

LETTER

Ecological and evolutionary consequences of niche construction for its agent

Grigoris Kylafis* and
Michel Loreau
Department of Biology, McGill
University, 1205 Avenue
Docteur Penfield, Montreal, QC
H3A 1B1, Canada
*Correspondence: E-mail:
grigoris.kylafis@mail.mcgill.ca

Abstract

Niche construction can generate ecological and evolutionary feedbacks that have been underinvestigated so far. We present an eco-evolutionary model that incorporates the process of niche construction to reveal its effects on the ecology and evolution of the niche-constructing agent. We consider a simple plant–soil nutrient ecosystem in which plants have the ability to increase the input of inorganic nutrient as an example of positive niche construction. On an ecological time scale, the model shows that niche construction allows the persistence of plants under infertile soil conditions that would otherwise lead to their extinction. This expansion of plants' niche, however, requires a high enough rate of niche construction and a high enough initial plant biomass to fuel the positive ecological feedback between plants and their soil environment. On an evolutionary time scale, we consider that the rates of niche construction and nutrient uptake coevolve in plants while a trade-off constrains their values. Different evolutionary outcomes are possible depending on the shape of the trade-off. We show that niche construction results in an evolutionary feedback between plants and their soil environment such that plants partially regulate soil nutrient content. The direct benefit accruing to plants, however, plays a crucial role in the evolutionary advantage of niche construction.

Keywords

Adaptive dynamics, niche construction, nutrient cycling, plant–soil interactions, positive feedback, regulation.

Ecology Letters (2008) 11: 1072–1081

INTRODUCTION

Niche construction, which portrays organisms as active agents that modify their environment rather than mere passive entities selected by their environment, has received increasing attention in ecology and evolutionary biology during the last decade (Odling-Smee *et al.* 1996, 2003; Laland & Sterelny 2006). Niche construction is described as a process by which organisms, through their metabolism, 'engineering' activities (e.g. burrows, nests) and habitat 'choice' (e.g. dispersal, immigration), actively modify abiotic and biotic features of their environment. By doing so, they generate feedbacks with their environment that may operate on both ecological and evolutionary time scales (Lewontin 1978; Odling-Smee *et al.* 2003; Hastings *et al.* 2007).

In its ecological dimension, niche construction is often viewed as synonymous with 'ecosystem engineering' (Jones *et al.* 1994). Through their activities, organisms bring about

significant, consistent and directed changes to the flows of energy and matter in ecosystems (Jones *et al.* 1994, 1997). Ecosystem engineering, however, is mainly focused on the feed-forward ecological effects of engineering activities on other species, and largely ignores feedbacks on the 'engineer', especially on evolutionary time scales. Niche construction was originally introduced as an evolutionary process that generates selection through an evolutionary feedback between organisms and their selective environment (Lewontin 1978; Odling-Smee *et al.* 2003; Han *et al.* 2006). This evolutionary feedback is adaptive provided it enhances the fitness of the organism that generates it (Free & Barton 2007). Adaptive feedback gives the niche-constructing agent the potential to regulate its own environment (Odling-Smee *et al.* 2003).

Theoretical studies of niche construction are in the very beginning of their development. So far, the majority of theoretical models that have been proposed to describe the

basic mechanism of niche construction are based on two-locus population genetic models, and confirm that niche construction can significantly alter evolutionary patterns (Laland *et al.* 1999; Hui & Yue 2005; Han *et al.* 2006). But we lack more realistic models that explicitly describe the feedback mechanisms generated by niche construction, and study their importance on ecological and evolutionary time scales.

Plants provide numerous examples of niche construction. Therefore, they are ideal organisms to investigate its causes and consequences. In terrestrial ecosystems, plants can alter various soil properties (e.g. humidity, temperature, fertility), and thus influence nutrient cycling (van Breemen & Finzi 1998; Knops *et al.* 2002). In particular, plants can modify nutrient mineralization, either through their litter quality (Pastor *et al.* 1984) or even by creating favourable abiotic conditions for decomposers under their canopy (Cross & Schlesinger 1999). They can also modify nutrient inputs in their local soil environment. Plant species that enrich the soil with nitrogen via symbiotic or non-symbiotic nitrogen fixation (Vitousek *et al.* 1987), or with other nutrients via uplift from previously inaccessible soil resources using deep roots (Berendse 1979; Chapin *et al.* 1997) are some of the best known examples. But nutrient input modification by plants can take on many other forms. For instance, some tree species are very efficient at retaining dry atmospheric inputs due to their large surface area and aerodynamic resistance (Marcos & Lancho 2002). Some shrub species alter airflow dynamics, and thereby accumulate mineral-rich clay materials under their canopy (Parsons *et al.* 1992).

In this article, we investigate the consequences of niche construction for the ecology and evolution of its agent. We use a simple ecological model proposed by Loreau & Holt (2004) as a baseline model. This model describes a nutrient-limited ecosystem with only two compartments, plants and inorganic soil nutrient. We then incorporate the ability of plants to modify the input of inorganic nutrient in the ecosystem. In this respect, our model has some similarities with that recently presented by Menge *et al.* (2008). Menge *et al.*'s model, however, is specifically focused on nitrogen fixation, whereas ours is designed to explore the ecology and evolution of niche construction much more generally. By comparing the ecological and evolutionary dynamics with and without niche construction, we analyse the conditions under which the plant-driven environmental modification becomes an important process. On an ecological time scale, we explore how plants foster their own persistence through a positive feedback generated by niche constructing activities. On an evolutionary time scale, we highlight the effect of niche construction on plants' evolutionary dynamics and the resulting adaptive regulation of the local soil nutrient pool.

