Spatial variation and density-dependent dispersal in competitive coexistence

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It is well known that dispersal from localities favourable to a species' growth and reproduction (sources) can prevent competitive exclusion in unfavourable localities (sinks). What is perhaps less well known is that too much emigration can undermine the viability of sources and cause regional competitive exclusion. Here, I investigate two biological mechanisms that reduce the cost of dispersal to source communities. The first involves increasing the spatial variation in the strength of competition such that sources can withstand high rates of emigration; the second involves reducing emigration from sources via density-dependent dispersal. I compare how different forms of spatial variation and modes of dispersal influence source viability, and hence source–sink coexistence, under dominance and pre-emptive competition. A key finding is that, while spatial variation substantially reduces dispersal costs under both types of competition, density-dependent dispersal does so only under dominance competition. For instance, when spatial variation in the strength of competition is high, coexistence is possible (regardless of the type of competition) even when sources experience high emigration rates; when spatial variation is low, coexistence is restricted even under low emigration rates. Under dominance competition, density-dependent dispersal has a strong effect on coexistence. For instance, when the emigration rate increases with density at an accelerating rate (Type III density-dependent dispersal), coexistence is possible even when spatial variation is quite low; when the emigration rate increases with density at a decelerating rate (Type II density-dependent dispersal), coexistence is restricted even when spatial variation is quite high. Under pre-emptive competition, density-dependent dispersal has only a marginal effect on coexistence. Thus, the diversity-reducing effects of high dispersal rates persist under pre-emptive competition even when dispersal is density dependent, but can be significantly mitigated under dominance competition if density-dependent dispersal is Type III rather than Type II. These results lead to testable predictions about source–sink coexistence under different regimes of competition, spatial variation and dispersal. They identify situations in which density-independent dispersal provides a reasonable approximation to species' dispersal patterns, and those under which consideration of density-dependent dispersal is crucial to predicting long-term coexistence.

Keywords: competition; density-dependent dispersal; dominance; pre-emption; spatial variation; source–sink dynamics

1. INTRODUCTION

It is well known that dispersal can allow species coexistence if spatial variation in the relative strengths of intra-specific and interspecific interactions creates a source–sink population structure (e.g. Levin 1974; Pacala & Roughgarden 1982; Shmida & Ellner 1984; Kishimoto 1990; Amarasekare & Nisbet 2001; Codeco & Grover 2001; Mouquet & Loreau 2002). For instance, immigration from localities where a given species experiences weaker interspecific than intraspecific competition (i.e. sources where the species can increase when rare) can prevent competitive exclusion in localities where it suffers stronger interspecific than intraspecific competition (i.e. sinks where the species cannot increase when rare). What is perhaps less well known is that this rescue effect imposes a cost of dispersal on sources. While emigration from source localities is necessary for maintaining species in sink localities, too much emigration can depress the *per capita* growth rates of sources and homogenize spatial variance in the strength of competition (Levin 1974; Pacala & Roughgarden 1982; Amarasekare & Nisbet 2001; Mouquet & Loreau 2002). Such homogenization can

cause region-wide exclusion of species that are inferior competitors or have lower initial abundances, thus reducing diversity below that observed in isolated communities.

The prediction that high dispersal rates should undermine diversity begs the question of whether there are biological mechanisms that can reduce the cost of dispersal to source communities. There are two basic mechanisms. The first involves strong spatial variation in the strength of competition; for example, if the competitive advantage in the source is strong relative to the competitive disadvantage in the sink, then the source may be able to withstand quite high rates of emigration. The second involves reducing the amount of emigration from source communities. One such mechanism is localized dispersal (e.g. Murrell & Law 2003; Snyder & Chesson 2003). If individuals do not move very far from their natal localities, they are less likely to leave areas favourable to their growth and reproduction. However, they are also less likely to rescue sink populations from extinction. Thus localized dispersal may increase source viability, but species diversity is likely to be lower than that observed under low levels of global dispersal. (Global here means a dispersal range that is sufficiently large to encompass both favourable and unfavourable localities of the landscape.)

A second, and much less well-studied, mechanism for reducing emigration from sources is density-dependent dispersal. All models that predict diversity-reducing effects of high dispersal assume dispersal to be density independent and global in extent (e.g. Levin 1974; Pacala & Roughgarden 1982; Shmida & Ellner 1984; Amarasekare & Nisbet 2001; Mouquet & Loreau 2002). Models of localized dispersal also assume density independence (e.g. Murrell & Law 2003; Snyder & Chesson 2003). Most real organisms, however, exhibit some form of density-dependent dispersal (Sutherland *et al.* 2002). Investigation of global density-dependent dispersal is important because this type of dispersal has the potential to rescue sink populations from extinction without unduly affecting source viability. Thus, density-dependent dispersal could increase species diversity above that observed under density-independent dispersal, whether local or global.

