Journal of Dynamics and Differential Equations
https://doi.org/10.1007/s10884-019-09763-0

Coexistence of Competing Species for Intermediate Dispersal Rates in a Reaction–Diffusion Chemostat Model

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Received: 20 August 2017 / Revised: 18 February 2019

Abstract
A diffusive chemostat model with two competing species and one nutrient is revisited in this paper. It is shown that at large diffusion rate, both species are washed out, while competition exclusion occurs at small diffusion rate. This implies that a stable coexistence only occurs at intermediate diffusion rate, and an explicit way of determining parameter ranges which support a stable coexistence steady state is given.

Keywords Chemostat · Reaction–diffusion · Competitive exclusion · Coexistence · Diffusion rate · Stability

Mathematics Subject Classification 35K57 · 35Q92 · 35B40 · 35B35 · 92D40

1 Introduction

Theoretical biologists conjecture/believe that coexistence of competing species are most likely when their dispersals are at intermediate levels (see, e.g., [27,30,31,45]). This is because when the dispersal rate is small, competitive exclusion happens in each local community that can be regarded as a closed system; and when the dispersal rate is large, the whole community is a closed system and the competitive exclusion also governs the interaction

Research supported by NSF of USA (Grant No. DMS-1313243), by a Fields Institute Postdoctoral Fellowship and by NSERC of Canada (Grant No. RGPIN-2016-04665).

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Published online: 29 May 2019

between competing species. In this paper, we will confirm such a conjecture/belief in a diffusive chemostat model with two competing species, and show that coexistence of the competing species is only possible for intermediate diffusion rates.

Ever since the design of chemostat by Novick and Szilard [35,36] to grow microbial species in laboratory, it has attracted numerous studies in biology and mathematics (e.g. [4–7,12,32–34,41,46–48]). A chemostat is an apparatus with a continuous constant inflow of nutrients for the growth of microorganisms and an outflow of mixed culture at the same rate to keep the volume unchanged. Besides its role in serving as an apparatus for laboratory bacterium cultivation, it can also be treated as an approximation of complicated microbial habitats such as ponds and lakes. As pointed out by Hsu and Waltman in [25], many theoretical studies are in agreement with the experiments in some simple situations, and this makes the mathematical researches on chemostats more intriguing.

Because chemostats are usually well-stirred for the purpose of uniform distribution of nutrients, most of the earlier chemostat models assume well-stirring of the culture, leading to spatially homogeneous densities of nutrients and microorganisms described by ordinary differential equation models. As a consequence, competitive exclusion for microorganisms is typically predicted in most of those models. For example, in the ODE Monod model [17,19, 20,43] and ODE Droop model [9,10,40], the coexistence of different microbial species is not possible. However, coexistence of different species has been observed both in laboratories and in nature. This suggests that the well-stirring assumption is not reasonable and motivates incorporation of passive diffusion and/or spatially heterogeneous parameters into models. There have been some efforts along this line, see, e.g., [6,7,12,21,23,25,32–34,47,48].

Among the aforementioned diffusive chemostat models is the most classic one introduced by Hsu and Waltman [25]:

$$\begin{cases} S_t = dS_{xx} - m_1 f_1(S)\,u - m_2 f_2(S)\,v, & x \in (0,1), \\ u_t = du_{xx} + m_1 f_1(S)\,u, & x \in (0,1), \\ v_t = dv_{xx} + m_2 f_2(S)\,v, & x \in (0,1), \\ S_x(0,t) = -S_0, \;\; S_x(1,t) + \gamma S(1,t) = 0, & \\ u_x(0,t) = 0, \;\; u_x(1,t) + \gamma u(1,t) = 0, & \\ v_x(0,t) = 0, \;\; v_x(1,t) + \gamma v(1,t) = 0, & \\ w(x,0) = w^0(x), & w = S, u, v, \end{cases} \tag{1.1}$$

where the nutrient uptake rate is Monod type

$$f_i(S) = \frac{S}{a_i + S}, \;\; i = 1, 2. \tag{1.2}$$

Here $S(x,t)$ is the concentration of the nutrients, and $u(x,t)$ and $v(x,t)$ are the concentrations of the two competing microorganisms at position x and time t, respectively. The diffusion terms S_{xx}, u_{xx} and v_{xx} represent the random motion of the nutrients and microorganisms with an identical diffusion rate d. The positive constant m_i is the growth rate of the microorganisms and a_i is the Michaelis–Menten half-saturation constant. The nutrients are pumped in at the rate of S_0, and the microorganisms cannot cross the boundary at position $x = 0$. The mixed culture containing nutrients and microorganisms are pumped out at the rate of γ at the position $x = 1$, which results in the Robin boundary conditions [25]. Indeed the loss of nutrients or microorganisms at $x = 1$ can be written as $dw_x(1,t) = -d\gamma w(1,t)$ for $w = S, u, v$, which is equivalent to $w_x(1,t) + \gamma w(1,t) = 0$. Other boundary conditions have also been considered especially when there is also a unidirectional flow in the chemostat [2]. The initial data S^0, u^0, and v^0 are nonnegative nontrivial continuous functions.

As shown in [25], the total concentration $S + u + v$ in the chemostat approaches a steady state

$$\phi(x) = S_0 \left(\frac{1+\gamma}{\gamma} - x \right), \tag{1.3}$$

and this fact allows (1.1) to have the following limiting system:

$$\begin{cases} u_t = du_{xx} + m_1 f_1(\phi - u - v)\, u, & x \in (0,1),\ t > 0, \\ v_t = dv_{xx} + m_2 f_2(\phi - u - v)\, v, & x \in (0,1),\ t > 0, \\ w_x(0,t) = 0,\ w_x(1,t) + \gamma w(1,t) = 0, & w = u, v, \\ u(x,0) = u^0(x), v(x,0) = v^0(x), u^0 + v^0 \le \phi. \end{cases} \tag{1.4}$$

It is not hard to check that the region $\{(u, v) \in C_+[0,1] \times C_+[0,1] : u + v \le \phi\}$ is invariant for (1.4). The steady states of (1.4) are the nonnegative solutions of the following elliptic system:

$$\begin{cases} du_{xx} + m_1 f_1(\phi - u - v)\, u = 0, & x \in (0,1), \\ dv_{xx} + m_2 f_2(\phi - u - v)\, v = 0, & x \in (0,1), \\ u'(0) = u'(1) + \gamma u(1) = 0, \quad v'(0) = v'(1) + \gamma v(1) = 0, \end{cases} \tag{1.5}$$

satisfying $u + v \le \phi$. The existence of positive solutions of (1.5) is investigated in [42] by a bifurcation method, and the dynamics of (1.4) are studied in [23–25]. We admit, and it is also pointed out in [25], that the assumption of the nutrients and microorganisms having the same diffusion rate d is not that biologically realistic, but this assumption is crucial in reducing (1.1) to the limiting system (1.4). For different diffusion rates, there were only very limited results known compared to the equal diffusion rate case (see, e.g., [2,13,14]). However, we would like to point out that (1.4) itself is also of great interest since it may be viewed as a variation of the Lotka–Volterra competition model.

Since (1.4) generates a strictly monotone dynamical system, by the theory of monotone dynamical systems (see, e.g., [18,24,39]), the dynamics of (1.4) is determined by the nonnegative steady states. As far as a chemostat model is concerned, positive co-existence steady states are particularly important and interesting, but are also most mathematically challenging. In [25], the authors conjectured that when the two semi-trivial steady states are unstable, there exists a unique coexistence steady state which is globally asymptotically stable. This conjecture still remains unsolved. To the authors' best knowledge, for similar diffusive chemostat models, the existence of stable coexistence steady state has only been proved when the two species are similar (for the current model, this means $m_1 \approx m_2$ and $a_1 \approx a_2$) by the perturbation technique and Lyapunov–Schmidt reduction [32–34]. In this paper, we prove the existence of a stable coexistence steady state for Problem (1.4) for a different range of parameters, and our main results provide partial support for the conjecture by Hsu and Waltman but the uniqueness of coexistence is still not known. The parameter range which supports a stable coexistence state is robust and explicit. An implicit condition on (a_i, m_i) and d for the existence of a stable coexistence state was first given in [25], but it was not clear whether such conditions can be achieved or not. We expect that our method can be applied to other diffusive chemostat models.

The following result has been proved in [25]:

1. When the diffusion coefficient d is large, then both species are washed out, meaning that the extinction steady state is globally asymptotically stable for (1.4) (see Theorem 2.1).

Our main results in this paper can be summarized as follows:

2. For fixed m_i, a_i satisfying $m_1/a_1 \neq m_2/a_2$, when the diffusion coefficient d is sufficiently small, then there is no coexistence steady state for (1.4), and the competition exclusion is the consequence meaning that one of the semi-trivial steady states is globally asymptotically stable (see Theorem 5.4);
3. When the diffusion coefficient d is fixed in an intermediate range which depends on a_1 and m_1, for small a_2 there is an interval of m_2 within which, both semi-trivial steady states are unstable and there is a stable coexistence steady state (see Theorem 4.6).

Our results indicate that coexistence in (1.4) occurs *only when the diffusion rate is at intermediate level*. Indeed fixing a_i and m_i, the coexistence steady state cannot occur if d is small (Theorem 5.4) or large (Theorem 2.1). This provides rigorous theoretical support to the theory that claims coexistence for intermediate diffusion rates in ecology [27,30,31,45].

Note that when the diffusion rate d is small, our results also suggest that the ratio m_i/a_i completely determines the competing ability of the species i. This is in consistence with the ODE result proved in [19,20], in which it was shown that the outcome of the competition is determined by $da_i/(m_i - d) \approx da_i/m_i$ when d is small. If the microorganisms live in an interval $(0, L)$ instead of $(0, 1)$, after a rescaling, we can find that the resulting diffusion rate d is proportional to L^{-2} in the sense that small diffusion rate corresponds to large interval size (see [22]).

We remark that besides chemostat models, coexistence phenomenon has been investigated in other reaction–diffusion competition systems such as Lotka–Volterra systems [15,16,26, 28], two-strain epidemic SIS model [1,44] and phytoplankton models [11,29]. Our methods may be adapted to these models to show the existence of coexistence steady states. The uniqueness of stable coexistence steady state for the Lotka–Volterra system has been shown in [15,26], and a complete classification of dynamics for the Lotka–Volterra system with weak competition has been achieved in [15,16]. The uniqueness of stable coexistence state and complete dynamics for all parameter ranges have not been obtained for other diffusive competition systems including (1.4).

The rest of the paper is organized as follows. In Sect. 2, we present some preliminary results. In Sect. 3, we study the single species model and consider the behaviour of the positive steady state as the parameters vary. Coexistence of the two species is studied in Sect. 4, and we prove the existence of a stable coexistence steady state for some parameter ranges. In Sect. 5, we determine the dynamics of the model for small diffusion rate d with other parameters fixed and prove that there is no coexistence if $m_1/d_1 \neq m_2/d_2$. Finally we present some numerical studies in Sect. 6.

2 Preliminaries

Consider the eigenvalue problem

$$\begin{cases} \psi''(x) + \lambda q(x)\psi(x) = 0, & x \in (0, 1), \\ \psi'(0) = \psi'(1) + \gamma\psi(1) = 0. \end{cases} \tag{2.1}$$

Suppose that $q(x) \in C[0,1]$, $q(x) \geq (\not\equiv) 0$ for $x \in (0,1)$, then (2.1) has a sequence of eigenvalues $0 < \lambda_1(q) < \lambda_2(q) < \cdots \lambda_k(q) < \cdots$ with $\lim_{k\to\infty} \lambda_k(q) = \infty$, and the eigenfunction ψ_1 associated with the principal eigenvalue $\lambda_1(q)$ can be chosen to be positive. From the variational characterization of $\lambda_1(q)$:

$$\lambda_1(q) = \inf_{\psi \in C^1[0,1], \int_0^1 q(x)\psi^2(x)dx \neq 0} \frac{\int_0^1 [\psi'(x)]^2 dx + \gamma\psi^2(1)}{\int_0^1 q(x)\psi^2(x)dx}, \tag{2.2}$$

we know the monotonicity of $\lambda_1(q)$ in the following sense: if $q_1(x) \geq (\not\equiv) q_2(x)$ for $x \in (0,1)$, then $\lambda_1(q_1) < \lambda_1(q_2)$.

A related eigenvalue problem is

$$\begin{cases} \theta''(x) + q(x)\theta(x) = \mu\theta(x), & x \in (0,1), \\ \theta'(0) = \theta'(1) + \gamma\theta(1) = 0. \end{cases} \tag{2.3}$$

For any $q(x) \in C[0,1]$, (2.3) has a sequence of eigenvalues $\mu_1(q) > \mu_2(q) > \cdots \mu_k(q) > \cdots$ with $\lim_{k\to\infty} \mu_k(q) = -\infty$, and the eigenfunction θ_1 associated with the principal eigenvalue $\mu_1(q)$ can be chosen to be positive. From the variational characterization of $\mu_1(q)$:

$$\mu_1(q) = -\inf_{\theta \in C^1[0,1], \theta \neq 0} \frac{\int_0^1 [\theta'(x)]^2 dx - \int_0^1 q(x)\theta^2(x)dx + \gamma\theta^2(1)}{\int_0^1 \theta^2(x)dx}, \tag{2.4}$$

we know the monotonicity of $\mu_1(q)$ in the following sense: if $q_1(x) \geq (\not\equiv) q_2(x)$ for $x \in (0,1)$, then $\mu_1(q_1) > \mu_1(q_2)$.

