EVOLUTION OF CONDITIONAL DISPERSAL: A REACTION-DIFFUSION-ADVECTION APPROACH

DISSERTATION

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By

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ABSTRACT

We study the evolution of conditional dispersal using a Lotka-Volterra reaction-diffusion-advection model for two competing species in a nonhomogeneous, temporally constant environment. We assume that the two species are identical except for their dispersal strategies. Both species employ random diffusion combined with advection upward along resource gradients. We use a perturbation argument to understand the evolution of these rates. When the advection rates are small relative to the diffusion rates, we find that stronger advection is preferred. However, when the advection rates are large relative to the diffusion rates, we find that weaker advection is preferred. We also studied the case where the two species have differing strategies, one with a very strong biased movement relative to diffusion, and the other with a more balanced approach. If the advection rate of the latter is small, the two species can coexist. But if its advection rate increases sufficiently, the second species drives the first to extinction. So we see in these results a preference against overly strong advection and in favor of a more balanced strategy, suggesting the existence of an optimal intermediate rate.

To Hope Elisabeth, may your thirst for knowledge never be quenched.

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CHAPTER 1

INTRODUCTION

In this paper we study the evolution of dispersal strategies via reaction-advection-diffusion models. Our goal is to better understand how dispersal strategies will affect the survival and extinction of the species. We will focus on conditional dispersal strategies, that is, dispersal strategies that are dependent on the spatial heterogeneity of the habitat.

Our approach in studying the evolution of dispersal will be to analyze the competition between two species in a closed environment. Throughout this paper we will assume that the two species are identical in all ecological aspects except for their dispersal strategies. In particular, they compete for the same resources and have the same intrinsic growth rates. The main goal is to determine which dispersal strategies can confer a competitive advantage and thus will evolve.

1.1 Background

The most basic dispersal strategy is simply dispersal by random diffusion. We let $u = u(x, t)$ and $v = v(x, t)$ be the densities of the two species at location x and time t, and $\mu, \nu > 0$ be the respective diffusion rates of the species. The spatially varying but time constant function $m(x)$ accounts for the intrinsic growth rate of the species at location x. Combining the diffusion with the classical Lotka-Volterra competition kinetics, we get the following system.

$$\begin{aligned} &u_t = \mu\Delta u + u(m-u-v) \quad \text{in} \quad \Omega \times (0,\infty),\\ &v_t = \nu\Delta v + v(m-u-v) \quad \text{in} \quad \Omega \times (0,\infty),\\ &\partial u/\partial n = \partial v/\partial n = 0 \quad \text{on} \quad \partial\Omega \times (0,\infty), \end{aligned} \tag{1.1}$$

where Δ is the Laplace operator, Ω is a domain in R^N with smooth boundary $\partial\Omega$, n is the outward unit normal vector on $\partial\Omega$, and the boundary conditions mean that no individuals cross the boundary.

Dockery et. al. [8] studied this system and showed that the slower diffuser is always the winner. More precisely, let $\theta = \theta(x;\mu)$ be a positive steady-state of the single species system

$$\begin{aligned} &\theta_t = \mu\Delta\theta + u(m-\theta) \quad \text{in} \quad \Omega \times (0,\infty),\\ &\partial\theta/\partial n = 0 \quad \text{on} \quad \partial\Omega \times (0,\infty). \end{aligned} \tag{1.2}$$

If $\mu < \nu$, then the semi-trivial steady state $(\theta(\cdot;\mu), 0)$ is globally asymptotically stable among all non-negative, non-identically zero initial data. They also showed that for more than 2 species with respective diffusion rates $d_1 < d_2 < \ldots < d_n$, the semi-trivial steady state $(\theta(\cdot;d_1), 0, \ldots, 0)$ is the only locally asymptotically stable semi-trivial steady state. In fact, all the other semi-trivial steady states are unstable and there are no other non-trivial non-negative steady states. However, they could not prove (and it is still not proven), that $(\theta(\cdot;d_1), 0, \ldots, 0)$ is globally asymptotically stable. This difference is mainly due to the fact that competition models for two species are monotone systems, while competition models for three or more species are not monotone in general.

Random diffusion alone does not usually explain well the movement of animals. Even the most simple species may exhibit some cognition of the local environment in their search for food, water, shelter, etc. Since resources are usually not distributed uniformly across the habitat, we expect to see some biased movement of animals in searching for resources, e.g., they may be able to track the gradient of resources to some extent. We identified $m(x)$ above as the intrinsic growth rate of the species, but we can also view m as the indicator of the quality of the habitat (the more suitable the habitat, the higher the growth rate). Hence as individuals set off in search of more food and better habitat, we expect to see movement upwards along the gradient of m. Of course, we still expect and even desire some random movement. Without any random diffusion the species will simply congregate at a local maximum for m (depending on their initial location). If the random movement is strong enough, however, some individuals may move away from the locally most desirable habitat to find another desirable area, thus likely increasing the overall population size and the survivability of the species.

Next we modify the system by allowing one species to move upward along the resource gradient in search of a better habitat while the other moves only by random diffusion. We come up with the following system:

$$\begin{aligned} &u_t = \nabla \cdot [\mu \nabla u - \alpha u \nabla m] + u(m - u - v) \quad \text{in } \ \Omega \times (0, \infty), \\ &v_t = \nu \Delta v + v(m - u - v) \quad \text{in } \ \Omega \times (0, \infty), \\ &[\mu \nabla u - \alpha u \nabla m] \cdot n = \nabla v \cdot n = 0 \quad \text{on } \ \partial\Omega \times (0, \infty). \end{aligned} \tag{1.3}$$

Here $\alpha \geq 0$ measures the tendency of the species to move upward along the resource gradient.

Cantrell et. al. [3] confirmed the results of Dockery et. al. [8] (with $\alpha = 0$) that the species with the slower diffusion rate has the advantage. They also showed that for convex domains, if α is small (but not too small with respect to the difference of μ and ν), the faster diffuser can be the winner.

If $\mu = \nu$ and Ω is convex, Cantrell et. al. [4] further showed that species u is always the winner, i.e., the dispersal strategy with a little biased movement will evolve. As shown in Cantrell et. al. [4], the assumption on the convexity of Ω is necessary. Hence, it is rather interesting to see that the geometry of the habitat can play an important role in the evolution of dispersal strategies.

An important result in Cantrell et. al. [4] is that for large values of α, the system may produce a stable positive steady state, i.e., the two species can coexist for large α. Hence, biased movement of species can provide a new mechanism of coexistence of competing species.

So while a little advection is advantageous, too much advection opens an opportunity for the second species to coexist with the first. Chen and Lou [5] further improved the results for the coexistence of the species for large α and also showed that if m has a unique local maximum, the population of u concentrates around this maximum for large values of α, a phenomenon which leaves other resources for species v to utilize.

1.2 The Mathematical Model

In this paper we want to look at the case where both species disperse both by random diffusion and directed movement upward along the resource gradient. While the dispersal rates may vary, we assume the species are identical in every other way. The respective diffusion rates for the species are given by $\mu, \nu > 0$, and the rates of advection by $\alpha, \beta \geq 0$. We assume that the intrinsic growth rate $m(x)$ varies in space but is constant in time. Adding in no flux conditions on the boundary we obtain the system

$$
\begin{aligned}
&u_t = \nabla \cdot [\mu \nabla u - \alpha u \nabla m] + u(m - u - v) \quad \text{in} \;\; \Omega \times (0, \infty), \\
&v_t = \nabla \cdot [\nu \nabla v - \beta v \nabla m] + v(m - u - v) \quad \text{in} \;\; \Omega \times (0, \infty), \\
&[\mu \nabla u - \alpha u \nabla m] \cdot n = [\nu \nabla v - \beta v \nabla m] \cdot n = 0 \quad \text{on} \;\; \partial\Omega \times (0, \infty).
\end{aligned}
\tag{1.4}
$$

Throughout this paper we will always assume that m is twice continuously differentiable, non-constant, and that $\int_\Omega m > 0$. The first assumption is reasonable to the biological context and needed for the approach used, the second simply says that there really is spatial diversity, and the last as we will see is sufficient for the existence of two semi-trivial equilibria of the system.

Our focus is on understanding the global dynamics of this system. As a major part of this, we will study the existence and stability of non-negative and non-trivial steady states of this model, that is, solutions (u, v) of

$$
\begin{aligned}
&\nabla \cdot [\mu \nabla u - \alpha u \nabla m] + u(m - u - v) = 0 \quad \text{in} \;\; \Omega, \\
&\nabla \cdot [\nu \nabla v - \beta v \nabla m] + v(m - u - v) = 0 \quad \text{in} \;\; \Omega, \\
&[\mu \nabla u - \alpha u \nabla m] \cdot n = [\nu \nabla v - \beta v \nabla m] \cdot n = 0 \quad \text{on} \;\; \partial\Omega.
\end{aligned}
\tag{1.5}
$$

But to understand the two species system, we first need a little information about the single species system. For one species with advection and diffusion and with no flux across the boundary, we have the equations

$$\begin{aligned} &\nabla \cdot [\mu \nabla \theta - \alpha \theta \nabla m] + \theta(m - \theta) = 0 \quad \text{in } \Omega, \\ &[\mu \nabla \theta - \alpha \theta \nabla m] \cdot n = 0 \quad \text{on } \partial\Omega. \end{aligned} \tag{1.6}$$

If the trivial solution $\theta \equiv 0$ is unstable, then there is a unique positive solution $\theta = \theta(x; \alpha, \mu)$ of (1.6) which is globally attracting among all positive initial data [3]. Thus if $\theta \equiv 0$ is unstable in the single species system (1.6), then the two species system (1.5) has two semi-trivial equilibria, denoted by $(\theta(x; \alpha, \mu), 0)$ and $(0, \theta(x; \beta, \nu))$. We will see that the stability of $(\theta(x; \alpha, \mu), 0)$ and $(0, \theta(x; \beta, \nu))$ play important roles in the dynamics of the system (1.4).

1.3 Main Results

In this paper we will establish several main results. The first two theorems deal with the case where the species are very similar and the dispersal strategies are not that much different. Biologically, one can envision that a mutation occurs and the question is whether the mutant species, which is not much different from the original species, can successfully establish itself in the habitat or not. Moreover, if invasion occurs, will it coexist with the resident species or will it drive the resident species to extinction?

Theorem 1.3.1. *Suppose* $\mu = \nu$, $\Omega = [0, 1]$, *m is twice continuously differentiable on* $[0, 1]$, $m_x > 0$ *on* $[0, 1]$.

(i) *If* $0 \le \beta < \nu / \max_{\overline{\Omega}} m$, *then there exists* $\delta_1 > 0$ *such that for* $\alpha \in (\beta, \beta + \delta_1)$, $(\theta(x; \alpha, \mu), 0)$ *is globally asymptotically stable.*

(ii) *If* $\beta > \nu / \min_{\overline{\Omega}} m$ *and* $m > 0$ *on* $[0, 1]$, *then there exists* $\delta_2 > 0$ *such that for* $\alpha \in (\beta, \beta + \delta_2)$, $(0, \theta(x; \beta, \nu))$ *is globally asymptotically stable.*

The first part of this theorem extends the results of Cantrell et. al. [3]. When the advection rates are small, the species with the stronger advection rate has the advantage. But the second part tells us that when the advection rates are large, the species with the weaker advection has the advantage and can even drive the other to extinction. Therefore, evolution is against both small and large advection rates, and some intermediate advection rate may give the optimal strategy.

Theorem 1.3.2. *Suppose* $\alpha = \beta$, $\Omega = [0, 1]$, *m is twice continuously differentiable on* $[0, 1]$, $m_x > 0$ *on* $[0, 1]$.

(i) *If* $0 \le \alpha < \mu / \max_{\overline{\Omega}} m$, *then there exists* $\delta_3 > 0$ *such that for* $\nu \in (\mu, \mu + \delta_3)$, $(\theta(x; \alpha, \mu), 0)$ *is globally asymptotically stable.*

(ii) *If* $\alpha > \max(\mu / \min_{\overline{\Omega}} m, \max_{\overline{\Omega}} m / \min_{\overline{\Omega}} m_x)$ *and* $m > 0$ *on* $[0, 1]$, *then there exists* $\delta_4 > 0$ *such that for* $\nu \in (\mu, \mu + \delta_4)$, $(0, \theta(x; \beta, \nu))$ *is globally asymptotically stable.*

In the first part of this theorem, we see that for small advection rates, the slower diffuser still has the advantage, the same as in the diffusion only system. But we again see a reversal for the large advection case, where the slower diffuser no longer has the advantage and in fact is always the loser in the competition. Therefore, the direction of the evolution of diffusion rates depends crucially on the magnitude of the advection rates.

The theorems above present some surprising results for two similar species with large advection. The following theorems continue to explore the effects of large advection. However, here we shall only assume that the first species has a large advection rate relative to its rate of diffusion, we no longer assume that the second species has a similar dispersal strategy.

Theorem 1.3.3. *Suppose that* $\int_\Omega m(x) > 0$ *and that the set of critical points of* m *has Lebesgue measure zero. Then there exists a positive constant* $\Lambda_1 = \Lambda_1(\mu, \nu, m, \Omega)$, *independent of* β, *such that if* $\alpha \geq \Lambda_1$ *and* $\beta/\nu \leq 1/\max_{\overline{\Omega}} m$, *the following hold:*

(i) *Both semi-trivial states* $(\theta(x; \alpha, \mu), 0)$ *and* $(0, \theta(x; \beta, \nu))$ *are unstable.*

(ii) *The system* (1.4) *has at least one stable positive steady state.*

(iii) *For any positive steady state* (U, V) *of* (1.4), $\|U\|_{L^2(\Omega)} \to 0$ *as* $\alpha \to \infty$. *If we further assume that the function* m *has at least one isolated global maximum, then there exists some positive constant* δ_0 *such that* $\max_{\overline{\Omega}} U \geq \delta_0$ *for all* $\alpha \geq \Lambda_1$.

This theorem for β/ν small extends the results of Cantrell et al [4] and Chen and Lou [5] for the case $\beta = 0$. Next we turn to the case where β/ν is sufficiently larger. But first we need an additional assumption on the function m.

(A1) The function $m(x)$ satisfies $\partial_n m < 0$ on $\partial\Omega$, m has only one critical point in $\overline{\Omega}$, denoted by x_0, and x_0 satisfies $x_0 \in \Omega$ with $D^2 m(x_0) < 0$.

$D^2 m(x_0)$ denotes the Hessian matrix of the function $m(x)$ at the point $x = x_0$, and

$D^2m(x_0) < 0$ means that the matrix is negative definite. What this means in the biological context is that there is a unique maximum for the habitability function that is located inside the habitat.

Theorem 1.3.4. *Suppose that* $m > 0$ *in* $\overline{\Omega}$ *and assumption* **(A1)** *holds. There exists an increasing function* $\Lambda_2(\cdot)$ *defined on* $[\nu/\min_{\overline{\Omega}} m, \infty)$ *such that if* $\alpha \geq \Lambda_2(\beta)$ *and* $\beta/\nu \geq 1/\min_{\overline{\Omega}} m$*, then the steady state* $(0, \theta(x; \beta, \nu))$ *is globally asymptotically stable.*

So we see that for small values of β, large advection gives room for the second species to coexist with the first. But if β is large enough, the second species can even drive the first species (which has a much larger advection rate) to extinction. So while some advection is good, too much advection can be harmful. This again suggests that there might be some intermediate advection rate that is most beneficial.

The rest of the paper is organized as follows. In Chapter 2 we will discuss some background results: define a strongly monotone system, introduce the single species equation and establish some estimates on the solution, and lastly establish an important result on a 1-dimensional domain. In Chapter 3 we will address the local stability of the semi-trivial steady states. In Chapter 4 we will turn our attention to the existence and non-existence of positive steady states. Chapter 5 will combine the previous results and discuss the global dynamics of the system. In Chapter 6 we conclude with a discussion of the results established and some open problems.

CHAPTER 2

PRELIMINARY RESULTS

In this chapter we will cover some preliminary ideas and some technical results that we will use later in establishing the main results of this thesis.

2.1 Monotone Dynamical Systems

First we want to show that (1.4) is a strongly monotone system and outline the results that gives us.

