IDEAL FREE DISPERSAL: DYNAMICS OF TWO AND THREE COMPETING SPECIES

DISSERTATION

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By

Daniel S. Munther, M.S.

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Dissertation Committee:

Professor Yuan Lou, Advisor

Professor Chiu-Yen Kao

Professor Barbara Keyfitz

ABSTRACT

We utilize reaction-diffusion-advection equations in an adaptive dynamic framework to study the evolution of dispersal of two competing species. The species are assumed to be identical except for their dispersal strategies which consist of random movement (diffusion) and biased movement (advection) upward along resource gradients. We focus on how spatial heterogeneity in the habitat influences selection. A key facet of this relationship is that diffusion creates a mismatch between a species population density at steady state and the resource function [9]. This led Cantrell et al. [9] to introduce a conditional strategy which can perfectly match the resource, resulting in the ideal free distribution of the species at equilibrium.

This ideal free strategy (IFS) serves as a basis for our study. Not only do we show that it is a global evolutionarily stable strategy, but we find conditions under which it is convergent stable, varying random dispersal rates, advection rates, or both of these parameters at the same time. For two similar strategies on the "same side" of the IFS we show that when resource function is monotone, the strategy which is closer to the IFS is generally selected. For nonmonotone resource functions, we find that there may exist nonideal free strategies which are locally evolutionarily stable and/or convergent stable [21]. In addition, we find that for certain nonmonotone resource functions, two similarly competing species can coexist, which enables us to also show how three species coexistence is possible.

A mi amada Daniellee

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For God, who said, "Light shall shine out of darkness," is the One who has shone in our hearts to give the Light of the knowledge of the glory of God in the face of Christ Jesus. But we have this treasure in earthen vessels, so that the surpassing greatness of the power will be of God and not from ourselves ...

-Paul of Tarsus

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VITA

1980	Born in New York, New York
2004	B.S. in Mathematics, The Ohio State University
2006	M.S. in Mathematics, The Ohio State University
2004-Present	Graduate Teaching Associate, The Ohio State University

PUBLICATIONS

I. Averill, Y. Lou, and D. Munther, On several conjectures from evolution of dispersal, *J. Biol. Dyn.*, in press.

R. Gejji, Y. Lou, D. Munther, and J. Peyton, Evolutionary convergence to ideal free dispersal strategies and coexistence, *Bulletin of Mathematical Biology*, in press.

FIELDS OF STUDY

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Application of differential equations to population dynamics and epidemiology

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CHAPTER 1

INTRODUCTION

As a broad aim of theoretical ecology is to determine how the interplay within a species and interactions between organisms and their environment influence the location, size and structure of a population, one quickly realizes that accounting for all such details is an unlikely task. Instead, one attempts to identify and describe the essential elements of these interactions, anticipating that such biological fundamentals can provide meaningful insight. Dispersal is one such aspect which is indispensable in determining the distribution, dynamics, and persistence of a species within its habitat. From an ecological point of view, the implications of the spread and movement of a population have received much attention from researchers (searching *Google Scholar* with key words “ecology” and “dispersal” produces over 140,000 hits for years later than 1992).

Another viewpoint which has also received considerable attention in the last two decades concerns the evolution of dispersal (again, searching *Google Scholar* with key words “evolution” and “dispersal” produces over 130,000 hits for years later than 1992). However, the rationale behind why certain dispersal strategies evolve has drawn much less attention [15]. One reason for this is that it is difficult to precisely identify and then assess mechanisms which are thought to influence evolution. Consequently, there remains somewhat of a disconnect between observable evolutionary data and proposed evolutionary theory [15].

While narrowing the gap between data and theory presents an imposing challenge, over the last few decades, studies have identified several mechanisms as being key players in the evolution of dispersal. These include habitat extinction risks, competition among relatives, temporal and spatial variability in environment quality, cost of dispersal, and inbreeding [15]. In order to shed light on how these processes affect the evolution of dispersal, researchers usually have taken an approach where they consider one factor more or less independently. The following three subsections highlight some of the recent major studies concerning the effect of environmental variability on selection for or against dispersal.

1.1 Recent Studies: A Brief Overview

1.1.1 Discrete Space, Discrete Time Models

While such models were not among the first to be studied, Holt and McPeek in [42] utilized the difference equation approach, observing some novel results concerning the effects of spatial and temporal variability on the evolution of dispersal. They considered a two patch, metapopulation model from a numerical perspective, demonstrating that some form of dispersal is usually selected. In addition, they noted that a necessary condition for such selection is variation in fitness between patches. Previous studies [20], [46], and [37], which ignored kin competition and asymmetric dispersal, suggested that in order for positive rates of dispersal to evolve, the habitat must vary both spatially and temporally. In contrast to these analyses, Holt and McPeek considered a conditional dispersal strategy (i.e. habitat dependent strategy), finding that spatial heterogeneity is enough to favor nonzero dispersal rates between patches. The underlying reason is that a species employing a conditional strategy is able to offset fitness costs by balancing their movement between both high and low fitness patches.

Building on their work, Holt and McPeek in [31] as well as Doebeli and Ruxton in [18] showed, once again using numerical methods, that in a spatially homogeneous habitat where population dynamics were cyclic or chaotic, dispersal is also preferred. These studies showed that the internal dynamics of a population, rather than external environmental factors alone, can give rise to spatiotemporal fluctuations needed to support conditions (like those in [37]) which favor dispersal [41]. Furthermore, both studies observed a phenomenon known as evolutionary branching. That is, two dispersal phenotypes can coexist, but as evolutionary time continues, these phenotypes progressively become more and more disparate [18].

In order to gain a more universal view of the evolution of dispersal, Kirkland et al. in [35] considered a general category of difference equation models, loosening the assumptions of Holt and McPeek [42] (as well as assumptions made in several other papers, including [27], [30], and [17]). In particular, they analytically investigated a spatially varying multi-patch model in which dispersal strategies can be either conditional or passive, with no symmetry conditions on such movement [35]. Relying on the theory of nonnegative matrices, they demonstrated that when restricting to unconditional dispersal strategies, dispersal is not selected. That is, similar to [27], they found that when comparing two competing species, the slower disperser will win. However, when considering competition among conditional dispersers (assuming no dispersal costs), they observed the existence of a "one-parameter family" of strategies that resist invasion and at equilibrium manifest a population distribution in which fitness is equilibrated throughout the environment. Not only did this result generalize the two-patch numerical findings of Holt and McPeek in [42], it also provided analytic support. Nevertheless, Kirkland et al. mentioned in [35] that one must take care when inferring about these “ideal-free strategies” in that the “slightest dispersal cost destroys this one-parameter family of evolutionary stable strategies and only leaves the non-dispersal strategy as a candidate for an evolution stable strategy.”

1.1.2 Discrete Space, Continuous Time Models

In 1983, Alan Hastings published a significant analytic study concerning the evolution of passive dispersal. Among other things, he considered a single species n-patch model in which movement between patches is symmetric in the sense that the net flux of each patch is zero. Taking into account the effects of spatial inhomogeneity on such movement, he asked “can spatial variation alone lead to selection for increased dispersal in a deterministic model?” [27]. He found that the slower diffuser is more likely to be selected as “passive diffusion takes individuals from more favorable regions to less favorable regions more often than it does the reverse...” [27].

Obtaining similar results to Hastings, Holt [30] explored a two patch single species model. Not only did he provide analytic justification as to why “passive dispersal should always be selectively disadvantageous (ignoring kin effects) in a spatially heterogenous but temporally constant environment”, but he also gave a “heuristic argument”, relying on optimal habitat theory [30]. In essence, Holt demonstrated that positive diffusion rates are not compatible with predictions from the theory of optimal habitat selection, which, in this two-patch context, assumes that individuals will seek the patch where fitness is greater and at evolutionary equilibrium, either all individuals will be in the patch with the higher fitness or individuals will be distributed in both patches such that each patch has the same fitness. While his discussion develops biological intuition, Holt also asserted that such an argument is able to extend Hastings’ conclusions to models that consider more than one species.

However, while such models describe the behavior of one or more species, the conclusions of Hastings and Holt only apply to the evolution of passive dispersal. In 2006, V. Padrón and M.C. Trevisan [43] used both analytic and numerical techniques to examine a single-species n-patch model with a spatially inhomogeneous but temporally constant environment. Their model generalized Hastings' approach as they allowed for asymmetric dispersal strategies which depend on the variability of the surrounding habitat. Similar to [42], assuming no costs of dispersal, Padrón and Trevisan, showed that there exists a conditional (non-passive) dispersal strategy which is evolutionarily stable. That is, individuals employing such a strategy of movement will not be able to be invaded by a small population of individuals with a different dispersal strategy. Furthermore, they noted that this ESS (evolutionarily stable strategy) exhibits a property commonly predicted by such dispersion models; that fitness is equilibrated throughout the environment. That is, with the progression of evolutionary time, rather than promoting a source-sink configuration, the population moves towards a "balanced population distribution" which closely fits the "environmental carrying capacity" [43]. This type of distribution is known as the ideal free distribution and will be further discussed in sections to follow.

1.1.3 Continuous space, Continuous Time Models

Perhaps one of the earliest papers in which reaction-diffusion equations are connected with a diffusive description of the dispersal of a population is "Random dispersal in theoretical populations" written by J.G. Skellam in 1951 [47]. R.S. Cantrell and C. Cosner, in their book [6], go so far as to refer to Skellam's work as the 'origin of this species', remarking that "his landmark paper..... profoundly affected the study of spatial ecology." While Skellam's contribution provided a new approach to dispersal problems, modeling such scenarios with reaction-diffusion equations increased significantly only in last few decades.

In terms of the effect of spatial variability on the selection of dispersal strategies, we again begin with Alan Hastings' work in [27]. In addition to the ODE n-patch model mentioned above, Hastings examined the dynamics of a single species diffusion equation. Considering only passive dispersal strategies, he found that dispersal is not selected as diffusion rates progress towards zero in evolutionary time.

Finding results similar to Hastings, Dockery et al. [17] studied a system of n reaction-diffusion equations which describe the dynamics of a species with n phenotypes (here the phenotypes differ only in their diffusion rates). While they were able to show analytically that "the only nontrivial equilibrium is a population dominated by the slowest diffusing phenotype", they were only able to numerically support the conjecture that selection will always be for the slowest diffuser. However, in the case when $n = 2$, they proved that the slower diffuser will in fact evolve.

Much like in [17], V. Hutson et al. [33] considered a reaction-diffusion model for two phenotypes, however they included temporal periodicity as well as spatial variability in the environment. As in other studies, they found that in a spatially heterogeneous but temporally constant environment, the faster diffuser will suffer defeat. But they also saw that when the environment varies in both space and time, the faster diffuser can be selected. At first glance, it would seem that the faster phenotype is selected as it is able to move to richer resources at any select time. However, they cautioned the plausibility of such an explanation as the slower diffuser wins in extremal cases of frequencies of environmental change [33].

The reaction-diffusion models mentioned so far all concern unconditional dispersal. While these models apply to organisms whose movement relies on factors such as wind, ocean currents, gravity, etc., Hastings reasoned that to understand the movement of animals, one must consider more than random movement [27]. He suggested that environmental cues may have a significant effect on the dispersal strategy of the species in question. In line with such rationale, Belgacem and Cosner [4] added an advection term to the well-known logistic reaction-diffusion equation for population growth, noting that in a spatially inhomogeneous environment, a population may move towards regions that are more favorable. This biased movement toward better locations within a habitat combined with random diffusion is known as a conditional dispersal strategy.

In particular, this notion of a conditional strategy motivated Cosner and Lou to ask "does movement toward better environments always benefit a population?" [13]. Utilizing a single species logistic reaction-diffusion equation, with the assumption of a spatially varying local growth rate, they found that increasing the advection in the direction of the gradient of the growth rate is advantageous for the population. However, this result depends largely on the shape of the environment. That is, Cosner and Lou [13] found that if the habitat is convex then the increase of advection will benefit the population, however, for some non-convex environments, such an increase may hurt the species as some of the best regions may be unattainable by moving upward along the environmental gradient.

Expanding the work of Cosner and Lou, Cantrell et al. [7] analyzed a reaction-diffusion-advection model for two competing phenotypes, differing only in their dispersal strategies. Specifically, one phenotype disperses with a conditional strategy, that is, random diffusion coupled with movement upward along resource gradients, while the other moves only by passive diffusion. Cantrell et al. determined that sometimes (under appropriate environmental conditions) the phenotype with the advective strategy, even though it may diffuse faster than the competitor exhibiting pure diffusion, gains a competitive advantage [7]. Hence, they concluded that the evolutionary trend towards a species with faster diffusion rates is likely if the species also develops the capacity to move towards better resources [7]. However, Cantrell et al. [8], using the same model as [7], noted that if both competitors have an arbitrary diffusion rate and the advection rate of the conditional disperser is significantly greater than its diffusion rate, coexistence is possible. Thus if the movement towards favorable resources is too strong, the pure diffuser is able to make use of the "leftovers", i.e. resources in less favorable locations, and thus survive.

Naturally following the work of Cantrell et al. in [7] and [8], Chen et al. [11] considered a similar model but allowed both competitors to employ conditional strategies. In particular, they assumed that the advective rate of one of the competitors is much higher than the other. Under this supposition, they discovered at least two phenomena. First, if the species with the more balanced strategy has an advection rate which is slightly less than its diffusion rate, coexistence can occur; however, if its advection rate is slightly more than its diffusion rate, it will win out over the species with high advection. Thus, Chen et al. concluded that "selection is against excessive advection along resource gradients, which suggests that an intermediate biased movement rate may evolve" [11].

Aiming to connect the results of [17], [7], [8], and [11], Hambrock and Lou [24] investigated a model similar to that of [11]. They established two main results. First, they set the advection rates of both species to be equal and let the diffusion rates vary. They found that if both diffusion rates are sufficiently close and larger than the advection rate, the slower diffuser wins, supporting Hastings' result. However, if both diffusion rates are sufficiently close and smaller than the advection rate (note here the advection rate must be large) then the faster diffuser wins. Thus, they concluded that the magnitude of the advection rates directly affects the course of the evolution of random diffusion [24].

Second, they let the diffusion rates of the species remain equal, varying the advection rates. In this case, they saw that if both advection rates are close enough and smaller than the diffusion rate, the species with larger advection evolves. Whereas, if the advection rates are close and larger than the diffusion rate, the species with less advection is selected. Hence, they indicated that evolution does not seem to favor small or large advection, rather some intermediate rate may be best [24].

In a slightly different direction, Cantrell et al. [9] noticed that the results of both [27] and [17] were closely related to the fact that diffusion produces a disparity between population density and the quality of the environment. They incorporated a conditional strategy of both advection and diffusion into a reaction-diffusion-advection model, allowing for the possibility that populations can "match environmental quality". We will call such a distribution at equilibrium an ideal free distribution (IFD) and call a corresponding strategy that allows for IFD, an ideal free strategy.

The notion of an ideal free distribution originates from the theory of habitat selection. Fretwell and Lucas [19] defined "ideal" in the sense that each individual within a species chooses the environment "most suitable to them" and individuals are "free" to move into any habitat [19]. As individuals at equilibrium can exactly match the habitat quality, their fitness (measured by the local intrinsic growth rate) will be equalized across the habitat. In this study, we adopt the IFD introduced in Cantrell et al. [8, 9], noting that a species at IFD has the properties that the net-movement and the local growth rate are both zero everywhere.

1.2 An Adaptive Dynamic Approach

1.2.1 Adaptive Dynamic Basics

Many factors are involved when trying to understand the adaptive evolution of a particular species. As these factors depend both on ecological aspects as well as the transfer of genetic information from parent to offspring, researchers have taken various perspectives, attempting to find some synthesis that adequately incorporates both ecology and genetics [22]. However, this has proven to be difficult. For example, in the context of the evolution of dispersal in a spatially variable environment, one tries to understand how interactions between members of a population and their habitat connect to the selective pressures that drive evolution [15]. As this interplay can be quite sophisticated, difficulties can arise when trying to simultaneously understand the genetic dynamics of the species [15].

In order to address some of these complications, J. Maynard Smith and G. R. Price [49] introduced an important concept adapted from game theory and from studies by MacArthur [39] as well as Hamilton [25] (see [22] for more details). In 1973 they published 'The logic of animal conflict', in which they proposed the notion of an evolutionary stable strategy or ESS. In general, an ESS is a strategy that allows for maximal reproductive fitness [49]. However, the game-theortic models in which evolutionary stable strategies were studied, had a tendency to "oversimplify strategies and feedbacks by relying on payoff matricies" [15]. Thus, new approaches for understanding phenotypic evolution were needed.

A more recent perspective which pertains to the evolution of phenotype is that of adaptive dynamics. A key part of this viewpoint concerns how the environment affects interactions on the individual level in a population, how these interactions affect the population at large and finally how the population affects the resulting environment. That is, "the deterministic dynamics of well-mixed populations is governed by a feedback loop at the ecological time scale" [16]. In addition, reproduction is assumed to be clonal, thus eliminating the complexity involved with the genotype $\rightarrow$ phenotype map. Roughly we start with a resident species (which is at equilibrium) and a rare invading species which can be thought of as a type of "mutant" offspring. By "mutant" we mean that the invading species is identical to the resident except for a slight variation in the specific aspect of the phenotype in question. Thus, questions concerning the survivability of the mutant population, replacement of the resident population by the invading population, and even the possible coexistence of both populations depend on the long-term growth rate of the invading species in the environmental situation determined by the resident [16].

Naturally, attempts to understand such inquiries cause one to ask if there is some unbeatable strategy which would ensure a resident species' sole existence. As was mentioned previously, such a strategy is an ESS, which appears in alternate approaches to evolutionary theory. What is significant about the adaptive dynamic setting is that it allows one to determine the existence and nature of evolutionary attractors. Such attractors are known as convergent stable strategies or CSS. Basically, a strategy is convergent stable if selection favors changes that are closer to it as opposed to those which are farther away.

While many of the studies discussed in Section 1.1 are approached from an ESS viewpoint, some of the later papers, such as [24] and [9] have an adaptive dynamic framework. For example, in [24], Hambrock and Lou showed that selection is against slow as well as fast advection rates, indicating that evolution seemed to be towards an intermediate advection rate. In the context of adaptive dynamics, this intermediate rate acts as a CSS. Furthermore, in [9], the authors showed that their ideal free strategy is a local ESS as well as a CSS along particular paths.

1.2.2 Main Questions and Findings

Concerning this present study, we aim to provide a context from which we can extend as well as connect some of the results of [24] and [9]. To do so we first explore the question of whether or not the ideal free strategy is a global ESS. Cantrell et al

[9] predicted that the ideal free strategy is indeed a global ESS and we show their conjecture to be true [1].

The second main question involves the following: if we start with a strategy which is not an ESS, to where and how is it driven by selection? In adaptive dynamic language, this question is closely related to finding and understanding the nature of convergent stable strategies. The fact that the ideal free strategy is a global ESS provides some footing with which to approach our second question as this strategy acts as a reference point from which we can compare competitions between species whose strategies both lie on the "same side" of the IFS.

We find that under certain conditions the ideal free strategy is a CSS. For a monotone resource curve, "by varying a single trait responsible for the dispersal strategy, the species whose traits are closer to an ideal free strategy will win. In many cases, subsequent invasions of species will allow nonideal free strategies to evolve towards ideal free strategies. However, if we vary two traits, it is possible for the species whose dispersal strategy is further away from ideal free to win and this allows for divergence away from ideal free strategies. Despite this possibility, results suggest that random perturbations of the two dispersal traits lead toward convergence to ideal free strategies [21]".

Not only are we interested in describing these conditions for evolutionary convergence to ideal free strategies, but also those that promote coexistence. Again, utilizing the IFS as a reference point we compare strategies which lie on "opposite sides" of the IFS, finding conditions for such two species coexistence. "For a resource function that is nonmontone, we show that there exists a new region of two species coexistence where neither species employs an ideal free strategy" and where both strategies lie on the "same side" of the IFS [21]. Numerically, we argue that convergent stable strategies may exist in this new region as well as a variety of evolutionary outcomes, including the possibility of evolutionary branching, which depend on the magnitude of difference between competing strategies [21]. Finally, we show that three species permanence is possible for suitable nonmonotone resource functions as well as the existence of a componentwise positive three species steady state.

1.3 Consumer Resource Models

1.3.1 Model Derivation

Given a bounded domain in $\mathbb{R}^N$, say Ω, suppose we let $R(x,t)$ denote the density of an immobile resource at $x \in \Omega$, and for some time $t > 0$. Also, suppose we have two competing consumers whose density in Ω at any time $t > 0$ is given by u and v. Classically, the dynamics of R when considering a non-spatial model are assumed to be logistic in the absence of consumers, see [50]. Although we include a spatial component, we can utilize the same approach, expressing the dynamics of R as

$$\epsilon R_t = R[m(x) - a_u u - a_v v - R] \quad \text{in} \quad \Omega \times (0, \infty). \tag{1.3.1}$$

Supposing that $0 < \epsilon \ll 1$, we assume that the resource dynamics are near quasi-steady state and we can thus write $R(x) = m(x) - a_u u - a_v v$ in Ω. Notice that in (1.3.1), $m(x)$ is the intrinsic growth rate of R and a_u, a_v are real parameters measuring the strength of competition (Note: here m can be thought of as the distribution of R's resources.) Because we want to consider competition between dispersive consumers and take into account spatial variance, we appeal to a logistic reaction-diffusion-advection model:

$$\begin{cases} u_t = \mu \nabla \cdot [\nabla u - u \nabla P(x)] + u(f_u(R) - d_u) & \text{in} \quad \Omega \times (0, \infty), \\ v_t = \nu \nabla \cdot [\nabla v - v \nabla Q(x)] + v(f_v(R) - d_v) & \text{in} \quad \Omega \times (0, \infty). \end{cases} \tag{1.3.2}$$

Here we consider two species, with densities $u(x,t)$ and $v(x,t)$ for $x \in \Omega$ and $t > 0$, which may differ in their intrinsic growth rates, as given by $f_u(R)$ and $f_v(R)$, as well as their dispersal strategies. Note that $u(x, 0)$ and $v(x, 0)$ are both nonnegative and not identically zero. Furthermore, we assume that the dispersal strategy, for either species, includes both random diffusion as well as directed movement along a specified gradient. The random diffusion rates are given by the real parameters $\mu, \nu > 0$. The functions $P(x)$, $Q(x) \in C^2(\bar{\Omega})$ provide advective directions as well as regulate the speeds in such directions. Typically, such P and Q can be taken as functions of $m(x)$; see for example [11], [8], and [9]. In such cases then, this means that the consumer is tracking the resource's resource. Finally, $d_u, d_v > 0$ are the natural death rates of u and v, respectively.

Since we want to consider only the effects of spatial variation and not temporal changes in the environment on such competition, we use our steady state assumption on R, substituting $R(x) = m(x) - a_u u - a_v v$ into (1.3.2). Also, taking $f_u(R) = f_v(R) = R$, $a_u = a_v = 1$, $d_u = d_v = d > 0$, upon substitution into (1.3.2) we have

$$\begin{cases} u_t = \mu\nabla \cdot [\nabla u - u\nabla P(x)] + u(m(x) - u - v - d) & \text{in} \quad \Omega \times (0, \infty), \\ v_t = \nu\nabla \cdot [\nabla v - v\nabla Q(x)] + v(m(x) - u - v - d) & \text{in} \quad \Omega \times (0, \infty). \end{cases} \tag{1.3.3}$$

Finally, we set $\tilde{m} = m - d$ on Ω. Dropping the tilde on $\tilde{m}$, and adding no-flux boundary conditions, we have the familiar Lotka-Volterra reaction-diffusion-advection model given by

$$\begin{cases} u_t = \mu\nabla \cdot [\nabla u - u\nabla P] + u(m - u - v) & \text{in} \quad \Omega \times (0, \infty), \\ v_t = \nu\nabla \cdot [\nabla v - v\nabla Q] + v(m - u - v) & \text{in} \quad \Omega \times (0, \infty), \\ [\nabla u - u\nabla P] \cdot n = [\nabla v - v\nabla Q] \cdot n = 0 & \text{on} \quad \partial\Omega \times (0, \infty). \end{cases} \tag{1.3.4}$$

Note that we assume $m(x) \in C^2(\bar{\Omega})$ is positive and nonconstant. Here $\partial\Omega$ is the smooth boundary of Ω (assuming $N \geq 2$) and n is the outward unit normal vector on $\partial\Omega$. Note that the boundary conditions mean that no member of species u or v can cross $\partial\Omega$.

1.3.2 Well-Posedness and Monotonicity of (1.3.4)

Concerning the existence and biological applicability of solutions of (1.3.4) we note that by the maximum principle for cooperative systems [45] and standard theory for parabolic equations [28], if the initial conditions of (1.3.4) are nonnegative and not identically zero, system (1.3.4) has a unique positive smooth solution which exists for all time and it defines a smooth dynamical system on $C(\bar{\Omega}) \times C(\bar{\Omega})$ [6, 29, 48]. The stability of steady states of (1.3.4) is understood with respect to the topology of $C(\bar{\Omega}) \times C(\bar{\Omega})$. The following result is a consequence of the maximum principle and the structure of (1.3.4); see Theorem 3, [9].

Theorem 1.3.1. *The system* (1.3.4) *is a strongly monotone dynamical system, i.e.,*

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

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

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

Because we are concerned with the global dynamics of system (1.3.4), our analysis depends a great deal on its nonnegative steady states. These steady states are nonnegative solutions (u,v) of

$$\begin{cases} \mu\nabla \cdot [\nabla u - u\nabla P] + u(m - u - v) = 0 \quad \text{in} \quad \Omega, \\ \nu\nabla \cdot [\nabla v - v\nabla Q] + v(m - u - v) = 0 \quad \text{in} \quad \Omega, \\ [\nabla u - u\nabla P] \cdot n = [\nabla v - v\nabla Q] \cdot n = 0 \quad \text{on} \quad \partial\Omega. \end{cases} \tag{1.3.5}$$

In order to guarantee the existence of such solutions, we appeal to the single species model described by the following:

$$\begin{cases} \mu\nabla \cdot [\nabla u^* - u^*\nabla P] + u^*(m - u^*) = 0 \quad \text{in } \Omega, \\ [\nabla u^* - u^*\nabla P] \cdot n = 0 \quad \text{on } \partial\Omega. \end{cases} \tag{1.3.6}$$

It is well known that if $m > 0$ in Ω, then Equation (1.3.6) has a unique positive steady state, denoted by u^*, which is globally asymptotically stable among nonnegative nontrivial initial data. Thus by symmetry, we see that (1.3.4) has two semi-trivial steady states written as $(u^*, 0)$ and $(0, v^*)$ respectively. Also of interest will be the existence and nature of coexistence states or positive steady states (i.e. both components are positive) of (1.3.4).

The following result is a consequence of Theorem 1.3.1 and the monotone dynamical system theory [29, 48, 40, 14]:

Theorem 1.3.2. *If system* (1.3.4) *has no coexistence state, then one of the semi-trivial steady states is unstable and the other one is globally asymptotically stable* [32]*; If both semi-trivial steady states are unstable, then* (1.3.4) *has at least one stable coexistence state* [14, 40]*.*

CHAPTER 2

EVOLUTIONARY STABILITY

Proceeding as in [9], we begin by considering the equilibrium equation for a single species

$$\mu\nabla \cdot [\nabla u^* - u^*\nabla P] + u^*(m - u^*) = 0 \quad \text{in } \Omega, \tag{2.0.1}$$

$$[\nabla u^* - u^*\nabla P] \cdot n = 0 \quad \text{on } \partial\Omega. \tag{2.0.2}$$

A key observation of Cantrell et al. [9] is that $P = \ln m$ if and only if $u^* = m$ is a solution of (2.0.1). In particular, if $P = \ln m$, the corresponding unique steady state $u^* = m$ satisfies (i) $u^* - m \equiv 0$ and (ii) $\nabla u^* - u^*\nabla P \equiv 0$ in Ω. Part (i) means that the fitness of the species, which is represented by its local growth rate, is zero across the habitat. Part (ii) means that there is no net movement of species. We shall refer to a choice of μ and $P = \ln m$ as an ideal free dispersal strategy if it gives rise to an ideal free distribution of the population density at equilibrium. Note, $P = \ln m$ is an ideal free dispersal strategy with any choice of positive μ. The advantage of ideal free dispersal strategies over other strategies is clearly illustrated by the following result:

Theorem 2.0.3. *Suppose that m is a positive nonconstant function, $P = \ln m$, and $Q - \ln m$ is nonconstant. Then, $(m, 0)$, as a steady state of (1.3.4), is globally asymptotically stable among all nonnegative, not-identically zero initial data.*

Theorem 2.0.3 was first established by Cantrell et al. [9] when Q is a small perturbation of $\ln m$ and $\mu = \nu$. The full generality in current form was recently given in [1]. In adaptive dynamic terms, this result says that the strategy $P = \ln m$ is a global ESS.

Before proving Theorem 2.0.3, we state a useful result concerning the linear stability of semi-trivial steady states of (1.3.4) (see, e.g. Lemma 5.5 in [11]).

Lemma 2.0.4. *The steady state $(u^*, 0)$ is linearly stable/unstable if and only if the following eigenvalue problem, for $(\lambda, \psi) \in \mathbb{R} \times C^2(\bar{\Omega})$, has a positive/negative principal eigenvalue:*

$$\begin{cases} \nu \cdot [\nabla\psi - \psi\nabla(\ln m + \epsilon R)] + (m - u^*)\psi = -\lambda\psi \quad \text{in } \Omega, \\ [\nabla\psi - \psi\nabla(\ln m + \epsilon R)] \cdot n = 0 \ \text{on } \partial\Omega, \end{cases}$$

where $\epsilon \in \mathbb{R}$ and $R \in C^2(\bar{\Omega})$. The criterion for the linearized stability of the semi-trivial steady state $(0, v^*)$ is analogous.

2.1 Proof of Theorem 2.0.3

In this section we let $P(x) = \ln m$, considering the following model:

$$\begin{cases} u_t = \mu\nabla \cdot [\nabla u - u\nabla \ln m] + u[m(x) - u - v] \quad \text{in } \Omega \times (0, \infty), \\ v_t = \nu\nabla \cdot [\nabla v - v\nabla Q(x)] + v[m(x) - u - v] \quad \text{in } \Omega \times (0, \infty), \\ [\nabla u - u\nabla(\ln m)] \cdot n = [\nabla v - v\nabla Q(x)] \cdot n = 0 \text{ on } \partial\Omega \times (0, \infty). \end{cases} \tag{2.1.1}$$

Theorem 2.1.1. [1] *Given any $\mu, \nu > 0$. Suppose that $Q(x) - \ln m$ is not a constant function. Then, the semi-trivial steady state $(u^*, 0)$ is globally asymptotically stable.*

Proof. First, we show that (2.1.1) has no positive steady states, arguing by contradiction. Suppose that u, v are positive steady states of (2.1.1), i.e. they satisfy

$$\begin{cases} \mu\nabla \cdot [\nabla u - u\nabla(\ln m)] + u[m(x) - u - v] = 0 \quad \text{in } \Omega, \\ \nu\nabla \cdot [\nabla v - v\nabla Q(x)] + v[m(x) - u - v] = 0 \quad \text{in } \Omega, \\ [\nabla u - u\nabla(\ln m)] \cdot n = [\nabla v - v\nabla Q(x)] \cdot n = 0 \text{ on } \partial\Omega. \end{cases} \tag{2.1.2}$$

Set $w = u/m$. Then w satisfies

$$\mu\nabla \cdot [m\nabla w] + mw(m-u-v) = 0 \text{ in } \Omega, \quad \frac{\partial w}{\partial n}|_{\partial\Omega} = 0.$$

Since $w > 0$, dividing the equation of w by w and integrating in Ω, we have

$$\mu\int_\Omega m\frac{|\nabla w|^2}{w^2} + \int_\Omega m(m-u-v) = 0. \tag{2.1.3}$$

Integrating the equations of u and v, we have

$$\int_\Omega u(m-u-v) = 0 \tag{2.1.4}$$

and

$$\int_\Omega v(m-u-v) = 0, \tag{2.1.5}$$

respectively.

Adding up (2.1.4) and (2.1.5) we have

$$\int_\Omega (u+v)(m-u-v) = 0. \tag{2.1.6}$$

Subtracting (2.1.6) from (2.1.3) we obtain

$$\mu\int_\Omega m\frac{|\nabla w|^2}{w^2} + \int_\Omega (m-u-v)^2 = 0,$$

which implies that $m - u - v \equiv 0$ and $w = s$ for some positive constant $s > 0$; i.e, $u/m = s$ for some constant s. Since $u > 0$ and $v > 0$, from $m-u-v = 0$ we see that $s \in (0,1)$ and $v = (1-s)m$. Substituting $(u,v) = (sm, (1-s)m)$ into the equation of v and dividing the result by $(1-s)$, we see that

$$\nu\nabla \cdot [m\nabla(\ln m - Q(x))] = 0 \quad \text{in } \Omega, \quad \nabla(\ln m - Q(x)) \cdot n|_{\partial\Omega} = 0. \tag{2.1.7}$$

By the maximum principle [45], $Q(x) - \ln m$ must be equal to some constant, which contradicts our assumption. This proves that (2.1.1) has no positive steady states.

Next, we show that $(0, v^*)$ is unstable. By Lemma 2.0.4, it suffices to show the smallest eigenvalue, denoted by λ_1, of the linear eigenvalue problem

$$\begin{cases} \mu\nabla\cdot[\nabla\varphi - \varphi\nabla\ln m] + (m - v^*)\varphi = -\lambda\varphi \quad \text{in } \Omega, \\ [\nabla\varphi - \varphi\nabla(\ln m)]\cdot n = 0 \text{ on } \partial\Omega \end{cases}$$

satisfies $\lambda_1 < 0$. Let φ_1 denote the positive eigenfunction of λ_1 uniquely determined by $\max_{\bar{\Omega}} \varphi_1 = 1$. Set $\psi = \varphi_1/m$. Then the previous equation can be written as

$$\mu\nabla\cdot[m\nabla\psi] + m(m - v^*)\psi = -\lambda_1 m\psi, \quad \nabla\psi\cdot n|_{\partial\Omega} = 0.$$

Dividing the equation of ψ by ψ and integrating the result in Ω, we have

$$\mu\int_\Omega m\frac{|\nabla\psi|^2}{\psi^2} + \int_\Omega m(m - v^*) = -\lambda_1\int_\Omega m. \tag{2.1.8}$$

Integrating the equation of v^* we have

$$\int_\Omega v^*(m - v^*) = 0. \tag{2.1.9}$$

Subtracting (2.1.9) from (2.1.8), we find that

$$\mu\int_\Omega m\frac{|\nabla\psi|^2}{\psi^2} + \int_\Omega (m - v^*)^2 = -\lambda_1\int_\Omega m.$$

Hence, $\lambda_1 < 0$ as long as $v^* \not\equiv m$. To this end, we argue by contradiction and suppose that $v^* \equiv m$. Then by the equation of v^*, we see that (2.1.7) holds, which implies that $Q(x) - \ln m$ is constant and we reach a contradiction. Hence, $v^* \not\equiv m$ and thus $\lambda_1 < 0$.

Finally, we show that the semi-trivial steady state $(u^*, 0)$ is globally asymptotically stable. This follows from Theorem 1.3.2, the fact that system (2.1.1) has no positive steady states, and the instability of the semi-trivial steady state $(0, v^*)$. □

The fact that $P = \ln m$ is a global ESS raises a natural question: Can one find dispersal strategies for two competing species such that the spatial distributions of both species at equilibrium are ideal free?

To address this question, we observe that if there exist nonnegative constants γ and τ such that $\gamma e^{P(x)} + \tau e^{Q(x)} \equiv m(x)$ in Ω, then $(u, v) = (\gamma e^{P(x)}, \tau e^{Q(x)})$ is a nonnegative steady state of (1.3.4) with "ideal free distribution" for both u and v; i.e., $m(x) - u - v \equiv 0$ in Ω and the net flux for both species in Ω is 0. Furthermore, we have the following result [21]:

Theorem 2.1.2. *Suppose that there exist positive constants γ and τ such that $\gamma e^{P(x)} + \tau e^{Q(x)} \equiv m(x)$ in Ω, and either $P - \ln m$ or $Q - \ln m$ is nonconstant. Then, $(u, v) = (\gamma e^{P(x)}, \tau e^{Q(x)})$ is the unique positive steady state of* (1.3.4)*, and it is globally asymptotically stable among all positive initial data.*

Remark 2.1.3. *When $\tau = 0$, $P - \ln m$ is constant and $Q - \ln m$ is nonconstant, Theorem* 2.1.2 *is reduced to Theorem* 2.0.3*. Hence, Theorem* 2.1.2 *generalizes Theorem* 2.0.3*.*

If both $P - \ln m$ and $Q - \ln m$ are constants, Theorem 2.1.2 fails since the system has a continuum of positive steady states of the form $\{(sm, (1 - s)m) : 0 < s < 1\}$. It is interesting that even if neither P nor Q alone can produce ideal free distribution (i.e., $P - \ln m, Q - \ln m$ are nonconstants), a linear combination of them can yield ideal free distributions for both competing species at equilibrium.

