Global dynamics of a Lotka–Volterra competitive system from river ecology: general boundary conditions

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Abstract

In this paper, we mainly study the population dynamics of a Lotka–Volterra competition system from river ecology. One interesting feature in this model concerns the boundary conditions at upstream and downstream ends, where the species can be exposed to a net loss of individuals, as tuned by parameters b_u and b_d measuring the magnitude of the loss. We establish a complete classification of all possible long time behaviors for this general model, and as an application, we further present a clear picture on the global dynamics by investigating a special case where two species are competing for the same resource.

1. Introduction

In this paper, we mainly investigate the population dynamics of the following general two-species Lotka–Volterra competition-diffusion-advection system arising in river ecology:

$$
\begin{cases}
u_t = d_1 u_{xx} - \alpha_1 u_x + u(r_1(x) - u - bv), & 0 < x < L,\ t > 0, \\
v_t = d_2 v_{xx} - \alpha_2 v_x + v(r_2(x) - cu - v), & 0 < x < L,\ t > 0, \\
d_1 u_x(0,t) - \alpha_1 u(0,t) = b_u \alpha_1 u(0,t), & t > 0, \\
d_1 u_x(L,t) - \alpha_1 u(L,t) = -b_d \alpha_1 u(L,t), & t > 0, \\
d_2 v_x(0,t) - \alpha_2 v(0,t) = b_u \alpha_2 v(0,t), & t > 0, \\
d_2 v_x(L,t) - \alpha_2 v(L,t) = -b_d \alpha_2 v(L,t), & t > 0, \\
u(x,0) = u_0(x) \geqslant, \neq 0, & 0 < x < L, \\
v(x,0) = v_0(x) \geqslant, \neq 0, & 0 < x < L,
\end{cases}
\tag{1}
$$

where u and v represent the population densities of two competing aquatic species living in a river with constantly unidirectional water flow. The river is abstracted here by a one-dimensional habitat denoted by an interval $(0,L)$. Populations are taking certain diffusive movement with rates $d_1, d_2 > 0$ due to water turbulence or self-propelling, and also some passive movement caused by unidirectional water flow with advection speeds $\alpha_1, \alpha_2 > 0$. The functions $r_1(x)$ and $r_2(x)$ stand for the intrinsic growth rates or local carrying capacities, and $b, c > 0$ signify the inter-specific competition intensities. The parameters $b_u, b_d \geqslant 0$ are used to measure the loss rate of individuals at the upstream and downstream ends relative to the flow rate, see [9].

Up to now, various special cases of system (1) have been widely investigated.

We begin with the spatially homogeneous case $r_1 = r_2 \equiv r_0$ with r_0 being a positive constant. If $d_1 \neq d_2$, $\alpha_1 = \alpha_2$, Lou, Lutscher [9] and Lou, Zhou [12], respectively, discussed $b_u = 0, b_d = 1$ and $b_u = 0, b_d \in [0,1)$, and they finally conclude that the competitor with faster diffusion rate would displace the slower one, that is, faster diffusion will evolve, in sharp contrast to the well-known 'slower diffuser wins' in *non-advective* case [4, 5]; while if $d_1 = d_2$, $\alpha_1 \neq \alpha_2$ and $b_u = b_d = 0$, it was confirmed by Lou *et al* [10] that weak advection is more beneficial for species to exclude its competitor; this conclusion was further extended to general case with $d_1 = d_2$, $\alpha_1 \neq \alpha_2$, $b_u = 0$, $0 < b_d \leqslant +\infty$ and spatially dependent resource function; see [15, 21]. For differing movement rates, i.e. $d_1 \neq d_2$, $\alpha_1 \neq \alpha_2$, Zhou [18] firstly treated $b_u = b_d = 0$, and among other things, he found: (i) the strategy of faster diffusion together with slower advection is always favorable, which can be seen as a generation of [10] and [12]; (ii) the strategy of faster diffusion but with much stronger advection (relative to diffusion) is always selected against; see also [20] for the generalization to $b_u = 0$ and $b_d \in (0,1]$.

For the inhomogeneous case $r_1 = r_2 := r(x)$, non-constant, system (1) is much more harder to deal with. Lam, Lou and Lutscher [8] seems to be the first attempt to talk about the case $d_1 \neq d_2$, $\alpha_1 = \alpha_2$ and $b_u = b_d = 0$, aiming at the existence and multiplicity of evolutionarily stable strategies by using some limiting arguments (in the sense of both diffusion and advection rates are sufficiently small and comparable). Zhao and Zhou [17], focusing on the special case $d_1 \neq d_2$, $\alpha_1 = 0 < \alpha_2$, $b_u = -1$ and $b_d = 0$, tried to reveal some different phenomena after involving spatial variations. The general case $d_1 \neq d_2$, $\alpha_1 \neq \alpha_2$, $b_u = 0$ and $b_d > 0$, was recently explored by Lou *et al* [11], where, by developing new techniques to overcome the difficult caused by non-self-adjoint operators, they obtained a deep understanding on the global dynamics.

A recent important advance on a bit more general setting of system (1) is due to Zhou and Xiao [19], where by assuming

$(H_1) \frac{d_2}{d_1} = \frac{\alpha_2}{\alpha_1} := k > 0$ (or equivalently $\frac{\alpha_1}{d_1} = \frac{\alpha_2}{d_2} = k^*$);
$(H_2) (b,c) \in A := \{(b,c) : b, c > 0 \text{ and } b \cdot c \leqslant 1\}$
$(H_3) r_1(x), r_2(x) \in C^{1,\gamma}([0,L], \mathbb{R}^+)$ with some $\gamma \in (0,1)$;
$(H_4) b_u = b_d = 0$;

they classified completely all possible long time behaviors of system (1): either one of these two species wins the final competition or both populations coexist eventually. Indeed, they discussed it in higher spatial dimensions.

Motivated by the above work, in this paper, we aim to consider system (1) under the basic hypotheses (H_1)–(H_3) but in a very general region for parameters b_u and b_d, that is,

$(\bar{H}_4) \qquad (b_u, b_d) \in [0, \infty] \times [0, \infty] \backslash (0,0),$

which includes various biological scenarios at the habitat ends, and also, may induce different types of boundary conditions from the mathematical point of view. We explain this further by taking b_d as an example. Specifically,

(1) $b_d = 0$ means that there is no loss at the downstream end, which indicates that populations cannot cross over the downstream end, and if we further have $b_u = 0$, then one sees the environment under consideration is closed [8, 18];
(2) $b_d = 1$ means that water flow will cause a hundred percent loss at the downstream end, which can be applied to describe the scenario 'stream to lake' [9, 14] and biologically is called 'free-flow' boundary condition (indeed, mathematically it matches the homogeneous Neumann type boundary condition);
(3) $0 < b_d < 1$ indicates that at the downstream end there is a partial loss relative to the water flow, and this seems to happen under certain artificial factors, e.g. at the interface of the stream and lake, there is a fishnet set up by human beings, which may block a portion of individuals to be washed out [20];
(4) $b_d > 1$ shows that both diffusive and advective movements will cause population loss at the downstream end, which in turn reflects an unfavorable environment nearby $x = L$, and mathematically, it gives rise to the Robin type boundary condition [9]; especially, if $b_d \to \infty$, then formally we get the Dirichlet type boundary condition, which can be used to model the situation 'stream to ocean' [13] (in the sequel, by $b_d = \infty$, we mean $u(x,t) = v(x,t) = 0$ at $x = L$; $b_u = \infty$ can be understood similarly).

