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Patch Dynamics, Persistence, and Species Coexistence in Metaecosystems

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abstract: We add an ecosystem perspective to spatially structured communities subject to colonization-extinction dynamics. We derive a plant-based metaecosystem model to analyze how the spatial flows of the biotic and abiotic forms of a limiting nutrient affect persistence and coexistence. We show that the proportion of patches supporting plants in a region has a considerable impact on local nutrient dynamics. Then we explicitly couple nutrient dynamics to patch dynamics. Our model shows strong feedback between local and regional dynamics mediated by nutrient flows. We find that nutrient flows can have either positive or negative effects on species persistence and coexistence. The essential feature of this local-regional coupling is the net direction of the nutrient flows between occupied and empty patches. A net flow of nutrients from occupied to empty patches leads to indirect facilitative interactions, such as an inferior competitor promoting the persistence of a superior competitor. We show that nutrient flows affect the potential diversity of the metaecosystem and key features of plant community dynamics, such as the shape of the competition-colonization trade-off and successional sequences. Our analysis revealed that integrating ecosystem and spatial dynamics can lead to various indirect interactions that contribute significantly to community organization.

Keywords: metaecosystem, metacommunity, ecosystem ecology, nutrient recycling, patch dynamics, coexistence.

Introduction

Understanding local community interactions has been a focus of community ecology, but recently ecologists have begun to investigate the reciprocal effects between the emergent regional properties of a metacommunity and local dynamics (reviewed in Holyoak et al. 2005). The metapopulation and metacommunity frameworks have been successful at addressing questions related to species persistence and coexistence in spatially structured communities (e.g., Tilman 1994; Bolker and Pacala 1999; Hanski 1999; Hubbell 2001; Mouquet and Loreau 2002; Abrams and Wilson 2004). However, these studies have mostly been restricted to the biotic components of ecosystems. A related body of research has demonstrated that ecosystems are best understood by explicitly accounting for the overall functioning of the system composed of both biotic and abiotic components (DeAngelis 1992; Jones and Lawton 1995; Loreau et al. 2002; Wardle 2002; Daufresne and Hedin 2005). Therefore, we may gain insight in spatial ecosystem ecology by integrating biotic and abiotic elements into a single coherent framework (see Loreau et al. 2003; Holt 2004; Loreau and Holt 2004; Leroux and Loreau 2008).

Spatial flows of organisms and materials are maintained by the heterogeneous spatial distribution of the different ecosystem compartments. Heterogeneity at the landscape level can be imposed by spatial variation of the environment, for example, temperature or nutrient supply rate. Because of the regional mass-balance constraint (Loreau et al. 2003), flows between a high-quality location and a low-quality location will affect their source-sink dynamics (Gravel et al. 2010). Alternatively, landscape heterogeneity can result from ecological processes themselves. Most landscapes are characterized by disturbances that create spatial heterogeneity in community structure. Local disturbances generate a mosaic of communities driven by ecological processes of succession (Watt 1947), which may structure landscapes over decades to centuries (Turner 2005). Interactions between neighboring ecosystems can further affect the ecological succession initiated by disturbance. For example, differential arrival of seeds from neighboring ecosystems may influence the sequence of community assembly during ecological succession. The patch dynamics model is a popular representation of such

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macroscopic dynamics of species within landscapes (Hastings 1980; Tilman 1994). Although it is very successful at synthesizing the regional dynamics of a metacommunity, this model does not account for the feedback of regional properties into local dynamics. Because spatial flows of material, energy, and organisms across ecosystem boundaries are ubiquitous, current patch dynamics theory must integrate the dynamical feedbacks between ecosystem and species-level processes.

Margalef (1963, 1968) built on the existence of such feedbacks between local and metaecosystem dynamics to propose that the exchange of resources and organisms between communities could influence colonization and species replacement dynamics. In this study, we build on this hypothetical feedback to explore the consequences of the spatial flows of a limiting nutrient on assembly dynamics in a competitive and spatially structured plant-based ecosystem. The objective of this study is to relate spatial flows of a limiting nutrient to persistence and coexistence in a plant metaecosystem. We first analyze a simple nutrient-plant-detritus ecosystem in a structured landscape to understand the consequences of spatial occupancy by a resident plant species for the ability of invaders to establish. We then expand this model to a multispecies patch dynamics model, following Hastings (1980) and Tilman (1994). We derive conditions for regional persistence of a single plant species and for the coexistence of two plant species and multispecies assemblages. Complex feedbacks emerge from the integration of nutrient and regional dynamics, leading to novel and counterintuitive community dynamics. Our results suggest that spatial flows of the soil solution and the litter—and, more generally, of inorganic and organic nutrients—could have considerable impacts on plant diversity and successional dynamics.

Model Description

We derive a model for plant spatial dynamics with explicit nutrient recycling. The model is, however, sufficiently general to apply to a broad range of organisms, from plants to animals, that obey patch dynamics (Leibold et al. 2004). The model has two distinctive dynamics and scales (see fig. 1). At the local scale, the model describes the dynamics of nutrient uptake by the plants and the dynamics of the nutrient's recycling. Within each locality (called a patch), plants deplete the limiting inorganic nutrient to support their growth. A patch could support from one to several plant individuals (Hastings 1980; Tilman 1994). The nutrient sequestered in the plant biomass is returned to the detritus compartment following natural death of tissues and individuals, from which is in turn mineralized to the inorganic-nutrient compartment. At the regional scale, nutrient dynamics is implemented through flows of the inorganic nutrient and detritus among patches. The inorganic nutrient diffuses among patches through the soil solution (root foraging also imposes a spatial flow of the inorganic nutrient, although the model is not specifically designed to account for this process). The detritus diffuses among patches through litter dispersal or translocation (e.g., by wind, macrofauna, or water runoff). We first analyze the model by imposing the fraction of occupied and empty patches. We then expand the model to explicitly describe patch dynamics—that is, the proportion of the region that is either occupied or empty—as a result of colonization and disturbance events.

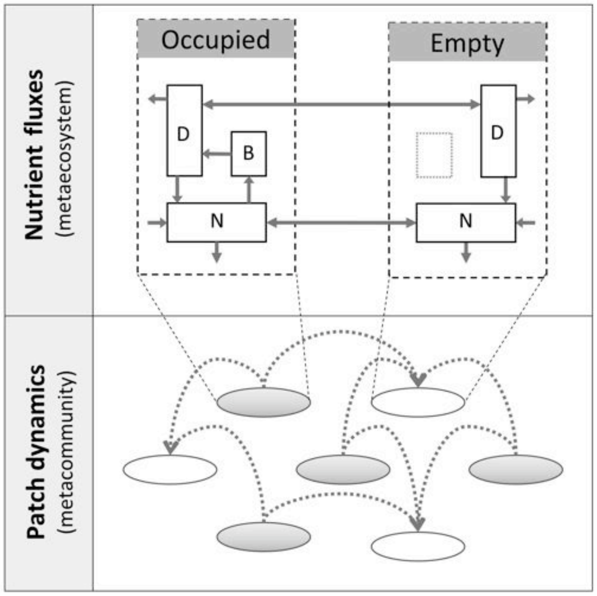

Figure 1: Schematic representation of the model structure. The model has two distinctive dynamics and scales. At the local scale, the model describes the dynamics of nutrient uptake by primary producers and nutrient recycling. The boxes represent the different ecosystem compartments, and the arrows represent the flows between them. The model represents the spatial structure of the metaecosystem by considering occupied and empty patches. At the regional scale, the model describes the dynamics of spatial occupancy on the basis of colonization and disturbance dynamics.