2.2 Proof of Theorem 2.1.2

To prove Theorem 2.1.2, we first prove the following result:

Lemma 2.2.1. [21] *Suppose that there exist positive constants γ and τ such that $\gamma e^{P(x)} + \tau e^{Q(x)} \equiv m(x)$ in Ω and either $P - \ln m$ or $Q - \ln m$ is nonconstant. Then, the system* (1.3.4) *has a unique positive steady state.*

Proof. Let (u^*, v^*) denote any positive steady state, i.e., it satisfies

$$\begin{cases} \mu\nabla \cdot [\nabla u^* - u^*\nabla P] + u^*(m(x) - u^* - v^*) = 0, \\ \nu\nabla \cdot [\nabla v^* - v^*\nabla Q] + v^*(m(x) - u^* - v^*) = 0, \\ [\nabla u^* - u^*\nabla P] \cdot n = [\nabla v^* - v^*\nabla Q] \cdot n|_{\partial\Omega} = 0. \end{cases} \tag{2.2.1}$$

Integrating the equations of u^* and v^* in Ω and adding up the results, we have

$$\int_\Omega (u^* + v^*)(m - u^* - v^*) = 0. \tag{2.2.2}$$

Dividing the equation of u^* by u^*/e^P and integrating in Ω, we have

$$\mu \int_\Omega \frac{e^{3P}}{(u^*)^2} \left|\nabla \frac{u^*}{e^P}\right|^2 + \int_\Omega e^P(m - u^* - v^*) = 0. \tag{2.2.3}$$

Dividing the equation of v^* by v^*/e^Q and integrating in Ω, we have

$$\nu \int_\Omega \frac{e^{3Q}}{(v^*)^2} \left|\nabla \frac{v^*}{e^Q}\right|^2 + \int_\Omega e^Q(m - u^* - v^*) = 0. \tag{2.2.4}$$

Multiplying (2.2.3) by γ and (2.2.4) by τ, and using $\gamma e^P + \tau e^Q \equiv m$ we have

$$\gamma\mu \int_\Omega \frac{e^{3P}}{(u^*)^2} \left|\nabla \frac{u^*}{e^P}\right|^2 + \tau\nu \int_\Omega \frac{e^{3Q}}{(v^*)^2} \left|\nabla \frac{v^*}{e^Q}\right|^2 + \int_\Omega m(m - u^* - v^*) = 0. \tag{2.2.5}$$

By (2.2.2) and (2.2.5) we have

$$\gamma\mu \int_\Omega \frac{e^{3P}}{(u^*)^2} \left|\nabla \frac{u^*}{e^P}\right|^2 + \tau\nu \int_\Omega \frac{e^{3Q}}{(v^*)^2} \left|\nabla \frac{v^*}{e^Q}\right|^2 + \int_\Omega (m - u^* - v^*)^2 = 0. \tag{2.2.6}$$

From (2.2.6) we see that $m - u^* - v^* = 0$ in Ω, $u^* = C_1 e^P$, and $v^* = C_2 e^Q$ for some positive constants C_1, C_2. Hence, $m = C_1 e^P + C_2 e^Q$ in Ω. This together with $\gamma e^{P(x)} + \tau e^{Q(x)} \equiv m(x)$ implies that $(C_1 - \gamma)e^P + (C_2 - \tau)e^Q = 0$. We claim that $C_1 = \gamma$. If not, we have $e^P = (C_2 - \tau)/(C_1 - \gamma)e^Q$. Substituting this expression into the equation of $\gamma e^{P(x)} + \tau e^{Q(x)} \equiv m(x)$ yields that $Q - \ln m$ is constant. Hence, $P - \ln m$ is also a constant. This contradicts our assumption. Hence, $C_1 = \gamma$, and consequently, $C_2 = \tau$. This shows that $(\gamma e^P, \tau e^Q)$ is the unique positive steady state. □

Lemma 2.2.2. [21] *Suppose that there exist positive constants γ and τ such that $\gamma e^{P(x)} + \tau e^{Q(x)} \equiv m(x)$ in Ω and either $P - \ln m$ or $Q - \ln m$ is nonconstant. Then both semi-trivial steady states $(\tilde{u}, 0)$ and $(0, \tilde{v})$ are unstable.*

Proof. The stability of $(\tilde{u}, 0)$ is determined by the principal eigenvalue of

$$\nu \nabla \cdot [\nabla \psi - \psi \nabla Q] + (m - \tilde{u})\psi = -\lambda \psi \quad \text{in } \Omega, \quad [\nabla \psi - \psi \nabla Q] \cdot n|_{\partial\Omega} = 0.$$

Dividing the above equation by ψ / e^Q and integrating the result in Ω, we have

$$-\lambda \int_\Omega e^Q = \nu \int_\Omega \frac{e^{3Q}}{\psi^2} \left| \nabla \frac{\psi}{e^Q} \right|^2 + \int_\Omega e^Q (m - \tilde{u}). \tag{2.2.7}$$

Dividing the equation of $\tilde{u}$ by $\tilde{u}/e^P$ and integrating the result in Ω, we have

$$0 = \mu \int_\Omega \frac{e^{3P}}{\tilde{u}^2} \left| \nabla \frac{\tilde{u}}{e^P} \right|^2 + \int_\Omega e^P (m - \tilde{u}). \tag{2.2.8}$$

Multiplying (2.2.7) by τ and (2.2.8) by γ, adding the results together, by $\gamma e^P + \tau e^Q = m$ we have

$$-\lambda \tau \int_\Omega e^Q = \nu \tau \int_\Omega \frac{e^{3Q}}{\psi^2} \left| \nabla \frac{\psi}{e^Q} \right|^2 + \gamma \mu \int_\Omega \frac{e^{3P}}{\tilde{u}^2} \left| \nabla \frac{\tilde{u}}{e^P} \right|^2 + \int_\Omega m(m - \tilde{u}).$$

Integrating the equation of $\tilde{u}$ in Ω, we have

$$\int_\Omega \tilde{u}(m - \tilde{u}) = 0.$$

Hence,

$$-\lambda \tau \int_\Omega e^Q = \nu \tau \int_\Omega \frac{e^{3Q}}{\psi^2} \left| \nabla \frac{\psi}{e^Q} \right|^2 + \gamma \mu \int_\Omega \frac{e^{3P}}{\tilde{u}^2} \left| \nabla \frac{\tilde{u}}{e^P} \right|^2 + \int_\Omega (m - \tilde{u})^2.$$

Therefore, $\lambda \leq 0$. We further show that $\lambda < 0$: if not, say $\lambda = 0$. Then $\tilde{u} - m \equiv 0$. This together with the equation of $\tilde{u}$ implies that $\tilde{u}/e^P$ is constant. As $\tilde{u} - m \equiv 0$, $P - \ln m$ is equal to some constant. This together with $\gamma e^P + \tau e^Q = m$ implies that $Q - lnm$ is also equal to some constant. Hence, both $P - \ln m$ and $Q - lnm$ are equal to constants, which is a contradiction. Hence, $\lambda < 0$ and $(\tilde{u}, 0)$ is unstable. Similarly, we can show that $(0, \tilde{v})$ is unstable. $\square$

Theorem 2.1.2 follows from the previous two lemmas and Theorem 1.3.2.

CHAPTER 3

CONVERGENT STABILITY

Another important idea in Adaptive Dynamics is that of convergent stable strategies (CSS), which act as attractors for evolutionary dynamics. Recall that a strategy is convergent stable if, roughly speaking, selection favors strategies that are closer to it over strategies that are further away.

Unless otherwise specified, we shall vary a single trait, i.e., we vary one parameter and fix all others, focusing on the convergent stability of the ideal free dispersal strategy for the following model:

$$\begin{cases} u_t = \nabla \cdot [\mu \nabla u - \alpha u \nabla \ln m] + u(m - u - v) \quad \text{in} \quad \Omega \times (0, \infty), \\ v_t = \nabla \cdot [\nu \nabla v - \beta v \nabla \ln m] + v(m - u - v) \quad \text{in} \quad \Omega \times (0, \infty), \\ [\mu \nabla u - \alpha u \nabla \ln m] \cdot n = [\nu \nabla v - \beta v \nabla \ln m] \cdot n = 0 \quad \text{on} \quad \partial\Omega \times (0, \infty), \end{cases} \tag{3.0.1}$$

where α, β are two non-negative constants that measure the speed of advection upward along the environmental gradient. Note that (1.3.4) can be reduced to (3.0.1) when $P = (\alpha/\mu) \ln m$ and $Q = (\beta/\nu) \ln m$. Note also that $\alpha = \mu$ is an ideal free strategy for species u, and $\beta = \nu$ represents an ideal free dispersal strategy for species v.

To state our results, we first consider the scalar equation

$$\begin{cases} u_t = \nabla \cdot [\mu \nabla u - \alpha u \nabla \ln m] + u(m - u) \quad \text{in} \quad \Omega \times (0, \infty), \\ [\mu \nabla u - \alpha u \nabla \ln m] \cdot n = 0 \quad \text{on} \quad \partial\Omega \times (0, \infty). \end{cases} \tag{3.0.2}$$

It is well known that if $m \in C^2(\bar{\Omega})$ and is positive, then (3.0.2) has a unique positive steady state, denoted by $\theta_{\alpha,\mu}$, for every $\alpha \geq 0$ and $\mu > 0$. Therefore, (3.0.1) has exactly two semi-trivial steady states, denoted as $(\theta_{\alpha,\mu}, 0)$ and $(0, \theta_{\beta,\nu})$, respectively.

Before we present our findings in this chapter, we will use the next three sections to establish some technical results.

3.1 Stability of Semitrivial Steady States

We begin by determining stability conditions for $(\theta_{\alpha,\mu}, 0)$. Given $\alpha, \mu > 0$, we want to investigate the stability of $(\theta_{\alpha,\mu}, 0)$ under a small perturbation of ν and β. The following lemma will be useful.

Lemma 3.1.1. *The steady state $(\theta_{\alpha,\mu}, 0)$ is stable/unstable if and only if the following eigenvalue problem, for $(\lambda, \varphi) \in \mathbb{R} \times C^2(\bar{\Omega})$, has a positive/negative principal eigenvalue λ^*:*

$$\begin{cases} \nabla \cdot [\nu \nabla \varphi - \beta \varphi \nabla \ln m] + \varphi(m - \theta_{\alpha,\mu}) = -\lambda \varphi \quad \text{in } \Omega, \\ [\nu \nabla \varphi - \beta \varphi \nabla \ln m] \cdot n = 0 \quad \text{on } \partial\Omega, \quad \varphi > 0 \quad \text{on } \bar{\Omega}. \end{cases} \tag{3.1.1}$$

The proof of Lemma 3.1.1 is similar to that of Lemma 5.5 in [10]. Consider the following parameterizations:

$$\nu = \mu + \delta, \quad \beta = \alpha + \epsilon, \tag{3.1.2}$$

where δ and ϵ are assumed to be small. Using the implicit function theorem, we know that λ^* and φ are both smooth functions of ϵ and δ (see Lemma 3.3.1 of [3]). Hence, we can write λ^* as $\lambda^* = \lambda_0 + \lambda_1 \epsilon + \lambda_2 \delta + O(\epsilon^2 + \delta^2)$ and $\varphi = \varphi_0 + \varphi_1 \epsilon + \varphi_2 \delta + O(\epsilon^2 + \delta^2)$.

It is easy to see that $\lambda_0 = 0$ and $\varphi_0 = \theta_{\alpha,\mu}$ after suitable scaling. Substituting these expansions into (3.1.1), we see that φ_1 and φ_2 are determined by

$$\begin{cases} \nabla \cdot [\mu \nabla \varphi_1 - \alpha \varphi_1 \nabla \ln m - \theta_{\alpha,\mu} \nabla \ln m] \\ + (m - \theta_{\alpha,\mu})\varphi_1 = -\lambda_1 \theta_{\alpha,\mu} \quad \text{in} \quad \Omega, \\ [\mu \nabla \varphi_1 - \alpha \varphi_1 \nabla \ln m - \theta_{\alpha,\mu} \nabla \ln m] \cdot n = 0 \quad \text{on} \quad \partial\Omega, \end{cases} \tag{3.1.3}$$

and

$$\begin{cases} \nabla \cdot [\mu \nabla \varphi_2 - \alpha \varphi_2 \nabla \ln m + \nabla \theta_{\alpha,\mu}] \\ + (m - \theta_{\alpha,\mu})\varphi_2 = -\lambda_2 \theta_{\alpha,\mu} \quad \text{in} \quad \Omega, \\ [\mu \nabla \varphi_2 - \alpha \varphi_2 \nabla \ln m + \nabla \theta_{\alpha,\mu}] \cdot n = 0 \quad \text{on} \quad \partial\Omega. \end{cases} \tag{3.1.4}$$

Furthermore, we have that λ_1 and λ_2 are determined by the following result:

Theorem 3.1.2. [21] *λ_1 satisfies*

$$\lambda_1 \int_\Omega e^{-\alpha/\mu \ln m} \theta_{\alpha,\mu}^2 = -\int_\Omega \nabla(e^{-\alpha/\mu \ln m} \theta_{\alpha,\mu}) \cdot \theta_{\alpha,\mu} \nabla \ln m, \tag{3.1.5}$$

and λ_2 satisfies

$$\lambda_2 \int_\Omega e^{-\alpha/\mu \ln m} \theta_{\alpha,\mu}^2 = \int_\Omega \nabla(e^{-\alpha/\mu \ln m} \theta_{\alpha,\mu}) \cdot \nabla \theta_{\alpha,\mu}. \tag{3.1.6}$$

Proof. If we multiply (3.1.3) by $e^{-\alpha/\mu \ln m}\theta_{\alpha,\mu}$, integrate the result over Ω and use the boundary condition for φ_1, we get

$$\begin{aligned} -\int_\Omega \nabla(e^{-\alpha/\mu \ln m} \theta_{\alpha,\mu}) \cdot (\mu \nabla \varphi_1 - \alpha \varphi_1 \nabla \ln m - \theta_{\alpha,\mu} \nabla \ln m) \\ + \int_\Omega e^{-\alpha/\mu \ln m} \theta_{\alpha,\mu} (m - \theta_{\alpha,\mu}) \varphi_1 = -\lambda_1 \int_\Omega e^{-\alpha/\mu \ln m} \theta_{\alpha,\mu}^2. \end{aligned} \tag{3.1.7}$$

Now, if we multiply the equation of $\theta_{\alpha,\mu}$ by $e^{-\alpha/\mu \ln m}\varphi_1$, integrate the result over Ω and use the boundary condition for $\theta_{\alpha,\mu}$ we find

$$\begin{aligned} &-\int_\Omega \nabla(e^{-\alpha/\mu \ln m} \varphi_1) \cdot (\mu \nabla \theta_{\alpha,\mu} - \alpha \theta_{\alpha,\mu} \nabla \ln m) \\ &+ \int_\Omega e^{-\alpha/\mu \ln m} \theta_{\alpha,\mu} (m - \theta_{\alpha,\mu}) \varphi_1 = 0. \end{aligned} \tag{3.1.8}$$

Evaluating $\nabla(e^{-\alpha/\mu \ln m}\theta_{\alpha,\mu})$, we have

$$\int_\Omega \nabla(e^{-\alpha/\mu \ln m}\theta_{\alpha,\mu}) \cdot (\mu\nabla\varphi_1 - \alpha\varphi_1\nabla \ln m) \tag{3.1.9}$$
$$= \int_\Omega e^{-\alpha/\mu \ln m}\left(\nabla\theta_{\alpha,\mu} - \frac{\alpha}{\mu}\theta_{\alpha,\mu}\nabla \ln m\right) \cdot (\mu\nabla\varphi_1 - \alpha\varphi_1\nabla \ln m).$$

Similarly, evaluating $\nabla(e^{-\alpha/\mu \ln m}\varphi_1)$, we have

$$\int_\Omega \nabla(e^{-\alpha/\mu \ln m}\varphi_1) \cdot (\mu\nabla\theta_{\alpha,\mu} - \alpha\theta_{\alpha,\mu}\nabla \ln m) \tag{3.1.10}$$
$$= \int_\Omega e^{-\alpha/\mu \ln m}\left(\nabla\theta_{\alpha,\mu} - \frac{\alpha}{\mu}\theta_{\alpha,\mu}\nabla \ln m\right) \cdot (\mu\nabla\varphi_1 - \alpha\varphi_1\nabla \ln m).$$

Now, subtracting (3.1.7) from (3.1.8) and using (3.1.9) and (3.1.10), we obtain our result for λ_1. Similarly, we can find the expression for λ_2, performing the same procedure as above. □

Remark 3.1.3. *We can rewrite the parameterizations in* (3.1.2) *using polar coordinates as follows. If we let* $\epsilon = r\cos\phi$ *and* $\delta = r\sin\phi$, *then* $\beta = \alpha + r\cos\phi$ *and* $\nu = \mu + r\sin\phi$, *where* $r > 0$ *and* $\phi \in [0, 2\pi)$. *Thus within a small neighborhood of* (α, μ), *as long as* $\lambda_1\cos\phi + \lambda_2\sin\phi \neq 0$ *and does not change sign, we can write* $\lambda^* = \lambda_1 r\cos\phi + \lambda_2 r\sin\phi + O(r^2) \neq 0$. *We will see that this alternate parameterization is more useful in demonstrating our main results in the two trait context.*

Now we seek conditions for the stability of the other semi-trivial steady state, $(0, \theta_{\beta,\nu})$. Similar to Lemma 3.1.1 we have the following.

Lemma 3.1.4. *The steady state* $(0, \theta_{\beta,\nu})$ *is stable/unstable if and only if the following eigenvalue problem, for* $(\eta, \varphi) \in \mathbb{R} \times C^2(\bar{\Omega})$, *has a positive/negative principal eigenvalue* η^**:*

$$\begin{cases} \nabla \cdot [\mu\nabla\varphi - \alpha\varphi\nabla \ln m] + \varphi(m - \theta_{\beta,\nu}) = -\eta\varphi \quad in \quad \Omega, \\ [\mu\nabla\varphi - \alpha\varphi\nabla \ln m] \cdot n = 0 \quad on \quad \partial\Omega, \quad \varphi > 0 \quad on \quad \bar{\Omega}. \end{cases} \tag{3.1.11}$$

Performing similar analysis as above and using the parameterization in Remark 3.1.3, we see that $\eta^* = \eta_1 r\cos\phi + \eta_2 r\sin\phi + O(r^2)$, where η_1 and η_2 satisfy

$$\eta_1 \int_\Omega e^{-\alpha/\mu \ln m}\theta_{\alpha,\mu}^2 = \int_\Omega \nabla(e^{-\alpha/\mu \ln m}\theta_{\alpha,\mu}) \cdot \theta_{\alpha,\mu}\nabla \ln m, \tag{3.1.12}$$

$$\eta_2 \int_\Omega e^{-\alpha/\mu \ln m}\theta_{\alpha,\mu}^2 = -\int_\Omega \nabla(e^{-\alpha/\mu \ln m}\theta_{\alpha,\mu}) \cdot \nabla\theta_{\alpha,\mu}. \tag{3.1.13}$$

3.2 Sign Analysis for Eigenvalue Expansions

In this section we always assume that $\Omega = (0,1)$, $m_x > 0$ on $[0,1]$ and $m \in C^2[0,1]$. In particular, $\theta_{\alpha,\mu}$ satisfies

$$\begin{cases} \left[\mu(\theta_{\alpha,\mu})_x - \alpha\theta_{\alpha,\mu}\dfrac{m_x}{m}\right]_x + \theta_{\alpha,\mu}[m - \theta_{\alpha,\mu}] = 0 \quad 0 < x < 1, \\ \mu(\theta_{\alpha,\mu})_x - \alpha\theta_{\alpha,\mu}\dfrac{m_x}{m} = 0 \quad \text{at } x = 0, 1. \end{cases} \tag{3.2.1}$$

In light of our expansions for λ^* and η^*, to determine the sign of both principal eigenvalues, we need to know the sign of $(e^{-(\alpha/\mu)\ln m}\theta_{\alpha,\mu})_x$ and $(\theta_{\alpha,\mu})_x$ on $(0,1)$ for both $\alpha < \mu$ and $\alpha > \mu$. When $\alpha < \mu$ this is possible as the sign of $(e^{-(\alpha/\mu)\ln m}\theta_{\alpha,\mu})_x$ determines the sign of $(\theta_{\alpha,\mu})_x$ (see Lemma 3.2.1 below); however, when $\alpha > \mu$, the sign of $(\theta_{\alpha,\mu})_x$ on $[0,1]$ cannot be determined in general and further assumptions are needed.

Lemma 3.2.1. [21] *If $\alpha < \mu$, then $\mu(\theta_{\alpha,\mu})_x - \alpha\dfrac{m_x}{m}\theta_{\alpha,\mu} > 0$ on $(0,1)$. In particular, $(\theta_{\alpha,\mu})_x > 0$ on $[0,1]$.*

Proof. Suppose that f is a solution of

$$\begin{cases} f_{xx} + b(x)f_x + \gamma(x)f[\kappa(x) - f] = 0 \quad x \in (0,1), \\ f_x(0) = f_x(1) = 0, \quad f > 0 \quad \text{in} \quad [0,1], \end{cases} \tag{3.2.2}$$

where $b, \gamma \in C[0,1], \kappa \in C^1[0,1]$, and $\gamma, \kappa > 0$ in $[0,1]$. Lemma 2.1 of [9] says that if $\kappa_x > 0$ in [0,1], then $f_x > 0$ in $(0,1)$. Let $f = e^{-(\alpha/\mu)\ln m}\theta_{\alpha,\mu}$, $b(x) = \dfrac{\alpha}{\mu}\left(\dfrac{m_x}{m}\right)$, $\gamma(x) =$

$\dfrac{1}{\mu}e^{(\alpha/\mu)\ln m}$, and $\kappa(x) = me^{-(\alpha/\mu)\ln m}$. Thus, we see that f satisfies (3.2.2). If $m_x > 0$ on [0,1], the sign of $\kappa_x = m_x e^{-(\alpha/\mu)\ln m}\left(1 - \dfrac{\alpha}{\mu}\right)$ depends on the size of $\dfrac{\alpha}{\mu}$. So if $\alpha < \mu$, we see that $\kappa_x > 0$ and hence $f_x > 0$. Notice that $f_x = e^{(-\alpha/\mu)\ln m}((\theta_{\alpha,\mu})_x - \dfrac{\alpha}{\mu}\dfrac{m_x}{m}\theta_{\alpha,\mu})$. Hence we have our result. □

Lemma 3.2.2. [21] *If* $\alpha > \mu$*, then* $\mu(\theta_{\alpha,\mu})_x - \alpha\dfrac{m_x}{m}\theta_{\alpha,\mu} < 0$ *on* $(0, 1)$*.*

Proof. Lemma 2.1 of Cantrell et al. [9] shows that if $\kappa_x < 0$ in [0,1], then $f_x < 0$ in $(0, 1)$. Using the same proof as in Lemma 3.2.1 and since we are assuming that $\alpha > \mu$, we have $\kappa_x < 0$ in [0,1] and thus we obtain our result. □

Lemma 3.2.3. [21] *If* $\alpha < \mu$*, then* $m(0) < \theta_{\alpha,\mu}(0)$ *and* $m(1) > \theta_{\alpha,\mu}(1)$*.*

Proof. Using Lemma 3.2.1 and the boundary conditions for $\theta_{\alpha,\mu}$, we see that $[\mu(\theta_{\alpha,\mu})_x - \alpha\dfrac{m_x}{m}\theta_{\alpha,\mu}]_x \geq 0$ at $x = 0$ and that $[\mu(\theta_{\alpha,\mu})_x - \alpha\dfrac{m_x}{m}\theta_{\alpha,\mu}]_x \leq 0$ at $x = 1$. Thus by (3.2.1), we have $m(0) \leq \theta_{\alpha,\mu}(0)$ and $m(1) \geq \theta_{\alpha,\mu}(1)$. Now if $m(0) = \theta_{\alpha,\mu}(0)$, the boundary condition of (3.2.1) at $x = 0$ gives us that $(\theta_{\alpha,\mu})_x < m_x$. So for some $\delta > 0$, $m > \theta_{\alpha,\mu}$ on $(0, \delta)$. But then (3.2.1) gives us that $[\mu(\theta_{\alpha,\mu})_x - \alpha\dfrac{m_x}{m}\theta_{\alpha,\mu}]_x < 0$ on $(0, \delta)$. Thus, $\mu(\theta_{\alpha,\mu})_x - \alpha\dfrac{m_x}{m}\theta_{\alpha,\mu} < 0$ on $(0, \delta)$. But this contradicts Lemma 3.2.1. Hence, $m(0) > \theta_{\alpha,\mu}(0)$. Similar analysis shows strict inequality at $x = 1$ as well. □

Lemma 3.2.4. [21] *If* $\alpha > \mu$*, then* $m(0) > \theta_{\alpha,\mu}(0)$ *and* $m(1) < \theta_{\alpha,\mu}(1)$*.*

Proof. The proof is similar to that of Lemma 3.2.3. □

For the following results, in order to determine the sign of $(\theta_{\alpha,\mu})_x$ on $[0, 1]$, we now impose some additional assumptions. First, we see that as long as α is large enough, we can show that $(\theta_{\alpha,\mu})_x > 0$ on $[0, 1]$ as illustrated by Lemma 3.2.5 below.

Lemma 3.2.5. [21] *Suppose* $m_x > 0$ *in* $[0, 1]$ *and* $\alpha \geq \dfrac{\int_0^1 m}{\min_{[0,1]}(m_x/m)}$*. Then* $(\theta_{\alpha,\mu})_x > 0$ *on* $[0, 1]$.

Proof. Let $y \in [0,1]$ be the smallest number such that $(\theta_{\alpha,\mu})_x(y) \le 0$. Since $(\theta_{\alpha,\mu})_x(0) > 0$ and $(\theta_{\alpha,\mu})_x(1) > 0$, and because $(\theta_{\alpha,\mu})_x$ is continuous, we see that $y \in (0,1)$ and $(\theta_{\alpha,\mu})_x(y) = 0$. Integrating the equation for $\theta_{\alpha,\mu}$ over $[0,y]$, and noticing that $\theta_{\alpha,\mu}$ is increasing on $[0,y]$, we see that

$$\alpha\theta_{\alpha,\mu}(y)\frac{m_x(y)}{m(y)} = \int_0^y \theta_{\alpha,\mu}(m-\theta_{\alpha,\mu}) \le \int_0^y \theta_{\alpha,\mu}m < \theta_{\alpha,\mu}(y)\int_0^1 m. \tag{3.2.3}$$

Thus we see that $\alpha < \dfrac{\int_0^1 m}{\min_{[0,1]}(m_x/m)}$. But this contradicts our assumption on α. Hence, it must be that $(\theta_{\alpha,\mu})_x > 0$ on $[0,1]$. $\square$

Now we want to determine the sign of $(\theta_{\alpha,\mu})_x$ on $[0,1]$, specifically when $\mu < \alpha$ and $m_x > 0$. The problem is that if, for example, we let $m(x) = \sin(10x)+10.01x+5$, clearly $m_x > 0$ on $[0,1]$, but we find that $(\theta_{\alpha,\mu})_x$ changes sign on $(0,1)$ (see Figure 3.5). Hence we consider a linear resource function. Without loss of generality, assume that $\mu = 1$.

Lemma 3.2.6. [21] *Assuming $\alpha \ne 1$ and m is linear, if $\theta_{\alpha,1}(\bar{x}) = m(\bar{x})$ for some $\bar{x} \in [0,1]$, then $(\theta_{\alpha,\mu})_x(\bar{x}) \ne m_x(\bar{x})$.*

Proof. Without loss of generality, assume that $\mu = 1$. Set $w = \dfrac{\theta_{\alpha,1}}{m}$. By assumption $\theta_{\alpha,1}(\bar{x}) = m(\bar{x})$, $w(\bar{x}) = 1$. Since

$$w_x(\bar{x}) = \frac{(\theta_{\alpha,1})_x m - \theta_{\alpha,1}m_x}{m^2}(\bar{x}) = \frac{(\theta_{\alpha,1})_x(\bar{x}) - m_x(\bar{x})}{m(\bar{x})},$$

it suffices to show that $w_x(\bar{x}) \ne 0$. Note that w satisfies (since m is linear)

$$\begin{cases} w_{xx} + (2-\alpha)\dfrac{m_x}{m}w_x + mw(1-w) = 0 & 0 < x < 1, \\ w_x + (1-\alpha)\left(\dfrac{m_x}{m}\right)w = 0 & x = 0,1. \end{cases} \tag{3.2.4}$$

Note that if $\bar{x} = 0$ or 1, by the boundary condition of (3.2.4), $w_x \ne 0$. So consider

$\bar{x} \in (0,1)$. Suppose that $w_x(\bar{x}) = 0$ and consider the following linear initial value problem:

$$\begin{cases} \phi_{xx} + (2-\alpha)\dfrac{m_x}{m}\phi_x - mw\phi = 0 \quad 0 < x < 1, \\ \phi_x(\bar{x}) = \phi(\bar{x}) = 0 \end{cases} \tag{3.2.5}$$

We see that $\phi \equiv 0$ is a solution to (3.2.5) and by ordinary differential equation theory, it is the unique solution on $(0,1)$ satisfying the initial value problem. We note that if we set $\phi = 1 - w$ that this too is a solution to (3.2.5). Hence it must be the case that $w \equiv 1$ on $(0,1)$ and extending by continuity, $w \equiv 1$ on $[0,1]$. But w satisfies the boundary conditions in (3.2.4) so $w_x(0) \neq 0$ and $w_x(1) \neq 0$. This is a contradiction. □

Theorem 3.2.7. [21] *Suppose m is linear, $m_x > 0$ in $[0,1]$, and $\alpha > \mu$. Then $\left(\frac{\theta_{\alpha,1}}{m}\right)_x > 0$ in $[0,1]$.*

Proof. Without loss of generality, assume that $\mu = 1$. First we note that by Lemma 3.2.4, there exists some $x_1 \in (0,1)$ such that $\theta_{\alpha,1} < m$ on $[0, x_1)$ and $\theta_{\alpha,1}(x_1) = m(x_1)$. By Lemma 3.2.6, we see that $\left(\frac{\theta_{\alpha,1}}{m}\right)_x (x_1) > 0$. We claim that $\left(\frac{\theta_{\alpha,1}}{m}\right)_x > 0$ on $(0, x_1)$. If not, there exists some $x_2 \in (0, x_1)$ such that $\left(\frac{\theta_{\alpha,1}}{m}\right)_x > 0$ on (x_2, x_1) and $\left(\frac{\theta_{\alpha,1}}{m}\right)_x (x_2) = 0$. Put $w = \frac{\theta_{\alpha,1}}{m}$. Note that $w_{xx}(x_2) \geq 0$. However, upon evaluating (3.2.4) at x_2, since $w_x(x_2) = 0$ and $0 < w(x_2) < 1$, we see that $w_{xx}(x_2) < 0$. This is a contradiction. So we see that $\left(\frac{\theta_{\alpha,1}}{m}\right)_x > 0$ on $(0, x_1]$

Next we claim that $w_x > 0$ on $(x_1, 1]$. Suppose w_x changes sign on $(x_1, 1]$. Then by continuity, there exists a $y \in (x_1, 1]$, such that $w_x > 0$ on (x_1, y) and $w_x(y) = 0$. Note that $w > 1$ on $(x_1, y]$. To see this, if $w = 1$ somewhere on $(x_1, y]$, then by the mean value theorem, there must be a point $p \in (x_1, y)$, such that $w_x(p) = 0$ and $w(p) > 1$. But

$$0 = w_x(p) = \frac{(\theta_{\alpha,1})_x m - \theta_{\alpha,1} m_x}{m^2}(p) = \left(\frac{m_x(p)}{m(p)}\right)\left(\frac{(\theta_{\alpha,1})_x(p)}{m_x(p)} - w(p)\right)$$
$$= \left(\frac{m_x(p)}{m(p)}\right)(1 - w(p)) < 0.$$

This is clearly a contradiction, so it must be the case that $w > 1$ on $(x_1, y]$. Note that $w_{xx}(y) \leq 0$. On the other hand, if we evaluate (3.2.4) at y, since $w_x(y) = 0$ and $w(y) > 1$, we see that $w_{xx}(y) > 0$. Again, we have a contradiction and obtain the fact that $w_x > 0$ on $(x_1, 1]$. This completes the proof. □

Corollary 3.2.8. [21] *Suppose m is linear, $m_x > 0$ in $[0, 1]$, and $\alpha > \mu$. Then, $(\theta_{\alpha,1})_x > 0$ on $[0, 1]$.*

Proof. Note that from Theorem 3.2.7, $\left(\frac{\theta_{\alpha,1}}{m}\right)_x > 0$ on $[0, 1]$. Since

$$\left(\frac{\theta_{\alpha,1}}{m}\right)_x = \frac{(\theta_{\alpha,1})_x m - \theta_{\alpha,1} m_x}{m^2},$$

we see that $(\theta_{\alpha,1})_x > \frac{\theta_{\alpha,1} m_x}{m} > 0$ on $[0, 1]$. □

Theorem 3.2.9. [21] *Suppose m is linear, $m_x > 0$ in $[0, 1]$, and $\alpha < \mu$. Then $\left(\frac{\theta_{\alpha,\mu}}{m}\right)_x < 0$ in $[0, 1]$.*

Proof. Without loss of generality, assume that $\mu = 1$. First we note that by Lemma 3.2.3, there exists some $x_1 \in (0, 1)$ such that $\theta_{\alpha,1} > m$ on $[0, x_1)$ and $\theta_{\alpha,1}(x_1) = m(x_1)$. Hence $m_x(x_1) \geq (\theta_{\alpha,1})_x(x_1)$. Let $w = \frac{\theta_{\alpha,1}}{m}$ as before. By Lemma 3.2.6 , we see that $m_x(x_1) > (\theta_{\alpha,1})_x(x_1)$, that is, $w_x(x_1) < 0$. We claim that $w_x < 0$ on $[0, x_1]$. Suppose not. Then there is an $x_2 \in (0, x_1)$ such that $w_x < 0$ on (x_2, x_1) and $w_x(x_2) = 0$. Note that $w_{xx}(x_2) \leq 0$. If, however, we evaluate (3.2.4) at x_2, since $w > 1$ and $w_x(x_2) = 0$, we get that $w_{xx}(x_2) > 0$. This is a contradiction, indicating that $w_x < 0$ on $[0, x_1]$.

Next we claim that $w_x < 0$ on $(x_1, 1]$. Suppose w_x changes sign on $(x_1, 1]$. Then by continuity, there exists a $y \in (x_1, 1]$, such that $w_x < 0$ on (x_1, y) and $w_x(y) = 0$. Note that $w < 1$ on $(x_1, y]$. To see this, if $w = 1$ somewhere on $(x_1, y]$, then by the mean value theorem, there must be a point $p \in (x_1, y)$, such that $w_x(p) = 0$ and $w(p) < 1$. But

$$\begin{aligned}
0 = w_x(p) &= \frac{(\theta_{\alpha,1})_x m - \theta_{\alpha,1} m_x}{m^2}(p) = \left(\frac{m_x(p)}{m(p)}\right)\left(\frac{(\theta_{\alpha,1})_x(p)}{m_x(p)} - w(p)\right) \\
&= \left(\frac{m_x(p)}{m(p)}\right)(1 - w(p)) > 0,
\end{aligned}$$

which is clearly a contradiction. So it must be the case that $w < 1$ on $(x_1, y]$. Note that $w_{xx}(y) \geq 0$. On the other hand, if we evaluate (3.2.4) at y, since $w_x(y) = 0$ and $w(y) < 1$, we see that $w_{xx}(y) < 0$. Again, we have a contradiction and obtain the fact that $w_x < 0$ on $(x_1, 1]$. This completes the proof. □

3.3 Nonexistence of Positive Steady States

In this section, we show that under specific conditions, system (3.0.1) has no positive steady states. Before stating and proving the result, we present several useful lemmas.

