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Global dynamics of a competition-diffusion-advection system with general boundary conditions

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Abstract. We study a general Lotka-Volterra competition-diffusion-advection system with general boundary conditions from river ecology. A complete classification on all possible long-time dynamical behaviors is established. Moreover, we investigate the joint effects of diffusion rates, advection rates, the inter-specific competition intensities and boundary conditions on global dynamics of the system. Finally, several numerical simulations are performed to verify the theoretical results. These results improve previously known ones by removing one condition and considering an interesting boundary condition where the species can be exposed to a net loss of individuals.

1. Introduction

The question of how the random dispersing affect the evolution of the population has fascinated ecologists and evolutionary biologists for many years. In recent decades, many works have been devoted to studying this topic [5, 8, 9, 12]. In addition to the random movement, the species may also take directed movement towards more favorable habitats in some special circumstances [1, 3, 4] or there exist some external environmental forces, such as water flow [17, 18]. River ecosystems are the typical example of environment featured by a constantly unidirectional flow that influences the dispersal of individuals. How populations resist washout and manage to persist? This question has attracted many researchers to investigate by employing an analytic or numerical approach based on some specific mathematical models. Speirs and Gurney [20] proposed the following single compartment model with diffusion, advection and a logistic growth from river ecosystems

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$$\begin{cases} u_t = du_{xx} - \alpha u_x + u[m(x) - u], & 0 < x < L,\ t > 0, \\ du_x(x,t) - \alpha u(x,t) = 0, & x = 0,\ t > 0, \\ u(x,t) = 0, & x = L,\ t > 0, \\ u(x,0) = u_0 \geq, \not\equiv 0, & 0 < x < L, \end{cases} \tag{1.1}$$

where u stands for the population density of an aquatic species. d characterizes random diffusion rate which is therefore assumed to be non-negative. α measures the tendency of the biased movement by water flow (sometimes we call α the advection speed/rate). L is the size of the habitat, and in the sequel, we call $x = 0$ the upstream end and $x = L$ the downstream end. We point out here that α should be positive since it is defined that $x = L$ is the downstream end. The function $m(x)$ accounts for intrinsic growth rate. It is assumed by the no-flux type condition at the upstream end and by the hostile condition at the downstream end. Their results suggested that a sufficient amount of diffusive movement can counterbalance the water flow and lead to population survival.

In this paper, we mainly study the population dynamics when a new or invasive species is introduced into such advective environments with more general boundary. To be more specific, the two-species Lotka-Volterra competition-diffusion-advection system with general boundary conditions:

$$\begin{cases} u_t = d_1 u_{xx} - \alpha_1 u_x + u[m_1(x) - u - bv], & 0 < x < L,\ t > 0, \\ v_t = d_2 v_{xx} - \alpha_2 v_x + v[m_2(x) - cu - v], & 0 < x < L,\ t > 0, \\ d_1 u_x(x,t) - \alpha_1 u(x,t) = b_u \alpha_1 u(x,t), & x = 0,\ t > 0, \\ d_1 u_x(x,t) - \alpha_1 u(x,t) = -b_d \alpha_1 u(x,t), & x = L,\ t > 0, \\ d_2 v_x(x,t) - \alpha_2 v(x,t) = b_u \alpha_2 v(x,t), & x = 0,\ t > 0, \\ d_2 v_x(x,t) - \alpha_2 v(x,t) = -b_d \alpha_2 v(x,t), & x = L,\ t > 0, \\ u(x,0) = u_0 \geq, \not\equiv 0, \quad v(x,0) = v_0 \geq, \not\equiv 0, & 0 < x < L, \end{cases} \tag{1.2}$$

where u and v represent the population densities of two aquatic competing species. d_i, α_i and m_i $(i = 1, 2)$ can be understood biologically in the same manner as that in (1.1). $b, c > 0$ signify the inter-specific competition intensities. The parameters $b_u, b_d \geq 0$ are used to measure the loss rate of individuals at the upstream and downstream ends relative to the flow rate, see [14]. It turns out that different values of parameters b_u and b_d may reflect different biological scenarios at the habitat ends, and also, may induce different types of boundary conditions from the mathematical point of view. To be more specific, we take b_d as an example to explain further: (1) $b_d = 0$ implies that there is no loss at the habitat ends, which indicates that individuals can not pass through the downstream end. Meanwhile, if $b_u = 0$, it means that the species live in an isolated environment [13]. (2) $b_d = 1$ means that there is a hundred percent loss at the downstream end relative to the water flow, which can be applied to describe the scenario stream to lake [14, 21] and biologically is called free-flow boundary condition (homogeneous Neumann type boundary condition). (3) $0 < b_d < 1$ indicates that at the downstream end, water flow cause a partial loss, and this seems to happen under certain artificial factors, e.g. at the interface of the stream and lake, there is a fishnet set up by human beings, which may prevent a portion of individuals from being washed out [31]. (4) $b_d > 1$ shows that both diffusive and advective movements will cause population loss at the downstream end, which in turn reflects an unfavorable environment nearby $x = L$ (Robin type boundary condition). If $b_d \to \infty$, it can be used to model the situation stream to ocean [20] (Dirichlet type boundary condition). In the past few years, several special cases of system (1.2) have been well understood.

We begin with the no-flux case, i.e., $b_u = b_d = 0$. In spatially homogeneous environment, that is $m_1(x) = m_2(x) = m_0$ with m_0 being a positive constant. Lou et al [15] confirmed that weak advection is more beneficial for species to exclude its competitor when $d_1 = d_2$ and $\alpha_1 \neq \alpha_2$. For differing movement rates, i.e., $d_1 \neq d_2$ and $\alpha_1 \neq \alpha_2$, Zhou [28] found that the strategy of faster diffusion together with slower advection is always favorable, which can be seen as a generation of [15]. For the inhomogeneous case $m_1 = m_2 = r(x)$, non-constant, Lam et al [13] seemed to be the first attempt to talk about, aiming at the existence and multiplicity of evolutionarily stable strategies by using some limiting arguments if $d_1 \neq d_2$ and $\alpha_1 = \alpha_2$ with both diffusion and advection rates are sufficiently small and comparable. Recently, if $m_1 \neq m_2$, an important advance on a bit more general setting of system (1.2) is due to Zhou and Xiao [30], they classified completely all possible long time behaviors of system (1.2) under a technical assumption:

$$(H) : \alpha_1/d_1 = \alpha_2/d_2 =: k > 0.$$

Lately, Guo et al [6] got a complete classification by removing the assumption (H) (see [[6], Corollary 5.1]). Zhou et al [29] also got a similar classification and presented a picture on the dynamics in $b - c$ plane, which was new. Indeed, Zhou and Xiao [30], Guo et al [6] and Zhou et al [29] all discussed in multi-dimensional space. For more investigations, we refer to [22, 23, 24].

In addition, there have been many researchers discuss other boundary conditions. For $m_1 = m_2 = m_0$, if $d_1 \neq d_2$ and $\alpha_1 = \alpha_2$, Lou and Lutscher [14] and Lou and Zhou [19], respectively, discussed $b_u = 0$, $b_d = 1$ and $b_u = 0$, b_d in $[0, 1)$, and they concluded that the competitor with faster diffusion rate would displace the slower one. If $d_1 = d_2$ and $\alpha_1 \neq \alpha_2$, Xu et al [25] talked about the case of $b_u = 0$ and $0 < b_d \leq +\infty$, and they showed that weak advection is more favorable, which extended the result in [15]. When $m_1 = m_2 = m(x)$, Zhao and Zhou [27], focusing on the special case $d_1 \neq d_2$, $\alpha_1 = 0 < \alpha_2$, $b_u = -1$ and $b_d = 0$, tried to reveal some different phenomena after involving spatial variations. Later, they [32] investigated the case of $d_1 = d_2$ and $\alpha_1 \neq \alpha_2$ with $b_u = 0$, $0 < b_d \leq +\infty$ which generalized [15]. Lou et al [16] explored a more general case $d_1 \neq d_2$, $\alpha_1 = \alpha_2$, $b_u = 0$ and $b_d > 0$, they obtained a deep understanding on the global dynamics by developing new techniques to overcome the difficulties caused by non-self-adjoint operators. The general boundary case (b_u, b_d) belongs to $[0, \infty] \times [0, \infty] \backslash (0, 0)$ was investigated by Xu et al [26] recently, where they discussed the global dynamics of system (1.2) under the technical condition (H).

In river ecosystems, advection speeds of aquatic species depend on many factors, such as water flow rate and so on. The condition that the diffusion rate of species is proportional to the advection rate is specific. It is obvious that condition $(H) : \alpha_1/d_1 = \alpha_2/d_2$ is harsh. To better describe the reality of nature, through the above discussion, we will remove the technical condition (H). Considering different scenarios in nature (e.g. stream to lake, stream to ocean and so on), we study the population dynamics of system (1.2) with general boundary. To explore the joint effects of diffusion rates, advection rates, the inter-specific competition intensities and the parameters b_u as well as b_d (boundary conditions) on the global dynamics of system (1.2), we will force the two species have the same growth rate.

Before stating our results, firstly, we make the following assumptions:

(H_1) $m_1(x)$ and $m_2(x)$ belong to $L^\infty(0, L)$;

(H_2) (b_u, b_d) belongs to $[0, \infty] \times [0, \infty] \backslash (0, 0)$.

In the sequel, when $b_u = b_d = \infty$, we mean that $u(0, t) = v(0, t) = u(L, t) = v(L, t) = 0$.

Set

$$k_0 = \begin{cases} e^{(\alpha_2/d_2 - \alpha_1/d_1)L}, & \frac{\alpha_1}{d_1} - \frac{\alpha_2}{d_2} \geq 0, \\ e^{(\alpha_1/d_1 - \alpha_2/d_2)L}, & \frac{\alpha_1}{d_1} - \frac{\alpha_2}{d_2} < 0. \end{cases} \tag{1.3}$$

It is obvious that k_0 is in $(0, 1]$. For every $\xi > 0$, define

$$\Pi_\xi := \{(b, c) \in \mathbb{R}^+ \times \mathbb{R}^+ : bc \leq \xi\}. \tag{1.4}$$

From the theory of monotone dynamical systems, to study the dynamics of system (1.2), we should study the stability of its semi-trivial steady states. Clearly, by similar arguments as in the proofs of existence and uniqueness results in [2], we see that there is a unique steady state for the following two equations, respectively

$$\begin{cases} u_t = d_1 u_{xx} - \alpha_1 u_x + u(m_1(x) - u), & 0 < x < L,\ t > 0, \\ d_1 u_x(x,t) - \alpha_1 u(x,t) = b_u \alpha_1 u(x,t), & x = 0,\ t > 0, \\ d_1 u_x(x,t) - \alpha_1 u(x,t) = -b_d \alpha_1 u(x,t), & x = L,\ t > 0, \end{cases} \tag{1.5}$$

and

$$\begin{cases} v_t = d_2 v_{xx} - \alpha_2 v_x + v(m_2(x) - v), & 0 < x < L,\ t > 0, \\ d_2 v_x(x,t) - \alpha_2 v(x,t) = b_u \alpha_2 v(x,t), & x = 0,\ t > 0, \\ d_2 v_x(x,t) - \alpha_2 v(x,t) = -b_d \alpha_2 v(x,t), & x = L,\ t > 0. \end{cases} \tag{1.6}$$

