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Ideal free dispersal in integrodifference models

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Abstract

In this paper, we use an integrodifference equation model and pairwise invasion analysis to find what dispersal strategies are evolutionarily stable strategies (also known as evolutionarily steady or ESS) when there is spatial heterogeneity and possibly seasonal variation in habitat suitability. In that case there are both advantages and disadvantages of dispersing. We begin with the case where all spatial locations can support a viable population, and then consider the case where there are non-viable regions in the habitat. If the viable regions vary seasonally, and the viable regions in summer and winter do not overlap, dispersal may really be necessary for sustaining a population. Our findings generally align with previous findings in the literature that were based on other modeling frameworks, namely that dispersal strategies associated with ideal free distributions are evolutionarily stable. In the case where only part of the habitat can sustain a population, we show that a partial occupation ideal free distribution that occupies only the viable region is associated with a dispersal strategy that is evolutionarily stable. As in some previous works, the proofs of these results make use of properties of line sum symmetric functions, which are analogous to those of line sum symmetric matrices but applied to integral operators.

Keywords Integrodifference · Ideal free distribution · Spatial ecology · Population dynamics · Migration · Dispersal

Mathematics Subject Classification 92D15 · 92D25 · 92D40

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1 Introduction

The main goal of this paper is to determine which dispersal strategies are predicted by pairwise invasion analysis to be evolutionarily stable (sometimes also known as evolutionarily steady or abbreviated as ESS) in the context of integrodifference models for population dynamics and dispersal in bounded regions. Integrodifference models are widely used in ecology because they are in some ways simpler to analyze and simulate than partial differential equations, they can describe a very wide range of dispersal patterns, and they are based on descriptions of dispersal that can be constructed in a natural way from empirical data; see Lutscher (2019). We consider both the cases where there is only a single season and the population occupies all of the region at each time step, which leads to a fairly typical integrodifference model, and those where there are two seasons and the occupancy may be partial, that is, populations may only occupy parts of the region in either season, which leads to a more complicated form of integrodifference model.

A secondary goal is to develop a framework for studying competition between populations using different dispersal strategies in the setting of integrodifference models which could be used to study the evolution of migration. Similar analyses of evolutionarily steady strategies have been done in various other modeling contexts, including patch models, reaction–diffusion–advection models, and integrodifferential models; see Averill et al. (2012), Cantrell et al. (2010), Cantrell et al. (2012a), Cantrell et al. (2012b), Cantrell et al. (2017), Cantrell and Cosner (2018) and Cosner (2014). In many of those settings the strategies that are evolutionarily stable are those that can produce an ideal free distribution of a population that uses them. The ideal free distribution originated as a verbal description of how a population would distribute itself if individuals could sense what their fitness would be in any given location, taking into account logistic types of crowding effects from the presence of conspecifics, and could move freely to locations where their fitness would be greatest. In spatially explicit models for population dynamics in environments that are heterogeneous in space but static in time a population with an ideal free distribution will exactly match the distribution of resources in the environment (Averill et al. 2012; Cantrell et al. 2010, 2012a, b, 2017; Cosner 2014). In various modeling contexts the notion of line sum symmetry from matrix theory or its extension to integral operators plays an important role in showing which dispersal strategies are evolutionarily steady. That turns out to be the case in the present setting as well. For general background on the evolution of dispersal in reaction-advection-diffusion systems and the ideal free distribution see Cosner (2014). For general background on integrodifference models see Lutscher (2019).

In Hardin et al. (1988) dispersal operators in integrodifference models for a single population were compared in terms of the spectral radii of the models linearized around zero. More specifically, the criterion used in Hardin et al. (1988) to rank a linear dispersal operator was the maximum over a class of growth functions of the infimum of the spectral radius of the linearization at zero population density of the full dispersal and growth operator. Their idea was to rank dispersal operators by asking which were the most likely to result in survival of populations under a range of possible environmental conditions modeled by a set of possible growth functions. They considered the cases of no dispersal at all, uniform dispersal everywhere, and dispersal described by diffusion-like kernels of the form $J(|x-y|)$ for some function $J(x)$. By their criterion they found that among those three types of dispersal, no movement at all is optimal in temporally static environments but dispersing everywhere is optimal in the temporally variable environments they considered. Their criterion is quite different from ours, but their conclusions are roughly consistent with those obtained for reaction-diffusion models when diffusion rates are compared by pairwise invasion analysis. In that setting, in temporally static environments, pairwise invasion analysis shows that there is selection for slower diffusion (see Hastings (1983); Dockery et al. (1998)), so that not diffusing at all is a convergent stable strategy, defined as a strategy such that mutants adopting a strategy closer to it are always selected for (Lam and Lou 2014) (this situation can change if there is advection as well as diffusion, see Lou and Lutscher (2014)).On the other hand, in time periodic environments, there may be selection for faster diffusion; see Hutson et al. (2001). In the temporally static case for both diffusion and integrodifference models there is a connection between the strategy of no movement and the ideal free distribution. In such environments a small logistically growing population that initially has a positive density everywhere will increase to exactly match the resource density wherever that is positive, and thereby the population will achieve an ideal free distribution. However, in temporally variable environments the time average of the population growth rate over time at every point in space might be too small to support a population, but at any given time it might always be large enough at some locations. In that situation a population that did not move would not survive but one that moved correctly might.

We will allow dispersal operators defined by fairly general kernels $k(x, y)$. The reason for this is because in most cases kernels of the form $k(x-y)$ cannot produce an ideal free distribution of population. This is analogous to the case of reaction-advection-diffusion models, where simple Fickian diffusion operators of the form $\nabla \cdot D(x)\nabla$ cannot usually produce an ideal free distribution, but certain more general advection-diffusion operators can. Kernels of the form $k(x-y)$ are not sufficiently flexible to support steady state equilibria that match general resource distributions. For example, because we are considering a population in a bounded region Ω, a kernel of the form $k(x-y)$ will cause some of the population to disperse outside the region. Our analysis of the pairwise invasion problem will be based on the theory of monotone semidynamical systems, so we will always assume that the population growth terms are qualitatively similar to those in the Beverton–Holt model. We first consider the case where there is only one season and populations occupy the entire environment. We then consider the more complicated case where there are distinct summer and winter seasons and populations may only partially occupy the environment. In that case we combine the two transitions from summer to winter and winter to summer to produce a single summer to summer map. Related ideas were used to capture periodic variation in rivers in Jacobsen et al. (2015). If the entire environment is viable and occupied during the summer, the mathematical analysis of the seasonal model can be reduced to that for the single season case. If only part of the environment is viable in the summer, the analysis of the seasonal model requires some new technical results that may be of independent interest. In all cases we give a definition of the ideal free distribution that is appropriate for the class of models, and show that populations using a dispersal strategy that leads to an ideal free distribution can invade and resist invasion by otherwise ecologically similar populations that use dispersal strategies which do not produce an ideal free distribution.

2 Model formulation and main results

In this section, we will construct an integrodifference equation model to study the dynamics of a single-species population that is sessile for most of the year, but redistributes in space twice a year to keep track of the seasonal changes in their habitat. The motivation of the model is that various types of organisms make seasonal migrations twice a year, often as summer turns to winter or as winter turns to summer. Those include bird species ranging from hummingbirds to geese that migrate between northern and southern regions, and ungulates such as elk that move between higher and lower altitudes, among many others. There are also species such as garter snakes that hibernate in groups in refuges over the winter but spread out during the summer. In our model, such redistribution of organisms in space is modeled by taking an integral transformation of the population densities, with an integral kernel referred to as the *redistribution kernel* or often as the *dispersal kernel*. The main variables of the model are $n_{s,t}(x)$ and $n_{w,t}(x)$, which are the density of the population at location x for year t at the beginning of summer (with subscript s) and winter (with subscript w). The habitat of the population is restricted in space to a compact subset Ω of $\mathbb{R}^L$, so that the population density outside Ω is always 0. In cases of applied interest, $1 \leq L \leq 3$.

The model framework is discrete in time. The population density $n_{s,t}(x)$ is mapped to $n_{w,t}(x)$, and then $n_{w,t}(x)$ to $n_{s,t+1}(x)$, $t = 0, 1, 2, \ldots$, by a pair of integral equations such as those below:

$$n_{w,t}(x) = \int_\Omega k_{ws}(x, y)\ Q_s(y)\ \frac{f_0\, n_{s,t}(y)}{1 + b_0 n_{s,t}(y)}\, dy, \tag{1a}$$

$$n_{s,t+1}(x) = \int_\Omega k_{sw}(x, y)\ Q_w(y)\ g_0 n_{w,t}(y)\, dy. \tag{1b}$$

In Eq. (1a), $n_{s,t}(x)$ is first mapped to

$$Q_s(y)\ \frac{f_0\, n_{s,t}(y)}{1 + b_0 n_{s,t}(y)}, \tag{2}$$

to account for the change in the population size when the population is sessile. We assume unless otherwise stated that the functions Q_s and Q_w are continuous on Ω and the kernels k_{ws} and k_{sw} are jointly continuous in x and y on $\Omega \times \Omega$. The function Q_s is a *habitat quality function* with range [0, 1] that describes the summer habitat quality at each location y relative to the maximum possible quality, thereby capturing the spatial heterogeneity of the environment. By multiplying the habitat quality function onto a Beverton–Holt type nonlinear growth function with parameters f_0 and b_0, it is assumed that the spatial heterogeneity of habitat quality affects population growth by rescaling the growth function with Q_s. The population density (2) is then mapped to $n_{w,t}(x)$ by the integral in (1a) with the redistribution kernel $k_{ws}(x, y)$ to account for the spatial redistribution before winter. The redistribution kernel is related to a probability density function: for any location y, $k_{ws}(x, y)$ is the probability density of an individual from location y being redistributed to location x.

Likewise, Eq. (1b) maps $n_{w,t}(x)$ to $n_{s,t+1}(x)$ in a similar way. The relative habitat quality is described by $Q_w(y)$, with range [0, 1], which is multiplied by a maximum population survival rate g_0 to give the absolute winter survival rate at location y. We assume that there is no population growth or density dependent loss during the winter, so that $g_0 \in (0, 1]$ is a constant, and the population density at the end of winter is $Q_w(y)g_0 n_{w,t}(y)$. That density is then mapped to $n_{s,t+1}(x)$ by the integral in (1b) with redistribution kernel $k_{sw}(x, y)$.

The idea of the scaling for habitat quality is that f_0 and g_0 are the maximum growth and survival rates for our populations, which are attained in habitats where the habitat quality is the best possible, corresponding to locations where Q_s and Q_w are equal to 1 and, in the case of the summer season, in locations where the population density approaches 0, because of the density dependence. Thus, we assume that there are always at least some places where the habitat quality achieves its maximum, at least if there is no population present.

We assume that there is no population growth during migration. That is, both k_{ws} and k_{sw} satisfy the no-growth condition

$$\int_\Omega k(x, y)\, dx \le 1, \quad \forall y. \tag{3}$$

2.1 The special case with no winter season

Let us first consider a special case where $k_{ws}(x, y) = \delta(x - y)$, $Q_w(y) \equiv 1$, and $g_0 = 1$. In this case, model (1) takes the condensed form

$$n_{s,t+1}(x) = \int_\Omega k_{sw}(x, y) Q_s(y) \frac{f_0\, n_{s,t}(y)}{1 + b_0 n_{s,t}(y)}\, dy. \tag{4}$$

Equation (4) reflects an absence of a distinct winter season. Instead of migrating twice a year, the population only disperses once a year after summer.

Dropping the s and sw subscripts, so that the density at $x \in \Omega$ and $t \in \mathbb{Z}$ is given by $n_t(x)$, and using a more abstract *fitness* function

$$g[y, n_t(y)] \tag{5}$$

to replace

$$\frac{f_0 Q_s(y)}{1 + b_0 n_t(y)}. \tag{6}$$

Equation (4) can be rewritten in the generalized form

$$n_{t+1}(x) = \int_\Omega k(x, y) g[y, n_t(y)]\, n_t(y)\, dy. \tag{7}$$

Since we assume that there is no population growth during dispersal or migration, $k(x, y)$ satisfies the no-growth condition (3).

When the population, hereafter referred to as population N, does not disperse at all, Eq. (7) becomes

$$n_{t+1}(x) = g[x, n_t(x)]\, n_t(x). \tag{8}$$

Throughout this section we assume that $g[x, n]$ satisfies the following conditions:

(G0) $g[x, n]$ is jointly continuous in x and n on $\Omega \times [0, \infty)$,
(G1) $\forall\, x \in \Omega,\ n > 0, g[x, n] > 0$,
(G2) $\forall\, x \in \Omega$, if $n_1 > n_2 \geq 0$, then $g[x, n_1] < g[x, n_2]$,
(G3) $\forall\, x \in \Omega$, if $n_1 > n_2 \geq 0$, then $g[x, n_1]\, n_1 > g[x, n_2]\, n_2$.

Clearly, the formulation (6), as a function of $n_t(x)$, with the assumption $\forall\, x \in \Omega$, $Q_s(x) > 0$, meets conditions (G0)–(G3). For most of the cases we consider (except in Sect. 2.3), we make an additional assumption:

(G4) $g[x, n(x)]$ is a function such that Eq. (8) has a unique nontrivial equilibrium $n^*(x)$ that is continuous and asymptotically stable, and

$$n^*(x) > 0,\ \forall x \in \Omega. \tag{9}$$

Since this equilibrium satisfies

$$g[x, n^*(x)] = 1, \tag{10}$$

it describes how a population would be distributed so that the fitness at each location would be 1, which would keep the population at equilibrium when there is no dispersal. Under condition G2, condition G4 implies that $g[x, 0] > 1$ on Ω.

