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Dynamical Behavior of a Lotka-Volterra Competitive System From River Ecology

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Abstract. This work is devoted to the study of a two-species competition model in advective homogenous environment from the river ecology. We assume that two species live in a special river where the upstream end has free-flow boundary conditions. This means that the upstream end is linked to a lake. On the other hand, at the downstream end the population may be exposed to differing magnitudes of individuals loss. We mainly study the influence of inter-specific competition intensities on the competition outcome and show that the contest is very complex — viz. either one of competitors becomes a single winner (exclusion), or both populations coexist, or both species go to extinction.

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1. Introduction

The dynamical models expressed by reaction-diffusion equations have been actively studied in recent years. In particular, such models can describe the uneven distribution of individuals across an area. This is an important issue in various fields of natural sciences and the two-species Lotka-Volterra competition-diffusion system is one of the most popular models used to investigate the problems mentioned — cf. [2,8,9,22].

In addition to traditional reaction-diffusion models, there are numerous studies focused on spatial population dynamics in advective environment. The advection is an inducement of an individual movement in a given direction caused by external environmental forces

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like lake water columns, streams, or rivers [2–5, 18–20]. The advection terms can be incorporated in these classical Lotka-Volterra competition-diffusion systems which results the competition-diffusion-advection systems. Most obviously, it occurs in rivers where individuals can be swept downstream by water flows. In order to study different ecological scenarios, Lou and Lutscher [14] considered various boundary conditions at the upstream and downstream ends. More exactly, the competition-diffusion-advection system with various boundary conditions has the form

$$\begin{array}{lll} u_t = d_1 u_{xx} - \alpha_1 u_x + u[r - u - av], & 0 < x < L, & t > 0, \\ v_t = d_2 v_{xx} - \alpha_2 v_x + v[r - cu - v], & 0 < x < L, & t > 0, \\ d_1 u_x(x,t) - \alpha_1 u(x,t) = b_1 \alpha_1 u(x,t), & x = 0, & t > 0, \\ d_1 u_x(x,t) - \alpha_1 u(x,t) = -b_2 \alpha_1 u(x,t), & x = L, & t > 0, \\ d_2 v_x(x,t) - \alpha_2 v(x,t) = b_1 \alpha_2 v(x,t), & x = 0, & t > 0, \\ d_2 v_x(x,t) - \alpha_2 v(x,t) = -b_2 \alpha_2 v(x,t), & x = L, & t > 0, \\ u(x,0) = u_0 \geq, \not\equiv 0, \;\; v(x,0) = v_0 \geq, \not\equiv 0, & 0 < x < L, & \end{array} \tag{1.1}$$

where $a > 0$, $c > 0$ are the inter-specific competition intensities, u, v the population densities of two aquatic competing species, $d_1 > 0$, $d_2 > 0$ random diffusion rates of the two species, and $\alpha_1 > 0$, $\alpha_2 > 0$ the effective advection rates caused by unidirectional water flow. Besides, r is the intrinsic growth rate or the local carrying capacity and L the size of the habitat. In what follows, $x = 0$ and $x = L$ are called the upstream and downstream ends. The parameters $b_1 \geq 0$ and $b_2 \geq 0$ are used to measure the respective loss rate of individuals at the upstream and downstream ends which are relative to the flow rate — [14]. More specifically, let us consider b_2 as an example. It is easily seen that $b_2 = 0, 1$ produces no-flux Neumann boundary conditions. The corresponding problem can be used in order to describe the scenario stream to lake [14, 27]. If $b_2 > 1$, it means that random and directed movements will cause population loss. Moreover, sufficiently large coefficient b_2 reflects a severe loss of individuals at the downstream end, which in turn indicates that the downstream area is unfavorable for organisms to survive. Formally, we can regard $b_2 = \infty$ as the Dirichlet boundary condition $u(L,t) = v(L,t) = 0$ for $t > 0$ which can be used to model the situation stream to ocean [24].

We note that various special cases and variants of the system (1.1) have been qualitatively investigated in last years. Under no-flux boundary conditions — i.e. if no individual passes through the upstream and downstream ends, Lou *et al.* [15] confirmed that a weaker advection is more beneficial for species to exclude its competitor when $d_1 = d_2$ and $\alpha_1 \neq \alpha_2$. For unequal movement rates $d_1 \neq d_2$ and $\alpha_1 \neq \alpha_2$, Zhou [31] found that the strategy of faster diffusion together with slower advection is always favorable. This result can be viewed as a generation of [15]. For other boundary conditions — e.g. if $d_1 \neq d_2$ and $\alpha_1 = \alpha_2$, Lou and Zhou [17] suggested that the competitor with faster diffusion rate will displace the slower one — i.e. the faster diffusion evolves for $b_1 = 0$ and $b_2 \in [0, 1)$. If $d_1 = d_2$ and $\alpha_1 \neq \alpha_2$, Xu *et al.* [30] considered the case $b_1 = 0$, $1/2 \leq b_2 \leq +\infty$ and showed that a weaker advection is more favorable for species to survive, thus extending results [15]. For higher spatial dimension studies, we refer the reader to [29, 32].

There are few recent works dealing with the case $b_1 = -1$, i.e. if the upstream end has the Neumann boundary condition. Assuming that $d_1 \neq d_2$, $\alpha_1 = \alpha_2$, Tang and Chen [25] note that a larger diffusion should be selected if $b_2 \in [0,1)$, while for $b_2 \in (1,\infty]$ a slower diffuser provides more competitive advantages. For $b_2 = 1$, the system (1.1) becomes degenerate in the sense that there is a compact attractor consisting of a continuum of steady states. Later on, Ma and Tang [21] investigated unequal movement rates $d_1 \neq d_2$, $\alpha_1 \neq \alpha_2$ and $b_2 = \infty$. They found that:

1. The strategy of a slower diffusion and faster advection is always favorable.

2. Two species will also coexist for a faster advection and faster diffusion.

Li and Xu [13] considered the case $d_2 > d_1 > 0$, $\alpha_1 = \alpha_2$ and unequal magnitudes of the population loss at the downstream end $x = L$, i.e.

$$\begin{aligned}
&d_1 u_x(x,t) - \alpha_1 u(x,t) = -b_1\alpha_1 u(x,t), \quad x = L, \quad t > 0,\\
&d_2 v_x(x,t) - \alpha_2 v(x,t) = -b_2\alpha_2 v(x,t), \quad x = L, \quad t > 0,
\end{aligned}$$

and $b_2 \geq b_1 \geq 1$. Their results suggest that slower dispersal is selected for, which can be viewed as the further development of [25].

However, different species have different abilities to compete, so that the influence of inter-specific competition intensities on the dynamics is extremely significant. Nevertheless, to the best of the author's knowledge, there is no work devoted to the impact of different inter-specific competition intensities on the dynamics of the system (1.1) in the case of the Neumann boundary conditions at the upstream end. Following the previous considerations, we note that if $d_1 \neq d_2$ and the population loss magnitudes are different at $x = L$, then either both species vanish or the slower diffuser species wins and these species cannot coexist when both inter-specific competition coefficients are normalized to 1. On the other hand, what happens to the competition outcome, if the inter-specific competition intensities differ? Is the coexistence of two populations possible in addition to competitive exclusion? Therefore, getting motivated by [13], here we investigate the following system:

$$\begin{aligned}
&u_t = d_1 u_{xx} - \alpha u_x + u(r - u - av), && 0 < x < L, \quad t > 0,\\
&v_t = d_2 v_{xx} - \alpha v_x + v(r - cu - v), && 0 < x < L, \quad t > 0,\\
&u_x(0,t) = v_x(0,t) = 0, && t > 0,\\
&d_1 u_x(L,t) - \alpha u(L,t) = -b_1 \alpha u(L,t), && t > 0,\\
&d_2 v_x(L,t) - \alpha v(L,t) = -b_2 \alpha v(L,t), && t > 0,\\
&u(x,0) = u_0 \geq,\not\equiv 0, \ \ v(x,0) = v_0 \geq,\not\equiv 0, && 0 < x < L
\end{aligned} \tag{1.2}$$

with the interpretation of variables and parameters in the same biological manner as for the system (1.1).

In order to present the main result, we need the following conditions:

(H_1) $0 < d_1 < d_2$;

(H_2) $1 < b_1 \leq b_2 \leq \infty$.

Note that condition (H_1) does not restrict the generality because of the system (1.2) symmetry. It is also easily seen that stronger diffusive movements leads to a greater loss of individuals, so that (H_1) yields assumption (H_2).

Since (1.2) generates a monotone dynamical system, its dynamics is largely determined by the corresponding steady states and their stability. Monotone dynamical systems are well studied [10,23]. In particular, the system (1.2) has the following types of nonnegative steady state solutions:

(i) $(u,v)=(0,0)$ is called a trivial steady state;

(ii) $(u,v)=(\widehat{u},0)$ or $(u,v)=(0,\widehat{v})$ is called a semi-trivial steady state, where $\widehat{u}>0$ and $\widehat{v}>0$;

(iii) $u^*>0, v^*>0$, and we call (u^*,v^*) a coexistence steady state.

