

# EVOLUTION OF CONDITIONAL DISPERSAL: A REACTION-DIFFUSION-ADVECTION MODEL

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**ABSTRACT.** To study evolution of conditional dispersal, a Lotka-Volterra reaction-diffusion-advection model for two competing species in a heterogeneous environment is proposed and investigated. The two species are assumed to be identical except their dispersal strategies: both species disperse by random diffusion and advection along environmental gradients, but one species has stronger biased movement (i.e., advection along the environmental gradients) than the other one. It is shown that at least two scenarios can occur: if only one species has a strong tendency to move upward the environmental gradients, the two species can coexist since one species mainly pursues resources at places of locally most favorable environments while the other relies on resources from other parts of the habitat; if both species have such strong biased movements, it can lead to overcrowding of the whole population at places of locally most favorable environments, which causes the extinction of the species with stronger biased movement. These results provide a new mechanism for the coexistence of competing species, and they also imply that selection is against excessive advection along environmental gradients, and an intermediate biased movement rate may evolve.

**KEYWORDS:** Evolution of dispersal, reaction, advection, competition

**AMS CLASSIFICATION:** 92D25, 35K57

## 1. Introduction

The evolution of dispersal has been an important topic in population dynamics (Levin et al. [30] and references therein). Two theories dominate current investigations on dispersal: (i) the “source-sink model” (Hastings [19]; Holt [25]; Hanski and Thomas [18]; Doebeli [14]; Travis and Dytham [44]), in which individuals disperse at fixed constant rates, regardless of the local environment; and (ii) the “balanced dispersal model” (McPeck and Holt [34]; Doncaster et al. [15]; Morris et al. [35]), in which the dispersal is conditional since the dispersal rate depends on a combination of local biotic and abiotic factors such as habitat quality. It has been well-recognized that conditional dispersal can be a crucial factor in population dynamics (Turchin [46]; Travis and French [45]; Bowler and Benton [4]). This paper is devoted to studying the evolution of conditional dispersal in the context of two competing species.

One important question in the evolution of dispersal is which patterns of dispersal can confer some sort of selective or ecological advantage? When habitat quality varies spatially

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but remains constant in time, the source-sink model predicts that the selection is for slow dispersal (Hastings [19]; Holt [25]). For instance, the results in [19] say that decreasing dispersal rate increases some measures of fitness in logistic models. It was shown in both discrete and continuous models (McPeck and Holt [34]; Dockery et al. [13]; Hutson et al. [27]) that for unconditional dispersal in spatially varying but temporally constant environments slower dispersal rate is selected. An interesting problem is whether the slowest diffuser always wins the competition in the context of  $k$  ( $\geq 3$ ) competing species, and we refer to Kirkland et al. [29] for recent progress in patch models. For unconditional dispersal in temporally varying environments, faster dispersal rates can be selected for both patch models [34] and diffusion models (Hutson et al. [28]).

In reality, species are neither completely ignorant of the surrounding environment nor will their movement perfectly track resource gradients. It is more likely that their movements are a combination of both random and biased ones: for instance, adding some amount of random motion to a purely directed movement dispersal strategy might help an individual escape a local environmental trap to find some distant but better sources (Armsworth and Roughgarden [1, 2]). In other words, a balanced combination of both random and directed movement might help the species better utilize overall resources. For two-patch models, it was shown in [34] that conditional dispersal can be advantageous in a spatially varying but temporally constant environment.

Diffusion models incorporating directed movement upward along resource gradients have been considered by Grindrod [17], Belgacem and Cosner [3], Cosner and Lou [11], Cantrell et al. [7, 8], Chen and Lou [10], Rowell [41], and references therein. In reaction-diffusion-advection models for a single population in a spatially varying but temporally constant environment, Belgacem and Cosner [3] and Cosner and Lou [11] showed that conditional dispersal involving both diffusion and directed movement up environmental gradients can sometimes (but not always) make persistence more likely. We also refer to Cantrell et al. [6] for recent progress on the evolution of ideal free distribution in patch models.

## 2. The Mathematical Model

This paper is concerned with the evolution of conditional dispersal strategies in the context of competition between two species that are ecologically identical except in their dispersal mechanisms.

Let  $u = u(x, t)$ ,  $v = v(x, t)$  denote the densities of two competing species at location  $x$  and time  $t$ . We assume that both species have the same per-capita growth rates, denoted by  $m(x)$ . This scenario can occur if the two species are competing for the same resources. To reflect the heterogeneity of environment, we assume that  $m(x)$  is a nonconstant function. In some sense,  $m(x)$  can reflect the quality and quantity of resources available at the location  $x$ , where the favorable region  $\{x \in \Omega : m(x) > 0\}$  acts as a source and the unfavorable part  $\{x \in \Omega : m(x) < 0\}$  is a sink region.

Since the resource is usually spatially unevenly distributed, the movement of species in general is not purely random. One of the simplest dispersal strategies is that the dispersal of species consists of two components: random diffusion and directed movement upward along the gradient of  $m(x)$ . In other words, the species can sense and evaluate local environment (but neglecting other important effects such as population density and nutrition dynamics) and move towards places with better resources. In particular, with such dispersal strategy it is more likely for the species to move from less favorable regions to more favorable ones, *e.g.*, sink regions to source regions. Intuitively, one possible consequence of such biased movement is to cause a certain degree of crowding in the source regions of the habitat and thus may change the outcome of the competition of two species. Our model and results can assess the degree of crowding induced by such biased movement, predict qualitatively when and where overcrowding of population will occur, and determine the effects of such biased movement on the population dynamics.

Under our assumptions, the dispersal of the two competitors can be described in terms of their fluxes

$$J_u = -\mu\nabla u + \alpha(\nabla m)u, \quad J_v = -\nu\nabla v + \beta(\nabla m)v,$$

respectively, where  $\mu\nabla u$  and  $\nu\nabla v$  account for random diffusion, and  $\alpha(\nabla m)u$  and  $\beta(\nabla m)v$  represent movement upward along the environmental gradient. The two non-negative constants  $\alpha$  and  $\beta$  measure the tendency of the two populations to move up along the gradient of  $m(x)$ , and  $\mu$  and  $\nu$  represent the random diffusion rates of two species, respectively. If we assume that there is no flux across  $\partial\Omega$ , we obtain the competition model

$$(2.1) \quad \begin{cases} u_t = \nabla \cdot [\mu\nabla u - \alpha u \nabla m] + (m - u - v)u \\ v_t = \nabla \cdot [\nu\nabla v - \beta v \nabla m] + (m - u - v)v \end{cases}$$

in  $\Omega \times (0, \infty)$ , with no-flux boundary conditions

$$(2.2) \quad \mu\partial_n u - \alpha u \partial_n m = \nu\partial_n v - \beta v \partial_n m = 0$$

on  $\partial\Omega \times (0, \infty)$ , where the habitat  $\Omega$  is a bounded region in  $\mathbb{R}^N$  with smooth boundary  $\partial\Omega$ ,  $n$  is the outward unit normal vector on  $\partial\Omega$ , and  $\partial_n u := \nabla u \cdot n$ . The zero-flux boundary condition in (2.2) means that no individuals cross the boundary of the habitat.

Our model is derived by the widely used approach based on fluxes (see, *e.g.*, Murray [36]). It should be mentioned that advection-diffusion equations can also be derived as limits of discrete models based on random walks (see, *e.g.*, Okubo and Levin [37]) or from transport equations (see, *e.g.*, Hillen [21]). We refer the interested readers to Cantrell and Cosner [5], Hillen [21], Holmes et al. [24], Murray [36], Okubo and Levin [37], Shigesada and Kawasaki [42], and references therein for motivation, derivation, and analysis of reaction-diffusion-advection models for ecological problems.

Throughout this paper, we shall always assume that the function  $m(x)$  is non-constant to reflect the spatial heterogeneity of the environment. Moreover,  $m$  is assumed to be twice

continuously differentiable in  $\bar{\Omega}$  and

$$(2.3) \quad \int_{\Omega} m(x) dx > 0$$

so that the following equation has a unique positive solution, denoted as  $\theta = \theta(x; \alpha, \mu)$ , for every  $\mu > 0$  and every  $\alpha \geq 0$  (see [11]):

$$(2.4) \quad \nabla \cdot [\mu \nabla \theta - \alpha \theta \nabla m] + \theta(m - \theta) = 0 \quad \text{in } \Omega, \quad \mu \partial_n \theta - \alpha \theta \partial_n m = 0 \quad \text{on } \partial\Omega.$$

Hence, whenever (2.3) holds, (2.1)-(2.2) has two semi-trivial non-negative steady states, denoted by  $(\theta(x; \alpha, \mu), 0)$  and  $(0, \theta(x; \beta, \nu))$ , for every  $\mu > 0$ ,  $\nu > 0$ , and  $\alpha, \beta \geq 0$ . As will be seen later, the local stability of these two semi-trivial steady states has strong implications on the dynamics of the full system (2.1)-(2.2).

### 3. Previous Work

For the system (2.1)-(2.2) with  $\alpha = \beta = 0$ , it was shown in [13] that if  $\mu < \nu$ , then the semi-trivial steady state  $(0, \theta(x; 0, \nu))$  is unstable and  $(\theta(x; 0, \mu), 0)$  is globally asymptotically stable among non-negative non-trivial initial data. That is, *the slower diffuser is the winner*. If  $\mu = \nu$ , then (2.1)-(2.2) with  $\alpha = \beta = 0$  has a continuum of positive steady states of the form  $\{(s\theta(x; 0, \mu), (1-s)\theta(x; 0, \mu)) : 0 \leq s \leq 1\}$ , which attracts all non-negative non-trivial initial data.