MODEL DESCRIPTION

We start with a simple model of a nutrient-limited ecosystem (Loreau & Holt 2004). It comprises two compartments, which describe the stocks of a limiting nutrient in inorganic form in the soil (N) and in plants (P) (Fig. 1). A constant input of inorganic nutrient, I , replenishes the soil nutrient pool through precipitation or dry deposit, while the nutrient is leached out of the soil at a rate e_N . Plants take up a quantity $u(N, P)$ of nutrient from the soil per unit time. Plant litter decomposes, part of which is recycled to the soil nutrient pool at a rate r , while another part is either lost from the ecosystem or made unavailable to plants at a rate e_P .

We assume for simplicity that plant nutrient uptake, $u(N, P)$, is proportional to the amount of available nutrient in the soil, N . We take into account the fact that plant nutrient uptake may be limited by intraspecific competition for other factors than the limiting nutrient (e.g. water, light) when plant biomass is high (Clark *et al.* 2005). Accordingly, plant nutrient uptake is described by the equation:

$$u(N, P) = \frac{uNP}{k + P} \quad (1)$$

where u is a parameter that measures plant nutrient uptake ability, and k is a parameter that determines the strength of plant limitation by other factors. When limitation by other factors is weak, parameter k is large, such that $k \gg P$ and

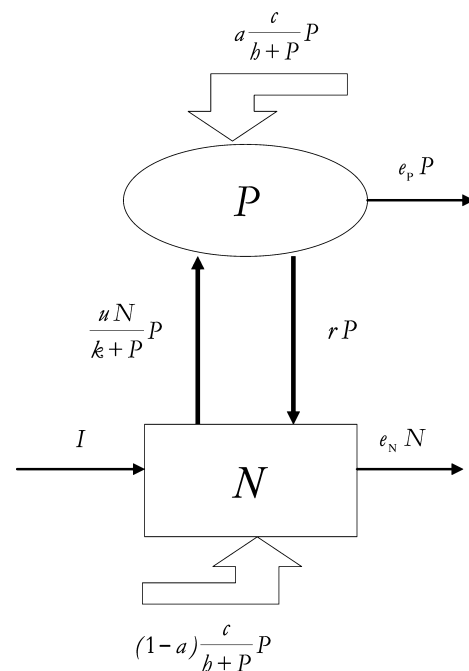


Figure 1 Flow diagram of the model system composed of a plant compartment (P) and a soil nutrient compartment (N).

eqn (1) becomes identical to the standard Lotka–Volterra interaction term. When limitation by other factors is strong, k is small, such that $k \ll P$ and eqn (1) becomes a linear donor-controlled function. Equation (1) may be viewed as a special case of the more general consumption function proposed by De Angelis *et al.* (1975) and Beddington (1975), in which saturation of plant nutrient uptake at high nutrient availability is assumed to be negligible because of strong nutrient limitation. We did not include this saturation effect because it considerably complicates the mathematical analysis of the model.

We now incorporate the ability of plants to add an amount $c(P)$ of nutrient to the system through their niche constructing activities. However, only a fraction a of the nutrient made available by niche construction directly benefits plants and is incorporated into their biomass. For instance, in savannas (Scholz *et al.* 2002) and probably in other tropical ecosystems, water and nutrients uplifted by deep-rooted plants flow from shallow roots into the surrounding soil. Therefore, we consider that the remained fraction $(1-a)$ of the nutrient coming from niche construction is added to the soil inorganic nutrient pool. One of the limitations of Menge *et al.*'s (2008) model was that nitrogen fixation was density independent, which creates the possibility of a boundless autocatalytic process leading to unlimited growth of nutrient stocks. To avoid this unrealistic feature, we consider niche construction to be density dependent. Density dependence represents a negative feedback on niche construction resulting from other limiting factors such as other resources and herbivory. As niche construction increases plants' biomass, their ability to perform further niche construction becomes limited such that

$$c(P) = \frac{cP}{b + P} \tag{2}$$

where c is the maximum rate of niche construction, and b is its half-saturation constant. The following differential equations then describe the dynamics of the plant–nutrient system:

$$\frac{dP}{dt} = \frac{uNP}{k + P} - e_P P - rP + a \frac{cP}{b + P}, \tag{3.a}$$

$$\frac{dN}{dt} = I - e_N N - \frac{uNP}{k + P} + rP + (1 - a) \frac{cP}{b + P}. \tag{3.b}$$

RESULTS

Ecological dynamics

We analyse the dynamical behaviour of the plant–nutrient system by setting eqns (3) to zero and examining their null

isoclines in the (N, P) phase plane. We first investigate the behaviour of the model when there is no niche construction (i.e. $c = 0$). In this case, two cases of soil fertility need to be distinguished (Loreau & Holt 2004): when

$$\frac{I}{e_N} > \frac{k(e_P + r)}{u},$$

the soil is fertile, whereas in the opposite case,

$$\frac{I}{e_N} < \frac{k(e_P + r)}{u},$$

the soil is infertile compared with plant requirements (Appendix S1, for more details). Combining analytical feasibility conditions and graphical results from isocline analysis, we obtain the following conclusions. Plants persist under fertile soil conditions (Appendix S1.1 [A3]) as the system then converges on an internal equilibrium point (Fig. 2a). In contrast, under infertile soil conditions (Appendix S1.1 [A4]), the only feasible equilibrium point is a boundary equilibrium point leading to plant extinction (Fig. 2d).

When there is niche construction ($c \neq 0$), the complexity of the dynamical system precludes a complete mathematical analysis. We were able, however, to study its behaviour analytically under a scenario of weak limitation of nutrient uptake by other factors, yielding a Lotka–Volterra interaction function (Appendix S1.2.i). The graphical analysis showed identical results in the general case; the maximum rate of niche construction c then modifies the curvature and position of the P -isocline. Based on these analytical and graphical results, we derive the following conclusions.