Lemma 3.3.1. [21] *Suppose that* (u, v) *is a positive steady state solution of* (3.0.1). *Then*

$$\begin{aligned}
&\int_\Omega \left[\mu e^{\alpha/\mu \ln m} - \nu e^{\beta/\nu \ln m}\right] \nabla(e^{-\alpha/\mu \ln m} u) \cdot \nabla(e^{-\beta/\nu \ln m} v) \\
&= \int_\Omega \left[e^{-\alpha/\mu \ln m} - e^{-\beta/\nu \ln m}\right] uv(m - u - v).
\end{aligned} \tag{3.3.1}$$

Proof. Note that we can rewrite the steady state system of (3.0.1) as

$$\begin{cases}
\mu \nabla \cdot [e^{\alpha/\mu \ln m} \nabla(e^{-\alpha/\mu \ln m} u)] + u(m - u - v) = 0 & x \in \Omega, \\
\nu \nabla \cdot [e^{\beta/\nu \ln m} \nabla(e^{-\beta/\nu \ln m} v)] + v(m - u - v) = 0 & x \in \Omega, \\
\nabla(e^{-\alpha/\mu \ln m} u) \cdot n = \nabla(e^{-\beta/\nu \ln m} v) \cdot n = 0 & x \in \partial\Omega.
\end{cases} \tag{3.3.2}$$

If we multiply the equation for u in (3.3.2) by $e^{-\beta/\nu \ln m} v$, integrate over $[0, 1]$ and use the boundary condition, we find that

$$\mu \int_\Omega e^{\alpha/\mu \ln m} \nabla(e^{-\beta/\nu \ln m} v) \cdot \nabla(e^{-\alpha/\mu \ln m} u) = \int_\Omega e^{-\beta/\nu \ln m} uv(m - u - v). \quad (3.3.3)$$

Also, if we multiply the equation for v in (3.3.2) by $e^{-\alpha/\mu \ln m} u$, integrate over Ω and use the boundary condition, we have

$$\nu \int_\Omega e^{\beta/\nu \ln m} \nabla(e^{-\beta/\nu \ln m} v) \cdot \nabla(e^{-\alpha/\mu \ln m} u) = \int_\Omega e^{-\alpha/\mu \ln m} uv(m - u - v) \quad (3.3.4)$$

Now, subtracting (3.3.3) from (3.3.4) we obtain the result. □

Using the polar parameterizations for ν and β, as discussed in Section 3.1, and Taylor expansions, we have the two following results:

Lemma 3.3.2. [21] *For* $0 < r \ll 1$,

$$\mu e^{\frac{\alpha}{\mu} \ln m} - \nu e^{\frac{\beta}{\nu} \ln m} = e^{\frac{\alpha}{\mu} \ln m} r \left[\ln m \left(\frac{\alpha}{\mu} \sin \phi - \cos \phi \right) - \sin \phi \right] + O(r^2). \quad (3.3.5)$$

Lemma 3.3.3. [21] *For* $0 < r \ll 1$,

$$e^{-\frac{\beta}{\nu} \ln m} - e^{-\frac{\alpha}{\mu} \ln m} = e^{-\frac{\alpha}{\mu} \ln m} r \left[\ln m \left(\frac{\alpha \sin \phi}{\mu^2} - \frac{\cos \phi}{\mu} \right) \right] + O(r^2). \quad (3.3.6)$$

Next we have

Lemma 3.3.4. [21] *Suppose* (u, v) *is a positive steady state solution of* (3.0.1). *Let the parametrization of* β *and* ν *be given as in Section* 3.1. *Then for some* $s \in [0, 1]$, $(u, v) \to (s\theta_{\alpha,\mu}, (1 - s)\theta_{\alpha,\mu})$ *in* $C^2(\bar{\Omega})$ *as* $r \to 0$.

Proof. By elliptic regularity and the Sobolev embedding theorem, for $0 < r \ll 1$, (u, v) is uniformly bounded in $C^{2,\gamma}(\bar{\Omega})$ for some $\gamma \in (0, 1)$ [23]. If we let $r \to 0$, passing to a subsequence if necessary, $(u,v) \to (\hat{u},\hat{v})$ where $(\hat{u},\hat{v}) \in C^2(\bar{\Omega})$ with $\hat{u},\hat{v} \geq 0$, and $(\hat{u},\hat{v})$ satisfy

$$\begin{cases} \nabla \cdot [\mu \nabla \hat{u} - \alpha \hat{u} \nabla \ln m] + \hat{u}(m - \hat{u} - \hat{v}) = 0 \quad x \in \Omega, \\ \nabla \cdot [\mu \nabla \hat{v} - \alpha \hat{v} \nabla \ln m] + \hat{v}(m - \hat{u} - \hat{v}) = 0 \quad x \in \Omega, \\ [\mu \nabla \hat{u} - \alpha \hat{u} \nabla \ln m] \cdot n = [\mu \nabla \hat{v} - \alpha \hat{v} \nabla \ln m] \cdot n = 0 \quad x \in \partial\Omega. \end{cases} \tag{3.3.7}$$

Adding the equation for $\hat{u}$ and $\hat{v}$ we have that $\hat{u}+\hat{v}$ is a solution of

$$\begin{cases} \nabla \cdot [\mu \nabla (\hat{u}+\hat{v}) - \alpha (\hat{u}+\hat{v}) \nabla \ln m] \\ \ + (\hat{u}+\hat{v})[m - (\hat{u}+\hat{v})] = 0 \quad x \in \Omega, \\ [\mu \nabla (\hat{u}+\hat{v}) - \alpha (\hat{u}+\hat{v}) \nabla \ln m] \cdot n = 0 \quad x \in \partial\Omega. \end{cases} \tag{3.3.8}$$

Hence we have that either $\hat{u}+\hat{v} = 0$ or $\hat{u}+\hat{v} = \theta_{\alpha,\mu}$. If $\hat{u}+\hat{v} = 0$, then since $\hat{u},\hat{v} \geq 0$, it must be that $\hat{u} = \hat{v} = 0$, i.e., $(u,v) \to (0,0)$ uniformly as $r \to 0$. As $m > 0$ in $\bar{\Omega}$, this implies that $m - u - v > 0$ for small positive r. Integrating the equation of u in Ω, we have $\displaystyle\int_\Omega u(m-u-v) = 0$, which is a contradiction. Thus, it must be the case that $\hat{u}+\hat{v} = \theta_{\alpha,\mu}$. Therefore, $(\hat{u},\hat{v})$ satisfies

$$\begin{cases} \nabla \cdot [\mu \nabla \hat{u} - \alpha \hat{u} \nabla \ln m] + \hat{u}(m - \theta_{\alpha,\mu}) = 0 \quad x \in \Omega, \\ \nabla \cdot [\mu \nabla \hat{v} - \alpha \hat{v} \nabla \ln m] + \hat{v}(m - \theta_{\alpha,\mu}) = 0 \quad x \in \Omega, \\ [\mu \nabla \hat{u} - \alpha \hat{u} \nabla \ln m] \cdot n = [\mu \nabla \hat{v} - \alpha \hat{v} \nabla \ln m] \cdot n = 0 \quad x \in \partial\Omega. \end{cases} \tag{3.3.9}$$

Since $\hat{u}$ is non-negative, either $\hat{u} = 0$ or $\hat{u} \not\equiv 0$. If $\hat{u} \not\equiv 0$, by the maximum principle we have $\hat{u} > 0$ in Ω. This together with the equation of $\theta_{\alpha,\mu}$ imply that $\hat{u} = s\theta_{\alpha,\mu}$ for some constant $s > 0$, f since both $\hat{u}$ and $\theta_{\alpha,\mu}$ are eigenfunctions for the principal eigenvalue 0. Similarly, $\hat{v} = \tau\theta_{\alpha,\mu}$ for some non-negative constant τ. Since $\hat{u}+\hat{v} = \theta_{\alpha,\mu}$, we see that $s + \tau = 1$. Therefore, $s \in [0,1]$. □

Lemma 3.3.5. [21] *Let (u,v) be any positive steady state solution of* (3.0.1) *with (β,ν) parameterized as in Section* 3.1. *If $(u,v) \to (0,\theta_{\alpha,\mu})$ in $L^\infty(\Omega)$ as $r \to 0$, then $u/||u||_\infty \to \theta_{\alpha,\mu}/||\theta_{\alpha,\mu}||_\infty$ in $C^2(\bar{\Omega})$.*

Proof. We divide the steady state equation of u in (3.0.1) by $||u||_\infty$ to get

$$\begin{cases} \nabla \cdot [\mu \nabla (u/||u||_\infty) - \alpha (u/||u||_\infty) \nabla \ln m] \\ \ + (u/||u||_\infty)[m - u - v] = 0 \quad x \in \Omega, \\ [\mu \nabla (u/||u||_\infty) - \alpha (u/||u||_\infty) \nabla \ln m] \cdot n|_{\partial\Omega} = 0. \end{cases} \tag{3.3.10}$$

By elliptic regularity and Sobolev embedding theorem [23], we notice that for all $0 < r \ll 1$, $u/||u||_\infty$ is uniformly bounded in $C^{2,\tau}(\bar{\Omega})$ for some $\tau \in (0,1)$. Thus, passing to a subsequence if necessary, as $r \to 0$, $u/||u||_\infty \to f$ in $C^2(\bar{\Omega})$, where f satisfies

$$\begin{cases} \nabla \cdot [\mu \nabla f - \alpha f \nabla \ln m] + f[m - \theta_{\alpha,\mu}] = 0 \quad x \in \Omega, \\ [\mu \nabla f - \alpha f \nabla \ln m] \cdot n|_{\partial\Omega} = 0. \end{cases} \tag{3.3.11}$$

Therefore, $f = k\theta_{\alpha,\mu}$ for some constant $k > 0$. Because $||f||_\infty = 1$, we see that $k = 1/||\theta_{\alpha,\mu}||_\infty$. Hence, $f = (\theta_{\alpha,\mu})/||\theta_{\alpha,\mu}||_\infty$. Thus, f is uniquely determined, implying that convergence $u/||u||_\infty \to f$ is independent of the subsequence. □

Lemma 3.3.6. [21] *Let* (u,v) *be any positive steady state solution of* (3.0.1) *with* (β,ν) *parameterized as in Section* 3.1. *If* $(u,v) \to (\theta_{\alpha,\mu}, 0)$ *in* $L^\infty(\Omega)$ *as* $r \to 0$, *then* $v/||v||_\infty \to (\theta_{\alpha,\mu})/||\theta_{\alpha,\mu}||_\infty$ *in* $C^2(\bar{\Omega})$.

The proof is similar to the previous Lemma. Finally, we state and prove the main result in this section:

Theorem 3.3.7. [21] *Fix* $\alpha, \mu > 0$. *Consider the parameterizations* $\beta = \alpha + r\cos\phi$ *and* $\nu = \mu + r\sin\phi$, *where* $r > 0$ *and* $\phi \in [0, 2\pi)$. *Suppose that*

$$\begin{aligned} &- \cos\phi \int_\Omega \theta_{\alpha,\mu} \nabla (e^{-\alpha/\mu \ln m} \theta_{\alpha,\mu}) \cdot \nabla \ln m \\ &+ \sin\phi \int_\Omega \nabla (e^{-\alpha/\mu \ln m} \theta_{\alpha,\mu}) \cdot \nabla \theta_{\alpha,\mu} \neq 0. \end{aligned} \tag{3.3.12}$$

Then for $0 < r \ll 1$, *system* (3.0.1) *has no positive steady state solutions.*

Proof. Suppose we have a positive solution (u, v) for every $0 < r \ll 1$. If we let $r \to 0$, from Lemma 3.3.4, Lemma 3.3.5, and Lemma 3.3.6 we see that there are three scenarios: (i) $(u, v) \to (s\theta_{\alpha,\mu}, (1-s)\theta_{\alpha,\mu})$ in $C^2(\bar{\Omega})$; (ii) $(u, v) \to (0, \theta_{\alpha,\mu})$ and $u/||u||_\infty \to (\theta_{\alpha,\mu})/||\theta_{\alpha,\mu}||_\infty$ in $C^2(\bar{\Omega})$; and finally (iii) $(u, v) \to (\theta_{\alpha,\mu}, 0)$ and $v/||v||_\infty \to (\theta_{\alpha,\mu})/||\theta_{\alpha,\mu}||_\infty$ in $C^2(\bar{\Omega})$.

We first consider the case $(u, v) \to (s\theta_{\alpha,\mu}, (1-s)\theta_{\alpha,\mu})$ for $s \in (0, 1)$ as $r \to 0$. Consider the formula (3.3.1). By the expansions from Lemma 3.3.2 and Lemma 3.3.3, we combine the first order terms in r and then divide the result by $s(1-s)$ to get

$$\begin{aligned}&\int_\Omega e^{\alpha/\mu \ln m}\left[\ln m\left(\frac{\alpha}{\mu}\sin\phi - \cos\phi\right) - \sin\phi\right]|\nabla(e^{-\alpha/\mu \ln m}\theta_{\alpha,\mu})|^2 \\ &= \int_\Omega e^{-\alpha/\mu \ln m}\ln m\left[\frac{\alpha\sin\phi}{\mu^2} - \frac{\cos\phi}{\mu}\right]\theta_{\alpha,\mu}^2(m - \theta_{\alpha,\mu}).\end{aligned} \tag{3.3.13}$$

Now consider case (ii). If we divide (3.3.1) by $||u||_\infty$, using our polar parameterizations as well as our expansions and combining the first order terms in r, we see that

$$\begin{aligned}&\int_\Omega e^{\alpha/\mu \ln m}\left[\ln m\left(\frac{\alpha}{\mu}\sin\phi - \cos\phi\right) - \sin\phi\right] \\ &\times \nabla(e^{-\alpha/\mu \ln m}\theta_{\alpha,\mu}) \cdot \nabla\left(e^{-\alpha/\mu \ln m}\frac{\theta_{\alpha,\mu}}{||\theta_{\alpha,\mu}||_\infty}\right)\end{aligned} \tag{3.3.14}$$

$$= \int_\Omega e^{-\alpha/\mu \ln m}\ln m\left[\frac{\alpha\sin\phi}{\mu^2} - \frac{\cos\phi}{\mu}\right]\frac{\theta_{\alpha,\mu}^2}{||\theta_{\alpha,\mu}||_\infty}(m - \theta_{\alpha,\mu}). \tag{3.3.15}$$

Notice that if we multiply (3.3.15) by $||\theta_{\alpha,\mu}||_\infty$, we obtain the expression in (3.3.13). Case (iii) can be handled in a similar manner. Thus we proceed, multiplying the equation for the semi-trivial steady state $\theta_{\alpha,\mu}$ by $e^{-\alpha/\mu \ln m}\theta_{\alpha,\mu}\ln m$ and using integration by parts we obtain the following:

$$
\begin{aligned}
&\int_\Omega e^{-\alpha/\mu \ln m}\theta_{\alpha,\mu}^2(m-\theta_{\alpha,\mu})\ln m \\
&= \mu\int_\Omega e^{\alpha/\mu \ln m}\nabla(e^{-\alpha/\mu \ln m}\theta_{\alpha,\mu}\ln m)\cdot\nabla(e^{-\alpha/\mu \ln m}\theta_{\alpha,\mu}) \\
&= \mu\int_\Omega e^{\alpha/\mu \ln m}[\nabla(e^{-\alpha/\mu \ln m}\theta_{\alpha,\mu})\ln m \\
&+ e^{-\alpha/\mu \ln m}\theta_{\alpha,\mu}\nabla \ln m]\cdot\nabla(e^{-\alpha/\mu \ln m}\theta_{\alpha,\mu}) \\
&= \mu\Big[\int_\Omega e^{\alpha/\mu \ln m}|\nabla(e^{-\alpha/\mu \ln m}\theta_{\alpha,\mu})|^2\ln m \\
&+ \int_\Omega \theta_{\alpha,\mu}\nabla(e^{-\alpha/\mu \ln m}\theta_{\alpha,\mu})\cdot\nabla\ln m\Big].
\end{aligned}
\tag{3.3.16}
$$

Combining this result with (3.3.13) we get

$$
\begin{aligned}
&-\sin\phi\int_\Omega e^{\alpha/\mu \ln m}|\nabla e^{-\alpha/\mu \ln m}\theta_{\alpha,\mu})|^2 \\
&= \left(\frac{\alpha\sin\phi-\mu\cos\phi}{\mu}\right)\left[-\int_\Omega e^{\alpha/\mu \ln m}\ln m|\nabla e^{-\alpha/\mu \ln m}\theta_{\alpha,\mu})|^2\right] \\
&\quad + \left(\frac{\alpha\sin\phi-\mu\cos\phi}{\mu}\right)\left[\frac{1}{\mu}\int_\Omega e^{-\alpha/\mu \ln m}\theta_{\alpha,\mu}^2(m-\theta_{\alpha,\mu})\right] \\
&= \left(\frac{\alpha\sin\phi-\mu\cos\phi}{\mu}\right)\int_\Omega \theta_{\alpha,\mu}\nabla\ln m\cdot\nabla(e^{-\alpha/\mu \ln m}\theta_{\alpha,\mu}).
\end{aligned}
\tag{3.3.17}
$$

By rearranging (3.3.17), we see that

$$
\begin{aligned}
&-\sin\phi\Big[\int_\Omega e^{\alpha/\mu \ln m}|\nabla(e^{-\alpha/\mu \ln m}\theta_{\alpha,\mu})|^2 \\
&+ \frac{\alpha}{\mu}\int_\Omega \theta_{\alpha,\mu}\nabla\ln m\cdot\nabla(e^{-\alpha/\mu \ln m}\theta_{\alpha,\mu})\Big] \\
&= -\cos\phi\int_\Omega \theta_{\alpha,\mu}\nabla\ln m\cdot\nabla(e^{-\alpha/\mu \ln m}\theta_{\alpha,\mu}).
\end{aligned}
\tag{3.3.18}
$$

Note also that

$$
\begin{aligned}
&e^{\alpha/\mu \ln m}|\nabla(e^{-\alpha/\mu \ln m}\theta_{\alpha,\mu})|^2 + \frac{\alpha}{\mu}\theta_{\alpha,\mu}\nabla\ln m\cdot\nabla(e^{-\alpha/\mu \ln m}\theta_{\alpha,\mu}) \\
&= \nabla(e^{-\alpha/\mu \ln m}\theta_{\alpha,\mu})\cdot\left[e^{\alpha/\mu \ln m}\nabla(e^{-\alpha/\mu \ln m}\theta_{\alpha,\mu}) + \frac{\alpha}{\mu}\theta_{\alpha,\mu}\nabla\ln m\right] \\
&= \nabla(e^{-\alpha/\mu \ln m}\theta_{\alpha,\mu})\cdot\nabla\theta_{\alpha,\mu}.
\end{aligned}
\tag{3.3.19}
$$

Finally, using (3.3.19) in the expression given by (3.3.18), we see that

$$-\cos\phi\int_\Omega \theta_{\alpha,\mu}\nabla(e^{-\alpha/\mu\ln m}\theta_{\alpha,\mu})\cdot\nabla\ln m+\sin\phi\int_\Omega \nabla(e^{-\alpha/\mu\ln m}\theta_{\alpha,\mu})\cdot\nabla\theta_{\alpha,\mu}=0,$$

which is a contradiction. □

3.4 Evolution of a Single Trait

We begin with a result on the global dynamics of (3.0.1).

Theorem 3.4.1. [21] *Let $m \in C^2(\bar{\Omega})$ such that $m > 0$, $m \not\equiv$ constant, and suppose that $\dfrac{\alpha}{\mu} = \dfrac{\beta}{\nu} \neq 1$. Then $(\theta_{\alpha,\mu}, 0)$ is globally asymptotically stable when $\mu < \nu$, and $(0, \theta_{\beta,\nu})$ is globally asymptotically stable when $\mu > \nu$.*

We note that when $\alpha = \beta = 0$, Theorem 3.4.1 is reduced to the findings in [17, 27]. As we assume that the ratio of advection to diffusion for two species is identical but not equal to one, our result in essence mirrors the single trait analysis in [17, 27] by showing that selection favors the slower diffuser when $\alpha/\mu = \beta/\nu$. Hence, Theorem 3.4.1 implies that zero dispersal rate is a convergent stable strategy along the line $\alpha/\mu = \beta/\nu$.

Remark 3.4.2. [21] *When $\dfrac{\alpha}{\mu} = \dfrac{\beta}{\nu} = 1$, Theorem 3.4.1 does not hold as (3.0.1) has a continuum of positive coexistent states $(sm, (1-s)m)$ for every $0 < s < 1$ and for any μ, ν. Biologically, the assumption $\dfrac{\alpha}{\mu} = \dfrac{\beta}{\nu} = 1$ means that both species u and v are using ideal free dispersal strategies and will thus coexist.*

3.4.1 Proof of Theorem 3.4.1

Before proving Theorem 3.4.1, we state and prove a useful lemma.

Lemma 3.4.3. [21] *Consider the following eigenvalue problem*

$$\begin{cases} \gamma\nabla\cdot\left(e^{\tau\ln m}\nabla\psi\right)+e^{\tau\ln m}h\psi=-\lambda e^{\tau\ln m}\psi \quad x\in\Omega, \\ \nabla\psi\cdot n=0 \quad x\in\partial\Omega. \end{cases} \tag{3.4.1}$$

where $\tau > 0$*,* $h \in C(\bar{\Omega})$*, and* h *is not a constant function. Then* $\bar{\lambda}$ *is a strictly increasing function of* γ*, where* $\bar{\lambda}$ *is the principle eigenvalue for* (3.4.1)*.*

Proof. We first note that $\bar{\lambda}$ satisfies

$$\begin{cases} \gamma\nabla\cdot\left(e^{\tau\ln m}\nabla\bar{\psi}\right)+e^{\tau\ln m}h\bar{\psi}=-\bar{\lambda}e^{\tau\ln m}\bar{\psi} \quad x\in\Omega, \\ \nabla\bar{\psi}\cdot n=0 \quad x\in\partial\Omega, \end{cases} \tag{3.4.2}$$

where $\bar{\psi} > 0$ on Ω. It is clear from the variational characterization that $\bar{\lambda}$ is an increasing function of γ. We claim that this function is strictly increasing. Considering (3.4.2), by the implicit function theorem we see that $\bar{\lambda}$, $\bar{\psi}$ are both differentiable functions of γ (see [3]). Hence we differentiate both sides of (3.4.2) with respect to γ to obtain

$$\begin{cases} \gamma\nabla\cdot\left(e^{\tau\ln m}\nabla\bar{\psi}'\right)+\nabla\cdot\left(e^{\tau\ln m}\nabla\bar{\psi}\right)+e^{\tau\ln m}\bar{\psi}'h \\ =-\bar{\lambda}'e^{\tau\ln m}\bar{\psi}-\bar{\lambda}e^{\tau\ln m}\bar{\psi}' \quad x\in\Omega, \\ \nabla\bar{\psi}'\cdot n=0 \quad x\in\partial\Omega. \end{cases} \tag{3.4.3}$$

If we multiply (3.4.3) by $\bar{\psi}$ and (3.4.2) by $\bar{\psi}'$, subtract the two equations, and finally using the boundary conditions, integrate by parts, we see that

$$\bar{\lambda}'\int_{\Omega}e^{\tau\ln m}\bar{\psi}^2=\int_{\Omega}|\nabla\bar{\psi}|^2e^{\tau\ln m}$$

Because $\bar{\psi} > 0$ on Ω, we have that $\bar{\lambda}' \geq 0$. Suppose $\bar{\lambda}' = 0$. Then it must be the case that $\bar{\psi} \equiv C > 0$, where C is constant. Hence, (3.4.1) gives us that $-\bar{\lambda} = h$ on Ω. But we assumed that h is not a constant on Ω and so we have a contradiction. Therefore, it follows that $\bar{\lambda}' > 0$ and hence that $\bar{\lambda}$ is strictly increasing. □

Now we prove Theorem 3.4.1

Proof. Fix $\alpha, \mu, \beta, \nu > 0$ such that $\dfrac{\alpha}{\mu} = \dfrac{\beta}{\nu} \neq 1$. Suppose that $\mu < \nu$, we first show that $(\theta_{\alpha,\mu}, 0)$ is locally stable. Linearizing (3.0.1) at $(\theta_{\alpha,\mu}, 0)$, we see that it suffices to consider

$$\begin{cases} \nabla \cdot [\nu \nabla \phi - \beta \phi \nabla \ln m] + \phi(m - \theta_{\alpha,\mu}) = -\lambda \phi & x \in \Omega, \\ [\nu \nabla \phi - \beta \phi \nabla \ln m] \cdot n = 0 & x \in \partial\Omega. \end{cases} \tag{3.4.4}$$

Set $\varphi = e^{-\beta/\nu \ln m} \phi$. Substituting this into (3.4.4), we see that φ satisfies

$$\begin{cases} \nu \nabla \cdot [e^{\beta/\nu \ln m} \nabla \varphi] + e^{\beta/\nu \ln m} \varphi(m - \theta_{\alpha,\mu}) = -\lambda e^{\beta/\nu \ln m} \varphi & x \in \Omega, \\ \nabla \varphi \cdot n = 0 & x \in \partial\Omega. \end{cases} \tag{3.4.5}$$

We can also rewrite the equation for $\theta_{\alpha,\mu}$ as

$$\begin{cases} \mu \nabla \cdot \left[e^{\alpha/\mu \ln m} \nabla (e^{-\alpha/\mu \ln m} \theta_{\alpha,\mu})\right] + \theta_{\alpha,\mu}(m - \theta_{\alpha,\mu}) = 0 & x \in \Omega, \\ \nabla (e^{-\alpha/\mu \ln m} \theta_{\alpha,\mu}) \cdot n = 0, & x \in \partial\Omega. \end{cases} \tag{3.4.6}$$

Set $\theta_0 = e^{-\alpha/\mu \ln m} \theta_{\alpha,\mu}$, we see that θ_0 satisfies

$$\begin{cases} \mu \nabla \cdot [e^{\alpha/\mu \ln m} \nabla \theta_0] + e^{\alpha/\mu \ln m} \theta_0(m - \theta_{\alpha,\mu}) = 0 & x \in \Omega, \\ \nabla \theta_0 \cdot n = 0, & x \in \partial\Omega. \end{cases} \tag{3.4.7}$$

Referring to Lemma 3.4.3, put $h = m - \theta_{\alpha,\mu}$. Furthermore, set $\tau = \dfrac{\alpha}{\mu} = \dfrac{\beta}{\nu}$. Note that from (3.4.7), since $\theta_{\alpha,\mu} > 0$ on Ω, which means that $\theta_0 > 0$ on Ω, we see that when $\gamma = \mu$, $\bar{\lambda}(\mu) = 0$. Furthermore, when $\gamma = \nu$, since we are assuming that $\mu < \nu$ by Lemma 3.4.3 we see that $\bar{\lambda}(\nu) > \bar{\lambda}(\mu) = 0$. This means then that $(\theta_{\alpha,\mu}, 0)$ is locally stable.

Finally, we prove that system (3.0.1) has no positive steady state solutions for our particular choice of α, μ, β, and ν. We argue by contradiction: suppose that (3.0.1) has a positive steady state solution (u, v). Let $h = m - u - v$ in Ω. Then we see that (u, v) satisfy

$$\begin{cases} \mu\nabla \cdot [\nabla u - (\alpha/\mu)u\nabla \ln m] + uh = 0 \quad x \in \Omega, \\ \nu\nabla \cdot [\nabla v - (\beta/\nu)v\nabla \ln m] + vh = 0 \quad x \in \Omega, \\ [\nabla u - (\alpha/\mu)u\nabla \ln m] \cdot n = [\nabla v - (\beta/\nu)v\nabla \ln m] \cdot n = 0 \quad x \in \partial\Omega. \end{cases} \tag{3.4.8}$$

Let $\bar{u} = e^{-\alpha/\mu \ln m}u$ and $\bar{v} = e^{-\beta/\nu \ln m}v$. Then the equations in (3.4.8) can be written as follows:

$$\begin{cases} \mu\nabla \cdot [e^{\alpha/\mu \ln m}\nabla \bar{u}] + e^{\alpha/\mu \ln m}\bar{u}h = 0 \quad x \in \Omega, \\ \nu\nabla \cdot [e^{\beta/\nu \ln m}\nabla \bar{v}] + e^{\beta/\nu \ln m}\bar{v}h = 0 \quad x \in \Omega, \\ \nabla \bar{u} \cdot n = \nabla \bar{v} \cdot n = 0 \quad x \in \partial\Omega. \end{cases} \tag{3.4.9}$$

Since $\alpha/\mu = \beta/\nu$, we see that $\bar{u}$ is the principle eigenfunction satisfying (3.4.1) when $\gamma = \mu$, and we see that $\bar{v}$ is the principle eigenfunction satisfying the same eigenvalue problem when $\gamma = \nu$. Since we are assuming that $\mu < \nu$, by Lemma 3.4.3, we know that $\bar{\lambda}(\mu) < \bar{\lambda}(\nu)$. But from (3.4.9), we see that $\bar{\lambda}(\mu) = 0 = \bar{\lambda}(\nu)$, which is a contradiction. Hence, (3.0.1) has no positive steady state solutions. Finally, since (3.0.1) has no positive steady states, by Theorem 1.3.2 we see that $(\theta_{\alpha,\mu}, 0)$ is globally asymptotically stable. The proof concerning the global asymptotic stability of $(0, \theta_{\beta,\nu})$ is similar. □

Theorem 3.4.1 raises a interesting question: in a temporally constant but spatially varying environment, is the smaller dispersal rate always favored by selection? The following result provides a partial answer:

Theorem 3.4.4. [21] *Suppose $m, m_x > 0$ on $\bar{\Omega} = [0, 1]$, and $\alpha = \beta$.*

(i) *If $0 \leq \alpha < \mu$, there is an $\epsilon_1 > 0$ such that for $\nu \in (\mu, \mu + \epsilon_1)$, $(\theta_{\alpha,\mu}, 0)$ is globally asymptotically stable.*

(ii) *If* $\alpha \geq \max\left\{\mu, \dfrac{\int_0^1 m}{\min_{[0,1]}(m_x/m)}\right\}$, *there is an* $\epsilon_2 > 0$ *such that for* $\nu \in (\mu, \mu + \epsilon_2)$, $(0, \theta_{\beta,\nu})$ *is globally asymptotically stable.*

Theorem 3.4.4 is motivated by [24], where a similar result is established for the model (3.0.1) with $P = Q = m$. It is an open question whether part (ii) holds for any $\alpha > \mu$.

Theorem 3.4.4 assumes that the advection rates of both species are set to be equal and the diffusion rates vary. If both diffusion rates are close and larger than the advection rate, the slower diffuser wins. However, if both diffusion rates are close but smaller than the advection rate then the faster dispersal rate is favored. In particular, Theorem 3.4.4 implies that the ideal free strategy $\mu = \alpha$ is a convergent stable strategy with respect to the evolution of the random diffusion rate. For each fixed $\alpha = \beta$, the species whose diffusion rate is closer to the (common) advection rate will win; i.e., selection prefers strategies which are closer to being ideal free.

3.4.2 Proof of Theorem 3.4.4

Proof. (i) We begin by showing that $(\theta_{\alpha,\mu}, 0)$ is locally stable. Referring to the eigenvalue problem in (3.1.1) and using the parameterizations in Remark 3.1.3, we have that the principal eigenvalue $\lambda^* = \lambda_1 r \cos\phi + \lambda_2 r \sin\phi + O(r^2)$, where λ_1 and λ_2 satisfy (3.1.5) and (3.1.6) respectively. However, since $\alpha = \beta$ is fixed, we consider only $\phi = \pi/2$. Thus, $\cos\phi = 0$ and λ^* has the same sign as λ_2 which satisfies

$$\lambda_2 \int_0^1 e^{-\alpha/\mu \ln m} \theta_{\alpha,\mu}^2 = \int_0^1 \left(e^{-\alpha/\mu \ln m} \theta_{\alpha,\mu}\right)_x (\theta_{\alpha,\mu})_x. \qquad (3.4.10)$$

From Lemma 3.2.1 we have that since $0 \leq \alpha < \mu$, $\left(e^{-(\alpha/\mu)\ln m}\theta_{\alpha,\mu}\right)_x, (\theta_{\alpha,\mu})_x > 0$ on $[0,1]$. Thus, $\lambda_2 > 0$, and there is an $\epsilon > 0$ such that for $r \in (0, \epsilon)$, $\lambda^* > 0$. Hence, $(\theta_{\alpha,\mu}, 0)$ is locally asymptotically stable. Similarly, using Lemma 3.2.1 and the expression for η_2 in (3.1.13), there exists a $\delta > 0$ such that if $r \in (0, \delta)$, the principal eigenvalue for (3.1.11), $\eta^* < 0$. Thus, $(0, \theta_{\beta,\nu})$ is unstable. By Theorem 3.3.7, we see there are no positive steady states and, as our system is strongly monotone, we know that by Theorem 1.3.2 for $0 < r < \epsilon_1 = \min\{\epsilon, \delta\}$, $(\theta_{\alpha,\mu}, 0)$ is globally asymptotically stable.

(ii) From Lemma 3.2.2, since $\alpha > \mu$, $\left(e^{-\alpha/\mu \ln m}\theta_{\alpha,\mu}\right)_x < 0$ on $[0,1]$ and since $\alpha > \dfrac{\int_0^1 m}{\min(m_x/m)}$, Lemma 3.2.5 gives us that $(\theta_{\alpha,\mu})_x > 0$ on $[0,1]$. Using the expression for η_2 in (3.1.13), again with $\phi = \pi/2$, we notice that

$$\eta_2 \int_0^1 e^{-\alpha/\mu \ln m}\theta_{\alpha,\mu}^2 = -\int_0^1 \left(e^{-\alpha/\mu \ln m}\theta_{\alpha,\mu}\right)_x (\theta_{\alpha,\mu})_x. \tag{3.4.11}$$

This shows that $\eta_2 > 0$, indicating that for sufficiently small $r > 0$, $\eta^* > 0$. Hence, $(0, \theta_{\beta,\nu})$ is locally asymptotically stable. In addition, from (3.4.10), $\lambda_1 < 0$, giving us that for sufficiently small $r > 0$, $\lambda^* < 0$. Thus $(\theta_{\alpha,\mu}, 0)$ is unstable. Combining the stability results of both semi-trivial steady states, recalling that our system has no positive steady states, and appealing to the strong monotonicity of our system, renders that for sufficiently small $r > 0$, $(0, \theta_{\beta,\nu})$ is globally asymptotically stable. □

As another example of selection favoring strategies closer to the ideal free strategy, we restate Theorem 2 of [9] in the framework of model (3.0.1), as follows.

Theorem 3.4.5. (*Theorem 2 in* [9]) *Suppose $m, m_x > 0$ on $\bar{\Omega} = [0,1]$ and $\mu = \nu$. If $\alpha < \beta < \mu$ or $\mu < \beta < \alpha$, $(\theta_{\alpha,\mu}, 0)$ is unstable and $(0, \theta_{\beta,\nu})$ is locally stable. Furthermore, give any $\alpha \neq \mu$, there exists a number $\zeta(\alpha) > 0$ such that if $\alpha < \beta < \alpha + \zeta < \mu$ or $\mu < \alpha - \zeta < \beta < \alpha$ then $(0, \theta_{\beta,\nu})$ is globally asymptotically stable.*

Notice in Theorem 3.4.5, we set $\mu = \nu$ and vary the advection rates. By varying advection rates, we see that the species with the advection rate closer to the (common) random dispersal rate is favored, indicating that $\mu = \alpha$ is a CSS. Hence, we show again that the species with the strategy closest to the ideal free dispersal strategy will win.

Remark 3.4.6. *If we relax the monotonicity assumption on* m*, then the first part of Theorem* 3.4.5 *may not hold. That is, for appropriately chosen* m, α, β, μ*, and* ν*, where* $\mu < \alpha < \beta$*, both* $(\theta_{\alpha,\mu}, 0)$ *and* $(0, \theta_{\beta,\nu})$ *can be unstable. This topic will be further explored in Section* 4.1.

Assuming that a one-dimensional trait is represented by a real parameter, then Theorems 3.4.1, 3.4.4, and 3.4.5 are in essence results concerning the evolution of one trait. These results can be summarized in Figure 3.1.

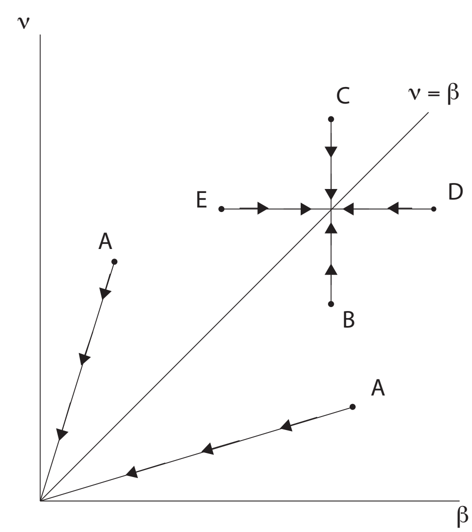

Figure 3.1: (Figure 1 in [21]) Illustration of Theorems 3.4.1, 3.4.4, 3.4.5. Each dot represents a resident with strategy (α, μ) and evolution is directed by the arrows. (A) illustrates Theorem 3.4.1. (B) and (C) illustrate Theorem 3.4.4. (D) and (E) illustrate Theorem 3.4.5. Note that selection drives each resident along its respective path towards the ideal free dispersal strategy (shown as the line $\nu = \beta$).

