Research Article

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Effects of anisotropic diffusion in a two-dimensional unstirred chemostat

https://doi.org/10.1515/ans-2023-0201
Received July 1, 2025; accepted September 12, 2025; published online October 1, 2025

Abstract: We investigate an unstirred chemostat model in which two species compete in a two-dimensional environment. The populations are assumed to disperse anisotropically, with distinct probabilities assigned to horizontal and vertical movements, which are interpreted as dispersal strategies. First, we analyze the dynamics of the single-species model and identify the conditions for the existence of positive steady states. Then, we classify the dynamical behavior of the two-species model into three scenarios based on the diffusion strategies: (i) extinction; (ii) competitive exclusion; and (iii) coexistence. Next, we provide sufficient conditions for the existence of coexistence steady states. Finally, our numerical simulations provide visual validation of our theoretical results and offer valuable insights for future researches.

Keywords: chemostat; anisotropic diffusion; dynamical behavior; bifurcation; numerical simulation

MSC 2020: 35A01; 35A02; 35B32; 35B35

1 Introduction

The chemostat is a widely employed laboratory apparatus for continuous microbial cultures, with significant applications in fields such as fermentation engineering and wastewater treatment. Moreover, it is often used as a simplified model to study more intricate microbial ecosystems, including ponds and lakes. Consequently, various mathematical models have been developed to characterize the interactions between nutrients and microorganisms in chemostats, integrating factors such as species growth, diffusion, and interspecies interactions; see, e.g., [1].

Initial formulations of chemostat dynamics were based on the premise of complete mixing within the culture vessel, thereby maintaining uniform nutrient dispersion. Under this assumption, the system is commonly modeled by ordinary differential equations that describe spatially homogeneous concentrations of nutrients and microbial populations; see, e.g., [2]. However, substantial discrepancies remain between these idealized chemostat models and the complexities of real natural environments. To bridge this gap and enhance ecological realism, subsequent research has led to substantial modifications of classical chemostat models, yielding a wide array of generalized formulations. Prominent examples encompass models incorporating periodic temporal variations [3]–[5], delayed responses [6], and the presence of inhibitors [7], [8].

The work is supported by the National Natural Science Foundation of China (12171296, 12461097).

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Diffusion is a widespread natural process, which has led to considerable interest in the analysis of unstirred chemostat models. Hsu and Waltman [9] introduced random diffusion into the chemostat model and derived results concerning the coexistence of two competing populations. Their findings revealed that diffusion plays a crucial role in population coexistence. In the context of unstirred chemostat models, Wu [10] studied the existence of coexistence states using global bifurcation theory. Subsequently, Wu and collaborators extended this line of research to unstirred chemostat models incorporating inhibitors [11], as well as models involving two resources [12], [13]. Furthermore, it is also noted in ref. [9] that assuming nutrients and microorganisms have identical diffusion rates is biologically unrealistic. Previous studies have presented various results for different random diffusion rates; see, e.g., [14]–[17].

However, population dispersal is often non-random due to heterogeneity in resource distribution, variability in topography and climate, and anthropogenic modifications, leading to directional movement biases. Anisotropic diffusion is one such form that captures these complexities. Bouin et al. [18] proposed a scenario where the population moves horizontally with probability $\frac{\theta}{2}$ and vertically with probability $\frac{1-\theta}{2}$, where $\theta \in [0,1]$. Moreover, they showed that in a model of two competing populations in two-dimensional heterogeneous environments, the optimal dispersal strategy for both populations is to migrate preferentially in the direction exhibiting lower variability in resource distribution. For more advanced theoretical studies concerning anisotropy or other diffusion mechanisms, the reader is referred to refs. [19]–[21].

Biologically, anisotropic diffusion may offer more adaptive possibilities for populations, enabling them to better align with available resources. This can enhance the likelihood of coexistence. Exploring the evolution of anisotropic diffusion in more biologically plausible environments would be both intriguing and significant.

Motivated by the works of refs. [9], [10], [18], we investigate in this study an unstirred chemostat model incorporating anisotropic diffusion.

$$\begin{aligned} &S_t = D_0 \Delta S - f_1(S)u - f_2(S)v, \\ &u_t = D(p)u_{xx} + D(1-p)u_{yy} + f_1(S)u, \\ &v_t = D(q)v_{xx} + D(1-q)v_{yy} + f_2(S)v \qquad \text{in } \Omega \times \mathbb{R}_+, \end{aligned} \tag{1.1}$$

subject to the boundary conditions

$$\begin{aligned} &D_0 \nabla S \cdot \nu + b(x,y)S = H(x,y), \\ &(D(p)u_x, D(1-p)u_y) \cdot \nu + b(x,y)u = 0, \\ &(D(q)v_x, D(1-q)v_y) \cdot \nu + b(x,y)v = 0 \quad \text{on } \partial\Omega \times \mathbb{R}_+, \end{aligned} \tag{1.2}$$

and the initial conditions

$$\begin{aligned} &S(x,y,0) = S_0(x,y) \ge 0, \\ &u(x,y,0) = u_0(x,y) \ge, \not\equiv 0, \\ &v(x,y,0) = v_0(x,y) \ge, \not\equiv 0 \quad \text{on } \overline{\Omega}. \end{aligned} \tag{1.3}$$

Here, $\Delta := \frac{\partial^2}{\partial x^2} + \frac{\partial^2}{\partial y^2}$ is the Laplace operator and $\nabla \cdot \nu$ is the normal derivative on the boundary, where $\nu = (\nu_x, \nu_y)$ denotes the outward unit normal vector. $S(x,y,t)$ represents the nutrient concentration, while $u(x,y,t)$ and $v(x,y,t)$ denote the population densities of two competitors within the unstirred chemostat. Ω is a strictly convex, open, bounded subset of $\mathbb{R}^2$ with a smooth boundary $\partial\Omega$. The function $D(\theta) := \underline{D} + (\overline{D} - \underline{D})\theta$ for any $\theta \in [0,1]$, where $0 < \underline{D} < \overline{D}$ to avoid the degeneracy [18]. In particular, we assume that

$$D_0 = D\left(\frac{1}{2}\right) = \frac{1}{2}\left(\underline{D} + \overline{D}\right).$$

The functions

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

where $m_i, a_i > 0$. Here, the constants $m_i > 0$, $i = 1, 2$, represent the maximal growth rates, and the constants $a_i > 0$, $i = 1, 2$, denote the Michaelis-Menten constants. The nutrients are supplied at the rate of $H(x, y)$ at position (x, y), where $H(x, y) \geq 0$. The mixture of nutrients and microorganisms is withdrawn at a spatially dependent rate $b(x, y)$ at location (x, y), leading to the Robin boundary conditions. The functions $b(x, y), H(x, y) \in C^{2+\alpha}(\partial\Omega)$ and $b(x, y), H(x, y) \geq, \not\equiv 0$ on $\partial\Omega$. We assume that $\partial\Omega$ is partitioned into two non-empty, pairwise disjoint subsets $\Gamma_i, i = 1, 2$, with $\partial\Omega = \Gamma_1 \cap \Gamma_2$, where $\Gamma_1 := \{(x, y) \in \partial\Omega : b(x, y) = 0\}$ and $H(x, y) \geq, \not\equiv 0$ on Γ_1. The boundary conditions (1.2) are intuitive and appropriate for this type of equations; see [9], [16], [22] for the derivation and explanation. Moreover, the initial values $(S_0, u_0, v_0) \in [C(\overline{\Omega})]^3$. For simplicity, the parameters not explicitly specified are treated as constants throughout this paper.

If the initial condition $v_0(x, y) \equiv 0$, formally equivalent to setting $v(x, y, t) \equiv 0$ in system (1.1)–(1.3), then this system can be reduced to

$$\begin{aligned} S_t &= D_0 \Delta S - f_1(S)u, \\ u_t &= D(p)u_{xx} + D(1-p)u_{yy} + f_1(S)u \qquad \text{in } \Omega \times \mathbb{R}_+, \\ D_0 \nabla S \cdot \nu + b(x, y)S &= H(x, y), \\ \big(D(p)u_x, D(1-p)u_y\big) \cdot \nu + b(x, y)u &= 0 \quad \text{on } \partial\Omega \times \mathbb{R}_+, \\ S(x, y, 0) &= S_0(x, y) \geq 0, \\ u(x, y, 0) &= u_0(x, y) \geq, \not\equiv 0 \qquad \text{on } \bar{\Omega}. \end{aligned} \tag{1.4}$$

Similarly, we obtain another single-species model

$$\begin{aligned} S_t &= D_0 \Delta S - f_2(S)v, \\ v_t &= D(q)v_{xx} + D(1-q)v_{yy} + f_2(S)v \qquad \text{in } \Omega \times \mathbb{R}_+, \\ D_0 \nabla S \cdot \nu + b(x, y)S &= H(x, y), \\ (D(q)v_x, D(1-q)v_y) \cdot \nu + b(x, y)v &= 0 \quad \text{on } \partial\Omega \times \mathbb{R}_+, \\ S(x, y, 0) &= S_0(x, y) \geq 0, \\ v(x, y, 0) &= v_0(x, y) \geq, \not\equiv 0 \qquad \text{on } \bar{\Omega}. \end{aligned} \tag{1.5}$$

Furthermore, it is well known that in the absence of species in this chemostat, the nutrient concentration $S(x, y, t)$ approaches a unique equilibrium, denoted by z; see Lemma 2.5.

Inspired by the seminal contribution of Bouin et al. [18], which established the concavity property of the principal eigenvalue for a certain class of elliptic operators with respect to the anisotropic diffusion parameter (denoted by either p or q), we significantly broaden this result. In particular, we establish the concavity property for a substantially wider class of elliptic eigenvalue problems encompassing more general functional response terms and boundary conditions in reaction-diffusion equations; see Lemma 2.1 for the precise statement.

By introducing anisotropic diffusion, where random diffusion can be seen as a special case when $p = q = \frac{1}{2}$ (e.g., [9]), we face several technical challenges. One such challenges is the failure of the conservation law in the chemostat, which prevents us from simplifying the models. As a result, we are compelled to work with higher-dimensional operators. Another challenge arises from the necessity of simultaneously considering both the average diffusion rate, $\frac{1}{2}(\underline{D} + \overline{D})$ (i.e., D_0), and the diffusion strategies, p and q, within these models.

Interestingly, our findings reveal a more intricate structure than that observed in the case of isotropic diffusion. To illustrate this, we examine the steady states of the single-species model (1.4). In the isotropic diffusion setting, the corresponding results (see, e.g., [9] or Lemma 2.7) are represented by the slice $p = \frac{1}{2}$ in the schematic bifurcation diagrams shown in Figure 1. From this figure, we observe that regardless of whether positive steady states exist in the isotropic case, variations in the anisotropic diffusion parameter p can induce the emergence or disappearance of such steady states.

We derive several key results concerning the dynamics of systems (1.1)–(1.5) are summarized briefly as follows.

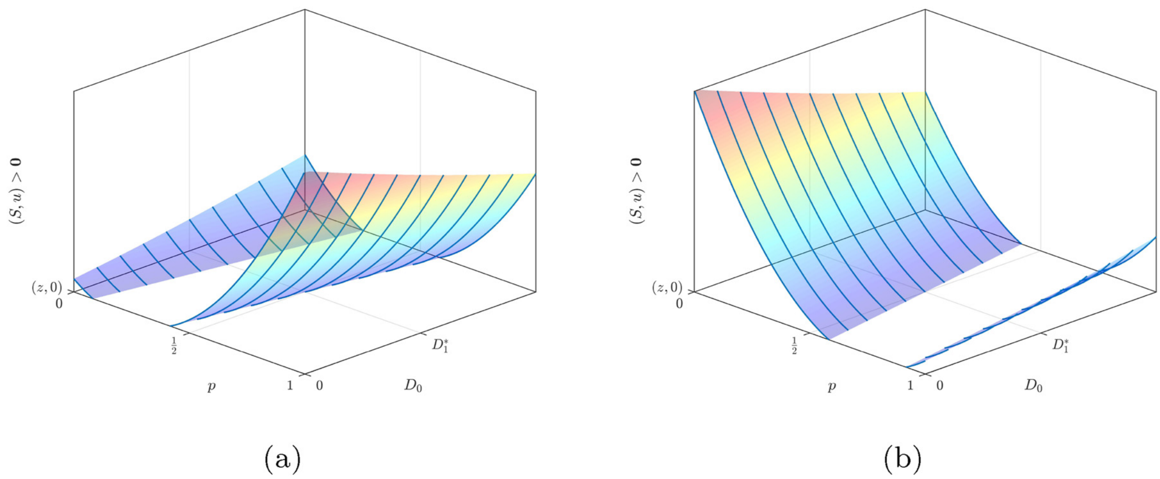


Figure 1: Schematic bifurcation diagrams of (S, u) for system (3.8); see Theorems 3.7–3.9.

(i) There exists a unique connected open interval $I_p \subset [0,1]$ such that the steady state $(z, 0)$ of system (1.4) is globally asymptotically stable for $p \in I_p$ (see Theorem 3.3), and system (1.4) is uniformly persistent for $p \in [0,1]\backslash\overline{I_p}$ (see Theorem 3.4). Moreover, system (1.4) admits at least one positive steady state for $p \in [0,1]\backslash\overline{I_p}$, and the positive steady state is locally asymptotically stable when the parameter p is near the outer boundary of the interval I_p (see Theorems 3.7–3.9 and Remarks there).

(ii) Similarly, there exists a unique connected open interval $I_q \subset [0,1]$ such that the steady state $(z, 0)$ of system (1.5) is globally asymptotically stable for $p \in I_q$, and system (1.5) is uniformly persistent for $q \in [0,1]\backslash\overline{I_q}$ (see Theorem 3.5). Moreover, system (1.5) admits at least one positive steady state for $q \in [0,1]\backslash\overline{I_q}$, and the positive steady state is locally asymptotically stable when the parameter q is near the outer boundary of the interval I_q (see Theorem 3.11 and Remark there).

(iii) There exists a unique connected region $\Sigma_0 \subset [0,1]^2$ such that the steady state $(z, 0, 0)$ of system (1.1)–(1.3) is globally asymptotically stable for $(p, q) \in \Sigma_0$ (see Theorem 4.2).

(iv) Competitive exclusion between the two species u, v in system (1.1)–(1.3) may occur if the average rate of anisotropic diffusion $\frac{1}{2}(\underline{D} + \overline{D})$ (i.e., D_0) is relatively low (see Theorem 4.3), where $(p, q) \in [0,1]^2\backslash\Sigma_0$.

(v) There may exist a region $\Sigma_1 \subset [0,1]^2$ located on the boundary of $[0,1]^2$ such that system (1.1)–(1.3) is uniformly persistent for $(p, q) \in \Sigma_1$ (see Theorem 4.4). Moreover, we derive the conditions for the linear stability of several special solutions (see Theorem 5.1). Additionally, we conclude that under certain additional conditions, system (1.1)–(1.3) admits at least one positive steady state when (p, q) lies within a specific region of Σ_1 (see Theorems 5.8 and 5.10), and the positive steady state is locally asymptotically stable when (p, q) is located in a very small region of Σ_1 (see Lemmas 5.5 and 5.6).

(vi) Moreover, we investigate the impact of anisotropic diffusion on system (1.1)–(1.3) using numerical simulations, with the goal of providing insights and support (see Section 6).

Based on the above analysis of the models, we found that it is more advantageous for the species to disperse in a single direction. This is because our conclusion shows that the diffusion strategies leading to extinction or competitive exclusion are typically positioned in the middle of their feasible area, exhibiting no distinct directional bias. In contrast, anisotropic diffusion can significantly enhance the potential for species coexistence, which is consistent with the conclusions drawn in ref. [18].

The organization of this paper is as follows. In Section 2, we present several findings that will be utilized in the subsequent analysis. Section 3 analyzes the dynamical behavior of the single-species models (1.4) and (1.5), and examines the existence and local stability of their positive steady states. The aim of Section 4 is to investigate the dynamic behavior of the two-species model (1.1)–(1.3). In Section 5, we further study the structure of coexistence steady states of system (1.1)–(1.3) using bifurcation theory. Furthermore, we discuss the local stability of some coexistence steady states using perturbation theory. Section 6 presents numerical simulations examining the effects of dispersal strategies. Finally, a brief discussion is provided in Section 7.

2 Preliminaries

In this section, we present some preliminary results that will be useful for the subsequent analysis.

Consider the following linear elliptic eigenvalue problem

$$\begin{aligned} &D(p)\varphi_{xx} + D(1-p)\varphi_{yy} + h(x,y)\varphi + \lambda\varphi = 0 \quad &&\text{in } \Omega, \\ &\big(D(p)\varphi_x, D(1-p)\varphi_y\big)\cdot \nu + b(x,y)\varphi = 0 &&\text{on } \partial\Omega, \end{aligned} \tag{2.1}$$

where $h \in L^\infty(\Omega)$. This problem admits a unique principal eigenvalue [23], denoted by $\lambda_1(p,h)$, with a positive eigenfunction $\varphi_1(p,h)$. The corresponding eigenfunction $\varphi_1(p,h)$ is unique up to a scalar multiple. We can normalize the positive eigenfunction $\varphi_1(p,h)$ by enforcing the condition $\int_\Omega \varphi_1^2 = 1$. The variational characterization of $\lambda_1(p,h)$ could be given by

$$\lambda_1(p,h) = \inf_{\substack{\varphi\in H^1(\Omega)\\ \varphi\not\equiv 0}} \left\{ \frac{\int_\Omega \big(D(p)(\varphi_x)^2 + D(1-p)(\varphi_y)^2 - h\varphi^2\big) + \int_{\partial\Omega} b(x,y)\varphi^2}{\int_\Omega \varphi^2} \right\}. \tag{2.2}$$

Furthermore, if $\varphi_1 \in H^1(\Omega)$, then in fact $\varphi_1 \in W^{2,r}(\Omega)$ for any $r \in (1,\infty)$; see, e.g., [24, Theorem 2.1 and Remarks there].

It is well known that $\lambda_1(p,h)$ varies smoothly with p. The implicit function theorem further implies that the corresponding principal eigenfuntion $\varphi_1(p,h) > 0$ on $\overline{\Omega}$ also depends continuously and differentiably on p; see, e.g., [24]. For convenience, we write $\frac{\partial\lambda_1(p,h)}{\partial p}$ and $\frac{\partial^2\lambda_1(p,h)}{\partial p^2}$ as λ_1' and λ_1'', respectively. Similarly, we denote $\frac{\partial\varphi_1(p,h)}{\partial p}$ by φ_1'. In particular, when h satisfies the following assumption, the principal eigenvalue $\lambda_1(p,h)$ exhibits more special properties. Recalling that $\Gamma_1 = \{(x,y) \in \partial\Omega : b(x,y) = 0\}$ and $H(x,y) \geq, \not\equiv 0$ on Γ_1, we introduce the following assumption.

(A) There does not exist an non-empty subset $\Omega_{\Gamma_1} \subset \Omega$, where $\Gamma_1 \subset \overline{\Omega_{\Gamma_1}}$, such that h is constant on $\overline{\Omega_{\Gamma_1}}$.

Motivated by ref. [18, Lemma 4.4], we have the following results.

Lemma 2.1. *The mapping $p \mapsto \lambda_1(p,h)$ is concave on the interval $[0,1]$. Furthermore, under the assumption (A), if there exists $p_0 \in [0,1]$ such that $\lambda_1'(p_0,h) = 0$, then $\lambda_1''(p_0,h) < 0$.*

Proof. Differentiating eigenvalue problem (2.1) with respect to p, we obtain

$$\begin{aligned} &D(p)(\varphi_1)'_{xx} + D(1-p)(\varphi_1)'_{yy} + h\varphi_1' + \lambda_1\varphi_1' + (\bar{D}-\underline{D})\big((\varphi_1)_{xx} - (\varphi_1)_{yy}\big) + \lambda_1'\varphi_1 = 0 \qquad \text{in } \Omega, \\ &\Big(D(p)(\varphi_1)'_x + (\bar{D}-\underline{D})(\varphi_1)_x, D(p)(\varphi_1)'_y - (\bar{D}-\underline{D})(\varphi_1)_y\Big)\cdot\nu + b(x,y)\varphi_1' = 0 \quad \text{on } \partial\Omega. \end{aligned} \tag{2.3}$$

By multiplying the first equation of (2.1) by φ_1' and integrating the result by parts over Ω, and then applying the second equation of (2.1), we obtain

$$-\int_{\partial\Omega} b(x,y)\varphi_1\varphi_1' - \int_\Omega \Big(D(p)(\varphi_1)_x(\varphi_1)'_x + D(1-p)(\varphi_1)_y(\varphi_1)'_y\Big) + \int_\Omega h\varphi_1\varphi_1' + \lambda_1\int_\Omega \varphi_1\varphi_1' = 0.$$

Similarly, by multiplying the first equation of (2.3) by φ_1, integrating the result by parts over Ω, and applying the second equation of (2.3), we derive

$$-\int_{\partial\Omega} b(x,y)\varphi_1'\varphi_1 - \int_{\Omega}\Big(D(p)(\varphi_1)_x'(\varphi_1)_x + D(1-p)(\varphi_1)_y'(\varphi_1)_y\Big) + \int_{\Omega} h\varphi_1\varphi_1'$$
$$+\lambda_1\int_{\Omega}\varphi_1'\varphi_1 - (\bar{D}-\underline{D})\int_{\Omega}\Big(\big((\varphi_1)_x\big)^2 - \big((\varphi_1)_y\big)^2\Big) + \lambda_1'\int_{\Omega}\varphi_1^2 = 0$$

Subtracting the above two equalities, we have

$$\lambda_1'\int_{\Omega}\varphi_1^2 = (\bar{D}-\underline{D})\int_{\Omega}\Big(\big((\varphi_1)_x\big)^2 - \big((\varphi_1)_y\big)^2\Big).$$

Since the eigenspace corresponding to λ_1 is one-dimensional, we can normalize the eigenfunction φ_1 by imposing $\int_\Omega \varphi_1^2 = 1$, so that it is uniquely determined. Then we obtain

$$\lambda_1' = (\bar{D}-\underline{D})\int_{\Omega}\Big(\big((\varphi_1)_x\big)^2 - \big((\varphi_1)_y\big)^2\Big). \tag{2.4}$$

Differentiating equation (2.4) with respect to p yields

$$\lambda_1'' = 2(\bar{D}-\underline{D})\int_{\Omega}\Big((\varphi_1)_x(\varphi_1)_x' - (\varphi_1)_y(\varphi_1)_y'\Big).$$

Multiplying the first equation of (2.3) by φ_1', integrating the result by parts over Ω, and applying the second equation of (2.3), we have

$$(\bar{D}-\underline{D})\int_{\Omega}\Big((\varphi_1)_x(\varphi_1)_x' - (\varphi_1)_y(\varphi_1)_y'\Big)$$
$$= -\int_{\partial\Omega} b(x,y)(\varphi_1')^2 - \int_{\Omega}\Big(D(p)\big((\varphi_1')_x\big)^2 + D(1-p)\big((\varphi_1')_y\big)^2\Big) + \int_{\Omega} h\varphi_1\varphi_1'$$
$$+\lambda_1\int_{\Omega}(\varphi_1')^2 + \lambda_1'\int_{\Omega}\varphi_1\varphi_1'.$$

Here the last term in the right-hand side vanishes due to the normalisation condition $\int_\Omega \varphi_1^2 = 1$, which implies that $\int_\Omega \varphi_1\varphi_1' = 0$. By the variational characterization of $\lambda_1(p,h)$ (see, e.g., equation (2.2)), we obtain

$$(\bar{D}-\underline{D})\int_{\Omega}\Big((\varphi_1)_x(\varphi_1)_x' - (\varphi_1)_y(\varphi_1)_y'\Big) \le 0.$$

It then follows that $\lambda_1'' \le 0$, with the equality holding if and only if φ_1' is a scalar multiple of φ_1. Since $\int_\Omega \varphi_1\varphi_1' = 0$ and $\varphi_1 > 0$ in Ω, we have that $\varphi_1' \equiv 0$ in Ω when $\lambda_1'' = 0$.

Now we show that if there exists $p_0 \in [0,1]$ such that $\lambda_1'(p_0,h) = 0$, then $\lambda_1''(p_0,h) < 0$ by contradiction arguments. Otherwise, $\lambda_1''(p_0,h) = 0$, then problem (2.3) reduces to

$$(\varphi_1)_{xx} - (\varphi_1)_{yy} = 0 \quad \text{in } \Omega,$$
$$(\varphi_1)_x\nu_x - (\varphi_1)_y\nu_y = 0 \quad \text{on } \partial\Omega.$$

In view of the boundary condition for φ in problem (2.1), we further have

$$(\varphi_1)_x \nu_x = (\varphi_1)_y \nu_y = -\frac{b\varphi_1}{\bar{D}+\underline{D}} \begin{cases} = 0 & \text{on } \Gamma_1, \\ < 0 & \text{in } \Gamma_2. \end{cases}$$

Under the assumption of strict convexity for the domain Ω, the components ν_x and ν_y of the outward normal vector ν are non-zero on the boundary $\partial\Omega$, except possibly on a set of measure zero. Since $\varphi_1 \in C^1(\overline{\Omega})$, we have $\nabla\varphi_1 = 0$ on Γ_1. Set $\eta = x + y$, $\zeta = x - y$ and $Z(\eta, \zeta) := \varphi_1(x, y)$. The function $Z(\eta, \zeta)$ then satisfies

$$\begin{aligned} Z_{\eta\zeta} &= 0 \quad \text{in } \Omega', \\ (Z_\eta, Z_\zeta) &= (0, 0) \quad \text{on } \Gamma_1', \end{aligned} \tag{2.5}$$

where Ω' and Γ_1' are the images of Ω and Γ_1 under the homeomorphic map $(x, y) \mapsto (\eta, \zeta)$, respectively. It follows from the first equation of (2.5) that $Z(\eta, \zeta) = f(\eta) + g(\zeta)$, where the functions f and g are to be determined. Moreover, the second equation of (2.5) implies that $f'(\eta) = g'(\zeta) = 0$ for all $(\eta, \zeta) \in \Gamma_1'$. Consequently, there exists a non-empty open subset $\Omega_0' \subset \Omega'$ such that Z is constant on Ω_0', where $\Gamma_1' \subset \partial\Omega_0'$. Hence, φ_1 is constant on $\overline{\Omega_0}$, where Ω_0 is the preimage of Ω_0'. Using the first equation of (2.1), we obtain that $h + \lambda_1(p_0, h) \equiv 0$ in Ω_0, which contradicts the assumption (A). This completes the proof. □

For any given $h \in L^\infty(\Omega)$, we define a function

$$F(p; h) := \int_\Omega \left(\left((\varphi_1(p, h))_x \right)^2 - ((\varphi_1(p, h))_y)^2 \right) \tag{2.6}$$

for $p \in [0, 1]$. Based on the proof of Lemma 2.1, it is straightforward to observe that $F'(p;\ h) \le 0$ in (0, 1). This function is closely aligned with the formulation in ref. [18, Theorem 2.1] and underpins the core arguments of the subsequent investigation. It quantifies the difference between the resource variations in horizontal and vertical directions. For $F > 0$, the resource distribution exhibits greater spatial variations in the horizontal direction, while for $F < 0$, the variation is more pronounced in the vertical direction.