In the case of a fertile soil environment

$$\frac{k(e_P + r)}{u} - \frac{kac}{bu} < \frac{k(e_P + r)}{u} < \frac{I}{e_N} \text{ and } c \geq 0,$$

the system shows the same dynamical behaviour as without niche construction, and plants persist (Fig. 2a). In the case of an infertile soil, there are several sub-cases depending on the value of the maximum niche construction rate, c (Appendix S1.2.i [A8–A10]). For high values of the maximum niche construction rate ($c > c_{(1)}$), the P -isocline is shifted to the left

$$\frac{k(e_P + r)}{u} - \frac{kac}{bu} < \frac{I}{e_N} < \frac{k(e_P + r)}{u}$$

compared with the equivalent case without niche construction (Fig. 2b). A stable internal equilibrium point appears along with a boundary point. The boundary point in this case is unstable, as opposed to the stable one without niche construction. Therefore, the plant population persists despite harsh soil conditions. For intermediate values of the maximum niche construction rate ($c_{(2)} < c < c_{(1)}$) and high values of b and k , niche construction is not sufficient to

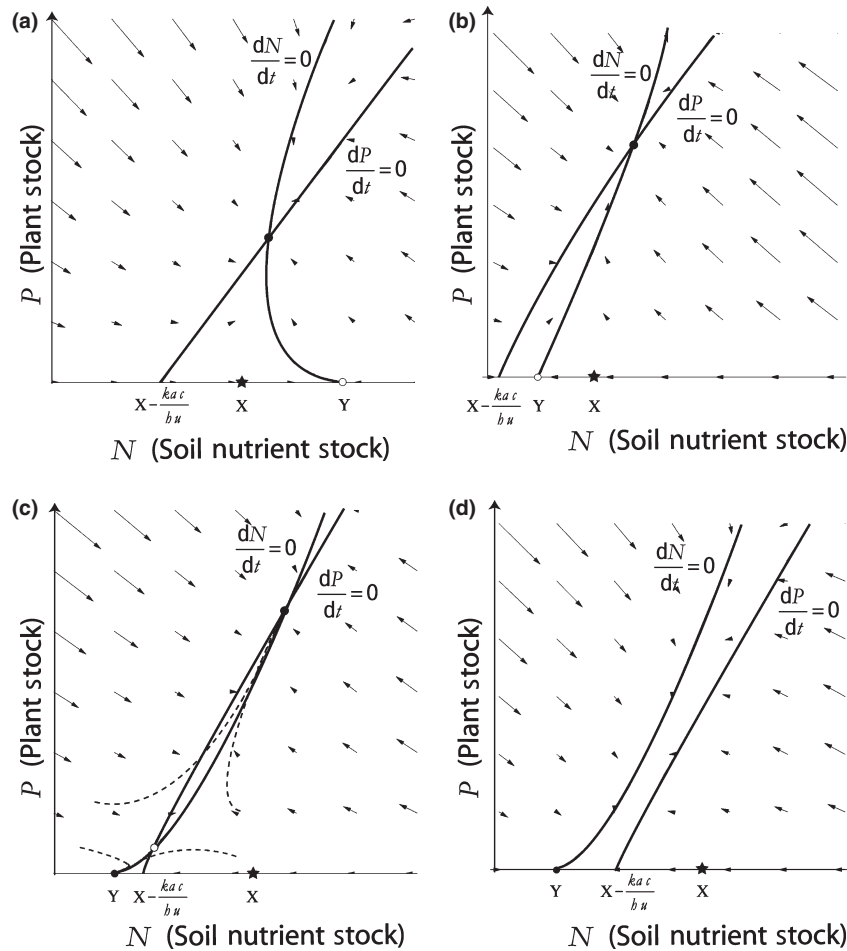


Figure 2 Isocline analysis of the plant-soil nutrient system in the case when there is niche construction (i.e. $c \neq 0$). The zero isoclines are formed by plotting $dN/dt = 0$ (N -isocline) and $dP/dt = 0$ (P -isocline), respectively. The growth rate of N is positive to the left side of its zero-isocline and negative to the right side. The opposite holds for the sign of the growth rate of P . (a) Under fertile soil conditions the system demonstrates the same dynamic behaviour as in the case without niche construction ($c = 0$ and P -isocline shifts to the intercept X). There are two equilibrium points, an unstable boundary equilibrium and an internal stable equilibrium. (b) Under infertile soil conditions and for high rate of niche construction, there are two equilibrium points, a stable interior and an unstable boundary point. (c) Under infertile soil conditions and for intermediate rate of niche construction, two stable equilibrium points are possible (internal and boundary). An unstable, internal, equilibrium also lies in between. Dotted lines represent dynamic trajectories for different initial conditions. A large initial plant population size allows for plant survival; otherwise plants go extinct. (d) Under infertile soil conditions and for very low maximum niche construction rate, the system demonstrates the same dynamic behaviour as in the case without niche construction ($c = 0$ and P -isocline shifts to the intercept X). Only one unstable boundary equilibrium is possible. Filled circles indicate locally stable equilibria and an open circles indicate locally unstable equilibria. Intercept values: $X = \frac{k(e_p+r)}{u}$, $Y = \frac{I}{e_N}$.

shift the P -isocline as much to the left as in the previous subcase

$$\frac{I}{e_N} < \frac{k(e_p+r)}{u} - \frac{kac}{bu} < \frac{k(e_p+r)}{u}$$

(Fig. 2c). Consequently, two internal equilibrium points and one boundary equilibrium point are feasible. The system converges either to the upper internal equilibrium point or to the boundary point depending on initial plant biomass (Fig. 2c). Finally, for low maximum rates of niche con-

struction, no intersection between the zero isoclines is feasible, and thus plants go extinct (Fig. 2d).

