

# Advection-Mediated Competition in General Environments

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## Abstract

We consider a reaction-diffusion-advection system of two competing species with one of the species dispersing by random diffusion as well as a biased movement upward along resource gradient, while the other species by random diffusion only. It has been shown that, under some non-degeneracy conditions on the environment function, the two species always coexist when the advection is strong. In this paper, we show that for general smooth environment function, in contrast to what is known, there can be competitive exclusion when the advection is strong, and, we give a sharp criterion for coexistence that includes all previously considered cases. Moreover, when the domain is one-dimensional, we derive in the strong advection limit a system of two equations defined on different domains. Uniqueness of steady states of this non-standard system is obtained when one of the diffusion rates is large.

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## 1. Introduction

In this paper, we are interested in the effect of dispersal on the competition of species. Our study is motivated by an interesting result obtained in [11] in which Dockery, Hutson, Mischaikow and Pernarowski considered the following two species competition model

$$\begin{cases} U_t = d_1 \Delta U + U(m(x) - U - V) & \text{in } \Omega \times (0, \infty), \\ V_t = d_2 \Delta V + V(m(x) - U - V) & \text{in } \Omega \times (0, \infty), \\ \partial_\nu U = \partial_\nu V = 0 & \text{on } \partial\Omega \times (0, \infty), \\ U(x, 0) = U_0(x), \quad V(x_0) = V_0(x) & \text{in } \Omega. \end{cases} \quad (1)$$

Here  $\Omega$  is a bounded smooth domain in  $\mathbb{R}^N$ , with  $\nu$  denoting the outward unit normal vector on the boundary  $\partial\Omega$  of  $\Omega$ , and  $\partial_\nu = \nu \cdot \nabla$  being the outer normal derivative.  $U$  and  $V$  represent the population densities of two different

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competing species, while  $m(x)$  captures the quality of the habitat  $\Omega$  at location  $x$ . If  $m(x)$  is nonconstant, it is shown that if  $0 < d_2 < d_1$ , then all positive solutions of (1), regardless of the initial values  $U_0(x)$ ,  $V_0(x)$ , converge uniformly to  $(0, \theta_{d_2})$  as  $t \rightarrow \infty$ , where  $\theta_{d_2}$  is the unique positive steady state of

$$\begin{cases} \theta_t = d_2 \Delta \theta + \theta(m - \theta) & \text{in } \Omega \times (0, \infty), \\ \partial_\nu \theta = 0 & \text{on } \partial\Omega \times (0, \infty). \end{cases} \quad (2)$$

In other words, in pure diffusion models with heterogeneous environment, slower diffusion rates is favored.

In [20], an important distinction was drawn between unconditional dispersal, which does not depend on habitat quality or population density, and conditional dispersal, which does depend on such factors. Passive diffusion, as considered in [11], is an example of unconditional dispersal. Diffusion combined with directed movement upward along environmental gradients, as considered in [2, 10], is a type of conditional dispersal.

As an attempt to determine whether conditional or unconditional dispersal strategy confers more ecological advantage, the following system was introduced in [5], following the approach in [11]:

$$\begin{cases} U_t = \nabla \cdot (d_1 \nabla U - \alpha U \nabla m) + U(m - U - V) & \text{in } \Omega \times (0, \infty), \\ V_t = d_2 \Delta V + V(m - U - V) & \text{in } \Omega \times (0, \infty), \\ d_1 \partial_\nu U - \alpha U \partial_\nu m = \partial_\nu V = 0 & \text{on } \partial\Omega \times (0, \infty). \end{cases} \quad (3)$$

While the two species  $U$  and  $V$  are ecologically equivalent, they adopt different dispersal strategies:  $V$  disperses purely randomly, and  $U$  adopts, in addition to diffusion, a directed movement upward along the environmental gradient  $\nabla m$ . Throughout this paper, we always assume

(M1)  $m \in C^2(\bar{\Omega})$  is nonconstant, and  $\int_\Omega m > 0$ .

Under assumption (M1), for all  $d_i > 0$  and  $\alpha \geq 0$ , system (3) has a trivial steady state  $(0, 0)$ , and two semi-trivial steady states  $(\tilde{u}, 0)$  and  $(0, \theta_{d_2})$ , where  $\theta_{d_2}$  is the unique positive steady state to (2) and  $\tilde{u}$  is the unique (globally asymptotically stable) positive steady state to

$$\begin{cases} \tilde{u}_t = \nabla \cdot (d_1 \nabla \tilde{u} - \alpha \tilde{u} \nabla m) + \tilde{u}(m - \tilde{u}) & \text{in } \Omega \times (0, \infty), \\ d_1 \partial_\nu \tilde{u} - \alpha \tilde{u} \partial_\nu m = 0 & \text{on } \partial\Omega \times (0, \infty). \end{cases} \quad (4)$$

**Theorem 1** (See [2]). *Suppose that (M1) holds. Then for all  $\alpha \geq 0$ , (4) has a unique positive steady state  $\tilde{u}$  which is globally asymptotically stable among nonnegative, nontrivial solutions.*

Significant progress is made in [6], prompting much subsequent work [3, 7, 8, 9, 13, 16, 17, 18]. In [6], the authors showed that when  $\alpha$  is positive and small, the effect of the advection upward resource gradient depends crucially on the shape of the habitat of the population: If the habitat is convex, the movement in the direction of the gradient of growth rate can be beneficial to the population, while such advection could be harmful for certain nonconvex domains. Furthermore, under a nondegeneracy condition on  $m$ , the two species co-exist for sufficiently large  $\alpha$ . The following co-existence result is first proved in [6] and generalized later in [9].

**Theorem 2** (See [6, 9]). *Suppose that (M1) holds and that the set of all critical points of  $m$  has Lebesgue measure zero. Then for every  $d_1, d_2 > 0$ , the system (3) has at least one stable positive steady state for all sufficiently large  $\alpha$ .*

Detailed information of the shape of such positive steady states are obtained in [3, 8, 9, 16, 17, 18]. For example, the limiting profiles of positive steady states are determined in [18].

**Theorem 3** (See [18]). *Let  $\Omega = (-1, 1)$  and denote the set of all local maximum points of  $m$  by  $\mathfrak{M}_{loc}$ . Suppose that all critical points of  $m$  are non-degenerate, and  $xm'(x) < 0$  at  $\pm 1$ . Then for any  $r > 0$  small, as  $\alpha \rightarrow \infty$ , any positive steady state  $(U, V)$  of (3) has the following properties:*

- (i)  $V \rightarrow \theta_{d_2}$  in  $C^{1,\gamma}(\bar{\Omega})$ , for all  $\gamma \in (0, 1)$ ;
- (ii)  $U \rightarrow 0$  exponentially in  $\Omega \setminus \cup_{x_0 \in \mathfrak{M}_{loc}} B_r(x_0)$ ;
- (iii) For any  $x_0 \in \mathfrak{M}_{loc}$ ,  $\|U(x) - \sqrt{2} \max\{m(x_0) - \theta_{d_2}(x_0), 0\} e^{\alpha[m(x) - m(x_0)]/d_1}\|_{L^\infty(B_r(x_0))} \rightarrow 0$ .

**Remark 1.1.** Under additional mild conditions on  $m$ , analogous results in higher dimensional domains are established in [17] by a different method.

As illustrated by Theorem 3, the more “intelligent” species  $U$  concentrates only at a selected subset of the local maximum points of  $m$ , and,  $\|U\|_{L^p(\Omega)} \rightarrow 0$  as  $\alpha \rightarrow \infty$ , leaving virtually all the resources  $m$  for  $V$  to consume. This seemingly peculiar phenomenon stems from the fact that  $m$  attains its local maxima only on a *discrete* set.

Thus, from either mathematical or ecological point of view, it seems desirable, perhaps even important, to consider *general* resource function  $m(x)$  which only satisfies (M1).

The focus of this paper is to investigate the advection-mediated co-existence phenomenon for general resource function  $m$ , whose critical points are not necessarily non-degenerate - in fact, we will pay special attention to those with local maxima assumed on a set with non-empty interior. Our primary purpose is to give a *sharp criterion for co-existence* in the competition system (3); in particular, to show that for general  $m(x)$  satisfying (M1), (3) does not necessarily support co-existence for large values of  $\alpha$ .

Our first main result is the following criterion for advection-mediated co-existence for general  $m(x)$ .

**Theorem 4.** If  $m \in C^2(\bar{\Omega})$  is non-constant, and satisfies

$$\int_{\{x \in \Omega: |\nabla m| > 0 \text{ and } m > 0\}} m + \int_{\{x \in \Omega: m \leq 0\}} m > 0, \quad (5)$$

then for all  $d_1, d_2 > 0$ , (3) has at least one stable co-existence steady state for all sufficiently large  $\alpha$ .

It is easy to see that Theorem 2 follows as a special case of Theorem 4. Furthermore, condition (5) is satisfied by any nonnegative, nonconstant  $m$ .

**Corollary 1.1.** If  $m \in C^2(\bar{\Omega})$  is nonconstant and nonnegative, then for all  $d_1, d_2 > 0$ , (3) has at least one co-existence steady state for all sufficiently large  $\alpha$ .

It is convenient to denote the set of all *global* maximum points of  $m(x)$  in  $\bar{\Omega}$  by  $\mathfrak{M}$  as it will play an important role in our approach.

Our next result shows that, in contrast to previous results (e.g. Theorem 2), for certain environment function satisfying (M1), there exists  $d_1, d_2 > 0$  such that  $U$  always wipes out  $V$  for sufficiently large  $\alpha$ . i.e. it pays to be “greedy” sometimes. This result in particular implies that Theorem 4 is sharp.

**Theorem 5.** Let  $\Omega \subset \mathbb{R}^N$  for some  $N \leq 3$ . Suppose, in addition to (M1), that  $\mathfrak{M} \cap \partial\Omega = \emptyset$  and

$$\int_{\Omega \setminus \mathfrak{M}} m < 0.$$

Then there exists  $d_1, d_2 > 0$  such that the steady state  $(\tilde{u}, 0)$  if (3) is globally asymptotically stable for all sufficiently large  $\alpha$ .

Next, we will show that the asymptotic behavior of (3) for general resource function  $m(x)$  can be significantly different from that of previously mentioned non-degenerate case, namely, Theorems 2 and 3. We now illustrate this by the following one-dimensional result.

**Theorem 6.** Let  $\Omega = (-2, 2)$ . Assume  $m \in C^2([-2, 2])$ , satisfying  $m > 0$  in  $[-2, 2]$ , and

$$m' > 0 \quad \text{in } [-2, -1), \quad m = 1 \quad \text{in } [-1, 1], \quad m' < 0 \quad \text{in } (1, 2].$$

Then for each  $\alpha$  large, (3) has at least one stable positive steady state. Moreover, if  $(U, V)$  is any positive steady state of (3), then by passing to a subsequence  $\alpha_k \rightarrow \infty$ ,  $U \rightarrow U_0$  in  $C^2([-1, 1])$ , and  $V \rightarrow V_0$  in  $C^{1,\beta}([-2, 2])$  for all  $\beta \in (0, 1)$ , where  $(U_0, V_0)$  is a positive solution to

$$\begin{cases} d_1 U'' + U(m(x) - U - V) = 0 & \text{in } (-1, 1), \\ d_2 V'' + V(m(x) - U - V) = 0 & \text{in } (-2, 2), \\ U' = 0 & \text{at } x = \pm 1, \\ V' = 0 & \text{at } x = \pm 2. \end{cases} \quad (6)$$

Here for the second equation, we set  $U = 0$  in  $(-2, -1] \cup [1, 2)$ .

Roughly speaking, when the directed movement of  $U$  is strong (sufficiently large  $\alpha$ ),  $U$  tends to be restricted to the locally most favorable regions, while  $V$  moves freely throughout the entire domain. One could also visualize this as if an “invisible membrane” is placed at  $x = \pm 1$  through which only  $V$  can pass. We conjecture that analogous results hold for multi-dimensional domains as well.

A novel feature of the limiting system (6) is that the underlying domains of the two equations in (6) are actually *different*! Fortunately, the maximum principle and the theory of monotone dynamical systems still apply, which makes it possible to handle (6). It turns out that from the limiting system (6) we can show that for  $d_2$  large, regardless of  $d_1 > 0$ , the positive steady state of (6) is *unique*, and thereby the profile of the co-existence steady state of (3) is determined.

**Theorem 7.** *Let  $m \in C^2([-2, 2])$  satisfy the hypothesis of Theorem 6, then there exists  $\underline{d}_2 > 0$ , independent of  $d_1$ , such that for all  $d_1 > 0$  and  $d_2 > \underline{d}_2$ , system (6) has a unique positive solution.*

The key to the proofs of Theorems 4 and 5 is a good understanding of the behavior of the positive solution  $\tilde{u}$  to (4). In case  $m(x)$  has only non-degenerate critical points, the positive steady state of (4) stays bounded in  $L^\infty(\Omega)$  for all  $\alpha$  large, and tends to 0 in  $L^p(\Omega)$ ,  $1 < p < \infty$  [8, 17, 18]. However, it seems interesting to note that positive steady states do not necessarily stay bounded for general  $m(x)$  as  $\alpha$  tends to  $\infty$ , as the following result shows. In fact, this is one of the main difficulties in handling the general case.

**Proposition 1.1.** *There exists  $m \in C^2(\bar{\Omega})$ , satisfying (M1), such that  $\|\tilde{u}\|_{L^1(\Omega)} \not\rightarrow 0$  and  $\|\tilde{u}\|_{L^\infty(\Omega)} \rightarrow \infty$  as  $\alpha \rightarrow \infty$ .*

This paper is organized as follows. Some preliminary estimates are given in Section 2. Proposition 1.1 and Theorem 6 will be proved in Section 3. After establishing a key lemma in Section 4, Theorem 4 will be shown in Section 5, under the additional assumption that  $\partial_\nu m|_{\partial\Omega} < 0$ . Subsequently, this additional assumption  $\partial_\nu m|_{\partial\Omega} < 0$  will be removed in Section 7. Section 6 is devoted to the proof of Theorem 5, and the uniqueness result, Theorem 7, will be proved in Section 8. Finally, some discussions are included in Section 9.

## 2. Preliminaries

The starting point of our analysis is the following estimate contained in [8].

**Theorem 8** (See [8]). *Suppose  $m \in C^2(\bar{\Omega})$  assumes a positive local maximum value  $M$  in a (closed) set  $\Omega_M \subset\subset \Omega$ ; more precisely, for some  $\epsilon > 0$ ,*

$$m = \begin{cases} M & \text{if } x \in \Omega_M, \\ < M & \text{if } x \in \Omega \setminus \Omega_M \text{ and } \text{dist}(x, \Omega_M) < \epsilon. \end{cases}$$

*Then for all  $K_1 > 0$  there exists  $K_2 > 0$ , such that the positive steady state of (4) satisfies that  $\tilde{u} > M$  in  $\Omega_M$  whenever  $d_1 \leq K_1$  and  $\alpha/d_1 \geq K_2$ .*

Suppose that (M1) holds. Let  $\bar{m} = \frac{1}{|\Omega|} \int_\Omega m$ . For each  $\kappa \in [0, \bar{m}]$ , define  $\tilde{u}_\kappa$  to be the unique positive solution to (see Theorem 1 for existence)

$$\begin{cases} \nabla \cdot (d_1 \nabla \tilde{u}_\kappa - \alpha \tilde{u}_\kappa \nabla m) + \tilde{u}_\kappa (m - \kappa - \tilde{u}_\kappa) = 0 & \text{in } \Omega, \\ d_1 \partial_\nu \tilde{u}_\kappa - \alpha \tilde{u}_\kappa \partial_\nu m = 0 & \text{on } \partial\Omega. \end{cases} \quad (7)$$

Recall that  $\mathfrak{M} = \{x \in \Omega : m(x) = \max_{\bar{\Omega}} m\}$ . The following corollary will be used to establish Theorem 5.