We are interested in the effects on persistence and coexistence of nutrient flows between occupied and empty patches. Nutrient concentration is lower in occupied patches because the plant consumes the inorganic nutrient (Tilman 1982). Consequently, the inorganic nutrient will passively flow along concentration gradients from empty to occupied patches. In contrast, plants are by definition absent from empty patches, and thus the detritus plants produce will tend to move from occupied to empty patches. Any inequality between these flows will create net nutrient importer and exporter patches. As a consequence, these flows are predicted to influence both the productivity of the resident species and the nutrient availability in empty patches (Gravel et al. 2010). We now detail our implementation of local and regional dynamics.

Nutrient Fluxes

We expand a local plant-based ecosystem model (nutrient-plant-detritus; DeAngelis 1992; Loreau 1998) to the regional scale, with spatial heterogeneity arising among occupied and empty patches. The nutrient could be in an inorganic form (e.g., inorganic N or P) or sequestered in live and dead biomass. Nutrients are exchanged between occupied and empty patches, occupying the fractions p and $1 - p$, respectively, of the region. Full details of the model analysis are provided in appendix A in the online edition of the American Naturalist.

The plant and detritus biomasses are assumed to be proportional to their nutrient contents. The model consequently describes the dynamics of the nutrient stocks across trophic compartments. The plant biomass of species i in patch x is B_{xi}. The inorganic nutrient and detritus compartments in occupied (index o) and empty (index e) patches are N_{xo} and N_{xe} and D_{xo} and D_{xe}, respectively. The metaecosystem is open to nutrient inputs and outputs. The inorganic-nutrient compartment in each local patch receives external inputs (e.g., atmospheric depositions, rock alteration) at rate I and is exported out of the metaecosystem at rate e_{N} (e.g., in-depth nutrient leaching). The plants consume the inorganic nutrient in a patch at rate a_i and die at rate b_i. Dead plant tissue (e.g., foliage) and individuals are completely incorporated into the local detritus compartment. The detritus is mineralized at rate r. A fraction of the detritus is lost from the ecosystem at rate e_{D} (e.g., because of transformation into recalcitrant dead organic matter; Moore et al. 2004).

The nutrient and detritus diffuse among patches at rates d_{N} and d_{D}, respectively. This dispersal function describes the balance between the outflows from and the inflows into a patch. It models passive spatial flows, such as water circulation in soils and leaf litter dispersal (e.g., Gomez-Aparicio and Canham 2008), or passive animal dispersal, such as excretion by large herbivores (e.g., Seagle 2003). These flows could vary by several orders of magnitude, from peatlands, where the soil solution is rich in dissolved organic matter and flows much faster than the mosses, up to forests with heavy soils, where the leaf litter dispersal is much more important than the flows from the soil solution. The model does not account for the spatially explicit distribution of the empty and occupied patches. We focused on global spatial flows for analytical tractability, but also to better highlight the impacts of nutrient exchanges. Spatially explicit dynamics are susceptible to forming spatial patterns (Rietkerk and van de Koppell 2008), which are important but beyond the scope of this study. We also assume that seed size is negligible compared with total biomass, which enables us to ignore nutrient transport through seed dispersal and focus explicitly on the consequences of spatial flows of materials (simulations revealed that the results are qualitatively unaffected by the spatial flows of nutrients contained in seeds; see app. B in the online edition of the *American Naturalist* and Gravel et al. 2010). The model is represented by the following dynamical equations:

$$
\begin{aligned}
\frac{dN_{xo}}{dt} &= I - e_{\mathrm{N}}N_{xo} - \sum_i a_iN_{xo}B_{xi} + rD_{xo} - d_{\mathrm{N}}(N_{xo} - \overline{N}),\\
\frac{dN_{xe}}{dt} &= I - e_{\mathrm{N}}N_{xe} + rD_{xe} - d_{\mathrm{N}}(N_{xe} - \overline{N}),\\
\frac{dB_{xi}}{dt} &= a_iN_{xo}B_{xi} - b_iB_{xi},\\
\frac{dD_{xo}}{dt} &= \sum_i b_iB_{xi} - rD_{xo} - e_{\mathrm{D}}D_{xo} - d_{\mathrm{D}}(D_{xo} - \overline{D}),\\
\frac{dD_{xe}}{dt} &= -rD_{xe} - e_{\mathrm{D}}D_{xe} - d_{\mathrm{D}}(D_{xe} - \overline{D}),
\end{aligned}
\tag{1}
$$

where

$$
\begin{aligned}
\overline{N} &= pN_{xo} + (1 - p)N_{xe},\\
\overline{D} &= pD_{xo} + (1 - p)D_{xe},
\end{aligned}
$$

and where the overbar (e.g., $\overline{N}$, $\overline{D}$) denotes a regional average. At equilibrium, the inflows balance the outflows. We solve the system of equations (1) to determine the equilibrium densities of each compartment.

The inorganic-nutrient availability in empty patches is a critical quantity that determines the ability of an inferior competitor to invade empty patches and thus coexist with resident species. It also informs us on the direction of the net flow between occupied and empty patches (Gravel et al. 2010). A net flow toward empty patches results in an increased equilibrium nutrient concentration in empty patches ($\hat{N}_{xe}$) above its expected value in absence of spatial flows (i.e., $\hat{N}_{xe} > I/e_{\mathrm{N}}$). For a plant species to persist in a single patch, the nutrient concentration in an empty patch must be larger than the minimum nutrient concentration required for positive population growth (the R^* rule; Tilman 1982). At equilibrium, this critical nutrient concentration for persistence in an occupied patch is $N_i^* =$

b_i/a_i. Equivalently, $N_i^* < \hat{N}_{xe}$ is the condition for a plant species to sustain a viable population in an empty patch.

We now analyze the effect of spatial nutrient flows on nutrient concentration in empty patches. We are more specifically interested in parameter values marking the reversal of net nutrient flow: from the situation where the nutrient flows from occupied to empty patches (benefiting the empty patches) to the situation where it flows from empty to occupied patches (benefiting the occupied patches). The difference between nutrient concentrations in empty patches in the presence and in the absence of spatial flows tells us whether the spatial flows enrich or impoverish empty patches. This transition can be formulated as a critical ratio of diffusion rates, $(d_D/d_N)^*$, by first setting $\hat{N}_{xe} - I/e_N = 0$ and then solving for d_D/d_N, yielding

$$\left(\frac{d_D}{d_N}\right)^* = \frac{-e_D(r + e_D)}{d_N e_D - r e_N}. \tag{2}$$

The spatial flow of the nutrient will enrich the empty patches, provided that $(d_D/d_N) > (d_D/d_N)^*$ (fig. 3*A*, 3*B*). This mechanism is also robust to nonlinear Type II functional responses for the plants (Gravel et al. 2010). Low recycling and output rates (r, e_N, and e_D) and low inorganic nutrient flow promote enrichment of the empty patches (eq. [2]; fig. 3*A*, 3*B*). Note that neither the resident species performance (N_i^*) in occupied patches, the patch fertility (nutrient input rate I), nor the spatial occupancy p are found in this criterion. This means that the direction of the net flow between empty and occupied patches depends on only the diffusion rates and the recycling efficiency. The magnitude of the enrichment (or impoverishment), however, is affected by these parameters (app. A; fig. 2). The flows also affect the equilibrium biomass in the occupied patches, as for a given spatial occupancy, p, an elevated d_D/d_N has a negative effect on local population size (fig. 3*C*, 3*D*). Because detritus flows from occupied to empty patches, it reduces the amount of nutrients available for growth and thus the equilibrium local plant biomass.

