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IDEA AND PERSPECTIVE

Niche construction in the light of niche theory

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Abstract

Ecological niche construction, the process whereby an organism improves its environment to enhance its growth and persistence, is an important missing element of niche theory. Niche theory has mainly focused on niche-deteriorating processes, such as resource consumption, predation and competition, which have negative effects on population growth. Here, we integrate niche construction explicitly into modern niche theory. We use a graphical approach to analyse how a species' niche-improving impacts interplay with niche-deteriorating impacts to modify its response to the environment. In a model of two consumers that compete for one limiting resource and one predator, we show how niche construction modifies the traditional niche-deteriorating impacts of its agent or of competing species, and hence the potential for species coexistence. By altering the balance between intraspecific and interspecific competitive effects, niche construction can either generate net interspecific facilitation or strengthen interspecific competition. The adaptive benefit derived from niche construction also strongly affects the realized niche of a niche-constructing species.

Keywords

Coexistence, competition, ecological and adaptive niche construction, niche impact, niche theory, positive and negative interactions, species response.

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INTRODUCTION

The niche concept and its history

Since its inception, the niche concept has been controversial and has captured the attention of ecologists. Grinnell (1917) first introduced the concept as describing a species' requirements, i.e. the environmental conditions under which the species exhibits positive response or growth. Hutchinson (1957) took this definition one step further by suggesting a quantitative formulation of the niche. He described the fundamental niche of a species as an *n*-dimensional hypervolume, in which each dimension represents an environmental factor (i.e. a resource or abiotic conditions) that constraints a species' response. In the presence of other species, however, this fundamental niche may shrink to a smaller realized niche because of additional ecological constraints on the species' response (e.g. apparent and resource competition). Both Hutchinson's and Grinnell's niche concepts focus on an organism's response to abiotic and biotic environmental constraints. In the meantime, Elton (1927) suggested a slightly different niche concept that describes the functional role of an organism in its environment and considers the environmental impacts of the organism as a result of its consuming and being consumed. Leibold (1995) proposed a synthesis of the two approaches by including both the impacts and requirements of a species in the definition of its niche. Organisms modify the level of various niche factors though their impacts; the modified levels of niche factors in turn determine the organisms' responses (see Glossary). This reciprocal interaction reveals the feedback between organisms and their environment (Lewontin 1978). Indeed, traits that shape the impacts of an organism on niche factors determine its response and therefore its realized niche.

Evolutionary niche construction

Odling-Smee *et al.* (1996, 2003) introduced the concept of niche construction to describe the modification of their environment by organisms, with a focus on the evolutionary consequences of this process. Similar to Hutchinson's description of the ecological niche as an *n*-dimensional space of ecological constraints on a species' growth and persistence, they described the evolutionary niche as an *n*-dimensional space of selective pressures acting on a species. Niche construction is then seen as a mechanism that modifies selective pressures to generate a better (or worse) fit between its agent and its environment, which they call positive (or negative) niche construction. Niche construction *sensu* Odling-Smee *et al.* involves such basic metabolic activities as the depletion of resources (e.g. dead or live tissues, nutrients) through assimilatory processes and the release of subsequent dissimilatory wastes. These processes are the main candidates for negative niche construction as they eventually deteriorate the environment, thereby generating selective pressures on organisms. Niche construction also includes physical state changes (i.e. ecosystem engineering) through the construction of artefacts such as nests and burrows (Jones *et al.* 1994, 1997a,b; Hastings *et al.* 2007), as well as niche choice, through which organisms relocate in space to modify the environment they experience (Laland & Sterelny 2006). These changes are the main candidates for positive niche construction as they can improve the niche and mitigate selective pressures as in the case of the warm, well-protected environment of a nest mound. The broad picture of niche construction provided by Odling-Smee *et al.* implies that almost every organism is engaged in niche-constructing processes, which has raised several arguments, especially among evolutionary biologists, against the pervasiveness of the concept (Dawkins 2004; Brodie 2005; Griffiths 2005; Sterelny 2005).

Ecological niche construction

Although niche construction has so far been mainly discussed in an evolutionary context (Odling-Smee *et al.* 1996, 2003; Laland *et al.* 1999; Erwin 2008), the concept would clearly gain much by being linked explicitly and formally to ecological niche theory. Rather than regarding niche construction as a process that modifies selective pressures, we focus here on its ecological consequences as a mechanism that improves the environment of its agent (Kylafis & Loreau 2008). This elementary form of niche construction is what we call ecological niche construction (seze Fig. 1; Glossary). In this definition, we make a distinction between the niche-improving and niche-deteriorating impacts of an organism, with the latter being the traditional focus of classical niche theory. For instance, organisms deplete limiting resources through their metabolic activities and offer food and shelter to predators and pathogens, thereby allowing them to sustain high abundances. Such niche-deteriorating impacts generate negative effects on the response of their agent.

Less attention has been paid, however, to niche-improving impacts, which usually generate positive effects on the response of their agent (Fig. 1). There is abundant evidence for plant impacts on soil and their subsequent feedback (intraspecific) effects (see Ehrenfeld *et al.* 2005 for a review in plant–soil feedbacks). The role of litter inputs has been perhaps most widely investigated (e.g. Berendse 1998; Chapin 2003). The feedback system in this case operates through litter quality, measured by C:N or N:lignin ratios, and its effects on microbial activity and the rate of nutrient mineralization. Invasions of N-fixing species into communities lacking such species also demonstrate this feedback. A widely cited example is the invasion of *Myrica faya* into Hawaiian forests. Vitousek and colleagues (Vitousek *et al.* 1987; Vitousek & Walker 1989) showed that the introduction of an N-fixing tree caused an increase in available N in the soil, which preferentially supported the growth of the introduced species. In contrast, animal-resource feedbacks are less abundant or more poorly known. For instance, in nutrient-poor tundra and desert ecosystems, some large herbivores are able to accelerate the turnover rates of nutrients, such as sodium and nitrogen, through the large quantity and high quality of their faeces, eventually promoting the production of their preferred forage plants (Jefferies *et al.* 1994; McNaughton *et al.* 1997; van der Wal *et al.* 2004).