And we denote the steady states of (1.5) and (1.6) by $\tilde{u}$ and $\tilde{v}$, respectively. Hence there are two semi-trivial steady states for system (1.2), in the sequel, denoted by $(\tilde{u}, 0)$ and $(0, \tilde{v})$. To characterize the linear stability properties of steady states, we define:

$$\Gamma := R^+ \times R^+ \times R^+ \times R^+ \qquad \text{and} \qquad R^+ = (0, \infty),$$

and

$$\Sigma_u := \{(d_1, \alpha_1, d_2, \alpha_2) \in \Gamma : (\tilde{u}, 0) \text{ is linearly stable}\},$$

$$\Sigma_v := \{(d_1, \alpha_1, d_2, \alpha_2) \in \Gamma : (0, \tilde{v}) \text{ is linearly stable}\},$$

$$\tilde{\Sigma}_u := \{(d_1, \alpha_1, d_2, \alpha_2) \in \Gamma : (\tilde{u}, 0) \text{ is neutrally stable}\},$$

$$\tilde{\Sigma}_v := \{(d_1, \alpha_1, d_2, \alpha_2) \in \Gamma : (0, \tilde{v}) \text{ is neutrally stable}\},$$

$$\tilde{\Sigma}_u^v := \tilde{\Sigma}_u \cap \tilde{\Sigma}_v,$$

$$\Sigma_o := \{(d_1, \alpha_1, d_2, \alpha_2) \in \Gamma : (\tilde{u}, 0) \text{ and } (0, \tilde{v}) \text{ are linearly unstable}\}.$$

In order to study the stability of semi-trivial steady states, we introduce the following auxiliary eigenvalue problem:

$$\begin{cases} d\varsigma_{xx} - \alpha\varsigma_x + r\varsigma + \tau\varsigma = 0, & 0 < x < L, \\ d\varsigma_x(x) - \alpha\varsigma(x) = b_u \alpha\varsigma(x), & x = 0, \\ d\varsigma_x(x) - \alpha\varsigma(x) = -b_d \alpha\varsigma(x), & x = L, \end{cases} \tag{1.7}$$

where d and α are greater than 0 and r belongs to $L^\infty([0, L])$. By the Krein-Rutman theorem [11], there exists a principal eigenvalue for problem (1.7), which is denoted by $\tau_1(d, \alpha, r)$, and its corresponding eigenfunction $\varsigma_1(d, \alpha, r)$ could be chosen to be strictly positive in $[0, L]$.

Now we state our main results as follows.

Theorem 1.1. *Assume that* (H_1) *and* (H_2) *hold. Let* $(b, c) \in \Pi_{k_0}$. *Then we have the following results:*

(i) *if* $\tau_1(d_1, \alpha_1, m_1) \geq 0$ *and* $\tau_1(d_2, \alpha_2, m_2) \geq 0$, *then* $(0,0)$ *is g.a.s;*

(ii) *if* $\tau_1(d_1, \alpha_1, m_1) \geq 0$ *and* $\tau_1(d_2, \alpha_2, m_2) < 0$, *then* $\Sigma_v = \Gamma$ *and* $(0, \tilde{v})$ *is g.a.s;*

(iii) *if* $\tau_1(d_1, \alpha_1, m_1) < 0$ *and* $\tau_1(d_2, \alpha_2, m_2) \geq 0$, *then* $\Sigma_u = \Gamma$ *and* $(\tilde{u}, 0)$ *is g.a.s;*

(iv) *if* $\tau_1(d_1, \alpha_1, m_1) < 0$ *and* $\tau_1(d_2, \alpha_2, m_2) < 0$, *then we have the following mutually disjoint decomposition of* Γ

$$\Gamma = (\Sigma_u \cup \tilde{\Sigma}_u \backslash \tilde{\Sigma}_u^v) \cup (\Sigma_v \cup \tilde{\Sigma}_v \backslash \tilde{\Sigma}_u^v) \cup \Sigma_o \cup \tilde{\Sigma}_u^v. \tag{1.8}$$

In particular,

$$(d_1, \alpha_1, d_2, \alpha_2) \in \tilde{\Sigma}_u^v \ \text{if and only if} \ \frac{\alpha_1}{d_1} = \frac{\alpha_2}{d_2}, \qquad bc = 1 \ \text{and} \ \frac{\tilde{u}}{\tilde{v}} \equiv b,$$

and the following statements are valid for system (1.2)*:*

(iv_1) *For all* $(d_1, \alpha_1, d_2, \alpha_2) \in (\Sigma_u \cup \tilde{\Sigma}_u \backslash \tilde{\Sigma}_u^v)$, $(\tilde{u}, 0)$ *is g.a.s;*

(iv_2) *For all* $(d_1, \alpha_1, d_2, \alpha_2) \in (\Sigma_v \cup \tilde{\Sigma}_v \backslash \tilde{\Sigma}_u^v)$, $(0, \tilde{v})$ *is g.a.s;*

(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 g.a.s;*

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

$$\{(\varrho\tilde{u}, (1-\varrho)\tilde{u}/b : \varrho \in [0,1])\}$$

connecting the two semi-trivial steady states;

where g.a.s means that the steady state is globally asymptotically stable among all non-negative and nontrivial initial conditions.

Remark 1.2. *We present a complete classification on all possible global dynamical behaviors of system* (1.2) *in Theorem* 1.1. *In* [25], *Xu et al. made a complete classification on the global dynamics of system* (1.2) *by assuming random diffusion rates and advection rates satisfying* $\alpha_1/d_1 = \alpha_2/d_2$. *Zhou et al* [29] *and Guo et al* [6] *displayed a similar complete classification in higher spatial dimensions and a closed environment, i.e.,* $b_u = b_d = 0$. *Here, we get rid of the condition that* $\alpha_1/d_1 = \alpha_2/d_2$ *and consider a more general boundary condition.*

It is highly challenging to precisely describe the geometric property of the sets Σ_u, Σ_v, $\tilde{\Sigma}_u$, $\tilde{\Sigma}_v$, $\tilde{\Sigma}_u^v$ and Σ_o. To investigate this issue further, we next turn to discuss the special case $m_1(x) = m_2(x) := m(x)$, that is:

$$\begin{cases} u_t = d_1 u_{xx} - \alpha_1 u_x + u[m(x) - u - bv], & 0 < x < L,\ t > 0, \\ v_t = d_2 v_{xx} - \alpha_2 v_x + v[m(x) - cu - v], & 0 < x < L,\ t > 0, \\ d_1 u_x(x,t) - \alpha_1 u(x,t) = b_u \alpha_1 u(x,t), & x = 0,\ t > 0, \\ d_1 u_x(x,t) - \alpha_1 u(x,t) = -b_d \alpha_1 u(x,t), & x = L,\ t > 0, \\ d_2 v_x(x,t) - \alpha_2 v(x,t) = b_u \alpha_2 v(x,t), & x = 0,\ t > 0, \\ d_2 v_x(x,t) - \alpha_2 v(x,t) = -b_d \alpha_2 v(x,t), & x = L,\ t > 0, \\ u(x,0) = u_0 \geq, \not\equiv 0, \quad v(x,0) = v_0 \geq, \not\equiv 0, & 0 < x < L. \end{cases} \tag{1.9}$$

Set

$$\beta_1 = \frac{d_1}{d_2} \qquad \text{and} \qquad \beta_2 = \frac{\alpha_1}{\alpha_2}.$$

For system (1.9), by using β_1, β_2 and b as variable parameters with others fixed, we obtain a more clear picture on the global dynamics as follows. Since the case of $\beta_1 = \beta_2$ has been studied in [26], we only consider $\beta_1 \neq \beta_2$.

Theorem 1.3. *Assume that* (H_1) *and* (H_2) *hold. For every* $b_d \geq 1/2$, *there exists* $\alpha_1^* > 0$ *and* $\alpha_2^* > 0$ *such that*

(i) *case* 1: $\beta_2 > \beta_1 > 1$,
 (i$_1$) *if* $\alpha_2 < \alpha_2^*$ *and* $\alpha_1^* < \alpha_1$, *then when* $(b,c) \in ((0,1] \times (0,1]) \cap \Pi_{k_0}$, $(0,\tilde{v})$ *is g.a.s;*
 (i$_2$) *if* $\alpha_2 > \alpha_2^*$, *then when* $(b,c) \in ((0,1] \times (0,1]) \cap \Pi_{k_0}$, $(0,0)$ *is g.a.s;*
 (i$_3$) *if* $\alpha_1 < \alpha_1^*$, *there exists* $b^* \in (0,1)$ *such that when* $(b,c) \in ([b^*,1] \times (0,1]) \cap \Pi_{k_0}$, $(0,\tilde{v})$ *is g.a.s, and system* (1.2) *has a unique coexistence steady state that is g.a.s when* $(b,c) \in ((0,b^*), \times(0,1]) \cap \Pi_{k_0}$.

(ii) *case* 2: $0 < \beta_2 < \beta_1 < 1$,
 (ii$_1$) *if* $\alpha_1 < \alpha_1^*$ *and* $\alpha_2^* < \alpha_2$, *then when* $(b,c) \in ((0,1] \times (0,1]) \cap \Pi_{k_0}$, $(\tilde{u},0)$ *is g.a.s;*
 (ii$_2$) *if* $\alpha_1 > \alpha_1^*$, *then when* $(b,c) \in ((0,1] \times (0,1]) \cap \Pi_{k_0}$, $(0,0)$ *is g.a.s;*
 (ii$_3$) *if* $\alpha_2 < \alpha_2^*$, *there exists* $c^* \in (0,1)$ *such that when* $(b,c) \in ((0,1] \times [c^*,1]) \cap \Pi_{k_0}$, $(\tilde{u},0)$ *is g.a.s, and system* (1.2) *has a unique coexistence steady state that is g.a.s when* $(b,c) \in ((0,1] \times (0,c^*)) \cap \Pi_{k_0}$.

Moreover, the formulas for b^* *and* c^* *are as follows*

$$b^* = \inf_{0 \neq \sigma \in H^1(0,L)} \frac{\int_0^L (d_1 \sigma_x^2 e^{(\alpha_1/d_1)x} - m\sigma^2 e^{(\alpha_1/d_1)x})dx + b_d \alpha_1 e^{(\alpha_1/d_1)L} \sigma^2(L) + b_u \alpha_1 \sigma^2(0)}{\int_0^L \tilde{v} e^{(\alpha_1/d_1)x} \sigma^2 \, dx},$$

and

$$c^* = \inf_{0 \neq \sigma \in H^1(0,L)} \frac{\int_0^L (d_2 \sigma_x^2 e^{(\alpha_2/d_2)x} - m\sigma^2 e^{(\alpha_2/d_2)x})dx + b_d \alpha_2 e^{(\alpha_2/d_2)L} \sigma^2(L) + b_u \alpha_2 \sigma^2(0)}{\int_0^L \tilde{u} e^{(\alpha_2/d_2)x} \sigma^2 \, dx}.$$

Remark 1.4. *By the subscripts of* α_1^* *and* α_2^*, *we mean that the values of* α_1^* *and* α_2^* *depend on* d_1 *and* d_2, *respectively. Indeed, if* $\beta_2 > \beta_1 > 1$, *the condition* $\alpha_2 < \alpha_2^*$ *in* (i$_1$) *means that* $\alpha_2 < \min\{\alpha_2^*, \alpha_1\}$ *and we can explain* (ii$_1$) *in the same way. In Theorem* 1.2, *we discuss the global dynamics of system* (1.2) *for the cases of* $\beta_2 > \beta_1 > 1$ *and* $0 < \beta_2 < \beta_1 < 1$. *Xu et al* [26] *explored the situation where* $\beta_2 = \beta_1$. *For the other cases, it is more complex to investigate and we leave these questions.*

Remark 1.5. *From a biological point of view, we make some interpretations for Theorem* 1.2. *For statement* (i), *when* $\beta_2 > \beta_1 > 1$, *statement* (i$_1$) *shows that if species v can persist in the long run while species u cannot persist without competition, then during the competition species v is in a good position and would finally take place of species u. Statement* (i$_2$) *suggests that if* $(\tilde{u}, 0)$ *and* $(0, \tilde{v})$ *do not exist without competition, then when competition is involved both species u and v will go extinct. Statement* (i$_3$) *reveals that species v is more competitive than species u in the sense that either it wipes out u completely in the final or coexists with u eventually. Moreover, whether the inter-specific competition intensity b crosses over a critical number* b^* *which is in* $(0, 1)$ *determines if species v will wipe out u eventually or coexist with u. For statement* (ii), *we can have the similar explanations.*

The rest of this paper is organized as follows. In Section 2, we present some preliminary results which will be used in verifying our results. Section 3 is devoted to establishing Theorem 1.1. In Section 4, we mainly prove Theorem 1.2. Some numerical simulations are performed in Section 5 to support and verify the theoretical results. Finally, a short discussion then completes this paper.