While several studies have investigated the role of density-dependent dispersal in the source-sink dynamics of single species (e.g. Pulliam 1988; Howe *et al.* 1991; Pulliam & Danielson 1991; Amarasekare 2004), I am aware of only one study that has investigated density-dependent dispersal in the source-sink dynamics of competing species (Nishimura & Kishida 2001). This study considered only one mode of dispersal (dispersal rate increasing in proportion to the species' density) for species engaged in dominance competition. Data, however, show that dispersal rate can both increase and decrease with increasing density (e.g. Denno & Peterson 1995; Herzig 1995; Fonseca & Hart 1996; Veit & Lewis 1996; Doncaster *et al.* 1997; Wolff 1997; Diffendorfer 1998; Aars & Ims 2000). Data also show that species engage in both dominance and pre-emptive competition, as well as combinations thereof. Therefore, a comprehensive investigation of how density-dependent dispersal influences source viability requires a comparative approach that considers different types of competition as well as different modes of dispersal.

Here, I present a model that investigates how spatial variation and density-dependent dispersal influence dispersal costs to sources under dominance and pre-emptive competition. I derive comparative predictions about how different types of competition, spatial variation and modes of dispersal influence source viability and hence source-sink coexistence. I discuss the implications of these results for species coexistence in patchy environments.

2. THE MODEL

Consider a patchy environment consisting of multiple localities, each inhabited by a local community of competing species. Within a given locality, competition occurs according to Lotka-Volterra dynamics. The communities are linked by emigration and immigration of competing species. A collection of such communities that occupies a particular region of the landscape constitutes a metacommunity. Dispersal is global in that all species can get to all habitable localities within the metacommunity.

The dynamics of a source-sink system of two competing species inhabiting two localities (j and l) are given by

$$\begin{aligned} \frac{dX_{1j}}{dt} = & r_1 X_{1j} \left(1 - \frac{X_{1j}}{K_{1j}} - \alpha_{1j} \frac{X_{2j}}{K_{1j}} \right) \\ & - D_1 X_{1j} \left(\frac{X_{1j} + \alpha_{1j} X_{2j}}{K_{1j}} \right)^s + D_1 X_{1l} \left(\frac{X_{1l} + \alpha_{1l} X_{2l}}{K_{1l}} \right)^s, \end{aligned}$$

$$\begin{aligned} \frac{dX_{2j}}{dt} = & r_2 X_{2j} \left(1 - \frac{X_{2j}}{K_{2j}} - \alpha_{2j} \frac{X_{1j}}{K_{2j}} \right) \\ & - D_2 X_{2j} \left(\frac{X_{2j} + \alpha_{2j} X_{1j}}{K_{2j}} \right)^s + D_2 X_{2l} \left(\frac{X_{2l} + \alpha_{2l} X_{1l}}{K_{2l}} \right)^s, \end{aligned} \quad (2.1)$$

where X_{ij} is the abundance, α_{ij} the competition coefficient and K_{ij} the carrying capacity of species i in locality j ($i, j, l = 1, 2; j \neq l$). The parameter r_i is the intrinsic growth rate of species i , and D_i is its *per capita* emigration rate. The quantity s denotes the strength of density dependence in dispersal.

I non-dimensionalize equation (2.1) using scaled quantities. Non-dimensional analysis allows the dynamic system to be described by a minimal set of parameters and also illuminates the scaling relations between the various dynamic processes (Murray 1993).

I use the following substitutions:

$$\begin{aligned} x_{ij} &= \frac{X_{ij}}{K_{ij}}, \quad a_{ij} = \alpha_{ij} \frac{K_{kj}}{K_{ij}}, \quad k_i = \frac{K_{il}}{K_{ij}}, \\ \beta_i &= \frac{D_i}{r_i}, \quad \rho = \frac{r_2}{r_1}, \quad \tau = r_1 t \quad (i, j, k, l = 1, 2; i \neq k, j \neq l), \end{aligned}$$

to transform equation (2.1) to its non-dimensional form.

The non-dimensional quantity x_{ij} represents the density of species i in locality j scaled by its carrying capacity, and a_{ij} represents the *per capita* competitive effect of species m on species i scaled by the ratio of their respective carrying capacities. The quantity k_i is the ratio of the carrying capacities in the two localities for species i , and β_i is its *per capita* emigration rate scaled by the intrinsic growth rate. The quantity ρ is the ratio of the intrinsic growth rates of the two species. The non-dimensional time metric τ expresses time in terms of species 1's intrinsic growth rate.

I substitute the non-dimensional quantities into equation (2.1) to obtain the following system of equations.

$$\begin{aligned} \frac{dx_{1j}}{d\tau} = & x_{1j} (1 - x_{1j} - a_{1j} x_{2j}) - \beta_1 x_{1j} (x_{1j} + a_{1j} x_{2j})^s \\ & + k_1 \beta_1 x_{1l} (x_{1l} + a_{1l} x_{2l})^s, \\ \frac{dx_{2j}}{d\tau} = & \rho x_{2j} (1 - x_{2j} - a_{2j} x_{1j}) - \rho \beta_2 x_{2j} (x_{2j} + a_{2j} x_{1j})^s \\ & + k_2 \rho \beta_2 x_{2l} (x_{2l} + a_{2l} x_{1l})^s. \end{aligned} \quad (2.2)$$

Unless otherwise noted, all variables and parameters from this point on are expressed as scaled quantities.

