Sink habitats can alter ecological outcomes for competing species

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Summary

1. Species often compete for breeding sites in heterogeneous landscapes consisting of sources and sinks. To understand how the presence or absence of sink breeding sites influence ecological outcomes, we extend Pulliam's source–sink model to competing species.
2. In a homogeneous landscape consisting of source sites, we prove that one species, the 'superior' competitor, competitively excludes the other. Dominance is determined by a simple rule: the species that at equilibrium acquires new breeding sites at a faster rate dominates.
3. We prove that the inclusion of sink sites can alter this ecological outcome by either mediating coexistence, reversing competitive dominance, or facilitating a priority effect.
4. Sink-mediated coexistence requires the species to exhibit asymmetries in acquiring sink sites, the 'inferior' species to have a competitive advantage on sink sites and the ratio of sink to source sites be sufficiently low.
5. For example, if the sink breeding sites are competitive refuges for the 'inferior' competitor and not too low in quality, coexistence occurs if the number of sink sites lies below a threshold. Alternatively, when the number of sink sites exceeds this threshold, competitive dominance is reversed and the 'superior' competitor is displaced.
6. Counter-intuitively, despite being unable to support species in isolation, sink habitats embedded in a geographical mosaic of sources and sinks can enhance biodiversity by mediating coexistence or alter species composition by reversing competitive interactions.

Key-words: competition, population dynamics, sink-mediated coexistence.

Introduction

Most species have birth and death rates that vary spatially due to variation in abiotic (e.g. temperature, precipitation, nutrient availability) and biotic (e.g. predation, competition, quality and availability of biotic resources) factors. For each species, this variability may result in a geographical mosaic of source and sink populations (Holt 1985; Pulliam 1988, 1996; Pulliam & Danielson 1991; Dias 1996; Holt 1997). In source populations, birth rates exceed death rates and emigration exceeds immigration. Hence, sources are net exporters of indi-

viduals. In sink populations, on the other hand, death rates exceed birth rates and immigration exceeds emigration. Sink habitats, by definition, cannot persist without immigration.

Despite their inability to persist in isolation, there is ample evidence that sink populations exist in nature (Donovan *et al*. 1995; Dias 1996; Pulliam 1996; Boughton 1999; Amezcua & Holyoak 2000; Foppen *et al*. 2000; Murphy 2001; Rosenheim 2001). The presence of sink populations raises two fundamental questions: why do these populations exist, and how do sink habitats affect ecological interactions and outcomes? Theory and empirical studies suggest that sink populations exist for a variety of reasons. Populations may exhibit an ideal pre-emptive distribution in which individuals move to sink habitats when all source habitats are occupied (Pulliam 1988; Pulliam & Danielson 1991). A dominance hierarchy can yield source–sink dynamics provided that subordinates have poorer prospects in the source

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habitat than in the sink habitat, but later may be able to return to the source habitat (B. Kotler, personal communication). While ideal free populations in which individuals move freely to maximize their per-capita fitness do not occupy sink habitats under equilibrium conditions (Holt 1985), they may occupy sink habitats under non-equilibrium conditions (Holt 1997; Jansen & Yoshimura 1998). Finally, organisms may exhibit maladaptive behaviour due to rapid shifts in the environment that prevent them from making optimal habitat-selection decisions (Remeš 2000). Theoretical and empirical work suggest that sink habitats can significantly affect ecological interactions. For instance, the addition of sink habitats can increase population abundance (Holt 1985; Pulliam 1988) by providing alternative habitats when the source habitats are overcrowded. The presence of sink refuges for predators (respectively, prey) can stabilize predator–prey interactions by decreasing predation rates when prey numbers are low (respectively, when predator numbers are high) (Holt 1985; Amezcua & Holyoak 2000). Alternatively, in environments subject to random disturbances, dispersal between sink habitats can result in population persistence at the regional scale even though persistence does not occur at a local scale (Jansen & Yoshimura 1998).

Here, we confront the issue of how the presence of sink habitats influences the ecological outcomes of competing species. We begin by introducing a model of species competing for breeding sites (more generally space) in a homogeneous landscape. For this model, we prove that one species always competitively excludes the other species. In light of this fact, we present and analyse two models that introduce sink (more generally lower-quality) breeding sites into the landscape. We derive conditions under which the presence of sink sites can mediate coexistence, facilitate a reversal of competitive dominance, or produce a priority effect in which neither species can invade when rare.

General model formulation

Our model extends a single species model of Pulliam (1988) to two species, species 1 and species 2, competing for a finite number of breeding sites of which N are higher-quality and $\tilde{N}$ are lower-quality. An annual census of the abundances, x_1 and x_2, of species 1 and 2 is taken in the spring, after individuals have dispersed and competed for breeding sites (Fig. 1). After the census, individuals from species i with $i = 1, 2$ occupying higher-quality breeding sites produce on average β_i progeny while individuals occupying lower-quality breeding sites produce on average $\tilde{\beta}_i$ progeny. By lower-quality, we mean $\beta_i > \tilde{\beta}_i$ for $i = 1, 2$. A long period of survival through autumn and winter follows, in which a fraction $1 - A_i$ of the adults and a fraction $1 - J_i$ of the juveniles of species i perish. Following winter survival, individuals disperse actively to breeding sites, making use of a breeding site if it is available, and always preferring a higher-quality site to a lower-quality site
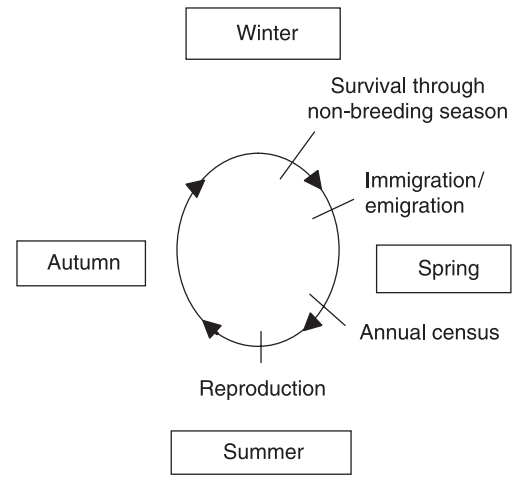
Fig. 1. The life-cycle: an annual census is taken in each habitat in the spring at the initiation of the breeding season (summer). Each female of species i produces β_i (respectively, $\tilde{\beta}_i$) juveniles in the high-quality (respectively, low-quality) breeding sites. Adults survive the non-breeding season (winter) with probability A_i and juveniles survive with probability J_i.

