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Evolutionary Convergence to Ideal Free Dispersal Strategies and Coexistence

Richard Gejji, Yuan Lou, Daniel Munther, Justin Peyton

Abstract We study a two species competition model in which the species have the same population dynamics but different dispersal strategies and show how these dispersal strategies evolve. We introduce a general dispersal strategy which can result in the ideal free distributions of both competing species at equilibrium and generalize the result of Averill et al. (2011). We further investigate the convergent stability of this ideal free dispersal strategy by varying random dispersal rates, advection rates, or both of these two parameters simultaneously. For monotone resource functions, our analysis reveals that among two similar dispersal strategies, selection generally prefers the strategy which is closer to the ideal free dispersal strategy. For nonmono-tone resource functions, our findings suggest that there may exist some dispersal strategies which are not ideal free, but could be locally evolutionarily stable and/or convergent stable, and allow for the coexistence of more than one species.

1 Introduction

Organisms disperse to feed, avoid predation, breed, and reduce kin competition. While dispersal of organisms is one of the most studied concepts in ecology and evolutionary biology, the understanding of its evolution and ecological effects remain limited (Bowler and Benten 2005; Johnson and Gaines 1990; Levin et al. 2003). Studies have identified several key mechanisms in the evolution of dispersal. They include habitat extinction risks, competition among relatives, temporal and spatial variability in environment quality, costs of dispersal, and inbreeding (Dieckmann et al. 1999). To investigate how these processes affect the evolution of dispersal, a common approach is to consider one factor at a time. We will focus solely on the effect of environmental variability on the evolution of dispersal.

Many of the early studies on the evolution of dispersal concern random dispersal only. In Hastings (1983), Hastings envisioned a resident species at equilibrium with the subsequent introduction of a mutant invader. The mutant is identical to the original phenotype except for its random dispersal rate. He showed that if the environment is spatially heterogeneous but temporally constant, the mutant can invade when rare if and only if it is the slower diffuser. Along the same line, Dockery et al. (1998) studied a system of reaction diffusion equations that describes the two species dynamics of competing phenotypes, where the phenotypes differ only in their random diffusion rates. They proved that the phenotype with smaller dispersal rate will always drive the other phenotype to extinction, regardless of the initial conditions. However, by using a reaction diffusion model for two competing phenotypes and an environment that varies in space and time, Hutson et al. (2001) found the faster disperser can be selected.

Dispersal of organisms is usually nonrandom (Clobert et al. 2001; Turchin 1998) as it is often conditional upon a combination of local biotic and abiotic factors such as climate, food, predators, parasites, or conspecifics. Hastings (1983) suggested that environmental cues may have a significant effect on the dispersal strategy of a species. In this connection, Belgacem and Cosner (1995) modeled movement toward regions that are locally more favorable by adding a spatially dependent advection term to the classical logistic reaction–diffusion model for the growth of a single species. This motivated Cosner and Lou (2003) to ask "does movement toward better environments always benefit a population?" They found that increasing the advection along the gradient of the growth rate is advantageous for the persistence of the species, when the habitat is convex. However, they also showed that for some nonconvex habitats, the species may be more likely to go extinct if it increases its advection upward along the gradient of its growth rate. The underlying biological reason is that some favorable regions for certain nonconvex habitats may become less accessible when the species adopts biased movement.

Extending the works in Belgacem and Cosner (1995), Cosner and Lou (2003) from a single species to competing species, Cantrell et al. (2006, 2007), Chen et al. (2008) analyzed a reaction–diffusion-advection model for two phenotypes, with the same population dynamics but different dispersal strategies. Here, the phenotypes disperse with conditional strategies that include a combination of random dispersal and biased movement upward along the environmental gradient. In this model, coexistence is possible if the advection rate for the first species is large and the second species has no biased movement (Cantrell et al. 2007). In this case, the first species, the conditional disperser, concentrates at some (not necessarily all) of the locally most favorable locations, and the random disperser is able to use the resources in less favorable locations to coexist (Chen and Lou 2008; Lam 2011; Lam preprint; Lam and Ni 2010). When both advection rates are larger than some threshold value but one of them is much larger than the other, the larger advection rate will go extinct and "selection is against excessive advection along resource gradients, which suggests that an intermediate biased movement rate may evolve" (Chen et al. 2008).

Aiming to connect the above results, Hambrock and Lou (2009) investigated the model from Chen et al. (2008) and established two main results. First, they found that when the advection rates of both species are small and equal, and the two random diffusion rates are close, then the slower diffuser wins. This echoes Hastings' result (Hastings 1983). However, if the advection rates of both species are large and equal, and the two random diffusion rates are close, the faster diffuser wins. Thus, the magnitude of the advection rates directly affects the evolution of the random diffusion rate. Second, they set the random diffusion rates of both species equal and varied the advection rates. For this case, they showed that if two advection rates are small and close, the species with the larger advection rate drives the other species to extinction. This is consistent with results from Cantrell et al. (2006). However, if two advection rates are large and close, the species with less advection drives the other species to extinction, in agreement with the result from Chen et al. (2008).

The results of Dockery et al. (1998), Hastings (1983) suggest that the equilibrium population density distribution of a species with only random diffusion undermatches the habitat quality at the most favorable places. In contrast, the results from Cantrell et al. (2010), Chen and Lou (2008), Chen et al. (2008), Hambrock and Lou (2009), Lam and Ni (2010) show that excessive advection along the environmental gradient causes the population density distribution to over-match the habitat quality at the most favorable places. These observations led Cantrell et al. (2010) to introduce a new type of conditional dispersal strategy, allowing for the possibility that the population density distribution can match habitat quality perfectly. We call such a distribution at equilibrium an ideal free distribution (IFD) and call a corresponding dispersal strategy that allows for IFD, an ideal free dispersal strategy.

The notion of ideal free distribution originates from the theory of habitat selection. Fretwell and Lucas (1970) 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 (Fretwell and Lucas 1970). 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 paper, we adopt the IFD introduced in Cantrell et al. (2007, 2010), noting that a species at IFD has the properties that the net-movement and the local growth rate are both zero everywhere.

The main goal of this paper is to further investigate the evolution of dispersal strategies. In particular, we are interested in determining conditions for evolutionary convergence to ideal free dispersal strategies or coexistence. We introduce a generalized description of ideal free dispersal strategies where both species are at a nonzero equilibrium and neither species experiences any net-movement. We find that for a monotone resource, 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 toward 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 generally lead toward convergence to ideal free strategies. For a nonmonotone resource, we prove the existence of a new region of coexistence where the species are not at an ideal free distribution. Numerics suggest the possibility that this new region contains convergent stable strategies and evolution toward this region may lead to evolutionary branching. Finally, these results reveal the necessity for discrete patch models to include more than two patches in order to capture possible coexistence dynamics suggested by this new region of coexistence.

There are several mathematical approaches in modeling dispersal and population dynamics that incorporate discrete and continuous space and time. In this paper, we use a continuous time and continuous space (reaction–diffusion) model framework. Parallel to the development of reaction-diffusion models, there have been extensive studies on the evolution of dispersal using difference models and patch models, and we refer the reader to Doebeli and Ruxton (1997), Holt (1985), Holt and McPeek (1996), Kirkland et al. (2006), Levin et al. (1984), McPeek and Holt (1992), Padrón and Trevisan (2006), and references therein.

This paper is organized as follows: in Sect. 2, we introduce the mathematical model and discuss both evolutionary stability and convergent stability of the ideal free dispersal strategy. Section 3 is a brief summary of well-posedness and monotonicity of our model. In Sect. 4, we establish a result which generalizes previous work of Averill et al. (2011). Sections 5–8 are devoted to the proofs of the main results on the convergent stability of the ideal free dispersal strategy. Numerical confirmation and extensions of the main results are presented in Sect. 9. Finally, in Sect. 10, we discuss some potential biological applications and some future directions.

2 The Mathematical Model and Main Results

Cantrell et al. (2010) proposed the following two species competition model, in which the species are assumed to have the same population dynamics but different dispersal strategies:

$$\begin{cases} u_t = \mu \nabla \cdot [\nabla u - u \nabla P] + u(m - u - v) & \text{in } \Omega \times (0, \infty), \\ v_t = \nu \nabla \cdot [\nabla v - v \nabla Q] + v(m - u - v) & \text{in } \Omega \times (0, \infty), \\ [\nabla u - u \nabla P] \cdot n = [\nabla v - v \nabla Q] \cdot n = 0 & \text{on } \partial\Omega \times (0, \infty), \end{cases} \tag{1}$$

where Ω is a bounded domain in $\mathbb{R}^N$, $P(x)$, $Q(x)$, $m(x) \in C^2(\bar{\Omega})$, and $m(x)$ is a positive and nonconstant function which accounts for environmental heterogeneity. The functions $u(x,t)$ and $v(x,t)$ denote the density of two competing species at $x \in \Omega$ and time $t > 0$, μ and ν are their positive random diffusion coefficients, respectively, and note that $u(x,0)$ and $v(x,0)$ are nonnegative and not identically zero. $\partial\Omega$ 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 in (1) mean that there is no flux for either species across the boundary $\partial\Omega$.

2.1 Evolutionary Stability

Following (Cantrell et al. 2010), we first consider the equilibrium equation for a single species

$$\begin{aligned} &\mu\nabla\cdot[\nabla U - U\nabla P] + U(m-U) = 0 \quad \text{in } \Omega, \\ &[\nabla U - U\nabla P]\cdot n = 0 \quad \text{on } \partial\Omega. \end{aligned} \tag{2}$$

A key observation of Cantrell et al. (2010) is that $P = \ln m$ if and only if $U = m$ is a solution of (2). 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 1 *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), *is globally asymptotically stable among all nonnegative, not-identically zero initial data.*

Theorem 1 was first established by Cantrell et al. (2010) when Q is a small perturbation of $\ln m$ and $\mu = \nu$. The full generality in current form was recently given in Averill et al. (2011). In terms of the theory of Adaptive Dynamics (Dieckmann 1997, 2003; Geritz et al. 1998, 1996), the strategy $P = \ln m$ is evolutionarily stable. We say a strategy is evolutionarily stable if a population using it cannot be invaded by any small population using a different strategy. We will use the standard abbreviation ESS for “evolutionarily stable strategy”.

A natural question aries: 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) 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.

Theorem 2 *Suppose that there exist nonnegative 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), *and it is globally asymptotically stable among all positive initial data.*

Remark 2.1 When $\tau = 0$, $P - \ln m$ is constant and $Q - \ln m$ is nonconstant, Theorem 2 is reduced to Theorem 1. Hence, Theorem 2 generalizes Theorem 1.

If both $P - \ln m$ and $Q - \ln m$ are constants, Theorem 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 Convergent Stability I: Evolution of a Single Trait

Another important idea in Adaptive Dynamics is that of convergent stable strategies, which act as attractors for evolutionary dynamics. We say that a strategy is convergent stable if, roughly speaking, selection favors strategies that are closer to it over strategies that are further away. We will use the abbreviation CSS for "convergent stable strategy".

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:

$$\begin{cases} u_t = \nabla \cdot [\mu \nabla u - \alpha u \nabla \ln m] + u(m - u - v) \quad \text{in } \Omega \times (0, \infty), \\ v_t = \nabla \cdot [\nu \nabla v - \beta v \nabla \ln m] + v(m - u - v) \quad \text{in } \Omega \times (0, \infty), \\ [\mu \nabla u - \alpha u \nabla \ln m] \cdot n = [\nu \nabla v - \beta v \nabla \ln m] \cdot n = 0 \quad \text{on } \partial\Omega \times (0, \infty), \end{cases} \tag{3}$$

where α, β are two nonnegative constants that measure the speed of advection upward along the environmental gradient. Note that (1) can be reduced to (3) 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

$$\begin{cases} u_t = \nabla \cdot [\mu \nabla u - \alpha u \nabla \ln m] + u(m - u) \quad \text{in } \Omega \times (0, \infty), \\ [\mu \nabla u - \alpha u \nabla \ln m] \cdot n = 0 \quad \text{on } \partial\Omega \times (0, \infty). \end{cases} \tag{4}$$

It is well known that if $m \in C^2(\bar{\Omega})$ and is positive, then (4) has a unique positive steady state, denoted by $\theta_{\alpha,\mu}$, for every $\alpha \geq 0$ and $\mu > 0$. Therefore, (3) has exactly two semitrivial steady states, denoted as $(\theta_{\alpha,\mu}, 0)$ and $(0, \theta_{\beta,\nu})$, respectively.

We begin with a result on the global dynamics of (3).

Theorem 3 *Let $m \in C^2(\bar{\Omega})$ such that $m > 0$, $m \not\equiv$ constant, and suppose that $\frac{\alpha}{\mu} = \frac{\beta}{\nu} \neq 1$. 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 is reduced to the findings in Dockery et al. (1998), Hastings (1983). 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 Dockery et al. (1998), Hastings (1983) by showing that selection favors the slower diffuser when $\alpha/\mu = \beta/\nu$. Hence, Theorem 3 implies that zero dispersal rate is a convergent stable strategy along the line $\alpha/\mu = \beta/\nu$.

Remark 2.2 When $\frac{\alpha}{\mu} = \frac{\beta}{\nu} = 1$, Theorem 3 does not hold as (3) has a continuum of positive coexistent states $(sm, (1-s)m)$ for every $0 < s < 1$ and for any μ, ν. Biologically, the assumption $\frac{\alpha}{\mu} = \frac{\beta}{\nu} = 1$ means that both species u and v are using ideal free dispersal strategies and will thus coexist.

Theorem 3 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 4 *Suppose* $m, m_x > 0$ *on* $\bar{\Omega} = [0,1]$, *and* $\alpha = \beta$.

