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The effect of positive interactions on community structure in a multi-species metacommunity model along an environmental gradient

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Abstract

Positive interactions are widely recognized as playing a major role in the organization of community structure and diversity. As such, recent theoretical and empirical works have revealed the significant contribution of positive interactions in shaping species’ geographical distributions, particularly in harsh abiotic conditions. In this report, we explore the joint influence of local dispersal and an environmental gradient on the spatial distribution, structure and function of communities containing positive interactions. While most previous theoretical efforts were limited to modelling the dynamics of single pairs of associated species being mutualist or competitor, here we employ a spatially explicit multi-species metacommunity model covering a rich range of interspecific interactions (mutualism, competition and exploitation) along an environmental gradient. We find that mutualistic interactions dominate in communities with low diversity characterized by limited species dispersal and poor habitat quality. On the other hand, the fraction of mutualistic interactions decreases at the expense of exploitation and competition with the increase in diversity caused by higher dispersal and/or habitat quality. Our multi-species model exemplifies the ubiquitous presence of mutualistic interactions and the role of mutualistic species as facilitators for the further establishment of species during ecosystem assembly. We therefore argue that mutualism is an essential component driving the origination of complex and diverse communities.

Keywords

positive interactions, mutualism, metacommunity, dispersal, multi-species model, environmental gradient, diversity
Positive interactions are ubiquitous in ecosystems and are now widely recognized as playing a major role in the organization of community structure and diversity (Bertness and Callaway 1994; Hacker and Gaines 1997; Stachowicz 2001; Bruno et al. 2003; Brooker et al. 2008; Okuyama and Holland 2008; Bastolla et al. 2009). Recent theoretical and empirical works have revealed the significant contribution of positive interactions in shaping a species’ geographical distribution, particularly in harsh abiotic conditions, because of their ability to extend the realized niche of the species' partner(s) (Pugnaire et al. 1996; Callaway et al. 2002; Travis et al. 2005; Maestre and Cortina 2004; Travis et al. 2006; Kéfi et al. 2008). Indeed, positive interactions, which are either beneficial for the two species involved (mutualism) or beneficial for one while creating no harm to the other (commensalism), make the local environment more favorable for the associated species by generating, directly or indirectly, nutritional, dispersal or reproduction services or by creating refuges from competitors, predators or physical pressures (Stachowicz 2001).

Simple two-species models have been used to investigate the environmental factors under which positive interactions should be expected to dominate (Wilson and Nisbet 1997; Travis et al. 2005; Yamamura et al. 2004; Travis et al. 2006). Studies have also explored the relationship between the mechanisms by which mutualistic species provide benefits and the resulting spatial distributions of the interacting species. For example, it has been
shown that, even along a smooth gradient of environmental stress, species composition can change abruptly whereby mutualists and competitors dominate different zones of the landscape that differ in extent and location depending on whether mutualism improves chances of survival or reproduction (Travis et al. 2006).

While these prior theoretical efforts have greatly improved our understanding of the correlation between environmental conditions, interspecific interactions and species’ spatial distributions, most of the models were limited to representing the dynamics of single pairs of associated species being either mutualists or competitors. However, species rarely coexist in isolated pairs. Natural communities usually form a complex web of many interacting species which are linked to each other through a wide range of possible interactions (Wootton 1994; Polis and Strong 1996). Moreover, mutualism is not restricted to pairwise interactions between two species since communities may contain rich guilds of mutualistic species (Stanton 2003) containing both specialist and generalist associates (Bascompte et al. 2003; Bascompte et al. 2006; Bastolla et al. 2009). As a result, the contribution of positive interactions in determining the spatial distribution of species is likely to be non-intuitive in multi-species assemblages.

In this report, we extend previous two-species models to investigate the relationship between an environmental gradient and the spatial distribution of multi-species communities containing positive interspecific interactions. We employ a spatially explicit multi-species metacommunity model which covers a rich range of interspecific interactions (mutualism, competition and exploitation) along an environmental gradient.
In recent years, metacommunity theory has received increased recognition as an innovative framework to study community structure and function at local and regional scales (Wilson 1992; Forbes and Chase 2002; Mouquet and Loreau 2002; Cottenie et al. 2003; Loreau et al. 2003; Leibold et al. 2004; Venail et al. 2008). Patterns of species richness, species relative abundances, productivity and stability can be seen as emerging properties of metacommunity dynamics where local communities are coupled via the dispersal of organisms. The principal objective of this article is to assess the joint influence of local dispersal and an environmental gradient on the metacommunity properties. The effect of local dispersal on this metacommunity was previously studied using a landscape with homogeneous environmental conditions (Filotas et al. submitted). Our investigation here is twofold. First, following closely our prior analysis we review the general effect of local dispersal on the properties of this heterogeneous metacommunity at the regional scale. We report on i) the average local and regional diversity and ii) on the average structure of the local interaction webs. Second, we explore in detail the change of the local community properties along the environmental gradient at specific values of the dispersal rate.