The criterion given in equation (2) is critical in order to understand the mechanism underlying subsequent results on the impact of spatial nutrient flows on persistence and coexistence. It determines whether the presence of a plant in the region increases or reduces nutrient availability in empty patches and, in return, how this feeds back to local plant biomass. The criterion in equation (2) determines whether the net nutrient flow is from occupied to empty patches or vice versa. Because the spatial occupancy has an important effect on the properties of both occupied and empty patches (fig. 2), we expect a strong feedback between nutrient dynamics and patch dynamics.

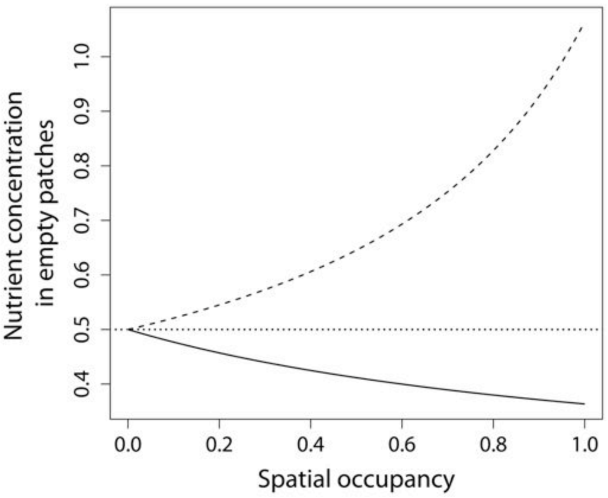

Figure 2: Effects of spatial occupancy on the available nutrient concentration in empty patches. *Solid line*, diffusion of detritus $d_D = 0.001$ (smaller than the $(d_D/d_N)^*$ threshold criteria for facilitative effect); *dashed line*, $d_D = 0.1$ (larger than the $(d_D/d_N)^*$ threshold criteria for facilitative effect). The horizontal dotted line represents the equilibrium nutrient concentration in the absence of consumption (I/e_N). Other parameter values are as follows: $I = 0.05$, $e_N = 0.1$, $e_D = 0.01$, $d_N = 0.1$, $r = 0.1$, $a = 1$, $b = 0.2$.

Patch Dynamics

We now relax the assumption of p as a fixed parameter to extend our metaecosystem model to the patch-dynamical perspective of metacommunity theory (Leibold et al. 2004). Our first objective is to relate among-patch nutrient flows (inorganic and organic forms, d_N and d_D) to metapopulation and metacommunity properties. Then we generalize our analysis to the multispecies assembly dynamics in a metaecosystem.

Metapopulation Persistence

We couple spatial occupancy to ecosystem dynamics, using Levins's metapopulation model (Levins 1969; Hanski 1999), where change in spatial occupancy p of patches is simply given by

$$\frac{dp}{dt} = cp(1 - p) - mp, \tag{3}$$

where c is the colonization rate (equivalent to the number of seeds produced per patch) and m is the disturbance (or extinction/mortality) rate. Central to metapopulation the-

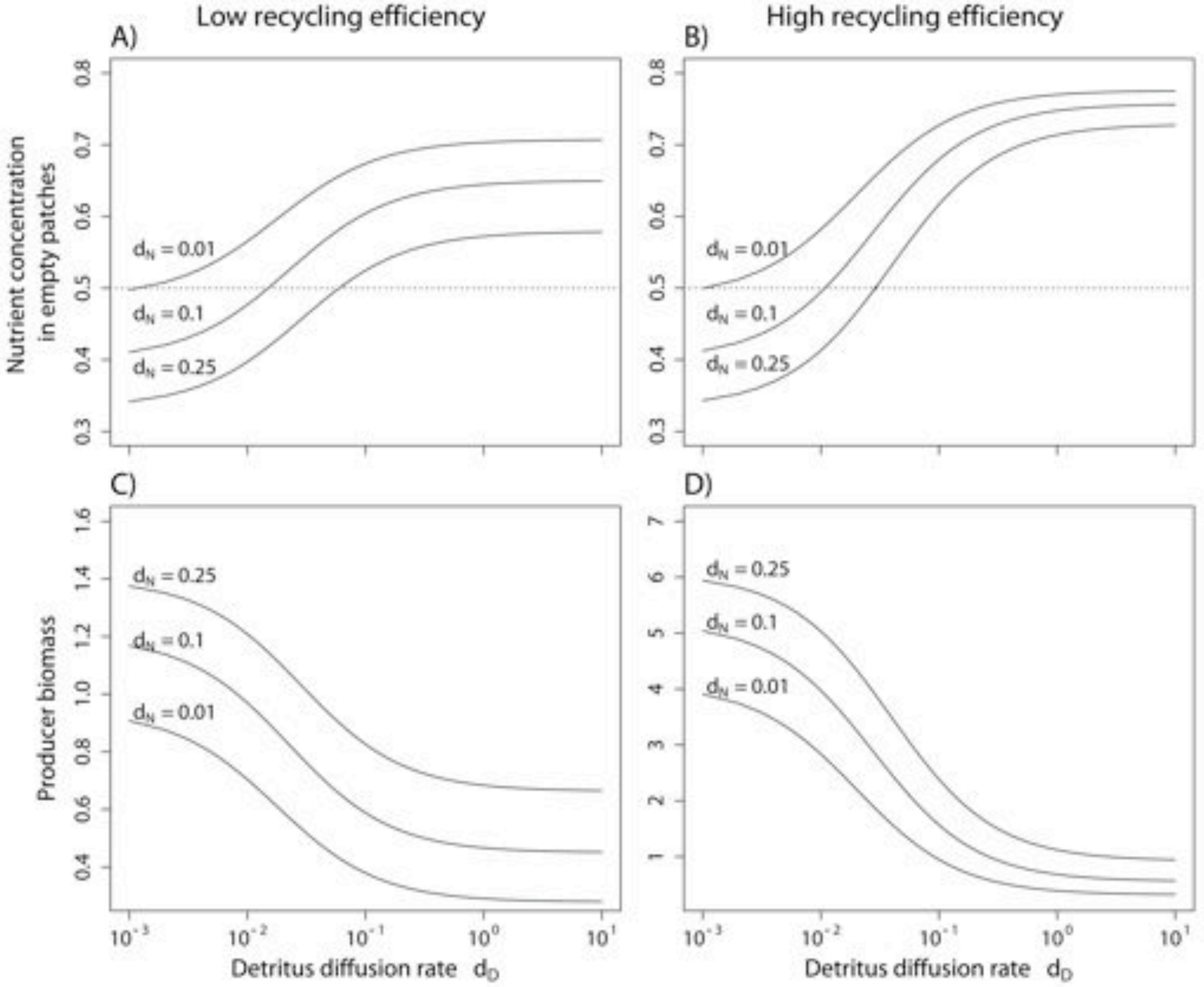

Figure 3: Effects on ecosystem properties of the ratio of indirect to direct nutrient diffusion. *A*, *B*, Nutrient concentration in empty patches. *C*, *D*, Plant biomass in occupied patches. Parameter values are the same as for figure 2, except for the recycling rate, which is $r = 0.05$ and 0.25 for the low and the high recycling efficiency, respectively. Spatial occupancy is fixed at $p = 0.5$. The horizontal dotted line represents the equilibrium nutrient concentration in absence of consumption (I/e_N).

ory is the idea that a metapopulation will persist in the region, despite local extinctions, given that the colonization rate is larger than the critical colonization rate $c^* = m$. At equilibrium there are always empty patches, and the proportion of the region that is occupied is given by $1 - m/c$. The model has been discussed in depth elsewhere (see Hastings and Harrison 1994; Hanski 1999; Mouquet et al. 2005), and thus we will restrict our discussion to its extension to metaecosystem dynamics.