(i.e. exhibit a pre-emptive ideal distribution, Pulliam & Danielson 1991).

Under these assumptions, we arrive at difference equations of the following form:

$$x_1' = A_1 x_1 + J_1 f_1(x_1, x_2)$$
$$x_2' = A_2 x_2 + J_2 f_2(x_1, x_2) \qquad \text{eqn 1}$$

where $f_i(x_1, x_2)$ are 'progeny functions' that represent the average number of progeny produced by species i. These functions will be specified later for different scenarios and depend on the parameters β_i, $\tilde{\beta}_i$, N and $\tilde{N}$. In all scenarios, the model for a single species with abundance x restricted to a single habitat type reduces to:

$$x' = Ax + Jf(x) \qquad \text{eqn 2}$$

with

$$f(x) = \begin{cases} \beta x, & \text{if } x \leq N \\ \beta N, & \text{if } x \geq N \end{cases}$$

For this model, if $A + J\beta < 1$, then the population is a sink population, or else it is a source and the population converges to the equilibrium density $x^* = J\beta N/(1 - A)$ (Pulliam 1988). In the next three sections, we analyse three realizations of this model. The first realization considers a homogeneous environment and results in a competitive exclusion principle. The second realization assumes that all individuals acquire higher-quality breeding sites on a 'first-come, first-served' basis and that only one species can acquire lower-quality breeding sites. We present this special case as it permits formulating the functions f_i explicitly and it illustrates clearly how the inclusion of sink habitats modifies ecological outcomes. Finally, we formulate and analyse

a model in which both species have access to the lower-quality sites and can exhibit asymmetries in their abilities to acquire breeding sites.

Competitive exclusion in a homogeneous environment

Assume that both species compete in a homogeneous environment for N breeding sites. Individuals exhibit lottery recruitment for breeding sites. To allow for competitive asymmetries in the species acquisition of breeding sites, let c_i denote the rate at which an individual of species i acquires a breeding site, i.e. on average, an individual of species i requires $1/c_i$ units of time to acquire a breeding site. If there are more breeding sites than individuals ($x_1 + x_2 \leq N$), then all individuals are assumed to acquire a breeding site. However, if there are more individuals than breeding sites ($x_1 + x_2 > N$), then all breeding sites become occupied and Appendix A proves that species i acquires $(1 - \exp(-c_i T))x_i$ breeding sites where $T = T(c, x)$ is the time it takes to occupy all breeding sites and is the unique solution to $\Sigma_i(1 - \exp(-c_i T))x_i = N$. In the special case of individuals acquiring breeding sites on a 'first-come, first-served' basis (i.e. $c_1 = c_2$), the expression $(1 - \exp(-c_i T))x_i$ for the number of breeding sites acquired by species i simplifies to $x_i N/(x_1 + x_2)$. Although it is not possible to write down an explicit formula for T when $c_1 \neq c_2$, we can still analyse and simulate these models. Under these assumptions, the progeny function f_i for species i is:

$$f_i(x_1, x_2) = \begin{cases} \beta_i x_i & \text{if } x_1 + x_2 \leq N \\ \beta_i x_i(1 - \exp(-c_i T)) & \text{if } x_1 + x_2 > N \end{cases} \quad \text{eqn 3}$$

The first term in these piecewise defined functions corresponds to the situation in which there are more breeding sites than individuals. Hence, all individuals of species i acquire a higher-quality breeding site in which they produce β_i progeny. The second term in these piecewise defined functions corresponds to the situation in which there are more individuals than breeding sites. Hence, only $x_i(1 - \exp(-c_i T))$ individuals of species i acquire breeding sites.

If the breeding sites are source sites for both species (i.e. $A_i + \beta_i J_i > 1$ for $i = 1, 2$), then the system (generically) admits only three equilibria, $(0, 0)$, $(x_1^*, 0)$ and $(0, x_2^*)$ where $x_i^* = J_i \beta_i N/(1 - A_i)$. As the lack of feasible equilibria suggests, the coexistence of both species is (generically) impossible. Indeed, Appendix B proves that if:

$$\left(1 - \frac{N}{x_1^*}\right)^{\frac{1}{c_1}} > \left(1 - \frac{N}{x_2^*}\right)^{\frac{1}{c_2}} \quad \text{eqn 4}$$

then species 1 competitively excludes species 2. Alternatively, if the opposite inequality holds, then species 2 competitively excludes species 1. An interpretation of this inequality is as follows: the species that at equilibrium can acquire newly introduced breeding sites at a faster rate is competitively superior. In the case of species acquiring breeding sites on a 'first-come, first-served' basis (i.e. $c_1 = c_2$), this rule of dominance simplifies to the species that attains the higher equilibrium density is competitively dominant.

Competition with a competitive refuge

The result of the preceding analysis is that species competing for breeding sites in a homogeneous environment cannot coexist. It is well known that introducing a competitive refuge for the inferior competitor can mediate coexistence if the inferior competitor can maintain a positive initial growth rate in the competitive refuge (see, e.g. Amarasekare & Nisbet 2001). The novel issue we address here is whether competitive refuges in which per-capita death rates always exceed per-capita birth rates can mediate coexistence. To address this issue, let species 1 be the superior competitor on the higher-quality breeding sites (i.e. in a landscape consisting only of higher-quality breeding sites, species 1 excludes species 2) and let species 2 have sole access to the lower-quality breeding sites. To simplify things, assume that individuals of both species acquire higher-quality nesting sites on a 'first-come, first-served' basis (i.e. $c_1 = c_2$).

