Ideal Free Dispersal in Integro-Difference Models

Robert Stephen Cantrell[1,3], Chris Cosner[1,3], and Ying Zhou[2]

1. Department of Mathematics, University of Miami

2. Department of Mathematics, Lafayette College

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1 Abstract

In this paper, we use an integrodifference equation model and pairwise invasion analysis to find what dispersal strategies are evolutionarily stable strategies (ESS) when there is spatial heterogeneity in habitat suitability, and there may be seasonal changes in this spatial heterogeneity, so that 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 that makes dispersal really 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, a partial occupation ideal free distribution that occupies only the viable region is shown to be 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 applies to integral operators.

2 Introduction

The main goal of this paper is to determine which dispersal strategies are predicted by pairwise invasion analysis to be evolutionarily steady (sometimes also known as evolutionarily stable 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 integrodiference 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, 2012a,b, 2017b), Cantrell and Cosner (2018), 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, 2017b, 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 K was the maximum over a class of growth functions $F \in \mathscr{F}$ of the infimum of the spectral radius of the linearization at $u = 0$ of the full dispersal and growth operator $\Phi(u) = K \circ F(u)$. 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 set of possible growth functions $\mathscr{F}$.) They considered the cases of no dispersal at all, uniform dispersal everywhere, and dispersal described by diffusion-like kernels $k(x, y) = J(|x - y|)$ 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, so that not diffusing at all is a convergence stable strategy; see Hastings (1983), Dockery et al. (1998). 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 $k(x, y)$. 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). The second case requires some new technical results that may be of independent interest. In both 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.

3 Model formulation and main results

In this section, we will construct a model to study the dynamics of a population of single-species organisms that disperse before every summer and winter to keep track of the seasonal changes in their habitat. 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 in a compact subset Ω of $\mathbb{R}^n$, so that the population density outside Ω is always 0. In cases of applied interest, $1 \leq n \leq 3$.

We adopt an integrodifference-equation framework, which is suitable for organisms whose dispersal occurs in short periods of time, so that the change in their population size during dispersal is negligible. The population we are studying is assumed to be sessile for most of the year, but redistribute in space twice a year. This redistribution in space is modeled by taking an integral transformation of the pre-dispersal population density, mapping it to the post-dispersal population density. The kernel of the integral transformation is referred to as the *redistribution kernel* or the *dispersal kernel*. 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 the pair of integral equations 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 equation (1a), $n_{s,t}(x)$ is first mapped to the pre-dispersal density,

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

to account for the change in the population size when the population is sessile. The function $Q_s(y)$ is a *habitat quality function* with range $[0,1]$ that describes the spatial heterogeneity of habitat quality at each location y. By multiplying the habitat quality function to 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 $Q_s(y)$. The pre-dispersal density (2) is then mapped to $n_{w,t}(x)$ by the integral in (1a) with the dispersal kernel $k_{ws}(x,y)$ to account for the spatial redistribution during the dispersal before winter. The dispersal 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. It is assumed that there is no population change during the dispersal, therefore

$$\int_\Omega k_{ws}(x,y)\, dx = 1, \quad \forall y. \tag{3}$$

Likewise, equation (1b) maps $n_{w,t}(x)$ to $n_{s,t+1}(x)$ in a similar way, with a linear population growth function that is rescaled by the habitat quality $Q_w(y)$ and then transformed by an integral transformation with dispersal kernel $k_{sw}(x,y)$. We also assume

$$\int_\Omega k_{sw}(x,y)\, dx = 1, \quad \forall y. \tag{4}$$

3.1 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

$$n_{s,t+1}(x) = \int_\Omega k_{sw}(x,y) Q_s(y) \frac{f_0\, n_{s,t}(y)}{1 + b_0 n_{s,t}(y)}\, dy. \tag{5}$$

Equation (5) reflects an absence of a distinct winter season, and the population only disperses once a year after summer.

Dropping the s and sw subscripts, and using a more abstract *fitness* function

$$g[y, n_t(y)] \tag{6}$$

to replace

$$\frac{f_0 Q_s(y)}{1 + b_0 n_t(y)}, \tag{7}$$

equation (5) can be rewritten in the generalized form

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

We still assume

$$\int_\Omega k(x,y)\, dx = 1, \quad \forall y. \tag{9}$$

When the population, hereafter referred to as population N, does not disperse at all, equation (8) becomes

$$n_{t+1}(x) = g[x, n_t(x)]\, n_t(x). \tag{10}$$

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

(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 (7), as a function of $n_t(x)$, with the assumption $\forall\, x \in \Omega,\ Q_s(x) > 0$, meets conditions (G1) $-$ (G3). In addition, for the cases we consider (except in section 2.3), we make an additional assumption:

(G4) $g[x, n(x)]$ is a function such that equation (10) has a unique nontrivial equilibrium $n^*(x)$ that is asymptotically stable, and

$$n^*(x) > 0,\ \forall x \in \Omega. \tag{11}$$

Since this equilibrium satisfies

$$g[x, n^*(x)] = 1, \tag{12}$$

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

In section 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.

Definition 1. *The population described by $n_t(x)$ in equation* (8) *is adopting an ideal free dispersal strategy $k(x,y)$ (relative to $n^*(x)$) if the dispersal kernel $k(x,y)$ satisfies*

$$n^*(x) = \int_\Omega k(x,y) n^*(y)\, dy, \tag{13}$$

where $n^*(x)$ is defined by (12).

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 (13) 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 let the two populations engage in a competitive relationship when it comes to resourses 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:

$$n_{t+1}(x) = \int_\Omega k_n(x,y) g[y, n_t(y) + m_t(y)]\, n_t(y)\, dy, \tag{14a}$$

$$m_{t+1}(x) = \int_\Omega k_m(x,y) g[y, n_t(y) + m_t(y)]\, m_t(y)\, dy. \tag{14b}$$

In system (14), $k_n(x,y)$ is an ideal free dispersal strategy relative to $n^*(x)$, $k_m(x,y)$ is not, but both kernels satisfy (9). In addition to assumptions (G1) $-$ (G3), we also assume system (14) 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* (8)*. This equilibrium is invasible by $m_t(x)$ if $m_t(x) \equiv 0$ is unstable relative to nonnegative initial data in equation* (14b)*. If $m_t(x) \equiv 0$ is stable relative to nonnegative initial data in equation* (14b)*, then $n(x)$ is not invasible.*

Definition 3. *A dispersal strategy $k(x,y)$ in* (13) *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 function $f(x,y)$ is said to be line-sum symmetric if it satisfies*

$$\int_{-\infty}^{\infty} f(y,x)\, dy = \int_{-\infty}^{\infty} f(x,y)\, dy. \tag{15}$$

Lemma 1. *Conditions* (9) *and* (13) *imply that the function $k(x,y)n^*(y)$ is line-sum symmetric.*

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

$$\begin{aligned}
\int_\Omega k(y,x)\, n^*(x)\, dy &= n^*(x) \int_\Omega k(y,x)\, dy && (16a)\\
&= n^*(x) \int_\Omega k(x,y)\, dx && (16b)\\
&= n^*(x) && (16c)\\
&= \int_\Omega k(x,y)\, n^*(y)\, dy. && (16d)
\end{aligned}$$

□

We will first restate Theorem 4 of (Cantrell et al. 2012b) below because we will make frequent use of this theorem.

Theorem 1. *(Cantrell et al. 2012b, Theorem 4) Let $f(x,y)$ be a nonnegative function for all x and y. Then $f(x,y)$ is line-sum symmetric if and only if*

$$\int_{-\infty}^{\infty}\int_{-\infty}^{\infty} f(x,y)\, \frac{\psi(x)}{\psi(y)}\, dx\, dy \geq \int_{-\infty}^{\infty}\int_{-\infty}^{\infty} f(x,y)\, dx\, dy \tag{17}$$

for all $\psi(x) > 0$ and $\psi(y) > 0$. In addition, if $f(x,y) > 0$, $\forall x$, $\forall y$, and $f(x,y)$ is line-sum symmetric, then equality in (17) *holds if and only if $\psi(x) \equiv \psi(y)$.*

Lemma 2. *Assume $k_n(x,y)$ and $k_m(x,y)$ are continuous functions that satisfy both condition* (9) *and the positivity condition*

$$k(x,y) > 0, \forall x,\ \forall y \in \Omega. \tag{18}$$

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. In addition, assume $g[x,n(x)]$ satisfies (G1) $-$ (G4). Then system (14) 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

$$n(x) = \int_\Omega k_n(x,y)\, g[y,n(y)+m(y)]\, n(y)\, dy, \tag{19a}$$

$$m(x) = \int_\Omega k_m(x,y)\, g[y,n(y)+m(y)]\, m(y)\, dy, \tag{19b}$$

with both components nonzero. Because of the positivity condition (18), the two components must be strictly positive:

$$n(x) > 0,\ m(x) > 0,\ \forall x \in \Omega. \tag{20}$$

We will show that this means population M also adopts an ideal free strategy, which contradicts the assumptions of the lemma.

To begin, we multiply both sides of equation (19a) with $\psi(x)$, where

$$\psi(x) = \frac{n^*(x)}{g[x,n(x)+m(x)]n(x)}. \tag{21}$$

This fraction is well-defined because of (20) and assumption (G1). Thus we obtain

$$\frac{n^*(x)}{g[x,n(x)+m(x)]} = \int_\Omega k_n(x,y)\frac{g[y,n(y)+m(y)]n^*(x)n(y)}{g[x,n(x)+m(x)]n(x)}\, dy \tag{22a}$$

$$= \int_\Omega k_n(x,y)n^*(y) \cdot \frac{g[y,n(y)+m(y)]n(y)}{g[x,n(x)+m(x)]n(x)} \cdot \frac{n^*(x)}{n^*(y)}\, dy \tag{22b}$$

$$= \int_\Omega k_n(x,y)n^*(y)\, \frac{\psi(x)}{\psi(y)}\, dy, \tag{22c}$$

while (11) is also invoked to ensure the fractions are well-defined. Integrating both sides with respect to x, we get

$$\int_\Omega \frac{n^*(x)}{g[x,n(x)+m(x)]}\, dx = \int_\Omega\int_\Omega k_n(x,y)n^*(y)\, \frac{\psi(x)}{\psi(y)}\, dydx \tag{23a}$$

$$\geq \int_\Omega\int_\Omega k_n(x,y)n^*(y)\, dydx. \tag{23b}$$

The inequality in the last step is due to inequality (17) and $k_n(x,y)n^*(y)$ being line-sum symmetric.

