

Notes and Comments

Coexistence in Metacommunities: The Regional Similarity Hypothesis

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Species richness has historically been studied with a separation between small- and large-scale processes. Species diversity has been approached, on the one hand, from a local perspective, based on niche theory (Pianka 1966; MacArthur and Levins 1967; Schoener 1974), and on the other hand, from a regional perspective, through island biogeography (MacArthur and Wilson 1967), with no strong interactions between these two levels. At the local scale, interactions between competing species constrain diversity, and coexistence is a function of niche dimensions and resource heterogeneity (MacArthur and Levins 1967) or differences in species life-history traits as in colonization-competition trade-off models (Hastings 1980; Tilman 1994). At the regional scale, the theory of island biogeography (MacArthur and Wilson 1967) ignores local dynamics and considers local diversity as the result of regional processes such as chance events of immigration and extinction. There are no limits to diversity except those arising from the size of the regional species pool (continent size) and the constraints on immigration events (continent-island distance). This apparent contradiction has been named "MacArthur's paradox" (Schoener 1983; Loreau and Mouquet 1999) because MacArthur's contribution has been central in both niche theory (Mac-

Arthur and Levins 1967) and island biogeography theory (MacArthur and Wilson 1967).

Despite this arbitrary separation of scales, many authors have pointed out that both regional and local processes are acting together to structure local species diversity (see Ricklefs 1987; Zobel 1997 for reviews). In a previous article (Loreau and Mouquet 1999), we studied the influence of immigration (regional scale) on the dynamics of local plant communities. We showed that immigration can be a key factor determining local species richness by maintaining a high diversity in communities in which a single species would persist if they were closed. Immigration intensity also had a considerable effect on species relative abundances and community properties.

In this article, we go further and study a network of communities linked by dispersal, in which each community acts as a source of immigrants for other communities in the region. Thus, immigration becomes an explicit function of emigration from other communities. Such a network is called a "metacommunity" (Wilson 1992; Holt 1997). We describe the environmental conditions and constraints on species parameters that promote coexistence in such a system. Finally, we investigate the dynamics of species diversity depending on the relative importance of dispersal between communities. Our approach potentially concerns any ecological system in which the dispersal dynamics leads to a spatial structure that permits a distinction between local and a regional dynamics. However, for simplicity we describe our model in terms that concern sessile organisms such as plants.

Model Presentation

Our metacommunity model incorporates spatial structure at two levels: within communities and between communities.

At the local scale (within communities), we consider the environment as a collection of identical discrete patches given that no patch is ever occupied by more than one individual. We use the classical formalism of meta-population models (Levins 1969, 1970) applied at the scale

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of the individual (Hasting 1980; Tilman 1994). As in our previous model (Loreau and Mouquet 1999), we assume indirect competition for space; thence, once a plant occupies a site, it keeps it until its “natural” death. There is no direct competitive exclusion because of interference or competition for other resources, a species’ competitive ability is determined by its capacity to occupy free sites (a reproduction parameter) and to keep them (mortality parameter), and no particular trade-off is assumed between these traits. Thus, the proportion of free sites obtained by a species is proportional to the quantity of propagules present. This is a simple extension of “competitive lottery” models as developed by Chesson and Warner (1981) with an infinite number of sites. We ignore direct interference because we wish to explore the effects of immigration/emigration uncluttered by other processes that may affect local diversity.

At the regional scale (between communities), we assume dispersal between communities through an immigration-emigration process. We also consider heterogeneity of environmental conditions at the regional scale by changing species-specific parameters in each community. Species exhibit different phenotypic responses in the different communities because various factors (i.e., resources, predators, microclimate, etc.) act differently in each community.