Several examples of organism–environment feedbacks have been also documented in the ecosystem engineering literature, when important abiotic parameters such as temperature, humidity, geomorphology, are altered by organisms for their own benefit. For instance, Jouquet *et al.* (2002) demonstrated that the termite *Odontotermes auperans* utilizes soil selectively, favouring finer particles and making structures that match their ecological needs (see also Jouquet *et al.* 2006 for a review in soil invertebrates–soil feedbacks).

Incorporating niche construction into niche theory

In this article, we highlight the ecological properties of niche construction in the light of niche theory. As in recent theoretical contributions (Vandermeer 2008; Krakauer *et al.* 2009), we view an organism's niche as a product of a dynamic two-way interaction between the organism and its environment. Accordingly, niche construction is considered an adaptive process that improves a niche factor, which in turn generates positive effects on the agent's response. The niche model presented in this article, however, differs from previous contributions in two important ways. First, a species' niche is here defined by two distinct components: impact and response (Leibold 1995). This allows classifying niche construction with respect to both its impact on niche factors and its effect on species response. Second, we assess the outcome of the interplay between niche construction and competition on species coexistence in a mechanistic and thus potentially testable way.

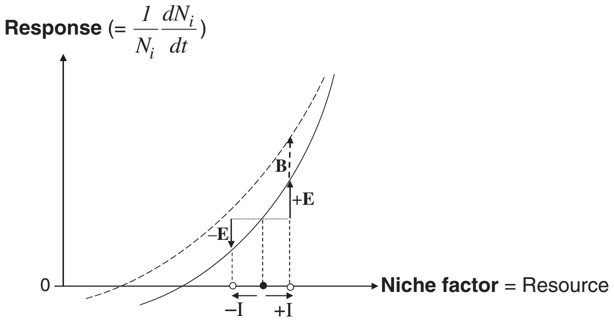

Figure 1 A unified niche concept that incorporates both a species' response to and its impact on niche factors (e.g. resource, predator, temperature). The absolute response of a species is here measured by its per capita population growth rate as a function of the amount of a limiting resource. Niche theory has focused so far on niche-deteriorating impacts (−I) on niche factors, such as consumption of a limiting resource leading to resource depletion, which generate negative effects on the response of their agent (−E). Little attention has been paid, however, to niche-improving impacts (+*I*), such as resource enrichment via nitrogen fixation, which usually generate positive effects on the response of their agent (+*E*). This is what we call ecological niche construction. Finally, we represent the adaptive benefit (*B*) that the niche construction trait confers to its agent by increasing the level of its absolute response. For instance, a legume derives a direct benefit from the symbiotically fixed nitrogen even though a significant part of fixed nitrogen may leak out of the plant and enrich the soil pool; as a result, its response to the enriched soil is enhanced. Enhancement of the response due to adaptive niche construction is represented by the dotted line.

We use a simple model of two consumers limited by one resource and one predator to explore how niche construction generates niche-improving impacts. We show that niche construction may modify (expand or shrink) the area of coexistence of its agent with competing species through modification of the relative slope of their niche-deteriorating impact vectors. Niche construction modifies the ratio of negative interspecific and intraspecific effects on species responses and, hence, the potential for coexistence. We also investigate the adaptive benefit that the niche construction trait confers to its agent as it affects its long-term response (here measured by its Zero Net Growth Isocline), resulting in an expansion of its realized niche. Finally, we show how all the above processes affect a species' occupation of the niche space.

ECOLOGICAL NICHE CONSTRUCTION AND ITS CONSEQUENCES

The study of the impacts of a species on its environment was until recently limited to deteriorating impacts. Organisms consume and deplete biotic or abiotic resources; therefore, they engage in competitive interactions with other species that share the same resources (i.e. resource competition). They can also be resources for other organisms, like predators, allowing the latter to sustain high abundances, which also generate negative interactions with other species that share the same predator (i.e. apparent competition). Here, we use a simple model of competition between two consumers limited by one resource and one predator to explore, first, the implications of classical niche theory focused on niche-deteriorating impacts, and second, the consequences of niche construction, which introduces the ability of organisms to have niche-improving impacts.

Classical niche theory in a system of two consumers limited by one resource and one predator

We consider a simplified model for competition between two consumers, species A (N_A) and species B (N_B), that compete along two niche axes: predator abundance (P) and resource abundance (R). The model is similar to Leibold's (1996). The equations describing the dynamics of the four compartments are the following:

$$\frac{dP}{dt} = P\left(\sum_i m_i c_i N_i - d_{\mathrm{P}}\right) \tag{1a}$$

$$\frac{dN_i}{dt} = N_i(f_i a_i R - m_i P - d_{N_i}) \tag{1b}$$

$$\frac{dR}{dt} = k(S - R) - \sum_i f_i N_i R, \tag{1c}$$

where $i = A$, B, m_i is the predator's attack rate on species N_i, d_{P} is the predator's death rate, c_i is the predator's conversion efficiency for species N_i, f_i is the resource consumption rate of species N_i, a_i is the consumer N_i's conversion efficiency, d_{Ni} is the consumer N_i's death rate, S is the resource supply rate, K is the resource turnover rate.