Since $k_n(x,y)$ integrates to 1 with respect to x,

$$\int_\Omega\int_\Omega k_n(x,y)n^*(y)\, dydx = \int_\Omega n^*(x)\, dx, \tag{24}$$

and the last inequality in (23) can be replaced by

$$\int_\Omega \frac{n^*(x)}{g[x,m(x)+n(x)]}\, dx \geq \int_\Omega n^*(x)\, dx. \tag{25}$$

Therefore

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

On the other hand, adding equation (19a) to equation (19b) and integrating both sides yields

$$\int_\Omega [m(x)+n(x)]\cdot\{1-g[x,m(x)+n(x)]\}\,dx = 0. \tag{27}$$

Subtracting equation (27) from inequality (26), we obtain

$$\int_\Omega \left\{\frac{n^*(x)}{g[x,m(x)+n(x)]}-[m(x)+n(x)]\right\}\cdot\{1-g[x,m(x)+n(x)]\}\,dx \geq 0. \tag{28}$$

Rewriting inequality (28) and using (12), we obtain

$$\int_\Omega \frac{n^*(x)-[m(x)+n(x)]g[x,m(x)+n(x)]}{g[x,m(x)+n(x)]}\cdot\{1-g[x,m(x)+n(x)]\}\,dx \tag{29a}$$

$$\tag{29b}$$

$$= \int_\Omega \frac{n^*(x)g(x,n^*(x))-[m(x)+n(x)]g[x,m(x)+n(x)]}{g[x,m(x)+n(x)]}\cdot\{g[x,n^*(x)]-g[x,m(x)+n(x)]\}\,dx \tag{29c}$$

$$\geq 0. \tag{29d}$$

But the integrand satisfies

$$\frac{n^*(x)g[x,n^*(x)]-[m(x)+n(x)]g[x,m(x)+n(x)]}{g[x,m(x)+n(x)]}\cdot\{g[x,n^*(x)]-g[x,m(x)+n(x)]\}\leq 0 \tag{30}$$

because the two factors

$$n^*(x)g[x,n^*(x)]-[m(x)+n(x)]g[x,m(x)+n(x)] \tag{31}$$

and

$$g[x,n^*(x)]-g[x,m(x)+n(x)] \tag{32}$$

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 less 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 nonnegative, the only possibility is that the integrand is 0. Therefore

$$n^*(x) = m(x)+n(x). \tag{33}$$

Meanwhile, this also means inequalities (23) and (28) are, in fact, both equalities. Therefore

$$\int_\Omega\int_\Omega k_n(x,y)n^*(y)\cdot\frac{\psi(x)}{\psi(y)}\,dydx = \int_\Omega\int_\Omega k_n(x,y)n^*(y)\,dydx. \tag{34}$$

Because the function $k_n(x,y)n^*(y)$ is line-sum-symmetric and strictly positive, Theorem 1 implies that equality (34) is achieved only if $\psi(x)=\psi(y)$. So we have

$$\frac{n^*(x)}{n(x)} = \frac{n^*(y)}{n(y)}. \tag{35}$$

Therefore it must be that both fractions are a constant, and there is some constant c so that

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

Thus we have

$$n(x) = cn^*(x), \tag{37}$$

and

$$m(x) = (1-c)n^*(x). \tag{38}$$

As a result, equation (19b) is equivalent to

$$\begin{aligned}
(1-c)n^*(x) &= \int_\Omega k_m(x,y)g[y, m(y)+n(y)](1-c)n^*(y)\,dy \\
&= \int_\Omega k_m(x,y)g[y, n^*(y)](1-c)n^*(y)\,dy \\
&= \int_\Omega k_m(x,y)(1-c)n^*(y)\,dy.
\end{aligned} \tag{39}$$

If $c \neq 1$, then

$$n^*(x) = \int_\Omega k_m(x,y)n^*(y)\,dy. \tag{40}$$

Equation (40) implies that $k_m(x,y)$ is also an ideal free strategy relative to $n^*(x)$, which is a contradiction to the assumptions of this lemma. Therefore system (14) 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. *We will make the same assumptions as the previous lemma, namely, that population N adopts an ideal free dispersal strategy $k_n(x,y)$ relative to $n^*(x)$, and population M adopts a dispersal strategy $k_m(x,y)$ that is not ideal free. Both dispersal kernels are positive in $\Omega\times\Omega$ and satisfy condition (9). The function $g[x,n(x)]$ is assumed to satisfy $(G1)-(G4)$. With these assumptions, if system (14) has a semitrivial equilibrium $(0,m^*)$, then this equilibrium $(0,m^*)$ must be unstable.*

Proof. Consider the eigenvalue problem

$$\lambda\phi(x) = \int_\Omega k_n(x,y)g[y,m^*(y)]\phi(y)\,dy. \tag{41}$$

With our assumptions, the integral operator defined by the right-hand side of equation (41) is completely continuous. (See Hardin et al. (1990). The reason the operator is completely continuous is that $\Omega\times\Omega$ is closed and bounded, and $k(x,y)$ is continuous on $\Omega\times\Omega$, so it is bounded and uniformly continuous there. Thus, the integral operator maps any bounded set of continuous functions into a set of functions that is uniformly bounded and equicontinuous.) Because $k_n(x,y)$ satisfies the positivity condition (18), the Krein-Rutman theorem (Krein and Rutman 1950) 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

$$m^*(x) > 0,\ \forall x \in \Omega, \tag{42}$$

because $k_m(x,y)$ meets the positivity condition (18). Multiplying both sides of the eigenvalue problem equation (41) by

$$\frac{n^*(x)}{\phi(x)g[x,m^*(x)]}, \tag{43}$$

we obtain

$$\frac{n^*(x)}{\phi(x)g[x,m^*(x)]}\cdot\lambda\phi(x) = \int_\Omega k_n(x,y)\cdot\frac{n^*(x)}{\phi(x)g[x,m^*(x)]}\cdot\phi(y)g[y,m^*(y)]\,dy \tag{44a}$$

$$= \int_\Omega k_n(x,y)n^*(x)\cdot\frac{\phi(y)g[y,m^*(y)]}{\phi(x)g[x,m^*(x)]}\,dy \tag{44b}$$

$$= \int_\Omega k_n(x,y)n^*(y)\cdot\frac{\phi(y)g[y,m^*(y)]/n^*(y)}{\phi(x)g[x,m^*(x)]/n^*(x)}\,dy. \tag{44c}$$

Therefore

$$\frac{\lambda n^*(x)}{g[x,m^*(x)]} = \int_\Omega k_n(x,y)n^*(y)\cdot\frac{\phi(y)g[y,m^*(y)]/n^*(y)}{\phi(x)g[x,m^*(x)]/n^*(x)}\,dy. \tag{45}$$

Integrating both sides, we get

$$\lambda\int_\Omega \frac{n^*(x)}{g[x,m^*(x)]}\,dx = \int_\Omega\int_\Omega k_n(x,y)n^*(y)\cdot\frac{\phi(y)g[y,m^*(y)]/n^*(y)}{\phi(x)g[x,m^*(x)]/n^*(x)}\,dydx. \tag{46}$$

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

$$\int_\Omega\int_\Omega k_n(x,y)n^*(y)\cdot\frac{\phi(y)g[y,m^*(y)]/n^*(y)}{\phi(x)g[x,m^*(x)]/n^*(x)}\,dydx \geq \int_\Omega\int_\Omega k_n(x,y)n^*(y)dydx = \int_\Omega n^*(x)\,dx. \tag{47}$$

Thus equation (46) can be replaced by the inequality

$$\lambda\int_\Omega \frac{n^*(x)}{g[x,m^*(x)]}\,dx \geq \int_\Omega n^*(x)\,dx. \tag{48}$$

The last inequality means that

$$(\lambda-1)\int_\Omega \frac{n^*(x)}{g[x,m^*(x)]}\,dx \geq \int_\Omega n^*(x)\left\{1-\frac{1}{g[x,m^*(x)]}\right\}\,dx = \int_\Omega n^*(x)\left\{\frac{g[x,m^*(x)]-1}{g[x,m^*(x)]}\right\}\,dx \tag{49}$$

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

$$m^*(x) = \int_\Omega k_m(x,y)g[y,m^*(y)]\,m^*(y)\,dy. \tag{50}$$

Integrating both sides of (50), and using the fact that $k_m(x,y)$ satisfies condition (9), we integrate both sides and get

$$\int_\Omega m^*(x)\,dx = \int_\Omega g[y,m^*(y)]\,m^*(y)\,dy = \int_\Omega g[x,m^*(x)]\,m^*(x)\,dx. \tag{51}$$