Since system (1) generates a monotone dynamical system, its dynamics will be largely determined by its steady states and their stability. Clearly, system (1) always has a trivial steady state $(0,0)$, and two possible semi-trivial steady states, which, in the sequel, are denoted by $(u_{d_1,\alpha_1,r_1}, 0)$ and $(0, v_{d_2,\alpha_2,r_2})$ respectively.

Let us introduce the following auxiliary linear eigenvalue problem

$$\begin{cases} d\phi_{xx} - \alpha\phi_x + r\phi + \tau\phi = 0, \ x \in (0,L), \\ d\phi_x(0) - \alpha\phi(0) = b_u\alpha\phi(0), \ d\phi_x(L) - \alpha\phi(L) = -b_d\alpha\phi(L), \end{cases} \tag{2}$$

where $d, \alpha > 0$ and $r(x) \in L^\infty(0,L)$. By the Krein–Rutman theorem [7], problem (2) admits a principal eigenvalue, denoted in the sequel, by $\tau_1(d, \alpha, r)$, and its corresponding eigenfunction $\phi_1(d, \alpha, r)$ can be chosen strictly positive in $[0,L]$.

Let us define

$$\Gamma := \mathbb{R}^+ \times \mathbb{R}^+ \times \mathbb{R}^+,$$

and

$$\Sigma_u := \{(d_1, \alpha_1, k) \in \Gamma : \ \tau_1(d_2, \alpha_2, r_2 - cu_{d_1,\alpha_1,r_1}) > 0, \ \text{i.e. } (u_{d_1,\alpha_1,r_1}, 0) \text{ is linearly stable}\};$$
$$\Sigma_v := \{(d_1, \alpha_1, k) \in \Gamma : \ \tau_1(d_1, \alpha_1, r_1 - bv_{d_2,\alpha_2,r_2}) > 0, \ \text{i.e. } (0, v_{d_2,\alpha_2,r_2} \text{ is linearly stable}\};$$
$$\Sigma_- := \{(d_1, \alpha_1, k) \in \Gamma : \ \tau_1(d_2, \alpha_2, r_2 - cu_{d_1,\alpha_1,r_1}) < 0 \text{ and } \tau_1(d_1, \alpha_1, r_1 - bv_{d_2,\alpha_2,r_2}) < 0 \ \ ,$$
$$\text{i.e. both } (u_{d_1,\alpha_1,r_1}, 0) \text{ and } (0, v_{d_2,\alpha_2,r_2}) \text{ are linearly unstable }\};$$
$$\Sigma_{u,0} := \{(d_1, \alpha_1, k) \in \Gamma : \ \tau_1(d_2, \alpha_2, r_2 - cu_{d_1,\alpha_1,r_1}) = 0, \ \text{i.e. } (u_{d_1,\alpha_1,r_1}, 0) \text{ is neutrally stable}\};$$
$$\Sigma_{v,0} := \{(d_1, \alpha_1, k) \in \Gamma : \ \tau_1(d_1, \alpha_1, r_1 - bv_{d_2,\alpha_2,r_2}) = 0, \ \text{i.e. } (0, v_{d_2,\alpha_2,r_2} \text{ is neutrally stable}\};$$
$$\Sigma_{0,0} := \{(d_1, \alpha_1, k) \in \Gamma : \ \tau_1(d_1, \alpha_1, r_1 - bv_{d_2,\alpha_2,r_2}) = \tau_1(d_2, \alpha_2, r_2 - cu_{d_1,\alpha_1,r_1}) = 0, \ \text{i.e. both}$$
$$(u_{d_1,\alpha_1,r_1}, 0) \text{ and } (0, v_{d_2,\alpha_2,r_2}) \text{ are neutrally stable }\}.$$

In the sequel, we say that a steady state $(U(x), V(x))$ of system (1) is g.a.s (globally asymptotically stable) if for any given initial data $(u_0(x), v_0(x))$ with $u_0(x), v_0(x) \geqslant, \not\equiv 0$ in $[0, L]$, the corresponding unique solution $(u(x, t), v(x, t))$ of system (1) satisfies

$$\lim_{t \to \infty} (u(x, t), v(x, t)) = (U(x), V(x)) \quad \text{uniformly for} \quad x \in [0, L],$$

in the standard $C([0, L]) \times C([0, L])$ topology. Moreover, a compact set $\mathcal{A} \subset C([0, L]) \times C([0, L])$ is said to be a global attractor of system (1) if for any given initial data $(u_0(x), v_0(x))$ with $u_0(x), v_0(x) \geqslant, \not\equiv 0$ in $[0, L]$, the corresponding unique solution $(u(x, t), v(x, t))$ of system (1) satisfies

$$\lim_{t \to \infty} d\Big(\big(u(x, t), v(x, t) \big), \mathcal{A} \Big) = 0 \quad \text{uniformly for} \quad x \in [0, L],$$

where $d\Big(\cdot, \mathcal{A} \Big) : C([0, L]) \times C([0, L]) \to \mathbb{R}$ is defined by

$$d\Big(m, \mathcal{A}. \Big) := \inf_{n \in \mathcal{A}.} d(m, n), \quad \text{for any} \quad m \in C([0, L]) \times C([0, L]).$$

Here the metric $d(\cdot, \cdot)$, again, is understood in the standard $C([0, L]) \times C([0, L])$ topology.

We now state our main result as follows.

Theorem 1.1. *Assume that (H_1)–(H_3) and $\bar{H}_4$ hold. Then, we have the following results:*

(i) *if $\tau_1(d_1, \alpha_1, r_1) \geqslant 0$ and $\tau_1(d_2, \alpha_2, r_2) \geqslant 0$, then $(0, 0)$ is g.a.s;*
(ii) *if $\tau_1(d_1, \alpha_1, r_1) \geqslant 0$ and $\tau_1(d_2, \alpha_2, r_2) < 0$, then $\Sigma_v = \Gamma$ and $(0, v_{d_2,\alpha_2,r_2})$ is g.a.s;*
(iii) *if $\tau_1(d_1, \alpha_1, r_1) < 0$ and $\tau_1(d_2, \alpha_2, r_2) \geqslant 0$, then $\Sigma_u = \Gamma$ and $(u_{d_1,\alpha_1,r_1}, 0)$ is g.a.s;*
(iv) *if $\tau_1(d_1, \alpha_1, r_1) < 0$ and $\tau_1(d_2, \alpha_2, r_2) < 0$, then*

$$\Gamma = \big(\Sigma_u \cup \Sigma_{u,0} \setminus \Sigma_{0,0} \big) \cup \big(\Sigma_v \cup \Sigma_{v,0} \setminus \Sigma_{0,0} \big) \cup \Sigma_- \cup \Sigma_{0,0},$$

and the following statements are valid:

(iv.1) *For all $(d_1, \alpha_1, k) \in \big(\Sigma_u \cup \Sigma_{u,0} \setminus \Sigma_{0,0} \big)$, $(u_{d_1,\alpha_1,r_1}, 0)$ is g.a.s;*
(iv.2) *For all $(d_1, \alpha_1, k) \in \big(\Sigma_v \cup \Sigma_{v,0} \setminus \Sigma_{0,0} \big)$, $(0, v_{d_2,\alpha_2,r_2})$ is g.a.s;*
(iv.3) *For all $(d_1, \alpha_1, k) \in \Sigma_-$, system (1) has a unique co-existence steady state that is g.a.s;*
(iv.4) *For all $(d_1, \alpha_1, k) \in \Sigma_{0,0}$, $u_{d_1,\alpha_1,r_1} \equiv bv_{d_2,\alpha_2,r_2}$ in $[0, L]$ and system (1) has a compact global attractor consisting of a continuum of steady states*

$$\left\{ \left(\varrho u_{d_1,\alpha_1,r_1}, \ (1 - \varrho) \frac{u_{d_1,\alpha_1,r_1}}{b} \right) : \ \varrho \in [0, 1] \right\}$$

connecting the two semi-trivial steady states.

Theorem 1.1 presents a complete classification of all possible long time behaviors of system (1) under the conditions (H_1)–(H_3) and $\bar{H}_4$. Recall the fact that the sign of $\tau_1(d_1, \alpha_1, r_1)$ and $\tau_1(d_2, \alpha_2, r_2)$ will exactly determine the existence of $(u_{d_1,\alpha_1,r_1}, 0)$ and $(0, v_{d_2,\alpha_2,r_2})$, respectively. Taking $\tau_1(d_1, \alpha_1, r_1)$ as an example, the semi-trivial steady state $(u_{d_1,\alpha_1,r_1}, 0)$ exists if and only if $\tau_1(d_1, \alpha_1, r_1) < 0$. Having this in mind, we obtain the following nice biological explanations: theorem 1.1 (*i*) reveals that if both $(u_{d_1,\alpha_1,r_1}, 0)$ and $(0, v_{d_2,\alpha_2,r_2})$ do not exist, that is, both species u and v cannot survive without competition, then two populations definitely will die out when competition is involved; Statement (*ii*) suggests that if species v can persist in the long run without competition while u cannot, then v takes an advantegeous position during the competition and would displace species u eventually; A similar interpretation can be seen from statement (*iii*). However, when both u and v can persist without competition, statement (*iv*) indicates that the final competitive consequence becomes very complicated, either one of these two competitors becomes the final winner (see (*iv*.1)–(*iv*.2)), or both of them coexist eventually (see (*iv*.3)), or even the system is degenerate in the sense that there is a compact global attractor consisting of a continuum of steady states (see (*iv*.4)).

As mentioned in [19], it is, in general, highly challenging to precisely describe the geometric property of the sets $\Sigma_u, \Sigma_{u,0}, \Sigma_v, \Sigma_{v,0}, \Sigma_{0,0}$ and Σ_-, as some of them may become empty in certain circumstance. To investigate this issue further, we next turn to discuss the special case $r_1(x) = r_2(x) := r(x)$, that is,

$$
\begin{cases}
u_t = d_1 u_{xx} - \alpha_1 u_x + u(r(x) - u - bv), & 0 < x < L, t > 0, \\
v_t = d_2 v_{xx} - \alpha_2 v_x + v(r(x) - cu - v), & 0 < x < L, t > 0, \\
d_1 u_x(0,t) - \alpha_1 u(0,t) = b_u \alpha_1 u(0,t), & t > 0, \\
d_1 u_x(L,t) - \alpha_1 u(L,t) = -b_d \alpha_1 u(L,t), & t > 0, \\
d_2 v_x(0,t) - \alpha_2 v(0,t) = b_u \alpha_2 v(0,t), & t > 0, \\
d_2 v_x(L,t) - \alpha_2 v(L,t) = -b_d \alpha_2 v(L,t), & t > 0, \\
u(x,0) = u_0(x) \geqslant, \neq 0, & 0 < x < L, \\
v(x,0) = v_0(x) \geqslant, \neq 0, & 0 < x < L.
\end{cases}
\tag{3}
$$

For system (3), we obtain a more clear picture on the global dynamics by using k, b, c as variable parameters. See below.

Theorem 1.2. *Assume that (H_1)–(H_3) and $\bar{H}_4$ hold. The following statements are true:*

(*i*) *If $k > 1$, we have $\tau_1(d_1, \alpha_1, r) < \tau_1(d_2, \alpha_2, r)$ and*

(*i*.1) *if $\tau_1(d_1, \alpha_1, r) < 0 \leqslant \tau_1(d_2, \alpha_2, r)$, then for any $(b,c) \in (0,1] \times (0,1]$, $(u_{d_1,\alpha_1,r}, 0)$ is g.a.s;*

(*i*.2) *if $\tau_1(d_1, \alpha_1, r) \geqslant 0$, then for any $(b,c) \in (0,1] \times (0,1]$, $(0,0)$ is g.a.s;*

(*i*.3) *if $\tau_1(d_2, \alpha_2, r) < 0$, there exists $c^* \in (0,1)$ such that for any $(b,c) \in (0,1] \times [c^*, 1]$, $(u_{d_1,\alpha_1,r}, 0)$ is g.a.s, and for any $(b,c) \in (0,1] \times (0,c^*)$, system (3) has a unique co-existence steady state that is g.a.s;*

(*ii*) *If $k < 1$, we have $\tau_1(d_1, \alpha_1, r) > \tau_1(d_2, \alpha_2, r)$ and*

(*ii*.1) *if $\tau_1(d_2, \alpha_2, r) < 0 \leqslant \tau_1(d_1, \alpha_1, r)$, then for any $(b,c) \in (0,1] \times (0,1]$, $(0, v_{d_2,\alpha_2,r})$ is g.a.s;*

(*ii*.2) *if $\tau_1(d_2, \alpha_2, r) \geqslant 0$, then for any $(b,c) \in (0,1] \times (0,1]$, $(0,0)$ is g.a.s;*

(*ii*.3) *if $\tau_1(d_1, \alpha_1, r) < 0$, there exists $b^* \in (0,1)$ such that for any $(b,c) \in [b^*, 1] \times (0,1]$, $(0, v_{d_2,\alpha_2,r})$ is g.a.s, while for any $(b,c) \in (0,b^*) \times (0,1]$, system (3) has a unique coexistence steady state that is g.a.s;*

(*iii*) *If $k = 1$, we have $\tau_1(d_1, \alpha_1, r) = \tau_1(d_2, \alpha_2, r)$ and*

(*iii*.1) *if $\tau_1(d_1, \alpha_1, r) \geqslant 0$, then for any $(b,c) \in (0,1] \times (0,1]$, $(0,0)$ is g.a.s;*

