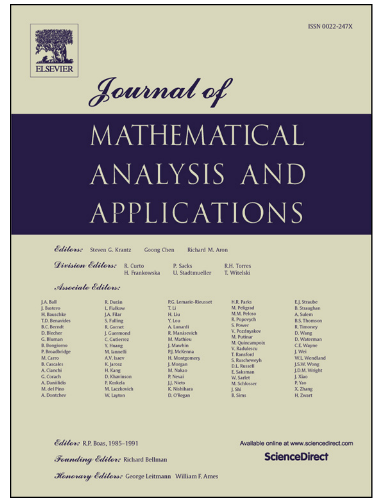

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PII: S0022-247X(17)31128-9
DOI: https://doi.org/10.1016/j.jmaa.2017.12.050
Reference: YJMAA 21911

To appear in: *Journal of Mathematical Analysis and Applications*

Received date: 12 May 2017

Dynamics of a Benthic-Drift Model for Two Competitive Species

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Abstract

Population dynamics of multiple interactive species in rivers and streams is important in river/stream ecology. In this paper, we consider a model for two competitive species living in a river environment where the populations grow and compete in the benthic zone and disperse in the drifting water zone. We establish threshold conditions for persistence and extinction of two species and obtain the existence of a positive steady state under persistence conditions. We also numerically investigate the influences of factors, such as advection rates, diffusion rates, river length, competition rates, transfer rates, and spatial heterogeneity on persistence of the two competitive species.

Keywords. Benthic-drift model, competition, principal eigenvalue, persistence, stability

AMS subject classifications. 35K10, 47A75, 92B05

1 Introduction

Numerous species and organisms live in river and stream environments. Population dynamics in rivers or streams have attracted increasing attentions of biologists, ecologists and mathematicians in recent years. There are two important issues in stream ecology. One is the "drift paradox" [16], which asks how stream dwelling organisms can persist in a river/stream environment when continuously subjected to a unidirectional water flow. The solution of this problem provides not only better understanding of ecodynamics inside a river, but also strategies for how to

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keep a native species persistent or how to control the growth of an invasive species. The other issue is called the "Instream Flow Needs" [9, 14], which asks how to design reasonable flows to maintain desired levels of ecosystem in a river/stream environment. With increasing demands for human beings' daily life, industry, agriculture, etc, for limited freshwater resources, it is crucial to understand how much water can human beings utilize without destroying the heath and diversity of river ecosystems. Mathematical models, such as ordinary or partial differential equations and integro-differential or integro-difference equations have been established to study the effect of population demography, individual movement and flow dynamics on spatial spread and persistence of populations in streams and rivers and to provide water management strategy for maintaining ecosystem in rivers (see e.g., [6, 7, 8, 10, 11, 14, 17, 19, 2]).

For a single species, in recent works [9] and [14], population dynamics has been described by reaction-diffusion-advection equations that couple population demography and hydraulic dynamics in the cases where a single species only lives in flowing water and where the species lives in both flowing water and river benthos, respectively. Three measures have been established to determine a population's fundamental niche, source and sink regions, and global persistence in a river, through the next generation operator, which maps the population from one generation to its next generation offsprings.

In natural rivers or streams, multiple species live in the same environment. They interact with each other and are also interfered with the physical and hydrological environment. The study of a single species cannot provide its accurate dynamics in a river, so it is important and necessary to consider the interactions of a species with other species and the habitat. Competition is a simple but typical interaction between species. The study of competitive models has been an interesting topic in river ecodynamics studies. Li et al (see e.g., [23]) studied spreading speeds and traveling waves or cooperative systems; their results can be applied to competitive models for river species. Vasilyeva and Lutscher [21] studied dynamics of competitive models in a spatially homogeneous river and approximated the dispersal terms by linear terms depending on the principal eigenvalue of the dispersal operator. Recently, Zhou and Zhao [25] studied a competitive model for two river/stream species. Their model consists of two reaction-diffusion-advection equations and they analyzed the dynamics of the model including the existence and stability of steady states.

In this work, we will extend the earlier works [9, 14, 25] and consider a competitive model for two river species that live not only in the flowing water but also on the benthos. Such species can be invertebrates, which live on the benthos of the river but jump into water and settle down to the bottom from time to time [1]. They actually spend most of their time on the benthos and only drift in water for a very short period every time. The species can also be those who stay in a transient storage zone on the benthos or near the river side, which suffers different physical or hydrological conditions from the flowing water and hence provides different ecological habitat than the water column [4, 15]. Therefore, it is very important to incorporate the benthic stage into a mathematical model for competitive species. Moreover, the model can also describe the dynamics of a species that has a storage zone in a river or it almost does not move in the zone close to the river bank. Hence, this work is a mathematical and biological extension of previous works.

In our model, we consider a one-dimensional river and assume that individuals reproduce and compete on the benthos but only disperse in the flowing water. This yields a system consisting of two reaction-diffusion-advection equations that describe dynamics in the free water, coupled to two ordinary differential equations that describe dynamics on the benthos. We consider very general competitors in our model so that all the parameters including the advection rates (see [20, 25] and references therein) may be different for two species. We are interested in the persistence criteria for such two species. Overall, there might be three cases for the dynamics of the species: none of them can survive, one species wins the competition, and two species coexist. Since there are two species, it is hard to define the next generation operator to map one population to its offspring and the resulted net reproductive rate. Because of the two ordinary differential equations, the solution maps of the system are not compact, and hence, traditional theories of eigenvalue problems in infinite-dimensional dynamical systems based on the Krein-Rutman theorem [5] (see e.g., [14]), are therefore not applicable to our model. Wang and Zhao [22] has developed a theory of eigenvalue problems for compartmental epidemic models of reaction-diffusion equations, where some of diffusion coefficients could be zeros. Hsu et al [6] has established estimates for the principal eigenvalue of second order differential operators with variable coefficients. We adapt these theories to our model and show that the eigenvalue problems corresponding to the linearized systems at the trivial steady state and semi-trivial steady states admit principal eigenvalues. Then we use the theories of monotone dynamical systems to show that these principal eigenvalues serve as thresholds for extinction and uniform persistence of one or two populations under investigation.

The paper is organized as follows. In the next section, we introduce a benthic-drift model for two competitive species in a river or stream. In section 3, we establish threshold conditions for existence and stability of the trivial steady state, semi-trivial steady states, and a coexistence steady state, by mainly using the theories of monotone dynamical systems and eigenvalue problems. In section 4, we numerically investigate how biotic and abiotic factors such as diffusion coefficients, competition rates, transfer rates, advection rates, and river length affect population persistence or extinction, by studying the dependence of the principal eigenvalues of corresponding eigenvalue problems on these factors. We also analyze the effect of spatial heterogeneity on population density distributions in the positive steady state. A short discussion section completes the paper.

2 The model

We consider two competitive species in a river. They live both in the water column and in the benthic zone, while they only reproduce in the benthic zone and disperse in water. They compete in the benthic zone for space and nutrients so that the reproduction of either species depends on the densities of both species in the benthic zone. The dynamics of these two species are then governed by the following system

$$\begin{cases} \frac{\partial N_{d,1}}{\partial t} = \frac{A_b(x)}{A_d(x)}\mu_1(x)N_{b,1} - \sigma_1(x)N_{d,1} - m_{d,1}(x)N_{d,1} - \frac{Q}{A_d(x)}\frac{\partial N_{d,1}}{\partial x} \\ \qquad\quad + \frac{1}{A_d(x)}\frac{\partial}{\partial x}\left[D_1(x)A_d(x)\frac{\partial N_{d,1}}{\partial x}\right], \\ \frac{\partial N_{b,1}}{\partial t} = f_1(x, N_{b,1}, N_{b,2})N_{b,1} - \mu_1(x)N_{b,1} + \frac{A_d(x)}{A_b(x)}\sigma_1(x)N_{d,1}, \\ \frac{\partial N_{d,2}}{\partial t} = \frac{A_b(x)}{A_d(x)}\mu_2(x)N_{b,2} - \sigma_2(x)N_{d,2} - m_{d,2}(x)N_{d,2} - \frac{\delta Q}{A_d(x)}\frac{\partial N_{d,2}}{\partial x} \\ \qquad\quad + \frac{1}{A_d(x)}\frac{\partial}{\partial x}\left[D_2(x)A_d(x)\frac{\partial N_{d,2}}{\partial x}\right], \\ \frac{\partial N_{b,2}}{\partial t} = f_2(x, N_{b,1}, N_{b,2})N_{b,2} - \mu_2(x)N_{b,2} + \frac{A_d(x)}{A_b(x)}\sigma_2(x)N_{d,2}, \end{cases} \tag{2.1}$$

in $(x,t) \in (0,L) \times (0,\infty)$ with boundary and initial value conditions

$$\begin{cases} \alpha_1 N(0,t) - \beta_1 \frac{\partial N}{\partial x}(0,t) = 0,\ t > 0,\ N = N_{d,1},\ N_{d,2}, \\ \alpha_2 N(L,t) + \beta_2 \frac{\partial N}{\partial x}(L,t) = 0,\ t > 0,\ N = N_{d,1},\ N_{d,2}, \\ \mathbf{N}(x,0) = \mathbf{N}^0(x) \geq 0,\ 0 < x < L,\ \mathbf{N} = (N_{d,1},\ N_{d,2},\ N_{b,1},\ N_{b,2}). \end{cases} \tag{2.2}$$

Here $N_{d,i}$ is the density of the drift population of species i ($i = 1,2$), $N_{b,i}$ is the density of the benthic population of species i, D_i is the diffusion rate of species i, $m_{d,i}$ is the death rate of drift population, σ_i is the transfer rate of the drift population to benthos, μ_i is the transfer rate of the benthic population to drifting water, f_i is the growth rate of species i (in the benthic zone), α_i and β_i are nonnegative constants, A_b and A_d are the cross-sectional areas of the benthic zone and the drift zone, respectively, Q is the water discharge, δ is a nonnegative constant that represents the ratio between the advection rates of two species. $\mathbf{N}^0$ represents the initial distribution of the population. For simplicity, we denote spatial operators as

$$\mathcal{L}_1[u] := -\frac{Q}{A_d(x)}\frac{\partial u}{\partial x} + \frac{1}{A_d(x)}\frac{\partial}{\partial x}\left[D_1(x)A_d(x)\frac{\partial u}{\partial x}\right],$$
$$\mathcal{L}_2[u] := -\frac{\delta Q}{A_d(x)}\frac{\partial u}{\partial x} + \frac{1}{A_d(x)}\frac{\partial}{\partial x}\left[D_2(x)A_d(x)\frac{\partial u}{\partial x}\right].$$

Throughout this paper, we make the following assumptions for the functions and parameters in model (2.1):

H(i) $\mu_i(x)$, $\sigma_i(x)$, and $m_{d,i}(x)$ are nonnegative continuous functions.

H(ii) $D_i,\ A_b,\ A_d \in C^2([0,L],(0,\infty))$, and there exist positive constants c_1 and c_2 such that $c_1 < A_d(x), A_b(x) < c_2$ for any $x \in [0,L]$.

H(iii) $f_i : [0,L] \times (0,\infty) \times (0,\infty) \to \mathbb{R}$ is continuous; f_i is monotonically decreasing and Liptschiz continuous with respect to $N_{b,1}$ and $N_{b,2}$; $f_i(x,0,0) < \infty$; $f_i(x,0,0) - \mu_i(x) < 0$ for all $x \in (0,L)$; there exist $K_1 > 0$ and $K_2 > 0$ such that for all $x \in [0,L]$, $f_1(x,N_{b,1},0) < 0$ for $N_{b,1} > K_1$, and $f_2(x,0,N_{b,2}) < 0$ for $N_{b,2} > K_2$.

Typical examples of f_1 and f_2 for two competitive species can be chosen as follows:

$$\begin{cases} f_1(x,N_{b,1},N_{b,2}) = r_1(x)\left(1 - \frac{N_{b,1}}{K_{11}(x)} - \frac{N_{b,2}}{K_{12}(x)}\right), \\ f_2(x,N_{b,1},N_{b,2}) = r_2(x)\left(1 - \frac{N_{b,1}}{K_{21}(x)} - \frac{N_{b,2}}{K_{22}(x)}\right), \end{cases} \tag{2.3}$$

where r_i is the intrinsic growth rate, K_{ii} is the carrying capacity, and $1/K_{ij}$ represents the competition rate.

3 Dynamics of model (2.1)

In this section, we investigate the dynamics of (2.1) and establish existence and stability conditions for all types of steady states of (2.1).

