Evolutionary stability of ideal free nonlocal dispersal

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We study the evolutionary stability of nonlocal dispersal strategies that can produce ideal free population distributions, that is, distributions where all individuals have equal fitness and there is no net movement of individuals at equilibrium. We find that the property of producing ideal free distributions is necessary and often sufficient for evolutionary stability. Our results extend those already developed for discrete diffusion models on finite patch networks to the case of nonlocal dispersal models based on integrodifferential equations. The analysis is based on the use of comparison methods and the construction of sub- and supersolutions.

\textbf{Keywords:} nonlocal dispersal; integrodifferential equations; ideal free distribution; evolutionarily stable strategy; evolution of dispersal

1. Introduction

The dispersal of organisms is an obvious feature of natural communities and has been the subject of investigation by various researchers [7]. One topic related to dispersal that has received considerable attention in recent years is the evolution of dispersal strategies [5]. A key question is what dispersal strategies can be expected to persist over the course of evolution. That question can be addressed in terms of the idea of evolutionary stability. A strategy is evolutionarily stable if a population using it cannot be invaded by a small population of mutants that use a different strategy but are otherwise similar to the original resident population. We will examine the evolutionary stability of a class of nonlocal dispersal strategies in continuous space and time. We will assume that the environment is variable in space but not in time. Our models will be integrodifferential equations. Mathematical models for dispersal in continuous time often take the form of reaction–diffusion–advection equations or their spatially discrete analogues. However, there has been some modelling based on integrodifferential equations with nonlocal dispersal [8,13,20,22]. (Of course, integrodifference equations have been used extensively in discrete-time models; see for example [23].)

It has been shown that in the case of symmetric dispersal strategies there will be selection for lower dispersal rates; see [16,19] for diffusion and [20] for the case of nonlocal dispersal. However,
if the dispersal process is nonsymmetric in such a way that it allows populations to exactly match the available resources, it may be evolutionarily stable even though the dispersal rate is far from zero. This has been shown for a fairly wide class of discrete diffusion models [4] and in certain reaction–advection–diffusion models [6]. Strategies that allow exact matching of resources are related to the concept of the ideal free distribution of organisms. The ideal free distribution is a verbal theory about how organisms would locate themselves if they were omniscient (ideal) and able to move as they wanted (free) [17]. Generally there is an assumption that crowding reduces the fitness of individuals in a given environment. The implication is that at equilibrium all organisms would have equal fitness (otherwise some would relocate themselves) and there would be no net movement (since by moving an individual would reduce its fitness, unless it traded places with another organism with equal fitness). Mathematically, this can be described by features of equilibria for equations describing population dynamics, where the intrinsic local population growth rate can be used as a proxy for fitness, and dispersal. The ideas and results in the present paper are extensions to integrodifferential models of those given for discrete diffusion models in [4]. Further discussion of the ideal free distribution and other background material are given in [4]. The main results of this paper show that for nonlocal dispersal there is a class of density-independent strategies that can lead to an ideal free distribution of the population, and among density-independent strategies those are typically the ones that are evolutionarily stable. The fact that it is possible to achieve an ideal free distribution without density-dependent dispersal is somewhat surprising because in our models fitness (as described by the per capita birth rate) is assumed to be density dependent. Specifically, we will assume that local population dynamics are governed by a logistic equation with a spatially varying local growth rate $m(x) - u$, where $u$ represents population density. The strategies we will consider may depend on $m$ but do not depend on $u$. Thus, individuals can choose a strategy that allows them to optimize their fitness relative to conspecifics in the sense envisioned in the ideal free distribution without being able to actually assess their fitness. In that sense the strategies we analyse are not strictly adaptive because they do not depend on fitness per se. It is known (and perhaps not surprising) that in the context of reaction–advection equations strategies that involve advection on fitness, including density-dependent terms, can produce an ideal free distribution [9]. Something similar may well be true in the nonlocal case, but we will not explore that question here partly because of the technical difficulties that arise in the analysis of models with density-dependent dispersal. Our general approach to assessing the invasibility of dispersal strategies by other strategies is based on using spatially explicit population models to assess the invasibility of equilibria arising from particular types of dispersal strategies. Our specific approach is adapted from the work of Hastings [19] on reaction–diffusion and discrete-diffusion models, as in [4]. A related but more sophisticated approach has been used in related contexts in [6,16,20,22], but we do not know how to address the technical problems that arise in applying that approach in the setting we are studying. A completely different approach to connecting the ideal free distribution with the evolution of dispersal strategies is based on game theory; see [14,15,24]. Although the technical aspects of the game theoretic approach are very different from those used in [4,6,16,19,20,22] and the present article, that approach leads to a similar conclusion that strategies resulting in an ideal free distribution of the population using them are likely to be evolutionarily stable.