(*iii*.2) *if* $\tau_1(d_1, \alpha_1, r) < 0$, *then for any* $(b, c) \in (0, 1) \times (0, 1)$, *system* (3) *has a unique co-existence steady state that is g.a.s;*

(*iii*.3) *if* $\tau_1(d_1, \alpha_1, r) < 0$, *then for any* $(b, c) \in \{1\} \times (0, 1)$, $(0, v_{d_2, \alpha_2, r})$ *is g.a.s;*

(*iii*.4) *if* $\tau_1(d_1, \alpha_1, r) < 0$, *then for any* $(b, c) \in (0, 1) \times \{1\}$, $(u_{d_1, \alpha_1, r}, 0)$ *is g.a.s;*

(*iii*.5) *if* $\tau_1(d_1, \alpha_1, r) < 0$ *and* $b = c = 1$, *then system* (3) *has a compact global attractor consisting of a continuum of steady states*

$$\left\{ \left(\varrho u_{d_1, \alpha_1, r_1}, \ (1 - \varrho) u_{d_1, \alpha_1, r_1} \right) : \ \varrho \in [0, 1] \right\}.$$

We make some biological interpretations for theorem 1.2. For statement (*i*) above, clearly the situation in (*i*.1) and (*i*.2) can be understood biologically in a similar way to that of theorem 1.1 (*i*)–(*iii*), while for the case that both *u* and *v* can survive without competition, (*i*.3) above shows that species *u* has relatively more competitive advantages in the sense that either it wipes out *v* completely in the final or coexists with *v* eventually depending on whether the inter-specific competition intensity $c \in (0, 1]$ crosses over a critical number $c^* \in (0, 1)$. To understand this phenomenon, we first explain two special cases: (1) $c = 1$ and (2) $c = 0$. If $c = 1$, from the reaction terms one sees that *u* is superior since the inter-specific competition intensity *b* is less than 1, and also, from the movement terms one finds that *v* is inferior as it has stronger advective movement $(k > 1)$ which is negative (as such movements always drive individuals to the downstream end $x = L$ where there is a net loss of populations measured by b_d), so finally species *u* is the winner. If $c = 0$, the equation of *v* is decoupled from that of *u*, and for this case, it is not difficult to prove that two species will coexist eventually at the steady state $(u^*, v_{d_2, \alpha_2, r})$, where u^* is the unique positive solution of

$$\begin{cases} 0 = d_1 u_{xx} - \alpha_1 u_x + u(r(x) - b v_{d_2, \alpha_2, r} - u), \quad 0 < x < L, \\ d_1 u_x(0) - \alpha_1 u(0) = b_u \alpha_1 u(0), \\ d_1 u_x(L) - \alpha_1 u(L) = -b_d \alpha_1 u(L). \end{cases}$$

(We note here that the existence of u^* is equivalent to $\tau_1(d_1, \alpha_1, r - b v_{d_2, \alpha_2, r}) < 0$, which can be established by using $\tau_1(d_2, \alpha_2, r - v_{d_2, \alpha_2, r}) = 0$, $k > 1$, $b < 1$ and lemma 3.1. The uniqueness of u^* is standard.) Based on the results of (1) and (2), it then seems natural to expect the critical value of c^* which connects these two different competitive consequences. Statement (*ii*) can be understood in a symmetric manner to (*i*). For statement (*iii*), (*iii*.1) is easy to see; (*iii*.2) shows that two weakly competing species $(b, c \in (0, 1))$ will coexist finally if they take the same movement and growth rate; (*iii*.3)–(*iii*.4) suggest that if one species takes a slightly strong competition ability, then it will be dominated provided the rest biological traits of two populations are identical; (*iii*.5) indicates that two populations cannot be distinguished if everything of them is the same.

As we see from theorem 1.2, the global dynamics of system (3) depends heavily on the sign of $\tau_1(d_1, \alpha_1, r)$ and $\tau_1(d_2, \alpha_2, r)$. To exactly determine the sign of $\tau_1(d_1, \alpha_1, r)$ and $\tau_1(d_2, \alpha_2, r)$, we find a feasible way by fixing $k^* > 0$ (recall k^* is given in (H_1)) and changing the diffusion rates d_1, d_2, and then obtain the following result on system (3).

Theorem 1.3. *Assume that* (H_1)–(H_3) *and* $\bar{H}_4$ *hold. Fix* $k^* > 0$. *Then there exists* $0 < d^* < +\infty$ *such that*

(*i*) *if* $d_1, d_2 \geqslant d^*$, *then* $(0, 0)$ *is g.a.s;*

(*ii*) *if* $d_1 \geqslant d^* > d_2$, *then* $(0, v_{d_2, d_2 k^*, r})$ *is g.a.s;*

(*iii*) *if* $d_2 \geqslant d^* > d_1$, *then* $(u_{d_1, d_1 k^*, r}, 0)$ *is g.a.s;*

(*iv*) *if* $d_1, d_2 < d^*$, *then we have the following results:*

(*iv*.1) if $d_1 < d_2$, then there exists $c^* \in (0,1)$ such that for any $(b,c) \in (0,1] \times [c^*,1]$, $(u_{d_1,\alpha_1,r}, 0)$ is g.a.s; while if $(b,c) \in (0,1] \times (0,c^*)$, system (3) has a unique co-existence steady state which is g.a.s.

(*iv*.2) if $d_2 < d_1$, then there exists $b^* \in (0,1)$ such that for any $(b,c) \in [b^*,1] \times (0,1]$, $(0, v_{d_2,\alpha_2,r})$ is g.a.s; while if $(b,c) \in (0,b^*) \times (0,1]$, system (3) has a unique co-existence steady state which is g.a.s.

(*iv*.3) if $d_1 = d_2$, then the following statements are true:

(*iv*.3.1) for any $(b,c) \in (0,1) \times (0,1)$, system (3) has a unique co-existence steady state that is g.a.s;

(*iv*.3.2) for any $(b,c) \in \{1\} \times (0,1)$, $(0, v_{d_2,\alpha_2,r})$ is g.a.s;

(*iv*.3.3) for any $(b,c) \in (0,1) \times \{1\}$, $(u_{d_1,\alpha_1,r}, 0)$ is g.a.s;

(*iv*.3.4) if $b = c = 1$, then system (3) has a compact global attractor consisting of a continuum of steady states

$$\left\{ \left(\varrho u_{d_1,\alpha_1,r_1}, \ (1-\varrho) u_{d_1,\alpha_1,r_1} \right) : \ \varrho \in [0,1] \right\}.$$

Biologically, theorem 1.3 (*i*)–(*iii*) suggest that if the advection is proportional to the diffusion at the same level for two populations ($d_1[u_{xx} - k^* u_x]$ and $d_2[v_{xx} - k^* v_x]$), then species with sufficiently large diffusive movement will never win the competition. This is not surprising because combining lemma 3.1(2) and the limiting behaviors in lemmas 3.2–3.4 together, one immediately finds that large diffusion is harmful for the survival of single species, and thus for two-species competition. Theorem 1.3 (*iv*) can be understood similarly to the counterpart in theorem 1.2 (*i*.3), (*ii*.3) and (*iii*.2)–(*iii*.5).