A question which consequently arises is as follows: Suppose we are given any (α, μ)

with $\alpha \neq \mu$, and we introduce a nearby mutant (β, ν). Can we construct a picture which integrates the results from Theorems 3.4.1, 3.4.4, and 3.4.5? This question prompts us to consider varying both random diffusion and advection simultaneously. Our results are shown in the next section.

3.5 Evolution of Two Traits

All of the previous results concern the evolution of a one-dimensional trait parameter. We allowed a single trait to vary while fixing all other parameters. By varying two trait parameters, we can make the problem more biologically realistic (see [21] for specific examples) and can refer to the variation of two parameters as the evolution of two traits.

In this section we use the model (3.0.1) to study the evolution of two traits; that is, we allow the random dispersal and advection rates to vary simultaneously in the model, while fixing other parameters. The following result provides an initial look into the evolution of two traits:

Theorem 3.5.1. [21] *Suppose that $m, m_x > 0$ on $[0,1]$. Given any $\alpha, \mu > 0$, let $B_\gamma(\alpha, \mu)$ denote the ball of radius γ centered at (α, μ). Then, there exists some $\epsilon > 0$ small such that the following hold:*

(i) *If $\alpha > \mu$, $(\beta, \nu) \in \left\{(\beta, \nu) : \nu \leq \mu, \dfrac{\nu}{\beta} \geq \dfrac{\mu}{\alpha}\right\} \cap B_\epsilon(\alpha, \mu)$, then $(0, \theta_{\beta,\nu})$ is globally asymptotically stable; if $(\beta, \nu) \in \left\{(\beta, \nu) : \nu \geq \mu, \dfrac{\nu}{\beta} \leq \dfrac{\mu}{\alpha}\right\} \cap B_\epsilon(\alpha, \mu)$, then $(\theta_{\alpha,\mu}, 0)$ is globally asymptotically stable.*

(ii) *If $\alpha < \mu$, $(\beta, \nu) \in \left\{(\beta, \nu) : \nu \leq \mu, \dfrac{\nu}{\beta} \leq \dfrac{\mu}{\alpha}\right\} \cap B_\epsilon(\alpha, \mu)$, then $(0, \theta_{\beta,\nu})$ is globally asymptotically stable; If $(\beta, \nu) \in \left\{(\beta, \nu) : \nu \geq \mu, \dfrac{\nu}{\beta} \geq \dfrac{\mu}{\alpha}\right\} \cap B_\epsilon(\alpha, \mu)$, then $(\theta_{\alpha,\mu}, 0)$ is globally asymptotically stable.*

3.5.1 Proof of Theorem 3.5.1

Here we suppose that $m \in C^2(\bar{\Omega})$, m is positive, non-constant and $\Omega = (0,1)$.

Lemma 3.5.2. [21] *Suppose* $\alpha, \mu > 0$ *and let* λ_1, λ_2 *be defined as in* (3.1.5) *and* (3.1.6)*, respectively.*

(i) *If* $\alpha < \mu$*, then* $0 < \dfrac{-\lambda_1}{\lambda_2} < \dfrac{\mu}{\alpha}$.

(ii) *If* $\alpha > \mu$*, then* $\dfrac{\alpha}{\mu} > \dfrac{-\lambda_2}{\lambda_1}$.

Furthermore, suppose that m *is linear. If* $\alpha < \mu$*, then* $\dfrac{\mu}{\alpha} > \dfrac{-\lambda_1}{\lambda_2} > 1$*. On the other hand, if* $\alpha > \mu$*, then* $\dfrac{\mu}{\alpha} < \dfrac{-\lambda_1}{\lambda_2} < 1$.

Proof. (i) When $\alpha < \mu$, Lemma 3.2.1 states that $\mu(\theta_{\alpha,\mu})_x - \alpha\dfrac{m_x}{m}\theta_{\alpha,\mu} > 0$ on $(0,1)$. Hence

$$\begin{aligned} 0 &< \int_0^1 (e^{-\alpha/\mu \ln m}\theta_{\alpha,\mu})_x \left(\mu(\theta_{\alpha,\mu})_x - \alpha\frac{m_x}{m}\theta_{\alpha,\mu}\right) \\ &= -\alpha\int_0^1 (e^{-\alpha/\mu \ln m}\theta_{\alpha,\mu})_x \frac{m_x}{m}\theta_{\alpha,\mu} + \mu\int_0^1 (e^{-\alpha/\mu \ln m}\theta_{\alpha,\mu})_x(\theta_{\alpha,\mu})_x. \end{aligned} \tag{3.5.1}$$

Note that using (3.1.5), (3.1.6), and (3.5.1) gives $0 < \alpha\lambda_1 + \mu\lambda_2$. Thus, because $\lambda_2 > 0$, we obtain our result.

(ii) If $\alpha > \mu$, then Lemma 3.2.2 gives us that $\mu(\theta_{\alpha,\mu})_x - \alpha\dfrac{m_x}{m}\theta_{\alpha,\mu} < 0$ on $(0,1)$. Proceeding as above, we see that $\alpha\lambda_1 + \mu\lambda_2 > 0$. Since $\lambda_1 > 0$, our result follows.

Now suppose that m is linear. By part (i) above, we have that $\dfrac{-\lambda_1}{\lambda_2} < \dfrac{\mu}{\alpha}$. From Theorem 3.2.9, we know that $(\theta_{\alpha,\mu})_x - \dfrac{m_x}{m}\theta_{\alpha,\mu} < 0$ on $[0,1]$. Thus,

$$\begin{aligned} 0 &> \int_0^1 (e^{-\alpha/\mu \ln m}\theta_{\alpha,\mu})_x \left((\theta_{\alpha,\mu})_x - \frac{m_x}{m}\theta_{\alpha,\mu}\right) \\ &= \int_0^1 (e^{-\alpha/\mu \ln m}\theta_{\alpha,\mu})_x(\theta_{\alpha,\mu})_x - \int_0^1 (e^{-\alpha/\mu \ln m}\theta_{\alpha,\mu})_x \frac{m_x}{m}\theta_{\alpha,\mu}. \end{aligned} \tag{3.5.2}$$

Now from (3.1.5), (3.1.6), and (3.5.2), it follows that $\lambda_2 + \lambda_1 < 0$. Since $(\theta_{\alpha,\mu})_x > 0$ on $[0,1]$, $\lambda_2 > 0$ and our result follows. The proof of the other case is similar. □

Similar to Lemma 3.5.2, we have the following result:

Lemma 3.5.3. [21] *Suppose* $\alpha, \mu > 0$ *and let* η_1, η_2 *be defined as in* (3.1.12) *and* (3.1.13), *respectively.*

(i) *If* $\alpha < \mu$, *then* $0 < \dfrac{-\eta_1}{\eta_2} < \dfrac{\mu}{\alpha}$.

(ii) *If* $\alpha > \mu$, *then* $\dfrac{\alpha}{\mu} > \dfrac{-\eta_2}{\eta_1}$.

In addition, suppose that m *is linear. If* $\alpha < \mu$, *then* $\dfrac{\mu}{\alpha} > \dfrac{-\eta_1}{\eta_2} > 1$. *Also, if* $\alpha > \mu$, *then* $\dfrac{\mu}{\alpha} < \dfrac{-\eta_1}{\eta_2} < 1$.

Theorem 3.5.4. [21] (*Theorem* 3.5.1) *Fix* $\mu, \alpha > 0$, *and set* $\beta = \alpha + r\cos\phi$ *and* $\nu = \mu + r\sin\phi$, *where* $r > 0$ *and* $\phi \in [0, 2\pi)$.

(i) *Suppose that* $\alpha < \mu$. *There exists* $0 < \gamma_1 \ll 1$ *such that if* $r < \gamma_1$ *and* $\phi \in [\tan^{-1}(\mu/\alpha) - \pi, 0]$, *then* $(0, \theta_{\beta,\nu})$ *is globally asymptotically stable. Furthermore, there is a* $0 < \gamma_2 \ll 1$ *such that if* $r < \gamma_2$ *and* $\phi \in [\tan^{-1}(\mu/\alpha), \pi]$, *then* $(\theta_{\alpha,\mu}, 0)$ *is globally asymptotically stable.*

(ii) *Suppose that* $\alpha > \mu$. *There exists* $0 < \gamma_3 \ll 1$ *such that if* $r < \gamma_3$ *and* $\phi \in [\pi, \cot^{-1}(\alpha/\mu) + \pi]$, *then* $(0, \theta_{\beta,\nu})$ *is globally asymptotically stable. Furthermore, there is a* $0 < \gamma_4 \ll 1$ *such that if* $r < \gamma_4$ *and* $\phi \in [0, \cot^{-1}(\alpha/\mu)]$, *then* $(\theta_{\alpha,\mu}, 0)$ *is globally asymptotically stable.*

Proof. (i) We know that as long as $\lambda_1\cos\phi + \lambda_2\sin\phi \neq 0$, but retains the same sign, $\lambda^* = \lambda_1 r\cos\phi + \lambda_2 r\sin\phi + O(r^2) \neq 0$ for $0 < r \ll 1$ and appropriate ϕ. Define the function g as $g(\phi) = \lambda_1\cos\phi + \lambda_2\sin\phi$. Clearly g is continuous in ϕ. Note that $g(-\pi/2) = -\lambda_2 < 0$ (see (3.1.6) and Lemma 3.2.1). We claim that on $[\tan^{-1}(\mu/\alpha) - \pi, 0]$, $g < 0$. Suppose this is not the case. That is, suppose that $g(\phi_0) = 0$ for some $\phi_0 \in [\tan^{-1}(\mu/\alpha) - \pi, 0]$. Then $\phi_0 \in [\tan^{-1}(\mu/\alpha) - \pi, -\pi/2)$ or $\phi_0 \in (-\pi/2, 0]$. Suppose $\phi_0 \in [\tan^{-1}(\mu/\alpha) - \pi, -\pi/2)$. On the one hand, since $g(\phi_0) =$

0, $\tan(\phi_0) = \dfrac{-\lambda_1}{\lambda_2}$, but on the other hand, $\tan(\phi_0) \geq \dfrac{\mu}{\alpha}$ on this interval. Lemma 3.5.2 states that $\dfrac{-\lambda_1}{\lambda_2} < \dfrac{\mu}{\alpha}$, giving us a contradiction. Next, if we suppose $\phi_0 \in (-\pi/2, 0]$, we obtain a contradiction since $\tan(\phi_0) \leq 0$, but by Lemma 3.5.2 , $\dfrac{-\lambda_1}{\lambda_2} > 0$. Finally, since g is continuous, it does not change sign on $[\tan^{-1}(\mu/\alpha) - \pi, -\pi/2) \cup (-\pi/2, 0]$, and $g(-\pi/2) = -\lambda_2 < 0$, we see that $g < 0$ on the desired interval. Thus for r small enough and $\phi \in [\tan^{-1}(\mu/\alpha) - \pi, 0]$, the principal eigenvalue λ^*, in conjunction with semi-trivial steady state $(\theta_{\alpha,\mu}, 0)$, has the same sign as $g(\phi)$. Since $g < 0$ on $[\tan^{-1}(\mu/\alpha) - \pi, 0]$, it must be that $\lambda^* < 0$. Hence, $(\theta_{\alpha,\mu}, 0)$ is unstable. Note that by Theorem 3.3.7, our system does not have any positive steady states. Hence, by Theorem 1.3.2, $(0, \theta_{\beta,\nu})$ is globally asymptotically stable.

For the second case, define $h(\phi) = \eta_1 \cos\phi + \eta_2 \sin\phi$. By the continuity of h, Lemma 3.5.3, (3.1.12), and (3.1.13), we see that $h > 0$ on $[\tan^{-1}(\mu/\alpha), \pi]$. Here we want to show that $(0, \theta_{\beta,\nu})$ is unstable. As above, we can express the principal eigenvalue $\eta^* = \eta_1 r \cos\phi + \eta_2 r \sin\phi + O(r^2)$ for small r and $\phi \in [\tan^{-1}(\mu/\alpha), \pi]$. For these values of r and ϕ, $\eta^* = rh(\phi) + O(r^2)$. Hence, $\eta^* > 0$, which shows that $(0, \theta_{\beta,\nu})$ is unstable. Again, by Theorem 3.3.7 our system does not have positive steady states, so by Theorem 1.3.2, $(\theta_{\alpha,\mu}, 0)$ is globally asymptotically stable.

(ii) The proof is quite similar to that of part (i). First we want to show that for small r and $\phi \in [\pi, \cot^{-1}(\alpha/\mu) + \pi]$, $\lambda^* < 0$, implying that $(\theta_{\alpha,\mu}, 0)$ is unstable. Again, we define $g(\phi) = \lambda_1 \cos\phi + \lambda_2 \sin\phi$. Using (3.1.6) and Lemma 3.2.2, we see that $g(\pi) = -\lambda_1 < 0$. We claim that $g < 0$ on $[\pi, \cot^{-1}(\alpha/\mu) + \pi]$. Suppose that $g(\phi_0) = 0$ for some $\phi_0 \in (\pi, \cot^{-1}(\alpha/\mu) + \pi]$. Then $\cot\phi = \dfrac{-\lambda_2}{\lambda_1}$. But on $[\pi, \cot^{-1}(\alpha/\mu) + \pi]$, $\cot\phi > \dfrac{\alpha}{\mu} > \dfrac{-\lambda_2}{\lambda_1}$, where the last inequality is given by Lemma 3.5.2. This is a contradiction and thus shows that $g < 0$ on the given interval. Hence, for small enough r and $\phi \in [\pi, \cot^{-1}(\alpha/\mu) + \pi]$, we can write $\lambda^* = rg(\phi) + O(r^2)$ and we have that $\lambda^* < 0$. Thus, $(\theta_{\alpha,\mu}, 0)$ is unstable. Again, by appealing to Theorem 3.3.7 and Theorem 1.3.2, $(0, \theta_{\beta,\nu})$ is globally asymptotically stable.

For the other case, we define $h(\phi) = \eta_1 \cos\phi + \eta_2 \sin\phi$. Following an argument similar to the above, we see that $h > 0$ on $[0, \cot^{-1}(\alpha/\mu)]$. We can then write $\eta^* = rh(\phi) + O(r^2)$ for small enough r and $\phi \in [0, \cot^{-1}(\alpha/\mu)]$. Thus, $\eta^* > 0$, which indicates that $(0, \theta_{\beta,\nu})$ is unstable. Finally, by Theorem 3.3.7 and Theorem 1.3.2, it must be that $(\theta_{\alpha,\mu}, 0)$ is globally asymptotically stable. □

Theorem 3.5.1 provides limited regions where we can conclude whether or not a semi-trivial steady state is globally asymptotically stable; see Figure 3.2. The picture is more complete, however, for linear resource functions. The underlying mathematical reason, which could be technical, is that the gradient of the single-species equilibrium solution $\theta_{\alpha,\mu}$ plays a crucial role in determining the stability of the semi-trivial steady states of (3.0.1). What is surprising is that there are monotone resource functions m on $\Omega = (0, 1)$ such that $\theta_{\alpha,\mu}$ are nonmonotone. We will give a more detailed discussion in Section 3.5.3 about such example(s). For now, this gives us reason to narrow our choice of resource function for the sake of finding an analytic picture which is more complete than Figure 3.2. We consider linear m in the next result.

Theorem 3.5.5. [21] *Suppose that m is linear, nonconstant and positive on $[0, 1]$. Given any $\alpha, \mu > 0$, there exists some $\epsilon > 0$ small such that*

(i) *If $\alpha > \mu$, $(\beta, \nu) \in \left\{(\beta, \nu) : \nu - \mu \geq \beta - \alpha, \dfrac{\nu}{\beta} \geq \dfrac{\mu}{\alpha}\right\} \cap B_\epsilon(\alpha, \mu)$, then $(0, \theta_{\beta,\nu})$ is globally asymptotically stable; If $(\beta, \nu) \in \left\{(\beta, \nu) : \nu - \mu \leq \beta - \alpha, \dfrac{\nu}{\beta} \leq \dfrac{\mu}{\alpha}\right\} \cap B_\epsilon(\alpha, \mu)$, then $(\theta_{\alpha,\mu}, 0)$ is globally asymptotically stable.*

(ii) *If $\alpha < \mu$, $(\beta, \nu) \in \left\{(\beta, \nu) : \nu - \mu \leq \beta - \alpha, \dfrac{\nu}{\beta} \leq \dfrac{\mu}{\alpha}\right\} \cap B_\epsilon(\alpha, \mu)$, then $(0, \theta_{\beta,\nu})$ is*

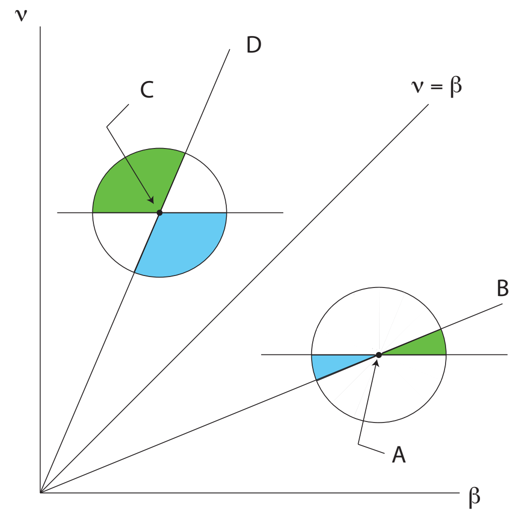

Figure 3.2: (Figure 2 in [21]) Illustration of Theorem 3.5.1. Part (i): Point (A) represents resident with strategy (α, μ), centering the ball B_ϵ. An invader with strategy (β, ν) located in the blue region wins over strategy (A). However, an invader with strategy in the green region loses to (A). Line B has slope $\dfrac{\mu}{\alpha}$ and the line $\nu = \beta$ represents the ideal free dispersal strategy. Part(ii): Illustrated as in part (i). Just replace point (A) with point (C) and line B with line D.

globally asymptotically stable; If $(\beta, \nu) \in \left\{(\beta, \nu) : \nu - \mu \geq \beta - \alpha, \dfrac{\nu}{\beta} \geq \dfrac{\mu}{\alpha}\right\} \cap B_\epsilon(\alpha, \mu)$, *then* $(\theta_{\alpha,\mu}, 0)$ *is globally asymptotically stable.*

3.5.2 Proof of Theorem 3.5.5

Before proving the Theorem 3.5.5, we reformulate it in terms of polar coordinates, and present the result in full generality.

Theorem 3.5.6. (*Theorem* 3.5.5) *Fix* $\mu, \alpha > 0$. (*Note that here we slightly extend the regions listed in Theorem* 3.5.5) *Consider the parameterizations* $\beta = \alpha + r\cos(\phi)$ *and* $\nu = \mu + r\sin(\phi)$, *where* $r > 0$ *and* $\phi \in [0, 2\pi)$.

(i) *Suppose that* $\alpha < \mu$*. Let* $0 < \tau_1 < \dfrac{-\lambda_1}{\lambda_2}$ *and* $\dfrac{-\lambda_1}{\lambda_2} < \rho_1$*. There exists* $0 < \gamma_1 \ll 1$ *such that if* $r < \gamma_1$ *and* $\phi \in [\tan^{-1}(\rho_1) - \pi, \tan^{-1}(\tau_1)]$*, then* $(0, \theta_{\beta,\nu})$ *is globally asymptotically stable.*

(ii) *Suppose that* $\alpha < \mu$*. Let* $\dfrac{-\eta_1}{\eta_2} < \tau_2$ *and* $0 < \rho_2 < \dfrac{-\eta_1}{\eta_2}$*. There exists* $0 < \gamma_2 \ll 1$ *such that if* $r < \gamma_2$ *and* $\phi \in [\tan^{-1}(\tau_2), \pi + \tan^{-1}(\rho_2)]$*, then* $(\theta_{\alpha,\mu}, 0)$ *is globally asymptotically stable.*

(iii) *Suppose that* $\alpha > \mu$*. Let* $\dfrac{-\lambda_1}{\lambda_2} < \tau_3$ *and* $0 < \rho_3 < \dfrac{-\lambda_1}{\lambda_2}$*. There exists* $0 < \gamma_3 \ll 1$ *such that if* $r < \gamma_3$ *and* $\phi \in [\tan^{-1}(\tau_3), \pi + \tan^{-1}(\rho_3)]$*, then* $(0, \theta_{\beta,\nu})$ *is globally asymptotically stable.*

(iv) *Suppose that* $\alpha > \mu$*. Let* $0 < \tau_4 < \dfrac{-\lambda_1}{\lambda_2}$ *and* $\dfrac{-\lambda_1}{\lambda_2} < \rho_4$*. There exists* $0 < \gamma_4 \ll 1$ *such that if* $r < \gamma_4$ *and* $\phi \in [\tan^{-1}(\rho_4) - \pi, \tan^{-1}(\tau_4)]$*, then* $(\theta_{\alpha,\mu}, 0)$ *is globally asymptotically stable.*

Proof. (i) We begin by showing that $(\theta_{\alpha,\mu}, 0)$ is unstable. As in the proof of Theorem 3.5.4, we seek a region where $\lambda_1 \cos\phi + \lambda_2 \sin\phi \neq 0$. Define $g(\phi) = \lambda_1 \cos\phi + \lambda_2 \sin\phi$. Note that by Lemma 3.2.1 and (3.1.6), $g(-\pi/2) = -\lambda_2 < 0$. We claim that $g < 0$ on $[\tan^{-1}(\rho_1) - \pi, \tan^{-1}(\tau_1)]$. Suppose that g changes sign on this interval. Then there is a $\phi_0 \in [\tan^{-1}(\rho_1) - \pi, -\pi/2) \cup (-\pi/2, \tan^{-1}(\tau_1)]$ where $g(\phi_0) = 0$. By definition of g, we see that $\tan(\phi_0) = \dfrac{-\lambda_1}{\lambda_2}$. Now if $\phi_0 \in [\tan^{-1}(\rho_1) - \pi, -\pi/2)$, then $\tan(\phi_0) \geq \rho_1 > \dfrac{-\lambda_1}{\lambda_2}$, which is a contradiction. Likewise, if $\phi \in (-\pi/2, \tan^{-1}(\tau_1)]$, $\tan(\phi) \leq \tau_1 < \dfrac{-\lambda_1}{\lambda_2}$, which is a contradiction. Thus, as g is continuous in ϕ and does not change sign, $g < 0$ on $[\tan^{-1}(\rho_1) - \pi, \tan^{-1}(\tau_1)]$. We can then write $\lambda^* = rg(\phi) + O(r^2) < 0$ for sufficiently small $r > 0$ and $\phi \in [\tan^{-1}(\rho_1) - \pi, \tan^{-1}(\tau_1)]$. It follows that $(\theta_{\alpha,\mu}, 0)$ is unstable. By Theorem 3.3.7 and Theorem 1.3.2, $(0, \theta_{\beta,\nu})$ is globally asymptotically stable. The other cases can be proved similarly. □

Theorem 3.5.5 is succinctly illustrated in Figure 3.3. Note that for part (ii) of Theorem 3.5.5, the picture is symmetric with respect to the line $\nu = \beta$.

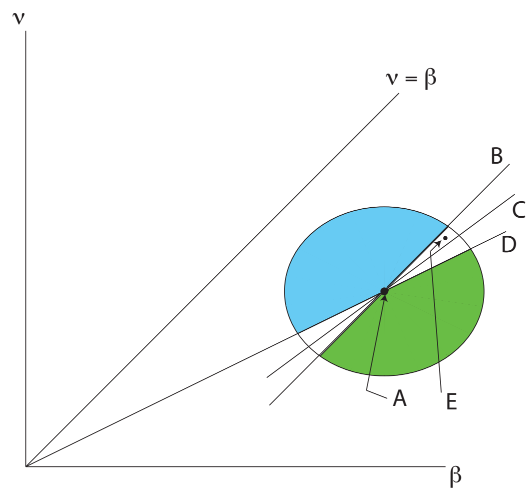

Figure 3.3: (Figure 3 in [21]) Illustration of Theorem 3.5.5, part (i). Point (A) represents resident with strategy (α, μ), centering the ball B_ϵ. Line B is parallel to the line $\nu = \beta$ (the ideal free dispersal strategy). Line C represents the line formed when $\lambda^* = 0$ (refer to parameterization in (3.1.2)). Line D has slope $\frac{\mu}{\alpha}$. An invader with strategy (β, ν) located in the blue region wins over (A). However, an invader with strategy in the green region loses to (A).

3.5.3 Numerical Results with Monotonic Resource

Before we present our specific numerical results in this section, we briefly discuss our numerical methods and introduce some terminology.

Numerical Methods

The numerical analysis of the PDE was performed using MATLAB's pdepe code [21]. In terms of simulating a competition between a resident and an invader, we begin with a resident of initial distribution $u_0 = \sin(2\pi x) + 2\sin(3\pi x) + 3$, $v_0 = 0$ and allow that resident's population size to evolve according to (3.0.1) up to time $t = 10^{15}$ [21]. This allows the resident distribution to essentially be at "equilibrium". This resulting "equilibrium" distribution becomes the new initial population of the resident. Next, we introduce an invader with initial distribution $v_0 = 0.05(\sin(2\pi x) + 2\sin(3\pi x) + 3)$ and run the new system for time $t = 10^{15}$ [21]. As in [21], a species survives if its maximum population size at any point in the domain is larger than 0.01, otherwise we consider the species extinct. To be a winner, a species must survive and all other competitors must go extinct.

In order to illustrate these competitions graphically (with respect to specific parameters), we use Pairwise Invasion Plots (PIP). "Each point corresponds to a different competition where the color of the point indicates the outcome of the competition. Green indicates the resident wins, blue the invader wins, and red implies that both species survive. Two types of PIP plots were generated: α v β where μ and ν are held constant while α and β are varied and β v ν where α and μ are held constant while β and ν are varied [21]."

Monotone Results

In this section, we numerically test our new results in Theorem 3.5.1 and Theorem 3.5.5 as well as broaden their applicability. To begin, we assume a resident has traits $\alpha = 0.5$ and $\mu = 1$ and the resource function $m(x) = 2x + 1$ [21]. We plot the results of resident versus invader competitions in a circular PIP where the invader traits are allowed to be small perturbations around $\alpha = 0.5$ and $\mu = 1$, see Figure 3.4(a).

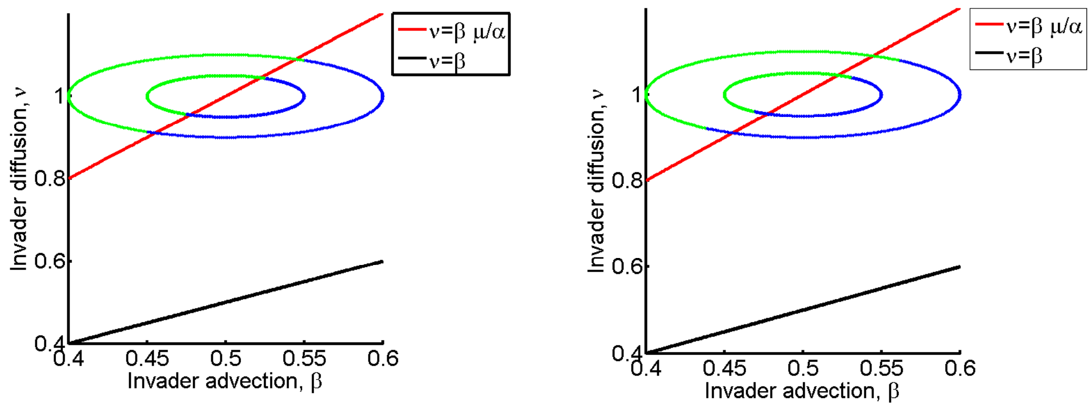

Figure 3.4: (Figure 4 in [21])(a) Linear and (b) monotonic circular PIP for $\alpha = 0.5$, $\mu = 1$. Green points indicate the resident wins, blue points indicate the invader wins, and red indicates coexistence.

Notice that we have an invader winning over the resident via a vertical perturbation under which μ decreases slightly. This is consistent with the result of [17] as the slower diffuser gains an advantage. However, if we consider a circular PIP around a resident with traits $\alpha = 1$ and $\mu = 0.5$, the picture will be symmetric relative to the $\nu = \beta$ line. This suggests, and is consistent with the result of Hambrock and Lou [24], that a vertical perturbation where μ increases slightly gives the faster diffuser the advantage. Thus we see that our numerics correspond to the analytic result in Theorem 3.5.1. In addition, we see in Figure 3.4 (a) that there are regions near the $\nu = \dfrac{\mu}{\alpha}\beta$ line where either the resident or invader wins. As Theorem 3.5.5 indicates, "these regions overlap the μ/α line, and are actually divided into two regions by the line representing $\lambda^* = 0$ (compare Figure 3.3 and 3.4)" [21].

Note that in Figure 3.5, we let $m(x) = \sin(10x) + 10.1x + 10$ which is clearly non-linear, but still monotone. Interestingly, for $\alpha = 3$ and $\mu = 0.1$, the steady state profile for the single resident species is not monotone, see Figure 3.5. However, referring to Figure 3.4(b), we see a similar picture as in the linear case (except with a larger region of overlap). Not only does this support our analytic findings, but it allows us to generally say that for a monotone resource m, the competitive species which is "closer" to the ideal free strategy will win.

We see then that the ideal free strategy provides a reference point from which we can more clearly understand the evolution of dispersal as well as interpret previous findings. As was mentioned above, Hambrock and Lou obtained almost an identical result to Theorem 3.5.1. In order to explain why sometimes the faster or slower diffuser gains the competitive advantage, Hambrock and Lou [24] suggested that "a balanced combination of random dispersal and biased movement along resource gradients is probably a good strategy . . . for the species as a whole". While this makes biological sense, it remains somewhat indefinite. Putting the whole picture

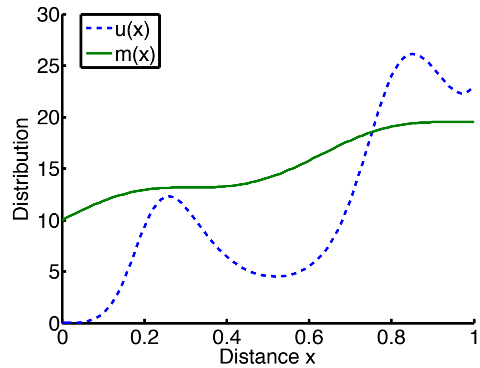

Figure 3.5: (Figure 5 in [21])Non-monotonic resident steady state (blue dashed curve) plotted against its monotonic resource (green solid curve).

together, our conclusion for monotone m allows us to precisely define this 'balanced combination' in terms of the ideal free strategy.

3.5.4 Evolutionary Paths

As in the one trait case, it is tempting to conjecture that the ideal free dispersal strategy $\nu = \beta$ is a CSS with respect to the Euclidean metric in the trait space (β, ν). That is, given a resident strategy (α, μ) with $\alpha \neq \mu$ (i.e., not an ideal free dispersal strategy for the resident), we would expect that an invading species with strategy (β, ν) will be able to invade when rare if the distance from (β, ν) to the line $\nu = \beta$ is shorter than the distance from (α, μ) to the line $\nu = \beta$. However, referring to Figure 3.3, note that the blue and green regions can be arbitrarily close to the line C (also refer to the generalized version in Theorem 3.5.6). Hence, an invader with strategy at (E), for example, can replace (A) and become the new resident even though its distance to the line $\nu = \beta$ is greater than the distance from (A) to the line $\nu = \beta$; see Figure 3.3. This means that there are certain paths along which selection will drive the dispersal strategy further away from the ideal free dispersal strategy.

It seems natural to ask the following question: along which paths (not necessarily straight lines) is the ideal free dispersal strategy a CSS in the trait space (β, ν)? Note that in the one trait case, we showed that along the vertical line, the horizontal line and the line $\alpha/\mu = \beta/\nu$, the ideal free dispersal strategy is indeed a CSS. To answer this question, we first give a definition. For $0 \le s \le 1$, define curves

$$\begin{aligned} \Gamma_- &:= \{(x(s), y(s)) : 0 < y(s) < x(s), \quad 0 \le s < 1, \quad x(1) = y(1)\}, \\ \Gamma_+ &:= \{(x(s), y(s)) : 0 < x(s) < y(s), \quad 0 \le s < 1, \quad x(1) = y(1)\}. \end{aligned} \tag{3.5.3}$$

We say that Γ_- or Γ_+ is a **convergent stable path** if for any $0 \le s < 1$, there exists $\delta > 0$ small enough such that for any $0 < \Delta s < \delta$, the semi-trivial steady state $(0, \theta_{\beta,\nu})$ of system (3.0.1) with $(\alpha, \mu, \beta, \nu) = (x(s), y(s), x(s + \Delta s), y(s + \Delta s))$ is globally asymptotically stable.

The following result provides a criterion for determining a convergent stable path:

Theorem 3.5.7. [21] *Suppose that m is linear, non-constant and positive on* $[0, 1]$. *Let $x(s), y(s)$ be two positive functions defined on* $[0, 1]$.

(i) *If we further assume that both $y(s) - x(s)$ and $\dfrac{y(s)}{x(s)}$ are monotonically decreasing functions for $s \in [0, 1)$, then Γ_+ is a convergent stable path.*

(ii) *If we assume that both $y(s) - x(s)$ and $\dfrac{y(s)}{x(s)}$ are monotonically increasing functions for $s \in [0, 1)$, then Γ_- is a convergent stable path.*

Proof. (i) By the monotonicity of $y - x$ and $\dfrac{y}{x}$ for $0 \le s < 1$ and $0 < \Delta s < 1 - s$, we have $y(s + \Delta s) - y(s) \le x(s + \Delta s) - x(s)$, and $\dfrac{y(s + \Delta s)}{y(s)} \ge \dfrac{x(s + \Delta s)}{x(s)}$. Choosing

$(\alpha, \mu, \beta, \nu) = (x(s), y(s), x(s+\Delta s), y(s+\Delta s))$, we have that $\nu - \mu \leq \beta - \alpha$ and $1 \leq \dfrac{\nu}{\mu} \leq \dfrac{\beta}{\alpha}$. Let γ_1 be as in Theorem 3.5.6. Fix $0 \leq s < 1$ and choose $0 < \delta \ll 1$ such that as long as $0 < \Delta s < \delta$, $(\beta - \alpha)^2 + (\nu - \mu)^2 < \gamma_1^2$. We can now apply Theorem 3.5.6 by setting $\tau_1 = 1$ and $\rho_1 = \dfrac{\mu}{\alpha}$, which says that $(0, \theta_{\beta,\nu})$ is globally asymptotically stable. The proof of (ii) is similar. □

Referring to Figure 3.3, Theorem 3.5.7 says that a path will be convergent stable as long as it stays within the blue cone formed by the lines $\dfrac{\nu}{\beta} = \dfrac{\mu}{\alpha}$ and $\nu - \mu = \beta - \alpha$. Essentially, this means that the path stays in the blue region as it progresses towards the line $\beta = \nu$.

