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

Authors
Elise Filotas, Martin Grant, Lael Parrott and Per Arne Rikvold

Affiliations and email adresses
Elise Filotas: elise.larose-filotas@umontreal.ca
Complex Systems Laboratory, Département de Géographie, Université de Montréal, C.P. 6128, Succursale Centre-ville, Montréal, Québec, H3C 3J7, Canada

Martin Grant: grant@physics.mcgill.ca
Department of Physics, McGill University, 3600 rue University, Montréal, Québec, H3A 2T8, Canada

Lael Parrott: lael.parrott@umontreal.ca
Complex Systems Laboratory, Département de Géographie, Université de Montréal, C.P. 6128, Succursale Centre-ville, Montréal, Québec, H3C 3J7, Canada

Per Arne Rikvold: prikvold@fsu.edu
Center for Materials Research and Technology, National High Magnetic Field Laboratory, and Department of Physics, Florida State University, Tallahassee, FL 32306, USA

Corresponding author
Lael Parrott: lael.parrott@umontreal.ca
Tel : +1 (514) 343 8032
Fax : +1 (514) 343 8008
Complex Systems Laboratory, Département de Géographie, Université de Montréal, C.P. 6128, Succursale Centre-ville, Montréal, Québec, H3C 3J7, Canada

1   **Abstract**

2   Positive interactions are widely recognized as playing a major role in the organization of

3   community structure and diversity. As such, recent theoretical and empirical works have

4   revealed the significant contribution of positive interactions in shaping species'

5   geographical distributions, particularly in harsh abiotic conditions. In this report, we

6   explore the joint influence of local dispersal and an environmental gradient on the spatial

7   distribution, structure and function of communities containing positive interactions.

8   While most previous theoretical efforts were limited to modelling the dynamics of single

9   pairs of associated species being mutualist or competitor, here we employ a spatially

10 explicit multi-species metacommunity model covering a rich range of interspecific

11 interactions (mutualism, competition and exploitation) along an environmental gradient.

12 We find that mutualistic interactions dominate in communities with low diversity

13 characterized by limited species dispersal and poor habitat quality. On the other hand, the

14 fraction of mutualistic interactions decreases at the expense of exploitation and

15 competition with the increase in diversity caused by higher dispersal and/or habitat

16 quality. Our multi-species model exemplifies the ubiquitous presence of mutualistic

17 interactions and the role of mutualistic species as facilitators for the further establishment

18 of species during ecosystem assembly. We therefore argue that mutualism is an essential

19 component driving the origination of complex and diverse communities.

20

1

2

1. Introduction

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

1   shown that, even along a smooth gradient of environmental stress, species composition

2   can change abruptly whereby mutualists and competitors dominate different zones of the

3   landscape that differ in extent and location depending on whether mutualism improves

4   chances of survival or reproduction (Travis et al. 2006).

5

6   While these prior theoretical efforts have greatly improved our understanding of the

7   correlation between environmental conditions, interspecific interactions and species'

8   spatial distributions, most of the models were limited to representing the dynamics of

9   single pairs of associated species being either mutualists or competitors. However,

10   species rarely coexist in isolated pairs. Natural communities usually form a complex web

11   of many interacting species which are linked to each other through a wide range of

12   possible interactions (Wootton 1994; Polis and Strong 1996). Moreover, mutualism is not

13   restricted to pairwise interactions between two species since communities may contain

14   rich guilds of mutualistic species (Stanton 2003) containing both specialist and generalist

15   associates (Bascompte et al. 2003; Bascompte et al. 2006; Bastolla et al. 2009). As a

16   result, the contribution of positive interactions in determining the spatial distribution of

17   species is likely to be non-intuitive in multi-species assemblages.

18

19   In this report, we extend previous two-species models to investigate the relationship

20   between an environmental gradient and the spatial distribution of multi-species

21   communities containing positive interspecific interactions. We employ a spatially explicit

22   multi-species metacommunity model which covers a rich range of interspecific

23   interactions (mutualism, competition and exploitation) along an environmental gradient.

1   In recent years, metacommunity theory has received increased recognition as an

2   innovative framework to study community structure and function at local and regional

3   scales (Wilson 1992; Forbes and Chase 2002; Mouquet and Loreau 2002; Cottenie et al.

4   2003; Loreau et al. 2003; Leibold et al. 2004; Venail et al. 2008). Patterns of species

5   richness, species relative abundances, productivity and stability can be seen as emerging

6   properties of metacommunity dynamics where local communities are coupled via the

7   dispersal of organisms. The principal objective of this article is to assess the joint

8   influence of local dispersal and an environmental gradient on the metacommunity

9   properties. The effect of local dispersal on this metacommunity was previously studied

10   using a landscape with homogeneous environmental conditions (Filotas et al. submitted).

11   Our investigation here is twofold. First, following closely our prior analysis we review

12   the general effect of local dispersal on the properties of this heterogeneous

13   metacommunity at the regional scale. We report on i) the average local and regional

14   diversity and ii) on the average structure of the local interaction webs. Second, we

15   explore in detail the change of the local community properties along the environmental

16   gradient at specific values of the dispersal rate.

17

18

19   **2. The Method**

20

21   2.1 Model description

22

1   The metacommunity model employed is a spatial generalization of an individual-based

2   community model conceived by Rikvold et al. (Rikvold and Zia 2003; Rikvold 2007) and

3   inspired by the Tangled-Nature model (Christensen and al. 2002), both of which are non-

4   spatial models of biological coevolution. The metacommunity is spatially explicit,

5   forming a two-dimensional square lattice composed of DxD communities of species with

6   periodic boundary conditions. The model includes a potential species pool (PSP) of 2^L

7   potential species. Species are represented by a bit string of length L, by analogy with a

8   genotype, and are numbered from 1 to 2^L (Eigen 1971; Eigen et al. 1988).

9

10    $$\mathbf{S}^i = (S_1^i, S_2^i, S_3^i,...,S_L^i) \quad \text{where } S_\nu^i = \pm 1 \text{ and } i = 1, 2,...,2^L. \tag{1}$$

11

12   Individuals of the same species are represented by the same vector of bits (i.e. there is a

13   one-to-one correspondence between phenotype and genotype in this model). The

14   individuals interact locally with other species of their community through a random

15   interaction matrix J, the elements of which will be described later. They reproduce

16   asexually, and their offspring may undergo mutation with a small but fixed probability.

17   Each community is open to the spontaneous arrival of newly introduced species via

18   evolution and to migration from and to neighboring communities. Not all potential

19   species from the PSP coexist locally. The dynamics has the effect of sampling the PSP at

20   a specific low rate to find stable configurations of species which depend strongly on how

21   those species interact together. In a previous report, we investigated the influence of local

22   dispersal, in a homogeneous landscape, on the dynamics of this multi-species

23   metacommunity model (Filotas et al. submitted). We found the realized communities and

1   their interaction webs to spontaneously self-organize through local level dispersal

2   dynamics and to vary in structural properties with changes in dispersal rate. Here we

3   extend this model by introducing an abiotic environmental gradient.

4

5   2.1.1 The environmental gradient

6   Environmental gradients may be associated with abiotic factors, such as disturbance (e.g.

7   wave action or wind), water and nutrient availability, salinity, heavy metal concentration,

8   etc. or biotic factors, such as the presence of competitors, pathogens, predators, etc.