Definition 2.1.1. *We say that* (1.4) *is a strongly monotone system if*

(1) $u_1(x,0) \geq u_2(x,0)$ *and* $v_1(x,0) \leq v_2(x,0)$ *for all* $x \in \Omega$*, and*

(2) $(u_1(x,0), v_1(x,0)) \not\equiv (u_2(x,0), v_2(x,0))$*,*

then $u_1(x,t) > u_2(x,t)$ *and* $v_1(x,t) < v_2(x,t)$ *for all* $x \in \overline{\Omega}$ *and for all* $t > 0$*.*

Theorem 2.1.2. *The system* (1.4) *is a strongly monotone system.*

Proof. We introduce the functions $w := e^{-(\alpha/\mu)m}u$, and $z := e^{-(\beta/\nu)m}v$. Then (w, z) satisfy

$$w_t = \mu\Delta w + \alpha\nabla w\nabla m + w(m - e^{(\alpha/\mu)m}w - e^{(\beta/\nu)m}z) \quad \text{in} \quad \Omega \times (0, \infty),$$
$$z_t = \nu\Delta z + \beta\nabla z\nabla m + z(m - e^{(\alpha/\mu)m}w - e^{(\beta/\nu)m}z) \quad \text{in} \quad \Omega \times (0, \infty), \tag{2.1}$$

with classical Neumann boundary conditions

$$\frac{\partial w}{\partial n} = \frac{\partial z}{\partial n} = 0 \quad \text{on} \quad \partial\Omega \times (0, \infty). \tag{2.2}$$

We will show that with the partial ordering

$$(w_1, z_1) \geq (w_2, z_2) \Leftrightarrow w_1 \geq w_2 \text{ and } z_1 \leq z_2, \tag{2.3}$$

if $(w_1(x, 0), z_1(x, 0)) \geq (w_2(x, 0), z_2(x, 0))$ then $(w_1(x, t), z_1(x, t)) \geq (w_2(x, t), z_2(x, t))$ for all $t > 0$. Further, if we assume that $(u_1(x, 0), v_1(x, 0)) \not\equiv (u_2(x, 0), v_2(x, 0))$, which gives us that $(w_1(x, 0), z_1(x, 0)) \not\equiv (w_2(x, 0), z_2(x, 0))$, the inequality is strict. We introduce $W := w_2 - w_1$ and $Z := z_1 - z_2$, and define

$$f(x, w, z) = w(m - e^{(\alpha/\mu)m}w - e^{(\beta/\nu)m}z),$$
$$g(x, w, z) = z(m - e^{(\alpha/\mu)m}w - e^{(\beta/\nu)m}z). \tag{2.4}$$

Then (W, Z) satisfy

$$W_t = \mu \Delta W + \alpha \nabla W \nabla m + f(x, w_2, z_2) - f(x, w_1, z_1) \quad \text{in} \;\; \Omega \times (0, \infty),$$

$$Z_t = \nu \Delta Z + \beta \nabla Z \nabla m + g(x, w_1, z_1) - g(x, w_2, z_2) \quad \text{in} \;\; \Omega \times (0, \infty), \tag{2.5}$$

$$\partial W / \partial n = \partial Z / \partial n = 0 \quad \text{on} \;\; \partial\Omega \times (0, \infty).$$

We rewrite

$$\begin{aligned} f(x, w_2, z_2) - f(x, w_1, z_1) &= f(x, w_2, z_2) - f(x, w_1, z_2) + f(x, w_1, z_2) - f(x, w_1, z_1) \\ &= f_w(x, w^*, z_2)W - f_z(x, w_1, z^*)Z \end{aligned}$$

$$\begin{aligned} g(x, w_1, z_1) - g(x, w_2, z_2) &= g(x, w_1, z_1) - g(x, w_1, z_2) + g(x, w_1, z_2) - g(x, w_2, z_2) \\ &= g_z(x, w_1, z^{**})Z - g_w(x, w^{**}, z_2)W \end{aligned} \tag{2.6}$$

for some $w^*, w^{**} \in (w_2, w_1)$ and some $z^*, z^{**} \in (z_1, z_2)$.

This gives us a weakly coupled parabolic system (see Protter and Weinberger, Ch. 3 [16])

$$W_t = \mu \Delta W + \alpha \nabla W \nabla m + f_w(x, w^*, z_2)W - f_z(x, w_1, z^*)Z \quad \text{in} \;\; \Omega \times (0, \infty),$$

$$Z_t = \nu \Delta z + \beta \nabla z \nabla m + g_z(x, w_1, z^{**})Z - g_w(x, w^{**}, z_2)W \quad \text{in} \;\; \Omega \times (0, \infty),$$

$$\partial W / \partial n = \partial Z / \partial n = 0 \quad \text{on} \;\; \partial\Omega \times (0, \infty). \tag{2.7}$$

We compute

$$f_z(x, w_1, z^*) = -w_1 e^{(\beta/\nu)m} < 0$$
$$g_w(x, w^{**}, z_2) = -z_2 e^{(\alpha/\mu)m} < 0, \tag{2.8}$$

so by Theorem 13 [16], both W and Z are negative in $\Omega \times (0, \infty)$ or identically 0 everywhere. Since we assumed $(w_1(x, 0), z_1(x, 0)) \not\equiv (w_2(x, 0), z_2(x, 0))$, it must be the former.

In addition, by Theorem 14 [16], if either W or Z are 0 on $\partial\Omega \times (0, \infty)$, then the outward normal derivative must be positive at that point. But since we have Neumann boundary conditions for both, this also cannot happen.

So we can conclude that $(w_1(x, t), z_1(x, t)) > (w_2(x, t), z_2(x, t))$ for all $x \in \overline{\Omega}$ and for all $t > 0$, that is, (2.1)-(2.2) is a strongly monotone system. Since the system (2.1)-(2.2) is equivalent to (1.4), (1.4) is also a strongly monotone system. □

Since (1.4) is a strongly monotone system, we have the following results (see, e.g., [10]):

1. If both semi-trivial steady states are unstable, then there is at least one stable positive steady state.

2. If the system has no positive equilibria, then one of the semi-trivial equilibria is unstable and the other is a global attractor.

2.2 Single-Species Equation

Next we look at the single-species equation

$$\nabla \cdot [\mu \nabla \theta - \alpha \theta \nabla m] + \theta(m - \theta) = 0 \quad \text{in } \Omega,$$
$$[\mu \nabla \theta - \alpha \theta \nabla m] \cdot n = 0 \quad \text{on } \partial\Omega. \tag{2.9}$$

In this section we want to establish conditions for the existence of a unique positive solution θ $(= \theta(x; \alpha, \mu))$ to the single-species equation. We begin by introducing $w = e^{-(\alpha/\mu)m}\theta$. Then w satisfies

$$\mu \Delta w + \alpha \nabla w \nabla m + w[m - e^{(\alpha/\mu)m} w] = 0 \quad \text{in } \Omega,$$
$$\partial w / \partial n = 0 \quad \text{on } \partial\Omega. \tag{2.10}$$

We consider the eigenvalue problem

$$\mu \Delta \varphi + \alpha \nabla \varphi \nabla m + \varphi m = \lambda \varphi \quad \text{in } \Omega,$$
$$\partial \varphi / \partial n = 0 \quad \text{on } \partial\Omega. \tag{2.11}$$

Lemma 2.2.1. *If $\int_\Omega m > 0$, then the principal eigenvalue λ_1 of* (2.11) *is negative for any $\mu > 0$, $\alpha \geq 0$.*

Proof. We choose the principal eigenfunction $\varphi > 0$. We multiply (2.11) by $e^{(\alpha/\mu)m}$, divide by φ and integrate over Ω to obtain

$$\int_\Omega \frac{\mu \nabla \cdot [e^{(\alpha/\mu)m} \nabla \varphi]}{\varphi} + \int_\Omega m e^{(\alpha/\mu)m} = -\lambda_1 \int_\Omega e^{(\alpha/\mu)m}. \tag{2.12}$$

We want to show that the LHS of (2.12) is positive. This will establish our result. We first show that $\int_\Omega me^{(\alpha/\mu)m} > 0$. We define

$$f(\alpha) = \int_\Omega me^{(\alpha/\mu)m} \tag{2.13}$$

Then $f(0) = \int_\Omega m > 0$ by our assumption. And we have

$$f'(\alpha) = \frac{1}{\mu}\int_\Omega m^2 e^{(\alpha/\mu)m} \geq 0 \tag{2.14}$$

Thus $\int_\Omega me^{(\alpha/\mu)m} > 0$ for all $\alpha \geq 0$.

Next we show that the first integral is nonnegative. Using the divergence theorem and the boundary conditions on φ, we have

$$\int_\Omega \frac{\mu\nabla\cdot[e^{(\alpha/\mu)m}\nabla\varphi]}{\varphi} = \int_\Omega \frac{\mu e^{(\alpha/\mu)m}|\nabla\varphi|^2}{\varphi^2} \geq 0 \tag{2.15}$$

This establishes the lemma. □

Theorem 2.2.2. *If $\int_\Omega m > 0$, then for any $\mu > 0,\ \alpha \geq 0$, (2.9) has a unique positive solution $\theta = \theta(x; \alpha, \mu)$.*

Proof. First we establish the existence of a positive solution. As above we define $w = e^{-(\alpha/\mu)m}\theta$. Then w satisfies

$$\begin{aligned} &\mu\Delta w + \alpha\nabla w\nabla m + w[m - e^{(\alpha/\mu)m}w] = 0 \quad \text{in } \Omega, \\ &\partial w/\partial n = 0 \quad \text{on } \partial\Omega. \end{aligned} \tag{2.16}$$

Then $\overline{w}$ is a supersolution to (2.16) for any constant $\overline{w} \geq max_{\overline{\Omega}}[me^{(-\alpha/\mu)m}]$. Next we find a subsolution $\underline{w} = \epsilon\varphi$ where φ is the principal eigenfunction of (2.11). We also normalize φ so that $\|\varphi\|_\infty = 1$. To be a subsolution of (2.16), $\epsilon\varphi$ must satisfy

$$\mu\Delta(\epsilon\varphi) + \alpha\nabla(\epsilon\varphi)\nabla m + \epsilon\varphi[m - e^{(\alpha/\mu)m}\epsilon\varphi] \geq 0 \tag{2.17}$$

Dividing the RHS of (2.17) by ϵ and using (2.11), we get

$$\begin{aligned} -\lambda_1\varphi + \varphi(-\epsilon\varphi e^{(\alpha/\mu)m}) &= \varphi(-\lambda_1 - \epsilon\varphi e^{(\alpha/\mu)m}) \\ &\geq \varphi(-\lambda_1 - \epsilon e^{(\alpha/\mu)m}) \\ &\geq \varphi(-\lambda_1 - \epsilon \max_{\overline{\Omega}} e^{(\alpha/\mu)m}) \end{aligned} \tag{2.18}$$

Thus if we choose $0 < \epsilon \leq -\lambda_1/(max_{\overline{\Omega}} e^{(\alpha/\mu)m})$, then $\epsilon\varphi$ is a subsolution to (2.16). If necessary, we can choose ϵ smaller or $\overline{w}$ larger to insure that $\underline{w} \leq \overline{w}$. Thus there exists a solution w to (2.16) with $\underline{w} \leq w \leq \overline{w}$, and thus a positive solution $\theta = we^{(\alpha/\mu)m}$ to (2.9).

Next we show that this solution is unique. Assume there are two solutions $\theta_1, \theta_2 > 0$ to (2.9) with $\theta_1 \not\equiv \theta_2$. Then there exist positive solutions $w_1 \not\equiv w_2$ to (2.16) given by $w_i = e^{-(\alpha/\mu)m}\theta_i$.

From above, we can choose $\epsilon \ll 1$ and $\overline{w} \gg 1$ so that we have a subsolution $\underline{w}$ and supersolution $\overline{w}$ with $\epsilon\varphi = \underline{w} \leq w_1, w_2 \leq \overline{w}$ in $\overline{\Omega}$. Thus there exist solutions $w_*(x), w^*(x) > 0$ of (2.16) such that $\underline{w} \leq w_* \leq w_1, w_2 \leq w^* \leq \overline{w}$. That is, w^* and w_* are maximal and minimal solutions, respectively (see, e.g., [15]). So then

$$\mu\nabla \cdot [e^{(\alpha/\mu)m}\nabla w_*] + e^{(\alpha/\mu)m}w_*(m - e^{(\alpha/\mu)m}w_*) = 0 \quad \text{in } \Omega,$$

$$\mu\nabla \cdot [e^{(\alpha/\mu)m}\nabla w^*] + e^{(\alpha/\mu)m}w^*(m - e^{(\alpha/\mu)m}w^*) = 0 \quad \text{in } \Omega, \tag{2.19}$$

$$\partial w_*/\partial n = \partial w^*/\partial n = 0 \quad \text{on } \partial\Omega.$$

Multiplying the first equation in (2.19) by w^* and the second by w_*, then subtracting the first from the second and integrating over Ω, we get

$$\mu \int_\Omega (w_* \nabla \cdot [e^{(\alpha/\mu)m} \nabla w^*] - w^* \nabla \cdot [e^{(\alpha/\mu)m} \nabla w_*]) + \int_\Omega e^{2(\alpha/\mu)m} w_* w^* (w_* - w^*) = 0 \quad (2.20)$$

Using the divergence theorem with the boundary conditions for $w_*(x)$ and $w^*(x)$ on the first integral above, we see that

$$\begin{aligned} &\int_\Omega (w_* \nabla \cdot [e^{(\alpha/\mu)m} \nabla w^*] - w^* \nabla \cdot [e^{(\alpha/\mu)m} \nabla w_*]) \\ &= \int_\Omega \nabla w^* \cdot [e^{(\alpha/\mu)m} \nabla w_*] - \int_\Omega \nabla w_* \cdot [e^{(\alpha/\mu)m} \nabla w^*] = 0 \end{aligned} \quad (2.21)$$

Thus we have simply

$$\int_\Omega e^{2(\alpha/\mu)m} w_* w^* (w_* - w^*) = 0 \quad (2.22)$$

Since $w_* \leq w^*$, this implies that $w_* = w^*$. But this contradicts $w_1 \not\equiv w_2$. This establishes the uniqueness of the positive solution for (2.16), and thus for (2.9). $\square$

2.3 Estimates on Single-Species Solution

We continue by establishing some bounds on the positive solution θ to (2.9).

Lemma 2.3.1. *If m is a non-constant function, then*

$$\min_{\overline{\Omega}} \left(m e^{-(\alpha/\mu)m} \right) < e^{-(\alpha/\mu)m(x)} \theta(x) < \max_{\overline{\Omega}} \left(m e^{-(\alpha/\mu)m} \right) \quad (2.23)$$

for every $x \in \overline{\Omega}$.