2. Preliminaries

Recall that $\tau_1(d, \alpha, r)$ is the principal eigenvalue of problem (1.7). By the variational approach, if $0 \le b_u, b_d < \infty$, then

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

if $b_u = b_d = \infty$, then

$$\tau_1(d, \alpha, r) = \inf_{\phi \in \mathscr{S}} \frac{\int_0^L (d\phi_x^2 e^{(\alpha/d)x} - r\phi^2 e^{(\alpha/d)x})dx}{\int_0^L e^{(\alpha/d)x} \phi^2 \, dx},$$

where $\mathscr{S} := \{\varsigma \in H^1(0,L) \mid \varsigma(0) = \varsigma(L) = 0,\ \varsigma \not\equiv 0\}$; if $b_u = \infty$ and $0 \le b_d < \infty$, then

$$\tau_1(d,\alpha,r) = \inf_{\phi \in \mathscr{S}_1} \frac{\int_0^L (d\phi_x^2 e^{(\alpha/d)x} - r\phi^2 e^{(\alpha/d)x})dx + b_d \alpha e^{\alpha L/d}\phi^2(L)}{\int_0^L e^{(\alpha/d)x}\phi^2\, dx}, \tag{2.1}$$

where $\mathscr{S}_1 := \{\varsigma \in H^1(0,L) \mid \varsigma(0) = 0,\ \varsigma \not\equiv 0\}$; and if $b_d = \infty$ and $0 \le b_u < \infty$, then

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

where $\mathscr{S}_2 := \{\varsigma \in H^1(0,L) \mid \varsigma(L) = 0,\ \varsigma \not\equiv 0\}$.

In order to prove Theorem 1.1, it is needed to introduce the following eigenvalue problem.

Let $\mu_1(a(x), q(x))$ be the principal eigenvalue of the following eigenvalue problem:

$$\begin{cases} (a(x)\varphi_x)_x + q(x)\varphi + \mu\varphi = 0, & 0 < x < L, \\ a(x)\varphi_x(x) = b_u \varphi(x), & x = 0, \\ a(x)\varphi_x(x) = -b_d \varphi(x), & x = L, \end{cases} \tag{2.2}$$

where $a \in \mathscr{C}^{1,\gamma}([0,L])$ is a positive function on $[0,L]$. Then we have the following variational characterization of $\mu_1(a(x), q(x))$:

$$\mu_1(a,q) = \inf_{0 \ne \phi \in H_1(0,L)} \frac{\int_0^L (a\phi x^2 - q\phi^2)dx + b_u\phi^2(0) + b_d\phi^2(L)}{\int_0^L \phi^2\, dx};$$

similarly, if $b_u = b_d = \infty$, then

$$\mu_1(a,q) = \inf_{0 \ne \phi \in \mathscr{H}(0,L)} \frac{\int_0^L (a\phi_x^2 - q\phi^2)dx}{\int_0^L \phi^2\, dx}, \tag{2.3}$$

where $\mathscr{H} := \{\varphi \in H_1(0,L) \mid \varphi(0) = \varphi(L) = 0\}$, moreover, if $b_u = \infty$ and $0 \le b_d < \infty$ and $b_u = \infty$ and $0 \le b_d < \infty$, in view of the variational characterizations of $\tau_1(d,\alpha,r)$, the variational characterizations of $\mu_1(a(x), q(x))$ can be obtained correspondingly.

Since system (1.2) generates a monotone dynamical system, It is useful to display the following lemma which is derived from the theory of monotone dynamical systems [10].

Lemma 2.1. *The following statements on system* (1.2) *are true:*

(i) *If system* (1.2) *has no coexistence steady state, then one of the semi-trivial steady state is unstable and the other is globally asymptotically stable;*

(ii) *If both semi-trivial steady states are unstable, then there is at least one stable coexistence steady state; moreover, if every coexistence steady state is asymptotically stable, then there exists a unique coexistence steady state which is globally asymptotically stable;*

(iii) *If every coexistence steady state is asymptotically stable, then either there exists a unique coexistence steady state which is globally asymptotically stable or there are no coexistence steady state and one of the semi-trivial steady state is unstable and the other is globally asymptotically stable.*

For linear stability of the trivial steady state $(0,0)$ and the two semi-trivial steady states $(\tilde{u},0)$ and $(0,\tilde{v})$ of system (1.2), we have the following relatively simple criterion.

Lemma 2.2. *The linear stability of $(\tilde{u},0)$, $(0,\tilde{v})$ and $(0,0)$ in system (1.2) are determined by the sign of $\tau_1(d_2,\alpha_2,m_2-c\tilde{u})$, $\tau_1(d_1,\alpha_1,m_1-b\tilde{v})$ and $\min\{\tau_1(d_1,\alpha_1,m_1),\tau_1(d_2,\alpha_2,m_2)\}$ respectively.*

The proof follows essentially from the same arguments as in that of [[12], Corollary 2.10] and therefore is omitted here.

We include some properties of $\tau_1(d,\alpha,r)$.

Lemma 2.3 (Monotonicity). *Assume that (H_2) holds. For given $d,\alpha>0$ and r in $L^\infty([0,L])$, the following statements on $\tau_1(d,\alpha,r)$ are true:*

(i) *If $r_1(x)\le,\not\equiv r_2(x)$ in $[0,L]$, then $\tau_1(d,\alpha,r_1)>\tau_1(d,\alpha,r_2)$;*

(ii) *$\tau_1(d,\alpha,r)$, as a function of α, is strictly monotonically increasing provided $b_d\ge\frac{1}{2}$.*

Proof. Statement (i) was proved in [2].

We next verify statement (ii) by using some idea from [7].

By the transformation $\varsigma=e^{(\alpha/d)x}\bar{\varsigma}$, the equation (1.7) becomes

$$\begin{cases} d\bar{\varsigma}_{xx}+\alpha\bar{\varsigma}_x+r\bar{\varsigma}+\tau_1\bar{\varsigma}=0, & 0<x<L,\\ d\bar{\varsigma}_x(x)=b_u\alpha\bar{\varsigma}(x), & x=0,\\ d\bar{\varsigma}_x(x)=-b_d\alpha\bar{\varsigma}(x), & x=L, \end{cases} \tag{2.4}$$

where $\bar{\varsigma}>0$ is uniquely determined by $\|\bar{\varsigma}\|^2_{L^2(0,L)}=1$. Let $\frac{\partial}{\partial\alpha}={}'$ denote differentiation with respect to α. Differentiating (2.4), we obtain

$$\begin{cases} d\bar{\varsigma}'_{xx}+\bar{\varsigma}_x+\alpha\bar{\varsigma}'_x+r\bar{\varsigma}'+\tau_1'\bar{\varsigma}+\tau_1\bar{\varsigma}'=0, & 0<x<L,\\ d\bar{\varsigma}'_x(x)=b_u\bar{\varsigma}(x)+b_u\alpha\bar{\varsigma}'(x), & x=0,\\ d\bar{\varsigma}'_x(x)=-b_d\bar{\varsigma}(x)-b_d\alpha\bar{\varsigma}'(x), & x=L. \end{cases} \tag{2.5}$$

Next, multiplying (2.4) by $e^{(\alpha/d)x}\bar{\varsigma}'$ and (2.5) by $e^{(\alpha/d)x}\bar{\varsigma}$, and then subtracting and integrating the resulting equations, one obtains

$$d[e^{(\alpha/d)x}\bar{\varsigma}_x'\bar{\varsigma}|_0^L - e^{(\alpha/d)x}\bar{\varsigma}'\bar{\varsigma}_x|_0^L] + \int_0^L e^{(\alpha/d)x}\bar{\varsigma}_x\bar{\varsigma}\,dx = -\tau_1'\int_0^L e^{(\alpha/d)x}\bar{\varsigma}^2\,dx.$$

Using the integration by parts and the boundary conditions, one obtains

$$-b_d e^{(\alpha/d)L}\bar{\varsigma}^2(L) - b_u\bar{\varsigma}^2(0) + e^{(\alpha/d)L}\frac{\bar{\varsigma}^2(L)}{2} - \frac{\bar{\varsigma}^2(0)}{2} - \frac{\alpha}{d}\int_0^L e^{(\alpha/d)x}\frac{\bar{\varsigma}^2}{2}\,dx$$
$$= -\tau_1'\int_0^L e^{(\alpha/d)x}\bar{\varsigma}^2\,dx,$$

from which we can further deduce that

$$\tau_1' = \frac{b_d e^{(\alpha/d)L}\bar{\varsigma}^2(L) + b_u\bar{\varsigma}^2(0) - e^{(\alpha/d)L}\frac{\bar{\varsigma}^2(L)}{2} + \frac{\bar{\varsigma}^2(0)}{2} + \frac{\alpha}{d}\int_0^L e^{(\alpha/d)x}\frac{\bar{\varsigma}^2}{2}\,dx}{\int_0^L e^{(\alpha/d)x}\bar{\varsigma}^2\,dx},$$

which, in view of $b_d \geq \frac{1}{2}$, implies $\tau_1' > 0$, as desired.

Lemma 2.4 (Limiting Behavior). *Assume that assumption (H_2) holds. For given $d, \alpha > 0$ and r in $L^\infty([0,L])$, we have*

(i) $\lim_{\alpha\to 0}\tau_1(d,\alpha,r) = \tau_1(d,0,r) < 0$;

(ii) $\lim_{\alpha\to\infty}\tau_1(d,\alpha,r) = +\infty$.

Proof. Clearly, $\tau_1(d,0,r) < 0$ follows directly from the positivity of $r(x)$. Next we prove $\lim_{\alpha\to\infty}\tau_1(d,\alpha,r) = +\infty$.

By variational representation of $\tau_1(d,\alpha,r)$ and a transformation $\phi = e^{-l(\alpha/d)x}\vartheta$, where l is a positive number to be determined later, we see

$$\tau_1 = \inf_{0\neq\vartheta\in H^1(0,L)}\left\{\frac{\int_0^L d\vartheta_x^2 e^{(1-2l)(\alpha/d)x} + \frac{\alpha^2 l^2}{d}\int_0^L \vartheta^2 e^{(1-2l)(\alpha/d)x}\vartheta^2\,dx}{\int_0^L e^{(1-2l)(\alpha/d)x}\vartheta^2\,dx}\right.$$
$$+\frac{b_d\alpha e^{(1-2l)(\alpha/d)L}\vartheta^2(L) + b_u\alpha\vartheta^2(0)}{\int_0^L e^{(1-2l)(\alpha/d)x}\vartheta^2\,dx}$$
$$\left.-\frac{\alpha l\int_0^L e^{(1-2l)(\alpha/d)x}(\vartheta^2)_x dx + \int_0^L r(x)\vartheta^2 e^{(1-2l)(\alpha/d)x}\,dx}{\int_0^L e^{(1-2l)(\alpha/d)x}\vartheta^2\,dx}\right\}$$
$$= \inf_{0\neq\vartheta\in H^1(0,L)}\left\{\frac{\int_0^L d\vartheta_x^2 e^{(1-2l)(\alpha/d)x} + \frac{\alpha^2 l^2}{d}\int_0^L \vartheta^2 e^{(1-2l)(\alpha/d)x}\vartheta^2\,dx}{\int_0^L e^{(1-2l)(\alpha/d)x}\vartheta^2\,dx}\right.$$
$$+\frac{b_d\alpha e^{(1-2l)(\alpha/d)L}\vartheta^2(L) + b_u\alpha\vartheta^2(0)}{\int_0^L e^{(1-2l)(\alpha/d)x}\vartheta^2\,dx}$$