**Corollary 2.1.** *Suppose that  $\mathfrak{M} \subset\subset \Omega$ . Then, for all  $d > 0$ , there exists  $\alpha_0 > 0$  such that for any  $\alpha \geq \alpha_0$  and any  $\kappa \in [0, \bar{m}]$ , we have*

$$\tilde{u}_\kappa(x) > \max_{\bar{\Omega}} m - \kappa \quad \text{on } \mathfrak{M}. \quad (8)$$

*Proof.* By the proof of Theorem 8, there exists  $\underline{u}_{\bar{m}} \in C^2(\bar{\Omega})$  satisfying

$$\underline{u}_{\bar{m}} \equiv \max_{\bar{\Omega}} m - \bar{m} \quad \text{in } \mathfrak{M} \quad \text{and} \quad \underline{u}_{\bar{m}}(x) \leq \max_{\bar{\Omega}} m - \bar{m} \quad \text{in } \Omega, \quad (9)$$

and  $\underline{u}_{\bar{m}}$  is a lower solution of (7) with  $\kappa = \bar{m}$  for  $\alpha \geq \alpha_0$ , for some  $\alpha_0 > 0$ . i.e.

$$\begin{cases} \nabla \cdot (d_1 \nabla \underline{u}_{\bar{m}} - \alpha \underline{u}_{\bar{m}} \nabla m) + \underline{u}_{\bar{m}}(m - \bar{m} - \underline{u}_{\bar{m}}) \geq 0 & \text{in } \Omega, \\ d_1 \partial_\nu \underline{u}_{\bar{m}} - \alpha \underline{u}_{\bar{m}} \partial_\nu m = 0 & \text{on } \Omega. \end{cases}$$

This proves (8) for the case  $\kappa = \bar{m}$ . Now for any  $\kappa \in [0, \bar{m})$ , define

$$\underline{u}_\kappa = \frac{\max_{\bar{\Omega}} m - \kappa}{\max_{\bar{\Omega}} m - \bar{m}} \underline{u}_{\bar{m}},$$

then  $d_1 \partial_\nu \underline{u}_\kappa - \alpha \underline{u}_\kappa \partial_\nu m = 0$  on  $\partial\Omega$ , and

$$\begin{aligned} & \nabla \cdot (d_1 \nabla \underline{u}_\kappa - \alpha \underline{u}_\kappa \nabla m) + \underline{u}_\kappa(m - \kappa - \underline{u}_\kappa) \\ &= \nabla \cdot (d_1 \nabla \underline{u}_{\bar{m}} - \alpha \underline{u}_{\bar{m}} \nabla m) + \underline{u}_\kappa(m - \bar{m} - \underline{u}_{\bar{m}}) + \underline{u}_\kappa(\bar{m} - \kappa + \underline{u}_{\bar{m}} - \underline{u}_\kappa) \\ &\geq \underline{u}_\kappa \left[ \bar{m} - \kappa - \frac{\bar{m} - \kappa}{\max_{\bar{\Omega}} m - \bar{m}} \underline{u}_{\bar{m}} \right] \geq 0 \end{aligned}$$

whenever  $\alpha \geq \alpha_0$ , since  $\frac{\underline{u}_{\bar{m}}}{\max_{\bar{\Omega}} m - \bar{m}} \leq 1$  by (9). Hence  $\underline{u}_\kappa$  is a lower solution of (7), and (8) follows.  $\square$

Next, we make an observation from the proof of Theorem 1.5(i) in [6].

**Theorem 9.** Let  $m \in C^2(\bar{\Omega})$  be nonconstant and positive somewhere, then  $\tilde{u} \rightarrow 0$  (weakly) in  $L^2(\{x \in \Omega : |\nabla m| > 0\})$  as  $\alpha \rightarrow \infty$ . In particular,  $\int_{\{x \in \Omega : |\nabla m| > 0\}} \tilde{u} \rightarrow 0$  as  $\alpha \rightarrow \infty$ . Moreover, if  $\{x \in \Omega : |\nabla m| = 0\}$  is of measure zero, then  $\tilde{u} \rightarrow 0$  (strongly) in  $L^2(\Omega)$  as  $\alpha \rightarrow \infty$ .

*Proof.* By integrating (4) over  $\Omega$ , we have

$$\int_{\Omega} \tilde{u}(m - \tilde{u}) = 0 \quad (10)$$

and hence

$$\|\tilde{u}\|_{L^2(\Omega)} \leq \|m\|_{L^2(\Omega)}. \quad (11)$$

Therefore, by passing to a subsequence, we may assume that  $\tilde{u} \rightharpoonup u^*$  weakly in  $L^2(\Omega)$ , for some nonnegative function  $u^* \in L^2(\Omega)$ . Multiplying (4) by  $\varphi \in \mathcal{S}$ , where  $\mathcal{S} = \{\varphi \in C^2(\bar{\Omega}) : \partial_\nu \varphi|_{\partial\Omega} = 0\}$ , and integrating in  $\Omega$ , we have

$$-d_1 \int_{\Omega} \nabla \tilde{u} \cdot \nabla \varphi + \alpha \int_{\Omega} \tilde{u} \nabla m \cdot \nabla \varphi = \int_{\Omega} \varphi \tilde{u}(\tilde{u} - m).$$

By the boundary condition of  $\varphi$ ,

$$\int_{\Omega} \nabla \tilde{u} \cdot \nabla \varphi = - \int_{\Omega} \tilde{u} \Delta \varphi.$$

Hence,

$$d_1 \int_{\Omega} \tilde{u} \Delta \varphi + \alpha \int_{\Omega} \tilde{u} (\nabla m \cdot \nabla \varphi) = \int_{\Omega} \varphi \tilde{u}(\tilde{u} - m). \quad (12)$$

Dividing (12) by  $\alpha$  and passing to the limit in (12) we have

$$\int_{\Omega} u^* \nabla m \cdot \nabla \varphi = 0. \quad (13)$$

Since (13) holds for any  $\varphi \in \mathcal{S}$  and  $\mathcal{S}$  is dense in  $W^{1,2}(\Omega)$ , we see that (13) holds for every  $\varphi \in W^{1,2}(\Omega)$ . In particular, we can choose  $\varphi = m$  in (13) so that

$$\int_{\Omega} u^* |\nabla m|^2 = 0.$$

Hence  $u^* |\nabla m|^2 = 0$  a.e. in  $\Omega$ . Therefore we conclude that  $\tilde{u} \rightharpoonup 0$  weakly in  $L^2(\Omega_r)$ , where  $\Omega_r = \{x \in \Omega : |\nabla m(x)| > 0\}$ . Moreover, if the set of critical points of  $m$  is of measure zero, then we see that  $u^* = 0$  a.e. in  $\Omega$ . Therefore  $\tilde{u} \rightarrow 0$  weakly in  $L^2(\Omega)$ , which implies by (10) that, as  $\alpha \rightarrow \infty$ ,

$$\int_{\Omega} \tilde{u}^2 = \int_{\Omega} \tilde{u} m \rightarrow 0.$$

$\square$

### 3. One-dimensional Results

Consider the steady state equation of (4) when  $\Omega = (-2, 2)$ .

$$\begin{cases} (d_1 \tilde{u}' - \alpha \tilde{u} m')' + \tilde{u}(m - \tilde{u}) = 0 & \text{in } (-2, 2), \\ d_1 \tilde{u}' - \alpha \tilde{u} m' = 0 & \text{at } x = \pm 2. \end{cases} \quad (14)$$

**Lemma 3.1.** *At any  $x_0 \in \Omega$ ,  $\limsup_{\alpha \rightarrow \infty} m'(x_0)[d_1 \tilde{u}'(x_0) - \alpha \tilde{u}(x_0)m'(x_0)] \leq 0$ .*

*Proof.* If  $m'(x_0) = 0$ , there is nothing to prove. Suppose  $m'(x_0) > 0$ . Assume to the contrary that there is a  $\epsilon_0 > 0$  such that along a sequence  $\alpha = \alpha_k \rightarrow \infty$ ,

$$d_1 \tilde{u}'(x_0) - \alpha \tilde{u}(x_0)m'(x_0) \geq \epsilon_0. \quad (15)$$

Choose  $x_1 > x_0$  so that  $m' > 0$  in  $[x_0, x_1]$  (i.e.  $[x_0, x_1]$  consist of regular points). For  $x \in [x_0, x_1]$ , by integrating the equation (14) from  $x_0$  to  $x$ , we have

$$d_1 \tilde{u}'(x) - \alpha \tilde{u}(x)m'(x) = d_1 \tilde{u}'(x_0) - \alpha \tilde{u}(x_0)m'(x_0) + \int_{x_0}^x \tilde{u}(\tilde{u} - m) \geq \epsilon_0 - \int_{x_0}^x \tilde{u}m \geq \frac{\epsilon_0}{2}$$

for all  $\alpha = \alpha_k$  large, by Theorem 9. Hence

$$d_1 \tilde{u}'(x) \geq \frac{\epsilon_0}{2} + \alpha \tilde{u}(x)m'(x) \geq \frac{\epsilon_0}{2} \quad \text{for all } x \in [x_0, x_1]$$

which is impossible, since  $\int_{x_0}^{x_1} \tilde{u} \rightarrow 0$ , as  $\alpha_k \rightarrow \infty$ , by Theorem 9. The other case  $m'(x_0) < 0$  can be treated in the same way.  $\square$

**Lemma 3.2.** *If  $m' > 0$  (resp.  $m' < 0$ ) in  $(x_0, x_1)$ , then  $\tilde{u} \rightarrow 0$  locally uniformly in  $[x_0, x_1]$  (resp.  $(x_0, x_1]$ ) as  $\alpha \rightarrow \infty$ .*

*Proof.* Assume  $m' > 0$  in  $(x_0, x_1)$ . By Theorem 9,  $\int_{x_0}^{x_1} \tilde{u} \rightarrow 0$ . Suppose to the contrary that for some  $\delta > 0$ ,  $\tilde{u}$  does not converge to zero uniformly in  $[x_0, x_1 - \delta]$ , then for some  $\alpha > 0$ , there exists  $y \in [x_0, x_1 - \delta]$  such that  $\tilde{u}'(y) < -\frac{1}{d_1} \int_{-2}^2 m^2$ . But we also have, by integrating the equation of  $\tilde{u}$  from  $y$  to 2,

$$d_1 \tilde{u}'(y) = \alpha \tilde{u}(y)m'(y) + \int_y^2 \tilde{u}(m - \tilde{u}) > - \int_{-2}^2 \tilde{u}^2 \geq - \int_{-2}^2 m^2$$

where we have used (10). This is a contradiction. The proof for the other case is similar.  $\square$

It is shown in [18] that if  $\Omega = (-2, 2)$ ,  $xm'(x) < 0$  for  $x = \pm 2$  and  $m$  has finitely many critical points, all being non-degenerate, then  $\|\tilde{u}\|_{L^\infty(\Omega)} \leq C$  for some  $C$  independent of  $\alpha \geq 0$ . (See [17] for analogous uniform  $L^\infty$  estimate for higher dimensions.) To the contrary, such an  $L^\infty$  estimate does not hold in general when the critical set of  $m$  is of positive measure. The following is a more precise version of Proposition 1.1.

**Proposition 3.1.** *Let  $m \in C^2([-2, 2])$  satisfies  $m = d_1 \pi^2$  in  $[-2, 0]$  and  $m' > 0$  in  $(0, 2]$ . Then as  $\alpha \rightarrow \infty$ ,*

(i)  $\tilde{u}|_{[-2, 0]} \rightarrow \omega$  in  $C^2([-2, 0])$ , where  $\omega$  is the unique positive solution to

$$\begin{cases} d_1 \omega'' + \omega(d_1 \pi^2 - \omega) = 0 & \text{in } (-2, 0), \\ \omega'(-2) = \omega(0) = 0. \end{cases} \quad (16)$$

(Note that  $\omega$  exists since  $d_1 \pi^2 > d_1 \pi^2/16$ , the latter being the principal eigenvalue of the Laplacian in  $(-2, 0)$  with the prescribed (mixed) boundary condition.)

(ii)  $\tilde{u} \rightarrow 0$  uniformly on compact subsets of  $[0, 2)$ .

(iii)  $\|\tilde{u}\|_{L^\infty(-2, 2)} \rightarrow \infty$ .

*Proof.* (ii) follows by Lemma 3.2. In particular,  $\tilde{u}(0) \rightarrow 0$  as  $\alpha \rightarrow \infty$ . Hence, (i) follows from the fact that  $\tilde{u}$  satisfies the equation

$$\begin{cases} d_1 \tilde{u}'' + \tilde{u}(d_1 \pi^2 - \tilde{u}) = 0 & \text{in } (-2, 0), \\ \tilde{u}'(-2) = 0, \quad \tilde{u}(0) \rightarrow 0, \end{cases}$$

and that by comparison,  $\tilde{u} \geq \omega$ , where  $\omega$  is the unique positive solution of (16). For (iii), one observes that since  $\int_0^2 \tilde{u} \rightarrow 0$  by Theorem 9, it suffices to show that  $\liminf_{\alpha \rightarrow \infty} \int_0^2 \tilde{u}^2 > 0$ . To this end, by (10)

$$\int_0^2 \tilde{u}^2 = \int_0^2 \tilde{u}m + \int_{-2}^0 \tilde{u}(m - \tilde{u}).$$

Letting  $\alpha \rightarrow \infty$ , by Theorem 9,

$$\lim_{\alpha \rightarrow \infty} \int_0^2 \tilde{u}^2 = \lim_{\alpha \rightarrow \infty} \int_0^2 \tilde{u}m + \lim_{\alpha \rightarrow \infty} \int_{-2}^0 \tilde{u}(m - \tilde{u}) = 0 + \int_{-2}^0 \omega(m - \omega) > 0.$$

□

**Remark 3.1.** In fact, by the methods in [17, 18], one may show that  $\|\tilde{u}\|_{L^\infty(\Omega)} = O(\alpha^{1/2})$ .

Next, we consider (3) in the one-dimensional case.

$$\begin{cases} (d_1 U' - \alpha U m')' + U(m - U - V) = 0 & \text{in } (-2, 2), \\ d_2 V'' + V(m - U - V) = 0 & \text{in } (-2, 2), \\ d_1 U' - \alpha U m' = V' = 0 & \text{at } x = \pm 2. \end{cases} \quad (17)$$

Suppose  $m$  satisfies the hypothesis of Theorem 6. We now give the proof of Theorem 6.

*Proof of Theorem 6.* The existence of positive steady state  $(U_\alpha, V_\alpha)$  follows from Theorem 4 which will be proved independently in Sections 5 and 7. Let  $\tilde{u}$  be the unique positive solution to (4). First, we claim

**Claim 1.**  $\|\tilde{u}\|_{C^1([-1, 1])}$  is bounded uniformly in  $\alpha$ .

Integrating (14) from  $-2$  to  $x$ , using the no-flux boundary condition, we have

$$d_1 \tilde{u}'(x) - \alpha \tilde{u}(x) m'(x) = \int_{-2}^x \tilde{u}(\tilde{u} - m).$$

Next, for all  $x \in [-1, 1]$ , we have  $m'(x) = 0$ . So by (11),

$$d_1 |\tilde{u}'(x)| \leq \int_{-2}^x |\tilde{u}(\tilde{u} - m)| \leq 2 \int_{-2}^2 m^2 \quad \text{for all } x \in [-1, 1]. \quad (18)$$

Claim 1 follows by interpolating (11) and (18).

