Population Dynamics in an Advective Environment

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Abstract

We consider a one-dimensional reaction-diffusion equation describing single and two-species population dynamics in an advective environment, based on the modeling frameworks proposed by Dockery et al. in 1998 and Lutscher, Lewis, and McCauley in 2006. We analyze the effect of rate of loss of individuals at both the upstream and downstream boundaries. In the single species case, we prove the existence of the critical domain size and provide explicit formulas in terms of model parameters. We further derive qualitative properties of the critical domain size and show that, in some cases, the critical domain size is either strictly decreasing over all diffusion rates, or monotonically increasing after first decreasing to a minimum. We also consider competition between species differing only in their diffusion rates. For two species having large diffusion rates, we give a sufficient condition to determine whether the faster or slower diffuser wins the competition. We also briefly discuss applications of these results to competition in species whose spatial niche is affected by shifting isotherms caused by climate change.

Keywords: Reaction-diffusion-advection, Critical domain size, Competition, Climate change

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 [3]. The idea that the "slower diffuser wins" was later reinforced by Dockery et al., who showed that in a population of finitely many phenotypes, differing solely in their diffusion rates, only the slowest diffuser may survive [1].

In those 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. The following model for competing species in a river was studied by Lou and Lutscher [4] and Lou and Zhou [5]:

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

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 [6] previously considered models of the form (1) in the single species case, and with $b=+\infty$, to study the "drift paradox" of species persistence in rivers. See also [7], which considered (1) for a single species with the "free-flow" condition $b=1$, and [8], which studied (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 [4, 5]. Thus, 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 slower diffuser persists [5].

In fact, Hao et al. [9] showed that the constant $b=\frac{3}{2}$ represents a critical threshold for the evolution of dispersal in (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 faster species becomes extinct.

1.1 The model

In (1), there is no flux at the upstream boundary $x = 0$. In this paper, we relax this assumption and consider the following system:

$$\begin{cases} u_t = \mu u_{xx} - \alpha u_x + u(r - \frac{u+v}{K}), & 0 < x < l, \ t > 0, \\ v_t = \nu v_{xx} - \alpha v_x + v(r - \frac{u+v}{K}), & 0 < x < l, \ t > 0, \\ \mu u_x(0,t) - \alpha u(0,t) = (b_0 - 1)\alpha u(0,t), & t > 0, \\ \mu u_x(l,t) - \alpha u(l,t) = -b_l \alpha u(l,t), & t > 0, \\ \nu v_x(0,t) - \alpha v(0,t) = (b_0 - 1)\alpha v(0,t), & t > 0, \\ \nu v_x(l,t) - \alpha v(l,t) = -b_l \alpha v(l,t), & t > 0, \end{cases} \tag{2}$$

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

There have been several recent works investigating Lotka-Volterra competition systems in advective environments; see, e.g., [10], which considered the global dynamics of (2) with $(b_0, b_l) = (1, 0)$, a spatially-dependent resource function $r(x)$, and possibly distinct advection rates for u and v; [11], which considered a similar model as in [10], with distinct resource functions for u and v; and [12], which studied (2) for $b_0 > 1$ and $b_0 > 0$, identical diffusion rates $\mu = \nu$, and possibly distinct advection rates. We also note a preprint by Yin Wang, Qingxiang Xu, and Peng Zhou, which determines the global dynamics of (2) under the condition that b_0 and b_l are not large. For a summary of recent developments concerning competitive reaction-diffusion-advection systems, we refer to the review [13].

In this work, we investigate (2) for slightly more general boundary conditions, and focus on competing species differing only in their dispersal rates. 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.

1.2 Motivation of our problem: climate change

In concert with rising temperatures, many species have been observed to migrate toward the poles [14]. To study these habitat shifts, Lewis and Potapov [15] considered a two-species model of the form

$$\begin{cases} u_t = \mu u_{xx} + u(r_1 - c_{11}u - c_{12}v), & 0 \le x + \alpha t \le l, \\ v_t = \nu v_{xx} + v(r_2 - c_{21}u - c_{22}v), & 0 \le x + \alpha t \le l, \\ u_t = \mu u_{xx} - \kappa_1 u, & x + \alpha t < 0 \text{ and } x + \alpha t > l, \\ v_t = \nu v_{xx} - \kappa_2 v, & x + \alpha t < 0 \text{ and } x + \alpha t > l. \end{cases} \tag{3}$$

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(See also [16], which considered the effect of a shifting habitat range on the dynamics of a single species. We also note recent work [17] 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 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), we have modified the equation in [15] 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 κ_i. Finally, only species densities which converge to 0 as $x \to \pm\infty$ 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 $x \to x + \alpha t$, (3) is converted to an equation in which the suitable habitat range of each species is fixed:

$$\begin{cases} u_t = \mu u_{xx} - \alpha u_x + u(r - \frac{u+v}{K}), & 0 \leq x \leq l, \\ v_t = \nu v_{xx} - \alpha v_x + v(r - \frac{u+v}{K}), & 0 \leq x \leq l, \\ u_t = \mu u_{xx} - \alpha u_x - \kappa_1 u, & x < 0 \text{ and } x > l, \\ v_t = \nu v_{xx} - \alpha v_x - \kappa_2 v, & x < 0 \text{ and } x > l. \end{cases} \tag{4}$$

As in [15], we assume that u_x, v_x, u, and v are continuous at $x = 0$ and $x = l$. Then, following Ludwig et al. [18], the set of equilibrium solutions to (4) can be identified with the set of stationary solutions for the following equation on a bounded domain:

$$\begin{cases} u_t = \mu u_{xx} - \alpha u_x + u(r - \frac{u+v}{K}), & 0 < x < l, \\ v_t = \nu v_{xx} - \alpha u_x + u(r - \frac{u+v}{K}), & 0 < x < l, \\ \mu u_x(0) - k_\mu^+ u(0) = \nu v_x(0) - k_\nu^+ v(0) = 0, \\ \mu u_x(l) - k_\mu^- u(l) = \nu v_x(l) - k_\nu^- v(l) = 0, \end{cases} \tag{5}$$

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 [15], corresponding stationary solutions of (4) and (5) are either both linearly unstable or stable. Thus, to consider steady states of (4) and their stability, we may instead consider the equilibrium solutions of (5). We note that in the single species case where $v = 0$, equilibrium solutions to (5) are equilibrium solutions of (2), with $b_0 = b_l = \frac{1+\sqrt{1+\frac{4\mu\kappa_1}{\alpha^2}}}{2}$.