9   (Wilson and Keddy 1988; Damgaard 2003). In theoretical studies, environmental

10   gradients are typically modelled by their direct effect on biotic parameters such as

11   reproduction or growth rate (Travis et al. 2005; Travis et al. 2006), mortality or extinction

12   rate (Travis et al. 2006; Holt and Keitt 2000), or strength of inter-specific interaction

13   (Damgaard 2003). Environmental gradients can also be modelled by their effect on

14   landscape structure such as habitat availability (Holt and Keitt 2000; Roy et al. 2008). In

15   the present investigation, we employ a gradient in carrying capacity. Though we are

16   aware that the concept of carrying capacity can be somewhat vague and mostly

17   theoretical (MacNab 1985; Dhondt 1988; Seidl and Tisdell 1999; del Monte-Luna et al.

18   2004; Schluter and Weir 2007), we make use of this concept since it permits a simple

19   generalization of the many abiotic factors known to restrict population growth. As

20   previously proposed (Bevers and Flather 1999), the carrying capacity in our model is a

21   non-energetic constraint and can be seen as a limit to the available space in a given

22   habitat of the metacommunity (e.g. breeding sites). The carrying capacity is modelled as

23   having an indirect effect on the species reproduction probability (see below). Each cell

1 (x,y) of the landscape corresponds to a habitat of a given carrying capacity $N_0(x,y)$. The

2 carrying capacity changes from one habitat to the next according to a horizontal

3 sinusoidal gradient spanning the interval $[N_0^{\min}, N_0^{\max}]$ (see fig. A1 in appendix A). The

4 sinusoidal gradient enables the carrying capacity to be varied in a smoother manner than

5 a linear gradient over a landscape with periodic boundaries.

6

7 2.1.2 Species interactions

8 Species in the PSP are connected by a fixed interaction matrix $\boldsymbol{J}$ of dimension $2^L \times 2^L$.

9 The elements J_{ij} of the interaction matrix represent the effect of species j on species i. It

10 is thus a measure of the biological interaction between the two species which is not

11 restricted to direct trophic interactions and hence does not express an energetic link. If

12 both elements J_{ij} and J_{ji} are negative, the two species are in competition. If they are both

13 positive, the species are mutualistic partners. Finally, if they have opposite signs, one

14 species benefits at the expense of the other species (as in parasitism or predation). We

15 will call the latter interaction "exploitation". Intra-species interactions have been set to

16 zero, $J_{ii} = 0$, to emphasize the dynamics resulting from interspecific interactions. The off-

17 diagonal elements are fully connected, uncorrelated and their distribution is triangular,

18 centered on 0 and randomly distributed between -1 and 1 (fig. 6b; also see appendix B for

19 a complete description of the matrix construction). For large values of L, the full matrix $\boldsymbol{J}$

20 cannot fit into standard computer memory and we must adopt an algorithm able to

21 generate the matrix entries in a deterministic, chaotic and numerically efficient way. The

22 triangular aspect of the distribution, chosen to account for the predominance of weak

23 interactions in real webs (Paine 1992), is also a result of this procedure.

1

2   2.1.3 The model's dynamics

3   The population dynamics is modeled at the level of individuals to incorporate

4   stochasticity in the demographic processes of reproduction and dispersal in non-

5   overlapping generations. It follows three steps: reproduction, mutation and dispersal.

6

7   *Reproduction*

8   Reproduction is an intra-community process. The reproduction probability is a time and

9   space varying function which measures how favorable the current community is for each

10   local species. A species can have a low reproduction probability in some communities but

11   a high one somewhere else in the landscape, depending on the local configuration of

12   species with which it interacts, their relative abundance and the local carrying capacity. In

13   a given community, the probability of reproduction is identical for all individuals of the

14   same species. At the beginning of a generation, each individual from each community is

15   given the possibility to reproduce. The probability for an individual of species i, located

16   in community (x,y) at generation t, to give birth is

17

18   $$p_{off_i}(x, y, t) = \frac{1}{1 + \exp[-\Phi_i(x, y, t)]} \qquad \in [0,1] \ . \qquad (2)$$

19

20   p_{off_i} has a simple functional form chosen to ensure a gradual variation between 0 (no

21   reproduction) and 1 (definite reproduction) (see fig. C1 in appendix C).

22

1   The function $\Phi_i(x,y,t)$ measures the impact of the local community at (x,y) on species i

2   at generation t, and is given by:

3

4     $$\Phi_i(x,y,t) = \frac{1}{N(x,y,t)}\sum_j J_{ij}n_j(x,y,t) - \frac{N(x,y,t)}{N_0(x,y)} \tag{3}$$

5

6   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

7   biomass (or total abundance) and $N_0(x,y)$ is the carrying capacity of the community at

8   (x,y). The sum over j in the first term represents the effects on species i by the other

9   species, j, through the elements of the interaction matrix, J_{ij}. One must see the system as

10   one in which energetic resources are abundant, although not explicitly represented in eq.

11   (3). For example, even if there is no direct food supply in this system, it is possible for a

12   single-species population to survive. The local total biomass $N(x,y,t)$ is limited by the

13   abiotic constraint $N_0(x,y)$ which expresses a non-energetic limitation such as the

14   availability of space. While for simplicity we assume that the carrying capacity reduces

15   the reproduction probability of each species of a given community in the same manner,

16   some species might be less affected than others depending on the nature and strength of

17   their interspecific interactions. For large positive $\Phi_i(x,y,t)$ the local conditions at (x,y)

18   are favorable to species i, and its individuals almost certainly reproduce. For large

19   negative $\Phi_i(x,y,t)$ the local conditions are harsh, and chances of reproduction for

20   individuals of species i are low. Note that even species benefiting from positive

21   interactions can have a low reproduction probability if the population size exceeds the

1   carrying capacity $N_0(x, y)$. The model mimics non-overlapping generations through

2   asexual reproduction. Individuals who reproduce are replaced by *F* offspring and

3   individuals who do not are removed from their community (they die). The model does not

4   assume mass-balance and the total biomass, at the local and regional scales, is allowed to

5   fluctuate stochastically through the individual-based dynamics. Nevertheless, the total

6   biomass does not grow unbounded since it is constrained by the carrying

7   capacity $N_0(x, y)$.

8

9   *Mutation*

10   Offspring produced during reproduction may undergo mutation, whereby each bit of their

11   "genome" can switch from -1 to 1 or inversely with a small probability p_{mut}. In this

12   process the offspring "genome" may become distinct from the one inherited by its parent.

13   If this is the case, the mutant either enters the community in the form of a new species or

14   adds to the abundance of another existing species. In both instances, the offspring

15   acquires a new set of interspecific interactions. Because there are no correlations between

16   changes in a species' "genome" and the resulting changes in its interspecies interactions,

17   mutation is not interpreted as part of a biological evolutionary process but mimics the

18   spontaneous introduction of a new individual in a community assembly process. It

19   differs, however, from immigration (see below) in that the possible mutants in a

20   particular community are limited to genotypic neighbors of the locally existing species.

21

22   *Dispersal*

1   Dispersal is an inter-community process. We motivate the process of dispersal in this

2   model by the fact that for many non-sessile organisms dispersal is a means to improve

3   their intrinsic condition based on factors such as local population size, resource

4   competition, habitat quality, habitat size, etc. (Bowler and Benton 2005). In our model,

5   individuals with low reproductive probability are allowed to escape from their

6   community in the "hope" of finding a more suitable one. Motivated by the

7   metapopulation model of Ruxton and Rohani (1999), we set up a tolerance threshold

8   called p_d (Filotas et al. 2008), which we simply refer to as the rate of dispersal. At each

9   generation of the model following the reproduction and mutation processes, the

10   reproduction probability of each species (eq. 2) is updated. An individual whose

11   reproduction probability is less than or equal to this threshold, $p_{off_i} \leq p_d$, moves randomly

12   to one of its neighboring communities. We choose a square neighborhood containing the

13   individual's initial community and the 8 immediately adjacent communities (also called

14   the next-nearest neighbors or the Moore neighborhood (Hogeweg 1988)). Therefore,

15   there is a 1/9 probability that an individual stays in its original habitat even for $p_{off_i} \leq p_d$.