For the case when  $\alpha > 0$  and  $\beta = 0$ , the system (2.1)-(2.2) was studied in [7, 8, 10]. Among other things, it was shown in [7, 8] that *if  $\Omega$  is convex,  $\mu = \nu$  and  $\beta = 0$ , then for positive small  $\alpha$ , the species  $u$  is always the winner, i.e., the semi-trivial steady state  $(\theta(x; \alpha, \mu), 0)$  is globally asymptotically stable*. Hence, at least for convex habitats, species with a small amount of biased movement have the advantage and biased movement can thus evolve. The convexity assumption on  $\Omega$  seems to be necessary as shown in [8]. It is rather interesting that the geometry of the habitat plays an important role in the evolution of dispersal.

In strong contrast to the case when  $\beta = 0$  and  $\alpha$  is positive small, it was shown in [8, 10] that *if the set of critical points of  $m(x)$  has Lebesgue measure zero, then for  $\beta = 0$  and large  $\alpha$ , both semi-trivial steady states are unstable and the system (2.1)-(2.2) has at least one stable positive steady state*. At the first look, such coexistence result appears to be counterintuitive. For instance, if  $\mu < \nu$  and  $\alpha$  is small, the species  $u$  always wins the competition, i.e., the slower diffuser wins. As  $\alpha$  increases, the species  $u$  has the tendency to move toward more favorable regions, so it should have more competitive advantage than the other species which moves around randomly. Loosely speaking, the species  $u$  looks “smarter” and should still be the sole winner of the competition. However, the above coexistence result informs us that the “smarter” species may not necessarily win the competition (of course, neither does it lose the competition in this case).

A biological explanation for such coexistence is that as  $\alpha$  becomes large, the “smarter” competitor moves toward and then concentrates at places of locally most favorable environments, leaving the other species to utilize other resources in the habitat. This is likely true

in general, and was shown in some situations. For instance, it was recently proved in [10] that when at equilibrium, the “smarter” species is concentrated at the global maximum of  $m(x)$ . More precisely, we proved in [10] that *if  $\partial_n m \leq 0$  on  $\partial\Omega$ , and there exists  $x_0 \in \Omega$  such that  $\{x \in \bar{\Omega} : \nabla m(x) = 0\} = \{x_0\}$  and  $\det(D^2 m(x_0)) \neq 0$ , then for any positive steady state solution  $(U, V)$  of (2.1)-(2.2) with  $\beta = 0$ , as  $\alpha \rightarrow \infty$ ,  $V \rightarrow \theta(\cdot; 0, \nu)$  in  $C^1(\bar{\Omega})$ , and*

$$(3.1) \quad U(x; \alpha) = e^{-(\alpha/\mu)[\max_{\bar{\Omega}} m - m(x)]} \{2^{N/2}[m(x_0) - \theta(x_0; 0, \nu)] + o(1)\}, \quad \forall x \in \bar{\Omega}.$$

Roughly speaking, this result says that if there is only one local maximum resource, then the “smarter” species is concentrated near this maximum. Interestingly, strong advection upward along environmental gradients provides a mechanism for coexistence of competing species. When  $m(x)$  has multiple local maxima, i.e, when there are multiple local maximum resources, it is an open problem whether the “smarter” species is concentrated near every local maximum of  $m(x)$ .

We also refer to Potapov and Lewis [39], Lutscher et al. [31, 32], and references therein for some other recent work on reaction-diffusion-advection models concerning the effects of dispersal patterns on competing species.

#### 4. Main results

Even though the dispersal strategies in (2.1)-(2.2) have same components for both species, i.e., random diffusion and biased movement along environmental gradients, they can be quite different: For instance, the species with stronger biased movement mainly pursues resources at places of locally most favorable environments, while the other species has a rather balanced dispersal strategy. In this paper, we study the case when both  $\alpha$  and  $\beta$  are positive, i.e., when both species are “smart”. Our main goal is to address the following issue:

**Question.** For arbitrary but fixed  $\beta > 0$ , do the two species always coexist if  $\alpha$  is sufficiently large?

By previous coexistence results for the case  $\beta = 0$  and ensuing discussions, one might naturally expect that the two species will still coexist stably. However, we will show that the answer depends crucially upon the ratio  $\beta/\nu$ , and at least two scenarios can occur. More precisely, we have the following two results which seem to complement and contrast each other. In the sequel,  $\mu$  and  $\nu$  are fixed positive constants.

**Theorem 1.** *Suppose that  $\int_{\Omega} m(x) dx > 0$  and that  $|\nabla m(x)| > 0$  for almost all  $x \in \Omega$ . Then there exists some positive constant  $\Lambda_1 = \Lambda_1(\mu, \nu, m, \Omega)$ , independent of  $\beta$ , such that when*

$$(4.1) \quad (\alpha, \beta) \in [\Lambda_1, \infty) \times \left[0, \frac{\nu}{\max_{\bar{\Omega}} m}\right],$$

*the following hold:*

- (1) **(invasion)** *both semi-trivial states  $(\theta(x; \alpha, \mu), 0)$  and  $(0, \theta(x; \beta, \nu))$  are unstable;*

- (2) **(coexistence)** *the system (2.1)-(2.2) has at least one stable positive steady state;*
- (3) **(concentration)** *for any positive steady state  $(U, V)$  of (2.1)-(2.2),  $\|U\|_{L^2(\Omega)} \rightarrow 0$  as  $\alpha \rightarrow \infty$ . If we further assume that the function  $m$  has at least one isolated global maximum, then there exists some positive constant  $\delta_0$  such that  $\max_{\bar{\Omega}} U \geq \delta_0$  for every  $(\alpha, \beta)$  in the range (4.1).*

Theorem 1 generalizes some of the main results in [8, 10] for the case  $\beta = 0$  as discussed earlier. What happens if  $\beta/\nu$  is suitably larger? It turns out that the answer is dramatically different and a new phenomenon occurs. To this end, we first introduce a technical condition on the function  $m(x)$ .

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

Here  $D^2m(x_0)$  denotes the Hessian matrix of the function  $m(x)$  at  $x = x_0$ , and  $D^2m(x_0) < 0$  means that the matrix is negative definite. Biologically, assumption (A1) means that the resource distribution has a unique maximum and it is located inside the habitat.

**Theorem 2.** *Suppose that  $m > 0$  in  $\bar{\Omega}$  and assumption (A1) holds. There exists an increasing function  $\Lambda_2(\cdot)$  defined on  $[\nu/\min_{\bar{\Omega}} m, \infty)$  such that when*

$$(4.2) \quad \alpha \geq \Lambda_2(\beta), \quad \beta \in \left[ \frac{\nu}{\min_{\bar{\Omega}} m}, \infty \right),$$

*the steady state  $(0, \theta(x; \beta, \nu))$  is globally asymptotically stable.*

Our results have applications to the evolution of dispersal and population dynamics.

- (1) Theorem 1 implies that strong advection along resource gradients can provide a new mechanism for the coexistence of two competing species. The biological insight is that if only one competitor has strong tendency to move upward along the gradient of  $m(x)$  and concentrate at places of locally most favorable environments, there will be no overcrowding and coexistence of two species can occur as the other species can rely on resources from other parts of the habitat.
- (2) Theorem 2 shows that strong advection along resource gradients can be disadvantageous under some circumstances, and can cause the extinction of the species which only pursues most favorable resources. From the biological point of view, strong biased movement along the gradient of  $m(x)$  of both species can induce overmatching of resources for both species at places of locally most favorable environments and thus lead to overcrowding of the whole population at such locations, which causes the extinction of the species which puts all of its bets on such places.

These results indicate that very strong advection along resource gradients can be disadvantageous and, under some circumstances, can cause the extinction of the species which only pursues most favorable resources. Previous result in [8] implies that at least for convex habitats, species with a small amount of biased movement can have the advantage (corresponding to the case when  $\alpha$  is positive small and  $\beta = 0$ ). These results for large and small advection suggest the possibility of a threshold value for the ratio  $\beta/\nu$  in the interval  $(1/\max_{\bar{\Omega}} m, 1/\min_{\bar{\Omega}} m)$ , and that the dispersal strategy with such intermediate biased movement rate may be evolutionarily stable since a balanced combination of random and biased movement may help the species better match the resources.

Our results combined can also assess the degree of crowding induced by the directed movement along the gradient of  $m(x)$ , determine when and where the overcrowding occurs, and give a qualitative prediction about the effects of crowding on the outcome of the competition, *i.e.*, coexistence or extinction. More detailed discussions, from both mathematical and biological point of views, will be given in Sect. 9.

The rest of the paper is organized as follows. In Sect. 5 we present some preliminary results. Sect. 6 is concerned with the stability of the two semi-trivial steady states. Sect. 7 is devoted to the proof of Theorem 1, and Theorem 2 will be established in Sect. 8. Finally, in Sect. 9 we will discuss our main results and their implications from both mathematical and biological point of views. Some open problems will also be touched upon.

## 5. Preliminary results

In this section we study various properties of  $\theta(x; \alpha, \mu)$ , which will be crucial in the proofs of Theorems 1 and 2.

