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COMPETITION BETWEEN TWO SIMILAR SPECIES IN THE UNSTIRRED CHEMOSTAT

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Abstract. This paper deals with the competition between two similar species in the unstirred chemostat. Due to the strict competition of the unstirred chemostat model, the global dynamics of the system is attained by analyzing the equilibria and their stability. It turns out that the dynamics of the system essentially depends upon certain function of the growth rate. Moreover, one of the semi-trivial stationary solutions or the unique coexistence steady state is a global attractor under certain conditions. Biologically, the results indicate that it is possible for the mutant to force the extinction of resident species or to coexist with it.

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 [16]). Hence, chemostat models have attracted the attention of both mathematicians and biologists. Analytic work on the chemostat models can be found in [2, 3, 13, 5, 6, 9, 10, 11, 12, 17, 16, 19, 20, 21] and references therein.

This paper deals with the basic N-dimensional competition model in the unstirred chemostat

$$\begin{array}{ll} S_t = \Delta S - auf(S,k_1) - bvf(S,k_2), & x\in\Omega, t>0,\\ u_t = \Delta u + auf(S,k_1), & x\in\Omega, t>0,\\ v_t = \Delta v + bvf(S,k_2), & x\in\Omega, t>0, \end{array} \tag{1}$$

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with boundary conditions and initial conditions

$$\begin{array}{l} \frac{\partial S}{\partial \nu} + \gamma(x)S = S^0(x), \quad x \in \partial\Omega, t > 0, \\ \frac{\partial u}{\partial \nu} + \gamma(x)u = \frac{\partial v}{\partial \nu} + \gamma(x)v = 0, \quad x \in \partial\Omega, t > 0, \\ S(x,0) = S_0(x) \geq 0, \quad x \in \Omega, \\ u(x,0) = u_0(x) \geq 0, \not\equiv 0, \quad v(x,0) = v_0(x) \geq 0, \not\equiv 0, \quad x \in \Omega, \end{array} \tag{2}$$

where Ω is a bounded region in $R^N (N \geq 1)$ with smooth boundary $\partial\Omega$, $a, b > 0$ are the maximal growth rates, and the response function

$$f(S, k_i) = \frac{S}{k_i + S}$$

with $k_i > 0$ is the Michaelis-Menten constant. $\gamma(x), S^0(x)$ are continuous and nonnegative on $\partial\Omega$. Let $\Gamma_1 = \{x \in \partial\Omega : \gamma(x) = 0\}$. Assume $\Gamma_1 \neq \emptyset$, $\Gamma_1 \neq \partial\Omega$ and $S^0(x) > 0$ on Γ_1.

Let $W = S + u + v$. Then W satisfies

$$W_t = \Delta W, \quad x \in \Omega, t > 0, \quad \frac{\partial W}{\partial \nu} + \gamma(x)W = S^0(x), \quad x \in \partial\Omega, t > 0.$$

By similar arguments as in Lemma 2.1 of [6], we have $\lim_{t\to\infty} W(x,t) = z(x)$ uniformly on $\overline{\Omega}$, where $z(x) > 0$ $(x \in \overline{\Omega})$ is the unique solution to the problem

$$\Delta z = 0, x \in \Omega, \quad \frac{\partial z}{\partial \nu} + \gamma(x)z = S^0(x), \ x \in \partial\Omega.$$

Hence, we concentrate on the following limiting system of (1)-(2):

$$\begin{array}{ll} u_t = \Delta u + auf(z - u - v, k_1), & x \in \Omega, t > 0, \\ v_t = \Delta v + bvf(z - u - v, k_2), & x \in \Omega, t > 0, \\ \frac{\partial u}{\partial \nu} + \gamma(x)u = \frac{\partial v}{\partial \nu} + \gamma(x)v = 0, & x \in \partial\Omega, t > 0, \\ u(x,0) = u_0(x) \geq 0, \not\equiv 0, \quad v(x,0) = v_0(x) \geq 0, \not\equiv 0, & \end{array} \tag{3}$$

and $u_0(x) + v_0(x) \leq z(x)$. Theorem 4.1 in [18] connects the dynamics of (1)-(2) to the dynamics of system (3), provided that we are able to show the existence of a stable attractor for (3). As only coexistence solutions (i.e. positive steady-state solutions) of (3) are meaningful, we redefine the response function as follows:

$$\bar{f}(S,k) = \begin{cases} f(S,k), & S \geq 0, \\ \tan^{-1}(2S/k + 1) - \pi/4, & S < 0. \end{cases}$$

It is easy to see that $\bar{f}(S,k) \in C^2(-\infty, +\infty) \times (0, +\infty)$. We will denote $\bar{f}(S,k)$ by $f(S,k)$ for simplicity.

This basic unstirred chemostat model has received considerable attention. The existence of positive steady state solutions is investigated in [2] by degree theory. The structure and local stability of the steady state solutions are studied in [17, 19, 1] by bifurcation theory. Some dynamical behaviors are considered in [6, 5] by the theory of uniform persistence. However, many crucial problems still remain open. In particular, it is very difficult to determine the uniqueness and stability of positive steady-state solutions. In fact, numerical computations in [17] strongly suggest that (3) has a unique positive steady state solution, and it is globally asymptotically stable under certain conditions. But no rigorous proof has been available. In [10, 3], partial results are obtained, which show that (3) has a unique positive steady-state solution when the maximal growth rates a, b are near the principal eigenvalues λ_1, σ_1, respectively, and the unique positive steady state solution is globally asymptotically stable under certain conditions (see [10]).

The goal of this paper is to study the uniqueness and stability of coexistence solutions of (3) and its global dynamics. It follows from Theorem 4.1 in [19] that if $k_1 = k_2 = k$ and $a > \lambda_0$, then (3) possesses positive steady-state solutions if and only if $a = b$. Moreover,

$$(u_s, v_s) = (s\theta(\cdot, a), (1-s)\theta(\cdot, a)), \quad 0 < s < 1$$

is a family of coexistence solutions in this case. Here λ_0 is the principal eigenvalue of the linear problem

$$\Delta\phi + \lambda f(z(x), k)\phi = 0 \quad \text{in} \quad \Omega, \quad \frac{\partial \phi}{\partial \nu} + \gamma(x)\phi = 0 \ \text{ on } \partial\Omega, \tag{4}$$

and $\theta(\cdot, a)$ is the unique positive solution (see Lemma 3.2 in [19]) of

$$\Delta u + auf(z-u, k) = 0 \quad \text{in} \quad \Omega, \quad \frac{\partial u}{\partial \nu} + \gamma(x)u = 0 \ \text{ on } \ \partial\Omega. \tag{5}$$

Our goal here is to determine how the structure of coexistence states changes under small perturbations. With this in mind, we can rewrite $k_1 = k, k_2 = k+\tau, b = a+\beta\tau$ and consider the following perturbed version of (3):

$$\begin{array}{ll} u_t = \Delta u + auf(z-u-v, k), & x \in \Omega, \ t > 0, \\ v_t = \Delta v + (a+\beta\tau)vf(z-u-v, k+\tau), & x \in \Omega, \ t > 0, \\ \frac{\partial u}{\partial \nu} + \gamma(x)u = \frac{\partial v}{\partial \nu} + \gamma(x)v = 0, & x \in \partial\Omega, \ t > 0, \end{array} \tag{6}$$

where $\tau > 0$ is a small parameter.

As mentioned earlier, if $\tau = 0$, we observe that the two species play an identical role, and system (6) can be reduced to the single species case, i.e., (6) possesses a family of coexistence states $(s\theta(\cdot, a), (1-s)\theta(\cdot, a))$, $0 < s < 1$, which attracts all solutions of system (6) with nonnegative, nontrivial initial data. An interesting problem is to find out what happens when the two species are slightly different, that is, $\tau > 0$ is small.

Before stating our main results, we start by recalling some well-known results on the one-species problem (5).

Lemma 1.1. [6, 19] *If $a \le \lambda_0$, then zero is the unique nonnegative solution of (5); if $a > \lambda_0$, then (5) has a unique positive solution, denoted by $\theta(\cdot, a)$. Moreover, $\theta(\cdot, a)$ satisfies the following properties:*

- (i) *$0 < \theta(\cdot, a) < z$;*
- (ii) *$\theta(\cdot, a)$ is continuously differentiable for $a \in (\lambda_0, +\infty)$, and is pointwisely increasing when a increases;*
- (iii) *$\lim_{a \to \lambda_0+} \theta(\cdot, a) = 0$ uniformly for $x \in \overline{\Omega}$, and $\lim_{a \to +\infty} \theta(\cdot, a) = z(x)$ for almost every $x \in \Omega$;*
- (iv) *Let $L_a = \Delta + af_1(z - \theta(\cdot, a), k) - a\theta(\cdot, a)f_1'(z - \theta(\cdot, a), k)$, where $f_1'(S, k) = \frac{\partial f(S,k)}{\partial S}$ denotes the partial derivative of $f(S, k)$ with respect to S. Then L_a is a differential operator in $C_B^2(\overline{\Omega}) = \{u \in C^2(\overline{\Omega}) : \frac{\partial u}{\partial \nu} + \gamma(x)u = 0\}$ and all eigenvalues of L_a are strictly negative.*