Setting

$$k_0=e^{(\frac{\alpha}{d_2}-\frac{\alpha}{d_1})L}, \tag{1.3}$$

we observe that k_0 is in $(0,1)$. For every $\xi>0$, define

$$\Pi_\xi := \big\{(a,c)\in\mathbb{R}^+\times\mathbb{R}^+ : ac\le\xi\big\}. \tag{1.4}$$

Theorem 1.1. *If (H_1) and (H_2) hold, then the system* (1.2) *has the following properties:*

(i) If $1<b_1\le b_2\le 1+rL/\alpha$, then for every $d_1,d_2>0$ and $\alpha>0$, there exist constants $a^*\in(0,+\infty)$ and $c^*\in(0,1)$ such that for every $(a,c)\in((0,\infty)\times[c^*,\infty))\cap\Pi_{k_0}$, $(\widehat{u},0)$ is GAS. Besides, for every $(a,c)\in((0,a^*)\times(0,c^*))\cap\Pi_{k_0}$, there exists a unique coexistence steady state for system (1.2) *that is GAS, and for every $(a,c)\in([a^*,+\infty)\times(0,+\infty))\cap\Pi_{k_0}$, $(0,\widehat{v})$ is GAS.*

(ii) If $1<b_1\le 1+rL/\alpha<b_2$, then for every $d_1>0$ and $\alpha>0$, there exists a positive constant $d_2^*=d_2^*(\alpha,r,L,b_2)$ such that

(ii_1) For every $d_2\ge d_2^*$ and $(a,c)\in\Pi_{k_0}$, $(\widehat{u},0)$ is GAS.

(ii_2) For every $d_2<d_2^*$, there exist two constants $a^*\in(0,+\infty)$ and $c^*\in(0,1)$ such that for every $(a,c)\in((0,\infty)\times[c^*,\infty))\cap\Pi_{k_0}$, $(\widehat{u},0)$ is GAS. Besides, for every $(a,c)\in((0,a^*)\times(0,c^*))\cap\Pi_{k_0}$, there exists a unique coexistence steady state for system (1.2) *that is GAS, and for every $(a,c)\in([a^*,+\infty)\times(0,+\infty))\cap\Pi_{k_0}$, $(0,\widehat{v})$ is GAS.*

(iii) If $1+rL/\alpha<b_1<b_2$, then for every $\alpha>0$, there exists positive constants $d_1^*=d_1^*(\alpha,r,L,b_1)$ and $d_2^*=d_2^*(\alpha,r,L,b_2)$ such that

(iii_1) For every $d_1\ge d_1^*$, $d_2\ge d_2^*$ and $(a,c)\in\Pi_{k_0}$, $(0,0)$ is GAS.

(iii_2) For every $d_1<d_1^*$, $d_2\ge d_2^*$ and $(a,c)\in\Pi_{k_0}$, $(\widehat{u},0)$ is GAS.

(iii_3) For every $d_1 < d_1^*$ and $d_2 < d_2^*$, there exist constants $a^* \in (0,+\infty)$ and $c^* \in (0,1)$ such that for every $(a,c) \in ((0,\infty)\times[c^*,\infty)) \cap \Pi_{k_0}$, $(\widehat{u},0)$ is GAS. Besides, for every $(a,c) \in ((0,a^*)\times(0,c^*)) \cap \Pi_{k_0}$, there exists a unique coexistence steady state for system (1.2) *that is GAS, an for every $(a,c) \in ([a^*,+\infty)\times(0,+\infty)) \cap \Pi_{k_0}$, $(0,\widehat{v})$ is GAS,*

where GAS means that the steady state is globally asymptotically stable among all non-negative and nontrivial initial conditions. And d_1^* and d_2^* are given in Lemma 3.3. *Moreover, a^* and c^* can be written as*

$$a^* = \inf_{0\neq\sigma\in H^1(0,L)} \frac{\int_0^L \left(d_1\sigma_x^2 e^{\frac{\alpha}{d_1}x} - r\sigma^2 e^{\frac{\alpha}{d_1}x}\right)dx + b_1\alpha e^{\frac{\alpha}{d_1}L}\sigma^2(L) - \alpha\sigma^2(0)}{\int_0^L \widehat{v} e^{\frac{\alpha}{d_1}x}\sigma^2 dx}, \tag{1.5}$$

$$c^* = \inf_{0\neq\sigma\in H^1(0,L)} \frac{\int_0^L \left(d_2\sigma_x^2 e^{\frac{\alpha}{d_2}x} - r\sigma^2 e^{\frac{\alpha}{d_2}x}\right)dx + b_2\alpha e^{\frac{\alpha}{d_2}L}\sigma^2(L) - \alpha\sigma^2(0)}{\int_0^L \widehat{u} e^{\frac{\alpha}{d_2}x}\sigma^2 dx}. \tag{1.6}$$

Remark 1.1. Theorem 1.1 thoroughly describes the global dynamics of system (1.2). Contrary to the case where the inter-specific competition intensities $a = c = 1$ in [13], our results suggest that the inter-specific competition intensity have a strong impact on the outcome of the competition. As was shown in [13], the two competing species never coexist. However, if the inter-specific competition intensities satisfy the condition $(a,c) \in ((0,a^*)\times(0,c^*)) \cap \Pi_{k_0}$, the above theorem shows that two species can coexist.

This paper is organized as follows. In Section 2, we present preliminary results which are used in what follows. Section 3 contains the main result. Numerical simulations carried out in Section 4 support and verify the theoretical results. Finally, a short discussion completes this work.

2. Preliminaries

Consider the following model of single species:

$$\begin{aligned}
&u_t = du_{xx} - \alpha u_x + u(r-u), && 0<x<L, \quad t>0,\\
&u_x(0,t) = 0, && t>0,\\
&du_x(L,t) - \alpha u(L,t) = -b\alpha u(L,t), && t>0,\\
&u(x,0) = u_0 \geq, \not\equiv 0, && 0<x<L,
\end{aligned} \tag{2.1}$$

where $d,\alpha,L>0$ and $b\in(1,\infty]$. We focus on the positive steady state of the system (2.1), i.e. on the positive solutions of the problem

$$\begin{aligned}
&du_{xx} - \alpha u_x + u(r-u) = 0, \quad 0<x<L,\\
&u_x(0) = 0,\\
&du_x(L) - \alpha u(L) = -b\alpha u(L).
\end{aligned} \tag{2.2}$$

Denoting the positive solution of the system (2.2) by $\theta(x)$, we first describe its properties.

Lemma 2.1 (cf. Tang & Chen, [25, Lemma 2.1]). *Fix $\alpha, r, L > 0$ and $b \in (1, \infty]$. If the positive steady state $\theta(x)$ of the problem* (2.2) *exists, then the following estimates hold:*

(i) $\theta(x) < r$ *in* $[0, L]$;

(ii) $\theta(x)_x < 0$ *in* $(0, L]$.

Proof. Since $\theta(x)$ is a positive solution of problem (2.2), we have

$$\begin{aligned} &d\theta_{xx} - \alpha\theta_x + \theta(r-\theta) = 0, \quad 0 < x < L, \\ &\theta_x(0) = 0, \quad d\theta_x(L) - \alpha\theta(L) = -b\alpha\theta(L). \end{aligned} \tag{2.3}$$

We first prove the assertion (i). By the maximum principle, $\theta(x) \le r$ in $[0, L]$. If the assertion (i) is wrong, then there exists $x_1 \in [0, L]$ such that

$$\theta(x_1) = \max_{0 \le x \le L} \theta(x) = r.$$

Note that $x_1 \in [0, L)$, since $b \in (1, \infty]$. It follows from (2.3), that $\theta_x(x_1) = 0$ and $\theta_{xx}(x_1) = 0$. The uniqueness of solutions of ODE yields $\theta_x \equiv 0$ in $[0, L]$, i.e. $\theta \equiv C_0$ in $[0, L]$ for a positive constant C_0. However, this contradicts the boundary condition at the point $x = L$.

To show (ii), we set $w = \theta_x/\theta$ and note that

$$\begin{aligned} &dw_{xx} + (2dw - \alpha)w_x - w\theta = 0, \quad 0 < x < L, \\ &w(0) = 0, \quad w(L) = (1-b)\frac{\alpha}{d}. \end{aligned} \tag{2.4}$$

The strong maximum principle [6] implies

$$(1-b)\frac{\alpha}{d} < w(x) < 0, \quad x \in (0, L).$$

Along with the boundary conditions, this gives (ii). □

Since the single model (2.1) is a monotone dynamical system and the nonlinear reaction term is of the logistic type, the existence of positive solutions of problem (2.4) can be determined by the linear stability of the zero solution [1]. Moreover, if (2.3) admits a positive steady state, then it is globally asymptotically stable. Therefore, we have to study the following eigenvalue problem:

$$d\varphi_{xx} - \alpha\varphi_x + m(x)\varphi + \lambda\varphi = 0, \quad 0 < x < L, \tag{2.5a}$$
$$\varphi_x(0) = 0, \tag{2.5b}$$
$$d\varphi_x(L) - \alpha\varphi(L) = -b\alpha\varphi(L), \tag{2.5c}$$

where $d, \alpha, L > 0$, $b \in (1, \infty]$ and $m(x) \in L^\infty(0, L)$. By the celebrated Krein-Rutman theorem [11], the problem (2.5) has a principal eigenvalue λ_1 and a strictly positive in $[0, L]$ eigenfunction φ_1 for the eigenvalue λ_1. In what follows, we write λ_1 as $\lambda_1(d, \alpha, m(x), b)$

to stress the dependence on the parameters but in some cases we also adopt notation $\lambda_1(\kappa)$ in order to show that λ_1 is regarded as a function of κ with the other parameters fixed. Moreover, by the variational approach, $\lambda_1(d,\alpha,m(x),b)$ can be characterized by

$$\lambda_1\big(d,\alpha,m(x),b\big)=\inf_{0\neq\sigma\in H^1(0,L)}\frac{\int_0^L\big(d\sigma_x^2e^{\frac{\alpha}{d}x}-m(x)\sigma^2e^{\frac{\alpha}{d}x}\big)dx+b\alpha e^{\frac{\alpha}{d}L}\sigma^2(L)-\alpha\sigma^2(0)}{\int_0^L e^{\frac{\alpha}{d}x}\sigma^2dx}.$$

