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A COMPETITION MODEL WITH DYNAMICALLY ALLOCATED TOXIN PRODUCTION IN THE UNSTIRRED CHEMOSTAT

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Abstract. This paper deals with a competition model with dynamically allocated toxin production in the unstirred chemostat. First, the existence and uniqueness of positive steady state solutions of the single population model is attained by the general maximum principle, spectral analysis and degree theory. Second, the existence of positive equilibria of the two-species system is investigated by the degree theory, and the structure and stability of nonnegative equilibria of the two-species system are established by the bifurcation theory. The results show that stable coexistence solution can occur with dynamic toxin production, which cannot occur with constant toxin production. Biologically speaking, it implies that dynamically allocated toxin production is sufficiently effective in the occurrence of coexisting. Finally, numerical results illustrate that a wide variety of dynamical behaviors can be achieved for the system with dynamic toxin production, including competition exclusion, bistable attractors, stable positive equilibria and stable limit cycles, which complement the analytic results.

1. Introduction.

The chemostat is a basic resource-based model for competition in an open system and a standard model for the laboratory bio-reactor, which plays an important role in the study of population dynamics and species interactions (see, e.g., [14, 27]).

The study on the problem of the influence of toxicants both on the growth of one population and on the competition of two species for a critical nutrient has received considerable attention in the past decades (see, e.g., [1, 2, 5, 11, 13, 21, 22, 18, 19, 20,

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28, 30, 31]). Particularly, there has been a lot of interest in the so called allelopathic competitions between species (see, e.g., [2, 5, 16, 21, 22, 18, 24, 28]). Allelopathy can be defined as the direct or indirect harmful effect of one species on another by releasing a chemical compound into the surrounding environment[25]. Allelopathic competition occurs between algal species[16], algae and bacteria[28], bacteria and bacteria[3], algae and aquatic plants[24] as well as plants and plants[2]. Several experimental results concerning bacterial competition show that the production of allelopathic chemical compound depends on the concentrations of populations through a quorum sensing mechanism [3, 12]. As a consequence, a general mathematical model was first proposed in [5] to model such a mechanism. In [5], the basic assumption is that the chemostat is well-stirred and the weaker competitor can devote some of its resources to the dynamically allocated production of an allelopathic agent (which is also called anti-competitor toxin or just toxin). Dynamically allocated production implies that the effort devoted to toxin production can be adjusted to reflect the state of the competition. For instance, if there is no competition, there is no resource devoted to the toxin production. The numerical examples in [5] show that some new interesting dynamical behaviors occur, including stable interior rest points and stable limit cycles, in contrast to the model with constant toxin production. This suggests a possible mechanism for coexistence. Rigorous mathematical analysis of allelopathic competition models with quorum sensing in the well-stirred chemostat-like environment can be found, for example, in [1, 11, 13].

Our goal here is to explore the role of the dynamic toxin production and spatial heterogeneity in the competition process. Thus we remove the well-stirred hypothesis and consider the following chemostat model with dynamically allocated toxin production and diffusion

$$\begin{array}{ll} S_t = dS_{xx} - \dfrac{1}{\eta_1} auf_1(S) - \dfrac{1}{\eta_2} bvf_2(S), & x \in (0, L), t > 0, \\ u_t = du_{xx} + auf_1(S) - cpu, & x \in (0, L), t > 0, \\ v_t = dv_{xx} + (1 - K(u, v))bvf_2(S), & x \in (0, L), t > 0, \\ p_t = dp_{xx} + K(u, v)bvf_2(S), & x \in (0, L), t > 0 \end{array} \tag{1}$$

with boundary conditions and initial conditions

$$\begin{array}{ll} S_x(0, t) = -S^0, \quad S_x(L, t) + \nu S(L, t) = 0, & t > 0, \\ u_x(0, t) = u_x(L, t) + \nu u(L, t) = 0, & t > 0, \\ v_x(0, t) = v_x(L, t) + \nu v(L, t) = 0, & t > 0, \\ p_x(0, t) = p_x(L, t) + \nu p(L, t) = 0, & t > 0, \end{array} \tag{2}$$

$$\begin{array}{ll} S(x, 0) = S_0(x) \geq 0, \quad u(x, 0) = u_0(x) \geq 0, \not\equiv 0, & x \in [0, L], \\ v(x, 0) = v_0(x) \geq 0, \not\equiv 0, \quad p(x, 0) = p_0(x) \geq 0, \not\equiv 0, & x \in [0, L]. \end{array} \tag{3}$$

Here $S(x, t)$ is the concentration of the nutrient in the vessel at time t, $u(x, t)$ is the concentration of the sensitive microorganism, $v(x, t)$ is the concentration of the toxin producing organism and $p(x, t)$ is the concentration of the toxicant. $S^0 > 0$ is the input concentration of the nutrient, which is assumed to be constant. L is the depth of the vessel, ν is a positive constant. d is the diffusion rate of the chemostat, $\eta_i (i = 1, 2)$ are the growth yield coefficients. a, b are the maximal growth rates of two microorganisms, respectively. The response functions are denoted by $f_i(S) = \frac{S}{k_i + S}, i = 1, 2$, where k_i are the Michaelis-Menten constants. The interaction between the toxin and the sensitive microorganisms is taken to be of mass action form $-cpu$, where the constant of proportionality $c > 0$. The function $K(u, v)$ represents the fraction of potential growth devoted to producing the toxin, which is assumed to be a smooth function satisfying $0 \leq K(u,v) < 1$. $K(u,v) \equiv 0$ produces a system asymptotic to the standard chemostat, and $K(u,v) \equiv k(\text{contant})$ is the system studied in [15, 18].

The production of anti-competitor toxins is of interest when the weaker competitor can produce toxins against its competitors. The introduction of the function $K(u,v)$ is based on the assumption that the effort devoted to toxin production can be dynamically allocated as a function of the state of the system, which reflects the mechanism of quorum sensing (see [3]). In [15], Hsu and Waltman assumed $K(u,v) \equiv k(\text{contant})$ and studied the competition in the well-stirred chemostat when the weaker competitor produces toxins. Considering spatial heterogeneity, the system (1)-(3) with $K(u,v) \equiv k(\text{contant})$ was investigated in [18]. The results in [15, 18] indicate that coexistence cannot occur when the effort devoted to toxin production is constant even if taking into account diffusion.

The focus of this study is to investigate the dynamical behavior of the system (1)-(3) in combination with the effects of dynamically allocated toxin production and diffusion, and to explain the coexistence of two species in competition on a single resource in the unstirred chemostat. To this end, we assume that the function $K(u,v)$ satisfies the hypotheses

$(H1): K(u,v)$ is C^1 continuous in $\mathbb{R}_+ \times \mathbb{R}_+$, where $\mathbb{R}_+ = [0,+\infty)$;
$(H2): 0 \leq K(u,v) < 1$ for any $u, v \in \mathbb{R}_+$;
$(H3): K(0,0) = 0, K(u,v) > 0$ for $u > 0, v > 0$, and $K_v(0,v) \geq 0$ for any $v \in \mathbb{R}_+$.

Meanwhile, we can extend the response functions $f_i : [0,+\infty) \to \mathbb{R}$ to $\bar{f}_i : \mathbb{R} \to \mathbb{R}$ such that $\bar{f}_i(S) = f_i(S)$ for $S \geq 0$, $\bar{f}_i(S) < 0$ for $S < 0$, and $\bar{f}_i \in C^1(\mathbb{R})$ (see [18, 21]). We will denote $\bar{f}_i(S)$ by $f_i(S)$ for simplicity.

By suitable scaling, we may take $S^0 = 1$, $\eta_i = 1 (i = 1,2)$ and $L = 1$. Then the original system (1)-(3) becomes

$$\begin{array}{ll} S_t = dS_{xx} - auf_1(S) - bvf_2(S), & x \in (0,1), t > 0, \\ u_t = du_{xx} + auf_1(S) - cpu, & x \in (0,1), t > 0, \\ v_t = dv_{xx} + (1 - K(u,v))bvf_2(S), & x \in (0,1), t > 0, \\ p_t = dp_{xx} + K(u,v)bvf_2(S), & x \in (0,1), t > 0 \end{array} \tag{4}$$

with boundary conditions

$$\begin{array}{ll} S_x(0,t) = -1, \quad S_x(1,t) + \nu S(1,t) = 0, & t > 0, \\ u_x(0,t) = u_x(1,t) + \nu u(1,t) = 0, & t > 0, \\ v_x(0,t) = v_x(1,t) + \nu v(1,t) = 0, & t > 0, \\ p_x(0,t) = p_x(1,t) + \nu p(1,t) = 0, & t > 0, \end{array} \tag{5}$$

and initial conditions (3).

As mentioned before, we concentrate on coexistence solutions (i.e. stable positive solutions) of the following steady state system

$$\begin{array}{ll} dS_{xx} - auf_1(S) - bvf_2(S) = 0, & x \in (0,1), \\ du_{xx} + auf_1(S) - cpu = 0, & x \in (0,1), \\ dv_{xx} + (1 - K(u,v))bvf_2(S) = 0, & x \in (0,1), \\ dp_{xx} + K(u,v)bvf_2(S) = 0, & x \in (0,1), \end{array} \tag{6}$$

with boundary conditions

$$\begin{array}{ll} S_x(0) = -1, \quad S_x(1) + \nu S(1) = 0, & u_x(0) = u_x(1) + \nu u(1) = 0, \\ v_x(0) = v_x(1) + \nu v(1) = 0, & p_x(0) = p_x(1) + \nu p(1) = 0. \end{array} \tag{7}$$

The main technical difficulties in our analysis come from the basic assumption that the weaker competitor can devote some of its resources to the dynamically allocated production of anti-competitor toxins. Consequently, the usual reduction of the system to a competitive system of one order lower through the conservation of nutrient principle is lost. Thus the system with toxin production is non-monotone, and the single population model can't be reduced to a scalar system. Hence, it is hard to study the uniqueness and stability of the semitrivial nonnegative equilibria.

The main goal of Section 2 is to study the uniqueness and some properties of single population equilibrium by the general maximum principle, spectral analysis and degree theory. The main results are given by Theorems 2.1 and 2.2. Since the single population model (9) can't be reduced to a scalar system, it is much more difficult to prove Theorem 2.2 than Theorem 2.1. The crucial point of proving Theorem 2.2 is to establish Lemma 2.4, which indicates that any positive solution of (9) is nondegenerative and has index 1. In Section 3, the existence of positive solutions of the steady state system (6)-(7) is investigated by the degree theory. The structure and stability of the nonnegative solutions of (6)-(7) is established by the bifurcation theory in Section 4. Lemma 2.4 and Remark 2.1 also play a key role in verifying the main outcomes (see Theorems 3.1, 4.2 and 4.3). It turns out that stable coexistence solutions can occur with dynamic toxin production, which cannot occur with constant toxin production. Biologically speaking, it implies that dynamically allocated toxin production is sufficiently effective in the occurrence of coexisting. Finally, some numerical results illustrate the existence of coexistence solutions, bi-stable attractors or stable limit cycles, which complement the analytic results.

2. **Uniqueness of single population equilibria.**

The goal of this section is to determine the properties of single population equilibria of (4)-(5). Mathematically, this means that u or v is set to zero in the system (4)-(5), or equivalently, the initial data $u_0(x) \equiv 0$ or $v_0(x) \equiv 0$, respectively. Hence, we obtain the following reduced boundary value problems

$$\begin{cases} dS_{xx} - auf_1(S) = 0, \quad x \in (0,1), \\ du_{xx} + auf_1(S) - cpu = 0, \quad x \in (0,1), \\ dp_{xx} = 0, \quad x \in (0,1), \\ S_x(0) = -1, \quad S_x(1) + \nu S(1) = 0, \\ u_x(0) = u_x(1) + \nu u(1) = 0, \quad p_x(0) = p_x(1) + \nu p(1) = 0, \end{cases} \tag{8}$$

$$\begin{cases} dS_{xx} - bvf_2(S) = 0, \quad x \in (0,1), \\ dv_{xx} + (1 - K(0,v))bvf_2(S) = 0, \quad x \in (0,1), \\ dp_{xx} + K(0,v)bvf_2(S) = 0, \quad x \in (0,1), \\ S_x(0) = -1, \quad S_x(1) + \nu S(1) = 0, \\ v_x(0) = v_x(1) + \nu v(1) = 0, \quad p_x(0) = p_x(1) + \nu p(1) = 0. \end{cases} \tag{9}$$

To work out the properties of the solutions of the reduced boundary value problems (8) and (9), we introduce λ_1, σ_1 as the principal eigenvalues of the problems respectively,

$$\begin{aligned} &d(\phi_1)_{xx} + \lambda_1 f_1(z)\phi_1 = 0 \ \text{ in } \ (0,1), \quad (\phi_1)_x(0) = (\phi_1)_x(1) + \nu\phi_1(1) = 0, \\ &d(\psi_1)_{xx} + \sigma_1 f_2(z)\psi_1 = 0 \ \text{ in } \ (0,1), \quad (\psi_1)_x(0) = (\psi_1)_x(1) + \nu\psi_1(1) = 0, \end{aligned} \tag{10}$$

with the associated eigenfunctions $\phi_1, \psi_1 > 0$ on $[0,1]$, normalized with $\max\limits_{[0,1]} \phi_1 = 1$, $\max\limits_{[0,1]} \psi_1 = 1$.

For the reduced boundary value problems (8), it is easy to see that $p \equiv 0$ on [0, 1], and (S, u) satisfies

$$\begin{array}{ll} dS_{xx} - auf_1(S) = 0, & x \in (0,1), \\ du_{xx} + auf_1(S) = 0, & x \in (0,1), \\ S_x(0) = -1,\ S_x(1) + \nu S(1) = 0, & u_x(0) = u_x(1) + \nu u(1) = 0. \end{array} \tag{11}$$

Let $W = S + u$. Then $dW_{xx} = 0, x \in (0,1),\quad W_x(0) = -1, W_x(1) + \nu W(1) = 0$, which implies $W = z(x) = \frac{1+\nu}{\nu} - x$ on [0, 1]. Hence, $S = z - u$, and u satisfies

$$du_{xx} + auf_1(z-u) = 0,\ x \in (0,1),\quad u_x(0) = u_x(1) + \nu u(1) = 0. \tag{12}$$

It follows from Theorem 2.1 in [20] that 0 is the unique nonnegative solution of (12) if $a \le \lambda_1$, and there exists a unique positive solution of (12) if $a > \lambda_1$, which is denoted by θ_a. Therefore, $(z, 0, 0)$ is the unique nonnegative solution of (8) if $a \le \lambda_1$, and there exists a unique positive solution $(z - \theta_a, \theta_a, 0)$ if $a > \lambda_1$. Furthermore, we have the following results.

Theorem 2.1. *If $a \le \lambda_1$, then $(z, 0, 0)$ is the unique nonnegative solution of the single population model (8); if $a > \lambda_1$, then (8) has a unique positive solution $(z - \theta_a, \theta_a, 0)$. Moreover, θ_a satisfies the following properties:*

(i) *$0 < \theta_a < z$;*
(ii) *θ_a is continuously differentiable for $a \in (\lambda_1, +\infty)$, and is pointwisely increasing when a increases;*
(iii) *$\lim_{a \to \lambda_1} \theta_a = 0$ uniformly for $x \in [0,1]$;*
(iv) *$\lim_{a \to \infty} \theta_a = z(x)$ uniformly for $x \in [0,1]$;*
(v) *Let $L_a = -d\frac{\mathrm{d}^2}{\mathrm{d}x^2} - af_1(z - \theta_a) + a\theta_a f_1'(z - \theta_a)$. Then L_a is a differentiable operator in $C_B^2[0,1] = \{u \in C^2[0,1] : u_x(0) = u_x(1) + \nu u(1) = 0\}$ and all eigenvalues of L_a are strictly positive, which implies that L_a is a nondegenerate and positive operator in $C_B^2[0,1]$.*

Proof. By Lemmas 3.3–3.4 in [32] and Propositions 2.3–2.4 in [20], one can conclude that θ_a satisfies the above properties (i)-(iii) and (v). Hence, we only need to show (iv).

Since $0 < \theta_a < z(x)$ and θ_a is pointwisely increasing with respect to $a \in (\lambda_1, \infty)$, we only need to show that for any $\epsilon > 0$, $\theta_a > (1-\epsilon)z(x)$ provided that a is large enough. To this end, let $\underline{\theta} \in C^\infty[0,1]$, and $(1-\epsilon)z(x) < \underline{\theta} < (1 - \frac{\epsilon}{2})z(x)$. Then

$$d\underline{\theta}_{xx} + a\underline{\theta} f_1(z - \underline{\theta}) = a[\frac{d}{a}\underline{\theta}_{xx} + \underline{\theta} f_1(z - \underline{\theta})] > a[\frac{d}{a}\underline{\theta}_{xx} + (1-\epsilon)zf_1(\frac{\epsilon}{2}z)] > 0,$$

provided that $\|\underline{\theta}_{xx}\|$ is bounded and a is large enough. That is, for any $\epsilon > 0$, there exists $A(\epsilon) > 0$ and $\underline{\theta} \in C^\infty[0,1]$, $(1-\epsilon)z(x) < \underline{\theta} < (1-\frac{\epsilon}{2})z(x)$, $\|\underline{\theta}_{xx}\|$ bounded and $-\underline{\theta}_x(0) \le 0, \underline{\theta}_x(1) + \nu\underline{\theta}(1) \le 0$ such that $d\underline{\theta}_{xx} + a\underline{\theta} f_1(z - \underline{\theta}) > 0$ provided that $a > A(\epsilon)$. Clearly, $z(x)$ is a super-solution of (12). Hence we have $z(x) > \theta_a > \underline{\theta} > (1-\epsilon)z(x)$ by the super- and sub- solution method and the uniqueness of positive solutions to (12). Letting $\epsilon \to 0$, we obtain $\lim_{a\to\infty} \theta_a = z(x)$ uniformly for $x \in [0,1]$. $\square$

Next, we begin to study nonnegative solutions of (9). If $K(0, v) \equiv 0$, then it is easy to see that $p \equiv 0$ and $S + v \equiv z(x)$ on [0, 1]. Hence, (9) can be reduced into the scalar system

$$dv_{xx} + bvf_2(z - v) = 0,\ x \in (0,1),\quad v_x(0) = v_x(1) + \nu v(1) = 0. \tag{13}$$

By similar arguments as in Theorem 2.1, we can conclude that 0 is the unique nonnegative solution of (13) if $b \le \sigma_1$, and there exists a unique positive solution of (13) if $b > \sigma_1$, which is denoted by ϑ_b. Moreover, by similar arguments as in Theorem 2.1 again, we have the following similar outcomes.