Proof. Let $w = e^{-(\alpha/\mu)m} \theta(x)$. We see that w satisfies

$$\begin{aligned} &\mu \nabla \cdot [e^{(\alpha/\mu)m} \nabla w] + e^{(\alpha/\mu)m} w \left[m - e^{(\alpha/\mu)m} w \right] = 0 \quad \text{in } \Omega, \\ &\partial w / \partial n = 0 \quad \text{on } \partial\Omega. \end{aligned} \quad (2.24)$$

Or, equivalently, multiplying the above by $e^{-(\alpha/\mu)m}$,

$$\begin{aligned} &\mu\Delta w + \alpha\nabla m \cdot \nabla w + w\left[m - e^{(\alpha/\mu)m}w\right] = 0 \quad \text{in } \Omega, \\ &\partial w/\partial n = 0 \quad \text{on } \partial\Omega. \end{aligned} \tag{2.25}$$

Let $x_0 \in \overline{\Omega}$ be a point such that $w(x_0) = \max_{\overline{\Omega}} w$. By the Hopf Boundary Lemma [16], for both cases $x_0 \in \Omega$ and $x_0 \in \partial\Omega$, we have $\nabla w(x_0) = 0$, and $\Delta w(x_0) \leq 0$. Hence, by (2.25) we get

$$\max_{\overline{\Omega}} w = w(x_0) \leq m(x_0)e^{-(\alpha/\mu)m(x_0)} \leq \max_{\overline{\Omega}} \left(me^{-(\alpha/\mu)m}\right). \tag{2.26}$$

Next we show that the second inequality in (2.23) is strict. Let $M_1 = \max_{\overline{\Omega}} \left(me^{-(\alpha/\mu)m}\right)$ and set $w_1(x) = M_1 - w(x)$. Then w_1 satisfies

$$-\mu\Delta w_1 - \alpha\nabla w_1 \cdot \nabla m + e^{(\alpha/\mu)m}(M_1 - w_1)\left[me^{-(\alpha/\mu)m} - M_1 + w_1\right] = 0 \quad \text{in } \Omega. \tag{2.27}$$

Multiplying this out and using the definition of M_1, we get

$$\begin{aligned} &-\mu\Delta w_1 - \alpha\nabla w_1 \cdot \nabla m + e^{(\alpha/\mu)m}w_1(2M_1 - me^{-(\alpha/\mu)m} - w_1) \\ &= e^{(\alpha/\mu)m}M_1\left[M_1 - me^{-(\alpha/\mu)m}\right] \geq 0, \end{aligned} \tag{2.28}$$

where the last inequality is not identically zero since m is a non-constant function. Recall that $\partial w_1/\partial n = 0$ on $\partial\Omega$, and by (2.26), $w_1 \geq 0$ in $\overline{\Omega}$. By the Strong Maximum Principle [16], we have $w_1 > 0$ in $\overline{\Omega}$. This establishes the second inequality in (2.23). For the first inequality, the proof is trivial if m is non-positive somewhere in $\overline{\Omega}$, hence it suffices to consider the case when $m > 0$ in $\overline{\Omega}$. Since the proof is almost identical to that of the second inequality, we omit it. □

Next we define

$$m^* = \max_{\overline{\Omega}} m.$$

Lemma 2.3.2. *Suppose that m is a non-constant function.*

(i) *If $\alpha/\mu \leq 1/\max_{\overline{\Omega}} m$, then*

$$\theta(x) < m^* e^{(\alpha/\mu)[m(x)-m^*]} \tag{2.29}$$

for every $x \in \overline{\Omega}$.

(ii) *If $m > 0$ in $\overline{\Omega}$ and $\alpha/\mu \geq 1/\min_{\overline{\Omega}} m$, then*

$$\theta(x) > m^* e^{(\alpha/\mu)[m(x)-m^*]} \tag{2.30}$$

for every $x \in \overline{\Omega}$.

Proof. By Lemma 2.3.1, we have

$$e^{-(\alpha/\mu)m(x)}\theta(x) < \max_{\overline{\Omega}} \left(me^{-(\alpha/\mu)m}\right) \tag{2.31}$$

for every $x \in \overline{\Omega}$. Since

$$\left(ye^{-(\alpha/\mu)y}\right)' = e^{-(\alpha/\mu)y}(1-(\alpha/\mu)y),$$

we see that $ye^{-(\alpha/\mu)y}$ is strictly increasing when $y < \mu/\alpha$. Hence, if $\alpha/\mu < 1/m^*$,

$$\max_{\overline{\Omega}} \left(me^{-(\alpha/\mu)m}\right) \leq m^* e^{-(\alpha/\mu)m^*}. \tag{2.32}$$

Combining this with (2.31) and multiplying by $e^{(\alpha/\mu)m}$, we get

$$\theta(x) < m^* e^{(\alpha/\mu)[m(x)-m^*]}, \tag{2.33}$$

establishing part (i).

For the proof of part (ii), we note that $\big(ye^{-(\alpha/\mu)y}\big)' < 0$ for $y > \mu/\alpha$. Thus if $m > 0$ in $\overline{\Omega}$ and $\alpha/\mu > 1/\min_{\overline{\Omega}} m$, then

$$m(x)e^{-(\alpha/\mu)m(x)} \geq m^* e^{-(\alpha/\mu)m^*} \tag{2.34}$$

for every $x \in \overline{\Omega}$. So again using Lemma 2.3.1 and multiplying by $e^{(\alpha/\mu)m}$, we get the desired result. □

By assumption **(A1)**, there exist positive constants κ_0, κ_1, and κ_2 such that

$$|\nabla m(x)| \geq \kappa_0 |x - x_0|, \qquad \kappa_2 |x - x_0|^2 \geq m^* - m(x) \geq \kappa_1 |x - x_0|^2 \qquad \forall\, x \in \overline{\Omega}. \tag{2.35}$$

These properties, together with $\partial m < 0$ on $\partial\Omega$ enables us to prove the following.

Lemma 2.3.3. *Suppose that assumption* **(A1)** *holds. There exists a positive constant* K*, independent of* α*, such that*

$$\theta(x; \alpha, \mu) \leq K e^{(\alpha/\mu)[m(x) - m^*]} \qquad \forall\, x \in \overline{\Omega}. \tag{2.36}$$

Proof. We define $w = e^{-(\alpha/\mu - 1)m}\theta$. Then w satisfies

$$\mu \Delta w + (\alpha - 2\mu)\nabla m \cdot \nabla w - \big[(\alpha - \mu)|\nabla m|^2 + \mu \Delta m + \theta - m\big] w = 0 \quad \text{in } \Omega,$$

$$[\nabla w - w \nabla m] \cdot n = 0 \quad \text{on } \partial\Omega. \tag{2.37}$$

Let $z^* = z^*(\alpha, \mu) \in \overline{\Omega}$ be a point such that $w(z^*) = \max_{\overline{\Omega}} w$. Since $\partial w/\partial n = w\ \partial m/\partial n < 0$ on $\partial\Omega$, we see that $z^* \in \Omega$. Hence, $\nabla w(z^*) = \mathbf{0}$ and $\Delta w(z^*) \leq 0$. It then follows that

$$(\alpha - \mu)|\nabla m(z^*)|^2 + \mu \Delta m(z^*) + \theta(z^*) \leq m(z^*). \tag{2.38}$$

Hence,

$$(\alpha-\mu)|\nabla m(z^*)|^2 \le m^* - \mu\Delta m(z^*) \le \mu\|m\|_{C^2(\overline{\Omega})} \tag{2.39}$$

and

$$\theta(z^*) \le m(z^*) - \mu\Delta m(z^*) \le \mu\|m\|_{C^2(\overline{\Omega})}. \tag{2.40}$$

It follows from (2.35) and (2.38) that

$$(\alpha-\mu)[m^* - m(z^*)] \le \frac{\kappa_2(\alpha-\mu)}{\kappa_0^2}|\nabla m(z^*)|^2 \le \frac{\kappa_2\mu\|m\|_{C^2(\overline{\Omega})}}{\kappa_0^2}.$$

Since $w(x) \le w(z^*)$, we have

$$\begin{aligned} e^{-\alpha[m(x)-m^*]}\theta(x) &\le e^{-\alpha[m(x)-m^*]}\theta(z^*)e^{(\alpha-\mu)[m(x)-m(z^*)]} \\ &= \theta(z^*)e^{[m^*-m(x)]+(\alpha-\mu)[m^*-m(z^*)]} \\ &\le \|m\|_{C^2(\overline{\Omega})}e^{2\|m\|_\infty+(\kappa_2\mu/\kappa_0^2)\|m\|_{C^2(\overline{\Omega})}} =: K \quad \forall\, x \in \overline{\Omega}. \end{aligned}$$

This implies (2.36). □

Next we consider the following eigenvalue problem:

$$\begin{aligned} &-\Delta\varphi - \alpha\nabla m\cdot\nabla\varphi + c\,\varphi = \lambda(\alpha)\varphi \qquad \text{in} \ \ \Omega, \\ &\partial_n\varphi = 0 \quad \text{on} \ \ \partial\Omega, \quad \varphi > 0 \quad \text{on} \ \overline{\Omega}, \end{aligned} \tag{2.41}$$

where $m \in C^2(\overline{\Omega})$ and $c \in C(\overline{\Omega})$. The following result was established in Chen and Lou [5]:

Theorem 2.3.4 ([5])**.** *Assume that all critical points of m are non-degenerate. Let $\mathcal{M}$ be the set of points of local maximum of m. Then*

$$\lim_{\alpha\to\infty}\lambda(\alpha) = \min_{x\in\mathcal{M}} c(x).$$

2.4 One-Dimension Result

Finally in this chapter we show a result when Ω is a one-dimensional domain.

Let $w \in C^2([0,1])$ with $w > 0$ satisfy

$$\begin{aligned} &\mu(w_{xx} + \gamma m_x w_x) + (me^{-\gamma m} - w)we^{\gamma m} = 0 \quad \text{on } (0,1), \\ &w_x(0) = w_x(1) = 0, \end{aligned} \tag{2.42}$$

where γ and μ are positive constants.

Lemma 2.4.1. *Suppose that $m > 0$ and $m_x > 0$ in $[0,1]$, and $\gamma > 1/\min_{\overline{\Omega}} m$. Then $w(0) < m(0)e^{-\gamma m(0)}$, $w(1) > m(1)e^{-\gamma m(1)}$, and $w_x(x) < 0$ for all $x \in (0,1)$.*

Proof. We first show that $w(0) < m(0)e^{-\gamma m(0)}$. We argue by contradiction: Suppose $w(0) \geq m(0)e^{-\gamma m(0)}$.

We define $h(x) = w(x) - m(x)e^{-\gamma m(x)}$. Thus $h(0) \geq 0$. And we note that $h_x(0) = w_x(0) - m_x(0)e^{-\gamma m(0)}(1 - \gamma m(0)) > 0$, since $m_x > 0$ on [0, 1] and $m(0) > 1/\gamma$.

Thus there exists $\delta > 0$ such that $h(x) > 0$ for $0 < x < \delta$. Then by (2.42) we have $w_{xx} + \gamma m_x w_x > 0$ on $(0, \delta)$. This tells us that $(e^{\gamma m} w_x)_x = e^{\gamma m}(w_{xx} + \gamma m_x w_x) > 0$ on $(0, \delta)$. Thus $e^{\gamma m(x)} w_x(x) > e^{\gamma m(0)} w_x(0) = 0$ for all $x \in (0, \delta)$, so $w_x > 0$ on $(0, \delta)$.

Since $w_x(1) = 0$, let $x^* \in (0, 1]$ be the smallest number such that $w_x(x^*) = 0$. Then $w_x > 0$ on $(0, x^*)$ and $(me^{-\gamma m})_x < 0$ on [0, 1], implying that $h_x > 0$ on $(0, x^*)$, so $h(x^*) > 0$. But $w_x(x^*) = 0$, $w_{xx}(x^*) \leq 0$, contradicting (2.42).

Next we want to show that $w(1) > m(1)e^{-\gamma m(1)}$. Again we argue by contradiction and assume that $w(1) \leq m(1)e^{-\gamma m(1)}$.

We define $h(x) = w(x) - m(x)e^{-\gamma m(x)}$. Then $h(1) \leq 0$, and $h_x(1) = w_x(1) - m_x(1)e^{-\gamma m(1)}(1 - \gamma m(1)) > 0$, thus $h(x) < 0$ for $1 - \delta < x < 1$ for some $\delta > 0$.

By (2.42), $w_{xx} + \gamma m_x w_x < 0$ on $(1 - \delta, 1)$, so $(e^{\gamma m} w_x)_x < 0$ on $(1 - \delta, 1)$. Thus $e^{\gamma m(x)} w_x(x) > e^{\gamma m(1)} w_x(1) = 0$ for all $x \in (1 - \delta, 1)$, so $w_x > 0$ on $(1 - \delta, 1)$.

Since $w_x(0) = 0$, let $\hat{x} \in [0, 1)$ be the largest such that $w_x(\hat{x}) = 0$. Then $w_x > 0$ on $(\hat{x}, 1)$ and $(me^{-\gamma m})_x < 0$ on $[0,\ 1]$, so $h_x > 0$ on $(\hat{x}, 1)$ and $h(\hat{x}) < 0$. But $w_{xx}(\hat{x}) \geq 0$, contradicting (2.42).

Finally, we show that $w_x(x) < 0$ for all $x \in (0,\ 1)$. Since $w(0) < m(0)e^{-\gamma m(0)}$ and $w_x(0) = 0$, from (2.42) we get that $w_{xx}(0) < 0$. Thus $w_x(x) < 0$ for all x in some interval $(0, \delta)$. Now suppose there exists $x \in (0, 1)$ such that $w_x(x) = 0$. Let x^* be the smallest such that $w_x(x^*) = 0$. We consider two different cases.

In case 1, we assume $w(x^*) < m(x^*)e^{-\gamma m(x^*)}$. But this immediately contradicts (2.42) since $w_{xx}(x^*) \geq 0$.

For case 2, assume $w(x^*) \geq m(x^*)e^{-\gamma m(x^*)}$. Since $w_x(x^*) = 0$ and $(me^{-\gamma m})_x \mid_{x=x^*} < 0$, $h(x) = w(x) - m(x)e^{-\gamma m(x)} > 0$ for all $x^* < x < x^* + \delta$. Again we have to consider two cases: whether $h(x)$ remains positive or is somewhere 0 on $(x^*, 1)$.

So suppose $h(x) > 0$ for all $x \in (x^*, 1)$. By (2.42), $w_{xx} + \gamma m_x w_x > 0$ on $(x^*, 1)$, so $(e^{\gamma m} w_x)_x > 0$ on $[x^*, 1]$. But $w_x(x^*) = w_x(1) = 0$, giving us a contradiction.

Finally we assume $h(x) = 0$ for some $x \in (x^*, 1)$. Let $\bar{x}$ be the smallest of these. Then $h(x) > 0$ on $(x^*, \bar{x})$, so $w_{xx} + \gamma m_x w_x > 0$ on $(x^*, \bar{x})$, and thus $(e^{\gamma m} w_x)_x > 0$ on $(x^*, \bar{x})$.

But $h_x(\bar{x}) = w_x(\bar{x}) - m_x(\bar{x})e^{-\gamma m(\bar{x})}(1 - \gamma m(\bar{x})) \leq 0$, giving us $w_x(\bar{x}) < 0$ since

$(me^{-\gamma m})_x$ is always negative. Thus we have $0 = w_x(x^*) < w_x(\bar{x})) < 0$, which is a contradiction.

Thus it must be that $w_x(x) < 0$ for all $x \in (0,\, 1)$. □

Lemma 2.4.2. *Suppose that* $m_x > 0$ *in* $[0,1]$ *and* $\gamma < 1/\max_{\overline{\Omega}} m$*. Then* $w(0) > m(0)e^{-\gamma m(0)}$*,* $w(1) < m(1)e^{-\gamma m(1)}$*, and* $w_x(x) > 0$ *for all* $x \in (0,1)$*.*

Proof. Since $m_x > 0$ in $[0,1]$ and $\gamma < 1/\max_{\overline{\Omega}} m$, we have $(me^{-\gamma m})' = e^{-\gamma m}m'(1 - \gamma m) > 0$ in $[0,1]$. The rest of the proof is almost identical to that of Lemma 2.4.1, so we omit it. □

CHAPTER 3

STABILITY OF SEMI-TRIVIAL STEADY STATES

From Theorem 2.2.2, if $\int_\Omega m > 0$ (an assumption we will make throughout this paper), then we see that the system (1.4) has two semi-trivial steady states, $(\theta(x;\alpha,\mu),0)$ and $(0,\theta(x;\beta,\nu))$ for every $\mu,\nu > 0$, $\alpha,\beta \geq 0$. For simplicity we will often use θ for both $\theta(x;\alpha,\mu)$ and $\theta(x;\beta,\nu)$. In all cases, the context should make it clear which is intended. In this chapter we look at the linearized stability of both semi-trivial steady states. In addition to being necessary for the proof of the main results in this paper, the stability of semi-trivial steady states is also of interest as it is related to the invasion of species when they are rare.

3.1 Eigenvalue Problem

The following fact will be used in the analysis of the stability or instability of the semi-trivial steady states.

Lemma 3.1.1. *The steady state $(\theta(\cdot;\alpha,\mu),0)$ is stable/unstable if and only if the following eigenvalue problem, for $(\lambda_1,\psi)\in\mathbb{R}\times C^2(\overline{\Omega})$, has a positive/negative eigenvalue λ_1:*

$$\begin{aligned}&\nabla\cdot(\nu\nabla\varphi-\beta\varphi\nabla m)+[m-\theta(\cdot;\alpha,\mu)]\varphi=-\lambda_1\varphi \quad \text{in } \Omega,\\ &(\nu\nabla\varphi-\beta\varphi\nabla m)\cdot n=0 \quad \text{on } \partial\Omega, \qquad\qquad \varphi>0 \text{ on } \overline{\Omega}.\end{aligned} \tag{3.1}$$

Proof. The full system for the eigenvalue problem is

$$\begin{aligned}\mathcal{L}_1\varphi &:= -\nabla\cdot(\mu\nabla\varphi-\alpha\varphi\nabla m)-[m-\theta(\cdot;\alpha,\mu)]\varphi=\lambda\varphi \quad \text{in } \Omega,\\ \mathcal{L}_2\psi &:= -\nabla\cdot(\nu\nabla\psi-\beta\psi\nabla m)-[m-2\theta(\cdot;\alpha,\mu)]\psi=\lambda\psi-\theta(\cdot;\alpha,\mu)\varphi \quad \text{in } \Omega\end{aligned}$$

with no-flux boundary conditions.

