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22. The properties of competitive communities with coupled local and regional dynamics

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Abstract

In this chapter we review the results from models which link local and regional scales and illustrate some of the mechanisms that can maintain biodiversity. First, we present a model of local competition for space in plant communities. The model is a classical metapopulation model, but we apply it to a population of individuals rather than to a population of populations, and we add an external source of immigration by a propagule rain. In such a system, we show that local coexistence is possible, and the number of coexisting species is a growing function of immigration intensity. To explain the origin of the propagule rain, we next present a model of a metacommunity, defined as a regional set of communities linked by dispersal. Assuming environmental heterogeneity at the regional scale, we show that the number of coexisting species cannot be greater than the number of different communities or habitats. A new concept arises from these conditions of coexistence, which we call regional similarity. To persist in a metacommunity, all species must have the same mean competitive ability at the regional (metacommunity) scale. In both models, communities change from low-diversity communities when local dynamic is important to high-diversity communities when regional dynamic is the most important process. Moreover, switching to local versus regional dynamics generates very different relationships between diversity and ecosystem processes such as plant productivity. Our second model describes the evolution of the properties of communities. Generally, the properties of communities like their composition, diversity and productivity that form over very long periods of time, will be determined by two constraints. As illustrated above, a first constraint is that the component species have to be able to coexist in a community. Secondly, a community will adapt under evolution and therefore a second constraint is that a community is evolutionarily stable. Only a subset of all communities that can coexist will be evolutionarily stable. To study the properties of evolutionarily stable assemblages, we present an evolutionary model for competitive communities. Our model is based on a framework to describe evolution in metapopulations. The local dynamics are specified by competition for a single resource, the regional dynamics by seasonal harvesting and redistribution of dispersing propagules. We let the characteristics of the competitive communities adapted through selection and small mutations. The properties of the evolutionarily stable ecosystem, in particular its biodiversity, the composition of the community, biomass composition depend on the maximum productivity and the length of the productive season. Our different models illustrate how the composition and properties of competitive communities is structured through the population and evolutionary dynamics, and how these, in turn, depend on the local and regional dynamics.

Keywords: Altruism, assemblage, biodiversity, biogeography, coexistence, competition for space, competitive exclusion, community properties, diversity, ecosystem processes, ESS, fitness, haystack model, immigration, inclusive fitness, kin selection, metacommunity, plant community, propagule rain, single-resource competition, source-sink.

Introduction

In some natural plant communities, more than 80 species can be found in a square meter (Zobel 1992). How such a large number of species can coexist on a limited number of resources is still not completely understood (see Tilman and Pacala 1993; Bengtsson *et al.* 1994 for reviews). A possible solution to this paradox lies in the different spatial scales on which ecological interactions work (Holt 1993; Loreau and Mouquet 1999).

Individuals predominantly interact with other individuals in their local environment. This results in a small characteristic spatial scale. However, the dynamics at the local scale also depends on the regional population through immigration (Holt 1993; Ricklefs and Schluter 1993; Zobel 1997; Cornell and Karlson 1998; Loreau and Mouquet 1999). This introduces two distinct spatial scales into the interaction: a local scale and a regional one (see Rand and Wilson 1995; De Roos *et al.* 1991; Wilson and Keeling 1999 for procedures to estimate the characteristic local spatial scale). To understand the effects on population dynamics, both experimental and theoretical works have concentrated on cases with a clear separation between these two scales. Typically, local interactions take place in sites or patches; the influence of regional interactions on local interaction is through immigration of individuals, which will be a function of some average of the density over all patches in the region.

Populations that cannot persist in a single location can persist in a collection of different patches. This observation, which lies at the heart of the theories of island biogeography (MacArthur and Wilson 1967) and metapopulations (Levins 1969; see Gilpin and Hanski 1991; Hastings and Harrison 1994; Hanski 1999 for reviews), may also explain the coexistence of many species on a limited number of resources. If all competitors inhabited a single location, the number of resources would limit the number of species. In a collection of patches, local populations may disappear from sites, but as long as each local population on average colonizes at least one new site, the metapopulation will persist. Many species can coexist in systems with local and regional dynamics, even on a single resource. In their simplest form, metapopulation models only describe empty and occupied patches, and thus completely ignore local dynamics, the colonization of new patches depending only on the number of occupied patches (Levins 1969).

The competitive dominance of one species is a robust result of models of competition for a single resource. With resources so limited and competition so fierce, how can species-rich communities nevertheless be explained? One possible explanation is that there exist underlying regional differences so that different species dominate in different sites. Another possible explanation is that there are no regional differences, but different species have different strategies to use space: some species go for local competitive advantage, whereas others go for spatial expansion. This idea has received much attention in the framework of the competition-colonization trade-off hypothesis (Hastings 1980; Tilman 1994). The basic assumptions of models including this trade-off are that each patch can be occupied by only one individual; being a superior competitor implies being a weaker colonizer (see Tilman 1990); and if a superior competitor invades an already-occupied patch, it immediately replaces any inferior competitor. Therefore, an inferior competitor (better colonizer) survives only in those patches that are left open by its superior competitors.

We shall study these two hypotheses with two different types of models. The first type of model relaxes the assumption of a trade-off between competitive and colonizing abilities, and focuses on the influence, through immigration, of regional process on local dynamics. The second type of model relaxes the assumption of immediate replacement of the inferior by the superior competitor and studies the properties of competitive communities from an

evolutionary perspective. In this chapter, we ask how species richness is maintained and how it is generated. Both types of models yield results on coexistence far more general than those described previously. As an extension, we will use them to explore the relationships between ecosystem functioning and species diversity, which emerge from these two approaches to species coexistence.