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) for a single species, given by the following equation:

$$\begin{cases} u_t = \mu u_{xx} - \alpha u_x + u(r - u/K), & 0 < x < l,\ t > 0, \\ \mu u_x(0) - \alpha u(0) = (b_0 - 1)\alpha u(0), \\ \mu u_x(l) - \alpha u(l) = -b_l \alpha u(l). \end{cases} \tag{6}$$

In particular, we are interested in the existence of positive steady state solutions of (6), which satisfy

$$\begin{cases} \mu u_{xx} - \alpha u_x + u(r - u/K) = 0, & 0 < x < l, \\ \mu u_x(0) - \alpha u(0) = (b_0 - 1)\alpha u(0), \\ \mu u_x(l) - \alpha u(l) = -b_l \alpha u(l). \end{cases} \tag{7}$$

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 to insulate the population from hostile conditions at the habitat edges. The minimal domain size required to sustain a population is known as the critical domain size [19], and we assert its existence for (6) in the following theorem:

Theorem 1. *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 (6) has a unique, positive, globally asymptotically stable steady state if and only if $l > l^*$. If $l \leq l^*$, then all solutions of (6) converge asymptotically to $u = 0$. Moreover, if we denote*

$$\hat{\mu} = \begin{cases} \frac{\alpha^2}{4r} & \text{if } \min\{b_0, b_l\} \geq \frac{1}{2} \\ \frac{\alpha^2 \min\{b_0,b_l\}(1-\min\{b_0,b_l\})}{r} & \text{if } 0 \leq \min\{b_0, b_l\} < \frac{1}{2}, \end{cases} \tag{8}$$

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

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

Remark. *Influential early work regarding the critical domain size for randomly dispersing species can be found in [19, 20]. The problem of critical domain size in an advective environment was first studied in [6] 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 [21]). Later on, this work was generalized in [22] 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 [5, 7, 9, 12]. In particular, in [12], a formula for the critical domain size of (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 $L \mapsto \lambda_1(L)$, where λ_1 is principal eigenvalue 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

Theorem 2. *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 (8) and define*

$$G(b_0, b_l) = \frac{1}{4} + (b_0 - \frac{1}{2})(b_l - \frac{1}{2}) - \frac{(b_0 + b_l - 1)^2}{3}. \tag{9}$$

eq:GG

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

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

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 $(b_0 + b_l - 1)^2 \geq 0.941(b_0 + b_l - 1 - 2b_0 b_l)^2$, and that either*

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

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 2 was proved previously by the combined efforts of [5] and [9] in the case $b_0 = 1$ and $b_l > 0$. When there is no flux 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 2 implies that, for sufficiently large diffusion rates, increasing μ 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 μ (Figure 1).

b=b0=bl

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

(a) *If* $\frac{1}{2} < \tilde{b} \leq \frac{1}{2}(1+\sqrt{3})$, *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* $\mu \gg 1$.

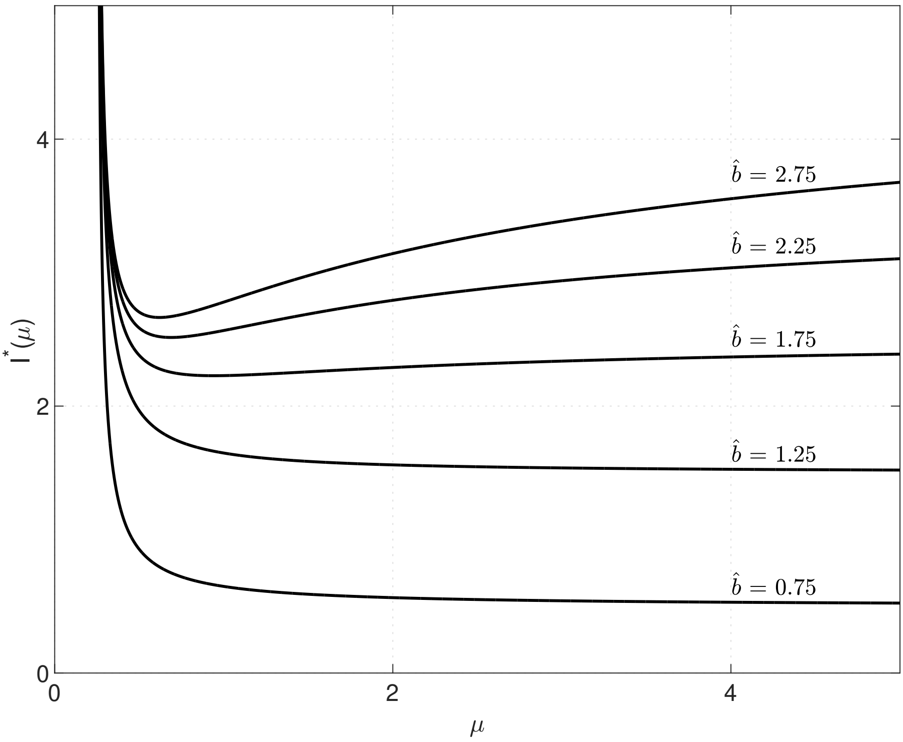

Fig. 1 Dependence of l^* on the diffusion rate μ for varying $\tilde{b} = b_0 = b_l$. l^* is strictly decreasing for $\mu \gg 1$ if $\tilde{b} \leq \frac{1}{2}(1+\sqrt{3})$, and strictly increasing for $\mu \gg 1$ if $\tilde{b} > \frac{1}{2}(1+\sqrt{3}) \approx 1.366$ (Corollary 1).

fig:l_p

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). 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.

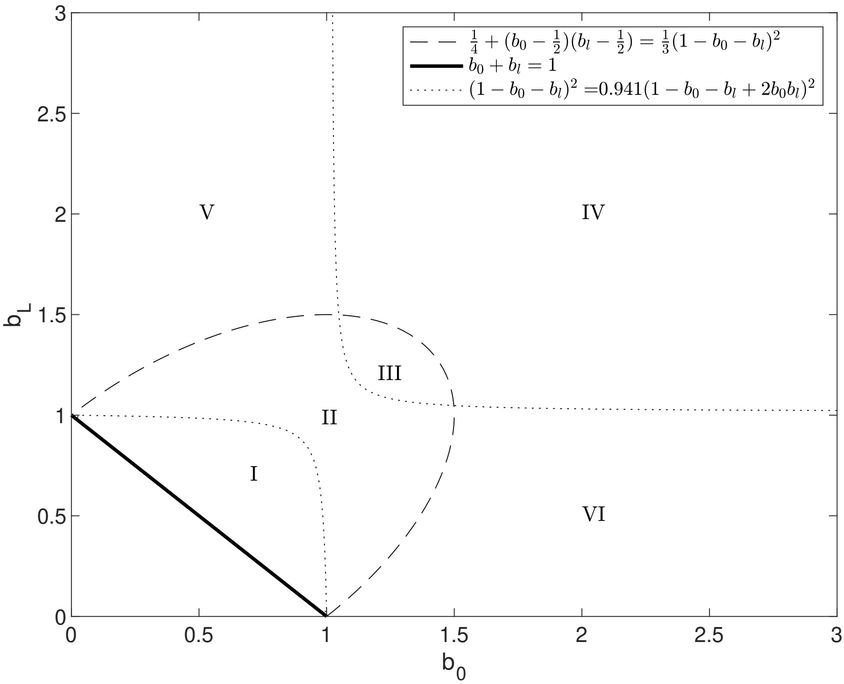

Fig. 2 $l^*(\mu)$ is strictly decreasing for $\mu \gg 1$ if (b_0, b_l) lies in regions I, II, or III above, and $l^*(\mu)$ is decreasing for all $\mu > \hat{\mu}$ if (b_0, b_l) lies in region II, and if $\min\{b_0, b_l\} \geq \frac{1}{2}$ (Theorem 2 (a)). On the other hand, $l^*(\mu)$ is strictly increasing 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 is monotonically increasing (Theorem 2 (b)). fig:lev

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 θ_μ denote the unique positive solution of (6), if it exists. We now state our main result on the competitive dynamics of (2):

etition **Theorem 3.** *Assume $b_0 + b_l > 1$ and recall the definition of $G(b_0, b_l)$ in (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 [9], where Theorem 3 was proved in the case $b_0 = 1$ and $b_l > 0$. We see that in (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 [3] and [1], where the slower diffuser always prevails.