Due to the strict competition of the basic chemostat model (6), we can determine the global dynamics of (6) by analyzing the equilibria and their stability. Here we say the system

$$\begin{array}{ll} u_t = \Delta u + F_1(u, v), & x \in \Omega, \, t > 0, \\ v_t = \Delta v + F_2(u, v), & x \in \Omega, \, t > 0 \end{array}$$

is strictly competitive if $\frac{\partial F_1}{\partial v} < 0, \frac{\partial F_2}{\partial u} < 0$ for $u, v > 0$. It turns out that, for $\tau > 0$ small, the dynamics and coexistence solutions of (6) essentially depend on the following function of $a \in (\lambda_0, +\infty)$, which is defined by

$$G(a) := \int_\Omega \theta^2(\cdot, a)[\beta f(z - \theta(\cdot, a), k) + a f_2'(z - \theta(\cdot, a), k)]\mathrm{d}x, \tag{7}$$

where $f_2'(S, k) = \frac{\partial f}{\partial k}(S, k)$ is the partial derivative of $f(S, k)$ with respect to k. By direct calculations, we have

$$G(a) = \int_\Omega \frac{\beta(k + z - \theta(\cdot, a)) - a}{(k + z - \theta(\cdot, a))^2}(z - \theta(\cdot, a))\theta^2(\cdot, a)\mathrm{d}x. \tag{8}$$

By Lemma 1.1(iii), it is easy to see that $\lim_{a \to \lambda_0 +} G(a) = 0$ and $G(a) < 0$ when a is large enough. Moreover, if $\beta k > \lambda_0$, one can conclude that there exists $\delta > 0$ such that for $a \in (\lambda_0, \lambda_0 + \delta)$, we have $\beta(k + z - \theta(\cdot, a)) - a > 0$ on $\overline{\Omega}$, which implies $G(a) > 0$ for $a \in (\lambda_0, \lambda_0 + \delta)$. Hence, for fixed $\beta > \frac{\lambda_0}{k}$, $G(a)$ must change sign in $a \in (\lambda_0, +\infty)$. Furthermore, numerical computations illustrate that the diagram of $G(a)$ looks like Figure 1.

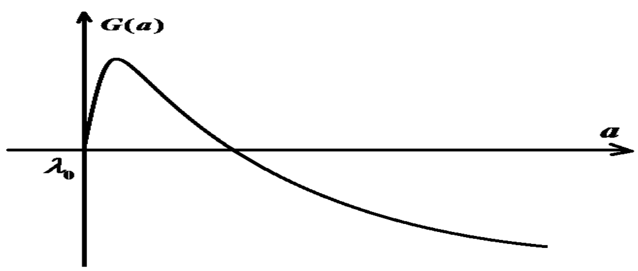

FIGURE 1. Possible diagram of the function $G(a)$.

Theorem 1.2. *Suppose $a_0 > \lambda_0$. Then*

(i) *if $G(a_0) > 0$, then there exists $\epsilon > 0$ such that for $a \in (a_0 - \epsilon, a_0 + \epsilon)$ and $\tau \in (0, \epsilon)$, system (6) has no coexistence solution, and $(0, \vartheta(\cdot, a, \tau))$ is the global attractor of (6);*

(ii) *if $G(a_0) < 0$, then there exists $\epsilon > 0$ such that for $a \in (a_0 - \epsilon, a_0 + \epsilon)$ and $\tau \in (0, \epsilon)$, system (6) has no coexistence solution, and $(\theta(\cdot, a), 0)$ is the global attractor of (6);*

(iii) *if $G(a_0) = 0$ and $G'(a_0) \neq 0$, then for any sufficiently small $\epsilon > 0$, there exists $\hat{\tau} = \hat{\tau}(\epsilon) > 0$ with the following property: For every $\tau \in (0, \hat{\tau})$, there exist $a_* < a^*$ with $a_*, a^* \in (a_0 - \epsilon, a_0 + \epsilon)$ such that for $a \in [a_0 - \epsilon, a_0 + \epsilon]$, (6) has a coexistence solution if and only if $a \in (a_*, a^*)$. Moreover, any coexistence solution (if it exists) is the global attractor of (6) provided $I_A \geq 0$, where $I_A = \int_\Omega \left(\frac{2a_0 k}{(k+z-\theta_0)^3} - \frac{a_0 + \beta k}{(k+z-\theta_0)^2} \right) \theta_0^2 A \mathrm{d}x$, $\theta_0 = \theta(\cdot, a_0)$ and A is given by (37).*

Remark 1. Here we say an equilibrium (u_e, v_e) is the global attractor if it is stable and for each nontrivial $(u_0(x), v_0(x)) \in C(\overline{\Omega}) \times C(\overline{\Omega})$ with $u_0(x) \geq 0, v_0(x) \geq 0$ one has $(u(x,t), v(x,t))$ converges to (u_e, v_e) in $C(\overline{\Omega}) \times C(\overline{\Omega})$ as $t \to \infty$, where $(u(x,t), v(x,t))$ is the solution of (6) with the initial conditions $u(x, 0) = u_0(x), v(x, 0) = v_0(x)$.

Remark 2. Numerical computations suggest that the integral I_A can be negative or positive. For example, we take $\Omega = (0, 1)$ and $\gamma(x) \equiv 1$ on [0,1] and choose the parameters as follows: $a = 1.2, k = 0.8, \beta = 0.5690$, we obtain that $G(1.2) \approx 0$ and $I_A = -0.7361$. Changing the parameters to $a = 2.5, k = 0.8, \beta = 2.1260525$, we get $G(2.5) \approx 0$ and $I_A = 37.7032$. We suspect that if I_A is negative, it may occur that both semi-trivial steady states are locally stable and the coexistence steady state is unstable. Hence the hypothesis $I_A \geq 0$ is reasonable.

Remark 3. From the biological perspective, the perturbed system (6) is motivated by the following considerations. Suppose that random mutation produces another phenotype of species which is slightly different from the resident species. For instance, the mutant has slightly different maximal growth rates and Michaelis-Menten constants. Two similar species might have to compete for the same limited resources. Two interesting questions arise in the study of the perturbed system (6): One is whether the mutant can invade when its initial population size is small. The other is that if the mutant does invade, whether it will drive the resident species to extinction or coexist with it. Theorem 1.2 indicates that global dynamics of the system (6) essentially depends upon the function $G(a)$ of the growth rate. Moreover, it is possible for the mutant to force the extinction of resident species or to coexist with it. Similar problems have been studied in [7, 8] and the references therein to reveal the effects of the spatial heterogeneity of environment on the invasion of the mutant and the coexistence of multiple species in classical Lotka-Volterra systems.

The method of analysis is based on Lyapunov-Schmidt reduction, stability analysis and the following well-known results on the monotone dynamical system.

Lemma 1.3. [4, 15] *For the monotone dynamical system,*

(i) *if there is no coexistence state, then one of the semi-trivial equilibria is unstable and the other one is the global attractor.*
(ii) *if there is a unique coexistence state and it is stable, then it is the global attractor (in particular, both semi-trivial equilibria are unstable).*
(iii) *if all coexistence states are asymptotically stable, then there is at most one of them.*

The organization of the paper is as follows: In Section 2, the stability of semi-trivial equilibria of (6) is investigated. Positive equilibria of (6) are constructed by Lyapunov-Schmidt reduction, and their stability is established by spectral analysis subsequently. Finally, Theorem 1.2 is proved by the monotone dynamical theory, which reveals the global dynamics of (6).

2. **Stability of semi-trivial equilibria.** The aim of this section is to study the stability of semi-trivial equilibria of (6). To this end, we first investigate the semi-trivial nonnegative solutions of the steady state system

$$\begin{cases} \Delta u + auf(z-u-v,k) = 0, & x \in \Omega, \\ \Delta v + (a+\beta\tau)vf(z-u-v,k+\tau) = 0, & x \in \Omega, \\ \frac{\partial u}{\partial \nu} + \gamma(x)u = \frac{\partial v}{\partial \nu} + \gamma(x)v = 0, & x \in \partial\Omega. \end{cases} \tag{9}$$

Clearly, it follows from Lemma 1.1 that (9) has the semi-trivial nonnegative solution $(\theta(\cdot, a), 0)$ if $a > \lambda_0$. In order to determine the other semi-trivial nonnegative solution, we introduce $\lambda_0(\tau)$ to be the principal eigenvalue of the following problem:

$$\Delta\phi + \lambda_0(\tau)f(z(x), k+\tau)\phi = 0 \quad \text{in} \quad \Omega, \quad \frac{\partial \phi}{\partial \nu} + \gamma(x)\phi = 0 \quad \text{on } \partial\Omega. \tag{10}$$

By similar arguments as in Lemma 2.3 of [10, 13], we have the following results.

Lemma 2.1. *The function* $\lambda_0(\tau) : [0,+\infty) \to \mathbb{R}_+$ *is continuously differentiable with respect to the parameter* τ *on* $[0,+\infty)$, *and it is strictly increasing on* $[0,+\infty)$. *Moreover,*

$$\lim_{\tau\to 0}\lambda_0(\tau) = \lambda_0, \quad \lambda_0'(0) = -\frac{\lambda_0\int_\Omega f_2'(z,k)\phi_0^2\mathrm{d}x}{\int_\Omega f(z,k)\phi_0^2\mathrm{d}x},$$

where λ_0, ϕ_0 *are the principal eigenvalue and eigenfunction of* (4).

