

Movement Toward Better Environments and the Evolution of Rapid Diffusion

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4. Research partially supported by NSF grant DMS-0211367

Abstract

We study a reaction-diffusion-advection model for two ecologically equivalent competitors with different dispersal strategies inhabiting a spatially heterogeneous environment. The competitors represent different phenotypes of the same species. One is assumed to disperse by simple diffusion, the other by diffusion together with directed movement toward more favorable environments. We show that under suitable conditions on the underlying spatial domain, the competitor that moves toward more favorable environments may have a competitive advantage even if it diffuses more rapidly than the other competitor. This is in contrast with the case in which both competitors disperse by pure diffusion, where the competitor that diffuses more slowly always has the advantage. We determine competitive advantage by examining the invasibility, i.e. stability or instability, of steady states with only one competitor present. The mathematical approach is a perturbation analysis of principal eigenvalues.

Keywords: reaction-diffusion-advection, competition, Lotka-Volterra, evolution of dispersal, heterogeneous environments, principal eigenvalues, eigenvalue perturbation

1 Introduction

The effects of dispersal on population dynamics, ecology, and evolution have been widely studied from a variety of viewpoints; see for example [1-7] and the references cited in those works. A natural question about dispersal is to determine which patterns of dispersal can be expected to confer some sort of selective or ecological advantage. This question has been examined by a number of investigators using various modeling approaches, including but certainly not limited to McPeck and Holt [2], Belgacem and Cosner [8], Holt and McPeck [4], Dockery et al. [5], Hutson et al. [6] and Cosner and Lou [9]. An important distinction is made by McPeck and Holt [2] between unconditional dispersal, which does not depend on habitat quality or population density, and conditional dispersal, which does depend on such factors. Passive diffusion, as considered by Dockery et al. [5] and Hutson et al. [6], is a type of unconditional dispersal. Diffusion combined with directed movement upward along resource gradients, as considered by Belgacem and Cosner [8] and Cosner and Lou [9], is an example of conditional dispersal, because the bias in the direction of dispersal depends on the spatial distribution of resources. There is evidence based on modeling that for unconditional dispersal in spatially varying but temporally constant environments slower dispersal rates can confer a selective advantage. This was shown in the context of a simple two-patch discrete time model by McPeck and Holt [2] and in the context of diffusion models by Dockery et al. [5]. However, for unconditional dispersal in environments that vary both in space and over time faster dispersal rates may be advantageous in both simple two-patch models [2] and diffusion models [6]. McPeck and Holt [2] also showed that in spatially variable but temporally constant environments certain types of conditional dispersal can confer a selective advantage, again in the context of simple two-patch models. In diffusion-advection models for a single population in a spatially varying but temporally constant environment, Belgacem and Cosner [8] and Cosner and Lou [9] showed that conditional dispersal involving both diffusion and directed movement up resource gradients can sometimes (but not always!) make persistence more likely. The purpose of the present article is to study that type of conditional dispersal in context of competition between two populations that are ecologically identical except in their dispersal mechanisms. This approach is very similar to that taken by Hutson et al. [6], and somewhat similar to but simpler than the approach taken by Dockery et al. [5]. The idea is to think of the competitors as representing different phenotypes of the same species which differ only in their dispersal behavior and to ask which type of dispersal behavior confers

a competitive, and thus presumably selective, advantage.

The specific modeling approach we take is to begin with a diffusive Lotka-Volterra model for two identical competitors in a closed but spatially varying environment and then perturb the model by changing the diffusion rate for one competitor while simultaneously changing the diffusion rate and introducing advection up resource gradients for the other. The modeling of movement toward more favorable habitats by introducing an advection term was done *ad hoc* in [8,9] but can be derived from a mechanistic analysis of individual movement via transport equations; see [10]. We assess whether or not this confers an advantage for either competitor by examining the invasibility of states where only one competitor is present by the other competitor. Mathematically, such states will be invulnerable if they are unstable but will not be invulnerable if they are stable. If the first competitor can invade when the second is at equilibrium but the second competitor cannot invade when the first is at equilibrium then the first competitor has an advantage in competition. We will determine the stability (i.e. invasibility) of single-species equilibria by a perturbation analysis of the principal eigenvalues of linearizations of system around those equilibria. Our conclusions are consistent with those of McPeck and Holt [2], namely that conditional dispersal can sometimes confer an advantage. However, Cosner and Lou [9] have shown that movement upward along resource gradients is not always beneficial for a single population, even in closed environments. Conditional dispersal can be expected to confer a competitive advantage only in cases where it is beneficial for a single species. Some cases where movement upward along resource gradients is always beneficial are when the underlying spatial environment is convex or one-dimensional; see [9] for further discussion of this point.

In the second section of this paper we describe the models and review the mathematical background needed for their analysis. In the third section we perform the perturbation analysis. In the fourth section we describe the conclusions in relatively nonmathematical terms. Some of the proofs of mathematical results are given in an Appendix.

2 Model Formulation and Mathematical Background

To analyze the combined effects of random and directed movement on competition we consider a situation where two competitors are ecologically identical in terms of their utilization of resources but may differ in their patterns or rates of dispersal. This is the same approach that was used by Dockery et.

al. [5], but we will make different assumptions about the dispersal patterns of the two competitors. Specifically, we will assume that there is a random component to the dispersal of both competitors but that when resources are distributed in a spatially heterogeneous way, one of the competitors also has a tendency to move upward along the resource gradient while the other does not. Such directed motion introduces a drift or advection term into the diffusion equation which describes random dispersal. Dispersal models for a single species which incorporate diffusion and movement up the resource gradient were considered by Belgacem and Cosner [8] and Cosner and Lou [9]. In those papers it was shown that directed movement up the resource gradient is beneficial to the population in some cases but not others, depending on the underlying spatial structure of the environment and the distribution of resources. Dockery et al. [5] showed that if two or more competitors inhabiting a temporally static environment are ecologically identical and the competitors all disperse by random diffusion, then reaction-diffusion models predict that the one with the lowest diffusion rate will have a competitive advantage over the others. We will see that this conclusion may be modified if one of the competitors has a tendency to move upward along resource gradients, but only in cases where such directed movement would be beneficial to that competitor by itself in a single-species model.