It is well known that the signs of $\lambda_1(d_1,\alpha,r,b_1)$ and $\lambda_1(d_2,\alpha,r,b_2)$ determine the existence of $\widehat{u}$ and $\widehat{v}$, respectively. Thus for the system (1.2), the signs of $\lambda_1(d_1,\alpha,r,b_1)$ and $\lambda_1(d_2,\alpha,r,b_2)$ determine the existence of $(\widehat{u},0)$ and $(0,\widehat{v})$. Following the ideas of [12, Corollary 2.10], we note that the linear stability of $(\widehat{u},0)$ and $(0,\widehat{v})$ is respectively determined by the signs of $\lambda_1(d_2,\alpha,r-c\widehat{u},b_2)$ and $\lambda_1(d_1,\alpha,r-a\widehat{v},b_1)$. More exactly, $(\widehat{u},0)$ is linearly stable (linearly unstable) if $\lambda_1(d_2,\alpha,r-c\widehat{u},b_2)>0$ ($\lambda_1(d_2,\alpha,r-c\widehat{u},b_2)<0$). We also say that $(\widehat{u},0)$ is neutrally stable if $\lambda_1(d_2,\alpha,r-c\widehat{u},b_2)=0$. The stability of $(0,\widehat{v})$ can be described analogously.

The following properties of λ_1 are useful for later analysis.

Lemma 2.2. *If $m\in C^1([0,L])$ and $L>0$, then*

$$\frac{\partial\lambda_1}{\partial d}=\frac{\int_0^L\big(\varphi_1e^{-\frac{\alpha}{d}x}\big)_x\varphi_{1x}dx}{\int_0^L\varphi_1^2e^{-\frac{\alpha}{d}x}dx}. \tag{2.6}$$

Furthermore, for $\lambda_1(d,\alpha,m(x),b)$ the following results hold:

(i) Suppose $m(x)\equiv m_0$ with m_0 being a constant and $b\in(1,\infty]$. Considering λ_1 as a function of d with the other parameters fixed we have $\partial\lambda_1/\partial d>0$.

(ii) Suppose that $b\in(1,\infty]$, $m(0)>0$, and $m_x(x)\geq 0$ in $(0,L)$. Regard λ_1 as a function of d (with others fixed). Then $\lambda_1(d)$ has at most one positive root. Moreover, if there exists d^* such that $\partial\lambda_1/\partial d(d^*)=0$, then $\partial\lambda_1/\partial d(d^*)>0$.

(iii) λ_1 is strictly decreasing in the weight function $m(x)$ in the $L^\infty([0,L])$ sense, that is, if $m_1(x)\leq,\not\equiv m_2(x)$ in $[0,L]$, then $\lambda_1(m_1)>\lambda_1(m_2)$.

(iv) Regard λ_1 as a function of b (with others fixed), then λ_1 is strictly increasing in b. That is, if $b_1<b_2$, then $\lambda_1(b_1)<\lambda_1(b_2)$.

Proof. Differentiating (2.5) with respect to d, one obtains

$$d\frac{\partial\varphi_{xx}}{\partial d}+\varphi_{xx}-\alpha\frac{\partial\varphi_x}{\partial d}+m(x)\frac{\partial\varphi}{\partial d}+\lambda_1\frac{\partial\varphi}{\partial d}+\frac{\partial\lambda_1}{\partial d}\varphi=0,\quad 0<x<L, \tag{2.7a}$$

$$\frac{\partial\varphi_x}{\partial d}(0)=0,\quad d\frac{\partial\varphi}{\partial d}(L)-\alpha\frac{\partial\varphi}{\partial d}(L)+\varphi_x(L)=-b\alpha\frac{\partial\varphi}{\partial d}(L). \tag{2.7b}$$

Multiplying the Eq. (2.7a) by $e^{-\alpha/d}\varphi$, and the Eq. (2.5a) by $e^{-\alpha/d}(\partial\varphi/\partial d)$, and integrating the difference of the resulting equations over $[0,L]$ yields

$$\begin{aligned}&\int_0^L \left[d\frac{\partial\varphi_x}{\partial d}-\alpha\frac{\partial\varphi}{\partial d}\right]_x e^{-\frac{\alpha}{d}x}\varphi dx-\int_0^L [d\varphi_x-\alpha\varphi]_x e^{-\frac{\alpha}{d}x}\frac{\partial\varphi}{\partial d}dx\\&+\int_0^L \varphi_{xx}e^{-\frac{\alpha}{d}x}\varphi dx+\frac{\partial\lambda_1}{\partial d}\int_0^L e^{-\frac{\alpha}{d}x}\varphi^2 dx=0.\end{aligned}$$

Using integration by parts and the boundary conditions, we obtain the relation (2.6).

The assertions (i),(iv) are established in [13, Proposition 2.1] and assertion (iii) is presented in [21, Remark 2]. The proof of assertion (ii) is similar to the proof of [21, Lemma 2.1]. □

3. Proof of Theorem 1.1

We start this section with the proof of the existence and uniqueness of positive steady states for system (2.1).

Lemma 3.1 (cf. Tang & Chen [25]). *Assume that $\alpha,r,L>0$. Then the following statements hold:*

(i) If $1<b\le 1+rL/\alpha$, then the system (2.1) *has a unique positive steady state for any $d>0$.*

(ii) If $b>1+rL/\alpha$, then there exists a positive constant $d^*=d^*(\alpha,r,L,b)$ such that the system (2.1) *has a unique positive steady state if and only if $d<d^*$.*

Proof. To make this work self-contained, we present details of the proof from [25] here. Since (2.1) is a monotone dynamical system and the nonlinear reaction term is of the logistic type, it has a positive steady state if and only if $u=0$ is linearly unstable, i.e. if $\lambda_1(d,\alpha,r)<0$, [1]. Moreover, if (2.1) has a unique positive steady state, then it is globally asymptotically stable. The proof of the uniqueness is standard — cf. [15, Proof of Lemma 2.1]. Therefore, only the existence of steady states has to be shown.

By Lemma 2.2(i), the principal eigenvalue $\lambda_1(d)$ is strictly increasing with respect to d. Later on, we estimate $\lim_{d\to\infty}\lambda_1(d)$ and $\lim_{d\to 0}\lambda_1(d)$. Choosing 1 as a test function and using variational characteristic yields

$$\lambda_1(d)\le\frac{-r\int_0^L e^{\frac{\alpha}{d}x}dx+b\alpha e^{\frac{\alpha}{d}L}-\alpha}{\int_0^L e^{\frac{\alpha}{d}x}dx},$$

which implies that $\lim_{d\to\infty}\lambda_1(d)$ is bounded.

Let $\{d_n\}$ be a positive sequence such that $\lim_{n\to\infty}d_n=\infty$. Recall that the principal eigenpair $(\lambda_1(d_n),\varphi_1(d_n))$ satisfies

$$\begin{aligned}&d_n\varphi_{xx}-\alpha\varphi_{1x}+r\varphi_1+\lambda_1\varphi_1=0,\quad 0<x<L,\\&\varphi_{1x}(0)=0,\ \ d_n\varphi_{1x}(L)-\alpha\varphi_1(L)=-b\alpha\varphi_1(L).\end{aligned}\tag{3.1}$$

Since $\max_{0\le x\le L}(\varphi_1(d_n))(x) = 1$ for any $d_n > 0$, we note that $\lim_{d\to\infty}\lambda_1(d)$ is bounded. Besides, one can also see that the set $\{\|\varphi_1(d_n)\|_{W^{2,p}(0,L)}\}$ is bounded for any $p \ge 1$. Passing to a subsequence, if necessary, and using the standard Sobolev embedding theorem, we deduce from (3.1) that $(\varphi_1(d_n))$ converges to a function $\overline{\varphi}$ in the topology of $C^1([0,L])$ as n tends to ∞, where $\overline{\varphi}$ satisfies the following relations in the weak form:

$$\begin{aligned} &\overline{\varphi}_{xx} = 0, \quad x \in (0,L),\\ &\overline{\varphi}_x = 0, \quad\ \ x = 0, L. \end{aligned}$$

This implies $\overline{\varphi} \equiv 1$ because $\max_{0\le x\le L}\overline{\varphi}(x) = 1$. Integrating $\varphi_1(d_n)$ over $(0,L)$ and passing to the limit, we obtain

$$\lim_{d_n\to\infty}\lambda_1(d_n) = \lim_{d_n\to\infty}\frac{-\int_0^L\{d_n\varphi_{1xx}(d_n) - \alpha\varphi_{1x}(d_n) + r\varphi_1(d_n)\}dx}{\int_0^L\varphi_1(d_n)dx} = -r + \frac{(b-1)\alpha}{L}.$$

Note that above we also used the boundary condition.