1. Source-sink dynamics in competitive plant communities

1.1. The propagule rain model

We first present a model that incorporates the influence of immigration from a regional pool on a community of plants competing for space (for more details, see Loreau and Mouquet 1999). As in metapopulation theory (Levins 1969; Levins 1970), the habitat is assumed to be discrete and we model the dynamics of extinction and colonization of patches. Our model differs from metapopulation models (Levins and Culver 1971; Horn and MacArthur 1972; Slatkin 1974; Hastings 1980) because each site can support only one plant (Tilman 1994; Goldwasser *et al.* 1994; Pacala and Rees 1998), and because we consider only indirect competition for space (i.e. a plant will release a site only at its death). The establishment of plants in vacant sites obeys a competitive lottery (Chesson and Warner 1981; Sale 1982).

We define P_i as the proportion of sites occupied by species i in the community. There are S such species that compete for a limited proportion of vacant sites, V . For each species i , we include seed production, short-distance dispersal, germination and seedling establishment in its local reproduction rate, c_i . All forms of natural death are encapsulated in its mortality rate, m_i . As in island-continent models (Gotelli 1991), we add an external source of immigrants in the form of a propagule rain. Parameter I_i describes the species-specific potential immigration rate of species i , which is determined by its long-distance dispersal capacity and its relative abundance in the regional source. Immigration intensity depends on the size of, and distance from, the regional source, and is defined by a parameter \mathbf{a} . Because only vacant sites can be occupied, potential reproduction (local reproduction + immigration) is not fully realized.

This model, which we call the propagule rain model, reads:

$$\frac{dP_i}{dt} = f_i(P_1, P_2, \dots, P_S) = (\mathbf{a}I_i + c_iP_i)V - m_iP_i \quad (1)$$

$$V = 1 - \sum_{j=1}^S P_j$$

First, consider a closed community in the absence of immigration ($\mathbf{a} = 0$), and let us define $r_i = c_i/m_i$ as species i 's local basic reproductive rate (Fagerström and Westoby 1997; Loreau 1998b) which is equivalent to its lifetime reproductive success in a vacant environment. The community reaches an equilibrium ($f_i = 0$) when $V = 1/r_i$. However, because there are as many different r_i 's as there are species in the system, only the species with the highest basic reproductive rate can persist at equilibrium.

Next, consider the general case of a community open to immigration of all species ($\mathbf{a} > 0$ and $I_i > 0 \forall i$). All species coexist because individuals arrive continuously from outside the

community. However, in this deterministic model many species are maintained at unrealistically low densities. In reality, rare species are subject to the risk of extinction by demographic stochasticity. We have studied the consequences of such extinction on coexistence in communities, with different immigration intensities. To mimic demographic stochasticity, we used a numerical approximation of equation (1) with a threshold proportion of sites, below which a species is considered to be extinct. Our results show that species richness at equilibrium increases continuously with immigration intensity \mathbf{a} (Fig. 22.1a). This increase is steepest at an intermediate value of \mathbf{a} when the contribution of immigration allows the potential recruitment of a number of individuals greater than the extinction threshold.

To describe community composition we measured equitability based on the classical Shannon diversity index (see Fig. 22.1). When equitability is equal to 1, all the species have the same proportion, and when equitability is low, there is one dominant species and many rare species. The increase in the number of species, and the increase in the proportion of sites occupied by new species, occur at different immigration intensities, therefore equitability first decreases (Fig. 22.1b). At higher immigration intensities, the amount of space occupied by the various species becomes more and more similar, and equitability increases until it reaches a ceiling. Therefore, there is a switch from a species-poor, non-equitable community to a species-rich, equitable community as the intensity of immigration increases.

1.2. The metacommunity model

The propagule rain model shows that immigration from an external source is able to maintain a high local diversity in a system that would otherwise experience competitive exclusion of all but one species. It does, however, raise the questions: Where does the propagule rain come from? And what about emigration? To answer these questions we formulated a model for a metacommunity, in which immigration to a community is a function of emigration from other communities. Our approach fits in with “mesoscale ecology”, which seeks to link local and regional processes (Roughgarden *et al.* 1988; Holt 1993). This type of approach has already been developed, both in population ecology (Levin 1974; Iwasa and Roughgarden 1986; Kishimoto 1990; Holt 1997) to explain the coexistence of competing species, and in population genetics (e.g. Levene 1953) to explain the maintenance of polymorphism.

We define a metacommunity as a regional set of communities linked by dispersal. As mentioned in the first chapter of this book, defining dispersal is not a trivial challenge. A metacommunity model encompasses two levels of dispersal: long-distance (i.e., inter-community) and short-distance (i.e., intra-community) dispersal. In the rest of this section, we use the word dispersal when referring to inter-community dispersal. Let P_{ij} be the proportion of sites occupied by species i in community j . There are S species that compete for a limited proportion of vacant sites, V_j , in N communities. Immigration of species i to community j , I_{ij} , is a function of emigration from other communities. For each community, there is a proportion of reproductive progeny that disperses, a , and a proportion of non-dispersers, $1-a$. Because a is taken to be the same for all species, it can be interpreted as the relative importance of local, as compared to regional, dynamics (depending on the size of, and distance between communities). Following Levin (1974), we assume heterogeneity of environmental conditions at the regional scale by changing species-specific parameters in each community.

