

has been increasingly recognized in recent years to understand such fundamental ecological issues as the relationship between biodiversity and ecosystem functioning, the interactions between food web structure and nutrient cycling, and the role of species in ecosystems (DeAngelis 1992; Jones and Lawton 1995; Loreau 2000b; Kinzig et al. 2002; Loreau et al. 2002; Sterner and Elser 2002). Within the field of spatial ecology, there is a similar need to integrate the perspectives of population and community ecology, including the metacommunity approach, on the one hand, and ecosystem and landscape ecology on the other hand. The metacommunity concept has so far had an exclusive focus on the biotic components of ecosystems. Many critical issues at the landscape or larger spatial scales, however, require consideration of abiotic constraints and feedbacks to biotic processes. We have recently proposed the metaecosystem concept as a theoretical framework for achieving this integration of the community and ecosystem perspectives within spatial ecology (Loreau et al. 2003a).

A *metaecosystem* is defined as a set of ecosystems connected by spatial flows of energy, materials, and organisms across ecosystem boundaries. In contrast to the metacommunity concept, which only considers connections among systems via the dispersal of organisms, the metaecosystem more broadly embraces all kinds of spatial flows among systems, including movements of inorganic nutrients, detritus, and living organisms, which are ubiquitous in natural systems. There has been considerable attention to impacts of spatial subsidies on local ecosystems (Polis et al. 1997). Such studies, however, are limited, in that a subsidy entering one local ecosystem must necessarily be drawn from another. Subsidies at one end are losses at another end, and as such should have impacts on both source and target ecosystems. Moreover, flows are rarely completely asymmetrical. Properties of the higher-level system that arise from movements among coupled ecosystems have seldom been considered explicitly.

Expanding the focus from metacommunities to metaecosystems allows one to understand critical functional properties and processes at spatial scales larger than that of the local ecosystems, which have been the object of greatest interest in classical ecology. Metaecosystems can be defined at any scale from that of an ecosystem cluster (Forman 1995), in which the focus is on small-scale spatial processes among contiguous ecosystems, to that of a region or even the entire globe, for some processes such as spatial flows driven by highly mobile organisms or global biogeochemical cycles involving large-scale air or sea currents. The metaecosystem concept provides a theoretical framework for investigating many of the issues that have been addressed form a more empirical perspective in landscape ecology. It focuses on the properties of the higher-level, spatially extended dynamical system that emerges from movement at landscape to global scales. Just as metacommunity theory is giving new concrete insights into the diversity and structure of ecological communities by explicitly considering interactions between local- and regional-scale processes, the metaecosystem concept provides a

CHAPTER 18

From Metacommunities to Metaecosystems

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Introduction

A defining feature of ecology over the last few decades has been a growing appreciation of the importance of considering processes operating at spatial scales larger than that of a single locality, from the scale of the landscape to that of the region (Ricklefs and Schluter 1993; Turner et al. 2001). Spatial ecology, however, has reproduced the traditional divide within ecology between the perspectives of population and community ecology on the one hand and ecosystem ecology on the other hand.

The population and community ecological perspective has focused on population persistence and species coexistence in spatially distributed systems (Hanski and Gilpin 1997; Tilman and Kareiva 1997), and has a strong background in theoretical ecology and simple, generic mathematical models. The metapopulation concept has occupied a prominent role in the development of this perspective (Hanski and Gilpin 1997; Hoopes et al. chapter 2; Mouquet et al. chapter 10). Its strength has been its ability to deliver specific testable hypotheses on the increasingly critical issue of conservation of fragmented populations in human-dominated landscapes. Because local extinction and colonization can be influenced by interspecific interactions such as predation and competition, a natural extension of the metapopulation concept is provided by the metacommunity concept (Holyoak et al., chapter 1). Significant novel insights are being gained from this new approach, as attested by the various contributions in this book.

Another perspective, however, has developed from ecosystem ecology, and is represented by landscape ecology. Landscape ecology is concerned with ecological patterns and processes in explicitly structured mosaics of nearby heterogeneous ecosystems (Turner 1989; Pickett and Cadenasso 1995; Forman 1995; Turner et al. 2001). It has a strong descriptive basis and a focus on whole-system properties, including abiotic processes. Models that address population persistence and conservation from this perspective are usually more detailed; they consider landscape structure and heterogeneity explicitly, and therefore aim to be more realistic and directly applicable to concrete problems than the more general abstract models of classical metapopulation and community ecology (Gustafson and Gardner 1996; With 1997; With et al. 1997).

The need to integrate the perspectives of community and ecosystem ecology

new tool to understand emergent constraints and properties that arise from spatial coupling of local ecosystems. Emergent properties have been widely discussed within hierarchy theory, which attempts to provide a framework for describing and understanding the spatiotemporal complexity of ecosystems (Allen and Starr 1982; O'Neill et al. 1986). These properties, however, have rarely been studied in a rigorous, quantitative way based on a firm foundation of lower-level interactions.

In this chapter we examine from a theoretical standpoint three examples of emergent properties that arise from spatial coupling of local systems and provide a brief account of the theory that explains the emergence of these properties. Our examples are taken from our recent work at the interface between metacommunities and metaecosystems, and concern three major issues of current interest: (1) the relationship between local and regional species diversity (a community ecology issue); (2) the relationship between species diversity and ecosystem productivity (an issue at the interface between community and ecosystem ecology); and (3) material flows and ecosystem organization at large spatial scales (an ecosystem ecology issue).