Therefore

$$\int_\Omega m^*(x)\{1-g[x,m^*(x)]\}\,dx = 0. \tag{52}$$

That means

$$\int_\Omega n^*(x)\left\{\frac{g[x,m^*(x)]-1}{g[x,m^*(x)]}\right\}\,dx \tag{53a}$$

$$= \int_\Omega \{n^*(x)-m^*(x)g[x,m^*(x)]\}\cdot\left\{\frac{g[x,m^*(x)]-1}{g[x,m^*(x)]}\right\}\,dx \tag{53b}$$

$$= \int_\Omega \{g[x,n^*(x)]n^*(x)-g[x,m^*(x)]m^*(x)\}\cdot\left\{\frac{g[x,m^*(x)]-g[x,n^*(x)]}{g(x,m^*(x))}\right\}\,dx \tag{53c}$$

$$\geq 0. \tag{53d}$$

Inequality (53) becomes an equality only when

$$g[x,m^*(x)] = g[x,n^*(x)] = 1, \tag{54}$$

and

$$m^*(x) = n^*(x), \tag{55}$$

resulting in

$$n^*(x) = m^*(x) = \int_\Omega k_m(x,y)g[y,m^*(y)]\,m^*(y)\,dy. \tag{56}$$

Since population M is not adopting an ideal free strategy, $k_m(x,y)$ would not be such a function that equation (56) holds. Therefore inequality (53) is strict, and

$$(\lambda - 1)\int_\Omega \frac{n^*(x)}{g[x, m^*(x)]}\,dx > 0. \tag{57}$$

Therefore

$$\lambda > 1, \tag{58}$$

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 (14) is globally asymptotically stable, and the ideal free dispersal strategy $k(x,y)$, as defined in Definition 1, is an evolutionarily-stable strategy.*

Proof. Let the spaces X_1 and X_2 be $X_i = BC(\Omega)$, the space of all bounded and continuous functions on Ω, for $i = 1, 2$. Let them be equipped with positive cones $X_i^+ = BC^+(\Omega)$, the set of all nonnegative functions in $BC(\Omega)$, 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

$$T\begin{bmatrix} n(x) \\ m(x) \end{bmatrix} = \begin{bmatrix} \int_\Omega k_n(x,y) g[y, n(y) + m(y)]\, n(y)\, dy \\ \int_\Omega k_m(x,y) g[y, n(y) + m(y)]\, m(y)\, dy \end{bmatrix}. \tag{59}$$

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

$$g(x, n + m) \cdot (n + m) < g(x, \bar{n} + m) \cdot (\bar{n} + m). \tag{60}$$

Expanding the terms in both sides yields

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

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

$$g(x, n + m) \cdot m > g(x, \bar{n} + m) \cdot m, \ \ \forall x \in \Omega. \tag{62}$$

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

$$g(x, \bar{n} + m) < g(x, \bar{n} + \bar{m}), \tag{63}$$

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 (12), 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

$$f(x, \alpha n) > \alpha f(x, n),\ \forall \alpha \in (0, 1). \tag{64}$$

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 (9) ensure that every orbit of T is bounded on $X_1 \times \{0\}$. The positivity assumption (18) 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 (18), 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 (14) 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 (14) 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 (14) 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.

$\square$

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

Now let us consider the two-season model (1). Equations (1a) and (1b) can be combined as one equation that maps $n_{s,t}(x)$ to $n_{s,t+1}(x)$,

$$n_{s,t+1}(x) = \int_\Omega \int_\Omega k_{sw}(x,z)\, Q_w(z)\, k_{ws}(z,y) \cdot \frac{f_0 g_0 Q_s(y)\, n_{s,t}(y)}{1 + b_0 n_{s,t}(y)}\, dydz, \tag{65}$$

Let

$$g[x, u(x)] = \frac{f_0 g_0\, Q_s(x)}{1 + b_0 u(x)}, \tag{66}$$

and let $n_s^*(x)$ be the solution to

$$g[x, n_s^*(x)] = 1. \tag{67}$$

Then we can think of $n_s^*(x)$ as the ideal free distribution in the summer season for the two-season case. Within this section, we assume that $n_s^*(x) > 0, \forall\, x \in \Omega$. Note that for an ideal free distribution we will want $n_s^*(x)$ to be an equilibrium of (65), so that using $g[x, n_s^*(x)] = 1$ we get

$$n_s^*(x) = \int_\Omega \int_\Omega k_{sw}(x,z)\, Q_w(z)\, k_{ws}(z,y)\, n_s^*(y)\, dydz. \tag{68}$$

Integrating in x and using Fubini's theorem and the assumption $\int_\Omega k(x,z)dx = 1$ we have

$$\int_\Omega n_s^*(x)dx = \int_\Omega \int_\Omega Q_w(z)\, k_{ws}(z,y)dz\, n_s^*(y)\, dy. \tag{69}$$

Since $Q_w(z) \le 1$, and in general we may have we have $Q_w(z) < 1$ for some z, unless we require $Q_w(z)\, k_{ws}(z,y) = k_{ws}(z,y)$ we would have

$$\int_\Omega Q_w(z)\, k_{ws}(z,y)dz < \int_\Omega k_{ws}(z,y)dz = 1, \tag{70}$$

which would create a contradiction in (69). Thus the condition $Q_w(z)k_{ws}(z,y) = k_{ws}(z,y)$ is necessary to achieve an ideal free distribution.

For the two-season case, a dispersal strategy is represented by two dispersal kernels, k_{sw} and k_{ws}. Therefore we consider a pair of equations that jointly define an ideal free strategy, as elaborated in the following definition.

Definition 5. *Let $n_s^*(x)$ be defined by (67). If the dispersal kernels $k_{sw}^*(x,z)$ and $k_{ws}^*(z,y)$ satisfy*

$$Q_w(z)k_{ws}^*(z,y) = k_{ws}^*(z,y) \tag{71}$$

and

$$n_s^*(x) = \int_\Omega \int_\Omega k_{sw}^*(x,z)k_{ws}^*(z,y)\, n_s^*(y)\, dz\, dy, \tag{72}$$

then $k_{sw}^*(x,z)$ and $k_{ws}^*(z,y)$ together define an ideal free dispersal strategy relative to $n_s^*(x)$.

We want to show that this ideal free strategy is an evolutionarily-stable strategy.

Since we can combine the two seasons to rewrite model (1) as equation (65), we consider a two-species competition model based on model (65),

$$n_{s,t+1}(x) = \int_\Omega \int_\Omega k_{sw}^*(x,z)Q_w(z)k_{ws}^*(z,y)\, g[y, n_{s,t}(y) + m_{s,t}(y)]n_{s,t}(y)\, dz\, dy, \tag{73a}$$

$$m_{s,t+1}(x) = \int_\Omega \int_\Omega k_{sw}(x,z)Q_w(z)k_{ws}(z,y)\, g[y, n_{s,t}(y) + m_{s,t}(y)]m_{s,t}(y)\, dz\, dy, \tag{73b}$$

for two competing species, which we label as N and M. Species N is adopting the pair of strategies k_{sw}^* and k_{ws}^*, and species M is adopting another pair of strategies k_{sw} and k_{ws}, so that either

$$Q_w(z)k_{ws}(z,y) \neq k_{ws}(z,y) \text{ for some } (z,y) \in \Omega \times \Omega \tag{74}$$

or

$$n_s^*(x) \neq \int_\Omega \int_\Omega k_{sw}(x,z)k_{ws}(z,y)\, n_s^*(y)\, dz\, dy \tag{75}$$

for some $x \in \Omega$. Meanwhile, all dispersal kernels k_{sw}^*, k_{ws}^*, k_{sw}, and k_{ws} satisfy the no-loss conditions (3) and (4).

We will first verify that the dispersal kernels $k_{sw}^*(x,z)$ and $k_{ws}^*(z,y)$, and the ideal free distribution $n_s^*(x)$, satisfy a line-sum symmetry condition. Let

$$K^*(x,y) = \int_\Omega k_{sw}^*(x,z)\, k_{ws}^*(z,y)\, n_s^*(y)\, dz, \tag{76}$$

then $K^*(x,y)$ is line-sum symmetric. This is true because conditions (3) and (4) imply that

$$\int_\Omega K^*(y,x)\, dy = \int_\Omega \int_\Omega k_{sw}^*(y,z)\, k_{ws}^*(z,x)\, n_s^*(x)\, dzdy \tag{77a}$$

$$= \int_\Omega k_{ws}^*(z,x)\, n_s^*(x)\, dz \tag{77b}$$

$$= n_s^*(x). \tag{77c}$$

Since the ideal free strategy requirement (72) can be rewritten as

$$\int_\Omega K^*(x,y)\, dy = n_s^*(x), \tag{78}$$

we have

$$\int_\Omega K^*(x,y)\, dy = \int_\Omega K^*(y,x)\, dy. \tag{79}$$

Therefore $K^*(x,y)$ is line-sum symmetric.

We now proceed to show that system (73) does not allow the two species to coexist at a coexistence equilibrium, and that any semi-trivial equilibrium of system (73) of the form $(0, m^*)$ must be unstable.