It is interesting to consider the behavior of solutions of (7) in the limit as $\mu \to \infty$. 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 (7) exists for all sufficiently large μ. Then as $\mu \to \infty$, we observe that solutions θ_μ of (7) converge to an ideal free distribution. Introduced by Fretwell and Lucas [23], 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 θ_μ of (7) converge to the positive, constant density $K\big(r - \frac{\alpha(b_0+b_l-1)}{l}\big)$ as $\mu \to \infty$, 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 [24–26]. We have seen that $\mu = +\infty$ is an IFD strategy of (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 3 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) [27]. On the other hand, if $G(b_0, b_l) < 0$, then $\mu^* = +\infty$ is not a CSS.

1.5 Discussion

We briefly discuss applications of our results to the moving habitat model studied in [15] and [16]. The set of steady states of the moving habitat model (4) and of equation (5), where the domain is bounded, are equivalent [15]. With appropriate choices for b_0 and b_l, equation (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 $b_0 + b_l = 1 + \sqrt{1 + \frac{4\mu\kappa_1}{\alpha^2}} > 1$.

It is interesting to consider our results in the context of the parameter α, which denotes the velocity of the shifting habitat in (3), and serves to capture the potential effects of climate change. Theorem 1 shows that increasing α 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 2. To apply these results for a single species, we assume that the death rate κ_1 is inversely proportional to μ, so that μ 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 2 says 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 $\alpha^2 < 2\mu\kappa_1$. In the former case, if it is also true that $\alpha^2 > 8\mu\kappa_1$, 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 κ_1.

Our results also apply to two-species competition in a moving habitat. 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 3 implies that faster diffusion is advantageous in rapidly-shifting habitats, while slower diffusion is advantageous if the habitat is moving slowly. In particular, if $\alpha^2 > C$, 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 ($\alpha^2 < C$), 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 Proofs for the critical domain size

In this section we demonstrate the existence of a critical domain size for (6). To this end, we consider the eigenvalue problem

$$\begin{cases} \mu\varphi_{xx} - \alpha\varphi_x + r\varphi = \lambda\varphi, & 0 < x < l, \\ \mu\varphi_x(0) - \alpha b_0\varphi(0) = \mu\varphi_x(l) + \alpha(b_l - 1)\varphi(l) = 0, \end{cases} \tag{10}$$

which arises from linearizing (6) about the steady state $u \equiv 0$.

2.1 Existence of principal eigenvalue

It is well-known that problem (10) admits a principal eigenvalue; see, e.g., [28].

Proposition 1. *Assume $b_0 + b_1 \geq 1$. Then the eigenvalues of (10) are given by*

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

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 λ_1 is the principal eigenvalue of (10).

2.2 Formula for the critical domain size

The notion of a critical domain size for (6) is based on the following well-known result; see, e.g., [29].

Theorem 4. *Let λ_1 be the principal eigenvalue of (10).*

(i) *If $\lambda_1 \leq 0$, then $\lim_{t\to\infty} \|u(\cdot,t)\|_{C^0([0,l])} = 0$ for every nonnegative solution of (6).*

(ii) *If $\lambda_1 > 0$, then (6) has a unique positive equilibrium θ. Moreover,*

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

for every nonnegative, nontrivial solution of (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 (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* (6) *if*

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

where λ_1 is the principal eigenvalue of (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., cosner_book [29].

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

$$l_1^* = \begin{cases} +\infty, & 0 < \mu \leq \frac{\alpha^2}{4r} \\ F_1(0;\ \mu, \alpha, r, b_0, b_l), & \mu > \frac{\alpha^2}{4r}. \end{cases} \tag{11}$$

eq:l1**

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

$$l_2^* = \begin{cases} +\infty, & 0 < \mu \leq \frac{\alpha^2 \min\{b_0,b_l\}(1-\min\{b_0,b_l\})}{r} \\ F_2(0;\ \mu, \alpha, r, b_0, b_l), & \frac{\alpha^2 \min\{b_0,b_l\}(1-\min\{b_0,b_l\})}{r} < \mu < \frac{\alpha^2}{4r} \\ -\frac{\alpha(b_0+b_l-1)}{4r(b_0-\frac{1}{2})(b_l-\frac{1}{2})}, & \mu = \frac{\alpha^2}{4r} \\ F_1(0;\ \mu, \alpha, r, b_0, b_l), & \mu > \frac{\alpha^2}{4r}. \end{cases} \tag{12}$$

eq:l2**

Here, F_1 and F_2 are given by

$$F_1(\lambda;\ \mu, \alpha, r, b_0, b_l) := \frac{2\mu}{\sqrt{4\mu(r-\lambda)-\alpha^2}}\left[\arctan\left(\frac{2\alpha(b_l-\frac{1}{2})}{\sqrt{4\mu(r-\lambda)-\alpha^2}}\right) - \arctan\left(\frac{-2\alpha(b_0-\frac{1}{2})}{\sqrt{4\mu(r-\lambda)-\alpha^2}}\right)\right], \tag{13}$$

eq:F1

$$F_2(\lambda;\ \mu, \alpha, r, b_0, b_l) := \frac{\mu}{\sqrt{\alpha^2-4\mu(r-\lambda)}} \cdot \log\frac{\left[\frac{1}{2}\sqrt{\alpha^2-4\mu(r-\lambda)}-\alpha(b_0-\frac{1}{2})\right]\left[\frac{1}{2}\sqrt{\alpha^2-4\mu(r-\lambda)}-\alpha(b_l-\frac{1}{2})\right]}{\left[\frac{1}{2}\sqrt{\alpha^2-4\mu(r-\lambda)}+\alpha(b_0-\frac{1}{2})\right]\left[\frac{1}{2}\sqrt{\alpha^2-4\mu(r-\lambda)}+\alpha(b_l-\frac{1}{2})\right]}. \tag{14}$$

eq:F2

Remark. *The case $(b_0, b_l) = (1, +\infty)$ is contained in* speirs *[6]; the case $(b_0, b_l) = (1, 1)$ is contained in* mckenzie *[22]; the case $(b_0, b_l) \in \{1\} \times (0, \infty)$ is contained in* lou_zhou *[5]; the case $(b_0, b_l) \in (1, \infty) \times (0, \infty)$ is contained in* xu *[12].*

Equation (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* $b_l \to \infty$, *we see from* (11) *that the critical domain size* $l^* \to \frac{2\mu}{\sqrt{4\mu r-\alpha^2}}\left(\frac{\pi}{2} - \arctan\left(\frac{-\alpha}{\sqrt{4\mu r-\alpha^2}}\right)\right)$, *which is consistent with the case of Dirichlet conditions at* $x = l$, *studied in* [6] *(we note that the expression for the critical domain size in* [6] *should be adjusted according to* (3.2) *in* [22]*). On the other hand, as* $b_l \to 0^+$, *we observe that the critical domain size* $l^* \to 0$ *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* $l > 0$, (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 [16]*, and is equivalent to* (26), *with* $b_0 = b_l = \frac{1+\sqrt{1+\frac{4\mu\kappa_1}{\alpha^2}}}{2}$.