Local and Regional Diversity

Species diversity has been studied historically within community ecology from two different, nonoverlapping perspectives: a local perspective, based on niche theory (MacArthur and Levins 1967), and a regional perspective, through island biogeography (MacArthur and Wilson 1967). In the local perspective, interactions between competing species constrain local diversity, and coexistence is viewed either as a function of niche dimensions and resource heterogeneity (MacArthur and Levins 1967) or of differences in species life-history traits (as in the so-called colonization-competition trade-off models; Hastings 1980; Tilman 1994). In the regional perspective, the theory of island biogeography ignores local dynamics and considers local diversity to be the result of regional processes of immigration and extinction. In this theory, there are no limits to diversity except those arising from the size of the regional species pool (continent size) and the constraints on immigration events (continent-island distance). This apparent contradiction was called "MacArthur's paradox" (Schoener 1983; Loreau and Mouquet 1999) because MacArthur's contributions were central in the development of both niche and island biogeography theory.

In reality the dynamics of species diversity at local and regional scales are not independent of one another. Local α diversity and regional γ diversity are mutually dependent through β diversity, the diversity among communities. It is therefore impossible to understand local diversity, regional diversity, and the relationship between them without considering the dynamics that occur across the two scales (Loreau 2000a). Although this mutual dependency of local and regional

diversity has been recognized in principle (Cornell and Lawton 1992; Cornell 1993; Rosenzweig 1995), it has generally been ignored in the interpretation of local-regional richness relationships (Cornell and Lawton 1992; Cornell 1993). Even within metacommunity theory (Holyoak et al. chapter 1), the species-sorting perspective (Leibold 1998) and much of the neutral theory (Hubbell 2001) are based on the implicit assumption that local diversity is influenced by regional diversity but there is no feedback of local diversity on regional diversity, just as in the classical theory of island biogeography. In a true metacommunity perspective, local and regional diversity should be emergent properties that arise from the dynamics of species interactions across scales and constrain each other. The source-sink metacommunity perspective that two of us have recently developed (Mouquet and Loreau 2002, 2003) shows precisely this.

Mouquet and Loreau's (2002) metacommunity model concerns sessile organisms with a dispersal stage, such as plants and some marine invertebrates, or territorial animals with natal dispersal. It incorporates spatial structure both within and among communities. At the local scale (within communities) the model considers the environment as a collection of identical discrete sites, each of which can be occupied by a single individual. It uses the classical formalism of metapopulation models (Levins 1969, 1970) applied at the scale of the individual (Hastings 1980, Tilman 1994; see also Mouquet et al. chapter 10). The model assumes exploitation competition for space; once a plant occupies a site, it keeps it until its death (Loreau and Mouquet 1999). There is no direct competitive exclusion because of interference or competition for other resources; a species' competitive ability is determined by its capacity to occupy new sites (reproduction parameter) and keep them (mortality parameter). Thus, the proportion of vacant sites obtained by each species is proportional to the quantity of propagules it produces. This is a simple extension of competitive lottery models as developed by Chesson and Warner (1981). At the regional scale (among communities), dispersal among communities is assumed to occur through a passive immigration-emigration process. Heterogeneity of environmental conditions at the regional scale is obtained by changing species-specific parameters in each community. This assumes that species exhibit different phenotypic responses in different communities as a result of different local environmental factors.

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

takes the parameters corresponding to that community. This model reads as follows:

$$\frac{dP_{ik}}{dt} = V_k \sum_{l=1}^N b_{ilk} P_{il} - m_{ik} P_{ik} \quad (18.1)$$

where

$$V_k = 1 - \sum_{j=1}^S P_{jk} \quad (18.2)$$

Mouquet and Loreau (2002) showed that a necessary condition for there to be an equilibrium in this model is $S \leq N$. Thus, there cannot be more species than communities in the metacommunity at equilibrium. This rule provides an equivalent to the competitive exclusion principle in a local community (Levin 1970). They further showed that at equilibrium each species satisfies:

$$\bar{R}_i = \frac{\sum_{k=1}^N R_{ik} W_{ik}}{\sum_{k=1}^N W_{ik}} = 1 \quad (18.3)$$

where

$$R_{ik} = V_k^* r_{ik} \quad (18.4)$$

$$r_{ik} = \frac{\sum_{l=1}^N b_{lki}}{m_{ik}}, \quad (18.5)$$

$$W_{ik} = \sum_{l=1}^N b_{ilk} P_{il}^* \quad (18.6)$$

The parameter r_{ik} can be interpreted as the local basic reproductive rate of species i in community k (equation 18.5). Multiplying r_{ik} by the proportion of vacant sites at equilibrium, V_k^* , we obtain the local net reproductive rate of species i in community k at equilibrium, R_{ik} (equation 18.4). Finally, w_{ik} is the total quantity of propagules produced by species i that arrive in community k per unit time at equilibrium (equation 18.6). Consequently, R_i is the regional average net reproductive rate of species i , weighted by the total quantity of propagules arriving in each community, at equilibrium (equation 18.3). Clearly, for the metacommunity to reach equilibrium, R_i must be equal to one (equation 18.3), that is, each individual of each species must produce one individual on average during its lifetime in the metacommunity as a whole.

Because all the regional average net reproductive rates must be equal at equilibrium, this sets a constraint of regional similarity between coexisting species. Whatever the local net reproductive rates, they have to be equal when averaged at the scale of the region. And since net reproductive rates are simply basic repro-

ductive rates multiplied by the proportion of vacant space in each community, this constrains basic reproductive rates too. The latter must be sufficiently balanced over the region for equation 18.3 to be possible. Local coexistence is then possible in a metacommunity when species are locally different but regionally similar with respect to their reproductive rates. Local coexistence is explained by compensations among species' competitive abilities at the scale of the region. As a corollary, the net reproductive rate, and hence also the basic reproductive rate, of any species cannot be lower than that of any other species in all communities simultaneously. This condition requires habitat differentiation among species, that is, each species should be competitively dominant in at least one community. Thus, in a metacommunity, the number of species that coexist locally and regionally will be highest when species have different niches (habitat differentiation constraint), but similar competitive abilities (regional similarity constraint), at the scale of the region.

