

Immigration and the Maintenance of Local Species Diversity

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ABSTRACT: Explaining the maintenance of high local species diversity in communities governed by competition for space has been a long-standing problem in ecology. We present a simple theoretical model to explore the influence of immigration from an external source on local coexistence, species abundance patterns, and ecosystem processes in plant communities. The model is built after classical metapopulation models but is applied to competition for space between individuals and includes immigration by a propagule rain and an extinction threshold for rare species. Our model shows that immigration can have a huge effect on local species diversity in competitive communities where competition for space would lead to the exclusion of all but one species if the community were closed. Local species richness is expected to increase strongly when immigration intensity increases beyond the threshold required for the successful establishment of one or a few individuals. Community structure and species relative abundances are also expected to change markedly with immigration intensity. Increasing immigration causes total space occupation by the community to increase but primary productivity on average to either decrease or stay constant with increasing diversity, depending on the relation between immigration and local reproduction rates. These results stress the need for a regional perspective to understand the processes that determine species diversity, species abundance patterns, and ecosystem functioning in local communities.

Keywords: model, immigration, plant community, competition for space, species diversity, ecosystem processes.

Explanations for the maintenance of species diversity in ecological communities have traditionally been sought at two distinct levels. First, species diversity has been explained by local processes such as competition, predation, mutualism, and spatio-temporal variations in abiotic factors. This approach has been classical since the studies by

MacArthur and others on niche differentiation and interspecific competition (Pianka 1966; MacArthur and Levins 1967; Schoener 1974). In this theory, species interactions limit and organize species diversity, and the latter is determined by resource heterogeneity. Despite the abundant literature on the subject, this explanation of species coexistence is still debated, especially for plant communities where many species seem to coexist on a few resources (see Tilman and Pacala 1993; Bengtsson et al. 1994 for reviews). A second approach has focused on larger-scale, regional processes such as colonization of new sites and extinction of populations. This approach has also been classical since MacArthur and Wilson's (1967) equilibrium theory of island biogeography. In this theory, there is no explicit mechanism of species interactions, and the niche concept is absent. Local diversity is considered to be a function of chance events of immigration and extinction. Thus, niche theory is a deterministic theory in which diversity is limited and organized by local processes, whereas island biogeography theory is a stochastic theory in which diversity is determined by regional processes and is not necessarily organized. How can two theories that are so different be invoked simultaneously to explain community structure when the issue is addressed at different scales? Because MacArthur played a major role in the development of both theories, we refer to this apparent contradiction as "MacArthur's paradox" (Schoener 1983). This paradox is the starting point of our work, in which we attempt to link local and regional processes, which thus fits in with the perspective of "ecology at the mesoscale" (Holt 1993).

Our aim is to introduce a regional perspective in the dynamics of local processes such as competition for space. It is clear that regional biota influence local communities (Cornell and Lawton 1992; Holt 1993; Ricklefs and Schluter 1993; Caley and Schluter 1997; Cornell and Karlson 1998). Hanski's (1982) "core and satellite species hypothesis" was an interesting attempt to link regional- and local-scale processes; some of the local patterns it predicts are consistent with observed patterns in plant and insect communities (e.g., Hanski 1982; Grubb 1986; Loreau 1994). Not all patterns are consistent with the model (Gaston and Lawton 1989), however, and its mechanistic basis has been

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questioned (Nee et al. 1991). Alternative theories are poorly developed. In the classical regional-scale models of island biogeography or metapopulation theory (Levins 1969, 1970), local dynamics are not considered, while in the local-scale models of interspecific competition, regional processes are not taken into account. Here we present a very simple theoretical model to investigate the influence of immigration from a regional pool (regional process) on a plant community governed by competition for space (local process). This model may be viewed as providing a formal and mechanistic theoretical foundation for the "mass-effect hypothesis" proposed by Shmida and Wilson (1985). We examine the influence of immigration on several community properties, in particular species diversity, but also explore its potential consequences for ecosystem processes such as primary productivity and total space occupation.

Our model potentially concerns any kind of sessile organisms that have a dispersal phase during their life cycle, compete for space, and do not select their habitat. However, we present and discuss the model in the context of plant communities for the following reasons: First, plant species with a similar growth form are similar enough in resource utilization for their dynamics to be characterized by the same mathematical model. Second, competition for space is critical in plants (Vance 1984; Yodzis 1986; Goldberg and Barton 1992). Third, our model is based on the "competitive community" concept (Yodzis 1986), which may be appropriate for plant communities. This concept postulates that species are confined in one habitat (local community), resources are indispensable (space), limited in supply (fixed number of sites) and homogeneously distributed, and there is no direct interference between species. Last, the processes we discuss in this article, that is, interspecific competition, species diversity, and ecosystem processes, have been well studied in grassland plant communities (see Goldberg and Barton 1992; Tilman and Pacala 1993; Bengtsson et al. 1994; Johnson et al. 1996; Tilman 1997 for reviews).

Our approach will be first and foremost analytical but will be complemented by numerical simulations to obtain more detailed results.

Model Presentation

Our model is built after classical metapopulation models (Levins 1969, 1970) that have been used to link regional and local processes (Levins and Culver 1971; Verboom et al. 1991; Gotelli and Kelley 1993; Harrison and Taylor 1997) and to study interactions between species that compete for space (Levins and Culver 1971; Horn and MacArthur 1972; Slatkin 1974; Hanski 1983; Nee et al. 1997). These classical models consider a regional group of local