As discussed in the previous section, the progeny function for species 1 is:

$$f_1(x_1, x_2) = \begin{cases} \beta_1 x_1, & \text{if } x_1 + x_2 \leq N \\ \beta_1 x_1 \dfrac{N}{x_1 + x_2}, & \text{if } x_1 + x_2 \geq N \end{cases} \quad \text{eqn 5}$$

On the other hand, as species 2 is assumed to exhibit an ideal pre-emptive distribution, individuals attempt to acquire lower-quality breeding sites only when all the higher-quality sites are occupied. When this occurs, $Nx_2/(x_1 + x_2)$ individuals of species 2 acquire higher-quality breeding sites and the remaining $x_2 - Nx_2/(x_1 + x_2)$ individuals of species 2 attempt to acquire the lower-quality breeding sites. If this latter number is less than $\tilde{N}$, then all these individuals acquire lower-quality breeding sites or else only $\tilde{N}$ individuals do. Thus, the progeny function for species 2 is:

$$f_2(x_1, x_2) = \begin{cases} \beta_2 x_2, \\ \qquad \text{if } x_1 + x_2 \leq N \\ \beta_2 x_2 \left(\dfrac{N}{x_1 + x_2}\right) + \tilde{\beta}_2 x_2 \left(1 - \dfrac{N}{x_1 + x_2}\right), \\ \qquad \text{if } x_1 + x_2 \geq N \text{ and } x_2\left(1 - \dfrac{N}{x_1 + x_2}\right) \leq \tilde{N} \\ \beta_2 x_2 \left(\dfrac{N}{x_1 + x_2}\right) + \tilde{\beta}_2 \tilde{N}, \\ \qquad \text{if } x_1 + x_2 \geq N \text{ and } x_2\left(1 - \dfrac{N}{x_1 + x_2}\right) \geq \tilde{N} \end{cases}$$

$$\text{eqn 6}$$

If the higher-quality habitat is a source habitat for both populations, then each species achieves a positive

equilibrium in the absence of the other. For species 1, this positive equilibrium is given by $x_1^* = \psi_1 N$ where $\psi_i = \beta_i J_i/(1 - A_i)$ for $i = 1, 2$. The equilibrium x_2^* achieved by species 2 in the absence of species 1 is described in Appendix C. An analysis of this model reveals that species 2 can invade the equilibrium x_1^* determined by species 1 if and only if:

$$(A_2 + J_2\beta_2)\frac{1}{\psi_1} + (A_2 + J_2\tilde{\beta}_2)\left(1 - \frac{1}{\psi_1}\right) > 1 \qquad \text{eqn 7}$$

i.e. a weighted sum of the intrinsic rates of growth of species 2 in the two sites is greater than 1.

This inequality is always met when the competitive refuge sites are source sites for species 2 (i.e. $A_2 + J_2\tilde{\beta}_2 > 1$) and also is met for a wide range of parameter values when the competitive refuge sites are sinks (Fig. 2). When species 2 can invade, the ecological consequences of the invasion depend on the number $\tilde{N}$ of competitive refuge breeding sites. When $\tilde{N}$ is below a critical threshold ϕ/x_1^* where $\phi = \tilde{\beta}_2/(\beta_2/\psi_2 - \beta_2/\psi_1)$, both species coexist about a globally stable equilibrium:

$$(x_1^{**}, x_2^{**}) = (x_1^* - \phi\tilde{N}, \phi\tilde{N}). \qquad \text{eqn 8}$$

Because $x_1^{**} + x_2^{**} = x_1^*$, the invasion of species 2 in this case has no effect on the equilibrium number of individuals occupying the landscape. On the other hand, if the number of competitive refuges sites exceeds x_1^*/ϕ, then the invasion of species 2 results in a competitive reversal; species 2 competitively displaces species 1. Moreover, the resulting invasion may increase or decrease the equilibrium number of individuals.

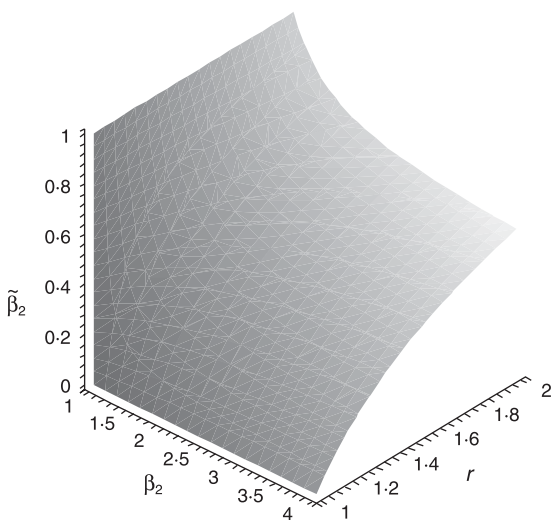Assuming that competitive refuges alter ecological outcomes, we analyse two scenarios of how the equilibrium abundances of both species vary as functions of the number of lower-quality breeding sites. The first scenario considers the effect of simply adding $\tilde{N}$ lower-quality breeding sites to a landscape initially consisting of N higher-quality breeding sites. This might occur when previously unusable habitat becomes converted to lower-quality habitat that can be utilized by one of the species. In this case, the abundance $\psi_1 N - \phi\tilde{N}$ of species 1 decreases linearly with $\tilde{N}$ until it is driven to extinction when $\tilde{N} \geq \psi_1 N/\phi$. This linear decline of species 1 is perfectly compensated by the linear increase of the abundance $\phi\tilde{N}$ of species 2; the total abundance of both species remains constant at $\psi_1 N$ for $\tilde{N} \leq \psi_1 N/\phi$. Following the extinction of species 1, adding more lower-quality sites to the landscape either results in a saturating piecewise linear increase of species 2 when the competitive refuge sites are sinks (Fig. 3a) or results in non-saturating piecewise linear increase when the competitive refuge sites are sources (Fig. 3b).

The second scenario considers converting $\tilde{N}$ of initially N higher-quality breeding sites to lower-quality breeding sites. Habitat conversion may be caused by or occur in response to anthropogenic and environmental disturbances. For instance, legislation with a goal of no net loss of wetlands has led to the creation of wetlands to replace destroyed natural wetlands (National Wetlands Policy Forum 1988). The created wetlands are often of lower quality than natural wetlands and not accessible to all species in the natural wetlands. Our analysis implies that, initially, conversion of higher-quality sites to lower-quality sites results in a linear decrease in the abundance $\psi_1(N - \tilde{N}) - \phi\tilde{N}$ of species 1 that is not compensated by the linear increase of the abundance $\phi\tilde{N}$ of species 2. Beyond a critical level $\tilde{N} \geq \psi_1/(\psi_1 + \phi)$ of habitat conversion, species 1 is competitively excluded. Continuing conversion results in species 2 decreasing in abundance ultimately to extinction if the competitive refuge sites are sinks or to a lower equilibrium abundance if the competitive refuge sites are sources (Fig. 3c,d).

