

# Mechanisms of Coexistence in Competitive Metacommunities

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**ABSTRACT:** Although there is a large body of theory on spatial competitive coexistence, very little of it involves comparative analyses of alternative mechanisms. We thus have limited knowledge of the conditions under which multiple spatial mechanisms can operate or of emergent properties arising from interactions between mechanisms. Here we present a mathematical framework that allows for comparative analysis of spatial coexistence mechanisms. The basis for comparison is mechanisms operating in spatially homogeneous competitive environments (e.g., life-history trade-offs) versus mechanisms operating in spatially heterogeneous competitive environments (e.g., source-sink dynamics). Our comparative approach leads to several new insights about spatial coexistence. First, we show that spatial variation in the expression of a life-history trade-off leads to a unique regional pattern that cannot be predicted by considering trade-offs or source-sink dynamics alone. This result represents an instance where spatial heterogeneity constrains rather than promotes coexistence, and it illustrates the kind of counterintuitive emergent properties that arise due to interactions between different classes of mechanisms. Second, we clarify the role of dispersal mortality in spatial coexistence. Previous studies have shown that coexistence can be constrained or facilitated by dispersal mortality. Our broader analysis distinguishes situations where dispersal mortality is not necessary for coexistence from those where such mortality is essential for coexistence because it preserves spatial variation in the strength of competition. These results form the basis for two important future directions: evolution of life-history traits in spatially heterogeneous environments and elucidation of the cause and effect relationship(s) between biodiversity and ecosystem functioning.

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Species diversity in spatially structured environments has received a great deal of attention, in part because of the loss of biodiversity from human-induced fragmentation of natural habitats. A large body of theory addresses how the interplay between competition and dispersal allows species coexistence in such fragmented environments.

Spatial coexistence mechanisms belong to two major classes depending on the nature of the competitive environment experienced by the interacting species. A species' competitive environment consists of biotic (e.g., natural enemies) and abiotic factors (e.g., temperature, nutrient availability) that influence its ability to exploit space or limiting resources that vary in space.

The first class of coexistence mechanisms operates in a spatially homogeneous competitive environment; that is, the species' competitive rankings do not change within the spatial extent of the landscape being considered. This situation typically occurs when differences in the way species exploit resources depend on life-history differences rather than on spatial variation in the species' biotic or abiotic environment. For example, plants that produce a few large seeds with limited dispersal ability may be competitively superior to plants that produce many small seeds with high dispersal ability (Levine and Rees 2002). Coexistence is possible if species exhibit trade-offs that allow niche differences in space (Chesson 2000*b*). For instance, superior competitors may be fecundity or dispersal limited and hence unable to exploit all the available space or the spatially variable resource. Inferior competitors can exploit such gaps in the landscape by virtue of high fecundity or dispersal ability (e.g., Levins and Culver 1971; Hastings 1980; Nee and May 1992; Tilman et al. 1994; Adler 1999; Kneitel and Chase 2004). Coexistence can be local or regional, depending on the spatial scale at which such trade-offs or other mechanisms involving spatially invariant competitive rankings operate (e.g., successional niche: Pacala and Rees 1998; differences in interaction neighborhoods: Murrell and Law 2003).

A spatially homogeneous competitive environment does

not imply that the biotic or abiotic environment is completely homogeneous in space. The distinguishing feature is that while species' vital rates may vary spatially, they do so without altering the species' competitive rankings (Amarasekare 2003).

The second class of coexistence mechanisms operates in a spatially heterogeneous competitive environment; that is, species' competitive rankings change within the spatial extent of the landscape being considered. This situation arises when spatial heterogeneity in the biotic or abiotic environment leads to spatial variation in the strength of competition. Species experience greater intraspecific than interspecific competition in favorable areas and vice versa in unfavorable areas (Chesson 2000*a*, 2000*b*). These mechanisms typically lead to regional coexistence, with each species restricted to favorable areas of the habitat. However, dispersal from favorable areas can prevent competitive exclusion in unfavorable areas, leading to local coexistence via source-sink dynamics (Levin 1974; Hamilton and May 1977; Pacala and Roughgarden 1982; Shmida and Ellner 1984; Kishimoto 1990; Loreau and Mouquet 1999; Moko and Iwasa 2000; Amarasekare and Nisbet 2001; Mouquet and Loreau 2002, 2003).

Most theory has focused on one class of mechanism or the other, making it difficult to gauge how the interaction between the two classes of mechanisms influences coexistence. For instance, the role of spatial variation in allowing coexistence when life-history trade-offs fail to do so has been investigated (Yu and Wilson 2001; Levine and Rees 2002), but the role of spatial variation in the actual expression of a life-history trade-off has not. Similarly, despite the fact that species engage in different types of competition and modes of dispersal, we know of no studies that have compared the operation of both classes of mechanisms under different competitive and dispersal regimes.

Here we present a theoretical framework that utilizes a common mathematical approach to accommodate both classes of mechanisms, thus allowing the study of interactions between mechanisms. This comparative framework is important for several reasons. First, it helps clarify the conditions under which each class of mechanism is likely to operate and, more importantly, identify the conditions under which both classes of mechanisms may operate simultaneously. Second, predictions resulting from such a comparative analysis can facilitate empirical progress on spatial coexistence. For instance, empirical studies that fail to detect a particular mechanism cannot distinguish between the absence of spatial effects and the presence of untested spatial mechanisms. Empirical studies that test comparative predictions for multiple mechanisms are much more powerful both in detecting spatial effects and in refining theory. A third reason for adopting a comparative approach is the potential it offers for advancing

spatial ecology in two new and exciting directions: understanding how life-history traits evolve in spatially structured environments and elucidating the cause and effect relationship(s) between species diversity and ecosystem functioning.

The framework we present is the simplest mathematical approach that can accommodate both spatially homogeneous and heterogeneous competitive environments. It thus constitutes a first step toward integrating what have been regarded as two fundamentally different approaches toward studying spatial coexistence. Despite its simplicity, the framework yields important insights into situations where the joint operation of both classes of mechanisms leads to unexpected emergent properties.

### Background

We briefly discuss the modeling approaches used to study the two classes of coexistence mechanisms. We use the terms spatially invariant versus spatially varying competitive rankings interchangeably with spatially homogeneous versus heterogeneous competitive environments.

Coexistence mechanisms that operate in spatially homogeneous competitive environments (e.g., life-history trade-offs) have most frequently been studied using the patch occupancy approach (Levins 1969, 1970) that tracks the presence or absence of species. It assumes that local competitive interactions occur on a faster timescale than dispersal (Cohen 1970; Levins and Culver 1971; Hastings 1980). Because of this decoupling of local and spatial dynamics, the primary role of dispersal is in colonizing empty patches. Emigration and immigration between occupied patches cannot influence local competitive interactions. Therefore, in this approach, species cannot coexist within the same patch. Species can however coexist on larger spatial scales provided that they exhibit a trade-off between competitive ability and other life-history traits, and that competition involves a strict dominance hierarchy that allows for spatial niche differences (Hastings 1980; Nee and May 1992; Tilman et al. 1994). Coexistence via a life-history trade-off cannot occur if competition is preemptive, because preemptive competition in itself does not provide the spatial niche differences required for coexistence (Comins and Noble 1985; Chesson and Huntly 1997; Yu and Wilson 2001).

Coexistence mechanisms that operate in spatially heterogeneous competitive environments (e.g., source-sink dynamics) have typically been studied via the explicit dynamics approach that tracks the population numbers of competing species. In this approach, competition and dispersal occur on comparable timescales such that dispersal can influence the outcome of competition. In contrast to life-history trade-offs in the patch occupancy framework,

coexistence is possible under both dominance and preemptive competition (Levin 1974; Pacala and Roughgarden 1982; Loreau and Mouquet 1999; Amarasekare and Nisbet 2001; Mouquet and Loreau 2002, 2003).

The different assumptions made by these two modeling approaches make it difficult to identify the conditions that allow simultaneous operation of coexistence mechanisms with and without spatial variation in competitive rankings. Understanding the relative importance of each mechanism and their joint operation requires that both classes of mechanisms be analyzed in a common mathematical framework. The next section lays the groundwork for such a framework.

### Theoretical Framework

The simplest way to incorporate spatially homogeneous and heterogeneous competitive environments in a common mathematical framework is to expand the patch occupancy formalism to include hierarchical spatial structure. Consider a set of competing species inhabiting a landscape with three spatial scales. The smallest spatial scale is a patch, or microsite, that is occupied by only one individual. The intermediate scale is a locality, a collection of a large number of identical patches. A locality contains a community of competing species, and is the scale at which mechanisms involving spatially invariant competitive rankings (e.g., life-history trade-offs) operate. The largest spatial scale is a region, a collection of localities. A region contains a metacommunity, a set of local communities linked by dispersal of multiple species (Wilson 1992). Because different communities may be subject to different biotic or abiotic environmental regimes, the region is the spatial scale at which mechanisms involving spatially varying competitive rankings (e.g., source-sink dynamics) operate.

