

Community Patterns in Source-Sink Metacommunities

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Submitted December 4, 2002; Accepted May 14, 2003;
Electronically published November 6, 2003

ABSTRACT: We present a model of a source-sink competitive metacommunity, defined as a regional set of communities in which local diversity is maintained by dispersal. Although the conditions of local and regional coexistence have been well defined in such systems, no study has attempted to provide clear predictions of classical community-wide patterns. Here we provide predictions for species richness, species relative abundances, and community-level functional properties (productivity and space occupation) at the local and regional scales as functions of the proportion of dispersal between communities. Local (α) diversity is maximal at an intermediate level of dispersal, whereas between-community (β) and regional (γ) diversity decline as dispersal increases because of increased homogenization of the metacommunity. The relationships between local and regional species richness and the species rank abundance distributions are strongly affected by the level of dispersal. Local productivity and space occupation tend to decline as dispersal increases, resulting in either a hump-shaped or a positive relationship between species richness and productivity, depending on the scale considered (local or regional). These effects of dispersal are buffered by decreasing species dispersal success. Our results provide a niche-based alternative to the recent neutral-metacommunity model and have important implications for conservation biology and landscape management.

Keywords: dispersal, metacommunity, local and regional species richness, species abundance patterns, source-sink, productivity.

It is well established that communities are organized at multiple scales and that the interactions between these scales determine both the local and the regional patterns

of species richness (Ricklefs 1987; Levin 1992; Zobel 1997; Loreau 2000). These considerations reflect the growing interest among ecologists in studying communities as organized into networks linked by dispersal, called metacommunities (Wilson 1992; Holt 1993; Leibold 1998; Hanski 1999; Hubbell 2001; Mouquet and Loreau 2002). The appreciation of both local and regional processes in the context of community ecology is not necessarily new, but only recently has the metacommunity concept been clearly defined (Wilson 1992; Holt 1993).

Various mechanisms of species coexistence have been proposed in such a metacommunity framework. The best known is the competition-colonization trade-off (Levins and Culver 1971; Horn and MacArthur 1972; Tilman 1994), where the combination of community extinction and recolonization and appropriate trade-offs between species' competitive and colonizing abilities explain a high level of species richness. The species-sorting perspective (Leibold 1998) explains local species richness as a function of differential priority effects and dispersal limitation at the scale of the region. More recently Hubbell (2001) has proposed a neutral theory in which mainland diversity is a function of speciation-extinction balance, whereas local-scale diversity adds a drift (local-extinction) component. Even if Hubbell's model is closer to a continent-island system than to a metacommunity in which communities are linked through immigration and emigration, it can be viewed as the endpoint of a continuum of coexistence mechanisms within the metacommunity framework, just as it is in metapopulation theory (Hanski and Gyllenberg 1993). Another very important mechanism of species coexistence in metacommunities is the source-sink effect (Levin 1974; Shmida and Ellner 1984; Holt 1993; Pulliam 2000; Mouquet and Loreau 2002). At the metacommunity scale, a source-sink (Pulliam 1988) or mass (Shmida and Ellner 1984) effect occurs because species are not excluded from communities where they are bad competitors, because they immigrate (Brown and Kodric-Brown 1977; Loreau and Mouquet 1999) from other communities where they are good competitors.

This idea of a source-sink dynamic at the metacommunity scale has been studied theoretically with weighted competitive-lottery models (Shmida and Ellner 1984;

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Chesson 1985; Iwasa and Roughgarden 1986; Mouquet and Loreau 2002) and classical Lotka-Volterra competition models (Levin 1974; Amarasekare and Nisbet 2001). These studies have provided strong evidence that the regional dimension of species interactions could promote the local coexistence of competing species through a transfer of the effects of regional habitat heterogeneity to the local scale (Levin 1974; Amarasekare and Nisbet 2001; Mouquet and Loreau 2002) and regional similarity between competing species (Mouquet and Loreau 2002). This approach provides a niche-based alternative to recent neutral-based metacommunity models because coexistence results from regional niche differentiation and dispersal between communities (Mouquet and Loreau 2002). It also differs from competition-colonization models because it does not concern transient local coexistence between species with different life cycles.

Although the conditions for local and regional coexistence in metacommunities have now been extensively investigated, few studies have provided clear predictions about classical community-ecological patterns. Some predictions are available from the neutral perspective (Hubbell 2001; Chave et al. 2002) and, to a certain extent, for the competition-colonization models (Tilman 1994; Kinzig et al. 1999; Chave et al. 2002; Mouquet et al. 2002), but none for source-sink metacommunities. Here we provide such predictions for species richness, species relative abundances, and community-level functional properties (productivity and space occupation) at the local and regional scales as functions of the proportion of dispersal between communities. We have also studied the consequences of varying the proportion of successful dispersal. We have found some clear patterns that vary as functions of the proportion of dispersal between communities.

These predictions are important for many reasons. They correspond to what ecologists commonly measure in the field and use to infer the mechanisms behind species coexistence (Hubbell 2001; but see Chave et al. 2002). They can be viewed as an alternative explanation of classical community patterns that has been revived by the recent neutral model proposed by Hubbell (2001). They address some fundamental issues in ecology, such as the relationship between local and regional species richness, the relationship between species diversity and productivity, and the consequences for biodiversity of altering landscape structure, within a common framework, and they are crucial to decisions about conservation biology and landscape management, in the context of increasing landscape perturbation by human activities (Lawton and May 1995; Turner et al. 2001).

Model and Methods

Because of its basic structure, our model portrays sessile organisms with a dispersal stage, such as plants or marine sessile organisms and, on a different scale, territorial organisms with natal dispersal, but the results are relevant to all kinds of organisms that make up competitive metacommunities.

The Model

We use a model (Mouquet and Loreau 2002) that includes three hierarchical levels (individual, community, and metacommunity) and in which local dynamics (community) are described by the formalism developed for meta-populations (Levins 1969, 1970), but each site is occupied by a single individual (as in Tilman 1994). The regional dynamic is obtained as in continent-island models through immigration (Gotelli 1991; Loreau and Mouquet 1999) but with an explicit origin for immigration that is a function of emigration from other communities in the metacommunity.