Remark. *As detailed in* [21]*, there is a connection between the critical domain size of* (6) *and the Fisher-KPP spreading speed. On the infinite domain* $-\infty < x < \infty$, *solutions to* (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* (6) *into the form of Fisher's equation via the change of variables* $x \mapsto x - \alpha t$*; see the discussion in* [21]*). Thus, the population spreads upstream if* $c^* > 0$, *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* (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* (12), *the critical domain size* l^* *is finite for* $\mu \in \left(\frac{\alpha^2 \min\{b_0,b_l\}(1-\min\{b_0,b_l\})}{r}, \frac{\alpha^2}{4r}\right)$, *so that the species will persist if the domain is large. However, for such* μ *we have* $c^* < 0$, *so that any bounded and initially compactly-supported solution to* (6) *on the infinite domain* $-\infty < x < \infty$ *will be eventually washed downstream.*

jection **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,*

$$l = F_1(\lambda_1;\ \mu, \alpha, r, b_0, b_l). \quad (15)$$ lcase1_

(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,*

$$l = \begin{cases} F_1(\lambda_1), & \lambda_1 < r - \frac{\alpha^2}{4\mu} \\ -\frac{\mu(b_0+b_l-1)}{\alpha(b_0-\frac{1}{2})(b_l-\frac{1}{2})}, & \lambda_1 = r - \frac{\alpha^2}{4\mu} \\ F_2(\lambda_1), & r - \frac{\alpha^2}{4\mu} < \lambda_1 < r - \frac{\alpha^2 \min\{b_0,b_l\}(1-\min\{b_0,b_l\})}{\mu}. \end{cases} \tag{16}$$

eq:lcas

Proof Suppose $b_0 + b_\ell > 1$, then thanks to Proposition 1, the elliptic problem (10) has a unique principal eigenvalue $\lambda_1 \in \mathbb{R}$ and positive eigenfunction ψ 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 λ_1. First, let $\psi = e^{-\frac{\alpha}{2\mu}x}\varphi$. Then (10) becomes

$$\begin{cases} \mu\psi_{xx} + (r - \frac{\alpha^2}{4\mu} - \lambda_1)\psi = 0, & 0 < x < l, \\ \mu\psi_x(0) - \alpha(b_0 - \frac{1}{2})\psi(0) = \mu\psi_x(l) + \alpha(b_l - \frac{1}{2})\psi(l) = 0. \end{cases} \tag{17}$$

eq:eig_

ambda1) **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 (17), ψ has the form

$$\psi = A\cos\Big(\frac{\sqrt{4\mu(r-\lambda_1) - \alpha^2}}{2\mu}(x - \eta)\Big), \tag{18}$$

eq:psi_

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

Now from the boundary conditions, we compute

$$-\frac{\alpha(b_0 - \frac{1}{2})}{\mu} = -\frac{\psi_x(0)}{\psi(0)} = \frac{\sqrt{4\mu(r-\lambda_1) - \alpha^2}}{2\mu}\tan\Big(\frac{\sqrt{4\mu(r-\lambda_1) - \alpha^2}}{2\mu}(-\eta)\Big) \tag{19}$$

eq:0con

and

$$\frac{\alpha(b_l - \frac{1}{2})}{\mu} = -\frac{\psi_x(l)}{\psi(l)} = \frac{\sqrt{4\mu(r-\lambda_1) - \alpha^2}}{2\mu}\tan\Big(\frac{\sqrt{4\mu(r-\lambda_1) - \alpha^2}}{2\mu}(l - \eta)\Big). \tag{20}$$

eq:lcon

Recall that ψ is positive on $[0, l]$, $b_0 + b_l > 1$, we observe that η and $l > 0$ are uniquely determined by (19) and (20). Hence, we may solve for l to obtain $l = F_1(\lambda_1)$. This proves Claim 1.

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

a^2/4d **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 ψ has the form

$$\psi(x) = Ax + B \quad \text{for some } A \in \{0, 1\}, \quad \text{and} \quad B \geq 0. \tag{21}$$

eq:line

Consider the two boundary conditions of (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 (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

$$l = -B - \frac{\mu}{\alpha(b_l - \frac{1}{2})} = -\mu\Big(\frac{1}{\alpha(b_0 - \frac{1}{2})} + \frac{1}{\alpha(b_l - \frac{1}{2})}\Big) < 0, \tag{22}$$

eq:l_ed

a contradiction.

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

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

By substituting into the boundary conditions, we find

$$\tanh\Big(\frac{\sqrt{\alpha^2 - 4\mu(r - \lambda_1)}}{2\mu}l\Big) = -\frac{2\alpha(b_0 + b_l - 1)\sqrt{\alpha^2 - 4\mu(r - \lambda_1)}}{\alpha^2 - 4\mu(r - \lambda_1) + 4\alpha^2(b_0 - \frac{1}{2})(b_l - \frac{1}{2})}. \tag{23}$$

eq:tanh

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

n b>1/2 **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 (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 (13) that $\lambda_1(l) \nearrow r - \frac{\alpha^2}{4\mu}$ as $l \to +\infty$ and $\lambda_1(l) \searrow -\infty$ as $l \to 0^+$. The mapping $l \mapsto \lambda_1(l)$, being a homeomorphism of $(0, \infty) \to (-\infty, r - \frac{\alpha^2}{4\mu})$, must be strictly increasing. This shows Claim 3. By Together, Claims 1, 2, and 3 establish part (i) of Lemma 1.

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

1-b)/d **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 (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

$$\alpha^2 - 4\mu(r - \lambda_1) + 4\alpha^2(b_0 - \frac{1}{2})(b_l - \frac{1}{2}) < -2\alpha(b_0 + b_l - 1)\sqrt{\alpha^2 - 4\mu(r - \lambda_1)}. \tag{24}$$

eq:tanh

In particular, since the right hand side of (24) is negative, we note that

$$\mu(r-\lambda_1) > \frac{\alpha^2}{4}[1+4(b_0-\frac{1}{2})(b_l-\frac{1}{2})] > \alpha^2 \max\{b_0,b_l\}(1-\max\{b_0,b_l\}). \quad (25)$$

eq:lamb

After some calculations, (24) implies that

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

By (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.

a2/4u

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 (23).

b < 1/2

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 (13), (22), and (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 λ_1, since

