CHAPTER 10

The World Is Patchy and Heterogeneous!

Trade-off and Source-Sink Dynamics in Competitive Metacommunities

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> When we discuss communities beyond their most essential attributes as open systems, generality may elude us, except the generality of diversity.
>
> WHITTAKER AND LEVIN, 1977

Introduction

Recognition that the world is patchy and heterogeneous has been the basis for many advances in both fundamental and applied ecology over the last thirty years (Levin 1992). This chapter reviews conceptual advances in the understanding of spatial mechanisms of competitive coexistence and places those advances in the context of metacommunity ecology. We discuss work from the past half century through extremely recent results in order to highlight unexpected links and reinterpretations. We show that apparently different mechanisms have common elements and we discuss options for integrating these elements into a broader theoretical framework. This framework could lead to a general theory of biological diversity for a natural world increasingly transformed by human activities.

For the sake of generality, ecologists frequently look for simple rules that apply to a wide range of taxa. Community ecology has provided one such simple law in the form of the competitive exclusion principle (Lack 1944; Hutchinson 1957; Hardin 1960) derived from the Lotka-Volterra models (Lotka 1925; Volterra 1926) and Gause's experiments (1934). This principle states that the number of coexisting species cannot exceed the number of limiting factors or ecological niches. It has brought community ecology into a modern synthesis led by the works of Hutchinson (1957), Hardin (1960), MacArthur (1967, 1972), and others. In reality, however, for the vast majority of communities, the competitive exclusion principle is too restrictive because it focuses only on local limiting factors in a homogeneous environment. The original theory could not explain high diversity found in natural systems with few identified limiting factors, especially for plants and aquatic communities (e.g., Hutchinson 1961). Ecology rejected niche theory reductionism in favor of complexity and entered a new era without a theory of diversity but with a diversity of theories explaining species richness (reviewed by Chesson 2000a, Barot and Gignoux 2004).

Forty years after Hutchinson discussed paradoxically high plankton diversity (Hutchinson 1961), recognition of the importance of patchiness and heterogeneity has led to more comprehensive and realistic theories of species diversity. Patchiness and heterogeneity are two interconnected forms of environmental variation. Patchy environments have spatially discrete elements either because of natural barriers (e.g., deep water between coral reefs, ponds separated by land, plant patches separated by a matrix inconducive to plant growth, etc.) or species characteristics (e.g., sessile species with a dispersal stage, territorial organisms with natal dispersal, etc.). Heterogeneity implies differences in the environmental conditions found in two patches (table 1.1), for example due to different limiting factors or historical context. Although early community ecologists recognized the discrete nature of habitats (Skellam 1951; Andrewartha and Birch 1954; Huffaker 1958), the idea became central to community ecology only after Levins defined metapopulations (Levins 1969, 1970), and Levins and Culver (1971) applied the concept to competition theory. The natural link between patchiness and regional heterogeneity has led ecologists to focus on mesoscale ecology (Roughgarden et al. 1988; Holt 1993; Ricklefs and Schluter 1993) to incorporate more realistically the dynamics of species diversity in metacommunities.

The recognition of spatial structure leads to differentiation between local (within patch) and regional (among patch) processes (see table 1.1). Since the work by Skellam (1951) there has been a separation in model formalism and assumptions between these two scales (figure 10.1). For example, models of coexistence in discrete, homogeneous environments have adopted the Levins (1969, 1970) metapopulation approach of describing dynamics in terms of extinctions and recolonization of patches. These models assume a net separation between local and regional time scales such that coexistence within a patch is impossible, and they explain regional coexistence given a trade-off between competitive and colonization abilities (Levins and Culver 1971; Horn and MacArthur 1972; Hastings 1980). In contrast, models that consider coexistence in heterogeneous environments have opened different perspectives on local species coexistence through source-sink or mass effects in metacommunities (see Holyoak et al., chapter 1 for definitions). These models have shown that local coexistence is possible through regional niche differentiation and dispersal between patches (Levin 1974; Shmida and Ellner 1984; Amarasekare and Nisbet 2001; Mouquet and Loreau 2002, 2003). This divergence has resulted for example, in competition-colonization trade-offs and source-sink dynamics being viewed as mutually exclusive mechanisms of coexistence when they should be studied in a common framework relevant to metacommunity ecology (Amarasekare et al. 2004).

Ecologists have recently begun to synthesize these two approaches into a common framework under metacommunity ecology (Wilson 1992; Holt 1993, 1997a;

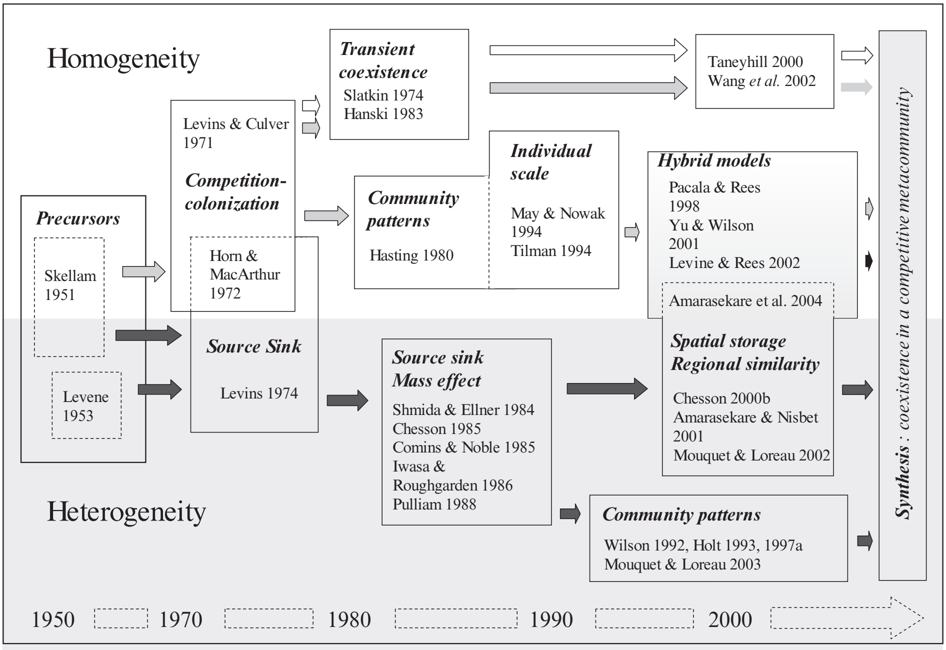

Figure 10.1 Representation of the chronology of some important papers that have studied the conditions of coexistence between competing species in patchy habitats. There was rapid separation between studies that considered homogeneous (white region) and heterogeneous (gray region) environments. Three main branches have emerged from the precursor works of Skellam (1951) and Levene (1953), respectively the source-sink hypothesis (dark gray arrows), the competition-colonization hypothesis (gray arrows) and a third branch that have studied the consequences of transient local coexistence in patch models (white arrows). We have added a chronological axis at the bottom of the figure. These papers are reviewed in the text and summarized in table 10.1. This list is not exhaustive, but rather represents what we think are the key papers.