The nature of density dependence in dispersal is mediated by the parameter s (figure 1). When $s = 0$, emigration is density independent and occurs at the *per capita* rate β_i . When $s \neq 0$, emigration is dependent on the effective density of the species (cf. Nishimura & Kishida 2001), which is a function of both intraspecific and interspecific competition (e.g. $x_{ij} + a_{ij} x_{mj}$, $i, m = 1, 2; i \neq m$). There are two basic modes of density-dependent dispersal, depending on the sign of s . When $s < 0$, emigration increases with density at a decelerating rate, akin to a Type II functional response at low resource abundances (Holling 1959). (The analogy is not perfect because the emigration rate does not necessarily saturate at high abundances; figure 1.) This mode of dispersal is likely to occur when individuals tend to emigrate from low-density populations, owing to difficulties in finding a mate or reduced

Figure 1. Modes of density-dependent dispersal. The x -axis is the abundance of species i in locality j (x_{ij}), and the y -axis is the emigration rate ($\beta_i x_{ij} (x_{ij} + \alpha_{ij} x_{kj})^s$). In the baseline case of density-independent dispersal ($s = 0$), emigration rate increases in proportion to density. (a) Type II density-dependent dispersal ($s < 0$) occurs when the emigration rate increases with abundance at a decelerating rate. (b) Type III density-dependent dispersal ($s > 0$) occurs when the emigration rate increases with abundance at an accelerating rate. Note that the dispersal function can be non-monotonic for $s \ll 0$, but this occurs for values of s that are not biologically feasible.

predator vigilance. Examples include insects (Herzig 1995; Kuussaari *et al.* 1998), birds (Birkhead 1977) and mammals (Wolff 1997; Diffendorfer 1998). When $s > 0$, emigration increases with density at an accelerating rate, akin to a Type III functional response at low resource abundances (Murdoch & Oaten 1975). This mode of dispersal is likely to occur when individuals tend to leave high-density populations owing to strong intraspecific and interspecific competition. Examples include insects

(Denno & Peterson 1995; Fonseca & Hart 1996; Rhainds *et al.* 1998) and territorial birds and mammals (Veit & Lewis 1996; Wolff 1997; Aars & Ims 2000).

Although the dynamic analogy with functional responses is not perfect, it is convenient to refer to the three dispersal modes as Type I ($s = 0$), Type II ($s < 0$) and Type III ($s > 0$). Note that Type III density-dependent dispersal is a generalization of the mode of density-dependent dispersal considered in Pulliam's (1988) model of single-species source-sink dynamics. In Pulliam's model, intraspecific competition occurs for resources that are spatially well defined and easily defensible (e.g. nesting sites or breeding territories). Individuals obey a habitat-selection rule such that emigration from the source to the sink occurs only after all breeding sites in the source locality are filled. Thus, dispersal involves only 'surplus' individuals whose departure does not affect the source population's *per capita* growth rate. The functional form of Type III density-dependent dispersal that I employ here generalizes such surplus dispersal to resources that are not as well-defined or defensible (e.g. essential nutrients and mobile prey).

Because I am interested in spatial variation in the strength of competition and density-dependent dispersal, I assume that species differ in their *per capita* competitive effects (α_{ij}) and dispersal rates (β_i) but are otherwise similar, i.e. $\rho = 1$, $k_1 = k_2$, $K_{1j} = K_{2j}$ ($j = 1, 2$). This yields the following simplified system:

$$\frac{dx_{ij}}{d\tau} = x_{ij}(1 - x_{ij} - \alpha_{ij}x_{mj}) - \beta_i x_{ij}(x_{ij} + \alpha_{ij}x_{mj})^s + \beta_i x_{il}(x_{il} + \alpha_{il}x_{ml})^s \quad i, j, m, l = 1, 2; i \neq m, j \neq l. \quad (2.3)$$

There are two basic types of competition to consider: dominance and pre-emption. This distinction is important because spatial variation arises in fundamentally different ways in the two types of competition, which in turn can cause significant differences in the dispersal costs incurred by source communities. Dominance competition implies that $\alpha_{1j} < 1$ and $\alpha_{2j} > 1$ ($j = 1, 2$), i.e. species 1 experiences greater intraspecific competition than interspecific competition, and species 2 experiences the opposite. Species 1 is hence the superior competitor and excludes species 2 in the absence of dispersal. Pre-emptive competition, on the other hand, implies that $\alpha_{1j} > 1$ and $\alpha_{2j} > 1$, i.e. both species experience stronger interspecific competition than intraspecific competition. Neither species is hence the superior competitor, and the species with the higher initial abundance excludes the other in the absence of dispersal.

The key issue is whether spatial variation and density-dependent dispersal reduce dispersal costs to sources below those expected under density-independent dispersal. I investigate this issue using a comparative analysis of dominance and pre-emptive competition.