Lemma 2.2. *Suppose $(H1)-(H3)$ hold and $K(0,v)\equiv 0$. Then if $b \le \sigma_1$, then $(z,0,0)$ is the unique nonnegative solution of the single population model (9); if $b > \sigma_1$, then (9) has a unique positive solution $(z-\vartheta_b, \vartheta_b, 0)$. Moreover, ϑ_b satisfies the following properties:*

(i) *$0 < \vartheta_b < z$;*

(ii) *ϑ_b is continuously differentiable for $b \in (\sigma_1, +\infty)$, and is pointwisely increasing when b increases;*

(iii) *$\lim\limits_{b\to\sigma_1} \vartheta_b = 0$ uniformly for $x \in [0,1]$, and $\lim\limits_{b\to\infty} \vartheta_b = z(x)$ uniformly for $x \in [0,1]$;*

(iv) *Let $L_b = -d\frac{\mathrm{d}^2}{\mathrm{d}x^2} - bf_2(z-\vartheta_b) + b\vartheta_b f_1'(z-\vartheta_b)$. Then L_b is a differentiable operator in $C_B^2[0,1]$ and all eigenvalues of L_b are strictly positive, which implies that L_b is a non-degenerate and positive operator in $C_B^2[0,1]$.*

If $K(0,v) \not\equiv 0$, then (9) cannot be reduced into a scalar system, which makes it difficult to study nonnegative solutions of (9). We first consider the decoupled subsystem

$$\begin{array}{l} dS_{xx} - bvf_2(S) = 0, \quad x \in (0,1), \\ dv_{xx} + (1-K(0,v))bvf_2(S) = 0, \quad x \in (0,1), \\ S_x(0) = -1,\ S_x(1) + \nu S(1) = 0, \quad v_x(0) = v_x(1) + \nu v(1) = 0. \end{array} \tag{14}$$

By similar arguments as in Lemmas 3.1–3.2 (see Page 11), we establish the priori estimates for nonnegative solutions of (14).

Lemma 2.3. *Suppose $(H1)-(H3)$ hold and let (S,v) be a nonnegative solution of (14) with $v \not\equiv 0$. Then $S+v<z$, $0<S<z$, $0<v<\vartheta_b$ on $[0,1]$. Moreover, $b>\sigma_1$.*

Next, we show the uniqueness of positive equilibria of (14) by the degree theory. To this end, let $\chi = z - S$. Then (14) is equivalent to

$$\begin{array}{l} d\chi_{xx} + bvf_2(z-\chi) = 0, \quad x \in (0,1), \\ dv_{xx} + (1-K(0,v))bvf_2(z-\chi) = 0, \quad x \in (0,1), \\ \chi_x(0) = \chi_x(1) + \nu\chi(1) = 0, \quad v_x(0) = v_x(1) + \nu v(1) = 0. \end{array} \tag{15}$$

Introduce the spaces:

$$\begin{array}{l} X_0 = C[0,1] \times C[0,1], \\ W_0 = \{(\chi,v) \in X_0 | \chi \ge 0, v \ge 0 \ \text{ for } \ x \in [0,1]\}, \\ \Omega_0 = \{(\chi,v) \in W_0 | \chi < z,\ v < \max\limits_{[0,1]} \vartheta_b + 1\}. \end{array}$$

Then W_0 is a cone of X_0 and Ω_0 is a bounded open set in W_0. We define A_τ : $[0,1] \times X_0 \to X_0$ by

$$A_\tau(\chi,v) := \left(-d\frac{\mathrm{d}^2}{\mathrm{d}x^2} + M\right)^{-1} \begin{pmatrix} \tau bvf_2(z-\chi) + M\chi \\ \tau(1-K(0,v))bvf_2(z-\chi) + Mv \end{pmatrix},$$

where $\left(-d\frac{\mathrm{d}^2}{\mathrm{d}x^2} + M\right)^{-1}$ is the inverse operator of $-d\frac{\mathrm{d}^2}{\mathrm{d}x^2} + M$ subject to the boundary conditions $v_x(0) = v_x(1) + \nu v(1) = 0$, M is large enough such that $M + \tau(1-$

$K(0, v))bf_2(z - \chi) > 0$ for all $(\chi, v) \in \Omega_0$, $\tau \in [0, 1]$ and $x \in [0, 1]$. Hence, for any $\tau \in [0, 1]$, we have $A_\tau : \Omega_0 \to W_0$. It follows from the standard elliptic regularity theory that A_τ is compact and continuously differentiable. Let $A = A_1$. By Lemma 2.3, (15) (or (14) equivalently) has a nonnegative solution if and only if the operator A has a fixed point in Ω_0. Moreover, similar arguments as in Lemma 2.3 indicate that A_τ has no fixed points on $\partial\Omega_0$.

Lemma 2.4. *Suppose* $(H1) - (H3)$ *hold. Then* (i) $\operatorname{index}(A, \Omega_0, W_0) = 1$; (ii) $\operatorname{index}(A, (0, 0), W_0) = 0$ *provided that* $b > \sigma_1$.

Proof. (i) It follows from similar arguments as in Lemma 2.3 that A_τ has no fixed points on $\partial\Omega_0$. By the homotopic invariance of the degree, we obtain

$$\operatorname{index}(A, \Omega_0, W_0) = \operatorname{index}(A_\tau, \Omega_0, W_0) = \operatorname{index}(A_0, \Omega_0, W_0).$$

Here $\operatorname{index}(A, \Omega_0, W_0)$ is the index of the compact operator A on Ω_0 in the cone W (see [8, 9, 10]). Clearly, $(0, 0)$ is the unique fixed point of A_0 in Ω_0. Hence,

$$\operatorname{index}(A, \Omega_0, W_0) = \operatorname{index}(A_0, \Omega_0, W_0) = \operatorname{index}(A_0, (0, 0), W_0).$$

By some standard calculations (see [8, 9, 10, 31]), we have $\operatorname{index}(A_0, (0, 0), W_0) = 1$. Hence, $\operatorname{index}(A, \Omega_0, W_0) = 1$.

(ii) Let $A'(0, 0)$ be the Fréchet derivative of A at $(0, 0)$ with respect to (χ, v). Suppose $A'(0, 0)(\phi, \psi)^\top = (\phi, \psi)^\top$ with $(\phi, \psi) \in \overline{W}_0 - (0, 0)$. Then

$$\begin{array}{l} d\phi_{xx} + bf_2(z)\psi = 0, \quad x \in (0, 1), \\ d\psi_{xx} + bf_2(z)\psi = 0, \quad x \in (0, 1), \\ \phi_x(0) = \phi_x(1) + \nu\phi(1) = 0, \quad \psi_x(0) = \psi_x(1) + \nu\psi(1) = 0. \end{array}$$

Since $b > \sigma_1$ and $\psi \geq 0$, it is easy to see that $\psi \equiv 0$, which implies $\phi \equiv 0$, a contradiction to $(\phi, \psi) \in \overline{W}_0 - (0, 0)$. Hence, $(0, 0)$ is an isolated fixed point of A in W_0.

Let $A'(0, 0)(\phi, \psi)^\top = \lambda(\phi, \psi)^\top$. Then

$$\begin{array}{ll} -\lambda d\phi_{xx} + (\lambda - 1)M\phi = bf_2(z)\psi, & x \in (0, 1), \\ -d\psi_{xx} + M\psi = \dfrac{1}{\lambda}(M + bf_2(z))\psi, & x \in (0, 1), \\ \phi_x(0) = \phi_x(1) + \nu\phi(1) = 0, \quad \psi_x(0) = \psi_x(1) + \nu\psi(1) = 0. & \end{array} \tag{16}$$

Consider the eigenvalue problem

$$- d\psi_{xx} - bf_2(z)\psi = \eta\psi, \ \psi_x(0) = \psi_x(1) + \nu\psi(1) = 0. \tag{17}$$

In view of $b > \sigma_1$, we can find that the least eigenvalue $\eta_1 < 0$ of (17). It follows from Lemma A.2 that the spectral radius

$$\lambda_0 := r\left(\left(M - d\frac{\mathrm{d}^2}{\mathrm{d}x^2}\right)^{-1}(M + bf_2(z))\right) > 1.$$

Note that $-\lambda d\frac{\mathrm{d}^2}{\mathrm{d}x^2} + (\lambda - 1)M$ is invertible subject to the boundary conditions $\phi_x(0) = \phi_x(1) + \nu\phi(1) = 0$ when $\lambda > 1$. We can conclude that the spectral radius λ_0 is an eigenvalue of $A'(0, 0)$. Hence, $A'(0, 0)$ has an eigenvalue greater than 1. It follows from Lemma A.3 that $\operatorname{index}(A, (0, 0), W_0) = 0$ provided that $b > \sigma_1$. $\square$

Lemma 2.5. *Suppose* $(H1) - (H3)$ *hold and* (S_0, v_0) *is a positive solution of* (14). *Then* (S_0, v_0) *is non-degenerative, and* $\operatorname{index}(A, (\chi_0, v_0), W_0) = 1$, *where* $\chi_0 = z - S_0$.

Proof. In order to show the nondegeneracy of (S_0, v_0), we only need to show that the linearization of (14) at (S_0, v_0) with respect to (S, v)

$$\begin{array}{l} L_1\phi - bf_2(S_0)\psi = 0, \quad x \in (0,1), \\ L_2\psi + (1-K(0,v_0))bv_0 f_2'(S_0)\phi = 0, \quad x \in (0,1), \\ \phi_x(0) = \phi_x(1) + \nu\phi(1) = 0, \quad \psi_x(0) = \psi_x(1) + \nu\psi(1) = 0. \end{array} \tag{18}$$

only has trivial solution, where

$$\begin{array}{l} L_1\phi = d\phi_{xx} - bv_0 f_2'(S_0)\phi, \\ L_2\psi = d\psi_{xx} + (1-K(0,v_0))bf_2(S_0)\psi - K_v(0,v_0)bv_0 f_2(S_0)\psi. \end{array}$$

We prove it by an indirect argument, which is motivated by [17]. Suppose $(\phi,\psi) \not\equiv (0,0)$. It follows from $bv_0 f_2'(S_0) > 0$ that the operator L_1 is invertible subject to the boundary conditions $\phi_x(0) = \phi_x(1) + \nu\phi(1) = 0$, and the principal eigenvalue of L_1 satisfies $\lambda_1(L_1) < 0$. Noting that the hypothesis $(H3)$ and

$$\begin{array}{l} d(v_0)_{xx} + (1-K(0,v_0))bv_0 f_2(S_0) = 0,\ x \in (0,1), \\ (v_0)_x(0) = (v_0)_x(1) + \nu v_0(1) = 0, \end{array} \tag{19}$$

we have $\lambda_1(L_2) \le 0$. The equality holds if $K_v(0,v) \equiv 0$.

We first claim that both ϕ, ψ must change sign in (0, 1). Suppose $\psi > 0$ in (0, 1) without loss of generality. Then it follows from the first equation of (18) that $L_1\phi > 0$ in (0, 1). By the strong maximum principle, we have $\phi < 0$ on [0, 1]. Multiplying the second equation of (18) by v_0 and (19) by ψ, integrating over (0, 1), and applying Green's formula, we have

$$\int_0^1 [K_v(0,v_0)f_2(S_0)\psi - (1-K(0,v_0))f_2'(S_0)\phi]bv_0^2 \mathrm{d}x = 0,$$

a contradiction to $\int_0^1 [K_v(0,v_0)f_2(S_0)\psi - (1-K(0,v_0))f_2'(S_0)\phi]bv_0^2 \mathrm{d}x > 0$. Assume $\phi > 0$ in (0, 1). There are two possibilities: (i)$K_v(0,v) \equiv 0$; (ii)$K_v(0,v) \ge 0, \not\equiv 0$. In case (i). Similar arguments as above lead to $\int_0^1 (1-K(0,v_0))bv_0^2 f_2'(S_0)\phi \mathrm{d}x = 0$, a contradiction. In case (ii), one can conclude that $\lambda_1(L_2) < 0$ and $L_2\psi = -(1-K(0,v_0))bv_0 f_2'(S_0)\phi < 0$ on [0, 1]. The strong maximum principle implies $\psi > 0$ on [0, 1]. Thus $L_1\phi = bf_2(S_0)\psi > 0$ in (0, 1). It follows from the strong maximum principle that $\phi < 0$ on [0, 1], a contradiction. Hence, both ϕ, ψ must change sign in (0, 1).

Second, we claim that ϕ, ψ have at most finitely many zeros in (0,1) where ϕ, ψ change sign. Suppose $\phi(x_n) = 0$ for an infinite sequence of distinct points $\{x_n\} \subset [0,1]$, and ϕ changes sign at any x_n. By compactness, we may assume that there is $x_\infty \in [0,1]$ such that $x_n \to x_\infty (n \to \infty)$ by passing to a subsequence if necessary. By the mean value theorem, we conclude that $\phi(x_\infty) = 0, \phi_x(x_\infty) = 0, \phi_{xx}(x_\infty) = 0$. It follows from the first equation of (18) that $\psi(x_\infty) = 0$. The maximum principle applied to the first equation of (18) shows that ψ must change sign in any neighborhood of x_∞. Thus $\psi_x(x_\infty) = 0$. It follows from the uniqueness of the Cauchy problem associated with (18) that $(\phi,\psi) = (0,0)$, which is a contradiction to $(\phi,\psi) \ne (0,0)$. The same assertion holds for the zeros where ψ changes sign.

Clearly, $\phi(0) \ne 0$ or $\psi(0) \ne 0$. Otherwise, $\phi(0) = 0, \psi(0) = 0$. By the uniqueness of the Cauchy problem associated with (18), we have $(\phi,\psi) \equiv (0,0)$, a contradiction. Hence, we may assume that $\phi(0) > 0$ and $0 < x_1 < x_2 < \cdots < x_m < 1$ are the finite sequence of zeros of ϕ in (0,1) where it changes sign. Then $\phi(x_i) = 0(i =$

$1, 2, \cdots, m$), and

$$\phi > 0 \text{ in } (x_{2i}, x_{2i+1}) \text{ for } i \geq 0, 2i+1 \leq m+1,$$
$$\phi < 0 \text{ in } (x_{2i-1}, x_{2i}) \text{ for } i \geq 1, 2i \leq m+1$$

where $x_0 = 0, x_{m+1} = 1$. We claim that

$$(-1)^j \psi(x_j) > 0, \quad j \in \{1, 2, \cdots, m\}.$$

We first claim that $\psi(x_1) < 0$ by an indirect argument. Suppose $\psi(x_1) \geq 0$. Note that $\phi > 0$ on $(0, x_1)$ and

$$L_2\psi = -(1 - K(0, v_0))bv_0 f_2'(S_0)\phi < 0 \text{ in } (0, x_1), \quad \psi_x(0) = 0, \ \psi(x_1) \geq 0. \tag{20}$$

There are two possibilities: (i)$K_v(0, v) \equiv 0$; (ii)$K_v(0, v) \geq 0, \not\equiv 0$.

(i) If $K_v(0, v) \equiv 0$, then $L_2\psi = d\psi_{xx} + (1 - K(0, v_0))bf_2(S_0)\psi$ and $L_2 v_0 = 0$ in $(0, x_1)$. The general maximum principle implies that ψ/v_0 cannot reach its nonpositive minimum in $(0, x_1)$. If $\min\limits_{x \in [0,1]} \psi/v_0 = \psi(0)/v_0(0) \leq 0$, then $\left(\frac{\psi}{v_0}\right)_x |_{x=0} > 0$ by the general maximum principle, which is a contradiction to $\left(\frac{\psi}{v_0}\right)_x |_{x=0} = 0$. Suppose $\min\limits_{x \in [0,1]} \psi/v_0 = \psi(x_1)/v_0(x_1) \leq 0$. In view of $\psi(x_1) \geq 0$, we have $\psi(x_1) = 0$ and $\psi > 0$ in $(0, x_1)$. Hence,

$$L_1\phi = bf_2(S_0)\psi > 0 \text{ in } (0, 1), \quad \phi_x(0) = 0, \ \phi(x_1) = 0.$$

By the strong maximum principle, we obtain $\phi < 0$ in $(0, x_1)$, a contradiction to $\phi > 0$ in $(0, x_1)$. Thus $\psi(x_1) < 0$.

(ii) If $K_v(0, v) \geq 0, \not\equiv 0$, then $\lambda_1(L_2) < 0$. The maximum principle applied to (20) shows that $\psi > 0$ in $(0, x_1)$. Hence,

$$L_1\phi = bf_2(S_0)\psi > 0 \text{ in } (0, 1), \quad \phi_x(0) = 0, \ \phi(x_1) = 0.$$

By the strong maximum principle, we obtain $\phi < 0$ in $(0, x_1)$, a contradiction to $\phi > 0$ in $(0, x_1)$. Thus $\psi(x_1) < 0$.

Next, assume that $\psi(x_i) < 0$ and $\phi < 0$ in (x_i, x_{i+1}) for $i \in \{1, 2, \cdots, m-1\}$. We prove $\psi(x_{i+1}) > 0$ by an indirect argument. Suppose $\psi(x_{i+1}) \leq 0$. Then

$$L_2\psi = -(1 - K(0, v_0))bv_0 f_2'(S_0)\phi > 0 \text{ in } (x_i, x_{i+1}), \quad \psi(x_i) < 0, \ \psi(x_{i+1}) \leq 0. \tag{21}$$

We also have two possibilities: (i)$K_v(0, v) \equiv 0$; (ii)$K_v(0, v) \geq 0, \not\equiv 0$.

(i) If $K_v(0, v) \equiv 0$, then $L_2\psi = d\psi_{xx} + (1 - K(0, v_0))bf_2(S_0)\psi$ and $L_2 v_0 = 0$ in (x_i, x_{i+1}). The general maximum principle implies that ψ/v_0 cannot reach its nonnegative maximum in (x_i, x_{i+1}). By virtue of $\psi(x_i) < 0$, one can conclude that ψ/v_0 cannot reach its nonnegative maximum at $x = x_i$. Assume that $\max\limits_{x \in [x_i, x_{i+1}]} \psi/v_0 = \psi(x_{i+1})/v_0(x_{i+1}) \geq 0$. By the hypothesis $\psi(x_{i+1}) \leq 0$, we get $\psi(x_{i+1}) = 0$ and $\psi(x)/v_0(x) < 0$ in (x_i, x_{i+1}). Hence,

$$L_1\phi = bf_2(S_0)\psi < 0 \text{ in } (x_i, x_{i+1}), \quad \phi(x_i) = 0, \ \phi(x_{i+1}) = 0.$$

By the strong maximum principle, we obtain $\phi > 0$ in (x_i, x_{i+1}), a contradiction to $\phi < 0$ in (x_i, x_{i+1}). Hence, $\psi(x_{i+1}) > 0$.