Competition in heterogeneous landscapes without refuges

The preceding analysis shows that the addition or removal of lower-quality competitive refuges, even if they are sinks, can alter ecological outcomes by reversing competitive dominance or mediating coexistence. Because populations may compete for all available breeding sites, we ask can sink habitats, more generally lower-quality habits, alter ecological outcomes when both competing species utilize them? Furthermore, are the only altered outcomes coexistence or competitive reversals?

To answer these questions, assume that both species have access to N higher-quality breeding sites and $\tilde{N}$ lower-quality breeding sites. Let c_i (respectively, $\tilde{c}_i$) denote the rate that individuals from species i acquire a higher-quality (respectively, lower-quality) breeding site.

Fig. 2. Necessary and sufficient conditions for coexistence in the competitive refuge model whenever the number of lower-quality breeding sites is not too large. The parameter values are $A_1 = A_2 = 0\cdot5$, $J_1 = J_2 = 0\cdot5$, and $r = \beta_1/\beta_2$ and $\tilde{\beta}_2$ vary as shown. For all these parameter values, the lower-quality habitat is a sink habitat for both species.
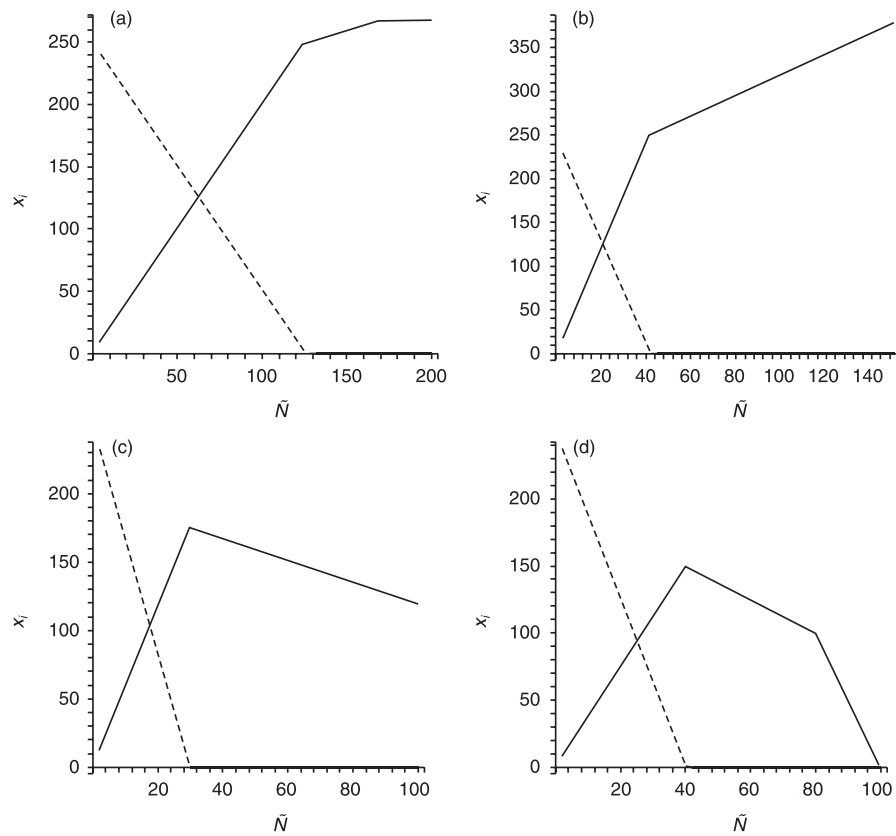
Fig. 3. Equilibrium density of species 1 (dashed line) and species 2 (solid line) for the competitive refuge model as functions of the number $\tilde{N}$ of lower-quality breeding sites. In all 11 figures, $A_1 = A_2 = 0{\cdot}5$, $J_1 = J_2 = 0{\cdot}5$, $\beta_1 = 2{\cdot}5$, and $\beta_2 = 2{\cdot}0$. In (a) and (b), lower-quality breeding sites are augmenting $N = 100$ higher-quality breeding sites. In (a), $\tilde{\beta}_2 = 0{\cdot}4$ and the lower-quality breeding sites are sinks. In (b), $\tilde{\beta}_2 = 1{\cdot}2$ and the lower-quality breeding sites are sources. In (c) and (d), lower-quality breeding sites are replacing higher-quality breeding sites, i.e. number of higher-quality breeding sites equals $100 - \tilde{N}$. In (c), $\tilde{\beta} = 1{\cdot}2$. In (d), $\tilde{\beta} = 0{\cdot}75$ and the lower-quality breeding sites are sinks.

If both species exhibit a pre-emptive distribution and $x_1 + x_2 > N$, then $(1 - \exp(c_i T))x_i$ individuals of species i acquire higher-quality breeding sites where T is the unique solution to $\Sigma_i(1 - \exp(-c_i T))x_i = N$. The remaining $\Sigma_i \exp(-c_i T)x_i$ individuals of both species attempt to acquire lower-quality breeding sites. If the remaining number of individuals is less than $\tilde{N}$, then all remaining individuals acquire lower-quality breeding sites. However, if the remaining number of individuals is greater than $\tilde{N}$, then the number of low-quality breeding sites acquired by species i is given by $(1 - \exp(-\tilde{c}_i \tilde{T}))\exp(-c_i T)x_i$ where $\tilde{T}$ is the unique solution to $\Sigma_i(1 - \exp(-\tilde{c}_i \tilde{T}))\exp(-c_i T)x_i = \tilde{N}$. Thus, the progeny function for species i is:

$$f_i(x_1, x_2) = \begin{cases} \beta_i x_i \\ \qquad \text{if } x_1 + x_2 \leq N \\ \beta_i x_i(1 - \exp(-c_i T)) + \tilde{\beta}_i \exp(-c_i T)x_i \\ \qquad \text{if } N < x_1 + x_2 \leq N + \tilde{N} \\ \beta_i x_i(1 - \exp(-c_i T)) + \\ \tilde{\beta}_i \exp(-c_i T)x_i(1 - \exp(-\tilde{c}_i \tilde{T})) \\ \qquad \text{if } N + \tilde{N} < x_1 + x_2 \end{cases}$$