Mouquet and Loreau 2002, 2003; Loreau et al. 2003; Leibold et al. 2004; Holyoak et al., chapter 1). Although we are not the first to make the link between these approaches (Yu and Wilson 2001; Levine and Rees 2002), a thorough clarification of the ideas underlying spatial coexistence is necessary for further progress in metacommunity ecology. Contemporary ecologists (including the authors of this chapter) have also often failed to recognize insightful contributions of early works such as Skellam (1951) and Levene (1953). This oversight is partially due to differences in focus between more recent metacommunity ecology and the early work on species coexistence in space. For example Levins and Culver (1971), only briefly considered the general topic of coexistence and species richness. Their focus instead was on the role of competition in the dynamics of rare species on island systems. The diversity of biological systems modeled also contributed to the lack of early synthesis because the questions addressed in marine versus terrestrial systems were not necessarily similar, and hence generalizations were difficult to make.

With a view toward clarification, in this chapter we review theory on coexistence in patchy environments, focusing on the competition-colonization (hereafter CC) and the source-sink (hereafter SS; also known as the mass effect) hypotheses. We retrace the chronology of these two approaches, highlighting their key results, differences, and similarities. We end with the basic elements of a more general framework that allows ecologists to examine patch dynamics and mass effects simultaneously. Table 10.1 and figure 10.1 provide an overview of these models that might be used as a guideline during the reading of this chapter. We focus only on theoretical studies since empirical evidence for spatial coexistence is presented elsewhere (Keddy 1982; Shmida and Ellner 1984; Kadmon and Shmida 1990; Gonzalez et al. 1998; Forbes and Chase 2002; Cottenie et al. 2003; Kneitel and Miller 2003; Urban 2004; Miller and Kneitel, chapter 5; Cottenie and De Meester, chapter 8; Chase et al., chapter 14). Our perception of the historical development of these ideas has probably biased our choices, but our goal is to be comprehensive rather than exhaustive.

The Precursors: Skellam (1951) and Levene (1953)

The works of Skellam and Levene are seminal to the development of metacommunity theory. Skellam used diffusion theory to study the consequences of dispersal for both local and regional species coexistence. He showed that a population could maintain itself in unfavorable regions by random dispersal from favorable regions. He stated that the stability of such a system depended "on the ability of the population in favorable habitats to make good the decline in the unfavorable ones" (Skellam 1951, 202). He also studied competition between two annual plants within the same habitat and showed that coexistence was possible given that "a disadvantage in direct competition may be offset by a superiority in reproductive capacity" (215). He further demonstrated that the advantage in reproductive capacity that an inferior competitor needs to persist depends on the density of the superior competitor (the effect of the superior competitor on the inferior competitor). Levene studied similar coexistence concepts with genes (1953; see also Levins and MacArthur 1966). He examined the conditions for the maintenance of polymorphism without any heterozygote advantage. He proposed a simple model of allele frequencies considering that "the existence of several ecological niches, with one allele favored in one niche and the other allele favored in another, might increase the possibilities for attainment of equilibrium with both alleles present in substantial proportions" (Levene 1953, 331). Under such conditions, he found that the polymorphism was maintained if the weighted arithmetic mean of the "relative fitnesses" of homozygotes was less than one. This condition, which is obviously true when the heterozygote has higher fitness, can also be obtained for particular parameter values without the heterozygote being superior to both homozygotes in any single niche.

Both authors, therefore, investigated the role of regional heterogeneity in local coexistence. Skellam's work also examines CC dynamics long before metapopulation theory (Levins 1969, 1970) brought it to mainstream attention (see next section). Skellam's work is seminal to the development of metacommunity theory because it provides the basis for both the competition-colonization trade-off and source-sink dynamics. Levene (1953) makes the fundamental link between niche theory and spatial coexistence. He is, to our knowledge, the first to propose such a regional vision of niche separation allowing local coexistence despite strong local niche overlap. Although neither author extended his results to community ecology or considered the consequences of variation in dispersal ability, these papers are the roots from which metacommunity ecology has grown, and they should be viewed as ecological masterpieces.

Competition, Patchiness and Spatial Heterogeneity

The Levins Metapopulation Model

Levins defined a metapopulation as a set of local populations with extinctions and recolonizations, giving us the most common formalism for metapopulation theory (1969, 1970). His work is based on three major assumptions: (1) The environment consists of an infinite number of patches ("localities" in the terminology of table 1.1) with identical environmental conditions, and each patch supports a local population. (2) Local dynamics operate on a faster timescale than regional dynamics, with each patch reaching carrying capacity instantaneously upon colonization. (3) Dispersal is infrequent, serving only to colonize empty patches and having no effect on within-patch population dynamics.

With these assumptions, the dynamics of patch occupation results in a balance between extinction (by stochasticity and disturbance) and recolonization from other patches in the region. Levins modeled the proportion of patches p occupied by a species at the regional scale:

$$\begin{gathered}\frac{dp}{dt} = cpV - ep \\ \text{with } V = 1 - p,\end{gathered} \tag{10.1}$$

where c is the recolonization rate of empty patches, and e is the extinction rate of occupied patches. This model assumes that the colonization probability for any patch is proportional to the proportion of patches already colonized. In order to highlight competition for empty habitat, we have modified the original model to isolate V, the proportion of empty patches in the region. The equilibrium is given by