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

Theorem 4 is motivated by Hambrock and Lou (2009), where a similar result is established for the model (3) with $P = Q = m$. It is an open question whether part (ii) holds for any $\alpha > \mu$.

Theorem 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 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. As another example of selection favoring strategies closer to the ideal free strategy, we restate Theorem 2 of Cantrell et al. (2010) in the framework of model (3), as follows.

Theorem 5 (Theorem 2 in Cantrell et al. (2010)) *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 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.

If we relax the monotonicity assumption on m, then the first part of Theorem 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. Similar to Theorem 6 of Averill et al. (2011), we have the following result.

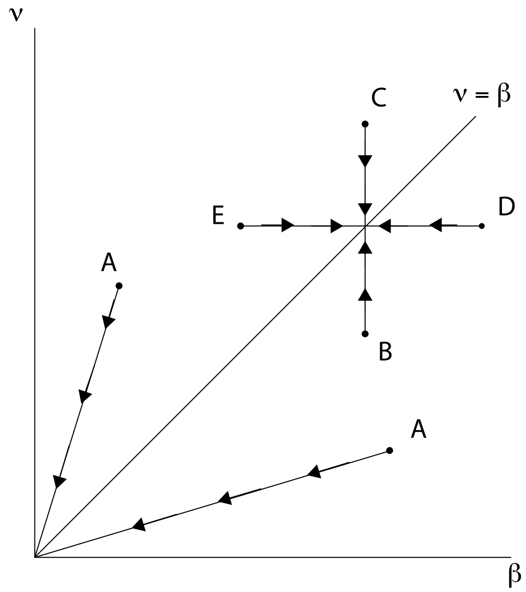


Fig. 1 Illustration of Theorems 3, 4, 5. Each dot represents a resident with strategy (α, μ) and evolution is directed by the arrows. (**A**) illustrates Theorem 3. (**B**) and (**C**) illustrate Theorem 4. (**D**) and (**E**) illustrate Theorem 5. Note that selection drives each resident along its respective path towards the ideal free dispersal strategy (shown as the line $\nu = \beta$)

Theorem 6 *Suppose that all critical points of m are nondegenerate and*

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

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

Then there exists $\mu_0 > 0$ *such that for each* $\mu > \mu_0$, *we can find some* $\delta > 0$ *small such that if* $1 < \frac{\alpha}{\mu} < 1 + \delta$, *and given any* $\nu > 0$, *both* $(\theta_{\alpha,\mu}, 0)$ *and* $(0, \theta_{\beta,\nu})$ *are unstable for large enough* $\beta > 0$. *Moreover,* (3) *has at least one stable positive steady state.*

Remark 2.3 Note that we can assume that $\mu = \nu$ in Theorem 6. 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 locally evolutionarily stable and/or convergent stable.

Assuming that a one-dimensional trait is represented by a real parameter, then Theorems 3, 4, and 5 are in essence results concerning the evolution of one trait. These results can be summarized in Fig. 1.

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, and 5? This question prompts us to consider varying both random diffusion and advection simultaneously. Our results are shown in the next subsection.

2.3 Convergent Stability II: 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

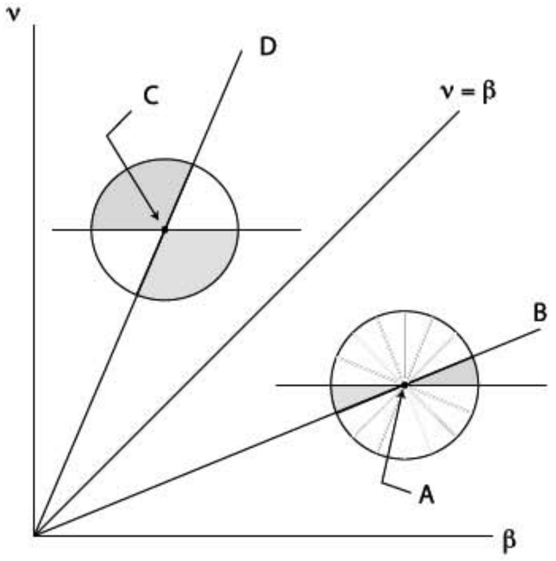


Fig. 2 (Color online) Illustration of Theorem 7. Part (i): Point (A) represents resident with strategy (α, μ), centering the ball B_ϵ. An invader with strategy (β, ν) located in the *blue region* wins over strategy (A). However, an invader with strategy in the *green region* loses to (A). Line B has slope $\frac{\mu}{\alpha}$ 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

trait parameters, we can make the problem more biologically realistic and can refer to the variation of two parameters as the evolution of two traits.

In this section, we use the model (3) 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 7 *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* $\alpha > \mu$, $(\beta, \nu) \in \{(\beta, \nu) : \nu \leq \mu, \frac{\nu}{\beta} \geq \frac{\mu}{\alpha}\} \cap B_\epsilon(\alpha, \mu)$, *then* $(0, \theta_{\beta,\nu})$ *is globally asymptotically stable*; *if* $(\beta, \nu) \in \{(\beta, \nu) : \nu \geq \mu, \frac{\nu}{\beta} \leq \frac{\mu}{\alpha}\} \cap B_\epsilon(\alpha, \mu)$, *then* $(\theta_{\alpha,\mu}, 0)$ *is globally asymptotically stable.*

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

Theorem 7 provides limited regions where we can conclude whether or not a semitrivial steady state is globally asymptotically stable; see Fig. 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 semitrivial steady states of (3). 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 Sect. 9 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 Fig. 2. We consider linear m in the next result.

Theorem 8 *Suppose that m is linear, nonconstant and positive on* $[0, 1]$. *Given any* $\alpha, \mu > 0$, *there exists some* $\epsilon > 0$ *small such that*

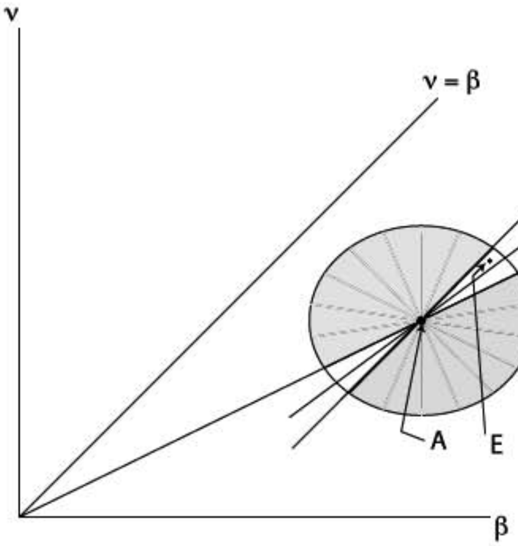


Fig. 3 (Color online) Illustration of Theorem 8, part (i). Point (A) represents resident with strategy (α, μ), centering the ball B_ϵ. Line B is parallel to the line $\nu = \beta$ (the ideal free dispersal strategy). Line C represents the line formed when $\lambda^* = 0$ (refer to parameterization in (16)). 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)

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

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

This result is succinctly illustrated in Fig. 3. Note that for part (ii) of Theorem 8, the picture is symmetric with respect to the line $\nu = \beta$.

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, note that the blue and green regions can be arbitrarily close to the line C (see the full generality of Theorem 8 in Sect. 8). 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 Fig. 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 $0 \leq s \leq 1$, define curves

$$\begin{aligned}
\Gamma_- &:= \big\{\big(x(s), y(s)\big) : 0 < y(s) < x(s), \quad 0 \leq s < 1,\ x(1) = y(1)\big\}, \\
\Gamma_+ &:= \big\{\big(x(s), y(s)\big) : 0 < x(s) < y(s), \quad 0 \leq s < 1,\ x(1) = y(1)\big\}.
\end{aligned} \tag{5}$$

We say that Γ_- or Γ_+ is a *convergent stable path* if for any $0 \leq s < 1$, there exists $\delta > 0$ small enough such that for any $0 < \Delta s < \delta$, the semitrivial steady state $(0, \theta_{\beta,\nu})$ of system (3) 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 9 *Suppose that* m *is linear, nonconstant, 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* $\frac{y(s)}{x(s)}$ *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* $\frac{y(s)}{x(s)}$ *are monotonically increasing functions for* $s \in [0, 1)$, *then* Γ_- *is a convergent stable path.*

Referring to Fig. 3, Theorem 9 says that a path will be convergent stable as long as it stays within the blue cone formed by the lines $\frac{\nu}{\beta} = \frac{\mu}{\alpha}$ and $\nu - \mu = \beta - \alpha$. Essentially, this means that the path stays in the blue region as it progresses toward the line $\beta = \nu$.

3 Well-Posedness and Monotonicity of (1)

Concerning the positivity of solutions of (1), we note that by the maximum principle (Protter and Weinberger 1984), if we assume initial data $u(x, 0)$ and $v(x, 0)$ are nonnegative and not identically zero, then $u(x, t), v(x, t) > 0$ for every $x \in \Omega$ and every $t > 0$. Also, using standard parabolic theory (Henry 1981), it is well known that (1) has a unique classical solution (u, v) which exists for all $t > 0$. In particular, as we are concerned with the global dynamics of (3), our analysis depends a great deal on its nonnegative steady states, which are nonnegative solutions of

$$\begin{cases} \nabla \cdot [\mu \nabla u - \alpha u \nabla \ln m] + u(m - u - v) = 0, & \text{in } \Omega, \\ \nabla \cdot [\nu \nabla v - \beta v \nabla \ln m] + v(m - u - v) = 0, & \text{in } \Omega, \\ [\mu \nabla u - \alpha u \nabla \ln m] \cdot n = [\nu \nabla v - \beta v \nabla \ln m] \cdot n = 0 & \text{on } \partial\Omega. \end{cases} \tag{6}$$

We mention two results that will help us in determining the global dynamics of (1). First, we note that (1) defines a smooth dynamical system on $C(\bar{\Omega}) \times C(\bar{\Omega})$ (see Smith 1995). Furthermore, as the following result indicates, this system is a strongly monotone dynamical system.

Theorem 10 *The system* (1) *is a strongly monotone dynamical system, that is*;

(i) $u_1(x, 0) \geq u_2(x, 0)$ *and* $v_1(x, 0) \leq v_2(x, 0)$ *for all* $x \in \Omega$ *and*
(ii) $(u_1(x, 0), v_1(x, 0)) \neq (u_2(x, 0), v_2(x, 0))$ *imply that* $u_1(x, t) > u_2(x, t)$ *and* $v_1(x, t) < v_2(x, t)$ *for all* $x \in \bar{\Omega}$ *and* $t > 0$.

For a proof of Theorem 10, see Theorem 3 in Cantrell et al. (2010). Theorem 10 as well as monotone dynamical system theory (Hess 1991; Smith 1995) imply the following result.

Theorem 11 (i) *If system* (1) *has no coexistence state, then one of the semitrivial steady states is unstable and the other one is globally asymptotically stable* (Hsu et al. 1996);

(ii) *If both semitrivial steady states are unstable, then* (1) *has at least one stable coexistence state* (Dancer 1995; Matano 1984); *Furthermore, if* (1) *has a unique positive steady state, then it is globally asymptotically stable.*

4 Proof of Theorem 2

By Remark 2.1, it suffices to consider the case when $\gamma > 0$ and $\tau > 0$. To prove Theorem 2, we first prove the following result.

Lemma 4.1 *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) *has a unique positive steady state.*

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

$$\begin{cases} \mu\nabla \cdot \big[\nabla u^* - u^*\nabla P\big] + u^*\big(m(x) - u^* - v^*\big) = 0, \\ \nu\nabla \cdot \big[\nabla v^* - v^*\nabla Q\big] + v^*\big(m(x) - u^* - v^*\big) = 0, \\ \big[\nabla u^* - u^*\nabla P\big]\cdot n = \big[\nabla v^* - v^*\nabla Q\big]\cdot n|_{\partial\Omega} = 0. \end{cases} \tag{7}$$

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

$$\int_\Omega (u^* + v^*)(m - u^* - v^*) = 0. \tag{8}$$

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

$$\mu\int_\Omega \frac{e^{3P}}{(u^*)^2}\left|\nabla\frac{u^*}{e^P}\right|^2 + \int_\Omega e^P(m - u^* - v^*) = 0. \tag{9}$$

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

$$\nu\int_\Omega \frac{e^{3Q}}{(v^*)^2}\left|\nabla\frac{v^*}{e^Q}\right|^2 + \int_\Omega e^Q(m - u^* - v^*) = 0. \tag{10}$$

Multiplying (9) by γ and (10) by τ, and using $\gamma e^P + \tau e^Q \equiv m$, we have

$$\gamma\mu\int_\Omega \frac{e^{3P}}{(u^*)^2}\left|\nabla\frac{u^*}{e^P}\right|^2 + \tau\nu\int_\Omega \frac{e^{3Q}}{(v^*)^2}\left|\nabla\frac{v^*}{e^Q}\right|^2 + \int_\Omega m(m - u^* - v^*) = 0. \tag{11}$$

By (8) and (11), we have

$$\gamma\mu\int_\Omega \frac{e^{3P}}{(u^*)^2}\left|\nabla\frac{u^*}{e^P}\right|^2 + \tau\nu\int_\Omega \frac{e^{3Q}}{(v^*)^2}\left|\nabla\frac{v^*}{e^Q}\right|^2 + \int_\Omega (m - u^* - v^*)^2 = 0. \tag{12}$$

From (12), 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 4.2 *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 both semitrivial 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

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

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

$$-\lambda \int_\Omega e^Q = \nu \int_\Omega \frac{e^{3Q}}{\psi^2} \left| \nabla \frac{\psi}{e^Q} \right|^2 + \int_\Omega e^Q (m - \tilde{u}). \tag{13}$$

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

$$0 = \mu \int_\Omega \frac{e^{3P}}{\tilde{u}^2} \left| \nabla \frac{\tilde{u}}{e^P} \right|^2 + \int_\Omega e^P (m - \tilde{u}). \tag{14}$$

Multiplying (13) by τ and (14) 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, $\lambda \le 0$. 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 $Q - \ln m$ is also equal to some constant. Hence, both $P - \ln m$ and $Q - \ln m$ 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 follows from the previous two lemmas and Theorem 11.