$$
- \frac{\alpha l e^{(1-2l)(\alpha/d)L}\vartheta^2(L) - \alpha l \vartheta^2(0) - l(1-2l)\frac{\alpha^2}{d}\int_0^L e^{(1-2l)(\alpha/d)x}\vartheta^2\,dx}{\int_0^L e^{(1-2l)(\alpha/d)x}\vartheta^2\,dx}
$$

$$
\left. - \frac{\int_0^L r(x)\vartheta^2 e^{(1-2l)(\alpha/d)x}\,dx}{\int_0^L e^{(1-2l)(\alpha/d)x}\vartheta^2\,dx} \right\}
$$

$$
= \inf_{0 \neq \vartheta \in H^1(0,L)} \left\{ \frac{[b_d - l]\alpha e^{(1-2l)(\alpha/d)L}\vartheta^2(L) + [l - l^2]\frac{\alpha^2}{d}\int_0^L e^{(1-2l)(\alpha/d)x}\vartheta^2\,dx}{\int_0^L e^{(1-2l)(\alpha/d)x}\vartheta^2\,dx} \right.
$$

$$
\left. + \frac{\int_0^L d\vartheta_x^2 e^{(1-2l)(\alpha/d)x} + \alpha l \vartheta^2(0) + b_u \alpha \vartheta^2(0)}{\int_0^L e^{(1-2l)(\alpha/d)x}\vartheta^2\,dx} - \frac{\int_0^L r(x)\vartheta^2 e^{(1-2l)(\alpha/d)x}\,dx}{\int_0^L e^{(1-2l)(\alpha/d)x}\vartheta^2\,dx} \right\}
$$

$$
\geq [l - l^2]\frac{\alpha^2}{d} - \max_{x \in [0,L]} r(x),
$$

provided $0 < l < \min\{b_d, 1\}$. The desired result would then follow by sending $\alpha \to +\infty$.

3. Proof of Theorem 1.1

Suppose that (U, V) is a coexistence steady state of system (1.2), then $U, V > 0$ in $[0, L]$ and satisfy

$$
\begin{cases}
d_1 U_{xx} - \alpha_1 U_x + U[m_1(x) - U - bV] = 0, & 0 < x < L, \\
d_2 V_{xx} - \alpha_2 V_x + U[m_2(x) - cU - V] = 0, & 0 < x < L, \\
d_1 U_x(x) - \alpha_1 U(x) = b_u \alpha_1 U(x), & x = 0, \\
d_1 U_x(x) - \alpha_1 U(x) = -b_d \alpha_1 U(x), & x = L, \\
d_2 V_x(x) - \alpha_2 V(x) = b_u \alpha_2 V(x), & x = 0, \\
d_2 V_x(x) - \alpha_2 V(x) = -b_d \alpha_2 V(x), & x = L.
\end{cases} \tag{3.1}
$$

Denote

$$
W = e^{-(\alpha_1/d_1)x} U, \qquad Z = e^{-(\alpha_2/d_2)x} V.
$$

Then (W, Z) satisfies the following system

$$
\begin{cases}
(d_1 e^{(\alpha_1/d_1)x} W_x)_x + W(e^{(\alpha_1/d_1)x} m_1 - e^{2(\alpha_1/d_1)x} W \\
\quad - b e^{(\alpha_1/d_1)x + (\alpha_2/d_2)x} Z) = 0, & 0 < x < L, \\
(d_2 e^{(\alpha_2/d_2)x} Z_x)_x + Z(e^{(\alpha_2/d_2)x} m_2 - c e^{(\alpha_1/d_1)x + (\alpha_2/d_2)x} W \\
\quad - e^{2(\alpha_2/d_2)x} Z) = 0, & 0 < x < L, \\
d_1 W_x(x) = b_u \alpha_1 W(x), \quad d_2 Z_x(x) = b_u \alpha_2 Z(x), & x = 0, \\
d_1 W_x(x) = -b_d \alpha_1 W(x), \quad d_2 Z_x(x) = -b_d \alpha_2 Z(x), & x = L.
\end{cases} \tag{3.2}
$$

Recall $(\tilde{u}, 0)$ and $(0, \tilde{v})$ are two semi-trivial steady states of system (1.2). Denote

$$\tilde{w} = e^{-(\alpha_1/d_1)x}\tilde{u}, \qquad \tilde{z} = e^{-(\alpha_2/d_2)x}\tilde{v}.$$

Then $\tilde{w}$ satisfies the following system

$$\begin{cases} (d_1 e^{(\alpha_1/d_1)x}\tilde{w}_x)_x + \tilde{w}(e^{(\alpha_1/d_1)x}m_1(x) - e^{2(\alpha_1/d_1)x}\tilde{w}) = 0, & 0 < x < L, \\ d_1\tilde{w}_x(x) = b_u\alpha_1\tilde{w}(x), & x = 0, \\ d_1\tilde{w}_x(x) = -b_d\alpha_1\tilde{w}(x), & x = L, \end{cases} \tag{3.3}$$

and $\tilde{z}$ satisfies the following system

$$\begin{cases} (d_2 e^{(\alpha_2/d_2)x}\tilde{z}_x)_x + \tilde{z}(e^{(\alpha_2/d_2)x}m_2(x) - e^{2(\alpha_2/d_2)x}\tilde{z}) = 0, & 0 < x < L, \\ d_2\tilde{z}_x(x) = b_u\alpha_2\tilde{z}(x), & x = 0, \\ d_2\tilde{z}_x(x) = -b_d\alpha_2\tilde{z}(x), & x = L. \end{cases} \tag{3.4}$$

Then we get to study the following system

$$\begin{cases} w_t = (d_1 e^{(\alpha_1/d_1)x}w_x)_x + w(e^{(\alpha_1/d_1)x}m_1 - e^{2(\alpha_1/d_1)x}w - be^{(\alpha_1/d_1)x+(\alpha_2/d_2)x}z), \\ \quad 0 < x < L,\ t > 0, \\ z_t = (d_2 e^{(\alpha_2/d_2)x}z_x)_x + z(e^{(\alpha_2/d_2)x}m_2 - ce^{(\alpha_1/d_1)x+(\alpha_2/d_2)x}w - e^{2(\alpha_2/d_2)x}z), \\ \quad 0 < x < L,\ t > 0, \\ d_1 w_x(x,t) = b_u\alpha_1 w(x,t), \quad d_2 z_x(x,t) = b_u\alpha_2 z(x,t), \\ \quad x = 0,\ t > 0, \\ d_1 w_x(x,t) = -b_d\alpha_1 w(x,t), \quad d_2 z_x(x,t) = -b_d\alpha_2 z(x,t), \\ \quad x = L,\ t > 0, \end{cases} \tag{3.5}$$

from above discussion, it is clear that (W, Z) is a coexistence steady state of system (3.5) and $(\tilde{w}, 0)$ and $(0, \tilde{z})$ are semi-trivial steady states of system (3.5).

Similarly, we can denote Σ_w, Σ_z, $\tilde{\Sigma}_w$, $\tilde{\Sigma}_z$, and $\tilde{\Sigma}_w^z$.

For $(\tilde{w}, 0)$ and $(0, \tilde{z})$, we have the following results which can be demonstrated in the same way as in [[12], Corollary 2.10].

Lemma 3.1. *The linear stability of* $(\tilde{w}, 0)$, $(0, \tilde{z})$ *and* $(0, 0)$ *of system* (3.5) *are determined by the sign of* $\mu_1(d_2 e^{\alpha_2 x/d_2}, e^{\alpha_2 x/d_2}m_2 - ce^{\alpha_1 x/d_1 + \alpha_2 x/d_2}\tilde{w})$, $\mu_1(d_1 e^{\alpha_1 x/d_1}, e^{\alpha_1 x/d_1}m_1 - be^{\alpha_1 x/d_1 + \alpha_2 x/d_2}\tilde{v})$ *and* $\min\{\mu_1(d_1 e^{\alpha_1 x/d_1}, e^{\alpha_1 x/d_1}m_1), \mu_1(d_2 e^{\alpha_2 x/d_2}, e^{\alpha_2 x/d_2}m_2)\}$, *respectively.*

Proof of Theorem 1.1. It is clear that the existence of semi-trivial steady state $(\tilde{u}, 0)$ if and only if $\tau_1(d_1, \alpha_1, m) < 0$ and the semi-trivial steady state $(0, \tilde{v})$ exists if and only if $\tau_1(d_2, \alpha_2, m) < 0$. In statement (i), both semi-trivial steady states do not exist; in statement (ii), only $(0, \tilde{v})$ exists; and in statement (iii), only $(\tilde{u}, 0)$ exists. The dynamics in these three statements can be obtained by using the standard upper and lower solution methods; see [[32], Lemma 5.1].

Next we prove statements (iv).

By transformation, to investigate the linear stability of $(\tilde{u}, 0)$, $(0, \tilde{v})$ and (U, V), we only need to investigate the linear stability of $(\tilde{w}, 0)$, $(0, \tilde{z})$ and (W, Z). We employ similar arguments in [6] to complete the proof of Theorem 1.1.

Linearizing the steady state problem (3.2) at (W, Z), we have

$$\begin{cases} (d_1 e^{(\alpha_1/d_1)x}\Phi_x)_x + \Phi(e^{(\alpha_1/d_1)x}m_1 - e^{2(\alpha_1/d_1)x}W \\ \quad - be^{(\alpha_1/d_1)x+(\alpha_2/d_2)x}Z) - W(e^{2(\alpha_1/d_1)x}\Phi \\ \quad + be^{(\alpha_1/d_1)x+(\alpha_2/d_2)x}\Psi) + \eta\Phi = 0, & 0 < x < L, \\ (d_2 e^{(\alpha_2/d_2)x}\Phi_x)_x + \Psi(e^{(\alpha_2/d_2)x}m_2 - ce^{(\alpha_1/d_1)x+(\alpha_2/d_2)x}W \\ \quad - e^{2(\alpha_2/d_2)x}Z) - Z(ce^{(\alpha_1/d_1)x+(\alpha_2/d_2)x}\Phi + e^{2(\alpha_2/d_2)x}\Psi) \\ \quad + \eta\Psi = 0, & 0 < x < L, \\ d_1\Phi_x(x) = b_u\alpha_1\Phi(x), \quad d_2\Psi_x(x) = b_u\alpha_2\Psi(x), & x = 0, \\ d_1\Phi_x(x) = -b_d\alpha_1\Phi(x), \quad d_2\Psi_x(x) = -b_d\alpha_2\Psi(x), & x = L, \end{cases} \tag{3.6}$$

by the Krein-Rutman theorem [11] again, there is a principal eigenvalue to system (3.6) denoted by η_1, and its corresponding eigenfunctions (Φ_1, Ψ_1) can be chosen to satisfy $\Phi_1 > 0 > \Psi_1$ in $(0, L)$.

Now we establish the a priori estimate regarding the linear stability of the coexistence steady state of system (3.2): for every $(d_1, \alpha_1, d_2, \alpha_2)$ in $\Gamma \backslash \tilde{\Sigma}_w^z$, every coexistence steady state of system (1.2), if it exists, is linearly stable. It suffices to show $\eta_1 > 0$ when $(d_1, \alpha_1, d_2, \alpha_2)$ is in $\Gamma \backslash \tilde{\Sigma}_w^z$.