**Lemma 5.1.** *If  $m$  is a non-constant function, then*

$$(5.1) \quad \min_{\bar{\Omega}} (me^{-(\alpha/\mu)m}) < e^{-(\alpha/\mu)m(x)}\theta(x; \alpha, \mu) < \max_{\bar{\Omega}} (me^{-(\alpha/\mu)m})$$

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

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

$$(5.2) \quad \mu \nabla \cdot [e^{(\alpha/\mu)m} \nabla w] + e^{(\alpha/\mu)m} w [m - e^{(\alpha/\mu)m} w] = 0 \quad \text{in } \Omega, \quad \partial_n w = 0 \quad \text{on } \partial\Omega.$$

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

$$(5.3) \quad \mu \Delta w + \alpha \nabla m \cdot \nabla w + w [m - e^{(\alpha/\mu)m} w] = 0 \quad \text{in } \Omega, \quad \partial_n w = 0 \quad \text{on } \partial\Omega.$$

Let  $x_0 \in \bar{\Omega}$  be a point such that  $w(x_0) = \max_{\bar{\Omega}} w$ . By the Hopf Boundary Lemma [40], for both cases  $x_0 \in \Omega$  and  $x_0 \in \partial\Omega$ , we have  $\nabla w(x_0) = 0$ , and  $\Delta w(x_0) \leq 0$ . Hence, by (5.3) we get

$$(5.4) \quad \max_{\bar{\Omega}} w = w(x_0) \leq m(x_0) e^{-(\alpha/\mu)m(x_0)} \leq \max_{\bar{\Omega}} (me^{-(\alpha/\mu)m}).$$

Next we show the second inequality in (5.1) is strict. Let  $M_1 = \max_{\bar{\Omega}} (me^{-(\alpha/\mu)m})$  and set  $w_1(x) = M_1 - w(x)$ . Then  $w_1$  satisfies

$$(5.5) \quad -\mu\Delta w_1 - \alpha\nabla w_1 \cdot \nabla m + e^{(\alpha/\mu)m}(M_1 - w_1) [me^{-(\alpha/\mu)m} - M_1 + w_1] = 0 \quad \text{in } \Omega.$$

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

$$-\mu\Delta w_1 - \alpha\nabla w_1 \cdot \nabla m + e^{(\alpha/\mu)m}w_1(2M_1 - me^{-(\alpha/\mu)m} - w_1) = e^{(\alpha/\mu)m}M_1 [M_1 - me^{-(\alpha/\mu)m}] \geq 0,$$

where the last inequality is not identically zero since  $m$  is a non-constant function. Recall that  $\partial_n w_1 = 0$  on  $\partial\Omega$ , and by (5.4),  $w_1 \geq 0$  in  $\bar{\Omega}$ . By the Strong Maximum Principle [40], we have  $w_1 > 0$  in  $\bar{\Omega}$ . This establishes the second inequality in (5.1). For the first inequality, the proof is trivial if  $m$  is non-positive somewhere in  $\bar{\Omega}$ , hence it suffices to consider the case when  $m > 0$  in  $\bar{\Omega}$ . Since the proof is almost identical to that of the second inequality, we omit it.  $\square$

Define

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

**Lemma 5.2.** *Suppose that  $m$  is a non-constant function.*

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

$$(5.6) \quad \theta(x; \alpha, \mu) < m^* \cdot e^{(\alpha/\mu)[m(x)-m^*]}$$

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

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

$$(5.7) \quad \theta(x; \alpha, \mu) > m^* \cdot e^{(\alpha/\mu)[m(x)-m^*]}$$

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

**Proof.** By Lemma 5.1, we have

$$(5.8) \quad e^{-(\alpha/\mu)m(x)}\theta(x; \alpha, \mu) < \max_{\bar{\Omega}} (me^{-(\alpha/\mu)m})$$

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

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

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

$$(5.9) \quad \max_{\bar{\Omega}} (me^{-(\alpha/\mu)m}) \leq m^* e^{-(\alpha/\mu)m^*}.$$

This along with (5.8) establishes the estimate (5.6).

For the proof of part (ii), note that  $ye^{-(\alpha/\mu)y}$  is strictly decreasing for  $y > \mu/\alpha$ . Hence, if  $m > 0$  in  $\bar{\Omega}$  and  $\alpha/\mu > 1/\min_{\bar{\Omega}} m$ , we have

$$(5.10) \quad m(x)e^{-(\alpha/\mu)m(x)} \geq m^* \cdot e^{-(\alpha/\mu)m^*}$$

for every  $x \in \bar{\Omega}$ . Part (ii) follows from Lemma 5.1 and (5.10).  $\square$

By assumption (A1), there exist positive constants  $\kappa_0$ ,  $\kappa_1$ , and  $\kappa_2$  such that

$$(5.11) \quad |\nabla m(x)| \geq \kappa_0 |x - x_0|, \quad \kappa_2 |x - x_0|^2 \geq m^* - m(x) \geq \kappa_1 |x - x_0|^2 \quad \forall x \in \bar{\Omega}.$$

This property, together with  $\partial_n m < 0$  on  $\partial\Omega$  enables us to prove the following.

**Lemma 5.3.** *Suppose that assumption (A1) holds. There exists a positive constant  $K$ , independent of  $\alpha$ , such that*

$$(5.12) \quad \theta(x; \alpha, \mu) \leq K e^{(\alpha/\mu)[m(x)-m^*]} \quad \forall x \in \bar{\Omega}.$$

**Proof.** Without loss of generality, assume that  $\mu = 1$  and abbreviate  $\theta(x; \alpha, \mu)$  either as  $\theta(x; \alpha)$  or simply as  $\theta$ . By the maximum principle and choosing  $K$  suitably, we see that (5.12) holds uniformly for  $\alpha \in [0, 2]$ . Hence, it suffices to consider the situation when  $\alpha \geq 2$ . Consider the function

$$w(x) = w(x; \alpha) = e^{-(\alpha-1)m(x)} \theta(x; \alpha).$$

Then in  $\Omega$ ,  $w$  satisfies

$$\Delta w + (\alpha - 2) \nabla m \cdot \nabla w - [(\alpha - 1) |\nabla m|^2 + \Delta m + \theta - m] w = 0.$$

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

$$(5.13) \quad (\alpha - 1) |\nabla m(z^*)|^2 + \Delta m(z^*) + \theta(z^*; \alpha) \leq m(z^*).$$

Hence,

$$(5.14) \quad (\alpha - 1) |\nabla m(z^*)|^2 \leq m^* - \Delta m(z^*) \leq \|m\|_{C^2(\bar{\Omega})}$$

and

$$\theta(z^*; \alpha) \leq m(z^*) - \Delta m(z^*) \leq \|m\|_{C^2(\bar{\Omega})}.$$

It follows from (5.11) and (5.14) that

$$(\alpha - 1) [m^* - m(z^*)] \leq \frac{\kappa_2 (\alpha - 1)}{\kappa_0^2} |\nabla m(z^*)|^2 \leq \frac{\kappa_2 \|m\|_{C^2(\bar{\Omega})}}{\kappa_0^2}.$$

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

$$\begin{aligned} e^{-\alpha[m(x)-m^*]} \theta(x; \alpha) &\leq e^{-\alpha[m(x)-m^*]} \theta(z^*, \alpha) e^{(\alpha-1)[m(x)-m(z^*)]} \\ &= \theta(z^*, \alpha) e^{[m^*-m(x)]+(\alpha-1)[m^*-m(z^*)]} \\ &\leq \|m\|_{C^2(\bar{\Omega})} e^{2\|m\|_\infty + (\kappa_2/\kappa_0^2)\|m\|_{C^2(\bar{\Omega})}} =: K \quad \forall x \in \bar{\Omega}. \end{aligned}$$

This implies (5.12).  $\square$

Next we consider the following eigenvalue problem:

$$(5.15) \quad -\Delta \varphi - \alpha \nabla m \cdot \nabla \varphi + c \varphi = \lambda(\alpha) \varphi \quad \text{in } \Omega, \quad \partial_n \varphi = 0 \quad \text{on } \partial\Omega, \quad \varphi > 0 \quad \text{on } \bar{\Omega},$$

where  $m \in C^2(\bar{\Omega})$  and  $c \in C(\bar{\Omega})$ . The following result was established in [10]:

**Theorem 3** ([10]). *Assume that all critical points of  $m$  are non-degenerate. Let  $\mathcal{M}$  be the set of points of local maximum of  $m$ . Then*

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

We also show that the system (2.1)-(2.2) is a strongly monotone one.