Suppose the steady state $(\theta(\cdot;\alpha,\mu),0)$ is unstable. Then there is a non-trivial solution (λ,φ,ψ) with $\mathrm{Re}(\lambda)<0$. Consider two cases: (i) $\varphi\not\equiv 0$; (ii) $\varphi\equiv 0$.

In case (i), we conclude that $\mathcal{L}_1$ has an eigenvalue with negative real parts. Hence its principal eigenvalue λ_1 is negative and (3.1) admits a solution.

Case (ii) does not happen since the principle eigenvalue of $\mathcal{L}_2$ is positive. To see this, let (λ,ψ) be an principal eigen pair of $\mathcal{L}_2$. So then $\psi>0$. Multiplying the equation of $\mathcal{L}_2$ by $\theta e^{-\alpha m/\mu}$ and using the equation satisfied by $\theta=\theta(\cdot;\alpha,\mu)$, we can derive

$$\begin{aligned}\lambda\int_\Omega \psi\theta e^{-\alpha m/\mu} &= -\int_\Omega e^{-\alpha m/\mu}\theta\nabla\cdot[e^{\beta m/\nu}\nabla(e^{-\alpha m/\mu}\psi)]+(m-2\theta)\theta\psi e^{-\alpha m/\mu}\\ &= -\int_\Omega e^{-\alpha m/\mu}\psi\nabla\cdot[e^{\alpha m/\mu}\nabla(e^{-\alpha m/\mu}\theta)]+(m-2\theta)\theta\psi e^{-\alpha m/\mu}\\ &= \int_\Omega \theta^2 e^{-\alpha m/\mu}\psi>0.\end{aligned}$$

Hence, the principal eigenvalue of $\mathcal{L}_2$ is positive.

Next, suppose the steady state $(\theta(\cdot;\alpha,\mu),0)$ is stable. Then (3.1) cannot have a solution with $\lambda_1 \le 0$. Indeed, suppose it has a solution with $\lambda_1 \le 0$. Then since the principal eigenvalue of $\mathcal{L}_2$ is positive, there is a unique solution ψ of $(\mathcal{L}_2 - \lambda_1)\psi = -\theta\varphi$. This implies that the full linearized problem has a non-trivial solution (λ,φ,ψ) with $\lambda = \lambda_1 \le 0$. But this contradicts the assumption that the steady state $(\theta(\cdot;\alpha,\mu),0)$ is (linearly) stable. □

Lemma 3.1.2. *The steady state* $(0,\ \theta(\cdot;\beta,\nu))$ *is stable/unstable if and only if the following eigenvalue problem, for* $(\lambda_1,\psi) \in \mathbb{R}\times C^2(\overline{\Omega})$*, has a positive/negative eigenvalue* λ_1*:*

$$\nabla\cdot(\mu\nabla\varphi - \alpha\varphi\nabla m) + [m - \theta(\cdot;\beta,\nu)]\varphi = -\lambda_1\varphi \quad \text{in} \ \ \Omega,$$
$$\mu\nabla\varphi - \alpha\varphi\nabla m)\cdot n = 0 \quad \text{on} \ \ \partial\Omega, \qquad\qquad \varphi > 0 \text{ on } \ \overline{\Omega}. \tag{3.2}$$

Proof. The proof is identical to that of Lemma 3.1.1, and thus is omitted. □

3.2 Stability of $(\theta(x;\alpha,\mu),0)$

By Lemma 3.1.1 above, for the stability of the semi-trivial steady state $(\theta(x;\alpha,\mu),0)$, it suffices to consider the smallest eigenvalue, denoted as λ_1, of the eigenvalue problem

$$\nabla\cdot[\nu\nabla\psi - \beta\psi\nabla m] + [m - \theta(\cdot;\alpha,\mu)]\psi = -\lambda_1\psi \quad \text{in } \Omega,$$
$$(\nu\nabla\psi - \beta\psi\nabla m)\cdot n = 0 \quad \text{on } \partial\Omega. \tag{3.3}$$

3.2.1 Stability of $(\theta(x;\alpha,\mu),0)$ for large α

In this section we will show that for α large enough, $(\theta(x;\alpha,\mu),0)$ is always unstable.

Lemma 3.2.1. *For any $\beta \geq 0$, $\int_\Omega m e^{(\beta/\nu)m} \geq \int_\Omega m$.*

Proof. Define $F(\beta) := \int_\Omega m e^{(\beta/\nu)m}$. Since

$$\frac{dF}{d\beta} = \frac{1}{\nu}\int_\Omega m^2 e^{(\beta/\nu)m} > 0,$$

we see that $F(\beta) \geq F(0) = \int_\Omega m$ for every $\beta \geq 0$. □

The following result was established in [4]:

Lemma 3.2.2. *Suppose that the set of critical points of m has measure zero. Then*

$$\lim_{\alpha\to\infty}\int_\Omega \theta^2(x;\alpha,\mu)\,dx = 0. \tag{3.4}$$

We are now ready to show that for any fixed β, $(\theta,0)$ is unstable for α large enough.

Theorem 3.2.1. *Suppose that $\int_\Omega m > 0$ and the set of critical points of m has measure zero. For any $\eta > 0$, there exists a positive constant $\Lambda_3 = \Lambda_3(\eta)$ such that for every $\beta \in [0,\eta]$ and $\alpha \geq \Lambda_3(\eta)$, $(\theta,0)$ is unstable.*

Proof. Let $\psi > 0$ denote the eigenfunction corresponding to λ_1 uniquely determined by $\max_{\overline{\Omega}}\psi = 1$. We consider the following equivalent form of (3.3):

$$\nu\nabla\cdot[e^{(\beta/\nu)m}\nabla(e^{-(\beta/\nu)m}\psi)] + (m-\theta)\psi = -\lambda_1\psi. \tag{3.5}$$

Dividing (3.5) by $e^{-(\beta/\nu)m}\psi$ and integrating over Ω, we have

$$\int_\Omega \frac{\nu\nabla\cdot[e^{(\beta/\nu)m}\nabla(e^{-(\beta/\nu)m}\psi)]}{e^{-(\beta/\nu)m}\psi} + \int_\Omega (m-\theta)e^{(\beta/\nu)m} = -\lambda_1 \int_\Omega e^{(\beta/\nu)m}. \tag{3.6}$$

Using the divergence theorem and the boundary condition for ψ, we obtain

$$\int_\Omega \frac{\nu\nabla\cdot[e^{(\beta/\nu)m}\nabla(e^{-(\beta/\nu)m}\psi)]}{e^{-(\beta/\nu)m}\psi} = \int_\Omega \frac{\nu e^{(\beta/\nu)m}}{(e^{-(\beta/\nu)m}\psi)^2}\cdot|\nabla(e^{-(\beta/\nu)m}\psi)|^2 \geq 0. \tag{3.7}$$

Hence,

$$\begin{aligned}
-\lambda_1\int_\Omega e^{(\beta/\nu)m} &\geq \int_\Omega (m-\theta)e^{(\beta/\nu)m} = \int_\Omega me^{(\beta/\nu)m} - \int_\Omega \theta e^{(\beta/\nu)m} \\
&\geq \int_\Omega me^{(\beta/\nu)m} - e^{(\beta/\nu)m^*}\int_\Omega \theta \\
&\geq \int_\Omega m - e^{(\eta/\nu)m^*}\int_\Omega \theta \\
&\geq \frac{1}{2}\int_\Omega m
\end{aligned} \tag{3.8}$$

provided that $\alpha \geq \Lambda_3 = \Lambda_3(\eta)$, where the last inequality follows from the fact that $\lim_{\alpha\to\infty}\int_\Omega \theta = 0$. Therefore, $\lambda_1 < 0$ provided that $\alpha \geq \Lambda_3$. □

3.2.2 Stability of $(\theta(x;\alpha,\mu),0)$ for $(\alpha,\mu)\approx(\beta,\nu)$

Finally we consider the stability of $(\theta(x;\alpha,\mu),0)$ for $(\alpha,\mu)\approx(\beta,\nu)$, i.e., when the two species are nearly identical in their dispersal strategies.

For any $\alpha_0 > 0$ and $\mu_0 > 0$, we define $\theta_0 = \theta(x;\alpha_0,\mu_0) > 0$ as the unique positive solution of

$$\begin{aligned}
&\nabla\cdot[\mu_0\nabla\theta_0 - \alpha_0\theta_0\nabla m] + (m-\theta_0)\theta_0 = 0, \\
&[\mu_0\nabla\theta_0 - \alpha_0\theta_0\nabla m]\cdot n = 0.
\end{aligned} \tag{3.9}$$

If (ν, β) is very close to (μ_0, α_0) (i.e. $(\nu, \beta) = (\alpha_0 + \epsilon\beta_1 + O(\epsilon^2), \mu_0 + \epsilon\nu_1 + O(\epsilon^2)))$, then after suitable scaling, $\psi = \theta_0 + \epsilon\psi_1 + O(\epsilon^2)$. By plugging into (3.3), we see that ψ_1 is determined by

$$\nabla \cdot [\mu_0 \nabla \psi_1 + \nu_1 \nabla \theta_0 - \alpha_0 \psi_1 \nabla m - \beta_1 \theta_0 \nabla m] + (m - \theta_0)\psi_1 - u_1\theta_0 = -\lambda_1 \theta_0,$$

$$[\mu_0 \nabla \psi_1 + \nu_1 \nabla \theta_0 - \alpha_0 \psi_1 \nabla m - \beta_1 \theta_0 \nabla m] \cdot n = 0. \tag{3.10}$$

If (μ, α) is also very close to (μ_0, α_0) (i.e. $(\mu, \alpha) = (\alpha_0 + \epsilon\alpha_1 + O(\epsilon^2), \mu_0 + \epsilon\mu_1 + O(\epsilon^2)))$, then $u = \theta_0 + \epsilon u_1 + O(\epsilon^2)$, where u_1 is determined by

$$\nabla \cdot [\mu_0 \nabla u_1 + \mu_1 \nabla \theta_0 - \alpha_0 u_1 \nabla m - \alpha_1 \theta_0 \nabla m] + (m - \theta_0)u_1 - \theta_0 u_1 = 0,$$

$$[\mu_0 \nabla u_1 + \mu_1 \nabla \theta_0 - \alpha_0 u_1 \nabla m - \alpha_1 \theta_0 \nabla m] \cdot n = 0. \tag{3.11}$$

Lemma 3.2.2.

$$-\lambda_1 \int_\Omega e^{-(\alpha_0/\mu_0)m} \theta_0^2 = \int_\Omega \nabla(e^{-(\alpha_0/\mu_0)m}\theta_0) \cdot [(\mu_1 - \nu_1)\nabla\theta_0 + (\beta_1 - \alpha_1)\theta_0 \nabla m]. \tag{3.12}$$

Proof. We begin by multiplying (3.10) by $e^{-(\alpha_0/\mu_0)m}\theta_0$ and integrating over Ω. Using the divergence theorem and the boundary conditions on ψ_1, we get

$$\begin{aligned} &-\int_\Omega \nabla(e^{-(\alpha_0/\mu_0)m}\theta_0) \cdot [\mu_0 \nabla \psi_1 + \nu_1 \nabla \theta_0 - \alpha_0 \psi_1 \nabla m - \beta_1 \theta_0 \nabla m] \\ &\quad + \int_\Omega e^{-(\alpha_0/\mu_0)m} \theta_0 [(m - \theta_0)\psi_1 - u_1 \theta_0] = -\lambda_1 \int_\Omega e^{-(\alpha_0/\mu_0)m} \theta_0^2. \end{aligned} \tag{3.13}$$

Next we multiply (3.11) by $e^{-(\alpha_0/\mu_0)m}\psi_1$ and integrate over Ω. Again using the divergence theorem and the boundary conditions on θ_0, we have

$$-\int_\Omega \nabla(e^{-(\alpha_0/\mu_0)m}\psi_1)\cdot[\mu_0\nabla\theta_0-\alpha_0\theta_0\nabla m]+\int_\Omega e^{-(\alpha_0/\mu_0)m}\psi_1(m-\theta_0)\theta_0=0. \quad (3.14)$$

Evaluating $\nabla(e^{-(\alpha_0/\mu_0)m}\theta_0)$, we see that

$$\begin{aligned}&-\int_\Omega \nabla(e^{-(\alpha_0/\mu_0)m}\theta_0)\cdot[\mu_0\nabla\psi_1-\alpha_0\psi_1\nabla m]\\ &\qquad=-\int_\Omega e^{-(\alpha_0/\mu_0)m}(\mu_0\nabla\theta_0-\alpha_0\theta_0\nabla m)(\nabla\psi_1-\frac{\alpha_0}{\mu_0}\psi_1\nabla m);\end{aligned} \quad (3.15)$$

and similarly,

$$\begin{aligned}&-\int_\Omega \nabla(e^{-(\alpha_0/\mu_0)m}\psi_1)\cdot[\mu_0\nabla\theta_0-\alpha_0\theta_0\nabla m]\\ &\qquad=-\int_\Omega e^{-(\alpha_0/\mu_0)m}(\nabla\psi_1-\frac{\alpha_0}{\mu_0}\psi_1\nabla m)(\mu_0\nabla\theta_0-\alpha_0\theta_0\nabla m).\end{aligned} \quad (3.16)$$

So subtracting (3.14) from (3.13), we are left with

$$\begin{aligned}&-\lambda_1\int_\Omega e^{-(\alpha_0/\mu_0)m}\theta_0^2=\\ &\quad-\int_\Omega \nabla(e^{-(\alpha_0/\mu_0)m}\theta_0)\cdot[\nu_1\nabla\theta_0-\beta_1\theta_0\nabla m]+\int_\Omega e^{-(\alpha_0/\mu_0)m}u_1\theta_0^2.\end{aligned} \quad (3.17)$$

Multiplying (3.11) by $e^{-(\alpha_0/\mu_0)m}\theta_0$ and integrating over Ω we get

$$\begin{aligned}&\int_\Omega e^{-(\alpha_0/\mu_0)m}u_1\theta_0^2\\ &\qquad=-\int_\Omega \nabla(e^{-(\alpha_0/\mu_0)m}\theta_0)\cdot[\mu_0\nabla u_1-\alpha_0u_1\nabla m+\mu_1\nabla\theta_0-\alpha_1\theta_0\nabla m]\\ &\qquad\quad+\int_\Omega e^{-(\alpha_0/\mu_0)m}\theta_0(m-\theta_0)u_1.\end{aligned} \quad (3.18)$$

Multiplying the first equation in (3.9) by $e^{-(\alpha_0/\mu_0)m}u_1$ and integrating over Ω we get

$$-\int_\Omega \nabla(e^{-(\alpha_0/\mu_0)m}u_1)\cdot[\mu_0\nabla\theta_0-\alpha_0\theta_0\nabla m]+\int_\Omega e^{-(\alpha_0/\mu_0)m}u_1(m-\theta_0)\theta_0=0. \quad (3.19)$$

Again we expand $\nabla(e^{-(\alpha_0/\mu_0)m}\theta_0$ to get

$$\begin{aligned}
&-\int_\Omega \nabla(e^{-(\alpha_0/\mu_0)m}\theta_0)\cdot[\mu_0\nabla u_1-\alpha_0 u_1\nabla m] \\
&\qquad = -\int_\Omega e^{-(\alpha_0/\mu_0)m}(\nabla\theta_0-\frac{\alpha_0}{\mu_0}\theta_0\nabla m)(\mu_0\nabla u_1-\alpha_0 u_1\nabla m).
\end{aligned} \tag{3.20}$$

And similarly,

$$\begin{aligned}
&-\int_\Omega \nabla(e^{-(\alpha_0/\mu_0)m}u_1)\cdot[\mu_0\nabla\theta_0-\alpha_0\theta_0\nabla m] \\
&\qquad = -\int_\Omega e^{-(\alpha_0/\mu_0)m}(\mu_0\nabla u_1-\alpha_0 u_1\nabla m)(\nabla\theta_0-\frac{\alpha_0}{\mu_0}\theta_0\nabla m).
\end{aligned} \tag{3.21}$$

Using these results and subtracting (3.19) from (3.18) we obtain

$$\int_\Omega e^{-(\alpha_0/\mu_0)m}u_1\theta_0^2 = -\int_\Omega \nabla(e^{-(\alpha_0/\mu_0)m}\theta_0)\cdot[\mu_1\nabla\theta_0-\alpha_1\theta_0\nabla m]. \tag{3.22}$$

Substituting this result into (3.17) and combining terms, we obtain the desired result,

$$-\lambda_1\int_\Omega e^{-(\alpha_0/\mu_0)m}\theta_0^2 = \int_\Omega \nabla(e^{-(\alpha_0/\mu_0)m}\theta_0)\cdot[(\mu_1-\nu_1)\nabla\theta_0+(\beta_1-\alpha_1)\theta_0\nabla m]. \tag{3.23}$$

□

While we cannot make broad conclusions from this information, there is an identity linking the two parts of the integral on the right. This does give us some insight into the sign of this integral.