(ii) If $K_v(0, v) \geq 0, \not\equiv 0$, then $\lambda_1(L_2) < 0$. The maximum principle applied to (21) shows that $\psi < 0$ in (x_i, x_{i+1}). Hence,

$$L_1\phi = bf_2(S_0)\psi < 0 \text{ in } (0, 1), \quad \phi_x(x_i) = 0, \ \phi(x_{i+1}) = 0.$$

By the strong maximum principle, we obtain $\phi > 0$ in (x_i, x_{i+1}), a contradiction to $\phi < 0$ in (x_i, x_{i+1}). Thus $\psi(x_{i+1}) > 0$.

Similar arguments show that if $\psi(x_i) > 0$ and $\phi > 0$ in (x_i, x_{i+1}), then $\psi(x_{i+1}) < 0$. These imply $(-1)^j\psi(x_j) > 0, \quad j \in \{1, 2, \cdots, m\}$.

At last, we focus on the last interval to establish a contradiction. We have two possibility to consider: (i) $\phi > 0$ in $(x_m, 1)$; (ii) $\phi < 0$ in $(x_m, 1)$.

(i) The case of $\phi > 0$ in $(x_m, 1)$. By the above arguments, we have $\psi(x_m) > 0$. Note that

$$\begin{aligned} &L_2\psi = -(1 - K(0, v_0))bv_0 f_2'(S_0)\phi < 0 \text{ in } (x_m, 1), \\ &\psi(x_m) > 0,\ \psi_x(1) + \nu\psi(1) = 0. \end{aligned} \tag{22}$$

Just as above, if $K_v(0, v) \equiv 0$, then $L_2\psi = d\psi_{xx} + (1 - K(0, v_0))bf_2(S_0)\psi$ and $L_2 v_0 = 0$ in $(x_m, 1)$. The general maximum principle implies that ψ/v_0 cannot reach its non-positive minimum in $(x_m, 1)$. By virtue of $\psi(x_m) > 0$, one can conclude that ψ/v_0 cannot reach its non-positive minimum at $x = x_m$. Then $\min_{x\in[x_m,1]} \psi/v_0 = \psi(1)/v_0(1) \le 0$. By the general maximum principle again, we have $\left(\frac{\psi}{v_0}\right)_x |_{x=1} < 0$. On the other hand, it is easy to see that $\left(\frac{\psi}{v_0}\right)_x |_{x=1} = \frac{\psi_x(1)v_0(1) - \psi(1)(v_0)_x(1)}{v_0^2(1)} = 0$, a contradiction. If $K_v(0, v) \ge 0, \not\equiv 0$, then $\lambda_1(L_2) < 0$. The maximum principle applied to (22) shows that $\psi > 0$ in $(x_m, 1)$. Hence,

$$L_1\phi = bf_2(S_0)\psi > 0 \text{ in } (0, 1), \quad \phi(x_m) = 0,\ \phi_x(1) + \nu\phi(1) = 0.$$

By the strong maximum principle, we obtain $\phi < 0$ in $(x_m, 1)$, a contradiction to $\phi > 0$ in $(x_m, 1)$.

(ii) The case of $\phi < 0$ in $(x_m, 1)$. By the above arguments, we have $\psi(x_m) < 0$. Note that

$$\begin{aligned} &L_2\psi = -(1 - K(0, v_0))bv_0 f_2'(S_0)\phi > 0 \text{ in } (x_m, 1), \\ &\psi(x_m) < 0,\ \psi_x(1) + \nu\psi(1) = 0. \end{aligned} \tag{23}$$

Similarly, if $K_v(0, v) \equiv 0$, then $L_2\psi = d\psi_{xx} + (1 - K(0, v_0))bf_2(S_0)\psi$ and $L_2 v_0 = 0$ in $(x_m, 1)$. The general maximum principle implies that ψ/v_0 cannot reach its nonnegative maximum in $(x_m, 1)$. Noting that $\psi(x_m) < 0$, one can conclude that ψ/v_0 cannot reach its nonnegative maximum at $x = x_m$. Then $\max_{x\in[x_m,1]} \psi/v_0 = \psi(1)/v_0(1) \ge 0$. By the general maximum principle again, we have $\left(\frac{\psi}{v_0}\right)_x |_{x=1} > 0$, a contradiction to $\left(\frac{\psi}{v_0}\right)_x |_{x=1} = \frac{\psi_x(1)v_0(1) - \psi(1)(v_0)_x(1)}{v_0^2(1)} = 0$. If $K_v(0, v) \ge 0, \not\equiv 0$, then $\lambda_1(L_2) < 0$. The maximum principle applied to (23) shows that $\psi < 0$ in $(x_m, 1)$. Hence,

$$L_1\phi = bf_2(S_0)\psi < 0 \text{ in } (0, 1), \quad \phi(x_m) = 0,\ \phi_x(1) + \nu\phi(1) = 0.$$

By the strong maximum principle, we obtain $\phi > 0$ in $(x_m, 1)$, a contradiction to $\phi < 0$ in $(x_m, 1)$.

Therefore, we have $(\phi, \psi) \equiv (0, 0)$, which implies that any positive solution of (14) is non-degenerative.

The remain task is to show $\text{index}(A, (\chi_0, v_0), W_0) = 1$, where $\chi_0 = z - S_0$. To this end, let $A'(\chi_0, v_0)$ be the Fréchet derivative operator of A at (χ_0, v_0) with respect to (χ, v). It follows from the arguments above that 1 is not an eigenvalue of $A'(\chi_0, v_0)$, and (χ_0, v_0) is a nondegenerate fixed-point of A in W_0. Hence,

$$\text{index}(A, (\chi_0, v_0), W_0) = \text{index}(A, (\chi_0, v_0), X_0) = \text{index}(A'(\chi_0, v_0), (0, 0), X_0) = (-1)^\sigma$$

by the Leray-Schauder formula, where σ is the sum of the multiplicities of all eigenvalues of $A'(\chi_0, v_0)$ which are greater than one. Suppose $\lambda > 1$ is an eigenvalue of

$A'(\chi_0, v_0)$ with the corresponding eigenfunction (ϕ, ψ). Then $A'(\chi_0, v_0)(\phi, \psi)^\top = \lambda(\phi, \psi)^\top$ leads to

$$\begin{aligned}
&\mathfrak{L}_1(\lambda)\phi = -bf_2(z-\chi_0)\psi, \qquad x \in (0,1),\\
&\mathfrak{L}_2(\lambda)\psi = (1-K(0,v_0))bv_0 f_2'(z-\chi_0)\phi, \qquad x \in (0,1),\\
&\phi_x(0) = \phi_x(1) + \nu\phi(1) = 0, \quad \psi_x(0) = \psi_x(1) + \nu\psi(1) = 0,
\end{aligned}$$

where

$$\mathfrak{L}_1(\lambda)\phi = \lambda d\phi_{xx} - (\lambda-1)M\phi - bv_0 f_2'(z-\chi_0)\phi,$$

$$\mathfrak{L}_2(\lambda)\psi = \lambda d\psi_{xx} - (\lambda-1)M\psi + (1-K(0,v_0))bf_2(z-\chi_0)\psi - K_v(0,v_0)bv_0 f_2(z-\chi_0)\psi.$$

It follows from $\lambda > 1$ and $bv_0 f_2'(z-\chi_0) > 0$ that the operator $\mathfrak{L}_1(\lambda)$ is invertible subject to the boundary conditions $\phi_x(0) = \phi_x(1) + \nu\phi(1) = 0$, and the principal eigenvalue of $\mathfrak{L}_1(\lambda)$ satisfies $\lambda_1(\mathfrak{L}_1(\lambda)) < 0$. Noting that the equation (19) and $\lambda > 1$, we have $\lambda_1(\mathfrak{L}_2(\lambda)) < 0$ by Lemma A.1. By similar arguments as we have dealt with (18), we can show $(\phi, \psi) = (0,0)$. Hence, $A'(\chi_0, U_0)$ has no eigenvalue greater than 1. Thus $\text{index}(A, (\chi_0, U_0), W_0) = (-1)^0 = 1$. □

Remark 1. Suppose $(H1)-(H3)$ hold and (S_0, v_0) is a positive solution of (14). It follows from the proof of Lemma 2.5 that for any $\lambda \geq 1$, the operator

$$\mathfrak{B}(\lambda) := \begin{pmatrix} \mathfrak{L}_1(\lambda) & bf_2(z-\chi_0) \\ -(1-K(0,v_0))bv_0 f_2'(z-\chi_0) & \mathfrak{L}_2(\lambda) \end{pmatrix}$$

is invertible in $C_B^2[0,1] \times C_B^2[0,1]$, where $C_B^2[0,1] = \{u \in C^2[0,1] : u_x(0) = u_x(1) + \nu u(1) = 0\}$. In particular, $\mathfrak{B} = \mathfrak{B}(1)$ is invertible in $C_B^2[0,1] \times C_B^2[0,1]$.

Theorem 2.6. *Suppose $(H1)-(H3)$ hold. Then*

(i) *the trivial solution (z, 0, 0) of (9) is the unique nonnegative solution provided that $b \leq \sigma_1$;*

(ii) *there exists a unique positive solution of (9) provided that $b > \sigma_1$, denoted by (S^*, v^*, p^*).*

Proof. (i) is a direct result of Lemma 2.3.

(ii) We first show there exists a unique positive solution of (14) provided that $b > \sigma_1$. It suffices to show A has a unique positive fixed point in Ω_0. It follows from Lemma 2.3 that the fixed points of A in Ω_0 are two types, which are the trivial fixed point $(0,0)$ and the positive fixed points (χ, v). It follows from Lemma 2.5 that any positive fixed point (χ_0, v_0) of A is non-degenerative and $\text{index}(A, (\chi_0, v_0), W_0) = 1$. Meanwhile, by the compactness argument on the operator A and the non-degeneracy of its fixed points (including $(0,0)$ and positive fixed points), one knows that there are at most finitely many positive fixed points in Ω_0. Let them be $(\chi_i, v_i)(i = 1, 2, \cdots, m)$. Then $\text{index}(A, (\chi_i, v_i), W_0) = 1$ for $i = 1, 2, \cdots, m$. By the additivity property of the fixed point index and Lemma 2.4, we have

$$1 = \text{index}(A, \Omega_0, W_0) = \text{index}(A, (0,0), W_0) + \sum_{i=1}^{m} \text{index}(A, (\chi_i, v_i), W_0) = m.$$

That is, there exists a unique positive solution of (14) provided that $b > \sigma_1$, which is denoted by (S^*, v^*). Let p^* be the unique solution to the problem

$$dp_{xx} + K(0, v^*)bv^* f_2(S^*) = 0, \quad x \in (0,1), \quad p_x(0) = p_x(1) + \nu p(1) = 0.$$

It follows from the strong maximum principle that $p^* > 0$ on [0, 1]. Hence, (9) has a unique positive solution (S^*, v^*, p^*) provided that $b > \sigma_1$. □

3. **Existence of positive solutions.** Clearly, $(z,0,0,0)$ is the trivial solution of (6)-(7). It follows from Theorems 2.1–2.2 that (6)-(7) possesses two semi-trivial nonnegative solutions $(z-\theta_a,\theta_a,0,0)$ and $(S^*,0,v^*,p^*)$ provided that $a>\lambda_1, b>\sigma_1$. The aim of this section is to establish the existence of positive solutions of (6)-(7). To this end, we first derive the priori estimates for nonnegative solutions of (6)-(7).

Lemma 3.1. *Suppose $(H1)-(H3)$ hold and (S,u,v,p) is a nonnegative solution of (6)-(7) with $u\not\equiv 0, v\not\equiv 0, p\not\equiv 0$. Then $S+u+v+p<z$, $0<S<z$, $0<u<\theta_a$, $0<v<\vartheta_b$, $0<p<\vartheta_b$, $0<v+p<\vartheta_b$ on [0, 1].*

Proof. Let $\Phi = z-(S+u+v+p)$. Then

$$-d\Phi_{xx}=cpu\geq 0,\not\equiv 0,\ x\in(0,1),\quad \Phi_x(0)=\Phi_x(1)+\nu\Phi(1)=0.$$

It follows from the strong maximum principle that $\Phi>0$ on [0, 1]. That is, $0\leq S+u+v+p<z(x)$ on [0, 1]. Noting that

$$\begin{aligned}&-dS_{xx}+(au\textstyle\int_0^1 f_1'(\tau S)d\tau+bv\int_0^1 f_2'(\tau S)d\tau)S=0,\quad x\in(0,1),\\ &S_x(0)=-1,\ S_x(1)+\nu S(1)=0.\end{aligned}$$

It follows from the strong maximum principle that $S>0$ on [0, 1]. Hence, $0<S<z-u-v-p$ on [0, 1]. In particular, $0<S<z$, $0<S<z-u$, $0<S<z-(v+p)$ and $0<S<z-v$ on [0, 1]. Similarly, we have

$$-du_{xx}+cpu=auf_1(S)\geq 0,\not\equiv 0,\ x\in(0,1),\quad u_x(0)=u_x(1)+\nu u(1)=0.$$

By the strong maximum principle, we obtain that $u>0$ on [0, 1]. In view of $0<S<z-u$ on [0, 1], we get

$$0=du_{xx}+auf_1(S)-cpu\leq du_{xx}+auf_1(z-u),\ x\in(0,1),\quad u_x(0)=u_x(1)+\nu u(1)=0,$$

which implies $u<\theta_a$ on [0, 1]. Namely, $0<u<\theta_a$ on [0, 1]. Similarly, by virtue of $0<S<z-(v+p)<z-v$ on [0, 1], we have $v,p>0$ and $v+p<\vartheta_b$ on [0, 1], which imply $0<v<\vartheta_b$, $0<p<\vartheta_b$ on [0, 1]. $\square$

Lemma 3.2. *Suppose $(H1)-(H3)$ hold and (S,u,v,p) is a nonnegative solution of (6)-(7) with $u\not\equiv 0, v\not\equiv 0, p\not\equiv 0$. Then*

(i) *$a>\lambda_1, b>\sigma_1$;*
(ii) *for $b>\sigma_1$ fixed, there exists some positive constant Λ_0 such that $a<\Lambda_0$.*

Proof. (i) It follows from Lemma 3.1 that $S,u,v,p>0$ and $S<z$ on [0, 1]. By Lemma A.1, we have

$$a=\lambda_1(cp,f_1(S))>\lambda_1(0,f_1(z))=\lambda_1,$$

where $\lambda_1(cp,f_1(S))$ is the principal eigenvalue of $-d\phi_{xx}+cp\phi=\lambda f_1(z)\phi,\ x\in(0,1),\ \phi_x(0)=\phi_x(1)+\nu\phi(1)$(cf. Lemma A.1). Similarly, we get

$$b=\lambda_1(K(u,v)bf_2(S),f_2(S))>\lambda_1(0,f_2(z))=\sigma_1.$$

(ii) Assume that (S_i,u_i,v_i,p_i) is a positive solution of (6)-(7) with $a=a_i$ and $a_i\to\infty$. Then it follows from the equation

$$-d(u_i)_{xx}+cp_iu_i=a_iu_if_1(S_i),\ x\in(0,1),\quad (u_i)_x(0)=(u_i)_x(1)+\nu u_i(1)=0,$$

that $a_i=\lambda_1(cp_i,f_1(S_i))<\lambda_1(c\vartheta_b,f_1(S_i))$. Noting that $a_i\to\infty$, one can find that $S_i\to 0$ a.e. in $(0,1)$ as $i\to\infty$. On the other hand, it follows from the equation

$$d(v_i)_{xx}+K(u_i,v_i)bv_if_2(S_i)=bv_if_2(S_i),\ x\in\Omega,\quad (v_i)_x(0)=(v_i)_x(1)+\nu v_i(1)=0$$

that $b = \lambda_1(K(u_i, v_i)bf_2(S_i), f_2(S_i))$, which implies $b \to \infty$ since $S_i \to 0$ a.e. in $(0,1)$ as $i \to \infty$. This is a contradiction. Hence, there exists some positive constant Λ_0 such that $a < \Lambda_0$. $\square$

Let $\chi = z - S$. Then the steady state system (6)-(7) is equivalent to

$$\begin{cases} d\chi_{xx} + auf_1(z-\chi) + bvf_2(z-\chi) = 0, & x \in (0,1), \\ du_{xx} + auf_1(z-\chi) - cpu = 0, & x \in (0,1), \\ dv_{xx} + (1-K(u,v))bvf_2(z-\chi) = 0, & x \in (0,1), \\ dp_{xx} + K(u,v)bvf_2(z-\chi) = 0, & x \in (0,1), \\ \chi_x(0) = \chi_x(1) + \nu\chi(1) = 0, \quad u_x(0) = u_x(1) + \nu u(1) = 0, & \\ v_x(0) = v_x(1) + \nu v(1) = 0, \quad p_x(0) = p_x(1) + \nu p(1) = 0. & \end{cases} \tag{24}$$

Moreover, by Lemma 3.1, (S, u, v, p) is a nonnegative solution of (6)-(7) if and only if (χ, u, v, p) is a nonnegative solution of (24). As mentioned before, nonnegative solutions of (24) can be divided into three types:

(i) the trivial solution $E_0 = (\chi, u, v, p) = (0, 0, 0, 0)$,
(ii) the semi-trivial solutions $E_1 = (\chi, u, v, p) = (\theta_a, \theta_a, 0, 0)$ exists if $a > \lambda_1$ and $E_2 = (\chi, u, v, p) = (z - S^*, 0, v^*, p^*)$ exists if $b > \sigma_1$,
(iii) positive solutions (χ, u, v, p) with $\chi, u, v, p > 0$ on $[0, 1]$.

