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Niche construction, co-evolution and biodiversity☆

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A B S T R A C T

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 conditions 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