**Lemma 5.4.** *Let  $(u_i(x, t), v_i(x, t))$ ,  $i = 1, 2$ , be two solutions of (2.1)-(2.2),  $u_1(x, 0) \geq u_2(x, 0)$  and  $v_1(x, 0) \leq v_2(x, 0)$  for  $x \in \Omega$ . Then  $u_1(x, t) \geq u_2(x, t)$  and  $v_1(x, t) \leq v_2(x, t)$  for  $x \in \Omega$  and  $t > 0$ . If we further assume that  $(u_1(x, 0), v_1(x, 0)) \not\equiv (u_2(x, 0), v_2(x, 0))$ , then  $u_1(x, t) > u_2(x, t)$  and  $v_1(x, t) < v_2(x, t)$  for  $x \in \bar{\Omega}$  and  $t > 0$ .*

**Proof.** Set  $w_i = e^{-(\alpha/\mu)m}u_i$  and  $z_i = e^{-(\beta/\nu)m}v_i$ . Then (2.1)-(2.2) become

$$(5.16) \quad \begin{cases} w_{i,t} = \mu \Delta w_i + \alpha \nabla m \cdot \nabla w_i + [m - e^{(\alpha/\mu)m}w_i - e^{(\beta/\nu)m}z_i] w_i & \text{in } \Omega \times (0, \infty), \\ z_{i,t} = \nu \Delta z_i + \beta \nabla m \cdot \nabla z_i + [m - e^{(\alpha/\mu)m}w_i - e^{(\beta/\nu)m}z_i] z_i & \text{in } \Omega \times (0, \infty), \\ \partial_n w_i = \partial_n z_i = 0 & \text{on } \partial\Omega \times (0, \infty). \end{cases}$$

Since  $w_1(x, 0) \geq w_2(x, 0)$ ,  $z_1(x, 0) \leq z_2(x, 0)$ , and (5.16) is a monotone dynamical system [20, 26], by the maximum principle [40] we have  $w_1(x, t) \geq w_2(x, t)$  and  $z_1(x, t) \leq z_2(x, t)$ . The rest of the proof follows similarly from the strong maximum principle [40].  $\square$

The following fact will be used in our subsequent analysis.

**Lemma 5.5.** *The steady state  $(0, \theta(\cdot; \beta, \nu))$  is stable/unstable if and only if the following eigenvalue problem, for  $(\lambda_1, \psi) \in \mathbb{R} \times C^2(\bar{\Omega})$ , has a positive/negative principal eigenvalue  $\lambda_1$ :*

$$(5.17) \quad \begin{cases} \nabla \cdot (\mu \nabla \varphi - \alpha \varphi \nabla m) + [m - \theta(\cdot; \beta, \nu)] \varphi = -\lambda_1 \varphi & \text{in } \Omega, \\ \mu \partial_n \varphi - \alpha \varphi \partial_n m = 0 & \text{on } \Omega, \quad \varphi > 0 \text{ on } \bar{\Omega}. \end{cases}$$

*The criterion for the stability of the steady state  $(\theta(\cdot; \alpha, \mu), 0)$  is analogous.*

**Proof.** The full system for the eigenvalue problem is

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

with no-flux boundary conditions.

Suppose the steady state  $(0, \theta(\cdot; \beta, \nu))$  is unstable. Then there is a non-trivial solution  $(\lambda, \varphi, \psi)$  with  $\text{Re}(\lambda) < 0$ . Consider two cases: (i)  $\varphi \not\equiv 0$  (ii)  $\varphi \equiv 0$ .

In case (i), we conclude that  $\mathcal{L}_1$  has an eigenvalue with negative real parts. Hence its principal eigenvalue  $\lambda_1$  is negative and (5.17) admits a solution.

Case (ii) does not happen since the principle eigenvalue of  $\mathcal{L}_2$  is positive. To see this, let  $(\lambda, \psi)$  be an principal eigen pair of  $\mathcal{L}_2$ . Then  $\psi > 0$ . Using the equation satisfied by

$\theta := \theta(\cdot; \beta, \nu)$  we can derive

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

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

Next, suppose the steady state  $(0, \theta(\cdot; \beta, \nu))$  is stable. Then (5.17) cannot have a solution with  $\lambda_1 \leq 0$ . Indeed, suppose it has a solution with  $\lambda_1 \leq 0$ . Then since the principal eigenvalue of  $\mathcal{L}_2$  is positive, there is a unique solution  $\psi$  of  $(\mathcal{L}_2 - \lambda_1)\psi = -\theta\varphi$ . This implies that the full linearized problem has a non-trivial solution  $(\lambda, \varphi, \psi)$  with  $\lambda = \lambda_1 \leq 0$ . But this contradicts the assumption that the steady state  $(0, \theta(\cdot; \beta, \nu))$  is (linearly) stable.  $\square$

## 6. Stability of Two Semi-trivial Steady States

This section is devoted to the study of linearized stability of both semi-trivial steady states, which will be needed in the proofs of the main results. Besides, the stability of semi-trivial steady states is of independent interest since it is related to the invasion of species when they are rare.

**6.1. Stability of  $(\theta(x; \alpha, \mu), 0)$ .** For the stability of the semi-trivial steady state  $(\theta(x; \alpha, \mu), 0)$ , it suffices to consider the smallest eigenvalue, denoted as  $\lambda_1$ , of the eigenvalue problem

$$(6.1) \quad \nabla \cdot [\nu \nabla \psi - \beta \psi \nabla m] + [m - \theta(x; \alpha, \mu)] \psi = -\lambda_1 \psi \quad \text{in } \Omega, \quad \nu \partial_n \psi - \beta \psi \partial_n m = 0 \quad \text{on } \partial\Omega.$$

For the sake of simplicity, we sometimes abbreviate  $\theta(x; \alpha, \mu)$  as  $\theta$  in this subsection.

**Lemma 6.1.** *For any  $\beta \geq 0$ ,  $\int_{\Omega} m e^{(\beta/\nu)m} \geq \int_{\Omega} m$ .*

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

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

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

The following result was established in [8]:

**Lemma 6.2.** *Suppose that the set of critical points of  $m$  has measure zero. Then*

$$(6.2) \quad \lim_{\alpha \rightarrow \infty} \int_{\Omega} \theta^2(x; \alpha, \mu) dx = 0.$$

We are now ready to establish the instability of  $(\theta, 0)$ :

**Lemma 6.3.** *Suppose that  $\int_{\Omega} m > 0$  and the set of critical points of  $m$  has measure zero. For any  $\eta > 0$ , there exists a positive constant  $\Lambda_3 = \Lambda_3(\eta)$  such that for every  $\beta \in [0, \eta]$  and  $\alpha \geq \Lambda_3(\eta)$ ,  $(\theta, 0)$  is unstable.*

**Proof.** Let  $\psi > 0$  denote the eigenfunction of  $\lambda_1$  uniquely determined by  $\max_{\bar{\Omega}} \psi = 1$ . We consider the following equivalent form of (6.1):

$$(6.3) \quad \nu \nabla \cdot [e^{(\beta/\nu)m} \nabla (e^{-(\beta/\nu)m} \psi)] + (m - \theta) \psi = -\lambda_1 \psi.$$

Dividing (6.3) by  $e^{-(\beta/\nu)m} \psi$  and integrating over  $\Omega$ , we have

$$(6.4) \quad \int_{\Omega} \frac{\nu \nabla \cdot [e^{(\beta/\nu)m} \nabla (e^{-(\beta/\nu)m} \psi)]}{e^{-(\beta/\nu)m} \psi} + \int_{\Omega} (m - \theta) e^{(\beta/\nu)m} = -\lambda_1 \int_{\Omega} e^{(\beta/\nu)m}.$$

Using the divergence theorem and the boundary condition for  $\psi$ , we find

$$(6.5) \quad \int_{\Omega} \frac{\nu \nabla \cdot [e^{(\beta/\nu)m} \nabla (e^{-(\beta/\nu)m} \psi)]}{e^{-(\beta/\nu)m} \psi} = \int_{\Omega} \frac{\nu e^{(\beta/\nu)m}}{(e^{-(\beta/\nu)m} \psi)^2} \cdot |\nabla (e^{-(\beta/\nu)m} \psi)|^2 \geq 0.$$

Hence,

$$(6.6) \quad \begin{aligned} -\lambda_1 \int_{\Omega} e^{(\beta/\nu)m} &\geq \int_{\Omega} (m - \theta) e^{(\beta/\nu)m} = \int_{\Omega} m e^{(\beta/\nu)m} - \int_{\Omega} \theta e^{(\beta/\nu)m} \\ &\geq \int_{\Omega} m e^{(\beta/\nu)m} - e^{(\beta/\nu)m^*} \int_{\Omega} \theta \\ &\geq \int_{\Omega} m - e^{(\eta/\nu)m^*} \int_{\Omega} \theta \geq \frac{1}{2} \int_{\Omega} m > 0 \end{aligned}$$

provided that  $\alpha \geq \Lambda_4 = \Lambda_4(\eta)$ , where the last inequality follows from  $\lim_{\alpha \rightarrow \infty} \int_{\Omega} \theta = 0$ . Therefore,  $\lambda_1 < 0$  provided that  $\alpha \geq \Lambda_4$ .  $\square$

**6.2. Stability of  $(0, \theta(x; \beta, \nu))$ .** In this section we consider the stability of  $(0, \theta(x; \beta, \nu))$ . For the sake of simplicity we sometimes abbreviate  $\theta(x; \beta, \nu)$  as  $\theta$ . We first establish the following preliminary result.

**Lemma 6.4.** *Suppose that  $m$  is a non-constant function and  $\int_{\Omega} m > 0$ . There exists a positive constant  $\Lambda_5 = \Lambda_5(\mu, \nu, m, \Omega)$  such that if  $0 \leq \beta \leq \nu / \max_{\bar{\Omega}} m$  and  $\alpha \geq \Lambda_5$ , we have*

$$(6.7) \quad \int_{\Omega} e^{(\alpha/\mu)m} (m - \theta) > 0.$$

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

$$(6.8) \quad \int_{\Omega} e^{(\alpha/\mu)(m - \|\theta\|_{\infty})} (m - \theta) = \int_{\Omega_+} e^{(\alpha/\mu)(m - \|\theta\|_{\infty})} (m - \theta) + \int_{\Omega_-} e^{(\alpha/\mu)(m - \|\theta\|_{\infty})} (m - \theta).$$

By part (i) of Lemma 5.2,  $\|\theta\|_{\infty} \leq \|m\|_{\infty}$  provided that  $\beta/\nu \leq 1 / \max_{\bar{\Omega}} m$ . Hence,

$$(6.9) \quad \left| \int_{\Omega_+} e^{(\alpha/\mu)(m - \|\theta\|_{\infty})} (m - \theta) \right| \leq \int_{\Omega_+} e^{(\alpha/\mu)(m - \|\theta\|_{\infty})} |m - \theta| \leq \int_{\Omega_+} |m - \theta| \leq 2 \|m\|_{\infty} |\Omega|.$$

Set

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

By part (i) of Lemma 5.2 and the continuity of  $\theta(x; \beta, \nu)$  with respect to  $\beta$ , we have  $\epsilon > 0$ .

