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### **Spatial Heterogeneity, Source-Sink Dynamics, and the Local Coexistence of Competing Species**

HERNANDEZ DE RODRIGUEZ Maria Josefina  
*Universidad Central de Venezuela  
Instituto de Zoología Tropical  
Facultad de Ciencias, Apartado 47058, 1041-A  
Caracas  
VENEZUELA*

# Spatial Heterogeneity, Source-Sink Dynamics, and the Local Coexistence of Competing Species

Priyanga Amarasekare<sup>1,\*</sup> and Roger M. Nisbet<sup>1,2,†</sup>

1. National Center for Ecological Analysis and Synthesis,  
University of California, Santa Barbara, California 93101-5504;  
2. Department of Ecology, Evolution, and Marine Biology,  
University of California, Santa Barbara, California 93106

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**ABSTRACT:** Patch occupancy theory predicts that a trade-off between competition and dispersal should lead to regional coexistence of competing species. Empirical investigations, however, find local coexistence of superior and inferior competitors, an outcome that cannot be explained within the patch occupancy framework because of the decoupling of local and spatial dynamics. We develop two-patch metapopulation models that explicitly consider the interaction between competition and dispersal. We show that a dispersal-competition trade-off can lead to local coexistence provided the inferior competitor is superior at colonizing empty patches as well as immigrating among occupied patches. Immigration from patches that the superior competitor cannot colonize rescues the inferior competitor from extinction in patches that both species colonize. Too much immigration, however, can be detrimental to coexistence. When competitive asymmetry between species is high, local coexistence is possible only if the dispersal rate of the inferior competitor occurs below a critical threshold. If competing species have comparable colonization abilities and the environment is otherwise spatially homogeneous, a superior ability to immigrate among occupied patches cannot prevent exclusion of the inferior competitor. If, however, biotic or abiotic factors create spatial heterogeneity in competitive rankings across the landscape, local coexistence can occur even in the absence of a dispersal-competition trade-off. In fact, coexistence requires that the dispersal rate of the overall inferior competitor not exceed a critical threshold. Explicit consideration of how dispersal modifies local competitive interactions shifts the focus from the patch occupancy approach with its emphasis on extinction-colonization dynamics to the realm of source-sink dynamics. The key to coexistence in this framework is spatial variance in fitness. Unlike in the patch occupancy framework, high rates of dispersal

can undermine coexistence, and hence diversity, by reducing spatial variance in fitness.

*Keywords:* competition, coexistence, spatial heterogeneity, source-sink dynamics, immigration, dispersal-competition trade-off.

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The issue of how species coexist in patchy environments is central to both basic and applied ecology. When competition for resources is asymmetric, a life-history trade-off between competitive and dispersal abilities can lead to coexistence in a patchy environment (Skellam 1951). This idea has been formalized in the patch occupancy metapopulation framework (Levins 1969, 1970). The patch occupancy approach assumes that local competitive interactions occur on a much faster time scale relative to extinction-colonization dynamics (Cohen 1970; Levins and Culver 1971; Slatkin 1974; Hastings 1980; Nee and May 1992; Tilman et al. 1994). For instance, when patches are colonized by both superior and inferior competitors, there is rapid exclusion of the inferior species. This restricts the inferior competitor to patches that the superior competitor cannot colonize. The predicted outcome is regional coexistence, with the two species occupying mutually exclusive subsets of patches in the metapopulation.

Empirical studies of dispersal-competition trade-offs, however, reveal a pattern that is at odds with the theoretical prediction of regional coexistence. For instance, in Lei and Hanski's (1998) study of two parasitoid species that attack the butterfly *Melitaea cinxia*, the superior competitor (*Cotesia melitaeorum*) was absent from some host populations, but the superior disperser (*Hyposoter horticola*) was present in all populations sampled. Another host-parasitoid system consisting of the harlequin bug (*Murgantia histrionica*) and its two egg parasitoids (*Trissolcus murgantiae* and *Ooencyrtus johnsonii*) also shows a similar pattern with local coexistence in some patches and the superior competitor absent in other patches (Amarasekare 2000a, 2000b).

The mismatch between patch occupancy theory and data may arise from the separation of time scales inherent in the patch occupancy framework. The assumption that local dynamics occur on a faster time scale relative to

\* Present address: Department of Ecology and Evolution, University of Chicago, Chicago, Illinois 60637-1573; e-mail: amarasek@uchicago.edu.

† E-mail: nisbet@lifesci.ucsb.edu.

spatial dynamics restricts the role of dispersal to colonizing empty, or locally extinct, patches. In the absence of any immigration among occupied patches, dispersal cannot influence local competitive interactions. This decoupling of local and spatial dynamics eliminates any possibility of local coexistence. Empirical observations of local coexistence, however, suggest that dispersal may be sufficiently rapid to counteract competitive exclusion. In fact, the two parasitoid species that attack *M. cinxia* appear to exhibit a dispersal-competition trade-off most convincingly at the scale of larval groups within local populations (Lei and Hanski 1998). Movement between such larval groups is likely to occur on a time scale comparable to local competitive interactions. The harlequin bug and its two parasitoids move among populations on a per-generation basis (Amarasekare 2000a, 2000b). Harrison et al.'s (1995) study of the insect herbivores of ragwort (*Senecio jacobea*) also demonstrated rapid dispersal of the cinnabar moth (*Tyria jacobeeae*) and other herbivores (*Botanophila seneciella* and *Contarina jacobeeae*) relative to the time scale of local competition.

These data present a puzzle for theory. Can a dispersal-competition trade-off lead to local coexistence when competition and dispersal operate on comparable time scales? Answering this question necessitates a shift in focus from extinction-colonization dynamics to source-sink dynamics. For instance, the issue now is not whether a superior ability to colonize empty patches prevents regional exclusion but whether a superior ability to immigrate among occupied patches prevents local exclusion.

### The Model

We use a two-patch model with Lotka-Volterra competitive dynamics within patches and emigration and immigration between patches. The dynamics are given by the following system of equations:

$$\begin{aligned} \frac{dX_i}{dt} &= r_x X_i \left( 1 - \frac{X_i}{K_{x,i}} - \phi_{x,i} \frac{Y_i}{K_{x,i}} \right) + d_x (X_j - X_i), \\ \frac{dY_i}{dt} &= r_y Y_i \left( 1 - \frac{Y_i}{K_{y,i}} - \phi_{y,i} \frac{X_i}{K_{y,i}} \right) + d_y (Y_j - Y_i), \end{aligned} \quad (1)$$

$i, j = 1, 2, \quad i \neq j,$

where  $X_i$  and  $Y_i$  are the abundances of each species in patch  $i$ ;  $\phi_{x,i}$  and  $\phi_{y,i}$  are the competition coefficients, and  $K_{x,i}$  and  $K_{y,i}$  are the carrying capacities for species 1 and 2 in patch  $i$ ;  $r_x$  and  $r_y$  are the per capita growth rates, and  $d_x$  and  $d_y$  are the per capita emigration rates of species 1 and 2, respectively.