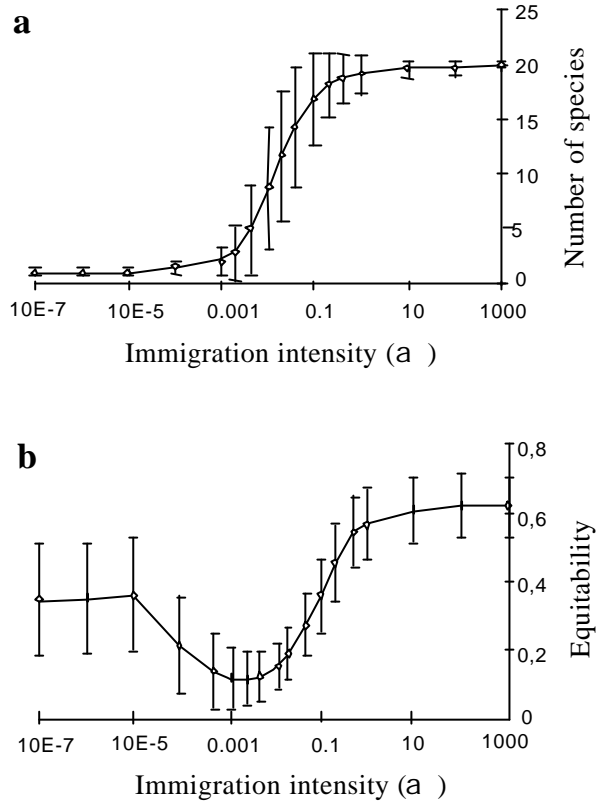


Figure 22.1. Variation of species richness and equitability (measured by Shannon's index: $E = -\sum P_i \ln P_i / \ln S$) at equilibrium, as a function of the immigration intensity α . Means and standard deviations obtained from 1000 simulations. The potential species pool comprises 20 species. The extinction threshold is fixed at 0.001. For each simulation we sampled parameters randomly from a potential species pool, and these species were allowed to compete for space until equilibrium was reached. We selected parameters randomly between 0 and 1 in a uniform distribution.

This model, which we call the metacommunity model, reads:

$$\frac{dP_{ij}}{dt} = f_{ij}(P_{1j}, P_{2j}, \dots, P_{Sj}) = (I_{ij} + (1-a)c_{ij}P_{ij})V_j - m_{ij}P_{ij} \quad (2)$$

$$V_j = 1 - \sum_{k=1}^S P_{kj} \quad \text{and} \quad I_{ij} = \frac{a}{N-1} \sum_{k \neq j}^N c_{ik} P_{ik}$$

This model is complex, and we present only general results here. A full analysis will be presented elsewhere (Mouquet and Loreau, unpublished). This model has allowed us to extend and generalize Iwasa and Roughgarden's (1986) results: at equilibrium, the number of species coexisting in each community cannot be greater than the number of different communities (habitats) at the regional scale. Each community acts as a source of immigrants for other communities in the region, provided that communities are different enough for different species to be competitively dominant there. This is a strict application of niche theory, because

it is not possible to have more coexisting species than the number of limiting factors. However, we have shifted the scale of heterogeneity from the local to the regional scale, which may be more relevant to natural systems.

Further, to persist in a metacommunity, all species must have the same mean competitive ability at the regional (metacommunity) scale. We have called this condition the regional similarity rule. Coexistence is then possible even if species are *locally different*, because they are *regionally similar*. Let the basic reproductive rate of species i in community j be $r_{ij} = c_{ij}/m_{ij}$. As an extreme case, we can define regional competitive ability for a species i as the product of its local reproductive rates in all communities ($r_i = \prod_{j=1}^N r_{ij}$). Therefore a sufficient condition for regional similarity is obtained when all r_i 's are equal. We have called this condition strict regional similarity.

We will now illustrate this result with the case of two species in two communities. Coexistence is then possible if $r_{11}r_{12} = r_{21}r_{22}$. What are the consequences of increasing the dispersal rate between the communities (i.e., increasing the relative importance of regional versus local dynamics)? For the case of strict similarity, we analyzed the stability of the equilibrium: stable coexistence is possible only for a value of dispersal smaller than 0.5. We also studied the concept of regional similarity, for divergence from this case. Because constraints on parameters are very strong (strict parameters combination), strict regional similarity between coexisting species is biologically unrealistic. So, let us define δ as a function of divergence from the strict similarity case:

$$d = \frac{r_{11}r_{12}}{r_{21}r_{22}} \quad (3)$$

When $\delta = 1$, we find the condition of strict similarity as defined above. To diverge from that case we fixed all parameters except c_{11} (the local reproductive ability of species 1 in community 1), which varied from 0 to 2. As in the propagule rain model, we solved the equations numerically and included an extinction threshold. Figure 22.2 shows that for low values of dispersal, coexistence is achieved even when species are not strictly similar. Therefore, regional similarity is defined as a product of species parameters, equilibrium values of coexisting species and the level of dispersal between communities. Furthermore, we have shown that the range of parameters which allows coexistence is wider at intermediate levels of dispersal, but as yet, we have not found an analytical expression for this range.

