

# Reaction-Diffusion Equations in Spatial Ecology

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## Abstract

In this work, we study two problems in mathematical ecology. These problems are formulated as partial differential equations of reaction-diffusion type.

In the first part of this work, we study the persistence of a single species or two species in a bounded domain subject to diffusive movement, environmental drift and boundary loss. These populations are described by a reaction-diffusion equation describing single- and two-species population dynamics. For the case of a single species, we establish the existence of the critical domain size, and analyze its dependence on the diffusion rate and rate of loss at each boundary point. We also consider the competition between two species which differ only in their dispersal rates. If the diffusion rates of both species are sufficiently large, we show that one species must exclude the other, and provide conditions under which the faster (or the slower) species will prevail.

In the second part of this work, we study the spreading speed of a predator population that is expanding its range. Specifically, we consider a diffusive Lotka-Volterra system describing the interaction of a predator species and a prey species. Motivated by the effect of global climate change, it is imposed that the efficiency with which predators convert prey to offspring is described by a function whose profile is fixed in the moving frame  $\xi = x - c_1 t$ . By applying the Hamilton-Jacobi approach, we completely determine the asymptotic spreading speed of the predator in the case

that the conversion efficiency is monotonically increasing with arbitrary value of  $c_1 > 0$ . When the conversion efficiency is monotonically decreasing, we determine the spreading speed if the speed  $c_1 > 0$  of the moving frame is sufficiently fast or slow.

*To Chunxiao, Liwu, Athena, and Grace*

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## Chapter 1: Introduction

### 1.1 Reaction-diffusion equations in spatial ecology

This thesis will be devoted to the analysis of systems of reaction-diffusion equations inspired by ecology. In 1951, Skellam [86] proposed that the two-dimensional population density of successive generations of a biological species be described according to a solution,  $u$ , of the heat equation  $u_t = d(u_{xx} + u_{yy})$ , where  $d$  is a positive parameter. Furthermore, Skellam showed that the approximately linear relationship between the square root of territorial area and time, inferred from data for the expanding habitat range of a population of invasive muskrats in central Europe, could be reproduced by his model. By adding a rule for population growth, Skellam obtained a reaction-diffusion equation of the form

$$u_t = d(u_{xx} + u_{yy}) + f(u), \tag{1.1}$$

where  $f(u)$  describes the rate of population growth independent of dispersal. In so doing, Skellam was the first to analyze reaction-diffusion equations in the context of population dynamics.

His work examined two fundamental issues that have since formed the basis for much study of reaction-diffusion equations in theoretical ecology: (i) the persistence

of species in spatially heterogeneous habitats, and (ii) the rate of spread of species into new territory. This work is divided into two parts, which are motivated by precisely these two questions.

The first part concerns our results which have appeared in publication [56]. Specifically, we consider the following reaction-diffusion-advection equation describing a single species in a bounded, one-dimensional domain  $[0, l]$ :

$$\begin{cases} u_t = \mu u_{xx} - \alpha u_x + u(r - u/K), & 0 < x < l, t > 0, \\ \mu u_x(0) - \alpha u(0) = (b_0 - 1)\alpha u(0), \\ \mu u_x(l) - \alpha u(l) = -b_l \alpha u(l). \end{cases} \quad (1.2)$$

Here, we are interested in the influence of parameters, such as dispersal rate, domain size, and boundary conditions, on the persistence of the species  $u$ .

Furthermore, as an extension of (1.2) we consider the following diffusive Lotka-Volterra system describing two species differing only in their dispersal rates:

$$\begin{cases} u_t = \mu u_{xx} - \alpha u_x + u(r - \frac{u+v}{K}), & 0 < x < l, t > 0, \\ v_t = \nu v_{xx} - \alpha v_x + v(r - \frac{u+v}{K}), & 0 < x < l, t > 0, \\ \mu u_x(0, t) - \alpha u(0, t) = (b_0 - 1)\alpha u(0, t), & t > 0, \\ \mu u_x(l, t) - \alpha u(l, t) = -b_l \alpha u(l, t), & t > 0, \\ \nu v_x(0, t) - \alpha v(0, t) = (b_0 - 1)\alpha v(0, t), & t > 0, \\ \nu v_x(l, t) - \alpha v(l, t) = -b_l \alpha v(l, t), & t > 0. \end{cases} \quad (1.3)$$

Here, we are interested in the influence of parameters on the competition between species  $u$  and  $v$ .

In the second part of this thesis, we present our results which have been submitted for publication [55]. Specifically, we consider the following diffusive Lotka-Volterra system describing the interaction of a predator and a prey species in a one-dimensional unbounded spatial domain  $\mathbb{R}^1$ :

$$\begin{cases} u_t = u_{xx} + (-1 - u + a(x - c_1 t)v)u & \text{in } (0, \infty) \times \mathbb{R} \\ v_t = dv_{xx} + r(1 - v - bu)v & \text{in } (0, \infty) \times \mathbb{R} \\ u(0, x) = u_0(x), \quad v(0, x) = v_0(x) & \text{in } \mathbb{R}. \end{cases} \quad (1.4)$$

Here, we are interested in the asymptotic spreading speed of the predator,  $u$ . In particular, we are interested in how the spreading speed depends on the environmental shifting speed  $c_1$  and the prey-to-predator conversion efficiency function,  $a$ .

The rest of this thesis is organized as follows. In Subsection 1.2 we briefly introduce our main results for (1.2) and (1.3), and present the complete statements and proofs in Chapter 2. In Subsection 1.3, we briefly introduce our main results for (1.4), and present the complete statements and proofs in Chapter 3.

## 1.2 Species persistence: the critical domain size

In the first part of this work, we study the population dynamics of a single species and of two competing species in a one-dimensional, bounded, advective environment.

For a single species, the population dynamics are represented by the following model:

$$\begin{cases} u_t = \mu u_{xx} - \alpha u_x + u(r - u/K), & 0 < x < l, \quad t > 0, \\ \mu u_x(0) - \alpha u(0) = (b_0 - 1)\alpha u(0), \\ \mu u_x(l) - \alpha u(l) = -b_l \alpha u(l). \end{cases} \quad (1.5)$$

We are particularly interested in the ability of the species  $u$  to persist. Our main result is to prove that there is a threshold domain length  $l^*$ , called the *critical domain size*, such that the species will persist if and only if  $l > l^*$ . By finding an explicit formula for  $l^*$  as a function of model parameters, we are able to analyze the effect of the dispersal rate  $\mu$ , the boundary parameters  $b_0$  and  $b_l$ , the advection rate  $\alpha$ , and the intrinsic growth rate  $r$  on the persistence of the species.

A key fact used in our analysis relates the asymptotic dynamics of (1.5) to the principal eigenvalue of the following eigenvalue problem, which arises from linearizing (1.5) about the steady state  $u \equiv 0$ :

$$\begin{cases} \mu \varphi_{xx} - \alpha \varphi_x + r \varphi = \lambda \varphi, & 0 < x < l, \\ \mu \varphi_x(0) - \alpha b_0 \varphi(0) = \mu \varphi_x(l) + \alpha (b_l - 1) \varphi(l) = 0. \end{cases} \quad (1.6)$$

It is well-known that problem (1.6) admits a *principal eigenvalue*,  $\lambda_1$  (see, e.g., [33]), in the sense that:

1.  $\lambda_1 \in \mathbb{R}$  is a simple eigenvalue.
2.  $\lambda_1 > \operatorname{Re} \lambda$  for all other eigenvalues  $\lambda$  of (1.6) (in fact, all eigenvalues of (1.6) are real-valued).
3.  $\lambda_1$  is the unique eigenvalue of (1.6) with a positive eigenfunction,  $\varphi_1$ .

The following well-known result (see [16, 57]) supplies a persistence criterion for the species, based on the sign of  $\lambda_1$ :

**Theorem 1.** *Let  $\lambda_1$  be the principal eigenvalue of (1.6).*

- (i) *If  $\lambda_1 \leq 0$ , then  $\lim_{t \rightarrow \infty} \|u(\cdot, t)\|_{C^0([0,l])} = 0$  for every nonnegative solution of (1.5).*
- (ii) *If  $\lambda_1 > 0$ , then (1.5) has a unique positive equilibrium  $\theta$ . Moreover,*

$$\lim_{t \rightarrow \infty} \|u(\cdot, t) - \theta\|_{C^0([0,l])} = 0$$

*for every nonnegative, nontrivial solution of (1.5).*

Thus, the solution  $u \equiv 0$  is globally asymptotically stable if and only if  $\lambda_1 \leq 0$ . Otherwise, if  $\lambda_1 > 0$ , any initially non-negative population will tend to a positive equilibrium, and the species persists. With this fact, the critical domain size can be defined as follows:

**Definition.** *Given  $\mu, \alpha, r > 0$ ,  $b_0 \geq 0$ , and  $b_l \geq 0$ , we say that  $l^* \in (0, \infty]$  is a critical domain size of (1.5) if*

$$\lambda_1 \begin{cases} > 0 & \text{for } l > l^* \\ = 0 & \text{for } l = l^* \\ < 0 & \text{for } l < l^*, \end{cases}$$

By showing that the mapping  $\lambda_1 \mapsto l$  is increasing, the existence of  $l^*$  is established for  $b_0 + b_l > 1$  (Ch. 2, Theorem 2). In Ch. 2, Theorem 3, we establish properties of the critical domain size  $l^*$  as a function of the dispersal rate, and determine values of  $b_0$  and  $b_l$  such that faster diffusion can be advantageous for persistence.

Finally, we consider competition between two species, which disperse at distinct rates  $\mu$  and  $\nu$ , but are otherwise identical:

$$\begin{cases} u_t = \mu u_{xx} - \alpha u_x + u(r - \frac{u+v}{K}), & 0 < x < l, t > 0, \\ v_t = \nu v_{xx} - \alpha v_x + v(r - \frac{u+v}{K}), & 0 < x < l, t > 0, \\ \mu u_x(0, t) - \alpha u(0, t) = (b_0 - 1)\alpha u(0, t), & t > 0, \\ \mu u_x(l, t) - \alpha u(l, t) = -b_l \alpha u(l, t), & t > 0, \\ \nu v_x(0, t) - \alpha v(0, t) = (b_0 - 1)\alpha v(0, t), & t > 0, \\ \nu v_x(l, t) - \alpha v(l, t) = -b_l \alpha v(l, t), & t > 0. \end{cases} \quad (1.7)$$

In Ch. 2, Theorem 4, we establish a sufficient condition to determine whether the faster or slower dispersing species wins the competition, so long as the dispersal rates of both species are sufficiently large.

### 1.3 Asymptotic spreading speed: a predator-prey system in a shifting environment

In the second part of this work, we study a predator-prey system inspired by the effects of changing climate. We consider the system:

$$\begin{cases} u_t = u_{xx} + (-1 - u + a(x - c_1 t)v)u & \text{in } (0, \infty) \times \mathbb{R} \\ v_t = dv_{xx} + r(1 - v - bu)v & \text{in } (0, \infty) \times \mathbb{R} \\ u(0, x) = u_0(x), \quad v(0, x) = v_0(x) & \text{in } \mathbb{R}. \end{cases} \quad (1.8)$$

Here,  $u$  represents the density of a predator species, and  $v$  represents the density of its prey. We are interested in the spreading properties of the solution  $u(t, x)$  of (1.8), i.e., the asymptotic spreading speed of the predator. Following Aronson and Weinberger

[4], we say that the species  $u$  spreads with speed  $c^* > 0$  if

$$\lim_{t \rightarrow \infty} \sup_{|x| > ct} u(t, x) = 0 \quad \text{for } c \in (c^*, \infty), \quad \text{and} \quad \lim_{t \rightarrow \infty} \inf_{|x| > ct} u(t, x) > 0 \quad \text{for } c \in (0, c^*).$$
(1.9)

Although predator-prey systems have been studied commonly in the ecological literature [16], before the papers of Pan in 2017 [79] and Ducrot et al. in 2019 [30], there were relatively few investigations into the asymptotic spreading dynamics of such systems from general initial conditions.

Neither [79] nor [30] considered spatially or temporally heterogeneous systems. In our work, the function  $a(x - c_1 t)$  leads to different spreading dynamics for the predator species. This function represents the efficiency with which predators produce offspring from consumption of prey. We assume that the profile of the conversion efficiency is fixed in the moving frame  $\xi = x - c_1 t$ , in the manner of other recent ecologically-motivated reaction-diffusion equations with interest in the effects of climate change [82, 10, 66, 11]. In our work, we are motivated particularly by trends in rising global temperatures. Here, the constant  $c_1 > 0$  corresponds to the velocity of moving temperature isotherms, while the fixed profile  $a(\xi)$  models the hypothesized dependence of the predator conversion efficiency on the climate.

The main result of our work is to characterize the spreading speed of the predator in the cases that (i)  $a(\xi)$  is monotonically increasing (Ch. 3, Theorem 7) and (ii)  $a(\xi)$  is monotonically decreasing and the velocity of climate shift is sufficiently fast or slow (Ch. 3, Theorem 8). The first case represents the situation when conversion efficiency declines with increasing temperature, which could be the case for predators already residing in a “thermally optimal” [51, 23, 15] habitat range. The case when



$a(\xi)$  is monotonically decreasing corresponds to the situation when conversion efficiency increases with warming, which has been observed experimentally in a microbial predator-prey system [22].

We briefly summarize our results in each case. In the case that the conversion efficiency is monotonically increasing, there are three possible spreading speeds of the predator, depending on the velocity of the climate shift. When the speed of climate shift is slow relative to the maximal spreading speed of the predator, then the predator spreads at its maximal speed, ie., the speed determined by the maximal limiting conversion rate  $a(+\infty)$  and an abundance of prey. When the climate shift is significantly faster than the predator's maximum speed, then the predator falls behind the shifting climate, and spreads at speed determined by the minimal limiting conversion rate,  $a(-\infty)$ . Finally, when the climate shifts at an intermediate speed, the predator spreads at a rate in between its minimal and maximal speeds, and is "non-locally pulled" [48, 42] by the shifting climate front.

In the case that  $a(\xi)$  is monotonically decreasing, the spreading speed of the predator is minimal when the climate shift is slow. On the other hand, when the climate shift is very fast, then the predator spreads at a maximal rate. For intermediate speeds of climate shift, we conjecture that the predator spreads at the same rate as the climate shift. However, this case is not covered in our work. A possible approach is to use the persistence theory as in [29].

## Chapter 2: Population Dynamics in an Advective Environment

### 2.1 Introduction

How does dispersal affect the ability of a species to persist? In spatially heterogeneous but temporally constant environments, Hastings showed that a small, passively diffusing population cannot survive in the presence of an established population of slower diffusers [46]. The idea that the “slower diffuser wins” was later reinforced by Dockery et al., who conjectured that in a population of finitely many phenotypes, differing solely in their diffusion rates, only the slowest diffuser may survive [25]. See [19, 58] for recent mathematical progress on this question.

In the above studies, species were assumed to disperse by passive diffusion alone. In advective environments, on the other hand, the diffusive movement of an organism is combined with an environmentally-imposed drift. Inspired by the earlier work of Speirs and Gurney [89], the following model for competing species in a river was

studied by Lou and Lutscher [72] and Lou and Zhou [74]:

$$\begin{cases} u_t = \mu u_{xx} - \alpha u_x + u(r - u - v), & 0 < x < l, t > 0, \\ v_t = \nu v_{xx} - \alpha v_x + v(r - u - v), & 0 < x < l, t > 0, \\ \mu u_x(0) - \alpha u(0) = 0, & t > 0, \\ \mu u_x(l) - \alpha u(l) = -b\alpha u(l), & t > 0, \\ \nu v_x(0) - \alpha v(0) = 0, & t > 0, \\ \nu v_x(l) - \alpha v(l) = -b\alpha v(l), & t > 0. \end{cases} \quad (2.1)$$

Here,  $l > 0$  is the length of the river,  $\mu > 0$  and  $\nu > 0$  are the diffusion rates of species  $u$  and  $v$ , respectively,  $\alpha > 0$  is the advection rate,  $r > 0$  is the intrinsic growth rate, and  $b \geq 0$  is a parameter which mediates the rate of population loss at the downstream boundary  $x = l$ . Speirs and Gurney [89] previously considered models of the form (2.1) in the single species case, and with  $b = +\infty$ , to study the “drift paradox” of species persistence in rivers. See also [92], which considered (2.1) for a single species with the “free-flow” condition  $b = 1$ , and [90], which studied (2.1) with the free-flow condition imposed at the upstream boundary.

It has been shown that for  $0 \leq b \leq 1$ , only the faster-dispersing species may persist [72, 74]. Thus, in homogeneous habitat with a “mildly hostile” downstream boundary, the presence of advection can disrupt the advantage of the slower diffuser. However, fast diffusion may be deleterious if the loss rate at the downstream boundary is severe. In particular, for  $b > \frac{3}{2}$ , it is possible for a sufficiently-fast diffuser to become extinct, while the relatively slower diffuser persists [74].

In fact, Hao et al. [45] showed that the constant  $b = \frac{3}{2}$  represents a critical threshold for the evolution of dispersal in (2.1). Given a population of two sufficiently fast diffusers, only the faster of the two may persist for  $0 \leq b < \frac{3}{2}$ . On the other hand, for  $b > \frac{3}{2}$ , if the diffusion rates of both species are sufficiently large then only the slower species can persist, while the relatively faster species becomes extinct.

### 2.1.1 The model

In (2.1), the no-flux boundary condition is imposed at the upstream boundary  $x = 0$ . In this paper, we relax this assumption and consider the following system:

$$\begin{cases} u_t = \mu u_{xx} - \alpha u_x + u(r - \frac{u+v}{K}), & 0 < x < l, t > 0, \\ v_t = \nu v_{xx} - \alpha v_x + v(r - \frac{u+v}{K}), & 0 < x < l, t > 0, \\ \mu u_x(0, t) - \alpha u(0, t) = (b_0 - 1)\alpha u(0, t), & t > 0, \\ \mu u_x(l, t) - \alpha u(l, t) = -b_l \alpha u(l, t), & t > 0, \\ \nu v_x(0, t) - \alpha v(0, t) = (b_0 - 1)\alpha v(0, t), & t > 0, \\ \nu v_x(l, t) - \alpha v(l, t) = -b_l \alpha v(l, t), & t > 0, \end{cases} \quad (2.2)$$

where  $u(x, t)$  and  $v(x, t)$  are the population densities of competing species which diffuse at positive rates  $\mu$  and  $\nu$ , respectively, and  $\alpha, r, K, b_0, b_l$  are positive parameters, with  $b_0 + b_l > 1$ .

There have been several other recent works investigating Lotka-Volterra competition systems in advective environments. The effect of distinct advection rates and a spatially heterogeneous resource function,  $r(x)$ , on the global dynamics of (2.2), with  $(b_0, b_l) = (1, 0)$ , was studied in [73], while [91] further considered the possibility of distinct resource functions  $r_1(x) \neq r_2(x)$  for the two species. The effect of distinct advection rates and identical dispersal rates on the global dynamics of (2.2) was studied in [104], with  $b_0 > 1$  and  $b_l > 0$ . We also mention [98], which determines the global dynamics of (2.2) under the condition that  $b_0$  and  $b_l$  are not large, and [38], where the global dynamics of a generalized river model were considered. For a summary of recent developments concerning competitive reaction-diffusion-advection systems, we refer to the review [84].

In this work, we investigate (2.2) for slightly more general boundary conditions, and focus on the effect of dispersal. We identify a function of the boundary loss

parameters  $b_0$  and  $b_l$  which divides the space of parameters  $b_0$  and  $b_l$  into two regions, and show that if both species diffuse rapidly, then relatively faster diffusion is advantageous in one, while slower diffusion is advantageous in the other.

### 2.1.2 Motivation of our problem: climate change

In concert with rising temperatures, many species have been observed to migrate toward the poles [80]. To study these habitat shifts, Lewis and Potapov [82] considered a two-species model of the form

$$\begin{cases} u_t = \mu u_{xx} + u(r_1 - c_{11}u - c_{12}v), & 0 \leq x + \alpha t \leq l, \\ v_t = \nu v_{xx} + v(r_2 - c_{21}u - c_{22}v), & 0 \leq x + \alpha t \leq l, \\ u_t = \mu u_{xx} - \kappa_1 u, & x + \alpha t < 0 \text{ and } x + \alpha t > l, \\ v_t = \nu v_{xx} - \kappa_2 v, & x + \alpha t < 0 \text{ and } x + \alpha t > l. \end{cases} \quad (2.3)$$

(See also [10], which considered the effect of a shifting habitat range on the dynamics of a single species. We also note recent work [2] regarding reaction-diffusion equations on time-dependent domains). The coefficients  $r_i$ ,  $c_{ii}$ , and  $c_{ij}$  ( $i \neq j$ ) correspond to the intrinsic growth rates, intraspecific competition rates, and interspecific competition rates, respectively, of species  $u$  and  $v$ . Species growth and competition occur in a domain of constant length  $l$ , corresponding to the suitable habitat range of both species, which shifts with velocity  $\alpha > 0$  (to ease the connection with models of the form (2.2), we have modified the equation in [82] to consider a habitat range that shifts from right to left). On the exterior of this domain, the environment is assumed to be unsuitable for species growth, and the species die at rates  $\kappa_i$ . Finally, only species densities which converge to 0 as  $x \rightarrow \pm\infty$  are considered.

We will assume that both species are identical in their intrinsic growth rates,  $r = r_1 = r_2$ , and that  $c_{ij} = \frac{1}{K}$  for  $1 \leq i, j \leq 2$ . By the change of variables  $x \rightarrow x + \alpha t$ , (2.3) is converted to an equation in which the suitable habitat range of each species

is fixed:

$$\begin{cases} u_t = \mu u_{xx} - \alpha u_x + u(r - \frac{u+v}{K}), & 0 \leq x \leq l, \\ v_t = \nu v_{xx} - \alpha v_x + v(r - \frac{u+v}{K}), & 0 \leq x \leq l, \\ u_t = \mu u_{xx} - \alpha u_x - \kappa_1 u, & x < 0 \text{ or } x > l, \\ v_t = \nu v_{xx} - \alpha v_x - \kappa_2 v, & x < 0 \text{ or } x > l. \end{cases} \quad (2.4)$$

As in [82], we assume that  $u_x$ ,  $v_x$ ,  $u$ , and  $v$  are continuous at  $x = 0$  and  $x = l$ .

Then, following Ludwig et al. [75], the set of equilibrium solutions to (2.4) can be identified with the set of stationary solutions for the following equation on a bounded domain:

$$\begin{cases} u_t = \mu u_{xx} - \alpha u_x + u(r - \frac{u+v}{K}), & 0 < x < l, \\ v_t = \nu v_{xx} - \alpha v_x + v(r - \frac{u+v}{K}), & 0 < x < l, \\ \mu u_x(0) - k_\mu^+ u(0) = \nu v_x(0) - k_\nu^+ v(0) = 0, \\ \mu u_x(l) - k_\mu^- u(l) = \nu v_x(l) - k_\nu^- v(l) = 0, \end{cases} \quad (2.5)$$

where

$$k_\mu^\pm = \frac{\alpha \pm \sqrt{\alpha^2 + 4\mu\kappa_1}}{2}, \quad \text{and} \quad k_\nu^\pm = \frac{\alpha \pm \sqrt{\alpha^2 + 4\nu\kappa_2}}{2}.$$

Moreover, by Theorem 3.1 in [82], corresponding stationary solutions of (2.4) and (2.5) are either both linearly unstable or stable. Thus, to consider steady states of (2.4) and their stability, we may instead consider the equilibrium solutions of (2.5). We note that in the single species case where  $v = 0$ , equilibrium solutions to (2.5) are equilibrium solutions of (2.2), with  $b_0 = b_l = \frac{1 + \sqrt{1 + \frac{4\mu\kappa_1}{\alpha^2}}}{2}$ .

### 2.1.3 The critical domain size

Meaningful competition may occur if at least one species is capable of persisting in the absence of the other. This leads us to study the dynamics of (2.2) for a single species, given by the following equation:

$$\begin{cases} u_t = \mu u_{xx} - \alpha u_x + u(r - u/K), & 0 < x < l, \quad t > 0, \\ \mu u_x(0) - \alpha u(0) = (b_0 - 1)\alpha u(0), \\ \mu u_x(l) - \alpha u(l) = -b_l \alpha u(l). \end{cases} \quad (2.6)$$

In particular, we are interested in the existence of positive steady state solutions of (2.6), which satisfy

$$\begin{cases} \mu u_{xx} - \alpha u_x + u(r - u/K) = 0, & 0 < x < l, \\ \mu u_x(0) - \alpha u(0) = (b_0 - 1)\alpha u(0), \\ \mu u_x(l) - \alpha u(l) = -b_l \alpha u(l). \end{cases} \quad (2.7)$$

If  $b_0 + b_l > 1$ , there is net population loss at one or both boundary points. In order for the species to persist, the habitat must be large enough for the overall population growth to overcome the hostile conditions at the habitat edges. The minimal size of habitat required to sustain a population is known as the critical domain size [53], and we assert its existence for (2.6) in the following theorem:

**Theorem 2.** *Fix  $\mu, \alpha, r > 0$ , and  $b_0, b_l \geq 0$  such that  $b_0 + b_l > 1$ . There exists a function  $l^* = l^*(\mu, \alpha, r, b_0, b_l)$  such that (2.6) has a unique, positive, globally asymptotically stable steady state if and only if  $l > l^*$ . If  $l \leq l^*$ , then all solutions of (2.6) converge asymptotically to  $u = 0$ . Moreover, if we denote*

$$\hat{\mu} = \begin{cases} \frac{\alpha^2}{4r} & \text{if } \min\{b_0, b_l\} \geq \frac{1}{2} \\ \frac{\alpha^2 \min\{b_0, b_l\}(1 - \min\{b_0, b_l\})}{r} & \text{if } 0 \leq \min\{b_0, b_l\} < \frac{1}{2}, \end{cases} \quad (2.8)$$

then  $l^*$  is finite if and only if  $\mu > \hat{\mu}(b_0, b_l)$ , and satisfies

$$\lim_{\mu \searrow \hat{\mu}} l^*(\mu, \alpha, r, b_0, b_l) = \infty, \text{ and } \lim_{\mu \rightarrow \infty} l^*(\mu, \alpha, r, b_0, b_l) = \frac{\alpha(b_0 + b_l - 1)}{r}.$$

**Remark.** *Influential early work regarding the critical domain size for randomly dispersing species can be found in [53, 86]. The problem of critical domain size in an advective environment was first studied in [89] in the context of a river habitat with the no-flux condition at the upstream boundary and a lethal downstream boundary (see also the review [64]). Later on, this work was generalized in [76] for the case of Danckwerts boundary conditions, and a rigorous argument was provided for the existence of critical domain size using a next generation approach. Further discussion*

of the critical domain size for river environments can be found in [92, 74, 45, 104]. In particular, in [104], a formula for the critical domain size of (2.6) as a function of the dispersal rate was derived for boundary conditions  $b_0 > 1, b_l > 0$ . Here our contribution is to give a different proof for slightly more general boundary conditions by showing that, with other parameters being fixed, the mapping  $l \mapsto \lambda_1(l)$ , from the domain size  $l$  to the principal eigenvalue  $\lambda_1$  of the linearized problem at the trivial equilibrium, is invertible.