Consider the scalar steady state equation

$$\begin{cases} dw'' + \dfrac{m(\phi - w)w}{a + \phi - w} = 0, & x \in (0,1), \\ w'(0) = w'(1) + \gamma w(1) = 0, \end{cases} \tag{2.5}$$

where $m, a > 0$ are constant and $\phi(x)$ is give by (1.3). Denote $f_a(\phi) = \phi/(a+\phi)$. Then for any $a > 0$, by [25, Theorem 3.2], (2.5) has a unique positive solution $w_*(x; m, a)$ with $0 < w_*(\cdot; m, a) < \phi$, if and only if $m > d\lambda_1(f_a(\phi))$. Based on this, we immediately see that Eq. (1.5) has the following trivial and semi-trivial solutions:

- trivial solution: $E_0 = (0, 0)$;
- semi-trivial solution: $E_1 = (w_*(\cdot; m_1, a_1), 0)$, if and only if $m_1 > d\lambda_1(f_1(\phi))$;
- semi-trivial solution: $E_2 = (0, w_*(\cdot; m_2, a_2))$, if and only if $m_2 > d\lambda_1(f_2(\phi))$.

Moreover, the following theorem summarizes the results on the stability of these steady states of (1.4), which is a combination of Theorems 3.6 and 3.7 in [25].

Theorem 2.1 *Let* $(u(x,t), v(x,t))$ *be the solution of* (1.4) *with any non-negative non-trivial initial condition.*

(i) *If* $m_1 \leq d\lambda_1(f_1(\phi))$ *and* $m_2 \leq d\lambda_1(f_2(\phi))$, *then*

$$\lim_{t\to\infty} u(x,t) = 0, \quad \lim_{t\to\infty} v(x,t) = 0 \quad \textit{uniformly on } [0,1]. \tag{2.6}$$

(ii) *If* $m_1 \leq d\lambda_1(f_1(\phi))$ *and* $m_2 > d\lambda_1(f_2(\phi))$, *then*

$$\lim_{t\to\infty} u(x,t) = 0, \quad \lim_{t\to\infty} v(x,t) = w_*(x; m_2, a_2) \quad \textit{uniformly on } [0,1]. \tag{2.7}$$

(iii) *If* $m_1 > d\lambda_1(f_1(\phi))$ *and* $m_2 \leq d\lambda_1(f_2(\phi))$*, then*

$$\lim_{t\to\infty} u(x,t) = w_*(x; m_1, a_1), \quad \lim_{t\to\infty} v(x,t) = 0 \quad \text{uniformly on } [0,1]. \tag{2.8}$$

(iv) *If* $m_1 > d\lambda_1(f_1(\phi))$ *and* $m_2 > d\lambda_1(f_2(\phi))$*, then* (2.7) *holds provided*

$$\frac{m_2}{m_1} > \max\left\{\frac{a_2}{a_1}, 1\right\}. \tag{2.9}$$

(v) *If* $m_1 > d\lambda_1(f_1(\phi))$ *and* $m_2 > d\lambda_1(f_2(\phi))$*, then* (2.8) *holds provided*

$$\frac{m_2}{m_1} < \min\left\{\frac{a_2}{a_1}, 1\right\}. \tag{2.10}$$

A nonnegative solution (u, v) of (1.5) is called a coexistence steady state of (1.4) if both u and v are non-trivial. Actually, it follows from the maximum principle that u and v are both strictly positive on $[0, 1]$, if (u, v) is a coexistence steady state.

The coexistence steady state problem was firstly addressed by So and Waltman [42] through a local bifurcation analysis. Their numerical simulation showed that the parameter range for the coexistence was very narrow. In Theorem 4.1 of [25], Hsu and Waltman proved a coexistence result under the conditions $m_1 > m_1^*$ and $m_2 > m_2^*$, where m_1^* is a constant depending on m_2 and m_2^* is a constant depending on m_1. Obviously these two conditions are not easy to verify. Moreover as pointed out in the discussion section of [25], more detailed information, especially the stability of the equilibria, is needed for a complete classification of the global dynamics of (1.4). Hence, it is worthwhile to revisit this model for a better (if not full) understanding of the global dynamics.

We know that (1.4) is strictly monotone and hence the following well-celebrated results on monotone dynamical system (e.g. see [18,24,39]) apply here.

Lemma 2.2 *Suppose that both of the two semi-trivial steady state solutions of* (1.4) *exist.*

(i) *If* E_1 *is stable,* E_2 *is unstable, and there is no coexistence steady state, then* E_1 *is globally stable; similarly if* E_2 *is stable,* E_1 *is unstable, and there is no coexistence steady state, then* E_2 *is globally stable.*
(ii) *If* E_1 *and* E_2 *are both unstable, then* (1.4) *has at least one stable coexistence steady state. If in addition, the coexistence steady state is unique, it is then globally stable.*
(iii) *If* E_1 *and* E_2 *are both stable, then* (1.4) *has at least one unstable coexistence steady state.*

3 Semi-trivial Steady State

In this section, we present some results about the unique positive solution $w_*(x; m, a)$ of (2.5), which provide additional information on the semi-trivial steady states of (1.4) and are helpful for studying the coexistence steady states of (1.4).

Proposition 3.1 *The following statements about the positive solution* $w_*(x; m, a)$ *of* (2.5) *hold.*

(i) *Suppose* $m > d\lambda_1(f_a(\phi))$ *so that* $w_*(x; m, a)$ *exists. Then it is linearly stable in the sense that all eigenvalues of the linearized eigenvalue equation*

$$\begin{cases} d\varphi'' + m\left[\dfrac{\phi - w_*}{a+\phi-w_*} - \dfrac{aw_*}{(a+\phi-w_*)^2}\right]\varphi = \mu\varphi, & x \in (0,1), \\ \varphi'(0) = \varphi'(1) + \gamma\varphi(1) = 0, \end{cases} \tag{3.1}$$

are negative.

(ii) *For fixed* $a, d > 0$, *the positive solution* $w_*(x; m, a)$ *exists if* $m \in (d\lambda_1(f_a(\phi)), \infty)$, *and it is strictly increasing in m, and*

$$\lim_{m \to d\lambda_1(f_a(\phi))^+} w_*(x; m, a) = 0, \quad \lim_{m\to\infty} w_*(x; m, a) = \phi(x) \quad \textit{uniformly on } [0, 1]. \tag{3.2}$$

(iii) *For fixed* $m, d > 0$ *with* $m > d\lambda_1(1)$, *the positive solution* $w_*(x; m, a)$ *exists if* $a \in (0, a_m)$, *and it is strictly decreasing in a, and*

$$\lim_{a\to 0^+} w_*(x; m, a) = h(x), \quad \lim_{a \to a_m^-} w_*(x; m, a) = 0 \quad \textit{uniformly on } [0, 1], \tag{3.3}$$

where a_m *is determined by* $m = d\lambda_1(f_{a_m}(\phi))$ *and h is given by*

$$h(x) = \begin{cases} \dfrac{\phi(x_0)}{\cos(\sqrt{m/d}\, x_0)} \cos(\sqrt{m/d}\, x) & 0 \le x \le x_0, \\ \phi(x) & x_0 < x \le 1, \end{cases} \tag{3.4}$$

with $x_0 \in (0, 1)$ *satisfying*

$$\sqrt{m/d}\tan(\sqrt{m/d}\, x_0)\left(\frac{\gamma+1}{\gamma} - x_0\right) = 1. \tag{3.5}$$

(iv) *For fixed* $a, m > 0$, *the positive solution* $w_*(x; m, a, d)$ *exists if* $d \in (0, m/\lambda_1(f_a(\phi)))$, *and it is strictly decreasing in d for all* $x \in [0, 1]$. *Moreover,*

$$\begin{aligned} &\lim_{d\to 0^+} w_*(x; m, a, d) \\ &= \phi(x) \quad \textit{and} \quad \lim_{d \to m/\lambda_1(f_a(\phi))^-} w_*(x; m, a, d) = 0 \quad \textit{uniformly on } [0, 1]. \end{aligned}$$

Proof For (i), let

$$q_1(x) = m\left[\frac{\phi - w_*}{a+\phi-w_*} - \frac{aw_*}{(a+\phi-w_*)^2}\right] \quad \text{and} \quad q_2(x) = \frac{m(\phi - w_*)}{a+\phi-w_*}. \tag{3.6}$$

Since the principal eigenvalue $\mu_1(q)$ is increasing in q, we have $\mu_1(q_1) < \mu_1(q_2)$. This together with $\mu_1(q_2) = 0$ (with eigenfunction $\theta_1(q_2) = w_*$) leads to $\mu_1(q_1) < 0$, implying that all eigenvalues of (3.1) are negative.

To prove (ii), let $L_1[\psi] = d\psi'' + q_1(x)\psi$ where q_1 is defined as in (3.6), and $\psi \in X_\gamma := \{\psi \in C^2[0, 1] : \psi'(0) = 0,\ \psi'(1) + \gamma\psi(1) = 0\}$. By $\mu_1(q_1) < 0$ and the maximum principle, for any $f \in X_\gamma$, $L_1[f] < 0$ implies that $f > 0$ on $[0, 1]$. From (2.5), w_* is continuously differentiable with respect to the parameters m and a. Let

$$\varphi_m(x) = \frac{\partial w_*(x; m, a)}{\partial m}, \quad \text{and} \quad \varphi_a(x) = \frac{\partial w_*(x; m, a)}{\partial a}.$$

Then φ_m satisfies

$$\begin{cases} d\varphi_m'' + m\left[\dfrac{\phi - w_*}{a+\phi-w_*} - \dfrac{aw_*}{(a+\phi-w_*)^2}\right]\varphi_m = -\dfrac{(\phi - w_*)w_*}{a+\phi-w_*}, & x \in (0,1), \\ \varphi_m'(0) = \varphi_m'(1) + \gamma\varphi_m(1) = 0. \end{cases} \tag{3.7}$$

Since $\varphi_m \in X_\gamma$ and $L_1[\varphi_m] = -(\phi - w_*)w_*/(a+\phi - w_*) < 0$, we conclude that $\varphi_m(x) > 0$, implying that $w_*(x; m, a)$ is strictly increasing in m for $x \in [0, 1]$.

Noticing $0 < w_* < \phi$, $w_*''(x) = -\frac{m(\phi - w_*)w_*}{a+\phi - w_*} \leq 0$, which implies that $w_*'(x)$ is decreasing on $[0, 1]$. Since $w_*'(0) = 0$ and $w_*'(1) = -\gamma w_*(1)$, $w_*'(x)$ is uniformly bounded for $x \in [0, 1]$ and $m > 0$. Therefore, by Arzela–Ascoli Theorem, there exists $w_i \in C[0, 1]$, $i = 1, 2$, with $0 \leq w_1 < \phi$ and $0 < w_2 \leq \phi$ such that $\lim_{m \to d\lambda_1(f_a(\phi))^+} w_*(\cdot; m, a) = w_1$ and $\lim_{m\to\infty} w_*(\cdot; m, a) = w_2$ in $C[0, 1]$.

To show that $w_1 = 0$, we assume on the contrary that w_1 is nontrivial. Since $(\phi - w)/(a+\phi - w)$ is uniformly bounded by 1, it follows from the L^p-estimates for $p \in (1, \infty)$ that $w_*(x; m, a)$ is uniformly bounded in $W^{2,p}(0, 1)$ for $m \in (d\lambda_1(f_a(\phi)), M]$, where M is a fixed number larger than $d\lambda_1(f_a(\phi))$. Hence, we have $\lim_{m \to d\lambda_1(f_a(\phi))^+} w_*(\cdot; m, a) = w_1$ weakly in $W^{2,p}(0, 1)$, where w_1 satisfies

$$\begin{cases} dw_1'' + d\lambda_1(f_a(\phi))\dfrac{(\phi - w_1)w_1}{a + \phi - w_1} = 0, & x \in (0, 1), \\ w_1'(0) = w_1'(1) + \gamma w_1(1) = 0. \end{cases} \tag{3.8}$$

Rewriting the first equation in (3.8) as $w_1'' + \lambda_1(f_a(\phi)) f_a(\phi - w_1)w_1 = 0$, one then infers that $\lambda_1(f_a(\phi)) = \lambda_1(f_a(\phi - w_1))$, which is a contradiction to the monotonicity of λ_1. Therefore $w_1 = 0$.