In Sect. 2.3 we consider cases where G1 and G4 are replaced by weaker conditions which allow cases where $g[x, 0] > 1$ only on part of Ω. However, in such cases we must assume some additional technical conditions on $g[x, n]$ and on the dispersal kernels.

We will hereafter refer to the dispersal kernel for population N as k^N, and assume that k^N satisfies the no-flux boundary condition

$$\int_\Omega k(x, y)\, dx = 1, \quad \forall y, \tag{11}$$

which is stronger than the no-growth condition (3). As we will see in the comment below Definition 1, condition (11) is necessary to produce an ideal free distribution if we already assume the no-growth condition (3).

Definition 1 The population N described by $n_t(x)$ in equation (7) is adopting an *ideal free dispersal strategy* $k^N(x, y)$ (relative to $n^*(x)$) on Ω if the dispersal kernel $k^N(x, y)$ satisfies the no-flux boundary condition (11) and

$$n^*(x) = \int_\Omega k^N(x, y) n^*(y)\, dy, \tag{12}$$

where $n^*(x)$ is defined by (10).

Comments: If k^N satisfies the no-growth condition (3), but $\int_\Omega k^N(x, y)dx < 1$ for some y, then integrating (12) over Ω with respect to x leads to the contradiction $\int_\Omega n^*(x)dx < \int_\Omega n^*(y)dy$, so the ideal free condition implicitly requires k^N to satisfy the no-flux boundary condition (11). Hence the assumption of condition (11) .

If $k(x, y)$ is positive and jointly continuous in x and y and satisfies (3), g satisfies (G0)–(G3), and there is a constant $C > 0$ such that $g(x, n) < 1$ for $n > C$, then the operator defined by

$$n(x) \mapsto \int_\Omega k(x, y) g[y, n(y)] n(y)\, dy$$

has compactness and monotonicity properties which imply that the model

$$n_{t+1}(x) = \int_\Omega k(x, y) g[y, n_t(y)] n_t(y)\, dy$$

has a unique positive equilibrium $\hat{n}(y)$, which is globally asymptotically stable among positive solutions, if and only if the equilibrium $n(y) \equiv 0$ is unstable. See for example the discussion in Lutscher (2019), Chs. 3 and 4. We will use these and related ideas later. In general, $\hat{n} \neq n^*$, where n^* is as in (10). In particular, it is usually not possible to achieve an ideal free distribution (that is, we have $\hat{n} \neq n^*$) in the case of a symmetric kernel of the form $k(|x - y|)$. This is analogous to the observation that in the reaction-diffusion setting, it is generally impossible to achieve an ideal free distribution via simple diffusion, although it is possible if there is advection that varies with location. This is the reason why we need to allow kernels of the form $k(x, y)$. One way to achieve an ideal free distribution would be to take $k(x, y) = k(x) = n^*(x)/\int_\Omega n^*(x)dx$, so that dispersal is not influenced by conditions at the departure point y but only by those at the arrival point x.

An ideal free dispersal strategy allows the population to reach an equilibrium that is the same as the equilibrium without dispersal. In what follows in this section, we will show that with proper assumptions, an ideal free strategy defined by (12) is an *evolutionarily stable strategy*, meaning it cannot be invaded by another population adopting a non-ideal-free strategy. To elaborate, we introduce a population of mutants, referred to as population M, whose density is described by $m_t(x)$ and kernel by $k^M(x, y)$, and let the two populations engage in a competitive relationship when it comes to resources and space. We assume that the two populations only differ in their dispersal, and are the same in other ecological aspects. Thus the competition between the two populations can be modeled by the following equations:

$$n_{t+1}(x) = \int_\Omega k^N(x, y) g[y, n_t(y) + m_t(y)]\, n_t(y)\, dy, \tag{13a}$$

$$m_{t+1}(x) = \int_\Omega k^M(x, y) g[y, n_t(y) + m_t(y)]\, m_t(y)\, dy. \tag{13b}$$

In system (13), $k^N(x, y)$ is an ideal free dispersal strategy relative to $n^*(x)$ adopted by species N, and $k^M(x, y)$ is the dispersal strategy adopted by species M, which is not ideal free. Both kernels satisfy (3). In addition to assumptions (G0)–(G3), we also assume system (13) has a unique semi-trivial equilibrium $(n^*(x), 0)$ when $m_t(x) \equiv 0$. We aim to show that this equilibrium $(n^*(x), 0)$ is globally asymptotically stable, which implies that the dispersal strategy $k^N(x, y)$ is an evolutionarily-stable strategy according to the following definitions.

Definition 2 Suppose $n^*(x)$ is an asymptotically stable equilibrium of (7). This equilibrium is *invasible* by $m_t(x)$ if $m_t(x) \equiv 0$ is unstable relative to nonnegative initial data in equation (13b). If $m_t(x) \equiv 0$ is stable relative to nonnegative initial data in equation (13b), then $n^*(x)$ is *not invasible*.

Definition 3 A dispersal strategy $k^N(x, y)$ in (12) with corresponding asymptotically stable equilibrium $n^*(x)$ is *evolutionarily stable* with respect to $n_t(x)$ if $n^*(x)$ is not invasible by any small population $m_t(x)$ using another dispersal strategy.

We will first establish a lemma regarding line-sum symmetry, as defined below.

Definition 4 (Cantrell et al. 2012b, Theorem 4) A continuous function f on the set $\Omega \times \Omega$ is said to be *line-sum symmetric* if it satisfies

$$\int_\Omega f(y, x)\, dy = \int_\Omega f(x, y)\, dy. \tag{14}$$

Lemma 1 *Conditions* (11) *and* (12) *imply that the function* $k^N(x, y)n^*(y)$ *is line-sum symmetric.*

Proof The fact that $k^N(x, y)n^*(y)$ is line-sum symmetric is verified by the calculation below:

$$\int_\Omega k^N(y, x)\, n^*(x)\, dy = n^*(x) \int_\Omega k^N(y, x)\, dy \tag{15a}$$

$$= n^*(x) \tag{15b}$$

$$= \int_\Omega k^N(x, y)\, n^*(y)\, dy. \tag{15c}$$

□

We will first restate Theorem 4 of (Cantrell et al. 2012b) below because we will make frequent use of this theorem. It is valid in any space dimension.

Theorem 1 (Cantrell et al. 2012b, Theorem 4) *Let f be a nonnegative continuous function on $\Omega \times \Omega$. Then f is line-sum symmetric if and only if*

$$\int_\Omega \int_\Omega f(x, y) \frac{\psi(x)}{\psi(y)} \, dx \, dy \geq \int_\Omega \int_\Omega f(x, y) \, dx \, dy \tag{16}$$

for any positive continuous function $\psi > 0$ on Ω. In addition, if f is line sum symmetric and

$f(x, y) > 0$, $\forall (x, y) \in \Omega \times \Omega$, then equality in (16) holds if and only if ψ is constant.

Lemma 2 *Assume $k^N(x, y)$ and $k^M(x, y)$ are continuous functions that satisfy both condition (3) and the positivity condition*

$$k(x, y) > 0, \forall (x, y) \in \Omega \times \Omega. \tag{17}$$

Assume also that the kernels $k^N(x, y)$ and $k^M(x, y)$ are such that population N, described by $n_t(x)$, adopts an ideal free dispersal strategy relative to $n^*(x)$, and population M, described by $m_t(x)$, does not adopt an ideal free dispersal strategy relative to $n^*(x)$. Finally, assume $g[x, n]$ satisfies (G0)–(G4). Then system (13) does not have a coexistence equilibrium $(n(x), m(x))$ where $n(x)$ and $m(x)$ are both nonzero.

Proof We will prove the lemma by contradiction. Suppose the contrary, that there is a solution $(n(x), m(x))$ to the system

$$n(x) = \int_\Omega k^N(x, y) \, g[y, n(y) + m(y)] \, n(y) \, dy, \tag{18a}$$

$$m(x) = \int_\Omega k^M(x, y) \, g[y, n(y) + m(y)] \, m(y) \, dy, \tag{18b}$$

with both components nonzero. Because of the positivity condition (17), the two components $n(x)$ and $m(x)$ must be strictly positive. We will show that this means population M also adopts an ideal free strategy relative to $n^*(x)$, which contradicts the assumptions of the lemma.

To begin, we multiply both sides of equation (18a) with $\psi(x)$, where

$$\psi(x) = \frac{n^*(x)}{g[x, n(x) + m(x)]n(x)}. \tag{19}$$

This fraction is well-defined because of the strict positivity of n and m and assumption (G1). Thus we obtain

$$\frac{n^*(x)}{g[x,n(x)+m(x)]} = \int_\Omega k^N(x,y)\frac{g[y,n(y)+m(y)]n^*(x)n(y)}{g[x,n(x)+m(x)]n(x)}\,dy \tag{20a}$$

$$= \int_\Omega k^N(x,y)n^*(y)\cdot\frac{g[y,n(y)+m(y)]n(y)}{g[x,n(x)+m(x)]n(x)}\cdot\frac{n^*(x)}{n^*(y)}\,dy \tag{20b}$$

$$= \int_\Omega k^N(x,y)n^*(y)\,\frac{\psi(x)}{\psi(y)}\,dy, \tag{20c}$$

while (9) is also invoked to ensure the fractions are well-defined. Integrating both sides with respect to x, we get

$$\int_\Omega \frac{n^*(x)}{g[x,n(x)+m(x)]}\,dx = \int_\Omega\int_\Omega k^N(x,y)n^*(y)\,\frac{\psi(x)}{\psi(y)}\,dydx \tag{21a}$$

$$\geq \int_\Omega\int_\Omega k^N(x,y)n^*(y)\,dydx. \tag{21b}$$

The inequality in the last step is due to inequality (16) and $k^N(x,y)n^*(y)$ being line-sum symmetric.

Since $k^N(x,y)$ is an ideal free dispersal strategy, $k^N(x,y)$ integrates to 1 with respect to x [condition (11)], so

$$\int_\Omega\int_\Omega k^N(x,y)n^*(y)\,dydx = \int_\Omega n^*(x)\,dx, \tag{22}$$

and the last inequality in (21) can be replaced by

$$\int_\Omega \frac{n^*(x)}{g[x,m(x)+n(x)]}\,dx \geq \int_\Omega n^*(x)\,dx. \tag{23}$$

Therefore

$$\int_\Omega n^*(x)\left\{\frac{1-g[x,m(x)+n(x)]}{g[x,m(x)+n(x)]}\right\}\,dx \geq 0. \tag{24}$$

On the other hand, adding Eqs. (18a)–(18b), integrating both sides, and using the conditions (11) for k^N and (3) for k^M yields

$$\int_\Omega [m(x)+n(x)]\cdot\{1-g[x,m(x)+n(x)]\}\,dx \leq 0. \tag{25}$$

Subtracting (25) from (24), we obtain

$$\int_\Omega \left\{\frac{n^*(x)}{g[x,m(x)+n(x)]} - [m(x)+n(x)]\right\}\cdot\{1-g[x,m(x)+n(x)]\}\,dx \geq 0. \tag{26}$$

Rewriting inequality (26) and using (10), we obtain

$$\int_\Omega \frac{n^*(x) - [m(x)+n(x)]g[x,m(x)+n(x)]}{g[x,m(x)+n(x)]} \cdot \{1 - g[x,m(x)+n(x)]\}\ dx \quad (27a)$$

$$= \int_\Omega \frac{n^*(x)g[x,n^*(x)] - [m(x)+n(x)]g[x,m(x)+n(x)]}{g[x,m(x)+n(x)]} \quad (27b)$$

$$\cdot \left\{g[x,n^*(x)] - g[x,m(x)+n(x)]\right\}\ dx \quad (27c)$$

$$\geq 0. \quad (27d)$$

But the integrand satisfies

$$\frac{n^*(x)g[x,n^*(x)] - [m(x)+n(x)]g[x,m(x)+n(x)]}{g[x,m(x)+n(x)]} \cdot \left\{g[x,n^*(x)] - g[x,m(x)+n(x)]\right\} \leq 0 \quad (28)$$

because the two factors

$$n^*(x)g[x,n^*(x)] - [m(x)+n(x)]g[x,m(x)+n(x)] \quad (29)$$

and

$$g[x,n^*(x)] - g[x,m(x)+n(x)] \quad (30)$$

are of opposite signs. This is because $g(x,n)$ is monotonically decreasing with respect to n but $g(x,n)n$ is monotonically increasing with respect to n. Depending on whether $n^*(x)$ is larger or smaller than $n(x)+m(x)$, one of the two factors is positive and the other is negative. Since the integral of a nonpositive integrand is nonpositive, the only possibility is that the integrand is 0. Therefore

$$n^*(x) = m(x) + n(x). \quad (31)$$

This also means inequalities (21) and (26) are, in fact, both equalities. Therefore

$$\int_\Omega \int_\Omega k^N(x,y)n^*(y) \cdot \frac{\psi(x)}{\psi(y)}\ dydx = \int_\Omega \int_\Omega k^N(x,y)n^*(y)\ dydx. \quad (32)$$

Because the function $k^N(x,y)n^*(y)$ is line-sum symmetric and strictly positive, Theorem 1 implies that equality (32) is achieved only if ψ is a constant. So we have

$$\frac{n^*(x)}{n(x)} = \frac{n^*(y)}{n(y)}. \quad (33)$$

Therefore $\frac{n^*(x)}{n(x)}$ must be constant, so for some constant $c > 0$ we have

$$\frac{n^*(x)}{n(x)} = \frac{1}{c}. \quad (34)$$

Thus we have

$$n(x) = cn^*(x), \tag{35}$$

and

$$m(x) = (1 - c)n^*(x). \tag{36}$$

As a result, Eq. (18b) is equivalent to

$$\begin{aligned}(1 - c)n^*(x) &= \int_\Omega k^M(x, y)g[y, m(y) + n(y)](1 - c)n^*(y)\, dy \\ &= \int_\Omega k^M(x, y)g[y, n^*(y)](1 - c)n^*(y)\, dy \\ &= \int_\Omega k^M(x, y)(1 - c)n^*(y)\, dy.\end{aligned} \tag{37}$$

If $c \neq 1$, then

$$n^*(x) = \int_\Omega k^M(x, y)n^*(y)\, dy. \tag{38}$$

If $\int_\Omega k^M(x, y)dx < 1$, then integrating equation (38) in x leads to the contradiction $\int_\Omega n^*(x)\, dx < \int_\Omega n^*(y)\, dy$. If $\int_\Omega k^M(x, y)dx = 1$, then (38) implies $k^M(x, y)$ is also an ideal free strategy relative to $n^*(x)$, which is a contradiction to the assumptions of this lemma. Therefore system (13) does not have a coexistence equilibrium $(n(x), m(x))$ where $n(x)$ and $m(x)$ are both nonzero, and the lemma is proved. □

Lemma 3 *Under the assumptions of the previous lemma, if system* (13) *has a semitrivial equilibrium* $(0, m^*)$*, then this equilibrium* $(0, m^*)$ *must be unstable.*

Proof Consider the eigenvalue problem

$$\lambda\phi(x) = \int_\Omega k^N(x, y)g[y, m^*(y)]\phi(y)\, dy. \tag{39}$$

With our assumptions, the integral operator defined by the right-hand side of Eq. (39) is completely continuous (see Hardin et al. (1990)). Because $k^N(x, y)$ satisfies the positivity condition (17), the Krein–Rutman theorem (Krein and Rutman 1962) guarantees this integral operator has an eigenfunction $\phi(x)$, corresponding to the dominant eigenvalue λ of the operator, that is strictly positive in Ω. In order to show that $(0, m^*)$ is unstable, we need to show that $\lambda > 1$.