The rest of this paper is organized as follows. In section 2 below, we establish theorem 1.1. Then in section 3, we prove theorems 1.2 and 1.3. Finally, we include a short discussion in section 4.

2. Proof of theorem 1.1

To verify theorem 1.1, according to the theory of monotone dynamical systems [6, proposition 9.1, theorem 9.2], we need to make an estimate on the linear stability of coexistence steady states.

Suppose that (u,v) is a coexistence steady state of system (1), that is,

$$\begin{cases} d_1 u_{xx} - \alpha_1 u_x + u(r_1(x) - u - bv) = 0, & 0 < x < L \\ d_2 v_{xx} - \alpha_2 v_x + v(r_2(x) - cu - v) = 0, & 0 < x < L \\ d_1 u_x(0) - \alpha_1 u(0) = b_u \alpha_1 u(0), \ d_2 v_x(0) - \alpha_2 v(0) = b_u \alpha_2 v(0), \\ d_1 u_x(L) - \alpha_1 u(L) = -b_d \alpha_1 u(L), \ d_2 v_x(L) - \alpha_2 v(L) = -b_d \alpha_2 v(L). \end{cases} \tag{4}$$

Linearizing system (4) at (u,v), we obtain the following linear eigenvalue problem

$$\begin{cases} d_1 \phi_{xx} - \alpha_1 \phi_x + \phi(r_1(x) - u - bv) - u(\phi + b\psi) + \lambda \phi = 0, \ 0 < x < L, t > 0, \\ d_2 \psi_{xx} - \alpha_2 \psi_x + \psi(r_2(x) - cu - v) - v(c\phi + \psi) + \lambda \psi = 0, \ 0 < x < L, t > 0, \\ d_1 \psi_x(0) - \alpha_1 \psi(0) = b_u \alpha_1 \psi(0), \ d_2 \psi_x(0) - \alpha_2 \psi(0) = b_u \alpha_2 \psi(0), \\ d_1 \phi_x(L) - \alpha_1 \phi(L) = -b_d \alpha_1 \phi(L), \ d_2 \psi_x(L) - \alpha_2 \psi(L) = -b_d \alpha_2 \psi(L). \end{cases} \tag{5}$$

Using the Krein–Rutman theorem [7] again, one sees that problem (5) admits a principal eigenvalue, denoted in the sequel by λ_1, and its corresponding eigenfunctions (ϕ, ψ) satisfying $\phi > 0 > \psi$ in $(0,L)$.

We now display a key lemma regarding the linear stability of any coexistence steady state, which plays an extremely important role in proving theorem 1.1.

Lemma 2.1. *Assume that (H₁)–(H₃) and $\bar{H}_4$ hold. Then for any $(d_1, \alpha_1, k) \in \Gamma\backslash\Sigma_{0,0}$, every coexistence steady state of system (1), if it exists, is linearly stable.*

Proof. It suffices to show that $\lambda_1 > 0$ when $(d_1, \alpha_1, k) \in \Gamma\backslash\Sigma_{0,0}$. We employ some idea from [19] to give this proof.

Multiplying the first equation in (5) by u and the first equation in (4) by ϕ, and then subtracting the resulting equations, one finds

$$(d_1\phi_{xx} - \alpha_1\phi_x)u - (d_1u_{xx} - \alpha_1u_x)\phi - u^2(\phi + b\psi) + \lambda_1\phi u = 0. \tag{6}$$

Multiplying (6) by $\frac{\phi^2}{u^2}e^{-\frac{\alpha_1}{d_1}x}$ and integrating over $(0, L)$, one attains

$$\int_0^L (d_1\phi_x - \alpha_1\phi)_x \frac{\phi^2}{u}e^{-\frac{\alpha_1}{d_1}x}dx - \int_0^L (d_1u_{xx} - \alpha_1u_x)\frac{\phi^3}{u^2}e^{-\frac{\alpha_1}{d_1}x}dx$$

$$- \int_0^L \phi^2(\phi + b\psi)e^{-\frac{\alpha_1}{d_1}x}dx + \lambda_1\int_0^L \frac{\phi^3}{u}e^{-\frac{\alpha_1}{d_1}x}dx = 0. \tag{7}$$

Set

$$I_1 := \int_0^L (d_1\phi_x - \alpha_1\phi)_x \frac{\phi^2}{u}e^{-\frac{\alpha_1}{d_1}x}dx \quad \text{and} \quad I_2 := \int_0^L (d_1u_x - \alpha_1u)_x \frac{\phi^3}{u^2}e^{-\frac{\alpha_1}{d_1}x}dx.$$

By integration by parts and boundary conditions, one can calculate

$$I_1 := -b_d\alpha_1 \frac{\phi^3(L)}{u(L)}e^{-\frac{\alpha_1}{d_1}L} - b_u\alpha_1 \frac{\phi^3(0)}{u(0)} + \int_0^L \frac{\alpha_1}{d_1}\frac{\phi^3}{u}(d_1\frac{\phi_x}{\phi} - \alpha_1)e^{-\frac{\alpha_1}{d_1}x}dx$$

$$- \int_0^L (d_1\frac{\phi_x}{\phi} - \alpha_1)\frac{\phi^3}{u}(2\frac{\phi_x}{\phi} - \frac{u_x}{u})e^{-\frac{\alpha_1}{d_1}x}dx, \tag{8}$$

and

$$I_2 := -b_d\alpha_1 \frac{\phi^3(L)}{u(L)}e^{-\frac{\alpha_1}{d_1}L} - b_u\alpha_1 \frac{\phi^3(0)}{u(0)} + \int_0^L \frac{\alpha_1}{d_1}\frac{\phi^3}{u}(d_1\frac{u_x}{u} - \alpha_1)e^{-\frac{\alpha_1}{d_1}x}dx$$

$$- \int_0^L \frac{\phi^3}{u}(d_1\frac{u_x}{u} - \alpha_1)(3\frac{\phi_x}{\phi} - 2\frac{u_x}{u})e^{-\frac{\alpha_1}{d_1}x}dx. \tag{9}$$

It follows from (8) and (9) that

$$I_1 - I_2 = -2d_1\int_0^L \frac{\phi^3}{u}(\frac{u_x}{u} - \frac{\phi_x}{\phi})^2 e^{-\frac{\alpha_1}{d_1}x}dx, \tag{10}$$

which, together with (7), gives

$$\lambda_1\int_0^L \frac{\phi^3}{u}e^{-\frac{\alpha_1}{d_1}x}dx = \int_0^L 2d_1\frac{\phi^3}{u}(\frac{u_x}{u} - \frac{\phi_x}{\phi})^2 e^{-\frac{\alpha_1}{d_1}x}dx + \int_0^L \phi^2(\phi + b\psi)e^{-\frac{\alpha_1}{d_1}x}dx. \tag{11}$$

Following the same idea as above, one can use the equations v and ψ satisfy to derive

$$\lambda_1 \int_0^L \frac{\psi^3}{v} e^{-\frac{\alpha_2}{d_2}x} dx = \int_0^L 2d_2 \frac{\psi^3}{v} (\frac{v_x}{v} - \frac{\psi_x}{\psi})^2 e^{-\frac{\alpha_2}{d_2}x} dx + \int_0^L \psi^2(c\phi + \psi) e^{-\frac{\alpha_2}{d_2}x} dx. \tag{12}$$