Evolutionary dynamics

The theory of adaptive dynamics (Metz *et al.* 1996; Geritz *et al.* 1997) assumes that once ecological dynamics brings the system to an ecological equilibrium, evolution takes place. This theory describes evolution as a process of small successive mutation steps. We follow this approach, and

consider that the two main plant traits under direct plant control coevolve: (i) the environment-altering trait, the maximum niche construction rate, c , and (ii) the recipient trait, the nutrient uptake ability, u , whose value depends on feedback from natural selection in the 'altered' environment. In our evolutionary model, the fitness of a rare mutant with strategy (c_m, u_m) is defined by its growth rate in the resident population with strategy (c, u) :

$$W_m(c_m, u_m, c, u) = \frac{1}{P_m} \frac{dP_m}{dt} = \frac{u_m}{k + P^*} N^* - \epsilon_p - r + a \frac{c_m}{b + P^*} \tag{4}$$

where N^* and P^* are the nutrient and plant stocks, respectively, at the equilibrium with the resident strategy alone. The mutant population invades the resident population if and only if its fitness is positive. The local selection gradient is a vector, defined as

$$\vec{S} = \left(\frac{\partial W_m}{\partial c_m}, \frac{\partial W_m}{\partial u_m} \right) \Big|_{c_m=c, u_m=u}$$

pointing in the direction of evolution.

Both the maximum niche construction rate, c , and the nutrient uptake ability, u , have energetic and material costs. Given that the energetic and nutrient contents of organisms are bounded, a trade-off should constrain the values of these traits. For example, the cost of nitrogen fixation compromises the ability of nitrogen-fixers to produce roots to appropriate soil nitrogen (Vitousek & Field 1999; Menge

et al. 2008). Likewise, the investment of some plants in deep roots limits their ability to efficiently consume nutrients from the shallow soil pool (Callaway *et al.* 2003).

As we are interested in the outcome of selection when there is a trade-off between two traits, we use the powerful graphical approach developed by de Mazancourt & Dieckmann (2004). Following their method, we first plot the attainability boundary (A-boundary) and the invasibility boundary (I-boundary) in the plane defined by the two coevolving traits (Appendix S2, for more details). Evolution proceeds in the direction of the local selection gradient and along the trade-off curve; it stops at the point where the local selection gradient becomes perpendicular to the trade-off curve (evolutionarily singular strategy).

We can visualize graphically the different evolutionary outcomes based on the shape of the trade-off function. A convex trade-off represents a low start-up cost for niche construction, but further investment in higher values of niche construction involves an increasing cost to the detriment of nutrient uptake ability. By contrast, a concave trade-off represents a high start-up cost, but further investment involves a decreasing cost (Fig. 3a).

Without niche construction

As in the case of ecological dynamics, we first study the evolutionary dynamics of the system when there is no niche construction. In this case, substituting the ecological equilibrium values of the plant and soil nutrient stocks into equation (5) yields:

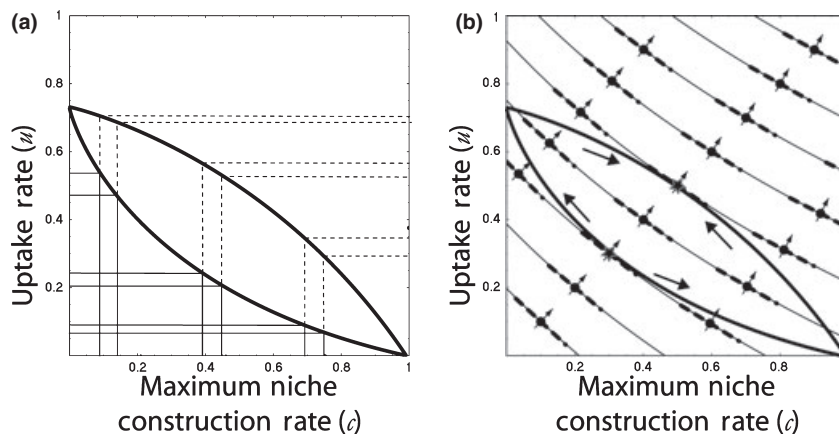


Figure 3 (a) Trade-off functions between niche construction rate (c) and soil nutrients uptake rate (u). A convex trade-off represents a low start-up cost for niche construction, but further investment to higher values of c (from left to right on the horizontal-axis), involves an increasing cost to the detriment of u (from top to bottom on the vertical-axis). A concave trade-off represents a high start-up cost for niche construction but further investment to higher values of c involves a decreasing cost to the detriment of u . (b) Evolutionary outcomes when there is niche construction (i.e. $c \neq 0$) for different trade-off functions. Thick solid lines represent trade-off curves. Parallel solid lines represent A-boundaries, short dotted lines represent I-boundaries, thin arrows represent the selection gradient. Stars represent evolutionarily singular strategies. A convex trade-off results in a continuously stable strategy (CSS); directional selection converges to the singular strategy where evolution ceases, as the thick arrows indicate. A concave trade-off results in an invulnerable repellor; directional evolution diverges from the singular strategy towards either very high values of c , if plants can afford the big start-up cost for niche construction, or very high values of u , in the opposite case, as the thick arrows indicate.

$$W_m(u_m, u) = \left(\frac{u_m}{u} - 1\right)(e_p + r). \tag{5}$$

This equation shows that the mutant’s fitness is not affected by soil parameters, but only by its nutrient uptake ability relative to the resident.

With niche construction

When there is niche construction, the mutant’s fitness is determined by an equation in which soil parameters come into play along with other model parameters (Appendix S2 [B1]). Plants modify their soil environment through niche construction, and the modified environment in turn affects their fitness. In other words, an evolutionary feedback between plants and soil emerges as a result of niche construction.

The graphical analysis of the evolutionary model shows that several evolutionary outcomes are possible (Fig. 3b). If the trade-off is convex, the singular strategy is evolutionarily and convergence stable, resulting in a continuously stable strategy (CSS). If the trade-off is concave then the singular strategy is evolutionarily and convergence unstable, resulting in an invisible repeller (i.e. evolution leads away from such a singular strategy). In the rest of our analysis, we focus on the case of a convex trade-off, for two reasons. First, this case may be more realistic as it involves increasing costs for higher values of niche construction and it generates stable evolutionary dynamics. Second, a concave trade-off generates qualitatively similar results regarding the effects of independent parameters on the outcome of evolution.