Numerical Results

As discussed in the previous section, sufficient criteria for a path to be convergent stable (for the linear resource case) is if it remains in the blue cone formed between the lines $\nu - \mu = \beta - \alpha$ and $\nu/\beta = \mu/\alpha$, refer to Figure 3.3. In order to test this claim and examine how evolution may proceed for more sophisticated resource functions, we set up another competition between a resident and an invader. This time, however, the invader's traits are given as a random perturbation which is 0.01 away from the resident's traits [21] (note that we can vary either a single trait (refer to Figure 3.1) or both traits). If the invader wins the competition or coexists, we make the invader the new resident. If the resident wins it remains. We repeat this process for finitely many steps. The resulting evolutionary path will be referred to as an 'acceptable path' [21]. Note that a convergent stable path is not the same as an acceptable path as the latter may move into a region of coexistence if the random perturbation is large enough [21]. Also note that the law of large numbers indicates that almost all acceptable paths will be "close to an average path, or trajectory" [36]. Such a trajectory is determined by the canonical equation (see [36]) which is

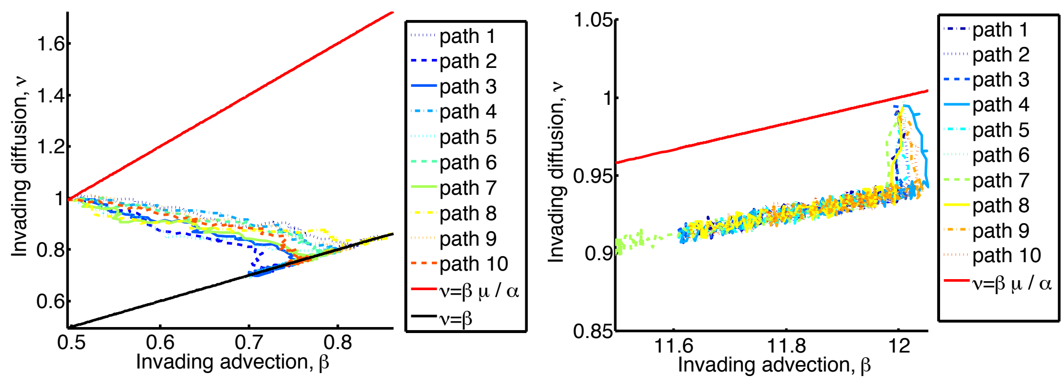

Figure 3.6: (Figure 10 in [21]) Acceptable paths for (a) linear resource with resident traits starting at $\alpha = 0.5$, $\mu = 1$, and (b) multiple peak resource with the resident traits starting at $\alpha = 12$, $\mu = 1$. Acceptable paths in the linear example allow deviations from the line $\nu = \beta\mu/\alpha$ to the ideal free strategy. Acceptable paths in the multi-peak example stay close to another line.

derived as a limiting process of small random trait perturbations. Thus our method of determining an acceptable path provides approximations to the "canonical path".

Referring to Figure 3.6 (a), we see that in the linear resource case the acceptable trait paths converge directly to the ideal free strategy. This supports our analytic result. We note that the acceptable paths in the nonlinear but monotone example ($m(x) = \sin(10x) + 10.1x + 10$) follow a similar trend as in Figure 3.6 (a), again supporting our analytic results. However, if we consider a multiple peak resource curve, $m(x) = \sin(3\pi x + \pi) + 2$, we see different behavior. As Figure 3.6 (b) suggests, the paths seem to be converging to a line different than the ideal free strategy. We see the diffusion decrease while the advection remains relatively unchanged until the path reaches this new line. However, we believe that the traits decrease along this line, eventually reaching the ideal free strategy at the origin, i.e. where both advection and diffusion are 0.

CHAPTER 4

COEXISTENCE RESULTS

4.1 Coexistence of Two Species

Because we want to understand the competition between species with differing dispersal strategies, we look for conditions that promote the coexistence of two competitors. We begin with some previous findings. Recently, Cantrell et al. [8] considered model (1.3.4) with $P = \frac{\alpha}{\mu}m$, $Q = \frac{\beta}{\nu}m$ and $\beta = 0$, in other words, comparing the competition between a conditional disperser and a species dispersing only via random diffusion. They proved the following to be true:

Theorem 4.1.1. (*Theorem* 1.5(*c*) *in* [8]) *Suppose that* m *is a non-constant function, and* $\int_\Omega m > 0$*. Also, suppose that the set of critical points of* m *has Lebesgue measure zero and that* m *has at least one isolated global maximum in* $\bar{\Omega}$*. Then for every* $\mu > 0$ *and* $\zeta > 0$*, there exists some positive constant* $\Lambda(\mu, \zeta, m, \Omega)$ *such that if* $\nu \geq \zeta$ *and* $\alpha \geq \Lambda$*, system* (1.3.4) *has at least one stable coexistence state.*

Building on their work, Chen et al [11] studied model (1.3.4) with $P = \frac{\alpha}{\mu}m$ and $Q = \frac{\beta}{\nu}m$, allowing both species to be conditional dispersers. Concerning the coexistence question, they asked that if species v has a fixed advection rate, say $\beta > 0$, then will species u and v coexist if the advection rate α, for u, is sufficiently large? We state their conclusion in the following theorem.

Theorem 4.1.2. (*Theorem* 1 *in* [11]) *Suppose that* $\int_\Omega m > 0$ *and that* $|\nabla m| > 0$ *for almost all* $x \in \Omega$. *Then there exists some positive constant* $\Lambda_1(\mu, \nu, m, \Omega)$, *independent of* β, *such that when* $\alpha \geq \Lambda_1$ *and* $0 \leq \beta \leq \dfrac{\nu}{\max_{\bar{\Omega}} m}$, *both semi-trivial steady states are unstable and system* (1.3.4) *has at least one stable positive steady state.*

Next, Cantrell et al. [9] considered model (1.3.4) with $P = Q = \ln m$ and were able to extend the above results. We present their assertion on coexistence in the context of system (3.0.1).

Theorem 4.1.3. (*Theorem* 2(*b*) *in* [9]) *Suppose that* $\mu = \nu$, $\Omega = (0, 1)$, *and* $m, m_x > 0$ *on* $\bar{\Omega}$. *If either* $\alpha < \mu < \beta$ *or* $\beta < \mu < \alpha$, *then both semi-trivial steady states are unstable and system* (3.0.1) *has at least one stable positive steady state.*

However, coexistence is possible with more general conditions on μ, ν, Ω, and m. Recently, we showed the following (we state the result and its proof in the context of system (3.0.1)):

Theorem 4.1.4. (*Theorem* 4 *in* [1]) *Suppose that* $m \in C^2(\bar{\Omega})$ *is positive and non-constant (here* Ω *is a bounded domain in* $\mathbb{R}^N$ *with smooth boundary). If* $(\alpha - \mu)(\beta - \nu) < 0$, *then both semi-trivial steady states are unstable and system* (3.0.1) *has at least one stable positive steady state.*

Proof. First we show that $(0, \theta_{\beta,\nu})$ is unstable. Let λ_1 denote the smallest eigenvalue of the following eigenvalue problem

$$\begin{cases} \nabla \cdot [\mu \nabla \varphi - \alpha \varphi \nabla \ln m] + \varphi(m - \theta_{\beta,\nu}) = -\lambda \varphi, & \text{in } \Omega, \\ [\mu \nabla \varphi - \alpha \varphi \nabla \ln m] \cdot n = 0, & \text{on } \partial\Omega, \end{cases} \tag{4.1.1}$$

and let φ_1 be the unique positive eigenfunction satisfying $\max_{\bar{\Omega}} \varphi_1 = 1$. Put $\psi = \varphi_1 m^{-\alpha/\mu}$. Then, ψ satisfies

$$\begin{cases} \mu \nabla \cdot [m^{\alpha/\mu} \nabla \psi] + \psi m^{\alpha/\mu}(m - \theta_{\beta,\nu}) = -\lambda_1 m^{\alpha/\mu} \psi, & \text{in } \Omega, \\ \nabla \psi \cdot n = 0, & \text{on } \partial\Omega. \end{cases} \tag{4.1.2}$$

Dividing equation (4.1.2) by ψ and integrating in Ω, we see that

$$-\lambda_1 \int_\Omega m^{\alpha/\mu} = \mu \int_\Omega \frac{m^{\alpha/\mu}|\nabla\psi|^2}{\psi^2} + \int_\Omega m^{\alpha/\mu}(m - \theta_{\beta,\nu}). \tag{4.1.3}$$

Note also that $\theta_{\beta,\nu}$ satisfies

$$\begin{cases} \nabla \cdot [\nu\nabla\theta_{\beta,\nu} - \beta\theta_{\beta,\nu}\nabla \ln m] + \theta_{\beta,\nu}(m - \theta_{\beta,\nu}) = 0, \quad \text{in } \Omega, \\ [\nu\nabla\theta_{\beta,\nu} - \beta\theta_{\beta,\nu}\nabla \ln m] \cdot n = 0, \quad \text{on } \partial\Omega. \end{cases} \tag{4.1.4}$$

Set $\theta = \theta_{\beta,\nu} m^{-\beta/\nu}$. We then have that θ satisfies

$$\begin{cases} \nu\nabla \cdot [m^{\beta/\nu}\nabla\theta] + \theta_{\beta,\nu}(m - \theta_{\beta,\nu}) = 0, \quad \text{in } \Omega, \\ \nabla\theta \cdot n = 0, \quad \text{on } \partial\Omega. \end{cases} \tag{4.1.5}$$

Multiplying equation (4.1.5) by θ^s and integrating in Ω, we have

$$\nu s \int_\Omega m^{\beta/\nu}\theta^{s-1}|\nabla\theta|^2 - \int_\Omega \frac{\theta_{\beta,\nu}^{s+1}}{m^{s\beta/\nu}}(m - \theta_{\beta,\nu}) = 0, \tag{4.1.6}$$

where $s > 0$ will be chosen later.

Combining equations (4.1.3) and (4.1.6) we obtain

$$\begin{aligned} -\lambda_1 \int_\Omega m^{\alpha/\mu} = \mu \int_\Omega \frac{m^{\alpha/\mu}|\nabla\psi|^2}{\psi^2} + \nu s \int_\Omega m^{\beta/\nu}\theta^{s-1}|\nabla\theta|^2 \\ + \int_\Omega \frac{m^{\alpha/\mu}m^{s\beta/\nu} - \theta_{\beta,\nu}^{s+1}}{m^{s\beta/\nu}}(m - \theta_{\beta,\nu}). \end{aligned} \tag{4.1.7}$$

Set $s = \dfrac{\nu(\alpha-\mu)}{\mu(\nu-\beta)}$. Then by assumption, $s > 0$. Thus,

$$-\lambda_1 \int_\Omega m^{\alpha/\mu} \geq \int_\Omega \frac{m^{s+1} - \theta_{\beta,\nu}^{s+1}}{m^{s\beta/\nu}}(m - \theta_{\beta,\nu}), \tag{4.1.8}$$

where equality holds if and only if ψ and θ are constants in Ω. Since $s > 0$, we have that

$$(m^{s+1} - \theta_{\beta,\nu}^{s+1})(m - \theta_{\beta,\nu}) \geq 0$$

in Ω and equality holds if and only if $m = \theta_{\beta,\nu}$. Thus, $\lambda_1 \leq 0$, and $\lambda_1 = 0$ if and only if $m - \theta_{\beta,\nu} = 0$. Suppose that $m = \theta_{\beta,\nu}$ in Ω. Then since θ satisfies equation (4.1.5) where the second term is now zero, by the maximum principle [45] we must have that $\theta \equiv C$ in Ω, where C is some constant. By the definition of θ, m must then be constant in Ω. But this is a contradiction. Hence, $\lambda_1 < 0$, which together with Lemma 2.0.4 implies that $(0, \theta_{\beta,\nu})$ is unstable.

By symmetry, we also have that if $(\alpha-\mu)(\beta-\nu) < 0$, $(\theta_{\alpha,\mu}, 0)$ is unstable. Because system (3.0.1) is a strongly monotone dynamical system, by Theorem 1.3.2, system (3.0.1) has at least a stable positive steady state. □

Essentially, Theorems 4.1.1, 4.1.2, 4.1.3, and 4.1.4 show that coexistence is possible for similar regions in trait space. For simplicity, we illustrate the region in Theorem 4.1.4 when $\nu = \mu$; see Figure 4.1.

Cantrell et al. [9] predicted that the only way system (3.0.1) could exhibit coexistence is if the dispersal strategies for both species satisfied $(\alpha - \mu)(\beta - \nu) < 0$ (the assumption from Theorem 4.1.4). In particular they conjectured that the first part of Theorem 3.4.5, namely if $\mu < \beta < \alpha$, then $(\theta_{\alpha,\mu}, 0)$ is unstable and $(0, \theta_{\beta,\nu})$ is locally stable, should hold for a larger class of functions than just those m with $m_x \neq 0$ on Ω. Biologically these predictions seem likely for two reasons. First, the strategy $\alpha = \mu$ is an ESS. Thus it seems likely that two species can coexist if their strategies are on "opposite sides" in trait space of the ideal free strategy, i.e. one species acts as a generalist, pursuing resources away from the local maxima of m and the other species acts as a specialist, focusing on resource maxima. Second, it seems that this is the only way two species can coexist as Cantrell et al. found that $\alpha = \mu$ is a CSS along certain paths [9]. That is, if two strategies are on the "same side" in trait space of the IFS (i.e. both competing as specialists or generalists) competitive exclusion suggests that only one species should survive.

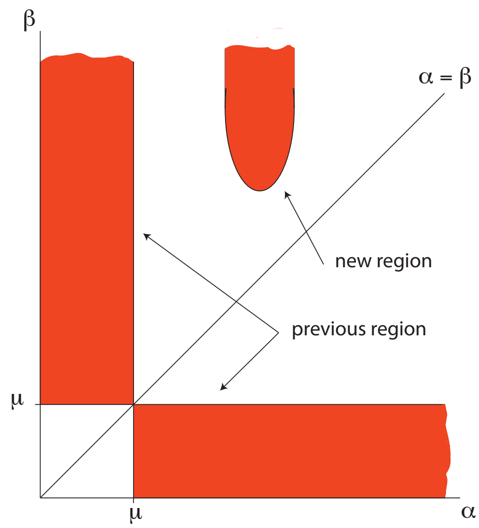

Figure 4.1: (Figure 7 in [21]) Coexistence is indicated by the red regions. The region along both axes illustrates Theorem 4.1.4. The elliptic region illustrates our new result given in Theorem 4.1.5.

However, we see that if we relax the monotonicity assumption on m, then the first part of Theorem 3.4.5 may not hold. That is, for appropriately chosen m, α, β, μ, and ν, where $\mu < \alpha < \beta$, (such trait values do not satisfy $(\alpha - \mu)(\beta - \nu) < 0$), both $(\theta_{\alpha,\mu}, 0)$ and $(0, \theta_{\beta,\nu})$ can be unstable. To construct such an m, we suppose m is positive in $\bar{\Omega}$ and satisfies the following assumption:

$(A1)$ There exists some $x_0 \in \bar{\Omega}$ such that x_0 is a local maximum of $m(x)$ and

$$\ln m(x_0) < \frac{\int_\Omega m^2 \ln m}{\int_\Omega m^2}.$$

Clearly, there exist functions $m \in C^2(\bar{\Omega})$ that satisfy $(A1)$ and if we perturb m slightly, we can say that all critical points of m are non-degenerate. Furthermore, notice that if m satisfies $(A1)$ it cannot be monotone as it must have at least two local maxima. That is, if we let $\bar{x}$ be any global maximum point of $m(x)$, we see that

$$\ln m(x_0) < \frac{\int_\Omega m^2 \ln m}{\int_\Omega m^2} \leq \ln m(\bar{x}).$$

Since $\ln(x)$ is an increasing function, we have that $m(x_0) < m(\bar{x})$.

Now, assuming that m satisfies $(A1)$, we want to find positive constants α, β, μ, and ν, such that $(\theta_{\alpha,\mu}, 0)$ is unstable. The underlying idea here is to first find $\alpha, \mu > 0$ such that species u under-matches the resource at some local maximum x_0. That is, for appropriate $\alpha, \mu > 0$, we want $m(x_0) - \theta_{\alpha,\mu}(x_0) > 0$. Next, we choose sufficiently large β so that species v will be inclined to concentrate close to the local maxima of m. Note that if we consider a small invader population v, the effective growth rate for v in a neighborhood of x_0 will be $m(x) - u(x) \approx m(x_0) - \theta_{\alpha,\mu}(x_0) > 0$. So, as long as enough of species v is concentrated near x_0, it will be able to invade. More rigorously, we have the following result:

Theorem 4.1.5. [21] *Suppose that m satisfies assumption $(A1)$ and all critical points of m are non-degenerate. Assume that in (1.3.4), $P = (\alpha/\mu)\ln m$ and $Q = (\beta/\nu)\ln m$. Then there exists $\mu_0 > 0$ such that if $\mu > \mu_0$, we can find some $\delta > 0$ small such that if $1 < \dfrac{\alpha}{\mu} < 1 + \delta$, and given any $\nu > 0$, both $(\theta_{\alpha,\mu}, 0)$ and $(0, \theta_{\beta,\nu})$ are unstable for large enough $\beta > 0$. Moreover, (1.3.4) has at least one stable positive steady state.*

4.1.1 Proof of Theorem 4.1.5

Next we seek to prove Theorem 4.1.5. Before doing so, we establish some useful lemmas.

Lemma 4.1.6. [21] *Given $\mu > 0$ and set $\alpha = (1+\delta)\mu$. Then, as $\delta \to 0+$,*

$$\frac{\theta_{\alpha,\mu} - m}{\delta} \to m(w^* + lnm)$$

uniformly in $\bar{\Omega}$, where w^* is the unique solution of

$$\mu\nabla \cdot [m\nabla w^*] - m^2 w^* = m^2 lnm, \quad \nabla w^* \cdot n|_{\partial\Omega} = 0. \tag{4.1.9}$$

Proof. Given any $\delta > 0$, let w denote the unique solution of

$$\mu\nabla \cdot [m\nabla w] - m^2 w = m^2 lnm - \sqrt{\delta}, \quad \nabla w \cdot n|_{\partial\Omega} = \sqrt{\delta}.$$

By elliptic regularity we see that $w \to w^*$ in $C^2(\bar{\Omega})$ as $\delta \to 0$. We claim that for $\delta > 0$ sufficiently small, $\bar{u} := m + \delta m(w + lnm)$ is a supersolution for (3.2.1). To check this, we first see that

$$\nabla\bar{u} - (1+\delta)\bar{u}\nabla(lnm) = \delta m\nabla w - \delta^2(w + lnm)\nabla m.$$

Hence, since w is uniformly bounded,

$$[\nabla\bar{u} - (1+\delta)\bar{u}\nabla(lnm)] \cdot n|_{\partial\Omega} = m\delta^{3/2} + O(\delta^2) > 0$$

for sufficiently small δ. Similarly,

$$\begin{aligned} &\mu\nabla \cdot [\nabla\bar{u} - (1+\delta)\bar{u}\nabla(lnm)] + \bar{u}[m - \bar{u}] \\ &= \mu\delta\nabla \cdot (m\nabla w) - \delta m^2(w + lnm) + O(\delta^2) = -\delta^{3/2} + O(\delta^2) \leq 0 \end{aligned}$$

for sufficiently small $\delta > 0$. Hence, $\bar{u} := m + \delta m(w + lnm)$ is a supersolution of (3.2.1).

Given any $\delta > 0$, let z denote the unique solution of

$$\mu\nabla \cdot [m\nabla z] - m^2 z = m^2 lnm + \sqrt{\delta}, \quad \nabla z \cdot n|_{\partial\Omega} = -\sqrt{\delta}.$$

Set $\underline{u} := m + \delta m(z + lnm)$. Similarly, we can show that $z \to w^*$ uniformly in $\bar{\Omega}$ as $\delta \to 0$ and $\underline{u}$ is a subsolution of (3.2.1). By the supersolution and subsolution method, $\underline{u} \leq \theta_{\alpha,\mu} \leq \bar{u}$ for sufficiently small $\delta > 0$ [44]. In particular,

$$m(z + lnm) \leq \frac{\theta_{\alpha,\mu} - m}{\delta} \leq m(w + lnm)$$

in $\bar{\Omega}$. Since both w and z converge to w^* uniformly as $\delta \to 0$, we see that $(\theta_{\alpha,\mu} - m)/\delta \to m(w^* + lnm)$ uniformly as $\delta \to 0$. □

Lemma 4.1.7. [21] *Suppose that* $m > 0$ *on* Ω *and satisfies assumption* (A1) *of Theorem* 4.1.5. *Then there exists* μ_0 *such that for each* $\mu > \mu_0$*, there exists some* $\delta > 0$ *small such that if* $1 < \alpha/\mu < 1 + \delta$*, then* $\theta_{\alpha,\mu}(x_0) - m(x_0) < 0$.

Proof. Recall that w^* is the unique solution of (4.1.9). By the maximum principle [45], w^* is uniformly bounded. By elliptic regularity and the Sobolev embedding theorem [23] we see that as $\mu \to \infty$, $w^* \to \bar{w} \equiv$ constant in $C^2(\bar{\Omega})$. Integrating the equation of w^*, we have

$$\int_\Omega m^2(w^* + \ln m) = 0.$$

Hence, we see that

$$\bar{w} \equiv -\frac{\int_\Omega m^2 \ln m}{\int_\Omega m^2}.$$

Therefore, using this fact and our assumption on m, there exists some $\mu_0 > 0$ such that if $\mu > \mu_0$, $w^*(x_0) + \ln m(x_0) < 0$. By Lemma 4.1.6, there exists some $\delta > 0$ such that if $1 < \alpha/\mu < 1+\delta$, $\theta_{\alpha,\mu}(x_0) - m(x_0) = \delta[m(x_0)(w^*(x_0) + \ln m(x_0)) + o(1)] < 0$. □

Lemma 4.1.8. [21] *Suppose that* $m > 0$ *on* Ω *satisfies assumption* (A1) *and all the critical points of* m *are non-degenerate. Then there exists* μ_0 *such that for each* $\mu > \mu_0$*, there exists some* $\delta > 0$ *small such that* $1 < \alpha/\mu < 1 + \delta$*, the semi-trivial steady state* $(\theta_{\alpha,\mu}, 0)$ *is unstable for sufficiently large* $\beta > 0$.

Proof. By Lemma 3.1.1, we need only show the principal eigenvalue, denoted by λ_0, of the eigenvalue problem

$$\begin{cases} \nabla \cdot [\nu \nabla \varphi - \beta \varphi \nabla \ln m] + \varphi(m - \theta_{\alpha,\mu}) = -\lambda \varphi & x \in \Omega \\ [\nu \nabla \varphi - \beta \varphi \nabla \ln m] \cdot n = 0 & x \in \partial\Omega, \end{cases} \tag{4.1.10}$$

is less than 0. Set $\psi = e^{-\beta/\nu \ln m} \varphi$. Then ψ satisfies

$$\begin{cases} \nu \nabla \cdot [e^{\beta/\nu \ln m} \nabla \psi] + e^{\beta/\nu \ln m} \psi (m - \theta_{\alpha,\mu}) = -\lambda e^{\beta/\nu \ln m} \psi & \text{in} \quad \Omega, \\ \nabla \psi \cdot n|_{\partial\Omega} = 0 \end{cases} \tag{4.1.11}$$

Simplifying the expression in (4.1.11), we see that ψ satisfies

$$-\nu\Delta\psi - \beta\nabla(\ln m)\cdot\nabla\psi + (\theta_{\alpha,\mu} - m)\psi = \lambda\psi \quad \text{in } \Omega, \;\; \nabla\psi\cdot n|_{\partial\Omega} = 0. \quad (4.1.12)$$

By Theorem 1.1 of [10] we have that

$$\lim_{\beta\to\infty} \lambda_0 = \min_{\mathcal{M}}(\theta_{\alpha,\mu} - m)$$

where $\mathcal{M}$ denotes the set of local maxima of m. Now,

$$\min_{\mathcal{M}}(\theta_{\alpha,\mu} - m) \le \theta_{\alpha,\mu}(x_0) - m(x_0).$$

Hence by Lemma 4.1.7 we see that for appropriate μ and α, $\theta_{\alpha,\mu}(x_0) - m(x_0) < 0$. Thus for large enough $\beta > 0$, we see that $\lambda_0 < 0$. □

Lemma 4.1.9. *Suppose that the set of critical points of $m(x)$ has Lebesgue measure zero. Recall that $\theta_{\beta,\nu}$ satisfies*

$$\begin{cases} \nabla\cdot[\nu\nabla\theta_{\beta,\nu} - \beta\theta_{\beta,\nu}\nabla\ln m] + \theta_{\beta,\nu}(m - \theta_{\beta,\nu}) = 0 \quad in \quad \Omega, \\ [\nu\nabla\theta_{\beta,\nu} - \beta\theta_{\beta,\nu}\nabla\ln m]\cdot n = 0 \quad on \quad \partial\Omega. \end{cases} \quad (4.1.13)$$

Then $\theta_{\beta,\nu} \to 0$ in $L^2(\Omega)$ as $\beta\to\infty$.

Proof. See the proof of Theorem 3.5 [8]. □

Lemma 4.1.10. [21] *Assume that the set of critical points of $m(x)$ has measure zero. Then for any $\mu > 0$, $\nu > 0$, and $\alpha > 0$, if β is sufficiently large, $(0, \theta_{\beta,\nu})$ is unstable.*

Proof. Once again, by Lemma 3.1.4 it is enough to show that the principal eigenvalue λ_0 of the eigenvalue problem

$$\begin{cases} \nabla\cdot[\mu\nabla\varphi - \alpha\varphi\nabla\ln m] + \varphi(m - \theta_{\beta,\nu}) = -\lambda\varphi \quad x\in\Omega \\ [\mu\nabla\varphi - \alpha\varphi\nabla\ln m]\cdot n = 0 \quad x\in\partial\Omega, \end{cases} \quad (4.1.14)$$

is less than 0. Let φ_0 denote the positive eigenfunction associated with λ_0. Set $\psi = e^{-\alpha/\mu \ln m}\varphi_0$. Then ψ satisfies

$$\begin{cases} \mu\nabla\cdot[e^{\alpha/\mu\ln m}\nabla\psi] + e^{\alpha/\mu\ln m}\psi(m-\theta_{\beta,\nu}) = -\lambda_0 e^{\alpha/\mu\ln m}\psi & \text{in} \quad \Omega, \\ \nabla\psi\cdot n|_{\partial\Omega} = 0 \end{cases} \tag{4.1.15}$$

Note that if we divide the expression ψ in Ω by ψ and then integrate in Ω, we obtain the following

$$\begin{aligned} -\lambda_0\int_\Omega e^{\alpha/\mu\ln m} &= \mu\int_\Omega \frac{e^{\alpha/\mu\ln m}|\nabla\psi|^2}{\psi^2} + \int_\Omega e^{\alpha/\mu\ln m}(m-\theta_{\beta,\nu}) \\ &\geq \int_\Omega m e^{\alpha/\mu\ln m} - ||e^{\alpha/\mu\ln m}||_{L^\infty}\int_\Omega \theta_{\beta,\nu} > 0, \end{aligned}$$

where the last inequality follows from Lemma 4.1.9 for large enough β. □

Putting together the results of the lemmas we can now prove Theorem 4.1.5

Proof. Lemmas 4.1.8 and 4.1.10 establish that both semi-trivial steady states of (1.3.4) are unstable. Thus by Theorem 1.3.2, there exists at least one stable coexistence state. □

Remark 4.1.11. *Note that we can assume that $\mu = \nu$ in Theorem* 4.1.5*. For large enough fixed random dispersal rate $\mu = \nu$, we suspect that there exists some $\alpha^* > 0$ such that if $\beta < \alpha \leq \alpha^*$ or $\alpha^* \leq \alpha < \beta$, then $(\theta_{\alpha,\mu}, 0)$ is stable. This would imply that for certain nonmonotone $m(x)$, there might exist some dispersal strategies which are not ideal free but are locally evolutionarily stable and/or convergent stable.*

Remark 4.1.12. *Notice that in Theorem* 4.1.5*, for fixed $\mu > 0$, we require that α be sufficiently close to μ. Thus, for this result to hold, we see that α cannot be too large, rather $\mu < \alpha < \alpha_*$, for some α_* which at least depends on m, Ω, and μ. However, if α is in a larger range, coexistence is not feasible. Bezuglyy and Lou* [5]*, considering system* (1.3.4) *with $P = \alpha m$ and $Q = \beta m$, showed the impossibility of two species* *coexisting for such α. More precisely, they demonstrated that for fixed $\mu, \nu > 0$, there exists some α^*, such that for every $\alpha > \alpha^*$, there exists some $\Lambda^* = \Lambda^*(\alpha) > 0$ such that if $\beta \geq \Lambda^*$, the semi-trivial steady state corresponding to the equation for α will be stable, whereas the other semi-trivial steady state will be unstable* (*see Theorem* 9 *in* [5]). *The main point here is if species u has an advection rate $\alpha > \alpha^*$, it will overmatch the resource function m at all local maxima, preventing the situation on which Theorem* 4.1.5 *depends.*

Remark 4.1.13. *It is also noteworthy that if m has multiple maxima all of the same height, we will not be able to follow the procedure above to construct counterexamples to the first part of Theorem* 3.4.5. *To see this, we can apply similar reasoning as in Theorem 1.3 from* [8]. *Our conclusion is cleaner than in Theorem* 1.3 *as we consider the equation for u in* (1.3.4) *with $P = (\alpha/\mu)\ln m$ rather than $P = (\alpha/\mu)m$. Thus we find that if $\alpha > \mu$, then $\max_{\bar{\Omega}} \theta_{\alpha,\mu} \geq \max_{\bar{\Omega}} m$. That is, the single species equilibrium $\theta_{\alpha,\mu}$ will overmatch the resource m at each maximum of m.*

4.2 Numerics for Two Species Coexistence

First we consider the monotone case where $m(x) = \sin(10x) + 10.1x + 10$ [21]. Referring to Figure 4.2 (a), we see that the red coexistence region is the same region as predicted by Theorem 4.1.4. For the nonmonotone case, we let $m(x) = \sin(3\pi x + \pi) + 2$ [21]. As predicted by Theorem 4.1.5, we see a "new region" of coexistence (see Figure 4.2(b)) as compared with the monotone case in Figure 4.2 (a). We suspect that a necessary condition for nonmonotone m to produce such a region is that m has peaks of different heights. We found that the "new region" disappeared when we shifted the resource curve to $m(x) = \sin(3\pi x + \pi/2) + 2$ [21].

Note that the circular PIP centered at the resident traits of $\alpha = 0.5$ and $\mu = 1$

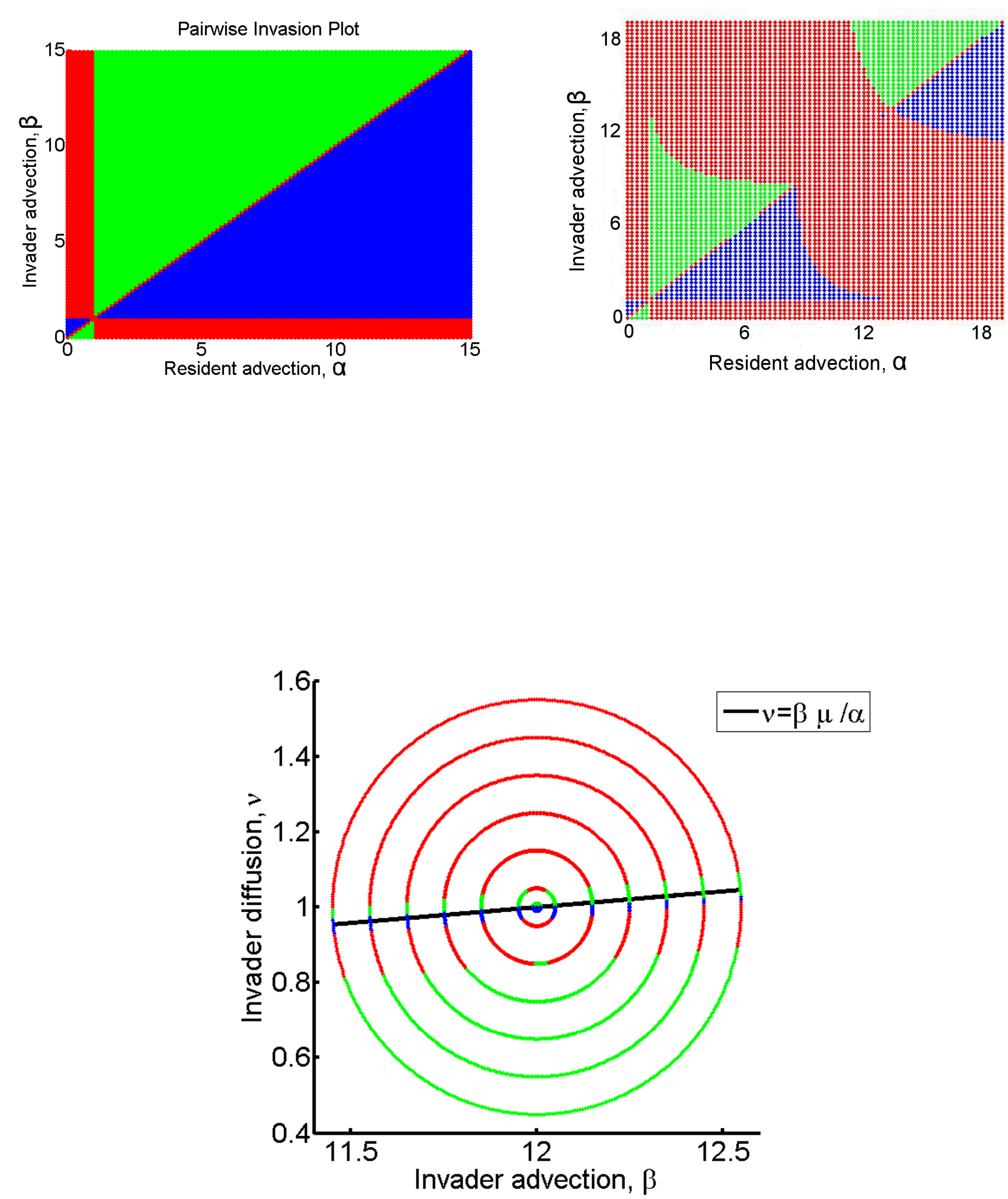

Figure 4.2: (Figure 7 in [21]) (a) Rectangular PIP for monotone m with $\mu = \nu = 1$ (b) Rectangular PIP for non-monotone m with $\mu = \nu = 1$ and (c) circular PIP for $\alpha = 12$, $\mu = 1$

for $m(x) = \sin(3\pi x + \pi) + 2$ is similar to the monotonic cases in Figure 3.4. However, if we consider a point within the "new region" of coexistence, say $\alpha = 12$ and $\mu = 1$, we find a markedly different picture (Figure 4.2(c)) (note that for monotone m with $\alpha = 12$ and $\mu = 1$, the circular PIP plot is similar to those in Figure 3.4) [21]. Figure 4.2(c) suggests that the size of the perturbation of the traits can produce several different outcomes. For instance, for sufficiently small perturbations (in both traits) either the resident or invader can win and for larger perturbations coexistence can occur. If we vary advection only, again we see that small perturbations lead to either competitor winning, but large enough perturbations lead to coexistence. If we vary diffusion only, then we see that large enough changes result in coexistence, while even larger perturbations result in the resident winning [21].

This new coexistence region is also interesting in conjunction with acceptable paths, especially when the red region is sufficiently close to the $\alpha = \beta$ line (Figure 4.2 (b)). For instance suppose we fix $\mu = 1$ and vary only advection. Beginning with a resident that has very large advection (say $\alpha > 18$), the PIP in Figure 4.2 (b) indicates that the path will evolve along decreasing advection until it reaches the coexistence region. Once inside the coexistence region, technically we need to analyze the situation via a three species model as we will have two residents and one invader. We suspect that there may be a variety of evolutionary outcomes, including evolutionary branching, once a path has entered this region. Notice that Figure 3.6 (b) treats the case of evolutionary paths beginning at $\alpha = 12$ and $\mu = 1$. Using the perturbation size of 0.01, the paths seem to converge to a line other than the ideal free line, however, we believe it will eventually reach the ideal free strategy at the origin. To conclude this section, we see that in addition to supporting our analytic results, the numerics show that perturbation size can markedly influence the direction and destiny of an evolutionary path when the resource function is multi-peaked.

4.3 Numerics for Three Species Coexistence

In the case that we have three species, it is natural to ask if coexistence can occur. We seek to apply the idea of a single species steady-state profile under-matching at a local maximum of m to provide a biologically interesting example of three species coexistence. We utilize Theorem 4.1.5 to help construct a coexistence scenario where species w, with possibly a large range of diffusion values and little to no advection, can coexist with species u and v. We use the resource function $m(x) = \sin(2.1\pi x - \pi/4) + 2$, which satisfies assumption $(A1)$.

Notice in Fig. 4.3(a), species u is at equilibrium, overmatching m at its global maximum and under-matching m at the local maximum on the boundary. Next, in Fig. 4.3(b), because of relatively large β, species v can overmatch both maxima of m. Notice in Fig. 4.3(c), that as species u and v compete, they approach a steady state where u overmatches the global maximum of m and v overmatches the local maximum of m.

We suggest that the profile in Fig. 4.3(c) provides biological motivation as to explaining how three species coexistence may occur. That is, as both species u and v have an established niche near the relative maxima of m, a relatively slowly diffusing competitor w, will be able to invade, focusing on resources away from these niches (i.e. away from the maxima of m). This is illustrated in Fig. 4.4, where we see all three species surviving together.