Next, we claim that  $\tilde{u}$  is bounded in  $L^\infty([-2, 2])$  uniformly in  $\alpha$ .

**Claim 2.**  $\|\tilde{u}\|_{L^\infty([-2, 2])}$  is bounded uniformly in  $\alpha$ .

Let  $\tilde{u}(x_\alpha) = \|\tilde{u}\|_{L^\infty([-2, 2])}$ . By Theorem 8,  $\tilde{u} > m$  in  $[-1, 1]$  for all  $\alpha$  large. By (4),  $\tilde{u}'' > 0$  in  $[-1, 1]$ . Thus  $x_\alpha \in [-2, -1) \cup (1, 2]$  and by Lemma 3.2 (passing to a subsequence)

$$x_\alpha \rightarrow 1^+ \quad \text{or} \quad x_\alpha \rightarrow -1^- \quad \text{as } \alpha \rightarrow \infty. \quad (19)$$

Integrating (14) from  $-2$  to  $y$ , multiplying by  $e^{-\alpha m/d_1}$  and integrating again, we have

Case (i):  $x_\alpha \rightarrow 1^+$ .

$$\begin{aligned}
 d_1 \frac{d}{dy} (e^{-\alpha m(y)/d_1} \tilde{u}(y)) &= e^{-\alpha m(y)/d_1} \int_{-2}^y \tilde{u}(\tilde{u} - m) dz \\
 d_1 e^{-\alpha m(x_\alpha)/d_1} u(x_\alpha) &= d_1 e^{-\alpha m(-1)/d_1} \tilde{u}(-1) + \int_{-1}^{x_\alpha} e^{-\alpha m(y)/d_1} \int_{-2}^y \tilde{u}(\tilde{u} - m) dz dy \\
 d_1 \tilde{u}(x_\alpha) &= d_1 e^{\alpha[m(x_\alpha)-m(-1)]/d_1} \tilde{u}(-1) + \int_{-1}^{x_\alpha} e^{\alpha[m(x_\alpha)-m(y)]/d_1} \int_{-2}^y \tilde{u}(\tilde{u} - m) dz dy \\
 &\leq d_1 \tilde{u}(-1) + |x_\alpha + 1| \cdot 2 \int_{-2}^2 m^2 \quad \text{by (11)} \\
 &\leq d_1 \|\tilde{u}\|_{C^1([-1,1])} + 5 \int_{-2}^2 m^2.
 \end{aligned}$$

Case (ii):  $x_\alpha \rightarrow -1^-$  can be treated similarly. Hence by Claim 1,  $\|\tilde{u}\|_{L^\infty([-2,2])}$  is bounded independent of  $\alpha$ . In particular, by Theorem 9 and interpolation,

$$\int_{-2}^{-1} \tilde{u}^2 + \int_1^2 \tilde{u}^2 \rightarrow 0 \quad \text{as } \alpha \rightarrow \infty. \quad (20)$$

Now given any positive steady state  $(U_\alpha, V_\alpha)$  of (17), one can deduce by comparison that,  $U_\alpha \leq \tilde{u}$  and  $V_\alpha \leq \theta_{d_2}$ . So  $\|V_\alpha\|_{L^\infty([-2,2])}$ ,  $\|U_\alpha\|_{L^\infty([-2,2])}$ , and by (17),  $\|U_\alpha''\|_{L^\infty([-1,1])}$  and  $\|V_\alpha''\|_{L^\infty([-2,2])}$  are bounded uniformly in  $\alpha \geq 0$ . Therefore passing to a subsequence,  $V_\alpha \rightarrow V_0$  in  $C^{1,\beta}([-2,2])$  and  $U_\alpha \rightarrow U_0$  in  $C^{1,\beta}([-1,1])$  with  $U_0, V_0$  solving (6) in the weak sense. Moreover, by the equation of  $U_\alpha$ ,  $U_\alpha \rightarrow U_0$  in  $C^2([-1,1])$ . It remains to check the boundary condition of  $U_0$  at  $x = \pm 1$ . Here we integrate the equation of  $U_\alpha$  from  $-2$  to  $-1$ , and deduce by (20) that

$$d_1 |U_\alpha'(-1)| = \left| \int_{-2}^{-1} U_\alpha(m - U_\alpha - V_\alpha) \right| \leq C \int_{-2}^{-1} U_\alpha^2 \leq C \int_{-2}^{-1} \tilde{u}^2 \rightarrow 0.$$

Hence  $U_0'(-1) = 0$ . Similarly, we can deduce that  $U_0'(1) = 0$ . This completes the proof.  $\square$

**Remark 3.2.** One can show that (6) has a unique positive steady states when  $d_2$  is sufficiently large. The key to the proof lies in the observation that the non-standard problem (6) describes the steady states of a monotone dynamical system. We defer the proof to the Appendix.

In fact, by the proof of Theorem 6, we can obtain the following result, which is perhaps more illustrative of the effect of large advection on the competition system.

**Theorem 10.** Assume  $\Omega = (-2, 2)$  and  $m \in C^2([-2, 2])$  satisfies

$$\begin{aligned}
 m' &> 0 & \text{in } [-2, -1], & \quad m = d_2\pi^2 + 2 & \text{in } [-1, 0], \\
 m' &< 0 & \text{in } (0, 1), & \quad m = d_2\pi^2 + 1 & \text{in } [1, 2], \quad m(-2) \geq d_2\pi^2 + 1.
 \end{aligned}$$

Then for each  $\alpha$  large, (17) has at least one stable positive steady state. Moreover, if  $(U, V)$  is any positive steady state, then by passing to a subsequence  $\alpha_k \rightarrow \infty$ ,  $U \rightarrow U_0$  in  $C^2([-1, 0] \cup [1, 2])$ , and  $V \rightarrow V_0$  in  $C^{1,\beta}([-2, 2])$ , where  $(U_0, V_0)$  is a positive solution to

$$\begin{cases} d_1 U_0'' + U_0(m(x) - U_0 - V_0) = 0 & \text{in } (-1, 0) \cup (1, 2), \\ d_2 V_0'' + V_0(m(x) - U_0 - V_0) = 0 & \text{in } (-2, 2), \\ U_0'(-1) = U_0'(2) = 0, & U_0'(0) = U_0'(1), \\ V_0'(-2) = V_0'(2) = 0, \end{cases} \quad (21)$$

where we set  $U_0 = 0$  in  $(-2, -1] \cup [0, 1]$  in the second equation.



*Proof.* The proof of Theorem 10 follows the same ideas in proving Theorem 6. Here we indicate the necessary modifications. Again, the existence follows from Theorem 4 which will be proved independently in Sections 5 and 7.

The uniform boundedness of  $\|\tilde{u}\|_{L^\infty([-2,2])}$  in  $\alpha$  can be deduced as before: Let  $\tilde{u}(x_\alpha) = \|\tilde{u}\|_{L^\infty([-2,2])}$ . First, by Theorem 8,  $\tilde{u} > m$  in  $[-1, 0]$ . Also, by verifying that

$$\bar{u} = (d_2\pi^2 + 1)e^{\alpha[m(x) - \pi^2 - 1]/d_1}$$

is an upper solution, we also have  $\tilde{u} < m$  in  $[1, 2]$  for all  $\alpha$  large. In particular,  $\tilde{u}'' > 0$  in  $[-1, 0]$  and  $\tilde{u}'' < 0$  in  $[1, 2]$ . Thus  $x_\alpha \in [-2, -1) \cup (0, 1)$  and by Lemma 3.2 (passing to a subsequence)

$$x_\alpha \rightarrow 0^+ \quad \text{or} \quad x_\alpha \rightarrow -1^-. \quad (22)$$

The uniform boundedness of  $\|\tilde{u}\|_{L^\infty([-2,2])}$  follows as before. Then, we may similarly show the boundedness of  $\|U_\alpha\|_{C^2([-1,1])}$  and  $\|V_\alpha\|_{C^2([-2,2])}$ , and that, up to a sequence, they converge to a weak solution  $(U_0, V_0)$  of (21). Finally, the boundary conditions  $U'_0(0) = U'_0(1)$  follows by integrating the equation of  $U_\alpha$  from 0 to 1

$$\left| d_1(U'_\alpha(1) - U'_\alpha(0)) \right| = \left| (d_1 U'_\alpha - \alpha U_\alpha m') \Big|_0^1 \right| = \int_0^1 |U_\alpha(U_\alpha + V_\alpha - m)| \rightarrow 0, \quad (23)$$

by Theorem 9 and the  $L^\infty$  boundedness of  $U_\alpha$  and  $V_\alpha$ . The rest of the proof follows in a completely analogous way.  $\square$

#### 4. A Key Lemma

For simplicity, we first show the following higher-dimensional analogue of Lemma 3.1 under the additional assumption  $\partial_\nu m|_{\partial\Omega} < 0$ . We will later remove the assumption in Section 7. In the following, we denote, for each  $t \in \mathbb{R}$ ,  $\Omega(t) = \{x \in \Omega : m(x) > t\}$  and  $\Gamma(t) = \{x \in \Omega : m(x) = t\}$ . Furthermore, we denote  $\tau(x) = -\frac{\nabla m}{|\nabla m|}$  for each  $x \in \bar{\Omega}$  such that  $\nabla m(x) \neq 0$ .

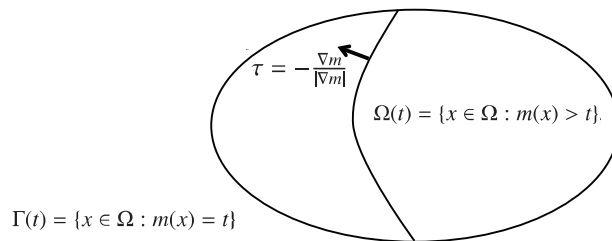


Figure 1. Illustrations of  $\Omega(t)$ ,  $\Gamma(t)$  and  $\tau$ .

**Lemma 4.1.** Suppose  $\partial_\nu m|_{\partial\Omega} < 0$ . Let  $\tilde{u}$  be the unique positive solution to (4), then for each regular value  $m_0$  of  $m$ ,

$$\liminf_{\alpha \rightarrow \infty} \int_{\Gamma(m_0)} (d_1 \partial_\tau \tilde{u} - \alpha \tilde{u} \partial_\tau m) \geq 0,$$

where  $\tau = \tau(x) = -\frac{\nabla m(x)}{|\nabla m(x)|}$  is the outer unit normal of  $\partial(\Omega(m_0))$  on  $\Gamma(m_0) = \Omega \cap \partial(\Omega(m_0))$ , and  $\partial_\tau = \tau \cdot \nabla$ .

By (4) and the Divergence Theorem, we have

**Corollary 4.2.** Under the hypotheses of Lemma 4.1,  $\liminf_{\alpha \rightarrow \infty} \int_{\Omega(m_0)} \tilde{u}(\tilde{u} - m) \geq 0$ .

We also have

**Corollary 4.3.** Under the hypotheses of Lemma 4.1, for each regular value  $\epsilon > 0$  of  $m$ ,

$$\limsup_{\alpha \rightarrow \infty} \int_{\Omega \setminus \Omega(\epsilon)} \tilde{u}^2 \leq \epsilon^2 |\Omega|.$$

*Proof.* By (10) and Corollary 4.2,

$$\limsup_{\alpha \rightarrow \infty} \int_{\Omega \setminus \Omega(\epsilon)} \tilde{u}(\tilde{u} - \epsilon) \leq \limsup_{\alpha \rightarrow \infty} \int_{\Omega \setminus \Omega(\epsilon)} \tilde{u}(\tilde{u} - m) = \limsup_{\alpha \rightarrow \infty} \int_{\Omega(\epsilon)} \tilde{u}(m - \tilde{u}) \leq 0.$$

So

$$\int_{\Omega \setminus \Omega(\epsilon)} \tilde{u}^2 \leq \epsilon \int_{\Omega \setminus \Omega(\epsilon)} \tilde{u} + o(1) \leq \epsilon |\Omega|^{\frac{1}{2}} \left( \int_{\Omega \setminus \Omega(\epsilon)} \tilde{u}^2 \right)^{\frac{1}{2}} + o(1)$$

and hence

$$\limsup_{\alpha \rightarrow \infty} \int_{\Omega \setminus \Omega(\epsilon)} \tilde{u}^2 \leq \epsilon^2 |\Omega|.$$

□

*Proof of Lemma 4.1.* Let  $m_0$  be a regular value of  $m$ . Assume to the contrary that for some  $\epsilon_0 > 0$  and some  $\alpha_k \rightarrow \infty$ , (taking  $\tau = -\frac{\nabla m}{|\nabla m|}$ )

$$\int_{\Gamma(m_0)} (d_1 \partial_\tau \tilde{u} - \alpha \tilde{u} \partial_\tau m) \leq -\epsilon_0 < 0 \quad \text{for all } \alpha = \alpha_k. \quad (24)$$

Given a regular value  $m_0$  of  $m$ , we divide into three cases:

- (i)  $m_0$  is not in the range of  $m$ ;
- (ii)  $m_0 = \max_{\bar{\Omega}} m$  (necessarily attained on  $\partial\Omega$ );
- (iii)  $m_0 \in [\min_{\bar{\Omega}} m, \max_{\bar{\Omega}} m)$ .