populations that are subject to extinction and connected by dispersal. Here, we consider a community of individuals rather than a population of populations (Iwasa and Roughgarden 1986; Goldwasser et al. 1994; Tilman 1994) because we are interested in the problem of local coexistence and the ultimate level of patchiness is the individual plant (Grubb 1986). We assume that competition for space is indirect, as in classical exploitation competition, unlike most previous metapopulation models that have, implicitly or explicitly, considered direct interference interactions (Levins and Culver 1971; Horn and MacArthur 1972; Slatkin 1974; Hastings 1980; Nee and May 1992; Tilman 1994). Once occupied, a site is released by a plant only at its death, and there is no direct competitive exclusion during the seedling stage. Thus, the establishment of plants in vacant sites obeys a "competitive lottery" (Sale 1977; Chesson and Warner 1981; Fagström and Westoby 1997). Although we recognize that direct interference during seedling establishment and growth can occur, particularly in fertile environments, we deliberately ignore it because we wish to explore the effects of immigration from an external source on their own, uncluttered by other processes that may affect local diversity. Taking into account interference competition and colonization-interference trade-offs (Hastings 1980; Tilman 1994) would lead to qualitatively similar conclusions regarding the effects of immigration but would dilute them with another potential mechanism for the maintenance of species diversity. Further, the "competitive lottery" may be a valid approximation for a number of plant communities with strong recruitment limitation (van der Maarel and Sykes 1993; Clark et al. 1998; Hubbell et al. 1999).

First, we generalize Levins's (1969, 1970) model to multispecies competition. Let P be the proportion of sites occupied by species i in the community. There are n such species that compete for a limited proportion of vacant sites, V . Each species i is characterized by its potential reproduction rate, c_i , which incorporates seed production, short-distance dispersal, germination and seedling establishment, and its mortality rate, m_i , which encapsulates all forms of "natural" death. Potential reproduction, however, is not fully realized because only vacant sites can be occupied.

Second, we add an external source of immigrants in the form of a "propagule rain," as in island-continent models (Gotelli 1991; Gotelli and Kelley 1993). Parameter I_i describes the species-specific immigration rate of species i , which is determined by its long-distance dispersal capacity and its relative abundance in the regional source. Another parameter, α , encapsulates the overall immigration intensity into the community, which depends on the size of, and distance from, the regional source.

The model thus reads

$$\frac{dP_i}{dt} = f_i(P_1, P_2, \dots, P_n), \quad (1a) \quad r_i = \frac{c_i}{m_i}. \quad (3)$$

with

$$f_i(P_1, P_2, \dots, P_n) = (\alpha I_i + c_i P_i) V - m_i P_i \quad (1b)$$

and

$$V = 1 - \sum_{j=1}^n P_j. \quad (1c) \quad f_i(P_1, P_2, \dots, P_n) = m_i P_i (r_i V - 1). \quad (4)$$

Note that there might be a relation between parameters I_i and c_i because both are linked to the seed production and dispersal abilities of species i . Three scenarios are then possible: (1) Parameters I_i and c_i are independent; that is, a species' immigration rate is unrelated to its potential reproduction rate. This is the typical case in island biogeography theory, where immigration is determined by the size of the regional pool (continent) and the degree of isolation of the community (distance between continent and island). (2) Parameter I_i is an increasing function of c_i . This case may arise when short- and long-distance dispersal abilities are correlated positively. (3) Parameter I_i is a decreasing function of c_i . This case involves a trade-off between local reproduction and long-distance dispersal.

For simplicity, we first study case 1, which is directly linked to island biogeography theory. Cases 2 and 3 involve a combination of biogeographical constraints and species traits. The properties of the model are generally qualitatively similar for the three cases; therefore, we shall only provide results for cases 2 and 3 when they differ qualitatively from those of case 1.

Analytical Results

Closed Community

We first analyze the limiting case when the immigration intensity α is 0, that is, when the community is closed. In this case, our model corresponds to a multispecies version of Levins's (1969, 1970) model, and equation (1b) reduces to

$$f_i(P_1, P_2, \dots, P_n) = c_i P_i V - m_i P_i. \quad (2)$$

Let us define r_i as

This parameter measures species i 's basic reproductive rate (Loreau 1998b), which is equivalent to its lifetime reproductive success in a vacant environment (Fagerström and Westoby 1997). Equation (2) can then be rewritten as

This equation shows that the community reaches an equilibrium ($f_i = 0$) when $V = 1/r_i$. But there are as many different r_i 's as there are species in the system. Therefore, only one species can persist at equilibrium: the species that, when at equilibrium ($f_i = 0$), drives all the others to extinction ($f_j < 0$, $j \neq i$) because it decreases the proportion of vacant sites V below the threshold required for their persistence. This species is the one with the highest basic reproductive rate, r . If we order species according to their basic reproductive rate (with species 1 having the highest r) and denote equilibrium values by a circumflex, there is a single equilibrium at

$$\hat{P}_i = 1 - \frac{1}{r_i}, \quad (5a)$$

$$\hat{P}_i = 0 \quad \forall i > 1, \quad (5b)$$

provided that $r_1 > 1$.

Thus, we rediscover the classical conclusion of interspecific competition theory: no more than one species can persist on a single resource. Here, \hat{V} plays the same role as Tilman's (1982) R^* .

This result is different from that usually found in metapopulation competition models (Levins and Culver 1971; Horn and MacArthur 1972; Slatkin 1974; Hastings 1980; Nee and May 1992; Tilman 1994). These models implicitly or explicitly allow interference competition between species within sites, and coexistence is obtained when there is a trade-off between competitive superiority and colonization ability. Because we do not consider interference, there is no possibility for such a trade-off in our model and, hence, coexistence in a closed community is impossible. As mentioned earlier, we deliberately ignore trade-offs associated with interference competition because we wish to explore the effects of immigration from an external source on their own.

Open Community

We now turn to the general case of an open community ($\alpha > 0$) and study the influence of the propagule rain on coexistence and other community properties.

When the community is open to immigration for all species ($I_i > 0 \forall i$), our deterministic model now suggests that species extinction never occurs because a certain number of individuals arrive continuously from outside the community. Indeed, when the population is very small ($P_i \approx 0$), invasion is guaranteed ($f_i > 0$).