Lemma 4. *Assume the dispersal kernels $k_{sw}^*(x,y)$, $k_{ws}^*(x,y)$, $k_{sw}(x,y)$, and $k_{ws}(x,y)$ are continuous functions that satisfy the no-loss condition* (9)*. In addition, the kernels $k_{sw}^*(x,y)$ and $k_{sw}(x,y)$ satisfy the positivity condition* (18)*. The kernels $k_{sw}^*(x,y)$ and $k_{ws}^*(x,y)$ are such that population N, described by $n_{s,t}(x)$, adopts an ideal free dispersal strategy relative to $n_s^*(x)$, and population M, described by $m_{s,t}(x)$, does not adopt an ideal free dispersal strategy. In addition, assume $g[x, n(x)]$ satisfies (G1) − (G4). Then system* (73) *does not have a coexistence equilibrium $(n(x), m(x))$ where $n(x)$ and $m(x)$ are both nonzero.*

Proof. We will again prove that system (73) does not have a nontrivial equilibrium by contradiction. Suppose, on the contrary, that there is a nontrivial equilibrium $(n(x), m(x))$ for the pair of equations (73). The positivity assumption (18) about the kernels $k_{sw}^*(x,z)$ and $k_{sw}(z,y)$, and the positivity assumption (G1) on function $g[x, n(x)]$ imply that $n(x)$ and $m(x)$ are both positive in Ω. The equilibrium $(n(x), m(x))$ satisfies

$$n(x) = \int_\Omega \int_\Omega k_{sw}^*(x,z)Q_w(z)k_{ws}^*(z,y)\, g[y, n(y)+m(y)]n(y)\, dz\, dy, \tag{80a}$$

$$m(x) = \int_\Omega \int_\Omega k_{sw}(x,z)Q_w(z)k_{ws}(z,y)\, g[y, n(y)+m(y)]m(y)\, dz\, dy. \tag{80b}$$

Integrating equation (80a) with respect to x, and using the ideal free condition (71) and the no-loss condition (9), we get

$$\int_\Omega n(x)\,dx = \int_\Omega \int_\Omega Q_w(z) k^*_{ws}(z,y) g[y, n(y)+m(y)] n(y)\,dydz \tag{81a}$$

$$= \int_\Omega \int_\Omega k^*_{ws}(z,y) g[y, n(y)+m(y)] n(y)\,dydz \tag{81b}$$

$$= \int_\Omega k^*_{ws}(z,y)\,dz \int_\Omega g[y, n(y)+m(y)] n(y)\,dy \tag{81c}$$

$$= \int_\Omega g[y, n(y)+m(y)] n(y)\,dy. \tag{81d}$$

Integrating equation (80b) with respect to x, we get

$$\int_\Omega m(x)\,dx = \int_\Omega \int_\Omega Q_w(z) k_{ws}(z,y) g[y, n(y)+m(y)] m(y)\,dydz \tag{82a}$$

$$\leq \int_\Omega \int_\Omega k_{ws}(z,y)\; g[y, n(y)+m(y)] m(y)\,dydz \tag{82b}$$

$$= \int_\Omega g[y, n(y)+m(y)] m(y)\,dy. \tag{82c}$$

In inequality (82b), equality holds only if

$$\int_\Omega Q_w(z) k_{ws}(z,y)\,dz = \int_\Omega k_{ws}(z,y)\,dz, \tag{83}$$

which is equivalent to

$$Q_w(z) k_{ws}(z,y) = k_{ws}(z,y) \tag{84}$$

because $Q_w(z) \leq 1$.

Adding the two integrals (81) and (82) together yields

$$\int_\Omega [n(x)+m(x)]\,dx \leq \int_\Omega g[x, n(x)+m(x)] \cdot [n(x)+m(x)]\,dx, \tag{85}$$

where the inequality is strict unless condition (83) is true.

Multiplying equation (80a) by

$$\Psi(x) = \frac{n^*_s(x)}{n(x) g[x, n(x)+m(x)]}, \tag{86}$$

and integrating both sides, we obtain

$$\int_\Omega \frac{n_s^*(x)}{g[x, n(x)+m(x)]}\,dx \tag{87a}$$

$$= \int_\Omega\int_\Omega\int_\Omega k_{sw}^*(x,z)Q_w(z)k_{ws}^*(z,y)\,g[y,n(y)+m(y)]n(y)\cdot\frac{n_s^*(x)}{g[x,n(x)+m(x)]n(x)}\,dz\,dy\,dx \tag{87b}$$

$$= \int_\Omega\int_\Omega\int_\Omega k_{sw}^*(x,z)Q_w(z)k_{ws}^*(z,y)\,n_s^*(y)\cdot\frac{g[y,n(y)+m(y)]n(y)n_s^*(x)}{g[x,n(x)+m(x)]n(x)n_s^*(y)}\,dz\,dy\,dx \tag{87c}$$

$$= \int_\Omega\int_\Omega\int_\Omega k_{sw}^*(x,z)k_{ws}^*(z,y)n_s^*(y)\cdot\frac{g[y,n(y)+m(y)]n(y)n_s^*(x)}{g[x,n(x)+m(x)]n(x)n_s^*(y)}\,dz\,dy\,dx \tag{87d}$$

$$= \int_\Omega\int_\Omega K^*(x,y)\cdot\frac{\Psi(x)}{\Psi(y)}\,dy\,dx \tag{87e}$$

$$\geq \int_\Omega\int_\Omega K^*(x,y)\,dy\,dx \tag{87f}$$

$$= \int_\Omega n_s^*(x)\,dx. \tag{87g}$$

Here, inequality (87f) is due to Theorem 1 and the line-sum symmetric property of $K^*(x,y)$.

Therefore we know

$$\int_\Omega \frac{n_s^*(x)}{g[x,n(x)+m(x)]}\,dx \geq \int_\Omega n_s^*(x)\,dx, \tag{88}$$

and thus

$$\int_\Omega n_s^*(x)\left\{\frac{1-g[x,n(x)+m(x)]}{g[x,n(x)+m(x)]}\right\} \geq 0. \tag{89}$$

Meanwhile, inequality (85) implies

$$\int_\Omega \{1-g[x,n(x)+m(x)]\}\cdot[n(x)+m(x)]\,dx \leq 0, \tag{90}$$

and

$$\int_\Omega g[x,n(x)+m(x)]\cdot[n(x)+m(x)]\cdot\left\{\frac{1-g[x,n(x)+m(x)]}{g[x,n(x)+m(x)]}\right\}\,dx \leq 0. \tag{91}$$

Subtracting inequalities (89) and (91), we get

$$\int_\Omega \{n_s^*(x)-g[x,n(x)+m(x)]\cdot[n(x)+m(x)]\}\cdot\left\{\frac{1-g[x,n(x)+m(x)]}{g[x,n(x)+m(x)]}\right\}\,dx \geq 0. \tag{92}$$

Replacing $n_s^*(x)$ with $g[x,n_s^*(x)]n_s^*(x)$, we obtain

$$\int_\Omega \{g[x,n_s^*(x)]n_s^*(x)-g[x,n(x)+m(x)]\cdot[n(x)+m(x)]\}\cdot\left\{\frac{1-g[x,n(x)+m(x)]}{g[x,n(x)+m(x)]}\right\}\,dx \geq 0. \tag{93}$$

Replacing 1 with $g[x,n_s^*(x)]$, we then obtain

$$\int_\Omega \{g[x,n_s^*(x)]n_s^*(x)-g[x,n(x)+m(x)]\cdot[n(x)+m(x)]\}\cdot\left\{\frac{g[x,n_s^*(x)]-g[x,n(x)+m(x)]}{g[x,n(x)+m(x)]}\right\}\,dx \geq 0. \tag{94}$$

The integrand of the integral in (94) is nonpositive because conditions (G2) and (G3) do not allow the two factors in the integrand to be of the same signs. Therefore inequality (94) is in fact an equality, which in turn implies the inequalities (82), (89), and (91) are equalities too. Meanwhile, the integrand of the integral in equation (94) must be 0, which means

$$n_s^*(x) = n(x) + m(x). \tag{95}$$

The fact that the equal sign holds in (94) means

$$\int_\Omega \int_\Omega K^*(x,y) \cdot \frac{\Psi(x)}{\Psi(y)} \, dydx \tag{96a}$$

$$= \int_\Omega \int_\Omega K^*(x,y) \, dydx. \tag{96b}$$

That means $\Psi(x) = \Psi(y)$, so $\Psi(x)$ is a constant. This constant is positive because the factors in $\Psi(x)$ in (86) are all positive in Ω. We can thus assume

$$\frac{n_s^*(x)}{n(x)} = \frac{1}{c}, \tag{97}$$

which means $n(x) = cn_s^*(x)$ and $m(x) = (1-c)n_s^*(x)$. From (80b) and (84),

$$m(x) = \int_\Omega \int_\Omega k_{sw}(x,z) \, k_{ws}(z,y) \, g[x, m(x) + n(x)] \, m(y) \, dy, \tag{98}$$

hence

$$m(x) = \int_\Omega \int_\Omega k_{sw}(x,z) \, k_{ws}(z,y) \, m(y) \, dy. \tag{99}$$

Substituting $(1-c)n_s^*(x)$ for $m(x)$, we have

$$n_s^*(x) = \int_\Omega \int_\Omega k_{sw}(x,z) \, k_{ws}(z,y) \, n_s^*(y) \, dy. \tag{100}$$

This is a contradiction with k_{sw} and k_{ws} being not ideal free strategies. Therefore a nontrivial equilibrium $(n(x), m(x))$ for equations (73) does not exist. $\square$

Lemma 5. *Assume the dispersal kernels $k_{sw}^*(x,z)$, $k_{ws}^*(z,y)$, $k_{sw}(x,z)$, and $k_{ws}(z,y)$ are continuous functions that satisfy condition* (9)*, and the two kernels $k_{sw}^*(x,z)$ and $k_{sw}(x,z)$ also satisfy the positivity condition* (18)*. The kernels $k_{sw}^*(x,z)$ and $k_{ws}^*(z,y)$ are such that population N, described by $n_{s,t}(x)$, adopts an ideal free dispersal strategy relative to $n_s^*(x)$, and population M, described by $m_{s,t}(x)$, does not adopt an ideal free dispersal strategy. In addition, assume $g[x, n(x)]$ satisfies (G1) − (G4). If system* (73) *has a semitrivial equilibrium $(0, m^*)$, then this equilibrium must be unstable.*