We can use the notion of a critical domain size to assess the relative advantages of distinct dispersal strategies. Our first result concerns the monotonicity of the critical domain size  $l^* = l^*(\mu)$  as a function of the diffusion rate:

**Theorem 3.** Fix  $r, \alpha > 0$ , and  $b_0, b_l \geq 0$  such that  $b_0 + b_l > 1$ . Let  $\hat{\mu}$  be given as in (2.8) and define

$$G(b_0, b_l) = \frac{1}{4} + (b_0 - \frac{1}{2})(b_l - \frac{1}{2}) - \frac{(b_0 + b_l - 1)^2}{3}. \quad (2.9)$$

(a) If  $G(b_0, b_l) > 0$ , then  $\mu \mapsto l^*(\mu)$  is strictly decreasing for  $\mu \gg 1$ . Suppose, in addition, that  $(b_0 + b_l - 1)^2 \geq 0.941(b_0 + b_l - 1 - 2b_0b_l)^2$ , and that either

$$\min\{b_0, b_l\} \geq \frac{1}{2} \quad \text{or} \quad \min\{b_0, b_l\} < \frac{1}{2} \quad \text{and} \quad \max\{b_0, b_l\} \leq 1.$$

Then  $\mu \mapsto l^*(\mu)$  is globally strictly decreasing on  $(\hat{\mu}, \infty)$ .

(b) If  $G(b_0, b_l) < 0$ , then  $\mu \mapsto l^*(\mu)$  is strictly increasing for  $\mu \gg 1$ . Suppose, in addition, that  $(b_0 + b_l - 1)^2 \geq 0.941(b_0 + b_l - 1 - 2b_0b_l)^2$  and  $\min\{b_0, b_l\} \geq \frac{1}{2}$ . Then there exists  $\tilde{\mu} > \frac{\alpha^2}{4r}$  such that  $\mu \mapsto l^*(\mu)$  is strictly decreasing on  $(\hat{\mu}, \tilde{\mu})$  and strictly increasing on  $(\tilde{\mu}, \infty)$ .



Theorem 3 was proved previously by the combined efforts of [74] and [45] in the case  $b_0 = 1$  and  $b_l > 0$ . When the no-flux condition ( $b_0 = 1$ ) is imposed at the upstream boundary, faster diffusion is advantageous for persistence if the population loss rate is low ( $b_l \leq \frac{3}{2}$ ), but may become deleterious when the loss rate is more severe ( $b_l > \frac{3}{2}$ ).

For general  $b_0$  and  $b_l$  satisfying  $b_0 + b_l > 1$ , a similar dichotomy holds. For example, suppose  $\tilde{b} := b_0 = b_l$ . Then Theorem 3 implies that, for sufficiently large diffusion rates, increasing  $\mu$  decreases the critical domain size when the boundary loss parameter  $\tilde{b}$  is mild, so that faster diffusion is advantageous for persistence. On the other hand, when  $\tilde{b}$  is large, the critical domain size is an increasing function of the diffusion rate for large  $\mu$  (Figure 2.1).

**Corollary 1.** *Suppose  $\tilde{b} := b_0 = b_l$ .*

- (a) *If  $\frac{1}{2} < \tilde{b} < \frac{1}{2}(1 + \sqrt{3})$ , then  $\mu \mapsto l^*(\mu)$  is strictly decreasing for  $\mu \gg 1$ .*
- (b) *If  $\tilde{b} > \frac{1}{2}(1 + \sqrt{3})$ , then  $\mu \mapsto l^*(\mu)$  is strictly increasing for  $\mu \gg 1$ .*

Interestingly, the threshold beyond which faster diffusion becomes disadvantageous (among sufficiently large diffusion rates) is nonlinear in the parameters  $b_0$  and  $b_l$  (Figure 2.2). For example, if the loss parameter  $b_0$  at the upstream boundary is fixed and  $1 < b_0 < \frac{3}{2}$ , then continuously increasing the downstream loss parameter  $b_l$  from  $b_l = 0$  results in two points at which the relative advantage of fast diffusion is reversed. Here, faster diffusion is not advantageous for persistence among large diffusion rates both when  $b_l \geq 0$  is sufficiently small or sufficiently large, while for intermediate values of  $b_l$ , the critical domain size is an increasing function for sufficiently fast rates of diffusion.

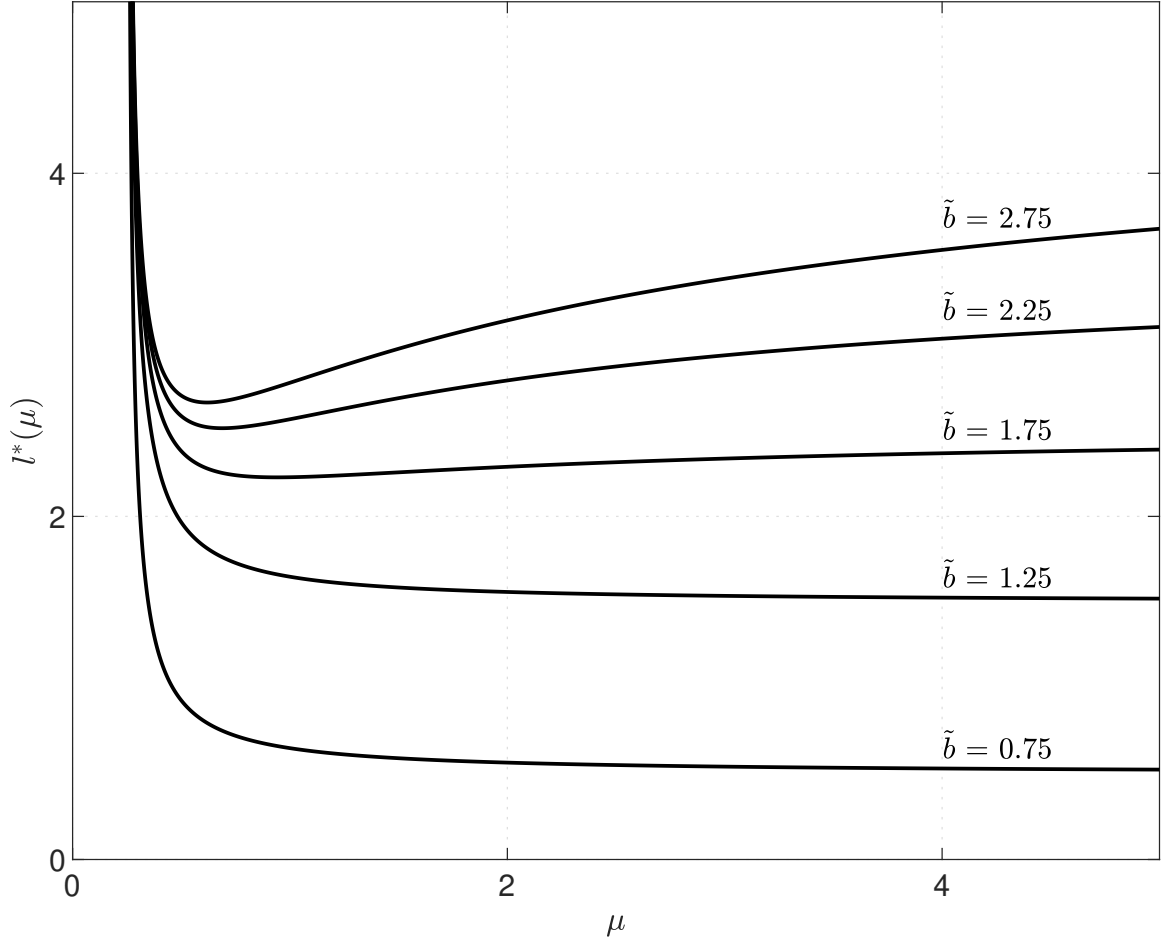


Figure 2.1: Dependence of  $l^*$  on the diffusion rate  $\mu$  for varying  $\tilde{b} = b_0 = b_l$ .  $l^*$  is strictly decreasing for  $\mu \gg 1$  if  $\tilde{b} < \frac{1}{2}(1 + \sqrt{3})$ , and strictly increasing for  $\mu \gg 1$  if  $\tilde{b} > \frac{1}{2}(1 + \sqrt{3}) \approx 1.366$  (Corollary 1).

### 2.1.4 Competitive dynamics

The relative advantages of distinct dispersal rates for the persistence of a single species suggest similar advantages in the competition between two species.

For  $\mu > 0$ , let  $\theta_\mu$  denote the unique positive solution of (2.6), if it exists. We now state our main result on the competitive dynamics of (2.2):

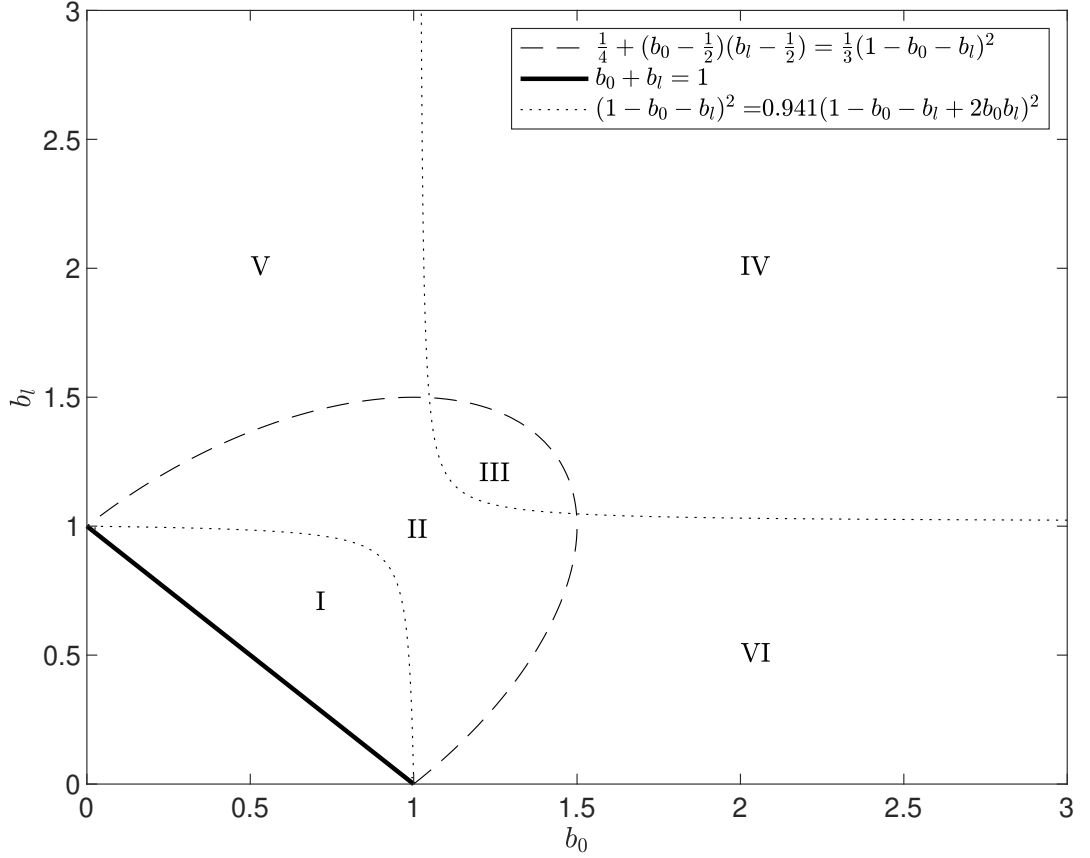


Figure 2.2:  $l^*(\mu)$  is strictly decreasing for  $\mu \gg 1$  if  $(b_0, b_l)$  lies in regions I, II, or III above, and  $l^*(\mu)$  is decreasing for all  $\mu > \hat{\mu}$  if  $(b_0, b_l)$  lies in region II and either  $\min\{b_0, b_l\} \geq \frac{1}{2}$ , or  $\min\{b_0, b_l\} < \frac{1}{2}$  and  $\max\{b_0, b_l\} \leq 1$  (Theorem 3 (a)). On the other hand,  $l^*(\mu)$  is strictly increasing for  $\mu \gg 1$  if  $(b_0, b_l)$  lies in regions IV, V, or VI. If  $(b_0, b_l)$  lies in regions V or VI, and  $\min\{b_0, b_l\} \geq \frac{1}{2}$ , then  $l^*(\mu)$  decreases to a global minimum, then becomes monotonically increasing (Theorem 3 (b)).

**Theorem 4.** *Let  $b_0 + b_l > 1$  and recall the definition of  $G(b_0, b_l)$  in (2.9).*

- (a) *If  $G(b_0, b_l) > 0$  and  $l > \frac{\alpha(b_0+b_l-1)}{r}$ , then there exists  $\underline{\mu} > 0$  such that for  $\mu > \nu \geq \underline{\mu}$ , the steady state  $(\theta_\mu, 0)$  is globally asymptotically stable.*

(b) *If  $G(b_0, b_l) < 0$  and  $l > \frac{\alpha(b_0+b_l-1)}{r}$ , then there exists  $\underline{\mu} > 0$  such that for  $\mu > \nu \geq \underline{\mu}$ , the steady state  $(0, \theta_\nu)$  is globally asymptotically stable.*

For two species with sufficiently large diffusion rates, the boundary conditions under which the faster-diffusing population will exclude the slower-diffusing one, and vice versa, correspond to those that determine whether the single species critical domain size is an eventually increasing or decreasing function of the diffusion rate. This extends previous work in [45], where Theorem 4 was proved in the case  $b_0 = 1$  and  $b_l > 0$ . We see that in (2.2), advection disrupts the selective advantage of a slower diffuser when there is mild loss at the habitat edges, in contrast to the systems considered in [46] and [25], where the slower diffuser always prevails.

It is interesting to consider the behavior of solutions of (2.7) in the limit as  $\mu \rightarrow \infty$ . Fix  $l > \frac{\alpha(b_0+b_l-1)}{r}$  and  $b_0, b_l \geq 0$  such that  $b_0 + b_l > 1$ , so that a unique solution of (2.7) exists for all sufficiently large  $\mu$ . Then as  $\mu \rightarrow \infty$ , we observe that solutions  $\theta_\mu$  of (2.7) converge to an ideal free distribution. Introduced by Fretwell and Lucas [37], the ideal free distribution (IFD) describes an arrangement achieved by individuals that: (i) have full knowledge of the conditions of their habitat and (ii) can freely relocate to regions that are more favorable to growth. For models involving species movement, an IFD is achieved when no individuals may benefit from relocation, so that further movement does not occur. We observe that solutions  $\theta_\mu$  of (2.7) converge to the positive, constant density  $K\left(r - \frac{\alpha(b_0+b_l-1)}{l}\right)$  as  $\mu \rightarrow \infty$ , which is an IFD, since for constant species densities the homogeneity of the intrinsic growth rate  $r$  and carrying capacity  $K$  implies that all individuals will have the same fitness.

It has been shown in several modeling applications that a species using an IFD movement strategy is resistant to invasion by an otherwise identical and rare species

that adopts a different movement strategy [17, 18, 6]. We have seen that  $\mu = +\infty$  is an IFD strategy of (2.2). For  $b_0, b_l \geq 0$  such that  $b_0 + b_l > 1$  and  $G(b_0, b_l) > 0$ , corresponding to “mild” boundary hostility, our results show that the species adopting a strategy that more closely approximates the IFD strategy (i.e. faster diffusion) is resistant to invasion by the other, so long as both diffusion rates are sufficiently large. However, the opposite situation occurs for  $b_0$  and  $b_l$  such that  $G(b_0, b_l) < 0$ . In such cases, although  $\mu = +\infty$  represents an IFD movement strategy, a fast-diffusing species can be invaded by a slower one.

In case  $G(b_0, b_l) > 0$ , we note Theorem 4 demonstrates that, for competition between species with large diffusion rates, i.e.  $\mu, \nu \gg 1$ , then the faster diffusing species is selected. In such a case,  $\mu^* = +\infty$  is called a convergence stable strategy (CSS) [24]. On the other hand, if  $G(b_0, b_l) < 0$ , then  $\mu^* = +\infty$  is not a CSS.

### 2.1.5 Discussion

We briefly discuss applications of our results to the moving habitat model studied in [82] and [10]. The set of steady states of the moving habitat model (2.4) and of equation (2.5), where the domain is bounded, are equivalent [82]. With appropriate choices for  $b_0$  and  $b_l$ , equation (2.5) can be viewed as a special case of our model. In particular, our results apply directly for  $b_0$  and  $b_l$  satisfying  $b_0 = b_l = \frac{1 + \sqrt{1 + \frac{4\mu\kappa_1}{\alpha^2}}}{2} = \frac{1 + \sqrt{1 + \frac{4\nu\kappa_2}{\alpha^2}}}{2}$ . Note that, in such a case, we have  $b_0 + b_l = 1 + \sqrt{1 + \frac{4\mu\kappa_1}{\alpha^2}} > 1$ .

We first consider our results in the context of the parameter  $\alpha$ , which denotes the velocity of the shifting habitat in (2.3), and serves to capture the potential effects of climate change. Theorem 2 shows that increasing  $\alpha$  increases the threshold diffusion rate  $\hat{\mu} = \frac{\alpha^2}{4r}$ , below which there can be no finite critical domain size. Thus, if the

habitat range shifts too rapidly, then it is not possible for the species to persist, regardless of the size of the habitat.

When the critical domain size is finite, its dependence on the diffusion rate is mediated crucially by the shifting of the habitat, as described in Theorem 3. We consider a single species, and assume that the death rate  $\kappa_1$  is inversely proportional to  $\mu$ , so that  $\mu$  may vary while  $b_0 = b_l = \frac{1 + \sqrt{1 + \frac{4\mu\kappa_1}{\alpha^2}}}{2}$  remains fixed. This means that the hostility of the external environment is assumed to decrease if the diffusion rate of the species is increased. Substituting  $b_0 = b_l = \frac{1 + \sqrt{1 + \frac{4\mu\kappa_1}{\alpha^2}}}{2}$ , Theorem 3 implies that the mapping  $\mu \mapsto l^*(\mu)$  is strictly decreasing for  $\mu \gg 1$  if  $\alpha^2 > 2\mu\kappa_1$ , and strictly increasing for  $\mu \gg 1$  if  $\alpha^2 < 2\mu\kappa_1$ . If  $\alpha^2 \geq 2\left(\frac{0.941}{0.059 + \sqrt{0.059}}\right)\mu\kappa_1$ , then  $\mu \mapsto l^*(\mu)$  is decreasing for all  $\mu > \hat{\mu}$ . We see that if the habitat is shifting rapidly, then faster diffusion (assuming that the product  $\mu\kappa_1$  is fixed) decreases the critical domain size among  $\mu \gg 1$ . On the other hand, if the habitat movement is slow, then faster diffusion increases the critical domain size among  $\mu \gg 1$ , despite a proportional decrease in the external death rate  $\kappa_1$ .

We may also apply our results in the case of two-species competition, with  $b_0 = b_l = \frac{1 + \sqrt{1 + \frac{4\mu\kappa_1}{\alpha^2}}}{2} = \frac{1 + \sqrt{1 + \frac{4\nu\kappa_2}{\alpha^2}}}{2}$ . For competing species with sufficiently large diffusion rates and death rates satisfying  $\mu\kappa_1 = \nu\kappa_2 = C$ , where  $C$  is some positive constant, Theorem 4 implies that faster diffusion is advantageous in rapidly-shifting habitats, while slower diffusion is advantageous if the habitat is moving slowly. In particular, if  $\alpha^2 > 2C$ , then the faster of two species will exclude the slower one (if they do not both go extinct), so long as both diffusion rates are sufficiently large. However, if the habitat movement is slow ( $\alpha^2 < 2C$ ), then the situation is reversed, and only the slower of two fast-diffusing species may persist. By the comparison principle, we

observe that these advantages are predictably maintained in some situations where the diffusion and death rates of each species are not in fixed proportion. For example, if the death rate of the “winning” species outside of the habitat is reduced, then the species will maintain its advantage. Similarly, if the death rate of the excluded species outside of the habitat is increased, then the species is still driven to extinction.

## 2.2 Proofs for the critical domain size

In this section we demonstrate the existence of a critical domain size for (2.6). To this end, we consider the eigenvalue problem

$$\begin{cases} \mu\varphi_{xx} - \alpha\varphi_x + r\varphi = \lambda\varphi, & 0 < x < l, \\ \mu\varphi_x(0) - \alpha b_0\varphi(0) = \mu\varphi_x(l) + \alpha(b_l - 1)\varphi(l) = 0, \end{cases} \quad (2.10)$$

which arises from linearizing (2.6) about the steady state  $u \equiv 0$ .

### 2.2.1 Existence of principal eigenvalue

It is well-known that problem (2.10) admits a principal eigenvalue; see, e.g., [33].

**Proposition 1.** *Let  $b_0 + b_l \geq 1$ . Then the eigenvalues of (2.10) are given by*

$$\lambda_1 \geq \lambda_2 \geq \lambda_3 \geq \cdots, \quad \text{with } \lim_{k \rightarrow \infty} \lambda_k = -\infty.$$

*Moreover,  $\lambda_1 = \lambda_1(\mu, \alpha, r, b_0, b_l, l)$  is a simple eigenvalue, and the only eigenvalue with a positive eigenfunction. The eigenvalue  $\lambda_1$  is the principal eigenvalue of (2.10).*

### 2.2.2 Formula for the critical domain size

The notion of a critical domain size for (2.6) can be related to the sign of the principal eigenvalue  $\lambda_1$ , based on the following well-known result; see [16, 57].

**Theorem 5.** *Let  $\lambda_1$  be the principal eigenvalue of (2.10).*

- (i) If  $\lambda_1 \leq 0$ , then  $\lim_{t \rightarrow \infty} \|u(\cdot, t)\|_{C^0([0, l])} = 0$  for every nonnegative solution of (2.6).
- (ii) If  $\lambda_1 > 0$ , then (2.6) has a unique positive equilibrium  $\theta$ . Moreover,

$$\lim_{t \rightarrow \infty} \|u(\cdot, t) - \theta\|_{C^0([0, l])} = 0$$

for every nonnegative, nontrivial solution of (2.6).

Thus, the trivial solution is globally asymptotically stable if and only if  $\lambda_1 = \lambda_1(\mu, \alpha, r, b_0, b_l, l) \leq 0$ . Otherwise, the trivial solution is linearly unstable, and any initially nonnegative, nonzero species density will converge to a positive equilibrium—i.e., the species will persist. We define the critical domain size of (2.6) to be the unique, minimal domain size at which the trivial solution loses stability.

**Definition.** Given  $\mu, \alpha, r > 0$ ,  $b_0 \geq 0$ , and  $b_l \geq 0$ , we say that  $l^* \in (0, \infty]$  is a critical domain size of (2.6) if

$$\lambda_1 \begin{cases} > 0 & \text{for } l > l^* \\ = 0 & \text{for } l = l^* \\ < 0 & \text{for } l < l^*, \end{cases}$$

where  $\lambda_1$  is the principal eigenvalue of (2.10).

Note that when  $\alpha = 0$  and  $b_0 = b_l = \infty$ , it is well-known that  $l^* = \pi \sqrt{\frac{d}{r}}$ ; see, e.g., [16].

Under the assumption that  $b_0, b_l > 0$  and  $b_0 + b_l > 1$ , we will establish that  $l^*$  is well-defined, and is given by the following explicit formulas:

- If  $\min\{b_0, b_l\} \geq \frac{1}{2}$ , then

$$l^* = \begin{cases} +\infty, & 0 < \mu \leq \frac{\alpha^2}{4r} \\ F_1(0; \mu, \alpha, r, b_0, b_l), & \mu > \frac{\alpha^2}{4r}. \end{cases} \quad (2.11)$$



- If  $0 < \min\{b_0, b_l\} < \frac{1}{2}$ , then

$$l^* = \begin{cases} +\infty, & 0 < \mu \leq \frac{\alpha^2 \min\{b_0, b_l\}(1 - \min\{b_0, b_l\})}{r} \\ F_2(0; \mu, \alpha, r, b_0, b_l), & \frac{\alpha^2 \min\{b_0, b_l\}(1 - \min\{b_0, b_l\})}{r} < \mu < \frac{\alpha^2}{4r} \\ -\frac{\alpha(b_0 + b_l - 1)}{4r(b_0 - \frac{1}{2})(b_l - \frac{1}{2})}, & \mu = \frac{\alpha^2}{4r} \\ F_1(0; \mu, \alpha, r, b_0, b_l), & \mu > \frac{\alpha^2}{4r}. \end{cases} \quad (2.12)$$

Here,  $F_1$  and  $F_2$  are given by

$$F_1(\lambda; \mu, \alpha, r, b_0, b_l) := \frac{2\mu}{\sqrt{4\mu(r - \lambda) - \alpha^2}} \left[ \arctan\left(\frac{2\alpha(b_l - \frac{1}{2})}{\sqrt{4\mu(r - \lambda) - \alpha^2}}\right) - \arctan\left(\frac{-2\alpha(b_0 - \frac{1}{2})}{\sqrt{4\mu(r - \lambda) - \alpha^2}}\right) \right], \quad (2.13)$$

$$F_2(\lambda; \mu, \alpha, r, b_0, b_l) := \frac{\mu}{\sqrt{\alpha^2 - 4\mu(r - \lambda)}} \cdot \log \frac{\left[ \frac{1}{2}\sqrt{\alpha^2 - 4\mu(r - \lambda)} - \alpha(b_0 - \frac{1}{2}) \right] \left[ \frac{1}{2}\sqrt{\alpha^2 - 4\mu(r - \lambda)} - \alpha(b_l - \frac{1}{2}) \right]}{\left[ \frac{1}{2}\sqrt{\alpha^2 - 4\mu(r - \lambda)} + \alpha(b_0 - \frac{1}{2}) \right] \left[ \frac{1}{2}\sqrt{\alpha^2 - 4\mu(r - \lambda)} + \alpha(b_l - \frac{1}{2}) \right]}. \quad (2.14)$$

**Remark.** The case  $(b_0, b_l) = (1, +\infty)$  is contained in [89]; the case  $(b_0, b_l) = (1, 1)$  is contained in [76]; the case  $(b_0, b_l) \in \{1\} \times (0, \infty)$  is contained in [74]; the case  $(b_0, b_l) \in (1, \infty) \times (0, \infty)$  is contained in [104].