(a) Dominance competition

As noted above, under dominance competition species 1 is the superior competitor and excludes species 2 in the absence of dispersal. In a spatially heterogeneous environment, however, there may be biotic or abiotic factors that cause spatial variation in the strength of competition. For instance, the superior competitor may be more susceptible

to a shared natural enemy whose abundance varies spatially, or to spatial variation in temperature, humidity or nutrient availability. Such variation allows the inferior competitor to increase when rare in localities where it suffers weaker interspecific than intraspecific competition (e.g. because high natural-enemy abundance causes high mortality in the superior competitor, or intolerance of a particular temperature–humidity regime reduces its resource-exploitation abilities) and to be driven extinct when rare in localities where it suffers stronger interspecific than intraspecific competition (e.g. because low natural-enemy abundances cause negligible mortality in the superior competitor, or temperature–humidity regimes enhance its resource-exploitation abilities). Spatial variation in the strength of competition thus creates a source–sink structure, with favourable localities where species experience weak interspecific competition and unfavourable localities where they experience strong interspecific competition. Given such variation, dispersal from favourable to unfavourable localities can allow *local* coexistence by preventing competitive exclusion in the unfavourable localities. This leads to a spatial pattern with both species being present in all localities of the landscape (barring any dispersal constraints) as opposed to being restricted to the source localities in the absence of dispersal.

A prerequisite for local coexistence is mutual invasibility. Each species should be able to increase when rare when the other species is at its carrying capacity. Invasion is possible if the dominant eigenvalue of the Jacobian of equation (2.3) is positive when evaluated at the appropriate boundary equilibrium $(x_{11}^*, x_{12}^*, x_{21}^*, x_{22}^*) = (1, 1, 0, 0)$ or $(x_{11}^*, x_{12}^*, x_{21}^*, x_{22}^*) = (0, 0, 1, 1)$. A little algebra shows that invasion can occur if

$$(1 - \alpha_{ij})(1 - \alpha_{il}) - \beta_i(\alpha_{il}^s(1 - \alpha_{ij}) + \alpha_{ij}^s(1 - \alpha_{il})) < 0, \quad (2.4)$$

where $1 - \alpha_{ij}$ is the initial *per capita* growth rate of species i in locality j in the absence of dispersal ($i, j, l = 1, 2; j \neq l$).

The invasion criterion has two terms. The first term is the product of the initial growth rates of species i in the two localities. The second term is the product of the *per capita* emigration rate and the weighted sum of the initial growth rates. Note that, when there is spatial variation in the strength of competition, one locality is a source and the other locality is a sink. Hence, the product of the initial growth rates is always negative. Invasibility therefore depends on the weighted sum of the initial growth rates. (In this model the coexistence equilibrium is stable when it is feasible, and hence invasibility also guarantees long-term coexistence.)

There are two situations under which invasion can occur. First, if the weighted sum of the initial growth rates is positive, invasion is possible as long as the emigration rate β_i is non-zero. Because only one of the initial growth rates is positive, positivity of the weighted sum requires the competitive advantage that a given species experiences in the source to be very strong relative to the competitive disadvantage it suffers in the sink. The key point to appreciate is that when spatial variation in the strength of competition is very strong, there is no dispersal cost to the source. Local coexistence is possible regardless of how high the emigration rate is. By contrast, if the weighted

sum of the initial growth rates is negative, invasion is possible only if the emigration rate is below a critical threshold:

$$\beta_i < \frac{(1 - \alpha_{ij})(1 - \alpha_{il})}{(\alpha_{il}^s(1 - \alpha_{ij}) + \alpha_{ij}^s(1 - \alpha_{il}))}. \quad (2.5)$$

Invasibility now depends on the interaction between spatial variation and dispersal, which in turn depends on the different forms of spatial variation and modes of dispersal.

As noted above, there are three basic modes of dispersal: Type I, Type II and Type III. Categorizing the different forms of spatial variation requires a consideration of the average competitive effect experienced by a given species across the landscape. When spatial variation is high, the competitive advantage in the source is stronger than the competitive disadvantage in the sink. As a result, intraspecific competition will be stronger than interspecific competition when averaged across source and sink localities. By contrast, when spatial variation is low, the competitive advantage in the source is weak compared with the competitive disadvantage in the sink. As a result, interspecific competition will be stronger than intraspecific competition when averaged across source and sink localities. Because each species can experience either of these two situations, the two-species system will exhibit three basic forms of spatial variation (Amarasekare & Nisbet 2001).

The first case occurs when species 1 is the superior competitor in locality 1 ($\alpha_{11} < 1$ and $\alpha_{21} > 1$) and species 2 is the superior competitor in locality 2 ($\alpha_{12} > 1$ and $\alpha_{22} < 1$) but the competitive advantage in the source is greater than the competitive disadvantage in the sink for both species. Hence the average competitive effect across the landscape is such that intraspecific competition is stronger than interspecific competition for both species ($\bar{\alpha}_1 < 1, \bar{\alpha}_2 < 1$). I call this regional niche partitioning.