At the local scale, P_{ik} is the proportion of sites occupied by species i in community k (note that i always refers to species and k to communities). Each community consists of S species that compete for a limited proportion of vacant sites, V_k . The metacommunity is constituted by N communities that differ in their local conditions, so species exhibit different phenotypic responses in the different communities. To take into account this regional heterogeneity, we used a multiple indexing of species life-history trait parameters. Each species i is characterized by a set of reproduction parameters, c_{ik} , each of which measures the potential local reproductive rate of species i in community k , and a set of mortality rates, m_{ik} .

At the regional scale we assumed a constant proportion a of dispersal between communities. In each community, this proportion represents the fraction of the local reproductive output that emigrates. For simplicity we assumed that this proportion was equal for all species in all communities, so it could be used as a simple measure of metacommunity connectivity. Roughly speaking, a measures the relative importance of regional and local influences in local communities, as well as the degree of coupling between population dynamics within the metacommunity.

For each species in each community, we considered an explicit immigration function I_{ik} . Emigrants were combined into a regional pool of dispersers that was equally redistributed to all other communities, except that no individual returned to the community it came from. After immigration, individuals took the parameters corresponding to the community they immigrated to. Dispersal success, θ , is the probability that a migrant will find a new

community. It depends on several factors such as mortality during dispersal or failure to find a suitable community.

Formally, the equations for such a metacommunity are

$$\frac{dP_{ik}}{dt} = [\theta I_{ik} + (1 - a)c_{ik}P_{ik}]V_k - m_{ik}P_{ik}, \quad (1)$$

where

$$I_{ik} = \frac{a}{N-1} \sum_{l \neq k}^N c_{il}P_{il} \quad (2)$$

and

$$V_k = 1 - \sum_{j=1}^S P_{jk}. \quad (3)$$

We define the local basic reproductive rate of a species as the ratio of its potential local reproductive and mortality rates:

$$r_{ik} = \frac{c_{ik}}{m_{ik}}. \quad (4)$$

It has been shown previously that, in such a system, this rate determines local competitive ability because competition for space takes the form of a weighted lottery (Loreau and Mouquet 1999).

Numerical Simulations

In general, we numerically simulated a metacommunity consisting of 20 species competing in 20 communities. We chose the matrix of species' local basic reproductive rates (eq. [4]) to fit the constraint of regional similarity (Mouquet and Loreau 2002). The rates were chosen such that each species was the best competitor in one community, the second best competitor in another community, the third in a third, and so on. The matrix corresponded to a deviation of 5% from the strict similarity case, in which the matrix of species parameters is completely symmetrical at the scale of the region (Mouquet and Loreau 2002). The values of local basic reproductive rates ranged from 0.66 to 16.66.

To study the relationship between local and regional species richness, we generated different regional species-pool sizes by varying the degree of regional heterogeneity. The maximal regional heterogeneity corresponded to the case presented above (20 communities with different local conditions). Species were characterized by a parameter x_i between 0 and 1 ($x_i = 0.0, 0.05, \dots, 1.0$), and environmental conditions in each community were characterized

by a parameter E_k between 0 and 1. We obtained the different levels of heterogeneity by choosing E_k from different classes of values H such that there were 1, 4, 6, 10, 13, 16, or 20 different types of communities (when $H = 1$, $E_k = 0.5$ for all k ; when $H = 20$, $E_k = E_{k-1} + 0.05$, where $E_1 = 0$; other cases were intermediate). We assumed that the closer a species' parameter was to the environmental value of a community, the more competitively successful that species was in that community ($c_{ik} = (1 - |E_k - x_i|) \times 3$). We considered mortality equal in all species ($m_i = 0.3$ for all i). The values of local basic reproductive rates therefore ranged from 0.5 to 10. To avoid any confounding effect, we considered only the case in which dispersal success was maximal ($\theta = 1$).

In both cases, we used a Euler approximation ($\Delta t = 0.001$) of equation (1) and ran the simulations until an equilibrium was reached in all communities. At the beginning of each simulation, we attributed the same proportion of sites to each species in all communities ($P_{ik} = 0.01$, for all i and k). After a period of time corresponding to the very early stage of community development, we assumed a species was extinct when its proportion of occupied sites was lower than 0.01, in order to mimic the effect of stochastic extinction. Considering an extinction threshold gives a good approximation of stochastic extinction in such lottery models (Loreau and Mouquet 1999).

For simplicity, the results we present here were obtained with a single set of species parameters, but the qualitative conclusions of our simulations are robust to significant deviations from those parameter values. To determine whether our results depended on a special distribution of species parameters, we performed simulations with different sets of species parameters with 5% and 15% deviation from the strict-similarity case (as defined above) and found no qualitative differences. To determine whether our results depended on initial conditions (initial proportion of sites occupied), we performed other simulations with different initial proportions of occupied sites, and we found no significant differences in the resulting equilibrium communities.

Community-Level Properties

Community-level properties were measured after the equilibrium was reached in all communities. We measured the three components of species diversity (Whittaker 1972): local within-community (α) diversity, diversity between communities (β), and total regional (γ) diversity. We related these components to each other using an additive partitioning

$$\gamma = \beta + \bar{\alpha} \quad (5)$$

(where $\bar{\alpha}$ is the mean α diversity in the metacommunity), rather than using Whittaker's original multiplicative form because this partitioning has well-defined statistical properties and can be used to compare communities with different levels of γ diversity (Lande 1996; Loreau 2000).

We assumed that each species' local productivity was determined by its local competitive ability (Tilman et al. 1997; Loreau 1998; Loreau and Mouquet 1999; Cardinale et al. 2000; Mouquet et al. 2002). Community productivity was therefore correlated with both the number of sites occupied per species and their local reproductive rates (which are correlated with species' competitive abilities in our model) in that community according to the following relationship (Loreau and Mouquet 1999):

$$\Phi_k = \sum_i^S c_{ik} P_{ik} \quad (6)$$

Space occupation was simply equal to the sum of the proportions of sites occupied by all species. We present average values of productivity and space occupation averaged over the whole metacommunity.