2. Modelling framework and background results

2.1. Basic models and results

There are a number of ways to formulate spatially explicit models for population dynamics with dispersal. In continuous time, two popular types of deterministic models are reaction–diffusion
equations (see [3,10]) and discrete diffusion models (for example [1,4]). Reaction–diffusion models incorporate the assumption that all movement is local, so they rule out movement by sudden long-distance jumps. Discrete diffusion models can allow global movement but assume space is discrete. Reaction–diffusion models can be derived as limits of transport equations or stochastic movement models such as random walks, but only under some fairly restrictive assumptions. Specifically, diffusion models arise from unbiased, uncorrelated random walks under specific scaling assumptions. However, different assumptions about the underlying transport process lead to models that involve nonlocal dispersal terms that can be formulated as integrals. For discussions of the derivation and biological significance of nonlocal dispersal models, see [18,25,27]. A recent application of a nonlocal dispersal model is given in [21]. The models we will consider describe deterministic population dynamics and the nonlocal transfer or movement of individuals. We do not have any specific populations in mind in our models, but the models describe populations of organisms inhabiting a region in continuous space (as do reaction–diffusion models) but in cases where the organisms can make long-distance jumps as well as local movements (as do discrete diffusion models). For a single population our models take the form

$$\frac{du(x,t)}{dt} = \int_\Omega k(x, y)u(y, t)\,dy - \int_\Omega k(y, x)u(x, t)\,dy + f(x, u(x, t))u(x, t) \quad \text{for } x \in \Omega \quad \text{and } t > 0,$$

$$u(x, 0) = u_0(x) \quad \text{for } x \in \Omega,$$  

where \(u\) represents a population density and \(\Omega\) is a bounded domain. We will denote the closure of \(\Omega\), that is, the union of \(\Omega\) and its boundary, by \(\bar{\Omega}\). The kernel \(k(x, y)\) describes the rate at which organisms move from point \(y\) to point \(x\). For comparison, if \(\Omega\) were replaced by a collection of patches and we let \(u_i\) and \(f_i(u_i)\) denote, respectively, the population density and growth rate on patch \(i\), the corresponding discrete diffusion model would be

$$\frac{du_i}{dt} = \sum_{j=1}^n d_{ij}u_j - \sum_{j=1}^n d_{ji}u_i + f_i(u_i)u_i \quad \text{for } i = 1, \ldots, n.$$  

The model Equation (1) has essentially the same structure as Equation (2) with the sums replaced by integrals, and if the patches in Equation (2) formed a grid we could interpret Equation (1) as being a continuum limit of Equation (2) arising from a scaling where the number of patches increased to infinity and the distance between them went to zero. We will assume that \(k(x, y)\) is nonnegative, that there exists a positive constant \(c_0\) such that in Equation (1) \(k(x, y) > c_0\) for all \(x \in \bar{\Omega}\), and that \(k(x, y)\) is continuous on \(\bar{\Omega} \times \bar{\Omega}\), but \(k\) need not be symmetric. The conditions on \(k\) imply the positivity of the integral operator and infinite speed of propagation; similar conditions are considered in [8,12]. We will assume that \(f(x, u)\) is continuous in \(x\) on \(\bar{\Omega}\) and that \(f(x, u)\) and its derivative with respect to \(u\) are continuous in \(u\). We will also assume that there are positive constants \(f_0\) and \(C_0\) so that \(f(x, u) \leq -f_0u < 0\) if \(u \geq C_0\) on \(\bar{\Omega}\). Our prototype is \(f(x, u) = m(x) - u\) but our results apply to more general forms of \(f\). Finally, we assume that \(u_0(x) \geq 0\) and \(u_0(x)\) is continuous on \(\bar{\Omega}\).

**Remark on notation:** We will say that a function is \(C^k\) if it has continuous derivatives of order up to and including \(k\). We will denote the class of continuous functions on \(\bar{\Omega}\) as \(C(\bar{\Omega})\) and the class of functions with continuous derivatives of order up to and including \(k\) on \(\bar{\Omega}\) as \(C^k(\bar{\Omega})\). This is standard mathematical notation.
We can define a supersolution \( \bar{u} \) of Equation (1) analogously by reversing the inequality in Equation (4). A function \( \underline{u}(x, t) \) is a subsolution to the equilibrium problem for Equation (1) if it satisfies Equation (4) with the term \( du(x, t)/dt \) on the left-hand side replaced by 0; for a supersolution of the equilibrium problem the inequality would be reversed but would still hold on the left-hand side. Any sub- or supersolution of the equilibrium problem for Equation (1) is also a sub- or supersolution of the original time-dependent model equation (1). Of course any solution of Equation (1) is both a subsolution and a supersolution of Equation (1), and any equilibrium of Equation (1) is both a sub- and supersolution of the equilibrium problem. Lemma 1 then implies the following results:

**Lemma 2** [20] Suppose that \( u(x, t) \) is a subsolution of Equation (1) and that \( \bar{u}(x, t) \) is a supersolution on \( \bar{\Omega} \times [0, T] \), with \( u(x, 0) \leq \bar{u}(x, 0) \) on \( \bar{\Omega} \). Then \( \underline{u}(x, t) \leq \bar{u}(x, t) \) in \( \bar{\Omega} \times [0, T] \). If \( \underline{u}(x_0, t_0) < \bar{u}(x_0, t_0) \) for some \( (x_0, t_0) \in \bar{\Omega} \times [0, T] \) then \( \underline{u}(x, t) < \bar{u}(x, t) \) in \( \bar{\Omega} \times (t_0, T] \).

**Lemma 3** [20] Suppose that \( \bar{u}(x) \) is a supersolution to the equilibrium problem for Equation (1). If \( u \) is the solution of Equation (1) with \( u(x, 0) = \bar{u}(x) \) then either \( u(x, t) \) is decreasing in \( t \) or \( \bar{u} \) is an equilibrium of Equation (1). The analogous result holds for subsolutions to the equilibrium problem.

**Remark 1** Lemma 2 follows by letting \( w = \bar{u}(x, t) - u(x, t) \), subtracting the inequality Equation (4) for \( u(x, t) \) from the analogous inequality for \( \bar{u} \) to obtain an inequality for \( w \), using the mean value theorem to write \( f(x, \bar{u})\bar{u} - f(x, u)u = c(x, t)w \), then applying Lemma 1 to \( w \).
For Lemma 3, if \( u(x, t) \) is the solution of Equation (1) with \( u(x, 0) = \bar{u}(x) \), then \( u \) is a subsolution of Equation (1), so since \( \bar{u}(x) \) is a supersolution, we have \( u(x, t) \leq \bar{u}(x) \) for \( t > 0 \) by Lemma 2. For any \( \tau > 0 \), we can let \( \hat{u}(x, t) = u(x, t + \tau) \) and observe that \( \hat{u} \) is a solution of Equation (1) with \( \hat{u}(x, 0) = u(x, \tau) \leq \bar{u}(x) = u(x, 0) \). Thus, by Lemma 2, we have \( \hat{u}(x, t) \leq u(x, t) \), which is equivalent to \( u(x, t + \tau) \leq u(x, t) \), so \( u(x, t) \) is nonincreasing in \( t \). Furthermore \( u(x, t) \) is either constant in \( t \) and thus equal to \( u(x, 0) = \bar{u} \), so that \( u(x, t) = \bar{u}(x) \) is an equilibrium, or \( \hat{u}(x, t) = u(x_0, \tau) < u(x_0, 0) \) for some \( x_0 \in \Omega \), so that \( \bar{u}(x, t) = u(x, t + \tau) < u(x, t) \) for \( t > t_0 \), and hence \( u(x, t) \) is decreasing in \( t \). Lemmas 2 and 3 are analogous to standard results for reaction–advection–diffusion equations and they follow from the maximum principle in the same way. The reaction–diffusion–advection case is treated in detail in [3,10].

Since \( u \equiv 0 \) is a subsolution and any solution is a supersolution, it follows that the model equation (1) preserves the nonnegativity of initial data. Since we assume that the dispersal kernel is continuous and hence bounded, the condition that \( f(x, u) \leq -f_0u \) if \( u \geq C_0 \) implies that any sufficiently large constant is a supersolution, so all solutions with bounded nonnegative initial data will exist globally. With some additional smoothness assumptions on \( k(x, y) \) the existence of a positive supersolution implies the existence of a positive equilibrium; see the proof of Theorem 3.6 in [20]. (In [20], it is assumed that \( k(x, y) \) is symmetric, but we will not make that assumption here. It is not needed for the results stated above. Under some assumptions on \( \int_{\Omega} k(y, x) dy + f_u(x, 0) \) one can show that the largest element of the spectrum of the operator obtained by linearizing Equation (1) at an equilibrium is the principal eigenvalue. This fact can be used to obtain various more precise results on the existence, uniqueness, and stability of equilibria. Specifically, if the principal eigenvalue \( \mu \) of \( \int_{\Omega} k(y, x) \phi(y) dy - \int_{\Omega} k(y, x) \phi(x) dy + f_u(x, 0) \phi(x) = \mu \phi(x) \) is positive, then there exists an equilibrium which attracts all solutions of the initial value problem. (This is shown in [12]. See also [2].)