Let $\tilde{X} = C([0,L],R^4)$ and $\tilde{X}^+ = C([0,L],R^4_+)$ with norm $||u|| = \max\limits_{1\le i\le 4}\max\limits_{x\in[0,L]}|u_i(x)|$ for $u = (u_1,u_2,u_3,u_4) \in \tilde{X}$ in the case of Robin boundary conditions for (2.1) or $\tilde{X} = C^1_0([0,L],R^4)$ and $\tilde{X}^+ = C^1_0([0,L],R^4_+)$ with norm $||u|| = \max\limits_{1\le i\le 4}(\max\limits_{x\in[0,L]}|u_i(x)| + \max\limits_{x\in[0,L]}|u_i'(x)|)$ for $u = (u_1,u_2,u_3,u_4) \in \tilde{X}$ in the case of Dirichlet boundary conditions for (2.1). Then $\tilde{X}^+$ is the positive cone in the Banach space $\tilde{X}$ with the above norm.

By [13, Proposition 3 and Remark 2.4], we can show that system (2.1) admits a unique solution for all $t > 0$ for each $\mathbf{N}^0 \in \tilde{X}^+$. Furthermore, $\tilde{X}^+$ is positively invariant for (2.1). Define the solution map of (2.1) as

$$\Phi_t(\mathbf{N}^0)(x) := (N_{d,1}(x,t), N_{b,1}(x,t), N_{d,2}(x,t), N_{b,2}(x,t)),\ \forall x \in [0,L],\ t \ge 0, \tag{3.1}$$

where $(N_{d,1}(x,t), N_{b,1}(x,t), N_{d,2}(x,t), N_{b,2}(x,t))$ is the solution of (2.1) with initial condition $(N_{d,1}(\cdot,0), N_{b,1}(\cdot,0), N_{d,2}(\cdot,0), N_{b,2}(\cdot,0)) = \mathbf{N}^0 \in \tilde{X}^+$.

We define the following quantities, which will be used to construct a positively invariant set for (2.1):

$$\begin{cases} K_{b,1} = \inf\{\rho > 0 : f_1(x,\rho,0) - \mu_1^{\min} + \frac{A_d^{\max}\sigma_1^{\max}}{A_b^{\min}} \frac{A_b^{\max}\mu_1^{\max}}{A_d^{\min}(\sigma_1^{\min}+m_{d,1}^{\min})} \le 0 \ \text{ in } [0,L]\}, \\ K_{b,2} = \inf\{\rho > 0 : f_2(x,0,\rho) - \mu_2^{\min} + \frac{A_d^{\max}\sigma_2^{\max}}{A_b^{\min}} \frac{A_b^{\max}\mu_2^{\max}}{A_d^{\min}(\sigma_2^{\min}+m_{d,2}^{\min})} \le 0 \ \text{ in } [0,L]\}, \\ K_{d,1} = \frac{A_b^{\max}\mu_1^{\max}}{A_d^{\min}(\sigma_1^{\min}+m_{d,1}^{\min})} K_{b,1}, \\ K_{d,2} = \frac{A_b^{\max}\mu_2^{\max}}{A_d^{\min}(\sigma_2^{\min}+m_{d,2}^{\min})} K_{b,2}, \end{cases} \tag{3.2}$$

where $g^{\max} = \max_{x\in[0,L]} g(x)$ and $g^{\min} = \min_{x\in[0,L]} g(x)$ for any $g \in C([0,L], R_+)$.

3.1 Existence and stability of trivial and semi-trivial steady states

It is easy to see that $E_0^* = (0,0,0,0)$ is a trivial steady state of (2.1). The linearization of (2.1) at E_0^* is

$$\begin{cases} \frac{\partial N_{d,1}}{\partial t} = \frac{A_b(x)}{A_d(x)}\mu_1(x)N_{b,1} - \sigma_1(x)N_{d,1} - m_{d,1}(x)N_{d,1} + \mathcal{L}_1[N_{d,1}], \\ \frac{\partial N_{b,1}}{\partial t} = f_1(x,0,0)N_{b,1} - \mu_1(x)N_{b,1} + \frac{A_d(x)}{A_b(x)}\sigma_1(x)N_{d,1}, \\ \frac{\partial N_{d,2}}{\partial t} = \frac{A_b(x)}{A_d(x)}\mu_2(x)N_{b,2} - \sigma_2(x)N_{d,2} - m_{d,2}(x)N_{d,2} + \mathcal{L}_2[N_{d,2}], \\ \frac{\partial N_{b,2}}{\partial t} = f_2(x,0,0)N_{b,2} - \mu_2(x)N_{b,2} + \frac{A_d(x)}{A_b(x)}\sigma_2(x)N_{d,2}, \\ \alpha_1 N(0,t) - \beta_1 \frac{\partial N}{\partial x}(0,t) = 0, \ t > 0, \ N = N_{d,1}, \ N_{d,2}, \\ \alpha_2 N(L,t) + \beta_2 \frac{\partial N}{\partial x}(L,t) = 0, \ t > 0, \ N = N_{d,1}, \ N_{d,2}, \\ \mathbf{N}(x,0) = \mathbf{N}^0(x) \ge 0, \ 0 < x < L, \ \mathbf{N} = (N_{d,1}, \ N_{d,2}, \ N_{b,1}, \ N_{b,2}), \end{cases} \tag{3.3}$$

which can be written as two decoupled systems

$$\begin{cases} \frac{\partial N_{d,1}}{\partial t} = \frac{A_b(x)}{A_d(x)}\mu_1(x)N_{b,1} - \sigma_1(x)N_{d,1} - m_{d,1}(x)N_{d,1} + \mathcal{L}_1[N_{d,1}], \\ \frac{\partial N_{b,1}}{\partial t} = f_1(x,0,0)N_{b,1} - \mu_1(x)N_{b,1} + \frac{A_d(x)}{A_b(x)}\sigma_1(x)N_{d,1}, \\ \alpha_1 N_{d,1}(0,t) - \beta_1 \frac{\partial N_{d,1}}{\partial x}(0,t) = 0, \ \alpha_2 N_{d,1}(L,t) + \beta_2 \frac{\partial N_{d,1}}{\partial x}(L,t) = 0, \ t > 0, \\ \mathbf{N}(x,0) = \mathbf{N}^0(x) \ge 0, \ 0 < x < L, \ \mathbf{N} = (N_{d,1}, \ N_{b,1}), \end{cases} \tag{3.4}$$

and

$$\begin{cases} \frac{\partial N_{d,2}}{\partial t} = \frac{A_b(x)}{A_d(x)}\mu_2(x)N_{b,2} - \sigma_2(x)N_{d,2} - m_{d,2}(x)N_{d,2} + \mathcal{L}_2[N_{d,2}], \\ \frac{\partial N_{b,2}}{\partial t} = f_2(x,0,0)N_{b,2} - \mu_2(x)N_{b,2} + \frac{A_d(x)}{A_b(x)}\sigma_2(x)N_{d,2}, \\ \alpha_1 N_{d,2}(0,t) - \beta_1 \frac{\partial N_{d,2}}{\partial x}(0,t) = 0, \ \alpha_2 N_{d,2}(L,t) + \beta_2 \frac{\partial N_{d,2}}{\partial x}(L,t) = 0, \ t > 0, \\ \mathbf{N}(x,0) = \mathbf{N}^0(x) \ge 0, \ 0 < x < L, \ \mathbf{N} = (N_{d,2}, \ N_{b,2}). \end{cases} \tag{3.5}$$

It follows from [9, Discussion] that if $f_i(x,0,0)-\mu_i(x)\geq 0$ then $(0,0)$ is always unstable for (3.4) or (3.5), and hence E_0^* is unstable for (3.3). If $f_i(x,0,0)-\mu_i(x)<0$, we substitute $N_{d,i}(x,t)=e^{\lambda t}\phi_{1,i}(x)$ and $N_{b,i}(x,t)=e^{\lambda t}\phi_{2,i}(x)$ into (3.4) and (3.5) and consider the following eigenvalue problem associated with (3.4) and (3.5):

$$\begin{cases}\lambda\phi_{1,i}=\frac{A_b(x)}{A_d(x)}\mu_i(x)\phi_{2,i}-\sigma_i(x)\phi_{1,i}-m_{d,i}(x)\phi_{1,i}+\mathcal{L}_i[\phi_{1,i}],\\ \lambda\phi_{2,i}=f_i(x,0,0)\phi_{2,i}-\mu_i(x)\phi_{2,i}+\frac{A_d(x)}{A_b(x)}\sigma_i(x)\phi_{1,i},\\ \alpha_1\phi_{1,i}(0)-\beta_1\frac{\partial\phi_{1,i}}{\partial x}(0)=0,\ \alpha_2\phi_{1,i}(L)+\beta_2\frac{\partial\phi_{1,i}}{\partial x}(L)=0,\end{cases}\tag{3.6}$$

for $i=1,2$. By [9, Theorem 3], we can obtain the following result.

Theorem 3.1. *Assume $\tilde{f}_i(x):=f_i(x,0,0)-\mu_i(x)<0$ and $\tilde{f}_i$ is locally Lipschitz at some maximum point $x_*\in[0,L]$. Then (3.6) admits a unique principal eigenvalue $\lambda_i^*\in(\lambda_{c,i},\infty)$, where $\lambda_{c,i}=\max\limits_{x\in[0,L]}\{\tilde{f}_i(x)\}$.*

Define

$$\lambda_i^*=\text{the unique principal eigenvalue of (3.6)},\ i=1,2.\tag{3.7}$$

It then follows from Lemma 4 and Theorem 5 in [9] that $(0,0)$ is stable for (3.4) if $\lambda_1^*<0$ and unstable if $\lambda_1^*>0$, and that $(0,0)$ is stable for (3.5) if $\lambda_2^*<0$ and unstable if $\lambda_2^*>0$. We then obtain the following theorem regarding the stability of E_0^*.

Theorem 3.2. *If $\lambda_1^*<0$ and $\lambda_2^*<0$, then E_0^* is globally asymptotically stable for (2.1) in $\tilde{X}^+$.*

Proof. When $\lambda_1^*<0$ and $\lambda_2^*<0$, E_0^* is the unique steady state of (2.1). By the dynamics of (3.4) and (3.5), we can obtain that E_0^* is globally asymptotically stable for (3.3) when $\lambda_1^*<0$ and $\lambda_2^*<0$. Note that by **H(iii)** we have $f_1(x,N_{b,1},N_{b,2})\leq f_1(x,0,0)$ and $f_2(x,N_{b,1},N_{b,2})\leq f_2(x,0,0)$ for $N_{b,1}\geq 0$ and $N_{b,2}\geq 0$. Hence, the comparison principle implies that the solution of (2.1) is controlled from above by the solution of (3.3). Thus, if $\lambda_1^*<0$ and $\lambda_2^*<0$, then E_0^* is globally asymptotically stable for (2.1) for any initial condition in $\tilde{X}^+$. □

Lemma 3.1. *(i) If $\lambda_1^*>0$, then the system*

$$\begin{cases}\frac{\partial N_{d,1}}{\partial t}=\frac{A_b(x)}{A_d(x)}\mu_1(x)N_{b,1}-\sigma_1(x)N_{d,1}-m_{d,1}(x)N_{d,1}+\mathcal{L}_1[N_{d,1}],\\ \frac{\partial N_{b,1}}{\partial t}=f_1(x,N_{b,1},0)N_{b,1}-\mu_1(x)N_{b,1}+\frac{A_d(x)}{A_b(x)}\sigma_1(x)N_{d,1},\\ \alpha_1N_{d,1}(0,t)-\beta_1\frac{\partial N_{d,1}}{\partial x}(0,t)=0,\ \alpha_2N_{d,1}(L,t)+\beta_2\frac{\partial N_{d,1}}{\partial x}(L,t)=0,\\ N_{d,1}(x,0)=N_{d,1}^0(x)\geq 0,\ N_{b,1}(x,0)=N_{b,1}^0(x)\geq 0,\ 0<x<L,\end{cases}\tag{3.8}$$

admits a unique positive steady state $(N_{d,1}^*(x),N_{b,1}^*(x))$, which is globally asymptotically stable for all initial functions in $C([0,L],R_+^2)\setminus\{(0,0)\}$.

(ii) If $\lambda_2^* > 0$, then the system

$$\begin{cases} \frac{\partial N_{d,2}}{\partial t} = \frac{A_b(x)}{A_d(x)}\mu_2(x)N_{b,2} - \sigma_2(x)N_{d,2} - m_{d,2}(x)N_{d,2} + \mathcal{L}_2[N_{d,2}], \\ \frac{\partial N_{b,2}}{\partial t} = f_2(x,0,N_{b,2})N_{b,2} - \mu_2(x)N_{b,2} + \frac{A_d(x)}{A_b(x)}\sigma_2(x)N_{d,2}, \\ \alpha_1 N_{d,2}(0,t) - \beta_1\frac{\partial N_{d,2}}{\partial x}(0,t) = 0,\ \alpha_2 N_{d,2}(L,t) + \beta_2\frac{\partial N_{d,2}}{\partial x}(L,t) = 0, \\ N_{d,2}(x,0) = N^0_{d,2}(x) \geq 0,\ \ N_{b,2}(x,0) = N^0_{b,2}(x) \geq 0,\ 0 < x < L, \end{cases} \tag{3.9}$$

admits a unique positive steady state $(N^*_{d,2}(x), N^*_{b,2}(x))$, which is globally asymptotically stable for all initial functions in $C([0,L], R^2_+) \setminus \{(0,0)\}$.