To begin, notice that $m^*(x)$ must satisfy the positivity condition

$$m^*(x) > 0,\ \forall x \in \Omega, \tag{40}$$

because $k^M(x, y)$ meets the positivity condition (17). Multiplying both sides of the eigenvalue problem equation (39) by

$$\frac{n^*(x)}{\phi(x)g[x, m^*(x)]}, \tag{41}$$

we obtain

$$\frac{n^*(x)}{\phi(x)g[x, m^*(x)]} \cdot \lambda\phi(x) = \int_\Omega k^N(x, y) \cdot \frac{n^*(x)}{\phi(x)g[x, m^*(x)]} \cdot \phi(y)g[y, m^*(y)]\, dy \tag{42a}$$

$$= \int_\Omega k^N(x, y)n^*(x) \cdot \frac{\phi(y)g[y, m^*(y)]}{\phi(x)g[x, m^*(x)]}\, dy \tag{42b}$$

$$= \int_\Omega k^N(x, y)n^*(y) \cdot \frac{\phi(y)g[y, m^*(y)]/n^*(y)}{\phi(x)g[x, m^*(x)]/n^*(x)}\, dy. \tag{42c}$$

Therefore

$$\frac{\lambda n^*(x)}{g[x, m^*(x)]} = \int_\Omega k^N(x, y)n^*(y) \cdot \frac{\phi(y)g[y, m^*(y)]/n^*(y)}{\phi(x)g[x, m^*(x)]/n^*(x)}\, dy. \tag{43}$$

Integrating both sides, we get

$$\lambda \int_\Omega \frac{n^*(x)}{g[x, m^*(x)]}\, dx = \int_\Omega \int_\Omega k^N(x, y)n^*(y) \cdot \frac{\phi(y)g[y, m^*(y)]/n^*(y)}{\phi(x)g[x, m^*(x)]/n^*(x)}\, dydx. \tag{44}$$

Since $k^N(x, y)$ is an ideal free strategy, function $k^N(x, y)n^*(y)$ is line-sum symmetric, and Theorem 1 implies

$$\int_\Omega \int_\Omega k^N(x, y)n^*(y) \cdot \frac{\phi(y)g[y, m^*(y)]/n^*(y)}{\phi(x)g[x, m^*(x)]/n^*(x)}\, dydx \geq \int_\Omega \int_\Omega k^N(x, y)n^*(y)dydx$$
$$= \int_\Omega n^*(x)\, dx. \tag{45}$$

Thus Eq. (44) can be replaced by the inequality

$$\lambda \int_\Omega \frac{n^*(x)}{g[x, m^*(x)]}\, dx \geq \int_\Omega n^*(x)\, dx. \tag{46}$$

The last inequality means that

$$(\lambda - 1) \int_\Omega \frac{n^*(x)}{g[x, m^*(x)]}\, dx \geq \int_\Omega n^*(x) \left\{1 - \frac{1}{g[x, m^*(x)]}\right\} dx$$
$$= \int_\Omega n^*(x) \left\{\frac{g[x, m^*(x)] - 1}{g[x, m^*(x)]}\right\} dx \tag{47}$$

Meanwhile, by definition, function $m^*(x)$ must satisfy the equation

$$m^*(x) = \int_\Omega k^M(x, y) g[y, m^*(y)]\, m^*(y)\, dy. \tag{48}$$

Integrating both sides of (48), and using the fact that $k^M(x, y)$ satisfies condition (3), we get

$$\int_\Omega m^*(x)\, dx \leq \int_\Omega g[y, m^*(y)]\, m^*(y)\, dy = \int_\Omega g[x, m^*(x)]\, m^*(x)\, dx. \tag{49}$$

Therefore

$$\int_\Omega m^*(x)\{1 - g[x, m^*(x)]\}\, dx \leq 0. \tag{50}$$

That means

$$\int_\Omega n^*(x) \left\{ \frac{g[x, m^*(x)] - 1}{g[x, m^*(x)]} \right\} dx \tag{51a}$$

$$\geq \int_\Omega \left\{ n^*(x) - m^*(x) g[x, m^*(x)] \right\} \cdot \left\{ \frac{g[x, m^*(x)] - 1}{g[x, m^*(x)]} \right\} dx \tag{51b}$$

$$= \int_\Omega \left\{ g[x, n^*(x)] n^*(x) - g[x, m^*(x)] m^*(x) \right\} \cdot \left\{ \frac{g[x, m^*(x)] - g[x, n^*(x)]}{g(x, m^*(x))} \right\} dx \tag{51c}$$

$$\geq 0. \tag{51d}$$

Inequality (51) becomes an equality only when

$$g[x, m^*(x)] = g[x, n^*(x)] = 1, \tag{52}$$

and

$$m^*(x) = n^*(x), \tag{53}$$

resulting in

$$n^*(x) = m^*(x) = \int_\Omega k^M(x, y) g[y, m^*(y)]\, m^*(y)\, dy. \tag{54}$$

Since population M is not adopting an ideal free strategy relative to $n^*(x)$, $k^M(x, y)$ cannot be such that Eq. (54) holds. Therefore inequality (51) is strict, and

$$(\lambda - 1) \int_\Omega \frac{n^*(x)}{g[x, m^*(x)]}\, dx > 0. \tag{55}$$

Therefore

$$\lambda > 1, \tag{56}$$

and the lemma is proved. □

Theorem 2 *With the same assumptions as the previous two lemmas, the semi-trivial equilibrium* $(n^*(x), 0)$ *of system* (13) *is globally asymptotically stable, and the ideal free dispersal strategy* $k^N(x, y)$*, as defined in Definition* 1*, is an evolutionarily stable strategy.*

Proof Let the spaces X_1 and X_2 be $X_i = C(\Omega)$, the space of all continuous functions on Ω, for $i = 1, 2$. Let them be equipped with positive cones $X_i^+ = C^+(\Omega)$, the set of all nonnegative functions in $C(\Omega)$, for $i = 1, 2$. The cones X_i^+ generate the order relations $\leq, <, \ll$ in the usual way. The cone $K = X_1^+ \times (-X_2^+)$ generates the partial order relations $\leq_K, <_K, \ll_K$ in the sense that $(n, m) \leq_K (\bar{n}, \bar{m})$ is equivalent to $n \leq \bar{n}$ and $\bar{m} \leq m$, and likewise for $<_K$ and $\ll_K$.

Let $X^+ = X_1^+ \times X_2^+$, and the operator $T : X^+ \to X^+$ be defined as

$$T \begin{bmatrix} n(x) \\ m(x) \end{bmatrix} = \begin{bmatrix} \int_\Omega k^N(x, y) g[y, n(y) + m(y)]\, n(y)\, dy \\ \int_\Omega k^M(x, y) g[y, n(y) + m(y)]\, m(y)\, dy \end{bmatrix}. \tag{57}$$

We will first verify the following properties of T:

(P1) T is order compact. That is, for every $(n, m) \in X^+$, $T([0, n] \times [0, m])$ has compact closure in X.
(P2) T is strictly order-preserving with respect to $<_K$. That is, $n < \bar{n}$ and $\bar{m} < m$ implies $T(n, m) <_K T(\bar{n}, \bar{m})$.
(P3) $T(X_1^+ \times \{0\}) \subset X_1^+ \times \{0\}$. There exists $\hat{n}$ such that $0 \ll \hat{n}$, $T(\hat{n}, 0) = (\hat{n}, 0)$, and $T^t(n_0, 0) \to (\hat{n}, 0)$, $\forall\, n_0,\ 0 < n_0$.

To verify property (P1), first notice that operator T is compact because Ω is a bounded set, and the dispersal kernels $k^N(x, y)$ and $k^M(x, y)$ are both continuous. Since any order interval pair $([0, n] \times [0, m])$ is bounded in X^+, it has a relatively compact image. Therefore T is order compact.

The fact that the order-preserving property in (P2) is satisfied comes from assumptions (G2) and (G3). For any $n < \bar{n}$ and $\bar{m} < m$, the monotonicity of $g(x, n) \cdot n$ means

$$g(x, n + m) \cdot (n + m) < g(x, \bar{n} + m) \cdot (\bar{n} + m). \tag{58}$$

Expanding the terms in both sides yields

$$g(x, n + m) \cdot n + g(x, n + m) \cdot m < g(x, \bar{n} + m) \cdot \bar{n} + g(x, \bar{n} + m) \cdot m \tag{59}$$

But the second terms on both sides are compared by the inequality

$$g(x, n+m) \cdot m > g(x, \bar{n}+m) \cdot m, \quad \forall x \in \Omega. \tag{60}$$

because $g(x, n)$ is monotonically decreasing. Therefore $g(x, n+m) \cdot n < g(x, \bar{n}+m) \cdot \bar{n}$. Meanwhile, $\bar{m} < m$ means

$$g(x, \bar{n}+m) < g(x, \bar{n}+\bar{m}), \tag{61}$$

and $g(x, \bar{n}+m) \cdot \bar{n} < g(x, \bar{n}+\bar{m}) \cdot \bar{n}$. Therefore $g(x, n+m) \cdot n < g(x, \bar{n}+\bar{m}) \cdot \bar{n}$ as well. A parallel argument can be made to show that $g(x, n+m) \cdot \bar{m} < g(x, \bar{n}+\bar{m}) \cdot m$, and we can conclude that $T(n, m) <_K T(\bar{n}, \bar{m})$.

It is clear that $T(X_1^+ \times \{0\}) \subset X_1^+ \times \{0\}$. To verify property (P3), we begin by noticing that the ideal free distribution $n^*(x)$, as defined in (10), satisfies $T(n^*(x), 0) = (n^*(x), 0)$. The interior of the cone X_1^+ consists of all functions that are positive everywhere in Ω, therefore by assumption (G4), $0 \ll n^*(x)$. To show that $T^t(n_0, 0) \to (n^*(x), 0), \forall\, n_0,\ 0 < n_0$, we will verify that T, when restricted to $X_1 \times \{0\}$, satisfies the assumptions of Theorem 2.3.4 of Zhao (2003). First of all, because of assumption (G3), T is monotone when restricted to X_1. Assumptions (G1)–(G3) also ensure that $f(x, n) = g(x, n) \cdot n$ satisfies

$$f(x, \alpha n) > \alpha f(x, n), \ \forall \alpha \in (0, 1). \tag{62}$$

Therefore T is also strongly subhomogeneous (Zhao 2003 Definition 2.3.1) on $X_1 \times \{0\}$. We know T is continuous and compact on $X_1 \times \{0\}$ so it is asymptotically smooth (Zhao 2003, Definition 1.1.2). The same is true of the Fréchet derivative of T at (0, 0). Assumptions (G1)–(G3) and condition (11) ensure that every orbit of T is bounded on $X_1 \times \{0\}$. The positivity assumption (17) being satisfied by $k^N(x, y)$ ensures that the Fréchet derivative of T at (0, 0), when restricted to $X_1 \times \{0\}$, is strongly positive. We can now invoke Theorem 2.3.4 of Zhao (2003) to conclude that either (0, 0) is the only fixed point of T on $X_1 \times \{0\}$, or there exists a semitrivial fixed point of T that is globally asymptotically stable when T is restricted to $X_1 \times \{0\}$. Because we have already shown the existence of a semitrivial fixed point $(n^*(x), 0)$, the latter is clearly the case. Thus, letting $\hat{n} = n^*(x)$ suffices for (P3).

Property (P3) shows that the resident population $n_t(x)$ is an "adequate" competitor in the sense that it can persist on its own when the other competitor is absent. Meanwhile, there are two possibilities when it comes to the invader population $m_t(x)$. Either there exists a semi-trivial equilibrium $(0, \tilde{m})$ such that $\tilde{m} \neq 0$, $T(0, \tilde{m}) = (0, \tilde{m})$, or such an equilibrium does not exist.