Equation (2.6) may be used to model a population in a river environment. In particular, setting  $b_0 = 1$  indicates no-flux conditions at the river source, while the degree of hostility downstream of the habitat can be tuned via the parameter  $b_l$ . As  $b_l \rightarrow \infty$ , we see from (2.11) that the critical domain size  $l^* \rightarrow \frac{2\mu}{\sqrt{4\mu r - \alpha^2}} \left( \frac{\pi}{2} - \arctan\left(\frac{-\alpha}{\sqrt{4\mu r - \alpha^2}}\right) \right)$ , which is consistent with the case of Dirichlet conditions at  $x = l$ , studied in [89] (we note that the expression for the critical domain size in [89] should be adjusted according to (3.2) in [76]). On the other hand, as  $b_l \searrow 0$ , we observe that the critical domain size  $l^* \rightarrow 0$  for all  $\mu > 0$ . This is consistent with the no-flux condition  $b_l = 0$  at the downstream end, for which it is clear that for any  $l > 0$ , (2.6) admits a unique, positive, globally asymptotically stable steady state.

For the case of a moving habitat on an infinite, one-dimensional domain, the critical domain size is given in formula (25) of [10], and is equivalent to (2.26), with  $b_0 = b_l = \frac{1 + \sqrt{1 + \frac{4\mu\kappa_1}{\alpha^2}}}{2}$ .

**Remark.** As detailed in [64], there is a connection between the critical domain size of (2.6) and the Fisher-KPP spreading speed. On the infinite spatial domain  $\mathbb{R}$ , solutions to (2.6) originating from compactly supported, nonnegative, and continuous initial conditions propagate upstream at rate  $c^* = 2\sqrt{\mu r} - \alpha$  (this can be seen by converting equation (2.6) into the form of Fisher's equation via the change of variables  $x \mapsto x - \alpha t$ ; see the discussion in [64]). Thus, the population spreads upstream if  $c^* > 0$  (i.e.  $\mu \in (\frac{\alpha^2}{4r}, \infty)$ ), but is washed downstream if  $c^* < 0$ . In the case  $\min\{b_0, b_l\} \geq \frac{1}{2}$ , there is a correspondence with our result for the critical domain size: by (2.11), if  $c^* > 0$  then the critical domain size is finite, and it is possible for the species to persist on a suitably large domain. However, if  $c^* \leq 0$ , then the critical domain size is infinite, and the species cannot persist.

Interestingly, if  $\min\{b_0, b_l\} < \frac{1}{2}$ , this correspondence no longer holds. By (2.12), the critical domain size  $l^*$  can be finite even if  $c^* < 0$ . In other words, the species will persist if the finite domain is sufficiently large but the same population will eventually be washed downstream in the infinite domain. The intuitive reason is that the smallness of one of the loss rates  $b_0, b_l$  enhances growth.

While it is well-known that the principal eigenvalue  $\lambda_1$  is a smooth function of the domain size  $l$ , the key to the existence of the critical domain size  $l^*$ , however, is the invertibility of  $l \mapsto \lambda_1(l)$ . Here we provide a proof of this fact. See also [76] for an alternative proof.

**Lemma 1.** Fix  $\mu, \alpha, r > 0$ , and  $b_0, b_l \geq 0$  such that  $b_0 + b_l > 1$ . Then  $\lambda_1 = \lambda_1(l)$  is a strictly increasing function such that

(i) If  $\min\{b_0, b_l\} \geq \frac{1}{2}$ , then  $l \mapsto \lambda_1$  is a bijection from  $(0, \infty)$  to  $(-\infty, r - \frac{\alpha^2}{4\mu})$ .

Moreover,

$$l = F_1(\lambda_1; \mu, \alpha, r, b_0, b_l). \quad (2.15)$$

(ii) If  $\min\{b_0, b_l\} < \frac{1}{2}$ , then  $l \mapsto \lambda_1$  is a bijection from  $(0, \infty)$  to

$(-\infty, r - \frac{\alpha^2 \min\{b_0, b_l\}(1 - \min\{b_0, b_l\})}{\mu})$ . Moreover,

$$l = \begin{cases} F_1(\lambda_1), & \lambda_1 < r - \frac{\alpha^2}{4\mu} \\ -\frac{\mu(b_0 + b_l - 1)}{\alpha(b_0 - \frac{1}{2})(b_l - \frac{1}{2})}, & \lambda_1 = r - \frac{\alpha^2}{4\mu} \\ F_2(\lambda_1), & r - \frac{\alpha^2}{4\mu} < \lambda_1 < r - \frac{\alpha^2 \min\{b_0, b_l\}(1 - \min\{b_0, b_l\})}{\mu}. \end{cases} \quad (2.16)$$

*Proof.* Suppose  $b_0 + b_l > 1$ , then thanks to Proposition 1, the elliptic problem (2.10) has a unique principal eigenvalue  $\lambda_1 \in \mathbb{R}$  and positive eigenfunction  $\psi$  for each  $l \in (0, \infty)$ . Thus  $l \mapsto \lambda_1(l)$  is a mapping from  $(0, \infty)$  to  $\mathbb{R}$ . To establish that this is a bijection, we derive in each case an expression for  $l$  depending on  $\lambda_1$ . First, let  $\psi = e^{-\frac{\alpha}{2\mu}x}\varphi$ . Then (2.10) becomes

$$\begin{cases} \mu\psi_{xx} + (r - \frac{\alpha^2}{4\mu} - \lambda_1)\psi = 0, & 0 < x < l, \\ \mu\psi_x(0) - \alpha(b_0 - \frac{1}{2})\psi(0) = \mu\psi_x(l) + \alpha(b_l - \frac{1}{2})\psi(l) = 0. \end{cases} \quad (2.17)$$

**Claim 1.** If  $\lambda_1 \in (-\infty, r - \frac{\alpha^2}{4\mu})$ , then  $l = F_1(\lambda_1)$ .

Indeed, suppose  $\lambda_1 < r - \frac{\alpha^2}{4\mu}$  for some  $l > 0$ . Then by solving the first equation of (2.17),  $\psi$  has the form

$$\psi = A \cos\left(\frac{\sqrt{4\mu(r - \lambda_1) - \alpha^2}}{2\mu}(x - \eta)\right), \quad (2.18)$$

where  $\eta \in \left(-\mu\frac{\pi}{\sqrt{4\mu(r - \lambda_1) - \alpha^2}}, \mu\frac{\pi}{\sqrt{4\mu(r - \lambda_1) - \alpha^2}}\right)$ .

Now from the boundary conditions, we compute

$$-\frac{\alpha(b_0 - \frac{1}{2})}{\mu} = -\frac{\psi_x(0)}{\psi(0)} = \frac{\sqrt{4\mu(r - \lambda_1) - \alpha^2}}{2\mu} \tan\left(\frac{\sqrt{4\mu(r - \lambda_1) - \alpha^2}}{2\mu}(-\eta)\right) \quad (2.19)$$

and

$$\frac{\alpha(b_l - \frac{1}{2})}{\mu} = -\frac{\psi_x(l)}{\psi(l)} = \frac{\sqrt{4\mu(r - \lambda_1) - \alpha^2}}{2\mu} \tan\left(\frac{\sqrt{4\mu(r - \lambda_1) - \alpha^2}}{2\mu}(l - \eta)\right). \quad (2.20)$$

Recall that  $\psi$  is positive on  $[0, l]$ ,  $b_0 + b_l > 1$ , we observe that  $\eta$  and  $l > 0$  are uniquely determined by (2.19) and (2.20). Hence, we may solve for  $l$  to obtain  $l = F_1(\lambda_1)$ . This proves Claim 1.

We first consider the case  $\min\{b_0, b_l\} \geq \frac{1}{2}$ .

**Claim 2.** *If  $\min\{b_0, b_l\} \geq \frac{1}{2}$ , then  $\lambda_1 \in (-\infty, r - \frac{\alpha^2}{4\mu})$ .*

Suppose to the contrary that  $\lambda_1 \geq r - \frac{\alpha^2}{4\mu}$ .

If  $\lambda_1 = r - \frac{\alpha^2}{4\mu}$ , then  $\psi$  has the form

$$\psi(x) = Ax + B \quad \text{for some } A \in \{0, 1\}, \quad \text{and } B \geq 0. \quad (2.21)$$

Consider the two boundary conditions of (2.17). Since  $(b_0, b_l) \neq (\frac{1}{2}, \frac{1}{2})$ , we have  $A \neq 0$ , which in turn implies  $b_0 \neq \frac{1}{2}$  and  $b_l \neq \frac{1}{2}$ . Hence,  $\min\{b_0, b_l\} > \frac{1}{2}$  and (2.21) holds for  $A = 1$  and some  $B \geq 0$ . We may then solve for  $B$  using the boundary condition at  $x = 0$  to obtain  $B = \frac{\mu}{\alpha(b_0 - \frac{1}{2})}$ . The boundary condition at  $x = l$  now yields

$$l = -B - \frac{\mu}{\alpha(b_l - \frac{1}{2})} = -\mu\left(\frac{1}{\alpha(b_0 - \frac{1}{2})} + \frac{1}{\alpha(b_l - \frac{1}{2})}\right) < 0. \quad (2.22)$$

This is a contradiction.

If  $\lambda_1 > r - \frac{\alpha^2}{4\mu}$ , then  $\psi$  has the form

$$\psi(x) = A \cosh\left(\frac{\sqrt{\alpha^2 - 4\mu(r - \lambda_1)}}{2\mu}x\right) + B \sinh\left(\frac{\sqrt{\alpha^2 - 4\mu(r - \lambda_1)}}{2\mu}x\right).$$

By substituting into the boundary conditions, we find

$$\tanh\left(\frac{\sqrt{\alpha^2 - 4\mu(r - \lambda_1)}}{2\mu}l\right) = -\frac{2\alpha(b_0 + b_l - 1)\sqrt{\alpha^2 - 4\mu(r - \lambda_1)}}{\alpha^2 - 4\mu(r - \lambda_1) + 4\alpha^2(b_0 - \frac{1}{2})(b_l - \frac{1}{2})}. \quad (2.23)$$

But this implies  $\tanh\left(\frac{\sqrt{\alpha^2 - 4\mu(r - \lambda_1)}}{2\mu}l\right) < 0$ , which cannot occur for any  $l > 0$ . This proves Claim 2.

**Claim 3.** *If  $\min\{b_0, b_l\} \geq \frac{1}{2}$ , the mapping  $l \mapsto \lambda_1(l)$  is a homeomorphism from  $(0, \infty)$  to  $(-\infty, r - \frac{\alpha^2}{4\mu})$ . In fact,  $l \mapsto \lambda_1(l)$  is strictly increasing.*

By Claim 2, the range of the mapping  $l \mapsto \lambda_1(l)$  is contained in  $(-\infty, r - \frac{\alpha^2}{4\mu})$ . It then follows from Claim 1 that it is a homeomorphism. Indeed, the mapping is injective since if  $\lambda_1(l) = \lambda_1(\tilde{l}) = \hat{\lambda}$  for some  $\hat{\lambda} \in (-\infty, r - \frac{\alpha^2}{4\mu})$ , then Claim 1 implies that  $l = \tilde{l} = F_1(\hat{\lambda})$ . It is surjective, since for any  $\hat{\lambda} \in (-\infty, r - \frac{\alpha^2}{4\mu})$ , we have  $\lambda_1(\hat{l}) = \hat{\lambda}$ , where  $\hat{l} = F_1(\hat{\lambda}) > 0$ . Indeed, the eigenfunction given by (2.18) with  $\lambda_1 = \hat{\lambda}$  is positive on  $[0, \hat{l}]$ . That  $\lambda_1(\hat{l}) = \hat{\lambda}$  then follows from the uniqueness of the principal eigenvalue. Thus  $l \mapsto \lambda_1(l)$  is bijective, and the inverse is given by  $F_1$ . Finally,  $l \mapsto \lambda_1(l)$  is continuous since  $F_1$  is. Now it follows from  $l = F_1(\lambda_1(l))$  and (2.13) that  $\lambda_1(l) \nearrow r - \frac{\alpha^2}{4\mu}$  as  $l \rightarrow +\infty$  and  $\lambda_1(l) \searrow -\infty$  as  $l \nearrow 0$ . The mapping  $l \mapsto \lambda_1(l)$ , being a homeomorphism of  $(0, \infty) \rightarrow (-\infty, r - \frac{\alpha^2}{4\mu})$ , must be strictly increasing. This shows Claim 3. Together, Claims 1, 2, and 3 establish part (i) of Lemma 1.

Next, we discuss the case  $\min\{b_0, b_l\} < \frac{1}{2}$ .

**Claim 4.** *If  $0 < \min\{b_0, b_l\} < \frac{1}{2}$ , then  $\lambda_1 \in (-\infty, r - \frac{\alpha^2 \min\{b_0, b_l\}(1 - \min\{b_0, b_l\})}{\mu})$ .*

Suppose that  $\lambda_1 > r - \frac{\alpha^2}{4\mu}$ . (If not, there is nothing to prove, since  $r - \frac{\alpha^2 \min\{b_0, b_l\}(1 - \min\{b_0, b_l\})}{\mu} > r - \frac{\alpha^2}{4\mu}$ .) Then, since  $0 < \tanh(x) < 1$  for  $x > 0$ , we

observe from (2.23) that

$$0 < -\frac{2\alpha(b_0 + b_l - 1)\sqrt{\alpha^2 - 4\mu(r - \lambda_1)}}{\alpha^2 - 4\mu(r - \lambda_1) + 4\alpha^2(b_0 - \frac{1}{2})(b_l - \frac{1}{2})} < 1.$$

Since  $b_0 + b_l > 1$ , this implies

$$\alpha^2 - 4\mu(r - \lambda_1) + 4\alpha^2(b_0 - \frac{1}{2})(b_l - \frac{1}{2}) < -2\alpha(b_0 + b_l - 1)\sqrt{\alpha^2 - 4\mu(r - \lambda_1)} < 0. \quad (2.24)$$

In particular, since the right hand side of (2.24) is negative, we note that

$$\mu(r - \lambda_1) > \frac{\alpha^2}{4}[1 + 4(b_0 - \frac{1}{2})(b_l - \frac{1}{2})] > \alpha^2 \max\{b_0, b_l\}(1 - \max\{b_0, b_l\}), \quad (2.25)$$

where we used  $(b_0 - \frac{1}{2})(b_l - \frac{1}{2}) > (\frac{1}{2} - \max\{b_0, b_l\})(\max\{b_0, b_l\} - \frac{1}{2})$ . After some calculations, (2.24) implies that

$$\begin{aligned} & [\mu(r - \lambda_1) - \alpha^2 \min\{b_0, b_l\}(1 - \min\{b_0, b_l\})] \\ & \cdot [\mu(r - \lambda_1) - \alpha^2 \max\{b_0, b_l\}(1 - \max\{b_0, b_l\})] > 0. \end{aligned}$$

By (2.25), this is only possible if  $\mu(r - \lambda_1) > \alpha^2 \min\{b_0, b_l\}(1 - \min\{b_0, b_l\})$ , i.e.,

$$\lambda_1 < r - \frac{\alpha^2 \min\{b_0, b_l\}(1 - \min\{b_0, b_l\})}{\mu},$$

which establishes the claim.

**Claim 5.** *If  $\lambda_1 > r - \frac{\alpha^2}{4\mu}$ , then  $l = F_2(\lambda_1)$ .*

The claim follows by solving for  $l$  in (2.23).

**Claim 6.** *If  $0 < \min\{b_0, b_l\} < \frac{1}{2}$ , then the mapping  $l \mapsto \lambda_1(l)$  is a strictly increasing homeomorphism from  $(0, \infty)$  to  $(-\infty, r - \frac{\alpha^2 \min\{b_0, b_l\}(1 - \min\{b_0, b_l\})}{\mu})$ .*

From Claim 4, the range of the mapping  $l \mapsto \lambda_1(l)$  is contained in  $(-\infty, r - \frac{\alpha^2 \min\{b_0, b_l\}(1 - \min\{b_0, b_l\})}{\mu})$ . By (2.13), (2.22), and (2.14), we have:

$$l = F_3(\lambda_1) := \begin{cases} F_1(\lambda_1), & \lambda_1 < r - \frac{\alpha^2}{4\mu} \\ -\frac{\mu(b_0 + b_l - 1)}{\alpha(b_0 - \frac{1}{2})(b_l - \frac{1}{2})}, & \lambda_1 = r - \frac{\alpha^2}{4\mu} \\ F_2(\lambda_1), & r - \frac{\alpha^2}{4\mu} < \lambda_1 < r - \frac{\alpha^2 \min\{b_0, b_l\}(1 - \min\{b_0, b_l\})}{\mu}. \end{cases}$$

Note that  $l$  is a continuous function of  $\lambda_1$ , since

$$\lim_{\lambda_1 \rightarrow (r - \frac{\alpha^2}{4\mu})^-} F_1(\lambda_1) = \lim_{\lambda_1 \searrow (r - \frac{\alpha^2}{4\mu})} F_2(\lambda_1) = -\frac{\mu(b_0 + b_l - 1)}{\alpha(b_0 - \frac{1}{2})(b_l - \frac{1}{2})}.$$

Now the claim follows by similar reasoning as in the case  $\min\{b_0, b_l\} \geq \frac{1}{2}$ . The mapping  $l \mapsto \lambda_1(l)$  is injective, since if  $\lambda_1(l) = \lambda_1(\tilde{l})$ , then letting  $\hat{\lambda}$  denote the common value, we have  $l = \tilde{l} = F_3(\hat{\lambda})$ . The mapping is surjective, since for any  $\hat{\lambda} \in (-\infty, r - \frac{\alpha^2 \min\{b_0, b_l\}(1 - \min\{b_0, b_l\})}{\mu})$ , we have  $\hat{\lambda} = \lambda_1(\hat{l})$ , where  $\hat{l} = F_3(\hat{\lambda})$  (note  $F_3(\hat{\lambda}) > 0$  since  $\min\{b_0, b_l\} < \frac{1}{2}$ ). That  $\hat{\lambda} = \lambda_1(\hat{l})$  follows from Proposition 1, and the positivity of the associated eigenfunction on  $[0, \hat{l}]$ . Thus,  $l \mapsto \lambda_1(l)$  is a bijection from  $(0, \infty)$  to  $(-\infty, r - \frac{\alpha^2 \min\{b_0, b_l\}(1 - \min\{b_0, b_l\})}{\mu})$ . Moreover,  $l \mapsto \lambda_1(l)$  is continuous, since its inverse  $F_3$  is continuous on the interval  $(-\infty, r - \frac{\alpha^2 \min\{b_0, b_l\}(1 - \min\{b_0, b_l\})}{\mu})$ . Since  $l = F_3(\lambda_1(l))$ , it follows from (2.14) that  $\lambda \nearrow r - \frac{\alpha^2 \min\{b_0, b_l\}(1 - \min\{b_0, b_l\})}{\mu}$  as  $l \rightarrow +\infty$ , and from (2.13) that  $\lambda \searrow -\infty$  as  $l \searrow 0$ . Thus, as a homeomorphism from  $(0, \infty)$  to  $(-\infty, r - \frac{\alpha^2 \min\{b_0, b_l\}(1 - \min\{b_0, b_l\})}{\mu})$ , the mapping  $l \mapsto \lambda_1(l)$  is strictly increasing. This shows Claim 6. Combined, Claims 1, 4, 5, and 6 prove part (ii). This concludes the proof.  $\square$

**Proposition 2.** Fix  $\mu, \alpha, r > 0$ , and  $b_0, b_l > 0$  such that  $b_0 + b_l > 1$ .

(a) If  $\min\{b_0, b_l\} \geq \frac{1}{2}$ , then the critical domain size is given by

$$l_1^* = \begin{cases} +\infty, & 0 < \mu \leq \frac{\alpha^2}{4r} \\ F_1(0; \mu, \alpha, r, b_0, b_l), & \mu > \frac{\alpha^2}{4r}. \end{cases} \quad (2.26)$$

(b) If  $0 < \min\{b_0, b_l\} < \frac{1}{2}$ , then the critical domain size is given by

$$l_2^* = \begin{cases} +\infty, & 0 < \mu \leq \frac{\alpha^2 \min\{b_0, b_l\}(1 - \min\{b_0, b_l\})}{r} \\ F_2(0; \mu, \alpha, r, b_0, b_l), & \frac{\alpha^2 \min\{b_0, b_l\}(1 - \min\{b_0, b_l\})}{r} < \mu < \frac{\alpha^2}{4r} \\ -\frac{\alpha(b_0 + b_l - 1)}{4r(b_0 - \frac{1}{2})(b_l - \frac{1}{2})}, & \mu = \frac{\alpha^2}{4r} \\ F_1(0; \mu, \alpha, r, b_0, b_l), & \mu > \frac{\alpha^2}{4r}. \end{cases} \quad (2.27)$$

Here,  $F_1$  and  $F_2$  are given in (2.13) and (2.14), respectively.

**Remark.** Under the additional assumption that  $b_0 > 1$ , (2.26)-(2.27) are given in [104, Sec. 2.2] in slightly different forms. Note that  $(b_u, b_d) = (b_0 - 1, b_l)$  under their notation.

**Remark.** For the case of a moving habitat, the critical domain size is given in formula (25) of [10], and is equivalent to (2.26), with  $b_0 = b_l = \frac{1 + \sqrt{1 + \frac{4\mu\kappa_1}{\alpha^2}}}{2}$ .

*Proof of Proposition 2.* Assertion (a) follows directly from Lemma 1. If  $\mu \leq \frac{\alpha^2}{4r}$ , then by Lemma 1(i), the range of  $l \mapsto \lambda_1(l)$  is contained in  $(-\infty, 0)$ , i.e.  $\lambda_1 < 0$  for all  $l > 0$ . If  $\mu > \frac{\alpha^2}{4r}$ , the critical value  $l_1^*$  is obtained from setting  $\lambda_1 = 0$  in (2.15). Now  $l_1^*$  is a critical domain size, since by Lemma 1,  $\lambda_1 = \lambda_1(l)$  is a strictly increasing function of  $l$ .

Similarly reasoning proves assertion (b). Lemma 1(ii) implies that  $\lambda_1 < 0$  for all  $l > 0$  if  $\mu \leq \frac{\alpha^2 \min\{b_0, b_l\}(1 - \min\{b_0, b_l\})}{r}$ . If  $\mu > \frac{\alpha^2 \min\{b_0, b_l\}(1 - \min\{b_0, b_l\})}{r}$ , then we set  $\lambda_1 = 0$  in (2.16) to obtain the critical value  $l_2^*$ . Now  $l_2^*$  is a critical domain size, since Lemma 1 implies that  $\lambda_1 = \lambda_1(l)$  is a strictly increasing function of  $l$ .  $\square$

## 2.2.3 Proof of Theorem 2

In this section, we consider the critical domain size  $l^*$  for persistence of the species  $u$  in (2.6).



*Proof of Theorem 2.* We define

$$l^* = \begin{cases} l_1^*, & \min\{b_0, b_l\} \geq \frac{1}{2} \\ l_2^*, & 0 \leq \min\{b_0, b_l\} < \frac{1}{2}. \end{cases} \quad (2.28)$$

By Proposition 2,  $l^*$  is the critical domain size of (2.6). It follows from Theorem 5(i) that if  $l > l^*$ , then (2.6) has a unique, positive equilibrium  $\theta$  such that

$$\lim_{t \rightarrow \infty} \|u(\cdot, t) - \theta\|_{C^0([0, l])} = 0$$

for every nonnegative, nontrivial solution  $u$  of (2.6). If  $l \leq l^*$ , then by Theorem 5(ii)

$$\lim_{t \rightarrow \infty} \|u(\cdot, t)\|_{C^0([0, l])} = 0$$

for every nonnegative solution of (2.6). This establishes Theorem 2.  $\square$

## 2.2.4 Monotonicity of the critical domain size

We now prove Theorem 3, which establishes the monotone dependence of the critical domain size on the diffusion coefficient when the diffusion rate is large, and, given additional assumptions on the boundary loss parameters  $b_0$  and  $b_l$ , provides a global characterization of the relationship between the critical domain size and the diffusion rate.

**Proposition 3.** *Fix  $r, \alpha > 0$ , and  $b_0, b_l \geq 0$  such that  $b_0 + b_l > 1$ . Let  $l^*(\mu, b_0, b_l)$  be given by (2.28).*

(a) *Fix  $\mu > \frac{\alpha^2}{4r}$ . Then  $l^*(\mu, b_0, b_l)$  is the first positive root in  $\left(0, \frac{\pi}{\sqrt{r\tau - \frac{\alpha^2\tau^2}{4}}}\right)$  of the equation*

$$g\left(\sqrt{r\tau - \frac{\alpha^2\tau^2}{4}}l^*\right) = l^* \left( \frac{r - \tau\frac{\alpha^2}{4} - \tau\alpha^2(b_0 - \frac{1}{2})(b_l - \frac{1}{2})}{\alpha(b_0 + b_l - 1)} \right), \quad (2.29)$$

where  $g(s) = s \cot s$  and  $\tau = \frac{1}{\mu}$ .

(b) Suppose that  $(b_0 + b_l - 1)^2 \geq 0.941(b_0 + b_l - 1 - 2b_0b_l)^2$ , and that there exists

$$\mu_0 \geq \frac{\alpha^2}{4r} \text{ for which } \frac{\partial l^*}{\partial \mu}(\mu_0, b_0, b_l) = 0.$$

(i) If  $\min\{b_0, b_l\} \geq \frac{1}{2}$ , then  $\mu_0 > \frac{\alpha^2}{4r}$  and  $\frac{\partial^2 l^*}{\partial \mu^2}(\mu_0, b_0, b_l) > 0$ .