The second case occurs when species 1 is the superior competitor in locality 1 and species 2 is the superior competitor in locality 2. Species 1 has a strong competitive advantage in the source, which overrides the disadvantage it suffers in the sink, but species 2 has only a weak advantage in the source, which is insufficient to overcome its disadvantage in the sink. Hence the average competitive effect across the landscape is such that species 1 is the superior competitor ($\bar{\alpha}_1 < 1, \bar{\alpha}_2 > 1$). I call this regional dominance.

The third case occurs when species 1 is the superior competitor in locality 1 and species 2 is the superior competitor in locality 2, but the competitive advantage in the source is weaker than the competitive disadvantage in the sink for both species. Hence the average competitive effect is such that interspecific competition is stronger than intraspecific competition for both species ($\bar{\alpha}_1 > 1, \bar{\alpha}_2 > 1$). I call this a regional priority effect.

Given that we have three forms of spatial variation and three modes of dispersal, the interplay between spatial variation and dispersal can lead to nine different outcomes. These are summarized in table 1 and figure 2. There are two key points to note. First, invasibility depends strongly on the form of spatial variation. Invasion success is greatest under regional niche partitioning and least under a regional priority effect. This is because under regional niche partitioning the competitive advantage in the source is greater than the competitive disadvantage in

Table 1. The interplay between spatial variation and the dispersal mode in determining local coexistence under dominance competition.

dispersal mode	spatial variation		
	regional niche partitioning ^a	regional dominance ^b	regional priority effect ^c
Type I ($s = 0$)	$\beta_i > 0$	$\beta_i < \beta_c$	$\beta_i < \beta_c$
Type II ($s < 0$)	$\beta_i > 0$ ($s \rightarrow 0$) $\beta_i < \beta_c$ ($s \ll 0$)	$\beta_i < \beta_c$	$\beta_i < \beta_c$
Type III ($s > 0$)	$\beta_i > 0$	$\beta_i > 0$ ($s > 1$) $\beta_i < \beta_c$ ($0 < s < 1$)	$\beta_i < \beta_c$

^a When dispersal is density independent ($s = 0$), the sum of the initial growth rates is always positive. Noting that $\alpha_{ij} < 1$, $\alpha_{il} > 1 \Rightarrow 1 - \alpha_{ij} > 0$, $1 - \alpha_{il} < 0$, it can be seen that when dispersal is density dependent ($s \neq 0$), the weighted sum of the initial growth rates will be positive only if $|\alpha_{il}^s(1 - \alpha_{ij})| > |\alpha_{ij}^s(1 - \alpha_{il})|$, $j, l = 1, 2$; $j \neq l$. This condition is always satisfied under Type III density-dependent dispersal ($s > 0$). It can be satisfied under Type II density-dependent dispersal ($s < 0$) if $s \rightarrow 0$. When $s \ll 0$, the species that experiences the higher *per capita* competitive effect can invade only if its dispersal rate is below the threshold β_c given by equation (2.5).

^b When dispersal is density independent, the sum of the initial growth rates of the overall inferior competitor is always negative. Hence, invasibility requires that β_i does not exceed the threshold β_c . With Type II density-dependent dispersal, the weighted sum is more negative than under density-independent dispersal, i.e. β_i needs to be smaller than it does under density-independent dispersal. With Type III density-dependent dispersal, the weighted sum can be positive if $s \gg 1$. Thus, invasion is possible regardless of the magnitude of β_i if Type III density-dependent dispersal is sufficiently strong.

^c Because neither species is the superior competitor overall, the weighted sum of the initial growth rates cannot be positive for either species. Mutual invasibility requires the dispersal rates of both species to be below the threshold β_c .

Figure 2. Effect of density-dependent dispersal on local coexistence under the three forms of spatial variation in the strength of dominance competition: (a) regional niche partitioning, (b) regional dominance and (c) regional priority effect. The x-axis denotes the strength of density dependence in dispersal (s) and the y-axis denotes the *per capita* emigration rate of species 2 (β_2), the overall inferior competitor. The solid curve depicts the dispersal threshold (equation (2.5)) that separates the region of the s - β parameter space allowing local coexistence everywhere in the landscape from that which causes regional exclusion of species 2. In general, Type III density-dependent dispersal ($s > 0$) facilitates coexistence, and Type II dispersal ($s < 0$) constrains it, compared with density-independent dispersal ($s = 0$). This effect, however, depends strongly on spatial variation in the strength of competition. Opportunities for coexistence are greatest under regional niche partitioning, and least under a regional priority effect. Parameter values are: $\alpha_{21} = 1.5$, $\alpha_{22} = 0.4$ for (a), $\alpha_{21} = 1.9$, $\alpha_{22} = 0.7$ for (b) and $\alpha_{21} = 1.9$, $\alpha_{22} = 0.9$ for (c).

the sink for both species. It therefore requires quite a high rate of emigration to depress the *per capita* growth rate of the source community. Under a regional priority effect the competitive advantage in the source is weaker than the competitive disadvantage in the sink for both species. Hence even small amounts of emigration can depress the *per capita* growth rate of the source.