We nondimensionalize equation (1) in order to describe the system in terms of a minimal set of parameters (Murray 1993). The following transformations,

$$\begin{aligned} x_i &= \frac{X_i}{K_{x,i}}, & y_i &= \frac{Y_i}{K_{y,i}}, & \tau &= r_x t, \\ a_{x,i} &= \phi_{x,i} \frac{K_{y,i}}{K_{x,i}}, & a_{y,i} &= \phi_{y,i} \frac{K_{x,i}}{K_{y,i}}, \\ k_x &= \frac{K_{x,j}}{K_{x,i}}, & k_y &= \frac{K_{y,j}}{K_{y,i}}, & \rho &= \frac{r_y}{r_x}, \\ \beta_x &= \frac{d_x}{r_x}, & \beta_y &= \frac{d_y}{r_y}, \end{aligned}$$

yield the nondimensional system

$$\begin{aligned} \frac{dx_i}{d\tau} &= x_i (1 - x_i - a_{x,i} y_i) + \beta_x (k_x x_j - x_i), \\ \frac{dy_i}{d\tau} &= \rho y_i (1 - y_i - a_{y,i} x_i) + \rho \beta_y (k_y y_j - y_i), \end{aligned} \quad (2)$$

$i, j = 1, 2, \quad i \neq j.$

The quantities  $x_i$  and  $y_i$  represent the densities of species 1 and 2 in the  $i$ th patch scaled by their respective carrying capacities, and  $a_{x,i}$  and  $a_{y,i}$  represent the per capita effect of species 2 on species 1 (and vice versa) scaled by the ratio of respective carrying capacities. Quantities  $k_x$  and  $k_y$  represent the ratio of carrying capacities in the two patches for species 1 and 2, respectively,  $\beta_x$  and  $\beta_y$  are the species-specific emigration rates scaled by their respective growth rates,  $\rho$  is the ratio of the per capita growth rates of the two species, and  $\tau$  is a time metric that is a composite of  $t$  and  $r_x$ , the growth rate of species 1. The dispersal scheme is such that individuals leaving one patch end up in the other patch, with no dispersal mortality in transit. This is equivalent to the island model of dispersal.

We are interested in a life-history trade-off between competitive and dispersal abilities. We describe such a trade-off in terms of competition coefficients (the per capita effect that a given species has on the other) and per capita dispersal rates. We assume the species and patches to be otherwise similar (i.e.,  $\rho = 1$ ,  $k_x = k_y = 1$ ,  $K_{x,i} = K_{y,i}$ ), which means that  $a_{x,i} = \phi_{x,i}$  and  $a_{y,i} = \phi_{y,i}$ . This leads to the following simplified two-patch system:

$$\begin{aligned} \frac{dx_i}{d\tau} &= x_i (1 - x_i - \phi_{x,i} y_i) + \beta_x (x_j - x_i), \\ \frac{dy_i}{d\tau} &= y_i (1 - y_i - \phi_{y,i} x_i) + \beta_y (y_j - y_i), \end{aligned} \quad (3)$$

$i, j = 1, 2, \quad i \neq j.$

In the absence of dispersal ( $\beta_x = \beta_y = 0$ ), competitive interactions within each patch lead to three basic outcomes (Volterra 1926; Lotka 1932): coexistence via niche partitioning ( $\phi_{x,i} < 1$ ,  $\phi_{y,i} < 1$ ), exclusion via priority effects ( $\phi_{x,i} > 1$ ,  $\phi_{y,i} > 1$ ), and exclusion via competitive asymmetry ( $\phi_{x,i} < 1$ ,  $\phi_{y,i} > 1$ , or vice versa). We focus exclusively on competitive asymmetry because this is the situation for which a life-history trade-off is most relevant.

When patches are linked by dispersal, spatial heterogeneity becomes an important consideration (Murdoch et al. 1992; Nisbet et al. 1993). We define spatial heterogeneity in terms of factors that affect the patch-specific competitive abilities of the two species  $\phi_{x,i}$  and  $\phi_{y,i}$ . For instance, when  $\phi_{x,i} = \phi_{x,j} < 1$  and  $\phi_{y,i} = \phi_{y,j} > 1$  (or vice versa), the competitive environment is spatially homogeneous and one species is consistently superior within all patches of the landscape. When  $\phi_{x,i} \neq \phi_{x,j}$  and  $\phi_{y,i} \neq \phi_{y,j}$  (e.g.,  $\phi_{x,i} < 1$ ,  $\phi_{x,j} > 1$ ,  $\phi_{y,i} > 1$ ,  $\phi_{y,j} < 1$ , or vice versa), competitive rankings vary over space such that the species that is the superior competitor in some parts of the landscape is the inferior competitor in the other parts of the landscape. This type of spatial heterogeneity can arise due to intrinsic factors such as genetic variability or phenotypic plasticity in competitive ability (Huel and Huel 1996; Morrison and Molofsky 1999). It can also arise via extrinsic factors that affect the species differently. Examples include spatial variation in microclimatic factors, availability of a second, critical resource (Tilman and Pacala 1993), disturbances (Connell 1978), and keystone predation (Paine 1966).

We investigate the conditions under which a trade-off between competition and dispersal can lead to local coexistence of superior and inferior competitors. We focus on three specific situations, each motivated by empirical studies of dispersal-competition trade-offs.

#### *Local Coexistence When the Inferior Competitor Has a Refuge*

The first situation we analyze is motivated by Lei and Hanski's (1998) study of the parasitoids of *Melitaea cinxia*. Their data show a spatial pattern of local coexistence versus patches occupied only by the superior disperser (inferior competitor). Can local coexistence result from a dispersal-competition trade-off?

We assume that the superior competitor does not move among occupied patches and is restricted to patch 1. Patch 2 is colonized solely by the inferior competitor and serves as a refuge from competition for that species. The inferior competitor also moves between the two patches at a rate  $\beta_y$ . This scenario leads to the following version of the model:

$$\begin{aligned}\frac{dx_1}{d\tau} &= x_1(1 - x_1 - \phi_{x,1} y_1), \\ \frac{dy_1}{d\tau} &= y_1(1 - y_1 - \phi_{y,1} x_1) + \beta_y(y_2 - y_1), \\ \frac{dy_2}{d\tau} &= y_2(1 - y_2) + \beta_y(y_1 - y_2),\end{aligned}\quad (4)$$

with  $x$  denoting the abundance of the superior, immobile competitor and  $y$  denoting that of the inferior, mobile competitor. Note that  $\phi_{x,1} < 1$  and  $\phi_{y,1} > 1$ .

In the absence of dispersal (i.e.,  $\beta_y = 0$ ), patch 1 is a sink for the inferior competitor. This is because the superior competitor increases in abundance at the expense of the inferior competitor, preventing the latter from maintaining a positive growth rate.

Equation (4) yields four feasible equilibria: first, both species extinct ( $x_1^*, y_1^*, y_2^*) = (0, 0, 0)$ ; second, superior competitor at carrying capacity (1, 0, 0); third, inferior competitor at carrying capacity (0, 1, 1); and finally, the coexistence equilibrium.

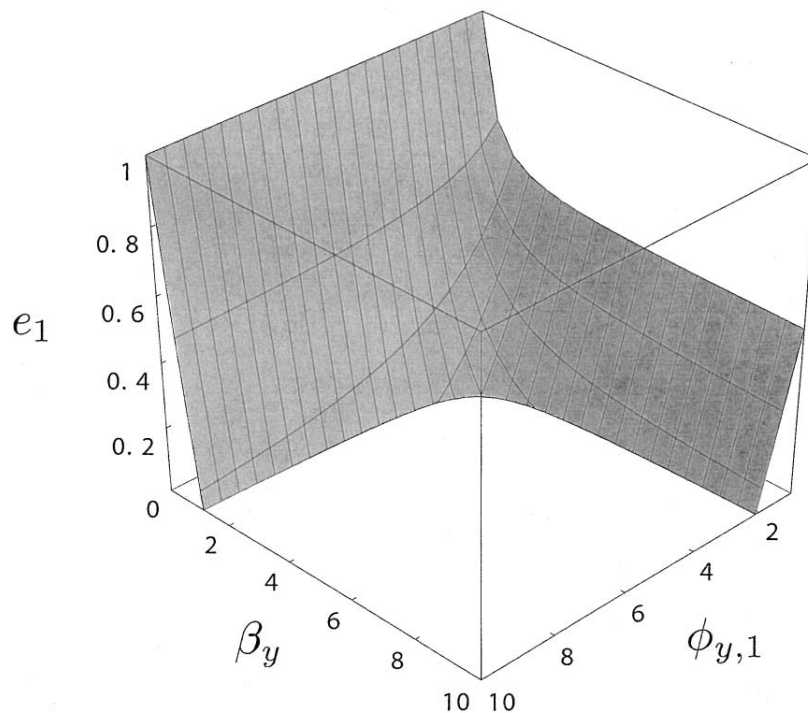
Local coexistence of inferior and superior competitors requires that the inferior competitor be able to invade a patch when the superior competitor is at carrying capacity and that the coexistence equilibrium be stable to small perturbations in the abundance of both species.