### 2.2. Evolutionary stability, invasibility and ideal free dispersal

A strategy is evolutionarily stable if a population using it can resist invasion by any small population of mutants using another strategy. We will use the specific formulation of this idea introduced by Hastings [19], adapted to the case of nonlocal dispersal. The same approach was used in [4] in the spatially discrete case. Suppose that \( u^* \) is a stable equilibrium of Equation (1) and that \( v \) represents the density of a population attempting to invade a system where the resident population is already at density \( u^* \). Then \( u^* \) satisfies

\[
0 = \int_{\Omega} k(x, y)u^*(y)\,dy - \int_{\Omega} k(y, x)u^*(x)\,dy + f(x, u^*)u^* \quad \text{for all } x \in \hat{\Omega}.
\]

To assess the invasibility of \( u^* \), we follow [19] and thus consider the model

\[
\frac{dv(x, t)}{dt} = \int_{\Omega} \tilde{k}(x, y)v(y, t)\,dy - \int_{\Omega} \tilde{k}(y, x)v(x, t)\,dy + f(x, u^* + v)v
\]

\[
v(x, 0) \in C(\hat{\Omega}), \quad v(x, 0) \geq 0.
\]

An assumption that the invading population is small enough that it does not have a significant impact on the resident population is implicit in the formulation used by Hastings [19]. We interpret Equation (6) as predicting invasibility if the equilibrium \( v = 0 \) is unstable and noninvasibility if \( v = 0 \) is stable. We will see that both of those outcomes are possible, so that the assumption that the invading population does not have a significant impact on the resident population is not in itself equivalent to assuming evolutionary stability for the strategy used by the resident. In the
case where $v = 0$ is unstable it would be expected that the invading population would eventually grow to an extent that the assumption that the invader does not have a significant impact on the resident population would break down and the model equation (6) would no longer be valid, but we are specifically interested in understanding what happens when the invading population is small. Thus, in our modelling framework, a strategy that results in an equilibrium $u^*$ will be viewed as evolutionarily stable if the equilibrium $v = 0$ is stable in Equation (6) for any choice of the dispersal strategy $\hat{k}(x, y)$. A more sophisticated way of assessing the evolutionary stability of the strategy arising from $k(x, y)$ would be to consider

$$\frac{du(x, t)}{dt} = \int_{\Omega} k(x, y)u(y, t) \, dy - \int_{\Omega} k(y, x)u(x, t) \, dy + f(x, u + v)u,$$

$$\frac{dv(x, t)}{dt} = \int_{\Omega} \hat{k}(x, y)v(y, t) \, dy - \int_{\Omega} \hat{k}(y, x)v(x, t) \, dy + f(x, u + v)v \quad \text{for all } x \in \bar{\Omega}. \quad (7)$$

In Equation (7) one would consider the stability of the equilibrium $(u^*, 0)$ to determine the evolutionary stability of the strategy defined by $k(x, y)$. That approach has been used to compare dispersal strategies in various settings [6,16,20,22] including nonlocal models [20,22], but in most of those problems linear stability analysis is adequate. Unfortunately, linear stability analysis is not adequate for treating strategies that lead to an ideal free distribution of the equilibrium population, because in that case the linearized system at such an equilibrium is generally neutrally stable. Nonlinear stability analysis is possible in some cases, specifically for certain types of reaction–advection–diffusion models [6], but there are serious open questions in the nonlinear analysis of models of the form Equation (7). We hope to address those issues in future work but for now we will use the formulation (6) to examine the invasibility of dispersal strategies. The analogous formulation in the case of discrete space was used in [4]. That formulation gives an advantage to the resident, so it underestimates the range of strategies that are evolutionarily unstable but overestimates the range of strategies that are evolutionarily stable. Thus, Equation (6) can give strong evidence that producing an ideal free distribution is a necessary condition for a dispersal strategy to be evolutionarily stable, but only weaker evidence that it is sufficient.

A strategy produces a version of the ideal free distribution if it has the features that at equilibrium fitness is equal for all individuals in all locations, and there is no net movement of individuals. If fitness is represented by the local population growth rate, then the equilibrium fitness should be zero since otherwise the population would grow. Thus, an equilibrium population density $u^*$ corresponding to an ideal free dispersal strategy should satisfy

$$f(x, u^*) \equiv 0 \quad \text{for all } x \in \bar{\Omega}. \quad (8)$$

Since there is no net movement of individuals at an ideal free equilibrium, it should also be the case that

$$\int_{\Omega} k(x, y)u^*(y) \, dy - \int_{\Omega} k(y, x)u^*(x) \, dy = 0 \quad \text{for all } x \in \bar{\Omega}. \quad (9)$$

These formulations of what constitutes an ideal free dispersal strategy are precisely analogous to those for reaction–diffusion–advection models or for discrete diffusion models; see [4–6] for more details.