eqn 9

As in the previous models, if the higher-quality breeding sites are source sites for both species, then species i achieves an unique positive equilibrium density x_i^* in the absence of the other species. The invasion rates g_i of species i when the competing species is at equilibrium determine three possible dynamics: coexistence if $g_1 > 1$ and $g_2 > 1$, displacement of species 2 (respectively, species 1) if $g_1 > 1$ and $g_2 < 1$ (respectively, $g_2 > 1$ and $g_1 < 1$) and a priority effect if $g_1 < 1$ and $g_2 < 1$. In the case of a priority effect, the species that establishes itself first prevents the establishment of its competitor. In the special case that there are no competitive asymmetries in the species abilities to acquire breeding sites (i.e. $c_1 = c_2$ and $\tilde{c}_1 = \tilde{c}_2$), it is easily shown that generically one species is dominant. Therefore, in the absence of asymmetries, the inclusion of lower-quality breeding sites can facilitate competitive reversals but, surprisingly, not mediate coexistence. For instance, competitive reversals can occur if the lower-quality sites are sources, or species 1 is dominant in the higher-quality sites (i.e. $\psi_1 > \psi_2$ where $\psi_i = \beta_i J_i/(1 - A_i)$) and species 2 has an advantage in the lower-quality sites (i.e. $\tilde{\psi}_2 > \tilde{\psi}_1$ where $\tilde{\psi}_i = \tilde{\beta}_i J_i/(1 - A_i)$).

When there are competitive asymmetries in the species' abilities to acquire nesting sites (i.e. $c_1 \neq c_2$ or $\tilde{c}_1 \neq \tilde{c}_2$),
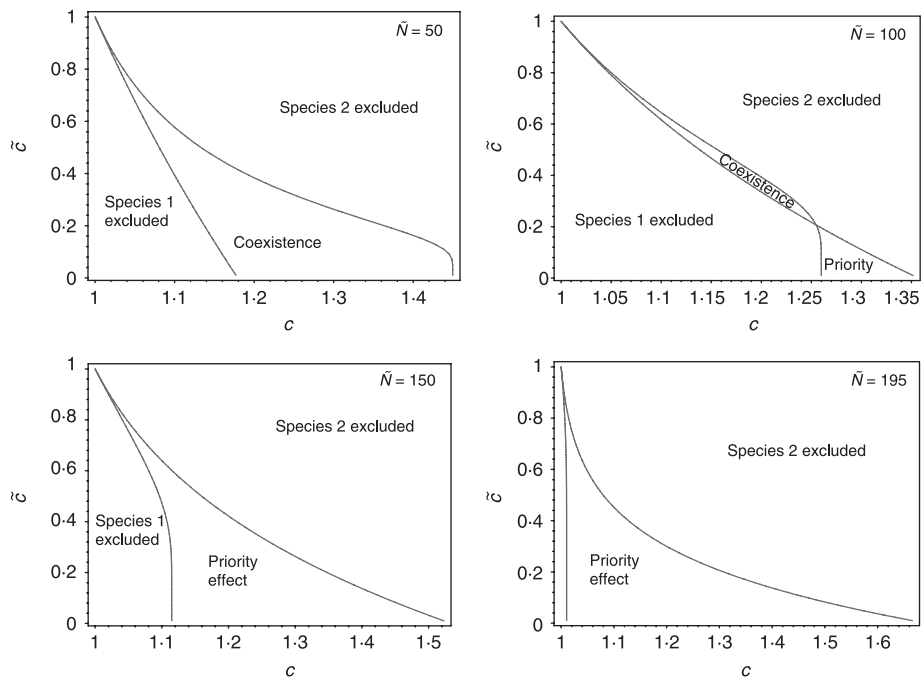
Fig. 4. Bifurcation diagrams for general model with $A_i = 0.9$, $J_i = 0.1$, $\beta_i = 2.0$, $\tilde{\beta}_i = 0.5$, $N = 100$. Parameters $\tilde{N}$, $c = c_1/c_2$ and $\tilde{c} = \tilde{c}_1/\tilde{c}_2$ vary as shown.

the complexity of the invasion rates g_i (Appendix D) limits our analysis to numerical simulations. Figure 4 illustrates how ecological outcomes depend on competitive asymmetries in the acquisition of breeding sites and the availability of sink breeding sites. These numerical simulations show that the inclusion of sink habitats can alter ecological outcomes only if each species has a competitive advantage in one of the habitat types and when there are not too many sinks or too many source sites. The inclusion of sinks alters ecological outcomes in three ways. First, if the ratio of sinks to source sites is not too great, then sink habitats can mediate coexistence (Fig. 4a,b). Secondly, if the ratio of sink to source sites is large and the competitive asymmetry in the two habitats is not too great, there can be a priority effect in which neither species can invade when rare (Fig. 4b–d). Thirdly, sink-facilitated competitive reversals can occur (Fig. 4b).

Discussion

We analyse the population dynamics of two species competing for a finite number of breeding sites. We prove that when this competition occurs in a homogeneous landscape, a simple rule of dominance determines the outcome; the species that at equilibrium attains new breeding sites at the fastest rate competitively displaces the other species. This dominance rule is similar to the R* rule for exploitative competition; the species that at equilibrium suppresses the resource to the lower density is competitively superior (Tilman 1982; Holt *et al.* 1994. The presence of lower-quality breeding sites can alter this ecological outcome by mediating coexistence,

reversing competitive dominance, or inducing a priority effect in which competitive exclusion is contingent upon initial conditions. Most notably, these altered outcomes occur even when neither population in isolation can persist on the lower-quality breeding sites, i.e. the lower-quality breeding sites are sinks.