We first investigate whether the inferior competitor can invade when rare in both patches. In appendix A, we show that invasion will succeed if

$$(1 - \phi_{y,1}) - \beta_y(2 - \phi_{y,1}) < 0. \quad (5)$$

The inferior competitor can invade when rare under two situations: if  $\phi_{y,1} < 2$ , invasion can occur as long as  $\beta_y > 0$ , and if  $\phi_{y,1} > 2$ , then invasion is possible only as long as  $\beta_y < (1 - \phi_{y,1}) / (2 - \phi_{y,1})$  (fig. 1). Stability analyses (app. A) show that the coexistence equilibrium is stable when it exists.

The key result is that stable local coexistence of inferior and superior competitors can occur, but is not guaranteed, as long as there are patches in the landscape that are colonized only by the inferior competitor. Immigration from such refuge populations rescues the inferior competitor from exclusion in patches that are colonized by both species. Coexistence in the face of competitive asymmetry depends on both dispersal rates and degree of asymmetry. When competitive asymmetry in patch 1 is low (e.g.,  $\phi_{x,1} < 1$  and  $1 < \phi_{y,1} < 2$ ), coexistence occurs provided the inferior competitor has a nonzero dispersal rate. When competitive asymmetry is high (e.g.,  $\phi_{x,1} < 1$  and  $\phi_{y,1} > 2$ ), coexistence occurs only as long as the dispersal rate is below a critical threshold. When the dispersal rate exceeds



**Figure 1:** Conditions for invasion by the inferior competitor when it has a refuge (eq. [4]). The eigenvalue  $e_1 = [b + (b^2 - 4c)^{1/2}]/2$  ( $b$  and  $c$  as defined in app. A) is plotted as a function of the competition coefficient ( $\phi_{y,1}$ ) and dispersal rate ( $\beta_y$ ) of the inferior competitor. The surface depicts the portion of the parameter space where  $e_1$  is positive (i.e., the inferior competitor can invade when rare). When  $\phi_{y,1} < 2$ , the invasion can occur as long as  $\beta_y > 0$ . When  $\phi_{y,1} > 2$ , invasion is possible only as long as  $\beta_y < [(1 - \phi_{y,1})/(2 - \phi_{y,1})]$ . Note that  $\beta_y$  is the ratio of per capita emigration to local growth (i.e.,  $\beta_y > 1$  means that rate of emigration from the patch exceeds the local growth rate).

this threshold, net emigration from source to sink populations causes the source population growth rate to be negative, and the inferior competitor is excluded from the entire metapopulation.

#### *Local Coexistence When the Inferior Competitor Has No Refuge*

In Harrison et al.'s (1995) study of the herbivores of ragwort, no patches were found that were empty of the superior competitor. This suggests that the superior competitor has a colonization ability comparable to that of the inferior competitors. Our full two-patch model (eq. [3]) describes the situation where no refuges exist for the inferior competitor and both the superior and inferior competitors are able to move among occupied patches. Now the issue becomes more challenging: Can a superior ability to immigrate among occupied patches allow an inferior competitor to coexist locally with a superior competitor?

We first investigate whether the inferior competitor can invade when the superior competitor is at carrying capacity

in both patches (i.e.,  $x_1^* = x_2^* = 1$ ). In appendix B, we show that successful invasion requires  $I < 0$ , where

$$I = (1 - \phi_{y,1})(1 - \phi_{y,2}) - \beta_y[(1 - \phi_{y,1}) + (1 - \phi_{y,2})]. \quad (6)$$

Note that the quantities  $1 - \phi_{y,1}$  and  $1 - \phi_{y,2}$  are the initial growth rates of the inferior competitor in patches 1 and 2 in the absence of dispersal (Pacala and Roughgarden 1982). Thus, the first term of  $I$  represents the product of the initial growth rates in the two patches and the second term their sum. The signs of these two quantities determine whether or not invasion can occur. For example, if the sum of the initial growth rates is positive and the product negative,  $I < 0$  as long as  $\beta_y > 0$ . If both sum and product are negative, then whether or not  $I < 0$  depends on the actual magnitude of  $\beta_y$ .

We first consider the situation where the competitive environment is spatially homogeneous. When  $\phi_{x,i} = \phi_{x,j} = \phi_x < 1$  and  $\phi_{y,i} = \phi_{y,j} = \phi_y > 1$ , species 1 is the superior competitor across the metapopulation. Then the

sum of the initial growth rates of the inferior competitor in the two patches is negative ( $2 - 2\phi_y < 0$ ) and the product positive ( $[1 - \phi_y]^2 > 0$ ), which means that  $I = (1 - \phi_y)^2 - \beta_y(2 - 2\phi_y) > 0$ . The equilibrium with the superior competitor at carrying capacity cannot be invaded by the inferior competitor. Invasion fails because the superior competitor increases at the expense of the inferior competitor in both patches, causing the initial growth rate of the latter to be negative across the metapopulation.

The key result is that when the competitive environment is spatially homogeneous (i.e., one species is consistently the superior competitor), and when both species have comparable colonization abilities such that local refuges for the inferior competitor do not exist, a superior ability to migrate among occupied patches is not sufficient to prevent exclusion of the inferior competitor.

#### *The Role of Spatial Heterogeneity*

The above analysis shows that invasion fails in a competitively homogeneous environment because the inferior competitor has a negative initial growth rate in both patches. This suggests that invasion may succeed if the inferior competitor can maintain a positive initial growth rate in at least one patch. Mathematically, this means that the product of the initial growth rates in the two patches should be negative (i.e.,  $[1 - \phi_{y,1}][1 - \phi_{y,2}] < 0$ ). Since competition is assumed to be asymmetric (i.e.,  $\phi_{x,i} < 1$  and  $\phi_{y,i} > 1$  or vice versa;  $i = 1, 2$ ), the only way this can happen is if there is spatial heterogeneity in competitive rankings such that the superior competitor suffers a disadvantage in at least some parts of the landscape (e.g.,  $\phi_{x,i} < 1$ ,  $\phi_{x,j} > 1$ ;  $i, j = 1, 2$ ;  $i \neq j$ ).

That inferior competitors can flourish in areas disadvantageous to superior competitors (e.g., keystone predation) is well known (Harper 1961; Paine 1966; Connell 1978; Lubchenco 1978). The novel issue we explore is whether dispersal from such areas allows the inferior competitor to persist in areas where the superior competitor itself flourishes. Because competitive rankings vary across space, the average competitive ability of each species becomes an important determinant of invasion and coexistence.

When the competitive environment is spatially heterogeneous, invasion can occur under three biologically distinct, and significant, circumstances. The first situation arises when competition is asymmetric at the scale of a local population but spatial averages of competition coefficients are such that niche partitioning occurs at the scale of the metapopulation. For instance, let  $\phi_{x,1} < 1$ ,  $\phi_{y,1} > 1$  in patch 1 and  $\phi_{x,2} > 1$ ,  $\phi_{y,2} < 1$  in patch 2. Let the average competitive coefficients be  $\bar{\phi}_x = [(\phi_{x,1} + \phi_{x,2})/2] < 1$  and  $\bar{\phi}_y = [(\phi_{y,1} + \phi_{y,2})/2] < 1$ . Then, species 1

is the superior competitor in patch 1 and species 2 is the superior competitor in patch 2, but neither species is superior in the sense that interspecific competition is weaker than intraspecific competition when averaged across the metapopulation. At the metapopulation scale, the two species meet the criteria for classical niche partitioning (Volterra 1926; Lotka 1932).