It was shown above that spatial occupancy affects local nutrient availability and plant biomass (fig. 2). The reproductive output in a single location should depend on local plant biomass, and given the above results, it should also depend on spatial occupancy. We explore this idea by expanding the Levins metapopulation model to include the effect of local plant biomass on colonization rate (dropping the i subscript for this section on metapopulation):

$$\frac{dp}{dt} = c'p(1 - p) - mp, \tag{4}$$

where the effective colonization rate (the number of seeds produced per patch) is defined as the product of the number of seeds produced per unit of biomass and the biomass ($c' = cB$). This constitutes the only addition to the Levins model to couple nutrient and patch dynamics. The original metapopulation framework assumes that properties of local populations are invariant to regional properties (B is independent of p), and it includes no explicit term for local biomass B. Because spatial occupancy p influences the biomass in a local patch, we consequently expect a feedback between nutrient and regional dynamics.

We emphasize that this approach assumes different timescales between local nutrient and regional dynamics (Levins 1969; Hastings 1980; Tilman 1994; Hanski 1999). In other words, the nutrient stocks in the various compartments of occupied and empty patches reach equilibrium between colonization/disturbance events. We explored how sensitive our results are to this assumption and found that, except when regional dynamics is very fast relative to local nutrient dynamics, resulting in frequent occurrence of disturbances, this assumption does not fundamentally alter our predictions (see app. B). When the pace of regional dynamics is increased relative to that of local dynamics, the predicted spatial occupancy and distribution of nutrient stocks remain close to the analytical predictions until a threshold is reached, and suddenly spatial occupancy collapses and the plant metapopulation becomes extinct. The explanation for this phenomenon is simple: when disturbances become too frequent, local populations do not have the time to build up after a disturbance, which prevents their reproduction and thus their persistence. This threshold rate thus gives us an indication of what should be considered as the minimal timescale separation for metapopulation persistence. It is unlikely that metapopulations near or beyond this threshold rate would be found in nature, as the disturbance return interval would be too small to allow the development and reproduction of the local plant populations. Plant communities that persist in nature have the time to develop until a disturbance occurs (e.g., forest stands do have time to reach maturity until a fire reinitiates succession).

The plant metapopulation will persist, given two conditions: (1) a single seed must be able to develop a viable population on an empty patch (the local invasion criterion defined above) and (2) the metapopulation must persist despite colonization/disturbance dynamics. The first criterion is met if $N^* < I/e_N$. For the second criterion, when a plant invades a landscape, it must grow enough to produce seeds and disperse. The above results show that the amount of nutrients in the few patches a plant initially colonizes depends on the spatial context. Consequently, the number of seeds produced in the patches it colonized first (the effective colonization rate) should also depend on the spatial context. Consequently, we must solve for the equilibrium local biomass of the invading population. Once the plant has invaded a single patch at population size B_{inv} (the subscript "inv" denotes an invader), it will successfully invade the region if $c > m/B_{\mathrm{inv}}$ (eq. [4]). We solve the model of nutrient dynamics (eq. [1]) for B_{inv} by assuming that p at invasion is negligible. This simplified system corresponds to

$$\begin{aligned}\frac{dN_{\mathrm{inv}}}{dt} &= I - e_N N_{\mathrm{inv}} - aN_{\mathrm{inv}}B_{\mathrm{inv}} + rD_{\mathrm{inv}} - d_N\left(N_{\mathrm{inv}} - \frac{I}{e_N}\right),\\ \frac{dB_{\mathrm{inv}}}{dt} &= aN_{\mathrm{inv}}B_{\mathrm{inv}} - bB_{\mathrm{inv}},\\ \frac{dD_{\mathrm{inv}}}{dt} &= bB_{\mathrm{inv}} - rD_{\mathrm{inv}} - e_D D_{\mathrm{inv}} - d_D D_{\mathrm{inv}},\end{aligned} \tag{5}$$

resulting in equilibrium biomass

$$\hat{B}_{\mathrm{inv}} = \frac{(e_N + d_N)(Ia - e_N b)(r + e_D + d_D)}{ame_N(e_D + d_D)}.$$

The critical colonization rate for metapopulation persistence thus becomes

$$c^* = \frac{mabe_N(e_D + d_D)}{(e_N + d_N)(Ia - e_N b)(r + e_D + d_D)}. \tag{6}$$

Now the spatial nutrient flows of the inorganic nutrient (d_N) and of detritus (d_D) determine the critical colonization rate for metapopulation persistence. By comparing the critical colonization rate given by equation (6) with and without spatial flows of resource and detritus, we find that $(d_D/d_N)^*$ (given in eq. [2]) marks the transition between positive and negative effects of spatial nutrient flows on metapopulation persistence. The persistence is enhanced when nutrients flow from empty to occupied patches (i.e., $(d_D/d_N) < (d_D/d_N)^*$). This slight addition to the Levins model provides us with our first important result for the dynamics of spatially connected ecosystems: metapopulation persistence is promoted by a net flow of nutrients from the empty to the occupied patches.

Metacommunities: Two-Species Coexistence

Disturbance-colonization dynamics prevent the complete occupancy of the landscape by the plant and leave unoccupied patches available for colonization by other species (Hastings 1980; Tilman 1994). The multispecies extension of the Levins model predicts that a very high number of species will coexist on a landscape subject to colonization-extinction dynamics, given a strict ordination of species traits along a competition-colonization tradeoff axis (Tilman 1994). Like the Levins model, the Hastings-Tilman model does not explicitly account for local dynamics. It assumes immediate replacement of inferior competitors when a superior competitor reaches a patch that is already occupied, presumably as a result of resource competition. There is thus only the implicit condition of a competition-colonization (c/N^*) trade-off, since the mechanism of resource competition is never defined. This limitation has been criticized because of the very stringent definition of competition (see Calcagno et al. 2006). Instead, our framework explicitly describes ecosystem processes underlying the competition-colonization trade-off necessary for coexistence because resource competition is treated mechanistically. In the following analysis, we identify two mechanisms by which nutrient flows between communities influence the regional coexistence of a weak local competitor for the nutrient (referred to as the weak competitor, for simplicity) with a strong local competitor for the nutrient (referred to as the strong competitor). First, at the local scale, the weak competitor species must be able to invade an empty patch; specifically, to have a positive growth rate, its N^* must be smaller than the nutrient concentration in the patch it colonizes. Second, at the regional scale, the weak competitor must be able to persist; therefore, the effective colonization rate must be higher than the disturbance rate.