We will now formulate our reaction-advection-diffusion model for dispersal and competition. Suppose that $\Omega \subseteq \mathbb{R}^n$ is a bounded domain with $\partial\Omega$ smooth. Let u and v denote the population densities of two competitors on Ω , and let $m(x)$ represent a local population growth rate which depends on location. We will assume that $m \in C^{2+\delta}(\bar{\Omega})$ so that we may use standard elliptic regularity theory. We envision that the local population growth rate $m(x)$ reflects the quality and quantity of resources available at the point x . If both competitors have a random component to their dispersal but the competitor with density u also responds to the gradient of m by moving upward along it, the dispersal of the two competitors may be described in terms of the fluxes $J_u = -\mu\nabla u + \alpha(\nabla m)u$ and $J_v = -\nu\nabla v$. (See [3] for a discussion of how advection-diffusion equations can be derived in terms of fluxes, and [10] for a mechanistic derivation from transport equations.) To correctly describe diffusion we must have $\mu, \nu > 0$. Also, to capture the hypothesis that the first competitor has a tendency to move up the gradient of m we will assume $\alpha \geq 0$. If we assume there is no flux across $\partial\Omega$, that is,

individuals do not cross $\partial\Omega$, we obtain the competition model

$$\begin{aligned}\frac{\partial u}{\partial t} &= \nabla \cdot [\mu \nabla u - \alpha u \nabla m] + (m - u - v)u \\ \frac{\partial v}{\partial t} &= \nabla \cdot [\nu \nabla v] + (m - u - v)v \quad \text{on } \Omega \times (0, \infty),\end{aligned}\tag{2.1}$$

with boundary conditions

$$\begin{aligned}J_u \cdot \vec{n} &= \mu \frac{\partial u}{\partial \vec{n}} - \alpha u \frac{\partial m}{\partial \vec{n}} = 0 \\ J_v \cdot \vec{n} &= \nu \frac{\partial v}{\partial \vec{n}} = 0 \quad \text{on } \partial\Omega \times (0, \infty),\end{aligned}\tag{2.2}$$

where \vec{n} denotes the outward normal to $\partial\Omega$. The boundary condition on v is a standard Neumann condition. The no-flux boundary condition on u would be a classical Robin condition if $\partial m / \partial \vec{n} < 0$ on $\partial\Omega$, but we do not want to impose that extra restriction on m . Note, however, that if we let $w = e^{-(\alpha/\mu)m}u$ then the system (2.1) becomes

$$\begin{aligned}\frac{\partial w}{\partial t} &= \mu \nabla^2 w + \alpha \nabla m \cdot \nabla w + [m - e^{(\alpha/\mu)m}w - v]w \\ \frac{\partial v}{\partial t} &= \nu \nabla^2 v + [m - e^{(\alpha/\mu)m}w - v]v \quad \text{on } \Omega \times (0, \infty),\end{aligned}\tag{2.3}$$

where the boundary conditions (2.2) become

$$\frac{\partial w}{\partial \vec{n}} = 0, \quad \frac{\partial v}{\partial \vec{n}} = 0 \quad \text{on } \partial\Omega \times (0, \infty).\tag{2.4}$$

The system (2.3) and (2.4) is now cast as a Lotka-Volterra competition model with classical Neumann boundary conditions. Thus, (2.3) and (2.4) generate a semiflow on various function spaces which is monotone with respect to the ordering $(w_1, v_1) \leq (w_2, v_2)$ if $w_1 \leq w_2$ and $v_1 \geq v_2$. (See for example [7,11,12].) Since (2.3), (2.4) is equivalent to (2.1), (2.2), and the map from w to u corresponds to multiplication by a positive function, these properties are shared by (2.1), (2.2) despite the possibility of nonclassical Robin boundary conditions on u in (2.2).

A considerable amount of the behavior of the system (2.1), (2.2) is determined by its equilibria and their stability properties. We will briefly review some of the standard results about how the dynamics of two-species competition models are influenced by their equilibria. For a more complete and

detailed discussion see [7] or [11]. The first observation is that the system admits solutions $(u, 0)$ and $(0, v)$ where u and v are solutions to the logistic equations

$$\begin{aligned} \frac{\partial u}{\partial t} &= \nabla \cdot [\mu \nabla u - \alpha u \nabla m] + (m - u)u \quad \text{on } \Omega \times (0, \infty), \\ \mu \frac{\partial u}{\partial \vec{n}} - \alpha u \frac{\partial m}{\partial \vec{n}} &= 0 \quad \text{on } \partial\Omega \times (0, \infty), \end{aligned} \tag{2.5}$$

and

$$\begin{aligned} \frac{\partial v}{\partial t} &= \nu \nabla^2 v + (m - v)v \quad \text{on } \Omega \times (0, \infty), \\ \frac{\partial v}{\partial \vec{n}} &= 0 \quad \text{on } \partial\Omega \times (0, \infty). \end{aligned} \tag{2.6}$$

As in (2.3), (2.4) we can set $w = e^{-(\alpha/\mu)u}$ in (2.5) to obtain the equivalent form

$$\begin{aligned} \frac{\partial w}{\partial t} &= \mu \nabla^2 w + \alpha \nabla m \cdot \nabla w + (m - e^{(\alpha/\mu)m} w)w \quad \text{on } \Omega \times (0, \infty) \\ \frac{\partial w}{\partial \vec{n}} &= 0 \quad \text{on } \partial\Omega \times (0, \infty). \end{aligned} \tag{2.7}$$

The behavior of diffusive logistic models such as (2.6) or (2.7) (and hence (2.5)) is fairly simple. If the equilibrium $v \equiv 0$ in (2.6) is stable then all positive solutions to (2.6) approach zero as $t \rightarrow \infty$; if $v \equiv 0$ is unstable then (2.6) has a unique positive equilibrium \tilde{v} which is globally attracting among positive solutions. (See for example [7,11].) Similarly, if $u \equiv 0$ is stable in (2.5) then all positive solutions approach zero as $t \rightarrow \infty$ while if $u \equiv 0$ is unstable then (2.5) has a unique positive equilibrium \tilde{u} which is globally attracting among positive solutions. (To apply the standard results directly it may be necessary to work with the equivalent form (2.7) because of the boundary conditions.) If (u_1, v_1) is a solution of (2.1), (2.2) then u_1 is a subsolution of (2.5), so in the case of (2.5) where the equilibrium $u \equiv 0$ is stable, we must have $u_1 \rightarrow 0$ as $t \rightarrow \infty$. (This follows from the fact that when $u \equiv 0$ is stable in (2.5) all positive solutions of (2.5) approach zero as $t \rightarrow \infty$ together with the fact that we can compare u_1 with the solution to (2.5) having initial data $u(x, 0) = u_1(x, 0)$.) The situation for (2.6) is analogous. We are interested in cases where the coefficients μ, α , and ν can influence the outcome of competition, and we will study those via perturbation of the case where $\mu = \nu$ and $\alpha = 0$. The stability of the equilibria $u \equiv 0$ and

$v \equiv 0$ in (2.5), (2.6) depends on the signs of the principal eigenvalues of the linearizations about 0 of the operators on the right hand sides of those equations. Those eigenvalues in turn depend continuously on μ, ν , and α , so to obtain any behavior other than extinction in (2.1), (2.2) we need to start with a value of μ for which $u \equiv 0$ is unstable in (2.5) for $\alpha = 0$ and $v \equiv 0$ is unstable in (2.6) for $\mu = \nu$. The stability of $v \equiv 0$ in (2.6) is determined by the sign of the principal eigenvalue of the problem

$$\begin{aligned} \nu \nabla^2 \psi + m(x)\psi &= \sigma \psi & \text{on } \Omega, \\ \frac{\partial \psi}{\partial \vec{n}} &= 0 & \text{on } \partial \Omega. \end{aligned} \tag{2.8}$$