Results

Community Patterns with Maximum Dispersal Success ($\theta = 1$)

Species Abundance Patterns. Figure 1 shows species relative abundances in a local community at equilibrium as a function of the proportion of dispersal within the metacommunity in the case when regional heterogeneity is maximal. When dispersal was zero, dominance by the best local competitor was complete (*Sp. A* in fig. 1). As dispersal increased, some species were rescued from competitive exclusion because they immigrated from communities where they were dominant. The local best competitor occupied fewer sites, and species relative abundances became more equitable and independent of their local competitive abilities (fig. 1). Under high dispersal, however, the potential for local coexistence decreased because the species that was the best competitor at the scale of the region (*Sp. B* in fig. 1a) progressively excluded other species from the metacommunity. Note that, under high dispersal ($a = 0.9$), a species other than species B was still present. This species was a good competitor at the scale of the region and could exist at such high dispersal value when other species were excluded, but this species was also finally excluded at very high dispersal values ($a > 0.9$). The locally best competitor was excluded relatively rapidly as dispersal value increased, because the determinant of species dominance changed from local to regional competitive ability. Species were ranked according to their local competitive

ability at low dispersal, but this relation disappeared as dispersal increased (fig. 1b).

To study species rank abundance distributions, we used a larger metacommunity (40 species and 40 communities). The matrix of species parameters was chosen such that each species was the best competitor in one community and the distribution of parameters corresponded to a deviation of 5% from the strict similarity case. Local basic reproductive rates ranged from 0.16 to 24. The extinction threshold was fixed at 0.001. The species rank abundance distributions were strongly affected by the level of dispersal between communities and the scale considered. At the local scale (fig. 2a; table 1), the distribution shifted from geometric at very low values of dispersal ($a = 0.001$) to lognormal at intermediate values of dispersal ($a = 0.5$) and to geometric again at high values of dispersal ($a = 0.98$). Patterns were also consistent with the log series and the broken-stick distribution at intermediate dispersal values. At the regional scale (fig. 2b; table 1) the trend was from a flat distribution to a log series or a broken-stick distribution at intermediate values of dispersal ($0.2 < a < 0.95$) and to a geometric series at high values of dispersal ($a = 0.98$).

Local and Regional Diversity. Increasing dispersal resulted in homogenization of the species composition within the metacommunity. When dispersal was zero, local (α) diversity was minimum (one species), whereas between-community (β) and regional (γ) diversities were maximum (fig. 3): in each community a different species was the locally best competitor. As dispersal increased to an intermediate value a_{\max} , more species were maintained by immigration above the extinction threshold, and local diversity increased. Communities then became more similar in species composition, and between-community diversity decreased. Because all species remained in the metacommunity, regional diversity remained constant. When dispersal was greater than a_{\max} , local diversity decreased because the best competitor at the scale of the region dominated each community, and other species were progressively excluded. In this case, the species that were not excluded were present in all communities, between-community diversity was zero, and regional diversity was equal to local diversity and decreased. Finally, when dispersal was highest, the metacommunity functioned as a single large community, in which the regionally best competitor excluded all other species; local and regional diversity were minimum.

When we varied the maximal regional species richness using different degrees of regional heterogeneity, we found the maximal local diversity for high values of regional heterogeneity and intermediate dispersal. Regional diversity was highest at high values of regional heterogeneity