These assumptions can be expressed in mathematical terms as follows. Define P_{ik} as the proportion of sites occupied by species i in community k . There are S species that compete for a limited proportion of vacant sites, V_k , in each community k , and there are N such communities. Each species i is characterized by a set of reproduction-dispersal parameters b_{ilk} , which describe the rate at which new individuals are produced in community l and establish in community k . When $k = l$, b_{ilk} corresponds to local reproduction, and when $k \neq l$, b_{ilk} corresponds to dispersal from community l to community k . Each species i dies in community k at a mortality rate m_{ik} . When a species immigrates in a particular community, it immediately takes the parameters corresponding to that community. This model reads

$$\frac{dP_{ik}}{dt} = V_k \sum_{l=1}^N b_{ilk} P_{il} - m_{ik} P_{ik}, \quad (1)$$

with

$$V_k = 1 - \sum_{j=1}^S P_{jk}. \quad (2)$$

Equation (1) is a very general model with no explicit hypotheses on the rules governing dispersal. Given that b_{ilk} is not explicitly defined, it could potentially encompass

any kind of rules concerning the relation between local reproduction, emigration, and immigration. This generality makes it very useful as a basic model to study general conditions of local and regional coexistence in a metacommunity.

Conditions for Species Coexistence

A Limiting Case: Zero Dispersal

In the limiting case where there is no connection between communities, we showed previously that local coexistence is impossible and that the species with the highest local basic reproductive rate excludes all the others (Loreau and Mouquet 1999). The local basic reproductive rate (r_{ik}) is the average number of offspring produced by an individual of species i in community k during its lifetime. It is equal to the total number of propagules produced per individual per unit of time, $\sum_l b_{ilk}$, multiplied by the mean life span of an individual, $1/m_{ik}$:

$$r_{ik} = \frac{\sum_l b_{ilk}}{m_{ik}}. \quad (3)$$

In the limiting case of no dispersal, $b_{ilk} = 0$ for $l \neq k$. At the local scale, the species with the highest local basic reproductive rate then drives all the others to extinction because it decreases the proportion of vacant sites, V_k , below the threshold required for their persistence. In this case, space can be considered as a homogeneous limiting resource and there can be no more than one species per locally limiting factor. Despite the impossibility for local coexistence, regional coexistence is possible if different factors are limiting in different communities (regional heterogeneity).

Limits to the Number of Coexisting Species

In the general case, the equilibrium obtained from equation (1) satisfies:

$$\hat{P}_{ik} = \frac{\hat{V}_k}{m_{ik}} \sum_{l=1}^N b_{ilk} \hat{P}_{il} \quad (4)$$

or

$$\sum_{l=1}^N \frac{b_{ilk} \hat{V}_k}{m_{ik}} \hat{P}_{il} - \hat{P}_{ik} = 0, \quad (5)$$

where \hat{P}_{ik} and \hat{V}_k denote the equilibrium values of P_{ik} and V_k , respectively.

There are N such equations for $k = 1$ to N , which can be rewritten in matrix form:

$$(\mathbf{Z}_i - \mathbf{I})\hat{\mathbf{P}}_i = 0, \tag{6}$$

where $\mathbf{Z}_i = (z_{ilk})$ is an $N \times N$ square matrix with $z_{ilk} = b_{ilk}\hat{V}_k/m_{ik}$, \mathbf{I} is an $N \times N$ identity matrix, and $\hat{\mathbf{P}}_i = (\hat{P}_{ik})$ is an N -column vector. The system of equations (6) has a nontrivial solution ($\hat{\mathbf{P}}_i \neq 0$) only if

$$\det(\mathbf{Z}_i - \mathbf{I}) = 0. \tag{7}$$

In this last equation, there are N unknowns, the \hat{V}_k for $k = 1$ to N , and there are S such equations, for $i = 1$ to S . Since a system of equations admits a general solution only if the number of equations is less than or equal to the number of variables, a necessary condition for there to be an equilibrium is $S \leq N$. In conclusion, an equilibrium is possible in the metacommunity only if there are no more coexisting species (locally and regionally) than the number of communities.