Proof. We consider the eigenvalue problem

$$\lambda \phi(x) = \int_\Omega \int_\Omega k_{sw}^*(x,z) \, Q_w(z) \, k_{ws}^*(z,y) \, g[y, m^*(y)] \, \phi(y) \, dz \, dy, \tag{101}$$

where

$$g[y, m^*(y)] = \frac{f_0 g_0 \, Q_s(y)}{1 + b_0 \, m^*(y)}. \tag{102}$$

Multiplying both sides of equation (101) by

$$\frac{n_s^*(x)}{\phi(x) g[x, m^*(x)]}, \tag{103}$$

we obtain

$$\frac{\lambda \, n_s^*(x)}{g[x, m^*(x)]} = \int_\Omega \int_\Omega k_{sw}^*(x,z) \, Q_w(z) \, k_{ws}^*(z,y) \, \frac{n_s^*(x)}{\phi(x) g[x, m^*(x)]} \, g[y, m^*(y)] \, \phi(y) \, dz \, dy \tag{104a}$$

$$= \int_\Omega \int_\Omega k_{sw}^*(x,z) \, Q_w(z) \, k_{ws}^*(z,y) \, n_s^*(x) \, \frac{\phi(y) g[y, m^*(y)]}{\phi(x) g[x, m^*(x)]} \, dz \, dy \tag{104b}$$

$$= \int_\Omega \int_\Omega k_{sw}^*(x,z) \, Q_w(z) \, k_{ws}^*(z,y) \, n_s^*(y) \, \frac{\Phi(y)}{\Phi(x)} \, dz \, dy, \tag{104c}$$

where

$$\Phi(x) = \frac{\phi(x) g[x, m^*(x)]}{n_s^*(x)}. \tag{105}$$

Integrating both sides, we obtain

$$\lambda \int_\Omega \frac{n_s^*(x)}{g[x, m^*(x)]}\, dx = \int_\Omega \int_\Omega \int_\Omega k_{sw}^*(x,z)\, Q_w(z)\, k_{ws}^*(z,y)\, n_s^*(y)\, \frac{\Phi(y)}{\Phi(x)}\, dz\, dy\, dx \tag{106a}$$

$$= \int_\Omega \int_\Omega K^*(x,y)\, \frac{\Phi(y)}{\Phi(x)}\, dy\, dx \tag{106b}$$

$$\geq \int_\Omega \int_\Omega K^*(x,y)\, dy\, dx \tag{106c}$$

$$= \int_\Omega n_s^*(x)\, dx. \tag{106d}$$

Therefore

$$\lambda \int_\Omega \frac{n_s^*(x)}{g[x, m^*(x)]}\, dx \geq \int_\Omega \frac{g[x, m^*(x)]}{g[x, m^*(x)]}\, n_s^*(x)\, dx, \tag{107}$$

and

$$(\lambda - 1) \int_\Omega \frac{n_s^*(x)}{g[x, m^*(x)]}\, dx \geq \int_\Omega n_s^*(x) \left\{ 1 - \frac{1}{g[x, m^*(x)]} \right\} dx. \tag{108}$$

Next we will show that the right hand side of equation (108) is nonnegative. To see this, we begin with observing that the equilibrium $m^*(x)$ must satisfy the equation

$$m^*(x) = \int_\Omega \int_\Omega k_{sw}(x,z)\, Q_w(z)\, k_{ws}(z,y)\, g[y, m^*(y)]\, m^*(y)\, dz\, dy. \tag{109}$$

Integrating both sides of equation (109), we obtain

$$\int_\Omega m^*(x)\, dx = \int_\Omega \int_\Omega \int_\Omega k_{sw}(x,z)\, Q_w(z)\, k_{ws}(z,y)\, g[y, m^*(y)]\, m^*(y)\, dz\, dy\, dx \tag{110a}$$

$$\leq \int_\Omega \int_\Omega \int_\Omega k_{sw}(x,z)\, k_{ws}(z,y)\, g[y, m^*(y)]\, m^*(y)\, dz\, dy\, dx \tag{110b}$$

$$= \int_\Omega g[y, m^*(y)]\, m^*(y)\, dy. \tag{110c}$$

Therefore

$$\int_\Omega m^*(x) \{1 - g[x, m^*(x)]\}\, dx \leq 0, \tag{111}$$

and

$$\int_\Omega m^*(x)\, \{g[x, m^*(x)] - 1\}\, dx \geq 0. \tag{112}$$

Subtracting the left-hand side of equation (112) from the right-hand side of equation (108), we obtain

$$\int_\Omega n_s^*(x) \left\{ 1 - \frac{1}{g[x, m^*(x)]} \right\} dx - \int_\Omega m^*(x)\, \{g[x, m^*(x)] - 1\}\, dx \tag{113a}$$

$$= \int_\Omega \{n_s^*(x) - m^*(x) g[x, m^*(x)]\}\, \frac{g[x, m^*(x)] - 1}{g[x, m^*(x)]}\, dx \tag{113b}$$

$$= \int_\Omega \{n_s^*(x) g[x, n_s^*(x)] - m^*(x) g[x, m^*(x)]\}\, \frac{g[x, m^*(x)] - g[x, n_s^*(x)]}{g[x, m^*(x)]}\, dx \tag{113c}$$

$$\geq 0. \tag{113d}$$

From inequalities (112) and (113), we know

$$\int_\Omega n_s^*(x)\left\{1-\frac{1}{g[x,m^*(x)]}\right\}dx \geq \int_\Omega m^*(x)\left\{g[x,m^*(x)]-1\right\}dx \geq 0. \tag{114}$$

Inequality (112) becomes an equality only when $Q_w(z)\,k_{ws}(z,y) = k_{ws}(z,y)$. Inequality (113) becomes an equality only when $g[x,m^*(x)] \equiv 1$, which requires $n_s^*(x) \equiv m^*(x)$, and

$$n_s^*(x) = \int_\Omega \int_\Omega k_{sw}(x,z)\,Q_w(z)\,k_{ws}(z,y)\,dz\,g[y,n_s^*(y)]\,n_s^*(y)\,dy \tag{115a}$$

$$= \int_\Omega \int_\Omega k_{sw}(x,z)\,Q_w(z)\,k_{ws}(z,y)\,dz\,n_s^*(y)\,dy. \tag{115b}$$

If k_{sw} and k_{ws} are kernels that do not satisfy the ideal free conditions (71) and (72), either one of the inequalities (112) and (113) will be strict. Therefore, with inequality (108), we know

$$(\lambda-1)\int_\Omega \frac{n_s^*(x)}{g[x,m^*(x)]}\,dx > 0, \tag{116}$$

and

$$\lambda > 1. \tag{117}$$

□

Just as in the single-season case, Lemmas 4 and 5 imply that the ideal free dispersal strategy, as defined in Definition 5, is an evolutionarily-stable strategy. The supporting argument for this result is a special case of Theorem 3 in the next section, and is not repeated here for the sake of brevity. In the next section, we show that the results in this section can be further extended to a more general case.

3.3 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, (18) is satisfied, so that $k_{sw}(x,y) > 0\ \forall (x,y) \in \Omega \times \Omega$. 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. In such a case, a population with an ideal free distribution cannot occupy sink environments. That is because under an ideal free distribution a population should have equal fitness everywhere, and at population equilibrium that fitness would have to be equal to 1, but our proxy for fitness is $g[x,n(x)]$ so that is impossible if $g[x,0] < 1$ in some locations. In the setting of patch models in continuous time, it was shown in Cantrell et al. (2017a) that in a habitat with both sources and sinks an ideal free distribution is only possible with partial occupancy. This turns out to be true in our present setting as well. In this section, 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 $n_s^*(x) > 0$, $\forall\, x \in \Omega$, i.e. condition (G4) is no longer assumed to hold. That is, in some regions of the habitat Ω, the habitat quality is not high enough to sustain a population over the two seasons. Here, $g[x,n(x)]$ is still defined as in (66). To address this case we need to extend our definition of ideal free dispersal and address some technical issues related to the function spaces we need to use in the analysis.

We will first redefine the ideal free distribution $n_s^*(x)$ using a piece-wise construction. Let

$$\Omega_1 = \{x \in \Omega : g[x,0] > 1\} = \{x \in \Omega : f_0 g_0\, Q_s(x) > 1\}. \tag{118}$$

To define the ideal free distribution we require

$$n_s^*(x) = \begin{cases} g[x,n_s^*(x)]n_s^*(x), & \text{for } x \in \Omega_1, \\ 0, & \text{for } x \in \Omega\backslash\Omega_1. \end{cases} \tag{119}$$

That is,

$$n_s^*(x) = \begin{cases} \dfrac{f_0 g_0\, Q_s(x) - 1}{b_0}, & \text{for } x \in \Omega_1, \\ 0, & \text{for } x \in \Omega \backslash \Omega_1. \end{cases} \tag{120}$$

Therefore $n_s^*(x)$ is well-defined and unique. We also know it has positivity properties $n_s^*(x) \geq 0, \forall x \in \Omega$ and $n_s^*(x) > 0, \forall x \in \Omega_1$. For the cases we consider, we will impose an additional assumption that will be needed for technical reasons which will be discussed later.

(D) $n_s^*(x)$ restricted to $\bar{\Omega}_1$ belongs to $C_0^1(\bar{\Omega}_1)$ and $D_\nu n_s^*(x) < -n_1$ for some $n_1 > 0$, where ν is any outward normal vector on $\partial\Omega_1$, and D_ν refers to the directional derivative in the direction of ν.

We can now generalize the definition of the ideal free dispersal strategy.