Table 10.1 Summary of important metacommunity models

Authors		Org	Comp	M	CCR	CCL	SSD	SST	Notes
Skellam	1951	TA, P	P	3, 5	No	Yes	Yes	No	Basis for CC and SS hypothesis.
Levene	1953	All	D	5	No	No	Yes	No	Explains allelic polymorphism without any higher adaptive value for the heterozygote.
Levins and Culver	1971	TA	D	1	Yes	No	No	No	Basis for CC models.
Horn and MacArthur	1972	All	D	1	Yes	No	No	Yes	CC model and proto-SS since a CC trade-off in habitat 1 allows species 2 to persist and maintain itself in habitat 2 via a SS effect.
Slatkin	1974	All	D	1	Yes	No	No	No	Recolonization from doubly-occupied patches enhances the potential for species coexistence.
Levin	1974	All	D	1, 2, 3	Yes	No	Yes	Yes	Perturbation theorem and first real SST.
Hastings	1980	MA	D	1	Yes	Yes	No	No	Assumes extinction is a result of disturbance and finds a hump-shaped relationship between species richness and disturbance rate.
Hanski	1981	TA	D	3	Yes	No	No	No	Spatial variance in the better competitor can be high due to inefficient dispersal.
Hanski	1983	TA	D	1	Yes	No	No	No	Rescue effect. Coexistence in patchy environment depends on the distinctness between local and regional time scales.
Shmida and Ellner	1984	P	P	4	Yes	Yes	Yes	No	Coined the term mass effect.
Chesson	1985	MA, P	P	4	No	No	Yes	No	Spatial and temporal storage effects.
Comins and Noble	1985	MA, P	P	4	No	No	Yes	No	Assuming that the environment is uniformly variable, every coexisting species must have its own transient spatial niche.
Iwasa and Roughgarden	1986	MA	P	1, 4	No	No	Yes	No	Number of locally coexisting species cannot exceed the number of communities in the region. Regional compensation between larval growth rates.
Kishimoto	1990	All	D	3	No	No	Yes	Yes	An infinite number of species can exist over two patches.
Wilson	1992	All	D	3	No	No	Yes	No	Coined the term metacommunity. Limitation to the founder effect argument proposed by Levin (1974).
Holt	1993	All	D	3	No	No	Yes	Yes	Mesoscale and metacommunity perspective.
Goldwasser et al.	1994	P	D	1	No	Yes	No	No	There is a limit to coexistence with the CC if one considers finite habitat size.
Tilman	1994	P	D	1	No	Yes	No	No	Applies the Hastings (1980) CC model at the individual scale.

Holmes and Wilson	1998	P	D	1	Yes	Yes	No	No	If the superior species is rare, it is possible for a long-distance disperser, which is both an inferior competitor and a bad reproducer, to coexist
Pacala and Rees	1998	P	P, D	1, 4	Yes	No	No	No	Model that combines CC and the successional niche.
Chesson	2000b	All	P, D	4, 5	No	No	Yes	No	Extends the concept of spatial storage effects.
Muko and Iwasa	2000	MA	P	4	No	No	Yes	No	Between habitat variation in mortality ratios promotes coexistence, while that of reproductive rates does not.
Taneyhill	2000	All	D	1	Yes	No	No	No	Migration from doubly occupied patches is always stabilizing.
Amarasekare and Nisbet	2001	TA	D	3	No	Yes	Yes	Yes	Perturbation theorem with spatial variance in species fitness. Limit to species competitive asymmetry.
Yu and Wilson	2001	All	P	1, 4	Yes	Yes	No	Yes	A dispersal fecundity trade-off can partition variation in patch density creating the conditions for SS based on a priority effect.
Levine and Rees	2002	P	P	5	No	Yes	Yes	No	Provide a hybrid model where coexistence occurs via SS dynamics and is facilitated by a CC trade-off.
Mouquet and Loreau	2002	All	P	1, 4	No	No	Yes	No	Definition of the regional similarity constraint. High local diversity at intermediate dispersal and regional species dissimilarity.
Wang et al.	2002	All	D	1	Yes	No	No	No	Stochastic local extinctions make it likely that species with strong competitive effects on each other can coexist.
Mouquet and Loreau	2003	All	P	1, 4	No	No	Yes	No	Community patterns in a source-sink metacommunity.
Amarasekare et al.	2004	All	P, D	1	Yes	Yes	Yes	Yes	Spatial variation in the expression of a life-history trade-off can constrain rather than promote coexistence.

Notes: *Org* refers to the type of organisms considered: (All) for all species (or undefined species), (TA) for terrestrial animals, (P) for plants, (MA) for marine animals. *Comp* refers to the type of competition, either by dominance (D) or by preemption (P). *M* refers to the type of model used: (1) patch dynamic, (2) diffusion reaction, (3) Lotka-Volterra, (4) lottery model, and (5) other. The next four columns describe the coexistence mechanism addressed: competition-colonization trade-off at the local (CCL) or regional (CCR) scales as well as source-sink directional (SSD) and threshold (SST) dynamics as defined in the text. *Notes* describes the contribution within the paper that motivated our choice to include it in the table. We acknowledge that there are many other metacommunity models that we did not include due either to our oversight or because they did not add any fundamentally new result. Some of these papers are also presented in figure 10.1.

$$\hat{p} = 1 - \frac{e}{c}$$
$$\hat{V} = \frac{e}{c}. \tag{10.2}$$

The minimum proportion of available patches to maintain a species in the metapopulation is $\hat{V}$, and the basic metapopulation growth rate of a species is $r = c/e$ (Fagerström and Westoby 1997; Loreau and Mouquet 1999). This growth rate is the change in the proportion of occupied patches when a species first enters a metapopulation. The persistence of a species requires that r be greater than or equal to 1 (recolonization must compensate for extinction) and that a minimum number of patches be available at the regional scale ($V > \hat{V}$). Note also that there will always be some empty patches at equilibrium because, as $\hat{V}$ tends toward zero, c tends toward infinity or e tends toward zero, both of which are biologically unrealistic (Tilman 1994). There is a strong similarity with models of resource competition if one considers available patches as a resource consumed by a species at a rate r. In this context the quantity $\hat{V}$ can be interpreted as Tilman's R^* (1982) since it is the minimum amount of resources (available patches) required for persistence in a metapopulation (Loreau and Mouquet 1999).

One can generalize equation 10.1 to multispecies competition if species differ only in their metapopulation growth rates.

$$\frac{dp_i}{dt} = c_i p_i V - e_i p_i$$
$$V = 1 - \sum_i p_i \tag{10.3}$$
$$r_i = \frac{c_i}{e_i}$$
$$V_i^* = \frac{1}{r_i},$$

where V_i^* is the minimum proportion of available patches for a particular species to persist alone (without competition) in the metacommunity. Competition then takes the form of a lottery (Sale 1977; Chesson and Warner 1981) with an infinite number of patches. At equilibrium, only the species with the highest r_i (i.e., lowest V_i^*) will persist. This species decreases the proportion of available patches below the threshold required for the persistence of other species and thus competitively excludes other species (Loreau and Mouquet 1999). This result matches competitive exclusion by the species with the lowest R^* as proposed by Tilman (1982). When competition takes the form of a simple lottery based on extinction and recolonization, V_i^*, therefore, defines species' competitive abilities.