Next, we summarize several results on $\lambda_1(p, h)$ obtained in prior studies, while the proofs are not repeated here.

Lemma 2.2 ([24]). *The following statements on eigenvalue $\lambda_1(p, h)$ hold true.*
(i) *$h_n \to h$ in $C(\overline{\Omega})$ implies $\lambda_1(p, h_n) \to \lambda_1(p, h)$.*
(ii) *$h_1 \ge h_2$ implies $\lambda_1(p, h_1) \le \lambda_1(p, h_2)$, and the equality holds if and only if $h_1 \equiv h_2$.*

Lemma 2.3. *Assume that $p = \frac{1}{2}$. Then eigenvalue problem* (2.1) *degenerates into*

$$\begin{aligned} D_0\Delta\varphi + h(x, y)\varphi + \lambda\varphi &= 0 \qquad \text{in } \Omega, \\ D_0\nabla\varphi \cdot \nu + b(x, y)\varphi &= 0 \quad \text{on } \partial\Omega. \end{aligned}$$

The principal eigenvalue $\lambda_1\left(\frac{1}{2}, h\right)$ is strictly increasing with respect to D_0 in $(0, +\infty)$. Moreover,

$$\lim_{D_0 \to 0+} \lambda_1\left(\frac{1}{2}, h\right) = -\max_{(x,y)\in\overline{\Omega}} h(x, y) \text{ and } \lim_{D_0 \to +\infty} \lambda_1\left(\frac{1}{2}, h\right) = \frac{1}{|\Omega|}\left(\int_{\partial\Omega} b(x, y) - \int_\Omega h(x, y) \right).$$

Therefore, if $\max_{(x,y)\in\bar{\Omega}} h(x,y) > 0$ *and* $\int_\Omega h(x,y) < \int_{\partial\Omega} b(x,y)$*, then there exists a unique* $D^*(h) \in (0,+\infty)$ *such that*

$$\begin{cases} \lambda_1\left(\frac{1}{2}, h\right) < 0 & \text{if } 0 < D_0 < D^*(h), \\ \lambda_1\left(\frac{1}{2}, h\right) = 0 & \text{if } D_0 = D^*(h), \\ \lambda_1\left(\frac{1}{2}, h\right) > 0 & \text{if } D_0 > D^*(h). \end{cases}$$

Remark 2.4. If the assumption $\int_\Omega h(x,y) < \int_{\partial\Omega} b(x,y)$ does not hold, then it follows that $\lambda_1\left(\frac{1}{2}, h\right) < 0$ for any $D_0 \in (0,+\infty)$, implying the nonexistence of $D^*(h)$. This observation considerably simplifies the subsequent analysis. Therefore, in the following, we focus on the case where $\int_\Omega h(x,y) < \int_{\partial\Omega} b(x,y)$. A similar but simpler analysis can be carried out for the case where $\int_\Omega h(x,y) \geq \int_{\partial\Omega} b(x,y)$.

The monotonicity of the principal eigenvalue $\lambda_1\left(\frac{1}{2}, h\right)$ with respect to D_0 can be established through its variational formulation; see, e.g., equation (2.2). By employing techniques similar to those used in the proofs of ref. [25, Propositions 1.3.16 and 1.3.19], we can prove the asymptotic behavior of $\lambda_1\left(\frac{1}{2}, h\right)$ in the limits $D_0 \to 0+$ and $D_0 \to +\infty$, respectively.

Then we restate some conclusions for certain degenerate cases without providing the proof.

Lemma 2.5 ([9], [10]). *The following system*

$$\begin{aligned} \bar{S}_t &= D_0 \Delta \bar{S} && \text{in } \Omega \times \mathbb{R}_+, \\ D_0 \nabla \bar{S} \cdot \nu + b(x,y)\bar{S} &= H(x,y) && \text{on } \partial\Omega \times \mathbb{R}_+, \\ \bar{S}(x,y,0) &= S_0(x,y) \geq 0 && \text{on } \bar{\Omega} \end{aligned} \tag{2.7}$$

admits a unique globally attractive positive steady state, denoted by z.

Remark 2.6. In view of the boundary condition in system (2.7), we conclude that there does not exist an non-empty subset $\Omega_{\Gamma_1} \subset \Omega$, where $\Gamma_1 \subset \overline{\Omega_{\Gamma_1}}$, such that z is constant on $\overline{\Omega_{\Gamma_1}}$.

For the sake of simplicity, unless otherwise specified, we shall assume that the following assumptions hold throughout the remainder of this paper:

$$\max\left\{ \int_\Omega f_1(z), \int_\Omega f_2(z) \right\} < \int_{\partial\Omega} b(x,y).$$

If $p = \frac{1}{2}$, then system (1.4) becomes

$$\begin{aligned} S_t &= D_0 \Delta S - f_1(S)u, \\ u_t &= D_0 \Delta u + f_1(S)u && \text{in } \Omega \times \mathbb{R}_+, \\ D_0 \nabla S \cdot \nu + b(x,y)S &= H(x,y), \\ D_0 \nabla u \cdot \nu + b(x,y)u &= 0 && \text{on } \partial\Omega \times \mathbb{R}_+, \\ S(x,y,0) &= S_0(x,y) \geq 0, \\ u(x,y,0) &= u_0(x,y) \geq, \not\equiv 0 && \text{on } \bar{\Omega}. \end{aligned} \tag{2.8}$$

Let $D_1^* := D^*\left(f_1(z)\right)$, where D^* is defined in Lemma 2.3. We have the following results.

Lemma 2.7 ([26]). *The following statements on system* (2.8) *are valid.*

(i) *If* $0 < D_0 < D_1^*$, *then system* (2.8) *admits a unique globally attractive positive steady state* $(z - \theta_1, \theta_1)$, *where* θ_1 *is the unique positive solution to*

$$\begin{aligned} D_0 \Delta\theta + f_1(z - \theta)\theta = 0 \qquad &\text{in } \Omega, \\ D_0 \nabla\theta \cdot \nu + b(x, y)\theta = 0 \quad &\text{on } \partial\Omega. \end{aligned} \tag{2.9}$$

(ii) *If* $D_0 \geq D_1^*$, *then the semi-trivial steady state* $(z, 0)$ *is globally attractive.*

Recall that $\lambda_1(p, f_1(z))$ is the principal eigenvalue of problem

$$\begin{aligned} D(p)\varphi_{xx} + D(1-p)\varphi_{yy} + f_1(z)\varphi + \lambda\varphi = 0 \qquad &\text{in } \Omega, \\ \big(D(p)\varphi_x, D(1-p)\varphi_y\big) \cdot \nu + b(x, y)\varphi = 0 \quad &\text{on } \partial\Omega \end{aligned} \tag{2.10}$$

with eigenfunction $\varphi_1(p, f_1(z))$, and $F\big(p; f_1(z)\big) = \int_\Omega \Big(\big((\varphi_1(p, f_1(z)))_x \big)^2 - \big((\varphi_1(p, f_1(z)))_y \big)^2 \Big)$. It follows that once the parameters $p, m_1, a_1, b(x, y)$, and the domain Ω are specified, the value of $F(p;\ f_1(z))$ is uniquely determined. For convenience, we write

$$F_1 := F\Big(\frac{1}{2}; f_1(z)\Big) = \int_\Omega \bigg(\Big(\Big(\varphi_1\Big(\frac{1}{2}, f_1(z)\Big)\Big)_x \Big)^2 - \Big(\Big(\varphi_1\Big(\frac{1}{2}, f_1(z)\Big)\Big)_y \Big)^2 \bigg).$$

By Lemmas 2.1 and 2.3, we obtain the following results. The proofs are similar to that of ref. [18, Theorem 5.2], thus we omit them here.

Proposition 2.8. *Assume that* $D_0 = D_1^*$. *Then one of the following statements is valid.*

(i) *If* $F_1 = 0$, *then* $\lambda_1(p, f_1(z)) < 0$ *for* $p \in [0,1] \backslash \{\frac{1}{2}\}$.

(ii) *If* $F_1 < 0$, *then there exists* $p^* \in \big[0, \frac{1}{2}\big)$ *such that* $\lambda_1(p, f_1(z)) < 0$ *for* $p \in [0,1] \backslash \big[p^*, \frac{1}{2}\big]$ *and* $\lambda_1(p, f_1(z)) > 0$ *for* $p \in \big(p^*, \frac{1}{2}\big)$, *where* $p^* = 0$ *if* $\lambda_1\big(0, f_1(z)\big) \geq 0$.

(iii) *If* $F_1 > 0$, *then there exists* $p^* \in \big(\frac{1}{2}, 1\big]$ *such that* $\lambda_1(p, f_1(z)) < 0$ *for* $p \in [0,1] \backslash \big[\frac{1}{2}, p^*\big]$ *and* $\lambda_1(p, f_1(z)) > 0$ *for* $p \in \big(\frac{1}{2}, p^*\big)$, *where* $p^* = 1$ *if* $\lambda_1\big(1, f_1(z)\big) \geq 0$.

Proposition 2.9. *Assume that* $D_0 > D_1^*$. *Then there exist* $0 \leq p_0^* < \frac{1}{2} < p_1^* \leq 1$ *such that* $\lambda_1(p, f_1(z)) > 0$ *for* $p \in \big(p_0^*, p_1^*\big)$ *and* $\lambda_1(p, f_1(z)) < 0$ *for* $p \in [0,1] \backslash \big[p_0^*, p_1^*\big]$, *where* $p_0^* = 0$ *if* $\lambda_1\big(0, f_1(z)\big) \geq 0$ *and* $p_1^* = 1$ *if* $\lambda_1\big(1, f_1(z)\big) \geq 0$.

Proposition 2.10. *Assume that* $0 < D_0 < D_1^*$. *Then one of the following statements is valid.*

(i) *If* $F_1 = 0$, *then* $\lambda_1(p, f_1(z)) < 0$ *for* $p \in [0,1]$.

(ii) *If* $F_1 < 0$, *then* $\lambda_1(p, f_1(z)) < 0$ *for* $p \in \big(\frac{1}{2} - \epsilon, 1\big]$, *where* $\epsilon > 0$ *is small enough. In particular, there may exist two points,* $0 \leq p_-^* \leq p_+^* < \frac{1}{2}$, *such that* $\lambda_1(p, f_1(z)) < 0$ *for* $p \in [0,1] \backslash \big[p_-^*, p_+^*\big]$ *and* $\lambda_1(p, f_1(z)) > 0$ *for* $p \in \big(p_-^*, p_+^*\big)$, *where* $p_-^* = 0$ *if* $\lambda_1\big(0, f_1(z)\big) \geq 0$.

(iii) *If* $F_1 > 0$, *then* $\lambda_1(p, f_1(z)) < 0$ *for* $p \in \big[0, \frac{1}{2} + \epsilon)$, *where* $\epsilon > 0$ *is small enough. In particular, there may exist two points,* $\frac{1}{2} < p_-^* \leq p_+^* \leq 1$, *such that* $\lambda_1(p, f_1(z)) < 0$ *for* $p \in [0,1] \backslash \big[p_-^*, p_+^*\big]$ *and* $\lambda_1(p, f_1(z)) > 0$ *for* $p \in \big(p_-^*, p_+^*\big)$, *where* $p_+^* = 1$ *if* $\lambda_1\big(1, f_1(z)\big) \geq 0$.

For convenience, we summarize the conclusions on the sign of $\lambda_1(p, f_1(z))$ in Table 1. Here $D_0, D_1 > 0$. The symbol "*" indicates that no specific requirements are imposed on the related parameters. In this table, the set $[0,1] \backslash \big[p_0^*, p_1^*\big]$ is empty when $p_0^* = 0$ and $p_1^* = 1$, and the set $\big(p_-^*, p_+^*\big)$ is empty when $p_-^* = p_+^*$ or when p_-^*, p_+^* do not exist. All other sets are non-empty.

Table 1: The results on the sign of $\lambda_1(p, f_1(z))$.

$D_0 - D_1^*$	F_1	p	$\lambda_1(p, f_1(z))$
+	*	$(p_0^*, p_1^*), 0 \le p_0^* < \frac{1}{2} < p_1^* \le 1$	+
		$[0,1]\backslash[p_0^*, p_1^*]$	−
0	+	$\left(\frac{1}{2}, p^*\right), \frac{1}{2} < p^* \le 1$	+
		$[0,1]\backslash\left[\frac{1}{2}, p^*\right]$	−
	0	$[0,1]\backslash\left\{\frac{1}{2}\right\}$	−
	−	$\left(p^*, \frac{1}{2}\right), 0 \le p^* < \frac{1}{2}$	+
		$[0,1]\backslash\left[p^*, \frac{1}{2}\right]$	−
−	+	$(p_-^*, p_+^*), \frac{1}{2} < p_-^* \le p_+^* \le 1$	+
		$[0,1]\backslash[p_-^*, p_+^*]$	−
	0	$[0,1]$	−
	−	$(p_-^*, p_+^*), 0 \le p_-^* \le p_+^* < \frac{1}{2}$	+
		$[0,1]\backslash[p_-^*, p_+^*]$	−

Table 2: The results on the sign of $\lambda_1(q, f_2(z))$.

$D_0 - D_2^*$	F_2	q	$\lambda_1(q, f_2(z))$
+	*	$(q_0^*, q_1^*), 0 \le q_0^* < \frac{1}{2} < q_1^* \le 1$	+
		$[0,1]\backslash[q_0^*, q_1^*]$	−
0	+	$\left(\frac{1}{2}, q^*\right), \frac{1}{2} < q^* \le 1$	+
		$[0,1]\backslash\left[\frac{1}{2}, q^*\right]$	−
	0	$[0,1]\backslash\left\{\frac{1}{2}\right\}$	−
	−	$\left(q^*, \frac{1}{2}\right), 0 \le q^* < \frac{1}{2}$	+
		$[0,1]\backslash\left[q^*, \frac{1}{2}\right]$	−
−	+	$(q_-^*, q_+^*), \frac{1}{2} < q_-^* \le q_+^* \le 1$	+
		$[0,1]\backslash[q_-^*, q_+^*]$	−
	0	$[0,1]$	−
	−	$(q_-^*, q_+^*), 0 \le q_-^* \le q_+^* < \frac{1}{2}$	+
		$[0,1]\backslash[q_-^*, q_+^*]$	−

Set $D_2^* := D^*(f_2(z))$ and $F_2 := F\left(\frac{1}{2}; f_2(z)\right)$. Similarly, Table 2 can be derived, which provides essential structural insights into the analysis of system (1.1)–(1.3).

3 Single-species model

To gain insight into the population dynamics in the absence of interspecific interactions, we examine the single-species models (1.4) and (1.5), aiming to determine the conditions for population persistence in the unstirred chemostat.

3.1 Dynamical behavior

In this subsection, we investgate the dynamical behavior of system (1.4). The local existence and uniqueness of its solution are established in refs. [27]–[30]. Recalling that the initial values $(S_0, u_0) \in [C(\overline{\Omega})]^2$ are nonnegative, we have the following conclusions.

Lemma 3.1 (local existence, [31]). *System* (1.4) *admits a unique nonnegative classical solution* (S, u) *in* $\overline{\Omega} \times (0, T_{\max})$*, where* $T_{\max} \in (0, +\infty]$*. Specifically, the solution satisfies*

$$(S, u) \in \left[C\left(\overline{\Omega} \times [0, T_{\max})\right) \cap C^{2,1}\left(\overline{\Omega} \times (0, T_{\max})\right)\right]^2.$$

Moreover, if $T_{\max} < +\infty$*, then*

$$\limsup_{t \to T_{\max}} \left(\| S(\cdot, \cdot, t)\|_{L^\infty(\Omega)} + \|u(\cdot, \cdot, t)\|_{L^\infty(\Omega)} \right) = +\infty.$$

Based on the approach used in the proof of ref. [32, Lemma 4.1], we demonstrate that the solution $(S(x, y, t), u(x, y, t))$ to system (1.4) is well-defined for all $t > 0$ and is bounded.

Lemma 3.2. *System* (1.4) *admits a unique solution* $(S(x, y, t), u(x, y, t))$ *for all* $(x, y) \in \overline{\Omega}$ *and* $t > 0$*. Moreover, there exist positive constants* K_1, K_2*, which depend on the initial values* $S_0(x, y), u_0(x, y)$*, such that for all* $(x, y) \in \overline{\Omega}$ *and* $t > 0$*,*

$$0 < S(x, y, t) \le K_1, \;\; 0 < u(x, y, t) \le K_2.$$

In particular, the solution $(S(x, y, t), u(x, y, t))$ *is ultimately bounded.*

Proof. The local existence and uniqueness of the solution to system (1.4) are shown in Lemma 3.1. We only need to establish the global existence and boundedness of the solution to system (1.4). Firstly, it follows from the maximum principle for parabolic equations that $S(x, y, t) > 0, u(x, y, t) > 0$ for all $(x, y) \in \overline{\Omega}$ and $t \in (0, T_{\max})$. Then we have

$$S_t \le D_0 \Delta S \quad \text{in } \Omega \times \mathbb{R}_+.$$

Recall that $\bar{S}(x, y, t)$ is the solution to system (2.7). The comparison principle for parabolic equations implies that $S(x, y, t) \le \bar{S}(x, y, t)$ for all $(x, y) \in \overline{\Omega}$ and $t > 0$. Moreover, $\bar{S}(\cdot, \cdot, t) \to z$ uniformly on $\overline{\Omega}$ as $t \to +\infty$. Hence, there exists a positive constant K_1, depending on the initial values $S_0(x, y)$, such that $0 < S(x, y, t) \le K_1$ for all $(x, y) \in \overline{\Omega}$ and $t > 0$.

Consequently,

$$u_t \le D(p)u_{xx} + D(1-p)u_{yy} + f_1(K_1)u \quad \text{in } \Omega \times \mathbb{R}_+.$$

Let $\tilde{\varphi} \in C^{1+\alpha}(\overline{\Omega})$ be the unit norm positive principal eigenfunction of problem (2.1) with $h = f_1(K_1)$, corresponding to the principal eigenvalue $\tilde{\lambda} := \lambda_1\left(p, f_1(K_1)\right)$; see Section 2. Note that $\bar{u} = c_1 \tilde{\varphi} e^{-\tilde{\lambda} t}$ is a solution to

$$\begin{aligned} \bar{u}_t &= D(p)\bar{u}_{xx} + D(1-p)\bar{u}_{yy} + f_1(K_1)\bar{u} && \text{in } \Omega \times \mathbb{R}_+, \\ \left(D(p)\bar{u}_x, D(1-p)\bar{u}_y\right) \cdot \nu + b(x, y)\bar{u} &= 0 && \text{on } \partial\Omega \times \mathbb{R}_+. \\ \bar{u}(x, y, 0) &= c_1 \tilde{\varphi} > 0 && \text{on } \bar{\Omega}. \end{aligned}$$

By choosing a sufficiently large positive constant c_1 such that $c_1 \tilde{\varphi} > u_0$ on $\overline{\Omega}$, the comparison principle for parabolic equations implies that $u(x, y, t) \le \bar{u}(x, y, t)$ for all $(x, y) \in \overline{\Omega}$ and $t > 0$. Hence, system (1.4) admits a unique solution $(S(x, y, t), u(x, y, t))$ for all $(x, y) \in \overline{\Omega}$ and $t > 0$.

In the following, we demonstrate that for all $(x, y) \in \overline{\Omega}$ and $t > 0$, the solution $u(x, y, t)$ is uniformly bounded. Let $\varphi_0 \in C^{1+\alpha}(\overline{\Omega})$ be the unit norm positive principal eigenfunction of problem (2.1) with $h = 0$, corresponding to the principal eigenvalue $\lambda_0 := \lambda_1\left(p, 0\right)$. Multiplying the equation for u in system (1.4) by φ_0 and integrating over Ω by parts, we obtain

$$\frac{\mathrm{d}}{\mathrm{d}t} \int_\Omega u\varphi_0 = \int_\Omega \left(f_1(S) - \lambda_0\right) u\varphi_0 \quad \text{for all } t > 0. \tag{3.1}$$

Set $G(t) = \int_\Omega (S + c_2 u\varphi_0)$, where $0 < c_2 \le (\max_{(x,y)\in\overline{\Omega}} \varphi_0)^{-1}$. By integrating the first equation of system (1.4) over Ω by parts, and subsequently adding c_2 times equation (3.1), we obtain that for all $t > 0$,

$$\frac{\mathrm{d}}{\mathrm{d}t}G(t) + \lambda_0 G(t) = \int_{\partial\Omega} (H - bS) + \int_\Omega f_1(S)(c_2\varphi_0 - 1)u + \lambda_0 \int_\Omega S \le \int_{\partial\Omega} H + \lambda_0|\Omega|K_1.$$

By Gronwall's inequality, we get the L^1 estimates

$$G(t) \le G(0)e^{-\lambda_0 t} + \frac{\int_{\partial\Omega} H + \lambda_0|\Omega|K_1}{\lambda_0}\left(1 - e^{-\lambda_0 t}\right) \quad \text{for all } t > 0.$$

Clearly, φ_0 is independent of t. Moreover, $\lambda_0 > 0$ by the variational characterization; see, e.g., equation (2.2). Hence, there exists a positive constant κ such that

$$\int_\Omega u < \kappa \quad \text{for all } t > 0. \tag{3.2}$$

Let $U(t) = \max_{(x,y)\in\overline{\Omega},\tau\in[0,t]} u(x,y,\tau)$. Clearly, $U(t)$ is nondecreasing. There exists a sequence $t_n \to +\infty$ such that $U(t_n) = \max_{(x,y)\in\overline{\Omega}} u(x,y,t_n)$. Suppose, by contradiction, that $U(t) \to +\infty$ as $t \to +\infty$, i.e., $U(t_n) \to +\infty$ as $n \to +\infty$. Assume without loss of generality that $t_n > 1$ for all $n \ge 1$. Define $\tilde{u}_n(x,y,t) = \frac{u(x,y,t+t_n-1)}{U(t_n)}$. It then follows that $\tilde{u}_n(x,y,t)$ satisfies

$$\begin{aligned}
&(\tilde{u}_n)_t = D(p)(\tilde{u}_n)_{xx} + D(1-p)(\tilde{u}_n)_{yy} + f_1\big(S(x,y,t+t_n-1)\big)\tilde{u}_n && \text{in } \Omega \times \mathbb{R}_+,\\
&(D(p)(\tilde{u}_n)_x, D(1-p)(\tilde{u}_n)_y)\cdot \nu + b(x,y)\tilde{u}_n = 0 && \text{on } \partial\Omega \times \mathbb{R}_+,\\
&0 < \tilde{u}_n(x,y,0) \le 1 && \text{on } \overline{\Omega}.
\end{aligned}$$

In view of $0 < f_1\big(S(x,y,t+t_n-1)\big) \le f_1(K_1)$ for all $(x,y) \in \overline{\Omega}$ and $t > 0$, the comparison principle for parabolic equations implies that $0 < \tilde{u}_n(x,y,t) \le e^{f_1(K_1)t}$ for all $(x,y) \in \overline{\Omega}$ and $t > 0$. It follows from the standard parabolic regularity theory that $\{\tilde{u}_n\}$ is bounded in $C^{1+\alpha,\alpha}\left(\overline{\Omega} \times \left[\frac{1}{2}, 2\right]\right)$ for any $\alpha \in (0,1)$. By passing to a subsequence if necessary, we get that $\tilde{u}_n \to \tilde{u}$ in $C^{1,0}\left(\overline{\Omega} \times \left[\frac{1}{2}, 2\right]\right)$. Noting $\max_{(x,y)\in\overline{\Omega}} \tilde{u}_n(x,y,1) = 1$ for any $n \ge 1$, we have $\max_{(x,y)\in\overline{\Omega}} \tilde{u}(x,y,1) = 1$. Due to the continuous differentiability of $\tilde{u}(x,y,1)$ with respect to (x,y) and the maximum principle for parabolic equations, we have $\int_\Omega \tilde{u}(x,y,1) \ge \delta > 0$. This implies that $\int_\Omega \tilde{u}_n(x,y,1) \ge \frac{\delta}{2}$ for all large n. Hence,

$$\int_\Omega u(x,y,t_n) = \int_\Omega \tilde{u}_n(x,y,1)U(t_n) \ge \frac{\delta}{2}U(t_n)|\Omega| \to +\infty \quad \text{as } n \to +\infty,$$

which contradicts (3.2). This implies that $u(x,y,t)$ is bounded for all $(x,y) \in \overline{\Omega}$ and $t > 0$. Consequently, there exists a positive constant K_2, depending on the initial data $u_0(x,y)$, such that $0 < u(x,y,t) \le K_2$ for all $(x,y) \in \overline{\Omega}$ and $t > 0$. This completes the proof. □

Then we have the following conclusions on system (1.4).