The following model describes the dynamics of the metacommunity:

$$\frac{dp_{ij}}{dt} = p_{ij}[f_{ij}(D_{ij}(a_i, c_{ij}, p_{ij}), V_{ij}(h_j, p_{kj})) - g_{ij}(p_{kj}, \dots, p_{mj}) - e_{ij}], \quad (1)$$

where  $p_{ij}$  is the fraction of patches occupied by species  $i$  in locality  $j$  ( $i = 1, \dots, m$ ;  $j = 1, \dots, n$ ). The function  $f_{ij}$  represents the rate of reproduction and establishment of species  $i$  in locality  $j$ , and  $g_{ij}$  represents the nature of competitive interactions between species. The parameter  $e_{ij}$  is the loss rate due to death of individuals of species  $i$ . The function  $f_{ij}$  is itself a composite of two other functions:

$D_{ij}$  describes the contribution to local reproduction by residents of locality  $j$  (at a per capita rate  $c_{ij}$ ) and by immigrants from other localities (at a species-specific per capita rate  $a_i$ );  $V_{ij}$  describes resource availability, which in a spatial context is the amount of habitat available to a given species within locality  $j$ . It depends on both the abundances of other species in the community ( $p_{kj}$ ) and the fraction of suitable habitat in locality  $j$  ( $h_j$ ). Note that the functions  $V_{ij}$  (resource availability) and  $g_{ij}$  (competition) distinguish between coexistence mechanisms with and without spatial variation in competitive rankings. We have used general notation to highlight the fact that equation (1) can incorporate a variety of mechanisms for competition and dispersal, including empirically derived functional relationships. Later sections illustrate the application of the model with specific mechanisms.

Our goal is to compare coexistence mechanisms in spatially homogeneous and heterogeneous competitive environments under different regimes of competition and dispersal. The next two sections describe the types of competition and dispersal we consider in the article.

### Competition within Localities

We consider the two major forms of competition that can operate in a patchy environment: dominance and preemption. In dominance competition, individuals of superior competitors can displace individuals of inferior competitors from patches the latter already occupy (Hastings 1980). This leads to a dominance hierarchy with  $g_{ij} > 0$  for  $k < i$  and  $V_{ij} = h_j - \sum_{k < i} p_{kj}$  in equation (1). In biological terms, this means that all species that are competitively superior to species  $i$  can displace individuals of species  $i$  from occupied patches and that species  $i$  can colonize only those patches not already occupied by superior competitors.

In preemptive (lottery) competition, there is no displacement of any species from occupied patches; that is,  $g_{ij} = 0$  in equation (1). All species compete for empty patches in proportion to their relative abundances; that is,  $V_{ij} = h_j - \sum_{i=1}^m p_{ij}$ . The superior competitor is the species with the highest local growth rate and hence the greatest capability of replacing an individual once it dies and leaves an empty patch (Comins and Noble 1985).

### Dispersal between Localities

Metacommunity dynamics result from the interplay between within-locality competition and between-locality dispersal. Dispersal can take two basic modes. The first mode involves “surplus” individuals from one locality colonizing patches in other localities. These are individuals that make no contribution to reproduction within their

“natal” locality regardless of whether they stay or disperse. For instance, they may be individuals that are forced out because of strong competition. This is the mode of dispersal considered in Pulliam’s (1988) model of single-species source-sink dynamics. It is also the dispersal mechanism implicit in patch occupancy models of trade-off-mediated coexistence (e.g., Hastings 1980). The important point is that the loss of these surplus individuals does not affect local dynamics in their natal locality. However, they may suffer dispersal mortality in transit, so the number of individuals surviving to reach another locality may be fewer than the number leaving a given locality.

The second mode of dispersal involves emigration of “reproductive” individuals. A fraction of propagules leaves without attempting to colonize empty patches within their natal locality. This is the mode of dispersal considered in explicit dynamics models of spatial variation and source-sink dynamics (e.g., Levin 1974; Pacala and Roughgarden 1982; Amarasekare and Nisbet 2001). The key point is that the loss of emigrants that would otherwise have reproduced in situ has a direct negative effect on local dynamics in the natal locality.

When between-locality dispersal involves surplus individuals, metacommunity dynamics are given by

$$\frac{dp_{ij}}{dt} = p_{ij} \left[ \left( c_{ij} + s_i \frac{\sum_{l \neq j} c_{il} p_{il}}{p_{ij}} \right) V_{ij} - g_{ij} - e_{ij} \right], \quad (2)$$

where  $D_{ij}$ , the reproduction and dispersal function, is  $c_{ij} + s_i(\sum_{l \neq j} c_{il} p_{il})/(p_{ij})$  and  $V_{ij}$  the resource availability function, is as defined above for the two forms of competition. The key parameter in  $D_{ij}$  is  $c_{ij}$ , the per capita colonization rate of species  $i$  propagules produced in locality  $j$ . It encapsulates both local reproduction and subsequent establishment of offspring via random dispersal. The parameter  $s_i$  is the species-specific fraction of dispersers from one locality that survive to reach another locality. Thus, in  $D_{ij}$   $c_{ij}$  is the per capita contribution to local reproduction and establishment by conspecific residents, and  $s_i(\sum_{l \neq j} c_{il} p_{il})/(p_{ij})$  is the contribution by conspecific colonists from other localities. The total amount of suitable habitat within the region is assumed constant; thus,  $\sum_j h_j = 1$  in  $V_{ij}$ . This condition determines resource limitation at the metacommunity scale. In dominance competition, the competition function is  $g_{ij} = \sum_{k < i} c_{kj} p_{kj} + s_k \sum_{k < i} \sum_{l \neq j} c_{kl} p_{kl}$ . Here  $\sum_{k < i} c_{kj} p_{kj}$  is the per capita contribution to competition by heterospecific residents, and  $s_k \sum_{k < i} \sum_{l \neq j} c_{kl} p_{kl}$  is the contribution by heterospecific colonists from other localities. In preemptive competition, the competition function is  $g_{ij} = 0$ . For both types of competition,  $e_{ij}$  is the per capita extinction rate of species  $i$  in locality  $j$ . This parameter encapsulates all forms of

density-independent mortality experienced by adults of species  $i$ .

When between-locality dispersal involves reproductive individuals, metacommunity dynamics are given by

$$\frac{dp_{ij}}{dt} = p_{ij} \left[ c_{ij} \left( 1 - a_i + \frac{s_i a_i}{n-1} \frac{\sum_{l \neq j} p_{il}}{p_{ij}} \right) V_{ij} - g_{ij} - e_{ij} \right], \quad (3)$$

where

$$D_{ij} = c_{ij} \left( 1 - a_i + \frac{s_i a_i}{n-1} \frac{\sum_{l \neq j} p_{il}}{p_{ij}} \right)$$

and  $V_{ij}$  is as defined in the previous section. In  $D_{ij}$ ,  $a_i$  is the fraction of species  $i$  propagules that emigrate from their natal locality,  $c_{ij}(1 - a_i)$  is the per capita contribution to local reproduction and establishment by conspecific residents, and

$$c_{ij} \left( \frac{s_i a_i}{n-1} \frac{\sum_{l \neq j} p_{il}}{p_{ij}} \right)$$

is the contribution by conspecific immigrants. The competition functions are  $g_{ij} = \sum_{k < i} c_{kj} [(1 - a_k) p_{kj} + (s_k a_k)/(n-1) \sum_{l \neq j} p_{kl}]$  for dominance and  $g_{ij} = 0$  for preemption. For dominance competition,  $\sum_{k < i} c_{kj} (1 - a_k) p_{kj}$  is the per capita contribution to interspecific competition by heterospecific residents, while  $\sum_{k < i} c_{kj} [(s_k a_k)/(n-1) \sum_{l \neq j} p_{kl}]$  is the contribution by heterospecific immigrants.

That the two modes of dispersal have quite different effects on within-locality dynamics is evident when looking at the per capita growth rate (quantities inside large square brackets in eqq. [2], [3]). Except in the extreme case of 100% dispersal mortality ( $s_i = 0$ ), dispersal of surplus individuals always has a positive effect on within-locality dynamics by augmenting the per capita growth rate above that in isolation. For instance, the growth rate when locality  $j$  is isolated is  $c_{ij} V_{ij} - g_{ij} - e_{ij}$ ; when connected by dispersal, it is  $[c_{ij} + s_i(\sum_{l \neq j} c_{il} p_{il})/(p_{ij})] V_{ij} - g_{ij} - e_{ij}$ . In contrast, when between-locality dispersal involves individuals that would otherwise have reproduced within their natal locality, per capita growth rate may increase or decrease depending on the species’ relative abundance in the various localities. For instance, if losses due to emigration from locality  $j$  outweigh gains due to immigration from other localities, growth rate within locality  $j$  can fall below that experienced in isolation; that is,

$$c_{ij} \left( 1 - a_i + \frac{s_i a_i}{n-1} \frac{\sum_{l \neq j} p_{il}}{p_{ij}} \right) V_{ij} - g_{ij} - e_{ij} < c_{ij} V_{ij} - g_{ij} - e_{ij}$$

because  $a_i > [(s_i a_i)/(n-1)] [(\sum_{l \neq j} p_{il})/p_{ij}]$ . Hence, dispersal

of reproductive individuals can have a positive or negative effect on within-locality dynamics.

We have outlined the basic formulas for competition and dispersal functions. We next investigate how the two types of competition (dominance vs. preemption) and modes of dispersal (surplus vs. reproductive individuals) influence coexistence in spatially homogeneous and heterogeneous environments.

### Coexistence in a Spatially Homogeneous Competitive Environment

As noted in the first section of this article, the defining feature of a spatially homogeneous competitive environment is that species' competitive rankings do not change within the region of the landscape that contains the metacommunity. In what follows, we use life-history trade-offs as an illustrative example, but the framework we present also applies to other mechanisms involving spatially invariant competitive rankings (e.g., successional niche; Pacala and Rees 1998).