16   While it is possible that the displacement brings the individual to a more favorable

17   environment, there is no guarantee that this happens. p_d is fixed and of equal value for all

18   species. Nonetheless, each species experiences the dispersal process differently since its

19   reproduction probability is distinct and varies with space and time. This mode of

20   community-driven dispersal was previously studied for a two-species predator-prey

21   model (Filotas et al. 2008) and a multispecies model (Filotas et al. submitted) and shown

22   to produce spatial pattern formation dependent on p_d, even in the absence of

1   environmental inhomogeneity. Dispersal completes one generation of the model, and the

2   above-mentioned sequence is repeated.

3

4   The local dynamics produced by this sequence is intermittent. The system settles into

5   long-lived quasi-stationary communities consisting of only a small subset of the potential

6   species contained in the PSP. Coexistence in this model never consists of a static

7   equilibrium. As a result of new species being introduced into the metacommunity via the

8   assembly process, quasi-stationary communities may get interrupted by rapid periods of

9   reorganization where a new community is sampled from the PSP (Christensen and al.

10   2002; Rikvold and Zia 2003). Consequently, under the model's dynamics, the abundance

11   $n_i(x, y, t)$ of each species, as well as the diversity and composition of local communities

12   change with time and spatial location. The interaction web linking the species of the

13   realized local communities may therefore have a structure quite different from the

14   interaction matrix $\boldsymbol{J}$ connecting all potential species together.

15

16   2.2 Parameter choice and simulation details

17

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

19

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

21

22   The choice of parameter values is justified as follows. The size D of the landscape was

23   chosen to be small enough for the model to stay numerically tractable yet sufficiently

1 larger than the dispersal neighborhood to allow for possible spatial correlations in the

2 composition of the communities to occur. Similarly, the value for L was chosen large

3 enough for the PSP to include a rich diversity of potential species but was also limited by

4 computational efficiency. The values of the carrying capacity, between 200 and 3800,

5 assure that the size of the local total population $N(x, y, t)$ is much lower than the number

6 of potential species contained in the PSP (i.e. $2^L = 8192$ species). Moreover, for these

7 values the average carrying capacity over the entire landscape is $\overline{N_0} = 2000$. This allows

8 easy comparison with our previous investigation of this metacommunity in which we

9 employed a homogeneous landscape of carrying capacity $N_0 = 2000$. The fecundity F

10 was determined by a stability analysis of the fixed points of the non-spatial model in the

11 limit where the mutation probability is zero (Rikvold and Zia 2003). Note that in this

12 limit, when the system is composed of a single species, the non-spatial model becomes

13 equivalent to a logistic growth model, and hence a variety of dynamical behaviors are

14 possible. We require that perturbations of the population size away from this single-

15 species fixed point should decrease monotonically and not in an oscillatory or chaotic

16 fashion. This ensures that any non-trivial behavior of the model necessarily results from

17 the interactions among the species. This restriction translates to the condition

18 $2 < F <\sim 4.5$, from which we chose $F = 4$. Finally, the chosen value for the probability of

19 mutation, p_{mut}, is sufficiently small so as to be inferior to the error threshold (Eigen 1971;

20 Eigen et al. 1988). This choice guarantees that the generated population of individuals at

21 each site is constrained to a few species and does not consist of a broad configuration

22 spanning the PSP in a random diffused manner (di Collobiano et al. 2003).

23

1   We initially assign a population of 100 individuals to one species chosen at random for

2   each site of the landscape. However, the model's dynamics is independent of the initial

3   conditions as long as the initial populations are substantially less than the size of the PSP

4   (Rikvold and Zia 2003). The interaction matrix is created randomly at the beginning of

5   the simulation and stays fixed thereafter. We do not focus here on the dynamics of the

6   metacommunity over evolutionary time scales. Monte Carlo simulations have a duration

7   of 65536 generations and the results are time averaged over 32768 consecutive

8   generations where the system is in a quasi-stationary state. The dynamics of the

9   metacommunity is investigated for values of the dispersal rate p_d between 0 (no dispersal)

10 and 1 (maximum dispersal). Depending on the degree of variability between simulations,

11 3 or 5 repetitions have been carried out for each value of p_d. Repetitions differ from each

12 other through the interaction matrix and initial conditions.

13

14 Throughout the simulations we recorded the temporal evolution of the local (α) and

15 regional (γ) diversity. Moreover, we recorded the abundance of each species in each

16 community of the metacommunity at four distinct times during the simulations, to assess

17 the local species assemblages and the local interaction webs.

18

19

20 **3. Results**

21

22 3.1 General impact of local dispersal

1   Local dispersal modifies the diversity and interspecific interactions of the local

2   communities through a sharp transition. This abrupt transition occurs for a species

3   dispersal rate around $p_d^* = 0.22$ and was first reported and thoroughly analyzed in our

4   previous investigation of this metacommunity using a homogeneous landscape with

5   carrying capacity $N_0 = 2000$ (Filotas et al. submitted). Figure 1 presents this transition in

6   two important community properties: the local and regional Shannon diversities (fig. 1a)

7   and the average structure of the local interaction webs (fig. 1b) as functions of the

8   dispersal rate. The average structure is measured by the average fraction of mutualistic,

9   competitive and exploitative pairs of interaction in local communities. The spatial

10   averages in figure 1 are performed over all communities of the landscape regardless of

11   their position on the carrying-capacity gradient.

12

13   We found that for low dispersal rates below the transition, communities are almost

14   isolated from each other due to the infrequent exchanges of individuals. As a result,

15   species coexistence is poor locally but rich regionally because most quasi-stable

16   communities on the landscape exhibit distinct assemblages of species (fig. 1a). With the

17   increase in the dispersal rate, neighbor communities start exchanging species of low local

18   reproduction probability, which improves the chance of survival of those species and

19   hence enhances local diversity. As the dispersal rate reaches the critical threshold the

20   local diversity rises abruptly at the expense of the regional diversity which drops as the

21   metacommunity becomes increasingly uniform in its species content (fig 1a). This

22   increased similarity amongst communities can be seen by the Shannon beta diversity,

23   defined as $\beta = \gamma - \alpha$ (Lande 1996, Jost 2006), dropping to zero above the transition.

1   Hence, the regional (γ) and average local (α) Shannon diversities become equivalent,

2   indicating that the metacommunity operates as one single large community for high

3   dispersal rates.

4

5   The occurrence of the transition is linked with the community-based dispersal process

6   employed in this model.   The dispersal rule allows individuals with reproduction

7   probability inferior to p_d to migrate to neighbor communities. At the point $p_d^* \approx 0.22$ the

8   number of individuals having a reproduction probability inferior to p_d, and hence being

9   allowed to disperse, becomes large enough to induce a homogenization in the species

10   composition of the communities (Filotas et al. submitted). Under a dispersal strategy that

11   does not depend on species density, we expect that a crossover between the low and high

12   diversity regimes would also occur, but that the details of the transition may differ.