Proof. We prove (i) and omit the proof of (ii).

By [13, Proposition 3 and Remark 2.4], we can show the local existence of solutions for system (3.8) with initial functions in $C([0,L], R^2_+)$, and we can also show that $C([0,L], R^2_+)$ is positively invariant for (3.8). Let

$$\Psi_t : C([0,L], R^2_+) \to C([0,L], R^2_+)$$

be the solution map associated with system (3.8), that is, for $x \in [0,L]$ and $t \geq 0$, $\Psi_t(N^0_{d,1}, N^0_{b,1})(x) := (N_{d,1}(x,t), N_{b,1}(x,t))$, where $(N_{d,1}(x,t), N_{b,1}(x,t))$ is the solution of (3.8) with $(N_{d,1}(x,0), N_{b,1}(x,0)) = (N^0_{d,1}(x), N^0_{b,1}(x)) \in C([0,L], R^2_+)$.

We first prove that for any $t > 0$, Ψ_t satisfies the following claims.

Claim 1. Ψ_t ***is strongly positive.***

Let $\mathbf{N^0} = (N^0_{d,1}, N^0_{b,1}) \geq 0$ with $\mathbf{N^0} \not\equiv 0$. We prove that $N_{d,1}(x,t) > 0$ and $N_{b,1}(x,t) > 0$ for all $t > 0$, $x \in [0,L]$.

Suppose $N_{d,1}(x_1,t_1) = 0$ for some $x_1 \in [0,L], t_1 > 0$. Then $-\frac{\partial N_{d,1}}{\partial t} - \sigma_1(x)N_{d,1} - m_{d,1}(x)N_{d,1} + \mathcal{L}_1[N_{d,1}] = -\frac{A_b(x)}{A_d(x)}\mu_1(x)N_{b,1} \leq 0$. If $x_1 \in (0,L)$, then strong maximum principle implies that $N_{d,1}(x,t) \equiv 0$ on $x \in [0,L]$, $t \geq 0$. Substituting $N_{d,1}(x,t) \equiv 0$ into the first equation of (3.8), we have $N_{b,1}(x,t) \equiv 0$ on $x \in [0,L]$, $t \geq 0$. Then it follows that $\mathbf{N^0} = (N^0_{d,1}, N^0_{b,1}) = (N_{d,1}(\cdot,0), N_{b,1}(\cdot,0) = (0,0)$, a contradiction. If $x_1 = 0$, we have $N_{d,1}(0,t_1) = 0$, and hence, $\partial N_{d,1}/\partial x(0,t_1) > 0$. So $\alpha_1 N_{d,1}(0,t_1) - \beta_1 \partial N_{d,1}/\partial x(0,t_1) < 0$. Contradiction. If $x_1 = L$, it follows from the boundary condition that $\partial N_{d,1}/\partial x(L,t_1) < 0$, contradiction again. Thus $N_{d,1}(x,t) > 0$ for all $x \in [0,L], t > 0$.

Suppose $N_{b,1}(x_2,t_2) = 0$ for some $x_2 \in [0,L]$, $t_2 > 0$. Then $\partial N_{b,1}/\partial t = A_d/A_b \sigma_1 N_{d,1} > 0$ at (x_2,t_2). So $N_{b,1}(x_2, t_2 - t_\delta) < N_{b,1}(x_2,t_2) = 0$ for some sufficiently small $t_\delta > 0$. This contradicts the fact $N_{b,1}(x,t) \geq 0$ for $t \in [0,t_2]$. Thus $N_{b,1}(x,t) > 0$ for all $x \in [0,L], t > 0$.

Therefore, $\mathbf{N^0} \geq 0$ with $\mathbf{N^0} \not\equiv (0,0)$ implies $(N_{d,1}(x,t), N_{b,1}(x,t)) \gg 0$ for all $x \in [0,L], t > 0$. Hence, for any $t > 0$, Ψ_t is strongly positive.

Claim 2. Ψ_t ***is strongly monotone.***

Let $(N^j_{d,1}(x,t,\mathbf{N}^{j0}), N^j_{b,1}(x,t,\mathbf{N}^{j0}))$ be the solution of (3.8) with initial condition $\mathbf{N}^{j0} = (N^{j0}_{d,1}, N^{j0}_{b,1})$, $j = 1, 2$, where $\mathbf{N}^{10} \geq \mathbf{N}^{20}$ and $\mathbf{N}^{10} \not\equiv \mathbf{N}^{20}$. Let $\bar{N}_{d,1} = N^1_{d,1} - N^2_{d,1}$, $\bar{N}_{b,1} = N^1_{b,1} - N^2_{b,1}$. Note that Ψ_t is monotone. Then $\bar{N}_{b,1} \geq 0$ and

$$\begin{aligned}
\frac{\partial \bar{N}_{d,1}}{\partial t} &= \frac{A_b(x)}{A_d(x)}\mu_1(x)\bar{N}_{b,1}(x,t) - (\sigma_1(x) + m_{d,1}(x))\bar{N}_{d,1}(x,t) + \mathcal{L}_1[\bar{N}_{d,1}](x,t),\\
\frac{\partial \bar{N}_{b,1}}{\partial t} &= -\mu_1(x)\bar{N}_{b,1} + \frac{A_d(x)}{A_b(x)}\sigma_1(x)\bar{N}_{d,1} + f_1(x, N^1_{b,1}, 0)N^1_{b,1} - f_1(x, N^2_{b,1}, 0)N^2_{b,1}\\
&\geq -L(x)\bar{N}_{b,1} - \mu_1(x)\bar{N}_{b,1} + \frac{A_d(x)}{A_b(x)}\sigma_1(x)\bar{N}_{d,1},
\end{aligned}$$

where $L(x) \geq 0$ is the Liptschiz constant of the function $f_1(x, N, 0)N$ with respect to N.

Consider the following system

$$\begin{aligned}
&\frac{\partial \tilde{N}_{d,1}}{\partial t} = \frac{A_b(x)}{A_d(x)}\mu_1(x)\tilde{N}_{b,1}(x,t) - (\sigma_1(x) + m_{d,1}(x))\tilde{N}_{d,1}(x,t) + \mathcal{L}_1[\tilde{N}_{d,1}](x,t),\\
&\frac{\partial \tilde{N}_{b,1}}{\partial t} = -L(x)\tilde{N}_{b,1} - \mu_1(x)\tilde{N}_{b,1} + \frac{A_d(x)}{A_b(x)}\sigma_1(x)\tilde{N}_{d,1},\\
&\alpha_1\tilde{N}_{d,1}(0,t) - \beta_1\frac{\partial \tilde{N}_{d,1}}{\partial x}(0,t) = 0,\ \alpha_2\tilde{N}_{d,1}(L,t) + \beta_2\frac{\partial \tilde{N}_{d,1}}{\partial x}(L,t) = 0,
\end{aligned}$$

with the initial condition $(\tilde{N}^0_{d,1}, \tilde{N}^0_{b,1}) = (N^{10}_{d,1} - N^{20}_{d,1}, N^{10}_{b,1} - N^{20}_{b,1}) \geq, \not\equiv (0,0)$. By the similar arguments to those in Claim 1, we can show that $(\tilde{N}_{d,1}(x,t), \tilde{N}_{b,1}(x,t)) \gg 0$, for all $x \in [0, L],\ t > 0$. Then by comparison principle, $(\bar{N}_{d,1}(x,t), \bar{N}_{b,1}(x,t)) \geq (\tilde{N}_{d,1}(x,t), \tilde{N}_{b,1}(x,t)) \gg 0$, for all $x \in [0, L],\ t > 0$. This implies that the solution map Ψ_t is strongly monotone.

Claim 3. ***Ψ_t is strictly subhomogenous.***

Assume that $(N_{d,1}(x,t,\mathbf{N^0}), N_{b,1}(x,t,\mathbf{N^0}))$ is a solution of (3.8) with initial condition $\mathbf{N^0} = (N^0_{d,1}, N^0_{b,1})$. For any $\lambda \in (0,1)$, $(\lambda N_{d,1}(x,t,\mathbf{N^0}), \lambda N_{b,1}(x,t,\mathbf{N^0}))$ satisfies

$$\begin{aligned}
\frac{\partial(\lambda N_{d,1})}{\partial t} &= \frac{A_b(x)}{A_d(x)}\mu_1(x)\lambda N_{b,1} - \sigma_1(x)\lambda N_{d,1} - m_{d,1}(x)\lambda N_{d,1} + \mathcal{L}_1[\lambda N_{d,1}],\\
\frac{\partial(\lambda N_{b,1})}{\partial t} &= f_1(x, N_{b,1}, 0)\lambda N_{b,1} - \mu_1(x)\lambda N_{b,1} + \frac{A_d(x)}{A_b(x)}\sigma_1(x)\lambda N_{d,1}\\
&\leq f_1(x, \lambda N_{b,1}, 0)\lambda N_{b,1} - \mu_1(x)\lambda N_{b,1} + \frac{A_d(x)}{A_b(x)}\sigma_1(x)\lambda N_{d,1}.
\end{aligned}$$

This implies that $(\lambda N_{d,1}(x,t,\mathbf{N^0}), \lambda N_{b,1}(x,t,\mathbf{N^0}))$ is a lower solution of the system (3.8). Hence $\Psi_t(\lambda\mathbf{N^0}) \geq \lambda\Psi_t(\mathbf{N^0})$ for any $\mathbf{N^0} \gg 0$ and $\lambda \in (0,1)$.

Let $\hat{N}_{d,1}(x,t) = N_{d,1}(x,t,\lambda\mathbf{N^0}) - \lambda N_{d,1}(x,t,\mathbf{N^0})$, $\hat{N}_{b,1}(x,t) = N_{b,1}(x,t,\lambda\mathbf{N^0}) - \lambda N_{b,1}(x,t,\mathbf{N^0})$. Then $\hat{N}_{d,1} \geq 0$, $\hat{N}_{b,1} \geq 0$, and $(\hat{N}_{d,1}, \hat{N}_{b,1})$ satisfies

$$\begin{aligned}
&\frac{\partial \hat{N}_{d,1}}{\partial t} = \frac{A_b(x)}{A_d(x)}\mu_1(x)\hat{N}_{b,1} - (\sigma_1(x) + m_{d,1}(x))\hat{N}_{d,1} + \mathcal{L}_1[\hat{N}_{d,1}],\\
&\frac{\partial \hat{N}_{b,1}}{\partial t} = -\mu_1(x)\hat{N}_{b,1} + \frac{A_d(x)}{A_b(x)}\sigma_1(x)\hat{N}_{d,1}\\
&\qquad + f_1(x, N_{b,1}(x,t,\lambda\mathbf{N^0}), 0)N_{b,1}(x,t,\lambda\mathbf{N^0}) - f_1(x, N_{b,1}(x,t,\mathbf{N^0}), 0)\lambda N_{b,1}(x,t,\mathbf{N^0}),\\
&\alpha_1\hat{N}_{d,1}(0,t) - \beta_1\frac{\partial \hat{N}_{d,1}}{\partial x}(0,t) = 0,\ \alpha_2\hat{N}_{d,1}(L,t) + \beta_2\frac{\partial \hat{N}_{d,1}}{\partial x}(L,t) = 0,\\
&\hat{N}_{d,1}(\cdot, 0) = 0,\ \hat{N}_{d,1}(\cdot, 0) = 0.
\end{aligned}$$

Let $T_d(t)$ be the semigroup generated by $\frac{\partial \hat{N}_{d,1}}{\partial t} = -(\sigma_1(x) + m_{d,1}(x))\hat{N}_{d,1} + \mathcal{L}_1[\hat{N}_{d,1}]$ and $(T_b(t)\phi)(x) = e^{-\mu_1(x)t}$. Then the solution of the above system can be written as

$$\begin{cases} \hat{N}_{d,1}(x,t) = \int_0^t T_d(t-s)\frac{A_b(x)}{A_d(x)}\mu_1(x)\hat{N}_{b,1}(x,s)ds, \\ \hat{N}_{b,1}(x,t) = \int_0^t T_b(t-s)[f_1(x, N_{b,1}(x,s,\lambda\mathbf{N^0}), 0)N_{b,1}(x,s,\lambda\mathbf{N^0}) \\ \qquad -f_1(x, N_{b,1}(x,s,\mathbf{N^0}),0)\lambda N_{b,1}(x,s,\mathbf{N^0}) + \frac{A_d(x)}{A_b(x)}\sigma_1(x)\hat{N}_{d,1}(x,s)]ds, \end{cases} \tag{3.10}$$

It follows from Claim 2 that $N_{b,1}(x,t,\lambda\mathbf{N^0}) \ll N_{b,1}(x,t,\mathbf{N^0})$. **H(iii)** then implies that

$$f_1(x, N_{b,1}(x,t,\lambda\mathbf{N^0}), 0) \geq, \not\equiv f_1(x, N_{b,1}(x,t,\mathbf{N^0}), 0).$$

Therefore, we have

$$f_1(x, N_{b,1}(x,t,\lambda\mathbf{N^0}),0)N_{b,1}(x,t,\lambda\mathbf{N^0}) - f_1(x, N_{b,1}(x,t,\mathbf{N^0}),0)\lambda N_{b,1}(x,t,\mathbf{N^0}) \geq, \not\equiv 0,$$

for all $x \in [0, L]$ and $t \geq 0$. This together with the second equation of (3.10) imply that $\hat{N}_{b,1}(x,t) \geq, \not\equiv 0$, and hence, $\hat{N}_{d,1}(x,t) > 0$, for all $x \in [0, L],\ t > 0$, due to the first equation of (3.10). Therefore, $\Psi_t(\lambda\mathbf{N^0}) > \lambda\Psi_t(\mathbf{N^0})$ for any $(N^0_{d,1}, N^0_{b,1}) \gg 0$, $t > 0$ and $\lambda \in (0,1)$, that is, Ψ_t is strictly subhomogeneous.