Under global niche partitioning, the sum of the initial growth rates is positive and the product negative, which means that  $I < 0$  as long as  $\beta_y > 0$ . The equilibrium with the locally superior competitor at carrying capacity (i.e.,  $x_1^*, x_2^*, y_1^*, y_2^* = 1, 1, 0, 0$  or  $0, 0, 1, 1$ ) can be invaded by the locally inferior competitor (species 2 or 1, respectively) as long as it has a nonzero dispersal rate ( $\beta_y > 0$  or  $\beta_x > 0$ , respectively).

The important point is that as long as competition is asymmetric locally and niche partitioning occurs globally, coexistence can occur even in the absence of a dispersal-competition trade-off. The patch in which the species has local competitive superiority acts as a source of immigrants for the patch in which it is locally inferior. Thus, source-sink dynamics allow each species to maintain small sink populations in areas of the landscape where it suffers a competitive disadvantage.

The second situation arises when competition is asymmetric both locally and globally. For example, species 1 is the superior competitor in patch 1 ( $\phi_{x,1} < 1$ ,  $\phi_{y,1} > 1$ ) and species 2 is the superior competitor in patch 2 ( $\phi_{x,2} > 1$ ,  $\phi_{y,2} < 1$ ), but now species 1 is the superior competitor when averaged across the metapopulation ( $\bar{\phi}_x < 1$  and  $\bar{\phi}_y > 1$ ).

The species that is the overall superior competitor can invade when rare as long as it has a nonzero dispersal rate (i.e.,  $\beta_x > 0$ ). The important issue is whether the overall inferior competitor can invade when rare. Global asymmetric competition means both the sum and the product of initial growth rates are negative. Invasibility now depends on the actual magnitude of  $\beta_y$ . Solving equation (6) for  $\beta_y$  shows that the inferior competitor can invade only if its dispersal rate is below a critical threshold:

$$\beta_y < \beta_{\text{critical}} = \frac{(1 - \phi_{y,1})(1 - \phi_{y,2})}{(1 - \phi_{y,1}) + (1 - \phi_{y,2})}.$$

When competition is asymmetric both locally and globally, local coexistence does not involve a dispersal-competition trade-off. In fact, local coexistence requires that the dispersal rate of the overall inferior competitor not exceed a critical threshold. Once the dispersal rate exceeds this threshold, the overall inferior competitor cannot increase when rare even when it is competitively superior in some parts of the landscape.

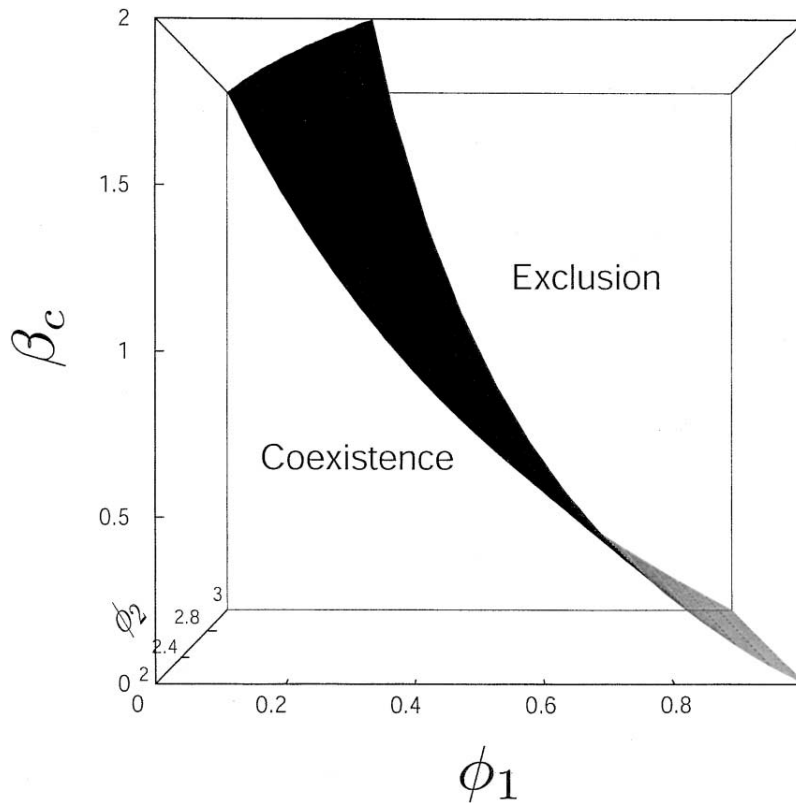
The critical dispersal threshold depends on spatial het-

erogeneity in competitive ability (fig. 2). The stronger the local competitive advantage to the overall inferior competitor in areas where the overall superior competitor is disadvantaged (e.g.,  $\phi_{y,i} > 1$ ,  $\phi_{y,j} \ll 1 \Rightarrow \bar{\phi}_y \rightarrow 1$ ), the larger the critical dispersal threshold and greater the possibility of local coexistence. If spatial heterogeneity in the environment is insufficient to create a strong local competitive advantage to the inferior competitor (e.g.,  $\phi_{y,i} > 1$ ,  $\phi_{y,j} \rightarrow 1 \Rightarrow \bar{\phi}_y > 1$ ), then the threshold becomes correspondingly small and conditions for coexistence restrictive.

The key to coexistence, therefore, is spatial heterogeneity in competitive ability. There should be sufficient spatial variation in the biotic or abiotic environment that the overall superior competitor suffers a disadvantage in some parts of the landscape. Immigration from populations where the overall inferior competitor has a local advantage

prevents its exclusion in areas where it has a local disadvantage. In contrast to global niche partitioning, however, coexistence is possible only as long as the dispersal rate of the overall inferior competitor is below a critical threshold. This is because individuals are moving from regions of the landscape where they are competitively superior and enjoy a positive growth rate (source populations) to regions where they are competitively inferior and suffer a negative growth rate (sink populations). If the net rate of emigration is sufficiently high relative to local reproduction that the growth rate of the source population becomes negative, the species loses its local competitive advantage and is excluded from the entire metapopulation.

So far, we have derived conditions for local coexistence for two situations: global niche partitioning and global competitive asymmetry. The third situation arises when



**Figure 2:** The relationship between spatial variance in competitive ability and the critical dispersal threshold ( $\beta_c$ ) when competition involves global asymmetry. The quantities  $\phi_1$  and  $\phi_2$  are the competition coefficients of the overall inferior competitor in patches 1 and 2, respectively. The overall inferior competitor enjoys a competitive advantage in patch 1 ( $\phi_1 < 1$ ) and suffers a competitive disadvantage in patch 2 ( $\phi_2 > 1$ ). Global asymmetry means that  $\phi_1 + \phi_2 > 2$  (or  $\bar{\phi} > 1$ ) for the inferior competitor. For any given value of  $\phi_2$ ,  $\beta_c$  reaches a maximum when  $\phi_1 \rightarrow 0$  ( $\lim_{\phi_1 \rightarrow 0} \beta_c = [(1 - \phi_2)/(2 - \phi_2)]$ );  $\beta_c > 0 \Rightarrow \phi_2 > 2$  and a minimum when  $\phi_1 \rightarrow 1$  ( $\lim_{\phi_1 \rightarrow 1} \beta_c = 0$ ). The larger  $\phi_2$  is the smaller the maximum value of  $\beta_c$  and steeper the decline of  $\beta_c$  with  $\phi_1$ . In biological terms, this means that for any level of the competitive disadvantage suffered by the species in one patch, the stronger its local competitive advantage in the other patch, the higher the critical dispersal threshold, and hence, the possibility of coexistence. However, if the competitive disadvantage suffered by the species in one patch is large relative to its competitive advantage in the other patch, the dispersal threshold is lowered and conditions for coexistence become restrictive.