Let  $x_0$  be a point such that  $m(x_0) = \max_{\bar{\Omega}} m$ . By part (i) of Lemma 5.2,  $x_0 \in \Omega_-$ . Hence, again by the continuity of  $\theta(x; \beta, \nu)$  with respect to  $\beta$ , we can choose  $\delta > 0$ , independent of  $\beta$ , such that for every  $\beta \in [0, \nu / \max_{\bar{\Omega}} m]$ ,

$$(6.10) \quad m(x) - \|\theta\|_{\infty} \geq \frac{1}{2} (\max_{\bar{\Omega}} m - \|\theta\|_{\infty}) \geq \epsilon, \quad \text{if } |x - x_0| \leq \delta.$$

Then

$$(6.11) \quad \begin{aligned} \int_{\Omega_-} e^{(\alpha/\mu)(m-\|\theta\|_{\infty})} (m - \theta) &\geq \int_{\{x \in \Omega : |x - x_0| \leq \delta\}} e^{(\alpha/\mu)(m-\|\theta\|_{\infty})} (m - \theta) \\ &\geq \int_{\{x \in \Omega : |x - x_0| \leq \delta\}} e^{(\alpha/\mu)\epsilon} \cdot \epsilon \\ &= \epsilon \cdot e^{(\alpha/\mu)\epsilon} |\{x \in \Omega : |x - x_0| \leq \delta\}| \rightarrow \infty \end{aligned}$$

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

$$(6.12) \quad \int_{\Omega} e^{(\alpha/\mu)(m-\|\theta\|_{\infty})} (m - \theta) > 0$$

provided that  $\alpha \geq \Lambda_5$ , where  $\Lambda_5$  is some positive constant independent of  $\alpha$  and  $\beta$ . Hence, (6.7) holds for  $\alpha \geq \Lambda_5$  and  $\beta/\nu \leq 1/\max_{\bar{\Omega}} m$ .  $\square$

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

**Lemma 6.5.** *Suppose that  $m$  is a non-constant function and  $\int_{\Omega} m > 0$ . If  $\alpha \geq \Lambda_5$  and  $0 \leq \beta \leq \nu / \max_{\bar{\Omega}} m$ , then  $(0, \theta(x; \beta, \nu))$  is unstable.*

**Proof.** We want to show that the principal eigenvalue, denoted by  $\lambda_1$ , for the problem

$$(6.13) \quad \nabla \cdot [\mu \nabla \varphi - \alpha \varphi \nabla m] + \varphi(m - \theta) = -\lambda \varphi \quad \text{in } \Omega, \quad \mu \partial_n \varphi - \alpha \varphi \partial_n m = 0 \quad \text{on } \partial \Omega$$

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

$$\mu \nabla \cdot [e^{(\alpha/\mu)m} \nabla \psi] + e^{(\alpha/\mu)m} \psi (m - \theta) = -\lambda_1 e^{(\alpha/\mu)m} \psi \quad \text{in } \Omega, \quad \partial_n \psi = 0 \quad \text{on } \partial \Omega.$$

We divide the differential equation by  $\psi$  and integrate over  $\Omega$  to get

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

The first integral in the left hand side is clearly non-negative. By Lemma 6.4, the second integral in the left hand side is positive for  $\alpha \geq \Lambda_5$  and  $0 \leq \beta/\nu \leq 1/\min_{\bar{\Omega}} m$ , thus we have  $\lambda_1 < 0$ .  $\square$

In strong contrast to Lemma 6.5, we have the following result.

**Lemma 6.6.** *Suppose that (A1) holds and  $m > 0$  in  $\bar{\Omega}$ . For any number  $\eta > 1/\min_{\bar{\Omega}} m$ , there exists some positive constant  $\Lambda_6 = \Lambda_6(\mu, \nu, m, \Omega, \eta)$  such that for  $\alpha \geq \Lambda_6$  and  $\beta/\nu \in [1/\min_{\bar{\Omega}} m, \eta]$ ,  $(0, \theta(x; \beta, \nu))$  is stable.*

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

$$\nabla \cdot [\mu \nabla \varphi - \alpha_i \varphi \nabla m] + \varphi [m - \theta(\cdot; \beta_i, \nu)] = -\lambda_i \varphi \quad \text{in } \Omega, \quad \mu \partial_n \varphi - \alpha_i \varphi \partial_n m = 0 \quad \text{on } \partial\Omega$$

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

$$(6.14) \quad \mu \Delta \psi_i + \alpha_i \nabla \psi_i \cdot \nabla m + \psi_i [m - \theta(\cdot; \beta_i, \nu)] = -\lambda_i \psi_i \quad \text{in } \Omega, \quad \partial_n \psi_i = 0 \quad \text{on } \partial\Omega.$$

Passing to a subsequence if necessary, we may assume that  $\beta_i \rightarrow \beta$  for some  $\beta/\nu \geq 1/\min_{\bar{\Omega}} m$ . By assumption (A1),  $\mathcal{M} = \{x_0\}$ . From part (ii) of Lemma 5.2 (with  $\alpha, \mu$  being replaced by  $\beta, \nu$ , respectively), we have  $-m(x_0) + \theta(x_0; \beta, \nu) > 0$ . Set

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

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

$$(6.15) \quad \mu \Delta \psi + \alpha_i \nabla \psi \cdot \nabla m + \psi [m - \theta(\cdot; \beta, \nu) + \epsilon] = -\lambda \psi \quad \text{in } \Omega, \quad \partial_n \psi = 0 \quad \text{on } \partial\Omega.$$

Since  $\theta(\cdot; \beta_i, \nu) \rightarrow \theta(\cdot; \beta, \nu)$  in  $L^\infty$ , for sufficiently large  $i$  we have  $\theta(\cdot; \beta_i, \nu) \geq \theta(\cdot; \beta, \nu) - \epsilon$  in  $\bar{\Omega}$ . By the comparison principle for principal eigenvalues we have  $\lambda_i \geq \lambda_i(\epsilon)$  for large  $i$ . This together with assumption  $\lambda_i \leq 0$  imply that  $\lambda_i(\epsilon) \leq 0$  for large  $i$ . However, by Theorem 3 in Sect. 5 we have

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

where the last inequality follows from the definition of  $\epsilon$ . This contradiction finishes the proof.  $\square$

## 7. Advection-induced coexistence and concentration

This section is devoted to the proof of Theorem 1. The instability of the two semi-trivial steady states  $(\theta(x; \alpha, \mu), 0)$  and  $(0, \theta(x; \beta, \nu))$  have been established in Lemmas 6.3 and 6.5, respectively. The existence of one stable positive steady state follows from the instability of  $(\theta(x; \alpha, \mu), 0)$  and  $(0, \theta(x; \beta, \nu))$  and monotone dynamical system theory [33, 22, 12]. In fact, according to a recent result in [23], (2.1)-(2.2) has at least one asymptotically stable positive steady state. This proves parts (i) and (ii) of Theorem 1.

Let  $(U, V)$  denote any positive steady state of (2.1)-(2.2). By the comparison principle, we have  $U \leq \theta(x; \alpha, \mu)$ . Hence, by Lemma 6.2, we have  $\|U\|_{L^2(\Omega)} \rightarrow 0$  as  $\alpha \rightarrow \infty$ .

Therefore, to complete the proof of Theorem 1, it suffices to establish the uniform lower bound of  $\max_{\bar{\Omega}} U$  for sufficiently large  $\alpha$ . To this end, we first show that if  $m$  has an isolated global maximum, then the principal eigenvalue  $\lambda_1$  of (6.13) is uniformly bounded from below

by some positive constant for sufficiently large  $\alpha$ . The uniform lower bound for  $U$  is then established in Lemma 7.2.

**Lemma 7.1.** *Suppose that  $\int_{\Omega} m > 0$  and  $m$  has an isolated global maximum, i.e., there exist  $x_0 \in \Omega$  and  $\epsilon > 0$  such that  $m(x_0) = \max_{\bar{\Omega}} m$  and  $m(x_0) > m(x)$  for every  $x \in B_{\epsilon}(x_0) \cap \Omega \setminus \{x_0\}$ . Then there exists  $\delta_0 > 0$  independent of  $\alpha$  such that for large  $\alpha$ ,  $\lambda_1 \leq -\delta_0$ .*

**Proof.** By variational characterizations of principal eigenvalues,

$$(7.1) \quad \lambda_1 = \inf_{\psi \neq 0, \psi \in C^1(\bar{\Omega})} \frac{\mu \int_{\Omega} e^{(\alpha/\mu)m} |\nabla \psi|^2 - \int_{\Omega} (m - \theta) e^{(\alpha/\mu)m} \psi^2}{\int_{\Omega} e^{(\alpha/\mu)m} \psi^2}$$

Let  $x_0$  be an isolated maximum of  $m$ . By part (i) of Lemma 5.2 and the continuity of  $\theta(x; \beta, \nu)$  with respect to  $\beta$ , we can choose  $R_1 > 0$ , independent of  $\beta$ , such that for every  $\beta \in [0, \nu / \max_{\bar{\Omega}} m]$ ,

$$(7.2) \quad C_0 := \min_{x \in B_{R_1}(x_0) \cap \bar{\Omega}} [m(x) - \theta(x; \beta, \nu)] > 0,$$

where  $B_{R_1}(x_0)$  is the closed ball centered at  $x_0$  with radius  $R_1$ . For the sake of simplicity, we denote  $B_{R_1}(x_0) \cap \bar{\Omega}$  by  $B_R$  for any  $R > 0$ . Here and thereafter,  $C_i$  ( $i = 1, 2, \dots$ ) denote positive constants which are independent of  $\alpha$  and  $\beta \in [0, \nu / \max_{\bar{\Omega}} m]$ .