The second key point is that invasibility depends crucially on the mode of dispersal. Invasion success is greatest under Type III density-dependent dispersal and least under Type II density-dependent dispersal (table 1 and

figure 2). This is because under Type III density-dependent dispersal the emigration rate is less than linear at low densities, so most individuals leave at high densities as a result of strong competition. Because these are surplus individuals that would not have contributed to local reproduction, this mode of dispersal incurs the least cost to source communities. Under Type II density-dependent dispersal, the emigration rate is disproportionately higher at lower abundances. This means that most individuals leave at low abundances, when competition is weak. Because these are individuals that could have contributed

to local reproduction, this mode of dispersal can make the source's *per capita* growth rate negative at abundances well below the source carrying capacity. It thus incurs the greatest cost to source communities.

This interplay between spatial variance and density-dependent dispersal leads to two important insights. First, when spatial variation in the strength of competition is strong, source communities can withstand quite high rates of emigration. For instance, when spatial variation is such that regional niche partitioning results, local coexistence is possible with no dispersal cost to the source except under very strong Type II density-dependent dispersal (table 1; figure 2a). Second, even when spatial variation is not strong, density-dependent dispersal can reduce dispersal costs by preventing emigration from source communities. For instance, when Type III density-dependent dispersal is sufficiently strong, coexistence can occur with no dispersal costs to sources except when spatial variance is very low (table 1; figure 2).

The above results were obtained for dominance competition, where the outcome of competition depends on the species' competitive abilities. An important question is how dispersal costs to sources are affected when competition changes from dominance to pre-emption. I address this issue next.

(b) *Pre-emptive competition*

Under pre-emptive competition $\alpha_{1j} > 1$, $\alpha_{2j} > 1$ ($j = 1, 2$), i.e. interspecific competition is stronger than intraspecific competition for both species. Hence, the species with the higher initial abundance excludes the other in the absence of dispersal. Levin (1974) has previously shown that local coexistence can occur with global density-independent dispersal, provided that different localities have different initial abundances of competing species. Dispersal incurs a cost to sources such that coexistence is possible only if the emigration rate is below a critical threshold. Too much emigration from the source to the sink homogenizes spatial variation in abundances, and the species with the higher overall abundance excludes the other (Levin 1974). The issue to investigate is what effects spatial variation and density-dependent dispersal have on coexistence.

Pure pre-emptive competition occurs when species have comparable competitive effects on each other (e.g. $\alpha_{1j} = \alpha_{2j}$, $j = 1, 2$) and differ only in their initial abundances. In this case invasibility is significantly more constrained than under dominance competition (figure 3a,c). This difference is a direct result of the way in which spatial variation arises under the two types of competition. Dominance competition involves spatial variation in species' competitive abilities, whereas pre-emptive competition involves spatial variation in species abundances. Thus even small amounts of emigration can disrupt the source-sink structure by equalizing abundances across localities. Because spatial variation in the strength of pre-emptive competition is so easily destroyed, density-dependent dispersal, even when it is Type III, has only a marginal effect in reducing the costs of dispersal to sources.

Pure pre-emptive competition assumes that species are equivalent in their competitive effects. This is somewhat unrealistic given that most species in nature tend to show differences in competitive ability even when the outcome

of competition is contingent on the initial conditions. Incorporation of such species differences leads to the notion of asymmetric pre-emptive competition, where species differ in the *per capita* competitive effects they experience (e.g. $\alpha_{1j} \neq \alpha_{2j}$, $j = 1, 2$). In the absence of dispersal, therefore, the species that suffers a lower *per capita* effect of interspecific competition has a larger domain of attraction for the boundary equilibrium with itself at carrying capacity and the other species extinct. This allows for spatial variation in the relative magnitudes of the competition coefficients (e.g. $\alpha_{1j}, \alpha_{2j} > 1$ but $\bar{\alpha}_1 \neq \bar{\alpha}_2$).

The key result is that, under asymmetric pre-emptive competition, invasion success becomes comparable to that under dominance competition (figure 3a,b). This is because spatial variation is much stronger when species differ in their *per capita* effects on each other. Thus it takes greater amounts of emigration to undermine the viability of source communities. This similarity in invasion success, however, belies the key differences between dominance and pre-emptive competition. Although spatial variation is key to reducing dispersal costs to sources and promoting local coexistence under both dominance and pre-emption, pre-emptive competition is much less sensitive to the dispersal mode than is dominance competition (figure 4). Under dominance competition the transition from Type I (density-independent) to Type II or Type III dispersal is associated with a large change in the parameter space that allows coexistence. Under pre-emptive competition, an equivalent transition induces only a marginal change in the parameter space that allows coexistence, particularly for Type II dispersal (figure 4). Thus, the diversity-reducing effects of high dispersal persist under pre-emptive competition even when dispersal is density dependent, while they can be significantly mitigated under dominance competition if the density-dependent dispersal is Type III rather than Type II.

3. DISCUSSION

Competing species inhabiting patchy or fragmented environments can coexist if dispersal from favourable areas prevents competitive exclusion in unfavourable areas (e.g. Levin 1974; Pacala & Roughgarden 1982; Shmida & Ellner 1984; Amarasekare & Nisbet 2001; Mouquet & Loreau 2002). However, too much emigration from favourable (source) localities can undermine their viability and reduce diversity below that observed in isolated communities. Long-term coexistence, therefore, requires mechanisms that reduce the cost of dispersal to source communities.