Species richness is only one aspect of species diversity, which we complemented by measuring equitability. We performed simulations in the simple case of strict similarity, as discussed above, for two species in two communities. When dispersal is zero, communities are closed, and there is local exclusion by the most competitive species (i.e. the species with the highest local competitive ability r_{ij}). Species richness is then equal to one and equitability is zero. When dispersal increases, local species richness becomes maximal (here, 2) and communities become more and more similar, until equitability reaches its maximum when dispersal is 0.5. It is possible to generalize this result to a metacommunity of S species and N communities. When dispersal is low, the most competitive species dominates in each community, and others, maintained by dispersal from other communities, are rare and therefore under constant extinction risk; thence species diversity is low. As dispersal increases, more and more species are maintained above the extinction threshold by immigration, and thus species richness and equitability increase.

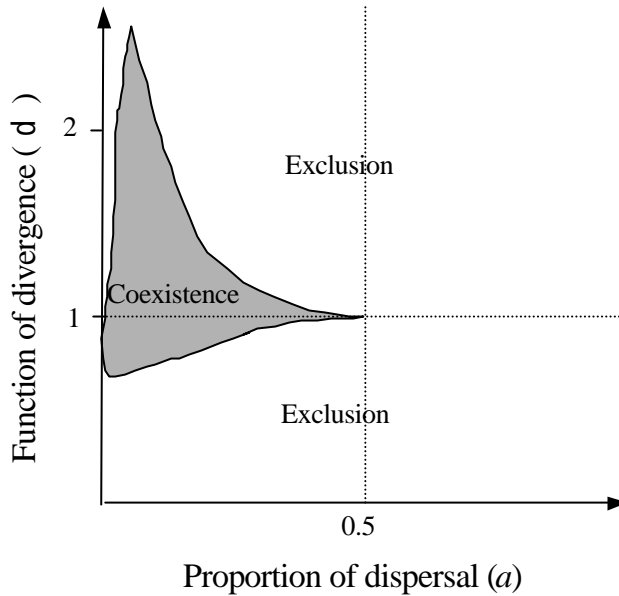


Figure 22.2. Zone of local coexistence (grey) as a function of divergence from the strict similarity case, d (Y -axis), and dispersal, a (X -axis). This result is obtained from a metacommunity of two species competing in two communities. Simulations were performed until equilibrium was reached. Parameters are $c_{12} = 0.5$, $c_{21} = 0.5$, $c_{22} = 0.8$ and $m_{11} = m_{12} = m_{21} = m_{22} = 0.3$. Divergence from the strict similarity case is obtained by varying parameter c_{11} . The extinction threshold is set at 0.01.

1.3. Community properties

We now explore some consequences of increasing the relative importance of regional versus local dynamics (increasing dispersal), on community properties such as total space occupation and primary productivity at equilibrium.

In the propagule rain model the proportion of vacant sites in the community, on average, decreases as immigration intensity increases (Fig. 22.3a). Assuming that a species' productivity is correlated with both the numbers of sites it occupies and its potential reproduction rate in a site, we approximate total plant (primary) productivity by:

$$\Phi = \sum_i c_i P_i \tag{4}$$

The effect of immigration intensity on productivity depends on the relationship between the immigration (I) and potential reproduction (c) rates. For example, consider the classical case of a trade-off between competitive and dispersal abilities. In our model, competitive ability is determined by r_i , which is proportional to c_i . Thus, this trade-off can be represented by a negative relationship between I and c . In this case, productivity decreases as diversity increases (Fig. 22.3a). For a low immigration intensity (α), the species that persist at equilibrium have a high potential reproduction rate c , hence productivity is high. As α increases, the immigration rate I becomes more important in determining dominance; because

dominant species have a low potential reproductive rate (c), productivity declines. Productivity was found to be roughly constant when immigration and local reproduction are positively correlated, and slightly decreasing with increasing immigration intensity when there is no correlation between immigration and local reproduction.