If the principal eigenvalue is positive, then $v \equiv 0$ is unstable. Similarly, $w \equiv 0$ in (2.7) and thus $u \equiv 0$ in (2.5) is unstable if the principal eigenvalue for

$$\begin{aligned} \mu \nabla^2 \psi + \alpha \nabla m \cdot \nabla \psi + m\psi &= \sigma \psi & \text{on } \Omega, \\ \frac{\partial \psi}{\partial \vec{n}} &= 0 & \text{on } \partial \Omega \end{aligned} \tag{2.9}$$

is positive. The principal eigenvalue for (2.8) will be positive for all $\nu > 0$ provided that

$$\int_{\Omega} m(x) dx > 0; \tag{2.10}$$

see for example [7]. We will assume that (2.10) holds. It follows as in [9], proposition 2.1, that

$$\int_{\Omega} m(x) e^{(\alpha/\mu)m(x)} dx > 0 \tag{2.11}$$

for $\alpha \geq 0$; also, (2.11) holds by continuity for α in a neighborhood of $\alpha = 0$. If (2.11) holds then the principal eigenvalue in (2.9) is positive so $w \equiv 0$ in (2.7) or equivalently $u \equiv 0$ in (2.5) is unstable. See [7,8,13-15] for further discussion of this and related points. In what follows we will assume that (2.10) holds, so that for positive μ, ν , and α the logistic models (2.5) and (2.6) have positive equilibria \tilde{u}, \tilde{v} which are unique and globally attracting among positive solutions.

Definition: The positive equilibria to (2.5) and (2.6) will be denoted as $\tilde{u} = \tilde{u}(\mu, \alpha)$ and $\tilde{v} = \tilde{v}(\nu)$ respectively.

Just as the behavior of the logistic models (2.5), (2.6) depends largely on the stability of the equilibria $u \equiv 0, v \equiv 0$, the behavior of the system (2.1),

(2.2) depends largely on the stability of the semi-trivial equilibria $(\tilde{u}, 0)$ and $(0, \tilde{v})$. If $(\tilde{u}, 0)$ is stable then solutions to (2.1), (2.2) with initial data near $(\tilde{u}, 0)$ will approach $(\tilde{u}, 0)$ as $t \rightarrow \infty$; thus, in that case, a small number of individuals of species v cannot invade the system if u is established at the equilibrium \tilde{u} . If $(\tilde{u}, 0)$ is unstable, then solutions (u, v) of (2.1), (2.2) with initial data close to $(\tilde{u}, 0)$ will converge to some equilibrium (u^*, v^*) of (2.1), (2.2) with $u^* < \tilde{u}$ and $v^* > 0$. Thus, in that case, a small number of individuals of species v can invade the system when u is already established at the equilibrium \tilde{u} . Similarly, if $(0, \tilde{v})$ is stable then a small number of individuals of species u cannot invade the system when v is already established at equilibrium, while if $(0, \tilde{v})$ is unstable then the system is invasible by u when v is established at equilibrium. (See [7,11] for additional discussion and references on competition models.) Because of the properties described above, it is reasonable to conclude that u has a competitive advantage over v if $(\tilde{u}, 0)$ is stable but $(0, \tilde{v})$ is unstable; similarly, v has an advantage over u if that situation is reversed. The stability of $(\tilde{u}, 0)$ and $(0, \tilde{v})$ is determined by the signs of the principal eigenvalues of the linearizations of (2.1), (2.2) about $(\tilde{u}, 0)$ and $(0, \tilde{v})$. The main goal of the present paper is to understand the dependence of those principal eigenvalues on μ, ν , and α . Specifically, $(\tilde{u}, 0)$ is stable if the principal eigenvalue for the problem

$$\begin{aligned} \nu \nabla^2 \psi + (m - \tilde{u})\psi &= \sigma\psi \quad \text{on } \Omega, \\ \frac{\partial \psi}{\partial \vec{n}} &= 0 \quad \text{on } \partial\Omega, \end{aligned} \tag{2.12}$$

is negative, and unstable if it is positive. Similarly, $(0, \tilde{v})$ is stable if the principal eigenvalue for

$$\begin{aligned} \nabla \cdot [\mu \nabla \psi - \alpha \psi \nabla m] + (m - \tilde{v})\psi &= \sigma\psi \quad \text{on } \Omega, \\ \mu \frac{\partial \psi}{\partial \vec{n}} - \alpha \psi \frac{\partial m}{\partial \vec{n}} &= 0 \quad \text{on } \partial\Omega, \end{aligned} \tag{2.13}$$

is negative and unstable if it is positive. (For additional discussion, again see [7] or [11].) As before, we can rewrite (2.13) as

$$\begin{aligned} \mu \nabla^2 \phi + \alpha \nabla m \cdot \nabla \phi + (m - \tilde{v})\phi &= \sigma\phi \quad \text{on } \Omega, \\ \frac{\partial \phi}{\partial \vec{n}} &= 0 \quad \text{on } \partial\Omega, \end{aligned} \tag{2.14}$$

by taking $\phi = e^{-(\alpha/\mu)m}\psi$. We will examine the effects of the diffusion rates μ and ν and the rate of directed movement α on the dynamics of the

competition model (2.1), (2.2) by studying how the principal eigenvalues in (2.12) and (2.13) (equivalently (2.14)) depend on those rates.

3 Mathematical Analysis

The main results of this paper will be based on a perturbation analysis of the principal eigenvalues of (2.12) and (2.13). That perturbation analysis is based on the following lemma:

Lemma 3.1: Suppose that $\mu_0, \nu_0 > 0$ and $\alpha_0 \geq 0$. The map from \mathbb{R}^2 to $C^{2+\delta}(\bar{\Omega})$ given by $(\mu, \alpha) \mapsto \tilde{u}(\mu, \alpha)$ is differentiable in some neighborhood of (μ_0, α_0) . The map from \mathbb{R} to $C^{2+\delta}(\bar{\Omega})$ given by $\nu \mapsto \tilde{v}(\nu)$ is differentiable in some neighborhood of ν_0 . Let $\sigma_0(\mu, \nu, \alpha)$ and $\tau_0(\mu, \nu, \alpha)$ denote the principal eigenvalues of (2.12) and (2.13) respectively; then for (μ, ν, α) in some neighborhood of (μ_0, ν_0, α_0) , $\sigma_0(\mu, \nu, \alpha)$ and $\tau_0(\mu, \nu, \alpha)$ depend differentiably on μ, ν , and α . The corresponding normalized eigenfunctions also depend differentiably on μ, ν , and α in a neighborhood of (μ_0, ν_0, α_0) .

A proof of the Lemma is given in the Appendix. Related results are discussed in [7,8,16,17].