When the fraction of direct niche construction benefits accruing to plants, a , increases, the CSS shifts along the trade-off curve towards higher values of c and lower values of u (Fig. 4). When the independent nutrient input, I , increases or soil when the nutrient leaching rate, e_N , decreases, the CSS shifts towards higher values of u and lower values of c (Fig. 4). In general, notice that plants adapt to soil enrichment (in the form of either increased I or decreased e_N) by decreasing their investment in niche construction and increasing their investment in soil nutrient uptake. Conversely, when the soil tends to impoverish (decreased I or increased e_N), plants respond to this environmental change by investing less in soil nutrient uptake and adding more nutrient into the system through a higher rate of niche construction. These results indicate an adaptive regulation of the soil nutrient level by plants.

This regulatory property is illustrated in Fig. 5, which shows how the equilibrium soil nutrient stock changes as the independent nutrient input, I , increases. As I varies, plants adjust the values of the two coevolving traits, which are linked via the trade-off function. When I is small, niche-constructing plants buffer, to a certain degree, the soil nutrient stock against variations in nutrient input. Their regulatory ability, however, attenuates with increasing I , for reasons that we discuss later, and the soil nutrient stock eventually varies linearly with the independent nutrient input, as in the case without niche construction. We obtain identical results when we vary the leaching rate e_N .

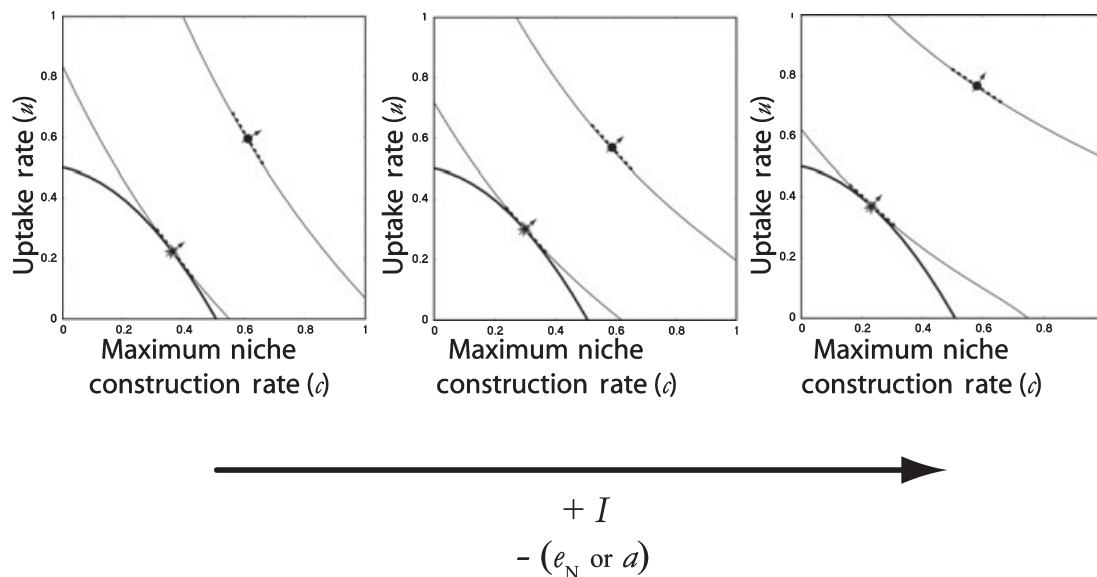


Figure 4 Results of coevolution of niche construction trait (c) and uptake rate (u), when the fraction of direct benefit from niche construction (a), the independent nutrient input (I) or soil leaching rate (e_N) change. A convex trade-off between c and u is considered. Increasing parameter I , or decreasing parameters a or e_N (from left to right), alters the dynamics of the system; A- and I- boundaries become shallower and it results in the shift of CSS toward higher values of u at the expense of lower values of c . The current figure has the same structure as Fig. 3.

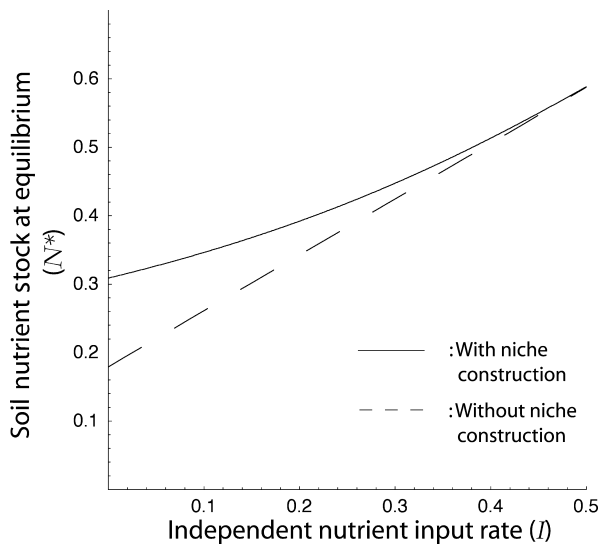


Figure 5 Graphical representation of the change of soil nutrients stock at equilibrium (N^*) as the independent nutrient input rate (I) changes. Plants adjust the values of coevolving traits c and u according to a convex trade-off function that results in a CSS. When there is niche construction, plants respond adaptively to the change of I . When, there is no niche construction plants do not show any adaptive response to the change of I . Used trade-off function: $u = -1.32 c^2 + 0.1 c + 0.45$. Solid line represents the case when there is niche construction and the dotted line represents when there is no niche construction.

DISCUSSION

Niche construction transforms the ecological and evolutionary dynamics of its agent. We have explored these ecological and evolutionary feedbacks using a simple ecological plant–nutrient ecosystem model that incorporates both population dynamical and mass-balance constraints, and that includes the ability of plants to enhance the input of a limiting nutrient to the system. Menge *et al.* (2008) recently made a first step in that direction by adding the ability of plants to modify nutrient input in a similar model system, but they focused on the special case of nitrogen fixation. Our model seeks greater generality as it accommodates various cases of input modification, it incorporates saturating effects of plant density on niche construction and soil nutrient uptake abilities, and it sheds light on generic ecological and evolutionary features of niche construction. We now discuss how our model improves our understanding of niche construction, and of the functioning and evolution of ecological systems.