A significant difference between the formulations (6) and (7) is that in Equation (7), if the single species equilibria $u^*$ and $v^*$ arising from $k(x, y)$ and $\hat{k}(x, y)$ are the same, which would be the case if for example $f(x, u) = m(x) - u$ and $k(x, y)$ and $\hat{k}(x, y)$ both produced ideal free distributions so that $u^* = v^* = m(x)$, then $(u, v) = (\alpha m(x), (1 - \alpha)m(x))$ would be an equilibrium of Equation (7) for any $\alpha \in [0, 1]$. All such equilibria would be neutrally stable and hence the model Equation (7) would allow coexistence of different ideal free dispersal strategies. That would not be the case in
the corresponding eigenvalue problem associated with \( L \). This distinction is also present in the spatially discrete case and is discussed in [4, Section 2.4] in that context.

Since \( u^* \) is an ideal free equilibrium, to analyse the linearization of Equation (6) at \( v = 0 \) we should study the spectrum of the operator \( L\psi = \int_\Omega \tilde{k}(x, y)\psi(y)\,dy - \int_\Omega \tilde{k}(y, x)\psi(x)\,dy \). The corresponding eigenvalue problem associated with \( L \) is

\[
\int_\Omega \tilde{k}(x, y)\psi(y)\,dy - \int_\Omega \tilde{k}(y, x)\psi(x)\,dy = \sigma \psi(x) \quad \text{for all } x \in \bar{\Omega}.
\]

By the Krein–Rutman theorem, taking \( \tilde{b}(x) = \int_\Omega \tilde{k}(y, x)\,dy \), we have that the operator

\[
\tilde{L}\psi = \frac{1}{\tilde{b}(x)} \int_\Omega \tilde{k}(x, y)\psi(y)\,dy
\]

has a principal eigenvalue. Also, integrating the eigenvalue problem \( \tilde{L}\psi = \lambda \psi \) over \( \Omega \) shows that the principal eigenvalue for \( \tilde{L} \) must be 1. It follows that \( L \) has zero as an eigenvalue with positive eigenvector. Furthermore, integrating Equation (10) with respect to \( x \) shows that any such eigenvalue must be zero. Since the spectrum of \( L \) is contained in \([ − \max \tilde{b}(x), 0] \) the equilibrium \( v = 0 \) is neutrally linearly stable.

It is natural to ask if there are actually any ideal free dispersal strategies. Suppose that \( u^* = m(x) \) satisfies \( f(x, u) = 0 \). If individuals leave the location \( y \) at a rate \( 1/m(y) \), so that the rate of leaving a given location is inversely proportional to its resource level, and then settle at random, uniformly across \( \bar{\Omega} \), the resulting dispersal strategy \( k(x, y) = 1/m(y) \) can be seen to be ideal free. This particular strategy does not require knowledge of the environment at any point other than the point of departure. Another ideal free dispersal strategy for nonlocal dispersal would be for individuals to leave all locations at the same rate but settle at new locations at a rate proportional to \( m(x) \). More generally, any strategy of the form \( k(x, y) = m(x)^\alpha m(y)^{\alpha - 1} \) will be ideal free. It is not clear if those are the only such strategies. Note that strategies involving the arrival point \( x \) as well as or instead of the departure point \( y \) require that individuals have global knowledge of their environment. It is reasonable to expect that there may be other strategies that involve the full fitness term \( m(x) − u \) which can result in an ideal free distribution. Such a strategy was found for advection–diffusion models in [9], but we have not explored that possibility here, partly because of the technical difficulties arising in the analysis of models with density-dependent dispersal.

**Remark 2** In models of biological diffusion where the decision to move depends on the departure point the dispersal term takes the form \( \Delta(D(x)u) \), where \( \Delta \) represents the Laplace operator; see [26, Section 5.4]. That formulation of diffusion is typically used in cross-diffusion models, but makes sense in other contexts as well. A model analogous to those we have considered in the present paper but using that form of dispersal would be \( \partial u/\partial t = \Delta(D(x)u) + f(x, u) \). In that modelling formulation, the dispersal strategy \( D(x) = 1/m(x) \) where organisms leave the departure point at a rate inversely proportional to the local resource level is analogous to the strategy \( k(x, y) = 1/m(y) \) described above for the nonlocal case, and it also results in an ideal free distribution of the population.

3. Main results

3.1. Sufficiency of ideal free dispersal for evolutionary stability

**Theorem 1** Suppose that \( u^* \) is an ideal free equilibrium of Equation (1) and that there is a constant \( f_1 > 0 \) so that \( f(x, u^* + v) \leq -f_1 v^2 \) for \( v \geq 0 \). Then the dispersal strategy leading to the
equilibrium \( u^* \) is evolutionarily stable in the sense that for any dispersal strategy \( \tilde{k}(x, y) \), any solution \( v(x, t) \) of Equation (6) converges uniformly to zero as \( t \to \infty \).