Identity 3.2.3.

$$\begin{aligned}
&\nabla(e^{-(\alpha_0/\mu_0)m}\theta_0)\cdot\nabla\theta_0-\tfrac{\alpha_0}{\mu_0}(\nabla(e^{-(\alpha_0/\mu_0)m}\theta_0)\cdot\nabla m)\theta_0 \\
&\qquad = e^{(\alpha_0/\mu_0)m}|\nabla(e^{-(\alpha_0/\mu_0)m}\theta_0)|^2.
\end{aligned} \tag{3.24}$$

It immediately follows from the above identity that

$$\begin{aligned}\int_\Omega \nabla(e^{-(\alpha_0/\mu_0)m}\theta_0)\cdot\nabla\theta_0 - \frac{\alpha_0}{\mu_0}\int_\Omega(\nabla(e^{-(\alpha_0/\mu_0)m}\theta_0)\cdot\nabla m)\theta_0 \\ = \int_\Omega e^{(\alpha_0/\mu_0)m}|\nabla(e^{-(\alpha_0/\mu_0)m}\theta_0)|^2 \geq 0.\end{aligned} \tag{3.25}$$

This tells us that whenever the second integral on the LHS is positive, the first must be also. And if the first integral is negative, the second integral must also be negative.

3.3 Stability of $(0, \theta(x; \beta, \nu))$

In this section we consider the stability of $(0, \theta(x; \beta, \nu))$. We first establish the following preliminary result.

3.3.1 Stability of $(0, \theta(x; \beta, \nu))$ for large α

Lemma 3.3.1. *Suppose that m is a non-constant function and $\int_\Omega m > 0$. There exists a positive constant $\Lambda_5 = \Lambda_5(\mu, \nu, m, \Omega)$ such that if $0 \leq \beta \leq \nu/\max_{\overline{\Omega}} m$ and $\alpha \geq \Lambda_5$, we have*

$$\int_\Omega e^{(\alpha/\mu)m}(m-\theta) > 0.$$

Proof. Define $\Omega_+ = \{x \in \Omega : m(x) \leq \|\theta\|_\infty\}$ and $\Omega_- = \{x \in \Omega : m(x) > \|\theta\|_\infty\}$. Then

$$\int_\Omega e^{(\alpha/\mu)(m-\|\theta\|_\infty)}(m-\theta) = \int_{\Omega_+} e^{(\alpha/\mu)(m-\|\theta\|_\infty)}(m-\theta) + \int_{\Omega_-} e^{(\alpha/\mu)(m-\|\theta\|_\infty)}(m-\theta). \tag{3.26}$$

By part (i) of Lemma 2.3.2, $\|\theta\|_\infty < \|m\|_\infty$ provided that $\beta/\nu \le 1/\max_{\overline{\Omega}} m$. Hence,

$$\left|\int_{\Omega_+} e^{(\alpha/\mu)(m-\|\theta\|_\infty)}(m-\theta)\right| \le \int_{\Omega_+} e^{(\alpha/\mu)(m-\|\theta\|_\infty)}|m-\theta| \le \int_{\Omega_+} |m-\theta| \le 2\|m\|_\infty|\Omega|. \tag{3.27}$$

Set

$$\epsilon = \tfrac{1}{2}\min_{0\le\beta\le\nu/\max_{\overline{\Omega}} m}(\max_{\overline{\Omega}} m - \|\theta\|_\infty).$$

By part (i) of Lemma 2.3.2 and the continuity of $\theta(x;\beta,\nu)$ with respect to β, we have $\epsilon > 0$.

Let x_0 be a point such that $m(x_0) = \max_{\overline{\Omega}} m$. By part (i) of Lemma 2.3.2, $x_0 \in \Omega_-$. Again by the continuity of $\theta(x;\beta,\nu)$ with respect to β, we can choose $\delta > 0$, independent of β, such that for every $\beta \in [0, \nu/\max_{\overline{\Omega}} m]$,

$$m(x) - \|\theta\|_\infty \ge \tfrac{1}{2}(\max_{\overline{\Omega}} m - \|\theta\|_\infty) \ge \epsilon, \qquad \text{if } \ |x-x_0| \le \delta. \tag{3.28}$$

Then

$$\begin{aligned}\int_{\Omega_-} & e^{(\alpha/\mu)(m-\|\theta\|_\infty)}(m-\theta)\\ &\ge \int_{\{x\in\Omega:|x-x_0|\le\delta\}} e^{(\alpha/\mu)(m-\|\theta\|_\infty)}(m-\theta)\\ &\ge \int_{\{x\in\Omega:|x-x_0|\le\delta\}} e^{(\alpha/\mu)\epsilon}\cdot\epsilon\\ &= \epsilon\cdot e^{(\alpha/\mu)\epsilon}|\{x\in\Omega : |x-x_0|\le\delta\}| \to \infty\end{aligned} \tag{3.29}$$

as $\alpha \to \infty$. Therefore,

$$\int_\Omega e^{(\alpha/\mu)(m-\|\theta\|_\infty)}(m-\theta) > 0 \tag{3.30}$$

provided that $\alpha \geq \Lambda_5$, where Λ_5 is some positive constant independent of α and β. Hence,

$$\int_\Omega e^{(\alpha/\mu)m}(m-\theta) > 0 \tag{3.31}$$

for $\alpha \geq \Lambda_5$ and $\beta/\nu \leq 1/\max_{\overline{\Omega}} m$. □

The next two lemmas are the main results of this section.

Lemma 3.3.2. *Suppose that m is a non-constant function and $\int_\Omega m > 0$. If $\alpha \geq \Lambda_5$ and $0 \leq \beta \leq \nu/\max_{\overline{\Omega}} m$, then $(0, \theta(x;\beta,\nu))$ is unstable.*

Proof. We want to show that the principal eigenvalue, denoted by λ_1, for the problem

$$\begin{aligned} &\nabla \cdot [\mu \nabla \varphi - \alpha \varphi \nabla m] + \varphi(m-\theta) = -\lambda \varphi \quad \text{in } \ \Omega, \\ &(\mu \nabla \varphi - \alpha \varphi \nabla m) \cdot n = 0 \quad \text{on } \ \partial\Omega \end{aligned} \tag{3.32}$$

is negative. We choose the corresponding principal eigenfunction $\varphi > 0$ with $\max_{\overline{\Omega}} \varphi = 1$ and set $\psi = e^{-(\alpha/\mu)m}\varphi$. Then $\psi > 0$ satisfies

$$\begin{aligned} &\mu \nabla \cdot [e^{(\alpha/\mu)m} \nabla \psi] + e^{(\alpha/\mu)m}\psi(m-\theta) = -\lambda_1 e^{(\alpha/\mu)m}\psi \quad \text{in } \ \Omega, \\ &\nabla \psi \cdot n = 0 \quad \text{on } \ \partial\Omega. \end{aligned} \tag{3.33}$$

We divide (3.33) by ψ and integrate over Ω to get

$$\mu \int_\Omega \frac{e^{(\alpha/\mu)m}|\nabla \psi|^2}{\psi^2} + \int_\Omega e^{(\alpha/\mu)m}(m-\theta) = -\lambda_1 \int_\Omega e^{(\alpha/\mu)m}.$$

The first integral in the left hand side is clearly non-negative and the integral on the right hand side is positive. By Lemma 3.3.1, the second integral in the left hand side is positive for $\alpha \geq \Lambda_5$ and $0 \leq \beta/\nu \leq 1/\max_{\overline{\Omega}} m$, thus we have $\lambda_1 < 0$. □

In strong contrast to Lemma 3.3.2 for the case when $\beta/\nu \leq 1/\max_{\overline{\Omega}} m$, we have the following result.

Lemma 3.3.3. *Suppose that* (A1) *holds. For any number $\eta > 1/\min_{\overline{\Omega}} m$, there exists some positive constant $\Lambda_6 = \Lambda_6(\mu, \nu, m, \Omega, \eta)$ such that for $\alpha \geq \Lambda_6$ and $\beta/\nu \in [1/\min_{\overline{\Omega}} m, \eta]$, $(0, \theta(x; \beta, \nu))$ is stable.*

Proof. We argue by contradiction. If not, suppose that there exists some $\eta > 1/\min_{\overline{\Omega}} m$, sequences $\{\alpha_i, \beta_i\}_{i=1}^{\infty}$ with $\alpha_i \to \infty$ and $\beta_i/\nu \in [1/\min_{\overline{\Omega}} m, \eta]$ such that the principal eigenvalue, denoted by λ_i, for

$$\begin{aligned} &\nabla \cdot [\mu \nabla \varphi - \alpha_i \varphi \nabla m] + \varphi[m - \theta(\cdot; \beta_i, \nu)] = -\lambda \varphi \quad \text{in} \ \ \Omega, \\ &(\mu \nabla \varphi - \alpha_i \varphi \nabla m) \cdot n = 0 \quad \text{on} \ \ \partial\Omega \end{aligned} \tag{3.34}$$

is non-positive for large i. We choose the corresponding principal eigenfunction $\varphi_i > 0$ and set $\psi_i = e^{-(\alpha_i/\mu)m} \varphi_i$. Then $\psi_i > 0$ satisfies

$$\begin{aligned} &\mu \Delta \psi_i + \alpha_i \nabla \psi_i \cdot \nabla m + \psi_i[m - \theta(\cdot; \beta_i, \nu)] = -\lambda_i \psi_i \quad \text{in} \ \ \Omega, \\ &\nabla \psi_i \cdot n = 0 \quad \text{on} \ \ \partial\Omega. \end{aligned} \tag{3.35}$$

Passing to a subsequence if necessary, we may assume that $\beta_i \to \beta$ for some $\beta/\nu \geq 1/\min_{\overline{\Omega}} m$. By assumption (A1), $\mathcal{M} = \{x_0\}$. From part (ii) of Lemma 2.3.2 (with α, μ being replaced by β, ν, respectively), we have $-m(x_0) + \theta(x_0; \beta, \nu) > 0$. Set

$$\epsilon = \tfrac{1}{2}[-m(x_0) + \theta(x_0; \beta, \nu)] > 0.$$

Let $\lambda_i(\epsilon)$ denote the principal eigenvalue of the eigenvalue problem

$$\mu\Delta\psi + \alpha_i \nabla\psi \cdot \nabla m + \psi[m - \theta(\cdot;\beta,\nu) + \epsilon] = -\lambda\psi \quad \text{in} \;\; \Omega,$$
$$\nabla\psi \cdot n = 0 \quad \text{on} \;\; \partial\Omega. \tag{3.36}$$

Since $\theta(\cdot;\beta_i,\nu) \to \theta(\cdot;\beta,\nu)$ in L^∞, for sufficiently large i we have $\theta(\cdot;\beta_i,\nu) \geq \theta(\cdot;\beta,\nu) - \epsilon$ in $\overline{\Omega}$. By the comparison principle for principal eigenvalues we have $\lambda_i \geq \lambda_i(\epsilon)$ for large i. This together with assumption $\lambda_i \leq 0$ imply that $\lambda_i(\epsilon) \leq 0$ for large i. However, by Theorem 2.3.4 in Chapter 2 we have

$$\lim_{i\to\infty} \lambda_i(\epsilon) = \min_{x\in\mathcal{M}}[-m(x) + \theta(x;\beta,\nu) - \epsilon] = -m(x_0) + \theta(x_0;\beta,\nu) - \epsilon > 0,$$

where the last inequality follows from the definition of ϵ. This contradiction finishes the proof. □

3.3.2 Stability of $(0,\theta(x;\beta,\nu))$ for $(\alpha,\mu) \approx (\beta,\nu)$

As with $(\theta(x;\alpha,\mu),0)$ above, we consider the stability of $(0,\theta(x;\beta,\nu))$ for $(\alpha,\mu) \approx (\beta,\nu)$.

Again if (μ,α) is very close to (μ_0,α_0), then $\varphi = \theta_0 + \epsilon\varphi_1 + O(\epsilon^2)$. From (3.5), φ_1 satisfies

$$\nabla \cdot [\mu_0\nabla\varphi_1 + \mu_1\nabla\theta_0 - \alpha_0\varphi_1\nabla m - \alpha_1\theta_0\nabla m] + (m-\theta_0)\varphi_1 - v_1\theta_0 = -\lambda_1\theta_0,$$
$$[\mu_0\nabla\varphi_1 + \mu_1\nabla\theta_0 - \alpha_0\varphi_1\nabla m - \alpha_1\theta_0\nabla m] \cdot n = 0. \tag{3.37}$$

And if (ν, β) is also very close to (μ_0, α_0), then $v = \theta_0 + \epsilon v_1 + O(\epsilon^2)$, where v_1 is determined by

$$\begin{aligned} &\nabla \cdot [\mu_0 \nabla v_1 + \nu_1 \nabla \theta_0 - \alpha_0 v_1 \nabla m - \beta_1 \theta_0 \nabla m] + (m - \theta_0) v_1 - \theta_0 v_1 = 0, \\ &[\mu_0 \nabla v_1 + \nu_1 \nabla \theta_0 - \alpha_0 v_1 \nabla m - \beta_1 \theta_0 \nabla m] \cdot n = 0. \end{aligned} \tag{3.38}$$

Lemma 3.3.1.

$$-\lambda_1 \int_\Omega e^{-(\alpha_0/\mu_0)m} \theta_0^2 = \int_\Omega \nabla(e^{-(\alpha_0/\mu_0)m} \theta_0) \cdot [(\nu_1 - \mu_1) \nabla \theta_0 + (\alpha_1 - \beta_1) \theta_0 \nabla m]. \tag{3.39}$$

Proof. The proof is symmetrical to that of Lemma 3.2.2 above, and so is omitted.

CHAPTER 4

POSITIVE STEADY STATES

After looking at the local stability of the semi-trivial steady states in the last chapter, in this chapter we turn our attention to positive steady states, particularly the existence or non-existence of positive steady states. This will help us in determining whether we might have coexistence or competitive exclusion.

4.1 Coexistence and Concentration for Large α

Theorem 4.1.1. *Suppose that* $\int_\Omega m > 0$ *and the set of critical points of* m *has measure zero. Then there exists a positive constant* $\Lambda_7 = \Lambda_7(\mu, \nu, m, \Omega)$ *such that if* $\alpha \geq \Lambda_7$ *and* $0 \leq \beta \leq \nu / \max_{\overline{\Omega}} m$*, then the system* (1.4) *has at least one stable positive steady state.*

Proof. From Lemmas 3.2.1 and 3.3.2, we have that the two semi-trivial equilibria are unstable. This fact along with monotone system theory guarantees the existence of at least one stable positive steady state [14, 11, 7]. □

Next we show that as $\alpha \to \infty$, the population of u concentrates in isolated locations. Let (U, V) denote any positive steady state of (1.4). By the comparison principle, we have $U(x) \leq \theta(x;\alpha,\mu)$. Hence it follows that $\|U\|_{L^2(\Omega)} \to 0$ as $\alpha \to \infty$ by Lemma 3.2.2. But we will show that $\|U\|_{L^\infty(\Omega)}$ is uniformly bounded away from 0 for large α.

