensis) on trees damaged by elephants than on undamaged trees, and elucidated the underlying mechanism of this distribution by mimicking the engineering effects of elephants. Bark stripping and branch splintering by elephants creates crevices large enough to serve as lizard refuges and produces exposed horizontal perches which are otherwise rare in the local tree species. Pringle transplanted lizards to artificially created perch+refuge trees, perch-only trees, refuge-only trees and control trees. He found that transplanted lizards remained three times longer on trees with refuges than on trees without, whereas perch presence or absence did not affect lizards' decision to stay. Furthermore, within five days after refuges were experimentally removed from ten elephant-damaged trees, seven of these trees were completely vacant, compared to none of the sham-manipulated trees. This study thus shows that elephant-engineered habitat can strongly increase local lizard population densities (Pringle, 2008).

Other recent studies of ecosystem engineers' importance for biodiversity and ecosystem functioning have a more observational character; they compare habitats with and without engineers. For example, patches of cushion plant Azorella monantha enable other species to survive in the harsh environment of the high Andes of Chile by reducing daily temperature fluctuations and increasing water and habitat availability, substrate stability and nitrogen concentrations (reviewed by Badano and Marquet, 2008). When comparing ecosystem functioning in landscapes with and without this ecosystem engineer, Badano and Marquet (2008) showed that both biomass and nitrogen accumulated increasingly with species richness in both landscape types, but more so in landscapes including the cushion plant.

Invasions of exotic species pose major threats to ecosystem functioning and diversity of native species (Vitousek et al., 1997; Godfray and Crawley, 1998; Chapin et al., 2000). Particularly large and cascading effects are expected when either the invading species modifies the physical structure of the invaded ecosystem (Crooks, 2002), or it removes the resident key ecosystem engineering species. An example of the first case is provided by an observational study on deciduous forests in New Jersey (Baiser et al., 2008). Here, white-tailed deer (Odocoileus virginianus) are so abundant that they overbrowse and, ultimately, eliminate understory and mid-canopy vegetation, creating the perfect conditions for Japanese stilt grass (Microstegium vimineum) to invade. As white-tailed deer have large home ranges that include both fragmented habitats with large stilt grass populations and more intact forests, they may also serve as primary dispersers of stilt grass propagules into the forest interior. The synergistic interactions of these two ecosystem engineers cause a drastic change in forest composition, structure, and successional pathways: they remove native understory and mid-canopy vegetation, resulting in significant decreases in birds that nest in these vegetation layers, and prevent regeneration of the dominant native canopy trees (Baiser et al., 2008).

The second way in which invasive species can lead to loss of biodiversity, namely by removing the key engineering species in an ecosystem, is illustrated by a case study in eastern Tasmania (Ling, 2008). Due to global warming-induced changes in ocean currents, the sea urchin (Centrostephanus rodgersii) has expanded its range southward, from New South Wales to the eastern coastline of Tasmania (Ling, 2008). There, it is currently starting to produce "barrens" habitat, grazed free of macroalgae. Of the 296 flora and fauna taxa recorded in intact reef habitats, only 72 were found in these incipient barrens. However, when the sea urchins were completely removed from barren patches, filamentous algae and macro-algal sporophytes recruited and started to overgrow the patch within one month of sea urchin removal, and within two years, 253 of the native taxa returned to these recovering patches (Ling, 2008). This study shows that climate-change induced range expansion of invasive species can lead to a dramatic loss of biodiversity when the invader removes the key niche constructor of the invaded ecosystem.

These studies illustrate three important points. First, they show that organisms can have strong impacts on ecosystem structure, function, and biodiversity. Second, they demonstrate that these impacts can be non-trophic in character, resulting directly from niche-constructing activities. Third, they provide several methods to identify key engineering species in ecosystems and quantify their effects, such as removing or adding the engineering species, comparing naturally occurring sites with and without the engineer, and experimentally mimicking engineering effects on the environment in the absence of the engineer (Boogert et al., 2006).

4.   Human niche construction

The studies described above illustrate that niche construction is an extremely general process, and humans are far from alone in their capacity to modify the environment. Nonetheless, human niche construction may be uniquely potent. In the last 100,000 years, humans have dispersed from East Africa around the globe, a success story that would not have been possible without their ability to modify environments to compensate for different climates and variable food availability. Humans overcame these and other challenges by, for instance, manufacturing clothes and shelters, controlling fire, devising agricultural practices, and domesticating livestock.