To prove that $w_2 = \phi$, we divide the first equation of (2.5) by mw_* and integrate the resulting equation over $(0, 1)$ to obtain

$$\frac{d}{m}\int_0^1 \frac{|w_*'|^2}{w_*^2}dx - \frac{d\gamma}{m} + \int_0^1 \frac{\phi - w_*}{a + \phi - w_*}dx = 0.$$

It then follows from $0 \leq w_*, w_2 \leq \phi$ that

$$0 \leq \int_0^1 \frac{\phi - w_*}{a + \phi - w_*}dx \leq \frac{d\gamma}{m},$$

and

$$\lim_{m\to\infty}\int_0^1 \frac{\phi - w_*}{a + \phi - w_*}dx = \int_0^1 \frac{\phi - w_2}{a + \phi - w_2}dx = 0.$$

Therefore we must have $w_2 = \phi$.

(iii) Since $\lambda_1(f_a(\phi))$ is strictly increasing in a with

$$\lim_{a\to 0} d\lambda_1(f_a(\phi)) = d\lambda_1(1) < m \quad \text{and} \quad \lim_{a\to\infty} \lambda_1(f_a(\phi)) = \infty,$$

there exists a unique $a_m > 0$ such that $m = d\lambda_1(f_{a_m}(\phi))$. Moreover, $m > d\lambda_1(f_a(\phi))$ if and only if $a \in (0, a_m)$. Therefore, positive solution $w_*(x; m, a)$ exists if $a \in (0, a_m)$.

Similar to the proof of (ii), we observe that φ_a satisfies

$$\begin{cases} d\varphi_a'' + m\left[\dfrac{\phi - w_*}{a + \phi - w_*} - \dfrac{aw_*}{(a + \phi - w_*)^2}\right]\varphi_a = \dfrac{m(\phi - w_*)w_*}{(a + \phi - w_*)^2}, & x \in (0, 1), \\ \varphi_a'(0) = \varphi_a'(1) + \gamma\varphi_a(1) = 0. \end{cases} \tag{3.9}$$

Noting $\varphi_a \in X_\gamma$ and $L_1[\varphi_a] = m(\phi - w_*)w_*/(a + \phi - w_*)^2 > 0$, we conclude that $\varphi_a(x) < 0$, implying that $w_*(x; m, a)$ is decreasing in a.

Since $(\phi - w)/(a + \phi - w)$ is uniformly bounded by 1, it follows from the L^p-estimates for $p \in (1, \infty)$ that $w(x; m, a)$ is uniformly bounded in $W^{2,p}(0, 1)$ for $a \in (0, a_m)$. So

$\lim_{a\to a_m^-} w_*(x;m,a) = g$ and $\lim_{a\to 0^+} w_*(x;m,a) = h$ weakly in $W^{2,p}(0,1)$ for some g, h with $0 \le g, h \le \phi$ (the convergence also holds in $C^1[0,1]$ by the Sobolev embedding theorem). Moreover, g satisfies

$$\begin{cases} dg'' + \dfrac{m(\phi-g)g}{a_m+\phi-g} = 0, & x \in (0,1). \\ g'(0) = g'(1) + \gamma g(1) = 0, \end{cases}$$

We show that $g \equiv 0$. Assume, for the sake of contradiction, that that $g \not\equiv 0$. Rewriting the first equation above as $g'' + (m/d) f_{a_m}(\phi - g)\, g = 0$, one sees that $m/d = \lambda_1(f_{a_m}(\phi-g))$. Then, the monotonicity of $\lambda_1(q)$ in q would yield $m/d = \lambda_1(f_{a_m}(\phi-g)) > \lambda_1(f_{a_m}(\phi))$, which contradicts the definition of a_m. Hence we have $g \equiv 0$.

To determine the function h, we first show that $\phi(x) - w_*(x;m,a)$ is decreasing in x on $[0,1]$ for any $m, a > 0$. To see this, let $v = \phi - w_*$. Then, $0 < v < \phi$ and v satisfies

$$\begin{cases} dv'' - \dfrac{m(\phi-v)v}{a+v} = 0, & x \in (0,1), \\ v'(0) = -S_0, \quad v'(1) + \gamma v(1) = 0. \end{cases}$$

Thus $v'' > 0$, and v' is increasing on $[0,1]$. By the boundary condition, $v'(1) = -\gamma v(1) < 0$ and hence $v'(x) < 0$ for $x \in [0,1]$. Hence v is strictly decreasing in x on $[0,1]$. It follows that $\phi - h$ is also non-increasing in x.

Next we show that $\phi - h \ge 0$ is non-trivial. Assume on the contrary that $\phi - h \equiv 0$, *i.e.* $h \equiv \phi$. Then $h'(0) = \phi'(0) = -S_0 < 0$. But $0 = w_*'(0;m,a) \to h'(0)$ by $w_*(\cdot;m,a) \to h$ as $a \to 0^+$ in $C^1[0,1]$. Hence $h'(0) = 0$, which is a contradiction. So $\phi - h$ is nontrivial.

We now show that $\phi - h$ is not positive for all $x \in [0,1)$. Assume on the contrary that $\phi - h > 0$ on $[0,1)$. Rewriting the first equation of (2.5) as $d(a+\phi-w)w'' + m(\phi-w)w = 0$ and taking the limit $a \to 0^+$, we have

$$\begin{cases} dh'' + mh = 0, & x \in (0,1), \\ h'(0) = 0, \quad h'(1) + \gamma h(1) = 0. \end{cases}$$

Since $h \ge w_*(x,m,a) > 0$, h is indeed an eigenfunction of (2.1) corresponding to the principal eigenvalue m/d. This implies $m/d = \lambda_1(1)$, which is a contradiction. Therefore, $\phi - h$ cannot be strictly positive in $[0,1)$.

From the above, we see that $\phi - h \ge 0$ is non-increasing, non-trivial, and not strictly positive on $[0,1)$. Thus, there exists $x_0 \in (0,1)$ such that $\phi - h > 0$ on $[0, x_0)$ and $\phi - h = 0$ on $[x_0, 1]$. Again rewriting (2.5) as $d(a+\phi-w)w'' + m(\phi-w)w = 0$ and taking the limit as $a \to 0^+$, we have

$$\begin{cases} dh'' + mh = 0, & x \in (0, x_0), \\ h'(0) = 0. \end{cases} \tag{3.10}$$

Since $\phi - h = 0$ on $[x_0, 1]$, we have

$$h(x_0) = \phi(x_0) \quad \text{and} \quad h'(x_0) = \phi'(x_0) = -S_0. \tag{3.11}$$

Solving (3.10), we have $h = k\cos(\sqrt{m/d}\,x)$ for some $k > 0$. By $h(x_0) = \phi(x_0)$, we have $k = \phi(x_0)/\cos(\sqrt{m/d}\,x_0)$. By $h'(x_0) = -S_0$, x_0 satisfies (3.5).

The proof of (iv) is similar to that of (ii), and we omit it here. □

4 Coexistence

This section is devoted to the existence of coexistence steady states of (1.4). We first introduce two threshold values to determines existence/non-existence of a coexistence steady state. It has been conjectured by Hsu and Waltman [25] that a coexistence steady state of (1.4), if any, is *always stable*. In Sect. 4.2, we show that there are ranges of parameters within which there is a *stable* coexistence steady state. Lastly in Sect. 4.3, we perform a global bifurcation analysis to show the existence of a branch of coexistence steady states using m_2 as the bifurcation parameter.

4.1 Classification of Coexistence Steady States

We have seen that for $i = 1, 2$, if $m_i > d\lambda_1(f_i(\phi))$ then (1.4) has the semi-trivial steady states E_i, where $E_1 = (\hat{u}, 0)$ and $E_2 = (0, \hat{v})$ with $\hat{u} = w_*(m_1, a_1)$ and $\hat{v} = w_*(m_2, a_2)$. We fix $a_1 > 0$, $a_2 > 0$, $m_1 > d\lambda_1(f_1(\phi))$, and view m_2 as a parameter variable. We define two critical values $\widehat{m}_2$ and $\widetilde{m}_2$ as follows. Let

$$\widehat{m}_2 = d\lambda_1\left(\frac{\phi - \hat{u}}{a_2 + \phi - \hat{u}}\right) = d\lambda_1\left(\frac{\phi - w_*(m_1, a_1)}{a_2 + \phi - w_*(m_1, a_1)}\right). \tag{4.1}$$

Let $m_2 = \widetilde{m}_2$ be the unique solution of

$$m_1 = d\lambda_1\left(\frac{\phi - \hat{v}}{a_1 + \phi - \hat{v}}\right) = d\lambda_1\left(\frac{\phi - w_*(m_2, a_2)}{a_1 + \phi - w_*(m_2, a_2)}\right). \tag{4.2}$$

To see that (4.2) has a unique solution, we note that [by Proposition 3.1(ii)]

$$\lim_{m_2 \to d\lambda_1(f_2(\phi))^+} w_*(x; m_2, a_2) = 0, \quad \lim_{m_2 \to \infty} w_*(x; m_2, a_2) = \phi(x), \quad \text{uniformly on } [0, 1]. \tag{4.3}$$

Therefore,

$$\begin{aligned} &\lim_{m_2 \to d\lambda_1(f_2(\phi))^+} d\,\lambda_1\left(\frac{\phi - w_*(m_2, a_2)}{a_1 + \phi - w_*(m_2, a_2)}\right) = d\,\lambda_1(f_1(\phi)) < m_1, \\ &\lim_{m_2 \to \infty} \lambda_1\left(\frac{\phi - w_*(m_2, a_2)}{a_1 + \phi - w_*(m_2, a_2)}\right) = \infty. \end{aligned} \tag{4.4}$$

Thus, the monotonicity of $\lambda_1(\cdot)$ together with (4.3) and (4.4) and Proposition 3.1(ii) implies that there is a unique value for $m_2 = \widetilde{m}_2 \in (d\lambda_1(f_2(\phi)), \infty)$ such that (4.2) holds with $m_2 = \widetilde{m}_2$. Moreover, we can easily see that $\widehat{m}_2, \widetilde{m}_2 > d\lambda_1(f_2(\phi))$.

The definitions of $\widehat{m}_2$ and $\widetilde{m}_2$ arise naturally from studying the stability of E_1 and E_2, which will be apparent in the proof of the following result.

Proposition 4.1 *For given $a_1, a_2 > 0$ and $m_1 > d\lambda_1(f_1(\phi))$, let $\widehat{m}_2$ and $\widetilde{m}_2$ be defined as above.*

(i) *If $m_2 < \widehat{m}_2$, the semi-trivial steady state E_1 is locally asymptotically stable; if $m_2 > \widehat{m}_2$, E_1 is unstable. Also, there holds*

$$\widehat{m}_2 \geq m_1 \min\left\{\frac{a_2}{a_1}, 1\right\}. \tag{4.5}$$

(ii) *Suppose $m_2 > d\lambda_1(f_2(\phi))$. If $m_2 < \widetilde{m}_2$, the semi-trivial steady state E_2 is unstable; if $m_2 > \widetilde{m}_2$, E_2 is locally asymptotically stable. Also, there holds*

$$\widetilde{m}_2 \le m_1 \max\left\{\frac{a_2}{a_1}, 1\right\}. \tag{4.6}$$

Proof We will only prove the stability results for E_1 and E_2, as (4.5) and (4.6) follow from these and Theorem 2.1.

(i) The stability of E_1 for (1.4) is determined by the following elliptic eigenvalue problem:

$$\begin{cases} d\xi'' + m_1\left[\dfrac{\phi-\hat{u}}{a_1+\phi-\hat{u}} - \dfrac{a_1\hat{u}}{(a_1+\phi-\hat{u})^2}\right]\xi - \dfrac{m_1a_1\hat{u}}{(a_1+\phi-\hat{u})^2}\eta = \mu\xi, & x\in(0,1),\\ d\eta'' + m_2\dfrac{\phi-\hat{u}}{a_2+\phi-\hat{u}}\eta = \mu\eta, & x\in(0,1),\\ \xi'(0)=\xi'(1)+\gamma\xi(1)=0, \quad \eta'(0)=\eta'(1)+\gamma\eta(1)=0. \end{cases} \tag{4.7}$$

Suppose $m_2 < \widehat{m}_2$ and let μ be an eigenvalue of (4.7) with corresponding eigenvector (ξ,η). If $\eta = 0$, then μ is an eigenvalue of (3.1). By Proposition 3.1(i), we have $\mu < 0$. If $\eta \neq 0$, then μ is an eigenvalue of

$$\begin{cases} d\eta'' + m_2\dfrac{\phi-\hat{u}}{a_2+\phi-\hat{u}}\eta = \mu\eta, & x\in(0,1),\\ \eta'(0)=\eta'(1)+\gamma\eta(1)=0. \end{cases} \tag{4.8}$$

The principal eigenvalue of (4.8) is 0 if and only if $m_2 = \widehat{m}_2$. Sine $m_2 < \widehat{m}_2$, the principal eigenvalue of (4.8) is less than 0, and thus, $\mu < 0$. Therefore, E_1 is stable.