**Proof** We know by the boundedness of the kernel \( \tilde{k}(x, y) \) and the condition that \( f(x, u) \leq -f_0 u \) for \( u \) large that any sufficiently large constant is a supersolution to the equilibrium problem for Equation (6). Thus, any solution \( v \) is pointwise bounded. Also, \( v \equiv 0 \) is a subsolution, so Equation (6) preserves nonnegativity. Integrating Equation (6) over \( \Omega \) with respect to \( x \) and using

\[
\int_{\Omega} \int_{\Omega} \tilde{k}(x, y) v(y) \, dy \, dx = \int_{\Omega} \int_{\Omega} \tilde{k}(y, x) v(x) \, dy \, dx
\]

yields

\[
\frac{d}{dt} \int_{\Omega} v \, dx = \int_{\Omega} f(x, u^* + v) v \, dx \leq -f_1 \int_{\Omega} v^2 \, dx \leq -f_1 \left( \int_{\Omega} v \, dx \right)^2.
\]

(11)

It follows that \( \int_{\Omega} v \, dx \to 0 \) as \( t \to \infty \). Since \( \tilde{k}(x, y) \) is bounded, it then follows that

\[
\int_{\Omega} \tilde{k}(x, y) v(y, t) \, dy \to 0
\]

as \( t \to \infty \). Thus, for any \( \epsilon > 0 \), there exists \( t_1 \) such that for \( t > t_1 \), Equation (6) implies

\[
\frac{dv(x, t)}{dt} \leq \epsilon - \int_{\Omega} \tilde{k}(x, y) v(x, t) \, dy - f_1 v(x, t)^2 \leq \epsilon - f_1 v(x, t)^2.
\]

(12)

It follows that there exists \( t_2 \) so that if \( t > t_2 \) then \( v < 2(\epsilon/f_1)^{1/2} \). Since \( \epsilon > 0 \) is arbitrary, it follows that \( v \to 0 \) uniformly as \( t \to \infty \), which is the desired result. \( \blacksquare \)

**3.2. Necessity of ideal free dispersal for evolutionary stability**

**Theorem 2** Suppose that \( u^* \) is a continuous equilibrium of Equation (1) that is not ideal free, so that \( f(x, u^*) \neq 0 \) for some \( x \in \bar{\Omega} \). Then the dispersal strategy \( k(x, y) \) leading to the equilibrium \( u^* \) is not evolutionarily stable.

**Proof** We will show that under the hypotheses of Theorem 2 there exists a dispersal strategy \( \tilde{k}(x, y) \) that admits arbitrarily small positive subsolutions in the equilibrium problem for Equation (6). If such a family of subsolutions exists, then by Lemma 3 there will be solutions of Equation (6) that are initially arbitrarily small but are nondecreasing over time, so that a small population can successful invade the resident population. Because of the regularity assumptions on \( f \), it suffices to find \( \underline{v} > 0 \) so that for some \( \delta > 0 \),

\[
\delta \underline{v}(x) \leq \int_{\Omega} \tilde{k}(x, y) \underline{v}(y) \, dy - \int_{\Omega} \tilde{k}(y, x) \underline{v}(x) \, dy + f(x, u^*) \underline{v}(x).
\]

(13)

Given such a \( \underline{v} \), we can use \( \eta \underline{v} \) for arbitrarily small \( \eta > 0 \) to obtain the necessary subsolutions.

Integrating Equation (5) over \( \Omega \) with respect to \( x \) yields (as in Equation (11))

\[
\int_{\Omega} f(x, u^*) u^* \, dx = 0.
\]

Hence, if \( f(x, u^*) \) is not identically zero, it must change sign, so by continuity there must be a point \( x_0 \in \Omega \) and a constant \( F_0 > 0 \) so that for some \( r > 0 \) we have \( f(x, u^*) > F_0 \) for \( x \in B(x_0, r) \),
where $B(x_0, r)$ denotes the ball of radius $r$ centred at $x_0$. Furthermore, there must be a constant $F_1 > 0$ so that $f(x, u^*) > -F_1$ on $\Omega$. Let $\rho < r$ and $\gamma \in (0, 1)$ be constants that will be chosen later. Define $\underline{v}$ to be a continuous function so that

\[
\underline{v}(x) = 1 \quad \text{for } x \in B(x_0, \rho),
\]
\[
\gamma \leq \underline{v}(x) \leq 1 \quad \text{for } x \in B(x_0, r) \setminus B(x_0, \rho),
\]
\[
\underline{v}(x) = \gamma \quad \text{for } x \in \tilde{\Omega} \setminus B(x_0, r).
\]

(14)

Let $\theta > r$ and $\epsilon \in (0, 1)$ be constants to be chosen later, and define the dispersal strategy $\tilde{k}(x, y) = \tilde{k}(x)$ to be a continuous function so that

\[
\tilde{k}(x) = 1 \quad \text{for } x \in B(x_0, r),
\]
\[
\epsilon \leq \tilde{k}(x) \leq 1 \quad \text{for } x \in B(x_0, \theta) \setminus B(x_0, r),
\]
\[
\tilde{k}(x) = \epsilon \quad \text{for } x \in \tilde{\Omega} \setminus B(x_0, \theta).
\]