5 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 5.1 *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^*:*

$$\begin{cases} \nabla \cdot [\nu \nabla \varphi - \beta \varphi \nabla \ln m] + \varphi(m - \theta_{\alpha,\mu}) = -\lambda \varphi \quad \text{in } \Omega, \\ [\nu \nabla \varphi - \beta \varphi \nabla \ln m] \cdot n = 0 \quad \text{on } \partial\Omega, \quad \varphi > 0 \quad \text{on } \bar{\Omega}. \end{cases} \tag{15}$$

The proof of Lemma 5.1 is similar to that of Lemma 5.5 in Chen and Lou (2008). Consider the following parameterizations:

$$\nu = \mu + \delta, \qquad \beta = \alpha + \epsilon, \tag{16}$$

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 Belgacem 1997). 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 (15), we see that φ_1 and φ_2 are determined by

$$\begin{cases} \nabla \cdot [\mu \nabla \varphi_1 - \alpha \varphi_1 \nabla \ln m - \theta_{\alpha,\mu} \nabla \ln m] + (m - \theta_{\alpha,\mu})\varphi_1 = -\lambda_1 \theta_{\alpha,\mu} \quad \text{in } \Omega, \\ [\mu \nabla \varphi_1 - \alpha \varphi_1 \nabla \ln m - \theta_{\alpha,\mu} \nabla \ln m] \cdot n = 0 \quad \text{on } \partial\Omega, \end{cases} \tag{17}$$

and

$$\begin{cases} \nabla \cdot [\mu \nabla \varphi_2 - \alpha \varphi_2 \nabla \ln m + \nabla \theta_{\alpha,\mu}] + (m - \theta_{\alpha,\mu})\varphi_2 = -\lambda_2 \theta_{\alpha,\mu} \quad \text{in } \Omega, \\ [\mu \nabla \varphi_2 - \alpha \varphi_2 \nabla \ln m + \nabla \theta_{\alpha,\mu}] \cdot n = 0 \quad \text{on } \partial\Omega. \end{cases} \tag{18}$$

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

Theorem 12 *λ_1 satisfies*

$$\lambda_1 \int_\Omega e^{-\alpha/\mu \ln m} \theta_{\alpha,\mu}^2 = -\int_\Omega \nabla\left(e^{-\alpha/\mu \ln m} \theta_{\alpha,\mu}\right) \cdot \theta_{\alpha,\mu} \nabla \ln m, \tag{19}$$

and λ_2 *satisfies*

$$\lambda_2 \int_{\Omega} e^{-\alpha/\mu \ln m} \theta_{\alpha,\mu}^2 = \int_{\Omega} \nabla\big(e^{-\alpha/\mu \ln m} \theta_{\alpha,\mu}\big) \cdot \nabla \theta_{\alpha,\mu}. \tag{20}$$

Proof If we multiply (17) by $e^{-\alpha/\mu \ln m}\theta_{\alpha,\mu}$, integrate the result over Ω and use the boundary condition for φ_1, we get

$$\begin{aligned} &-\int_{\Omega} \nabla\big(e^{-\alpha/\mu \ln m}\theta_{\alpha,\mu}\big) \cdot (\mu \nabla \varphi_1 - \alpha \varphi_1 \nabla \ln m - \theta_{\alpha,\mu} \nabla \ln m) \\ &\quad + \int_{\Omega} e^{-\alpha/\mu \ln m} \theta_{\alpha,\mu} (m - \theta_{\alpha,\mu}) \varphi_1 = -\lambda_1 \int_{\Omega} e^{-\alpha/\mu \ln m} \theta_{\alpha,\mu}^2. \end{aligned} \tag{21}$$

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

$$\begin{aligned} &-\int_{\Omega} \nabla\big(e^{-\alpha/\mu \ln m}\varphi_1\big) \cdot (\mu \nabla \theta_{\alpha,\mu} - \alpha \theta_{\alpha,\mu} \nabla \ln m) \\ &\quad + \int_{\Omega} e^{-\alpha/\mu \ln m} \theta_{\alpha,\mu} (m - \theta_{\alpha,\mu}) \varphi_1 = 0. \end{aligned} \tag{22}$$

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

$$\begin{aligned} &\int_{\Omega} \nabla\big(e^{-\alpha/\mu \ln m}\theta_{\alpha,\mu}\big) \cdot (\mu \nabla \varphi_1 - \alpha \varphi_1 \nabla \ln m) \\ &\quad = \int_{\Omega} e^{-\alpha/\mu \ln m} \left(\nabla \theta_{\alpha,\mu} - \frac{\alpha}{\mu} \theta_{\alpha,\mu} \nabla \ln m\right) \cdot (\mu \nabla \varphi_1 - \alpha \varphi_1 \nabla \ln m). \end{aligned} \tag{23}$$

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

$$\begin{aligned} &\int_{\Omega} \nabla\big(e^{-\alpha/\mu \ln m}\varphi_1\big) \cdot (\mu \nabla \theta_{\alpha,\mu} - \alpha \theta_{\alpha,\mu} \nabla \ln m) \\ &\quad = \int_{\Omega} e^{-\alpha/\mu \ln m} \left(\nabla \theta_{\alpha,\mu} - \frac{\alpha}{\mu} \theta_{\alpha,\mu} \nabla \ln m\right) \cdot (\mu \nabla \varphi_1 - \alpha \varphi_1 \nabla \ln m). \end{aligned} \tag{24}$$

Now, subtracting (21) from (22) and using (23) and (24), we obtain our result for λ_1. Similarly, we can find the expression for λ_2, performing the same procedure as above. □

Remark 5.1 We can rewrite the parameterizations in (16) 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 semitrivial steady state, $(0, \theta_{\beta,\nu})$. Similar to Lemma 5.1, we have the following.

Lemma 5.2 *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^*:

$$\begin{cases} \nabla \cdot [\mu \nabla \varphi - \alpha \varphi \nabla \ln m] + \varphi(m - \theta_{\beta,\nu}) = -\eta \varphi \quad \text{in } \Omega, \\ [\mu \nabla \varphi - \alpha \varphi \nabla \ln m] \cdot n = 0 \quad \text{on } \partial\Omega, \quad \varphi > 0 \quad \text{on } \bar{\Omega}. \end{cases} \tag{25}$$

Performing similar analysis as above and using the parameterization in Remark 5.1, we see that $\eta^* = \eta_1 r \cos\phi + \eta_2 r \sin\phi + O(r^2)$, where η_1 and η_2 satisfy

$$\eta_1 \int_\Omega e^{-\alpha/\mu \ln m} \theta_{\alpha,\mu}^2 = \int_\Omega \nabla\left(e^{-\alpha/\mu \ln m} \theta_{\alpha,\mu}\right) \cdot \theta_{\alpha,\mu} \nabla \ln m, \tag{26}$$

$$\eta_2 \int_\Omega e^{-\alpha/\mu \ln m} \theta_{\alpha,\mu}^2 = -\int_\Omega \nabla\left(e^{-\alpha/\mu \ln m} \theta_{\alpha,\mu}\right) \cdot \nabla \theta_{\alpha,\mu}. \tag{27}$$

6 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

$$\begin{cases} [\mu(\theta_{\alpha,\mu})_x - \alpha \theta_{\alpha,\mu} \frac{m_x}{m}]_x + \theta_{\alpha,\mu}[m - \theta_{\alpha,\mu}] = 0, \quad 0 < x < 1, \\ \mu(\theta_{\alpha,\mu})_x - \alpha \theta_{\alpha,\mu} \frac{m_x}{m} = 0 \quad \text{at } x = 0, 1. \end{cases} \tag{28}$$

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 6.1 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 6.1 *If* $\alpha < \mu$, *then* $\mu(\theta_{\alpha,\mu})_x - \alpha \frac{m_x}{m} \theta_{\alpha,\mu} > 0$ *on* $(0, 1)$. *In particular,* $(\theta_{\alpha,\mu})_x > 0$ *on* $[0, 1]$.

Proof Suppose that f is a solution of

$$\begin{cases} f_{xx} + b(x) f_x + \gamma(x) f[\kappa(x) - f] = 0, \quad x \in (0, 1), \\ f_x(0) = f_x(1) = 0, \quad f > 0 \quad \text{in } [0, 1], \end{cases} \tag{29}$$

where $b, \gamma \in C[0, 1]$, $\kappa \in C^1[0, 1]$, and $\gamma, \kappa > 0$ in $[0, 1]$. Lemma 2.1 of Cantrell et al. (2010) says that if $\kappa_x > 0$ in $[0, 1]$, then $f_x > 0$ in $(0, 1)$. Let $f = e^{-(\alpha/\mu)\ln m} \theta_{\alpha,\mu}$,

$b(x) = \frac{\alpha}{\mu}(\frac{m_x}{m})$, $\gamma(x) = \frac{1}{\mu}e^{(\alpha/\mu)\ln m}$, and $\kappa(x) = me^{-(\alpha/\mu)\ln m}$. Thus, we see that f satisfies (29). If $m_x > 0$ on $[0, 1]$, the sign of $\kappa_x = m_x e^{-(\alpha/\mu)\ln m}(1 - \frac{\alpha}{\mu})$ depends on the size of $\frac{\alpha}{\mu}$. So, if $\alpha < \mu$, we see that $\kappa_x > 0$, and hence $f_x > 0$. Notice that $f_x = e^{(-\alpha/\mu)\ln m}((\theta_{\alpha,\mu})_x - \frac{\alpha}{\mu}\frac{m_x}{m}\theta_{\alpha,\mu})$. Hence, we have our result. □

Lemma 6.2 *If* $\alpha > \mu$, *then* $\mu(\theta_{\alpha,\mu})_x - \alpha\frac{m_x}{m}\theta_{\alpha,\mu} < 0$ *on* $(0, 1)$.

Proof Lemma 2.1 of Cantrell et al. (2010) shows that if $\kappa_x < 0$ in $[0, 1]$, then $f_x < 0$ in $(0, 1)$. Using the same proof as in Lemma 6.1 and since we are assuming that $\alpha > \mu$, we have $\kappa_x < 0$ in $[0, 1]$ and thus we obtain our result. □

Lemma 6.3 *If* $\alpha < \mu$, *then* $m(0) < \theta_{\alpha,\mu}(0)$ *and* $m(1) > \theta_{\alpha,\mu}(1)$.

Proof Using Lemma 6.1 and the boundary conditions for $\theta_{\alpha,\mu}$, we see that $[\mu(\theta_{\alpha,\mu})_x - \alpha\frac{m_x}{m}\theta_{\alpha,\mu}]_x \geq 0$ at $x = 0$ and that $[\mu(\theta_{\alpha,\mu})_x - \alpha\frac{m_x}{m}\theta_{\alpha,\mu}]_x \leq 0$ at $x = 1$. Thus, by (28), 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 (28) 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 (28) gives us that $[\mu(\theta_{\alpha,\mu})_x - \alpha\frac{m_x}{m}\theta_{\alpha,\mu}]_x < 0$ on $(0, \delta)$. Thus, $\mu(\theta_{\alpha,\mu})_x - \alpha\frac{m_x}{m}\theta_{\alpha,\mu} < 0$ on $(0, \delta)$. But this contradicts Lemma 6.1. Hence, $m(0) > \theta_{\alpha,\mu}(0)$. Similar analysis shows strict inequality at $x = 1$ as well. □

Lemma 6.4 *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 6.3. □

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 6.5.

Lemma 6.5 *Suppose* $m_x > 0$ *in* $[0, 1]$ *and* $\alpha \geq \frac{\int_0^1 m}{\min_{[0,1]}(m_x/m)}$. *Then* $(\theta_{\alpha,\mu})_x > 0$ *on* $[0, 1]$.

Proof Let $y \in [0, 1]$ be the smallest number such that $(\theta_{\alpha,\mu})_x(y) \leq 0$. 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

$$\alpha\theta_{\alpha,\mu}(y)\frac{m_x(y)}{m(y)} = \int_0^y \theta_{\alpha,\mu}(m - \theta_{\alpha,\mu}) \leq \int_0^y \theta_{\alpha,\mu}m < \theta_{\alpha,\mu}(y)\int_0^1 m. \tag{30}$$

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

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 Fig. 5). Hence, we consider a linear resource function. Without loss of generality, assume that $\mu = 1$.