Assume it is the first case. Then we can show that T satisfies the assumptions of Theorem A in Hsu et al. (1996), which are the following:

- (H1) T is order compact. That is, for every $(n, m) \in X^+$, $T([0, n] \times [0, m])$ has compact closure in X.
- (H2) T is strictly order-preserving with respect to $<_K$. That is, $n < \bar{n}$ and $\bar{m} < m$ implies $T(n, m) <_K T(\bar{n}, \bar{m})$.

(H3) $T(0) = 0$, and 0 is a repelling point in the sense that there exists a neighborhood U of 0 in X^+ such that $\forall\,(n, m) \in U \backslash \{0\}$, $\exists\, t$, $t \in Z$, such that $T^t(n, m) \notin U$.

(H4) $T(X_1^+ \times \{0\}) \subset X_1^+ \times \{0\}$. There exists $0 \ll \hat{n}$ such that $T(\hat{n}, 0) = (\hat{n}, 0)$, and $T^t(n_0, 0) \to (\hat{n}, 0)$, $\forall\, n_0 > 0$. Likewise for T on $\{0\} \times X_2$, with fixed point $(0, \tilde{m})$.

(H5) If $(n_1, m_1) <_K (n_2, m_2)$, and either (n_1, m_1) or (n_2, m_2) belongs to $Int(X^+)$, then $T(n_1, m_1) \ll_K T(n_2, m_2)$. If $(n, m) \in X^+$ satisfies $n, m \neq 0$, then $T(n, m) \gg 0$.

Assumptions (H1) and (H2) are the same as (P1) and (P2). Assumption (H3) is true, because the positivity condition in assumption (G4) means $g[x, 0] > 1$, $\forall\, x \in \Omega$. The first part of assumption (H4) is the same as property (P3), and the second part is true because in the case where the semi-trivial equilibrium $(0, \tilde{m})$ exists, it also has the property that $\forall\, m_0$, $0 < m_0$, $T^t(0, m_0) \to (0, \tilde{m})$ as $t \to \infty$. This is true because all assumptions of Theorem 2.3.4 of Zhao (2003) are satisfied by T when restricted to $\{0\} \times X_2$, just like in the case of T restricted on $X_1 \times \{0\}$. The interiors of $X_i^+, i = 1, 2$ both consist of strictly positive functions on Ω. Because $k^N(x, y)$ and $k^M(x, y)$ both satisfy the positivity condition (17), if $(n, m) \in X^+$ satisfies $n \neq 0$, $m \neq 0$, then both components of $T(n, m)$ are strictly positive functions, and therefore $T(n, m) \gg 0$. Likewise, for $(n_1, m_1) <_K (n_2, m_2)$, $T(n_1, m_1) \ll_K T(n_2, m_2)$. Therefore (H5) is satisfied as well.

Since we have shown in Lemma 2 that there is not a nontrivial equilibrium of system (13) with both components nonzero, and operator T satisfies conditions (H1) − (H5), from Theorem A in Hsu et al. (1996), $\forall\,(n, m) \in X^+$, either $T^t(n, m) \to (\hat{n}, 0)$ or $T^t(x) \to (0, \tilde{m})$. Since Lemma 3 showed the latter cannot be the case, it must be that $T^t(n, m) \to (\hat{n}, 0) = (n^*(x), 0)$. Therefore the semi-trivial equilibrium $(n^*(x), 0)$ of system (13) is globally asymptotically stable. This implies that $n^*(x)$ is not invasible, and by Definition 3, the ideal free dispersal strategy $k^N(x, y)$ is an evolutionarily-stable strategy.

If it is the case that a semi-trivial equilibrium $(0, \tilde{m})$ does not exist, the argument in the second half of Theorem 3.3 of Kirkland et al. (2006) applies, and we can still conclude that the semi-trivial equilibrium $(n^*(x), 0)$ of system (13) is globally asymptotically stable. Thus, with the assumptions of this theorem, the ideal free dispersal strategy $k^N(x, y)$ is an evolutionarily stable strategy. □

2.2 The two-season case with both summer and winter seasons

Now let us consider the two-season model (1). We use k_{sw}^N and k_{ws}^N to represent the redistribution kernels for the population N. Equations (1a) and (1b) can be combined as one equation that maps $n_{s,t}(x)$ to $n_{s,t+1}(x)$,

$$n_{s,t+1}(x) = \int_\Omega \int_\Omega k_{sw}^N(x, z)\; Q_w(z)\; k_{ws}^N(z, y) \;\cdot\; \frac{f_0 g_0 Q_s(y)\, n_{s,t}(y)}{1 + b_0 n_{s,t}(y)}\, dy dz. \quad (63)$$

Let

$$g[x, u(x)] = \frac{f_0 g_0\, Q_s(x)}{1 + b_0 u(x)}, \tag{64}$$

and let

$$k^N(x, y) = \int_\Omega k^N_{sw}(x, z)\, Q_w(z)\, k^N_{ws}(z, y)dz. \tag{65}$$

Note that since we assume in general that (3) holds for kernels k^N_{ws} and k^N_{sw}, and also $0 \le Q_w(z) \le 1$, we have

$$\int_\Omega k^N(x, y)dx \le \int_\Omega Q_w(z)\, k^N_{ws}(z, y)dz \le \int_\Omega k^N_{ws}(z, y)dz \le 1, \tag{66}$$

so that $k^N(x, y)$ satisfies (3) as well. We can now rewrite (63) as

$$n_{s,t+1}(x) = \int_\Omega k^N(x, y)g[y, n_{s,t}(y)]n_{s,t}(y)\, dy, \tag{67}$$

which exactly recovers (7). Thus, we can reduce the two-season case to a single season model for $n_{s,t}(x)$ of the type we have already treated. Then we can define an ideal free distribution in terms of the solution $n^*_s(x)$ of

$$g[x, n^*_s(x)] = 1 \tag{68}$$

exactly as in the single season case by using Definition 1. We can think of $n^*_s(x) = n^*(x)$ as the ideal free distribution in the summer season for the two-season case, which then determines the ideal free distribution in the winter via equation (1a).

To show the evolutionary stability of ideal free dispersal, we consider the two-species competition model based on model (63), (64):

$$n_{s,t+1}(x) = \int_\Omega \int_\Omega k^N_{sw}(x, z)Q_w(z)k^N_{ws}(z, y)\, g[y, n_{s,t}(y) + m_{s,t}(y)]n_{s,t}(y)\, dz\, dy, \tag{69a}$$

$$m_{s,t+1}(x) = \int_\Omega \int_\Omega k^M_{sw}(x, z)Q_w(z)k^M_{ws}(z, y)\, g[y, n_{s,t}(y) + m_{s,t}(y)]m_{s,t}(y)\, dz\, dy, \tag{69b}$$

and convert it to the single season system (13) by defining $k^M(x, y)$ in the same way as $k^N(x, y)$. By applying Theorem 2 to that system, we obtain the following.

Theorem 3 *Suppose that the densities of populations M and N satisfy* (69) *and the kernel $k^N(x, y)$ defined in* (65)*, the analogous kernel $k^M(x, y)$, and $g[x, n(x)]$ satisfy the hypotheses of Lemma* 2*. Then the semi-trivial equilibrium $(n^*(x), 0)$ of system* (69) *is globally asymptotically stable, and the ideal free dispersal strategy $k^N(x, y)$,* *as defined in Definition 1, is an evolutionarily-stable strategy relative to strategies that are not ideal free.*

Discussion: The interesting issue that remains is to determine what conditions on $k_{sw}^N, k_{ws}^N, k_{sw}^M, k_{ws}^M$, and Q_w are needed for k^N and k^M to have the necessary continuity and positivity properties, and for k^N to satisfy the ideal free condition in Definition 1. We also need to understand what those conditions mean biologically. Let us first consider the requirements we impose on all our redistribution kernels, whether they are ideal free or not. Recall that $Q_s(x)$ and $Q_w(x)$ describe the spatial distribution of habitat quality, which we have arbitrarily scaled to the range [0, 1], and the maximum summer growth rate and winter survival rate are given by f_0 and g_0. So the effective local fitness in winter at location x would be described by $g_0 Q_w(x)$, while in summer it would be $Q_s(x)$ multiplied by a density dependent growth term scaled by f_0. If Q_s and Q_w are positive and continuous on Ω, and the kernels k_{ws}^M, k_{ws}^N, k_{sw}^M, and k_{sw}^N are positive and jointly continuous in x and y on $\Omega \times \Omega$ and satisfy (3), then the kernels $k^N(x, y)$ and $k^M(x, y)$ will be positive and jointly continuous in x and y, and by (66) they will satisfy (3). Since we need $g[x, n(x)] > 0$ in Ω, we need $Q_s(x) > 0$ in Ω.

Now let us consider what conditions can be weakened. It is clear that $k_{sw}^N(x, z)$ and $k_{sw}^M(x, z)$ need to be continuous in x and positive for $x \in \Omega$. However, because k_{ws}^N, k_{ws}^M, and Q_w only occur in integrated forms, we do not always need to require $Q_w(z)$, $k_{ws}^N(z, y)$ or $k_{ws}^M(z, y)$ to be positive for all z, or to be continuous, for $k^N(x, y)$ and $k^M(x, y)$ to have the desired properties. In particular, our models allow for the possibility that there are places that are uninhabitable in winter, so that $Q_w(z) = 0$ for some locations $z \in \Omega$; and also the possibility that only part of the overall environment Ω is occupied during the winter, so that $k_{ws}^N(z, y) = 0$ or $k_{ws}^M(z, y) = 0$ for some z. On the other hand, to allow the corresponding possibility that Ω is only partially occupied in the summer requires either a change in the modeling set-up, or some additional technicalities, or both. We will consider such a possibility in the next section.

Example 1 Suppose that $\Omega_0 \subset \Omega$ and $k_{ws}^N(z, y) = (1/|\Omega_0|)\chi_{\Omega_0}(z)$, so that only Ω_0 is occupied in winter, and assume further that $Q_w(z) = Q_0 > 0$ for $z \in \Omega_0$ and $Q_w(z) = 0$ otherwise, and $k_{sw}^N(x, z) = k(x)$ with $k(x)$ positive and continuous on Ω, and bounded by $1/(Q_0|\Omega|)$. We then have $k^N(x, y) = Q_0 k(x)$, and k^N satisfies our basic hypotheses on dispersal kernels. Biologically, these assumptions would correspond to a situation where the population spreads everywhere in Ω during the summer but only occupies a restricted region Ω_0 in the winter.

Example 2 For a more extreme example, we could take $Q_w(z)$ to be any continuous function with range [0, 1] that is positive at $z = z_0$ and let $k_{ws}^N(z, y) = \delta(z - z_0)$ and $k_{sw}^N(x, z) = k(x)$ with $k(x)$ positive, continuous, and bounded by $1/(Q(z_0)|\Omega|)$. Then $k^N(x, y) = k(x)Q_w(z_0)$, which will again satisfy our basic continuity and boundedness conditions. (This could be extended to $k_{ws}^N(z, y) = \sum_{i=0}^{\ell} \gamma_i \delta(z - z_i)$ with $\gamma_i > 0$ and $\sum_{i=0}^{\ell} \gamma_i = 1$.) Such choices of kernels would correspond biologically to a situation where large numbers of individuals gather in one place, or a few places, to hibernate during the winter. This type of behavior has been observed in garter snakes and bats.

If we want to satisfy the ideal free condition in Definition 1, additional conditions are needed on $k_{sw}^N(x,z)$, k_{ws}^N (z,y), and $Q_w(z)$. If we integrate (12) over Ω we obtain

$$\begin{aligned}\int_\Omega n^*(x)dx &= \int_\Omega \int_\Omega k^N(x,y)n^*(y)dydx\\ &= \int_\Omega \left[\int_\Omega k^N(x,y)dx\right] n^*(y)dy,\end{aligned} \tag{70}$$

which in view of (3) can be satisfied only if $k^N(x,y)$ satisfies (11). That in turn requires

$$1 = \int_\Omega \int_\Omega k_{sw}^N(x,z)\ Q_w(z)\ k_{ws}^N(z,y)dzdx = \int_\Omega \int_\Omega k_{sw}^N(x,z)\ Q_w(z)\ k_{ws}^N(z,y)dxdz.$$

Since k_{sw}^N and k_{ws}^N satisfy (3) and $Q_w(z) \le 1$, this is possible only if $k_{sw}^N(x,z)$ satisfies (11) and $\int_\Omega Q_w(z)\,k_{ws}^N(z,y)dz = 1$ for all $y \in \Omega$. This last condition will be satisfied in Example 1 if for all $y \in \Omega$, the support of $k_{ws}^N(z,y)$ as a function of z is in a region $\Omega_1 \subset \Omega_0$ so that $Q_w(z) = 1$, and $\int_{\Omega_1} k_{ws}^N(z,y)dz = 1$. In other words, the population has to spend the winter in some region where the habitat quality is at its maximum possible value. In the second example, if $Q_w(z_0) = 1$ then we could use $k_{ws}^N(z,y) = \delta(z - z_0)$ and obtain a similar result.

Example 3 In Example 1, if $Q_0 = 1$ we could define an ideal free dispersal strategy by taking $k_{ws}^N(z,y) = (1/|\Omega_0|)\chi_{\Omega_0}(z)$ and $k_{sw}(x,y) = n^*(x)/\int_\Omega n^*(x)dx$. The biological interpretation of these examples (and ideal free dispersal in general in the two season case) is that to disperse optimally, a population should spend the winter in the best possible habitat, then distribute itself to match the resource distribution in the summer as in the single season case. Since there is no density dependence in the winter population dynamics, the exact distribution of the population within the region of maximum winter habitat quality does not matter, so we could replace Ω_0 with any subset of Ω_0 with positive measure, and we would still get an ideal free distribution. It is not necessary to have $Q_w(z) = 1$ everywhere, but it is necessary to have $Q_w(z) = 1$ in the part of Ω that is occupied in winter. If $g_0 < 1$ then there will still be a net loss of population in winter, but so far we are assuming that f_0 is sufficiently large that $g[x,0] > 1$ for all $x \in \Omega$, so that a population that disperses optimally can survive. In the next section we will weaken the assumption, and include the case of partial occupancy in the summer.