It follows from Lemma 2.1 that if $a > \lambda_0$, then $a + \beta\tau > \lambda_0(\tau)$ for τ small enough. By Lemma 1.1, (9) possesses the other semi-trivial nonnegative solution $(0, \vartheta(\cdot, a, \tau))$ if $a > \lambda_0$ and $\tau > 0$ is small enough. Here $\vartheta(\cdot, a, \tau)$ is the unique positive solution of (5) with $(a, k) = (a+\beta\tau, k+\tau)$. The purpose of this section is to study the linearized stability of the semi-trivial nonnegative solutions $(\theta(\cdot, a), 0)$ and $(0, \vartheta(\cdot, a, \tau))$. Throughout this paper, for simplicity we denote $\theta(\cdot, a)$ and $\vartheta(\cdot, a, \tau)$ by θ and ϑ, respectively.

First, we study the stability of $(\theta(\cdot, a), 0)$. To this end, we consider the following linearized problem of (9) at $(\theta(\cdot, a), 0)$:

$$\begin{cases} \Delta\varphi + a(f(z-\theta,k) - \theta f_1'(z-\theta,k))\varphi - a\theta f_1'(z-\theta,k)\psi = -\lambda\varphi, \quad x\in\Omega, \\ \Delta\psi + (a+\beta\tau)f(z-\theta,k+\tau)\psi = -\lambda\psi, \quad x\in\Omega, \\ \frac{\partial\varphi}{\partial\nu} + \gamma(x)\varphi = \frac{\partial\psi}{\partial\nu} + \gamma(x)\psi = 0, \quad x\in\partial\Omega, \end{cases}$$

where $f_1'(S,k) = \frac{\partial f(S,k)}{\partial S}$ denotes the partial derivative of $f(S,k)$ with respect to S. In view of Lemma 1.1, one can conclude that the stability of $(\theta, 0)$ is determined by the principal eigenvalue of the scalar problem

$$\Delta\psi + (a+\beta\tau)f(z-\theta,k+\tau)\psi = -\lambda\psi \quad \text{in} \quad \Omega, \quad \frac{\partial\psi}{\partial\nu} + \gamma(x)\psi = 0 \quad \text{on } \partial\Omega. \tag{11}$$

Let $\lambda_1(\tau)$ be the principal eigenvalue of (11) and $\psi_1(\cdot, \tau)$ be the corresponding eigenfunction such that $\psi_1 > 0$ on $\overline{\Omega}$ and $\max_{\overline{\Omega}}\psi_1 = \max_{\overline{\Omega}}\theta$. Then we have

$$\Delta\psi_1 + (a+\beta\tau)f(z-\theta,k+\tau)\psi_1 = -\lambda_1(\tau)\psi_1 \quad \text{in} \quad \Omega, \quad \frac{\partial\psi_1}{\partial\nu} + \gamma(x)\psi_1 = 0 \quad \text{on } \partial\Omega.$$

It is easy to see that $\psi_1(\cdot, 0) = \theta, \lambda_1(0) = 0$. Multiplying this equation by θ, and integrating over Ω by parts, we have

$$\lambda_1(\tau)\int_\Omega \psi_1\theta\mathrm{d}x = \int_\Omega [af(z-\theta,k) - (a+\beta\tau)f(z-\theta,k+\tau)]\psi_1\theta\mathrm{d}x.$$

Expanding the eigenfunction ψ_1 in the form $\psi_1 = \theta + \tau\Psi(\cdot, \tau)$, we obtain

$$\begin{aligned}\lambda_1(\tau)\int_\Omega \psi_1\theta\mathrm{d}x = & -\tau G(a) + \tau^2\Big[\int_\Omega \frac{(\beta(k+z-\theta)-a)(z-\theta)\theta^2}{(k+z-\theta)^2(k+\tau+z-\theta)}\mathrm{d}x \\ & - \int_\Omega \frac{(\beta(k+z-\theta)-a)(z-\theta)\theta\Psi}{(k+z-\theta)(k+\tau+z-\theta)}\mathrm{d}x\Big],\end{aligned}$$

where $G(a)$ is given by (7). Hence the stability of $(\theta(\cdot, a), 0)$ is determined by the sign of $G(a)$ when τ is small, and the following lemma holds.

Lemma 2.2. *Suppose* $a > \lambda_0$. *Then there exists* $\delta_1 > 0$ *such that for any* $0 < \tau < \delta_1$ *the semi-trivial solution* $(\theta_a, 0)$ *is stable provided* $G(a) < 0$, *and unstable provided* $G(a) > 0$.

Next, we study the stability of $(0, \vartheta(\cdot, a, \tau))$. To this end, we consider the following linearized problem of (9) at $(0, \vartheta(\cdot, a, \tau))$:

$$\begin{array}{l}\Delta\varphi + af(z-\vartheta, k)\varphi = -\sigma\varphi, \quad x \in \Omega,\\ \Delta\psi + (a+\beta\tau)[f(z-\vartheta, k+\tau) - \vartheta f_1'(z-\vartheta, k+\tau)]\psi\\ \qquad -(a+\beta\tau)\vartheta f_1'(z-\vartheta, k)\varphi = -\sigma\psi, \qquad x \in \Omega,\\ \frac{\partial\varphi}{\partial\nu} + \gamma(x)\varphi = \frac{\partial\psi}{\partial\nu} + \gamma(x)\psi = 0, \quad x \in \partial\Omega.\end{array}$$

By virtue of Lemma 1.1, it is easy to check that the stability of $(0, \vartheta(\cdot, a, \tau))$ is determined by the principal eigenvalue of the scalar eigenvalue problem

$$\Delta\varphi + af(z-\vartheta(\cdot, a, \tau), k)\varphi = -\sigma\varphi \quad \text{in} \quad \Omega, \quad \frac{\partial\varphi}{\partial\nu} + \gamma(x)\varphi = 0 \quad \text{on } \partial\Omega. \tag{12}$$

Let $\sigma_1(\tau)$ be the principal eigenvalue of (12) and $\varphi_1(\cdot, \tau)$ be the corresponding eigenfunction such that $\varphi_1 > 0$ on $\overline{\Omega}$ and $\max_{\overline{\Omega}} \varphi_1 = \max_{\overline{\Omega}} \theta$. Then we have

$$\Delta\varphi_1 + af(z-\vartheta(\cdot, a, \tau), k)\varphi_1 = -\sigma\varphi_1 \quad \text{in} \quad \Omega, \quad \frac{\partial\varphi_1}{\partial\nu} + \gamma(x)\varphi_1 = 0 \quad \text{on } \partial\Omega.$$

Clearly, $\vartheta(\cdot, a, 0) = \theta$, $\sigma_1(0) = 0$, and $\varphi_1(\cdot, 0) = \theta$. Multiplying this equation by ϑ, and integrating over Ω by parts, we have

$$\begin{aligned}\sigma_1(\tau)\int_\Omega \varphi_1\vartheta \mathrm{d}x &= \int_\Omega [(a+\beta\tau)f(z-\vartheta, k+\tau) - af(z-\vartheta, k)]\varphi_1\vartheta \mathrm{d}x\\ &= \tau\int_\Omega \frac{\beta(k+z-\vartheta) - a}{(k+z-\vartheta)(k+\tau+z-\vartheta)}(z-\vartheta)\varphi_1\vartheta \mathrm{d}x\\ &= \tau(G(a) + O(\tau)).\end{aligned}$$

Similarly, the stability of $(0, \vartheta(\cdot, a, \tau))$ is determined by the sign of $G(a)$ when τ is small, and the following lemma holds.

Lemma 2.3. *Suppose $a > \lambda_0$. Then there exists $\delta_2 > 0$ such that for any $0 < \tau < \delta_2$ the semi-trivial solution $(0, \vartheta(\cdot, a, \tau))$ is stable provided $G(a) > 0$, and unstable provided $G(a) < 0$.*

3. **Lyapunov-Schmidt reduction.** In this section, we construct positive solutions of (9) by Lyapunov-Schmidt reduction near the surface

$$\Sigma_a := \{(a, s\theta(\cdot, a), (1-s)\theta(\cdot, a)) : a > \lambda_0, s \in [0, 1]\}.$$

Note that for every $a > \lambda_0$, Σ_a is the set of nontrivial nonnegative solutions of (9) when $\tau = 0$. Moreover, for any small τ, (9) has the semi-trivial solutions $(\theta(\cdot, a), 0)$ and $(0, \vartheta(\cdot, a, \tau))$ if $a > \lambda_0$.

Introduce the following spaces:

$$\begin{array}{l}X = \{(\omega, \chi) \in W^{2,p}(\Omega) \times W^{2,p}(\Omega) : \frac{\partial\omega}{\partial\nu} + \gamma(x)\omega = \frac{\partial\chi}{\partial\nu} + \gamma(x)\chi = 0 \text{ on } \partial\Omega\},\\ X_1 = \text{span}\{(\theta, -\theta)\},\\ X_2 = \{(\omega, \chi) \in X : \int_\Omega (\omega - \chi)\theta \mathrm{d}x = 0\},\\ Y = L^p(\Omega) \times L^p(\Omega),\end{array}$$

where $\theta = \theta(\cdot, a)$.