Definition 6. *The population described by system* (1) *is adopting an ideal free dispersal strategy relative to $n_s^*(x)$, as defined in* (119)*, if its dispersal kernels $k_{sw}^*(z, y)$ and $k_{ws}^*(x, z)$ satisfy conditions* (71) *and* (72)*, where $n_s^*(x)$ is defined by* (119)*.*

The ideal free dispersal strategy must move all of the population into the favorable habitat Ω_1 during the summer. That means $k_{sw}^*(x, z)$ must satisfy $k_{sw}^*(x, z) = 0$ for $x \in \Omega\backslash\Omega_1$ and z such that $k_{ws}^*(z, y) > 0$ for some $y \in \Omega_1$. To see this, we integrate both sides of (72) for $x \in \Omega\backslash\Omega_1$, and get

$$\int_\Omega \int_\Omega \left(\int_{\Omega\backslash\Omega_1} k_{sw}^*(x, z)\, dx \right) k_{ws}^*(z, y)\, n^*(y)\, dz\, dy = 0. \tag{121}$$

Therefore

$$\int_{\Omega\backslash\Omega_1} k_{sw}^*(x, z)\, dx = 0, \tag{122}$$

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

$$k_{sw}^*(x, z) = 0 \;\text{ for }\; x \in \Omega\backslash\Omega_1 \;\text{ and }\; z \in \Omega \text{ with } k_{ws}^*(z, y) > 0 \text{ for some } y \in \Omega_1. \tag{123}$$

The overall dispersal operator from summer to summer defined by $k_{sw}^*(x, z) k_{ws}^*(z, y)$ then maps Ω_1 into itself. Therefore the ideal free strategy restricts dispersal to Ω_1, the habitat of good quality. Thus the no-loss condition

$$\int_\Omega k_{sw}^*(x, y)\, dx = 1, \;\; \forall y \tag{124}$$

is equivalent to

$$\int_{\Omega_1} k_{sw}^*(x, y)\, dx = 1, \;\; \forall y. \tag{125}$$

Correspondingly, the positivity condition (18) can be modified as

$$k_{sw}^*(x, y) > 0, \;\; \forall\, x \in \Omega_1, \; \forall\, y \in \Omega. \tag{126}$$

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. That will not be the case if we use $X_1 = C_0(\bar{\Omega}_1)$ with positive cone $P_1 = \{n(x) \in C_0(\bar{\Omega}_1) | n(x) \geq 0, \forall\, x \in \Omega_1\}$ because the interior of P_1 is empty. A similar difficulty arises in formulating homogeneous Dirichlet problems for parabolic partial differential equations. In both cases the problem arises because we want functions that are zero on the boundary of a region but positive in the interior to belong to a positive cone that has nonempty interior. However, it can be addressed in both cases by using order unit norms; see Amann (1976), Mierczyński (1998). The idea of order unit norms is, roughly speaking, to find a suitable function $e(x) \in P_1$ 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) $k^*_{sw}(x,y) \in C^1(\bar{\Omega}_1 \times \Omega)$, and for $\forall x \in \partial\Omega_1,\ \forall y \in \Omega,\ k^*_{sw}(x,y) = 0$ and $D_\nu k^*_{sw}(x,y) \le -k_1$ for some $k_1 > 0$, 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.

For the population M we could retain the positivity condition (18) 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 $k_{sw}(x,y) = 0$ on $\Omega \backslash \Omega_2$ for some open subset $\Omega_2 \subset \Omega$ and impose a positivity condition analogous to (126):

$$k_{sw}(x,y) > 0,\ \ \forall\, x \in \Omega_2,\ \forall\, y \in \Omega. \tag{127}$$

In that case we will also need an additional assumption analogous to (D1):

(D2) $k_{sw}(x,y) \in C^1(\bar{\Omega}_2 \times \Omega)$, and for $\forall x \in \partial\Omega_2,\ \forall y \in \Omega_2,\ k_{sw}(x,y) = 0$ and $D_\nu k_{sw}(x,y) \le -k_2$ for some $k_2 > 0$, 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.

Let $K^*(x,y)$ be defined by equation (76), where $x \in \Omega_1$ and $y \in \Omega_1$. Then $K^*(x,y)$ remains line-sum symmetric with the generalized definition of the ideal free distribution and the ideal free dispersal strategy. To see this, let us first observe that (72) implies

$$n^*_s(x) = \int_{\Omega_1}\int_{\Omega} k^*_{sw}(x,z)k^*_{ws}(z,y)\, n^*_s(y)\, dz\, dy = \int_{\Omega_1} K^*(x,y)\, dy \tag{128}$$

because $n^*_s(y)$ in the integrand is 0 outside of Ω_1. Meanwhile,

$$\int_{\Omega_1} K^*(y,x)\, dy = \int_{\Omega_1}\int_{\Omega} k^*_{sw}(y,z)\, k^*_{ws}(z,x)\, n^*_s(x)\, dz\, dy \tag{129a}$$

$$= \int_{\Omega} k^*_{ws}(z,x)\, n^*_s(x)\, dz \tag{129b}$$

$$= n^*_s(x) \tag{129c}$$

because of the no-loss condition (125) and

$$\int_{\Omega} k^*_{ws}(z,x)\, dz = 1. \tag{130}$$

Therefore

$$\int_{\Omega_1} K^*(x,y)\, dy = \int_{\Omega_1} K^*(y,x)\, dy, \tag{131}$$

and $K^*(x,y)$ is line-sum symmetric on $\Omega_1 \times \Omega_1$.

We now turn to the issue of positivity in the case of partial occupancy.

The following two lemmas generalize Lemmas 4 and 5, respectively. They will again show that system (73) does not allow the two species to coexist at a coexistence equilibrium, and that any semi-trivial equilibrium of system (73) of the form $(0, m^*)$ must be unstable.

Lemma 6. *Assume that condition (D) holds and the dispersal kernels $k^*_{ws}(x,y)$, $k_{sw}(x,y)$, and $k_{ws}(x,y)$ are continuous functions that satisfy condition (9), and the kernel $k^*_{sw}(x,y)$ satisfies conditions (125) and (D1). In addition, the kernel $k^*_{sw}(x,y)$ also satisfies the positivity condition (126), and $k_{sw}(x,y)$ satisfies the positivity condition (18) or both (127) and condition (D2). The kernels $k^*_{sw}(x,y)$ and $k^*_{ws}(x,y)$ are such that population N, described by $n_{s,t}(x)$, adopts an ideal free dispersal strategy relative to $n^*_s(x)$ in (119), and population M, described by $m_{s,t}(x)$, does not adopt an ideal free dispersal strategy. In addition, assume $g[x,n(x)]$ satisfies (G1) $-$ (G3), and Ω_1 is not empty. Then system (73) 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 (73), which satisfies equations (80). (In the case where $k_{sw}(x, y)$ satisfies both (127) and condition (D2), extend $m(x)$ to be 0 on $\Omega\backslash\Omega_2$.) Because of (123), we know from (80a) that

$$n(x) = 0 \text{ for } x \in \Omega\backslash\Omega_1. \tag{132}$$

Meanwhile, the positivity condition (126) ensures that

$$n(x) > 0 \text{ for } x \in \Omega_1. \tag{133}$$

Integrating both sides of (80a) on Ω, with the same calculations as those in equation (81), we obtain

$$\int_\Omega n(x)\, dx = \int_\Omega g[y, n(y) + m(y)]\, n(y)\, dy, \tag{134}$$

which is equivalent to

$$\int_{\Omega_1} n(x)\, dx = \int_{\Omega_1} g[y, n(y) + m(y)]\, n(y)\, dy \tag{135}$$

because of (132). Likewise, following the calculations in (82), integrating both sides of (80b) yields

$$\int_\Omega m(x)\, dx \le \int_\Omega g[y, n(y) + m(y)]\, m(y)\, dy \tag{136a}$$

$$= \int_{\{y: m(y)>0\}} g[y, n(y) + m(y)]\, m(y)\, dy, \tag{136b}$$

and the inequality is strict unless

$$k_{ws}(z, y) = Q_w(z)\, k_{ws}(z, y) \tag{137}$$

where $m(y) > 0$.

Adding (134) and (136) together, we obtain inequality (85) again. To proceed, we need to construct a piece-wise function similar to the function $\Psi(x)$ in (86). Let

$$\tilde{\Psi}(x) = \begin{cases} \dfrac{n^*(x)}{n(x) g[x, n(x) + m(x)]} \text{ on } \Omega_1, \\ 0 \text{ on } \Omega\backslash\Omega_1. \end{cases} \tag{138}$$

This function is well-defined because of the positivity condition (133).

Multiplying both sides of equation (80a) by $\tilde{\Psi}(x)$ and integrating, we get

$$\int_{\Omega} \tilde{\Psi}(x)n(x)\,dx = \int_{\Omega_1} \tilde{\Psi}(x)n(x)\,dx \tag{139a}$$

$$= \int_{\Omega_1} \frac{n_s^*(x)}{g[x,n(x)+m(x)]}\,dx \tag{139b}$$

$$= \int_{\Omega_1}\int_{\Omega_1}\int_{\Omega} k_{sw}^*(x,z)Q_w(z)k_{ws}^*(z,y)\; g[y,n(y)+m(y)]n(y)\;\frac{n_s^*(x)}{g[x,n(x)+m(x)]n(x)}\,dz\,dy\,dx \tag{139c}$$

$$= \int_{\Omega_1}\int_{\Omega_1}\int_{\Omega} k_{sw}^*(x,z)Q_w(z)k_{ws}^*(z,y)\; n_s^*(y)\;\frac{g[y,n(y)+m(y)]n(y)n_s^*(x)}{g[x,n(x)+m(x)]n(x)n_s^*(y)}\,dz\,dy\,dx \tag{139d}$$

$$= \int_{\Omega_1}\int_{\Omega_1}\int_{\Omega} k_{sw}^*(x,z)k_{ws}^*(z,y)n_s^*(y)\;\frac{g[y,n(y)+m(y)]n(y)n_s^*(x)}{g[x,n(x)+m(x)]n(x)n_s^*(y)}\,dz\,dy\,dx \tag{139e}$$

$$= \int_{\Omega_1}\int_{\Omega_1} K^*(x,y)\,\frac{\tilde{\Psi}(x)}{\tilde{\Psi}(y)}\,dy\,dx \tag{139f}$$

$$\geq \int_{\Omega_1}\int_{\Omega_1} K^*(x,y)\,dy\,dx \tag{139g}$$

$$= \int_{\Omega_1} n_s^*(x)\,dx. \tag{139h}$$

The inequality is again due to Theorem 1 and the fact that $K^*(x,y)$ 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

$$\int_{\Omega_1} \frac{n_s^*(x)}{g[x,n(x)+m(x)]}\,dx \geq \int_{\Omega_1} n_s^*(x)\,dx, \tag{140}$$

and thus

$$\int_{\Omega_1} n_s^*(x)\left\{\frac{1-g[x,n(x)+m(x)]}{g[x,n(x)+m(x)]}\right\} \geq 0. \tag{141}$$

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

$$\int_{\Omega} n_s^*(x)\left\{\frac{1-g[x,n(x)+m(x)]}{g[x,n(x)+m(x)]}\right\} \geq 0 \tag{142}$$

is also true.