These rules place strong constraints on both local and regional species diversity. Within these constraints, however, a wide variation of local and regional diversity is possible, and this variation is driven in particular by changes in dispersal among communities. To demonstrate the effect of dispersal on species diversity, assume for simplicity that a proportion of the total reproductive output remains resident while the rest emigrates through a regional pool of dispersers that are equally redistributed in all other communities, and that the proportions of dispersers (a) and nondispersers ($1 - a$) are equal for all species and all communities. Parameter a may thus also be interpreted as a measure of the relative importance of regional versus local dynamics. With these assumptions,

$$b_{ik} = (1 - a)c_{ij} \text{ for } k = i, \quad (18.7a)$$

$$b_{ik} = \frac{a}{N-1} c_{ij} \text{ for } k \neq i, \quad (18.7b)$$

in equation (18.1). Here c_{ij} is the potential reproductive rate of species i in community j , which encapsulates local reproduction, short-distance dispersal and establishment capacities. The model can then be rewritten as

$$\frac{dP_{ik}}{dt} = V_k \left[\frac{a}{N-1} \sum_{l \neq k} c_{il} P_{il} + (1-a)c_{ik} P_{ik} \right] - m_{ik} P_{ik} \quad (18.8)$$

This model was simulated until equilibrium for a metacommunity consisting of twenty species competing in twenty communities. Simulations used an extinction threshold of 0.01, which provides a good approximation of stochastic extinctions at low population size (Loreau and Mouquet 1999), and a matrix of species' local basic reproductive rates corresponding to a deviation of 5% from strict regional similarity. In the case of strict regional similarity the matrix is completely symmetrical with each species being the best competitor in one community

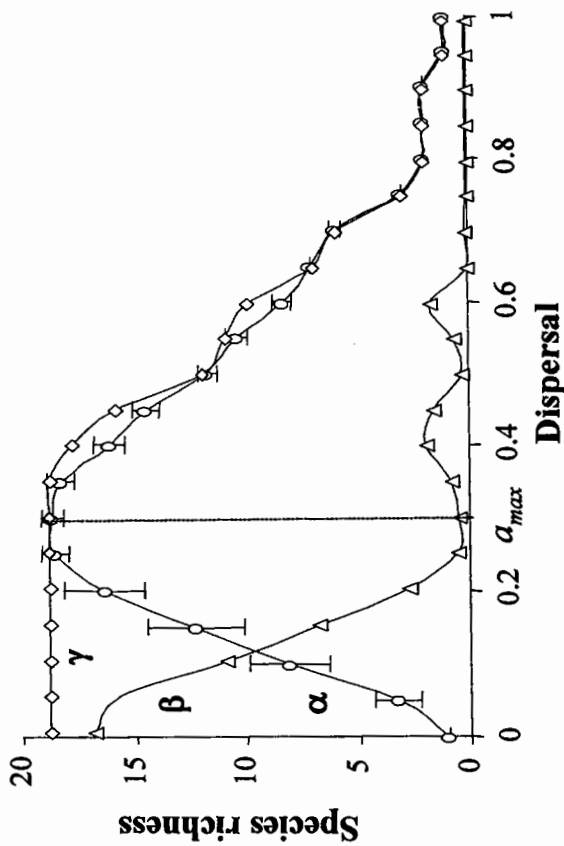


Figure 18.1 Local (α , circles, mean \pm standard deviation across communities), among-community (β , triangles), and regional (γ , diamonds) diversity as functions of dispersal (proportion of dispersers a) in a competitive metacommunity; a_{max} is the dispersal value at which local species diversity is maximal. Modified from Mouquet and Loreau (2003).

(Mouquet and Loreau 2002). The three components of species diversity (α , β and γ) were related through the additive partitioning advocated by Lande (1996) and Loreau (2000a):

$$\gamma = \beta + \bar{\alpha}, \quad (9)$$

where $\bar{\alpha}$ is the mean alpha diversity of local communities.

Varying dispersal has a dramatic effect on the three components of diversity (figure 18.1; Mouquet and Loreau 2003). When dispersal is zero, local (α) diversity is minimal (1 species) whereas among-community (β) and regional (γ) diversities are maximal; in each community a different species is locally the best competitor. As dispersal increases to an intermediate value a_{max} , an increasing number of species are maintained by immigration above the extinction threshold so that α diversity increases, while at the same time communities become more similar in composition so that β diversity decreases. Regional diversity, however, remains relatively constant. As dispersal increases above a_{max} , both local and regional diversity decrease while β diversity stays close to zero because the best competitor at the scale of the region tends to dominate each community, and other species are progressively excluded. At high dispersal, the metacommunity functions effectively as a single community in which one species outcompetes all others. A hump-shaped relationship between local diversity and dispersal emerges from these constraints:

In the ascending part of the curve, γ diversity is determined by regional environmental heterogeneity, and dispersal acts to transfer its effect from the among-community (β) to the local (α) component of diversity. In the descending part of the curve, dispersal leads to homogenization of the metacommunity, which has a negative effect on regional, and hence also local, diversity.