(ii) If  $\min\{b_0, b_l\} < \frac{1}{2}$ , then  $\frac{\partial^2 l^*}{\partial \mu^2}(\mu_0, b_0, b_l) > 0$  if  $\mu_0 > \frac{\alpha^2}{4r}$ , and

$$\lim_{\mu \searrow \mu_0} \frac{\partial^2 l^*}{\partial \mu^2}(\mu_0, b_0, b_l) > 0 \text{ if } \mu_0 = \frac{\alpha^2}{4r}.$$

(c) If  $\min\{b_0, b_l\} < \frac{1}{2}$  and  $\max\{b_0, b_l\} \leq 1$ , then  $\frac{\partial l^*}{\partial \mu}(\mu_0, b_0, b_l) < 0$  for

$$\frac{\alpha^2}{r} \min\{b_0, b_l\}(1 - \min\{b_0, b_l\}) < \mu < \frac{\alpha^2}{4r}.$$

*Proof of Proposition 3(a).* Recall from (2.13) that  $l^*$  satisfies

$$\frac{l^* \sqrt{4\mu r - \alpha^2}}{2\mu} = \arctan\left(\frac{2\alpha(b_l - \frac{1}{2})}{\sqrt{4\mu r - \alpha^2}}\right) - \arctan\left(\frac{-2\alpha(b_0 - \frac{1}{2})}{\sqrt{4\mu r - \alpha^2}}\right).$$

Using the identity  $\cot(x - y) = \frac{1 + \tan(x)\tan(y)}{\tan(x) - \tan(y)}$ , for  $x, y \in (-\frac{\pi}{2}, \frac{\pi}{2})$  and  $x - y \in (0, \pi)$ ,

we deduce that

$$\cot\left(\frac{l^* \sqrt{4\mu r - \alpha^2}}{2\mu}\right) = \frac{4\mu r - \alpha^2 - 4\alpha^2(b_0 - \frac{1}{2})(b_l - \frac{1}{2})}{2\alpha(b_0 + b_l - 1)\sqrt{4\mu r - \alpha^2}}.$$

Thus,

$$\frac{l^* \sqrt{4\mu r - \alpha^2}}{2\mu} \cot\left(\frac{l^* \sqrt{4\mu r - \alpha^2}}{2\mu}\right) = l^* \left(\frac{r - \frac{\alpha^2}{4\mu} - \frac{\alpha^2}{\mu}(b_0 - \frac{1}{2})(b_l - \frac{1}{2})}{\alpha(b_0 + b_l - 1)}\right),$$

and substituting  $\tau = \frac{1}{\mu}$  gives the desired result.  $\square$

*Proof of Proposition 3(b).* Fix  $b_0, b_l \geq 0$  such that  $(b_0 + b_l - 1)^2 \geq 0.941(b_0 + b_l - 1 - 2b_0b_l)^2$ . Denote  $\tau_0 := \frac{1}{\mu_0}$ , and set

$$L(\tau) := l^*(\mu, b_0, b_l), \quad ' := \frac{\partial}{\partial \tau}, \quad M(\tau) := \sqrt{r\tau - \frac{\alpha^2\tau^2}{4}},$$

and

$$N(\tau) := \frac{r - \tau\alpha^2(\frac{1}{4} + (b_0 - \frac{1}{2})(b_l - \frac{1}{2}))}{\alpha(b_0 + b_l - 1)}.$$

By Proposition 3(a),  $l^*$  satisfies (2.29) for  $\mu > \frac{\alpha^2}{4r}$ . Differentiating (2.29) with respect to  $\tau$ , we have

$$g'(ML)(M'L + ML') = L'N + LN' \quad \text{for } \tau \in (0, \frac{4r}{\alpha^2}). \quad (2.30)$$

Differentiating again and rearranging, we obtain

$$L''(N - g'(ML)M) = g''(ML)(M'L + ML')^2 + g'(ML)(M''L + 2M'L') - 2L'N' \quad (2.31)$$

for  $\tau \in (0, \frac{4r}{\alpha^2})$ .

Assume  $\min\{b_0, b_l\} \geq \frac{1}{2}$ . Then clearly  $\mu_0 > \frac{\alpha^2}{4r}$ , since  $l^*$  is finite if and only if  $\mu > \frac{\alpha^2}{4r}$  (Theorem 2). Thus, we have  $L'(\tau_0) = 0$  for some  $\tau_0 \in (0, \frac{4r}{\alpha^2})$ , so that setting  $\tau = \tau_0$  in (2.31), we obtain

$$\left[ L''(N - g'(ML)M) = g''(ML)(M'L)^2 + g'(ML)(M''L) \right]_{\tau=\tau_0}. \quad (2.32)$$

We first consider the case  $\tau_0 = \frac{2r}{\alpha^2}$ , where  $M'(\tau_0) = 0$ . Letting  $\tau_0 = \frac{2r}{\alpha^2}$  in (2.30), we have  $N'(\tau_0) = -\alpha \left( \frac{\frac{1}{4} + (b_0 - \frac{1}{2})(b_l - \frac{1}{2})}{b_0 + b_l - 1} \right) = 0$ , which implies that  $(b_0 - \frac{1}{2})(b_l - \frac{1}{2}) = -\frac{1}{4}$ . Moreover, we compute  $M(\frac{2r}{\alpha^2}) = \frac{r}{\alpha}$ , and  $M''(\frac{2r}{\alpha^2}) = -\frac{\alpha^3}{4r}$ , so that by setting  $\tau_0 = \frac{2r}{\alpha^2}$  in (2.31), we obtain

$$\begin{aligned} \left[ L'' = \frac{g'(ML)M''L}{N - Mg'(ML)} \right]_{\tau=\frac{2r}{\alpha^2}} &= -\frac{\alpha^4}{4r^2} \left[ \frac{g'(ML)L}{\frac{\frac{1}{2} - 2(b_0 - \frac{1}{2})(b_l - \frac{1}{2})}{b_0 + b_l - 1} - g'(ML)} \right]_{\tau=\frac{2r}{\alpha^2}} \\ &= -\frac{\alpha^4}{4r^2} \left[ \frac{g'(ML)L}{\frac{1}{b_0 + b_l - 1} - g'(ML)} \right]_{\tau=\frac{2r}{\alpha^2}}. \end{aligned}$$

Since  $g'(x) < 0$  for  $x \in (0, \pi)$ , it follows that  $L''(\frac{2r}{\alpha^2}) > 0$ . This is equivalent to  $\frac{\partial^2 l^*}{\partial \mu^2}(\frac{\alpha^2}{2r}) > 0$ , and establishes assertion (i) for  $\mu_0 = \frac{\alpha^2}{2r}$ .

If  $\tau_0 \neq \frac{2r}{\alpha^2}$ , we proceed in steps.

**Step 1.** We show that for  $\tau = \tau_0$ ,

$$L''(N - g'(ML)M) = \left(\frac{N'L}{g'(ML)}\right)^2 \left[ g''(ML) - \frac{g'(ML)}{ML} \left( \frac{\alpha^2}{4(N')^2} g'(ML)^2 + 1 \right) \right]. \quad (2.33)$$

Setting  $\tau = \tau_0$  in (2.30), we have

$$0 > g'(ML) \Big|_{\tau=\tau_0} = \frac{N'(\tau_0)}{M'(\tau_0)} = -\alpha \left( \frac{\frac{1}{4} + (b_0 - \frac{1}{2})(b_l - \frac{1}{2})}{b_0 + b_l - 1} \right) \left( \frac{2M(\tau_0)}{r - \frac{\alpha^2 \tau_0}{2}} \right). \quad (2.34)$$

Further, we note that

$$M'' = \left( \frac{r - \frac{\alpha^2 \tau}{2}}{2M} \right)' = - \left( \frac{\alpha^2}{4M} + \frac{(M')^2}{M} \right). \quad (2.35)$$

Now recalling (2.32) and applying (2.34) and (2.35), we compute

$$\begin{aligned} L''(N - g'(ML)M) &= g''(ML)(M'L)^2 + g'(ML)(M''L) \\ &= g''(ML) \left( \frac{N'L}{g'(ML)} \right)^2 - g'(ML) \left( \frac{\alpha^2}{4M} + \frac{(M')^2}{M} \right) L \\ &= \left( \frac{N'L}{g'(ML)} \right)^2 \left[ g''(ML) - \frac{g'(ML)}{ML} \left( \frac{\alpha^2}{4(N')^2} g'(ML)^2 + 1 \right) \right] \end{aligned}$$

for  $\tau = \tau_0$ .

**Step 2.** Next, we observe

$$\left[ N - g'(ML)M \right]_{\tau=\tau_0} > 0. \quad (2.36)$$

Recalling (2.34), a direct computation yields

$$\left[ N - g'(ML)M \right]_{\tau=\tau_0} = \frac{\alpha^2 \tau_0 \left[ \frac{1}{4} + (b_0 - \frac{1}{2})(b_l - \frac{1}{2}) \right] + r - \frac{\alpha^2 \tau_0}{2}}{\frac{\alpha}{r} (b_0 + b_l - 1) \left( r - \frac{\alpha^2 \tau_0}{2} \right)}.$$

Since  $b_0 + b_l - 1 > 0$ , (2.34) implies that  $\frac{1}{4} + (b_0 - \frac{1}{2})(b_l - \frac{1}{2})$  and  $r - \frac{\alpha^2 \tau_0}{2}$  have the same sign, from which (2.36) follows.

**Step 3.** Finally, we show that

$$\left[ g''(ML) - \frac{g'(ML)}{ML} \left( \frac{\alpha^2}{4(N')^2} g'(ML)^2 + 1 \right) \right]_{\tau=\tau_0} > 0. \quad (2.37)$$

By Lemma 3, we have

$$g''(s) - \frac{g'(s)}{s}[Cg'(s)^2 + 1] > 0 \quad \text{for } 0 < s < \pi$$

if  $C \geq 0.941$ . Thus, (2.37) holds if  $\frac{\alpha^2}{4(N')^2} \geq 0.941$ , which follows from the assumption  $(1 - b_0 - b_l)^2 \geq 0.941(1 - b_0 - b_l + 2b_0b_l)^2$ .

Together, (2.33), (2.36), and (2.37) imply that  $L''(\tau_0) > 0$ . This concludes the proof of assertion (i).

To prove assertion (ii), we assume  $\min\{b_0, b_l\} < \frac{1}{2}$  and suppose that  $\frac{\partial l^*}{\partial \mu}(\mu_0, b_0, b_l) = 0$  for some  $\mu_0 \geq \frac{\alpha^2}{4r}$ . If  $\mu_0 > \frac{\alpha^2}{4r}$ , then  $l^*$  satisfies (2.29), so that the proof of assertion (i) also holds for (ii). Thus, we need only consider the case  $\mu_0 = \frac{\alpha^2}{4r}$ , i.e.,  $\tau_0 = \frac{4r}{\alpha^2}$ .

We use the expressions

$$M' = \frac{r - \frac{\alpha^2\tau}{2}}{2M} \quad \text{and} \quad M'' = -\frac{\frac{\alpha^2}{4} + (M')^2}{M}$$

for  $\tau \in (0, \frac{4r}{\alpha^2})$  to rewrite (2.31) as follows:

$$\begin{aligned} L''(N - g'(ML)M) &= g''(ML)(M'L + ML')^2 - \frac{g'(ML)}{ML}\left(\frac{\alpha^2}{4} + M'^2\right)L^2 \\ &\quad + \frac{g'(ML)}{ML}\left(r - \frac{\alpha^2\tau}{2}\right)LL' - 2L'N' \\ &= (M'L)^2\left[g''(ML) - \frac{g'(ML)}{ML}\left(\frac{\alpha^2}{4(M')^2} + 1\right)\right] \\ &\quad + \frac{g'(ML)}{ML}\left(r - \frac{\alpha^2\tau}{2}\right)LL' \\ &\quad + g''(ML)\left[\left(r - \frac{\alpha^2\tau}{2}\right)L'L + (ML')^2\right] - 2L'N' \end{aligned} \quad (2.38)$$

for  $\tau \in (0, \frac{4r}{\alpha^2})$ .

Denoting the right hand side of (2.38) by  $R(\tau)$ , we will show that both

$$\lim_{\tau \rightarrow \frac{4r}{\alpha^2}^-} [N - g'(ML)M] > 0 \quad \text{and} \quad \lim_{\tau \rightarrow \frac{4r}{\alpha^2}^-} R(\tau) > 0.$$

Thus, sending  $\tau \rightarrow \frac{4r}{\alpha^2}^-$  in (2.38), we conclude that

$$\lim_{\tau \rightarrow \frac{4r}{\alpha^2}^-} L''(\tau) > 0,$$

as desired.

Using the expansions  $\frac{g'(s)}{s} = -\frac{2}{3} - \frac{4}{45}s^2 + o(s^3)$  and  $g''(s) = -\frac{2}{3} - \frac{12}{45}s^2 + o(s^3)$ , we compute

$$\lim_{\tau \rightarrow \frac{4r}{\alpha^2}^-} [N - g'(ML)M] = \frac{-4r(b_0 - \frac{1}{2})(b_l - \frac{1}{2})}{\alpha(b_0 + b_l - 1)} > 0,$$

and

$$\begin{aligned} \lim_{\tau \rightarrow \frac{4r}{\alpha^2}^-} R(\tau) &= \lim_{\tau \rightarrow \frac{4r}{\alpha^2}^-} \left[ (ML)^2 \left( g''(ML) - \frac{g'(ML)}{ML} \right) + \frac{\alpha^2}{6} L^2 \right] \\ &= \lim_{\tau \rightarrow \frac{4r}{\alpha^2}^-} \left[ L^4 (2r - \alpha^2 \tau)^2 \left( \frac{g''(ML) - \frac{g'(ML)}{ML}}{16(ML)^2} \right) + \frac{\alpha^2}{6} L^2 \right] \\ &= \left[ L^2 \left( \frac{\alpha^2}{6} - \frac{4r^2}{90} L^2 \right) \right]_{\tau = \frac{4r}{\alpha^2}} \\ &= \frac{1}{96} \left( \frac{\alpha^2(b_0 + b_l - 1)}{r(b_0 - \frac{1}{2})(b_l - \frac{1}{2})} \right)^2 \left( 1 - \frac{(b_0 + b_l - 1)^2}{60(b_0 - \frac{1}{2})^2(b_l - \frac{1}{2})^2} \right). \end{aligned}$$

(We recall from (2.27) that  $L(\frac{4r}{\alpha^2}) = -\frac{\alpha(b_0 + b_l - 1)}{4r(b_0 - \frac{1}{2})(b_l - \frac{1}{2})}$ ).

By Lemma 4,  $L'(\frac{4r}{\alpha^2}) = 0$  only if  $(b_0 + b_l - 1)^2 = 12(b_0 - \frac{1}{2})(b_l - \frac{1}{2})[\frac{1}{4} + (b_0 - \frac{1}{2})(b_l - \frac{1}{2})]$ .

That  $\lim_{\tau \rightarrow \frac{4r}{\alpha^2}^-} R(\tau) > 0$  now follows by observing that

$$\begin{aligned} 1 - \frac{(b_0 + b_l - 1)^2}{60(b_0 - \frac{1}{2})^2(b_l - \frac{1}{2})^2} &= 1 - \frac{\frac{1}{4} + (b_0 - \frac{1}{2})(b_l - \frac{1}{2})}{5(b_0 - \frac{1}{2})(b_l - \frac{1}{2})} \\ &= \frac{4(b_0 - \frac{1}{2})(b_l - \frac{1}{2}) - \frac{1}{4}}{5(b_0 - \frac{1}{2})(b_l - \frac{1}{2})} > 0. \end{aligned}$$

This concludes the proof. □

*Proof of Proposition 3(c).* We will use an argument similar to that of Proposition 2.2 in [74]. By (2.27),  $l^* = F_2(0; \mu, b_0, b_l)$  for  $\mu \in (\frac{\alpha^2}{r} \min\{b_0, b_l\}(1 - \min\{b_0, b_l\}), \frac{\alpha^2}{4r})$ .

Thus, it suffices to show that  $F_2(0; \mu, b_0, b_l)$  is a decreasing function of  $\mu$  for  $\mu \in (\frac{\alpha^2}{r} \min\{b_0, b_l\}(1 - \min\{b_0, b_l\}), \frac{\alpha^2}{4r})$ .

For ease of notation, we denote

$$F(\mu) := F_2(0; \mu, b_0, b_l) = \frac{\mu}{2M} \log \frac{k_1}{k_2},$$

where  $M := \frac{1}{2}\sqrt{\alpha^2 - 4\mu r}$ ,  $k_1 := [M - \alpha(b_0 - \frac{1}{2})][M - \alpha(b_l - \frac{1}{2})]$ , and  $k_2 := [M + \alpha(b_0 - \frac{1}{2})][M + \alpha(b_l - \frac{1}{2})]$ .

Suppose that  $b_l < \frac{1}{2}$ ,  $b_0 \leq 1$ . We will show that  $F'(\mu) < 0$  for  $\mu \in (\frac{\alpha^2 b_l(1-b_l)}{r}, \frac{\alpha^2}{4r})$ .

We compute

$$\begin{aligned} F'(\mu) &= \frac{2M^2 + \mu r}{4M^3} \log \frac{k_1}{k_2} + \frac{\mu r \alpha (b_0 + b_l - 1) (\alpha^2 (b_0 - \frac{1}{2})(b_l - \frac{1}{2}) - M^2)}{2M^2 k_1 k_2} \\ &= \frac{1}{4M^3 k_1 k_2} \left( (2M^2 + \mu r) (k_1 k_2) \log \frac{k_1}{k_2} \right. \\ &\quad \left. + 2M \mu r \alpha (b_0 + b_l - 1) (\alpha^2 (b_0 - \frac{1}{2})(b_l - \frac{1}{2}) - M^2) \right). \end{aligned} \quad (2.39)$$

We note that  $4M^3 k_1 k_2 > 0$  for  $\mu \in (\frac{\alpha^2 b_l(1-b_l)}{r}, \frac{\alpha^2}{4r})$ .

We now consider the numerator of (2.39) as a function,  $h$ , of  $b_l$ . Differentiating in  $b_l$ , we obtain

$$\begin{aligned} h'(b_l) &= 2\alpha(2M^2 + \mu r) (\alpha^2 (b_0 - \frac{1}{2})^2 - M^2) (M + \alpha(b_l - \frac{1}{2})) \log \frac{k_1}{k_2} \\ &\quad + 2M \mu r \alpha [2\alpha^2 (b_0 - \frac{1}{2})(b_l - \frac{1}{2}) - M^2 + \alpha^2 (b_0 - \frac{1}{2})^2], \\ h''(b_l) &= 2\alpha^2 (2M^2 + \mu r) (\alpha^2 (b_0 - \frac{1}{2})^2 - M^2) \\ &\quad \cdot \left[ \log \frac{k_1}{k_2} + (b_l - \frac{1}{2}) \frac{2\alpha M (\alpha^2 (b_0 - \frac{1}{2})^2 - M^2)}{k_1 k_2} \right] + 4M \mu r \alpha^3 (b_0 - \frac{1}{2}), \\ h'''(b_l) &= \frac{8\alpha^3 M (2M^2 + \mu r) (\alpha^2 (b_0 - \frac{1}{2})^2 - M^2)^2}{(k_1 k_2)^2} \\ &\quad \cdot \left[ k_1 k_2 + \alpha^2 (b_l - \frac{1}{2})^2 (M^2 - \alpha^2 (b_0 - \frac{1}{2})^2) \right]. \end{aligned}$$

For  $\mu \in (\frac{\alpha^2 b_l(1-b_l)}{r}, \frac{\alpha^2}{4r})$ , we have

$$\begin{aligned} k_1 k_2 + \alpha^2 (b_l - \frac{1}{2})^2 (M^2 - \alpha^2 (b_0 - \frac{1}{2})^2) &= (\frac{\alpha^2}{4} - \mu r) (\alpha^2 b_0 (1 - b_0) - \mu r) \\ &< (\frac{\alpha^2}{4} - \mu r) (\alpha^2 b_l (1 - b_l) - \mu r) \\ &< 0. \end{aligned}$$

Thus, for  $\mu \in (\frac{\alpha^2 b_l(1-b_l)}{r}, \frac{\alpha^2}{4r})$ ,  $0 < b_l < \frac{1}{2}$ , and  $b_0 \leq 1$ , we have

$$\begin{aligned} h'''(b_l) < 0 &\implies h''(b_l) < h''(1 - b_0) = 2\alpha^3 M (b_0 - \frac{1}{2}) (4\mu r - \alpha^2) < 0 \\ &\implies h'(b_l) < h'(1 - b_0) = 4\alpha^3 M^3 b_0 (b_0 - 1) \leq 0 \\ &\implies h(b_l) < h(1 - b_0) = 0. \end{aligned}$$

It follows from (2.39) that  $F'(\mu) < 0$  for  $\mu \in (\frac{\alpha^2 b_l(1-b_l)}{r}, \frac{\alpha^2}{4r})$ . The proof for the case  $0 < b_0 < \frac{1}{2}$ ,  $b_l \leq 1$  is similar, and we omit the details.  $\square$

*Proof of Theorem 3.* Using the same notation as in the proof of Proposition 3(b), we will show the existence of

$$-L'(0) = \lim_{\mu \rightarrow \infty} \mu^2 \frac{\partial l^*}{\partial \mu}, \quad (2.40)$$

and use this relation to deduce the eventual monotonicity of  $l^*(\mu)$ .

From (2.30), we have

$$\begin{aligned} L' \left[ \frac{r - \tau \frac{\alpha^2}{4} - \tau \alpha^2 (b_0 - \frac{1}{2})(b_l - \frac{1}{2})}{\alpha(b_0 + b_l - 1)} \right] - \alpha L \left[ \frac{\frac{1}{4} + (b_0 - \frac{1}{2})(b_l - \frac{1}{2})}{b_0 + b_l - 1} \right] \\ = \frac{g'(ML)}{ML} \left[ \frac{L^2}{2} (r - \frac{\alpha^2 \tau}{2}) + M^2 LL' \right] \end{aligned} \quad (2.41)$$

for  $\tau \in (0, \frac{4r}{\alpha^2})$ , where  $g(s) = s \cot s$ . Recalling that  $\lim_{\mu \rightarrow \infty} l^*(\mu) = \frac{\alpha(b_0 + b_l - 1)}{r}$  and  $\frac{g'(s)}{s} = -\frac{2}{3} + o(1)$ , we let  $\tau \rightarrow 0$  to obtain

$$L'(0) = \frac{\alpha^3 (b_0 + b_l - 1)}{r^2} \left( \frac{1}{4} + (b_0 - \frac{1}{2})(b_l - \frac{1}{2}) - \frac{(b_0 + b_l - 1)^2}{3} \right).$$



To prove part (a), suppose  $G(b_0, b_l) > 0$ . Then  $L'(0) > 0$ , so (2.40) implies that  $\mu \mapsto l^*(\mu)$  is strictly decreasing for  $\mu \gg 1$ . Suppose, in addition, that  $(b_0 + b_l - 1)^2 \geq 0.941(b_0 + b_l - 1 - 2b_0b_l)^2$ . Then if  $\min\{b_0, b_l\} \geq \frac{1}{2}$ , Proposition 3(b)(i) implies that  $\frac{\partial}{\partial \mu} l^*(\mu, b_0, b_l) < 0$  for all  $\mu > \hat{\mu}$ , where  $\hat{\mu}$  is given in (2.8). If  $\min\{b_0, b_l\} < \frac{1}{2}$ ,  $\max\{b_0, b_l\} \leq 1$ , then Proposition 3(b)(ii) and (c) imply that  $\frac{\partial}{\partial \mu} l^*(\mu, b_0, b_l) < 0$  for all  $\mu > \hat{\mu}$ . This proves (a).

If  $G(b_0, b_l) < 0$ , then  $L'(0) < 0$ , so that  $\mu \mapsto l^*(\mu)$  is strictly increasing for  $\mu \gg 1$ . Since  $l^*(\mu) \rightarrow \infty$  as  $\mu \searrow \hat{\mu}$  (Theorem 2),  $l^*(\mu)$  obtains a global minimum for some  $\tilde{\mu} \in (\hat{\mu}, \infty)$ . Suppose also that  $(b_0 + b_l - 1)^2 \geq 0.941(b_0 + b_l - 1 - 2b_0b_l)^2$ . If  $\min\{b_0, b_l\} \geq \frac{1}{2}$ , then Proposition 3(b)(i) implies that  $\tilde{\mu}$  is unique,  $\frac{\partial}{\partial \mu} l^*(\mu) < 0$  for  $\mu \in (\hat{\mu}, \tilde{\mu})$ , and  $\frac{\partial}{\partial \mu} l^*(\mu) > 0$  for  $\mu > \tilde{\mu}$ . This proves (b), and completes the proof.  $\square$

### 2.3 Proof of competition dynamics

We consider the equation:

$$\begin{cases} u_t = \mu u_{xx} - \alpha u_x + u(r - \frac{u+v}{K}), & 0 < x < l, t > 0, \\ v_t = \nu v_{xx} - \alpha v_x + v(r - \frac{u+v}{K}), & 0 < x < l, t > 0, \\ \mu u_x(0, t) - \alpha u(0, t) = (b_0 - 1)\alpha u(0, t), & t > 0 \\ \mu u_x(l, t) - \alpha u(l, t) = -b_l \alpha u(l, t), & t > 0 \\ \nu v_x(0, t) - \alpha v(0, t) = (b_0 - 1)\alpha v(0, t), & t > 0 \\ \nu v_x(l, t) - \alpha v(l, t) = -b_l \alpha v(l, t), & t > 0, \end{cases} \quad (2.42)$$

in which the species  $u$  and  $v$  diffuse at rates  $\mu > 0$  and  $\nu > 0$ , respectively, and  $\alpha, r, K, b_0, b_l$  are positive constants.

We note that  $(0, 0)$  is a trivial equilibrium of system (2.42), while  $(\theta_\mu(x), 0)$  and  $(0, \theta_\nu(x))$  are semi-trivial equilibria, where  $\theta_\mu(x)$  is the unique positive solution (whenever it exists) of the equation

$$\begin{cases} \mu\theta_{xx} - \alpha\theta_x + (r - \theta/K)\theta = 0, & 0 < x < l \\ \mu\theta_x(0) - \alpha\theta(0) = (b_0 - 1)\alpha\theta(0) \\ \mu\theta_x(l) - \alpha\theta(l) = -b_l\alpha\theta(l). \end{cases} \quad (2.43)$$

The linear stability of the equilibrium solution  $(\theta_\mu, 0)$  is given by the sign of the principal eigenvalue  $\Lambda(\mu, \nu)$  of the following problem; see, e.g., [82, 85]:

$$\begin{cases} \nu\Psi_{xx} - \alpha\Psi_x + (r - \theta_\mu/K)\Psi = \Lambda\Psi, & 0 < x < l \\ \nu\Psi_x(0) - \alpha\Psi(0) = (b_0 - 1)\alpha\Psi(0) \\ \nu\Psi_x(l) - \alpha\Psi(l) = -b_l\alpha\Psi(l). \end{cases}$$

We perform the change of variables  $\xi = \frac{1}{\mu}$ ,  $\tau = \frac{1}{\nu}$ ,  $\Lambda(\xi, \tau) = \Lambda(\mu, \nu)$ . Then  $\Lambda(\xi, \tau)$  is the principal eigenvalue of:

$$\begin{cases} \Phi_{xx} - \alpha\tau(1 - 2b_0)\Phi_x + \tau\left[\alpha^2b_0\tau(b_0 - 1) + \left(r - \frac{e^{\alpha b_0 \xi x}}{K}\eta\right)\right]\Phi = \tau\Lambda\Phi, \\ \Phi_x(0) = \Phi_x(l) + \tau\alpha(b_0 + b_l - 1)\Phi(l) = 0, \end{cases}$$

where the first equation holds for  $0 < x < l$ ,  $\Phi = e^{-\alpha b_0 \tau x}\Psi$ , and  $\eta_\xi(x)$  is the unique positive solution of

$$\begin{cases} \eta_{xx} - \alpha\xi(1 - 2b_0)\eta_x + \xi\left[\alpha^2b_0\xi(b_0 - 1) + \left(r - \frac{e^{\alpha b_0 \xi x}}{K}\eta\right)\right]\eta = 0, & 0 < x < l \\ \eta_x(0) = \eta_x(l) + \xi\alpha(b_0 + b_l - 1)\eta(l) = 0. \end{cases}$$

**Lemma 2.** Fix  $\alpha > 0$ ,  $r > 0$ ,  $b_0, b_l$  and  $r$  such that  $b_0 + b_l > 1$ , and  $0 \leq \frac{\alpha(b_0 + b_l - 1)}{r} < l$ .