Multiplying (11) by c^3 and subtracting (12) by the resulting equations, one finds

$$\lambda_1 \int_0^L (c^3 \frac{\phi^3}{u} e^{-\frac{\alpha_1}{d_1}x} - \frac{\psi^3}{v} e^{-\frac{\alpha_2}{d_2}x}) dx \geqslant \int_0^L (c\phi + \psi)^2(c\phi - \psi) e^{-\frac{\alpha_1}{d_1}x} dx$$

$$+ \int_0^L 2d_1 c^3 \frac{\phi^3}{u} (\frac{u_x}{u} - \frac{\phi_x}{\phi})^2 e^{-\frac{\alpha_1}{d_1}x} dx - \int_0^L 2d_2 \frac{\psi^3}{v} (\frac{v_x}{v} - \frac{\psi_x}{\psi})^2 e^{-\frac{\alpha_2}{d_2}x} dx$$

$$\geqslant 0, \tag{13}$$

where we have used $\frac{\alpha_1}{d_1} = \frac{\alpha_2}{d_2}$, $bc \leqslant 1$ and $\phi > 0 > \psi$ in $(0, L)$. So, $\lambda_1 \geqslant 0$.

It remains to exclude $\lambda_1 = 0$ under the given conditions. By (13), we know that $\lambda_1 = 0$ if and only if

$$bc = 1, \quad \frac{u_x}{u} = \frac{\phi_x}{\phi}, \frac{v_x}{v} = \frac{\psi_x}{\psi} \text{ and } \psi = c\phi,$$

which implies

$$bc = 1 \quad \text{and} \quad \frac{u_x}{u} = \frac{v_x}{v}.$$

The above second condition further yields

$$u = \rho v \quad \text{for some constant} \quad \rho > 0. \tag{14}$$

By applying (14) to the equations of (u, v), one can derive from the uniqueness of positive steady state of the single species problem that

$$(1 + \frac{b}{\rho})u = u_{d_1,\alpha_1,r_1} \quad \text{and} \quad (1 + c\rho)v = v_{d_2,\alpha_2,r_2},$$

which, in view of $bc = 1$, gives $\frac{u_{d_1,\alpha_1,r}}{v_{d_2,\alpha_2,r}} = b$. This in turn shows

$$\tau_1(d_2, \alpha_2, r_2 - cu_{d_1,\alpha_1,r_1}) = \tau_1(d_2, \alpha_2, r_2 - v_{d_2,\alpha_2,r_2}) = 0$$

and

$$\tau_1(d_1, \alpha_1, r_1 - bv_{d_2,\alpha_2,r_2}) = \tau_1(d_1, \alpha_1, r_1 - u_{d_1,\alpha_1,r_1}) = 0,$$

contradicting our assumption. Thus, $\lambda_1 > 0$. $\qquad\qquad\square$

Remark 2.1. We note here that when b_u or b_d equals infinity, that is, the Dirichlet boundary condition holds, the above proof still works. Indeed, one should keep in mind

$$\frac{\phi}{u}\big|_{x=0,L} = \frac{\phi'}{u'}\big|_{x=0,L} \quad \text{and} \quad \frac{\psi}{v}\big|_{x=0,L} = \frac{\psi'}{v'}\big|_{x=0,L},$$

where we have used the Hopf boundary lemma.

We next give the proof of theorem 1.1 as follows.

Proof. In statement (*i*), both semi-trivial steady states do not exist; in statement (*ii*), only $(0, v_{d_2, \alpha_2, r_2})$ exists; and in statement (*iii*), only $(u_{d_1, \alpha_1, r_1}, 0)$ exists. The dynamics in these three statements can be obtained by using the standard upper and lower solution method; see [21, lemma 5.1].

Statement (*iv*) holds mainly due to the estimate in lemma 2.1. Since the rest proof is quite similar to [19, theorem 1.2], we omit the details here. □

3. Proof of theorems 1.2 and 1.3

Recall $\tau_1(d, \alpha, r)$ for problem (2). By the variational approach, if $0 \leqslant b_u, b_d < \infty$, then

$$\tau_1(d, \alpha, r) = \inf_{0 \neq \psi \in H^1(0, L)} \frac{\int_0^L (d\psi_x^2 e^{\frac{\alpha}{d}x} - r\psi^2 e^{\frac{\alpha}{d}x}) dx + b_d \alpha e^{\frac{\alpha L}{d}} \psi^2(L) + b_u \alpha \psi^2(0)}{\int_0^L e^{\frac{\alpha}{d}x} \psi^2 dx};$$

if $b_u = b_d = \infty$, then

$$\tau_1(d, \alpha, r) = \inf_{\psi \in \mathcal{S}} \frac{\int_0^L (d\psi_x^2 e^{\frac{\alpha}{d}x} - r\psi^2 e^{\frac{\alpha}{d}x}) dx}{\int_0^L e^{\frac{\alpha}{d}x} \psi^2 dx},$$

where $\mathcal{S} := \{\phi \in H^1(0, L) | \phi(0) = \phi(L) = 0, \phi \not\equiv 0\}$; if $b_u = \infty$ and $0 \leqslant b_d < \infty$, then

$$\tau_1(d, \alpha, r) = \inf_{\psi \in \mathcal{S}_1} \frac{\int_0^L (d\psi_x^2 e^{\frac{\alpha}{d}x} - r\psi^2 e^{\frac{\alpha}{d}x}) dx + b_d \alpha e^{\frac{\alpha L}{d}} \psi^2(L)}{\int_0^L e^{\frac{\alpha}{d}x} \psi^2 dx}, \tag{15}$$

where $\mathcal{S}_1 := \{\phi \in H^1(0, L) | \phi(0) = 0, \phi \not\equiv 0\}$; and if $0 \leqslant b_u < \infty$ and $b_d = \infty$, then

$$\tau_1(d, \alpha, r) = \inf_{\psi \in \mathcal{S}_2} \frac{\int_0^L (d\psi_x^2 e^{\frac{\alpha}{d}x} - r\psi^2 e^{\frac{\alpha}{d}x}) dx + b_u \alpha \psi^2(0)}{\int_0^L e^{\frac{\alpha}{d}x} \psi^2 dx},$$

where $\mathcal{S}_2 := \{\phi \in H^1(0, L) | \phi(L) = 0, \phi \not\equiv 0\}$. Then the following result is standard.

Lemma 3.1. *Assume that* $d, \alpha > 0, 0 \leqslant b_u, b_d \leqslant \infty, |b_u| + |b_d| \neq 0$ *and* $m(x) \in L^\infty([0, L])$. *Then the following statements on* $\tau_1(d, \alpha, m)$ *are true:*

(1) $\tau_1(d, \alpha, m)$ *is strictly decreasing in the weight function* $m(x)$ *in the* L^∞ *sense, that is, if* $m_1(x) \leqslant, \not\equiv m_2(x)$ *in* $[0, L]$, *then* $\tau_1(d, \alpha, m_1) > \tau_1(d, \alpha, m_2)$;
(2) if $\beta > 1$, *then* $\tau_1(\frac{d}{\beta}, \frac{\alpha}{\beta}, m) < \tau_1(d, \alpha, m) < \tau_1(\beta d, \beta \alpha, m)$.