Claim 4. ***Ψ_t is κ-contracting.***

Let k be the Kuratowski measure of noncompactness defined by $\kappa(B) = \inf\{r : B$ has a finite cover of diameter $< r\}$ for any bounded set B (see e.g., [24]). By using the assumptions **H(i)-H(iii)**, similarly as in Lemma 4.1 in [7], we can prove Ψ_t is κ-contracting in the sense that $\lim_{t\to\infty} \kappa(\Psi_t(B)) = 0$ for any bounded set $B \subset C([0, L], R^2_+)$.

Now we prove the existence of a unique positive steady state of (3.8).

Let

$$Y^+ = \{(u_1, u_2) \in C([0, L], R^2_+) : (u_1, u_2) \leq (K_{d,1}, K_{b,1})\}, \tag{3.11}$$

and

$$Y_0 = Y^+ \setminus \{(0, 0)\} \tag{3.12}$$

where $(K_{d,1}, K_{b,1})$ is defined in (3.2). Since $(K_{d,1}, K_{b,1})$ is an upper solution of (3.8), we obtain that for any $t > 0$, the solution map Ψ_t of (3.8) is point dissipative (i.e., solutions of (3.8) are ultimately bounded) and uniformly bounded on Y^+.

Let $\bar{t} > 0$. Since $\Psi_{\bar{t}}$ is κ-contracting on Y^+, $\Psi_{\bar{t}}$ is point dissipative on Y^+, and positive orbits of bounded subsets of Y^+ for $\Psi_{\bar{t}}$ are bounded, it follows from Theorem 2.6 in [12] that $\Psi_{\bar{t}}$ has a global attractor that attracts each bounded set in Y^+. Note that Theorem 5 in [9] implies that $\Psi_{\bar{t}}$ is weakly uniformly persistent with respect to $(Y_0, \partial Y_0)$ when $\lambda_1^* > 0$. It follows from Theorem 1.3.3 in [24] that $\Psi_{\bar{t}}$ is uniformly persistent with respect to $(Y_0, \partial Y_0)$ in the sense that there exists $\epsilon > 0$

such that $\liminf_{t\to\infty} ||\Psi_{\bar{t}}(P)|| \geq \epsilon$, for all $P \in Y_0$. Then $\Psi_{\bar{t}} : Y_0 \to Y_0$ admits a global attractor A_0. Note that $\Psi_{\bar{t}}$ is strongly monotone and strictly subhomogeneous. Since A_0 is in Y_0 and $A_0 = \Psi_{\bar{t}}(A_0)$, we have $A_0 \subseteq Int(C([0,L]), R_+^2)$. Then by Theorem 2.3.2 in [24] with $K = A_0$ that $\Psi_{\bar{t}}$ has a fixed point $\mathbf{e} \gg 0$ in Y_0 such that $A_0 = \{\mathbf{e}\}$. Since (3.8) is an autonomous system, we can consider it as a $\bar{t}$-periodic system. For any $t \geq 0$, we have $\Psi_t(\mathbf{e}) = \Psi_t(\Psi_{\bar{t}}(\mathbf{e})) = \Psi_{\bar{t}}(\Psi_t(\mathbf{e}))$, which implies that $\Psi_t(\mathbf{e})$ is a fixed point of $\Psi_{\bar{t}}$. Hence, $\Psi_t(\mathbf{e}) = \mathbf{e}$ for all $t \geq 0$ since the fixed point of $\Psi_{\bar{t}}$ is unique. Thus, $\mathbf{e}$ is a globally attractive steady state of the system (3.8) in Y_0. The comparison principle guarantees the local stability of $\mathbf{e}$. Hence, $\mathbf{e}$ is globally asymptotically stable in Y_0.

For any initial value $\mathbf{N}^0 = (N_{d,1}^0, N_{b,1}^0) \in C([0,L], R_+^2) \setminus \{(0,0)\}$, we can find a constant $\zeta \geq 1$, such that $\mathbf{N}^0 \in \hat{Y}^+ = \{(u_1,u_2) \in C([0,L], R_+^2) : (u_1,u_2) \leq \zeta(K_{d,1}, K_{b,1})\}$. By the comparison principle, we have $\Psi_t : \hat{Y}^+ \to \hat{Y}^+$, and hence Ψ_t is point dissipative and uniformly bounded on $\hat{Y}^+$ for all $t > 0$. Therefore, applying the above proof for Ψ_t on $\hat{Y}^+$, we can obtain that there exists a unique globally attractive steady state $\hat{\mathbf{e}}$ of the system (3.8) in $\hat{Y}^+ \setminus \{(0,0)\}$. Note that $Y_0 \subset \hat{Y}^+ \setminus \{(0,0)\}$. By the uniqueness of the globally attractive steady state in $\hat{Y}^+ \setminus \{(0,0)\}$, we have $\mathbf{e} = \hat{\mathbf{e}}$, which implies $\lim_{t\to\infty} ||\Psi_t(\mathbf{N}^0) - \mathbf{e}|| = 0$. Therefore, we have proved that $\mathbf{e}$ attracts any solution of (3.8) in $C([0,L], R_+^2) \setminus \{(0,0)\}$. Hence, $\mathbf{e}$ is globally asymptotically stable in $C([0,L], R_+^2) \setminus \{(0,0)\}$.

We then complete the proof of Lemma 3.1 (i) by writing $\mathbf{e} = (N_{d,1}^*(x), N_{b,1}^*(x))$. □

It follows from Lemma 3.1 that system (2.1) admits a semi-trivial steady state $E_1^*(x) = (N_{d,1}^*(x), N_{b,1}^*(x), 0, 0)$ when $\lambda_1^* > 0$ and that it admits a semi-trivial steady state $E_2^*(x) = (0, 0, N_{d,2}^*(x), N_{b,2}^*(x))$ when $\lambda_2^* > 0$.

The linearization of (2.1)-(2.2) at E_1^* is

$$\begin{aligned}
\frac{\partial N_{d,1}}{\partial t} &= \frac{A_b(x)}{A_d(x)}\mu_1(x)N_{b,1} - \sigma_1(x)N_{d,1} - m_{d,1}(x)N_{d,1} + \mathcal{L}_1[N_{d,1}], \\
\frac{\partial N_{b,1}}{\partial t} &= \left(f_1(x, N_{b,1}^*, 0) + \frac{\partial f_1(x, N_{b,1}^*, 0)}{\partial N_{b,1}} N_{b,1}^*\right) N_{b,1} - \mu_1(x)N_{b,1} \\
&\quad + \frac{A_d(x)}{A_b(x)}\sigma_1(x)N_{d,1} + \frac{\partial f_1(x, N_{b,1}^*, 0)}{\partial N_{b,2}} N_{b,1}^* N_{b,2}, \\
\frac{\partial N_{d,2}}{\partial t} &= \frac{A_b(x)}{A_d(x)}\mu_2(x)N_{b,2} - \sigma_2(x)N_{d,2} - m_{d,2}(x)N_{d,2} + \mathcal{L}_2[N_{d,2}], \\
\frac{\partial N_{b,2}}{\partial t} &= f_2(x, N_{b,1}^*, 0)N_{b,2} - \mu_2(x)N_{b,2} + \frac{A_d(x)}{A_b(x)}\sigma_2(x)N_{d,2}, \\
&\quad \text{with initial and boundary value conditions as in (2.2).}
\end{aligned} \tag{3.13}$$

The linearization of (2.1)-(2.2) at E_2^* is

$$\begin{aligned}
\frac{\partial N_{d,1}}{\partial t} &= \frac{A_b(x)}{A_d(x)}\mu_1(x)N_{b,1} - \sigma_1(x)N_{d,1} - m_{d,1}(x)N_{d,1} + \mathcal{L}_1[N_{d,1}],\\
\frac{\partial N_{b,1}}{\partial t} &= \left(f_1(x,0,N_{b,2}^*)\right) N_{b,1} - \mu_1(x)N_{b,1} + \frac{A_d(x)}{A_b(x)}\sigma_1(x)N_{d,1},\\
\frac{\partial N_{d,2}}{\partial t} &= \frac{A_b(x)}{A_d(x)}\mu_2(x)N_{b,2} - \sigma_2(x)N_{d,2} - m_{d,2}(x)N_{d,2} + \mathcal{L}_2[N_{d,2}],\\
\frac{\partial N_{b,2}}{\partial t} &= \left(f_2(x,0,N_{b,2}^*) + \frac{\partial f_2(x,0,N_{b,2}^*)}{\partial N_{b,2}}N_{b,2}^* - \mu_2(x)\right) N_{b,2} + \frac{A_d(x)}{A_b(x)}\sigma_2(x)N_{d,2}\\
&\quad + \frac{\partial f_2(x,0,N_{b,2}^*)}{\partial N_{b,1}}N_{b,2}^*N_{b,1},\\
&\quad \text{with initial and boundary value conditions as in (2.2).}
\end{aligned} \tag{3.14}$$

Lemma 3.2. *(i). If $f_2(x,N_{b,1}^*,0) - \mu_2(x) < 0$ and $\lambda_1^* > 0$, then the eigenvalue problem*

$$\begin{cases}
\lambda\phi_{1,2} = \frac{A_b(x)}{A_d(x)}\mu_2(x)\phi_{2,2} - \sigma_2(x)\phi_{1,2} - m_{d,2}(x)\phi_{1,2} + \mathcal{L}_2[\phi_{1,2}],\\
\lambda\phi_{2,2} = f_2(x,N_{b,1}^*,0)\phi_{2,2} - \mu_2(x)\phi_{2,2} + \frac{A_d(x)}{A_b(x)}\sigma_2(x)\phi_{1,2},\\
\alpha_1\phi_{1,2}(0) - \beta_1\frac{\partial\phi_{1,2}}{\partial x}(0) = 0,\ \alpha_2\phi_{1,2}(L) + \beta_2\frac{\partial\phi_{1,2}}{\partial x}(L) = 0,
\end{cases} \tag{3.15}$$

associated with

$$\begin{cases}
\frac{\partial N_{d,2}}{\partial t} = \frac{A_b(x)}{A_d(x)}\mu_2(x)N_{b,2} - \sigma_2(x)N_{d,2} - m_{d,2}(x)N_{d,2} + \mathcal{L}_2[N_{d,2}],\\
\frac{\partial N_{b,2}}{\partial t} = f_2(x,N_{b,1}^*,0)N_{b,2} - \mu_2(x)N_{b,2} + \frac{A_d(x)}{A_b(x)}\sigma_2(x)N_{d,2},\\
\alpha_1 N_{d,2}(0) - \beta_1\frac{\partial N_{d,2}}{\partial x}(0) = 0,\ \alpha_2 N_{d,2}(L) + \beta_2\frac{\partial N_{d,2}}{\partial x}(L) = 0,
\end{cases} \tag{3.16}$$

admits a unique principal eigenvalue $\lambda_{E_1}^*$ with a corresponding positive eigenfunction $(\phi_{1,2}^*, \phi_{2,2}^*)$.