- (a) If  $\Lambda_\tau(0, 0) < 0$ , then there exists  $\underline{\mu} > 0$  such that if  $\mu > \nu \geq \underline{\mu}$ , then  $(\theta_\mu, 0)$  is globally asymptotically stable among all nonnegative, nontrivial solutions of (2.42).
- (b) If  $\Lambda_\tau(0, 0) > 0$ , then there exists  $\underline{\mu} > 0$  such that if  $\mu > \nu \geq \underline{\mu}$ , then  $(0, \theta_\nu)$  is globally asymptotically stable among all nonnegative, nontrivial solutions of (2.42).

*Proof.* Our proof follows the arguments in Lemma 6.1 of [45]. First, we show that if  $\Lambda_\tau(0,0) \neq 0$ , then (2.42) has no positive equilibria for  $\mu, \nu$  sufficiently large. Otherwise, let  $\mu_j \rightarrow \infty$  and  $\nu_j \rightarrow \infty$  such that for each  $j \geq 1$ ,  $(u_j, v_j)$  is a positive solution to (2.42) with  $(\mu, \nu) = (\mu_j, \nu_j)$ . Then for  $(\xi_j, \tau_j) = (\frac{1}{\mu_j}, \frac{1}{\nu_j})$ , we observe that  $(\tilde{u}_j, \tilde{v}_j)$  satisfies the equation:

$$\begin{cases} \tilde{u}_{j,xx} - \alpha \xi_j (1 - 2b_0) \tilde{u}_{j,x} + \xi_j \left[ \alpha^2 b_0 \xi_j (b_0 - 1) + \left( r - \frac{u_j + v_j}{K} \right) \right] \tilde{u}_j = 0, & 0 < x < l \\ \tilde{v}_{j,xx} - \alpha \tau_j (1 - 2b_0) \tilde{v}_{j,x} + \tau_j \left[ \alpha^2 b_0 \tau_j (b_0 - 1) + \left( r - \frac{u_j + v_j}{K} \right) \right] \tilde{v}_j = 0, & 0 < x < l \\ \tilde{u}_{j,x}(0) = \tilde{u}_{j,x}(l) + \xi_j \alpha (b_0 + b_l - 1) \tilde{u}_j(l) = 0 \\ \tilde{v}_{j,x}(0) = \tilde{v}_{j,x}(l) + \tau_j \alpha (b_0 + b_l - 1) \tilde{v}_j(l) = 0, \end{cases} \quad (2.44)$$

where  $\tilde{u}_j = e^{-\alpha b_0 \xi_j x} u_j$  and  $\tilde{v}_j = e^{-\alpha b_0 \tau_j x} v_j$ ,  $j \geq 1$ .

Denoting by  $\tilde{\Lambda}(\tau; h(\cdot))$  the principal eigenvalue of

$$\begin{cases} \phi_{xx} - \alpha \tau (1 - 2b_0) \phi_x + \tau \left[ \alpha^2 b_0 \tau (b_0 - 1) + \left( r - \frac{h(x)}{K} \right) \right] \phi = \tau \Lambda \phi, & 0 < x < l \\ \phi_x(0) = \phi_x(l) + \tau \alpha (b_0 + b_l - 1) \phi(l) = 0, \end{cases}$$

we observe from (2.44) that

$$\tilde{\Lambda}(\xi_j; u_j + v_j) = 0 = \tilde{\Lambda}(\tau_j; u_j + v_j) \quad \text{for } j \geq 1.$$

Now by Rolle's theorem, there exists  $\tau'_j \rightarrow 0$  such that

$$\tilde{\Lambda}_\tau(\tau'_j; u_j + v_j) = 0, \quad (2.45)$$

where  $\tilde{\Lambda}_\tau$  is the partial derivative of  $\tilde{\Lambda}$  with respect to  $\tau$  and  $\tau'_j$  lies between  $\xi_j$  and  $\tau_j$  for  $j \geq 1$ .

**Claim 7.** *By passing to a subsequence,*

$$\tilde{u}_j \rightarrow C_u, \quad \text{and} \quad \tilde{U}_j := \frac{\tilde{u}_j}{\|\tilde{u}_j\|_\infty} \rightarrow 1 \quad \text{uniformly in } [0, l],$$

where  $C_u \geq 0$  is a constant. A similar conclusion holds for  $\tilde{v}_j$  and  $\tilde{V}_j = \frac{\tilde{v}_j}{\|\tilde{v}_j\|_\infty}$ .

First, we observe that  $\|\tilde{u}_j\|_\infty \leq C$ ,  $\|\tilde{v}_j\|_\infty \leq C$ , where  $C = \max\{rK, [r + \alpha^2 b_0 \xi(b_0 - 1)]K\}$ . Indeed,  $\tilde{u}_j$  is a subsolution and  $C$  is a supersolution of the equation

$$u_{xx} - \alpha\xi(1 - 2b_0)u_x + \xi[\alpha^2 b_0 \xi(b_0 - 1) + (r - \frac{e^{\alpha b_0 \xi x}}{K}u)]u = 0, \quad 0 < x < l.$$

That  $\|\tilde{u}_j\|_\infty \leq C$  now follows by applying the maximum principle. By similar reasoning, we conclude that  $\|\tilde{v}_j\|_\infty \leq C$ .

Now, by standard elliptic estimates, we may pass to a subsequence and assume  $\tilde{u}_j$  and  $\tilde{v}_j$  converge weakly in  $W^{2,p}(0, l)$ ,  $p > 1$ , to some limit functions  $\tilde{u}$  and  $\tilde{v}$ , respectively.

Letting  $\xi_j \rightarrow 0$  in (2.44), we obtain

$$\tilde{u}_{xx} = 0 \quad \text{for } 0 < x < l \quad \text{and} \quad \tilde{u}_x(0) = 0 = \tilde{u}_x(l),$$

so that  $\tilde{u} = C_u$  for some constant  $C_u \geq 0$ .

Dividing the equations for  $\tilde{u}_j$  and  $\tilde{v}_j$  by  $\|\tilde{u}_j\|_\infty$  and  $\|\tilde{v}_j\|_\infty$ , respectively, we observe that  $\tilde{U}_j$  and  $\tilde{V}_j$  satisfy

$$\begin{cases} \tilde{U}_{j,xx} - \alpha\xi_j(1 - 2b_0)\tilde{U}_{j,x} + \xi_j \left[ \alpha^2 b_0 \xi_j (b_0 - 1) + (r - \frac{u_j + v_j}{K}) \right] \tilde{U}_j = 0, & 0 < x < l \\ \tilde{V}_{j,xx} - \alpha\tau_j(1 - 2b_0)\tilde{V}_{j,x} + \tau_j \left[ \alpha^2 b_0 \tau_j (b_0 - 1) + (r - \frac{u_j + v_j}{K}) \right] \tilde{V}_j = 0, & 0 < x < l \\ \tilde{U}_{j,x}(0) = \tilde{U}_{j,x}(l) + \xi_j \alpha (b_0 + b_l - 1) \tilde{U}_j(l) = 0 \\ \tilde{V}_{j,x}(0) = \tilde{V}_{j,x}(l) + \tau_j \alpha (b_0 + b_l - 1) \tilde{V}_j(l) = 0. \end{cases} \quad (2.46)$$

By the same reasoning as for  $\tilde{u}_j$ , we observe that  $\tilde{U}_j$  converges to a constant as  $j \rightarrow \infty$ , which must be 1.

Similarly, we conclude that  $\tilde{v}_j \rightarrow C_v$  for some constant  $C_v \geq 0$ , and that  $\tilde{V}_j \rightarrow 1$  uniformly in  $[0, l]$ .

**Claim 8.**  $C_u + C_v = K \left[ r - \frac{\alpha(b_0 + b_l - 1)}{l} \right]$ .

First, we show that  $C_u + C_v > 0$ . Dividing the first equation in (2.46) by  $\tilde{U}_j$  and integrating by parts over  $(0, l)$ , we have

$$\begin{aligned} & \xi_j \left( -\alpha(1 - 2b_0) [\log(\tilde{U}_j)]_{x=0}^l + \int \alpha^2 b_0 \xi_j (b_0 - 1) + \left(r - \frac{u_j + v_j}{K}\right) dx \right) \\ &= - \left[ \frac{\tilde{U}_{j,x}}{\tilde{U}_j} \right]_{x=0}^l - \int \left( \frac{\tilde{U}_{j,x}}{\tilde{U}_j} \right)^2 dx \leq \xi_j \alpha (b_0 + b_l - 1), \end{aligned}$$

where the inequality arises from the boundary conditions of  $\tilde{U}_j$ . Since  $u_j + v_j \rightarrow C_u + C_v$  uniformly and  $\tilde{U}_j \rightarrow 1$  uniformly, we may divide the above inequality by  $\xi_j$  and take the limit as  $j \rightarrow \infty$  to obtain

$$\left( r - \frac{C_u + C_v}{K} \right) l \leq \alpha (b_0 + b_l - 1).$$

Since  $l > \frac{\alpha(b_0 + b_l - 1)}{r}$ , this implies  $C_u + C_v > 0$ .

Now integrating the equations for  $\tilde{u}_j$  and  $\tilde{v}_j$  over  $(0, l)$ , and applying the boundary conditions, we have

$$\begin{aligned} \xi_j \alpha (b_0 - b_l) \tilde{u}_j(l) + \alpha \xi_j (1 - 2b_0) \tilde{u}_j(0) + \xi_j \int \left[ \alpha^2 b_0 \xi_j (b_0 - 1) + \left(r - \frac{u_j + v_j}{K}\right) \right] \tilde{u}_j dx &= 0, \\ \tau_j \alpha (b_0 - b_l) \tilde{v}_j(l) + \alpha \tau_j (1 - 2b_0) \tilde{v}_j(0) + \tau_j \int \left[ \alpha^2 b_0 \tau_j (b_0 - 1) + \left(r - \frac{u_j + v_j}{K}\right) \right] \tilde{v}_j dx &= 0. \end{aligned}$$

Dividing the first and second equations by  $\xi_j$  and  $\tau_j$ , respectively, and passing to the limit, we obtain

$$\alpha(1 - b_0 - b_l)C_u + l\left(r - \frac{C_u + C_v}{K}\right)C_u = \alpha(1 - b_0 - b_l)C_v + l\left(r - \frac{C_u + C_v}{K}\right)C_v = 0.$$

Adding these equations yields

$$(C_u + C_v) \left[ \alpha(1 - b_0 - b_l) + l\left(r - \frac{C_u + C_v}{K}\right) \right] = 0.$$

Since  $C_u + C_v > 0$ , this implies  $C_u + C_v = K \left[ r - \frac{\alpha(b_0 + b_l - 1)}{l} \right]$ .

Now by the continuous dependence of  $\tilde{\Lambda}(\tau, h)$  on  $\tau$  and  $h$ , letting  $j \rightarrow \infty$  in (2.45) gives

$$\Lambda_\tau(0, 0) = \tilde{\Lambda}_\tau \left( 0, K \left[ r - \frac{\alpha(b_0 + b_l - 1)}{l} \right] \right) = 0,$$

where the smooth extension of  $\eta_\xi$  up to  $\xi = 0$  is given by the constant  $K \left[ r - \frac{\alpha(b_0 + b_l - 1)}{l} \right]$  (see Remark 5.1 in [45]). But this contradicts our assumption  $\Lambda_\tau(0, 0) \neq 0$ . Thus, if  $\Lambda_\tau(0, 0) \neq 0$ , then (2.42) has no positive equilibria for  $\mu, \nu$  sufficiently large.

To prove part (a), we observe that there exists  $\delta_1 > 0$  such that for  $(\xi, \tau) \in [0, \delta_1]^2$ , (2.42) has no positive equilibrium and  $\Lambda_\tau(\xi, \tau) < 0$ , i.e.

$$\Lambda_\nu(\mu, \nu) > 0 \quad \text{for all } \mu, \nu \geq \frac{1}{\delta_1}.$$

Since  $\Lambda(\mu, \mu) = 0$  for  $\mu > 0$ , this implies

$$\Lambda(\nu, \mu) > 0 > \Lambda(\mu, \nu) \quad \text{for } \mu > \nu \geq \frac{1}{\delta_1}.$$

So  $(\theta_\mu, 0)$  is linearly stable and  $(0, \theta_\nu)$  is linearly unstable. Since (2.42) has no positive equilibria, we conclude by Theorem B of [49] and Theorem 1.3 of [59] that  $(\theta_\mu, 0)$  is globally asymptotically stable among all nonnegative, nontrivial solutions of (2.42). The proof of part (b) follows similar reasoning, and we omit the details.  $\square$

**Theorem 6.** *Assume  $b_0 + b_l > 1$ , and recall the definition of  $G(b_0, b_l)$  in (2.9).*

(a) *If  $G(b_0, b_l) > 0$  and  $l > \frac{\alpha(b_0 + b_l - 1)}{r}$ , there exists  $d > 0$  such that for  $\mu > \nu \geq d$ , the steady state  $(\theta_\mu, 0)$  is globally asymptotically stable.*

(b) *If  $G(b_0, b_l) < 0$  and  $l > \frac{\alpha(b_0 + b_l - 1)}{r}$ , there exists  $d > 0$  such that for  $\mu > \nu \geq d$ , the steady state  $(0, \theta_\nu)$  is globally asymptotically stable.*

*Proof.* Let  $l > \frac{\alpha(b_0+b_l-1)}{r}$ . Theorem 2 implies that there exists  $\underline{\mu} > 0$  such that (2.43) has a positive solution  $\theta_\mu$  for all  $\mu > \underline{\mu}$ . Thus,  $\Lambda$  is well-defined for all  $(\xi, \tau) \in [0, 1/\underline{\mu}]^2$ . If  $G(b_0, b_l) > 0$ , then by Lemma 6, we have  $\Lambda_\tau(0, 0) = -\alpha^2[\frac{1}{4} + (b_0 - \frac{1}{2})(b_l - \frac{1}{2}) - \frac{(b_0+b_l-1)^2}{3}] < 0$ . Now by Lemma 2(a), there exists  $\underline{\mu}' > \underline{\mu}$  such that for  $\mu > \nu \geq \underline{\mu}'$ ,  $(\theta_\mu, 0)$  is globally asymptotically stable among all nonnegative, nontrivial solutions of (2.42). This proves assertion (a).

If  $G(b_0, b_l) < 0$ , then Lemma 6 implies  $\Lambda_\tau(0, 0) = -\alpha^2[\frac{1}{4} + (b_0 - \frac{1}{2})(b_l - \frac{1}{2}) - \frac{(b_0+b_l-1)^2}{3}] > 0$ . By Lemma 2(b), there exists  $\underline{\mu}' > \underline{\mu}$  such that for  $\mu > \nu \geq \underline{\mu}'$ ,  $(0, \theta_\nu)$  is globally asymptotically stable among all nonnegative, nontrivial solutions of (2.42). This proves assertion (b).  $\square$

## 2.4 Appendix

### 2.4.1 Computations for Prop. 3(b)

**Lemma 3.** *Let  $g(s) = s \cot s$ , and  $C \geq 0.941$ . Then*

$$g''(s) - \frac{g'(s)}{s}[1 + Cg'(s)^2] > 0 \quad (2.47)$$

for  $0 < s < \pi$ .

*Proof.* Our proof is similar to that of Lemma A.12 of [45]. There, the claim is shown for  $C \geq 1$ , so we may fix  $0.941 \leq C < 1$ . Observe  $g'(s) = \cot s - s \csc^2(s)$  and  $g''(s) = 2 \csc^2(s)(g(s) - 1)$ . We compute

$$\begin{aligned} 1 + Cg'(s)^2 &= 1 + C(\cot^2(s) - 2s \cot(s) \csc^2(s) + s^2 \csc^4(s)) \\ &= (1 - C) + C(1 + \cot^2(s) - 2s \cot(s) \csc^2(s) + s^2 \csc^4(s)) \\ &= (1 - C) + C \csc^2(s)((g - 1)^2 + s^2). \end{aligned}$$

By the above expression, and since  $\frac{-g'(s)}{s} \geq \frac{2}{3}$  for  $s \in (0, \pi)$  (see [45] Lemma A.12), we observe

$$\begin{aligned} g'' - \frac{g'}{s}(1 + Cg'^2) &= 2 \csc^2(s)(g - 1) - \frac{g'}{s} \left[ (1 - C) + C \csc^2(s)((g - 1)^2 + s^2) \right] \\ &\geq \frac{2}{3} \csc^2(s) \left[ 3(g - 1) + (1 - C) \sin^2(s) + C((g - 1)^2 + s^2) \right]. \end{aligned} \quad (2.48)$$

Furthermore, we have

$$\begin{aligned} C(g - 1)^2 + 3(g - 1) + Cs^2 + (1 - C) \sin^2(s) &\geq C \left[ (g - 1)^2 + \frac{3}{C}(g - 1) + s^2 \right] \\ &\geq C \left( s^2 - \frac{9}{4C^2} \right), \end{aligned} \quad (2.49)$$

where the second inequality is deduced by completing the square. Combining (2.48) and (2.49), we find that (2.47) holds for  $s \in (\frac{3}{2C}, \pi)$ .

It remains to consider  $s \in (0, \frac{3}{2C}]$ . For  $C \geq 0.941$ , we have  $\frac{3}{2C} < \sqrt{6}$ . Thus, we have

$$\frac{-s^2/3 + s^4/30 - s^6/720}{1 - s^2/6 + s^4/120} < g(s) - 1 < \frac{s(1 - s^2/2 + s^4/24)}{s - s^3/6} - 1 \leq -s^2/3$$

and

$$\sin^2(s) > \left( s - \frac{s^3}{6} \right)^2$$

for  $s \in (0, \frac{3}{2C}]$ . It follows that

$$\begin{aligned} C(g - 1)^2 + 3(g - 1) + Cs^2 + (1 - C) \sin^2(s) &\geq C \frac{s^4}{9} + \frac{-s^2 + s^4/10 - s^6/240}{1 - s^2/6 + s^4/120} \\ &\quad + Cs^2 + (1 - C) \left( s - \frac{s^3}{6} \right)^2 \\ &= \frac{s^4}{1 - \frac{s^2}{6} + \frac{s^4}{120}} \left( \frac{4C}{9} - \frac{2}{5} \right. \\ &\quad \left. + \frac{189 - 220C}{2160} s^2 + \frac{9C - 8}{1080} s^4 \right. \\ &\quad \left. + \frac{1 - C}{4320} s^6 \right) \end{aligned} \quad (2.50)$$



for  $s \in (0, \frac{3}{2C}]$ . We observe that the right hand side of (2.50) is positive if

$$\frac{4C}{9} - \frac{2}{5} + \frac{189 - 220C}{2160}s^2 + \frac{9C - 8}{1080}s^4 + \frac{1 - C}{4320}s^6 > 0, \quad (2.51)$$

and (2.51) holds for  $s \in (0, \frac{3}{2C}]$  if

$$C > \frac{2/5 - 7s^2/80 + s^4/135 - s^6/4320}{4/9 - 11s^2/108 + s^4/120 - s^6/4320} =: f(s). \quad (2.52)$$

Denote  $h(C) := \frac{3}{2C}$ . To complete the proof, we must show that  $C > f(s)$  for all  $0 < s \leq \frac{3}{2C} = h(C)$ . First, we compute

$$f'(s) = \frac{-8s(s^8 - 31s^6 + 262s^4 + 384s^2 - 8640)}{(-s^6 + 36s^4 - 440s^2 + 1920)^2} > 0 \text{ for } 0 < s < \sqrt{6}$$

and

$$h'(C) = -\frac{3}{2C^2} < 0.$$

Thus,  $f(s)$  is increasing for  $0 < s < \sqrt{6}$  and  $h(C)$  is decreasing. Moreover,  $f(s^*) = h^{-1}(s^*) = \frac{3}{2s^*}$  for  $s^* \approx 1.59438 \in (0, \sqrt{6})$ . It follows that if  $C \geq 0.941 > f(s^*) \approx 0.9408$ , then  $h(C) < h(f(s^*)) = h(h^{-1}(s^*)) = s^*$ . In turn, we have  $C > f(s^*) > f(h(C)) \geq f(s)$  for  $0 < s < \frac{3}{2C} = h(C)$ , as desired, since  $f$  is increasing. Now by (2.48) and (2.50)-(2.52), we conclude that (2.47) also holds for  $s \in (0, \frac{3}{2C}]$ , which concludes the proof.  $\square$

**Lemma 4.** *Suppose  $\min\{b_0, b_l\} < \frac{1}{2}$ . If  $\frac{\partial l^*}{\partial \mu} = 0$  for  $\mu = \frac{\alpha^2}{4r}$ , then*

$$(b_0 + b_l - 1)^2 = 12(b_0 - \frac{1}{2})(b_l - \frac{1}{2})\left[\frac{1}{4} + (b_0 - \frac{1}{2})(b_l - \frac{1}{2})\right].$$

*Proof.* Let  $\tau = \frac{1}{\mu}$ , set  $L(\tau) := l^*(\mu)$  and  $M(\tau) := \sqrt{r\tau - \frac{\alpha^2\tau^2}{4}}$ , and let ' denote differentiation with respect to  $\tau$ . Then  $\frac{\partial l^*}{\partial \mu} = 0$  for  $\mu = \frac{\alpha^2}{4r}$  if and only if  $L'(\frac{4r}{\alpha^2}) = 0$ .

We recall from (2.41) that  $L'(\tau)$  satisfies

$$\begin{aligned} L' \left[ \frac{r - \tau \frac{\alpha^2}{4} - \tau \alpha^2 (b_0 - \frac{1}{2})(b_l - \frac{1}{2})}{\alpha(b_0 + b_l - 1)} \right] - \alpha L \left[ \frac{\frac{1}{4} + (b_0 - \frac{1}{2})(b_l - \frac{1}{2})}{b_0 + b_l - 1} \right] \\ = \frac{g'(ML)}{ML} \left[ M^2 L L' + \frac{L^2}{2} \left( r - \frac{\alpha^2 \tau}{2} \right) \right] \end{aligned}$$

for  $0 < \tau < \frac{4r}{\alpha^2}$ , where  $g(s) = s \cot s$ . Since  $L'(\frac{4r}{\alpha^2}) = 0$ ,  $L(\frac{4r}{\alpha^2}) = -\frac{\alpha(b_0 + b_l - 1)}{4r(b_0 - \frac{1}{2})(b_l - \frac{1}{2})}$  (by (2.27)), and  $\frac{g'(s)}{s} = -\frac{2}{3} + o(s)$ , sending  $\tau \rightarrow \frac{4r}{\alpha^2}^-$  yields

$$\alpha^2 \left[ \frac{\frac{1}{4} + (b_0 - \frac{1}{2})(b_l - \frac{1}{2})}{4r(b_0 - \frac{1}{2})(b_l - \frac{1}{2})} \right] = \frac{r}{3} \left[ \frac{\alpha(b_0 + b_l - 1)}{4r(b_0 - \frac{1}{2})(b_l - \frac{1}{2})} \right]^2.$$

Multiplying both sides of the above equality by  $\frac{r}{\alpha^2}$  and rearranging, we obtain the desired result.  $\square$

## 2.4.2 Computation of $\Lambda_\tau(0, 0)$

The proofs in this section follow analogous results in [45].

**Lemma 5.** *For each  $0 \leq \tau < \frac{4r}{\alpha^2}$ , the eigenvalue  $\Lambda(0, \tau)$  satisfies*

$$\begin{aligned} 1 - \frac{l}{\alpha(b_0 + b_l - 1)} \left[ \Lambda + \frac{\alpha^2 \tau}{4} + \alpha^2 \tau (b_0 - \frac{1}{2})(b_l - \frac{1}{2}) \right] \\ = g \left( l \sqrt{\left( \frac{\alpha(b_0 + b_l - 1)}{l} - \Lambda \right) \tau - \frac{\alpha^2 \tau^2}{4}} \right), \end{aligned} \quad (2.53)$$

where  $g(s) = s \cot(s)$ .

*Proof.* We recall from Proposition 3(a) that, for  $\nu > \frac{\alpha^2}{4r}$ , the critical domain size  $l^* = l^*(\nu, b_0, b_l) > 0$  for which there exists a positive solution to the equation

$$\begin{cases} \nu \psi_{xx} - \alpha(1 - 2b_0)\psi_x + \left( \frac{\alpha^2 b_0}{\nu} (b_0 - 1) + r \right) \psi = 0 & \text{for } x \in (0, l^*), \\ \psi_x(0) = 0 \\ \nu \psi_x(l^*) + \alpha(b_0 + b_l - 1)\psi(l^*) = 0 \end{cases}$$

satisfies

$$\tan \left( \frac{\sqrt{4\nu r - \alpha^2}}{2\nu} l^* \right) = \frac{2\alpha(b_0 + b_l - 1)\sqrt{4\nu r - \alpha^2}}{4\nu r - \alpha^2 - 4\alpha^2(b_0 - \frac{1}{2})(b_l - \frac{1}{2})}. \quad (2.54)$$

Now for  $\Lambda = \Lambda(0, \tau)$ , there exists a positive solution to the equation

$$\begin{cases} \nu\psi_{xx} - \alpha(1 - 2b_0)\psi_x + \left(\frac{\alpha^2 b_0}{\nu}(b_0 - 1) + r(1 - \frac{\eta_0}{K}) - \Lambda\right)\psi = 0 & \text{for } x \in (0, l), \\ \psi_x(0) = 0 \\ \nu\psi_x(l) + \alpha(b_0 + b_l - 1)\psi(l) = 0, \end{cases}$$

if and only if  $l^* = l$  satisfies (2.54) with  $r(1 - \frac{\eta_0}{K}) - \Lambda$  replacing  $r$ , where  $\eta_0 = K(1 - \frac{\alpha(b_0 + b_l - 1)}{rl})$ . Setting  $l^* = l$ ,  $\tau = \frac{1}{\nu}$ , and  $r = r(1 - \frac{\eta_0}{K}) - \Lambda = \frac{\alpha(b_0 + b_l - 1)}{l} - \Lambda$  in (2.54), we arrive at the desired result.  $\square$

**Lemma 6.** *Let  $b_0 + b_l > 1$  and  $l > \frac{\alpha(b_0 + b_l - 1)}{r}$ . Then  $\Lambda_\tau(0, 0) = -\alpha^2[\frac{1}{4} + (b_0 - \frac{1}{2})(b_l - \frac{1}{2}) - \frac{(b_0 + b_l - 1)^2}{3}]$ .*

*Proof.* Using the expansion  $s \cot(s) = 1 - \frac{s^2}{3} - \frac{s^4}{45} + \dots$ , we can express (2.53) as

$$\begin{aligned} 1 - \frac{l}{\alpha(b_0 + b_l - 1)} \left[ \Lambda + \frac{\alpha^2 \tau}{4} + \alpha^2 \tau (b_0 - \frac{1}{2})(b_l - \frac{1}{2}) \right] \\ = 1 - \frac{l^2}{3} \left[ \left( \frac{\alpha(b_0 + b_l - 1)}{l} - \Lambda \right) \tau - \frac{\alpha^2 \tau^2}{4} \right] \\ - \frac{l^4}{45} \left[ \left( \frac{\alpha(b_0 + b_l - 1)}{l} - \Lambda \right) \tau - \frac{\alpha^2 \tau^2}{4} \right]^2 + O(|\tau|^3), \end{aligned} \quad (2.55)$$

where  $\Lambda = \Lambda(0, \tau)$ . Differentiating (2.55) in  $\tau$ , and setting  $\tau = 0$ , we have

$$-\frac{l}{\alpha(b_0 + b_l - 1)} \left[ \Lambda_\tau(0, 0) + \frac{\alpha^2}{4} + \alpha^2 (b_0 - \frac{1}{2})(b_l - \frac{1}{2}) \right] = -\frac{l\alpha(b_0 + b_l - 1)}{3},$$

so that

$$\Lambda_\tau(0, 0) = -\alpha^2 \left[ \frac{1}{4} + (b_0 - \frac{1}{2})(b_l - \frac{1}{2}) - \frac{(b_0 + b_l - 1)^2}{3} \right].$$

$\square$

## Chapter 3: Predator-prey Dynamics in a Shifting Environment

### 3.1 Introduction

A fundamental challenge in ecology is to understand the persistence and spread of a given species in an environment. These issues are receiving a renewed interest as changes in climatic conditions can dramatically impact the suitability of a habitat for a species' survival and growth. As temperatures rise, many species have moved in the directions of the poles or toward higher elevations, in an apparent attempt to keep pace with shifting temperature isotherms [80, 63]. As species establish in new regions, new biotic interactions take place [41], which in turn can have significant consequences for species abundance and biodiversity [94, 69, 88], the functioning of ecosystems [88, 93, 100], the spread of disease [81, 103] and human welfare [81]. The ecological effects of a changing climate are complex and various. While many species are vulnerable to a changing climate, for many others climate-related changes may facilitate expansion to new areas and population growth [95, 5, 13, 47].