13

14   We found that species-poor communities at low spatial interconnectedness self-organized

15   into an interaction web presenting a high fraction of mutualistic interaction pairs (figure

16   1b; the calculation to find the number of interacting pairs will be explained later). On the

17   other hand, species-rich communities at high spatial interconnectedness have an

18   interaction web supporting a wider diversity of interspecific interactions (fig. 1b).

19

20   3.2 Impact of the carrying capacity

21   The carrying capacity in this model affects the local communities in two significant ways:

22   the number of species which can coexist in a given community and the total population

23   size. As we will show, varying the carrying capacity across the landscape thus has non-

1   trivial effects on the change of diversity and structure of the communities with dispersal

2   rates. For simplicity, in the analysis that follows we demonstrate these effects on three

3   typical dispersal rates: p_d = 0.0 (below the transition), p_d = 0.22 (at the transition) and p_d

4   = 1.0 (above the transition). The metacommunity properties as a function of carrying

5   capacities will be presented by averaging over communities of identical carrying

6   capacity. We start by illustrating the spatial distribution along the environmental gradient

7   of the metacommunity properties discussed above. Figure 2 gives snapshots of the

8   Shannon diversity and fraction of mutualistic interaction pairs at a given moment during a

9   simulation run of the. Throughout this section we will refer to this figure since it displays

10   the spatial aspect of the presented averaged properties.

11

12   *Diversity patterns along the gradient*

13   Figure 3 gives the variation of the local diversity (in species richness, fig. 3a) and of the

14   Shannon diversity (fig. 3b) as a function of the carrying capacity (N_0). At p_d = 0.0, both

15   curves increase with the augmentation in N_0 (see also fig. 2a). However, we observe a

16   saturation of the local species diversity for large values of N_0. We believe this saturation

17   to be caused by the limited number of species which can be drawn from the PSP to form

18   a stable configuration. At p_d = 1.0, species richness and Shannon diversity are much

19   higher everywhere in the landscape than at p_d = 0.0, in accordance with figure 1a (see

20   also fig. 2c). However, we observe that contrary to species richness, Shannon diversity

21   decreases with carrying capacity at high dispersal rates. This behaviour, as we will

22   explain, can be understood by the change in species abundance distributions with

23   dispersal rates and carrying capacities.

1

2   At $p_d = 0.22$, the transition from isolated communities of low diversity to rich and similar

3   communities, does not proceed uniformly on all sites of the landscape. Indeed, we note

4   that at this point while local diversity increases on all communities of the landscape (fig.

5   3a), the communities with carrying capacity lower than about $N_0 \cong 1500$, which have

6   lower diversity, are subjected to a higher relative increase in species richness than

7   communities with larger carrying capacity (approximately 70% in the former and 40% in

8   the latter). In a way, for that intermediate value of the dispersal rate, half of the landscape

9   (constituted of communities of low N_0) has entered the species-rich phase while the other

10   half (with communities of high N_0) is still in the species-poor phase (fig. 2b). Hence, the

11   transition proceeds in a wave-like manner along the carrying capacity gradient, affecting

12   first the communities of low N_0 and then the richer communities of higher N_0 as p_d

13   continues to increase (see inset of fig. 3a where the local diversity at $p_d = 0.2, 0.21$ and

14   0.22 has been represented). This is an important difference from the homogeneous case

15   we have previously examined where the transition was sharp, affecting all communities

16   of the landscape at the same dispersal rate. Hence the environmental gradient attenuates

17   the severity of the transition.

18

19   The sampling of the PSP at low dispersal rates, which produces communities with

20   spatially uncoupled dynamics, and at high dispersal rates, which produces communities

21   with coupled dynamics, favors assemblages of species with different distributions of

22   abundances (fig. 4). At low dispersal rates, a typical community is formed of a core of 2

23   ($N_0 = 200$) to 4 ($N_0 = 3800$) highly abundant species constituting most of the

1 community's total population (fig. 4a). The rest of the community's total population is

2 distributed amongst a large but restricted number of low-abundance species each of

3 which usually does not exceed a population of 8 individuals. These low-abundance

4 species are basically mutants with reproduction probabilities that are not high enough to

5 allow them to successfully invade the assemblage's core. The number of low-abundance

6 species increases slightly with carrying capacity contributing to the diversity

7 augmentation. On the other hand, the distribution of species abundances at high dispersal

8 rates has a different shape and consists of a continuous range between the most common

9 species (with an abundance representing about 20% of the total population size) and the

10 rarer species (of abundance 1) with species of subsequently decreasing intermediate

11 abundances (fig. 4b). Hence the population size of the species' core found at low

12 dispersal rates is reduced, allowing the communities to accommodate more intermediate

13 and low-abundance species. The number of these additional species increases

14 considerably with carrying capacity. Because the relative abundance of large-population

15 species decreases given the large number of species of lower abundance, the local

16 Shannon diversity (fig. 3b) therefore decreases slightly along the gradient even if the

17 species richness increases (fig. 3a).

18

19 *Community structure*

20 We explore the structure of a community's interaction web by considering the sub-web

21 containing the most abundant species and disregarding the rarer species (with abundances

22 lower than 8 individuals). We investigate the structure of the interaction sub-webs as a

23 function of the local carrying capacity by counting the fraction of interaction pairs of

1 each possible sign combination for each community: $(+,+)$ for mutualistic pairs, $(+,-)$ for

2 exploitative pairs and $(-,-)$ for competitive pairs.

3

4 Figure 5 gives these fractions for the three typical dispersal rates ($p_d = 0.0$, $p_d = 0.22$ and

5 $p_d = 1.0$). We see that low dispersal rates (open circles) favor the emergence of

6 communities dominated by mutualistic interactions (fig. 5a), as is also the case when

7 employing a homogeneous carrying capacity landscape (Filotas et al. submitted) as well

8 as in the non-spatial version of the model (Christensen et al. 2002; Rikvold and Zia 2003;

9 Rikvold 2007). Nevertheless, we observe a slight decrease in the dominance of

10 mutualism with the increase in carrying capacity (fig. 5a). We can also see this small

11 reduction in the spatial distribution of the fraction of mutualistic pairs (fig. 2d).

12

13 At $p_d = 0.22$ during the transition (grey diamonds), the average fraction of mutualistic

14 pairs varies in a peculiar fashion along the carrying capacity gradient (fig. 5a and fig. 2e)

15 in a way that seems to follow the changes in local diversity (fig. 3a-inset and fig. 2b). We

16 observe that the fraction of exploitative (fig. 5b) and competitive pairs (fig. 5c) follows

17 the inverse trend. The fraction of mutualistic pairs decreases in every community of the

18 landscape following the increase in diversity due to local migration. The decrease is

19 stronger for communities of carrying capacity lower than $N_0 \cong 1500$ which are subjected

20 to a higher relative increase in species richness. However, for communities of carrying

21 capacity ranging from approximately $N_0 \cong 1500$ to 3000, the fraction of mutualistic pairs

22 is only slightly lower than at $p_d = 0.0$ and is higher than everywhere else in the landscape

23 (this is clearly visible from the white bands in fig. 2e). Communities in this zone are at

1   the boundary between communities with distinct species content (N_0>3000) and with

2   similar species content (N_0<1500). We believe that the flux of individuals coming from

3   communities of lower carrying capacity to communities in this zone is not large enough

4   to homogenize the species content of these communities. On the other hand, the few

5   individuals migrating away from distinct communities toward similar communities are

6   likely to find themselves in habitats where the species assemblage is difficult to invade

7   and hence they will not survive. As a result, the local diversity in the communities of this

8   zone does not increase much along the gradient (fig. 3a-inset) and communities conserve

9   their large fraction of mutualistic pairs of interaction. This mechanism does not occur in

10   communities with N_0>2500 because their large carrying capacity allows them to

11   accommodate a few immigrants without affecting their community structure.