Multiplying the first equation in (3.6) by W, the first equation in (3.2) by Φ_1, and subtracting the resulting equations, one then finds

$$\left(d_1 e^{(\alpha_1/d_1)x} W^2 \left(\frac{\Phi_1}{W}\right)_x\right)_x = W^2(e^{2(\alpha_1/d_1)x}\Phi_1 + be^{(\alpha_1/d_1)x+(\alpha_2/d_2)x}\Psi_1) - \eta_1 W\Phi_1.$$

Multiplying both sides of the above equality by $\frac{\Phi_1^2}{W^2}$ and integrating over $(0, L)$, we obtain

$$\begin{aligned} d_1 e^{(\alpha_1/d_1)x} W^2 \left(\frac{\Phi_1}{W}\right)_x \frac{\Phi_1^2}{W^2}\bigg|_0^L - 2\int_0^L d_1 e^{(\alpha_1/d_1)x} W\Phi_1 \left(\frac{\Phi_1}{W}\right)_x^2 dx \\ = \int_0^L \Phi_1^2(e^{2(\alpha_1/d_1)x}\Phi_1 + be^{(\alpha_1/d_1)x+(\alpha_2/d_2)x}\Psi_1)dx - \eta_1 \int_0^L \frac{\Phi_1^3}{W}\, dx. \end{aligned}$$

By the boundary conditions

$$
\begin{aligned}
&d_1 e^{(\alpha_1/d_1)x} W^2 \left(\frac{\Phi_1}{W}\right)_x \frac{\Phi_1^2}{W^2}\bigg|_0^L \\
&\quad = d_1 e^{(\alpha_1/d_1)L} W^2(L) \frac{\Phi_{1x}(L)W(L) - \Phi_1(L)W_x(L)}{W^2(L)} \frac{\Phi_1^2(L)}{W^2(L)} \\
&\qquad - d_1 W^2(0) \frac{\Phi_{1x}(0)W(0) - \Phi_1(0)W_x(0)}{W^2(0)} \frac{\Phi_1^2(0)}{W^2(0)} \\
&\quad = d_1 e^{(\alpha_1/d_1)L} \left[-\frac{b_d}{d_1}\alpha_1 \Phi_1(L)W(L) + \Phi_1(L)\frac{b_d}{d_1}\alpha_1 W(L)\right] \frac{\Phi_1^2(L)}{W^2(L)} \\
&\qquad - d_1 \left[\frac{b_u}{d_1}\alpha_1 \Phi_1(0)W(0) - \Phi_1 \frac{b_u}{d_1}\alpha_1 W(0)\right] \\
&\quad = 0,
\end{aligned}
$$

then

$$
\begin{aligned}
\eta_1 \int_0^L \frac{\Phi_1^3}{W}\, dx = &\int_0^L \Phi_1^2 (e^{2(\alpha_1/d_1)x}\Phi_1 + b e^{(\alpha_1/d_1)x + (\alpha_2/d_2)x}\Psi_1) dx \\
&+ 2\int_0^L d_1 e^{(\alpha_1/d_1)x} W \Phi_1 \left(\frac{\Phi_1}{W}\right)_x^2 dx.
\end{aligned}
$$

Similarly, we can derive the following identity:

$$
\begin{aligned}
\eta_1 \int_0^L \frac{\Psi_1^3}{Z}\, dx = &\int_0^L \Psi_1^2 (e^{2(\alpha_2/d_2)x}\Phi_1 + c e^{(\alpha_1/d_1)x + (\alpha_2/d_2)x}\Psi_1) dx \\
&+ 2\int_0^L d_2 e^{(\alpha_2/d_2)x} Z \Psi_1 \left(\frac{\Psi_1}{Z}\right)_x^2 dx.
\end{aligned}
$$

Denote $(\bar{\Phi}_1, \bar{\Psi}_1) := (\Phi_1, -\Psi_1)$. It holds that $\bar{\Phi}_1, \bar{\Psi}_1 > 0$ on $[0, L]$. By Hölder's inequality, we have

$$
\begin{aligned}
-\eta_1 \int_0^L \frac{\bar{\Phi}_1^3}{W}\, dx &\le \int_0^L b e^{(\alpha_1/d_1)x + (\alpha_2/d_2)x} \bar{\Phi}_1^2 \bar{\Psi}_1\, dx - \int_0^L e^{2(\alpha_1/d_1)x} \bar{\Phi}_1^3\, dx \\
&\le \int_0^L b e^{(\alpha_1/d_1)x + (\alpha_2/d_2)x} \bar{\Phi}_1^2 \bar{\Psi}_1\, dx \\
&\quad - \min_{x\in[0,L]} e^{(\alpha_1/d_1)x - (\alpha_2/d_2)x} \int_0^L e^{(\alpha_1/d_1)x + (\alpha_2/d_2)x} \bar{\Phi}_1^3\, dx \\
&\le \left(\int_0^L e^{(\alpha_1/d_1)x + (\alpha_2/d_2)x} \bar{\Phi}_1^3\, dx\right)^{2/3} \cdot \min_{x\in[0,L]} e^{(\alpha_1/d_1)x - (\alpha_2/d_2)x}
\end{aligned}
$$

$$\cdot\left[b\max_{x\in[0,L]}e^{(\alpha_1/d_1)x-(\alpha_2/d_2)x}\left(\int_0^L e^{(\alpha_1/d_1)x+(\alpha_2/d_2)x}\bar{\Psi}_1^3\,dx\right)^{1/3}\right.$$
$$\left.-\left(\int_0^L e^{(\alpha_1/d_1)x+(\alpha_2/d_2)x}\bar{\Phi}_1^3\,dx\right)^{1/3}\right] \tag{3.7}$$

and

$$-\eta_1\int_0^L\frac{\bar{\Psi}_1^3}{Z}\,dx\le\int_0^L ce^{(\alpha_1/d_1)x+(\alpha_2/d_2)x}\bar{\Phi}_1\bar{\Psi}_1^2\,dx-\int_0^L e^{2(\alpha_2/d_2)x}\bar{\Psi}_1^3\,dx$$
$$\le\left(\int_0^L e^{(\alpha_1/d_1)x+(\alpha_2/d_2)x}\bar{\Psi}_1^3\,dx\right)^{2/3}\cdot\min_{x\in[0,L]}e^{(\alpha_2/d_2)x-(\alpha_1/d_1)x}$$
$$\cdot\left[c\max_{x\in[0,L]}e^{(\alpha_2/d_2)x-(\alpha_1/d_1)x}\left(\int_0^L e^{(\alpha_1/d_1)x+(\alpha_2/d_2)x}\bar{\Phi}_1^3\,dx\right)^{1/3}\right.$$
$$\left.-\left(\int_0^L e^{(\alpha_1/d_1)x+(\alpha_2/d_2)x}\bar{\Psi}_1^3\,dx\right)^{1/3}\right]. \tag{3.8}$$

Denote

$$\zeta_1=b\max_{x\in[0,L]}e^{(\alpha_1/d_1)x-(\alpha_2/d_2)x}\qquad\text{and}\qquad\zeta_2=c\max_{x\in[0,L]}e^{(\alpha_2/d_2)x-(\alpha_1/d_1)x},$$

then

$$\zeta_1\zeta_2=bc\max_{x\in[0,L]}e^{(\alpha_1/d_1)x-(\alpha_2/d_2)x}\max_{x\in[0,L]}e^{(\alpha_2/d_2)x-(\alpha_1/d_1)x}$$
$$=bc\frac{\max_{x\in[0,L]}e^{(\alpha_1/d_1)x-(\alpha_2/d_2)x}}{\min_{x\in[0,L]}e^{(\alpha_1/d_1)x-(\alpha_2/d_2)x}}.$$

By the assumption that $(b,c)\in\Pi_{k_0}$

$$bc\frac{\max_{x\in[0,L]}e^{(\alpha_1/d_1)x-(\alpha_2/d_2)x}}{\min_{x\in[0,L]}e^{(\alpha_1/d_1)x-(\alpha_2/d_2)x}}\le 1,$$

one sees

$$-\eta_1\left[\frac{\varsigma_2\int_0^L\frac{\bar{\Phi}_1^3}{W}\,dx}{(\int_0^L\bar{\Phi}_1^3\,dx)^{2/3}}+\frac{\int_0^L\frac{\bar{\Psi}_1^3}{Z}\,dx}{(\int_0^L\bar{\Psi}_1^3\,dx)^{2/3}}\right]$$
$$\le\left(bc\frac{\max_{x\in[0,L]}e^{(\alpha_1/d_1)x-(\alpha_2/d_2)x}}{\min_{x\in[0,L]}e^{(\alpha_1/d_1)x-(\alpha_2/d_2)x}}-1\right)\left(\int_0^L\bar{\Psi}_1^3\,dx\right)^{1/3}$$
$$\le 0, \tag{3.9}$$

which implies that $\eta_1\ge 0$.

We next show that $\eta_1 = 0$ could not happen under our assumptions. In fact, $\eta_1 = 0$ if and only if

$$bc = \frac{\min_{x\in[0,L]} e^{(\alpha_1/d_1)x-(\alpha_2/d_2)x}}{\max_{x\in[0,L]} e^{(\alpha_1/d_1)x-(\alpha_2/d_2)x}},$$

and all the above inequalities involved in the proof become equalities. In other words, $\eta_1 = 0$ if and only if

$$\frac{\alpha_1}{d_1} = \frac{\alpha_2}{d_2}, \qquad \bar{\Phi} \propto U \propto \bar{\Psi} \propto V, \qquad bc = 1 \qquad \text{and} \qquad \frac{\bar{\Phi}}{\bar{\Psi}} \equiv b,$$

where $\bar{\Phi} \propto U$ means $\bar{\Phi}/U \equiv \text{const.}$

In addition, if $\eta_1 = 0$, denote $\theta = W/Z$, which is a positive constant. Then W and Z satisfy the following equations:

$$\begin{cases} (d_1 e^{(\alpha_1/d_1)x} W_x)_x + W\big(e^{(\alpha_1/d_1)x} m_1 - e^{2(\alpha_1/d_1)x}\big(1 + b\tfrac{1}{\theta}\big) W\big) & \\ \quad = 0, & 0 < x < L, \\ (d_2 e^{(\alpha_2/d_2)x} Z_x)_x + Z(e^{(\alpha_2/d_2)x} m_2 - e^{2(\alpha_2/d_2)x}(c\theta + 1) Z) & \\ \quad = 0, & 0 < x < L, \\ d_1 W_x(x) = b_u \alpha_1 W(x), \quad d_2 Z_x(x) = b_u \alpha_2 Z(x), & x = 0, \\ d_1 W_x(x) = -b_d \alpha_1 W(x), \quad d_2 Z_x(x) = -b_d \alpha_2 Z(x), & x = L, \end{cases} \tag{3.10}$$

by the uniqueness of positive steady state of single system, we obtain that $\big(1 + b\frac{1}{\theta}\big) W = \tilde{w}$ and $(c\theta + 1) Z = \tilde{z}$. Therefore,

$$\frac{\tilde{w}}{\tilde{z}} = b \qquad \text{and} \qquad W + bZ = \tilde{w}.$$

Then, one can easily check

$$\begin{aligned} &\mu(d_2 e^{(\alpha_2/d_2)x}, e^{(\alpha_2/d_2)x} m_2 - c e^{(\alpha_1/d_1)x + (\alpha_2/d_2)x} \tilde{w}) \\ &\qquad = \mu(d_2 e^{(\alpha_2/d_2)x}, e^{(\alpha_2/d_2)x} m_2 - e^{(\alpha_1/d_1)x + (\alpha_2/d_2)x} \tilde{z}) = 0 \end{aligned}$$

and

$$\begin{aligned} &\mu(d_1 e^{(\alpha_1/d_1)x}, e^{(\alpha_1/d_1)x} m_1 - b e^{(\alpha_1/d_1)x + (\alpha_2/d_2)x} \tilde{z}) \\ &\qquad = \mu(d_1 e^{(\alpha_1/d_1)x}, e^{(\alpha_1/d_1)x} m_1 - e^{(\alpha_1/d_1)x + (\alpha_2/d_2)x} \tilde{w}) = 0, \end{aligned}$$

which contradicts our assumption. Thus, $\eta_1 > 0$.

By the similar way in [6], we can finish the proof of statements (iv_1)–(iv_4) and we omit the details here.