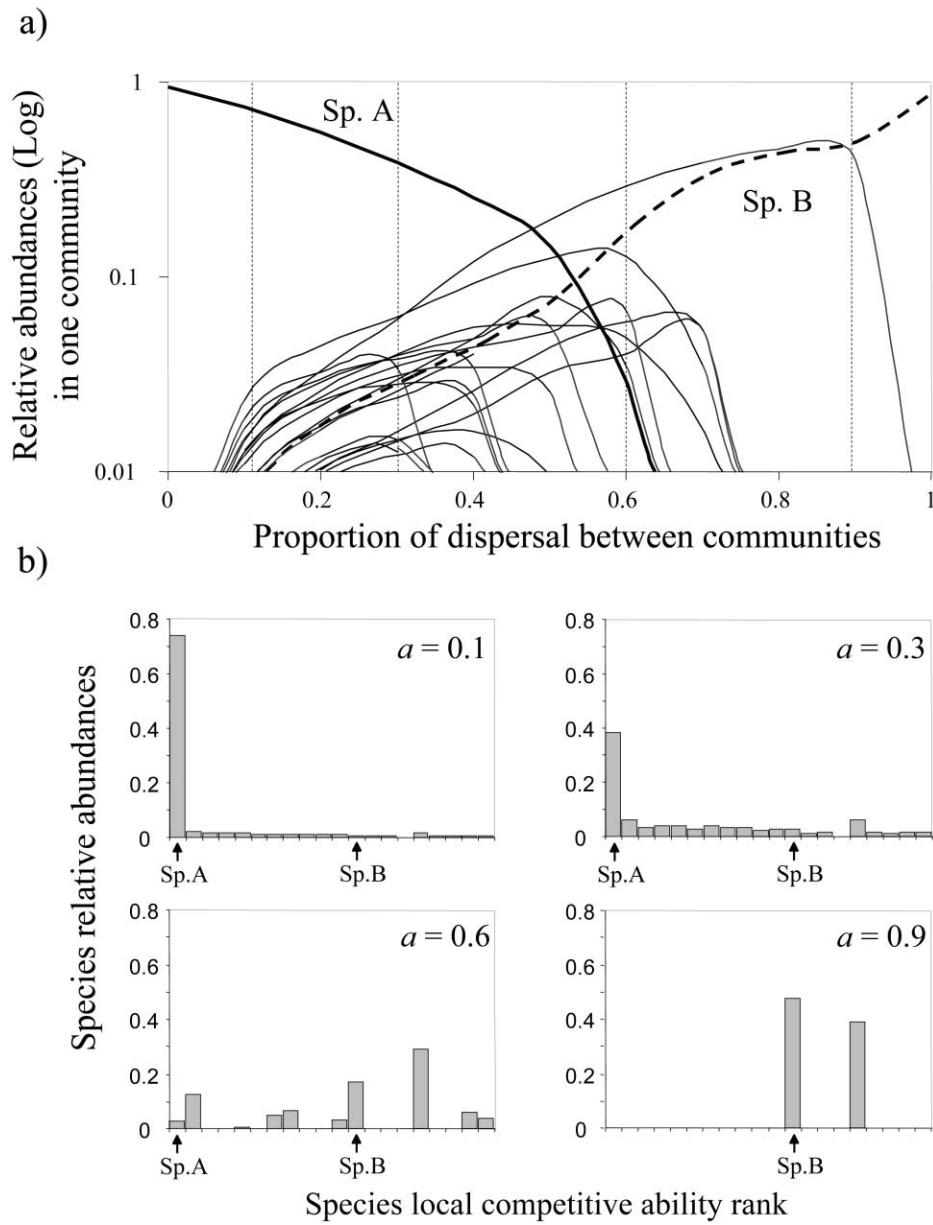


Figure 1: *a*, Species relative abundance (logarithm) at equilibrium in one community of the metacommunity as a function of dispersal between communities. The bold curve represents the best local competitor (*Sp. A*), and the dashed curve represents the best regional competitor (*Sp. B*). The other lines represent other species. *b*, Species relative abundances in the same community with species ranked in order of their local competitive abilities for four different values of dispersal, 0.1, 0.3, 0.6, and 0.9 (corresponding to the four vertical dashed lines in *a*). Results are from numerical simulations for a metacommunity of 20 species competing in 20 communities and an extinction threshold of 0.01 and $\theta = 1$. The matrix of species' local basic reproductive rates is as defined in the text for the general case.

and low dispersal. Figure 4 illustrates how the relationship between local and regional diversity varied with increasing dispersal when we obtained the gradient of regional diversity by varying regional heterogeneity. At low dispersal, regardless of regional species richness, the local species richness was limited by the locally dominant species, and

the resulting relationship between local and regional diversity was saturated. At intermediate to high dispersal, local species richness was maximal and equal to the regional species richness; the relationship was linear.

Community-Level Functional Properties. The average pro-

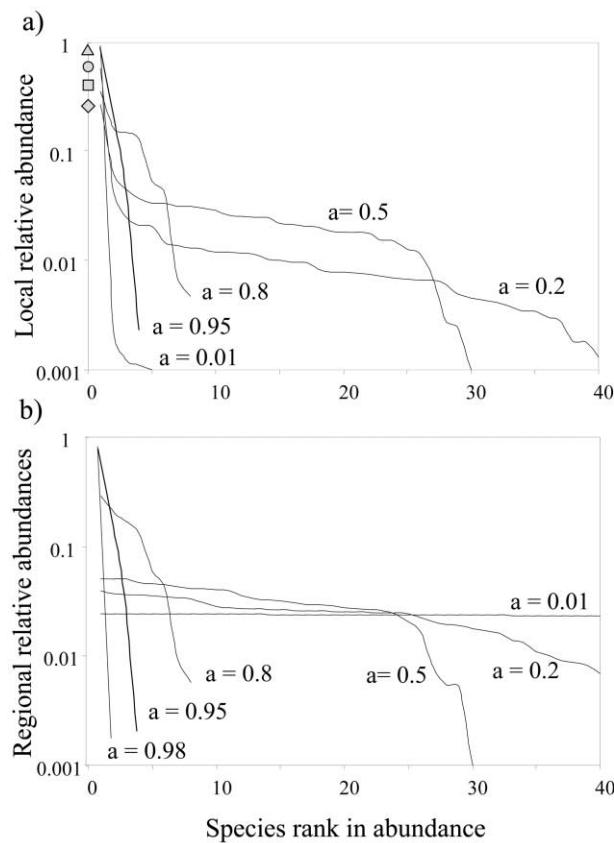


Figure 2: Species rank abundance curves at equilibrium for different values of dispersal. The abundance of each species is plotted on a logarithmic scale against the species rank, in order from the most abundant to the least abundant species. *a*, Local relative species abundances in one community of the metacommunity. For clarity, symbols have been used to differentiate between the starting points of the different curves: diamond, $a = 0.5$; square, $a = 0.8$; circle, $a = 0.2$; triangle, $a = 0.01$. The curves for $a = 0.001$ and $a = 0.98$ have been omitted because they were confounded with the curve obtained for $a = 0.01$. *b*, Regional relative species abundances: average of local species abundances over the whole metacommunity. The curve for $a = 0.001$ has been omitted because it was confounded with the curve obtained for $a = 0.01$. Results are from numerical simulations for a metacommunity of 40 species competing in 40 communities.

ductivity and space occupation decreased as dispersal increased (fig. 5*a*). When dispersal was low, the dominant species in each community was the one with the highest local basic reproductive rate, and it occupied most of the sites. Equation (6) shows that productivity was then high. As dispersal increased, species with low local reproductive rates were maintained by immigration, occupying more sites, but, on average, fewer sites were occupied in the whole community, and species rescued by immigration had lower c_{ik} , which resulted in decreasing average productivity. We plotted average productivity against local

species richness in figure 5*b*. Because the local species richness shows a hump-shaped relationship with dispersal (fig. 3), whereas productivity continuously decreases (fig. 5*a*), a humped curve emerged, which shows that at the local scale the relationship between productivity and local species diversity can be positive or negative depending on which side of the hump is observed. At the regional scale, however, the relationship between regional species richness and productivity was either positive or null (fig. 5*c*) because the regional species richness was constant or decreased with increasing dispersal (fig. 3).

Community Patterns with Varying Dispersal Success

We consider the effect of dispersal success (θ) on community-level properties and ecosystem functioning in figure 6. In all cases, the shapes of the relationships between species dispersal and the community-level properties were qualitatively similar, but varying θ did alter the position of the curve.