Since this section considers competitive abilities determined by life-history differences that are invariant in space, there will be one species that is the superior competitor across the region. For example, of the two parasitoids of the red scale (*Aonidiella aurantii*), *Aphytis melinus* is competitively superior to *Aphytis lingnanensis* over the entire range of their overlap (Luck and Podoler 1985). *Aphytis melinus*'s competitive superiority arises from the ability to obtain female offspring from a smaller-sized scale than *A. lingnanensis* (Luck and Podoler 1985; Murdoch et al. 1996). Similarly, of the two egg parasitoids of the harlequin bug (*Murgantia histrionica*), *Ooencyrtus johnsonii* is competitively superior to *Trissolcus murgantiae* in all habitats where they co-occur in southern California (Amarasekare 2000a, 2000b). *Ooencyrtus johnsonii*'s competitive superiority arises from the ability to kill and consume larvae of *T. murgantiae* during within-host larval competition (Amarasekare 2000b).

Previous work has shown that a life-history trade-off can lead to coexistence under dominance, but not preemptive, competition (e.g., Hastings 1980; Comins and Noble 1985). We first check whether metacommunity dynamics arising from hierarchical spatial structure alter these outcomes. We then investigate the consequences for coexistence when there is spatial variation in the expression of a life-history trade-off, an aspect previously not investigated in spatial competition theory.

*Role of Metacommunity Dynamics in Trade-off-Mediated Coexistence.* In the interests of analytical tractability, we consider a model of two competing species inhabiting two

localities. The following model describes the metacommunity dynamics:

$$\frac{dp_{ij}}{dt} = p_{ij}[D_{ij}(a_i, c_{ij}, p_{ij})V_{ij} - g_{ij} - e_{ij}], \quad (4)$$

with  $D_{ij} = c_{ij} + s_i c_{il}(p_{il}/p_{ij})$  and  $D_{ij} = c_{ij}[1 - a_i + a_i(p_{il}/p_{ij})]$ , respectively, for dispersal of surplus and reproductive individuals;  $V_{ij} = h_j - \sum_{i=1}^2 p_{ij}$  and  $g_{ij} = 0$  for preemptive competition; and  $V_{ij} = h_j - \sum_{k \leq i} p_{kj}$  and  $g_{ij} > 0$  for  $k < i$  for dominance competition ( $g_{ij} = c_{kj}p_{kj} + s_k c_{kl}p_{kl}$  and  $c_{kj}[(1 - a_k)p_{kj} + a_k p_{kl}]$ , respectively, for dispersal of surplus and reproductive individuals;  $i, j, k, l = 1, 2$ ). We let  $s_i$  and  $s_k = 1$  in the case of reproductive dispersal because dispersal mortality simply reduces the emigration rates  $a_i$  and  $a_k$  without any qualitative effects on coexistence (see "Coexistence in a Spatially Heterogeneous Competitive Environment").

Coexistence requires that each species be able to invade when its competitor is at equilibrium. Successful invasion by species  $i$  requires that the dominant eigenvalue of the Jacobian of equation (4) be positive when evaluated at the boundary equilibrium  $p_{ij} = 0$ ,  $p_{kj} > 0$ . This requirement leads to the following invasion criterion when between-locality dispersal involves surplus individuals:

$$(c_{ij}V_{ij} - g_{ij} - e_{ij})(c_{il}V_{il} - g_{il} - e_{il}) - c_{ij}V_{ij}c_{il}V_{il}s_i^2 < 0. \quad (5)$$

When between-locality dispersal involves reproductive individuals, the invasion criterion is

$$(c_{ij}V_{ij} - g_{ij} - e_{ij})(c_{il}V_{il} - g_{il} - e_{il}) - a_i[c_{il}V_{il}(c_{ij}V_{ij} - g_{ij} - e_{ij}) + c_{ij}V_{ij}(c_{il}V_{il} - g_{il} - e_{il})] < 0. \quad (6)$$

In equations (5) and (6), the quantity  $c_{ij}V_{ij} - g_{ij} - e_{ij}$  is the initial per capita growth rate of species  $i$  in locality  $j$  when species  $k$  is at equilibrium ( $p_{kj}^*$ ), with  $V_{ij} = h_j - p_{kj}^*$ . With dominance competition,  $g_{ij} = c_{kj}p_{kj}^* + s_k c_{kl}p_{kl}^*$  and  $g_{ij} = c_{kj}[(1 - a_k)p_{kj}^* + a_k p_{kl}^*]$  for dispersal of surplus and reproductive individuals, respectively.

If species  $i$  is the inferior competitor, it can invade when rare only if its initial growth rate is positive when averaged across localities. Note that since competitive ability is species specific rather than habitat specific, the inferior competitor's initial growth rate will be positive in both localities if it is positive in either locality. A positive average initial growth rate, however, does not guarantee invasibility. Invasion success depends on the type of competition. In preemptive competition, where no displacement is possible (i.e.,  $V_{ij} = V_{2j} = h_j - p_{1j} - p_{2j}$ ), competitive ability itself is defined by the species' reproductive ability relative

to its longevity (e.g.,  $c_{ij}/e_{ij}$ ). Although initial growth rates of both species can be positive when  $c_{ij}V_{ij} > e_{ij}$ , the  $R^*$  rule (Tilman 1982) operates, and the species with the higher  $c_{ij}/e_{ij}$  ratio excludes the other. Dispersal between localities cannot counteract competitive exclusion.

In dominance competition, where displacement is possible, species  $i$  can invade when rare if its competitive inferiority is compensated for by greater reproductive ability or longevity; that is,  $c_{ij}V_{ij} - e_{ij} > g_{ij}$  ( $j = 1, 2$ ). In this case, a life-history trade-off allows coexistence within localities regardless of dispersal between localities.

While dispersal between localities has no qualitative effect on coexistence under dominance competition, it can alter species' equilibrium abundances (mass effect; Shmida and Ellner 1984) given spatial variation in habitat size or vital rates (fig. 1). The mass effect illustrates two features that are crucial for empirical investigations of trade-off-mediated coexistence. First, inferior competitors can have higher absolute abundances than superior competitors in localities of small habitat area that are isolated or experience low levels of either surplus or reproductive dispersal (fig. 1a, 1d). Second, reproductive dispersal between localities can increase the relative abundances of inferior competitors in localities of large habitat area (fig. 1f).

*Role of Metacommunity Dynamics with Spatial Variation in the Expression of a Trade-off.* Models of trade-off-mediated coexistence generally assume that if a trade-off exists, it is expressed everywhere; that is, it is based on traits that are genetically invariant or not phenotypically plastic on time-scales relevant to ecological dynamics. These models typically do not consider whether spatial heterogeneity in the environment can affect the expression of a life-history trade-off. Considering spatial variation in the expression of a trade-off allows us to investigate whether metacommunity dynamics have a qualitative effect on trade-off-mediated coexistence.

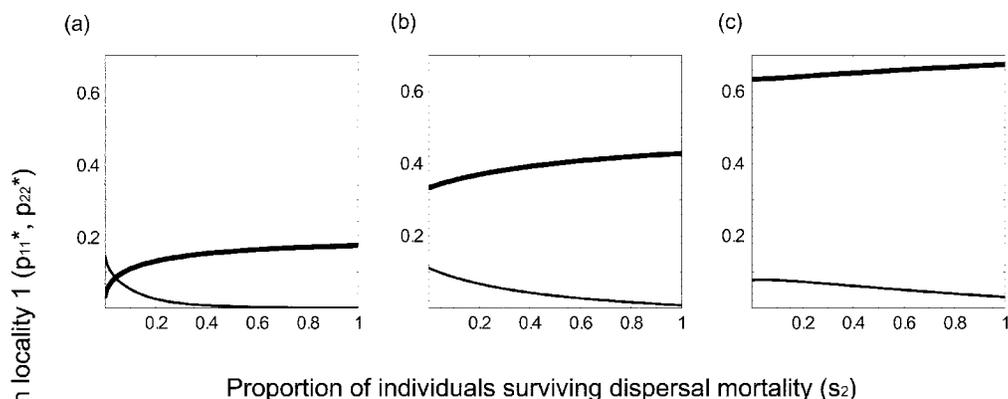
While the expression of some life-history trade-offs is largely invariant with respect to spatial variation in the biotic or abiotic environment (e.g., production of a few large seeds as opposed to many small seeds in plants, greater energy allocation to egg load rather than flight muscles in insects), the expression of others may be dependent on such variation. By way of illustration, consider an interspecific trade-off between resource exploitation and susceptibility to a natural enemy. One species allocates more energy to natural enemy defense (e.g., a plant that produces chemicals that make it unpalatable to herbivores) than to reproduction or other life-history traits that influence its resource exploitation abilities (e.g., lower seed set or reduced growth). Individuals of the other species allocate more energy to growth than to natural enemy defense. The latter species is therefore competitively su-

perior but suffers additional mortality because of greater susceptibility to the natural enemy. We assume dominance competition where superior competitors can displace inferior competitors. (Since species' competitive rankings are spatially invariant, the same species is the superior competitor everywhere within the metacommunity.) There is spatial variation in natural enemy abundance such that it is present in some localities but not others. This scenario can be incorporated into equation (4) by a simple alteration of parameters. Both superior and inferior competitors (species 1 and 2, respectively) have comparable colonization abilities ( $c_{1j} = c_{2j} = c_j$ ,  $j = 1, 2$ ), but the superior competitor suffers greater mortality in locality  $j$  due to natural enemy attack such that  $\hat{e}_{1j} = e_{1j} + e_{1N}N > e_{2j}$ . The parameter  $e_{1N}$  is the per capita mortality rate of species 1 due to natural enemy attack, and  $N$  is the fraction of species 1 patches attacked by the natural enemy. For simplicity, we assume that natural enemy dynamics are decoupled from competitive dynamics such that  $N$  is constant over the timescale of competition. Relaxing this assumption makes the analyses a great deal less tractable but does not alter the conclusions that follow.