12

13   Above the transition at $p_d = 1.0$ (black squares), while mutualism is still the preferred

14   interaction type, its fraction has diminished and is replaced by competition and

15   exploitation (fig. 5 and fig. 2f). The saturation in the decrease of the fraction of

16   mutualistic pairs in communities of large carrying capacity seems to parallel the

17   saturation in local species richness (fig. 3a). We also note that while increased migration

18   produces a wider variety of interactions, the assemblage of interaction pairs is not

19   random, since if it were, the fractions would be equal to the ones found in the PSP: 0.5

20   for exploitation, 0.25 for competition and 0.25 for mutualism.

21

22   Figure 6 gives the distributions of the strengths of the realized interactions in the sub-

23   webs containing all species of abundance higher than 8 in habitats of lowest ($N_0 = 200$)

1 and highest (N_0 = 3800) carrying capacity. We observe that interactions are strongly

2 positive when dispersal is limited but their strength decreases with the increase in

3 carrying capacity (fig. 6a). However, with increased dispersal, the distribution contains an

4 increasing proportion of negative and weak interactions (fig. 6b). At low carrying

5 capacities the interactions are still markedly strong and positive but at high carrying

6 capacities the bias toward positive interactions decreases and the distribution resembles

7 the distribution of the PSP.

8

9 **4. Discussion**

10 Our results show that local species coexistence increases in the metacommunity as a

11 result of the increase in habitat carrying capacity (fig. 3) and, in a more drastic manner, as

12 a result of the increase in species dispersal rate (fig. 1a). This augmentation of the local

13 diversity has considerable consequences for the structure of the species web of

14 interactions: the fraction and strength of positive pairs of interactions diminish with the

15 augmentation of local diversity at the expense of weak competitive and exploitative

16 interaction pairs (figs. 5 and 6). Additional simulations (not shown) suggest that these

17 transformations in community properties are robust under changes of parameter values

18 for D, the landscape size, L, which determines the size of the PSP and p_{mut} the mutation

19 probability per gene (given that it remains at a value below the error threshold). The

20 emergence of strong mutualistic webs at low dispersal rates is independent of the

21 triangular form of the PSP distribution of interactions employed in our investigation.

22 Rikvold and Zia (2003) have shown that the same mutualistic webs emerge in the non-

23 spatial version of this model when the elements of the PSP interactions matrix are

1   randomly and uniformly distributed over the interval $[-1,1]$. However, for large dispersal

2   rates the distribution of interactions of the realized webs seems to correspond

3   approximately to the triangular distribution of the PSP. Moreover, removing the

4   assumption of zero intraspecific interactions does not affect the emergence of mutualistic

5   interaction web at low dispersal rates or at low carrying capacities. In fact, while negative

6   non-zero intraspecific interactions limit the growth of abundant mutualistic species and

7   permits the survival of a few species with other interaction types, mutualism still

8   dominates the interaction web (Filotas et al. submitted). For example, when intraspecific

9   interactions are uniformly distributed on the interval $[-1,0)$, the fraction of mutualistic

10   pairs of interactions goes from ca. 0.92 to 0.84 at $p_d = 0.0$ in a landscape with

11   homogeneous carrying capacity $N_0 = 2000$.

12

13   This dynamics suggests that mutualistic interactions play a determining role in the

14   assemblage of species-rich communities. Mutualist species act as ecological engineers

15   (Crain and Bertness 2006). Without their initial establishment, the habitat cannot support

16   a more complex web comprising competitive or exploitative interspecific interactions.

17   While the fraction of mutualistic pairs of interactions decreases with the increase in

18   diversity, the number of species participating in mutualistic interactions does not

19   decrease. Figure 7 gives a schematic representation of the growth of the species

20   assemblage with the increase in the dispersal rate and carrying capacity for one given

21   local community. Mutualistic species form the core of the assemblage and serve as

22   facilitators for the further establishment of new species. Communities relying on such

23   mutualistic associations abound in nature (Stanton 2003; Thompson 2005) ranging from

1   coral reefs formed by the mutualism between corals and dinoflagellates (Knowlton and

2   Rohwer 2003), to the rich mutualistic networks formed by plant species and their

3   pollinators (Herrera 1988; Elberling and Olesen 1999; Bascompte et al. 2003). The core

4   of mutualistic species can also be exemplified by trees relying on multiple positive

5   interspecific interactions for growth: mycorhizal fungal for the uptake of nutrients and

6   water, pollinators for reproduction and insects, birds or mammals for seed dispersal

7   (Thompson 2006). In turn, trees create a favourable habitat for numerous other species by

8   providing shade on the forest floor and by altering light and moisture regimes (Bruno et

9   al. 2003). Mutualist foundation species form the basic structure for the development of a

10   more complex community and henceforth influence the dynamics of species at all levels

11   of the trophic web (Hacker and Bertness 1996).

12

13   The dominance of strong mutualistic species pairs in the habitats with poorest carrying

14   capacity appears to mimic an important feature seen in numerous plant systems

15   characterized by severe environmental conditions, for example in alpine plant

16   communities (Choler et al. 2001; Callaway et al. 2002), salt marsh plants (Bertness and

17   Hacker 1994) or arctic shrub tundra (Shevtsova et al. 1995). This dominance has also

18   been demonstrated in two-species models studying the interplay of positive and negative

19   interactions across a gradient of environmental severity, when mutualism confers a

20   reproductive advantage (Travis et al. 2005; Travis et al. 2006). Mutualist species hence

21   permit competitors and exploiters to extend their spatial range. While the carrying

22   capacity and the severity of a habitat have different interpretations, both concepts are

23   modeled (here and in the models cited above) so as to reduce the reproduction probability

24   (or rate) of the species and hence it seems reasonable that they engender similar effects at

1   the community level. However, an important difference between these prior studies and

2   ours is that mutualists in our model are never excluded by species with negative

3   interspecific interactions even in domains with favourable environmental conditions.

4   Even if few observations support this prediction (e.g. Barnes and Archer 1996), positive

5   interactions are not necessarily expected to disappear in more clement abiotic conditions.

6   As Brooker and Callaghan (1998) argue, the impact of positive interactions is probably

7   masked in natural systems by the relatively greater impact of competition.

8

9   Our results also show that at $p_d = 0.22$ near the transition, mutualist species dominate in

10   communities of intermediate carrying capacity (fig. 2e and fig. 5a), thereby creating a

11   boundary between zones of high and low community similarity which both contain a

12   larger fraction of negative interactions. This pattern is a consequence of the community-

13   dependent dispersal rule employed in this model. During the transition, the flux of

14   dispersing individuals in this zone of the landscape is not large enough to disturb the

15   already existing assemblages of species and hence communities conserve their large

16   fraction of mutualistic pairs of interaction. Even if we do not expect the pattern produced

17   by this specific dispersal rule to be universal, it nevertheless highlights that species

18   dispersal may produce irregular distributions of positive and negative interactions on an

19   environmental gradient. While it has been suggested that the 'currency' through which

20   mutualism operates (e.g. by improving fecundity or reducing mortality) may explain the

21   hump-shape distribution of positive interactions along a severity gradient in certain plant

22   communities (Maestre and Cortina 2004; Travis et al. 2006); we propose that in addition

1 to this mechanism, the manner in which species (or their propagules) disperse may also

2 contribute to generating this non-linear pattern.