Figure 6*a* shows that, as dispersal success decreased, higher dispersal values were needed before any species could be rescued from competitive exclusion and before exclusion by the regionally best competitor occurred. Note that at high dispersal values species extinction resulted from both competition with the regionally competitive species and the loss of too many individuals during the dispersal event. The relationship between the proportion of dispersal and local species richness shifted to the right (fig. 6*b*). In other words, the importance of regional dynamics decreased as dispersal success decreased, and

Table 1: The shape of the species rank abundances obtained in one community (local) and averaged over all communities (regional) for different values of dispersal (shown in fig. 2)

Dispersal	Local scale		Regional scale	
	N	Distribution	N	Distribution
.001	2	Geometric	40	Flat
.01	4	Log series	40	Flat
.2	40	Log series	40	Broken stick
.5	26	Log normal	26	Log series
.8	8	Broken stick	8	Broken stick
.95	4	Log series	4	Log series
.98	2	Geometric	2	Geometric

Note. We have used four classical species abundance models: geometric, log series, log normal, and broken stick (May 1975) plus a flat model (all species abundances equal). Expected values were obtained as by Magurran (1988) and were compared to observed values with a χ^2 goodness-of-fit test. For each dispersal value we have selected the model that best fit the observed distribution.

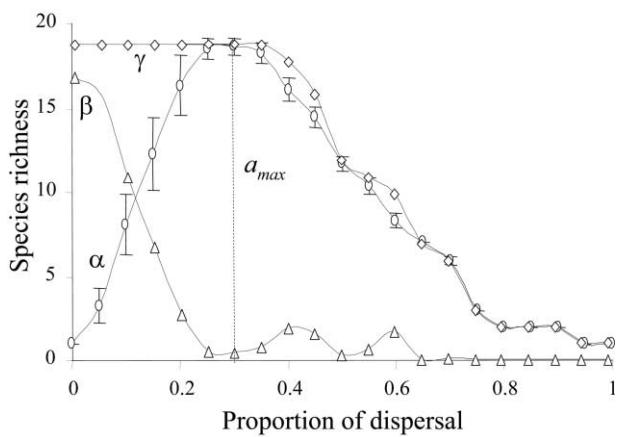


Figure 3: Species richness as a function of the proportion of dispersal between communities. Circles = local (α); triangles = between-community (β); diamonds = regional (γ). a_{max} is the dispersal value at which species diversity is maximal.

higher values of dispersal were needed to generate the same effects of dispersal on local and regional coexistence.

The effect of dispersal success on local productivity depended on dispersal values (fig. 6c). When dispersal was zero, productivity was high regardless of dispersal success. For intermediate values of dispersal, because the intensity of regional dynamics decreased as dispersal success decreased, the negative effect of dispersal on productivity was buffered, and local productivity was higher for low dispersal-success values. Finally, for high values of dispersal ($a > 0.8$), too many individuals were lost during the dispersal phase, local species abundances decreased strongly, and productivity was lower for low dispersal-success values.

Discussion

Our results help to generalize and complement previous results on source-sink metacommunities (Levin 1974; Shmida and Ellner 1984; Chesson 1985; Iwasa and Roughgarden 1986; Wilson 1992; Holt 1993; Pulliam 2000; Amarasekare and Nisbet 2001; Mouquet and Loreau 2002). They provide the first predictions about the composition and properties of source-sink metacommunities. The relevance of our model to other theoretical approaches is discussed elsewhere (Mouquet and Loreau 2002); here we focus on interpreting our results and their limitation.

Dispersal as a Link between Local and Regional Species Richness

We found a humped relationship between local (α) species richness and dispersal values (see also Mouquet and Loreau 2002). Dispersal acts to transfer the effects of regional heterogeneity to the local scale, such that species that can only coexist regionally when communities are closed also coexist locally when communities are open. Because dispersal leads to a progressive homogenization of the metacommunity, it also has an overall negative effect on local and regional species richness from intermediate to high dispersal values.

From our results, one would expect that systems in which regional processes make a moderate contribution to local dynamics (intermediate dispersal) should have higher local species richness than systems with a large difference between the strengths of regional and local processes. For example, Forbes and Chase (2002) studied the effects of habitat connectivity in experimental zooplankton metacommunities and found that increasing connectivity (dispersal in our model) led to a decrease in both regional and between-community diversities. This effect appeared to be driven by one species, which could be interpreted as the regionally best competitor. In another recent study, using data on 34 neighboring ponds in an interconnected pond system, Cottenie et al. (2003) showed that the degree of connectivity of the metacommunity and local environmental conditions were important determinants of species

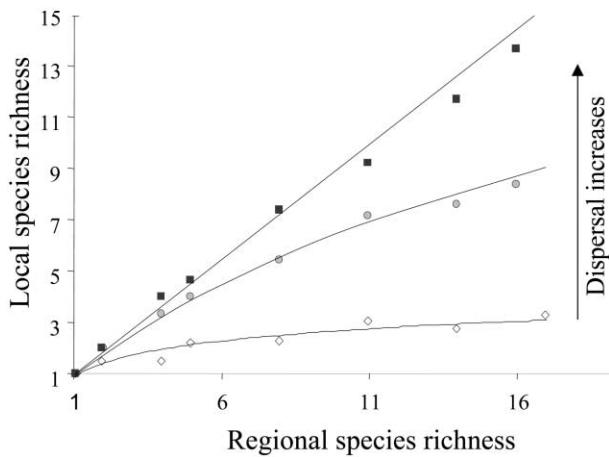


Figure 4: Relationship between local and regional species richness for different values of dispersal between communities ($a = 0.1$, black squares; $a = 0.075$, gray circles; $a = 0.025$, white diamonds). For each dispersal value, we obtained the gradient of regional species richness by varying the degree of regional heterogeneity. These results were obtained for dispersal at low to intermediate values. At high dispersal, local and regional diversity are equal and the relationship is linear.

