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Dynamics of a diffusion-advection Lotka-Volterra competition model with stage structure in a spatially heterogeneous environment

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Abstract

In this paper, we study a diffusion-advection Lotka-Volterra competition model with stage structure in a spatially heterogeneous environment. The existence and local asymptotic stability of spatially non-homogeneous semi-trivial steady-state solutions and spatially non-homogeneous positive steady-state solutions are obtained by the implicit function theorem and spectral analysis. We show that three scenarios can occur: if random diffusion rates of two species are sufficiently large, both species go extinct; if random diffusion rates of two species are relatively small, two competing species coexist; if one species has a large random diffusion rate and the other has a small random diffusion rate, the species with a large random diffusion rate are driven to extinction. An interesting finding is that a large delay does not lead to Hopf bifurcation at the spatially non-homogeneous steady-state solution, but makes this steady-state solution approach zero. We numerically demonstrate the effects of spatial heterogeneity on spatiotemporal dynamics.

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Keywords: Lotka-Volterra competition; Advection; Stage structure; Time delay; Bifurcation; Spatially heterogeneous; Stability

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1. Introduction

Spatial heterogeneity of the environment has attracted extensive attention from researchers recently [1–8]. Since the distribution of resources is non-uniform, the diffusion of the species will also have moved along a certain direction in addition to random diffusion. Based on the species will move along the gradient of resources, Belgacem and Cosner [1] proposed the following mathematical model:

$$\begin{cases} \dfrac{\partial u}{\partial t} = \nabla \cdot [d\nabla u - au\nabla m] + u\,[m(x) - u]\,, & x \in \Omega, t > 0, \\ u(x,t) = 0, & x \in \partial\Omega, t > 0, \end{cases} \tag{1.1}$$

where $u(x,t)$ represents the population density at location x and time t, and Ω is a bounded domain in $\mathbb{R}^n$ with a smooth boundary, $m(x)$ denotes the intrinsic growth rate of species at location x, a measures the tendency of population to move up or down along the gradient of $m(x)$. The Dirichlet boundary condition represents the environment surrounding the habitat Ω is lethal.

Chen *et al*. [9] considered the effect of the time delay on model (1.1),

$$\begin{cases} \dfrac{\partial u}{\partial t} = \nabla \cdot [d\nabla u - \alpha u\nabla m] + u(x,t)\,[m(x) - u(x,t-\tau)]\,, & x \in \Omega, t > 0, \\ u(x,t) = 0, & x \in \partial\Omega, t > 0, \end{cases} \tag{1.2}$$

where $\tau > 0$ represents the maturation time. They found that the time delay will lead to the Hopf bifurcation of the system in the positive steady-state solution, resulting in a spatially non-homogeneous periodic solution. The classical Lotka-Volterra competition model is widely studied when considering the dynamics of two competing species. See [3,6,10–23] and the references therein. On the basis of (1.1), Chen *et al*. [10,12] introduced two competing species. They investigated the following two-species competition-diffusion-advection model in spatially heterogeneous environments:

$$\begin{cases} u_t = d_1\Delta u - \alpha_1\nabla\cdot[u\nabla m_1(x)] + u[m_1(x) - a_{11}u - a_{12}v] & x \in \Omega, t > 0, \\ v_t = d_2\Delta v - \alpha_2\nabla\cdot[v\nabla m_2(x)] + v[m_2(x) - a_{21}u - a_{22}v] & x \in \Omega, t > 0, \end{cases} \tag{1.3}$$

with no-flux boundary conditions

$$d_1\partial_n u - \alpha_1 u\partial_n m_1 = d_2\partial_n v - \alpha_2 v\partial_n m_2 = 0, \tag{1.4}$$

where $d_1, d_2 > 0$ represent diffusion coefficients of species u and v; a_{11}, a_{22} represent intra-specific competition coefficients, and a_{12}, a_{21} are inter-specific competition coefficients; $m_1(x), m_2(x)$ and α_1, α_2 have the same meaning as m and a in model (1.1) above. They assumed $d_1 = d_2$, $a_{11} = a_{12} = a_{21} = a_{22} = 1$, $m_1(x) = m_2(x)$, and indicated that very strong advection along resource gradients can be disadvantageous and can cause the extinction of the species under some conditions. In the special case $\alpha_1 = \alpha_2 = 0$, $m_1(x) = m_2(x)$, if $a_{11} = a_{12} = a_{21} = a_{22} = 1$, Dockery [3] et al. proved that species with slow diffusion always win, if $0 < a_{12}a_{21} \le 1$, He and Ni [16] showed a complete classification of global dynamics, they establish the results that determine the global asymptotic stability of semi-trivial as well as coexistence steady-state solutions.

For the case of $d_1 \neq d_2$, $\alpha_1 \neq \alpha_2$, $m_1(x) \neq m_2(x)$, Ma and Guo [24] investigated the existence and local stability of steady-state solutions by the Lyapunov-Schmidt reduction method.

The discrete time delay can be used to represent species growth models with stage structure consisting of immature and mature stages. Single-species models and two-species competitive models with stage structure have been studied extensively. See [5,8,25–30] and the references given there.

Motivated by [5,12], we investigate a diffusion-advection-competition Lotka-Volterra model with stage structure in a spatially heterogeneous environment under homogeneous Dirichlet boundary condition, given by

$$\begin{cases} \dfrac{\partial u}{\partial t} =\nabla \cdot [d_1 \nabla u(x,t) - \alpha_1 u(x,t)\nabla m_1] + m_1(x) e^{-\gamma\tau} u(x,t-\tau) \\ \qquad - u^2(x,t) - bu(x,t)v(x,t), \qquad x \in \Omega, t > 0, \\ \dfrac{\partial v}{\partial t} =\nabla \cdot [d_2 \nabla v(x,t) - \alpha_2 v(x,t)\nabla m_2] + m_2(x) e^{-\gamma\tau} v(x,t-\tau) \\ \qquad - cu(x,t)v(x,t) - v^2(x,t), \qquad x \in \Omega, t > 0, \\ u(x,t) = v(x,t) = 0, \qquad x \in \partial\Omega, t > 0, \\ u(x,t) = \psi_1(x,t), v(x,t) = \psi_2(x,t), \qquad x \in \Omega, t \in [-\tau, 0], \end{cases} \tag{1.5}$$

where $\psi_i \in \mathcal{C} := C([-\tau, 0], Y)$, and $Y = L^2(\Omega)$; $u(x,t)$ and $v(x,t)$ denote the concentration of mature species; $\gamma > 0$ denotes the death rate of immature stage of the species u and v; $\tau > 0$ is the length of time from immature's birth to maturity of the species u and v; $b, c > 0$ are interspecific competition coefficients; $d_1, d_2, \alpha_1, \alpha_2, m_1(x), m_2(x)$ have the same meanings as those in (1.3). We assume species are growing in a poorly bounded and heterogeneous environment.

Here we consider the species that do not perform random or directional movements in the immature stage. For example, the chicks of some birds, they are not yet developed when they emerge from the shell, they cannot walk, and they need to be fed by the parent birds and continue to complete the development process in the nest. As they mature, they can make random or directional movements.

From now on we make the assumption:

(H1) $m_i(x) \in C^2(\overline{\Omega}),\ m_i(x) > 0$ on $\overline{\Omega}$, $i = 1, 2$.

As the variable transformation in [1], letting $\tilde{u} = e^{-(\alpha_1/d_1)m_1}u$, $\tilde{v} = e^{-(\alpha_2/d_2)m_2}v$, $\tilde{t} = d_1 t$, denoting $\tilde{\alpha_1} = \alpha_1/d_1$, $\tilde{\alpha_2} = \alpha_2/d_2$, $\lambda_1 = 1/d_1$, $\tilde{\tau} = d\tau$, and dropping the tilde sign, system (1.5) can be transformed to:

$$\begin{cases} \dfrac{\partial u}{\partial t} =e^{-\alpha_1 m_1}\nabla \cdot \left[e^{\alpha_1 m_1}\nabla u(x,t)\right] + \lambda_1 m_1(x) e^{-\gamma\tau} u(x,t-\tau) \\ \qquad - \lambda_1 u(x,t)(e^{\alpha_1 m_1} u(x,t) + be^{\alpha_2 m_2} v(x,t)), \qquad x \in \Omega, t > 0, \\ \dfrac{\partial v}{\partial t} =\dfrac{d_2}{d_1} e^{-\alpha_2 m_2}\nabla \cdot \left[e^{\alpha_2 m_2}\nabla v(x,t)\right] + \lambda_1 m_2(x) e^{-\gamma\tau} v(x,t-\tau) \\ \qquad - \lambda_1 v(x,t)(ce^{\alpha_1 m_1} u(x,t) + e^{\alpha_2 m_2} v(x,t)), \qquad x \in \Omega, t > 0, \\ u(x,t) = v(x,t) = 0, \qquad x \in \partial\Omega, t > 0, \\ u(x,t) = e^{-\alpha_1 m_1}\psi_1(x,t), v(x,t) = e^{-\alpha_2 m_2}\psi_2(x,t), \qquad x \in \Omega, t \in [-\tau, 0]. \end{cases} \tag{1.6}$$

For two competing species, permanence and extinction of the species is an important issue. Two competing species coexist, or one species survives while the other species go extinct, or both species go extinct, which are expressed as positive solutions, semi-trivial solutions and trivial solutions respectively in the mathematical model.

Different from the results of three scenarios in [12], we show that there are two critical random diffusion rates $1/\lambda_{1*}$ and $1/\lambda_{2*}$. If the random diffusion rates of both species are greater than these two critical random diffusion rates, the extinction of both species will be driven; If the random diffusion rates of both species are lower than these two critical random diffusion rates, the two species coexist; If one species has a random dispersal rate greater than its critical dispersal rate and another species has a random dispersal rate less than its critical dispersal rate, the species with a large random dispersal rate are driven to extinction.

In this paper, due to the Dirichlet boundary condition, and the spatially heterogeneous resource functions of the two species are neither equal nor proportional, both the semi-trivial solutions and positive solutions of (1.5) are spatially non-homogeneous. For the semi-trivial solution, we use the single eigenvalue bifurcation theorem to obtain the existence theorem (see Theorem 3.3). However, for the positive solution, single eigenvalue bifurcation theorem cannot be applied because the multiplicity of the 0 eigenvalue is double, we use the most primitive implicit function theorem to overcome the difficulties (see Theorem 3.6).

Moreover, we further analyze the local stability of trivial solutions (Theorem 4.1), semi-trivial solutions (Theorem 4.2, 4.3) and positive solutions (Theorem 4.5) by analyzing the distribution of the eigenvalues of the infinitesimal generator of the solution semigroup corresponding to the linearization operator. In particular, we take advantage of the power series expansion of the exponential function of e to deal with the difficulties posed by the stage structure. Under certain assumptions, the positive solution is locally asymptotically stable, which is different from the result in [9,17,31], where the positive solution becomes unstable and a Hopf bifurcation occurs as the delay increases. The time delay in this paper does not make the steady-state solution unstable through Hopf bifurcation and generate periodic oscillation.

In addition, we analyze the effects of the stage structure and spatial heterogeneity on the steady-state solution of (1.5). From Lemma 3.4, we find that the upper bound of the steady-state solution is related to the stage structure. The stage structure can affect the persistence and extinction of species. With the increase of τ, the upper bound of the steady-state solution tends to 0, which implies that the two competing species will go from coexistence to extinction. This is also a natural consequence in biology. Moreover, we numerically demonstrate the influence of spatial heterogeneity on the steady-state solution.

The rest of the paper is organized as follows. In Section 2, we give preliminaries and the steady-state system. The existence of semi-trivial solutions and non-trivial solutions are obtained in Section 3. Section 4 is devoted to the local stability of the steady-state solutions. Numerical simulations are shown in Section 5, and we analyzed the effect of stage structure and spatial heterogeneity on steady-state solution.

Throughout this paper, we denote spaces $X = H^2(\Omega, \mathbb{R}) \cap H_0^1(\Omega, \mathbb{R})$, $Y = L^2(\Omega, \mathbb{R})$. We also define the complexification of a linear space Z to be $Z_{\mathbb{C}} := Z \oplus iZ = \{x_1 + ix_2 | x_1, x_2 \in Z\}$, the domain of a linear operator L by $\mathcal{D}(L)$, the kernel of L by $\mathcal{N}(L)$, and the range of L by $\mathcal{R}(L)$. For the complex-valued Hilbert space $Y_{\mathbb{C}}^2$, we use the standard inner product $\langle u, v\rangle = \int_\Omega \overline{u}(x)^T v(x) dx$.

2. Preliminaries and steady-state equation

We first recall the elliptic eigenvalue problem. Denote by $\lambda_*(\alpha, q, m)$ and $\mu_*(\alpha, q, m)$ the principal eigenvalue of the eigenvalue problem

$$\begin{cases} \nabla \cdot \left[e^{\alpha q(x)} \nabla \varphi\right] + \lambda e^{\alpha q(x)} m(x)\varphi = 0, & x \in \Omega, \\ \varphi(x) = 0, & x \in \partial\Omega, \end{cases} \tag{2.1}$$

and

$$\begin{cases} e^{-\alpha q(x)} \nabla \cdot \left[e^{\alpha q(x)} \nabla \varphi\right] + m(x)\varphi = \mu\varphi, & x \in \Omega, \\ \varphi(x) = 0, & x \in \partial\Omega. \end{cases} \tag{2.2}$$

The principal eigenvalue is the only positive eigenvalue admitting a positive eigenfunction, and it is a simple eigenvalue.

In view of [2,24,32], we have the following important properties of $\lambda_*(\alpha, q, m)$ and $\mu_*(\alpha, q, m)$.

Lemma 2.1. *Suppose that $\alpha > 0,\ q \in C^1(\Omega),\ m \in L^\infty(\Omega)$.*

(i) The principal eigenvalue of (2.1) and (2.2)are given by

(a)

$$\lambda_*(\alpha, q, m) = \inf_{\substack{\varphi \in W_0^{1,2}(\Omega), \varphi \neq 0, \\ \int_\Omega e^{\alpha q(x)} m(x)\varphi^2 \mathrm{d}x > 0}} \left[\frac{\int_\Omega e^{\alpha q(x)} |\nabla\varphi|^2 \mathrm{d}x}{\int_\Omega e^{\alpha q(x)} m(x)\varphi^2 \mathrm{d}x} \right], \tag{2.3}$$

(b)

$$\mu_*(\alpha, q, m) = \sup_{\varphi \in W_0^{1,2}(\Omega), \varphi \neq 0} \left[\frac{\int_\Omega e^{\alpha q(x)} m(x)\varphi^2 dx - \int_\Omega e^{\alpha q(x)} |\nabla\varphi|^2 \mathrm{d}x}{\int_\Omega e^{\alpha q(x)} \varphi^2 \mathrm{d}x} \right]. \tag{2.4}$$

(ii) $\mu_*(\alpha, q, m) > 0$ for all $\lambda_*(\alpha, q, m) < 1$, $\mu_*(\alpha, q, m) = 0$ for all $\lambda_*(\alpha, q, m) = 1$, $\mu_*(\alpha, q, m) < 0$ for all $\lambda_*(\alpha, q, m) > 1$.

(iii) $\mu_*(\alpha, q, m_1) < \mu_*(\alpha, q, m_2)$ if $m_1(x) \leq\not\equiv m_2(x)$ in Ω.

Let $\lambda_2 = 1/d_2$, we obtain the steady-state system as follows,

$$\begin{cases} e^{-\alpha_1 m_1} \nabla \cdot \left[e^{\alpha_1 m_1} \nabla u\right] + \lambda_1 m_1(x) e^{-\gamma\tau} u - \lambda_1 u(e^{\alpha_1 m_1} u + b e^{\alpha_2 m_2} v) = 0, & x \in \Omega, \\ e^{-\alpha_2 m_2} \nabla \cdot \left[e^{\alpha_2 m_2} \nabla v\right] + \lambda_2 m_2(x) e^{-\gamma\tau} v - \lambda_2 v(c e^{\alpha_1 m_1} u + e^{\alpha_2 m_2} v) = 0, & x \in \Omega, \\ u(x) = v(x) = 0, & x \in \partial\Omega. \end{cases} \tag{2.5}$$

Therefore, the corresponding eigenvalue problem of (2.5) is

$$\begin{cases} \nabla \cdot \left[e^{\alpha_i m_i} \nabla \phi_i\right] + \lambda_i m_i(x) e^{\alpha_i m_i} e^{-\gamma\tau} \phi_i = 0, & x \in \Omega, \\ \phi_i(x) = 0, & x \in \partial\Omega. \end{cases} \tag{2.6}$$

For simplicity, we denote

$$\lambda_{i*} \triangleq \lambda_*(\alpha_i, m_i, m_i(x)e^{-\gamma\tau}) = \inf_{\substack{\phi_i \in W_0^{1,2}(\Omega), \phi_i \neq 0, \\ \int_\Omega e^{\alpha_i m_i(x)} m_i(x) e^{-\gamma\tau}\phi_i^2 \mathrm{d}x > 0}} \left[\frac{\int_\Omega e^{\alpha_i m_i(x)} |\nabla \phi_i|^2 \mathrm{d}x}{\int_\Omega e^{\alpha_i m_i(x)} m_i(x) e^{-\gamma\tau} \phi_i^2 \mathrm{d}x} \right], \tag{2.7}$$

be the principal eigenvalue and ϕ_{i*} $(i = 1, 2)$ be the corresponding principal eigenfunction.

Let $\lambda = (\lambda_1, \lambda_2)$, $\lambda_* = (\lambda_{1*}, \lambda_{2*})$. Denote $\Phi_{1*} = (\phi_{1*}, 0)^T$, $\Phi_{2*} = (0, \phi_{2*})^T$, $y = (y_1, y_2)^T$, and define

$$L = \begin{pmatrix} L_1 & 0 \\ 0 & L_2 \end{pmatrix} \tag{2.8}$$

with its domain $\mathcal{D}(L) = X^2$, where

$$\begin{aligned} L_1 &= \nabla \cdot \left[e^{\alpha_1 m_1} \nabla \right] + \lambda_{1*} e^{\alpha_1 m_1} m_1(x) e^{-\gamma\tau}, \\ L_2 &= \nabla \cdot \left[e^{\alpha_2 m_2} \nabla \right] + \lambda_{2*} e^{\alpha_2 m_2} m_2(x) e^{-\gamma\tau}, \end{aligned} \tag{2.9}$$

Actually, we have the following decompositions:

$$X^2 = \mathcal{N}(L) \oplus X_1^2, \quad Y^2 = \mathcal{N}(L) \oplus Y_1^2,$$

where

$$\mathcal{N}(L) = \mathrm{span}\{\Phi_{1*}, \Phi_{2*}\},$$
$$X_1^2 = \{y \in X^2 : \langle \Phi_{1*}, y \rangle = \langle \Phi_{2*}, y \rangle = 0\},$$
$$Y_1^2 = \mathcal{R}(L) = \{y \in Y^2 : \langle \Phi_{1*}, y \rangle = \langle \Phi_{2*}, y \rangle = 0\}.$$

Clearly, $dim(\mathcal{N}(L)) = codim(\mathcal{R}(L)) = 2$. This implies that 0 is the double eigenvalue of operator L, so the well-known bifurcation theorem from single eigenvalue in [33] is no longer applicable.

In this paper, we take λ_1 and λ_2 as bifurcation parameters to discuss the existence and stability of steady-state solutions for system (2.5):

(i) Trivial solutions: $(u, v) = (0, 0)$;
(ii) Semi-trivial solutions: $u \geq, \not\equiv 0$, $v \equiv 0$ or $u \equiv 0$, $v \geq, \not\equiv 0$;
(iii) Non-trivial solutions (Coexistence steady-state solutions): $u \geq, \not\equiv 0$, $v \geq \not\equiv 0$.

For the competitive system, semi-trivial solutions of the system naturally exist under spatial homogeneous environments and Neumann boundary conditions. However, for system (2.5) in spatially heterogeneous environments, the existence of semi-trivial and non-trivial solutions is proved by the bifurcation theorem and the implicit function theorem.

3. Existence of solutions

3.1. The existence of semi-trivial solutions

In this section, we study the existence of semi-trivial steady-state solutions to system (1.6). Noting that semi-trivial steady-state solutions are of the form $(u, 0)$ and $(0, v)$, where u and v are the positive steady-state solutions of the following single species model (3.1) and (3.2), respectively.

$$\begin{cases} e^{-\alpha_1 m_1}\nabla\cdot\left[e^{\alpha_1 m_1}\nabla u\right]+\lambda_1 m_1(x)e^{-\gamma\tau}u-\lambda_1 e^{\alpha_1 m_1}u^2=0, & x\in\Omega,\\ u(x)=0, & x\in\partial\Omega. \end{cases} \tag{3.1}$$

$$\begin{cases} e^{-\alpha_2 m_2}\nabla\cdot\left[e^{\alpha_2 m_2}\nabla v\right]+\lambda_2 m_2(x)e^{-\gamma\tau}v-\lambda_2 e^{\alpha_2 m_2}v^2=0, & x\in\Omega,\\ v(x)=0, & x\in\partial\Omega. \end{cases} \tag{3.2}$$

Due to the combined effect of the Dirichlet boundary condition and the spatially heterogeneous environment, model (3.1) and (3.2) do not have constant steady-state solutions. It is worth noting that the results in [1, Proposition 2.2] yielding the existence of solutions for model (3.1) and (3.2). The corresponding results are given in the following theorems, which can also be proved by using the bifurcation theorem [33].

Theorem 3.1. *Assume that (H1) holds. Let λ_{1*} and ϕ_{1*} be defined in* (2.7).

(i) If $\lambda_1 < \lambda_{1*}$, 0 is the unique non-negative solution of (3.1);
(ii) If $\lambda_1 > \lambda_{1*}$, (3.1) *has a unique positive solution, denoted as u_{λ_1}.*

Theorem 3.2. *Assume that (H1) holds. Let λ_{2*} and ϕ_{2*} be defined in* (2.7).

(i) If $\lambda_2 < \lambda_{2*}$, 0 is the unique non-negative solution of (3.2);
(ii) If $\lambda_2 > \lambda_{2*}$, (3.2) *has a unique positive solution, denoted as v_{λ_2}.*

From Theorems 3.1 and 3.2, we immediately have the following theorem for system (1.6).

Theorem 3.3. *Assume that (H1) holds. There are semi-trivial steady-state solutions $(u_{\lambda_1}, 0)$ for $(\lambda_1, \lambda_2) \in (\lambda_{1*}, \lambda_{1*} + \delta) \times (0, +\infty)$ and $(0, v_{\lambda_2})$ for $(\lambda_1, \lambda_2) \in (0, +\infty) \times (\lambda_{2*}, \lambda_{2*} + \delta)$ of system* (1.6)*, where $0 < \delta \ll 1$ is a constant.*

3.2. The existence of non-trivial solutions

In this section, we investigate the existence of non-trivial steady-state solutions to system (1.6). By using the maximum principle, we immediately have the lemma below.

Lemma 3.4. *If the non-negative steady-state solution (u, v) of system* (1.6) *satisfies $u \not\equiv 0$ and $v \not\equiv 0$, then (u, v) is bounded. Moreover, $0 < u \le \frac{e^{-\gamma\tau}}{\alpha_1 e}$ and $0 < v \le \frac{e^{-\gamma\tau}}{\alpha_2 e}$ on Ω.*

Proof. If $u \not\equiv 0$ and $v \not\equiv 0$, then $u > 0$ and $v > 0$ on Ω by the strong maximum principle. From (2.5), we have

$$\begin{cases} 0 = \nabla \cdot \left[e^{\alpha_1 m_1} \nabla u\right] + \lambda_1 m_1(x) e^{\alpha_1 m_1} e^{-\gamma\tau} u - \lambda_1 u (e^{2\alpha_1 m_1} u + b e^{\alpha_1 m_1 + \alpha_2 m_2} v) \\ \quad \le \nabla \cdot \left[e^{\alpha_1 m_1} \nabla u\right] + \lambda_1 u (m_1(x) e^{\alpha_1 m_1} e^{-\gamma\tau} - e^{2\alpha_1 m_1} u), \quad x \in \Omega, \\ 0 = \nabla \cdot \left[e^{\alpha_2 m_2} \nabla v\right] + \lambda_2 m_2(x) e^{\alpha_2 m_2} e^{-\gamma\tau} v - \lambda_2 v (c e^{\alpha_1 m_1 + \alpha_2 m_2} u + e^{2\alpha_2 m_2} v) \\ \quad \le \nabla \cdot \left[e^{\alpha_2 m_2} \nabla v\right] + \lambda_2 v (m_2(x) e^{\alpha_2 m_2} e^{-\gamma\tau} - e^{2\alpha_2 m_2} v), \quad x \in \Omega, \\ u(x) = v(x) = 0, \quad x \in \partial\Omega. \end{cases} \tag{3.3}$$

We consider the following elliptic problem

$$\begin{cases} \nabla \cdot \left[e^{\alpha_1 m_1} \nabla u\right] + \lambda_1 u (m_1(x) e^{\alpha_1 m_1} e^{-\gamma\tau} - e^{2\alpha_1 m_1} u) \ge 0, & x \in \Omega, \\ u(x) \ge 0, & x \in \partial\Omega. \end{cases}$$

Let $u(w_0) = \max_{x \in \overline{\Omega}} u(x)$, hence $w_0 \in \Omega$ satisfies $\nabla u(w_0) = 0$ and $\Delta u(w_0) \le 0$. Moreover, at $x = w_0$ we have

$$e^{\alpha_1 m_1(w_0)} \Delta u(w_0) + \lambda_1 u(w_0)(m_1(w_0) e^{\alpha_1 m_1(w_0)} e^{-\gamma\tau} - e^{2\alpha_1 m_1(w_0)} u(w_0)) \ge 0.$$

It follows [34, Proposition 2.2] that

$$\lambda_1 u(w_0)(m_1(w_0) e^{\alpha_1 m_1(w_0)} e^{-\gamma\tau} - e^{2\alpha_1 m_1(w_0)} u(w_0)) \ge 0,$$

which yields

$$u(w_0) \le \frac{e^{-\gamma\tau} m_1(w_0)}{e^{\alpha_1 m_1(w_0)}}. \tag{3.4}$$

It is evident that

$$\frac{e^{-\gamma\tau} m_1(w_0)}{e^{\alpha_1 m_1(w_0)}} \le \frac{e^{-\gamma\tau}}{\alpha_1 e}, \tag{3.5}$$

the equal sign holds if and only if $m_1(w_0) = \frac{1}{\alpha_1}$. Likewise, let $v(z_0) = \max_{x \in \overline{\Omega}} v(x)$, we obtain

$$v(z_0) \le \frac{e^{-\gamma\tau} m_2(z_0)}{e^{\alpha_2 m_2(z_0)}} \le \frac{e^{-\gamma\tau}}{\alpha_2 e}. \tag{3.6}$$

Combining comparison principle and (3.3), (3.4), (3.5), and (3.6), we can assert that

$$0 < u \le \frac{e^{-\gamma\tau}}{\alpha_1 e}, \quad 0 < v \le \frac{e^{-\gamma\tau}}{\alpha_2 e}. \tag{3.7}$$

Remark 1. Lemma 3.4 proves that the steady-state solution (u, v) of system (1.6) is bounded, and the upper bound is related to the time delay τ. With the increase of τ, the bound of the steady-state solution gradually decreases to 0.

Theorem 3.5. *If system* (1.6) *has a positive steady-state solution* (u, v) *with* $u > 0$ *and* $v > 0$, *then* $\lambda_1 > \lambda_{1*}$ *and* $\lambda_2 > \lambda_{2*}$.

Proof. Suppose (u, v) is the positive solution of (2.5) with $u > 0$ and $v > 0$, multiplying both sides of the first equation of (2.5) by u and integrating on Ω, we get

$$\begin{aligned}\int_\Omega e^{\alpha_1 m_1}|\nabla u|^2 \mathrm{d}x &= \lambda_1 \int_\Omega e^{\alpha_1 m_1} u^2[m_1(x)e^{-\gamma\tau} - (e^{\alpha_1 m_1}u + be^{\alpha_2 m_2}v)]\mathrm{d}x \\ &< \lambda_1 \int_\Omega e^{\alpha_1 m_1} u^2 m_1(x)e^{-\gamma\tau}\mathrm{d}x.\end{aligned} \tag{3.8}$$

From the variational property of the principal eigenvalue, we have

$$\int_\Omega e^{\alpha_1 m_1}|\nabla u|^2 \mathrm{d}x \geq \lambda_{1*} \int_\Omega e^{\alpha_1 m_1} u^2 m_1(x)e^{-\gamma\tau}\mathrm{d}x. \tag{3.9}$$

Combining (3.8) and (3.9), which yields $\lambda_1 > \lambda_{1*}$. Similarly, multiplying both sides of the second equation of (2.5) by v and integrating on Ω, and so $\lambda_2 > \lambda_{2*}$.

Remark 2. Since $\lambda_1 = \frac{1}{d_1}$ and $\lambda_2 = \frac{1}{d_2}$, Theorem 3.5 shows that positive steady-state solution (u, v) with $u \not\equiv 0$ and $v \not\equiv 0$ may exist when the diffusion coefficients d_1 and d_2 are sufficiently small.

For simplicity, we denote

$$\begin{aligned} &k_{11} \triangleq \int_\Omega e^{2\alpha_1 m_1}\phi_{1*}^3 \mathrm{d}x,\ k_{12} \triangleq b\int_\Omega e^{\alpha_1 m_1+\alpha_2 m_2}\phi_{1*}^2\phi_{2*}\mathrm{d}x, \\ &k_{21} \triangleq c\int_\Omega e^{\alpha_1 m_1+\alpha_2 m_2}\phi_{1*}\phi_{2*}^2\mathrm{d}x,\ k_{22} \triangleq \int_\Omega e^{2\alpha_2 m_2}\phi_{2*}^3 \mathrm{d}x, \\ &k_1 \triangleq \int_\Omega e^{\alpha_1 m_1}m_1(x)\phi_{1*}^2 \mathrm{d}x,\ k_2 \triangleq \int_\Omega e^{\alpha_2 m_2}m_2(x)\phi_{2*}^2 \mathrm{d}x, \\ &k_3 \triangleq \int_\Omega e^{\alpha_1 m_1}\phi_{1*}^2 \mathrm{d}x, \qquad k_4 \triangleq \int_\Omega e^{\alpha_2 m_2}\phi_{2*}^2 \mathrm{d}x. \end{aligned} \tag{3.10}$$

In biological models, we care more about the positive solution, so we make further assumptions.

(H2) $D \triangleq k_{11}k_{22} - k_{12}k_{21} \neq 0$.
(H3) $\mathrm{sign}(D) = \mathrm{sign}((\lambda_2 - \lambda_{2*})\lambda_1 k_{11}k_2 - (\lambda_1 - \lambda_{1*})\lambda_2 k_{21}k_1) = \mathrm{sign}((\lambda_1 - \lambda_{1*})\lambda_2 k_{22}k_1 - (\lambda_2 - \lambda_{2*})\lambda_1 k_{12}k_2)$.

Theorem 3.6. *Assume that* **(H1)-(H2)** *hold. Let λ_{i*} and ϕ_{i*} be defined in (2.7). Then, there exists a constant $\delta > 0$ and a continuously differentiable mapping $\lambda \mapsto (\xi_{1\lambda}, \xi_{2\lambda}, \beta_{1\lambda}, \beta_{2\lambda})$ from $B(\lambda_*, \delta)$ to $X_1^2 \times \mathbb{R}^2$, system (1.6) has a non-constant steady-state solution $(u_\lambda, v_\lambda)^T$ given by*

$$\begin{cases} u_\lambda = \beta_{1\lambda}[\phi_{1*} + \xi_{1\lambda}], \\ v_\lambda = \beta_{2\lambda}[\phi_{2*} + \xi_{2\lambda}], \end{cases} \tag{3.11}$$

where

$$\begin{aligned} \beta_{1\lambda} &= \frac{e^{-\gamma\tau}[(\lambda_2 - \lambda_{2*})\lambda_1 k_{11} k_2 - (\lambda_1 - \lambda_{1*})\lambda_2 k_{21} k_1]}{\lambda_1 \lambda_2 D}, \\ \beta_{2\lambda} &= \frac{e^{-\gamma\tau}[(\lambda_1 - \lambda_{1*})\lambda_2 k_{22} k_1 - (\lambda_2 - \lambda_{2*})\lambda_1 k_{12} k_2]}{\lambda_1 \lambda_2 D}, \end{aligned} \tag{3.12}$$

and $(\xi_{1\lambda}, \xi_{2\lambda}) \in X_1^2$ *be the unique solution of the following equation:*

$$\begin{cases} L_1\xi_1 + (\lambda_1 - \lambda_{1*}) e^{\alpha_1 m_1} m_1(x) e^{-\gamma\tau}(\phi_{1*} + \xi_1) \\ -\lambda_1(\phi_{1*} + \xi_1)[e^{2\alpha_1 m_1}\beta_{1\lambda}(\phi_{1*} + \xi_1) + b e^{\alpha_1 m_1 + \alpha_2 m_2}\beta_{2\lambda}(\phi_{2*} + \xi_2)] = 0, \\ L_2\xi_2 + (\lambda_2 - \lambda_{2*}) e^{\alpha_2 m_2} m_2(x) e^{-\gamma\tau}(\phi_{2*} + \xi_2) \\ -\lambda_2(\phi_{2*} + \xi_2)[c e^{\alpha_1 m_1 + \alpha_2 m_2}\beta_{1\lambda}(\phi_{1*} + \xi_1) + e^{2\alpha_2 m_2}\beta_{2\lambda}(\phi_{2*} + \xi_2)] = 0. \end{cases} \tag{3.13}$$

In particular, $\beta_{1\lambda_*} = \beta_{2\lambda_*} = \xi_{1\lambda_*} = \xi_{2\lambda_*} = 0$. *Furthermore, if the assumption* **(H3)** *holds, the positive steady-state solution exists in* $(\lambda_1, \lambda_2) \in (\lambda_{1*}, \lambda_1^*) \times (\lambda_{2*}, \lambda_2^*)$, *where* $\lambda_i^* < \lambda_{i*} + \delta$, $i = 1, 2$. *As* $\lambda \to \lambda_*$, *the positive steady-state solution tends to the trivial solution.*

Proof. Suppose that system (2.5) has a solution of form

$$\begin{cases} u = \beta_1[\phi_{1*} + \xi_1], \\ v = \beta_2[\phi_{2*} + \xi_2], \end{cases} \tag{3.14}$$

where $\beta_i = O(\|\lambda - \lambda_*\|)$, $\xi_i = O(\|\lambda - \lambda_*\|)$, $i = 1, 2$. Substituting (3.14) into (2.5), we define a continuous map $T = (T_1, T_2) : X_1^2 \times \mathbb{R}^2 \times (\mathbb{R}^+)^2 \to Y^2$ be

$$\begin{cases} \quad T_1(\xi_1, \xi_2, \beta_1, \beta_2, \lambda) \\ = L_1\xi_1 + (\lambda_1 - \lambda_{1*}) e^{\alpha_1 m_1} m_1(x) e^{-\gamma\tau}(\phi_{1*} + \xi_1) \\ \quad -\lambda_1(\phi_{1*} + \xi_1)[e^{2\alpha_1 m_1}\beta_1(\phi_{1*} + \xi_1) + b e^{\alpha_1 m_1 + \alpha_2 m_2}\beta_2(\phi_{2*} + \xi_2)], \\ \quad T_2(\xi_1, \xi_2, \beta_1, \beta_2, \lambda) \\ = L_2\xi_2 + (\lambda_2 - \lambda_{2*}) e^{\alpha_2 m_2} m_2(x) e^{-\gamma\tau}(\phi_{2*} + \xi_2) \\ \quad -\lambda_2(\phi_{2*} + \xi_2)[c e^{\alpha_1 m_1 + \alpha_2 m_2}\beta_1(\phi_{1*} + \xi_1) + e^{2\alpha_2 m_2}\beta_2(\phi_{2*} + \xi_2)]. \end{cases}$$

It is easy to check that

$$T_i(0, 0, 0, 0, \lambda_*) = 0, \quad i = 1, 2.$$

The Fréchet derivative of T respect to $(\xi_{\lambda_1}, \xi_{\lambda_2}, \beta_{\lambda_1}, \beta_{\lambda_2})$ at $(0, 0, 0, 0, \lambda_*)$ is

$$D_{(\xi_1,\xi_2,\beta_1,\beta_2)}T(0,0,0,0,\lambda_*)[\zeta_1,\zeta_2,\epsilon_1,\epsilon_2]$$
$$=\begin{pmatrix} L_1\zeta_1-\lambda_1(\epsilon_1 e^{2\alpha_1 m_1}\phi_{1*}^2+b\epsilon_2 e^{\alpha_1 m_1+\alpha_2 m_2}\phi_{1*}\phi_{2*}) \\ L_2\zeta_2-\lambda_2(c\epsilon_1 e^{\alpha_1 m_1+\alpha_2 m_2}\phi_{1*}\phi_{2*}+\epsilon_2 e^{2\alpha_2 m_2}\phi_{2*}^2) \end{pmatrix}.$$

We claim that

$$D_{(\xi_1,\xi_2,\beta_1,\beta_2)}T(0,0,0,0,\lambda_*)$$

is a bijection from $X_1^2\times\mathbb{R}^2$ to Y^2. In fact, if

$$D_{(\xi_1,\xi_2,\beta_1,\beta_2)}T(0,0,0,0,\lambda_*)[\zeta_1,\zeta_2,\epsilon_1,\epsilon_2]=0,$$

that is

$$\begin{cases} L_1\zeta_1-\lambda_1(\epsilon_1 e^{2\alpha_1 m_1}\phi_{1*}^2+b\epsilon_2 e^{\alpha_1 m_1+\alpha_2 m_2}\phi_{1*}\phi_{2*})=0, \\ L_2\zeta_2-\lambda_2(c\epsilon_1 e^{\alpha_1 m_1+\alpha_2 m_2}\phi_{1*}\phi_{2*}+\epsilon_2 e^{2\alpha_2 m_2}\phi_{2*}^2)=0, \end{cases} \tag{3.15}$$

take the inner product of the first and the second equation of (3.15) with ϕ_{1*} and ϕ_{2*}, respectively. It follows from assumption **(H2)** that $\epsilon_1=\epsilon_2=0$, then $L_i\zeta_i=0,\ i=1,2$, since $\zeta=(\zeta_1,\zeta_2)\in X_1^2$, we have $\zeta_1=\zeta_2=0$, which yields that $D_{(\xi_1,\xi_2,\beta_1,\beta_2)}T(0,0,0,0,\lambda_*)$ is a injection.

On the other hand, let

$$D_{(\xi_1,\xi_2,\beta_1,\beta_2)}T(0,0,0,0,\lambda_*)[\zeta_1,\zeta_2,\epsilon_1,\epsilon_2]=p, \tag{3.16}$$

where $p=(p_1,p_2)\in Y^2$, we decompose $p_i=p_{i1}+p_{i2}$, where $p_{i1}\in\mathcal{N}(L_i),\ \ p_{i2}\in\mathcal{R}(L_i)$. Taking the inner product of Eq. (3.16) with Φ_{1*} and Φ_{2*}, respectively. We obtain

$$\begin{cases} \lambda_1(k_{11}\epsilon_1+k_{12}\epsilon_2)=-\langle\phi_{1*},p_{11}\rangle, \\ \lambda_2(k_{21}\epsilon_1+k_{22}\epsilon_2)=-\langle\phi_{2*},p_{21}\rangle. \end{cases} \tag{3.17}$$

By assumption **(H2)**, there exists a unique solution

$$\begin{cases} \epsilon_1=\dfrac{-\langle\phi_{1*},p_{11}\rangle\lambda_2 k_{22}-\langle\phi_{2*},p_{21}\rangle\lambda_2 k_{12}}{\lambda_1\lambda_2 D}, \\ \epsilon_2=\dfrac{-\langle\phi_{2*},p_{21}\rangle\lambda_1 k_{11}-\langle\phi_{1*},p_{11}\rangle\lambda_2 k_{21}}{\lambda_1\lambda_2 D}. \end{cases}$$

Therefore,

$$\begin{pmatrix} p_1+\lambda_1(\epsilon_1 e^{2\alpha_1 m_1}\phi_{1*}^2+b\epsilon_2 e^{\alpha_1 m_1+\alpha_2 m_2}\phi_{1*}\phi_{2*}) \\ p_2+\lambda_2(c\epsilon_1 e^{\alpha_1 m_1+\alpha_2 m_2}\phi_{1*}\phi_{2*}+\epsilon_2 e^{2\alpha_2 m_2}\phi_{2*}^2) \end{pmatrix}\in\mathcal{R}(L).$$

Since $L:X_1^2\to Y_1^2$ is bijective, there exists

$$\zeta=L^{-1}\begin{pmatrix} p_1+\lambda_1(\epsilon_1 e^{2\alpha_1 m_1}\phi_{1*}^2+b\epsilon_2 e^{\alpha_1 m_1+\alpha_2 m_2}\phi_{1*}\phi_{2*}) \\ p_2+\lambda_2(c\epsilon_1 e^{\alpha_1 m_1+\alpha_2 m_2}\phi_{1*}\phi_{2*}+\epsilon_2 e^{2\alpha_2 m_2}\phi_{2*}^2) \end{pmatrix},$$

then $D_{(\xi_1,\xi_2,\beta_1,\beta_2)}T(\xi_{1\lambda_*},\xi_{2\lambda_*},\beta_{1\lambda_*},\beta_{2\lambda_*},\lambda_*)$ is a surjection.

Therefore, the implicit function theorem implies that there exists a constant $\delta > 0$ and a continuously differentiable mapping $\lambda \mapsto (\xi_{1\lambda},\xi_{2\lambda},\beta_{1\lambda},\beta_{2\lambda})$ from $B(\lambda_*,\delta)$ to $X_1^2 \times \mathbb{R}^2$ such that

$$T(\xi_{1\lambda},\xi_{2\lambda},\beta_{1\lambda},\beta_{2\lambda},\lambda) = 0. \tag{3.18}$$

(3.12) and (3.13) can be calculated from the inner product of Eq. (3.18) and Φ_* and Φ_{2*}, respectively. In Particular, $\beta_{1\lambda_*} = \beta_{2\lambda_*} = \xi_{1\lambda_*} = \xi_{2\lambda_*} = 0$ when $\lambda = \lambda_*$. Moreover, combining Theorem 3.5 and assumption **(H3)**, the positive steady-state exists in $(\lambda_1,\lambda_2) \in (\lambda_{1*},\lambda_1^*) \times (\lambda_{2*},\lambda_2^*)$. This theorem is completely proved.

4. Local stability of solutions

In this section, we consider the local stability of the trivial steady-state solution, semi-trivial steady-state solutions, and the positive steady-state solution. Since Theorem 3.6 proves the local existence of positive steady-state solutions, in the rest of this paper, we always assume that positive steady-state solutions exist in the parameter region $(\lambda_{1*},\lambda_1^*) \times (\lambda_{2*},\lambda_2^*)$, where $\lambda_i^* < \lambda_{i*} + \delta,\ i = 1,2$.

In order to describe the local asymptotic stability of solutions, we give the linearized system of (1.6) at the solution (u_*, v_*) as follows,

$$\begin{cases} \widetilde{u}_t = e^{-\alpha_1 m_1}\nabla\cdot\left[e^{\alpha_1 m_1}\nabla\widetilde{u}\right] - 2\lambda_1 e^{\alpha_1 m_1}u_*\widetilde{u} - b\lambda_1 e^{\alpha_2 m_2}(u_*\widetilde{v} + v_*\widetilde{u}) \\ \qquad + \lambda_1 m_1(x)e^{-\gamma\tau}\widetilde{u}(t-\tau), \qquad x\in\Omega, t>0, \\ \widetilde{v}_t = d_2\lambda_1 e^{-\alpha_2 m_2}\nabla\cdot\left[e^{\alpha_2 m_2}\nabla\widetilde{v}\right] - 2\lambda_1 e^{\alpha_2 m_2}v_*\widetilde{v} - c\lambda_1 e^{\alpha_1 m_1}(u_*\widetilde{v} + v_*\widetilde{u}) \\ \qquad + \lambda_1 m_2(x)e^{-\gamma\tau}\widetilde{v}(t-\tau), \qquad x\in\Omega, t>0, \\ \widetilde{u}(x,t) = \widetilde{v}(x,t) = 0, \qquad x\in\partial\Omega, t>0. \end{cases} \tag{4.1}$$

Substituting $\widetilde{u} = \Phi e^{\mu t}$ and $\widetilde{v} = \Psi e^{\mu t}$ into (4.1) gives the eigenvalue problem

$$\begin{cases} \mu\Phi = e^{-\alpha_1 m_1}\nabla\cdot\left[e^{\alpha_1 m_1}\nabla\Phi\right] - 2\lambda_1 e^{\alpha_1 m_1}u_*\Phi - b\lambda_1 e^{\alpha_2 m_2}(u_*\Psi + v_*\Phi) \\ \qquad + \lambda_1 m_1(x)e^{-\gamma\tau}e^{-\mu\tau}\Phi, \qquad x\in\Omega, \\ \mu\Psi = d_2\lambda_1 e^{-\alpha_2 m_2}\nabla\cdot\left[e^{\alpha_2 m_2}\nabla\Psi\right] - 2\lambda_1 e^{\alpha_2 m_2}v_*\Psi - c\lambda_1 e^{\alpha_1 m_1}(u_*\Psi + v_*\Phi) \\ \qquad + \lambda_1 m_2(x)e^{-\gamma\tau}e^{-\mu\tau}\Psi, \qquad x\in\Omega, \\ \Phi(x) = \Psi(x) = 0, \qquad x\in\partial\Omega. \end{cases} \tag{4.2}$$

Let μ_* be the principal eigenvalue of (4.2) (the existence of the principal eigenvalues could be found in [5]). In what follows, as in [32], we call the steady-state solution

(i) (u_*, v_*) is linearly stable if $\mu_* < 0$,
(ii) (u_*, v_*) is neutrally stable if $\mu_* = 0$,
(iii) (u_*, v_*) is linearly unstable if $\mu_* > 0$.

Moreover, the steady-state solution is asymptotically stable (unstable) if it is linearly stable (linearly unstable) (see [35]).

4.1. Local stability of the trivial solution

For $(u_*, v_*) = (0,0)$, the corresponding eigenvalue problem is

$$\begin{cases} \mu\Phi = e^{-\alpha_1 m_1}\nabla\cdot\left[e^{\alpha_1 m_1}\nabla\Phi\right] + \lambda_1 m_1(x)e^{-\gamma\tau}e^{-\mu\tau}\Phi, & x\in\Omega,\\ \mu\Psi = d_2\lambda_1 e^{-\alpha_2 m_2}\nabla\cdot\left[e^{\alpha_2 m_2}\nabla\Psi\right] + \lambda_1 m_2(x)e^{-\gamma\tau}e^{-\mu\tau}\Psi, & x\in\Omega,\\ \Phi(x)=\Psi(x)=0, & x\in\partial\Omega. \end{cases} \tag{4.3}$$

Theorem 4.1. *Assume that* **(H1)** *holds. Let λ_{i*} be defined in (2.7). Trivial steady-state solution $(0,0)$ of system (1.6) is locally asymptotically stable when $(\lambda_1,\lambda_2)\in[0,\lambda_{1*})\times[0,\lambda_{2*})$, and $(0,0)$ is unstable when $\lambda_1>\lambda_{1*}$ or $\lambda_2>\lambda_{2*}$.*

Proof. Since $(\Phi,\Psi)\neq(0,0)$, if $\Phi\neq 0$, then $\mu\le\mu_*(\alpha_1,m_1,\lambda_1 e^{-\gamma\tau}e^{-\mu\tau}m_1(x))$. If $\Psi\neq 0$, then $d_1\lambda_2\mu\le\mu_*(\alpha_2,m_2,\lambda_2 e^{-\gamma\tau}e^{-\mu\tau}m_2(x))$. Hence,

$$\mu\le\max\{\mu_*(\alpha_1,m_1,\lambda_1 e^{-\gamma\tau}e^{-\mu\tau}m_1(x)),\ (d_1\lambda_2)^{-1}\mu_*(\alpha_2,m_2,\lambda_2 e^{-\gamma\tau}e^{-\mu\tau}m_2(x))\}. \tag{4.4}$$

By applying the results in [5,36],

$$\operatorname{sign}(\mu_*(\alpha_i,m_i,\lambda_i e^{-\gamma\tau}e^{-\mu\tau}m_i(x))) = \operatorname{sign}(\mu_*(\alpha_i,m_i,\lambda_i e^{-\gamma\tau}m_i(x))),\ i=1,2. \tag{4.5}$$

Now

$$\mu_*(\alpha_1,m_1,\lambda_1 e^{-\gamma\tau}m_1(x))=0, \quad \text{if } \lambda_1=\lambda_{1*}, \tag{4.6}$$

which is due to the fact that

$$\begin{cases} e^{-\alpha_1 m_1}\nabla\cdot\left[e^{\alpha_1 m_1}\nabla\right]\phi_{1*} + \lambda_{1*}e^{-\gamma\tau}m_1(x)\phi_{1*}=0, & x\in\Omega,\\ \phi_{1*}(x)=0, & x\in\partial\Omega. \end{cases}$$

Further, by (iii) of Lemma 2.1, we have

$$\begin{cases} \mu_*(\alpha_1,m_1,\lambda_1 e^{-\gamma\tau}m_1(x))<0, & \text{if } \lambda_1<\lambda_{1*},\\ \mu_*(\alpha_1,m_1,\lambda_1 e^{-\gamma\tau}m_1(x))>0, & \text{if } \lambda_1>\lambda_{1*}. \end{cases}$$

Similarly,

$$\begin{cases} \mu_*(\alpha_2,m_2,\lambda_2 e^{-\gamma\tau}m_2(x))=0, & \text{if } \lambda_2=\lambda_{2*},\\ \mu_*(\alpha_2,m_2,\lambda_2 e^{-\gamma\tau}m_2(x))<0, & \text{if } \lambda_2<\lambda_{2*},\\ \mu_*(\alpha_2,m_2,\lambda_2 e^{-\gamma\tau}m_2(x))>0, & \text{if } \lambda_2>\lambda_{2*}. \end{cases}$$

Therefore, all eigenvalues of (4.3) have negative real parts when $\lambda_1<\lambda_{1*}$ and $\lambda_2<\lambda_{2*}$, then $(0,0)$ is linearly stable, and when $\lambda_1>\lambda_{1*}$ or $\lambda_2>\lambda_{2*}$, $(0,0)$ is linearly unstable.

4.2. Local stability of semi-trivial solutions

For $(u_*, v_*) = (u_{\lambda_1}, 0)$, the corresponding eigenvalue problem is

$$\begin{cases} \mu\Phi = e^{-\alpha_1 m_1}\nabla\cdot\left[e^{\alpha_1 m_1}\nabla\Phi\right] - 2\lambda_1 e^{\alpha_1 m_1}u_{\lambda_1}\Phi - b\lambda_1 e^{\alpha_2 m_2}u_{\lambda_1}\Psi \\ \qquad + \lambda_1 m_1(x)e^{-\gamma\tau}e^{-\mu\tau}\Phi, \qquad x\in\Omega, t>0, \\ \mu\Psi = d_2\lambda_1 e^{-\alpha_2 m_2}\nabla\cdot\left[e^{\alpha_2 m_2}\nabla\Psi\right] - c\lambda_1 e^{\alpha_1 m_1}u_{\lambda_1}\Psi \\ \qquad + \lambda_1 m_2(x)e^{-\gamma\tau}e^{-\mu\tau}\Psi, \qquad x\in\Omega, t>0, \\ \Phi(x) = \Psi(x) = 0, \qquad x\in\partial\Omega. \end{cases} \tag{4.7}$$

Theorem 4.2. *Assume that* **(H1)** *holds. Let λ_{i*} be defined in (2.7). Semi-trivial steady-state solution $(u_{\lambda_1}, 0)$ of system (1.6) is locally asymptotically stable if $(\lambda_1, \lambda_2) \in (\lambda_{1*}, \lambda_1^*) \times (0, \lambda_{2*})$, and $(u_{\lambda_1}, 0)$ is unstable if $(\lambda_1, \lambda_2) \in (\lambda_{1*}, \lambda_1^*) \times (\lambda_{2*}, +\infty)$.*

Proof. If $\Psi \neq 0$, according to the properties of the principal eigenvalue,

$$d_1\lambda_2\mu \le \mu_*(\alpha_2, m_2, \lambda_2 e^{-\gamma\tau}e^{-\mu\tau}m_2(x) - c\lambda_2 e^{\alpha_1 m_1}u_{\lambda_1}). \tag{4.8}$$

If $\Psi \equiv 0$, then $\Phi \neq 0$, from the first equation of (4.7) we obtain that

$$\mu \le \mu_*(\alpha_1, m_1, \lambda_1 e^{-\gamma\tau}e^{-\mu\tau}m_1(x) - 2\lambda_1 e^{\alpha_1 m_1}u_{\lambda_1}).$$

Then

$$\begin{aligned} \mu \le \max\{&(d_1\lambda_2)^{-1}\mu_*(\alpha_2, m_2, \lambda_2 e^{-\gamma\tau}e^{-\mu\tau}m_2(x) - c\lambda_2 e^{\alpha_1 m_1}u_{\lambda_1}), \\ &\mu_*(\alpha_1, m_1, \lambda_1 e^{-\gamma\tau}e^{-\mu\tau}m_1(x) - 2\lambda_1 e^{\alpha_1 m_1}u_{\lambda_1})\}. \end{aligned}$$

It follows from [5,36] that

$$\begin{aligned} &\mathrm{sign}(\mu_*(\alpha_2, m_2, \lambda_2 e^{-\gamma\tau}e^{-\mu\tau}m_2(x) - c\lambda_2 e^{\alpha_1 m_1}u_{\lambda_1})) \\ =&\mathrm{sign}(\mu_*(\alpha_2, m_2, \lambda_2 e^{-\gamma\tau}m_2(x) - c\lambda_2 e^{\alpha_1 m_1}u_{\lambda_1})), \\ &\mathrm{sign}(\mu_*(\alpha_1, m_1, \lambda_1 e^{-\gamma\tau}e^{-\mu\tau}m_1(x) - 2\lambda_1 e^{\alpha_1 m_1}u_{\lambda_1})) \\ =&\mathrm{sign}(\mu_*(\alpha_1, m_1, \lambda_1 e^{-\gamma\tau}m_1(x) - 2\lambda_1 e^{\alpha_1 m_1}u_{\lambda_1})). \end{aligned} \tag{4.9}$$

Note that u_{λ_1} is the steady-state solution of system (3.1), hence

$$\mu_*(\alpha_1, m_1, \lambda_1 e^{-\gamma\tau}m_1(x) - \lambda_1 e^{\alpha_1 m_1}u_{\lambda_1}) = 0. \tag{4.10}$$

By (iii) of Lemma 2.1,

$$\begin{aligned} &\mu_*(\alpha_1, m_1, \lambda_1 e^{-\gamma\tau}m_1(x) - 2\lambda_1 e^{\alpha_1 m_1}u_{\lambda_1}) \\ <&\mu_*(\alpha_1, m_1, \lambda_1 e^{-\gamma\tau}m_1(x) - \lambda_1 e^{\alpha_1 m_1}u_{\lambda_1}) = 0. \end{aligned}$$

Thus, the stability of $(u_{\lambda_1}, 0)$ is mainly determined by $\text{sign}(\mu_*(\alpha_2, m_2, \lambda_2 e^{-\gamma\tau} m_2(x) - c\lambda_2 e^{\alpha_1 m_1} u_{\lambda_1}))$. It is easily seen that $\lim_{\lambda_1 \to \lambda_{1*}} u_{\lambda_1} = 0$. Letting $\lambda_1 \to \lambda_{1*}$, we see that

$$\mu_*(\alpha_2, m_2, \lambda_2 e^{-\gamma\tau} m_2(x) - c\lambda_2 e^{\alpha_1 m_1} u_{\lambda_1}) = 0, \quad \text{if } \lambda_2 = \lambda_{2*},$$

Applying (iii) of Lemma 2.1 again,

$$\begin{cases} \mu_*(\alpha_2, m_2, \lambda_2 e^{-\gamma\tau} m_2(x) - c\lambda_2 e^{\alpha_1 m_1} u_{\lambda_1}) < 0, & \text{if } \lambda_2 < \lambda_{2*}, \\ \mu_*(\alpha_2, m_2, \lambda_2 e^{-\gamma\tau} m_2(x) - c\lambda_2 e^{\alpha_1 m_1} u_{\lambda_1}) > 0, & \text{if } \lambda_2 > \lambda_{2*}. \end{cases}$$

Consequently, when $(\lambda_1, \lambda_2) \in (\lambda_{1*}, \lambda_1^*) \times (0, \lambda_{2*})$, all eigenvalues of (4.7) have negative real parts, $(u_{\lambda_1}, 0)$ is locally asymptotically stable. When $(\lambda_1, \lambda_2) \in (\lambda_{1*}, \lambda_1^*) \times (\lambda_{2*}, +\infty)$, $(u_{\lambda_1}, 0)$ is unstable.

For $(u_*, v_*) = (0, v_{\lambda_2})$, the corresponding eigenvalue problem is

$$\begin{cases} \mu\Phi = e^{-\alpha_1 m_1} \nabla \cdot \left[e^{\alpha_1 m_1} \nabla \Phi \right] - b\lambda_1 e^{\alpha_2 m_2} v_{\lambda_2} \Phi \\ \qquad + \lambda_1 m_1(x) e^{-\gamma\tau} e^{-\mu\tau} \Phi, & x \in \Omega, \\ \mu\Psi = d_2 \lambda_1 e^{-\alpha_2 m_2} \nabla \cdot \left[e^{\alpha_2 m_2} \nabla \Psi \right] - 2\lambda_1 e^{\alpha_2 m_2} v_{\lambda_2} \Psi - c\lambda_1 e^{\alpha_1 m_1} v_{\lambda_2} \Phi \\ \qquad + \lambda_1 m_2(x) e^{-\gamma\tau} e^{-\mu\tau} \Psi, & x \in \Omega, \\ \Phi(x) = \Psi(x) = 0, & x \in \partial\Omega. \end{cases} \tag{4.11}$$

Using a similar proof method to Theorem 4.2, we have

Theorem 4.3. *Assume that* **(H1)** *holds. Let λ_{i*} be defined in* (2.7). *Semi-trivial steady-state solution $(0, v_{\lambda_2})$ of system* (1.6) *is locally asymptotically stable if $(\lambda_1, \lambda_2) \in (0, \lambda_{1*}) \times (\lambda_{2*}, \lambda_2^*)$, and $(0, v_{\lambda_2})$ is unstable if $(\lambda_1, \lambda_2) \in (\lambda_{1*}, +\infty) \times (\lambda_{2*}, \lambda_2^*)$.*

4.3. Local stability of the non-trivial solution

We now consider the local stability of the positive steady-state solution (u_λ, v_λ).
The linearization of system (1.6) at positive steady-state solution (u_λ, v_λ) is given by

$$\begin{cases} \widetilde{u}_t = e^{-\alpha_1 m_1} \nabla \cdot \left[e^{\alpha_1 m_1} \nabla \widetilde{u} \right] - 2\lambda_1 e^{\alpha_1 m_1} u_\lambda \widetilde{u} - b\lambda_1 e^{\alpha_2 m_2} (u_\lambda \widetilde{v} + v_\lambda \widetilde{u}) \\ \qquad + \lambda_1 m_1(x) e^{-\gamma\tau} \widetilde{u}(t-\tau), & x \in \Omega, t > 0, \\ \widetilde{v}_t = d_2 \lambda_1 e^{-\alpha_2 m_2} \nabla \cdot \left[e^{\alpha_2 m_2} \nabla \widetilde{v} \right] - 2\lambda_1 e^{\alpha_2 m_2} v_\lambda \widetilde{v} - c\lambda_1 e^{\alpha_1 m_1} (u_\lambda \widetilde{v} + v_\lambda \widetilde{u}) \\ \qquad + \lambda_1 m_2(x) e^{-\gamma\tau} \widetilde{v}(t-\tau), & x \in \Omega, t > 0, \\ \widetilde{u}(x,t) = \widetilde{v}(x,t) = 0, & x \in \partial\Omega, t > 0. \end{cases} \tag{4.12}$$

Introduce linear operator $A(\lambda) : X_{\mathbb{C}}^2 \to Y_{\mathbb{C}}^2$ defined by

$$A(\lambda) = \begin{pmatrix} a_{11} & 0 \\ 0 & a_{22} \end{pmatrix}, \tag{4.13}$$

and

$$B(\lambda) = \begin{pmatrix} -\lambda_1 e^{\alpha_1 m_1} u_\lambda & -b\lambda_1 e^{\alpha_2 m_2} u_\lambda \\ -c\lambda_1 e^{\alpha_1 m_1} v_\lambda & -\lambda_1 e^{\alpha_2 m_2} v_\lambda \end{pmatrix}, \tag{4.14}$$

$$C(\lambda) = \begin{pmatrix} \lambda_1 m_1(x) e^{-\gamma\tau} & 0 \\ 0 & \lambda_1 m_2(x) e^{-\gamma\tau} \end{pmatrix}, \tag{4.15}$$

where

$$\begin{aligned} a_{11} &\triangleq e^{-\alpha_1 m_1} \nabla \cdot \left[e^{\alpha_1 m_1} \nabla \right] - \lambda_1 e^{\alpha_1 m_1} u_\lambda - b\lambda_1 e^{\alpha_2 m_2} v_\lambda, \\ a_{22} &\triangleq d_2 \lambda_1 e^{-\alpha_2 m_2} \nabla \cdot \left[e^{\alpha_2 m_2} \nabla \right] - \lambda_1 e^{\alpha_2 m_2} v_\lambda - c\lambda_1 e^{\alpha_1 m_1} u_\lambda. \end{aligned} \tag{4.16}$$

From [9], the semigroup induced by solutions of Eq. (4.1) has the infinitesimal generator $A_\tau(\lambda)$ given by

$$A_\tau(\lambda)\psi = \dot{\psi},$$

with domain

$$\mathcal{D}(A_\tau(\lambda)) = \left\{ \psi \in (\mathcal{C}_\mathbb{C} \cap \mathcal{C}^1_\mathbb{C})^2 : \psi(0) \in X^2_\mathbb{C}, \dot{\psi}(0) = (A(\lambda) + B(\lambda))\psi(0) + C(\lambda)\psi(-\tau) \right\},$$

where $\mathcal{C}^1_\mathbb{C} = C^1([-\tau, 0], Y_\mathbb{C})$, $\psi = (\psi_1, \psi_2)^T \in Y^2_\mathbb{C}$. Moreover, $\mu \in \mathbb{C}$ is an eigenvalue of $A_\tau(\lambda)$, if and only if there exists $y = (y_1, y_2)^T (\neq (0,0)^T) \in X^2_\mathbb{C}$ such that

$$\Delta(\lambda, \mu, \tau) y = 0, \tag{4.17}$$

where

$$\Delta(\lambda, \mu, \tau) := A(\lambda) + B(\lambda) + C(\lambda) e^{-\mu\tau} - \mu I,$$

I is identity matrix in $\mathbb{R}^{2\times 2}$. By [37], the eigenvalues of $A_\tau(\lambda)$ continuously depend on τ, thus $A_\tau(\lambda)$ has an eigenvalue μ for some $\tau \geq 0$, if and only if

$$[A(\lambda) + B(\lambda) + C(\lambda) e^{-\mu\tau} - \mu I] y = 0, \quad y (\neq (0,0)^T) \in X^2_\mathbb{C}. \tag{4.18}$$

Note that

$$[A(\lambda) + C(\lambda)][(u_\lambda, v_\lambda)^T] = 0$$

and (3.11) satisfies (2.5), we obtain

$$[A(\lambda) + C(\lambda)][\Phi_{i*}] = 0, \; i = 1, 2. \tag{4.19}$$

Moreover, for any $\Phi, \Psi \in X^2_\mathbb{C}$,

$$\langle \Phi, [A(\lambda) + C(\lambda)]\Psi \rangle = \langle [A(\lambda) + C(\lambda)]\Phi, \Psi \rangle. \tag{4.20}$$

Eq. (4.17) is equivalent to

$$\begin{pmatrix} e^{\alpha_1 m_1} & 0 \\ 0 & e^{\alpha_2 m_2} \end{pmatrix} \Delta(\lambda, \mu, \tau) y = 0. \tag{4.21}$$

Via ignoring a scalar factor, suppose that

$$y = p\Phi_{1*} + q\Phi_{2*} + \|\lambda - \lambda_*\| \eta(x) \tag{4.22}$$

where $y(\neq (0,0)^T) \in X_{\mathbb{C}}^2$, $p, q \in \mathbb{C}^2$, $\eta = (\eta_1, \eta_2) \in X_{\mathbb{C}}^2$ satisfies $\langle \Phi_{1*}, \eta \rangle = \langle \Phi_{2*}, \eta \rangle = 0$. Let Φ_{1*} and Φ_{2*} be the inner product of (4.21), respectively, we get

$$\begin{aligned}
&\left\langle \Phi_{1*}, \begin{pmatrix} e^{\alpha_1 m_1} & 0 \\ 0 & e^{\alpha_2 m_2} \end{pmatrix} \mu y \right\rangle \\
=&\left\langle \Phi_{1*}, \begin{pmatrix} e^{\alpha_1 m_1} & 0 \\ 0 & e^{\alpha_2 m_2} \end{pmatrix} [A(\lambda) y + B(\lambda) y + C(\lambda) e^{-\mu\tau} y] \right\rangle \\
=&\left\langle \Phi_{1*}, \begin{pmatrix} e^{\alpha_1 m_1} & 0 \\ 0 & e^{\alpha_2 m_2} \end{pmatrix} [A(\lambda) y + C(\lambda) y] \right\rangle \\
&+ \left\langle \Phi_{1*}, \begin{pmatrix} e^{\alpha_1 m_1} & 0 \\ 0 & e^{\alpha_2 m_2} \end{pmatrix} [B(\lambda) y + C(\lambda)(e^{-\mu\tau} - 1) y] \right\rangle \\
=&\left\langle \begin{pmatrix} e^{\alpha_1 m_1} & 0 \\ 0 & e^{\alpha_2 m_2} \end{pmatrix} [A(\lambda) + C(\lambda)] \Phi_{1*}, y \right\rangle \\
&+ \left\langle \Phi_{1*}, \begin{pmatrix} e^{\alpha_1 m_1} & 0 \\ 0 & e^{\alpha_2 m_2} \end{pmatrix} [B(\lambda) y + C(\lambda)(e^{-\mu\tau} - 1) y] \right\rangle \\
=&\left\langle \Phi_{1*}, \begin{pmatrix} e^{\alpha_1 m_1} & 0 \\ 0 & e^{\alpha_2 m_2} \end{pmatrix} [B(\lambda) y + C(\lambda)(e^{-\mu\tau} - 1) y] \right\rangle,
\end{aligned} \tag{4.23}$$

where the third and fourth equalities can be obtained from (4.19) and (4.20), respectively. Similarly,

$$\begin{aligned}
&\left\langle \Phi_{2*}, \begin{pmatrix} e^{\alpha_1 m_1} & 0 \\ 0 & e^{\alpha_2 m_2} \end{pmatrix} \mu y \right\rangle \\
=&\left\langle \Phi_{2*}, \begin{pmatrix} e^{\alpha_1 m_1} & 0 \\ 0 & e^{\alpha_2 m_2} \end{pmatrix} [B(\lambda) y + C(\lambda)(e^{-\mu\tau} - 1) y] \right\rangle.
\end{aligned} \tag{4.24}$$

Moreover,

$$e^{-\mu\tau} - 1 = -\mu\tau + \frac{\mu^2\tau^2}{2!} - \frac{\mu^3\tau^3}{3!} + \cdots. \tag{4.25}$$

Let $\mu = j\|\lambda - \lambda_*\|$, we can rewrite (3.11) as

$$\begin{cases} u_\lambda = \varrho_1 \|\lambda - \lambda_*\| [\phi_{1*} + O(\|\lambda - \lambda_*\|)], \\ v_\lambda = \varrho_2 \|\lambda - \lambda_*\| [\phi_{2*} + O(\|\lambda - \lambda_*\|)], \end{cases} \tag{4.26}$$

where

$$\varrho_1 = \frac{e^{-\gamma\tau}[\cos\omega\lambda_1 k_{11}k_2 - \sin\omega\lambda_2 k_{21}k_1]}{\lambda_1\lambda_2 D},$$
$$\varrho_2 = \frac{e^{-\gamma\tau}[\sin\omega\lambda_2 k_{22}k_1 - \cos\omega\lambda_1 k_{12}k_2]}{\lambda_1\lambda_2 D},$$

$\omega \in (0, \frac{\pi}{2})$. Substituting Eq. (4.26), Eq. (4.22) and Eq. (4.25) into Eq. (4.23) and Eq. (4.24),

$$\begin{aligned}
& j\int_\Omega e^{\alpha_1 m_1}\phi_{1*}(p\phi_{1*} + \|\lambda-\lambda_*\|\eta_1)dx \\
=& -\lambda_1 \int_\Omega e^{2\alpha_1 m_1}\phi_{1*}\varrho_1[\phi_{1*} + O(\|\lambda-\lambda_*\|)](p\phi_{1*} + \|\lambda-\lambda_*\|\eta_1)dx \\
& -\lambda_1 b\int_\Omega e^{\alpha_1 m_1+\alpha_2 m_2}\phi_{1*}\varrho_1[\phi_{1*} + O(\|\lambda-\lambda_*\|)](q\phi_{2*} + \|\lambda-\lambda_*\|\eta_2)dx \\
& +\lambda_1 \int_\Omega e^{\alpha_1 m_1} m_1(x) e^{-\gamma\tau}(-j\tau + O(\|\lambda-\lambda_*\|))\phi_{1*}(p\phi_{1*} + \|\lambda-\lambda_*\|\eta_1)dx, \\
& j\int_\Omega e^{\alpha_2 m_2}\phi_{2*}(q\phi_{2*} + \|\lambda-\lambda_*\|\eta_2)dx \\
=& -\lambda_2 \int_\Omega e^{2\alpha_2 m_2}\phi_{2*}\varrho_2[\phi_{2*} + O(\|\lambda-\lambda_*\|)](q\phi_{2*} + \|\lambda-\lambda_*\|\eta_2)dx \\
& -\lambda_2 c\int_\Omega e^{\alpha_1 m_1+\alpha_2 m_2}\phi_{2*}\varrho_2[\phi_{2*} + O(\|\lambda-\lambda_*\|)](p\phi_{1*} + \|\lambda-\lambda_*\|\eta_1)dx \\
& +\lambda_2 \int_\Omega e^{\alpha_2 m_2} m_2(x) e^{-\gamma\tau}(-j\tau + O(\|\lambda-\lambda_*\|))\phi_{2*}(q\phi_{2*} + \|\lambda-\lambda_*\|\eta_2)dx.
\end{aligned}$$

Comparing the coefficients of $O(\|\lambda-\lambda_*\|)$ gives

$$\begin{cases} jpk_3 = -\lambda_1[(k_{11}\varrho_1 + k_1 j\tau e^{-\gamma\tau})p + k_{12}\varrho_1 q], \\ jqk_4 = -\lambda_2[k_{21}\varrho_2 p + (k_{22}\varrho_2 + k_2 j\tau e^{-\gamma\tau})q], \end{cases} \tag{4.27}$$

where $k_{11},\ k_{12},\ k_{21},\ k_{22},\ k_1,\ k_2,\ k_3,\ k_4$ are defined in (3.10). In fact, (4.27) is equivalent to

$$Q\begin{pmatrix} p \\ q \end{pmatrix} = 0$$

where

$$Q = \begin{pmatrix} -\lambda_1 k_{11}\varrho_1 - (k_3 + \lambda_1 \tau e^{-\gamma\tau} k_1) j & -\lambda_1 k_{12}\varrho_1 \\ -\lambda_2 k_{21}\varrho_2 & -\lambda_2 k_{22}\varrho_2 - (k_4 + \lambda_2 \tau e^{-\gamma\tau} k_2) j \end{pmatrix}.$$

Eq. (4.27) has a non-trivial solution (p, q) if and only if $\det Q = 0$, we have the following quadratic equation

$$Aj^2 + Bj + C = 0, \tag{4.28}$$

where

$$\begin{aligned} A &= (k_3 + \lambda_1 \tau e^{-\gamma\tau} k_1)(k_4 + \lambda_2 \tau e^{-\gamma\tau} k_2) > 0, \\ B &= (k_3 + \lambda_1 \tau e^{-\gamma\tau} k_1)\lambda_2 k_{22}\varrho_2 + (k_4 + \lambda_2 \tau e^{-\gamma\tau} k_2)\lambda_1 k_{11}\varrho_1 > 0, \\ C &= \lambda_1 \lambda_2 \varrho_1 \varrho_2 D. \end{aligned}$$

Eq. (4.28) has two roots

$$j_\pm = \frac{-B \pm \sqrt{B^2 - 4AC}}{2A}. \tag{4.29}$$

Lemma 4.4. *Assume that* **(H1)**-**(H3)** *hold.* 0 *is not an eigenvalue of Eq.* (4.18).

Proof. Conversely, if 0 is an eigenvalue of the characteristic equation (4.18), bring $j = 0$ into the equation (4.28), then $D = 0$, which contradicts the assumption.

Theorem 4.5. *Assume that* **(H1)**-**(H3)** *hold. The coexistence steady-state solution* (u_λ, v_λ) *that exists in* $(\lambda_1, \lambda_2) \in (\lambda_{1*}, \lambda_1^*) \times (\lambda_{2*}, \lambda_2^*)$ *is locally asymptotically stable if condition* $D > 0$ *is satisfied, and unstable if* $D < 0$*, where* D *is defined in* (H2).

Proof. From Eq. (4.29), when $D > 0$, all eigenvalues have negative real parts, It's easy to verify that when $D \le 0$, there are eigenvalues of non-negative real parts.

Remark 3. Combining Theorem 4.5 with Remark 1, we deduce that as the delay τ increases, Hopf bifurcation does not occur, which is different from the Hopf bifurcation caused by the delay τ in literature [9,17,31,38]. On the contrary, as τ increases, the bound of steady-state solution will gradually become smaller or even tend to zero.

Remark 4. Note that when $m_1(x) = m_2(x) \equiv C$, where C is a positive constant, the condition of $D > 0$ is equivalent to the weak competition condition $bc < 1$.

Based on the analysis in the previous sections, we briefly sketch the existence of steady-state solutions to system (1.6) in different parameter regions, see Fig. 1. We summarize the existence and stability of the solution of (2.5) as follows.

(i) $(\lambda_1, \lambda_2) \in (0, \lambda_{1*}) \times (0, \lambda_{2*})$: there is trivial solution $(0, 0)$ of system (2.5). Moreover, trivial solution $(0, 0)$ is asymptotically stable,

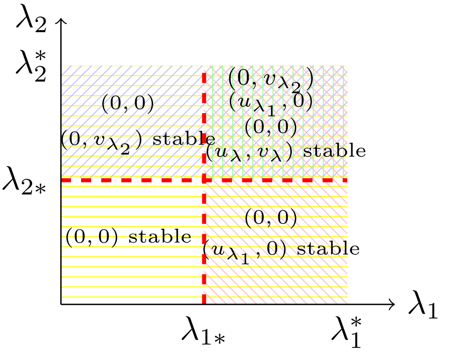


Fig. 1. Local bifurcation graph with λ_1 and λ_2 as parameters.

(ii) $(\lambda_1, \lambda_2) \in (\lambda_{1*}, \lambda_1^*) \times (0, \lambda_{2*})$: there are trivial solution $(0, 0)$ and the semi-trivial solution $(u_{\lambda_1}, 0)$ of system (2.5). Moreover, trivial solution $(0, 0)$ is unstable, the semi-trivial solution $(u_{\lambda_1}, 0)$ is asymptotically stable,

(iii) $(\lambda_1, \lambda_2) \in (0, \lambda_{1*}) \times (\lambda_{2*}, \lambda_2^*)$: there are trivial solutions $(0, 0)$ and the semi-trivial solution $(0, v_{\lambda_2})$ of system (2.5). Moreover, trivial solution $(0, 0)$ is unstable, the semi-trivial solution $(0, v_{\lambda_2})$ is asymptotically stable,

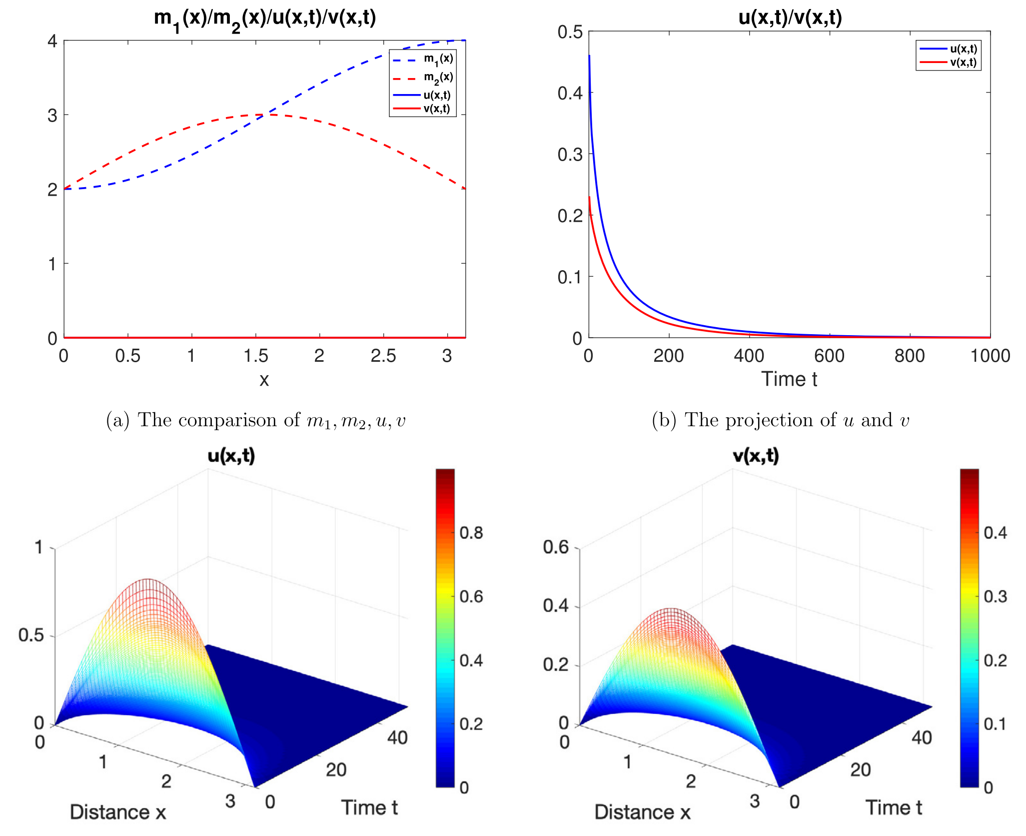
(iv) $(\lambda_1, \lambda_2) \in (\lambda_{1*}, \lambda_1^*) \times (\lambda_{2*}, \lambda_2^*)$: there are trivial solutions $(0, 0)$, the semi-trivial solution $(u_{\lambda_1}, 0)$, the semi-trivial solution $(0, v_{\lambda_2})$, and the non-trivial solution (coexistence steady-state solution) (u_λ, v_λ) system (2.5). Moreover, trivial solution $(0, 0)$, the semi-trivial solution $(u_{\lambda_1}, 0)$ and the semi-trivial solution $(0, v_{\lambda_2})$ are unstable, the coexistence steady-state solution (u_λ, v_λ) is asymptotically stable.

Remark 5. If $m_1(x) = m_2(x) = m(x)$, $\alpha_1 = \alpha_2 = \alpha > 0$, $b = c = 1$, we have $\lambda_{1*} = \lambda_{2*}$. Note that $\lambda_i = \frac{1}{d_i}$, from Fig. 1, we show that there is an intermediate random dispersal rate and three scenarios may occur: (i) If the random dispersal rate of two competing species is both greater than this rate, then both species go to extinction; (ii) If the random diffusion rate of both competing species is smaller than this rate (near the intermediate diffusion rate), then two competing species coexist; (iii) If one diffusion rate is larger than the critical rate and the other is smaller than the critical rate, the species with the larger diffusion rate goes to extinction. These results are different from the results in [12]. However, if $m_1(x) = m_2(x) = m(x)$, $\alpha_1 = \alpha_2 = 0$, $b = c = 1$, large random dispersal rates will drive species extinction, which is consistent with the results obtained in [3].

5. Numerical simulations

In this section, we support the results obtained by our theoretical analysis with numerical simulations. Furthermore, we show the effect of the stage structure and spatial heterogeneity on the steady-state solution.

Let $b = 0.3$, $c = 0.1$, $\gamma = 1$, $\alpha_1 = 0.5$, $\alpha_2 = 0.4$. Choose $m_1(x) = 3 - \cos x$, $m_2(x) = \sin x + 2$. Hence, $\lambda_{1*} = 0.5263$, $\lambda_{2*} = 0.4167$. We fix $\tau = 0.5$ and simulate the steady-state solution of system (1.5) in the four regions of (λ_1, λ_2) in Fig. 2, Fig. 3, Fig. 4, Fig. 5, respectively, which are consistent with Fig. 1.



(a) The comparison of m_1, m_2, u, v

(b) The projection of u and v

(c) The solution of $u(x,t)$

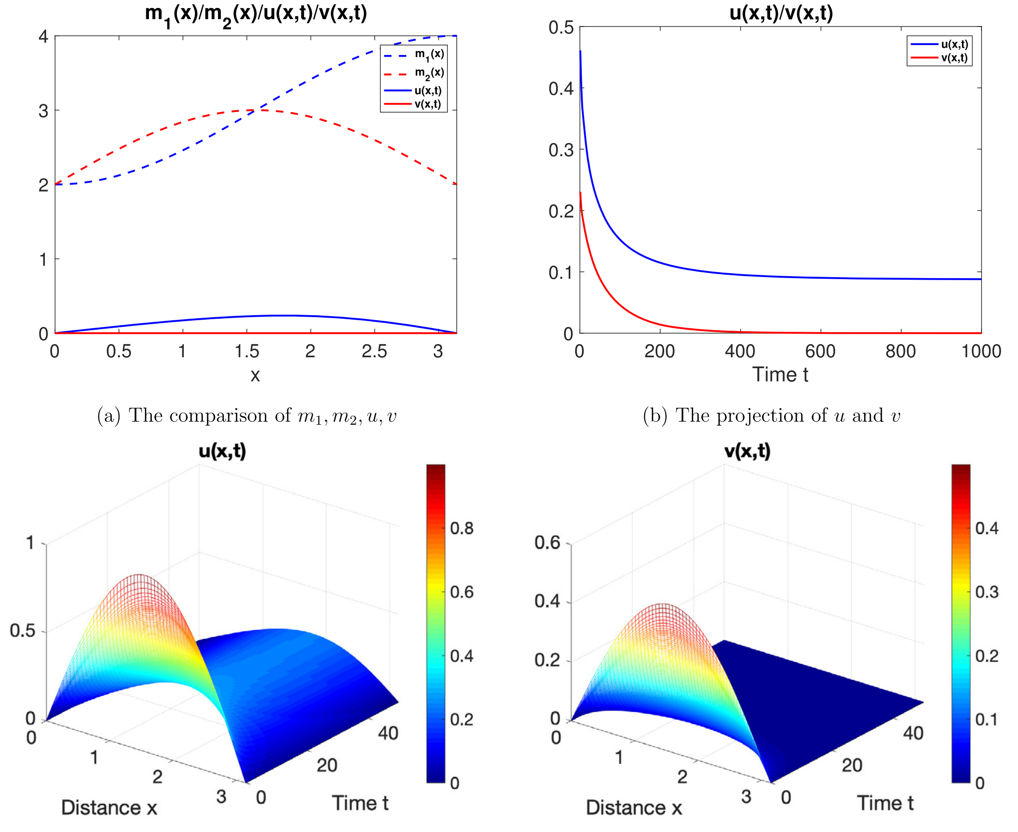
(d) The solution of $v(x,t)$

Fig. 2. Here, $\lambda_1 = 0.5$, $\lambda_2 = 0.4$, $(\lambda_1, \lambda_2) \in (0, \lambda_{1*}) \times (0, \lambda_{2*})$: The solution of (1.5) tends to (0, 0).

In this paper, we obtain the local existence and local asymptotic stability of the positive steady-state solution of system (1.5). In Fig. 6, we numerically provide the long-term behavior of the positive steady-state solution far away from the bifurcation point $(\lambda_{1*}, \lambda_{2*})$. Furthermore, from numerical simulations, we see that the positive steady-state solution is unique. We conjecture that the positive steady-state solution is unique, but it is a pity that we have not yet been able to prove it theoretically, and this will be a problem to be considered in the future.

5.1. Influence of stage structure on the steady-state solution

From Lemma 3.4, the upper bound of the steady-state solution is related to the stage structure. As the time delay τ increases, the upper bound of the steady-state solution gradually decreases and tends to 0. The resource function $m_i(x)$ is usually taken in the form of a sine or cosine function, see for example [9,31]. Here we let $m_1(x) = 3 - \cos 2x$, $m_2(x) = 3 + \sin 5x$. Figs. 7, 8, 9 and 10 show the effect of the stage structure on the steady-state solution when the resource environment is spatially heterogeneous. In Fig. 7, Fig. 8, Fig. 9 and Fig. 10, parameters are the same except for the time delay τ. As the time delay τ increasing, the positive steady-state



(a) The comparison of m_1, m_2, u, v

(b) The projection of u and v

(c) The solution of $u(x, t)$

(d) The solution of $v(x, t)$

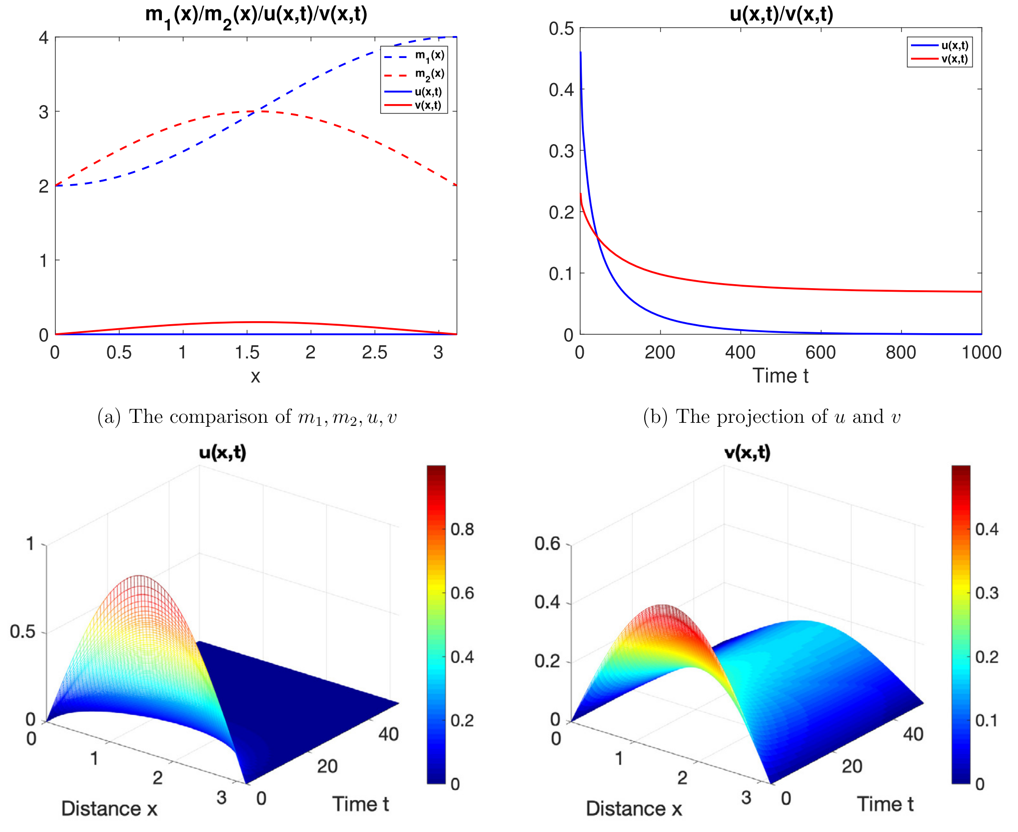
Fig. 3. Here, $\lambda_1 = 0.6250$, $\lambda_2 = 0.3846$, $(\lambda_1, \lambda_2) \in (\lambda_{1*}, \lambda_1^*) \times (0, \lambda_{2*})$: The solution of (1.5) tends to $(u_{\lambda_1}, 0)$.

solution gradually becomes smaller and then tends to 0, which means that the species u and v go from coexistence to extinction.

The increase of time delay τ implies a longer maturity period of the species. For insects and other invertebrates in temperate and subtropical regions, adverse environmental conditions can cause periods of developmental arrest. This a phenomenon known as diapause. See for example [39,40]. Newly mature species are rare if the maturation period is long. The species will be on the verge of extinction. This is also naturally in line with biological phenomena.

5.2. Influence of spatial heterogeneity on steady-state solution

Another interesting thing is to consider the effect of spatial heterogeneity on steady-state solution. The expression of the positive steady-state solution we obtained in Theorem 3.6 is related to the principal eigenfunction ϕ_{i*}, which in turn is related to the resource function $m_i(x)$. Therefore we may conjecture that the positive steady-state solution and the resource function are positively correlated. Due to the complexity of spatial heterogeneity, we are unable to prove it at this time, but numerical simulations of our model lend credence to this conjecture.



(a) The comparison of m_1, m_2, u, v

(b) The projection of u and v

(c) The solution of $u(x,t)$

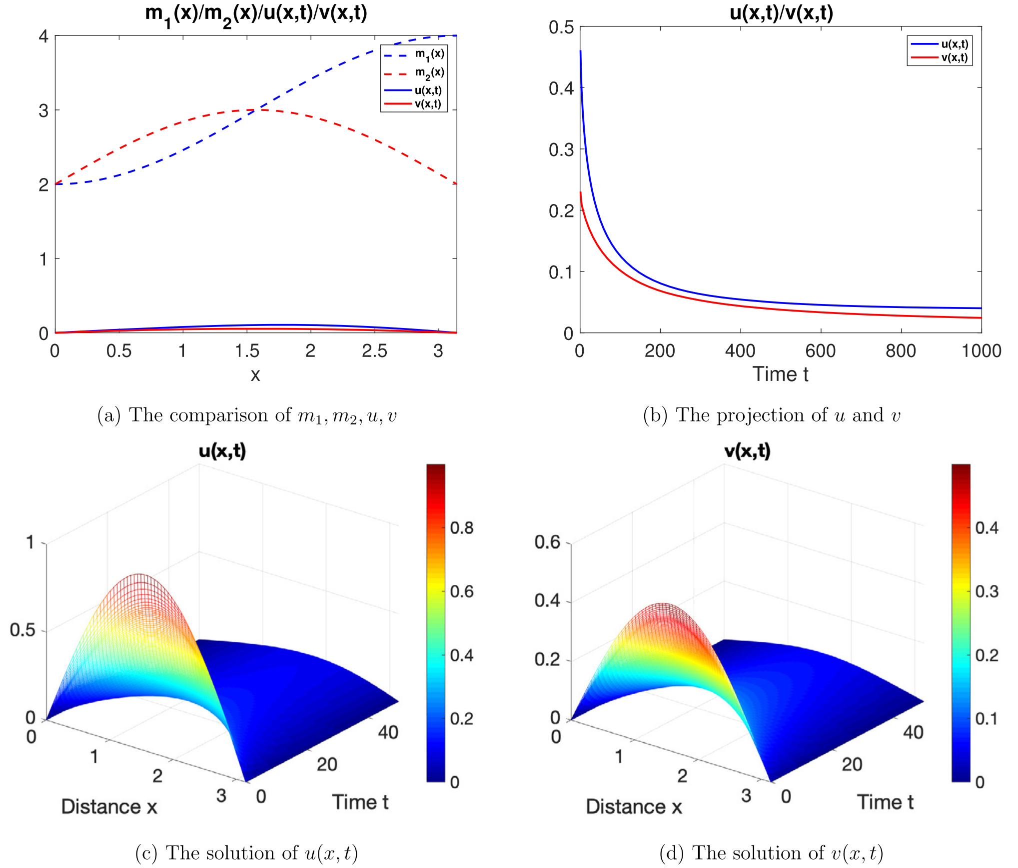
(d) The solution of $v(x,t)$

Fig. 4. Here, $\lambda_1 = 0.5$, $\lambda_2 = 0.4762$, $(\lambda_1, \lambda_2) \in (0, \lambda_{1*}) \times (\lambda_{2*}, \lambda_2^*)$: The solution of (1.5) tends to $(0, v_{\lambda_2})$.

Fig. 11 shows that the profile of the resource function and the principal eigenfunction are basically the same, and Fig. 7 shows that the profile of the resource function and the steady-state solution are basically the same. In Fig. 7, we find that the profiles of u and v are roughly the same as the distribution of resource functions $m_1(x)$ and $m_2(x)$. However, in Fig. 5, the shape of v matches the distribution of the resource function and the shape of u does not match, which is caused by the boundary condition of our model is the Dirichlet boundary condition. Although there are favorable living resources on the boundary, the species still die when they reach the boundary since the boundary is fatal. Therefore, the distribution of the solution is the joint effect of the combination of boundary conditions and resource distribution.

6. Discussion

In this paper, we consider a diffusion-advection-competition Lotka-Volterra model with stage structure under homogeneous Dirichlet boundary conditions. Moreover, the environments of the two species are spatially heterogeneous. Therefore, both semi-trivial steady-state solutions and the coexistence steady-state solution of the system are spatially non-homogeneous, and the diffusion-advection operator is not a self-adjoint, these all bring many difficulties to our analysis.



(a) The comparison of m_1, m_2, u, v

(b) The projection of u and v

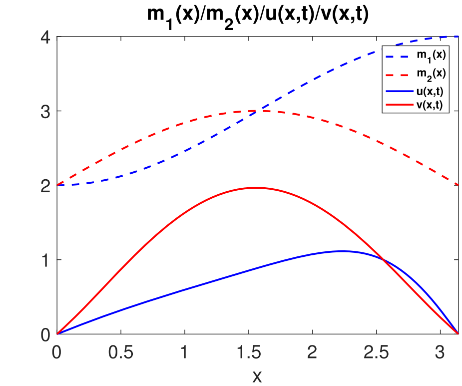
(c) The solution of $u(x,t)$

(d) The solution of $v(x,t)$

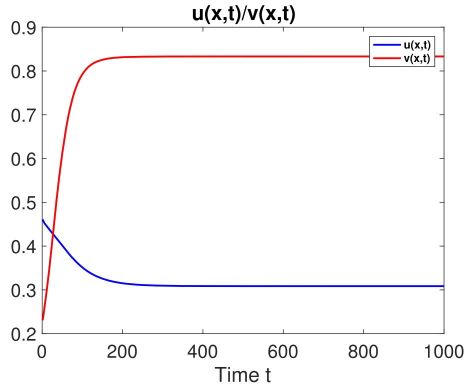
Fig. 5. Here, $\lambda_1 = 0.5882$, $\lambda_2 = 0.4545$, $(\lambda_1, \lambda_2) \in (\lambda_{1*}, \lambda_1^*) \times (\lambda_{2*}, \lambda_2^*)$: The solution of (1.5) tends to $(u_{\lambda_1}, v_{\lambda_2})$.

However, the single eigenvalue bifurcation theorem does not apply to the existence of the coexistence steady-state solution, we explore the existence of the coexistence steady-state solution by using the implicit function theorem. Stability is analyzed by methods such as comparison principle and eigenvalue analysis. We found that the increase of time delay will not destabilize the coexistence steady-state solution and generate periodic solutions through the Hopf bifurcation, the large time delay can lead to the extinction of species, which is different from the results in the existing work [9,31]. Using the reciprocal of diffusion coefficients of the two species as bifurcation parameters, we show the local existence and local asymptotic stability of steady-state solutions in different regions, see Fig. 1. If the random dispersal rates of both species are sufficiently large, both species go extinct. There are two critical values for the random dispersal rate of two species. If random diffusion rates of both species are less than the critical value, the two species can coexist; if one is greater than the critical value and the other is less than the critical value, then the species less than the critical value survives.

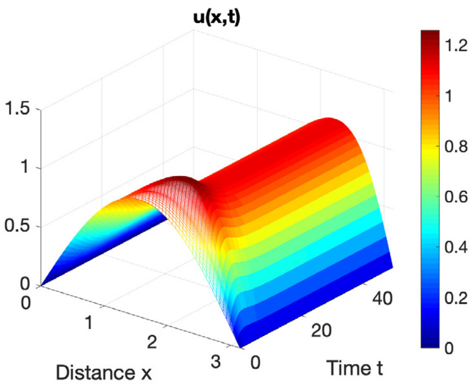
In numerical simulations, we observed that the steady-state solution exists not only locally but also globally. Furthermore, we show the effects of the stage structure and spatial heterogeneity on the steady-state solution. However, the proof of the global existence and global stability of the



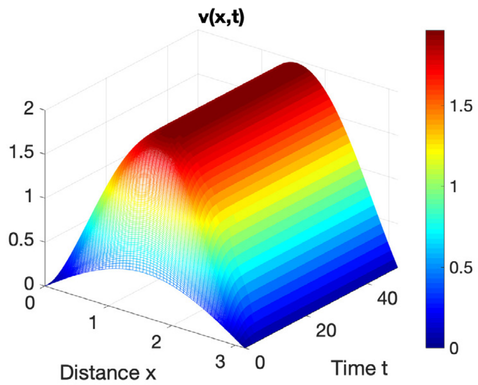
(a) The comparison of m_1, m_2, u, v



(b) The projection of u and v



(c) The solution of $u(x, t)$



(d) The solution of $v(x, t)$

Fig. 6. This figure shows that the positive steady-state solution still exists when the parameters are far away from the bifurcation point $(\lambda_{1*}, \lambda_{2*})$. Here, $\lambda_1 = 2.5, \lambda_2 = 2$.

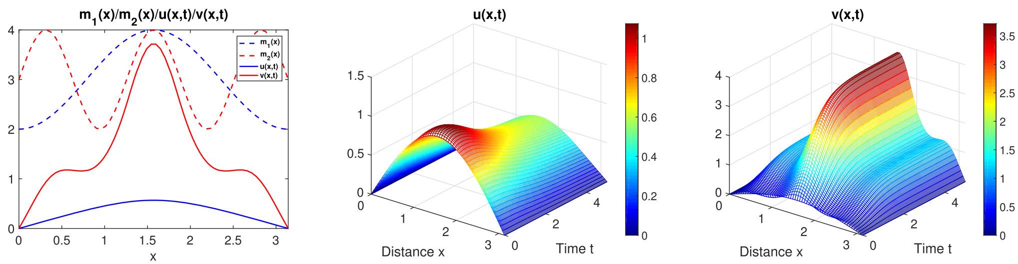


Fig. 7. $b = 0.3$, $c = 0.1$, $\gamma = 1$, $\alpha_1 = 0.5$, $\alpha_2 = 0.4$, $\lambda_1 = 0.5882$, $\lambda_2 = 0.4545$, $m_1(x) = 3 - \cos 2x$, $m_2(x) = 3 + \sin 5x$, $\tau = 0.05$.

steady-state solution is a difficult problem, and how the resource function affects the permanence and extinction of species remains an open question, which needs a new method.

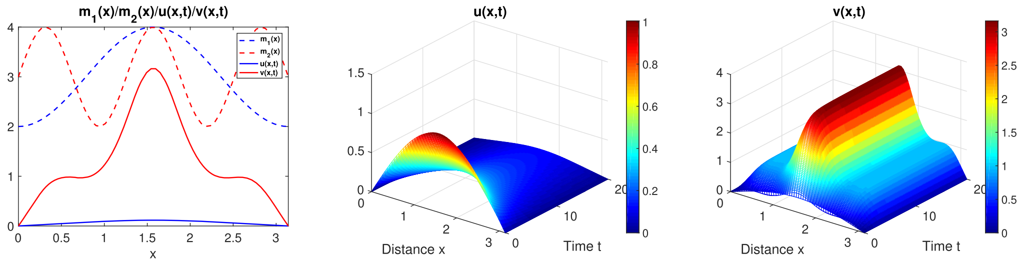


Fig. 8. $b = 0.3$, $c = 0.1$, $\gamma = 1$, $\alpha_1 = 0.5$, $\alpha_2 = 0.4$, $\lambda_1 = 0.5882$, $\lambda_2 = 0.4545$, $m_1(x) = 3 - \cos 2x$, $m_2(x) = 3 + \sin 5x$, $\tau = 0.2$.

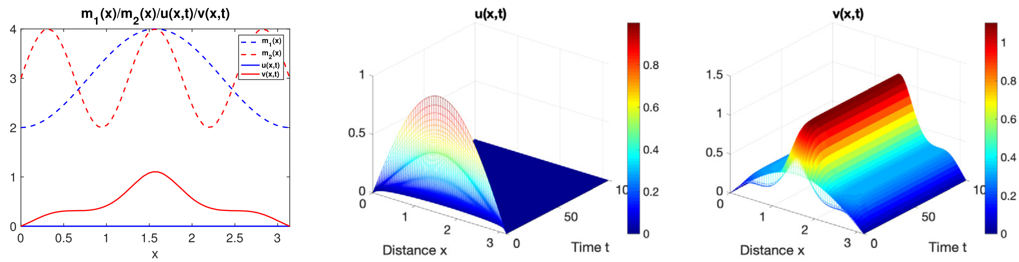


Fig. 9. $b = 0.3$, $c = 0.1$, $\gamma = 1$, $\alpha_1 = 0.5$, $\alpha_2 = 0.4$, $\lambda_1 = 0.5882$, $\lambda_2 = 0.4545$, $m_1(x) = 3 - \cos 2x$, $m_2(x) = 3 + \sin 5x$, $\tau = 1$.

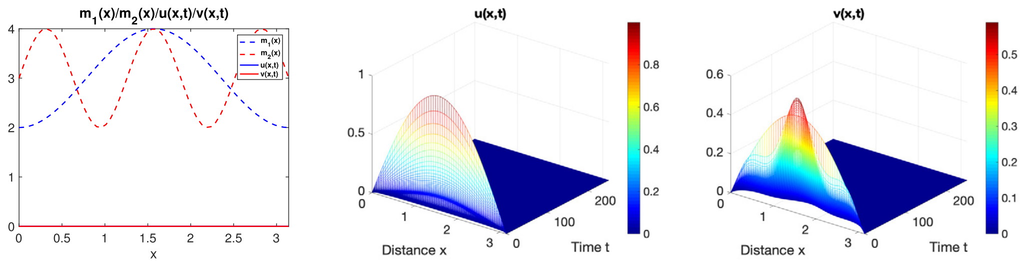


Fig. 10. $b = 0.3$, $c = 0.1$, $\gamma = 1$, $\alpha_1 = 0.5$, $\alpha_2 = 0.4$, $\lambda_1 = 0.5882$, $\lambda_2 = 0.4545$, $m_1(x) = 3 - \cos 2x$, $m_2(x) = 3 + \sin 5x$, $\tau = 2.5$.

Data availability

This is an article describes entirely theoretical research, data sharing is not applicable to this article as no datasets were generated or analyzed during the current study.

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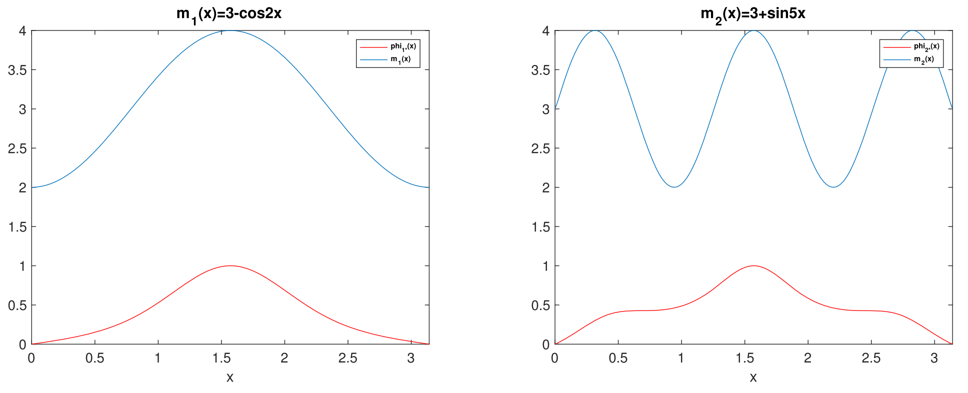

Fig. 11. The left is the profile of $\phi_{1*}(x)$ and $m_1(x)$. The right is the profile of $\phi_{2*}(x)$ and $m_2(x)$.

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