Recalling the monotonicity of the principal eigenvalue $\lambda_1(d)$ with respect to d implies

$$\lim_{d\to\infty}\lambda_1(d) = -r + \frac{(b-1)\alpha}{L}. \tag{3.2}$$

To estimate $\lim_{d\to 0}\lambda_1(d)$, we consider the boundary value problem

$$\begin{aligned} &d\zeta_{xx} - \alpha\zeta_x + \zeta(r-\zeta) = 0, \quad 0 < x < L,\\ &\zeta_x(0) = 0, \quad \zeta(L) = 0, \end{aligned} \tag{3.3}$$

and the corresponding linear eigenvalue problem — i.e.

$$\begin{aligned} &d\psi_{xx} - \alpha\psi_x + r\psi + \hat{\lambda}\psi = 0, \quad 0 < x < L,\\ &\psi_x(0) = 0, \quad \psi(L) = 0. \end{aligned} \tag{3.4}$$

Let $\hat{\lambda}_1(d,\alpha,r)$ and ψ_1 be the principal eigenvalue and the associated eigenfunction such that $\max_{0\le x\le L}\psi_1(x) = 1$, respectively. Similar to the proof of Lemma 2.1, we obtain that

$$\frac{\partial\hat{\lambda}_1}{\partial\alpha} < 0$$

for any $\alpha > 0$. Therefore,

$$\hat{\lambda}_1(d,\alpha,r) < \hat{\lambda}_1(d,0,r)$$

for any $\alpha > 0$. Set

$$K := \inf_{\sigma\in S}\frac{\int_0^L\sigma_x^2dx}{\int_0^L\sigma^2dx} > 0,$$

where

$$S := \left\{\sigma \in H^1(0,L) \mid \sigma \not\equiv 0 \text{ and } \sigma(L) = 0\right\}.$$

The variational characteristic yields

$$\hat{\lambda}_1(d,0,r) \le 0 \quad \text{for any} \quad d \le \frac{r}{K},$$

so that for any $\alpha > 0, d \le r/K$ we have

$$\hat{\lambda}_1(d,\alpha,r) < 0.$$

Therefore, the problem (3.3) has a unique positive solution ζ provided that $d \le r/K$. Obviously, ζ is a sub-solution of the Eq. (2.2) and r is a super-solution of the Eq. (2.2). Employing standard methods of sub and super-solutions, we obtain that the Eq. (2.2) has a positive solution provided that $d \le r/K$. This implies that

$$\lim_{d\to 0} \lambda_1(d) < 0. \tag{3.5}$$

Combining the relations (3.2), (3.5), and Lemma 2.2(i) gives the assertions (i) and (ii). $\square$

Lemma 3.2. *Assume that (H$_1$) and (H$_2$) hold. If the semi-trivial steady state $(0,\hat{v})$ exists, then there is a^* such that*

(i) $(0,\hat{v})$ *is linearly unstable for* $(a,c) \in (0,a^*) \times (0,+\infty)$;

(ii) $(0,\hat{v})$ *is linearly stable for* $(a,c) \in (a^*,+\infty) \times (0,+\infty)$;

(iii) $(0,\hat{v})$ *is neutrally stable for* $(a,c) \in \{a^*\} \times (0,+\infty)$.

Proof. It is known that the linear stability of $(0,\hat{v})$ is determined by the sign of $\lambda_1(d_1,\alpha, r-b\hat{v},b_1)$. Suppose that $(0,\hat{v})$ exists. Since assumption (H$_2$) holds, Lemma 3.1 shows that $(\hat{u},0)$ exists. Therefore,

$$\lambda_1(d_1,\alpha,r,b_1)|_{a=0} < 0.$$

Using variational approach, one immediately obtains that

$$\lim_{a\to\infty} \lambda_1(d_1,\alpha,r-a\hat{v},b_1) = +\infty.$$

Then there exists a^* such that

$$\begin{aligned}
&\lambda_1(d_1,\alpha,r-a\hat{v},b_1) < 0, \quad \text{if} \quad a < a^*,\\
&\lambda_1(d_1,\alpha,r-a\hat{v},b_1) = 0, \quad \text{if} \quad a = a^*,\\
&\lambda_1(d_1,\alpha,r-a\hat{v},b_1) > 0, \quad \text{if} \quad a > a^*.
\end{aligned}$$

In other words, for $(a,c) \in (0,a^*) \times (0,+\infty)$, for $(a,c) \in (a^*,+\infty) \times (0,+\infty)$ the state $(0,\hat{v})$ is linearly stable, and for $(a,c) \in \{a^*\} \times (0,+\infty)$ the state $(0,\hat{v})$ is neutrally stable. $\square$

Let $R^+ = (0,\infty)$ and $\Gamma = R^+ \times R^+ \times R^+ \times R^+ \times R^+$. To characterize the linear stability of the steady states, we introduce the sets

$$\Sigma_u := \big\{(d_1,d_2,\alpha,b_1,b_2) \in \Gamma : \lambda_1(d_2,\alpha,r-c\hat{u},b_2) > 0, \text{ i.e. } (\hat{u},0) \text{ is linearly stable}\big\},$$

$$
\begin{aligned}
\Sigma_v &:= \big\{(d_1,d_2,\alpha,b_1,b_2)\in\Gamma : \lambda_1(d_1,\alpha,r-a\widehat{v},b_1)>0,\ \text{i.e. } (0,\widehat{v}) \text{ is linearly stable}\big\},\\
\tilde{\Sigma}_u &:= \big\{(d_1,d_2,\alpha,b_1,b_2)\in\Gamma : \lambda_1(d_2,\alpha,r-c\widehat{u},b_2)=0,\ \text{i.e. } (\widehat{u},0) \text{ is neutrally stable}\big\},\\
\tilde{\Sigma}_v &:= \big\{(d_1,d_2,\alpha,b_1,b_2)\in\Gamma : \lambda_1(d_1,\alpha,r-a\widehat{v},b_1)=0,\ \text{i.e. } (0,\widehat{v}) \text{ is neutrally stable}\big\},\\
\tilde{\Sigma}_u^v &:= \tilde{\Sigma}_u\cap\tilde{\Sigma}_v,\\
\Sigma_o &:= \big\{(d_1,d_2,\alpha,b_1,b_2)\in\Gamma : \lambda_1(d_2,\alpha,r-c\widehat{u},b_2)<0 \text{ and } \lambda_1(d_1,\alpha,r-a\widehat{v},b_1)<0,\\
&\qquad\quad \text{i.e. } (\widehat{u},0) \text{ and } (0,\widehat{v}) \text{ are linearly unstable}\big\}.
\end{aligned}
$$

Lemma 3.3. *Assume that the conditions (H$_1$) and (H$_2$) hold and $(a,c)\in\Pi_{k_0}$. Then*

(i) If $\lambda_1(d_1,\alpha,r,b_1)\geq 0$ and $\lambda_1(d_2,\alpha,r,b_2)\geq 0$, then $(0,0)$ is GAS.

(ii) If $\lambda_1(d_1,\alpha,r,b_1)<0$ and $\lambda_1(d_2,\alpha,r,b_2)\geq 0$, then $\Sigma_u=\Gamma$ and $(\widehat{u},0)$ is GAS.

(iii) If $\lambda_1(d_1,\alpha,r,b_1)<0$ and $\lambda_1(d_2,\alpha,r,b_2)<0$, then

$$
\Gamma=\big(\Sigma_u\cup\tilde{\Sigma}_u\setminus\tilde{\Sigma}_u^v\big)\cup\big(\Sigma_v\cup\tilde{\Sigma}_v\setminus\tilde{\Sigma}_u^v\big)\cup\Sigma_o\cup\tilde{\Sigma}_u^v, \tag{3.6}
$$

the system (1.2) has the following properties:

(iii$_1$) For all $(d_1,d_2,\alpha,b_1,b_2)\in(\Sigma_u\cup\tilde{\Sigma}_u\setminus\tilde{\Sigma}_u^v)$, $(\widehat{u},0)$ is GAS.

(iii$_2$) For all $(d_1,d_2,\alpha,b_1,b_2)\in(\Sigma_v\cup\tilde{\Sigma}_v\setminus\tilde{\Sigma}_u^v)$, $(0,\widehat{v})$ is GAS.

(iii$_3$) For all $(d_1,d_2,\alpha,b_1,b_2)\in\Sigma_o$, the system (1.2) has a coexistence steady state that is GAS.

(iii$_4$) For all $(d_1,d_2,\alpha,b_1,b_2)\in\tilde{\Sigma}_u^v$, $u^*\equiv av^*$ in $[0,L]$ and the system (1.2) has a compact global attractor consisting of a continuum of steady states

$$
\big\{(\varrho u^*,(1-\varrho)u^*/a:\varrho\in[0,1]\big\}
$$

connecting the two semi-trivial steady states.

Remark 3.1. Lemma 3.3 provides a complete classification of all possible global dynamical behaviors of the system (1.1) when the upstream end has free-flow boundary conditions.

Remark 3.2. Theorem 1.1 provides a complete classification on all possible global dynamical behaviors of the system (1.1) under conditions (H$_1$) and (H$_2$). If for every $d_1,d_2,\alpha_1,\alpha_2>0$ and resource functions $m_1(x)$, $m_2(x)$ we consider the term

$$
k_1=\begin{cases} e^{(\frac{\alpha_2}{d_2}-\frac{\alpha_1}{d_1})L}, & \text{if } \dfrac{\alpha_1}{d_1}-\dfrac{\alpha_2}{d_2}\geq 0,\\[2mm] e^{(\frac{\alpha_1}{d_1}-\frac{\alpha_2}{d_2})L}, & \text{if } \dfrac{\alpha_1}{d_1}-\dfrac{\alpha_2}{d_2}<0,\end{cases} \tag{3.7}
$$

then for $(a,c)\in\Pi_{k_1}$ the following result holds:

(i) If $\lambda_1(d_1,\alpha_1,m_1)\geq 0$ and $\lambda_1(d_2,\alpha_2,m_2)\geq 0$, then $(0,0)$ is GAS.