This also ensures that the community reaches a feasible stable equilibrium. From equations (1) and (3), the equilibrium satisfies

$$\hat{P}_i = \frac{\alpha I_i \hat{V}}{m_i(1 - r_i \hat{V})} \quad (6a)$$

and

$$\hat{V} + \sum_j \hat{P}_j = 1. \quad (6b)$$

This equilibrium is feasible if $\hat{P}_i > 0$ for all species, which, from equation (6a), requires $0 < \hat{V} < 1/r_1$, where species 1 is again defined as the species with the highest basic reproductive rate r . But \hat{P}_i is a monotonic increasing function of \hat{V} that varies from 0 to $+\infty$ when \hat{V} increases from 0 to $1/r_1$. Thus, the left-hand side of equation (6b) is also a monotonic increasing function of \hat{V} that varies from 0 to $+\infty$ when \hat{V} increases from 0 to $1/r_1$. Therefore, there is one and only one value of \hat{V} that satisfies equation (6b) in the range $0 < \hat{V} < 1/r_1$, and the equilibrium is indeed feasible.

A full stability analysis of this equilibrium is not possible because equations (6a) and (6b) do not admit an explicit general solution. However, the equilibrium is easily seen to be stable against perturbations in V because if $V < \hat{V}$, then $f_i < 0$ for all i , and V increases; and if $V > \hat{V}$, then $f_i > 0$ for all i , and V decreases.

Thus, in both cases the equilibrium value \hat{V} is restored. Although this is not formally sufficient to ensure stability against perturbations in the P_i 's, it is a strong indication of local stability. A stronger stability criterion is mutual invasibility, and, as mentioned above, this condition is always met. Numerical simulations further indicated that the equilibrium is globally stable.

Thus, there is always stable coexistence in a community with a propagule rain. This conclusion, however, is true to the extent that our deterministic model is a valid approximation of reality. Even though arbitrary coexistence is possible in this deterministic model, many species will

be lost because they are maintained at unrealistically low densities in the community. These species will be under the risk of extinction by demographic stochasticity (Shaffer 1981) or simply because there is less than one individual in the population. The criteria for persistence should therefore be that the P_i 's must be greater than a threshold value that is inversely proportional to the total number of sites available in the community.

Effect of Varying Immigration Intensity

Because of this threshold proportion of occupied sites to ensure persistence of a species, it is important to understand the effect of varying the overall immigration intensity α on the diversity and characteristics of species in the community. Since equations (6a) and (6b) do not admit an explicit general solution, we limit our analysis to the two limiting cases when immigration intensity is either very small ($\alpha \rightarrow 0$) or very large ($\alpha \rightarrow +\infty$).

The appendix shows that, for a very small immigration intensity, most species have a density that is close to 0 and, hence, are expected to be under the extinction threshold. The species with the highest basic reproductive rate is dominant, and species diversity is low. At the other extreme, when immigration intensity is very large, the proportion of sites occupied by a species becomes proportional to its I/m ratio and is independent of its potential reproduction rate c . Numerical dominance is determined by the I/m ratio, and species diversity is expected to be high. Thus, as immigration intensity increases, we expect communities to change from low-diversity communities in which numerical dominance is determined by r to high-diversity communities in which numerical dominance is determined by the I/m ratio.

Our model also predicts that the equilibrium proportion of vacant sites decreases from $1/r_1$ to 0 as the immigration intensity is increased from 0 to ∞ (see appendix). Thus, space is expected to be more fully occupied by the community as a whole when immigration intensity increases.

Numerical Results

Our analytical approach provided detailed results only for the two limiting cases of a very small and a very large immigration intensity α . A numerical study will now be used to improve our understanding of the system's properties between those two extremes, taking into account species extinctions at unrealistically low densities. We focus on the effects of increased immigration intensity on plant species diversity and other ecosystem-level patterns and properties.

Methods

We used two methods to account for the extinction of rare species in our numerical simulations. First, we used a Euler approximation of equations (1) with a threshold proportion of sites below which extinction of a species occurs. We assumed that this threshold corresponds to the presence of a single individual and, thus, is simply determined by the inverse of the total number of available sites in the community. And, second, we used a stochastic version of the model, in which establishment in a site and mortality are probabilistic events. In this version, establishment in a vacant site was obtained by random sampling from the pool of potential occupants, constituted by both immigrants and new individuals produced by local reproduction.

The two methods were found to give similar results for most of the issues addressed in this work. Therefore, we shall only provide results from the first method, which is closer to the original deterministic model.

For each simulation, we sampled parameters randomly from a potential species pool corresponding to the “null community” concept (Zobel 1992), that is, a pool of species capable of living in the community in the absence of interspecific interactions. These species were then allowed to compete for space until an equilibrium was reached.

We ran simulations with randomly sampled parameters because it allowed us to explore the general properties of our model without choosing particular combinations of competing species. Thus, we studied an average community rather than various particular communities. Accordingly, for each issue investigated, we performed 1,000 simulations and present results in the form of a mean and a standard deviation. We arbitrarily selected parameters randomly between 0 and 1 in a uniform distribution, set the number of species in the pool to 20, and set the threshold proportion of sites for extinction to 0.001 (corresponding to 1,000 sites in total).

Species Diversity

As expected from our mathematical analysis, species richness at equilibrium increases continuously when immigration intensity α increases (fig. 1, *top*). This increase, however, is not linear. Species richness on average starts increasing as soon as immigration intensity allows the potential recruitment of a number of individuals equivalent to the extinction threshold (here, a single individual in the community; fig. 1, *bottom*). It then increases most steeply when immigration intensity is intermediate and reaches the ceiling set by regional richness when immigration is unrealistically high, that is, when immigration contributes

many more individuals than does local reproduction (fig. 1).

This result emphasizes the critical role of extinction of rare species when the intensity of immigration is low. Although the deterministic model without extinction threshold would predict unlimited coexistence under all circumstances as long as immigration is nonzero, including the extinction threshold leads to the more realistic result that species richness decreases to 1 as immigration becomes weaker and the community tends to be closed.