competition is asymmetric locally but a priority effect occurs globally (i.e., species 1 is the superior competitor in patch 1 [ $\phi_{x,1} < 1$ ,  $\phi_{y,1} > 1$ ], and species 2 is the superior competitor in patch 2 [ $\phi_{x,2} > 1$ ,  $\phi_{y,2} < 1$ ]), but interspecific competition is stronger than intraspecific competition when averaged across the metapopulation ( $\bar{\phi}_x > 1$  and  $\bar{\phi}_y > 1$ ). Now each species has a critical dispersal threshold above which coexistence cannot occur:

$$\beta < \beta_{\text{critical}} = \frac{(1 - \phi_{x,1})(1 - \phi_{y,2})}{(1 - \phi_{x,1}) + (1 - \phi_{y,2})}.$$

As with global asymmetry, the magnitude of the dispersal threshold depends on spatial heterogeneity in competitive ability (fig. 3). If the two species differ in the degree of local asymmetry but have the same competitive ability on average (e.g.,  $\phi_{x,1} \neq \phi_{y,2}$ ,  $\phi_{x,2} \neq \phi_{y,1}$ ;  $\bar{\phi}_x = \bar{\phi}_y > 1$ ), then local coexistence is determined by the dispersal ability of the species that experiences lower spatial heterogeneity and hence the lower dispersal threshold (fig. 3). If the species are sufficiently different that their average competition coefficients are unequal (e.g.,  $\bar{\phi}_x > 1$ ,  $\bar{\phi}_y > 1$ ;  $\bar{\phi}_x < \bar{\phi}_y$ ), then local coexistence is determined by the dispersal ability of the species with the higher average competition coefficient (lower competitive ability). For instance, if  $\bar{\phi}_x < \bar{\phi}_y$ , then  $\beta_{y,\text{critical}} < \beta_{x,\text{critical}}$ , and the dispersal threshold for species 2 determines the transition from coexistence to exclusion.

The key to coexistence, again, is spatial heterogeneity in competitive ability. When heterogeneity is low ( $\bar{\phi} > 1$ ), the region of the parameter space where each species can invade when rare is small (fig. 3B); when heterogeneity is high ( $\bar{\phi} \rightarrow 1$ ), this region is correspondingly larger (fig. 3C). An important difference between global asymmetry and a global priority effect is that while coexistence is determined by the dispersal ability of the overall inferior competitor in the former, dispersal abilities of both competing species determine conditions for coexistence in the latter. If both species have dispersal rates that exceed their respective thresholds, neither species can invade when rare and coexistence is impossible either locally or regionally.

These results lead to a set of comparative predictions (table 1). The three situations under which local coexistence can occur in a competitively heterogeneous environment can be distinguished by their response to the transition from low to high dispersal. In the absence of dispersal, all three situations exhibit global coexistence with each species flourishing in areas where it has a local competitive advantage. Under low dispersal, source-sink dynamics ensure local coexistence in all three cases. High dispersal, however, elicits qualitatively different dynamical responses. For instance, when competition involves global

niche partitioning, local coexistence prevails. When competition involves global asymmetry, global exclusion of the overall inferior competitor results. When competition involves a global priority effect, the outcome is global exclusion of the species with the lower dispersal threshold.

Another key distinction between the three situations is the relative sensitivity of competing species to a perturbation that increases dispersal between patches. Neither species is sensitive to such a perturbation under global niche partitioning, only the inferior competitor is sensitive under global asymmetry, and both species are sensitive under a global priority effect. In other words, there are no constraints on the dispersal abilities when global niche partitioning occurs, while constraints exist on one or both species when global asymmetry or priority effects occur. This suggests that species that experience local competitive asymmetry but partition niches globally have the highest likelihood of coexistence, while those that experience global priority effects have the least.

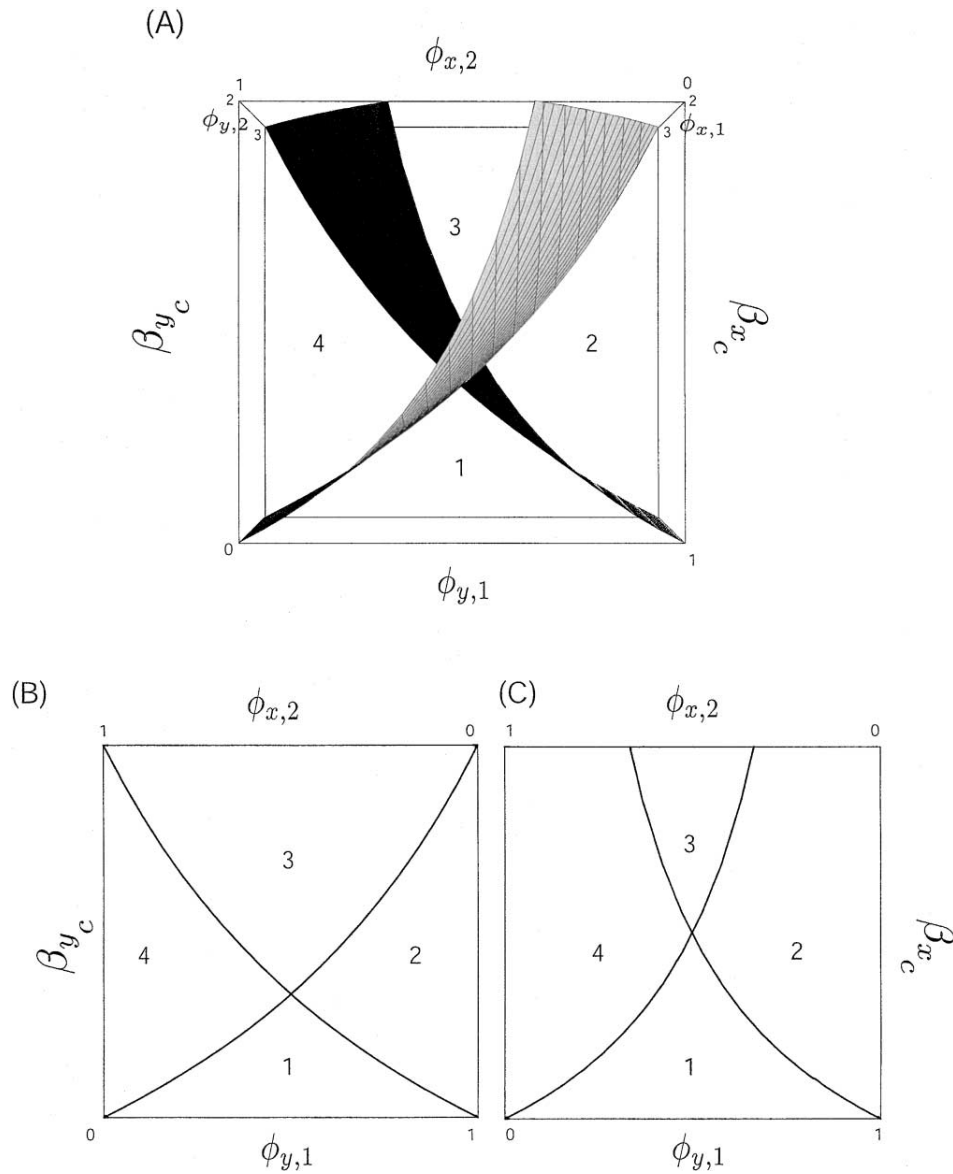
## Discussion

This study was motivated by empirical investigations of dispersal-competition trade-offs in insect systems. Observations of local coexistence in these studies are at odds with the prediction of regional coexistence from patch occupancy theory. These observations suggest that dispersal may be sufficiently rapid to counteract competitive exclusion, a possibility that cannot be addressed in the patch occupancy framework because of the decoupling of local and spatial dynamics. We developed models that explicitly consider local dynamics in which spatial processes of emigration and immigration operate on the same time scale as local competitive interactions. Our objective was to determine the conditions under which the interaction between competition and dispersal could lead to local coexistence.