Consider a two-species situation with a strong competitor (labeled 1) and a weak competitor (labeled 2). If we assume that nutrient dynamics are much faster than regional dynamics, the weak competitor will be able to colonize only vacant patches (with high nutrient levels), while the strong competitor will be able to colonize both empty and occupied patches. The strong competitor will rapidly displace the weak competitor by lowering the nutrient availability in the patches it occupies. The regional dynamics for the two species is then

$$\frac{dp_1}{dt} = c_1' p_1(1 - p_1) - mp_1,$$

$$\frac{dp_2}{dt} = c_2' p_2(1 - p_1 - p_2) - mp_2 - c_1' p_1 p_2, \qquad (7)$$

where again the effective colonization rate is the product of the biomass ($c_i' = c_i B_i$) and the number of seeds produced per unit biomass. The strong competitor is not directly influenced by the weak competitor, although (in contrast to the Hastings-Tilman model) the total spatial occupancy ($p_1 + p_2$) indirectly influences its local biomass B_1 via spatial nutrient flows (figs. 3, 4). The weak competitor, however, directly interacts with the strong competitor, as it can colonize only unoccupied patches (first term) and is competitively excluded from the patches occupied by the strong competitor (second term).

The relative importance of inorganic-nutrient and detritus flows (d_D/d_N) affects the capacity of a weak competitor to coexist with a strong competitor on the landscape. To assess coexistence, we solve the equilibrium nutrient availability in the empty patches and spatial occupancy in the presence the strong competitor. The spatial occupancy is considered to be constant when nutrient flows at equilibrium are assessed, and, similarly, the equilibrium local biomass is considered to be constant when patch dynamics is assessed. In doing so, we find the equilibrium spatial occupancy (fig. 4*A*, 4*B*) of the resident plant species (denoted by the subscript "res") by solving equation (1) for the biomass B_{res} at equilibrium as a function of spatial occupancy p_{res}. We substitute the resulting function for B_{res} into equation (4) and solve for equilibrium p_{res} (which is locally stable; app. D in the online edition of the *American Naturalist*).

The nutrient concentration in empty patches increases with d_D/d_N for fixed spatial occupancy of the resident strong competitor (fig. 3*A*, 3*B*), but the equilibrium spatial occupancy decreases with increasing d_D/d_N (fig. 4*A*, 4*B*). As the nutrient is exported outside of empty patches with increasing d_D/d_N, there are fewer nutrients for biomass and seed production, consequently reducing spatial occupancy. The nutrient recycling rate and the input and output rates determine the magnitude of the effect of d_D/d_N on the spatial occupancy. These two interacting processes result in a unimodal relationship between nutrient concentration in empty patches and d_D/d_N (fig. 4*C*, 4*D*).

A strong competitor will promote the establishment of a weak competitor in an empty patch if it increases the inorganic nutrient concentration of this patch relative to the concentration expected in an unoccupied landscape. The critical d_D/d_N for a facilitative effect is found by solving $\hat{N}_{xe}^{\text{res}} - I/e_N = 0$ for d_D/d_N. The nutrient concentration in the empty patch in the presence of the superior competitor will exceed that expected in an unoccupied landscape, provided that $(d_D/d_N) > (d_D/d_N)^*$, with $(d_D/d_N)^*$ given by equation (2). This is our second important result: nutrient availability in empty patches could increase above the critical N^* of a weak competitor by a net flow of nutrients from occupied to empty patches when a strong competitor is resident, resulting in a facilitative interaction between the strong and the weak competitor.

The direction of the net flow of nutrients between occupied and empty patches also affects the critical colonization rate of the weak competitor because it affects the biomass of the patch it invades (B_{inv}) and the availability of empty patches ($1 - p_{\text{res}}$). The biomass of the weak competitor in the patch where it invades, in the presence of a resident strong competitor, is calculated as in equation (5). The solution is algebraically complex, but we plotted it to show how the critical colonization rate for persistence of a weak competitor is modified by d_D/d_N (fig. 5*A*). The net

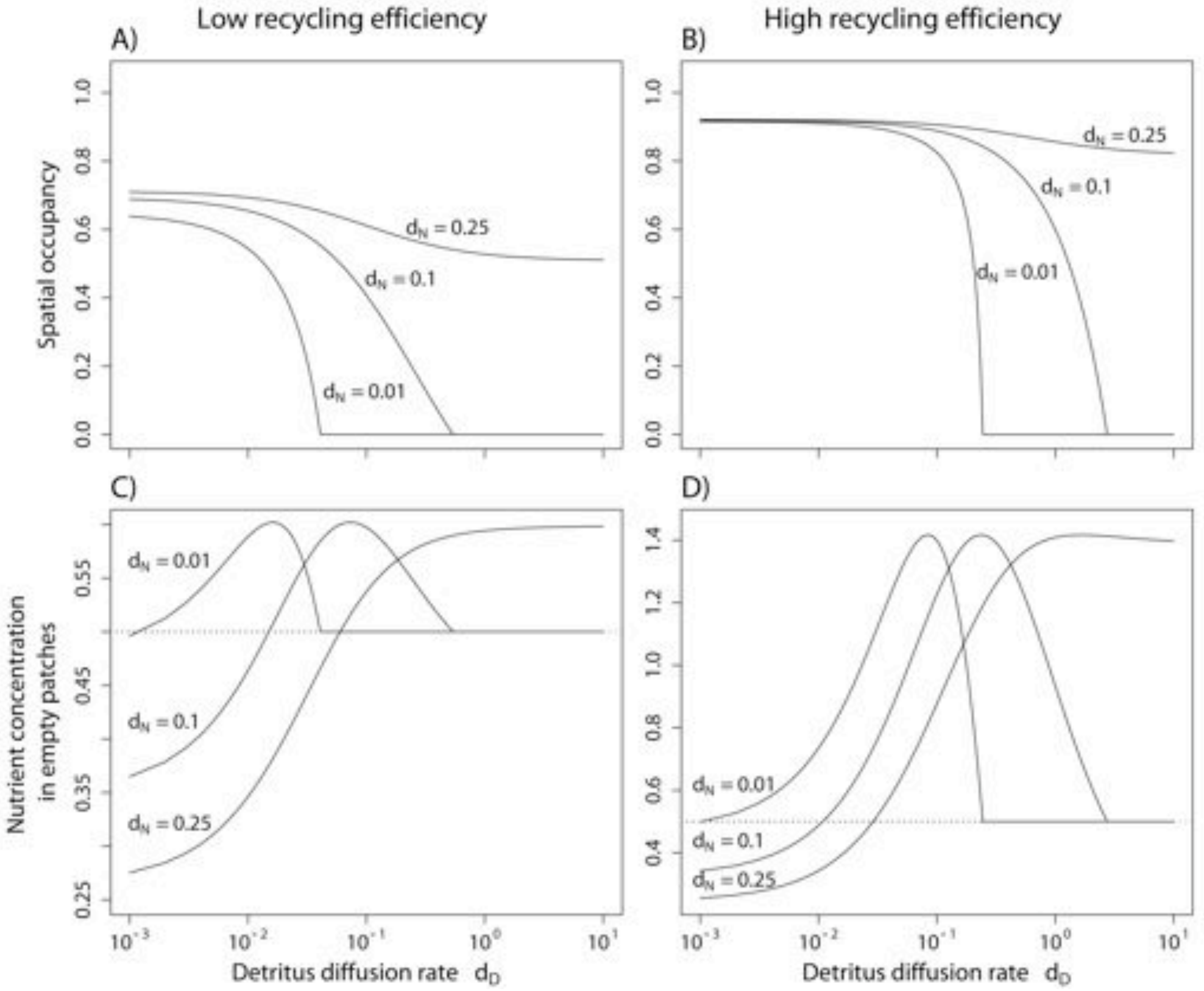

Figure 4: Effects of the ratio of indirect to direct nutrient diffusion on metapopulation properties. *A*, *B*, Spatial occupancy. *C*, *D*, Nutrient concentration in empty patches. Parameter values are as follows: $I = 0.05$, $e_N = 0.1$, $e_D = 0.01$, $d_N = 0.1$, $a = 1.5$, $b = 0.2$, $m = 0.5$, $c = 1.25$, and, for the low and the high recycling efficiency, $r = 0.05$ and 0.25, respectively. The horizontal dotted line represents the equilibrium nutrient concentration in the absence of consumption (I/e_N).