Constraints on Species Parameters

It is possible to derive additional information on the constraints imposed on species parameters in such a system for there to be local coexistence at equilibrium. Multiplying both sides of equation (4) by b_{ikl} and summing over l and k gives

$$\sum_{k=1}^N \sum_{l=1}^N b_{ikl} \hat{P}_{ik} = \sum_{k=1}^N \left(\sum_{l=1}^N b_{ikl} \frac{\hat{V}_k}{m_{ik}} \right) \left(\sum_{l=1}^N b_{ilk} \hat{P}_{il} \right). \tag{8}$$

Since

$$\sum_{k=1}^N \sum_{l=1}^N b_{ikl} \hat{P}_{ik} = \sum_{k=1}^N \sum_{l=1}^N b_{ilk} \hat{P}_{il},$$

this equation can be rearranged to obtain

$$\bar{R}_i = \frac{\sum_{k=1}^N R_{ik} w_{ik}}{\sum_{k=1}^N w_{ik}} = 1, \tag{9}$$

where

$$R_{ik} = \hat{V}_k r_{ik}, \tag{10}$$

$$w_{ik} = \sum_{l=1}^N b_{ilk} \hat{P}_{il}, \tag{11}$$

and r_{ik} is, as before, the local basic reproductive rate of species i in community k (eq. [3]). Multiplying this by the proportion of vacant sites, \hat{V}_k , we obtain the local net reproductive rate of species i in the community k , R_{ik} . Finally, w_{ik} is the total quantity of propagules of species i arriving in community k per unit of time.

Consequently, \bar{R}_i is the regional average net reproductive rate of species i , weighted by the total quantity of propagules arriving in each community. At equilibrium, this must be equal to 1; that is, each individual of each species must produce one individual on average during its lifetime at the scale of the metacommunity. Because all the regional average net reproductive rates must be equal at equilibrium, this sets a constraint of regional similarity between coexisting species. Whatever the local net reproductive rates, they have to be equal when averaged at the scale of the region. And since net reproductive rates are simply basic reproductive rates multiplied by the proportion of free space in each community, this constrains basic reproductive rates, too. The latter must be sufficiently balanced over the region for equality (9) to be possible. Local coexistence is then possible in a metacommunity when species are locally different but regionally similar with respect to their reproductive rates. Local coexistence is explained by compensations between species' competitive abilities at the scale of the region.

As a corollary, however, the net reproductive rate of a species i , and hence also its basic reproductive rate, cannot be lower than that of any other species in all communities. This condition requires habitat differentiation among species. In principle, it could be met by both habitat specialists (species that are each the best competitor in at least one community) and habitat generalists (species that are never the best competitors and never the worst competitors). Using numerical simulations of our model with three species in three communities, however, we were unable to find the persistence of a generalist species in a metacommunity made up of two specialists and one generalist. This suggests that in our model the habitat differentiation constraint takes the form of a stronger habitat specialization constraint; that is, to coexist at equilibrium in the metacommunity, each species should be the best competitor in at least one community. More simulation work is needed, however, to draw conclusions on this issue.

To summarize, in a metacommunity, both local and regional species diversity will be highest when species have different niches at the scale of the region (habitat differentiation constraint) and when they have similar competitive abilities at the scale of the region (regional similarity constraint).

Explicit Dispersal and Multispecies Dynamics

To study the consequence of varying dispersal between communities, we have constructed a specific model that is a particular case of equation (1). In each community, we consider that a proportion of the total reproductive output remains resident, and the rest emigrates through a regional pool of dispersers that are equally redistributed in all other communities. Thus, for species i in community k , immigration (I_{ik}) is the sum of all emigrants from other communities, divided by the number of communities minus one. For simplicity we assume that the proportions of dispersers (a) and nondispersers ($1 - a$) are equal for all species and all communities. Parameter a may thus also be interpreted as a measure of the relative importance of regional versus local dynamics. With these assumptions, we have

$$b_{ik} = (1 - a)c_{il} \quad \text{for } k = l, \quad (12a)$$

$$b_{ik} = \frac{a}{N - 1} c_{il} \quad \text{for } k \neq l, \quad (12b)$$

where parameter c_{il} is the potential reproductive rate of species i in community l , which encapsulates local reproduction, short-distance dispersal, and establishment capacities. The model then reads:

$$\frac{dP_{ik}}{dt} = [I_{ik} + (1 - a)c_{ik}P_{ik}]V_k - m_{ik}P_{ik}, \quad (13)$$

$$I_{ik} = \frac{a}{N - 1} \sum_{l \neq k}^N c_{il}P_{il}, \quad (14)$$

with V_k as defined in equation (2).