Case (i) implies that the integral is empty, which is in contradiction with (24). Case (ii) implies that  $\{x \in \Omega : m(x) = \max_{\bar{\Omega}} m\} \cap \Omega = \emptyset$ . Thus for all  $x_0 \in \{x \in \Omega : m(x) = \max_{\bar{\Omega}} m\}$ , we have  $x_0 \in \partial\Omega$  and  $\tau = \frac{\nabla m}{|\nabla m|}$  coincide with the unit normal vector of  $\partial\Omega$  at  $x_0$ . Hence

$$\int_{\Gamma(\max_{\bar{\Omega}} m)} (d_1 \partial_\tau \tilde{u} - \alpha \tilde{u} \partial_\tau m) = 0$$

by the no-flux boundary conditions satisfied by  $\tilde{u}$  on  $\partial\Omega$ , which again contradicts (24). It suffices to consider the remaining case (iii). Since  $\bar{\Omega}$  is compact, the set of critical values of  $m$  is closed and of measure zero (Sard's Theorem). Hence, the set of regular values of  $m$  is open and dense in the range of  $m$ ,  $m(\bar{\Omega})$ . We may assume that there exists  $\delta > 0$  such that  $[m_0, m_0 + \delta]$  consists entirely of regular values of  $m$ . Then for all  $t \in [0, \delta]$ , (taking  $\tau = -\frac{\nabla m}{|\nabla m|}$ )

$$\left( - \int_{\Gamma(m_0+t)} + \int_{\Gamma(m_0)} \right) (d_1 \partial_\tau \tilde{u} - \alpha \tilde{u} \partial_\tau m) = \int_{\Omega(m_0) \setminus \Omega(m_0+t)} \tilde{u}(\tilde{u} - m) \geq - \int_{\Omega(m_0) \setminus \Omega(m_0+\delta)} \tilde{u}m \rightarrow 0$$

as  $\alpha_k \rightarrow \infty$ , by Theorem 9. Hence by (24), for all  $t \in [0, \delta]$ ,

$$\int_{\Gamma(m_0+t)} (d_1 \partial_\tau \tilde{u} - \alpha \tilde{u} \partial_\tau m) \leq -\frac{\epsilon_0}{2} \quad \text{for all } \alpha_k \text{ large.} \quad (25)$$

Next, let  $0 < s \leq t \leq \delta$ . For all  $y_s \in \Gamma(m_0 + s)$ , define  $\phi_{t-s}(y_s) = \phi(t-s, y_s)$  by the ODE

$$\frac{d\phi}{dt} = \frac{\nabla m(\phi)}{|\nabla m(\phi)|^2}, \quad \phi(0, y_s) = y_s.$$

By the boundary condition  $\partial_\nu m|_{\partial\Omega} < 0$ , one can deduce that for all  $0 < s \leq t \leq \delta$ , and all  $y_s \in \Gamma(m_0 + s)$ ,  $\phi_{t-s}$  is an injective, differentiable mapping from  $\Gamma(m_0 + s)$  to  $\Gamma(m_0 + t)$ . The existence of  $\phi_{t-s}$  follows from the regularity of  $m$  ( $\nabla m$  is  $C^1$  and non-zero), along with our assumption that  $\partial_\nu m|_{\partial\Omega} < 0$ . The latter implies in particular that if

$y_s \in \Gamma(m_0 + s) \subset \bar{\Omega}$ , then  $\phi_{t-s}(y_s) \in \bar{\Omega}$  for all  $t \in [0, \delta]$ . Observe that  $\frac{d}{dt}[m(\phi_{t-s})] = \nabla m(\phi_{t-s}) \cdot \frac{\nabla m(\phi_{t-s})}{|\nabla m(\phi_{t-s})|^2} = 1$ , so  $m(\phi_{t-s}) = m_0 + t$  for all  $0 < s \leq t \leq \delta$ . The rest follows from uniqueness and smooth dependence on initial conditions of the ODE. Also, note that for  $0 < s_1 < s_2 \leq t \leq \delta$ ,

$$\phi_{t-s_1}(\Gamma(m_0 + s_1)) \subset \phi_{t-s_2}(\Gamma(m_0 + s_2)) \subset \Gamma(m_0 + t). \quad (26)$$

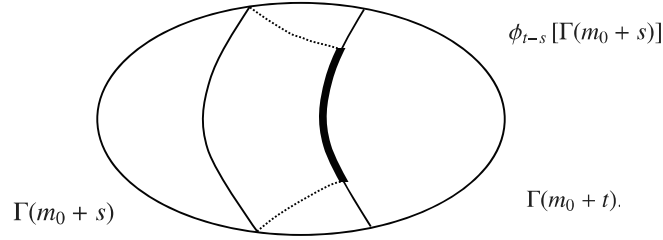


Figure 2.  $\phi_{t-s}$  as an injective mapping from  $\Gamma(m_0 + s)$  into  $\Gamma(m_0 + t)$ .

Define, for  $0 < s \leq t \leq \delta$ ,

$$\begin{aligned} \Phi(t, s) &= \int_{\Gamma(m_0+s)} \tilde{u}(\phi_{t-s}(y_s)) |\nabla m(\phi_{t-s}(y_s))| |J\phi_{t-s}(y_s)| dS_{y_s} \\ &= \int_{\phi_{t-s}(\Gamma(m_0+s))} \tilde{u}(y) |\nabla m(y)| dS_y, \end{aligned}$$

where  $J\phi_{t-s}$  is the Jacobian of  $\phi_{t-s} : \Gamma(m_0 + s) \rightarrow \Gamma(m_0 + t)$ , while  $dS_{y_s}$  and  $dS_y$  are the area elements of  $\Gamma(m_0 + s)$  and  $\Gamma(m_0 + t)$  respectively. Now,  $\phi_0 = Id$  gives  $J\phi_0 \equiv 1$ . Hence, by taking  $\delta > 0$  smaller,  $||J\phi_{t-s}| - 1| < \frac{1}{2}$  for all  $0 < s \leq t \leq \delta$ , and all  $y_s \in \Gamma(m_0 + s)$ . In particular,

$$\Phi(s, s) = \int_{\Gamma(m_0+s)} \tilde{u}(y_s) |\nabla m(y_s)| dS_{y_s}.$$

It suffices then to show that for some  $\epsilon_1 > 0$  (independent of  $\alpha$ ),

$$\Phi(t, t) \geq \epsilon_1 t \quad \text{for all } t \in [0, \delta]. \quad (27)$$

For, assuming (27), we have

$$0 < \frac{\epsilon_1 \delta_2}{2} \leq \int_0^\delta \Phi(s, s) ds = \int_{\Omega(m_0) \setminus \Omega(m_0+\delta)} \tilde{u} |\nabla m| \leq \int_{\{x \in \Omega : |\nabla m| > 0\}} \tilde{u} |\nabla m|.$$

But this contradicts the fact that  $\int_{\{x \in \Omega : |\nabla m| > 0\}} \tilde{u} \rightarrow 0$  (Theorem 9). To show (27), we first observe that,

$$\Phi(t, s) \text{ is non-decreasing in } s, \quad (28)$$

which follows by (26). Now,  $\frac{d}{ds}[\Phi(s, s)] \geq \left[ \frac{d}{dt}[\Phi(t, s)] \right]_{t=s}$  by (28).

Hence,

$$\begin{aligned}
 \frac{d}{ds}[\Phi(s, s)] &= \frac{d}{dt} \left[ \int_{\Gamma(m_0+s)} \tilde{u}(\phi_{t-s}(y_s)) |\nabla m(\phi_{t-s}(y_s))| |J\phi_{t-s}(y_s)| dS_{y_s} \right]_{t=s} \\
 &= \left[ \int_{\Gamma(m_0+s)} \nabla \tilde{u}(\phi_{t-s}(y_s)) \cdot \left[ \frac{d}{dt} \phi_{t-s}(y_s) \right] |\nabla m(\phi_{t-s}(y_s))| |J\phi_{t-s}(y_s)| dS_{y_s} \right]_{t=s} \\
 &\quad + \left[ \int_{\Gamma(m_0+s)} \tilde{u}(\phi_{t-s}(y_s)) \frac{d}{dt} [|\nabla m(\phi_{t-s}(y_s))| |J\phi_{t-s}(y_s)|] dS_{y_s} \right]_{t=s} \\
 &= \int_{\Gamma(m_0+s)} \nabla \tilde{u}(y_s) \cdot \frac{\nabla m(y_s)}{|\nabla m(y_s)|^2} |\nabla m(y_s)| dS_{y_s} + \int_{\Gamma(m_0+s)} \tilde{u}(y_s) \frac{d}{dt} [|\nabla m(\phi_{t-s}(y_s))| |J\phi_{t-s}(y_s)|]_{t=s} dS_{y_s} \\
 &\geq \int_{\Gamma(m_0+s)} \partial_\tau \tilde{u} dS_{y_s} - C\Phi(s, s) \\
 &\geq \frac{\epsilon_0}{2d_1} - C\Phi(s, s),
 \end{aligned}$$

where  $C$  is a positive constant independent of  $\delta > 0$  small. The last inequality follows from (25). This gives

$$e^{Ct} \Phi(t, t) \geq \frac{\epsilon_0 t}{2d_1} + \Phi(0, 0) \geq \frac{\epsilon_0 t}{2d_1},$$

which implies (27).  $\square$

## 5. Advection-mediated Co-existence

In this section, we show Theorem 4 under the additional assumption  $\partial_\nu m|_{\partial\Omega} < 0$ .

**Theorem 11.** *If  $m \in C^2(\bar{\Omega})$  is non-constant,  $\partial_\nu m|_{\partial\Omega} < 0$  and*

$$\int_{\{x \in \Omega: |\nabla m| > 0 \text{ and } m > 0\}} m + \int_{\{x \in \Omega: m \leq 0\}} m > 0, \quad (29)$$

*then for all  $d_1, d_2 > 0$ , (3) has at least one stable co-existence steady state for all  $\alpha$  sufficiently large.*

In particular, (29) is satisfied by any nonnegative, nonconstant  $m$ .

**Corollary 5.1.** *If  $m \in C^2(\bar{\Omega})$  is nonconstant, nonnegative and that  $\partial_\nu m|_{\partial\Omega} < 0$ , then for all  $d_1, d_2 > 0$ , there exists  $\alpha_0 > 0$  such that (3) has at least one co-existence steady state for all  $\alpha \geq \alpha_0$ .*

*Proof of Theorem 11.* By the general theory of monotone dynamical systems, it suffices to show the instability of  $(\bar{u}, 0)$  and  $(0, \theta_{d_2})$ . First we show the instability of  $(0, \theta_{d_2})$ . To this end, consider the principal eigenvalue  $\lambda_\nu$  of

$$\begin{cases} \nabla \cdot (d_1 \nabla \varphi - \alpha \varphi \nabla m) + (m - \theta_{d_2}) \varphi + \lambda_\nu \varphi = 0 & \text{in } \Omega, \\ d_1 \partial_\nu \varphi - \alpha \varphi \partial_\nu m = 0 & \text{on } \partial\Omega. \end{cases} \quad (30)$$

By the transformation  $\psi = e^{-\alpha m/d_1} \varphi$ , (30) is equivalent to

$$\begin{cases} \nabla \cdot (d_1 e^{\alpha m/d_1} \nabla \psi) + (m - \theta_{d_2}) e^{\alpha m/d_1} \psi + \lambda_\nu e^{\alpha m/d_1} \psi = 0 & \text{in } \Omega, \\ \partial_\nu \psi = 0 & \text{on } \partial\Omega, \end{cases}$$

which admits the variational characterization,

$$\lambda_\nu = \inf_{\psi \in H^1(\Omega)} \frac{\int_\Omega e^{\alpha m/d_1} [d_1 |\nabla \psi|^2 + (\theta_{d_2} - m) \psi^2]}{\int_\Omega e^{\alpha m/d_1} \psi^2}.$$

Observe that by maximum principle that  $\sup_{\bar{\Omega}} m - \|\theta_{d_2}\|_{L^\infty(\Omega)} > 0$ , since  $\bar{\theta} \equiv \max_{\bar{\Omega}} m$  is a strict upper solution of (2).

**Claim 3.** For any  $d_1, d_2 > 0$ ,  $\limsup_{\alpha \rightarrow \infty} \lambda_v < 0$ .

Let  $0 < \epsilon_0 < \sup_{\bar{\Omega}} m - \|\theta_{d_2}\|_{L^\infty(\Omega)}$ . Then let  $\psi$  be a test function satisfying

$$\psi = \begin{cases} 1 & \text{if } m(x) \geq \max_{\bar{\Omega}} m - \frac{\epsilon_0}{2}, \\ 0 & \text{if } m(x) \leq \max_{\bar{\Omega}} m - \epsilon_0. \end{cases}$$

Then

$$\begin{aligned} \lambda_v &\leq \frac{\int_{\Omega} e^{\alpha m/d_1} [d_1 |\nabla \psi|^2 + (\theta_{d_2} - m) \psi^2]}{\int_{\Omega} e^{\alpha m/d_1} \psi^2} \\ &\leq \frac{d_1 \int_{\{x \in \Omega : m(x) \leq \max_{\bar{\Omega}} m - \frac{\epsilon_0}{2}\}} e^{\alpha m/d_1} |\nabla \psi|^2}{\int_{\{x \in \Omega : m(x) \geq \max_{\bar{\Omega}} m - \frac{\epsilon_0}{3}\}} e^{\alpha m/d_1} \psi^2} + \frac{\int_{\Omega} e^{\alpha m/d_1} (\theta_{d_2} - m) \psi^2}{\int_{\Omega} e^{\alpha m/d_1} \psi^2} \\ &\leq C e^{-\frac{\alpha \epsilon_0}{6d_1}} + \sup_{\text{supp } \psi} (\theta_{d_2} - m) \\ &\leq C e^{-\frac{\alpha \epsilon_0}{6d_1}} + \|\theta_{d_2}\|_{L^\infty(\Omega)} - \sup_{\bar{\Omega}} m + \epsilon_0. \end{aligned}$$

Letting  $\alpha \rightarrow \infty$ , we have

$$\limsup_{\alpha \rightarrow \infty} \lambda_v \leq \|\theta_{d_2}\|_{L^\infty(\Omega)} - \sup_{\bar{\Omega}} m + \epsilon_0 < 0.$$

This proves the instability of  $(0, \theta_{d_2})$  in Claim 3.

Next, we prove the instability of  $(\tilde{u}, 0)$ . Consider the principal eigenvalue  $\lambda_u$  of

$$\begin{cases} d_2 \Delta \varphi + (m - \tilde{u}) \varphi + \lambda_u \varphi = 0 & \text{in } \Omega, \\ \partial_\nu \varphi = 0 & \text{on } \partial\Omega. \end{cases} \quad (31)$$

Now dividing (31) by  $\varphi$  and integrating by parts, we have

$$d_2 \int_{\Omega} \frac{|\nabla \varphi|^2}{\varphi^2} + \int_{\Omega} (m - \tilde{u}) + |\Omega| \lambda_u = 0 \quad (32)$$

The instability ( $\lambda_u < 0$ ) for large  $\alpha$  follows from (29), (32), and the following lemma, which we shall prove at the end of this section.

**Lemma 5.2.** Suppose  $m$  is nonconstant and  $\partial_\nu m|_{\partial\Omega} < 0$ . Then for each  $d_1 > 0$ ,

$$\liminf_{\alpha \rightarrow \infty} \int_{\Omega} (m - \tilde{u}) \geq \int_{\{x \in \Omega : |\nabla m| > 0, m > 0\}} m + \int_{\{x \in \Omega : m \leq 0\}} m. \quad (33)$$

**Remark 5.1.** The assumption  $\partial_\nu m|_{\partial\Omega} < 0$  in the statement of Theorem 11 is only needed for Lemmas 4.1 and 5.2 and will be removed in Section 7.

□

*Proof of Lemma 5.2.* Let  $\Omega_c = \{x \in \Omega : |\nabla m| = 0\}$ . Then by Sard's Theorem, the set of critical values of  $m$ , denoted by  $m(\Omega_c)$ , has Lebesgue measure zero. Fix a regular value  $\epsilon_0 > 0$ , then for all  $\delta > 0$ , there exists a sequence of disjoint open intervals  $(a_i, b_i)$  such that  $a_i = \epsilon_0$  for some  $i$ , and

$$m(\Omega_c \cap \Omega(\epsilon_0)) \subset \cup_{i=1}^{\infty} (a_i, b_i) \quad (\text{disjoint union}), \text{ and } \sum_{i=1}^{\infty} (b_i - a_i) < \delta.$$

Here  $a_i, b_i$  are necessarily regular values of  $m$ . Moreover, we can choose an integer  $K = K(\delta)$  such that

$$\left| \left\{ x \in \Omega : m(x) \in \cup_{i=K+1}^{\infty} (a_i, b_i) \right\} \right| = \left| \cup_{i=K+1}^{\infty} m^{-1}(a_i, b_i) \right| < \frac{\delta^2}{\int_{\Omega} m^2}, \quad (34)$$

since  $S_K := \cup_{i=K+1}^{\infty} m^{-1}(a_i, b_i)$  is decreasing in  $K$  and contained in a set  $\bar{\Omega}$  of finite measure. Hence  $\lim_{k \rightarrow \infty} m(S_k) = m\left(\lim_{k \rightarrow \infty} S_k\right) = m(\emptyset) = 0$ . Rename the indices such that  $b_1 > \max_{\bar{\Omega}} m$  and

$$\epsilon_0 = a_K < b_K < a_{K-1} < b_{K-1} < \dots < a_1 < b_1. \quad (35)$$

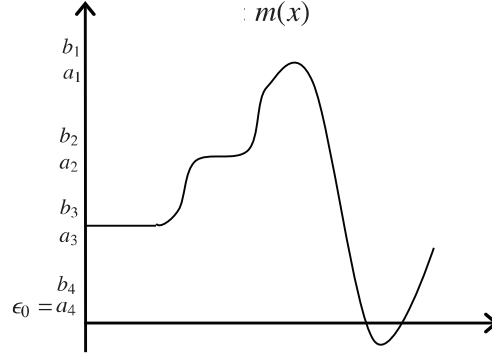


Figure 3. Illustrations of  $a_i, b_i$ .