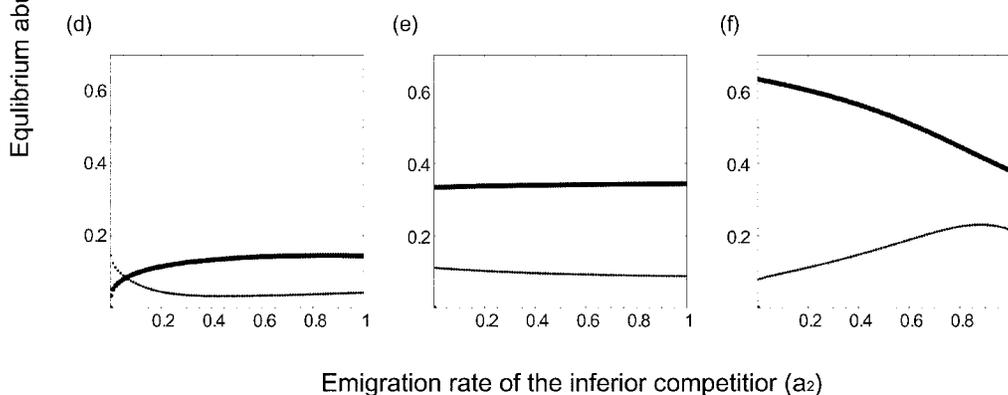
In the absence of dispersal between localities, the invasion criteria (eqq. [5], [6]) reduce to  $c_jV_{2j} - g_{2j} - e_{2j}$  with  $V_{2j} = h_j - p_{1j}^* - p_{2j}$ ,  $g_{2j} = c_jp_{1j}^*$ , and  $p_{1j}^* = h_j - \hat{e}_{1j}/c_j$  ( $j = 1, 2$ ). Biologically, this means that the inferior competitor can invade locality  $j$  if its initial growth rate in the absence of dispersal is positive when the superior competitor is at its equilibrium abundance. Noting that  $V_{1j} = h_j - p_{1j}^*$  and  $g_{1j} = 0$ , a little algebra shows that invasion is possible if  $p_{1j}^* < (\hat{e}_{1j} - e_{2j})/c_j$ . Thus,  $\hat{e}_{1j} > e_{2j}$  is a necessary condition for coexistence in the presence of the natural enemy; that is, the superior competitor should suffer greater mortality due to natural enemy attack. A sufficient condition is that mortality suffered by species 1 due to natural enemy attack should be sufficiently high to offset the inferior resource exploitation ability of species 2. In locality  $l$  where the natural enemy is absent so that  $\hat{e}_{1l} = e_{1l}$  and  $p_{1l}^* = h_l - e_{1l}/c_l$  ( $l = 1, 2$ ), coexistence is impossible unless some other trade-off is operating (e.g., inferior competitor has a smaller background mortality rate with  $e_{2l} < e_{1l}$ ).

These results have significant biological implications. In the absence of dispersal, spatial variation in the expression of a trade-off leads to a spatial pattern distinct from that expected when only one class of mechanism (spatially invariant vs. spatially varying competitive rankings) is operating (table 1). In localities where the natural enemy 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 natural enemy defense (a net cost now with no benefit) gives it an overall competitive disadvantage.

## Dispersal of surplus individuals



## Dispersal of reproductive individuals



**Figure 1:** Effect of between-locality dispersal on species abundances, given spatial variation in habitat size, when local coexistence occurs via a trade-off. In each row, panels from left to right represent increasing habitat size in locality 1 ( $h_1 = 0.2, 0.5, \text{ and } 0.8$ ). Because the total habitat size is constant, this implies a corresponding decrease (from left to right) in habitat size in locality 2 ( $h_2 = 0.8, 0.5, \text{ and } 0.2$ ). For surplus dispersal (*top row*), the X-axis is the proportion of individuals surviving dispersal mortality, with increasing survivorship implying an increase in the inferior competitor's colonization rate. For reproductive dispersal, the X-axis is the emigration rate of the inferior competitor. For both modes of dispersal, the Y-axis is the equilibrium abundance of competing species within locality 1. The thick solid line depicts the abundance of the superior competitor (species 1), and the thin solid line depicts that of the inferior competitor (species 2). The two modes of dispersal have qualitatively different effects on equilibrium abundances when habitat size is either very low or very high. When habitat size in locality 1 is low (*a, d*), the inferior competitor has a higher abundance at zero or low dispersal rates. This is because the superior competitor is more strongly affected by a reduction in habitat size. As the dispersal rate increases, the superior competitor's abundance increases because of input from locality 2, which because of its larger size has a higher abundance of that species. Under surplus dispersal, the inferior competitor can even be driven extinct if dispersal mortality is very low ( $s_2 \rightarrow 1$ ). When habitat size is very large in locality 1 (*e, f*), the superior competitor has a higher abundance than the inferior competitor in the absence of dispersal. The abundance of the inferior competitor increases with reproductive dispersal but not surplus dispersal. This is because of the cost of dispersal to the superior competitor; that is, emigration of reproductive individuals from the larger to the smaller locality depresses its equilibrium abundance. Because the inferior competitor is less affected by habitat loss, its abundance increases with dispersal regardless of the smaller size of locality 2. Since surplus dispersal incurs no cost to the locality with large habitat area, the superior competitor's abundance continues to increase with increasing dispersal rate (*c*). Parameter values are  $c_{11} = 0.6, c_{12} = 0.8, c_{21} = 5.4, c_{22} = 5.6$ , and  $e_{11} = e_{12} = e_{21} = e_{22} = 0.1$  for both modes of dispersal, with  $s_1 = s_2$  and  $a_1 = a_2$  for surplus and reproductive dispersal, respectively.

**Table 1:** Coexistence patterns under mechanisms that operate in spatially homogeneous and heterogeneous competitive environments

Dispersal	Coexistence mechanism		
	Spatially homogeneous competitive environment (e.g., trade-offs) <sup>a</sup>		Spatially heterogeneous competitive environment (e.g., source-sink dynamics) <sup>b</sup>
	Expressed everywhere	Spatial variation in expression	
No dispersal	Local coexistence everywhere	Local coexistence where expressed, exclusion of inferior competitor elsewhere	Regional coexistence
Low dispersal <sup>c</sup>	Local coexistence everywhere	Local coexistence everywhere	Local coexistence everywhere
High dispersal <sup>c</sup>	Local coexistence everywhere	Regional exclusion of inferior competitor	Regional exclusion of inferior competitor

<sup>a</sup> Competitive rankings are spatially invariant; that is, the same species is the superior competitor throughout the region that contains the metacommunity.

<sup>b</sup> Competitive rankings vary spatially such that different species are superior competitors in different localities of the metacommunity.

<sup>c</sup> Outcomes are the same for both surplus and reproductive dispersal.

In contrast to the commonly studied case of spatially invariant life-history trade-offs, dispersal plays a key role when there is spatial variation in the trade-off's expression. Emigration from localities in which the trade-off is expressed (sources for the inferior competitor) can rescue the inferior competitor from exclusion in localities in which the trade-off is not expressed (sinks for the inferior competitor). Thus, dispersal enables local coexistence everywhere. Coexistence, however, is possible only if the dispersal rate is low enough to preserve between-locality differences in the expression of the trade-off. By manipulating equation (5), it can be shown that coexistence under surplus dispersal requires the fraction of inferior competitor colonists that survive dispersal mortality to be nonzero ( $s_2 > 0$ ) and the fraction of superior competitor colonists that survive dispersal mortality to be below a critical threshold:

$$s_1 < \frac{-b + \sqrt{b^2 - 4c}}{2}, \quad (7)$$

where

$$b = \frac{-[c_j p_{1j}^* (c_j V_{2j} - g_{2j} - e_{2j}) + c_l p_{1l}^* (c_l V_{2l} - g_{2l} - e_{2l})]}{c_j p_{1j}^* c_l p_{1l}^*}, \quad (8)$$

$$c = \frac{(c_j V_{2j} - g_{2j} - e_{2j})(c_l V_{2l} - g_{2l} - e_{2l})}{c_j p_{1j}^* c_l p_{1l}^*} - \frac{c_j V_{2j} c_l V_{2l} s_2^2}{c_j p_{1j}^* c_l p_{1l}^*}, \quad (9)$$

with  $V_{2j} = h_j - p_{1j}^*$  and  $g_{2j} = c_j p_{1j}^*$ . Note that  $p_{1j}^*$  is now the equilibrium abundance of the superior competitor in the presence of dispersal when the inferior competitor is extinct.