Each consumer's niche is determined by its niche impact, which depends on the slope of its impact vector, C_i, and its Zero Net Growth Isocline (ZNGI$_i$) (Fig. 2a). The impact vector C_i, illustrates the per capita effect of consumer i on resource and predator abundances. Its slope $\left(\frac{m_i c_i P}{f_i R}\right)$ is defined by the ratio of two rates: the numerator represents the rate at which a consumer individual contributes to predator's birth rate ($m_i c_i P$), while the denominator is its rate of resource consumption ($f_i R$). The population abundances P and R that determine the slope of the impact vector do not necessarily correspond to equilibrium abundances (Leibold 1995). If we consider that the absolute response of a consumer is measured by its per capita population growth rate $\left(\frac{1}{N_i}\frac{dN_i}{dt}\right)$ (Fig. 1), then its ZNGI represents zero absolute response and the area below the isocline, where absolute response is positive, the fundamental niche of the consumer. Indeed, the ZNGI is a line that represents abundances of the niche factors, R and P, when the consumer is at equilibrium. The slope of $ZNGI_i\left(=\frac{f_i a_i}{m_i}\right)$ and its intercept with the resource axis, $R_i^{min}\left(=\frac{d_{N_i}}{f_i a_i}\right)$ determine the position of the isocline in the niche space and therefore the response of the consumer relative to that of its competitor (i.e. relative response). When ZNGI$_A$ lies above ZNGI$_B$, species A has a higher growth than species B and dominates. Both the impact vector C_i and ZNGI$_i$ are linked through consumer traits such as the consumption rate f_i and mortality rate m_i.

As shown by Leibold (1996), the coexistence of the two consumers requires that their ZNGIs cross as shown in Fig. 2a. This in turn requires that there is a trade-off between their resource exploitation ability and their tolerance to predation, i.e. the species with the higher resource exploitation ability $\left(\text{i.e. with the lowest } R_i^{min} = \frac{d_{N_i}}{f_i a_i}\right)$ is more vulnerable to predation (i.e. it has a shallower ZNGI). In the case illustrated in Fig. 2, without losing generality, we consider that species A is the one with the above competitive attributes $\left(\text{i.e. } \frac{d_{N_A}}{f_A a_A} < \frac{d_{N_B}}{f_B a_B} \text{ and slope of } ZNGI_A = \frac{f_A a_A}{m_A} < \frac{f_B a_B}{m_B} = \text{slope of } ZNGI_B\right)$.

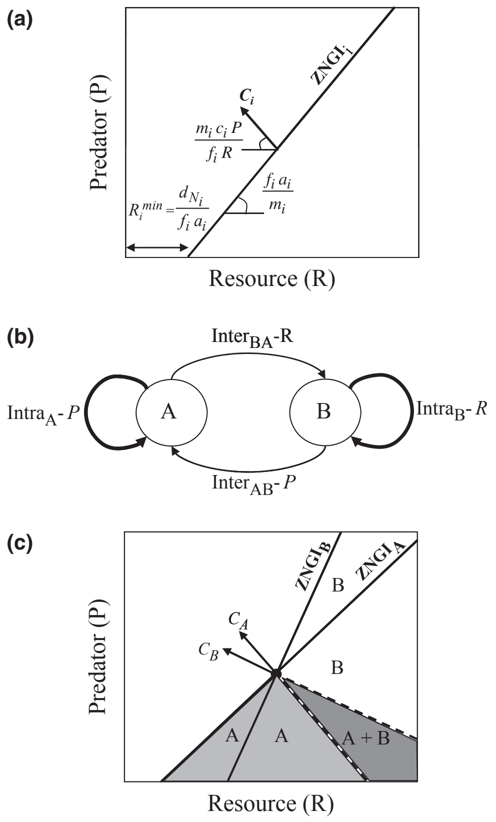

Figure 2 (a) Graphical representation of the Zero Net Growth Isocline (ZNGI) and impact vector C_i of a consumer i in the niche space defined by predator abundance, P, and resource abundance, R. The ZNGI$_i$ represents all the combinations of P and R that yield zero absolute response of the consumer $\left(\text{i.e. } \frac{1}{N_i}\frac{\mathrm{d}N_i}{\mathrm{d}t} = 0 \rightarrow P = \frac{f_i a_i}{m_i}R - \frac{d_{N_i}}{m_i}\right)$. Below the line the absolute response is positive, and above the line it is negative. The slope of the ZNGI$_i$ and the R^i_{min} value (i.e. intercept of ZNGI$_i$ with the R-axis) determine the position of the ZNGI$_i$ in the niche space, and hence the relative response of the consumer. Vector C_i represents the impact of the consumer i on P and R. (b) Schematic representation of the negative density-dependent effects within (intra) and between (inter) two species A and B. The response of species A is limited through a density-dependent effect via predator abundance P, whereas the response of species B is limited through a density-dependent effect via resource abundance R. Species A also limits the response of species B through a negative density-dependent effect via R, whereas species B limits the response of species A through a negative density-dependent effect via P. The equilibrium point is stable provided that the negative intraspecific effect is stronger than the negative interspecific effect in both species (i.e. intra$_A$-P > inter$_{BA}$-R and intra$_B$-R > inter$_{AB}$-P). (c) Realized niches of a consumer species A and another consumer species B when they compete for the same niche space. In this case, species A is a better resource exploiter (lower $R^A{}_{\mathrm{min}}$), but is less tolerant to predation than species B (i.e. shallower slope of ZNGI$_A$). The extensions of the impact vectors, shown as dashed lines, set the limits to niche overlap where species stably coexist. Therefore, the realized niche of species A consists of a dominant part (light grey area) and an overlap part (dark grey area). Similarly, the realized niche of species B consists of the same overlap part and a dominant part (white area) Note: the ZNGI corresponds to Grinnell's and Hutchinson's niche concept, whereas the impact vector C corresponds to Elton's niche concept (Chase & Leibold 2003). The locally stable equilibrium point (filled circle) lies at the intersection of the two ZNGIs.