Community Composition

We now examine how immigration intensity changes the composition and species abundance pattern of the community.

When immigration intensity is low, diversity is low (fig. 1) and communities are dominated by a single, very competitive species that occupies almost all sites (fig. 2A). When immigration intensity is high enough to get over the extinction threshold for competitively inferior species, diversity increases (fig. 1) and communities are composed of one dominant species and a few rare species (fig. 2B, 2C). The distribution of the proportion of occupied sites is then bimodal; the dominant species still occupies most sites, but rare species are maintained by immigration. When immigration intensity is high, diversity is high (fig. 1); there is no dominant species any more, and the distribution is unimodal (fig. 2D). Thus, there is a switch from a community with one dominant species to a community without dominant species as immigration intensity increases.

It is interesting to discriminate between the three scenarios for the relation between the species-specific immigration rate I and the potential reproduction rate c . Figure 3 illustrates the changes in the proportions of sites occupied by three species at equilibrium as immigration intensity increases. When there is a negative correlation between I and c , the dominance relationships between species are reversed as α increases (fig. 3A). When there is a positive correlation between I and c , these dominance relationships are preserved, although the most competitive species usually occupies fewer sites when immigration intensity increases (fig. 3C). The case when I and c are independent is intermediate, dominance depending on the selected parameters (fig. 3B).

Thus, as expected from our analytical results, the relation between immigration rate (I) and potential reproduction rate (c) determines the changes in dominance as immigration intensity (α) increases. Therefore, the dominance hierarchy observed in natural communities should depend not only on local species-specific traits but also on immigration intensity.

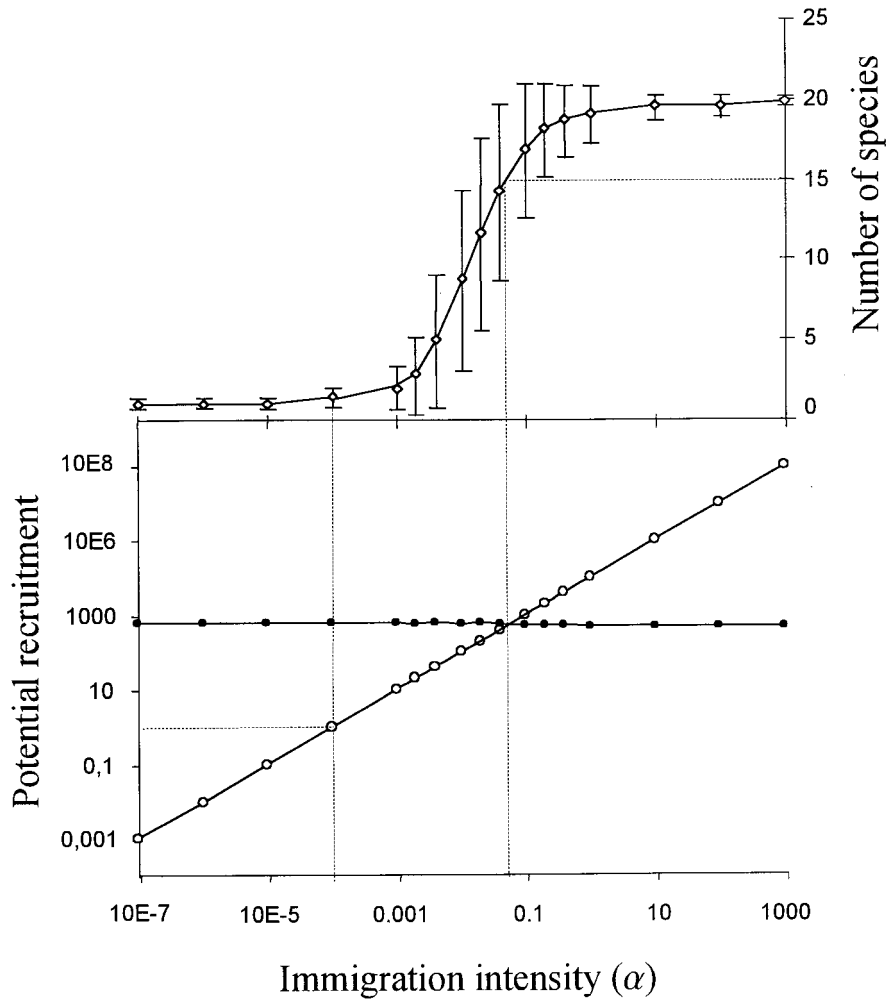


Figure 1: Species richness at equilibrium ($\bar{X} \pm SD$) as a function of the immigration intensity α (top), and respective contributions of local reproduction ($\sum_j c_j P_j$, solid circles) and immigration ($\alpha \sum_j I_j$, open circles) to the total potential recruitment in the community (bottom). The left dotted vertical line shows the immigration intensity allowing the potential recruitment of one immigrating individual on average in the community. The right dotted line shows the immigration intensity at which the local and regional contributions to total potential recruitment are equal. The potential species pool comprises 20 species.

Implications for Ecosystem Processes

We now explore the potential consequences of the intensity of the propagule rain on ecosystem properties and processes such as space occupation and primary productivity. Because there is a direct relationship between immigration intensity and diversity, these consequences might be important for an understanding of the relationship between biodiversity and ecosystem functioning.

As predicted by our mathematical analysis, the proportion of vacant sites in the community, on average, decreases as immigration intensity is increased (fig. 4). Assuming that site occupation and plant cover are related,

this suggests that plant cover should increase with immigration intensity.