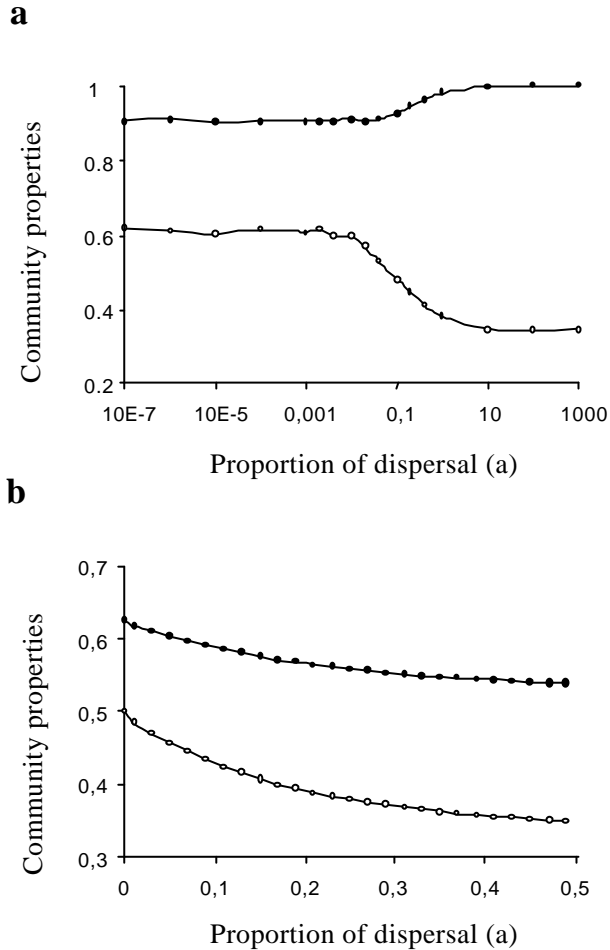


Figure 22.3. Community properties as a function of the proportion of dispersal, which measures the relative importance of local versus regional dynamics: space occupation (filled circles) and primary productivity (open circles). (a) Results from the propagule rain model (means from 1000 simulations), in which the immigration rate I is a decreasing function of the potential reproduction rate c ($I_i = 1 - c_i$). (b) Results from the metacommunity model with two species competing in two communities, in the case of strict similarity. Simulations are performed until equilibrium is reached. Parameters are $c_{11} = 0.8$, $c_{12} = 0.5$, $c_{21} = 0.5$, $c_{22} = 0.8$ and $m_{11} = m_{12} = m_{21} = m_{22} = 0.3$.

In the metacommunity model, we have used an equivalent to equation (4) summed over all j to approximate local plant productivity in a metacommunity. Figure 22.3b shows that

both productivity and space occupation decrease as dispersal increases. Let us calculate the P_{ij} 's equilibrium values from equation (2):

$$\hat{P}_{ij} = \frac{\hat{I}_{ij} \hat{V}_j}{m_{ij}(1 - (1 - a)r_{ij}\hat{V}_j)} \quad (5)$$

When dispersal (a) is low, the dominant species in each community is the one with the highest local competitive ability r_{ij} (i.e. a high local reproduction parameter c_{ij}). Thus, it can be understood from equation (5) that space occupation ($\sum \hat{P}_{ij}$) and productivity ($\sum c_{ij} \hat{P}_{ij}$) are high. As dispersal increases, species with low c_{ij} are maintained by immigration, occupying more sites whereas dominant species occupy fewer sites, which results in decreasing productivity and space occupation. As discussed above, productivity and space occupation are then negatively correlated with diversity, because diversity is positively correlated with dispersal.

2. Evolution in competitive communities

In the real world, the properties of species evolve. In most ecological models, species characteristics are chosen arbitrarily, as if they were formed by some creation event. This would also lead to equally arbitrary communities, as other characteristics could result in entirely different communities. For instance, in classical metapopulation models for a competitive community (Hastings 1980; Tilman 1994), a major assumption is that a superior competitor immediately and completely replaces an inferior competitor. In order for two species to coexist, the inferior competitor needs to be a much better colonizer to make up for the patches lost to the superior competitor. Therefore a good competitor casts a competitive shadow in trait space (Nowak and May 1994). If the best competitor happens to have a small population size, this shadow will be short and many species can coexist; if it happens to have a high population size, only few species can coexist. The composition of the community thus depends strongly on the arbitrarily chosen properties of the dominant competitor.

Although the idea that the natural world has arbitrarily chosen characteristics has a respectable pedigree reaching back several millennia, here we let species characteristics be determined by evolution. We consider a system in which occasionally mutants appear which may replace the wild type if they have a selective advantage, so that a species' traits gradually evolve. Such a process of gradual evolution leads to an assemblage of species with a typical community structure in which evolution of a species depends on the characteristics of the other species in the community.

Under gradual evolution the assumption of immediate replacement in metapopulation models has important consequences for biodiversity and community structure, of competitive communities. Because a superior competitor will immediately replace marginally less-competitive types, a superior competitor grows as if it has the environment for itself. A marginally less competitive type will be in the competitive shadow cast by a superior competitor and disappear altogether. Through this mechanism the successive appearance (through mutations) of marginally better competitors will lead to an increase of the competitiveness of the superior competitor. A better competitor is a weaker colonizer (Tilman 1990, 1994), therefore the equilibrium densities decrease with increased competitiveness. The evolutionary process will only stop if the superior competitor has reached a very low density. All other competitors will be subject to a similar evolutionary process and will evolve towards maximal competitiveness and minimal population sizes. In these models biodiversity is

therefore not maintained unless new, less competitive species are continuously created through mutation.

2.1 Model formulation

Here, we describe a model in which we relax the assumption of immediate replacement. Our model is of the haystack type (Maynard Smith 1964; Cohen and Eshel 1976): a large number patches are simultaneously seeded with various numbers of individuals. We assume a random distribution of seeds according to a Poisson distribution. These local populations “incubate” for some time, after which the local populations produce a new generation of individuals that are then redistributed. Although our model can be easily generalized to suit many biological scenarios, we will interpret the dispersing units as seeds and the incubation period as a growing season in which annual plants compete within a site. Our model has an explicit description of the within-patch dynamics that we solve by separation of time scales. This approximate solution enables us to analyze the evolutionarily stable assemblage, i.e. a community of species with evolutionarily stable growth rates. To keep the technical details to a minimum, we will only present the typical structure of our model and some results. The details will be presented elsewhere (Jansen and Mulder 1999).