Theorem 3.1. *Suppose that $a_0 > \lambda_0$. Then there exist a neighborhood U of Σ_{a_0} in $(\lambda_0, +\infty) \times X$ and $\delta > 0$ with the following properties:*

(i) *if $G(a_0) \neq 0$, then for $\tau \in (0, \delta)$ there is no positive solution of (9) in U;*

(ii) *if $G(a_0) = 0$ and $G'(a_0) \neq 0$, then for $\tau \in (0, \delta)$, the set of solutions of (9) in U consists of the semi-trivial solutions $(a, \theta(\cdot, a), 0)$ and $(a, 0, \vartheta(\cdot, a, \tau))$ and the set $\Gamma \cap U$, where Γ is a smooth curve given by*

$$\Gamma = \{(a(\tau, s), u(\tau, s), v(\tau, s)) : -\delta \leq s \leq 1 + \delta\}.$$

Here $(\tau, s) \mapsto (u(\tau, s), v(\tau, s)) \in X$ and $(\tau, s) \mapsto a(\tau, s) \in (\lambda_0, +\infty)$ are smooth functions on $[0, \delta) \times (-\delta, 1 + \delta)$ satisfying the following properties:

$$\begin{aligned} &(u(\tau, 0), v(\tau, 0)) = (0, \vartheta(\cdot, a(\tau, 0), \tau)), \\ &(u(\tau, 1), v(\tau, 1)) = (\theta(\cdot, a(\tau, 1)), 0), \\ &(a(0, s), u(0, s), v(0, s)) = (a_0, s\theta(\cdot, a_0), (1 - s)\theta(\cdot, a_0)). \end{aligned} \tag{13}$$

Namely, a branch of positive solution bifurcates from the branch of semi-trivial nonnegative solutions $\{(a, \theta(\cdot, a), 0) : a > \lambda_0\}$ at $a = a(\tau, 1)$, and meets the other branch of semi-trivial nonnegative solutions $\{(a, 0, \vartheta(\cdot, a, \tau)) : a \in \mathbb{R}\}$ at $a = a(\tau, 0)$. For $\tau = 0$, the branch coincides with Σ_{a_0}.

Proof. It is easy to see that each solution (u, v) of (9) with (a, u, v) near Σ_{a_0} can be written as

$$u = s\theta(\cdot, a) + \omega, \quad v = (1 - s)\theta(\cdot, a) + \chi, \tag{14}$$

where $s \in \mathbb{R}$, and $(\omega, \chi) \in X_2$ is in a neighborhood of $(0, 0)$. Moreover, (ω, χ) satisfies

$$\begin{aligned} &\Delta\omega + a\omega f(z - \theta - \omega - \chi, k) + as\theta(f(z - \theta - \omega - \chi, k) - f(z - \theta, k)) = 0, \ \ x \in \Omega, \\ &\Delta\chi + (a + \beta\tau)\chi f(z - \theta - \omega - \chi, k + \tau) \\ &\quad + (1 - s)\theta[(a + \beta\tau)f(z - \theta - \omega - \chi, k + \tau) - af(z - \theta, k)] = 0, \quad x \in \Omega, \\ &\tfrac{\partial\omega}{\partial\nu} + \gamma(x)\omega = \tfrac{\partial\chi}{\partial\nu} + \gamma(x)\chi = 0, \quad x \in \partial\Omega. \end{aligned}$$

For small $\delta > 0$, define the map $F : X \times (a_0 - \delta, a_0 + \delta) \times (-\delta, \delta) \times (-\delta, 1 + \delta) \to Y$ by

$$\begin{aligned} &F(\omega, \chi, a, \tau, s) \\ &= \begin{pmatrix} \Delta\omega + a\omega f(z - \theta - \omega - \chi, k) \\ \quad + as\theta(f(z - \theta - \omega - \chi, k) - f(z - \theta, k)) \\ \Delta\chi + (a + \beta\tau)\chi f(z - \theta - \omega - \chi, k + \tau) \\ \quad + (1 - s)\theta[(a + \beta\tau)f(z - \theta - \omega - \chi, k + \tau) - af(z - \theta, k)] \end{pmatrix} \end{aligned} \tag{15}$$

Clearly, F is smooth and (u, v) given by (14) satisfies (9) if and only if $F(\omega, \chi, a, \tau, s) = 0$ with $(\omega, \chi) \in X_2$. Note that the semi-trivial equilibria can be written as

$$\begin{aligned} &(\theta(\cdot, a), 0) = (\theta(\cdot, a), 0) + (0, 0), \\ &(0, \vartheta(\cdot, a)) = (s\theta(\cdot, a), (1 - s)\theta(\cdot, a)) + (\rho(a, \tau), \eta(a, \tau)) \ \text{ with } s = \sigma(a, \tau), \end{aligned}$$

where $(\rho(a, \tau), \eta(a, \tau))$ and σ are smooth functions of (a, τ) taking values in X_2 and $\mathbb{R}$, respectively. Clearly,

$$\sigma(a, 0) = 0, \quad (\rho(a, 0), \eta(a, 0)) = (0, 0)$$

due to $\vartheta(\cdot, a, 0) = \theta(\cdot, a)$. Hence, one can conclude that

$$\begin{aligned} &F(0, 0, a, 0, s) = 0, \\ &F(0, 0, a, \tau, 1) = 0, \\ &F(\rho(a, \tau), \eta(a, \tau), a, \tau, \sigma(a, \tau)) = 0 \end{aligned} \tag{16}$$

for all admissible values of a, s and τ.

Define the linearized operator $L(a, s) : X \to Y$ by

$$L(a, s) = \mathrm{D}_{(\omega, \chi)}F(0, 0, a, 0, s).$$

By straightforward calculations, we can find that $L(a,s)$ is given by

$$L(a,s)\begin{pmatrix}\varphi\\ \psi\end{pmatrix}=\begin{pmatrix}\Delta\varphi+af(z-\theta,k)\varphi-as\theta f_1'(z-\theta,k)(\varphi+\psi)\\ \Delta\psi+af(z-\theta,k)\psi-a(1-s)\theta f_1'(z-\theta,k)(\varphi+\psi)\end{pmatrix}$$

Clearly, $L(a,s)$ is a Fredholm operator of zero index. Moreover,

$$\begin{aligned}\ker(L(a,s))&=\operatorname{span}\{(\theta,-\theta)\}=X_1,\\ \mathrm{R}(L(a,s))&=\{(\varphi,\psi)\in Y:\textstyle\int_\Omega((1-s)\varphi-s\psi)\theta\mathrm{d}x=0\},\end{aligned}$$

where $\ker(L(a,s))$ and $\mathrm{R}(L(a,s))$ stand for the kernel and the range of L, respectively.

Let the operator $P(a,s)$ on Y be defined by

$$P\begin{pmatrix}\omega\\ \chi\end{pmatrix}=\frac{1}{\int_\Omega\theta^2\mathrm{d}x}\left[\int_\Omega\theta((1-s)\omega-s\chi)\mathrm{d}x\right]\begin{pmatrix}\theta\\ -\theta\end{pmatrix}. \tag{17}$$

Then one can show that $\mathrm{R}(P)=X_1$, $P^2=P$ and $P(a,s)L(a,s)=0$, which means that P is the projection of Y onto X_1 along the range $\mathrm{R}(L(a,s))$.

By the Lyapunov-Schmidt procedure, we consider the system

$$\begin{aligned}&P(a,s)F(\omega,\chi,a,\tau,s)=0,\\ &(I-P(a,s))F(\omega,\chi,a,\tau,s)=0,\end{aligned} \tag{18}$$

where $(\omega,\chi)\in X_2$. It is easy to see that $L(a,s)$ is an isomorphism from X_2 to $\mathrm{R}(L(a,s))$. Hence we can apply the Implicit Function Theorem to solve the second equation of (18) for (ω,χ). Meanwhile, by the application of a compactness argument, we can conclude that there exist $\delta_0>0$, a neighborhood U_1 of $(0,0)$ in X_2, and a smooth function

$$(a,\tau,s)\mapsto(\omega_1(a,\tau,s),\chi_1(a,\tau,s)):(a_0-\delta_0,a_0+\delta_0)\times(-\delta_0,\delta_0)\times(-\delta_0,1+\delta_0)\to X_2$$

such that $\omega_1(a,0,s)=\chi_1(a,0,s)=0$ and $(\omega,\chi,a,\tau,s)\in U_1\times(a_0-\delta_0,a_0+\delta_0)\times(-\delta_0,\delta_0)\times(-\delta_0,1+\delta_0)$ satisfies $F(\omega,\chi,a,\tau,s)=0$ if and only if $\omega=\omega_1(a,\tau,s)$, $\chi=\chi_1(a,\tau,s)$ and (a,τ,s) satisfies

$$P(a,s)F(\omega_1(a,\tau,s),\chi_1(a,\tau,s),a,\tau,s)=0.$$

It follows from (16) that ω_1 and χ_1 satisfy

$$\begin{aligned}&\omega_1(a,0,s)=\chi_1(a,0,s)=0,\\ &\omega_1(a,\tau,1)=\chi_1(a,\tau,1)=0,\\ &\omega_1(a,\tau,\sigma(a,\tau))=\chi_1(a,\tau,\sigma(a,\tau))=(\rho(a,\tau),\eta(a,\tau)).\end{aligned} \tag{19}$$

Next, we define $\xi(a,\tau,s)$ by

$$\xi(a,\tau,s)\begin{pmatrix}\theta\\ -\theta\end{pmatrix}=P(a,s)F(\omega_1(a,\tau,s),\chi_1(a,\tau,s),a,\tau,s). \tag{20}$$