Suppose $m_2 > \widehat{m}_2$. Then, (4.8) has a principal eigenvalue $\mu > 0$ with corresponding eigenvector $\eta > 0$. Since μ is not an eigenvalue of (3.1), by Fredholm theorem, there exists a unique ξ solving the following problem

$$\begin{cases} d\xi'' + m_1\left[\dfrac{\phi-\hat{u}}{a_1+\phi-\hat{u}} - \dfrac{a_1\hat{u}}{(a_1+\phi-\hat{u})^2}\right]\xi - \dfrac{m_1a_1\hat{u}}{(a_1+\phi-\hat{u})^2}\eta = \mu\xi, & x\in(0,1),\\ \xi'(0)=\xi'(1)+\gamma\xi(1)=0. \end{cases}$$

Therefore, $\mu > 0$ is an eigenvalue of (4.7) with corresponding eigenvector (ξ,η). Hence, E_1 is unstable.

(ii) The stability of E_2 for (1.4) is determined by the following elliptic eigenvalue problem:

$$\begin{cases} d\xi'' + m_1\dfrac{\phi-\hat{v}}{a_1+\phi-\hat{v}}\xi = \mu\xi, & x\in(0,1),\\ d\eta'' - \dfrac{m_2a_2\hat{v}}{(a_2+\phi-\hat{v})^2}\xi + m_2\left[\dfrac{\phi-\hat{v}}{a_2+\phi-\hat{v}} - \dfrac{a_2\hat{v}}{(a_2+\phi-\hat{v})^2}\right]\eta = \mu\eta, & x\in(0,1),\\ \xi'(0)=\xi'(1)+\gamma\xi(1)=0, \quad \eta'(0)=\eta'(1)+\gamma\eta(1)=0. \end{cases} \tag{4.9}$$

By the definition of $\widetilde{m}_2$, the eigenvalue problem

$$\begin{cases} d\xi'' + m_1 \dfrac{\phi - \hat{v}}{a_1 + \phi - \hat{v}} \xi = \mu \xi, & x \in (0, 1), \\ \xi'(0) = \xi'(1) + \gamma \xi(1) = 0, \end{cases} \tag{4.10}$$

has principal eigenvalue 0 if and only if $m_2 = \widetilde{m}_2$. Since $\hat{v}$ is strictly increasing in m_2, the principal eigenvalue of (4.10) is positive if $m_2 < \widetilde{m}_2$ and negative if $m_2 > \widetilde{m}_2$. By a similar argument in (i), E_2 is unstable if $m_2 < \widetilde{m}_2$ and stable if $m_2 > \widetilde{m}_2$. □

We can explore a little bit more about the two thresholds $\widehat{m}_2 = \widehat{m}_2(a_1, a_2)$ and $\widetilde{m}_2 = \widetilde{m}_2(a_1, a_2)$, with given $m_1 > d\lambda_1(f_1(\phi))$. Firstly, by the monotonicity of $w_*(m, a)$ in m and a established in Proposition 3.1, and the monotonicity of $\lambda_1(\cdot)$, we can easily see that both $\widehat{m}_2(a_1, a_2)$ and $\widetilde{m}_2(a_1, a_2)$ are decreasing in a_1 and increasing in a_2. When $a_1 = a_2$, it is obvious that $\widehat{m}_2 = \widetilde{m}_2 = m_1$. Therefore, if $a_1 > a_2$, then $\widehat{m}_2(a_1, a_2) < \widehat{m}_2(a_2, a_2) = m_1$. Moreover, if $a_1 > a_2$, then

$$\begin{aligned} m_1 =& d\lambda_1 \left(\frac{\phi - w_*(\widetilde{m}_2(a_1, a_2), a_2)}{a_1 + \phi - w_*(\widetilde{m}_2(a_1, a_2), a_2)} \right) \\ =& d\lambda_1 \left(\frac{\phi - w_*(\widetilde{m}_2(a_2, a_2), a_1)}{a_1 + \phi - w_*(\widetilde{m}_2(a_2, a_2), a_1)} \right) = d\lambda_1 \left(\frac{\phi - w_*(m_1, a_1)}{a_1 + \phi - w_*(m_1, a_1)} \right) = m_1, \end{aligned}$$

which implies that $\widetilde{m}_2(a_1, a_2) < \widetilde{m}_2(a_2, a_2) = m_1$.

By Lemma 2.2 and Proposition 4.1, we have the following classification of steady states in terms of $\widehat{m}_2$ and $\widetilde{m}_2$.

Theorem 4.2 *Fix a_1, a_2, m_1 and d such that $a_1 \geq a_2$ and $m_1 > d\lambda_1(f_1(\phi))$. Let $\widehat{m}_2$ and $\widetilde{m}_2$ be defined as above.*

(i) *Suppose $\widehat{m}_2 < \widetilde{m}_2$. If $m_2 < \widehat{m}_2$, then the semi-trivial steady state E_1 is locally asymptotically stable, and E_2 is unstable if it exists. If $m_2 > \widetilde{m}_2$, then E_1 is unstable, and E_2 is locally asymptotically stable. If $m_2 \in (\widehat{m}_2, \widetilde{m}_2)$, then E_1 and E_2 are both unstable, and (1.4) has at least one stable coexistence steady state.*
(ii) *Suppose $\widehat{m}_2 > \widetilde{m}_2$. If $m_2 < \widetilde{m}_2$, then the semi-trivial steady state E_1 is locally asymptotically stable, and E_2 is unstable if it exists. If $m_2 > \widehat{m}_2$, then E_1 is unstable, and E_2 is locally asymptotically stable. If $m_2 \in (\widetilde{m}_2, \widehat{m}_2)$, then E_1 and E_2 are both stable, and (1.4) has at least one unstable coexistence steady state.*
(iii) *Suppose $\widehat{m}_2 = \widetilde{m}_2$. If $m_2 < \widetilde{m}_2$, then the semi-trivial steady state E_1 is locally asymptotically stable, and E_2 is unstable if it exists. If $m_2 > \widetilde{m}_2$, then E_1 is unstable, and E_2 is locally asymptotically stable.*

4.2 Existence of Stable Coexistence Steady States

In this subsection, we will confirm that there are parameter ranges within which there exists a *stable* coexistence steady state. By Theorem 4.2, we just need to seek ranges for the parameters for which, $\widehat{m}_2 < \widetilde{m}_2$ holds.

Let $\alpha \in (0, \pi/2)$ be the unique root of the transcendental equation

$$\alpha \tan(\alpha) = \gamma. \tag{4.11}$$

Recall that γ is the pump-out rate for the mixed culture. Our results are stated under the condition

$$m_1 > d\lambda_1\left(f_1(\phi - \frac{\phi(1)}{\cos\alpha}\cos(\alpha x))\right) = d\lambda_1\left(\frac{\phi - \frac{S_0}{\gamma\cos\alpha}\cos(\alpha x)}{a_1 + \phi - \frac{S_0}{\gamma\cos\alpha}\cos(\alpha x)}\right). \tag{4.12}$$

Since the eigenvalue λ_1 in (4.12) is independent of m_1 and d, for fixed a_1, if m_1 is large or d is small, then (4.12) holds.

The following result is about the limit of $\widetilde{m}_2$ as $a_2 \to 0$.

Lemma 4.3 *Suppose that $d, m_1, a_1 > 0$. If (4.12) holds, then*

$$\lim_{a_2\to 0^+} \widetilde{m}_2 > d\alpha^2 = d\lambda_1(1).$$

To prove Lemma 4.3, we need the following lemma.

Lemma 4.4 *For any $x_0 \in (0, 1)$, the equation*

$$x\tan(x_0 x)\left(\frac{1+\gamma}{\gamma} - x_0\right) = 1 \tag{4.13}$$

has a unique solution x in $(0, \frac{\pi}{2x_0})$, which is greater than α.

Proof Let $g(x) = x\tan(x_0 x)\left(\frac{1+\gamma}{\gamma} - x_0\right) - 1$. Since $g(0) = -1$, $g(\frac{\pi}{2x_0}) = \infty$, and g is strictly increasing in $(0, \frac{\pi}{2x_0})$, g has a unique root in $(0, \frac{\pi}{2x_0})$. It then suffices to show that $g(\alpha) < 0$, *i.e.*

$$g(\alpha) = \alpha\tan(x_0\alpha)\left(\frac{1+\alpha\tan(\alpha)}{\alpha\tan(\alpha)} - x_0\right) - 1 < 0.$$

This is equivalent to

$$\tan(x_0\alpha) - \tan(\alpha) + \alpha(1 - x_0)\tan(x_0\alpha)\tan(\alpha) < 0.$$

Noticing $\tan(x_0\alpha) - \tan(\alpha) = -\tan((1-x_0)\alpha)[1 + \tan(\alpha)\tan(x_0\alpha)]$, we only need to show

$$-\tan((1-x_0)\alpha) + [(1-x_0)\alpha - \tan((1-x_0)\alpha)]\tan(\alpha)\tan(x_0\alpha) < 0,$$

which is obvious since $(1-x_0)\alpha - \tan((1-x_0)\alpha) < 0$. □

Proof of Lemma 4.3 By the definition of $\widetilde{m}_2$, there exists a positive eigenvector ψ associated with $\lambda_1(f_1(\phi - w_*(\widetilde{m}_2, a_2))) = m_1/d$. Moreover ψ is unique if we normalize it such that $\psi(0) = 1$. Hence $w := w_*(\widetilde{m}_2, a_2)$ satisfies

$$\begin{cases} dw'' + \dfrac{\widetilde{m}_2(\phi - w)w}{a_2 + \phi - w} = 0, & x \in (0, 1), \\ w'(0) = w'(1) + \gamma w(1) = 0, \end{cases} \tag{4.14}$$

and ψ satisfies

$$\begin{cases} d\psi'' + \dfrac{m_1(\phi - w)}{a_1 + \phi - w}\psi = 0, & x \in (0, 1), \\ \psi'(0) = \psi'(1) + \gamma\psi(1) = 0, \quad \psi(0) = 1. \end{cases} \tag{4.15}$$

By $0 < w < \phi$ and (4.15), $\psi'' < 0$ which implies $\psi' \le \psi'(0) = 0$. Hence ψ is decreasing and thus $\psi \le 1$ on $[0, 1]$. Fix $p > 1$. Noticing $0 < \widetilde{m}_2 \le m_1$ and by the L^p estimates, w

and ψ are uniformly bounded in $W^{2,p}(0,1)$ for all $a_2 > 0$. Then there exists a decreasing sequence $\{a_{2,n}\}$ with $\lim_{n\to\infty} a_{2,n} = 0$ such that the corresponding $\widetilde{m}_{2,n}$, w_n, and ψ_n satisfy that

$$\lim_{n\to\infty} \widetilde{m}_{2,n} = dc^2,$$

and

$$\lim_{n\to\infty} w_n = \rho, \quad \lim_{n\to\infty} \psi_n = \Psi, \quad \text{weakly in } W^{2,p}(0,1),$$

for some $c \geq 0$ and $\rho, \Psi \in W^{2,p}(0,1)$ (The convergence of w_n and ψ_n is also in $C^1[0,1]$ by the Sobolev embedding theorem). By the proof of Proposition 3.1, $\phi - w_n$ is decreasing in x with $0 < \phi - w_n < \phi$, and hence, $\phi - \rho$ is also decreasing in x with $0 \leq \phi - \rho \leq \phi$. If $\phi - \rho = \phi$, *i.e.* $\rho = 0$, then by (4.15), Ψ is an eigenvector corresponding to the principal eigenvalue $m_1/d = \lambda_1(f_1(\phi))$, which contradicts the assumption $m_1 > d\lambda_1(f_1(\phi))$. If $\phi - \rho = 0$, *i.e.* $\rho = \phi$, then $\rho'(0) = \phi'(0) = -S_0$. However, this contradicts $\lim_{n\to 0} w_n'(0) = \rho'(0) = 0$. Hence, we have two cases by the monotonicity of $\phi - \rho$:

Case 1 $\phi - \rho > 0$ on $[0,1)$.