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

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 (14) that $\lambda \nearrow r-\frac{\alpha^2\min\{b_0,b_l\}(1-\min\{b_0,b_l\})}{\mu}$ as $l \to +\infty$, and from (13) that $\lambda \searrow -\infty$ as $l \to 0^+$. 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), concluding the proof. □

formula **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*

$$l_1^* = \begin{cases} +\infty, & 0 < \mu \leq \frac{\alpha^2}{4r} \\ F_1(0;\ \mu, \alpha, r, b_0, b_l), & \mu > \frac{\alpha^2}{4r}. \end{cases} \tag{26}$$

eq:l1*

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

$$l_2^* = \begin{cases} +\infty, & 0 < \mu \leq \frac{\alpha^2 \min\{b_0,b_l\}(1-\min\{b_0,b_l\})}{r} \\ F_2(0;\ \mu, \alpha, r, b_0, b_l), & \frac{\alpha^2 \min\{b_0,b_l\}(1-\min\{b_0,b_l\})}{r} < \mu < \frac{\alpha^2}{4r} \\ -\frac{\alpha(b_0+b_l-1)}{4r(b_0-\frac{1}{2})(b_l-\frac{1}{2})}, & \mu = \frac{\alpha^2}{4r} \\ F_1(0;\ \mu, \alpha, r, b_0, b_l), & \mu > \frac{\alpha^2}{4r}. \end{cases} \tag{27}$$

eq:l2*

Here, F_1 and F_2 are given in (13) and (14), respectively.

Remark. *Under the additional assumption that $b_0 > 1$ is given in* xu *[12, Sec. 2.2]. Note that $(b_u, b_d) = (b_0 - 1, b_\ell)$ under their notation.*

Remark. *For the case of a moving habitat on an infinite, one-dimensional domain, the critical domain size is given in formula (25) of* berestycki *[16], and is equivalent to (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), $\lambda_1 < 0$ for all $l > 0$. If $\mu > \frac{\alpha^2}{4r}$, the critical value l_1^* is obtained from setting $\lambda_1 = 0$ in (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 (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. □

2.3 Proof of Theorem 1

In this section, we show that the critical domain size l^* is the minimal domain size required for persistence of the species u in (6).

Proof of Theorem 1 We define

$$l^* = \begin{cases} l_1^*, & \min\{b_0, b_l\} \geq \frac{1}{2} \\ l_2^*, & 0 \leq \min\{b_0, b_l\} < \frac{1}{2}. \end{cases} \tag{28}$$

eq:l*

By Proposition 2, l^* is the critical domain size of (6). It follows from Theorem 4(i) that if $l > l^*$, then (6) has a unique, positive equilibrium θ such that

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

for every nonnegative, nontrivial solution u of (6). If $l \le l^*$, then by Theorem 4(ii)

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

for every nonnegative solution of (6). This establishes Theorem 1. □

2.4 Monotonicity of the critical domain size

We now prove Theorem 2, 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.

and L2

Proposition 3. *Fix $r, \alpha > 0$, and $b_0, b_l \ge 0$ such that $b_0 + b_l > 1$. Let $l^*(\mu, b_0, b_l)$ be given by (28).*

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

$$g\Big(\sqrt{r\tau - \frac{\alpha^2\tau^2}{4}}\, l^*\Big) = l^*\Big(\frac{r - \tau\frac{\alpha^2}{4} - \tau\alpha^2(b_0 - \frac{1}{2})(b_l - \frac{1}{2})}{\alpha(b_0 + b_l - 1)}\Big), \tag{29}$$

eq:g

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

(b) *Suppose that $(b_0 + b_l - 1)^2 \ge 0.941(b_0 + b_l - 1 - 2b_0b_l)^2$, and that there exists $\mu_0 \ge \frac{\alpha^2}{4r}$ for which $\frac{\partial l^*}{\partial \mu}(\mu_0, b_0, b_l) = 0$.*
   (i) *If $\min\{b_0, b_l\} \ge \frac{1}{2}$, 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 $\lim_{\mu\to\mu_0^+} \frac{\partial^2 l^*}{\partial \mu^2}(\mu_0, b_0, b_l) > 0$ if $\mu_0 = \frac{\alpha^2}{4r}$.*

(c) *If $\min\{b_0, b_l\} < \frac{1}{2}$ and $\max\{b_0, b_l\} \le 1$, 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 (13) that l^* satisfies

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

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

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

Thus,

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

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

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

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

By Proposition 3(a), l^* satisfies (29) for $\mu > \frac{\alpha^2}{4r}$. Differentiating (29) with respect to τ, we have

$$g'(ML)(M'L + ML') = L'N + LN' \quad \text{for } \tau \in (0, \frac{4r}{\alpha^2}). \tag{30}$$

eq:[g(M

Differentiating again and rearranging, we obtain

$$L''(N - g'(ML)M) = g''(ML)(M'L + ML')^2 + g'(ML)(M''L + 2M'L') - 2L'N' \tag{31}$$

eq:l''

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 1). Thus, we have $L'(\tau_0) = 0$ for some $\tau_0 \in (0, \frac{4r}{\alpha^2})$, so that setting $\tau = \tau_0$ in (31), we obtain

$$\Big[L''(N - g'(ML)M) = g''(ML)(M'L)^2 + g'(ML)(M''L)\Big]_{\tau=\tau_0}. \tag{32}$$

eq:l''

We first consider the case $\tau_0 = \frac{2r}{\alpha^2}$, where $M'(\tau_0) = 0$. Letting $\tau_0 = \frac{2r}{\alpha^2}$ in (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 (31), we obtain

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

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

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 $\tau = \tau_0$,

$$L''(N - g'(ML)M) = \left(\frac{N'L}{g'(ML)}\right)^2\left[g''(ML) - \frac{g'(ML)}{ML}\left(\frac{\alpha^2}{4(N')^2}g'(ML)^2 + 1\right)\right]. \tag{33}$$

eq:step

Setting $\tau = \tau_0$ in (30), we have

$$0 > g'(ML)\big|_{\tau=\tau_0} = \frac{N'(\tau_0)}{M'(\tau_0)} = -\alpha\left(\frac{\frac{1}{4} + (b_0 - \frac{1}{2})(b_l - \frac{1}{2})}{b_0 + b_l - 1}\right)\left(\frac{2M(\tau_0)}{r - \frac{\alpha^2\tau_0}{2}}\right). \tag{34}$$

eq:g'(M

Further, we note that

$$M'' = \Big(\frac{r - \frac{\alpha^2\tau}{2}}{2M}\Big)' = -\Big(\frac{\alpha^2}{4M} + \frac{(M')^2}{M}\Big). \tag{35}$$

eq:M''

Now recalling (32) and applying (34) and (35), we compute

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

for $\tau = \tau_0$.

Step 2. Next, we observe

$$\Big[N - g'(ML)M\Big]_{\tau=\tau_0} > 0. \tag{36}$$

eq:step

Recalling (34), a direct computation yields

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

Since $b_0 + b_l - 1 > 0$, (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 (36) follows.