Note that by (11) and (34), one can prove, by Hölder's inequality, and  $\int_{\Omega} \tilde{u}^2 \leq \int_{\Omega} m^2$ , that

$$\int_{\cup_{i=K+1}^{\infty} \Omega(a_i) \setminus \Omega(b_i)} \tilde{u} < \delta. \quad (36)$$

**Lemma 5.3.** For all  $\alpha > 0$ ,

$$\int_{\Omega(a_1)} (\tilde{u} - m) \leq \frac{1}{a_1} \int_{\Omega(a_1)} \tilde{u}(\tilde{u} - m) + \frac{\|m\|_{L^\infty(\Omega)}^2}{\epsilon_0^2} (b_1 - a_1) |\Omega|. \quad (37)$$

Furthermore, for all  $i = 1, \dots, K-1$ ,

$$\int_{\Omega(a_{i+1}) \setminus \Omega(a_i)} (\tilde{u} - m) \leq \frac{1}{a_{i+1}} \int_{\Omega(a_{i+1}) \setminus \Omega(a_i)} \tilde{u}(\tilde{u} - m) + \frac{\|m\|_{L^\infty(\Omega)}^2}{\epsilon_0^2} (b_{i+1} - a_{i+1}) |\Omega| \quad (38)$$

$$+ \frac{\|m\|_{L^\infty(\Omega)}}{\epsilon_0} \int_{\Omega(b_{i+1}) \setminus \Omega(a_i)} \tilde{u} - \int_{\Omega(b_{i+1}) \setminus \Omega(a_i)} (m - \tilde{u})_+, \quad (39)$$

where  $g_+ = \max\{g, 0\}$  for any function  $g$ .

*Proof.*

$$\begin{aligned} \int_{\Omega(a_1)} (\tilde{u} - m) &= \int_{\Omega(a_1)} (\tilde{u} - m)_+ - \int_{\Omega(a_1)} (m - \tilde{u})_+ \\ &\leq \frac{1}{a_1} \int_{\Omega(a_1)} \tilde{u}(\tilde{u} - m)_+ - \frac{1}{b_1} \int_{\Omega(a_1)} \tilde{u}(m - \tilde{u})_+ \\ &\leq \frac{1}{a_1} \int_{\Omega(a_1)} \tilde{u}(\tilde{u} - m) + \left( \frac{1}{a_1} - \frac{1}{b_1} \right) \|m\|_{L^\infty(\Omega)} \int_{\Omega(a_1)} \tilde{u}. \end{aligned}$$

where the second line follows since in  $\text{supp}(\tilde{u} - m)_+ \cap \Omega(a_1)$ , we have  $\tilde{u} \geq m > a_1$ , and in  $\text{supp}(m - \tilde{u})_+$ ,  $\tilde{u} \leq m \leq \max_{\bar{\Omega}} m < b_1$ . Hence, (37) follows from this, and

$$\int_{\Omega} \tilde{u} \leq \sqrt{|\Omega| \int_{\Omega} \tilde{u}^2} \leq \sqrt{|\Omega| \int_{\Omega} m^2} \leq |\Omega| \|m\|_{L^\infty(\Omega)} \quad (40)$$

(by (11)). Similarly, for  $i = 1, \dots, K - 1$ ,

$$\begin{aligned}
 & \int_{\Omega(a_{i+1}) \setminus \Omega(a_i)} (\tilde{u} - m) \\
 &= \int_{\Omega(a_{i+1}) \setminus \Omega(a_i)} (\tilde{u} - m)_+ - \int_{\Omega(a_{i+1}) \setminus \Omega(a_i)} (m - \tilde{u})_+ \\
 &\leq \frac{1}{a_{i+1}} \int_{\Omega(a_{i+1}) \setminus \Omega(a_i)} \tilde{u}(\tilde{u} - m)_+ - \frac{1}{b_{i+1}} \int_{\Omega(a_{i+1}) \setminus \Omega(b_{i+1})} \tilde{u}(m - \tilde{u})_+ - \int_{\Omega(b_{i+1}) \setminus \Omega(a_i)} (m - \tilde{u})_+ \\
 &\leq \frac{1}{a_{i+1}} \int_{\Omega(a_{i+1}) \setminus \Omega(a_i)} \tilde{u}(\tilde{u} - m) + \left( \frac{1}{a_{i+1}} - \frac{1}{b_{i+1}} \right) \int_{\Omega} \tilde{u}(m - \tilde{u})_+ \\
 &\quad + \frac{1}{a_{i+1}} \int_{\Omega(b_{i+1}) \setminus \Omega(a_i)} \tilde{u}(m - \tilde{u})_+ - \int_{\Omega(b_{i+1}) \setminus \Omega(a_i)} (m - \tilde{u})_+.
 \end{aligned}$$

Thus (38)-(39) follow in a similar fashion.  $\square$

By induction, one can prove the following.

**Lemma 5.4.** For each  $\delta > 0$ , if  $\alpha$  is sufficiently large, then for all  $i = 1, \dots, K$ ,

$$\begin{aligned}
 \int_{\Omega(a_i)} (\tilde{u} - m) + \frac{\delta}{a_1} &\leq \frac{1}{a_i} \left[ \int_{\Omega(a_i)} \tilde{u}(\tilde{u} - m) + \delta \right] + \frac{\|m\|_{L^\infty(\Omega)}^2}{\epsilon_0^2} |\Omega| \sum_{j=1}^i (b_j - a_j) \\
 &\quad + \frac{\|m\|_{L^\infty(\Omega)}}{\epsilon_0} \int_{\cup_{j=2}^i [\Omega(b_j) \setminus \Omega(a_{j-1})]} \tilde{u} - \int_{\cup_{j=2}^i [\Omega(b_j) \setminus \Omega(a_{j-1})]} (m - \tilde{u})_+.
 \end{aligned}$$

*Proof.* When  $i = 1$ , the claim follows from (37). Assume the claim is true for some  $i < K$ , then

$$\begin{aligned}
 & \int_{\Omega(a_{i+1})} (\tilde{u} - m) + \frac{\delta}{a_1} \\
 &= \int_{\Omega(a_i)} (\tilde{u} - m) + \frac{\delta}{a_1} + \int_{\Omega(a_{i+1}) \setminus \Omega(a_i)} (\tilde{u} - m) \\
 &\leq \frac{1}{a_i} \left[ \int_{\Omega(a_i)} \tilde{u}(\tilde{u} - m) + \delta \right] + \frac{\|m\|_{L^\infty(\Omega)}^2}{\epsilon_0^2} |\Omega| \sum_{j=1}^i (b_j - a_j) \\
 &\quad + \frac{\|m\|_{L^\infty(\Omega)}}{\epsilon_0} \int_{\cup_{j=2}^i [\Omega(b_j) \setminus \Omega(a_{j-1})]} \tilde{u} - \int_{\cup_{j=2}^i [\Omega(b_j) \setminus \Omega(a_{j-1})]} (m - \tilde{u})_+ + \int_{\Omega(a_{i+1}) \setminus \Omega(a_i)} (\tilde{u} - m) \\
 &\leq \frac{1}{a_{i+1}} \left[ \int_{\Omega(a_{i+1})} \tilde{u}(\tilde{u} - m) + \delta \right] + \frac{\|m\|_{L^\infty(\Omega)}^2}{\epsilon_0^2} |\Omega| \sum_{j=1}^{i+1} (b_j - a_j) \\
 &\quad + \frac{\|m\|_{L^\infty(\Omega)}}{\epsilon_0} \int_{\cup_{j=2}^{i+1} [\Omega(b_j) \setminus \Omega(a_{j-1})]} \tilde{u} - \int_{\cup_{j=2}^{i+1} [\Omega(b_j) \setminus \Omega(a_{j-1})]} (m - \tilde{u})_+
 \end{aligned}$$

by (39) and the fact that the expressions in the square brackets are positive for  $\alpha$  large (Corollary 4.2).  $\square$

Now we continue our proof of Lemma 5.2. Setting  $i = K$  in Lemma 5.4, we have

$$\begin{aligned}
 \int_{\Omega(\epsilon_0)} (\tilde{u} - m) + \frac{\delta}{a_1} &\leq \frac{1}{\epsilon_0} \left[ \int_{\Omega(\epsilon_0)} \tilde{u}(\tilde{u} - m) + \delta \right] + \frac{\|m\|_{L^\infty(\Omega)}^2 \delta}{\epsilon_0^2} |\Omega| \\
 &\quad + \frac{\|m\|_{L^\infty(\Omega)}}{\epsilon_0} \int_{\cup_{j=K+1}^\infty [\Omega(a_i) \setminus \Omega(b_i)] \cup \Omega_r} \tilde{u} - \int_{\Omega(\epsilon_0) \setminus \cup_{j=1}^\infty [\Omega(a_i) \setminus \Omega(b_i)]} (m - \tilde{u})_+.
 \end{aligned}$$

By (10) and Corollary 4.3,

$$\int_{\Omega(\epsilon_0)} \tilde{u}(\tilde{u} - m) = \int_{\Omega \setminus \Omega(\epsilon_0)} \tilde{u}(m - \tilde{u}) \leq \left( \sup_{\Omega \setminus \Omega(\epsilon_0)} (m - \tilde{u}) \right) \int_{\Omega \setminus \Omega(\epsilon_0)} \tilde{u} \leq \epsilon_0^2 |\Omega| + \delta. \quad (41)$$

provided  $\alpha$  is large. Hence we have

$$\begin{aligned} \int_{\Omega(\epsilon_0)} (\tilde{u} - m) + \frac{\delta}{a_1} &\leq \frac{1}{\epsilon_0} [\epsilon_0^2 |\Omega| + 2\delta] + \frac{\|m\|_{L^\infty(\Omega)}^2 \delta}{\epsilon_0^2} |\Omega| \\ &\quad + \frac{\|m\|_{L^\infty(\Omega)}}{\epsilon_0} \int_{\cup_{i=K+1}^\infty [\Omega(a_i) \setminus \Omega(b_i)] \cup \Omega_r} \tilde{u} - \int_{\Omega(\epsilon_0) \setminus \cup_{i=1}^\infty [\Omega(a_i) \setminus \Omega(b_i)]} (m - \tilde{u})_+. \end{aligned}$$

Taking  $\limsup$  on both sides as  $\alpha \rightarrow \infty$ , and using  $\lim_{\alpha \rightarrow \infty} \int_{\Omega_r} \tilde{u} \rightarrow 0$  (Theorem 9) and (36), we have

$$\limsup_{\alpha \rightarrow \infty} \int_{\Omega(\epsilon_0)} (\tilde{u} - m) + \frac{\delta}{a_1} \leq \epsilon_0 |\Omega| + \frac{2\delta}{\epsilon_0} + \frac{\|m\|_{L^\infty(\Omega)} \delta}{\epsilon_0^2} (|\Omega| \|m\|_{L^\infty(\Omega)} + \epsilon_0) - \int_{\Omega(\epsilon_0) \setminus \cup_{i=1}^\infty [\Omega(a_i) \setminus \Omega(b_i)]} m. \quad (42)$$

We may assume without loss that  $\cup_{i=1}^\infty [\Omega(a_i) \setminus \Omega(b_i)]$  is chosen to be monotonically decreasing as  $\delta \searrow 0$ . Hence by Monotone Convergence Theorem

$$\lim_{\delta \rightarrow 0} \int_{\Omega(\epsilon_0) \setminus \cup_{i=1}^\infty [\Omega(a_i) \setminus \Omega(b_i)]} m = \int_{\Omega(\epsilon_0) \cap \Omega_r} m,$$

where  $\Omega_r$  denotes the set of regular points of  $m$ . Letting  $\delta \rightarrow 0$  in (42), we have

$$\limsup_{\alpha \rightarrow \infty} \int_{\Omega(\epsilon_0)} (\tilde{u} - m) \leq \epsilon_0 |\Omega| - \int_{\Omega(\epsilon_0) \cap \Omega_r} m. \quad (43)$$

On the other hand, by Corollary 4.3,

$$\limsup_{\alpha \rightarrow \infty} \int_{\Omega \setminus \Omega(\epsilon_0)} (\tilde{u} - m) \leq \epsilon_0 |\Omega| - \int_{\Omega \setminus \Omega(\epsilon_0)} m. \quad (44)$$

Adding (43) and (44), and letting  $\epsilon_0 \rightarrow 0$ ,

$$\limsup_{\alpha \rightarrow \infty} \int_{\Omega} (\tilde{u} - m) \leq - \int_{\Omega(0) \cap \Omega_r} m - \int_{\Omega \setminus \Omega(0)} m.$$

This proves Lemma 5.2, which, together with (29), implies the instability of  $(\tilde{u}, 0)$ .  $\square$

## 6. Large Biased Movement vs. Large Diffusion

In this section we present the proof of Theorem 5. In fact, we will prove a more precise result, from which Theorem 5 follows.

**Theorem 12.** Let  $\Omega \subset \mathbb{R}^N$  for some  $N \leq 3$ . Suppose, in addition to (M1), that  $\mathfrak{M} \cap \partial\Omega = \emptyset$  and

$$\int_{\bar{\Omega} \setminus \mathfrak{M}} m < 0.$$

Then for all  $d_1 > 0$ , there exists  $\underline{d} > 0$  such that for all  $d_2 > \underline{d}$ ,  $(\tilde{u}, 0)$  is globally asymptotically stable for all sufficiently large  $\alpha$ .

Let  $m \in C^2(\bar{\Omega})$  be such that  $\max_{\bar{\Omega}} m > 0$ ,  $\partial\Omega \cap \mathfrak{M} = \emptyset$  (where  $\mathfrak{M} = \{x \in \Omega : m(x) = \max_{\bar{\Omega}} m\}$ ),

$$\int_{\Omega} m > 0 \quad \text{and} \quad \int_{\Omega \setminus \mathfrak{M}} m < 0. \quad (45)$$

First, we show the instability of  $(0, \theta_{d_2})$  for all sufficiently large  $\alpha$ .



**Lemma 6.1.** For all  $d_1, d_2 > 0$ ,  $(0, \theta_{d_2})$  is unstable for all sufficiently large  $\alpha$ .

*Proof.* Refer to Claim 3 in the proof of Theorem 11.  $\square$

Next, we show the non-existence of positive steady state.

**Lemma 6.2.** Let  $\Omega \subset \mathbb{R}^N$  and  $N \leq 3$ . For all  $d_1 > 0$ , there exists  $d'' > 0$  such that for  $d_2 > d''$ , (3) has no co-existence steady state for all sufficiently large  $\alpha$ .