Since  $m$  has an isolated global maximum at  $x_0$ , we can choose  $R_2 > 0$  with  $R_2 \leq R_1/2$  such that

$$(7.3) \quad \min_{B_{R_2}} m > \max_{B_{R_1} \setminus B_{R_1/2}} m.$$

For simplicity, let  $M_1 = \max_{B_{R_1} \setminus B_{R_1/2}} m$ ,  $M_2 = \min_{B_{R_2}} m$ . Therefore,  $M_1 < M_2$ .

Choose a test function  $\psi \in C^1(\bar{\Omega})$  such that

$$(7.4) \quad \psi = \begin{cases} 1 & \text{in } B_{R_1/2}, \\ \in [0, 1] & \text{in } (B_{R_1} \setminus B_{R_1/2}), \\ 0 & \text{otherwise,} \end{cases}$$

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

$$(7.5) \quad \lambda_1 \leq \frac{\mu \int_{\Omega} e^{(\alpha/\mu)m} |\nabla \psi|^2}{\int_{\Omega} e^{(\alpha/\mu)m} \psi^2} - \frac{\int_{\Omega} (m - \theta) e^{(\alpha/\mu)m} \psi^2}{\int_{\Omega} e^{(\alpha/\mu)m} \psi^2}.$$

Since

$$(7.6) \quad \begin{aligned} \mu \int_{\Omega} e^{(\alpha/\mu)m} |\nabla \psi|^2 &= \mu \int_{(B_{R_1} \setminus B_{R_1/2})} e^{(\alpha/\mu)m} |\nabla \psi|^2 \\ &\leq \mu C_1^2 \int_{B_{R_1} \setminus B_{R_1/2}} e^{(\alpha/\mu)m} \leq C_2 e^{(\alpha/\mu)M_1}, \end{aligned}$$

$$(7.7) \quad \int_{\Omega} e^{(\alpha/\mu)m} \psi^2 \geq \int_{B_{R_2}} e^{(\alpha/\mu)m} \psi^2 \geq C_3 e^{(\alpha/\mu)M_2},$$

and

$$(7.8) \quad \begin{aligned} \int_{\Omega} (m - \theta) e^{(\alpha/\mu)m} \psi^2 &= \int_{B_{R_1}} (m - \theta) e^{(\alpha/\mu)m} \psi^2 \\ &\geq C_0 \int_{B_{R_1}} e^{(\alpha/\mu)m} \psi^2 = C_0 \int_{\Omega} e^{(\alpha/\mu)m} \psi^2, \end{aligned}$$

we have

$$(7.9) \quad \lambda_1 \leq \frac{C_2}{C_3} e^{(\alpha/\mu)(M_1 - M_2)} - C_0 \leq -\frac{1}{2} C_0$$

for sufficiently large  $\alpha$ , which completes the proof.  $\square$

**Lemma 7.2.** *Suppose that  $m$  has an isolated global maximum. For  $\alpha \gg 1$ ,  $\|U\|_{L^\infty(\Omega)} \geq \delta_0$ , where  $\delta_0$  is given in Lemma 7.1.*

*Proof.* By comparison principle, for any positive steady state  $(U, V)$  of (2.1)-(2.2), we have  $V \leq \theta(x; \beta, \nu)$  (in the following we abbreviate  $\theta(x; \beta, \nu)$  as  $\theta$ ). Thus

$$(7.10) \quad \nabla \cdot [\mu \nabla U - \alpha U \nabla m] + U(m - \theta - U) \leq 0.$$

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

$$(7.11) \quad \nabla \cdot [\mu \nabla u^* - \alpha u^* \nabla m] + u^*(m - \theta - u^*) = 0 \quad \text{in } \Omega, \quad \mu \partial_n u^* - \alpha u^* \partial_n m = 0 \quad \text{on } \partial\Omega.$$

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

$$(7.12) \quad \nabla \cdot [\mu \nabla \varphi - \alpha \varphi \nabla m] + \varphi(m - \theta) = -\lambda \varphi \quad \text{in } \Omega, \quad \mu \partial_n \varphi - \alpha \varphi \partial_n m = 0 \quad \text{on } \partial\Omega.$$

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

$$(7.13) \quad \nabla \cdot [\mu \nabla(\delta\varphi) - \alpha(\delta\varphi) \nabla m] + (\delta\varphi)(m - \theta - \delta\varphi) = (\delta\varphi)[- \lambda_1 - \delta\varphi] \geq (\delta\varphi)(- \lambda_1 - \delta) \geq 0.$$

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

$$(7.14) \quad \max_{\bar{\Omega}} U \geq -\lambda_1 \max_{\bar{\Omega}} \varphi = -\lambda_1 \geq \delta_0,$$

where the last inequality follows from Lemma 7.1. This completes the proof.  $\square$

## 8. Advection-induced extinction

This section is devoted to the proof of Theorem 2. In fact, we will prove a stronger result which can be stated as follows.

**Theorem 4.** *Suppose that  $m > 0$  in  $\bar{\Omega}$  and assumption (A1) holds. Given any number  $\eta > \nu / \min_{\bar{\Omega}} m$ , there exists some positive constant  $\Lambda_7 = \Lambda_7(\mu, \nu, m, \Omega, \eta)$  such that if  $\alpha \geq \Lambda_7$  and  $\beta \in [\nu / \min_{\bar{\Omega}} m, \eta]$ ,  $(0, \theta(x; \beta, \nu))$  is globally asymptotically stable.*

Clearly, Theorem 2 is included in Theorem 4. Throughout this section we always assume that  $m > 0$  in  $\bar{\Omega}$  and assumption (A1) holds. Let  $(U_i, V_i)$  denote any positive steady state of (2.1)-(2.2) with  $(\alpha, \beta) = (\alpha_i, \beta_i)$ .

**Lemma 8.1.** *Suppose that  $\alpha_i \rightarrow \infty$  and  $\beta_i \rightarrow \beta \in [0, \infty)$ . Then  $V_i \rightarrow \theta(x; \beta, \nu)$  in  $C^1(\bar{\Omega})$ .*

**Proof.** By Lemma 5.3, for any  $p > 1$ ,  $\|U_i\|_{L^p} \rightarrow 0$  as  $i \rightarrow \infty$ . By standard elliptic regularity [16],  $V_i \rightarrow \theta(x; \beta, \nu)$  in  $W^{2,p}(\Omega)$  weakly for any  $p > 1$ . By Sobolev embedding theorem [16],  $V_i \rightarrow \theta(x; \beta, \nu)$  in  $C^1$ .  $\square$

**Lemma 8.2.** *Given any  $\eta > \nu / \min_{\bar{\Omega}} m$ , there exists positive constant  $\Lambda_8 = \Lambda_8(\mu, \nu, m, \Omega, \eta)$  such that if  $\alpha \geq \Lambda_8$  and  $\beta \in [\nu / \min_{\bar{\Omega}} m, \eta]$ , system (2.1)-(2.2) has no positive steady state.*

**Proof.** We argue by contradiction. Suppose that there exist sequences  $\{\alpha_i, \beta_i\}_{i=1}^{\infty}$  with  $\alpha_i \rightarrow \infty$  and  $\beta_i \in [\nu / \min_{\bar{\Omega}} m, \eta]$  such that system (2.1)-(2.2) with  $(\alpha, \beta) = (\alpha_i, \beta_i)$  has a positive steady state, denoted as  $(U_i, V_i)$ , for every  $i$ . Without loss of generality, assume that  $\mu = 1$  and  $\beta_i \rightarrow \beta \in [\nu / \min_{\bar{\Omega}} m, \infty)$ . Set  $W_i = e^{-\alpha_i m} U_i$ . Then  $W_i > 0$  satisfies

$$(8.1) \quad \nabla \cdot [e^{\alpha_i m} \nabla W_i] + e^{\alpha_i m} (m - U_i - V_i) W_i = 0 \quad \text{in } \Omega, \quad \partial_n W_i = 0 \quad \text{on } \partial\Omega.$$

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

$$(8.2) \quad \nabla \cdot [e^{\alpha_i m} \nabla \varphi] + e^{\alpha_i m} [m - (1 - \epsilon)\theta(x; \beta, \nu)] = -\lambda e^{\alpha_i m} \varphi \quad \text{in } \Omega, \quad \partial_n \varphi = 0 \quad \text{on } \partial\Omega.$$