Next, we turn to study positive solutions of (24). To this end, we introduce the spaces

$$\begin{aligned} &C_+[0,1] = \{u \in C[0,1] : u \geq 0 \text{ on } [0,1]\}, \\ &X = C[0,1] \times C[0,1] \times C[0,1] \times C[0,1], \\ &W = C_+[0,1] \times C_+[0,1] \times C_+[0,1] \times C_+[0,1], \\ &\Omega = \{(\chi, u, v, p) \in W : \chi < z,\ u < \max_{[0,1]} \theta_a + 1,\ v < \max_{[0,1]} \vartheta_b + 1, p < \max_{[0,1]} \vartheta_b + 1\}, \end{aligned}$$

Then W is a cone of X and Ω is a bounded open set in W. Define a differential operator $\mathcal{A}_\tau : [0,1] \times \Omega \to X$ by

$$\mathcal{A}_\tau(\chi, u, v, p) := \left(-d\frac{\mathrm{d}^2}{\mathrm{d}x^2} + M\right)^{-1} \begin{pmatrix} \tau auf_1(z-\chi) + \tau bvf_2(z-\chi) + M\chi \\ \tau auf_1(z-\chi) - \tau cpu + Mu \\ \tau(1-K(u,v))bvf_2(z-\chi) + Mv \\ \tau K(u,v)bvf_2(z-\chi) + Mp \end{pmatrix},$$

where $\left(-d\frac{\mathrm{d}^2}{\mathrm{d}x^2} + M\right)^{-1}$ is the inverse operator of $-d\frac{\mathrm{d}^2}{\mathrm{d}x^2} + M$ subject to the boundary conditions $v_x(0) = v_x(1) + \nu v(1) = 0$, M is large enough such that $M - cp > 0$ for all $(\chi, u, v, p) \in \Omega$ and $x \in [0,1]$. Hence, for any $\tau \in [0,1]$, we have $\mathcal{A}_\tau : \Omega \to W$. It follows from standard elliptic regularity theory that $\mathcal{A}_\tau$ is compact and continuously differentiable. Let $\mathcal{A} = \mathcal{A}_1$. By Lemma 3.1, there exists a nonnegative solution of (6)-(7) (or (24) equivalently) if and only if there exists a fixed point of the operator $\mathcal{A}$ in Ω. Moreover, similar arguments as in Lemma 3.1 indicate that $\mathcal{A}_\tau$ has no fixed points on $\partial\Omega$. To figure out whether there exist positive fixed points of $\mathcal{A}$ or not, we need to calculate the index of the trivial and semi-trivial fixed points of $\mathcal{A}$ firstly.

Let $\hat{\lambda}_1, \hat{\sigma}_1$ be the principal eigenvalues of the problems respectively,

$$\begin{cases} -d(\hat{\phi}_1)_{xx} + cp^*\hat{\phi}_1 = \hat{\lambda}_1 f_1(S^*)\hat{\phi}_1,\ x \in (0,1), \\ (\hat{\phi}_1)_x(0) = (\hat{\phi}_1)_x(1) + \nu\hat{\phi}_1(1) = 0, \\ d(\hat{\psi}_1)_{xx} + \hat{\sigma}_1(1 - K(\theta_a, 0))f_2(z-\theta_a)\hat{\psi}_1 = 0,\ x \in (0,1), \\ (\hat{\psi}_1)_x(0) = (\hat{\psi}_1)_x(1) + \nu\hat{\psi}_1(1) = 0, \end{cases} \tag{25}$$

with the corresponding eigenfunctions $\hat{\phi}_1, \hat{\psi}_1 > 0$ on $[0,1]$, normalized with $\max\limits_{[0,1]} \hat{\phi}_1 = 1$, $\max\limits_{[0,1]} \hat{\psi}_1 = 1$. It follows from Lemma 3.1 and Lemma A.1 that

$$\hat{\lambda}_1 = \lambda_1\left(cp^*, f_1(S^*)\right) > \lambda_1(0, f_1(z)) = \lambda_1.$$

Similarly,

$$\hat{\sigma}_1 = \lambda_1\left(0, (1-K(\theta_a,0))f_2(z-\theta_a)\right) > \lambda_1(0, f_2(z)) = \sigma_1.$$

Moreover, it follows from Theorem 2.1 and Lemma A.1 that the function $\hat{\sigma}_1(a)$ depends continuously on the parameter a on $[\lambda_1, +\infty)$ with $\lim\limits_{a\to\lambda_1} \hat{\sigma}_1(a) = \sigma_1$ and $\lim\limits_{a\to+\infty} \hat{\sigma}_1(a) = +\infty$. Furthermore, if $K_u(u,v) \geq 0$, then $\hat{\sigma}_1(a)$ is strictly increasing on $[\lambda_1, +\infty)$. That is, the following lemma holds, whose proof is exactly similar to Lemma 2.3 in [23].

Lemma 3.3. *Suppose $(H1)-(H3)$ hold and $K_u(u,v) \geq 0$. Then the function $\hat{\sigma}_1(a)$ depends continuously on the parameter a on $[\lambda_1, +\infty)$, and is strictly increasing on $[\lambda_1, +\infty)$. Moreover, $\lim\limits_{a\to\lambda_1} \hat{\sigma}_1(a) = \sigma_1$ and $\lim\limits_{a\to+\infty} \hat{\sigma}_1(a) = +\infty$.*

Lemma 3.4. *Suppose $(H1)-(H3)$ hold and $a > \lambda_1, b > \sigma_1$. Then*

(i) $\mathrm{index}(\mathcal{A}, \Omega, W) = 1$;
(ii) $\mathrm{index}(\mathcal{A}, E_0, W) = 0$;
(iii) $\mathrm{index}(\mathcal{A}, E_1, W) = 0$ *if* $b > \hat{\sigma}_1$, *and* $\mathrm{index}(\mathcal{A}, E_1, W) = 1$ *if* $b < \hat{\sigma}_1$;
(iv) $\mathrm{index}(\mathcal{A}, E_2, W) = 0$ *if* $a > \hat{\lambda}_1$, *and* $\mathrm{index}_W(\mathcal{A}, E_2, W) = 1$ *if* $a < \hat{\lambda}_1$.

Proof. (i)-(ii) can be shown by similar arguments as in Lemma 2.4, and we omit it here.

(iii) To calculate $\mathrm{index}(\mathcal{A}, E_1, W)$, we decompose X into

$$X_1 = \{(\chi, u, 0, 0) : \chi, u \in C[0,1]\}, \quad X_2 = \{(0, 0, v, p) : v, p \in C[0,1]\}.$$

Let $W_1 = W \cap X_1, W_2 = W \cap X_2$ and $U = N(E_1) \cap W_1$, where $N(E_1)$ is a small neighborhood of E_1 in W. Then U is relatively open and bounded. Choosing $\epsilon > 0$ small enough, we have

$$\mathrm{index}(\mathcal{A}, E_1, W) = \deg_W(I - \mathcal{A}, U \times W_2(\epsilon), 0),$$

where $W_2(\epsilon) = \{(0,0,v,p) \in W_2 : \|(v,p)\|_{X_2} < \epsilon\}$. Let $Q : X \to X_1$ be the projection such that $Q(\chi, u, v, p) = (\chi, u)$. Denote $\mathcal{A}_1 = Q\mathcal{A}, \mathcal{A}_2 = (I-Q)\mathcal{A}$. Then we have $\mathcal{A}(\chi, u, v, p) = (\mathcal{A}_1(\chi, u, v, p), \mathcal{A}_2(\chi, u, v, p))$. Moreover, $\mathcal{A}_2(\chi, u, 0, 0) \equiv 0$ for $(\chi, u) \in \overline{U}$ and $\mathcal{A}_1(\chi, u, 0, 0) \neq (\chi, u)$ for $(\chi, u) \in \partial U$.

Next, we determine the spectral radius $r(\mathcal{A}_2'(E_1)|_{W_2})$ of the operator $\mathcal{A}_2'(E_1)|_{W_2}$. Direct computation leads to

$$\mathcal{A}_2'(E_1)|_{W_2} = \left(-d\frac{\mathrm{d}^2}{\mathrm{d}x^2} + M\right)^{-1} \begin{pmatrix} (1-K(\theta_a,0))bf_2(z-\theta_a) + M & 0 \\ K(\theta_a,0)bf_2(z-\theta_a) & M \end{pmatrix}.$$

Hence, $\mathcal{A}_2'(E_1)|_{W_2}(\psi, \zeta)^\top = \lambda(\psi, \zeta)^\top$ gives

$$\begin{aligned} &-d\psi_{xx} + M\psi = \frac{1}{\lambda}[(1-K(\theta_a,0))bf_2(z-\theta_a)\psi + M\psi], && x \in (0,1), \\ &-d\zeta_{xx} + M\zeta = \frac{1}{\lambda}[K(\theta_a,0)bf_2(z-\theta_a)\psi + M\zeta], && x \in (0,1), \\ &\psi_x(0) = \psi_x(1) + \nu\psi(1) = 0, \quad \zeta_x(0) = \zeta_x(1) + \nu\zeta(1) = 0. && \end{aligned} \tag{26}$$

Consider the eigenvalue problem

$$\begin{aligned}&-d\psi_{xx}-b(1-K(\theta_a,0))f_2(z-\theta_a)\psi=\eta\psi, \quad x\in(0,1),\\&\psi_x(0)=\psi_x(1)+\nu\psi(1)=0.\end{aligned}\tag{27}$$

Noting that

$$\begin{aligned}&d(\hat{\psi}_1)_{xx}+\hat{\sigma}_1(1-K(\theta_a,0))f_2(z-\theta_a)\hat{\psi}_1=0,\ x\in(0,1),\\&(\hat{\psi}_1)_x(0)=(\hat{\psi}_1)_x(1)+\nu\hat{\psi}_1(1)=0,\end{aligned}$$

we can find that the least eigenvalue $\eta_1<0$ of (27) if $b>\hat{\sigma}_1$, and the least eigenvalue $\eta_1>0$ of (27) if $b<\hat{\sigma}_1$. It follows from Lemma A.2 that the spectral radius

$$r\left[(M-d\frac{\mathrm{d}^2}{\mathrm{dx}^2})^{-1}(M+(1-K(\theta_a,0))bf_2(z-\theta_a))\right]>1$$

if $b>\hat{\sigma}_1$, and

$$r\left[(M-d\frac{\mathrm{d}^2}{\mathrm{dx}^2})^{-1}(M+(1-K(\theta_a,0))bf_2(z-\theta_a))\right]<1$$

if $b<\hat{\sigma}_1$. In view of the spectral radius $r\left(M-d\frac{\mathrm{d}^2}{\mathrm{dx}^2}\right)^{-1}(M)<1$, we can conclude that (26) has eigenvalues greater than 1 and 1 is not an eigenvalue of (26) corresponding to a positive eigenvector provided that $b>\hat{\sigma}_1$, and (26) has no eigenvalues greater than or equal to 1 provided that $b<\hat{\sigma}_1$. Hence, the spectral radius $r(\mathcal{A}_2'(E_1)|_{W_2})>1$ and 1 is not an eigenvalue of $\mathcal{A}_2'(E_1)|_{W_2}$ corresponding to a positive eigenvector provided that $b>\hat{\sigma}_1$ and the spectral radius $r(\mathcal{A}_2'(E_1)|_{W_2})<1$ provided that $b<\hat{\sigma}_1$. It follows from Lemma A.4 that for $\epsilon>0$ small,

$$\operatorname{index}(\mathcal{A},E_1,W)=\deg_W(I-\mathcal{A},U\times W_2(\epsilon),0)=\begin{cases}0 & \text{if } b>\hat{\sigma}_1,\\ \deg_{W_1}(I-\mathcal{A}_1|_{W_1},U,0) & \text{if } b<\hat{\sigma}_1.\end{cases}$$

By Leray-Schauder degree theory, $\deg_{W_1}(I-\mathcal{A}_1|_{W_1},U,0)=(-1)^m$, where m is the sum of the multiplicities of all eigenvalues of the Fréchet derivative $\mathcal{A}_1'(E_1)$ which are greater than one. Consider the eigenvalue problem $\mathcal{A}_1'(E_1)|_{W_1}(\xi,\phi)^\top=\lambda(\xi,\phi)^\top$. Then we have

$$\begin{aligned}&-\lambda d\xi_{xx}+(\lambda-1)M\xi=-a\theta_af_1'(z-\theta_a)\xi+af_1(z-\theta_a)\phi,\ x\in(0,1),\\&-\lambda d\phi_{xx}+(\lambda-1)M\phi=af_1(z-\theta_a)\phi-a\theta_af_1'(z-\theta_a)\xi,\quad x\in(0,1),\\&\xi_x(0)=\xi_x(1)+\nu\xi(1)=0,\quad \phi_x(0)=\phi_x(1)+\nu\phi(1)=0.\end{aligned}$$

Let $\Phi=\xi-\phi$. Then

$$-d\Phi_{xx}=\frac{1-\lambda}{\lambda}M\Phi,\ x\in(0,1),\Phi_x(0)=\Phi_x(1)+\nu\Phi(1)=0.$$

If $\Phi\equiv0$, then

$$\begin{aligned}&-d\phi_{xx}+M\phi=\frac{1}{\lambda}[af_1(z-\theta_a)-a\theta_af_1'(z-\theta_a)+M]\phi,\ x\in(0,1),\\&\phi_x(0)=\phi_x(1)+\nu\phi(1)=0.\end{aligned}\tag{28}$$

Noting that the first eigenvalue of the eigenvalue problem

$$\begin{aligned}&-d\varphi_{xx}-[af_1(z-\theta_a)-a\theta_af_1'(z-\theta_a)]\varphi=\eta\varphi,\ x\in(0,1),\\&\varphi_x(0)=\varphi_x(1)+\nu\varphi(1)=0.\end{aligned}$$

is larger than 0. It follows from Lemma A.2 that the spectral radius

$$r\left[(M-d\frac{\mathrm{d}^2}{\mathrm{dx}^2})^{-1}(M+af_1(z-\theta_a)-a\theta_af_1'(z-\theta_a))\right]<1.$$

Hence, (28) has no eigenvalues greater than or equal to 1. If $\Phi \not\equiv 0$, then it is easy to see that $\lambda < 1$. Hence, $\mathcal{A}_1'(E_1)|_{W_1}$ has no eigenvalues greater than or equal to 1. It follows that for $\epsilon > 0$ small

$$\text{index}(\mathcal{A}, E_1, W) = \deg_W(I - \mathcal{A}, U \times W_2(\epsilon), 0) = \deg_{W_1}(I - \mathcal{A}_1|_{W_1}, U, 0) = (-1)^0 = 1$$

provided that $b < \hat{\sigma}_1$.

(iv) In order to calculate index$(\mathcal{A}, E_2, W)$, we decompose X into $X_1 = \{(\chi, 0, v, p) : \chi, v, p \in C[0,1]\}$, $X_2 = \{(0, u, 0, 0) : u \in C[0,1]\}$. Let $W_1 = W \cap X_1, W_2 = W \cap X_2$ and $U = N(E_2) \cap W_1$, where $N(E_2)$ is a small neighborhood of E_2 in W. Then U is relatively open and bounded. Choosing $\epsilon > 0$ small enough, we have

$$\text{index}(\mathcal{A}, E_2, W) = \deg_W(I - \mathcal{A}, U \times W_2(\epsilon), 0),$$

where $W_2(\epsilon) = \{(0, u, 0, 0) \in W_2 : \|u\|_{C[0,1]} < \epsilon\}$. Let $Q : X \to X_1$ be the projection such that $Q(\chi, u, v, p) = (\chi, v, p)$. Denote $\mathcal{A}_1 = Q\mathcal{A}, \mathcal{A}_2 = (I - Q)\mathcal{A}$. Then we have

$$\mathcal{A}(\chi, u, v, p) = (\mathcal{A}_1(\chi, u, v, p), \mathcal{A}_2(\chi, u, v, p)).$$

Moreover, $\mathcal{A}_2(\chi, 0, v, p) \equiv 0$ for $(\chi, v, p) \in \overline{U}$ and $\mathcal{A}_1(\chi, 0, v, p) \neq (\chi, v, p)$ for $(\chi, v, p) \in \partial U$.

Next, we determine the spectral radius $r(\mathcal{A}_2'(E_2)|_{W_2})$ of the operator $\mathcal{A}_2'(E_2)|_{W_2}$. Direct computation leads to

$$\mathcal{A}_2'(E_1)|_{W_2} = \left(-d\frac{\mathrm{d}^2}{\mathrm{d}x^2} + M\right)^{-1} (af_1(S^*) - cp^* + M).$$

Hence, $\mathcal{A}_2'(E_2)|_{W_2}\phi = \lambda\phi$ gives

$$\begin{aligned} &-d\phi_{xx} + M\phi = \frac{1}{\lambda}(af_1(S^*)\phi - cp^*\phi + M\phi),\ x \in (0,1), \\ &\phi_x(0) = \phi_x(1) + \nu\phi(1) = 0. \end{aligned} \tag{29}$$

Consider the eigenvalue problem

$$-d\varphi_{xx} + cp^*\varphi - af_1(S^*)\varphi = \eta\varphi,\ x \in (0,1), \quad \varphi_x(0) = \varphi_x(1) + \nu\varphi_1(1) = 0. \tag{30}$$

If $a > \hat{\lambda}_1$, then the first eigenvalue of the eigenvalue problem (30) is less than 0. It follows from Lemma A.2 that the spectral radius

$$r\left[(-d\frac{\mathrm{d}^2}{\mathrm{d}x^2} + M)^{-1}(af_1(S^*) - cp^* + M)\right] > 1,$$

and 1 is not an eigenvalue of (29) corresponding to a positive eigenvector. That is, the spectral radius $r(\mathcal{A}_2'(E_1)|_{W_2}) > 1$ and 1 is not an eigenvalue of $\mathcal{A}_2'(E_1)|_{W_2}$ corresponding to a positive eigenvector provided that $a > \hat{\lambda}_1$. If $a < \hat{\lambda}_1$, then the first eigenvalue of the eigenvalue problem (30) is larger than 0. It follows from Lemma A.2 that the spectral radius $r(\mathcal{A}_2'(E_2)|_{W_2}) < 1$ provided that $a < \hat{\lambda}_1$. It follows from Lemma A.4 that for $\epsilon > 0$ small,

$$\text{index}(\mathcal{A}, E_2, W) = \deg_W(I – \mathcal{A}, U \times W_2(\epsilon), 0) = \begin{cases} 0 & \text{if } a > \hat{\lambda}_1, \\ \deg_{W_1}(I - \mathcal{A}_1|_{W_1}, U, 0) & \text{if } a < \hat{\lambda}_1. \end{cases}$$