By (4.14), we have $d(a_{2,n} + \phi - w_n)w_n'' + \widetilde{m}_{2,n}(\phi - w_n)w_n = 0$. Taking $n \to \infty$, we have

$$\begin{cases} \rho'' + c^2\rho = 0, & x \in (0,1), \\ \rho'(0) = \rho'(1) + \gamma\rho(1) = 0, \end{cases}$$

Since ρ is nonnegative and nontrivial, we must have $c^2 = \lambda_1(1)$. It is easy to check that $\cos(\alpha x)$ is an eigenvector corresponding to $\lambda_1(1) = \alpha^2$. Hence $c = \alpha$. Moreover $\rho = A\cos(\alpha x)$ for some $A > 0$. It then follows from $\phi - \rho \geq 0$ that $A \leq \phi(1)/\cos(\alpha)$. Hence,

$$\rho \leq \frac{\phi(1)}{\cos(\alpha)} \cos(\alpha x).$$

By (4.15), we have

$$\begin{cases} d\Psi'' + \dfrac{m_1(\phi - \rho)}{a_1 + \phi - \rho}\Psi = 0, & x \in (0,1), \\ \Psi'(0) = \Psi'(1) + \gamma\Psi(1) = 0, \quad \Psi(0) = 1. \end{cases}$$

This implies

$$\frac{m_1}{d} = \lambda_1(f_1(\phi - \rho)) \leq \lambda_1\left(f_1\left(\phi - \frac{\phi(1)}{\cos(\alpha)}\cos(\alpha x)\right)\right). \tag{4.16}$$

Case 2 There exists $x_0 \in (0,1)$ such that $\phi - \rho > 0$ on $[0, x_0)$ and $\phi - \rho = 0$ on $[x_0, 1]$. Since $\rho \in C^1[0,1]$, we have $\rho(x_0) = \phi(x_0)$ and $\rho'(x_0) = \phi'(x_0) = -S_0$. Similar to Case 1, it follows from (4.14) that

$$\begin{cases} \rho'' + c^2\rho = 0, & x \in (0, x_0), \\ \rho'(0) = 0, \quad \rho(x_0) = \phi(x_0), \quad \rho'(x_0) = \phi'(x_0) = -S_0. \end{cases}$$

Hence we must have

$$\rho = \frac{\phi(x_0)}{\cos(x_0 c)} \cos(cx),$$

with $c \in (0, \frac{\pi}{2x_0})$ satisfying

$$c \tan(x_0 c) \left(\frac{1+\gamma}{\gamma} - x_0 \right) = 1.$$

Moreover by Lemma 4.4, we have $c > \alpha$.

In view of the two cases, our assumption (4.12) implies that Case 1 is impossible due to (4.16). Hence we must have $\lim_{a_2 \to 0^+} \widetilde{m}_2 > d\alpha^2$ (The monotonicity of $\widetilde{m}_2$ implies that the limit exists). □

Our next result is about the limit of $\widehat{m}_2$ as a_2 approaches zero. Since its proof is similar to but simper than that of Lemma 4.3, we sketch it here.

Lemma 4.5 *Suppose that $d, m_1, a_1 > 0$ are fixed with $m_1 > d\lambda_1(f_1(\phi))$. Then*

$$\lim_{a_2 \to 0^+} \widehat{m}_2 = d\alpha^2 = d\lambda_1(1).$$

Proof By the definition of $\widehat{m}_2$, there exists a positive eigenvector ψ associated with $\lambda_1(f_2(\phi - \hat{u})) = \widehat{m}_2/d$. Moreover, ψ is unique if we normalize it such that $\psi(0) = 1$. So, ψ satisfies

$$\begin{cases} d\psi'' + \dfrac{\widehat{m}_2(\phi - \hat{u})}{a_2 + \phi - \hat{u}}\psi = 0, & x \in (0, 1), \\ \psi'(0) = \psi'(1) + \gamma\psi(1) = 0, \quad \psi(0) = 1. \end{cases} \tag{4.17}$$

Similar to the proof of Lemma 4.3, there exists a decreasing sequence $\{a_{2,n}\}$ with $\lim_{n\to\infty} a_{2,n} = 0$ such that the corresponding $\widehat{m}_{2,n}$ and ψ_n satisfy that

$$\lim_{n\to\infty} \widehat{m}_{2,n} = dc^2,$$

and

$$\lim_{n\to\infty} \psi_n = \Psi \quad \text{weakly in } W^{2,p}(0, 1),$$

for some $c \geq 0$ and $\Psi \in W^{2,p}(0, 1)$ (The convergence of ψ_n is also in $C^1[0, 1]$ by the Sobolev embedding theorem). Since $\phi > \hat{u}$, we have

$$\begin{cases} \Psi'' + c^2\Psi = 0, & x \in (0, 1), \\ \Psi'(0) = \Psi'(1) + \gamma\Psi(1) = 0, \quad \Psi(0) = 1. \end{cases}$$

Since Ψ is nonnegative and nontrivial, we must have $c^2 = \lambda_1(1)$. It has been shown in the proof of Lemma 4.3 that $\lambda_1(1) = \alpha^2$. Therefore, $c = \alpha$ and $\lim_{a_2 \to 0^+} \widehat{m}_2 = d\alpha^2$ (The limit exists by the monotonicity of $\widehat{m}_2$). □

Combining the previous two lemmas, we can verify that $\widetilde{m}_2 > \widehat{m}_2$ under the condition (4.12) and small a_2, which implies the existence of a stable coexistence steady state of (1.4) for some parameter ranges.

Theorem 4.6 *Suppose that d, m_1, a_1 are fixed. If (4.12) holds, then there exists $a_2^* < a_1$ such that $\widetilde{m}_2 > \widehat{m}_2$ for all $a_2 \in (0, a_2^*)$. For such a_2, (1.4) possesses a stable coexistence steady state for $m_2 \in (\widehat{m}_2, \widetilde{m}_2)$.*

Proof The existence of a_2^* follows from Lemmas 4.3 and 4.5, and the existence of a stable coexistence steady state for $m_2 \in (\widehat{m}_2, \widetilde{m}_2)$ follows from Theorem 4.2. □

4.3 Bifurcation of Coexistence Solutions

In this subsection, we perform a bifurcation analysis to show the existence of coexistence steady states. We note that a local bifurcation analysis was conducted in [42] by casting (1.5) into a system of integral equations.

We fix a_1, a_2, m_1 and d such that $a_1 \geq a_2$ and $m_1 > d\lambda_1(f_1(\phi))$, and use m_2 as a bifurcation parameter. Recall $X_\gamma = \{\psi \in C^2[0,1] : \psi'(0) = 0,\ \ \psi'(1) + \gamma\psi(1) = 0\}$. Then, in the space $\mathbb{R} \times X_\gamma^2$, (1.5) has three branches of trivial or semi-trivial solutions:

$$\begin{aligned}\Gamma_0 &= \{(m_2, 0, 0) : m_2 > 0\},\\ \Gamma_u &= \{(m_2, w_*(m_1, a_1), 0) : m_2 > 0\},\\ \Gamma_v &= \{(m_2, 0, w_*(m_2, a_2)) : m_2 > d\lambda_1(f_2(\phi))\}.\end{aligned} \tag{4.18}$$

For convenience, we still let $\hat{u} = w_*(m_1, a_1)$ and $\hat{v} = w_*(m_2, a_2)$.

We prove that there is a branch of positive solutions of (1.5) bifurcating from Γ_u as stated in the following:

Theorem 4.7 *There is a smooth curve $\Gamma = \{(m_2(s), u(s), v(s)) : s \in (-\epsilon, \epsilon)\}$, such that $(m_2(s), u(s), v(s))$ is a solution of (1.5) for $s \in (-\epsilon, \epsilon)$ which is positive for $s \in (0, \epsilon)$, where $m_2(0) = \widehat{m}_2$, $u(s) = \hat{u} + s\varphi_0 + o(s)$, and $v(s) = s\psi_0 + o(s)$ with $\psi_0 > 0$ being a principal eigenfunction of the problem*

$$\begin{cases}\psi''(x) + \lambda f_2(\phi - \hat{u})\psi(x) = 0, & x \in (0,1),\\ \psi'(0) = \psi'(1) + \gamma\psi(1) = 0,\end{cases} \tag{4.19}$$

corresponding to the eigenvalue $\lambda = \widehat{m}_2/d$ and $\varphi_0 < 0$ satisfying

$$\begin{cases}d\varphi_0'' + m_1\left[f_1(\phi - \hat{u}) - \dfrac{a_1\hat{u}}{(a_1 + \phi - \hat{u})^2}\right]\varphi_0 = \dfrac{m_1 a_1 \hat{u}}{(a_1 + \phi - \hat{u})^2}\psi_0, & x \in (0,1),\\ \varphi_0'(0) = \varphi_0'(1) + \gamma\varphi_0(1) = 0.\end{cases} \tag{4.20}$$

Moreover,

$$m_2'(0) = \widehat{m}_2 \frac{\displaystyle\int_0^1 \frac{a_2(\varphi_0 + \psi_0)\psi_0^2}{(a_2 + \phi - \hat{u})^2}dx}{\displaystyle\int_0^1 f_2(\phi - \hat{u})\psi_0^2 dx}. \tag{4.21}$$

Proof We apply the local bifurcation theorem in [8]. Define $F : \mathbb{R} \times X_\gamma^2 \to Y^2$ (where $Y = C[0,1]$) by

$$F(m_2, u, v) = \begin{pmatrix} du'' + m_1 f_1(\phi - u - v)u \\ dv'' + m_2 f_2(\phi - u - v)v \end{pmatrix}. \tag{4.22}$$

Then, we can compute

$$\begin{aligned}&F_{(u,v)}(m_2, u, v)[\varphi, \psi]\\ &= \begin{pmatrix} d\varphi'' \\ d\psi'' \end{pmatrix} + \begin{pmatrix} m_1 f_1(\phi - u - v) - \frac{m_1 a_1 u}{(a_1+\phi-u-v)^2} & -\frac{m_1 a_1 u}{(a_1+\phi-u-v)^2} \\ -\frac{m_2 a_2 v}{(a_2+\phi-u-v)^2} & m_2 f_2(\phi - u - v) - \frac{m_2 a_2 v}{(a_2+\phi-u-v)^2} \end{pmatrix}\begin{pmatrix} \varphi \\ \psi \end{pmatrix}.\end{aligned}$$

Evaluating it at $(\widehat{m}_2, \hat{u}, 0)$, we have

$$F_{(u,v)}(\widehat{m}_2, \hat{u}, 0)[\varphi, \psi] = \begin{pmatrix} d\varphi'' + p\varphi - q\psi \\ d\psi'' + \widehat{m}_2 f_2(\phi - \hat{u})\psi \end{pmatrix},$$

with

$$p = m_1 f_1(\phi - \hat{u}) - \frac{m_1 a_1 \hat{u}}{(a_1 + \phi - \hat{u})^2}, \quad q = \frac{m_1 a_1 \hat{u}}{(a_1 + \phi - \hat{u})^2}.$$

It then follows that the kernel of $F_{(u,v)}(\widehat{m}_2, \hat{u}, 0)$ is

$$N(F_{(u,v)}(\widehat{m}_2, \hat{u}, 0)) = span\{(\varphi_0, \psi_0)\}.$$

To see this, let $F_{(u,v)}(\widehat{m}_2, \hat{u}, 0)[\varphi, \psi] = 0$. Noticing $\widehat{m}_2 = d\lambda(f_2(\phi - \hat{u}))$, we have $\psi = k\psi_0$ for some $k \in \mathbb{R}$, where ψ_0 is a positive principal eigenvector of problem (4.19). By Proposition 3.1(i) and Fredholm theory, there is a unique φ_0 solving (4.20). Moreover, by the maximum principle, $\varphi_0 < 0$.

We claim that the range of $F_{(u,v)}(\widehat{m}_2, \hat{u}, 0)$ is

$$R(F_{(u,v)}(\widehat{m}_2, \hat{u}, 0)) = \left\{(h_1, h_2) \in Y^2 : \int_0^1 h_2\psi_0 dx = 0\right\}. \tag{4.23}$$

To see this, we note that $(h_1, h_2) \in Y^2$ is in the range if and only if there exists $(\varphi, \psi) \in X_\gamma^2$ such that

$$d\varphi'' + p\varphi - q\psi = h_1, \tag{4.24}$$
$$d\psi'' + \widehat{m}_2 f_2(\phi - \hat{u})\psi = h_2. \tag{4.25}$$

The Eq. (4.24) always has a unique solution in X_γ for any $\psi, h_1 \in L^p(0, 1)$ by Proposition 3.1(i) and Fredholm theory. Hence the claim is equivalent to that $(h_1, h_2) \in Y^2$ is in the range if and only if $\int_0^1 h_2\psi_0 dx = 0$. And this can be derived by the Fredholm theory, because the solutionz of the equation $d\psi'' + \widehat{m}_2 f_2(\phi - \hat{u})\psi = 0$ in X_γ consist of $span\{\psi_0\}$.

To apply the bifurcation theorem from a simple eigenvalue by Crandall and Rabinowitz [8], we then only need to check the transversality condition $F_{m_2,(u,v)}(\widehat{m}_2, \hat{u}, 0)[\varphi_0, \psi_0] \notin R(F_{(u,v)}(\widehat{m}_2, \hat{u}, 0))$. To see this, we compute

$$F_{m_2}(m_2, u, v) = \begin{pmatrix} 0 \\ f_2(\phi - u - v)v \end{pmatrix}$$

and

$$F_{m_2,(u,v)}(m_2, u, v)[\varphi, \psi] = \begin{bmatrix} 0 \\ -\frac{a_2 v\varphi}{(a_2+\phi-u-v)^2} + (f_2(\phi - u - v) - \frac{a_2 v}{(a_2+\phi-u-v)^2})\psi \end{bmatrix}.$$

This implies

$$F_{m_2,(u,v)}(\widehat{m}_2, \hat{u}, 0)[\varphi_0, \psi_0] = \begin{bmatrix} 0 \\ f_2(\phi - \hat{u})\psi_0 \end{bmatrix}, \tag{4.26}$$

and so the transversality condition holds by (4.23) and $\int_0^1 f_2(\phi - \hat{u})\psi_0^2 dx > 0$.