The Competition-Colonization Trade-off Hypothesis

The first models to consider competition in a metapopulation focused on dominance competition. These models are variations of the Levins (1969, 1970) model and all explore coexistence without classical niche partitioning mechanisms but with species differing in the way they use a single resource—space. Levins and Culver (1971) proposed the first such model. They assumed that the competitive effect between species affected their relative extinction or colonization rates. For example, for two competing species the extinction and colonization parameters of species 1 can be written as

$$e_1 = e_{12}p_2 + e_{10}(1 - p_2) \tag{10.4}$$

and

$$c_1 = c_{12}p_2 + c_{10}(1 - p_2), \tag{10.5}$$

where e_{12}, c_{12} are the respective extinction and colonization rates for species 1 in patches with species 2. Similarly, e_{10}, c_{10} are the respective extinction and colonization rates for species 1 in patches that do not contain species 2. The proportion of patches occupied by species 2 is p_2. When competition affects extinction (equation 10.4), they found that coexistence is possible if:

$$c_1 > e_{12} - e_{10}, \tag{10.6}$$

which can be interpreted as a requirement that the colonization rate of species 1 must be higher than the competitive effect of species 2 on species 1. They found that when competition affects colonization (equation 10.5), coexistence is possible if

$$\frac{c_{10}}{c_{10} - c_{12}} > 1, \tag{10.7}$$

which is always true, given that $c_{10} \neq 0$ and $c_{12} > 0$. The main result is thus that there must be a trade-off between the colonization and competitive effects for coexistence (equation 10.6) when competition affects species' extinction rates.

Following Levins and Culver (1971), Horn and MacArthur (1972) studied competition in an environment with two kinds of habitat. They used the same model and varied the fraction of habitat where each species outcompeted the other. They found no limit to the number of species that can coexist in such a heterogeneous environment as long as there is a supply of unoccupied patches and the colonization rate increases for each successive new competitor. They also found that the inferior competitor needs only to persist in one habitat to persist in both habitats. While Horn and MacArthur examined equal within- and between-habitat dispersal values, Levin (1974) then examined a similar model in which local (within-habitat) dispersal is much higher than regional (B habitats) dispersal. This case is relevant when patches tend to be clumped according to types. He showed that coexistence in this system does not require two types of patches if both species have within-habitat dispersal parameters sufficiently high that enough colonists of each species are present to replace lost populations.

Hastings (1980) developed a simpler model also adapted from the original single species metapopulation model. He assumed that competition is sufficiently rapid (or patches sufficiently small) that inferior competitors are instantaneously excluded, and no patch contains more than a single species. He acknowledged that the extreme result of this assumption is the modeling of microsites, or patches that hold only a single individual (table 1.1). Hastings (1980) also assumed a strict hierarchy of competitive dominance and added the possibility of extinction by external disturbances. For two species, the model reads

$$\begin{aligned} \frac{dp_1}{dt} &= c_1 p_1(1 - p_1) - ep_1 \\ \frac{dp_2}{dt} &= c_2 p_2(1 - p_1 - p_2) - c_1 p_1 p_2 - ep_2. \end{aligned} \tag{10.8}$$

This corresponds to a very strong, unidirectional competitive effect with species extinctions that are independent of competition. One can reformulate Hastings's model in terms of V^* as we did for the simple metapopulation model. The equilibrium is then

$$\begin{aligned} \hat{p}_1 &= 1 - V_1^* \\ \hat{p}_2 &= V_1^* - V_2^* \\ V_1^* &= \frac{e}{c_1} \\ V_2^* &= \frac{c_1 \hat{p}_1}{c_2} + \frac{e}{c_2}. \end{aligned} \tag{10.9}$$

Species 1's performance is determined solely by its own life-history characteristics, while that of species 2 also depends on species 1's ability to exclude it $(c_1\hat{p}_1/c_2)$. For species 2 to coexist at equilibrium with the superior competitor, the equation must satisfy $\hat{p}_2 > 0$, that is $V_2^* < V_1^*$. The competitive advantage of species 1 is then more than compensated by the ability of species 2 to get free patches, that is the worse competitor has to be a better colonizer (low V^*). This result is interesting because it helps to differentiate between two aspects of a species' competitive ability: dominance competition that is based on direct displacement of one species by a superior competitor and spatial competition that is based on the ability to colonize empty sites and linked to species V^*. Hastings (1980) also found a hump-shaped relationship between species richness and disturbance rate. At low disturbance rates the best competitor excludes all other species; at intermediate disturbance rates coexistence is most likely; but at high disturbance rates coexistence is impossible because species do not have sufficiently high colonization rates to compensate for extinction.

Hastings's (1980) model opened the way for extremely local, microsite (table 1.1) applications of CC models to plant communities and parasite strains (Nee and May 1992; May and Nowak 1994; Tilman 1994). These more recent models explicitly assume that only one individual can occupy a microsite, that is, that the ultimate level of patchiness is the individual itself (Grubb 1986). In this context the extinction rate of Hastings's (1980) model is equivalent to a mortality rate, and the colonization rate is equivalent to the species' reproductive rate. Both of these new parameters are independent of local competition. As in Hastings's (1980) model, these formulations all assume a strict competitive hierarchy and instantaneous exclusion of inferior competitors. These models predict that a virtually infinite number of species can coexist locally given an appropriate trade-off between competitive ability and fecundity or mortality (but see Adler and Mosquera 2000).

Some other models yield similar results. Models based on other types of competition yield similar results. For example, Hanski (1981) introduced spatial heterogeneity (spatial variance in abundances) into the Lotka-Volterra competition model in the context of patchy habitats. He studied regional coexistence in cases where local coexistence was not possible. His analysis suggests that an inferior competitor might survive regionally if the spatial variance in abundance of the better competitor is high, for example, due to a low rate of dispersal. Shmida and Ellner (1984) proposed a pure lottery model (Sale 1977; Chesson and Warner 1981) with plant species competing for microsites (table 1.1). They found basically the same constraint on species parameters: differences in life-history strategies in terms of competitive versus colonizing abilities explain local coexistence between competing species.