Theorem 3.3. *Assume that* $\lambda_1(p, f_1(z)) > 0$*; see* Table 1. *Then the steady state* $(z, 0)$ *of system* (1.4) *is globally asymptotically stable.*

Proof. It follows from Lemma 3.2 that the solution $(S(x,y,t), u(x,y,t))$ satisfies $S(x,y,t) > 0$, $u(x,y,t) > 0$ for all $(x,y) \in \Omega$ and $t > 0$. Hence, we have

$$S_t \le D_0\Delta S \quad \text{in } \Omega \times \mathbb{R}_+.$$

The comparison principle for parabolic equations implies that

$$\limsup_{t\to+\infty} S(\cdot,\cdot,t) \le z \quad \text{uniformly on } \overline{\Omega}, \tag{3.3}$$

where z is the unique globally attractive positive steady state of system (2.7). This implies that for any $\epsilon > 0$, there exists $t_1 > 0$ such that $S < z + \epsilon$ for all $(x, y) \in \overline{\Omega}$ and $t > t_1$. By arguments similar to those in the proof of ref. [9, Theorem 3.1], we conclude that if $\lambda_1(p, f_1(z)) > 0$, then

$$\lim_{t\to+\infty} u(\cdot,\cdot,t) = 0 \quad \text{uniformly on } \overline{\Omega} \text{ in an exponential manner.} \tag{3.4}$$

In view of (3.4), we conclude that for any $\epsilon > 0$, there exists $t_2 > t_1$ such that $u(x, y, t) < \epsilon$ for all $(x, y) \in \overline{\Omega}$ and $t > t_2$. It follows from arguments similar to those in the proof of ref. [26, Theorem 1.1] that

$$\liminf_{t\to+\infty} S(\cdot,\cdot,t) \ge z \quad \text{uniformly on } \overline{\Omega}. \tag{3.5}$$

Inequalities (3.3) and (3.5) imply that $\lim_{t\to+\infty} S(\cdot,\cdot,t) = z$ uniformly on $\overline{\Omega}$. The proof is completed. □

Theorem 3.4. *Assume that* $\lambda_1(p, f_1(z)) < 0$*; see* Table 1. *Then system* (1.4) *is uniformly persistent in the sense that there exists* $\epsilon > 0$ *such that the solution* $(S(x, y, t), u(x, y, t))$ *of system* (1.4) *satisfying*

$$\liminf_{t\to+\infty} S(\cdot,\cdot,t) \ge \epsilon \text{ and } \liminf_{t\to+\infty} u(\cdot,\cdot,t) \ge \epsilon \text{ uniformly on } \overline{\Omega}.$$

Proof. We first claim that there exists $\epsilon_1 > 0$ such that $\liminf_{t\to+\infty} S(\cdot,\cdot,t) \ge \epsilon_1$. It follows from Lemma 3.2 that

$$S_t \ge D_0 \Delta S - K_2 f_1(S) \quad \text{in } \Omega \times \mathbb{R}_+.$$

The comparison principle for parabolic equations implies that $S(x, y, t) \ge \tilde{S}(x, y, t)$ for all $(x, y) \in \overline{\Omega}$ and $t > 0$, where $\tilde{S}(x, y, t)$ is the solution to

$$\begin{aligned} \tilde{S}_t &= D_0 \Delta \tilde{S}_{xx} - K_2 f_1(\tilde{S}) && \text{in } \Omega \times \mathbb{R}_+, \\ D_0 \nabla \tilde{S} \cdot \nu + b(x, y)\tilde{S} &= H(x, y) && \text{on } \partial\Omega \times \mathbb{R}_+, \\ \tilde{S}(x, y, 0) &= S_0(x, y) && \text{on } \bar{\Omega}. \end{aligned} \tag{3.6}$$

By arguments similar to those in ref. [33, Lemmas 2.2 and 4.2], we conclude that $\tilde{S}(\cdot,\cdot,t) \to z_{K_2}$ uniformly on $\overline{\Omega}$ as $t \to +\infty$, where z_{K_2} is the unique positive steady state of system (3.6). Hence, we have that $\liminf_{t\to+\infty} S(\cdot,\cdot,t) \ge \epsilon_1$, where $\epsilon_1 = \min_{\overline{\Omega}} z_{K_2}$.

Next, we aim to apply the abstract persistence theory in refs. [34], [35]. With this in mind, we let

$$\begin{aligned} P_1 &= \left\{ (S, u) \in C(\overline{\Omega}) \times C(\overline{\Omega}) : S \ge 0, u \ge 0 \quad \text{on } \overline{\Omega} \right\}, \\ P_1^0 &= \{(S, u) \in P_1 : u \not\equiv 0\}, \\ \partial P_1^0 &= P_1 \backslash P_1^0 = \{(S, u) \in P_1 : u \equiv 0\}. \end{aligned}$$

Clearly, ∂P_1^0 contains the steady state $(z, 0)$. Define Φ_t as the solution semiflow generated by system (1.4) on P_1. It follows from the standard parabolic regularity theory that Φ_t is compact for any $t > 0$. By Lemma 3.2, we have that Φ_t is point dissipative. Then it follows from ref. [36, Theorem 2.6] that Φ_t has a global compact attractor that attracts each bounded set in P_1.

Let $M'_\partial = \left\{ (S_0, u_0) \in \partial P_1^0 : \Phi_t(S_0, u_0) \in \partial P_1^0,\ \forall\ t \ge 0 \right\}$ and $\omega_1((S_0, u_0))$ be the omega limit set of the forward orbit $\gamma_1^+((S_0, u_0)) := \{\Phi_t(S_0, u_0) : t \ge 0\}$. We then claim that

$$\cup_{(S_0,u_0)\in M'_\partial} \omega_1((S_0, u_0)) = \{(z, 0)\}.$$

In fact, for any $(S_0, u_0) \in M'_\partial$, we have $\Phi_t(S_0, u_0) \in \partial P_1^0$ for all $t \geq 0$. Hence, $u(x, y, t) \equiv 0$ on $\overline{\Omega}$ for all $t \geq 0$. Then $S(x, y, t)$ satisfies system (2.7). It follows that $\lim_{t\to+\infty} S(\cdot, \cdot, t) = z$ uniformly on $\overline{\Omega}$. This claim is valid.

We now show that $(z, 0)$ is a uniform weak repeller. That is, there exists $\delta_0 > 0$ such that for all $(S_0, u_0) \in P_1^0$,

$$\limsup_{t\to+\infty} \|\Phi_t(S_0, u_0) - (z, 0)\|_\infty \geq \delta_0.$$

If not, then for any $\delta > 0$, there exists $(S_0, u_0) \in P_1^0$ such that $\limsup_{t\to+\infty} \|\Phi_t(S_0, u_0) - (z, 0)\|_\infty < \delta$. This implies that there exists $t_0 > 0$ such that for $t > t_0$,

$$\|S(\cdot, \cdot, t) - z\|_\infty < \delta, \ \|u(\cdot, \cdot, t)\|_\infty < \delta. \tag{3.7}$$

By the continuity of function $f_1(S)$, we can choose $\epsilon > 0$ small such that for all $(x, y) \in \overline{\Omega}$ and $t \geq t_0$, $f_1(S) > f_1(z) - \epsilon$. Thus, we obtain

$$u_t \geq D(p)u_{xx} + D(1-p)u_{yy} + \big(f_1(z) - \epsilon\big)u \quad \text{in } \Omega \times (t_0, +\infty).$$

In view of $(S_0, u_0) \in P_1^0$, it follows from the maximum principle that $u(x, y, t_0) > 0$ for all $(x, y) \in \overline{\Omega}$. Hence, there exists $\kappa > 0$ such that $u(\cdot, \cdot, t_0) \geq \kappa\varphi_1$, where $\varphi_1 := \varphi_1(p, f_1(z))$ is the principal eigenfunction of problem (2.10) corresponding to the principal eigenvalue $\lambda_1 := \lambda_1(p, f_1(z))$. Let $\tilde{u}(x, y, t) = \kappa e^{(\lambda_1+\epsilon)(t_0-t)}\varphi_1(x, y)$ for all $(x, y) \in \overline{\Omega}$ and $t \geq t_0$. Then $\tilde{u}$ satisfies

$$\begin{aligned} \tilde{u}_t &= D(p)\tilde{u}_{xx} + D(1-p)\tilde{u}_{yy} + \big(f_1(z) - \epsilon\big)\tilde{u} && \text{in } \Omega \times (t_0, +\infty), \\ \big(D(p)\tilde{u}_x, D(1-p)\tilde{u}_y\big) \cdot \nu + b(x, y)\tilde{u} &= 0 && \text{on } \partial\Omega \times (t_0, +\infty), \\ \tilde{u}(x, y, t_0) &= \kappa\varphi_1(x, y) && \text{on } \bar{\Omega}. \end{aligned}$$

By the comparison principle for parabolic equations, we conclude that $u(x, y, t) \geq \tilde{u}(x, y, t)$ for all $(x, y) \in \overline{\Omega}$ and $t \geq t_0$. Since $\lambda_1(p, f_1(z)) < 0$, we can choose $\epsilon > 0$ small such that $\lambda_1(p, f_1(z)) + \epsilon < 0$. This implies that $\lim_{t\to+\infty} u(\cdot, \cdot, t) = +\infty$, which contradicts (3.7). Hence, $(z, 0)$ is a uniform weak repeller and $\{(z, 0)\}$ is an isolated invariant set in P_1.

Define a continuous function $\mathcal{D}_1 : P_1 \to [0, +\infty)$ by $\mathcal{D}_1(S, u) := \min_{\overline{\Omega}} u(x, y)$ for any $(S, u) \in P_1$. It is easy to see that $\mathcal{D}_1^{-1}(0, +\infty) \subseteq P_1^0$, and $\mathcal{D}_1$ satisfies the condition that if $\mathcal{D}_1((S, u)) > 0$ or $(S, u) \in P_1^0$ with $\mathcal{D}_1((S, u)) = 0$, then $\mathcal{D}_1(\Phi_t(S, u)) > 0$ for all $t > 0$. Thus $\mathcal{D}_1$ is a generalized distance function for the semiflow $\Phi_t : P_1 \to P_1$ [35]. Moreover, the stable set $W^s(\{(z, 0)\}) \cap \mathcal{D}_1^{-1}(0, +\infty) = \emptyset$. Therefore, no subset of $\{(z, 0)\}$ forms a cycle in M'_∂. It follows from [ref. 35, Theorem 3] that there exists $\epsilon_2 > 0$ such that

$$\min_{(S,u)\in\omega_1((S_0,u_0))} \mathcal{D}_1((S, u)) > \epsilon_2,$$

which implies that for any $(S_0, u_0) \in P_1^0$, $\liminf_{t\to+\infty} u(\cdot, \cdot, t) \geq \epsilon_2$ uniformly on $\overline{\Omega}$. Set $\epsilon = \min\{\epsilon_1, \epsilon_2\}$. This completes the proof. □

For another single-species model (1.5), analogous results can be obtained by similar arguments.

Theorem 3.5. *For system* (1.5)*, one of the following statements is valid.*
(i) *Assume that* $\lambda_1(q, f_2(z)) > 0$*; see* Table 2. *Then the steady state* $(z, 0)$ *of system* (1.5) *is globally asymptotically stable.*
(ii) *Assume that* $\lambda_1(q, f_2(z)) < 0$*; see* Table 2. *Then system* (1.5) *is uniformly persistent.*

3.2 Further study on positive steady states

In order to better understand the coexistence states of system (1.4), we further study the following steady-state system.

$$\begin{aligned} &D_0\Delta S - f_1(S)u = 0, \\ &D(p)u_{xx} + D(1-p)u_{yy} + f_1(S)u = 0 \qquad \text{in } \Omega, \\ &D_0\nabla S\cdot\nu + b(x,y)S = H(x,y), \\ &\big(D(p)u_x, D(1-p)u_y\big)\cdot\nu + b(x,y)u = 0 \quad \text{on } \partial\Omega. \end{aligned} \tag{3.8}$$

We first derive *a priori* estimates for the positive solutions to system (3.8).

Lemma 3.6. *Assume that* (S,u) *is a nonnegative solution to system* (3.8) *with* $S \not\equiv 0$ *and* $u \not\equiv 0$. *Then*
(i) $\lambda_1(p, f_1(z)) < 0$;
(ii) $0 < S < z$, *and there exists a positive constant* C *such that* $0 < u < C$ *on* $\overline{\Omega}$.

Proof. It is easy to see that $S > 0$, $u > 0$ on $\overline{\Omega}$ by the strong maximum principle. By the equation for S, we have

$$0 = D_0\Delta S - f_1(S)u < D_0\Delta S.$$

Noting that z is the unique positive steady state of system (2.7), we conclude that $S < z$ by the upper and lower solution method.

By the equation for u, we have $\lambda_1(p, f_1(S)) = 0$. In view of Lemma 2.2(ii) and $0 < S < z$, we have

$$\lambda_1(p, f_1(z)) < \lambda_1(p, f_1(S)) = 0.$$

By applying integration by parts to the first two equations of system (3.8) over Ω, we obtain

$$\int_{\partial\Omega} bu = \int_{\partial\Omega} (H - bS).$$

Clearly, there exist a constant $\epsilon > 0$ and a non-empty subset $\Gamma_2^\epsilon \subset \Gamma_2$ (recall that $b(x,y) > 0$ in Γ_2) such that $b(x,y) \geq \epsilon$ on $\overline{\Gamma_2^\epsilon}$. Thus, we have

$$\epsilon\int_{\Gamma_2^\epsilon} u \leq \int_{\partial\Omega} bu = \int_{\partial\Omega} (H - bS) \leq \int_{\partial\Omega} H.$$

This implies that there exists $C_0 > 0$ such that $\min_{\overline{\Omega}} u \leq \min_{\overline{\Gamma_2^\epsilon}} u \leq C_0$. Note that the domain $\Omega \subset \mathbb{R}^2$ is assumed to be bounded and strictly convex, and its boundary $\partial\Omega$ is a $C^{2+\alpha}$ smooth curve. The Harnack inequality implies the existence of a constant $C_1 > 0$ such that $\max_{\overline{\Omega}} u \leq C_1 \min_{\overline{\Omega}} u$. Therefore, there exists a constant $C > 0$ satisfying $0 < u < C$ throughout $\overline{\Omega}$. □

Next, we analyze the structure and linear stability of the nonnegative solutions to the steady-state system (3.8) using a bifurcation approach; see, e.g., [32], [37]. Taking p as the bifurcation parameter, we construct a positive solution branch that bifurcates from the semi-trivial branch $\Gamma_p := \{(p, z, 0) : p \in [0,1]\}$. By Proposition 2.8, we have that for $D_0 = D_1^*$, the critical value p^* satisfies $p^* \in \left[0, \frac{1}{2}\right)$ if $F_1 < 0$, and $p^* \in \left(\frac{1}{2}, 1\right]$ if $F_1 > 0$. We define

$$\underline{p} := \min\left\{p^*, \frac{1}{2}\right\}, \ \overline{p} := \max\left\{p^*, \frac{1}{2}\right\}.$$

To facilitate the understanding of the bifurcation phenomena described in Theorems 3.7–3.9, we present schematic bifurcation diagrams illustrating two representative scenarios for the solutions (S, u) of system (3.8), with respect to the parameters p and D_0; see Figure 1.

Theorem 3.7. *Assume that $D_0 = D_1^*$ and $F_1 \neq 0$. Then one of the following statements is valid.*

(i) *If $p^* = 0$ (respectively, $p^* = 1$), then system* (3.8) *admits a continuum of positive solutions that bifurcates from the semi-trivial solution branch Γ_p at $\left(\frac{1}{2}, z, 0\right)$. This continuum can be extended to the plane $\{(1, S, u): S > 0, u > 0 \text{ on } \bar{\Omega}\}$ (respectively, $\{(0, S, u): S > 0, u > 0 \text{ on } \bar{\Omega}\}$).*

(ii) *If $0 < p^* < 1$, then there exist two continua of positive solutions to system* (3.8)*, bifurcating from the semi-trivial solution branch Γ_p at the points $(\underline{p}, z, 0)$ and $(\overline{p}, z, 0)$, respectively. Each of these continua can be extended to the planes $\{(0, S, u): S > 0, u > 0 \text{ on } \bar{\Omega}\}$ and $\{(1, S, u): S > 0, u > 0 \text{ on } \bar{\Omega}\}$, respectively.*

That is, system (3.8) *has at least one positive solution if and only if $p \in [0, 1] \setminus [\underline{p}, \overline{p}]$. Furthermore, if $p \in [0, 1]$ is sufficiently close to $\frac{1}{2}$ or p^*, then the positive solution is linearly stable.*

Remark 3.8. If $F_1 = 0$, then $\underline{p} = \overline{p} = \frac{1}{2}$, and consequently, $\lambda_1(p, f_1(z)) < 0$ for any $p \in [0, 1] \setminus \{\frac{1}{2}\}$; see Table 1. Since system (3.8) is continuous in all parameters within the specified range, it can be concluded that system (3.8) admits at least one positive solution if and only if $p \in [0, 1] \setminus \{\frac{1}{2}\}$, and the positive solution is linearly stable if p is sufficiently close to $\frac{1}{2}$.

Proof of Theorem 3.7. It is easy to see that $F_1 \neq 0$ implies that $p^* \neq \frac{1}{2}$, and if $0 < p^* < 1$, then $\lambda_1(p^*, f_1(z)) = 0$. By Lemma 2.1, we deduce that necessarily $F\left(p^*; f_1(z)\right) \neq 0$. Hence, we can prove that both $\left(\frac{1}{2}, z, 0\right)$ and $\left(p^*, z, 0\right)$ are bifurcation points with respect to Γ_p. For brevity, we present the proof only for $\left(\frac{1}{2}, z, 0\right)$, as the case of $\left(p^*, z, 0\right)$ can be treated analogously. To enhance clarity, the proof is structured in three distinct steps.

Step 1. Local bifurcation. Let $w = z - S$. Then system (3.8) is equivalent to

$$\begin{aligned} D_0 \Delta w + f_1(z - w)u &= 0, \\ D(p)u_{xx} + D(1-p)u_{yy} + f_1(z - w)u &= 0 \qquad \text{in } \Omega, \\ D_0 \nabla w \cdot \nu + b(x, y)w &= 0, \\ \left(D(p)u_x, D(1-p)u_y\right) \cdot \nu + b(x, y)u &= 0 \quad \text{on } \partial\Omega. \end{aligned} \tag{3.9}$$

Here w and u in the boundary conditions are interpreted as the traces of $w \in W^{2,r}(\Omega)$ and $u \in W^{2,r}(\Omega)$ on $\partial\Omega$; see, e.g., [24, Theorem 1.6] and Remarks there. Define $T_1: (0, 1) \times X_1 \to Y_1 \times \left[W^{1,r}(\partial\Omega)\right]^2$ by

$$T_1(p, w, u) = \begin{pmatrix} D_0 \Delta w + f_1(z - w)u \\ D(p)u_{xx} + D(1-p)u_{yy} + f_1(z - w)u \\ D_0 \nabla w \cdot \nu + b(x, y)w \\ (D(p)u_x, D(1-p)u_y) \cdot \nu + b(x, y)u \end{pmatrix}, \tag{3.10}$$

where $X_1 = \left[W^{2,r}(\Omega)\right]^2$ and $Y_1 = \left[L^r(\Omega)\right]^2$ with $r \in (1, \infty)$. Then $W^{2,r}(\Omega)$ embeds compactly in $C(\overline{\Omega})$; see, e.g., [24, Theorem 1.7]. Let $D_{(w,u)}T_1(p, 0, 0)$ be the Fréchet derivative of $T_1(p, w, u)$ with respect to (w, u) at (0, 0). It is easy to see that $D_{(w,u)}T_1(p, 0, 0)$ is a Fredholm operator with index zero.

Set $D_{(w,u)}T_1(\frac{1}{2},0,0)(\phi,\psi)^\top = \mathbf{0}$ with $(\phi,\psi) \neq (0,0)$, i.e.,

$$\begin{aligned} D_0\Delta\phi + f_1(z)\psi &= 0, \\ D_0\Delta\psi + f_1(z)\psi &= 0 \qquad \text{in } \Omega, \\ D_0\nabla\phi\cdot\nu + b(x,y)\phi &= 0, \\ D_0\nabla\psi\cdot\nu + b(x,y)\psi &= 0 \quad \text{on } \partial\Omega. \end{aligned}$$

By Lemma 2.3, we have $\lambda_1\left(\frac{1}{2}, f_1(z)\right) = 0$. Thus, the kernal of $D_{(w,u)}T_1\left(\frac{1}{2},0,0\right)$ is

$$\mathcal{N}\left(D_{(w,u)}T_1\left(\frac{1}{2},0,0\right)\right) = \operatorname{span}\{(\phi_0,\psi_0)\}.$$

Here ψ_0 is a positive principal eigenfunction of problem (2.1) with $p=\frac{1}{2}$ and $h=f_1(z)$. The variational characterization of $\lambda_1\left(\frac{1}{2},0\right)$ (see, e.g., equation (2.2)) implies that $\lambda_1\left(\frac{1}{2},0\right)>0$. Thus, we have $\phi_0 = \left(D_0\Delta\right)^{-1}\left(-f_1(z)\psi_0\right)$ with the boundary conditions $D_0\nabla\phi_0\cdot\nu + b(x,y)\phi_0 = 0$, and $\phi_0 > 0$ on $\overline{\Omega}$ by the general maximum principle [38].

We next claim that the rangle of $D_{(w,u)}T_1\left(\frac{1}{2},0,0\right)$ is

$$\mathcal{R}\left(D_{(w,u)}T_1\left(\frac{1}{2},0,0\right)\right) = \left\{(\phi^*,\psi^*,\xi_1,\xi_2) \in Y_1\times\left[W^{1,r}(\partial\Omega)\right]^2 : l_1(\phi^*,\psi^*,\xi_1,\xi_2) = 0\right\},$$

where $l_1 : Y_1\times\left[W^{1,r}(\partial\Omega)\right]^2 \to \mathbb{R}$ is a linear functional in $\left(Y_1\times\left[W^{1,r}(\partial\Omega)\right]^2\right)^*$ defined by

$$l_1(\phi^*,\psi^*,\xi_1,\xi_2) = \int_\Omega \psi^*\psi_0 - \int_{\partial\Omega}\xi_2\psi_0.$$

In order to prove this claim, we need to consider the following problem

$$\begin{aligned} D_0\Delta\phi + f_1(z)\psi &= \phi^*, \\ D_0\Delta\psi + f_1(z)\psi &= \psi^* \qquad \text{in } \Omega, \\ D_0\nabla\phi\cdot\nu + b(x,y)\phi &= \xi_1, \\ D_0\nabla\psi\cdot\nu + b(x,y)\psi &= \xi_2 \quad \text{on } \partial\Omega. \end{aligned} \tag{3.11}$$

We begin by examining the problem

$$\begin{aligned} D_0\Delta\psi + f_1(z)\psi &= \psi^* \qquad \text{in } \Omega, \\ D_0\nabla\psi\cdot\nu + b(x,y)\psi &= \xi_2 \quad \text{on } \partial\Omega. \end{aligned} \tag{3.12}$$

Clearly, there exists a constant $M>0$ such that $M - f_1(z) > 0$ on $\overline{\Omega}$. Problem (3.12) is equivalent to

$$\begin{aligned} -D_0\Delta\psi + \left(M - f_1(z)\right)\psi &= M\psi - \psi^* \qquad \text{in } \Omega, \\ D_0\nabla\psi\cdot\nu + b(x,y)\psi &= \xi_2 \quad \text{on } \partial\Omega. \end{aligned}$$

It follows from the standard elliptic regularity theory (see, e.g., [24, Theorem 1.6]) that for any $\xi_2 \in W^{1,r}(\partial\Omega)$, the following problem

$$\begin{aligned} -D_0\Delta\psi + \left(M - f_1(z)\right)\psi &= 0 \qquad \text{in } \Omega, \\ D_0\nabla\psi\cdot\nu + b(x,y)\psi &= \xi_2 \quad \text{on } \partial\Omega \end{aligned}$$

has a unique solution $\psi \in W^{2,r}(\Omega)$, denoted by ψ_1. Setting $\tilde{\psi} := \psi - \psi_1$, we have

$$\begin{aligned} -D_0\Delta\tilde{\psi} + \big(M - f_1(z)\big)\tilde{\psi} &= M\psi - \psi^* \quad \text{in } \Omega, \\ D_0\nabla\tilde{\psi}\cdot\nu + b(x,y)\tilde{\psi} &= 0 \quad \text{on } \partial\Omega. \end{aligned} \tag{3.13}$$

Denote

$$K := M\big(-D_0\Delta + M - f_1(z)\big)^{-1} \text{ and } \Psi := M(\tilde{\psi} + \psi_1) - \psi^*,$$

where $K: L^r(\Omega) \to W^{2,r}(\Omega)$ with $r \in (1, \infty)$. The Rellich–Kondrachov theorem implies that for any r, $W^{1,r}(\Omega)$ embeds compactly in $L^r(\Omega)$; see, e.g., [39, Theorem 9.16]. Thus, K is compact on $L^r(\Omega)$. Then problem (3.13) is equivalent to

$$(I - K)\Psi = M\psi_1 - \psi^*. \tag{3.14}$$

Note that ψ_0 satisfies

$$\begin{aligned} D_0\Delta\psi_0 + f_1(z)\psi_0 &= 0 \quad \text{in } \Omega, \\ D_0\nabla\psi_0\cdot\nu + b(x,y)\psi_0 &= 0 \quad \text{on } \partial\Omega. \end{aligned} \tag{3.15}$$

By direct computation, we have that with the boundary conditions $D_0\nabla\psi\cdot\nu + b(x,y)\psi = 0$,

$$\mathcal{N}(I - K^*) = \mathcal{N}\Big(\big(-D_0\Delta - f_1(z)\big)^*\Big) = \operatorname{span}\{\psi_0\}.$$

It follows from the Fredholm alternative theorem (see, e.g., [39, Theorem 6.6]) that equation (3.14) has a solution if and only if

$$\langle\psi_0, M\psi_1 - \psi^*\rangle = \int_\Omega \big(M\psi_1 - \psi^*\big)\psi_0 = 0,$$

where $\langle , \rangle$ denotes the scalar product in the duality pairing. Here

$$\int_\Omega M\psi_1\psi_0 = \int_\Omega \big(D_0\Delta\psi_1 + f_1(z)\psi_1\big)\psi_0 = \int_{\partial\Omega} \xi_2\psi_0.$$

Therefore, problem (3.12) has a solution $\psi = \tilde{\psi} + \psi_1$ if and only if $\int_\Omega \psi^*\psi_0 - \int_{\partial\Omega}\xi_2\psi_0 = 0$. By the standard elliptic regularity theory, we conclude that for any $\phi^* \in L^r(\Omega)$, $\psi \in W^{2,r}(\Omega)$ and $\xi_1 \in W^{1,r}(\partial\Omega)$, the following problem

$$\begin{aligned} D_0\Delta\phi &= \phi^* - f_1(z)\psi \quad \text{in } \Omega, \\ D_0\nabla\phi\cdot\nu + b(x,y)\phi &= \xi_1 \quad \text{on } \partial\Omega \end{aligned}$$

has a unique solution $\phi \in W^{2,r}(\Omega)$. This completes the proof of the claim.