We assume that the different types interact within a patch through competition for a single resource. This is described by a set of non-linear differential equations of the form (Hofbauer and Sigmund 1988):

$$\begin{aligned} \frac{dX}{dt} &= X \left(z - \frac{X + X^*}{k} \right) \\ \frac{dX^*}{dt} &= X^* \left(z^* - \frac{X + X^*}{k} \right) \end{aligned} \tag{6}$$

The amount of biomass of each type is given by X and X^* . The traits z and z^* represent the growth rates of the respective types, and k the carrying capacity or quality of the local environment. We assume that the environment affects only the carrying capacity and not the growth rates. Because competition is for a single resource, no two different types can coexist within a patch indefinitely. The fraction of a type ($F = \frac{X^*}{X + X^*}$) changes over time as:

$$\frac{dF}{dt} = (z^* - z)F(1 - F)$$

in which the logistic equation can be recognized. The initial value of this fraction depends on the precise amount of seeds of each type that this patch has received. In this way, the amount of biomass at the end of the season, which is the fraction times the total amount, can be approximated. Locally, species with a higher growth rate, z , will tend to replace species with a low z , so that the growth rate z is therefore a measure of competitive ability.

Note that if the types are very different ($z^* \gg z$ or $z^* \ll z$) one type is replaced quickly by the other and the immediate replacement scenario is recovered. However, if the two types are very similar, the fraction changes slowly, slower than the growth of the total amount of biomass, which we have assumed to be a fast process. The total amount of biomass therefore goes to a quasi-steady state that is a linear combination of the biomass equilibria the respective types would have had if they had had a patch completely to themselves. This procedure can be

made mathematically precise for a large class of local dynamics, and allows us to approximate the amount of biomass of each type at the end of the season (Jansen and Mulder 1999).

At the end of the season all biomass is harvested so that all patches are empty again. Biomass is converted into seeds according to a constraint that relates the growth rate to fecundity. The trade-off is chosen such that a good competitor has a low fecundity. The particular function for the fecundity we use here is $f(z) = (z_{\max} - z)/z$ where z_{\max} is the maximum trait value at which no seeds are produced. Such a trade-off between growth rate and fecundity arises if plants can store part of their assimilates for later seed production. To avoid this function reaching infinite values, we also introduce a minimum value for z : $z_{\min} > 0$. After all patches are emptied, the seeds are redistributed over the patches, according to a Poisson distribution, before the next season starts.

2.2 A description of the global dynamics of a rare mutant

To describe a globally rare mutant we need to know the dynamics across the seasons. Again, we first consider a single type, with a trait with value z . In all patches that have received at least one seed, the biomass at the end of the season will be $\tilde{X} = zk$ (\tilde{X} is the equilibrium amount of biomass of type z in a patch where no z^* is present). The number of seeds produced in these patches is $f(z)\tilde{X}$. If the average seed number per patch is given by N , the fraction of patches with at least one seed is $1 - e^{-N}$; hence, in the next season the average number of seeds per patch is:

$$N' = f(z)\tilde{X}(1 - e^{-N}) \tag{7}$$

This defines the seasonal dynamics of the seed number that goes to a unique and stable equilibrium \tilde{N} if $f(z)\tilde{X} = k(z_{\max} - z) > 1$.

To find out which mutants are selected in an environment dominated by this type, we consider a rare mutant type with growth rate z^* and a background population of residents with trait z at equilibrium density \tilde{N} , and ask whether or not the average number of mutant seeds in a patch, N^* , increases. If so, the mutant can invade the resident population. The within-patch dynamics can be approximated as outlined above: the fraction of mutants in a patch, F , changes logistically. If the mutant is rare, the fraction of patches with two or more mutant seeds is negligible, while the probability of receiving a single seed is approximately linear in N^* . The dynamics of a rare mutant is therefore approximately:

$$N^*{}' = W(z, z^*)N^* \tag{8}$$

The invasion rate of the mutant, $W(z, z^*)$, is a measure of the mutant's fitness (Metz *et al.*, 1992). A mutant's fitness depends both on its own trait and on the trait of the resident. It can be derived from the population dynamics; and because the mutant is rare and the resident at equilibrium, this can be done through a linearization around $N = \tilde{N}$ and $N^* = 0$. It is:

$$W(z, z^*) = \sum_{i=0}^{\infty} f(z^*)F_t : [\tilde{X} + F_t(\tilde{X}^* - \tilde{X})] e^{-\tilde{N}} \tilde{N}^i / i! \tag{9}$$

where i is the number of resident seeds in a patch, and $i!$ is the factorial of i . The number of seeds produced in a patch is $f(z) [\tilde{x} + F_t (\tilde{x}^* - \tilde{x})]$ where $\tilde{x}^* = z^* k$ is the amount of biomass a mutant produces in a patch without residents, and F_t is the fraction of mutants at the end of the season. A fraction F_t of the total seeds are mutant seeds. This fitness is a canonical form of a rare and similar mutant for a large class of haystack models with different local dynamics. The total amount of biomass (the term in square brackets) is determined both by the mutant and by the resident, and reflects how the types interact.

With this expression for fitness, the evolutionarily stable traits \tilde{z} can be derived in the usual way by finding the fitness maximum for z^* (Maynard Smith 1982, Metz *et al.* 1992, Geritz *et al.* 1998). For every value of k , z_{min} is evolutionarily stable (this is due to the particular form of the fecundity trade off.). Fig. 22.4a shows that there is a second evolutionarily stable trait (thick line) whose value depends on the quality of the environment, k . For very poor environments z_{min} is the only evolutionarily stable growth rate; in richer environments the second evolutionarily stable growth rate exists, which corresponds to a stronger competitor. Generally, an increase in environmental quality causes the evolutionarily stable type to be even more competitive. This is because in richer environments the population densities tend to be larger, patches receive more seeds, and competition within a patch becomes more important so that more competitive types evolve.