Ecological consequences

On an ecological time scale, positive niche construction generates new equilibrium points that would otherwise be

unfeasible. Our ecological model shows niche construction to be particularly important under harsh soil conditions. When plants grow on a nutrient-poor soil, they can foster their own persistence through a positive feedback caused by their environment-altering activities. Plants increase nutrient supply through niche construction, leading to a higher population size, which can further increase nutrient supply. Positive feedback mechanisms between primary producers and environmental conditions have been identified for a wide variety of systems, especially for plants (Wilson & Agnew 1992).

Our model also demonstrates the importance of the intensity of niche construction on ecosystem dynamics. At high rates of niche construction, the plant population always reaches a feasible, stable equilibrium. For intermediate rates of niche construction, multiple stable states are possible. In this case, plants' persistence depends on their initial population size, and not on the initial inorganic soil nutrient stock (see Fig. 2c). A large initial population size can create the necessary conditions for plant survival by amplifying the positive feedback mechanism that is generated by niche construction; otherwise the plant population goes extinct. Various mathematical studies have shown that positive feedback between plants and their environment may induce alternative stable states for the vegetation–soil system (Rietkerk & van de Koppel 1997; van de Koppel *et al.* 2001). The presence of alternative stable states also implies sensitivity of the system to perturbations. For instance, a human-induced decrease in plant abundance might push the system into the basin of attraction that leads to the collapse of the plant population. These theoretical predictions agree with the fact that plant strategies such as nitrogen fixation, deep-rooting systems (Canadell *et al.* 1996) and retention of nutrients by canopy (Miller *et al.* 1980) are important ecological mechanisms that permit them to thrive in nutrient-poor ecosystems. Finally, low rates of niche construction do not allow plants to improve their fate under harsh soil conditions.

Evolutionary consequences

On an evolutionary time scale, we considered directional, frequency-dependent coevolution of two plant traits: the maximum niche construction rate, c , and the soil nutrient uptake rate, u . In the absence of niche construction ($c = 0$), we showed that the fitness of a mutant, and consequently the outcome of its competition with the resident plant strategy, is independent of soil-related parameters.

Our evolutionary model reveals an evolutionary feedback between niche-constructing plants and their soil environment. In this respect, it differs from Menge *et al.*'s (2008) model, in which abiotic soil parameters (such as I and e_N) played no role in the evolution of N-fixation. In our work,

plants modify their soil environment, which in turn enhances their fitness, thereby generating an adaptive feedback. This difference is attributable to the saturation of plants' ability to perform niche construction, in our model. Our model further predicts different evolutionary outcomes depending on the shape of the trade-off between the two coevolving traits. When the trade-off is convex, implying an increasingly costly mechanism of niche construction, it results in an evolutionarily and convergence stable strategy (CSS). The end point of evolution is a strategy that allows plants to exploit a combination of the soil resource and the resource generated by niche constructing activities. When the trade-off is concave, implying a decreasingly costly niche construction, the end point of evolution is an unstable strategy (i.e. an invulnerable repellor). Eventually, plants diverge towards a strategy that involves a more intensive exploitation of either the soil resource or the resource generated by niche construction. These results agree with previous theoretical studies on the evolution of a species that exploits two resources but faces a trade-off in its ability to exploit these resources (Levins 1963; Abrams 1986; Rueffler *et al.* 2006).

Our evolutionary model predicts that an increase in the direct benefit of niche constructing activities to plants, a , results in selection for higher values of the maximum niche construction rate, c , and lower values of the nutrient uptake rate, u . By investing more energy and nutrients in niche construction, plants replenish the soil with the limiting nutrient, which may eventually become available to potential invaders. The higher the direct advantage to the niche-constructing plants, the less vulnerable they are to invasion by 'cheaters' that are able to consume the available soil nutrient without cost. Some studies on the evolution of facilitation, and in particular of nitrogen fixation, (Vitousek & Howarth 1991; Vitousek & Field 1999), suggest that the benefit must be high enough for the process to be evolutionary advantageous. Parameter a deserves more attention and further investigation for the different cases of input modification.

When the soil becomes more nutrient poor as a result of either a decrease in the independent nutrient input, I , or an increase of leaching rate, e_N , evolution favours a higher rate of niche construction and a lower rate of soil nutrient uptake; the result is reversed when soil fertility increases. This conclusion agrees with the experimentally observed ability of nitrogen-fixers to regulate, through a trade-off, the extent to which they rely on fixed N vs. soil N on ecological time scales depending on soil conditions (Peoples & Craswell 1992). When intermediate levels of soil N are available, legumes rely on a combination of fixed and soil N (Neyra 1978), while N fixation in many legumes ceases at high soil nitrate concentrations (Marschner 1995). An analogous mechanism has been suggested to explain the

dominance of shallower root systems in nutrient-rich soils, and of deeper roots in nutrient-poor soils (Becker *et al.* 1999), as well as in other forms of niche construction that do not involve nutrient input modification. For instance, plants tend to invest in either their ability to modify nutrient mineralization via litter quality or their growth ability to adapt to different soil conditions (Berendse 1994; Aerts & Chapin 2000).

This adaptive response of niche constructing plants to changes in their external environment, as illustrated in Fig. 5 by a change in I , results in the emergence of a regulatory process on evolutionary time scales. We showed that plants tend to regulate the amount of available soil nutrient through their adaptive dynamics, although only for relatively low levels of soil fertility. When nutrient input is too high, their control over the soil nutrient pool tends to vanish because their ability to consume the soil nutrient is a saturating function of their biomass. As the soil is replenished with a higher independent nutrient input, it supports a higher plant biomass. When plant biomass is high enough, the nutrient consumption by the plant population becomes approximately a linear donor-controlled function of the amount of soil nutrient (see Model description). As a consequence, plants stop controlling the soil nutrient. Several authors used detailed process-based models to describe the coupled dynamics of nitrogen fixers and non-fixers (Schwinning & Parsons 1996; Tyrrell 1999; Lenton & Klausmeier 2006). They showed that these systems are strongly self-regulated with respect to nitrogen, although in this case, regulation results from changes in species abundances instead of evolution. Jobbagy & Jackson (2004) also showed empirically how plant uplift of heavy minerals from deeper soils regulate their availability at the soil surface as a result of decades of succession of deep and shallow-rooted plants.