2. The Method

2.1 Model description
The metacommunity model employed is a spatial generalization of an individual-based community model conceived by Rikvold et al. (Rikvold and Zia 2003; Rikvold 2007) and inspired by the Tangled-Nature model (Christensen and al. 2002), both of which are non-spatial models of biological coevolution. The metacommunity is spatially explicit, forming a two-dimensional square lattice composed of $D \times D$ communities of species with periodic boundary conditions. The model includes a potential species pool (PSP) of $2^L$ potential species. Species are represented by a bit string of length $L$, by analogy with a genotype, and are numbered from 1 to $2^L$ (Eigen 1971; Eigen et al. 1988).

\[ S^i = (S_1^i, S_2^i, S_3^i, \ldots, S_L^i) \quad \text{where} \quad S_i^i = \pm 1 \quad \text{and} \quad i = 1, 2, \ldots, 2^L. \]  

Individuals of the same species are represented by the same vector of bits (i.e. there is a one-to-one correspondence between phenotype and genotype in this model). The individuals interact locally with other species of their community through a random interaction matrix $J$, the elements of which will be described later. They reproduce asexually, and their offspring may undergo mutation with a small but fixed probability. Each community is open to the spontaneous arrival of newly introduced species via evolution and to migration from and to neighboring communities. Not all potential species from the PSP coexist locally. The dynamics has the effect of sampling the PSP at a specific low rate to find stable configurations of species which depend strongly on how those species interact together. In a previous report, we investigated the influence of local dispersal, in a homogeneous landscape, on the dynamics of this multi-species metacommunity model (Filotas et al. submitted). We found the realized communities and
their interaction webs to spontaneously self-organize through local level dispersal
dynamics and to vary in structural properties with changes in dispersal rate. Here we
extend this model by introducing an abiotic environmental gradient.

2.1.1 The environmental gradient

Environmental gradients may be associated with abiotic factors, such as disturbance (e.g.
wave action or wind), water and nutrient availability, salinity, heavy metal concentration,
etc. or biotic factors, such as the presence of competitors, pathogens, predators, etc.
(Wilson and Keddy 1988; Damgaard 2003). In theoretical studies, environmental
gradients are typically modelled by their direct effect on biotic parameters such as
reproduction or growth rate (Travis et al. 2005; Travis et al. 2006), mortality or extinction
rate (Travis et al. 2006; Holt and Keitt 2000), or strength of inter-specific interaction
(Damgaard 2003). Environmental gradients can also be modelled by their effect on
landscape structure such as habitat availability (Holt and Keitt 2000; Roy et al. 2008). In
the present investigation, we employ a gradient in carrying capacity. Though we are
aware that the concept of carrying capacity can be somewhat vague and mostly
theoretical (MacNab 1985; Dhondt 1988; Seidl and Tisdell 1999; del Monte-Luna et al.
2004; Schluter and Weir 2007), we make use of this concept since it permits a simple
generalization of the many abiotic factors known to restrict population growth. As
previously proposed (Bevers and Flather 1999), the carrying capacity in our model is a
non-energetic constraint and can be seen as a limit to the available space in a given
habitat of the metacommunity (e.g. breeding sites). The carrying capacity is modelled as
having an indirect effect on the species reproduction probability (see below). Each cell
(x,y) of the landscape corresponds to a habitat of a given carrying capacity $N_0(x,y)$. The carrying capacity changes from one habitat to the next according to a horizontal sinusoidal gradient spanning the interval $[N_0^{\text{min}}, N_0^{\text{max}}]$ (see fig. A1 in appendix A). The sinusoidal gradient enables the carrying capacity to be varied in a smoother manner than a linear gradient over a landscape with periodic boundaries.

2.1.2 Species interactions

Species in the PSP are connected by a fixed interaction matrix $J$ of dimension $2^L \times 2^L$. The elements $J_{ij}$ of the interaction matrix represent the effect of species $j$ on species $i$. It is thus a measure of the biological interaction between the two species which is not restricted to direct trophic interactions and hence does not express an energetic link. If both elements $J_{ij}$ and $J_{ji}$ are negative, the two species are in competition. If they are both positive, the species are mutualistic partners. Finally, if they have opposite signs, one species benefits at the expense of the other species (as in parasitism or predation). We will call the latter interaction “exploitation”. Intra-species interactions have been set to zero, $J_{ii} = 0$, to emphasize the dynamics resulting from interspecific interactions. The off-diagonal elements are fully connected, uncorrelated and their distribution is triangular, centered on 0 and randomly distributed between -1 and 1 (fig. 6b; also see appendix B for a complete description of the matrix construction). For large values of $L$, the full matrix $J$ cannot fit into standard computer memory and we must adopt an algorithm able to generate the matrix entries in a deterministic, chaotic and numerically efficient way. The triangular aspect of the distribution, chosen to account for the predominance of weak interactions in real webs (Paine 1992), is also a result of this procedure.
2.1.3 The model’s dynamics

The population dynamics is modeled at the level of individuals to incorporate stochasticity in the demographic processes of reproduction and dispersal in non-overlapping generations. It follows three steps: reproduction, mutation and dispersal.