Lemma 6.6 *Assuming $\alpha \neq 1$ and m is linear, if $\theta_{\alpha,1}(\bar{x}) = m(\bar{x})$ for some $\bar{x} \in [0, 1]$, then $(\theta_{\alpha,\mu})_x(\bar{x}) \neq m_x(\bar{x})$.*

Proof Without loss of generality, assume that $\mu = 1$. Set $w = \frac{\theta_{\alpha,1}}{m}$. 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 $w_x(\bar{x}) \neq 0$. Note that w satisfies (since m is linear)

$$\begin{cases} w_{xx} + (2-\alpha)\frac{m_x}{m} w_x + mw(1-w) = 0, & 0 < x < 1, \\ w_x + (1-\alpha)(\frac{m_x}{m})w = 0 & x = 0, 1. \end{cases} \tag{31}$$

Note that if $\bar{x} = 0$ or 1, by the boundary condition of (31), $w_x \neq 0$. So, consider $\bar{x} \in (0, 1)$. Suppose that $w_x(\bar{x}) = 0$ and consider the following linear initial value problem:

$$\begin{cases} \phi_{xx} + (2-\alpha)\frac{m_x}{m}\phi_x - mw\phi = 0, & 0 < x < 1, \\ \phi_x(\bar{x}) = \phi(\bar{x}) = 0. \end{cases} \tag{32}$$

We see that $\phi \equiv 0$ is a solution to (32) 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 (32). 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 (31) so $w_x(0) \neq 0$ and $w_x(1) \neq 0$. This is a contradiction. □

Theorem 13 *Suppose m is linear, $m_x > 0$ in $[0, 1]$, and $\alpha > \mu$. Then $(\frac{\theta_{\alpha,1}}{m})_x > 0$ in $[0, 1]$.*

Proof Without loss of generality, assume that $\mu = 1$. First, we note that by Lemma 6.4, 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 6.6, we see that $(\frac{\theta_{\alpha,1}}{m})_x(x_1) > 0$. We claim that $(\frac{\theta_{\alpha,1}}{m})_x > 0$ on $(0, x_1)$. If not, there exists some $x_2 \in (0, x_1)$ such that $(\frac{\theta_{\alpha,1}}{m})_x > 0$ on (x_2, x_1) and $(\frac{\theta_{\alpha,1}}{m})_x(x_2) = 0$. Put $w = \frac{\theta_{\alpha,1}}{m}$. Note that $w_{xx}(x_2) \geq 0$. However, upon evaluating (31) 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 $(\frac{\theta_{\alpha,1}}{m})_x > 0$ 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

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

This is clearly a contradiction, so it must be the case that $w > 1$ on $(x_1, y]$. Note that $w_{xx}(y) \le 0$. On the other hand, if we evaluate (31) 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 6.7 *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 13, $(\frac{\theta_{\alpha,1}}{m})_x > 0$ 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 14 *Suppose* m *is linear,* $m_x > 0$ *in* $[0, 1]$, *and* $\alpha < \mu$. *Then* $(\frac{\theta_{\alpha,\mu}}{m})_x < 0$ *in* $[0, 1]$.

Proof Without loss of generality, assume that $\mu = 1$. First, we note that by Lemma 6.3, 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, $m_x(x_1) \ge (\theta_{\alpha,1})_x(x_1)$. Let $w = \frac{\theta_{\alpha,1}}{m}$ as before. By Lemma 6.6, 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 $w_{xx}(x_2) \le 0$. If, however, we evaluate (31) 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

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

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 (31) 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. □

7 Nonexistence of Positive Steady-States

In this section, we show that under specific conditions, system (6) has no positive steady states. Before stating and proving the result, we present several useful lemmas.

Lemma 7.1 *Suppose that* (u, v) *is a positive solution of* (6). *Then*

$$\begin{aligned}\int_\Omega \big[\mu e^{\alpha/\mu \ln m} - \nu e^{\beta/\nu \ln m}\big]\nabla\big(e^{-\alpha/\mu \ln m}u\big)\cdot\nabla\big(e^{-\beta/\nu \ln m}v\big)\\ = \int_\Omega \big[e^{-\alpha/\mu \ln m} - e^{-\beta/\nu \ln m}\big]uv(m-u-v).\end{aligned} \tag{33}$$

Proof Note that we can rewrite (6) as

$$\begin{cases}\mu\nabla\cdot[e^{\alpha/\mu \ln m}\nabla(e^{-\alpha/\mu \ln m}u)] + u(m-u-v) = 0, & x \in \Omega,\\ \nu\nabla\cdot[e^{\beta/\nu \ln m}\nabla(e^{-\beta/\nu \ln m}v)] + v(m-u-v) = 0, & x \in \Omega,\\ \nabla(e^{-\alpha/\mu \ln m}u)\cdot n = \nabla(e^{-\beta/\nu \ln m}v)\cdot n = 0, & x \in \partial\Omega.\end{cases} \tag{34}$$

If we multiply the equation for u in (34) by $e^{-\beta/\nu \ln m}v$, integrate over [0, 1] and use the boundary condition, we find that

$$\mu\int_\Omega e^{\alpha/\mu \ln m}\nabla\big(e^{-\beta/\nu \ln m}v\big)\cdot\nabla\big(e^{-\alpha/\mu \ln m}u\big) = \int_\Omega e^{-\beta/\nu \ln m}uv(m-u-v). \tag{35}$$

Also, if we multiply the equation for v in (34) by $e^{-\alpha/\mu \ln m}u$, integrate over Ω and use the boundary condition, we have

$$\nu\int_\Omega e^{\beta/\nu \ln m}\nabla\big(e^{-\beta/\nu \ln m}v\big)\cdot\nabla\big(e^{-\alpha/\mu \ln m}u\big) = \int_\Omega e^{-\alpha/\mu \ln m}uv(m-u-v). \tag{36}$$

Now, subtracting (35) from (36), we obtain the result. □

Using the polar parameterizations for ν and β, as discussed in Sect. 5, and Taylor expansions, we have the two following results.

Lemma 7.2 *For* $0 < r \ll 1$,

$$\mu e^{\frac{\alpha}{\mu}\ln m} - \nu e^{\frac{\beta}{\nu}\ln m} = e^{\frac{\alpha}{\mu}\ln m} r\left[\ln m\left(\frac{\alpha}{\mu}\sin\phi - \cos\phi\right) - \sin\phi\right] + O\big(r^2\big). \tag{37}$$

Lemma 7.3 *For* $0 < r \ll 1$,

$$e^{-\frac{\beta}{\nu}\ln m} - e^{-\frac{\alpha}{\mu}\ln m} = e^{-\frac{\alpha}{\mu}\ln m} r\left[\ln m\left(\frac{\alpha\sin\phi}{\mu^2} - \frac{\cos\phi}{\mu}\right)\right] + O\big(r^2\big). \tag{38}$$

Next we have

Lemma 7.4 *Suppose* (u, v) *is a positive solution of* (6). *Let the parameterization of* β *and* ν *be given as in Sect.* 5. *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 $\gamma \in (0, 1)$ (Gilbarg and Trudinger 1983). 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

$$\begin{cases} \nabla\cdot[\mu\nabla\hat{u} - \alpha\hat{u}\nabla\ln m] + \hat{u}(m - \hat{u} - \hat{v}) = 0, & x \in \Omega, \\ \nabla\cdot[\mu\nabla\hat{v} - \alpha\hat{v}\nabla\ln m] + \hat{v}(m - \hat{u} - \hat{v}) = 0, & x \in \Omega, \\ [\mu\nabla\hat{u} - \alpha\hat{u}\nabla\ln m]\cdot n = [\mu\nabla\hat{v} - \alpha\hat{v}\nabla\ln m]\cdot n = 0, & x \in \partial\Omega. \end{cases} \tag{39}$$

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

$$\begin{cases} \nabla\cdot[\mu\nabla(\hat{u} + \hat{v}) - \alpha(\hat{u} + \hat{v})\nabla\ln m] + (\hat{u} + \hat{v})[m - (\hat{u} + \hat{v})] = 0 & x \in \Omega, \\ [\mu\nabla(\hat{u} + \hat{v}) - \alpha(\hat{u} + \hat{v})\nabla\ln m]\cdot n = 0, & x \in \partial\Omega. \end{cases} \tag{40}$$

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 $\int_\Omega u(m - u - v) = 0$, which is a contradiction. Thus, it must be the case that $\hat{u} + \hat{v} = \theta_{\alpha,\mu}$. Therefore, $(\hat{u}, \hat{v})$ satisfies

$$\begin{cases} \nabla\cdot[\mu\nabla\hat{u} - \alpha\hat{u}\nabla\ln m] + \hat{u}(m - \theta_{\alpha,\mu}) = 0, & x \in \Omega, \\ \nabla\cdot[\mu\nabla\hat{v} - \alpha\hat{v}\nabla\ln m] + \hat{v}(m - \theta_{\alpha,\mu}) = 0, & x \in \Omega, \\ [\mu\nabla\hat{u} - \alpha\hat{u}\nabla\ln m]\cdot n = [\mu\nabla\hat{v} - \alpha\hat{v}\nabla\ln m]\cdot n = 0, & x \in \partial\Omega. \end{cases} \tag{41}$$

Since $\hat{u}$ is nonnegative, 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 nonnegative constant τ. Since $\hat{u} + \hat{v} = \theta_{\alpha,\mu}$, we see that $s + \tau = 1$. Therefore, $s \in [0, 1]$. □

Lemma 7.5 *Let* (u, v) *be any positive solution of* (6) *with* (β, ν) *parameterized as in Sect.* 5. *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 equation of u in (6) by $\|u\|_\infty$ to get

$$\begin{cases} \nabla \cdot [\mu \nabla(u/\|u\|_\infty) - \alpha(u/\|u\|_\infty)\nabla \ln m] \\ \quad + (u/\|u\|_\infty)[m - u - v] = 0, \quad x \in \Omega, \\ [\mu \nabla(u/\|u\|_\infty) - \alpha(u/||u||_\infty)\nabla \ln m] \cdot n|_{\partial\Omega} = 0. \end{cases} \tag{42}$$

By elliptic regularity and Sobolev embedding theorem (Gilbarg and Trudinger 1983), 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

$$\begin{cases} \nabla \cdot [\mu \nabla f - \alpha f \nabla \ln m] + f[m - \theta_{\alpha,\mu}] = 0, \quad x \in \Omega, \\ [\mu \nabla f - \alpha f \nabla \ln m] \cdot n|_{\partial\Omega} = 0. \end{cases} \tag{43}$$

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 7.6 *Let* (u, v) *be any positive solution of* (6) *with* (β, ν) *parameterized as in Sect.* 5. *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 15 *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*

$$\begin{aligned} &-\cos\phi \int_\Omega \theta_{\alpha,\mu} \nabla(e^{-\alpha/\mu \ln m}\theta_{\alpha,\mu}) \cdot \nabla \ln m \\ &\quad + \sin\phi \int_\Omega \nabla(e^{-\alpha/\mu \ln m}\theta_{\alpha,\mu}) \cdot \nabla\theta_{\alpha,\mu} \neq 0. \end{aligned} \tag{44}$$

Then for $0 < r \ll 1$, *system* (6) *has no positive solutions.*

Proof Suppose we have a positive solution (u, v) for every $0 < r \ll 1$. If we let $r \to 0$, from Lemmas 7.4, 7.5, and 7.6 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 (33). By the expansions from Lemmas 7.2 and 7.3, we combine the first order terms in r and then divide the result by $s(1 - s)$ to get

$$\int_\Omega e^{\alpha/\mu\ln m}\left[\ln m\left(\frac{\alpha}{\mu}\sin\phi-\cos\phi\right)-\sin\phi\right]\left|\nabla\left(e^{-\alpha/\mu\ln m}\theta_{\alpha,\mu}\right)\right|^2$$
$$=\int_\Omega e^{-\alpha/\mu\ln m}\ln m\left[\frac{\alpha\sin\phi}{\mu^2}-\frac{\cos\phi}{\mu}\right]\theta_{\alpha,\mu}^2(m-\theta_{\alpha,\mu}). \tag{45}$$

Now consider case (ii). If we divide (33) by $\|u\|_\infty$, using our polar parameterizations as well as our expansions and combining the first order terms in r, we see that

$$\int_\Omega e^{\alpha/\mu\ln m}\left[\ln m\left(\frac{\alpha}{\mu}\sin\phi-\cos\phi\right)-\sin\phi\right]$$
$$\times\nabla(e^{-\alpha/\mu\ln m}\theta_{\alpha,\mu})\cdot\nabla\left(e^{-\alpha/\mu\ln m}\frac{\theta_{\alpha,\mu}}{\|\theta_{\alpha,\mu}\|_\infty}\right)$$
$$=\int_\Omega e^{-\alpha/\mu\ln m}\ln m\left[\frac{\alpha\sin\phi}{\mu^2}-\frac{\cos\phi}{\mu}\right]\frac{\theta_{\alpha,\mu}^2}{\|\theta_{\alpha,\mu}\|_\infty}(m-\theta_{\alpha,\mu}). \tag{46}$$

Notice that if we multiply (46) by $\|\theta_{\alpha,\mu}\|_\infty$, we obtain the expression in (45). Case (iii) can be handled in a similar manner. Thus, we proceed, multiplying the equation for the semitrivial 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:

$$\int_\Omega e^{-\alpha/\mu\ln m}\theta_{\alpha,\mu}^2(m-\theta_{\alpha,\mu})\ln m$$
$$=\mu\int_\Omega e^{\alpha/\mu\ln m}\nabla\left(e^{-\alpha/\mu\ln m}\theta_{\alpha,\mu}\ln m\right)\cdot\nabla\left(e^{-\alpha/\mu\ln m}\theta_{\alpha,\mu}\right)$$
$$=\mu\int_\Omega e^{\alpha/\mu\ln m}\left[\nabla\left(e^{-\alpha/\mu\ln m}\theta_{\alpha,\mu}\right)\ln m+e^{-\alpha/\mu\ln m}\theta_{\alpha,\mu}\nabla\ln m\right]$$
$$\times\nabla\left(e^{-\alpha/\mu\ln m}\theta_{\alpha,\mu}\right)$$
$$=\mu\left[\int_\Omega e^{\alpha/\mu\ln m}\left|\nabla\left(e^{-\alpha/\mu\ln m}\theta_{\alpha,\mu}\right)\right|^2\ln m+\int_\Omega\theta_{\alpha,\mu}\nabla\left(e^{-\alpha/\mu\ln m}\theta_{\alpha,\mu}\right)\right.$$
$$\left.\times\nabla\ln m\right]. \tag{47}$$