Our findings provide potential explanations for the patterns seen in several insect systems. For instance, in Lei and Hanski's (1998) study of the parasitoids of *Melitaea cinxia*, the inferior competitor is found in patches that are not colonized by the superior competitor, suggesting that it has a superior colonization ability. The observed pattern of local coexistence in some patches versus the inferior competitor by itself in other patches could arise if immigration from the latter prevents competitive exclusion in the former.

In contrast to the butterfly system, however, the two parasitoids of the harlequin bug have comparable colonization abilities (Amarasekare 2000a). In such a situation, immigration could counteract competitive exclusion if there is spatial variance in competitive rankings. However, one parasitoid species is consistently the superior com-





**Figure 3:** The relationship between spatial variance in competitive ability and the critical dispersal threshold when competition involves a global priority effect. *A*, The three-dimensional parameter space with the critical dispersal threshold for each species as a function of its competitive coefficients in the two patches. The black surface depicts this relationship for species 2 and the gray surface for species 1. Note that the X-axis goes from 1 to 0 for species 1. *B*, *C*, Two-dimensional slices of the parameter space for  $\phi_{x,1} = \phi_{y,2} = 3$  and  $\phi_{x,1} = \phi_{y,2} = 2$ , respectively. Region 1 represents the portion of the parameter space where both species can invade when the other species is at carrying capacity. The long-term outcome is stable coexistence. Region 2 represents the parameter space where species 2 cannot invade when rare, and region 4, where species 1 cannot invade when rare. The long-term outcome is exclusion of species 2 and 1, respectively. Region 3 represents the parameter space where neither species can invade when rare. The long-term outcome is global exclusion of the species that exhibits the lower dispersal threshold. When spatial heterogeneity is low (i.e., local competitive advantage enjoyed by a species in one patch is small relative to the disadvantage it suffers in the other patch), the region where both species can invade is small and the region where neither species can invade is large (*B*). When spatial heterogeneity is high, the region of mutual invasibility increases relative to the region of mutual noninvasibility (*C*).

**Table 1:** Comparative predictions for invasion and local coexistence under different regimes of spatial heterogeneity

Competitive environment	Isolation	Low dispersal	High dispersal
Local asymmetry, global niche partitioning	Locally inferior competitor cannot invade Global coexistence $\beta_x, \beta_y = 0$	Both species can invade Local coexistence $\beta_x, \beta_y > 0$	Both species can invade Local coexistence $\beta_x, \beta_y > 0$
Local asymmetry, global asymmetry	Locally inferior competitor cannot invade Global coexistence $\beta_x, \beta_y = 0$	Both species can invade Local coexistence $0 < \beta_y < \beta_{critical}, \beta_x > 0$	Overall inferior competitor cannot invade <sup>a</sup> Global exclusion of inferior competitor $\beta_y > \beta_{critical}, \beta_x > 0$
Local asymmetry, global priority effect	Locally inferior competitor cannot invade Global coexistence $\beta_x, \beta_y = 0$	Both species can invade Local coexistence $0 < \beta_x, \beta_y < \beta_{critical}$	Neither species can invade <sup>b</sup> Global exclusion of species with lower dispersal threshold $\beta_x, \beta_y > \beta_{critical}$

<sup>a</sup> Transition from low to high dispersal affects inferior competitor only.

<sup>b</sup> Transition from low to high dispersal affects both species.

petitor all across the landscape, and experimental manipulations of dispersal rates have no effect on patterns of local coexistence (Amarasekare 2000a, 2000b). This study exemplifies a situation where lack of spatial variance in competitive ability precludes coexistence via source-sink dynamics.

Harrison et al.'s (1995) study of the herbivores of ragwort (*Senecio jacobea*) illustrates how rapid dispersal and spatial variance in competitive ability may counteract local exclusion. At the authors' study site in Silwood Park, Ascot, Berkshire, United Kingdom, the cinnabar moth (*Tyria jacobaeae*) is the superior competitor and depresses the abundances of the flower head-feeding fly *Botanophila seneciella* and the flower galler *Contarina jacobaeae*. However, local competitive exclusion is not observed even in patches heavily defoliated by the moth. Cinnabar moths are sufficiently mobile so that no ragwort patches exist that are empty of the moths. There is, however, spatial variation in cinnabar moth performance; the moth consistently defoliates dense patches of ragwort but performs consistently less well in patches that are heavily mown or in which the ragwort is sparsely distributed. The authors suggest that the patches of sparse ragwort may serve as refuges for *B. seneciella* and *C. jacobaeae*. Both species have good dispersal abilities (*B. seneciella* is in fact a faster disperser than the cinnabar moth) and are able to invade areas where ragwort has been extensively defoliated. This suggests that immigration from patches where the moth performs poorly may be counteracting competitive exclusion of *B. seneciella* and *C. jacobaeae* in patches where defoliation by the moth is extensive.

While there is certainly a potential for spatial dynamics

to counteract competitive exclusion, we frequently observe instances of region-wide competitive displacement. The displacement of the native asexual gecko *Lepidodactylus lugubris* by the introduced sexual species *Hemidactylus frenatus* in the tropical Pacific (Case et al. 1994; Petren and Case 1996) and that of *Aphytis lingnanensis*, a parasitoid of the red scale (*Aonidiella aurantii*), by its congener *Aphytis melinus* in southern California (Luck and Podoler 1985; Murdoch et al. 1996) provide some of the more well studied examples. These observations suggest that, in some cases at least, spatial processes cannot counteract competitive exclusion because of insufficient spatial variance in competitive ability. If one species is competitively superior and is sufficiently mobile so that no refuges for the inferior competitor exist, then all local populations are essentially sinks for the inferior competitor. Dispersal from one location to another cannot prevent competitive exclusion. Typically, one would expect such large-scale exclusion to occur when competitive ability is determined by traits that are fixed within and across populations. For example, *A. melinus* gains a competitive advantage over *A. lingnanensis* because of a life-history difference; *A. melinus* is able to obtain female offspring from a smaller-sized scale than *A. lingnanensis* (Luck and Podoler 1985). Using a stage-structured host-parasitoid model, Murdoch et al. (1996) showed that this subtle difference is sufficient to explain the rapid displacement of *A. lingnanensis* from inland areas of southern California. If, however, the life-history traits influencing competitive ability are plastic, or if competitive ability is determined by extrinsic factors that are either biotic (predators, parasites, and pathogens) or abiotic (temperature, humidity, and disturbances), then

spatial variation in these factors could provide conditions under which source-sink dynamics can lead to local coexistence. One would expect global niche partitioning to provide the broadest conditions for coexistence because this situation imposes no constraints on dispersal ability. Field measurements required to quantify the nature of the competitive environment include any measure of fitness or competitive ability such as growth rates or competitive coefficients and some measure of dispersal either through direct mark-recapture experiments or indirectly by using genetic markers (e.g., Dias 1996).