*Proof.* Fix  $d_1 > 0$ . Assume to the contrary, then (3) necessarily has a coexistence steady state  $(U_j, V_j)$  for  $d_{2,j} \rightarrow \infty$  and  $\alpha_j \rightarrow \infty$ .

By comparison principle,  $\|V_j\|_{L^\infty(\Omega)} \leq \|m\|_{L^\infty(\Omega)}$  and  $U_j \leq \tilde{u}$ . This and (11) implies, by elliptic  $L^p$  estimates, that  $\|V_j\|_{W^{2,2}(\Omega)}$  is bounded uniformly in  $j$ . Since  $N \leq 3$ , we may assume without loss that  $V_j \rightarrow \kappa$  in  $L^\infty(\Omega)$  for some constant  $\kappa \in [0, \bar{m}]$ . Similarly,  $V_j/\|V_j\|_{L^\infty(\Omega)} \rightarrow 1$  in  $L^\infty(\Omega)$ . Hence, for all  $\epsilon > 0$ ,

$$V_j < \kappa + \epsilon \quad \text{for } j \text{ sufficiently large,} \quad (46)$$

and  $U_j > \tilde{u}_j$ , where  $\tilde{u}_j$  is the unique positive solution to

$$\begin{cases} \nabla \cdot (d_1 \nabla \tilde{u}_j - \alpha_j \tilde{u}_j \nabla m) + \tilde{u}_j(m - \kappa - \epsilon - \tilde{u}_j) = 0 & \text{in } \Omega, \\ d_1 \partial_\nu \tilde{u}_j - \alpha_j \tilde{u}_j \partial_\nu m = 0 & \text{on } \partial\Omega. \end{cases}$$

Hence by Corollary 2.1 (replacing  $m$  by  $m - \kappa - \epsilon$ ),

$$U_j > m - \kappa - \epsilon \quad \text{on } \mathfrak{M} \quad (47)$$

for all  $j$  sufficiently large. Dividing the second equation of (3) (with  $(U, V, \alpha) = (U_j, V_j, \alpha_j)$ ) by  $\|V_j\|_{L^\infty(\Omega)}$  and integrating, we deduce

$$0 = \int_{\Omega} \frac{V_j}{\|V_j\|_{L^\infty(\Omega)}} (m - U_j - V_j) < \int_{\Omega} \frac{V_j}{\|V_j\|_{L^\infty(\Omega)}} (m - (m - \kappa - \epsilon)X_{\mathfrak{M}} - V_j).$$

Letting  $j \rightarrow \infty$ , we have  $V_j \rightarrow \kappa$  and

$$0 \leq \int_{\Omega} (m - \kappa) - \int_{\mathfrak{M}} (m - \kappa - \epsilon) \leq \int_{\Omega \setminus \mathfrak{M}} m + \epsilon |\mathfrak{M}|.$$

Since this is true for all  $\epsilon > 0$ , we have  $\int_{\Omega \setminus \mathfrak{M}} m \geq 0$ , a contradiction to (45).  $\square$

*Proof of Theorem 12.* Since, (i)  $(0, \theta_{d_2})$  is unstable (by Lemma 6.1), and (ii) there are no positive steady states (Lemma 6.2). By the theory of monotone dynamical systems,  $(\tilde{u}, 0)$  is globally asymptotically stable.  $\square$

## 7. Advection-mediated Co-existence, General Case

In this section we shall prove the general version of Theorem 11. By Remark 5.1, it suffices to remove the assumption  $\partial_\nu m|_{\partial\Omega} < 0$  in Lemma 5.2. First, we give a definition

**Definition 1.** Let  $m|_{\partial\Omega}$  be the restriction of  $m$  in  $\partial\Omega$ . We say that  $m_0$  is a regular value of  $m$  and  $m|_{\partial\Omega}$ , if it is a regular value of  $m$  and a regular value of  $m|_{\partial\Omega}$ .

**Lemma 7.1.** Suppose  $m \in C^2(\bar{\Omega})$  is nonconstant and is positive somewhere. Then for each  $d_1 > 0$ ,

$$\liminf_{\alpha \rightarrow \infty} \int_{\Omega} (m - \tilde{u}) \leq \int_{\{x \in \Omega: |\nabla m| > 0, m > 0\}} m + \int_{\{x \in \Omega: m \leq 0\}} m.$$

*Proof.* Fix a positive regular value  $\epsilon_0$  of  $m$  and  $m|_{\partial\Omega}$ , and (small)  $\delta > 0$ , and choose as in the proof of Lemma 5.2, a sequence of disjoint open intervals  $\{(a_i, b_i)\}_{i=1}^\infty$  whose union contains the set of critical values of  $m$  and  $m|_{\partial\Omega}$  in  $(\epsilon_0, \infty)$ . Moreover, there exists  $K$  such that (35) holds and

$$\sum_{i=1}^{\infty} (b_i - a_i) < \delta \quad \text{and} \quad |m^{-1}\{\cup_{i=K+1}^{\infty} (a_i, b_i)\}| < \frac{\delta^2}{\int_{\Omega} m^2}. \quad (48)$$

Also, since  $a_i, b_i$  are regular values of  $m$ , the latter being an open set in  $\mathbb{R}$ , there exists  $\epsilon_i < \frac{b_i - a_i}{3}$  such that  $[a_i, a_i + \epsilon_i] \cup [b_i - \epsilon_i, b_i]$  are regular values of  $m$  and  $m|_{\partial\Omega}$ .

Now, we will follow largely the arguments in Lemma 5.2. We primarily work with the level set of  $L$ , a modified version of  $m$ .

**Lemma 7.2.** *For any  $\eta > 0$  small, there exists  $L \in C^2(\bar{\Omega})$  such that*

- (i)  $L(x) = m(x)$  if  $\text{dist}(x, \partial\Omega) \geq \eta$ ,
- (ii)  $\partial_\nu L < 0$  if  $x \in \partial\Omega$ , and  $m(x) \in \cup_{i=1}^K ([a_i - \epsilon_i, a_i + \epsilon_i] \cup [b_i - \epsilon_i, b_i + \epsilon_i])$ ,
- (iii)  $\|L - m\|_{L^\infty(\Omega)} \leq \eta$ ,
- (iv)  $\nabla L \cdot \nabla m \geq 0$  if  $m(x) \in \cup_{i=1}^K ([a_i - \epsilon_i, a_i + \epsilon_i] \cup [b_i - \epsilon_i, b_i + \epsilon_i])$ .

Moreover,  $\eta > 0$  is chosen such that

$$\eta < \min_{0 \leq i \leq K} \{\epsilon_i/3\} \quad \text{and} \quad \eta < \min_{1 \leq i \leq K} \{(b_i - a_i)/3\}. \quad (49)$$

And that there exists  $\tilde{a}_i, \tilde{b}_i, \tilde{\epsilon}_i$  such that  $\cup_{i=1}^K [\tilde{a}_i, \tilde{a}_i + \tilde{\epsilon}_i] \cup [\tilde{b}_i - \tilde{\epsilon}_i, \tilde{b}_i]$  are regular values of  $L$  satisfying

$$[\tilde{a}_i, \tilde{a}_i + \tilde{\epsilon}_i] \subseteq [a_i, a_i + \epsilon_i], \quad [\tilde{b}_i - \tilde{\epsilon}_i, \tilde{b}_i] \subseteq [b_i - \epsilon_i, b_i], \quad (50)$$

and

$$L^{-1}\{[\tilde{a}_i, \tilde{a}_i + \tilde{\epsilon}_i]\} \subset m^{-1}\{[a_i, a_i + \epsilon_i]\} \quad \text{and} \quad L^{-1}\{[\tilde{b}_i - \tilde{\epsilon}_i, \tilde{b}_i]\} \subset m^{-1}\{[b_i - \epsilon_i, b_i]\}. \quad (51)$$

for all  $1 \leq i \leq K$ .

The proof of Lemma 7.2 is contained in the Appendix.

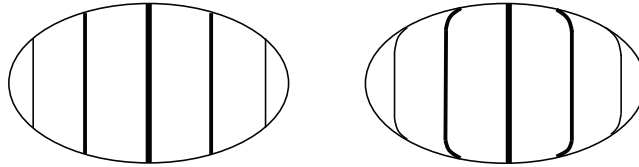


Figure 4. Example of  $L(x)$  corresponding to  $m(x) = 1 - (x_1)^2$ . On the left: Level set of  $m(x)$ , the thickness of the line represents the magnitude of  $m(x)$ . On the right: Level set of the corresponding  $L(x)$ .

Given  $\epsilon_0, \delta > 0$ , let  $L(x)$  be given by Lemma 7.2. In the following we denote

$$\Omega'(\tilde{a}) = \{x \in \Omega : L(x) > \tilde{a}\} \quad \text{and} \quad \Gamma'(\tilde{a}) = \{x \in \Omega : L(x) = \tilde{a}\}$$

and  $\tilde{a} = \tilde{a}_i$  for some  $1 \leq i \leq K$ .

**Lemma 7.3** (Lemma 4.1'). *Assume (M1), if  $\tilde{a} = \tilde{a}_i$  for some  $1 \leq i \leq K$  then*

$$\liminf_{\alpha \rightarrow \infty} \int_{\Gamma'(\tilde{a})} (d_1 \partial_\tau \tilde{u} - \alpha \tilde{u} \partial_\tau m) \geq 0,$$

where  $\tau = -\frac{\nabla L(x)}{|\nabla L(x)|}$  on  $\Gamma'(\tilde{a})$  and  $\partial_\tau = \tau \cdot \nabla$ .

The proof of Lemma 7.3 is completely analogous to Lemma 4.1 and is omitted. The next two corollaries follow from Lemma 7.3 as their counterparts in Section 4 do.

**Corollary 7.4** (Corollary 4.2'). Assume (M1), then  $\liminf_{\alpha \rightarrow \infty} \int_{\Omega'(\tilde{a})} \tilde{u}(\tilde{u} - m) \geq 0$ .

**Corollary 7.5** (Corollary 4.3'). Assume (M1), then there exists a constant  $C > 0$  such that for each regular value  $\epsilon$  of  $m$ ,

$$\limsup_{\alpha \rightarrow \infty} \int_{\Omega \setminus \Omega(\epsilon)} \tilde{u}^2 \leq C\epsilon^2 |\Omega|.$$

**Lemma 7.6** (Lemma 5.6'). For all  $\alpha > 0$ ,

$$\int_{\Omega'(\tilde{a}_1)} (\tilde{u} - m) \leq \frac{1}{\tilde{a}_1 - \eta} \int_{\Omega'(\tilde{a}_1)} \tilde{u}(\tilde{u} - m) + \frac{\|m\|_{L^\infty(\Omega)}^2}{(\epsilon_0/2)^2} 3(\tilde{b}_1 - \tilde{a}_1) |\Omega|.$$

And for all  $1 < i \leq K$ ,

$$\begin{aligned} \int_{\Omega'(\tilde{a}_{i+1}) \setminus \Omega'(\tilde{a}_i)} (\tilde{u} - m) &\leq \frac{1}{\tilde{a}_{i+1} - \eta} \int_{\Omega'(\tilde{a}_{i+1}) \setminus \Omega'(\tilde{a}_i)} \tilde{u}(\tilde{u} - m) + \frac{\|m\|_{L^\infty(\Omega)}^2}{(\epsilon_0/2)^2} 3(\tilde{b}_{i+1} - \tilde{a}_{i+1}) |\Omega| \\ &\quad + \frac{\|m\|_{L^\infty(\Omega)}}{\epsilon_0/2} \int_{\Omega'(\tilde{b}_{i+1}) \setminus \Omega'(\tilde{a}_i)} \tilde{u} - \int_{\Omega'(\tilde{b}_{i+1}) \setminus \Omega'(\tilde{a}_i)} (m - \tilde{u})_+. \end{aligned}$$

*Proof.* Since  $\|m - L\|_{L^\infty(\Omega)} \leq \eta$ ,

$$\begin{aligned} \int_{\Omega'(\tilde{a}_1)} (\tilde{u} - m) &= \int_{\Omega'(\tilde{a}_1)} (\tilde{u} - m)_+ - \int_{\Omega'(\tilde{a}_1)} (m - \tilde{u})_+ \\ &\leq \frac{1}{\tilde{a}_1 - \eta} \int_{\Omega'(\tilde{a}_1)} \tilde{u}(\tilde{u} - m)_+ - \frac{1}{\tilde{b}_1 + \eta} \int_{\Omega'(\tilde{a}_1)} \tilde{u}(m - \tilde{u})_+ \\ &\leq \frac{1}{\tilde{a}_1 - \eta} \int_{\Omega'(\tilde{a}_1)} \tilde{u}(\tilde{u} - m) + \left( \frac{1}{\tilde{a}_1 - \eta} - \frac{1}{\tilde{b}_1 + \eta} \right) \|m\|_{L^\infty(\Omega)} \int_{\Omega'(\tilde{a}_1)} \tilde{u} \\ &\leq \frac{1}{\tilde{a}_1 - \eta} \int_{\Omega'(\tilde{a}_1)} \tilde{u}(\tilde{u} - m) + \left( \frac{\tilde{b}_1 - \tilde{a}_1 + 2\eta}{(\tilde{a}_1 - \eta)(\tilde{b}_1 + \eta)} \right) \|m\|_{L^\infty(\Omega)} \int_{\Omega'(\tilde{a}_1)} \tilde{u} \end{aligned}$$

And the case  $i = 1$  follows by  $\tilde{b}_i + \eta > \tilde{a}_i - \eta > \epsilon_0/2$ , (49) and (40). For  $1 < i \leq K$ ,

$$\begin{aligned} \int_{\Omega'(\tilde{a}_{i+1}) \setminus \Omega'(\tilde{a}_i)} (\tilde{u} - m) &= \int_{\Omega'(\tilde{a}_{i+1}) \setminus \Omega'(\tilde{a}_i)} (\tilde{u} - m)_+ - \int_{\Omega'(\tilde{a}_{i+1}) \setminus \Omega'(\tilde{a}_i)} (m - \tilde{u})_+ \\ &\leq \frac{1}{\tilde{a}_{i+1} - \eta} \int_{\Omega'(\tilde{a}_{i+1}) \setminus \Omega'(\tilde{a}_i)} \tilde{u}(\tilde{u} - m)_+ - \frac{1}{\tilde{b}_{i+1} + \eta} \int_{\Omega'(\tilde{a}_{i+1}) \setminus \Omega'(\tilde{b}_{i+1})} \tilde{u}(m - \tilde{u})_+ \\ &\quad - \int_{\Omega'(\tilde{b}_{i+1}) \setminus \Omega'(\tilde{a}_i)} (m - \tilde{u})_+ \\ &\leq \frac{1}{\tilde{a}_{i+1} - \eta} \int_{\Omega'(\tilde{a}_{i+1}) \setminus \Omega'(\tilde{a}_i)} \tilde{u}(\tilde{u} - m) + \left( \frac{1}{\tilde{a}_{i+1} - \eta} - \frac{1}{\tilde{b}_{i+1} + \eta} \right) \int_{\Omega} \tilde{u}(m - \tilde{u})_+ \\ &\quad + \frac{1}{\tilde{a}_{i+1} - \eta} \int_{\Omega'(\tilde{b}_{i+1}) \setminus \Omega'(\tilde{a}_i)} \tilde{u}(m - \tilde{u})_+ - \int_{\Omega'(\tilde{b}_{i+1}) \setminus \Omega'(\tilde{a}_i)} (m - \tilde{u})_+. \end{aligned}$$