2.3 More general case with partial occupancy

In previous sections, we assumed condition (G4), which requires that the entire habitat Ω is suitable for reproduction, so that $n_s^*(x) > 0$, which in turn requires that $g[x,0] > 1$ on Ω. In that setting, it is natural to assume all of Ω is occupied during the summer, that is, (17) is satisfied, so that $k_{sw}^N(x,y) > 0$, $\forall(x,y) \in \Omega\times\Omega$. In ecological terms, condition (G4) means that all of Ω consists of source habitats during the summer. That may not always be the case. In a heterogeneous habitat, it is possible that only some regions are sources, while others are sinks, even during the summer season. A biologically important case is where there exist locations x and y with $x \neq y$ where summer growth rates and winter survival rates are large enough that $f_0 g_0 Q_s(x) Q_w(y) > 1$, but both locations x and y are sink locations in the sense that $f_0 g_0 Q_s(x) Q_w(x) < 1$ and $f_0 g_0 Q_s(y) Q_w(y) < 1$. In those cases, an ideal free distribution (or even the mere survival of a population) will require exploiting the most favorable habitats via partial occupancy and migration in both seasons. This is quite different from the case of a uniformly favorable habitat, where a sedentary population could achieve an ideal free distribution via population growth without migration or dispersal. In the setting of patch models in continuous time, it was shown in Cantrell et al. (2012a, 2017) that in a habitat with both sources and sinks, an ideal free distribution is only possible with partial occupancy. We will show that this is true in our present setting as well.

In this section, condition (G4) is no longer assumed to hold. We generalize the results in the previous section to the case where $g[x, 0] < 1$ for some x so that $g[x, n]$ does not guarantee $n_s^*(x) > 0 \ \forall \ x \in \Omega$. Here, $g[x, n(x)]$ is still defined as in (64). In other words, in some regions of the habitat Ω, the habitat quality in summer is not high enough to sustain a population over the two seasons. In this case, a population with an ideal free distribution cannot occupy sink environments. This is because a population under an ideal free distribution should have equal fitness everywhere, and the fitness should be 1 at population equilibrium, which is impossible if $g[x, 0] < 1$ in some locations occupied by the population. Therefore we expect that, as in the case of patch models (Cantrell et al. 2012a, 2017), a population with an ideal free distribution in an environment with sinks will not occupy sink habitats. However, to achieve an ideal free distribution, a population also should occupy all habitats where $g[x, n(x)] > 1$, so if $g(x, n)$ is continuous then we would have $g(x, 0) = 1$ on the boundary of the occupied region. In that case we would have $n^*(x) = 0$ on the boundary and exterior of the occupied region and $n^*(x) > 0$ on the interior. A population that does not have an ideal free distribution may occupy all of Ω or a subset of Ω which contains both sources and sinks. If so, the region it occupies will contain points where $g(x, 0) = 1$. This situation creates some technical issues related to the positive cones used in our analysis of the models. Many mathematical results on integrodifference equation models, including those in this paper, use versions of the Krein–Rutman theorem that require the dispersal operators in the models to be strongly positive, which means they must be defined on function spaces whose positive cones have nonempty interior. Similar issues arise in using the theory of positive operators to study second order elliptic and parabolic partial differential equations with Dirichlet boundary conditions. The new mathematical constructions and analysis in this section address the issue of setting up the models in spaces which have positive cones with nonempty interior, and where dispersal operators are strongly positive.

To make these ideas precise we will first convert the two season model to a single season model as we did before, and use $n(x)$ in place of $n_s(x)$ except in places where we write out the explicit form of the two season model. Then we redefine the ideal free distribution $n^*(x)$ using a piece-wise construction. Let

$$\Omega_1 = \{x \in \Omega : g[x, 0] > 1\} = \{x \in \Omega : f_0 g_0 \, Q_s(x) > 1\} . \tag{71}$$

To define the ideal free distribution, we require

$$n^*(x) = \begin{cases} g[x, n^*(x)]n^*(x), & \text{for } x \in \Omega_1, \\ 0, & \text{for } x \in \Omega \backslash \Omega_1. \end{cases} \tag{72}$$

That is,

$$n^*(x) = \begin{cases} \dfrac{f_0 g_0\, Q_s(x) - 1}{b_0}, & \text{for } x \in \Omega_1, \\ 0, & \text{for } x \in \Omega \backslash \Omega_1. \end{cases} \tag{73}$$

Therefore $n^*(x)$ is well-defined and unique. We also know it has positivity properties $n^*(x) \geq 0, \forall x \in \Omega$ and $n^*(x) > 0, \forall x \in \Omega_1$.

To proceed we now need to define appropriate function spaces and positive cones. There are a couple of possible approaches. If we assume that g is continuous then we must have $n^*(x) = 0$ on $\partial\Omega_1$. If we try to use $X = C(\bar{\Omega}_1)$ with positive cone X^+ consisting of functions that are positive on $\bar{\Omega}_1$ then n^* is not in the interior of the positive cone. If we use $X = C_0(\bar{\Omega}_1)$ and use the positive cone X^+ consisting of functions that are positive on the interior of Ω_1, then X^+ has an empty interior. We cannot use our abstract results based on the Krein–Rutman theorem in either of those situations. What we can do is to follow the approach used to handle the case of Dirichlet boundary conditions in reaction-diffusion systems and related models based on partial differential equations. Specifically, we can follow Amann (1976) and use a cone that requires functions that are positive inside a domain and zero on the boundary to have negative normal derivatives. It is then possible to define a cone with a nonempty interior that contains n^*.

Comment: A different approach entirely (suggested by one of the referees of the original version of this paper) would be to abandon the requirement that $g[x, n]$ and $n^*(x)$ be continuous and think of the overall environment as consisting of a network of patches that all have some spatial extent, rather than being viewed as points, where each patch is either entirely a source (that is, $g[x, n] > 1$) or entirely a sink ($g[x, n] < 1$). In that case we could define a system of integrodifference equations, one for each patch, but perhaps with some coupling between equations so that individuals could move from patch to patch. This might lead to something like a version of the results on patch models in Cantrell et al. (2012a, 2017) but where each patch has spatial extent. The suggestion is good, and we may pursue it in later work, but here we specifically want to think about a single environment where there is continuous variation in habitat quality and any patchiness in population distributions arises from dispersal strategies that are conditional on habitat quality.

For the cases we consider, we will impose an additional assumption that will be needed for technical reasons which will be discussed later.

(D) $\partial\Omega_1$ is compact, $\bar{\Omega}_1$ is contained in the interior of Ω, $g[x, 0] < 1$ on $\Omega\backslash\bar{\Omega}_1$, $n^*(x)$ restricted to $\bar{\Omega}_1$ belongs to $C_0^1(\bar{\Omega}_1)$, and $D_\nu n^*(x) < 0$ on $\partial\Omega_1$, where ν is any outward normal vector on $\partial\Omega_1$, and D_ν refers to the directional derivative in the direction of ν. (It follows that $D_\nu n^*(x) < -n_1$ on $\partial\Omega_1$ for some $n_1 > 0$.)

Comment: In the case of second order elliptic or parabolic partial differential equations, solutions that are positive on the interior of some domain and zero on the boundary automatically satisfy condition D because of the strong maximum principle. In the present setting, since the set where $n_s^*(x) = 0$ is the level set $g[x, 0] = 1$, whether condition D is satisfied or not depends on g, so we need to impose condition D. In one space dimension , if $g[x, n(x)] = 1$ then $n'(x) = -\frac{\partial g/\partial x}{\partial g/\partial n}$ so condition D would fail if $\partial g/\partial x = 0$ for x such that $g[x, n(x)] = 1$ but would be satisfied if $\partial g/\partial x$ and $\partial g/\partial n$ are nonzero and have the right combination of signs at points where $g[x, n(x)] = 1$.

We will retain the assumption that there is no population growth during migration, namely condition (3). As before, in the ideal free case, we will need to assume there is no loss during migration, which will again require the no-flux boundary conditions (11). Note that in the case of partial occupancy we would have

$$\int_{\Omega} k_{sw}(x, y)\, dx = \int_{\Omega_1} k_{sw}(x, y)\, dx. \tag{74}$$

As in the case of full occupancy, we can define a combined operator from $n_{s,t}$ to $n_{s,t+1}$ as in (63). However, since we have partial occupancy, $n_{s,t}$ is always zero outside of Ω_1. Thus the combined model can be written as

$$\begin{aligned} n_{s,t+1}(x) &= \int_{\Omega}\int_{\Omega} k_{sw}^N(x, z)\, Q_w(z)\, k_{ws}^N(z, y) \cdot \frac{f_0 g_0 Q_s(y)\, n_{s,t}(y)}{1 + b_0 n_{s,t}(y)}\, dydz, \\ &= \int_{\Omega}\int_{\Omega_1} k_{sw}^N(x, z)\, Q_w(z)\, k_{ws}^N(z, y) \cdot \frac{f_0 g_0 Q_s(y)\, n_{s,t}(y)}{1 + b_0 n_{s,t}(y)}\, dydz, \\ &= \int_{\Omega_1}\int_{\Omega} k_{sw}^N(x, z)\, Q_w(z)\, k_{ws}^N(z, y) dz \cdot \frac{f_0 g_0 Q_s(y)\, n_{s,t}(y)}{1 + b_0 n_{s,t}(y)}\, dy. \end{aligned} \tag{75}$$

We can define a combined kernel $k^N(x, y)$ as before by (65), so that

$$n_{s,t+1}(x) = \int_{\Omega_1} k^N(x, y) \cdot \frac{f_0 g_0 Q_s(y)\, n_{s,t}(y)}{1 + b_0 n_{s,t}(y)}\, dy.$$

From this point on we will generally replace $n_{s,t}(x)$ with $n_t(x)$, and similarly for $m_{s,t}$ and their corresponding equilibria, since we have reduced our model to the form of a single season case.

If a dispersal strategy moves all of the population into Ω_1 during the summer, and yields a positive population there, then $n_{t+1}(x) = n_{s,t+1}(x) = 0$ on $\Omega\backslash\Omega_1$, so $k^N(x, y)$ and hence k_{sw}^N must satisfy $k^N(x, z) = 0$ for $x \in \Omega\backslash\Omega_1$, and hence $k_{sw}^N(x, z) = 0$ for $x \in \Omega\backslash\Omega_1$. To yield a positive population on Ω_1 it must be the case that $k^N(x, y) > 0$ for $x \in \Omega_1$, and there must be some z such that $k_{ws}^N(z, y) > 0$ for some $y \in \Omega_1$. It follows that

$$\int_{\Omega\backslash\Omega_1} k^N(x, y)\, n(y)\, dy \; = 0$$

We can now define an ideal free dispersal strategy again as in the single season case by (12):

$$n^*(x) = \int_\Omega k^N(x, y) n^*(y)\, dy.$$

By Lemma 1, $k^N(x, y)n^*(y)$ is line sum symmetric, so Theorem 1 applies to it. Since we know that $n^*(x)$ and $k^N(x, y)$ are zero outside Ω_1, the ideal free condition (12) in this case can be expressed as

$$n^*(x) = \int_{\Omega_1} k^N(x, y) n^*(y)\, dy. \tag{76}$$

To see this, recall the definition (65) and refer back to (63). We integrate both sides of (12) for $x \in \Omega \backslash \Omega_1$, and get

$$\int_\Omega \int_\Omega \left(\int_{\Omega \backslash \Omega_1} k^N_{sw}(x, z)\, dx \right) Q^N_w(z) k^N_{ws}(z, y)\, n^*(y)\, dz\, dy = 0. \tag{77}$$

Therefore

$$\int_{\Omega \backslash \Omega_1} k^N_{sw}(x, z)\, dx = 0, \tag{78}$$

for all $z \in \Omega$ such that $k^N_{ws}(z, y) > 0$ for some $y \in \Omega_1$. Since $k^N_{sw}(x, z)$ is nonnegative,

$$k^N_{sw}(x, z) = 0 \quad \text{for} \quad x \in \Omega \backslash \Omega_1 \ \text{ and } \ z \in \Omega \text{ with } k^N_{ws}(z, y) > 0 \text{ for some } y \in \Omega_1.$$

It follows that

$$k^N(x, y) = 0 \quad \text{for} \quad x \in \Omega \backslash \Omega_1 \text{ with } k^N(x, y) > 0 \text{ for some } y \in \Omega_1. \tag{79}$$

The overall dispersal operator from summer to summer defined by $k^N(x, y)$ then maps Ω_1 into itself. Therefore the ideal free strategy restricts dispersal to Ω_1, the habitat of good quality. Thus the no flux condition

$$\int_\Omega k^N(x, y)\, dx = 1, \quad \forall y \tag{80}$$

is equivalent to

$$\int_{\Omega_1} k^N(x, y)\, dx = 1, \quad \forall y. \tag{81}$$

Correspondingly, the positivity condition (17) can be modified as

$$k^N(x, y) > 0, \quad \forall\, x \in \Omega_1, \ \forall\, y \in \Omega_1. \tag{82}$$

That condition is adequate for the extension of some of our results to the case of partial occupancy, but the proofs of others require the spaces X_1 and X_2 to have positive cones with nonempty interiors and the operator T or its derivatives to be strongly positive. For this reason, as noted in the discussion following (73), we cannot use the standard positive cone $P_1 = \{n(x) \in C_0(\bar{\Omega}_1) | n(x) \geq 0, \forall x \in \Omega_1\}$ in $C_0(\bar{\Omega}_1)$. This problem can be addressed in both our case and the case of partial differential equations with Dirichlet conditions by using order unit norms; see Amann (1976) and Mierczyński (1998). The idea of order unit norms is, roughly speaking, to find a suitable function $e(x)$ with $e(x) = 0$ on $\partial\Omega_1$ and $e(x) > 0$ inside Ω_1 such that the first component of T maps nonzero $n(x) \in P_1$ into $\{n(x) \in C_0(\bar{\Omega}_1) : \alpha e(x) \leq n(x) \leq \beta e(x)\}$ for some positive α and β, and then use $e(x)$ to define the norm and ordering for a new subspace X_e of $C_0(\bar{\Omega}_1)$ whose positive cone has a nonempty interior that can be used to replace X_1. This is described in more detail when we prove the main theorem in the section. A condition related to (D) will be needed in that construction:

(D1) $k^N_{sw}(x, y) \in C^1(\bar{\Omega}_1 \times \Omega)$, and for $\forall x \in \partial\Omega_1$, $\forall y \in \Omega$, $k^N_{sw}(x, y) = 0$ and $D_\nu k^N_{sw}(x, y) < 0$, where ν is any normal vector on $\partial\Omega_1$, and D_ν refers to the directional derivative relative to the variable x in the direction of ν. (It follows that $D_\nu k^N_{sw}(x, y) \leq -k_1$ for some $k_1 > 0$).