Finally, we compute $m_2'(0)$ by the formula (see [37])

$$m_2'(0) = -\frac{\langle l, F_{(u,v),(u,v)}(\widehat{m}_2, \hat{u}, 0)[\varphi_0, \psi_0]^2\rangle}{2\langle l, F_{m_2,(u,v)}(\widehat{m}_2, \hat{u}, 0)[\varphi_0, \psi_0]\rangle}, \tag{4.27}$$

where l is a linear functional on Y^2 given by $\langle l, [h_1, h_2]\rangle = \int_0^1 h_2(x)\psi_0(x)dx$ for any $(h_1, h_2) \in Y^2$. To this end, we compute

$$F_{(u,v),(u,v)}(m_2, u, v)[\varphi, \psi]^2$$
$$= \begin{pmatrix} * \\ -m_2\left(\frac{2a_2v\varphi^2}{(a_2+\phi-u-v)^3} + 2\varphi\psi(\frac{2a_2v}{(a_2+\phi-u-v)^3} + \frac{a_2}{(a_2+\phi-u-v)^2}) + \psi^2(\frac{2a_2}{(a_2+\phi-u-v)^2} + \frac{2a_2v}{(a_2+\phi-u-v)^3})\right) \end{pmatrix}$$

and

$$F_{(u,v),(u,v)}(\widehat{m}_2, \hat{u}, 0)[\varphi_0, \psi_0]^2 = \begin{pmatrix} * \\ \frac{-2\widehat{m}_2a_2(\varphi_0+\psi_0)\psi_0}{(a_2+\phi-\hat{u})^2} \end{pmatrix}. \tag{4.28}$$

Hence, the formula (4.21) follows from (4.26) to (4.28). □

We then prove that there is a branch of positive solutions of (1.5) bifurcating from Γ_v. The proof of this result is similar to (1.5), so we only sketch it here.

Theorem 4.8 *There is a smooth curve $\Gamma' = \{(m_2(s), u(s), v(s)) : s \in (-\epsilon, \epsilon)\}$, such that $(m_2(s), u(s), v(s))$ is a solution of (1.5) for $s \in (-\epsilon, \epsilon)$ which is positive for $s \in (0, \epsilon)$, where $m_2(0) = \widetilde{m}_2$, $u(s) = s\tilde{\varphi}_0 + o(s)$, and $v(s) = \hat{v}_0 + s\tilde{\psi}_0 + o(s)$ with $\hat{v}_0 = w_*(\widetilde{m}_2, a_2)$, and $\tilde{\varphi}_0 > 0$ being a principal eigenfunction of the problem*

$$\begin{cases} \varphi''(x) + \lambda f_1(\phi - \hat{v}_0)\varphi(x) = 0, & x \in (0, 1), \\ \varphi'(0) = \varphi'(1) + \gamma\varphi(1) = 0, \end{cases} \tag{4.29}$$

corresponding to the eigenvalue $\lambda = m_1/d$, and $\tilde{\psi}_0 < 0$ satisfying

$$\begin{cases} d\tilde{\psi}_0'' + \widetilde{m}_2\left[f_2(\phi - \hat{v}_0) - \dfrac{a_2\hat{v}_0}{(a_2 + \phi - \hat{v}_0)^2}\right]\tilde{\psi}_0 = \dfrac{\widetilde{m}_2a_2\hat{v}_0}{(a_2 + \phi - \hat{v}_0)^2}\tilde{\varphi}_0, & x \in (0, 1), \\ \tilde{\psi}_0'(0) = \tilde{\psi}_0'(1) + \gamma\tilde{\psi}_0(1) = 0. \end{cases} \tag{4.30}$$

Moreover,

$$m_2'(0) = -\frac{\displaystyle\int_0^1 \frac{(\tilde{\varphi}_0 + \tilde{\psi}_0)\tilde{\varphi}_0^2}{(a_1 + \phi - \hat{v}_0)^2}dx}{\displaystyle\int_0^1 \frac{\hat{v}_{\widetilde{m}_2}\tilde{\psi}_0^2}{(a_1 + \phi - \hat{v}_0)^2}dx}, \tag{4.31}$$

where $\hat{v}_{\widetilde{m}_2}$ is the unique positive solution of

$$\begin{cases} d\hat{v}_{\widetilde{m}_2}'' + \widetilde{m}_2\left[f_2(\phi - \hat{v}_0) - \dfrac{a_2\hat{v}_0}{(a_2 + \phi - \hat{v}_0)^2}\right]\hat{v}_{\widetilde{m}_2} = -\dfrac{\phi - \hat{v}_0}{a_2 + \phi - \hat{v}_0}\hat{v}_0, & x \in (0, 1), \\ \hat{v}_{\widetilde{m}_2}'(0) = \hat{v}_{\widetilde{m}_2}'(1) + \gamma\hat{v}_{\widetilde{m}_2}(1) = 0. \end{cases}$$

Proof Define $\tilde{F} : \mathbb{R} \times X_\gamma^2 \to Y^2$ by

$$\tilde{F}(m_2, u, w) = \begin{pmatrix} du'' + m_1 f_1(\phi - u - \hat{v} - w)u \\ dw'' + d\hat{v}'' + m_2 f_2(\phi - u - \hat{v} - w)(\hat{v} + w) \end{pmatrix},$$

where $\hat{v} = w_*(m_2, a_2)$. Then we have $\tilde{F}(m_2, 0, 0) = 0$ and

$$\tilde{F}_{(u,w)}(\widetilde{m}_2, 0, 0)[\varphi, \psi] = \begin{pmatrix} d\varphi'' + m_1 f_1(\phi - \hat{v}_0)\varphi \\ d\psi'' + \widetilde{m}_2 \left(f_2(\phi - \hat{v}_0) - \frac{a_2 \hat{v}_0}{(a_2+\phi-\hat{v}_0)^2} \right) \psi - \frac{\widetilde{m}_2 a_2 \hat{v}_0 \varphi}{(a_2+\phi-\hat{v}_0)^2} \end{pmatrix},$$

where $\hat{v}_0 = w_*(\widetilde{m}_2, a_2)$. It then follows that the kernel of $\tilde{F}_{(u,w)}(\widetilde{m}_2, 0, 0)$ is

$$N(\tilde{F}_{(u,w)}(\widetilde{m}_2, 0, 0)) = span\{(\tilde{\varphi}_0, \tilde{\psi}_0)\},$$

and the range of $\tilde{F}_{(u,w)}(\widetilde{m}_2, 0, 0)$ is

$$R(\tilde{F}_{(u,w)}(\widetilde{m}_2, 0, 0)) = \left\{ (h_1, h_2) \in Y^2 : \int_0^1 h_1 \tilde{\varphi}_0 dx = 0 \right\}. \tag{4.32}$$

By

$$\tilde{F}_{m_2,(u,w)}(\widetilde{m}_2, 0, 0)[\tilde{\varphi}_0, \tilde{\psi}_0] = \begin{bmatrix} -\frac{m_1 a_1 \hat{v}_{\widetilde{m}_2} \tilde{\varphi}_0}{(a_1+\phi-\hat{v}_0)^2} \\ * \end{bmatrix}, \tag{4.33}$$

$\hat{v}_{\widetilde{m}_2} > 0$, and (4.32), the transversality condition holds. Finally, $m_2'(0)$ can be computed by

$$m_2'(0) = -\frac{\langle l, \tilde{F}_{(u,w),(u,w)}(\widetilde{m}_2, 0, 0)[\tilde{\varphi}_0, \tilde{\psi}_0]^2 \rangle}{2\langle l, \tilde{F}_{m_2,(u,w)}(\widetilde{m}_2, 0, 0)[\tilde{\varphi}_0, \tilde{\psi}_0] \rangle}, \tag{4.34}$$

where l is a linear functional on Y^2 given by $\langle l, [h_1, h_2] \rangle = \int_0^1 h_1(x)\tilde{\varphi}_0(x)dx$ for any $(h_1, h_2) \in Y^2$. Then the formula (4.31) follows from (4.33), (4.34) and

$$\tilde{F}_{(u,w),(u,w)}(\widetilde{m}_2, 0, 0)[\tilde{\varphi}_0, \tilde{\psi}_0]^2 = -\begin{pmatrix} \frac{2m_1 a_1 \tilde{\varphi}_0(\tilde{\varphi}_0+\tilde{\psi}_0)}{(a_1+\phi-\hat{v}_0)^2} \\ * \end{pmatrix}. \tag{4.35}$$

□

We remark that although (4.21) and (4.31) provide formulas for the direction of bifurcation at $m_2 = \widetilde{m}_2$ and $m_2 = \widehat{m}_2$, the actual direction is not clear as the sign of $\varphi_0 + \psi_0$ or $\tilde{\varphi}_0 + \tilde{\psi}_0$ is not known. So, we can not rule out possible multiple coexistence steady state solutions for some values of m_2.

Next, we perform a global bifurcation analysis and prove that the two bifurcation continua in Theorems 4.7 and 4.8 are connected. We need the following result.

Lemma 4.9 *Suppose that $m_1 > d\lambda_1(f_1(\phi))$. If (u, v) is a nonnegative solution of (1.5), then we have $u \le \hat{u}$.*

Proof Since u satisfies $0 = du'' + m_1 f_1(\phi - u - v) \le du'' + m_1 f_1(\phi - u)$, u is a lower solution of

$$\begin{cases} dw'' + \dfrac{m_1(\phi - w)w}{a_1 + \phi - w} = 0, & x \in (0, 1), \\ w'(0) = w'(1) + \gamma w(1) = 0. \end{cases} \tag{4.36}$$

It is easy to check that ϕ is an upper solution. Hence by the method of upper/lower solutions and the uniqueness of the solution of (4.36), we have $u \le w_*(m_1, a_1) = \hat{u}$. □

Define

$$S = \{(m_2, u, v) \in \mathbb{R}_+ \times X_\gamma^2 : u > 0, v > 0, (m_2, u, v) \text{ satisfies } (1.5)\}. \tag{4.37}$$

Theorem 4.10 *Suppose that $m_1 > d\lambda_1(f_1(\phi))$. Then there exists a connected component $\mathcal{C}^*$ of S such that the closure of $\mathcal{C}^*$ contains two bifurcation points $(\widehat{m}_2, \hat{u}, 0)$ and $(\widetilde{m}_2, 0, \hat{v}_0)$ with $\hat{v}_0 = w_*(\widetilde{m}_2, a_2)$. In other words, the two bifurcation continua Γ and Γ' in Theorem 4.7 and 4.8 are connected to each other.*

Proof We apply the global bifurcation theorem [38, Theorem 4.4] and follow the process in [38, Theorem 4.7]. Let $F : \mathbb{R}_+ \times P_\varepsilon^2 \to Y^2$ be defined as in (4.22), where $P_\varepsilon = \{u \in X_\gamma : u > -\varepsilon\}$ for some $\varepsilon > 0$. Let $P = \{u \in X_\gamma : u > 0\}$. By Theorem 4.7, there is a smooth curve $\Gamma = \{(m_2(s), u(s), v(s)) : s \in (-\epsilon, \epsilon)\}$ of solutions of (1.5) emanating from the bifurcation point $(\hat{m}_2, \hat{u}, 0)$ from Γ_u. Let $\Gamma^+ = \{(m_2(s), u(s), v(s)) : s \in (0, \epsilon)\}$ and $\Gamma^- = \{(m_2(s), u(s), v(s)) : s \in (-\epsilon, 0)\}$ be the positive and negative components of Γ, respectively. Let $\mathcal{C}$ be the connected component of solutions in $\mathbb{R}_+ \times P_\varepsilon^2$ bifurcating from $(\widehat{m}_2, \hat{u}, 0)$. Let $\mathcal{C}^+$ be the connected component of $\mathcal{C}\backslash\Gamma^-$ which contains Γ^+. Let $\mathcal{C}^* = \mathcal{C}^+ \cap (\mathbb{R}_+ \times P^2)$. Then $\mathcal{C}^* \subset \mathcal{C}^+$ and contains Γ^+.

By [38, Theorem 4.4], $\mathcal{C}^+$ satisfies one of the following alternatives: (I) it is not compact in $\mathbb{R}_+ \times P_\epsilon^2$; (II) it contains a point $(m_*, \hat{u}, 0)$ with $m_* \neq \hat{m}_2$; (III) it contains a point $(m_2, \hat{u} + u_1, u_2)$, where (u_1, u_2) is nontrivial and belongs to the complement of $span\{(\varphi_0, \psi_0)\}$, i.e.

$$\int_0^1 (u_1\varphi_0 + u_2\psi_0)dx = 0, \tag{4.38}$$

where (φ_0, ψ_0) is specified in Theorem 4.7 with $\varphi_0 < 0$ and $\psi_0 > 0$. Here, (I) is equivalent to either $\mathcal{C}^+$ intersects $\mathbb{R}_+ \times \partial P_\varepsilon^2$ (∂P_ε^2 is the boundary of P_ε^2) or $\mathcal{C}^+$ is unbounded by the elliptic regularity theory.

We claim that either (I)–(III) implies that $\bar{\mathcal{C}^*} \cap (\mathbb{R}_+ \times \partial P^2)$ contains a point (m_*, u_*, v_*), distinct from $(\widehat{m}_2, \hat{u}, 0)$, where ∂P^2 is the boundary of P^2. We prove the claim now. Suppose that (I) holds. If $\mathcal{C}^+$ intersects $\mathbb{R}_+ \times \partial P_\varepsilon^2$, it insects $\mathbb{R}_+ \times \partial P^2$. So, we may assume that $\mathcal{C}^+$ is unbounded. If $\mathcal{C}^*$ does not intersect $\mathbb{R}_+ \times \partial P^2$, by the boundedness of positive solutions, there exists an unbounded interval $I \subset \mathbb{R}_+$ with $\widehat{m}_2 \in I$ such that, for each $m_2 \in I$, (1.5) has a positive solution. However, if $0 < m_2 < m_1a_2/a_1$ or $m_2 > m_1$, by Theorem 2.1, (1.5) has no positive solution. This contradicts the unboundedness of I. (II) is obvious. Suppose that (III) holds. If $(\hat{u} + u_1, u_2)$ is not nonnegative, then the claim holds. So, suppose $\hat{u} + u_1 \geq 0$ and $u_2 \geq 0$. By Lemma 4.9, we have $u_1 \leq 0$. By (4.38), we must have $(u_1, u_2) = (0, 0)$, which contradicts that (u_1, u_2) is nontrivial. This proves the claim.

Since $(m_*, u_*, v_*) \in \mathbb{R}_+ \times \partial P^2$, by the maximum principle, either $u_* = 0$ or $u_* > 0$ on [0, 1], and either $v_* = 0$ or $v_* > 0$ on [0, 1]. Thus, there are three possible cases: (1) $(m_*, u_*, v_*) = (m_*, 0, 0)$; (2) $(m_*, u_*, v_*) = (m_*, \hat{u}, 0)$ with $m_* \neq \widehat{m}_2$; (3) $(m_*, u_*, v_*) = (m_*, 0, v_*)$ with $v_* = w_*(m_*, a_2)$. Whichever the case, (m_*, u_*, v_*) is a bifurcation point for positive solutions of (1.5). (2) can be easily ruled out since $(\widehat{m}_2, \hat{u}, 0)$ is the only bifurcation point of positive solutions from Γ_u. To rule out (1), we compute

$$F_{(u,v)}(m_*, 0, 0)[\varphi, \psi] = \begin{pmatrix} d\varphi'' + m_1 f_1(\phi)\varphi \\ d\psi'' + m_* f_2(\phi)\psi \end{pmatrix}.$$

Since $m_1 > d\lambda(f_1(\phi))$, the only bifurcation point of nonnegative solutions from Γ_0 is $m_* = \lambda(f_2(\phi))/d$. It is not hard to see that the corresponding bifurcation curve is

$(m_2, 0, w_*(m_2, a_2))$. Therefore, $(m_*, 0, 0)$ can not be a bifurcation point for positive solutions. Therefore, (3) holds. From the proof of Theorem 4.8, the only possible bifurcation point of positive solutions from Γ_v is $(m_*, 0, v_*) = (\widetilde{m}_2, 0, \hat{v}_0)$ with $\hat{v}_0 = w_*(\widetilde{m}_2, a_2)$. This proves the result. □

We remark that the bifurcation results proved in this subsection hold without extra conditions on parameters (d, a_1, a_2, m_1) (except for $m_1 > d\lambda_1(f_1(\phi))$), and bifurcation analysis can be performed using parameters a_1, a_2 or m_1. However, with the result $\widetilde{m}_2 > \widehat{m}_2$ proved in Sect. 4.2, we have more information on the bifurcation branch $\mathcal{C}^*$:

Corollary 4.11 *Suppose that d, m_1, a_1 are fixed such that (4.12) holds. Let $a_2^* > 0$ be defined in Theorem 4.6 such that $\widetilde{m}_2 > \widehat{m}_2$ when $0 < a_2 < a_2^*$. Then the projection of the continuum $\mathcal{C}^*$ of positive solutions onto m_2-axis contains the interval $(\widehat{m}_2, \widetilde{m}_2)$.*

5 Non-coexistence for Small *d*

In this section, we consider the dynamics of (1.4) when the diffusion rate d is small. We fix a_1, a_2, m_1, m_2 and make d small enough such that $m_1 > d\lambda(f_1(\phi))$ and $m_2 > d\lambda(f_2(\phi))$. Then the two semi-trivial steady states both exist, and we denote them by $(\hat{u}, 0)$ and $(0, \hat{v})$, respectively.

As pointed out in the previous section, the stability of $(\hat{u}, 0)$ is determined by the sign of μ_1^*, which is the principal eigenvalue of the problem

$$\begin{cases} d\eta'' + m_2 \dfrac{\phi - \hat{u}}{a_2 + \phi - \hat{u}} \eta = \mu\eta, & x \in (0, 1), \\ \eta'(0) = \eta'(1) + \gamma\eta(1) = 0. \end{cases} \tag{5.1}$$

Similarly, the stability of $(0, \hat{v})$ is determined by the sign of μ_2^*, which is the principal eigenvalue of the problem

$$\begin{cases} d\eta'' + m_1 \dfrac{\phi - \hat{v}}{a_1 + \phi - \hat{v}} \eta = \mu\eta, & x \in (0, 1), \\ \eta'(0) = \eta'(1) + \gamma\eta(1) = 0. \end{cases} \tag{5.2}$$

We first prove the following instability result regarding the semi-trivial steady states.

Lemma 5.1 *If $m_1/a_1 < m_2/a_2$, then there exists $d_1 > 0$ such that $(\hat{u}, 0)$ is unstable for all $d < d_1$; if $m_1/a_1 > m_2/a_2$, then there exists $d_2 > 0$ such that $(0, \hat{v})$ is unstable for all $d < d_2$.*

Proof Suppose that $m_1/a_1 < m_2/a_2$. Notice that $\hat{u}$ satisfies

$$\begin{cases} d\hat{u}'' + \dfrac{m_1(\phi - \hat{u})\hat{u}}{a_1 + \phi - \hat{u}} = 0, & x \in (0, 1), \\ \hat{u}'(0) = \hat{u}'(1) + \gamma\hat{u}(1) = 0. \end{cases} \tag{5.3}$$

Multiplying both sides of the first equation of (5.3) by $\hat{u}$ and integrating it over $(0, 1)$, we have

$$d\int_0^1 |\hat{u}'|^2 dx + dr\hat{u}^2(1) = \int_0^1 \frac{m_1(\phi - \hat{u})}{a_1 + \phi - \hat{u}} \hat{u}^2 dx.$$

The variational formula gives

$$\begin{aligned}\mu_1^* &= -\inf_{\varphi\in C^1([0,1]),\varphi\neq 0}\frac{d\int_0^1|\varphi'|^2dx + dr\varphi^2(1) - \int_0^1\frac{m_2(\phi-\hat u)}{a_2+\phi-\hat u}\varphi^2dx}{\int_0^1\varphi^2dx}\\ &\geq -\frac{d\int_0^1|\hat u'|^2dx + dr\hat u^2(1) - \int_0^1\frac{m_2(\phi-\hat u)}{a_2+\phi-\hat u}\hat u^2dx}{\int_0^1\hat u^2dx}\\ &= -\frac{1}{\int_0^1\hat u^2dx}\int_0^1\left[\frac{m_1}{a_1+\phi-\hat u}-\frac{m_2}{a_2+\phi-\hat u}\right](\phi-\hat u)\hat u^2dx.\end{aligned}$$

Since $\hat u \to \phi$ in $C[0,1]$ as $d\to 0$ by Proposition 3.1 and $m_1/a_1 < m_2/a_2$, there exists $d_1>0$ such that $\mu_1^*>0$ for all $d<d_1$. Thus $(\hat u, 0)$ is unstable for all $d<d_1$. The proof for the case $m_1/a_1 > m_2/a_2$ is similar. □

We next prove a local stability result for the semi-trivial steady states. The main technique is a min–max representation formula of the principal eigenvalue $\mu_1(d,q)$ (see [3]) of the following problem

$$\begin{cases} d\theta''(x)+q(x)\theta(x)=\mu\theta(x), & x\in(0,1),\\ \theta'(0)=\theta'(1)+\gamma\theta(1)=0.\end{cases}\tag{5.4}$$

The principal eigenvalue $\mu_1(d,q)$ of (5.4) is given by

$$\mu_1(d,q)=\inf_{\theta\in X_\gamma^+}\sup_{x\in(0,1)}\frac{d\theta''(x)+q(x)\theta(x)}{\theta(x)},\tag{5.5}$$

where

$$X_\gamma^+=\{\theta\in C^2[0,1]:\theta>0 \text{ in } (0,1) \quad\text{and}\quad \theta'(0)=\theta'(1)+\gamma\theta(1)=0\}.$$

Lemma 5.2 *If $m_1/a_1 < m_2/a_2$, then there exists $d_3>0$ such that $(0,\hat v)$ is locally asymptotically stable for all $d<d_3$; if $m_1/a_1 > m_2/a_2$, then there exists $d_4>0$ such that $(\hat u, 0)$ is locally asymptotically stable for all $d<d_4$.*

Proof Suppose that $m_1/a_1 < m_2/a_2$. By the variational formula, we have

$$\begin{aligned}\mu_2^* &= \inf_{\theta\in X_\gamma^+}\sup_{x\in(0,1)}\left\{\frac{d\theta''(x)}{\theta(x)}+\frac{m_1(\phi(x)-\hat v(x))}{a_1+\phi(x)-\hat v(x)}\right\}\\ &\leq \sup_{x\in(0,1)}\left\{\frac{d\hat v''(x)}{\hat v(x)}+\frac{m_1(\phi(x)-\hat v(x))}{a_1+\phi(x)-\hat v(x)}\right\}\\ &= \sup_{x\in(0,1)}\left\{-\frac{m_2(\phi(x)-\hat v(x))}{a_2+\phi(x)-\hat v(x)}+\frac{m_1(\phi(x)-\hat v(x))}{a_1+\phi(x)-\hat v(x)}\right\}\\ &= \sup_{x\in(0,1)}\left\{(\phi(x)-\hat v(x))\left(-\frac{m_2}{a_2+\phi(x)-\hat v(x)}+\frac{m_1}{a_1+\phi(x)-\hat v(x)}\right)\right\}.\end{aligned}$$

Since $\hat v\to\phi$ uniformly as $d\to 0$ by Proposition 3.1 and $m_1/a_1 < m_2/a_2$, there exists $d_3>0$ such that $\mu_2^*<0$ for all $d>d_3$. Hence $(0,\hat v)$ is stable for all $d<d_3$. The case of $m_1/a_1 > m_2/a_2$ can be proved analogously. □

To completely determine the global dynamics of (1.4) for small diffusion rate d, we only need to prove the nonexistence of positive solutions of (1.5).

Lemma 5.3 *Suppose that $m_1/a_1 \neq m_2/a_2$. Then there exists $d_5 > 0$ such that* (1.4) *has no positive steady state for all $d < d_5$.*

Proof Without loss of generality, suppose $m_1/a_1 < m_2/a_2$. Assume on the contrary that such a d_5 does not exist. Then there exists a sequence $\{d_n\}$ such that $d_n \to 0$ as $n \to \infty$, and problem (1.5) with $d = d_n$ has a positive solution (u_n, v_n). By the first equation of (1.5), we have

$$d_n \int_0^1 \frac{u_n''}{u_n} dx + \int_0^1 \frac{m_1(\phi - u_n - v_n)}{a_1 + \phi - u_n - v_n} dx = 0.$$

Noticing the boundary conditions $u'(0) = u'(1) + \gamma u(1)$, the above equation leads to

$$d_n \int_0^1 \frac{|u_n'|^2}{u_n^2} dx + \int_0^1 \frac{m_1(\phi - u_n - v_n)}{a_1 + \phi - u_n - v_n} dx = d_n \gamma.$$

Since $\phi - u - v \geq 0$ for all $d > 0$, by the Ries-z-Fisher theorem, there exists a subsequence (still denote by $\{d_n\}$) with $d_n \to 0$ as $n \to \infty$ such that the corresponding positive solutions (u_n, v_n) satisfy that $u_n + v_n \to \phi$ pointwisely a.e. in $[0, 1]$ as $n \to \infty$.

By (1.5) and $\phi - u_n - v_n \geq 0$, u_n'' and v_n'' are both negative. Hence u_n' and v_n' are strictly decreasing in $[0, 1]$. Since $u_n'(0) = v_n'(0) = u_n'(1) + \gamma u_n(1) = v_n'(1) + \gamma v_n(1) = 0$, $\{u_n' + v_n'\}$ are uniformly bounded in $[0, 1]$. Noticing that $\{u_n\}$ and $\{v_n\}$ are uniformly bounded, it follows from the Arzela–Ascoli Theorem that there exists a subsequence of $\{d_n\}$ (still denoted by $\{d_n\}$) such that the corresponding positive solutions (u_n, v_n) of (1.5) satisfy that $u_n + v_n \to \phi$ in $C[0, 1]$ as $n \to \infty$. For $d = d_n$, multiplying the first equation of (1.5) by v_n and the second the equation by u_n, and integrating the difference over $[0, 1]$, we get

$$\int_0^1 u_n v_n (\phi - u_n - v_n) \left[\frac{m_1}{a_1 + \phi - u_n - v_n} - \frac{m_2}{a_2 + \phi - u_n - v_n} \right] = 0. \tag{5.6}$$

Since $m_1/a_1 < m_2/a_2$ and $u_n + v_n \to \phi$ in $C[0, 1]$ as $n \to \infty$, there exists $N > 0$ such that the left hand side of (5.6) is negative for all $n > N$. This is a contradiction. Therefore, there exists $d_5 > 0$ such that (1.4) has no positive steady state for all $d < d_5$. The case $m_1/a_1 > m_2/a_2$ can be proved analogously. □

Combining Lemma 2.2 and Lemmas 5.1–5.3, we have obtained a complete description of the dynamic behavior of (1.4) when $m_1/a_1 \neq m_2/a_2$ for small diffusion rate d.

Theorem 5.4 *Suppose that $m_1/a_1 \neq m_2/a_2$. If $m_1/a_1 < m_2/a_2$, then there exists $d_a > 0$ such that problem* (1.4) *has no positive steady state and the semi-trivial steady state $(0, \hat{v})$ is globally asymptotically stable for all $d < d_a$; if $m_1/a_1 > m_2/a_2$, then there exists $d_b > 0$ such that problem* (1.4) *has no positive steady state and the semi-trivial steady state $(\hat{u}, 0)$ is globally asymptotically stable for all $d < d_b$.*

By Theorems 2.1(i), 4.6 and 5.4, for fixed m_1, m_2, a_1 and a_2, we have proved that coexistence steady states can only exist for intermediate d.

Remark 5.5 A corresponding result of Theorem 5.4 holds for large m_1 and m_2 with fixed d, a_1 and a_2: There exists $m > 0$ such that if $m_1, m_2 > m$ problem (1.4) has no positive steady state. Moreover, $(0, \hat{v})$ is globally asymptotically stable if $m_1/a_1 < m_2/a_2$, and $(\hat{u}, 0)$ is globally asymptotically stable if $m_1/a_1 > m_2/a_2$.

6 Numerical Studies

We first summarize our theoretical results in Fig. 1, which shows parameter ranges of (m_1, m_2) with different dynamic behavior for (1.4). For convenience, we suppose $a_1 > a_2$. In region A, $E_0 = (0, 0)$ is globally asymptotically stable by Theorem 2.1(i); In region $B \cup C$ (or $D \cup E$), $E_2 = (0, \hat{v})$ (or $E_1 = (\hat{u}, 0)$) is globally asymptotically stable by part (ii) and (iv) [or (iii) and (v)] of Theorem 2.1, respectively. If the conditions in Theorem 4.6 hold, then $\widehat{m}_2 < \widetilde{m}_2$ and there exists a stable coexistence steady state in region F. In region G (or H), E_2 (or E_1) is locally asymptotically stable while E_1 (or E_2) is unstable by Theorem 4.2. Note that Fig. 1 is for illustration only, so it is not up to scale, and the curves of $m_2 = \widetilde{m}_2$ and $m_2 = \widehat{m}_2$ are not necessarily straight lines. Also we are not able to estimate the magnitude of $\widetilde{m}_2$ and $\widehat{m}_2$ if (4.12) is not satisfied, and this leaves a blank region between $m_1 = d\lambda_1(f_1(\phi))$ and $m_1 = d\lambda_1\left(f_1(\phi - \frac{\phi(1)}{\cos\alpha}\cos(\alpha x))\right)$. It is worth noting that the curves of $\hat{m}_2$ and $\tilde{m}_2$ are bounded by Remark 5.5.

Next, we present some numerical simulations. We first provide some numerical evidence that the inequality $\widehat{m}_2 < \widetilde{m}_2$ can hold. To this end, we fix $S_0 = 1$ and $\gamma = 0.5$, and choose different values for d, m_1, a_1, a_2, and then compute $\widehat{m}_2$ and $\widetilde{m}_2$. For all the cases in Table 1, we obtain $\widehat{m}_2 < \widetilde{m}_2$, which means that (1.4) has a stable coexistence steady state if $m_2 \in (\widehat{m}_2, \widetilde{m}_2)$ by Theorem 4.2.

Then, we fix $S_0 = 1$, $\gamma = 0.5$, $a_1 = 1.5$, $a_2 = 0.2$, $m_1 = 1$ (first set of parameter values in Table 1), and explore different values for m_2. We compute $\lambda_1(f_1(\phi)) = \lambda_1(\phi/(a_1 + \phi)) = 0.9342930$, and $\lambda_1(f_2(\phi)) = \lambda_1(\phi/(a_2 + \phi)) = 0.4948056$. Choose $d = 0.5$ such that $d\lambda_1(f_1(\phi)) < m_1$, which means that E_1 exists. By Table 1, we have $\widehat{m}_2 = 0.323612$ and $\widetilde{m}_2 = 0.324587$. Choose initial data $u_0 = v_0 = 0.5\cos(\alpha x)$, where α is the solution of (4.11). We choose three different values for m_2 to perform numerical simulations.

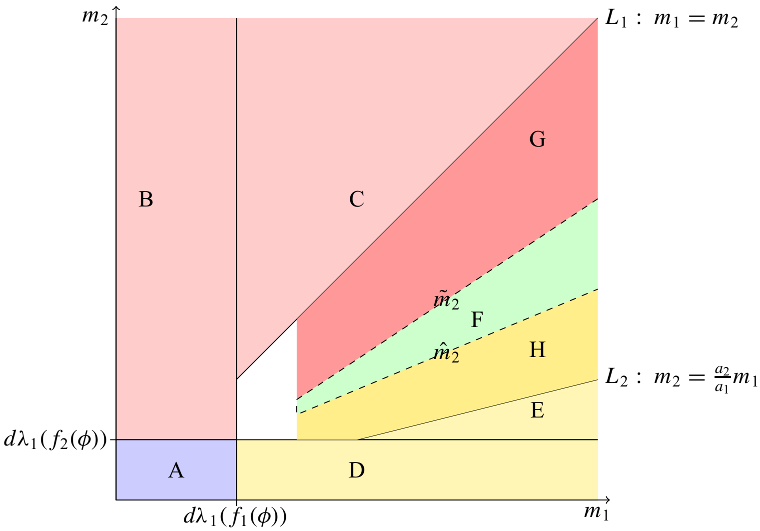
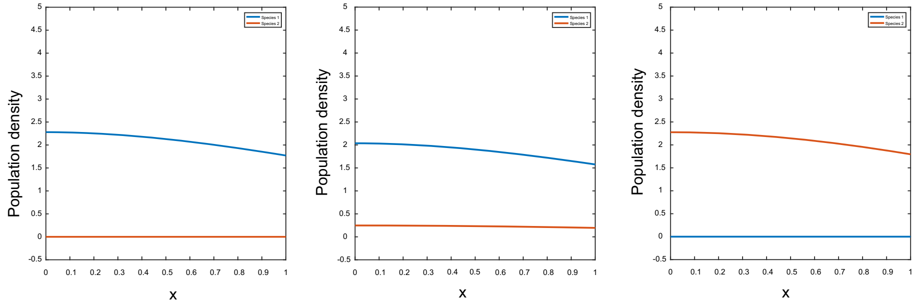


Fig. 1 Regions in (m_1, m_2) plane with different asymptotical dynamics

Table 1 $\widehat{m}_2$ and $\widetilde{m}_2$ for different parameter values

d	m_1	a_1	a_2	$\widehat{m}_2$	$\widetilde{m}_2$
0.5	1	1.5	0.2	0.323612	0.324587
0.5	0.5	1.5	0.2	0.252095	0.252117
0.5	2	1.5	0.2	0.479253	0.486946
0.25	1	1.5	0.2	0.239627	0.243473
1	1	1.5	0.2	0.504191	0.504233
0.5	1	1	0.2	0.381601	0.383848
0.5	1	2	0.2	0.295132	0.295596
0.5	1	1.5	0.1	0.269303	0.270197
0.5	1	1.5	1.2	0.845441	0.845478



(a) $m_2 = 0.32 < \widehat{m}_2$ **(b)** $m_2 = 0.3245 \in (\widehat{m}_2, \widetilde{m}_2)$ **(c)** $m_2 = 0.33 > \widetilde{m}_2$

Fig. 2 The densities of the two species at $t = 2000$. The parameters for the three sub-figures are the same except for m_2: $S_0 = 1, \gamma = 0.5, a_1 = 1.5, a_2 = 0.2, m_1 = 1$ and $d = 0.5$

(I) Choose $m_2 = 0.32$. Then, $d\lambda_1(f_2(\phi)) < m_2$ and E_2 exists. As $m_2 < \widehat{m}_2$, by Theorem 4.2, E_1 is locally asymptotically stable and E_2 is unstable. The numerical simulation shows that species 1 excludes species 2 (see Fig. 2a).

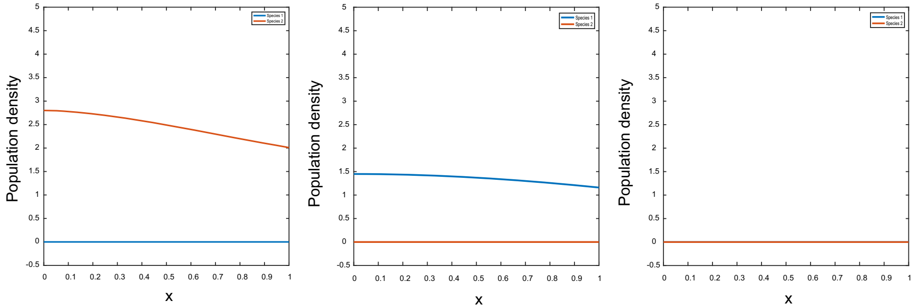
(II) Choose $m_2 = 0.33$. Then, $m_2 > \widetilde{m}_2$ and E_2 exists. By Theorem 4.2, E_2 is locally asymptotically stable and E_1 is unstable. The numerical simulation shows that species 2 excludes species 1 (see Fig. 2c).

(III) Choose $m_2 = 0.3245$. Then, $m_2 \in (\widehat{m}_2, \widetilde{m}_2)$. By Theorem 4.2, there exists a stable coexistence steady state. The numerical simulation shows that two species may coexist (see Fig. 2b).

Finally, to explore the impact of the diffusion rate d, we keep the values of all parameters the same as in Fig. 2b except for replacing $d = 0.5$ by $d = 0.1, 1, 2$, respectively ($S_0 = 1, \gamma = 0.5, a_1 = 1.5, a_2 = 0.2, m_1 = 1, m_2 = 0.3245$). The results corresponding to different values of d are summarized below:

(i) Choose $d = 0.1$ (small diffusion rate). We can compute $\widehat{m}_2 = 0.193758$ and $\widetilde{m}_2 = 0.198186$. So, $m_2 > \widetilde{m}_2$. By Theorem 4.2, E_2 is locally asymptotically stable and E_1 is unstable. In Theorem 5.4, we prove that one species will drive the other one to extinction when d is small. Note that $m_1/a_1 = 0.67$ and $m_2/a_2 = 1.62$, which means that species 2 has competitive advantage over species 1 by Theorem 5.4. The numerical simulation confirms this (see Fig. 3a).

(ii) Choose $d = 0.5$ (see Fig. 2b). Two species may coexist in this case.



(a) d=0.1 **(b)** d=1 **(c)** d=2

Fig. 3 The densities of the two species at $t = 2000$ with the same parameter values as for simulations in Fig. 2b except for d: $S_0 = 1, \gamma = 0.5, a_1 = 1.5, a_2 = 0.2, m_1 = 1, m_2 = 0.3245$

(iii) Choose $d = 1$. Numerical simulation shows that species 1 has competitive advantage over species 2 and drives it to extinction (see Fig. 3b).

(iv) Choose $d = 2$ (large diffusion rate). Numerical simulation shows that both species become extinct (see Fig. 3c).

Our numerical simulations confirm that coexistence of the two species is only possible for intermediate ranges of d.

Acknowledgements The authors would like to thank the anonymous referee for his valuable comments which have led to a significant improvement in the presentation of the paper.

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