Reproduction

Reproduction is an intra-community process. The reproduction probability is a time and space varying function which measures how favorable the current community is for each local species. A species can have a low reproduction probability in some communities but a high one somewhere else in the landscape, depending on the local configuration of species with which it interacts, their relative abundance and the local carrying capacity. In a given community, the probability of reproduction is identical for all individuals of the same species. At the beginning of a generation, each individual from each community is given the possibility to reproduce. The probability for an individual of species $i$, located in community $(x,y)$ at generation $t$, to give birth is

$$p_{off,i}(x,y,t) = \frac{1}{1 + \exp[-\Phi_i(x,y,t)]} \in [0,1] \quad (2)$$

$p_{off,i}$ has a simple functional form chosen to ensure a gradual variation between 0 (no reproduction) and 1 (definite reproduction) (see fig. C1 in appendix C).
The function $\Phi_i(x, y, t)$ measures the impact of the local community at $(x,y)$ on species $i$ at generation $t$, and is given by:

$$\Phi_i(x, y, t) = \frac{1}{N(x, y, t)} \sum_j J_{ij} n_j(x, y, t) - \frac{N(x, y, t)}{N_0(x, y)}$$

(3)

where $n_j(x, y, t)$ is the abundance of species $j$, $N(x, y, t) = \sum_i n_i(x, y, t)$ is the total biomass (or total abundance) and $N_0(x, y)$ is the carrying capacity of the community at $(x,y)$. The sum over $j$ in the first term represents the effects on species $i$ by the other species, $j$, through the elements of the interaction matrix, $J_{ij}$. One must see the system as one in which energetic resources are abundant, although not explicitly represented in eq. (3). For example, even if there is no direct food supply in this system, it is possible for a single-species population to survive. The local total biomass $N(x, y, t)$ is limited by the abiotic constraint $N_0(x, y)$ which expresses a non-energetic limitation such as the availability of space. While for simplicity we assume that the carrying capacity reduces the reproduction probability of each species of a given community in the same manner, some species might be less affected than others depending on the nature and strength of their interspecific interactions. For large positive $\Phi_i(x, y, t)$ the local conditions at $(x, y)$ are favorable to species $i$, and its individuals almost certainly reproduce. For large negative $\Phi_i(x, y, t)$ the local conditions are harsh, and chances of reproduction for individuals of species $i$ are low. Note that even species benefiting from positive interactions can have a low reproduction probability if the population size exceeds the
carrying capacity $N_0(x,y)$. The model mimics non-overlapping generations through asexual reproduction. Individuals who reproduce are replaced by $F$ offspring and individuals who do not are removed from their community (they die). The model does not assume mass-balance and the total biomass, at the local and regional scales, is allowed to fluctuate stochastically through the individual-based dynamics. Nevertheless, the total biomass does not grow unbounded since it is constrained by the carrying capacity $N_0(x,y)$.

**Mutation**

Offspring produced during reproduction may undergo mutation, whereby each bit of their “genome” can switch from -1 to 1 or inversely with a small probability $p_{\text{mut}}$. In this process the offspring “genome” may become distinct from the one inherited by its parent. If this is the case, the mutant either enters the community in the form of a new species or adds to the abundance of another existing species. In both instances, the offspring acquires a new set of interspecific interactions. Because there are no correlations between changes in a species’ “genome” and the resulting changes in its interspecies interactions, mutation is not interpreted as part of a biological evolutionary process but mimics the spontaneous introduction of a new individual in a community assembly process. It differs, however, from immigration (see below) in that the possible mutants in a particular community are limited to genotypic neighbors of the locally existing species.

**Dispersal**
Dispersal is an inter-community process. We motivate the process of dispersal in this model by the fact that for many non-sessile organisms dispersal is a means to improve their intrinsic condition based on factors such as local population size, resource competition, habitat quality, habitat size, etc. (Bowler and Benton 2005). In our model, individuals with low reproductive probability are allowed to escape from their community in the “hope” of finding a more suitable one. Motivated by the metapopulation model of Ruxton and Rohani (1999), we set up a tolerance threshold called \( p_d \) (Filotas et al. 2008), which we simply refer to as the rate of dispersal. At each generation of the model following the reproduction and mutation processes, the reproduction probability of each species (eq. 2) is updated. An individual whose reproduction probability is less than or equal to this threshold, \( p_{off} \leq p_d \), moves randomly to one of its neighboring communities. We choose a square neighborhood containing the individual’s initial community and the 8 immediately adjacent communities (also called the next-nearest neighbors or the Moore neighborhood (Hogeweg 1988)). Therefore, there is a 1/9 probability that an individual stays in its original habitat even for \( p_{off} \leq p_d \). While it is possible that the displacement brings the individual to a more favorable environment, there is no guarantee that this happens. \( p_d \) is fixed and of equal value for all species. Nonetheless, each species experiences the dispersal process differently since its reproduction probability is distinct and varies with space and time. This mode of community-driven dispersal was previously studied for a two-species predator-prey model (Filotas et al. 2008) and a multispecies model (Filotas et al. submitted) and shown to produce spatial pattern formation dependent on \( p_d \), even in the absence of
environmental inhomogeneity. Dispersal completes one generation of the model, and the above-mentioned sequence is repeated.