Lower-quality breeding sites mediate coexistence provided that at least three conditions hold. First, the species inferior with respect to the source sites has a competitive advantage on the lower-quality sites. Secondly, there are competitive asymmetries in the species' abilities to acquire breeding sites. The most extreme form of this asymmetry occurs when the lower-quality sites are competitive refuges for the inferior species. Thirdly, there are some but not too many lower-quality breeding sites. When lower-quality breeding sites can mediate coexistence, there is a threshold effect. If the number of lower-quality sites lies below a threshold, coexistence is mediated. If the number of lower-quality sites exceeds this threshold, a competitive reversal in which the once inferior species displaces the previously superior species or a priority effect occurs. In particular, our study shows that fast-directed dispersal (i.e. in populations exhibiting an ideal pre-emptive distribution; Pulliam 1988; Pulliam & Danielson 1991) can mediate coexistence. In contrast, when dispersal is passive, Amarasekare & Nisbet (2001) found that if there is spatial heterogeneity in competitive rankings across the landscape, local coexistence can occur provided that the dispersal rate of the overall inferior competitor does not exceed a critical threshold.

Amarasekare & Nisbet (2001) showed that spatial heterogeneity could mediate coexistence if all patches

in the absence of competitive interactions are sources for each of the competing species. Our results show that even spatial heterogeneity generated by sink sites can mediate coexistence. This sink-mediated coexistence provides an example of when two sink populations coupled by dispersal make a source population. More specifically, when the species superior on the source sites is isolated and at equilibrium, restricting the inferior species to either habitat results in a sink population. Restricted to the sink sites, the inferior species perishes by definition. Restricted to the source sites, the inferior species is competitively displaced. However, by actively dispersing between these two sink habitats, the inferior species can invade and coexist with the superior species. A different mechanism for the persistence of two sink populations linked by dispersal has been described by Jansen & Yoshimura (1998).

They considered a single population that can disperse between two patches. One patch is a deterministic sink in which the population exhibits a gradual steady decline. The other patch is a stochastic sink, in which frequent favourable periods are punctuated by large disturbances. Coupling these habitats by passive dispersal promotes persistence, the deterministic sink providing a refuge from catastrophes and the stochastic sink providing frequent opportunities for growth. Thus, coupled sink populations may become source populations when spatial heterogeneity is coupled with temporal heterogeneity or is coupled with heterogeneity of species.

Our model makes several simplifying assumptions that warrant further investigation. On the deterministic front, the models assume that adult survivorship is independent of the quality of the breeding site in which they reside, species share habitat selection preferences, there is no density dependence in reproductive success after acquiring a breeding site and individuals have equal pre-emptive abilities regardless of the breeding site from which they came. The model also does not account for the intrinsic discreteness of breeding sites and individuals. For instance, a lattice version of our model is presented in Appendix A. As illustrated by comparing Fig. 5 to Fig. 4d, lattice effects are most pronounced in parameter regimens (e.g. small number of breeding sites) where our original models have a low population abundance at the positive equilibrium. As in these parameter regimens demographic stochasticity may be pronounced, individual-based stochastic counterparts of our model may provide insights into how competition in source–sink landscapes influences coexistence and population persistence.

In conclusion, the use of source–sink theory in conservation biology has focused almost exclusively on single-species dynamics and how sink sites modulate population abundance and population persistence times (Dias 1996; Fauth 2001; With & King 2001). As species are often competing with each other, we have shown that sink habitats can affect biodiversity. On one hand, habitat heterogeneity provided by sinks promotes biodiversity by mediating coexistence. On
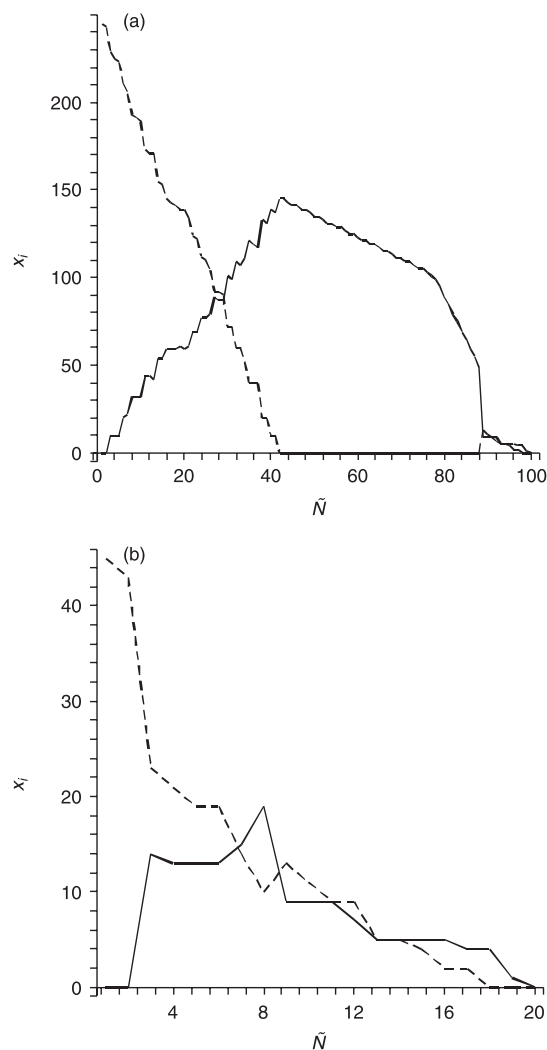
Fig. 5. Equilibrium density of species 1 (dashed line) and species 2 (solid line) for the discrete competitive refuge model as functions of the number $\tilde{N}$ of lower-quality breeding sites. In all figures, lower-quality breeding sites are replacing higher-quality breeding sites, $A_1 = A_2 = 0.5$, $J_1 = J_2 = 0.5$, $\beta_1 = 2.5$, $\beta_2 = 2.0$ and $\tilde{\beta} = 0.75$. In (a), total number of breeding sites is 100 and in (b), total number of breeding sites is 20.

the other hand, excessive conversion of source habitats to sink habitats can decrease species richness. Because habitat fragmentation may be rapidly converting sources to sinks throughout the world, future work on understanding how species interactions and the structures of source–sink mosaics influence biodiversity will be critical.

