frontiers | Frontiers in Physics

TYPE Original Research
PUBLISHED 27 July 2023
DOI 10.3389/fphy.2023.1205571

OPEN ACCESS

EDITED BY
Xiaoming Zheng,
Central Michigan University, United States

REVIEWED BY
Xueyong Zhou,
Xinyang Normal University, China
Raid Naji,
University of Baghdad, Iraq

*CORRESPONDENCE
Zhiguo Wang,
zgwang@snnu.edu.cn

RECEIVED 14 April 2023
ACCEPTED 06 July 2023
PUBLISHED 27 July 2023

CITATION
Zhang W, Nie H and Wang Z (2023), Dynamics of an unstirred chemostat model with Beddington–DeAngelis functional response.
Front. Phys. 11:1205571.
doi: 10.3389/fphy.2023.1205571

Dynamics of an unstirred chemostat model with Beddington–DeAngelis functional response

Wang Zhang, Hua Nie and Zhiguo Wang*

School of Mathematics and Statistics, Shaanxi Normal University, Xi'an, China

This paper deals with an unstirred competitive chemostat model with the Beddington–DeAngelis functional response. With the help of the linear eigenvalue theory and the monotone dynamical system theory, we establish a relatively clear dynamic classification of this system in terms of the growth rates of two species. The results indicate that there exist several critical curves, which may classify the dynamics of this system into three scenarios: 1) extinction; 2) competitive exclusion; and 3) coexistence. Comparing with the classical chemostat model [26], our theoretical results reveal that under the weak–strong competition cases, the role of intraspecific competition can lead to species coexistence. Moreover, the simulations suggest that under different competitive cases, coexistence can occur for suitably small diffusion rates and some intermediate diffusion rates. These new phenomena indicate that the intraspecific competition and diffusion have a great influence on the dynamics of the unstirred chemostat model of two species competing with the Beddington–DeAngelis functional response.

KEYWORDS

unstirred chemostat model, coexistence, competitive exclusion, bifurcation, numerical simulation

1 Introduction

It is well known that the chemostat is a laboratory apparatus used for the continuous culture of microorganisms, while the chemostat models are extensively applied in ecology to simulate the growth of single-celled algal plankton in oceans and lakes [1–4]. Most of the earlier chemostat models assume the well-stirring of culture, which leads to chemostat models generally described by ordinary differential equation models (see, e.g., [2, 4, 5]). However, this idealized mixing is quite different from the real environment in which microbial populations live. Since the ability of microorganisms to move in a random fashion plays an important role in determining the survival and extinction of populations, many unstirred chemostat models have sprung up in which populations and resources are distributed in spatially variable habitats; please refer to [6–10] for small sampling of such works.

There are various types of response functions; among them, Holling types I–IV [11] are usually introduced to model the growth of microorganisms. Particularly, the various chemostat models with Holling type II functional response have been extensively studied (see, e.g., [4, 10, 12, 13]). As far as we know, for the unstirred competitive chemostat models with Holling type II functional response, So and Waltman [14] first obtained the local coexistence by standard bifurcation theorems. Later, Hsu and Waltman [6] obtained the asymptotic behavior of solutions by the theory of uniform persistence in an infinite-dimensional dynamical system and the theory of strongly order-preserving semi-dynamical system. To explore the effect of diffusion, Shi et al. [8] further studied this model and confirmed that stable coexistence solutions only occur at the intermediate diffusion rates. In addition, a diffusive predator–prey chemostat model with Holling type II functional response was studied by Nie et al. [7], and their analytical and numerical results show that a relatively small diffusion is conducive to the coexistence of species.

However, in nature, it is known that there is not only competition between two species but also mutual interference in species. Therefore, it is necessary to consider mutual interference in species. To this end, Beddington [15] and DeAngelis et al. [16] (simplified as B.–D.) proposed the following B.–D. functional response:

$$f_1(S,u) = \frac{S}{k_1 + S + \beta_1 u}, \quad f_2(S,v) = \frac{S}{k_2 + S + \beta_2 v}, \tag{1.1}$$

where $k_i > 0$ ($i = 1, 2$) are the Michaelis–Menten constants, S represents the density of the resources, u and v represent the density of two species, respectively, and $\beta_i > 0$ ($i = 1, 2$) model the mutual interference between two species.

As illustrated by Harrision [17], the B.–D. functional response with intraspecific interference competition was superior to well-known Holling type II functional response in modeling the resource uptake of species. Therefore, there appear successively many works to describe the population dynamics by using the B.–D. functional response. For instance, Jiang et al. [18] discussed a competition model with the B.–D. functional response, and they applied the fixed-point index theory to obtain the sufficient conditions for the existence of positive solutions. In addition, a predator–prey model with a heterogeneous environment and the B.–D. functional response was constructed by Zhang and Wang [19], and the existence of positive stationary solutions was obtained by using the fixed-point index theory. We also refer the recent works [20–22] about population models with the B.–D. functional response.

Particularly, the unstirred chemostat models with the B.–D. functional response have also received considerable attention in the past decades. Wang et al. [23] obtained the sufficient conditions for the existence of positive steady-state solutions and studied the effect of parameter β_1 on coexistence states by the fixed-point index theory, the perturbation technique, and the bifurcation theory. Meanwhile, Nie and Wu [24] studied the unstirred chemostat model with the B.–D. functional response and inhibitor, and the uniqueness, multiplicity, and stability of the coexistence solutions were obtained by the degree theory in cones, bifurcation theory, and perturbation technique. More works on chemostat models with the B.–D. functional response can be found in [25–27] and the references therein.

Mathematically speaking, these sufficient conditions for the existence of coexistence solutions are usually established in terms of the principal eigenvalues of the corresponding linearized eigenvalue problems at trivial or semi-trivial steady states (see, e.g., [18, 19, 23, 24]). It is worth noting that these principal eigenvalues depend heavily on the model parameters, which motivates us to explore how these model parameters affect the existence of coexistence solutions and establish the dynamics classification of this system in terms of these model parameters. Moreover, it should be noted that studying the asymptotic analysis of steady states of chemostat models is non-trivial, and some new techniques need to be introduced. Overall, for the unstirred chemostat system with the B.–D. functional response, we are concerned with the following questions:

(1) How do parameters such as diffusion rates, growth rates, and intraspecific competition parameters affect the dynamics of the unstirred chemostat system with the B.–D. functional response?
(2) Can we establish a clear dynamic classification of the unstirred chemostat system with the B.–D. functional response in terms of these parameters?
(3) Will there arise a new phenomenon if one introduces the B.–D. functional response into the unstirred chemostat model?

The purpose of this paper is to address these problems. We hope that the approaches in this paper might provide some new insights on the dynamical behavior of the unstirred chemostat models.

This paper is organized as follows. In Section 2, we introduce an unstirred chemostat model with the B.–D. functional response and its corresponding limiting system. In Section 3, some preliminary results are given. In Section 4, we aim to investigate the dynamics of this limiting system and obtain a relatively clear dynamic classification of this limiting system in the $m_1 - m_2$ plane. In Section 5, the coexistence solution for this limiting system is established by a bifurcation argument. In Section 6, we study the effect of diffusion on system dynamics by numerical approaches. In Section 7, a discussion is presented from the opinion of analytic and numerical results. Finally, the proofs of some theoretical results are deferred to the Supplementary Appendix in Supplementary Section S8.

2 The model

In this paper, we consider following the unstirred chemostat system with the B.–D. functional response:

$$\begin{cases} S_t = dS_{xx} - m_1 u f_1(S,u) - m_2 v f_2(S,v), & x \in (0,1),\ t > 0, \\ u_t = du_{xx} + m_1 u f_1(S,u), & x \in (0,1),\ t > 0, \\ v_t = dv_{xx} + m_2 v f_2(S,v), & x \in (0,1),\ t > 0, \\ S_x(0,t) = -S^0, S_x(1,t) + \gamma S(1,t) = 0, & t > 0, \\ u_x(0,t) = u_x(1,t) + \gamma u(1,t) = 0, & t > 0, \\ v_x(0,t) = v_x(1,t) + \gamma v(1,t) = 0, & t > 0, \\ S(x,0) = S_0(x) \geq 0, & x \in [0,1], \\ u(x,0) = u_0(x) \geq, \not\equiv 0, v(x,0) = v_0(x) \geq, \not\equiv 0, & x \in [0,1], \end{cases} \tag{2.1}$$

where $S(x, t)$ is the concentration of the nutrient and $u(x, t)$ and $v(x, t)$ represent the population density for the two competing microorganisms with location x and time t, respectively. The positive constants m_1 and m_2 are corresponding to the growth rates of species u and v with nutrient concentration S. $d > 0$ is the diffusion rate of the nutrient and microorganisms. The initial data $S_0(x)$, $u_0(x)$, and $v_0(x)$ are non-negative non-trivial continuous functions. In the reactor, the nutrients are pumped with the rate of

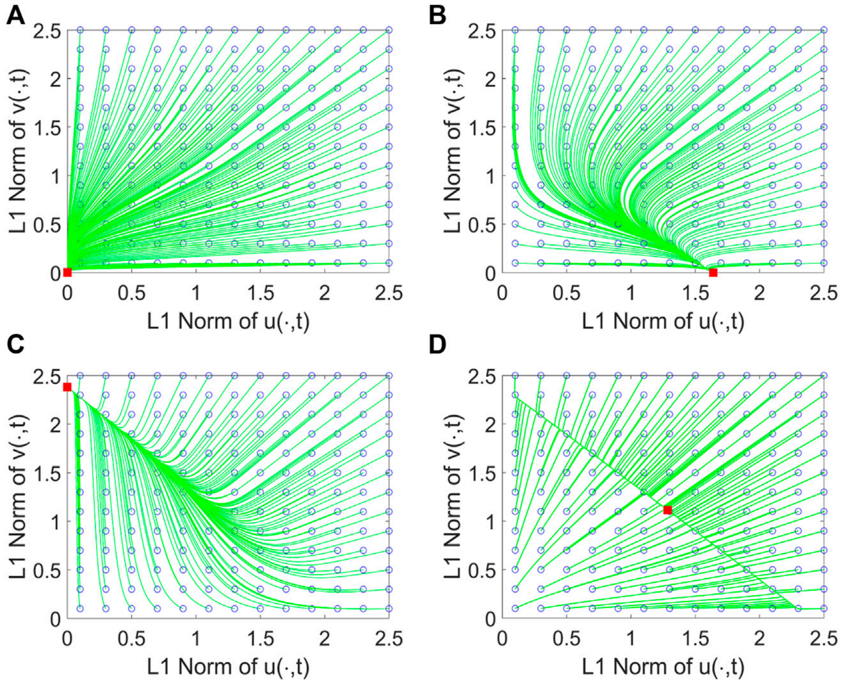

FIGURE 1
Phase portrait graphs of system (2.2) for different growth rates m_1 and m_2. Here, we take $\beta_1 = 0.01$, $\beta_2 = 0.01$, $L = 1$, $S^0 = 1$, $d = 0.5$, $\gamma = 0.5$, $k_1 = 1$, and $k_2 = 0.4$. As shown, (0,0) is globally asymptotically stable (simplified as g.a.s) in **(A)** with $m_1 = 0.2$, $m_2 = 0.1$; $(\hat{u}, 0)$ is g.a.s. in **(B)** with $m_1 = 1$, $m_2 = 0.1$; $(0, \hat{v})$ is g.a.s. in **(C)** with $m_1 = 0.2$, $m_2 = 1$; and there exist stable coexistence steady states in **(D)** with $m_1 = 1$, $m_2 = 0.545$.

$S^0 > 0$ at position $x = 0$, and the mixed cultures containing nutrients and microorganisms are pumped out with the rate of $\gamma > 0$ at the position $x = 1$, which results in the Robin boundary conditions at $x = 1$ [6]. Here, $f_1(S, u)$, $f_2(S, v)$ satisfying Eq. 1.1 are the nutrient uptake of species u and v at nutrient concentration S. Moreover, we redefine $f_1(S, u)$, $f_2(S, v)$ as follows [10]:

$$\hat{f}_1(S,u) = \begin{cases} f_1(S,u), & S \ge 0,\ u \ge 0, \\ 0, & \text{others}, \end{cases}$$

$$\hat{f}_2(S,v) = \begin{cases} f_2(S,v), & S \ge 0,\ v \ge 0, \\ 0, & \text{others}. \end{cases}$$

For convenience, we still denote $\hat{f}_i(S,u)$ $(i = 1, 2)$ as $f_i(S, u)$, throughout this paper.

It is worth pointing out that system (2.1) satisfies the conservation law [4]. In other words, the total biomass concentration $S + u + v$ in the chemostat approaches asymptotically a steady state $\phi(x) = S^0\left(\frac{1+\gamma}{\gamma} - x\right)$ (see [14], Lemma 2.1); that is,

$$\lim_{t\to\infty} (S(x,t) + u(x,t) + v(x,t)) = \phi(x) \text{ uniformly for } x \in [0,1].$$

Hence, we apply the classical internal chain transitive theory [[28], Lemma 2.1] to reduce system (2.1) into the following limiting system:

$$\begin{cases} u_t = du_{xx} + m_1 f_1(\phi(x) - u - v, u)u, & x \in (0,1),\ t > 0, \\ v_t = dv_{xx} + m_2 f_2(\phi(x) - u - v, v)v, & x \in (0,1),\ t > 0, \\ u_x(0,t) = u_x(1,t) + \gamma u(1,t) = 0,\ v_x(0,t) = v_x(1,t) + \gamma v(1,t) = 0, & t > 0, \\ u(x,0) = u_0(x) \ge, \not\equiv 0, v(x,0) = v_0(x) \ge, \not\equiv 0, u_0(x) + v_0(x) \le \phi(x) & x \in [0,1]. \end{cases} \tag{2.2}$$

In this paper, we are mainly concerned with the dynamics classification of system (2.2). Based on the competition relationship of two species, system (2.2) generates a strictly monotone dynamical system in the partial competitive order induced by the cone $K = \{(u, v) \in C[0, 1] \times C[0, 1]: u \ge 0,\ v \le 0\}$ (see [27], Proposition 1.3 in Chapter 8). Since the dynamics of Eq. 2.2 are related to the stability of non-negative steady states [29], we also focus on the following steady-state system:

$$\begin{cases} du_{xx} + m_1 f_1(\phi(x) - u - v, u)u = 0, & x \in (0,1), \\ dv_{xx} + m_2 f_2(\phi(x) - u - v, v)v = 0, & x \in (0,1), \\ u_x(0) = u_x(1) + \gamma u(1) = 0,\ v_x(0) = v_x(1) + \gamma v(1) = 0. \end{cases} \tag{2.3}$$

The contribution of this paper is to explore the effect of these model parameters on the dynamics of system (2.2). Precisely, we first apply the linear eigenvalue theory and the monotone dynamical system theory to establish the threshold dynamics of system (2.2) in terms of growth rates and intraspecific competition parameters (see Theorems 4.1, 4.2). Moreover, we give a relatively clear dynamic classification of system (2.2) in the $m_1 - m_2$ plane (Figure 2). Finally, by numerical simulations, we further investigate the effect of diffusion on the dynamics of system (2.2) (Figures 3–5). Particularly, the numerical results show that under the different competitive cases, coexistence occurs for suitably small diffusion rates and some intermediate diffusion rates, which reveals that the dynamics of system (2.2) are relatively complicated.

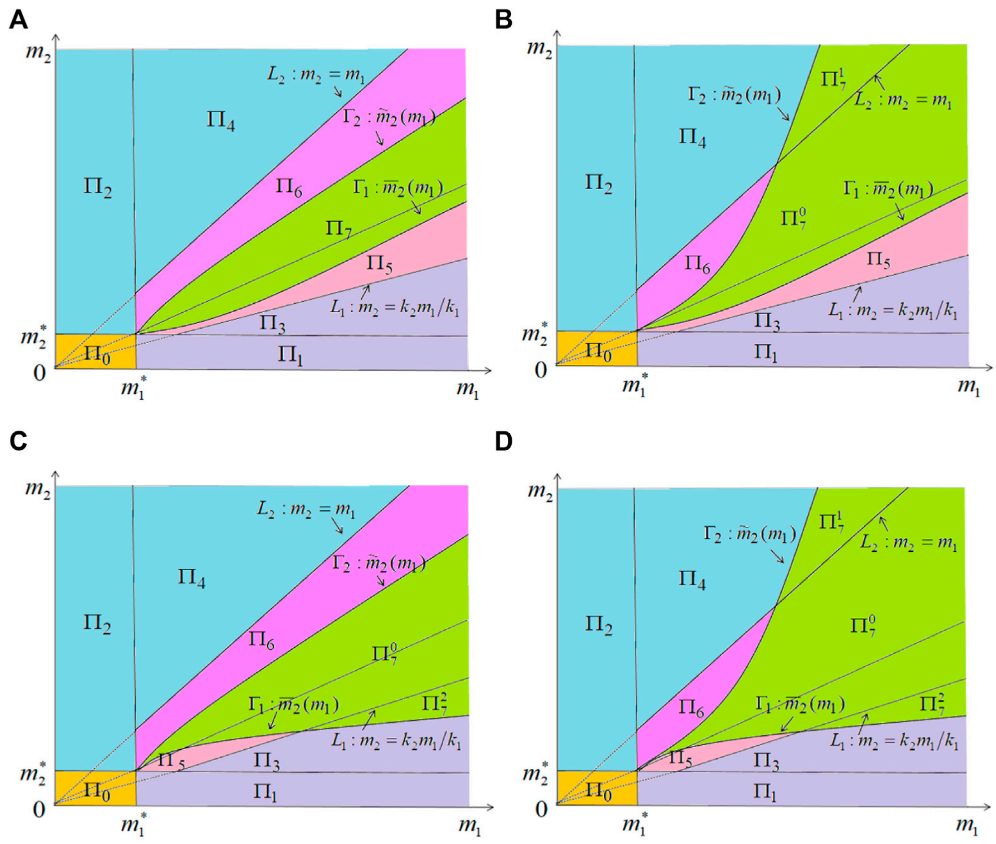

FIGURE 2
Illustration of the dynamics of system (2.2) in the $m_1 - m_2$ plane for the case of $k_1 > k_2 > 0$. More precisely, **(A)** $0 < \beta_1 \le \beta_1^0$ and $0 < \beta_2 \le \beta_2^0$; **(B)** $0 < \beta_1 \le \beta_1^0$ and $\beta_2 > \beta_2^\star$; **(C)** $\beta_1 > \beta_1^\star$ and $0 < \beta_2 \le \beta_2^0$; and **(D)** $\beta_1 > \beta_1^\star$ and $\beta_2 > \beta_2^\star$. Then, (0,0) is g.a.s in region Π_0; $(\hat{u}, 0)$ is g.a.s in region $\Pi_1 \cup \Pi_3$; $(0, \hat{v})$ is g.a.s in region $\Pi_2 \cup \Pi_4$; $(\hat{u}, 0)$ is locally asymptotically stable in region Π_5 and unstable in region $\Pi_6 \cup \Pi_7$; $(0, \hat{v})$ is locally asymptotically stable in region Π_6 and unstable in region $\Pi_5 \cup \Pi_7$; and there exist stable coexistence steady states in Π_7. Here, we note that **(B)** $\Pi_7 = \Pi_7^0 \cup \Pi_7^1$, **(C)** $\Pi_7 = \Pi_7^0 \cup \Pi_7^2$, and **(D)** $\Pi_7 = \Pi_7^0 \cup \Pi_7^1 \cup \Pi_7^2$.

3 Preliminaries

In this section, some preliminary results are presented, which are helpful in the following analysis.

We first consider a linear eigenvalue problem

$$\begin{cases} d\varphi_{xx} + q(x)\varphi = \mu\varphi, & x \in (0,1), \\ \varphi_x(0) = \phi_x(1) + \gamma\varphi(1) = 0, \end{cases} \tag{3.1}$$

where γ is a positive constant and $q(x) \in C[0,1]$. For fixed $d > 0$, it is well known that problem (3.1) admits a principal eigenvalue $\mu_1(q(x))$ [29], which corresponds to a positive eigenfunction $\varphi_1(\cdot, q(x))$ normalized by $\max_{x\in[0,1]} \varphi_1 = 1$. Furthermore, by the variation characterization of the principal eigenvalue [29], we have

$$\mu_1(q(x)) = -\inf_{\varphi\in H^1(0,1),\varphi\neq 0} \frac{d\int_0^1 (\varphi_x)^2 dx + d\gamma\varphi^2(1) - \int_0^1 q(x)\varphi^2 dx}{\int_0^1 \varphi^2 dx}. \tag{3.2}$$

Moreover, the principal eigenvalue $\mu_1(q(x))$ has the following properties.

Lemma 3.1. (See [21], Lemma 2.1). *The following statements on the principal eigenvalue $\mu_1(q(x))$ are true:*

(i) *$\mu_1(q(x))$ depends continuously and differentially on parameter d in $(0, +\infty)$, and it is strictly decreasing with respect to d in $(0, +\infty)$.*
(ii) *$q_n(x) \to q(x)$ in $C[0,1]$ implies $\mu_1(q_n(x)) \to \mu_1(q(x))$.*
(iii) *$q_1(x) \ge q_2(x)$ implies that $\mu_1(q_1(x)) \ge \mu_1(q_2(x))$, and the equality holds only if $q_1(x) \equiv q_2(x)$. Particularly, $\mu_1(0) < 0$.*

We consider the following single-species model:

$$\begin{cases} \omega_t = d\omega_{xx} + mf(\phi - \omega, \omega)\omega, & x \in (0,1),\ t > 0, \\ \omega_x(0,t) = \omega_x(1,t) + \gamma\omega(1,t) = 0, & t > 0, \\ \omega(x,0) = \omega_0(x) \ge, \not\equiv 0, & x \in [0,1], \end{cases} \tag{3.3}$$

where $d, m > 0$ are constants and $f(\phi - \omega, \omega) = \frac{\phi - \omega}{k + \phi + (\beta - 1)\omega}$. For fixed d, $k > 0$, let $\mu_1(mf(\phi, 0))$ be the principal eigenvalue of

$$\begin{cases} d\varphi_{xx} + mf(\phi, 0)\varphi = \mu\varphi, & x \in (0,1),\ t > 0, \\ \varphi_x(0) = \varphi_x(1) + \gamma\varphi(1) = 0, \end{cases}$$

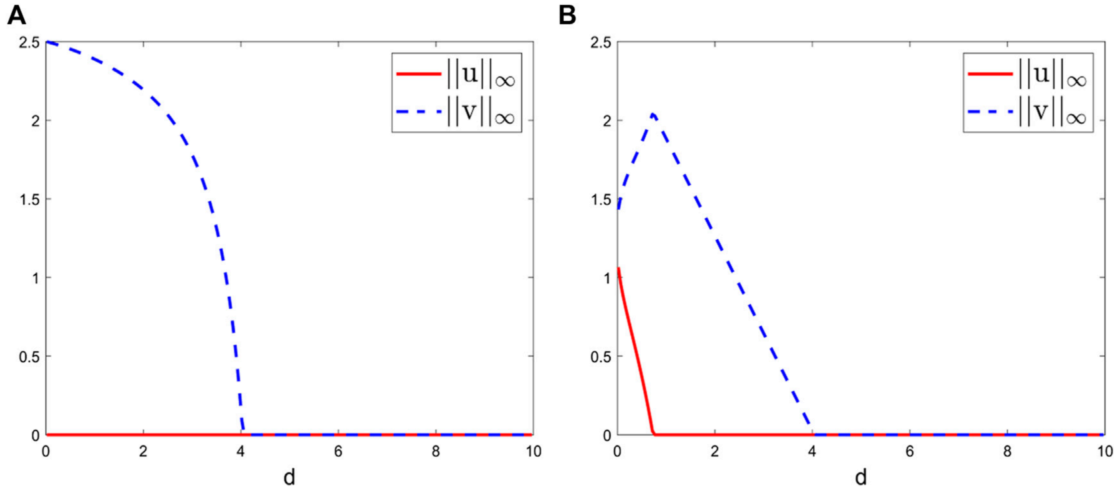

FIGURE 3
Bifurcation diagrams of the positive steady-state solutions to system (2.2) at $t = 2000$ with the bifurcation parameter d ranging from 0.01 to 10. Here, we take $L = 1$, $S^0 = 1$, $\gamma = 0.5$, $k_1 = 1$, $k_2 = 0.4$, $m_1 = 1$, and $m_2 = 2$ and **(A)** $\beta_1 = 0.01$, $\beta_2 = 0.01$ and **(B)** $\beta_1 = 0.01$, $\beta_2 = 1$.

where $f(\phi, 0) = \frac{\phi}{k+\phi}$. Then, we can conclude from Lemma 3.1(iii) that $\mu_1(mf(\phi, 0))$ is strictly increasing with respect to m in $(0, +\infty)$. Moreover, $\lim_{m\to 0^+} \mu_1(mf(\phi,0)) = \mu_1(0) < 0$ by Lemma 3.1(iii), and $\lim_{m\to+\infty} \mu_1(mf(\phi,0)) = +\infty$ by Eq. 3.2. For fixed $d, k > 0$, there exists a unique critical value $m^\star$ such that

$$\begin{cases} \mu_1(mf(\phi,0)) < 0 & \text{if} \quad 0 < m < m^*, \\ \mu_1(mf(\phi,0)) = 0 & \text{if} \quad m = m^*, \\ \mu_1(mf(\phi,0)) > 0 & \text{if} \quad m > m^*. \end{cases} \tag{3.4}$$

To stress the dependence of the unique positive steady state of system (3.3) on m and β, let us denote it by $\omega_*(\cdot; m, \beta)$.

Lemma 3.2. *Suppose d, m, β, $k > 0$. Let $\omega(x, t)$ be the solution of system* (3.3). *Then,*

(i) *if $m > m^*$, system* (3.3) *admits a unique positive steady state $0 < \omega_*(\cdot; m, \beta) < \phi(x)$ for $x \in [0, 1]$, and $\lim_{t\to\infty} \omega(x,t) = \omega_*(\cdot; m, \beta)$ uniformly on* [0,1];
(ii) *if $m \le m^*$, system* (3.3) *has no positive steady state and $\lim_{t\to\infty} \omega(x,t) = 0$ uniformly on* [0,1].

The proof of Lemma 3.2 is similar to the arguments in [6], Theorem 3.2. So, we omit it here.

We next give some asymptotic properties of the unique positive steady state $\omega_*(\cdot; m, \beta)$ of system (3.3) by taking m and β as the variable parameters.

Lemma 3.3. suppose that $m > m^*$ holds. The following statements about the positive solution $\omega_*(; m, \beta)$ will hold.

(i) For fixed d, k, $\beta > 0$, there exists positive solution $\omega_*(; m, \beta)$, which is continuously differentiable with respect to m in $(m^*, +\infty)$, and it is point-wise strictly increasing in $m \in (m^*, +\infty)$. Moreover,

$$\lim_{m\to(m^*)^+} \omega_*(\cdot; m, \beta) = 0, \quad \lim_{m\to+\infty} \omega_*(\cdot; m, \beta) = \phi(x) \quad \text{uniformly on } [0,1]. \tag{3.5}$$

(ii) For fixed $d, k > 0$ and $m > m^*$, there exists positive solution $\omega_*(\cdot; m, \beta)$, which is continuously differentiable with respect to β in $(0, +\infty)$, and it is point-wise strictly decreasing in $\beta \in (0, +\infty)$. Moreover,

$$\lim_{\beta\to+\infty} \omega_*(\cdot; m, \beta) = 0 \quad \text{uniformly on } [0,1]. \tag{3.6}$$

Proof. For (i), it follows from Lemma 3.2 that $\omega_*(\cdot; m, \beta)$ exists if and only if $m > m^*$. Moreover, $\omega_*(\cdot; m, \beta)$ is continuously differentiable with respect to m in $(m^*, +\infty)$ refering to the arguments in [30], Lemma 5.4(ii). Differentiating the equation of $\omega_*(\cdot; m, \beta)$ with respect to m and denoting $P_m(x) = \partial\omega_*(\cdot; m, \beta)/\partial m$, $P_m(x)$ satisfies

$$\begin{cases} dP_m'' + m\left[f(\phi - \omega_*, \omega_*) - \dfrac{(k+\beta\phi)\omega_*}{[k+\phi+(\beta-1)\omega_*]^2}\right] \\ P_m = -f(\phi - \omega_*, \omega_*)\omega_*, x \in (0,1), \\ P_m'(0) = P_m'(1) + \gamma P_m(1) = 0. \end{cases} \tag{3.7}$$

We define $\mathbb{X} = \{\psi \in C^2[0,1]: \psi'(0) = \psi'(1) + \gamma\psi(1) = 0\}$ and denote $L_1(\psi) = d\psi'' + m\left[f(\phi - \omega_*, \omega_*) - \frac{(k+\beta\phi)\omega_*}{[k+\phi+(\beta-1)\omega_*]^2}\right]\psi$. It is easy to see that $\mu^1(L^1) < \mu^1(mf(\phi - \omega^*, \omega^*)) = 0$ by Lemma 3.1(iii). Noting that $P_m(x) \in \mathbb{X}$ and $L^1(P^m) = -f(\phi - \omega^*, \omega^*)\omega^* < 0$, we have $P^m(x) > 0$ on [0,1] by the generalized maximum principle [23, Theorem 5], which implies that $\omega^*(\cdot; m, \beta)$ is point-wise strictly increasing in $m \in (m, +\infty)$.

Since $0 < \omega_*(\cdot; m, \beta) < \phi$ and $\omega_*'' = -\frac{m}{d} f(\phi - \omega_*, \omega_*)\omega_* < 0$, ω_*' is decreasing on [0,1]. Note that the boundary conditions $\omega_*'(0) = 0$, $\omega_*'(1) = -\gamma\omega_*(1)$. Then, $\omega_*'(x)$ is uniformly bounded for $x \in [0, 1]$. It follows from the Arzela–Ascoli theorem that there exist $\omega_1, \omega_2 \in C[0, 1]$ with $0 \le \omega_1 \le \phi$ and $0 \le \omega_2 \le \phi$ such that

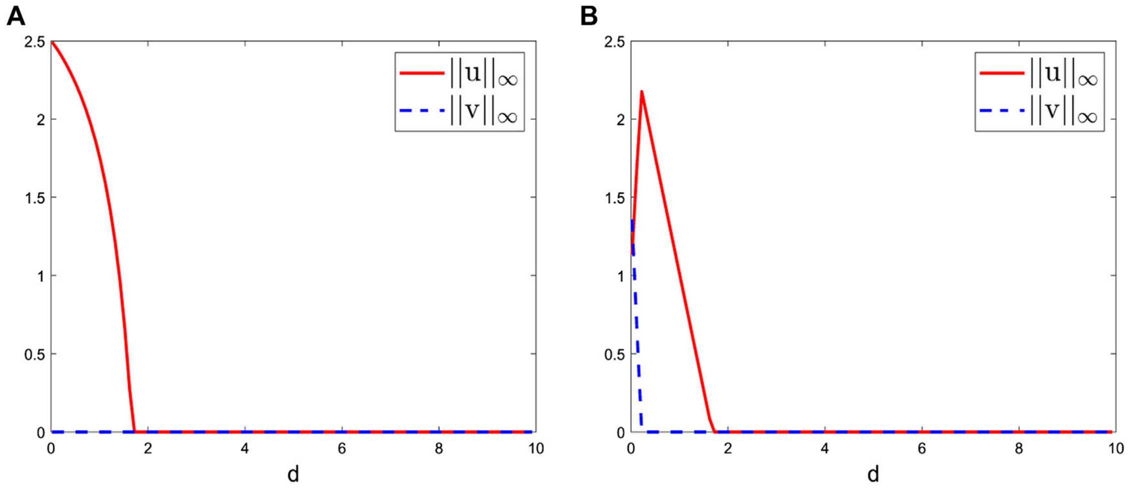

FIGURE 4
Bifurcation diagrams of the positive steady-state solutions to system (2.2) at $t = 2000$ with the bifurcation parameter d ranging from 0.01 to 10. Here, we take $L = 1$, $S^0 = 1$, $\gamma = 0.5$, $k_1 = 1$, $k_2 = 0.4$, $m_1 = 1$, and $m_2 = 0.2$ and **(A)** $\beta_1 = 0.01$, $\beta_2 = 0.01$ and **(B)** $\beta_1 = 1$, $\beta_2 = 0.01$.

$$\lim_{m\to(m^*)^+} \omega_*(\cdot; m,\beta) = \omega_1, \quad \lim_{m\to+\infty} \omega_*(\cdot; m,\beta) = \omega_2 \text{ in } C[0,1].$$

To prove $\omega_1 = 0$ on [0,1], we assume by contradiction that $\omega_1 \not\equiv 0$ on [0,1]. Since $0 < f(\phi - \omega_*, \omega_*) < 1$, the standard L^p-estimate implies that $\omega_*(\cdot; m, \beta)$ is uniformly bounded in $W^{2,p}(0, 1)$ with $p \in (1, \infty)$ for $m \in (m^*, M]$, where M is a fixed constant larger than m^*. Therefore, $\lim_{m\to(m^*)^+} \omega_*(\cdot; m,\beta) = \omega_1$ weakly in W^2, p (0, 1) and the convergence also holds in $C^1[0, 1]$ by the Sobolev embedding theorem. Then, ω^1 satisfies

$$\begin{cases} d\omega_1'' + m^* f(\phi - \omega_1, \omega_1)\omega_1 = 0, & x \in (0,1), \\ \omega_1'(0) = \omega_1'(1) + \gamma\omega_1(1) = 0. \end{cases} \tag{3.8}$$

Since $\omega_1 \not\equiv 0$ on [0,1], we have $\omega_1 > 0$ on [0,1] by the strong maximum principle. It is easy to see that $\mu_1(m^* f(\phi, 0)) > \mu_1(m^* f(\phi - \omega_1, \omega_1)) = 0$ by Lemma 3.1(iii), a contradiction to the definition of m^* (Eq. 3.4). Thus, $\omega_1 = 0$.

We next prove $\omega_2 = \phi(x)$ on [0,1]. We recall that $\omega_*(\cdot; m, \beta)$ satisfies

$$\begin{cases} d\omega_*'' + m f(\phi - \omega_*, \omega_*)\omega_* = 0, & x \in (0,1), \\ \omega_*'(0) = \omega_*'(1) + \gamma\omega_*(1) = 0. \end{cases} \tag{3.9}$$

Dividing the first equation of Eq. 3.9 by $m\omega_*$ and integrating over (0,1),

$$\frac{d}{m}\int_0^1 \frac{|\omega_*'|^2}{\omega_*^2} dx - \frac{d\gamma}{m} + \int_0^1 f(\phi - \omega_*, \omega_*) dx = 0,$$

which implies

$$0 \le \int_0^1 f(\phi - \omega_*, \omega_*) dx \le \frac{d\gamma}{m}.$$

Note $\lim_{m\to+\infty} \omega_*(\cdot; m,\beta) = \omega_2$ in $C[0, 1]$. Taking $m \to +\infty$, we have $\int_0^1 f(\phi - \omega_2, \omega_2)dx = 0$, which means $\omega_2 = \phi(x)$ on [0,1] by $0 \le \omega_2 \le \phi$.

(ii) The monotonicity of $\omega_*(\cdot; m, \beta)$ with respect to β in $(0, +\infty)$ can be proved by the similar arguments as in the proof of (i) and $\lim_{\beta\to+\infty} \omega_*(\cdot; m,\beta) = 0$ uniformly on $[0,1]$ holds (see [23], Remark 1.2).

It is clear that system (2.2) generates a monotone dynamical system in the partial competitive order induced by the cone $K = \{(u, v) \in C[0, 1] \times C[0, 1]\colon u \ge 0, v \le 0\}$ (see [27], Proposition 1.3 in Chapter 8). Hence, we can recall the well-known results on the monotone dynamical system as follows.

Lemma 3.4. [9]. For the monotone dynamical system,

(i) if two semi-trivial steady states are asymptotically stable, then it has at least one unstable coexistence steady state.
(ii) if two semi-trivial steady states are unstable, then it has at least one stable coexistence steady state. Furthermore, if its coexistence steady states are all linearly stable, then there is a unique coexistence steady state that is globally asymptotically stable.
(iii) if there is no coexistence steady state and if one semi-trivial solution is linearly unstable, the other semi-trivial solution is globally asymptotically stable.

4 The dynamics analysis of system (2.2)

As we already know, the local dynamics of system (2.2) are related to the stability of semi-trivial solutions [29]. Hence, we next establish the stability of semi-trivial solutions, including local and some global stability results. Recalling $f_i(\phi, 0) = \frac{\phi}{k_i+\phi}$ $(i = 1, 2)$, by the similar arguments as in (3.4), we can define m_i^* such that

$$\begin{cases} \mu_1(m_i f_i(\phi, 0)) < 0 & \text{if } 0 < m_i < m_i^*, \\ \mu_1(m_i f_i(\phi, 0)) = 0 & \text{if } m_i = m_i^*, \\ \mu_1(m_i f_i(\phi, 0)) > 0 & \text{if } m_i > m_i^*. \end{cases} \tag{4.1}$$

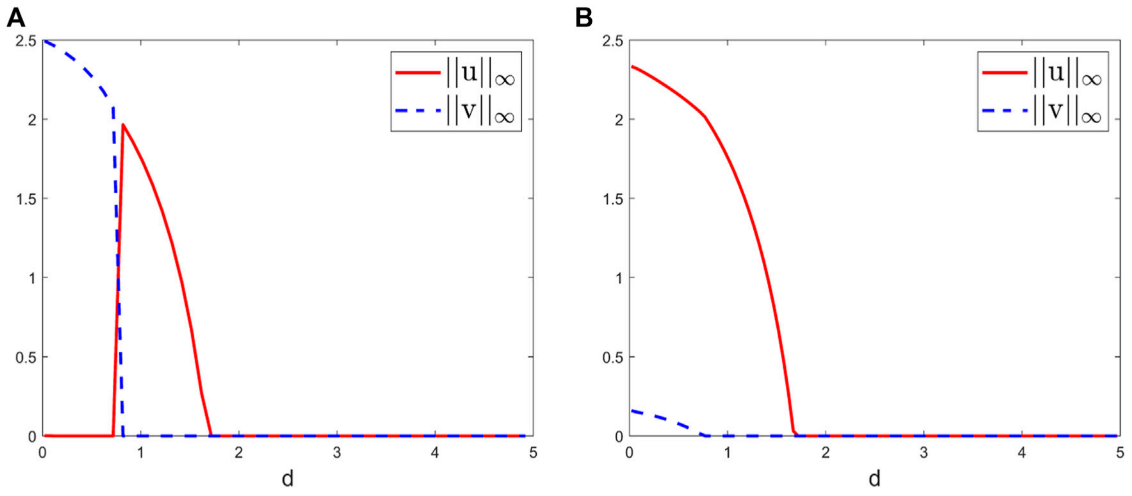

FIGURE 5
Bifurcation diagrams of the positive steady state solutions to system (2.2) at $t = 2000$ with the bifurcation parameter d ranging from 0.01 to 5. Here we take $L = 1$, $S^0 = 1$, $\gamma = 0.5$, $k_1 = 1$, $k_2 = 0.4$, $m_1 = 1$, and $m_2 = 0.6$ and **(A)** $\beta_1 = 0.01$, $\beta_2 = 0.01$ and **(B)** $\beta_1 = 0.01$, $\beta_2 = 1$.

Clearly, m_i^* $(i = 1, 2)$ are dependent on k_i but not on β_i.

Proposition 4.1. For fixed $d > 0$, the following statements hold:

$$\text{(i)}\ \frac{k_2}{k_1} < \frac{m_2^*}{m_1^*} < 1\ if\ k_1 > k_2 > 0;$$

$$\text{(ii)}\ 1 < \frac{m_2^*}{m_1^*} < \frac{k_2}{k_1}\ if\ k_2 > k_1 > 0;$$

$$\text{(iii)}\ m_1^* = m_2^*\ if\ k_1 = k_2 > 0.$$

Proof. (i) Since

$$\mu_1\left(\frac{m_1^*\phi}{k_1+\phi}\right) = 0 \text{ and } \mu_1\left(\frac{m_2^*\phi}{k_2+\phi}\right) = 0, \tag{4.2}$$

it is easy to check that $m_1^* > m_2^*$ by $k_1 > k_2 > 0$ and Lemma 3.1(iii). Note that Eq. 4.2) is equivalent to $\mu_1\left(\frac{m_1^*\phi/k_1}{1+\phi/k_1}\right) = 0$ and $\mu_1\left(\frac{m_2^*\phi/k_2}{1+\phi/k_2}\right) = 0$. Since $\frac{\phi}{1+\phi/k_1} > \frac{\phi}{1+\phi/k_2}$ based on $k^1 > k^2 > 0$, we have $\frac{m_1^*}{k_1} < \frac{m_2^*}{k_2}$; that is, $\frac{k_2}{k_1} < \frac{m_2^*}{m_1^*}$. Therefore, $\frac{k_2}{k_1} < \frac{m_2^*}{m_1^*} < 1$. (ii) can be obtained similarly. For (iii), it is easy to obtain $m_1^* = m_2^*$ by the fact of $k^1 = k^2 > 0$ and $\mu_1(m_i^* f_i(\phi, 0)) = 0$.

As the consequence of Lemma 3.2, system (2.2) admits the following trivial and semi-trivial solutions: trivial solution (0,0); semi-trivial solution $(\omega_*(\cdot; m_1, \beta_1), 0)$ exists if and only if $m_1 > m_1^*$; semi-trivial solution $(0, \omega_*(\cdot; m_2, \beta_2))$ exists if and only if $m_2 > m_2^*$. For convenience, we denote $\hat{u} = \omega_*(\cdot; m_1, \beta_1)$, $\hat{v} = \omega_*(\cdot; m_2, \beta_2)$, and next, we give an *a priori* estimate for the positive steady-state solution of system (2.2).

Lemma 4.1. Suppose that $(u(x), v(x))$ is a non-negative solution of system (2.2) with $u \not\equiv 0$ and $v \not\equiv 0$ on [0,1]. Then,

(i) $0 < u(x) \le \hat{u}$ and $0 < v(x) \le \hat{v}$ for $x \in [0, 1]$
(ii) $0 < u(x) + v(x) < \phi(x)$ for $x \in [0, 1]$

The proof of Lemma 4.1 is exactly similar to that in [10], Lemma 4.2; hence, it is omitted here.

We next establish the linear stability of $(\hat{u}, 0)$ and $(0, \hat{v})$. First, the linearized operator of system (2.3) at $(\hat{u}, 0)$ is given by

$$\begin{cases} d\varphi_{xx} + m_1[f_1(\phi-\hat{u},\hat{u}) + \hat{u} f_1^u(\phi-\hat{u},\hat{u})]\varphi + m_1\hat{u} f_1^v(\phi-\hat{u},\hat{u})\psi = \mu\varphi, & x \in (0,1), \\ d\psi_{xx} + m_2 f_2(\phi-\hat{u},0)\psi = \mu\psi, & x \in (0,1), \\ \varphi_x(0) = \varphi_x(1) + \gamma\varphi(1) = 0, & \\ \psi_x(0) = \psi_x(1) + \gamma\psi(1) = 0, & \end{cases} \tag{4.3}$$

where $f_1^u(\phi-\hat{u},\hat{u}) = -\frac{k_1+\beta_1\phi}{[k_1+\phi+(\beta_1-1)\hat{u}]^2} < 0$, $f_1^v(\phi-\hat{u},\hat{u}) = -\frac{k_1+\beta_1\hat{u}}{[k_1+\phi+(\beta_1-1)\hat{u}]^2} < 0$. By the Riesz–Schauder theory, the eigenvalues of Eq. 4.3 consist of the eigenvalues of the following two operators:

$$\mathcal{B}_1(m_1) = d\frac{\mathrm{d}^2}{\mathrm{d}x} + m_1(f_1(\phi-\hat{u},\hat{u}) + \hat{u} f_1^u(\phi-\hat{u},\hat{u})),\quad \mathcal{B}_2(m_2) = d\frac{\mathrm{d}^2}{\mathrm{d}x} + m_2 f_2(\phi-\hat{u},0), \tag{4.4}$$

subject to the corresponding boundary conditions. It follows from Lemma 3.1 (iii) that $\mu_1(m_1(f_1(\phi-\hat{u},\hat{u}) + \hat{u} f_1^u(\phi-\hat{u},\hat{u}))) < \mu_1(m_1 f_1(\phi-\hat{u},\hat{u}))$. Moreover, $\mu_1(m_1 f_1(\phi-\hat{u},\hat{u})) = 0$ with eigenfunction $\varphi_1(m_1 f_1(\phi-\hat{u},\hat{u})) = \hat{u}$, which implies $\mu_1(m_1(f_1(\phi-\hat{u},\hat{u}) + \hat{u} f_1^u(\phi-\hat{u},\hat{u}))) < 0$. Hence, the stability of $(\hat{u}, 0)$ is determined by the sign of the principal eigenvalue $\mu_1(m_2 f_2(\phi-\hat{u},0))$ of $\mathcal{B}_2(m_2)$. More precisely, $(\hat{u}, 0)$ is asymptotically stable if $\mu_1(m_2 f_2(\phi-\hat{u},0)) < 0$, while $(\hat{u}, 0)$ is unstable if $\mu_1(m_2 f_2(\phi-\hat{u},0)) > 0$.

The linearized operator of system (2.3) at $(0, \hat{v})$ is given by

$$\begin{cases} d\varphi_{xx} + m_1 f_1(\phi-\hat{v},0)\varphi = \mu\varphi, & x \in (0,1), \\ d\psi_{xx} + m_2[f_2(\phi-\hat{v},\hat{v}) + \hat{v} f_2^v(\phi-\hat{v},\hat{v})]\psi + m_2\hat{v} f_2^u(\phi-\hat{v},\hat{v})\varphi = \mu\psi, & x \in (0,1), \\ \varphi_x(0) = \varphi_x(1) + \gamma\varphi(1) = 0, & \\ \psi_x(0) = \psi_x(1) + \gamma\psi(1) = 0, & \end{cases} \tag{4.5}$$

where
$f_2^u(\phi-\hat{v},\hat{v}) = -\frac{k_2+\beta_2\hat{v}}{[k_2+\phi+(\beta_2-1)\hat{v}]^2} < 0$, $f_2^v(\phi-\hat{v},\hat{v}) = -\frac{k_2+\beta_2\phi}{[k_2+\phi+(\beta_2-1)\hat{v}]^2} < 0$.
We denote

$$\mathcal{B}_3(m_2) = d\frac{\mathrm{d}^2}{\mathrm{d}x} + m_1 f_1(\phi-\hat{v},0),$$

$$\mathcal{B}_4(m_2) = d\frac{\mathrm{d}^2}{\mathrm{d}x} + m_2[f_2(\phi-\hat{v},\hat{v}) + \hat{v} f_2^v(\phi-\hat{v},\hat{v})]. \tag{4.6}$$

Similarly, $(0, \hat{v})$ is asymptotically stable if $\mu_1(m_1 f_1(\phi - \hat{v}, 0)) < 0$, while $(0, \hat{v})$ is unstable if $\mu_1(m_1 f_1(\phi - \hat{v}, 0)) > 0$.

Theorem 4.1. *We consider $d, k_1, k_2 > 0$ fixed. Let $(u(x, t), v(x, t))$ be the solution of (2.2) with any non-negative non-trivial initial condition. The following statements hold:*

(i) *We consider $\beta_1, \beta_2 > 0$ fixed.*
(i.1) *If $m_1 \le m_1^\star$ and $m_2 \le m_2^\star$, then*

$$\lim_{t\to+\infty} u(x,t) = 0, \quad \lim_{t\to+\infty} v(x,t) = 0 \text{ uniformly on } [0,1]. \tag{4.7}$$

(i.2) *If $m_1 \le m_1^\star$ and $m_2 > m_2^\star$, then*

$$\lim_{t\to+\infty} u(x,t) = 0, \quad \lim_{t\to+\infty} v(x,t) = \hat{v} \text{ uniformly on } [0,1]. \tag{4.8}$$

(i.3) *If $m_1 > m_1^\star$ and $m_2 \le m_2^\star$, then*

$$\lim_{t\to+\infty} u(x,t) = \hat{u}, \quad \lim_{t\to+\infty} v(x,t) = 0 \text{ uniformly on } [0,1]. \tag{4.9}$$

(ii) *We consider $m_1 > m_1^\star$, $m_2 > \max\{m_2^\star, \max\{\frac{k_2}{k_1}, 1\}m_1\}$, and $\beta_1 > 0$ fixed. Then, $(\hat{u}, 0)$ is unstable. Moreover,*
(ii.1) (4.8) *holds provided*

$$0 < \beta_2 \le \beta_2^0 := \frac{(m_2 k_1 - m_1 k_2)\gamma}{m_1 S^0 (1+\gamma)}, \tag{4.10}$$

(ii.2) *there exists a unique $\beta_2^\star \in (\beta_2^0, +\infty)$ such that $(0, \hat{v})$ is asymptotically stable when $0 < \beta_2 < \beta_2^\star$; $(0, \hat{v})$ is unstable when $\beta_2 > \beta_2^\star$, and system (2.2) admits at least one stable coexistence steady state when $\beta_2 > \beta_2^\star$.*

(iii) *We consider $m_2 > m_2^\star$, $m_1 > \max\{m_1^\star, \max\{\frac{k_1}{k_2}, 1\}m_2\}$, and $\beta_2 > 0$ fixed. Then, $(0, \hat{v})$ is unstable. Moreover,*
(iii.1) Eq. 4.9 *holds provided*

$$0 < \beta_1 \le \beta_1^0 := \frac{(m_1 k_2 - m_2 k_1)\gamma}{m_2 S^0 (1+\gamma)}, \tag{4.11}$$

(iii.2) *there exists a unique $\beta_1^\star \in (\beta_1^0, +\infty)$ such that $(\hat{u}, 0)$ is asymptotically stable when $0 < \beta_1 < \beta_1^\star$; $(\hat{u}, 0)$ is unstable when $\beta_1 > \beta_1^\star$, and system (2.2) admits at least one stable coexistence steady state when $\beta_1 > \beta_1^\star$.*

Proof. (i) can be proved by the similar arguments as in [6], Theorems 3.5, 3.6, and we omit it here. Next, we only prove (ii), since (iii) can be proved by similar arguments.

Claim 1. For $m_1 > m_1^*$, $m_2 \ge \max\{\frac{k_2}{k_1}, 1\}m_1$, and $\beta_1 > 0$ fixed, $(\hat{u}, 0)$ is unstable.

Note that $\hat{u}$ satisfies

$$\begin{cases} d\hat{u}_{xx} + m_1 f_1(\phi - \hat{u}, \hat{u})\hat{u} = 0, & x \in (0,1), \\ \hat{u}_x(0) = \hat{u}_x(1) + \gamma\hat{u}(1) = 0, \end{cases} \tag{4.12}$$

which implies $\mu_1(m_1 f_1(\phi - \hat{u}, \hat{u})) = 0$. We recall that $(\hat{u}, 0)$ is asymptotically stable if $\mu_1(m_2 f_2(\phi - \hat{u}, 0)) < 0$ and it is unstable if $\mu_1(m_2 f_2(\phi - \hat{u}, 0)) > 0$. Then, we conclude from $m_2 \ge \max\{\frac{k_2}{k_1}, 1\}m_1$ and $0 < \hat{u} < \phi$ on [0,1] that

$$\begin{aligned} m_1 f_1(\phi - \hat{u}, \hat{u}) - m_2 f_2(\phi - \hat{u}, 0) &< m_1 f_1(\phi - \hat{u}, 0) - m_2 f_2(\phi - \hat{u}, 0) \\ &= \frac{m_1 k_2 - m_2 k_1 + (m_1 - m_2)(\phi - \hat{u})}{(k_1 + \phi - \hat{u})(k_2 + \phi - \hat{u})}(\phi - \hat{u}), \\ &\le 0, \end{aligned}$$

which means that $\mu_1(m_2 f_2(\phi - \hat{u}, 0)) > \mu_1(m_1 f_1(\phi - \hat{u}, \hat{u})) = 0$ by Lemma 3.2(iii). That is, $(\hat{u}, 0)$ is unstable.

Claim 2. (1) For $m_1 > m_1^*$, $m_2 > \max\{m_2^*, \max\{\frac{k_2}{k_1}, 1\}m_1\}$, and $\beta_1 > 0$ fixed, $(0, \hat{v})$ is asymptotically stable when $0 < \beta_2 \le \beta_2^0$, where β_2^0 is defined by Eq. 4.10.

(2) There exists a unique $\beta_2^* > \beta_2^0$ such that $(0, \hat{v})$ is asymptotically stable when $0 < \beta_2 < \beta_2^*$, and $(0, \hat{v})$ is unstable when $\beta_2 > \beta_2^*$.

For (1), we recall that $(0, \hat{v})$ is asymptotically stable if $\mu_1(m_1 f_1(\phi - \hat{v}, 0)) < 0$ and unstable if $\mu_1(m_1 f_1(\phi - \hat{v}, 0)) > 0$. Similarly, we can conclude from $m_2 > \max\{m_2^*, \max\{\frac{k_2}{k_1}, 1\}m_1\}$ and $0 < \hat{v} < \phi(x) < \frac{S^0(1+\gamma)}{\gamma}$ on [0,1] that

$$\begin{aligned} & m_1 f_1(\phi - \hat{v}, 0) - m_2 f_2(\phi - \hat{v}, \hat{v}) \\ = & \frac{m_1 k_2 - m_2 k_1 + (m_1 - m_2)(\phi - \hat{v}) + m_1\beta_2\hat{v}}{[k_2 + \phi + (\beta_2 - 1)\hat{v}](k_1 + \phi - \hat{v})}(\phi - \hat{v}), \\ < & \ 0 \end{aligned}$$

provided $0 < \beta_2 \le \beta_2^0 := \frac{(m_2 k_1 - m_1 k_2)\gamma}{m_1 S^0 (1+\gamma)}$. It follows from Lemma 3.2(iii) that $\mu_1(m_1 f_1(\phi - \hat{v}, 0)) < \mu_1(m_2 f_2(\phi - \hat{v}, \hat{v})) = 0$ when $0 < \beta_2 \le \beta_2^0$. That is, $(0, \hat{v})$ is asymptotically stable when $0 < \beta_2 \le \beta_2^0$.

For (2), since $\hat{v}(\cdot; m_2, \beta_2)$ is point-wise strictly decreasing in $\beta_2 \in (0, +\infty)$ and $\lim_{\beta_2\to+\infty} \hat{v}(\cdot; m_2, \beta_2) = 0$ uniformly on [0,1] (see Lemma 3.3(ii)), we can obtain from Lemma 3.2(iii) that $\mu_1(m_1 f_1(\phi - \hat{v}(\cdot; m_2, \beta_2), 0))$ is strictly increasing in $\beta_2 \in (0, +\infty)$. Furthermore,

$$\lim_{\beta_2\to+\infty} \mu_1(m_1 f_1(\phi - \hat{v}(\cdot; m_2, \beta_2), 0)) = \mu_1(m_1 f_1(\phi, 0)) > 0,$$

based on $m_1 > m_1^*$ (Eq. 4.1). Moreover, $\mu_1(m_1 f_1(\phi - \hat{v}(\cdot; m_2, \beta_2), 0)) < 0$ when $0 < \beta_2 \le \beta_2^0$. Therefore, there exists a unique $\beta_2^* > \beta_2^0$ such that

$$\mu_1(m_1 f_1(\phi - \hat{v}(\cdot; m_2, \beta_2), 0)) \begin{cases} < 0 & \text{if } 0 < \beta_2 < \beta_2^*, \\ = 0 & \text{if } \beta_2 = \beta_2^*, \\ > 0 & \text{if } \beta_2 > \beta_2^*, \end{cases}$$

which means that $(0, \hat{v})$ is asymptotically stable when $0 < \beta_2 < \beta_2^*$, while it is unstable when $\beta_2 > \beta_2^*$.

Claim 3. For $m_1 > m_1^*$, $m_2 > \max\{m_2^*, \max\{\frac{k_2}{k_1}, 1\}m_1\}$, and $\beta_1 > 0$ fixed, system (2.2) has no positive steady states when $0 < \beta_2 \le \beta_2^0$.

We assume by contradiction that system (2.2) admits a positive steady state $(\bar{u}, \bar{v})$, which satisfies

$$\begin{cases} d\bar{u}_{xx} + m_1 f_1(\phi - \bar{u} - \bar{v}, \bar{u})\bar{u} = 0, & x \in (0,1), \\ d\bar{v}_{xx} + m_2 f_2(\phi - \bar{u} - \bar{v}, \bar{v})\bar{v} = 0, & x \in (0,1), \\ \bar{u}_x(0) = \bar{u}_x(1) + \gamma\bar{u}(1) = 0, \\ \bar{v}_x(0) = \bar{v}_x(1) + \gamma\bar{v}(1) = 0. \end{cases} \tag{4.13}$$

Multiplying the first equation of (4.13) by $\bar{v}$ and the second equation by $\bar{u}$, integrating over (0,1), and then, subtracting the resulting equations, we have

$$\int_0^1 \frac{m_1 k_2 - m_2 k_1 + (m_1 - m_2)(\phi - \bar{u} - \bar{v}) + m_1\beta_2\bar{v} - m_2\beta_1\bar{u}}{[k_1 + \phi + (\beta_1 - 1)\bar{u} - \bar{v}][k_2 + \phi + (\beta_2 - 1)\bar{v} - \bar{u}]}\bar{u}\bar{v}(\phi - \bar{u} - \bar{v})dx = 0. \tag{4.14}$$

Since $\bar{u} + \bar{v} < \phi(x) < \frac{S^0(1+\gamma)}{\gamma}$ on [0,1], we can conclude from $m_1 > m_1^*$ and $m_2 > \max\{m_2^*, \max\{\frac{k_2}{k_1}, 1\}m_1\}$ that the left side of (4.14) is less than 0, when $0 < \beta_2 \le \beta_2^0 := \frac{(m_2 k_1 - m_1 k_2)\gamma}{m_1 S^0 (1+\gamma)}$. That is a contradiction.

In conclusion, we can deduce that (ii.1) holds from Claim 1, Claim 2(1), Claim 3, and Lemma 3.4(iii). In addition, (ii.2) is the direct result of Claim 1, Claim 2(2), and Lemma 3.4(ii). The proof is completed.

Remark 4.1. Theorem 4.1(i) implies that both species with sufficiently small growth rates are washed out, while competition exclusion occurs and the species with a sufficiently faster growth rate will finally win the competition. In particular, when both species admit sufficient fast growth rates, Theorem 4.1(ii.1) suggests that the species v with stronger growth ability ($\frac{m_2}{k_2}$ is large) and weaker intraspecific competition (β_2 is small) will finally win the competition. This is consistent with the biological intuition that the species with stronger growth ability and weaker intraspecific competition has more competitive advantages. Theorem 4.1(iii.1) illustrates the similar biological phenomenon.

We next investigate the local dynamics of system (2.2). Note that the stability of $(\hat{u}(m_1,\beta_1),0)$ is determined by the sign of $\mu_1(m_2 f_2(\phi-\hat{u}(m_1,\beta_1),0))$, and the stability of $(0,\hat{v}(m_2,\beta_2))$ is determined by the sign of $\mu_1(m_1 f_1(\phi-\hat{v}(m_1,\beta_1),0))$. Clearly, $\mu_1(m_2 f_2(\phi-\hat{u}(m_1,\beta_1),0))$ depends on m_1, m_2, and β_1, and $\mu_1(m_1 f_1(\phi-\hat{v}(m_2,\beta_2),0))$ depends on m_1, m_2, and β_2. To this end, we define

$$\sigma_1(m_1,m_2,\beta_1) := \mu_1(m_2 f_2(\phi-\hat{u}(m_1,\beta_1),0)) \text{ for } m_1 > m_1^*,\ m_2>0,\ \beta_1>0,$$

$$\tau_1(m_1,m_2,\beta_2) := \mu_1(m_1 f_1(\phi-\hat{v}(m_2,\beta_2),0)) \text{ for } m_1>0,\ m_2>m_2^*,\ \beta_2>0.$$

Lemma 4.2. The principal eigenvalues $\sigma_1(m_1, m_2, \beta_1)$ and $\tau_1(m_1, m_2, \beta_2)$ have the following properties:

(i) For fixed d, k_1, $k_2>0$ and $m_1>m_1^*$,
- (i.1) $\sigma_1(m_1, m_2, \beta_1)$ is strictly decreasing with respect to m_1 in $(m_1^*,+\infty)$,
- (i.2) $\sigma_1(m_1, m_2, \beta_1)$ is strictly increasing with respect to β_1 in $(0, +\infty)$,
- (i.3) $\sigma_1(m_1, m_2, \beta_1)$ is strictly increasing with respect to m_2 in $(m_2^*,+\infty)$; moreover,

$$\lim_{m_2\to (m_2^*)^+}\sigma_1(m_1,m_2,\beta_1) = \mu_1(m_2^* f_2(\phi-\hat{u},0))<0,\quad \lim_{m_2\to+\infty}\sigma_1(m_1,m_2,\beta_1) = +\infty .$$

(ii) For fixed d, k_1, $k_2>0$ and $m_2>m_2^*$,
- (ii.1) $\tau_1(m_1, m_2, \beta_2)$ is strictly increasing with respect to m_1 in $(m_1^*,+\infty)$,
- (ii.2) $\tau_1(m_1, m_2, \beta_2)$ is strictly increasing with respect to β_2 in $(0, +\infty)$,
- (ii.3) $\tau_1(m_1, m_2, \beta_2)$ is strictly decreasing with respect to m_2 in $(m_2^*,+\infty)$; moreover,

$$\lim_{m_2\to (m_2^*)^+}\tau_1(m_1,m_2,\beta_2) = \mu_1(m_1 f_1(\phi,0))>0,\quad \lim_{m_2\to+\infty}\tau_1(m_1,m_2,\beta_2) = \mu_1(0)<0.$$

Proof. For (i), (i.1) can be obtained by Lemma 3.1(iii) and Lemma 3.3(i). Similarly, (i.2) is followed by Lemma 3.1(iii) and Lemma 3.3(ii). To prove (i.3), it is obvious that $\sigma_1(m_1, m_2, \beta_1)$ is strictly increasing with respect to m_2 in $(m_2^*,+\infty)$ by Lemma 3.1(iii) and $\lim_{m_2\to+\infty}\sigma_1(m_1,m_2,\beta_1)=+\infty$ by (3.2). We recall $\mu_1(m_2^* f_2(\phi,0))=0$. Then, we can conclude from Lemma 3.1(ii)(iii) that

$$\lim_{m_2\to (m_2^*)^+}\sigma_1(m_1,m_2,\beta_1) = \mu_1(m_2^* f_2(\phi-\hat{u},0))<\mu_1(m_2^* f_2(\phi,0)) = 0.$$

For (ii), (ii.1) can be obtained by Lemma 3.1(iii), and (ii.2) can be proved by Lemma 3.1(iii) and Lemma 3.3(ii). We then prove (ii.3). Since $\hat{v}(m_2,\beta_2)$ is point-wise strictly increasing in $m_2\in(m_2^*,+\infty)$ by Lemma 3.3(i), it follows from Lemma 3.1(iii) that $\tau_1(m_1, m_2, \beta_2)$ is strictly decreasing with respect to m_2 in $(m_2^*,+\infty)$. Noting that $\lim_{m_2\to(m_2^*)^+}\hat{v}(m_2,\beta_2)=0$ by (3.5), we can conclude from Lemma 3.1(ii) that

$$\lim_{m_2\to (m_2^*)^+}\tau_1(m_1,m_2,\beta_2) = \mu_1(m_1 f_1(\phi,0))>0,$$

based on $m_1>m_1^*$ (see (4.1)). Moreover, since $\lim_{m_2\to+\infty}\hat{v}(m_2,\beta_2)=\phi(x)$ on [0,1] (see (3.5)), we can obtain from Lemma 3.1(ii) (iii) that

$$\lim_{m_2\to+\infty}\tau_1(m_1,m_2,\beta_2) = \mu_1(m_1 f_1(\phi-\hat{v}(m_2,\beta_2),0)) = \mu_1(0)<0.$$

The proof is completed.

Clearly, both $\sigma_1(m_1, m_2, \beta_1)$ and $\tau_1(m_1, m_2, \beta_2)$ depend on m_1 and m_2. To investigate the local dynamics of system (2.2) in the $m_1 - m_2$ plane, we fix $\beta_1, \beta_2>0$ and denote them by $\sigma_1(m_1, m_2)$ and $\tau_1(m_1, m_2)$.

Lemma 4.3. Suppose $m_i>m_i^*$ $(i=1,2)$. For fixed $d, \beta_1, \beta_2, k_1, k_2>0$, there exist two continuous critical curves

$$\Gamma_1:\ m_2=\bar{m}_2(m_1)\ for\ m_1\in(m_1^*,+\infty),$$
$$\Gamma_2:\ m_2=\tilde{m}_2(m_1)\ for\ m_1\in(m_1^*,+\infty),$$

where $\bar{m}_2(m_1)$ and $\tilde{m}_2(m_1)$ are differentially dependent on m_1 and uniquely determined by

$$\mu_1(\bar{m}_2(m_1) f_2(\phi-\hat{u},0))=0\quad and\quad \mu_1(m_1 f_1(\phi-\hat{v}(\cdot;\tilde{m}_2(m_1)),0)) = 0, \tag{4.15}$$

respectively. Then,

(i) the semi-trivial steady state $(\hat{u},0)$ is locally asymptotically stable if $(m_1,m_2)\in(m_1^*,+\infty)\times(m_2^*,\bar{m}_2(m_1))$, neutrally stable if $(m_1,m_2)\in(m_1^*,+\infty)\times\{\bar{m}_2(m_1)\}$, and unstable if.

(ii) the semi-trivial steady state $(0,\hat{v})$ is locally asymptotically stable if $(m_1,m_2)\in(m_1^*,+\infty)\times\{\tilde{m}_2(m_1),+\infty\}$, neutrally stable if $(m_1,m_2)\in(m_1^*,+\infty)\times\{\tilde{m}_2(m_1)\}$, and unstable if $(m_1,m_2)\in(m_1^*,+\infty)\times(m_2^*,\tilde{m}_2(m_1))$.

Proof. (i) By Lemma 4.2(i), we conclude that for any $m_1\in(m_1^*,+\infty)$ given, there exists a unique $\bar{m}_2(m_1)>m_2^*$ such that

$$\sigma_1(m_1,m_2)\begin{cases} <0 & \text{if } m_2^*<m_2<\bar{m}_2(m_1),\\ =0 & \text{if } m_2=\bar{m}_2(m_1),\\ >0 & \text{if } m_2>\bar{m}_2(m_1).\end{cases}$$

Therefore, $(\hat{u},0)$ is locally asymptotically stable for $m_2^*<m_2<\bar{m}_2(m_1)$, neutrally stable for $m_2=\bar{m}_2(m_1)$, and unstable for $m_2>\bar{m}_2(m_1)$.

(ii) Similarly, we can conclude from Lemma 4.2(ii) that for any $m_1\in(m_1^*,+\infty)$ given, there exists a unique $\tilde{m}_2(m_1)>m_2^*$ such that

$$\tau_1(m_1,m_2)\begin{cases} >0 & \text{if} \quad m_2^* < m_2 < \tilde{m}_2(m_1),\\ =0 & \text{if} \quad m_2 = \tilde{m}_2(m_1),\\ <0 & \text{if} \quad m_2 > \tilde{m}_2(m_1).\end{cases}$$

Therefore, $(0,\hat{v})$ is unstable for $m_2^* < m_2 < \tilde{m}_2(m_1)$, neutrally stable for $m_2 = \tilde{m}_2(m_1)$, and locally asymptotically stable for $m_2 > \tilde{m}_2(m_1)$. The proof is completed.

Combining with Lemma 3.4 and Lemma 4.3, we obtain the following results.

Theorem 4.2. Suppose $m_i > m_i^*$ $(i=1,2)$. For fixed d, k_1, k_2, β_1, $\beta_2 > 0$, $\bar{m}_2$ and $\tilde{m}_2$ are defined by Eq. 4.15, respectively, and the following statements hold.

(i) Suppose $\bar{m}_2 < \tilde{m}_2$. If $m_2 < \bar{m}_2$, then $(\hat{u},0)$ is locally asymptotically stable, and $(0,\hat{v})$ is unstable if it exists. If $m_2 > \tilde{m}_2$, then $(\hat{u},0)$ is unstable, and $(0,\hat{v})$ is locally asymptotically stable. If $m_2 \in (\bar{m}_2,\tilde{m}_2)$, then $(\hat{u},0)$ and $(0,\hat{v})$ are both unstable, and system (2.2) admits at least one stable coexistence steady state.

(ii) Suppose $\bar{m}_2 > \tilde{m}_2$. If $m_2 < \tilde{m}_2$, then $(\hat{u},0)$ is locally asymptotically stable, and $(0,\hat{v})$ is unstable. If $m_2 > \bar{m}_2$, then $(\hat{u},0)$ is unstable, and $(0,\hat{v})$ is locally asymptotically stable. If $m_2 \in (\tilde{m}_2,\bar{m}_2)$, then $(\hat{u},0)$ and $(0,\hat{v})$ are both stable, and system (2.2) admits at least one unstable coexistence steady state.

(iii) Suppose $\bar{m}_2 = \tilde{m}_2$. If $m_2 < \bar{m}_2$, then $(\hat{u},0)$ is locally asymptotically stable, and $(0,\hat{v})$ is unstable. If $m_2 > \bar{m}_2$, then $(\hat{u},0)$ is unstable, and $(0,\hat{v})$ is locally asymptotically stable.

For fixed d, k_1, k_2, β_1, $\beta_2 > 0$, Lemma 4.3 and Theorem 4.2 imply that there exist two critical curves Γ_1 and Γ_2 in the $m_1 - m_2$ plane, which divide the local dynamics of Eq. 2.2 into competitive exclusion, bi-stability, and coexistence. To further characterize classification on the dynamics of system (2.2) in the $m_1 - m_2$ plane, we next give some properties of critical curves Γ_1 and Γ_2. We recall

$$\mu_1(\bar{m}_2 f_2(\phi-\hat{u}(\cdot;m_1,\beta_1),0))=0 \quad \text{and} \quad \mu_1(m_1 f_1(\phi-\hat{v}(\cdot;\tilde{m}_2,\beta_2),0))=0.$$

Clearly, $\bar{m}_2$ depends on m_1 and β_1 and $\tilde{m}_2$ depends on m_1 and β_2. To emphasize these parameters, we denote $\bar{m}_2$ and $\tilde{m}_2$ by $\bar{m}_2(m_1,\beta_1)$ and $\tilde{m}_2(m_1,\beta_2)$, respectively.

Proposition 4.2. We consider d, k_1, $k_2 > 0$ fixed. The critical curve $\bar{m}_2(m_1,\beta_1)$ has the following properties.

(i) For any $\beta_1 > 0$ given, $\bar{m}_2(m_1,\beta_1)$ is strictly increasing with respect to m$_1$ in $(m_1^*,+\infty)$. Moreover,

$$\lim_{m_1\to(m_1^*)^+}\bar{m}_2(m_1,\beta_1)=m_2^*.$$

(ii) For any $m_1 > m_1^*$ given, $\bar{m}_2(m_1,\beta_1)$ is strictly decreasing with respect to β_1 in $(0,+\infty)$ and

$$m_2^* < \bar{m}_2(m_1,\beta_1) < \max\left\{\frac{k_2}{k_1},1\right\}m_1 \quad \text{and} \quad \lim_{\beta_1\to+\infty}\bar{m}_2(m_1,\beta_1)=m_2^*. \tag{4.16}$$

Particularly,

$$\max\left\{m_2^*,\ \min\left\{\frac{k_2}{k_1},1\right\}m_1\right\} \le \bar{m}_2(m_1,\beta_1) < \max\left\{\frac{k_2}{k_1},1\right\} m_1 \ \text{provided}\ 0<\beta_1\le\beta_1^0. \tag{4.17}$$

(iii) For any $m_1 > m_1^*$ given,

$$\lim_{\beta_1\to+\infty}\dot{\bar{m}}_2(m_1,\beta_1)=0, \tag{4.18}$$

where $\dot{\bar{m}}_2(m_1,\beta_1)$ is the derivative of $\bar{m}_2(m_1,\beta_1)$ with respect to m_1 in $(m_1^*,+\infty)$.

Proof. (i) For any $\beta_1 > 0$ given, we can conclude from Lemma 4.2(i.1) (i.3) that $\mu_1(m_2 f_2(\phi-\hat{u}),0)$ is strictly decreasing with respect to m_1 in $(m_1^*,+\infty)$ and strictly increasing with respect to m_2 in $(m_2^*,+\infty)$. Then, it follows from $\mu_1(\bar{m}_2(m_1,\beta_1) f_2(\phi-\hat{u},0))=0$ and the implicit function theorem that $\bar{m}_2(m_1,\beta_1)$ is strictly increasing with respect to m_1 in $(m_1^*,+\infty)$. Since $\mu_1(\bar{m}_2(m_1,\beta_1)f_2(\phi-\hat{u}),0)=0$, we can obtain $\lim_{m_1\to(m_1^*)^+}\bar{m}_2(m_1,\beta_1)=m_2^*$ based on $\mu_1(m_2^* f_2(\phi,0))=0$ and $\lim_{m_1\to(m_1^*)^+}\hat{u}=0$ uniformly on [0,1] (see Eq. 3.5).

(ii) For any $m_1 > m_1^*$ given, it follows from Lemma 4.2(i.2) (i.3) that $\mu_1(m_2 f_2(\phi-\hat{u}),0)$ is strictly increasing with respect to β_1 in $(0,+\infty)$ and strictly increasing with respect to m_2 in $(m_2^*,+\infty)$. Then, we can obtain from $\mu_1(\bar{m}_2(m_1,\beta_1)f_2(\phi-\hat{u},0))=0$ and the implicit function theorem that $\bar{m}_2(m_1,\beta_1)$ is strictly decreasing with respect to β_1 in $(0,+\infty)$. Then,

$$\lim_{\beta_1\to+\infty}\bar{m}_2(m_1,\beta_1) < \bar{m}_2(m_1,\beta_1) < \lim_{\beta_1\to0^+}\bar{m}_2(m_1,\beta_1) \ \text{for}\ m_1>m_1^*.$$

Substituting $\beta_1 \to 0^+$ in $\mu_1(\bar{m}_2(m_1,\beta_1)f_2(\phi-\hat{u},0))=0$, we have $\mu_1(\bar{m}_2(m_1,0)f_2(\phi-u_0,0))=0$ by Lemma 3.1(ii). Here, u_0 satisfies

$$\begin{cases} d(u_0)_{xx}+\dfrac{m_1(\phi-u_0)u_0}{k_1+\phi-u_0}=0, & x\in(0,1),\\ (u_0)_x(0)=(u_0)_x(1)+\gamma u_0(1)=0. \end{cases}$$

Then, we can deduce from [26], Theorem 2.1 that $\lim_{\beta_1\to0^+}\bar{m}_2(m_1,\beta_1)\le\max\{\frac{k_2}{k_1},1\}m_1$. Substituting $\beta_1 \to +\infty$ in $\mu_1(\bar{m}_2(m_1,\beta_1)f_2(\phi-\hat{u},0))=0$, we have $\lim_{\beta_1\to+\infty}\bar{m}_2(m_1,\beta_1)=m_2^*$ based on $\mu_1(m_2^* f_2(\phi,0))=0$ and $\lim_{\beta_1\to+\infty}\hat{u}=0$ uniformly on [0,1] (see (3.6)). The estimate of $\bar{m}_2(m_1,\beta_1)$ in Eq. 4.16 is obtained.

Finally, when $m_1 > m_1^*$, $m_2^* < m_2 < \min\{\frac{k_2}{k_1},1\}m_1$, Theorem 4.1(iii.1) shows that $(\hat{u},0)$ is globally asymptotically stable provided $0<\beta_1\le\beta_1^0$. Therefore, $\bar{m}_2(m_1,\beta_1)\ge\max\{m_2^*,\ \min\{\frac{k_2}{k_1},1\}m_1\}$ provided $0<\beta_1\le\beta_1^0$. Combining with Eq. 4.16, 4.17 is obtained.

(iii) Let $\psi_1 > 0$ with $\|\psi_1\|_\infty = 1$ be the corresponding principal eigenfunction of $\mu_1(\bar{m}_2 f_2(\phi-\hat{u},0))=0$. Then, ψ_1 satisfies

$$\begin{cases} d(\psi_1)_{xx}+\bar{m}_2 f_2(\phi-\hat{u},0)\psi_1=0, & x\in(0,1),\\ (\psi_1)_x(0)=(\psi_1)_x(1)+\gamma\psi_1(1)=0. \end{cases} \tag{4.19}$$

By differentiating Eq. 4.19 with respect to m_1, denoting $\frac{\partial}{\partial m_1}=\dot{}$, we have

$$\begin{cases} d(\dot{\psi}_1)_{xx} + \dot{\bar{m}}_2 f_2(\phi - \hat{u}, 0)\psi_1 + \bar{m}_2 \\ \left[f_2(\phi - \hat{u}, 0)\dot{\psi}_1 - \dfrac{k_2}{(k_2 + \phi - \hat{u})^2} \cdot \dfrac{\partial \hat{u}(m_1, \beta_1)}{\partial m_1}\psi_1 \right] = 0, \quad x \in (0,1), \\ (\dot{\psi}_1)_x(0) = (\dot{\psi}_1)_x(1) + \gamma\dot{\psi}_1(1) = 0, \end{cases} \tag{4.20}$$

where $\frac{\partial \hat{u}(m_1,\beta_1)}{\partial m_1}$ is the derivative of $\hat{u}(m_1,\beta_1)$ with respect to m_1 in $(m_1^*, +\infty)$. Multiplying Eq. 4.19 by $\dot{\psi}_1$ and Eq. 4.20 by ψ_1, integrating over (0,1), and then, subtracting the two resulting equations,

$$\dot{\bar{m}}_2(m_1,\beta_1) = \frac{\bar{m}_2 \int_0^1 \frac{k_2}{(k_2+\phi-\hat{u})^2} \cdot \frac{\partial \hat{u}(m_1,\beta_1)}{\partial m_1} \psi_1^2 dx}{\int_0^1 f_2(\phi - \hat{u}, 0)\psi_1^2 dx}. \tag{4.21}$$

We next show that $\lim_{\beta_1 \to +\infty} \frac{\partial \hat{u}(m_1,\beta_1)}{\partial m_1} = \frac{\partial}{\partial m_1} \lim_{\beta_1 \to +\infty} \hat{u}(m_1,\beta_1) = 0$. We choose an increasing sequence $\{\beta^{1,n}\}$ with $\lim_{n\to+\infty} \beta_{1,n} = +\infty$. Then, $\hat{u}_n := \hat{u}(m_1, \beta_{1,n})$ is the unique positive solution of

$$\begin{cases} d(\hat{u}_n)_{xx} + m_1 f_1^{(n)}(\phi - \hat{u}_n, \hat{u}_n)\hat{u}_n = 0, & x \in (0,1), \\ (\hat{u}_n)_x(0) = (\hat{u}_n)_x(1) + \gamma(\hat{u}_n)(1) = 0, \end{cases} \tag{4.22}$$

where $f_1^{(n)}(\phi - \hat{u}_n, \hat{u}_n) = \frac{\phi - \hat{u}_n}{k_1 + \phi + (\beta_{1,n} - 1)\hat{u}_n}$. Note that $0 < \hat{u}_n < \phi$ and $f_1^{(n)}(\phi - \hat{u}_n, \hat{u}_n)$ is uniformly bounded on [0,1]. By L^p estimates for $p \in (1, +\infty)$ and the Sobolev embedding theorem, we may assume that $\lim_{n\to+\infty} \hat{u}_n = U_1(x)$ in $C^1[0, 1]$ by passing to a subsequence if necessary. Since $\hat{u}_n$ is continuously differentiable with respect to m_1 in $(m_1^*, +\infty)$ (see Lemma 3.3(i)), we differentiate (4.22) with respect to m_1, denote $\frac{\partial}{\partial m_1} = \dot{}$, and obtain

$$\begin{cases} d(\dot{\hat{u}}_n)_{xx} + m_1 \\ \left[f_1^{(n)}(\phi - \hat{u}_n, \hat{u}_n) - \dfrac{(k_1 + \beta_{1,n}\phi)\hat{u}_n}{[k_1 + \phi + (\beta_{1,n} - 1)\hat{u}_n]^2} \right] \dot{\hat{u}}_n = -f_1^{(n)}(\phi - \hat{u}_n, \hat{u}_n)\hat{u}_n, \quad x \in (0,1), \\ (\dot{\hat{u}}_n)_x(0) = (\dot{\hat{u}}_n)_x(1) + \gamma\dot{\hat{u}}_n(1) = 0. \end{cases} \tag{4.23}$$

Since $0 < \hat{u}_n < \phi$, $f_1^{(n)}(\phi - \hat{u}_n, \hat{u}_n)\hat{u}_n$, and $f_1^{(n)}(\phi - \hat{u}_n, \hat{u}_n) - \frac{(k_1+\beta_{1,n}\phi)\hat{u}_n}{[k_1+\phi+(\beta_{1,n}-1)\hat{u}_n]^2}$ are uniformly bounded on [0,1], we can use L^p estimates for $p \in (1, +\infty)$ and the Sobolev embedding theorem again to assume that $\lim_{n\to+\infty} \dot{\hat{u}}_n = U_2(x)$ in $C^1[0, 1]$ by passing to a subsequence if necessary. Therefore, $\lim_{\beta_1\to+\infty} \frac{\partial \hat{u}(m_1,\beta_1)}{\partial m_1} = \frac{\partial}{\partial m_1} \lim_{\beta_1\to+\infty} \hat{u}(m_1,\beta_1) = 0$ based on $\lim_{\beta_1\to+\infty} \hat{u}(m_1,\beta_1) = 0$ uniformly on [0,1] (see Lemma 3.3(ii)). Finally, taking $\beta^1 \to +\infty$ in (4.21) and noting that $\lim_{\beta_1\to+\infty} \bar{m}_2(m_1,\beta_1) = m_2^*$ (see (4.16)), we have $\lim_{\beta_1\to+\infty} \dot{\bar{m}}_2(m_1,\beta_1) = 0$. The proof is completed.

Proposition 4.3. *We consider $d, k_1, k_2 > 0$ fixed. The critical curve $\tilde{m}_2(m_1,\beta_2)$ has the following properties:*

(i) *For any $\beta_2 > 0$ given, $\tilde{m}_2(m_1,\beta_2)$ is strictly increasing with respect to m_1 in $(m_1^*, +\infty)$. Moreover,*

$$\lim_{m_1\to(m_1^*)^+} \tilde{m}_2(m_1,\beta_2) = m_2^*.$$

(ii) *For any $m_1 > m_1^*$ given, $\tilde{m}_2(m_1,\beta_2)$ is strictly increasing with respect to β_2 in $(0, +\infty)$ and*

$$\max\left\{m_2^*, \min\left\{\frac{k_2}{k_1}, 1\right\}m_1\right\} < \tilde{m}_2(m_1,\beta_2) < +\infty. \tag{4.24}$$

Particularly,

$$\max\left\{m_2^*, \min\left\{\frac{k_2}{k_1}, 1\right\}m_1\right\} < \tilde{m}_2(m_1,\beta_2) \le \max\left\{\frac{k_2}{k_1}, 1\right\}m_1 \quad \text{provided } 0 < \beta_2 \le \beta_2^0. \tag{4.25}$$

(iii) For any $m_1 > m_1^*$ given,

$$\lim_{\beta_2\to+\infty} \dot{\tilde{m}}_2(m_1,\beta_2) = +\infty, \tag{4.26}$$

where $\dot{\tilde{m}}_2(m_1,\beta_2)$ is the derivative of $\tilde{m}_2(m_1,\beta_2)$ with respect to m_1 in $(m_1^*, +\infty)$.

Proof. (i) For any $\beta_2 > 0$ given, we can conclude from Lemma 4.2(ii.1) (ii.3) that $\mu_1(m_1 f_1(\phi - \hat{v}(\cdot; m_2, \beta_2), 0))$ is strictly increasing with respect to m_1 in $(m_1^*, +\infty)$ and strictly decreasing with respect to m_2 in $(m_2^*, +\infty)$. Then, $\tilde{m}_2(m_1,\beta_2)$ is strictly increasing with respect to m_1 in $(m_1^*, +\infty)$ by $\mu_1(m_1 f_1(\phi - \hat{v}(\cdot; \tilde{m}_2, \beta_2), 0)) = 0$ and the implicit function theorem. Substituting $m_1 \to (m_1^*)^+$ in $\mu_1(m_1 f_1(\phi - \hat{v}(\cdot; \tilde{m}_2, \beta_2), 0)) = 0$, we have $\lim_{m_1\to(m_1^*)^+} \hat{v}(\cdot; \tilde{m}_2, \beta_2) = 0$ based on $\mu_1(m_1^* f_1(\phi, 0)) = 0$. Therefore, $\lim_{m_1\to(m_1^*)^+} \tilde{m}_2(m_1,\beta_2) = m_2^*$ by $\lim_{\tilde{m}_2\to(m_2^*)^+} \hat{v}(\cdot; \tilde{m}_2, \beta_2) = 0$ uniformly on [0,1] (Eq. 3.5).

(ii) For any $m_1 > m_1^*$ given, it follows from Lemma 4.2(ii.2) (ii.3) that $\mu_1(m_1 f_1(\phi - \hat{v}(\cdot; m_2, \beta_2), 0))$ is strictly increasing with respect to β_2 in $(0, +\infty)$ and strictly decreasing with respect to m_2 in $(m_2^*, +\infty)$. Then, we can conclude from $\mu_1(m_1 f_1(\phi - \hat{v}(\cdot; \tilde{m}_2, \beta_2), 0)) = 0$ and the implicit function theorem that $\tilde{m}_2(m_1,\beta_2)$ is strictly increasing with respect to β_2 in $(0, +\infty)$. Therefore,

$$\lim_{\beta_2\to0^+} \tilde{m}_2(m_1,\beta_2) < \tilde{m}_2(m_1,\beta_2) < \lim_{\beta_2\to+\infty} \tilde{m}_2(m_1,\beta_2) \text{ for } m_1 > m_1^*.$$

Similarly, substituting $\beta_2 \to 0^+$ in $\mu_1(m_1 f_1(\phi - \hat{v}(\cdot; \tilde{m}_2, \beta_2), 0)) = 0$, we can deduce from [8], Theorem 2.1 again that $\max\{m_2^*, \min\{\frac{k_2}{k_1}, 1\}m_1\} \le \lim_{\beta_2\to0^+} \tilde{m}_2(m_1,\beta_2)$. Moreover, $\lim_{\beta_2\to+\infty} \tilde{m}_2(m_1,\beta_2) = +\infty$. Hence, the inequality about $\tilde{m}_2(m_1,\beta_2)$ in Eq. 4.24 is obtained.

When $m_1 > m_1^*$, $m_2 > \max\{m_2^*, \max\{\frac{k_2}{k_1}, 1\}m_1\}$, Theorem 4.1(ii.1) implies that $(0, \hat{v})$ is globally asymptotically stable provided $0 < \beta_2 \le \beta_2^0$. Therefore, $\tilde{m}_2(m_1,\beta_2) \le \max\{\frac{k_2}{k_1}, 1\}m_1$ provided $0 < \beta_2 \le \beta_2^0$. Combining with 4.24, 4.25 holds.

(iii) Let φ_1 with $\|\varphi_1\|_\infty = 1$ be the corresponding principal eigenfunction of $\mu_1(m_1 f_1(\phi - \hat{v}(\tilde{m}_2, \beta_2), 0)) = 0$. Then, φ_1 satisfies

$$\begin{cases} d(\varphi_1)_{xx} + m_1 f_1(\phi - \hat{v}(\tilde{m}_2, \beta_2), 0)\varphi_1 = 0, & x \in (0,1), \\ (\varphi_1)_x(0) = (\varphi_1)_x(1) + \gamma\varphi_1(1) = 0. \end{cases} \tag{4.27}$$

By differentiating Eq. 4.27 with respect to m_1 and denoting $\frac{\partial}{\partial m_1} = \dot{}$, we have

$$\begin{cases} d(\dot{\varphi}_1)_{xx} + f_1(\phi - \hat{v}, 0)\varphi_1 + m_1 \\ \left[f_1(\phi - \hat{v}, 0)\dot{\varphi}_1 - \dfrac{k_1}{(k_1 + \phi - \hat{v})^2} \cdot \dfrac{\partial \hat{v}(\tilde{m}_2, \beta_2)}{\partial m_2} \times \dot{\tilde{m}}_2(m_1)\varphi_1 \right] = 0, \quad x \in (0,1), \\ (\dot{\varphi}_1)_x(0) = (\dot{\varphi}_1)_x(1) + \gamma\dot{\varphi}_1(1) = 0, \end{cases} \tag{4.28}$$

where $\frac{\partial \hat{v}(\tilde{m}_2,\beta_2)}{\partial m_2}$ is the derivative of $\hat{v}$ with respect to m_2 at $m_2 = \tilde{m}_2$. Multiplying (4.27) by $\dot{\varphi}_1$ and (4.28) by φ_1, integrating over (0,1), and then, subtracting the two resulting equations,

$$\dot{\tilde{m}}_2(m_1,\beta_2) = \frac{\int_0^1 f_1(\phi-\hat{v},0)\varphi_1^2 \mathrm{d}x}{m_1\int_0^1 \frac{k_1}{(k_1+\phi-\hat{v})^2}\cdot\frac{\partial\hat{v}(\tilde{m}_2,\beta_2)}{\partial m_2}\varphi_1^2\mathrm{d}x}. \quad (4.29)$$

Similar to Proposition 4.2(iii), we can show $\lim_{\beta_2\to+\infty}\frac{\partial\hat{v}(\tilde{m}_2,\beta_2)}{\partial m_2} = \frac{\partial}{\partial m_2}\lim_{\beta_2\to+\infty}\hat{v}(\tilde{m}_2,\beta_2) = 0$ based on $\lim_{\beta_2\to+\infty}\hat{v}(\tilde{m}_2,\beta_2) = 0$ uniformly on [0,1] (see Lemma 3.3(ii)). Substituting $\beta_2 \to +\infty$ in (4.29), it is easy to obtain $\lim_{\beta_2\to+\infty}\dot{\tilde{m}}_2(m_1,\beta_2) = +\infty$.

We assume $k_1 > k_2 > 0$ without loss of generality. Then, there exist six critical curves: $m_1 = m_1^*,\ m_2 = m_2^*$,

$$L_1\colon m_2 = \frac{k_2}{k_1}m_1,\quad L_2\colon m_1 = m_2,\quad \Gamma_1\colon m_2 = \bar{m}_2(m_1),\quad \Gamma_2\colon m_2 = \tilde{m}_2(m_1),$$

in the $m_1 - m_2$ plane (Figure 2), which classify the dynamics of system (2.2) into extinction of both species, competitive exclusion and coexistence. Clearly, it follows from Proposition 4.1(i) that line $m_2 = \frac{m_2^*}{m_1^*}m_1$ is located above line L_1 and below line L_2 under the assumption $k_1 > k_2 > 0$. Propositions 4.2(i) and 4.3(i) suggest that Γ_1 and Γ_2 are increasing with respect to $m_1 \in (m_1^*,+\infty)$, respectively. Moreover, $\lim_{m_1\to(m_1^*)^+}\bar{m}_2(m_1) = \lim_{m_1\to(m_1^*)^+}\tilde{m}_2(m_1) = m_2^*$, which implies that Γ^1 and Γ^2 intersect at point (m_1^*, m_2^*). In addition, due to the effect of β^1 and β^2, Propositions 4.2(ii) (iii) and 4.3(ii) (iii) indicate that the locations of Γ^1 and Γ^2 in the $m^1 - m^2$ plane have the following four occasions shown in Figures 2A–D. Here, we assume that Γ^2 is always located above Γ^1 in this region (Figure 2). We set

$$\Pi_0 := (0,m_1^*]\times(0,m_2^*];\ \Pi_1 := (m_1^*,+\infty)\times(0,m_2^*];\ \Pi_2 := (0,m_1^*]\times(m_2^*,+\infty).$$

Now, we are ready to illustrate the dynamical classification of system (2.2) in the $m_1 - m_2$ plane under the assumption $k_1 > k_2 > 0$, by dividing the following four cases.

Case I: $0<\beta_1\le\beta_1^0,\ 0<\beta_2\le\beta_2^0$ (Figure 2A). Then, (4.17) holds provided $0<\beta_1\le\beta_1^0$; that is, $\frac{k_2}{k_1}m_1 < \bar{m}_2(m_1,\beta_1) < m_1$ under the assumption $k_1 > k_2 > 0$. Similarly, (4.25) holds provided $0<\beta_2\le\beta_2^0$, which means $\frac{k_2}{k_1}m_1 < \tilde{m}_2(m_1,\beta_1) < m_1$. These suggest that both Γ_1 and Γ_2 lie between lines L_1 and L_2 (Figure 2A). It follows from Theorem 4.1(i.1) that (0,0) is g.a.s in region $(m_1, m_2) \in \Pi_0$. In particular, the phase portrait graph of system (2.2) with $(m_1, m_2) = (0.2, 0.1) \in \Pi_0$ is illustrated in Figure 1A, which shows that (0,0) is g.a.s in this case. Then, $(\hat{u},0)$ is g.a.s when $(m_1, m_2) \in \Pi_1 \cup \Pi_3$ by Theorem 4.1(i.3), (iii.1). Particularly, the phase portrait graph of system (2.2) with $(m_1, m_2) = (1, 0.1) \in \Pi_1 \cup \Pi_3$ is shown in Figure 1B. $(0,\hat{v})$ is g.a.s in region $(m_1, m_2) \in \Pi_2 \cup \Pi_4$ by Theorem 4.1(i.2) and (ii.1). Moreover, the specific phase portrait graph with $(m_1, m_2) = (0.2, 1) \in \Pi_2 \cup \Pi_4$ is displayed in Figure 1C. Furthermore, by Lemma 4.3, $(\hat{u},0)$ is locally asymptotically stable in region Π_5 and unstable in region $\Pi_6 \cup \Pi_7$; $(0,\hat{v})$ is locally asymptotically stable in region Π_6 and unstable in region $\Pi_5 \cup \Pi_7$. Then, we can conclude from Theorem 4.2(i) that there exist stable coexistence steady states in Π_7, and the specific phase portrait graph with $(m_1, m_2) = (1, 0.545) \in \Pi_7$ is presented in Figure 1D.

Case II: $0<\beta_1\le\beta_1^0,\ \beta_2>\beta_2^*$ (Figure 2B). Then, (4.17) holds and Γ_1 still lies between lines L_1 and L_2 when $0<\beta_1\le\beta_1^0$. Moreover, (4.24) holds when $\beta_2>\beta_2^*$; that is, $\tilde{m}_2(m_1,\beta_2) > \max\{m_2^*, \frac{k_2}{k_1}m_1\}$ under the assumption $k_1 > k_2 > 0$. This implies that Γ_2 lies above lines L_1 and $m_2 = m_2^*$. Note that $\lim_{m_1\to(m_1^*)^+}\tilde{m}_2(m_1,\beta_2) = m_2^*$ by Proposition 4.3(i) and $m_1^* > m_2^*$ if $k^1 > k^2 > 0$ (see Proposition 4.1). Then, $\tilde{m}_2(m_1,\beta_2) < m_1$ when m^1 is near m_1^*, which means that there exists sufficiently small $\epsilon > 0$ such that Γ^2 lies below line L^2 for $m_1 \in (m_1^*, m_1^* + \epsilon)$.

Next, we illustrate two-fold that Γ_2 will first intersect L_2 and then lie above L_2 as m_1 increases (Figure 2B). On one hand, Theorem 4.1(ii) indicates that when $m_1 > m_1^*$ and $m_2 > \max\{m_2^*, m_1\}$, there exists a unique β_2^* such that $(0,\hat{v})$ is unstable when $\beta_2>\beta_2^*$. This means that there exist regions above L_2 such that $(0,\hat{v})$ is unstable when $\beta_2>\beta_2^*$. Note that Γ_2 is strictly increasing with respect to β_2 in $(0, +\infty)$ by Proposition 4.3(ii). Hence, when $\beta_2>\beta_2^*$, we can conclude from Lemma 4.3(ii) that the critical curve Γ_2 for the stability change of $(0,\hat{v})$ must intersect L_2 and then lie above L_2 as m_1 is suitably large. This implies that there exist regions above line L_2 and below Γ_2 such that $(0,\hat{v})$ is unstable when $\beta_2>\beta_2^*$. On the other hand, Proposition 4.3(iii) implies $\lim_{\beta_2\to+\infty}\dot{\tilde{m}}_2(m_1,\beta_2) = +\infty$, which means that the slope of Γ^2 will be bigger than 1 for suitably large β^2. This, in turn, suggests that for large β^2, there exists $\bar{m}_1^* > m_1^*$ such that Γ^2 must intersect L^2 and then locates above L^2 for all $m_1 > \bar{m}_1^*$. Therefore, the region Π_7^1 occurs for large β^2. This region is denoted as Π_7^1 in Figure 2B. Then, we deduce from Theorem 4.2(i) that there exist stable coexistence steady states in $\Pi_7 = \Pi_7^0 \cup \Pi_7^1$. The other regions $\Pi^0 - \Pi^6$ can be similarly defined as in Case I.

Case III: $\beta_1>\beta_1^*,\ 0<\beta_2\le\beta_2^0$ (see Figure 2C). Similar to Case II, (4.25) holds provided $0<\beta_2\le\beta_2^0$; that is, line Γ_2 lies between lines L_1 and L_2 when $0<\beta_2\le\beta_2^0$. Moreover, (4.16) holds when $\beta_1>\beta_1^*$; that is, $m_2^* < \bar{m}_2(m_1,\beta_1) < m_1$ under the assumption $k_1 > k_2 > 0$. This implies that Γ_1 lies below line L_2 and above line $m_2 = m_2^*$. Furthermore, note that $\lim_{m_1\to(m_1^*)^+}\bar{m}_2(m_1,\beta_1) = m_2^*$ by Proposition 4.2(i) and $m_2^* > \frac{k_2}{k_1}m_1^*$ if $k^1 > k^2 > 0$ by Proposition 4.1. Then, $\bar{m}_2(m_1,\beta_1) > \frac{k_2}{k_1}m_1$, when m^1 is near m_1^*, which means that there exists sufficiently small $\varepsilon > 0$ such that Γ^1 lies above L^1 for $m_1 \in (m_1^*, m_1^* + \varepsilon)$.

Similarly, we next illustrate that Γ_1 will first intersect L_1 and then lie below L_1 as m_1 increases (see Figure 2C). On one hand, Theorem 4.1(iii) suggests that when $m_1 > m_1^*$ and $m_2^* < m_2 < \frac{k_2}{k_1}m_1$, there exists a unique β_1^* such that $(\hat{u},0)$ is unstable when $\beta_1>\beta_1^*$. This means that there exist regions below L_1 such that $(\hat{u},0)$ is unstable when $\beta_1>\beta_1^*$. Note that Γ_1 is strictly decreasing with respect to β_1 in $(0,+\infty)$ by Proposition 4.2(ii). Hence, when $\beta_1>\beta_1^*$, we can deduce from Lemma 4.3(i) that the critical curve Γ_1 for the stability change of $(\hat{u},0)$ must intersect L_1 and then lie below L_1 as m_1 is suitably large. This implies that there exist regions below L_1 and above Γ_1 such that $(\hat{u},0)$ is unstable when $\beta_1>\beta_1^*$.

On the other hand, Proposition 4.2(iii) gives $\lim_{\beta_1\to+\infty}\dot{\bar{m}}_2(m_1,\beta_1) = 0$, which implies that the slope of Γ_1 will be smaller than $\frac{k_2}{k_1}$ for suitably large β_1. This, in turn, suggests that, for large β_1, there exists $\bar{m}_1^{**} > m_1^*$ such that Γ_1 must intersect L_1 and then lie below L_1 for all $m_1 > \bar{m}_1^{**}$. Therefore, the region Π_7^2 occurs for large β_1. This region is denoted as Π_7^2 in Figure 2C. Then, we obtain from Theorem 4.2(i) that there exist stable coexistence steady states in $\Pi_7 = \Pi_7^0 \cup \Pi_7^2$. The other regions $\Pi_0 - \Pi_6$ can be similarly illustrated as in Case I.

Case IV: $\beta_1 > \beta_1^*$, $\beta_2 > \beta_2^*$ (Figure 2D). Combining the analysis of $\beta_1 > \beta_1^*$ in Case II and $\beta_2 > \beta_2^*$ in Case III, we know that both the regions Π_7^1 and Π_7^2 exist. It follows from Theorem 4.2(i) that there exist stable coexistence steady states in $\Pi_7 = \Pi_7^0 \cup \Pi_7^1 \cup \Pi_7^2$. The other regions $\Pi_0 - \Pi_6$ can be similarly illustrated as in Case I.

We next make a comparison with the results in [8]. When the intraspecific competition is relatively weak (i.e., for the case of $0 < \beta_1 \le \beta_1^0$ and $0 < \beta_2 \le \beta_2^0$), the competitive dynamics of system (2.2) (Figure 2A) are similar to the unstirred chemostat model with Holling type II functional response (see [8], Theorems 2.1, 2.4] and Figure 1 in [8]), which suggests that the weak intraspecific competition has little effect on the competition outcomes of species.

However, when the intraspecific competition becomes strong, some new phenomena may occur. For instance, for the standard unstirred chemostat models, competition exclusion always happens for the weak–strong competition of two species (see [26], Theorem 2.1), while coexistence may occur in the unstirred chemostat model with B.–D. functional response with the increase of intraspecific competition, under the weak–strong competition cases (see Theorem 4.1 and Figures 2B–D). More precisely, under the weak–strong competition case $m_2 > \max\{\frac{k_2}{k_1}, 1\} m_1$ (i.e., species v has a stronger growth ability compared to species u), the competitive ability of species v becomes weak with the increase of β_2, which may result in the coexistence of the two species (see Theorem 4.1(ii.2) and Figure 2B). Similarly, under the weak–strong competition case $m_2 < \min\{\frac{k_2}{k_1}, 1\} m_1$ (i.e., species u has a stronger growth ability compared to species v), the competitive ability of species u becomes weak with the increase of β_1, which may cause the coexistence of the two species (see Theorem 4.1(iii.2) and Figure 2C). In particular, Theorem 4.1(ii.2), (iii.2) and Figure 2D suggest that coexistence is more likely to happen, when the intraspecific competition of two species is strong.

In summary, these theoretical results indicate that for the weak–strong competition cases, if the intraspecific competition parameter of the species with stronger growth ability is suitably large, we can observe different results from [8] that coexistence may occur. This new phenomenon suggests that the intraspecific competition parameters β_1 and β_2 have a great influence on the competitive outcomes of two species.

5 Positive solution branches of system (2.2)

We define $X = W^{2,p}(0,1) \times W^{2,p}(0,1)$ and $Y = L^p(0,1) \times L^p(0,1)$, where $p > 1$. For fixed $d, k_1, k_2, \beta_1, \beta_2 > 0$ and $m_1 > m_1^*$, system (2.2) admits three branches of trivial or semi-trivial solutions in the space $\mathbb{R}_+ \times X$: $\Gamma_0 = \{(m_2, 0, 0)\colon m_2 > 0\}$, $\Gamma_u = \{(m_2, \hat{u}, 0)\colon m_2 > 0\}$ and $\Gamma_v = \{(m_2, 0, \hat{v})\colon m_2 > m_2^*\}$, where $\hat{u} = \omega^*(\cdot; m_1, \beta_1)$ and $\hat{v} = \omega^*(\cdot; m_2, \beta_2)$. In this section, we will regard m_2 as the bifurcation parameter and study separately positive solutions bifurcating from the semi-trivial branches Γ_u and Γ_v by the Crandall–Rabinowitz bifurcation theorem in [31].

We first show that there exists a positive solution branch that bifurcates from the semi-trivial solution $(\hat{u}, 0)$. Moreover, the bifurcation of positive solutions from $(\hat{u}, 0)$ can only occur at $m_2 = \bar{m}_2$ by Lemma 4.3.

Theorem 5.1. For fixed $d, k_1, k_2, \beta_1, \beta_2 > 0$ and $m_1 > m_1^*$, there is a smooth non-constant solutions curve $\Gamma_1 = \{(m_2(s), u(s), v(s))\colon s \in (-\epsilon, \epsilon)\}$ such that $(m_2(s), u(s), v(s))$ is a positive solution of system (2.2) for $s \in (0, \epsilon)$ and satisfies $m_2(0) = \bar{m}_2$, $u(s) = \hat{u} + s\varphi_0 + o(s)$, and $v(s) = s\psi_0 + o(s)$. Here, $\psi_0 > 0$ *is the principal eigenfunction corresponding to the eigenvalue* $\mu_1(\bar{m}_2 f_2(\phi - \hat{u}, 0)) = 0$, which satisfies

$$\begin{cases} \mathcal{B}_2(\bar{m}_2)\psi_0 = 0, & x \in (0,1), \\ \psi_0'(0) = \psi_0'(1) + \gamma\psi_0(1) = 0, \end{cases} \tag{5.1}$$

and $\varphi_0 < 0$ satisfies

$$\begin{cases} \mathcal{B}_1(m_1)\varphi_0 = -m_1\hat{u} f_1^v(\phi - \hat{u}, \hat{u})\psi_0, & x \in (0,1), \\ \varphi_0'(0) = \varphi_0'(1) + \gamma\varphi_0(1) = 0. \end{cases} \tag{5.2}$$

Moreover,

$$m_2'(0) = -\frac{\int_0^1 \bar{m}_2 [f_2^u(\phi - \hat{u}, 0)\varphi_0 + f_2^v(\phi - \hat{u}, 0)\psi_0]\psi_0^2 dx}{\int_0^1 f_2(\phi - \hat{u}, 0)\psi_0^2 dx}, \tag{5.3}$$

where $f_2^u(\phi - \hat{u}, 0) = -\frac{k_2 + \beta_2\hat{u}}{(k_2 + \phi - \hat{u})^2}$ and $f_2^v(\phi - \hat{u}, 0) = -\frac{k_2 + \beta_2\phi}{(k_2 + \phi - \hat{v})^2}$.

Theorem 5.1. can be proved by the similar arguments as in [35], Theorem 6.2. For completeness, we defer the proof of Theorem 5.1 to the Supplementary Appendix.

Theorem 5.2. For fixed $d, k_1, k_2, \beta_1, \beta_2 > 0$ and $m_2 > m_2^*$, there is a smooth non-constant solutions curve $\Gamma_2 = \{(m_2(s), u(s), v(s))\colon s \in (-\epsilon, \epsilon)\}$ such that $(m_2(s), u(s), v(s))$ is a positive solution of (2.2) for $s \in (0, \epsilon)$ and satisfies $m_2(0) = \tilde{m}_2$, $u(s) = s\tilde{\varphi}_0 + o(s)$, *and* $v(s) = \hat{v} + s\tilde{\psi}_0 + o(s)$ $(\hat{v} = \hat{v}(\cdot; \tilde{m}_2, \beta_2))$. *Here,* $\tilde{\varphi}_0 > 0$ *is the principal eigenfunction corresponding to* $\mu_1(m_1 f_1(\phi - \hat{v}(\cdot; \tilde{m}_2, \beta_2), 0)) = 0$, *which satisfies*

$$\begin{cases} \mathcal{B}_3(\tilde{m}_2)\tilde{\varphi}_0 = 0, & x \in (0,1), \\ \tilde{\varphi}_0'(0) = \tilde{\varphi}_0'(1) + \gamma\tilde{\varphi}_0(1) = 0, \end{cases} \tag{5.4}$$

and $\tilde{\psi}_0 < 0$ *satisfies*

$$\begin{cases} \mathcal{B}_4(\tilde{m}_2)\tilde{\psi}_0 = -\tilde{m}_2\hat{v} f_2^u(\phi - \hat{v}, \hat{v})\tilde{\varphi}_0, & x \in (0,1), \\ \tilde{\psi}'(0) = \tilde{\psi}'(1) + \gamma\tilde{\psi}(1) = 0. \end{cases} \tag{5.5}$$

Moreover,

$$m_2'(0) = -\frac{\int_0^1 [f_1^u(\phi - \hat{v}, 0)\tilde{\varphi}_0 + f_1^v(\phi - \hat{v}, 0)\tilde{\psi}_0]\tilde{\varphi}_0^2 dx}{\int_0^1 \hat{v}' f_1^v(\phi - \hat{v}, 0)\tilde{\varphi}_0^2 dx}, \tag{5.6}$$

where $f_1^u(\phi - \hat{v}, 0) = -\frac{k_1 + \beta_1\phi}{(k_1 + \phi - \hat{v})^2}$, $f_1^v(\phi - \hat{v}, 0) = -\frac{k_1 + \beta_1\hat{v}}{(k_1 + \phi - \hat{v})^2}$, and $\hat{v}'$ is the derivative of $\hat{v}$ with respect to m_2 at $m_2 = \tilde{m}_2$.

The proof of Theorem 5.2 is similar to the arguments in Theorem 5.1, and we omit it here.

We define $\Omega = \{(m_2, u, v) \in \mathbb{R}_+ \times X\colon u > 0, v > 0, (m_2, u, v)$ satisfies system (2.3)$\}$. The following results show that the two bifurcation continua Γ_1 and Γ_2 in Theorems 5.1 and 5.2 are connected.

Theorem 5.3. We consider $d, k_1, k_2, \beta_1, \beta_2 > 0$ and $m_1 > m_1^*$ fixed. Then, there exists a connected component Γ of Ω, which bifurcates from the semi-trivial solution branch Γ_u at $(\bar{m}_2, \hat{u}, 0)$ and meets the other semi-trivial solution branch Γ_v at $(\tilde{m}_2, 0, \hat{v})$. In particular, system (2.3) admits a positive solution (u, v) if m_2 lies between $\bar{m}_2$ and $\tilde{m}_2$.

The proof is motivated by the methods in [13], Theorem 6.4 (see also [8], Theorem 4.10]). For readability, the proof is given in Supplementary Appendix.

6 Numerical descriptions

In this section, we will study the effect of diffusion rates d on the dynamics of system (2.2). It follows from Eqs 4.1, 4.15 that the threshold values $m_1^*, m_2^*, \bar{m}_2$, and $\tilde{m}_2$ depend on the diffusion rates d. Since these threshold values are dependent on d and they are non-monotone in d, we cannot theoretically establish the threshold dynamics of system (2.2) in terms of d. In order to explore the effect of d on the dynamics of system (2.2), in this subsection, we resort to numerical approaches. We fix $L = 1$, $S^0 = 1$, $\gamma = 0.5$, $k_1 = 1$, $k_2 = 0.4$, and $m_1 = 1$ as mentioned before. Then, by presenting the bifurcation diagrams of positive equilibrium solution of system (2.2) with the bifurcation parameter d increasing, the results are divided into the following three cases.

Case I: $m_2 > \max\{\frac{k_2}{k_1}, 1\}m_1$. We take $m_2 = 2$ such that $\frac{m_2}{k_2} = 5 > \frac{m_1}{k_1} = 1$, which means that species v has a stronger growth ability compared to species u. We can call this case the weak–strong competition [13]. To identify the effect of intraspecific competition, we fix $\beta_1 = 0.01$ and let β_2 change from $\beta_2 = 0.01$ to $\beta_2 = 1$.

First, if $\beta_1 = 0.01$, $\beta_2 = 0.01$, there is no coexistence and the competitive exclusion principle holds (species v with a stronger growth ability will win the competition) when d is sufficiently small (Figure 3A). As d increases, both species go extinct, which is consistent with our biological intuition that the sufficiently large diffusion rates will put species at a disadvantage. These numerical observations in Figure 3A coincide with [26], Theorem 5.4.

Second, if $\beta_1 = 0.01$, $\beta_2 = 1$. Clearly, under this weak–strong competition case, though species v has stronger growth ability compared to species u, the increase of β_2 makes the competitive ability of v weaker. This is consistent with our biological intuition that the stronger intraspecific competition will put species at a disadvantage. Moreover, coexistence may occur when d is sufficiently small (Figure 3B), which is different from [8], Theorem 5.4. As d increases, species v wins the competition. As d further increases, the sufficiently large diffusion rates drive both species to extinction.

Case II: $m_1 > \max\{\frac{k_1}{k_2}, 1\}m_2$. We take $m_2 = 0.2$ such that $m_1 = 1 > \max\{\frac{k_1}{k_2}, 1\}m_2 = 0.5$, which implies that species u has a stronger growth ability compared to species v. Similarly, we call this case the weak–strong competition case [13]. We fix $\beta_2 = 0.01$ and let β_1 change from $\beta_1 = 0.01$ to $\beta_1 = 1$. Similar to Case I, when $\beta_1 = 0.01$, $\beta_2 = 0.01$, results similar to those in Figure 3A are shown in Figure 4A. When $\beta_1 = 1$, $\beta_2 = 0.01$, the increase of β_1 makes the competitive ability of u weaker. Then, we can observe that coexistence may occur when d is sufficiently small (see Figure 4B), which is quite different from [26], Theorem 5.4.

Case III: $\frac{k_2}{k_1}m_1 < m_2 < m_1$. We take $m_2 = 0.6$ such that $\frac{k_2}{k_1}m_1 = 0.4 < m_2 = 0.6 < m_1 = 1$. We call this case the evenly matched competition [13]. Moreover, the fact of $\frac{m_1}{k_1} < \frac{m_2}{k_2}$ suggests that though the growth ability of the two species is evenly matched, the competitive ability of species v is still slightly better than that of species u. Then, for this evenly matched competition case, we fix $\beta_1 = 0.01$ and let β_2 change from $\beta_2 = 0.01$ to $\beta_2 = 1$.

For $\beta_1 = 0.01$, $\beta_2 = 0.01$, as shown in Figure 5A, the diffusion rates have a significant effect on the dynamics of system (2.2). More precisely, the dynamics of system (2.2) shift between four scenarios with the bifurcation parameter d increasing; that is, 1) competitive exclusion occurs and species v wins the competition, when d is sufficiently small; 2) coexistence occurs as d increases; 3) competitive exclusion occurs again and species u wins the competition, as d further increases; and 4) both species are washed out as d continues to increase. These suggest that system (2.2) may show a trade-off among extinction, exclusion, and coexistence as d increases. Particularly, coexistence occurs at the intermediate diffusion rates, which is in line with the theoretical results in [8].

For $\beta_1 = 0.01$, $\beta_2 = 1$, as stated before, the increase of β_2 will make the competitive ability of v weaker. Then, we can observe from Figure 5B that both species can coexist when d is sufficiently small. As d increases, competitive exclusion happens and species u wins the competition. As d further increases, the large diffusion rates drive two species to extinction.

In shorts, for different competition Cases (I)–(III), we investigate the effect of diffusion on the dynamics of system (2.2) by taking different intraspecific competition parameters β_1, β_2. As shown in Figures 3–5, the impacts of diffusion and intraspecific competition on the competitive outcomes of species are complex, which further suggests that diffusion and intraspecific competition play a key role in determining the dynamics of system (2.2).

7 Discussion

In this paper, we investigate an unstirred chemostat model with the Beddington–DeAngelis functional response (see system (2.2)). The analytical and numerical results show that the intraspecific competition and diffusion have an important biological effect on the dynamics of system (2.2).

Theoretically, we first adopt a basic strategy regarding the growth rates as variable/bifurcation parameters to study the effect of growth rates on system (2.2). The results show that there exist six critical curves

$$m_1 = m_1^*,\ m_2 = m_2^*,\ L_1\colon m_2 = \frac{k_2}{k_1}m_1,\ L_2\colon m_1 = m_2,\ \Gamma_1\colon m_2 = \bar{m}_2(m_1),\ \Gamma_2\colon m_2 = \tilde{m}_2(m_1)$$

in the $m_1 - m_2$ plane, which may classify the dynamics of system (2.2) into extinction of both species, competitive exclusion and coexistence (see Theorems 4.1, 4.2). To further understand the effect of β_i, $(i = 1, 2)$ on the dynamics of (2.2), we explore the properties of critical curves Γ_1 and Γ_2 (see Propositions 4.2 and 4.3) and get a relatively clear dynamics classification of system (2.2) in the $m_1 - m_2$ plane (Figure 2).

Numerically, since diffusion plays a key role in determining the competition outcomes of two species, we study the effect of diffusion on the dynamics of system (2.2). More precisely, for two weak–strong competition cases, due to the effect of intraspecific competition parameters β_1 and β_2, the coexistence may occur at sufficiently small diffusion rates (Figures 3B, 4B), while for the evenly matched competition case, the dynamics of system (2.2) shift between different scenarios (competitive exclusion, coexistence, and extinction) when β_1 and β_2 are small and the coexistence only occurs at the intermediate diffusion rates (Figure 5A). When β_2 is larger than β_1, we observe from Figure 5B that coexistence may occur at sufficiently small diffusion rates.

In conclusion, in this paper, the dynamics classification of system (2.2) in the $m_1 - m_2$ plane is established by the linear eigenvalue theory and the monotone dynamical system theory (Figure 2). Due to the effect of intraspecific competition parameters β_1 and β_2, the dynamics of system (2.2) are more complex than that of the unstirred chemostat model with Holling type II functional response (see Figure 1 of [8]). Numerically, we study the effect of diffusion on system (2.2) and obtain rich numerical results (Figures 3–5). These numerical observations reveal that, under different competition cases, the effects of diffusion and intraspecific competition on the dynamics of system (2.2) are complex. This, in turn, suggests that the B.–D. functional response is more biologically realistic and superior to the well-known Holling type II functional response in modeling the resource uptake of species.

Data availability statement

The original contributions presented in the study are included in the article/Supplementary Material; further inquiries can be directed to the corresponding author.

Author contributions

The theory part and simulation were obtained by the first author WZ. The second and third authors HN and ZW guided the work. All authors contributed to the article and approved the submitted version.

Funding

This work was supported by the National Natural Science Foundation of China (12071270 and 12171296) and the Natural Science Basic Research Program of Shaanxi (No. 2023-JC-JQ-03).

Acknowledgments

The authors are very grateful to the referees and the handling co editor-in-chief for their kind and valuable suggestions leading to a substantial improvement of the manuscript.

Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Publisher's note

Supplementary material

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fphy.2023.1205571/full#supplementary-material

References

1. Bayen T, Cazenave-Lacroutz H, Coville J. Stability of the chemostat system including a linear coupling between species. *Discrete Contin Dyn Syst Ser B* (2023) 28(2023):2104–29. doi:10.3934/dcdsb.2022160

2. Hsu SB, Jin Y. The dynamics of a two host-two virus system in a chemostat environment. *Discrete Contin Dyn Syst Ser B* (2021) 26:415–41. doi:10.3934/dcdsb.2020298

3. Nie H, Hsu SB, Grover JP. Algal competition in a water column with excessive dioxide in the atmosphere. *J Math Biol* (2016) 72:1845–92. doi:10.1007/s00285-015-0926-8

4. Smith HL, Waltman P. *The theory of the chemostat*. Cambridge: Cambridge University, Press (1995).

5. Dellal M, Bar B. Global analysis of a model of competition in the chemostat with internal inhibitor. *Discrete Contin Dyn Syst Ser B* (2021) 26:1129–48. doi:10.3934/dcdsb.2020156

6. Hsu SB, Waltman P. On a system of reaction-diffusion equations arising from competition in an unstirred chemostat. *SIAM J Appl Math* (1993) 53:1026–44. doi:10.1137/0153051

7. Nie H, Shi Y, Wu JH. The effect of diffusion on the dynamics of a predator-prey chemostat model. *SIAM J Appl Math* (2022) 3:821–48. doi:10.1137/21m1432090

8. Shi JP, Wu YX, Zou XF. Coexistence of competing species for intermediate dispersal rates in a reaction-diffusion chemostat model. *J Dynam Differential Equations* (2020) 32:1085–112. doi:10.1007/s10884-019-09763-0

9. Smith HL. Monotone dynamical systems: An introduction to the theory of competitive and cooperative systems. In: *Mathematical surveys and monographs*. Providence, RI: American Mathematical Society (1995).

10. Wu JH. Global bifurcation of coexistence state for the competition model in the chemostat. *Nonlinear Anal* (2000) 39:817–35. doi:10.1016/s0362-546x(98)00250-8

11. Holling CS. The functional response of predator to prey density and its role in mimicry and population regulation. *Mem Entonmol Soc Can* (1965) 45:1–60.

12. Zhang W, Nie H, Wu JH. A reaction-diffusion-advection chemostat model in a flowing habitat: Mathematical analysis and numerical simulations. *Internat J Bifur Chaos Appl Sci Engrg* (2023) 33:1245–74. doi:10.1142/s0218127423500736

13. Zhang W, Nie H, Wu JH. Dynamics of a reaction-diffusion-advection model with two species competing in a flow reactor. *Discrete Contin Dyn Syst Ser B* (2023) 28:3453–86. doi:10.3934/dcdsb.2022226

14. So WH, Waltman P. A nonlinear boundary value problem arising from competition in the chemostat. *Appl Math Comput* (1989) 32:169–83. doi:10.1016/0096-3003(89)90092-1

15. Beddington JR. Mutual interference between parasites or predators and its effect on searching efficiency. *J Anim Ecol* (1975) 44:331–40. doi:10.2307/3866

16. DeAngelis DL, Goldstein RA, O'Neill RV. A model for trophic interaction. *Ecology* (1975) 56:661–892.

17. Harrision GW. Comparing predator-prey models to Luckinbill's experiment with didinium and paramecium. *Ecology* (1995) 76:357–69.

18. Jiang HL, Wu JH, Wang LJ, Guo GH. Qualitative analysis for a competition model with B-D functional response and numerical simulation. *Numer Methods Partial Differential Equations* (2014) 30:1575–94. doi:10.1002/num.21848

19. Zhang GH, Wang XL. Extinction and coexistence of species for a diffusive intraguild predation model with B-D functional response. *Discrete Contin Dyn Syst Ser B* (2018) 23:3755–86. doi:10.3934/dcdsb.2018076

20. Meng Q, Yang L. Steady state in a cross-diffusion predator-prey model with the Beddington-DeAngelis functional response. *Nonlinear Anal Real World Appl* (2019) 45: 401–13. doi:10.1016/j.nonrwa.2018.07.012

21. He X, Zheng SN. Protection zone in a diffusive predator-prey model with Beddington-DeAngelis functional response. *J Math Biol* (2017) 75:239–57. doi:10.1007/s00285-016-1082-5

22. Feng XZ, Sun C, Yang WB, Li CT. Dynamics of a predator-prey model with nonlinear growth rate and B-D functional response. *Nonlinear Anal Real World Appl* (2023) 70:103766. in press. doi:10.1016/j.nonrwa.2022.103766

23. Wang YE, Wu JH, Guo GH. Coexistence and stability of an unstirred chemostat model with Beddington-DeAngelis function. *Comput Math Appl* (2010) 60:2497–507. doi:10.1016/j.camwa.2010.08.057

24. Nie H, Wu JH. Coexistence of an unstirred chemostat model with Beddington-DeAngelis functional response and inhibitor. *Nonlinear Anal Real World Appl* (2010) 11:3639–52. doi:10.1016/j.nonrwa.2010.01.010

25. Feng XZ, Sun SP, Zhang TQ, An XM. The effect of parameters on positive solutions and asymptotic behavior of an unstirred chemostat model with B-D functional response. *Adv Difference Equ* (2018) 23:181–204. doi:10.1186/s13662-018-1587-x

26. Zhang S, Tan D, Chen LS. Chaotic behavior of a chemostat model with Beddington-DeAngelis functional response and periodically impulsive invasion. *Chaos Solitons Fractals* (2006) 29:474–82. doi:10.1016/j.chaos.2005.08.026

27. Zhou X, Song X, Shi X. Analysis of competitive chemostat models with the Beddington-DeAngelis functional response and impulsive effect. *Appl Math Model* (2007) 31:2299–312. doi:10.1016/j.apm.2006.08.010

28. Hirsch MW, Smith HL, Zhao XQ. Chain transitivity, attractivity, and strong repellors for semidynamical systems. *J Dynam Differential Equations* (2001) 13:107–31. doi:10.1023/a:1009044515567

29. Cantrell R, Cosner C. *Spatial ecology via reaction-diffusion equations*. Chester, UK: John Wiley and Sons Ltd (2003).

30. Lou Y, Nie H, Wang YE. Coexistence and bistability of a competition model in open advective environments. *Math Biosci* (2018) 306:10–9. doi:10.1016/j.mbs.2018.09.013

31. Crandall MG, Rabinowitz PH. Bifurcation from simple eigenvalues. *J Funct Anal* (1971) 8:321–40. doi:10.1016/0022-1236(71)90015-2

32. Protter MH, Weinberger HF. *Maximum principles in differential equations*. New York: Springer-Verlag (1984).

33. Shi JP. Persistence and bifurcation of degenerate solutions. *J Funct Anal* (1999) 169:494–531. doi:10.1006/jfan.1999.3483

34. Shi JP, Wang XF. On global bifurcation for quasilinear elliptic systems on bounded domains. *J Differential Equations* (2009) 246:2788–812. doi:10.1016/j.jde.2008.09.009

35. L´opez-G´omez J. Global bifurcation for Fredholm operators. *Rend Istit Mat Univ Trieste* (2016) 48:539–64. doi:10.13137/2464-8728/13172