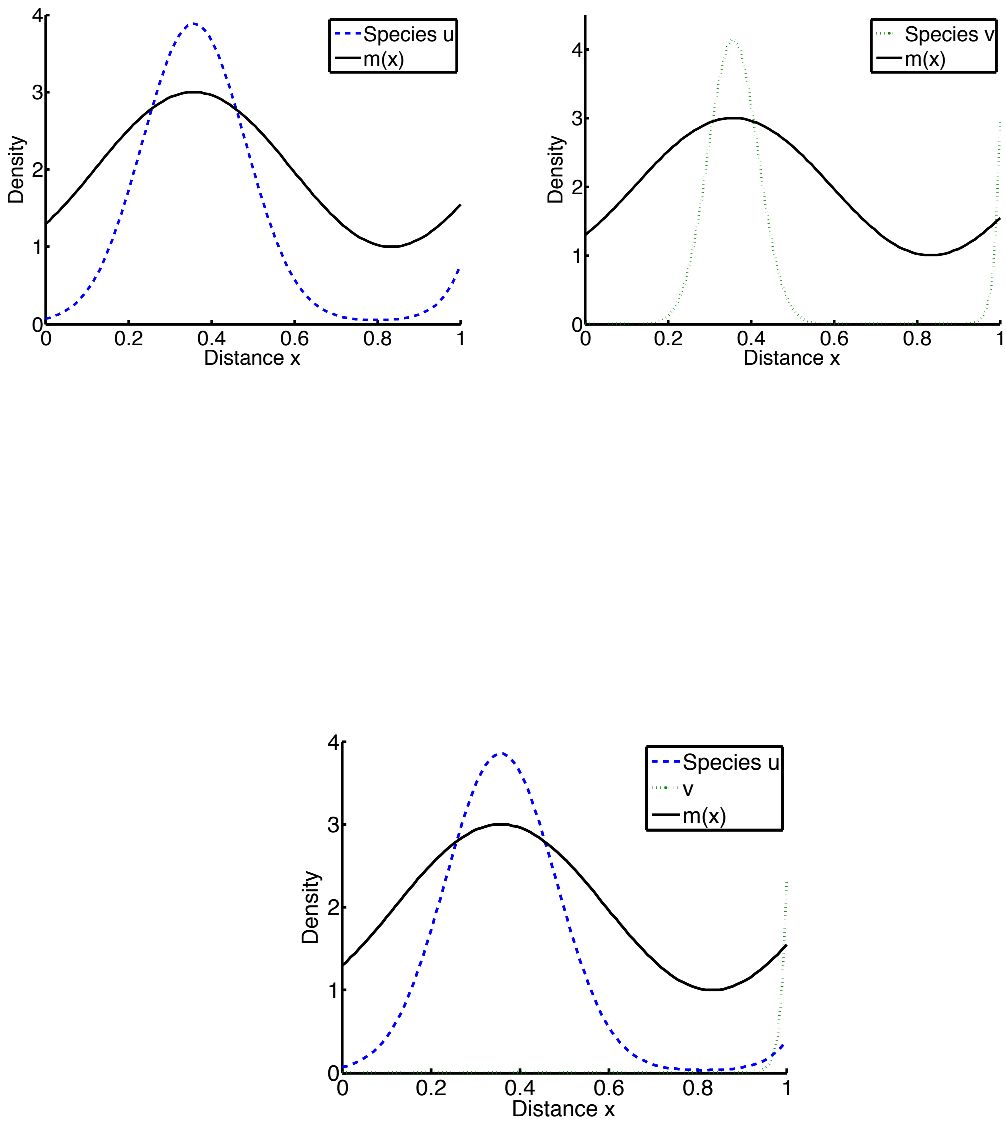

Figure 4.3: (Figure 8 in [21]) "New region" coexistence: (a) single species u (red), $\mu = .1$, $\alpha = .5$ (b) single species v (green), $\nu = .1$, $\beta = 2$ (c) coexistence of competing u and v. (Note: $m(x) = \sin(2.1\pi x - \pi/4) + 2$ is black on each graph.)

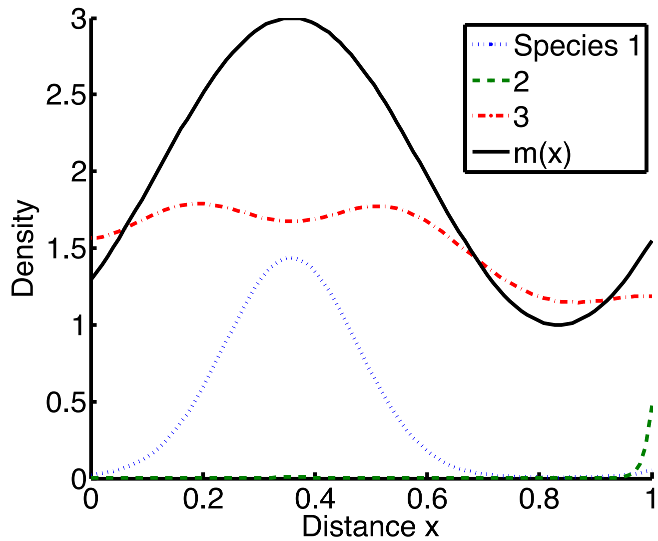

Figure 4.4: (Figure 9 in [21]) Three species coexistence. Species 1 with diffusion and advection rates (0.1,0.5) (blue), species 2 with rates (0.1,2) (green), and species 3 with (0.01,0) (red).

CHAPTER 5

PERMANENCE OF THREE COMPETING SPECIES

5.1 The Competition Model and Definition of Permanence

Consider the following parabolic system

$$\begin{cases} u_t = \mu\nabla\cdot[\nabla u - \alpha u\nabla\ln m] + u(m-u-v-w) \quad \text{in} \quad \Omega\times(0,\infty), \\ v_t = \nu\nabla\cdot[\nabla v - \beta v\nabla\ln m] + v(m-u-v-w) \quad \text{in} \quad \Omega\times(0,\infty), \\ w_t = \gamma\Delta w + w(m-u-v-w) \quad \text{in} \quad \Omega\times(0,\infty), \\ [\nabla u - \alpha u\nabla\ln m]\cdot n = [\nabla v - \beta v\nabla\ln m]\cdot n = \\ \nabla w\cdot n = 0 \quad \text{on} \quad \partial\Omega\times(0,\infty), \end{cases} \tag{5.1.1}$$

where Ω is a bounded domain in $\mathbb{R}^N$ with smooth boundary $\partial\Omega$, $u(x,t)$, $v(x,t)$, and $w(x,t)$ represent the densities of three competing species, μ, ν, and γ are their respective random diffusion coefficients, α and β are the advection rates of the respective species u and v. The function $m(x)$ represents the intrinsic growth rate of all three species. We assume that $m\in C^2(\bar{\Omega})$, and m is nonconstant and positive in $\bar{\Omega}$. We consider initial data $u(x,0)$, $v(x,0)$, and $w(x,0)$ which is nonnegative and not identically zero. Also, n is the outward unit normal vector on $\partial\Omega$, and the boundary conditions in (5.1.1) indicate that there is no flux for any of the three species across the boundary $\partial\Omega$.

5.1.1 Ecological Permanence

Initial uses of mathematical models to predict the long term coexistence of a number of species, involved an equilibrium approach [6]. For example, in the case of a Lotka-Volterra ordinary differential equation model for an n species community, one would try to find a componentwise constant solution and then observe the system's behavior under a local perturbation from the equilibrium solution [6]. The weakness of this technique is revealed in the event that the solution does not converge to an equilibrium or a periodic cycle. In such scenarios one cannot adequately provide criterion for long term survival of the species in question [6].

Cantrell and Cosner [6], however, highlight some key aspects of a criterion for predicting coexistence:

- "Robustness over a range of models."
- "Robustness with respect to qualitative features of a model when all species in question are in abundance."
- "Robustness with respect to quantitative changes in the parameters of a model when at least one species is at low density."
- "Independent of the initial state of the system so long as it is componentwise positive."

Together, these features describe what is known as **permanence**. In other words, "permanence is essentially a *qualitative* criterion for addressing the qualitative issue of whether a model for interacting biological species predicts the coexistence of all the species in question" [6]. However, we would like to express the notion of permanence in terms of a range of parameters of the model such that the resulting prediction of the model is biologically tractable. Practically, we say that "permanence in a model system for the densities of a collection of interacting species means the system possesses both an asymptotic 'ceiling' and a positive asymptotic 'floor' on the densities of all the species in question, the 'heights' of which are independent of the initial state of the system so long as each component is positive" [6]. Working from such a description, we utilize the following definition of ecological permanence as presented in [6].

Definition 1. *The system* (5.1.1) *is* **ecologically permanent**, *if there exist numbers* $K, k > 0$ *with* $k < K$ *such that if* $(u(x,t), v(x,t), w(x,t))$ *is a solution to* (5.1.1) *with nonnegative and not identically zero initial data* $(u(x,0), v(x,0), w(x,0))$, *then there is a* $T_0 > 0$ *which depends only on the initial condition such that* $k \leq u(x,t) \leq K$, $k \leq v(x,t) \leq K$, *and* $k \leq w(x,t) \leq K$ *for all* $x \in \Omega$ *and all* $t \geq T_0$.

Our goal is to find nonmontone resource functions m and a range of dispersal parameters such that system (5.1.1) displays ecological permanence. Our approach is related to that of section 4.1. We will assume that m satisfies $(A1)$ so that we can have one species concentrating at the global maximum of m and another concentrating near x_0 (at a local maximum of m). In this setting, we will show that in order to have three species coexisting, we will require that the local maximum of m at x_0 cannot be too small. Thus, we formulate a second condition on m which allows us to prove the permanence result.

5.2 Lower Bound for Species w

Let u^* denote the unique positive solution of

$$\begin{cases} \mu \nabla \cdot [\nabla u - \alpha u \nabla \ln m] + u(m - u) = 0 \quad \text{in} \quad \Omega, \\ [\nabla u - \alpha u \nabla \ln m] \cdot n = 0 \quad \text{on} \quad \partial\Omega. \end{cases} \tag{5.2.1}$$

The existence, uniqueness and positivity of u^* is well-known as we are assuming $m > 0$ and nonconstant on Ω. Clearly, when $\alpha = 1$, then $u^* = m$. The following result illustrates some properties of u^* when $\alpha \neq 1$.

Lemma 5.2.1. *Suppose that m is strictly positive in $\bar{\Omega}$ and nonconstant. Then for every $\alpha > 1$, $\int_\Omega u^* < \int_\Omega m$; for every $\alpha \in [0, 1)$, $\int_\Omega u^* > \int_\Omega m$.*

Proof. Rewrite the equation of u^* as

$$\begin{cases} \mu \nabla \cdot \left[m^\alpha \nabla \left(\frac{u^*}{m^\alpha} \right) \right] + u^*(m - u^*) = 0 \text{ in } \Omega, \\ \nabla \left(\frac{u^*}{m^\alpha} \right) \cdot n = 0 \text{ on } \partial\Omega. \end{cases} \tag{5.2.2}$$

Multiplying (5.2.2) by $\left(\frac{u^*}{m^\alpha} \right)^{1/(\alpha-1)}$ and integrating the result in Ω we have

$$\begin{aligned} &\int_\Omega \left(\frac{u^*}{m} \right)^{\alpha/(\alpha-1)} (m - u^*) \\ &= \frac{\mu}{\alpha - 1} \int_\Omega m^\alpha \left(\frac{u^*}{m^\alpha} \right)^{(2-\alpha)/(\alpha-1)} \left| \nabla \left(\frac{u^*}{m^\alpha} \right) \right|^2 . \end{aligned} \tag{5.2.3}$$

Hence,

$$\begin{aligned} &\int_\Omega (m - u^*) \\ &= \left[\int_\Omega (m - u^*) - \int_\Omega \left(\frac{u^*}{m} \right)^{\alpha/(\alpha-1)} (m - u^*) \right] + \int_\Omega \left(\frac{u^*}{m} \right)^{\alpha/(\alpha-1)} (m - u^*) \\ &= \int_\Omega (m - u^*) \frac{m^{\alpha/(\alpha-1)} - (u^*)^{\alpha/(\alpha-1)}}{m^{\alpha/(\alpha-1)}} \\ &+ \frac{\mu}{\alpha - 1} \int_\Omega m^\alpha \left(\frac{u^*}{m^\alpha} \right)^{(2-\alpha)/(\alpha-1)} \left| \nabla \left(\frac{u^*}{m^\alpha} \right) \right|^2 . \end{aligned} \tag{5.2.4}$$

We first claim that if $\alpha \neq 1$,

$$\int_\Omega m^\alpha \left(\frac{u^*}{m^\alpha} \right)^{(2-\alpha)/(\alpha-1)} \left| \nabla \left(\frac{u^*}{m^\alpha} \right) \right|^2 > 0. \tag{5.2.5}$$

It suffices to show that u^*/m^α is non-constant. We argue by contradiction. Suppose that u^*/m^α is constant, then from (5.2.2), we see that $u^* = m$. This implies that

m/m^α is a constant. Since $\alpha \neq 1$ we must have that m is constant, which is a contradiction.

To complete the proof, we consider two cases:

Case 1. $\alpha > 1$. For this case, $(m - u^*)[m^{\alpha/(\alpha-1)} - (u^*)^{\alpha/(\alpha-1)}] \geq 0$ in Ω. This together with (5.2.4) and (5.2.5) imply that if $\alpha > 1$, then $\int_\Omega (m - u^*) > 0$.

Case 2. $\alpha < 1$. For this case, $(m - u^*)[m^{\alpha/(\alpha-1)} - (u^*)^{\alpha/(\alpha-1)}] \leq 0$ in Ω. This together with (5.2.4) and (5.2.5) imply that $\int_\Omega (m - u^*) < 0$, as long as $\alpha < 1$. □

Remark 5.2.2. *For $\alpha = 0$, it was first observed in* [38] *that* $\int_\Omega u^* > \int_\Omega m$. *Lemma* 5.2.1 *is a generalization of this result.*

Lemma 5.2.3. *Let $\tilde{u}$ be a positive solution to*

$$\begin{cases} u_t = \mu\nabla \cdot [\nabla u - \alpha u \nabla \ln m] + u(m - u) & \text{in} \quad \Omega \times (0, \infty), \\ [\nabla u - \alpha u \nabla \ln m] \cdot n = 0 \quad \text{on} \quad \partial\Omega \times (0, \infty). \end{cases} \tag{5.2.6}$$

Then $\tilde{u}(x, t) \to u^*(x)$ uniformly as $t \to \infty$, where u^* satisfies (5.2.1).

Proof. See [6] for details. □

Similarly, we have the following result.

Lemma 5.2.4. *Let $\tilde{v}$ be a positive solution to*

$$\begin{cases} v_t = \nu\nabla \cdot [\nabla v - \beta v \nabla \ln m] + v(m - v) & \text{in} \quad \Omega \times (0, \infty), \\ [\nabla v - \beta v \nabla \ln m] \cdot n = 0 \quad \text{on} \quad \partial\Omega \times (0, \infty). \end{cases} \tag{5.2.7}$$

Then $\tilde{v}(x, t) \to v^*(x)$ uniformly as $t \to \infty$, where v^* is the unique positive steady state of (5.2.7)

Corollary 5.2.5. *Let (u, v, w) be any positive solution of* (5.1.1). *Then* $\limsup_{t\to\infty} u(x, t) \leq u^*$ *and* $\limsup_{t\to\infty} v(x, t) \leq v^*$. *In particular, for each β, there is a $T(\beta) > 0$ such that if $t \geq T(\beta)$, $u(x, t) \leq u^* + 1/\beta$ and $v(x, t) \leq v^* + 1/\beta$ on Ω.*

Theorem 5.2.6. *Let w be the last component of any positive solution (u, v, w) of* (5.1.1). *Suppose that the critical points of m have Lebesgue measure zero. Then for any μ, ν, $\gamma > 0$ (where these are the diffusion rates from* (5.1.1)) *and for any $\alpha > 1$, there is a β_1 such that for all $\beta > \beta_1$ there exists a $\delta_1 > 0$ such that for all $x \in \Omega$,* $\liminf_{t\to\infty} w(x,t) \geq \delta_1 > 0$.

Proof. From (5.1.1), we see that w is a super-solution to the following equation:

$$\begin{cases} \tilde{w}_t = \gamma \Delta \tilde{w} + \tilde{w}(m - u^* - v^* - 2/\beta - \tilde{w}) \quad \text{in} \quad \Omega \times (T(\beta), \infty), \\ \nabla \tilde{w} \cdot n = 0 \quad \text{on} \quad \partial\Omega \times (T(\beta), \infty), \\ \tilde{w}(x, T(\beta)) = w(x, T(\beta)) \quad \text{in} \quad \bar{\Omega}, \end{cases} \tag{5.2.8}$$

where we will choose $\beta > 0$ to be sufficiently large later. Now by Lemma 5.2.1, if we let $\alpha > 1$ then $\int_\Omega u^* < \int_\Omega m$. We also have from Theorem 3.5 in [8] that as $\beta \to \infty$, $\int_\Omega v^* \to 0$. Hence we can choose $\beta > \beta_1$ such that

$$\int_\Omega (m - u^* - v^* - 2/\beta) > 0.$$

We claim $\tilde{w} \to w^*$ uniformly as $t \to \infty$ where w^* is the unique positive solution of the equation

$$\begin{cases} \gamma \Delta w^* + w^*(m - u^* - v^* - 2/\beta - w^*) = 0 \quad \text{in} \quad \Omega, \\ \nabla w^* \cdot n = 0 \quad \text{on} \quad \partial\Omega. \end{cases} \tag{5.2.9}$$

Note that w^* exists for all γ since $\int_\Omega (m - u^* - v^* - 2/\beta) > 0$. Also, because $\int_\Omega (m - u^* - v^* - 2/\beta) > 0$, the zero solution to (5.2.9) is unstable and $\tilde{w} \to w^*$ uniformly as $t \to \infty$ [6]. By Corollary 5.2.5, w is super-solution of (5.2.8), that is for all $t \geq T(\beta)$, $w(x,t) \geq \tilde{w}(x,t)$ on Ω. Finally, because $\tilde{w} \to w^*$ uniformly, we can choose $\delta_1 = \min_{\bar{\Omega}} w^*$ such that for all $x \in \Omega$, $\liminf_{t\to\infty} w(x,t) \geq \delta_1 > 0$. □

5.3 Lower Bound for Species u

Theorem 5.3.1. *Suppose m is such that $\{x \in \bar{\Omega} : |\nabla m(x)| = 0\}$ has Lebesgue measure zero. Let u be the first component of any positive solution (u, v, w) of* (5.1.1)*. Then for any μ, ν, and $\gamma > 0$ and for any $\alpha > 1$, there exists a β_2 such that for all $\beta > \beta_2$, there is a $\delta_2 > 0$ such that for all $x \in \Omega$, $\liminf_{t\to\infty} u(x,t) \geq \delta_2 > 0$.*

To show this, we consider the following equations of u and w (coming from (5.1.1)).

$$\begin{cases} u_t = \mu\nabla \cdot [\nabla u - \alpha u \nabla \ln m] + u(m - u - v - w) \quad \text{in} \quad \Omega \times (0,\infty), \\ w_t = \gamma \Delta w + w(m - u - v - w) \quad \text{in} \quad \Omega \times (0,\infty), \\ [\nabla u - \alpha u \nabla \ln m] \cdot n = \nabla w \cdot n = 0 \quad \text{on} \quad \partial\Omega \times (0,\infty). \end{cases} \tag{5.3.1}$$

Note that by Corollary 5.2.5 that $v(x,t) \leq v^*(x) + 1/\beta$ for $t \geq T(\beta)$ and hence we see that

$$\begin{cases} u_t \geq \mu\nabla \cdot [\nabla u - \alpha u \nabla \ln m] \\ \;+ u(m - u - (v^* + 1/\beta) - w) \quad \text{in} \quad \Omega \times (T(\beta),\infty), \\ w_t \leq \gamma \Delta w + w(m - u - w) \quad \text{in} \quad \Omega \times (T(\beta),\infty), \\ [\nabla u - \alpha u \nabla \ln m] \cdot n = \nabla w \cdot n = 0 \quad \text{on} \quad \partial\Omega \times (T(\beta),\infty). \end{cases} \tag{5.3.2}$$

Thus we consider the following system:

$$\begin{cases} \bar{u}_t = \mu\nabla \cdot [\nabla \bar{u} - \alpha \bar{u} \nabla \ln m] \\ \;+ \bar{u}(m - \bar{u} - (v^* + 1/\beta) - \bar{w}) \quad \text{in} \quad \Omega \times (T(\beta),\infty), \\ \bar{w}_t = \gamma \Delta \bar{w} + \bar{w}(m - \bar{u} - \bar{w}) \quad \text{in} \quad \Omega \times (T(\beta),\infty), \\ [\nabla \bar{u} - \alpha \bar{u} \nabla \ln m] \cdot n = \nabla \bar{w} \cdot n = 0 \quad \text{on} \quad \partial\Omega \times (T(\beta),\infty), \\ \bar{u}(x,T(\beta)) = u(x,T(\beta)), \;\; \bar{w}(x,T(\beta)) = w(x,T(\beta)) \;\text{ in }\; \bar{\Omega}. \end{cases} \tag{5.3.3}$$

Proof. We first note that (5.3.3) is a strongly monotone system (by Theorem 1.20 in [6] and the strong maximum principle). We claim that the semi-trivial steady state

$(0, \bar{w}^*)$ of (5.3.3) is unstable. Upon showing this, by monotone dynamical system theory [29, 48], we will have that any solution with nonnegative initial data will either be attracted to $(\bar{u}^*, 0)$ or an order interval bounded above and below by positive equilibria of (5.3.3). In any case, there exists a $\delta_2 > 0$ such that for all $x \in \Omega$, and for $t > T_2$, where T_2 depends on the initial conditions and β, $\bar{u}(x,t) \geq \delta_2 > 0$. Since $u(x,t) \geq \bar{u}(x,t)$ on Ω and for $t > T_2$, we see that $\liminf_{t\to\infty} u(x,t) \geq \delta_2 > 0$.

To show that $(0, \bar{w}^*)$ is unstable, we consider the following eigenvalue problem:

$$\begin{cases} \mu\nabla \cdot [\nabla\varphi - \alpha\varphi\nabla \ln m] + \varphi(m - (v^* + 1/\beta) - \bar{w}^*) = -\lambda\varphi \quad \text{in} \quad \Omega, \\ [\nabla\varphi - \alpha\varphi\nabla \ln m] \cdot n = 0 \quad \text{on} \quad \partial\Omega. \end{cases} \tag{5.3.4}$$

Let λ_1 denote the smallest eigenvalue of (5.3.4) and let φ_1 be a positive eigenfunction associated to λ_1. Put $\psi = \dfrac{\varphi_1}{m^\alpha}$. Then ψ satisfies

$$\begin{cases} \mu\nabla \cdot [m^\alpha\nabla\psi] + \psi m^\alpha(m - (v^* + 1/\beta) - \bar{w}^*) = -\lambda_1\psi m^\alpha \quad \text{in} \quad \Omega, \\ \nabla\psi \cdot n = 0 \quad \text{on} \quad \partial\Omega. \end{cases} \tag{5.3.5}$$

Dividing (5.3.5) by ψ and integrating the resulting equation over Ω, we obtain

$$\mu\int_\Omega m^\alpha \frac{|\nabla\psi|^2}{\psi^2} + \int_\Omega m^\alpha(m - \bar{w}^*) - \int_\Omega m^\alpha(v^* + 1/\beta) = -\lambda_1\int_\Omega m^\alpha. \tag{5.3.6}$$

Also note that $\bar{w}^*$ satisfies

$$\begin{cases} \gamma\Delta\bar{w}^* + \bar{w}^*(m - \bar{w}^*) = 0 \quad \text{in} \quad \Omega, \\ \nabla\bar{w}^* \cdot n = 0 \quad \text{on} \quad \partial\Omega. \end{cases} \tag{5.3.7}$$

If we multiply (5.3.7) by $(\bar{w}^*)^{\alpha-1}$ and integrate the resulting equation over Ω we have that

$$0 = \gamma(\alpha - 1)\int_\Omega (\bar{w}^*)^{\alpha-2}|\nabla\bar{w}^*|^2 - \int_\Omega (\bar{w}^*)^\alpha(m - \bar{w}^*). \tag{5.3.8}$$

Combining (5.3.6) and (5.3.8), we get

$$\gamma(\alpha-1)\int_\Omega (\bar{w}^*)^{\alpha-2}|\nabla \bar{w}^*|^2 + \mu\int_\Omega m^\alpha \frac{|\nabla\psi|^2}{\psi^2} \\ + \int_\Omega [m^\alpha - (\bar{w}^*)^\alpha](m-\bar{w}^*) - \int_\Omega m^\alpha(v^* + 1/\beta) = -\lambda_1 \int_\Omega m^\alpha. \tag{5.3.9}$$

Since $\gamma > 0$, $\alpha > 1$, and $\bar{w}^* > 0$ on Ω, we notice that

$$-\lambda_1 \int_\Omega m^\alpha \geq \int_\Omega [m^\alpha - (\bar{w}^*)^\alpha](m-\bar{w}^*) - \int_\Omega m^\alpha(v^* + 1/\beta), \tag{5.3.10}$$

where equality holds if and only if both $\bar{w}^*$ and ψ are constant functions. Now notice that $[m^\alpha - (\bar{w}^*)^\alpha](m-\bar{w}^*) \geq 0$ in Ω with equality if and only if $m = \bar{w}^*$. Hence $\int_\Omega [m^\alpha - (\bar{w}^*)^\alpha](m-\bar{w}^*) = 0$ if and only if $m \equiv \bar{w}^*$ in Ω. We claim that $\int_\Omega [m^\alpha - (\bar{w}^*)^\alpha](m-\bar{w}^*) > 0$. To see this, suppose that $m \equiv \bar{w}^*$ in Ω. Then m must satisfy equation (5.3.7) and by the maximum principle, $m \equiv$ constant in Ω. This is a contradiction and thus $\int_\Omega [m^\alpha - (\bar{w}^*)^\alpha](m-\bar{w}^*) > 0$. By Theorem 3.5 in [8] we know that as $\beta \to \infty$, $\int_\Omega v^* \to 0$. Hence for large enough β,

$$\begin{aligned} -\lambda_1 \int_\Omega m^\alpha &\geq \int_\Omega [m^\alpha - (\bar{w}^*)^\alpha](m-\bar{w}^*) - \int_\Omega m^\alpha(v^* + 1/\beta) \\ &\geq \int_\Omega [m^\alpha - (\bar{w}^*)^\alpha](m-\bar{w}^*) - ||m^\alpha||_{L^\infty}\left(\int_\Omega v^* + (1/\beta)|\Omega|\right) > 0. \end{aligned} \tag{5.3.11}$$

From (5.3.11) we have that $\lambda_1 < 0$, proving that $(0, \bar{w}^*)$ is unstable. □

5.4 Lower Bound for Species v

As we mentioned in section 5.1.1, we work with nonmonotone functions m that satisfy assumption $(A1)$, looking for parameter values that cause species u to concentrate at the global maximum of m, species v to concentrate at the local maximum of m at x_0, and species w to pursue resources away from these maxima. However, for v to be able to concentrate at x_0 and persist, we need at least that its growth rate near

x_0 be positive (note that we will need a further condition on m). That is, we need $m(x) - \tilde{u}(x) - \tilde{w}(x) > 0$ in a neighborhood of x_0 (here $(\tilde{u}, \tilde{w})$ is a positive solution to the three species model when $v \equiv 0$). So, we first seek to understand the structure of the solution set $(\tilde{u}, \tilde{w})$ as we vary the advection parameter α near $\alpha = 1$.

5.4.1 Structure of Two Species Positive Steady States

Consider the following two species model: (this is system (5.1.1) with $v = 0$ and $\alpha = 1 + \epsilon$)

$$\begin{cases} \mu\nabla \cdot [\nabla\tilde{u} - (1+\epsilon)\tilde{u}\nabla \ln m] + \tilde{u}(m - \tilde{u} - \tilde{w}) = 0 \quad \text{in} \quad \Omega, \\ \gamma\Delta\tilde{w} + \tilde{w}(m - \tilde{u} - \tilde{w}) = 0 \quad \text{in} \quad \Omega, \\ [\nabla\tilde{u} - (1+\epsilon)\tilde{u}\nabla \ln m] \cdot n = \nabla\tilde{w} \cdot n = 0 \quad \text{on} \quad \partial\Omega. \end{cases} \tag{5.4.1}$$

We note that for $\alpha > 1$, there exists at least one steady state $(\tilde{u}, \tilde{w})$ of system (5.4.1) where both $\tilde{u}$ and $\tilde{w}$ are positive in Ω (see Theorem 1.4 in [1]). We also know that when $\alpha = 1$ that $(m, 0)$ is a solution of (5.4.1). Essentially, we will show that for α slightly larger than 1, system (5.4.1) has a unique branch of positive steady states bifurcating from $(m, 0)$ at $\alpha = 1$.

Let $u = \dfrac{\tilde{u}}{m^{1+\epsilon}}$. Then $(u, \tilde{w})$ satisfies

$$\begin{cases} \mu\nabla \cdot [m^{1+\epsilon}\nabla u] + m^{1+\epsilon}u(m - m^{1+\epsilon}u - \tilde{w}) = 0 \quad \text{in} \quad \Omega, \\ \gamma\Delta\tilde{w} + \tilde{w}(m - m^{1+\epsilon}u - \tilde{w}) = 0 \quad \text{in} \quad \Omega, \\ \nabla u \cdot n = \nabla\tilde{w} \cdot n = 0 \quad \text{on} \quad \partial\Omega. \end{cases} \tag{5.4.2}$$

Note that (5.4.2) reduces to:

$$\begin{cases} \mu\Delta u + \mu\nabla \ln(m^{1+\epsilon})\nabla u + u(m - m^{1+\epsilon}u - \tilde{w}) = 0 \quad \text{in} \quad \Omega, \\ \gamma\Delta\tilde{w} + \tilde{w}(m - m^{1+\epsilon}u - \tilde{w}) = 0 \quad \text{in} \quad \Omega, \\ \nabla u \cdot n = \nabla\tilde{w} \cdot n = 0 \quad \text{on} \quad \partial\Omega. \end{cases} \tag{5.4.3}$$

We begin by defining a map $\hat{\mathbf{F}} : (-r,r) \times C_n^{2,\tau}(\bar{\Omega}) \times C_n^{2,\tau}(\bar{\Omega}) \to C^{\tau}(\bar{\Omega}) \times C^{\tau}(\bar{\Omega})$ for some $\tau \in (0,1)$ and for some $r > 0$, where $C_n^{2,\tau}(\bar{\Omega}) = \{f \in C^{2,\tau}(\bar{\Omega}) : \nabla f \cdot n|_{\partial\Omega} = 0\}$, by

$$\hat{\mathbf{F}}(\epsilon, u, \tilde{w}) = \begin{pmatrix} \mu\Delta u + \mu\nabla \ln(m^{1+\epsilon})\nabla u + u(m - m^{1+\epsilon}u - \tilde{w}) \\ \gamma\Delta\tilde{w} + \tilde{w}(m - m^{1+\epsilon}u - \tilde{w}) \end{pmatrix}$$

Now $\hat{\mathbf{F}}(\epsilon, u_\epsilon, 0) = 0$ where $(u_\epsilon, 0)$ satisfies (5.4.3). In particular, note that $u_0 = 1$, so $\hat{\mathbf{F}}(0,1,0) = 0$. Next define a map $\mathbf{F}$ with the same domain and target spaces as $\hat{\mathbf{F}}$ but with formula

$$\mathbf{F}(\epsilon, u, \tilde{w}) = \hat{\mathbf{F}}(\epsilon, u + u_\epsilon, \tilde{w}).$$

Then $\mathbf{F}(\epsilon, 0, 0) = 0$ for $\epsilon \in (-r, r)$ and we note that

$$\mathbf{F}(\epsilon, u, \tilde{w}) = \tag{5.4.4}$$
$$\begin{pmatrix} \mu\Delta(u + u_\epsilon) + \mu\nabla \ln(m^{1+\epsilon})\nabla(u + u_\epsilon) + (u + u_\epsilon)[m - m^{1+\epsilon}(u + u_\epsilon) - \tilde{w}] \\ \gamma\Delta\tilde{w} + \tilde{w}[m - m^{1+\epsilon}(u + u_\epsilon) - \tilde{w}] \end{pmatrix}$$

Because we want to understand the solution structure of $\mathbf{F}(\epsilon, u, \tilde{w}) = 0$ near $(0,0,0)$, we make use of the following result from bifurcation theory.

Theorem 5.4.1. (*Crandall−Rabinowitz*) [34] *Suppose that* $\mathbf{F}(\epsilon, 0) = 0$ *for all* $\epsilon \in \mathbb{R}$, *dim Ker*$(\mathbf{F}_y(\epsilon_0, 0))$ = *codim Range*$(\mathbf{F}_y(\epsilon_0, 0)) = 1$, $\mathbf{F} \in C^2(V \times U)$, *where* $0 \in U$ *is an open set of a Banach space and* $\epsilon_0 \in V$ *is an open set of* $\mathbb{R}$, *Ker*$(\mathbf{F}_y|_{(\epsilon_0,0)})$ = *span* $\{v_0\}$, *and* $\mathbf{F}_{y\epsilon}(\epsilon_0, 0)v_0 \notin$ *Range*$(\mathbf{F}_y(\epsilon_0, 0))$. *Then there is a non-trivial continuously differentiable curve through* $(\epsilon_0, 0)$, $\{(\epsilon(s), x(s)) : s \in (-\delta, \delta), (\epsilon(0), x(0)) = (\epsilon_0, 0)\}$, *such that* $\mathbf{F}(\epsilon(s), x(s)) = 0$ *for* $s \in (-\delta, \delta)$, *and all solutions of* $\mathbf{F}(\epsilon, x) = 0$ *in a neighborhood of* $(\epsilon_0, 0)$ *are on the trivial solution line or on the curve* $(\epsilon(s), x(s))$.

We establish several lemmas which show that $\mathbf{F}$ as defined in (5.4.4) satisfies the hypotheses of Theorem 5.4.1. Differentiating $\mathbf{F}$ with respect to $(u, \tilde{w})$ and evaluating the derivative at $(\epsilon, 0, 0)$ gives us

$$\mathcal{L}_\epsilon = D_{(u,\tilde{w})}\mathbf{F}|_{(\epsilon,0,0)} = \begin{pmatrix} \mu\Delta + \mu\nabla\ln(m^{1+\epsilon})\nabla + m - 2m^{1+\epsilon}u_\epsilon & -u_\epsilon \\ 0 & \gamma\Delta + m - m^{1+\epsilon}u_\epsilon \end{pmatrix}.$$

Recall $u_0 = 1$ and let $\mathcal{L}_\epsilon = \mathcal{L}$ when $\epsilon = 0$. Put $\mathbf{X} = C_n^{2,\tau}(\bar{\Omega}) \times C_n^{2,\tau}(\bar{\Omega})$. Then given a vector $(\varphi, \psi) \in \mathbf{X}$ we see that

$$\mathcal{L}\begin{pmatrix} \varphi \\ \psi \end{pmatrix} = \begin{pmatrix} \mu\Delta\varphi + \mu\nabla\ln m\nabla\varphi - m\varphi - \psi \\ \gamma\Delta\psi \end{pmatrix} \in C^\tau(\bar{\Omega}) \times C^\tau(\bar{\Omega}).$$

Lemma 5.4.2. *Ker*$(\mathcal{L})$ = *span* $(\bar{\varphi}, 1)$*, where* $\bar{\varphi}$ *is the unique solution to*

$$\begin{cases} \mu\Delta\bar{\varphi} + \mu\nabla\ln m\nabla\bar{\varphi} - m\bar{\varphi} - 1 = 0 \quad \text{in} \quad \Omega, \\ \nabla\bar{\varphi}\cdot n = 0 \quad \text{on} \quad \partial\Omega. \end{cases} \tag{5.4.5}$$

Proof. Let $(\varphi, \psi) \in \text{Ker}(\mathcal{L})$. Then $\gamma\Delta\psi = 0$ in Ω with $\nabla\psi\cdot n|_{\partial\Omega} = 0$. Using integration by parts and the boundary condition, we have that $\psi \equiv$ constant in Ω. Note that if $\psi = 0$ in Ω, then $\varphi = 0$ as well. To see this, we multiply the equation of φ by $m\varphi$ and integrate by parts to obtain

$$\mu\int_\Omega |\nabla\varphi|^2 m + \int_\Omega m^2\varphi^2 = 0. \tag{5.4.6}$$

This implies that $\varphi \equiv 0$ in Ω. Hence, ψ is a non-zero constant. Normalizing ψ, substituting it into the equation for φ (from the definition of $\mathcal{L}$) and multiplying by m we have

$$\mu\nabla\cdot[m\nabla\varphi] - m^2\varphi = m \quad \text{in } \Omega, \quad \nabla\varphi\cdot n|_{\partial\Omega} = 0. \tag{5.4.7}$$

We claim that the operator $S : C_n^{2,\tau}(\bar{\Omega}) \to C_n^{\tau}(\bar{\Omega})$, defined by $S(\varphi) = \mu\nabla \cdot [m\nabla\varphi] - m^2\varphi$ is invertible. To prove this, we note that the principal eigenvalue λ of S satisfies $\mu\nabla \cdot [m\nabla\phi] - m^2\phi = -\lambda\phi$ in Ω where $\nabla\phi \cdot n|_{\partial\Omega} = 0$ and $\phi > 0$ in Ω. Multiplying the equation of ϕ by ϕ and integrating by parts, we see that λ satisfies

$$\mu \int_\Omega |\nabla\phi|^2 m + \int_\Omega m^2\phi^2 = \lambda \int_\Omega \phi^2. \tag{5.4.8}$$

Thus we have that $\lambda > 0$, indicating that S is invertible. Taking $\bar{\varphi} = S^{-1}(m)$ we complete the proof. $\square$

Lemma 5.4.3. *Rng*$(\mathcal{L}) = \left\{(f, g) \in C^\tau(\bar{\Omega}) \times C^\tau(\bar{\Omega}) : \int_\Omega g = 0\right\}$ *and hence is of co-dimension 1 in* $C^\tau(\bar{\Omega}) \times C^\tau(\bar{\Omega})$.