Although the CC hypothesis has received much attention from ecologists, it has also generated confusion because of its application at both local and regional scales. One source of confusion is that colonization subsumes a suite of species characteristics (e.g., fecundity, long and short distance dispersal, and colonization rate) and that competition is not always clearly separated from these characteristics, particularly fecundity. In actuality, trade-offs between any two of these features may lead to coexistence (Holmes and Wilson 1998, Yu and Wilson 2001). For example, Yu and Wilson (2001) showed that a trade-off between dispersal and fecundity could enhance the potential for species coexistence. Holmes and Wilson (1998) examined the nature of dispersal and demonstrated that, when the superior competitor is not very abundant, an inferior competitor with low fecundity but long distance dispersal can persist. This confusion about the nature of the trade-off is increased by confusion about the nature of competition. As we illustrated with Hastings's (1980) model, the notion of competitive superiority can be defined from different perspectives. A fugitive species that is supposed to be a bad competitor in models of dominance competition can be defined as a good competitor for available patches (a species with a low V^*) in models involving spatial competition. An additional source of confusion is that very different factors drive the dynamics of available patches at the different scales, and these dynamics are crucial to coexistence. At the regional scale (table 1.1), availability of localities results from stochasticity or deterministic disturbances (as in Hastings 1980), while at local scales, microsites become available through individual mortality (as in Tilman 1994). Even if these different causes of patch vacancy are necessarily related, their interpretations in terms of population dynamics are different.

Transient Local Coexistence

One of the main criticisms of patch dynamic models based on the original Levins (1969, 1970) formulation is the unrealistic assumption that colonization leads instantaneously to exclusion of inferior competitors and carrying capacity populations of dominant competitors (Hanski 1983; Levine and Rees 2002). Yu and Wilson (2001) pointed out (following Chesson and Warner 1981; Comins and Noble 1985; Chesson and Huntly 1997) that when this assumption is abandoned and seedlings only compete for available patches, as in a lottery system, local coexistence cannot occur via a CC trade-off alone. Therefore, several models have included transient patches in which inferior and superior competitors coexist. Slatkin (1974) pioneered this approach with a hybrid between Cohen's model (1970) and Levins and Culver's (1971) model. In their original paper, Levins and Culver assumed that species were distributed independently. This assumption allowed simplifications of the mathematics in their model, but Slatkin pointed out that species cannot both sort independently and affect each other's colonization or extinction rates (see also Levin 1974). Slatkin argued that Levins and Culver's assumption overestimates the number of patches where species co-occur and hence overestimates reciprocal competitive effects. Slatkin instead included four patch states: unoccupied by either species, occupied by species 1 or 2 alone, or co-occupied by both species. He found that migration from co-occupied patches increases the likelihood of coexistence by allowing rare species to colonize patches while increasing the extinction rates of common species.

Hanski (1983) found an exception to Slatkin's result if extinction is a function of patch occupancy (as colonization is for all patch dynamic models) so that the probability of extinction for a given species is negatively correlated with the proportion of sites occupied by that species in the region (but see Nee et al. 1991). He called this dependence of extinction on patch occupancy "the rescue effect" (cf. table 1.1). The rescue effect weakens intraspecific competition, thus changing the balance of inter- and intraspecific competition on the regional scale, such that the species with the wider initial distribution can outcompete the other species.

Taneyhill (2000) elaborated on the effects of co-occupied patches by integrating these two previous models into a broader framework. He showed that immigration from co-occupied patches is always stabilizing and that the rescue effect (as defined by Hanski 1983) is typically destabilizing for the less widespread competitor. Wang et al. (2000, 2002) extended these results by adding stochastic extinction and considering extinction to be a function of local abundance. They found that stochastic local extinctions make it more likely for strongly competing species to coexist.

The key result to emerge from these studies is that colonization from co-occupied patches increases the probability of coexistence between competing species. In these models, doubly-occupied patches introduce an element of spatial heterogeneity (variation in spatial abundances) because they act somewhat as a refuge for the inferior competitor. Co-occupied patches supply colonizers that are already removed from the fraction of patches occupied solely by the inferior competitor. As Chesson has pointed out (2000b), such heterogeneity in propagule production or resource-use contributes to coexistence by creating spatial niches. To simplify his model, Slatkin (1974) also examined species with similar colonization and extinction rates, an approach continued by others examining doubly-occupied patches (Taneyhill 2000; Wang, Zhang, et al. 2000; Wang, Wang, et al. 2002). These models also, therefore, reveal that ecologically similar species that would exclude each other in a uniform environment may coexist in a patchy environment (Slatkin 1974; Taneyhill 2000; Wang, Zhang, et al. 2000; Wang, Wang, et al. 2002). The following section focuses specifically on spatial heterogeneity, which is more commonly associated with SS models.

Regional Heterogeneity and Source-Sink Dynamics

The SS perspective focuses on spatial heterogeneity of the environment rather than variation in species' life-history traits. All SS models share a set of common assumptions: (1) the environment is divided into patches, and each patch has different environmental conditions (regional heterogeneity); (2) local and regional dynamics operate on the same time scale; and (3) immigration is frequent and can change the outcome of local competition (a mass effect *sensu* Shmida and Whittaker 1981). This idea has been applied to a wide range of taxa and different modes of competition, and investigated using either the Lotka-Volterra model (for both dominance and preemptive competition) or lottery models (for preemptive competition).

LOTKA-VOLTERRA MODELS (LV)

Aside from the initial work of Skellam (1951) and Levene (1953), the first person to apply SS ideas to community ecology was Levin (1974). He developed a two-patch LV model of competition in which founder effects (random differences in initial abundances) allow different species to dominate numerically in different patches (preemptive competition leading to a priority effect). Dispersal from safe areas maintains species in communities from which they would otherwise be excluded (due to lower initial abundance). Given the perturbation theorem (when different stable boundary equilibria occur in different places in space, small perturbations can create stable interior equilibria; see Amarasekare 2000 for a review) the coexistence equilibrium is stable when dispersal between communities is low. Levin suggested that dispersal has the potential to increase species richness but that high dispersal rates reduce local species richness below that in isolation. This finding suggests that intermediate dispersal maintains differences between the localities and communities.