To assess the effects of diffusion and directed movement on competition we will examine the results of perturbing the parameters (μ, ν, α) in (2.1) from $(\mu_0, \mu_0, 0)$ for some $\mu_0 > 0$. When $\mu = \nu = \mu_0$ and $\alpha = 0$, the single species equilibria \tilde{u} and \tilde{v} of (2.5) and (2.6) respectively are given by $\tilde{u} = \tilde{v} = \theta$ where θ is the unique positive solution of

$$\begin{aligned} \mu_0 \nabla^2 \theta + (m(x) - \theta)\theta &= 0 \quad \text{in } \Omega, \\ \frac{\partial \theta}{\partial \bar{n}} &= 0 \quad \text{on } \partial\Omega. \end{aligned} \tag{3.1}$$

Let $(\mu, \nu, \alpha) = (\mu(s), \nu(s), \alpha(s))$ where $\mu(s), \nu(s)$, and $\alpha(s)$ are smooth functions with $\mu(0) = \nu(0) = \mu_0$ and $\alpha(0) = 0$. Observe that when $\mu = \nu = \mu_0$ and $\alpha = 0$, i.e. when $s = 0$, we can choose $\psi = p_0\theta > 0$ in (2.12) with $\sigma = 0$ and $\phi = p_0\theta > 0$ in (2.14) with $\sigma = 0$ for any positive p_0 . Thus, we have $\sigma_0(\mu_0, \mu_0, 0) = \tau_0(\mu_0, \mu_0, 0) = 0$, since the principal eigenvalues of (2.12) and (2.14) (recall that (2.13) and (2.14) are equivalent) are the unique eigenvalues with positive eigenfunctions. To be consistent with the formulations given in the proof of Lemma 3.1, we would choose $p_0 = 1 / \int_{\Omega} \theta^2 dx$ and require that the eigenfunctions ψ_0 and ϕ_0 corresponding to σ_0 and τ_0

respectively satisfy

$$\int_{\Omega} \psi_0^2 dx = 1, \quad \int_{\Omega} e^{(\alpha/\mu)m} \phi_0^2 dx = 1. \quad (3.2)$$

(Here ψ_0 corresponds to (2.12) and ϕ_0 to (2.14).) It then follows from Lemma 3.1 and the assumptions on $(\mu(s), \nu(s), \alpha(s))$ that we may write the parameters μ, ν, α , the equilibria \tilde{u}, \tilde{v} , the normalized eigenfunctions ψ_0, ϕ_0 and the principal eigenvalues σ_0, τ_0 as

$$\begin{aligned} \mu &= \mu_0 + s\mu_1 + o(s), & \nu &= \mu_0 + s\nu_1 + o(s), & \alpha &= \alpha_1 s + o(s), \\ \tilde{u} &= \theta + u_1 s + o(s), & \tilde{v} &= \theta + v_1 s + o(s), \\ \psi_0 &= p_0 \theta + \psi_1 s + o(s), & \phi_0 &= p_0 \theta + \phi_1 s + o(s), \\ \sigma_0 &= \sigma_1 s + o(s), & \tau_0 &= \tau_1 s + o(s). \end{aligned} \quad (3.3)$$

If we substitute these expressions into (2.1) (for \tilde{u} and \tilde{v}) and (2.12) or (2.14) (for $\tilde{u}, \tilde{v}, \psi_0, \phi_0, \sigma_0$, and τ_0) the terms of order 0 in s drop out. The terms of order s satisfy the following relations:

(for \tilde{u})

$$\mu_1 \nabla^2 \theta + \mu_0 \nabla^2 u_1 - \nabla \cdot (\alpha_1 \theta \nabla m) + (m - 2\theta) u_1 = 0 \quad \text{on } \Omega, \quad (3.4)$$

(for \tilde{v})

$$\nu_1 \nabla^2 \theta + \mu_0 \nabla^2 v_1 + (m - 2\theta) v_1 = 0 \quad \text{on } \Omega, \quad (3.5)$$

(for ψ_0 and σ_0)

$$p_0 \nu_1 \nabla^2 \theta + \mu_0 \nabla^2 \psi_1 + (m - \theta) \psi_1 - u_1 p_0 \theta = \sigma_1 p_0 \theta \quad \text{on } \Omega, \quad (3.6)$$

and (for ϕ_0 and τ_0)

$$p_0 \mu_1 \nabla^2 \theta + \mu_0 \nabla^2 \phi_1 + \alpha_1 p_0 \nabla \theta \cdot \nabla m + (m - \theta) \phi_1 - p_0 v_1 \theta = \tau_1 p_0 \theta \quad \text{on } \Omega. \quad (3.7)$$

Note that (3.7) is derived from (2.14). In (3.4)-(3.7) the terms representing state variables $(\theta, u_1, v_1, \phi_1, \psi_1)$ satisfy the boundary conditions:

$$\begin{aligned} \frac{\partial \theta}{\partial \vec{n}} &= \frac{\partial v_1}{\partial \vec{n}} = \frac{\partial \phi_1}{\partial \vec{n}} = \frac{\partial \psi_1}{\partial \vec{n}} = 0, \\ \mu_0 \frac{\partial u_1}{\partial \vec{n}} - \alpha_1 \theta \frac{\partial m}{\partial \vec{n}} &= 0 \quad \text{on } \partial \Omega. \end{aligned} \quad (3.8)$$

To analyze how σ_0 depends on the perturbation we write (3.6) as

$$\mu_0 \nabla^2 \psi_1 + (m - \theta) \psi_1 + p_0 \nu_1 \nabla^2 \theta - u_1 p_0 \theta = \sigma_1 p_0 \theta \quad (3.9)$$

then multiply by θ and integrate over Ω . We have by the divergence theorem and (3.8)

$$\int \theta \nabla^2 \psi_1 dx = \int (\nabla^2 \theta) \psi_1 dx, \quad \int_{\Omega} \theta \nabla^2 \theta dx = - \int_{\Omega} |\nabla \theta|^2 dx \quad (3.10)$$

so after using (3.1) the first two terms in (3.9) drop out. Dividing by p_0 then yields

$$-\nu_1 \int_{\Omega} |\nabla \theta|^2 dx - \int_{\Omega} u_1 \theta^2 dx = \sigma_1 \int_{\Omega} \theta^2 dx. \quad (3.11)$$

To evaluate the second integral in (3.11) we can write (3.4) as

$$\mu_0 \nabla^2 u_1 + (m - \theta) u_1 + \mu_1 \nabla^2 \theta - \nabla \cdot (\alpha_1 \theta \nabla m) = \theta u_1. \quad (3.12)$$

Multiplying (3.12) by θ , integrating over Ω , applying the divergence theorem, and using (3.1) yields

$$\int_{\partial\Omega} \mu_0 \theta \frac{\partial u_1}{\partial \vec{n}} ds - \mu_1 \int_{\Omega} |\nabla \theta|^2 dx + \alpha_1 \int_{\Omega} \theta \nabla \theta \cdot \nabla m dx - \int_{\partial\Omega} \alpha_1 \theta \frac{\partial m}{\partial \vec{n}} ds = \int_{\Omega} u_1 \theta^2 dx. \quad (3.13)$$