(ii) If $\lambda_1(d_1,\alpha_1,m_1)\geq 0$ and $\lambda_1(d_2,\alpha_2,m_2)<0$, then $\Sigma_v=\Gamma$ and $(0,\widehat{v})$ is GAS.

(iii) If $\lambda_1(d_1,\alpha_1,m_1)<0$ and $\lambda_1(d_2,\alpha_2,m_2)\geq 0$, then $\Sigma_u=\Gamma$ and $(\widehat{u},0)$ is GAS.

(iv) If $\lambda_1(d_1,\alpha_1,m_1)<0$ and $\lambda_1(d_2,\alpha_2,m_2)<0$, then

$$\Gamma=\left(\Sigma_u\cup\tilde{\Sigma}_u\setminus\tilde{\Sigma}_u^v\right)\cup\left(\Sigma_v\cup\tilde{\Sigma}_v\setminus\tilde{\Sigma}_u^v\right)\cup\Sigma_o\cup\tilde{\Sigma}_u^v. \tag{3.8}$$

In particular, $(d_1,\alpha_1,d_2,\alpha_2)\in\tilde{\Sigma}_u^v$ if and only if $\alpha_1/d_1=\alpha_2/d_2$, $ac=1$, $\widehat{u}/\widehat{v}\equiv a$. Besides, for the system (1.2) the following relations hold:

(iv_1) For all $(d_1,\alpha_1,d_2,\alpha_2)\in(\Sigma_u\cup\tilde{\Sigma}_u\setminus\tilde{\Sigma}_u^v)$, $(\widehat{u},0)$ is GAS.

(iv_2) For all $(d_1,\alpha_1,d_2,\alpha_2)\in(\Sigma_v\cup\tilde{\Sigma}_v\setminus\tilde{\Sigma}_u^v)$, $(0,\widehat{v})$ is GAS.

(iv_3) For all $(d_1,\alpha_1,d_2,\alpha_2)\in\Sigma_o$, system (1.2) has a coexistence steady state that is GAS.

(iv_4) For all $(d_1,\alpha_1,d_2,\alpha_2)\in\tilde{\Sigma}_u^v$, $\widehat{u}\equiv a\widehat{v}$ in $[0,L]$ and system (1.2) has a compact global attractor consisting of a continuum of steady states

$$\left\{(\varrho\widehat{u},(1-\varrho)\widehat{u}/a:\varrho\in[0,1]\right\}$$

connecting the two semi-trivial steady states.

Proof of Lemma 3.3. In the assertion (i), both semi-trivial steady states do not exist and in (ii), the only $(\widehat{u},0)$ exists. In this situation, the dynamics can be established by the upper and lower solution method — cf. [33, Lemma 5.1].

To show assertion (iii), we follow [32] to first obtain

$$\Gamma=\left(\Sigma_u\cup\tilde{\Sigma}_u\setminus\tilde{\Sigma}_u^v\right)\cup\left(\Sigma_v\cup\tilde{\Sigma}_v\setminus\tilde{\Sigma}_u^v\right)\cup\Sigma_o\cup\tilde{\Sigma}_u^v,$$

and then (3.6). Proceeding similar to the approach of [7, 32, 34], we can establish the desired results. □

Proof of Theorem 1.1. Let us demonstrate the stability of the semi-trivial steady state $(\widehat{u},0)$.

Assertion (i). $1<b_1\leq b_2\leq 1+rL/\alpha$.

Lemma 3.1 shows that $\widehat{u}$ and $\widehat{v}$ exist for every $d_1,d_2>0$ and $\alpha>0$. To establish the stability of the semi-trivial steady state $(\widehat{u},0)$, it suffices to determine the sign of $\lambda_1(d_2,\alpha,r-c\widehat{u},b_2)$. Using the equation of $(0,\widehat{v})$ and Lemma 2.2(iii), we write

$$\begin{aligned}&\lambda_1(d_2,\alpha,r-\widehat{v},b_2)=0,\\&\lambda_1(d_2,\alpha,r,b_2)<0.\end{aligned}\tag{3.9}$$

On the other hand, the equation of $(\widehat{u},0)$ yields

$$\lambda_1(d_1,\alpha,r-\widehat{u},b_1)=0.$$

Taking into account the condition $d_1 < d_2$, Lemmas 2.1(ii) and 2.2(ii), 2.1(iv), we obtain

$$0 < \lambda_1(d_2, \alpha, r - \widehat{u}, b_2). \tag{3.10}$$

Combining (3.9) and (3.10) gives

$$\begin{aligned} &\lambda_1(d_2, \alpha, r - c\widehat{u}, b_2)|_{c=0} < 0, \\ &\lambda_1(d_2, \alpha, r - c\widehat{u}, b_2)|_{c=1} > 0. \end{aligned}$$

Hence, there exists a constant $c^* \in (0,1)$ such that

$$\begin{aligned} &\lambda_1(d_2, \alpha, r - c\widehat{u}, b_2) < 0, \quad \text{if} \quad c \in [0, c^*), \\ &\lambda_1(d_2, \alpha, r - c\widehat{u}, b_2) = 0, \quad \text{if} \quad c = c^*, \\ &\lambda_1(d_2, \alpha, r - c\widehat{u}, b_2) > 0, \quad \text{if} \quad c \in (c^*, \infty). \end{aligned} \tag{3.11}$$

Summarising, we note

1. If $(a, c) \in (0, a^*) \times (0, c^*)$, then both semi-trivial steady states are linearly unstable.
2. If $(a, c) \in (0, \infty) \times [c^*, \infty)$, then $(\widehat{u}, 0)$ is either linearly stable ($(a, c) \in (0, +\infty) \times (c^*, +\infty)$) or neutrally stable ($(a, c) \in (0, \infty) \times \{c^*\}$).

Assertion (i) now follows from Lemmas 3.2 and 3.3.

Assertion (ii). $1 < b_1 \le 1 + rL/\alpha < b_2$.

It follows from Lemma 3.1 that if $d_1 > 0$, then a positive steady state $\widehat{u}$ exists for every $\alpha > 0$. Besides, there exists a constant $d_2^* \in (0, \infty)$ such that a positive steady state $\widehat{v}$ exists if and only if $d_2 < d_2^*$. Thus if $d_2 \ge d_2^*$, a positive steady state $\widehat{v}$ does not exists — i.e.

$$\lambda_1(d_2, \alpha, r, b_2) > 0.$$

Lemma 2.2(iii) implies

$$\lambda_1(d_2, \alpha, r - c\widehat{u}, b_2) > 0,$$

so that $(\widehat{u}, 0)$ is linearly stable. The assertion (ii) now follows from Lemma 3.3.

If $d_2 < d_2^*$ and $d_1 > 0$, both $\widehat{u}$ and $\widehat{v}$ exist for every $\alpha > 0$. By the equation of $(\widehat{u}, 0)$ and Lemma 2.2(ii),(iv), we obtain

$$0 = \lambda_1(d_1, \alpha, r - \widehat{u}, b_1) < \lambda_1(d_2, \alpha, r - \widehat{u}, b_2),$$

and from the equation of $(0, \widehat{v})$ and Lemma 2.2(iii)

$$\lambda_1(d_2, \alpha, r, b_2) < \lambda_1(d_2, \alpha, r - \widehat{v}, b_2) = 0.$$

Hence, there is a constant $c^* \in (0,1)$ such that the Eq. (3.11) holds. The proof of (ii) is similar to the proof of (i).

Assertion (iii). $1 + rL/\alpha < b_1 < b_2$.

According to Lemma 3.1, there are constants $d_1^* \in (0, \infty)$ and $d_2^* \in (0, \infty)$ such that $\widehat{u}$ exists if and only if $d_1 < d_1^*$, and $\widehat{v}$ exists if and only if $d_2 < d_2^*$.

Firstly, we claim that if $b_1 \leq b_2$, then $d_1^* \geq d_2^*$. Recalling the definition of d_1^* and d_2^*, we obtain

$$\lambda_1(d_1^*, \alpha, r, b_1) = \lambda_1(d_2^*, \alpha, r, b_2) = 0. \tag{3.12}$$

Since $b_1 \leq b_2$, Lemma 2.2(iv) gives

$$\lambda_1(d_1^*, \alpha, r, b_1) \leq \lambda_1(d_1^*, \alpha, r, b_2). \tag{3.13}$$

Using again Lemma 2.2(iv) along with (3.12), (3.13), one immediately obtains $d_1^* \geq d_2^*$.

Combining the above claim with the condition $d_1 < d_2$, we consider the following cases:

Case 1. $d_1 \geq d_1^*$ and $d_2 \geq d_2^*$.
Case 2. $d_1 < d_1^*$ and $d_2 \geq d_2^*$.
Case 3. $d_1 < d_1^*$ and $d_2 < d_2^*$.

In the case $d_1 \geq d_1^*$ and $d_2 \geq d_2^*$, Lemma 3.1 shows that $\widehat{u}$ and $\widehat{v}$ do not exist. Therefore,

$$\lambda_1(d_1, \alpha, r, b_1) > 0, \quad \lambda_1(d_2, \alpha, r, b_2) > 0,$$

and by Lemma 3.3, the trivial steady state $(0, 0)$ is GAS.