Subsequent studies focused on the maintenance of spatial variation in fitness and the effects of this variation on diversity. Following Levin, Kishimoto (1990) showed that many species can coexist in a two-patch system if the reciprocal competitive effects between the two dominant species are sufficiently strong (high reciprocal competition coefficients) and dispersal between the two patches is intermediate. The interaction between strong competitors results in a resource surplus because these species can maintain themselves at low resource levels. The surplus becomes open to other less competitive species. As the number of species increases, the resource surplus decreases, and further invasion becomes less likely. Again, competitive superiority can be due to either differences in initial abundances for species engaged in preemptive competition, or due to differences in competitive ability for species engaged in dominance competition, for example, different limiting factors in each locality. Amarasekare and Nisbet (2001) have since clarified the conditions for species undergoing dominance competition by considering spatial variation in the strength of competition at the regional scale (spatial variance in fitness). They have shown that when competitive asymmetry between species is high, local coexistence is possible only below a critical dispersal threshold. High dispersal rates undermine the potential for coexistence by reducing spatial variance in fitness (see also Nichimura and Kishida 2001).

An important result from Levin (1974) is that spatial variance in fitness can result only from heterogeneity in initial species abundances, provided competition is preemptive. Wilson (1992) found somewhat different results by considering patches colonized at random by individuals from a disperser pool. Species then interact in a closed system; since the outcome is dependent on initial conditions, the patches end up with different combinations of species. The Wilson (1992) model then pools species at the metacommunity scale to generate a new pool of dispersers for a second metacommunity assembly process. In this context, the species composition at the regional scale converges toward the species composition at the local scale. The founder effect does not hold in the long term if one considers extinctions and recolonizations based on species abundances at the metacommunity scale. Note, however, that the difference between Levin's (1974) and Wilson's (1992) results is at least partly because Wilson does not consider a mass effect that would rescue species from local extinction, regardless of the metacommunity assembly rules.

LOTTERY SS MODELS

The SS concept has been well-integrated into lottery models (Sale 1977; Chesson and Warner 1981). Because they consider recruitment as central, immigration and emigration can be crucial in these models. For example, some authors (Shmida and Ellner 1984; Kadmon and Shmida 1990; Loreau and Mouquet 1999) have included immigration from a regional pool in the form of a mass effect, which maintains high local species richness in plant communities. In these models, plants compete for available microsites, and the species with the highest number of seeds at a site wins. Given such rules for site attribution, immigration from outside the community can maintain inferior species in the system.

Lottery models with SS dynamics have also been applied to several aquatic systems. These systems are essentially competitive metacommunities with sessile adults and mobile larvae. Planktonic larvae produced in all the local communities enter a common pool and are equally redistributed among communities. Chesson (1985) developed a stochastic model with regional heterogeneity such that each locality favors the adults of a different species (via increased survival). He showed that species can coexist locally with emigration-immigration and higher adult survival in favorable localities. As with the temporal storage effect (Chesson and Warner 1981; Chesson 1983, 1984) in which a population sustains a positive average growth rate in a temporally fluctuating environment if growth rates in good years more than compensate for bad years, here a "spatial storage effect" promotes coexistence because it buffers a species from poor recruitment in patches where it has a negative growth rate (See also Hoopes et al., chapter 2). Iwasa and Roughgarden (1986; see also Muko and Iwasa 2000) found similar results in another model of marine systems.

While the above studies suggest that spatial heterogeneity is important for coexistence, Comins and Noble (1985) showed that spatial heterogeneity does not have to be permanent to promote coexistence. In their model coexistence requires each species to be dominant in site establishment under some environmental conditions although there are no permanent differences between parts of the habitat. Rather, the environment is uniformly variable in the sense that the long-term statistical distribution of environmental conditions is the same in all patches (transient niches). They found that every coexisting species must have its own transient niche. They also found that the stabilizing effect (coexistence) of environmental variability in the basic model can be obtained either with a few patches and complete mixing or with a large number of patches and little mixing.

Chesson (2000b) recently proposed a generalization of these results where coexistence results from a spatial storage effect, as defined above (see also Hoopes et al., chapter 2). Two other mechanisms driven by spatial variation contribute to the storage effect but can also act alone to allow coexistence: spatial variation in the degree of nonlinearity in species competitive responses (spatial relative nonlinearity) and localized dispersal that concentrates an invading species in areas favorable to its growth and reproduction (growth-density covariance; see Chesson 2000b and Chesson et al., chapter 12 for more details).

Mouquet and Loreau (2002, 2003; Loreau et al., chapter 18) have recently developed a metacommunity model of lottery competition, which, because it shares some characteristics with metapopulation CC models, helps to compare the outcomes of SS and CC models. This model is based on equation 10.3 applied at the individual level and assumes that localities receive a constant number of immigrants from other localities in the metacommunity. The model is given by

$$\begin{aligned} \frac{dP_{ik}}{dt} &= (I_{ik} + [1 - a]c_{ik}P_{ik})V_k - m_{ik}P_{ik} \\ I_{ik} &= \frac{a}{N-1}\sum_{l \neq k}^{N} c_{il}P_{il} \\ V_k &= 1 - \sum_{i=1}^{S} P_{ik}. \end{aligned} \tag{10.10}$$

Here i refers to species and k to localities. The parameter a describes the proportion of local reproduction that emigrates into other localities, and I_{ik} is the immigration term. At the local scale, S species compete for a limited proportion of vacant microsites, V_k. The metacommunity consists of N localities that differ in their local conditions. When there is no dispersal between localities, the species with the highest local basic reproductive rate ($r_{ik} = c_{ik}/m_{ik}$) excludes all other species in the locality because it decreases the proportion of vacant sites, V_k, below the threshold required for their persistence. If however localities are linked by dispersal, and different species dominate in different localities (due to spatial heterogeneity in competitive rankings), local coexistence is possible. Individuals emigrating from source areas prevent competitive exclusion in sink areas (where they are competitively inferior). At equilibrium each individual of each species must on average during its lifetime produce one individual that survives somewhere in the metacommunity so that each species' average net reproductive rate at the scale of the metacommunity is:

$$\bar{R}_i = \frac{\sum_{k=1}^{N} \hat{V}_k r_{ik} w_{ik}}{\sum_{k=1}^{N} w_{ik}} = 1. \tag{10.11}$$

Here w_{ik} is the total quantity of propagules of species i in community k per unit of time:

$$w_{ik} = (1 - a)c_{ik}\hat{P}_{ik} + \frac{a}{N-1}\sum_{l \neq k}^{N} c_{il}\hat{P}_{il}. \tag{10.12}$$

In this lottery model, a species' competitive ability is directly related to its reproductive rate. Thus equation 10.11 can be interpreted as a constraint of regional competitive similarity (or equivalency) between coexisting species. For instance, each species' basic reproductive rate r_{ik} must be balanced over the metacommunity for equation 10.11 to hold. Local basic reproductive rates can be different locally so that different species will dominate in each locality, but they are equivalent when averaged over the region. Conditions for species coexistence are then a function of the proportion of dispersal between communities. When dispersal is too high, the metacommunity is homogenized, and species richness declines because the species that is the best competitor at the regional scale excludes all other species from the metacommunity.