Denote the eigenfunction corresponding to  $\lambda_i(\epsilon)$  by  $\varphi_i$ , which is uniquely determined by  $\varphi_i > 0$  in  $\bar{\Omega}$  and  $\int_{\Omega} \varphi_i^2 dx = 1$ . Multiplying (8.1) by  $\varphi_i$  and the equation of  $\varphi_i$  by  $W_i$ , subtracting them and integrating in  $\Omega$ , we have

$$(8.3) \quad \int_{\Omega} e^{\alpha_i m} [U_i + V_i - (1 - \epsilon)\theta(x; \beta, \nu)] dx = -\lambda_i(\epsilon) \int_{\Omega} e^{\alpha_i m} \varphi_i W_i.$$

Fix  $\epsilon \in (0, 1)$ . Since  $V_i \rightarrow \theta(x; \beta, \nu)$  uniformly in  $\Omega$  (Lemma 8.1), there exists  $i^*$  such that for  $i \geq i^*$ ,

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

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

$$(8.4) \quad \lambda_i(\epsilon) < 0.$$

By assumption (A1), we see that  $\mathcal{M} = \{x_0\}$ . Hence, by Theorem 3 we have

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

This along with (8.4) implies that  $m(x_0) \geq (1 - \epsilon)\theta(x_0; \beta, \nu)$ . Let  $\epsilon \rightarrow 0+$ , we have  $m(x_0) \geq \theta(x_0; \beta, \nu)$ . However, this is a contradiction since by Lemma 5.2 we know that  $\theta(x_0; \beta, \nu) > m(x_0)$  (recall that  $\beta/\nu \geq 1/\min_{\bar{\Omega}} m$ ).  $\square$

**Proof of Theorem 4.** By Lemma 5.4, (2.1)-(2.2) is a strongly monotone dynamical system. Hence, the global asymptotic stability of  $(0, \theta(x; \beta, \nu))$  follows from Lemmas 6.3, 6.6, 8.2, and the monotone dynamical system theory [20, 26, 43].  $\square$

## 9. Discussions

We studied a Lotka-Volterra reaction-diffusion-advection model for two competing species in a heterogeneous environment. The two species are ecologically identical except their dispersal strategies: both species disperse by random movement and advection along environmental gradients, but one species has much stronger biased movement than the other one. We first show that strong advection along environmental gradients for *one species* can provide a new mechanism for the coexistence of two competing species. The new biological insight is that the species with very strong biased movement mainly pursues resources at places of locally most favorable environments, coexistence of two species is thus possible since the other species can rely on resources from other parts of the habitat. In strong contrast, strong advection along environmental gradients of *both species* can cause the extinction of the species which has much stronger biased movement. Biologically, strong biased movements of both species along environmental gradients can lead to overcrowding of the whole population at places of locally most favorable environments, which causes the extinction of the species which only pursues most favorable resources. They seem to imply that selection is against excessive advection along environmental gradients due to overcrowding, which suggests that an intermediate biased movement rate may evolve in our model.

The key assumption of our model, *i.e.*, the species moving along the gradient of  $m(x)$ , neglects important effects such as nutrition dynamics and population density. In our model, the species can only sense and assess local environment partially and other important effects such as local population density are neglected. In Grindrod's model [17] the advection term  $\nabla m$  is being replaced by the more realistic term  $\nabla(m - u - v)$ . That is, instead of moving along the gradient of the intrinsic growth rate, the species moves in the direction of increasing effective growth rate which is given by  $m - u - v$ . It will be interesting to compare these two different dispersal strategies and determine which one will evolve. The nutrition dynamics is also neglected in our model: it will be important to incorporate the nutrition dynamics and see what dispersal strategies will evolve. Our next steps are to build on the models and approaches in this paper and earlier work, and to include both local population density as in [17] and the nutrition dynamics, and to address their effects on population dynamics. We refer to [9] and [41] for recent analytical and modeling work on dispersal mechanisms for single species based upon local information about both the environment and population density.

Though our current model lacks some important factors, it may still provide potentially some new insights into the implications of dispersal strategies for populations in heterogeneous landscapes. In our model the species pursues movement along environmental gradients and is more likely to move from less favorable regions to more favorable ones, *e.g.*, from sink regions to source ones. Intuitively, one consequence of such biased movement is to cause some degree of crowding in the favorable regions of the habitat and thus change the source-sink dynamics. Our results indicate that if both species strongly pursue such biased movements, it does lead to overcrowding of the population, causing the extinction of the species which

has the stronger biased movement rate. In strong contrast, if only one species strongly pursue such biased movement, overcrowding does not occur and the two species can coexist. Therefore, our model and results can assess the degree of crowding induced by directed movement along environmental gradients, predict qualitatively when and where overcrowding of population will occur, and determine the effects of such biased movement on the population dynamics. Our model and results may also be useful for further studies on more realistic models that incorporate nutrition dynamics or local population density. For instance, the species may not perfectly follow the gradient of  $m - u - v$  as in [17] but rather track the gradient of  $m - \gamma(u + v)$  for some  $\gamma > 0$ . Our model is a good approximation of the situation when  $\gamma$  is positive small, *i.e.*, when the species is much less sensitive to the population density than the landscape, and may also be helpful in understanding situations when  $\gamma$  is not necessarily small.

To connect Theorems 1, 2, 4 and earlier results in [13, 8, 10], we take a global bifurcation point of view, with  $\alpha$  as the bifurcation parameter. The global bifurcation diagram is far from being clear and many open questions still remain. Our goal is to use rigorous results from this paper and earlier work to make some reasonable (but maybe oversimplified) predictions on the global picture of the dynamics of system (2.1)-(2.2).

To interpret our results biologically, we regard the species with density  $u$  as the invading species and the species with density  $v$  as the resident species. We try to find the dispersal strategies for the invading species so that it can invade when rare and also to determine the winning strategies for the invading species. We say that a dispersal strategy is a *winning strategy* for the invading species if the species can apply the strategy to invade when rare and also drive the resident species to extinction, regardless of the initial condition.

We consider two cases: (i)  $\beta$  is small (e.g.,  $\beta \leq \nu / \max_{\bar{\Omega}} m$ ); (ii)  $\beta$  is large (e.g.,  $\beta \geq \nu / \min_{\bar{\Omega}} m$ ). The following result will be useful in our discussions ([38]):

**Theorem 5.** *Suppose that  $\alpha = \beta(\mu/\nu)$ . Then  $(\theta(\cdot; \alpha, \mu), 0)$  is globally asymptotically stable if  $\mu < \nu$ , and  $(0, \theta(\cdot; \beta, \nu))$  is globally asymptotically stable if  $\mu > \nu$ .*

Theorem 5 is a generalization of the case when  $\alpha = \beta = 0$  as in [13], *i.e.*, the slower diffuser always wins. The proof uses the monotonicity of the principal eigenvalue of some self-adjoint operator with respect to the diffusion coefficient as in [13, 28], and we refer the details of proofs to [13, 28].

**9.1. The small  $\beta$  case.** Biologically, this is when the resident species is not quite sensitive to the local environment. We will first describe the dynamics of (2.1)-(2.2) from the bifurcation point of view, and then proceed to corresponding biological discussions/predictions.

**Bifurcation diagrams.** Fix  $\mu, \nu, m, \Omega$ , and  $\beta$  and we will vary  $\alpha$ , starting from large  $\alpha$ . We should caution the readers that some of the bifurcation pictures described below are conjectures rather than theorems.

- (1) Since  $\beta/\nu \leq 1/\max_{\bar{\Omega}} m$ , by Theorem 1 we see that (2.1)-(2.2) has at least one stable positive steady state for every  $\alpha \geq \Lambda_1$ . From bifurcation point of view, these steady

states, denoted by  $(U, V)$ , may lie on a smooth solution curve  $\{(U, V, \alpha)\}$  that is contained in the product space  $C^2(\bar{\Omega}) \times C^2(\bar{\Omega}) \times (0, \infty)$ . We denote this solution curve and its extensions (before it connects one of the two semi-trivial steady states as we decrease  $\alpha$ ) by  $\Gamma_1$ .

- (2) The key question is whether  $\Gamma_1$  will connect one of the two semi-trivial steady states as we decrease  $\alpha$ ; if so, which one will it connect? We restrict our discussions to the case  $\mu < \nu$ . By Theorem 5,  $(\theta(\cdot; \alpha, \mu), 0)$  is globally asymptotically stable at  $\alpha = \beta\mu/\nu$ . By perturbation argument we see that there exists some small constant  $\delta_1 > 0$ , independent of  $\alpha$ , such that for  $\alpha \in (\beta\mu/\nu - \delta_1, \beta\mu/\nu + \delta_1)$ ,  $(\theta(\cdot; \alpha, \mu), 0)$  is globally asymptotically stable. Therefore, if  $\mu < \nu$ , as we decrease  $\alpha$ , the simplest situation for  $\Gamma_1$  is to connect  $(\theta(\cdot; \alpha, \mu), 0)$  at  $\alpha = \alpha_1$  for some  $\alpha_1 > \beta\mu/\nu$ .
- (3) The dynamics of (2.1)-(2.2) for  $\alpha \in [0, \beta\mu/\nu - \delta_1]$  can be rather complicated, e.g., when both  $\alpha$  and  $\beta$  are small, the results of [8] suggest that the dynamics can depend upon the geometry of the domain  $\Omega$ . As the general situation is unclear, we further restrict our discussions to the situation when  $\Omega$  is convex,  $\beta > 0$  small and  $\mu < \nu$  are so chosen that  $(0, \theta(\cdot; \beta, \nu))$  is globally asymptotically stable for system (2.1)-(2.2) with  $\alpha = 0$  (see Theorem 1.1, [8]). Note that the faster diffuser wins here. By perturbation argument, we see that there exists some  $\delta_2 > 0$  such that for  $\alpha \in [0, \delta_2)$ ,  $(0, \theta(\cdot; \beta, \nu))$  is globally asymptotically stable.
- (4) Previous assumptions and discussions for  $\alpha \in [0, \delta_2) \cup (\beta\mu/\nu - \delta_1, \beta\mu/\nu + \delta_1)$  imply that both semi-trivial steady states have to change their stability at least once for  $\alpha \in (\delta_2, \beta\mu/\nu - \delta_1)$ . The simplest scenario will be that there exist  $\alpha_2 > \alpha_3 > 0$  such that  $(0, \theta(\cdot; \beta, \nu))$  is globally asymptotically stable for  $\alpha \in [0, \alpha_3)$ ,  $(\theta(\cdot; \alpha, \mu), 0)$  is globally asymptotically stable for  $\alpha \in (\alpha_2, \alpha_1)$ , and in between another branch of positive steady states connects the two semi-trivial steady states  $(\theta(\cdot; \alpha, \mu), 0)$  and  $(0, \theta(\cdot; \beta, \nu))$  at  $\alpha = \alpha_2, \alpha_3$ , respectively. Determining this global bifurcation diagram is an open problem.