Now we prove the decomposition is mutually disjoint. To prove the disjoint property, by definition, it suffices to show

$$(\Sigma_w \cup \tilde{\Sigma}_w \backslash \tilde{\Sigma}_w^z) \cap (\Sigma_z \cup \tilde{\Sigma}_z \backslash \tilde{\Sigma}_w^z) = \emptyset. \tag{3.11}$$

Multiplying the equation for $\tilde{w}$ by $\tilde{w}$ and integrating over $(0, L)$, we obtain that

$$\begin{aligned}\int_0^L d_1 e^{(\alpha_1/d_1)x} \tilde{w}_x^2 \, dx = \int_0^L & (e^{(\alpha_1/d_1)x} m_1 - e^{2(\alpha_1/d_1)x} \tilde{w}) \tilde{w}^2 \, dx \\ & - b_d \alpha_1 e^{(\alpha_1/d_1)L} \tilde{w}^2(L) - b_u \alpha_1 \tilde{w}^2(0). \end{aligned} \tag{3.12}$$

By (3.12) and Hölder's inequality, choosing $\tilde{w}$ as a test function in the variational characterization for $\mu(d_1 e^{(\alpha_1/d_1)x}, e^{(\alpha_1/d_1)x} m_1 - b e^{(\alpha_1/d_1)x + (\alpha_2/d_2)x} \tilde{z})$, we obtain that

$$\begin{aligned}
&\mu(d_1 e^{(\alpha_1/d_1)x}, e^{(\alpha_1/d_1)x} m_1 - b e^{(\alpha_1/d_1)x + (\alpha_2/d_2)x} \tilde{z}) \\
&\quad = \inf_{0 \neq \phi \in H^1(0,L)} \left(\frac{\int_0^L d_1 e^{(\alpha_1/d_1)x} \phi_x^2 \, dx + \int_0^L (b e^{(\alpha_1/d_1)x + (\alpha_2/d_2)x} \tilde{z} - e^{(\alpha_1/d_1)x} m_1) \phi^2 \, dx}{\int_0^L \phi^2 \, dx} \right. \\
&\qquad \left. + \frac{+ b_u \alpha_1 \phi^2(0) + b_d \alpha_1 \phi^2(L)}{\int_0^L \phi^2 \, dx} \right) \\
&\quad \leq \frac{\int_0^L d_1 e^{(\alpha_1/d_1)x} \tilde{w}_x^2 \, dx + \int_0^L (b e^{(\alpha_1/d_1)x + (\alpha_2/d_2)x} \tilde{z} - e^{(\alpha_1/d_1)x} m_1) \tilde{w}^2 \, dx}{\int_0^L \tilde{w}^2 \, dx} \\
&\quad = \frac{\int_0^L (b e^{(\alpha_1/d_1)x + (\alpha_2/d_2)x} \tilde{z} - e^{2(\alpha_1/d_1)x} \tilde{w}) \tilde{w}^2 \, dx}{\int_0^L \tilde{w}^2 \, dx} \\
&\quad \leq \left(\int_0^L e^{(\alpha_1/d_1)x + (\alpha_2/d_2)x} \tilde{w}^3 \, dx \right)^{2/3} \cdot \min_{x \in [0,L]} e^{(\alpha_1/d_1)x - (\alpha_2/d_2)x} \\
&\qquad \cdot \left[b \max_{x \in [0,L]} e^{(\alpha_1/d_1)x - (\alpha_2/d_2)x} \left(\int_0^L e^{(\alpha_1/d_1)x + (\alpha_2/d_2)x} \tilde{z}^3 \, dx \right)^{1/3} \right. \\
&\qquad \left. - \left(\int_0^L e^{(\alpha_1/d_1)x + (\alpha_2/d_2)x} \tilde{w}^3 \, dx \right)^{1/3} \right] \cdot \int_0^L \tilde{w}^2 \, dx.
\end{aligned} \tag{3.13}$$

Similarly, choosing $\tilde{z}$ as a test function in the variational characterization for $\mu(d_2 e^{(\alpha_2/d_2)x}, e^{(\alpha_2/d_2)x} m_2 - c e^{(\alpha_1/d_1)x + (\alpha_2/d_2)x} \tilde{w})$ and by Hölder's inequality, we obtain that

$$\mu(d_2 e^{(\alpha_2/d_2)x}, e^{(\alpha_2/d_2)x} m_2 - c e^{(\alpha_1/d_1)x+(\alpha_2/d_2)x}\tilde{w})$$
$$\leq \left(\int_0^L e^{(\alpha_1/d_1)x+(\alpha_2/d_2)x}\tilde{z}^3\,dx\right)^{2/3}\cdot \min_{x\in[0,L]} e^{(\alpha_2/d_2)x-(\alpha_1/d_1)x}$$
$$\cdot\left[c\max_{x\in[0,L]} e^{(\alpha_2/d_2)x-(\alpha_1/d_1)x}\left(\int_0^L e^{(\alpha_1/d_1)x+(\alpha_2/d_2)x}\tilde{w}^3\,dx\right)^{1/3}\right.$$
$$\left.-\left(\int_0^L e^{(\alpha_1/d_1)x+(\alpha_2/d_2)x}\tilde{z}^3\,dx\right)^{1/3}\right]\cdot\int_0^L \tilde{z}^2\,dx. \tag{3.14}$$

Following from (3.13) and (3.14), one derives that

$$\frac{\zeta_2\mu(d_1 e^{(\alpha_1/d_1)x}, e^{(\alpha_1/d_1)x} m_1 - b e^{(\alpha_1/d_1)x+(\alpha_2/d_2)x}\tilde{z})\int_0^L \tilde{w}^2\,dx}{(\int_0^L \tilde{w}^3\,dx)^{2/3}}$$
$$+\frac{\mu(d_2 e^{(\alpha_2/d_2)x}, e^{(\alpha_2/d_2)x} m_2 - c e^{(\alpha_1/d_1)x+(\alpha_2/d_2)x}\tilde{w})\int_0^L \tilde{z}^2\,dx}{(\int_0^L \tilde{z}^3\,dx)^{2/3}}$$
$$\leq\left(bc\frac{\max_{x\in[0,L]} e^{(\alpha_1/d_1)x-(\alpha_2/d_2)x}}{\min_{x\in[0,L]} e^{(\alpha_1/d_1)x-(\alpha_2/d_2)x}}-1\right)\left(\int_0^L \tilde{z}^3\,dx\right)^{1/3}\leq 0. \tag{3.15}$$

Then $\mu(d_1 e^{(\alpha_1/d_1)x}, e^{(\alpha_1/d_1)x} m_1 - b e^{(\alpha_1/d_1)x+(\alpha_2/d_2)x}\tilde{z})$ and $\mu(d_2 e^{(\alpha_2/d_2)x}, e^{(\alpha_2/d_2)x} m_2 - c e^{(\alpha_1/d_1)x+(\alpha_2/d_2)x}\tilde{w})$ can not be positive simultaneously.

Then by Lemma 3.1, Theorem 1.1 follows directly from the above statements.

4. Proof of Theorem 1.2

Proof. We first verify that, if $1 < \beta_1 < \beta_2$ and $b_d \geq 1/2$, it holds that $\tau_1(\beta_1 d, \beta_2\alpha, m) > \tau_1(d, \alpha, m)$.

Without loss of generality, we assume that $b_u = \infty$ and $1/2 \leq b_d < \infty$. By the Krein-Rutman theorem [11], there exists a principal eigen-pair $(\tau_1(\beta_1 d, \beta_2\alpha, m), \varsigma_1(\beta_1 d, \beta_2\alpha, m))$ for problem (1.7), where $\varsigma_1(\beta_1 d, \beta_2\alpha, m)$ can be chosen strictly positive on $(0, L]$. For simplicify, we denote $\varsigma_1(\beta_1 d, \beta_2\alpha, m)$ by ς_1. By Lemma 2.3, we have that

$$\tau_1(\beta_1 d, \beta_2\alpha, m) > \tau_1(\beta_1 d, \beta_1\alpha, m).$$

It is obvious that $\tau_1(\beta_1 d, \beta_1\alpha, m)$, ς_1 satisfy

$$\tau_1(\beta_1 d, \beta_1 \alpha, m) = \frac{\int_0^L (\beta_1 d|\varsigma_{1x}|^2 e^{(\alpha/d)x} - m\varsigma_1^2 e^{(\alpha/d)x})dx + b_d \beta_1 \alpha e^{\alpha L/d} \varsigma_1^2(L)}{\int_0^L e^{(\alpha/d)x} \varsigma_1^2 \, dx}$$
$$> \frac{\int_0^L (d|\varsigma_{1x}|^2 e^{(\alpha/d)x} - m\varsigma_1^2 e^{(\alpha/d)x})dx + b_d \alpha e^{\alpha L/d} \varsigma_1^2(L)}{\int_0^L e^{(\alpha/d)x} \varsigma_1^2 \, dx}$$
$$= \tau_1(d, \alpha, m). \tag{4.1}$$

From the above inequalities, one obtains that

$$\tau_1(\beta_1 d, \beta_2 \alpha, m) > \tau_1(d, \alpha, m).$$

Hence, we have

$$\tau_1(d_2, \alpha_2, m) < \tau_1(d_1, \alpha_1, m).$$

When $b_d \geq 1/2$, by Lemma 2.3 (ii) and Lemma 2.4, there exists a critical number $\alpha_i^* > 0$ $(i = 1, 2)$ such that

$$\tau_1(d_i, \alpha_i, m) \begin{cases} < 0, & \text{if } 0 < \alpha < \alpha_i^*, \\ = 0, & \text{if } \alpha = \alpha_i^*, \\ > 0, & \text{if } \alpha > \alpha_i^*. \end{cases}$$

Recall that the semi-trivial steady state $(\tilde{u}, 0)$ exists if and only if $\tau_1(d_1, \alpha_1, m) < 0$ and the semi-trivial steady state $(0, \tilde{v})$ exists if and only if $\tau_1(d_2, \alpha_2, m) < 0$. If $\alpha_2 < \alpha_2^*$ and $\alpha_1^* < \alpha_1$, it holds that $\tau_1(d_2, \alpha_2, m) < 0 \leq \tau_1(d_1, \alpha_1, m)$, then only $(0, \tilde{v})$ exists. If $\alpha_2 > \alpha^*$, we obtain that $\tau_1(d_1, \alpha_1, m) > \tau_1(d_2, \alpha_2, m) > 0$, therefore both semi-trivial steady states do not exist. Statements (i_1) and (i_2) can be obtained by using the standard upper and lower solution method; see [[32], Lemma 5.1].

With regard to statement (i_3), we have $\tau_1(d_2, \alpha_2, m) < \tau_1(d_1, \alpha_1, m) < 0$ if $\alpha_1 < \alpha^*$, that is both $\tilde{u}$ and $\tilde{v}$ exist. Now, we would show that $(\tilde{u}, 0)$ is linearly unstable. It suffices to show that $\tau_1(d_2, \alpha_2, m - c\tilde{u}) < 0$. Actually, by Lemma 2.3, we have

$$\tau_1(d_2, \alpha_2, m - c\tilde{u}) \leq \tau_1(d_2, \alpha_2, m - \tilde{u}) < \tau_1(d_1, \alpha_1, m - \tilde{u}) = 0,$$

which implies that $(\tilde{u}, 0)$ is linearly unstable.