For the population M we can define a combined kernel $k^M(x, y)$ by (65). We could retain the positivity condition (17) and use $X_2 = C(\Omega)$, but that condition implies that the population M occupies all of Ω, and if there is a semi-trivial equilibrium $m^*(x)$ then it is positive everywhere. However, even if the dispersal strategy for M is not ideal free, that population may also avoid sink habitats to some extent so that both populations have partial occupancy. To address that situation, we could allow $k^M_{sw}(x, y) = 0$ on $\Omega \backslash \Omega_2$ for some open subset $\Omega_2 \subset \Omega$ and impose a positivity condition analogous to (82):

$$k^M_{sw}(x, y) > 0, \quad \forall\, x \in \Omega_2,\ \forall\, y \in \Omega. \tag{83}$$

In that case we will also need to impose condition D on Ω_2 and an additional assumption analogous to (D1):

(D2) $k^M_{sw}(x, y) \in C^1(\bar{\Omega}_2 \times \Omega)$, and for $\forall x \in \partial\Omega_2$, $\forall y \in \Omega_2$, $k^M_{sw}(x, y) = 0$ and $D_\nu k^M_{sw}(x, y) < 0$, where ν is any normal vector on $\partial\Omega_2$, and D_ν refers to the directional derivative relative to the variable x in the direction of ν. (It follows that $D_\nu k^M_{sw}(x, y) \leq -k_2$ for some $k_2 > 0$.)

As before, we require $k^M(x, y)$ to satisfy the no growth condition (3).

The kernel $k^N(x, y)$ satisfies the ideal free condition (12) and hence the no flux boundary condition (11) relative to Ω_1, so by Lemma 1 it is line sum symmetric relative to Ω_1.

The following two lemmas generalize Lemmas 2 and 3, respectively. They will again show that system (69) does not allow the two species to coexist at a coexistence equilibrium, and that any semi-trivial equilibrium of system (69) of the form $(0, m^*)$ must be unstable.

Lemma 4 *Assume* (i) $k^N(x, y)$ *and* $k^M(x, y)$ *are continuous.* (ii) *Condition (D) holds for* Ω_1 *and the kernel* $k^N_{sw}(x, y)$ *satisfies conditions* (81) *and (D1), and* $k^N_{ws}(x, y)$ *satisfies condition* (11)*. The kernel* $k^N(x, y)$ *also satisfies the positivity condition* (82). (iii) *Either* $\Omega_2 = \Omega$ *and* $k^M(x, y) > 0, \forall x, \ \forall y \in \Omega$ *or condition(D) holds for* Ω_2 *and the kernel* $k^M(x, y)$ *satisfies conditions (D2), and* (83)*. In either case* $k^M(x, y)$ *satisfies* (3). (iv) *The kernel* $k^N(x, y)$ *is such that population N, described by* $n_t(x)$*, adopts an ideal free dispersal strategy relative to* $n^*(x)$ *in* (72)*, and the kernel* $k^M(x, y)$ *is such that the population M, described by* $m_{s,t}(x)$*, does not adopt an ideal free dispersal strategy relative to* $n^*(x)$*. (v)* $g[x, n]$ *satisfies (G0)–(G3), and* Ω_1 *is not empty. Then system* (69) *does not have a coexistence equilibrium* $(n(x), m(x))$ *where* $n(x)$ *and* $m(x)$ *are both nonzero.*

Proof Suppose that there is a nontrivial equilibrium $(n(x), m(x))$ for system (69), which then satisfies the equations

$$n(x) = \int_\Omega \int_\Omega k^N_{sw}(x, z) Q_w(z) k^N_{ws}(z, y) \, g[y, n(y) + m(y)] n(y) \, dz \, dy \tag{84a}$$

$$m(x) = \int_\Omega \int_\Omega k^M_{sw}(x, z) Q_w(z) k^M_{ws}(z, y) \, g[y, n(y) + m(y)] m(y) \, dz \, dy. \tag{84b}$$

which are equivalent to

$$n(x) = \int_\Omega k^N(x, y) \, g[y, n(y) + m(y)] n(y) \, dy \tag{85a}$$

$$m(x) = \int_\Omega k^M(x, y) \, g[y, n(y) + m(y)] m(y) \, dy. \tag{85b}$$

(In the case where $k^M_{sw}(x, y)$ satisfies both (83) and condition (D2), extend $m(x)$ to be 0 outside Ω_2.)
Because of (79), we know from (85a) that

$$n(x) = 0 \quad \text{for} \quad x \in \Omega \backslash \Omega_1. \tag{86}$$

Meanwhile, the positivity condition (82) ensures that

$$n(x) > 0 \quad \text{for} \quad x \in \Omega_1. \tag{87}$$

Integrating both sides of (85a) on Ω and using the ideal free condition (12) and the no flux boundary condition (11) we obtain

$$\int_\Omega n(x) \, dx = \int_\Omega g[y, n(y) + m(y)] \, n(y) \, dy, \tag{88}$$

which is equivalent to

$$\int_{\Omega_1} n(x) \, dx = \int_{\Omega_1} g[y, n(y) + m(y)] \, n(y) \, dy \tag{89}$$

because of (86). Likewise, integrating both sides of (84b) and using the no growth boundary condition (3) yields

$$\int_{\Omega} m(x)\,dx \le \int_{\Omega} g[y, n(y)+m(y)]\,m(y)\,dy \tag{90a}$$

$$= \int_{\{y:m(y)>0\}} g[y, n(y)+m(y)]\,m(y)\,dy, \tag{90b}$$

and the inequality is strict unless $k^M(x, y)$ satisfies the no flux boundary condition (11) for all y where $m(y) > 0$.

Adding (88) and (90) together, we obtain the inequality

$$\int_{\Omega} [n(x)+m(x)]\,dx \le \int_{\Omega} g[x, n(x)+m(x)]\cdot[n(x)+m(x)]\,dx. \tag{91}$$

To proceed, we need to construct a piece-wise function similar to the function ψ in (19). Let

$$\tilde{\Psi}(x) = \begin{cases} \dfrac{n^*(x)}{n(x)g[x, n(x)+m(x)]} & \text{on } \Omega_1, \\ 0 & \text{on } \Omega\backslash\Omega_1. \end{cases} \tag{92}$$

This function is well-defined because of the positivity condition (87).

Multiplying both sides of Eq. (84a) by $\tilde{\Psi}(x)$ and integrating, then using (76), (89) and Theorem 1 we get

$$\int_{\Omega} \tilde{\Psi}(x)n(x)\,dx = \int_{\Omega_1} \tilde{\Psi}(x)n(x)\,dx \tag{93a}$$

$$= \int_{\Omega_1} \frac{n^*(x)}{g[x, n(x)+m(x)]}\,dx \tag{93b}$$

$$= \int_{\Omega_1}\int_{\Omega_1} k^N(x, y)\,g[y, n(y)+m(y)]n(y) \frac{n^*(x)}{g[x, n(x)+m(x)]n(x)}\,dy\,dx \tag{93c}$$

$$= \int_{\Omega_1}\int_{\Omega_1} k^N(x, y)\,n^*(y)\,\frac{g[y, n(y)+m(y)]n(y)n^*(x)}{g[x, n(x)+m(x)]n(x)n^*(y)}\,dy\,dx \tag{93d}$$

$$= \int_{\Omega_1}\int_{\Omega_1} k^N(x, y)n^*(y)\,\frac{\tilde{\Psi}(x)}{\tilde{\Psi}(y)}\,dy\,dx \tag{93e}$$

$$\ge \int_{\Omega_1}\int_{\Omega_1} k^N(x, y)n^*(y)\,dy\,dx \tag{93f}$$

$$= \int_{\Omega_1} n^*(x)\,dx. \tag{93g}$$

The inequality is again due to Theorem 1 and the fact that $k^N(x,y)n^*(y)$ is line-sum symmetric on $\Omega_1 \times \Omega_1$. It is a strict inequality unless $\tilde{\Psi}(x) = \tilde{\Psi}(y)$ in Ω_1. Therefore we have

$$\int_{\Omega_1} \frac{n^*(x)}{g[x, n(x)+m(x)]}\, dx \geq \int_{\Omega_1} n^*(x)\, dx, \tag{94}$$

and thus

$$\int_{\Omega_1} n^*(x) \left\{ \frac{1 - g[x, n(x)+m(x)]}{g[x, n(x)+m(x)]} \right\} \geq 0. \tag{95}$$

Note that we can extend the integral domain to Ω because $n^*(x) = 0$ outside Ω_1, so

$$\int_{\Omega} n^*(x) \left\{ \frac{1 - g[x, n(x)+m(x)]}{g[x, n(x)+m(x)]} \right\} \geq 0 \tag{96}$$

is also true.

Meanwhile, the calculations from (85) to (91) are still valid in the present setting. Inequality (91) says

$$\int_{\Omega} \{1 - g[x, n(x)+m(x)]\}\, [n(x)+m(x)]\, dx \leq 0, \tag{97}$$

from which we have

$$\int_{\Omega} g[x, n(x)+m(x)] \cdot [n(x)+m(x)] \cdot \left\{ \frac{1 - g[x, n(x)+m(x)]}{g[x, n(x)+m(x)]} \right\} dx \leq 0. \tag{98}$$

Combining (96) and (98), we get

$$\int_{\Omega} \left\{ n^*(x) - g[x, n(x)+m(x)] \cdot [n(x)+m(x)] \right\} \cdot \left\{ \frac{1 - g[x, n(x)+m(x)]}{g[x, n(x)+m(x)]} \right\} dx \geq 0. \tag{99}$$

Therefore, if

$$I_1 = \int_{\Omega_1} \left\{ n^*(x) - g[x, n(x)+m(x)] \cdot [n(x)+m(x)] \right\} \cdot \left\{ \frac{1 - g[x, n(x)+m(x)]}{g[x, n(x)+m(x)]} \right\} dx, \tag{100}$$

and

$$I_2 = \int_{\Omega \setminus \Omega_1} \left\{ n^*(x) - g[x, n(x)+m(x)] \cdot [n(x)+m(x)] \right\} \cdot \left\{ \frac{1 - g[x, n(x)+m(x)]}{g[x, n(x)+m(x)]} \right\} dx \tag{101a}$$

$$= \int_{\Omega \setminus \Omega_1} \{-g[x, n(x)+m(x)] \cdot [n(x)+m(x)]\} \cdot \left\{ \frac{1 - g[x, n(x)+m(x)]}{g[x, n(x)+m(x)]} \right\} dx, \tag{101b}$$

then

$$I_1 + I_2 \geq 0. \tag{102}$$

Both integrals I_1 and I_2 should be less than or equal to 0. We know $I_1 \leq 0$ because

$$I_1 = \int_{\Omega_1} \left\{ g[x, n^*(x)]n^*(x) - g[x, n(x) + m(x)] \cdot [n(x) + m(x)] \right\} \cdot \left\{ \frac{g[x, n^*(x)] - g[x, n(x) + m(x)]}{g[x, n(x) + m(x)]} \right\} dx, \tag{103}$$

and the integrand contains two factors that must be of opposite signs. We know $I_2 \leq 0$ because $g[x, n(x)+m(x)] \in (0, 1]$ for $x \in \Omega \backslash \Omega_1$ and $n(x)$ and $m(x)$ are nonnegative. Therefore, the only possibility is

$$I_1 = I_2 = 0. \tag{104}$$

The fact that $I_1 = 0$ implies

$$n^*(x) = n(x) + m(x), \quad \forall\, x \in \Omega_1. \tag{105}$$

With the same arguments as before, this implies that $\tilde{\Psi}(x)$ is a constant on Ω_1. So we can assume that for some constant c,

$$\frac{n^*(x)}{n(x)} = \frac{1}{c}, \quad x \in \Omega_1. \tag{106}$$

As before, this leads to $n(x) = cn^*(x)$ and $m(x) = (1-c)n^*(x)$, $x \in \Omega_1$. Meanwhile, we have

$$m(x) + n(x) = 0, \quad \forall\, x \in \Omega \backslash \Omega_1, \tag{107}$$

from $I_2 = 0$. From (86), it must be the case that

$$m(x) = 0, \quad \forall\, x \in \Omega \backslash \Omega_1. \tag{108}$$

From equations (85b) and (105), we then have, for $x \in \Omega_1$,

$$m(x) = \int_{\Omega} k^M(x, y)\, g[x, n(x) + m(x)]\, m(y)\, dy, \tag{109a}$$

$$= \int_{\Omega} k^M(x, y)\, m(y)\, dy. \tag{109b}$$

Thus (108) and (109b) imply

$$m(x) = \int_{\Omega_1} k^M(x, y)\, m(y)\, dy, \quad \forall x \in \Omega_1. \tag{110}$$

Substituting $m(x)$ with $(1-c)n^*(x)$, we have

$$n^*(x) = \int_{\Omega_1} \int_{\Omega} k^M(x, y)\, n^*(y)\, dy, \quad \forall x \in \Omega_1. \tag{111}$$

This together with the fact of strict inequality in (90) unless $k^M(x, y)$ satisfies the no flux boundary condition (11) conflicts with the assumption that $k^M(x, y)$ does not form an ideal free strategy. Therefore system (69) does not have a coexistence equilibrium $(n(x), m(x))$ where $n(x)$ and $m(x)$ are both nonzero. □

Lemma 5 *Assume that conditions of the preceding lemma hold. If system* (69) *has a semitrivial equilibrium* $(0, m^*(x))$*, then this equilibrium must be unstable.*

Proof Suppose system (69) has a semitrivial equilibrium $(0, m^*(x))$. We will show that this equilibrium must be unstable.