The local dynamics produced by this sequence is intermittent. The system settles into long-lived quasi-stationary communities consisting of only a small subset of the potential species contained in the PSP. Coexistence in this model never consists of a static equilibrium. As a result of new species being introduced into the metacommunity via the assembly process, quasi-stationary communities may get interrupted by rapid periods of reorganization where a new community is sampled from the PSP (Christensen and al. 2002; Rikvold and Zia 2003). Consequently, under the model’s dynamics, the abundance $n_i(x,y,t)$ of each species, as well as the diversity and composition of local communities change with time and spatial location. The interaction web linking the species of the realized local communities may therefore have a structure quite different from the interaction matrix $J$ connecting all potential species together.

2.2 Parameter choice and simulation details

In the simulations reported here, we used the following parameters:

\[ D = 64, \quad L = 13, \quad N_0(x,y) \in [200,3800], \quad F = 4, \quad p_{\text{mut}} = 0.001/L. \]  

The choice of parameter values is justified as follows. The size $D$ of the landscape was chosen to be small enough for the model to stay numerically tractable yet sufficiently
larger than the dispersal neighborhood to allow for possible spatial correlations in the composition of the communities to occur. Similarly, the value for $L$ was chosen large enough for the PSP to include a rich diversity of potential species but was also limited by computational efficiency. The values of the carrying capacity, between 200 and 3800, assure that the size of the local total population $N(x, y, t)$ is much lower than the number of potential species contained in the PSP (i.e. $2^L = 8192$ species). Moreover, for these values the average carrying capacity over the entire landscape is $\bar{N}_0 = 2000$. This allows easy comparison with our previous investigation of this metacommunity in which we employed a homogeneous landscape of carrying capacity $N_0 = 2000$. The fecundity $F$ was determined by a stability analysis of the fixed points of the non-spatial model in the limit where the mutation probability is zero (Rikvold and Zia 2003). Note that in this limit, when the system is composed of a single species, the non-spatial model becomes equivalent to a logistic growth model, and hence a variety of dynamical behaviors are possible. We require that perturbations of the population size away from this single-species fixed point should decrease monotonically and not in an oscillatory or chaotic fashion. This ensures that any non-trivial behavior of the model necessarily results from the interactions among the species. This restriction translates to the condition $2 < F < 4.5$, from which we chose $F = 4$. Finally, the chosen value for the probability of mutation, $p_{mut}$, is sufficiently small so as to be inferior to the error threshold (Eigen 1971; Eigen et al. 1988). This choice guarantees that the generated population of individuals at each site is constrained to a few species and does not consist of a broad configuration spanning the PSP in a random diffused manner (di Collobiano et al. 2003).
We initially assign a population of 100 individuals to one species chosen at random for each site of the landscape. However, the model’s dynamics is independent of the initial conditions as long as the initial populations are substantially less than the size of the PSP (Rikvold and Zia 2003). The interaction matrix is created randomly at the beginning of the simulation and stays fixed thereafter. We do not focus here on the dynamics of the metacommunity over evolutionary time scales. Monte Carlo simulations have a duration of 65536 generations and the results are time averaged over 32768 consecutive generations where the system is in a quasi-stationary state. The dynamics of the metacommunity is investigated for values of the dispersal rate $p_d$ between 0 (no dispersal) and 1 (maximum dispersal). Depending on the degree of variability between simulations, 3 or 5 repetitions have been carried out for each value of $p_d$. Repetitions differ from each other through the interaction matrix and initial conditions.

Throughout the simulations we recorded the temporal evolution of the local ($\alpha$) and regional ($\gamma$) diversity. Moreover, we recorded the abundance of each species in each community of the metacommunity at four distinct times during the simulations, to assess the local species assemblages and the local interaction webs.

3. Results

3.1 General impact of local dispersal
Local dispersal modifies the diversity and interspecific interactions of the local communities through a sharp transition. This abrupt transition occurs for a species dispersal rate around $p_d^* = 0.22$ and was first reported and thoroughly analyzed in our previous investigation of this metacommunity using a homogeneous landscape with carrying capacity $N_0 = 2000$ (Filotas et al. submitted). Figure 1 presents this transition in two important community properties: the local and regional Shannon diversities (fig. 1a) and the average structure of the local interaction webs (fig. 1b) as functions of the dispersal rate. The average structure is measured by the average fraction of mutualistic, competitive and exploitative pairs of interaction in local communities. The spatial averages in figure 1 are performed over all communities of the landscape regardless of their position on the carrying-capacity gradient.

We found that for low dispersal rates below the transition, communities are almost isolated from each other due to the infrequent exchanges of individuals. As a result, species coexistence is poor locally but rich regionally because most quasi-stable communities on the landscape exhibit distinct assemblages of species (fig. 1a). With the increase in the dispersal rate, neighbor communities start exchanging species of low local reproduction probability, which improves the chance of survival of those species and hence enhances local diversity. As the dispersal rate reaches the critical threshold the local diversity rises abruptly at the expense of the regional diversity which drops as the metacommunity becomes increasingly uniform in its species content (fig 1a). This increased similarity amongst communities can be seen by the Shannon beta diversity, defined as $\beta = \gamma - \alpha$ (Lande 1996, Jost 2006), dropping to zero above the transition.
Hence, the regional ($\gamma$) and average local ($\alpha$) Shannon diversities become equivalent, indicating that the metacommunity operates as one single large community for high dispersal rates.