By Leray-Schauder degree theory, $\deg_{W_1}(I - \mathcal{A}_1|_{W_1}, U, 0) = (-1)^m$, where m is the sum of the multiplicities of all eigenvalues of the Fréchet derivative $\mathcal{A}_1'(E_2)$

which are greater than one. Suppose $\lambda \geq 1$ is an eigenvalue of $\mathcal{A}_1'(E_2)|_{W_1}$ with the corresponding eigenfunction $(\xi, \psi, \zeta) \neq (0, 0, 0)$. Then

$$\begin{array}{l}
\mathcal{L}_1(\lambda)\xi = -bf_2(S^*)\psi,\ \ x \in (0,1),\\
\mathcal{L}_2(\lambda)\psi = (1 - K(0, v^*))bv^* f_2'(S^*)\xi, \quad x \in (0,1),\\
\mathcal{L}_3(\lambda)\zeta = -K(0, v^*)bf_2(S^*)\psi - K_v(0, v^*)bv^* f_2(S^*)\psi\\
\qquad\qquad +K(0, v^*)bv^* f_2'(S^*)\xi, \quad x \in (0,1),\\
\xi_x(0) = \xi_x(1) + \nu\xi(1) = 0, \quad \psi_x(0) = \psi_x(1) + \nu\psi(1) = 0,\\
\zeta_x(0) = \zeta_x(1) + \nu\zeta(1),
\end{array} \tag{31}$$

where

$$\mathcal{L}_1(\lambda)\xi = \lambda d\xi_{xx} - (\lambda - 1)M\xi - bv^* f_2'(S^*)\xi, \qquad \mathcal{L}_3(\lambda)\zeta = \lambda d\zeta_{xx} - (\lambda - 1)M\zeta,$$

$$\mathcal{L}_2(\lambda)\psi = \lambda d\psi_{xx} - (\lambda - 1)M\psi + (1 - K(0, v^*))bf_2(S^*)\psi - K_v(0, v^*)bv^* f_2(S^*)\psi.$$

We first consider the decoupled system

$$\begin{array}{ll}
\mathcal{L}_1(\lambda)\xi = -bf_2(S^*)\psi, & x \in (0,1),\\
\mathcal{L}_2(\lambda)\psi = (1 - K(0, v^*))bv^* f_2'(S^*)\xi, & x \in (0,1),\\
\xi_x(0) = \xi_x(1) + \nu\xi(1) = 0, \quad \psi_x(0) = \psi_x(1) + \nu\psi(1) = 0. &
\end{array} \tag{32}$$

It follows from $\lambda \geq 1$ and $bv^* f_2'(S^*) > 0$ that the operator $\mathcal{L}_1(\lambda)$ is invertible subject to the boundary conditions $\xi_x(0) = \xi_x(1) + \nu\xi(1) = 0$, and the principal eigenvalue of $\mathcal{L}_1(\lambda)$ satisfies $\lambda_1(\mathcal{L}_1(\lambda)) < 0$. Noting that (S^*, v^*) is the unique positive solution to (14), we can find that for $\lambda \geq 1$, the principal eigenvalue $\lambda_1(\mathfrak{L}_2(\lambda)) \leq 0$. The equality holds if and only if $K_v(0, v) \equiv 0$ and $\lambda = 1$. It follows from Remark 1 that for any $\lambda \geq 1$, the operator

$$\mathcal{B}(\lambda) := \begin{pmatrix} \mathcal{L}_1(\lambda) & bf_2(S^*) \\ -(1 - K(0, v^*))bv^* f_2'(S^*) & \mathcal{L}_2(\lambda) \end{pmatrix}$$

is invertible, which implies $(\xi, \psi) = (0, 0)$. Meanwhile, it is easy to see that $\mathcal{L}_3(\lambda)$ is invertible, which leads to $\zeta = 0$ on [0, 1]. This is a contradiction to $(\xi, \psi, \zeta) \neq (0, 0, 0)$. Thus $\mathcal{A}_1'(E_2)|_{W_1}$ has no eigenvalues greater than or equal to 1. That is, $m = 0$. It follows that for $\epsilon > 0$ small

$$\text{index}(\mathcal{A}, E_2, W) = \deg_W(I - \mathcal{A}, U \times W_2(\epsilon), 0) = \deg_{W_1}(I - \mathcal{A}_1|_{W_1}, U, 0) = (-1)^0 = 1$$

provided that $a < \hat{\lambda}_1$. $\square$

Theorem 3.5. *Suppose* $(H1)-(H3)$ *hold. Then the steady state system* (6)-(7) *has at least one positive solution if* (i) $a > \hat{\lambda}_1, b > \hat{\sigma}_1$ or (ii) $\lambda_1 < a < \hat{\lambda}_1, \sigma_1 < b < \hat{\sigma}_1$.

Proof. It suffices to show that (24) has at least a positive solution. Suppose (24) has no positive solutions. In view of, $a > \lambda_1, b > \sigma_1$, the system (24) has only the trivial solution $E_0 = (0, 0, 0, 0)$, and the semi-trivial solutions $E_1 = (\theta_a, \theta_a, 0, 0)$ and $E_2 = (z - S^*, 0, v^*, p^*)$. By the additivity of the index, we have

$$\text{index}(\mathcal{A}, \Omega, W) = \text{index}(\mathcal{A}, E_0, W) + \text{index}(\mathcal{A}, E_1, W) + \text{index}(\mathcal{A}, E_2, W).$$

It follows from Lemma 3.4 that

$$\begin{aligned}
&\text{index}(\mathcal{A}, E_0, W) + \text{index}(\mathcal{A}, E_1, W) + \text{index}(\mathcal{A}, E_2, W)\\
&= \begin{cases} 0 & \text{if } a > \hat{\lambda}_1, b > \hat{\sigma}_1,\\ 2 & \text{if } \lambda_1 < a < \hat{\lambda}_1, \sigma_1 < b < \hat{\sigma}_1, \end{cases}
\end{aligned}$$

which is a contradiction to $\text{index}(\mathcal{A}, \Omega, W) = 1$. Hence, (6)-(7) has at least one positive solution in the case of (i) or (ii). $\square$

4. **Global bifurcation and stability.** The aim of this section is devoted to study the structure and stability of the nonnegative solutions of the steady state system (6)-(7). Clearly, (6)-(7) has trivial solution $(S,u,v,p)=(z,0,0,0)$, which always exists. If $a>\lambda_1, b>\sigma_1$, then it follows from Theorems 2.1-2.6 that (6)-(7) has two semi-trivial solution branches

$$\Gamma_1=\{(a,z-\theta_a,\theta_a,0,0):a>\lambda_1\} \text{ and } \Gamma_2=\{(a,S^*,0,v^*,p^*):a\in\mathbb{R}_+\}.$$

We first study the stability of the trivial solution $(z,0,0,0)$ and the semi-trivial solutions $(z-\theta_a,\theta_a,0,0)$ and $(S^*,0,v^*,p^*)$.

Theorem 4.1. *Suppose $(H1)-(H3)$ hold. Then*

(i) *the trivial solution $(z,0,0,0)$ is stable if $a<\lambda_1$ and $b<\sigma_1$, and unstable if $a>\lambda_1$ or $b>\sigma_1$;*

(ii) *the semi-trivial solution $(z-\theta_a,\theta_a,0,0)$ is stable if $b<\hat{\sigma}_1$, and unstable if $b>\hat{\sigma}_1$;*

(iii) *if $K(0,v)\equiv 0$, then $(S^*,0,v^*,p^*)=(z-\vartheta_b,0,\vartheta_b,0)$, and it is stable if $a<\hat{\lambda}_1$, and unstable if $a>\hat{\lambda}_1$.*

Proof. The proof of (i) is standard, and is omitted here.

(ii) Consider the following linearized eigenvalue problem of (6)-(7) at $(z-\theta_a,\theta_a,0,0)$

$$\begin{cases} d\xi_{xx}-a\theta_a f_1'(z-\theta_a)\xi-af_1(z-\theta_a)\phi-bf_2(z-\theta_a)\psi+\lambda\xi=0, & x\in(0,1),\\ d\phi_{xx}+af_1(z-\theta_a)\phi+a\theta_a f_1'(z-\theta_a)\xi-c\theta_a\zeta+\lambda\phi=0, & x\in(0,1),\\ d\psi_{xx}+(1-K(\theta_a,0))bf_2(z-\theta_a)\psi+\lambda\psi=0, & x\in(0,1),\\ d\zeta_{xx}+K(\theta_a,0)bf_2(z-\theta_a)\psi+\lambda\zeta=0, & x\in(0,1),\\ \xi_x(0)=\xi_x(1)+\nu\xi(1)=0, \quad \phi_x(0)=\phi_x(1)+\nu\phi(1)=0,\\ \psi_x(0)=\psi_x(1)+\nu\psi(1)=0, \quad \zeta_x(0)=\zeta_x(1)+\nu\zeta(1)=0. \end{cases} \tag{33}$$

Let $\Phi=\xi+\phi$ and $\Psi=\psi+\zeta$. Then $\xi=\Phi-\phi,\zeta=\Psi-\psi$ and (ϕ,Φ,Ψ,ψ) satisfies

$$\begin{cases} d\phi_{xx}+af_1(z-\theta_a)\phi-a\theta_a f_1'(z-\theta_a)\phi+a\theta_a f_1'(z-\theta_a)\Phi\\ \qquad -c\theta_a\Psi+c\theta_a\psi+\lambda\phi=0, & x\in(0,1),\\ d\Phi_{xx}-c\theta_a\Psi-bf_2(z-\theta_a)\psi+c\theta_a\psi+\lambda\Phi=0, & x\in(0,1),\\ d\Psi_{xx}+bf_2(z-\theta_a)\psi+\lambda\Psi=0, & x\in(0,1),\\ d\psi_{xx}+(1-K(\theta_a,0))bf_2(z-\theta_a)\psi+\lambda\psi=0, & x\in(0,1),\\ \phi_x(0)=\phi_x(1)+\nu\phi(1)=0, \quad \Phi_x(0)=\Phi_x(1)+\nu\Phi(1)=0,\\ \Psi_x(0)=\Psi_x(1)+\nu\Psi(1)=0, \quad \psi_x(0)=\psi_x(1)+\nu\psi(1)=0. \end{cases} \tag{34}$$

It is easy to see that λ is an eigenvalue of (34) if and only if λ is an eigenvalue of one of the following four operators:

$$-d\frac{\mathrm{d}^2}{\mathrm{d}x^2}-af_1(z-\theta_a)+a\theta_a f_1'(z-\theta_a), \quad -d\frac{\mathrm{d}^2}{\mathrm{d}x^2},$$
$$-d\frac{\mathrm{d}^2}{\mathrm{d}x^2}, \quad -d\frac{\mathrm{d}^2}{\mathrm{d}x^2}-(1-K(\theta_a,0))bf_2(z-\theta_a)$$

subject to the homogeneous Robin boundary conditions: $\phi_x(0)=\phi_x(1)+\nu\phi(1)=0$. Clearly, all eigenvalues of the operator $-d\frac{\mathrm{d}^2}{\mathrm{d}x^2}$ subject to the homogeneous Robin boundary conditions: $\phi_x(0)=\phi_x(1)+\nu\phi(1)=0$ are larger than 0. By Theorem 2.1, all eigenvalues of the operator $L_a=-d\frac{\mathrm{d}^2}{\mathrm{d}x^2}-af_1(z-\theta_a)+a\theta_a f_1'(z-\theta_a)$ subject to the homogeneous Robin boundary conditions: $\phi_x(0)=\phi_x(1)+\nu\phi(1)=0$ are greater than 0. Meanwhile, it follows from Lemma A.1 that all eigenvalues of the operator $-d\frac{\mathrm{d}^2}{\mathrm{d}x^2}-(1-K(\theta_a,0))bf_2(z-\theta_a)$ are larger than 0 if $b<\hat{\sigma}_1$, and it has an eigenvalue less than 0 if $b>\hat{\sigma}_1$. Therefore, (ii) holds.

(iii) If $K(0,v)\equiv 0$, then it follows from Lemma 2.2 that $(S^*,0,v^*,p^*)=(z-\vartheta_b,0,\vartheta_b,0)$. To investigate the stability of the semi-trivial solution $(z-\vartheta_b,0,\vartheta_b,0)$, we consider the linearized eigenvalue problem of (6)-(7) at $(z-\vartheta_b,0,\vartheta_b,0)$

$$\begin{aligned}
&d\xi_{xx}-b\vartheta_b f_2'(z-\vartheta_b)\xi-af_1(z-\vartheta_b)\phi-bf_2(z-\vartheta_b)\psi+\lambda\xi=0,\\
&d\phi_{xx}+af_1(z-\vartheta_b)\phi+\lambda\phi=0,\\
&d\psi_{xx}+bf_2(z-\vartheta_b)\psi-K_u(0,\vartheta_b)b\vartheta_b f_2(z-\vartheta_b)\phi\\
&\qquad+b\vartheta_b f_2'(z-\vartheta_b)\xi+\lambda\psi=0,\\
&d\zeta_{xx}+K_u(0,\vartheta_b)b\vartheta_b f_2(z-\vartheta_b)\phi+\lambda\zeta=0,\\
&\xi_x(0)=\xi_x(1)+\nu\xi(1)=0,\quad \phi_x(0)=\phi_x(1)+\nu\phi(1)=0,\\
&\psi_x(0)=\psi_x(1)+\nu\psi(1)=0,\quad \zeta_x(0)=\zeta_x(1)+\nu\zeta(1)=0.
\end{aligned}\tag{35}$$

Let $\Phi=\xi+\psi$. Then $\psi=\Phi-\xi$ and (ξ,Φ,ζ,ϕ) satisfies

$$\begin{aligned}
&d\xi_{xx}-b\vartheta_b f_2'(z-\vartheta_b)\xi-af_1(z-\vartheta_b)\phi\\
&\qquad-bf_2(z-\vartheta_b)(\Phi-\xi)+\lambda\xi=0,\ x\in(0,1),\\
&d\Phi_{xx}-af_1(z-\vartheta_b)\phi-K_u(0,\vartheta_b)b\vartheta_b f_2(z-\vartheta_b)\phi+\lambda\Phi=0,\ x\in(0,1),\\
&d\zeta_{xx}+K_u(0,\vartheta_b)b\vartheta_b f_2(z-\vartheta_b)\phi+\lambda\zeta=0,\ x\in(0,1),\\
&d\phi_{xx}+af_1(z-\vartheta_b)\phi+\lambda\phi=0,\ x\in(0,1),\\
&\xi_x(0)=\xi_x(1)+\nu\xi(1)=0,\quad \Phi_x(0)=\Phi_x(1)+\nu\Phi(1)=0,\\
&\zeta_x(0)=\zeta_x(1)+\nu\zeta(1)=0,\quad \psi_x(0)=\psi_x(1)+\nu\psi(1)=0.
\end{aligned}\tag{36}$$

It is easy to see that λ is an eigenvalue of (36) if and only if λ is an eigenvalue of one of the following four operators:

$$-d\frac{\mathrm{d}^2}{\mathrm{d}x^2}-bf_2(z-\vartheta_b)+b\vartheta_b f_2'(z-\vartheta_b),\quad -d\frac{\mathrm{d}^2}{\mathrm{d}x^2},\quad -d\frac{\mathrm{d}^2}{\mathrm{d}x^2},\quad -d\frac{\mathrm{d}^2}{\mathrm{d}x^2}-af_1(z-\vartheta_b)$$

subject to the homogeneous Robin boundary conditions: $\phi_x(0)=\phi_x(1)+\nu\phi(1)=0$. Clearly, all eigenvalues of the operator $-d\frac{\mathrm{d}^2}{\mathrm{d}x^2}$ subject to the homogeneous Robin boundary conditions: $\phi_x(0)=\phi_x(1)+\nu\phi(1)=0$ are larger than 0. By Lemma 2.2, all eigenvalues of the operator $L_b=-d\frac{\mathrm{d}^2}{\mathrm{d}x^2}-bf_2(z-\vartheta_b)+b\vartheta_b f_2'(z-\vartheta_b)$ subject to the homogeneous Robin boundary conditions: $\phi_x(0)=\phi_x(1)+\nu\phi(1)=0$ are greater than 0. Meanwhile, it follows from Lemma A.1 that all eigenvalues of the operator $-d\frac{\mathrm{d}^2}{\mathrm{d}x^2}-af_1(z-\vartheta_b)$ are larger than 0 if $a<\hat{\lambda}_1$, and it has an eigenvalue less than 0 if $a>\hat{\lambda}_1$. Therefore, (iii) holds. □

Remark 2. In Lemma 4.1, we only establish the stability of the semi-trivial solution $(S^*,0,v^*,p^*)=(z-\vartheta_b,0,\vartheta_b,0)$ when $K(0,v)\equiv 0$. For the general case of $K(0,v)\not\equiv 0$, in view of Remark 1, we can show that the semi-trivial solution $(S^*,0,v^*,p^*)$ is unstable if $a>\hat{\lambda}_1$ by similar arguments as in Theorem 4.1. However, for $a<\hat{\lambda}_1$, the stability of the semi-trivial solution $(S^*,0,v^*,p^*)$ remains open although lots of numerical simulations strongly suggest that $(S^*,0,v^*,p^*)$ is stable. In fact, for $a<\hat{\lambda}_1$, we can prove that the linearized eigenvalue problem of (6)-(7) at $(S^*,0,v^*,p^*)$ has no eigenvalues less than or equal to 0 (c.f. Lemma 2.5). However, it is very difficult to figure out whether the linearized eigenvalue problem of (6)-(7) at $(S^*,0,v^*,p^*)$ has an eigenvalue with real part less than 0 or not.

Next, we focus on positive solutions of (6)-(7). The main tool is the bifurcation theorem[6, 26]. The main idea is to construct positive solutions of (6)-(7) bifurcating from the semi-trivial solution branch Γ_2 by taking $b>\sigma_1$ fixed and

a as the bifurcation parameter. To this end, let $\chi = z - S$. Then the system (6)-(7) is equivalent to (24). Moreover the change of variables maps the trivial solution $(S, u, v, p) = (z, 0, 0, 0)$ of (6)-(7) to $(\chi, u, v, p) = (0, 0, 0, 0)$, and maps the semi-trivial nonnegative solution branches Γ_1 and Γ_2 of (6)-(7) to the semi-trivial nonnegative ones

$$\Gamma_1' = \{(a, \theta_a, \theta_a, 0, 0) : a > \lambda_1\} \text{ and } \Gamma_2' = \{(a, z - S^*, 0, v^*, p^*) : a \in \mathbb{R}_+\}.$$

Let $\mathbf{X} = W^{2,q}(0,1) \times W^{2,q}(0,1) \times W^{2,q}(0,1) \times W^{2,q}(0,1)$ with $q > 1$. Then $\mathbf{X} \hookrightarrow C^1[0,1] \times C^1[0,1] \times C^1[0,1] \times C^1[0,1]$. For a small $\epsilon > 0$, we define

$$\begin{aligned} \Omega_\epsilon = \ &\{(\chi, u, v, p) \in \mathbf{X} : -\epsilon < \chi < z,\ -\epsilon < u < \max_{[0,1]} \theta_a + 1, \\ &-\epsilon < v < \max_{[0,1]} \vartheta_b + 1, -\epsilon < p < \max_{[0,1]} \vartheta_b + 1\}. \end{aligned}$$

Then Ω_ϵ is an open connected subset of $\mathbf{X}$. By Lemma 3.1, any nonnegative solution $(\chi, u, v, p) \in \Omega_\epsilon$ of (24). Moreover, Lemma 3.2 implies that the necessary conditions for the existence of a positive solution of (6)-(7) are $a > \lambda_1, b > \sigma_1$, and there exists some positive constant Λ_0 such that $a < \Lambda_0$ provided that $b > \sigma_1$ fixed. Hence, for $b > \sigma_1$ fixed and $\lambda_1 < a < \Lambda_0$, there exists a positive constant M large enough such that

$$M + af_1(z - \chi) - cp > 0 \tag{37}$$

for all $(\chi, u, v, p) \in \Omega_\epsilon$ and $x \in [0,1]$.