Combining this result with (45), we get

$$-\sin\phi\int_\Omega e^{\alpha/\mu\ln m}\left|\nabla\left(e^{-\alpha/\mu\ln m}\theta_{\alpha,\mu}\right)\right|^2$$
$$=\left(\frac{\alpha\sin\phi-\mu\cos\phi}{\mu}\right)\left[-\int_\Omega e^{\alpha/\mu\ln m}\ln m\left|\nabla\left(e^{-\alpha/\mu\ln m}\theta_{\alpha,\mu}\right)\right|^2\right]$$
$$+\left(\frac{\alpha\sin\phi-\mu\cos\phi}{\mu}\right)\left[\frac{1}{\mu}\int_\Omega e^{-\alpha/\mu\ln m}\theta_{\alpha,\mu}^2(m-\theta_{\alpha,\mu})\right]$$
$$=\left(\frac{\alpha\sin\phi-\mu\cos\phi}{\mu}\right)\int_\Omega\theta_{\alpha,\mu}\nabla\ln m\cdot\nabla\left(e^{-\alpha/\mu\ln m}\theta_{\alpha,\mu}\right). \tag{48}$$

By rearranging (48), we see that

$$
\begin{aligned}
&-\sin\phi\left[\int_{\Omega} e^{\alpha/\mu \ln m}\left|\nabla\left(e^{-\alpha/\mu \ln m}\theta_{\alpha,\mu}\right)\right|^2+\frac{\alpha}{\mu}\int_{\Omega}\theta_{\alpha,\mu}\nabla \ln m\cdot\nabla\left(e^{-\alpha/\mu \ln m}\theta_{\alpha,\mu}\right)\right]\\
&\quad=-\cos\phi\int_{\Omega}\theta_{\alpha,\mu}\nabla\ln m\cdot\nabla\left(e^{-\alpha/\mu \ln m}\theta_{\alpha,\mu}\right). \qquad (49)
\end{aligned}
$$

Note also that

$$
\begin{aligned}
&e^{\alpha/\mu \ln m}\left|\nabla\left(e^{-\alpha/\mu \ln m}\theta_{\alpha,\mu}\right)\right|^2+\frac{\alpha}{\mu}\theta_{\alpha,\mu}\nabla\ln m\cdot\nabla\left(e^{-\alpha/\mu \ln m}\theta_{\alpha,\mu}\right)\\
&\quad=\nabla\left(e^{-\alpha/\mu \ln m}\theta_{\alpha,\mu}\right)\cdot\left[e^{\alpha/\mu \ln m}\nabla\left(e^{-\alpha/\mu \ln m}\theta_{\alpha,\mu}\right)+\frac{\alpha}{\mu}\theta_{\alpha,\mu}\nabla\ln m\right]\\
&\quad=\nabla\left(e^{-\alpha/\mu \ln m}\theta_{\alpha,\mu}\right)\cdot\nabla\theta_{\alpha,\mu}. \qquad (50)
\end{aligned}
$$

Finally, using (50) in the expression given by (49), we see that

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

which is a contradiction. □

8 New Analytic Results

In this section, we prove the main analytic results of the paper. We begin with the results that concern single trait evolution and then move on to the two trait theorems. Finally, we prove the coexistence result for the new region as illustrated in Fig. 7.

8.1 1 Trait Analysis

Before proving Theorem 3, we state a useful lemma.

Lemma 8.1 *Consider the following eigenvalue problem*

$$
\begin{cases}
\gamma\nabla\cdot(e^{\tau\ln m}\nabla\psi)+e^{\tau\ln m}h\psi=-\lambda e^{\tau\ln m}\psi, & x\in\Omega,\\
\nabla\psi\cdot n=0, & x\in\partial\Omega
\end{cases}
\qquad (51)
$$

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 (51).

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

$$
\begin{cases}
\gamma\nabla\cdot\left(e^{\tau\ln m}\nabla\bar{\psi}\right)+e^{\tau\ln m}h\bar{\psi}=-\bar{\lambda}e^{\tau\ln m}\bar{\psi}, & x\in\Omega,\\
\nabla\bar{\psi}\cdot n=0, & x\in\partial\Omega,
\end{cases}
\qquad (52)
$$

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 (52), by the implicit function theorem we see that $\bar{\lambda}$, $\bar{\psi}$ are both differentiable functions of γ (see Belgacem 1997). Hence, we differentiate both sides of (52) with respect to γ to obtain

$$\begin{cases} \gamma\nabla\cdot\left(e^{\tau\ln m}\nabla\bar{\psi}'\right)+\nabla\cdot\left(e^{\tau\ln m}\nabla\bar{\psi}\right)+e^{\tau\ln m}\bar{\psi}'h \\ \quad =-\bar{\lambda}'e^{\tau\ln m}\bar{\psi}-\bar{\lambda}e^{\tau\ln m}\bar{\psi}', \quad x\in\Omega, \\ \nabla\bar{\psi}'\cdot n=0, \quad x\in\partial\Omega. \end{cases} \tag{53}$$

If we multiply (53) by $\bar{\psi}$ and (52) 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, (51) 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. □

Theorem 16 (Theorem 3) *Let $m \in C^2(\bar{\Omega})$ such that $m > 0$, $m \not\equiv$ constant and suppose that $\frac{\alpha}{\mu} = \frac{\beta}{\nu} \neq 1$. Then $(\theta_{\alpha,\mu}, 0)$ is globally asymptotically stable when $\mu < \nu$, and $(0, \theta_{\beta,\nu})$ is globally asymptotically stable when $\mu > \nu$.*

Proof Fix $\alpha, \mu, \beta, \nu > 0$ such that $\frac{\alpha}{\mu} = \frac{\beta}{\nu} \neq 1$. Suppose that $\mu < \nu$, we first show that $(\theta_{\alpha,\mu}, 0)$ is locally stable. Linearizing (3) at $(\theta_{\alpha,\mu}, 0)$, we see that it suffices to consider

$$\begin{cases} \nabla\cdot[\nu\nabla\phi-\beta\phi\nabla\ln m]+\phi(m-\theta_{\alpha,\mu})=-\lambda\phi, \quad x\in\Omega, \\ [\nu\nabla\phi-\beta\phi\nabla\ln m]\cdot n=0, \quad x\in\partial\Omega. \end{cases} \tag{54}$$

Set $\varphi = e^{-\beta/\nu\ln m}\phi$. Substituting this into (54), we see that φ satisfies

$$\begin{cases} \nu\nabla\cdot[e^{\beta/\nu\ln m}\nabla\varphi]+e^{\beta/\nu\ln m}\varphi(m-\theta_{\alpha,\mu})=-\lambda e^{\beta/\nu\ln m}\varphi, \quad x\in\Omega, \\ \nabla\varphi\cdot n=0, \quad x\in\partial\Omega. \end{cases} \tag{55}$$

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

$$\begin{cases} \mu\nabla\cdot[e^{\alpha/\mu\ln m}\nabla(e^{-\alpha/\mu\ln m}\theta_{\alpha,\mu})]+\theta_{\alpha,\mu}(m-\theta_{\alpha,\mu})=0, \quad x\in\Omega, \\ \nabla(e^{-\alpha/\mu\ln m}\theta_{\alpha,\mu})\cdot n=0, \quad x\in\partial\Omega. \end{cases} \tag{56}$$

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

$$\begin{cases} \mu\nabla\cdot[e^{\alpha/\mu\ln m}\nabla\theta_0]+e^{\alpha/\mu\ln m}\theta_0(m-\theta_{\alpha,\mu})=0, \quad x\in\Omega, \\ \nabla\theta_0\cdot n=0, \quad x\in\partial\Omega. \end{cases} \tag{57}$$

Referring to Lemma 8.1, put $h = m - \theta_{\alpha,\mu}$. Furthermore, set $\tau = \frac{\alpha}{\mu} = \frac{\beta}{\nu}$. Note that from (57), 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 8.1 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 (6) has no positive solutions for our particular choice of α, μ, β, and ν. We argue by contradiction: suppose that (6) has a positive solution (u, v). Let $h = m - u - v$ on Ω. Then we see that (u, v) satisfy

$$\begin{cases} \mu\nabla\cdot[\nabla u - (\alpha/\mu)u\nabla\ln m] + uh = 0, & x \in \Omega, \\ \nu\nabla\cdot[\nabla v - (\beta/\nu)v\nabla\ln m] + vh = 0, & x \in \Omega, \\ [\nabla u - (\alpha/\mu)u\nabla\ln m]\cdot n = [\nabla v - (\beta/\nu)v\nabla\ln m]\cdot n = 0, & x \in \partial\Omega. \end{cases} \tag{58}$$

Let $\bar{u} = e^{-\alpha/\mu \ln m}u$ and $\bar{v} = e^{-\beta/\nu \ln m}v$. Then the equations in (58) can be written as follows:

$$\begin{cases} \mu\nabla\cdot[e^{\alpha/\mu\ln m}\nabla\bar{u}] + e^{\alpha/\mu\ln m}\bar{u}h = 0, & x \in \Omega, \\ \nu\nabla\cdot[e^{\beta/\nu\ln m}\nabla\bar{v}] + e^{\beta/\nu\ln m}\bar{v}h = 0, & x \in \Omega, \\ \nabla\bar{u}\cdot n = \nabla\bar{v}\cdot n = 0, & x \in \partial\Omega. \end{cases} \tag{59}$$

Since $\alpha/\mu = \beta/\nu$, we see that $\bar{u}$ is the principle eigenfunction satisfying (51) 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 8.1, we know that $\bar{\lambda}(\mu) < \bar{\lambda}(\nu)$. But from (59), we see that $\bar{\lambda}(\mu) = 0 = \bar{\lambda}(\nu)$, which is a contradiction. Hence, (6) has no positive solutions. Finally, since (6) has no positive steady states, by Theorem 11 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 17 (Theorem 4) *Suppose m is as in Theorem* 16 *with* $\Omega = (0, 1)$, $m_x > 0$ *on* $[0, 1]$, *and* $\alpha = \beta$.

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

Proof (i) We begin by showing that $(\theta_{\alpha,\mu}, 0)$ is locally stable. Referring to the eigenvalue problem in (15) and using the parameterizations in Remark 5.1, 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 (19) and (20) 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

$$\lambda_2\int_0^1 e^{-\alpha/\mu\ln m}\theta_{\alpha,\mu}^2 = \int_0^1 \left(e^{-\alpha/\mu\ln m}\theta_{\alpha,\mu}\right)_x(\theta_{\alpha,\mu})_x. \tag{60}$$

From Lemma 6.1, we have that since $0 \le \alpha < \mu$, $(e^{-(\alpha/\mu)\ln m}\theta_{\alpha,\mu})_x, (\theta_{\alpha,\mu})_x > 0$ 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 6.1 and the expression for η_2 in (27), there exists a $\delta > 0$ such that if $r \in (0, \delta)$, the principal eigenvalue for (25), $\eta^* < 0$. Thus, $(0, \theta_{\beta,\nu})$ is unstable. By Theorem 15, we see there are no positive steady states and, as our system is strongly monotone, we know that by Theorem 11 for $0 < r < \epsilon_1 = \min\{\epsilon, \delta\}$, $(\theta_{\alpha,\mu}, 0)$ is globally asymptotically stable.

(ii) From Lemma 6.2, since $\alpha > \mu$, $(e^{-\alpha/\mu \ln m}\theta_{\alpha,\mu})_x < 0$ on $[0, 1]$ and since $\alpha > \frac{\int_0^1 m}{\min(m_x/m)}$, Lemma 6.5 gives us that $(\theta_{\alpha,\mu})_x > 0$ on $[0, 1]$. Using the expression for η_2 in (27), again with $\phi = \pi/2$, we notice that

$$\eta_2 \int_0^1 e^{-\alpha/\mu \ln m}\theta_{\alpha,\mu}^2 = -\int_0^1 \left(e^{-\alpha/\mu \ln m}\theta_{\alpha,\mu}\right)_x (\theta_{\alpha,\mu})_x. \tag{61}$$

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 (60), $\lambda_1 < 0$, giving us that for sufficiently small $r > 0$, $\lambda^* < 0$. Thus $(\theta_{\alpha,\mu}, 0)$ is unstable. Combining the stability results of both semitrivial 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. □

8.2 2 Trait Analysis

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

Lemma 8.2 *Suppose* $\alpha, \mu > 0$ *and let* λ_1, λ_2 *be defined as in* (19) *and* (20), *respectively.*

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

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

Proof (i) When $\alpha < \mu$, Lemma 6.1 states that $\mu(\theta_{\alpha,\mu})_x - \alpha\frac{m_x}{m}\theta_{\alpha,\mu} > 0$ on $(0, 1)$. Hence,

$$\begin{aligned} 0 &< \int_0^1 \left(e^{-\alpha/\mu \ln m}\theta_{\alpha,\mu}\right)_x \left(\mu(\theta_{\alpha,\mu})_x - \alpha\frac{m_x}{m}\theta_{\alpha,\mu}\right) \\ &= -\alpha \int_0^1 \left(e^{-\alpha/\mu \ln m}\theta_{\alpha,\mu}\right)_x \frac{m_x}{m}\theta_{\alpha,\mu} + \mu \int_0^1 \left(e^{-\alpha/\mu \ln m}\theta_{\alpha,\mu}\right)_x (\theta_{\alpha,\mu})_x. \end{aligned} \tag{62}$$

Note that using (19), (20), and (62) gives $0 < \alpha\lambda_1 + \mu\lambda_2$. Thus, because $\lambda_2 > 0$, we obtain our result.