The occurrence of the transition is linked with the community-based dispersal process employed in this model. The dispersal rule allows individuals with reproduction probability inferior to $p_d$ to migrate to neighbor communities. At the point $p_d^* \approx 0.22$ the number of individuals having a reproduction probability inferior to $p_d$, and hence being allowed to disperse, becomes large enough to induce a homogenization in the species composition of the communities (Filotas et al. submitted). Under a dispersal strategy that does not depend on species density, we expect that a crossover between the low and high diversity regimes would also occur, but that the details of the transition may differ.

We found that species-poor communities at low spatial interconnectedness self-organized into an interaction web presenting a high fraction of mutualistic interaction pairs (figure 1b; the calculation to find the number of interacting pairs will be explained later). On the other hand, species-rich communities at high spatial interconnectedness have an interaction web supporting a wider diversity of interspecific interactions (fig. 1b).

3.2 Impact of the carrying capacity

The carrying capacity in this model affects the local communities in two significant ways: the number of species which can coexist in a given community and the total population size. As we will show, varying the carrying capacity across the landscape thus has non-
trivial effects on the change of diversity and structure of the communities with dispersal rates. For simplicity, in the analysis that follows we demonstrate these effects on three typical dispersal rates: $p_d = 0.0$ (below the transition), $p_d = 0.22$ (at the transition) and $p_d = 1.0$ (above the transition). The metacommunity properties as a function of carrying capacities will be presented by averaging over communities of identical carrying capacity. We start by illustrating the spatial distribution along the environmental gradient of the metacommunity properties discussed above. Figure 2 gives snapshots of the Shannon diversity and fraction of mutualistic interaction pairs at a given moment during a simulation run of the. Throughout this section we will refer to this figure since it displays the spatial aspect of the presented averaged properties.

Diversity patterns along the gradient

Figure 3 gives the variation of the local diversity (in species richness, fig. 3a) and of the Shannon diversity (fig. 3b) as a function of the carrying capacity ($N_0$). At $p_d = 0.0$, both curves increase with the augmentation in $N_0$ (see also fig. 2a). However, we observe a saturation of the local species diversity for large values of $N_0$. We believe this saturation to be caused by the limited number of species which can be drawn from the PSP to form a stable configuration. At $p_d = 1.0$, species richness and Shannon diversity are much higher everywhere in the landscape than at $p_d = 0.0$, in accordance with figure 1a (see also fig. 2c). However, we observe that contrary to species richness, Shannon diversity decreases with carrying capacity at high dispersal rates. This behaviour, as we will explain, can be understood by the change in species abundance distributions with dispersal rates and carrying capacities.
At $p_d = 0.22$, the transition from isolated communities of low diversity to rich and similar communities, does not proceed uniformly on all sites of the landscape. Indeed, we note that at this point while local diversity increases on all communities of the landscape (fig. 3a), the communities with carrying capacity lower than about $N_0 \approx 1500$, which have lower diversity, are subjected to a higher relative increase in species richness than communities with larger carrying capacity (approximately 70% in the former and 40% in the latter). In a way, for that intermediate value of the dispersal rate, half of the landscape (constituted of communities of low $N_0$) has entered the species-rich phase while the other half (with communities of high $N_0$) is still in the species-poor phase (fig. 2b). Hence, the transition proceeds in a wave-like manner along the carrying capacity gradient, affecting first the communities of low $N_0$ and then the richer communities of higher $N_0$ as $p_d$ continues to increase (see inset of fig. 3a where the local diversity at $p_d = 0.2, 0.21$ and 0.22 has been represented). This is an important difference from the homogeneous case we have previously examined where the transition was sharp, affecting all communities of the landscape at the same dispersal rate. Hence the environmental gradient attenuates the severity of the transition.

The sampling of the PSP at low dispersal rates, which produces communities with spatially uncoupled dynamics, and at high dispersal rates, which produces communities with coupled dynamics, favors assemblages of species with different distributions of abundances (fig. 4). At low dispersal rates, a typical community is formed of a core of 2 ($N_0 = 200$) to 4 ($N_0 = 3800$) highly abundant species constituting most of the
community’s total population (fig. 4a). The rest of the community’s total population is
distributed amongst a large but restricted number of low-abundance species each of
which usually does not exceed a population of 8 individuals. These low-abundance
species are basically mutants with reproduction probabilities that are not high enough to
allow them to successfully invade the assemblage’s core. The number of low-abundance
species increases slightly with carrying capacity contributing to the diversity
augmentation. On the other hand, the distribution of species abundances at high dispersal
rates has a different shape and consists of a continuous range between the most common
species (with an abundance representing about 20% of the total population size) and the
rarer species (of abundance 1) with species of subsequently decreasing intermediate
abundances (fig. 4b). Hence the population size of the species’ core found at low
dispersal rates is reduced, allowing the communities to accommodate more intermediate
and low-abundance species. The number of these additional species increases
considerably with carrying capacity. Because the relative abundance of large-population
species decreases given the large number of species of lower abundance, the local
Shannon diversity (fig. 3b) therefore decreases slightly along the gradient even if the
species richness increases (fig. 3a).