Define $T : \mathbb{R}_+ \times \Omega_\epsilon \to \mathbf{X}$ by

$$T(a, \chi, u, v, p) := \left(-d\frac{\mathrm{d}^2}{\mathrm{d}x^2} + M\right)^{-1} \begin{pmatrix} auf_1(z-\chi) + bvf_2(z-\chi) + M\chi \\ auf_1(z-\chi) - cpu + Mu \\ (1 - K(u,v))bvf_2(z-\chi) + Mv \\ K(u,v)bvf_2(z-\chi) + Mp \end{pmatrix},$$

where $\left(-d\frac{\mathrm{d}^2}{\mathrm{d}x^2} + M\right)^{-1}$ is the inverse operator of $-d\frac{\mathrm{d}^2}{\mathrm{d}x^2} + M$ subject to the boundary conditions $u_x(0) = u_x(1) + \nu u(1) = 0$. By standard elliptic regularity theory, $T : \mathbb{R}_+ \times \Omega_\epsilon \to \mathbf{X}$ is completely continuous. Let

$$G(a, \chi, u, v, p) = (\chi, u, v, p)^\top - T(a, \chi, u, v, p).$$

Then $G : \mathbb{R}_+ \times \Omega_\epsilon \to \mathbf{X}$ is C^1 smooth, and the zeros of $G(a, \chi, u, v, p) = 0$ with $0 \le \chi < z, 0 \le u < \theta_a, 0 \le v < \vartheta_b, 0 \le p < \vartheta_b$ correspond to the nonnegative solutions of (24).

Let $\mathrm{D}_{(\chi,u,v,p)}G(a, z-S^*, 0, v^*, p^*)$ be the Fréchet derivative of $G(a, \chi, u, v, p)$ with respect to (χ, u, v, p) at $(z - S^*, 0, v^*, p^*)$. Clearly, $\mathrm{D}_{(\chi,u,v,p)}G(a, z - S^*, 0, v^*, p^*)$ is a Fredholm operator, and $\mathrm{D}_{(\chi,u,v,p)}G(a, z - S^*, 0, v^*, p^*)(\xi, \phi, \psi, \zeta)^\top = 0$ gives

$$\begin{aligned} &d\xi_{xx} - bv^* f_2'(S^*)\xi + af_1(S^*)\phi + bf_2(S^*)\psi = 0, \quad x \in (0,1), \\ &d\phi_{xx} + af_1(S^*)\phi - cp^*\phi = 0, \quad x \in (0,1), \\ &d\psi_{xx} + (1 - K(0,v^*))bf_2(S^*)\psi - K_v(0,v^*)bv^* f_2(S^*)\psi \\ &\qquad -(1 - K(0,v^*))bv^* f_2'(S^*)\xi - K_u(0,v^*)bv^* f_2(S^*)\phi = 0, \quad x \in (0,1), \\ &d\zeta_{xx} - K(0,v^*)bv^* f_2'(S^*)\xi + K_u(0,v^*)bv^* f_2(S^*)\phi \\ &\qquad +K(0,v^*)bf_2(S^*)\psi + K_v(0,v^*)bv^* f_2(S^*)\psi = 0, \quad x \in (0,1), \\ &\xi_x(0) = \xi_x(1) + \nu\xi(1) = 0, \quad \phi_x(0) = \phi_x(1) + \nu\phi(1) = 0, \\ &\psi_x(0) = \psi_x(1) + \nu\psi(1) = 0, \quad \zeta_x(0) = \zeta_x(1) + \nu\zeta(1) = 0. \end{aligned}$$

If $\phi \equiv 0$ on [0, 1], then (ξ, ψ, ζ) satisfies (31) with $\lambda = 1$. Recalling the operator

$$\mathcal{B}(1) := \begin{pmatrix} \mathcal{L}_1(1) & bf_2(S^*) \\ -(1-K(0,v^*))bv^* f_2'(S^*) & \mathcal{L}_2(1) \end{pmatrix}$$

is invertible, one can deduce that $(\xi, \psi) = (0, 0)$. It follows that $\zeta = 0$ on [0, 1]. That is, the operator

$$\mathbf{B} := \begin{pmatrix} \mathcal{L}_1(1) & bf_2(S^*) & 0 \\ -(1-K(0,v^*))bv^* f_2'(S^*) & \mathcal{L}_2(1) & 0 \\ -K(0,v^*)bv^* f_2'(S^*) & K(0,v^*)bf_2(S^*)+K_v(0,v^*)bv^* f_2(S^*) & d\dfrac{\mathrm{d}^2}{\mathrm{d}x^2} \end{pmatrix}$$

is invertible. Hence $\phi \not\equiv 0$.

Take $a = \hat{\lambda}_1,\ \phi = \hat{\phi}_1$, where $\hat{\lambda}_1, \hat{\phi}_1$ are the principal eigenvalue and eigenfunction of (25) respectively. In view of the invertibility of the operator $\mathbf{B}$, we can deduce that the null space of $\mathrm{D}_{(\chi,u,v,p)}G(a, z-S^*, 0, v^*, p^*)$ is

$$\mathbf{N}(\mathrm{D}_{(\chi,u,v,p)}G(a, z-S^*, 0, v^*, p^*)) = \mathrm{span}\{(\xi_1, \hat{\phi}_1, \psi_1, \zeta_1)\},$$

where (ξ_1, ψ_1, ζ_1) is the unique solution to

$$\mathbf{B}(\xi, \psi, \zeta) = (-af_1(S^*)\hat{\phi}_1, K_u(0,v^*)bv^* f_2(S^*)\hat{\phi}_1, -K_u(0,v^*)bv^* f_2(S^*)\hat{\phi}_1)^\top. \quad (38)$$

That is, $\dim \mathbf{N}(\mathrm{D}_{(\chi,u,v,p)}G(a, z-S^*, 0, v^*, p^*)) = 1$.

Next, we determine the range of the operator $\mathrm{D}_{(\chi,u,v,p)}G(\hat{\lambda}_1, z-S^*, 0, v^*, p^*)$. To this end, suppose that $(\chi, u, v, p) \in \mathbf{R}(\mathrm{D}_{(\chi,u,v,p)}G(\hat{\lambda}_1, z-S^*, 0, v^*, p^*))$, which is the range of the operator $\mathrm{D}_{(\chi,u,v,p)}G(\hat{\lambda}_1, z-S^*, 0, v^*, p^*)$. Then there exists $(\xi, \phi, \psi, \zeta) \in \mathbf{X}$ such that

$$\mathrm{D}_{(\chi,u,v,p)}G(\hat{\lambda}_1, z-S^*, 0, v^*, p^*)(\xi, \phi, \psi, \zeta)^\top = (\chi, u, v, p)^\top.$$

Direct computation leads to

$$\begin{aligned} &d\xi_{xx} - bv^* f_2'(S^*)\xi + \hat{\lambda}_1 f_1(S^*)\phi + bf_2(S^*)\psi = d\chi_{xx} - M\chi, \quad x \in (0,1), \\ &d\phi_{xx} + \hat{\lambda}_1 f_1(S^*)\phi - cp^*\phi = du_{xx} - Mu, \quad x \in (0,1), \\ &d\psi_{xx} + (1-K(0,v^*))bf_2(S^*)\psi - K_v(0,v^*)bv^* f_2(S^*)\psi - (1-K(0,v^*))bv^* f_2'(S^*)\xi \\ &\qquad - K_u(0,v^*)bv^* f_2(S^*)\phi = dv_{xx} - Mv, \quad x \in (0,1), \\ &d\zeta_{xx} - K(0,v^*)bv^* f_2'(S^*)\xi + K_u(0,v^*)bv^* f_2(S^*)\phi \\ &\qquad + K(0,v^*)bf_2(S^*)\psi + K_v(0,v^*)bv^* f_2(S^*)\psi = dp_{xx} - Mp, \quad x \in (0,1), \\ &\xi_x(0) = \xi_x(1) + \nu\xi(1) = 0, \quad \phi_x(0) = \phi_x(1) + \nu\phi(1) = 0, \\ &\psi_x(0) = \psi_x(1) + \nu\psi(1) = 0, \quad \zeta_x(0) = \zeta_x(1) + \nu\zeta(1) = 0. \end{aligned} \quad (39)$$

Note that $\hat{\phi}_1$ satisfies

$$-d(\hat{\phi}_1)_{xx} + cp^*\hat{\phi}_1 = \hat{\lambda}_1 f_1(S^*)\hat{\phi}_1,\ x \in (0,1), \quad (\hat{\phi}_1)_x(0) = (\hat{\phi}_1)_x(1) + \nu\hat{\phi}_1(1) = 0.$$

Multiplying this equation by ϕ and the second equation of (39) by $\hat{\phi}_1$, and integrating over (0, 1) by parts, we get

$$\int_0^1 [M + \hat{\lambda}_1 f_1(S^*) - cp^*]\hat{\phi}_1 u \mathrm{d}x = 0.$$

The invertibility of the operator $\mathbf{B}$ implies that the range of $\mathrm{D}_{(\chi,u,v,p)}G(\hat{\lambda}_1, z - S^*, 0, v^*, p^*)$ is

$$\begin{aligned}&\mathbf{R}(\mathrm{D}_{(\chi,u,v,p)}G(\hat{\lambda}_1, z-S^*, 0, v^*, p^*))\\ =&\{(\chi,u,v,p)\in\mathbf{X} : \int_0^1 [M+\hat{\lambda}_1 f_1(S^*)-cp^*]\hat{\phi}_1 u\mathrm{d}x = 0\}.\end{aligned}$$

What's more,

$$\begin{aligned}&\mathrm{D}^2_{a(\chi,u,v,p)}G(\hat{\lambda}_1, z-S^*, 0, v^*, p^*)(\xi_1,\hat{\phi}_1,\psi_1,\zeta_1)^\top\\ =&-(-d\frac{\mathrm{d}^2}{\mathrm{d}x^2}+M)^{-1}(f_1(S^*)\hat{\phi}_1, f_1(S^*)\hat{\phi}_1, 0, 0)^\top\end{aligned}$$

By virtue of $(-d\frac{\mathrm{d}^2}{\mathrm{d}x^2}+M)^{-1}(f_1(S^*)\hat{\phi}_1) > 0$ and (37), we have

$$-\int_0^1 [M+\hat{\lambda}_1 f_1(S^*)-cp^*]\hat{\phi}_1(-d\frac{\mathrm{d}^2}{\mathrm{d}x^2}+M)^{-1}(f_1(S^*)\hat{\phi}_1)\mathrm{d}x < 0.$$

Hence,

$$\mathrm{D}^2_{a(\chi,u,v,p)}G(\hat{\lambda}_1, z–S^*, 0, v^*, p^*)(\xi_1,\hat{\phi}_1,\psi_1,\zeta_1)^\top \notin \mathbf{R}(\mathrm{D}_{(\chi,u,v,p)}G(\hat{\lambda}_1, z–S^*, 0, v^*, p^*)).$$

Let

$$\begin{aligned}\mathbf{Z} =&\mathbf{R}(\mathrm{D}_{(\chi,u,v,p)}G(\hat{\lambda}_1, z-S^*, 0, v^*, p^*))\\ =&\{(\chi,u,v,p)\in\mathbf{X} : \int_0^1 [M+\hat{\lambda}_1 f_1(S^*)-cp^*]\hat{\phi}_1 u\mathrm{d}x = 0\}.\end{aligned}$$

Then $\mathrm{span}\{(\xi_1,\hat{\phi}_1,\psi_1,\zeta_1)\}\oplus\mathbf{Z} = \mathbf{X}$. Now, we are ready to apply the bifurcation theorem from a simple eigenvalue (see Theorem 1.7 in [6] or Theorem 4.3 in [26]). It follows that there exists a $\tau_0 > 0$ and C^1 curve $(a(\tau), Q(\tau), \Phi(\tau), \Psi(\tau), P(\tau)) : (-\tau_0, \tau_0) \mapsto (-\infty, +\infty)\times\mathbf{Z}$ such that

(i) $a(0) = \hat{\lambda}_1$,
(ii) $Q(0) = 0, \Phi(0) = 0, \Psi(0) = 0, P(0) = 0$,
(iii) $G(a(\tau), \chi(\tau), u(\tau), v(\tau), p(\tau)) = 0$ for $|\tau| < \tau_0$,

where $\chi(\tau) = z - S^* + \tau(\xi_1 + Q(\tau))$, $u(\tau) = \tau(\hat{\phi}_1 + \Phi(\tau))$, $v(\tau) = v^* + \tau(\psi_1 + \Psi(\tau))$, $p(\tau) = p^* + \tau(\zeta_1 + \tau P(\tau))$ with $|\tau| < \tau_0$. Namely, $(\chi(\tau), u(\tau), v(\tau), p(\tau))$ is the solution of the system (24) with $a = a(\tau)$. Let $S(\tau) = z - \chi(\tau)$. Then the bifurcation branch

$$\Gamma' = \{(a(\tau), S(\tau), u(\tau), v(\tau), p(\tau)) : \tau\in(0,\tau_0)\}$$

is exactly the positive solution branch of the system (6)-(7). That is, we have the following local bifurcation result.

Lemma 4.2. *Suppose $(H1)-(H3)$ hold and $b > \sigma_1$ fixed. Then the positive solutions of (6)−(7) bifurcate from the semitrivial solution branch $\Gamma_2 = \{(a, S^*, 0, v^*, p^*) : a\in\mathbb{R}_+\}$ if and only if $a = \hat{\lambda}_1$, and the set of positive solutions to (6) − (7) near $(\hat{\lambda}_1, S^*, 0, v^*, p^*)$ is a smooth curve*

$$\Gamma' = \{(a(\tau), S(\tau), u(\tau), v(\tau), p(\tau)) : \tau\in(0,\tau_0)\}$$

for some $\tau_0 > 0$, where $S(\tau) = S^* - \tau(\xi_1 + Q(\tau))$, $u(\tau) = \tau(\hat{\phi}_1 + \Phi(\tau))$, $v(\tau) = v^* + \tau(\psi_1 + \Psi(\tau))$ and $p(\tau) = p^* + \tau(\zeta_1 + \tau P(\tau))$ with $|\tau| < \tau_0$. $a(\tau), Q(\tau), \Phi(\tau), \Psi(\tau)$ and $P(\tau)$ are smooth functions with respect to τ, which satisfy $a(0) = \hat{\lambda}_1, Q(0) = 0, \Phi(0) = 0, \Psi(0) = 0, P(0) = 0$ and $(Q(\tau), \Phi(\tau), \Psi(\tau), P(\tau)) \in \mathbf{Z}$.

Next, we extend the local bifurcation Γ' to the global one by the global bifurcation results for Fredholm operators (see Theorems 4.3-4.4 in [26]). Noting that $T : \mathbb{R}_+ \times \Omega_\epsilon \to \mathbf{X}$ is C^1 smooth and compact, we can conclude that the Fréchet derivative $\mathrm{D}_{(\chi,u,v,p)}G(a, \chi, u, v, p)$ is Fredholm with index zero for any $(a, \chi, u, v, p) \in \mathbb{R}_+ \times \Omega_\epsilon$. Now we can apply Theorem 4.3 in [26] to obtain a connected component Υ of the set

$$\{(a, \chi, u, v, p) \in \mathbb{R}_+ \times \Omega_\epsilon : G(a, \chi, u, v, p) = 0, (\chi, u, v, p) \neq (z - S^*, 0, v^*, p^*)\}$$

emanating from Γ_2' at $(\hat{\lambda}_1, z - S^*, 0, v^*, p^*)$. Moreover, either Υ is not compact in $\mathbb{R}_+ \times \Omega_\epsilon$ or Υ contains a point $(\bar{a}, z - S^*, 0, v^*, p^*)$ with $\bar{a} \neq \hat{\lambda}_1$. Set $\Upsilon' = \{(a, S, u, v, p) : S = z - \chi,$ and $(a, \chi, u, v, p) \in \Upsilon\}$. Then $\Gamma' \subset \Upsilon'$. Let $\mathbf{X}_0 = \{(S, u, v, p) \in C^1[0, 1] \times C^1[0, 1] \times C^1[0, 1] \times C^1[0, 1] : S > 0, u > 0, v > 0, p > 0$ on $[0, 1]\}$. Then $\Upsilon' \cap (\mathbb{R}_+ \times \mathbf{X}_0) \neq \emptyset$.

Let $\Gamma = \Upsilon' \cap (\mathbb{R}_+ \times \mathbf{X}_0)$. Then Γ consists of the local positive solution branch Γ' near the bifurcation point $(\hat{\lambda}_1, S^*, 0, v^*, p^*)$. Let Υ^+ be the connected component of $\Upsilon' \backslash \{(a(\tau), S(\tau), u(\tau), v(\tau), p(\tau)) : \tau \in (-\tau_0, 0)\}$. Then $\Gamma \subset \Upsilon^+$. It follows from Theorem 4.4 in [26] that Υ^+ satisfies one of the following alternatives

(i) it is not compact;

(ii) it contains a point $(\bar{a}, S^*, 0, v^*, p^*)$ with $\bar{a} \neq \hat{\lambda}_1$;

(iii) it contains a point $(a, S^* + S, u, v^* + v, p^* + p)$, where $(S, u, v, p) \neq 0$ and $(S, u, v, p) \in \mathbf{Z}$.