Mathematical modeling can be used to determine why certain species decline while others prosper under the changing climate. The study of species persistence and spread often depend on the spatial context, and much analysis in the classical

literature has been based on reaction-diffusion models. A prominent example is the Fisher-KPP equation [36, 54], which describes the spreading of a single population

$$u_t = du_{xx} + ru(1 - u) \quad \text{for } x \in \mathbb{R}, t > 0, \quad (3.1)$$

where  $d$  corresponds to the dispersal rate and  $r$  the intrinsic growth rate of a species  $u$ . For a given population density  $u(t, x)$ , Aronson and Weinberger [3, 4] introduced the key notion of spreading speed, which refers to the number  $c^* > 0$  such that

$$\begin{aligned} \lim_{t \rightarrow \infty} \sup_{|x| > ct} u(t, x) &= 0 \quad \text{for } c \in (c^*, \infty), \quad \text{and} \\ \lim_{t \rightarrow \infty} \inf_{|x| > ct} u(t, x) &> 0 \quad \text{for } c \in (0, c^*). \end{aligned}$$

The problem of spreading speed for more general equations of the form

$$u_t = du_{xx} + f(u) \quad \text{for } x \in \mathbb{R}, t > 0, \quad (3.2)$$

was first investigated by Kolmogorov et al. [54] for heaviside initial condition, who showed under certain assumptions on the growth function  $f(u)$  that

$$c^* = 2\sqrt{df'(0)}.$$

This result was later generalized to any compactly supported initial data and in higher spatial dimensions by Aronson and Weinberger [4]. This theoretical spreading speed has yielded good estimates for range expansion observed in nature [85].

Various studies have since revisited Fisher's model with an interest in the impact of a shifting environment. To consider climate change, it is often assumed that the behavior of the species depends on the variable  $\xi = x - ct$ , where the constant  $c$  corresponds to the velocity of a shifting climate [82, 10, 66, 11]. See also [35], which studied a similar model in the context of an SIS model, and [97], for a survey on

reaction-diffusion models in shifting environments. Many models have proposed the case where the growth rate  $ru(1 - u)$  in (3.1) is replaced by a shifting logistic form  $u(r(x - ct) - u)$ , where  $r(x - ct)$  denotes the species' intrinsic growth rate [82, 10]. These works assumed the growth rate  $r(\xi)$  to be positive on a bounded patch of suitable habitat and negative elsewhere, and were broadly interested in the effects of a shifting climate on the persistence of the species.

A shifting environment also leads to new spreading phenomena. In [60], the spreading speed for solutions of Fisher's equation with growth rate  $f(u, x - ct) = (r(x - ct) - u)u$  was determined using the Hamilton-Jacobi method, in the case that the intrinsic growth rate of the species is positive and monotone. They showed that, for a certain range of velocities of climate shift, the species spreads with speed distinct from either of the limiting KPP invasion speeds in a phenomenon called non-local pulling [48, 42]. When the growth rate is non-monotone, the existence of forced waves and their attractivity is studied in [11].

In addition to single species equations, the spreading dynamics for systems of equations has received considerable attention. Building on the earlier works on order-preserving systems (such as cooperative systems and competitive systems of two species) [65, 99, 67, 68], the spreading of two competing species in a shifting habitat is studied in [106, 26].

By contrast, for predator-prey systems a comparison principle is not immediately available and many studies regarding propagation phenomena in these systems have focused on the dynamics of traveling wave solutions. The existence of traveling wave

solutions for two-species predator-prey equations was established in [32, 40], and studied further in [50, 77], while some results on the stability of traveling wave solutions were established in [39].

Until recently, few works have treated the spreading dynamics of predator-prey systems with general initial data. In [79], Pan determined the spreading speed of the predator for a predator-prey system with initially constant prey density and compactly-supported predator. Shortly thereafter, Ducrot, Giletti, and Matano [30] used methods from uniform persistence theory to characterize the spreading dynamics when both predator and prey are initially compactly supported. They showed that the behavior can be classified based on the speeds of the prey in the absence of predator, and of the predator when prey is abundant (see also [31], for the case of a predator-prey equation with non-local dispersal, and [27, 78]). Since these works, the spreading speeds regarding the Cauchy problem for predator-prey systems with three species was studied in [29] (see also [101]). There, it was shown that the nonlocal pulling phenomenon can occur in a system with two predators and one prey.

For other types of non-cooperative systems and their spreading speeds, we refer to [96], which characterizes the spreading speed for a general class of non-cooperative reaction diffusion systems as the minimal traveling wave speed. We also note [28], which determined the spreading speed of infectious disease in an epidemic model, and [71], which considered the spreading dynamics for competition between three species. Spreading dynamics are also studied for nonlocal diffusion problems, here we mention [105, 102] for such results in predator-prey models in the absence of shifting environment.

### 3.1.1 The predator-prey model in a shifting environment

We are interested in the effect of the heterogeneous shifting profile of the conversion efficiency of prey to predator, represented below by the function  $\tilde{a}(x - c_1t)$ , on the spreading dynamics. Though the temperature-dependence of the conversion efficiency is not well-understood, there is some evidence that the conversion efficiency is impacted by climate. Using an experimental system of predator and prey, Daugaard et al. [22] found that the conversion efficiency of the predator increased with warming, and in a recent meta-analysis Lang et. al [61] identified a trend toward increasing efficiency of energy assimilation by consumers with increasing temperature. On the other hand, many biological processes depend unimodally on temperature, such that measures of species performance and fitness decline once temperature increases sufficiently beyond a “thermal optimum” [51, 23, 15]. It is thus plausible that predators currently experiencing climates at or near their thermal optimum may experience declines in conversion efficiency with additional warming.

To this end, we propose the following predator-prey model of reaction-diffusion type to analyze the consequence of such effects on the population dynamics and spread of species:

$$\begin{cases} \tilde{u}_t = d_1 \tilde{u}_{xx} + \tilde{u}(-\kappa - \alpha_1 \tilde{u} + \tilde{a}(x - c_1t)\tilde{v}) & \text{in } (0, \infty) \times \mathbb{R}, \\ \tilde{v}_t = d_2 \tilde{v}_{xx} + \tilde{v}(\tilde{r} - \alpha_2 \tilde{v} - \tilde{b}\tilde{u}) & \text{in } (0, \infty) \times \mathbb{R}, \\ \tilde{u}(0, x) = \tilde{u}_0(x), \quad \tilde{v}(0, x) = \tilde{v}_0(x) & \text{in } \mathbb{R}. \end{cases} \quad (3.3)$$

Here the predator and prey densities are represented by  $\tilde{u}(t, x)$  and  $\tilde{v}(t, x)$ . It is assumed that the predator cannot persist in the absence of prey, and competes with other predators, while in the absence of predation the prey exhibits logistic growth and is described by the standard Fisher-KPP equation. The interaction rates between predator and prey are mediated by the consumption rate  $\tilde{b} > 0$  of prey by predator,



and by the predator's conversion efficiency function  $\tilde{a}(x - c_1 t)$ , which describes the degree to which consumed prey can be successfully converted to additional predators. For simplicity, we assume that conversion efficiency has a fixed profile in the moving coordinate  $y = x - c_1 t$  with constant velocity  $c_1$ . Finally,  $\tilde{d}_i, \tilde{\alpha}_i, \kappa, \tilde{r}$  are positive parameters, where  $\tilde{d}_i$  are the random dispersal rates,  $\alpha_i$  are the intraspecific competition rates,  $\kappa$  is the natural death rate of the predator species and  $\tilde{r}$  is the natural birth rate of the prey species.

Without loss of generality, we may non-dimensionalize the problem (3.3) and obtain the following model:

$$\begin{cases} u_t = u_{xx} + (-1 - u + a(x - c_1 t)v)u & \text{in } (0, \infty) \times \mathbb{R} \\ v_t = dv_{xx} + r(1 - v - bu)v & \text{in } (0, \infty) \times \mathbb{R} \\ u(0, x) = u_0(x), \quad v(0, x) = v_0(x) & \text{in } \mathbb{R}. \end{cases} \quad (3.4)$$

We assume the following throughout our study of (3.4).

**(H1)** The function  $a : \mathbb{R} \rightarrow \mathbb{R}$  is monotone, and satisfies

$$\beta := 1 - b(\|a\|_\infty - 1) > 0, \quad \inf_{s \in \mathbb{R}} a(s) > \frac{1}{\beta}, \quad \text{and} \quad \|a\|_\infty > 1.$$

By observing (via maximum principle) that the density of the predator is bounded from above by  $\|a\|_\infty - 1$ , it follows that the quantity  $\beta := 1 - b(\|a\|_\infty - 1)$  corresponds to the minimum carrying capacity for the prey.

**Remark.** *It is documented in a microbial predator-prey system [22] that the quantity of predators produced for each prey consumed increases when temperature is increased. This corresponds to the case when  $c_1 > 0$  and  $a(\cdot)$  is decreasing. We also study the case when increasing temperature decreases the predator efficiency, i.e.  $a(\cdot)$  is increasing.*

We are interested in the situation when the initial data of the predator is compactly supported, while that of the prey has a positive upper and lower bound. For simplicity, we will assume throughout the discussion that  $(u_0, v_0) \in C^2(\mathbb{R})$  satisfies

**(IC)**  $0 \leq u_0 \leq \|a\|_\infty - 1$ ,  $\beta \leq v_0 \leq 1$ , and  $u_0$  has compact support.

Finally, we define the following limiting growth rates (at  $\pm\infty$ ), to be used later in the proofs.

$$\begin{cases} r_1 = a(-\infty) - 1, & r_2 = a(+\infty) - 1, \\ \underline{r}_1 = \beta a(-\infty) - 1, & \underline{r}_2 = \beta a(+\infty) - 1. \end{cases} \quad (3.5)$$

Here,  $\underline{r}_1$  and  $\underline{r}_2$  correspond to the limiting growth rates of the predator behind and ahead of the environmental shift, respectively, when the prey density is at its minimum value  $v = \beta$ , while  $r_1$  and  $r_2$  are the limiting growth rates of the predator behind and ahead of the shift, respectively, when the prey density is at its maximum value  $v = 1$ .

### 3.1.2 Main Results

In this paper, we are interested in the asymptotic speed of spread (or spreading speed) as the predator species  $u$  expands its territory. Up to a change of coordinates  $x \mapsto -x$ , it is enough to focus our discussion on the rightward spreading speed, while allowing the spatial heterogeneity  $a(\cdot)$  to be monotonically increasing or decreasing.

In the remainder of this paper, we will refer to the rightward spreading speed  $c^*$  simply as the spreading speed, which is defined as follows.

**Definition.** *Let  $u$  be the solution of (3.4), where  $u_0$  and  $v_0$  satisfy (IC). We say that the species  $u$  has spreading speed given by  $c^* > 0$  if*

$$\limsup_{t \rightarrow \infty} \sup_{x > ct} u(t, x) = 0 \quad \text{for each } c \in (c^*, \infty), \quad (3.6)$$

$$\liminf_{t \rightarrow \infty} \inf_{0 < x < ct} u(t, x) > 0 \quad \text{for each } c \in (0, c^*). \quad (3.7)$$

Following [44, Definition 1.2], we introduce the closely related notion of maximal and minimal speed  $\bar{c}_*$ ,  $\underline{c}_*$ :

**Definition.** Let  $u$  be the solution of (3.4), where  $u_0$  and  $v_0$  satisfy (IC).

$$\begin{cases} \bar{c}_* & := \inf \left\{ c > 0 \mid \limsup_{t \rightarrow \infty} \sup_{x > ct} u(t, x) = 0 \right\}, \\ \underline{c}_* & := \sup \left\{ c > 0 \mid \liminf_{t \rightarrow \infty} \inf_{0 \leq x < ct} u(t, x) > 0 \right\}. \end{cases} \quad (3.8)$$

**Remark.** The species  $u$  has a spreading speed if and only if  $\bar{c}_* = \underline{c}_*$ . In such a case, the spreading speed  $c^*$  is given by the common value  $\bar{c}_* = \underline{c}_*$ .

The following two main theorems characterize the spreading speed of  $u$  for the cases (i)  $a(\cdot)$  is monotonically increasing and (ii)  $a(\cdot)$  is monotonically decreasing, respectively. Assuming the positive axis points poleward and temperature is rising, they correspond to the cases when the conversion efficiency of the predator is suppressed or enhanced by the warming climate.

**Theorem 7.** Let  $c_1 > 0$  be given,  $a : \mathbb{R} \rightarrow \mathbb{R}$  be increasing, and suppose **(H1)** holds. If  $(u(t, x), v(t, x))$  is the solution of (3.4) with initial data satisfying **(IC)**, then the spreading speed of  $u$  exists, and is given by

$$c^* := \begin{cases} 2\sqrt{r_2} & \text{if } c_1 \leq 2\sqrt{r_2} \\ \frac{c_1}{2} - \sqrt{r_2 - r_1} + \frac{r_1}{\frac{c_1}{2} - \sqrt{r_2 - r_1}} & \text{if } 2\sqrt{r_2} < c_1 < 2\sqrt{r_1} + 2\sqrt{r_2 - r_1} \\ 2\sqrt{r_1} & \text{if } c_1 \geq 2\sqrt{r_1} + 2\sqrt{r_2 - r_1}. \end{cases} \quad (3.9)$$

**Theorem 8.** Let  $a : \mathbb{R} \rightarrow \mathbb{R}$  be decreasing such that **(H1)** holds, and let  $c_1 \in \mathbb{R} \setminus (2\sqrt{r_2}, 2\sqrt{r_1})$  be given. If  $(u(t, x), v(t, x))$  is the solution of (3.4) with initial data satisfying **(IC)**, then the spreading speed of  $u$  exists, and is given by

$$c^* = \begin{cases} 2\sqrt{r_2} & \text{if } c_1 \leq 2\sqrt{r_2}, \\ 2\sqrt{r_1} & \text{if } c_1 \geq 2\sqrt{r_1}. \end{cases}$$

**Remark.** Note that the case  $c_1 \in (2\sqrt{r_2}, 2\sqrt{r_1})$  is not covered by Theorem 8. In that case the Hamilton-Jacobi approach does not apply. We conjecture that  $c^* = c_1$  in that case and the predator advances in locked step with the environment. See [11, 35] for results regarding a single species in a shifting habitat. A possible approach is to use the persistence theory as in [29].

**Remark.** In the case of  $a(\cdot) \equiv a_0$  being a constant and  $v_0 \equiv 1$ , the spreading speed of the predator was determined by Pan in [79, Theorem 2.1].

For the proof of Theorems 7 and 8, see Subsection 3.5.2

We also show the convergence of  $(u, v)$  to the homogeneous state in the moving frames with speed different from  $c_1$  and  $c^*$ . Let us first define, for  $i = 1, 2$ ,

$$u_i = \frac{a_i - 1}{1 + a_i b}, \quad v_i = \frac{1 + b}{1 + a_i b} \quad (3.10)$$

where  $a_1 := a(-\infty)$  and  $a_2 := a(+\infty)$ .

**Theorem 9.** Let  $(u, v)$  be the solution of (3.4), where  $(u_0, v_0) \in C^2(\mathbb{R})$  satisfies (IC).

(a) For any  $\eta > 0$ ,

$$\lim_{t \rightarrow \infty} \sup_{|x| \geq (c^* + \eta)t} \|(u, v) - (0, 1)\| = 0. \quad (3.11)$$

where  $\|\cdot\|$  denotes the Euclidean norm in  $\mathbb{R}^2$ .

(b) Suppose  $c_1 \geq c^*$ . For any  $\eta \in (0, c^*/2)$ ,

$$\lim_{t \rightarrow \infty} \sup_{|x| < (c^* - \eta)t} \|(u, v) - (u_1, v_1)\| = 0, \quad (3.12)$$

where  $(u_1, v_1)$  is defined in (3.10).

(c) Suppose  $c_1 < c^*$ . For any  $\eta \in (0, c_1/2)$ ,

$$\lim_{t \rightarrow \infty} \sup_{|x| < (c_1 - \eta)t} \|(u, v) - (u_1, v_1)\| = 0, \quad (3.13)$$

and for any  $\eta \in (0, (c^* - c_1)/2)$ ,

$$\lim_{t \rightarrow \infty} \sup_{(c_1 + \eta)t < x < (c^* - \eta)t} \|(u, v) - (u_2, v_2)\| = 0, \quad (3.14)$$

where  $(u_i, v_i)$  is defined in (3.10).

For the proof of Theorem 9, see Section 3.6.

To consolidate the formulas for the spreading speeds in Theorems 7 and 8, we will denote  $\lambda^* = \frac{c_1}{2} - \sqrt{|r_2 - r_1|}$ . Then the spreading speed for all cases can be given by

$$\sigma(c_1; r_1, r_2) = \begin{cases} 2\sqrt{r_2} & \text{if } r_1 < r_2 \text{ and } c_1 \leq 2\sqrt{r_2} \\ \lambda^* + \frac{r_1}{\lambda^*} & \text{if } r_1 < r_2 \text{ and } 2\sqrt{r_2} < c_1 < 2\sqrt{r_1} + 2\sqrt{r_2 - r_1} \\ 2\sqrt{r_1} & \text{if } r_1 < r_2 \text{ and } c_1 \geq 2\sqrt{r_1} + 2\sqrt{r_2 - r_1}, \\ 2\sqrt{r_2} & \text{if } r_1 > r_2 \text{ and } c_1 \leq 2\sqrt{r_2} \\ 2\sqrt{r_1} & \text{if } r_1 > r_2 \text{ and } c_1 \geq 2\sqrt{r_1}, \end{cases} \quad (3.15)$$

or, equivalently,

$$\sigma(c_1; r_1, r_2) = \begin{cases} 2\sqrt{r_2} & \text{if } c_1 \leq 2\sqrt{r_2} \\ \lambda^* + \frac{r_1}{\lambda^*} & \text{if } r_1 < r_2 \text{ and } 2\sqrt{r_2} < c_1 < 2\sqrt{r_1} + 2\sqrt{r_2 - r_1} \\ 2\sqrt{r_1} & \text{if } c_1 \geq 2\sqrt{r_1} + 2\sqrt{\max\{0, r_2 - r_1\}}, \end{cases} \quad (3.16)$$

### 3.1.3 Related mathematical results

We also mention a closely related work of Choi, Giletti, and Guo [21], where they considered a two-species predator-prey system similar to (3.4), with the intrinsic growth rate  $r = r(x - c_1 t)$  for the prey subject to the climate shift instead of the coefficient  $a$ . They considered the case when both initial data  $u_0$  and  $v_0$  are compactly supported and a non-decreasing profile for the growth rate with  $r$  changing sign,  $r(-\infty) < 0 < r(\infty)$ . In the case of local dispersal, they showed that the prey persists

by spreading if and only if the maximal speed of the prey exceeds the environmental speed (i.e.,  $2\sqrt{dr(+\infty)} > c_1$ ), while the predator persists by spreading at the speed given by the smaller of the prey and maximal predator spreading speeds. In their setting both species tends to zero in  $\{(t, x) : x < c_1 t\}$ , while in the zone ahead of the environmental shift, the density of the prey is strictly decreasing so there is no nonlocal pulling phenomenon. We also mention [43] for the case of two weak-competing predators and one prey, and [1], for the case of one predator and two preys. For compactly supported initial data, the invasion wave of the prey resembles the effect of a shifting environment studied in our paper. However, the exact spreading speed of the predator(s) is not completely determined.

Finally, we mention the work of Bramson [14], which established using probabilistic techniques a correction term of  $\frac{3}{2} \log t$  which separates the the location of the spreading front for solutions to the Fisher-KPP equation (3.1) and the asymptotic location of the minimal traveling wave solution. This result was later generalized using maximum principle arguments by Lau to KPP-like nonlinearities  $f(s)$  satisfying  $f'(s) \leq f'(0)$  on  $[0, 1]$  [62]. For systems of equations of predator-prey type, the existence and characterization of such a delay between the spreading front and the asymptotic rate of spread is a challenging open question.

### 3.1.4 Organization of the paper

The rest of the paper will be organized as follows. In Section 3.2, we give a quick proof of the upper estimate of the spreading speed (namely,  $\bar{c}_* \leq \sigma(c_1; r_1, r_2)$ ) by invoking the recent results on the diffusive logistic equation in shifting environment due to [60]. In Section 3.3, we derive some rough estimates for the prey density  $v(t, x)$ ,

and state five separate cases for the key parameters  $c_1, r_1, r_2$  where the spreading speed has to be treated separately. In Section 3.4, we outline, in several lemmas, the conceptual steps to estimate the spreading speed from below via explicit solution of some Hamilton-Jacobi equation (3.29) obtained as the limiting problem of the first equation of (3.4). These lemmas will be proved in Subsections 3.4.1, 3.4.2 and 3.4.3. In Section 3.5, we determine the explicit formulas of the unique solution  $\hat{\rho}$  to the limiting problem in each case, and prove that the upper bound of  $c^*$  obtained in Section 3.3 is also the lower bound. This finishes the proofs of Theorems 7 and 8 regarding the spreading speed. In Section 3.6, we prove Theorem 9 regarding the convergence to homogeneous state. Finally, in the Appendix, we collect some useful comparison results regarding the limiting Hamilton-Jacobi equations in [60], which are rephrased in a format suitable for our purpose here.

### 3.2 Upper bound on spreading speed

In this section, we give a quick proof of  $\bar{c}_* \leq \sigma(c_1; r_1, r_2)$ , where  $\sigma(c_1; r_1, r_2)$  is given by the first three cases of (3.15), i.e., the spreading speed  $c^*$  is bounded above by  $\sigma(c_1; r_1, r_2)$ .

First, we establish some preliminary estimates on the solutions  $u$  and  $v$  of (3.4).

**Lemma 7.** *Assume  $0 \leq u_0 \leq \|a\|_\infty - 1$  and  $\beta \leq v_0 \leq 1$ . Then the corresponding solutions  $u(t, x)$  and  $v(t, x)$  of (3.4) satisfy  $0 \leq u(t, x) \leq \|a\|_\infty - 1$  and  $\beta \leq v(t, x) \leq 1$  for all  $(t, x) \in (0, \infty) \times \mathbb{R}$ .*

*Proof.* By the classical theory of reaction-diffusion equations, there exists a unique solution  $(u, v)$  satisfying (3.4) for all  $(t, x) \in (0, \infty) \times \mathbb{R}$ ; see, e.g. [87]. Moreover, since  $0 \leq u_0 \leq \|a\|_\infty - 1$  and  $\beta \leq v_0 \leq 1$ , the maximum principle (see [83, Chapter

3, Section 6, Theorem 10] or [57, Theorem 6.2.1]) implies  $0 \leq u \leq \|a\|_\infty - 1$  and  $\beta \leq v \leq 1$  on  $(0, \infty) \times \mathbb{R}$ .  $\square$

The global upper bound for  $v$  established in Lemma 7, combining with existing results for the diffusive logistic equations with heterogeneous shifting coefficients [60], can be used to determine an upper bound for the spreading speed of  $u$ .

**Proposition 4.** *Let  $(u(t, x), v(t, x))$  be the solution of (3.4), with the associated maximal spreading speed  $\bar{c}_*$  as given in (3.8). Then*

$$\lim_{t \rightarrow \infty} \sup_{x \geq (\sigma + \eta)t} u(t, x) = 0 \quad \text{for each } \eta > 0. \quad (3.17)$$

In particular,  $\bar{c}_* \leq \sigma$ , where  $\sigma = \sigma(c_1; r_1, r_2)$  is defined in (3.16).

*Proof.* By Lemma 7,  $v(t, x) \leq 1$  for all  $(t, x) \in (0, \infty) \times \mathbb{R}$ , hence we may regard  $u(t, x)$  as a subsolution of the following scalar problem

$$\begin{cases} \bar{u}_t = \bar{u}_{xx} + \bar{u}(-1 - \bar{u} + a(x - c_1 t)) & \text{in } (0, \infty) \times \mathbb{R} \\ \bar{u}(0, x) = u_0(x) & \text{in } \mathbb{R}. \end{cases} \quad (3.18)$$

Let  $\bar{u}$  be the classical solution of (3.18) with initial data  $u_0(x)$ . By the parabolic maximum principle we have

$$u(t, x) \leq \bar{u}(t, x) \quad \text{for all } (t, x) \in (0, \infty) \times \mathbb{R}. \quad (3.19)$$

In the case  $r_2 > r_1$ , we may invoke [60, Theorem 6] to deduce that  $\bar{u}$  satisfies

$$\lim_{t \rightarrow \infty} \sup_{x \geq (\sigma + \eta)t} \bar{u}(t, x) = 0 \quad \text{for each } \eta > 0, \quad (3.20)$$

where  $\sigma = \sigma(c_1; r_1, r_2)$  is given in (3.16).

In case  $r_1 > r_2$ , we define

$$U(t, x) = \begin{cases} \exp(-\sqrt{r_1}x + 2r_1 t) & \text{if } c_1 \geq 2\sqrt{r_1}, \\ \min\{r_1, \exp(-\lambda(x - c_1 t))\} & \text{if } 2\sqrt{r_2} < c_1 < 2\sqrt{r_1}, \lambda = \frac{1}{2} \left( c_1 - \sqrt{c_1^2 - 4r_2} \right) \\ \min\{r_1, \exp(-\sqrt{r_2}x + 2r_2 t)\} & \text{if } 0 < c_1 \leq 2\sqrt{r_2}. \end{cases}$$



Then it can be verified that  $\bar{u}$  is a generalized supersolution of (3.18) (see [57, Definition 1.1.1] or [12, Definition 4.2] for the definition). Hence, we again deduce that

(3.20) holds where

$$\sigma = \begin{cases} 2\sqrt{r_2} & \text{if } c_1 \leq 2\sqrt{r_2}, \\ 2\sqrt{r_1} & \text{if } c_1 \geq 2\sqrt{r_1}, \\ c_1 & \text{otherwise.} \end{cases}$$

Combining with (3.19), we conclude that

$$\lim_{t \rightarrow \infty} \sup_{x \geq (\sigma + \eta)t} u(t, x) = 0 \quad \text{for each } \eta > 0,$$

where  $\sigma$  is given in (3.16) (and  $\sigma = c_1$ , in case  $2\sqrt{r_1} > c_1 > 2\sqrt{r_2}$ ). This completes the proof.  $\square$

### 3.3 Rough Estimate for $v(t, x)$

Having established that the spreading speed is bounded above by  $\sigma = \sigma(c_1; r_1, r_2)$ , we may also deduce in the following lemma that  $v(t, x)$  converges to its carrying capacity as  $t \rightarrow \infty$  in the region  $\{(x, t) : x > \sigma t\}$ .

**Lemma 8.** *Let  $(u(t, x), v(t, x))$  be the solution of (3.4). Then*

$$\lim_{t \rightarrow \infty} \sup_{x \geq (\sigma + \eta)t} |v(t, x) - 1| = 0 \quad \text{for each } \eta > 0, \quad (3.21)$$

where  $\sigma$  is given by (3.16).

*Proof.* Since  $v(t, x) \leq 1$  (thanks to Lemma 7), it suffices to show the lower bound. We shall follow the proof of Theorem 5.1 in [29]. Fix  $c > \sigma(c_1; r_1, r_2)$ . we may suppose for contradiction that there exists a sequence  $\{(t_n, x_n)\}$  with  $t_n \rightarrow \infty$  and  $x_n \geq ct_n$  such that  $\limsup_{n \rightarrow \infty} v(t_n, x_n) < 1$ . Denote  $(u_n, v_n)(t, x) = (u, v)(t + t_n, x + x_n)$ . By standard parabolic estimates, we may pass to a further subsequence so that  $(u_n, v_n)$  converges

to an entire in time solution  $(u_\infty, v_\infty)$  of (3.4) in  $C_{loc}(\mathbb{R}^2)$ . Since  $c > \sigma(c_1; r_1, r_2)$ , by Lemma 4, we have  $u_\infty \equiv 0$ . Thus,  $v_\infty$  is an entire solution satisfying the equation

$$(v_\infty)_t = D(v_\infty)_{xx} + rv_\infty(1 - v_\infty) \quad \text{for } (t, x) \in \mathbb{R}^2.$$

Since  $v \geq \beta$  for all  $(t, x) \in (0, \infty) \times \mathbb{R}$ , we deduce that  $v_\infty \geq \beta$  for all  $(t, x) \in \mathbb{R}^2$ . By the classification of entire solution of the diffusive logistic equation (see, e.g. [70, Lemma 2.3(d)]) we have  $v_\infty \equiv 1$ . This is in contradiction with the statement  $\limsup_{n \rightarrow \infty} v(t_n, x_n) < 1$ .  $\square$

Having established the upper bound of the spreading speed, the outstanding task is to estimate the spreading speed from below. We will do so by adopting the Hamilton-Jacobi approach [34]. To this end, define

$$F^\epsilon(t, x) = -1 + v\left(\frac{t}{\epsilon}, \frac{x}{\epsilon}\right)a\left(\frac{x}{\epsilon} - \frac{c_1 t}{\epsilon}\right) \quad (3.22)$$

and its (lower) half-relaxed limit [8]

$$F_*(t, x) = \liminf_{\substack{\epsilon \rightarrow 0 \\ (t', x') \rightarrow (t, x)}} F^\epsilon(t', x'). \quad (3.23)$$

We will divide the proof of the spreading speed into the following cases, depending on the speed of environmental shift  $c_1$  and the profile of the conversion efficiency  $a(x - c_1 t)$ .

**Case 1(a):**  $r_1 < r_2$  and  $c_1 < 2\sqrt{r_2}$

**Case 1(b):**  $r_1 < r_2$  and  $2\sqrt{r_2} < c_1 < 2(\sqrt{r_1} + \sqrt{r_2 - r_1})$

**Case 1(c):**  $r_1 < r_2$  and  $c_1 > 2(\sqrt{r_1} + \sqrt{r_2 - r_1})$

**Case 2(a):**  $r_1 > r_2$  and  $c_1 < 2\sqrt{r_2}$

**Case 2(b):**  $r_1 > r_2$  and  $c_1 \geq 2\sqrt{r_1}$

In Case 1(a) - (c), we have  $r_1 < r_2$ , and we let

$$R_1(s) = \begin{cases} R_{1a}(s) = \begin{cases} r_2 & \text{for } s \geq 2\sqrt{r_2} \\ r_2 & \text{for } c_1 \leq s < 2\sqrt{r_2} \\ r_1 & \text{for } s < c_1 \end{cases} & \text{if } c_1 < 2\sqrt{r_2}, \\ R_{1b}(s) = \begin{cases} r_2 & \text{for } s \geq c_1, \\ r_1 & \text{for } \lambda + \frac{r_1}{\lambda} \leq s < c_1 \\ r_1 & \text{for } s < \lambda + \frac{r_1}{\lambda} \end{cases} & \text{if } 2\sqrt{r_2} < c_1 < 2(\sqrt{r_1} + \sqrt{r_2 - r_1}), \\ R_{1c}(s) = \begin{cases} r_2 & \text{for } s \geq c_1, \\ r_1 & \text{for } 2\sqrt{r_1} \leq s < c_1 \\ r_1 & \text{for } s < 2\sqrt{r_1} \end{cases} & \text{if } c_1 > 2(\sqrt{r_1} + \sqrt{r_2 - r_1}) \end{cases} \quad (3.24)$$

In Cases 2(a)-(b), we have  $r_1 > r_2$ , and we let

$$R_2(s) = \begin{cases} R_{2a}(s) = \begin{cases} r_2 & \text{for } s \geq 2\sqrt{r_2}, \\ r_2 & \text{for } c_1 \leq s < 2\sqrt{r_2} \\ r_1 & \text{for } s < c_1. \end{cases} & \text{if } c_1 < 2\sqrt{r_2} \\ R_{2b}(s) = \begin{cases} r_2 & \text{for } s \geq c_1, \\ r_1 & \text{for } 2\sqrt{r_1} \leq s < c_1 \\ r_1 & \text{for } s < 2\sqrt{r_1} \end{cases} & \text{if } c_1 > 2\sqrt{r_1}. \end{cases} \quad (3.25)$$

**Lemma 9.**  $F_*(t, x) \geq R_i(x/t)$  in cases 1(a)-(c) and 2(a)-(b).

*Proof.* The lemma follows from the definition of  $F_*$ , in (3.23), and the global bounds  $\beta \leq v(t, x) \leq 1$  (Lemma 7).  $\square$

### 3.4 Lower bound on the spreading speed

We will use the Hamilton-Jacobi method to prove a lower bound for the spreading speed. To this end, define the WKB-Ansatz [34]

$$w^\epsilon(t, x) = -\epsilon \log u^\epsilon(t, x) \quad \text{where} \quad u^\epsilon(t, x) = u(t/\epsilon, x/\epsilon), \quad (3.26)$$

and consider the half-relaxed limits [9]

$$w^*(t, x) = \limsup_{\substack{\epsilon \rightarrow 0 \\ (t', x') \rightarrow (t, x)}} w^\epsilon(t', x') \quad \text{and} \quad w_*(t, x) = \liminf_{\substack{\epsilon \rightarrow 0 \\ (t', x') \rightarrow (t, x)}} w^\epsilon(t', x'). \quad (3.27)$$

In the following lemma, we show that  $w^*(t, x)$  and  $w_*(t, x)$  can be related to one dimensional-functions  $\rho^*(s)$  and  $\rho_*(s)$ , respectively,

**Lemma 10.** *Let  $w^*$  and  $w_*$  be defined as in (3.27). Then  $w^*(t, x) = t\rho^*(x/t)$  and  $w_*(t, x) = t\rho_*(x/t)$  for some functions  $\rho^*$  and  $\rho_*$ .*

*Proof.* For the existence of  $\rho^*$ , we may compute

$$w^*(t, x) = \limsup_{\substack{\epsilon \rightarrow 0 \\ (t', x') \rightarrow (t, x)}} -\epsilon \log u\left(\frac{t'}{\epsilon}, \frac{x'}{\epsilon}\right) = t \limsup_{\substack{\epsilon \rightarrow 0 \\ (t'', x'') \rightarrow (1, x/t)}} -(\epsilon/t) \log u\left(\frac{t''}{\epsilon/t}, \frac{x''}{\epsilon/t}\right).$$

Thus  $w^*(t, x) = tw^*(1, x/t)$ , and the first part of the result is proved if we take  $\rho^*(s) = w^*(1, s)$ . The proof of the second part is analogous.  $\square$

Next, we describe a bird's eye view of the Hamilton-Jacobi approach in order to achieve our final goal of bounding the spreading speed from below by the optimal constant  $\sigma > 0$ . For clarity, we will state the necessary lemmas and provide their proofs later on.

We start with the following lemma which is due to [34] for the KPP equation, the proof is presented Subsection 3.4.1.

**Lemma 11.** *Suppose that there is  $s_0 > 0$  such that  $\rho^*(s) = 0$  for all  $s \in [0, s_0]$ . Then there exists  $\delta_0 > 0$  such that*

$$\liminf_{t \rightarrow \infty} \inf_{\eta t < x < (s_0 - \eta)t} u(t, x) \geq \delta_0 \quad \text{for each } \eta > 0 \text{ sufficiently small.}$$

Hence, a lower bound of the spreading speed (and hence the complete proofs of our main theorems) can be obtained by determining the set  $\{s : \rho^*(s) = 0\}$ . Precisely, it is sufficient to show that  $\rho^*(s) = 0$  for  $s \in [0, \sigma]$ , where  $\sigma = \sigma(c_1; r_1, r_2)$  as in (3.16).

To this end, we derive a limiting Hamilton-Jacobi equation for  $w^*$  and then for  $\rho^*$ . Observe that  $w^\epsilon$  satisfies

$$w_t^\epsilon - \epsilon w_{xx}^\epsilon + |w_x^\epsilon|^2 + (F^\epsilon(t, x) - u^\epsilon) = 0 \quad \text{for } (t, x) \in (0, \infty) \times \mathbb{R}, \quad (3.28)$$

where  $F^\epsilon$  is given in (3.22). By the fact that  $F_*(t, x) \geq R(x/t)$ , it is standard [34, 60] to deduce the following.

**Lemma 12.** *Suppose  $F_*(t, x) \geq R(x/t)$ , then  $\rho^*$  is a viscosity subsolution of*

$$\min\{\rho - s\rho' + |\rho'|^2 + R(s), \rho\} = 0 \quad \text{for } s \in (0, \infty). \quad (3.29)$$

Moreover,

$$\rho^*(0) = 0 \quad \text{and} \quad \rho^*(s) < \infty \quad \text{for all } s \in [0, \infty). \quad (3.30)$$

*Proof.* We postpone the proof to Subsection 3.4.2. □

By the comparison principle, discussed in Section 3.4.3, the Hamilton-Jacobi equation (3.29) has a unique viscosity solution.

**Lemma 13.** *For any given case  $(i, j) \in \{(1, a), (1, b), (1, c), (2, a), (2, b)\}$  as stated in Section 3.3, let  $R$  be given by  $R = R_{ij}$ . The Hamilton-Jacobi equation (3.29) has a unique viscosity solution,  $\hat{\rho}$ , satisfying*

$$\hat{\rho}(0) = 0 \quad \text{and} \quad \lim_{s \rightarrow \infty} \frac{\hat{\rho}(s)}{s} = \infty. \quad (3.31)$$

Moreover,  $\hat{\rho}$  is nondecreasing in  $s$ , i.e.

$$\hat{\rho}(s) \equiv 0 \quad \text{for } 0 \leq s \leq \sup\{s' \geq 0 : \hat{\rho}(s') = 0\}. \quad (3.32)$$

Furthermore, the following Lemma holds:

**Lemma 14.** *For any given case  $(i, j) \in \{(1, a), (1, b), (1, c), (2, a), (2, b)\}$  as stated in Section 3.3, let  $R$  be given by  $R = R_{ij}$  and let  $\hat{\rho}$  be the unique solution of (3.29) as specified in Lemma 13. Then*

$$0 \leq \rho^*(s) \leq \hat{\rho}(s) \quad \text{for } s \geq 0.$$

The statement (3.32) and Lemma 14 imply that

$$\rho^*(s) = 0 \quad \text{for } 0 \leq s \leq \sup\{s' \geq 0 : \hat{\rho}(s') = 0\}. \quad (3.33)$$

Together with Lemma 11, this enables us to establish

$$\underline{c}_* \geq \sup\{s \geq 0 : \hat{\rho}(s) = 0\}.$$

Next, we will establish the explicit formula of the unique solution  $\hat{\rho}$  satisfying (3.29) in viscosity sense and (3.31) in classical sense in Lemma 17.

For example, in Case 1(a) ( $r_1 < r_2$  and  $c_1 < 2\sqrt{r_2}$ ), we will show that

$$\hat{\rho}(s) = \begin{cases} \frac{s^2}{4} - r_2 & \text{for } s > 2\sqrt{r_2} \\ 0 & \text{for } 0 \leq s \leq 2\sqrt{r_2}. \end{cases} \quad (3.34)$$

Hence, we deduce from Lemma 14 that

$$0 \leq \rho^*(s) \leq \hat{\rho}(s) = 0 \quad \text{for } 0 \leq s \leq 2\sqrt{r_2}.$$

By Lemma 11, we conclude that  $\underline{c}_* \geq 2\sqrt{r_2}$ . This establishes the lower bound of the spreading speed in Case 1(a). The spreading speed in Case 1(a) is thus determined, since  $2\sqrt{r_2}$  is also the upper bound of spreading speed (thanks to Proposition 4).

In the next couple subsections, we present the proofs of the above lemmas.

### 3.4.1 Proof of Lemma 11

*Proof of Lemma 11.* Our proof is adapted from Theorem 1.1 of [34]. Fix a small  $0 < \eta \ll 1$ . It is sufficient to show that there exists  $\delta_0 = \delta_0(\eta) > 0$  such that

$$\liminf_{\epsilon \rightarrow 0} \inf_K u^\epsilon(t, x) \geq \delta_0 \quad (3.35)$$

for any compact set given by  $K = \{(1, x) : \eta \leq x \leq s_0 - \eta\} \subset \subset \{(t, x) : 0 < x/t < s_0\}$ .

Indeed,

$$\liminf_{t \rightarrow \infty} \inf_{\eta t < x < (s_0 - \eta)t} u(t, x) = \liminf_{\epsilon \rightarrow 0} \inf_K u^\epsilon(t, x) \geq \delta_0.$$

To show (3.35), we first observe that  $w^*(t, x) = t\rho^*(x/t) = 0$  in some compact subset  $\tilde{K}$  such that

$$K \subset \text{Int } \tilde{K} \subset \{(t, x) : 0 < x/t < s_0\},$$

which implies  $w^\epsilon(t, x) \rightarrow 0$  uniformly in a neighborhood of  $K$ . Now for  $(t_0, x_0) \in K$ , let  $\psi(t, x) = (t - t_0)^2 + (x - x_0)^2$ . Then  $w^* - \psi$  has a strict local maximum at  $(t_0, x_0)$ . Since  $w^\epsilon \rightarrow 0$  uniformly in a neighborhood of  $K$ , for each  $\epsilon > 0$  sufficiently small, the function  $w^\epsilon - \psi$  has a local maximum at  $(t_\epsilon, x_\epsilon) \in K$ , where  $(t_\epsilon, x_\epsilon) \rightarrow (t_0, x_0)$  as  $\epsilon \rightarrow 0$ . Thus,

$$o(1) = \partial_t \psi - \epsilon \partial_{xx} \psi + |\partial_x \psi|^2 \leq \partial_t w^\epsilon - \epsilon \partial_{xx} w^\epsilon + |\partial_x w^\epsilon|^2 = u^\epsilon - F^\epsilon \leq u^\epsilon - \delta_0 \quad (3.36)$$

at  $(t, x) = (t_\epsilon, x_\epsilon)$ , where  $\delta_0 = \beta \inf_{s \in \mathbb{R}} a(s) - 1 > 0$ .

Using the fact that  $w^\epsilon - \psi$  has a local maximum at  $(t_\epsilon, x_\epsilon)$ , we deduce that

$$w^\epsilon(t_\epsilon, x_\epsilon) \geq (w^\epsilon - \psi)(t_\epsilon, x_\epsilon) \geq (w^\epsilon - \psi)(t_0, x_0) = w^\epsilon(t_0, x_0)$$

which implies that  $u^\epsilon(t_0, x_0) \geq u^\epsilon(t_\epsilon, x_\epsilon)$ . Combining with (3.36), we have

$$u^\epsilon(t_0, x_0) \geq u^\epsilon(t_\epsilon, x_\epsilon) \geq \delta_0 + o(1).$$

Since the above argument is uniform for arbitrary  $(t_0, x_0) \in K$ , this implies (3.35).  $\square$

### 3.4.2 Proof of Lemma 12

We recall the definition of viscosity solutions of (3.29).

**Definition.** We recall the definition of viscosity solution of Hamilton-Jacobi equations with discontinuous Hamiltonian, following [8] and originating from [52]. In the following let  $R^*$  and  $R_*$  be the upper and lower envelope of  $R$ , which is given by

$$R^*(s) = \limsup_{s' \rightarrow s} R(s') \quad \text{and} \quad R_*(s) = \liminf_{s' \rightarrow s} R(s').$$

- A lower semicontinuous function  $\hat{\rho}$  is called a viscosity super-solution of (3.29) if  $\hat{\rho} \geq 0$ , and for any test function  $\phi \in C^1$ , if  $s_0$  is a strict local minimum of  $\hat{\rho} - \phi$ , then

$$\hat{\rho}(s_0) - s_0\phi'(s_0) + |\phi'(s_0)|^2 + R^*(s_0) \geq 0.$$

- An upper semicontinuous function  $\hat{\rho}$  is called a viscosity sub-solution of (3.29) if for any test function  $\phi \in C^1$ , if  $s_0$  is a strict local maximum of  $\hat{\rho} - \phi$  and  $\hat{\rho}(s_0) > 0$ , then

$$\hat{\rho}(s_0) - s_0\phi'(s_0) + |\phi'(s_0)|^2 + R_*(s_0) \leq 0.$$

- We say  $\hat{\rho}$  is a viscosity solution of (3.29) if  $\hat{\rho}$  is a viscosity super- and sub-solution.

We will first show that  $\rho^*$  is nonnegative and that  $\rho^*(0) = 0$ .

**Lemma 15.** Let  $\rho^*$  be defined as in Lemma 10. Then

$$\rho^*(0) = 0 \quad \text{and} \quad \rho^*(s) \geq 0 \quad \text{for } s \geq 0. \quad (3.37)$$



*Proof.* We first show  $w^*(t, x) \geq 0$  for  $(t, x) \in [0, \infty) \times \mathbb{R}$ . Indeed, since  $u(t, x) \leq \max\{r_2, r_1\}$  for all  $(t, x) \in [0, \infty) \times \mathbb{R}$ , by the definition of  $w^*$  we have

$w^\epsilon \geq -\epsilon \log(\max\{r_2, r_1\})$  for each  $\epsilon > 0$  and  $(t, x) \in [0, \infty) \times \mathbb{R}$ , and we may compute

$$w^*(t, x) = \limsup_{\substack{\epsilon \rightarrow 0 \\ (t', x') \rightarrow (t, x)}} w^\epsilon(t', x') \geq 0 \quad \text{for } (t, x) \in [0, \infty) \times \mathbb{R}. \quad (3.38)$$

In particular,  $w^*(t, 0) \geq 0$  for  $t > 0$ .

The proof will be complete once we show  $w^*(t, 0) \leq 0$  for  $t > 0$ . Denote  $\underline{r} = r_1 \wedge r_2$ . Then using the lower bound  $v \geq \beta$ , we see that  $u$  is a super-solution of

$$\underline{u}_t - \underline{u}_{xx} = \underline{u}(\underline{r} - \underline{u}) \quad \text{in } (0, \infty) \times \mathbb{R}. \quad (3.39)$$

Let  $\underline{u}(t, x)$  be the solution of (3.39) with identical (compactly supported) initial condition as  $u(t, x)$ , then the classical spreading result for the diffusive logistic equation [4] says that  $\underline{u}$  has spreading speed  $2\sqrt{\underline{r}}$ . In particular,

$$\liminf_{t \rightarrow \infty} \inf_{|x| < \sqrt{\underline{r}t}} t \underline{u}(t, x) \geq 2\delta_1 \quad \text{for some } \delta_1 > 0.$$

By the comparison principle,  $u \geq \underline{u}$ , i.e. there exists  $t_1 > 0$  such that

$$\inf_{|x| < \sqrt{\underline{r}t}} u(t, x) \geq \delta_1 \quad \text{for } t \geq t_1,$$

which implies

$$\sup_{\substack{|x| < \sqrt{\underline{r}t} \\ t \geq \epsilon t_1}} w^\epsilon(t, x) \leq -\epsilon \log \delta_1. \quad (3.40)$$

Now, fix an arbitrary  $t_0 > 0$ . Let  $(t, x) \rightarrow (t_0, 0)$  and  $\epsilon \rightarrow 0$ , we deduce

$$w^*(t_0, 0) = \limsup_{\substack{\epsilon \rightarrow 0 \\ (t, x) \rightarrow (t_0, 0)}} w^\epsilon(t, x) \leq 0. \quad (3.41)$$

Combining (3.38) and (3.41), we have

$$w^*(t, 0) = 0 \quad \text{for all } t > 0. \quad (3.42)$$

We recall  $w^*(t, x) = t\rho^*(x/t)$  (thanks to Lemma 10), so that (3.37) directly follows from (3.38) and (3.42). This completes the proof.  $\square$

The following lemma implies that  $\rho^*(s) < \infty$  for  $s \in [0, \infty)$ .

**Lemma 16.** *Let  $w^\epsilon$  be a solution of (3.28). Then for each compact subset  $Q$  of  $(0, \infty) \times \mathbb{R}$ , there is a constant  $C(Q)$  independent of  $\epsilon$  such that*

$$w^\epsilon(t, x) \leq C(Q) \quad \text{for } (t, x) \in Q \text{ and } \epsilon \in (0, 1/C(Q)].$$

*In particular,*

$$w^*(t, x) < +\infty \quad \text{for each } (t, x) \in (0, \infty) \times \mathbb{R} \quad \text{and} \quad \rho^*(s) < +\infty \quad \text{for each } s \in [0, \infty). \quad (3.43)$$

*Proof.* We only prove the bound for  $Q \subset (0, \infty) \times [0, \infty)$ . The case for  $Q \subset (0, \infty) \times (-\infty, 0]$  is similar and is omitted. Our proof follows the ideas in [34]. Fix  $\delta \in (0, 1)$  such that  $Q \subset [\delta, 1/\delta] \times [0, 1/\delta]$ . Define

$$z^\epsilon(t, x) = \frac{|x + 2\delta|^2}{4t} + \frac{\epsilon}{2} \log t + C_\delta(1 + t).$$

By taking  $C_\delta > 0$  to be a large constant depending on  $\delta$ ,  $z^\epsilon$  is a (classical) supersolution of (3.28) in  $(0, \infty) \times (0, \infty)$ .

By (3.42) in the proof of Lemma 15 and the definition of  $w^*$ , there is a constant  $C_\delta > 0$  such that,

$$\sup_{0 < \epsilon \leq 1/2} w^\epsilon(t + \delta/2, 0) \leq C_\delta \quad \text{for } t \in [0, 1/\delta].$$

Observe that for  $\epsilon$  sufficiently small, we have

$$\begin{cases} w^\epsilon(\delta/2, x) < \infty = z^\epsilon(0, x) & \text{for } x \geq 0 \\ w^\epsilon(t + \delta/2, 0) \leq C_\delta \leq z^\epsilon(t, 0) & \text{for } t \in [0, 1/\delta]. \end{cases}$$

It follows from the maximum principle that

$$w^\epsilon(t + \delta/2, x) \leq z^\epsilon(t, x) \quad \text{for } (t, x) \in [0, 1/\delta] \times [0, \infty).$$

Taking supremum over  $[\delta/2, 1/\delta] \times [0, 1/\delta]$ , we have

$$\sup_{[\delta/2, 1/\delta] \times [0, 1/\delta]} w^\epsilon(t + \delta/2, x) \leq C'_\delta := \sup_{[\delta/2, 1/\delta] \times [0, 1/\delta]} \left[ \frac{|x + 2\delta|^2}{4t} + \log t + C_\delta(1 + t) \right]. \quad (3.44)$$

This completes the proof.  $\square$

Next, we prove Lemma 12.

*Proof of Lemma 12.* Since (3.30) is a consequence of Lemma 15 and (3.43), it remains to show that  $\rho^*$  is a viscosity subsolution of (3.29).