Considering the case $d_1 < d_1^*$ and $d_2 \geq d_2^*$, we recall Lemma 3.1 and obtains that $\widehat{u}$ exists but $\widehat{v}$ does not exist. Since $\widehat{v}$ does not exist, Lemma 2.2(iii) gives

$$\lambda_1(d_2, \alpha, r, b_2) > 0, \quad \lambda_1(d_2, \alpha, r - c\widehat{u}, b_2) > 0,$$

so that $(\widehat{u}, 0)$ is linearly stable. Applying Lemma 3.3, we arrive at the assertion (iii$_2$).

Finally, we consider the situation $d_1 < d_1^*$ and $d_2 < d_2^*$. Using again Lemma 3.1, we note that both $\widehat{u}$ and $\widehat{v}$ exist. Applying Lemma 2.2(ii),(iv) and the equation of $(\widehat{u}, 0)$,gives

$$\lambda_1(d_2, \alpha, r - \widehat{u}, b_2) > \lambda_1(d_1, \alpha, r - \widehat{u}, b_1) = 0.$$

Besides, Lemma 2.2(iii) and the equation of $(0, \widehat{v})$ imply

$$\lambda_1(d_2, \alpha, r, b_2) < \lambda_1(d_2, \alpha, r - \widehat{v}, b_2) = 0.$$

Therefore, there is a constant $c^* \in (0, 1)$ such that (3.11) holds. The the assertion (iii$_3$) can be now obtained similar to the assertion (i), and proof of (iii) is complete.

Finally we determine a^* and c^*. We only show (1.6). The proof of (1.5) is analogous. Note that the stability of $(\widehat{u}, 0)$ is determined by the sign of $\lambda_1(d_2, \alpha, r - c\widehat{u}, b_2)$, which satisfies the following eigenvalue problem:

$$\begin{aligned}
&d_2\varphi_{xx} - \alpha\varphi_x + (r - c\widehat{u})\varphi + \lambda_1\varphi = 0,\\
&\varphi_x(0) = 0,\\
&d_2\varphi_x(L) - \alpha\varphi(L) = -b_2\alpha\varphi(L).
\end{aligned} \tag{3.14}$$

Setting $c=c^*$, $\lambda_1=0$, we write (3.14) as

$$
\begin{aligned}
&d_2\varphi_{0xx}-\alpha\varphi_{0x}+r\varphi_0=c^*\widehat{u}\varphi_0,\\
&\varphi_{0x}(0)=0,\\
&d_2\varphi_{0x}(L)-\alpha\varphi_0(L)=-b_2\alpha\varphi_0(L),
\end{aligned}
$$

where $\varphi_0>0$ is the corresponding eigenfunction of $\lambda_1(d_2,\alpha,r-c^*\widehat{u},b_2)$, uniquely determined by the normalization condition $\|\varphi_0\|^2_{L^2(0,L)}=1$.

Let $\overline{\varphi}_0=\varphi_0 e^{-\alpha/d_2 x}$. Then $\overline{\varphi}_0$ satisfies

$$
\begin{aligned}
&\Big[d_2 e^{\frac{\alpha}{d_2}x}(\overline{\varphi}_0)_x\Big]_x+re^{\frac{\alpha}{d_2}x}\overline{\varphi}_0=c^*\widehat{u}e^{\frac{\alpha}{d_2}x}\overline{\varphi}_0,\quad 0<x<L,\\
&d_2(\overline{\varphi}_0)_x(0)=-\alpha\overline{\varphi}_0(0),\\
&d_2(\overline{\varphi}_0)_x(L)=-b_2\alpha\overline{\varphi}_0(L).
\end{aligned}
$$

Analogously, we can obtain

$$
c^*=\inf_{0\neq\sigma\in H^1(0,L)}\frac{\int_0^L\Big(d_2\sigma_x^2e^{\frac{\alpha}{d_2}x}-r\sigma^2e^{\frac{\alpha}{d_2}x}\Big)dx+b_2\alpha e^{\frac{\alpha}{d_2}L}\sigma^2(L)-\alpha\sigma^2(0)}{\int_0^L\widehat{u}e^{\frac{\alpha}{d_2}x}\sigma^2dx}.
$$

The Eq. (1.6) is proven. This and the above discussion complete the proof Theorem 1.1. □

4. Numerical Simulations

Let us present numerical results that complement and illustrate our analytical findings. To investigate the effects of dispersal, boundary conditions and the inter-specific competition intensities on the outcome of competition, we fix the other competition conditions. In particular, we assume that $\alpha=1, r=1, L=1$, which yields $1+rL/\alpha=2$. We carry out numerical simulations with the initial value

$$
(u_0,v_0)=(0.45-0.08\cos x,0.45-0.08\sin x).
$$

Recalling the conditions (H_1) and (H_2), we first consider the case $1<b_1\le b_2\le 1+rL/\alpha$ with the parameters shown in Table 1. To demonstrate the influence of the inter-specific competition coefficients a and c on the dynamics of the system (1.2), we fix all parameters except a and c. The corresponding numerical simulations of spatial-temporal

Table 1: Simulation parameters.

b_1	b_2	d_1	d_2	k_0	a	c
3/2	5/3	0.4	0.6	0.4346	0.3	0.95
3/2	5/3	0.4	0.6	0.4346	2	0.5
3/2	5/3	0.4	0.6	0.4346	0.3	0.5

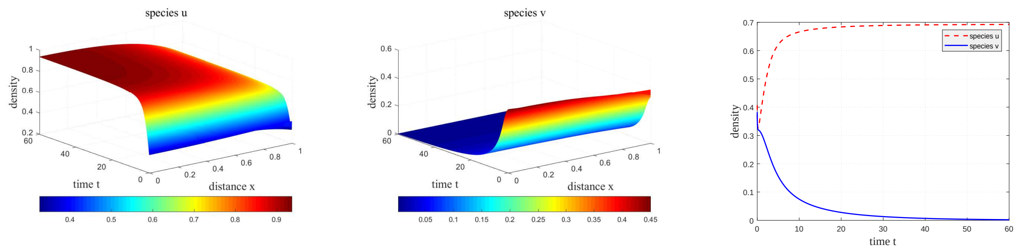

Figure 1: Numerical simulations of the asymptotics of system (1.2) solution, $b_1 = 3/2$, $b_2 = 5/3$, $d_1 = 0.4$, $d_2 = 0.6$, $a = 0.3$, $c = 0.95$.

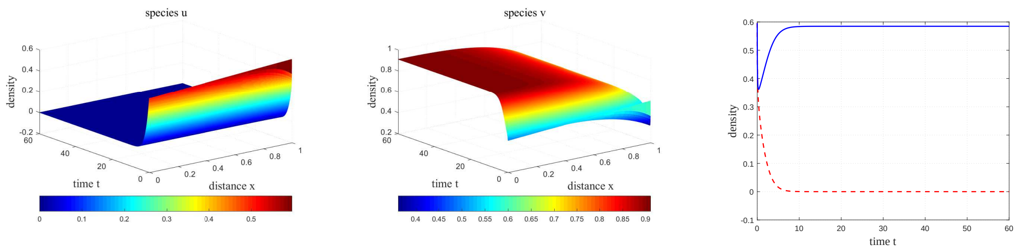

Figure 2: Numerical simulations of the asymptotics of system (1.2) solution, $b_1 = 3/2$, $b_2 = 5/3$, $d_1 = 0.4$, $d_2 = 0.6$, $a = 2$, $c = 0.5$.

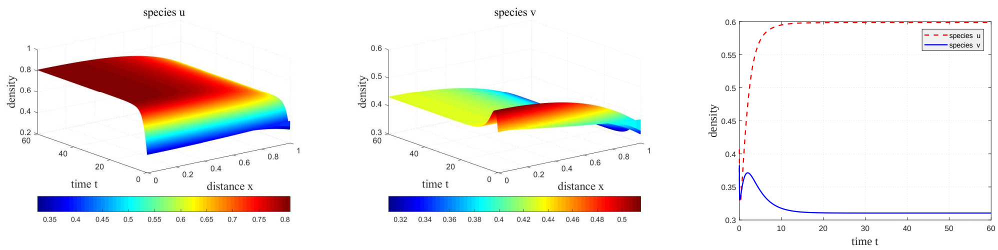

Figure 3: Numerical simulations of the asymptotic of system (1.2) solution, $b_1 = 3/2$, $b_2 = 5/3$, $d_1 = 0.4$, $d_2 = 0.6$, $a = 0.3$, $c = 0.5$.

patterns and the temporal evolutions for two competing species are displayed in Figs. 1-3. Fig. 1 shows that species u persist in the long run, but v will die out eventually. Fig. 2 shows that species v wipe out species u in the long run, and Fig. 3 demonstrates the coexistence of two competing species. Note that for $1 < b_1 \leq b_2 \leq 1 + rL/\alpha$, whether u wipes out or coexists with v depends on whether the inter-specific competition coefficient c crosses over a critical number $c^* \in (0,1)$.

Considering the case $1 < b_1 \leq 1 + rL/\alpha < b_2$ with the parameters listed in Table 2, we demonstrate the influence of the diffusion rate d_2 and the inter-specific competition coefficients a and c on dynamics of system (1.2). The corresponding numerical simulations of the spatial-temporal patterns and the temporal evolution for two competing species are shown in Figs. 4-7. According to Fig. 4, species u will displace species v eventually. On the other hand, Fig. 5 shows that species u persist in the long run but species v go to extinction finally. Fig. 6 shows that species v wipe out species u in the long run. On the other hand, Fig. 7 demonstrates that species u and v coexist in the end.