Technology and culture are clearly critical factors underlying the potency of human niche construction: agriculture was not independently invented by each farmer, nor is its presence an unlearned outcome of human gene expression. Findings of geneticists analysing the human genome point to gene-culture interactions as co-directors of human evolution

(Wang et al., 2006), and this perspective is supported by some well-established cases of gene-culture co-evolution. The most famous example of culturally induced genetic responses to human agriculture is the co-evolution of dairy farming and the gene for lactose absorption (Durham, 1991). Theoretical and empirical studies have provided convincing evidence that dairy farming must have spread prior to the allele for lactose absorption and generated a selection pressure favouring this gene in some human pastoralist societies (Feldman and Cavalli-Sforza, 1989; Holden and Mace, 1997; Burger et al., 2007). Another case study of gene-culture co-evolution involves Kwa-speaking yam cultivators in West Africa, people whose forest clearing activities to grow crops initiated a cascade of unforeseen consequences (Durham, 1991). The forest clearings increased the amount of standing water, which provided better breeding grounds for mosquitoes and increased the prevalence of malaria. This increased malaria prevalence, in turn, modified natural selection pressures in favour of an increased sickle-cell S allele frequency, as this allele provides protection against malaria in the heterozygous condition. The fact that other Kwa-speakers with different agricultural practices do not show the same increase in S allele frequency supports the conclusion that culture can drive genetic evolution (Durham, 1991). Modern Asian tyre manufacturing turns out to generate the same selection pressures as yam cultivation: mosquitoes infest pools of rainwater that collect in tyres stored outside, and tyre export is contributing to the spread of malaria and dengue (Hawley et al., 1987). Malaria became a major health problem only after the invention of farming, a cultural niche-constructing practice, yet there are several additional genes that appear to have been selected because they provide resistance to malaria (Balter, 2005; Wang et al., 2006). Other modern diseases that seem to drive the selection of resistance-conferring genes include AIDS, smallpox and hypertension (Balter, 2005). In all these cases, human modifications of the environment triggered or modified selection on human genes. Undoubtedly our niche constructing activities have affected the evolution of numerous other species too (Odling-Smee et al., 2003).

Niche construction provides a non-Lamarckian route by which acquired characteristics can influence the selective environment. While the information acquired by individuals through ontogenetic processes cannot be inherited because it is lost when they die, processes such as learning can nonetheless still be of considerable importance to subsequent generations because learned knowledge can guide niche construction in ways that do modify natural selection. This route is considerably enhanced by social learning, which allows animals to learn from each other. Hundreds of species of mammals, birds and fishes, and even invertebrates, are now known to learn socially (Zentall and Galef, 1988; Heyes and Galef, 1996; Leadbeater and Chittka, 2007), allowing novel learned traits to sweep through populations, and exposing individuals to novel selection pressures. This process is further amplified with stable trans-generational culture, and it is now widely believed that such characters were probably important to hominid evolution (Cavalli-Sforza and Feldman, 1981; Richerson and Boyd, 2005).

Theoretical analyses exploring the evolutionary ramifications of human cultural niche construction show it to be

potent. Laland et al. (2001) found that cultural niche construction can overwhelm or reverse natural selection, accelerate the rate at which favoured genes spread, initiate novel evolutionary events and trigger hominid speciation. As cultural processes typically operate faster than natural selection, Laland and colleagues concluded that cultural niche construction is likely to have more profound consequences than gene-based niche construction.

In addition to being crucial for our own evolutionary adaptation, gene-culture co-evolution has also driven co-evolutionary interactions with other species, including domesticated animals and plants (Smith 2007a,b), commensal species adapted to human-constructed environments (e.g. rats, mice, insects) and microbes (Boni and Feldman, 2005). However, the lesson from the aforementioned studies of the ecological impact of niche construction is that organisms can transform ecosystems, not just by outcompeting and directly consuming other species, but also by constructing and destroying habitat and resources used by other species, a lesson germane to our own species. After all, there is currently great concern that human activities are precipitating a major global extinction, but few environmentalists believe that this tragedy is brought about exclusively through our predatory behaviour. Siberian tigers, golden lion tamarins, checkerspot butterflies, and millions of other endangered species, are vulnerable not primarily because we eat them or their predators, but because of our habitat degradation, deforestation, industrial and urban development, agricultural practices, livestock grazing, pesticide use, and so forth—that is, our niche construction. Such activities destroy the (engineering) control webs that underlie ecosystems.