Proof. It is well-known that $\gamma\Delta\psi = g$ has a solution $\psi \in W^{1,2}(\Omega)$ where $\nabla\psi \cdot n|_{\partial\Omega} = 0$ if and only if $\int_\Omega g = 0$. By elliptic regularity and the Sobolev embedding theorem, we see that $\psi \in C^{2,\tau}(\Omega)$. Using a similar argument as in the proof of Lemma 5.4.2, namely the invertibility of S, we justify the existence of $\varphi \in C^{2,\tau}(\bar{\Omega})$, such that $\mu\Delta\varphi + \mu\nabla \ln m\nabla\varphi - m\varphi - \psi = f$ in Ω with $\nabla\varphi \cdot n|_{\partial\Omega} = 0$. To see that Range$(\mathcal{L})$ is of co-dimension 1, we note that $(f, g) = \left(f, g - \frac{1}{|\Omega|}\int_\Omega g\right) + \left(0, \frac{1}{|\Omega|}\int_\Omega g\right)$. $\square$

Note that by the implicit function theorem u_ϵ is a differentiable function of ϵ near 0 (see Section 3.4 in [6]). Using this fact, we can justify the computation that

$$D_\epsilon\mathcal{L}_\epsilon = \begin{pmatrix} \mu\nabla \ln m\nabla - 2[m^{1+\epsilon}\ln m u_\epsilon + m^{1+\epsilon}u'_\epsilon] & -u'_\epsilon \\ 0 & -[m^{1+\epsilon}(\ln m)u_\epsilon + m^{1+\epsilon}u'_\epsilon] \end{pmatrix}$$

where $u'_\epsilon = \frac{d}{d\epsilon}(u_\epsilon)$. Evaluating at $\epsilon = 0$, we have

$$D_\epsilon\mathcal{L} = \begin{pmatrix} \mu\nabla \ln m\nabla - 2[m\ln m + mu'_0] & -u'_0 \\ 0 & -[m\ln m + mu'_0] \end{pmatrix}.$$

Since the kernel of $\mathcal{L}$ is spanned by one vector, we want to show that $D_\epsilon\mathcal{L}(\bar{\varphi}, 1) \notin \text{Range}(\mathcal{L})$. Since

$$D_\epsilon\mathcal{L}\begin{pmatrix}\bar{\varphi}\\ 1\end{pmatrix} = \begin{pmatrix}\mu\nabla\ln m\nabla\bar{\varphi} - 2[m\ln m + mu_0']\bar{\varphi} - u_0'\\ -[m\ln m + mu_0']\end{pmatrix},$$

we want that

$$\int_\Omega (m\ln m + mu_0') \neq 0.$$

To check this integral, we first need an expression for u_0'. Because u is a differentiable function of ϵ, we consider its first order expansion at 0, i.e. $u_\epsilon = 1+\epsilon u_0' + O(\epsilon^2)$. Plugging in such an expression into system (5.4.3) (here $\tilde{w} = 0$), we have that u_0' satisfies:

$$\begin{cases}\mu\Delta u_0' + \mu\nabla\ln m\nabla u_0' - [mu_0' + m\ln m] = 0 \quad \text{in} \quad \Omega,\\ \nabla u_0'\cdot n = 0 \quad \text{on} \quad \partial\Omega.\end{cases} \tag{5.4.9}$$

Consider the following Lemma:

Lemma 5.4.4. *Let u_1 denote the unique solution of*

$$\begin{cases}\mu\nabla\cdot[m\nabla u_1 - \nabla m] - m^2u_1 = 0 \quad \textit{in} \quad \Omega,\\ [m\nabla u_1 - \nabla m]\cdot n = 0 \quad \textit{on} \quad \partial\Omega.\end{cases} \tag{5.4.10}$$

Suppose m is nonconstant. Then $\int_\Omega mu_1 < 0$.

Proof. We first show that $\int_\Omega mu_1e^{u_1} < 0$. Notice that if we multiply (5.4.10) by e^{u_1}/m and integrate the resulting equation in Ω, we see that

$$\begin{aligned}\int_\Omega mu_1e^{u_1} &= \mu\int_\Omega \nabla\cdot[m\nabla u_1 - \nabla m]\cdot\frac{e^{u_1}}{m}\\ &= -\mu\int_\Omega [m\nabla u_1 - \nabla m]\cdot\nabla\left(\frac{e^{u_1}}{m}\right)\\ &= -\mu\int_\Omega m\nabla(u_1 - \ln m)\cdot\nabla(e^{u_1-\ln m})\\ &= -\mu\int_\Omega e^{u_1}|\nabla(u_1-\ln m)|^2 < 0,\end{aligned}$$

where the last inequality is strict since $u_1 - \ln m$ is nonconstant as m is nonconstant. To complete the proof of the lemma, it suffices to show that $\int_\Omega m u_1 \le \int_\Omega m u_1 e^{u_1}$. To this end, for every $p \in \mathbb{R}$, define

$$h(p) = \int_\Omega m u_1 e^{p u_1}.$$

Since $h'(p) = \int_\Omega m u_1^2 e^{p u_1} \ge 0$, we see that $h(1) \ge h(0)$. This completes the proof. □

We notice that $u_0' = u_1 - \ln m$. Hence, Lemma 5.4.4 gives us that

$$\int_\Omega (m \ln m + m u_0') < 0$$

and we see that $D_\epsilon \mathcal{L}(\bar{\varphi}, 1) \notin \text{Range}(\mathcal{L})$, allowing us to use Theorem 5.4.1. We then can parameterize u, $\tilde{w}$, and ϵ for small s by the following:

$$\begin{cases} u(s) = s\bar{\varphi} + \psi(s), \\ \tilde{w}(s) = s + \tau(s), \\ \epsilon(s) = \lambda(s), \end{cases} \tag{5.4.11}$$

where both ψ and τ are of order at least two in s. Recall that $\text{Ker}(\mathcal{L})$ is spanned by $(\bar{\varphi}, 1)$. We claim that ϵ and s are of the same order and sign. We proceed to show this by first expanding $\epsilon(s) = \lambda(0) + s\lambda'(0) + O(s^2) = s\lambda'(0) + O(s^2)$. Now we substitute the expressions in (5.4.11) and the expansion for ϵ in terms of s, back into the equation $\mathbf{F} = 0$ and calculate the first and second order terms in s. Doing so gives us the following equation in Ω

$$\gamma\Delta(s + \tau(s)) + (s + \tau(s))[m- \tag{5.4.12}$$

$$(m + s\lambda'(0) m \ln m + O(s^2))(s\bar{\varphi} + 1 + s\lambda'(0) u_0' + O(s^2)) - (s + \tau(s))] = 0.$$

From (5.4.12) we have the following equation:

$$\gamma\Delta\left(\frac{\tau(s)}{s^2}\right) - m\bar{\varphi} - m\lambda'(0) u_0' - \lambda'(0) m \ln m - 1 = O(s) \quad \text{in} \quad \Omega. \tag{5.4.13}$$

Thus if we integrate both sides of (5.4.13), letting $s \to 0$ and using the fact that $\nabla\tilde{w}\cdot n|_{\partial\Omega} = 0$, we obtain

$$\lambda'(0) = \frac{-\int_\Omega (m\bar{\varphi}+1)}{\int_\Omega (mu_0' + m\ln m)}. \tag{5.4.14}$$

By Lemma 5.4.4 we see that the denominator of (5.4.14) must be negative. We claim that the numerator of (5.4.14) is negative as well.

Lemma 5.4.5. *For any* $\mu > 0$, $\displaystyle\int_\Omega (m\bar{\varphi}+1) > 0$.

Proof. To see this, recall that $\bar{\varphi}$ satisfies (5.4.5). If we multiply (5.4.5) by $m\bar{\varphi}$ and integrate the result in Ω, we have

$$\mu\int_\Omega m|\nabla\bar{\varphi}|^2 + \int_\Omega m\bar{\varphi}(m\bar{\varphi}+1) = 0.$$

So, we have that

$$\begin{aligned}\int_\Omega (m\bar{\varphi}+1) &= \int_\Omega (m\bar{\varphi}+1)^2 - \int_\Omega m\bar{\varphi}(m\bar{\varphi}+1)\\ &= \int_\Omega (m\bar{\varphi}+1)^2 + \mu\int_\Omega m|\nabla\bar{\varphi}|^2 > 0,\end{aligned}$$

where strict inequality holds as $\bar{\varphi}$ is nonconstant. □

By Lemmas 5.4.4 and 5.4.5 we see that both the numerator and the denominator of (5.4.14) must be negative. Hence, $\lambda'(0) > 0$ and for both s and ϵ small,

$$s = \frac{\epsilon}{\lambda'(0)} + O(\epsilon^2). \tag{5.4.15}$$

Noticing that $\tilde{u} = m^{1+\epsilon}(u + u_\epsilon)$, we have demonstrated that we can parameterize the positive solution $(\tilde{u}, \tilde{w})$ of system (5.4.1) in terms of ϵ as follows:

Theorem 5.4.6. *Let* $(\tilde{u}, \tilde{w})$ *be a positive solution pair of system* (5.4.1). *Then for sufficiently small* ϵ,

$$\begin{cases}\tilde{u} = m + \epsilon m[\Lambda\bar{\varphi} + \ln m + u_0'] + O(\epsilon^2),\\ \tilde{w} = \epsilon\Lambda + O(\epsilon^2),\end{cases} \tag{5.4.16}$$

where $\Lambda = 1/\lambda'(0)$.

The next two results establish the fact that for α slightly larger than 1, the only positive steady state solutions $(\tilde{u}, \tilde{w})$ of (5.4.1) are on the solution branch bifurcating from $(m, 0)$ as described by Theorem 5.4.1. This completes the global picture for positive solutions of (5.4.1) for α slightly larger than 1. In fact, (5.4.1) has no positive solutions for $\alpha \leq 1$ and close to 1.

Lemma 5.4.7. *Consider a positive solution* $(\tilde{u}, \tilde{w})$ *to* (5.4.1)*. Then* $\lim_{\epsilon \to 0^+} (\tilde{u}, \tilde{w}) = (m, 0)$.

Proof. By elliptic regularity and the Sobolev embedding theorem, for $0 < \epsilon \ll 1$, $(\tilde{u}, \tilde{w})$ is uniformly bounded in $C^{2,\tau}(\bar{\Omega})$ for some $\tau \in (0, 1)$ [23]. If we let $\epsilon \to 0^+$, passing to a subsequence if necessary, then by the Ascoli-Arzelá lemma, we see that $(\tilde{u}, \tilde{w})$ converges to $(\hat{u}, \hat{w})$ in $C^2(\bar{\Omega})$, where $(\hat{u}, \hat{w})$ satisfies

$$\begin{cases} \mu \nabla \cdot [\nabla \hat{u} - \hat{u} \nabla \ln m] + \hat{u}(m - \hat{u} - \hat{w}) = 0 \quad \text{in} \quad \Omega, \\ \gamma \Delta \hat{w} + \hat{w}(m - \hat{u} - \hat{w}) = 0 \quad \text{in} \quad \Omega, \\ [\nabla \hat{u} - \hat{u} \nabla \ln m] \cdot n|_{\partial\Omega} = \nabla \hat{w} \cdot n|_{\partial\Omega} = 0. \end{cases} \tag{5.4.17}$$

By Theorem 2 of [1], we know that (5.4.17) has no strictly positive steady states, rather it has a two semi-trivial steady states $(m, 0)$ and $(0, \hat{w}^*)$. Thus $(\hat{u}, \hat{w}) = (0, 0)$, $(0, \hat{w}^*)$, or $(m, 0)$.

Suppose $(\hat{u}, \hat{w}) = (0, 0)$. Set $u = \tilde{u}/||\tilde{u}||_\infty$. By elliptic regularity and the equation of $\tilde{u}$ we see that $u \to u_1$ in $C^2(\bar{\Omega})$ for some $u_1 \geq 0$ in Ω, which satisfies $||u_1||_\infty = 1$ and

$$\begin{cases} \mu \nabla \cdot [\nabla u_1 - u_1 \nabla \ln m] + u_1 m = 0 \quad \text{in} \quad \Omega, \\ [\nabla u_1 - u_1 \nabla \ln m] \cdot n|_{\partial\Omega} = 0. \end{cases} \tag{5.4.18}$$

Integrating both sides of equation (5.4.18) over Ω and using the boundary condition, we see that

$$\int_\Omega u_1 m = 0.$$

But this is a contradiction since $m > 0$ and $u_1 \geq 0$, $u_1 \not\equiv 0$ on Ω.

Now suppose $(\hat{u}, \hat{w}) = (0, \hat{w}^*)$. Again we set $u = \tilde{u}/||\tilde{u}||_\infty$ and see that by elliptic regularity and the equation of $\tilde{u}$ we see that $u \to u_1$ in $C^2(\bar{\Omega})$ for some $u_1 \geq 0$ in Ω, which satisfies $||u_1||_\infty = 1$ and

$$\begin{cases} \mu\nabla \cdot [\nabla u_1 - u_1 \nabla \ln m] + u_1(m - \hat{w}^*) = 0 \quad \text{in} \quad \Omega, \\ [\nabla u_1 - u_1 \nabla \ln m] \cdot n|_{\partial\Omega} = 0. \end{cases} \tag{5.4.19}$$

Since $u_1 \geq 0$, $u_1 \not\equiv 0$, we see 0 is the principal eigenvalue for the eigenvalue problem

$$\begin{cases} \mu\nabla \cdot [\nabla \phi - \phi \nabla \ln m] + \phi(m - \hat{w}^*) = -\lambda\phi \quad \text{in} \quad \Omega, \\ [\nabla \phi - \phi \nabla \ln m] \cdot n|_{\partial\Omega} = 0. \end{cases} \tag{5.4.20}$$

But this contradicts the result in Theorem 2 of [1] which says that the above eigenvalue problem has a negative principal eigenvalue. Hence, we must have that $(\hat{u}, \hat{w}) = (m, 0)$. □

Lemma 5.4.8. *There exists $\epsilon_0 > 0$ such that for all ϵ with $0 < \epsilon < \epsilon_0$, $(\tilde{u}^*, \tilde{w}^*)$ is the unique steady state of* (5.4.1) *and is linearly stable.*

Proof. Note for suitably small ϵ the uniqueness of $(\tilde{u}^*, \tilde{w}^*)$ as the steady state of (5.4.1) follows from Lemma 5.4.7 and Theorem 5.4.1 (Crandall-Rabinowitz).

Consider the following system

$$\begin{cases} u_t = \mu\nabla \cdot [\nabla u - (1+\epsilon)u\nabla \ln m] + u(m - u - w) \quad \text{in} \quad \Omega, \\ w_t = \gamma\Delta w + w(m - u - w) \quad \text{in} \quad \Omega, \\ [\nabla u - (1+\epsilon)u\nabla \ln m] \cdot n = \nabla w \cdot n = 0 \quad \text{on} \quad \partial\Omega. \end{cases} \tag{5.4.21}$$

Linearizing and then perturbing the above system about $(\tilde{u}^*, \tilde{w}^*)$, we put $u = \tilde{u}^* +$

$\delta\phi e^{-\eta t}+O(\delta^2)$ and $w = \tilde{w}^*+\delta\psi e^{-\eta t}+O(\delta^2)$, substitute these expressions into (5.4.21), divide by $\delta e^{-\eta t}$ and let $\delta \to 0$ to obtain the following eigenvalue problem

$$\begin{cases} -\eta\phi = \mu\nabla\cdot[\nabla\phi - (1+\epsilon)\phi\nabla\ln m] - \tilde{u}^*(\phi+\psi) \\ +\phi(m-\tilde{u}^*-\tilde{w}^*) \quad \text{in} \quad \Omega, \\ -\eta\psi = \gamma\Delta\psi + \psi(m-\tilde{u}^*-\tilde{w}^*) - \tilde{w}^*(\psi+\phi) \quad \text{in} \quad \Omega, \\ [\nabla\phi - (1+\epsilon)\phi\nabla\ln m]\cdot n|_{\partial\Omega} = \nabla\psi\cdot n|_{\partial\Omega} = 0. \end{cases} \tag{5.4.22}$$

By Lemma 5.4.7, we know that when $\epsilon = 0$, $\tilde{u}^* = m$, $\tilde{w}^* = 0$, $\eta = 0$ (here 0 is the principal eigenvalue), $\phi = m\bar{\varphi}$ (where $\bar{\varphi}$ satisfies (5.4.5)), and $\psi = 1$, after suitable scaling. Using the implicit function theorem, we know that the principal eigenvalue η and corresponding eigenfunctions ϕ and ψ are smooth functions of ϵ (see Lemma 3.3.1 of [3]). Hence, we can write $\eta = 0+\epsilon\eta_1+O(\epsilon^2)$, $\phi = m\bar{\varphi}+\epsilon m\phi_1+O(\epsilon^2)$, and $\psi = 1+\epsilon\psi_1+O(\epsilon^2)$, after suitable scaling. Recall that $\tilde{u}^* = m^{1+\epsilon}(u+u_\epsilon)$. Using this and the fact that $s = \epsilon\Lambda$, where $\Lambda = 1/\lambda'(0)$ we can write $\tilde{u}^* = (m+\epsilon m\ln m)(\Lambda\epsilon\bar{\varphi}+1+\epsilon u_0')+O(\epsilon^2)$ and $\tilde{w}^* = \epsilon\Lambda+O(\epsilon^2)$.

Substituting these expansions into the second equation of (5.4.22) we obtain the following equation in Ω

$$\begin{aligned} -\epsilon\eta_1 &= \gamma\Delta(1+\epsilon\psi_1) + (1+\epsilon\psi_1)[m - (\epsilon\Lambda m\bar{\varphi} + m + \epsilon m\ln m) - \epsilon\Lambda] \\ &\quad - \epsilon\Lambda(m\bar{\varphi}+\epsilon m\phi_1 + 1 + \epsilon\psi_1) + O(\epsilon^2), \quad \nabla\psi_1\cdot n|_{\partial\Omega} = 0. \end{aligned} \tag{5.4.23}$$

Dividing both sides by ϵ and letting $\epsilon \to 0$, we see that

$$-\eta_1 = \gamma\Delta\psi_1 - 2\Lambda(m\bar{\varphi}+1) - mu_0' - m\ln m \ \text{ in } \ \Omega, \quad \nabla\psi_1\cdot n|_{\partial\Omega} = 0. \tag{5.4.24}$$

Thus if we integrate both sides of (5.4.24), using the boundary condition and the definition of Λ, we see that

$$\eta_1 = -\frac{1}{|\Omega|}\int_\Omega (mu_0' + m\ln m) > 0. \tag{5.4.25}$$

Because $\eta_1 > 0$, we conclude that for sufficiently small positive ϵ, $\eta > 0$. □

5.4.2 Bounds on Solutions of the Three Species System

Given a solution $(u(x,t), v(x,t), w(x,t))$ of system (5.1.1), we aim to establish upper bounds on $u(x,t)$ and $w(x,t)$ in $\Omega \times (T, \infty)$ for some T which depends on the non-negative, not identically zero initial data of the solution (u, v, w). The main result of this section is

Theorem 5.4.9. *Let (u, v, w) be any positive solution of* (5.1.1). *Assume that $\{x \in \Omega : |\nabla m(x)| = 0\}$ has Lebesgue measure zero. Then there exists an $\epsilon_0 > 0$ such that for all $0 < \epsilon < \epsilon_0$, there exists $\tilde{\Gamma}$ such that for all $\beta > \tilde{\Gamma}$, there exists a $T > 0$ such that $u(x,t) \le \tilde{u}^*(x) + 1/\beta$ and $w(x,t) \le \tilde{w}^*(x) + 1/\beta$ on $\Omega \times (T, \infty)$.*

To establish this result, we make use of appropriate "sub/super" systems as follows.

Lemma 5.4.10. *Consider the system*

$$\begin{cases} \check{u}_t = \mu \nabla \cdot [\nabla \check{u} - (1+\epsilon)\check{u} \nabla \ln m] \\ \quad + \check{u}(m - \check{u} - \hat{w} - (v^* + 1/\beta)) \quad in \quad \Omega \times (T(\beta), \infty), \\ \hat{w}_t = \gamma \Delta \hat{w} + \hat{w}(m - \check{u} - \hat{w}) \quad in \quad \Omega \times (T(\beta), \infty), \\ [\nabla \check{u} - (1+\epsilon)\check{u} \nabla \ln m] \cdot n = \nabla \hat{w} \cdot n = 0 \quad on \quad \partial\Omega \times (T(\beta), \infty), \\ \check{u}(x, T(\beta)) = u(x, T(\beta)), \;\; \hat{w}(x, T(\beta)) = w(x, T(\beta)), \quad in \quad \Omega. \end{cases} \tag{5.4.26}$$

where v^* is the unique positive steady state of (5.2.7). *Let $(\check{u}^*_\beta, \hat{w}^*_\beta)$ be a positive steady state of* (5.4.26). *Let $\epsilon_0 > 0$ be as in Lemma* 5.4.8. *Then for all ϵ with $0 < \epsilon < \epsilon_0$, there exists $\bar{\beta}(\epsilon)$ such that if $\beta > \bar{\beta}(\epsilon)$, $(\check{u}^*_\beta, \hat{w}^*_\beta)$ is linearly stable.*

Proof. We know that for each $\beta > 0$, the system linearized at $(\breve{u}^*_\beta, \hat{w}^*_\beta)$ has principal eigenfunctions (f, g) in $W^{1,2}(\Omega)$ such that, $f, g > 0$, $||f||^2_{L^2} + ||g||^2_{L^2} = 1$ and

$$\begin{cases} -\eta f = \mu \nabla \cdot [\nabla f - (1+\epsilon) f \nabla \ln m] - \breve{u}^*_\beta (f+g) \\ \qquad\qquad + f(m - \breve{u}^*_\beta - \hat{w}^*_\beta - (v^* + 1/\beta)) \quad \text{in} \quad \Omega, \\ -\eta g = \gamma \Delta g + g(m - \breve{u}^*_\beta - \hat{w}^*_\beta) \quad \text{in} \quad \Omega, \\ [\nabla f - (1+\epsilon) f \nabla \ln m] \cdot n = \nabla g \cdot n = 0 \quad \text{on} \quad \partial\Omega, \end{cases} \tag{5.4.27}$$

where η is the associated principal eigenvalue. By elliptic regularity [23], we see that (f, g) are uniformly bounded in $W^{2,2}(\bar{\Omega})$. By the Sobolev embedding theorem [23], this sequence is uniformly bounded in $C^{1,\tau}(\bar{\Omega})$ for some $\tau \in (0, 1)$. Thus passing to a subsequence if necessary, we see that as $\beta \to \infty$, (f, g) converges to a limit (f^*, g^*) in $C^1(\bar{\Omega})$ where $f^*, g^* \geq 0$, $||f^*||^2_{L^2} + ||g^*||^2_{L^2} = 1$, and

$$\begin{cases} -\eta^* f^* = \mu \nabla \cdot [\nabla f^* - (1+\epsilon) f^* \nabla \ln m] - \tilde{u}^* (f^* + g^*) \\ \qquad\qquad + f^*(m - \tilde{u}^* - \tilde{w}^*) \quad \text{in} \quad \Omega, \\ -\eta^* g^* = \gamma \Delta g^* + g^*(m - \tilde{u}^* - \tilde{w}^*) \quad \text{in} \quad \Omega, \\ [\nabla f^* - (1+\epsilon) f^* \nabla \ln m] \cdot n = \nabla g^* \cdot n = 0 \quad \text{on} \quad \partial\Omega, \end{cases} \tag{5.4.28}$$

where $(\tilde{u}^*, \tilde{w}^*)$ is as in Lemma 5.4.8. Note that for small enough positive ϵ, as $\beta \to \infty$, $(\breve{u}^*_\beta, \hat{w}^*_\beta)$ converges to $(\tilde{u}^*, \tilde{w}^*)$ in $C^1(\bar{\Omega})$. To see this notice that by elliptic regularity and the Sobolev embedding theorem [23], a subsequence of $(\breve{u}^*_\beta, \hat{w}^*_\beta)$ converges to $(\tilde{u}^*, \tilde{w}^*)$ in $C^1(\bar{\Omega})$. For sufficiently small positive ϵ, the positive steady state of (5.4.1) is uniquely determined by Lemma 5.4.8. Thus, we see that convergence is independent of the subsequence.

Now we establish the uniqueness of the limit (f^*, g^*). Since $\tilde{u}^*, \tilde{w}^* > 0$ in Ω, we must have that $f^*, g^* > 0$ in Ω. Thus, we see that the triple (f^*, g^*, η^*) satisfies the eigenvalue problem in Equation (5.4.22) and because of the positivity of both f^* and g^*, η^* must be the principal eigenvalue. Note η^* is simple and since $||f^*||^2_{L^2} + ||g^*||^2_{L^2} =$

1, it must be that the triple (f^*, g^*, η^*) is uniquely determined. This proves that convergence is independent of the subsequence.

By Lemma 5.4.8, we know then that for $0 < \epsilon < \epsilon_0$, $\eta^* > 0$. Hence for $\beta > \bar{\beta}(\epsilon)$, the principal eigenvalue η, associated to $(\check{u}^*_\beta, \hat{w}^*_\beta)$ is positive. □

Lemma 5.4.11. *Consider the system*

$$\begin{cases} \hat{u}_t = \mu\nabla\cdot[\nabla\hat{u} - (1+\epsilon)\hat{u}\nabla\ln m] + \hat{u}(m - \hat{u} - \check{w}) \quad \textit{in} \quad \Omega\times(T(\beta),\infty), \\ \check{w}_t = \gamma\Delta\check{w} + \check{w}(m - \hat{u} - \check{w} - (v^* + 1/\beta)) \quad \textit{in} \quad \Omega\times(T(\beta),\infty), \\ [\nabla\hat{u} - (1+\epsilon)\hat{u}\nabla\ln m]\cdot n = \nabla\check{w}\cdot n = 0 \quad \textit{on} \quad \partial\Omega\times(T(\beta),\infty), \\ \hat{u}(x,T(\beta)) = u(x,T(\beta)), \;\; \check{w}(x,T(\beta)) = w(x,T(\beta)), \quad \textit{in} \quad \Omega. \end{cases} \tag{5.4.29}$$

where v^* is the unique steady state of (5.2.7)*. Let $(\hat{u}^*_\beta, \check{w}^*_\beta)$ be a positive steady state of* (5.4.29)*. Let $\epsilon_0 > 0$ be as in Lemma* 5.4.8*. Then for ϵ with $0 < \epsilon < \epsilon_0$, there exists $\tilde{\beta}(\epsilon)$ such that if $\beta > \tilde{\beta}(\epsilon)$, $(\hat{u}^*_\beta, \check{w}^*_\beta)$ is linearly stable.*

Proof. The proof is similar to that of Lemma 5.4.10. □

Lemma 5.4.12. *Assume that $\{x \in \Omega : |\nabla m(x)| = 0\}$ has Lebesgue measure zero. There exists β_s such that for all $\beta > \beta_s$ the semi-trivial steady states, $(\check{u}^*, 0)$ and $(0, \hat{w}^*)$, of system* (5.4.26) *are unstable.*

Proof. To show that $(\check{u}^*, 0)$ is unstable, we must show that the principal eigenvalue λ, satisfying the following eigenvalue problem, is negative:

$$\begin{cases} \gamma\Delta\phi + \phi(m - \check{u}^*) = -\lambda\phi \quad \text{in} \quad \Omega, \\ \nabla\phi\cdot n|_{\partial\Omega} = 0. \end{cases} \tag{5.4.30}$$

Note that in equation (5.4.30) we can choose the principal eigenfunction ϕ so that $\phi > 0$ in Ω. Dividing the equation of ϕ by ϕ, integrating the resulting equation over Ω and using the boundary conditions, we have

$$-\lambda|\Omega| = \gamma\int_\Omega \frac{|\nabla\phi|^2}{\phi^2} + \int_\Omega (m - \check{u}^*). \tag{5.4.31}$$

By the comparison principle, $\check{u}^* \leq u^*$, where u^* is the unique positive solution of (5.2.1). By Lemma 5.2.1, if $\alpha > 1$, $\int_\Omega u^* < \int_\Omega m$. Hence, $\int_\Omega \check{u}^* < \int_\Omega m$. This together with (5.4.31) implies that $\lambda < 0$ for all β.

Next, we want to prove that $(0, \hat{w}^*)$ is unstable. The proof is almost identical to that of Theorem 5.3.1. Working through the corresponding eigenvalue problem for system (5.4.26), we finally arrive at the following expression for the principal eigenvalue λ:

$$-\lambda \int_\Omega m^{1+\epsilon} \geq \int_\Omega [m^{1+\epsilon} - (\hat{w}^*)^{1+\epsilon}](m - \hat{w}^*) - \int_\Omega m^{1+\epsilon}(v^* + 1/\beta). \tag{5.4.32}$$

As in the proof of Theorem 5.3.1, we cannot have $m = \hat{w}^*$ in Ω. Thus, $\int_\Omega [m^{1+\epsilon} - (\hat{w}^*)^{1+\epsilon}](m - \hat{w}^*) > 0$. Also, we know that as $\beta \to \infty$, $\int_\Omega v^* \to 0$ and $1/\beta \to 0$. Thus because $||m^{1+\epsilon}||_{L^\infty} < \infty$, there exists a β_s such that if $\beta > \beta_s$ then right hand side of (5.4.32) will be positive. Hence, $\lambda < 0$, proving that $(0, \hat{w}^*)$ is unstable. □

Lemma 5.4.13. *Assume that $\{x \in \Omega : |\nabla m(x)| = 0\}$ has Lebesgue measure zero. There exists β_p such that for all $\beta > \beta_p$ the semi-trivial steady states, $(\hat{u}^*, 0)$ and $(0, \check{w}^*)$, of system* (5.4.29) *are unstable.*

Proof. The proof is similar to that of the previous Lemma. □

Theorem 5.4.14. *Assume that $\{x \in \Omega : |\nabla m(x)| = 0\}$ has Lebesgue measure zero. Let $\epsilon_0 > 0$ be as in Lemma* 5.4.8. *Then for all ϵ, with $0 < \epsilon < \epsilon_0$, there exists a Γ_ϵ, such that for all $\beta > \Gamma_\epsilon$, both systems* (5.4.26) *and* (5.4.29) *have unique positive steady states $(\check{u}^*_\beta, \hat{w}^*_\beta)$ and $(\hat{u}^*_\beta, \check{w}^*_\beta)$, respectively. Furthermore, as $\beta \to \infty$, both $(\check{u}^*_\beta, \hat{w}^*_\beta)$ and $(\hat{u}^*_\beta, \check{w}^*_\beta)$ converge to $(\tilde{u}^*, \tilde{w}^*)$ in $C^1(\bar{\Omega})$, where $(\tilde{u}^*, \tilde{w}^*)$ is as in Lemma* 5.4.8.

Proof. Let $\epsilon \in (0, \epsilon_0)$. If $\beta > \bar{\beta}(\epsilon)$, then by Lemma 5.4.10, $(\check{u}^*_\beta, \hat{w}^*_\beta)$ has a corresponding positive principal eigenvalue. From Lemma 5.4.12 we know that for $\beta > \beta_s$, both semi-trivial steady states of system (5.4.26) are unstable. Thus because system

(5.4.26) is strongly monotone, for $\beta > \max\{\bar{\beta}(\epsilon), \beta_s\}$, by monotone dynamical system theory [48], $(\check{u}^*_\beta, \hat{w}^*_\beta)$ is globally asymptotically stable and hence unique.

In addition, by Lemma 5.4.11, $(\hat{u}^*_\beta, \check{w}^*_\beta)$ has a corresponding positive principal eigenvalue for $\beta > \tilde{\beta}(\epsilon)$. From Lemma 5.4.13 we have that for $\beta > \beta_p$, both semi-trivial steady states of system (5.4.29) are unstable. Again, by monotone dynamical system theory [48], since (5.4.29) is a strongly monotone system, for $\beta > \max\{\tilde{\beta}(\epsilon), \beta_p\}$, $(\hat{u}^*_\beta, \check{w}^*_\beta)$ is globally asymptotically stable and thus unique.

Therefore, if we let $\Gamma_\epsilon = \max\{\beta_s, \beta_p, \bar{\beta}(\epsilon), \tilde{\beta}(\epsilon)\}$, then for $\beta > \Gamma_\epsilon$, both positive steady states are unique for their respective systems.

Finally, we reference the proof of Lemma 5.4.10 for justification of the result that as $\beta \to \infty$, both $(\check{u}^*_\beta, \hat{w}^*_\beta)$ and $(\hat{u}^*_\beta, \check{w}^*_\beta)$ converge to $(\tilde{u}^*, \tilde{w}^*)$ in $C^1(\bar{\Omega})$, where $(\tilde{u}^*, \tilde{w}^*)$ is as in Lemma 5.4.8. □

Corollary 5.4.15. *Assume that* $\{x \in \Omega : |\nabla m(x)| = 0\}$ *has Lebesgue measure zero. For all* ϵ*, where* $0 < \epsilon < \epsilon_0$*, there exists* $\tilde{\Gamma}$ *such that for all* $\beta > \tilde{\Gamma}$*, there exists a* $T_\beta > 0$ *such that* $\hat{u}(x,t) \le \tilde{u}^*(x) + 1/\beta$ *and* $\hat{w}(x,t) \le \tilde{w}^*(x) + 1/\beta$ *on* $\Omega \times (T_\beta, \infty)$. (*Note:* $\hat{u}$ *comes from the solution pair* $(\hat{u}, \check{w})$ *satisfying* (5.4.29) *and* $\hat{w}$ *comes from the solution pair* $(\check{u}, \hat{w})$ *satisfying* (5.4.26).)

Proof. Let $\epsilon \in (0, \epsilon_0)$ and let $\beta > \Gamma_\epsilon$. Then from Theorem 5.4.14, $(\check{u}^*_\beta, \hat{w}^*_\beta)$ is a globally asymptotically stable positive steady state for system (5.4.26) and $(\hat{u}^*_\beta, \check{w}^*_\beta)$ is a globally asymptotically stable steady state for system (5.4.29). Thus for a solution $(\check{u}, \hat{w})$ to system (5.4.26) with prescribed nonnegative initial data, there exists a $T_w > 0$ such that if $t > T_w$, $\hat{w}(x,t) \le \hat{w}^*_\beta(x) + 1/(2\beta)$ in Ω. Similarly, for a solution $(\hat{u}, \check{w})$ to system (5.4.29), there exists a $T_u > 0$ such that if $t > T_u$, $\hat{u}(x,t) \le \hat{u}^*_\beta + 1/(2\beta)$ in Ω.

By Theorem 5.4.14, as $\beta \to \infty$, $(\check{u}^*_\beta, \hat{w}^*_\beta) \to (\tilde{u}^*, \tilde{w}^*)$ in $C^1(\bar{\Omega})$. Hence, there exists Γ_1 such that if $\beta > \Gamma_1$, $\hat{w}^*_\beta(x) \le \tilde{w}^* + 1/(2\beta)$ in Ω and $\hat{u}^*_\beta(x) \le \tilde{u}^* + 1/(2\beta)$ in Ω.

Thus if we let $\beta > \tilde{\Gamma} = \max\{\Gamma_\epsilon, \Gamma_1\}$ and then put $T_\beta = \max\{T_u, T_w\}$, we obtain our result. $\square$

To prove Theorem 5.4.9, we simply apply Corollary 5.4.15 and $u \leq \hat{u}$ and $w \leq \hat{w}$ on $\Omega \times (T, \infty)$ for some $T > 0$.