Meanwhile, the calculations from (80) and (85) are still valid in the present setting. Inequality (85) says

$$\int_{\Omega} \{1-g[x,n(x)+m(x)]\}\,[n(x)+m(x)]\,dx \leq 0, \tag{143}$$

from which we have

$$\int_{\Omega} g[x,n(x)+m(x)]\cdot[n(x)+m(x)]\cdot\left\{\frac{1-g[x,n(x)+m(x)]}{g[x,n(x)+m(x)]}\right\}\,dx \leq 0. \tag{144}$$

Combining (142) and (144), we get

$$\int_{\Omega} \{n_s^*(x) - g[x,n(x)+m(x)]\cdot[n(x)+m(x)]\}\cdot\left\{\frac{1-g[x,n(x)+m(x)]}{g[x,n(x)+m(x)]}\right\}\,dx \geq 0. \tag{145}$$

Therefore, if

$$I_1 = \int_{\Omega_1} \{n_s^*(x) - g[x, n(x) + m(x)] \cdot [n(x) + m(x)]\} \cdot \left\{ \frac{1 - g[x, n(x) + m(x)]}{g[x, n(x) + m(x)]} \right\} dx, \tag{146}$$

and

$$I_2 = \int_{\Omega \backslash \Omega_1} \{n_s^*(x) - g[x, n(x) + m(x)] \cdot [n(x) + m(x)]\} \cdot \left\{ \frac{1 - g[x, n(x) + m(x)]}{g[x, n(x) + m(x)]} \right\} dx \tag{147a}$$

$$= \int_{\Omega \backslash \Omega_1} \{-g[x, n(x) + m(x)] \cdot [n(x) + m(x)]\} \cdot \left\{ \frac{1 - g[x, n(x) + m(x)]}{g[x, n(x) + m(x)]} \right\} dx, \tag{147b}$$

then

$$I_1 + I_2 \geq 0. \tag{148}$$

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

$$I_1 = \int_{\Omega_1} \{g[x, n_s^*(x)] n_s^*(x) - g[x, n(x) + m(x)] \cdot [n(x) + m(x)]\} \cdot \left\{ \frac{g[x, n_s^*(x)] - g[x, n(x) + m(x)]}{g[x, n(x) + m(x)]} \right\} dx, \tag{149}$$

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

$$I_1 = I_2 = 0. \tag{150}$$

The fact that $I_1 = 0$ implies

$$n_s^*(x) = n(x) + m(x), \;\; \forall\, x \in \Omega_1. \tag{151}$$

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,

$$\frac{n_s^*(x)}{n(x)} = \frac{1}{c}, \;\; x \in \Omega_1. \tag{152}$$

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

$$m(x) + n(x) = 0, \;\; \forall\, x \in \Omega \backslash \Omega_1, \tag{153}$$

from $I_2 = 0$. From (132), it must be the case that

$$m(x) = 0, \;\; \forall\, x \in \Omega \backslash \Omega_1. \tag{154}$$

From equations (80b), (137), and (151), we have, for $x \in \Omega_1$,

$$m(x) = \int_\Omega \int_\Omega k_{sw}(x, z)\, k_{ws}(z, y)\, g[x, n(x) + m(x)]\, m(y)\, dz\, dy, \tag{155a}$$

$$= \int_\Omega \int_\Omega k_{sw}(x, z)\, k_{ws}(z, y)\, m(y)\, dz\, dy. \tag{155b}$$

Thus (155b) implies

$$m(x) = \int_{\Omega_1} \int_\Omega k_{sw}(x, z)\, k_{ws}(z, y)\, m(y)\, dz\, dy, \;\; \forall x \in \Omega_1. \tag{156}$$

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

$$n_s^*(x) = \int_{\Omega_1} \int_\Omega k_{sw}(x, z)\, k_{ws}(z, y)\, n_s^*(y)\, dz\, dy, \;\; \forall x \in \Omega_1. \tag{157}$$

This together with (137) conflicts with the assumption that $k_{sw}(x, z)$ and $k_{ws}(z, y)$ do not form an ideal free strategy. Therefore system (73) does not have a coexistence equilibrium $(n(x), m(x))$ where $n(x)$ and $m(x)$ are both nonzero. □

Lemma 7. *Assume that condition (D) holds and the dispersal kernels $k^*_{ws}(x,y)$, $k_{sw}(x,y)$, and $k_{ws}(x,y)$ are continuous functions that satisfy condition* (9)*, and the kernel $k^*_{sw}(x,y)$ satisfies conditions* (125) *and (D1). In addition, the kernel $k^*_{sw}(x,y)$ also satisfies the positivity condition* (126)*, and $k_{sw}(x,y)$ satisfies the positivity condition* (18) *or both* (127) *and condition (D2). The kernels $k^*_{sw}(x,y)$ and $k^*_{ws}(x,y)$ are such that population N, described by $n_{s,t}(x)$, adopts an ideal free dispersal strategy relative to $n^*_s(x)$ in* (119)*, and population M, described by $m_{s,t}(x)$, does not adopt an ideal free dispersal strategy. In addition, assume $g[x,n(x)]$ satisfies (G1) $-$ (G3), and Ω_1 is not empty. If system* (73) *has a semitrivial equilibrium $(0,m^*(x))$, then this equilibrium must be unstable.*

Proof. Suppose system (73) has a semitrivial equilibrium $(0,m^*(x))$. We will show that this equilibrium must be unstable.

As before, consider the eigenvalue problem

$$\lambda\phi(x) = \int_\Omega\int_\Omega k^*_{sw}(x,z)\,Q_w(z)\,k^*_{ws}(z,y)\,g[y,m^*(y)]\,\phi(y)\,dz\,dy, \tag{158}$$

where

$$g[y,m^*(y)] = \frac{f_0 g_0\,Q_s(y)}{1+b_0\,m^*(y)}. \tag{159}$$

(In the proof of the next result we will verify conditions which imply that a principal eigenvalue exists in the present case.) Because of (123) and (126), we know

$$\phi(x)=0 \text{ for } x\in\Omega\backslash\Omega_1 \text{ and } \phi(x)>0 \text{ for } x\in\Omega_1. \tag{160}$$

Also, we have $g[x,m^*(x)]>0$ for $x\in\Omega_1$, so

$$G(x) = \begin{cases} \dfrac{n^*_s(x)}{\phi(x)g[x,m^*(x)]}, x\in\Omega_1, \\ 0, x\in\Omega\backslash\Omega_1, \end{cases} \tag{161}$$

is well defined. Multiplying both sides of equation (158) by G we obtain, for $x\in\Omega_1$,

$$\frac{\lambda\,n^*_s(x)}{g[x,m^*(x)]} = \int_\Omega\int_\Omega k^*_{sw}(x,z)\,Q_w(z)\,k^*_{ws}(z,y)\,\frac{n^*_s(x)}{\phi(x)g[x,m^*(x)]}\,g[y,m^*(y)]\,\phi(y)\,dz\,dy \tag{162a}$$

$$= \int_{\Omega_1}\int_\Omega k^*_{sw}(x,z)\,Q_w(z)\,k^*_{ws}(z,y)\,\frac{n^*_s(x)}{\phi(x)g[x,m^*(x)]}\,g[y,m^*(y)]\,\phi(y)\,dz\,dy \tag{162b}$$

$$= \int_{\Omega_1}\int_\Omega k^*_{sw}(x,z)\,Q_w(z)\,k^*_{ws}(z,y)\,n^*_s(x)\,\frac{\phi(y)g[y,m^*(y)]}{\phi(x)g[x,m^*(x)]}\,dz\,dy \tag{162c}$$

$$= \int_{\Omega_1}\int_{\Omega_1} k^*_{sw}(x,z)\,Q_w(z)\,k^*_{ws}(z,y)\,n^*_s(y)\,\frac{\Phi(y)}{\Phi(x)}\,dz\,dy, \tag{162d}$$

where

$$\Phi(x) = \frac{\phi(x)g[x,m^*(x)]}{n^*_s(x)}, x\in\Omega_1. \tag{163}$$

Integrating both sides, we obtain from (128) and (131)

$$\lambda\int_{\Omega_1}\frac{n^*_s(x)}{g[x,m^*(x)]}\,dx = \int_{\Omega_1}\int_{\Omega_1}\int_\Omega k^*_{sw}(x,z)\,Q_w(z)\,k^*_{ws}(z,y)\,n^*_s(y)\,\frac{\Phi(y)}{\Phi(x)}\,dz\,dy\,dx \tag{164a}$$

$$= \int_{\Omega_1}\int_{\Omega_1} K^*(x,y)\,\frac{\Phi(y)}{\Phi(x)}\,dy\,dx \tag{164b}$$

$$\geq \int_{\Omega_1}\int_{\Omega_1} K^*(x,y)\,dy\,dx \tag{164c}$$

$$= \int_{\Omega_1} n^*_s(x)\,dx. \tag{164d}$$

Therefore

$$\lambda \int_{\Omega_1} \frac{n_s^*(x)}{g[x, m^*(x)]}\, dx \geq \int_{\Omega_1} \frac{g[x, m^*(x)]}{g[x, m^*(x)]}\, n_s^*(x)\, dx, \tag{165}$$

and

$$(\lambda - 1) \int_{\Omega_1} \frac{n_s^*(x)}{g[x, m^*(x)]}\, dx \geq \int_{\Omega_1} n_s^*(x) \left\{1 - \frac{1}{g[x, m^*(x)]}\right\} dx. \tag{166}$$