These results clearly show that dispersal is a major determinant of the relationship between local and regional diversity. To further explore this issue, Mouquet and Loreau (2003) varied maximum regional species richness by varying the degree of regional environmental heterogeneity in the metacommunity for each dispersal value. Variation in environmental heterogeneity was obtained by defining a parameter E_k measuring the environmental condition of community k in a range from 0 to 1, and a parameter H_i measuring the niche preference of species i to environmental conditions, also in a range from 0 to 1. The potential reproductive rate of species i in community k , c_{ik} , was assumed to be greater as its niche optimum was closer to the local environmental condition $\{c_{ik} = (1 - |E_k - H_i|) \times 3\}$. Variation of regional environmental heterogeneity was then generated by varying the distribution of E_k values across communities. Figure 18.2 shows the resulting relationships between local and regional diversity for various levels of

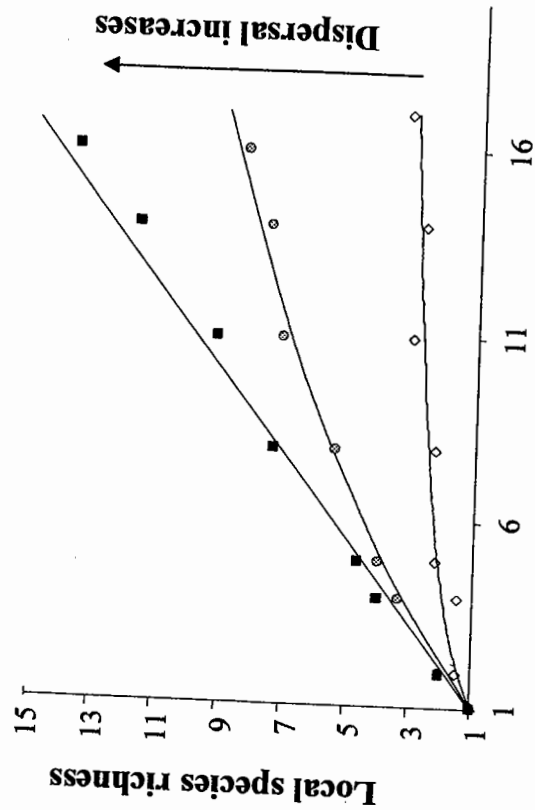


Figure 18.2 Relationships between local and regional species richness for various values of dispersal in a competitive metacommunity ($a = 0.1$, black squares; $a = 0.075$, gray circles; $a = 0.025$, white diamonds). For each dispersal value the gradient of regional species richness was obtained by varying the degree of regional heterogeneity. These results were obtained for low to intermediate dispersal values. At high dispersal, local and regional diversities are equal and the relationship is linear. Modified from Mouquet and Loreau (2003).

dispersal. When dispersal is low, local species richness is limited by the locally dominant species irrespective of regional species richness, and the resulting relationship between local and regional diversity is saturating. When dispersal is higher, local species richness becomes equal to regional species richness and the relationship between local and regional diversity is linear.

Local versus regional diversity plots have often been interpreted as indicative of community saturation; unsaturating linear curves would be typical for unsaturated, noninteractive communities, whereas saturating curves would indicate saturated, interactive communities (Terborgh and Faaborg 1980; Cornell and Lawton 1992; Cornell 1993). The above results show that this interpretation is unwarranted (see also Shurin and Srivastava, chapter 17). Saturation of local regional richness curves does not tell us anything about community saturation arising from species interactions, but is more fundamentally related to the scale at which a local community is defined and the dispersal properties of the organisms considered (Loreau 2000a). Generally speaking, expanding the scale at which local communities are defined amounts to transferring the environmental heterogeneity that is responsible for the bulk of diversity from the regional to the local scale, hence from β to α diversity. Increasing dispersal across the landscape has a similar effect. The effects of scale and dispersal can be studied quantitatively using modeling frameworks such as that presented here.

Species Diversity and Ecosystem Productivity

The relationship between species richness and ecosystem properties such as productivity has become a central issue in ecological and environmental sciences (see reviews in Tilman 1999; Waide et al. 1999; Loreau 2000b; Mittelbach et al. 2001; Loreau et al. 2001, 2002; Kinzig et al. 2002). It is a unifying fundamental question that requires merging concepts from ecosystem and community ecology. These two subdisciplines have increasingly diverged historically, and merging them is a challenge for modern ecology. This challenge is made particularly important by the current need to understand the potential consequences of biodiversity loss for ecosystem functioning. The traditional approach to diversity-productivity relationships has been to regress species diversity on productivity—or, more exactly on factors, such as climate and soil fertility, that determine productivity—across sites with different environmental characteristics (Huston 1994; Waide et al. 1999; Grime 2001). In contrast, recent experimental and theoretical work has focused on the specific effect of species diversity on productivity when all other factors are held constant (Tilman 1999; Loreau 2000b; Loreau et al. 2001, 2002; Kinzig et al. 2002). The two approaches have led to different results, which can be reconciled by recognizing that they address different causal relationships at different scales (Loreau 1998, 2000b; Loreau et al. 2001).

Diversity-productivity relationships are also expected to depend strongly on

the kind of diversity present in a community, that is, on the coexistence mechanisms that are responsible for the maintenance of diversity within the community (Mouquet et al. 2002). Different coexistence mechanisms involve different environmental and evolutionary constraints on organisms, and these constraints shape both the diversity and productivity of the communities and ecosystems these organisms form. Diversity-productivity relationships then emerge as products of environmental and evolutionary constraints, in which diversity determines productivity as much as productivity determines diversity. What kind of diversity-productivity relationship emerges from source-sink processes in a metacommunity?

Mouquet and Loreau (2003) and Loreau et al. (2003b) explored this issue with two different metacommunity models. The first model is the one presented above, which describes exploitation competition for space. In this model, each species' local productivity is assumed to be determined by its local competitive ability (Tilman et al. 1997; Loreau 1998; Mouquet et al. 2002). Ecosystem productivity in community k , Φ_k , is therefore taken to be the product of the proportion of sites occupied by each species and its local reproductive rate (which is correlated with competitive ability in this model), summed over all species (Loreau and Mouquet 1999):

$$\Phi_k = \sum_{i=1}^s c_{ik} P_{ik} \quad (18.10)$$

Similarly, space occupation by the community as a whole is taken to be simply the summed proportions of sites occupied by all species.