Next, we consider the stability of $(0, \tilde{v})$. It suffices to consider the sign of $\tau_1(d_1, \alpha_1, m - b\tilde{v})$. On the one hand, we have $\tau_1(d_1, \alpha_1, m) < 0$. On the other hand, by (4.2)

$$\tau_1(d_1, \alpha_1, m - \tilde{v}) > \tau_1(d_2, \alpha_2, m - \tilde{v}) = 0,$$

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

$$\tau_1(d_1,\alpha_1,m-b\tilde{v})\begin{cases} <0, & \text{for } b\in(0,b^*),\\ =0, & \text{for } b=b^*,\\ >0, & \text{for } b\in(b^*,1],\end{cases}$$

which implies that for $(b,c)\in(0,b^*)\times(0,1]$, both semi-trivial steady states are linearly unstable and for $(b,c)\in[b^*,1]\times(0,1]$, $(0,\tilde{v})$ is either linearly stable ($(b,c)\in(b^*,1]\times(0,1]$) or neutrally stable ($(b,c)\in\{b^*\}\times(0,1]$), but $(\tilde{u},0)$ is always linearly unstable. By Theorem 1.1 and the assumption that $(b,c)\in\Pi_{k_0}$, statement (i_3) is valid.

If $0<\beta_2<\beta_1<1$ and $b_d\geq 1/2$, it holds that $\tau_1(d_1,\alpha_1,m)>\tau_1(d_2,\alpha_2,m)$. By a similar way, statement (ii) can be established.

Finally we calculate the value of b^*. We know that the stability of $(0,\tilde{v})$ is determined which satisfies the following eigenvalue by the sign of $\tau_1(d_1,\alpha_1,m-b\tilde{v})=0$ problem

$$\begin{cases} d_1\varsigma_{xx}-\alpha_1\varsigma_x+(m-b\tilde{v})\varsigma+\tau_1\varsigma=0, & 0<x<L,\\ d_1\varsigma_x(x)-\alpha_1\varsigma(x)=b_u\alpha_1\varsigma(x), & x=0,\\ d_1\varsigma_x(x)-\alpha_1\varsigma(x)=-b_d\alpha_1\varsigma(x), & x=L,\end{cases} \tag{4.2}$$

rewrite (4.3) (with $b=b^*$ and $\tau_1=0$) as

$$\begin{cases} d_1(\varsigma_0)_{xx}-\alpha_1(\varsigma_0)_x+m\varsigma_0=b^*\tilde{v}\varsigma_0, & 0<x<L,\\ d_1(\varsigma_0)_x(x)-\alpha_1\varsigma_0(x)=b_u\alpha_1\varsigma_0(x), & x=0,\\ d_1(\varsigma_0)_x(x)-\alpha_1\varsigma_0(x)=-b_d\alpha_1\varsigma_0(x), & x=L,\end{cases}$$

where $\varsigma_0>0$ is the corresponding eigenfunction of $\tau_1(d_1,\alpha_1,m-b\tilde{v})=0$, which is uniquely determined by the normalization $\|\varsigma_0\|^2_{L^2(0,L)}=1$.

Let $\overline{\varsigma_0}=\varsigma_0e^{-(\alpha_1/d_1)x}$. Then $\overline{\varsigma_0}$ satisfies

$$\begin{cases} [d_1e^{(\alpha_1/d_1)x}(\overline{\varsigma_0})_x]_x+me^{(\alpha_1/d_1)x}\overline{\varsigma_0}=b^*\tilde{v}e^{(\alpha_1/d_1)x}\overline{\varsigma_0}, & 0<x<L,\\ d_1(\overline{\varsigma_0})_x(x)=b_u\alpha_1\overline{\varsigma_0}(x), & x=0,\\ d_1(\overline{\varsigma_0})_x(x)=-b_d\alpha_1\overline{\varsigma_0}(x), & x=L.\end{cases}$$

By using variational formulation, we obtain

$$b^*=\inf_{0\neq\phi\in H^1(0,L)}\frac{\int_0^L(d_1\phi_x^2e^{(\alpha_1/d_1)x}-m\phi^2e^{(\alpha_1/d_1)x})dx+b_d\alpha_1e^{(\alpha_1/d_1)L}\phi^2(L)+b_u\alpha_1\phi^2(0)}{\int_0^L\tilde{v}e^{(\alpha_1/d_1)x}\phi^2\,dx}.$$

Similarly, we can obtain

$$c^*=\inf_{0\neq\phi\in H^1(0,L)}\frac{\int_0^L(d_2\phi_x^2e^{(\alpha_2/d_2)x}-m\phi^2e^{(\alpha_2/d_2)x})dx+b_d\alpha_2e^{(\alpha_2/d_2)L}\phi^2(L)+b_u\alpha_2\phi^2(0)}{\int_0^L\tilde{u}e^{(\alpha_2/d_2)x}\phi^2\,dx}.$$

The proof of Theorem 1.2 is completed.

5. Numerical simulations

The purpose of this section is to study the global dynamics of system (1.2) via numerical approach. To investigate the effects of dispersal and the inter-specific competition intensities on the competition outcomes, we set other competition conditions to be the same, and hence in the following we assume that

$$b_u = 1, \qquad b_d = \frac{1}{2}, \qquad L = 1.$$

We shall implement the numerical simulations by the Matlab solver with the following initial value

$$(u_0, v_0) = (0.9 + 0.08\cos(\pi x), 0.9 - 0.08\sin(\pi x)).$$

As shown in Theorem 1.2, the critical advection rate α^* plays a significant role in determining the stability of steady states. As we know, the value of α^* changes as the value of $m(x)$ as well as d changes, and our purpose is to investigate the effects of dispersal on the competition outcomes. In order to determine the value of α^*, we shall simply set $m(x) = 1$ and numerically compute by varying the diffusion rates.

From the numerical result, we know that, $\alpha^* = 0.8324$ when $d = 0.6$, $\alpha^* = 0.8164$ when $d = 0.8$ and $\alpha^* = 0.7978$ when $d = 1$. In the following, we divide our numerical simulations into two broad categories: $\beta_2 > \beta_1 > 1$ and $0 < \beta_2 < \beta_1 < 1$. The two broad categories also contain three cases, respectively.

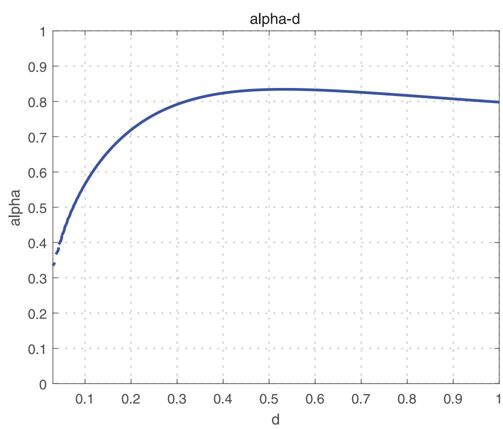

Fig. 5.1. The critical advection rate α^* when d ranges from 0 to 1.

Table 5.1. The values of parameters for simulations:

case	α_1	α_2	k_0	b	c
1	0.9	0.7	0.9753	0.5	0.5
2	1	0.9	0.8824	0.5	0.5
3	0.6	0.4	0.9048	0.8	0.5
	0.6	0.4	0.9048	0.1	0.5

Category I: $\beta_2 > \beta_1 > 1$.

Without loss of generality, we choose $d_1 = 1$ and $d_2 = 0.8$. By the above numerical result of α^*, if $d_1 = 1$ and $d_2 = 0.8$, we can obtain that $\alpha_1^* = 0.7978$ and $\alpha_2^* = 0.8164$.

For case 1: $\alpha_2 < \alpha_2^*$ and $\alpha_1^* < \alpha_1$, the numerical simulations of spatial-temporal patterns and the temporal evolutions for the two competing species are plotted in Figure 5.2. As shown in Figure 5.2, as times goes by, the density of species u tends to 0 and the density of species v converge to corresponding steady states, which imply that, species u will die out eventually and species v will persist in the long run. The numerical simulations shown in Figure 5.3 is for case 2: $\alpha_2 > \alpha_2^*$. It can be seen that the densities of species u and v both are convergent to 0, that is, the two competing species u and v

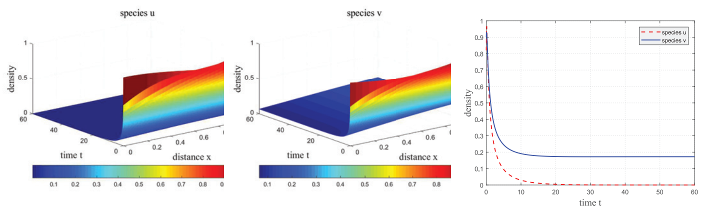

Fig. 5.2. Numerical simulations of the asymptotic behavior of the solution for system (1.9) when $d_1 = 1$, $d_2 = 0.8$, $\alpha_1 = 0.9$, $\alpha_2 = 0.7$ and $b = c = 0.5$.

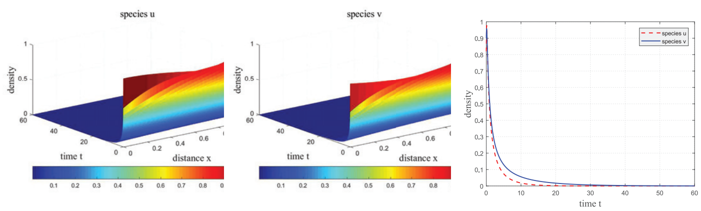

Fig. 5.3. Numerical simulations of the asymptotic behavior of the solution for system (1.9) when $d_1 = 1$, $d_2 = 0.8$, $\alpha_1 = 1$, $\alpha_2 = 0.9$ and $b = c = 0.5$.

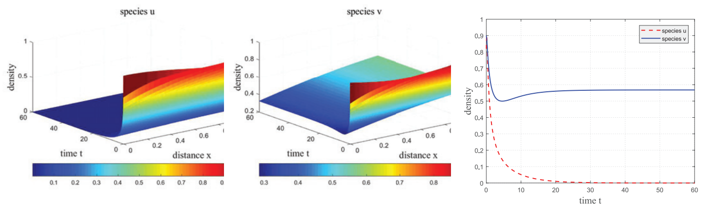

Fig. 5.4. Numerical simulations of the asymptotic behavior of the solution for system (1.9) when $d_1 = 1$, $d_2 = 0.8$, $\alpha_1 = 0.6$, $\alpha_2 = 0.4$, $b = 0.8$ and $c = 0.5$.

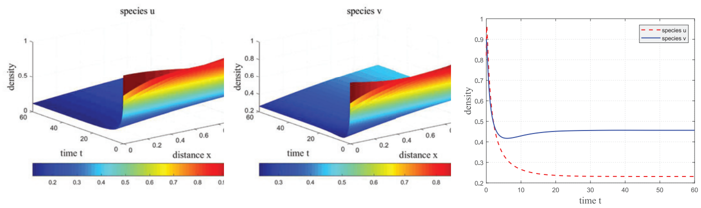

Fig. 5.5. Numerical simulations of the asymptotic behavior of the solution for system (1.9) when $d_1 = 1$, $d_2 = 0.8$, $\alpha_1 = 0.6$, $\alpha_2 = 0.4$, $b = 0.1$ and $c = 0.5$.

both will extinct as time goes on. Case 3: $\alpha_1 < \alpha_1^*$. In Figure 5.4, we choose $b = 0.8$ and $c = 0.5$ and in Figure 5.5, we choose $b = 0.1$ and $c = 0.5$. From Figure 5.4, we can see that, after a long time, species u goes extinct and species v survive. Figure 5.5 shows that the densities of species u and v will converge to their corresponding steady states, which means that, the two competing species will coexist finally. From case 3, we can derive that there exists a critical value for the inter-specific competition intensity (denoted by b^*) in system (1.9) which changes the stability of steady state. Moreover, when b lies above the critical value c^*, the semi-trivial steady state $(0, \tilde{v})$ is g.a.s, and the coexistence steady state (U, V) is g.a.s when b lies below the critical value b^*. Then the numerical simulations shown in Figure 5.4 and Figure 5.5 verify the results (i_3) in Theorem 1.2.

Category II: $0 < \beta_2 < \beta_1 < 1$.