Community structure

We explore the structure of a community’s interaction web by considering the sub-web
containing the most abundant species and disregarding the rarer species (with abundances
lower than 8 individuals). We investigate the structure of the interaction sub-webs as a
function of the local carrying capacity by counting the fraction of interaction pairs of
each possible sign combination for each community: (+,+) for mutualistic pairs, (+,−) for exploitative pairs and (−,−) for competitive pairs.

Figure 5 gives these fractions for the three typical dispersal rates ($p_d = 0.0$, $p_d = 0.22$ and $p_d = 1.0$). We see that low dispersal rates (open circles) favor the emergence of communities dominated by mutualistic interactions (fig. 5a), as is also the case when employing a homogeneous carrying capacity landscape (Filotas et al. submitted) as well as in the non-spatial version of the model (Christensen et al. 2002; Rikvold and Zia 2003; Rikvold 2007). Nevertheless, we observe a slight decrease in the dominance of mutualism with the increase in carrying capacity (fig. 5a). We can also see this small reduction in the spatial distribution of the fraction of mutualistic pairs (fig. 2d).

At $p_d = 0.22$ during the transition (grey diamonds), the average fraction of mutualistic pairs varies in a peculiar fashion along the carrying capacity gradient (fig. 5a and fig. 2e) in a way that seems to follow the changes in local diversity (fig. 3a-inset and fig. 2b). We observe that the fraction of exploitative (fig. 5b) and competitive pairs (fig. 5c) follows the inverse trend. The fraction of mutualistic pairs decreases in every community of the landscape following the increase in diversity due to local migration. The decrease is stronger for communities of carrying capacity lower than $N_0 \approx 1500$ which are subjected to a higher relative increase in species richness. However, for communities of carrying capacity ranging from approximately $N_0 \approx 1500$ to 3000, the fraction of mutualistic pairs is only slightly lower than at $p_d = 0.0$ and is higher than everywhere else in the landscape (this is clearly visible from the white bands in fig. 2e). Communities in this zone are at
the boundary between communities with distinct species content ($N_0 > 3000$) and with similar species content ($N_0 < 1500$). We believe that the flux of individuals coming from communities of lower carrying capacity to communities in this zone is not large enough to homogenize the species content of these communities. On the other hand, the few individuals migrating away from distinct communities toward similar communities are likely to find themselves in habitats where the species assemblage is difficult to invade and hence they will not survive. As a result, the local diversity in the communities of this zone does not increase much along the gradient (fig. 3a-inset) and communities conserve their large fraction of mutualistic pairs of interaction. This mechanism does not occur in communities with $N_0 > 2500$ because their large carrying capacity allows them to accommodate a few immigrants without affecting their community structure.

Above the transition at $p_d = 1.0$ (black squares), while mutualism is still the preferred interaction type, its fraction has diminished and is replaced by competition and exploitation (fig. 5 and fig. 2f). The saturation in the decrease of the fraction of mutualistic pairs in communities of large carrying capacity seems to parallel the saturation in local species richness (fig. 3a). We also note that while increased migration produces a wider variety of interactions, the assemblage of interaction pairs is not random, since if it were, the fractions would be equal to the ones found in the PSP: 0.5 for exploitation, 0.25 for competition and 0.25 for mutualism.

Figure 6 gives the distributions of the strengths of the realized interactions in the subwebs containing all species of abundance higher than 8 in habitats of lowest ($N_0 = 200$)
and highest \((N_0 = 3800)\) carrying capacity. We observe that interactions are strongly positive when dispersal is limited but their strength decreases with the increase in carrying capacity (fig. 6a). However, with increased dispersal, the distribution contains an increasing proportion of negative and weak interactions (fig. 6b). At low carrying capacities the interactions are still markedly strong and positive but at high carrying capacities the bias toward positive interactions decreases and the distribution resembles the distribution of the PSP.

4. Discussion

Our results show that local species coexistence increases in the metacommunity as a result of the increase in habitat carrying capacity (fig. 3) and, in a more drastic manner, as a result of the increase in species dispersal rate (fig. 1a). This augmentation of the local diversity has considerable consequences for the structure of the species web of interactions: the fraction and strength of positive pairs of interactions diminish with the augmentation of local diversity at the expense of weak competitive and exploitative interaction pairs (figs. 5 and 6). Additional simulations (not shown) suggest that these transformations in community properties are robust under changes of parameter values for \(D\), the landscape size, \(L\), which determines the size of the PSP and \(p_{mut}\) the mutation probability per gene (given that it remains at a value below the error threshold). The emergence of strong mutualistic webs at low dispersal rates is independent of the triangular form of the PSP distribution of interactions employed in our investigation. Rikvold and Zia (2003) have shown that the same mutualistic webs emerge in the non-spatial version of this model when the elements of the PSP interactions matrix are
randomly and uniformly distributed over the interval $[-1,1]$. However, for large dispersal rates the distribution of interactions of the realized webs seems to correspond approximately to the triangular distribution of the PSP. Moreover, removing the assumption of zero intraspecific interactions does not affect the emergence of mutualistic interaction web at low dispersal rates or at low carrying capacities. In fact, while negative non-zero intraspecific interactions limit the growth of abundant mutualistic species and permits the survival of a few species with other interaction types, mutualism still dominates the interaction web (Filotas et al. submitted). For example, when intraspecific interactions are uniformly distributed on the interval $[-1,0)$, the fraction of mutualistic pairs of interactions goes from ca. 0.92 to 0.84 at $p_d = 0.0$ in a landscape with homogeneous carrying capacity $N_0 = 2000$.