CONCLUSIONS AND PERSPECTIVES

Niche construction is a significant force that changes the abiotic environment, and hence the ecology and evolution of its agent. Our model reveals the ecological and evolutionary feedbacks generated by positive niche construction, and their properties. We urge theoreticians to explicitly address these feedbacks in future ecological models. The emergence of an adaptive environmental regulation, given simple trade-off between niche construction and resource exploitation, is a noteworthy outcome of niche construction.

Our model offers a simple, general platform for studying different cases of nutrient modification by plants within the broader framework of niche construction. An exciting future challenge for experimental ecology and evolution will be to test the efficiency of the ecological and evolutionary

feedbacks generated by niche construction and the sensitivity of plants' adaptive responses to natural and human-induced changes in the soil environment. Understanding the ability of plants to regulate soil nutrients may also be of high interest to ecosystem managers and agronomists aiming at sustaining soil nutrients at a desired level.

ACKNOWLEDGMENTS

We are grateful to C. de Mazancourt for her valuable help in the graphical analysis of our evolutionary model. We thank M. Perring, S. Leroux and three anonymous reviewers for constructive comments on the manuscript.

REFERENCES

- Abrams, P.A. (1986). Character displacement and niche shift analyzed using consumer–resource models of competition. *Theor. Popul. Biol.*, 29, 107–160.
- Aerts, R. & Chapin, F.S. (2000). The mineral nutrition of wild plants revisited: a re-evaluation of processes and patterns. *Adv. Ecol. Res.*, 30, 1–67.
- Becker, P., Sharbini, N. & Yahya, R. (1999). Root architecture and root:shoot allocation of shrubs and saplings in two lowland tropical forests: implications for life-form composition. *Biotropica*, 31, 93–101.
- Beddington, J.R. (1975). Mutual interference between parasites or predators and its effect on searching efficiency. *J. Anim. Ecol.*, 44, 331–340.
- Berendse, F. (1979). Competition between plant-populations with different root depths. 1. Theoretical considerations. *Oecologia*, 43, 19–26.
- Berendse, F. (1994). Litter decomposability – a neglected component of plant fitness. *J. Ecol.*, 82, 187–190.
- van Breemen, N. & Finzi, A.C. (1998). Plant–soil interactions: ecological aspects and evolutionary implications. *Biogeochemistry*, 42, 1–19.
- Callaway, R.M., Pennings, S.C. & Richards, C.L. (2003). Phenotypic plasticity and interactions among plants. *Ecology*, 84, 1115–1128.
- Canadell, J., Jackson, R.B., Ehleringer, J.R., Mooney, H.A., Sala, O.E. & Schulze, E.D. (1996). Maximum rooting depth of vegetation types at the global scale. *Oecologia*, 108, 583–595.
- Chapin, F.S., Walker, B.H., Hobbs, R.J., Hooper, D.U., Lawton, J.H., Sala, O.E. *et al.* (1997). Biotic control over the functioning of ecosystems. *Science*, 277, 500–504.
- Clark, B.R., Hartley, S.E., Suding, K.N. & de Mazancourt, C. (2005). The effect of recycling on plant competitive hierarchies. *Am. Nat.*, 165, 609–622.
- Cross, A.F. & Schlesinger, W.H. (1999). Plant regulation of soil nutrient distribution in the northern Chihuahuan Desert. *Plant Ecol.*, 145, 11–25.
- De Angelis, D.L., Goldstein, R.A. & Oneill, R.V. (1975). Model for trophic interaction. *Ecology*, 56, 881–892.
- Free, A. & Barton, N.H. (2007). Do evolution and ecology need the Gaia hypothesis? *Trends Ecol. Evol.*, 22, 611–619.
- Geritz, S.A.H., Metz, J.A.J., Kisdi, E. & Meszina, G. (1997). Dynamics of adaptation and evolutionary branching. *Phys. Rev. Lett.*, 78, 2024–2027.
- Han, X.Z., Li, Z.Z., Hui, C. & Zhang, F. (2006). Polymorphism maintenance in a spatially structured population: a two-locus genetic model of niche construction. *Ecol. Model.*, 192, 160–174.
- Hastings, A., Byers, J.E., Crooks, J.A., Cuddington, K., Jones, C.G., Lambrinos, J.G. *et al.* (2007). Ecosystem engineering in space and time. *Ecol. Lett.*, 10, 153–164.
- Hui, C. & Yue, D.X. (2005). Niche construction and polymorphism maintenance in metapopulations. *Ecol. Res.*, 20, 115–119.
- Jobbagy, E.G. & Jackson, R.B. (2004). The uplift of soil nutrients by plants: biogeochemical consequences across scales. *Ecology*, 85, 2380–2389.
- Jones, C.G., Lawton, J.H. & Shachak, M. (1994). Organisms as ecosystem engineers. *Oikos*, 69, 373–386.
- Jones, C.G., Lawton, J.H. & Shachak, M. (1997). Positive and negative effects of organisms as physical ecosystem engineers. *Ecology*, 78, 1946–1957.
- Knops, J.M.H., Bradley, K.L. & Wedin, D.A. (2002). Mechanisms of plant species impacts on ecosystem nitrogen cycling. *Ecol. Lett.*, 5, 454–466.
- van de Koppel, J., Herman, P.M.J., Thoolen, P. & Heip, C.H.R. (2001). Do alternate stable states occur in natural ecosystems? Evidence from a tidal flat. *Ecology*, 82, 3449–3461.
- Laland, K.N. & Sterelny, K. (2006). Seven reasons (not) to neglect niche construction. *Evolution*, 60, 1751–1762.
- Laland, K.N., Odling-Smee, F.J. & Feldman, M.W. (1999). Evolutionary consequences of niche construction and their implications for ecology. *Proc. Natl Acad. Sci. USA*, 96, 10242–10247.
- Lenton, T.M. & Klausmeier, C.A. (2006). Co-evolution of phytoplankton C:N:P stoichiometry and the deep ocean N:P ratio. *Biogeosci. Discuss.*, 3, 1023–1047.
- Levins, R. (1963). Theory of fitness in a heterogeneous environment. 1. Developmental flexibility and niche selection. *Am. Nat.*, 97, 75–90.
- Lewontin, R.C. (1978). Adaptation. *Sci. Am.*, 239, 212–230.
- Loreau, M. & Holt, R.D. (2004). Spatial flows and the regulation of ecosystems. *Am. Nat.*, 163, 606–615.
- Marcos, G.M. & Lancho, J.F.G. (2002). Atmospheric deposition in oligotrophic Quercus pyrenaica forests: implications for forest nutrition. *Forest. Ecol. Manag.*, 171, 17–29.
- Marschner, H. (1995). *Mineral Nutrition of Higher Plants*. Academic Press, London.
- de Mazancourt, C. & Dieckmann, U. (2004). Trade-off geometries and frequency-dependent selection. *Am. Nat.*, 164, 765–778.
- Menge, D.N.L., Levin, S.A. & Hedin, L.O. (2008). Evolutionary tradeoffs can select against nitrogen fixation and thereby maintain nitrogen limitation. *Proc. Natl Acad. Sci. USA*, 105, 1573–1578.
- Metz, J.A.J., Geritz, S.A.H., Meszina, G., Jacobs, F.J.A. & van Heerwaarden, J.S. (1996). Adaptive dynamics, a geometrical study of the consequences of nearly faithful reproduction. In: *Stochastic and Spatial Structures of Dynamical Systems* (eds van Strien, S.J. & Verduyn, S.M.). Lunel, KNAW Verhandlungen, Amsterdam, pp. 183–231.
- Miller, H.G., Miller, J.D. & Cooper, J.M. (1980). Biomass and nutrient accumulation at different growth-rates in thinned plantations of Corsican pine. *Forestry*, 53, 23–39.
- Neyra, C.A. (1978). Interactions of plant photosynthesis with dinitrogen fixation and nitrate assimilation. In: *Limitations and Potentials for Biological Nitrogen Fixation in the Tropics* (eds