Theorem 4.3. *Suppose $(H1) - (H3)$ hold and $b > \sigma_1$ fixed. Then there exists a continuum of positive solutions to (6)-(7), denoted by $\Gamma = \{(a, S, u, v, p)\} \subset \mathbb{R}_+ \times \mathbf{X}_0$, which bifurcates from the semi-trivial solution branch $\Gamma_2 = \{(a, S^*, 0, v^*, p^*) : a \in \mathbb{R}_+\}$ at $(\hat{\lambda}_1, S^*, 0, v^*, p^*)$, and meets the other semi-trivial solution branch $\Gamma_1 = \{(a, z - \theta_a, \theta_a, 0, 0) : a > \lambda_1\}$ at $(\bar{a}, z - \theta_{\bar{a}}, \theta_{\bar{a}}, 0, 0)$. In particular, (6)-(7) has a positive solution (S, u, v, p) if a lies between $\hat{\lambda}_1$ and $\bar{a}$. Here $\bar{a}$ is determined by $b = \hat{\sigma}_1(\bar{a})$.*

Proof. For any $(a, S, u, v, p) \in \Gamma$, we have $u > 0$ on $[0, 1]$. Hence, $\int_0^1 [M + \hat{\lambda}_1 f_1(S^*) - cp^*]\hat{\phi}_1 u dx > 0$, a contradiction to $(S, u, v, p) \in \mathbf{Z}$. Thus (iii) is impossible. Suppose (ii) holds. Then we can find a sequence of points $(a_n, S_n, u_n, v_n, p_n) \subset \Gamma \cap (\mathbb{R}_+ \times \mathbf{X}_0)$, which converges to $(\bar{a}, S^*, 0, v^*, p^*)$ in $\mathbb{R}_+ \times \mathbf{X}_0$. It follows from the equation for u_n, we have $a_n = \lambda_1(cp_n, f_1(S_n))$. Letting $n \to \infty$, we get $\bar{a} = \lambda_1(cp^*, f_1(S^*)) = \hat{\lambda}_1$. Thus (ii) can not occur.

By Lemmas 3.1-3.2, any nonnegative solution of (6)-(7) with $u \not\equiv 0$, $v \not\equiv 0$, $p \not\equiv 0$ satisfies

$$0 < S \leq z, 0 < u < \theta_a, 0 < v < \vartheta_b, 0 < p < \vartheta_b,$$

and there exists some positive constant Λ_0 such that $\lambda_1 < a < \Lambda_0$ when $b > \sigma_1$ fixed. By L^p estimates and Sobolev embedding theorems, we can deduce that $\|S\|_{C^1}, \|u\|_{C^1}, \|v\|_{C^1}, \|p\|_{C^1}$ are bounded. Hence, for $b > \sigma_1$ fixed, Γ is bounded in $\mathbb{R}_+ \times \mathbf{X}_0$. Thus (i) implies that $\Gamma \cap (\mathbb{R}_+ \times \partial\mathbf{X}_0)$ contains a point $(\bar{a}, \bar{S}, \bar{u}, \bar{v}, \bar{p})$ other than $(\hat{\lambda}_1, S^*, 0, v^*, p^*)$. That is, there exists $(\bar{a}, \bar{S}, \bar{u}, \bar{v}, \bar{p}) \in \{\Gamma - (\hat{\lambda}_1, S^*, 0, v^*, p^*)\} \cap (\mathbb{R}_+ \times \partial\mathbf{X}_0)$ which is the limit of a sequence

$$(a_n, S_n, u_n, v_n, p_n) \subset \Gamma \cap (\mathbb{R}_+ \times \mathbf{X}_0), S_n > 0, u_n > 0, v_n > 0, p_n > 0 \text{ on } [0, 1].$$

Clearly, $\lambda_1 \leq \bar{a} \leq \Lambda_0$. It follows from the maximum principle that $\bar{S} > 0$ on $[0, 1]$. Hence $(\bar{a}, \bar{S}, \bar{u}, \bar{v}, \bar{p}) \in \mathbb{R}_+ \times \partial\mathbf{X}_0$ means either (i) $\bar{u} \geq 0, \bar{u}(x_0) = 0$ for some point

$x_0 \in [0,1]$ or (ii) $\bar{v} \geq 0, \bar{v}(x_0) = 0$ for some point $x_0 \in [0,1]$ or (iii) $\bar{p} \geq 0, \bar{p}(x_0) = 0$ for some point $x_0 \in [0,1]$. Note that $\bar{u}$ satisfies

$$-d\bar{u}_{xx} + c\bar{p}\bar{u} = a\bar{u}f_1(\bar{S}),\ x \in (0,1), \quad \bar{u}_x(0) = \bar{u}_x(1) + \nu\bar{u}(1) = 0.$$

By the maximum principle, we have $\bar{u} \equiv 0$ if $\bar{u}(x_0) = 0$ for some point $x_0 \in [0,1]$. Similarly, we can show $\bar{v} \equiv 0$, $\bar{p} \equiv 0$ for the other two cases. Therefore, we have the following alternatives (i)$(\bar{S},\bar{u},\bar{v},\bar{p}) \equiv (z,0,0,0)$; (ii)$(\bar{S},\bar{u},\bar{v},\bar{p}) \equiv (S^*,0,v^*,p^*)$; (iii)$(\bar{S},\bar{u},\bar{v},\bar{p}) \equiv (z-\theta_a,\theta_a,0,0)$.

Suppose $(\bar{S},\bar{u},\bar{v},\bar{p}) \equiv (z,0,0,0)$. Then the sequence (a_n,S_n,u_n,v_n,p_n) satisfies $a_n \to \bar{a}$, $(S_n,u_n,v_n,p_n) \to (z,0,0,0)$ in $\mathbf{X}$ as $n \to \infty$. It follows from the equation for v_n, we have $b = \lambda_1(0,(1-K(u_n,v_n))f_2(S_n)) \to \lambda_1(0,f_2(z)) = \sigma_1$ as $n \to \infty$. Namely, $b = \sigma_1$, a contradiction.

Suppose $(\bar{S},\bar{u},\bar{v},\bar{p}) \equiv (S^*,0,v^*,p^*)$. Then the sequence (a_n,S_n,u_n,v_n,p_n) satisfies that $a_n \to \bar{a}$, $(S_n,u_n,v_n,p_n) \to (S^*,0,v^*,p^*)$ in $\mathbf{X}$ as $n \to \infty$. It follows from the equation for u_n, we have $a_n = \lambda_1(cp_n,f_1(S_n))$. Letting $n \to \infty$, we get $\bar{a} = \lambda_1(cp^*,f_1(S^*)) = \hat{\lambda}_1$, a contradiction to $\bar{a} \neq \hat{\lambda}_1$.

Thus the remaining possibility is $(\bar{S},\bar{u},\bar{v},\bar{p}) \equiv (z-\theta_a,\theta_a,0,0)$. Then the sequence

$$(a_n,S_n,u_n,v_n,p_n) \to (\bar{a},z-\theta_{\bar{a}},\theta_{\bar{a}},0,0)$$

in $\mathbb{R}_+ \times \mathbf{X}$ as $n \to \infty$. It follows from the equation for v_n, we have

$$\begin{aligned} b &= \lambda_1(0,(1-K(u_n,v_n))f_2(S_n)) \\ &\to \lambda_1(0,(1-K(\theta_{\bar{a}},0))f_2(z-\theta_{\bar{a}})) = \lambda_1((1-K(\theta_{\bar{a}},0))f_2(z-\theta_{\bar{a}})) = \hat{\sigma}_1(\bar{a}) \end{aligned}$$

as $n \to \infty$. Note that the function $\hat{\sigma}_1(a)$ depends continuously on the parameter a on $[\lambda_1,+\infty)$ with $\lim\limits_{a\to\lambda_1} \hat{\sigma}_1(a) = \sigma_1$ and $\lim\limits_{a\to+\infty} \hat{\sigma}_1(a) = +\infty$. Hence, for $b > \sigma_1$ fixed, there exists a $\bar{a} \in (\lambda_1,+\infty)$ such that $b = \hat{\sigma}_1(\bar{a})$. □

Remark 3. Suppose $(H1)-(H3)$ hold and $K_u(u,v) \geq 0$ for $u,v \geq 0$. By Lemma 3.3, the eigenvalue $\hat{\sigma}_1(a)$ is continuous and strictly increasing on $[\lambda_1,+\infty)$ with $\lim\limits_{a\to\lambda_1} \hat{\sigma}_1(a) = \sigma_1$ and $\lim\limits_{a\to+\infty} \hat{\sigma}_1(a) = +\infty$. Hence, for $b > \sigma_1$ fixed, there exists a unique $\bar{a} \in (\lambda_1,+\infty)$ such that $b = \hat{\sigma}_1(\bar{a})$. Thus, (6)-(7) has a positive solution if a lies between $\hat{\lambda}_1$ and $\bar{a}$.

Next, we turn to investigate the direction and stability of the bifurcation solution Γ' near the bifurcation point. To this end, substituting the local bifurcation solution $(a(\tau),S(\tau),u(\tau),v(\tau),p(\tau))$ with $\tau \in (0,\tau_0)$ into the second equation of (6), differentiating with respect to τ at $\tau = 0$, where $S(\tau) = S^* - \tau(\xi_1 + Q(\tau))$, $u(\tau) = \tau(\hat{\phi}_1 + \Phi(\tau))$, $v(\tau) = v^* + \tau(\psi_1 + \Psi(\tau))$ and $p(\tau) = p^* + \tau(\zeta_1 + \tau P(\tau))$, we have

$$d\dot{\Phi}(0)_{xx} + \dot{a}(0)\hat{\phi}_1 f_1(S^*) + \hat{\lambda}_1\dot{\Phi}(0)f_1(S^*) - \hat{\lambda}_1\hat{\phi}_1 f_1'(S^*)\xi_1 - cp^*\dot{\Phi}(0) - c\zeta_1\hat{\phi}_1 = 0, \tag{40}$$

where $\dot{\Phi}(0), \dot{a}(0)$ are the derivative of $\Phi(\tau), a(\tau)$ with respect to τ at $\tau = 0$ respectively. Note that

$$\begin{aligned} &d(\hat{\phi}_1)_{xx} + \hat{\lambda}_1 f_1(S^*)\hat{\phi}_1 - cp^*\hat{\phi}_1 = 0,\ x \in (0,1), \\ &(\hat{\phi}_1)_x(0) = (\hat{\phi}_1)_x(1) + \nu\hat{\phi}_1(1) = 0. \end{aligned} \tag{41}$$

Multiplying the equation (40) by $\hat{\phi}_1$ and the equation (41) by $\dot{\Phi}(0)$, and integrating over $(0,1)$ by parts, we obtain

$$\dot{a}(0)\int_0^1 f_1(S^*)\hat{\phi}_1^2 \mathrm{d}x = \hat{\lambda}_1 \int_0^1 f_1'(S^*)\hat{\phi}_1^2\xi_1 \mathrm{d}x + c\int_0^1 \hat{\phi}_1^2\zeta_1 \mathrm{d}x.$$

Here (ξ_1, ψ_1, ζ_1) is the unique solution to (38). Since it is hard to determine the sign of ξ_1, ζ_1, we cannot determine the direction and stability of the local bifurcation solution Γ' near the bifurcation point. However, if $K(0, v) \equiv 0$, then the semi-trivial solution $(S^*, 0, v^*, p^*) = (z - \vartheta_b, 0, \vartheta_b, 0)$, and the semi-trivial solution branch $\Gamma_2 = \{(a, S^*, 0, v^*, p^*) : a \in \mathbb{R}_+\}$ becomes $\Gamma_2 = \{(a, z - \vartheta_b, 0, \vartheta_b, 0) : a \in \mathbb{R}_+\}$. What's more, $K_v(0, \vartheta_b) \equiv 0$. It follows from (38) that

$$-d(\zeta_1)_{xx} = K_u(0, \vartheta_b) b \vartheta_b f_2(z - \vartheta_b)\hat{\phi}_1, \quad x \in (0,1), \quad (\zeta_1)_x(0) = (\zeta_1)_x(1) + \nu\zeta_1(1) = 0.$$

By the strong maximum principle, we have $\zeta_1 > 0$ provided that $K_u(0, \vartheta_b) > 0$. Hence, we have the following result on the direction and stability of the local bifurcation solution Γ' near the bifurcation point.

Theorem 4.4. *Suppose $(H1) - (H3)$ hold, $K(0, v) \equiv 0$, $K_u(0, v) > 0$ for $v > 0$. Let $b > \sigma_1$ fixed. Then there exists a positive constant C large enough such that for $c \geq C$, the positive solution branch Γ' of (6)-(7) is to the right, and it is stable.*

Proof. Clearly, $\zeta_1 > 0$, and

$$\dot{a}(0) \int_0^1 f_1(z - \vartheta_b)\hat{\phi}_1^2 \mathrm{d}x = \hat{\lambda}_1 \int_0^1 f_1'(z - \vartheta_b)\hat{\phi}_1^2 \xi_1 \mathrm{d}x + c \int_0^1 \hat{\phi}_1^2 \zeta_1 \mathrm{d}x. \tag{42}$$

under the hypotheses $(H1) - (H3)$ and $K(0, v) \equiv 0$, $K_u(0, v) > 0$. Hence, there exists a positive constant C large enough such that for $c \geq C$, we have $\dot{a}(0) > 0$, which implies that the positive solution branch Γ' of (6)-(7) is to the right when $c \geq C$. That is, there exists $\delta > 0$ sufficiently small such that $\dot{a}(\tau) > 0$ with $0 < \tau < \delta$.

Next, we study the linearized stability of positive solutions lying on the bifurcation branch Γ'. Let $\mathcal{L}(a(\tau), S(\tau), u(\tau), v(\tau), p(\tau))$ be the linearized operator of (6)-(7) at $(a(\tau), S(\tau), u(\tau), v(\tau), p(\tau))$. By the application of Corollary 1.13 in [7], there exist C^1 functions $a \to (\mu(a), \aleph(a))$, $\tau \to (\eta(\tau), \hbar(\tau))$ defined on the neighborhoods of $\hat{\lambda}_1$ and 0 into $\mathbb{R} \times \mathbf{X}$ respectively, such that

$$(\mu(\hat{\lambda}_1), \aleph(\hat{\lambda}_1)) = (0, \xi_1, \hat{\phi}_1, \psi_1, \zeta_1) = (\eta(0), \hbar(0))$$

and on these neighborhoods

$$\begin{aligned} &\mathcal{L}(a, z - \vartheta_b, 0, \vartheta_b, 0)\aleph(a) + \mu(a)\aleph(a) = 0 && \text{for } |a - \hat{\lambda}_1| \ll 1, \\ &\mathcal{L}(a(\tau), S(\tau), u(\tau), v(\tau), p(\tau))\hbar(\tau) + \eta(\tau)\hbar(\tau) = 0 && \text{for } |\tau| \ll 1. \end{aligned}$$

It follows from Theorem 1.16 in [7] that $\eta(\tau) \sim -\tau\dot{a}(\tau)\dot{\mu}(\hat{\lambda}_1)$ for $0 < \tau < \delta$. Meanwhile, similar arguments as in Theorem 4.1(iii) indicate that $\mu(a)$ is a simple eigenvalue of

$$d\phi_{xx} + af_1(z - \vartheta_b)\phi + \mu(a)\phi = 0, \quad x \in (0,1), \quad \phi_x(0) = \phi_x(1) + \nu\phi(1) = 0.$$

and the derivative $\dot{\mu}(\hat{\lambda}_1) < 0$ by Lemma A.1. Thus $\eta(\tau) > 0$, which implies that the positive solution branch Γ' of (6)-(7) is stable when $c \geq C$. $\square$

Remark 4. Take $K(u, v) = \frac{\alpha u}{\beta + u + v}$ (see [5]) and the parameters $\alpha, \beta > 0$ such that $0 \leq K(u, v) < 1$. Then the hypotheses $(H1) - (H3)$ hold, and $K(0, v) \equiv 0$, $K_u(u, v) = \frac{\alpha(\beta + v)}{(\beta + u + v)^2} > 0$ for $u, v \geq 0$. Hence, it follows from Theorems 4.3-4.4 and Remark 3 that for $b > \sigma_1$ fixed,

(i) there exists a continuum of positive solutions to (6)-(7), denoted by $\Gamma = \{(a, S, u, v, p)\} \subset \mathbf{X}_0$, which bifurcates from the semi-trivial solution branch $\Gamma_2 = \{(a, z - \vartheta_b, 0, \vartheta_b, 0) : a \in \mathbb{R}_+\}$ at $(\hat{\lambda}_1, z - \vartheta_b, 0, \vartheta_b, 0)$, and meets the other semi-trivial solution branch $\Gamma_1 = \{(a, z - \theta_a, \theta_a, 0, 0) : a > \lambda_1\}$ at $(\bar{a}, z - \theta_{\bar{a}}, \theta_{\bar{a}}, 0, 0)$, where $\bar{a}$ is uniquely determined by $b = \hat{\sigma}_1(\bar{a})$. In particular, (6)-(7) has a positive solution if a lies between $\hat{\lambda}_1$ and $\bar{a}$.

(ii) there exists a positive constant C large enough such that for $c \geq C$, the positive solution branch Γ' of (6)-(7) is to the right, and it is stable.

In [18], the unstirred chemostat model with constant toxin production (that is, $K(u, v) \equiv K_0(\text{constant})$) has been studied. The results show that when the parameter c, which measures the effect of toxins, is large enough, the model only has unstable positive solutions. Moreover, the species v always lose the competition. However, it follows from Theorem 4.4 that the unstirred chemostat model with dynamically allocated toxin production possesses stable positive solutions(i.e. coexistence solutions). From the biological point of view, dynamically allocated toxin production has a positive effect on coexistence of species.

5. **Numerical simulations and discussion.** In this section, we present some results of our numerical simulations performed with Matlab, which complement the analytic results of the previous sections.

As [5], we consider two special cases that represent the extremes for reasonable functions

$$K(u, v) = \frac{\alpha v}{\beta + u + v}, \tag{43}$$

$$K(u, v) = \frac{\alpha u}{\beta + u + v}, \tag{44}$$

where α, β are positive constants and chosen so that $0 < K(u, v) < 1$ for $u, v > 0$. (43) is monotone increasing in v while (44) is monotone increasing in u. These reflect two opposite strategies. For (43), if v is large, it devotes more of its resources to producing the toxin, which guards against invasion. For (44), if u is large, v increases the toxin production since it is already losing the competition and facing extinction, which is a desperation strategy. The advantage of this strategy is that if there is no competition, no resource is wasted on toxin production.

The numerical simulations show that a wide variety of dynamical behaviors can be achieved for the system with dynamically allocated toxin production, including competition exclusion, bistable attractors, stable positive equilibria and stable limit cycles. The most interesting numerical results are stable positive equilibria and stable limit cycles, which cannot occur in the system with constant toxin production. Stable positive equilibria and limit cycles provide coexistence, which suggest a possible mechanism to explain coexistence phenomena. In all of our figures except Figure 4(c)(d), the L_1 norms of the solutions $(S(\cdot, t), u(\cdot, t), v(\cdot, t), p(\cdot, t))$ to (4)-(5) are plotted versus the temporal variable. In Figure 4(c)(d), two positive equilibria of (4)-(5) are plotted versus the spatial variable.