Note that this model can be viewed as a direct extension of the propagule-rain models presented in our previous article (Loreau and Mouquet 1999) and of the continent-island model proposed by Gotelli (1991).

We investigated the dynamics of a metacommunity consisting of 20 species competing in 20 communities using numerical simulations. We kept the mortality rates constant and equal for all species but used different sets of potential reproductive rates to vary local basic reproductive rates among species (in this model the local basic reproductive rate of species i in community k is $r_{ik} = c_{ik}/m_{ik}$). We chose species potential reproductive rates to fit the constraint of regional similarity at different degrees. First, we considered an extreme formulation of this constraint based on a strict regional equivalence between species basic reproductive rates, which we call ‘‘strict regional similarity’’ (SRS). Under the SRS constraint, each species is most competitive in one community, second in another community, third in a third community, and so forth, and

has the same set of local basic reproductive rates but distributed differently among communities. This assumption is of course biologically unrealistic since the probability of finding such a strict combination of parameters in natural systems is extremely small, but it is useful as a baseline case. Second, we used combinations of species parameters that deviate from the SRS constraint to various degrees; we changed all the potential reproductive rates by either 5% or 25% (see fig. 1 for details). Third, we used a randomly generated matrix of potential reproductive rates. To make the results clearer and more realistic, we assumed extinction of rare species by setting a threshold proportion of sites below which extinction of a species occurs ($P_{ik} < 0.01$).

Local (within-community) diversity is plotted as a function of dispersal between communities for these various scenarios in figure 1. When dispersal is 0, communities are closed; in each community, there is local exclusion by the most competitive species and local diversity is lowest. As dispersal increases, more and more species are maintained by immigration above the extinction threshold, and thus local diversity increases. Local diversity then reaches a maximum value (equal to the number of communities under SRS), after which it stays constant under SRS, whereas it decreases in the other cases. When SRS is not

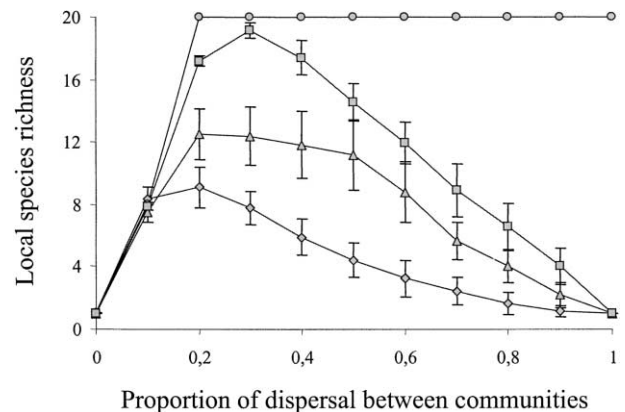


Figure 1: Local species richness as a function of the proportion of dispersal between communities, for different sets of species parameters: first, a metacommunity that meets strict regional similarity (SRS; circles); second, deviation from SRS to different degrees: all potential reproductive rates are increased or decreased by either 5% (squares) or 25% (triangles) compared with SRS, and the direction of the variation is chosen randomly; third, the potential reproductive rates are generated randomly (diamonds). Results from numerical simulations for metacommunities of 20 species competing in 20 communities and an extinction threshold of 0.01. Mortality parameters were all equal ($m_{ij} = m = 0.3$), and reproductive parameters (c_{ij}) varied from 0 to 3 depending on the competitive hierarchy. Simulations are run until the equilibrium is reached. Except for SRS, each scenario was replicated 25 times; the figure shows the means and standard deviations.

met, dispersal contributes to homogenize the metacommunity, and coexistence is no longer tolerated; the most competitive species at the scale of the region progressively excludes other species from all communities, and local diversity decreases. When the SRS condition is met, there is not any species more competitive at the scale of the region and the local diversity stays constant. The shape and the maximum of the species richness curve depend on both the degree of deviation from the SRS constraint and the dispersal rate. Note that local coexistence becomes more and more difficult as species become more dissimilar in the distribution of their local basic reproductive rates, but the potential for local coexistence in a metacommunity is still high even when species parameters are chosen randomly.