There is no direct relationship between plant productivity and the parameters of our model describing spatial dynamics. However, to explore some potential implications of immigration for primary productivity, we make some simplifying assumptions and consider that a species' productivity is correlated with its local recruitment potential, hence, with both the number of sites it occupies and its potential reproduction rate in a site. This assumes that a higher production means production of more propagules of a higher quality (Loreau 1998b). Thus, we approximate total plant (primary) productivity by

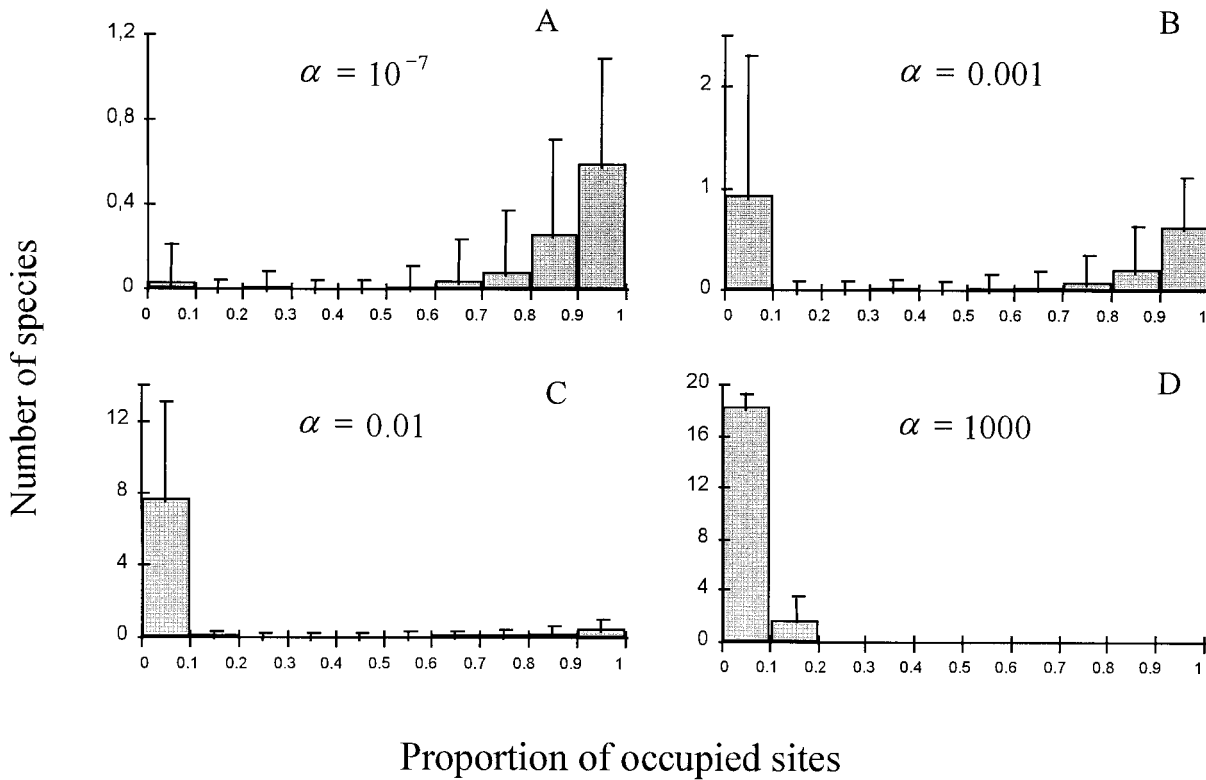


Figure 2: Frequency distribution ($\bar{x} \pm SD$) of the proportion of sites occupied by the various species at equilibrium for various values of the immigration intensity α .

$$\Phi = \sum_j c_j P_j. \quad (7)$$

The effect of immigration intensity on productivity then depends on the relationship between immigration rate (I) and potential reproductive rate (c).

When I and c are negatively correlated (fig. 5A), productivity on average decreases as immigration intensity increases. In this case, dominance was shown to shift when immigration intensity increases (fig. 3A). For small values of α , the species that persist at equilibrium have a high potential reproduction rate c , hence productivity is high. When α increases, the immigration rate I becomes more important in determining dominance; dominant species have a low potential reproduction rate c because of the negative correlation between I and c , hence productivity is lower.

When I and c are positively correlated, productivity is roughly constant on average (fig. 5C). In this case, it is always the same species that are dominant, and space occupation increases (fig. 4); thus, we might expect productivity to increase. But at the same time, dominant species usually occupy fewer sites when α increases (fig. 3C).

Therefore, the two effects tend to counterbalance each other, and productivity is not affected on average. The situation is intermediate when I and c are independent (fig. 5B).

These results show that even though space occupation increases, productivity is expected to stay constant or even decrease when immigration intensity increases. This may seem surprising because primary productivity is simply the product of the average productivity per occupied site, $\sum_j c_j P_j / \sum_j P_j$, and the number of sites occupied, $\sum_j P_j$. This counterintuitive pattern is explained entirely by the changes in dominance when immigration intensity increases. However, it should be kept in mind that this is true for an average community. It is of course possible for a particular community to have a productivity that increases with increasing immigration intensity.

Discussion

Immigration and the Maintenance of Local Species Diversity

Our model shows that immigration from an external source can have a huge effect on local coexistence and