Table 2: Simulation parameters.

b_1	b_2	d_1	d_2	k_0	a	c
3/2	4	0.4	3	0.1145	0.3	0.3
3/2	4	0.4	0.6	0.4346	0.3	0.9
3/2	4	0.4	0.6	0.4346	2	0.9
3/2	4	0.4	0.6	0.4346	0.3	0.3

Table 3: Simulation parameters.

b_1	b_2	d_1	d_2	k_0	a	c
3	5	4	6	0.9200	0.5	0.5
3	5	0.4	3	0.1145	0.3	0.3
3	5	0.4	0.6	0.4346	0.3	0.9
3	5	0.4	0.6	0.4346	2	0.9
3	5	0.4	0.6	0.4346	0.3	0.3

Finally, considering the case $1 + rL/\alpha < b_1 < b_2$ with the parameters are listed in Table 3, we demonstrate the influence of the diffusion rates d_1, d_2 and the inter-specific competition coefficients a, c on the dynamics of system (1.2). The results of numerical simulations of the spatial-temporal patterns and the temporal evolutions for the two competing species are shown in Figs. 8-12. Fig. 8 shows that both species u and v will go to extinction.

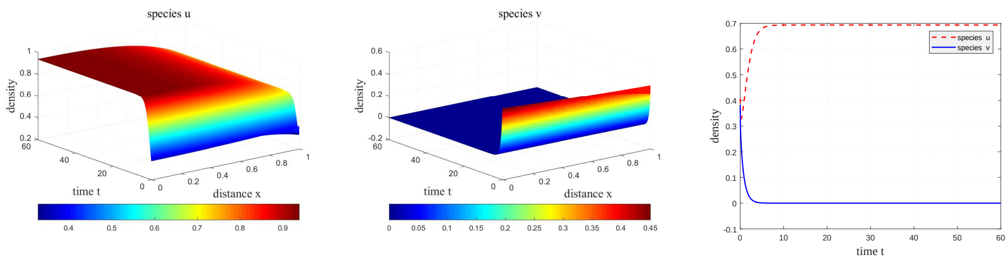

Figure 4: Numerical simulations of the asymptotic of system (1.2) solution, $b_1 = 3/2$, $b_2 = 4$, $d_1 = 0.4$, $d_2 = 3$, $a = 0.3$, $c = 0.3$.

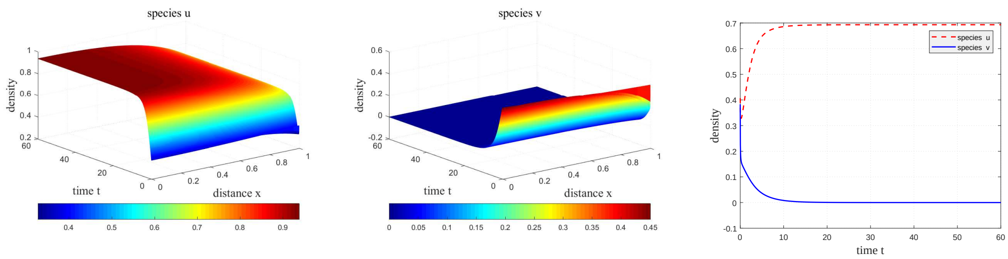

Figure 5: Numerical simulations of the asymptotic of system (1.2) solution, $b_1 = 3/2$, $b_2 = 4$, $d_1 = 0.4$, $d_2 = 0.6$, $a = 0.3$, $c = 0.9$.

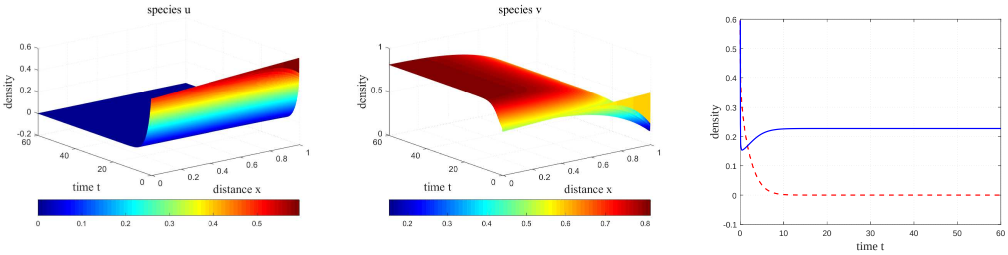

Figure 6: Numerical simulations of the asymptotic of system (1.2) solution, $b_1 = 3/2$, $b_2 = 4$, $d_1 = 0.4$, $d_2 = 0.6$, $a = 2$, $c = 0.3$.

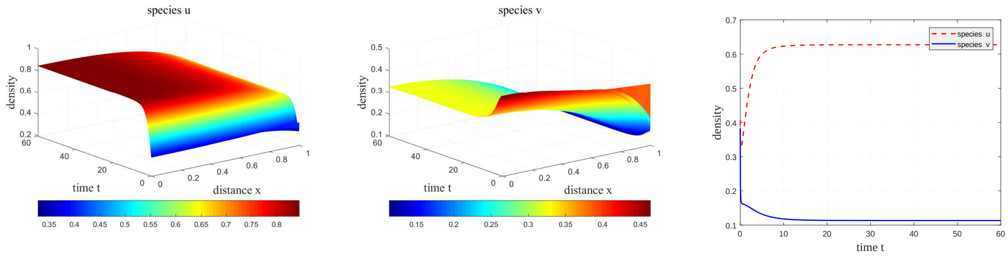

Figure 7: Numerical simulations of the asymptotic of system (1.2) solution, $b_1 = 3/2$, $b_2 = 4$, $d_1 = 0.4$, $d_2 = 0.6$, $a = 0.3$, $c = 0.3$.

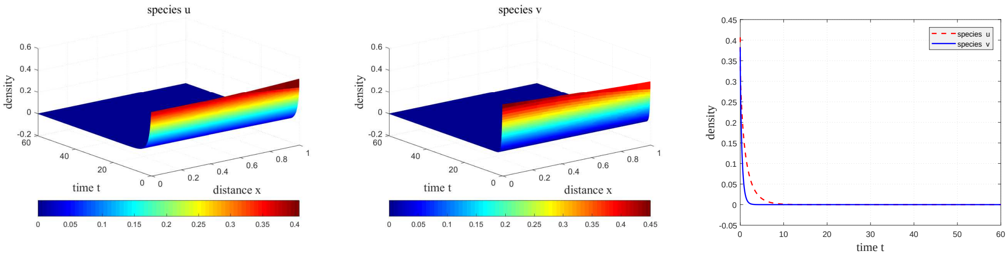

Figure 8: Numerical simulations of the asymptotic of system (1.2) solution, $b_1 = 3$, $b_2 = 5$, $d_1 = 4$, $d_2 = 6$, $a = 0.5$, $c = 0.5$.

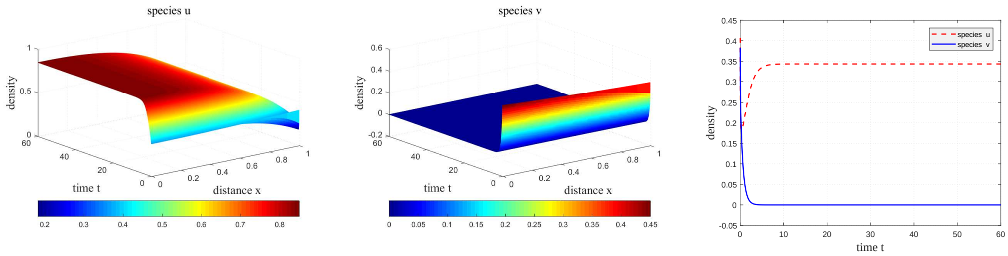

Figure 9: Numerical simulations of the asymptotic of system (1.2) solution, $b_1 = 3$, $b_2 = 5$, $d_1 = 0.4$, $d_2 = 3$, $a = 0.3$, $c = 0.3$.

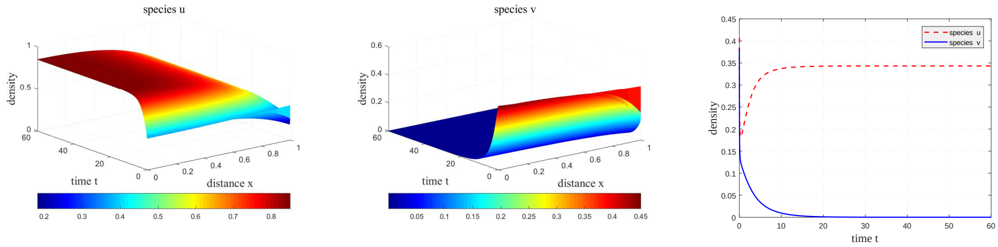

Figure 10: Numerical simulations of the asymptotic of system (1.2) solution, $b_1 = 3$, $b_2 = 5$, $d_1 = 0.4$, $d_2 = 0.6$, $a = 0.3$, $c = 0.9$.