Proof. The proof of statement (1) is standard; see, e.g. [1–3].

We next verify statement (2). Without loss of generality, we assume that $b_u = \infty$ and $0 \leqslant b_d < \infty$. By the Krein–Rutman theorem [7], problem (2) admits a principal eigen-pair $(\tau_1(\beta d, \beta \alpha, m), \psi_1(\beta d, \beta \alpha, m))$, where $\psi_1(\beta d, \beta \alpha, m) \in \mathcal{S}_1$ can be chosen strictly positive on $(0, L)$. For simplify, we denote $\psi_1(\beta d, \beta \alpha, m)$ by ψ_1. Clearly, $(\tau_1(\beta d, \beta \alpha, m), \psi_1)$ satisfies

$$
\begin{aligned}
\tau_1(\beta d, \beta\alpha, m) &= \frac{\int_0^L (\beta d\psi_{1,x}^2 e^{\frac{\alpha}{d}x} - m\psi_1^2 e^{\frac{\alpha}{d}x})\mathrm{d}x + b_d\beta\alpha e^{\frac{\alpha L}{d}}\psi_1^2(L)}{\int_0^L e^{\frac{\alpha}{d}x}\psi_1^2\mathrm{d}x} \\
&> \frac{\int_0^L (d\psi_{1,x}^2 e^{\frac{\alpha}{d}x} - m\psi_1^2 e^{\frac{\alpha}{d}x})\mathrm{d}x + b_d\alpha e^{\frac{\alpha L}{d}}\psi_1^2(L)}{\int_0^L e^{\frac{\alpha}{d}x}\psi_1^2\mathrm{d}x} \\
&\geqslant \inf_{\psi\in\mathcal{S}_1} \frac{\int_0^L (d\psi_x^2 e^{\frac{\alpha}{d}x} - m\psi^2 e^{\frac{\alpha}{d}x})\mathrm{d}x + b_d\alpha e^{\frac{\alpha L}{d}}\psi^2(L)}{\int_0^L e^{\frac{\alpha}{d}x}\psi^2\mathrm{d}x} \\
&= \tau_1(d, \alpha, m),
\end{aligned}
$$

where we have used $d, \alpha > 0$, $b_d \geqslant 0$, $\beta > 1$, ψ_1 is not a constant on $[0, L]$, and the variational approach (15). Similarly, one can obtain $\tau_1(\frac{d}{\beta}, \frac{\alpha}{\beta}, m) < \tau_1(d, \alpha, m)$. This completes the proof. $\qquad\square$

We now are ready to verify theorem 1.2.

Proof. Since the proofs are similar, we only prove case (i).

By the assumption, $k > 1$, that is, $d_2 > d_1$. By lemma 3.1, we have $\tau_1(d_1, \alpha_1, r) < \tau_1(d_2, \alpha_2, r)$. Then $(i.1)$ and $(i.2)$ are the direct results of theorem 1.1. For $(i.3)$, we have $\tau_1(d_1, \alpha_1, r) < \tau_1(d_2, \alpha_2, r) < 0$, that is $u_{d_1,\alpha_1,r}$ and $v_{d_2,\alpha_2,r}$ exist. Now, we will show that $(0, v_{d_2,\alpha_2,r})$ is linearly unstable. It suffices to show that $\tau_1(d_1, \alpha_1, r - bv_{d_2,\alpha_2,r}) < 0$. Actually, by lemma 3.1, we have

$$
\tau_1(d_1, \alpha_1, r - bv_{d_2,\alpha_2,r}) \leqslant \tau_1(d_1, \alpha_1, r - v_{d_2,\alpha_2,r}) < \tau_1(d_2, \alpha_2, r - v_{d_2,\alpha_2,r}) = 0,
$$

where we used $0 < b < 1$, $d_2 > d_1$, the equation of $v_{d_2,\alpha_2,r}$ and $v_{d_2,\alpha_2,r} > 0$ in $(0, L)$.

Next, we consider the stability of $(u_{d_1,\alpha_1,r}, 0)$. It suffices to consider the sign of $\tau_1(d_1 k, \alpha_1 k, r - cu_{d_1,\alpha_1,r})$. Since $\tau_1(d_1, \alpha_1, r) < 0$, by lemma 3.1 and theorem 1.1, it suffices to show that $\tau_1(d_1 k, \alpha_1 k, r - u_{d_1,\alpha_1,r}) > 0$. Indeed, by lemma 3.1, we have

$$
\tau_1(d_1 k, \alpha_1 k, r - u_{d_1,\alpha_1,r}) > \tau_1(d_1, \alpha_1, r - u_{d_1,\alpha_1,r}) = 0,
$$

where, we used $k > 1$ and the equation of $u_{d_1,\alpha_1,r}$. $\qquad\square$

To prove theorem 1.3, we need the following lemmas.

Lemma 3.2. *For any given $d, L, k > 0$, $0 < b_d < +\infty$, $0 \leqslant b_u < +\infty$ and $r(x) > 0$ in $(0, L)$, we have*

$(i)\ \lim_{d\to 0}\tau_1(d, dk, r) < 0;$
$(ii)\ \lim_{d\to\infty}\tau_1(d, dk, r) = +\infty.$

Proof. By variational representation, choosing 1 as a test function, we have

$$
\lim_{d\to 0}\tau_1(d, dk, r) < -\frac{\int_0^L re^{kx}\mathrm{d}x}{\int_0^L e^{kx}\mathrm{d}x} < 0,
$$

where we have used $r > 0$ in $(0, L)$.

On the other hand, by a transformation $\varphi = \mathrm{e}^{\epsilon k x} \psi$, where ϵ is a positive number to be determined later, we have