We then check the transversality condition

$$D_{p(w,u)}T_1\Big(\frac{1}{2}, 0, 0\Big)(\phi_0, \psi_0)^\top \notin \mathcal{R}\Big(D_{(w,u)}T_1\Big(\frac{1}{2}, 0, 0\Big)\Big).$$

Direct computation gives

$$D_{p(w,u)}T_1\Big(\frac{1}{2}, 0, 0\Big)(\phi_0, \psi_0)^\top = \begin{pmatrix} 0 \\ \big(\overline{D} - \underline{D}\big)\big((\psi_0)_{xx} - (\psi_0)_{yy}\big) \\ 0 \\ \big(\overline{D} - \underline{D}\big)\big((\psi_0)_x, -(\psi_0)_y\big)\cdot\nu \end{pmatrix}.$$

and

$$l_1\Big(D_{p(w,u)}T_1\Big(\frac{1}{2}, 0, 0\Big)(\phi_0, \psi_0)^\top\Big) = -\big(\overline{D} - \underline{D}\big)\int_\Omega \Big(\big((\psi_0)_x\big)^2 - \big((\psi_0)_y\big)^2\Big).$$

If $F_1 \neq 0$, then

$$l_1\Big(D_{p(w,u)}T_1\Big(\frac{1}{2}, 0, 0\Big)(\phi_0, \psi_0)^\top\Big) \neq 0.$$

Thus, the transversality condition is satisfied.

Let

$$Z_1 = \left\{ (\Phi, \Psi) \in X_1 \colon \int_\Omega \Psi \psi_0 = 0 \right\}.$$

Then $\operatorname{span}\{(\phi_0, \psi_0)\} \oplus Z_1 = X_1$. By applying the standard bifurcation theorem from a simple eigenvalue [40], we conclude that there exist $s_0 > 0$ and C^1 curve

$$\big(p(s), \Phi(s), \Psi(s)\big) \colon (-s_0, s_0) \to \mathbb{R} \times Z_1,$$

such that (i) $p(0) = \frac{1}{2}$, (ii) $\Phi(0) = 0$, $\Psi(0) = 0$, (iii) $T_1\big(p(s), w(s), u(s)\big) = 0$ for $|s| < s_0$, where

$$\big(p(s), w(s), u(s)\big) = \big(p(s), s(\phi_0 + \Phi(s)), s(\psi_0 + \Psi(s))\big).$$

Let $S(s) = z - w(s)$. Noting that $\phi_0, \psi_0 > 0$ on $\overline{\Omega}$, we conclude that the bifurcation branch

$$\Gamma_1^+ = \big\{ \big(p(s), S(s), u(s)\big) \colon 0 < s < s_0 \big\}$$

is exactly the positive solution to system (3.8).

Lemma 3.6(i) implies that there is no positive solution to system (3.8) when $\lambda_1(p, f_1(z)) \geq 0$. Thus, we conclude that for $0 < s < s_0$, the derivative $p'(s) < 0$ when $F\big(\frac{1}{2}; f_1(z)\big) > 0$, and $p'(s) > 0$ when $F\big(\frac{1}{2}; f_1(z)\big) < 0$. This implies that

(a) if $F\big(\frac{1}{2}; f_1(z)\big) > 0$, then the positive solution branch Γ_1^+ lies to the left, which implies that there exists $\sigma_- > 0$ small such that system (3.8) has at least one positive solution when $p \in \big(\frac{1}{2} - \sigma_-, \frac{1}{2}\big)$;

(b) if $F\big(\frac{1}{2}; f_1(z)\big) < 0$, then the positive solution branch Γ_1^+ lies to the right, which implies that there exists $\sigma_+ > 0$ small such that system (3.8) has at least one positive solution when $p \in \big(\frac{1}{2}, \frac{1}{2} + \sigma_+\big)$.

Step 2. Local stability. We then investigate the linear stability of the bifurcation solutions lying on the local branch Γ_1^+. Based on Step 1 of this proof, it is easy to see that 0 is an I_0-simple eigenvalue of $D_{(w,u)}T_1\big(\frac{1}{2}, 0, 0\big)$, where the map $I_0 \colon X_1 \to Y_1 \times \big[W^{1,r}(\partial\Omega)\big]^2$ is defined by $I_0(\phi, \psi) = (\phi, \psi, 0, 0)$. Then by [41, Corollary 1.13], there exist continuously differentiable functions

$$p \mapsto (\rho_1(p), \mathbf{u}_1(p)), \;\; s \mapsto (\varrho_1(s), \mathbf{v}_1(s))$$

defined on the eighborhoods of $p = \frac{1}{2}$ and $s = 0$, respectively, mapping onto $\mathbb{R} \times X_1$, such that

$$\rho_1\Big(\frac{1}{2}\Big) = 0, \;\; \mathbf{u}_1\Big(\frac{1}{2}\Big) = (\phi_0, \psi_0)^\top, \;\; \varrho_1(0) = 0, \;\; \mathbf{v}_1(0) = (\phi_0, \psi_0)^\top,$$

and

$$\begin{aligned} &D_{(w,u)}T_1(p, 0, 0)\mathbf{u}_1(p) = (\rho_1(p)\mathbf{u}_1(p), \mathbf{0})^\top && \text{for } \Big|p - \frac{1}{2}\Big| \ll 1, \\ &D_{(w,u)}T_1(p(s), w(s), u(s))\mathbf{v}_1(s) = (\varrho_1(s)\mathbf{v}_1(s), \mathbf{0})^\top && \text{for } |s| \ll 1. \end{aligned}$$

It follows from ref. [41, Theorem 1.16] that $\rho_1'\big(\frac{1}{2}\big) \neq 0$. Furthermore, for $|s| \ll 1$, if $\varrho_1(s) \neq 0$, then $\varrho_1(s)$ has the same sign as $-sp'(s)\rho_1'\big(\frac{1}{2}\big)$.

Noting that $\mathbf{u}_1(p) = (\phi(p), \psi(p))$ satisfies

$$\begin{aligned} D_0\Delta\phi(p) + f_1(z)\psi(p) &= \rho_1(p)\phi(p), \\ D(p)\big(\psi(p)\big)_{xx} + D(1-p)\big(\psi(p)\big)_{yy} + f_1(z)\psi(p) &= \rho_1(p)\psi(p) \qquad \text{in } \Omega, \\ D_0\nabla\phi(p)\cdot\nu + b(x,y)\phi(p) &= 0, \\ \big(D(p)(\psi(p))_x, D(1-p)(\psi(p))_y\big)\cdot\nu + b(x,y)\psi(p) &= 0 \quad \text{on } \partial\Omega, \end{aligned} \tag{3.16}$$

we have $\psi(p) > 0$ for $|p - \frac{1}{2}| \ll 1$ since $\psi\left(\frac{1}{2}\right) = \psi_0 > 0$. Hence, $\rho_1(p)$ is the principal eigenvalue of the second equation in (3.16), i.e., $\rho_1(p) = -\lambda_1(p, f_1(z))$ when $|p - \frac{1}{2}| \ll 1$. Recalling equation (2.4), we have that

$$\rho_1'\left(\frac{1}{2}\right) = -\frac{\partial\lambda_1(p, f_1(z))}{\partial p}\bigg|_{p=\frac{1}{2}} = -\left(\overline{D} - \underline{D}\right)F\left(\frac{1}{2}; f_1(z)\right).$$

It follows from Step 1 of this proof that for $0 < s < s_0$, the derivative $p'(s) < 0$ when $F\left(\frac{1}{2}; f_1(z)\right) > 0$, and $p'(s) > 0$ when $F\left(\frac{1}{2}; f_1(z)\right) < 0$. We then conclude that for $0 < s < s_0$,

(a) if $F\left(\frac{1}{2}; f_1(z)\right) > 0$, then $\rho_1'\left(\frac{1}{2}\right) < 0$ and $p'(s) < 0$, which implies $\varrho_1(s) < 0$;

(b) if $F\left(\frac{1}{2}; f_1(z)\right) < 0$, then $\rho_1'\left(\frac{1}{2}\right) > 0$ and $p'(s) > 0$, which implies $\varrho_1(s) < 0$.

Therefore, the bifurcation solutions to system (3.8) that lie on the local branch Γ_1^+ are linearly stable.

Step 3. Global bifurcation. By invoking the global bifurcation framework for Fredholm operators [42], the local branch Γ_1^+ is extended to a global branch.

By [40, Theorem 3.3], we conclude that for any $(p, w, u) \in (0,1)\times X_1$, the Fréchet derivative $D_{(w,u)}T_1(p, w, u)$ is a Fredholm operator with index zero and $T_1: (0,1)\times X_1 \to Y_1 \times \left[W^{1,r}(\partial\Omega)\right]^2$ is C^1 smooth. Similar to the definition in ref. [42, Theorem 1.2], let C_0 be the component of the set of nontrivial solutions to $T_1(p, w, u) = 0$, such that $\left(\frac{1}{2}, 0, 0\right) \in C_0$. Set

$$C_1 = \{(p, S, u): S = z - w, (p, w, u) \in C_0\}.$$

Let C_1^+ be the connected component of $C_1 \backslash \{(p(s), S(s), u(s)): -s_1 < s < 0\}$. Then $\Gamma_1^+ \subset C_1^+$. It follows from ref. [42, Theorem 1.2] that C_1^+ satisfies one of the following alternatives:

(i) it is not compact in $(0,1)\times X_1$;

(ii) it contains a point $(\tilde{p}, z, 0)$ with $\tilde{p} \neq \frac{1}{2}$;

(iii) it contains a point $(p, z + \Phi, \Psi)$, where $(\Phi, \Psi) \not\equiv (0, 0)$ and $(\Phi, \Psi) \in Z_1$.

We define

$$X_1^+ = \left\{(S, u) \in X_1: S > 0, u > 0 \quad \text{on } \overline{\Omega}\right\}.$$

Consequently, we have $C_1 \cap ((0,1)\times X_1^+) \neq \emptyset$. Let $C_1^* = C_1 \cap ((0,1)\times X_1^+)$. Then C_1^* consists of the local positive solution branch Γ_1^+ near the bifurcation point $\left(\frac{1}{2}, z, 0\right)$ and $C_1^* \subset C_1^+$.

Suppose (iii) holds. For any $(p, z + \Phi, \Psi) \in C_1^+$ with $(\Phi, \Psi) \not\equiv (0, 0)$, we have $(p, z + \Phi, \Psi) \in C_1^*$, which implies that $\Psi > 0$ on $\overline{\Omega}$. Hence, $\int_\Omega \Psi\psi_0 > 0$, which contradicts $(\Phi, \Psi) \in Z_1$. Therefore, (iii) is impossible.

Suppose (ii) holds. Then there exists a sequence of points $\{(p_n, S_n, u_n)\} \subset C_1^*$, which converges to $(\tilde{p}, z, 0)$ on $(0,1)\times\overline{X_1^+}$. By the equation for u_n in system (3.8), we have $\lambda_1(p_n, f_1(S_n)) = 0$. Letting $n \to \infty$, we get $\lambda_1(\tilde{p}, f_1(z)) = 0$ by continuity. Recall that $\lambda_1\left(\frac{1}{2}, f_1(z)\right) = 0$. Without loss of generality, we assume $\tilde{p} > \frac{1}{2}$. It follows from Lemma 2.1 that $\lambda_1(p, f_1(z)) > 0$ for all $p \in \left(\frac{1}{2}, \tilde{p}\right)$. However, by Lemma 3.6(i), we have that if there exists $p_0 \in \left(\frac{1}{2}, \tilde{p}\right)$ such that $(p_0, S, u) \in C_1^*$, then $\lambda_1(p_0, f_1(z)) < 0$, which is a contradiction. Hence, the component C_1^+ cannot connect $\left(\frac{1}{2}, z, 0\right)$ and $(\tilde{p}, z, 0)$ in $(0,1)\times X_1$, meaning that $(\tilde{p}, z, 0) \notin C_1^+$. Thus, (ii) can not occur.

The alternative (i) for C_1^+ is equivalent to "the closure of C_1^+ intersects $\partial((0,1)\times X_1^+)$ or is unbounded in norm of $(0,1)\times X_1^+$". It follows from Lemma 3.6 and the standard elliptic regularity theory that any positive solution (S,u) to system (3.8) remains bounded in X_1^+ uniformly for all $p\in[0,1]$. Thus, (i) implies that there exists a point $(\tilde p,\tilde S,\tilde u)\in\left(\overline{C_1^*}\backslash\{\left(\frac{1}{2},z,0\right)\}\right)\cap\partial\left((0,1)\times X_1^+\right)$, which is the limit of a sequence $\{(p_n,S_n,u_n)\}\subset C_1^*$. We only consider the case where $F_1>0$, i.e.,

$$F_1=\frac{1}{\overline{D}-\underline{D}}\frac{\partial\lambda_1(p,f_1(z))}{\partial p}\bigg|_{p=\frac{1}{2}}>0.$$

A similar analysis can be applied to another case where $F_1<0$. If $F_1>0$, then there exists $\epsilon>0$ such that $\lambda_1(p,f_1(z))>0$ for all $p\in\left(\frac{1}{2},\frac{1}{2}+\epsilon\right)$. This implies that there is no point $(p,S,u)\in C_1^*$ for $p\in\left(\frac{1}{2},\frac{1}{2}+\epsilon\right)$, and that $\tilde p$ satisfies $0\le\tilde p<\frac{1}{2}$, which in turn implies that $\lambda_1(\tilde p,f_1(z))<0$. Hence, $(\tilde p,\tilde S,\tilde u)\in\partial\left((0,1)\times X_1^+\right)$ implies that:

(1) $\tilde S\ge0$ and $\tilde S(x_0,y_0)=0$ for a point $(x_0,y_0)\in\overline{\Omega}$; or
(2) $\tilde u\ge0$ and $\tilde u(x_1,y_1)=0$ for a point $(x_1,y_1)\in\overline{\Omega}$; or
(3) $\tilde p=0$ and $\tilde S>0,\tilde u>0$ on $\overline{\Omega}$, i.e., $(\tilde S,\tilde u)\in X_1^+$.

It follows from the strong maximum principle that $\tilde S>0$ on $\overline{\Omega}$. Hence, (1) is impossible. By applying the strong maximum principle again, we conclude that (2) implies $\tilde u\equiv0$, which leads to $(\tilde S,\tilde u)=(z,0)$.

Suppose $(\tilde S,\tilde u)=(z,0)$. Then the sequence $\{(p_n,S_n,u_n)\}$ satisfies $p_n\to\tilde p$ and $(S_n,u_n)\to(z,0)$ in X_1 as $n\to\infty$. By the equation for u_n in system (3.8), we have $\lambda_1(p_n,f_1(S_n))=0$. Letting $n\to\infty$, we get $\lambda_1(\tilde p,f_1(z))=0$ by continuity, which contradicts $\lambda_1(\tilde p,f_1(z))<0$.

The remainning possibility is $\tilde p=0$ with $\tilde S>0,\tilde u>0$ on $\overline{\Omega}$, which implies that the global bifurcation branch C_1^+ meets the plane $\{(0,S,u):S>0,u>0\quad\text{on }\overline{\Omega}\}$ at the point $(0,\tilde S,\tilde u)$ as $p\to0$. This completes the proof. □

By arguments similar to those in the proof of Theorem 3.7, and recalling Propositions 2.9 and 2.10 (or Table 1), we derive the following conclusions.

Theorem 3.9. *One of the following statements is valid.*

(i) *Assume that $D_0>D_1^*$ and $0\le p_0^*<\frac{1}{2}<p_1^*\le1$. Then system* (3.8) *has at least one positive solution if and only if $p\in[0,1]\backslash\left[p_0^*,p_1^*\right]$. Furthermore, if p is sufficiently close to p_0^* or p_1^*, then the positive solution is linearly stable.*

(ii) *Assume that $0<D_0<D_1^*$, and that there exist p_-^* and p_+^* such that either $0\le p_-^*<p_+^*<\frac{1}{2}$ or $\frac{1}{2}<p_-^*<p_+^*\le1$. Then system* (3.8) *has at least one positive solution if and only if $p\in[0,1]\backslash\left[p_-^*,p_+^*\right]$. Furthermore, if p is sufficiently close to p_-^* or p_+^*, then the positive solution is linearly stable. In particular, if $p=\frac{1}{2}$, then $(z-\theta_1,\theta_1)$ is the unique globally attractive positive solution, as stated in Lemma* 2.7.

Remark 3.10. In case (i) where $D_0>D_1^*$, if $p_0^*=0$ and $p_1^*=1$, then the set $[0,1]\backslash\left[p_0^*,p_1^*\right]$ is empty. Consequently, system (3.8) admits no positive solution for any $p\in(0,1)$. By arguments similar to those in Remark 3.8, in case (ii) where $0<D_0<D_1^*$, if there exists $p_\pm^*\in\left(0,\frac{1}{2}\right)\cup\left(\frac{1}{2},1\right)$ such that $p_\pm^*=p_-^*=p_+^*$, then system (3.8) admits at least one positive solution if and only if $p\in[0,1]\backslash\left\{p_\pm^*\right\}$, and the positive solution is linearly stable if p is sufficiently close to $p_\pm^*$.

Consider another single-species steady state model

$$\begin{aligned} D_0\Delta S - f_2(S)v &= 0, \\ D(q)v_{xx} + D(1-q)v_{yy} + f_2(S)v &= 0 \qquad \text{in } \Omega, \\ D_0\nabla S\cdot \nu + b(x,y)S &= H(x,y), \\ (D(q)v_x, D(1-q)v_y)\cdot \nu + b(x,y)v &= 0 \quad \text{on } \partial\Omega. \end{aligned} \tag{3.17}$$

As shown in Table 2, when $D_0 = D_2^*$, the critical value q^* satisfies $q^* \in \left[0,\frac{1}{2}\right)$ if $F_2 < 0$, and $q^* \in \left(\frac{1}{2},1\right]$ if $F_2 > 0$. We define

$$\underline{q} := \min\left\{q^*, \frac{1}{2}\right\},\ \ \overline{q} := \max\left\{q^*, \frac{1}{2}\right\}.$$

Then we can derive the following results in a similar manner.

Theorem 3.11. *One of the following statements is valid.*

(i) *Assume that $D_0 = D_2^*$ and $F_2 \neq 0$. Then system* (3.17) *has at least one positive solution if and only if $q \in [0,1]\backslash[\underline{q},\overline{q}]$. Furthermore, if $q \in [0,1]$ is sufficiently close to $\frac{1}{2}$ or q^*, then the positive solution is linearly stable.*

(ii) *Assume that $D_0 > D_2^*$ and $0 \le q_0^* < \frac{1}{2} < q_1^* \le 1$. Then system* (3.17) *has at least one positive solution if and only if $q \in [0,1]\backslash\left[q_0^*, q_1^*\right]$. Furthermore, if q is sufficiently close to q_0^* or q_1^*, then the positive solution is linearly stable.*

(iii) *Assume that $0 < D_0 < D_2^*$, and that there exist q_-^* and q_+^* such that either $0 \le q_-^* < q_+^* < \frac{1}{2}$ or $\frac{1}{2} < q_-^* < q_+^* \le 1$. Then system* (3.17) *has at least one positive solution if and only if $q \in [0,1]\backslash\left[q_-^*, q_+^*\right]$. Furthermore, if q is sufficiently close to q_-^* or q_+^*, then the positive solution is linearly stable. In particular, if $q = \frac{1}{2}$, then $(z-\theta_2, \theta_2)$ is the unique globally attractive positive solution.*

Remark 3.12. In case (i) where $D_0 = D_2^*$, if $F_2 = 0$, then $\underline{q} = \overline{q} = \frac{1}{2}$. Consequently, system (3.17) admits at least one positive solution if and only if $q \in [0,1]\backslash\{\frac{1}{2}\}$, and the positive solution is linearly stable if q is sufficiently close to $\frac{1}{2}$. In case (ii) where $D_0 > D_2^*$, if $q_0^* = 0$ and $q_1^* = 1$, then the set $[0,1]\backslash\left[q_0^*, q_1^*\right]$ is empty. Thus, system (3.17) admits no positive solution for any $q \in (0,1)$. In case (iii) where $0 < D_0 < D_2^*$, if there exists $q_\pm^* \in \left(0,\frac{1}{2}\right) \cup \left(\frac{1}{2},1\right)$ such that $q_\pm^* = q_-^* = q_+^*$, then system (3.17) admits at least one positive solution if and only if $q \in [0,1]\backslash\left\{q_\pm^*\right\}$, and the positive solution is linearly stable if q is sufficiently close to $q_\pm^*$.

4 Dynamics of the two-species model

This section is devoted to investigating the dynamic behavior of system (1.1)–(1.3). With this in mind, we first show that this system has a unique solution $(S(x,y,t), u(x,y,t), v(x,y,t))$, which is defined for all $t > 0$ and is bounded. The proof is similar to that of Lemma 3.2, we thus omit it here.

Lemma 4.1. *System* (1.1)–(1.3) *admits a unique solution $(S(x,y,t), u(x,y,t), v(x,y,t))$ for all $(x,y) \in \overline{\Omega}$ and $t > 0$. Moreover, there exist positive constants ρ_1, ρ_2 depending on the initial values $S_0(x,y), u_0(x,y), v_0(x,y)$, such that for all $(x,y) \in \overline{\Omega}$ and $t > 0$,*

$$0 < S(x,y,t) \le \rho_1,\ \ 0 < u(x,y,t) \le \rho_2,\ \ 0 < v(x,y,t) \le \rho_2.$$

In particular, the solution $(S(x,y,t), u(x,y,t), v(x,y,t))$ is ultimately bounded.

The proof of the following result is similar to that of Theorem 3.3, and thus, we omit it here.

Theorem 4.2. *Assume that* $\lambda_1(p, f_1(z)) > 0$ *and* $\lambda_1(q, f_2(z)) > 0$*; see* Tables 1 and 2. *Then the steady state* $(z, 0, 0)$ *of system* (1.1)–(1.3) *is globally asymptotically stable.*

Recalling Lemma 2.7 and $D_2^* = D^*\big(f_2(z)\big)$, we conclude that if $0 < D_0 < D_2^*$ and $q = \frac{1}{2}$, then system (1.5) admits a unique globally attractive positive steady state $(z - \theta_2, \theta_2)$, where θ_2 is the unique positive solution to system (2.9) with f_1 replaced by f_2. Recalling Tables 1 and 2, we have the following conclusions.

Theorem 4.3. *The following statements is valid.*

(i) *Assume that* $0 < D_0 < D_1^*$ *and* $p = \frac{1}{2}$, *and that there exist* q_-^* *and* q_+^* *such that either* $0 \le q_-^* < q_+^* < \frac{1}{2}$ *or* $\frac{1}{2} < q_-^* < q_+^* \le 1$. *Then the positive steady state* $(z - \theta_1, \theta_1, 0)$ *of system* (1.1)–(1.3) *is globally asymptotically stable for* $q \in \big(q_-^*, q_+^*\big)$.

(ii) *Assume that* $0 < D_0 < D_2^*$ *and* $q = \frac{1}{2}$, *and that there exist* p_-^* *and* p_+^* *such that either* $0 \le p_-^* < p_+^* < \frac{1}{2}$ *or* $\frac{1}{2} < p_-^* < p_+^* \le 1$. *Then the positive steady state* $(z - \theta_2, 0, \theta_2)$ *of system* (1.1)–(1.3) *is globally asymptotically stable for* $p \in \big(p_-^*, p_+^*\big)$.