And the case  $1 < i \leq K$  follows in a similar fashion.  $\square$

By summing the results of Lemma 7.6, we have

**Lemma 7.7** (Lemma 5.7'). For all  $1 \leq i \leq K$ ,

$$\begin{aligned} \int_{\Omega'(\tilde{a}_i)} (\tilde{u} - m) + \frac{\delta}{\tilde{a}_1 - \eta} &\leq \frac{1}{\tilde{a}_i - \eta} \left[ \int_{\Omega'(\tilde{a}_i)} \tilde{u}(\tilde{u} - m) + \delta \right] + \frac{\|m\|_{L^\infty(\Omega)}^2}{(\epsilon_0/2)^2} |\Omega| 3 \sum_{j=1}^i (\tilde{b}_j - \tilde{a}_j) \\ &\quad + \frac{\|m\|_{L^\infty(\Omega)}}{\epsilon_0/2} \int_{\cup_{j=2}^i [\Omega'(\tilde{b}_j) \setminus \Omega'(\tilde{a}_{j-1})]} \tilde{u} - \int_{\cup_{j=2}^i [\Omega'(\tilde{b}_j) \setminus \Omega'(\tilde{a}_{j-1})]} (m - \tilde{u})_+ \end{aligned}$$

The proof of Lemma 7.7 is similar to that of Lemma 5.4 and is omitted. Next, we take  $i = K$  in Lemma 7.7, then

$$\begin{aligned} \int_{\Omega'(\tilde{a}_K)} (\tilde{u} - m) &\leq \frac{1}{\tilde{a}_K - \eta} \left[ \int_{\Omega'(\tilde{a}_K)} \tilde{u}(\tilde{u} - m) + \delta \right] + \frac{\|m\|_{L^\infty(\Omega)}^2}{(\epsilon_0/2)^2} |\Omega| 3 \sum_{j=1}^K (\tilde{b}_j - \tilde{a}_j) \\ &\quad + \frac{\|m\|_{L^\infty(\Omega)}}{\epsilon_0/2} \int_{\cup_{j=2}^K [\Omega'(\tilde{b}_j) \setminus \Omega'(\tilde{a}_{j-1})]} \tilde{u} - \int_{\cup_{j=2}^K [\Omega'(\tilde{b}_j) \setminus \Omega'(\tilde{a}_{j-1})]} (m - \tilde{u})_+. \end{aligned}$$

Similar to (41), we have

$$\int_{\Omega'(\tilde{a}_K)} \tilde{u}(\tilde{u} - m) = \int_{\Omega \setminus \Omega'(\tilde{a}_K)} \tilde{u}(m - \tilde{u}) \leq \|m\|_{L^\infty(\Omega \setminus \Omega'(\tilde{a}_K))} \int_{\Omega \setminus \Omega'(\tilde{a}_K)} \tilde{u} \leq C\epsilon^2 + \delta.$$

We also have the following set inclusions.

$$\cup_{j=2}^K [\Omega'(\tilde{b}_j) \setminus \Omega'(\tilde{a}_{j-1})] \subset \Omega_r \cup \left\{ \cup_{j=2}^K [\Omega(b_j) \setminus \Omega(a_{j-1})] \right\} \subset \cup_{i=K+1}^\infty [\Omega(a_i) \setminus \Omega(b_i)] \cup \Omega_r \quad (52)$$

$$\cup_{j=2}^K [\Omega'(\tilde{b}_j) \setminus \Omega'(\tilde{a}_{j-1})] \supset \cup_{j=2}^K [\Omega(b_j) \setminus \Omega(a_{j-1})] \supset \Omega(\epsilon_0) \setminus \left\{ \cup_{i=1}^\infty [\Omega(a_i) \setminus \Omega(b_i)] \right\} \quad (53)$$

Hence we deduce that

$$\begin{aligned} \int_{\Omega(2\epsilon_0)} \tilde{u} - \int_{\Omega(\epsilon_0/2)} m &\leq \frac{2}{\epsilon_0} [C\epsilon_0^2 + 2\delta] + \frac{\|m\|_{L^\infty(\Omega)}^2 12|\Omega|}{\epsilon_0^2} \delta \\ &\quad + \frac{2\|m\|_{L^\infty(\Omega)}}{\epsilon_0} \int_{\cup_{i=K+1}^\infty [\Omega(a_i) \setminus \Omega(b_i)] \cup \Omega_r} \tilde{u} - \int_{\Omega(\epsilon_0) \setminus \left\{ \cup_{i=1}^\infty [\Omega(a_i) \setminus \Omega(b_i)] \right\}} (m - \tilde{u})_+. \end{aligned}$$

Taking  $\limsup_{\alpha \rightarrow \infty}$  on both sides, using also (36),

$$\limsup_{\alpha \rightarrow \infty} \int_{\Omega(2\epsilon_0)} \tilde{u} - \int_{\Omega(\epsilon_0/2)} m \leq C\epsilon_0|\Omega| + \frac{C\delta}{\epsilon_0} + \frac{C\delta}{\epsilon_0^2} - \int_{\Omega(\epsilon_0) \setminus \left\{ \cup_{i=1}^\infty [\Omega(a_i) \setminus \Omega(b_i)] \right\}} m$$

Together with Corollary 4.3, we have

$$\limsup_{\alpha \rightarrow \infty} \int_{\Omega} (\tilde{u} - m) \leq C'\epsilon_0|\Omega| + \frac{C\delta}{\epsilon_0^2} + \frac{C\delta}{\epsilon_0} - \int_{\Omega(\epsilon_0) \setminus \left\{ \cup_{i=1}^\infty [\Omega(a_i) \setminus \Omega(b_i)] \right\}} m - \int_{\Omega \setminus \Omega(\epsilon_0/2)} m.$$

Finally, Lemma 7.1 follows by taking  $\delta \rightarrow 0$  and then  $\epsilon_0 \rightarrow 0$  same as before.  $\square$

## 8. Uniqueness for the Limiting System

In this section, we show the uniqueness and global asymptotic stability of positive solution to (6), which is stated as Theorem 7 in the Introduction. Consider the parabolic counterpart of (6)

$$\begin{cases} U_t = d_1 U'' + U(m - U - V) & \text{in } (-1, 1) \times (0, \infty), \\ V_t = d_2 V'' + V(m - U\chi_{[-1,1]} - V) & \text{in } (-2, 2) \times (0, \infty), \\ U'(\pm 1) = V'(\pm 2) = 0. \end{cases} \quad (54)$$

**Theorem 13.** Suppose that  $m \in C^2([-2, 2])$  satisfies the assumptions of Theorem 6. Then there exists  $\underline{d}_2$ , independent of  $d_1$ , such that (54) has a unique positive steady state for all  $d_1 > 0$  and  $d_2 > \underline{d}_2$ .

It is well-known that a two-species competition system generates a monotone flow [14, 15, 21]. Our situation here is slightly different from the standard case, as the governing equations for  $U$  and  $V$  are defined in different domains  $(-1, 1)$  and  $(-2, 2)$ . Nonetheless, we can proceed in a similar fashion. Denoting the cones of all nonnegative functions in  $C([-1, 1])$  and  $C([-2, 2])$  by  $K_1$  and  $K_2$ , respectively, we define that  $(U, V) \leq (\tilde{U}, \tilde{V})$  whenever  $\tilde{U} - U \in K_1$  and  $V - \tilde{V} \in K_2$ . Now, setting  $X = C([-1, 1]) \times C([-2, 2])$  and  $K = K_1 \times K_2$ , one can easily check that the standard theory carries over to our situation. Thus, we can apply the maximum principle and the theory of monotone dynamical systems to obtain the following proposition.

**Proposition 8.1.** Suppose that for some  $d_1, d_2, \alpha > 0$ , one of the semi-trivial steady states of (54) is linearly unstable, and that every positive steady state of (54), if exists, is asymptotically stable. Then one of the following holds:

- (i) There exists a unique positive steady state  $(U_0, V_0)$  ( $U_0 > 0$  in  $[-1, 1]$  and  $V_0 > 0$  in  $[-2, 2]$ ) which is globally asymptotically stable.
- (ii) One of the two semi-trivial steady states is globally asymptotically stable.

Before we prove Theorem 13, we first derive the existence and limiting profile of positive states of (54).

**Lemma 8.1.** The system (54) has at least one stable positive steady state  $(U_\alpha, V_\alpha)$ . Moreover, for any positive steady state  $(U, V)$  of (54),

$$(U, V) \rightarrow (2(1 - \bar{m}), 2\bar{m} - 1) \quad (55)$$

in  $L^\infty([-1, 1]) \times L^\infty([-2, 2])$  as  $d_2 \rightarrow \infty$ , uniformly in  $d_1 > 0$ .

*Proof.* First, we observe that  $\bar{m} = \frac{1}{4} \int_{-2}^2 m \in (1/2, 1)$ . Note that the system (54) has two semi-trivial steady states:  $(1, 0)$  and  $(0, \theta_{d_2})$ , where  $\theta_{d_2}$  is the unique positive steady state of (2). We claim that both semi-trivial steady states are unstable for any  $d_1, d_2 > 0$ . The stability of the semi-trivial steady state  $(1, 0)$  is determined by the principal eigenvalue  $\lambda_u$  of

$$d_2 \psi'' + (m - X_{[-1, 1]})\psi + \lambda_u \psi = 0 \quad \text{in } (-2, 2) \quad \text{and} \quad \psi'(\pm 2) = 0.$$

Dividing the equation by  $\psi$  and integrating by parts, we have

$$d_2 \int_{-2}^2 \frac{(\psi')^2}{\psi^2} + \int_{-2}^2 (m - X_{[-1, 1]}) + 4\lambda_u = 0.$$

Since  $m - X_{[-1, 1]}$  is non-negative and non-trivial, one deduces readily that  $\lambda_u < 0$ . Similarly, the stability of  $(0, \theta_{d_2})$  is determined by the principal eigenvalue  $\lambda_v$  of

$$d_1 \phi'' + (1 - \theta_{d_2})\phi + \lambda_v \phi = 0 \quad \text{in } (-1, 1) \quad \text{and} \quad \phi'(\pm 1) = 0.$$

Again, dividing by  $\phi$  and integrating by parts, we have

$$d_1 \int_{-1}^1 \frac{(\phi')^2}{\phi^2} + \int_{-1}^1 (1 - \theta_{d_2}) + 2\lambda_v = 0.$$

And the negativity of  $\lambda_v$  follows from the fact that  $\theta_{d_2} < 1 = \max_{[-2, 2]} m$ , which is a consequence of the maximum principle. By the theory of monotone dynamical systems, at least one stable positive steady state exists, as both of the semi-trivial steady states are unstable.

Next, we show (55). Suppose that  $(U, V)$  is a positive steady state of (54). By the maximum principle, one has  $\|U\|_{L^\infty([-1, 1])}, \|V\|_{L^\infty([-2, 2])} \leq 1$ . Next, divide the second equation of (6) by  $d_2$  and let  $d_2 \rightarrow \infty$ . By passing to a subsequence, we may assume that  $V \rightarrow C_v$  and, by the equation of  $U$ ,  $U \rightarrow C_u$ , for some non-negative constants  $C_u, C_v$ .

We claim that both  $C_v > 0$  and  $C_u > 0$ . Suppose that  $C_u = 0$ . Then  $U \rightarrow 0$  in  $L^\infty([-1, 1])$ . From the second equation of (6), it follows that  $V \rightarrow \bar{m} \in (1/2, 1)$ . Now integrating the first equation of (6) gives

$$0 = \int_{-1}^1 U(1 - U - V) = \int_{-1}^1 U(1 - \bar{m} + o(1)) > 0,$$

which is a contradiction. Next, suppose  $C_v = 0$ . Then we must have  $V \rightarrow 0$ , and thus  $U \rightarrow 1$ . Since  $V/\|V\|_{L^\infty([-2, 2])} \rightarrow \tilde{V}$ , where  $\tilde{V} > 0$ , we have, by integrating the second equation of (6) and dividing by  $\|V\|_{L^\infty([-2, 2])}$ ,

$$0 = \int_{-1}^1 \frac{V}{\|V\|_{L^\infty([-2, 2])}} (1 - U - V) + \int_{(-2, 2) \setminus (-1, 1)} \frac{V}{\|V\|_{L^\infty([-2, 2])}} (m - V).$$

Letting  $d_2 \rightarrow \infty$ , we have

$$0 = \lim_{d_2 \rightarrow \infty} \int_{-1}^1 \frac{V}{\|V\|_{L^\infty([-2, 2])}} (1 - U - V) + \lim_{d_2 \rightarrow \infty} \int_{(-2, 2) \setminus (-1, 1)} \frac{V}{\|V\|_{L^\infty([-2, 2])}} (m - V) = \int_{(-2, 2) \setminus (-1, 1)} \tilde{V} m > 0,$$

which is again a contradiction. Therefore,  $C_u > 0$  and  $C_v > 0$ . Finally, by integrating (6) and passing  $d_2 \rightarrow \infty$ , we see that  $C_u, C_v$  solves

$$C_u(1 - C_u - C_v) = 0 \quad \text{and} \quad C_v \left( \bar{m} - \frac{1}{2} C_u - C_v \right) = 0.$$

Hence  $(C_u, C_v) = (2(1 - \bar{m}), 2\bar{m} - 1)$ .  $\square$

Next, we show that every positive steady state of (54) is locally asymptotically stable, provided that  $d_2$  is large.

**Lemma 8.2.** *There exists  $\underline{d}_2 > 0$  such that every positive steady state of (54) is locally asymptotically stable for all  $d_1 > 0$  and  $d_2 > \underline{d}_2$ .*

*Proof.* Let  $(U, V)$  be a positive steady state of (6). As (54) generates a monotone dynamical system, it suffices to consider the linear stability of  $(U, V)$  via the following eigenvalue problem

$$\begin{cases} d_1 \phi'' + (1 - 2U - V)\phi - U\psi + \lambda\phi = 0 & \text{in } (-1, 1), \\ d_2 \psi'' - VX_{[-1, 1]}\phi + (m - UX_{[-1, 1]} - 2V)\psi + \lambda\psi = 0 & \text{in } (-2, 2), \\ \phi'(\pm 1) = \psi'(\pm 2) = 0. \end{cases} \quad (56)$$

Although (56) is not a standard cooperative system, it is straightforward to check that (56) has a principal eigenvalue  $\lambda_1 \in \mathbb{R}$  with least real part among all eigenvalues. Moreover,  $\lambda_1$  is simple and one can choose its eigenfunction  $(\phi, \psi)$  so that  $\phi > 0$  in  $[-1, 1]$  and  $\psi < 0$  in  $[-2, 2]$  and that the corresponding principal eigenfunction can be used to construct a family of super and subsolution which in turn give the local asymptotic stability of  $(U, V)$ . Hence, it suffices to show that  $\lambda_1 > 0$  for all  $d_2$  large.