Table 5.2. The values of parameters for simulations:

case	α_1	α_2	k_0	b	c
4	0.5	0.9	0.9355	0.8	0.6
5	0.9	1	0.6065	0.8	0.6
6	0.3	0.6	0.9048	0.8	0.7
	0.3	0.6	0.9048	0.8	0.1

In this situation, for convenience, we set $d_1 = 0.6$ and $d_2 = 1$. In the same way, by the above numerical result of α^*, $\alpha_1^* = 0.8324$ and $\alpha_2^* = 0.7978$ when $d_1 = 0.6$ and $d_2 = 1$.

For case 4: $\alpha_1 < \alpha_1^*$ and $\alpha_2^* < \alpha_2$, the numerical simulations in Figure 5.6 demonstrate that the density of species v tends to 0 and the density of species u converge to corresponding steady states after a period of time. It means that species u would displace species v eventually and persist in the long run. Figure 5.7 describes the case 5: $\alpha_1^* < \alpha_1$. From Figure 5.7, we can see that the densities of species u and v both converge to 0, which imply that both species u and v die out in the end. Case 6: $\alpha_2 < \alpha_2^*$. In Figure 5.8, we choose $b = 0.8$ and $c = 0.7$ and in Figure 5.9, we choose $b = 0.8$ and $c = 0.1$.

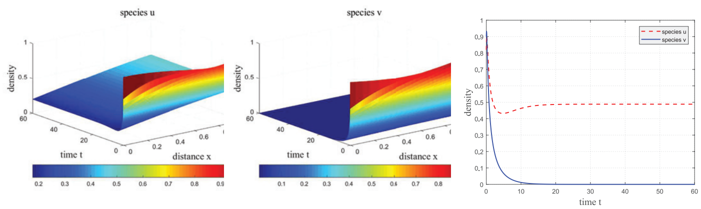

Fig. 5.6. Numerical simulations of the asymptotic behavior of the solution for system (1.9) when $d_1 = 0.6$, $d_2 = 1$, $\alpha_1 = 0.5$, $\alpha_2 = 0.9$, $b = 0.8$ and $c = 0.6$.

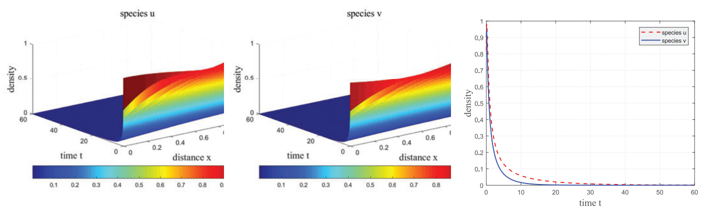

Fig. 5.7. Numerical simulations of the asymptotic behavior of the solution for system (1.9) when $d_1 = 0.6$, $d_2 = 1$, $\alpha_1 = 0.9$, $\alpha_2 = 1$, $b = 0.8$ and $c = 0.6$.

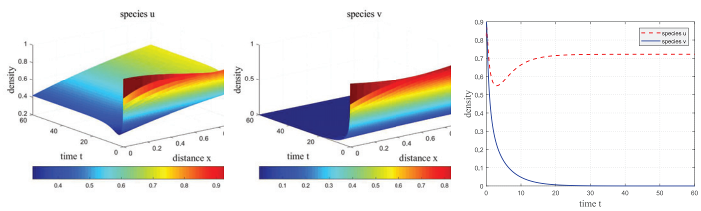

Fig. 5.8. Numerical simulations of the asymptotic behavior of the solution for system (1.9) when $d_1 = 0.6$, $d_2 = 1$, $\alpha_1 = 0.3$, $\alpha_2 = 0.6$, $b = 0.8$ and $c = 0.7$.

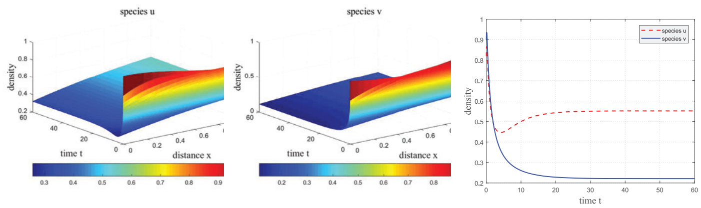

Fig. 5.9. Numerical simulations of the asymptotic behavior of the solution for system (1.9) when $d_1 = 0.6$, $d_2 = 1$, $\alpha_1 = 0.3$, $\alpha_2 = 0.6$, $b = 0.8$ and $c = 0.1$.

It is shown in Figure 5.8 that species u can persist in the long run while species v extinct. Instead, Figure 5.9 demonstrates that the densities of species u and v reach a coexistence steady state, then the two competing species will coexist eventually. In case 6, it implies that a critical value for the inter-specific competition intensity exists (denoted by c^*) for system (1.9) which changes the stability of steady state of the system. Moreover, when c lies above the critical value c^*, the semi-trivial steady state $(\tilde{u}, 0)$ is g.a.s, and the coexistence steady state (U, V) is g.a.s when c lies below the critical value c^*. Our numerical simulations in Figure 5.8 and Figure 5.9 verify the results (ii$_3$) in Theorem 1.2.

6. Discussion

In this paper, we investigate the global dynamics of a general Lotka-Volterra competition-diffusion-advection system from river ecology. It is assumed that the upstream and downstream ends allow individuals pass through, and we use two parameters b_u and b_d to measure the loss rates of individuals at the upstream and downstream ends, respectively. In mathematics, the boundary conditions include the standard Neumann, Robin and Dirichlet types.

For this general model, we get rid of the condition that $\alpha_1/d_1 = \alpha_2/d_2$ and make a discussion on the condition that $bc \leq k_0$. We obtain a complete classification on all possible global dynamical behaviors of system (1.2); see Theorem 1.1. This result generalizes [26] where the authors supposed that the ratios of the diffusion rates and advection rates for two competitors are the same. Resting on this, we apply Theorem 1.1 to discuss a special situation in which two species complete for the same resource, that is, $m_1 = m_2$. When $b_d \geq 1/2$ and $\beta_1 > \beta_2 > 1$ or $0 < \beta_1 < \beta_2 < 1$, a more clear picture on the global dynamics of system (1.2) is obtained by regarding β_1, β_2, b and c as variable parameters; see Theorem 1.2.

Although we have made some progress in understanding the general system (1.2), there are still several significant problems left for further investigation. Firstly, in spite of relaxing the limits on the diffusion rates and advection rates for two competitors, the ranges of the inter-specific competition intensities b and c correspondingly shrink. It is interesting to explore whether these limits can be further relaxed. The second one refers to the picture on the global dynamics of system (1.2), which, currently is obtained when b_d is in $[1/2, +\infty]$, $\beta_1 > \beta_2 > 1$ or $0 < \beta_1 < \beta_2 < 1$, and identical growth rate. What about the case of differing growth rates. Moreover, on account of the monotony property of eigenvalue with respect to the advection rate, the accurate lower bound of parameter b_d, at present, we know this bound should not be greater than $1/2$. But it is not determined the precise value. In addition, what about the case of other values of β_1 and β_2. These questions all need to be explored.

Conflict of interest

All authors declare no conflicts of interest in this paper.

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References

[1] F. Belgacem and C. Cosner, The effects of dispersal along environmental gradients on the dynamics of populations in heterogeneous environment, Canadian Appl. Math. Quarterly, **3** (1995), 379–397.

[2] R. S. Cantrell and C. Cosner, Spatial Ecology via Reaction-Diffusion Equations, Series in Mathematical and Computational Biology, John Wiley and Sons, Chichester, UK, 2003.

[3] X. F. Chen and Y. Lou, Principal eigenvalue and eigenfunctions of an elliptic operator with large advection and its application to a competition model, Indiana Univ. Math. J., **57** (2008), 627–658.

[4] X. F. Chen and Y. Lou, Effects of diffusion and advection on the smallest eigenvalue of an elliptic operator and their applications, Indiana Univ. Math. J., **61** (2012), 45–80.

[5] J. Dockery, V. Hutson, K. Mischaikow and M. Pernarowski, The evolution of slow dispersal rates: a reaction-diffusion model, J. Math. Biol., **37** (1998), 61–83.

[6] 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** (2020), 6547–6573.

[7] R. Hambrock and Y. Lou, The evolution of conditional dispersal strategy in spatially heterogeneous habitats, Bull. Math. Biol., **71** (2009), 1793–1817.

[8] A. Hasting, Can spatial variation alone lead to selection for dispersal? Theor. Popul., **24** (1983), 244–251.

[9] X. Q. He and W.-M. Ni, Global dynamics of the Lokta-Volterra competition-diffusion system: Diffusion and spatial heterogeneity, I, Comm. Pure Appl. Math., **69** (2016), 981–1014.
[10] P. Hess, Periodic-Parabolic Boundary Value Problems and Positivity, Pitman Res. Notes Math. Ser., vol. 247, Longman/Wiley, Harlow, UK/New York, 1991.
[11] M. G. Krein and M. A. Rutman, Linear operators leaving invariant a cone in a Banach space, Usp. Mat. Nauk, **3** (1948), 3–95.
[12] K.-Y. Lam and W.-M. Ni, Uniqueness and coomplete dynamics in the heterogeneous competition-diffusion systems, SIAM. J. Appl. Math., **72** (2012), 1695–1712.
[13] K. Y. Lam, Y. Lou and F. Lutscher, Evolution of dispersal in closed advective environments, J. Biol. Dyn., **9** (2015), 188–212.
[14] Y. Lou and F. Lutscher, Evolution of dispersal in open advective environments, J. Math. Biol., **69** (2014), 1319–1342.
[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** (2016), 953–969.
[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** (2019), 47–82.
[17] F. Lutscher, M. A. Lewis and E. McCauley, Effects of heterogeneity on spread and persistence in rivers, Bull. Math. Biol., **68** (2006), 2129–2160.
[18] F. Lutscher, E. Pachepsky and M. A. Lewis, The effect of dispersal patterns on stream populations, SIAM Rev., **47** (2005), 749–772.
[19] Y. Lou and P. Zhou, Evolution of dispersal in advective homogeneous environment: the effect of boundary conditions, J. Differential Equations, **259** (2015), 141–171.
[20] D. C. Speirs and W. S. C. Gurney, Population dynamics in rivers and estuaries, Ecology, **82** (2001), 1219–1237.
[21] O. Vasilyeva and F. Lutscher, Population dynamics in rivers: analysis of steady states, Can. Appl. Math. Q., **18** (2011), 439–469.
[22] D. Tang and P. Zhou, On a Lotka-volterra competition-diffusion-advection system: Homogeneity vs heterogeneity, J. Differential Equations, **268** (2020), 1570–1599.
[23] Qi Wang, Some global dynamics of a Lotka-Volterra competition-diffusion-advection system, Commun. Pure Appl. Anal., **19** (2020), 3245–3255.
[24] 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** (2021), 564–582.
[25] F. F. Xu and W. Z. Gan, On a Lotka-Volterra type competieion model from river ecology, Nonlinear Anal. Real World Appl., **47** (2019), 373–384.
[26] F. F. Xu, W. Z. Gan and D. Tang, Global dynamics of a Lotka-Volterra competitive system from river ecology: general boundary conditions, Nonlinerity, **33** (2020), 1528–1541.
[27] X.-Q. Zhao and P. Zhou, On a Lotka-Volterra competition model: the effects of advection and spatial variation, Calc. Var. Partial Differential Equations, **55** (2016), 73.
[28] P. Zhou, On a Lotka-Volterra competition system: diffusion vs advection, Calc. Var. Partial Differential Equations, **55** (2016), 137.
[29] P. Zhou, D. Tang and D.-M. Xiao, On Lotka-Volterra competitive parabolic systems: Exclusion, coexistence and bistability, J. Differ. Equ., **282** (2021), 596–625.
[30] P. Zhou and D. M. Xiao, Global dynamics of a classical Lotka-Volterra competition-diffusion-advection system, J. Funct. Anal., **275** (2018), 356–380.

[31] P. Zhou and X.-Q. Zhao, Global dynamics of a two species competition model in open stream environments, J. Dyn. Differ. Equ., **30** (2018), 613–636.

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

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