This dynamics suggests that mutualistic interactions play a determining role in the assemblage of species-rich communities. Mutualist species act as ecological engineers (Crain and Bertness 2006). Without their initial establishment, the habitat cannot support a more complex web comprising competitive or exploitative interspecific interactions. While the fraction of mutualistic pairs of interactions decreases with the increase in diversity, the number of species participating in mutualistic interactions does not decrease. Figure 7 gives a schematic representation of the growth of the species assemblage with the increase in the dispersal rate and carrying capacity for one given local community. Mutualistic species form the core of the assemblage and serve as facilitators for the further establishment of new species. Communities relying on such mutualistic associations abound in nature (Stanton 2003; Thompson 2005) ranging from
coral reefs formed by the mutualism between corals and dinoflagellates (Knowlton and Rohwer 2003), to the rich mutualistic networks formed by plant species and their pollinators (Herrera 1988; Elberling and Olesen 1999; Bascompte et al. 2003). The core of mutualistic species can also be exemplified by trees relying on multiple positive interspecific interactions for growth: mycorhizal fungal for the uptake of nutrients and water, pollinators for reproduction and insects, birds or mammals for seed dispersal (Thompson 2006). In turn, trees create a favourable habitat for numerous other species by providing shade on the forest floor and by altering light and moisture regimes (Bruno et al. 2003). Mutualist foundation species form the basic structure for the development of a more complex community and henceforth influence the dynamics of species at all levels of the trophic web (Hacker and Bertness 1996).

The dominance of strong mutualistic species pairs in the habitats with poorest carrying capacity appears to mimic an important feature seen in numerous plant systems characterized by severe environmental conditions, for example in alpine plant communities (Choler et al. 2001; Callaway et al. 2002), salt marsh plants (Bertness and Hacker 1994) or arctic shrub tundra (Shevtsova et al. 1995). This dominance has also been demonstrated in two-species models studying the interplay of positive and negative interactions across a gradient of environmental severity, when mutualism confers a reproductive advantage (Travis et al. 2005; Travis et al. 2006). Mutualist species hence permit competitors and exploiters to extend their spatial range. While the carrying capacity and the severity of a habitat have different interpretations, both concepts are modeled (here and in the models cited above) so as to reduce the reproduction probability (or rate) of the species and hence it seems reasonable that they engender similar effects at
the community level. However, an important difference between these prior studies and ours is that mutualists in our model are never excluded by species with negative interspecific interactions even in domains with favourable environmental conditions. Even if few observations support this prediction (e.g. Barnes and Archer 1996), positive interactions are not necessarily expected to disappear in more clement abiotic conditions. As Brooker and Callaghan (1998) argue, the impact of positive interactions is probably masked in natural systems by the relatively greater impact of competition.

Our results also show that at $p_d = 0.22$ near the transition, mutualist species dominate in communities of intermediate carrying capacity (fig. 2e and fig. 5a), thereby creating a boundary between zones of high and low community similarity which both contain a larger fraction of negative interactions. This pattern is a consequence of the community-dependent dispersal rule employed in this model. During the transition, the flux of dispersing individuals in this zone of the landscape is not large enough to disturb the already existing assemblages of species and hence communities conserve their large fraction of mutualistic pairs of interaction. Even if we do not expect the pattern produced by this specific dispersal rule to be universal, it nevertheless highlights that species dispersal may produce irregular distributions of positive and negative interactions on an environmental gradient. While it has been suggested that the ‘currency’ through which mutualism operates (e.g. by improving fecundity or reducing mortality) may explain the hump-shape distribution of positive interactions along a severity gradient in certain plant communities (Maestre and Cortina 2004; Travis et al. 2006); we propose that in addition
to this mechanism, the manner in which species (or their propagules) disperse may also contribute to generating this non-linear pattern.

5. Conclusion

We have presented a spatially explicit multi-species metacommunity model along an environmental gradient in carrying capacity. The model displays reproduction and dispersal mechanisms centered at the level of individuals and based on interspecific interactions covering a broad spectrum: competition, exploitation and mutualism. The model is simple yet general and serves as a mathematical metaphor to evaluate the joint influence of local dispersal and an environmental gradient on the spatial distribution and structure of communities containing positive interactions. The dispersal process permits species with low reproductive probability to disperse locally to nearby communities and is motivated by the fact that for many non-sessile organisms dispersal is a means to improve their intrinsic condition. Species in real ecosystems certainly adopt more complex and more varied processes of reproduction and dispersal, which might moreover operate on different temporal and spatial scales. Also, the model describes a system in which energetic resources are abundant but are not explicitly represented. As a result, given a pool of sufficiently varied interactions, assembly by random draws from the pool under limited dispersal and limited carrying capacity, favours the spontaneous emergence of communities of a few strongly interacting mutualistic species benefiting from each other’s presence. While this can be seen as an unrealistic feature, it creates an advantageous framework to evaluate the conditions in an environmental gradient under
which these mutualistic interactions permit the establishment of additional species and
contribute to the development of complex webs of species with various interaction types.