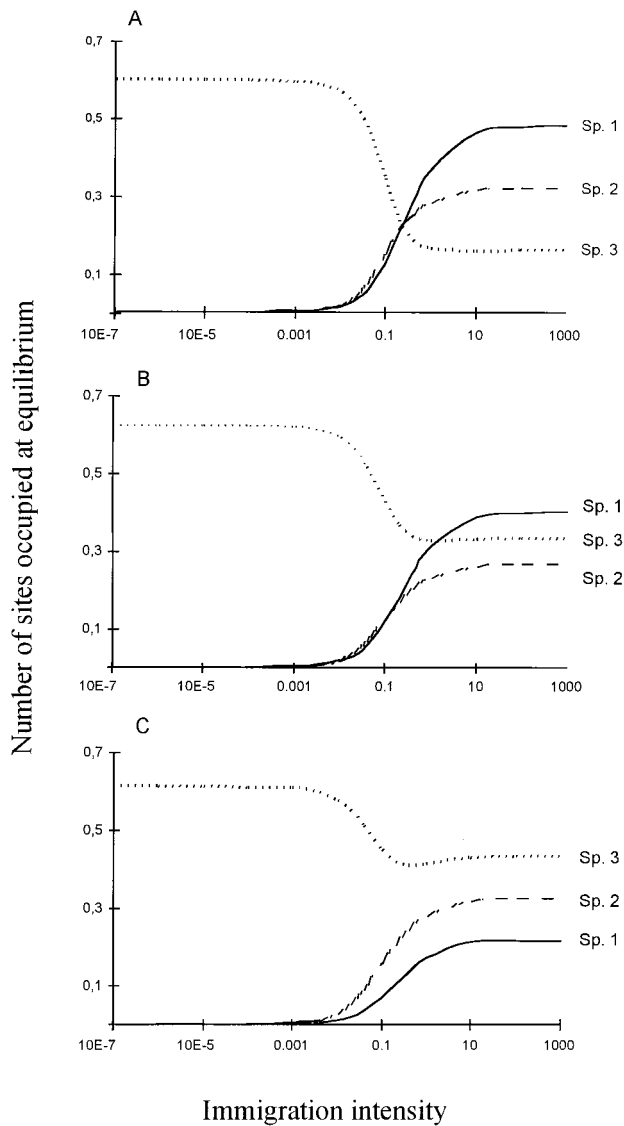


Figure 3: Changes in the dominance relationships in a community of three species as the immigration intensity α is increased, under three scenarios for the relation between the species-specific immigration rate I and the potential reproduction rate c : A, I is a decreasing function of c ($I = 1 - c$); B, I and c are independent; C, I is an increasing function of c ($I = c$).

diversity in competitive communities where competition for a single resource (space) would lead to the exclusion of all but one species if the community were closed. Local species richness is expected to increase strongly when immigration intensity increases beyond the threshold required for the successful establishment of one or a few individuals. Incorporating other mechanisms of local coexistence (such as niche differentiation or trade-off between interference competitive superiority and coloniza-

tion ability) may reduce the relative importance of immigration in the maintenance of local diversity but is unlikely to affect the basic trends identified in this work.

How do these results relate to actual processes in natural plant communities? A growing number of field studies demonstrate the importance of species pools and regional processes in regulating local species richness (Cornell 1993; Gough et al. 1994; Caley and Schluter 1997; Grace and Pugsek 1997; Zobel et al. 1998). Studying plants on a sea sand dune, Keddy (1981, 1982) showed that the density of a species on the poor side (in habitat quality) was a function of its density on the rich side. In this case, dispersal was strong and asymmetric, a phenomenon that was later named a "source-sink" relationship by Pulliam (1988), who generalized it to all kinds of organisms. Field studies by Shmida and his collaborators (Shmida and Ellner 1984; Shmida and Wilson 1985; Auerbach and Shmida 1987; Kadmon and Shmida 1990) provided similar results at the community level. They showed that some species are maintained solely because of immigration in plant communities. Another study (Grubb 1986) showed no correlation between the number of flowers in a year and the number of plants in the next year for rare species, whereas this correlation did exist for dominant species. Houle and Phillips (1989) and Tilman (1997) added seeds experimentally into plant communities and showed an important influence of immigration on local diversity. Thus, the regional species pool does appear to affect local diversity in plant communities, especially through the maintenance of rare species.

Our approach mimics the mass-effect hypothesis developed by Shmida and Wilson (1985), but here we build a mechanistic model of competition for space and obtain testable predictions on processes other than species diversity. It is also related to the source-sink hypothesis (Pulliam 1988) since all species but one would go extinct if the local community were closed and, hence, the latter acts as a sink for them. It is only immigration from an external source that allows them to persist in the community. Thus, our model explores the consequences of source-sink dynamics on species diversity at the community level.

Our model suggests that a plant community, or more exactly a subset of the community comprising similar species, may be viewed as a system constituted of one or a few species adapted to local environmental conditions associated with numerous other species, the persistence of which is assured by regional processes such as immigration.

Coexistence: Spatial Dynamics versus Trade-Offs

Our model shows that long-term coexistence in a closed community is impossible when plants compete indirectly

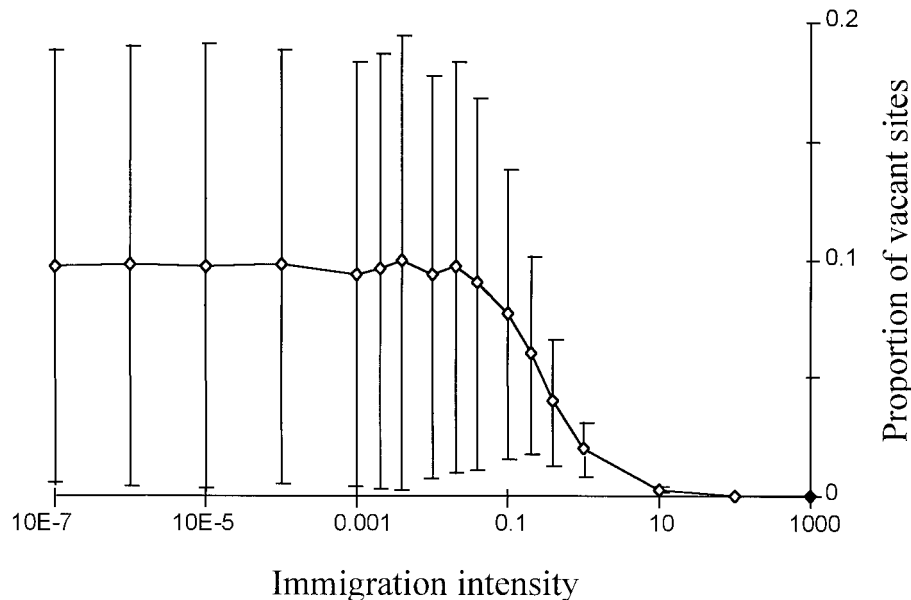


Figure 4: Proportion of vacant sites ($\bar{X} \pm SD$) as a function of the immigration intensity α