Proof. By Lemma 4.1, the solution $(S(x,y,t), u(x,y,t), v(x,y,t))$ of system (1.1)–(1.3) satisfies $S(x,y,t) > 0$, $u(x,y,t) > 0$, $v(x,y,t) > 0$ for all $(x,y) \in \Omega$ and $t > 0$. Hence, we have

$$\begin{aligned} &S_t \le D_0 \Delta S - f_1(S)u \\ &u_t = D_0 \Delta u + f_1(S)u \quad \text{in } \Omega \times \mathbb{R}_+. \end{aligned} \tag{4.1}$$

Let $w(x,y,t) = S(x,y,t) + u(x,y,t)$. The comparison principle for parabolic equations implies that $w(x,y,t) \le \bar{w}(x,y,t)$ for all $(x,y) \in \overline{\Omega}$ and $t > 0$, where $\bar{w}$ is the solution to

$$\begin{aligned} \bar{w}_t &= D_0 \Delta \bar{w} && \text{in } \Omega \times \mathbb{R}_+, \\ D_0 \nabla \bar{w} \cdot \nu + b(x,y)\bar{w} &= H(x,y) && \text{on } \partial\Omega \times \mathbb{R}_+, \\ \bar{w}(x,y,0) = S_0(x,y) + u_0(x,y) &\ge 0 && \text{on } \bar{\Omega}. \end{aligned} \tag{4.2}$$

Thus, for all $(x,y) \in \overline{\Omega}$ and $t > 0$, we have $S(x,y,t) + u(x,y,t) \le \bar{w}(x,y,t)$, or equivalently, $S(x,y,t) \le \bar{w}(x,y,t) - u(x,y,t)$. It follows from Lemma 2.5 that $\bar{w}(\cdot,\cdot,t) \to z$ uniformly on $\overline{\Omega}$ as $t \to +\infty$. This implies that for any $\epsilon > 0$, there exists $T_1 > 0$ such that $S < z + \epsilon - u$ for all $(x,y) \in \overline{\Omega}$ and $t > T_1$. The comparison principle for parabolic equations implies that $v(x,y,t) \le \bar{v}(x,y,t)$ for all $(x,y) \in \overline{\Omega}$ and $t > T_1$, where $\bar{v}$ is the solution to

$$\begin{aligned} \bar{v}_t = D(q)\bar{v}_{xx} + D(1-q)\bar{v}_{yy} + f_2(z + \epsilon - u)\bar{v} &\quad \text{in } \Omega \times (T_1, +\infty), \\ \big(D(q)\bar{v}_x, D(1-q)v_y\big) \cdot \nu + b(x,y)\bar{v} = 0 &\quad \text{on } \partial\Omega \times (T_1, +\infty), \\ \bar{v}(x,y,T_1) = v_1(x,y,T_1) &\quad \text{on } \bar{\Omega}. \end{aligned} \tag{4.3}$$

Note that if there exist q_-^* and q_+^* such that either $0 \le q_-^* < q_+^* < \frac{1}{2}$ or $\frac{1}{2} < q_-^* < q_+^* \le 1$, then $\lambda_1(q, f_2(z)) > 0$ for $q \in \big(q_-^*, q_+^*\big)$; see Table 2. By Lemma 2.2(i), one may select ϵ sufficiently small so that $\lambda_1(q, f_2(z - \epsilon)) > 0$. Consequently, it follows from Lemma 2.2(ii) that

$$\lambda_1\big(q, f_2(z + \epsilon - u)\big) > \lambda_1\big(q, f_2(z - \epsilon)\big) > 0.$$

By applying the separation of variables to system (4.3), we conclude that $\bar{v}(\cdot,\cdot,t) \to 0$ uniformly on $\overline{\Omega}$ as $t \to +\infty$ in an exponential manner, which implies

$$\lim_{t \to +\infty} v(\cdot,\cdot,t) = 0 \quad \text{uniformly on } \overline{\Omega} \text{ in an exponential manner.} \tag{4.4}$$

Substituting $S \le \bar{w} - u$ into the equation for u in system (1.1)–(1.3), we obtain that

$$u_t \le D_0 \Delta u + f_1(\bar{w} - u)u \quad \text{in } \Omega \times (0, +\infty).$$

By applying the comparison principle for parabolic equations again, we conclude that $u(x, y, t) \le \bar{u}(x, y, t)$ for all $(x, y) \in \overline{\Omega}$ and $t > 0$, where $\bar{u}$ is the solution to

$$\begin{aligned} \bar{u}_t &= D_0 \Delta \bar{u} + f_1(\bar{w} - \bar{u})\bar{u} && \text{in } \Omega \times \mathbb{R}_+, \\ D_0 \nabla \bar{u} \cdot \nu + b(x, y)\bar{u} &= 0 && \text{on } \partial\Omega \times \mathbb{R}_+, \\ \bar{u}(x, y, 0) &= u_0(x, y) \ge 0 && \text{on } \bar{\Omega}. \end{aligned} \tag{4.5}$$

Note that $\bar{w}(\cdot, \cdot, t) \to z$ uniformly on $\overline{\Omega}$ as $t \to +\infty$, and that θ_1 is the unique positive solution to system (2.9). Then by arguments similar to those in the proof of ref. [9, Theorem 3.2], we deduce that if $0 < D_0 < D_1^*$, i.e., $\lambda_1\left(\frac{1}{2}, f_1(z)\right) < 0$, then θ_1 is the unique globally attractive positive steady state of system (4.5). Hence,

$$\limsup_{t \to +\infty} u(\cdot, \cdot, t) \le \theta_1 \quad \text{uniformly on } \overline{\Omega}. \tag{4.6}$$

In view of (4.4), we have that for any $\epsilon > 0$, there exists $T_2 > 0$ such that $v(x, y, t) < \epsilon$ for all $(x, y) \in \overline{\Omega}$ and $t > T_2$. It follows from Lemma 4.1 that

$$S_t \ge D_0 \Delta S - f_1(S)u - f_2(\rho_1)\epsilon \quad \text{in } \Omega \times (T_2, +\infty).$$

Recall that $w = S + u$. The comparison principle for parabolic equations implies that $w(x, y, t) \ge w_\epsilon(x, y, t)$ for all $(x, y) \in \overline{\Omega}$ and $t > T_2$, where w_ϵ is the solution to

$$\begin{aligned} &(w_\epsilon)_t = D_0 \Delta w_\epsilon - f_2(\rho_1)\epsilon && \text{in } \Omega \times (T_2, +\infty), \\ &D_0 \nabla w_\epsilon \cdot \nu + b(x, y) w_\epsilon = H(x, y) && \text{on } \partial\Omega \times (T_2, +\infty), \\ &w_\epsilon(x, y, T_2) = S(x, y, T_2) + u(x, y, T_2) \ge 0 && \text{on } \overline{\Omega}. \end{aligned} \tag{4.7}$$

Hence, $S(x, y, t) \ge w_\epsilon(x, y, t) - u(x, y, t)$ for all $(x, y) \in \overline{\Omega}$ and $t > T_2$. Substituting it into the equation for u in system (1.1)–(1.3), we obtain that

$$u_t \ge D_0 \Delta u + f_1(w_\epsilon - u)u \quad \text{in } \Omega \times (T_2, +\infty).$$

By the comparison principle for parabolic equations, we conclude that $u(x, y, t) \ge \underline{u}(x, y, t)$ for all $(x, y) \in \overline{\Omega}$ and $t > T_2$, where $\underline{u}$ is the solution to

$$\begin{aligned} \underline{u}_t &= D_0 \Delta \underline{u} + f_1(w_\epsilon - \underline{u})\underline{u} && \text{in } \Omega \times (T_2, +\infty), \\ D_0 \nabla \underline{u} \cdot \nu + b(x, y)\underline{u} &= 0 && \text{on } \partial\Omega \times (T_2, +\infty), \\ \underline{u}(x, y, T_2) &= u(x, y, T_2) && \text{on } \bar{\Omega}. \end{aligned}$$

By arguments similar to those in ref. [33, Lemmas 2.2 and 4.2], we conclude that $w_\epsilon(\cdot, \cdot, t) \to z_\epsilon$ uniformly on $\overline{\Omega}$ as $t \to +\infty$, where z_ϵ is the unique positive steady state of system (4.7). Moreover, it follows from the standard elliptic regularity theory that $\lim_{\epsilon \to 0} z_\epsilon = z$ uniformly on $\overline{\Omega}$. By applying arguments similar to those presented above, we conclude

$$\liminf_{t \to +\infty} u(\cdot, \cdot, t) \ge \theta_1 \quad \text{uniformly on } \overline{\Omega}. \tag{4.8}$$

Inequalities (4.6) and (4.8) imply that $\lim_{t \to +\infty} u(\cdot, \cdot, t) = \theta_1$ uniformly on $\overline{\Omega}$. Similarly, we deduce that $\lim_{t \to +\infty} S(\cdot, \cdot, t) = z - \theta_1$ uniformly on $\overline{\Omega}$. The proof is completed. □

Theorems 3.7–3.11 and the corresponding Remarks imply that for all other parameters fixed, there exist semi-trivial steady states $\left(S_p^i, u_p^i, 0\right)$ for $i = 1, \dots, k_1$, where $k_1 \geq 1$, if and only if p satisfies $\lambda_1\left(p, f_1(z)\right) < 0$. Similarly, there exist semi-trivial steady states $\left(S_q^j, 0, v_q^j\right)$ for $j = 1, \dots, k_2$, where $k_2 \geq 1$, if and only if q satisfies $\lambda_1(q, f_2(z)) < 0$. In particular, if $q = \frac{1}{2}$, then $k_1 = 1$ and $\left(S_p^1, u_p^1, 0\right) = (z - \theta_1, \theta_1, 0)$; if $p = \frac{1}{2}$, then $k_2 = 1$ and $\left(S_q^1, 0, v_q^1\right) = (z - \theta_2, 0, \theta_2)$. Moreover, it follows from Lemma 3.6 that all of $S_p^i, S_q^j < z$ on $\overline{\Omega}$. Hence, by Lemma 2.2(ii), $\lambda_1\left(p, f_1(z)\right) < \lambda_1\left(p, f_1\left(S_q^j\right)\right)$ and $\lambda_1\left(q, f_2(z)\right) < \lambda_1\left(q, f_2\left(S_p^i\right)\right)$ for any $(p, q) \in [0, 1]^2$ and $1 \leq i \leq k_1, 1 \leq j \leq k_2$.

Theorem 4.4. *Assume that $\lambda_1\left(q, f_2\left(S_p^i\right)\right) < 0$ for any $i = 1, \dots, k_1$ and $\lambda_1\left(p, f_1\left(S_q^j\right)\right) < 0$ for any $j = 1, \dots, k_2$. Then system* (1.1)–(1.3) *is uniformly persistent in the sense that there exists $\sigma > 0$ such that the solution $(S(x, y, t), u(x, y, t), v(x, y, t))$ of system* (1.1)–(1.3) *satisfying*

$$\liminf_{t\to+\infty} S(\cdot, \cdot, t) \geq \sigma, \ \liminf_{t\to+\infty} u(\cdot, \cdot, t) \geq \sigma, \ \text{and} \liminf_{t\to+\infty} v(\cdot, \cdot, t) \geq \sigma \ \text{uniformly on } \overline{\Omega}.$$

Proof. This proof is similar to that of Theorem 3.4, so we only sketch it here. By the comparison principle for parabolic equations, Lemma 4.1 and [33, Lemmas 2.2 and 4.2], there exists $\sigma_1 > 0$ such that $\liminf_{t\to+\infty} S(\cdot, \cdot, t) \geq \sigma_1$. Let

$$\begin{aligned} P &= \left\{(S, u, v) \in C(\overline{\Omega}) \times C(\overline{\Omega}) \times C(\overline{\Omega}) : S \geq 0, u \geq 0, v \geq 0 \quad \text{on } \overline{\Omega}\right\}, \\ P^0 &= \{(S, u, v) \in P : u \not\equiv 0 \text{ and } v \not\equiv 0\}, \\ \partial P^0 &= P \backslash P^0 = \{(S, u, v) \in P : u \equiv 0 \text{ or } v \equiv 0\}. \end{aligned}$$

Define Ψ_t as the solution semiflow generated by system (1.1)–(1.3) on P, where Ψ_t is compact and point dissipative. By [36, Theorem 2.6], we conclude that Ψ_t has a global compact attractor that attracts each bounded set in P.

Set $\Theta := \left(S_0, u_0, v_0\right)$. Define $M_\partial := \left\{\Theta \in \partial P^0 : \Psi_t\Theta \in \partial P^0, \ \forall\ t \geq 0\right\}$, and let $\omega\left(\Theta\right)$ denote the omega limit set of the forward orbit $\gamma^+\left(\Theta\right) := \{\Psi_t\Theta : t \geq 0\}$. It is easily observed that

$$\cup_{\Theta\in M_\partial}\omega(\Theta) = \left\{(z, 0, 0), \left(S_p^i, u_p^i, 0\right), \left(S_q^j, 0, v_q^j\right), i = 1, \dots, k_1 \text{ and } j = 1, \dots, k_2 \text{ with } k_1, k_2 \geq 1\right\}.$$

Similar to the proof of Theorem 3.4, we conclude by contradiction that if $\lambda_1\left(p, f_1(z)\right) < 0$ or $\lambda_1\left(q, f_2(z)\right) < 0$, then $(z, 0, 0)$ is a uniform weak repeller for P^0. We now claim that if $\lambda_1\left(q, f_2\left(S_p^1\right)\right) < 0$, then $\left(S_p^1, u_p^1, 0\right)$ is a uniform weak repeller for P^0. That is, there exists $\delta_1 > 0$ such that for all $(S_0, u_0, v_0) \in P^0$,

$$\limsup_{t\to+\infty} \|\Psi_t(S_0, u_0, v_0) - \left(S_p^1, u_p^1, 0\right)\|_\infty \geq \delta_1.$$

If not, then for any $\delta > 0$, there exists $(S_0, u_0, v_0) \in P^0$ such that $\limsup_{t\to+\infty} \|\Psi_t(S_0, u_0, v_0) - \left(S_p^1, u_p^1, 0\right)\|_\infty < \delta$. This implies that there exists $T_0 > 0$ such that for $t > T_0$,

$$\|S(\cdot, \cdot, t) - S_p^1\|_\infty < \delta, \|u(\cdot, \cdot, t) - u_p^1\|_\infty < \delta, \|v(\cdot, \cdot, t)\|_\infty < \delta. \tag{4.9}$$

By the continuity of function $f_1(S)$, we can choose $\epsilon > 0$ small such that for all $(x, y) \in \overline{\Omega}$ and $t \geq T_0$, $f_1(S) > f_1\left(S_p^1\right) - \epsilon$. Thus, we obtain

$$v_t \geq D_0\Delta v + \left(f_1\left(S_p^1\right) - \epsilon\right)v \quad \text{in } \Omega \times (T_0, +\infty).$$

In view of $(S_0, u_0, v_0) \in P^0$, it follows from the maximum principle that $v(\cdot, \cdot, T_0) > 0$. Hence, there exists $\kappa > 0$ such that $v(\cdot, \cdot, T_0) \geq \kappa\varphi_1\left(q, f_2\left(S_p^1\right)\right)$, where $\varphi_1\left(q, f_2\left(S_p^1\right)\right)$ is the principal eigenfunction corresponding to the principal eigenvalue $\lambda_1\left(q, f_2\left(S_p^1\right)\right)$. Let $\underline{v}(x, y, t) = \kappa e^{\left(\lambda_1\left(q, f_2\left(S_p^1\right)\right)+\epsilon\right)(T_0-t)}\varphi_1\left(q, f_2\left(S_p^1\right)\right)$ for all $(x, y) \in \overline{\Omega}$ and $t \geq T_0$. Then $\underline{v}$ satisfies

$$\begin{aligned} \underline{v}_t &= D_0\Delta\underline{v} + \left(f_2\left(S_p^1\right) - \epsilon\right)\underline{v} && \text{in } \Omega \times (T_0, +\infty), \\ D_0\nabla\underline{v} \cdot \nu + b(x, y)\underline{v} &= 0 && \text{on } \partial\Omega \times (T_0, +\infty), \\ \underline{v}(x, y, T_0) &= \kappa\varphi_1\left(q, f_2\left(S_p^1\right)\right) && \text{on } \bar{\Omega}. \end{aligned}$$

By the comparison principle for parabolic equations, we conclude that $v(x, y, t) \geq \underline{v}(x, y, t)$ for all $(x, y) \in \overline{\Omega}$ and $t \geq T_0$. Since $\lambda_1\left(q, f_2\left(S_p^1\right)\right) < 0$, there exists a sufficiently small $\epsilon > 0$ such that $\lambda_1\left(q, f_2\left(S_p^1\right)\right) + \epsilon < 0$. This implies that $\lim_{t\to+\infty} v(\cdot, \cdot, t) = +\infty$, which contradicts (4.9). This claim is valid. Similarly, we deduce that if $\lambda_1\left(q, f_2\left(S_p^i\right)\right) < 0$ and $\lambda_1\left(p, f_1\left(S_q^j\right)\right) < 0$ for all $i = 1, \ldots, k_1$ and $j = 1, \ldots, k_2$ with $k_1, k_2 \geq 1$, then all of $\left(S_p^i, u_p^i, 0\right)$ and $\left(S_q^j, 0, v_q^j\right)$ are uniform weak repellers for P^0.

Define a continuous function $\mathcal{D}: P \to [0, +\infty)$ by $\mathcal{D}(S, u, v) := \left\{\min_{\overline{\Omega}} u(x, y), \min_{\overline{\Omega}} v(x, y)\right\}$ for any $(S, u, v) \in P$. It is easy to see that $\mathcal{D}^{-1}(0, +\infty) \subseteq P^0$, and $\mathcal{D}$ satisfies that if $\mathcal{D}((S, u, v)) > 0$ or $(S, u, v) \in P^0$ with $\mathcal{D}((S, u, v)) = 0$, then $\mathcal{D}(\Psi_t(S, u, v)) > 0$ for all $t > 0$. Thus $\mathcal{D}$ is a generalized distance function for the semiflow $\Psi_t: P \to P$ [35].

Denote $E := E_0 \cup \left(\cup_{i=1}^{k_1} E_p^i\right) \cup \left(\cup_{j=1}^{k_2} E_q^j\right)$, where $E_0 = \{(z, 0, 0)\}$, $E_p^i = \left\{\left(S_p^i, u_p^i, 0\right)\right\}$ and $E_q^j = \left\{\left(S_q^j, 0, v_q^j\right)\right\}$. By arguments presented above, we conclude that all of the sets E_0, E_p^i, E_q^j, where $i = 1, \ldots, k_1$ and $j = 1, \ldots, k_2$ with $k_1, k_2 \geq 1$, are isolated in P. Moreover, the stable set $W^s(E) \cap \mathcal{D}^{-1}(0, +\infty) = W^s\left(E_p^i\right) \cap \mathcal{D}^{-1}(0, +\infty) = W^s\left(E_q^j\right) \cap \mathcal{D}^{-1}(0, +\infty) = \emptyset$, where $i = 1, \ldots, k_1$ and $j = 1, \ldots, k_2$ with $k_1, k_2 \geq 1$. Therefore, no subset of E forms a cycle in M'_∂. It follows from ref. [35, Theorem 3] that there exists $\sigma_2 > 0$ such that

$$\min_{(S,u,v)\in\omega_a((S_0,u_0,v_0))} \mathcal{D}((S, u, v)) > \sigma_2,$$

which implies that for any $(S_0, u_0, v_0) \in P^0$, $\liminf_{t\to+\infty} u(\cdot, \cdot, t) \geq \sigma_2$ and $\liminf_{t\to+\infty} v(\cdot, \cdot, t) \geq \sigma_2$ uniformly on $\overline{\Omega}$. Set $\sigma = \min\{\sigma_1, \sigma_2\}$. This completes the proof. □

5 Further study on coexistence of the two-species model

In this section, we aim to further investigate the structure and stability of the positive steady states of system (1.1)–(1.3). Hence, we focus on the positive solutions to the following steady-state system

$$\begin{aligned} D_0\Delta S - f_1(S)u - f_2(S)v &= 0, \\ D(p)u_{xx} + D(1-p)u_{yy} + f_1(S)u &= 0, \\ D(q)v_{xx} + D(1-q)v_{yy} + f_2(S)v &= 0 \qquad \text{in } \Omega, \\ D_0\nabla S \cdot \nu + b(x, y)S &= H(x, y), \\ (D(p)u_x, D(1-p)u_y) \cdot \nu + b(x, y)u &= 0, \\ (D(q)v_x, D(1-q)v_y) \cdot \nu + b(x, y)v &= 0 \qquad \text{on } \partial\Omega. \end{aligned} \tag{5.1}$$

It is easy to see that system (5.1) has the following three types nonnegative solutions.

(i) There always exists the trivial solution $(z, 0, 0)$.

(ii) There exists at least one semi-trivial solution of the form $(S_p, u_p, 0)$, where $S_p > 0, u_p > 0$ on $\overline{\Omega}$, if and only if p satisfies $\lambda_1(p, f_1(z)) < 0$ with all other parameters fixed; see Theorems 3.7–3.9. Moreover, there exists at least one semi-trivial solution of the form $(S_q, 0, v_q)$, where $S_q > 0, v_q > 0$ on $\overline{\Omega}$, if and only if q satisfies $\lambda_1(q, f_2(z)) < 0$ with all other parameters fixed; see Theorem 3.11. In particular, (1) if $p = \frac{1}{2}$ and

$0 < D_0 < D_1^*$, then the semi-trivial solution $(S_p, u_p, 0) = (z - \theta_1, \theta_1, 0)$ is unique; (2) if $q = \frac{1}{2}$ and $0 < D_0 < D_2^*$, then the semi-trivial solution $(S_q, 0, v_q) = (z - \theta_2, 0, \theta_2)$ is unique.

(iii) The existence of positive solutions (S, u, v), where $S, u, v > 0$ on $\overline{\Omega}$, is to be determined.

We can readily analyze the linear stability of $(z, 0, 0)$, $(z - \theta_1, \theta_1, 0)$ and $(z - \theta_2, 0, \theta_2)$ using eigenvalue analysis.

Theorem 5.1. *The following statements is valid.*

(i) $(z, 0, 0)$ *is linearly stable if* $\lambda_1(p, f_1(z)) > 0$ *and* $\lambda_1(q, f_2(z)) > 0$*, and it is unstable if* $\lambda_1(p, f_1(z)) < 0$ *or* $\lambda_1(q, f_2(z)) < 0$*; see* Tables 1 and 2.

(ii) *Assume that* $p = \frac{1}{2}$ *and* $0 < D_0 < D_1^*$*. Then* $(z - \theta_1, \theta_1, 0)$ *is linearly stable if* $\lambda_1(q, f_2(z - \theta_1)) > 0$*, and it is unstable if* $\lambda_1(q, f_2(z - \theta_1)) < 0$*.*

(iii) *Assume that* $q = \frac{1}{2}$ *and* $0 < D_0 < D_2^*$*. Then* $(z - \theta_2, 0, \theta_2)$ *is linearly stable if* $\lambda_1(p, f_1(z - \theta_2)) > 0$*, and it is unstable if* $\lambda_1(p, f_1(z - \theta_2)) < 0$*.*

Proof. The proof of part (i) is standard and omitted here. We present the proof for part (ii) only, as part (iii) follows similarly. Let $w = z - S$. Then system (5.1) is equivalent to

$$\begin{aligned} D_0\Delta w + f_1(z - w)u + f_2(z - w)v &= 0, \\ D_0\Delta u + f_1(z - w)u &= 0, \\ D(q)v_{xx} + D(1 - q)v_{yy} + f_2(z - w)v &= 0 \qquad \text{in } \Omega, \\ D_0\nabla w \cdot \nu + b(x, y)w &= 0, \\ D_0\nabla u \cdot \nu + b(x, y)u &= 0, \\ \big(D(q)v_x, D(1 - q)v_y\big) \cdot \nu + b(x, y)v &= 0 \quad \text{on } \partial\Omega. \end{aligned} \tag{5.2}$$

Consider the following linearized eigenvalue problem for system (5.2) at $(\theta_1, \theta_1, 0)$,

$$\begin{aligned} D_0\Delta\zeta - f_1'(z - \theta_1)\theta_1\zeta + f_1(z - \theta_1)\eta + f_2(z - \theta_1)\vartheta + \lambda\zeta &= 0, \\ D_0\Delta\eta + f_1(z - \theta_1)\eta - f_1'(z - \theta_1)\theta_1\zeta + \lambda\eta &= 0, \\ D(q)\vartheta_{xx} + D(1 - q)\vartheta_{yy} + f_2(z - \theta_1)\vartheta + \lambda\vartheta &= 0 \quad \text{in } \Omega, \end{aligned}$$

subject to the homogeneous boundary conditions. Let $\chi = \zeta - \eta$. Then (ζ, χ, ϑ) satisfies

$$\begin{aligned} D_0\Delta\zeta - f_1'(z - \theta_1)\theta_1\zeta + f_1(z - \theta_1)\eta + f_2(z - \theta_1)\vartheta + \lambda\zeta &= 0, \\ D_0\Delta\chi - f_2(z - \theta_1)\vartheta + \lambda\chi &= 0, \\ D(q)\vartheta_{xx} + D(1 - q)\vartheta_{yy} + f_2(z - \theta_1)\vartheta + \lambda\vartheta &= 0 \quad \text{in } \Omega \end{aligned} \tag{5.3}$$

subject to the homogeneous boundary conditions. It is easy to see that λ is an eigenvalue of problem (5.3) if and only if λ is an eigenvalue of the following three operators,

$$I_1 := D_0\Delta - f_1'(z - \theta_1)\theta_1, \; I_2 := D_0\Delta, \; I_3 := D(q)\partial_{xx} + D(1 - q)\partial_{yy} + f_2(z - \theta_1).$$

It follows from the variational characterization of the principal eigenvalue (see, e.g., equation (2.2)) that the principal eigenvalues of I_1 and I_2 are positive. Moreover, the principal eigenvalue of I_3 is equal to $\lambda_1(q, f_2(z - \theta_1))$. This completes the proof. □

Then we derive *a priori* estimates for the positive solutions to system (5.1). The proof is similar to that of Lemma 3.6, we thus omit it here.

Lemma 5.2. *Assume that (S, u, v) is a nonnegative solution to system (5.1) with $S \not\equiv 0$, $u \not\equiv 0$ and $v \not\equiv 0$. Then*
(i) $\lambda_1(p, f_1(z)) < 0$ *and* $\lambda_1(q, f_1(z)) < 0$;
(ii) $0 < S < z$, *and there exist positive constants C_u, C_v such that $0 < u < C_u$ and $0 < v < C_v$ on $\overline{\Omega}$.*

Next, by taking q as the bifurcation parameter, we derive the corresponding branches of positive solutions; see, e.g., [17], [43]–[45].

5.1 Local bifurcation and stability

We begin by examining the branch of positive solutions to system (5.1) that bifurcates from the semi-trivial branch $\Gamma_u = \{(q, z - \theta_1, \theta_1, 0) : q \in [0, 1]\}$. For technical reasons, we need to impose the following conditions.
(H1) $p = \frac{1}{2}$ and $0 < D_0 < D_1^*$, which ensures that $\Gamma_u \neq \emptyset$.
(H2) There exists $\hat{q} \in (0, 1)$ such that $\lambda_1(\hat{q}, f_2(z - \theta_1)) = 0$.
(H3) $F(\hat{q}; f_2(z - \theta_1)) \neq 0$, where F is defined in (2.6).

Lemma 5.3. *Assume that* (H1)–(H3) *hold. Then there exists a C^1 curve*

$$\Gamma_u^{\pm} = \{(q(s), S(s), u(s), v(s)) : s \in (-s_1, s_1)\},$$

such that $((q(s), S(s), u(s), v(s)))$ is a solution to system (5.1) *for any $s \in (-s_1, s_1)$, and the solution is positive for any $s \in (0, s_1)$, where*

$$S(s) = z - \theta_1 - s(\zeta_0 + W(s)),\ \ u(s) = \theta_1 + s(\eta_0 + U(s)) \text{ and } v(s) = s(\vartheta_0 + V(s)).$$

Here,

$$q(0) = \hat{q},\ \ W(0) = 0,\ \ U(0) = 0,\ \ V(0) = 0 \text{ and } (W(s), U(s), V(s)) \in Z,$$

where $Z = \{(W, U, V) \in X : \int_\Omega V\vartheta_0 = 0\}$ with ϑ_0 being a positive principal eigenfunction corresponding $\lambda_1(\hat{q}, f_2(z - \theta_1))$, and (ζ_0, η_0) satisfies

$$\begin{aligned} D_0\Delta\zeta_0 - f_1'(z - \theta_1)\theta_1\zeta_0 + f_1(z - \theta_1)\eta_0 + f_2(z - \theta_1)\vartheta_0 &= 0, \\ D_0\Delta\eta_0 + f_1(z - \theta_1)\eta_0 - f_1'(z - \theta_1)\theta_1\zeta_0 &= 0 \qquad \text{in } \Omega, \\ D_0\nabla\zeta_0 \cdot \nu + b(x, y)\zeta_0 &= 0, \\ D_0\nabla\eta_0 \cdot \nu + b(x, y)\eta_0 &= 0 \quad \text{ on } \partial\Omega. \end{aligned}$$

Remark 5.4. The concavity of $\lambda_1(q, f_2(z - \theta_1))$ with respect to q implies that there exist at most two bifurcation points of positive solutions bifurcating from the semi-trivial branch Γ_u.

Proof of Lemma 5.3. Let $X = \left[W^{2,r}(\Omega)\right]^3$ and $Y = \left[L^r(\Omega)\right]^3$ with $r \in (1, \infty)$. Then $W^{2,r}(\Omega)$ embeds compactly in $C(\overline{\Omega})$. In system (5.2), w, u, v in the boundary condition are interpreted as the traces of $w, u, v \in W^{2,r}(\Omega)$ on $\partial\Omega$; see, e.g., [24, Theorem 1.6] and Remarks there. Define $T : (0, 1) \times X \to Y \times \left[W^{1,r}(\partial\Omega)\right]^3$ by

$$T(q, w, u, v) = \begin{pmatrix} D_0\Delta w + f_1(z - w)u + f_2(z - w)v \\ D_0\Delta u + f_1(z - w)u \\ D(q)v_{xx} + D(1 - q)v_{yy} + f_2(z - w)v \\ D_0\nabla w \cdot \nu + b(x, y)w \\ D_0\nabla u \cdot \nu + b(x, y)u \\ (D(q)v_x, D(1 - q)v_y) \cdot \nu + b(x, y)v \end{pmatrix}. \tag{5.4}$$

Let $D_{(w,u,v)}T(q,\theta_1,\theta_1,0)$ be the Fréchet derivative of $T(q,w,u,v)$ with respect to (w,u,v) at $(\theta_1,\theta_1,0)$. It is easy to see that $D_{(w,u,v)}T(q,\theta_1,\theta_1,0)$ is a Fredholm operator with index zero.