Here, I investigate two biological mechanisms that reduce the cost of dispersal to source communities. The first involves increasing spatial variation in the strength of competition such that source communities can withstand high rates of emigration. The second involves reducing the amount of emigration from sources via density-dependent dispersal. A key finding is that, while both mechanisms are important in reducing dispersal costs under dominance competition, spatial variation is much more important than density-dependent dispersal under pre-emptive competition. For species engaged in dominance competition, spatial variation in the strength of competition is greatest under regional niche partitioning. In this

Figure 3. Effect of density-dependent dispersal on local coexistence under (a) regional dominance, (b) asymmetric pre-emption and (c) pure pre-emption. Under both regional dominance and asymmetric pre-emption, high rates of Type II (and to a lesser extent Type I) dispersal lead to the exclusion of species 2, the overall inferior competitor. Under pure pre-emption either species 1 or species 2 could be excluded depending on the relative magnitudes of β_1 and β_2 . In general, coexistence is most restricted under pure pre-emptive competition, an effect that is not ameliorated even under strong Type III density-dependent dispersal. Parameter values are: $\alpha_{11} = 0.2$, $\alpha_{12} = 1.2$, $\alpha_{21} = 1.9$, $\alpha_{22} = 0.7$ for (a), $\alpha_{11} = 1.4$, $\alpha_{12} = 1.7$, $\alpha_{21} = 2.4$, $\alpha_{22} = 1.3$ for (b), $\alpha_{11} = \alpha_{12} = \alpha_{21} = \alpha_{22} = 1.7$ for (c), and $\beta_1 = 0.01$ for all three forms of competition.

Figure 4. Local coexistence in the face of spatial variation in the strength of competition for regional dominance (a–c) and asymmetric pre-emptive competition (d–f). Spatial variation is introduced by allowing α_{21} to vary (the x-axis) while holding all other competition coefficients constant. An increase in the magnitude of α_{21} implies a reduction in competitive ability and a reduction in spatial variation in the strength of competition for species 2, the overall inferior competitor. The solid curve denotes the dispersal threshold that separates the parameter space allowing local coexistence from that which leads to competitive exclusion of species 2. The threshold was calculated using equation (2.5) for dominance competition, and via numerical simulation for pre-emptive competition. Parameter values are: $\alpha_{22} = 0.7$ for (a–c), $\alpha_{11} = 1.1$, $\alpha_{12} = 1.4$, $\alpha_{22} = 1.1$, $\beta_1 = 0.01$ for (d–f), and $s = -0.2$ and $s = 1$, respectively, for Type II and Type III density-dependent dispersal.

case, coexistence is possible even under very high rates of emigration. By contrast, spatial variation is least under a regional priority effect. Now coexistence is possible only for very low emigration rates. For any given form of spatial

variation under dominance competition, Type III density-dependent dispersal incurs the least cost to source communities. It thus increases local and regional diversity above that observed under density-independent dispersal.

Table 2. Patterns of local and regional coexistence under different modes of density-independent and density-dependent dispersal. (Results apply to both dominance and pre-emptive competition, but the effects of dispersal mode are much weaker under pre-emptive competition.)

dispersal mode	dispersal rate		
	zero	low	high
global, density independent	regional coexistence	local coexistence, regional coexistence	regional exclusion of inferior competitor ^a
local, density independent	regional coexistence	↓ local coexistence ^b , ↑ regional coexistence ^b	regional coexistence
global, density dependent Type II	regional coexistence	↓ local coexistence ^b , ↓ regional coexistence ^b	regional exclusion at lower dispersal rate ^b
global, density dependent Type III	regional coexistence	↑ local coexistence ^b , ↑ regional coexistence ^b	regional exclusion at higher dispersal rate ^b

^a The species with inferior competitive ability in dominance competition and lower initial abundance in pre-emptive competition.

^b Compared with global density-independent dispersal.

This is because most individuals leave at high densities owing to strong resource limitation. Because such surplus individuals play no role in local reproduction, emigration has no detrimental effect on the *per capita* growth rates of source communities. With Type III density-dependent dispersal, therefore, coexistence is possible even when spatial variation in the strength of competition is quite low. By contrast, Type II density-dependent dispersal incurs the greatest cost to source communities. It thus reduces local and regional diversity compared with density-independent dispersal. This is because a disproportionately higher fraction of individuals leave at lower densities as a result of mate-finding difficulties or other social phenomena such as reduced predator vigilance. Thus emigration has a strong detrimental effect on the *per capita* growth rates of source communities. With this mode of dispersal coexistence is restricted even when spatial variation in the strength of competition is very high. In general, dispersal costs to sources are much greater, and hence local coexistence much more restrictive, under pre-emptive competition than under dominance competition. This is because spatial variation arises due to differences in initial abundances rather than due to differences in species' competitive abilities. Hence the balance between competition and dispersal is much more easily disrupted under pre-emptive competition. Introducing spatial variation in species' competitive abilities reduces dispersal costs by allowing sources to withstand higher rates of emigration, but density-dependent dispersal has only a marginal effect on dispersal costs.