**Claim 4.** *There exists  $C > 0$  such that  $\lambda_1 \geq -C$  for all  $d_1, d_2 > 0$ .*

Multiplying the first and second equation of (56) by  $\phi$  and  $\psi$  respectively and integrating by parts, we have, upon adding,

$$\lambda \left( \int_{-1}^1 \phi^2 + \int_{-2}^2 \psi^2 \right) = d_1 \int_{-1}^1 |\phi'|^2 + d_2 \int_{-2}^2 |\psi'|^2 + \int_{-1}^1 f_1 \phi^2 + \int_{-1}^1 f_2 \phi \psi + \int_{-2}^2 f_3 \psi^2$$

where  $f_i(x)$ ,  $i = 1, 2, 3$  depends on  $x, U(x), V(x)$ . As  $\|U\|_{L^\infty([-1, 1])} + \|V\|_{L^\infty([-2, 2])}$  is bounded, so is  $\|f_i\|_{L^\infty}$ ,  $i = 1, 2, 3$ . Hence there exists  $C > 0$  independent of  $\alpha$  such that

$$\lambda \left( \int_{-1}^1 \phi^2 + \int_{-2}^2 \psi^2 \right) \geq -C \left( \int_{-1}^1 \phi^2 + \int_{-2}^2 \psi^2 \right)$$

This proves the claim.

Suppose to the contrary that along a sequence of positive steady states  $(U_k, V_k)$  such that

$$\lambda_1 = \lambda_1(k) \leq 0 \quad \text{with} \quad d_2 = d_2(k) \rightarrow \infty, \quad d_1 = d_1(k) \in (0, \infty).$$

Then  $\lambda_1$  is bounded from above and below and we may assume that  $\lambda_1 \rightarrow \hat{\lambda}_1 \leq 0$ . Upon dividing the second equation of (56) by  $d_2$ , and normalizing by  $\|\phi\|_{L^\infty([-1, 1])} + \|\psi\|_{L^\infty([-2, 2])} = 1$ , we see that  $\psi \rightarrow -C_\psi < 0$ .

**Claim 5.**  $\phi \rightarrow C_\phi = \frac{C_u C_\psi}{C_u - \lambda_1}$  as  $d_2 \rightarrow \infty$ , uniformly in  $d_1$ .

The claim follows by observing that  $\phi$  solves

$$d_1 \phi'' + (1 - 2U - V + \lambda_1) \phi = U\psi \quad \text{in } (-1, 1), \quad \phi'(\pm 1) = 0,$$

with  $(1 - 2U - V + \lambda_1) \rightarrow -C_u + \hat{\lambda}_1 < 0$  and  $U\psi \rightarrow -C_u C_\psi$ .

Next, integrating the second equation of (56) and letting  $d_2 \rightarrow \infty$ , we have

$$-\frac{1}{2} C_v C_\phi + \left( \bar{m} - \frac{1}{2} C_u - 2C_v \right) (-C_\psi) + \hat{\lambda}_1 (-C_\psi) = 0.$$

By  $\bar{m} = \frac{1}{2} C_u + C_v$ , one deduces that

$$-\frac{1}{2} C_v C_\phi + C_v C_\psi + \hat{\lambda}_1 (-C_\psi) = 0. \quad (57)$$

Combining Claim 5 and (57), we have

$$\begin{pmatrix} \hat{\lambda}_1 - C_u & C_u \\ \frac{1}{2} C_v & \hat{\lambda}_1 - C_v \end{pmatrix} \begin{pmatrix} C_\phi \\ C_\psi \end{pmatrix} = \begin{pmatrix} 0 \\ 0 \end{pmatrix}$$

and hence

$$\hat{\lambda}_1 = \frac{C_u + C_v}{2} \pm \sqrt{\left( \frac{C_u + C_v}{2} \right)^2 - \frac{C_u C_v}{2}} = \frac{C_u + C_v}{2} \pm \frac{1}{2} \sqrt{C_u^2 + C_v^2} > 0.$$

This contradicts the fact that  $\hat{\lambda}_1$  as the limit of a non-positive sequence  $\lambda_1$ , must be non-positive.  $\square$

*Proof of Theorem 13.* By Lemma 8.1, (54) has at least one positive steady state  $(U_0, V_0)$  such that  $(U_0, V_0) \rightarrow (2(1 - \bar{m}), 2\bar{m} - 1)$  as  $d_2 \rightarrow \infty$ . Moreover, every positive steady state is locally asymptotically stable by Lemma 8.2. Therefore, by Proposition 8.1, (54) has a unique positive steady state  $(U_0, V_0)$ , which is globally asymptotically stable.  $\square$

## 9. Discussion

Biological dispersal strategies have important consequences on population dynamics, disease spread and distribution of species. A reaction-diffusion-advection model is proposed by [5] to compare the relative advantage of conditional and unconditional dispersal strategies. More precisely, we envision two species  $U$  and  $V$  possessing the same ecological properties, but different dispersal strategies:  $U$  is assumed to disperse by a combination of passive diffusion and directed movement up the environmental gradient while  $V$  adopts passive diffusion only. In the previous work by Cantrell et al. [6] and subsequently by Chen and Lou [9], under certain nondegeneracy conditions for  $m$ , the so-called “advection-mediated co-existence” is demonstrated. i.e. the two species *always* co-exist when  $\alpha$  is large. One possible explanation is that for large values of  $\alpha$ ,  $U$  specializes on the locally most favorable points of the habitat (which is assumed to be of measure zero), while the ‘generalist’  $V$  survives by utilizing the remaining resources.

However, depending on scales, it is conceivable that natural organisms may not be as sensitive when the local environment is favorable. This motivates us to study the case when the environment is represented by an arbitrary function in  $C^2(\bar{\Omega})$ . In particular, this allows the local maximum of  $m$ , as perceived by the organism, to be assumed over a region rather than a point.

To summarize, we have shown the following in this paper:

- (Theorem 4) A criterion on the environmental function  $m$  for the “advection-mediated coexistence” is established. For any  $m$  satisfying the criterion, and for any  $d_1, d_2 > 0$ , (3) has at least one coexistence steady state for all  $\alpha$  large. Moreover, in contrast to the non-degenerate case (when  $U$  always concentrates on isolated points and therefore has small total population), the limiting total population of  $u$  is not necessarily small.
- (Theorem 5) The above coexistence criterion is sharp.

- (Theorem 6) Suppose that  $\Omega \subset \mathbb{R}^N$  and  $m \in C^2(\bar{\Omega})$  has a single maximum attained over an interval. Then for  $\alpha$  large, every steady state satisfies, in the limit, a special system where the two species coexist, and  $U$  is confined in the local maximum points of  $m$  while  $V$  diffuses throughout the entire domain, and they compete only within the set of maximum points of  $m$ .

We conjecture that the last result can be extended to higher dimensional domains, possibly with additional conditions on  $m$ .

## Appendix A. Construction of $L(x)$

*Proof of Lemma 7.2.* Recall the basic fact that for some  $\eta_0 = \eta_0(\partial\Omega) > 0$ , the map  $T : \partial\Omega \times (-\eta_0, \eta_0) \rightarrow \{x \in \mathbb{R}^N : \text{dist}(x, \partial\Omega) < \eta_0\}$  defined as

$$(x_0, t) \mapsto x_0 - t\nu(x_0)$$

where  $\nu(x_0)$  is the outward unit normal vector with respect to  $\partial\Omega$  at  $x_0$ , is a diffeomorphism. For  $x \in \bar{\Omega}$  that is close enough to  $\partial\Omega$ , let  $x_0 \in \partial\Omega$  be the unique point on  $\partial\Omega$  closest to  $x$  and we define in the following  $\nu(x) = \nu(x_0)$ . For  $x$  close to  $\partial\Omega$ , we regard  $m$  as a function defined on  $\partial\Omega \times [0, \eta_0]$ , and define  $\nabla_{\partial\Omega} m$  by the decomposition

$$\nabla m = (\partial_\nu m)\nu + \nabla_{\partial\Omega} m, \quad \text{where} \quad \partial_\nu m(x) = \nu(x) \cdot \nabla m(x).$$

We also claim, without proof, the following calculus fact.

**Claim 6.** Given  $\eta \in (0, \eta_0)$ , define

$$g(t) := \begin{cases} 0 & \text{for } t \geq \eta, \\ \frac{1}{3\eta^2}(\eta - t)^3 & \text{for } -\eta < t \leq \eta, \end{cases}$$

then  $g \in C^2((-\eta, \infty))$ ,  $g'(0) = -1$ ,  $g'(\eta) = g''(\eta) = 0$ .

Now, let

$$D := \{x \in \Omega : m(x) \in \cup_{i=1}^K ([a_i - \epsilon_i, a_i + \epsilon_i] \cup [b_i - \epsilon_i, b_i + \epsilon_i]) \text{ and } \text{dist}(x, \partial\Omega) < \eta_0\}.$$

(Note that, as we are dealing with regular values of both  $m$  and  $m|_{\partial\Omega}$ , by taking  $\eta_0$  smaller, we may assume that  $D \subset \{x \in \Omega : |\nabla m| > 0 \text{ and } |\nabla_{\partial\Omega} m| > 0\}$ .) Choose positive constants  $\delta_1, \eta$  such that

$$\delta_1 := \frac{\inf_D |\nabla_{\partial\Omega} m|^2}{2\|\nabla m\|_{L^\infty(\Omega)}} \quad \text{and} \quad \eta < \min \left\{ \frac{3 \inf_D |\nabla_{\partial\Omega} m|^2}{2\|\nabla m\|_{L^\infty(\Omega)}\|\nabla^2 m\|_{L^\infty(\Omega)}}, \eta_0 \right\}. \quad (\text{A.1})$$

Define for any  $x = x_0 - t\nu = x_0 - t(x)\nu(x) \in \bar{\Omega}$ ,

$$L(x) = m(x) + (\delta_1 - \partial_\nu m(x_0))g(t).$$

it remains to check that  $L(x)$  satisfies all the requirements of Lemma 7.2. We first consider  $x \in \Omega$  such that  $\text{dist}(x, \partial\Omega) \geq \eta$ , then  $L(x) = m(x)$  and hence  $\nabla L \cdot \nabla m = |\nabla m|^2 \geq 0$ . Next, consider  $x \in D$  such that  $\text{dist}(x, \partial\Omega) < \eta$ , then

$$\nabla L = \nabla m + \nu g'(t)(\delta_1 + \partial_\nu m(x_0)) - g(t)\nabla F,$$

where  $F(x) := \partial_\nu m(x_0)$ . Note that  $F(x)$  depends only on the projection of  $x$  onto  $\partial\Omega$ , so  $\nabla F \perp \nu(x)$ . Thus, for all  $x_0 \in \partial\Omega \cap \bar{D}$ ,

$$\partial_\nu L(x_0) = \partial_\nu m(x_0) - (\delta_1 + \partial_\nu m(x_0)) = -\delta_1 < 0.$$

It suffices to check that  $\nabla L \cdot \nabla m \geq 0$  in  $\{x \in D : \text{dist}(x, \partial\Omega) < \eta\}$ . Now,

$$\begin{aligned} \nabla L \cdot \nabla m &= |\nabla m(x)|^2 + \partial_\nu m(x)g'(t)(\delta_1 + \partial_\nu m(x_0)) - g(t)(\nabla m \cdot \nabla F) \\ &\geq |\nabla_{\partial\Omega} m(x)|^2 - |\partial_\nu m(x)| |\partial_\nu m(x) - \partial_\nu m(x_0)| - |\partial_\nu m(x)| \delta_1 - g(t)(\nabla m \cdot \nabla F) \\ &\geq \inf_D |\nabla_{\partial\Omega} m|^2 - \delta_1 \|\nabla m\|_{L^\infty(\Omega)} - \frac{2}{3} \eta \|\nabla m\|_{L^\infty(\Omega)} \|\nabla^2 m\|_{L^\infty(\Omega)} \\ &\geq 0 \end{aligned}$$

by our choice of  $\delta_1$  and  $\eta$  in (A.1). The rest of Lemma 7.2 follow by choosing  $\tilde{a}_i, \tilde{a}_i + \tilde{\epsilon}_i, \tilde{b}_i - \tilde{\epsilon}_i, \tilde{b}_i$  from the set of dense, open regular values of  $L$ . We omit the details here.  $\square$



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## References

- [1] I. Averill, *The effect of intermediate advection on two competing species*, Doctoral Thesis, Ohio State University, 2012.
- [2] F. Belgacem and C. Cosner, *The effects of dispersal along environmental gradients on the dynamics of populations in heterogeneous environment*, Can. Appl. Math. Q. **3** (1995) 379–397.
- [3] A. Bezugly and Y. Lou, *Reaction-diffusion models with large advection coefficients*, Appl. Anal. **89** (2010) 983–1004.
- [4] R. S. Cantrell, C. Cosner, *Spatial Ecology via Reaction-Diffusion Equations*, Series in Mathematical and Computational Biology, John Wiley and Sons, 2003.
- [5] R. S. Cantrell, C. Cosner and Y. Lou, *Movement towards better environments and the evolution of rapid diffusion.*, Math. Biosci. **240** (2006) 199–214.
- [6] R. S. Cantrell, C. Cosner and Y. Lou, *Advection-mediated coexistence of competing species*, Proc. Roy. Soc. Edinburgh Sect. A **137** (2007) 497–518.
- [7] X. Chen, R. Hambrock and Y. Lou, *Evolution of conditional dispersal, a reaction-diffusion-advection model*, J. Math. Biol. **57** (2008) 361–386.
- [8] X. Chen, K.-Y. Lam and Y. Lou, *Dynamics of a reaction-diffusion-advection model for two competing species*, Discrete Contin. Dyn. Syst. A **32** (2012) 3841–3859.
- [9] X. Chen and Y. Lou, *Principal eigenvalue and eigenfunctions of an elliptic operator with large advection and its application to a competition model*, Indiana Univ. Math. J. **57** (2008) 627–657.
- [10] C. Cosner and Y. Lou, *Does movement toward better environments always benefit a population?*, J. Math. Anal. Appl. **277** (2003) 489–503.
- [11] J. Dockery, V. Hutson, K. Mischaikow and M. Pernarowski, *The evolution of slow dispersal rates: A reaction-diffusion model*, J. Math. Biol. **37** (1998) 61–83.
- [12] D. Gilbarg and N.S. Trudinger, *Elliptic Partial Differential Equations of Second Order*, Grundlehren der Mathematischen Wissenschaften 224, Springer-Verlag, Berlin, 1983.
- [13] R. Hambrock and Y. Lou, *The evolution of conditional dispersal strategy in spatially heterogeneous habitats*, Bull. Math. Biol. **71** (2009) 1793–1817.
- [14] P. Hess, *Periodic-Parabolic Boundary Value Problems and Positivity*, Pitman, New York, 1991.
- [15] S. Hsu, H. Smith and P. Waltman, *Competitive exclusion and coexistence for competitive systems on ordered Banach spaces*, Trans. Amer. Math. Soc. **394** (1996) 4083–4094.
- [16] K.-Y. Lam, *Concentration phenomena of a semilinear elliptic equation with large advection in an ecological model*, J. Differential Equations **250** (2011) 161–181.
- [17] K.-Y. Lam, *Limiting profiles of semilinear elliptic equations with large advection in population dynamics II*, SIAM J. Math. Anal. **44** (2012) 1808–1830.
- [18] K.-Y. Lam and W.-M. Ni, *Limiting profiles of semilinear elliptic equations with large advection in population dynamics*, Discrete Contin. Dyn. Syst. **28** (2010) 1051–1067.
- [19] W.-M. Ni, *The Mathematics of Diffusion*, CBMS Reg. Conf. Ser. Appl. Math. **82**, SIAM, Philadelphia, 2011.
- [20] M.A. McPeck and R.D. Holt, *The evolution of dispersal in spatially and temporally varying environments*, Am. Nat. **140** (1992) 1010–1027.
- [21] H. Smith, *Monotone Dynamical Systems. Mathematical Surveys and Monographs 41*. American Mathematical Society, Providence, Rhode Island, U.S.A., 1995.