(15)

We can now estimate the terms in Equation (13). For any $x \in \Omega$,

\[
\int_{\Omega} \tilde{k}(y, x) \underline{v}(x) \, dy = \underline{v}(x) \int_{\Omega} \tilde{k}(y) \, dy \leq \underline{v}(x) [|B(x_0, \theta)| + \epsilon |\Omega|].
\]

(16)

Similarly,

\[
\int_{\Omega} \tilde{k}(x, y) \underline{v}(y) \, dy = \tilde{k}(x) \int_{\Omega} \underline{v}(y) \, dy \geq \tilde{k}(x) [|B(x_0, \rho)| + \gamma |\Omega \setminus B(x_0, \rho)|].
\]

(17)

For $x \in B(x_0, r)$, we have $\tilde{k}(x) = 1$, so by Equations (16) and (17) we have

\[
\int_{\Omega} \tilde{k}(y, x) \underline{v}(x) \, dy - \int_{\Omega} \tilde{k}(y, x) \underline{v}(x) \, dy + f(x, u^*) \underline{v}(x)
\]
\[
\geq [|B(x_0, \rho)| + \gamma |\Omega \setminus B(x_0, \rho)|] - \underline{v}(x) [|B(x_0, \theta)| + \epsilon |\Omega|] + F_0 \underline{v}(x)
\]
\[
\geq [F_0 - \epsilon |\Omega| - |B(x_0, \theta)| + |B(x_0, \rho)|] \underline{v}(x).
\]

(18)

By choosing $\epsilon > 0$ sufficiently small and choosing $\rho$ and $\theta$ with $\rho < r < \theta$ but $|\theta - \rho|$ sufficiently small, we can see from Equation (18) that for $x \in B(x_0, r)$, inequality Equation (13) will hold with $\delta = F_0/2$.

For $x \in \tilde{\Omega} \setminus B(x_0, r)$, we have $\underline{v}(x) = \gamma$ and $\tilde{k}(x) \geq \epsilon$ so that

\[
\int_{\Omega} \tilde{k}(y, x) \underline{v}(y) \, dy - \int_{\Omega} \tilde{k}(y, x) \underline{v}(y) \, dy + f(x, u^*) \underline{v}(x)
\]
\[
\geq \epsilon [|B(x_0, \rho)| + \gamma |\Omega \setminus B(x_0, \rho)|] - \gamma [|B(x_0, \theta)| + \epsilon |\Omega|] - \gamma F_1
\]
\[
\geq \epsilon |B(x_0, \rho)| - \gamma [|B(x_0, \theta)| + \epsilon |\Omega| + F_1].
\]

(19)

From Equation (19), it follows that by choosing $\gamma > 0$ sufficiently small, we can satisfy Equation (13) with $\delta = \epsilon/2$. This completes the proof of Theorem 2. ■
4. Discussion

Our main results show that in spatially heterogeneous but temporally constant environments in continuous space, the only evolutionarily stable nonlocal dispersal strategies are those that support an ideal free distribution of the population. They suggest that strategies which produce an ideal free distribution are evolutionarily stable. This is in contrast to the case studied in [20] where the class of nonlocal dispersal strategies that was considered did not allow strategies that could lead to an ideal free distribution. In that case, there is selection for slower dispersal. (Note that having no dispersal at all is a strategy that leads to an ideal free population distribution.) The results for nonlocal dispersal in continuous space are similar to those obtained in [4] for discrete diffusion models. The results of [4] treat models for systems of interacting species such as competitors or predators and prey. It is likely that the results of the present paper could be extended to some systems of those types. It is well known that for simple diffusive dispersal in heterogeneous environments there is selection for slower dispersal [16,19]. Recently, it has been found that in some cases dispersal strategies involving a combination of diffusion and advection can produce ideal free population distributions, and in that context those are the strategies that are evolutionarily stable [6]. It would be of interest to treat nonlocal dispersal strategies that can produce ideal free distributions from the viewpoint of competing populations as has been done for other classes of strategies in [6,16,20,22]. It would also be of interest to extend the study of evolutionary stability to broader classes of dispersal strategies that include both nonlocal and advection–diffusion strategies that can induce ideal free population distributions. It seems likely that in many cases such strategies may be evolutionarily stable.