Then it suffices to solve $\xi(a,\tau,s)=0$. By (16) and (19), we immediately have the following properties of $\xi(a,\tau,s)$:

$$\xi(a,0,s)=0,\quad \xi(a,\tau,1)=0,\quad \xi(a,\tau,\sigma(a,\tau))=0, \tag{21}$$

which imply that $\xi(a,\tau,s)$ can be expressed as

$$\xi(a,\tau,s)=\tau(1-s)(\sigma(a,\tau)-s)\xi_1(a,\tau,s) \tag{22}$$

for some smooth function $\xi_1(a,\tau,s)$. Thus we only need to solve $\xi_1(a,\tau,s)=0$. Differentiating both sides of (20) with respect to τ at $\tau=0$, we have

$$\begin{aligned}\xi_\tau(a,0,s)\begin{pmatrix}\theta\\-\theta\end{pmatrix} &= P(a,s)L(a,s)\begin{pmatrix}\omega_{1\tau}(a,0,s)\\ \chi_{1\tau}(a,0,s)\end{pmatrix}+P(a,s)F_\tau(0,0,a,0,s)\\ &= P(a,s)F_\tau(0,0,a,0,s).\end{aligned} \tag{23}$$

On the other hand, from (17) and (15), we obtain

$$P(a,s)F_\tau(0,0,a,0,s)=P(a,s)\begin{pmatrix}0\\(1-s)\theta[\beta f(z-\theta,k)+af_2'(z-\theta,k)]\end{pmatrix},$$

where $f_2'(S,k)=\frac{\partial f}{\partial k}(S,k)$ is the partial derivative of $f(S,k)$ with respect to k. Hence

$$P(a,s)F_\tau(0,0,a,0,s)=\frac{-s(1-s)\int_\Omega\theta^2(\beta f(z-\theta,k)+af_2'(z-\theta,k))\mathrm{d}x}{\int_\Omega\theta^2\mathrm{d}x}\begin{pmatrix}\theta\\-\theta\end{pmatrix}. \tag{24}$$

It follows from (22), (23) and (24) that

$$\xi_1(a,0,s)=\frac{G(a)}{\int_\Omega\theta^2\mathrm{d}x}, \tag{25}$$

where $G(a)$ is given by (7).

If $G(a_0)\neq 0$, choosing δ_1 smaller if necessary, by (25) we can assert that the equation $\xi_1(a,\tau,s)=0$ has no solution in $(a_0-\delta_1,a_0+\delta_1)\times(-\delta_1,\delta_1)\times(-\delta_1,1+\delta_1)$. This implies that (9) has no coexistence solutions near Σ_{a_0}. That is, part (i) holds.

If $G(a_0)=0$, then

$$\frac{\partial\xi_1}{\partial a}(a_0,0,s)=\frac{G'(a_0)}{\int_\Omega\theta(\cdot,a_0)^2\mathrm{d}x}\neq 0.$$

By Implicit Function Theorem, there exists some $\delta_2>0$ such that all solutions of $\xi_1(a,\tau,s)=0$ in $(a_0-\delta_2,a_0+\delta_2)\times(-\delta_2,\delta_2)\times(-\delta_2,1+\delta_2)$ are given by

$$a=\alpha(\tau,s),\quad \tau\in(-\delta_2,\delta_2),\ s\in(-\delta_2,1+\delta_2),$$

where $\alpha(\tau,s)$ is a smooth function satisfying $\alpha(0,s)=a_0$. Noting that (21), one can conclude that $\xi(a,\tau,s)=0$ has the family of solutions

$$\{(\alpha(\tau,s),\tau,s):\ \tau\in(-\delta_2,\delta_2),\ s\in(-\delta_2,1+\delta_2)\}. \tag{26}$$

In this family of solutions, the point $(\alpha(\tau,1),\tau,1)$ is also contained in the set of solutions found in (21), which coincide with the semi-trivial solution $(\theta(\cdot,a),0)$ with $a=\alpha(\tau,1)$. Next, we look for points $(\alpha(\tau,s),\tau,s)$ in the set of solutions (26) associated with the semi-trivial solution $(0,\vartheta(\cdot,a,\tau))$. It follows from (21) that

$$s=\sigma(\alpha(\tau,s),\tau). \tag{27}$$

Since $\sigma(a,0)\equiv 0$, we obtain $\frac{\partial\sigma}{\partial a}(a,0)\equiv 0$. By Implicit Function Theorem, for τ small, there exists a unique solution $s=\bar{s}(\tau)$ of (27) with $\bar{s}(0)=0$, and it depends smoothly on τ. Thus for τ small, $(\alpha(\tau,\bar{s}(\tau)),\tau,\bar{s}(\tau))$ is a point contained in the set of solution (26) which corresponds to the semi-trivial solution $(0,\vartheta(\cdot,a,\tau))$ with $a=\alpha(\tau,\bar{s}(\tau))$. Introduce the change $\widehat{s}=\bar{s}(\tau)+s(1-\bar{s}(\tau))$ with $0\le s\le 1$, and define

$$\begin{aligned}u(\tau,s)&=\widehat{s}\theta(\cdot,\alpha(\tau,\widehat{s}))+\omega(\alpha(\tau,\widehat{s}),\tau,\widehat{s}),\\ v(\tau,s)&=(1-\widehat{s})\theta(\cdot,\alpha(\tau,\widehat{s}))+\chi(\alpha(\tau,\widehat{s}),\tau,\widehat{s}),\\ a(\tau,s)&=\alpha(\tau,\widehat{s}).\end{aligned}$$

Then $u(\tau,s), v(\tau,s)$ and $\alpha(\tau,s)$ are smooth functions of $(\tau,s)\in(-\delta,\delta)\times(-\delta,1+\delta)$ if δ is sufficiently small, and $(u(\tau,s),v(\tau,s))$ is a solution of (9) with $a=\alpha(\tau,s)$. By construction, these solutions, including the semi-trivial equilibria, contain all solutions of (9) in a small neighborhood of Σ_{a_0} for $\tau\in(0,\delta)$. Noting that $\omega_1(a,0,s)=\chi_1(a,0,s)=0$, $\alpha(0,s)=a_0$ and $\bar{s}(0)=0$, we conclude that

$$(a(0,s),u(0,s),v(0,s))=(a_0,s\theta(\cdot,a_0),(1-s)\theta(\cdot,a_0)).$$

Similarly, by virtue of (19), we can deduce that

$$(u(\tau,0),v(\tau,0))=(0,\vartheta(\cdot,a(\tau,0),\tau)),\quad (u(\tau,1),v(\tau,1))=(\theta(\cdot,a(\tau,1)),0).$$

This completes the proof. □

Next, we show that all positive solutions have been found by the local bifurcation analysis.

Lemma 3.2. *Let the hypotheses of Theorem 3.1 be satisfied. Then for any neighborhood U of the curve Σ_{a_0} in $(\lambda_0,+\infty)\times X$, there exists $\delta>0$ such that for $\tau\in(0,\delta)$ all solutions (a,u,v) of (9) with $u,v\geq 0$ and $|a-a_0|<\delta$ are contained in U.*

Proof. It suffices to show that if $\tau_i\to 0+$, $a_i\to a_0$, and (u_i,v_i) is the nonnegative solution of (9) with $a=a_i,\tau=\tau_i$, then (a_i,u_i,v_i) converges to the curve Σ_{a_0}. By Lemma 4.2 in [19], we have

$$u_i\leq\theta(\cdot,a)<z(x),\quad v_i\leq\vartheta(\cdot,a,\tau)<z(x).$$

By standard elliptic regularity, passing to a subsequence we may assume that $(u_i,v_i)\to(\hat{u},\hat{v})$ in X, where $(\hat{u},\hat{v})\geq 0$ in $\overline{\Omega}$, and

$$\begin{array}{ll}\Delta\hat{u}+a_0\hat{u}f(z-\hat{u}-\hat{v},k)=0, & x\in\Omega,\\ \Delta\hat{v}+a_0\hat{v}f(z-\hat{u}-\hat{v},k)=0, & x\in\Omega,\\ \frac{\partial\hat{u}}{\partial\nu}+\gamma(x)\hat{u}=\frac{\partial\hat{v}}{\partial\nu}+\gamma(x)\hat{v}=0, & x\in\partial\Omega.\end{array}$$

Clearly, $(\hat{u},\hat{v})$ is contained on the curve Σ_{a_0}. □

4. Stability of coexistence solutions.

To study the stability of positive solutions to (9), we consider the corresponding linear eigenvalue problem

$$\begin{array}{l}\Delta\varphi+a(f(z-u-v,k)-uf_1'(z-u-v,k))\varphi\\ \quad -auf_1'(z-u-v,k)\psi=-\mu\varphi,\quad x\in\Omega,\\ \Delta\psi+(a+\beta\tau)[f(z-u-v,k+\tau)-vf_1'(z-u-v,k+\tau)]\psi\\ \quad -(a+\beta\tau)f_1'(z-u-v,k+\tau)\varphi=-\mu\psi,\quad x\in\Omega,\\ \frac{\partial\varphi}{\partial\nu}+\gamma(x)\varphi=\frac{\partial\psi}{\partial\nu}+\gamma(x)\psi=0,\quad x\in\partial\Omega.\end{array}\tag{28}$$

It is well-known (see [4]) that if (u,v) is a positive solution, then (28) has a principal eigenvalue μ_1 which is real, algebraically simple and all other eigenvalues have their real parts greater than μ_1. Moreover, the principal eigenvalue μ_1 corresponds to an eigenfunction (φ,ψ) satisfying $\varphi>0,\psi<0$, and μ_1 is the only eigenvalue with such no sign-changing eigenfunction. The linearized stability of (u,v) is determined by the sign of the principal eigenvalue: (u,v) is stable if $\mu_1>0$; it is unstable if $\mu_1<0$. Hence, the next crucial step is to calculate the principal eigenvalue μ_1.