(ii). If $f_1(x,0,N_{b,2}^*) - \mu_1(x) < 0$ and $\lambda_2^* > 0$, then the eigenvalue problem

$$\begin{cases}
\lambda\phi_{1,1} = \frac{A_b(x)}{A_d(x)}\mu_1(x)\phi_{2,1} - \sigma_1(x)\phi_{1,1} - m_{d,1}(x)\phi_{1,1} + \mathcal{L}_1[\phi_{1,1}],\\
\lambda\phi_{2,1} = f_1(x,0,N_{b,2}^*)\phi_{2,1} - \mu_1(x)\phi_{2,1} + \frac{A_d(x)}{A_b(x)}\sigma_1(x)\phi_{1,1},\\
\alpha_1\phi_{1,1}(0) - \beta_1\frac{\partial\phi_{1,1}}{\partial x}(0) = 0,\ \alpha_2\phi_{1,1}(L) + \beta_2\frac{\partial\phi_{1,1}}{\partial x}(L) = 0,
\end{cases} \tag{3.17}$$

associated with

$$\begin{cases}
\frac{\partial N_{d,1}}{\partial t} = \frac{A_b(x)}{A_d(x)}\mu_1(x)N_{b,1} - \sigma_1(x)N_{d,1} - m_{d,1}(x)N_{d,1} + \mathcal{L}_1[N_{d,1}],\\
\frac{\partial N_{b,1}}{\partial t} = f_1(x,0,N_{b,2}^*)N_{b,1} - \mu_1(x)N_{b,1} + \frac{A_d(x)}{A_b(x)}\sigma_1(x)N_{d,1},\\
\alpha_1 N_{d,1}(0) - \beta_1\frac{\partial N_{d,1}}{\partial x}(0) = 0,\ \alpha_2 N_{d,1}(L) + \beta_2\frac{\partial N_{d,1}}{\partial x}(L) = 0,
\end{cases} \tag{3.18}$$

admits a unique principal eigenvalue $\lambda_{E_2}^*$ with a corresponding positive eigenfunction $(\phi_{1,1}^*, \phi_{2,1}^*)$.

Proof. The proof is similar to the proof of Theorem 3.1. □

Denote

$$\lambda^*_{\mathbf{E_1}} : \text{the principal eiganvalue of (3.15) },$$
$$\lambda^*_{\mathbf{E_2}} : \text{the principal eiganvalue of (3.17).}$$

We can prove the following results about the stability of the trivial and semi-trivial steady states of (2.1).

Theorem 3.3. *For model (2.1),*

(i) if $\lambda_1^* < 0$ and $\lambda_2^* > 0$, then E_0^* is unstable and E_2^* is globally asymptotically stable;

(ii) if $\lambda_1^* > 0$ and $\lambda_2^* < 0$, then E_0^* is unstable and E_1^* is globally asymptotically stable;

(iii) if $\lambda_1^* > 0$, $\lambda_2^* > 0$, $\lambda^*_{E_1} < 0$ and $\lambda^*_{E_2} > 0$, then E_0^* is unstable, E_1^* is stable, E_2^* is unstable;

(iv) if $\lambda_1^* > 0$, $\lambda_2^* > 0$, $\lambda^*_{E_1} > 0$ and $\lambda^*_{E_2} < 0$, then E_0^* is unstable, E_1^* is unstable, E_2^* is stable;

(v) if $\lambda_1^* > 0$, $\lambda_2^* > 0$, $\lambda^*_{E_1} < 0$ and $\lambda^*_{E_2} < 0$, then E_0^* is unstable, E_1^* is stable, E_2^* is stable.

Proof. It follows from Theorem 5 in [9] that E_0^* is unstable for (2.1) if $\lambda_1^* > 0$ or $\lambda_2^* > 0$, so we only need to prove stability for E_1^* and E_2^*. We provide the proof for (i) and (iii). The other results can be similarly proved.

(i). Note that $f_1(x, N_{b,1}, N_{b,2}) \leq f_1(x, N_{b,1}, 0)$ for all $N_{b,1}, N_{b,2} \geq 0$. Theorem 5 in [9] implies that when $\lambda_1^* < 0$, $(0, 0)$ is stable for (3.8). It then follows from the comparison principle that every solution of (2.1) satisfies $N_{d,1} \to 0$ and $N_{b,1} \to 0$ as $t \to \infty$. Hence, (3.9) is the limiting system of (2.1), which admits a unique, positive, globally asymptotically stable steady state $(N^*_{d,2}(x), N^*_{b,2}(x))$, when $\lambda_2^* > 0$. Recall that Φ_t is the solution semiflow of (2.1). Let ω be the ω-limit set of $\Phi_t(\mathbf{N^0})$ for $\mathbf{N^0} = (N^0_{d,1}, N^0_{b,1}, N^0_{d,2}, N^0_{b,2}) \in \tilde{X}^+$. Then $\omega = \{(0, 0)\} \times \tilde{\omega}$, $\tilde{\omega} \in C([0, L], R^2_+)$. Restricting Φ_t on ω, we have $\Phi_t|_\omega(0, 0, N_{d,2}, N_{b,2}) = (0, 0, \tilde{\Psi}_t(N_{d,2}, N_{b,2}))$, where $\tilde{\Psi}_t$ is the solution semiflow of (3.9). By [24, Lemma 1.2.1'], ω is an internal chain transitive set for Φ_t. Thus by the relationship between ω and $\tilde{\omega}$, we have $\tilde{\omega}$ is an internal chain transitive set for $\tilde{\Psi}_t$. Since for (3.9) there are only two steady states $(0, 0)$ and $(N^*_{d,2}(x), N^*_{b,2}(x))$ when $\lambda_2^* > 0$ and $(N^*_{d,2}(x), N^*_{b,2}(x))$ is globally asymptotically stable in $C([0, L], R^2_+) \setminus \{(0, 0)\}$, by the continuous time version of [24, Theoren 1.2.2], $\tilde{\omega}$ should be $(0, 0)$ or $(N^*_{d,2}(x), N^*_{b,2}(x))$. If $\tilde{\omega} = (0, 0)$, then $\omega = E_0^*$, which contradicts to the fact the E_0^* is unstable. Therefore, $\tilde{\omega} = (N^*_{d,2}(x), N^*_{b,2}(x))$, and hence, $\omega = (0, 0, N^*_{d,2}(x), N^*_{b,2}(x)) = E^*_2$. That is, E^*_2 is globally asymptotically stable for (2.1).

(iii). If $\lambda^*_{E_2} > 0$, then $(0, 0)$ is unstable for the first two equations of (3.14), hence, $(0, 0, 0, 0)$ is unstable for (3.14). The comparison principle implies that E^*_2 is unstable for (2.1). When $\lambda^*_{E_1} < 0$, $N_{d,2} \to 0$ and $N_{b,2} \to 0$ for the solution of (3.13). Therefore, the limiting system of (3.13) is

$$\begin{aligned} \frac{\partial N_{d,1}}{\partial t} &= \frac{A_b(x)}{A_d(x)}\mu_1(x)N_{b,1} - \sigma_1(x)N_{d,1} - m_{d,1}(x)N_{d,1} + \mathcal{L}_1[N_{d,1}], \\ \frac{\partial N_{b,1}}{\partial t} &= \left(f_1(x, N^*_{b,1}, 0) + \frac{\partial f_1(x, N^*_{b,1}, 0)}{\partial N_{b,1}} N^*_{b,1}\right) N_{b,1} - \mu_1(x)N_{b,1} + \frac{A_d(x)}{A_b(x)}\sigma_1(x)N_{d,1}, \end{aligned} \tag{3.19}$$

which is the linearization of (3.8) at $(N^*_{d,1}(x), N^*_{b,1}(x))$. It follows from Lemma 3.1 that $(0, 0)$ is globally asymptotically stable for (3.19) when $\lambda^*_1 > 0$. By similar arguments as in the proof for (i), we can prove that $(0, 0, 0, 0)$ is asymptotically stable for (3.14), which then implies that E^*_1 is locally asymptotically stable for (2.1).

□

3.2 Existence of a coexistence steady state

In this subsection, we will prove that system (2.1) admits a coexistence steady state when all the trivial and semi-trivial steady states are unstable. Throughout this subsection, we assume $\lambda^*_1 > 0$, $\lambda^*_2 > 0$, $\lambda^*_{E_1} > 0$ and $\lambda^*_{E_2} > 0$, which implies the existence of both semi-trivial steady states E^*_1 and E^*_2.

Let

$$X^+ := \{(u_1, u_2, u_3, u_4) \in \tilde{X}^+ : 0 \le (u_1, u_2, u_3, u_4) \le (K_{d,1}, K_{b,1}, K_{d,2}, K_{b,2})\}, \tag{3.20}$$

with $K_{b,i}$'s and $K_{d,i}$'s defined in (3.2). By using **H(iii)**, (3.2), and monotonicity of systems (3.8) and (3.9), we can show that X^+ is positively invariant for (2.1), and hence, the solution map of (2.1) $\Phi_t : X^+ \to X^+$ is point dissipative and uniformly bounded on X^+.

Let

$$M\begin{pmatrix}\phi_1\\ \phi_2\end{pmatrix}(x) = \begin{pmatrix} M_{11}(x) & M_{12}(x) \\ M_{21}(x) & M_{22}(x)\end{pmatrix}, \ \forall x \in [0, L],$$

where

$$\begin{aligned} M_{11} &= f_1(\cdot, \phi_1, \phi_2) + \frac{\partial f_1(\cdot, \phi_1, \phi_2)}{\partial N_{b,1}}\phi_1 - \mu_1, \qquad M_{12} = \frac{\partial f_1(\cdot, \phi_1, \phi_2)}{\partial N_{b,2}}\phi_1, \\ M_{21} &= \frac{\partial f_2(\cdot, \phi_1, \phi_2)}{\partial N_{b,1}}\phi_2, \qquad M_{22} = f_2(\cdot, \phi_1, \phi_2) + \frac{\partial f_2(\cdot, \phi_1, \phi_2)}{\partial N_{b,2}}\phi_2 - \mu_2, \end{aligned}$$

for all $\phi = (\phi_1, \phi_2) \in C([0, L], R^2_+)$ with $0 \le \phi(x) \le (K_{b,1}, K_{b,2})$ for all $x \in [0, L]$. Assume

H(iv) There exists a constant $\chi > 0$ such that $\mathbf{v}^T M(\phi(x))\mathbf{v} \le -\chi \mathbf{v}^T \mathbf{v}$, for any $\mathbf{v} \in \mathbb{R}^2$, $\phi \in C([0,L], R_+^2)$ with $0 \le \phi(x) \le (K_{b,1}, K_{b,2})$ for all $x \in [0,L]$.

Due to the loss of two diffusion terms in (2.1), the associated solution maps are not compact. However, under the assumptions **H(i)-H(iv)**, we can prove by similar arguments as in Lemma 4.3 of [8] that Φ_t is κ-contracting in the sense that $\lim\limits_{t\to\infty} \kappa(\Phi_t(B)) = 0$ for any bounded set $B \subset X^+$. It then follows from Theorem 2.6 in [12] that Φ_t admits a global attractor that attracts each bounded set in X^+. Then we can prove the following main result in this subsection.

Theorem 3.4. *If $\lambda_1^* > 0$, $\lambda_2^* > 0$, $\lambda_{E_1}^* > 0$ and $\lambda_{E_2}^* > 0$, then (2.1) admits a positive steady state $E^{**}(x) = (N_{d,1}^{**}(x), N_{b,1}^{**}(x), N_{d,2}^{**}(x), N_{b,2}^{**}(x))$.*

Proof. Let $X_0 = \{(\phi_1, \phi_2, \phi_3, \phi_4) \in X^+ : \phi_i \not\equiv 0,\ \forall\ 1 \le i \le 4\}$, $\partial X_0 = X^+ \setminus X_0 = \{(\phi_1, \phi_2, \phi_3, \phi_4) \in X^+ : \phi_1 \equiv 0 \text{ or } \phi_2 \equiv 0 \text{ or } \phi_3 \equiv 0 \text{ or } \phi_4 \equiv 0\}$. Then $\Phi_t(X_0) \subset X_0$. We will use M_∂ to denote the maximal positively invariant set of the semiflow Φ_t in ∂X_0, that is,

$$M_\partial := \{P \in \partial X_0 : \Phi_t(P) \in \partial X_0,\ \forall\ t \ge 0\},$$

and let $\omega(P)$ be the ω-limit set of the forward orbit $\gamma^+(P) := \{\Phi_t(P) : t \ge 0\}$.

Claim. $\bigcup_{P\in M_\partial} \omega(P) \subset \{E_0^*\} \cup \{E_1^*\} \cup \{E_2^*\}$.