Leibold (1996) also showed that the local stability of the equilibrium point depends on the slopes of the impact vectors. When the species with the shallower ZNGI (here, species A) also has the steeper impact vector, the equilibrium is locally stable. Therefore, the condition for local stability can be summarized as follows: if $\frac{f_A a_A}{m_A} < \frac{f_B a_B}{m_B}$ then it is required that $\frac{m_A c_A}{f_A} > \frac{m_B c_B}{f_B}$. One way to interpret this condition is that each species must have a greater impact on the niche factor that most limits its growth. Thus, species A must have a greater impact on its most limiting factor, predator abundance, and similarly, species B must have a greater impact on its most limiting factor, resource abundance (see Fig. 2a). Another way to interpret the stability condition is through the balance between intraspecific and interspecific density-dependent effects (Chesson 2000). The stability condition implies that each species depresses its own growth through a negative density-dependent feedback effect via its most limiting niche factor (intraspecific negative effect) more than it depresses the growth of the other species through a negative density-dependent effect via its least limiting niche factor (interspecific negative effect). This condition is equivalent to that in the classical Lotka–Volterra model for resource competition: intraspecific competition has to be stronger than interspecific competition for coexistence to be stable. Therefore, the negative effect on the response of species A is generated through the high predator abundance P and is stronger than the negative effect of A on the response of species B through the limited resource abundance R ($\text{intra}_A\text{-}P > \text{inter}_{BA}\text{-}R$; see Fig. 2b). Similarly, the negative effect on the response of species B is generated through the limited resource abundance R and is stronger than the negative effect of B on the response of species A through the high predator abundance P ($\text{intra}_B\text{-}R > \text{inter}_{AB}\text{-}P$; see Fig. 2b).

The realized niche of each consumer is graphically represented by its ZNGI and the impact vector of the competing consumer (see Fig. 2c). In the case presented here, the two species can stably coexist at the intersection of the ZNGIs, where the unique coexistence equilibrium lies, for initial niche conditions (i.e. resource and predator densities) that reside in the region of overlap (Fig. 2c; Tilman 1980). From now on, we call this part of the realized niche, the zone of coexistence. For initial niche conditions outside the zone of coexistence, however, the system converges to one of the two boundary equilibria where only one of the two consumers persists. In particular, for initial niche conditions above (below) the zone of coexistence, consumer A (consumer B) goes extinct.

Niche construction in the system of two consumers limited by one resource and one predator

To illustrate the concept of ecological niche construction, we now extend the above model to include niche construction by consumer species A. The conditions for the local stability of the coexistence equilibrium modified by niche construction are provided in the Appendix S1 of Supporting Information. As we are interested here in illustrating the qualitative outcomes of niche construction, we keep the model as simple as possible by choosing linear functions to quantify niche construction. Species A is assumed to modify its niche-deteriorating impacts on either resource or predator abundance proportionally to its own abundance, N_A, and at constant rates, n_R or n_P. Niche construction by species A contributes to improve its own niche. This can be done in two different ways:

(1) In a direct way, which we call direct niche construction, either by decreasing the predation pressure it experiences, $m_A c_A$, or by increasing the resource turnover rate k;

(2) In an indirect way, which we call indirect niche construction, by deteriorating the niche conditions that its competitor B experiences through either an increase in its predation pressure, $m_B c_B$, or a decrease in its resource consumption rate, f_B. Cases (a–d) below describe four cases of niche construction that affect the dynamics of the niche factors R and P.

a. Niche construction increases the resource turnover rate k. For instance, nitrogen-fixing plants improve soil conditions by enriching the soil with fixed nitrogen.

$$\frac{dR}{dt} = (k + n_R N_A)(S - R) - f_A N_A R - f_B N_B R \tag{2a}$$

b. Niche construction modifies the interaction between the competing species B and the resource in a way that inhibits its resource consumption rate, f_B. For example, *Sphagnum* plant species create cold and anoxic peat bogs that affect the growth of competing plants negatively (van Breemen 1995).

$$\frac{dR}{dt} = k(S - R) - f_A N_A R - f_B(1 - n_R N_A) N_B R \tag{2b}$$

c. Niche construction decreases predation pressure on its agent, $m_A c_A$, through direct or indirect defence mechanisms. For instance, plants commonly offer food and shelter to ants in return for protection from other herbivores (Heil & McKey 2003). We represent this effect in the form of a negative density-dependent function:

$$\frac{dP}{dt} = P[m_A c_A N_A(1 - n_\mathrm{P} N_A) + m_B c_B N_B - d_\mathrm{P}] \tag{2c}$$

d. Niche construction increases predation pressure on the competing species B, $m_B c_B$, by modifying the interaction between the predator and species B (environmentally mediated interaction modification, *sensu* Wootton 2002). For instance, corals provide shelter to crabs that in return selectively remove competitive seaweeds (Stachowicz & Hay 1999). We represent this effect in the form of a positive density-dependent functional response:

$$\frac{dP}{dt} = P[m_A c_A N_A + m_B c_B N_B(1 + n_P N_A) - d_\mathrm{P}] \tag{2d}$$

Modification of niche-deteriorating impacts due to niche construction

Without taking into account niche construction, the slope of the consumer impact vectors is $\frac{m_i c_i P}{f_i R}$ (where $i = A$, B). With direct niche construction the impact vector of species A becomes $\frac{m_A c_A P^*}{f_A R^* - n_R(S - R^*)}$ or $\frac{m_A c_A P^*(1 - n_P N_A^*)}{f_A R^*}$ depending on the niche factor that is being modified (see eqns 2a and 2c), whereas with indirect niche construction, the impact vector of species B becomes $\frac{m_B c_B P^*}{f_B(1 - n_R N_A^*)R^*}$ or $\frac{m_B c_B P^*(1 + n_P N_A^*)}{f_B R^*}$ (see eqns 2b and 2d). Note that the population abundances that appear in the modified vector slopes are calculated at the new coexistence equilibrium modified by niche construction (see Supporting Information). Thus, niche construction affects the ecological impacts of species A or B at equilibrium through a rotation of their impact vector (Fig. 3).

More specifically, if niche-constructing species A increases resource turnover rate [case (a)], then niche construction diminishes its deteriorating impact on the resource by n_R (S − R*). Therefore, the negative effect of species A on species B through the resource abundance decreases, which results in the expansion of the zone of

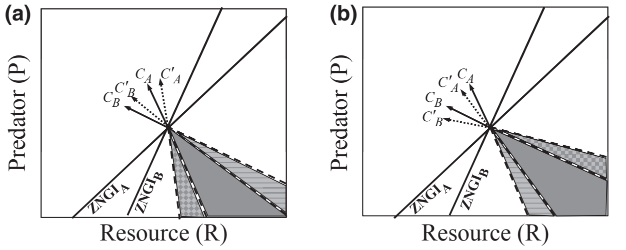

Figure 3 Graphical representation of the effects of niche construction on the impact vectors of consumer A or B under the assumption that the intraspecific negative effect is stronger than the interspecific one in both species. (a) The slope of species A's impact vector, $C_A\left(=\frac{m_A c_A P}{f_A R}\right)$, increases and the area of coexistence expands towards lower values of resource abundance R (diced area) when either species A performs direct niche construction by increasing the resource turnover rate $k\left(C'_A=\frac{m_A c_A P^*}{(f_A R^* - n_R(S-R^*))}\right)$, or species B performs indirect niche construction by either increasing predation pressure on species A or inhibiting species A's resource consumption rate $\left(C'_A=\frac{m_A c_A P^*(1+n_p N_B^*)}{f_A R^*}\right.$ or $\left.\frac{m_A c_A P^*}{f_A(1-n_R N_B^*)R^*}\right.$, respectively$\left.\right)$. The slope of species B's impact vector, $C_B\left(=\frac{m_B c_B P}{f_B R}\right)$increases and the area of coexistence shrinks (hatched area) when either species A performs indirect niche construction by either increasing the predation pressure on species B or decreasing the resource consumption rate of species B $\left(C'_\mathrm{B}=\frac{m_B c_B P^*(1+n_P N_A^*)}{f_B R^*}\right.$ or $\frac{m_B c_B P^*}{f_B(1-n_R N_A^*)R^*}$, respectively$\left.\right)$, or species B performs direct niche construction by increasing the resource turnover rate $\left(C'_B=\frac{m_B c_B P^*}{(f_B R^* - n_R(S-R^*))}\right)$. (b) In the same way, the slope of C_A decreases and the area of coexistence shrinks (hatched area) when species A performs direct niche construction by decreasing predation pressure on itself $\left(C'_A=\frac{m_A c_A P^*(1-n_P N_A^*)}{f_A R^*}\right)$. Finally, the slope of C_B decreases and the area of coexistence expands (diced area) when species B performs direct niche construction by decreasing predation pressure on itself $\left(C'_B=\frac{m_B c_B P^*(1-n_P N_B^*)}{f_B R^*}\right)$. Notice that in all modified impact vectors the abundances are calculated at the new equilibrium modified by niche construction.

coexistence inside the realized niche of species A (diced area in Fig. 3a). This is what we call direct facilitative niche construction, as it allows species B to survive under niche conditions of resource and predator abundances that would not allow its persistence in the absence of niche construction.

In contrast, a decrease in the resource consumption rate of species B induced by species A [case (b)] diminishes the deteriorating impact of species B on the resource by $n_R N^*_A$. As species B is mostly limited by a negative intraspecific effect through resource abundance, niche construction mitigates the strength of this negative effect. Thus, the relative importance of the negative effect of species B on A through predator abundance increases, causing an expansion of the realized niche of species B inside the zone of coexistence (hatched area in Fig. 3a). This is what we call indirect facilitative niche construction as it expands the dominance of species B (see Glossary), although with a negative repercussion on species coexistence. We obtain the same outcome when species A increases predation pressure on species B through niche construction by $n_P N^*_A$ [case (d)]. The increased impact of species B on the predator, which limits less its own growth and more the growth of species A, leads to an increase in predator abundance, which strengthens the negative interspecific effect on species A.

Similarly, when species A, which is limited by a negative intraspecific effect through predator abundance, decreases predation pressure on itself [case (c)], niche construction decreases the importance of the negative effect it experiences. Thus, the relative importance of the negative effect of species A on the response of species B increases and the area of coexistence shrinks to the detriment of species B (hatched area in Fig. 3b). This is what we call direct competitive niche construction (see Glossary).

We obtain the opposite outcomes when species B is the niche-constructing species involved in the above four cases (a–d) of niche improvement. In particular, in case (a), direct facilitative niche construction becomes direct competitive niche construction (hatched area in Fig. 3a), in cases (b) and (d), indirect facilitative niche construction becomes indirect competitive niche construction, but with a positive repercussion on the area of coexistence (diced area in Fig. 3a), and in case (c), direct competitive niche construction becomes direct facilitative niche construction (diced area in Fig. 3b).

ADAPTIVE NICHE CONSTRUCTION AND ITS CONSEQUENCES

After investigating the consequences of niche-improving impacts and their effects on the relative growth rates of the competing species, we now focus on the net benefit that the niche-constructing species reaps from the trait responsible for niche construction. The question is how much better individuals that bear the niche-construction trait respond to their 'constructed' environment relative to other individuals that do not bear this trait, but experience the same environment. The significance of this net benefit is twofold. First, it is crucial for the persistence and evolution of niche construction (Kylafis & Loreau 2008; Krakauer *et al.* 2009) because it determines whether the niche-construction trait is advantageous in the long run: this is what we call adaptive niche construction. Adaptive niche construction confers a relative selective advantage to its agent over other organisms (Dawkins 2004), which ensures that niche construction is selected for. Second, as we will see below, the net benefit of niche construction has an important influence on the ability of a species to fill the niche space.

The absolute response of species A or B is measured by its per capita population growth rate, $W_i=\frac{1}{N_i}\frac{dN_i}{dt}$ $(i = A$ and $B)$. As explained earlier, the relative position of the ZNGIs in the niche space defined by predator abundance P and resource abundance R determines which species is fitter. Any change in the absolute response function of a species causes a change in the position of its ZNGI, and hence its realized niche.

When species A performs direct niche construction, the direct benefit it generates may be represented in the response of species A as follows:

$$W_A = f_A a_A R - m_A P - d_{N_A} + n'_R R(or + n'_P P) \tag{3a}$$

When indirect niche construction modifies the niche impacts of the competing species B, the benefit is only indirect and may be represented in the response of species B as follows:

$$W_B = f_B a_B R - m_B P - d_{N_B} - n'_R N_A R(or - n'_P N_A P) \tag{3b}$$

The additional parameters $n'_R n'_P$ in the above equations represent the rate of benefit generated by direct or indirect niche construction. These rates are assumed to be proportional to the rates of niche construction, n_R and n_P, respectively. For the sake of simplicity, we choose simple linear functions to quantify this benefit. More precisely, a positive linear function of the abundance of the compartment modified by niche construction, $n'_R R$ or $n'_P P$, enhances the response of the niche-constructing species (i.e. absolute benefit to the agent), whereas a negative linear function of the abundances of both the modified compartment and the niche-constructing species, $n'_R N_A R$ or $n'_P N_A P$, deteriorates the competitor's response (i.e. relative benefit to the agent).

In cases when niche construction provides an absolute benefit to its agent, either ZNGI$_A$ becomes steeper and shifts to the left when niche construction enriches the resource or ZNGI$_A$ only becomes

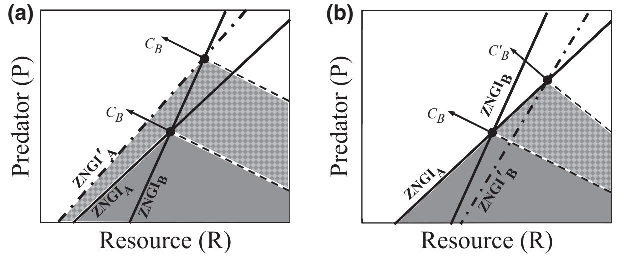

Figure 4 Graphical representation of adaptive niche construction performed by species *A* and its associated benefit to species *A* (absolute benefit if it enhances the long-term response of species *A*, relative benefit if it impairs the long-term response of the competing species *B*). (a) Absolute benefit due to direct niche construction: the ZNGI of species *A* becomes steeper and shifts to the left when niche construction leads to resource enrichment $\left(\text{slope of ZNGI}'_A = \frac{(f_A a_A + n'_R)}{m_A} \text{ and } {R'_A}^{\min} = \frac{d_{N_A}}{(f_A a_A + n'_R)}\right)$, or becomes only steeper when niche construction reduces predation pressure on species *A* $\left(\text{slope of ZNGI}'_A = \frac{f_A a_A}{(m_A - n'_P)}\right)$. In both cases, the realized niche of the niche-constructing species *A* expands from the initial grey area to the diced area, inside the realized niche of species *B* and towards the harsh part of the niche space (i.e. low initial resource abundance, high initial predator abundance). (b) Relative benefit due to indirect niche construction: the ZNGI of species *B* becomes shallower and shifts to the right when niche construction inhibits the resource uptake rate of species *B* $\left(\text{slope of ZNGI}'_B = \frac{(f_B a_B - n'_R N_A *)}{m_B} \text{ and } {R'_B}^{\min} = \frac{d_{N_B}}{(f_B a_B - n'_R N_A *)}\right)$, or becomes only shallower when niche construction increases predation pressure on species *B* $\left(\text{slope of ZNGI}'_B = \frac{f_B a_B}{(m_B + n'_P N_A *)}\right)$. Note that the abundance of species *A* is calculated at the coexistence equilibrium modified by niche construction. In both cases the realized niche of species *A* expands inside the realized niche of species *B,* as represented by the hatched area.

steeper when niche construction decreases predation pressure (Fig. 4a). In both cases, the realized niche of species *A* expands towards the harsh part of the niche space (i.e. high initial predator abundance, low initial resource abundance) and inside the realized niche of the competing species *B*.

In contrast, a relative benefit either shifts the ZNGI of the competitor *B* to the right and decreases its slope when niche construction reduces the resource consumption rate of species *B*, or only decreases its slope when niche construction increases predation pressure on species *B* (Fig. 4b). These changes result in the expansion of the realized niche of the species *A* inside the realized niche of species *B*. In all the above cases of adaptive niche construction, the final result is the expansion of the realized niche of the niche-constructing species *A* and the shrinkage of the realized niche of the competing species *B*.

As adaptive niche construction confers a competitive advantage to its agent over competing species, their ZNGIs diverge, which changes the coexistence equilibrium (see Supporting Information) and the position of the zone of coexistence in the niche space. As illustrated in Fig. 5a, when species *A*, which is mostly limited by the predator, performs adaptive niche construction, the equilibrium abundances of both the resource and the predator increase. On the other hand, the area of coexistence moves towards the upper right part of the niche space (i.e. higher levels of *N* and *P*). Conversely, when species *B*, which is mostly limited by the resource, performs adaptive niche construction, as illustrated in Fig. 5b, the equilibrium abundances of both the predator and the resource decrease. Finally, the area of coexistence moves towards the lower left part of the niche space.

Note, however, that niche construction may not always be adaptive and confer a net benefit to its agent. For instance, nest mounds of red wood ants are long-lived, warm, humid and rich in organic matter.

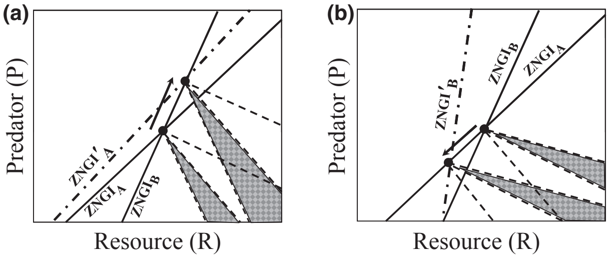

Figure 5 Graphical representation of adaptive niche construction in two different instances of direct facilitative niche construction: (a) Species *A* enriches the resource by increasing the resource turnover rate (*k*) and (b) Species *B* decreases predation pressure (m_B) on itself. The diced area of coexistence represents the positive effect of facilitative niche construction on species coexistence.

Nest construction thereby confers ants a higher fitness. But the high-energy inputs of ants in their nest also favour the growth of heterotrophic decomposer microbes, which may increase their exposure to pathogens (Jouquet *et al.* 2006). Therefore, nest construction can negatively affect ant performance and act as a negative selective feedback mechanism. Similarly, plant species that are provided protection against other herbivores by ants in return for food and shelter very often suffer high consumption by ants. Thus, under certain conditions, the cost may counterbalance the benefit that is offered (Frederickson & Gordon 2007). In these cases, the realized niche of the niche-constructing species shrinks, and niche destruction takes place.

DISCUSSION

The primary aim of our work was to integrate niche construction into modern niche theory. We propose the concept of ecological niche construction as a way to analyse the dialectic relationship between organisms and their environment over ecological time-scales. Modern niche theory has largely focused on cases where organisms induce niche-deteriorating impacts that generate negative effects on their response, but has neglected niche-improving impacts and their positive effects, whether direct or indirect, generated by niche construction. Since both kinds of impacts take place simultaneously within communities, we are interested in their interplay and in their outcome on the relative responses of competing species.

We use a simple mechanistic niche model to illustrate the dynamics of two consumers that compete for two dynamic niche factors, a resource and a predator. Trade-offs between species' niche-deteriorating impacts and their response function give rise to negative effects at the intraspecific and interspecific levels that account for coexistence: each species has to limit its growth more than that of the other species. Niche construction can improve its agent's environment either directly, by increasing resource availability or decreasing predator abundance, or indirectly, by undermining the persistence of the competing species through reduced access to the resource or increased predation pressure. The complex interplay of these impacts and the traditional niche-deteriorating impacts modify the potential for coexistence in various ways.

The net benefit that a niche-constructing species derives from its modified environment makes niche construction an adaptive process with important quantitative consequences on equilibrium abundances and the absolute position of the area of coexistence in the niche space. We now discuss the properties of adaptive direct and indirect niche construction and their relevance to the existing ecological literature.

Adaptive direct niche construction

This form of niche construction is equivalent to positive interactions mediated by changes in the abiotic environment or other organisms. Positive or facilitative interactions have gained increasing attention in contemporary ecological research (Hunter & Aarssen 1988; Callaway 1995; Bruno *et al.* 2003; Lortie *et al.* 2004). Our work shows that facilitation of competing species results from environmental improvement only when the niche-constructing species enhances the niche factor that limits more the growth of the competing species than its own growth. This increases the importance of intraspecific competition relative to interspecific competition to the benefit of the competing species. For instance, the hosting sites of the anemone fish (*Amphiprion*) are increased by its mutualistic interaction with its host anemone species. However, the limited ability of the fish to defend new host sites, as host area increases, leads to weaker interspecific competition. In fact, its competitor, the damselfish (*Dascyllus*), is facilitated by the new, poorly defended host sites, and coexistence between the two fish species is promoted (Schmitt & Holbrook 2003).