In our models, the interaction between competition and dispersal leads to a threshold effect. Levin (1974) documented a similar phenomenon for competition involving local priority effects. Since local dynamics themselves involve a threshold phenomenon in Levin's model, perhaps it is not surprising that this effect should persist when local populations are linked by dispersal. However, the models we have analyzed involve asymmetric competition that leads to deterministic extinction of inferior competitors in the absence of ameliorating forces. A threshold effect arises in our models when patches are coupled by dispersal, but only when competition involves global asymmetry or a global priority effect. A similar effect has been observed in some population genetic models as well. For instance, in Slatkin's (1994) model of epistatic, directional selection for complex adaptive traits, fixation of the adaptive genotype occurs in the absence of gene flow. With small amounts of gene flow, a stable polymorphism results with the less adaptive genotypes being maintained in the population. With large amounts of gene flow, the polymorphism disappears and the system reverts to monomorphism. The same dynamical phenomenon is observed in the classical migration-selection models with directional selection for a recessive allele (Wright 1931, 1969; Hartl and Clark 1997). A polymorphism arises under small amounts of gene flow and disappears under large amounts of gene flow. In contrast, competition-dispersal balance with global niche partitioning (this study) or migration-selection balance with directional selection for a dominant allele (Wright 1931, 1969; Hartl and Clark 1997) do not lead to threshold phenomena. In these cases, the transition from weak to strong coupling has no impact on coexistence.

A threshold effect resulting from the interaction between competition and dispersal has also been observed in a

diffusion model (Pacala and Roughgarden 1982), suggesting that the phenomenon may operate in both patchy and spatially continuous environments. Pacala and Roughgarden investigated the role of habitat suitability in the invasion success of competing species. They modeled habitat suitability in terms of spatially varying carrying capacities and derived critical dispersal thresholds for a diffusion model as well as a discrete compartment analogue. They found that invasion could sometimes succeed when both sides of the environment were unsuitable and that it could sometimes fail when both sides of the environment were suitable. The authors attribute this result to the cost incurred when dispersal interacts directly with local population dynamics (i.e., individuals are moving from areas of higher to lower fitness). In Pacala and Roughgarden's (1982) model, as in ours, dispersal is costly because it is random. If dispersal were directional or density dependent, then conclusions about competitive coexistence might be different from what we have obtained above. In fact, density-dependent dispersal may be sufficiently nonlinear to counteract competitive exclusion even in a competitively homogeneous environment. This possibility remains to be explored.

In summary, explicit consideration of the interaction between competition and dispersal takes us away from the patch occupancy framework with its emphasis on extinction-colonization dynamics to the realm of source-sink dynamics. The key to coexistence in this framework is spatial variance in fitness. Unlike in the patch occupancy framework where local and spatial dynamics are essentially decoupled, high rates of dispersal can undermine coexistence, and hence diversity, by reducing spatial variance in fitness.

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## APPENDIX A

### Invasion and Stability Analyses for the Model with a Refuge for the Inferior Competitor

The Jacobian matrix of equation (4) is given by

$$\begin{bmatrix} 1 - 2x_1^* - \phi_{x,1}y_1^* & -\phi_{x,1}x_1^* & 0 \\ -\phi_{y,1}y_1^* & 1 - 2y_1^* - \phi_{y,1}x_1^* - \beta_y & \beta_y \\ 0 & \beta_y & 1 - 2y_2^* - \beta_y \end{bmatrix}.$$

Note that the Jacobian is a tridiagonal, quasi-symmetric matrix (i.e., all nonzero off-diagonal elements  $A_{i,i+1}$  and  $A_{i+1,i}$  have the same sign [Wilkinson 1965]). All eigenvalues of a quasi-symmetric matrix are real (see Wilkinson 1965, p. 336). This means that the transition from stability to instability involves a zero real root rather than a complex root with zero real parts. Hence, the system defined by equation (4) does not exhibit oscillatory instability (Gurney and Nisbet 1998).

The inferior competitor can invade when the superior competitor is at carrying capacity if the dominant eigenvalue of the Jacobian is positive when evaluated at  $(x_1^*, y_1^*, y_2^*) = (1, 0, 0)$ .

The eigenvalues are  $-1$  and  $[b \pm (b^2 - 4c)^{1/2}]/2$ , where  $b = (1 - \phi_{y,1} - \beta_y)$  and  $c = (1 - \phi_{y,1} - \beta_y)(1 - \beta_y) - \beta_y^2$ . The equilibrium  $(x_1^*, y_1^*, y_2^*) = (1, 0, 0)$  is unstable to invasion by the inferior competitor if the eigenvalue  $[b + (b^2 - 4c)^{1/2}]/2 > 0$ . This occurs when  $c < 0$  and leads to the invasion criterion (eq. [5]) in main text.

The characteristic equation for the Jacobian of equation (4) is:

$$\lambda^3 + A_1\lambda^2 + A_2\lambda + A_3 = 0,$$

where

$$\begin{aligned} A_1 &= -(1 - 2x_1^* - \phi_{x,1}y_1^*) - (1 - 2y_1^* - \phi_{y,1}x_1^* - \beta_y) - (1 - 2y_2^* - \beta_y), \\ A_2 &= (1 - 2y_1^* - \phi_{y,1}x_1^* - \beta_y)[(1 - 2x_1^* - \phi_{x,1}y_1^*) + (1 - 2y_2^* - \beta_y)] \\ &\quad + (1 - 2x_1^* - \phi_{x,1}y_1^*)(1 - 2y_2^* - \beta_y) - \phi_{x,1}x_1^*\phi_{y,1}y_1^* - \beta_y^2, \end{aligned}$$

and

$$A_3 = (1 - 2x_1^* - \phi_{x,1}y_1^*)\beta_y^2 + \phi_{x,1}x_1^*\phi_{y,1}y_1^*(1 - 2y_2^* - \beta_y) - (1 - 2x_1^* - \phi_{x,1}y_1^*)(1 - 2y_1^* - \phi_{y,1}x_1^* - \beta_y)(1 - 2y_2^* - \beta_y).$$

We were unable to derive a rigorous proof of local stability of the coexistence equilibrium. As the roots of the characteristic equation are real, stability is guaranteed if  $A_1 > 0$ ,  $A_2 > 0$ , and  $A_3 > 0$ . It is easy to show that  $A_1$  is positive, so proving stability involves proving positivity of  $A_2$  and  $A_3$ . We obtained a convincing numerical demonstration that these coefficients are positive by noting that the model has only three parameters ( $\beta_y$ ,  $\phi_{x,1}$ , and  $\phi_{y,1}$ ) that are related to the equilibrium conditions by the equations:

$$\begin{aligned} \beta_y &= \frac{y_2^*(1 - y_2^*)}{y_2^* - y_1^*}, \\ \phi_{x,1} &= \frac{1 - x_1^*}{y_1^*}, \\ \phi_{y,1} &= \frac{1 - y_1^*}{x_1^*} + \frac{y_2^*(1 - y_2^*)}{x_1^*y_1^*}. \end{aligned}$$

The scaled equilibrium populations are restricted to the range  $(0, 1)$ , so we divided the unit cube in three-dimensional  $(x_1^*, y_1^*, y_2^*)$  space into a fine grid (intervals of 0.005 in each variable) and evaluated  $A_2$  and  $A_3$  for all points  $(x_1^*, y_1^*, y_2^*)$  that yielded  $\phi_{x,1} < 1$ ,  $\phi_{y,1} > 1$ , and  $\beta_y > 0$ . No unstable equilibria were found.

## APPENDIX B

### Invasion and Stability Analyses for the Model with No Refuge for the Inferior Competitor

The Jacobian matrix for equation (3) is:

$$\begin{bmatrix} 1 - 2x_1^* - \phi_{x,1}y_1^* - \beta_x & \beta_x & -\phi_{x,1}x_1^* & 0 \\ \beta_x & 1 - 2x_2^* - \phi_{x,2}y_2^* - \beta_x & 0 & -\phi_{x,2}x_2^* \\ -\phi_{y,1}y_1^* & 0 & 1 - 2y_1^* - \phi_{y,1}x_1^* - \beta_y & \beta_y \\ 0 & -\phi_{y,2}y_2^* & \beta_y & 1 - 2y_2^* - \phi_{y,2}x_2^* - \beta_y \end{bmatrix}.$$

The Jacobian is a quasi-symmetric matrix. All eigenvalues are therefore real, and hence the system defined by equation (3) does not exhibit oscillatory instability (Gurney and Nisbet 1998).