5.1. **Numerical results with $K(u, v) = \frac{\alpha v}{\beta + u + v}$.** At first, we choose the basic parameters of the species to be $a = 1.17, b = 1.17, k_1 = 0.017, k_2 = 0.025$ and $\nu = 0.6$. Namely, we assume that u is the better competitor in the absence of toxins. Taking the parameters $d = 0.1, \alpha = 0.2, \beta = 0.01$, and varying the parameter values of c, we observe competitive exclusion independent of initial conditions and competitive exclusion that depends on initial conditions (bistability).

More precisely, for small c, the species u can competitively exclude the species v independent of initial conditions (see Figure 1(a)). Increasing the parameter c, bistability occurs and either species u or species v is competitively excluded

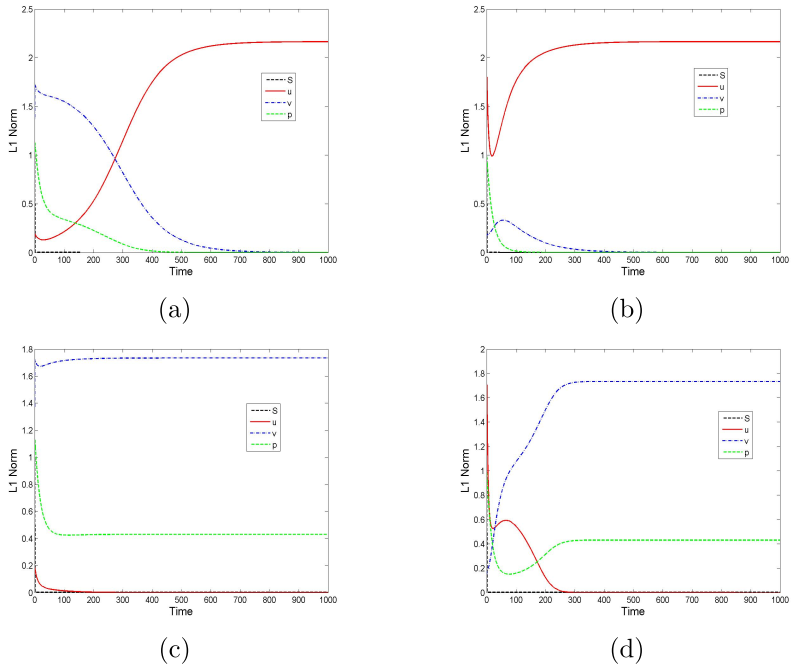

FIGURE 1. We further fix $d = 0.1, \alpha = 0.2, \beta = 0.01$, and observe the effects of the parameter c: bi-stability is observed in (b)(c) when the parameter $c = 0.1$; competitive exclusion occurs in (a)(d) when $c = 0.05, 0.2$ respectively.

depending on their initial conditions (see Figure 1(b)(c)). Increasing c eventually causes the species v can competitively exclude the species u independent of initial conditions (see Figure 1(d)). Biologically speaking, the numerical results show that toxins can help the weaker competitor to win in the competition.

Secondly, we assume that v is the better competitor in the absence of toxins and take the basic parameters of the species to be $a = 1.17, b = 1.17, k_1 = 1.7, k_2 = 0.025$ and $\nu = 0.6$. Taking the parameters $\alpha = 0.8, \beta = 0.001, c = 0.2$, and varying the diffusion rate d, we observe competitive exclusion independent of initial conditions, stable positive equilibria and stable limit cycles.

More precisely, for small d, the species v can competitively exclude the species u independent of initial conditions (see Figure 2(a)). Increasing the diffusion rate d can destabilize the system and cause it to switch to a stable limit cycle. Moreover, the amplitude decreases when d increases(see Figure 2(b)(c)(d)). If one continues to increase the diffusion rate d, the system generates a stable positive equilibrium (see Figure 2(e)). Stable positive equilibria and stable limit cycles provide coexistence, which can be called diffusion-driven coexistence. Increasing d eventually causes the system to converge to the washout solution. That is, all species including two competitors u, v and the toxin p go to zero eventually (see Figure 2(f)). As mentioned before, diffusion-driven coexistence can not occur when $K(u, v)$ is constant. Hence our numerical results imply that dynamically allocated toxin production is sufficiently effective in the occurrence of coexisting.

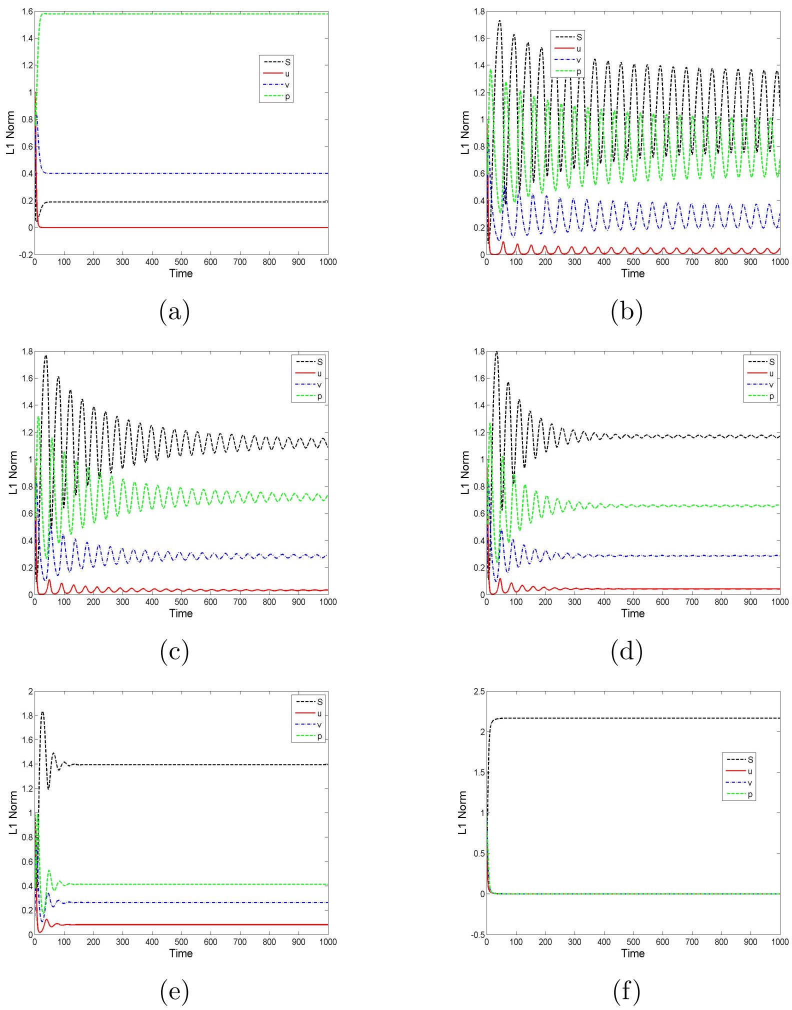

FIGURE 2. We further fix $\alpha = 0.8, \beta = 0.001, c = 0.2$, take the diffusion rates $d = 0.4, 0.6, 0.65, 0.7, 0.9, 1.5$ in (a)-(f), and observe the effects of the diffusion rate d: (a) competition exclusion, (b)-(d) stable limit cycles, (e) stable positive equilibrium, (f) washout solution.

5.2. **Numerical results with** $K(u,v) = \frac{\alpha u}{\beta+u+v}$**.** The basic assumption continues that u is the better competitor in the absence of toxins. Thus we take the basic parameters of the species to be $a = 1.1, b = 1.1, k_1 = 0.0567, k_2 = 0.06$ and $\nu = 0.6$. Taking the parameters $d = 0.1, \alpha = 0.2, \beta = 1$, and varying the parameter values of c, we observe competitive exclusion, bistable attractors and coexistence in the form of stable equilibria.

More precisely, for small c, the species u can competitively exclude the species v independent of initial conditions (see Figure 3(a)). Increasing the parameter c, bistable attractors occur (see Figure 4(a)(b)). In this case, two positive equilibria appear, one stable and the other unstable(see Figure 4(c)(d)). The stable positive equilibrium and the semitrivial solution $(z - \theta_a, \theta_a, 0, 0)$ are the bistable

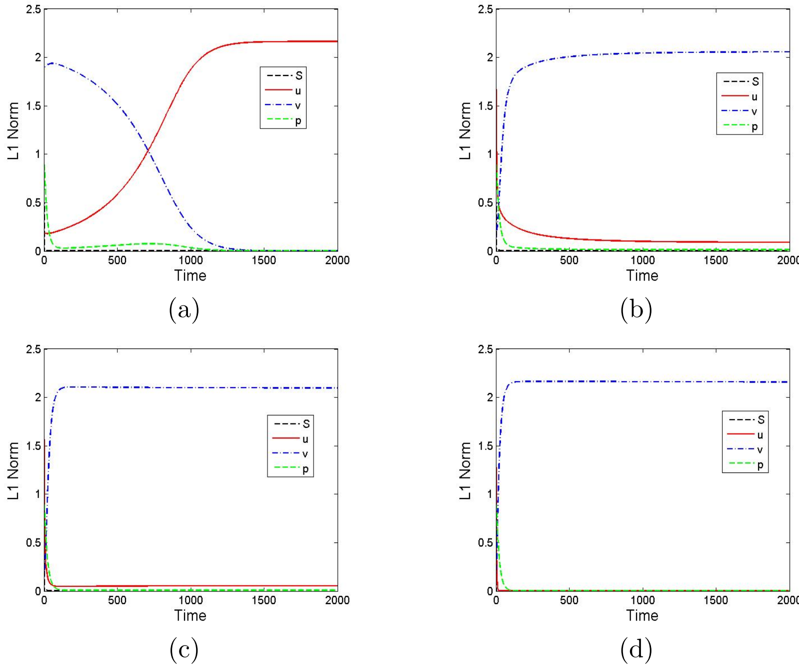

FIGURE 3. We further fix $d = 0.1, \alpha = 0.2, \beta = 1$, and observe the effects of the parameter c: coexistence in the form of equilibria is observed in (b)(c) when $c = 0.2, 0.3$ respectively; competitive exclusion occurs in (a)(d) when $c = 0.01, 0.6$ respectively.

attractors and the result of the competition is determined by the initial conditions. If one continues to increase the parameter c, coexistence is observed in the form of equilibria(see Figure 3(b)(c)). Increasing c eventually causes the species v can competitively exclude the species u independent of initial conditions (see Figure 3(d)). Biologically speaking, the numerical results indicate that dynamically allocated toxin production is sufficiently effective in the occurrence of coexisting, and toxins can help the weaker competitor to win in the competition.

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Appendix. We state some well-known lemmas as appendix without proof, which is useful for obtaining the main results in this paper.

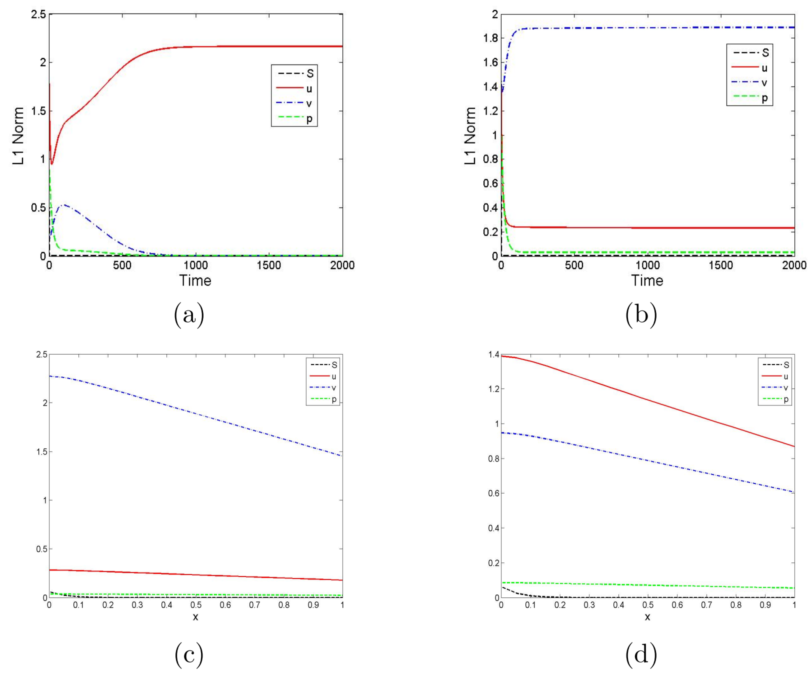

FIGURE 4. Taking $d = 0.1, \alpha = 0.2, \beta = 1$, and $c = 0.1$, bistable attractors occur, which are plotted in (a) and (b). Moreover, two positive equilibria appear (see (c) and (d)).

Lemma A.1 ([4]). *Assume that $c(x), q(x) \in C(\overline{\Omega})$, and $c(x) \geq 0, q(x) \geq 0$ on $\overline{\Omega}$ in the eigenvalue problem*

$$-\Delta\varphi + c(x)\varphi = \lambda q(x)\varphi, \quad x \in \Omega, \quad \frac{\partial \varphi}{\partial n} + \gamma(x)\varphi = 0, \quad x \in \partial\Omega, \tag{A.1}$$

where $\gamma(x) \in C(\partial\Omega)$ and $\gamma(x) \geq 0$. Then all eigenvalues of (A.1) can be listed in order

$$0 < \lambda_1(c,q) < \lambda_2(c,q) \leq \lambda_3(c,q) \leq \cdots \to \infty,$$

and

$$\lambda_1(c,q) = \inf_{\varphi} \frac{\int_\Omega (|\nabla\varphi|^2 + c(x)\varphi^2)\mathrm{d}x + \int_{\partial\Omega} \gamma(x)\varphi^2 \mathrm{d}s}{\int_\Omega q(x)\varphi^2 \mathrm{d}x}$$

is a simple eigenvalue with the associated eigenfunction $\varphi_1 > 0$ on $\bar{\Omega}$, which is called the principal eigenvalue. Moreover, $\lambda_i(c,q) (i = 1, 2, \cdots)$ is continuous with respect to c and q, and the following comparison principles hold:

(i) *$\lambda_i(c_1, q) \leq \lambda_i(c_2, q)$ if $c_1 \leq c_2$ on $\overline{\Omega}$ and the strict inequality holds if $c_1 \not\equiv c_2$,*
(ii) *$\lambda_i(c, q_1) \geq \lambda_i(c, q_2)$ if $q_1 \leq q_2$ on $\overline{\Omega}$ and the strict inequality holds if $q_1 \not\equiv q_2$.*

In particular, we denote $\lambda_i(0, q(x)) = \lambda_i(q)$.

Lemma A.2 ([29]). *Let Ω be a bounded domain in $\mathbb{R}^n$ with boundary surface $\partial\Omega \in C^{2+\gamma}$, $q(x) \in C(\overline{\Omega})$ and P be a positive constant such that $P - q(x) > 0$ on*

$\overline{\Omega}$. Let $\lambda_1(q(x))$ be the principal eigenvalue of the eigenvalue problem

$$-\sum_{i,j=1}^{n} \mathrm{D}_j(a_{ij}(x)\mathrm{D}_i\varphi) + q(x)\varphi = \lambda\varphi,\ x \in \Omega,$$
$$\sum_{i,j=1}^{n} a_{ij}(x)\mathrm{D}_i\varphi\cos(n, x_j) + b(x)\varphi = 0,\ x \in \partial\Omega,$$

where $a_{ij}(x) \in C^1(\overline{\Omega}), b(x) \in C(\partial\Omega)$, $b(x) \geq 0$, and n is the outward unit normal vector on $\partial\Omega$. Then the following conclusions hold

(i) *if $\lambda_1(q(x)) < 0$ then the spectral radius $r[(P - \mathrm{D}_j(a_{ij}(x)\mathrm{D}_i))^{-1}(P - q(x))] > 1$;*
(ii) *if $\lambda_1(q(x)) > 0$ then the spectral radius $r[(P - \mathrm{D}_j(a_{ij}(x)\mathrm{D}_i))^{-1}(P - q(x))] < 1$;*
(iii) *if $\lambda_1(q(x)) = 0$ then the spectral radius $r[(P - \mathrm{D}_j(a_{ij}(x)\mathrm{D}_i))^{-1}(P - q(x))] = 1$.*

Lemma A.3 ([8, 9]). *Let $F : W \to W$ be a compact, continuously differentiable operator, W be a cone in the Banach space E with zero Θ. Suppose that $W - W$ is dense in E and that $\Theta \in W$ is a fixed point of F and $A_0 = F'(\Theta)$. Then the following results hold:*

(i) $\mathrm{index}(F, \Theta, W) = 1$ *if the spectral radius $r(A_0) < 1$;*
(ii) $\mathrm{index}(F, \Theta, W) = 0$ *if A_0 has eigenvalue greater than 1 and Θ is an isolated solution of $x = F(x)$, that is $h \neq A_0 h$ if $h \in \overline{W} - \Theta$.*

Here $\mathrm{index}(F, \Theta, W)$ *is the index of the compact operator F at Θ in the cone W.*

Lemma A.4 ([8, 9, 10]). *Let E_1 and E_2 be ordered Banach spaces with positive cones W_1 and W_2, respectively. Let $E = E_1 \times E_2$ and $W = W_1 \times W_2$. Then E is an ordered Banach space with positive cone W. Let Ω be an open set in W containing 0 and $A_i : \overline{\Omega} \to W_i$ be completely continuous operators, $i = 1, 2$. Denote by (u, v) a general element in W with $u \in W_1$ and $v \in W_2$, and define $A : \overline{\Omega} \to W$ by $A(u, v) = (A_1(u, v), A_2(u, v))$. Let $W_2(\epsilon) = \{v \in W_2 : \|v\|_{E_2} < \epsilon\}$. Suppose $U \subset W_1 \cap \Omega$ is relatively open and bounded, and $A_1(u, 0) \neq u$ for $u \in \partial U$, $A_2(u, 0) \equiv 0$ for $u \in \overline{U}$. Suppose $A_2 : \Omega \to W_2$ extends to a continuously differentiable mapping of a neighborhood of Ω into E_2, $W_2 - W_2$ is dense in E_2 and $T = \{u \in U : u = A_1(u, 0)\}$. Then the following conclusions are true:*

(i) *$deg_W(I - A, U \times W_2(\epsilon), 0) = 0$ for $\epsilon > 0$ small, if for any $u \in T$, the spectral radius $r(A_2'(u, 0)|_{W_2}) > 1$ and 1 is not an eigenvalue of $A_2'(u, 0)|_{W_2}$ corresponding to a positive eigenvector.*
(ii) *$deg_W(I - A, U \times W_2(\epsilon), 0) = deg_{W_1}(I - A_1|_{W_1}, U, 0)$ for $\epsilon > 0$ small, if for any $u \in T$, the spectral radius $r(A_2'(u, 0)|_{W_2} < 1$.*

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