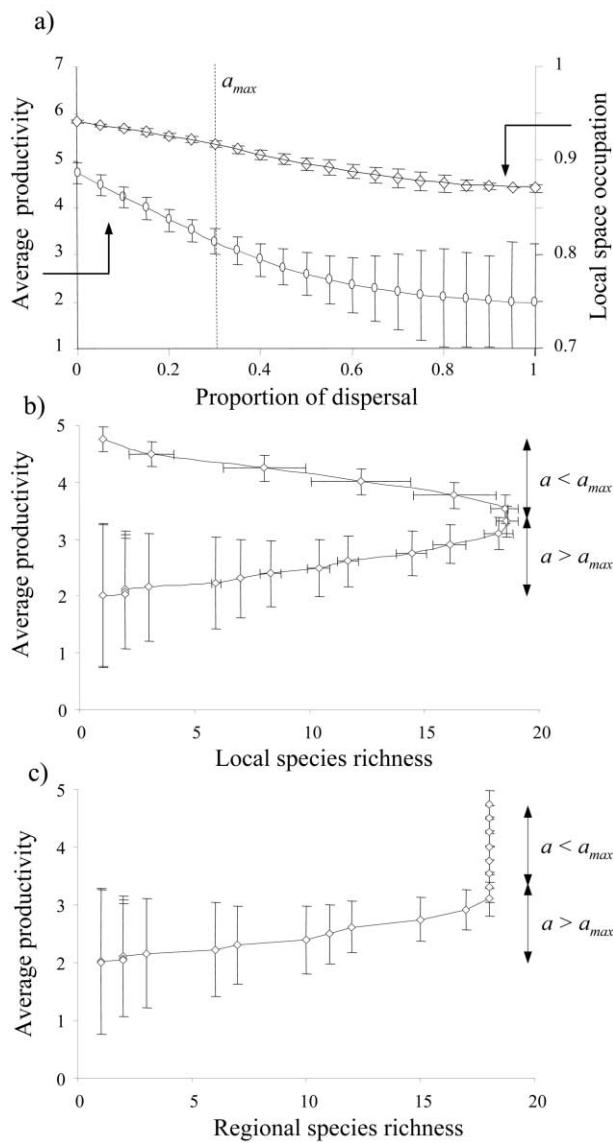


Figure 5: *a*, Average productivity (circles) and space occupation (diamonds) as functions of the proportion of dispersal between communities. *b*, The relation between local species richness and local productivity when dispersal was varied. *c*, The relation between regional species richness and local productivity when dispersal was varied. Simulation details as in figure 1. a_{max} is the dispersal value at which species richness is maximal.

richness. Even though these studies concerned multitrophic communities, whereas our model concerns competitive metacommunities, they do illustrate the possibility we found in our model for either a positive or a negative effect of dispersal on species coexistence in a metacommunity.

We also found that the shape of the relationship between local and regional species richness was a function of dispersal between communities. The shape of this relation-

ship has been used to infer the relative importance of local and regional processes in the formation of natural communities (see Srivastava 1999 for review). Classically, a saturated relationship is interpreted as indicating that local processes are acting, whereas a linear relationship suggests that regional processes are more important (after Terborgh and Faaborg 1980), but this interpretation has recently been criticized (Huston 1999; Srivastava 1999; Loreau 2000; Shurin et al. 2000; Mouquet et al. 2003). Our metacommunity model shows that a simple mechanism of local interaction can generate different relationships between local and regional species richness given particular values for the dispersal between communities and the degree of regional heterogeneity. Dispersal acts as a homogenizing factor, transferring the effect of regional heterogeneity to the local scale and thus from the β to the α component of species diversity (Loreau 2000). Our results therefore confirm that the shape of the relationship between local and regional species richness cannot reveal the underlying ecological processes. Detailed knowledge of dispersal processes and species interactions is necessary to interpretation of these relationships.

Species Abundance Patterns

Our model shows that species abundance patterns vary with the level of dispersal between communities. They are therefore functions of both dispersal and local and regional competitive abilities rather than of local competitive ability alone. Smoother distributions like the lognormal are found at low and intermediate values of dispersal because some species are maintained by a mass effect. High dispersal tends to homogenize the metacommunity, making the species rank abundance relationship steeper. Moreover, we show that spatial scale has a critical effect on the shape of these patterns. For example, at very low dispersal, a geometric curve is found at the local scale, whereas a flat curve is found at the regional scale.

Species rank abundance distributions are often supposed to give a better picture of the community structure than simple measures of richness or diversity (May 1975; but see Hughes 1986 and Loreau 1992). Recently the work by Hubbell (2001) on neutral metacommunities has emphasized the interest in such community patterns. Hubbell claimed that the excellent matching between real data and predictions from his model validated the neutral model (but see Chave et al. 2002). Our results show that similar species abundance patterns can be generated in the context of the niche theory applied at the metacommunity scale. Like Hubbell, we show that the dispersal is important in shaping this relationship and that the equilibrium distribution becomes steeper and more geometric-like with increasing community isolation (as dispersal decreases).