5.4.3 A Key Estimate and Instability of $(\tilde{u}^*, 0, \tilde{w}^*)$

We begin this section with a useful result concerning u_0' for large μ.

Lemma 5.4.16. *The following holds:*

$$\lim_{\mu \to \infty} \int_\Omega (m u_0' + m \ln m) < 0,$$

where u_0' is the unique solution satisfying (5.4.9)*.*

Proof. Consider equation (5.4.9). If we let $\mu \to \infty$, then we have uniform convergence of

$$u_0' \to -\frac{\int_\Omega m^2 \ln m}{\int_\Omega m^2}.$$

Thus,

$$\lim_{\mu \to \infty} \int_\Omega (m u_0' + m \ln m) = -\left(\int_\Omega m\right)\left(\frac{\int_\Omega m^2 \ln m}{\int_\Omega m^2} - \frac{\int_\Omega m \ln m}{\int_\Omega m}\right).$$

It suffices to show that

$$\frac{\int_\Omega m^2 \ln m}{\int_\Omega m^2} > \frac{\int_\Omega m \ln m}{\int_\Omega m}.$$

Define f as

$$f(p) = \frac{\int_\Omega m^p \ln m}{\int_\Omega m^p}, \quad p > 0.$$

Then

$$f'(p) = \frac{\int_\Omega m^p (\ln m)^2 \int_\Omega m^p - (\int_\Omega m^p \ln m)^2}{(\int_\Omega m^p)^2} > 0,$$

where the numerator of $f'(p)$ is positive by Hölder's inequality. Thus, f is a strictly increasing function of p and our result follows. $\square$

Next, we establish the following beautiful inequality coming from Hardy, Littlewood, and Pólya [26].

Lemma 5.4.17. [26] *Let E be a measurable subset of $\mathbb{R}^N$. Suppose that $a \leq f \leq b$, where a and b are in $\mathbb{R}$, and that f is almost never equal to a and b; that p, the "weight function", is finite and positive everywhere in E, and integrable over E. Further, suppose that $\phi''(t)$ is positive and finite for $a < t < b$. Then*

$$\phi\left(\frac{\int_E fp}{\int_E p}\right) \leq \frac{\int_E \phi(f)p}{\int_E p},$$

whenever the right-hand side exists and is finite. Also, note that equality holds when f is effectively constant.

Proof. Note that we can normalize p such that $\displaystyle\int_E p = 1$ and suppose that $Q = \displaystyle\int_E fp < \infty$ (this is the case in which we are interested, but one can refer to [26] for cases when $Q = \pm\infty$). If $f \not\equiv C$, then $a < Q < b$. Also, since f is finite and $a < f < b$ almost everywhere in E, we see that by Taylor's theorem

$$\phi(f) = \phi(Q) + (f-Q)\phi'(Q) + (1/2)(f-Q)^2\phi''(c),$$

where c is between f and Q, which implies that $a < c < b$. Thus

$$\int_E \phi(f)p \geq \phi(Q) = \phi\left(\int_E fp\right).$$

Here we have equality only if $(f-Q)^2\phi''(c) \equiv 0$. As $a < c < b$, $\phi''(c) > 0$. Hence $f \equiv Q$ almost everywhere in E. □

Lemma 5.4.18. *For $m > 0$, nonconstant and in $C^2(\bar{\Omega})$ (note: these are our assumptions on m without assumption (A1)),*

$$\frac{\int_\Omega m^2}{\int_\Omega m} < e^{\frac{\int_\Omega m^2 \ln m}{\int_\Omega m^2}}.$$

Proof. We apply Lemma 5.4.17 by choosing $\phi(t) = t \ln t$, $p = m$, $f = m$ and $E = \Omega$. □

Using the inequality in Lemma 5.4.18, we are now ready to make our "key estimate" on the size of $m(x_0)$. As we discussed in section 5.4, this result is fundamental to establishing the instability of $(\tilde{u}, 0, \tilde{w})$ and lower bound for v.

Lemma 5.4.19. *Suppose that $m > 0$, nonconstant and in $C^2(\bar{\Omega})$. Furthermore, suppose that*

$$\ln\left(\frac{\int_\Omega m^2}{\int_\Omega m}\right) < \ln(m(x_0)) < \frac{\int_\Omega m^2 \ln m}{\int_\Omega m^2}$$

for $x_0 \in \Omega$, where x_0 is a local maximum of m. Then there exists some $\bar{\mu}$ such that for all $\mu > \bar{\mu}$, there exists an $\bar{\epsilon} > 0$ such that for all $0 < \epsilon < \bar{\epsilon}$,

$$\tilde{u}^*(x_0) + \tilde{w}^*(x_0) - m(x_0) < 0,$$

where $(\tilde{u}^*, \tilde{w}^*)$ is the unique positive steady state of (5.4.1) *as shown by Lemma 5.4.8.*

Proof. Using our expansions (5.4.16), for $0 < \epsilon < \epsilon_0$,

$$\begin{cases} \tilde{u}^* = m + \epsilon m[\Lambda\bar{\varphi} + u_0' + \ln m] + O(\epsilon^2) \\ \tilde{w}^* = \epsilon\Lambda + O(\epsilon^2) \end{cases} \tag{5.4.33}$$

which gives us

$$\begin{aligned} \tilde{u}^* + \tilde{w}^* - m &= \epsilon\Lambda[m\bar{\varphi} + 1] + \epsilon[m \ln m + u_0' m] + O(\epsilon^2) \\ &= \epsilon B + O(\epsilon^2), \end{aligned} \tag{5.4.34}$$

where $\Lambda = 1/\lambda'(0) > 0$, $B = \Lambda[m\bar{\varphi} + 1] + [m \ln m + u_0' m]$. Let $\mu \to \infty$. Then we know that $\bar{\varphi} \to \dfrac{-\int_\Omega m}{\int_\Omega m^2}$ and $u_0' \to \dfrac{-\int_\Omega m^2 \ln m}{\int_\Omega m^2}$. Hence, as $\mu \to \infty$

$$
\begin{aligned}
\Lambda \to & \frac{\int_\Omega [m \ln m + \left(\frac{-\int_\Omega m^2 \ln m}{\int_\Omega m^2} \right) m]}{-\int_\Omega [m \left(\frac{-\int_\Omega m}{\int_\Omega m^2} \right) + 1]} \\
= & \frac{\int_\Omega m^2 \int_\Omega m \ln m - \int_\Omega m \int_\Omega m^2 \ln m}{\left(\int_\Omega m \right)^2 - |\Omega| \int_\Omega m^2}
\end{aligned} \tag{5.4.35}
$$

If we use our expression in (5.4.35) for Λ, then as $\mu \to \infty$

$$
\begin{aligned}
B \to & \left(\frac{\int_\Omega m^2 \int_\Omega m \ln m - \int_\Omega m \int_\Omega m^2 \ln m}{\left(\int_\Omega m \right)^2 - |\Omega| \int_\Omega m^2} \right) \left[m \left(\frac{-\int_\Omega m}{\int_\Omega m^2} \right) + 1 \right] \\
& + \left[m \ln m + m \left(\frac{-\int_\Omega m^2 \ln m}{\int_\Omega m^2} \right) \right] \\
= & \frac{(\int_\Omega m^2 \int_\Omega m \ln m - \int_\Omega m \int_\Omega m^2 \ln m)(-m \int_\Omega m + \int_\Omega m^2)}{(\int_\Omega m^2)((\int_\Omega m)^2 - |\Omega| \int_\Omega m^2)} \\
& + \frac{(m \ln m \int_\Omega m^2 - m \int_\Omega m^2 \ln m)((\int_\Omega m)^2 - |\Omega| \int_\Omega m^2)}{(\int_\Omega m^2)((\int_\Omega m)^2 - |\Omega| \int_\Omega m^2)}.
\end{aligned}
$$

Put $A = \left(\int_\Omega m^2 \right) \left(\left(\int_\Omega m \right)^2 - |\Omega| \int_\Omega m^2 \right) < 0$, then $B \to \dfrac{D}{A}$ as $\mu \to \infty$, where

$$
\begin{aligned}
D = & \left(\int_\Omega m^2 \int_\Omega m \ln m - \int_\Omega m \int_\Omega m^2 \ln m \right) \left(-m \int_\Omega m + \int_\Omega m^2 \right) \\
& + \left(m \ln m \int_\Omega m^2 - m \int_\Omega m^2 \ln m \right) \left(\left(\int_\Omega m \right)^2 - |\Omega| \int_\Omega m^2 \right).
\end{aligned}
$$

Note that by our assumption (A1) on m, at x_0, $m \ln m \int_\Omega m^2 - m \int_\Omega m^2 \ln m < 0$. Also, by Lemma 5.4.16, we see that $\int_\Omega m^2 \int_\Omega m \ln m - \int_\Omega m \int_\Omega m^2 \ln m < 0$. Now if we want $D > 0$ (evaluated at x_0), then rearranging the above expression for D gives us

$$\begin{aligned}D(x_0) =& m(x_0)\int_\Omega m\left(-\int_\Omega m^2\int_\Omega m\ln m+\int_\Omega m\int_\Omega m^2\ln m\right)\\&+m(x_0)\left(\ln m(x_0)\int_\Omega m^2-\int_\Omega m^2\ln m\right)\left(\left(\int_\Omega m\right)^2-|\Omega|\int_\Omega m^2\right)\\&-\left(-\int_\Omega m^2\int_\Omega m\ln m+\int_\Omega m\int_\Omega m^2\ln m\right)\int_\Omega m^2.\end{aligned}$$

Manipulating the above expression gives us that $D(x_0) > 0$ is equivalent to

$$m(x_0) > \frac{\int_\Omega m^2}{\int_\Omega m + \frac{ST}{C}}, \tag{5.4.36}$$

where $S = -\ln m(x_0)\int_\Omega m^2 + \int_\Omega m^2\ln m > 0$, $T = \dfrac{-A}{\int_\Omega m^2} > 0$ and $C = -\int_\Omega m^2\int_\Omega m\ln m + \int_\Omega m\int_\Omega m^2\ln m > 0$.

Assuming our nonmonotonicity condition (A1) for m, we see that if we want $D(x_0) > 0$ and hence $B < 0$ at x_0, then we need the lower bound for $m(x_0)$ as given in (5.4.36). Thus, if we impose the following condition on m,

$$(A2): \quad m(x_0) > \frac{\int_\Omega m^2}{\int_\Omega m},$$

we see that in light of Lemma 5.4.18 that this extra condition (A2) will not contradict the simultaneous assumption on m given by (A1). Clearly (A2) is equivalent to assuming that $\ln\left(\dfrac{\int_\Omega m^2}{\int_\Omega m}\right) < \ln(m(x_0))$. Furthermore, since $\dfrac{ST}{C} > 0$, we see for m satisfying both (A1) and (A2), $D(x_0) > 0$ and hence for large enough μ and small enough ϵ, $\tilde{u}^* + \tilde{w}^* - m < 0$ at x_0. □

Theorem 5.4.20. *Suppose that $m > 0$, nonconstant, in $C^2(\bar{\Omega})$, and all critical points of m are nondegenerate. Furthermore, suppose that*

$$\ln\left(\frac{\int_\Omega m^2}{\int_\Omega m}\right) < \ln(m(x_0)) < \frac{\int_\Omega m^2\ln m}{\int_\Omega m^2}$$

for some $x_0 \in \Omega$, where x_0 is a local maximum of m. Then there exists $\bar{\mu} > 0$ such that for all $\mu > \bar{\mu}$, there exists $\bar{\epsilon} > 0$ (from the previous Lemma) such that if $1 < \alpha < 1 + \epsilon$ (where $0 < \epsilon < \bar{\epsilon}$), for all $\gamma > 0$, $\nu \geq 0$, there exists a $\bar{\beta}(\mu, \epsilon, \gamma, \nu)$ such that for any $\beta > \bar{\beta}$ the positive steady state solution of $\mathbf{F}(\epsilon, u, \tilde{w}) = 0$ bifurcating from the trivial solution is unstable in the larger three equation system (5.1.1). In other words, $(\tilde{u}^*, 0, \tilde{w}^*)$ is unstable.

Proof. We consider the following eigenvalue problem:

$$\begin{cases} \nu\nabla \cdot [\nabla\phi - \beta\phi\nabla \ln m] + \phi(m - \tilde{u}^* - \tilde{w}^*) = -\lambda\phi \quad \text{in} \quad \Omega, \\ \nabla\phi \cdot n = 0 \quad \text{on} \quad \partial\Omega, \end{cases} \tag{5.4.37}$$

where $\tilde{u}^*$ and $\tilde{w}^*$ satisfy (5.4.1) for $0 < \epsilon < \epsilon_0$. Set $\zeta = e^{-\beta \ln m}\phi$. Then ζ satisfies

$$\begin{cases} \nu\nabla \cdot [e^{\beta \ln m}\nabla\zeta] + e^{\beta \ln m}\zeta(m - \tilde{u}^* - \tilde{w}^*) = -\lambda e^{\beta \ln m}\zeta \quad \text{in} \quad \Omega, \\ \nabla\phi \cdot n = 0 \quad \text{on} \quad \partial\Omega. \end{cases} \tag{5.4.38}$$

Simplifying the expression in (5.4.38), we see that ζ satisfies

$$-\nu\Delta\zeta - \nu\beta\nabla \ln m\nabla\zeta + (\tilde{u}^* + \tilde{w}^* - m)\zeta = \lambda\zeta \quad \text{in} \quad \Omega, \quad \nabla\zeta \cdot n|_{\partial\Omega} = 0. \tag{5.4.39}$$

Let λ^* denote the principal eigenvalue of Equation (5.4.37). Then from Theorem 1 of [10], we have

$$\lim_{\beta\to\infty} \lambda^* = \min_{M}(\tilde{u}^* + \tilde{w}^* - m), \tag{5.4.40}$$

where M denotes the set of local maxima of m. From Lemma 5.4.19, we know that for small enough ϵ, $\tilde{u}^*(x_0) + \tilde{w}^*(x_0) - m(x_0) < 0$. Thus for large enough β, we see that $\lambda^* < 0$. This completes the proof. □

Remark 5.4.21. *Suppose we let $m(x) = 3e^{-50(x-.2)^2} + .1e^{-200(x-.8)^2} + .1$ on $[0, 1]$. Then m has a local max at $x_0 = .8$ and m satisfies condition (A1). However, if we formally let $\mu \to \infty$, then $D < 0$ and $B \approx .006$, where D and B are as above. Hence* *for small ϵ and large μ, we see that $\tilde{u} + \tilde{w} - m > 0$ at x_0. This means that $(\tilde{u}, 0, \tilde{w})$ is stable. Therefore, we need to impose an additional assumption on m in order to guarantee the coexistence of three species.*

5.4.4 Proof of Lower Bound for Species v

Lemma 5.4.22. *Consider the following single equation system:*

$$\begin{cases} \check{v}_t = \nu \nabla \cdot [\nabla \check{v} - \beta \check{v} \nabla \ln m] \\ \quad + \check{v}(m - \tilde{u}^* - \tilde{w}^* - 2/\beta - \check{v}) \quad in \quad \Omega \times (T, \infty), \\ [\nabla \check{v} - \beta \check{v} \nabla \ln m] \cdot n = 0 \quad on \quad \partial\Omega \times (T, \infty), \\ \check{v}(x, T) = v(x, T) \quad in \quad \bar{\Omega}. \end{cases} \tag{5.4.41}$$

Suppose that m satisfies assumptions $(A1)$ and $(A2)$ and that the critical points of m are nondegenerate. Then there exists $\bar{\mu} > 0$ such that for all $\mu > \bar{\mu}$, there exists $\bar{\epsilon} > 0$ such that for $0 < \epsilon < \bar{\epsilon}$ and for all $\gamma > 0$, $\nu \geq 0$, there exists $\hat{\beta}(\epsilon, \mu, \gamma, \nu)$ such that if $\beta > \hat{\beta}$, the zero solution is unstable. (Note: $\bar{\epsilon} > 0$ and $\bar{\mu} > 0$ are as in Theorem 5.4.20.)

Proof. To show that zero is unstable, we must show that the principle eigenvalue λ of the following eigenvalue problem is negative:

$$\begin{cases} \nu \nabla \cdot [\nabla \varphi - \beta \varphi \nabla \ln m] + \varphi(m - \tilde{u}^* - \tilde{w}^* - 2/\beta) = -\lambda \varphi \quad \text{in} \quad \Omega, \\ [\nabla \varphi - \beta \varphi \nabla \ln m] \cdot n|_{\partial\Omega} = 0. \end{cases} \tag{5.4.42}$$

Note that we can choose $\varphi > 0$ in Ω as the corresponding eigenfunction to λ. If we let $\phi = \varphi / m^\beta$, then (5.4.42) becomes

$$\begin{cases} \nu \nabla \cdot [m^\beta \nabla \phi] + \phi m^\beta (m - \tilde{u}^* - \tilde{w}^* - 2/\beta) = -\lambda m^\beta \phi \quad \text{in} \quad \Omega, \\ \nabla \phi \cdot n|_{\partial\Omega} = 0. \end{cases} \tag{5.4.43}$$

Expanding and simplifying (5.4.43), we have

$$
\begin{aligned}
&-\nu\Delta\phi - \nu\beta\nabla\ln m\nabla\phi + (\tilde{u}^* + \tilde{w}^* + 2/\beta - m)\phi = \lambda\phi \quad \text{in} \quad \Omega, \\
&\nabla\phi\cdot n|_{\partial\Omega} = 0. \qquad (5.4.44)
\end{aligned}
$$

Now let $\delta_l > 0$ be any constant. Choose $\beta_l >> 1$ such that $2/\beta \leq \delta_l$ for all $\beta \geq \beta_l$. Consider the following eigenvalue problem

$$
\begin{cases}
-\nu\Delta\phi_l - \nu\beta\nabla\ln m\nabla\phi_l + (\tilde{u}^* + \tilde{w}^* + \delta_l - m)\phi = \lambda_1\phi_l \quad \text{in} \quad \Omega, \\
\nabla\phi_l\cdot n|_{\partial\Omega} = 0,
\end{cases} \qquad (5.4.45)
$$

where λ_l is the principal eigenvalue. By Theorem 1 of [10],

$$
\lim_{\beta\to\infty}\lambda_l = \min_M(\tilde{u}^* + \tilde{w}^* + \delta_l - m), \qquad (5.4.46)
$$

where M denotes the set of local maxima of m. Choosing

$$
\delta_l = \frac{1}{2}\left[m(x_0) - \tilde{u}^*(x_0) - \tilde{w}^*(x_0)\right] > 0,
$$

we see that by the choice of δ_l and Lemma 5.4.19

$$
\min_M(\tilde{u}^* + \tilde{w}^* + \delta_l - m) \leq \frac{1}{2}\left[\tilde{u}^*(x_0) + \tilde{w}^*(x_0) - m(x_0)\right] < 0.
$$

Hence, $\lambda_l < 0$ for $\beta \gg 1$. By the comparison principle, $\lambda_l \geq \lambda$ for $\beta \geq \beta_l$. Therefore, for $\beta \geq \beta_l$, $\lambda < 0$. $\square$

Finally, we can state and prove the lower bound result for species v.

Theorem 5.4.23. *Let m satisfy both assumptions (A1) and (A2). Assume that $\{x \in \Omega : |\nabla m(x)| = 0\}$ has Lebesgue measure zero and all the critical points of m are nondegenerate. Let v be the second component of any positive solution (u, v, w) of* (5.1.1)*. Let $\bar{\mu} > 0$ be as in Theorem* 5.4.20*. Then for all $\mu > \bar{\mu}$, there exists $0 < \bar{\epsilon}$ (where $\bar{\epsilon}$ is as above and is less than ϵ_0) such that for all $1 < \alpha < 1 + \bar{\epsilon}$, and for all $\gamma > 0$, $\nu \geq 0$, there exists an $\beta_3 = \max\{\tilde{\Gamma}, \hat{\beta}\}$ (where $\tilde{\Gamma}$ is from Corollary* 5.4.15 *and*

$\hat{\beta}$ is from Lemma 5.4.22), such that for all $\beta > \beta_3$, there exists a $\delta_3 > 0$ such that for all $x \in \Omega$, $\liminf_{t\to\infty} v(x,t) \geq \delta_3 > 0$.

Proof. Comparing system (5.4.26) and system (5.4.29) to system (5.1.1) and using Corollary 5.4.15, we see that v is a super solution to (5.4.41) for $t > T_\beta$ where T_β is as in Corollary 5.4.15. That is, for all $x \in \Omega$ and for all $t > T_\beta$, $v(x,t) \geq \check{v}(x,t)$. By Lemma 5.4.22, we know that zero is unstable for system (5.4.41) which implies that $\check{v}(x,t)$ tends to a unique positive equilibrium of (5.4.41) as $t \to \infty$. Hence we see that there exists a $\delta_3 > 0$ such that for all $x \in \Omega$, $\liminf_{t\to\infty} v(x,t) \geq \delta_3 > 0$. □

5.5 Three Species Permanence

Putting the results of Theorems 5.2.6, 5.3.1, and 5.4.23 together, we demonstrate that for appropriate parameters, any solution, with nonnegative and not identically zero initial data, of (5.1.1) eventually has a positive lower bound which is independent of the initial conditions.

Theorem 5.5.1. *Let $m > 0$, nonconstant and satisfy both (A1) and (A2). Assume that $\{x \in \Omega : |\nabla m(x)| = 0\}$ has Lebesgue measure zero and all the critical points of m are nondegenerate. There exists $\bar{\mu} > 0$ (as in Theorem 5.4.20) such that for all $\mu > \bar{\mu}$, there exists $0 < \bar{\epsilon}$ (where $\bar{\epsilon}$ is as in Theorem 5.4.23) such that for all $1 < \alpha < 1+\bar{\epsilon}$, and for all $\gamma > 0$, $\nu \geq 0$, there exists an $M = \max\{\beta_1, \beta_2, \beta_3\}$ such that for all $\beta > M$, there exists a $k = \min\{\delta_1, \delta_2, \delta_3\} > 0$ such that for any solution (u, v, w) of (5.1.1) with nonnegative and not identically zero initial data, $\liminf_{t\to\infty} u(x,t)$, $\liminf_{t\to\infty} v(x,t)$, $\liminf_{t\to\infty} w(x,t) \geq k > 0$, for all $x \in \Omega$.*

As the hard work has been completed, we turn to the upper bound result:

Theorem 5.5.2. *Given any positive solution* (u, v, w) *of system* (5.1.1)*, for* $m > 0$ *and nonconstant, if we let*

$$K = \max\{\sup_{\Omega} u^*(x), \sup_{\Omega} v^*(x), \sup_{\Omega} w^*(x)\} + \chi,$$

where $\chi > 0$ *and* $u^*(x), v^*(x), w^*(x)$ *are the steady state solutions of* (5.1.1) *when only one species is present, then* $\limsup_{t\to\infty} u(x,t)$*,* $\limsup_{t\to\infty} v(x,t)$*,* $\limsup_{t\to\infty} w(x,t) < K$*.*

Proof. Let (u, v, w) be a positive solution to (5.1.1). From Corollary 5.2.5 we know that $\limsup_{t\to\infty} u(x,t) \leq u^*$ and $\limsup_{t\to\infty} v(x,t) \leq v^*$ in Ω. Examining the single species equation for w, i.e. the equation for w in (5.1.1) when $u = v = 0$, we obtain a similar result for $w(x,t)$. That is, $\limsup_{t\to\infty} w(x,t) \leq w^*$. Putting these results together we complete the proof. □

Combining the results from Theorems 5.5.1 and 5.5.2 we have the following conclusion.

Theorem 5.5.3. *Given the assumptions in Theorem* 5.5.1*, a solution* (u, v, w) *of system* (5.1.1) *with nonnegative and not identically zero initial data will exhibit ecological permanence as defined in section* 5.1.1*.*

To conclude this section, we see that for nonmonotone m satisfying (A1) and (A2), for a suitable range of parameters, three species can survive together. Biologically, we note that species u and v both have an established niche as u concentrates near the global maximum of m and v concentrates near the local maximum of m at x_0. Species w, on the other hand, has a more evenly spread distribution. In short, we say that u pursues the "best" resources, v pursues the "second best", and w goes after the "rest."

5.6 Existence of a Componentwise Positive Equilibrium

In order to demonstrate that our permanence result implies the existence of a componentwise positive steady state for the three species model (5.1.1), we first rewrite (5.1.1) as follows

$$\begin{cases} \tilde{u}_t = \mu m^{-\alpha}\nabla \cdot [m^\alpha \nabla \tilde{u}] + \tilde{u}(m - m^\alpha \tilde{u} - m^\beta \tilde{v} - w) \quad \text{in} \quad \Omega \times (0,\infty), \\ \tilde{v}_t = \nu m^{-\beta}\nabla \cdot [m^\beta \nabla \tilde{v}] + \tilde{v}(m - m^\alpha \tilde{u} - m^\beta \tilde{v} - w) \quad \text{in} \quad \Omega \times (0,\infty), \\ w_t = \gamma \Delta w + w(m - u - v - w) \quad \text{in} \quad \Omega \times (0,\infty), \\ \nabla \tilde{u} \cdot n = \nabla \tilde{v} \cdot n = \nabla w \cdot n = 0 \quad \text{on} \quad \partial\Omega \times (0,\infty), \end{cases} \tag{5.6.1}$$

where $\tilde{u} = um^{-\alpha}$ and $\tilde{v} = vm^{-\beta}$ in Ω. Using the theory of analytic semi-groups and parabolic partial differential equations, we can recast system (5.6.1) as a semi-dynamical system $\Pi[(\tilde{u}^0, \tilde{v}^0, w^0), t]$ defined on the space $C(\bar{\Omega}) \times C(\bar{\Omega}) \times C(\bar{\Omega}) = [C(\bar{\Omega})]^3$, where $\Pi[(\tilde{u}^0, \tilde{v}^0, w^0), t]$ denotes the unique solution $(\tilde{u}(x,t), \tilde{v}(x,t), w(x,t))$ to (5.6.1) such that $(\tilde{u}(x,0), \tilde{v}(x,0), w(x,0)) = (\tilde{u}^0, \tilde{v}^0, w^0)$ [6]. As we are interested in nonnegative solutions of (5.6.1), we restrict Π to the cone V of $[C(\bar{\Omega})]^3$ where each of the components of an element of V are nonnegative. Note that V is a closed subspace of $[C(\bar{\Omega})]^3$ and hence is a Banach space. Also, by the maximum principle [48], V has nonempty interior. Note that $\Pi[(\cdot,\cdot), t] : V \to V$ for any $t > 0$ is compact by Theorem 1.12 in [6].

For the remainder of this section, we fix m and parameters $\mu, \alpha, \nu, \beta, \gamma$ such that the hypotheses of Theorems 5.5.1 and 5.5.2 are satisfied. So, there exists positive numbers k and K, such that if (u, v, w) is a solution of (5.1.1) with nonnegative initial data, there exists a $T_0 > 0$ such that $k < u < K$, $k < v < K$, and $k < w < K$ in $\Omega \times [T_0, \infty)$. In light of system (5.6.1), we have $k < \tilde{u}m^\alpha < K$, $k < \tilde{v}m^\beta < K$, and $k < w < K$ in $\Omega \times [T_0, \infty)$. Because m^α and m^β are bounded above and below by positive bounds, there are positive bounds b and B such that $b < \tilde{u} < B$, $b < \tilde{v} < B$, and $b < w < B$ in $\Omega \times [T_0, \infty)$.

Define $W^* = \{f : f \in [C(\bar{\Omega})]^3, f = (f_1, f_2, f_3) \text{ where } b < f_i < B \text{ in } \Omega\}$. Clearly, W^* is a nonempty, open, bounded, and convex subset of $[C(\bar{\Omega})]^3$. Following [6], we note that the crux of our proof of the existence of a positive steady state for (5.6.1) and hence for (5.1.1) depends on showing that for any $t > 0$, $\Pi[\cdot, t]$ has a fixed point in W^*. To show this, we rely on the Asymptotic Schauder Fixed Point Theorem which we state as follows:

Theorem 5.6.1. [51] *Let G be a nonempty bounded open convex set in a Banach space X. Let the operator $A : X \to X$ be compact and suppose for some prime $p \geq 2$ we have that $A^k(\bar{G}) \subseteq G$ where $k = p, p+1$. Then A has a fixed point in G.*

Consider the following result.

Lemma 5.6.2. *Let $t^* > 0$. There exists an integer $n_0 > 0$ such that $\Pi[\bar{W}^*, nt^*] \subseteq W^*$ for all $n \geq n_0$.*

Proof. Suppose there is an increasing sequence (n_j) of positive integers and there exists an $\vec{x} \in \bar{W}^*$ such that $\Pi[\vec{x}, n_j t^*] \notin W^*$ for all n_j. Suppose we have a solution to (5.6.1) with initial data $(\tilde{u}^0, \tilde{v}^0, w^0) = \vec{x}$. Then according to our permanence result above, $\Pi[\vec{x}, t] \in W^*$ for all $t \geq t_0$ where t_0 depends on $\vec{x}$. But this contradicts our previous assumption and completes the proof. □

Note that Lemma 5.6.2 allows us to apply Theorem 5.6.1 to Π acting on $\bar{W}^*$ and hence we have shown that for any $t > 0$, $\Pi[\cdot, t]$ has a fixed point in W^*.

It follows then that system (5.6.1) has an equilibrium point in W^* (see Lemma 3.7 in [2]). By definition of W^* this point is positive in each component. It is clear then that system (5.1.1) also has a positive equilibrium and we summarize our result as follows:

Theorem 5.6.3. *Under the assumptions of Theorem* 5.5.1*,* (5.1.1) *has a positive equilibrium solution* $(u_e(x), v_e(x), w_e(x))$ *in* Ω*.*

CHAPTER 6

DISCUSSION AND FUTURE DIRECTIONS

Recalling our brief review in the introduction, we see that there are various modeling approaches to studying the evolution of dispersal. In this study we utilize reaction-diffusion-advection equations in an adaptive dynamic framework to study both the evolution of diffusion or advection alone and the evolution of both traits simultaneously. We specifically focus on the interplay between evolution and the underlying spatial variation of the environment. A fundamental aspect of this relationship was noted in [9] as the authors suggested that the results of [17] and [27] are due to the mismatch diffusion creates between the species population density at steady state and the resource. This led Cantrell et al. [9] to introduce a conditional strategy capable of perfectly matching the resource curve. As mentioned above, this special strategy is the ideal free strategy as a species using it exhibits an ideal free distribution at equilibrium.

The ideal free strategy serves as a foundation for our current study. We show that if a single resident species employs the ideal free strategy versus an invading species using an alternate strategy, the resident species will win. In adaptive dynamic language, this means that the ideal free strategy is a global evolutionarily stable strategy (ESS). Intuitively, if the resident species is able to distribute itself as to perfectly match the resource, then an invading species will have no resources and its effective growth rate will eventually be negative, leading to extinction.

The above result depends on the fact that one species is able to use an ideal free strategy (IFS). However, we can generalize this concept by searching for strategies such that two competing species at equilibrium have distributions that are ideal free. In particular we find that given any $\mu, \nu > 0$, if $\gamma e^P + \tau e^Q = m$ in Ω for some $\gamma, \tau > 0$, $(\gamma e^P, \tau e^Q)$ is a unique positive steady state of (1.3.4) such that the fitness of both species is identically equal to zero in the habitat. In other words, two species can have a combined equilibrium population that perfectly matches the resource while both species exhibit an ideal free distribution. In this case we say that two such species form an "ideal free pair". With this in mind we want to pursue the co-evolution of competing species in two directions:

- Given two species whose strategies P_1 and P_2 form an ideal free pair (P_1, P_2) as described above, if we introduce a third species with strategy P_3 such that neither (P_1, P_3) nor (P_2, P_3) form an ideal free pair, then we conjecture that species P_3 will go extinct.

- Given two resident species, each giving rise to mutant species, we ask what evolutionary trends will arise in this context? To answer this we consider the following model (an extension of (1.3.4)):

$$\begin{cases} u_t = \mu\nabla\cdot[\nabla u - u\nabla P] + u(m - u - v - \tilde{u} - \tilde{v}), & \text{in} \quad \Omega\times(0,\infty), \\ v_t = \nu\nabla\cdot[\nabla v - v\nabla Q] + v(m - u - v - \tilde{u} - \tilde{v}), & \text{in} \quad \Omega\times(0,\infty), \\ \tilde{u}_t = \mu\nabla\cdot[\nabla \tilde{u} - \tilde{u}\nabla \tilde{P}] + \tilde{u}(m - u - v - \tilde{u} - \tilde{v}), & \text{in} \quad \Omega\times(0,\infty), \\ \tilde{v}_t = \nu\nabla\cdot[\nabla \tilde{v} - \tilde{v}\nabla \tilde{Q}] + \tilde{v}(m - u - v - \tilde{u} - \tilde{v}), & \text{in} \quad \Omega\times(0,\infty), \\ [\nabla u - u\nabla P]\cdot n = [\nabla v - v\nabla Q]\cdot n = 0 \text{ on } \partial\Omega\times(0,\infty), \\ [\nabla \tilde{u} - \tilde{u}\nabla \tilde{P}]\cdot n = [\nabla \tilde{v} - \tilde{v}\nabla \tilde{Q}]\cdot n = 0 \text{ on } \partial\Omega\times(0,\infty). \end{cases}$$

Note that both these directions are interesting as they directly generalize our results as well as incorporate models which are nonmonotone.

Coming back to our present work, we consider competing species having strategies on the "same side" of the IFS. For monotone resource functions, we notice that for each point in evolutionary time, the system in general exhibits competitive exclusion. Roughly we find that the species whose strategy is closer to being ideal free will win. That is, even a species with a dispersal strategy far from being ideal will evolve towards the ideal free strategy. In this sense, we show that for monotone resource functions, the IFS is generally a CSS. However, we cannot conclude that the IFS is strictly a CSS (with respect to the two dimensional Euclidean metric) as even with linear resource curves, selection may at times drive strategies away from the IFS.

For nonmonotone resource functions, the situation is more delicate. Our work implies that there may exist nonideal free strategies which are locally evolutionarily stable and/or convergent stable [21]. More specifically, we find that for certain nonmonotone resource functions, competing species on the "same side" of the IFS can coexist. It is within this novel coexistence zone that certain nonideal free strategies may be locally superior or attractive. Moreover, these results suggest that there is probably not a general trend of dispersal strategies converging towards the IFS, rather an evolutionary path may enter a coexistence zone where multiple outcomes are possible including evolutionary branching.

This new coexistence region also provides insight as to how three species can survive together. Chris Cosner [12] recently asked if three competing species with the same population dynamics but different dispersal strategies can coexist. We answer his question in the affirmative, showing that for nonmontone resource functions, with a global maximum in Ω as well as a local maximum which is neither too large nor too small in $\bar{\Omega}$ (see assumptions (A1) and (A2)), there is a range of parameters in which three species permanence is possible. While our work provides an initial answer, we suspect there are other parameter regions (which may be quite narrow) such that a nonmonotone resource function can support three species. For a numerical example, referring to model (5.1.1), if we fix $\mu = \nu = .1$, $\alpha = .04$, $\beta = .3$, then we see for γ near .01, three species can survive. However, if we make γ too small we see that species v dies; if we make γ too large then species w dies. This type of coexistence is quite different than in Chapter 5 as species u and v display competitive coexistence having strategies on "opposite sides" of the IFS, but seem to leave enough resources for species w to persist.

Returning to the context of two competing species, we also observe competitive coexistence. We consider species with strategies on "opposite sides" of the IFS, showing that for any positive resource function such species can coexist. The significance here is that our assumption on the resource function is much more general than results from earlier studies [8, 9, 11] and our result holds in an arbitrarily large spatial dimension.

These conclusions for competing traits on the "same side" and "opposite sides" of the IFS depend on our assumption in the model (1.3.4) that both P and Q are multiples of $\ln m$ in Ω. It would be insightful to allow $P = \ln m + rR$ and $Q = \ln m + sR$ for a fixed $R \in C^2(\bar{\Omega})$ and arbitrary $r, s \in \mathbb{R}$. Thinking of R as a small perturbation, we can widen the range of possible dispersal strategies but still allow for the possibility of an IFS (when r or s is 0). Furthermore, we can preserve the referential use of the IFS by considering the signs of r and s; that is, strategies lie on "opposite sides" when r and s have different signs and strategies lie on the "same side" when both r and s have the same sign.

Finally, a direction that is of great interest concerns the inclusion of resource dynamics in a two species competition model. The difficulty here is that the resulting dynamical system is not monotone. We suggest that the permanence theory we use in order to prove the coexistence of three competing species as well as the existence of a positive steady state for the three species model, may be beneficial in addressing such models and may open the door to new methods in dealing with nonmonotone systems.

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