As dispersal increases, average productivity and space occupation across the metacommunity decrease (figure 18.3A). This occurs because the mass effect (Shmida and Ellner 1984), which maintains local species diversity at low to moderate dispersal, also acts to dilute the locally best adapted species—the best competitor—in a mass of locally less adapted species (Loreau and Mouquet 1999). Combining this result with the hump-shaped relationship between local species diversity and dispersal (figure 18.1), a hump-shaped relationship between local species average productivity and local species richness (figure 18.3B; note that productivity is on the vertical axis, so that the humped relationship is portrayed in a vertical configuration relative to productivity-diversity plots with productivity on the horizontal axis). At the regional scale, however, the relationship between average productivity and regional species richness is either positive or null (figure 18.3C) because regional species richness is constant or decreases with increasing dispersal (figure 18.1).

These results provide theoretical support for the hypothesis that different diversity-productivity relationships may emerge at different spatial scales, although the mechanisms involved are different from those proposed in other studies (Bond and Chase 2002; Chase and Leibold 2002). Bond and Chase (2002),

using a verbal model, suggested that regional complementarity among species could lead to a positive relationship between productivity and regional species richness. In contrast, a hump-shaped relationship would be found at the local scale because local species richness would increase first through local niche complementarity (generating a positive relationship with productivity) and then through a source-sink effect (generating a negative relationship with productivity). Mouquet and Loreau's (2003) results confirm Bond and Chase's intuition, but they involve no local niche complementarity. Both the local hump-shaped and the regional positive diversity-productivity relationships arise from pure source-sink metacommunity processes.

Loreau et al. (2003) developed a more mechanistic consumer-resource model to explore the effects of species diversity on ecosystem productivity and its temporal stability in a metacommunity or metaecosystem under fluctuating environmental conditions. This model makes similar assumptions to the previous one, in particular the fact that dispersal is global and identical for all species, and dispersers are redistributed uniformly across the landscape. The main differences lie in the presence of an explicit consumer-resource local interaction, which allows a more straightforward measurement of productivity, and the presence of environmental fluctuations. The model reads as follows:

$$\frac{dN_{ij}(t)}{dt} = [e_{ij}c_{ij}(t)R_j(t) - m_{ij}]N_{ij}(t) + \frac{a}{M-1} \sum_{k \neq j} N_{ik}(t) - aN_{ij}(t) \tag{18.11}$$

$$\frac{dR_j(t)}{dt} = I_j - I_jR_j(t) - R_j(t) \sum_{i=1}^S c_{ij}(t)N_{ij}(t) \tag{18.12}$$

where $N_{ij}(t)$ is the biomass of species i (e.g., a plant) and $R_j(t)$ is the amount of limiting resource (e.g., a nutrient such as nitrogen) in community j at time t . The metacommunity consists of M communities and S species in total. Species i consumes the resource at a rate $c_{ij}(t)$, converts it into new biomass with efficiency e_{ij} , and dies at rate m_{ij} in community j . The resource is renewed locally through a constant input flux I_j , and is lost at a rate I_jR_j . All species disperse at a consumption rate $c_{ij}(t)$ vary as local environmental conditions change through time, and are assumed to reflect the matching between species traits and environmental conditions as above. Defining again H_i as the constant trait value of species i and $E_j(t)$ as the fluctuating environmental value of community j , consumption rates are given specifically by:

$$c_{ij}(t) = 1.5 - |H_i - E_j(t)|. \tag{18.13}$$

Fluctuations of local environmental values are assumed to be sinusoidal with period T :

$$E_j(t) = \frac{1}{2} \left[\sin \left(x_j + \frac{2\pi t}{T} \right) + 1 \right], \tag{18.14}$$