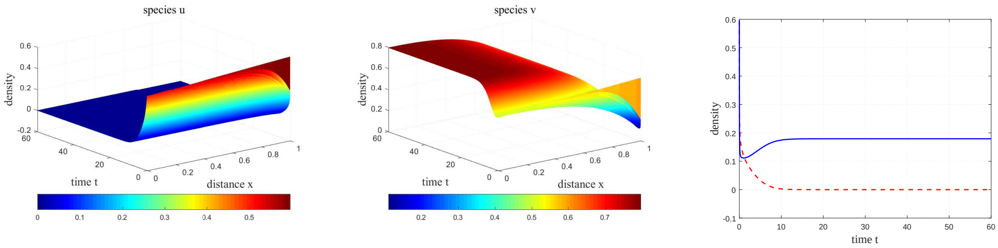

Figure 11: Numerical simulations of the asymptotic of system (1.2) solution, $b_1 = 3$, $b_2 = 5$, $d_1 = 0.4$, $d_2 = 0.6$, $a = 2$, $c = 0.9$.

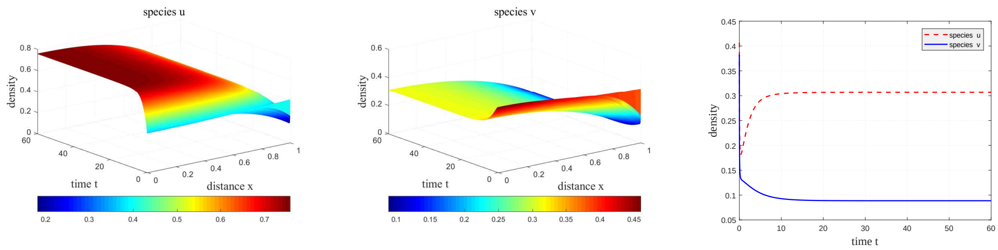

Figure 12: $b_1 = 3$, $b_2 = 5$, $d_1 = 0.4$, $d_2 = 0.6$, $a = 0.3$, $c = 0.3$.

Fig. 9 shows that species u will wipe out species v in the long run. Fig. 10 demonstrates that species u will replace species v, whereas Fig. 11 indicates that species v persist and u goes to extinction. Finally, Fig. 12 shows that the two species coexist in the end.

5. Conclusion

We study the global dynamics of a two-species Lotka-Volterra competition-diffusion-advection system in homogenous environments. We investigate the effects of the inter-specific competition intensities together with diffusion rates and loss rates at the down-stream end to the global dynamics of system (1.2). Here the flow-free boundary condition is considered at the upstream end which implies the upstream end is linked to a lake. However, we assume that both water flow and diffusive movement could cause the loss at the downstream end and due to the differing diffusing rates the differing magnitudes of population loss is considered.

Our results suggest that there are three outcomes of competition: either both two species go to extinction or one of the two competitors becomes the final single winner (exclusion), or species u and v coexist. This differs from the situation of both inter-specific competition coefficients normalized to 1, in which case two species cannot coexist. Note that the competition outcome is determined by the diffusion and loss rates, and by the inter-specific competition intensities. Besides, a coexistence steady state exists only if both two positive steady states $\widehat{u}$ and $\widehat{v}$ exist and the inter-specific competition intensities take the appropriate values.

Although we made a progress in understanding of the system (1.2), there are significant problems for further investigation. The one is related to two species having different advection rates and the other to species living in spatially heterogenous environment — cf. [16, 26, 28] for the case where there is no loss at the upstream end).

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References

[1] R.S. Cantrell and C. Cosner, *Spatial Ecology via Reaction-Diffusion Equations*, Series in Mathematical and Computational Biology, John Wiley and Sons (2003).

[2] Y. Du and S.B. Hsu, *Concentration phenomena in a nonlocal quasi-linear problem modeling phytoplankton: I. Existence*, SIAM J. Math. Anal. **40**, 1419–1440 (2008).

[3] Y. Du and S.B. Hsu, *Concentration phenomena in a nonlocal quasi-linear problem modeling phytoplankton: II. Limiting profile*, SIAM J. Math. Anal. **40**, 1441–1470 (2008).

[4] Y. Du and S.B. Hsu, *On a nonlocal reaction-diffusion problem arising from the modeling phytoplankton growth*, SIAM J. Math. Anal. **42**, 1305–1333 (2012).

[5] Y. Du and L.F. Mei, *On a nonlocal reaction-diffusion-advection equation modelling phytoplankton dynamics*, Nonlinearity **24**, 319–349 (2011).

[6] D. Gilbarg and N.S. Trudinger, *Elliptic Partial Differential Equations of Second Order*, Springer-Verlag (2001).

[7] Q. Guo, X.Q. He and W.-M. Ni, *Global dynamics of a general Lotka-Volterra competition-diffusion system in heterogeneous environments*, Discrete Contin. Dyn. Syst. **40**, 6547–6573 (2020).

[8] X. He and W.-M. Ni, *Global dynamics of the Lokta-Volterra competition-diffusion system: Diffusion and spatial heterogeneity, I*, Comm. Pure Appl. Math. **69**, 981–1014 (2016).

[9] X. He and W.-M. Ni, *Global dynamics of the Lotka-Volterra competition-diffusion system with equal amount of total resources, II*, Calc. Var. Partial Differential Equations **55**, 25 (2016).

[10] P. Hess, *Periodic-Parabolic Boundary Value Problems and Positivity*, Pitman Research Notes in Mathematics Series **247**, Longman Scientific (1991).

[11] M.G. Krein and M.A. Rutman, *Linear operators leaving invariant a cone in a Banach space*, Usp. Mat. Nauk **3**, 3–95 (1948).

[12] K.-Y. Lam and N.-W. Ni, *Uniqueness and complete dynamics in the heterogeneous competition-diffusion systems*, SIAM J. Appl. Math. **72**, 1695–1712 (2012).

[13] K. Li and F. Xu, *Global dynamics of a population model from river ecology*, J. Appl. Anal. Comput. **10**, 1698–1707 (2020).

[14] Y. Lou and F. Lutscher, *Evolution of dispersal in open advective environments*, J. Math. Biol. **69**, 1319–1342 (2014).

[15] Y. Lou, D.M. Xiao and P. Zhou, *Qualitative analysis for a Lotka-Volterra competition system in advective homogeneous environment*, Discrete Contin. Dyn. Syst. Ser. A **36**, 953–969 (2016).

[16] Y. Lou, X.-Q. Zhao and P. Zhou, *Global dynamics of a Lotka-Volterra competition-diffusion-advection system in heterogeneous environments*, J. Math. Pures Appl. **121**, 47–82 (2019).

[17] Y. Lou and P. Zhou, *Evolution of dispersal in advective homogeneous environment: The effect of boundary conditions*, J. Differential Equations **259**, 141–171 (2015).

[18] F. Lutscher, M.A. Lewis and E. McCauley, *Effects of heterogeneity on spread and persistence in rivers*, Bull. Math. Biol. **68**, 2129–2160 (2006).

[19] F. Lutscher, E. McCauley and M.A. Lewis, *Spatial patterns and coexistence mechanisms in systems with unidirectional flow*, Theor. Popul. Biol. **71**, 267–277 (2007).

[20] F. Lutscher, E. Pachepsky and M.A. Lewis, *The effect of dispersal patterns on stream populations*, SIAM Rev. **47**, 749–772 (2005).

[21] L. Ma and D. Tang, *Evolution of dispersal in advective homogenous environments*, Discrete Contin. Dyn. Syst. Ser. A **40**, 5815–5830 (2020).

[22] W.-M. Ni, *The Mathematics of Diffusion*, CBMS-NSF Regional Conference Series in Applied Mathematics **82**, SIAM (2011).

[23] H. Smith, *Monotone Dynamical Systems: An Introduction to the Theory of Competitive and Cooperative Systems*, Math. Surveys Monogr. **41**, AMS (1995).

[24] D.C. Speirs and W.S.C. Gurney, *Population dynamics in rivers and estuaries*, Ecology **82**, 1219–1237 (2001).

[25] D. Tang and Y. M. Chen, *Global dynamics of a Lotka-Volterra competition-diffusion system in advective homogeneous environments*, J. Differential Equations **269**, 1465–1483 (2020).

[26] D. Tang and P. Zhou, *On a Lotka-Volterra competition-diffusion-advection system: Homogeneity vs heterogeneity*, J. Differential Equations **268**, 1570–1599 (2020).

[27] O. Vasilyeva and F. Lutsccher, *Population dynamics in rivers: Analysis of steady states*, Can. Appl. Math. Q. **18**, 439–469 (2011).

[28] J.Y. Wei and B. Liu, *Global dynamics of a Lotka-Volterra competition-diffusion-advection system for small diffusion rates in heterogenous environment*, Math. Biosci. Eng. **18**, 564–582 (2011).

[29] J.Y. Wei and B. Liu, *Coexistence in a competition-diffusion-advection system with equal amount of total resources*, Math. Biosci. Eng. **18**, 3543–3558 (2021).

[30] F.F. Xu and W.Z. Gan, *On a Lotka-Volterra type competieion model from river ecology*, Nonlinear Anal. Real World Appl. **47**, 373–384 (2019).

[31] P. Zhou, *On a Lotka-Volterra competition system: Diffusion vs advection*, Calc. Var. Partial Differential Equations, **55** (2016), 137.

[32] P. Zhou and D.M. Xiao, *Global dynamics of a classical Lotka-Volterra competition-diffusion-advection system*, J. Funct. Anal. **275**, 356–380 (2018).

[33] P. Zhou and X.-Q. Zhao, *Evolution of passive movement in advective environments: general boundary condition*, J. Differential Equations **264**, 4176–4198 (2018).

[34] P. Zhou, D. Tang and D.-M. Xiao, *On Lotka-Volterra competitive parabolic systems: Exclusion, coexistence and bistability*, J. Differential Equations **282**, 596–625 (2021).