The SS models discussed above assume that extrinsic spatial heterogeneity drives spatial variance in fitness. However, as shown by Levin (1974), intrinsic heterogeneity can also arise from founder effects or other random factors that generate spatial variation in initial species abundances. More recently, Yu and Wilson (2001) incorporated such spatial variation in patch density in what is essentially a CC lottery model at the microsite scale (based on appendix E in Chesson and Huntly 1997) without dominance competition. Yu and Wilson varied the fraction *h* of available habitat in each community. In models with complete mixing, they showed that inferior competitors can be rescued from competitive exclusion in communities with high *h* by emigrating from communities with low *h* (where the best competitor cannot persist or is at very low density) because of the CC trade-off. Yu and Wilson also showed that including a trade-off between dispersal and fecundity can increase the potential for coexistence via spatial variation in patch density. In other words, CC itself cannot lead to coexistence in a lottery model with preemptive competition, but can allow coexistence via SS dynamics. Levine and Rees (2002) also found that a competition-colonization trade-off could not lead to coexistence when the assumption of a strict dominance hierarchy was relaxed. If coexistence could occur via spatial heterogeneity and SS dynamics, however, a competition-colonization trade-off operating simultaneously can predict the abundance patterns observed in annual plant communities (Levine and Rees 2002).

SYNTHESIS ON SOURCE-SINK DYNAMICS

Despite the differences in their mathematical formulations, LV and lottery models yield similar results. First, local coexistence in a SS metacommunity results from spatial variation in the strength of competition. Second, coexistence is most likely for intermediate dispersal rates. There is a critical dispersal threshold below which dispersal is too low to prevent local competitive exclusion and a critical dispersal threshold above which coexistence is impossible because spatial variation in fitness is homogenized by immigration. Third, species have limits to regional dissimilarity or competitive asymmetry that are a function of dispersal between communities.

Spatial heterogeneity is essential for coexistence in these models. It arises from spatial variation in abiotic or biotic factors that cause spatial variation in the strength of competition or from spatial variation in species abundances due to founder effects or other random phenomena. As pointed out by Amarasekare (2000), these two kinds of heterogeneity correspond to two different types of local dynamics—threshold and directional. Threshold dynamics occur in systems where the outcome of competition depends on initial abundances (e.g., preemptive competition) such that coexistence is possible given spatial variation in species abundances. In contrast, systems with directional local dynamics (e.g., dominance competition) are driven by spatial environmental heterogeneity and phenotypic plasticity. Threshold systems are highly sensitive to large perturbations, and it is likely that increasing dispersal will rapidly decrease species richness (following an initial increase at very low dispersal rates). Directional systems are less sensitive to perturbation, and they are more likely to have higher species richness at high dispersal rates. In both systems, however, very high dispersal values tend to homogenize spatial variance and reduce species richness. The results obtained with threshold systems (Levin 1974; Kishimoto 1990; Amarasekare 2000; Yu and Wilson 2001; Levine and Rees 2002) are striking because species can coexist only because the environment is patchy (but otherwise homogeneous), and abundances vary in space. Regional niche differentiation is not needed for species to coexist in such a metacommunity.

Because coexistence in SS models is frequently dependent on maintaining spatial variation in fitness, these models point toward generalizations about limits to similarity and regional niche differentiation. For instance, the condition of regional similarity defined by Mouquet and Loreau (2002) casts coexistence in terms of niche theory and thereby alludes to earlier models. Iwasa and Roughgarden do not interpret their results in the context of niche theory, but they state (in theorem 2) that coexistence requires compensation between larval productivity of species at the regional scale, that is, that species must have similar larval productivity at the scale of the region (1986, 198). This idea of regional compensation is also evident in Chesson's (1985) work on the spatial storage effect (see also Chesson 2000b). Models based on the LV framework produce the same regional similarity constraint. For instance, Amarasekare and Nisbet (2001) define a limit to competitive asymmetry that is equivalent to a constraint of similarity between coexisting species. These different results can be interpreted in the context of niche theory given that each locality has a different limiting factor (resulting in a different species dominating each community). Niche differentiation occurs at the regional scale and registers at the local scale through dispersal. Defining species as similar at particular spatial scales helps to reconcile niche theory with the high species diversity observed in natural systems and helps interpret niche theory in the context of metacommunity ecology. Further work to integrate classic limiting similarity concepts with the idea of regional niche differentiation will improve our understanding of competitive metacommunities (Chesson 1991).

Toward a General Framework

Although CC and the SS models have typically been regarded as two different approaches to studying spatial coexistence, elements of both classes of mechanisms are likely to operate simultaneously in natural communities. We present several key points of contact between CC- and SS-mediated coexistence and propose the basis for a general framework.

Convergence

As pointed out by Chesson (2000a), coexistence always requires intraspecific competition to be stronger than interspecific competition. This requirement allows spatial coexistence mechanisms such as CC and SS to be interpreted in the context of classical niche theory. In CC models with displacement competition, spatial niche differences arise because superior competitors can displace inferior competitors from occupied patches, but inferior competitors can only occupy patches not colonized by the superior competitors. This is equivalent to resource partitioning with inferior competitors, by virtue of their superior dispersal abilities that are better at acquiring empty patches, and superior competitors that because of their superior displacement abilities are better at acquiring occupied patches. In the case of SS models, niche differences between species arise at the regional scale due to spatial heterogeneity in the environment. For instance, if spatial variation in abiotic factors such as temperature, humidity, salinity or presence of an essential nutrient (or toxin) alters the relative strengths of intra- versus interspecific competition for a limiting resource in different locations of the landscape (for examples see Miller and Kneitel, chapter 5; Cottenie and De Meester, chapter 8; Kolasa and Romanuk, chapter 9), then space itself constitutes a second niche axis along which species exhibit differences.