By the boundary condition (3.8) on u_1 , the first and last terms on the left in (3.13) cancel, so that

$$-\mu_1 \int_{\Omega} |\nabla \theta|^2 dx + \alpha_1 \int_{\Omega} \theta \nabla \theta \cdot \nabla m dx = \int_{\Omega} u_1 \theta^2 dx. \quad (3.14)$$

Substituting (3.14) into (3.11) and solving for σ_1 yields

$$\sigma_1 = \frac{(\mu_1 - \nu_1) \int_{\Omega} |\nabla \theta|^2 dx - \alpha_1 \int_{\Omega} \theta \nabla \theta \cdot \nabla m dx}{\int_{\Omega} \theta^2 dx}. \quad (3.15)$$

The analysis for τ_0 is roughly analogous to that for σ_0 . Multiplying (3.7) by θ , integrating, applying the divergence theorem, using (3.1) to eliminate some terms, and dividing by p_0 yields in analogy to (3.11) the relation

$$-\mu_1 \int_{\Omega} |\nabla \theta|^2 dx + \alpha_1 \int_{\Omega} \theta \nabla \theta \cdot \nabla m dx - \int_{\Omega} v_1 \theta^2 dx = \tau_1 \int_{\Omega} \theta^2 dx. \quad (3.16)$$

Multiplying (3.5) by θ , integrating, and using (3.1) yields

$$-\nu_1 \int_{\Omega} |\nabla \theta|^2 dx = \int_{\Omega} v_1 \theta^2 dx; \quad (3.17)$$

substituting into (3.16) and solving for τ_1 yields

$$\tau_1 = -\sigma_1 = \frac{(\nu_1 - \mu_1) \int_{\Omega} |\nabla \theta|^2 dx + \alpha_1 \int_{\Omega} \theta \nabla \theta \cdot \nabla m dx}{\int_{\Omega} \theta^2 dx}. \quad (3.18)$$

Discussion: Recall that the stability of the equilibria $(\tilde{u}, 0)$ and $(0, \tilde{v})$ depends on the principal eigenvalues σ_0 and τ_0 , respectively. If $\sigma_0 < 0$ then $(\tilde{u}, 0)$ is locally stable, that is, it is not invasible by v for low densities of v . If $\sigma_0 > 0$ then $(\tilde{u}, 0)$ is invasible by v . Similarly, if $\tau_0 < 0$ then $(0, \tilde{v})$ is stable, that is, not invasible by u at low densities of u , while if $\tau_0 > 0$ then $(0, \tilde{v})$ is invasible. For $(\mu, \nu, \alpha) = (\mu_0, \mu_0, 0)$ we have $\sigma_0 = \tau_0 = 0$; thus, for small perturbations of $(\mu_0, \mu_0, 0)$ in the direction of (μ_1, ν_1, α_1) the signs of σ_0 and τ_0 are the same as those of σ_1 and τ_1 . Notice that $\tau_1 = -\sigma_1$, so if σ_1 and τ_1 are nonzero the perturbation has opposite effects on the signs of σ_1 and τ_1 . In the case $\alpha_1 = 0$, (3.15) implies the sign of σ_1 is the same sign as $\mu_1 - \nu_1$ while (3.18) implies that τ_1 has the opposite sign. If $m(x)$ is nonconstant we have $\nabla \theta \neq 0$ for some x , so we have $\sigma_1 < 0$ and hence $\sigma_0 < 0$ for small s if $\nu_1 > \mu_1$. Similarly $\tau_1 > 0$ and so $\tau_0 > 0$ for small s if $\nu_1 > \mu_1$. In that situation $(\tilde{u}, 0)$ will not be invasible by v but $(0, \tilde{v})$ will be invasible by u . Hence the competitor with the lower diffusion rate, in this case u , will have the advantage. This is consistent with the results of Dockery et al. [5]. If $\alpha_1 \neq 0$ the situation depends on the sign of $\int_{\Omega} \theta \nabla \theta \cdot \nabla m dx$ and the relative sizes of μ_1, ν_1 , and α_1 . We will now examine the sign of that integral. The analysis is closely related to the results of [8,9] on the effects of directed movement in single-species logistic models with diffusion and advection along resource gradients. That is not surprising, because movement upward along the resource gradient can be expected to contribute toward an advantage in competition if it is beneficial for a single species.

Lemma 3.2: The integral $\int_{\Omega} \theta \nabla \theta \cdot \nabla m dx$ is positive if $\Omega \subseteq \mathbb{R}$ is an interval or if $\Omega \subseteq \mathbb{R}^n$ is convex.

A proof of the lemma is given in the Appendix.

If $n \geq 2$ there exist nonconvex domains $\Omega \subseteq \mathbb{R}^n$ and growth rates m such that the integral is negative. This phenomenon can occur in situations analogous to those studied in [9] where movement upward along environmental gradients is harmful in single-species models. We will explore this topic further in another paper.

The requirement that Ω must be convex to insure that the integral in Lemma 3.2 is positive if $n \geq 2$ is not surprising, because there are examples of nonconvex domains where movement upward along resource gradients can be disadvantageous in single-species models; see [9].

Our main result now follows immediately from (3.18) and Lemma 3.2:

Theorem 3.3: Suppose that $\Omega \subseteq \mathbb{R}$ or that $\Omega \subseteq \mathbb{R}^n$ and Ω is convex, so that

$$\int_{\Omega} \theta \nabla \theta \cdot \nabla m dx > 0.$$

Let $(\mu, \nu, \alpha) = (\mu_0 + \mu_1 s + o(s), \mu_0 + \nu_1 s + o(s), \alpha_1 s + o(s))$. Then for $s > 0$ sufficiently small we have

$$\sigma_0(\mu, \nu, \alpha) < 0 < \tau_0(\mu, \nu, \alpha) \tag{3.19}$$

provided that

$$\alpha_1 > (\mu_1 - \nu_1) \left[\int_{\Omega} |\nabla \theta|^2 dx / \int_{\Omega} \theta \nabla \theta \cdot \nabla m dx \right]. \tag{3.20}$$

Proof: Recall that $\sigma_0(\mu_0, \mu_0, 0) = \tau_0(\mu_0, \mu_0, 0) = 0$. By Lemma 3.1 it follows that for $s > 0$ sufficiently small the signs of σ_0 and τ_0 are the same as those of σ_1 and τ_1 respectively. By (3.18) $\sigma_1 < 0$ and $\tau_1 > 0$ if (3.20) holds.

Discussion: If $\nu_1 > \mu_1$, so that the perturbation from $(\mu, \nu) = (\mu_0, \mu_0)$ causes $\nu > \mu$ for $s > 0$ small then (3.20) holds with $\alpha_1 = 0$. In other words, a perturbation which causes the diffusion rate for the second competitor to exceed that of the first competitor always favors the first competitor. This is consistent with Dockery et al. [5]. However, even when $\mu_1 > \nu_1$, so that the perturbation makes the diffusion rate of the first competitor larger than that of the second, the first competitor may still gain an advantage if $\alpha_1 > 0$ is large enough that (3.20) holds. The implication is that the advantage gained from directed movement upward along resource gradients can counterbalance the disadvantage created by more rapid diffusion.

4 Conclusions

Our analysis shows that in the context of reaction-diffusion-advection models with environmental variation in space but not in time, conditional dispersal can sometimes confer a competitive advantage. Specifically, directed movement upward along resource gradients can be advantageous, even if it is accompanied by an increased rate of random diffusion. In general terms this conclusion is consistent with results of McPeck and Holt [2] on discrete-time two-patch models. In single species models such directed movement is not always beneficial, but is beneficial if the underlying spatial environment is convex [9]. To conclude that directed movement can confer a competitive advantage requires analogous assumptions. Dockery et al. [5] showed that without directed movement the competitor with the slowest rate of diffusion (unconditional dispersal) has the advantage in the reaction-diffusion context. This is also consistent with McPeck and Holt [2]. It is at least plausible that increasing the rate of diffusion might be a necessary tradeoff for the ability to detect and follow environmental gradients, because some amount of random sampling of the environment in different locations might be needed to measure them. Our analysis suggests that such a trade-off may sometimes be advantageous. Thus, a species might tend to evolve faster rates of diffusion on a spatially varying but temporally constant environment if by doing so it could improve its ability to move toward more favorable regions.

References

- [1] A. Okubo, *Diffusion and Ecological Problems: Mathematical Models*, Biomathematics 10, Springer-Verlag, New York, 1980.
- [2] M.A. McPeck and R.D. Holt, The evolution of dispersal in spatially and temporally varying environments, *Am. Nat.* 140 (1992), 1010.
- [3] J.D. Murray, *Mathematical Biology*, 2nd ed., Biomathematics Texts 19, Springer-Verlag, New York, 1993.
- [4] R.D. Holt and M.A. McPeck, Chaotic population dynamics favors the evolution of dispersal. *Am. Nat.* 148 (1996), 709.
- [5] J. Dockery, V. Hutson, K. Mischaikow, and M. Pernarowski, The evolution of slow dispersal rates: a reaction-diffusion model. *J. Math. Biol.* 37 (1998), 61.
- [6] V. Hutson, K. Mischaikow, and P. Polacik, The evolution of dispersal rates in a heterogeneous time-periodic environment. *J. Math. Biol.* 43 (2001), 501.
- [7] R.S. Cantrell and C. Cosner, *Spatial Ecology Via Reaction-Diffusion Equations*. Wiley, Chichester, West Sussex, U.K., 2003.
- [8] F. Belgacem and C. Cosner, The effects of dispersal along environmental gradients on the dynamics of populations in heterogeneous environments. *Canadian Appl. Math. Quarterly* 3 (1995), 379.
- [9] C. Cosner and Y. Lou, Does movement toward better environments always benefit a population? *J. Math. Anal. Appl.* 277 (2003), 489.
- [10] T. Hillen, Transport equations with resting phases, *Eur. J. Appl. Math* 14 (2003), 613.
- [11] P. Hess, *Periodic-Parabolic Boundary Value Problems and Positivity*, Pitman Research Notes in Mathematics 247. Longman, Harlow, Essex, U.K., 1991.
- [12] H. Smith, *Monotone Dynamical Systems*. Mathematical Surveys and Monographs 41. American Mathematical Society, Providence, Rhode Island, U.S.A., 1995.

- [13] S. Senn, On a nonlinear elliptic eigenvalue problem with Neumann boundary conditions, with an application to population genetics. *Comm. PDE* 8 (1983), 1199.
- [14] S. Senn and P. Hess, On positive solutions of a linear elliptic boundary value problem with Neumann boundary conditions. *Math. Ann.* 258 (1982), 459.
- [15] F. Belgacem, Boundary value problems with indefinite weights: variational formulations of the principal eigenvalue and applications, Pitman Research Notes in Mathematics 368, Longman, Harlow, Essex, U.K., 1997.
- [16] R.S. Cantrell and C. Cosner, On the steady-state problem for the Volterra-Lotka competition model with diffusion. *Houston J. Math.* 13 (1987), 337.
- [17] R.S. Cantrell, C. Cosner, and Y. Lou, Multiple reversals of competitive dominance in ecological reserves via external habitat degradation. *J. Dynamics and Differential Equations*, 16 (2004), 973.
- [18] R.G. Casten and C. Holland, Instability results for reaction-diffusion equations with Neumann boundary conditions. *J. Differential Equations* 27 (1978), 266.
- [19] H. Matano, Asymptotic behavior and stability of solutions of semilinear diffusion equations. *Publ. Res. Inst. Math. Sci.* 15 (1979), 401.

Appendix

Proof of Lemma 3.1

There are two parts to the proof. First we observe that \tilde{u} depends differentiably on μ and α and that \tilde{v} depends differentiably on ν . Then we show that σ_0 and τ_0 depend differentiably on μ , ν , and α . Both parts use the implicit function theorem.

The differentiable dependence of \tilde{v} on ν follows by taking $\nu = 1/\lambda$ in Proposition 3.6 of [7] and the remarks that follow it. The sense in which \tilde{v} depends differentiably on ν is that the map $\nu \rightarrow \tilde{v}(\nu)$ is differentiable as a map from \mathbb{R} into $Y = \{y \in C^{2+\delta}(\overline{\Omega}) : \partial y / \partial \vec{n} = 0 \text{ on } \partial\Omega\}$. To show that \tilde{u} depends differentiably on μ and α , we would rewrite the equation (2.5) for \tilde{u} as the corresponding equilibrium equation for (2.7), where $\tilde{w} = e^{-(\alpha/\mu)m(x)}\tilde{u}$:

$$\begin{aligned} \mu \nabla^2 \tilde{w} + \alpha \nabla m \cdot \nabla \tilde{w} + (m - e^{(\alpha/\mu)m})\tilde{w} &= 0 \quad \text{on } \Omega, \\ \frac{\partial \tilde{w}}{\partial \vec{n}} &= 0 \quad \text{on } \partial\Omega. \end{aligned} \tag{A.1}$$

Equation (A.1) may be rewritten by multiplying by $e^{(\alpha/\mu)m}$:

$$\begin{aligned} \mu \nabla \cdot e^{(\alpha/\mu)m} \nabla \tilde{w} + (m - e^{(\alpha/\mu)m})e^{(\alpha/\mu)m}\tilde{w} &= 0 \quad \text{on } \Omega, \\ \frac{\partial \tilde{w}}{\partial \vec{n}} &= 0 \quad \text{on } \partial\Omega. \end{aligned} \tag{A.2}$$

The continuous dependence of \tilde{w} and hence \tilde{u} on α and μ then follows essentially as in Proposition 3.6 of Cantrell and Cosner (2003). To be more specific, we would (again) let

$$Y = \{y \in C^{2+\delta}(\overline{\Omega}) : \partial y / \partial \vec{n} = 0 \text{ on } \partial\Omega\} \tag{A.3}$$

and define $F : \mathbb{R} \times \mathbb{R} \times Y \rightarrow C^\delta(\overline{\Omega})$ by $(\mu, \alpha, w) \rightarrow \mu \nabla \cdot e^{(\alpha/\mu)m} \nabla w + (m - e^{(\alpha/\mu)m}w)e^{(\alpha/\mu)m}w$. The remainder of the proof consists of computing $D_w F$, showing that $D_w F$ is invertible via eigenvalue comparison, and applying the implicit function theorem. The calculations are very similar to those in the proof of Proposition 3.6 of [7] so we omit the details.

The differentiable dependence of σ_0 and τ_0 on μ , ν , and α (possibly via \tilde{u} and \tilde{v}) can be shown by arguments along the lines of Example 3.5 of [7] but there are enough differences that it seems worthwhile to sketch the proof.

We will consider the equation (2.14) for τ_0 . Multiplying (2.14) by $e^{(\alpha/\mu)m}$, we may rewrite it as

$$\begin{aligned} \nabla \cdot \mu e^{(\alpha/\mu)m} \nabla \phi + (m - \tilde{v}) e^{(\alpha/\mu)m} \phi &= \sigma e^{(\alpha/\mu)m} \phi \quad \text{in } \Omega, \\ \frac{\partial \phi}{\partial \bar{n}} &= 0 \quad \text{on } \partial\Omega, \end{aligned} \tag{A.4}$$

in analogy to (A.2). Let the space Y be as in (A.3) and define the map $G : (\mathbb{R}^2 \times Y) \times (Y \times \mathbb{R}) \rightarrow C^\delta(\bar{\Omega}) \times \mathbb{R}$ as

$$\begin{aligned} G(\alpha, \mu, \tilde{v}, \phi, \sigma) &= (\nabla \cdot \mu e^{(\alpha/\mu)m} \nabla \phi + (m - \tilde{v}) e^{(\alpha/\mu)m} \phi - \sigma e^{(\alpha/\mu)m} \phi, \\ &\int_{\Omega} e^{(\alpha/\mu)m} \phi^2 dx - 1). \end{aligned}$$

The linearization of G with respect to ϕ and σ is

$$\begin{aligned} D_{(\phi, \sigma)} G(\alpha, \mu, \tilde{v}, \phi, \sigma)(\xi, \rho) &= (\nabla \cdot \mu e^{(\alpha/\mu)m} \nabla \xi + (m - \tilde{v}) e^{(\alpha/\mu)m} \xi \\ &\quad - \sigma e^{(\alpha/\mu)m} \xi - \rho e^{(\alpha/\mu)m} \phi, 2 \int_{\Omega} e^{(\alpha/\mu)m} \phi \xi dx). \end{aligned}$$

Let $\tau_0^* = \tau_0(\mu_0, \nu_0, \alpha_0)$ be the principal eigenvalue of (A.4) (equivalently (2.13) or (2.14)) corresponding to $\alpha = \alpha_0$, $\mu = \mu_0$, and $\tilde{v} = \tilde{v}(\nu_0)$, and let ϕ_0 be the corresponding eigenfunction for (A.4) normalized by

$$\int_{\Omega} e^{(\alpha_0/\mu_0)m} \phi_0^2 dx = 1.$$

To determine whether $D_{(\phi, \sigma)} G$ is invertible at $(\alpha_0, \mu_0, \tilde{v}(\nu_0), \phi_0, \tau_0^*)$ we must consider the problem

$$\begin{aligned} \nabla \cdot \mu_0 e^{(\alpha_0/\mu_0)m} \nabla \xi + (m - \tilde{v}(\nu_0)) e^{(\alpha_0/\mu_0)m} \xi \\ - \tau_0^* e^{(\alpha_0/\mu_0)m} \xi - \rho e^{(\alpha_0/\mu_0)m} \phi_0 &= g(x), \\ 2 \int_{\Omega} e^{(\alpha_0/\mu_0)m} \phi_0 \xi dx &= r. \end{aligned} \tag{A.5}$$

Since τ_0^* is a simple eigenvalue for the differential operator in (A.5), standard elliptic theory based on the Fredholm alternative implies that the first equation in (A.5) can be solved for $\xi \in Y$ for a given $g \in C^\delta(\bar{\Omega})$ provided

$$0 = \int_{\Omega} [\rho e^{(\alpha_0/\mu_0)m} \phi_0 + g] \phi_0 dx$$

so that by the normalization of ϕ_0 , ρ is uniquely determined as $\rho = -\int_{\Omega} \phi_0 g dx$. The solution ξ then has the form $\xi = \xi_0 + s\phi_0$ where ξ_0 is any particular solution and $s \in \mathbb{R}$. Substituting into the second equation of (A.5) and again using the normalization of ϕ_0 yields

$$2 \int_{\Omega} e^{(\alpha_0/\mu_0)m} \phi_0 \xi_0 dx + 2s = r$$

which uniquely determines s as

$$s = (r/2) - \int_{\Omega} e^{(\alpha_0/\mu_0)m} \phi_0 \xi_0 dx,$$

so that (A.5) has a unique solution in $Y \times \mathbb{R}$ for any $(g, r) \in C^\delta(\bar{\Omega}) \times \mathbb{R}$. Standard results in operator theory and the theory of elliptic equations then imply that $D_{(\phi, \sigma)}G$ is an invertible operator from $Y \times \mathbb{R}$ onto $C^\delta(\bar{\Omega}) \times \mathbb{R}$ when $(\alpha, \mu, \tilde{\nu}) = (\alpha_0, \mu_0, \tilde{\nu}(\nu_0))$. It then follows from the implicit function theorem that the relation $G(\alpha, \mu, \tilde{\nu}, \phi, \sigma) = 0$ determines $(\phi, \sigma) \in Y \times \mathbb{R}$ as a differentiable function of α, μ , and $\tilde{\nu}$ in a neighborhood of $(\alpha_0, \mu_0, \tilde{\nu}(\nu_0))$ in $\mathbb{R} \times Y$. Since $\tilde{\nu}(\nu)$ depends differentiably on ν and $G(\alpha_0, \mu_0, \tilde{\nu}(\nu_0), \phi_0, \tau_0^*) = 0$, it then follows that $\tau_0 = \tau_0(\mu, \nu, \alpha)$ with $\tau_0(\mu_0, \nu_0, \alpha_0) = \tau_0^*$ and with differentiable dependence on μ, ν , and α in some neighborhood of (μ_0, ν_0, α_0) . A similar argument yields the analogous result for σ_0 .

Proof of Lemma 3.2.

By rescaling the spatial variables we may assume without loss of generality that $\mu_0 = 1$.

If $\Omega = (a, b) \subseteq \mathbb{R}$ is an interval, note that because $\theta > 0$ satisfies

$$\begin{aligned} \frac{d^2\theta}{dx^2} + (m - \theta)\theta &= 0 \quad \text{on } (a, b), \\ \frac{d\theta}{dx} &= 0 \quad \text{at } x = a, b, \end{aligned} \tag{A.6}$$

the principal eigenvalue of

$$\begin{aligned} \frac{d^2\phi}{dx^2} + (m - \theta)\phi &= \rho\phi \quad \text{on } (a, b), \\ \frac{d\phi}{dx} &= 0 \quad \text{at } x = a, b \end{aligned}$$

is zero, with a corresponding eigenfunction that is a multiple of θ . Thus, the principal eigenvalue ρ_1 for the corresponding problem with Dirichlet boundary conditions must be negative. Observe that differentiating (A.6) with respect to x leads to the equation

$$\frac{d^2}{dx^2} \left(\frac{d\theta}{dx} \right) + (m - \theta) \frac{d\theta}{dx} + \frac{\theta dm}{dx} - \frac{\theta d\theta}{dx} = 0 \quad \text{on } (a, b). \quad (\text{A.7})$$

Multiplying (A.7) by $\frac{d\theta}{dx}$ and integrating (using integration by parts in the first term) yields

$$\begin{aligned} & \int_a^b \left\{ - \left[\frac{d}{dx} \left(\frac{d\theta}{dx} \right) \right]^2 + (m - \theta) \left(\frac{d\theta}{dx} \right)^2 \right\} dx + \int_a^b \theta \frac{d\theta}{dx} \frac{dm}{dx} dx \\ & - \int_a^b \theta \left(\frac{d\theta}{dx} \right)^2 dx = 0. \end{aligned} \quad (\text{A.8})$$

By the boundary conditions on θ in (A.6), $d\theta/dx$ satisfies Dirichlet boundary conditions, so by the variational characterization of the principal eigenvalue we have

$$\begin{aligned} & \int_a^b \left\{ - \left[\frac{d}{dx} \left(\frac{d\theta}{dx} \right) \right]^2 + (m - \theta) \left(\frac{d\theta}{dx} \right)^2 \right\} dx \\ & \leq \rho_1 \int_a^b \left(\frac{d\theta}{dx} \right)^2 dx < 0. \end{aligned}$$

Since the third term in (A.8) is clearly negative (because $\theta > 0$) we must have $\int_a^b \theta \frac{d\theta}{dx} \frac{dm}{dx} dx > 0$, as claimed.

For $\Omega \subseteq \mathbb{R}^n$ the essential idea of the proof is the same but the analysis is more complicated and requires Ω to be convex. (This is not surprising, because it can be shown that if Ω is nonconvex then it is possible that directed motion upward along resource gradients may sometimes be detrimental to a single population, even with no-flux boundary conditions (See [9]). The technical issues addressed here are similar to those in that paper.) Suppose that θ satisfies

$$\begin{aligned} \Delta\theta + (m(x) - \theta)\theta &= 0 \quad \text{in } \Omega \\ \frac{\partial\theta}{\partial\vec{n}} &= 0 \quad \text{on } \partial\Omega \end{aligned} \quad (\text{A.9})$$

where $\Delta = \nabla^2$. Differentiating (A.9) and taking the dot product with $\nabla\theta$ we have

$$\nabla\theta \cdot \nabla(\Delta\theta) + |\nabla\theta|^2(m - 2\theta) + \theta\nabla\theta \cdot \nabla m = 0 \quad \text{in } \Omega. \quad (\text{A.10})$$

Using the identity

$$\nabla\theta \cdot \nabla(\Delta\theta) + |\text{Hess } \theta|^2 = \frac{1}{2}\Delta(|\nabla\theta|^2),$$

we have

$$\frac{1}{2}\Delta(|\nabla\theta|^2) - |\text{Hess } \theta|^2 + [m - 2\theta]|\nabla\theta|^2 + \theta\nabla\theta \cdot \nabla m = 0 \quad \text{in } \Omega. \quad (\text{A.11})$$

Integrating (A.11) over Ω we have

$$\int_{\Omega} \theta\nabla\theta \cdot \nabla m dx = \int_{\Omega} [|\text{Hess } \theta|^2 - (m - 2\theta)|\nabla\theta|^2] dx - \frac{1}{2} \int_{\partial\Omega} \frac{\partial}{\partial \vec{n}} (|\nabla\theta|^2) dS. \quad (\text{A.12})$$

As in the case of $\Omega \subseteq \mathbb{R}$, note that $\theta > 0$ in (A.9) so that the principal eigenvalue ρ_1 of

$$\nabla^2\phi + (m - \theta)\phi = \rho\phi \quad \text{in } \Omega \quad (\text{A.13})$$

$$\frac{\partial\phi}{\partial \vec{n}} = 0 \quad \text{on } \partial\Omega$$

is zero. Thus, by the variational characterization of eigenvalues, we have

$$\int_{\Omega} [-|\nabla\phi|^2 + (m - \theta)\phi^2] dx \leq \rho_1 \int_{\Omega} \phi^2 dx \leq 0 \quad (\text{A.14})$$

for any $\phi \in W^{1,2}(\Omega)$. If $\psi \in W^{2,2}(\Omega)$ then for each x_i we have

$$\int_{\Omega} [-|\nabla\psi_{x_i}|^2 + (m - \theta)\psi_{x_i}^2] dx \leq 0;$$

summing over i yields

$$\int_{\Omega} [-|\text{Hess } \psi|^2 + (m - \theta)|\nabla\psi|^2] dx \leq 0. \quad (\text{A.15})$$

We may rewrite (A.12) as

$$\begin{aligned} \int_{\Omega} \theta\nabla\theta \cdot \nabla m dx &= \int_{\Omega} [|\text{Hess } \theta|^2 - (m - \theta)|\nabla\theta|^2] dx \\ &+ \int_{\Omega} \theta|\nabla\theta|^2 dx - \frac{1}{2} \int_{\partial\Omega} \frac{\partial}{\partial \vec{n}} (|\nabla\theta|^2) dS \\ &\geq \int_{\Omega} \theta|\nabla\theta|^2 dx - \frac{1}{2} \int_{\partial\Omega} \frac{\partial}{\partial \vec{n}} (|\nabla\theta|^2) dS. \end{aligned} \quad (\text{A.16})$$

If Ω is convex then since $\partial\theta/\partial\vec{n} = 0$ on $\partial\Omega$ it follows from results of Casten and Holland [18] and Matano [19] that

$$\int_{\partial\Omega} \frac{\partial}{\partial\vec{n}} (|\nabla\theta|^2) dS \leq 0. \quad (\text{A.17})$$

Since we are assuming m is nonconstant, θ must also be nonconstant, so the integral on the left side of (A.16) must be strictly positive.