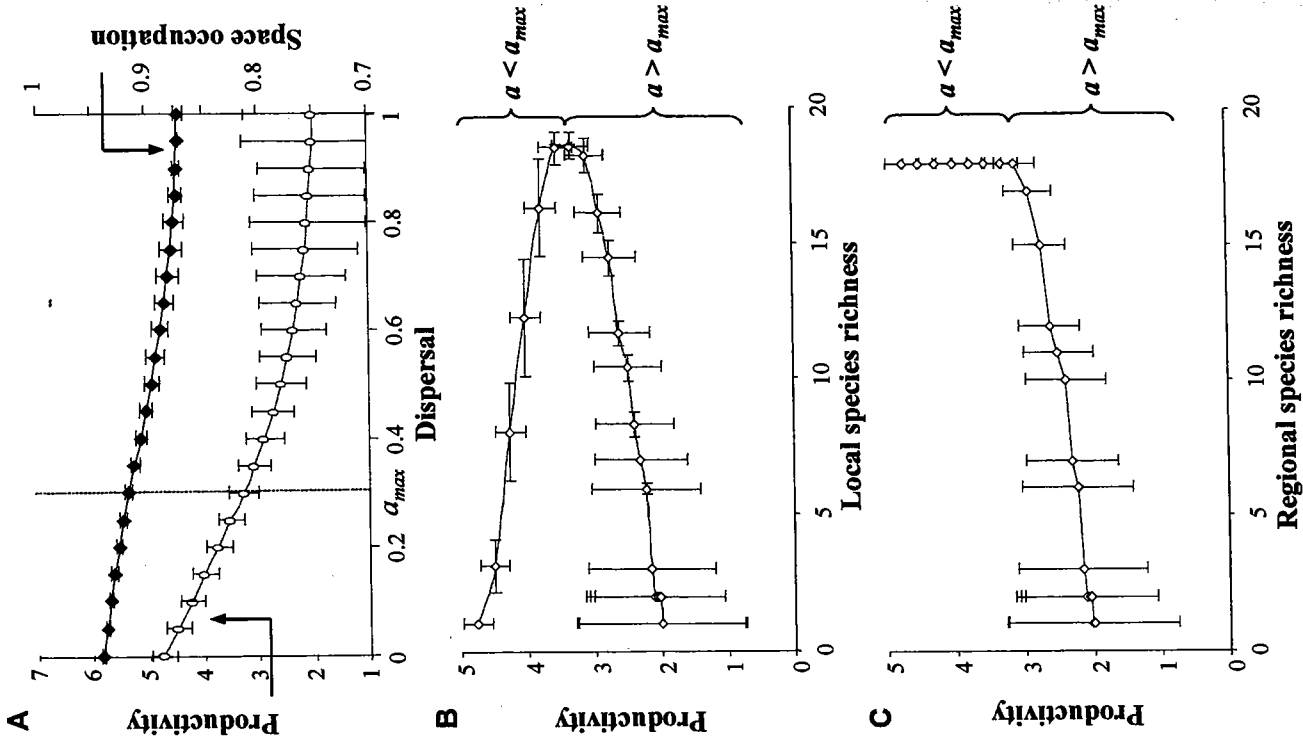


Figure 18.3 (A) Productivity (white circles) and space occupation (solid diamonds) (mean \pm standard deviation across communities) as functions of dispersal (proportion of dispersers a) in a competitive metacommunity. (B) The relationship between local species richness and local productivity when dispersal varies. (C) The relationship between regional species richness and local productivity when dispersal varies; a_{max} is the dispersal value at which species richness is maximal. Modified from

and to be out of phase in the various communities, by choosing x_j such that $E_j(0) = 1$ and $E_j(0) = E_{j-1}(0) - 1/6$ for $j = 2$ to 7 . With this assumption, there is always a community in which each species is superior, but because of temporal fluctuations, that community shifts in space over time, thus requiring some dispersal for long-term coexistence. The period of fluctuations was chosen to be large enough so that there was competitive exclusion in the absence of dispersal.

Lastly, ecosystem productivity at time t is defined as the production of new biomass per unit time, which, averaged across the metacommunity, is

$$\Phi(t) = \frac{\sum_{i=1}^S \sum_{j=1}^M e_{ij} c_{ij}(t) R_j(t) N_{ij}(t)}{M} \quad (18.14)$$

This model leads to the same hump-shaped relationship between local diversity and dispersal as does the previous model (figure 18.4A). In contrast to the previous model, however, average productivity here follows a hump-shaped pattern similar to that of species diversity (figure 18.4B). Similarly, the coefficient of variation of productivity—a common standardized measure of variability (Doak et al. 1998; Ives et al. 1999; Lehman and Tilman 2000; Ives and Hughes 2002)—follows an inverse pattern (figure 18.4C). As a consequence, variations in dispersal rate generate strongly nonlinear, parallel variations in local species diversity, average productivity, and the stability (sensu reduced variability) of productivity.

Differences from the previous model are explained by the specific effects of biodiversity made possible by environmental fluctuations. Biodiversity has been shown to act as biological insurance for local ecosystem functioning by allowing functional compensation among species or phenotypes in time (McNaughton 1977; Yachi and Loreau 1999; Ives et al. 1999; Lehman and Tilman 2000; Norberg et al. 2001). Such insurance effects include an increase in the temporal mean of productivity when there is selection for adaptive responses to environmental fluctuations, and a decrease in productivity's temporal variability because of temporal complementarity among species responses (Yachi and Loreau 1999; Loreau 2000b). Here, however, these effects occur despite the fact that local coexistence is impossible, and thus no temporal insurance effect can occur within a closed system. Therefore, insurance effects shown by this model are entirely generated by the spatial dynamics of the metacommunity. When different systems experience different environmental conditions and fluctuate asynchronously, different species thrive in each system at each point in time, and dispersal ensures that the species adapted to the new environmental conditions locally are available to replace less adapted ones as the environment changes. As a result, biodiversity enhances and buffers ecosystem processes through spatial exchanges among local systems in a heterogeneous landscape, even when such effects do not occur in a closed homogeneous system. This is the spatial insurance hypothesis (Loreau et al. 2003).

As shown by figure 18.4, however, spatial insurance effects are strongly

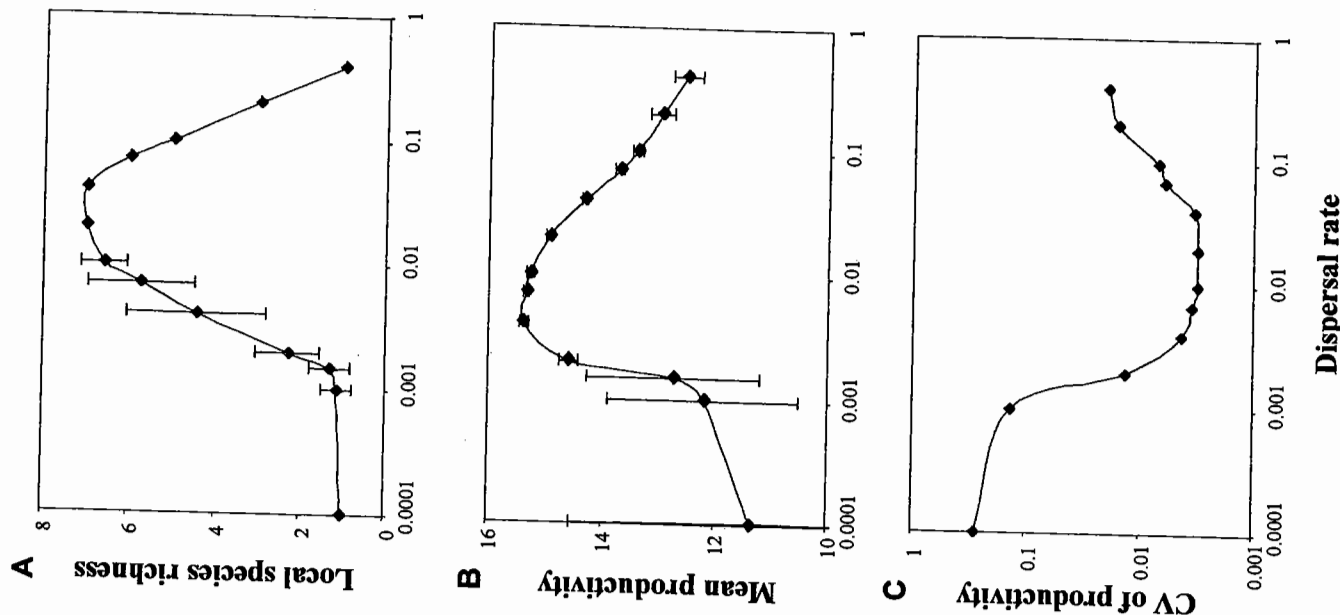


Figure 18.4 Local species richness (A), temporal mean of ecosystem productivity (B), and coefficient of variation of ecosystem productivity through time (C) as functions of dispersal rate (mean \pm standard deviation across communities) in a competitive metacommunity.