Step 3. Finally, we show that

$$\Big[g''(ML) - \frac{g'(ML)}{ML}\Big(\frac{\alpha^2}{4(N')^2}g'(ML)^2 + 1\Big)\Big]_{\tau=\tau_0} > 0. \tag{37}$$

eq:step

By Lemma A.1, we have

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

if $C \geq 0.941$. Thus, (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, (33), (36), and (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 (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 (31) as follows:

$$\begin{aligned} L''(N - g'(ML)M) = g''(ML)(M'L + ML')^2 - \frac{g'(ML)}{ML}(\frac{\alpha^2}{4} + M'^2)L^2 \\ + \frac{g'(ML)}{ML}(r - \frac{\alpha^2\tau}{2})LL' - 2L'N' \end{aligned}$$

$$= (M'L)^2\Big[g''(ML) - \frac{g'(ML)}{ML}\Big(\frac{\alpha^2}{4(M')^2}+1\Big)\Big]$$
$$+ \frac{g'(ML)}{ML}(r - \frac{\alpha^2\tau}{2})LL'$$
$$+ g''(ML)\Big[(r-\frac{\alpha^2\tau}{2})L'L + (ML')^2\Big] - 2L'N' \qquad (38)$$

eq:step

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

Denoting the right hand side of (38) by $R(\tau)$, we will show that both

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

Thus, sending $\tau \to \frac{4r}{\alpha^2}^-$ in (38), we conclude that

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

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

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

and

$$\lim_{\tau\to\frac{4r}{\alpha^2}^-} R(\tau) = \lim_{\tau\to\frac{4r}{\alpha^2}^-}\Big[(M'L)^2\big(g''(ML) - \frac{g'(ML)}{ML}\big) + \frac{\alpha^2}{6}L^2\Big]$$
$$= \lim_{\tau\to\frac{4r}{\alpha^2}^-}\Big[L^4(2r-\alpha^2\tau)^2\Big(\frac{g''(ML) - \frac{g'(ML)}{ML}}{16(ML)^2}\Big) + \frac{\alpha^2}{6}L^2\Big]$$
$$= \Big[L^2\Big(\frac{\alpha^2}{6} - \frac{4r^2}{90}L^2\Big)\Big]_{\tau=\frac{4r}{\alpha^2}}$$
$$= \frac{1}{96}\Big(\frac{\alpha^2(b_0+b_l-1)}{r(b_0-\frac{1}{2})(b_l-\frac{1}{2})}\Big)^2\Big(1 - \frac{(b_0+b_l-1)^2}{60(b_0-\frac{1}{2})^2(b_l-\frac{1}{2})^2}\Big).$$

(We recall from (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 A.2, $L'(\frac{4r}{\alpha^2}) = 0$ only if $(b_0+b_l-1)^2 = 12(b_0-\frac{1}{2})(b_l-\frac{1}{2})\big[\frac{1}{4}+(b_0-\frac{1}{2})(b_l-\frac{1}{2})\big]$. That $\lim_{\tau\to\frac{4r}{\alpha^2}^-} R(\tau) > 0$ now follows by observing that

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

This concludes the proof. □

Proof of Proposition 3(c) We will use an argument similar to that of Proposition 2.2 in lou_zhou [5]. By (27), $l^* = F_2(0;\ \mu, b_0, b_l)$ for $\mu \in \big(\frac{\alpha^2}{r}\min\{b_0,b_l\}(1-\min\{b_0,b_l\}), \frac{\alpha^2}{4r}\big)$.

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

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

Suppose that $b_l < \frac{1}{2}$, $b_0 \le 1$. 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

$$\begin{aligned}F'(\mu) &= \frac{2M^2+\mu r}{4M^3}\log\frac{k_1}{k_2} + \frac{\mu r\alpha(b_0+b_l-1)\left(\alpha^2(b_0-\frac{1}{2})(b_l-\frac{1}{2}) - M^2\right)}{2M^2k_1k_2}\\ &= \frac{1}{4M^3k_1k_2}\Big((2M^2+\mu r)(k_1k_2)\log\frac{k_1}{k_2}\\ &\quad + 2M\mu r\alpha(b_0+b_l-1)\big(\alpha^2(b_0-\frac{1}{2})(b_l-\frac{1}{2}) - M^2\big)\Big). \end{aligned} \tag{39}$$

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We note that $4M^3k_1k_2 > 0$ for $\mu \in (\frac{\alpha^2 b_l(1-b_l)}{r}, \frac{\alpha^2}{4r})$.

We now consider the numerator of (39) as a function, h, of b_l. Differentiating in b_l, we obtain

$$\begin{aligned}h'(b_l) &= 2\alpha(2M^2+\mu r)\big(\alpha^2(b_0-\frac{1}{2})^2 - M^2\big)\big(M+\alpha(b_l-\frac{1}{2})\log\frac{k_1}{k_2}\big)\\ &\quad + 2M\mu r\alpha\big[2\alpha^2(b_0-\frac{1}{2})(b_l-\frac{1}{2}) - M^2 + \alpha^2(b_0-\frac{1}{2})^2\big],\\ h''(b_l) &= 2\alpha^2(2M^2+\mu r)\big(\alpha^2(b_0-\frac{1}{2})^2 - M^2\big)\\ &\quad \cdot\Big[\log\frac{k_1}{k_2} + (b_l-\frac{1}{2})\frac{2\alpha M(\alpha^2(b_0-\frac{1}{2})^2 - M^2)}{k_1k_2}\Big] + 4M\mu r\alpha^3(b_0-\frac{1}{2}),\\ h'''(b_l) &= \frac{8\alpha^3M(2M^2+\mu r)\big(\alpha^2(b_0-\frac{1}{2})^2-M^2\big)^2}{(k_1k_2)^2}\\ &\quad \cdot\Big[k_1k_2 + \alpha^2(b_l-\frac{1}{2})^2\big(M^2 - \alpha^2(b_0-\frac{1}{2})^2\big)\Big].\end{aligned}$$

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

$$\begin{aligned}k_1k_2 + \alpha^2(b_l-\frac{1}{2})^2\big(M^2 - \alpha^2(b_0-\frac{1}{2})^2\big) &= (\frac{\alpha^2}{4} - \mu r)(\alpha^2 b_0(1-b_0) - \mu r)\\ &< (\frac{\alpha^2}{4} - \mu r)(\alpha^2 b_l(1-b_l) - \mu r)\\ &< 0.\end{aligned}$$

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

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

It follows from (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 $0 < b_0 < \frac{1}{2}$, $b_l \le 1$ is similar, and we omit the details. □

Proof of Theorem 2 Using the same notation as in the proof of Proposition 3(b), we will show the existence of

$$-L'(0) = \lim_{\mu\to\infty} \mu^2 \frac{\partial l^*}{\partial \mu}, \tag{40}$$

eq:l* l

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

From (30), we have

$$\begin{aligned} L'\Big[\frac{r - \tau\frac{\alpha^2}{4} - \tau\alpha^2(b_0 - \frac{1}{2})(b_l - \frac{1}{2})}{\alpha(b_0+b_l-1)}\Big] - \alpha L\Big[\frac{\frac{1}{4} + (b_0 - \frac{1}{2})(b_l - \frac{1}{2})}{b_0+b_l-1}\Big] \\ = \frac{g'(ML)}{ML}\Big[\frac{L^2}{2}(r - \frac{\alpha^2\tau}{2}) + M^2LL'\Big] \end{aligned} \tag{41}$$

eq:l'