A similar manipulation of equation (6) shows that coexistence under reproductive dispersal requires the emi-

gration rate of the inferior competitor to be below a critical threshold:

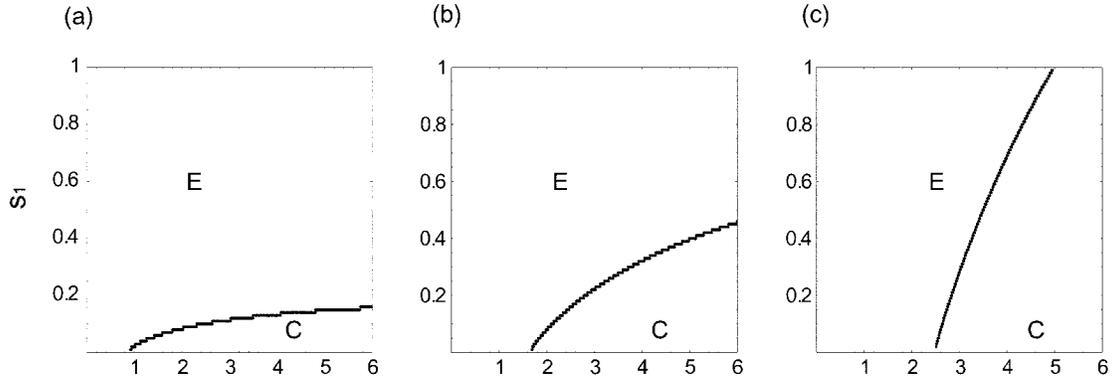
$$a_2 < \frac{(c_j V_{2j} - g_{2j} - e_{2j})(c_l V_{2l} - g_{2l} - e_{2l})}{c_l V_{2l} (c_j V_{2j} - g_{2j} - e_{2j}) + c_j V_{2j} (c_l V_{2l} - g_{2l} - e_{2l})}, \quad (10)$$

with  $V$  and  $g$  as defined in equation (6). Figure 2 illustrates the operation of these dispersal thresholds under spatial variation in habitat size.

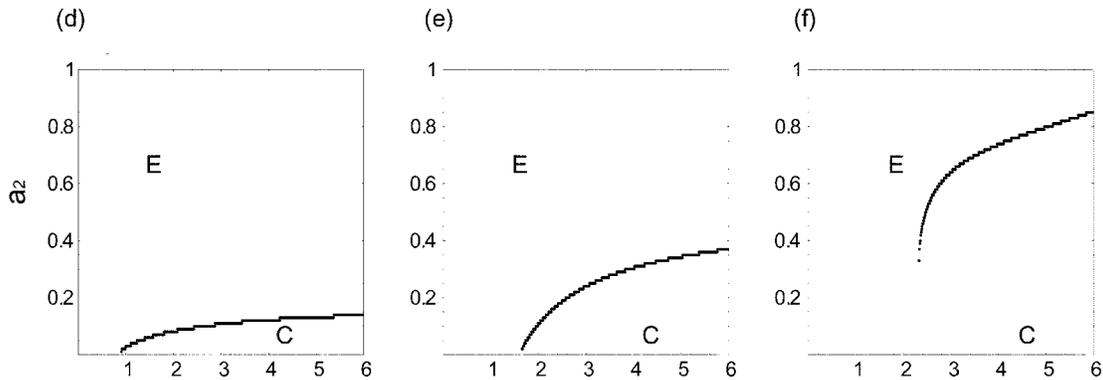
To summarize results for a spatially homogeneous competitive environment, our broader framework both accommodates previous results on trade-off-mediated coexistence and offers new insights into the operation of trade-offs in the face of spatial variation in the biotic or abiotic environment. When a life-history trade-off is expressed everywhere, dispersal has no qualitative effect on coexistence but can generate a mass effect. When there is spatial variation in the expression of the trade-off, however, dispersal is key to local coexistence. This new result illuminates the conditions under which both trade-offs and source-sink dynamics contribute to spatial coexistence. It provides the basis for a broader comparative analysis of coexistence mechanisms in spatially homogeneous and heterogeneous competitive environments (see "Discussion").

We have considered the scenario where spatial heterogeneity in the biotic or abiotic environment alters the expression of a life-history trade-off in space but does not alter species' competitive rankings. This means that the same species is the superior competitor throughout the region, and coexistence within a given locality depends on whether traits that allow other species to compensate for their inferior competitive abilities (e.g., greater resistance to natural enemy attack) are expressed in that locality. Quite a different scenario emerges if spatial variation alters the expression of life-history traits (assuming they are ge-

## Dispersal of surplus individuals



## Dispersal of reproductive individuals



## Mortality rate of the superior competitor

**Figure 2:** Local coexistence when there is spatial variation in the expression of a life-history trade-off. In each row, panels from left to right represent increasing habitat size in the locality where the trade-off is expressed ( $h_1 = 0.2, 0.5,$  and  $0.8$ ). In each panel, the X-axis is the mortality rate of the superior competitor in the locality where the natural enemy is present ( $\hat{e}_{1j}$ ). For surplus dispersal (*top row*), the Y-axis is the fraction of colonists of the superior competitor that survive dispersal mortality ( $s_1$ ), and for reproductive dispersal (*bottom row*), it is the emigration rate of the inferior competitor ( $a_2$ ). In all panels, the region marked C denotes local coexistence in both localities via source-sink dynamics, and the region marked E denotes exclusion of the inferior competitor from the locality where the trade-off is expressed. Both modes of dispersal have qualitatively the same effects on coexistence except when the size of the locality where the trade-off is expressed is very large (*c, f*). For sufficiently high mortality rates, coexistence is possible with surplus dispersal even with no dispersal mortality in the superior competitor ( $s_1 = 1$ ; *c*). In contrast, coexistence with reproductive dispersal is subject to an upper dispersal threshold for the inferior competitor even under high mortality rates of the superior competitor (*f*). Parameter values are  $c_{11} = c_{12} = c_{21} = c_{22} = 6.0$  and  $e_{12} = e_{21} = e_{22} = 0.1$  for both modes of dispersal.

netically variable or phenotypically labile) to such an extent that trade-offs are not possible. For instance, sufficiently high mortality in areas where the natural enemy is present may outweigh the resource exploitation advantage of an otherwise superior competitor and cause its exclusion. In this case, the competitive environment is no longer spatially homogeneous because competitive rankings now depend on spatial variation in the biotic or abiotic environment. We consider this situation next.

### *Coexistence in a Spatially Heterogeneous Competitive Environment*

A spatially heterogeneous competitive environment is one where differential responses by competing species to a spatially varying environment leads to spatial variation in their competitive rankings. Such variation is most likely to arise in the absence of mechanisms involving spatially invariant competitive rankings (e.g., life-history trade-offs). In fact, previous studies find that mechanisms involving spatially varying competitive rankings are necessary when life-history trade-offs fail to ensure coexistence (Yu and Wilson 2001; Levine and Rees 2002). For example, consider two competing species that share a predator whose abundance varies spatially. The species differ in their susceptibility to predation but do not exhibit a trade-off in that the species less susceptible to predation does not suffer a reduction in resource exploitation ability, and the species more susceptible to predation does not enjoy an increase in resource exploitation ability. Now, species' competitive rankings may shift with predator presence (Paine 1966; Connell 1971) such that the species less susceptible to predation will be the superior competitor in the presence of the predator (i.e., it will experience weaker interspecific than intraspecific competition because its competitor is affected by predation) and the inferior competitor in the absence of the predator (i.e., it will experience stronger interspecific than intraspecific competition because its competitor is released from predation). Similar spatial variation in the strength of competition can also result from differential responses of competing species to abiotic factors (e.g., temperature, humidity, salinity, nutrient availability).

The crucial difference between a spatially heterogeneous competitive environment and spatial variation in the expression of a life-history trade-off is that the latter, because it operates in a spatially homogeneous competitive environment, leads to a source-sink structure in the inferior competitor but not the superior competitor. In a spatially heterogeneous competitive environment, all species experience a source-sink structure with favorable areas where they can increase when rare and unfavorable areas where they cannot.

Previous work has shown that spatial variation in the

relative strengths of intraspecific and interspecific competition can lead to regional coexistence (Chesson 2000a, 2000b). Here we investigate how such regional coexistence mechanisms operating in concert with metacommunity dynamics allow local coexistence. Our analysis differs from previous studies by identifying conditions for coexistence under different regimes of competition and dispersal. For instance, the consequences of surplus versus reproductive dispersal for competitive coexistence have not previously been investigated for dominance or preemptive competition.

Equation (4) gives metacommunity dynamics in a spatially heterogeneous competitive environment, with  $D_{ij}$  as defined above for the two modes of dispersal. The distinguishing feature is spatial variation in the strength of competition, expressed via the functions  $V_{ij}$  and  $g_{ij}$ . For dominance competition,  $V_{ij} = h_j - p_{ij} - p_{kj}$  and  $g_{ij} > 0$  in locality  $j$ , and  $V_{il} = h_l - p_{il}$  and  $g_{il} = 0$  in locality  $l$  ( $g_{ij}$  as defined in eq. [4] for the two modes of dispersal). For preemptive competition,  $g_{ij} = 0$  and  $V_{ij} = h_j - \sum_{i=1}^2 p_{ij}$  ( $i, j, k, l = 1, 2; i \neq k, j \neq l$ ). Biologically, this means that species  $i$  is the inferior competitor in locality  $j$  and the superior competitor in locality  $l$ . Our representation of spatial variation in the strength of competition is phenomenological, which we do in the interests of analytical tractability. However, our model is sufficiently flexible to incorporate specific mechanisms that cause such variation (e.g., spatial storage effect or spatial relative nonlinearity) via the functions  $V_{ij}$  and  $g_{ij}$ .