$$
\begin{aligned}
\tau_1(d, \mathrm{d}k, r) &= \inf_{0 \neq \psi \in H^1(0,L)} \frac{b_d \mathrm{d}k \mathrm{e}^{kL} \psi^2(L) + b_u \mathrm{d}k \psi^2(0) + \int_0^L (\mathrm{d}\psi_x^2 \mathrm{e}^{kx} - r \psi^2 \mathrm{e}^{kx}) \mathrm{d}x}{\int_0^L \mathrm{e}^{kx} \psi^2 \mathrm{d}x} \\
&= \inf_{0 \neq \varphi \in H^1(0,L)} \left\{ \frac{b_d \mathrm{d}k \mathrm{e}^{(1-2\epsilon)kL} \varphi^2(L) + b_u \mathrm{d}k \varphi^2(0) - \int_0^L r \varphi^2 \mathrm{e}^{(1-2\epsilon)kx} \mathrm{d}x}{\int_0^L \mathrm{e}^{(1-2\epsilon)kx} \varphi^2 \mathrm{d}x} \right. \\
&\quad + \left. \frac{\int_0^L [\mathrm{d}\varphi_x^2 + \mathrm{d}\epsilon^2 k^2 \varphi^2 - \epsilon \mathrm{d}k(\varphi^2)_x] \mathrm{e}^{(1-2\epsilon)kx} \mathrm{d}x}{\int_0^L \mathrm{e}^{(1-2\epsilon)kx} \varphi^2 \mathrm{d}x} \right\} \\
&= \inf_{0 \neq \varphi \in H^1(0,L)} \left\{ \frac{b_d \mathrm{d}k \mathrm{e}^{(1-2\epsilon)kL} \varphi^2(L) + b_u \mathrm{d}k \varphi^2(0) + \int_0^L [\mathrm{d}\varphi_x^2 + \mathrm{d}\epsilon^2 k^2 \varphi^2] \mathrm{e}^{(1-2\epsilon)kx} \mathrm{d}x}{\int_0^L \mathrm{e}^{(1-2\epsilon)kx} \varphi^2 \mathrm{d}x} \right. \\
&\quad - \frac{\epsilon \mathrm{d}k \varphi^2(L) \mathrm{e}^{(1-2\epsilon)kL} - \epsilon \mathrm{d}k \varphi^2(0) + \int_0^L r \varphi^2 \mathrm{e}^{(1-2\epsilon)kx} \mathrm{d}x}{\int_0^L \mathrm{e}^{(1-2\epsilon)kx} \varphi^2 \mathrm{d}x} \\
&\quad + \left. \frac{\epsilon(1-2\epsilon) \mathrm{d}k^2 \int_0^L \varphi^2 \mathrm{e}^{(1-2\epsilon)kx} \mathrm{d}x}{\int_0^L \mathrm{e}^{(1-2\epsilon)kx} \varphi^2 \mathrm{d}x} \right\} \\
&= \inf_{0 \neq \varphi \in H^1(0,L)} \left\{ \frac{(b_d - \epsilon) \mathrm{d}k \mathrm{e}^{(1-2\epsilon)kL} \varphi^2(L) + \int_0^L \mathrm{d}\varphi_x^2 \mathrm{e}^{(1-2\epsilon)kx} \mathrm{d}x + (b_u + \epsilon) \mathrm{d}k \varphi^2(0)}{\int_0^L \mathrm{e}^{(1-2\epsilon)kx} \varphi^2 \mathrm{d}x} \right. \\
&\quad + \left. \frac{\epsilon(1-\epsilon) \mathrm{d}k^2 \int_0^L \varphi^2 \mathrm{e}^{(1-2\epsilon)kx} \mathrm{d}x - \int_0^L r \varphi^2 \mathrm{e}^{(1-2\epsilon)kx} \mathrm{d}x}{\int_0^L \mathrm{e}^{(1-2\epsilon)kx} \varphi^2 \mathrm{d}x} \right\} \\
&\geqslant \epsilon(1-\epsilon) \mathrm{d}k^2 - \|r\|_{L^\infty(0,L)},
\end{aligned}
\tag{16}
$$

provided $0 < \epsilon < \min\{b_d, 1\}$. Let $d \to +\infty$, part *(ii)* follows directly from the above inequality. $\qquad\square$

Lemma 3.3. *For any given $d, L, k > 0$, $b_d = 0$, $0 < b_u < +\infty$ and $r(x) > 0$ in $(0,L)$, we obtain*

(i) $\lim_{d \to 0} \tau_1(d, \mathrm{d}k, r) < 0$;
(ii) $\lim_{d \to +\infty} \tau_1(d, \mathrm{d}k, r) = +\infty$.

Proof. The proof is similar to that of lemma 3.2, and thus is omitted. $\qquad\square$

Lemma 3.4. *For any given $d, L, k > 0$ and $r \in C^{0,\gamma}([0,L], \mathbb{R}^+)$, if one of the following cases holds: case (1) $b_u = b_d = +\infty$; case (2) $b_u = +\infty$ and $0 \leqslant b_d < +\infty$; case (3) $b_d = +\infty$ and $0 \leqslant b_u < +\infty$; then, one obtains*

(i) $\lim_{d \to 0} \tau_1(d, \mathrm{d}k, r) < 0$;
(ii) $\lim_{d \to +\infty} \tau_1(d, \mathrm{d}k, r) = +\infty$.

Proof. Since the proofs of these cases are similar, we only consider case (2), i.e. $b_u = +\infty$ and $0 \leqslant b_d < +\infty$.

Choosing x as a text function and recalling (15), one attains that $\lim_{d \to 0} \tau_1(d, dk, r) < 0$, which finishes (*i*). For (*ii*), one can continue to use the idea in lemma 3.2 (*ii*) (with easy modifications) to establish the desired result. □

Finally, we establish theorem 1.3.

Proof. Based on theorem 1.2 and $\frac{\alpha_1}{d_1} = \frac{\alpha_2}{d_2} = k^*$, it suffices to consider the signs of $\tau_1(d_1, d_1 k^*, r)$ and $\tau_1(d_2, d_2 k^*, r)$. By lemma 3.1 (2), we know that $\tau_1(d, dk^*, r)$ is strictly increasing about d. Then it suffices to show that

$$\lim_{d \to 0} \tau_1(d, dk^*, r) < 0$$

and

$$\lim_{d \to +\infty} \tau_1(d, dk^*, r) > 0$$

which are immediately derived from lemmas 3.2–3.4. □

4. Discussion

In this paper, we primarily studied the population dynamics of a general model from river ecology as shown in system (1), where an interesting feature of the system structure lies in two parameters b_u and b_d appearing in the boundary conditions, which are used to measure the loss rates of individuals at the upstream and downstream ends, respectively. These two parameters, beside obviously important biological interpretations, also play a significant role in mathematics, as different values of them may yield different types of boundary conditions, including the standard Neumann, Robin and Dirichlet types.

For this general model, our first contribution is to establish a complete classification of all possible long time dynamical behaviors under certain mild conditions on system parameters; see theorem 1.1. This result provides a first angle to understand the global dynamics of system (1), and more importantly, it implies that the *global* dynamics could be determined by the *local* dynamics. Resting on this, we then further apply theorem 1.1 to discuss a special situation where two species are competing for the same resource. By regarding k or k^*, b, c and diffusion rates as variable parameters, we obtain a more clear picture on the global dynamics of system (3); see theorems 1.2 and 1.3.

Although in the current work we have made some progress in understanding the general system (1), there are several important problems that are unsolved and deserve further investigation. The first one concerns the technical condition (H_1), which, biologically means that the movement rates of diffusion and advection for two competitors are proportional. It is interesting to explore to what extent this condition can be relaxed; see also [19]. The second one refers to the local stability of semi-trivial steady states, which, currently is well understood in the case of identical growth rate. What about the case of differing growth rates? Lastly, we should point out that even the existence of semi-trivial steady states is non-trivial in general due to the appearance of parameters b_u and b_d. For the homogeneous case, that is, the growth function is a constant, recently we made some new insights to this issue in [16]; but for general functions especially those that are admitted to change sign in the domain $(0, L)$, it is far from being completely understood. We leave these interesting and challenging problems for future exploration.

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