3

4

5 **5. Conclusion**

6 We have presented a spatially explicit multi-species metacommunity model along an

7 environmental gradient in carrying capacity. The model displays reproduction and

8 dispersal mechanisms centered at the level of individuals and based on interspecific

9 interactions covering a broad spectrum: competition, exploitation and mutualism. The

10 model is simple yet general and serves as a mathematical metaphor to evaluate the joint

11 influence of local dispersal and an environmental gradient on the spatial distribution and

12 structure of communities containing positive interactions. The dispersal process permits

13 species with low reproductive probability to disperse locally to nearby communities and

14 is motivated by the fact that for many non-sessile organisms dispersal is a means to

15 improve their intrinsic condition. Species in real ecosystems certainly adopt more

16 complex and more varied processes of reproduction and dispersal, which might moreover

17 operate on different temporal and spatial scales. Also, the model describes a system in

18 which energetic resources are abundant but are not explicitly represented. As a result,

19 given a pool of sufficiently varied interactions, assembly by random draws from the pool

20 under limited dispersal and limited carrying capacity, favours the spontaneous emergence

21 of communities of a few strongly interacting mutualistic species benefiting from each

22 other's presence. While this can be seen as an unrealistic feature, it creates an

23 advantageous framework to evaluate the conditions in an environmental gradient under

1   which these mutualistic interactions permit the establishment of additional species and

2   contribute to the development of complex webs of species with various interaction types.

3

4   We show that the increase in species dispersal rate and the increase in habitat carrying

5   capacity produce an augmentation of the local species coexistence in the metacommunity

6   and hence permit the creation of species-rich communities. This increase of the local

7   diversity has marked consequences on the structure of the local communities. As local

8   webs accumulate new species, the predominance of strongly interacting mutualistic

9   species decreases and benefits the increase of species participating in weak exploitative

10   and competitive interactions.

11

12   Our model emphasizes that the biodiversity and structure of multi-species communities

13   relying on positive interactions to ameliorate the local conditions can change markedly

14   depending on the level of species dispersal and the severity of those local conditions. In

15   addition, the results from our model are in agreement with previous two-species models

16   (Travis et al. 2005; Travis et al. 2006) predicting the dominance of mutualistic

17   interactions in harsh habitats where species growth is limited. Finally, the multi-species

18   approach we have presented is novel and exemplifies the importance of considering the

19   relative influence of mutualism in a species-rich context beyond the traditional pairwise

20   perspective (Stanton 2003) because of its fundamental role in the assemblage and

21   organization of countless natural communities on Earth.

22

23

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Figure captions

3 **Figure 1: Diversity and community structure as a function of the dispersal rate (p_d). a) Average local**

4 **(α) (black circles), regional (γ) (open squares) and beta (β) (grey diamonds) Shannon diversities.**

5 **b) Average fraction of interacting pairs of type mutualistic (open circles), exploitative (black squares)**

6 **and competitive (grey diamonds) for the sub-webs containing species with abundance larger than 8**

7 **individuals. Averages are performed over all 4096 communities of the landscape regardless of their**

8 **carrying capacity. The diversity is averaged over a period of time of 32768 generations. The fractions**

9 **of interacting pairs are averaged over four different moments during one simulation run (t=40960,**

10 **49152, 57344 and 65536). All measures are also averaged over 5 simulation runs for points in the p_d**

11 **interval 0.21-0.29 and over 3 simulation runs for all other points.**

12

13 **Figure 2: Snapshots at one moment during the simulation of the Shannon diversity at a) $p_d = 0.0$, b)**

14 **$p_d = 0.22$ and c) $p_d = 1.0$. Snapshots of the fraction of mutualistic pairs at d) $p_d = 0.0$, e) $p_d = 0.22$**

15 **and f) $p_d = 1.0$.**

16

17 **Figure 3: a) Average local diversity (in species richness) and b) average local Shannon diversity, as a**

18 **function of the carrying capacity at $p_d = 0.0$ (open circles), $p_d = 0.22$ (grey diamonds) and $p_d = 1.0$**

19 **(black squares). Inset of a) represents the average local diversity at $p_d = 0.22$ (grey diamonds) in**

20 **comparison with $p_d = 0.21$ (upward pointing triangles) and $p_d = 0.2$ (downward pointing triangles).**

21 **Note how the local diversity increases in a wave-like manner from communities of low carrying**

22 **capacity to communities of high carrying capacity with the increase in p_d from 0.2 to 0.22.**

23 **Biodiversity measures are averaged over all communities having the same carrying capacity and over**

24 **time for a period of 32768 generations. All measures are also averaged over 5 simulation runs at**

25 **$p_d = 0.22$ and $p_d = 0.21$, and over 3 simulation runs at $p_d = 0.0$, $p_d = 0.2$ and $p_d = 1.0$.**

26

1

2 **Figure 4: Species abundance distribution at: a) $p_d = 0.0$ and b) at $p_d = 1.0$ for $N_0 = 200$ (black)**

3 **and $N_0 = 3800$ (white). Measures are averaged over all communities having the same carrying**

4 **capacity, over time for a period of 32768 generations and over 3 simulation runs.**

5

6 **Figure 5: Average fraction of interacting pairs of type a) mutualistic, b) exploitative and c)**

7 **competitive as a function of the carrying capacity, for the sub-webs containing species with**

8 **abundance larger than 8 individuals at $p_d = 0.0$ (open circles), $p_d = 0.22$ (grey diamonds) and**

9 **$p_d = 1.0$ (black squares). Note the different scales of the y-axis. The fractions of interacting pairs are**

10 **averaged over all communities having the same carrying capacity and over four different moments**

11 **during one simulation run (t=40960, 49152, 57344 and 65536). All measures are also averaged over 5**

12 **simulation runs at $p_d = 0.22$ and over 3 simulation runs at $p_d = 0.0$ and $p_d = 1.0$.**

13

14 **Figure 6: Distributions of the interaction strengths at a) $p_d = 0.0$ and b) $p_d = 1.0$ for the**

15 **communities of carrying capacity $N_0 = 200$ (black) and $N_0 = 3800$ (grey). The distribution of the**

16 **interaction strengths in the PSP matrix is presented in b) (stripes). The frequency distributions are**

17 **averaged over all communities having the same carrying capacity, over four different moments**

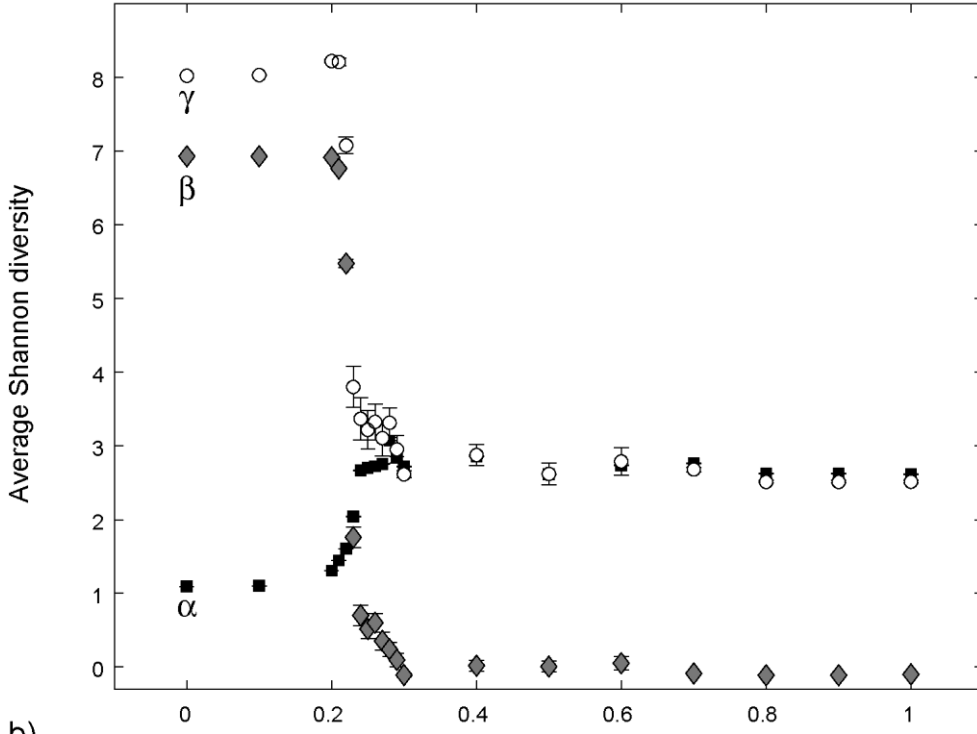18 **during one simulation run (t=40960, 49152, 57344 and 65536) and over 3 simulation runs.**