dependent on dispersal rate, which determines metacommunity connectivity. Local species diversity and the insurance effects that it generates are highest at an intermediate dispersal rate, and collapse at both low and high dispersal rates. At both ends of the dispersal gradient functional compensations and adaptive shifts between species are prevented, leading to a relatively low average productivity as well as large fluctuations in productivity as the single surviving species tracks environmental fluctuations.

Material Flows and Ecosystem Organization

The last example of an emergent property arising from spatial coupling of local systems is the pattern of material flows in a metaecosystem. Flows of nutrients, whether in the form of inorganic elements, detritus, or living organisms, can exert important influences on the functioning of local ecosystems (Polis et al. 1997). Less appreciated is the fact that these flows may also impose global constraints at the scale of the entire metaecosystem, thereby generating a strong interdependence among local ecosystems.

To highlight these constraints, we concentrate on the simplest possible model of a closed nutrient-limited metaecosystem. Consider two connected local ecosystems, 1 and 2, each of which in turn consists of two interacting compartments, plants (with nutrient stock P) and inorganic nutrients (with stock N). Spatial flows among ecosystems are assumed to occur among similar compartments (i.e., from inorganic nutrient to inorganic nutrient, and from plants to plants). They are also assumed to be independent of local interactions among ecosystem compartments, such that spatial flows and local growth rate are additive in the dynamical equation for each ecosystem compartment. Let F_{xij} denote the directed spatial flow of nutrient stored in compartment X from ecosystem i to ecosystem j , Φ_i primary production in ecosystem i , and R_i the flow of recycled nutrient within ecosystem i . Local and global mass balance leads to the following set of equations describing the dynamics of the metaecosystem:

$$\frac{dN_1}{dt} = F_{N21} - F_{N12} - \Phi_1 + R_1, \quad (18.15a)$$

$$\frac{dN_2}{dt} = F_{N12} - F_{N21} - \Phi_2 + R_2, \quad (18.15b)$$

$$\frac{dP_1}{dt} = F_{P21} - F_{P12} - \Phi_1 + R_1, \quad (18.15c)$$

$$\frac{dP_2}{dt} = F_{P12} - F_{P21} - \Phi_2 + R_2, \quad (18.15d)$$

This description in terms of directed flows among ecosystems and compartments (figure 18.5A) can be reduced to a simpler description in terms of net flows as follows:

$$\frac{dN_1}{dt} = F_N - G_1, \quad (18.16a)$$

$$\frac{dN_2}{dt} = -F_N + G_2, \quad (18.16b)$$

$$\frac{dP_1}{dt} = F_P - G_1, \quad (18.16c)$$

$$\frac{dP_2}{dt} = -F_P + G_2, \quad (18.16d)$$

where $F_X = F_{X21} - F_{X12}$ is the net spatial flow of nutrient of compartment X from ecosystem 2 to ecosystem 1, and G_i is net local plant growth in ecosystem i .

Note that, as required for closed systems, local mass is conserved in the absence of spatial flows and global mass is conserved with spatial flows. Additional constraints emerge from spatial coupling of local ecosystems as the metaecosystem reaches equilibrium. At equilibrium the left-hand side of equations 18.15 and 18.16 vanishes, which imposes

$$F_N^* = -F_P^* = G_1^* = -G_2^*, \quad (18.17)$$

where asterisks denote functions evaluated at equilibrium. This set of equalities can be interpreted as a double constraint, which can easily be generalized to metaecosystems with an arbitrary number of local ecosystems and an arbitrary number of ecosystem compartments (Loreau et al. 2003a): (1) A *source-sink constraint within* ecosystem compartments. For each compartment, positive growth in some ecosystems must be balanced by negative growth in other ecosystems at equilibrium, which means that some local ecosystems must be sources whereas others must be sinks; and (2) A *source-sink constraint between* ecosystem compartments. The total net spatial flow across the boundaries of each ecosystem must vanish at equilibrium, which means that some compartments must be sources whereas others must be sinks.

In our simple metaecosystem with two ecosystems and two compartments, these constraints result in a global material cycle such that net flows at equilibrium are either in the direction $N_1 \rightarrow P_1 \rightarrow P_2 \rightarrow N_2 \rightarrow N_1$ (figure 18.5B) or in the opposite direction depending on the sign of F_N^* (or any other function) in equation 18.17. In this global cycle, even though production and nutrient recycling occur within each ecosystem (figure 18.5A), one ecosystem acts as a net global pro-

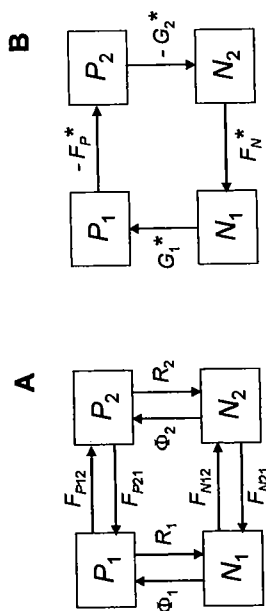


Figure 18.5 Material flows in a closed nutrient-limited metaecosystem consisting of two connected local ecosystems, 1 and 2, each of which in turn consists of two interacting compartments, plants (P) and inorganic nutrient (N): (A) directed nutrient flows, and (B) net nutrient flows at equilibrium.

ducer ($N_1 \rightarrow P_1$) whereas the other acts as a net global recycler ($P_2 \rightarrow N_2$) (figure 18.5B). When there are more than two ecosystem compartments and local ecosystems, the pattern of material circulation in the metaecosystem may be more complex, but all local ecosystems are embedded in a web of material flows constrained by the functioning of the metaecosystem as a whole (Loreau et al. 2003a).