We show that the increase in species dispersal rate and the increase in habitat carrying
capacity produce an augmentation of the local species coexistence in the metacommunity
and hence permit the creation of species-rich communities. This increase of the local
diversity has marked consequences on the structure of the local communities. As local
webs accumulate new species, the predominance of strongly interacting mutualistic
species decreases and benefits the increase of species participating in weak exploitative
and competitive interactions.

Our model emphasizes that the biodiversity and structure of multi-species communities
relying on positive interactions to ameliorate the local conditions can change markedly
depending on the level of species dispersal and the severity of those local conditions. In
addition, the results from our model are in agreement with previous two-species models
(Travis et al. 2005; Travis et al. 2006) predicting the dominance of mutualistic
interactions in harsh habitats where species growth is limited. Finally, the multi-species
approach we have presented is novel and exemplifies the importance of considering the
relative influence of mutualism in a species-rich context beyond the traditional pairwise
perspective (Stanton 2003) because of its fundamental role in the assemblage and
organization of countless natural communities on Earth.
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11 Loreau, M., Naeem, S., Inchausti, P., Bengtsson, J., Grime, J.P., Hector, A., Hooper,


Figure captions

Figure 1: Diversity and community structure as a function of the dispersal rate ($p_d$). a) Average local ($\alpha$) (black circles), regional ($\gamma$) (open squares) and beta ($\beta$) (grey diamonds) Shannon diversities. b) Average fraction of interacting pairs of type mutualistic (open circles), exploitative (black squares) and competitive (grey diamonds) for the sub-webs containing species with abundance larger than 8 individuals. Averages are performed over all 4096 communities of the landscape regardless of their carrying capacity. The diversity is averaged over a period of time of 32768 generations. The fractions of interacting pairs are averaged over four different moments during one simulation run ($t=40960, 49152, 57344$ and $65536$). All measures are also averaged over 5 simulation runs for points in the $p_d$ interval 0.21-0.29 and over 3 simulation runs for all other points.

Figure 2: Snapshots at one moment during the simulation of the Shannon diversity at a) $p_d = 0.0$, b) $p_d = 0.22$ and c) $p_d = 1.0$. Snapshots of the fraction of mutualistic pairs at d) $p_d = 0.0$, e) $p_d = 0.22$ and f) $p_d = 1.0$.

Figure 3: a) Average local diversity (in species richness) and b) average local Shannon diversity, as a function of the carrying capacity at $p_d = 0.0$ (open circles), $p_d = 0.22$ (grey diamonds) and $p_d = 1.0$ (black squares). Inset of a) represents the average local diversity at $p_d = 0.22$ (grey diamonds) in comparison with $p_d = 0.21$ (upward pointing triangles) and $p_d = 0.2$ (downward pointing triangles). Note how the local diversity increases in a wave-like manner from communities of low carrying capacity to communities of high carrying capacity with the increase in $p_d$ from 0.2 to 0.22. Biodiversity measures are averaged over all communities having the same carrying capacity and over time for a period of 32768 generations. All measures are also averaged over 5 simulation runs at $p_d = 0.22$ and $p_d = 0.21$, and over 3 simulation runs at $p_d = 0.0$, $p_d = 0.2$ and $p_d = 1.0$. 
Figure 4: Species abundance distribution at: a) $p_d = 0.0$ and b) $p_d = 1.0$ for $N_0 = 200$ (black) and $N_0 = 3800$ (white). Measures are averaged over all communities having the same carrying capacity, over time for a period of 32768 generations and over 3 simulation runs.

Figure 5: Average fraction of interacting pairs of type a) mutualistic, b) exploitative and c) competitive as a function of the carrying capacity, for the sub-webs containing species with abundance larger than 8 individuals at $p_d = 0.0$ (open circles), $p_d = 0.22$ (grey diamonds) and $p_d = 1.0$ (black squares). Note the different scales of the y-axis. The fractions of interacting pairs are averaged over all communities having the same carrying capacity and over four different moments during one simulation run ($t=40960, 49152, 57344$ and $65536$). All measures are also averaged over 5 simulation runs at $p_d = 0.22$ and over 3 simulation runs at $p_d = 0.0$ and $p_d = 1.0$.

Figure 6: Distributions of the interaction strengths at a) $p_d = 0.0$ and b) $p_d = 1.0$ for the communities of carrying capacity $N_0 = 200$ (black) and $N_0 = 3800$ (grey). The distribution of the interaction strengths in the PSP matrix is presented in b) (stripes). The frequency distributions are averaged over all communities having the same carrying capacity, over four different moments during one simulation run ($t=40960, 49152, 57344$ and $65536$) and over 3 simulation runs.

Figure 7: Schematic representation of typical local assemblages of species as a function of the carrying capacity and the dispersal rate. Each square box represents one community of the landscape. Each circle represents a species whose abundance (in log 10) is proportional to the circle’s radius. Open circles depict the core of species having only mutualistic interactions with each other. Filled circles depict species having at least one negative interaction with one of the species of the core. Note that there is no representation of space at the local community scale in this model; hence the spatial dimension in each box is simply an artifact of the illustration.