Lemma 4.1.1. *Suppose $\int_\Omega m > 0$ and m has an isolated global maximum. Then there exists $\delta_0 > 0$ independent of α such that for sufficiently large α, $\lambda_1 \leq -\delta_0$.*

Proof. By the variational characterization of principal eigenvalues,

$$\lambda_1 = \inf_{\psi\neq 0,\ \psi\in C^1(\overline{\Omega})} \frac{\mu\int_\Omega e^{(\alpha/\mu)m}|\nabla\psi|^2 - \int_\Omega (m-\theta)e^{(\alpha/\mu)m}\psi^2}{\int_\Omega e^{(\alpha/\mu)m}\psi^2} \tag{4.1}$$

(Note: Here and in the remainder of this section, $\theta = \theta(x;\beta,\nu)$).

Since m has an isolated global maximum at x_0, by Lemma 2.3.2 we can choose $R_1 > 0$ and $\delta > 0$ such that $m(x) - \theta(x) \geq \delta$ for all $x \in B_{R_1}(x_0)$. Further we can choose R_2 with $R_2 \leq R_1/2$ such that

$$\min_{B_{R_2}(x_0)} m > \max_{B_{R_1}(x_0)\setminus B_{R_1/2}(x_0)} m. \tag{4.2}$$

For simplicity, let $M_1 = \max_{B_{R_1}(x_0)\setminus B_{R_1/2}(x_0)} m$, $M_2 = \min_{B_{R_2}(x_0)} m$, and $B_R(x_0) = B_R$ for any R. Then we choose $\psi \in C^1(\overline{\Omega})$ such that

$$\psi \begin{cases} = 1 & \text{in } B_{R_1/2}\cap\Omega, \\ \in [0,1] & \text{in } (B_{R_1}\setminus B_{R_1/2})\cap\Omega, \\ = 0 & \text{otherwise.} \end{cases} \tag{4.3}$$

with $|\nabla\psi|_{L^\infty} \leq C_1$. Then

$$\begin{aligned} \mu\int_\Omega e^{(\alpha/\mu)m}|\nabla\psi|^2 &= \mu\int_{(B_{R_1}\setminus B_{R_1/2})\cap\Omega} e^{(\alpha/\mu)m}|\nabla\psi|^2 \\ &\leq C_2\int_{(B_{R_1}\setminus B_{R_1/2})\cap\Omega} e^{(\alpha/\mu)m} \\ &\leq C_3 e^{(\alpha/\mu)M_1}, \end{aligned} \tag{4.4}$$

and

$$\int_\Omega e^{(\alpha/\mu)m}\psi^2 \geq \int_{B_{R_1/2}\cap\Omega} e^{(\alpha/\mu)m}\psi^2 \geq \int_{B_{R_2}\cap\Omega} e^{(\alpha/\mu)m}\psi^2 \geq C_5 e^{(\alpha/\mu)M_2}. \tag{4.5}$$

So

$$\frac{\mu\int_\Omega e^{(\alpha/\mu)m}|\nabla\psi|^2}{\int_\Omega e^{(\alpha/\mu)m}\psi^2} \leq \frac{C_3 e^{(\alpha/\mu)M_1}}{C_5 e^{(\alpha/\mu)M_2}} = \frac{C_3}{C_5}e^{(\alpha/\mu)(M_1-M_2)} \to 0 \tag{4.6}$$

as $\alpha \to \infty$.

By our choice of R_1,

$$\begin{aligned}\frac{\int_\Omega (m-\theta)e^{(\alpha/\mu)m}\psi^2}{\int_\Omega e^{(\alpha/\mu)m}\psi^2} &= \frac{\int_{B_{R_1}\cap\Omega}(m-\theta)e^{(\alpha/\mu)m}\psi^2}{\int_{B_{R_1}\cap\Omega} e^{(\alpha/\mu)m}\psi^2} \\ &\geq \frac{\delta\int_{B_{R_1}\cap\Omega} e^{(\alpha/\mu)m}\psi^2}{\int_{B_{R_1}\cap\Omega} e^{(\alpha/\mu)m}\psi^2} = \delta\end{aligned} \tag{4.7}$$

Thus we have

$$\lambda_1 \leq \frac{C_3}{C_5}e^{(\alpha/\mu)(M_1-M_2)} - \delta \leq -\frac{\delta}{2} \tag{4.8}$$

for sufficiently large α, which completes the proof. □

Lemma 4.1.2. *Suppose that m has an isolated global maximum. For $\alpha \gg 1$, $\|U\|_{L^\infty(\Omega)} \geq \delta_0$, where δ_0 is given in Lemma* 4.1.1.

Proof. By the comparison principle, for any positive steady state (U, V) of (1.4), we have $V \leq \theta(x;\beta,\nu)$ $(=\theta)$. Thus

$$\nabla\cdot[\mu\nabla U - \alpha U\nabla m] + U(m-\theta-U) \leq 0. \tag{4.9}$$

Again by the comparison principle, $U \geq u^*$ where u^* satisfies

$$\begin{aligned}&\nabla\cdot[\mu\nabla u^* - \alpha u^*\nabla m] + u^*(m-\theta-u^*) = 0 \quad \text{in} \quad \Omega,\\ &(\mu\nabla u^* - \alpha u^*\nabla m)\cdot n = 0 \quad \text{on} \quad \partial\Omega.\end{aligned} \tag{4.10}$$

Next we show that $\|u^*\|_{L^\infty(\Omega)} \geq \delta_0 > 0$. Consider the principal eigenfunction $\varphi > 0$ with $\|\varphi\|_{L^\infty} = 1$ of

$$\nabla \cdot [\mu \nabla \varphi - \alpha \varphi \nabla m] + \varphi(m - \theta) = -\lambda \varphi \quad \text{in } \Omega,$$
$$(\mu \nabla \varphi - \alpha \varphi \nabla m) \cdot n = 0 \quad \text{on } \partial\Omega. \tag{4.11}$$

By direct calculation, for any $\delta \in (0, -\lambda_1]$,

$$\nabla \cdot [\mu \nabla(\delta\varphi) - \alpha(\delta\varphi)\nabla m] + (\delta\varphi)(m - \theta - \delta\varphi)$$
$$= (\delta\varphi)[-\lambda_1 - \delta\varphi] \geq (\delta\varphi)(-\lambda_1 - \delta) \geq 0. \tag{4.12}$$

By the comparison principle, $u^* \geq \delta\varphi$ in $\overline{\Omega}$. Hence, choosing $\delta = -\lambda_1$, we have $U \geq u^* \geq \delta\varphi = -\lambda_1\varphi$, which implies that

$$\max_{\overline{\Omega}} U \geq -\lambda_1 \max_{\overline{\Omega}} \varphi = -\lambda_1 \geq \delta_0, \tag{4.13}$$

where the last inequality follows from Lemma 4.1.1. This completes the proof. □

4.2 Non-existence of Positive Steady States for Large α

Next we look at some conditions under which we can state with certainty that no positive steady states exist. For this section we will always assume that $m > 0$ in $\overline{\Omega}$ and that assumption (A1) holds. We will show that for $\beta \geq \nu / \min_{\overline{\Omega}} m$ and α large enough, (1.4) has no positive steady states. We will argue by contradiction. Let (U_i, V_i) denote any positive steady state of (1.4) for $(\alpha, \beta) = (\alpha_i, \beta_i)$.

Lemma 4.2.1. *Suppose that* $\alpha_i \to \infty$ *and* $\beta_i \to \beta \in [0, \infty)$*. Then* $V_i \to \theta(x; \beta, \nu)$ *in* $C^1(\overline{\Omega})$*.*

Proof. From Lemma 2.3.3, we see that for any $p > 1$, $\|U_i\|_{L^p} \to 0$ as $i \to \infty$. By standard elliptic regularity [9], $V_i \to \theta(x; \beta, \nu)$ in $W^{2,p}(\Omega)$ weakly for any $p > 1$. By the Sobolev embedding theorem [9], $V_i \to \theta(x; \beta, \nu)$ in C^1. □

Lemma 4.2.2. *Given any* $\eta > 1/\min_{\overline{\Omega}} m$*, there exists a positive constant* $\Lambda_8 = \Lambda_8(\mu, \nu, m, \Omega, \eta)$ *such that if* $\alpha \geq \Lambda_8$ *and* $\beta/\nu \in [1/\min_{\overline{\Omega}} m, \eta]$*, the system* (1.4) *has no positive steady state.*

Proof. We argue by contradiction. Suppose that there exist sequences $\{\alpha_i, \beta_i\}_{i=1}^{\infty}$ with $\alpha_i \to \infty$ and $\beta_i/\nu \in [1/\min_{\overline{\Omega}} m, \eta]$ such that system (1.4) with $(\alpha, \beta) = (\alpha_i, \beta_i)$ has a positive steady state, denoted as (U_i, V_i), for every i. Without loss of generality, assume that $\mu = 1$ and $\beta_i \to \beta \in [\nu/\min_{\overline{\Omega}} m, \infty)$. Set $W_i = e^{-\alpha_i m} U_i$. Then $W_i > 0$ satisfies

$$\begin{aligned} &\nabla \cdot [e^{\alpha_i m} \nabla W_i] + e^{\alpha_i m}(m - U_i - V_i) W_i = 0 \qquad \text{in } \Omega, \\ &\partial_n W_i = 0 \quad \text{on } \partial\Omega. \end{aligned} \tag{4.14}$$

Given any $\epsilon \in (0, 1)$, let $\lambda_i(\epsilon)$ be the principal eigenvalue of the eigenvalue problem

$$\begin{aligned} &\nabla \cdot [e^{\alpha_i m} \nabla \varphi] + e^{\alpha_i m}[m - (1 - \epsilon)\theta(x; \beta, \nu)] = -\lambda e^{\alpha_i m} \varphi \quad \text{in } \Omega, \\ &\partial_n \varphi = 0 \quad \text{on } \partial\Omega. \end{aligned} \tag{4.15}$$

Denote the eigenfunction corresponding to $\lambda_i(\epsilon)$ by φ_i, which is uniquely determined by $\varphi_i > 0$ in $\overline{\Omega}$ and $\int_\Omega \varphi_i^2\, dx = 1$. Multiplying (4.14) by φ_i and (4.15) by W_i, subtracting the first equation from the second, and integrating over Ω, we have

$$\int_\Omega e^{\alpha_i m}[U_i + V_i - (1-\epsilon)\theta(x;\beta,\nu)]\, dx = -\lambda_i(\epsilon)\int_\Omega e^{\alpha_i m}\varphi_i W_i. \tag{4.16}$$

Now we fix $\epsilon \in (0,1)$. Since $V_i \to \theta(x;\beta,\nu)$ uniformly in Ω (Lemma 4.2.1), there exists i^* such that for $i \geq i^*$,

$$V_i - (1-\epsilon)\theta(x;\beta,\nu) \geq \tfrac{\epsilon}{2}\theta(x;\beta,\nu) > 0 \qquad \text{in } \overline{\Omega}.$$

Hence, for $i \geq i^*$,

$$\lambda_i(\epsilon) < 0. \tag{4.17}$$

By assumption (A1), we see that $\mathcal{M} = \{x_0\}$. Hence, by Theorem 2.3.4 we have

$$\lim_{i\to\infty} \lambda_i(\epsilon) = \min_{x\in\mathcal{M}}[-m(x) + (1-\epsilon)\theta(x;\beta,\nu)] = -m(x_0) + (1-\epsilon)\theta(x_0;\beta,\nu).$$

This along with (4.17) implies that

$$m(x_0) \geq (1-\epsilon)\theta(x_0;\beta,\nu).$$

Letting $\epsilon \to 0^+$, we have

$$m(x_0) \geq \theta(x_0;\beta,\nu).$$

However, this is a contradiction since by Lemma 2.3.2 we know that $\theta(x_0;\beta,\nu) > m(x_0)$ for $\beta/\nu \geq 1/\min_{\overline{\Omega}} m$. □

4.3 Non-existence of Positive Steady States for $\alpha \approx \beta$

Finally we show that under a certain condition, for α close to β, the system (1.4) has no internal positive steady states. Thus if $\int_\Omega m > 0$, the only equilibria are the two semi-trivial steady states.

Theorem 4.3.1. *The system* (1.5) *has no internal equilibria, provided that*

$$(\mu_1 - \nu_1) \int_\Omega \nabla(e^{-(\alpha_0/\mu_0)m}\theta) \cdot \nabla\theta - (\alpha_1 - \beta_1) \int_\Omega \theta\nabla(e^{-(\alpha_0/\mu_0)m}\theta) \cdot \nabla m \neq 0 \quad (4.18)$$

Before proving the theorem, we want to establish a couple lemmas which we will use in the proof.

Lemma 4.3.2.

$$\begin{aligned} &\int_\Omega [\mu e^{(\alpha/\mu)m} - \nu e^{(\beta/\nu)m}]\nabla(e^{-(\alpha/\mu)m}u) \cdot \nabla(e^{-(\beta/\nu)m}v) \\ &\quad = \int_\Omega [e^{-(\beta/\nu)m} - e^{-(\alpha/\mu)m}]uv(m - u - v) \end{aligned} \quad (4.19)$$

Proof. We rewrite the equations as

$$\mu\nabla \cdot [e^{(\alpha/\mu)m}\nabla(e^{-(\alpha/\mu)m}u)] + u(m - u - v) = 0 \quad \text{in } \Omega,$$

$$\nu\nabla \cdot [e^{(\beta/\nu)m}\nabla(e^{-(\beta/\nu)m}v)] + v(m - u - v) = 0 \quad \text{in } \Omega, \quad (4.20)$$

$$\nabla(e^{-(\alpha/\mu)m}u) \cdot n = \nabla(e^{-(\beta/\nu)m}v) \cdot n = 0 \quad \text{on } \partial\Omega.$$

We multiply the first equation in (4.20) by $e^{-(\beta/\nu)m}v$ and integrate over Ω using the divergence theorem and the boundary condition. From this we get

$$\mu \int_\Omega e^{(\alpha/\mu)m} \nabla(e^{-(\alpha/\mu)m}u) \cdot \nabla(e^{-(\beta/\nu)m}v) = \int_\Omega e^{-(\beta/\nu)m} uv(m-u-v). \tag{4.21}$$

Similarly, multiplying the second equation in (4.20) by $e^{-(\alpha/\mu)m}u$ and integrating over Ω we have

$$\nu \int_\Omega e^{(\beta/\nu)m} \nabla(e^{-(\alpha/\mu)m}u) \cdot \nabla(e^{-(\beta/\nu)m}v) = \int_\Omega e^{-(\alpha/\mu)m} uv(m-u-v). \tag{4.22}$$

Subtracting (4.22) from (4.21) gives us the desired result. □

Lemma 4.3.3. *Using the parametrization*

$$\begin{cases} \mu = \mu_0 + \epsilon\mu_1 + O(\epsilon^2), \\ \nu = \mu_0 + \epsilon\nu_1 + O(\epsilon^2), \\ \alpha = \alpha_0 + \epsilon\alpha_1 + O(\epsilon^2), \\ \beta = \alpha_0 + \epsilon\beta_1 + O(\epsilon^2), \end{cases} \tag{4.23}$$

$$\mu e^{(\alpha/\mu)m} - \nu e^{(\beta/\nu)m} = e^{(\alpha_0/\mu_0)m}\epsilon(\mu_1 - \nu_1 + \frac{\alpha_1\mu_0 - \alpha_0\mu_1 - \beta_1\mu_0 + \alpha_0\nu_1}{\mu_0}m) \tag{4.24}$$

and

$$e^{-(\beta/\nu)m} - e^{-(\alpha/\mu)m} = e^{(\alpha_0/\mu_0)m}[\epsilon(\frac{\alpha_1\mu_0 - \alpha_0\mu_1}{\mu_0^2} - \frac{\beta_1\mu_0 - \alpha_0\nu_1}{\mu_0^2})m + O(\epsilon^2)] \tag{4.25}$$

Proof. We use the Taylor expansion around $\epsilon = 0$, giving us

$$\begin{aligned}
\mu e^{(\alpha/\mu)m} &= (\mu_0 + \epsilon\mu_1 + O(\epsilon^2)) \exp[\frac{\alpha_0 + \epsilon\alpha_1 + O(\epsilon^2)}{\mu_0 + \epsilon\mu_1 + O(\epsilon^2)} m] \\
&= (\mu_0 + \epsilon\mu_1 + O(\epsilon^2)) \exp[(\alpha_0/\mu_0)m + \epsilon\frac{\alpha_1\mu_0 - \alpha_0\mu_1}{\mu_0^2} m + O(\epsilon^2)] \\
&= e^{(\alpha_0/\mu_0)m}(\mu_0 + \epsilon\mu_1 + O(\epsilon^2)) \exp[\epsilon\frac{\alpha_1\mu_0 - \alpha_0\mu_1}{\mu_0^2} m + O(\epsilon^2)] \qquad (4.26) \\
&= e^{(\alpha_0/\mu_0)m}(\mu_0 + \epsilon\mu_1 + O(\epsilon^2))[1 + \epsilon\frac{\alpha_1\mu_0 - \alpha_0\mu_1}{\mu_0^2} m + O(\epsilon^2)] \\
&= e^{(\alpha_0/\mu_0)m}[\mu_0 + \epsilon\mu_1 + \epsilon\frac{\alpha_1\mu_0 - \alpha_0\mu_1}{\mu_0} m + O(\epsilon^2)]
\end{aligned}$$

Similarly,

$$\nu e^{(\beta/\nu)m} = e^{(\alpha_0/\mu_0)m}[\mu_0 + \epsilon\nu_1 + \epsilon\frac{\beta_1\mu_0 - \alpha_0\nu_1}{\mu_0} m + O(\epsilon^2)] \qquad (4.27)$$

Subtracting (4.27) from (4.26) gives us the first equation.