for space, in agreement with the classical theory of resource competition. Thus, contrary to widespread beliefs, competitive lotteries do not make for species coexistence (Chesson and Huntly 1997; Fagerström and Westoby 1997; Loreau 1998*b*). Huston and DeAngelis (1994) recently developed a model of plant competition for a soil nutrient without direct interference interactions and explained coexistence by the fact that the plants themselves create spatial heterogeneity by depleting the nutrient only in a local site. While their theory is very useful to account for short-term plant coexistence, it does not explain coexistence in the long term because it does not take the spatial dynamics of site occupation into account. Local spatial dynamics in such a system obey the same rule as in our model and would result in competitive exclusion of all but one species in a closed community. What maintained long-term coexistence in Huston and DeAngelis's (1994) simulations was the fact that they sampled new occupants of vacant sites from a regional pool, thus mimicking an immigration process as in the present model.

Coexistence between competing species in plant communities has often been ascribed to a trade-off between competitive ability and colonization ability (Levins and Culver 1971; Horn and MacArthur 1972; Slatkin 1974; Nee and May 1992; Tilman 1994). This trade-off hypothesis is very likely to be valid when species from early and late successional stages are compared but is unlikely to be the sole explanation of coexistence between plants from the same successional stage. Field studies that demonstrate

this trade-off are scarce. Tilman (1988) provided interesting results supporting this trade-off hypothesis, but his results were based on data from 50 yr of community dynamics, and thus species with different strategies may have come from different successional stages. Immigration from an external source offers an alternative, complementary hypothesis for explaining the coexistence of species from the same successional stage in a community.

Species Abundance and Distribution Patterns

Our model generates three distinct species abundance patterns as immigration intensity increases (fig. 2): a unimodal distribution of abundance (or proportion of sites occupied) with a peak at high abundance, a bimodal distribution with two peaks at low and high abundances, and a unimodal distribution with a peak at low abundance.

Unimodal and bimodal distributions of the number of sites occupied are often discussed in biogeography and metapopulation theory in relation to species abundance and distribution patterns. A unimodal distribution is predicted by Levins's (1969, 1970) metapopulation model. Stochastic variation in extinction rates leads to a unimodal distribution of the number of sites occupied by one species at different times or by several species at the same time (Hanski 1982). In contrast, a bimodal distribution is predicted by Hanski's (1982) core and satellite species hypothesis. This hypothesis is based on a model similar to Levins's, with the additional assumption that the extinc-

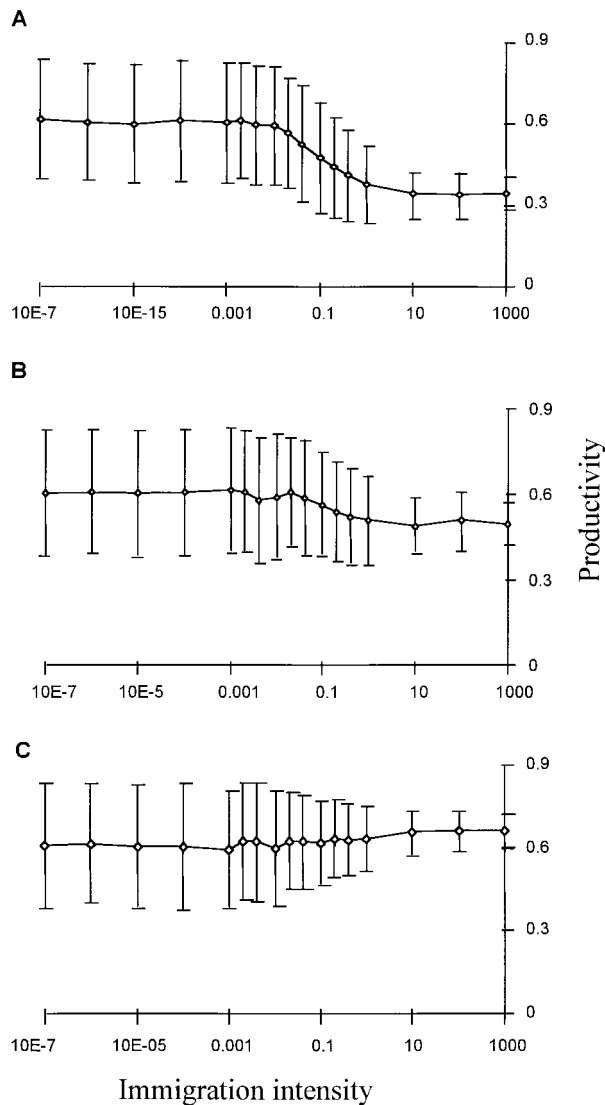


Figure 5: Primary productivity ($\bar{X} \pm SD$) as a function of the immigration intensity α under three scenarios for the relation between the species-specific immigration rate I and the potential reproduction rate c : A, I is a decreasing function of c ($I = 1 - c$); B, I and c are independent; C, I is an increasing function of c ($I = c$).

tion rate is a decreasing function of the proportion of sites occupied. Although Hanski's explanation was severely criticized (Brown 1984; Nee et al. 1991), bimodal distributions of the number of sites occupied have been found in a number of studies (Hanski 1982; Gotelli and Simberloff 1987; Collins and Glenn 1990; Maurer 1990; Gotelli 1991; Hanski and Gyllenberg 1993; Scheiner and Rey-Benayas 1997). In this study, a bimodal distribution was found from a theoretical model, so that Brown's (1984) sampling effect hypothesis can be rejected.

These two kinds of distributions have been found in numerous studies (see Scheiner and Rey-Benayas 1997 for a review) and, thus, may correspond to real ecological patterns. Our work shows that both can be traced to a single process. Depending on immigration intensity, communities vary from closed communities that are structured by local competition and have a low diversity to open communities that are structured by immigration and have a high diversity. The bimodal distribution is generated by an intermediate situation where local competition and immigration are roughly balanced.