- Dobereiner, J., Burris, R.H., Hollaender, A., Franco, A.A., Neyra, C.A. & Scott, D.B. (1999). Plenum, New York, pp. 111–120.
- Odling-Smee, F.J., Laland, K.N. & Feldman, M.W. (1996). Niche construction. *Am. Nat.*, 147, 641–648.
- Odling-Smee, F.J., Laland, K.N. & Feldman, M.W. (2003). *Niche Construction – The Neglected Process in Evolution*. Princeton University Press, Princeton, NJ.
- Parsons, A.J., Abrahams, A.D. & Simanton, J.R. (1992). Microtopography and soil-surface materials on semiarid piedmont hillslopes, Southern Arizona. *J. Arid Environ.*, 22, 107–115.
- Pastor, J., Aber, J.D., McLaugherty, C.A. & Melillo, J.M. (1984). Above-ground production of N and P cycling along a nitrogen mineralization gradient on Blackhawk island, Wisconsin. *Ecology*, 65, 256–268.
- Peoples, M.B. & Craswell, E.T. (1992). Biological nitrogen-fixation – investments, expectations and actual contributions to agriculture. *Plant Soil*, 141, 13–39.
- Rietkerk, M. & van de Koppel, J. (1997). Alternate stable states and threshold effects in semi-arid grazing systems. *Oikos*, 79, 69–76.
- Rueffler, C., Van Dooren, T.J.M. & Metz, J.A.J. (2006). The evolution of resource specialization through frequency-dependent and frequency-independent mechanisms. *Am. Nat.*, 167, 81–93.
- Scholz, F.G., Bucci, S.J., Goldstein, G., Meinzer, F.C. & Franco, A.C. (2002). Hydraulic redistribution of soil water by neotropical savanna trees. *Tree Physiol.*, 22, 603–612.
- Schwinning, S. & Parsons, A.J. (1996). A spatially explicit population model of stoloniferous N-fixing legumes in mixed pasture with grass. *J. Ecol.*, 84, 815–826.
- Tyrrell, T. (1999). The relative influences of nitrogen and phosphorus on oceanic primary production. *Nature*, 400, 525–531.
- Vitousek, P.M. & Field, C.B. (1999). Ecosystem constraints to symbiotic nitrogen fixers: a simple model and its implications. *Biogeochemistry*, 46, 179–202.
- Vitousek, P.M. & Howarth, R.W. (1991). Nitrogen limitation on land and in the sea – how can it occur. *Biogeochemistry*, 13, 87–115.
- Vitousek, P.M., Walker, L.R., Whiteaker, L.D., Muellerdombois, D. & Matson, P.A. (1987). Biological invasion of *Myrica faya* alters ecosystem development in Hawaii. *Science*, 238, 802–804.
- Wilson, J.B. & Agnew, A.D.Q. (1992). Positive-feedback switches in plant-communities. *Adv. Ecol. Res.*, 23, 263–336.

SUPPORTING INFORMATION

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

Appendix S1 Ecological equilibria and feasibility conditions.
Appendix S2 Analytical study of the evolutionary dynamics.

Please note: Blackwell publishing are not responsible for the content or functionality of any supporting materials supplied by the authors. Any queries (other than missing material) should be directed to the corresponding author for the article.

Editor, Shahid Naeem

Manuscript received 9 May 2008

Manuscript accepted 5 June 2008