A key issue in integrating CC and SS ideas in a common framework involves identifying the conditions under which both classes of mechanisms can contribute to coexistence. While the role of spatial heterogeneity and source-sink dynamics in allowing coexistence when life-history trade-offs cannot do so has been investigated (e.g., Yu and Wilson 2001; Levene and Rees 2002), how spatial variation influences trade-off mediated coexistence has not received much theoretical attention. For example, spatial heterogeneity in the biotic or abiotic environment can lead to spatial variation in the expression of a life-history trade-off. Contrary to the conventional wisdom that environmental heterogeneity promotes species coexistence, heterogeneity that influences the expression of a life-history trade-off can also constrain opportunities for coexistence (Amarasekare et al. 2004). In such a situation, source-sink dynamics can play a key role in enhancing opportunities for coexistence. For example, consider an interspecific trade-off between resource exploitation and susceptibility to a predator (as in McPeek 1996). The species that allocates more energy to reproduction at the cost of reduced predator defense is competitively superior to the species that employs the opposite allocation strategy. There is spatial variation in predator abundance such that it is present in some localities but not others. In localities where the predator is present, the trade-off is expressed and local coexistence is possible. In localities where the natural enemy is absent, the inferior competitor is excluded because energy allocated to predator defense (a net cost now with no benefit) gives it an overall competitive disadvantage. If there is dispersal between localities, however, coexistence is possible everywhere (see Amarasekare et al. 2004 for a formal mathematical analysis). This result is due to emigration from localities in which the trade-off is expressed (sources for the inferior competitor) rescuing the inferior competitor from exclusion in localities in which the trade-off is not expressed (sinks for the inferior competitor). Thus, simultaneous operation of trade-offs and source-sink dynamics can increase opportunities for coexistence.

The models we have presented in this review have considered fundamentally different types of competitive interactions that should be carefully considered when testing spatial theory. The key distinction between dominance and preemptive competition is that, because the former involves displacement of inferior competitors by superior competitors, the ability of the inferior competitor to persist is an explicit function of both the superior competitor's colonization ability and its abundance. In contrast, in preemptive competition species compete to replace individuals that have died, and no displacement occurs. The ability of any given species to persist is a function solely of its colonization and extinction rates. The key results we have reviewed in this chapter can be summarized as follows. Under dominance competition coexistence can occur either via a CC trade-off in a spatially homogeneous environment, or via SS dynamics in a spatially heterogeneous environment. When competition is preemptive, coexistence cannot occur via a CC trade-off unless there is some spatial heterogeneity and a trade-off between species competitive ability for distinct limiting resources.

Hybrid Models

The fact that CC and SS models have been considered alternative mechanisms has made it difficult to identify conditions under which elements of both mechanisms operate. This underscores the need for a more general framework that accommodates both approaches and allows predictions about the relative importance of competition-colonization and source-sink in mediating spatial coexistence in nature (Amarasekare et al. 2004).

Hybrid models have opened the way for an integrated framework (figure 10.1). The Horn and MacArthur model (1972) is a notable example because it demonstrates that a combination between CC and SS processes can explain coexistence between competing species. More recently Pacala and Rees (1998) proposed a model that combined competition-colonization and the successional niche. They showed that coexistence between species of different successional stages can result from competition-colonization, successional niche partitioning where early successional species have a greater ability to exploit resource-rich conditions of recently disturbed habitats, or a combination of the two. The model by Yu and Wilson (2001) makes the link with source-sink for preemptive competition, and that of Levine and Rees (2002) makes the link with SS for CC models with dominance competition but no strict asymmetry. In all of these examples, a combination of competition-colonization and source-sink can elevate species richness. More recently Amarasekare et al. (2004) combined competition-colonization and source-sink in a single framework and compared their operation under different types of competition and dispersal. They showed that counterintuitive properties arise due to interactions between these two different classes of mechanisms. For instance, spatial variation in the expression of a life-history trade-off (spatial heterogeneity) can constrain rather than promote coexistence.

A general framework may be obtained most easily by incorporating hierarchical spatial structure and spatial heterogeneity into the patch occupancy framework. Patch occupancy models (following Levins and Culver 1971) are attractive because of their analytical tractability for large numbers of patches, but they lack real world applications because of the unrealistic assumption of instantaneous local dynamics. This assumption has been important in developing simple metapopulation models but “there is no reason to believe that natural systems fall into two distinct classes with respect to the difference between the local and the regional time scales” (Hanski 1983). Explicit local dynamics will be required to track local abundances and details of local competitive interactions that influence coexistence and give predictions that correspond to what ecologists can measure in the field. Such hybrid models should also be able to vary the relative contribution of CC and SS mechanisms. Because the type of competition can alter the conditions for coexistence, preemptive and dominance competition should both be considered.

Several different avenues for further research have been investigated, but many more still require investigation.

(1) Classical SS effects at the regional scale with threshold versus directional local dynamics.
(2) Classical CC trade-offs at regional or local scales as well as a combination at different scales. Consideration of whether competition-colonization can lead to coexistence when dispersal occurs on the same timescale as competition may also be important.
(3) A combination of CC trade-offs and source-sink at the regional scale as in the successional perspective discussed above. This may extend the conditions

under which competition-colonization can increase opportunities for coexistence via SS dynamics.

(4) Regional competition-colonization between groups of species that have very distinct life-history strategies and source-sink between species of the same group. This point seems promising to merge the niche and the neutral theories of species diversity (Hubbell 2001; Mouquet and Loreau 2003; Chase et al., chapter 14).

(5) Regional source-sink between groups of species that would use very different resources and competition-colonization (either local or regional) between the species with similar resource use.

Conclusions

The world is patchy and heterogeneous, the recognition of which has been central to many theories of species coexistence over the last thirty years. Only recently have ecologists integrated these ideas into the emerging field of metacommunity ecology. In this chapter we have focused on the long history of spatial models based either on competition-colonization or source-sink dynamics, and we have discussed how these two approaches provide alternative mechanisms for species coexistence in metacommunities. We have shown that these apparently different mechanisms have common elements that could be integrated into a broader theoretical framework. We have also emphasized how these mechanisms could be interpreted in the context of niche theory and how this interpretation can help broaden the niche concept to include regional phenomena. Our focus was somewhat restrictive in that we concentrated exclusively on competitive metacommunities with no consideration of trophic interactions (Nowak and May 1994; Holt 1997a; Nee et al. 1997; Hassell 2000; Hoopes et al., chapter 2; Holt and Hoopes, chapter 3) or genetic polymorphisms (Karlin and McGregor 1972a, 1972b; De Meeus et al. 1993), both of which are integral components of biological diversity in patchy environments. A complete synthesis of coexistence in spatially heterogeneous environments would require assembling these other pieces of the same puzzle. Understanding mechanisms that maintain species diversity in patchy environments will allow for the development of a general theory of biological diversity that is needed now more than ever, given the catastrophic loss of biodiversity due to increasing human encroachment.

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