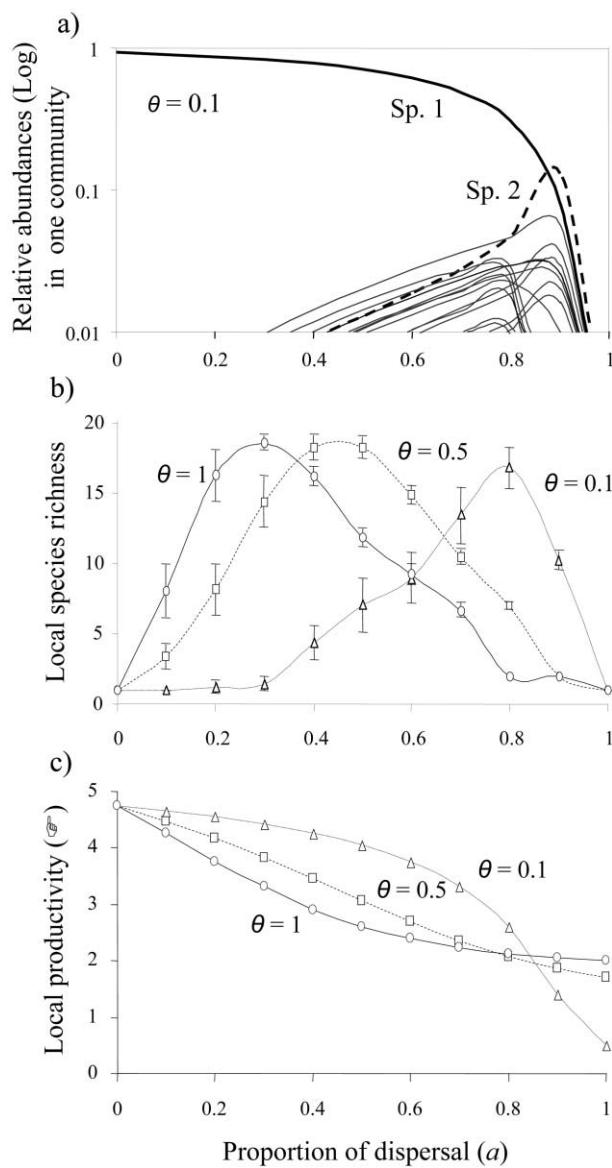


Figure 6: *a*, Species relative abundance (logarithm) in one community of the metacommunity as a function of the proportion of dispersal between communities when the species dispersal success (θ) is 0.1. The bold curve represents the best local competitor (*Sp. 1*), and the dashed curve the best regional competitor (*Sp. 2*). *b*, Local species richness and local productivity (*c*), as functions of the proportion of dispersal, for three values of dispersal success: $\theta = 1$ (circles), 0.5 (squares), and 0.1 (triangles). Means and standard deviations are given in *b*; standard deviations are omitted for clarity in *c*. Except for θ values, the simulation details are as in figure 1.

However, Hubbell found this geometric distribution because the local communities are isolated and drift is important, whereas in our model, it results from competitive exclusion by the locally best competitor. Moreover, unlike

Hubbell, we show that the distribution reverts to a geometric series at very high values of dispersal because of competitive exclusion by the regionally best competitor.

Our source-sink metacommunity model based on strong competitive interactions and regional niche differentiation therefore has the same predictive power for species abundance patterns as does the neutral model. We do not argue that either model is better than the other at explaining natural data—as Hubbell (2001) suggests, they can be viewed as complementary—but we stress the need to reevaluate carefully the use of species abundance patterns in community ecology to infer processes behind species coexistence.

Relationship between Productivity and Species Richness

Our results support the view that the current debate on the relationship between ecosystem functioning and species richness can gain insight from examination of the scale at which species richness is considered (Bond and Chase 2002; Chase and Leibold 2002) and of the mechanism that promotes coexistence (Mouquet et al. 2002).

Our model stresses the influence of dominant species on community-level functional properties such as productivity. As we have shown, the most locally abundant species is not necessarily the best local competitor, that is, the most productive species. When dispersal increases from low to intermediate, local species richness can increase at the same time as the numerical dominance (and thus primary productivity) of the best local competitor decreases. The result is a negative relationship between local species richness and productivity. At the regional scale, however, regional species richness does not vary and has no relationship with productivity. When dispersal further increases to high values, local species richness and regional species richness become equal and decrease just as does productivity, thereby generating a positive correlation between productivity and species richness at both local and regional scales. Interestingly, our model, in which the mechanism for coexistence is a source-sink relationship and regional niche complementarity, makes some predictions that are the opposite of those from models based on local niche complementarity (Tilman et al. 1997; Loreau 1998).

It has also recently been proposed that the productivity-diversity relationship was a function of the scale considered (Bond and Chase 2002). Using a verbal model, Bond and Chase (2002) argued on the basis of Mouquet and Loreau (2002) that in the context of a metacommunity a regional complementarity among species could lead to a positive relationship between productivity and regional species richness, whereas a hump-shaped relationship could be found at the local scale. Our results confirm their intuition

at the regional scale, but at the local scale we found the same pattern (hump-shaped relationship) in the absence of any local niche differentiation. Bond and Chase consider that local species richness increases first through local niche complementarity (generating a positive relationship with productivity) and then through a source-sink effect (generating a negative relationship with productivity). In contrast, our model demonstrates the possibility of a homogenization effect at high dispersal values, which results in a decline in species richness and productivity. This result suggests that, in the context of a metacommunity, the shape of the relationship between species richness and productivity will result from a coupling between local and regional niche differentiation and dispersal of organisms between communities.

To measure community productivity, we assumed that species productivity is correlated with species abundances and reproductive rates. Because reproductive rate determines species competitive ability, the better a species is at competing the more productive it will be (Tilman et al. 1997; Loreau 1998; Loreau and Mouquet 1999; Cardinale et al. 2000; Mouquet et al. 2002). This assumption can be criticized, so we have developed a more mechanistic version of our model with competition for nutrients, in which the best competitor is the species with the highest uptake of the limiting nutrient. This model predicts qualitatively similar results (Loreau et al. 2003).

Altering the Flux of Individuals between Communities

Our understanding of the consequences of habitat perturbation might change when we view systems as organized into metacommunities. Human perturbation can either reduce or increase the flux of organisms between communities by changing species' dispersal abilities or by changing the nature of the environment itself (through addition of obstacles to dispersal or corridors). Our work shows that dispersal has both positive and negative effects on species richness (fig. 3) and that these effects are buffered when species dispersal success varies (fig. 6b). Therefore, when systems are organized into metacommunities, the consequences of altering the flux of individuals between communities can be positive, negative, or null depending on dispersal before the perturbation and species characteristics. Connectivity (dispersal in our model) must therefore be a key issue in ecological management decisions (Doak 1995; Huxel and Hastings 1999). More will be presented on this topic elsewhere.

Limitations

Like any model, ours involves a number of simplifying assumptions. We have assumed that all species have the

same dispersal ability, whereas in reality species are likely to differ in this trait, for example, in the case of a trade-off between dispersal and local competitive ability (Levins and Culver 1971; Hastings 1980; Tilman 1994). Integrating different dispersal strategies into our model is beyond the scope of this discussion, but we can suggest some general predictions. First, a trade-off between dispersal ability and local competitive ability would make coexistence more difficult, because each species that would potentially be a good competitor in at least one locality would have a lower ability to disperse from source to sink areas. If the trade-off involved regional competitive ability, however, the potential for local coexistence would be higher because regional competitive exclusion would require higher dispersal values.

Our model requires differentiation between two or more spatial scales that are identical for the interacting species. This differentiation is present in plants or marine sessile organisms whose life cycles include a fixed and a mobile stage. For mobile animals this distinction can be set by the environment itself, as for fish communities living on coral reefs, or can result from territoriality. In the general case, however, each species perceives the environment at its own scale, and we acknowledge that our separation of it into two scales (local and regional) is an oversimplification. Future models should integrate a species-specific perception of scales.