The inferior competitor can invade when rare in both patches if the dominant eigenvalue of the Jacobian is positive when evaluated at  $(x_1^*, x_2^*, y_1^*, y_2^*) = (1, 1, 0, 0)$ . The eigenvalues are  $-1$ ,  $-1 - 2\beta_y$ , and  $[b \pm (b^2 - 4c)^{1/2}]/2$ , where  $b = (1 - \phi_{y,1} - \beta_y) + (1 - \phi_{y,2} - \beta_y)$  and  $c = (1 - \phi_{y,1} - \beta_y)(1 - \phi_{y,2} - \beta_y) - \beta_y^2$ . The equilibrium  $(x_1^*, x_2^*, y_1^*, y_2^*) = (1, 1, 0, 0)$  is unstable to invasion by the inferior competitor if the eigenvalue  $[b + (b^2 - 4c)^{1/2}]/2 > 0$ . This leads to the invasion criterion (eq. [6]) in the main text.

Local stability criteria for the coexistence equilibrium cannot be derived analytically. Numerical explorations over the parameter range  $\phi_{x,1} = (0, 1)$ ,  $\phi_{y,1} = (1, 5)$ ,  $\phi_{x,2} = (1, 5)$ ,  $\phi_{y,2} = (0, 1)$ ,  $\beta_x = (0, 5)$ ,  $\beta_y = (0, 5)$  show all four eigenvalues to be negative for all positive values of the coexistence equilibrium.

### Literature Cited

- Amarasekare, P. 2000a. Spatial dynamics in a host-multi-parasitoid community. *Journal of Animal Ecology* 69: 201–213.
- . 2000b. Coexistence of competing parasitoids on a patchily distributed host: local vs. spatial mechanisms. *Ecology* 81:1286–1296.
- Case, T. J., D. T. Bolger, and K. Petren. 1994. Invasions and competitive displacement among house geckos in the tropical Pacific. *Ecology* 75:464–477.
- Cohen, J. E. 1970. A Markov contingency-table model for replicated Lotka-Volterra systems near equilibrium. *American Naturalist* 104:547–560.
- Connell, J. H. 1978. Diversity in tropical rainforests and coral reefs. *Science (Washington, D.C.)* 199:1302–1310.
- Dias, P. C. 1996. Sources and sinks in population biology. *Trends in Ecology & Evolution* 11:326–330.
- Gurney, W. S. C., and R. M. Nisbet. 1998. *Ecological dynamics*. Oxford University Press, New York.
- Harper, J. L. 1961. Approaches to the study of plant competition. Pages 1–39 in F. L. Milthrope, ed. *Mechanisms in biological competition*. Society for Experimental Biology Symposium 15. Cambridge University Press, Cambridge.
- Harrison, S., C. D. Thomas, and T. M. Lewinsohn. 1995. Testing a metapopulation model of coexistence in the insect community of ragwort (*Senecio jacobea*). *American Naturalist* 145:546–562.
- Hartl, D. L., and A. G. Clark. 1997. *Principles of population genetics*. Sinauer, Sunderland, Mass.
- Hastings, A. 1980. Disturbance, coexistence, history and competition for space. *Theoretical Population Biology* 18:363–373.
- Huel, D. G., and P. Huel. 1996. Genotypic variation for competitive ability in spring wheat. *Plant Breeding* 115: 325–329.
- Lei, G., and I. Hanski. 1998. Spatial dynamics of two competing specialist parasitoids in a host metapopulation. *Journal of Animal Ecology* 67:422–433.
- Levin, S. A. 1974. Dispersion and population interactions. *American Naturalist* 108:207–228.
- Levins, R. 1969. Some demographic and genetic consequences of environmental heterogeneity for biological control. *Bulletin of the Entomological Society of America* 15:237–240.
- . 1970. Extinction. Pages 75–107 in M. Gerstenhaber, ed. *Some mathematical problems in biology*. American Mathematical Society, Providence, R.I.
- Levins, R., and D. Culver. 1971. Regional coexistence of species and competition between rare species. *Proceedings of the National Academy of Sciences of the USA* 68:1246–1248.
- Lotka, A. J. 1932. The growth of mixed populations: two species competing for a common food supply. *Journal of the Washington Academy of Sciences* 22:461–469.
- Lubchenco, J. 1978. Plant species diversity in a marine intertidal community: importance of herbivore food performance and algal competitive abilities. *American Naturalist* 112:23–39.
- Luck, R. F., and H. Podoler. 1985. Competitive exclusion of *Aphytis lingnanensis* by *Aphytis melinus*: potential role of host size. *Ecology* 66:904–913.
- Morrison, S. L., and J. Molofsky. 1999. Environmental and genetic effects on the early survival and growth of the invasive grass *Phalaris arundinacea*. *Canadian Journal of Botany* 77:1447–1453.
- Murdoch, W. W., C. J. Briggs, R. M. Nisbet, W. S. C. Gurney, and A. Stewart-Oaten. 1992. Aggregation and stability in metapopulation models. *American Naturalist* 140:41–58.

- Murdoch, W. W., C. J. Briggs, and R. M. Nisbet. 1996. Competitive displacement and biological control in parasitoids: a model. *American Naturalist* 148:807–826.
- Murray, J. D. 1993. *Mathematical biology*. Springer, New York.
- Nee, S., and R. M. May. 1992. Dynamics of metapopulations: habitat destruction and competitive coexistence. *Journal of Animal Ecology* 61:37–40.
- Nisbet, R. M., C. J. Briggs, W. S. C. Gurney, W. W. Murdoch, and A. Stewart-Oaten. 1993. Two-patch metapopulation dynamics. Pages 125–135 *in* S. A. Levin, T. Powell, and J. Steele, eds. *Patch dynamics in freshwater, terrestrial and aquatic ecosystems*. Springer, Berlin.
- Pacala, S. W., and J. Roughgarden. 1982. Spatial heterogeneity and interspecific competition. *Theoretical Population Biology* 21:92–113.
- Paine, R. T. 1966. Food web complexity and species diversity. *American Naturalist* 100:65–75.
- Petren, K., and T. J. Case. 1996. An experimental demonstration of exploitation competition in an ongoing invasion. *Ecology* 77:118–132.
- Skellam, J. G. 1951. Random dispersal in theoretical populations. *Biometrika* 38:196–218.
- Slatkin, M. 1974. Competition and regional coexistence. *Ecology* 55:128–134.
- . 1994. Epistatic selection opposed by migration in multiple locus genetic systems. *Journal of Evolutionary Biology* 8:623–633.
- Tilman, D., and S. Pacala. 1993. The maintenance of species richness in plant communities. Pages 13–25 *in* R. Ricklefs and D. Schluter, eds. *Species diversity in ecological communities*. University of Chicago Press, Chicago.
- Tilman, D., R. M. May, C. L. Lehman, and M. A. Nowak. 1994. Habitat destruction and the extinction debt. *Nature* 371:65–66.
- Volterra, V. 1926. Variations and fluctuations of the numbers of individuals in animal species living together. Pages 409–448 *in* R. N. Chapman, ed. *Animal ecology*. McGraw-Hill, New York.
- Wilkinson, J. H. 1965. *The algebraic eigenvalue problem*. Clarendon, Oxford.
- Wright, S. 1931. Evolution in Mendelian populations. *Genetics* 16:97–159.
- . 1969. *Evolution and the genetics of populations*. Vol. 2. *The theory of gene frequencies*. University of Chicago Press, Chicago.

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