effect is a lower critical colonization rate (higher likelihood of coexistence) with increasing d_D/d_N. This is our third important result: coexistence of an inferior competitor is promoted by a net flow of nutrients from occupied to empty patches.

Interestingly, this last result also affects the persistence of the strong competitor. Under a strong disturbance regime (high *m* relative to *c*), persistence of a strong competitor can be unsuccessful because of its low colonization rate (Nee and May 1992; Tilman et al. 1994). A weak competitor can, in this case, increase the nutrient concentration in empty patches, therefore increasing the biomass of the strong competitor in the patch where invasion occurs. The presence of the weak competitor can thus promote the persistence of the strong competitor by reducing its critical colonization rate (the dotted line in fig. 5*B*). However, the strong competitor cannot completely displace the weak competitor. This situation occurs because the presence of the weak competitor is necessary to redistribute the nutrient to the patches occupied by the strong competitor and promote its effective colonization rate.

Metacommunities: N*-Species Coexistence*

The two-species model could be generalized to *N*-species metacommunities (Hastings 1980; Tilman 1994). The species are ranked from the best competitor (with the lowest

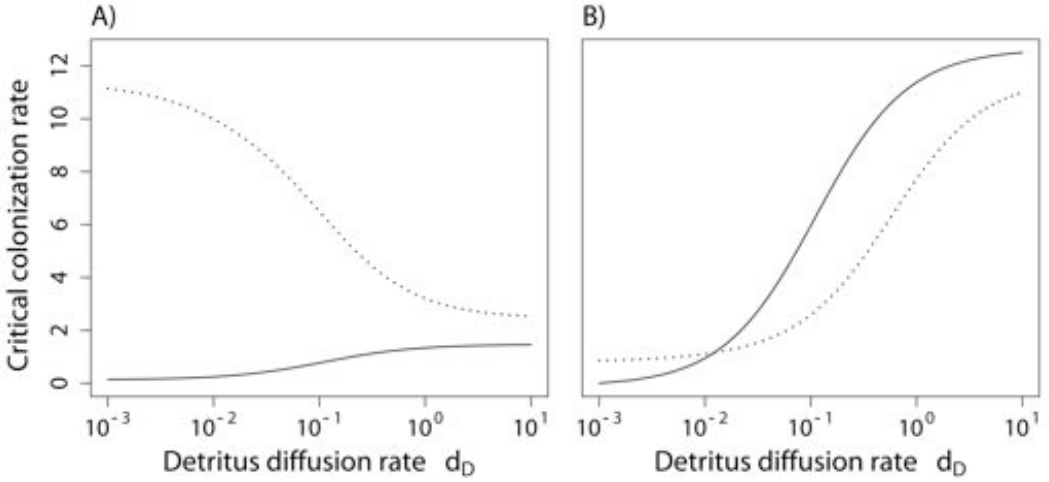

Figure 5: Effects of the ratio of indirect to direct nutrient diffusion on regional persistence. *A*, Invasion of the inferior competitor in the absence (*solid line*) and the presence (*dotted line*) of the superior competitor. *B*, Invasion of the superior competitor in the absence (*solid line*) and the presence (*dotted line*) of the inferior competitor. Parameter values are as follows: $I = 0.05$, $e_N = 0.1$, $e_D = 0.01$, $d_N = 0.1$, $r = 0.1$, $a_{sup} = 1.5$, $a_{inf} = 1.25$, $b = 0.2$, $m = 0.5$, $c_{sup} = 1.25$, $c_{inf} = 1.5$.

N^* value; species 1) to the worst. The dynamics of species i is

$$\frac{dp_i}{dt} = c_i' p_i\left(1 - \sum_{j=1}^{i} p_j\right) - mp_i - \sum_{j=1}^{i-1} c_j' p_j p_i. \tag{8}$$

Full details on the N-species model are provided in appendix C in the online edition of the *American Naturalist*.

Our model has no analytical solution for more than two species because of the incorporation of local dynamics into the metacommunity model. However, it is still possible to calculate the critical colonization rate for invasion from equations (5) and (6) after successive invasion events. To do this, we performed simulations of successive invasions, from the strongest to the weakest competitor. The community consisted of 25 species with equidistant N^* (recall $N_i^* = b_i/a_i$) ranging from 0.25 to 1.45. We calculated the critical colonization rate for a successful invasion given the equilibrium spatial occupancy of the resident community. The invading species was attributed a colonization rate corresponding to 110% of this critical colonization rate value. This value was chosen to allow persistence while preventing the resident species from occupying most of the available space.

The direction of the net spatial flow between occupied and empty patches constrains the shape of the competition-colonization trade-off required for multispecies coexistence (fig. 6*A*). With a net flow from empty to occupied patches, new colonizers require a relatively high colonization rate for a given competitive ability (N^*). This requirement is much less stringent, with a net flow from occupied to empty patches (fig. 5*A*). For a given competition-colonization trade-off (c/N^*), this will result in a positive relationship between species richness and the relative importance of nutrient and detritus flows (d_D/d_N; fig. 6*B*). As described above for two-species dynamics, this relationship arises as a consequence of two mechanisms. First, a net flow from occupied to empty patches will allow colonization of weak competitors that are otherwise unable to invade empty patches. Second, a net flow from empty to occupied patches is more stringent on the critical colonization rate for a given competitive ability N^*.