## Biological discussions

- (1) With suitable choices of  $\beta$ ,  $\mu < \nu$  and assuming that the habitat is convex, for  $\alpha \in [0, \delta_2)$ , the resident species has a competitive advantage even if it diffuses more rapidly than the invading species. The underlying mechanism is that the advantage gained by the resident species from the directed movement upward resource gradients can counterbalance the disadvantage created by its faster diffusion. The bifurcation diagram can be different for some non-convex habitat  $\Omega$ , and we refer to [8] for more details.
- (2) If  $\mu < \nu$ , for  $\alpha \in (\beta\mu/\nu - \delta_1, \beta\mu/\nu + \delta_1)$ , the invading species has the winning dispersal strategy, which says that the slower diffuser is the winner if the relative strengths of advection over random diffusion are similar for both species.

- (3) An interesting prediction is that both species can coexist for some intermediate parameter regions of  $\alpha$  contained in  $(\delta_2, \beta\mu/\nu - \delta_1)$ . We do not know the corresponding biological interpretation for such coexistence, and one possible explanation is that the two species are rather similar in their dispersal strategies for such parameter ranges.
- (4) For the case  $\alpha \in (\Lambda_1, \infty)$ , the two species have very different dispersal strategies: The invading species has much stronger biased movement and it mainly pursues resources at places of locally most favorable environments. Hence, such dispersal strategy leaves enough resources for the resident species so that both species can coexist.

These discussions indicate that if the resident species has a weak tendency to move upward along resource gradients, it might be a winning dispersal strategy for the invading species to adopt a stronger biased movement. However, if the invading species adopts too strong biased movement along resource gradients, then its dispersal strategy is neither a winning one nor a losing one. We predict that when the resident species is not quite sensitive to the surrounding environment, it will be advantageous for the invading species to be a slower diffuser and more (but not too much more) sensitive to the environment.

**9.2. The large  $\beta$  case.** Biologically, this corresponds to the situation when the resident species is very sensitive to the local environments. Again, we will use results from this paper and earlier work to make some predictions on the global bifurcation diagram.

**Bifurcation diagram.** Fix  $\mu, \nu, m, \Omega$ . Let  $\Lambda_1$  be given in Theorem 1. For simplicity we assume that  $\Lambda_1 > \mu/\min_{\bar{\Omega}} m$ . Otherwise, replace  $\Lambda_1$  by  $\max\{\Lambda_1, \mu/\min_{\bar{\Omega}} m + 1\}$ . Let  $\Lambda_7$  be given in Theorem 4 and set  $\eta = \Lambda_1$ , i.e.,  $\Lambda_7 = \Lambda_7(\mu, \nu, m, \Omega, \Lambda_1)$ . Choose  $\beta$  such that  $\beta \geq \max\{\Lambda_1, \Lambda_7\}$ . We fix  $\beta$  and let  $\alpha$  vary from zero to infinity this time.

- (1) We start from  $\alpha = 0$  and then increase  $\alpha$ . By  $\beta \geq \Lambda_1$  and Theorem 1, for every  $\alpha \in [0, \mu/\max_{\bar{\Omega}} m]$ , both semi-trivial steady states are unstable and there is at least one stable positive steady state. We remind the reader that the roles of  $\alpha$  and  $\beta$ ,  $\mu$  and  $\nu$  are switched here in applying Theorem 1. The simplest scenario is that there exists a branch of positive steady state of (2.1)-(2.2) for  $\alpha \in [0, \mu/\max_{\bar{\Omega}} m]$ . We denote this branch of solutions and its extensions (before it connects one of the two semi-trivial steady states) by  $\Gamma_2$ .
- (2) By  $\beta \geq \Lambda_7$  and Theorem 4 we see that for every  $\alpha \in [\mu/\min_{\bar{\Omega}} m, \Lambda_1]$ ,  $(\theta(x; \alpha, \mu), 0)$  is globally asymptotically stable. Again, note that the roles of  $\alpha$  and  $\beta$ ,  $\mu$  and  $\nu$  are switched here in order to apply Theorem 4 and the two semi-trivial steady states are also switched accordingly. This suggests that the simplest scenario for  $\Gamma_2$  is to connect the semi-trivial solution  $(\theta(x; \alpha, \nu), 0)$  at some  $\alpha_4$  with  $\alpha_4/\mu \in (1/\max_{\bar{\Omega}} m, 1/\min_{\bar{\Omega}} m)$ .
- (3) Let  $\Lambda_2 = \Lambda_2(\mu, \nu, m, \Omega, \beta)$  be given in Theorem 2. By  $\beta/\nu \geq 1/\min_{\bar{\Omega}} m$  and Theorem 2, for every  $\alpha \geq \Lambda_2$ ,  $(0, \theta(\cdot; \beta, \nu))$  is globally asymptotically stable. This also implies  $\Lambda_2 > \Lambda_1$  as  $(\theta(x; \alpha, \mu), 0)$  is globally asymptotically stable for  $\alpha \in (\mu/\min_{\bar{\Omega}} m, \Lambda_1)$ .

Hence, as  $\alpha$  varies from  $\Lambda_1$  to  $\Lambda_2$ ,  $(0, \theta(\cdot; \beta, \nu))$  changes from unstable to stable, and  $(\theta(\cdot; \alpha, \mu), 0)$  changes from stable to unstable. The simplest scenario will be that there exist  $\alpha_5 < \alpha_6$  such that  $(\theta(\cdot; \alpha, \mu), 0)$  is globally asymptotically stable for  $\alpha \in (\alpha_4, \alpha_5)$ ,  $(0, \theta(\cdot; \beta, \nu))$  is globally asymptotically stable for  $\alpha > \alpha_6$ , and a branch of positive steady states connects the two semi-trivial steady states  $(\theta(\cdot; \alpha, \mu), 0)$  and  $(0, \theta(\cdot; \beta, \nu))$  at  $\alpha = \alpha_5, \alpha_6$ , respectively. Again, determining such global bifurcation diagram is an open problem.

**Remark 9.1.** *From previous discussions and Theorem 5, we suspect that (i)  $\beta(\mu/\nu) \in (\alpha_4, \alpha_5)$  when  $\mu < \nu$ ; (ii)  $\beta(\mu/\nu) \in (\alpha_6, \infty)$  when  $\mu > \nu$ ; (iii)  $\alpha_5 = \alpha_6 = \beta$  when  $\mu = \nu$ .*

### Biological discussions

- (1) For  $\alpha \in [0, \mu/\max_{\bar{\Omega}} m]$  and possibly for  $\alpha \in [0, \alpha_4)$ , the invading species can invade when rare and the two species will coexist. For this case, the resident species has stronger biased movement and mainly pursues resources at places of locally most favorable environments, while the invading species can use resources elsewhere.
- (2) For  $\alpha \in [\mu/\min_{\bar{\Omega}} m, \Lambda_1]$  and possibly for  $\alpha \in (\alpha_4, \alpha_5)$ , the invading species has the winning dispersal strategy, most likely because both the invading species has a balanced dispersal strategy and can also compete effectively at places of locally most favorable environments, where the resident species puts all of its bets.
- (3) We predict that both species can coexist for some intermediate parameter region  $(\alpha_5, \alpha_6)$  of  $\alpha$ . Again, we do not know the corresponding biological interpretation for such coexistence. One possibility is that the two species are similar to each other in their dispersal strategies.
- (4) The case  $\alpha \in (\alpha_6, \infty)$  is opposite to case (2). It says that when the resident species has a strong tendency to move upward along resource gradient, if the invading species adopts a much stronger biased movement strategy, it will go extinct. This seems to indicate that under some situations the selection can be against very strong biased movement.

These discussions indicate that if the resident species has a strong tendency to move upward along resource gradients, it will be a losing dispersal strategy for the invading species to adopt an even stronger biased movement. If the invading species adopts a less aggressive biased movement, it might find some intermediate range of biased movement rates which will yield winning dispersal strategies. We predict that when the resident species is very sensitive to the surrounding environment, it will be advantageous for the invading species to be less (but not too much less) sensitive to the environment.

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