(ii) If $\alpha > \mu$, then Lemma 6.2 gives us that $\mu(\theta_{\alpha,\mu})_x - \alpha\frac{m_x}{m}\theta_{\alpha,\mu} < 0$ 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 $\frac{-\lambda_1}{\lambda_2} < \frac{\mu}{\alpha}$. From Theorem 14, we know that $(\theta_{\alpha,\mu})_x - \frac{m_x}{m}\theta_{\alpha,\mu} < 0$ on $[0, 1]$. Thus,

$$
\begin{aligned}
0 &> \int_0^1 \left(e^{-\alpha/\mu \ln m}\theta_{\alpha,\mu}\right)_x \left((\theta_{\alpha,\mu})_x - \frac{m_x}{m}\theta_{\alpha,\mu}\right) \\
&= \int_0^1 \left(e^{-\alpha/\mu \ln m}\theta_{\alpha,\mu}\right)_x (\theta_{\alpha,\mu})_x - \int_0^1 \left(e^{-\alpha/\mu \ln m}\theta_{\alpha,\mu}\right)_x \frac{m_x}{m}\theta_{\alpha,\mu}. \qquad (63)
\end{aligned}
$$

Now from (19), (20), and (63), 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 8.2, we have the following result.

Lemma 8.3 *Suppose* $\alpha, \mu > 0$ *and let* η_1, η_2 *be defined as in* (26) *and* (27), *respectively.*

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

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

Theorem 18 (Theorem 7) *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* $\phi \in [\tan^{-1}(\frac{\mu}{\alpha}) - \pi, 0]$, *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* $\phi \in [\tan^{-1}(\frac{\mu}{\alpha}), \pi]$, *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* $\phi \in [\pi, \cot^{-1}(\frac{\alpha}{\mu}) + \pi]$, *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* $\phi \in [0, \cot^{-1}(\frac{\alpha}{\mu})]$, *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 $g(-\pi/2) = -\lambda_2 < 0$ (cf. (20) and Lemma 6.1). We claim that on $[\tan^{-1}(\frac{\mu}{\alpha}) - \pi, 0]$, $g < 0$. Suppose this is not the case. That is, suppose that $g(\phi_0) = 0$ for some $\phi_0 \in [\tan^{-1}(\frac{\mu}{\alpha}) - \pi, 0]$. Then $\phi_0 \in [\tan^{-1}(\frac{\mu}{\alpha}) - \pi, -\pi/2)$ or $\phi_0 \in (-\pi/2, 0]$. Suppose $\phi_0 \in [\tan^{-1}(\frac{\mu}{\alpha}) - \pi, -\pi/2)$. On the one hand, since $g(\phi_0) = 0$, $\tan(\phi_0) = \frac{-\lambda_1}{\lambda_2}$, but on the other hand, $\tan(\phi_0) \geq \frac{\mu}{\alpha}$ on this interval. Lemma 8.2 states that $\frac{-\lambda_1}{\lambda_2} < \frac{\mu}{\alpha}$, 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 8.2, $\frac{-\lambda_1}{\lambda_2} > 0$. Finally, since g is continuous, it does not change the sign on $[\tan^{-1}(\frac{\mu}{\alpha}) - \pi, -\pi/2) \cup (-\pi/2, 0]$, and $g(-\pi/2) =$

$-\lambda_2 < 0$, we see that $g < 0$ on the desired interval. Thus, for r small enough and $\phi \in [\tan^{-1}(\frac{\mu}{\alpha}) - \pi, 0]$, the principal eigenvalue λ^*, in conjunction with semitrivial steady state $(\theta_{\alpha,\mu}, 0)$, has the same sign as $g(\phi)$. Since $g < 0$ on $[\tan^{-1}(\frac{\mu}{\alpha}) - \pi, 0]$, it must be that $\lambda^* < 0$. Hence, $(\theta_{\alpha,\mu}, 0)$ is unstable. Note that by Theorem 15, our system does not have any positive steady states. Hence, by Theorem 11, $(0, \theta_{\beta,\nu})$ 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 8.3, (26), and (27), we see that $h > 0$ on $[\tan^{-1}(\frac{\mu}{\alpha}), \pi]$. 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 $\phi \in [\tan^{-1}(\frac{\mu}{\alpha}), \pi]$. 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 15 our system does not have positive steady states, so by Theorem 11, $(\theta_{\alpha,\mu}, 0)$ 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 $\phi \in [\pi, \cot^{-1}(\frac{\alpha}{\mu}) + \pi]$, $\lambda^* < 0$, implying that $(\theta_{\alpha,\mu}, 0)$ is unstable. Again, we define $g(\phi) = \lambda_1 \cos\phi + \lambda_2 \sin\phi$. Using (20) and Lemma 6.2, we see that $g(\pi) = -\lambda_1 < 0$. We claim that $g < 0$ on $[\pi, \cot^{-1}(\frac{\alpha}{\mu}) + \pi]$. Suppose that $g(\phi_0) = 0$ for some $\phi_0 \in (\pi, \cot^{-1}(\frac{\alpha}{\mu}) + \pi]$. Then $\cot\phi = \frac{-\lambda_2}{\lambda_1}$. But on $[\pi, \cot^{-1}(\frac{\alpha}{\mu}) + \pi]$, $\cot\phi > \frac{\alpha}{\mu} > \frac{-\lambda_2}{\lambda_1}$, where the last inequality is given by Lemma 8.2. This is a contradiction and thus shows that $g < 0$ on the given interval. Hence, for small enough r and $\phi \in [\pi, \cot^{-1}(\frac{\alpha}{\mu}) + \pi]$, 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 15 and Theorem 11, $(0, \theta_{\beta,\nu})$ 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 $[0, \cot^{-1}(\frac{\alpha}{\mu})]$. We can then write $\eta^* = rh(\phi) + O(r^2)$ for small enough r and $\phi \in [0, \cot^{-1}(\frac{\alpha}{\mu})]$. Thus, $\eta^* > 0$, which indicates that $(0, \theta_{\beta,\nu})$ is unstable. Finally, by Theorem 15 and Theorem 11, it must be that $(\theta_{\alpha,\mu}, 0)$ is globally asymptotically stable. □

When m is linear, by Lemmas 8.2 and 8.3, we see that both $\frac{-\lambda_1}{\lambda_2}$ and $\frac{-\eta_1}{\eta_2}$ are bounded between 1 and $\frac{\mu}{\alpha}$. This observation, which relies on the fact that $(\theta_{\alpha,\mu})_x > 0$ on $[0, 1]$, enables us to expand the regions in Theorem 18 to obtain the following result.

Theorem 19 (Theorem 8) *Fix $\mu, \alpha > 0$. (Note that here we slightly extend the regions listed in Theorem 8.) 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 $0 < \tau_1 < \frac{-\lambda_1}{\lambda_2}$ and $\frac{-\lambda_1}{\lambda_2} < \rho_1$. 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 $\frac{-\eta_1}{\eta_2} < \tau_2$ and $0 < \rho_2 < \frac{-\eta_1}{\eta_2}$. 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* $\frac{-\lambda_1}{\lambda_2} < \tau_3$ *and* $0 < \rho_3 < \frac{-\lambda_1}{\lambda_2}$. *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* $0 < \tau_4 < \frac{-\lambda_1}{\lambda_2}$ *and* $\frac{-\lambda_1}{\lambda_2} < \rho_4$. *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 18, 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 6.1 and (20), $g(-\pi/2) = -\lambda_2 < 0$. 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 $\tan(\phi_0) = \frac{-\lambda_1}{\lambda_2}$. Now if $\phi_0 \in [\tan^{-1}(\rho_1) - \pi, -\pi/2)$, then $\tan(\phi_0) \geq \rho_1 > \frac{-\lambda_1}{\lambda_2}$, which is a contradiction. Likewise, if $\phi \in (-\pi/2, \tan^{-1}(\tau_1)]$, $\tan(\phi) \leq \tau_1 < \frac{-\lambda_1}{\lambda_2}$, 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 15 and Theorem 11, $(0, \theta_{\beta,\nu})$ is globally asymptotically stable. The other cases can be proved similarly. □

8.3 Convergent Stable Paths

Theorem 20 *Suppose that m is linear, nonconstant and positive on* $[0, 1]$ *and let* Γ_+ *and* Γ_- *be as in* (5).

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

(ii) *If we assume that both* $y - x$ *and* $\frac{y}{x}$ *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 $\frac{y}{x}$ for $0 \leq s < 1$ and $0 < \Delta s < 1 - s$, we have $y(s + \Delta s) - y(s) \leq x(s + \Delta s) - x(s)$, and $\frac{y(s+\Delta s)}{y(s)} \geq \frac{x(s+\Delta s)}{x(s)}$. 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 $1 \leq \frac{\nu}{\mu} \leq \frac{\beta}{\alpha}$. Let γ_1 be as in Theorem 19. 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 19 by setting $\tau_1 = 1$ and $\rho_1 = \frac{\mu}{\alpha}$, which says that $(0, \theta_{\beta,\nu})$ is globally asymptotically stable. The proof of (ii) is similar. □

8.4 Proof of Coexistence Result

Next we seek to prove Theorem 6. Before doing so, we establish some useful lemmas.

Lemma 8.4 *Given* $\mu > 0$ *and set* $\alpha = (1 + \delta)\mu$. *Then, as* $\delta \to 0+$,

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

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

$$\mu\nabla\cdot[m\nabla w^*]-m^2w^*=m^2\ln m,\qquad \nabla w^*\cdot n|_{\partial\Omega}=0. \tag{64}$$

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

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

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, $\bar{u}:=m+\delta m(w+\ln m)$ is a supersolution for (28). To check this, we first see that

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

Hence, since w is uniformly bounded,

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

for sufficiently small δ. Similarly,

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

for sufficiently small $\delta>0$. Hence, $\bar{u}:=m+\delta m(w+\ln m)$ is a supersolution of (28).

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

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

Set $\underline{u}:=m+\delta m(z+\ln m)$. Similarly, we can show that $z\to w^*$ uniformly in $\bar{\Omega}$ as $\delta\to 0$ and $\underline{u}$ is a subsolution of (28). By the supersolution and subsolution method, $\underline{u}\le\theta_{\alpha,\mu}\le\bar{u}$ for sufficiently small $\delta>0$ (Pao 1992). In particular,

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

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

Lemma 8.5 *Suppose that* $m>0$ *on* Ω *and satisfies assumption* (A) *of Theorem* 6. *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 (64). By the maximum principle (Protter and Weinberger 1984), w^* is uniformly bounded. By elliptic regularity and the Sobolev embedding theorem (Gilbarg and Trudinger 1983), 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 8.4, 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 8.6 *Suppose that $m > 0$ on Ω satisfies assumption* (A) *and all the critical points of m are nondegenerate. 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 semitrivial steady state $(\theta_{\alpha,\mu}, 0)$ is unstable for sufficiently large $\beta > 0$.*

Proof By Lemma 5.1, we need only show the principal eigenvalue, denoted by λ_0, of the eigenvalue problem

$$\begin{cases} \nabla \cdot [\nu\nabla\varphi - \beta\varphi\nabla \ln m] + \varphi(m - \theta_{\alpha,\mu}) = -\lambda\varphi, & x \in \Omega \\ [\nu\nabla\varphi - \beta\varphi\nabla \ln m] \cdot n = 0, & x \in \partial\Omega, \end{cases} \tag{65}$$

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

$$\begin{cases} \nu\nabla \cdot [e^{\beta/\nu \ln m}\nabla\psi] + e^{\beta/\nu \ln m}\psi(m - \theta_{\alpha,\mu}) = -\lambda e^{\beta/\nu \ln m}\psi & \text{in } \Omega, \\ \nabla\psi \cdot n|_{\partial\Omega} = 0. \end{cases} \tag{66}$$

Simplifying the expression in (66), we see that ψ satisfies

$$-\nu\Delta\psi - \beta\nabla(\ln m) \cdot \nabla\psi + (\theta_{\alpha,\mu} - m)\psi = \lambda\psi \quad \text{in } \Omega,\ \nabla\psi \cdot n|_{\partial\Omega} = 0. \tag{67}$$

By Theorem 1.1 of Chen and Lou (2008) 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 8.5, 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 8.7 *Suppose that the set of critical points of $m(x)$ has Lebesgue measure zero. Recall that $\theta_{\beta,\nu}$ satisfies*

$$\begin{cases} \nabla \cdot [\nu\nabla\theta_{\beta,\nu} - \beta\theta_{\beta,\nu}\nabla \ln m] + \theta_{\beta,\nu}(m - \theta_{\beta,\nu}) = 0 & \text{in } \Omega, \\ [\nu\nabla\theta_{\beta,\nu} - \beta\theta_{\beta,\nu}\nabla \ln m] \cdot n = 0 & \text{on } \partial\Omega. \end{cases} \tag{68}$$

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

Proof See the proof of Theorem 3.5 (Cantrell et al. 2007). □

Lemma 8.8 *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 5.2 it is enough to show that the principal eigenvalue λ_0 of the eigenvalue problem

$$\begin{cases} \nabla \cdot [\mu \nabla \varphi - \alpha \varphi \nabla \ln m] + \varphi(m - \theta_{\beta,\nu}) = -\lambda \varphi, & x \in \Omega \\ [\mu \nabla \varphi - \alpha \varphi \nabla \ln m] \cdot n = 0, \quad x \in \partial \Omega, \end{cases} \tag{69}$$

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

$$\begin{cases} \mu \nabla \cdot \left[e^{\alpha/\mu \ln m} \nabla \psi \right] + e^{\alpha/\mu \ln m} \psi (m - \theta_{\beta,\nu}) = -\lambda_0 e^{\alpha/\mu \ln m} \psi & \text{in } \Omega, \\ \nabla \psi \cdot n|_{\partial \Omega} = 0. \end{cases} \tag{70}$$

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

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

where the last inequality follows from Lemma 8.7 for large enough β. □

Theorem 21 (Theorem 6) *Suppose that* m *satisfies assumption* (A) *and all critical points of* m *are nondegenerate. Then there exists* $\mu_0 > 0$ *such that for each* $\mu > \mu_0$, *there exists some* $\delta > 0$ *such that if* $1 < \alpha/\mu < 1 + \delta$, *for any* $\nu > 0$, *both* $(\theta_{\alpha,\mu}, 0)$ *and* $(0, \theta_{\beta,\nu})$ *are unstable for large enough* $\beta > 0$. *Moreover,* (3) *has at least one stable positive steady state.*

Proof Lemmas 8.6 and 8.8 establish that both semitrivial steady states of (6) are unstable. Thus, by Theorem 11, there exists at least one stable coexistence state. □

9 Numerical Results

In this section, we verify and extend many of the above analytic results. Specifically, we numerically check the results for the linear and monotone cases against Theorem 7 and Theorem 8. We show that resource monotonicity does not necessarily imply a monotonic species distribution in the single species case.

We then show results about what may occur if the resource has multiple peaks of unequal height. In particular, we numerically verify the existence of a new region of coexistence that Theorem 6 suggests exists, and show that this new region may lead to evolutionary branching of one resident species to two coexisting resident species. We then show that under certain conditions numerical results can imply three species coexisting. This leaves open the question of whether or not further evolutionary branching may be possible and we conclude with some results on convergent stable paths, verifying results in Theorem 9.

9.1 Numerical Methods

All numerical analysis of the PDE was performed using MATLAB's pdepe code which uses Skeel and Berzin's method for discretizing the spatial domain (Skeel and Berzins 1990) in order to apply the method of lines coupled with MATLAB's stiff variable order ode solver, ode15s. In order to construct a competition between a resident and an invader, we start off 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) up to time $t = 10^{15}$. We set the resulting distribution as the new initial equilibrium distribution of the resident. Afterward, 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 $t = 10^{15}$. We say a species survives if the maximum population size at any location is greater than 0.01, dead otherwise, and it wins the competition if it survives and all other species die out.

Pairwise invasion plots (PIP), are plotted based on running a competition between a resident with specified parameters in competition with an invader with specified parameters. 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: $\alpha \vee \beta$ where μ and ν are held constant while α and β are varied and $\beta \vee \nu$ where α and μ are held constant while β and ν are varied.

In order to evaluate how evolution could proceed, we allow our resident trait to compete with a random invader. The winner of this competition will become the new resident trait. Specifically, we choose the traits of the invader to be a small random perturbation that is 0.01 away from one of the resident's traits. We say a species survives if the maximum population size at any location is greater than 0.01, dead otherwise. All who survive become the residents of the next iteration. We repeat the procedure for a fixed number of iterations or until we encounter a region of coexistence. In this manner, we can choose to vary a single trait or both traits. In single trait evolution diagrams, we allow only advection to change while we let both traits change in two trait evolution diagrams. Such an evolutionary path will be referred to as an acceptable path. In comparison to a convergent stable path, the results of a small perturbation may lead to coexistence if the random perturbation is large enough.

9.2 Numerical Confirmation of Monotone Results

In Hambrock and Lou (2009), it was established that for the monotone case when $\alpha = \beta > \mu$, the fast diffuser wins; but when $\alpha = \beta < \mu$, the slow diffuser wins. In Theorems 7 and 8, we state new results for who wins between an invader with perturbed diffusion and advection from the resident. Here, we test these results numerically, first assuming $m(x)$ is linear. We set $m(x) = 2x + 1$, and examine the results

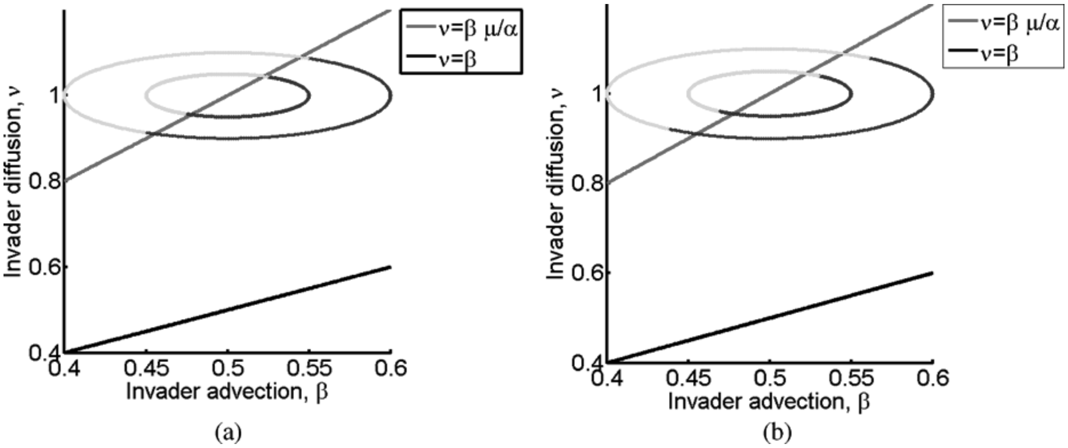


Fig. 4 (Color online) (**a**) Linear and (**b**) monotonic circular PIP for $\alpha = 0.5$, $\mu = 1$. *Green points* indicate the resident wins, *blue points* indicate the invader wins, and *red* indicates coexistence

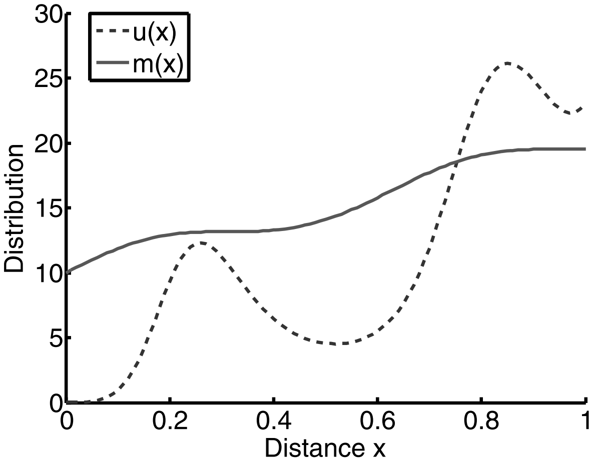


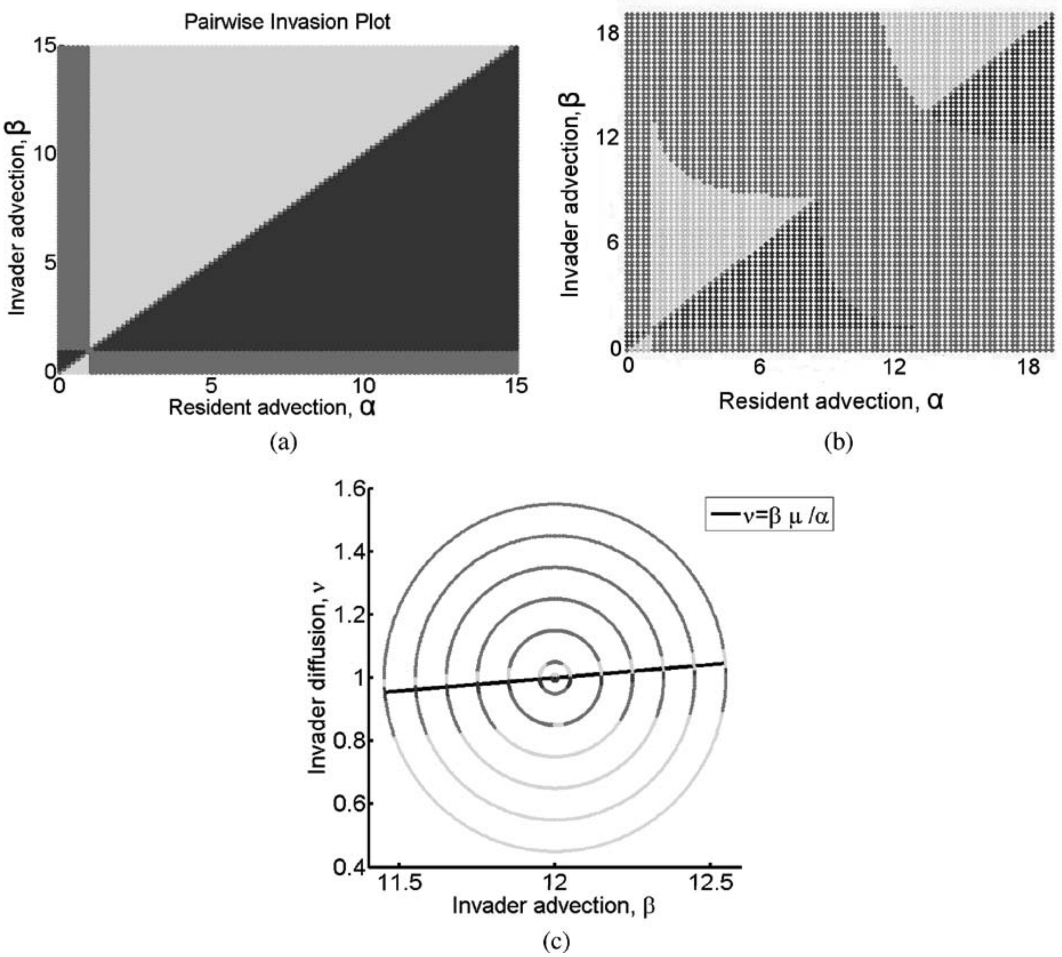
Fig. 5 (Color online) Nonmonotonic resident steady state (*blue dashed curve*) plotted against its monotonic resource (*green solid curve*)

varying the two invader traits against the resident traits of $\alpha = 0.5$ and $\mu = 1$. We plot the results in a circular PIP where the invader traits are small perturbations around the resident trait; see Fig. 4. As the results in Hambrock and Lou (2009) suggest, we see that around our resident parameter values, the survivor of a vertical perturbation will be the one closer to the line $\beta = \nu$. Furthermore, we see that around the $\nu = \frac{\mu}{\alpha}\beta$ line there are regions where either the resident or the invader wins. As Theorem 8 suggests, these regions overlap the μ/α line, and are actually divided into two regions by the line representing $\lambda^* = 0$ (compare Figs. 3 and 4). This shows that the numerics match our analytic results.

For a nonlinear but monotonically increasing case, we set $m(x) = \sin(10x) + 10.1x + 10$. This case differs significantly from the linear case in that if we plot out the resident distribution with no invader, we do not see monotonicity in the resident distribution for $\alpha = 3$ and $\mu = 0.1$; see Fig. 5. This numerically shows that a monotone resource does not necessarily imply monotone distribution of the resident species. The PIP plot around the region $\alpha = 0.5$ and $\mu = 1$ looks similar, but with greater overlap over the circle (see Fig. 4(b)), suggesting similar dynamics as the resident is replaced subsequent invasions as the linear case.

In the case where monotonicity is violated, we can consider multiple peaked resources of different heights such as $m(x) = \sin(3\pi x + \pi) + 2$. We see a new region of coexistence that was not present with other resource functions (compare Fig. 6(a) where $m(x) = \sin(10x) + 10.1x + 10$ and Fig. 6(b) where $m(x) = \sin(3\pi x + \pi) + 2$). If we look at the circular PIP plot of resident traits of $\alpha = 0.5$ and $\mu = 1$, we see a similar picture as the linear and monotonic cases above (Fig. 4). If instead we try to zoom in on a point inside the coexistence region, at $\alpha = 12$ and $\mu = 1$, we see something very different (Fig. 6(c)) (note that for monotone m with $\alpha = 12$ and $\mu = 1$, the circular PIP plot is similar to those in Fig. 4). There now appears to be regions of coexistence inside the regions where the resident wins and the invader wins by changing the diffusion above some threshold. The rectangular PIP plot, Fig. 6(b), also suggests that if we change the invader advection above some small threshold, then coexistence can occur.

To determine if the presence of the multiple peaks is sufficient for the new regions of coexistence, we shifted the resource curve to $m(x) = \sin(3\pi x + \pi/2) + 2$ and



(a)

(b)

(c)

Fig. 6 (Color online) (**a**) Rectangular PIP for monotone m with $\mu = \nu = 1$. (**b**) Rectangular PIP for nonmonotone m with $\mu = \nu = 1$, and (**c**) circular PIP for $\alpha = 12$, $\mu = 1$

found the region of coexistence is no longer present. This suggests that peaks of differing heights are necessary for this type of coexistence region.

In comparison, these conditions for coexistence between two competing species are different from that of Averill et al. (2011). They showed the following (we again state the result in the context of system (3)) theorem.

Theorem 22 (Theorem 4 in Averill et al. (2011)) *Suppose that* $m \in C^2(\bar{\Omega})$ *is positive and nonconstant. If* $(\alpha - \mu)(\beta - \nu) < 0$, *then both semitrivial steady states are unstable and system* (3) *has at least one stable positive steady state.*

For simplicity, we illustrate the region in Theorem 22 when $\nu = \mu$; see Fig. 7. What is significant about our result, however, is that we demonstrate the possibility of coexistence in a completely different location in the first quadrant of $\alpha - \beta$ space (see Fig. 7). That is, we provide a partial answer to the question of when two species, both having advection larger than their respective diffusion rates, can coexist. This notion directly connects to a conjecture made in Cantrell et al. (2010), which speaks against the existence of such a region. In particular, applying the prediction of Cantrell et al. (2010) to the model in (3), they conjectured that the first part of Theorem 6, 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. Somewhat surprisingly, as shown in Theorem 6, one can build nonmonotone functions m such that both $(\theta_{\alpha,\mu}, 0)$ and $(0, \theta_{\beta,\nu})$ are unstable for appropriate positive constants α, β, μ, and ν. Figure 8 illustrates the steady state coexistence profile of species u and v for dispersal traits in the "new region" as specified by Theorem 6.

Under certain resource curves, this new region may become arbitrarily close to the $\alpha = \beta$ line; see Fig. 6(b). When this occurs, by following acceptable evolutionary paths, which consist of randomly choosing the invader trait based on a small perturbation of the resident trait, the species may jump to a region of coexistence. Consider

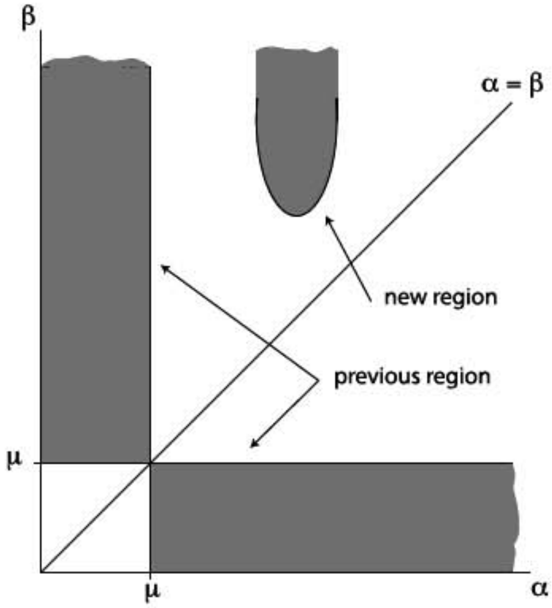


Fig. 7 (Color online) Coexistence is indicated by the *red* regions. The region along *both axes* illustrates Theorem 22. The *other region* illustrates our new result given in Theorem 6

Fig. 6(b); if the resident starts with large advection, then invaders with lower advection will take over. This trend will continue until the new region of coexistence is reached. Once within the region of coexistence, evolutionary branching has occurred and we need to consider a three species model with two residents and one invader. Zooming in on the point $\alpha = 12$, $\mu = 1$ within the region of coexistence, it is possible to do a two trait perturbation analysis; see Fig. 6(c). For sufficiently small perturbations, either the resident or the invader will win. Varying diffusion alone, large enough perturbations result in coexistence while even larger fluctuations may result in the resident winning. Introducing an invader with larger advection will result in the invader taking over, if the advection is sufficiently small, and pushing the trait to the branching point. Large advection invaders however can coexist; see Fig. 6(b), (c). This example illustrates the case where two species whose traits are close to each other, but not equal, results in either the invader or resident taking over. If the two species traits are sufficiently different, then coexistence will occur.

9.4 Coexistence of Three Species

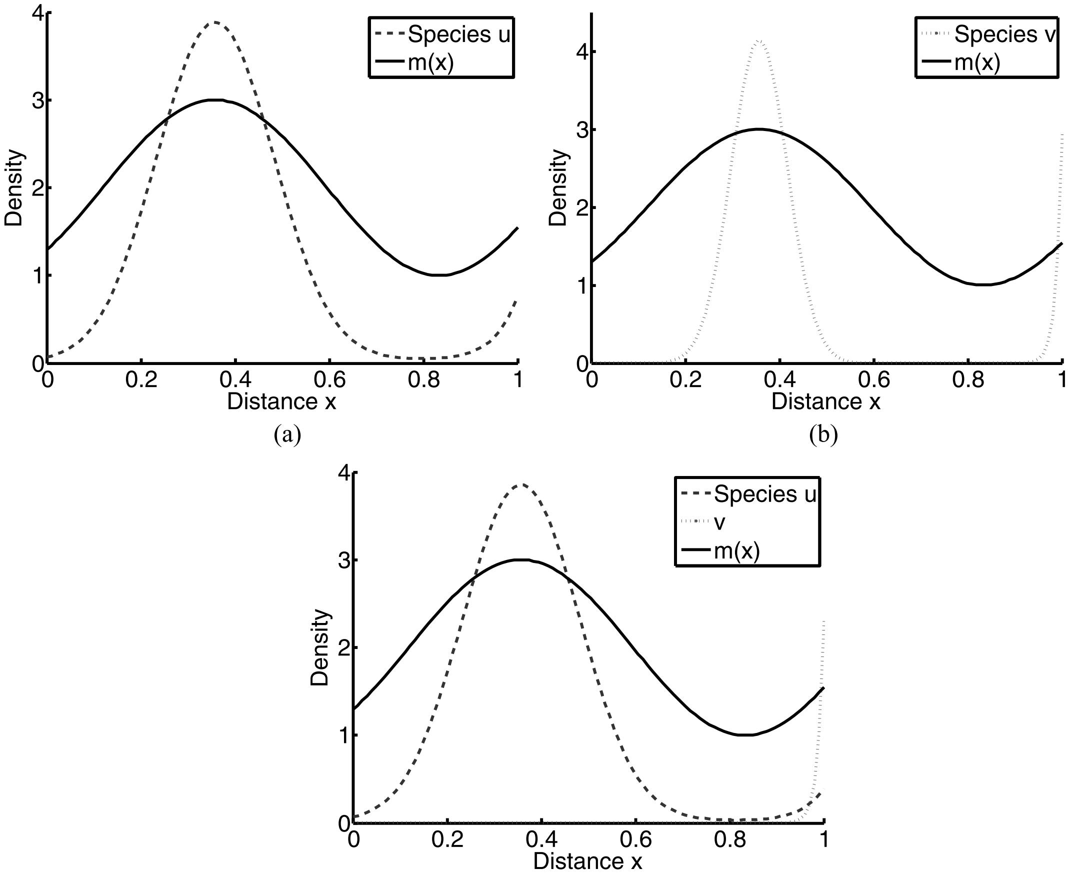
In the case that we have three species, it is natural to ask if coexistence can occur. In other words, we seek to apply the idea of a single species steady-state profile under-matching at a local maximum of m to provide a biologically interesting example of three species coexistence. We utilize Theorem 6 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 again use the resource function $m(x) = \sin(2.1\pi x - \pi/4) + 2$, which satisfies assumption (**A**).

Notice in Fig. 8(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. 8(b), because of relatively large β, species v can overmatch both maxima of m. Notice in Fig. 8(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. 8(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. 9, where we see all three species surviving together.

9.5 Two Trait Evolutionary Paths

Theorem 9 suggests that a sufficient condition for a path to be acceptable in the linear case is if it is in the blue cone formed between the lines $\nu - \mu = \beta - \alpha$ and $\nu/\beta = \mu/\alpha$, refer to Fig. 3. To test this result as well as generate acceptable paths for more complicated resource distributions, we take our resident trait and have it compete against a random invader. Specifically, we choose the traits of the invader to be a small random perturbation, that is 0.01, away from the resident's traits. If the invader either wins or coexists, we set the invader as a new resident. If the resident wins, it



(a) (b)

(c)

Fig. 8 (Color online) "New region" coexistence: (**a**) single species u (*red*), $\mu = 0.1$, $\alpha = 0.5$ (**b**) single species v (*green*), $\nu = 0.1$, $\beta = 2$ (**c**) coexistence of competing u and v. (Note: $m(x) = \sin(2.1\pi x - \pi/4) + 2$ is *black* on each graph)

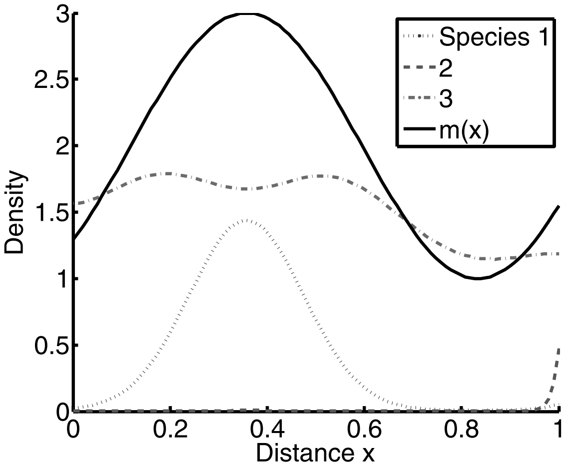
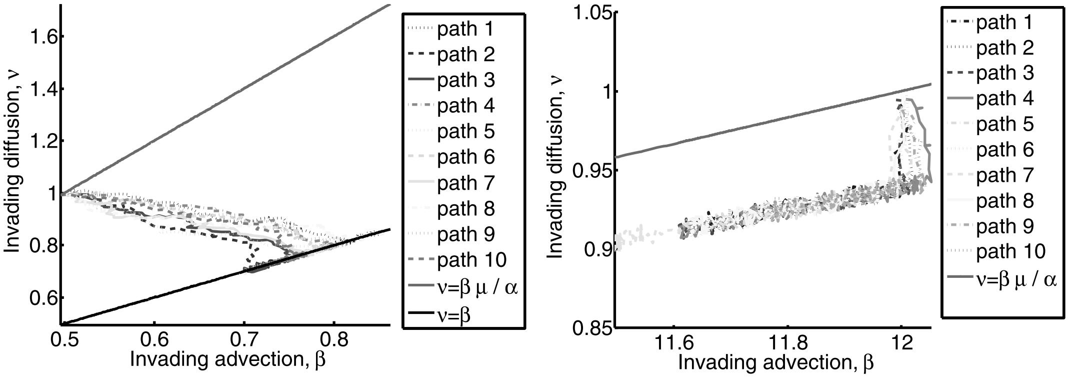


Fig. 9 (Color online) Three species coexistence. Species 1 with diffusion and advection rates $(0.1, 0.5)$ (*blue*), species 2 with rates $(0.1, 2)$ (*green*), and species 3 with $(0.01, 0)$ (*red*)

stays. In either case, we repeat the procedure for a fixed number of generations. This method is related to the canonical equation where one finds paths to the ideal free distribution by varying the traits, except here we vary the traits randomly and not deterministically.



(a) (b)

Fig. 10 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 multipeak example stay close to another line

Plotting the results, we see that in the linear case, the species traits converge straight to the ideal free distribution, $\nu = \beta$; see Fig. 10(a). The monotone example also has similar structure again in agreement with the analytic results. However, the multiple peak example has convergence to what seems to be another line; see Fig. 10(b). The diffusion of the trait decreases, followed by a subsequent decrease in the advection of the resident species as the traits start approaching zero. In this case, the species traits first go away from the ideal free distribution and we suspect reach it only at the origin where residents traits are 0.

10 Discussion Notes

Studying evolution with two traits is an important step for biological modeling because it is common for multiple traits to be under the same selective pressure. For example, the blackcap *Sylvia atricapill* has two distinct inheritable traits that govern their migration. The first controls the direction of migration, while the second controls the distance (Berthold and Pulido 1994; Berthold and Querner 1981). A single evolutionary trait is not sufficient to understand what will happen to this species when selection pressures change. When evolutionary models are extended to more traits we can better model these types of situations, and our models become more biologically relevant.

Our model is interesting in that it can provide an abstract exploration of trait based evolution towards ideal free strategies as well as insight into potential settings for sympatric speciation. In many cases, the traits evolve toward ideal free strategies, allowing a species to exhibit an ideal free distribution. In other cases, the traits evolve toward regions of coexistence. In particular, the region of coexistence in the multipeak cases allows for temporally divergent evolutionary branching when the invader's advection is allowed to change randomly between generations while keeping the diffusion constant. As residents are subsequently replaced with successful invaders, the sequence ultimately enters the region of coexistence (Fig. 6(b), (c)). Once there, two species can coexist as residents and a third species, that is close (trait-wise) to one of the two others, may be introduced. In nature, it is quite possible that some other selection pressure would begin to act on some of the traits that coevolved with advection and result in sympatric speciation of the species. The possibility of evolutionary branching resulting from dispersal strategies is a topic that is open and may be addressed in future work.

In a more specific setting, understanding dispersal strategies is beneficial when considering the evolution of crop rotation resistance in the western corn rootworm *Diabrotica virgifera*. The larvae of this maize pest damage the roots and root nodes. The control of this pest is a major expenditure in corn growing regions. One technique for controlling the rootworm is crop rotation (Gassmann et al. 2009; Meinke et al. 2009). By rotating the crops, farmers have changed the relative merits of high and low diffusion. When corn is planted in the same field every year, low diffusion is evolutionarily favored. When corn is rotated, however, higher diffusion is favored. Because of this shift, some strains of this rootworm have started laying eggs in surrounding fields and thus a crop rotation resistant strain is born. By allowing the environment to be variable in time, the effects of crop rotation, for instance, can be studied. We note that there has been work on dispersal in such situations, showing that there may be selection for faster diffusion (Hutson et al. 2001; McPeek and Holt 1992). If our model was to be extended to a resource that was a function of time, it might provide more subtle insights into how a resistant strain can appear. It might also suggest strategies for both controlling the resistant rootworm and slowing the evolution of the nonresistant strains.

Advection diffusion models can also be helpful in predicting the future location of sea life. This information can be used to inform management policies of fisheries. This is particularly important for management of species such as tuna where fishing is not uniform (Sibert et al. 1999; Adam and Sibert 2002). Furthering advection diffusion models is important because it may provide insights that better equip management agencies to protect fisheries.

Our results also yield surprising insights into the underpinnings of advection diffusion models. We generalize conditions for convergence to the ideal free strategies and prove the existence of regions of coexistence that had been previously conjectured to not exist (Cantrell et al. 2010). The observation that monotone resource does not necessarily imply monotone species distribution is also counter-intuitive. Originally, we expected the species to be monotonically increasing if the resource is. However, the change in concavity in $m(x)$ appears to have an effect on the monotonicity of the $\theta(x)$.

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