This simple metaecosystem model shows that strong constraints on local ecosystem functioning emerge from spatial coupling of ecosystems. When these constraints can be met, they imply that local ecosystems can no longer be governed by local interactions alone. Instead, by being part of the larger-scale metaecosystem, local ecosystems are constrained to become permanent sources and sinks for different compartments, and thereby to fulfill different functions in the metaecosystem. It is also conceivable, however, that these constraints may be impossible to meet in some cases; during transient dynamics parts of the metaecosystem will then absorb others by progressively depriving them of the limiting nutrient. Specifically, nutrient source-sink dynamics within metaecosystems may drive or accelerate successional changes, until equilibrium is achieved and the final metaecosystem state becomes compatible with global source-sink constraints. Whether energy and material transfers across ecosystem boundaries are strong enough to drive succession, however, depends on their magnitude relative to that of the colonization processes that bring new species into local ecosystems and thereby change their properties. This suggests that combining an explicit accounting of spatial flows of energy and materials with the dynamics of colonization of new patches by organisms in an integrated metaecosystem approach may provide a promising novel perspective on succession theory.

Conclusions

Extending metacommunity theory to a full theory of metaecosystems represents an important and timely development for spatial ecology—a development that

has the potential to integrate the perspectives of community, ecosystem, and landscape ecology. At a time when humans are profoundly altering the structure and functioning of natural landscapes, understanding and predicting the consequences of these changes is critical for designing appropriate conservation and management strategies. Metacommunity and metaecosystem perspectives provide powerful tools to meet this goal. By explicitly considering the spatial interconnections among systems, they have the potential to provide novel fundamental insights into the dynamics and functioning of ecosystems from local to regional scales, and to increase our ability to predict the consequences of land-use changes on biodiversity and the provision of ecosystem services to human societies.

In this chapter we have provided some examples of significant emergent properties that arise from spatial coupling of local ecosystems. These range from the coupled dynamics of local and regional diversity, through diversity-productivity relationships at local and regional scales, to patterns of nutrient flows from landscape to global scales. In all these examples, metaecosystem connectivity, as determined by the spatial arrangement of component ecosystems and the movements of organisms, energy, and inorganic substances across these ecosystems, exerts strong constraints on the structure, functioning, and stability of the system at both local and regional scales. It also drives many of the community and ecosystem properties that are traditionally studied at separate scales without consideration of these critical connections among scales. This shows that the metaecosystem and metaecosystem perspectives offer a promising theoretical framework to explore hierarchical systems and emergent properties in a spatial context.

We acknowledge that the theoretical models we have reviewed have a number of simplifying assumptions and hence a number of limitations, and that empirical support is still largely missing. The assumptions that are probably most critical in our metacommunity models concern the rules that constrain local interactions (competitive lottery), and the nature of the dispersal process (global, passive dispersal, with no life-history correlates). Modifying these assumptions to make the models better suited for organisms other than plants is likely to change some of the emergent properties we have investigated (such as diversity-productivity relationships), although others (such as local-regional diversity relationships) may be more robust because the mechanisms involved are relatively general. In contrast, our metaecosystem model can be made very general (Loreau et al. 2003a). The challenge here will be to devise more detailed, yet tractable, models capable of providing new insights into more targeted issues for specific systems.

The objective of the models presented in this chapter, however, was not to provide detailed predictions for specific systems, but instead to examine the potential of metacommunity and metaecosystem approaches for exploring new issues and providing new insights into old issues. We feel that, in this respect, these

approaches have proven very successful and offer a rich avenue for future theoretical, experimental, and empirical developments. Our hope is also that they will help stimulate the emergence of a mechanistic theoretical landscape ecology.

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CHAPTER 19

Adaptive and Coadaptive Dynamics in Metacommunities

Tracking Environmental Change at Different Spatial Scales

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Introduction

It has long been recognized that community processes operate at numerous scales and that the dynamics of these processes occur differently when they are manifest at these different scales. The metacommunity concept we have championed in this book provides one way of exploring these issues in a general framework that remains conceptually transparent and draws attention to numerous features of multiscale ecological processes.

The work described in the earlier chapters of this book and in previously published works illustrates numerous ways that local and regional dynamics of communities are illuminated by this approach. The effects of metacommunity dynamics can be discerned in many important aspects of community and metacommunity structure including patterns of population structure, coexistence, biodiversity, food web architecture, and ecosystem attributes. These studies also show that these various patterns are interrelated; specific patterns predicted by theory and that at times observable in experimental and observational work are contingent on each other. Thus, for example, the observation of patterns that correlate local diversity with regional diversity, despite having strong local saturation of local communities, may be contingent on the dynamics of food web assembly (Shurin and Srivastava, chapter 17). Similarly, observed scaling relations in biomass of organisms at different trophic levels, may also be contingent on how food web assembly processes and community shifts in composition among redundant species occur in metacommunities.

It seems clear that a metacommunity perspective can strongly modify the way we view how communities are regulated and how community structure is related to environmental conditions. In this chapter we evaluate how community structure might be related to environmental conditions by thinking of communities as "complex adaptive systems" (see Levin 1998) and explore how metacommunity dynamics constrain the processes that affect the behavior of such systems. We start with the following propositions that are strongly suggested by work to date on metacommunities: