Evolution of Dispersal in Advective Homogeneous Environment: the Effect of Boundary Conditions*

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Abstract: We consider a single species model and a two-species competition model in a one-dimensional advective homogeneous environment. One interesting feature in these models concerns the boundary condition at the downstream end, where the species can be exposed to a net loss of individuals, as tuned by a parameter b which measures the magnitude of the loss. We first determine necessary and sufficient conditions for the persistence of a single species for general value of b, in terms of the critical habitat size and the critical advection rate. Then for the competition model, we assume that two species are identical except their random diffusion rates. We obtain complete understanding when $0 \le b < 1$, and our result indicates that larger diffusion rate is selected, extending an earlier work [20] ($b = 1$). However, for $b > 1$ the dynamics can be quite different, and particularly we illustrate that some intermediate diffusion rate may be selected when $b > \frac{3}{2}$.

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1 Introduction

Individuals in a wide variety of environments are confronted with unidirectional drift (advection) that drives them out of the system and thus induces decline in population. Examples include gut-dwelling bacteria [2, 3, 17, 18], benthic marine species along coastlines with dominant long-shore currents [4], and even the oases in the desert moved by wind [7, 8]. However, perhaps the most salient example are these aquatic organisms, living in streams and rivers, where they are constantly subject to downstream advection due to water movement. See [14, 15, 19, 21, 22, 23, 24, 26] and references therein.

Why can populations persist in streams when they are constantly washed downstream? This question, termed as the "drift paradox" in literatures, has received considerable attentions [1, 12, 28]. Speirs and Gurney [26] argued that diffusive movement of organisms can allow persistence in an advective environment and considered the following mathematical model in [26]:

$$\begin{cases} u_t = du_{xx} - \alpha u_x + u[r-u], & 0 < x < L, t > 0, \\ du_x(0,t) - \alpha u(0,t) = 0, & t > 0, \\ u(L,t) = 0, & t > 0, \end{cases} \tag{1.1}$$

where $u(x,t)$ denotes the population density at location x and time t, d is the diffusion rate, L is the size of the habitat, and in the sequel, we call $x = 0$ the upstream end and $x = L$ the downstream end. α is the effective speed of the current (sometimes we also call α the advection speed/rate, and we remark here that α should be positive since $x = L$ is defined to be the downstream end). The constant $r > 0$ accounts for the intrinsic growth rate, which indicates that the environment is spatially homogeneous. We assume that d, r, α, L are all positive constants.

Speirs and Gurney [26] studied the local stability of steady state $u \equiv 0$ and concluded that it is unstable if and only if $\alpha < \sqrt{4dr}$ and $L > L^*$, where

$$L^* = 2d \frac{\pi - \arctan\left(\frac{\sqrt{4dr-\alpha^2}}{\alpha}\right)}{\sqrt{4dr - \alpha^2}}.$$

That is, the persistence is only likely when advection is slow and the stream is sufficiently long. It is natural to inquire whether such predictions still hold for more general situations. To this end, we consider the following single species problem:

$$\begin{cases} u_t = du_{xx} - \alpha u_x + u[r-u], & 0 < x < L, t > 0, \\ du_x(0,t) - \alpha u(0,t) = 0, & t > 0, \\ du_x(L,t) - \alpha u(L,t) = -b\alpha u(L,t), & t > 0. \end{cases} \tag{1.2}$$

We first give some comments on the boundary conditions in (1.2). At the upstream end $x = 0$, the organism is assumed to satisfy the no-flux boundary condition, which means that no individuals will pass through this boundary. While at the downstream end $x = L$, there appears an additional parameter b, which measures the loss rate of individuals at the boundary relative to the flow rate (see [21] for a detailed derivation). Clearly, for $b = 0$, we obtain the no-flux condition again, which together with the no-flux upstream condition, for instance, can be effectively used to study the sinking, self-shading phytoplankton model (see, e.g., [13, 14, 15]). For $b = 1$, one obtains the free-flow condition, referred as the Danckwerts condition, can be applied to the situation *stream to lake* (see [27]). When b becomes sufficiently large, i.e., $b \to \infty$, we get the hostile conditions, which can be used in the scenario *stream to ocean* (see [26]). Hence, the case of zero Dirichlet boundary condition $u(L,t) = 0$ can be formally regarded as $b = +\infty$.

For the case $b = 1$, Vasilyeva and Lutscher [27] proved that the species can persist when $\alpha < \sqrt{4dr}$ and $L > L^*$, where

$$L^* \triangleq \begin{cases} 2d\dfrac{\arctan \frac{\alpha\sqrt{4dr-\alpha^2}}{2rd-\alpha^2}}{\sqrt{4dr-\alpha^2}} & \text{for } 0 < \alpha \le \sqrt{2dr}, \\ 2d\dfrac{\pi + \arctan \frac{\alpha\sqrt{4dr-\alpha^2}}{2rd-\alpha^2}}{\sqrt{4dr-\alpha^2}} & \text{for } \sqrt{2dr} < \alpha < \sqrt{4dr}. \end{cases} \tag{1.3}$$

On the other hand, it is easy to see that if $b = 0$, then for any α, $L > 0$, problem (1.2) admits a unique positive steady state which is globally asymptotically stable among all non-negative and not identically zero initial data. Can we synthesize these results?

It turns out that the transition occurs at $b = \frac{1}{2}$. Namely, if $b \ge \frac{1}{2}$, the persistence happens when $\alpha < \sqrt{4dr}$ and $L > L^*$ for some positive number L^* depending on b, α, d, r; If $0 < b < \frac{1}{2}$, the persistence occurs when $\alpha < \sqrt{\frac{dr}{b(1-b)}}$ and $L > L^*$. As $b \to 0^+$, $\sqrt{\frac{dr}{b(1-b)}} \to \infty$ and $L^* \to 0^+$, which is consistent with the case $b = 0$. The explicit expressions of L^* are given in the next section, where we will also show that L^* is always a strictly increasing function of α, and it is a strictly decreasing function of d provided that $b \in (0,1)$. This suggests that when $b \in (0,1)$, the persistence is more likely if we increase the diffusion rate. A natural question arises: will large diffusion always be selected during the course of evolution? The second part of our paper intends to address this question.

It has now been well accepted that as long as the organisms disperse by only random diffusion, slow diffusion rate will be selected provided that the environments under consideration are spatially heterogeneous but temporally constant. More specifically, co-existence between phenotypes of differing diffusion rates is impossible, as the one with faster diffusion rate will be completely wiped out (see, e.g., [9, 11]). The intuitive explanation for this phenomenon is that slower diffusion helps individuals to better track favorable regions whereas faster diffusion makes it easier for population to move away from such "good" regions, and to lose competitive advantages.

Nevertheless, for the situation where the organisms are adopting a dispersal strategy that includes both random and passive movements, the mechanism behind the evolution of dispersal rates is not yet completely understood. Next we will consider a system of reaction-diffusion-advection equations for two logistically growing and competing populations, where the individuals undergo diffusive movements due to self-propelling and/or water turbulence and passive movements caused by water flow, and the only phenotypic difference between the two species is the diffusion rate. To be more precise, we consider

$$\begin{cases} u_t = d_1 u_{xx} - \alpha u_x + u[r-u-v], & 0<x<L, t>0, \\ v_t = d_2 v_{xx} - \alpha v_x + v[r-u-v], & 0<x<L, t>0, \\ d_1 u_x(0,t) - \alpha u(0,t) = 0, & t>0, \\ d_1 u_x(L,t) - \alpha u(L,t) = -b\alpha u(L,t), & t>0, \\ d_2 v_x(0,t) - \alpha v(0,t) = 0, & t>0, \\ d_2 v_x(L,t) - \alpha v(L,t) = -b\alpha v(L,t), & t>0 \\ u(x,0) = u_0(x) \geq, \not\equiv 0, & 0<x<L, \\ v(x,0) = v_0(x) \geq, \not\equiv 0, & 0<x<L, \end{cases} \tag{1.4}$$

where $u(x,t)$ and $v(x,t)$ represent the population density of two competing species at location x and time $t>0$, respectively. d_1, $d_2>0$ denote the random diffusion rates of two species.

Recently, system (1.4) with $b=1$ (i.e., with Danckwerts boundary conditions) has been qualitatively studied in [20], where the authors showed that populations with higher dispersal rate will always displace those with lower dispersal rate, in contrast to the evolution of slow random dispersal in non-advective but spatially heterogeneous environments. This finding, to some extent, suggests that advection can put slow diffusers at a disadvantage and thus fast diffusers can evolve. In this paper, we will completely determine the dynamics of system (1.4) when $0 \leq b < 1$ and also illustrate some different dynamics of system (1.4) when $b > \frac{3}{2}$.

We remark here that for system (1.4), due to the introduction of the parameter b in the boundary conditions, even the local stability of the semi-trivial steady states cannot be established by the arguments used in [20], but the new method developed in this paper can be equally applied to deal with the case $b=1$. Moreover, to obtain the global dynamics of system (1.4), it seems non-trivial to prove the non-existence result of any co-existence steady state, for which we will introduce some new ideas and techniques to overcome the emerging difficulty.

This paper is organized as follows. In section 2 we focus on the global dynamics of model (1.2) and determine necessary and sufficient conditions for the persistence of a single species. In section 3 we provide a complete understanding of the global dynamics of system (1.4) when $b \in [0,1)$ and some results on the global dynamics of system (1.4) when $b > \frac{3}{2}$. Section 4 is devoted to discussions of the main results.

2 Persistence of single specie

In this section we investigate the dynamics of the single species model (1.2). In particular, we are interested in conditions under which the species can persist in the long run. To this end, we study the steady states of (1.2), i.e.

$$\begin{cases} du_{xx} - \alpha u_x + u[r-u] = 0, \quad 0 < x < L, \\ du_x(0) - \alpha u(0) = 0, \\ du_x(L) - \alpha u(L) = -b\alpha u(L). \end{cases} \tag{2.1}$$

This in turn leads to the study of the linear eigenvalue problem

$$\begin{cases} d\varphi_{xx} - \alpha\varphi_x + r\varphi + \lambda\varphi = 0, \quad 0 < x < L, \\ d\varphi_x(0) - \alpha\varphi(0) = 0, \\ d\varphi_x(L) - \alpha\varphi(L) = -b\alpha\varphi(L). \end{cases} \tag{2.2}$$

It is well known that (see, e.g., [16, 25]) problem (2.2) admits a principal eigenvalue, denoted by λ_1, which is simple, and its corresponding eigenfunction, denoted by φ_1, can be chosen positive in $[0, L]$. In what follows, we restrict our attention to the dependence of λ_1 on various parameters.

2.1 Critical habitat size and its dependence on α

In this section we first prove the existence of the critical habitat size, denoted by L^*. By investigating the dependence of L^* on α, we also establish the existence of the critical advection rate.

Proposition 2.1 For any given d, r, L, $b > 0$, we have

(a) $\lim_{\alpha\to 0^+} \lambda_1 = -r < 0$;

(b) $\lim_{\alpha\to +\infty} \lambda_1 = +\infty$.

Proof: Part (a) is trivial. We focus on the proof of part (b).

Let $\psi = e^{-\frac{\alpha}{d}x}\varphi$, then (2.2) becomes

$$\begin{cases} d\psi_{xx} + \alpha\psi_x + [r+\lambda]\psi = 0, \quad 0 < x < L, \\ \psi_x(0) = 0, \\ d\psi_x(L) = -b\alpha\psi(L). \end{cases} \tag{2.3}$$

By the variational method, λ_1 can be characterized by

$$\lambda_1 = \inf_{0 \neq \psi \in W^{1,2}} \frac{b\alpha e^{\frac{\alpha}{d}L}\psi^2(L) + d\int_0^L e^{\frac{\alpha}{d}x}\psi_x^2 \mathrm{d}x - r\int_0^L e^{\frac{\alpha}{d}x}\psi^2 \mathrm{d}x}{\int_0^L e^{\frac{\alpha}{d}x}\psi^2 \mathrm{d}x}.$$

By a transformation $\psi = e^{-\delta\frac{\alpha}{d}x}\zeta$, where δ is a positive number to be determined later, we see

$$\begin{aligned}
\lambda_1 =& \inf_{0\neq\zeta\in W^{1,2}}\Big\{\frac{b\alpha e^{(1-2\delta)\frac{\alpha}{d}L}\zeta^2(L) + d\int_0^L e^{(1-2\delta)\frac{\alpha}{d}x}\zeta_x^2\mathrm{d}x + \frac{\alpha^2\delta^2}{d}\int_0^L e^{(1-2\delta)\frac{\alpha}{d}x}\zeta^2\mathrm{d}x}{\int_0^L e^{(1-2\delta)\frac{\alpha}{d}x}\zeta^2\mathrm{d}x} \\
&- \frac{\alpha\delta\int_0^L e^{(1-2\delta)\frac{\alpha}{d}x}[\zeta^2]_x\mathrm{d}x + r\int_0^L e^{(1-2\delta)\frac{\alpha}{d}x}\zeta^2\mathrm{d}x}{\int_0^L e^{(1-2\delta)\frac{\alpha}{d}x}\zeta^2\mathrm{d}x}\Big\} \\
=& \inf_{0\neq\zeta\in W^{1,2}}\Big\{\frac{b\alpha e^{(1-2\delta)\frac{\alpha}{d}L}\zeta^2(L) + d\int_0^L e^{(1-2\delta)\frac{\alpha}{d}x}\zeta_x^2\mathrm{d}x + \frac{\alpha^2\delta^2}{d}\int_0^L e^{(1-2\delta)\frac{\alpha}{d}x}\zeta^2\mathrm{d}x}{\int_0^L e^{(1-2\delta)\frac{\alpha}{d}x}\zeta^2\mathrm{d}x} \\
&- \frac{\alpha\delta e^{(1-2\delta)\frac{\alpha}{d}L}\zeta^2(L) - \alpha\delta\zeta^2(0) - \delta(1-2\delta)\frac{\alpha^2}{d}\int_0^L e^{(1-2\delta)\frac{\alpha}{d}x}\zeta^2\mathrm{d}x}{\int_0^L e^{(1-2\delta)\frac{\alpha}{d}x}\zeta^2\mathrm{d}x} \\
&- \frac{r\int_0^L e^{(1-2\delta)\frac{\alpha}{d}x}\zeta^2\mathrm{d}x}{\int_0^L e^{(1-2\delta)\frac{\alpha}{d}x}\zeta^2\mathrm{d}x}\Big\} \\
=& \inf_{0\neq\zeta\in W^{1,2}}\Big\{\frac{[b-\delta]\alpha e^{(1-2\delta)\frac{\alpha}{d}L}\zeta^2(L) + [\delta-\delta^2]\frac{\alpha^2}{d}\int_0^L e^{(1-2\delta)\frac{\alpha}{d}x}\zeta^2\mathrm{d}x}{\int_0^L e^{(1-2\delta)\frac{\alpha}{d}x}\zeta^2\mathrm{d}x} \\
&+ \frac{d\int_0^L e^{(1-2\delta)\frac{\alpha}{d}x}\zeta_x^2\mathrm{d}x + \alpha\delta\zeta^2(0)}{\int_0^L e^{(1-2\delta)\frac{\alpha}{d}x}\zeta^2\mathrm{d}x} - \frac{r\int_0^L e^{(1-2\delta)\frac{\alpha}{d}x}\zeta^2\mathrm{d}x}{\int_0^L e^{(1-2\delta)\frac{\alpha}{d}x}\zeta^2\mathrm{d}x}\Big\} \\
\geq& [\delta-\delta^2]\frac{\alpha^2}{d} - r,
\end{aligned}$$

provided $0 < \delta < \min\{b, 1\}$. By sending $\alpha \to +\infty$, part (b) follows directly from the above inequality, and so the proof is complete. □

Lemma 2.1 Fix d, $r > 0$ and $0 < b < \frac{1}{2}$. Then the following statements hold:

(a) For any $0 < \alpha < \sqrt{\frac{dr}{b(1-b)}}$, there exists a critical number $L^* = L^*(d, \alpha, r, b) > 0$ such that

$$\lambda_1 > 0 \text{ if } 0 < L < L^*,\ \lambda_1 = 0 \text{ if } L = L^*,\ \lambda_1 < 0 \text{ if } L > L^*;$$

while if $\alpha \geq \sqrt{\frac{dr}{b(1-b)}}$, then $\lambda_1 > 0$ for any $L > 0$.

(b) For any $L > 0$, there exists a critical number $\alpha^* = \alpha^*(d, r, L, b) \in (0, \sqrt{\frac{dr}{b(1-b)}})$ such that

$$\lambda_1 < 0 \text{ if } 0 < \alpha < \alpha^*,\ \lambda_1 = 0 \text{ if } \alpha = \alpha^*,\ \lambda_1 > 0 \text{ if } \alpha > \alpha^*.$$

Proof: The main idea of this proof is to determine all possible roots of λ_1. It turns out that these roots can be exactly described by a continuous curve (see (2.12) below).

Let $\psi_1 = e^{-\frac{\alpha}{2d}x}\varphi_1$, then (2.2) becomes

$$\begin{cases} d\psi_{1xx} + [r - \frac{\alpha^2}{4d} + \lambda_1]\psi_1 = 0, & 0 < x < L, \\ \psi_{1x}(0) - \frac{\alpha}{2d}\psi_1(0) = \psi_{1x}(L) - \frac{1-2b}{2d}\alpha\psi_1(L) = 0. \end{cases} \tag{2.4}$$

If $4d(r + \lambda_1) - \alpha^2 > 0$, then ψ_1 has the expression

$$\psi_1 = A\cos\frac{\sqrt{4d(r+\lambda_1)-\alpha^2}}{2d}x + B\sin\frac{\sqrt{4d(r+\lambda_1)-\alpha^2}}{2d}x, \tag{2.5}$$

and if $4d(r + \lambda_1) - \alpha^2 < 0$, then ψ_1 has a different expression

$$\psi_1 = Ae^{\frac{\sqrt{\alpha^2-4d(r+\lambda_1)}}{2d}x} + Be^{-\frac{\sqrt{\alpha^2-4d(r+\lambda_1)}}{2d}x}. \tag{2.6}$$

If ψ_1 takes the form (2.5), one then is able to derive from the boundary conditions that

$$\begin{cases} B\sqrt{4d(r+\lambda_1)-\alpha^2} = \alpha A, \\ F_1(L,\lambda_1) \triangleq \frac{\tan(\frac{\sqrt{4d(r+\lambda_1)-\alpha^2}}{2d}L)}{\sqrt{4d(r+\lambda_1)-\alpha^2}} - \frac{b\alpha}{2d(r+\lambda_1)-b\alpha^2} = 0. \end{cases}$$

Note that as long as $4d(r + \lambda_1) - \alpha^2 > 0$, $2d(r + \lambda_1) - b\alpha^2 > 0$ due to $0 < b < \frac{1}{2}$. Set $\lambda_1 = 0$. We find

$$L = L_1(\alpha) \triangleq 2d\frac{\arctan\frac{b\alpha\sqrt{4dr-\alpha^2}}{2rd-b\alpha^2}}{\sqrt{4dr-\alpha^2}}, \quad \text{for } 0 < \alpha < \sqrt{4dr}. \tag{2.7}$$

We claim that $L_1(\alpha)$ is a monotonically increasing function for $0 < \alpha < \sqrt{4dr}$. Indeed, differentiating L_1 with respect to α, after a series of calculations one obtains

$$\frac{L_1'(\alpha)}{2d} = \frac{f_1}{4dr-\alpha^2}, \text{ for } \alpha \in (0, \sqrt{4dr}),$$

where

$$f_1 := \frac{b[2dr + (b-1)\alpha^2]}{rd + b(b-1)\alpha^2} + \frac{\alpha}{\sqrt{4dr-\alpha^2}}\arctan\frac{b\alpha\sqrt{4dr-\alpha^2}}{2rd-b\alpha^2}.$$

Regard f_1 as a function of b and recall $b \in (0, \frac{1}{2})$. Then

$$f_1'(b) = \frac{4d^2r^2 + (4b-4b^2-1)dr\alpha^2 + b(b-1)\alpha^4}{2[rd+b(b-1)\alpha^2]^2} \triangleq \frac{f_2(b)}{2[rd+b(b-1)\alpha^2]^2}.$$

A further calculation gives

$$f_2'(b) = \alpha^2(1-2b)(4dr-\alpha^2) \geq 0 \text{ for } 0 < b < \frac{1}{2} \text{ and } 0 < \alpha < \sqrt{4dr},$$

and hence

$$f_2(b) \geq f_2(0) = dr(4dr - \alpha^2) > 0 \text{ for } 0 < b < \frac{1}{2} \text{ and } 0 < \alpha < \sqrt{4dr}.$$

Thus $f_1(b) > 0$ for all $0 < b < \frac{1}{2}$, that is, $L_1{}'(\alpha) > 0$. Therefore, the above claim holds. This monotonic property also gives

$$0 < L_1(\alpha) < \frac{b}{\frac{1}{2} - b}\sqrt{\frac{d}{r}} = \lim_{\alpha \to \sqrt{4dr}} L_1(\alpha).$$

To ensure that $\lambda_1 = 0$ is a principal eigenvalue, we have to check that the corresponding eigenfunction $\psi_1 = A\cos\frac{\sqrt{4dr-\alpha^2}}{2d}x + B\sin\frac{\sqrt{4dr-\alpha^2}}{2d}x$ does not change sign in $(0, L)$. Note that $B\sqrt{4dr - \alpha^2} = \alpha A$ and $L = L_1(\alpha)$. Let $A = 1/\alpha$. Then

$$\psi_1 = \sqrt{\frac{1}{\alpha^2} + \frac{1}{4dr - \alpha^2}}\sin(\frac{\sqrt{4dr - \alpha^2}}{2d}x + \theta),$$

where $\theta \in (0, \frac{\pi}{2})$ and $\tan\theta = \sqrt{4dr - \alpha^2}/\alpha$. Since $x < L_1(\alpha)$,

$$\frac{\sqrt{4dr - \alpha^2}}{2d}x \in (0, \arctan\frac{b\alpha\sqrt{4dr - \alpha^2}}{2rd - b\alpha^2}) \subset (0, \frac{\pi}{2}).$$

Hence, $\frac{\sqrt{4dr-\alpha^2}}{2d}x + \theta \in (0, \pi)$, which infers that ψ_1 does not change sign in $(0, L)$. By the uniqueness of the principle eigenvalue, we now can conclude that if ψ_1 takes the form (2.5), then

$$\lambda_1 = 0 \Leftrightarrow L = L_1(\alpha), \quad 0 < \alpha < \sqrt{4dr}. \tag{2.8}$$

If ψ_1 takes the form (2.6), we can derive from the boundary conditions that

$$\begin{cases} B = \frac{\sqrt{\alpha^2-4d(r+\lambda_1)}-\alpha}{\sqrt{\alpha^2-4d(r+\lambda_1)}+\alpha}A, \\ F_2(L, \lambda_1) \triangleq e^{\frac{L}{d}\sqrt{\alpha^2-4d(r+\lambda_1)}} - \frac{2d(r+\lambda_1)-b\alpha^2+b\alpha\sqrt{\alpha^2-4d(r+\lambda_1)}}{2d(r+\lambda_1)-b\alpha^2-b\alpha\sqrt{\alpha^2-4d(r+\lambda_1)}} = 0. \end{cases}$$

Set $\lambda_1 = 0$. We find

$$L = L_2(\alpha) \triangleq \ln\frac{2dr - b\alpha^2 + b\alpha\sqrt{\alpha^2 - 4dr}}{2dr - b\alpha^2 - b\alpha\sqrt{\alpha^2 - 4dr}} \cdot \frac{d}{\sqrt{\alpha^2 - 4dr}}, \tag{2.9}$$

for $\sqrt{4dr} < \alpha < \sqrt{\frac{dr}{b(1-b)}}$, where $\alpha = \sqrt{\frac{dr}{b(1-b)}}$ is determined from $2dr - b\alpha^2 - b\alpha\sqrt{\alpha^2 - 4dr} = 0$. We claim that $L_2(\alpha)$ is also a monotonically increasing function for $\sqrt{4dr} < \alpha < \sqrt{\frac{dr}{b(1-b)}}$. In fact, differentiating L_2 with respect to α produces

$$L_2'(\alpha) = \frac{h}{(\alpha^2 - 4dr)(dr + b^2\alpha^2 - b\alpha^2)\sqrt{\alpha^2 - 4dr}}, \text{ for } \alpha \in (\sqrt{4dr}, \sqrt{\frac{dr}{b(1-b)}}),$$

where

$$h := 2bd[(1-b)\alpha^2 - 2dr]\sqrt{\alpha^2-4dr} - d\alpha[dr + b^2\alpha^2 - b\alpha^2]\cdot \ln\frac{h_1}{h_2},$$

and where we denote

$$h_1 = 2dr - b\alpha^2 + b\alpha\sqrt{\alpha^2-4dr} \text{ and } h_2 = 2dr - b\alpha^2 - b\alpha\sqrt{\alpha^2-4dr}$$

for brevity. Regard h as a function of b. Then by a series of computations, we obtain

$$h'(b) = 2d[(1-2b)\alpha^2 - 2dr]\sqrt{\alpha^2-4dr} + (1-2b)d\alpha^3\ln\frac{h_1}{h_2} - d\alpha^2\sqrt{\alpha^2-4dr},$$

$$h''(b) = -4d\alpha^2\sqrt{\alpha^2-4dr} - 2d\alpha^3\ln\frac{h_1}{h_2} + d\alpha^4\sqrt{\alpha^2-4dr}\frac{1-2b}{dr-b\alpha^2+b^2\alpha^2},$$

and

$$h'''(b) = \frac{d\alpha^4\sqrt{\alpha^2-4dr}}{(dr-b\alpha^2+b^2\alpha^2)^2}\cdot(\alpha^2-4dr).$$

Clearly, for $0 < b < \frac{1}{2}$ and $\sqrt{4dr} < \alpha < \sqrt{\frac{dr}{b(1-b)}}$,

$$h'''(b) > 0 \Rightarrow h''(b) > h''(0) = \alpha^2\sqrt{\alpha^2-4dr}[\frac{\alpha^2}{r} - 4d] > 0$$

$$\Rightarrow h'(b) > h'(0) = d(\alpha^2-4dr)^{3/2} > 0 \Rightarrow h(b) > h(0) = 0.$$

Hence, $L_2'(\alpha) > 0$ for $\alpha \in (\sqrt{4dr}, \sqrt{\frac{dr}{b(1-b)}})$, as we wanted. Since

$$\lim_{\alpha\to\sqrt{4dr}} L_2(\alpha) = \frac{b}{\frac{1}{2}-b}\sqrt{\frac{d}{r}} \quad\text{and}\quad \lim_{\alpha\to\sqrt{\frac{dr}{b(1-b)}}} L_2(\alpha) = +\infty,$$

$L_2(\alpha) \in (\frac{b}{\frac{1}{2}-b}\sqrt{\frac{d}{r}}, +\infty)$ for $\alpha \in (\sqrt{4dr}, \sqrt{\frac{dr}{b(1-b)}})$ (the first limit can be obtained by using $\ln(1+x) \approx x$ as $x \to 0$). To guarantee $\lambda_1 = 0$ is a principal eigenvalue, we now have to check $\psi_1 = Ae^{\frac{\sqrt{\alpha^2-4dr}}{2d}x} + Be^{-\frac{\sqrt{\alpha^2-4dr}}{2d}x}$ does not change sign in $(0, L)$. Clearly, we can first choose $A > 0$ to ensure $\psi_1(0) = A + B = 2\frac{\sqrt{\alpha^2-4dr}}{\sqrt{\alpha^2-4dr}+\alpha}A > 0$, and so $\psi_1'(0) > 0$ due to the boundary condition. We next claim that $\psi_1 > 0$ in $[0, L]$. If $\psi_1(x_0) \le 0$ for some $x_0 \in (0, L]$. Then ψ_1 must attain a positive local maximum in $(0, x_0)$, say $x_1 \in (0, x_0)$. Evaluating the first equation in (2.4) at x_1, one can easily deduce a contradiction. Hence, ψ_1 does not change sign in $(0, L)$. We now can conclude that if ψ_1 takes the form (2.6), then

$$\lambda_1 = 0 \Leftrightarrow L = L_2(\alpha), \quad \sqrt{4dr} < \alpha < \sqrt{\frac{dr}{b(1-b)}}. \tag{2.10}$$

For the special case $4d(r+\lambda_1)-\alpha^2=0$, it is easy to derive from (2.4) that

$$\lambda_1 = 0 \Leftrightarrow \alpha^2 = 4dr \text{ and } L = \frac{b}{\frac{1}{2}-b}\sqrt{\frac{d}{r}}. \tag{2.11}$$

This case can be seen as a degenerate case, since now the eigenfunction ψ_1 is a linear function.

Based on the above analysis, we now can conclude from (2.8), (2.10) and (2.11) that

$$\lambda_1 = 0 \Leftrightarrow L = L^*(\alpha),\ 0<\alpha<\sqrt{\frac{dr}{b(1-b)}}, \tag{2.12}$$

where

$$L^*(\alpha) \triangleq \begin{cases} L_1(\alpha) & \text{for } 0<\alpha\le\sqrt{4dr}, \\ L_2(\alpha) & \text{for } \sqrt{4dr}<\alpha<\sqrt{\frac{dr}{b(1-b)}}. \end{cases}$$

Clearly, L^* is a continuous and strictly increasing function for $0<\alpha<\sqrt{\frac{dr}{b(1-b)}}$, and its range is $(0,+\infty)$.

By Proposition 2.1, we further have

$$\lambda_1 < 0 \Leftrightarrow 0<\alpha<\sqrt{\frac{dr}{b(1-b)}} \text{ and } L > L^*(\alpha), \tag{2.13}$$

and

$$\lambda_1 > 0 \Leftrightarrow 0<\alpha<\sqrt{\frac{dr}{b(1-b)}} \text{ and } L < L^*(\alpha),\ \text{ or } \alpha \ge \sqrt{\frac{dr}{b(1-b)}}. \tag{2.14}$$

Clearly, part (a) follows directly from (2.12), (2.13) and (2.14).

To establish part (b), let us define the inverse of L^*, that is,

$$\alpha^* \triangleq L^{*-1},\ \text{for } 0<L<+\infty.$$

It is easy to see that the range of α^* is $(0,\sqrt{\frac{dr}{b(1-b)}})$, and it is also an increasing function and satisfies

$$\alpha>\alpha^* \Leftrightarrow L<L^*, \alpha=\alpha^* \Leftrightarrow L=L^*, \alpha<\alpha^* \Leftrightarrow L>L^*.$$

This, together with (2.12), (2.13) and (2.14), immediately gives part (b). The proof of this lemma is finished. □

Lemma 2.2 Fix d, $r>0$ and $b\ge\frac{1}{2}$. Then the following statements hold:

(a) For any $0 < \alpha < \sqrt{4dr}$, there exists a critical number $L^* = L^*(d, \alpha, r, b) > 0$ such that

$$\lambda_1 > 0 \text{ if } 0 < L < L^*,\ \lambda_1 = 0 \text{ if } L = L^*,\ \lambda_1 < 0 \text{ if } L > L^*;$$

While if $\alpha \geq \sqrt{4dr}$, then $\lambda_1 > 0$ for any $L > 0$.

(b) For any $L > 0$, there exists a critical number $\alpha^* = \alpha^*(d, r, L, b) \in (0, \sqrt{4dr})$ such that

$$\lambda_1 < 0 \text{ if } 0 < \alpha < \alpha^*,\ \lambda_1 = 0 \text{ if } \alpha = \alpha^*,\ \lambda_1 > 0 \text{ if } \alpha > \alpha^*.$$

Proof: We prove this result by a similar argument as the above lemma, and we still consider the above eigenvalue problem (2.4).

We first claim that for $b \geq \frac{1}{2}$, $4d(r + \lambda_1) - \alpha^2 < 0$ would not happen, i.e., ψ_1 cannot be in the form of (2.6). Otherwise, $F_2(L, \lambda_1) = 0$ makes sense, that is,

$$e^{\frac{L}{d}\sqrt{\alpha^2 - 4d(r+\lambda_1)}} = \frac{2d(r + \lambda_1) - b\alpha^2 + b\alpha\sqrt{\alpha^2 - 4d(r + \lambda_1)}}{2d(r + \lambda_1) - b\alpha^2 - b\alpha\sqrt{\alpha^2 - 4d(r + \lambda_1)}} > 1.$$

Since $b \geq \frac{1}{2}$, $2d(r + \lambda_1) - b\alpha^2 - b\alpha\sqrt{\alpha^2 - 4d(r + \lambda_1)} < 0$, which together with the above inequality implies

$$2d(r+\lambda_1) - b\alpha^2 + b\alpha\sqrt{\alpha^2 - 4d(r + \lambda_1)} < 2d(r+\lambda_1) - b\alpha^2 - b\alpha\sqrt{\alpha^2 - 4d(r + \lambda_1)} < 0.$$

Clearly, this is impossible, and so the claim is true.

Suppose that ψ_1 takes the form (2.5). Then

$$F_1(L, \lambda_1) \triangleq \frac{\tan(\frac{\sqrt{4d(r+\lambda_1)-\alpha^2}}{2d}L)}{\sqrt{4d(r + \lambda_1) - \alpha^2}} - \frac{b\alpha}{2d(r + \lambda_1) - b\alpha^2} = 0.$$

Set $\lambda_1 = 0$. We find that if $b = \frac{1}{2}$, then

$$L = L_1^*(\alpha) \triangleq 2d\frac{\arctan\frac{b\alpha\sqrt{4dr-\alpha^2}}{2rd-b\alpha^2}}{\sqrt{4dr - \alpha^2}} = \frac{2d\arctan\left(\frac{\alpha}{\sqrt{4dr-\alpha^2}}\right)}{\sqrt{4dr - \alpha^2}},\quad 0 < \alpha < \sqrt{4dr}, \tag{2.15}$$

and if $b > \frac{1}{2}$, then

$$L = L_2^*(\alpha) \triangleq \begin{cases} 2d\frac{\arctan\frac{b\alpha\sqrt{4dr-\alpha^2}}{2rd-b\alpha^2}}{\sqrt{4dr-\alpha^2}} & \text{for } 0 < \alpha \leq \sqrt{\frac{2dr}{b}}, \\ 2d\frac{\pi+\arctan\frac{b\alpha\sqrt{4dr-\alpha^2}}{2rd-b\alpha^2}}{\sqrt{4dr-\alpha^2}} & \text{for } \sqrt{\frac{2dr}{b}} < \alpha < \sqrt{4dr}. \end{cases} \tag{2.16}$$

Clearly, $\lim_{\alpha\to\sqrt{4dr}} L_1^*(\alpha) = \lim_{\alpha\to\sqrt{4dr}} L_2^*(\alpha) = +\infty$. (Note that $L_2^*(\alpha)$ is continuous at $\alpha = \sqrt{\frac{2dr}{b}}$.)

We now first discuss the monotonicity of $L_1^*(\alpha)$. By a direct computation, one sees

$$\frac{L_1^{*\prime}(\alpha)}{2d} = \frac{1+\frac{\alpha}{\sqrt{4dr-\alpha^2}}\arctan\frac{\alpha}{\sqrt{4dr-\alpha^2}}}{4dr-\alpha^2} > 0, \text{ for } \alpha \in (0, \sqrt{4dr}),$$

hence $L_1^*(\alpha)$ is strictly increasing in $0<\alpha<\sqrt{4dr}$.

As for $L_2^*(\alpha)$, we first consider $0<\alpha\le\sqrt{\frac{2dr}{b}}$. By some computations,

$$\frac{L_2^{*\prime}(\alpha)}{2d} = \frac{h_1}{4dr-\alpha^2}, \text{ for } \alpha \in (0, \sqrt{\tfrac{2dr}{b}}],$$

where

$$h_1 := \frac{b[2dr+(b-1)\alpha^2]}{rd+b(b-1)\alpha^2} + \frac{\alpha}{\sqrt{4dr-\alpha^2}}\arctan\frac{b\alpha\sqrt{4dr-\alpha^2}}{2rd-b\alpha^2}.$$

Clearly,

$$2dr+(b-1)\alpha^2 \ge b\alpha^2+(b-1)\alpha^2 = (2b-1)\alpha^2 > 0,$$

and

$$rd+b(b-1)\alpha^2 \ge \frac{1}{2}b\alpha^2+b(b-1)\alpha^2 = b(b-\frac{1}{2})\alpha^2 > 0,$$

so $h_1>0$, and so

$$L_2^{*\prime}(\alpha) > 0 \text{ for } 0<\alpha\le\sqrt{\frac{2dr}{b}}.$$

While for $\sqrt{\frac{2dr}{b}}<\alpha<\sqrt{4dr}$,

$$\frac{L_2^{*\prime}(\alpha)}{2d} = \frac{h_2}{4dr-\alpha^2}, \text{ for } \alpha \in (\sqrt{\frac{2dr}{b}}, \sqrt{4dr}),$$

where

$$h_2 := \frac{b[2dr+(b-1)\alpha^2]}{rd+b(b-1)\alpha^2} + \frac{\alpha}{\sqrt{4dr-\alpha^2}}[\pi+\arctan\frac{b\alpha\sqrt{4dr-\alpha^2}}{2rd-b\alpha^2}].$$

Since now $dr>\frac{\alpha^2}{4}$, we see

$$2dr+(b-1)\alpha^2 > \frac{\alpha^2}{2}+(b-1)\alpha^2 = (b-\frac{1}{2})\alpha^2 > 0,$$

and

$$rd+b(b-1)\alpha^2 > \frac{\alpha^2}{4}+b(b-1)\alpha^2 = (b-\frac{1}{2})^2\alpha^2 > 0.$$

Moreover, since $\sqrt{\frac{2dr}{b}}<\alpha<\sqrt{4dr}$, $\arctan\frac{b\alpha\sqrt{4dr-\alpha^2}}{2rd-b\alpha^2}\in(-\frac{\pi}{2},0)$. These guarantee $h_2>0$, and so

$$L_2^{*\prime}(\alpha) > 0 \text{ for } \sqrt{\frac{2dr}{b}}<\alpha<\sqrt{4dr}.$$

By similar analysis as in Lemma 2.1, one can conclude that if $b = \frac{1}{2}$, then

$$\lambda_1 = 0 \Leftrightarrow L = L_1^*(\alpha),\ 0 < \alpha < \sqrt{4dr};$$

and if $b > \frac{1}{2}$, then

$$\lambda_1 = 0 \Leftrightarrow L = L_2^*(\alpha),\ 0 < \alpha < \sqrt{4dr}.$$

The rest proof can be dealt with in the same spirit of Lemma 2.1, and so we omit the details here. □

Remark 2.1 For the case $b = 0$, it is easy to see that $\lambda_1 \equiv -r < 0$, and the corresponding eigenfunction can be chosen as $\varphi_1 = Ce^{\frac{\alpha}{d}x}$, with C being any positive constant. In particular, when $b = 0$, problem (1.2) always has a unique positive steady state, and it is globally asymptotically stable among non-negative, not identically zero initial data.

We now state the main result of this subsection.

Theorem 2.1 Assume that d, r, $b > 0$. Set $\hat{\alpha} = \sqrt{dr/b(1-b)}$ for $b \in (0, \frac{1}{2}]$ and $\hat{\alpha} = \sqrt{4dr}$ for $b \geq \frac{1}{2}$.

(a) If $\alpha \geq \hat{\alpha}$, then for any $L > 0$, the trivial steady state $u = 0$ is globally asymptotically stable among all solutions of (1.2) with non-negative and not identically zero initial data; If $0 < \alpha < \hat{\alpha}$, then there exists $L^* = L^*(d, r, b, \alpha) > 0$ such that for $L > L^*$, (1.2) admits a unique positive steady state which is globally asymptotically stable, and for $0 < L \leq L^*$, $u = 0$ is globally asymptotically stable.

(b) For every $L > 0$, there exists $\alpha^* = \alpha^*(d, r, b, L) \in (0, \hat{\alpha})$ such that for $0 < \alpha < \alpha^*$, (1.2) admits a unique positive steady state which is globally asymptotically stable, and for $\alpha \geq \alpha^*$, $u = 0$ is globally asymptotically stable.

Here L^*, α^* are determined in Lemmas 2.1 and 2.2, respectively.

Part (a) of Theorem 2.1 implies that when the advection rate is larger than $\hat{\alpha}$, the single species can not persist for any habitat size. For any advection rate smaller than $\hat{\alpha}$, there exists some critical habitat size such that the species can persist if and only if the habitat size is greater than the critical size. Complementary, part (b) ensures that there always exist a critical advection rate, and the species can persist if and only if its advection rate is less than the critical rate.

Proof: As the single equation for u is a monotone dynamical system and the nonlinear reaction term is of the logistic type, it is well known that the existence of a positive steady state for problem (1.2) is equivalent to that $u = 0$ is unstable (i.e., $\lambda_1 < 0$) [5]. Moreover, if problem (1.2) admits a positive steady state, then it must be globally asymptotically stable. For these reasons, in what follows, we only include the details for the uniqueness result.

Suppose that problem (2.1) has two different positive solutions, then by a transformation $v = e^{-\frac{\alpha}{d}x}u$, we see that the following problem has two positive solutions

$$\begin{cases} dv_{xx} + \alpha v_x + v[r - e^{\frac{\alpha}{d}x}v] = 0, \quad 0 < x < L, \\ v_x(0) = 0, \\ dv_x(L) + b\alpha v(L) = 0. \end{cases} \tag{2.17}$$

This infers that the principal eigenvalue μ_1 of the eigenvalue problem

$$\begin{cases} d\psi_{xx} + \alpha\psi_x + r\psi + \mu\psi = 0, \quad 0 < x < L, \\ \psi_x(0) = 0, \\ d\psi_x(L) + b\alpha\psi(L) = 0, \end{cases}$$

should be negative. Let us denote by ψ_1 the corresponding eigenfunction. It is easy to check that $\overline{v} = M(> r)$ and $\underline{v} = \epsilon\psi_1$ are a pair of super- and sub- solution of problem (2.17). Moreover, since M and ϵ can be chosen arbitrarily large and small, respectively, one can easily show that the maximal solution of (2.17), denoted by v_1, and the minimal solution, denoted by v_2, satisfy

$$v_1 > v_2 > 0 \text{ in } [0, L]. \tag{2.18}$$

Multiply the equation of v_1 by $e^{\frac{\alpha}{d}x}v_2$ and the equation of v_2 by $e^{\frac{\alpha}{d}x}v_1$, subtract the resulting equations and then integrate over $[0, L]$, one finally gets

$$\int_0^L e^{\frac{2\alpha}{d}x} v_1 v_2 [v_1 - v_2] \mathrm{d}x = 0,$$

which contradicts (2.18). This contradiction finishes the proof. □

2.2 Monotone dependence of L^* on d

As can be seen from Lemmas 2.1 and 2.2, the critical habitat size L^* is an increasing function of the advection speed α. In this subsection, we continue to explore the dependence of L^* on the diffusion rate d.

Let us first rewrite L^* as a function of the diffusion rate d. For $0 < b < \frac{1}{2}$,

$$L^* = L_1^*(d) \triangleq \begin{cases} 2d\dfrac{\arctan\frac{b\alpha\sqrt{4dr-\alpha^2}}{2rd-b\alpha^2}}{\sqrt{4dr-\alpha^2}} & \text{as } d \geq \frac{\alpha^2}{4r}, \\ \ln\dfrac{2dr-b\alpha^2+b\alpha\sqrt{\alpha^2-4dr}}{2dr-b\alpha^2-b\alpha\sqrt{\alpha^2-4dr}} \cdot \dfrac{d}{\sqrt{\alpha^2-4dr}} & \text{as } \frac{\alpha^2 b(1-b)}{r} < d < \frac{\alpha^2}{4r}; \end{cases} \tag{2.19}$$

for $b = \frac{1}{2}$,

$$L^* = L_2^*(d) \triangleq 2d\frac{\arctan\frac{b\alpha\sqrt{4dr-\alpha^2}}{2rd-b\alpha^2}}{\sqrt{4dr-\alpha^2}}, \quad \text{as } d > \tfrac{\alpha^2}{4r}; \tag{2.20}$$

and for $b > \frac{1}{2}$,

$$L^* = L_3^*(d) \triangleq \begin{cases} 2d\frac{\arctan\frac{b\alpha\sqrt{4dr-\alpha^2}}{2rd-b\alpha^2}}{\sqrt{4dr-\alpha^2}} & \text{as } d \geq \frac{\alpha^2 b}{2r}, \\ 2d\frac{\pi+\arctan\frac{b\alpha\sqrt{4dr-\alpha^2}}{2rd-b\alpha^2}}{\sqrt{4dr-\alpha^2}} & \text{as } \frac{\alpha^2}{4r} < d < \frac{\alpha^2 b}{2r}. \end{cases} \tag{2.21}$$

For notational simplicity, let us denote

$$f(d) \triangleq 2d\frac{\arctan\frac{b\alpha\sqrt{4dr-\alpha^2}}{2rd-b\alpha^2}}{\sqrt{4dr-\alpha^2}},$$

$$g(d) \triangleq \ln\frac{k_1}{k_2}\cdot\frac{d}{\sqrt{\alpha^2-4dr}},$$

with $k_1 = 2dr - b\alpha^2 + b\alpha\sqrt{\alpha^2-4dr}$ and $k_2 = 2dr - b\alpha^2 - b\alpha\sqrt{\alpha^2-4dr}$, and

$$h(d) \triangleq 2d\frac{\pi + \arctan\frac{b\alpha\sqrt{4dr-\alpha^2}}{2rd-b\alpha^2}}{\sqrt{4dr-\alpha^2}} = \frac{2d\pi}{\sqrt{4dr-\alpha^2}} + f(d).$$

The first result of this subsection is as follows.

Proposition 2.2 The following statements hold:

(1) $L_1^*(d)$ defined in (2.19) is a decreasing function of d;

(2) $L_2^*(d)$ defined in (2.20) is a decreasing function of d;

(3) $L_3^*(d)$ defined in (2.21) is a decreasing function of d provided $\frac{1}{2} < b < 1$.

Proof: We first prove part (1). It is easy to check that $L_1^*(d)$ is continuous at $d = \frac{\alpha^2}{4r}$ (actually, one can directly compute $L_1^*(\frac{\alpha^2}{4r}) = \frac{b\alpha}{(1-2b)r}$). Hence, to establish part (1), we only have to show $L_1^*(d)$ is decreasing in both $(\frac{\alpha^2}{4r}, \infty)$ and $(\frac{\alpha^2 b(1-b)}{r}, \frac{\alpha^2}{4r})$.

For $d > \frac{\alpha^2}{4r}$, a direct calculation gives

$$\begin{aligned}(4dr-\alpha^2)L_1^{*\prime}(d) &= (4dr-\alpha^2)f'(d) \\ &= f_1 \triangleq 2\frac{2dr-\alpha^2}{\sqrt{4dr-\alpha^2}}\cdot\arctan\frac{b\alpha\sqrt{4dr-\alpha^2}}{2dr-b\alpha^2} + \alpha\frac{b(1-b)\alpha^2-2bdr}{dr+(b^2-b)\alpha^2}.\end{aligned}$$

Regard f_1 as a function of b. By some computations one attains

$$
\begin{aligned}
{f_1}'(b) =& 2\frac{2dr-\alpha^2}{\sqrt{4dr-\alpha^2}} \cdot \frac{\frac{\alpha\sqrt{4dr-\alpha^2}(2dr-b\alpha^2)+b\alpha^3\sqrt{4dr-\alpha^2}}{(2dr-b\alpha^2)^2}}{1+\frac{b^2\alpha^2(4dr-\alpha^2)}{(2dr-b\alpha^2)^2}} \\
&+\alpha\frac{[(1-2b)\alpha^2-2dr]\cdot[dr+(b^2-b)\alpha^2]-b(2b-1)\alpha^2[(1-b)\alpha^2-2dr]}{[dr+(b^2-b)\alpha^2]^2} \\
=&\frac{\alpha(2dr-\alpha^2)}{dr+(b^2-b)\alpha^2}+\alpha dr\frac{\alpha^2(1+2b^2-2b)-2dr}{[dr+(b^2-b)\alpha^2]^2} \\
=&\frac{(b^2-b)\alpha^3(4dr-\alpha^2)}{[dr+(b^2-b)\alpha^2]^2} \\
<&0, \text{ (due to } 0<b<\frac{1}{2})
\end{aligned}
$$

and hence $f_1(b) < f_1(0) = 0$, which immediately implies

$$
L_1^{*\prime}(d) < 0 \text{ for } d > \frac{\alpha^2}{4r}. \tag{2.22}
$$

For $\frac{\alpha^2 b(1-b)}{r} < d < \frac{\alpha^2}{4r}$, we have

$$
\begin{aligned}
L_1^{*\prime}(d) =& g'(d) \\
=&\frac{\alpha^2-2dr}{(\alpha^2-4dr)\sqrt{\alpha^2-4dr}}\cdot\ln\frac{k_1}{k_2}+\frac{d}{\sqrt{\alpha^2-4dr}}\cdot(\ln\frac{k_1}{k_2})'_d \\
=&\frac{\alpha^2-2dr}{(\alpha^2-4dr)\sqrt{\alpha^2-4dr}}\cdot\ln\frac{k_1}{k_2}-\frac{b\alpha}{\alpha^2-4dr}\cdot\frac{(1-b)\alpha^2-2dr}{dr+(b^2-b)\alpha^2} \\
=&\frac{(\alpha^2-2dr)\cdot[dr+(b^2-b)\alpha^2]\cdot\ln\frac{k_1}{k_2}-b\alpha\sqrt{\alpha^2-4dr}\cdot[(1-b)\alpha^2-2dr]}{(\alpha^2-4dr)\cdot\sqrt{\alpha^2-4dr}\cdot[dr+(b^2-b)\alpha^2]} \\
\triangleq&\frac{g_1}{(\alpha^2-4dr)\cdot\sqrt{\alpha^2-4dr}\cdot[dr+(b^2-b)\alpha^2]}.
\end{aligned}
$$

Regard g_1 as a function of b. By a series of computations,

$$
\begin{aligned}
{g_1}'(b) =& \alpha(\alpha^2-2dr)\cdot\sqrt{\alpha^2-4dr}+\alpha^2(2b-1)\cdot(\alpha^2-2dr)\cdot\ln\frac{k_1}{k_2} \\
&-[(1-2b)\alpha^3-2dr\alpha]\cdot\sqrt{\alpha^2-4dr},
\end{aligned}
$$

$$
\begin{aligned}
{g_1}''(b) =& 2\alpha^2(\alpha^2-2dr)\cdot\ln\frac{k_1}{k_2}+\alpha^3(2b-1)\cdot(\alpha^2-2dr)\cdot\frac{\sqrt{\alpha^2-4dr}}{dr+(b^2-b)\alpha^2} \\
&+2\alpha^3\sqrt{\alpha^2-4dr},
\end{aligned}
$$

and

$$
{g_1}'''(b) = -\frac{\alpha^3(\alpha^2-2dr)\cdot\sqrt{\alpha^2-4dr}\cdot(\alpha^2-4dr)}{[dr+(b^2-b)\alpha^2]^2}.
$$

Since $\frac{\alpha^2 b(1-b)}{r} < d < \frac{\alpha^2}{4r}$ and $0 < b < \frac{1}{2}$,

$$g_1'''(b) < 0 \Rightarrow g_1''(b) < g_1''(0) = \frac{\alpha^3\sqrt{\alpha^2 - 4dr}}{dr}[4dr - \alpha^2] < 0$$
$$\Rightarrow g_1'(b) < g_1'(0) = 0 \Rightarrow g_1(b) < g_1(0) = 0.$$

Hence,

$$L_1^{*\prime}(d) < 0 \text{ for } \frac{\alpha^2 b(1-b)}{r} < d < \frac{\alpha^2}{4r}. \tag{2.23}$$

Part (1) follows from (2.22) and (2.23).

By a careful reading, one finds that $f_1'(b) < 0$ for all $b \in (0,1)$ and $d > \frac{\alpha^2}{4r}$, and thus

$$f_1 < 0 \text{ for all } b \in (0,1) \text{ and } d > \frac{\alpha^2}{4r}. \tag{2.24}$$

This immediately gives the monotonicity of $L_2^*(d)$ in $(\frac{\alpha^2}{4r}, \infty)$ and $L_3^*(d)$ in $(\frac{\alpha^2 b}{2r}, \infty)$. Now, it remains to show $L_3^{*\prime}(d) < 0$ in $(\frac{\alpha^2}{4r}, \frac{\alpha^2 b}{2r})$. In fact, for $d \in (\frac{\alpha^2}{4r}, \frac{\alpha^2 b}{2r})$,

$$L_3^{*\prime}(d) = h'(d) = \frac{2\pi(2dr - \alpha^2)}{\sqrt{4dr - \alpha^2}(4dr - \alpha^2)} + f'(d) < 0,$$

where the inequality used $\frac{\alpha^2}{4r} < d < \frac{\alpha^2 b}{2r} < \frac{\alpha^2}{2r}$ and (2.24). The proof is finished. □

Set $\hat{d} = \alpha^2 b(1-b)/r$ when $0 < b \leq 1/2$ and $\hat{d} = \alpha^2/(4r)$ when $b \geq 1/2$. As a consequence of Proposition 2.2 we have

Theorem 2.2 Given any $d > 0, r > 0, L > 0$, we have

$$\lim_{d \to \hat{d}^-} L^* = +\infty, \quad \lim_{d \to +\infty} L^* = \frac{b\alpha}{r}.$$

If $b \in (0,1)$, then L^* is a strictly decreasing function of d.

Remark 2.2 The monotonicity of L^* with respect to d indicates that large diffusion rate increases the likelihood of the persistence of a single species. This, to some extent, gives us a hint that if one considers a two-species competing system instead of the single species model, and assumes that the two species are identical except their diffusion rates, then the species with larger diffusion rate may win the competition. We will make this intuitive idea more transparent in the next section.

Remark 2.3 It is natural to ask whether the critical habitat size L^* is still a monotonically decreasing function of d when $b \geq 1$. It turns out that this situation is complicated, and we will include some discussions in the final section.

Similar to Theorem 2.1, the main result of this subsection can be stated as follows.

Theorem 2.3 Assume that $\alpha > 0$, $r > 0$, $b \in (0, 1)$.

(a) If $0 < d \leq \hat{d}$, then for any $L > 0$, the trivial steady state $u = 0$ is globally asymptotically stable among all solutions of (1.2) with non-negative and not identically zero initial data; If $d > \hat{d}$, then there exists $L^* = L^*(d, r, b, \alpha) > 0$ such that for $L > L^*$, (1.2) admits a unique positive steady state which is globally asymptotically stable, and for $0 < L \leq L^*$, $u = 0$ is globally asymptotically stable.

(b) If $0 < L \leq \frac{b\alpha}{r}$, then for any $d > 0$, $u = 0$ is globally asymptotically stable; If $L > \frac{b\alpha}{r}$, then there exists $d^* = d^*(\alpha, r, b, L) > 0$ such that for $d > d^*$, (1.2) admits a unique positive steady state which is globally asymptotically stable, and for $0 < d \leq d^*$, $u = 0$ is globally asymptotically stable.

Theorem 2.3 follows from Theorem 2.2. As the proof is similar as that of Theorem 2.1, we omit the details.

Part (a) of Theorem 2.3 implies that when the dispersal rate is less than $\hat{d}$, the single species can not persist for any habitat size. For any dispersal rate greater than $\hat{d}$, there exists some critical habitat size such that the single species can persist if and only if the habitat size is greater than the critical size. Complementary, part (b) ensures that there exists a critical diffusion rate if and only if the habitat size is larger than $\frac{b\alpha}{r}$, and the single species can persist if and only if its diffusion rate is larger than the critical diffusion rate. We caution the readers that these results hold under the assumption $b \in (0, 1)$.

3 Global dynamics for two-species competition model

In this section, we first focus our attention on the study of the two-species competition system (1.2) with $0 \leq b < 1$. Due to the monotonicity of such systems, to a large extent, its dynamics can be determined by the stability/instability of the semi-trivial solutions of the stationary problem

$$\begin{cases} d_1 u_{xx} - \alpha u_x + u[r - u - v] = 0, & 0 < x < L, \\ d_2 v_{xx} - \alpha v_x + v[r - u - v] = 0, & 0 < x < L, \\ d_1 u_x(0) - \alpha u(0) = 0, \\ d_1 u_x(L) - \alpha u(L) = -b\alpha u(L), \\ d_2 v_x(0) - \alpha v(0) = 0, \\ d_2 v_x(L) - \alpha v(L) = -b\alpha v(L). \end{cases} \tag{3.1}$$

This in turn leads us to the study of some corresponding eigenvalue problems obtained by the linearization method. We discuss this in subsection 3.1. However, to obtain a complete understanding of the global dynamics, in general one needs to establish the non-existence of the co-existence steady state, or the stability of the co-existence steady state (if it exists). This will be covered by subsection 3.2. In subsection 3.3, we summarize the results obtained in previous sections and present our final conclusion for $0 \leq b < 1$. In the last part, subsection 3.4, we want to show that system (1.2) may have different dynamics provided b crosses over 1.

3.1 Local stability of semi-trivial steady states

We start with the local stability of the two semi-trivial steady states of system (1.4), which are respectively denoted by $(\widetilde{u}, 0)$ and $(0, \widetilde{v})$ in the sequel. For the sake of notation simplicity, we are going to unify some symbols associated with the linearized version of problem (1.4).

Linearizing problem (1.4) at $(\widetilde{u}, 0)$ and $(0, \widetilde{v})$ respectively, we obtain the following two eigenvalue problems:

$$\begin{cases} -[d_2\psi_x - \alpha\psi]_x - [r - \widetilde{u}]\psi = \mu\psi, \quad 0 < x < L, \\ d_2\psi_x(0) - \alpha\psi(0) = 0, \\ d_2\psi_x(L) - \alpha\psi(L) = -b\alpha\psi(L), \end{cases} \tag{3.2}$$

and

$$\begin{cases} -[d_1\varphi_x - \alpha\varphi]_x - [r - \widetilde{v}]\varphi = \lambda\varphi, \quad 0 < x < L, \\ d_1\varphi_x(0) - \alpha\varphi(0) = 0, \\ d_1\varphi_x(L) - \alpha\varphi(L) = -b\alpha\varphi(L). \end{cases} \tag{3.3}$$

Denote by (μ_1, ψ_1) and (λ_1, φ_1) the first pair of eigenvalue-eigenfunction of problem (3.2) and (3.3), respectively.

It is well known that (see, e.g., [16, 25]) both μ_1 and λ_1 are simple, and their corresponding eigenfunctions ψ_1 and φ_1 can be chosen strictly positive in $[0, L]$. We say that $(\widetilde{u}, 0)$ is linearly stable (resp. linearly unstable) if $\mu_1 > 0$ (resp. $\mu_1 < 0$); similarly $(0, \widetilde{v})$ is linearly stable (resp. linearly unstable) provided $\lambda_1 > 0$ (resp. $\lambda_1 < 0$). Moreover, if a steady state is linearly stable (resp. linearly unstable), then it should be asymptotically stable (resp. unstable) (see, e.g., Theorem 7. 6. 2 in [25]).

Before giving the local stability of the semi-trivial steady states, we first establish an identity which is very useful in later analysis.

Consider the auxiliary eigenvalue problem

$$\begin{cases} -[d\zeta_x - \alpha\zeta]_x - m(x)\zeta = \tau\zeta, \quad 0 < x < L, \\ d\zeta_x(0) - \alpha\zeta(0) = 0, \\ d\zeta_x(L) - \alpha\zeta(L) = -b\alpha\zeta(L), \end{cases} \tag{3.4}$$

where $m(x) \in L^\infty([0, L])$. We denote the first pair of eigenvalue-eigenfunction of problem (3.4) by (τ_1^d, ζ_1^d) to emphasize the dependence on the parameter d, then we have

Lemma 3.1 For any $0 < d_1 < d_2$, the following identity holds:

$$\tau_1^{d_1} - \tau_1^{d_2} = (d_1 - d_2)\frac{\int_0^L (\zeta_1^{d_1})_x [e^{-\frac{\alpha}{d_2}x}\zeta_1^{d_2}]_x \mathrm{d}x}{\int_0^L e^{-\frac{\alpha}{d_2}x}\zeta_1^{d_1}\zeta_1^{d_2}\mathrm{d}x}.$$

Proof: Rewrite the equations of $(\tau_1^{d_1}, \zeta_1^{d_1})$ and $(\tau_1^{d_2}, \zeta_1^{d_2})$ as follows:

$$\begin{cases} d_2(\zeta_1^{d_1})_{xx} - \alpha(\zeta_1^{d_1})_x + [m(x) + \tau_1^{d_1}]\zeta_1^{d_1} = (d_2 - d_1)(\zeta_1^{d_1})_{xx}, & 0 < x < L, \\ d_2(\zeta_1^{d_2})_{xx} - \alpha(\zeta_1^{d_2})_x + [m(x) + \tau_1^{d_2}]\zeta_1^{d_2} = 0, & 0 < x < L, \\ d_2(\zeta_1^{d_1})_x(0) - \alpha\zeta_1^{d_1}(0) = (d_2 - d_1)(\zeta_1^{d_1})_x(0), \\ d_2(\zeta_1^{d_1})_x(L) - \alpha\zeta_1^{d_1}(L) = -b\alpha\zeta_1^{d_1}(L) + (d_2 - d_1)(\zeta_1^{d_1})_x(L), \\ d_2(\zeta_1^{d_2})_x(0) - \alpha\zeta_1^{d_2}(0) = 0, \\ d_2(\zeta_1^{d_2})_x(L) - \alpha\zeta_1^{d_2}(L) = -b\alpha\zeta_1^{d_2}(L). \end{cases}$$

Multiply the first equation by $e^{-\frac{\alpha}{d_2}x}\zeta_1^{d_2}$ and the second one by $e^{-\frac{\alpha}{d_2}x}\zeta_1^{d_1}$, subtract the resulting equations and then integrate over $[0, L]$, one finally obtains

$$\begin{aligned} (\tau_1^{d_1} - \tau_1^{d_2}) \int_0^L e^{-\frac{\alpha}{d_2}x}\zeta_1^{d_1}\zeta_1^{d_2}\mathrm{d}x + \left\{[d_2(\zeta_1^{d_1})_x - \alpha\zeta_1^{d_1}]e^{-\frac{\alpha}{d_2}x}\zeta_1^{d_2}\right\}|_0^L \\ - \left\{[d_2(\zeta_1^{d_2})_x - \alpha\zeta_1^{d_2}]e^{-\frac{\alpha}{d_2}x}\zeta_1^{d_1}\right\}|_0^L \\ = [d_2 - d_1]\left\{(\zeta_1^{d_1})_x e^{-\frac{\alpha}{d_2}x}\zeta_1^{d_2}\right\}|_0^L - [d_2 - d_1]\int_0^L (\zeta_1^{d_1})_x [e^{-\frac{\alpha}{d_2}x}\zeta_1^{d_2}]_x \mathrm{d}x. \end{aligned}$$

Using the boundary conditions, one further derives

$$(\tau_1^{d_1} - \tau_1^{d_2}) \int_0^L e^{-\frac{\alpha}{d_2}x}\zeta_1^{d_1}\zeta_1^{d_2}\mathrm{d}x = [d_1 - d_2]\int_0^L (\zeta_1^{d_1})_x [e^{-\frac{\alpha}{d_2}x}\zeta_1^{d_2}]_x \mathrm{d}x,$$

which is exactly our claim. Hence the proof is finished. □

We now go to discuss the stability/instability of $(\widetilde{u}, 0)$ and $(0, \widetilde{v})$. In view of the results obtained in section 2, $\widetilde{u}$ and $\widetilde{v}$ do not always exist, and their existence depends on the parameters in the equation. In the next two lemmas, we assume that they exist, and discuss their stability properties. The precise version will be given in the final conclusion (see subsection 3.3), by combining results from section 2.