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Appendix A: model derivation

In this Appendix we develop the breeding-site acquisition functions for competing species. To describe these acquisition dynamics, let x_i denote the number of individuals of species i that are competing for N breeding sites, $n(t)$ be the number of available breeding sites at time t, $y_i(t)$ denote the number of individuals that have not acquired a breeding site by time t, and c_i the per-capita rate at which species i acquire breeding sites. We assume that initially there are more individuals than breeding sites (i.e. $N < x_1 + x_2$). If we assume that species acquire breeding sites at a rate proportional to their abundance and upon acquiring a breeding site individuals do not attempt to acquire more breeding sites, then we obtain the following linear differential equations:

$$\frac{dy_i}{dt} = -c_i y_i \quad y_i(0) = x_i$$

$$\frac{dn}{dt} = -c_1 y_1 - c_2 y_2 \quad n(0) = N$$

eqn 10

Solving these partially coupled linear differential equations yields $y_i(t) = x_i \exp(-c_i t)$ and $n(t) = N - \Sigma_i (1 - \exp(-c_i t)) x_i$. Because we have assumed that $x_1 + x_2 > N$, there exists a unique $T > 0$ such that:

$$\sum_i (1 - \exp(-c_i T)) x_i = N \qquad \text{eqn 11}$$

In the special case that $c_1 = c_2 = c$ (i.e. 'first-come, first-served') we obtain:

$$(1 - \exp(-cT)) x_i = \frac{x_i N}{x_1 + x_2}$$

whenever $x_1 + x_2 > N$.

Appendix B: homogeneous competition

In this Appendix, we analyse the spatially homogeneous model. We assume $A_i + J_i \beta_i > 1$ for $i = 1, 2$ (i.e. the habitat is a source for both species) and $A_1 + J_1 \beta_1 \neq A_2 + J_2 \beta_2$. Solving for equilibria yields three: $(0, 0)$, $(x_1^*, 0)$ and $(0, x_2^*)$ where $x_i^* = J_i \beta_i N / (1 - A_i)$. The invasion rate of species i at the equilibrium determined by the competing species $j \neq i$ is given by $g_i = A_i + J_i \beta_i (1 - \exp(-c_i T_j))$ where, where T_j is the unique solution to $(1 - \exp(-c_j T_j)) x_j^* = N$. Solving for T_j yields

$$T_j = -\frac{1}{c_j} \ln \left(1 - \frac{N}{x_j^*} \right) \qquad \text{eqn 12}$$

Substituting this expression for T_j into $g_i = A_i + J_i\beta_i(1 - \exp(-c_iT_j))$ and simplifying yields:

$$g_i = A_i + J_i\beta_i - J_i\beta_i\left(1 - \frac{M}{x_j^*}\right)^{c_i/c_j} \qquad \text{eqn 13}$$

Using this expression, one can show that $g_1 > 1$ (respectively, $g_2 > 1$) if and only if $(1 - N/x_1^*)^{1/c_1} > (1 - N/x_2^*)^{1/c_2}$ (respectively, reverse inequality). Hence, $g_1 > 1$ (respectively, $g_2 > 1$) if and only if $g_2 < 1$ (respectively, $g_1 < 1$). Lemma 6·2 of Franke & Yakubu (1993) can be used to prove that the invasion rate predictions extend to the entire phase space, i.e. competitive exclusion occurs for all positive initial conditions.

Appendix C: competitive refuge model

Let $\psi_i = J_i\beta_i/(1 - A_i)$ for $i = 1, 2$ and $\tilde{\psi}_2 = J_2\tilde{\beta}_2/(1 - A_2)$. Assume that $\psi_i > 1$ for $i = 1, 2$ (i.e. the main breeding sites are sources) and $\tilde{\beta}_2 < \beta_2$. The competitive refuge model has two non-trivial equilibria on the axes, namely $(x_1^*, 0)$ and $(0, x_2^*)$ where $x_1^* = \psi_1 N$ and

$$x_2^* = \begin{cases} \dfrac{\psi_2 - \tilde{\psi}_2}{1 - \tilde{\psi}_2}N & \text{if } N(\psi_2 - 1) \le \tilde{N}(1 - \tilde{\psi}_2) \\[2ex] \psi_2 N + \tilde{\psi}_2\tilde{N} & \text{if } N(\psi_2 - 1) \ge \tilde{N}(1 - \tilde{\psi}_2) \end{cases} \qquad \text{eqn 14}$$

We also have an equilibrium lying off the axes and given by:

$$(x_1^* - \phi\tilde{N}, \phi\tilde{N}) \qquad \text{eqn 15}$$

where $\phi = \tilde{\beta}_2/(\beta_2/\psi_2 - \beta_2/\psi_1)$. This interior equilibrium lies in the positive quadrant if and only if $\psi_1 > \psi_2$ (species 1 is superior on the common breeding sites) and $\tilde{N} < x_1^*/\phi$. These conditions are consistent with the analysis of the species' invasion rates. Evaluating the per-capita growth rate of species 1 at the point $(0, x_2^*)$ yields species 1 invasion rate:

$$g_1 = \begin{cases} A_1 + \dfrac{J_1\beta_1(1 - \tilde{\psi}_2)}{\psi_2 - \tilde{\psi}_2}, & \text{if } N(\psi_2 - 1) \le \tilde{N}(1 - \tilde{\psi}_2) \\[2ex] A_1 + \dfrac{J_1\beta_1 N}{\psi_2 N + \tilde{\psi}_2\tilde{N}}, & \text{if } N(\psi_2 - 1) \ge \tilde{N}(1 - \tilde{\psi}_2) \end{cases} \qquad \text{eqn 16}$$

Evaluating the per-capita growth rate of species 1 at the point $(x_1^*, 0)$ yields species 2 invasion rate:

$$g_2 = A_2 + J_2\beta_2\frac{1}{\psi_1} + J_2\tilde{\beta}_2(1 - 1/\psi_1) \qquad \text{eqn 17}$$

Let us view $g_1 = g_1(\tilde{N})$ as a function of $\tilde{N}$, because we assumed that species 1 is competitively superior on the higher-quality breeding sites (i.e. $\psi_1 > \psi_2$), $g_1(0) = A_1 + J_1\beta_1/\psi_2 > 1$. Moreover, $g_1(\tilde{N})$ is a non-increasing function, and $\lim_{\tilde{N}\to\infty} g_1(\tilde{N}) = A_1 < 1$ if the lower-quality sites are sources (i.e. $\psi_2 > 1$), or else equals $A_1 + J_1\beta_1(1 - \tilde{\psi}_2)/(\psi_2 - \tilde{\psi}_2)$. A little algebra reveals that