These results provide for a comparative framework for the roles of competition and dispersal in local and regional coexistence (table 2). Previous studies have suggested that localized density-independent dispersal could prevent excessive emigration and allow initially rare species to build up densities in favourable localities (e.g. Murrell & Law 2003; Snyder & Chesson 2003). While localized density-independent dispersal does reduce dispersal costs to source communities, it also reduces the probability that sinks are rescued from extinction. Thus, localized density-independent dispersal reduces local diversity compared with global density-independent dispersal. Global Type III density-dependent dispersal, however, can rescue sinks from extinction without undermining the viability of

sources. One would therefore expect the greatest enhancement of local and regional diversity under this mode of dispersal. Type II density-dependent dispersal, because it has a stronger detrimental effect on source viability and a weaker rescue effect than density-independent dispersal, imposes the greatest constraints on local and regional diversity. In fact, the four modes of dispersal lead to four distinct patterns of local and regional coexistence (table 2). These predictions about diversity patterns, because they are comparative, have the advantage of allowing for simultaneous tests of multiple hypotheses about the interplay between competition and dispersal. This type of comparative analysis has not previously been conducted for competitive coexistence in the face of density-dependent dispersal. It is particularly informative because the competitive regimes considered include not only pure dominance and pure pre-emption but also intermediate situations, where spatial variation introduces an element of dominance into pre-emptive competition.

The predictions arising from the comparative analysis also identify taxa and communities that are likely to exhibit a particular pattern of diversity. For instance, species that emigrate at higher densities in response to strong competition (e.g. territorial invertebrates, birds and mammals; Birkhead 1977; Wolff 1997; Diffendorfer 1998; Sutherland *et al.* 2002) should experience an enhancement of local diversity in communities that are linked by dispersal compared with ones that are relatively isolated. By contrast, species that emigrate at lower densities in response to social phenomena such as mate-finding difficulties or reduced predator vigilance (e.g. plants, insects and mammals; Lamont *et al.* 1993; Herzig 1995; Wolff 1997; Diffendorfer 1998; Kuussaari *et al.* 1998) should experience a decrease in diversity in communities that are linked by dispersal compared with isolated ones. Similarly, species engaged in pure pre-emptive competition should be more susceptible to reductions in diversity as a result of perturbations that reduce spatial variation or increase emigration compared with species engaged in dominance competition or asymmetric pre-emption.

The above findings have important implications when applying source-sink theory to conservation problems. The scarcity of data, particularly for multi-species systems, necessitates making assumptions about density dependence

in both population growth and dispersal. Knowing when density-independent dispersal provides a reasonable approximation to density-dependent dispersal is therefore crucial in implementing management strategies. In general, density-independent dispersal is not a reasonable approximation for species engaging in dominance competition that have a propensity to leave small populations owing to Allee effects, or large populations owing to strong resource limitation. In the former case, competing species are likely to exhibit Type II density-dependent dispersal, in which case density-independent dispersal overestimates the range of dispersal rates that allows local coexistence. In the latter case, competing species, particularly those that compete for spatially well-defined and defensible resources (e.g. nest sites or breeding territories), are likely to exhibit Type III density-dependent dispersal. In this case density-independent dispersal severely underestimates the range of dispersal rates that allows local coexistence. The same is true for species engaged in asymmetric pre-emptive competition. Thus, density-independent dispersal would yield an overly optimistic view of long-term coexistence when the actual dispersal mode is Type II, and an overly pessimistic view when the actual dispersal mode is Type III. It does, however, provide a reasonable approximation of both Type II and Type III density-dependent dispersal when species engaging in dominance competition exhibit a regional priority effect (figure 2) or when competition involves pure pre-emption (figure 3). Thus, density-independent dispersal can be used to predict long-term coexistence in communities where initial conditions or historical contingencies play a key role in competitive interactions (e.g. plants and sessile marine invertebrates), but not in communities structured by strong dominance hierarchies (e.g. insect parasitoid guilds, territorial invertebrates, birds and mammals).

The model presented here considers a two-species two-locality system, which was done in the interests of analytical tractability. The model can easily be extended to multiple interacting species inhabiting multiple localities. An important future direction would be to use a multi-species model to investigate community properties such as species richness and biomass under different regimes of competition and dispersal. Such an analysis can yield expectations about community patterns that can be contrasted with predictions from the neutral theory of biodiversity (Hubbell 2001) and niche-based but variation-independent mechanisms such as competition-colonization trade-offs. A second future direction involves investigating the role of dispersal strategies in competitive coexistence. Most real organisms exhibit age- or sex-biased dispersal strategies, but such variability is typically ignored in dynamic models of species coexistence. Investigations of how such strategies influence spatial coexistence allow for the development of a conceptual framework that integrates individual-level behavioural phenomena with the community-level dynamic processes that determine diversity patterns.

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