As before, consider the eigenvalue problem

$$\lambda\phi(x) = \int_{\Omega} k^N(x, y)\, g[y, m^*(y)]\, \phi(y)\, dy, \tag{112}$$

where

$$g[y, m^*(y)] = \frac{f_0 g_0\, Q_s(y)}{1 + b_0\, m^*(y)}. \tag{113}$$

(In the proof of the next result we will verify conditions which imply that a principal eigenvalue exists in the present case.) Because of (79) and (82), we know

$$\phi(x) = 0 \quad \text{for } x \in \Omega \backslash \Omega_1 \text{ and } \phi(x) > 0 \text{ for } x \in \Omega_1. \tag{114}$$

Also, we have $g[x, m^*(x)] > 0$ for $x \in \Omega$, so

$$G(x) = \begin{cases} \dfrac{n^*(x)}{\phi(x) g[x, m^*(x)]}, & x \in \Omega_1, \\ 0, & x \in \Omega \backslash \Omega_1, \end{cases} \tag{115}$$

is well defined. Multiplying both sides of equation (112) by G we obtain, for $x \in \Omega_1$,

$$\frac{\lambda\, n^*(x)}{g[x, m^*(x)]} = \int_{\Omega} k^N(x, y)\, \frac{n^*(x)}{\phi(x) g[x, m^*(x)]}\, g[y, m^*(y)]\, \phi(y)\, dy \tag{116a}$$

$$= \int_{\Omega_1} k^N(x, y)\, \frac{n^*(x)}{\phi(x) g[x, m^*(x)]}\, g[y, m^*(y)]\, \phi(y)\; dy \tag{116b}$$

$$= \int_{\Omega_1} k^N(x, y)\, n^*(x)\, \frac{\phi(y) g[y, m^*(y)]}{\phi(x) g[x, m^*(x)]}\; dy \tag{116c}$$

$$= \int_{\Omega_1} k^N(x, y)\, n^*(y)\, \frac{\Phi(y)}{\Phi(x)}\, dy, \tag{116d}$$

where

$$\Phi(x) = \frac{\phi(x)g[x, m^*(x)]}{n^*(x)}, x \in \Omega_1. \tag{117}$$

Integrating both sides, we obtain by Theorem 1 and the fact that $k^N(x, y)n^*(y)$ is line-sum symmetric on $\Omega_1 \times \Omega_1$

$$\lambda \int_{\Omega_1} \frac{n^*(x)}{g[x, m^*(x)]}\, dx \geq \int_{\Omega_1}\int_{\Omega_1} k^N(x, y)n^*(y)\, dy\, dx \tag{118a}$$

$$= \int_{\Omega_1} n^*(x)\, dx. \tag{118b}$$

Therefore

$$\lambda \int_{\Omega_1} \frac{n^*(x)}{g[x, m^*(x)]}\, dx \geq \int_{\Omega_1} \frac{g[x, m^*(x)]}{g[x, m^*(x)]}\, n^*(x)\, dx, \tag{119}$$

and

$$(\lambda - 1) \int_{\Omega_1} \frac{n^*(x)}{g[x, m^*(x)]}\, dx \geq \int_{\Omega_1} n^*(x) \left\{1 - \frac{1}{g[x, m^*(x)]}\right\} dx. \tag{120}$$

Next we will show that the right hand side of (120) is nonnegative. To see this, we begin with observing that the equilibrium $m^*(x)$ must satisfy the equation

$$m^*(x) = \int_{\Omega} k^M(x, y)\, g[y, m^*(y)]\, m^*(y)\, dy. \tag{121}$$

Integrating both sides of Eq. (121), we obtain

$$\int_{\Omega} m^*(x)\, dx = \int_{\Omega}\int_{\Omega} k^M(x, y)\, g[y, m^*(y)]\, m^*(y)\, dy\, dx \tag{122a}$$

$$\leq \int_{\Omega} g[y, m^*(y)]\, m^*(y)\, dy \tag{122b}$$

by the no growth boundary condition (3). Therefore

$$\int_{\Omega} m^*(x)\{1 - g[x, m^*(x)]\}\, dx \leq 0, \tag{123}$$

and

$$\int_{\Omega} m^*(x)\, \{g[x, m^*(x)] - 1\}\, dx \geq 0. \tag{124}$$

Splitting the integral into two integrals, we have

$$\int_{\Omega_1} m^*(x)\left\{g[x,m^*(x)]-1\right\}dx+\int_{\Omega\backslash\Omega_1} m^*(x)\left\{g[x,m^*(x)]-1\right\}dx\geq 0. \tag{125}$$

For $x\in\Omega\backslash\Omega_1$, we have

$$g[x,m^*(x)]\leq 1. \tag{126}$$

Therefore

$$\int_{\Omega\backslash\Omega_1} m^*(x)\left\{g[x,m^*(x)]-1\right\}dx\leq 0, \tag{127}$$

because $m^*(x)$ is nonnegative, rendering the integrand less than or equal to 0. The inequality (127) will be strict unless for each $x\in\Omega\backslash\Omega_1$ either $m^*(x)=0$ or $g[x,m^*(x)]=1$. The case $g[x,m^*(x)]=1$ is ruled out because $g[x,s]$ is strictly decreasing in s so that $g[x,m^*(x)]\leq g[x,0]\leq 1$, but by condition (D), $g[x,0]<1$ for each $x\in\Omega\backslash\Omega_1$. Hence (127) is strict unless $m^*(x)=0$ for $x\in\Omega\backslash\Omega_1$. Therefore (127) implies

$$\int_{\Omega_1} m^*(x)\left\{g[x,m^*(x)]-1\right\}dx\geq 0, \tag{128}$$

with strict inequality unless $m^*(x)=0$ for $x\in\Omega\backslash\Omega_1$. Subtracting the left-hand side of inequaltiy (128) from the right-hand side of (120), we obtain

$$\int_{\Omega_1} n^*(x)\left\{1-\frac{1}{g[x,m^*(x)]}\right\}dx-\int_{\Omega_1} m^*(x)\left\{g[x,m^*(x)]-1\right\}dx \tag{129a}$$

$$=\int_{\Omega_1}\left\{n^*(x)-m^*(x)g[x,m^*(x)]\right\}\cdot\frac{g[x,m^*(x)]-1}{g[x,m^*(x)]}\,dx \tag{129b}$$

$$=\int_{\Omega_1}\left\{n^*(x)g[x,n^*(x)]-m^*(x)g[x,m^*(x)]\right\}\cdot\frac{g[x,m^*(x)]-g[x,n^*(x)]}{g[x,m^*(x)]}\,dx. \tag{129c}$$

Since we assume $Q_s(x)>0$ for $x\in\Omega$, we have $g[x,s]$ strictly decreasing and $sg[x,s]$ strictly increasing in s for $x\in\Omega_1$. Therefore the integrand in the last line of (129) is nonnegative, and is strictly positive unless either $n^*(x)g[x,n^*(x)]=m^*(x)g[x,m^*(x)]$ or $g[x,m^*(x)]=g[x,n^*(x)]$. Either of those implies $n^*(x)=m^*(x)$ on Ω_1. It follows that

$$\int_{\Omega_1} n^*(x)\left\{1-\frac{1}{g[x,m^*(x)]}\right\}dx\geq\int_{\Omega_1} m^*(x)\left\{g[x,m^*(x)]-1\right\}dx\geq 0. \tag{130}$$

The first inequality is strict unless $n^*(x) = m^*(x)$ on Ω_1. The second is strict $m^*(x) = 0$ for $x \in \Omega\backslash\Omega_1$. If either inequality is strict we have $\lambda > 1$ by (120) so that $(0, m^*(x))$ is unstable. The conditions $n^*(x) = m^*(x)$ on Ω_1 and $m^*(x) = 0$ for $x \in \Omega\backslash\Omega_1$ imply that $n^*(x) = m^*(x)$. We then have

$$n^*(x) = \int_\Omega k^M(x, y)\, g[y, n^*(y)]\, n^*(y)\, dy \tag{131a}$$

$$= \int_\Omega k^M(x, y)\, n^*(y)\, dy. \tag{131b}$$

This is also required for inequality (129) to be an equality. Therefore, if $k^M(x, y)$ is a kernel that does not satisfy the ideal free conditions (12) and (11), the inequalities (128) and (129) will be strict. Therefore, with inequality (129), we know

$$(\lambda - 1) \int_\Omega \frac{n^*(x)}{g[x, m^*(x)]}\, dx > 0, \tag{132}$$

and

$$\lambda > 1. \tag{133}$$

Therefore, the equilibrium $(0, m^*(x))$, if existing, must be unstable. □

Theorem 4 *Assume that either*

(i) *(full occupancy) g[x,n] satisfies (G0)–(G4) and the hypotheses of Lemmas 2 and 3 are satisfied*
or
(ii) *(partial occupancy)* $g[x, n]$ *satisfies (G0)–(G3),* Ω_1 *is nonempty, condition (D) holds, and the hypotheses of Lemmas 4 and 5 are satisfied.*

Suppose the kernel k^N *(defined by the combined kernel in (65) in the two season cases) is such that population N, described by* $n_{s,t}(x)$*, adopts an ideal free dispersal strategy relative to* $n_s^*(x)$ *as in Definition 1 on* Ω *in case (i) and on* Ω_1 *in case (ii), and population M, described by* $m_{s,t}(x)$*, does not adopt an ideal free dispersal strategy. Then the semi-trivial equilibrium* $(n_s^*(x), 0)$ *is a globally asymptotically stable equilibrium, and the ideal free dispersal strategy, as defined in Definition 1 is an evolutionarily-stable strategy.*

Proof We will give a detailed proof for the case where N has partial occupancy but M occupies all of Ω. First we will formulate the abstract setting for the case of partial occupancy by N on Ω_1. If M has partial occupancy on Ω_2 we would make the corresponding construction for M on Ω_2. For cases with full occupancy for both M and N we would use the original space $X_1 \times X_2$ as in the single season case. Recall that Ω_1 is defined by (71). Let space X_1 be

$$X_1 = C_0(\bar{\Omega}_1) := \{n(x) \in C(\bar{\Omega}_1) | n(x) = 0, \forall\, x \in \partial\, \Omega_1\}, \tag{134}$$

equipped with the cone

$$P_1 = \{n(x) \in C_0(\bar{\Omega}_1) | n(x) \geq 0, \forall\, x \in \Omega_1\}, \tag{135}$$

and $X_2 = C(\Omega)$, equipped with the cone $P_2 = C_+(\Omega)$. Let $X = X_1 \times X_2$, with cone $X^+ = P_1 \times P_2$, and let $T : X^+ \to X^+$ be the operator

$$T \begin{bmatrix} n(x) \\ m(x) \end{bmatrix} = \begin{bmatrix} \int_\Omega \int_\Omega k_{sw}^N(x, z) Q_w(z) k_{ws}^N(z, y)\, dz\, g[y, n(y) + m(y)]\, n(y)\, dy \\ \int_\Omega \int_\Omega k_{sw}^M(x, z) Q_w(z) k_{ws}^M(z, y)\, dz\, g[y, n(y) + m(y)]\, m(y)\, dy \end{bmatrix} \tag{136}$$

which can be condensed as

$$T \begin{bmatrix} n(x) \\ m(x) \end{bmatrix} = \begin{bmatrix} \int_\Omega k^N(x, y)\, g[y, n(y) + m(y)]\, n(y)\, dy \\ \int_\Omega k^M(x, y)\, g[y, n(y) + m(y)]\, m(y)\, dy \end{bmatrix}. \tag{137}$$

The cone P_1 has an empty interior, so we will use order unit norms (Amann 1976) to construct an alternative space X_e which possesses a cone P_e with a nonempty interior. For the current purpose, it is natural to use $e = n_s^*(x)$, but any choice of $e(x)$ with $e(x) > 0$ in Ω_1, $e(x) = 0$ on $\partial\Omega_1$, and $e(x)$ satisfying condition (D) would produce an equivalent result. For $e = n_s^*(x)$, we have $e \in X_1 \backslash \{0\}$. Following Amann (1976) , we can then use the Minkowski functional

$$||x||_e = \inf\{\lambda > 0 | -\lambda e \leq x \leq \lambda e\} \tag{138}$$

to construct the normed vector space

$$X_e = (\cup\{\lambda[-e, e] | \lambda \in \mathbb{R}_+\}, || \cdot ||_e)\,, \tag{139}$$

and define a cone P_e as

$$P_e = \cup\{\lambda[-e, e] | \lambda \in \mathbb{R}_+\} \cap P_1. \tag{140}$$

By Theorem 2.3 of Amann (1976) , (X_e, P_e) is an ordered Banach space, and $\mathring{P}_e \neq \varnothing$, i. e. the interior of P_e is nonempty.