Set $D_{(w,u,v)}T(\hat{q},\theta_1,\theta_1,0)(\zeta,\eta,\vartheta)^\top = \mathbf{0}$ with $(\zeta,\eta,\vartheta)\neq(0,0,0)$, i.e.,

$$\begin{aligned}
D_0\Delta\zeta - f_1'(z-\theta_1)\theta_1\zeta + f_1(z-\theta_1)\eta + f_2(z-\theta_1)\vartheta &= 0,\\
D_0\Delta\eta + f_1(z-\theta_1)\eta - f_1'(z-\theta_1)\theta_1\zeta &= 0,\\
D(\hat{q})\vartheta_{xx} + D(1-\hat{q})\vartheta_{yy} + f_2(z-\theta_1)\vartheta &= 0 \qquad \text{in } \Omega,\\
D_0\nabla\zeta\cdot\nu + b(x,y)\zeta &= 0,\\
D_0\nabla\eta\cdot\nu + b(x,y)\eta &= 0,\\
\big(D(\hat{q})\vartheta_x, D(1-\hat{q})\vartheta_y\big)\cdot\nu + b(x,y)\vartheta &= 0 \quad \text{on } \partial\Omega,
\end{aligned}$$

where the function $f_1'(z-\theta_1) = \frac{m_1a_1}{(a_1+z-\theta_1)^2}$. Suppose $\vartheta\equiv 0$ on $\overline{\Omega}$. Then (ζ,η) satisfies

$$\begin{aligned}
D_0\Delta\zeta - f_1'(z-\theta_1)\theta_1\zeta + f_1(z-\theta_1)\eta &= 0,\\
D_0\Delta\eta - f_1'(z-\theta_1)\theta_1\zeta + f_1(z-\theta_1)\eta &= 0 \qquad \text{in } \Omega,\\
D_0\nabla\zeta\cdot\nu + b(x,y)\zeta &= 0,\\
D_0\nabla\eta\cdot\nu + b(x,y)\eta &= 0 \quad \text{on } \partial\Omega.
\end{aligned}$$

Let $\chi = \zeta - \eta$. Then χ satisfies

$$\begin{aligned}
\Delta\chi &= 0 \qquad \text{in } \Omega,\\
D_0\nabla\chi\cdot\nu + b(x,y)\chi &= 0 \quad \text{on } \partial\Omega.
\end{aligned}$$

The strong maximum principle implies that $\chi = 0$, i.e., $\zeta = \eta$ on $\overline{\Omega}$. Hence, ζ satisfies

$$\begin{aligned}
D_0\Delta\zeta + \big(f_1(z-\theta_1) - f_1'(z-\theta_1)\theta_1\big)\zeta &= 0 \qquad \text{in } \Omega,\\
D_0\nabla\zeta\cdot\nu + b(x,y)\zeta &= 0 \quad \text{on } \partial\Omega.
\end{aligned}$$

It follows from Lemma 2.2(ii) and the equation for u in system (5.1) that

$$\lambda_1\Big(\frac{1}{2}, f_1(z-\theta_1) - f_1'(z-\theta_1)\theta_1\Big) > \lambda_1\Big(\frac{1}{2}, f_1(z-\theta_1)\Big) = 0.$$

The general maximum principle [38] implies that $\zeta = \eta = 0$ on $\overline{\Omega}$. This contradicts the condition $(\zeta,\eta,\vartheta)\neq(0,0,0)$. Hence, $\vartheta\not\equiv 0$ on $\overline{\Omega}$. Moreover, based on the analysis above, we conclude that the operator

$$\mathcal{A} := \begin{pmatrix} D_0\Delta - f_1'(z-\theta_1)\theta_1 & f_1(z-\theta_1)\\ -f_1'(z-\theta_1)\theta_1 & D_0\Delta + f_1(z-\theta_1)\end{pmatrix}$$

is invertible with the boundary conditions $D_0\nabla\zeta\cdot\nu + b(x,y)\zeta = 0$, $D_0\nabla\eta\cdot\nu + b(x,y)\eta = 0$ on $\partial\Omega$. Note that $\lambda_1(\hat{q}, f_2(z-\theta_1)) = 0$. We then deduce that the kernel

$$N\big(D_{(w,u,v)}T(\hat{q},\theta_1,\theta_1,0)\big) = \operatorname{span}\{(\zeta_0,\eta_0,\vartheta_0)\},$$

where ϑ_0 is a positive principal eigenfunction of problem (2.1) with $p=\hat{q}$, $h = f_2(z-\theta_1)$, and (ζ_0,η_0) is the unique solution to

$$\begin{aligned}
\mathcal{A}(\zeta_0,\eta_0)^\top &= (-f_2(z-\theta_1)\vartheta_0, 0)^\top \qquad \text{in } \Omega,\\
D_0\nabla\zeta_0\cdot\nu + b(x,y)\zeta_0 &= 0,\\
D_0\nabla\eta_0\cdot\nu + b(x,y)\eta_0 &= 0 \quad \text{on } \partial\Omega.
\end{aligned}$$

We next claim that the rangle of $D_{(w,u,v)}T(\hat{q},\theta_1,\theta_1,0)$ is

$$R(D_{(w,u,v)}T(\hat{q},\theta_1,\theta_1,0)) \\ =\Big\{ \big(\zeta^*,\eta^*,\vartheta^*,\xi_1,\xi_2,\xi_3\big) \in Y\times\big[W^{1,r}(\partial\Omega)\big]^3 : l(\zeta^*,\eta^*,\vartheta^*,\xi_1,\xi_2,\xi_3)=0\Big\},$$

where $l: Y\times\big[W^{1,r}(\partial\Omega)\big]^3 \to \mathbb{R}$ is a linear functional in $\Big(Y\times\big[W^{1,r}(\partial\Omega)\big]^3\Big)^*$ defined by

$$l(\zeta^*,\eta^*,\vartheta^*,\xi_1,\xi_2,\xi_3) = \int\limits_{\Omega} \vartheta^*\vartheta_0 - \int\limits_{\partial\Omega}\xi_3\vartheta_0.$$

In order to prove this claim, we need to consider the following problem

$$\begin{aligned} D_0\Delta\zeta - f_1'(z-\theta_1)\theta_1\zeta + f_1(z-\theta_1)\eta + f_2(z-\theta_1)\vartheta &= \zeta^*, \\ D_0\Delta\eta + f_1(z-\theta_1)\eta - f_1'(z-\theta_1)\theta_1\zeta &= \eta^*, \\ D(\hat{q})\vartheta_{xx} + D(1-\hat{q})\vartheta_{yy} + f_2(z-\theta_1)\vartheta &= \vartheta^* \qquad \text{in } \Omega, \\ D_0\nabla\zeta\cdot\nu + b(x,y)\zeta &= \xi_1, \\ D_0\nabla\eta\cdot\nu + b(x,y)\eta &= \xi_2, \\ \big(D(\hat{q})\vartheta_x, D(1-\hat{q})\vartheta_y\big)\cdot\nu + b(x,y)\vartheta &= \xi_3 \quad \text{on } \partial\Omega. \end{aligned} \tag{5.5}$$

By arguments similar to those in the proof of Theorem 3.7, we conclude that the problem

$$\begin{aligned} D(\hat{q})\vartheta_{xx} + D(1-\hat{q})\vartheta_{yy} + f_2(z-\theta_1)\vartheta &= \vartheta^* \qquad \text{in } \Omega, \\ \big(D(\hat{q})\vartheta_x, D(1-\hat{q})\vartheta_y\big)\cdot\nu + b(x,y)\vartheta &= \xi_3 \quad \text{on } \partial\Omega \end{aligned}$$

has a solution, denoted by ϑ_1, if and only if $\int_\Omega \vartheta^*\vartheta_0 - \int_{\partial\Omega}\xi_3\vartheta_0 = 0$. It follows from the standard elliptic regularity theory that for any constant $c<0$ and $\xi_1,\xi_2\in W^{1,r}(\partial\Omega)$, the problem

$$\begin{aligned} D_0\Delta\zeta + c\zeta &= 0, \\ D_0\Delta\eta + c\eta &= 0 \qquad \text{in } \Omega, \\ D_0\nabla\zeta\cdot\nu + b(x,y)\zeta &= \xi_1, \\ D_0\nabla\eta\cdot\nu + b(x,y)\eta &= \xi_2 \quad \text{on } \partial\Omega \end{aligned}$$

has a unique solution, denoted by (ζ_1,η_1). Substituting $\vartheta=\vartheta_1$ into problem (5.5) and setting $\tilde{\zeta}=\zeta-\zeta_1$, $\tilde{\eta} = \eta-\eta_1$, we obtain

$$\begin{aligned} \mathcal{A}(\tilde{\zeta},\tilde{\eta})^\top &= (g_1,g_2)^\top \qquad \text{in } \Omega, \\ D_0\nabla\tilde{\zeta}\cdot\nu + b(x,y)\tilde{\zeta} &= 0, \\ D_0\nabla\tilde{\eta}\cdot\nu + b(x,y)\eta \tilde{=} 0 & \quad \text{on } \partial\Omega, \end{aligned} \tag{5.6}$$

where

$$\begin{aligned} g_1 &= \zeta^* + \big(f_1'(z-\theta_1)\theta_1 + c\big)\zeta_1 - f_1(z-\theta_1)\eta_1 - f_2(z-\theta_1)\vartheta_1, \\ g_2 &= \eta^* + f_1'(z-\theta_1)\theta_1\zeta_1 + \big(c - f_1(z-\theta_1)\big)\eta_1. \end{aligned}$$

Since the operator $\mathcal{A}$ is invertible with the boundary conditions $D_0\nabla\tilde{\zeta}\cdot\nu + b(x,y)\tilde{\zeta}=0$, $D_0\nabla\tilde{\eta}\cdot\nu+b(x,y)\tilde{\eta} = 0$ on $\partial\Omega$, we conclude that for any $\zeta^*,\eta^*\in L^r(\Omega)$, $\zeta_1,\eta_1,\vartheta_1\in W^{2,r}(\Omega)$, problem (5.6) always have a unique solution. Therefore, $\big(\zeta^*,\eta^*,\vartheta^*,\xi_1,\xi_2,\xi_3\big)\in Y\times\big[W^{1,r}(\partial\Omega)\big]^3$ is in the range $R\big(D_{(w,u,v)}T(\hat{q},\theta_1,\theta_1,0)\big)$ if and only if $\int_\Omega\vartheta^*\vartheta_0 - \int_{\partial\Omega}\xi_3\vartheta_0 = 0$.

We then check the transversality condition

$$D_{q(w,u,v)}T(\hat{q},\theta_1,\theta_1,0)(\zeta_0,\eta_0,\vartheta_0)^\top \notin R(D_{(w,u,v)}T(\hat{q},\theta_1,\theta_1,0)). \tag{5.7}$$

By direct computation, we have

$$D_{q(w,u,v)}T(\hat{q},\theta_1,\theta_1,0)(\zeta_0,\eta_0,\vartheta_0)^\top = \begin{pmatrix} 0 \\ 0 \\ (\overline{D}-\underline{D})\big((\vartheta_0)_{xx}-(\vartheta_0)_{yy}\big) \\ 0 \\ 0 \\ (\overline{D}-\underline{D})\big((\vartheta_0)_x,-(\vartheta_0)_y\big)\cdot\nu \end{pmatrix},$$

and

$$\begin{aligned} l\big(D_{q(w,u,v)}T(\hat{q},\theta_1,\theta_1,0)(\zeta_0,\eta_0,\vartheta_0)^\top\big) &= (\overline{D}-\underline{D})\int_\Omega \vartheta_0\big((\vartheta_0)_{xx}-(\vartheta_0)_{yy}\big) \\ &\quad - (\overline{D}-\underline{D})\int_{\partial\Omega} \vartheta_0\big((\vartheta_0)_x,-(\vartheta_0)_y\big)\cdot\nu \\ &= -(\overline{D}-\underline{D})\int_\Omega \Big(\big((\vartheta_0)_x\big)^2-\big((\vartheta_0)_y\big)^2\Big). \end{aligned}$$

If $F(\hat{q}; f_2(z-\theta_1)) \neq 0$, then

$$l\Big(D_{p(w,u)}T\big(\hat{q},\theta_1,\theta_1,0\big)\big(\zeta_0,\eta_0,\vartheta_0\big)^\top\Big) \neq 0.$$

This implies that the transversality condition is satisfied.

Let

$$Z = \left\{(W,U,V)\in X\colon \int_\Omega V\vartheta_0 = 0\right\}.$$

Then $\operatorname{span}\{(\zeta_0,\eta_0,\vartheta_0)\}\oplus Z = X$. By applying the standard bifurcation theorem from a simple eigenvalue [40], we conclude that there exist $s_1>0$ and C^1 curve

$$\big(q(s),W(s),U(s),V(s)\big)\colon \big(-s_1,s_1\big)\to\mathbb{R}\times Z,$$

such that (i) $q(0)=\hat{q}$, (ii) $W(0)=0$, $U(0)=0$, $V(0)=0$, (iii) $T\big(q(s),w(s),u(s),v(s)\big)=0$ for $|s|<s_1$, where

$$\big(q(s),w(s),u(s),v(s)\big) = \big(q(s),\theta_1+s(\zeta_0+W(s)),\theta_1+s(\eta_0+U(s)),s(\vartheta_0+V(s))\big).$$

Let $S(s)=z-w(s)=z-\theta_1-s(\zeta_0+W(s))$. Noting that $\vartheta_0>0$ on $\overline{\Omega}$, we conclude that the bifurcation branch

$$\Gamma_u^+ = \big\{\big(q(s),S(s),u(s),v(s)\big)\colon 0<s<s_1\big\}$$

is exactly the positive solution to system (5.1). The non-trivial nonnegative solutions to system (5.1) near $(\hat{q},z-\theta_1,\theta_1,0)$ lie on either the branch $\{(q,z-\theta_1,\theta_1,0)\colon q\in[0,1]\}$ or the branch Γ_u^+. This completes the proof. □

We then investigate the linear stability of the bifurcation solution near the bifurcation point $(\hat{q},z-\theta_1,\theta_1,0)$.

Lemma 5.5. *Assume that* (H1)–(H3) *hold. If* $\int_\Omega f_2'(z-\theta_1)\zeta_0\vartheta_0^2>0$, *then the bifurcation solutions to system* (5.1) *that lie on the local branch* Γ_u^+ *are linearly stable.*

Proof. According to the proof of Lemma 5.3, it is clear that 0 is an I_Y-simple eigenvalue of $D_{(w,u,v)}T(\hat{q},\theta_1,\theta_1,0)$, where the map $I_Y : X \to Y \times [W^{1,r}(\partial\Omega)]^3$ is defined by $I_Y(\zeta,\eta,\vartheta) = (\zeta,\eta,\vartheta,0,0,0)$. Then by [41, Corollary 1.13], there exist continuously differentiable functions

$$q \mapsto (\rho(q),\mathbf{u}(q)),\ \ s \mapsto (\varrho(s),\mathbf{v}(s))$$

defined on the eighborhoods of $\hat{q}$ and 0, respectively, mapping onto $\mathbb{R} \times X$, such that

$$\rho(\hat{q}) = 0,\ \ \mathbf{u}(\hat{q}) = (\zeta_0,\eta_0,\vartheta_0)^\top,\ \ \varrho(0) = 0,\ \ \mathbf{v}(0) = (\zeta_0,\eta_0,\vartheta_0)^\top,$$

and

$$D_{(w,u,v)}T(q,\theta_1,\theta_1,0)\mathbf{u}(q) = (\rho(q)\mathbf{u}(q),\mathbf{0})^\top \quad \text{for } \left|\hat{q} - \frac{1}{2}\right| \ll 1,$$

$$D_{(w,u,v)}T(q(s),w(s),u(s),v(s))\mathbf{v}(s) = (\varrho(s)\mathbf{v}(s),\mathbf{0})^\top \qquad \text{for } |s| \ll 1.$$

It follows from ref. [41, Theorem 1.16] that $\rho'(\hat{q}) \neq 0$ and $\varrho(s)$ has the same sign with $-sq'(s)\rho'(\hat{q})$ if $\varrho(s) \neq 0$ and $|s| \ll 1$.

Noting that $\mathbf{u}(q) = (\zeta(q),\eta(q),\vartheta(q))$ satisfies

$$\begin{aligned}
D_0\Delta\zeta(q) - f_1'(z-\theta_1)\theta_1\zeta(q) - f_1(z-\theta_1)\eta(q) + f_2(z-\theta_1)\vartheta(q) &= \rho(q)\zeta(q),\\
D_0\Delta\eta(q) + f_1(z-\theta_1)\eta(q) + f_1'(z-\theta_1)\theta_1\zeta(q) &= \rho(q)\eta(q),\\
D(q)\big(\vartheta(q)\big)_{xx} + D(1-q)\big(\vartheta(q)\big)_{yy} + f_2(z-\theta_1)\vartheta(q) &= \rho(q)\vartheta(q) \qquad \text{in } \Omega,\\
D_0\nabla\zeta(q)\cdot\nu + b(x,y)\zeta(q) &= 0,\\
D_0\nabla\eta(q)\cdot\nu + b(x,y)\eta(q) &= 0,\\
\Big(D(q)\big(\vartheta(q)\big)_x, D(1-q)\big(\vartheta(q)\big)_y\Big)\cdot\nu + b(x,y)\vartheta(q) &= 0 \quad \text{on } \partial\Omega,
\end{aligned} \tag{5.8}$$

we have $\vartheta(q) > 0$ for $|q-\hat{q}| \ll 1$ since $\vartheta(\hat{q}) = \vartheta_0 > 0$ on $\overline{\Omega}$. Hence, $\rho(q)$ is the principal eigenvalue of the third equation in (5.8), i.e., $\rho(q) = -\lambda_1(q, f_2(z-\theta_1))$ when $|q-\hat{q}| \ll 1$. Recalling equation (2.4), we conclude that

$$\rho'(\hat{q}) = -\frac{\partial\lambda_1(q, f_2(z-\theta_1))}{\partial q}\bigg|_{q=\hat{q}} = -(\overline{D} - \underline{D})F(\hat{q}; f_2(z-\theta_1)) \neq 0.$$

Then we compute $q'(0)$ by the formula [46, equation (4.5)],

$$q'(0) = -\frac{\langle l, D^2_{(w,u,v)}T(\hat{q},\theta_1,\theta_1,0)\big[(\zeta_0,\eta_0,\vartheta_0)^\top,(\zeta_0,\eta_0,\vartheta_0)^\top\big]\rangle}{2\langle l, D_{q(w,u,v)}T(\hat{q},\theta_1,\theta_1,0)(\zeta_0,\eta_0,\vartheta_0)^\top\rangle},$$

where $l: Y \times [W^{1,r}(\partial\Omega)]^3 \to \mathbb{R}$ is a linear functional in $\left(Y \times [W^{1,r}(\partial\Omega)]^3\right)^*$ (see the proof of Lemma 5.3) defined by

$$l(\zeta^*,\eta^*,\vartheta^*,\xi_1,\xi_2,\xi_3) = \int_\Omega \vartheta^*\vartheta_0 - \int_{\partial\Omega} \xi_3\vartheta_0.$$

To this end, we compute

$$D^2_{(w,u,v)}T(\hat{q},\theta_1,\theta_1,0)\big[(\zeta_0,\eta_0,\vartheta_0)^\top,(\zeta_0,\eta_0,\vartheta_0)^\top\big] = \begin{pmatrix} f_1''(z-\theta_1)\theta_1\zeta_0^2 - 2f_1'(z-\theta_1)\zeta_0\eta_0 - 2f_2'(z-\theta_1)\zeta_0\vartheta_0\\ f_1''(z-\theta_1)\theta_1\zeta_0^2 - 2f_1'(z-\theta_1)\zeta_0\eta_0\\ -2f_2'(z-\theta_1)\zeta_0\vartheta_0\\ 0\\ 0\\ 0 \end{pmatrix}.$$

Hence, we have

$$q'(0) = -\frac{\int_\Omega f_2'(z-\theta_1)\zeta_0\vartheta_0^2}{(\overline{D}-\underline{D})\int_\Omega \left(\left((\vartheta_0)_x\right)^2 - \left((\vartheta_0)_y\right)^2\right)}.$$

The denominator on the right-hand side of this equation has the same sign as $F(\hat{q}; f_2(z-\theta_1))$. Under the assumption that $\int_\Omega f_2'(z-\theta_1)\zeta_0\vartheta_0^2 > 0$, we conclude that for $0 < s \ll 1$,

(i) if $F(\hat{q}; f_2(z-\theta_1)) > 0$, then $\rho'(\hat{q}) < 0$ and $q'(s) < 0$, which implies $\varrho(s) < 0$;

(ii) if $F(\hat{q}; f_2(z-\theta_1)) < 0$, then $\rho'(\hat{q}) > 0$ and $q'(s) > 0$, which implies $\varrho(s) < 0$.

Therefore, the bifurcation solutions to system (5.1) that lie on the local branch Γ_u^+ are linearly stable. □

Similarly, we conclude that there is a branch of positive solutions to system (5.1) bifurcating from the semi-trivial branch $\Gamma_v = \{(p, z-\theta_2, 0, \theta_2): p \in [0,1]\}$. For technical reasons, we need to impose the following additional conditions.

(H1*) $q = \frac{1}{2}$ and $0 < D_0 < D_2^*$, which ensures that $\Gamma_v \neq \emptyset$.

(H2*) There exists $\hat{p} \in (0,1)$ such that $\lambda_1(\hat{p}, f_1(z-\theta_2)) = 0$.

(H3*) $F(\hat{p}; f_1(z-\theta_2)) \neq 0$, where F is defined in (2.6).

Lemma 5.6. *Assume that* (H1*)–(H3*) *hold. Then there exists a* C^1 *curve*

$$\Gamma_v^\pm = \{(p(s), S(s), u(s), v(s)): s \in (-s_2, s_2)\},$$

such that $((p(s), S(s), u(s), v(s)))$ *is a solution to system* (5.1) *for any* $s \in (-s_2, s_2)$, *and the solution is positive for any* $s \in (0, s_2)$, *where*

$$S(s) = z - \theta_2 - s(\hat{\zeta}_0 + \hat{W}(s)),\ \ u(s) = s(\hat{\eta}_0 + \hat{U}(s)) \text{ and } v(s) = \theta_2 + s(\hat{\vartheta}_0 + \hat{V}(s)).$$

Here,

$$p(0) = \hat{p},\ \ \hat{W}(0) = 0, \hat{U}(0) = 0,\ \ \hat{V}(0) = 0 \text{ and } (\hat{W}(s), \hat{U}(s), \hat{V}(s)) \in \hat{Z},$$

where $\hat{Z} = \{(\hat{W}, \hat{U}, \hat{V}) \in X: \int_\Omega \hat{U}\hat{\eta}_0 = 0\}$ *with* $\hat{\eta}_0$ *being a positive principal eigenfunction corresponding* $\lambda_1(\hat{p}, f_1(z-\theta_2))$, *and* $(\hat{\zeta}_0, \hat{\vartheta}_0)$ *satisfies*

$$\begin{aligned} D_0\Delta\hat{\zeta}_0 - f_2'(z-\theta_2)\theta_2\hat{\zeta}_0 + f_2(z-\theta_2)\hat{\vartheta}_0 + f_1(z-\theta_2)\hat{\eta}_0 = 0, & \\ D_0\Delta\hat{\vartheta}_0 + f_2(z-\theta_2)\hat{\vartheta}_0 - f_2'(z-\theta_2)\theta_2\hat{\zeta}_0 = 0 & \quad \text{in } \Omega, \\ D_0\nabla\hat{\zeta}_0 \cdot \nu + b(x,y)\hat{\zeta}_0 = 0, & \\ D_0\nabla\hat{\vartheta}_0 \cdot \nu + b(x,y)\hat{\vartheta}_0 = 0 & \quad \text{on } \partial\Omega. \end{aligned}$$

Moreover, if $\int_\Omega f_1'(z-\theta_2)\hat{\zeta}_0\hat{\eta}_0^2 > 0$, *then the bifurcation solutions to system* (5.1) *that lie on the local branch* $\Gamma_v^+ = \{(p(s), S(s), u(s), v(s)) \in \Gamma_v^\pm: s \in (0, s_2)\}$ *are linearly stable.*

Remark 5.7. The concavity of $\lambda_1(p, f_1(z-\theta_2))$ with respect to p implies that there exist at most two bifurcation points of positive solutions bifurcating from the semi-trivial branch Γ_v.

5.2 Global bifurcation

In this subsection, we extend the local solution branches Γ_u^+ and Γ_v^+ in Lemmas 5.3 and 5.6 by applying the global bifurcation results for Fredholm operators.

Initially, we extend the local solution branches Γ_u^+. Before proceeding, we first introduce a few additional assumptions. Consider

$$f_1(z) - f_2(z) = \frac{m_1 a_1 z}{(a_1+z)(a_2+z)}\left[(m_1-m_2)\frac{z}{m_1 a_1} + \frac{a_2}{a_1} - \frac{m_2}{m_1}\right].$$

It is easy to see that if one of the following condition holds, then $f_1(z) \leq, \not\equiv f_2(z)$ on $\overline{\Omega}$.

(1) $m_1 > m_2$, $\frac{a_2}{a_1} < \frac{m_2}{m_1}$, $0 < z \leq, \not\equiv \frac{m_2 a_1 - m_1 a_2}{m_1 - m_2}$ on $\overline{\Omega}$.
(2) $m_1 = m_2$, $\frac{a_2}{a_1} < \frac{m_2}{m_1}$.
(3) $m_1 < m_2$, $\frac{a_2}{a_1} \leq \frac{m_2}{m_1}$.
(4) $m_1 < m_2$, $\frac{a_2}{a_1} > \frac{m_2}{m_1}$, $z \geq, \not\equiv \frac{m_2 a_1 - m_1 a_2}{m_1 - m_2}$ on $\overline{\Omega}$.

We now present two additional conditions.
(H4) $\max_{q\in[0,1]} \lambda_1(q, f_2(z)) = \lambda_1(q_{\mathrm{m}}, f_2(z)) \geq 0$.
(H5) (1) $m_1 = m_2$, $a_1 > a_2$; or (2) $m_1 < m_2$, $\frac{a_2}{a_1} \leq \frac{m_2}{m_1}$.