The replacement sequence illustrates the complex interplay between local and regional dynamics (fig. 7). We simulated succession sequences with 25 species constrained by the competition-colonization trade-off corresponding to the scenario of $d_D/d_N = 1$ in figure 6*A*. Initial conditions consisted of all species having equal densities. Replacement sequences are highly sensitive to the net direction of the spatial flows between occupied and empty patches. The sequence where net nutrient flow is from empty to occupied patches shows a strong negative effect of nutrient flows on coexistence (fig. 7*A*). The good colonizers that are able to invade empty patches ($N_i^* < I/e_N$) are the first species to grow in abundance. Competitive exclusion is followed by local replacement of these initial invaders by stronger competitors because of local nutrient competition. Metacommunity theory predicts that strong colonizers can reinvade newly disturbed patches following

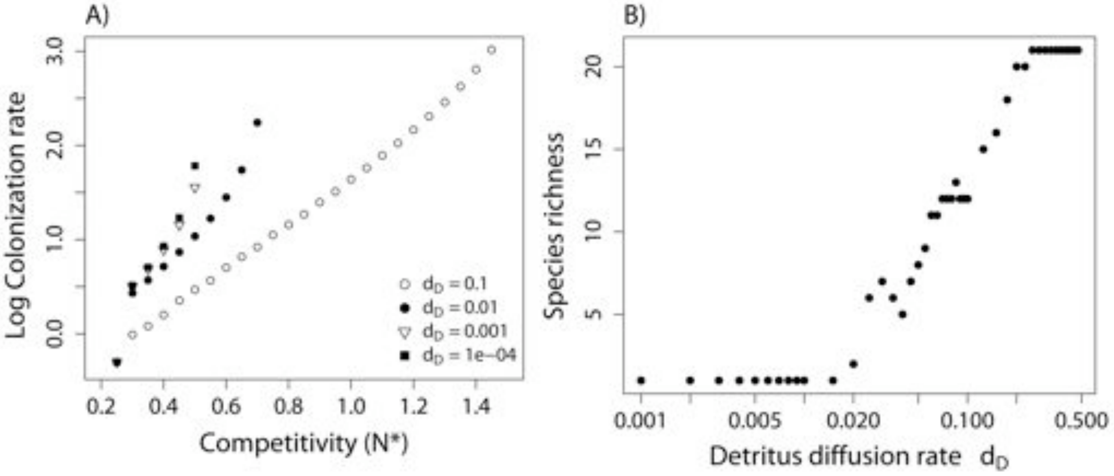

Figure 6: *A*, Simulated assemblage of a producer community for different diffusion rates of detritus, showing the required trade-off between colonization and competition. Each species of the 25-species pool is ranked by its N^* value. Assemblage proceeds from the most to the least competitive species, until a species could not invade further because of insufficient nutrient availability in the empty patches. For each species, its colonization rate is calculated as 110% of the critical colonization rate for a successful invasion, as in figure 4*A*. The numbers of coexisting species vary with the diffusion rate and are 25, 10, 6, and 6 for detritus diffusion rates (d_D) of 0.1, 0.01, 0.001, and 0.0001, respectively. Parameter values are as follows: $I = 0.075$, $e_N = 0.1$, $e_D = 0.01$, $d_N = 0.1$, $r = 0.2$, $b = 0.2$, $m = 0.6$. The colonization rate of the most competitive species is $c_0 = 0.5$. *B*, Effect of d_D/d_N on species richness for a fixed c/N^* trade-off. For the simulations, we used the c/N^* trade-off in *A* that corresponds to the case where $d_D/d_N = 1$.

local exclusion (Hastings 1980; Tilman 1994). In contrast, our metaecosystem model predicts that these fugitive dynamics are prevented at a low d_D/d_N. We can explain this reinforcement of competitive exclusion by the increase in regional abundance of the top competitor (i.e., high nutrient use efficiency). The increase in abundance concentrates nutrients in occupied patches, leading to the regional competitive exclusion of other species. This replacement sequence thus reveals a feedback between local and regional mechanisms of competitive exclusion that limits the importance of competition-colonization trade-offs as a mechanism of coexistence.

In contrast, the replacement sequence in the situation where the net nutrient flow is from occupied to empty patches shows a strong positive effect of nutrient flows on coexistence (fig. 7*B*). The facilitative effects emerging from ecosystem-community feedbacks affect the replacement sequence. The first species to invade are moderate colonizers that are able to sustain positive growth on an unoccupied metaecosystem. They initially dominate because they rapidly expand through the landscape, but they are later replaced by more competitive species with lower colonization rates. As strong competitors increase their regional abundance, they increase the spatial redistribution of the nutrient and the inorganic-nutrient availability builds up in empty patches. This enrichment of empty patches allows invasion from species that were initially unable to invade because nutrient availability was below their requirements (the good colonizers). The resulting community at equilibrium thus includes species relying on the presence of stronger competitors (fig. 7*B*). Because species with low competitive ability have high colonization rates, they increase rapidly, in abundance, simultaneously with the decrease of the more competitive species that facilitated their invasion. This increase in the abundance of weak competitors is associated with decreasing average nutrient use efficiency (as imposed by the c/N^* trade-off) and nutrient concentration in empty patches. This leads to the extinction of the weakest competitors, which initiates a second wave of colonization by more competitive and nutrient-efficient species. This pattern of successive invasion-exclusion cycles is repeated several times before a stable assemblage and equilibrium densities are eventually reached (fig. 7*B*). This leads to our fourth important result: in contrast to Tilman (1994), where only the traits of the superior competitors affect a species equilibrium abundance, here the equilibrium densities of a given species will depend on the traits of both superior and inferior competitors.

Discussion

It has long been suggested that mature ecosystems could exploit the energy accumulated in neighboring immature

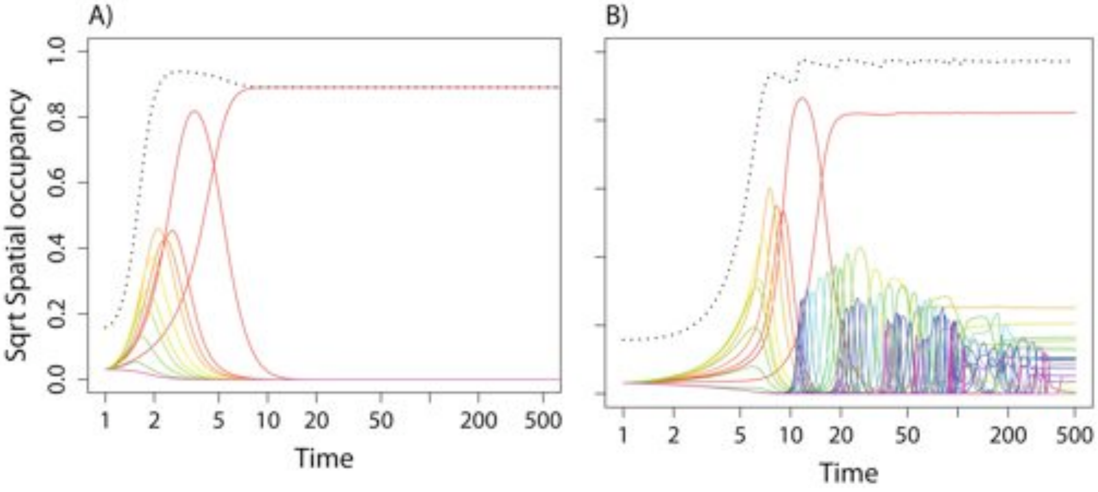

Figure 7: Simulated successional sequences of spatial occupancy. For the simulations, we used the c/N^* trade-off in figure 5*A* corresponding to the case where $d_D/d_N = 1$. Species are color coded from the most competitive (*red*) to the least competitive (*violet*). The dotted black line represents the total regional occupancy. Parameter values are as follows: in *A*, $d_D/d_N = 0.01$; in *B*, $d_D/d_N = 1$.

ones, thereby reducing or even preventing their further development (Margalef 1963, 1968). This hypothesis more generally suggests that nutrient flows between successional stages could feed back into the process of succession itself. Our study provides an explicit and formal exploration of this feedback, integrating local and regional dynamics into a metaecosystem framework. We accomplished this by coupling local (within-patch) nutrient-plant-detritus dynamics within regional dynamics of patch colonization and extinction. Our model best applies to plant dynamics, where a patch consists of one to several individuals, but it could be extended to other situations characterized by patch dynamics and nutrient exchanges, such as interconnected ponds, tidal pools, or other ephemeral habitats.