Next we will show that the right hand side of (166) is nonnegative. To see this, we begin with observing that the equilibrium $m^*(x)$ must satisfy the equation

$$m^*(x) = \int_\Omega \int_\Omega k_{sw}(x, z)\, Q_w(z)\, k_{ws}(z, y)\, g[y, m^*(y)]\, m^*(y)\, dz\, dy. \tag{167}$$

Integrating both sides of equation (167), we obtain

$$\int_\Omega m^*(x)\, dx = \int_\Omega \int_\Omega \int_\Omega k_{sw}(x, z)\, Q_w(z)\, k_{ws}(z, y)\, g[y, m^*(y)]\, m^*(y)\, dz\, dy\, dx \tag{168a}$$

$$\leq \int_\Omega \int_\Omega \int_\Omega k_{sw}(x, z)\, k_{ws}(z, y)\, g[y, m^*(y)]\, m^*(y)\, dz\, dy\, dx \tag{168b}$$

$$= \int_\Omega g[y, m^*(y)]\, m^*(y)\, dy. \tag{168c}$$

Therefore

$$\int_\Omega m^*(x)\{1 - g[x, m^*(x)]\}\, dx \leq 0, \tag{169}$$

and

$$\int_\Omega m^*(x)\, \{g[x, m^*(x)] - 1\}\, dx \geq 0. \tag{170}$$

Splitting the integral into two integrals, we have

$$\int_{\Omega_1} m^*(x)\, \{g[x, m^*(x)] - 1\}\, dx + \int_{\Omega\backslash\Omega_1} m^*(x)\, \{g[x, m^*(x)] - 1\}\, dx \geq 0. \tag{171}$$

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

$$g[x, m^*(x)] \leq f_0\, g_0\, Q_s(x) \leq 1. \tag{172}$$

Therefore

$$\int_{\Omega\backslash\Omega_1} m^*(x)\, \{g[x, m^*(x)] - 1\}\, dx \leq 0, \tag{173}$$

because $m^*(x)$ is nonnegative, rendering the integrand less than or equal to 0. The inequality (173) will be strict unless for each $x \in \Omega\backslash\Omega_1$ either $m^*(x) = 0$ or $g[x, m^*(x)] = 1$. The case $g[x, m^*(x)] = 1$ would be possible only if $Q_s(x) > 0$, but then $g[x, s]$ is strictly decreasing in s so that $g[x, m^*(x)] < g[x, 0] \leq 1$ if $m^*(x)) > 0$, so that case is ruled out. Hence (173) is strict unless unless $m^*(x) = 0$ for $x \in \Omega\backslash\Omega_1$. Therefore (173) implies

$$\int_{\Omega_1} m^*(x)\, \{g[x, m^*(x)] - 1\}\, dx \geq 0, \tag{174}$$

with strict inequality unless $m^*(x) = 0$ for $x \in \Omega\backslash\Omega_1$. Subtracting the left-hand side of inequaltiy (174) from the right-hand side of (166), we obtain

$$\int_{\Omega_1} n_s^*(x) \left\{1 - \frac{1}{g[x, m^*(x)]}\right\} dx - \int_{\Omega_1} m^*(x)\, \{g[x, m^*(x)] - 1\}\, dx \tag{175a}$$

$$= \int_{\Omega_1} \{n_s^*(x) - m^*(x) g[x, m^*(x)]\} \cdot \frac{g[x, m^*(x)] - 1}{g[x, m^*(x)]}\, dx \tag{175b}$$

$$= \int_{\Omega_1} \{n_s^*(x) g[x, n_s^*(x)] - m^*(x) g[x, m^*(x)]\} \cdot \frac{g[x, m^*(x)] - g[x, n_s^*(x)]}{g[x, m^*(x)]}\, dx. \tag{175c}$$

(175d)

Since we assume $Q_s(x) > 0$ for $x \in \Omega_1$, 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 (175) is nonegative, and is strictly positive unless either $n_s^*(x)g[x,n_s^*(x)] = m^*(x)g[x,m^*(x)]$ or $g[x,m^*(x)] = g[x,n_s^*(x)]$. Either of those implies $n_s^*(x) = m^*(x)$ on Ω_1. It follows that

$$\int_{\Omega_1} n_s^*(x)\left\{1 - \frac{1}{g[x,m^*(x)]}\right\} dx \geq \int_{\Omega_1} m^*(x)\left\{g[x,m^*(x)] - 1\right\} dx \geq 0. \tag{176}$$

The first inequality is strict unless $n_s^*(x) = m^*(x)$ on Ω_1. The second is strict unless unless $m^*(x) = 0$ for $x \in \Omega\backslash\Omega_1$. If either inequality is strict we have $\lambda > 1$ by (166) so that $(0, m^*(x))$ is unstable. The conditions $n_s^*(x) = m^*(x)$ on Ω_1 and $m^*(x) = 0$ for $x \in \Omega\backslash\Omega_1$ imply that $n_s^*(x) = m^*(x)$. We then have

$$n_s^*(x) = \int_\Omega \int_\Omega k_{sw}(x,z)\, Q_w(z)\, k_{ws}(z,y)\, dz\, g[y, n_s^*(y)]\, n_s^*(y)\, dy \tag{177a}$$

$$= \int_\Omega \int_\Omega k_{sw}(x,z)\, Q_w(z)\, k_{ws}(z,y)\, dz\, n_s^*(y)\, dy. \tag{177b}$$

This is also required for inequality (175) to be an equality. Therefore, if k_{sw} and k_{ws} are kernels that do not satisfy the ideal free conditions (71) and (72), the inequalities (174) and (175) will be strict. Therefore, with inequality (175), we know

$$(\lambda - 1)\int_\Omega \frac{n_s^*(x)}{g[x,m^*(x)]}\, dx > 0, \tag{178}$$

and

$$\lambda > 1. \tag{179}$$

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

Theorem 3. *Assume that either*
(i) (full occupancy) g[x,n] satisfies (G1)-(G4) and the hypotheses of Lemmas 4 and 5 are satisfied
or
(ii)(partial occupancy) g[x,n] satisfies (G1)-(G3), Ω_1 is nonempty, condition (D) holds, and the hypotheses of Lemmas 6 and 7 are satisfied.

Suppose the kernels $k_{sw}^*(x,z)$ and $k_{ws}^*(z,y)$ are such that population N, described by $n_{s,t}(x)$, adopts an ideal free dispersal strategy relative to $n_s^*(x)$, as in Definition 5 in case (i) and Definition 6 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 5 (case(i)) or Definition 6 (case(ii)), 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 (118). Let space X_1 be

$$X_1 = C_0(\bar{\Omega}_1) := \{n(x) \in C(\bar{\Omega}_1) | n(x) = 0, \forall\, x \in \partial\,\Omega_1\}, \tag{180}$$

equipped with the cone

$$P_1 = \{n(x) \in C_0(\bar{\Omega}_1) | n(x) \geq 0, \forall\, x \in \Omega_1\}, \tag{181}$$

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

$$T\begin{bmatrix} n(x) \\ m(x) \end{bmatrix} = \begin{bmatrix} \int_\Omega \int_\Omega k^*_{sw}(x,z)Q_w(z)k^*_{ws}(z,y)\,dz\,g[y,n(y)+m(y)]\,n(y)\,dy \\ \int_\Omega \int_\Omega k_{sw}(x,z)Q_w(z)k_{ws}(z,y)\,dz\,g[y,n(y)+m(y)]\,m(y)\,dy \end{bmatrix}. \tag{182}$$

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

$$||x||_e = \inf\{\lambda > 0| - \lambda e \le x \le \lambda e\} \tag{183}$$

to construct the normed vector space

$$X_e = (\cup\{\lambda[-e,e]|\lambda \in \mathbb{R}_+\}, ||\cdot||_e), \tag{184}$$

and define a cone P_e as

$$P_e = \cup\{\lambda[-e,e]|\lambda \in \mathbb{R}_+\} \cap P_1. \tag{185}$$

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 $C^1_0(\bar\Omega_1)$. Let $F = \pi_1 \circ T$, where π_1 is the projection onto the first coordinate. By condition (D1), $u \in C^1_0(\bar\Omega_1)$. Also, for each component x_i of x,

$$\frac{\partial k^*_{sw}}{\partial x_i} \in C^1_0(\bar\Omega_1 \times \bar\Omega_1). \tag{186}$$

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,

$$\frac{\partial u}{\partial x_i} = \int_{\Omega_1}\int_\Omega \frac{\partial k^*_{sw}(x,z)}{\partial x_i} Q_w(z)k^*(z,y)g[y,n_0(y)]n_0(y)\,dy, \tag{187}$$

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

$$||\nabla u||_0 \le C||n_0||_0, \tag{188}$$

where $||\ \ ||_0$ 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 (188) 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 (126) 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 (158) 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, sand 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 (127), and choosing, for example, $e_2(x) = \int_\Omega k_{sw}(x,y)dy$, 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

$$(n,m) \le_P (\bar n, \bar m) \Longleftrightarrow n \le \bar n, \text{ and } \bar m \le m, \tag{189}$$

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 compact under the original norm on $X_1 \times X_2$, because Ω is a compact set, and $k_{sw}(x, z)$ and $k^*_{sw}(x, z)$ 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 $k \in \mathbb{N}$,
$$u(x_k) < \frac{1}{k} \cdot e(x_k), \;\; x_k \in \bar{\Omega}_1. \tag{190}$$
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 $k_{sw}(x, z) > 0, \forall x \in \Omega, \forall z \in \Omega$. 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 6 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 7 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. □

4 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 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 formulation we have developed in the present paper.

Our primary focus here is on the evolutionary advantages of dispersal that produces 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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