Proceeding with the invasion analyses as before, we obtain the following criteria for the invasibility of species  $i$  when species  $k$  is at equilibrium in both localities. When dispersal involves surplus individuals, the invasion criterion is

$$(c_{ij}V_{ij} - g_{ij} - e_{ij})(c_{il}V_{il} - e_{il}) - c_{ij}V_{ij}c_{il}V_{il}s_i^2 < 0. \quad (11)$$

When dispersal involves reproductive individuals, the invasion criterion is

$$(c_{ij}V_{ij} - g_{ij} - e_{ij})(c_{il}V_{il} - e_{il}) - a_i[c_{il}V_{il}(c_{ij}V_{ij} - g_{ij} - e_{ij}) + c_{ij}V_{ij}(c_{il}V_{il} - e_{il})] < 0. \quad (12)$$

For dominance competition,  $V_{ij} = h_j - p_{kj}^*$ ,  $V_{il} = h_l$  and  $g_{ij} = c_{kj}p_{kj}^* + s_k c_{kl}p_{kl}^*$  and  $c_{kl}[(1 - a_k)p_{kl}^* + a_k p_{kj}^*]$  for surplus and reproductive dispersal, respectively. For preemptive competition,  $V_{ij} = h_j - p_{kj}^*$ ,  $V_{il} = h_l - p_{kl}^*$  and  $g_{ij} = 0$ . The quantities  $p_{kj}^*$  and  $p_{kl}^*$  are the respective boundary equilibria for species  $k$  in localities  $j$  and  $l$  when species  $i$  is extinct.

With spatial heterogeneity in the competitive environment, each species has a locality within which its initial growth rate can be positive (i.e.,  $c_{il}V_{il} - e_{il} > 0$ ;  $i, l = 1, 2$ )

because interspecific competition is weaker than intraspecific competition. Whether or not emigration from such source localities can prevent competitive exclusion in sink localities depends on both the type of competition and mode of dispersal. Table 2 summarizes the key results of this section, and the following subsections elaborate these results.

*Dispersal of Surplus Individuals.* When between-locality dispersal involves surplus individuals, mutual invasibility depends on the type of competition. In dominance competition, each species can invade when rare as long as the initial growth rate in the favorable locality is positive ( $c_{ii}V_{ii}/e_{ii} > 1$ ) and dispersal mortality is not 100% ( $s_i > 0$ ). In preemptive competition, invasion is possible only if the fraction surviving dispersal mortality is below a critical threshold:

$$s_i^2 < \frac{(c_{ij}V_{ij} - e_{ij})(c_{ii}V_{ii} - e_{ii})}{c_{ij}V_{ij}c_{ii}V_{ii}}. \quad (13)$$

The threshold in equation (13) arises because the total rate at which a species colonizes patches at a given locality consists of its rate of reproduction and establishment within that locality plus the equivalent rate from the other

locality weighted by the fraction surviving dispersal mortality (i.e.,  $D_{ij} = c_{ij}p_{ij} + s_i c_{ii}p_{ii}$ ). If the survivorship of dispersers moving between localities is too high ( $s_i \rightarrow 1$ ), spatial variation in competitive abilities (arising because of different  $c_{ij}/e_{ij}$  ratios) averages out such that the species with the lower average ratio ( $\bar{c}_i/\bar{e}_i$ ) has a negative per capita growth rate overall. In fact, when  $s_i = 1$ ,  $D_{ij}$  is the same for all localities, and coexistence is impossible under preemptive competition.

*Dispersal of Reproductive Individuals.* When between-locality dispersal involves reproductive individuals, the initial growth rate is positive in the favorable locality and negative in the unfavorable locality. Hence, the product of the initial growth rates (first term of eq. [12]) is always negative. Mutual invasibility is possible under two situations. First, if the sum of the growth rates is positive (i.e., the competitive advantage the species enjoys in the favorable locality is strong relative to the disadvantage it suffers in the unfavorable locality), each species can invade when rare as long as it has a nonzero dispersal rate ( $a_i > 0$ ). Second, if the sum of the initial growth rates is negative (i.e., the competitive advantage the species enjoys in the favorable locality is weak relative to the disadvantage it suffers in the unfavorable locality), invasion is possible only as long as  $a_i$  is below a critical threshold:

**Table 2:** Local coexistence under mechanisms operating in spatially homogeneous (e.g., trade-offs) and spatially heterogeneous (e.g., source-sink dynamics) competitive environments for different types of competition and modes of dispersal

	Dominance competition			Preemptive competition	
	Spatial homogeneity			Spatial homogeneity	Spatial heterogeneity
	Trade-off expressed everywhere	Spatial variation in expression	Spatial heterogeneity		
No dispersal	Coexistence	Coexistence where expressed, exclusion elsewhere	No coexistence	No coexistence	No coexistence
Dispersal of surplus individuals	Coexistence	Coexistence via source-sink dynamics subject to upper threshold <sup>a</sup>	Coexistence via source-sink dynamics, no upper threshold	No coexistence	Coexistence via source-sink dynamics subject to upper threshold <sup>b</sup>
Dispersal of reproductive individuals	Coexistence	Coexistence via source-sink dynamics subject to upper threshold <sup>b</sup>	Coexistence via source-sink dynamics, subject to upper threshold <sup>b</sup>	No coexistence	Coexistence via source-sink dynamics subject to upper threshold <sup>b</sup>

<sup>a</sup> For superior competitor.

<sup>b</sup> For inferior competitor.

$$a_i < \frac{(c_{ij}V_{ij} - g_{ij} - e_{ij})(c_{ii}V_{ii} - e_{ii})}{c_{ii}V_{ii}(c_{ij}V_{ij} - g_{ij} - e_{ij}) + c_{ij}V_{ij}(c_{ii}V_{ii} - e_{ii})}. \quad (14)$$

The key point to note is that when dispersal involves reproductive individuals, invasion success does not depend on the type of competition but on the balance between dispersal and spatial variation in the relative strengths of intraspecific and interspecific competition. For instance, if spatial heterogeneity in biotic or abiotic factors causes high spatial variance in the strength of competition (i.e., the numerator and denominator of eq. [14] are comparable in magnitude), mutual invasibility is possible under relatively high rates of dispersal. If spatial heterogeneity in such environmental factors is low or the species' responses to heterogeneity are weak, invasibility is possible only under low dispersal rates.

The balance between competition and dispersal arises because of the cost of dispersal to source communities in terms of loss of reproductive output. The upper dispersal threshold (eq. [14]) exists because too much emigration of reproductive individuals can reduce the per capita growth rate of sources, thus reducing spatial variation in the strength of competition across the region. If the emigration rate of a given species exceeds the upper threshold, its growth rate within its source community will become negative. Since there is no longer any spatial variation in the strength of competition, that species will be excluded from the entire region. This outcome is robust for both dominance and preemptive competition.

It is interesting to note that dispersal mortality ( $s_i < 1$ ) has a qualitative effect on coexistence under surplus dispersal but not under reproductive dispersal. This distinction can be seen by comparing the total rate at which a given species colonizes empty patches ( $D_{ij}$ ). With surplus dispersal, this rate is the same for all localities unless there is mortality during dispersal (i.e.,  $D_{ij} = c_{ij}p_{ij} + s_i c_{ii}p_{ii}$ ). With reproductive dispersal,  $D_{ij}$  is a function of the per capita rate of reproduction and establishment within a locality ( $c_{ij}$ ) weighted by the sum of disperser and non-disperser abundance; that is,  $D_{ij} = c_{ij}[(1 - a_i)p_{ij} + s_i a_i p_{ii}]$ . Thus, local differences in competitive ability are preserved as long as the dispersal rate  $a_i$  is not too high. Dispersal mortality can increase the threshold below which coexistence occurs (eq. [14]) by reducing the dispersal rate  $a_i$ , but it cannot influence the existence of the threshold as in surplus dispersal.

*Mechanism Underlying Dispersal-Mediated Coexistence.* In the absence of dispersal, the inferior competitor's per capita growth rate declines linearly with increasing density. In the presence of dispersal, the growth rate declines with