We will now show that $T(X_1 \times \{0\})$ embeds continuously, in fact compactly, into $C_0^1(\bar{\Omega}_1)$. Let $F = \pi_1 \circ T$, where π_1 is the projection onto the first coordinate. By condition (D1), $u \in C_0^1(\bar{\Omega}_1)$. Also, for each component x_i of x,

$$\frac{\partial k_{sw}^N}{\partial x_i} \in C_0^1(\bar{\Omega}_1 \times \bar{\Omega}_1). \tag{141}$$

Thus, both $k^*_{sw}(x, y)$ and its first derivatives in the x variables are uniformly continuous on $\bar{\Omega}_1 \times \bar{\Omega}_1$. It follows that for each i,

$$\frac{\partial u}{\partial x_i} = \int_{\Omega_1}\int_{\Omega} \frac{\partial k^N_{sw}(x,z)}{\partial x_i} Q_w(z) k^N(z,y) g[y, n_0(y)] n_0(y)\, dy, \tag{142}$$

so $\frac{\partial u}{\partial x_i}$ is well defined and uniformly continuous on $\bar{\Omega}_1$. Hence the functions in the image under F of a bounded set in $C_0(\bar{\Omega}_1)$, and their first derivatives, will be equicontinuous and uniformly bounded , so that image will have compact closure in $C^1_0(\bar{\Omega}_1)$ by Arzela–Ascoli. Thus, F is a completely continuous map from $X_1 \times \{0\}$ into $C^1_0(\bar{\Omega}_1)$. Also, by $(D1)$, it follows that

$$||\nabla u||_0 \le C||n_0||_0, \tag{143}$$

where $||\cdot||_0$ denotes the sup norm on $C(\bar{\Omega}_1)$ and C is a constant independent of n_0. It follows from conditions (D), (D1) and (143) that there exists $\beta = \beta(n_0) > 0$ sufficiently large that $0 \le u \le \beta e(x)$. Additionally, it can be seen from (D), (D1), and (82) that if $n_0 \in X_1\backslash\{0\}$ then $u(x) \ge \alpha e(x)$ for some $\alpha > 0$. Hence, F is a completely continuous map from $X_1 \times \{0\}$ into $C^1_0(\bar{\Omega}_1)$. Finally, the embedding of $C^1_0(\bar{\Omega}_1)$ into X_e is continuous by Mierczyński (1998), Proposition 2.2. Since the map F from $X_1 \times \{0\}$ into $C^1_0(\bar{\Omega}_1)$ is completely continuous, so its composition with the embedding of $C^1_0(\bar{\Omega}_1)$ into X_e is, as well. Additionally, it maps $X_1\backslash\{0\} \times \{0\}$ into the interior of the cone P_e so it is strongly positive.

This argument shows that the eigenvalue problem (112) has a principal eigenvalue, since it allows us to apply the Krein-Rutman Theorem in X_e. A similar argument implies that $T(X_1 \times X_2) \subset C^1_0(\bar{\Omega}_1) \times X_2$. The map obtained by restricting T to the second component is completely continuous; see the comments after Lemma 3, and again $C^1_0(\bar{\Omega}_1) \times X_2$ embeds continuously into $X_e \times X_2$, so we can work in that space. For the case where there is partial occupancy by M, a similar construction with order units using condition (D2) and (83), and choosing, for example, $e_2(x) = \int_\Omega k^M_{sw}(x, y)dy$, would allow us to work in $X_e \times X_{e_2}$. If N has full occupancy we can work in the original space $X_1 \times X_2$.

The cones P_e and P_2 define the order relations $\le, <, \ll$ in the usual way. Let $P = P_e \times (-P_2)$, then P defines the order relation

$$(n, m) \le_P (\bar{n}, \bar{m}) \Longleftrightarrow n \le \bar{n}, \text{ and } \bar{m} \le m, \tag{144}$$

and likewise the order relations $<_P$ and $\ll_P$.

We want to show that T satisfies the following assumptions:

(H1) T is order compact, meaning for every $(n, m) \in P_e \times P_2$, $T([0, n] \times [0, m])$ has compact closure in X.

(H2) T is strictly order-preserving with respect to $<_P$. That is, $n < \bar{n}$ and $\bar{m} < m$ implies $T(n, m) <_P T(\bar{n}, \bar{m})$.

(H3) $T(0,0) = (0,0)$, and $(0,0)$ is a repelling point in the sense that there exists a neighborhood U of 0 in $P_e \times P_2$ such that $\forall\, (n,m) \in U\backslash\{0\}$, $\exists\, t, t \in Z$, such that $T^t(n,m) \notin U$.

(H4) $T(X_e^+ \times \{0\}) \subset X_e^+ \times \{0\}$. There exists $0 \ll \hat{n}$ such that $T(\hat{n},0) = (\hat{n},0)$, and $T^t(n_0,0) \to (\hat{n},0)$, $\forall\, n_0 > 0$. Likewise for T on $\{0\} \times X_2$, with fixed point $(0,\tilde{m})$.

(H5) If $(n_1,m_1) <_P (n_2,m_2)$, both are elements of $P_e \times P_2$, and either (n_1,m_1) or (n_2,m_2) belongs to $\mathring{P}_e \times \mathring{P}_2$, then $T(n_1,m_1) \ll_P T(n_2,m_2)$. If $(n,m) \in P_e \times P_2$ satisfies $x_i \neq 0$, $i = 1,2$, then $T(n,m) \gg 0$.

We will now show that these assumptions are met.

(H1) The operator T is completely continuous on $X_e \times X_2$ under our hypotheses by the previous arguments. (For case (i) we know that the operator T is completely continuous under the original norm on $X_1 \times X_2$, because Ω is a compact set, and $k_{sw}^M(x,z)$ and $k_{sw}^N(x,z)$ are continuous dispersal kernels.) Any order interval pair $([0,n] \times [0,m])$ in $X_1 \times X_2$ or $X_e \times X_2$ relative to the positive cones in those spaces is bounded in their respective norms, and thus has a relatively compact image. Therefore $T([0,n] \times [0,m])$ is also relatively compact in $X_e \times X_2$. Therefore T is order compact.

(H2) The argument is the same as in Theorem 2 and is omitted here.

(H3) It is clear that $T(0,0) = (0,0)$. The point $(0,0)$ is a repelling point because $g[y,0] > 1,\ \forall\, y \in \Omega_1$.

(H4) We know that $e = n_s^*(x)$ is a fixed point of T when restricted to $X_e \times \{0\}$. By definition of X_e, $n_s^*(x) \gg 0$. Let $\hat{n} = n_s^*(x)$. To show convergence of trajectories towards $(\hat{n},0)$, we will first show that T is strongly positive when restricted to X_e. That is, we want to show that $\forall\, n_0 \in X_e\backslash\{0\}$, $\exists\, \alpha > 0$, s.t. $F[n_0] > \alpha \cdot e$. Suppose the contrary, then there exists a sequence $\{x_k\}_{k=1}^{\infty}$ such that for each $k \in \mathbb{N}$,

$$u(x_k) < \frac{1}{k} \cdot e(x_k), \quad x_k \in \bar{\Omega}_1. \tag{145}$$

Following the arguments in Proposition 2.2 of Mierczyński (1998) again, we can show that this eventually leads again to a contradiction with the assumptions about $D_\nu(n_s^*(x))$.

To show that $T^t(n_0,0) \to (\hat{n},0)$, $\forall n_0 > 0$, we will use the same argument in Theorem 2 that invokes Theorem 2.3.4 of Zhao (2003). The only difference in the argument is that the strong positivity of the Fréchet derivative of T at $(0,0)$ can be concluded with an argument very similar to how T is strongly positive on X_e, replacing the nonlinear population growth function with its linearization at 0. Therefore the existence of a semitrivial equilibrium $(\hat{n},0)$ means $T^t(n_0,0) \to (\hat{n},0)$, $\forall\, n_0 \in X_e\backslash\{0\}$. For the behavior of T on $\{0\} \times X_2$, we can still assume, without loss of generality, that there exists a semitrivial equilibrium $(0,\tilde{m})$. In the case where such an equilibrium $(0,\tilde{m})$ does not exist, we can use the same argument from the proof of Theorem 2, which cites the proof in Theorem 3.3 of Kirkland et al. (2006). Assuming there exists a semitrivial equilibrium $(0, \tilde{m})$, then $0 \ll \tilde{m}$ because of the positivity conditions on the dispersal kernels. Thus we can invoke Theorem 2.3.4 of Zhao (2003) again to show the convergence of initial data on $\{0\} \times X_2$ to $(0, \tilde{m})$.

(H5) We already showed T is strongly positive when restricted to $X_e \times \{0\}$. The strong positivity of T on $X_e \times X_2$ then comes from the positivity assumption that $k_{sw}^M(x, z) > 0, \forall x \in \Omega, \forall z \in \Omega$. Now let $x = (x_1, x_2)$ and $y = (y_1, y_2)$ be two elements of $P_e \times P_2$, and $x <_P y$. From (H2) we know that $T(x) <_P T(y)$. The fact that $T(x) \ll_P T(y)$ comes from the strong positivity of T.

As we have seen, operator T satisfies conditions (H1)-(H5). By Lemma 4 and Theorem A in Hsu et al. (1996), $\forall x = (x_1, x_2) \in X^+$, either $T^n(x) \to (\hat{x}_1, 0)$ or $T^n(x) \to (0, \tilde{x}_2)$. Since Lemma 5 showed the latter cannot be the case, it must be that $T^n(x) \to (\hat{x}_1, 0) = (n_s^*(x), 0)$. The global asymptotic stability of the equilibrium $(n_s^*(x), 0)$ implies that the ideal free dispersal strategy is an evolutionarily stable strategy by Definition 3. This completes the proof of this theorem. □

3 Discussion

Our main conclusion is that it is possible to define the ideal free distribution for integrodifference models in spatially heterogeneous environments with either one or two seasons, and if the population dynamical terms are such that the integrodifference models generate a monotone semidynamical system (e.g. Beverton–Holt dynamics), then dispersal strategies (i.e. choices of dispersal kernels) which lead to an ideal free distribution are evolutionarily steady (ESS) and neighborhood invaders (NIS) relative to strategies that do not produce an ideal free distribution. (A neighborhood invader strategy is one that allows a small population using it to invade established populations that use other strategies.) A secondary conclusion is that the class of strategies that can produce an ideal free distribution is quite restricted, at least during the growing season, and it appears that to achieve an ideal free distribution typically requires a complete knowledge of the spatial distribution of habitat that is favorable for population growth during the growing season. This is in contrast with the case of reaction-advection-diffusion and integrodifferential models in temporally constant but spatially varying environments where there are multiple strategies that can produce an ideal free distribution, and all (for reaction-diffusion-advection) or at least some (in the case of integrodifferential models) of those strategies can be achieved on the basis of purely local information. See Averill et al. (2012), Cantrell et al. (2010, 2012b), Cosner et al. (2012), Korobenko and Braverman (2014). For reaction-advection-diffusion models in time periodic environments, however, nonlocal information is needed to achieve an ideal free distribution Cantrell and Cosner (2018).

The fact that a rather complete knowledge of the environment in the growing season is typically needed to achieve an ideal free distribution in the setting of integrodifference models raises the question of how organisms can obtain the information. There are several possible answers. In an environment where population growth is possible at every location, a population that simply stays in place will grow to match the level of resources wherever it is initially present. If it is initially present everywhere that will lead to an ideal free distribution. That strategy would not be available to a population colonizing new habitats, however. Another possibility would be for organisms to update their dispersal strategies (i.e. modify their dispersal kernels) by learning. We are currently thinking about how to build mechanisms to account for learning from experience and memory into our models. It seems plausible that in an environment that was relatively benign but not necessarily universally favorable a population that initially used the strategy of going everywhere but learned from experience might be able to survive long enough to eventually learn the resource distribution well and thus approximate ideal free dispersal. Such a process might involve social learning, which is known to be important in sustaining existing migrations; for discussion of social learning and a spatially implicit model see Fagan et al. (2012). It would be possible and might be of interest to construct related spatially explicit migration models with social learning by using the sort of formulation we have developed in the present paper.

Our primary focus here is on the evolutionary advantages of dispersal or migration strategies that produce an ideal free distribution, but there may be some other phenomena which the models support that are also of interest. For example, we assume no density dependent effects during the winter, but for an ideal free distribution a population must spend the winter in regions that optimize survival. If those regions are small such a strategy could produce high densities of organisms during the winter. In fact, wintering (and hibernating) in large groups has been observed in ladybird beetles, garter snakes, and some species of bats.

The theoretical framework we have developed allows us to study interacting populations that may only occupy part of the environment during either season from the viewpoint of discrete semidynamical systems. A key issue is that with partial occupancy we may have population densities that are zero in some places. That causes difficulties with regard to using results based on strong positivity such as the strong version of the Krein-Rutman theorem. To address that issue we set up the partial occupancy model on spaces with positive cones similar to those used in treating diffusion models with Dirichlet boundary conditions. That construction may be useful in formulating and analyzing other integrodifference models for situations that involve partial occupancy.

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