We have considered competition to obey a lottery (Chesson and Warner 1981) with an infinite number of sites and single-site occupancy. This type of competitive model may be valid for a number of plant and animal communities with strong recruitment limitation (Sale 1982; van der Maarel and Sykes 1993; Hubbell et al. 1999). We recognize that other types of competition rules might change some of our results (Pacala and Rees 1998), but similar results were obtained for other metacommunity models based on different forms of competition, such as direct interference (Amarasekare and Nisbet 2001) and exploitation competition for a limiting nutrient (Loreau et al. 2003). We therefore believe that our main findings are qualitatively robust.

Because local competitive ability is related to the ratio of potential local reproduction to mortality, we have only varied local reproductive parameters to vary species competitive ability, but the assumption for equal mortality might be important in such a lottery model (Muko and Iwasa 2000). More research is needed before a conclusion on this point can be reached.

Unlike other metapopulation models, ours does not consider the possibility of stochastic extinction of local populations because we wished to explore the effects of dispersal uncluttered by coexistence mechanisms other than the source-sink effect. Stochastic extinction might be

an important process, particularly for metacommunities constituted of small populations, and it would be an interesting extension of the model to explore.

We have assumed that dispersers are naïve, that is, do not actively select their habitat. MacArthur (1972; Holt 1997) pointed out that an organism from a source should have no interest in dispersing to a sink, so naïve dispersal should be selected against. However, Holt (1997) demonstrated that, when environmental conditions in a habitat fluctuate, dispersing offspring to sink habitats can increase the long-term growth rate of a population because dispersal into sinks can be advantageous if sinks sometimes become sources and vice versa.

Finally, we assume that each species is a good competitor in at least one community and thus that species are locally adapted, but from an evolutionary point of view, local adaptation is a negative function of immigration intensity (Slatkin 1987). A metacommunity organization should therefore lead to a kind of decoupling between the traits of species and the conditions they experience in a local community (Thompson 1999). In closed systems species should be well adapted to local constraints, whereas in open systems they should escape from local selective pressures and be "nonadapted" (Wright 1930; Holt 1993). The degree of dispersal between communities should therefore fix a limit to dispersal between communities in the long term, beyond which species will not be locally adapted and the promotion of coexistence by the source-sink effect will vanish.

Metacommunity Ecology in the Field

Metacommunity ecology is just emerging, and much remains to be done if we are to understand the different kinds of mechanisms acting to promote coexistence in such multiscale organized systems (i.e., competition-colonization, species sorting, neutral, and source-sink). Species diversity in natural communities probably results from a combination of these different mechanisms along a continuum, and their relative contributions to phenomena that ecologists observe in the field must now be determined. Doing so would require reviewing the patterns predicted by the four different models of metacommunities in a comparative study designed to find patterns specific to each model and to differentiate among the processes behind the patterns.

Our study opens the way, showing that the patterns of rank abundance can probably not be used to differentiate between the neutral (Hubbell 2001) and source-sink mechanisms because the two models overlap in their predictions. The only difference appears at high dispersal values, where the source-sink model predicts a reversion to a geometric rank abundance distribution at the local scale.

Unfortunately, we do not know of any field study that has demonstrated such a pattern and would permit the differentiation between the two models. Some elements of comparison between the neutral and the competition-colonization models also appear in recent work by Chave et al. (2002). To go further in quantifying the relative contributions of these different processes to the properties of ecological communities, one must build models that will incorporate these different mechanisms into the same framework. Such a thorough and complete comparison of predicted patterns is essential but is beyond the scope of the present study. We hope our work will stimulate ecologists to go further in this direction.

Another issue important to empirical tests of the validity of metacommunity models is identification of parameters that can be measured in the field. Hubbell's neutral model has few adjustable parameters and is therefore broadly applicable, but at the same time these parameters are descriptive and very difficult to measure in the field unless they are inferred from the community-level patterns the model is supposed to describe, a process that introduces an important element of circularity. Source-sink metacommunity models (Wilson 1992; Holt 1993; Amarasekare and Nisbet 2001; Mouquet and Loreau 2002; the present paper) require parameters that are more likely to be measured in the field, like species dispersal, competitive ability, and dispersal success. For example, we have shown that any kind of species rank abundance patterns can be generated by variation of only one parameter, dispersal (connectivity), which can be measured in the field. Ecologists will now have to cross the community patterns observed in the field with species and landscape characteristics to test empirically the validity of the source-sink effect as a potential mechanism of species coexistence in ecological metacommunities.

Conclusions

Local communities are shaped by local ecological factors but also by exchanges with neighboring or more distant systems through dispersal. We have shown how the metacommunity approach can change and improve our understanding of the patterns in ecological communities. Our results stress the need for more approaches in community ecology that mix the different scales of ecological systems to explain the essence of community-level properties and to make more accurate predictions (at appropriate scales) for conservation biology and landscape management. Our simple model requires more complex modeling approaches that will incorporate different species' life-history traits, landscape complexity, as well as demography and evolution into the same framework to elucidate fully the effects of dispersal on species diversity in a metacommunity.

Acknowledging the openness of ecological systems and considering explicit immigration-emigration dynamics also provide a new perspective on ecological niche theory. We have shown that, even when niche theory does not do a good job of predicting community patterns at the local scale, pushing some ecologists toward other views of communities, like those in neutral models, it may nevertheless be appropriate when applied at the regional scale. We do not argue that one model is better than another but that the niche theory will gain from being reinterpreted in the broader context of metacommunity ecology, which should therefore not be excluded from any attempt to establish unified theories of biodiversity.

Acknowledgments

We thank J. Chase and T. E. Miller for their encouragement and for comments on the manuscript. We thank B. Bolker, P. Morin, and one anonymous reviewer for comments on the manuscript. A. B. Thistle kindly edited the manuscript. This work was funded in part by the School of Computational Science and Information Technology at Florida State University, by National Science Foundation grant DEB 1308-431-22, and by a grant from the Centre National de la Recherche Scientifique, Programme Populations Fragmentées, Extinction, Sélection d'Habitat, et Biologie de la Conservation.

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Associate Editor: Peter J. Morin