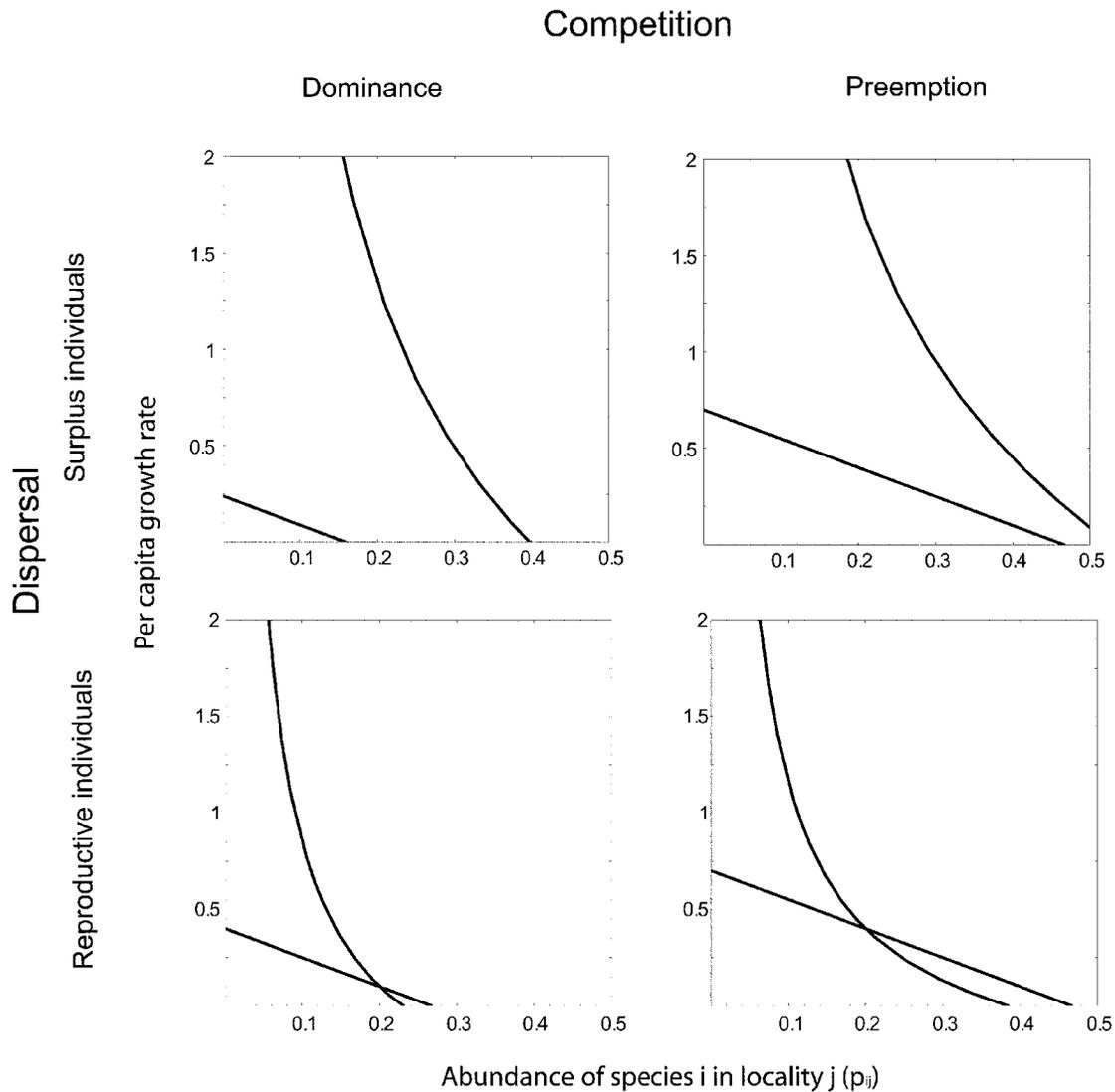
density in a nonlinear fashion (fig. 3). The negative density dependence induced by dispersal increases the strength of intraspecific competition relative to that of interspecific competition and prevents competitive exclusion. For instance, the per capita growth rate at low abundances is greater than that in isolation (fig. 3). This enhances the ability of species to increase when rare. The key point to note is that dispersal itself is density independent, but it creates a negative density-dependent effect akin to self-limitation (see also Holt 1993). This negative feedback in turn leads to nonlinearity in the per capita growth rates of competing species. When dispersal fails to allow local coexistence, it is because the negative density dependence induced in the per capita growth rate is insufficient to counteract interspecific competition.

*Effects of Habitat Availability on Coexistence.* Given that spatial coexistence involves species competing for space or a resource whose abundance varies in space, how habitat availability influences spatial coexistence becomes an important issue. As the size of one locality increases, the species that is competitively superior in that locality gains an overall advantage. (Since the total habitat size is constant, an increase in size of one locality implies a decrease in size for the other locality and thus resource limitation at the metacommunity scale.) Hence, opportunities for local coexistence are greatest when spatial variation in habitat size is the least (fig. 4) because lower spatial variation in habitat size means greater spatial variation in the strength of competition. For both modes of dispersal, opportunities for coexistence are greater under dominance than for preemptive competition. For both types of competition, smaller rates of reproductive dispersal provide greater opportunities for coexistence. With surplus dispersal, coexistence is always possible under dominance competition, but under preemptive competition, coexistence is impossible in the absence of dispersal mortality (fig. 4).

## Discussion

Although there is a vast body of theory on spatial coexistence, very little of it involves comparative analyses of alternative mechanisms. We thus know relatively little about the conditions under which multiple spatial mechanisms can operate, or about emergent properties that arise from interactions between mechanisms.

Here we have presented a simple mathematical framework that allows for comparative analysis of spatial coexistence mechanisms. The basis of comparison is mechanisms that operate in spatially homogeneous versus heterogeneous competitive environments. This framework allows us to identify the conditions under which each class



**Figure 3:** Per capita growth rate of species  $i$  in locality  $j$  as a function of its abundance ( $p_{ij}$ ) for the two modes of competition and dispersal when the competitive environment is spatially heterogeneous. When there is no dispersal between localities, per capita growth rate declines linearly with increasing abundance. When there is dispersal, per capita growth rate declines nonlinearly with abundance. Note that when dispersal involves surplus individuals (*top row*), per capita growth rate is always augmented above that in isolation. When dispersal involves reproductive individuals (*bottom row*), per capita growth rate is increased relative to that in isolation when the species' abundance is low but decreased relative to that in isolation when the abundance is relatively high. Increase in the growth rate at low abundances reflects the benefit to sinks via the rescue effect, while the decrease in the growth rate at high abundances reflects the cost to sources via loss of reproductive output. Parameter values are  $c_{11} = 3.0$ ,  $c_{12} = 1.6$ ,  $c_{21} = 1.5$ ,  $c_{22} = 3.5$ ,  $e_{11} = e_{12} = e_{21} = e_{22} = 0.2$ , and  $s_1 = 0.5$ ,  $s_2 = 0.8$  for surplus dispersal and  $a_1 = 0.5$ ,  $a_2 = 0.8$  for reproductive dispersal.

of mechanism is likely to operate and conditions under which both classes of mechanisms may operate simultaneously. We compare the operation of the two classes of mechanisms under different types of competition and modes of dispersal, and we derive comparative predictions that allow simultaneous tests of multiple mechanisms of coexistence.

We wish to emphasize three key points that emerge from

our comparative analysis and discuss their implications for future theoretical and empirical work. The first issue concerns the simultaneous operation of coexistence mechanisms with and without spatial variation in competitive rankings. Previous studies of life-history trade-offs have assumed that, if trade-offs exist that provide the appropriate niche differences required for coexistence, no constraints prevent their operation (e.g., Hastings 1980; Nee

and May 1992; Tilman et al. 1994). Studies that have simultaneously investigated trade-offs and source-sink dynamics (Yu and Wilson 2001; Levine and Rees 2002) have found that source-sink dynamics are important for coexistence when trade-offs fail to provide niche differences. No previous study to our knowledge has considered the possibility that spatial heterogeneity may influence the expression of a life-history trade-off that otherwise provides the requisite niche differences for coexistence.

Using an example of a trade-off between resource exploitation and susceptibility to a natural enemy, we have shown that spatial variation in natural enemy abundance can constrain coexistence and lead to a unique regional pattern that can be predicted only by simultaneous consideration of trade-offs and spatial heterogeneity. Previous studies have examined the conditions under which spatial variation in the abiotic environment promotes coexistence (e.g., Chesson 2000a; Muko and Iwasa 2000; Snyder and Chesson 2003). Here we show that spatial heterogeneity that influences the expression of a life-history trade-off can in fact constrain coexistence. In such a situation, dispersal can increase opportunities for coexistence via source-sink dynamics, provided the dispersal rate is sufficiently low that most individuals remain in localities where they experience weaker interspecific than intraspecific competition. While the example we have used is simple and phenomenological, the framework we present can be used to analyze more complicated instances of spatial variation in the expression of a life-history trade-off.