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References

[1] P. Amarasekare, Spatial dynamics of communities with intraguild predation: the role of dispersal strategies, Am. Nat. 170 (2007), pp. 819–831.
[2] P. Bates and G. Zhao, Existence, uniqueness, and stability of the stationary solution to a nonlocal equation arising in population dispersal, J. Math. Anal. Appl. 332 (2007), pp. 428–440.
[3] R.S. Cantrell and C. Cosner, Spatial Ecology via Reaction–Diffusion Equations, Wiley, Chichester, 2003.
[4] R.S. Cantrell, C. Cosner, D.L. DeAngelis, and V. Padrón, The ideal free distribution as an evolutionarily stable strategy, J. Biol. Dyn. 1 (2007), pp. 249–271.
[5] R.S. Cantrell, C. Cosner, and Y. Lou, Evolution of dispersal in heterogeneous landscapes, in Spatial Ecology, R.S. Cantrell, C. Cosner, and S. Ruan, eds., Chapman Hall/CRC, Boca Raton, FL, 2009.
[6] R.S. Cantrell, C. Cosner, and Y. Lou, Evolution of dispersal and the ideal free distribution, Math. Biosci. Eng. 7 (2010), pp. 17–36.
[7] J. Clobert, E. Danchin, A. Dhondt, and J. Nichols (eds.), Dispersal, Oxford University Press, Oxford, 2001.
[8] C. Cortázár, J. Coville, M. Elgueta, and S. Martínez, A nonlocal inhomogeneous dispersal process, J. Differential Equations 241 (2007), pp. 332–358.
[9] C. Cosner, A dynamic model for the ideal free distribution as a partial differential equation, Theoret. Popul. Biol. 67 (2005), pp. 101–108.
[10] C. Cosner, Reaction–diffusion equations and ecological modeling, in Tutorials in Mathematical Biosciences IV, Lecture Notes in Mathematics Vol. 1922, A Friedman ed., Springer, New York, 2008, pp. 77–116.
[11] J. Coville, Remarks on the strong maximum principle for nonlocal operators, Electron. J. Differential Equations 66 (2008), pp. 1–10.
[12] J. Coville, On a simple criterion for the existence of a principal eigenfunction of some nonlocal operators, J. Differential Equations 249 (2010), pp. 2921–2953.
[13] J. Coville, J. Dávila, and S. Martínez, Existence and uniqueness of solutions to a nonlocal equation with monostable nonlinearity, SIAM J. Math. Anal. 39 (2008), pp. 1693–1709.
[14] R. Cressman and V. Krivan, Migration dynamics for the ideal free distribution, Am. Nat. 168 (2006), pp. 384–397.
[15] R. Cressman, V. Krivan, and J. Garay, *Ideal free distributions, evolutionary games, and population dynamics in multiple-species environments*, Am. Nat. 164 (2004), pp. 473–489.

[16] J. Dockery, V. Hutson, K. Mischaikow, and M. Pernarowski, *The evolution of slow dispersal rates: a reaction diffusion model*, J. Math. Biol. 37 (1998), pp. 61–83.

[17] S.D. Fretwell and H.L. Lucas Jr., *On territorial behavior and other factors influencing habitat selection in birds. Theoretical development*, Acta Biotheoretica 19 (1970), pp. 16–36.

[18] K.P. Hadeler, *Reaction-transport systems in biological modelling*, in *Mathematics Inspired by Biology*, Lecture Notes Mathematics Vol. 1714, V. Capasso and O. Diekmann eds., Springer, New York, 1999, pp. 95–150.

[19] A. Hastings, *Can spatial variation alone lead to selection for dispersal?*, Theoret. Popul. Biol. 24 (1983), pp. 244–251.

[20] V. Hutson, S. Martínez, K. Mischaikow, and G.T. Vickers, *The evolution of dispersal*, J. Math. Biol. 47 (2003), pp. 483–517.

[21] Y. Jin and M.A. Lewis, *Seasonal influences on population spread and persistence in streams II: critical domain size*, SIAM J. Appl. Math. (in press).

[22] C.-Y. Kao, Y. Lou, and W. Shen, *Random dispersal vs. non-local dispersal*, Discrete and Continuous Dynamical Systems-A 26 (2010), pp. 551–596.

[23] M. Kot, M. Lewis, and P. van Driessche, *Dispersal data and the spread of invading organisms*, Ecology 77 (1996), pp. 2027–2042.

[24] V. Krivan, R. Cressman, and C. Schneider, *The ideal free distribution: a review and synthesis of the game theoretic perspective*, Theoret. Popul. Biol. 73 (2008), pp. 403–425.

[25] F.J.R. Meysman, B.P. Boudreau, and J.J. Middelburg, *Relations between local, nonlocal, discrete and continuous models of bioturbation*, J. Mar. Res. 61 (2003), pp. 391–410.

[26] A. Okubo, *Diffusion and Ecological Problems: Mathematical Models*, Springer, Berlin, 1980.

[27] H.G. Othmer, S.R. Dunbar, and W. Alt, *Models of dispersal in biological systems*, J. Math. Biol. 26 (1988), pp. 263–298.