Lemma 4.1. *Suppose that (u,v) solves (9), and $\mu_1(\tau)$ is the principal eigenvalue of (28). Then*

$$\mu_1(\tau)\int_\Omega\left(\frac{\varphi^3}{u}-\frac{\psi^3}{v}\right)\mathrm{d}x=I_1+I_2+I_3,$$

where

$$\begin{aligned} I_1 &= 2\int_\Omega u\varphi|\nabla\left(\frac{\varphi}{u}\right)|^2\mathrm{d}x, \\ I_2 &= -2\int_\Omega v\psi|\nabla\left(\frac{\psi}{v}\right)|^2\mathrm{d}x, \\ I_3 &= \int_\Omega (af_1'(z-u-v,k)\varphi^2-(a+\beta\tau)f_1'(z-u-v,k+\tau)\psi^2)(\varphi+\psi)\mathrm{d}x. \end{aligned}$$

Proof. Let $\Phi=\frac{\varphi}{u}$ and $\Psi=\frac{\psi}{v}$. Then $\varphi=u\Phi$, $\psi=v\Psi$, and $\Phi>0>\Psi$ on $\overline{\Omega}$. Direct computation leads to

$$\begin{cases} \Delta\Phi+\frac{2\nabla u\cdot\nabla\Phi}{u}-af_1'(z-u-v,k)(\varphi+\psi)=-\mu\Phi, & x\in\Omega, \\ \Delta\Psi+\frac{2\nabla v\cdot\nabla\Psi}{v}-(a+\beta\tau)f_1'(z-u-v,k+\tau)(\varphi+\psi)=-\mu\Psi, & x\in\Omega, \\ \frac{\partial\Phi}{\partial\nu}=\frac{\partial\Psi}{\partial\nu}=0, & x\in\partial\Omega. \end{cases} \tag{29}$$

Multiplying the first equation of (29) by φ^2, the second equation of (29) by ψ^2 and subtracting, we obtain

$$\begin{aligned} & \mu_1(\tau)(\Phi\varphi^2-\Psi\psi^2) \\ = & -\varphi^2\Delta\Phi+\psi^2\Delta\Psi-2\varphi\Phi\nabla u\cdot\nabla\Phi+2\psi\Psi\nabla v\cdot\nabla\Psi \\ & +[af_1'(z-u-v,k)\varphi^2-(a+\beta\tau)f_1'(z-u-v,k+\tau)\psi^2](\varphi+\psi). \end{aligned}$$

Integrating this equation over Ω, we get

$$\begin{aligned} & \mu_1(\tau)\int_\Omega\left(\frac{\varphi^3}{u}-\frac{\psi^3}{v}\right)\mathrm{d}x \\ = & -\int_\Omega\varphi^2\Delta\Phi\mathrm{d}x+\int_\Omega\psi^2\Delta\Psi\mathrm{d}x-2\int_\Omega\varphi\Phi\nabla u\cdot\nabla\Phi\mathrm{d}x+2\int_\Omega\psi\Psi\nabla v\cdot\nabla\Psi\mathrm{d}x \\ & +\int_\Omega[af_1'(z-u-v,k)\varphi^2-(a+\beta\tau)f_1'(z-u-v,k+\tau)\psi^2](\varphi+\psi)\mathrm{d}x \\ = & 2\int_\Omega\varphi\nabla\varphi\cdot\nabla\Phi\mathrm{d}x-2\int_\Omega\psi\nabla\psi\cdot\nabla\Psi\mathrm{d}x-2\int_\Omega\varphi\Phi\nabla u\cdot\nabla\Phi\mathrm{d}x \\ & +2\int_\Omega\psi\Psi\nabla v\cdot\nabla\Psi\mathrm{d}x+I_3 \\ = & 2\int_\Omega\varphi(u\nabla\Phi+\Phi\nabla u)\cdot\nabla\Phi\mathrm{d}x-2\int_\Omega\psi(v\nabla\Psi+\Psi\nabla v)\cdot\nabla\Psi\mathrm{d}x \\ & -2\int_\Omega\varphi\Phi\nabla u\cdot\nabla\Phi\mathrm{d}x+2\int_\Omega\psi\Psi\nabla v\cdot\nabla\Psi\mathrm{d}x+I_3 \\ = & 2\int_\Omega u\varphi|\nabla\Phi|^2\mathrm{d}x-2\int_\Omega v\psi|\nabla\Psi|^2\mathrm{d}x+I_3 \\ = & I_1+I_2+I_3. \end{aligned}$$

This completes the proof. □

Next, we turn to study the stability of positive solutions on the curve Γ. To this end, let

$$(a,u,v)=(\alpha(\tau,s),u(\tau,s),v(\tau,s))\in\Gamma.$$

Clearly, if $\tau=0$, we have $(u,v)=(s\theta_0,(1-s)\theta_0)$, and the principal eigenvalue $\mu_1=0$ of (28) with associated eigenfunction $(\theta_0,-\theta_0)$, where $\theta_0=\theta(\cdot,a_0)$. By standard spectral perturbation theory [14], for $\tau>0$ small, (28) has a unique eigenvalue denoted by $\mu_1(\tau, s)$ such that $\lim_{\tau\to 0}\mu_1(\tau, s) = 0$, and the real parts of all the other eigenvalues of (28) are positive and uniformly bounded away from zero for any $s \in [0, 1]$ and $\tau > 0$ small. Hence, the sign of $\mu_1(\tau, s)$ determines the stability of positive solutions on Γ. By Theorem 3.1, we know that $(a(\tau, 0), 0, \vartheta(\cdot, a(\tau, 0), \tau))$ and $(a(\tau, 1), \theta(\cdot, a(\tau, 1)), 0)$ are bifurcation points because they are the intersection points of Γ with the semi-trivial solution branches. Hence,

$$\mu_1(\tau, 0) = \mu_1(\tau, 1) = 0. \tag{30}$$

Moreover, we can expand the principal eigenfunction (φ, ψ) in the form

$$\begin{array}{l}\varphi = \theta_0 + \tau\varphi_1(\cdot, s) + \tau^2\varphi_2(\cdot, \tau, s),\\ \psi = -\theta_0 + \tau\psi_1(\cdot, s) + \tau^2\psi_2(\cdot, \tau, s)\end{array} \tag{31}$$

with $\varphi_1, \varphi_2, \psi_1$ and ψ_2 being smooth functions. From now on, we normalize the principal eigenfunction (φ, ψ) such that $\int_\Omega \varphi^2 \mathrm{d}x + \int_\Omega \psi^2 \mathrm{d}x = 2\int_\Omega \theta_0^2 \mathrm{d}x$ and $\varphi > 0 > \psi$. In particular, $\varphi = \theta_0, \psi = -\theta_0$ when $\tau = 0$.

It follows from Lemma 4.1 that the crucial step to determine the stability of positive solution (u, v) is to study the signs of the integrals $\int_\Omega \left(\frac{\varphi^3}{u} - \frac{\psi^3}{v}\right) \mathrm{d}x$ and $I_i (i = 1, 2, 3)$. It follows from (13) that for $s \in (0, 1)$ and $0 < \tau \ll 1$, the functions $u(\tau, s), v(\tau, s), a(\tau, s)$ can be expanded into

$$\begin{array}{l}u(\tau, s) = s\theta_0 + \tau u_1(\cdot, s) + O(\tau^2),\\ v(\tau, s) = (1 - s)\theta_0 + \tau v_1(\cdot, s) + O(\tau^2),\\ a(\tau, s) = a_0 + \tau a_1(s) + O(\tau^2),\end{array} \tag{32}$$

where $u_1(\cdot, s), v_1(\cdot, s)$ and $a_1(s)$ are smooth functions of s. At first, by using (31) and (32), it is easy to check that for $0 < \tau \ll 1$,

$$\int_\Omega \left(\frac{\varphi^3}{u} - \frac{\psi^3}{v}\right) \mathrm{d}x > 2\int_\Omega \theta_0^2 \mathrm{d}x + O(\tau) > 0. \tag{33}$$

Next, we turn to investigate the signs of the integrals I_1, I_2 and I_3. As $\varphi > 0 > \psi$, we see that $I_1 > 0$ and $I_2 > 0$. It suffices to find the sign of I_3.