For any given $P \in M_\partial$, we have $\Phi_t(P) \in M_\partial$, $\forall\ t \ge 0$. Then for each $t \ge 0$, we have $N_{d,1}(\cdot,t,P) \equiv 0$ or $N_{b,1}(\cdot,t,P) \equiv 0$ or $N_{d,2}(\cdot,t,P) \equiv 0$ or $N_{b,2}(\cdot,t,P) \equiv 0$. In the case where $N_{d,1}(\cdot,t,P) \equiv 0$, $\forall\ t \ge 0$. From the first equation of (2.1), we see that $N_{b,1}(\cdot,t,P) \equiv 0$, $\forall\ t \ge 0$. Thus, $(N_{d,2}(\cdot,t,P), N_{b,2}(\cdot,t,P))$ satisfies system (3.9). It follows from Lemma 3.1 that either

$$\lim_{t\to\infty} (N_{d,2}(\cdot,t,P), N_{b,2}(\cdot,t,P)) = (N_{d,2}^*(x), N_{b,2}^*(x)), \text{ uniformly for } x \in [0,L],$$

or

$$\lim_{t\to\infty} (N_{d,2}(\cdot,t,P), N_{b,2}(\cdot,t,P)) = (0,0), \text{ uniformly for } x \in [0,L].$$

In the case where $N_{d,1}(\cdot,t_1,P) \not\equiv 0$, for some $t_1 \ge 0$. Then we can show that $(N_{d,1}(\cdot,t,P), N_{b,1}(\cdot,t,P)) \gg (0,0)$, $\forall\ t > t_1$. Then for each $t > t_1$, we have $N_{d,2}(\cdot,t,P) \equiv 0$ or $N_{b,2}(\cdot,t,P) \equiv 0$. In the case where $N_{d,2}(\cdot,t,P) \equiv 0$, $\forall\ t > t_2$. From the third equation of (2.1), we see that $N_{b,2}(\cdot,t,P) \equiv 0$, $\forall\ t > t_1$. Thus, $(N_{d,1}(\cdot,t,P), N_{b,1}(\cdot,t,P))$ satisfies system (3.8), for all $t > t_1$. It follows from Lemma 3.1 that either

$$\lim_{t\to\infty} (N_{d,1}(\cdot,t,P), N_{b,1}(\cdot,t,P)) = (N_{d,1}^*(x), N_{b,1}^*(x)), \text{ uniformly for } x \in [0,L],$$

or

$$\lim_{t\to\infty}(N_{d,1}(\cdot,t,P),N_{b,1}(\cdot,t,P))=(0,0),\ \text{uniformly for } x\in[0,L].$$

In the case where $N_{d,2}(\cdot,t_2,P)\not\equiv 0$, for some $t_2>t_1$. Then we can show that $(N_{d,2}(\cdot,t,P),N_{b,2}(\cdot,t,P))\gg(0,0)$, $\forall\ t>t_2$, which is a contradiction. By the above discussions, the claim is proved.

Claim. For $j=0,1,2$, there exists $\delta_j>0$ such that

$$\limsup_{t\to\infty}|\Phi_t(P)-E_j^*|\geq\delta_j,\ \forall\ P\in X_0.$$

We prove the claim for E_0^*. Assume that ϕ_1^* and ϕ_2^* are positive eigenfunctions of the eigenvalue problems associated with (3.4) and (3.5) corresponding to the principal eigenvalues $\lambda_1^*>0$ and $\lambda_2^*>0$, respectively. Similarly as in Theorem 3 in [9], we can prove that for sufficiently small $\epsilon>0$, the eigenvalue problem

$$\begin{cases}\frac{A_b(x)}{A_d(x)}\mu(x)N_{b,i}-\sigma_i(x)N_{d,i}-m_{d,i}(x)N_{d,i}+\mathcal{L}_iN_{d,i}=\lambda N_{d,i}, & x\in(0,L),t>0,\\ (f_i(x,0,0)-\epsilon-\mu_i(x))N_{b,i}+\frac{A_d(x)}{A_b(x)}\sigma_i(x)N_{d,i}=\lambda N_{b,i}, x\in(0,L),t>0,\\ \alpha_1N_{d,i}(0,t)-\beta_1\frac{\partial N_{d,i}}{\partial x}(0,t)=0, \quad t>0,\\ \alpha_2N_{d,i}(L,t)+\beta_2\frac{\partial N_{d,i}}{\partial x}(L,t)=0, \quad t>0,\end{cases}\tag{3.21}$$

admits a principal eigenvalue $\lambda_{i,\epsilon}^*$ with a positive eigenfunction $\phi_{i,\epsilon}^*(x)$, where $i=1,2$. Moreover, $\lambda_{i,\epsilon}^*\to\lambda_i^*$ as $\epsilon\to 0$. Then, there exists a small $\bar\epsilon>0$ such that $\lambda_{i,\epsilon}^*>0$ for all $\epsilon\in(0,\bar\epsilon)$. Take $\epsilon_0\in(0,\bar\epsilon)$. By the continuity of f_i, there exists a $\delta_0>0$ such that $|f_i(x,N_{b,1},N_{b,2})-f_i(x,0,0,)|<\epsilon_0$ for both $i=1$ and 2 when $|\ N_{b,j}\ |<\delta_0$ for all $x\in[0,L]$ and $j=1,2$. Assume, for the sake of contradiction, that there exists $P_0\in X_0$ and a positive solution $(N_{d,1}(x,t),N_{b,1}(x,t),N_{d,2}(x,t),N_{b,2}(x,t))$ of (2.1) with the initial value P_0 such that

$$\limsup_{t\to\infty}||(N_{d,1}(x,t),N_{b,1}(x,t),N_{d,2}(x,t),N_{b,2}(x,t))-(0,0)||<\delta_0.\tag{3.22}$$

Then there exists a large $t_0>0$, such that $N_{b,j}(x,t)<\delta_0$ and $f_i(x,N_{b,1}(x,t),N_{b,2}(x,t))$ $>f_i(x,0,0)-\epsilon_0$ for all $x\in[0,L]$ and $t\geq t_0$. Therefore,

$$\begin{cases}\frac{\partial N_{d,i}}{\partial t}=\frac{A_b(x)}{A_d(x)}\mu_i(x)N_{b,i}-\sigma_i(x)N_{d,i}-m_{d,i}(x)N_{d,i}+\mathcal{L}N_{d,i}, & x\in(0,L),\\ \frac{\partial N_{b,i}}{\partial t}\geq(f_i(x,0,0)-\epsilon)N_{b,i}-\mu_i(x)N_{b,i}+\frac{A_d(x)}{A_b(x)}\sigma_i(x)N_{d,i},\ x\in(0,L),\end{cases}\tag{3.23}$$

for all $t\geq t_0$. Since $N_{d,i}(t_0,x)\gg 0, N_{b,i}(t_0,x)\gg 0$ in the interior of $[0,L]$, we can choose a sufficiently small number $\eta>0$, such that $(N_{d,i}(t_0,\cdot),N_{b,i}(t_0,\cdot))\geq\eta\phi_{i,\epsilon_0}^*(\cdot)$, where $\phi^*_{i,\epsilon_0}(\cdot)$ is the positive eigenfunction of (3.21) (with $\epsilon = \epsilon_0$) corresponding to λ^*_{i,ϵ_0}. Note that $\eta e^{\lambda^*_{i,\epsilon_0}(t-t_0)}\phi^*_{i,\epsilon_0}(x)$ is a solution of

$$\begin{cases} \frac{\partial N_{d,i}}{\partial t} = \frac{A_b(x)}{A_d(x)}\mu_i(x)N_{b,i} - \sigma_i(x)N_{d,i} - m_{d,i}(x)N_{d,i} + \mathcal{L}N_{d,i}, \quad x \in (0,L), \\ \frac{\partial N_{b,i}}{\partial t} = (f_i(x,0,0) - \epsilon)N_{b,i} - \mu_i(x)N_{b,i} + \frac{A_d(x)}{A_b(x)}\sigma_i(x)N_{d,i}, \ x \in (0,L), \end{cases} \tag{3.24}$$

for $t \geq t_0$. Then it follows from the comparison principle that $(N_{d,i}(x,t), N_{b,i}(x,t)) \geq \eta e^{\lambda^*_{i,\epsilon_0}(t-t_0)}\phi^*_{i,\epsilon_0}(x)$ for all $x \in [0,L], t \geq t_0$, and hence, $\max_{x\in[0,L]} N_{d,i}(x,t) \to \infty$ and $\max_{x\in[0,L]} N_{b,i}(x,t) \to \infty$ as $t \to \infty$, which contradicts (3.22). Therefore, $\limsup_{t\to\infty} |\Phi_t(P_0) - E^*_0| > \delta_0$ for any $P_0 \in X_0$. We can similarly prove $\limsup_{t\to\infty} |\Phi_t(P_0) - E^*_j| > \delta_j$ for $j = 1,2$ and $P \in X_0$. The claim is proved.

For $\phi \in X^+$, we define $p(\phi) := \min_{1\leq i\leq 4}\{\min_{x\in[0,L]} \phi_i(x)\}$ in the case of Robin boundary conditions for (2.1) or $p(\phi) := \sup\{\beta \in R_+ : \phi_i(x) \geq \beta\tilde{e}(x), \forall x \in [0,L], 1 \leq i \leq 4\}$ in the case of Dirichlet boundary conditions for (2.1), where $\tilde{e}$ is a given element in $Int(C^1_0([0,L], R^4_+))$. Clearly, $p^{-1}(0,\infty) \subseteq X_0$. Furthermore, one can show that p is a generalized distance function for the semiflow Φ_t in the sense that p has the property that if $p(\phi) > 0$ or $\phi \in X_0$ with $p(\phi) = 0$, then $p(\Phi_t(\phi)) > 0, \ \forall \ t > 0$ (see, e.g., [18]). By the above claims, it follows that any forward orbit of Φ_t in M_∂ converges to $\{E^*_0\}$ or $\{E^*_1\}$ or $\{E^*_2\}$. Further, $\{E^*_j\}$ is isolated in X^+, for $j = 0,1,2$ and $W^s(\{E^*_j\}) \cap X_0 = \emptyset, \ \forall \ j = 0,1,2$, where $W^s(\{E_j\})$ is the stable set of $\{E_j\}$ (see [18]). It is easy that no subsets of $\{\{E^*_0\}, \{E^*_1\}, \{E^*_2\}\}$ forms a cycle in M_∂.

It then follows from Theorem 3 in [18] that there exists $\eta > 0$ such that $\liminf_{t\to\infty} p(\Phi_t(\phi)) > \eta$ for any $\phi \in X_0$. That is, $[\Phi_t(\phi)]_i(x) > \eta$ $(1 \leq i \leq 4)$ in the case of Robin boundary conditions or $[\Phi_t(\phi)]_i(x) > \eta\tilde{e}(x)$ $(1 \leq i \leq 4)$ in the case of Dirichlet boundary conditions, for any $\phi \in X_0$. Clearly, this implies that Φ_t is uniformly persistent with respect to $(X_0, \partial X_0)$. Then Theorem 1.3.7 in [24] implies that Φ_t has a stationary coexistence state $E^{**} \in X_0$, i.e., $\Phi_t(E^{**}) = E^{**}$, $t \geq 0$, or $E^{**}(x) = (N^{**}_{d,1}(x), N^{**}_{b,1}(x), N^{**}_{d,2}(x), N^{**}_{b,2}(x))$ is a positive steady state of (2.1).

□

4 Influences of parameters on population persistence

In this section, by virtue of numerical simulations, we study the dependence of the principal eigenvalues λ^*_i's and $\lambda^*_{E_i}$'s on parameters of model (2.1) in order to understand how different factors influence population persistence and extinction for (2.1).

To calculate λ_i^*'s and $\lambda_{E_i}^*$'s, we use the finite difference method to discretize (3.6), (3.15), and (3.17) with the zero-flux condition at the upstream end and the free-flow condition at the downstream end, that is,

$$\begin{cases} D_i(0)\frac{\partial \phi_{1,i}}{\partial x}(0,t) - v_i(0)\phi_{1,i}(0,t) = 0, \ t > 0, \ i = 1, 2, \\ \frac{\partial \phi_{1,i}}{\partial x}(L,t) = 0, \ t > 0, \ i = 1, 2, \end{cases} \tag{4.1}$$

and then use the principal eigenvalues of the resulted matrix operators to approximate λ_i^*'s and $\lambda_{E_i}^*$'s. In all numerical simulations, we choose logistic growth and competition as

$$f_1(x, N_{b,1}, N_{b,2}) = r_1 \left(1 - \frac{N_{b,1}}{K_{11(x)}} - \frac{N_{b,2}}{K_{12}}\right),$$
$$f_2(x, N_{b,1}, N_{b,2}) = r_2 \left(1 - \frac{N_{b,1}}{K_{21}} - \frac{N_{b,2}}{K_{22(x)}}\right),$$

where $r_i > 0$ is the intrinsic growth rate, $K_{ii} > 0$ is the carrying capacity, and $1/K_{ij} > 0$ is the competition rate.

Upon our interest, the following parameters are fixed for all simulations in this section: $A_d = A_b = 1$, $m_{d,1} = m_{d,2} = 0.000001$. Other parameter values will be specified in each figure.