$A_1 + J_1\beta_1(1 - \tilde{\psi}_2)/(\psi_2 - \tilde{\psi}_2) < 1$ if and only if $g_2 > 1$. From these observations, we arrive at two conclusions. First, if $g_2 < 1$, then $g_1(\tilde{N}) > 1$ for all $\tilde{N} > 0$. Secondly, if $g_2 > 1$, then there exists a critical value of $\tilde{N}$ such that if $\tilde{N}$ is less than this critical value $g_1 > 1$ (i.e. coexistence), or else $g_1 < 1$ (i.e. competitive reversal). Assuming $g_2 > 1$ and solving the equation $A_1 + J_1\beta_1 N/(\psi_2 N + \tilde{\psi}_2\tilde{N})$ yields that $g_2(\tilde{N}) \le 1$ for $\tilde{N} \ge N(\psi_1 - \psi_2)/\tilde{\psi}_2 = x_1^*/\phi$. Notice that we have recovered the two conditions that must be satisfied in order for the interior equilibrium for this system to lie in the positive quadrant. We may also solve $N(\psi_2 - \tilde{\psi}_2)/(1 - \tilde{\psi}_2) = \psi_2 N + \tilde{\psi}_2\tilde{N}$ to find that the critical value of $\tilde{N}$ above which the invasion rate of species 1 is constant (assuming the competitive refuge sites are sinks) is $\tilde{N}^{**} = N(\psi_2 - 1)/(1 - \tilde{\psi}_2)$.

To go from local to global conclusions about the dynamics, we can use the results of Franke & Yakubu (1993) and Smith & Thieme (2001). Whenever we have $g_1 > 1$ and $g_2 < 1$ (respectively, $g_1 < 1$ and $g_2 > 1$), Lemma 6·2 of Franke & Yakubu (1993) implies that competitive exclusion of species 2 (respectively, species 1) occurs for all positive initial conditions. On the other hand, when $g_1 > 1$ and $g_2 > 1$, Theorem 2 of Smith & Thieme (2001) implies that the unique positive equilibrium is globally stable.

Appendix D: invasion rates for general model

Let $\psi_i = J_i\beta_i/(1 - A_i)$ and $\tilde{\psi}_i = J_i\tilde{\beta}_i/(1 - A_i)$ and for $i = 1, 2$. Solving for the non-trivial boundary equilibria $(x_1^*, 0)$ and $(0, x_2^*)$ of the general model yields:

$$x_i^* = \begin{cases} N\dfrac{\psi_i - \tilde{\psi}_i}{1 - \tilde{\psi}_i} & \text{if } \tilde{N}(1 - \tilde{\psi}_i) \ge N(\psi_i - 1) \\[2ex] N\psi_i + \tilde{N}\tilde{\psi}_i & \text{if } \tilde{N}(1 - \tilde{\psi}_i) \le N(\psi_i - 1) \end{cases} \qquad \text{eqn 18}$$

To determine the invasion rates of the missing species at these boundary equilibria, we solve $(1 - \exp(-c_iT))x_i = 0$ for T at the equilibria $x_i = x_i^*$. This yields $T_i = \ln(1 - N/x_i^*)/c_i$. On the other hand, when $x_i^* > N + \tilde{N}$, solving $(1 - \exp(-\tilde{c}_i\tilde{T}))(x_i^* - N) = 0$ for $\tilde{T}$ yields. $\tilde{T}_i = \ln(1 - \tilde{N}/(x_i^* - N))/\tilde{c}_i$. Using these quantities, we can express the invasion rate of species i at the equilibrium determined by its competitor as:

$$g_i = \begin{cases} A_i + J_i(\beta_i(1 - \exp(-c_iT_j)) + \tilde{\beta}_i\exp(-c_iT_j)) \\ \qquad\qquad \text{if } \tilde{N}(1 - \tilde{\psi}_i) \ge N(\psi_i - 1) \\[1ex] A_i + J_i(\beta_i(1 - \exp(-c_iT_j)) + \\ \tilde{\beta}_i(1 - \exp(-\tilde{c}_i\tilde{T}_i))\exp(-c_iT_j)) \\ \qquad\qquad \text{if } \tilde{N}(1 - \tilde{\psi}_i) \le N(\psi_i - 1) \end{cases} \qquad \text{eqn 19}$$

Appendix E: a discrete version of the competitive refuge model

To account for discreteness of individuals and breeding sites, we describe the discrete version of the competitive refuge model. This model discretizes (1) the number of

breeding sites acquired by either species, (2) the number of juveniles that make it to the next breeding season and (3) the number of adults that survive to the next breeding season. We let $\lfloor x \rfloor$ denote the floor of the number x.

$$x_1' = \lfloor A_1 x_1 \rfloor + \lfloor J_1 f_1(x_1, x_2) \rfloor$$
$$x_2' = \lfloor A_2 x_2 \rfloor + \lfloor J_2 f_2(x_1, x_2) \rfloor$$

eqn 20

where:

$$f_1(x_1, x_2) = \begin{cases} \beta_1 x_1, & \text{if } x_1 + x_2 \le N \\ \beta_1 \left\lfloor \dfrac{x_1 N}{x_1 + x_2} \right\rfloor, & \text{if } x_1 + x_2 \ge N \end{cases}$$

and

$$f_2(x_1, x_2) = \begin{cases} \beta_2 x_2, \\ \quad \text{if } x_1 + x_2 \le N \\ \beta_2 \left\lfloor \dfrac{x_2 N}{x_1 + x_2} \right\rfloor + \tilde{\beta}_2 \left(x_2 - \left\lfloor \dfrac{x_2 N}{x_1 + x_2} \right\rfloor \right), \\ \quad \text{if } x_1 + x_2 \ge N \text{ and } x_2 - \left\lfloor \dfrac{x_2 N}{x_1 + x_2} \right\rfloor \le \tilde{N} \\ \beta_2 \left\lfloor \dfrac{x_2 N}{x_1 + x_2} \right\rfloor + \tilde{\beta}_2 \tilde{N}, \\ \quad \text{if } x_1 + x_2 \ge N \text{ and } x_2 - \left\lfloor \dfrac{x_2 N}{x_1 + x_2} \right\rfloor \ge \tilde{N} \end{cases}$$