5.   Managing the environment

If ecosystems are threaded by engineering control webs, then the disappearance of key niche constructors may lead to abrupt changes in the resources and selection created by them, greatly affecting other species. Populations that have become dependent on engineered habitat and resources may be unable to cope with the loss, while genetic adaptation across generations is often too slow to counteract environmental modifications, leading to further declines in biodiversity and ecosystem functioning. This highlights the importance of preserving species that construct or maintain habitat and resources for other species (Boogert et al., 2006; Crain and Bertness, 2006; Ehlers et al., 2008).

However, many niche constructors are flexible organisms able to deal with novel environmental conditions. For example, earthworm populations are not negatively affected by regular anthropogenic short-term flooding of woodland in the "Lange Erlen" in Switzerland, where this flooding regime recharges groundwater and has been providing economic drinking water production for almost a century (Schütz et al., 2008). In fact, some earthworm species benefit from the temporal floods, and their interactions regenerate soil structure, stimulate microbial biomass, prevent clogging and enhance infiltration rates, thus contributing to the functioning of the "Lange Erlen" filtration system for almost 100 years now (Schütz et al., 2008). Other ecosystem engineers cope with

environmental changes through their creation of suitable habitats and other resources, a capability called "counteractive" niche construction by Odling-Smee et al. (2003), who document this phenomenon as being extremely prevalent. Counteractive niche construction may also protect other populations that are dependent on engineered habitats and resources from otherwise harmful environmental changes and buffer them from dramatic shifts in selection pressures.

Even if a key niche-constructing species is permanently removed, all may not be lost. Ecosystem restoration following environmental degradation could be facilitated by introducing ecosystem engineers with desirable activities. Byers et al. (2006) suggest that ecosystem engineers might provide a cheaper, easier, faster and more sustainable solution to restoration problems than other human interventions can achieve, and provide convincing examples: the Australian salt pans could be restored by introducing salt-tolerant trees and shrubs with different rooting depths that would promote more even distribution of salts in the currently hyper-saline soil, whereas productivity in the Negev desert could be enhanced by microphytic crust communities, shrubs and mound-creating organisms that would provide rain runoff sources and sinks, and could thereby prevent or reverse desertification (Byers et al., 2006).

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, however (e.g. Myers, 1997; Vitousek et al., 1997; Godfray and Crawley, 1998; Chapin et al., 2000; Crooks, 2002).

One might avoid unforeseen negative consequences of introducing engineering species by replenishing the niche constructors' effects on the environment, rather than the organisms themselves (Odling-Smee et al., 2003). Some examples of the ways in which we might be able to mimic engineering effects include introduction of artificial mussel mats (Crooks and Khim, 1999), artificially created leaf ties otherwise produced by caterpillars (Lill and Marquis, 2003), and relocalization of natural structures to provide lizard refuges (Pringle, 2008).

Obviously, a major research investment is required to explore the extent to which these manipulations can be successful, efficient, affordable and feasible at scales relevant to conservation goals. However, the studies and scenarios presented here and in recent papers (e.g. Boogert et al., 2006; Byers et al., 2006; Crain and Bertness, 2006) point to the importance and potential of key ecosystem engineers for the conservation and restoration of ecosystem structure and functioning. Boogert et al. (2006) suggest that a possible implementation strategy to conserve ecosystems through the conservation of ecosystem engineering activities might include the following steps:

1) Set conservation goals for the target ecosystem.
2) Determine the key engineers in the target ecosystem, which will often require additional research.
3) Conduct pilot studies to explore which of the following procedures might be most feasible and effective: (a) enhancing key engineers' current activity by introducing more conspecifics or providing them with the resources required for population growth, (b) enhancing key engineering activities

by introducing different species that engineer in the same manner, (c) introducing artificially manufactured products of the key engineers, and (d) creating optimal levels of abiotic and biotic factors to facilitate key engineers through trophic or nontrophic links. When the ecosystem is negatively affected by invading engineers, one could investigate the effectiveness of equivalent steps to reduce their impact.
4) Implement the optimal engineering strategy or combination of strategies on a small scale. Follow up by monitoring and assessment. 5) If step 4) has the desired outcome, implement the successful engineering strategy on a large scale.

While in this article we have concentrated on conservation objectives, a niche-construction perspective is potentially equally relevant to other aspects of environment management, including sustainable agriculture and development, renewable resource management and efficient environmental policies. In these and other domains, it will pay dividends to recognize the network of niche-constructed connections between living organisms in ecosystems.

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