Lemma 3.2 Assume that $0 < d_1 < d_2$, α, r, $L > 0$, and $0 \le b < 1$, and that $(\widetilde{u}, 0)$ exists. Then $(\widetilde{u}, 0)$ must be unstable.

Proof: Note that (μ_1, ψ_1) (defined at the beginning of this subsection) satisfies

$$\begin{cases} -[d_2\psi_{1x} - \alpha\psi_1]_x - [r - \widetilde{u}]\psi_1 = \mu_1\psi_1, & 0 < x < L, \\ d_2\psi_{1x}(0) - \alpha\psi_1(0) = 0, \\ d_2\psi_{1x}(L) - \alpha\psi_1(L) = -b\alpha\psi_1(L), \end{cases}$$

and that

$$\begin{cases} -[d_1\widetilde{u}_x - \alpha\widetilde{u}]_x - [r - \widetilde{u}]\widetilde{u} = 0, \quad 0 < x < L, \\ d_1\widetilde{u}_x(0) - \alpha\widetilde{u}(0) = 0, \\ d_1\widetilde{u}_x(L) - \alpha\widetilde{u}(L) = -b\alpha\widetilde{u}(L). \end{cases}$$

Set $m(x) = r - \widetilde{u}$ in (3.4), then by Lemma 3.1, we see

$$\mu_1 = [d_2 - d_1]\frac{\int_0^L \widetilde{u}_x[e^{-\frac{\alpha}{d_2}x}\psi_1]_x \mathrm{d}x}{\int_0^L e^{-\frac{\alpha}{d_2}x}\widetilde{u}\psi_1 \mathrm{d}x}. \tag{3.5}$$

Let $w = \frac{\widetilde{u}_x}{\widetilde{u}}$ and $z = \frac{\psi_{1x}}{\psi_1}$. Then after some tedious but straightforward calculations we have

$$\begin{cases} -d_1 w_{xx} + [\alpha - 2d_1 w]w_x + \widetilde{u}w = 0, \qquad 0 < x < L, \\ w(0) = \frac{\alpha}{d_1} > 0,\ w(L) = (1-b)\frac{\alpha}{d_1} > 0, \end{cases} \tag{3.6}$$

and

$$\begin{cases} -d_2 z_{xx} + [\alpha - 2d_2 z]z_x = -\widetilde{u}_x, \qquad 0 < x < L, \\ z(0) = \frac{\alpha}{d_2} > 0,\ z(L) = (1-b)\frac{\alpha}{d_2} > 0. \end{cases} \tag{3.7}$$

An application of the maximum principle to (3.6) yields that $0 < w < \frac{\alpha}{d_1}$ in $(0, L)$, and so

$$\widetilde{u}_x > 0 \text{ in } (0, L). \tag{3.8}$$

Hence, using the maximum principle again, we see from (3.7) that $z = \frac{\psi_{1x}}{\psi_1} < \frac{\alpha}{d_2}$, which particularly implies

$$[e^{-\frac{\alpha}{d_2}x}\psi_1]_x < 0 \text{ in } (0, L). \tag{3.9}$$

Substituting (3.8) and (3.9) into (3.5), one immediately gets $\mu_1 < 0$, which gives the instability of $(\widetilde{u}, 0)$. The proof is complete. □

By using similar arguments, we can establish the local stability of $(0, \widetilde{v})$ as follows.

Lemma 3.3 Assume that $0 < d_1 < d_2$, α, r, $L > 0$, and $0 \le b < 1$, and that $(0, \widetilde{v})$ exists. Then $(0, \widetilde{v})$ must be (locally) stable.

3.2 Non-existence of co-existence steady state

This subsection is devoted to studying whether system (1.4) has a co-existence steady state or not. To establish the non-existence result, we first establish several preliminary results (Lemmas 3.4 and 3.5 below), which will be frequently used in Lemma 3.6, the main result of this subsection.

Lemma 3.4 Assume that $0 < d_1 < d_2$, α, r, $L > 0$ and $0 \le b < 1$. If (u, v) is a co-existence steady state of system (1.4) (that is, (u, v) solves problem (3.1) and $u, v > 0$), then for any two points $0 \le y_1 \le y_2 \le L$, we have the following identities:

$$\begin{aligned} [d_1 - d_2] \int_{y_1}^{y_2} v_x [e^{-\frac{\alpha}{d_1}x} u]_x \mathrm{d}x =& [d_1 u_x(y_2) v(y_2) - d_2 v_x(y_2) u(y_2)] e^{-\frac{\alpha}{d_1} y_2} \\ & - [d_1 u_x(y_1) v(y_1) - d_2 v_x(y_1) u(y_1)] e^{-\frac{\alpha}{d_1} y_1}; \end{aligned} \tag{3.10}$$

and

$$\begin{aligned} [d_2 - d_1] \int_{y_1}^{y_2} u_x [e^{-\frac{\alpha}{d_2}x} v]_x \mathrm{d}x =& [d_2 v_x(y_2) u(y_2) - d_1 u_x(y_2) v(y_2)] e^{-\frac{\alpha}{d_2} y_2} \\ & - [d_2 v_x(y_1) u(y_1) - d_1 u_x(y_1) v(y_1)] e^{-\frac{\alpha}{d_2} y_1}. \end{aligned} \tag{3.11}$$

Proof: Here we only include the proof for identity (3.10), since the other case can be treated similarly.

Rewrite the equations of (u, v), i.e., (3.1), as follows

$$\begin{cases} d_1 \big\{ e^{\frac{\alpha}{d_1}x} [e^{-\frac{\alpha}{d_1}x} u]_x \big\}_x + u[r - u - v] = 0, & 0 < x < L, \\ d_1 \big\{ e^{\frac{\alpha}{d_1}x} [e^{-\frac{\alpha}{d_1}x} v]_x \big\}_x + v[r - u - v] = [d_1 - d_2] v_{xx}, & 0 < x < L. \end{cases}$$

Multiplying the first equation by $e^{-\frac{\alpha}{d_1}x} v$, the second one by $e^{-\frac{\alpha}{d_1}x} u$, subtracting the resulting equations and then integrating over $[y_1, y_2]$, we get

$$\begin{aligned} -\big\{ [d_1 u_x - \alpha u] e^{-\frac{\alpha}{d_1}x} v \big\}\big|_{y_1}^{y_2} =& [d_1 - d_2] \int_{y_1}^{y_2} v_{xx} e^{-\frac{\alpha}{d_1}x} u \mathrm{d}x - \big\{ [d_1 v_x - \alpha v] e^{-\frac{\alpha}{d_1}x} u \big\}\big|_{y_1}^{y_2} \\ =& [d_1 - d_2] \big\{ v_x e^{-\frac{\alpha}{d_1}x} u \big\}\big|_{y_1}^{y_2} - [d_1 - d_2] \int_{y_1}^{y_2} v_x [e^{-\frac{\alpha}{d_1}x} u]_x \mathrm{d}x \\ & - \big\{ [d_1 v_x - \alpha v] e^{-\frac{\alpha}{d_1}x} u \big\}\big|_{y_1}^{y_2}, \end{aligned}$$

and so

$$\begin{aligned} & [d_1 - d_2] \int_{y_1}^{y_2} v_x [e^{-\frac{\alpha}{d_1}x} u]_x \mathrm{d}x = [d_1 - d_2][v_x(y_2) e^{-\frac{\alpha}{d_1} y_2} u(y_2) - v_x(y_1) e^{-\frac{\alpha}{d_1} y_1} u(y_1)] \\ & \quad - \big\{ [d_1 v_x(y_2) - \alpha v(y_2)] e^{-\frac{\alpha}{d_1} y_2} u(y_2) - [d_1 v_x(y_1) - \alpha v(y_1)] e^{-\frac{\alpha}{d_1} y_1} u(y_1) \big\} \\ & \quad + \big\{ [d_1 u_x(y_2) - \alpha u(y_2)] e^{-\frac{\alpha}{d_1} y_2} v(y_2) - [d_1 u_x(y_1) - \alpha u(y_1)] e^{-\frac{\alpha}{d_1} y_1} v(y_1) \big\} \\ & = [d_1 u_x(y_2) v(y_2) - d_2 v_x(y_2) u(y_2)] e^{-\frac{\alpha}{d_1} y_2} - [d_1 u_x(y_1) v(y_1) - d_2 v_x(y_1) u(y_1)] e^{-\frac{\alpha}{d_1} y_1}, \end{aligned}$$

which coincides with (3.10). Thus the proof is finished. □

For any co-existence solution (u, v) (suppose it exists), define

$$T := \frac{u_x}{u} \quad \text{and} \quad S := \frac{v_x}{v}. \tag{3.12}$$

After some computations, one gets

$$\begin{cases} -d_1T_{xx} + [\alpha - 2d_1T]T_x + uT + vS = 0, \quad 0 < x < L, \\ -d_2S_{xx} + [\alpha - 2d_2S]S_x + uT + vS = 0, \quad 0 < x < L, \\ T(0) = \frac{\alpha}{d_1} > 0, \ T(L) = (1-b)\frac{\alpha}{d_1} > 0, \\ S(0) = \frac{\alpha}{d_2} > 0, \ S(L) = (1-b)\frac{\alpha}{d_2} > 0. \end{cases} \tag{3.13}$$

We now include some properties of T and S in the following lemma.

Lemma 3.5 Let T and S be defined as in (3.12). Then

$$-d_1T_x + \alpha T - d_1T^2 = -d_2S_x + \alpha S - d_2S^2, \text{ for any } x \in [0, L]. \tag{3.14}$$

In addition, the following situations for T and S cannot occur:

(1) T (resp. S) achieves a positive local maximum in (x_1, x_2) and $S \geq 0$ (resp. $T \geq 0$) in $[x_1, x_2]$;

(2) T (resp. S) achieves a negative local minimum in (x_1, x_2) and $S \leq 0$ (resp. $T \leq 0$) in $[x_1, x_2]$.

where $[x_1, x_2]$ is any interval in $[0, L]$.

Proof: We first prove the identity (3.14). From the equations of (u, v), we see

$$\frac{-d_1u_{xx} + \alpha u_x}{u} = \frac{-d_2v_{xx} + \alpha v_x}{v} = 1 - u - v,$$

and thereby

$$-d_1\frac{u_{xx}u - u_x^2}{u^2} + \alpha\frac{u_x}{u} - d_1\frac{u_x^2}{u^2} = -d_2\frac{v_{xx}v - v_x^2}{v^2} + \alpha\frac{v_x}{v} - d_2\frac{v_x^2}{v^2},$$

which is exactly the identity (3.14).

Next, we prove part (1). If T attains a positive local maximum in (x_1, x_2), say $x^* \in (x_1, x_2)$, then

$$T(x^*) > 0, \ T'(x^*) = 0, \text{ and } T''(x^*) \leq 0.$$

Evaluating the first equation of (3.13) at x^*, one easily sees $S(x^*) < 0$, contradicting our assumption. So this case would not happen. Clearly, all other cases in part (1) and part (2) can be verified similarly, so the proof is complete. □

Based on previous two results, we next move to establish the main result of this subsection.

Lemma 3.6 Assume that $0 < d_1 < d_2$, α, r, $L > 0$ and $0 \leq b < 1$. Then system (1.4) has no co-existence steady state.

Proof: Arguing indirectly, we suppose that there is a co-existence steady state of system (1.4), denoted by (u,v). For clarity, we prove this result by several claims.
Claim 1. Both u_x and v_x must change sign in $[0,L]$.

If u_x does not change sign in $[0,L]$, then $u_x\ge 0$ in $[0,L]$ (note $u_x(0)=\frac{\alpha}{d_1}u(0)>0$). Recall the identity (3.11) and let y_2 there be L and y_1 there be 0. Then

$$\int_0^L u_x[e^{-\frac{\alpha}{d_2}x}v]_x\mathrm{d}x=\int_0^L u_x[v_x-\frac{\alpha}{d_2}v]e^{-\frac{\alpha}{d_2}x}\mathrm{d}x=0.$$

We first make an assertion that $v_x-\frac{\alpha}{d_2}v$ must change sign in $[0,L]$. Otherwise, $u_x[v_x-\frac{\alpha}{d_2}v]e^{-\frac{\alpha}{d_2}x}\equiv 0$ in $[0,L]$. Clearly, $u_x\not\equiv 0$. Hence, $v_x-\frac{\alpha}{d_2}v\equiv 0$ in some interval $[x_1,x_2]\subset[0,L]$, and so $v(x)=v(x_1)e^{\frac{\alpha}{d_2}(x-x_1)}$ for $x\in[x_1,x_2]$. On the other hand, due to $v_x-\frac{\alpha}{d_2}v\equiv 0$ in $[x_1,x_2]$, $v_{xx}-\frac{\alpha}{d_2}v_x\equiv 0$ in $[x_1,x_2]$. By the equation of v, we see $u+v-r\equiv 0$, which in turn gives $d_1u_{xx}-\alpha u_x\equiv 0$, and thus $d_1u_x-\alpha u\equiv C$ in $[x_1,x_2]$ for some constant C. Substitute the expression $u(x)=r-v(x)=r-v(x_1)e^{\frac{\alpha}{d_2}(x-x_1)}$ into $d_1u_x-\alpha u\equiv C$, one then can easily deduce $d_1=d_2$, contradicting our assumption. Hence, the above assertion holds.

Let $x^*\in[0,L]$ be such that $v_x(x^*)-\frac{\alpha}{d_2}v(x^*)>0$, i.e., $S(x^*)>\frac{\alpha}{d_2}$. Since $S(0)=\frac{\alpha}{d_2}$ and $S(L)=(1-b)\frac{\alpha}{d_2}\le\frac{\alpha}{d_2}$, we can find two numbers $0\le x_1^*<x^*<x_2^*\le L$ such that

$$S(x_1^*)=S(x_2^*)=\frac{\alpha}{d_2},S(x)>\frac{\alpha}{d_2}\text{ in }(x_1^*,x_2^*),$$

which implies that S must attain a positive local maximum in (x_1^*,x_2^*). Clearly, $T\ge 0$ in $[x_1^*,x_2^*]$ due to $u_x\ge 0$ in $[0,L]$. But Lemma 3.5 tells us this is impossible. Hence, u_x must change sign in $[0,L]$.

The conclusion for v_x can be established by the identity (3.10) and a similar argument as above, so we omit the details.
Claim 2. v_x must reach the first zero point before u_x.

Lemma 6.6 in [20] indicates that u_x and v_x cannot be zero at the same time, so, if Claim 2 is not true, then there exists $x_0\in(0,L)$ such that

$$u_x>0\text{ in }[0,x_0),\ u_x(x_0)=0,\ v_x(x)>0\text{ in }[0,x_0].$$

Evaluating the identity (3.10) at $(y_1,y_2)=(0,x_0)$, one attains

$$0<d_2u(x_0)v_x(x_0)e^{-\frac{\alpha}{d_1}x_0}=[d_2-d_1]\int_0^{x_0}v_x[e^{-\frac{\alpha}{d_1}x}u]_x\mathrm{d}x. \tag{3.15}$$

On the other hand, we integrate the equation of u from 0 to x_0 to see $\int_0^{x_0}u[r-u-v]\mathrm{d}x=\alpha u(x_0)>0$, which implies that $r-u-v$ must be positive somewhere in $[0,x_0]$. Observing that $r-u-v$ is a strictly decreasing function in $[0,x_0]$, there are two possibilities of $r-u-v$: (i): $r-u-v>0$ in $[0,x_0)$; or (ii): $r-u-v>0$ in

$[0, x')$ and $r - u - v < 0$ in $(x', x_0]$. Case (i) shows that $[d_1 u_x - \alpha u]_x < 0$ in $[0, x_0)$, and hence $d_1 u_x - \alpha u < 0$ in $(0, x_0]$ due to $d_1 u_x - \alpha u|_{x=0} = 0$; Case (ii) shows that $d_1 u_x - \alpha u$ first declines and then increases to $d_1 u_x - \alpha u|_{x=x_0} = -\alpha u(x_0) < 0$, so again, we obtain $d_1 u_x - \alpha u < 0$ in $(0, x_0]$. Clearly, this immediately leads to a contradiction with inequality (3.15). Thus, the proof for Claim 2 is finished.

Let us now denote the first zero point of v_x by $z_1 \in (0, L)$; also we can choose $(z_1 <)\ z_2 < z_3 < L$ such that

$$u_x \geq 0 \text{ in } [0, z_2],\ u_x < 0 \text{ in } (z_2, z_3),\ \text{and } u_x(z_3) = 0.$$

(The existence of such z_i $(i = 1, 2, 3)$ is guaranteed by Claims 1 and 2 and $u_x(L) > 0$.)
Claim 3. v_x cannot be nonnegative in $[z_1, z_2]$.

Otherwise, $v_x \geq 0$ in $[z_1, z_2]$. By an integration of the equation of u over $[0, z_2]$, we find $\int_0^{z_2} u[r - u - v]\mathrm{d}x = \alpha u(z_2) > 0$. Note that in $[0, z_2]$, $u_x \geq 0$ and $v_x \geq 0$. Hence, one can apply a similar argument as in Claim 2 to establish $d_1 u_x - \alpha u < 0$ in $(0, z_2]$, that is, $[e^{-\frac{\alpha}{d_1}x} u]_x < 0$ in $(0, z_2]$.

Recall the identity (3.10) and let $(y_1, y_2) = (0, z_2)$. Then

$$0 < d_2 u(z_2) v_x(z_2) e^{-\frac{\alpha}{d_1} z_2} = [d_2 - d_1] \int_0^{z_2} v_x [e^{-\frac{\alpha}{d_1}x} u]_x \mathrm{d}x < 0,$$

a contradiction. (We point out here that $v_x(z_2)$ in the above inequality must be positive due to Lemma 6.6 in [20].) This contradiction completes the proof of this claim.
Claim 4. v_x cannot be non-positive in $[z_1, z_2]$.

Arguing indirectly, we suppose $v_x \leq 0$ in $[z_1, z_2]$. Using Lemma 6.6 in [20] again, we actually have $v_x(z_2) < 0$. Since $v_x(L) = (1 - b)\frac{\alpha}{d_2} v(L) > 0$, v_x must have at least one zero point in (z_2, L). Let z_4 be the one that is closest to z_2.

We first prove $z_4 \in (z_2, z_3)$. If not, then $z_4 \geq z_3$, and we have

$$u_x < 0 \text{ in } (z_2, z_3),\ u_x(z_2) = u_x(z_3) = 0,\ v_x \leq 0 \text{ in } [z_2, z_3].$$

This immediately tells us that T must attain a negative local minimum in (z_2, z_3), and $S \leq 0$ in $[z_2, z_3]$, which is impossible in view of Lemma 3.5. Hence, $z_4 \in (z_2, z_3)$.

It is easy to see that

$$T(z_2) = 0,\ T'(z_2) \leq 0,\ \text{and } S(z_2) < 0.$$

Restricting the identity (3.14) at $x = z_2$, one finds

$$d_2 S'(z_2) = d_1 T'(z_2) + \alpha S(z_2) - d_2 S^2(z_2) < 0,\ \text{i.e., } S'(z_2) < 0.$$

Clearly, $S'(z_4) \geq 0$. Hence, S must achieve a negative local minimum in $(z_2, z_4) \subset (z_2, z_3)$, in which T is non-positive. This contradicts Lemma 3.5 again, so the above claim holds.

In view of Claims 3 and 4, v_x must change sign in $[z_1, z_2]$. By Lemma 6.6 in [20], $v_x(z_2) \neq 0$, so

$$\text{either } v_x(z_2) > 0 \text{ or } v_x(z_2) < 0. \tag{3.16}$$

Claim 5. $v_x(z_2)$ cannot be negative.

Suppose for contradiction that $v_x(z_2) < 0$. Since now v_x changes sign in $[z_1, z_2]$, let $z^* \in (z_1, z_2)$ be such that $v_x(z^*) > 0$. Observing that $v_x(z_1) = 0$ and $v_x(z_2) < 0$, there must be two numbers $z_1 \leq \underline{z} < \overline{z} < z_2$ such that

$$v_x(\underline{z}) = v_x(\overline{z}) = 0, \ v_x > 0 \text{ in } (\underline{z}, \overline{z}).$$

Again, we find that S has a positive local maximum in $(\underline{z}, \overline{z})$ while T is nonnegative in $[\underline{z}, \overline{z}]$, which is impossible due to Lemma 3.5. This confirms the above claim.

Claim 6. $v_x(z_2)$ cannot be positive.

If $v_x(z_2) > 0$, then $S(z_2) > 0$. This together with the fact that $S(z_1) = 0$, $T(z_1) > 0$ and $T(z_2) = 0$ implies that T must intersect S at least once in (z_1, z_2). Let $\widetilde{z}$ be the first intersection point in (z_1, z_2). Clearly,

$$T > S \text{ in } [z_1, \widetilde{z}), \ T(\widetilde{z}) = S(\widetilde{z}) > 0.$$

(We remark here that $T(\widetilde{z}) = S(\widetilde{z}) = 0$ could not happen due to Lemma 6.6 in [20].) Therefore,

$$T'(\widetilde{z}) \leq S'(\widetilde{z}). \tag{3.17}$$

Recall the identity (3.14) and evaluate it at $x = \widetilde{z}$ to obtain

$$d_2 S'(\widetilde{z}) = (d_1 - d_2) T^2(\widetilde{z}) + d_1 T'(\widetilde{z}). \tag{3.18}$$

If $T'(\widetilde{z}) \leq 0$, then $S'(\widetilde{z}) < 0$, which together with $S(z_1) = 0$ and $S(\widetilde{z}) > 0$ tells us that S must have a positive local maximum in $(z_1, \widetilde{z})$. Obviously, T is nonnegative in $[z_1, \widetilde{z}]$. These again result in a contradiction with Lemma 3.5.

While if $T'(\widetilde{z}) > 0$, then $S'(\widetilde{z}) > 0$ by the virtue of (3.17). Moreover, one can deduce from (3.18) that

$$0 > (d_1 - d_2) T^2(\widetilde{z}) = d_2 S'(\widetilde{z}) - d_1 T'(\widetilde{z}) \geq d_1 S'(\widetilde{z}) - d_1 T'(\widetilde{z}) \geq 0.$$

This contradiction finishes the proof of Claim 6.

The obvious contradiction caused by (3.16) and Claims 5 and 6 shows that the co-existence steady state (u, v) could not exist. We now complete the whole proof of this lemma. □

3.3 Final conclusion for $0 \le b < 1$

In this subsection, we present our final conclusion for system (1.4).

Theorem 3.1 Assume that $0 < d_1 < d_2$, α, r, $L > 0$ and $0 \le b < 1$. If $(0, \widetilde{v})$ exists, then it must be globally asymptotically stable among all solutions with non-negative and not identically zero initial data; while if $(0, \tilde{v})$ does not exist, then $(0, 0)$ is globally asymptotically stable.

Proof: By the monotone dynamical system theory [25], the first part of Theorem 3.1 follows from Lemmas 3.2, 3.3 and 3.6. To establish the rest of Theorem 3.1, it suffices to show that if $(0, \widetilde{v})$ does not exist, then $(\widetilde{u}, 0)$ does not exist, too. If this is true, then $(0, 0)$ is globally asymptotically stable.

We argue by contradiction. Assume that $(0, \widetilde{v})$ does not exist, but $(\widetilde{u}, 0)$ exists. Consider the following two eigenvalue problems

$$\begin{cases} d_1\varphi_{xx} - \alpha\varphi_x + (r + \lambda)\varphi = 0, & 0 < x < L, \\ d_1\varphi_x(0) - \alpha\varphi(0) = 0, \\ d_1\varphi_x(L) - \alpha\varphi(L) = -b\alpha\varphi(L), \end{cases} \tag{3.19}$$

and

$$\begin{cases} d_2\psi_{xx} - \alpha\psi_x + (r + \mu)\psi = 0, & 0 < x < L, \\ d_2\psi_x(0) - \alpha\psi(0) = 0, \\ d_2\psi_x(L) - \alpha\psi(L) = -b\alpha\psi(L). \end{cases} \tag{3.20}$$

Denote by (λ_1, φ_1) and (μ_1, ψ_1) the first pair of eigenvalue-eigenfunction of problem (3.19) and problem (3.20), respectively. Then in view of the above assumption,

$$\lambda_1 < 0 \text{ and } \mu_1 \ge 0.$$

In addition, by Lemma 3.1 (set $m(x) = r$ in (3.4)), we have

$$0 > \lambda_1 - \mu_1 = (d_1 - d_2)\frac{\int_0^L \varphi_{1x}[e^{-\frac{\alpha}{d_2}x}\psi_1]_x \mathrm{d}x}{\int_0^L e^{-\frac{\alpha}{d_2}x}\varphi_1\psi_1 \mathrm{d}x}. \tag{3.21}$$

Let $z = \frac{\varphi_{1x}}{\varphi_1}$ and $\widehat{z} = \frac{\psi_{1x}}{\psi_1}$. Then

$$\begin{cases} -d_1 z_{xx} + [\alpha - 2d_1 z]z_x = 0, & 0 < x < L, \\ z(0) = \frac{\alpha}{d_1} > 0,\ z(L) = (1 - b)\frac{\alpha}{d_1} > 0, \end{cases} \tag{3.22}$$

and

$$\begin{cases} -d_2 \widehat{z}_{xx} + [\alpha - 2d_2 \widehat{z}]\widehat{z}_x = 0, & 0 < x < L, \\ \widehat{z}(0) = \frac{\alpha}{d_2} > 0,\ \widehat{z}(L) = (1 - b)\frac{\alpha}{d_2} > 0. \end{cases} \tag{3.23}$$

By the maximum principle, one sees from (3.22) and (3.23) that for $0 < x < L$,

$$(1-b)\frac{\alpha}{d_1} < z < \frac{\alpha}{d_1} \text{ and } (1-b)\frac{\alpha}{d_2} < \widehat{z} < \frac{\alpha}{d_2},$$

which particularly implies

$$\varphi_{1x} > 0 \text{ and } [e^{-\frac{\alpha}{d_2}x}\psi_1]_x < 0, \text{ for } 0 < x < L. \tag{3.24}$$

Putting (3.24) into (3.21), one then easily deduces a contradiction $0 > \lambda_1 - \mu_1 > 0$, and this contradiction ends the proof. □

Combining the results from section 2 with the above theorem, we attain a more specific and precise version as follows.

Theorem 3.2 Assume that $0 < d_1 < d_2$, α, r, $L > 0$ and $0 < b < 1$. For $0 < \alpha < \alpha^*$, $(0, \widetilde{v})$ is globally asymptotically stable among all solutions with non-negative and not identically zero initial data, while for $\alpha \geq \alpha^*$, $(0,0)$ is globally asymptotically stable. Here α^* is determined in Lemmas 2.1 and 2.2, respectively.

3.4 Global stability of $(\tilde{u}, 0)$ when $b > \frac{3}{2}$

It is natural to inquire about the dynamics of two-species competition models when the loss at the downstream end is severe. To this end, we illustrate some major differences between the cases $b < 1$ and $b > \frac{3}{2}$.

3.4.1 Non-monotone dependence of L^* on d

Theorem 2.3 says that if $b < 1$, the critical habitat size is a decreasing function of the diffusion rate. However, such conclusion does not hold for general values of loss rate b. The following result gives an example.

Lemma 3.7 Given any $d > 0$, $r > 0$, and $\alpha > 0$. If $b > \frac{3}{2}$, then L^* is strictly increasing in d for sufficiently large d; if $b < \frac{3}{2}$, L^* is strictly decreasing in d for sufficiently large d.

In strong contrast to Theorem 2.3, Lemma 3.7 implies that L^* is strictly increasing in d for sufficiently large d. For general values of b, the exact dependence of L^* on d has not been fully determined. For the special case $b = \infty$, it is straightforward to show that L^*, as a function of d with domain $(\frac{\alpha^2}{4r}, +\infty)$, has a unique critical point (and thus it must be the global minimum), denoted as d^*: L^* is strictly decreasing in $(\frac{\alpha^2}{4r}, d^*)$ and strictly increasing in $(d^*, +\infty)$. We suspect that such result also holds for $b > \frac{3}{2}$.

Proof: By direct calculations, we have

$$\begin{aligned}(4dr-\alpha^2)L^{*\prime}(d) =& 2\frac{2dr-\alpha^2}{\sqrt{4dr-\alpha^2}}\cdot\arctan\frac{b\alpha\sqrt{4dr-\alpha^2}}{2dr-b\alpha^2}+\alpha\frac{b(1-b)\alpha^2-2bdr}{dr+(b^2-b)\alpha^2}\\ =& 2\frac{2dr-\alpha^2}{\sqrt{4dr-\alpha^2}}\cdot[\frac{b\alpha\sqrt{4dr-\alpha^2}}{2dr-b\alpha^2}-\frac{1}{3}\frac{b^3\alpha^3(4dr-\alpha^2)^{\frac{3}{2}}}{(2dr-b\alpha^2)^3}]\\ &+b\alpha\frac{(1-b)\alpha^2-2dr}{dr+(b^2-b)\alpha^2}+o(\frac{1}{d^2})\\ =& 2\frac{b^2\alpha^3}{r}\cdot[\frac{2}{3}b-1]\cdot\frac{1}{d}+o(\frac{1}{d^2}).\end{aligned}$$

Clearly, if $b>\frac{3}{2}$, then for sufficiently large d, $L^{*\prime}(d)>0$; while if $b<\frac{3}{2}$, then $L^{*\prime}(d)<0$ for sufficiently large d. □

3.4.2 Global stability of $(\tilde{u},0)$ when $d_1<d_2$ and $b>3/2$

Theorem 3.1 ensures that if $b<1$ and $d_1<d_2$, then $(\tilde{u},0)$, if exists, is always unstable. That is, when the loss rate is small, the faster diffuser can invade the slower diffuser when rare. However, as we will show below, the opposite conclusion can hold for $b>\frac{3}{2}$.

Fix $b>0, r>0$ and $\alpha>0$. Define

$$L_*=\inf_{d>0}L^*,$$

where L^* is given in Theorem 2.1. In contrast to Theorem 3.1, we have the following result:

Theorem 3.3 Given $r>0$ and $\alpha>0$. Suppose that $b>\frac{3}{2}$ and $L\in(L_*,\frac{b\alpha}{r})$. Then there exist two constants d_*,d^* with $d^*>d_*>\frac{\alpha^2}{4r}$, such that for any $d_1\in(d_*,d^*)$, $(\tilde{u},0)$ exists. Furthermore, if d_2 is sufficiently large, then $(\tilde{u},0)$ is globally asymptotically stable.

Theorem 3.3 implies that when the loss of individuals at the downstream end is severe, larger diffusion rate can be selected against, in contrast to the case when $b\le 1$. It also supports previous analysis [20] which suggests that some intermediate diffusion rate is selected when $b=\infty$.

Proof: We first establish the existence of $\tilde{u}$. By part (a) of Theorem 2.1, $\tilde{u}$ exists if and only if $\alpha<\sqrt{4d_1r}$ and $L>L^*=L^*(d_1,r,b,\alpha)$. Since $\lim_{d_1\to\alpha^2/(4r)}L^*=+\infty$ and $\lim_{d_1\to\infty}=\frac{b\alpha}{r}$, L_* is well defined and $L_*\le\frac{b\alpha}{r}$. By Lemma 3.7, we see that if $b>\frac{3}{2}$, then

$$L_*<\frac{b\alpha}{r}.$$

Now choose $L \in (L_*, \frac{b\alpha}{r})$ (which is no-empty). Then we can find positive constants d_*, d^* such that $L > L^*$ for any $d_1 \in (d_*, d^*)$. Hence, $\tilde{u}$ exists provided that $b > \frac{3}{2}$, $L \in (L_*, \frac{b\alpha}{r})$ and $d_1 \in (d_*, d^*)$.

We next claim that if d_2 is sufficiently large, then $(0, \tilde{v})$ does not exist. To establish this assertion, we note that by part (a) of Theorem 2.1, $\tilde{v}$ exists if and only if $\alpha < \sqrt{4d_2 r}$ and $L > L^* = L^*(d_2, r, b, \alpha)$. Since $\lim_{d_2\to\infty} L^* = \frac{b\alpha}{r}$, by assumption $L < \frac{b\alpha}{r}$ and Lemma 3.7, we find that if $b > \frac{3}{2}$, $L < L^*(d_2, r, b, \alpha)$ for sufficiently large d_2. Therefore, $(0, \tilde{v})$ does not exist.

Finally, we show that under the assumption of Theorem 3.3, given any non-negative and not identically zero initial data $(u(x, 0), v(x, 0))$, $(u(x, t), v(x, t)) \to (\tilde{u}, 0)$ in $C([0, L])$ as $t \to \infty$. By the maximum principle, $u(x, t) > 0$ and $v(x, t) > 0$ for any $x \in [0, L]$ and $t > 0$. Therefore, by (1.4), $v(x, t)$ satisfies

$$\begin{cases} v_t < d_2 v_{xx} - \alpha v_x + v[r - v], & 0 < x < L, t > 0, \\ d_2 v_x(0, t) - \alpha v(0, t) = 0, & t > 0, \\ d_2 v_x(L, t) - \alpha v(L, t) = -b\alpha v(L, t), & t > 0 \\ v(x, 0) = v_0(x) \geq, \not\equiv 0, & 0 < x < L. \end{cases}$$

That is, $v(x, t)$ is a sub-solution of the equation

$$\begin{cases} w_t = d_2 w_{xx} - \alpha w_x + w[r - w], & 0 < x < L, t > 0, \\ d_2 w_x(0, t) - \alpha w(0, t) = 0, & t > 0, \\ d_2 w_x(L, t) - \alpha w(L, t) = -b\alpha w(L, t), & t > 0 \\ w(x, 0) = v_0(x) \geq, \not\equiv 0, & 0 < x < L. \end{cases} \tag{3.25}$$

By the comparison principle for parabolic equations, $w(x, t) \geq v(x, t)$ for any x and t. Since $\tilde{v}$ does not exist, i.e., (3.25) has no positive steady state, we have $w(x, t) \to 0$ in $C([0, L])$ as $t \to \infty$. Hence, $v(x, t) \to 0$ in $C([0, L])$ as $t \to \infty$, which in turn implies that $u(x, t) \to \tilde{u}$ in $C([0, L])$ as $t \to \infty$. This completes the proof. $\square$

4 Discussions

We studied a single species model and a two-species competition model in a one-dimensional advective homogeneous environment. The species can be exposed to a net loss of individuals at the downstream end. We first determine necessary and sufficient conditions for the persistence of a single species, in terms of the critical habitat size and the critical advection rate. For the competition model, we assume that two species have the same population dynamics but differ in random diffusion rate. We show that when the magnitude of the loss at the downstream end is small ($b < 1$), the species with higher diffusion rate will always displace the species with smaller rate; i.e., larger diffusion rate will be selected in this case. On the other hand, when the loss at the downstream end is severe ($b > \frac{3}{2}$), larger diffusion might not be favored. It seems that the dynamics of two-species competition model (1.4) has some major differences between the cases $b < 1$ and $b > \frac{3}{2}$.

We first offer some intuitive reasoning for the case $b \leq 1$, which is closely related with the ideal free distribution. The ideal free distribution (IFD), introduced by Fretwell and Lucas in [10], describes how organisms distribute themselves so that individuals optimize their fitness, assuming that individuals have complete knowledge of the environment and can move without any cost. For population models with movement, the IFD corresponds to an equilibrium state where all individuals have the same fitness, because otherwise some individuals would move to increase their fitness. For our single species model with population density $\tilde{u}$, the fitness of the species is measured by the effective growth rate $r - \tilde{u}$. It is easy to see that for any $d_1 > 0$, the fitness $r - \tilde{u}$ is never equal to a constant. For the case $b < 1$, if $L \leq \frac{b\alpha}{r}$, then $\tilde{u}$ does not exist for any d_1, so we restrict to $L > \frac{b\alpha}{r}$. When $L > \frac{b\alpha}{r}$, $\tilde{u}$ exists for all sufficiently large d_1. Furthermore, as $d_1 \to \infty$, $\tilde{u} \to r - \frac{b\alpha}{L}$ in $L^\infty([0, L])$. That is, the species approaches the IFD as its diffusion rate tends to infinity. It is generally believed that strategies leading to the ideal free distribution of populations should be evolutionarily stable; See [6] and references therein. Hence, we expect that faster diffusion rate will be favored when $b < 1$.

The case $b > \frac{3}{2}$ is different: $\tilde{u}$ exists for some intermediate range of d_1, but it does not exist for sufficiently large d_1. This suggests that large diffusion rate might be selected against, and some intermediate diffusion rate is favored in this case. It seems quite challenging to fully determine the global dynamics of system (1.4) for general parameter values of b, d, α, r, L.

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