Here, (H5) implies that $f_1(h) < f_2(h)$ for any $h > 0$ on $\overline{\Omega}$. Define

$$\Upsilon_q = \left\{(q, S, u, v) \in \mathbb{R} \times X : S > 0, u > 0, v > 0, (q, S, u, v) \text{ satisfies system (5.1) with } p = \frac{1}{2}\right\}.$$

Theorem 5.8. *Assume that* (H1)–(H5) *hold. If (i)* $\hat{q} \geq \frac{1}{2}$ *and* $F(\hat{q}; f_2(z-\theta_1)) > 0$, *or (ii)* $\hat{q} \leq \frac{1}{2}$ *and* $F(\hat{q}; f_2(z-\theta_1)) < 0$, *then there exists a continuum* C_q^* *of* Υ_q *bifurcating from* Γ_u *at* $(\hat{q}, z-\theta_1, \theta_1, 0)$ *and meeting another semi-trivial branch* $\{(q, S_q, 0, v_q) : \lambda_1(q, f_2(z)) < 0\}$ *at the point* $(\tilde{q}, S_{\tilde{q}}, 0, v_{\tilde{q}})$, *where* $\tilde{q}$ *satisfies* $\lambda_1\left(\frac{1}{2}, f_1(S_{\tilde{q}})\right) = 0$. *In particular, system* (5.1) *has at least one positive solution for any q between* $\hat{q}$ *and* $\tilde{q}$.

Proof. In view of ref. [40, Theorem 3.3], we conclude that for any $(q, w, u, v) \in (0,1) \times X$, the Fréchet derivative $D_{(w,u,v)}T(q, w, u, v)$ is a Fredholm operator with index zero; recall (5.4) for the definition of operator T. Moreover, $T : (0,1) \times X \to Y \times [W^{1,r}(\partial\Omega)]^3$ is C^1 smooth. Similar to the definition in ref. [42, Theorem 1.2], let $\tilde{C}_q$ be the component of the set of nontrivial solutions to $T(q, w, u, v) = \mathbf{0}$ with $(\hat{q}, \theta_1, \theta_1, 0) \in \tilde{C}_q$. Set

$$C_q = \{(q, S, u, v) : S = z - w, (q, w, u, v) \in \tilde{C}_q\}.$$

Let C_q^+ be the connected component of $C_q \backslash \{(q(s), S(s), u(s), v(s)) : -s_1 < s < 0\}$. Then $\Gamma_u^+ \subset C_q^+$. It follows from ref. [42, Theorem 1.2] that C_q^+ satisfies one of the following alternatives:
(i) it is not compact in $(0,1) \times X$;
(ii) it contains a point $(\tilde{q}, z-\theta_1, \theta_1, 0)$ with $\tilde{q} \neq \hat{q}$;
(iii) it contains a point $(q, z-\theta_1+W, \theta_1+U, V)$, where $(W, U, V) \not\equiv (0,0,0)$ and $(W, U, Z) \in Z$.

We set

$$X^+ = \left\{(S, u, v) \in X : S > 0, u > 0, v > 0 \quad \text{on } \overline{\Omega}\right\}.$$

Consequently, $C_q \cap ((0,1) \times X^+) \neq \emptyset$. Let $C_q^* = C_q \cap ((0,1) \times X^+)$. Then C_q^* consists of the local positive solution branch Γ_u^+ near the bifurcation point $(\hat{q}, z-\theta_1, \theta_1, 0)$ and $C_q^* \subset C_q^+$.

Suppose (iii) holds. For any $(q, z-\theta_1+W, \theta_1+U, V) \in C_q^+$ with $(W, U, V) \not\equiv (0,0,0)$, we have $(q, z-\theta_1+W, \theta_1+U, V) \in C_q^*$, which implies that $V > 0$ on $\overline{\Omega}$. Hence, $\int_\Omega V\vartheta_0 > 0$, which contradicts $(W, U, V) \in Z$.

Suppose (ii) holds. Then we may construct a sequence $\{(q_n, S_n, u_n, v_n)\} \subset C_q^*$ converging to $(\tilde{q}, z-\theta_1, \theta_1, 0)$ in $(0,1) \times \overline{X^+}$. By the equation for v_n in system (5.1), we have $\lambda_1(q_n, f_2(S_n)) = 0$. Letting $n \to \infty$, we get $\lambda_1(\tilde{q}, f_2(z-\theta_1)) = 0$ by continuity. (H2) implies that $\lambda_1(\hat{q}, f_2(z-\theta_1)) = 0$. Without loss of generality, we assume $\hat{q} < \tilde{q}$. It follows from Lemma 2.1 that $\lambda_1(q, f_2(z-\theta_1)) \leq 0$ for all $q \in [0,1] \backslash (\hat{q}, \tilde{q})$. Note that $\max_{q\in[0,1]} \lambda_1(q, f_2(z)) = \lambda_1(q_{\mathrm{m}}, f_2(z)) \geq 0$ and $\lambda_1(q, f_2(z)) < \lambda_1(q, f_2(z-\theta_1)) \leq 0$ for all $q \in [0,1] \backslash (\hat{q}, \tilde{q})$; see Lemma 2.2(ii) and (H4). From this, we deduce that $q_{\mathrm{m}} \in (\hat{q}, \tilde{q})$. However, Lemma 5.2(i) implies that if $\lambda_1(q_{\mathrm{m}}, f_2(z)) \geq 0$, then system (5.1) has no nonnegative solution (S, u, v) such that $(q_{\mathrm{m}}, S, u, v) \in C_q^*$. Hence, the component C_q^+ cannot connect $(\hat{q}, z - \theta_1, \theta_1, 0)$ and $(\tilde{q}, z - \theta_1, \theta_1, 0)$ in $(0,1) \times X$, meaning that $(\tilde{q}, z - \theta_1, \theta_1, 0) \notin C_q^+$. Thus, (ii) can not occur.

The alternative (i) for C_q^+ is equivalent to "the closure of C_q^+ intersects $\partial((0,1) \times X^+)$ or is unbounded in norm of $(0,1) \times X^+$"; see, e.g., the proof of ref. [40, Theorem 4.7]. It follows from Lemma 5.2 and the standard elliptic regularity theory that any positive solution (S, u, v) to system (5.1) is bounded in X^+ uniformly for all $q \in [0,1]$. Thus, (i) implies that there exists a point $(\tilde{q}, \tilde{S}, \tilde{u}, \tilde{v}) \in (\overline{C_q^*} \backslash \{(\hat{q}, z - \theta_1, \theta_1, 0)\}) \cap \partial((0,1) \times X^+)$, which is the limit of a sequence $\{(q_n, S_n, u_n, v_n)\} \subset C_q^*$.

We only consider the case where $\hat{q} \geq \frac{1}{2}$ and $F(\hat{q}; f_2(z - \theta_1)) > 0$, i.e., $\frac{\partial \lambda_1(q, f_2(z-\theta_1))}{\partial q}|_{q=\hat{q}} > 0$. The same analytical framework can be applied to other cases. In view of Lemma 2.1 and (H4), $\lambda_1(q, f_2(z))$ attains a unique maximum at a point $q_{\mathrm{m}} \in (\hat{q}, 1]$ such that $\lambda_1(q_{\mathrm{m}}, f_2(z)) \geq 0$. However, Lemma 5.2(i) implies that if $\lambda_1(q_{\mathrm{m}}, f_2(z)) \geq 0$, then system (5.1) has no nonnegative solution (S, u, v) such that $(q_{\mathrm{m}}, S, u, v) \in C_q^*$. Hence, we conclude that the component C_q^+ cannot intersect with the plane $\left\{(1, S, u, v) : S, u, v > 0 \quad \text{on } \overline{\Omega}\right\}$. Thus, $(\tilde{q}, \tilde{S}, \tilde{u}, \tilde{v}) \in \partial((0,1) \times X^+)$ implies that

(1) $\tilde{S} \geq 0$ and $\tilde{S}(x_0, y_0) = 0$ for a point $(x_0, y_0) \in \overline{\Omega}$; or
(2) $\tilde{u} \geq 0$ and $\tilde{u}(x_1, y_1) = 0$ for a point $(x_1, y_1) \in \overline{\Omega}$; or
(3) $\tilde{v} \geq 0$ and $\tilde{v}(x_2, y_2) = 0$ for a point $(x_2, y_2) \in \overline{\Omega}$; or
(4) $\tilde{q} = 0$ and $\tilde{S} > 0, \tilde{u} > 0, \tilde{v} > 0$ on $\overline{\Omega}$, i.e., $(\tilde{S}, \tilde{u}, \tilde{v}) \in X^+$.

It follows from the strong maximum principle that $\tilde{S} > 0$ on $\overline{\Omega}$. Hence, (1) is impossible.

(4) implies that the bifurcation branch C_q^+ meet the plane $\{(0, S, u, v) : S, u, v > 0 \quad \text{on } \overline{\Omega}\}$ at the point $(0, \tilde{S}, \tilde{u}, \tilde{v})$ as $q \to 0$. By the equations for u and v in system (5.1), we have $\lambda_1\left(\frac{1}{2}, f_1(S)\right) = \lambda_1(0, f_2(S)) = 0$. In view of Lemma 2.2(ii) and (H5), we have $\lambda_1\left(\frac{1}{2}, f_2(S)\right) < \lambda_1\left(\frac{1}{2}, f_1(S)\right) = 0$. It follows from Lemma 5.2(ii) and (H4) that $\lambda_1(q_{\mathrm{m}}, f_2(S)) > \lambda_1(q_{\mathrm{m}}, f_2(z)) \geq 0$. By the concavity of $\lambda_1(q, f_2(S))$ with respect to q on [0, 1], we deduce that $0 < q_{\mathrm{m}} < \frac{1}{2}$. However, in the case where $\hat{q} \geq \frac{1}{2}$ and $F(\hat{q}; f_2(z - \theta_1)) > 0$, i.e., $\frac{\partial \lambda_1(q, f_2(z-\theta_1))}{\partial q}|_{q=\hat{q}} > 0$, noting that $\lambda_1(q_{\mathrm{m}}, f_2(z - \theta_1)) > \lambda_1(q_{\mathrm{m}}, f_2(z)) \geq 0$, we deduce $q_{\mathrm{m}} > \hat{q} \geq \frac{1}{2}$, which is a contradiction.

By applying the strong maximum principle again, we conclude that (2) and (3) imply $\tilde{u} \equiv 0$ or $\tilde{v} \equiv 0$, which leads to the following three alternatives: (a) $(\tilde{S}, \tilde{u}, \tilde{v}) = (z, 0, 0)$; (b) $(\tilde{S}, \tilde{u}, \tilde{v}) = (z - \theta_1, \theta_1, 0)$; (c) $(\tilde{S}, \tilde{u}, \tilde{v}) = (S_{\tilde{q}}, 0, v_{\tilde{q}})$.

Suppose $(\tilde{S}, \tilde{u}, \tilde{v}) = (z, 0, 0)$. Then the sequence $\{(q_n, S_n, u_n, v_n)\}$ satisfies $q_n \to \tilde{q}$ and $(S_n, u_n, v_n) \to (z, 0, 0)$ in X as $n \to \infty$. By the equation for u_n in system (5.1), we have $\lambda_1\left(\frac{1}{2}, f_1(S_n)\right) = 0$. Letting $n \to \infty$, we get $\lambda_1\left(\frac{1}{2}, f_1(z)\right) = 0$ by continuity. In view of Lemma 2.3 and (H1), we have $\lambda_1\left(\frac{1}{2}, f_1(z)\right) < 0$, a contradiction.

Suppose $(\tilde{S}, \tilde{u}, \tilde{v}) = (z - \theta_1, \theta_1, 0)$. Then using similar arguments as those in the analysis of case (ii), we obtain that $\lambda_1(\tilde{q}, f_2(z - \theta_1)) = 0$ and if $\tilde{q} \neq \hat{q}$, then $(\tilde{q}, z - \theta_1, \theta_1, 0) \notin C_q^+$, which leads to a contradiction.

The remainning possibility is $(\tilde{S}, \tilde{u}, \tilde{v}) = (S_{\tilde{q}}, 0, v_{\tilde{q}})$, which implies that the global bifurcation branch C_q^+ meet another semi-trivial branch $\left\{(q, S_q, 0, v_q) : \lambda_1(q, f_2(z)) < 0\right\}$ at the point $(\tilde{q}, S_{\tilde{q}}, 0, v_{\tilde{q}})$, where $\tilde{q}$ satisfies $\lambda_1\left(\frac{1}{2}, f_1(S_{\tilde{q}})\right) = 0$. This completes the proof. □

Remark 5.9. Theorem 5.8 implies that $(\tilde{q}, S_{\tilde{q}}, 0, v_{\tilde{q}})$ is a bifurcation point from the semi-trivial branch $\left\{(q, S_q, 0, v_q) : \lambda_1(q, f_2(z)) < 0\right\}$.

Similarly, we extend the local solution branches Γ_v^+. For technical reasons, we need to impose the following additional conditions.

(H4*) $\max_{p \in [0,1]} \lambda_1(p, f_1(z)) = \lambda_1\big(p_{\mathrm{m}}, f_1(z)\big) \geq 0$.
(H5*) (1) $m_1 = m_2, a_1 < a_2$; or (2) $m_1 > m_2, \frac{a_2}{a_1} \geq \frac{m_2}{m_1}$.

Here, (H5*) implies that $f_1(h) < f_2(h)$ for any $h > 0$ on $\overline{\Omega}$. Define

$$\Upsilon_p = \left\{(p, S, u, v) \in \mathbb{R} \times X: S > 0, u > 0, v > 0, (p, S, u, v) \text{ satisfies system (5.1) with } q = \frac{1}{2}\right\}.$$

Theorem 5.10. *Assume that* (H1*)–(H5*) *hold. Then if (i)* $\hat{p} \geq \frac{1}{2}$ *and* $F(\hat{p}; f_1(z - \theta_2)) > 0$*, or (ii)* $\hat{p} \leq \frac{1}{2}$ *and* $F(\hat{p}; f_1(z - \theta_2)) < 0$*, then there exists a continuum* C_p^* *of* Υ_p *bifurcating from* Γ_u *at* $(\hat{p}, z - \theta_2, 0, \theta_2)$ *and meeting another semi-trivial branch* $\left\{(p, S_p, u_p, 0): \lambda_1(p, f_1(z)) < 0\right\}$ *at the point* $(\tilde{p}, S_{\tilde{p}}, u_{\tilde{p}}, 0)$*, where* $\tilde{p}$ *satisfies* $\lambda_1\left(\frac{1}{2}, f_2(S_{\tilde{p}})\right) = 0$*. In particular, system* (5.1) *has at least one positive solution for any p between* $\hat{p}$ *and* $\tilde{p}$*.*

Remark 5.11. Theorem 5.10 implies that $(\tilde{p}, S_{\tilde{p}}, u_{\tilde{p}}, 0)$ is a bifurcation point from the semi-trivial branch $\left\{(p, S_p, u_p, 0): \lambda_1(p, f_1(z)) < 0\right\}$.

6 Numerical simulation

We perform numerical experiments in this section to enhance the qualitative understanding of the results and to gain further insights. The computations are primarily executed with FreeFEM++, an open-source finite element software [47]. We first assume that the domain Ω is fixed and defined as a disk of radius 2 centered at the origin. Specifically, $\partial\Omega = \{(x, y): x = 2\cos\theta,\ y = 2\sin\theta,\ \theta \in [0, 2\pi)\}$. Moreover, we assume that

$$\Gamma_b = \left\{(x, y) \in \partial\Omega: x = 2\cos\theta, y = 2\sin\theta, \theta \in \left(-\frac{\pi}{4}, \frac{\pi}{4}\right)\right\},$$
$$\Gamma_H = \left\{(x, y) \in \partial\Omega: x = 2\cos\theta, y = 2\sin\theta, \theta \in \left(\frac{3\pi}{4}, \frac{5\pi}{4}\right)\right\}.$$

For $x = 2\cos\theta, y = 2\sin\theta$, we take

$$b(x, y) = \begin{cases} \frac{1}{2}(1 + \cos 4\theta), & (x, y) \in \Gamma_b, \\ 0, & (x, y) \in \partial\Omega\backslash\Gamma_b, \end{cases}$$

$$H(x, y) = \begin{cases} \frac{3}{2}(1 + \cos 4\theta), & (x, y) \in \Gamma_H, \\ 0, & (x, y) \in \partial\Omega\backslash\Gamma_H. \end{cases}$$

6.1 The principal eigenvalue

We first consider $\lambda_1(p, f_1(z))$, which is the principal eigenvalue of problem (2.1) with $h = f_1(z)$. The parameter values are given in this subsection as follows

$$\underline{D} = 0.1,\ \overline{D} = 10,\ a_1 = 5.$$

Figure 2 displays numerical results for the principal eigenvalue $\lambda_1(p, f_1(z))$, where $p \in [0, 1]$ and $m_1 = 0.2, 0.25, 0.3$. From this figure, we observe that $\lambda_1(p, f_1(z))$ is a concave function with respect to p. Moreover, for all $p \in [0, 1]$, $\lambda_1(p, f_1(z))$ decreases uniformly as m_1 increases. This observation aligns with the conclusions of Lemmas 2.1 and 2.2(ii).

6.2 The two-species model

Now we investigate system (1.1)–(1.3). In this subsection, we fix the parameter values as follows

$$\underline{D} = 0.1,\ \overline{D} = 10,\ m_1 = 0.2,\ m_2 = 0.3,\ a_1 = 4,\ a_2 = 5,\ S_0 = 0,\ u_0 = 3,\ v_0 = 3.$$

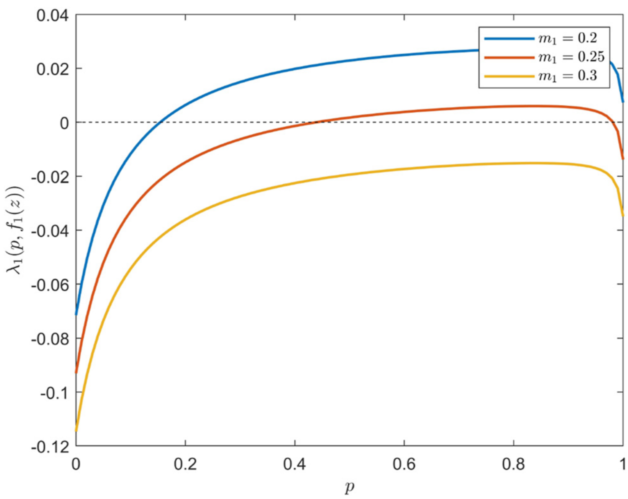


Figure 2: The principal eigenvalue $\lambda_1(p, f_1(z))$, where $p \in [0, 1]$ and $m_1 = 0.2, 0.25, 0.3$.

Figure 3 displays numerical results for the evolution of $\|S(\cdot,\cdot,t)\|_{L^\infty(\Omega)}$, $\|u(\cdot,\cdot,t)\|_{L^\infty(\Omega)}$ and $\|v(\cdot,\cdot,t)\|_{L^\infty(\Omega)}$ for system (1.1)–(1.3), where $(p, q) = (0.7, 0.05)$, $(0.7, 0.5)$, $(0.15, 0.5)$, $(0.0948, 1)$. In both subfigures (a)–(b), $\|v(\cdot,\cdot,t)\|_{L^\infty(\Omega)}$ reaches a steady state, while $\|u(\cdot,\cdot,t)\|_{L^\infty(\Omega)}$ diminishes asymptotically to zero. By comparing subfigures (a)–(b), we observe that when $(p, q) = (0.7, 0.05)$, the value of $\|v(\cdot,\cdot,t)\|_{L^\infty(\Omega)}$ at equilibrium is significantly higher than when $(p, q) = (0.7, 0.5)$. This suggests that as the anisotropic diffusion of the surviving population v becomes stronger, the population distribution tends to become more concentrated. This implies that anisotropic diffusion may benefit the survival of the population. In subfigure (c), $\|u(\cdot,\cdot,t)\|_{L^\infty(\Omega)}$ reaches a steady state, while $\|v(\cdot,\cdot,t)\|_{L^\infty(\Omega)}$ gradually approaches zero. In subfigure (d), both curves progressively stabilize to steady states. The numerical simulations shown in Figure 3 have the same parameters except for the diffusion strategies (p, q). This indicates that variations in the diffusion strategies can have complex and diverse effects on the dynamics of system (1.1)–(1.3).

Figure 4 depicts the spatiotemporal dynamics of (S, u, v) for system (1.1)–(1.3). The simulation parameters are identical to those in Figure 3(d). The figure shows points on the curves in Figure 3(d) in the $x - y$ plane. It can be observed from the figure that the diffusion patterns of the two populations are not identical. Furthermore, based on Figures 3(d) and 4, it can be observed that the single-directional diffusion strategy leads to the aggregation of the population within localized regions. This suggests that anisotropic diffusion provides more possibilities for species coexistence.

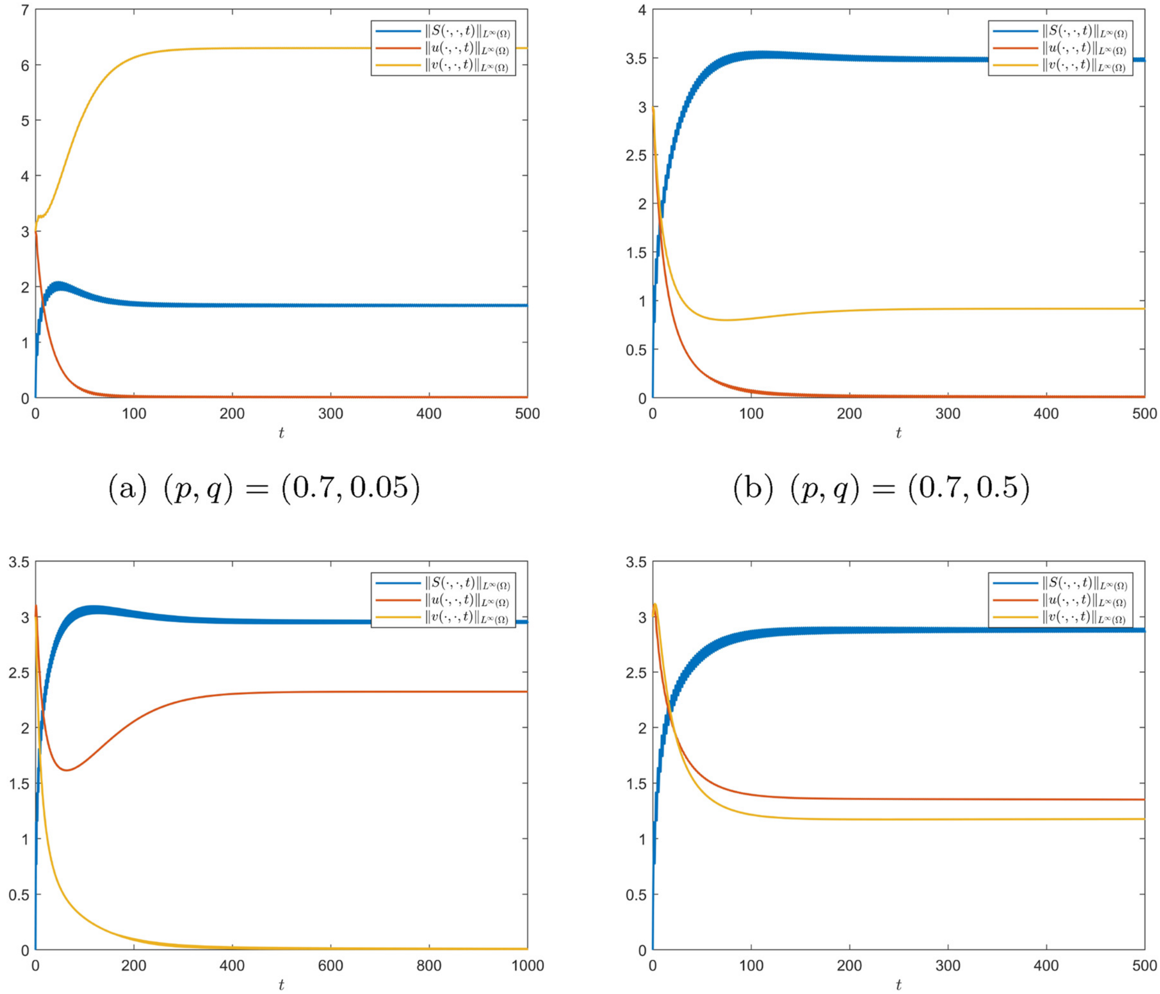
Then we further study the steady states of system (1.1)–(1.3). All parameters remain unchanged except for (p, q). Figure 5 displays numerical results for the bifurcation diagrams of steady states for system (1.1)–(1.3), where $q = 0.5$ and the bifurcation parameter p ranging from 0 to 1. This figure shows that when $q = 0.5$ and $p \in [0, 1]\backslash[0.13, 0.18]$, the two populations undergo competitive exclusion, whereas when $q = 0.5$, $p \in (0.13, 0.18)$, both populations coexist. By comparing the values $\frac{m_1}{a_1} < \frac{m_2}{a_2}$, it is clear that the population u has lower survival capability than v. However, when p takes smaller values, the population u can still survive as one of the competitors in competitive exclusion or coexist with the population v. This once again demonstrates that anisotropic diffusion introduces a rich variety of changes to the dynamics behavior of this system.

6.3 The rectangular model

Finally, we present numerical simulations for some scenarios with $\Omega = [0, 1]^2$, a setting that has not yet been addressed in the theoretical analysis. These simulations could be valuable in guiding future research and exploration.

For ease of comparison, the parameters used in Figures 6 and 7, except for Ω, b, H, are the identical to those employed in the previous numerical simulations. Here, we first assume that

$$\hat{\Gamma}_b = \{(x, y) \in \partial\Omega : x = 1, 0 \le y \le 1\}, \ \hat{\Gamma}_H = \{(x, y) \in \partial\Omega : x = 0, 0 \le y \le 1\}.$$



(a) $(p,q) = (0.7, 0.05)$ (b) $(p,q) = (0.7, 0.5)$

(c) $(p,q) = (0.15, 0.5)$ (d) $(p,q) = (0.0948, 1)$

Figure 3: The evolution of $\|S(\cdot,\cdot,t)\|_{L^\infty(\Omega)}$, $\|u(\cdot,\cdot,t)\|_{L^\infty(\Omega)}$ and $\|v(\cdot,\cdot,t)\|_{L^\infty(\Omega)}$ for system (1.1)–(1.3), where $(p,q) = (0.7, 0.05)$, $(0.7, 0.5)$, $(0.15, 0.5)$, $(0.0948, 1)$. The thicker parts of the curves in this figure are caused by dense oscillations.

Take

$$b(x,y) = \begin{cases} \frac{1}{2}\big(1+\cos(2y-1)\pi\big), & (x,y) \in \hat{\Gamma}_b, \\ 0, & (x,y) \in \partial\Omega \backslash \hat{\Gamma}_b, \end{cases}$$

$$H(x,y) = \begin{cases} \frac{3}{2}\big(1+\cos(2y-1)\pi\big), & (x,y) \in \hat{\Gamma}_H, \\ 0, & (x,y) \in \partial\Omega \backslash \hat{\Gamma}_H. \end{cases}$$

Figure 6 displays the spatiotemporal dynamics of (S, u, v) obtained under the prescribed parameter setting. We find that the system appears to reach equilibrium more quickly. However, unlike the case when Ω is a disk, both populations u and v tend to approach very small values, which seems to suggest that both populations may eventually go extinct.

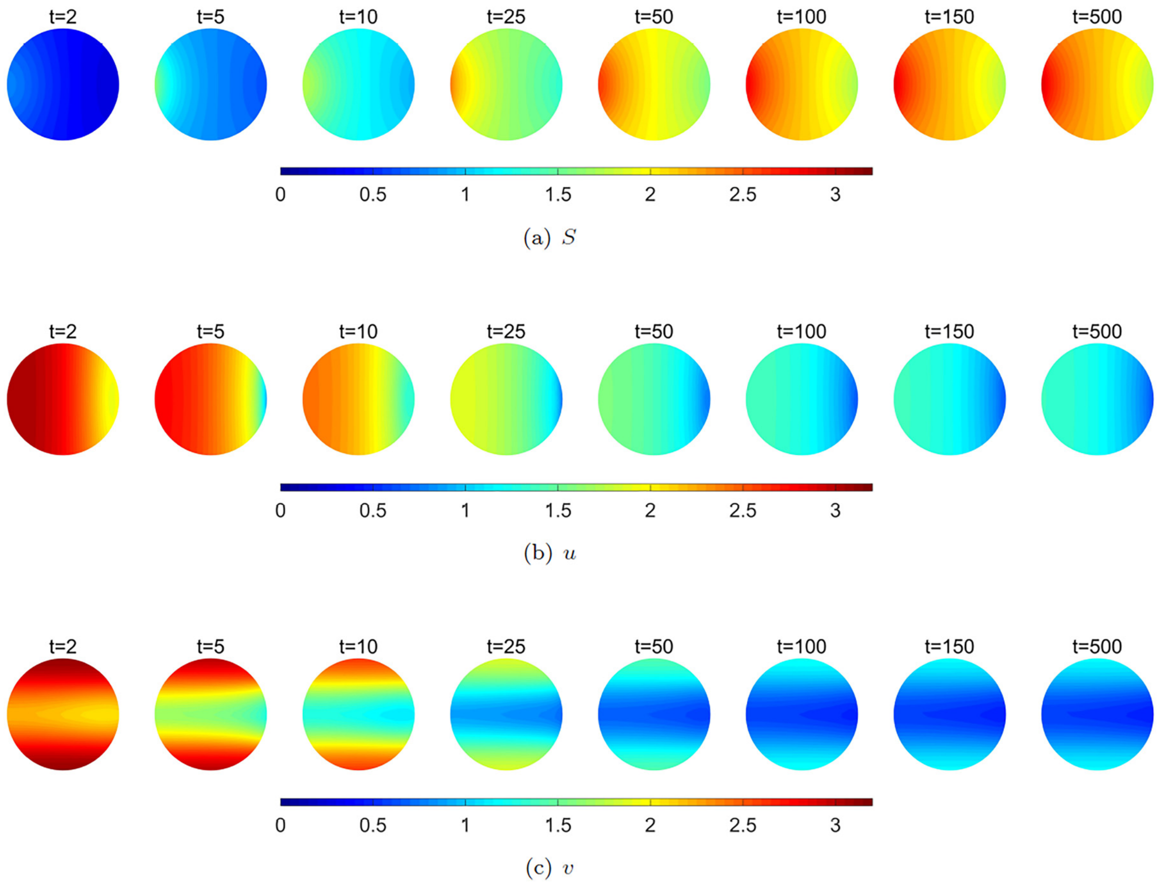


Figure 4: The solution (S, u, v) for system (1.1)–(1.3) at different moments, where $(p, q) = (0.0948, 1)$.

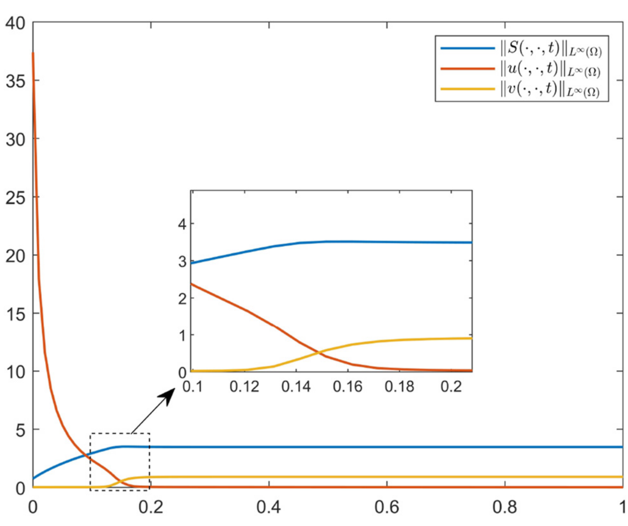


Figure 5: Bifurcation diagrams of steady states for system (1.1)–(1.3), where $q = 0.5$ and $p \in [0, 1]$.

We then consider another scenario where

$$\tilde{\Gamma}_b^1 = \{(x, y) \in \partial\Omega : x = 1, 0 \le y \le 1\}, \quad \tilde{\Gamma}_b^2 = \{(x, y) \in \partial\Omega : 0 \le x \le 1, y = 1\},$$
$$\tilde{\Gamma}_H^1 = \{(x, y) \in \partial\Omega : x = 0, 0 \le y \le 1\}, \quad \tilde{\Gamma}_H^2 = \{(x, y) \in \partial\Omega : 0 \le x \le 1, y = 0\}.$$

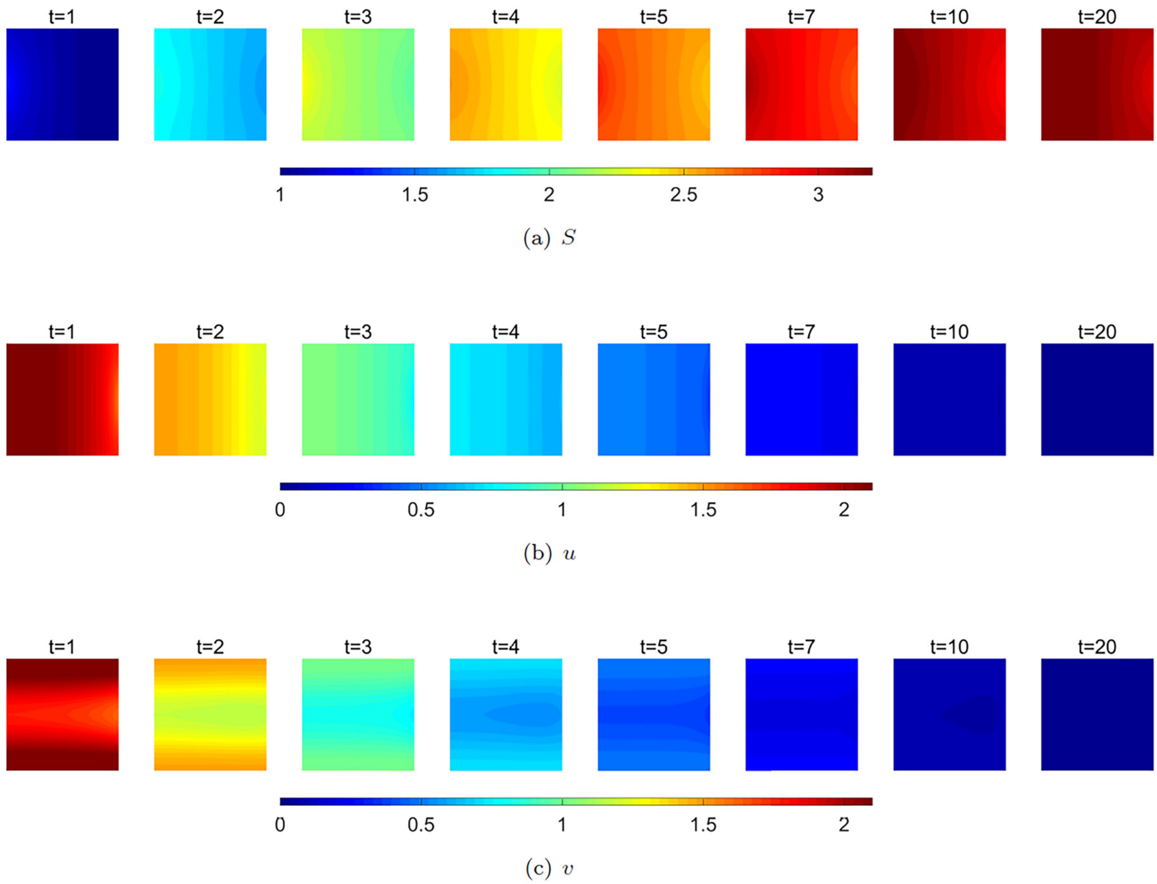


Figure 6: The solution (S, u, υ) for system (1.1)–(1.3) at different moments, where $(p, q) = (0.0948, 1)$.

Take

$$b(x,y) = \begin{cases} \frac{1}{2}\left(1+\cos(2y-1)\pi\right), & (x,y) \in \tilde{\Gamma}_b^1, \\ \frac{1}{2}\left(1+\cos(2x-1)\pi\right), & (x,y) \in \tilde{\Gamma}_b^2, \\ 0, & (x,y) \in \partial\Omega \backslash \left(\tilde{\Gamma}_b^1 \cap \tilde{\Gamma}_b^2\right), \end{cases}$$

$$H(x,y) = \begin{cases} \frac{3}{2}\left(1+\cos(2y-1)\pi\right), & (x,y) \in \tilde{\Gamma}_H^1, \\ \frac{3}{2}\left(1+\cos(2x-1)\pi\right), & (x,y) \in \tilde{\Gamma}_H^2, \\ 0, & (x,y) \in \partial\Omega \backslash \left(\tilde{\Gamma}_H^1 \cap \tilde{\Gamma}_H^2\right). \end{cases}$$

Figure 7 displays the spatiotemporal dynamics of (S, u, υ) obtained under the prescribed parameter setting. Similarly, the system appears to reach equilibrium more quickly, with both populations u and υ approaching near-zero levels, indicating a potential trajectory toward extinction for both species.

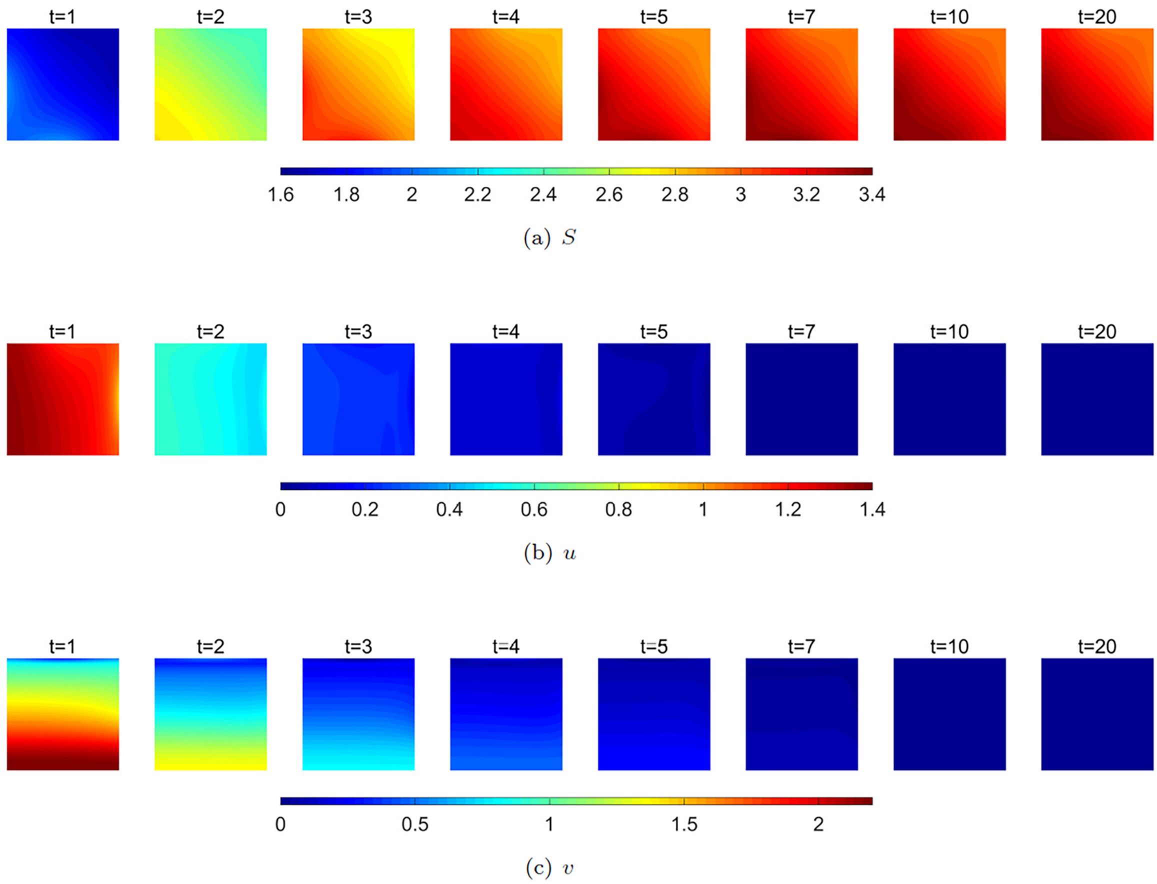


Figure 7: The solution (S, u, v) for system (1.1)–(1.3) at different moments, where $(p, q) = (0.0948, 1)$.

Furthermore, we also identified coexistence of the two species by varying other parameters, as illustrated in Figures 8 and 9. The time required to reach equilibrium is comparable to that observed when Ω is a disk. The parameter values used in the numerical simulation shown in Figure 8 are

$$\underline{D} = 0.1,\ \overline{D} = 10,\ m_1 = 0.2,\ m_2 = 0.3,\ a_1 = 4,\ a_2 = 6.07,\ S_0 = 0,\ u_0 = 3,\ v_0 = 3,$$

and

$$b(x,y) = \begin{cases} \frac{1}{10}\left(1 + \cos(2y-1)\pi\right), & (x,y) \in \hat{\Gamma}_b, \\ 0, & (x,y) \in \partial\Omega \backslash \hat{\Gamma}_b, \end{cases}$$

$$H(x,y) = \begin{cases} \frac{1}{2}\left(1 + \cos(2y-1)\pi\right), & (x,y) \in \hat{\Gamma}_H, \\ 0, & (x,y) \in \partial\Omega \backslash \hat{\Gamma}_H, \end{cases}$$

while those used in Figure 9 are

$$\underline{D} = 0.1,\ \overline{D} = 10,\ m_1 = 0.2,\ m_2 = 0.3,\ a_1 = 2.4243,\ a_2 = 5,\ S_0 = 0,\ u_0 = 3,\ v_0 = 3,$$

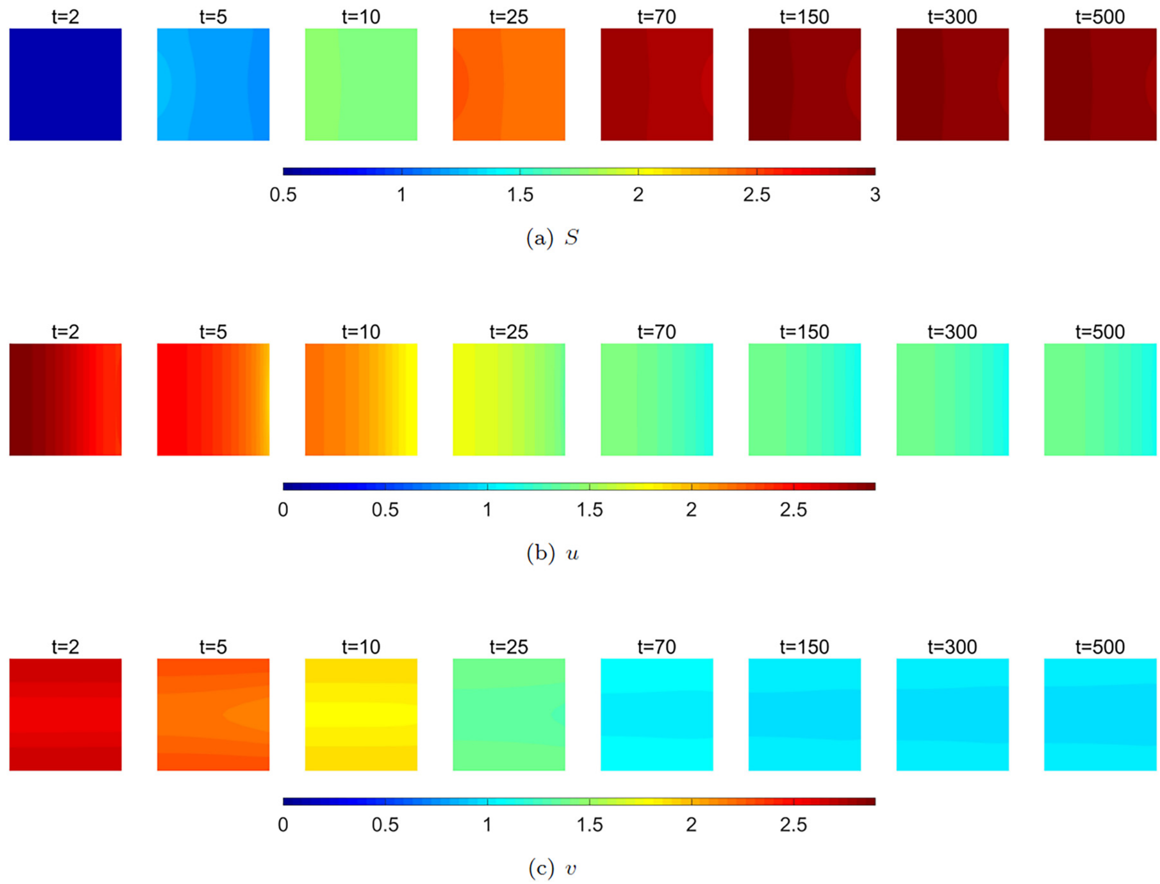


Figure 8: The solution (S, u, v) for system (1.1)–(1.3) at different moments, where $(p, q) = (0.01, 1)$.

and

$$b(x,y) = \begin{cases} \frac{1}{20}\big(1+\cos(2y-1)\pi\big), & (x,y) \in \tilde{\Gamma}_b^1, \\ \frac{1}{20}\big(1+\cos(2x-1)\pi\big), & (x,y) \in \tilde{\Gamma}_b^2, \\ 0, & (x,y) \in \partial\Omega \backslash \big(\tilde{\Gamma}_b^1 \cap \tilde{\Gamma}_b^2\big), \end{cases}$$

$$H(x,y) = \begin{cases} \frac{1}{4}\big(1+\cos(2y-1)\pi\big), & (x,y) \in \tilde{\Gamma}_H^1, \\ \frac{1}{4}\big(1+\cos(2x-1)\pi\big), & (x,y) \in \tilde{\Gamma}_H^2, \\ 0, & (x,y) \in \partial\Omega \backslash \big(\tilde{\Gamma}_H^1 \cap \tilde{\Gamma}_H^2\big). \end{cases}$$

A comparison between the parameter settings in Figures 6 and 8 suggests that coexistence of the two populations occurs only when both $b(x,y)$ and $H(x,y)$ are relatively small. By comparing the parameters used in Figures 8 and 9, it can be observed that although the values of $b(x,y)$ differ, their integrals over $\partial\Omega$ are identical. The same holds true for $H(x,y)$. Consequently, the non-zero regions of $b(x,y)$ and $H(x,y)$ in Figure 9 are larger than those in Figure 8, which results in relatively smaller maximum values for $b(x,y)$ and $H(x,y)$.

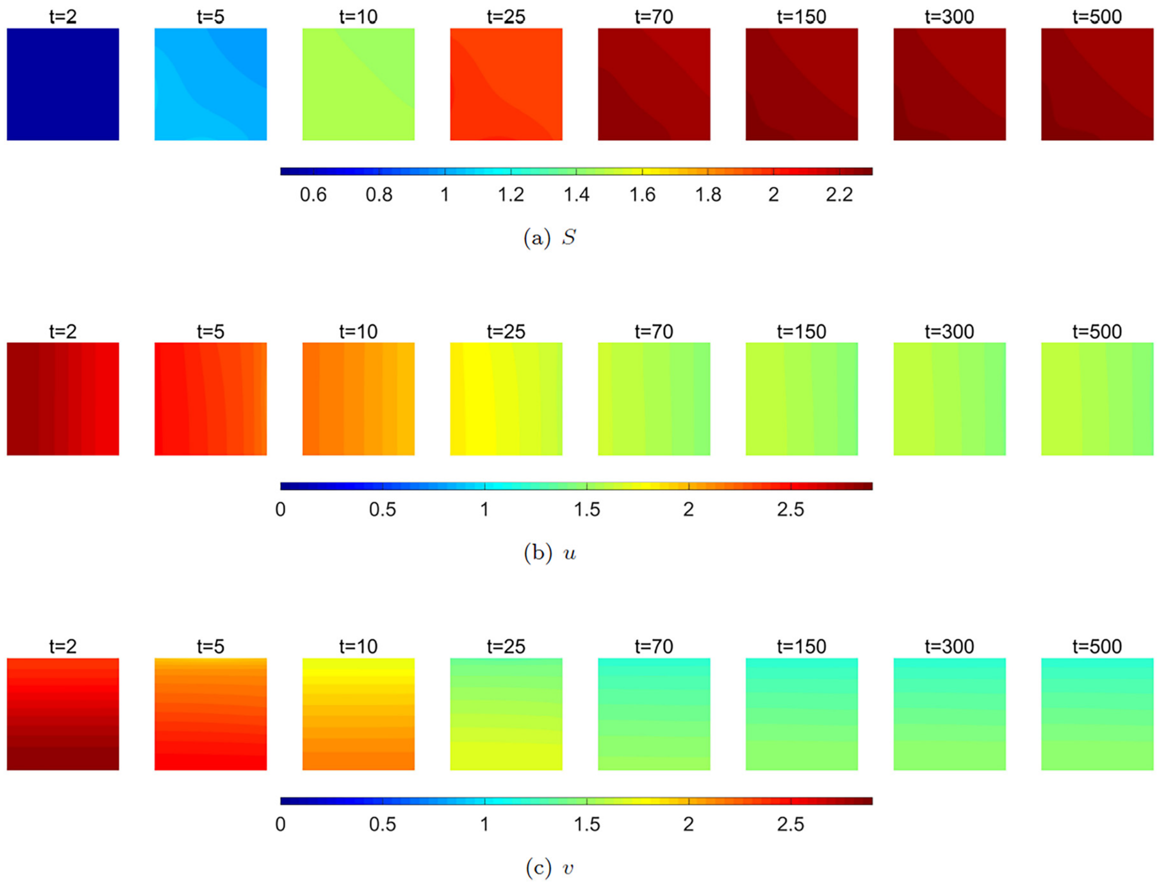


Figure 9: The solution (S, u, v) for system (1.1)–(1.3) at different moments, where $(p, q) = (0.01, 1)$.

7 Discussion

In this paper, we investigate an unstirred chemostat model for two competing populations in a bounded two-dimensional domain. Population dispersal is assumed to be anisotropic, with direction-specific probabilities interpreted as strategies.

We initially investigated the single-species models (1.4) and (1.5). Our findings demonstrate that there exists a unique continuous open interval contained within [0, 1] such that the steady state $(z, 0)$ is globally asymptotically stable when the dispersal strategy is located in the interval; see Theorems 3.3 and 3.5(i). Moreover, the single-species model is uniformly persistent when the dispersal strategy is outside the interval; see Theorems 3.4 and 3.5(ii). Moreover, we found that the single-species model admits at least one positive steady state when the conditions for uniform persistence in the model are satisfied; see Theorems 3.7–3.11. Additionally, the positive steady state is locally asymptotically stable when the dispersal strategy is near the outer boundary of the interval; see Theorems 3.7–3.11.

Then we investigated the two-species model (1.1)–(1.3). We classified the dynamical behavior of the model into three scenarios based on the diffusion strategies: (i) extinction (see Theorem 4.2); (ii) competitive exclusion (see Theorem 4.3); (iii) coexistence (see Theorem 4.4). Before studying the coexistence steady states of the model, we deduced the conditions for the linear stability of several special solutions; see Theorem 5.1. This provided a reference for selecting bifurcation points in the following. In the bifurcation analysis, we observed that the solution structure of the model is more complex. Furthermore, the parameter conditions constructed to classify the dynamic behavior of the model cannot be directly applied to the bifurcation analysis, necessitating the development of new parameter conditions; see Lemmas 5.3, 5.5 and 5.6. Additionally, we further studied the linear stability of the positive steady states when (p, q) is located in a very small part in $[0, 1]^2$; see Lemmas 5.5 and 5.6. Finally, we provide sufficient conditions for the coexistence steady states in the two-species model; see Theorems 5.8 and 5.10.

Based on the analysis of the models above, we found that it is more beneficial for the species to choose one direction only. Because our conclusion shows that the diffusion strategies leading to extinction or competitive exclusion are often positioned in the middle of their feasible area, with no distinct directional bias. This finding is in agreement with the results of ref. [18]. Therefore, anisotropic diffusion provides more possibilities for species coexistence.

This paper raises several interesting questions. One of the key questions is whether more precise conditions can be established for the existence of coexistence equilibria in system (1.1)–(1.3), and how the structure of all possible equilibria can be comprehensively and accurately characterized.

Acknowledgments: The authors are grateful to anonymous referees for valuable comments and suggestions which led to great improvement of this paper.
Research ethics: Not applicable.
Informed consent: Not applicable.
Author contributions: All authors have accepted responsibility for the entire content of this manuscript and approved its submission.
Use of Large Language Models, AI and Machine Learning Tools: We use ChatGPT to improve language.
Conflict of interest: The authors state no conflict of interest.
Research funding: The research is supported by the National Natural Science Foundation of China (12171296, 12461097).
Data availability: Not applicable.

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