Note that

$$\begin{aligned}
&(af_1'(z - u - v, k)\varphi^2 - (a + \beta\tau)f_1'(z - u - v, k + \tau)\psi^2)(\varphi + \psi)\\
= &\left(a\frac{k}{(k + z - u - v)^2}\varphi^2 - (a + \beta\tau)\frac{k + \tau}{(k + \tau + z - u - v)^2}\psi^2\right)(\varphi + \psi)\\
= &\frac{ak(\varphi + \psi)^2(\varphi - \psi)}{(k + \tau + z - u - v)^2} + \tau\frac{2ak\varphi^2 - (a + \beta k)(k + z - u - v)\psi^2}{(k + z - u - v)(k + \tau + z - u - v)^2}(\varphi + \psi)\\
&+\tau^2\frac{ak\varphi^2 - \beta(k + z - u - v)^2\psi^2}{(k + z - u - v)^2(k + \tau + z - u - v)^2}(\varphi + \psi).
\end{aligned}$$

We have

$$I_3 = I_{31} + I_{32} + I_{33}, \tag{34}$$

where

$$\begin{aligned}
I_{31} &= \int_\Omega \frac{ak(\varphi + \psi)^2(\varphi - \psi)}{(k + \tau + z - u - v)^2}\mathrm{d}x,\\
I_{32} &= \tau\int_\Omega \frac{2ak\varphi^2 - (a + \beta k)(k + z - u - v)\psi^2}{(k + z - u - v)(k + \tau + z - u - v)^2}(\varphi + \psi)\mathrm{d}x,\\
I_{33} &= \tau^2\int_\Omega \frac{ak\varphi^2 - \beta(k + z - u - v)^2\psi^2}{(k + z - u - v)^2(k + \tau + z - u - v)^2}(\varphi + \psi)\mathrm{d}x.
\end{aligned}$$

As $\varphi > 0 > \psi$, we see that $I_{31} > 0$. It follows from (32) and (31) that for $s \in [0,1]$ and $0 < \tau \ll 1$,

$$\begin{aligned} I_{32} &= \tau \int_\Omega \frac{2ak\varphi^2 - (a+\beta k)(k+z-u-v)\psi^2}{(k+z-u-v)(k+\tau+z-u-v)^2}(\varphi+\psi)\mathrm{d}x \\ &= \tau^2 \int_\Omega \frac{2a_0k - (a_0+\beta k)(k+z-\theta_0)}{(k+z-\theta_0)^3}\theta_0^2(\varphi_1(s)+\psi_1(s))\mathrm{d}x + O(\tau^3), \end{aligned} \tag{35}$$

and

$$I_{33} = \tau^2 \int_\Omega \frac{ak\varphi^2 - \beta(k+z-u-v)^2\psi^2}{(k+z-u-v)^2(k+\tau+z-u-v)^2}(\varphi+\psi)\mathrm{d}x = O(\tau^3). \tag{36}$$

By Lemma 4.1 and equations (30), (33), (35) and (36), we see that if

$$\int_\Omega \frac{2a_0k - (a_0+\beta k)(k+z-\theta_0)}{(k+z-\theta_0)^3}\theta_0^2(\varphi_1(s)+\psi_1(s))\mathrm{d}x \geq 0,$$

we have $\mu_1(\tau, s) > 0$ for $s \in (0,1)$ and $0 < \tau \ll 1$, which implies that positive solutions on the curve Γ are stable. Hence, we need to investigate the sign of the above integral.

To this end, we first introduce some notations. Let $L^2(\Omega)$ be the usual Hilbert space with norm $\|\cdot\|$ and inner product $(\cdot,\cdot)$. Take $\Theta = \mathrm{span}\{\theta_0\}$ and $\Theta^\perp$ is its orthogonal complement. Let

$$\mathcal{L} = \Delta + a_0 f(z-\theta_0, k), \quad \text{and} \quad \mathcal{L}_1 = \Delta + a_0 f(z-\theta_0,k) - a_0\theta_0 f_1'(z-\theta_0,k)$$

with the boundary conditions $\frac{\partial\phi}{\partial\nu} + \gamma(x)\phi = 0$. Clearly, 0 is the principal eigenvalue of $\mathcal{L}$, and $\mathcal{L}_1$ has the bounded inverse $\mathcal{L}_1^{-1}$ on $L^2(\Omega)$ corresponding to the boundary condition $\frac{\partial\phi}{\partial\nu} + \gamma(x)\phi = 0$. We define $\mathcal{L}^{-1}$ on $\Theta^\perp$ by setting $\mathcal{L}^{-1}\psi = \phi$ if and only if $\mathcal{L}\phi = \psi$ and $\phi, \psi \in \Theta^\perp$. Noting that $G(a_0) = 0$, that is,

$$\int_\Omega \theta_0^2[\beta f(z-\theta_0,k) + a_0 f_2'(z-\theta_0,k)]\mathrm{d}x = 0,$$

we have $\theta_0[\beta f(z-\theta_0,k) + a_0 f_2'(z-\theta_0,k)] \in \Theta^\perp$. Let

$$\begin{aligned} A &= \mathcal{L}_1^{-1}(\theta_0(\beta f(z-\theta_0,k) + a_0 f_2'(z-\theta_0,k))), \\ B &= a_1(s)\mathcal{L}_1^{-1}(\theta_0 f(z-\theta_0,k)), \\ C &= \mathcal{L}^{-1}(\theta_0(\beta f(z-\theta_0,k) + a_0 f_2'(z-\theta_0,k))). \end{aligned} \tag{37}$$

Then we have the following results.

Lemma 4.2. *Let $a_0 > \lambda_0$ and $I_A = \int_\Omega \left(\frac{2a_0k}{(k+z-\theta_0)^3} - \frac{a_0+\beta k}{(k+z-\theta_0)^2}\right)\theta_0^2 A\mathrm{d}x$. Then positive solutions on the curve Γ are stable provided $I_A \geq 0$.*

Proof. By Lemma 4.1 and the above calculations, one can find the conclusion of this lemma holds if $\varphi_1 + \psi_1 = A$. Hence, we only need to show $\varphi_1 + \psi_1 = A$. To this end, substituting (31) and (32) into (28) and noting that $\mu_{1\tau}(0,s) = 0$, we can find that $\varphi_1(\cdot,s), \psi_1(\cdot,s)$ satisfy

$$\begin{cases} \Delta\varphi_1 + a_0\varphi_1 f(z-\theta_0,k) + a_1(s)\theta_0 f(z-\theta_0,k) - a_0 f_1'(z-\theta_0,k)(u_1+v_1)\theta_0 \\ \qquad -a_0 s\theta_0 f_1'(z-\theta_0,k)(\varphi_1+\psi_1) = 0, \quad x \in \Omega, \\ \Delta\psi_1 + a_0\psi_1 f(z-\theta_0,k) - (a_1(s)+\beta)\theta_0 f(z-\theta_0,k) \\ \qquad +a_0 f_1'(z-\theta_0,k)(u_1+v_1)\theta_0 - a_0(1-s)\theta_0 f_1'(z-\theta_0,k)(\varphi_1+\psi_1) \\ \qquad -a_0\theta_0 f_2'(z-\theta_0,k) = 0, \quad x \in \Omega, \\ \frac{\partial\varphi_1}{\partial\nu} + \gamma(x)\varphi_1 = \frac{\partial\psi_1}{\partial\nu} + \gamma(x)\psi_1 = 0, \quad x \in \partial\Omega. \end{cases} \tag{38}$$

Adding the first and second equation of (38), we obtain

$$\mathcal{L}_1(\varphi_1+\psi_1)=\theta_0(\beta f(z-\theta_0,k)+a_0 f_2'(z-\theta_0,k)).$$

It follows from (37) that $\varphi_1+\psi_1=A$. The proof is complete. □

5. **The proof of Theorem 1.2.** The goal of this section is to establish Theorem 1.2. To this end, we first derive more information on the positive solutions on the curve Γ.

Lemma 5.1. *For some $\zeta\in\mathbb{R}$, we have*

$$\begin{aligned} u_1(\cdot,s) &= s(1-s)(C-A)-sB+\zeta\theta_0,\\ v_1(\cdot,s) &= -(1-s)((1-s)A+B+sC)-\zeta\theta_0. \end{aligned}$$

Proof. Substituting (32) into (9), one can find that $u_1(\cdot,s), v_1(\cdot,s)$ satisfy

$$\begin{cases} \Delta u_1+a_0u_1f(z-\theta_0,k)+a_1(s)s\theta_0 f(z-\theta_0,k)\\ \quad -a_0s\theta_0 f_1'(z-\theta_0,k)(u_1+v_1)=0, \qquad x\in\Omega,\\ \Delta v_1+a_0v_1f(z-\theta_0,k)+(a_1(s)+\beta)(1-s)\theta_0 f(z-\theta_0,k)\\ \quad -a_0(1-s)\theta_0 f_1'(z-\theta_0,k)(u_1+v_1)\\ \quad +a_0(1-s)\theta_0 f_2'(z-\theta_0,k)=0, \qquad x\in\Omega,\\ \frac{\partial u_1}{\partial\nu}+\gamma(x)u_1=\frac{\partial v_1}{\partial\nu}+\gamma(x)v_1=0, \quad x\in\partial\Omega. \end{cases} \tag{39}$$

Adding the first and second equation of (39), we obtain

$$\mathcal{L}_1(u_1+v_1)=-(1-s)\theta_0[\beta f(z-\theta_0,k)+a_0 f_2'(z-\theta_0,k)]-a_1(s)\theta_0 f(z-\theta_0,k).$$

It follows from (37) that

$$u_1+v_1=-(1-s)A-B. \tag{40}$$

Multiplying the first equation of (39) by $1-s$, the second equation of (39) by s and subtracting, we obtain

$$\mathcal{L}((1-s)u_1-sv_1)=s(1-s)\theta_0(\beta f(z-\theta_0,k)+a_0 f_2'(z-\theta_0,k)).$$