Again using the above parametrization and the Taylor expansion, we get

$$\begin{aligned}
e^{-(\alpha/\mu)m} &= \exp[-(\alpha_0/\mu_0)m - \epsilon\frac{\alpha_1\mu_0 - \alpha_0\mu_1}{\mu_0^2} m + O(\epsilon^2)] \\
&= e^{(\alpha_0/\mu_0)m}(1 - \epsilon\frac{\alpha_1\mu_0 - \alpha_0\mu_1}{\mu_0^2} m + O(\epsilon^2))
\end{aligned} \qquad (4.28)$$

and

$$e^{-(\beta/\nu)m} = e^{(\alpha_0/\mu_0)m}(1 - \epsilon\frac{\beta_1\mu_0 - \alpha_0\nu_1}{\mu_0^2} m + O(\epsilon^2)) \qquad (4.29)$$

Subtracting (4.28) from (4.29) gives us the second equation. □

Lemma 4.3.4. *Let (U, V) be any positive steady state of (1.5). Then for $(\alpha, \beta, \mu, \nu)$ parameterized as above, $(U, V) \to (s\theta_0, (1-s)\theta_0)$ as $\epsilon \to 0$ for $s \in [0, 1]$.*

Proof. Let (U, V) be any positive equilibrium of (1.5). As $\epsilon \to 0$, then (U, V) will approach some limit $(\hat{u}, \hat{v})$, with $\hat{u}, \hat{v} \geq 0$, where $(\hat{u}, \hat{v})$ satisfy

$$\nabla \cdot [\mu_0 \nabla \hat{u} - \alpha_0 \hat{u} \nabla m] + \hat{u}(m - \hat{u} - \hat{v}) = 0 \quad \text{in} \ \ \Omega,$$

$$\nabla \cdot [\mu_0 \nabla \hat{v} - \alpha_0 \hat{v} \nabla m] + \hat{v}(m - \hat{u} - \hat{v}) = 0 \quad \text{in} \ \ \Omega, \tag{4.30}$$

$$[\mu_0 \nabla \hat{u} - \alpha_0 \hat{u} \nabla m] \cdot n = [\mu_0 \nabla \hat{v} - \alpha_0 \hat{v} \nabla m] \cdot n = 0 \quad \text{on} \ \ \partial\Omega.$$

Adding the equations we see that $\hat{u} + \hat{v}$ satisfies

$$\nabla \cdot [\mu_0 \nabla(\hat{u} + \hat{v}) - \alpha_0(\hat{u} + \hat{v}) \nabla m] + (\hat{u} + \hat{v})(m - (\hat{u} + \hat{v})) = 0 \quad \text{in} \ \ \Omega,$$

$$\tag{4.31}$$

$$[\mu_0 \nabla(\hat{u} + \hat{v}) - \alpha_0(\hat{u} + \hat{v}) \nabla m] \cdot n = 0 \quad \text{on} \ \ \partial\Omega.$$

Thus either $\hat{u} + \hat{v} = \theta_0$ or $\hat{u} + \hat{v} \equiv 0$. We exclude the possibility $\hat{u} + \hat{v} \equiv 0$. Set $w = e^{-(\alpha/\mu)m} U$. Then w satisfies

$$\mu \nabla \cdot [e^{(\alpha/\mu)m} \nabla w] + w e^{(\alpha/\mu)m}(m - U - V) = 0$$

in Ω and $\partial w / \partial_n = 0$ on $\partial\Omega$. Dividing the above equation by w and integrating in Ω, similarly as before we find that

$$\int_\Omega e^{(\alpha/\mu)m}(m - U - V) \leq 0.$$

Since $(U, V) \to (\hat{u}, \hat{v}) = (0, 0)$, passing to the limit in the above equation we have

$$\int_\Omega e^{(\alpha/\mu)m} m \leq 0,$$

which is a contradiction.

Hence, $\hat{u} + \hat{v} = \theta_0$. Since both $\hat{u}, \hat{v} \geq 0$, this gives the desired result. □

Lemma 4.3.5. *If* $(U, V) \to (0, \theta_0)$ *as* $\epsilon \to 0$, *then* $U/\|U\|_\infty \to \theta_0/\|\theta_0\|_\infty$.

Proof. We begin by dividing (1.5) by $\|U\|_\infty$ to get

$$\begin{aligned} &\nabla \cdot [\mu \nabla \frac{U}{\|U\|_\infty} - \alpha \frac{U}{\|U\|_\infty} \nabla m] + \frac{U}{\|U\|_\infty}(m - U - V) = 0 \quad \text{in} \;\; \Omega, \\ &[\mu \nabla \frac{U}{\|U\|_\infty} - \alpha \frac{U}{\|U\|_\infty} \nabla m] \cdot n = 0 \quad \text{on} \;\; \partial\Omega. \end{aligned} \tag{4.32}$$

As $\epsilon \to 0$, then $U/\|U\|_\infty \to z$ where z satisfies

$$\begin{aligned} &\nabla \cdot [\mu_0 \nabla z - \alpha_0 z \nabla m] + z(m - \theta_0) = 0 \quad \text{in} \;\; \Omega, \\ &[\mu_0 \nabla z - \alpha_0 z \nabla m] \cdot n = 0 \quad \text{on} \;\; \partial\Omega. \end{aligned} \tag{4.33}$$

So we get that $z = k\theta_0$ for some constant $k > 0$. Since $\|z\|_\infty = 1$, $k = 1/\|\theta_0\|_\infty$, i.e. $z = \theta_0/\|\theta_0\|_\infty$. □

Lemma 4.3.6. *If* $(U, V) \to (\theta_0, 0)$ *as* $\epsilon \to 0$, *then* $V/\|V\|_\infty \to \theta_0/\|\theta_0\|_\infty$.

Proof. The proof is similar to Lemma 4.3.5 above, and thus is omitted. □

We are now ready to prove the theorem.

Proof of Theorem 4.3.1. Assume there is an internal equilibrium (U, V). As shown in the preceding lemmas, there are three possibilities. As $\epsilon \to 0$,

1. $(U, V) \to (s\theta_0, (1 - s)\theta_0)$ for $s \in (0, 1)$,

2. $(U, V) \to (0, \theta_0)$ and $U/\|U\|_\infty \to \theta_0/\|\theta_0\|_\infty$, or

3. $(U,V) \to (\theta_0, 0)$ and $V/\|V\|_\infty \to \theta_0/\|\theta_0\|_\infty$.

We will address each of these three possibilities and see that they quickly merge. First, suppose that $(U,V) \to (s\theta_0, (1-s)\theta_0)$ for $s \in (0,1)$ as $\epsilon \to 0$. Then we can parameterize $(U,V) = (s\theta_0 + O(\epsilon), (1-s)\theta_0 + O(\epsilon))$ where θ_0 satisfies

$$\begin{aligned} &\mu_0 \nabla \cdot [e^{(\alpha_0/\mu_0)m} \nabla (e^{-(\alpha_0/\mu_0)m}\theta_0)] + \theta_0(m - \theta_0) = 0 \quad \text{in} \;\; \Omega, \\ &\nabla (e^{-(\alpha_0/\mu_0)m}\theta_0) \cdot n = 0 \quad \text{on} \;\; \partial\Omega. \end{aligned} \tag{4.34}$$

We use the results from Lemma 4.3.3 along with this parametrization and that of $(\alpha, \beta, \mu, \nu)$ above, plug into (4.19), and combine the first-order terms in ϵ to get

$$\begin{aligned} &\int_\Omega e^{(\alpha_0/\mu_0)m} \Big[\mu_1 - \nu_1 + \frac{\alpha_1\mu_0 - \alpha_0\mu_1 - \beta_1\mu_0 + \alpha_0\nu_1}{\mu_0} m\Big] |\nabla (e^{-(\alpha_0/\mu_0)m}\theta_0)|^2 \\ &\qquad = \int_\Omega e^{-(\alpha_0/\mu_0)m} \Big[\frac{\alpha_1\mu_0 - \alpha_0\mu_1}{\mu_0^2} - \frac{\beta_1\mu_0 - \alpha_0\nu_1}{\mu_0^2}\Big] m\theta_0^2(m - \theta_0) \end{aligned} \tag{4.35}$$

Now if $(U,V) \to (0, \theta_0)$ as $\epsilon \to 0$, we parameterize $(U/\|U\|_\infty, V) = (\theta_0/\|\theta_0\|_\infty + O(\epsilon), \theta_0 + O(\epsilon))$. Then we first divide (4.19) by $\|U\|_\infty$ before using the results from Lemma 4.3.3. Then plugging in this parametrization and that of $(\alpha, \beta, \mu, \nu)$ and combining first-order terms in ϵ we get

$$\begin{aligned} &\int_\Omega e^{(\alpha_0/\mu_0)m} \Big[\mu_1 - \nu_1 + \frac{\alpha_1\mu_0 - \alpha_0\mu_1 - \beta_1\mu_0 + \alpha_0\nu_1}{\mu_0} m\Big] \nabla \Big(e^{-(\alpha_0/\mu_0)m} \frac{\theta_0}{\|\theta_0\|_\infty}\Big) \cdot \nabla (e^{-(\alpha_0/\mu_0)m}\theta_0) \\ &\qquad = \int_\Omega e^{-(\alpha_0/\mu_0)m} \Big[\frac{\alpha_1\mu_0 - \alpha_0\mu_1}{\mu_0^2} - \frac{\beta_1\mu_0 - \alpha_0\nu_1}{\mu_0^2}\Big] m \frac{\theta_0^2}{\|\theta_0\|_\infty}(m - \theta_0) \end{aligned} \tag{4.36}$$

Multiplying by $\|\theta_0\|_\infty$ gets us back to (4.35).

Lastly, if $(U,V) \to (\theta_0, 0)$ as $\epsilon \to 0$, then we parameterize $(U, V/\|V\|_\infty) = (\theta_0 + O(\epsilon), \theta_0/\|\theta_0\|_\infty + O(\epsilon))$, divide (4.19) by $\|V\|_\infty$, and proceed as above.

Once we have (4.35), we multiply (4.34) by $e^{-(\alpha_0/\mu_0)m}\theta_0 m$, integrate over Ω, and use the divergence theorem to get

$$\begin{aligned}\int_\Omega e^{-(\alpha_0/\mu_0)m}\theta_0^2(m-\theta_0)m &= -\mu_0\int_\Omega e^{-(\alpha_0/\mu_0)m}\theta_0 m\cdot\nabla[e^{(\alpha_0/\mu_0)m}\nabla(e^{-(\alpha_0/\mu_0)m}\theta_0)]\\ &= \mu_0\int_\Omega e^{(\alpha_0/\mu_0)m}\nabla(e^{-(\alpha_0/\mu_0)m}\theta_0)\cdot\nabla(e^{-(\alpha_0/\mu_0)m}\theta_0 m)\\ &= \mu_0\Big[\int_\Omega e^{(\alpha_0/\mu_0)m}m|\nabla(e^{-(\alpha_0/\mu_0)m}\theta_0)|^2\\ &\qquad + \int_\Omega \theta_0\nabla(e^{-(\alpha_0/\mu_0)m}\theta_0)\cdot\nabla m\Big]\end{aligned} \tag{4.37}$$

Using this result with (4.35), we now have

$$\begin{aligned}(\mu_1-\nu_1)&\int_\Omega e^{(\alpha_0/\mu_0)m}|\nabla(e^{-(\alpha_0/\mu_0)m}\theta_0)|^2\\ &\qquad + \frac{\alpha_1\mu_0-\alpha_0\mu_1-\beta_1\mu_0+\alpha_0\nu_1}{\mu_0}\int_\Omega e^{(\alpha_0/\mu_0)m}m|\nabla(e^{-(\alpha_0/\mu_0)m}\theta_0)|^2\\ &= \frac{\alpha_1\mu_0-\alpha_0\mu_1-\beta_1\mu_0+\alpha_0\nu_1}{\mu_0}\Big[\int_\Omega e^{(\alpha_0/\mu_0)m}m|\nabla(e^{-(\alpha_0/\mu_0)m}\theta_0)|^2\\ &\qquad + \int_\Omega \theta_0\nabla(e^{-(\alpha_0/\mu_0)m}\theta_0)\cdot\nabla m\Big]\end{aligned} \tag{4.38}$$

Thus

$$\begin{aligned}(\mu_1-\nu_1)&\int_\Omega e^{(\alpha_0/\mu_0)m}|\nabla(e^{-(\alpha_0/\mu_0)m}\theta_0)|^2\\ &= \frac{\alpha_1\mu_0-\alpha_0\mu_1-\beta_1\mu_0+\alpha_0\nu_1}{\mu_0}\int_\Omega \theta_0\nabla(e^{-(\alpha_0/\mu_0)m}\theta_0)\cdot\nabla m \qquad (4.39)\\ &= \Big[\alpha_1-\beta_1+\frac{\alpha_0(\nu_1-\mu_1)}{\mu_0}\Big]\int_\Omega \theta_0\nabla(e^{-(\alpha_0/\mu_0)m}\theta_0)\cdot\nabla m\end{aligned}$$

Bringing the last integral over to the LHS we get

$$\begin{aligned}(\mu_1 - \nu_1)\Big[\int_\Omega e^{(\alpha_0/\mu_0)m}|\nabla(e^{-(\alpha_0/\mu_0)m}\theta_0)|^2 + \frac{\alpha_0}{\mu_0}\int_\Omega \theta_0\nabla(e^{-(\alpha_0/\mu_0)m}\theta_0)\cdot\nabla m\Big] \\ = (\alpha_1 - \beta_1)\int_\Omega \theta_0\nabla(e^{-(\alpha_0/\mu_0)m}\theta_0)\cdot\nabla m\end{aligned} \tag{4.40}$$

Finally, using the fact that

$$\begin{aligned}& e^{(\alpha_0/\mu_0)m}|\nabla(e^{-(\alpha_0/\mu_0)m}\theta_0)|^2 + \frac{\alpha_0}{\mu_0}\theta_0\nabla(e^{-(\alpha_0/\mu_0)m}\theta_0)\cdot\nabla m \\ &= \nabla(e^{-(\alpha_0/\mu_0)m}\theta_0)\cdot[e^{(\alpha_0/\mu_0)m}\nabla(e^{-(\alpha_0/\mu_0)m}\theta_0) + \frac{\alpha_0}{\mu_0}\theta_0\nabla m] \\ &= \nabla(e^{-(\alpha_0/\mu_0)m}\theta_0)\cdot[e^{(\alpha_0/\mu_0)m}(e^{-(\alpha_0/\mu_0)m}\nabla\theta_0 + \theta_0 e^{-(\alpha_0/\mu_0)m}\Big(-\frac{\alpha_0}{\mu_0}\Big)\nabla m) \\ &\qquad + \frac{\alpha_0}{\mu_0}\theta_0\nabla m] \\ &= \nabla(e^{-(\alpha_0/\mu_0)m}\theta_0)\cdot\nabla\theta_0,\end{aligned} \tag{4.41}$$

we end up with

$$(\mu_1 - \nu_1)\int_\Omega \nabla(e^{-(\alpha_0/\mu_0)m}\theta_0)\cdot\nabla\theta_0 - (\alpha_1 - \beta_1)\int_\Omega \theta_0\nabla(e^{-(\alpha_0/\mu_0)m}\theta_0)\cdot\nabla m = 0, \tag{4.42}$$

a contradiction to the assumption (4.18). □

CHAPTER 5

GLOBAL DYNAMICS

After considering the existence and local stability of positive equilibria, in this chapter we turn our focus to the global dynamics of the system. Again we will look at two different situations, when one species has a large advection rate and when the two species have nearly identical dispersal strategies.

5.1 Global Dynamics for Large α

Theorem 5.1.1. *Suppose that* $m > 0$ *in* $\overline{\Omega}$ *and assumption* (A1) *holds. Given any number* $\eta > 1/\min_{\overline{\Omega}} m$*, there exists some positive constant* $\Lambda_8 = \Lambda_8(\mu, \nu, m, \Omega, \eta)$ *such that if* $\alpha \geq \Lambda_8$ *and* $\beta/\nu \in [1/\min_{\overline{\Omega}} m, \eta]$, $(0, \theta(x; \beta, \nu))$ *is globally asymptotically stable.*

Proof. From Theorem 2.1.2, (1.4) is a strongly monotone system. From Lemma 3.2.1, we know that $(\theta(x; \alpha, \mu), 0)$ is locally unstable and by Lemma 3.3.3, $(0, \theta(x; \beta, \nu))$ is locally stable. Lemma 4.2.2 tells us that the system has no positive steady states. Thus, by the monotone system theory [10, 12, 17], $(0, \theta(x; \beta, \nu))$ is globally asymptotically stable.

5.2 1-Dimensional Dynamics with $(\alpha, \mu) \approx (\beta, \nu)$

Here we consider the special case where the species have very similar dispersal strategies ($(\alpha, \mu) \approx (\beta, \nu)$), the habitat is one-dimensional ($\Omega = [0, 1]$), and the quality of resources is strictly increasing along the habitat (i.e., $m_x > 0$ on $[0, 1]$).

We first consider the case where $\mu = \nu$ and $\alpha \approx \beta$. We perturb (α, β) slightly, letting $(\alpha, \beta) = (\alpha_0 + \epsilon\alpha_1 + O(\epsilon^2), \alpha_0 + \epsilon\beta_1 + O(\epsilon^2))$. So both species have the same diffusion rate, both are a little smart, and species u is a little smarter than species v (i.e., $\alpha_1 > \beta_1$). We find different results when the advection is large and when the advection is small.

Theorem 5.2.1. *Suppose $\mu = \nu$ and $\alpha_1 > \beta_1$. Let $\Omega = [0, 1], m$ be twice continuously differentiable on $[0, 1]$, $m_x > 0$ on $[0, 1]$.*

(i) *If $\alpha_0 < \mu/max_{\overline{\Omega}}m$, then $(\theta(x; \alpha, \mu), 0)$ is globally asymptotically stable.*

(ii) *If $m > 0$ on $[0, 1]$ and $\alpha_0 > \mu/min_{\overline{\Omega}}m$, then $(0, \theta(x; \beta, \nu))$ is globally asymptotically stable.*

Proof. (i) First we show that $(\theta(x; \alpha, \mu), 0)$ is locally stable. By Lemma 3.2.2, we have that the principal eigenvalue λ_1 of (3.1) is given by

$$-\lambda_1 \int_\Omega e^{-(\alpha_0/\mu_0)m}\theta_0^2 = (\beta_1 - \alpha_1) \int_\Omega (e^{-(\alpha_0/\mu_0)m}\theta_0)_x \cdot \theta_0 m_x \qquad (5.1)$$

From Lemma 2.4.2, with $w = e^{-(\alpha_0/\mu_0)m}\theta_0$ and $\gamma = \alpha_0/\mu_0$, we see that $(e^{-(\alpha_0/\mu_0)m}\theta_0)_x > 0$. Since $\theta_0 > 0$ and $m_x > 0$ by assumption, the principal eigenvalue λ_1 of (3.1) is positive. Thus by Lemma 3.1.1, $(\theta(x; \alpha, \mu), 0)$ is locally asymptotically stable.

Similarly, from Lemmas 2.4.2 and 3.3.1, the principal eigenvalue of (3.2) is negative, so $(0, \theta(x; \beta, \nu))$ is unstable.

Since there are no positive steady states by Theorem 4.3.1 (note that (4.18) is satisfied), from the monotone system theory we can conclude that $(\theta(x; \alpha, \mu), 0)$ is globally asymptotically stable for all positive initial data.

(ii) With the same identifications as above, this time by Lemma 2.4.1 we have $(e^{-(\alpha_0/\mu_0)m}\theta_0)_x < 0$. We still have $\theta_0 > 0$ and $m_x > 0$, so the principal eigenvalue of (3.1) is negative. Thus by Lemma 3.1.1, $(\theta(x; \alpha, \mu), 0)$ is unstable.

By Lemma 3.3.1, the principal eigenvalue of λ_1 (3.2) is given by

$$-\lambda_1 \int_\Omega e^{-(\alpha_0/\mu_0)m}\theta_0^2 = (\alpha_1 - \beta_1) \int_\Omega (e^{-(\alpha_0/\mu_0)m}\theta_0)_x \cdot \theta_0 m_x \tag{5.2}$$

So the principal eigenvalue of (3.2) is positive, thus by Lemma 3.1.2, $(0, \theta(x; \beta, \nu))$ is locally asymptotically stable.

Again, Theorem 4.3.1 assures that we do not have any positive steady states, so by the monotone system theory we can conclude that $(0, \theta(x; \beta, \nu))$ is globally asymptotically stable. □

So for small advection rates relative to the rate of diffusion, we find that the smarter species survives. But if the advection rate is too large, the smarter species loses.

Next we consider the case where $\alpha = \beta$ and $\mu \approx \nu$. We parameterize $(\mu, \nu) = (\mu_0 + \epsilon\mu_1 + O(\epsilon^2), \mu_0 + \epsilon\nu_1 + O(\epsilon^2))$. Again we consider the two subcases with small and large advection rates.

Theorem 5.2.2. *Suppose $\alpha = \beta$ and $\mu_1 < \nu_1$. Let $\Omega = [0, 1]$, m be twice continuously differentiable on $[0, 1]$, $m_x > 0$ on $[0, 1]$.*

(i) *If* $\alpha < \mu_0/\max_{\overline{\Omega}} m$*, then* $(\theta(x;\alpha,\mu),0)$ *is globally asymptotically stable.*

(ii) *If* $m > 0$ *on* $[0,1]$ *and* $\alpha > \max(\mu_0/\min_{\overline{\Omega}} m, \max_{\overline{\Omega}} m/\min_{\overline{\Omega}} m_x)$*, then* $(0,\theta(x;\beta,\nu))$ *is globally asymptotically stable.*

Proof. (i) Since $\alpha_1 = \beta_1$, from Lemma 3.2.2, we now have that the principal eigenvalue λ_1 of (3.1) is given by

$$-\lambda_1 \int_\Omega e^{-(\alpha_0/\mu_0)m}\theta_0^2 = (\mu_1 - \nu_1)\int_\Omega \nabla(e^{-(\alpha_0/\mu_0)m}\theta_0)\cdot\nabla\theta_0 \tag{5.3}$$

In Lemma 2.4.2, we again identify $w = e^{-(\alpha_0/\mu_0)m}\theta_0$, so that $\theta_0 = we^{(\alpha_0/\mu_0)m}$. So then $(\theta_0)_x = e^{(\alpha_0/\mu_0)m}(w_x + (\alpha_0/\mu_0)m_x w) > 0$ since w_x, w, and m_x are all positive. Thus $\lambda_1 > 0$, so by Lemma 3.1.1 $(\theta(x;\alpha,\mu),0)$ is locally asymptotically stable.

Likewise, from Lemma 3.3.1, the principal eigenvalue of (3.2) is negative, so $(0,\theta(x;\beta,\nu))$ is unstable.

And again by Theorem 4.3.1, since there are no positive steady states, monotone system theory tells us that $(\theta(x;\alpha,\mu),0)$ is globally asymptotically stable.

(ii) By Lemma 2.4.1 we have that $(e^{-(\alpha_0/\mu_0)m}\theta_0)_x < 0$. We want to show that $(\theta_0)_x > 0$. We argue by contradiction. Let $x^* \in [0,1]$ be the least such that $(\theta_0)_x(x^*) \le 0$. Since $(\theta_0)_x(0) > 0$ and $(\theta_0)_x(1) > 0$, by the continuity of $(\theta_0)_x$, $x^* \in (0,1)$ and $(\theta_0)_x(x^*) = 0$. Integrating (3.9) over $[0,x^*]$ we get

$$\alpha\theta_0(x^*)m_x(x^*) = \int_0^{x^*}\theta_0(m-\theta_0) \le \int_0^{x^*}\theta_0 m \le \max_{[0,1]} m\cdot\int_0^{x^*}\theta_0 \tag{5.4}$$

Since θ_0 is increasing on $[0,x^*]$, we have

$$\alpha\theta_0(x^*)\min_{[0,1]} m_x \le \max_{[0,1]} m\cdot\theta_0(x^*) \tag{5.5}$$

From this, since $\theta_0(x^*) > 0$ and $\min_{[0,1]} m_x > 0$, we get $\alpha \le \max_{[0,1]} m / \min_{[0,1]} m_x$, contradicting our choice of α.

Thus $(\theta_0)_x > 0$ on $[0,1]$, so the principle eigenvalue of (3.1) is negative, therefore $(\theta(x;\alpha,\mu),0)$ is unstable.

From Lemma 3.3.1, the principal eigenvalue λ_1 of (3.2) is given by

$$-\lambda_1 \int_\Omega e^{-(\alpha_0/\mu_0)m}\theta_0^2 = (\nu_1 - \mu_1) \int_\Omega \nabla(e^{-(\alpha_0/\mu_0)m}\theta_0) \cdot \nabla\theta_0 \tag{5.6}$$

So we see that the principal eigenvalue of (3.2) is positive, and thus by Lemma 3.1.2, $(0, \theta(x;\beta,\nu))$ is locally asymptotically stable.

Theorem 4.3.1 shows that there are no positive steady states, so the monotone system theory tells us that $(\theta(x;\alpha,\mu),0)$ is globally asymptotically stable. □

CHAPTER 6

DISCUSSIONS AND OPEN PROBLEMS

6.1 Discussion

In this paper we show some interesting results and insights into the best dispersal strategy for a species. We see in the case where both species have similar dispersal strategies, $(\alpha, \mu) \approx (\beta, \nu)$, that the size of the advection rate relative to the diffusion rate is important. When the rate of advection is small relative to the rate of diffusion $(\alpha/\mu < 1/\max_{\overline{\Omega}} m)$, we see that the results of Dockery et. al. [8] and Cantrell et. al. [3] are extended. When advection rates are equal, evolution favors slower diffusion. When diffusion rates are equal, evoultion favors stronger advection.

The situation is reversed however if the rate of advection is larger relative to the rate of diffusion $(\alpha/\mu > 1/\min_{\overline{\Omega}} m > 0)$. Then faster diffusion is preferred when advection rates are equal and weaker advection is preferred when diffusion rates are equal.

So we see that if α/μ is small enough, then an advantage is gained if advection increases and diffusion decreases, that is if α/μ increases. While if α/μ is already large enough, then the species fares better if advection decreases and diffusion increases, that is if α/μ decreases.

The conclusion of Cantrell et. al. [3] that the faster diffuser can win if the advection rate is large enough (but not too large) can be strengthened. We have shown that too large of an advection rate is a disadvantage to the species. So for small advection rates, not only does an increase in advection *allow* for an increase in diffusion, but if the advection rate increases enough, the diffusion rate *must* increase. If advection becomes too strong relative to diffusion, then the species will be wiped out by its competitor.

To put it in the biological context, searching for and following better environments is a beneficial strategy for survival. But this must be balanced with an appropriate amount of random movement to ensure that the species is exposed to new opportunities and does not become too focused on the immediate environment. While individual members of a species may suffer by wandering into a less friendly environment, the gain and colonization of new habitat from such exploration is good for the species as a whole.

Returning to the mathematics, we see that for $\beta/\nu < \alpha/\mu < 1/\max_{\overline{\Omega}} m$, $(\theta(x;\alpha,\mu),0)$ is the global attractor. But for $\alpha/\mu > \beta/\nu > 1/\min_{\overline{\Omega}} m > 0$, $(0,\theta(x;\beta,\nu))$ is the global attractor. So for $1/\max_{\overline{\Omega}} m < \beta/\nu < \alpha/\mu < 1/\min_{\overline{\Omega}} m$, both semi-trivial steady states must change stability at least once. This strongly suggests that there is one strategy that is optimal, i.e. for fixed μ, there is an advection rate $\alpha^* \in [\mu/\max_{\overline{\Omega}} m, \mu/\min_{\overline{\Omega}} m]$ such that for $\beta/\nu \neq \alpha^*/\mu$, $(\theta(x;\alpha^*,\mu),0)$ is globally asymptotically stable. One thing that is uncertain is what if $\beta/\nu = \alpha^*/\mu$ but $\beta \neq \alpha^*$? Are all dispersal strategies with this ratio equal or is one better than the others?

This argument for an optimal rate is further strengthened by Identity 3.2.3 and Lemma 3.2.2. For a given domain Ω and resource function m, if α and μ are such that stronger advection is preferred, then slower diffusion *must* also be preferred, i.e. larger α/μ is favored. And if faster diffusion is preferred, weaker advection *must* also be preferred, i.e. the preference is for smaller α/μ. However the converse is not true. A large enough decrease in diffusion allows for weaker advection.

When the species have dissimilar dispersal strategies and α is large relative to μ, we again see that advection must be balanced with diffusion. When one species reacts strongly to the availability of resources and the quality of the environment with little random movement, a less intelligent species that relies almost entirely on random movement for dispersal can actually coexist. But as the second species gets smarter (β increases), the second species can not only invade but even drive the first species to extinction. But by the same token, if the second species gets too smart without increasing diffusion, it will be driven to extinction. So a large increase in advection must be accompanied by an increase in diffusion. As a species gets smarter, it must increase its efforts to explore new areas to avoid becoming overconcentrated in a few locations.

6.2 Open Problems

The results we obtained were for $(\alpha, \mu) \approx (\beta, \nu)$ and for α large. Do the same results hold if the diffusion or advection rates are not so close or not so far apart? Specifically we ask the following questions:

1. If $0 \leq \beta < \alpha < \mu/max_{\overline{\Omega}}m$, $\mu = \nu$, is $(\theta(\cdot; \alpha, \mu), 0)$ globally asymptotically stable?

2. If $\alpha > \beta > \mu/min_{\overline{\Omega}}m$, $\mu = \nu$, and $m > 0$, is $(0, \theta(\cdot; \beta, \nu))$ globally asymptotically stable?

3. If $0 \leq \alpha/\mu < 1/max_{\overline{\Omega}}m$, $\alpha = \beta$, is $(\theta(\cdot; \alpha, \mu), 0)$ globally asymptotically stable for any $\nu > \mu$?

4. If $\alpha > \max(\mu/\min_{\overline{\Omega}} m, \max_{\overline{\Omega}} m/\min_{\overline{\Omega}} m_x)$, $\alpha = \beta$ and $\nu > \mu$, is $(0, \theta(x; \beta, \nu))$ globally asymptotically stable?

5. Is there a unique r such that if $\alpha/\mu = r$ and $\beta/\nu \neq r$, then $(\theta(\cdot; \alpha, \mu), 0)$ is globally asymptotically stable?

   In addition, we have the following conjectures which we proved for a one-dimensional domain with $m_x > 0$. Do these hold in general for higher-dimensional domains and more general m?

6. Is $\int_\Omega \nabla(e^{-(\alpha_0/\mu_0)m}\theta_0) \cdot \nabla\theta_0 < 0$ for $\alpha \gg 1$?

7. Is $\int_\Omega (\nabla(e^{-(\alpha_0/\mu_0)m}\theta_0) \cdot \nabla m)\theta_0 < 0$ for $\alpha \gg 1$?

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