The feedback between nutrient and patch dynamics generates three mechanisms affecting persistence and coexistence. We find that a net nutrient flow from occupied to empty patches causes (1) a reduction of population size of a resident species, reducing its effective colonization rate and thus its persistence; (2) an enrichment of empty patches, allowing the nutrient concentration in these patches to meet the minimal requirements of weak competitors; and (3) an increase of the effective colonization rate of invading species, generating a facilitative interaction between the resident species and the invader. We have also shown these mechanisms to have profound impacts on the shape of the competition-colonization trade-off, species richness, and successional dynamics. We demonstrate how the spatial occupancy of species across the landscape feeds back into local ecosystem dynamics through its control of nutrient flows. Our metaecosystem approach, therefore, provides an emergent mechanism for coupling diversity and ecosystem functioning at the regional scale (Cardinale et al. 2000; Mouquet and Loreau 2003).

The basis of these mechanisms is a simple prediction: the net flow of nutrients is expected to be from occupied to empty patches when the spatial flow of nutrients sequestered in dead biomass is much larger than the flow of the inorganic nutrients. The relative importance of inorganic-nutrient and detritus flows, or, more generally, of direct and indirect nutrient flows (Gravel et al. 2010), drives a shift from an "exploitative" situation (sensu Margalef 1968), which prevents ecosystem development (see fig. 7*A*), to a facilitative situation where diversity reinforces ecosystem development (see fig. 7*B*). Spatial occupancy of species affects local dynamics because of the net flow of nutrients toward empty patches and also because of its effect on the population density of invading and resident species. These properties of local ecosystems, in turn, feed back to the regional space occupancy dynamics because the critical colonization rate for regional persistence is established by local population densities.

Our model extends current metapopulation and metacommunity theories by integrating explicit resource dynamics within a patch-dynamic metacommunity. The original metapopulation model assumed that local equilibrium population size was invariant to regional spatial occupancy with no explicit link between local and regional dynamics (Levins 1969). More recently, population size has been integrated as a local variable within metapopulation models (Hastings and Wolin 1989; Gyllenberg and Hanski 1992), and this integration has revealed feedbacks between regional metapopulation and local immigration processes, resulting in bistability (Hastings and Harrison 1994). Recent nonequilibrium metapopulation models have also found that regional metacommunity properties can feed back into local dynamics to generate complex spatiotemporal dynamics (Guichard et al. 2003; Guichard 2005). Here we integrate nutrient dynamics, which includes recycling, into the framework and show how local equilibrium concentrations across trophic compartments depend on spatial occupancy in the presence of spatial flows of a limiting nutrient. Our model reveals the importance of the coupling between nutrient and patch dynamics on fundamental predictions of persistence and coexistence.

This metaecosystem perspective promises a stimulating revision of some classic ecological theories, including the theory of island biogeography (MacArthur and Wilson 1967; Hanski and Gyllenberg 1997). This theory explains species diversity on islands as the balance between species colonization and extinction events. Island area is assumed to affect colonization and extinction rates because smaller islands receive fewer colonists and experience stronger demographic stochasticity. Island biogeography is known to be a special case of the more general metapopulation theory (Hanski 1999), for which islands are patches embedded in a dynamic landscape. Our framework adds a new dimension to this theory by providing an explicit link between colonization-extinction dynamics and patch geography (size and isolation) mediated by ecosystem function. For instance, perimeter : area decreases with patch area, and therefore we expect that processes that are responsible for direct resource flows will be strongest along the perimeter of small patches (Polis and Hurd 1995). Our metaecosystem framework thus predicts higher establishment rate on small patches because of these perimeter effects.

In addition to species diversity, our results provide a regional and ecosystemic perspective to the classic succession model (Connell and Slatyer 1977). The model is based on three fundamental mechanisms, facilitation, tolerance, and inhibition, and it has been very useful for understanding primary succession (e.g., Chapin et al. 1994). Here we added a regional dimension to this conceptual model. Neighboring ecosystems influence the properties of newly disturbed areas and can drive the successional sequence because of nutrient flows. Under a low d_D/d_N regime, the limiting nutrient will move from disturbed to occupied localities, inhibiting the establishment of weak competitors. Only the best competitors will tolerate this reduced nutrient concentration, and succession will be prevented. The opposite situation will arise under high d_D/d_N regimes, thus facilitating the establishment of good colonizers (poor competitors).

The metaecosystem perspective on patch dynamics may be applied to natural phenomena such as the relationship between ungulate foraging and forest succession. Ungulates are known to directly influence energy flow and nutrient fluxes in various ecosystems (e.g., McNaughton et al. 1988; Pastor et al. 1988). Seagle (2003) proposed that white-tailed deer foraging could indirectly affect forest ecosystem nutrient budgets because deer transport nutrients from surrounding foraging habitats with high N load—for example, urban and crop areas—into forests. In the same study, allometric relationships also predicted that deer contribution to N deposition could be equal or even larger than atmospheric N deposition, thus providing an explicit parallel to our nutrient ratio hypothesis (Seagle 2003). This hypothesis could be extended to boreal forest landscapes where pioneer species rapidly establish in recently disturbed patches that have high nutrient availability (Likens and Bormann 1995). These pioneer species are preferred by grazing ungulates (Cote et al. 2004); therefore, by analogy to the cropland-forest example cited above, we should expect the net flow of nutrients from the early successional areas into mature forests to slow ecological succession.

The model we presented should be extended to explore the impacts of habitat destruction and fragmentation in metaecosystems. Metacommunity models based on the competition-colonization trade-off predict that the best competitors are the first to become extinct following habitat destruction because of their poor colonizing ability (Nee and May 1992; Tilman et al. 1994; but see Klausmeier 1998). Our results suggest that the interruption of some essential spatial flows for diversity maintenance could trigger cascading extinction events. Our results emphasize the role of strong local competitors for nutrients as keystone species in metaecosystems because they are the drivers of spatial nutrient flows. The best competitors for nutrients are, by definition, the most efficient at exploiting limiting nutrients. If the nutrient flows from empty to occupied patches, habitat-driven extinctions of strong competitors would be mediated by an increased persistence of the remaining species. On the other hand, if the nutrient flows from occupied to empty patches, such extinctions would have a negative effect on weaker competitors that rely on nutrient inputs from stronger competitors. Overall, a small amount of habitat destruction could result in abrupt extinction of both strong and weak competitors because of the mutualistic interactions involved (Klausmeier 2001).

The metaecosystem perspective presented here provides a simple theoretical framework to link metacommunity and ecosystem phenomena. As humans profoundly alter the structure and functioning of natural landscapes and, in particular, nutrient flows (e.g., drainage, impermeable infrastructure), understanding and predicting the consequences of these changes is critical for designing appropriate conservation and management strategies. The metaecosystem perspective provides a powerful tool toward this goal.

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Nepenthe, "an accurate drawing made … from a pitcher that had been rendered transparent. … Embedded in this fleshy frill, lie many elongated, cylindrical glands, like guns on a fortification." From "The Structure of the Pitcher Plant" by J. G. Hunt, M.D. (*American Naturalist*, 1869, 3:13–17).