4.1 Influence of the river length and advection rates on population persistence

We first consider the influence of the river length L and advection rates on λ_i^*'s and $\lambda_{E_i}^*$'s. Assume that all the parameters for the two species are the same except that the advection rate of species 2 is only half of the advection rate of species 1 (i.e., $\delta = 0.5$). Figure 4.1 shows that λ_1^* and λ_2^* increase from negative to positive as L increases . This indicates that when the river becomes longer, the stability of the trivial solution $(0, 0)$ of the single species models (3.8) and (3.9) changes from stable to unstable, and hence the dynamics of a single species may change from extinction to persistence when the river length increases. This coincides with the earlier results in [9]. Note that λ_2^* becomes positive at smaller L values than λ_1^* does. This means that small advection rate helps population persistence in short rivers, which also coincides with earlier results. Then we see that once $E_1^*(x) = (N_{d,1}^*(x), N_{b,1}^*(x), 0, 0)$ and $E_2^*(x) = (0, 0, N_{d,2}^*(x), N_{b,2}^*(x))$ both exist, that is, when both λ_1^* and λ_2^* are positive, we have $\lambda_{E_1}^* > 0$ but $\lambda_{E_2}^* < 0$, which implies that E_1^* is unstable but E_2^* is stable. Note that in this case $E_0^* = (0, 0, 0, 0)$ is unstable and there exists no positive equilibrium. Therefore, for such two species with only different advection rates, the species with smaller advection rate wins the competition. The length of the river does not seem to change the stability of E_1^* or E_2^* once they exist.

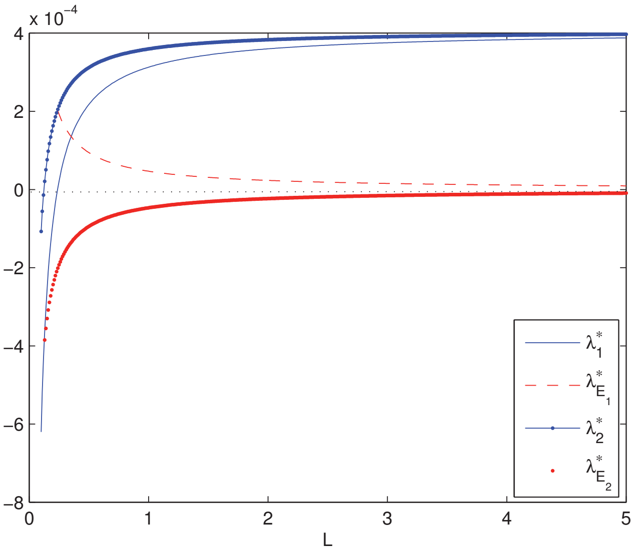


Figure 4.1: The relationship between λ_i^*'s, $\lambda_{E_i}^*$'s, and the length of the river L. Parameter values are: $Q = 0.0005$, $\delta = 0.5$, $\mu_1 = \mu_2 = 0.5$, $\sigma_1 = \sigma_2 = 2.2$, $D_1 = D_2 = 0.3$, $r_1 = r_2 = 0.000499$, $K_{11} = K_{12} = K_{21} = K_{22} = 998$.

4.2 Influence of diffusion and advection rates on population persistence

We then consider the influence of different diffusion and advection rates of two species on λ_i^*'s and $\lambda_{E_i}^*$'s. Assuming that all parameters are the same except that the diffusion rate of species 1 is larger than that of species 2 (i.e., $D_1 > D_2$), we vary the ratio δ between two advection rates. For parameter values in the simulation, we obtain $\lambda_1^* > 0$, which implies the existence of E_1^*. When δ increases, $\lambda_{E_1}^*$ decreases from positive to negative, λ_2^* decreases from positive (when E_2^* exists) to negative (when E_2^* does not exist) but $\lambda_{E_2}^*$ increases from negative to positive. See Figure 4.2. Therefore, if the advection rate of species 2 is far less than the advection rate of species 1, then E_1^* is unstable but E_2^* is stable if exists; if the advection rate of species 2 is larger than the advection rate of species 1, then E_1^* is stable but E_2^* is unstable if exists. This indicates that high advection rate decreases the competition ability of a species and hence reduces the possibility of existence. The results in Figure 4.2 coincide with the results in [25] where the model did not include benthic stages for two competitive species and only in the case of $D_1 > D_2$.

We then vary both the diffusion rates and the advection rates and obtain the influence of D_2 and δ on $\lambda_{E_i}^*$'s in the case where D_1 and Q are fixed. See Figure 4.3. When D_2 and δ are both small (i.e., the diffusion rate and the advection rate of species 2 are much smaller than those of species 1), both $\lambda_{E_1}^*$ and $\lambda_{E_2}^*$ are negative.

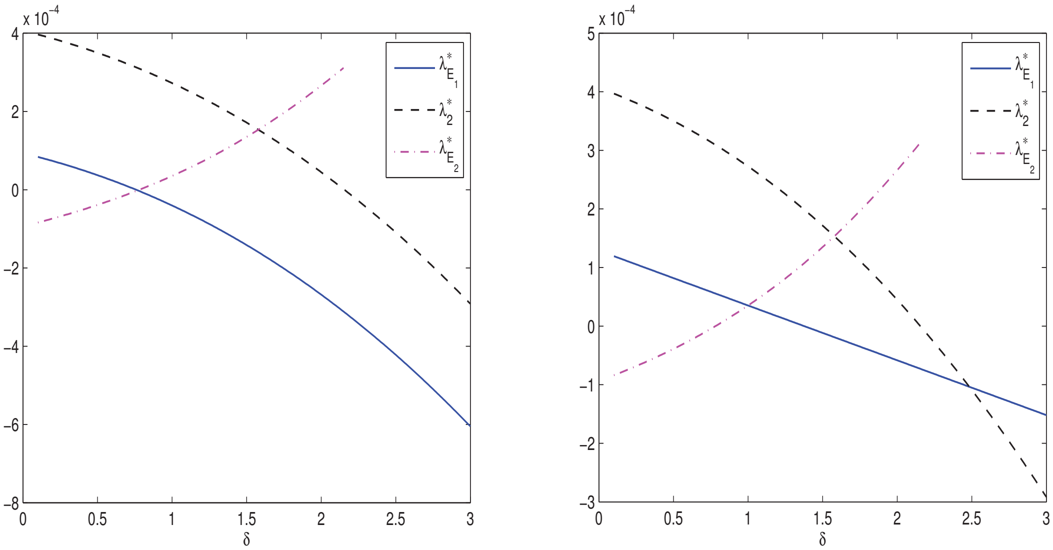


Figure 4.2: The relationship between λ_2^*, $\lambda_{E_i}^*$'s, and δ. Parameter values for D_i's: left figure: $D_1 = 0.5$, $D_2 = 0.0002$; right figure: $D_1 = 0.0002$, $D_2 = 0.5$. Other parameter values: $L = 1$, $Q = 0.0005$, $\mu_1 = \mu_2 = 0.5$, $\sigma_1 = \sigma_2 = 2.2$, $r_1 = r_2 = 0.000499$, $K_{11} = K_{12} = K_{21} = K_{22} = 998$. Here $\lambda_1^* = 0.00031292$.

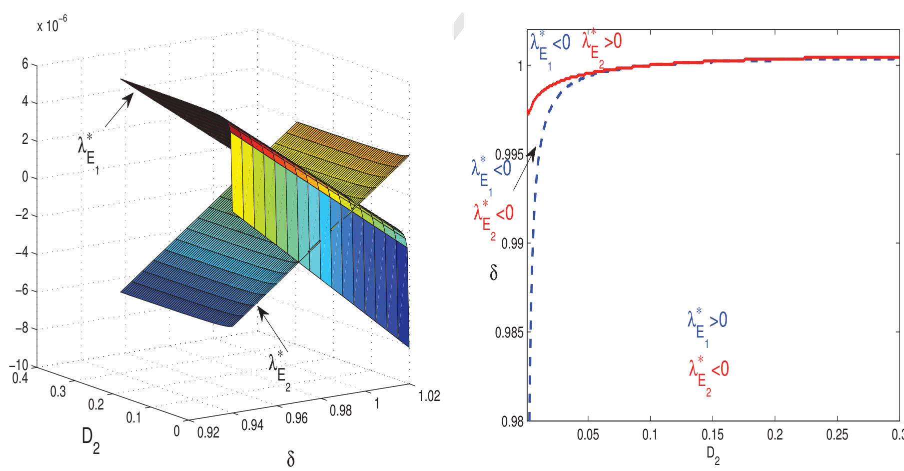


Figure 4.3: The influence of D_2 and δ on $\lambda_{E_i}^*$'s. Parameter values are the same as in Figure 4.2 except that $D_1 = 0.1$. In the right figure, the dash curve represents $\lambda_{E_1}^* = 0$; the solid curve represents $\lambda_{E_2}^* = 0$.

When δ is small (i.e., the advection rate of species 2 is small) but the diffusion rate D_2 becomes larger, $\lambda_{E_1}^* > 0$ and $\lambda_{E_2}^* < 0$, and hence E_1^* is unstable but E_2^* is stable. When δ becomes larger, $\lambda_{E_1}^* < 0$ and $\lambda_{E_2}^* > 0$, and hence E_1^* is stable but E_2^* is

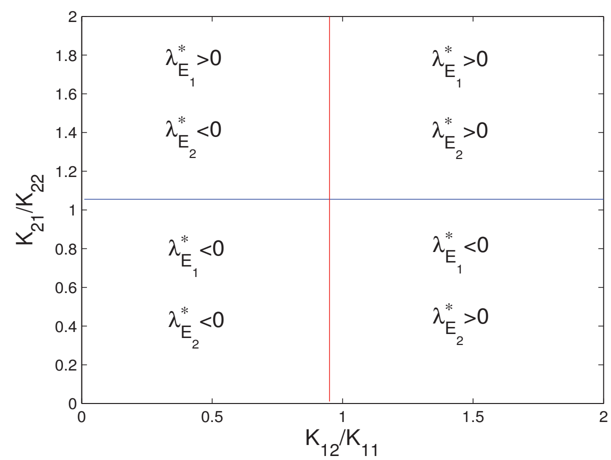


Figure 4.4: The influence of competition rates on $\lambda^*_{E_i}$'s. Parameter values are: $L = 1$, $Q = 0.00005$, $\delta = 1$, $\mu_1 = \mu_2 = 0.5$, $\sigma_1 = \sigma_2 = 2.2$, $D_1 = D_2 = 0.01$, $r_1 = r_2 = 0.5$, $K_{11} = 1050$, $K_{22} = 1000$.

unstable. Therefore, when the advection rate of species 2 is small, the increase of the diffusion rate D_2 helps species 2 persist and easily destroys the persistence of species 1. However, when the advection rate of species 2 is large, species 2 may not be persistent no matter what its diffusion rate is. In this case, species 1 easily win the competition.

4.3 The influence of competition on population persistence

We then consider the influence of the competition rates on $\lambda^*_{E_i}$'s. We assume all parameters are the same for the two species except the competition rates. In particular, we fix K_{11} and K_{22} but vary K_{12} and K_{21} to obtain Figure 4.4, which shows the regions for values of K_{12} and K_{21} where $\lambda^*_{E_1}$ and $\lambda^*_{E_2}$ have different signs. If inter-species competition rates (i.e., $1/K_{12}$ and $1/K_{21}$) are larger than the intra-species competition rates (i.e., $1/K_{11}$ and $1/K_{22}$), both $\lambda^*_{E_1}$ and $\lambda^*_{E_2}$ are negative and hence E_1^* and E_2^* are both locally asymptotically stable. In this case, either species could win the competition depending on the initial distribution of the populations. If inter-species competition rates are smaller than the intra-species competition rates, then both $\lambda^*_{E_1}$ and $\lambda^*_{E_2}$ are positive and two species may coexist. If the competition rate of species i is higher than the competition rate of species j, then species i wins the competition (i.e., $\lambda^*_{E_i} < 0$ but $\lambda^*_{E_j} > 0$). These results coincide with the dynamics of the nonspatial logistic competition model.