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

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

To prove part (a), suppose $G(b_0, b_l) > 0$. Then $L'(0) > 0$, so (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 (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 $l^*(\mu) \to \infty$ as $\mu \to \hat{\mu}^+$ (Theorem 1), $l^*(\mu)$ 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 $\mu > \tilde{\mu}$. If $\min\{b_0, b_l\} < \frac{1}{2}$, $\max\{b_0, b_l\} \leq 1$, then by Proposition 3(b)(ii) and (c), the same conclusion holds. This proves (b), and completes the proof. □

3 Proof of competition dynamics

We consider the equation:

$$\begin{cases} u_t = \mu u_{xx} - \alpha u_x + u(r - \frac{u+v}{K}), & 0 < x < l,\ t > 0, \\ v_t = \nu v_{xx} - \alpha v_x + v(r - \frac{u+v}{K}), & 0 < x < l,\ t > 0, \\ \mu u_x(0,t) - \alpha u(0,t) = (b_0 - 1)\alpha u(0,t), & t > 0 \\ \mu u_x(l,t) - \alpha u(l,t) = -b_l \alpha u(l,t), & t > 0 \\ \nu v_x(0,t) - \alpha v(0,t) = (b_0 - 1)\alpha v(0,t), & t > 0 \\ \nu v_x(l,t) - \alpha v(l,t) = -b_l \alpha v(l,t), & t > 0, \end{cases} \tag{42}$$

eq:two-

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

We note that $(0,0)$ is a trivial equilibrium of system (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

$$\begin{cases} \mu\theta_{xx} - \alpha\theta_x + (r-\theta/K)\theta = 0, & 0<x<l \\ \mu\theta_x(0) - \alpha\theta(0) = (b_0-1)\alpha\theta(0) \\ \mu\theta_x(l) - \alpha\theta(l) = -b_l\alpha\theta(l). \end{cases} \tag{43}$$

eq:one-

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., potapov, shigesada [15, 30]:

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

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:

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

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

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

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

(a) *If $\Lambda_\tau(0,0) < 0$, then there exists $\underline{\mu} > 0$ such that if $\mu > \nu \ge \underline{\mu}$, then $(\theta_\mu,0)$ is globally asymptotically stable among all nonnegative, nontrivial solutions of* (42)*.*

(b) *If $\Lambda_\tau(0,0) > 0$, then there exists $\underline{\mu} > 0$ such that if $\mu > \nu \ge \underline{\mu}$, then $(0,\theta_\nu)$ is globally asymptotically stable among all nonnegative, nontrivial solutions of* (42)*.*

Proof Our proof follows the arguments in Lemma 6.1 of hao [9]. First, we show that if $\Lambda_\tau(0,0) \neq 0$, then (42) has no positive equilibria for μ,ν sufficiently large. Otherwise, let $\mu_j \to \infty$ and $\nu_j \to \infty$ such that for each $j \ge 1$, (u_j,v_j) is a positive solution to (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:

$$\begin{cases} \tilde{u}_{j,xx} - \alpha\xi_j(1-2b_0)\tilde{u}_{j,x} + \xi_j\Big[\alpha^2 b_0\xi_j(b_0-1) + (r - \frac{u_j+v_j}{K})\Big]\tilde{u}_j = 0, & 0<x<l \\ \tilde{v}_{j,xx} - \alpha\tau_j(1-2b_0)\tilde{v}_{j,x} + \tau_j\Big[\alpha^2 b_0\tau_j(b_0-1) + (r - \frac{u_j+v_j}{K})\Big]\tilde{v}_j = 0, & 0<x<l \\ \tilde{u}_{j,x}(0) = \tilde{u}_{j,x}(l) + \xi_j\alpha(b_0+b_l-1)\tilde{u}_j(l) = 0 \\ \tilde{v}_{j,x}(0) = \tilde{v}_{j,x}(l) + \tau_j\alpha(b_0+b_l-1)\tilde{v}_j(l) = 0, \end{cases} \tag{44}$$

eq:two_

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

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

we observe from (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 $\tau_j'\to 0$ such that

$$\tilde{\Lambda}_\tau(\tau_j';\ u_j+v_j) = 0, \tag{45}$$

eq:dLam

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

Claim 7. *By passing to a subsequence,*

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

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 $\xi_j\to 0$ in (44), we obtain

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

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

$$\begin{cases} \tilde{U}_{j,xx} - \alpha\xi_j(1-2b_0)\tilde{U}_{j,x} + \xi_j\Big[\alpha^2 b_0\xi_j(b_0-1) + (r - \frac{u_j+v_j}{K})\Big]\tilde{U}_j = 0, & 0<x<l \\ \tilde{V}_{j,xx} - \alpha\tau_j(1-2b_0)\tilde{V}_{j,x} + \tau_j\Big[\alpha^2 b_0\tau_j(b_0-1) + (r - \frac{u_j+v_j}{K})\Big]\tilde{V}_j = 0, & 0<x<l \\ \tilde{U}_{j,x}(0) = \tilde{U}_{j,x}(l) + \xi_j\alpha(b_0+b_l-1)\tilde{U}_j(l) = 0 \\ \tilde{V}_{j,x}(0) = \tilde{V}_{j,x}(l) + \tau_j\alpha(b_0+b_l-1)\tilde{V}_j(l) = 0. \end{cases} \tag{46}$$

eq:U_j

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

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

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

First, we show that $C_u + C_v > 0$. Dividing the first equation in (46) by $\tilde{U}_j$ and integrating by parts over $(0, l)$, we have

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

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

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

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

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

Dividing the first and second equations by ξ_j and τ_j, respectively, and passing to the limit, we obtain

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

Adding these equations yields

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

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

Now by the continuous dependence of $\tilde{\Lambda}(\tau, h)$ on τ and h, letting $j \to \infty$ in (45) gives

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

where the the smooth extension of η_ξ up to $\xi = 0$ is given by the constant $K\big[r - \frac{\alpha(b_0+b_l-1)}{l}\big]$ (see Remark 5.1 in hao [9]). But this contradicts our assumption $\Lambda_\tau(0,0) \neq 0$. Thus, if $\Lambda_\tau(0,0) \neq 0$, then (42) has no positive equilibria for μ, ν sufficiently large.

To prove part (a), we observe that there exists $\delta_1 > 0$ such that for $(\xi, \tau) \in [0, \delta_1]^2$, (42) has no positive equilibrium and $\Lambda_\tau(\xi, \tau) < 0$, i.e.

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

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

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

So $(\theta_\mu, 0)$ is linearly stable and $(0, \theta_\nu)$ is linearly unstable. Since (42) has no positive equilibria, we conclude by Theorem B of [31] and Theorem 1.3 of [32] that $(\theta_\mu, 0)$ is globally asymptotically stable among all nonnegative, nontrivial solutions of (42). The proof of part (b) follows similar reasoning, and we omit the details. □

Theorem 5. *Assume $b_0 + b_l > 1$, and recall the definition of $G(b_0, b_l)$ in (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 1 implies that there exists $\underline{\mu} > 0$ such that (43) has a positive solution θ_μ for all $\mu > \underline{\mu}$. Thus, Λ is well-defined for all $(\xi, \tau) \in [0, 1/\underline{\mu}]^2$. If $G(b_0, b_l) > 0$, then by Lemma B.2, we have $\Lambda_\tau(0, 0) = -\alpha^2 \left[\frac{1}{4} + (b_0 - \frac{1}{2})(b_l - \frac{1}{2}) - \frac{(b_0+b_l-1)^2}{3}\right] < 0$. 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 (42). This proves assertion (a).