19

20 **Figure 7: Schematic representation of typical local assemblages of species as a function of the**

21 **carrying capacity and the dispersal rate. Each square box represents one community of the**

22 **landscape. Each circle represents a species whose abundance (in log 10) is proportional to the circle's**

23 **radius. Open circles depict the core of species having only mutualistic interactions with each other.**

24 **Filled circles depict species having at least one negative interaction with one of the species of the core.**

25 **Note that there is no representation of space at the local community scale in this model; hence the**

26 **spatial dimension in each box is simply an artifact of the illustration.**
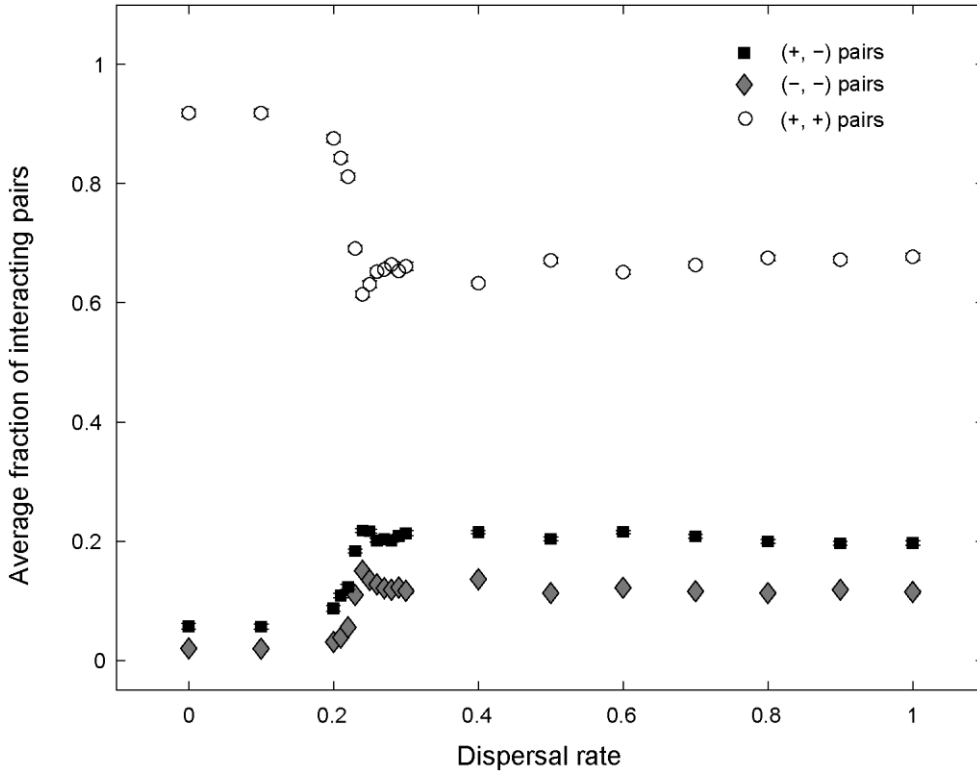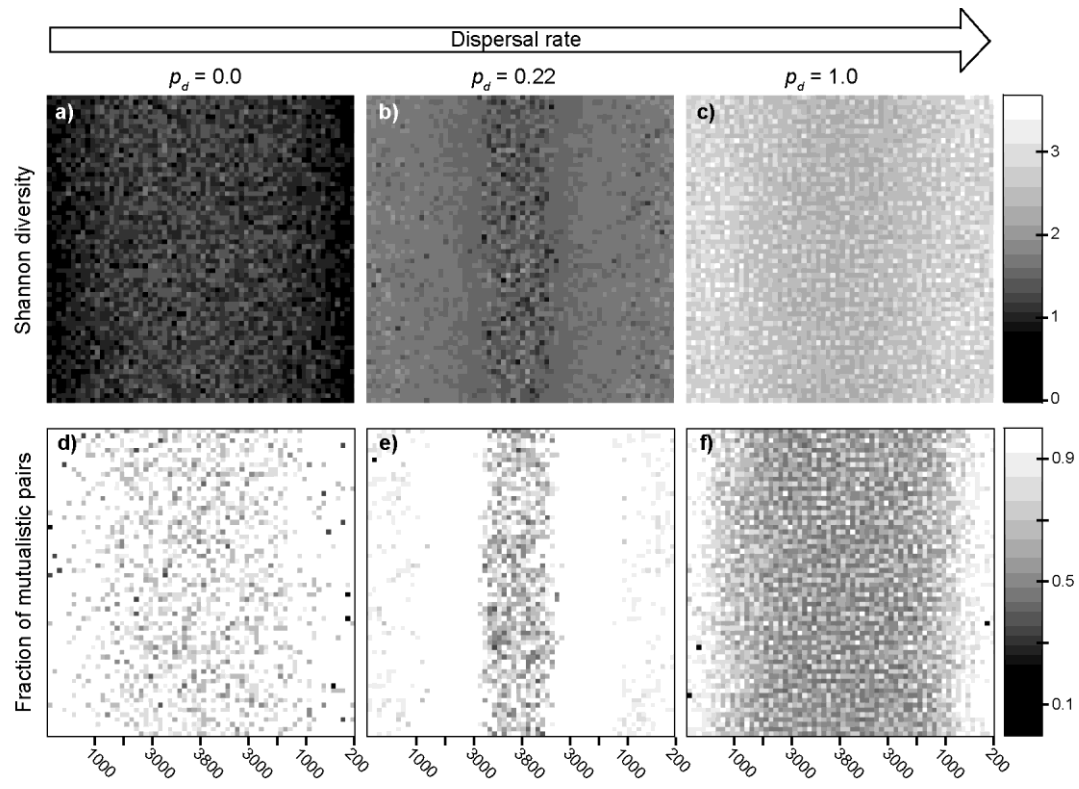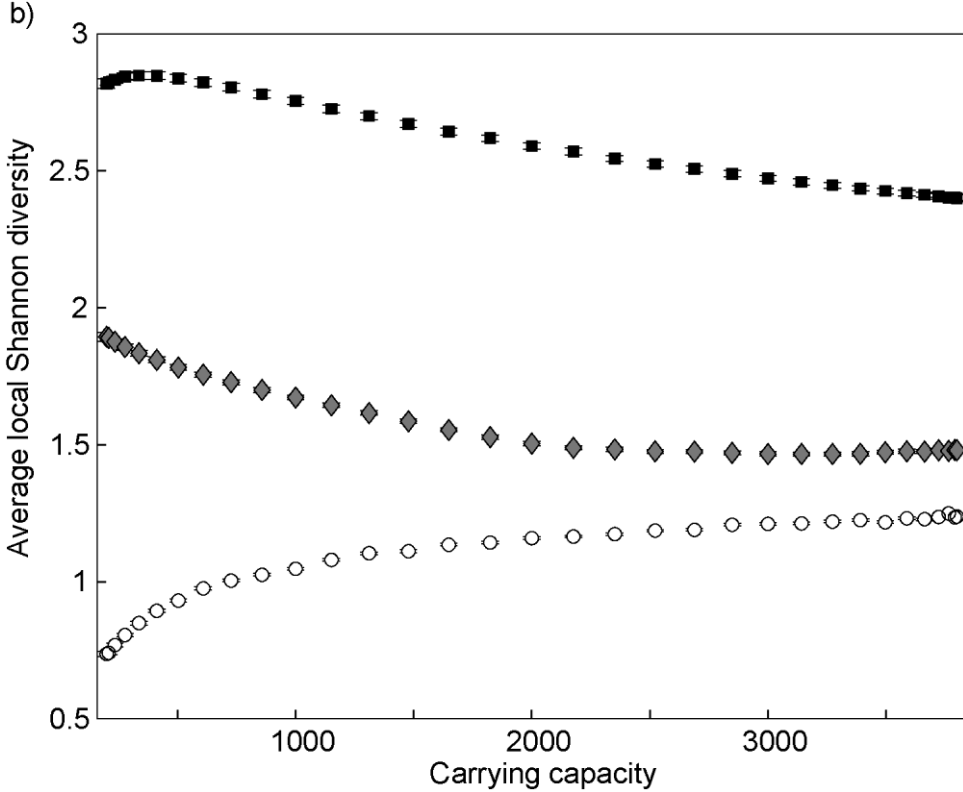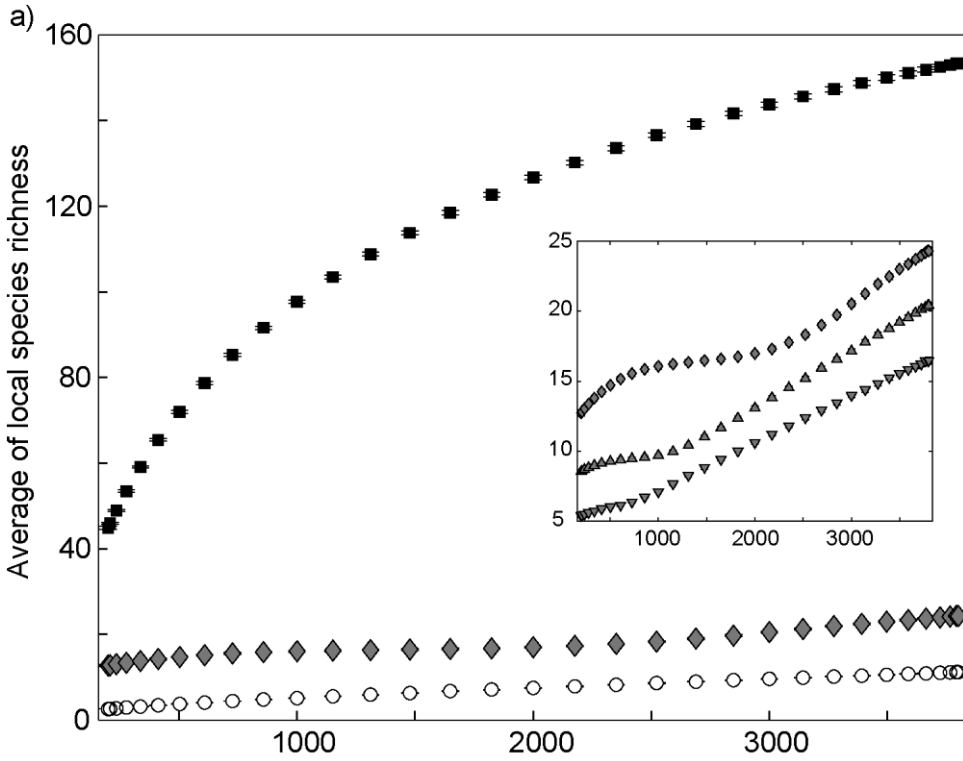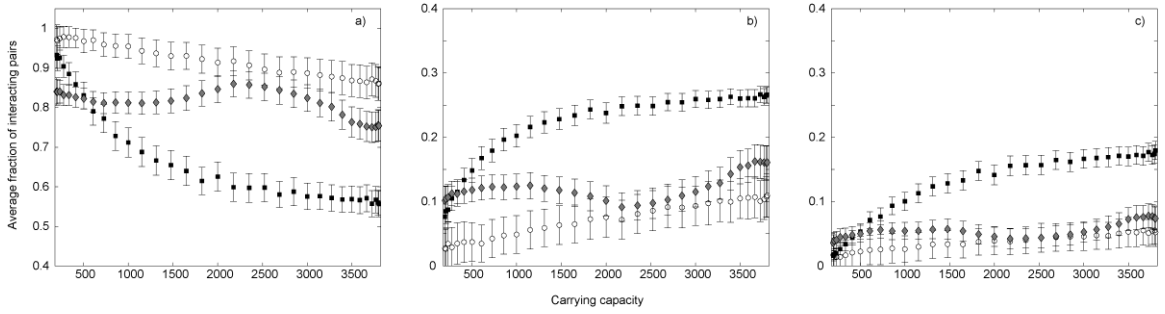
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a)