In view of $G(a_0)=0$, that is $\int_\Omega \theta_0^2(\beta f(z-\theta_0,k)+a_0f_2'(z-\theta_0,k))\mathrm{d}x=0$, we can conclude that there exists some $\zeta\in\mathbb{R}$ such that

$$(1-s)u_1-sv_1=s(1-s)C+\zeta\theta_0. \tag{41}$$

By (40) and (41), we get the expression of $u_1(\cdot,s), v_1(\cdot,s)$. □

Lemma 5.2. *Let $G'(a_0)$ be the derivative of $G(a)$ at $a=a_0$. Then*

$$a_1(s)=\frac{J_1(s)+J_2(s)+J_3(s)}{G'(a_0)},$$

where

$$\begin{aligned} J_1(s) &= \int_\Omega \frac{\beta(k+z-\theta_0)-a_0}{(k+z-\theta_0)^2}\theta_0(z-\theta_0)(2(1-s)(A-C)+C)\mathrm{d}x,\\ J_2(s) &= \int_\Omega \frac{\theta_0^2}{(k+z-\theta_0)^2}[(\beta(k+z-\theta_0)-a_0)(1-s)A-\beta(1-s)A(z-\theta_0)]\mathrm{d}x,\\ J_3(s) &= \int_\Omega \frac{\beta(k+z-\theta_0)-a_0}{(k+z-\theta_0)^3}(2(1-s)A+1)(z-\theta_0)\theta_0^2\mathrm{d}x. \end{aligned}$$

Proof. Multiplying the first equation of (9) by v and the second equation of (9) by v, subtracting and integrating over Ω, we obtain

$$\int_\Omega [af(z-u-v,k)-(a+\beta\tau)f(z-u-v,k+\tau)]uv\mathrm{d}x=0.$$

Namely,

$$\int_\Omega \frac{a-\beta(k+z-u-v)}{(k+z-u-v)(k+\tau+z-u-v)}uv(z-u-v)\mathrm{d}x=0.$$

Substituting (32) into this equation and noting that $G(a_0)=0$, we have

$$\begin{aligned}&\int_\Omega \frac{a_0-\beta(k+z-\theta_0)}{(k+z-\theta_0)^2}\theta_0(z-\theta_0)((1-s)u_1+sv_1)\mathrm{d}x\\&-s(1-s)[\int_\Omega \frac{a_0-\beta(k+z-\theta_0)}{(k+z-\theta_0)^2}\theta_0^2(u_1+v_1)\mathrm{d}x-\int_\Omega \frac{a_1+\beta(u_1+v_1)}{(k+z-\theta_0)^2}\theta_0^2(z-\theta_0)\mathrm{d}x\\&-\int_\Omega \frac{a_0-\beta(k+z-\theta_0)}{(k+z-\theta_0)^3}(2(u_1+v_1)-1)\theta_0^2(z-\theta_0)\mathrm{d}x]=0.\end{aligned}$$

By Lemma 5.1, we get

$$\begin{aligned}&\int_\Omega \frac{a_0-\beta(k+z-\theta_0)}{(k+z-\theta_0)^2}\theta_0(z-\theta_0)(-2(1-s)A-2B+(1-2s)C))\mathrm{d}x\\&+\int_\Omega \frac{a_0-\beta(k+z-\theta_0)}{(k+z-\theta_0)^2}\theta_0^2((1+s)A+B)\mathrm{d}x\\&+\int_\Omega \frac{a_1-\beta((1+s)A+B)}{(k+z-\theta_0)^2}\theta_0^2(z-\theta_0)\mathrm{d}x\\&-\int_\Omega \frac{a_0-\beta(k+z-\theta_0)}{(k+z-\theta_0)^3}(2(1-s)A+2B+1)\theta_0^2(z-\theta_0)\mathrm{d}x]=0.\end{aligned}\tag{42}$$

Differentiating both sides of $\Delta\theta(\cdot,a)+a\theta(\cdot,a)f(z-\theta(\cdot,a),k)=0$ with respect to a at $a=a_0$, we have

$$\mathcal{L}_1\frac{\partial\theta(\cdot,a_0)}{\partial a}=-\theta_0 f(z-\theta_0,k).$$

By virtue of $B=a_1(s)\mathcal{L}_1^{-1}(\theta_0 f(z-\theta_0,k))$, we have $B=-a_1(s)\frac{\partial\theta(\cdot,a_0)}{\partial a}$. Substituting $B=-a_1(s)\frac{\partial\theta(\cdot,a_0)}{\partial a}$ into (42), we obtain $a_1(s)=\frac{J_1(s)+J_2(s)+J_3(s)}{G'(a_0)}$ by some direct computation. □

Remark 4. As A,C is independent of s, one can conclude that $J_1(s),J_2(s)$ and $J_3(s)$ are linear functions with respect to s. Thus, $a_1(s)$ is a linear function of s, which implies $a_1(s)$ must be monotone with respect to s.

Proof of Theorem 1.2. By Theorem 3.1 and Lemma 3.2, it is easy to see that if $G(a_0)\neq 0$, then there exists $\epsilon>0$ such that for $a\in(a_0-\epsilon,a_0+\epsilon)$ and $\tau\in(0,\epsilon)$, (9) has no positive solution. Moreover, if $G(a_0)>0$, we can choose $\epsilon>0$ small enough such that $G(a)>0$ in $(a_0-\epsilon,a_0+\epsilon)$. It follows from Lemmas 2.2-2.3 that for $a\in(a_0-\epsilon,a_0+\epsilon)$ and $\tau\in(0,\epsilon)$, $(0,\vartheta(\cdot,a,\tau))$ is stable and $(\theta(\cdot,a),0)$ is unstable. By Lemma 1.3, we can conclude that for $a\in(a_0-\epsilon,a_0+\epsilon)$ and $\tau\in(0,\epsilon)$, $(0,\vartheta(\cdot,a,\tau))$ is the global attractor of (9) provided $G(a_0)>0$. Namely, (i) holds. Similarly, we can prove (ii) holds.

It remains to prove part (iii). By Theorem 3.1 and Lemma 3.2 again, we know that for $a \approx a_0$ and $\tau \approx 0$, all positive solutions lie on the curve Γ. Moreover, we have

$$a(\tau, s) = a_0 + \tau a_1(s) + O(\tau^2)$$

on the curve Γ. It follows from Lemma 5.2 and Remark 4 that $a_1(s)$ is a linear function of s, which implies that $a_1(s)$ is monotone with respect to s. Hence, $a(\tau, s)$ is also monotone with respect to s. Let

$$a_* = \min_{s\in[0,1]} a(\tau, s), \quad a^* = \max_{s\in[0,1]} a(\tau, s).$$

The monotonicity of $a(\tau, s)$ implies that (9) has a positive solution if and only if $a \in (a_*, a^*)$. Moreover, the positive solution is unique for each fixed $a \in (a_*, a^*)$. By virtue of Lemma 4.2, positive solutions on the curve Γ are stable provided $I_A \geq 0$. By Lemma 1.3, we can conclude that the unique and stable positive solution is the global attractor of (9). The proof is complete. □

6. **Discussion.** The purpose of this paper is to study the uniqueness and stability of coexistence solutions of (3) and its global dynamics. In [10, 3], partial results are obtained, which show that (3) has a unique positive steady-state solution when the maximal growth rates a, b are near the principal eigenvalues λ_1, σ_1, respectively, and the unique positive steady state solution is globally asymptotically stable under certain conditions (see [10]). Here we assume the random mutation can produce another phenotype of species v which is similar to the resident species u. That is, the mutant has slightly different maximal growth rates and Michaelis-Menten constants. For survival, these two species might have to compete for the same limited resources. There are two key questions. One is whether the mutant v can invade when rare. The other is if the mutant v does invade, whether it will drive the resident species u to extinction or coexist with it. Mathematically, the questions lead to the study of the perturbed version (6) of the system (3).

Analytical results show that global dynamics of the system (6) essentially depends upon the function $G(a)$ of the growth rate (see Theorem 1.2). More precisely, if $G(a_0) > 0$, then $(0, \vartheta(\cdot, a, \tau))$ is the global attractor of (6) when $a \in (a_0 - \epsilon, a_0 + \epsilon)$ and $\tau \in (0, \epsilon)$. If $G(a_0) < 0$, then $(\theta(\cdot, a), 0)$ is the global attractor of (6) when $a \in (a_0 - \epsilon, a_0 + \epsilon)$ and $\tau \in (0, \epsilon)$. If $G(a_0) = 0$ and $G'(a_0) \neq 0$, then for every $\tau \in (0, \hat{\tau}(\epsilon))$, there exist $a_* < a^*$ with $a_*, a^* \in (a_0 - \epsilon, a_0 + \epsilon)$ such that (6) has a coexistence solution if and only if $a \in (a_*, a^*)$. Moreover, any coexistence solution (if it exists) is the global attractor of (6) provided $I_A \geq 0$.

Biologically, the results imply there is an index that predicts the mutant and the resident species can coexist or not. More precisely, the mutant v always drives the resident species u to extinction if $G(a_0) > 0$, and the mutant can not invade if $G(a_0) < 0$. If $G(a_0) = 0$ and $G'(a_0) \neq 0$, the mutant and the resident species can coexist when $a \in (a_*, a^*)$ and $I_A \geq 0$. Numerical computations suggest that the integral I_A can be negative or positive (see Remark 2). We suspect that if I_A is negative, it may occur that both semi-trivial steady states are locally stable and the coexistence steady state is unstable. Meanwhile, numerical computations also suggest that the diagram of $G(a)$ looks like Figure 1. Hence, it is possible for the mutant to force the extinction of resident species or to coexist with it.

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