If $G(b_0, b_l) < 0$, then Lemma B.2 implies $\Lambda_\tau(0, 0) = -\alpha^2 \left[\frac{1}{4} + (b_0 - \frac{1}{2})(b_l - \frac{1}{2}) - \frac{(b_0+b_l-1)^2}{3}\right] > 0$. 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 (42). This proves assertion (b). □

Appendix A Computations for Prop. 3(b)

Lemma A.1. *Let $g(s) = s \cot s$, and $C \geq 0.941$. Then*

$$g''(s) - \frac{g'(s)}{s}[1 + Cg'(s)^2] > 0 \tag{A1}$$

for $0 < s < \pi$.

Proof Our proof is similar to that of Lemma A.12 of [9]. 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

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

$$= (1-C) + C\csc^2(s)\big((g-1)^2+s^2\big).$$

By the above expression, and since $\frac{-g'(s)}{s} \geq \frac{2}{3}$ for $s \in (0,\pi)$ (see [9] Lemma A.12), we observe

$$\begin{aligned} g'' - \frac{g'}{s}(1+Cg'^2) &= 2\csc^2(s)(g-1) - \frac{g'}{s}\Big[(1-C) + C\csc^2(s)\big((g-1)^2+s^2\big)\Big] \\ &\geq \frac{2}{3}\csc^2(s)\Big[3(g-1) + (1-C)\sin^2(s) + C\big((g-1)^2+s^2\big)\Big]. \end{aligned} \tag{A2}$$

Furthermore, we have

$$\begin{aligned} C(g-1)^2 + 3(g-1) + Cs^2 + (1-C)\sin^2(s) &\geq C\big[(g-1)^2 + \frac{3}{C}(g-1) + s^2\big] \\ &\geq C(s^2 - \frac{9}{4C^2}), \end{aligned} \tag{A3}$$

where the second inequality is deduced by completing the square. Combining (A2) and (A3), we find that (A1) 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

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

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

$$\begin{aligned} C(g-1)^2 + 3(g-1) + Cs^2 + (1-C)\sin^2(s) &\geq C\frac{s^4}{9} + \frac{-s^2 + s^4/10 - s^6/240}{1 - s^2/6 + s^4/120} \\ &\quad + Cs^2 + (1-C)(s - \frac{s^3}{6})^2 \\ &= \frac{s^4}{1 - \frac{s^2}{6} + \frac{s^4}{120}}\Big(\frac{4C}{9} - \frac{2}{5} \\ &\quad + \frac{189-220C}{2160}s^2 + \frac{9C-8}{1080}s^4 \\ &\quad + \frac{1-C}{4320}s^6\Big) \end{aligned} \tag{A4}$$

for $s \in (0, \frac{3}{2C}]$. We observe that the right hand side of (A4) is positive if

$$\frac{4C}{9} - \frac{2}{5} + \frac{189-220C}{2160}s^2 + \frac{9C-8}{1080}s^4 + \frac{1-C}{4320}s^6 > 0, \tag{A5}$$

and (A5) holds for $s \in (0, \frac{3}{2C}]$ if

$$C > \frac{2/5 - 7s^2/80 + s^4/135 - s^6/4320}{4/9 - 11s^2/108 + s^4/120 - s^6/4320} =: f(s). \tag{A6}$$

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 (A2) and (A4)-(A6), we conclude that (A1) also holds for $s \in (0, \frac{3}{2C}]$, which concludes the proof. □

a: l'=0

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

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

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 τ. 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 (41) that $L'(\tau)$ satisfies

$$L'\Big[\frac{r - \tau\frac{\alpha^2}{4} - \tau\alpha^2(b_0 - \frac{1}{2})(b_l - \frac{1}{2})}{\alpha(b_0 + b_l - 1)}\Big] - \alpha L\Big[\frac{\frac{1}{4} + (b_0 - \frac{1}{2})(b_l - \frac{1}{2})}{b_0 + b_l - 1}\Big]$$
$$= \frac{g'(ML)}{ML}\Big[M^2LL' + \frac{L^2}{2}(r - \frac{\alpha^2\tau}{2})\Big]$$

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 (27)), and $\frac{g'(s)}{s} = -\frac{2}{3} + o(s)$, sending $\tau \to \frac{4r}{\alpha^2}^-$ 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. □

Appendix B Computation of $\Lambda_\tau(0, 0)$

bda_tau

The proofs in this section follow analogous results in [9].

(0,tau)

Lemma B.1. *For each* $0 \leq \tau < \frac{4r}{\alpha^2}$, *the eigenvalue* $\Lambda(0, \tau)$ *satisfies*

$$1 - \frac{l}{\alpha(b_0 + b_l - 1)}\Big[\Lambda + \frac{\alpha^2\tau}{4} + \alpha^2\tau(b_0 - \frac{1}{2})(b_l - \frac{1}{2})\Big]$$
$$= g\Big(l\sqrt{(\frac{\alpha(b_0 + b_l - 1)}{l} - \Lambda)\tau - \frac{\alpha^2\tau^2}{4}}\Big), \quad \text{(B7)}$$

eq:Lamb

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

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

satisfies

$$\tan\Big(\frac{\sqrt{4\nu r - \alpha^2}}{2\nu} l^*\Big) = \frac{2\alpha(b_0+b_l-1)\sqrt{4\nu r-\alpha^2}}{4\nu r - \alpha^2 - 4\alpha^2(b_0-\frac{1}{2})(b_l-\frac{1}{2})}. \tag{B8}$$

eq:impl

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

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

if and only if $l^* = l$ satisfies (B8) with $r(1-\frac{\eta_0}{K}) - \Lambda$ replacing r, where $\eta_0 = K\big(1 - \frac{\alpha(b_0+b_l-1)}{rl}\big)$. 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 (B8), we arrive at the desired result. □

au(0,0)

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

Proof Using the expansion $s\cot(s) = 1 - \frac{s^2}{3} - \frac{s^4}{45} + \dots$, we can express (B7) as

$$\begin{aligned} 1 - \frac{l}{\alpha(b_0+b_l-1)}\Big[\Lambda + \frac{\alpha^2\tau}{4} + \alpha^2\tau(b_0-\frac{1}{2})(b_l-\frac{1}{2})\Big] \\ = 1 - \frac{l^2}{3}\Big[\Big(\frac{\alpha(b_0+b_l-1)}{l} - \Lambda\Big)\tau - \frac{\alpha^2\tau^2}{4}\Big] \\ - \frac{l^4}{45}\Big[\Big(\frac{\alpha(b_0+b_l-1)}{l} - \Lambda\Big)\tau - \frac{\alpha^2\tau^2}{4}\Big]^2 + O(|\tau|^3), \end{aligned} \tag{B9}$$

eq:Lamb

where $\Lambda = \Lambda(0,\tau)$. Differentiating (B9) in τ, and setting $\tau = 0$, we have

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

so that

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

□

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