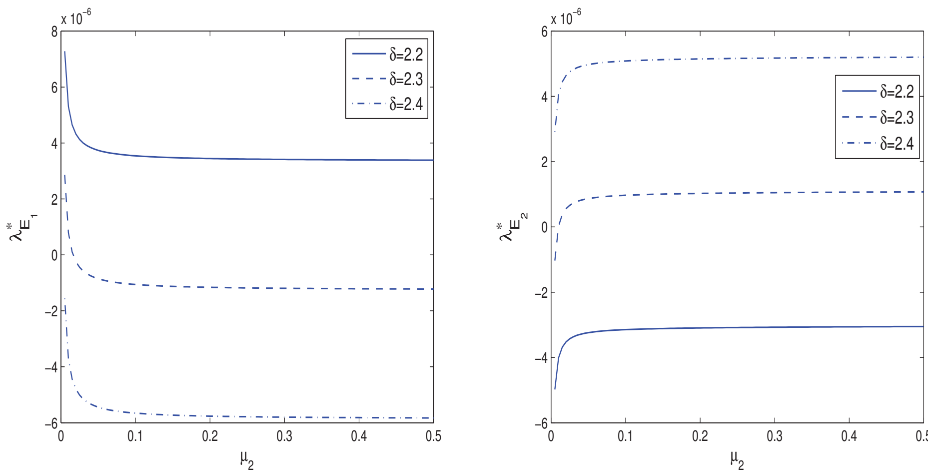
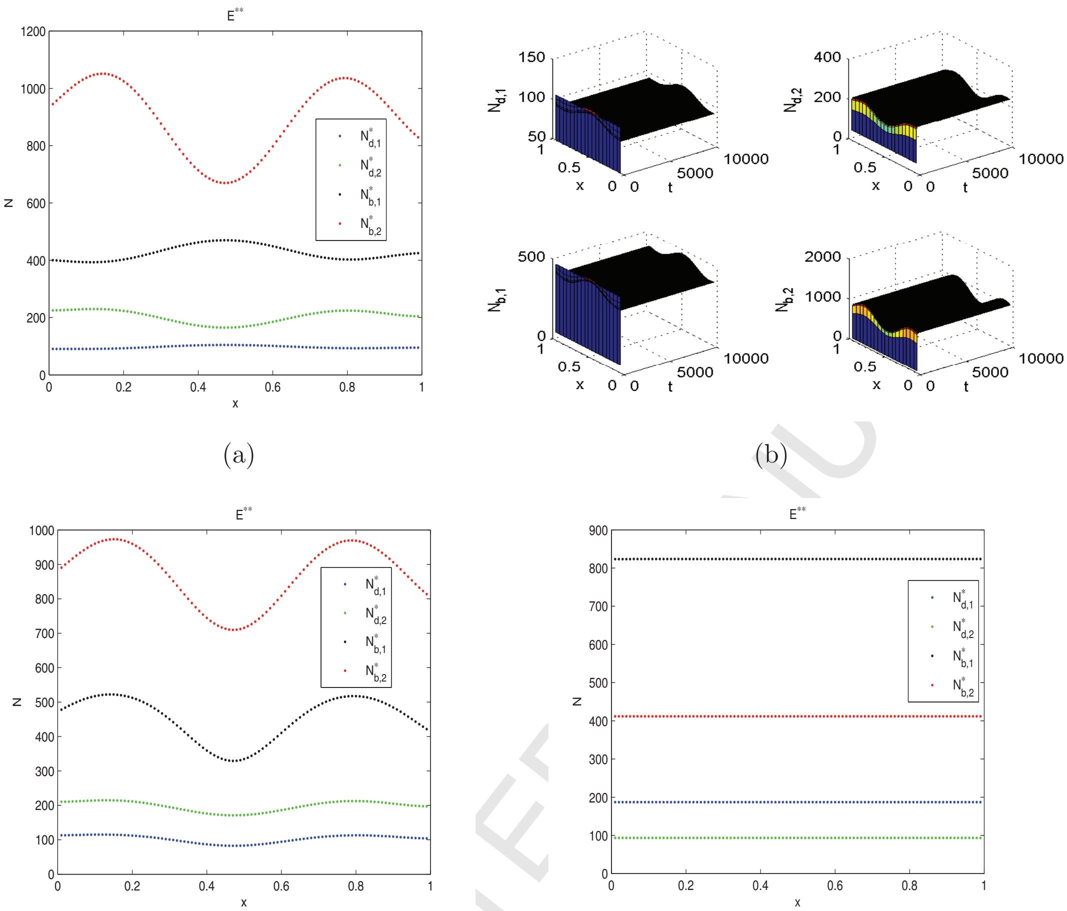


Figure 4.5: The influence of transfer rates on $\lambda^*_{E_i}$'s. Parameter values are: $L = 1$, $Q = 0.00005$, $\mu_1 = 0.5$, $\sigma_1 = 2.2$, $D_1 = D_2 = 0.01$, $r_1 = r_2 = 0.5$, $K_{11} = K_{12} = K_{21} = K_{22} = 1000$, $\mu_2/\sigma_2 = 0.1$.

4.4 The influence of transfer rates on population persistence

We study the influence of transfer rates on $\lambda^*_{E_i}$'s, and hence on persistence of the species. Assume all parameters of the two species are the same except the transfer rates and the advection rates. In particular, we fix the transfer rates of species 1 and vary those of species 2 with a fixed ratio between μ_2 and σ_2. Figure 4.5 shows that if the ratio μ_2/σ_2 is fixed, then as μ_2 and σ_2 become larger, $\lambda^*_{E_1}$ decreases and $\lambda^*_{E_2}$ increases. Both $\lambda^*_{E_1}$ and $\lambda^*_{E_2}$ quickly approach some limit values when the transfer rates are not very large. This indicates that when the transfer rates of species 1 are fixed, the more species 2 transfer between the water column and the benthic zone, the easier for species 1 to persist and the harder for species 2 to persist or compete with species 1. Moreover, we change the value of δ and compare the values of $\lambda^*_{E_i}$'s for different δ values. It turns out that when δ becomes larger, that is, when the advection rate of species 2 becomes larger, $\lambda^*_{E_1}$ is smaller and $\lambda^*_{E_2}$ is larger. This also coincides with our previous understanding of river population dynamics. Larger advection rate of species 2 decreases the chance of species 2 to persist or compete and hence increases the possibility of species 1 to persist. For Figure 4.5, $\mu_2/\sigma_2 = 0.1 < \mu_1/\sigma_1 = 0.5/2.2$. However, when we change the ratio μ_2/σ_2 (for example when $\mu_2/\sigma_2 > \mu_1/\sigma_1$), we obtain similar results.



(a) (b)

(c) (d)

Figure 4.6: A positive (co-existence) steady state of (2.1) and the time evolution of (2.1) with initial values $N_{b,i} = N_{d,i} = 200$ for $i = 1, 2$. Parameters: $L = 1$, $Q = 0.00005$, $\delta = 0.5$, $\mu_1 = \mu_2 = 0.5$, $\sigma_1 = \sigma_2 = 2.2$, $D_1 = D_2 = 0.01$, $r_1 = r_2 = 0.5$. Other parameters and values: (a) and (b): $K_{11} = 800 + 50\sin(10x)$, $K_{22} = 1100 + 300\sin(10x)$, $K_{12} = K_{21} = 1900$, $\lambda^*_{E_1} = 0.2386$, $\lambda^*_{E_2} = 0.1788$; (c): $K_{11} = 800 + 350\sin(10x)$, $K_{22} = 1100 + 300\sin(10x)$, $K_{12} = K_{21} = 1900$, $\lambda^*_{E_1} = 0.2503$, $\lambda^*_{E_2} = 0.1788$; (d): $K_{11} = 1050$, $K_{12} = 1910$, $K_{21} = 1400$, $K_{22} = 1000$, $\lambda^*_{E_1} = 0.1027$, and $\lambda^*_{E_2} = 0.1971$. The values of λ^*_i's are all about 0.4199.

4.5 Stability of the positive steady state $E^{**}(x)$ and the effect of spatial heterogeneity on $E^{**}(x)$

Theorem 3.4 guarantees the existence of a positive steady state $E^{**}(x)$ under the conditions $\lambda^*_1 > 0$, $\lambda^*_2 > 0$, $\lambda^*_{E_1} > 0$ and $\lambda^*_{E_2} > 0$, but does not imply the stability of $E^{**}(x)$. We choose parameters satisfying these conditions and numerically solve

(2.1) with $\partial N_{b,i}/\partial t = 0$ and $\partial N_{d,i}/\partial t = 0$ for $i = 1, 2$ to obtain $E^{**}(x)$. See Figure 4.6(a). We also numerically solve (2.1) with the same parameters and for constant initial values. The time evolution is shown in Figure 4.6(b), which indicates that the solution approaches $E^{**}(x)$ as time t becomes larger. Therefore, we can conclude that the positive steady state $E^{**}(x)$ obtained in Theorem 3.4 might be asymptotically stable. In this simulation, we only find one positive steady state, but we are not able to prove the uniqueness.

We also consider the influence of spatial heterogeneity on distribution of the positive steady state $E^{**}(x)$. In Figure 4.6, we obtained the steady state in three different situations, (a) and (c) for (2.1) with spatially varying carrying capacities of two species, (d) for (2.1) with spatially homogeneous carrying capacities of two species. Since two species are competitive, we assume that the carrying capacities are large or small in the same locations. When K_{11} is overall lower than K_{22} and its amplitude is much less than K_{22}'s, in the positive steady state, the density of species 2 reaches its maximum (minimum) where its carrying capacity is the largest (smallest), while the density distribution of species 1 reaches its maximum (minimum) where its carrying capacity is the smallest (largest); see Figure 4.6(a). When K_{11} is overall lower than K_{22} but K_{11}'s amplitude is not too much smaller or even larger than K_{22}'s, the density distributions in the positive steady state all reach the maximum (minimum) where the carrying capacities are the largest (smallest); see Figure 4.6(c). When all the parameters are constants, the density distributions in the positive steady state all slightly increase from the upstream to the downstream, due to the effect of the boundary conditions; see Figure 4.6(d).

4.6 Bistability

For parameter values $L = 1$, $Q = 0.00005$, $\delta = 1$, $\mu_1 = \mu_2 = 0.5$, $\sigma_1 = \sigma_2 = 2.2$, $D_1 = D_2 = 0.01$, $r_1 = r_2 = 0.5$, $K_{11} = 1050$, $K_{22} = 1000$, $k_{12} = 600$ and $K_{21} = 500$, we obtain that $\lambda_1^* = 0.4199 > 0$, $\lambda_2^* = 0.4199 > 0$, $\lambda_{E_1}^* = -0.4289 < 0$ and $\lambda_{E_2}^* = -0.2649 < 0$. This is the case of bistability, in which both semitrivial steady states are locally stable and the outcome of model (2.1) depends on initial conditions. While theoretical results have not been established, our computation shows that when bistability occurs, it is unlikely to have long-term coexistence steady states for (2.1).

5 Discussion

In this paper, we investigated the dynamics of a competitive model for two river species living both in the flowing water and in the benthic zone of the river. We established existence of the trivial steady state, the semi-trivial steady states, and a co-existence steady state, as well as the conditions for stability of the trivial steady state and the semi-trivial steady states, by using the theories of monotone dynamical systems and eigenvalue problems. We also conducted numerical simulations to understand the influences of biotic and abiotic factors such as the river length, the diffusion coefficients, the advection rates, the competition rates, and the transfer rates on the principal eigenvalues of eigenvalue problems corresponding to linearization of the system at steady states, and hence on existence and stability of the above mentioned steady states, which imply population persistence or extinction of one or two species. We also considered the effect of spatially varying carrying capacities on density distributions in the positive steady states.

The solution maps of our model (2.1) and its linearized systems are not compact due to the ordinary differential equations in the systems, so we proved a weaker result that the solution maps are κ-contracting, which by using the theory of monotone dynamical systems can guarantee the existence of positive steady states for corresponding systems under our model assumptions.

The results in this work extend the understanding of existing non-spatial competitive models or competitive models of only parabolic equations [25]. To our knowledge, this is the first time that the dynamics of a benthic-drift competitive model is comprehensively analyzed in a spatially heterogeneous habitat. We analyzed the existence and stability of the trivial and semi-trivial steady states in all situations, proved the existence of co-existence steady state and verified its stability numerically when other steady states are unstable. We also numerically found the possibility of non-existence of a positive steady state when two semi-trivial steady states are locally stable. Numerical simulations showed that for such two benthic-drift competitive species, factors such as the diffusion rates, the advection rates are critical on population persistence and extinction. We also saw that higher birth rate increases the possibility of one species to win, which is easily understandable, so we did not include any simulation results here.

The concept of persistence measure in [9] and [14] can also be extended to a competitive system. In [9] and [14], for a single species living only in flowing water or both in flowing water and on river benthos, the net reproductive rate R_0 was defined to describe the average number of offsprings that a single individual can produce during its lifetime and R_0 was used to determine population persistence (extinction) when $R_0 > 1$ ($R_0 < 1$). For two competitive species considered in this paper, we can apply the theory in [14] to define R_{01} and R_{02} for (3.8) and (3.9), respectively, as the net reproductive rates for isolated species 1 and species 2, respectively, satisfying $R_{0i} > (<) 1$ equivalent to $\lambda_i^* > (<) 0$. Similarly, we can define $R_0^{E_i^*}$ for (3.16) and (3.18) satisfying $R_0^{E_i^*} > (<) 1$ equivalent to $\lambda_{E_j}^* > (<) 0$, representing the net reproductive rate of species i when species j is at its steady state. Theorem 3.4 then implies that if either species can persist in a habitat without the other species and in a habitat with the other species in its steady state, then both species can coexist. Theorems 3.2 and 3.3 indicate that none species can survive in a competitive environment if either of them cannot persist in an isolated environment, that a species who cannot survive itself cannot win the competition, and that the species who can persist in the habitat with the other species wins the competition.

Acknowledgment. The authors greatly appreciated valuable discussions with Professors Sze-Bi Hsu and Xiao-Qiang Zhao. Y. J. was supported by NSF Grant DMS 1411703. Y. J. also acknowledged the hospitality of National Center for Theoretical Sciences (NCTS) in Taiwan while she visited there in summer 2016. F.-B.Wang was supported in part by Ministry of Science and Technology of Taiwan, National Center for Theoretical Sciences (NCTS), National Taiwan University, and Chang Gung Memorial Hospital (BMRPD18 and NMRPD5F0541).

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