Therefore, an amelioration of a limiting niche parameter allows a competing species to survive under niche conditions, such as low initial resource abundance (when species A enhances resource turnover rate) or high initial predator abundance (when species B decreases predation pressure on itself), that it is unable to tolerate on its own. The Stress Gradient Hypothesis makes a similar prediction, i.e. positive interactions should be predominant in communities under high physical stress or under high consumer pressure (Bertness & Callaway 1994; Callaway & Walker 1997; Stachowicz 2001; Brooker *et al.* 2008; Maestre *et al.* 2009). When we take into account the net benefit on the long-term response of the niche-constructing agent, however, the interspecific facilitative effect of niche construction, as being reflected in the expansion of the area of coexistence, prevails under higher initial resource abundances (Fig. 5a) or lower initial predator abundances (Fig. 5b). Therefore, our work suggests that facilitation theory would improve understanding of the complex interplay between competition and facilitation along stress gradients if it expanded its focus to include the adaptive benefit derived from niche construction by its agent.

A significant new insight from our analysis is that direct niche construction does not generate facilitative impacts on the competing species when its agent improves the niche parameter that limits most its own growth. In this case, niche construction deteriorates the negative intraspecific effects that stabilize the niche-constructing species and increases the intensity of interspecific competition. Therefore, direct niche construction contributes to generate negative interactions in communities.

Adaptive indirect niche construction

Adaptive indirect niche construction has some similarities with interference competition such as allelopathy and intraguild predation (Amarasekare 2002). By modelling changes in both the competitor and the modified niche compartment explicitly, however, we were able to unveil counterintuitive competitive outcomes. In particular, indirect competitive niche construction may promote species coexistence while, conversely, indirect facilitative niche construction may compromise species coexistence. In the first case, a species can increase intraspecific competition in a superior competitor, so that the competitive interaction strengthens to the benefit of the former species and coexistence is promoted. In the second case, a species can decrease intraspecific competition in an inferior competitor, and thus facilitate the latter to the detriment of their coexistence. As far as we are aware, these cases have not been reported in the ecological literature so far, and could offer new insights into species coexistence and the maintenance of biodiversity.

CONCLUSIONS

Our work extends recent contributions to niche theory (Leibold 1995; Chase & Leibold 2003), which showed that coexistence between species involves more than mere niche partitioning. Coexistence hinges on differences between species in their impacts on their environment, which in turn generate different interspecific and intraspecific effects on their responses to the changed environment. Our model goes one step further by offering a theoretical framework for the investigation of the complex interplay between niche-improving and niche-deteriorating impacts and their effects on species coexistence. As Holt (2009) aptly stated, a fully formed theory of community ecology should embrace both positive and negative interactions and include the careful articulation of specific mechanisms of organism-environment feedbacks. The simplicity of our model, however, does not allow us to draw general conclusions about more diverse ecosystems where non-transitive competitive interactions via multiple resources and enemies may interplay with niche construction to generate counterintuitive results. Thus, more complex models that incorporate more diverse organism–environment interactions will be necessary for a deeper understanding of the theoretical significance of niche construction (e.g. Goudard & Loreau 2008).

Our work also highlights the importance of new experimental work on organism–environment interactions and the feedbacks they generate. There has been a proliferation of studies on plant–soil feedbacks (PSF) in plant ecology during the past 5 years (Kulmatiski *et al.* 2008). This research is based on two main ideas that are explored in our work: (1) plants cause species-specific changes in the soil (Bever 1994; Ehrenfeld *et al.* 2005) and (2) they demonstrate species-specific responses to these changes. Therefore, PSF experiments offer a valuable tool for quantifying the differential response of experimentally introduced species in the soil ‘constructed’ by a known plant (i.e. interspecific effects). There is also increasing interest in experiments that quantify the impacts of introduced plant species on soil processes, such as nutrient cycling via tissue nutrient content (Ehrenfeld 2003), and the feedbacks these processes generate on the response of introduced species. A promising avenue for future research would be to combine these two experimental approaches to quantify simultaneously both the impacts of organisms on their environment and the interspecific and intraspecific effects that these generate on species responses in either plant or animal consumer communities. This would unveil currently neglected species-specific functional roles that largely determine community structure and ecosystem functioning.

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GLOSSARY

Niche factor: Any environmental factor that determines the per capita population growth rate of a species. Niche factors can be abiotic parameters such as resource abundance and temperature, or biotic parameters such as predation and parasitism.

Level of niche factor: An appropriate measure of a niche factor (e.g. abundance, °C).

Response: Effect of a niche factor on the per capita population growth rate of a species.

Long-term response: Effect of a niche factor on the per capita population growth rate of a species at equilibrium, which is graphically represented by its Zero Net Growth Isocline.

Impact: Effect of a species on the level of a niche factor (resource abundance or predator abundance in our model).

Niche-deteriorating (improving) impact: Negative (positive) effect of a species on a niche factor that favours its growth (e.g. resource abundance), or positive (negative) effect on a niche factor that inhibits its growth (e.g. predator abundance).

Ecological niche construction: Activities of a species that result in niche-improving impacts. Ecological niche construction can be either direct when the niche-constructing species improves its own niche, or indirect when it deteriorates the niche of competing species.

Facilitative (competitive) niche construction: Ecological niche construction that results in either (a) increasing (decreasing) the difference between intraspecific and interspecific negative effects generated by its agent (*direct niche construction*), or (b) decreasing (increasing) the difference between intraspecific and interspecific negative effects generated by competing species (*indirect niche construction*). In the first case the area of coexistence expands (shrinks), whereas in second case the area of coexistence shrinks (expands).

Adaptive niche construction: Niche construction in which the niche-constructing trait confers a direct or indirect net benefit to its bearer.

SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Analytical proof of graphical results.

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