Similar types cannot invade populations with an evolutionarily stable trait. However, for types that are very different we found immediate replacement, and therefore types that are much weaker competitors and which fall outside the competitive shadow cast by the evolutionarily stable traits can invade and coexist. Whenever these two types have seeds in the same patch, the better competitor excludes the weaker competitor in this patch almost completely within a season. Weaker competitors, therefore, are dependent on those patches that the good competitor leaves unoccupied. The good competitor's dynamics remain virtually unchanged by the presence of the weaker competitors, therefore also its evolutionary stability properties remain unchanged, and much weaker competitors do not change the value of the best competitor's evolutionarily stable trait.

Weaker competitors perceive the presence of the good competitor only as a reduction in the number of available patches. In this smaller number of patches, the weaker competitors can evolve independently of the strong competitor. By applying a similar argument as in the previous section, a third evolutionarily stable growth rate can be found. Because the third type is independent of the second type, apart from a reduction in the number of patches available, the evolutionarily stable growth rate of the third type is the same as that of the second type in a smaller number of patches. Because the fitness (eq. 9) is linear in the quality of the environment, this reduced number of patches can also be expressed as a reduction in the quality of the environment. The evolutionarily stable growth rate of the third type is therefore the same as the evolutionarily stable growth rate of a superior competitor in a poorer environment. In this way the evolutionarily stable growth rates of successively weaker competitors, which live in the patches unoccupied by superior competitors, can be found; these types are represented in Fig 22.4a by thinner lines under the thick curve. We can iterate this procedure until the number of available patches is so far reduced that no further types can be added. In this way the types that constitute the evolutionarily stable assemblage can be determined.

2.3 Properties of the evolutionarily stable assemblage

Fig. 22.4a gives the trait values of all types in the stable assemblage. The assemblage has well-defined types, which differ from other types by a limiting similarity and consists of an integer number of species. This is a feature that is caused by evolution: in our model any number of species can coexist, but not every community is evolutionarily stable. The number of species initially increases with increased environmental quality, but eventually decreases, causing a humped curve in the number of species (Fig 22.4d, dotted line). An intuitive explanation for this fact is that the local production of seeds is higher in richer environments. For the best competitor, this will result in an increase in equilibrium population density. For the remaining species in the assemblage, there is a second effect of increased richness: because of the increase in the superior competitor's density they have to survive in fewer patches. The combination of these opposed effects will result in an optimum number of species for an intermediate quality of the environment. Such relationships are well documented: the average number of species tends to have a humped curve when plotted against productivity (Rosenzweig 1995). Although our results resemble those from metapopulation models

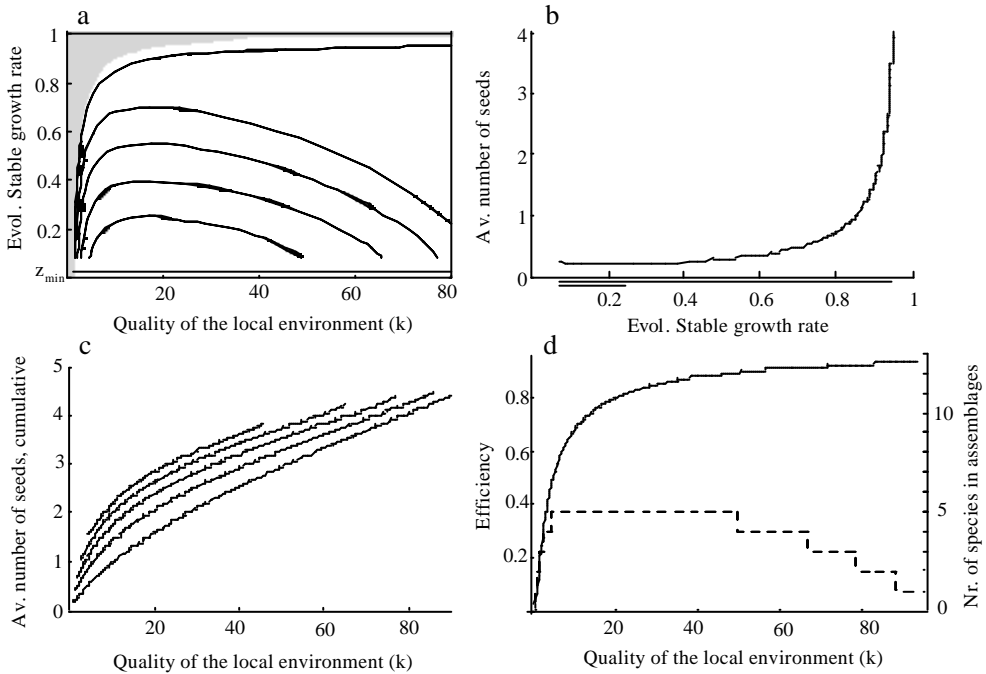


Figure 22.4. (a) The values of the evolutionarily stable growth rate as a function of the quality of the environment, k , in the evolutionary model. (b) The number of dispersers as a function of the evolutionarily stable growth rate. Note that this relation is increasing for large values of the growth rates but decreasing for very small values. The domains of the evolutionarily stable growth rates of the most (top bar) and the least (lower bar) competitive types are indicated with bars under the axis. (c) The cumulative number of dispersers as a function of the quality of the environment. The spacing between the different lines represents the number of dispersers that the next species adds to the total. (d) The efficiency, that is, the amount of biomass at the end of the season before seed conversion, divided by the quality of the environment k , as a function of k . The dashed line represents the number of different types in the evolutionarily stable assemblage.