Discussion

Together with results from previous studies (Levin 1974; Chesson 1985; Iwasa and Roughgarden 1986; Holt 1993, 1997; Loreau and Mouquet 1999), our work provides a theoretical foundation for the “mass effect theory” (Shmida and Wilson 1985) at the metacommunity scale. These mechanisms of maintenance of local diversity may be compared with a kind of source-sink dynamics (Dias 1996, for a review) applied at the metacommunity scale. As we showed, our approach is entirely consistent with niche theory (Pianka 1966; MacArthur and Levins 1967; Schoener 1974), for it is not possible to have more species coexisting at equilibrium than the number of limiting factors (number of different communities). However, the scale of heterogeneity (niche differentiation) that is responsible for coexistence is here shifted from the local to the regional scale, which may be more relevant in many natural systems. Local coexistence then requires a form of regional niche differentiation, or habitat differentiation (Whittaker et al. 1973). “MacArthur’s paradox” (Schoener 1983; Loreau and Mouquet 1999) finds a possible resolution in our work because niche differentiation takes place at the regional scale and emigration/immigration processes are acting to promote coexistence at the local scale.

This result brings us to define a condition of regional similarity between coexisting species. This constraint can be interpreted as a regional compensation between local competitive abilities (Chesson and Huntly 1997). All species have equivalent competitive abilities when averaged at the scale of the region, but their spatial distributions are different; there is a kind of spatial “storage effect” (Chesson 1984). We have shown that this constraint is a function of the proportion of dispersal and that the divergence from strict regional similarity is better tolerated at intermediate proportion of dispersal, indicating high potential for local coexistence at this level of dispersal.

Similarity between species has long been invoked to explain local coexistence between competing species (see Hubbell 2001 for a review). Our work switches the scale of similarity from the local community to the region. It shows that local coexistence at equilibrium is possible without requiring any local similarity and that it is indeed regional niche differentiation between species that explains local coexistence in a metacommunity through the immigration/emigration process.

Our model assumes that the world is patchy and heterogeneous. Heterogeneity is one of the most important properties of ecological systems from local to regional scales (Levin 1992). A consequence of heterogeneity is that the environment may be viewed as a mosaic of patches varying in their local conditions. The dispersal distance of organisms should act in parallel with the scale of heterogeneity to promote coexistence in a metacommunity. Each scale of heterogeneity could be considered as a potential scale for defining a metacommunity; it is the dispersal abilities of organisms that should determine which scale is important (Addicot et al. 1987). More precisely, it is the ratio of an individual’s sampling area or home range during its nondispersal period over its potential dispersal distance, rather than dispersal distance alone, that should determine which scale of heterogeneity is relevant. Thus, the scale at which metacommunity dynamics should be studied can vary from small to large depending on which groups of organisms are considered.

Some of our results on coexistence in a competitive metacommunity are similar to those that have been found in previous theoretical studies in which species interactions were studied with a regional perspective. For example, Levin (1974; see also Amarasekare 2000; Amarasekare and Nisbet 2001) studied a patchy environment in which differential founder effects allowed different species to dominate numerically in different patches. He showed that at low proportion of dispersal species can be maintained in communities where they are not dominant as overflow from their safe areas. Chesson (1985) developed a stochastic model for competition among sessile marine organisms that live in a patchy and varying environment. He showed that species could coexist with an emigration/immigration process and special values of survival in favored patches. Iwasa and Roughgarden (1986) studied what was essentially a competitive metacommunity (even though they did not use the term), again for marine sessile animals. They found results similar to ours; that is, the number of coexisting species must be less than or equal to the number of communities, and each must be specialized in a different community. Although some of our results are in agreement with these previous studies, never before were they all generated with a unique, simple, and

general model that follows the style initiated by Levins (1969, 1970) and others.

Conclusions

Our model emphasizes the critical importance of dispersal between habitats to understand the structure of communities. We have shown that dispersal between communities can lead to a shift of regional heterogeneity at the local scale and increases the potential for local coexistence through a source-sink effect. Coexistence in a metacommunity is then obtained through a regional compensation of local competitive abilities. As a consequence, species are locally different but regionally similar. Local species diversity is then a function of the degree of regional heterogeneity, the proportion of dispersal between communities, and the degree of regional similarity between species.

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