Let  $\phi \in C^1$  be a test function and suppose that  $\rho^* - \phi$  has a strict local maximum at  $s = s_0$ , and that  $\rho^*(s_0) > 0$ . Without loss of generality, we may assume that  $\rho^* - \phi \leq 0$  for all  $s$  near  $s_0$ , with equality holding only at  $s = s_0$ . We will show that

$$\rho^*(s_0) - s_0\phi'(s_0) + |\phi'(s_0)|^2 + R(s_0) \leq 0.$$

First, we note that  $w^*(t, x) = \rho^*(x/t)$  and that  $w^*(t, x) - t\phi(x/t) - (t - 1)^2 \leq 0$  for all  $(t, x)$  near  $(1, s_0)$ , with equality holding only at  $(t, x) = (1, s_0)$ . Define, in terms of  $\phi$ , a two variable test function

$$\varphi(t, x) = t\phi(x/t) - (t - 1)^2.$$

Then by the definition of  $w^*$ , there exists a sequence  $\epsilon_n \rightarrow 0$  and sequence of points  $(t_n, x_n) \rightarrow (1, s_0)$  as  $n \rightarrow \infty$  such that:  $w^{\epsilon_n} - \varphi$  has a local maximum at  $(t_n, x_n)$ , and  $w^{\epsilon_n}(t_n, x_n) \rightarrow w^*(t_0, x_0) > 0$ . Thus, for  $(t, x) = (t_n, x_n)$ , we have

$$\begin{aligned} \partial_t \varphi &= \partial_t w^{\epsilon_n} = \epsilon_n \partial_{xx} w^{\epsilon_n} - |\partial_x w^{\epsilon_n}|^2 - (F^{\epsilon_n} - u^{\epsilon_n}) \\ &\leq \epsilon_n \partial_{xx} \varphi - |\partial_x \varphi|^2 - (F^{\epsilon_n} - u^{\epsilon_n}). \end{aligned}$$

Thus,

$$\partial_t \varphi - \epsilon_n \partial_{xx} \varphi + |\partial_x \varphi|^2 + (F^{\epsilon_n} - u^{\epsilon_n}) \leq 0 \quad (3.45)$$

for  $(t, x) = (t_n, x_n)$ . Letting  $n \rightarrow \infty$ , we obtain

$$\partial_t \varphi(t_0, x_0) + |\partial_x \varphi(t_0, x_0)|^2 + F_*(t_0, x_0) \leq 0, \quad (3.46)$$

where we have used the fact that  $w^{\epsilon_n}(t_n, x_n) \rightarrow w^*(t_0, x_0) > 0$  implies  $u^{\epsilon_n}(t_n, x_n) \rightarrow 0$ .

Since  $F_*(t_0, x_0) \geq R(x_0/t_0)$ , it follows from (3.46) that

$$\phi(s_0) - s_0 \phi'(s_0) + |\phi'(s_0)|^2 + R(s_0) \leq 0.$$

Thus,  $\rho^*$  is a viscosity sub-solution of (3.29). □

### 3.4.3 Proof of Lemmas 13 and 14

*Proof of Lemma 13.* Observe, in each case  $i = 1, 2$ , that our choice of  $R$  satisfies (B1)-(B2) of the Appendix. By Corollary 3 of the Appendix, there exists a unique  $\hat{\rho}$  satisfying (3.29) in the viscosity sense, and the boundary condition (3.31) in the classical sense. Moreover,  $s \mapsto \hat{\rho}$  is nondecreasing. This proves Lemma 13. □

*Proof of Lemma 14.* We observe that  $\rho^*$  is a viscosity subsolution (by Lemma 12) and that  $\hat{\rho}$  is a viscosity super-solution (by Lemma 13). Moreover, by (3.30) and (3.31),

we have

$$\rho^*(0) = \hat{\rho}(0) = 0, \quad \text{and} \quad \lim_{s \rightarrow \infty} \frac{\rho^*(s)}{s} \leq +\infty = \lim_{s \rightarrow \infty} \frac{\hat{\rho}(s)}{s}.$$

We can therefore apply the comparison principle (see Lemma 18 of the Appendix) to derive

$$\rho^*(s) \leq \hat{\rho}(s) \quad \text{for } s \geq 0.$$

Finally,  $\rho^*(s) \geq 0$  is proved in Lemma 15. □

### 3.5 Solving for spreading speed via explicit formulas for $\hat{\rho}$

For each of the cases 1(a)-(c), 2(a), and 2(b), we will propose an explicit formula for  $\hat{\rho}$  in Subsection 3.5.1. Thanks to the uniqueness result in Lemma 13, it is enough to verify (separately for each of the cases) that the given expression defines a viscosity solution of (3.29). This will be done in Subsection 3.5.2.

#### 3.5.1 Explicit formulas for $\hat{\rho}$

Below, we state the explicit formula for  $\hat{\rho}$  in each case. Subsequently, we will verify in Lemma 17 that  $\hat{\rho}$  solves (3.29) by invoking the definition of the viscosity solution [8].

- **Case 1(a):**  $r_1 < r_2$  and  $c_1 < 2\sqrt{r_2}$ .

$$\hat{\rho}(s) = \begin{cases} \frac{s^2}{4} - r_2 & \text{for } s > 2\sqrt{r_2} \\ 0 & \text{for } 0 \leq s \leq 2\sqrt{r_2}, \end{cases} \quad (3.47)$$

- **Case 1(b):**  $r_1 < r_2$  and  $2\sqrt{r_2} < c_1 < 2(\sqrt{r_1} + \sqrt{r_2 - r_1})$ .

$$\hat{\rho}(s) = \begin{cases} \frac{s^2}{4} - r_2 & \text{for } s > c_1 \\ \lambda s - (\lambda^2 + r_1) & \text{for } (\lambda + \frac{r_1}{\lambda}) < s \leq c_1 \\ 0 & \text{for } 0 \leq s \leq \lambda + \frac{r_1}{\lambda}, \end{cases} \quad (3.48)$$

where  $\lambda = \frac{c_1}{2} - \sqrt{r_2 - r_1}$ .

- **Case 1(c):**  $r_1 < r_2$  and  $c_1 > 2(\sqrt{r_1} + \sqrt{r_2 - r_1})$

$$\hat{\rho}(s) = \begin{cases} \frac{s^2}{4} - r_2 & \text{for } s > c_1 \\ \lambda s - (\lambda^2 + r_1) & \text{for } 2\lambda < s \leq c_1 \\ \frac{s^2}{4} - r_1 & \text{for } 2\sqrt{r_1} < s \leq 2\lambda \\ 0 & \text{for } 0 \leq s \leq 2\sqrt{r_1}. \end{cases} \quad (3.49)$$

- **Case 2(a):**  $r_1 > r_2$  and  $c_1 < 2\sqrt{r_2}$ .

$$\hat{\rho}(s) = \begin{cases} \frac{s^2}{4} - r_2 & \text{for } s > 2\sqrt{r_2} \\ 0 & \text{for } 0 \leq s \leq 2\sqrt{r_2}, \end{cases} \quad (3.50)$$

- **Case 2(b):**  $r_1 > r_2$  and  $c_1 \geq 2\sqrt{r_1}$ .

$$\hat{\rho}(s) = \begin{cases} \frac{s^2}{4} - r_2 & \text{for } s > 2\tilde{\lambda} \\ \tilde{\lambda}s - (\tilde{\lambda}^2 + r_2) & \text{for } c_1 < s \leq 2\tilde{\lambda} \\ \frac{s^2}{4} - r_1 & \text{for } 2\sqrt{r_1} < s < c_1 \\ 0 & \text{for } 0 \leq s \leq 2\sqrt{r_1}, \end{cases} \quad (3.51)$$

where  $\tilde{\lambda} = \frac{c_1}{2} + \sqrt{r_1 - r_2}$ .

### 3.5.2 $\hat{\rho}$ solves the HJE (3.29) in the viscosity sense

**Lemma 17.** *The unique viscosity solution  $\hat{\rho}$  of (3.29) satisfying (in the classical sense)*

$$\hat{\rho}(0) = 0 \quad \text{and} \quad \lim_{s \rightarrow \infty} \frac{\hat{\rho}(s)}{s} = \infty,$$

*is given by the formulas of Subsection 3.5.1.*

*Proof.* We prove that the above formulas determine the the unique viscosity solution guaranteed by Lemma 13. To do that, it is enough to show that, in each case,  $\hat{\rho}$  as given above, satisfies (i) the Hamilton-Jacobi equation (3.29) in the viscosity sense, as well as (ii) the boundary condition (3.31) in the classical sense. In view of the explicit formulas, (ii) is obvious. Thus, it remains to verify that  $\hat{\rho}$  is a viscosity solution of

(3.29) in each case. Since the proof only differs slightly in each case, we consider only two representative cases 1(b) and 2(b) here, and omit the verification of the rest.

Let us proceed with Case 1(b), where we fix  $r_1, r_2, c_1$  satisfying

$$r_1 < r_2, \quad \text{and} \quad 2\sqrt{r_2} < c_1 < 2(\sqrt{r_1} + \sqrt{r_2 - r_1}). \quad (3.52)$$

Next, we set

$$R(s) = R_{1b}(s) = \begin{cases} r_2 & \text{for } s \geq c_1, \\ r_1 & \text{for } \lambda + \frac{r_1}{\lambda} \leq s < c_1 \\ r_1 & \text{for } s < \lambda + \frac{r_1}{\lambda}. \end{cases}$$

and

$$\hat{\rho}(s) = \begin{cases} \frac{s^2}{4} - r_2 & \text{for } s > c_1 \\ \lambda s - (\lambda^2 + r_1) & \text{for } (\lambda + \frac{r_1}{\lambda}) < s \leq c_1 \\ 0 & \text{for } 0 \leq s \leq \lambda + \frac{r_1}{\lambda}, \end{cases} \quad (3.53)$$

where  $\lambda = \frac{c_1}{2} - \sqrt{r_2 - r_1}$ .

First, observe that  $\hat{\rho}$  is continuous, thanks to our choice of  $\lambda$ .

Next, we show that  $\hat{\rho}$  is a viscosity subsolution of (3.29). To this end, observe that  $\hat{\rho}$  satisfies the equation (3.29) in the classical sense almost everywhere in  $[0, \infty)$ . (In fact, it satisfies the equation classically for  $s \in \mathbb{R} \setminus \{c_1, \lambda + r_1/\lambda\}$ .) By the convexity of the Hamiltonian, we can apply [7, Proposition 5.1] to conclude that it is in fact a viscosity sub-solution of (3.29).

Next, we show that  $\hat{\rho}$  is a viscosity super-solution of (3.29). Suppose  $\hat{\rho} - \phi$  obtains a strict local minimum at  $s_0 \in [0, \infty)$  for some  $\phi \in C^1$ . Now,  $\hat{\rho}$  is a classical solution of (3.29) for all  $s \notin \{\lambda + \frac{r_1}{\lambda}, c_1\}$ , so it automatically satisfies (3.29) in the viscosity sense. We need only consider  $s_0 \in \{\lambda + \frac{r_1}{\lambda}, c_1\}$ . Suppose  $s_0 = \lambda + \frac{r_1}{\lambda}$ . Then  $0 \leq \phi'(s_0) \leq \lambda$ . Therefore,  $R(s_0) = r_1$  and at the point  $s = s_0$ , it holds that

$$\rho - s_0\phi' + |\phi'|^2 + R^* = -(\lambda + \frac{r_1}{\lambda})\phi' + |\phi'|^2 + r_1 = (\phi' - \lambda)(\phi' - \frac{r_1}{\lambda}) \geq 0,$$

where the last inequality is a consequence of  $\phi'(s_0) \leq \lambda < \frac{r_1}{\lambda}$  (which in turn follows from the choice of  $\lambda$  and the condition (3.52)).

If  $s_0 = c_1$ , then  $R^*(s_0) = \max\{r_1, r_2\} = r_2$ , and we have

$$\begin{aligned} \rho - s_0\phi' + |\phi'|^2 + R^* &= \left(\frac{c_1^2}{4} - r_2\right) - c_1\phi' + |\phi'|^2 + r_2 \\ &= \left(\phi' - \frac{c_1}{2}\right)^2 \geq 0. \end{aligned}$$

This proves that  $\hat{\rho}$  is a viscosity super-solution.

This completes the proof that the unique viscosity solution  $\hat{\rho}$  as guaranteed by Lemma 13 is given by the explicit formula (3.53) for the first representative Case 1(b).

Let us proceed with Case 2(b), where we fix  $r_1, r_2, c_1$  satisfying

$$r_1 > r_2, \quad \text{and} \quad c_1 \geq 2\sqrt{r_1}. \quad (3.54)$$

Next, we set

$$R(s) = R_{2b}(s) = \begin{cases} r_2 & \text{for } s \geq c_1, \\ r_1 & \text{for } 2\sqrt{r_1} \leq s < c_1 \\ r_1 & \text{for } s < 2\sqrt{r_1} \end{cases}$$

and

$$\hat{\rho}(s) = \begin{cases} \frac{s^2}{4} - r_2 & \text{for } s > 2\tilde{\lambda} \\ \tilde{\lambda}s - (\tilde{\lambda}^2 + r_2) & \text{for } c_1 < s \leq 2\tilde{\lambda} \\ \frac{s^2}{4} - r_1 & \text{for } 2\sqrt{r_1} < s < c_1 \\ 0 & \text{for } 0 \leq s \leq 2\sqrt{r_1}, \end{cases} \quad (3.55)$$

where  $\tilde{\lambda} = \frac{c_1}{2} + \sqrt{r_1 - r_2}$ .

Again, we first observe that  $\hat{\rho}$ , as given in (3.55), is continuous, and satisfies the equation (3.29) in the classical sense for  $s \in [0, \infty) \setminus \{c_1, 2\sqrt{r_1}\}$  (note that it is in fact continuously differentiable in a neighborhood of  $s = 2\tilde{\lambda}$ ). It then follows again from [7, Proposition 5.1] that  $\hat{\rho}$  is a viscosity sub-solution of (3.29).



Next, we verify that it is also a viscosity super-solution. Suppose  $\hat{\rho} - \phi$  obtains a strict local minimum at  $s_0 \in [0, \infty)$  for some  $\phi \in C^1$ . Since  $\hat{\rho}$  is a classical solution of (3.29) for all  $s \notin \{c_1, 2\sqrt{r_1}\}$ , we need only consider  $s_0 \in c_1$  or  $s_0 = 2\sqrt{r_1}$ . Suppose  $s_0 = c_1$ , then

$$\rho - s_0\phi' + |\phi'|^2 + R^* = \left(\frac{c_1^2}{4} - r_1\right) - c_1\phi' + |\phi'|^2 + r_1 = \left(\phi' - \frac{c_1}{2}\right)^2 \geq 0 \quad \text{at } s = s_0.$$

Suppose  $s_0 = 2\sqrt{r_1}$ , then

$$\rho - s_0\phi' + |\phi'|^2 + R^* = 0 - (2\sqrt{r_1})\phi' + |\phi'|^2 + r_1 = (\phi' - \sqrt{r_1})^2 \geq 0 \quad \text{at } s = s_0.$$

This verifies that  $\hat{\rho}$  is a viscosity super-solution of (3.29). This completes the proof that the unique viscosity solution  $\hat{\rho}$  as guaranteed by Lemma 13 is given by the explicit formula (3.55) for the first representative Case 2(b).

We omit the verification of the other cases since they are analogous.  $\square$

**Corollary 2.** *Suppose either that (1)  $r_1 < r_2$ , or that (2)  $r_1 > r_2$  and  $c_1 \notin (2\sqrt{r_1}, 2\sqrt{r_2})$ .*

*Then there exists  $\delta_0 > 0$  such that for each  $\eta > 0$ ,*

$$\liminf_{t \rightarrow \infty} \inf_{|x| < (\sigma - \eta)t} u(t, x) \geq \delta_0 \quad \text{for each } \eta > 0 \text{ small enough,}$$

*where  $\sigma = \sigma(c_1; r_1, r_2)$  is given in (3.16). In particular, we have*

$$\underline{c}_* \geq \sigma(c_1; r_1, r_2). \tag{3.56}$$

*Proof.* Observe that

$$u_t \geq u_{xx} + u(\delta' - u) \quad \text{for } (t, x) \in (0, \infty) \times \mathbb{R}$$

where  $\delta' = \beta \inf_{s \in \mathbb{R}} a(s) - 1 > 0$ , thanks to (H1). Since  $u$  has compactly supported initial data, it follows from standard theory that the spreading speed of  $u$  is bounded

from below by  $2\sqrt{\delta'}$ , i.e.

$$\liminf_{t \rightarrow \infty} \inf_{|x| < 3\sqrt{\delta'}t/2} u(t, x) \geq \delta_0. \quad (3.57)$$

For given  $c_1, r_1, r_2 > 0$  satisfying any of the cases 1(a)-(c) and 2(a)-(b), Lemma 17 says that the unique solution  $\hat{\rho}$  guaranteed in Lemma 13 is given as in Subsection 3.5.1. If we define

$$\hat{s} := \sup\{s \geq 0 : \hat{\rho}(s) = 0\},$$

then it is easy to see that  $\hat{s} = \sigma(c_1; r_1, r_2)$ , where the latter is given in (3.16). By Lemmas 14 and 15,  $0 \leq \rho^*(s) \leq \hat{\rho}(s)$  for  $s \geq 0$ . Thus,  $\rho^*(s) = 0$  for all  $s \in [0, \sigma]$ , where  $\sigma = \sigma(c_1; r_1, r_2)$ .

It follows from Lemma 11 that

$$\liminf_{t \rightarrow \infty} \inf_{\eta t < x < (\sigma - \eta)t} u(t, x) \geq \delta_0 \quad \text{for each } \eta > 0 \text{ small enough,} \quad (3.58)$$

and a similar statement holds for  $x < 0$ . The desired result follows by combining with (3.57).  $\square$

*Proof of Theorems 7 and Theorem 8.* We recall that  $\underline{c}_* \leq \bar{c}_*$ , by construction. On the other hand, by Lemma 4,  $\bar{c}_* \leq \sigma_1(c_1; r_1, r_2)$ , and by Corollary 2,  $\underline{c}_* \geq \sigma_1(c_1; r_1, r_2)$ . It follows that  $\underline{c}_* = \bar{c}_* = \sigma_1(c_1; r_1, r_2)$ , so that the spreading speed of  $u$  is given by  $c^* = \sigma_1(c_1; r_1, r_2)$ .  $\square$

### 3.6 Convergence to homogeneous state

In this section, we apply the previous spreading result to characterize the long-term behavior of solutions of (3.4) in the moving frame where the predator persists.

Having established the existence of the spreading speed  $c^*$ , and recalling Lemma 8, it follows that  $(u, v) \rightarrow (0, 1)$  locally uniformly in any moving frame with speed above

$c^*$ , and that  $u$  persists in any moving frame with speed below  $c^*$ . In the following we discuss the asymptotic behavior of the solutions in the latter case. Define, for  $i = 1, 2$ ,

$$u_i = \frac{a_i - 1}{1 + a_i b}, \quad v_i = \frac{1 + b}{1 + a_i b} \quad (3.59)$$

where  $a_1 := a(-\infty)$  and  $a_2 := a(+\infty)$ . Then  $(u_i, v_i)$  is the unique positive root of the algebraic system

$$u(-1 - u + a_i v) = 0 = rv(1 - v - bu).$$

*Proof of Theorem 9.* Denote  $c^* = \sigma(c_1; r_1, r_2)$ . Thanks to Corollary 2, for each  $\eta > 0$ , there exists  $T = T(\eta) > 0$  and  $\delta_0 > 0$  such that

$$u(t, x) \geq \delta_0 \quad \text{for } t \geq T, \quad -\eta t \leq x \leq (c^* - \eta/2)t. \quad (3.60)$$

Suppose for a contradiction that there exists  $\epsilon_0, \eta > 0$  and a sequence  $(t_k, x_k)$  with  $t_k \rightarrow \infty$  and  $0 \leq x_k < (c^* - \eta)t_k$  (the case for  $x_k \leq 0$  is similar), such that  $\|(u, v)(t_k, x_k) - (\tilde{u}, \tilde{v})\| > \epsilon_0$  for all  $k \geq 1$ , where

$$(\tilde{u}, \tilde{v}) = \begin{cases} (u_2, v_2) & \text{if } c_1 < c^* \quad \text{and } x_k \in ((c_1 + \eta)t_k, (c^* - \eta)t_k), \\ (u_1, v_1) & \text{otherwise.} \end{cases} \quad (3.61)$$

Let

$$u_k(t, x) := u(t + t_k, x + x_k) \quad \text{and} \quad v_k(t, x) := v(t + t_k, x + x_k),$$

then

$$u_k(t, x) \geq \delta_0 \quad \text{in } \Omega_k,$$

where

$$\Omega_k = \{(t, x) : t + t_k \geq T, \quad -\eta(t + t_k) \leq x + x_k \leq (c^* - \eta/2)(t + t_k)\}.$$

**Claim.**  $\Omega_k \rightarrow \mathbb{R}^2$ , i.e. for any compact subset  $K \subset \mathbb{R}^2$  there exists  $k_1 > 1$  such that

$$K \subset \Omega_k \quad \text{for all } k \geq k_1.$$

Indeed, given  $K$ , choose  $R > 0$  such that  $K \subset [-R, R] \times [-R, R]$ . Then for  $k \gg 1$ , we have

$$\begin{aligned} K &\subset [-R, R]^2 \\ &\subseteq \{(t, x) : |t| \leq R, \quad \eta(R - t_k) \leq x \leq -(c^* - \eta/2)R + \eta t_k/2\} \\ &\subseteq \{(t, x) : |t| \leq R, \quad -\eta(t + t_k) \leq x \leq (c^* - \eta/2)t + \eta t_k/2\} \\ &\subseteq \{(t, x) : t + t_k \geq T, \quad -\eta(t + t_k) - x_k \leq x \leq (c^* - \eta/2)t - x_k + (c^* - \eta/2)t_k\} \\ &= \Omega_k. \end{aligned}$$

This proves the claim.

It follows from the claim and Lemma 7 that there exists constants  $0 < \delta_1 < 1$  independent of  $k$  such that

$$\delta_1 \leq u_k \leq \frac{1}{\delta_1} \quad \text{and} \quad \delta_1 \leq v_k \leq \frac{1}{\delta_1} \quad \text{in } \Omega_k \quad (3.62)$$

Using the above  $L^\infty$  bounds and parabolic  $L^p$  estimates we may deduce, re-labelling a sub-sequence if necessary, that  $(u_k, v_k)$  weakly in  $W_{loc}^{2,1,p}(\mathbb{R}^2)$  (and strongly in  $C_{loc}^{1+\alpha, (1+\alpha)/2}(\mathbb{R}^2)$  thanks to Sobolev embedding) to an entire solution  $(u_\infty, v_\infty)$  of the system

$$\begin{cases} u_t &= u_{xx} + u(-1 - u + \tilde{a}v) \\ v_t &= dv_{xx} + rv(1 - v - bu), \end{cases}$$

where  $\tilde{a} = a_2$  if  $c_1 < c^*$  and  $x_k \in ((c_1 + \eta)t_k, (c^* - \eta)t_k)$ , and  $\tilde{a} = a_1$  otherwise.

Moreover, (3.62) also implies that

$$\delta_1 \leq u_\infty \leq \frac{1}{\delta_1} \quad \text{and} \quad \delta_1 \leq v_\infty \leq \frac{1}{\delta_1} \quad \text{in } \mathbb{R}^2. \quad (3.63)$$

Having established the positive upper and lower bounds for  $(u_\infty, v_\infty)$  on  $\mathbb{R}^2$ , one can then repeat a standard argument via Lyapunov functional (see the proof of Lemma 4.1 in [29]) that  $(u_\infty, v_\infty)$  is identically equal to the homogeneous steady state  $(\tilde{u}, \tilde{v})$  given in (3.61), i.e.,  $(u_k, v_k) \rightarrow (\tilde{u}, \tilde{v})$  in  $C_{loc}(\mathbb{R}^2)$ . This in particular implies

$$(u, v)(t_k, x_k) = (u_k, v_k)(0, 0) \rightarrow (\tilde{u}, \tilde{v}) \quad \text{as } k \rightarrow \infty.$$

But this is a contradiction, which completes the proof.  $\square$

## 3.7 Appendix

### 3.7.1 Comparison Principle

Recall the Hamilton-Jacobi equation

$$\min\{\rho - s\rho' + |\rho'|^2 + \tilde{R}(s), \rho\} = 0 \quad \text{for } s \in (0, \infty). \quad (3.64)$$

We prove a comparison principle for (3.64) for discontinuous  $\tilde{R} : \mathbb{R} \rightarrow \mathbb{R}$  that is locally monotone [20].

**Definition.** A function  $h : \mathbb{R} \rightarrow \mathbb{R}$  is locally monotone if for every  $s_0 \in \mathbb{R}$ , either

$$\lim_{\delta \rightarrow 0} \inf_{\substack{|s_i - s_0| < \delta \\ s_1 > s_2}} (h(s_1) - h(s_2)) \geq 0 \quad \text{or} \quad \lim_{\delta \rightarrow 0} \sup_{\substack{|s_i - s_0| < \delta \\ s_1 > s_2}} (h(s_1) - h(s_2)) \leq 0.$$

The assumptions on  $\tilde{R}$  are stated precisely as follows.

(B1)  $\tilde{R}(s)$  is locally monotone;

(B2)  $\tilde{R}^*(s) = \tilde{R}_*(s)$  almost everywhere, and  $\inf_{s>0} R(s) > 0$ , where  $\tilde{R}^*$  and  $\tilde{R}_*$  are defined by

$$\tilde{R}^*(s) = \limsup_{s' \rightarrow s} \tilde{R}(s') \quad \text{and} \quad \tilde{R}_*(s) = \liminf_{s' \rightarrow s} \tilde{R}(s').$$

**Lemma 18.** *Suppose  $\tilde{R}(s)$  satisfies (B1)-(B2). Let  $\bar{\rho}$  and  $\underline{\rho}$  be non-negative viscosity super- and sub-solutions, respectively, of (3.64) such that*

$$\underline{\rho}(0) \leq \bar{\rho}(0) \quad \text{and} \quad \lim_{s \rightarrow \infty} \frac{\underline{\rho}(s)}{s} \leq \lim_{s \rightarrow \infty} \frac{\bar{\rho}(s)}{s}. \quad (3.65)$$

*Then  $\underline{\rho} \leq \bar{\rho}$  in  $(0, \infty)$ .*

*Proof.* We apply the results of [60]. The specific form of the Hamilton-Jacobi equation (3.64) and assumptions (B1)-(B2), imply that [60, (H1)-(H6)] hold. Hence, [60, Proposition 2.11] applies.  $\square$

**Corollary 3.** *Let  $\tilde{R} : \mathbb{R} \rightarrow \mathbb{R}$  satisfy the assumptions (B1)-(B2). Then there exists a unique viscosity solution  $\hat{\rho}$  to (3.64) satisfying the boundary conditions*

$$\hat{\rho}(0) = 0 \quad \text{and} \quad \lim_{s \rightarrow \infty} \frac{\hat{\rho}(s)}{s} = \infty. \quad (3.66)$$

*Moreover,  $\hat{\rho}$  is nondecreasing.*

*Proof.* Thanks to (B1)-(B2), [60, Proposition 1.7(b)] applies. Next, by applying [60, Lemma 2.9], we deduce that  $s \mapsto \hat{\rho}(s)$  is nondecreasing.  $\square$

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