(Tilman *et al.* 1994; Tilman 1994; Nowak and May 1994; May and Nowak 1994) there is a fundamental difference, in the sense that in these models, gradual evolution would lead to selection for ever-more-competitive types (Nowak and May 1994; Lehman and Tilman 1998), which have ever-smaller population densities.

All types in a stable assemblage have a locally evolutionarily stable growth rate. Although the types are different, their evolutionarily stable growth rate is formed through the same processes for all types. Therefore, a link between the number of dispersers and the growth rate emerges, through the evolutionary interaction (Fig. 22.4b). This link is the same for all types, but the qualitative relationship can appear to be very different for different types. For the most competitive type, the number of produced seeds mostly increases with the growth rate; for the least competitive type it decreases.

Evolutionarily stable assemblages can be used to study the properties of competitive communities. The total number of dispersers in the community increases sharply with the quality of the environment; for better environments this increase is less steep (Fig 22.4c). In Fig. 22.4d we relate the diversity to ecosystem functioning: we measure ecosystem efficiency as the total amount of biomass at the end of the season relative to the quality of the environment k . This measure can be also linked to ecosystem productivity. We found an increase in ecosystem efficiency with increasing environmental quality.

3. Discussion

Our models show two important ways in which dispersal can mitigate competition for space as a single common limiting resource, and hence maintain local species coexistence.

In our metacommunity model, this is obtained through habitat heterogeneity at the regional scale: different sites support different dominant species, which creates a source-sink dynamics at the metacommunity scale and maintains local diversity in all sites. Numerous field studies have shown an influence of regional processes on local species richness. Keddy (1981; 1982), studying plants on a sand dune, showed that the density of a species on the poor habitat quality side was a function of its density on the rich side. Field studies by Shmida and his collaborators (Auerbach and Shmida 1987; Shmida and Ellner 1984; Shmida and Wilson 1985; Kadmon and Shmida 1990) provided similar results at the community level. Seed addition experiments, too, have stressed the influence of immigration on local diversity (Houle and Phillips 1989; Tilman 1997). This concerns especially the maintenance of rare species that correspond, in the source-sink models, to intermediate intensity of immigration or low dispersal between communities. These results are related to the "mass-effect" theory (Shmida and Wilson 1985), and to the source-sink hypothesis (Pulliam 1988), since all species but one would go extinct if the local community was closed (although the latter result depends on the assumption of a constant environment [Jansen and Yoshimura 1998]).

In our evolutionary model, coexistence is obtained through a difference in the strategies by which space is exploited: some species go for local competitive advantage whereas others go for spatial expansion. Several earlier studies have reported the same result (Hastings 1980, Tilman 1994), but the results of those models are dominated by the properties that the dominant competitor happens to have. Our result is novel in that an assemblage of species is the outcome of evolution. In the assemblage, competition works very much as is assumed in the models by Hastings (1980) and Tilman (1994), in that superior competitors quickly replace inferior competitors. However, this same assumption will lead to spurious results if it is

applied to evolutionary processes in which competition between similar strains plays a predominant role.

Our evolutionary model shows another consequence of dispersal: the more dispersers there are, the larger the average number of seeds per patch and the larger the chance of meeting competitors in a patch. Therefore, under conditions that give rise to more dispersers, more competitive types evolve. Dispersal from a patch is often considered a form of altruism, because it reduces competition between kin (Hamilton and May 1977). Here, more dispersers will increase immigration, which reduces relatedness, so that dispersal will cause less altruistic types to evolve.

In the two types of models, the community properties that emerge lead to some counter-intuitive patterns in the relation between species diversity and ecosystem processes. In the propagule rain and metacommunity models, the increased species diversity is accompanied by a decreased average local competitive ability, which generates a negative relationship between diversity and primary productivity or total space occupation (in the metacommunity model), as predicted by Loreau (1998a). In the evolutionary model, a positive relation between efficiency and species diversity emerges for poor environments. But in richer environments, diversity decreases through the dominance of the most competitive species, and a negative correlation with efficiency appears. In this case, variations in diversity and variations in productivity are both determined by variations in the quality of the environment among different sites. This provides another example of across-site comparisons that lead to counter-intuitive patterns, as predicted by Loreau (1998a). Both types of models stress the role of dominant species on community properties. Species diversity increases when the competitive ability of the dominant species decreases, either because of increased dispersal in sink areas or a because of lower quality of the environment. Thus, counter-intuitively, the magnitude of ecosystem processes (such as primary productivity, efficiency or space occupation) tends to decrease as diversity increases.

This emphasizes the critical importance of dispersal between habitats in understanding the structure and functioning of communities and ecosystems. Local communities and ecosystems are shaped not only by local ecological factors, but also by exchanges with neighbouring or more distant systems, and by the evolutionary history of these spatial interactions. Dispersal links local and regional processes, and thus contributes to regulating the composition, diversity, and functional properties of local competitive communities. While the effect of regional processes on local communities has been increasingly recognized recently (see e.g. chapters in Ricklefs and Schluter 1993), the reciprocal effect of local processes on regional diversity has received much less attention. A comprehensive multi-scale theory of species diversity and ecosystem properties incorporating this feedback still waits to be developed. We hope the models presented in this chapter will contribute to this goal.

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