Ecosystem Processes

Our model predicts space occupation and, hence, likely also plant cover, to increase with increasing immigration intensity. Tilman's (1997) field study agrees with this theoretical result. Tilman added seeds in plant communities and found a positive correlation between species diversity resulting from seed addition and plant cover. Our model, just as Tilman's (1994), predicts that there should always be some vacant space in a plant community. Contrary to Tilman's (1997) experimental results, however, local species are here affected by the arrival of new species and occupy fewer sites. Whether species interact directly or indirectly, it seems normal that invasion of new species through sustained immigration affects other species in the community. If local species were not affected, this would mean that competition is absent between species maintained by local processes and species added by immigration.

Studies on the relationship between the productivity and diversity of ecosystems have developed dramatically in recent years (see Johnson et al. 1996 for a review). Recently Tilman et al. (1997) and Loreau (1998a) showed, using theoretical models, that a positive relation between productivity and diversity is expected for complementary species (i.e., species that occupy distinct niches), but Loreau's (1998a) model makes clear that a variety of relationships are possible for similar species, the average being a flat response of productivity to diversity. The present model considers similar species (i.e., species that compete for the same spatial resources) and shows that, when diversity is maintained by an immigration process, productivity should on average either stay constant or decrease when diversity increases, depending on the relationship between local reproduction and immigration among species. When local reproduction and immigration are correlated positively, increasing immigration intensity—and hence diversity—does not much affect productivity on average. But when local reproduction and immigration are either independent or correlated negatively, increasing immigration intensity and diversity results in a decreased produc-

tivity on average. This is explained by the fact that species sustained by immigration are usually not those that are the best competitors locally, and when a higher diversity is associated with a lower average competitive ability, productivity is expected to decrease with diversity (Loreau 1998a). Thus, both immigration intensity and the relationship between species-specific immigration rates and local reproduction rates may significantly influence the relationship between productivity and diversity in a community.

Although our measure of primary productivity is only indirect and rests on a number of assumptions that may make it more closely related to seed production than to biomass production, our results do suggest a counter-intuitive pattern and suggest that it would be worthwhile to collect more data on the relationship between local and regional dispersal and productivity, as well as experimentally to measure total production and seed production in plant communities under different immigration intensities.

Where Does the Propagule Rain Come From?

Our model shows that immigration from an external source is able to maintain a high local diversity in a system that would otherwise tend toward competitive exclusion of all but one species. But the operation of this process requires that diversity be maintained in the source itself, which looks like transferring the problem of the maintenance of diversity to the source. This apparent contradiction can be resolved by taking into account spatial heterogeneity of the environment at the regional scale. Each community can act as a source of immigrants for other communities in the region; provided that environmental conditions are different enough for different species to be competitively dominant in different communities, these constitute a “metacommunity” at the regional scale, which is capable of maintaining local diversity in each community. We reserve this important, complex issue for another work (N. Mouquet and M. Loreau, unpublished data).

Conclusion

We have shown that immigration from a regional source can have a considerable influence on local patterns in plant communities. We here summarize our main conclusions: Coexistence of numerous species on a single resource (space) is possible if immigration by a propagule rain is allowed into local communities. Local species richness at equilibrium is then a function of immigration intensity. Community structure and species abundance patterns can be strongly influenced by immigration intensity. Immi-

gration from an external source causes space occupation to increase but productivity on average to decrease or stay constant with increasing diversity.

Classically, ecologists have studied local diversity and its relationship with other local community processes or patterns. Here, we demonstrate that local diversity, community patterns, and ecosystem processes can be strongly influenced by regional processes such as immigration. This does not invalidate the other mechanisms habitually invoked to explain diversity in ecological communities (see Tilman and Pacala 1993; Bengtsson et al. 1994 for reviews), but it stresses the need to integrate local and regional processes in the explanation of local species diversity and, in particular, to put an emphasis on the regional processes that are still too often forgotten in the study of ecological communities.

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APPENDIX

Effect of Varying Immigration Intensity

This appendix analyzes the effect of varying the overall immigration intensity α on the diversity and characteristics of species in the community in the two limiting cases when immigration intensity is either very small ($\alpha \rightarrow 0$) or very large ($\alpha \rightarrow +\infty$).

Immigration Intensity Is Very Small ($\alpha \rightarrow 0$)

By continuity with the case where $\alpha = 0$, we have

$$\hat{V} \rightarrow \frac{1}{r_1},$$

$$\hat{P}_i = \frac{\alpha I_i}{m_i(r_1 - r_i)} \rightarrow 0 \quad \forall i > 1,$$

and

$$\hat{P}_1 \rightarrow 1 - \frac{1}{r_1}.$$

Thus, only the species with the highest basic reproductive rate persists at a high density. All other species have a very low density and are under the risk of extinction.

Among these species, relative abundance is determined

by two factors, r and the I/m ratio. However, it is its r that first determines whether a species is dominant or rare.

Immigration Intensity Is Very Large ($\alpha \rightarrow \infty$)

Equation (6a) can be rearranged to give

$$\hat{V} = \frac{\hat{P}_i}{\alpha I_i/m_i + r_i \hat{P}_i}.$$

Therefore, $\hat{V} \rightarrow 0$ as $\alpha \rightarrow \infty$, and, from equation (6a),

$$\hat{P}_i \rightarrow \frac{\alpha I_i \hat{V}}{m_i}.$$

From equation (6b), we obtain

$$\hat{V} \rightarrow \frac{1}{\alpha \sum_j I_j/m_j}$$

and, finally,

$$\hat{P}_i \rightarrow \frac{I_i/m_i}{\sum_j I_j/m_j}.$$

Thus, when immigration intensity is very large, the proportion of sites occupied by a species is proportional to its I/m ratio and is independent of its potential reproduction rate c .

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