b)

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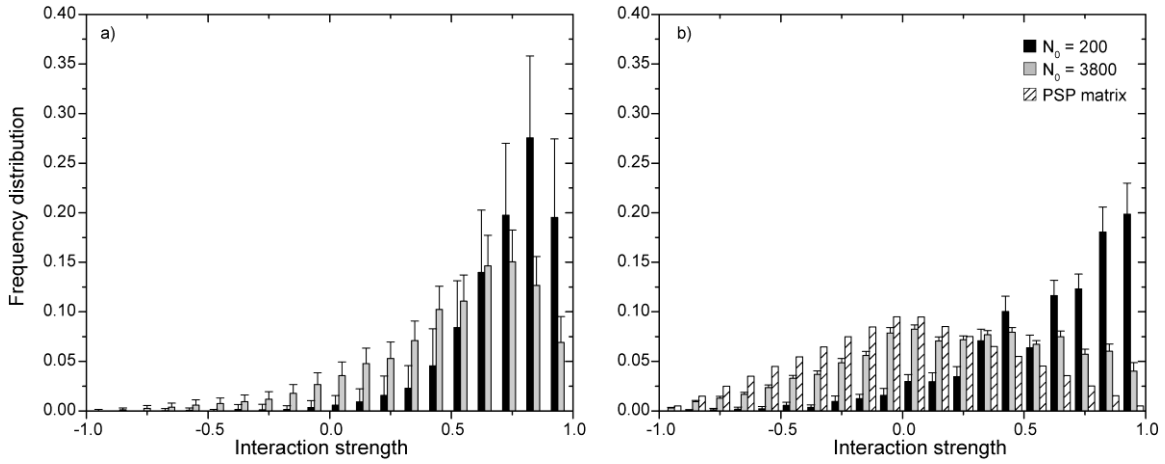4
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$N_0 = 200$ $N_0 = 2000$ $N_0 = 3800$

Carrying capacity

Dispersal rate

$p_d = 0.0$

$p_d = 1.0$

1