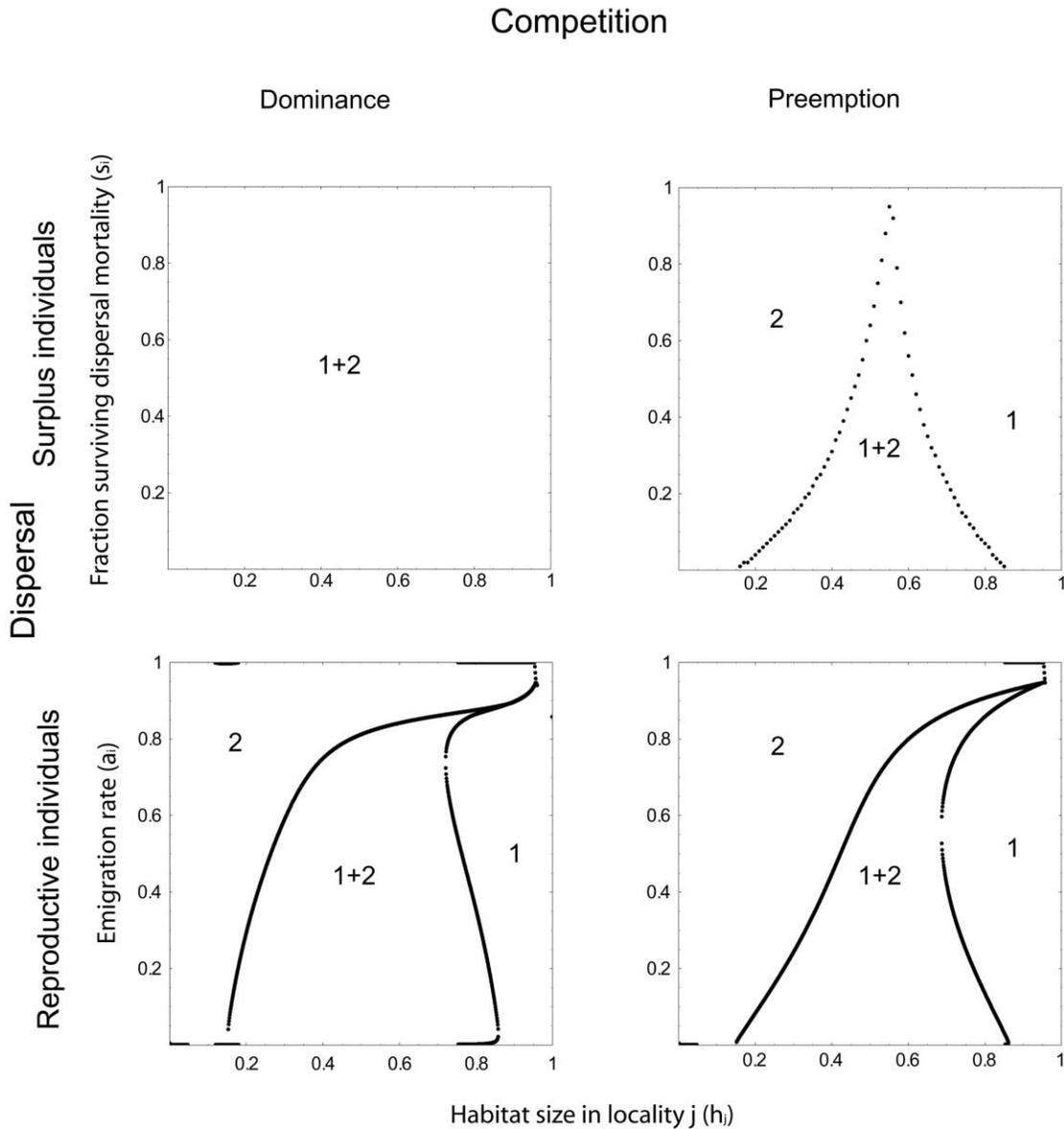
The demonstration that spatial heterogeneity can influence the operation of life-history trade-offs begs the question of how to distinguish such spatially variable trade-offs from mechanisms that involve spatial variation in competitive rankings (e.g., source-sink dynamics). The distinction we make between coexistence in spatially homogeneous versus spatially heterogeneous competitive environments is crucial in this regard. The basis for this distinction is spatial variation in the relative strengths of intraspecific and interspecific competition. Life-history trade-offs operate in a spatially homogeneous competitive environment, where competitive abilities are intrinsic to the species themselves such that the same species is the superior competitor everywhere in the landscape. Spatial variation does not alter species' competitive rankings but rather the expression of life-history traits that compensate for inferior resource exploitation abilities. In contrast, mechanisms such as source-sink dynamics operate in a spatially heterogeneous competitive environment where no single species is the superior competitor across the landscape. Interestingly, the two cases lead to unique spatial patterns of coexistence in the absence of dispersal but converge on the same pattern in the presence of dispersal (table 1). Distinguishing between the two mechanisms in

practice therefore necessitates measuring competition coefficients (or other measures of competitive ability) in multiple localities to determine whether there is spatial variation in competitive rankings, and preventing or constraining dispersal between localities to determine which of the two spatial patterns ensues.

The second key point we wish to emphasize concerns how mechanisms involving spatial variation in competitive rankings operate under different regimes of competition and dispersal. This type of comparative analysis has not previously been conducted in models of spatial variation and source-sink dynamics. Our analysis yields comparative predictions that can facilitate empirical investigations. For instance, when dispersal involves surplus individuals, local coexistence is possible under dominance but not preemptive competition unless there is mortality during dispersal. Dispersal mortality is necessary to preserve spatial variation in the strength of preemptive competition. Because surplus individuals, by definition, do not affect the local reproductive output of source communities, sinks can be rescued without an undue effect on sources, but the rescue effect may be weakened by dispersal mortality. This reduces opportunities for coexistence under preemptive competition compared with dominance competition. In contrast, when dispersal involves individuals that constitute a fraction of the reproductive output of their natal locality, coexistence is possible under both dominance and preemptive competition provided the emigration rate is below a critical threshold. Now dispersal mortality has no effect on spatial variation in the strength of competition, but the emigration rate itself does. This outcome occurs because the dispersal rate of individuals that would otherwise have reproduced in situ, if sufficiently high, can cause per capita growth rates of source communities themselves to become negative. Thus, while too much dispersal only reduces opportunities for coexistence under surplus dispersal, it can cause region-wide exclusion of a species under reproductive dispersal.

As with spatial variation in the expression of trade-offs, some of our results for source-sink dynamics are counterintuitive and could not have been predicted without a comparative analysis. For instance, previous studies show dispersal mortality to have only a quantitative effect on coexistence; that is, coexistence is possible in its absence but can be constrained or facilitated in its presence (e.g., Hanski and Gilpin 1997; Amarasekare 1998; Mouquet and Loreau 2003). Our analyses distinguish situations where dispersal mortality is not necessary for coexistence (e.g., reproductive dispersal) from those where such mortality is essential for coexistence because it preserves spatial variation in the strength of competition (e.g., surplus dispersal and preemptive competition).

The third point we want to emphasize concerns whether



**Figure 4:** Local coexistence in a spatially heterogeneous competitive environment as a function of habitat size in locality  $j$ . When dispersal involves surplus individuals (*top row*), the invasion criterion is expressed in terms of the fraction of colonists of species  $i$  that survive dispersal mortality, that is, by solving equation (11) for  $s_i$  ( $i = 1, 2$ ). When dispersal involves reproductive individuals (*bottom row*), the criterion is expressed in terms of the emigration rate of species  $i$ , that is, by solving equation (12) for  $a_i$ . For dominance competition with dispersal of surplus individuals (*top left*), mutual invasibility is possible as long as  $s_i > 0$ . For preemptive competition with dispersal of surplus individuals, mutual invasibility is possible if dispersal mortality is high ( $s_i$  is low) and habitat size is intermediate (*top right*). For both dominance and preemptive competition, mutual invasibility when dispersal involves reproductive individuals (*bottom row*) is greatest at intermediate habitat sizes and low to moderate emigration rates. However, the region of mutual invasibility is narrower (and opportunities for coexistence more restrictive) for preemptive competition (*bottom right*) than for dominance competition (*bottom left*). As a general rule, opportunities for coexistence are greatest when spatial variation in habitat size is the least (i.e.,  $h_j \sim h_l \sim 0.5$ ). Parameter values are  $c_{11} = 1.4$ ,  $c_{12} = 0.5$ ,  $c_{21} = 0.6$ ,  $c_{22} = 1.5$ , and  $e_{11} = e_{12} = e_{21} = e_{22} = 0.2$ .

mechanisms involving spatially invariant competitive rankings can influence the operation of mechanisms that require spatial variation in such rankings. Because the former, by definition, operate in the absence of spatial var-

iation in the strength of competition, it is difficult to envision how they may modify the latter. Thus, the current approach of considering mechanisms with and without spatial variation in competitive rankings in a purely eco-

logical context provides for a rather narrow depiction of their joint operation. A broader analysis of the interaction between the two classes of mechanisms requires a model that adopts a mechanistic basis for life-history trade-offs (i.e., by incorporating energy allocation strategies at the individual level) and investigates how such strategies evolve in the face of mutation and gene flow in a spatially heterogeneous environment. Adaptive dynamics (Hofbauer and Sigmund 1988) seems a promising avenue for such an investigation.

While we have focused on life-history trade-offs and source-sink dynamics as representative examples of coexistence mechanisms in spatially homogeneous and heterogeneous competitive environments, the framework we present can accommodate other mechanisms that operate in spatially homogeneous competitive environments (e.g., successional niche: Pacala and Rees 1998; interaction neighborhoods: Murrell and Law 2003) as well as more mechanistic representations of spatial variation in the strength of competition (e.g., the spatial storage effect, spatial nonlinearity, and growth density covariance; Chesson 2000*a*, 2000*b*). Expanding our comparative analysis to incorporate these factors is an important next step.

The framework presented here forms the basis for two important future directions. The first involves the evolution of life-history traits in spatially heterogeneous environments. As ecologists, we tend to think of trade-offs in terms of consequences rather than causes; that is, we focus on the negative correlations between species abundances that supposedly arise from complementary life-history trade-offs rather than on the energy allocation strategies that give rise to such trade-offs. This affords us only a myopic view of how life-history trade-offs may influence source-sink dynamics, because ignoring the individual-level allocation strategies constrains us to assume that individuals exhibiting particular life-history traits that enhance their fitness in a particular environment do not suffer a reduction in fitness when they immigrate into a different environment. Our expectations about dispersal effects on life-history trade-offs may be altered radically once we consider the possibility that mutation and gene flow can alter the average energy allocation strategy adopted by individuals of a given species.

The second future direction involves elucidating the cause and effect relationship between biodiversity and ecosystem functioning, an issue of intense current interest. Most studies have considered the macroscopic properties of diversity and ecosystem functions without consideration of underlying coexistence mechanisms (see Kinzig et al. 2001). A comparative analysis of coexistence mechanisms in spatially homogeneous versus heterogeneous competitive environments is essential for developing a predictive framework for biodiversity and ecosystem functioning that

is also of practical utility. Expanding the model we have presented to incorporate trophic interactions (e.g., predator-prey, host-parasite, plant-herbivore) constitutes an important first step in developing such a framework.

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