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On a system of reaction–diffusion equations arising from competition with internal storage in an unstirred chemostat

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ABSTRACT

In this paper we study a system of reaction–diffusion equations arising from competition of two microbial populations for a single-limited nutrient with internal storage in an unstirred chemostat. The conservation principle is used to reduce the dimension of the system by eliminating the equation for the nutrient. The reduced system (limiting system) generates a strongly monotone dynamical system in its feasible domain under a partial order. We construct suitable upper, lower solutions to establish the existence of positive steady-state solutions. Given the parameters of the reduced system, we answer the basic questions as to which species survives and which does not in the spatial environment and determine the global behaviors. The primary conclusion is that the survival of species depends on species's intrinsic biological characteristics, the external environment forces and the principal eigenvalues of some scalar partial differential equations. We also lift the dynamics of the limiting system to the full system.

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1. Introduction and the model

Chemostat is a laboratory apparatus for continuous culture of bacteria. It is a model for a very simple lake where exploitative competition is easily studied. Basically, the chemostat consists of a nutrient input, pumped at a constant rate into a well-mixed culture vessel whose volume is kept constant by pumping the nutrient and bacteria out at the same rate. The classical model is assumed that the nutrient uptake rate is proportional to its per capita rate of reproduction and the constant of proportionality is called the yield constant. As a consequence of the assumed constant value of the yield, the classical model is sometimes referred to as the constant-yield model [5]. For the constant-yield model, the mathematical analysis [1,7,10] shows the competitive exclusion principle holds, i.e., only one of the species survives.

In phytoplankton ecology, it has long been known that the yield is not a constant and it can vary depending on the growth rate. This led Droop [4] to formulate the following internal storage model:

$$
\begin{gathered}
\frac{dS}{dt} = \big(S^{(0)} - S\big)D - f_1(S, Q_1)u - f_2(S, Q_2)v, \\
\frac{du}{dt} = \big(\mu_1(Q_1) - D\big)u, \\
\frac{dQ_1}{dt} = f_1(S, Q_1) - \mu_1(Q_1)Q_1, \\
\frac{dv}{dt} = \big(\mu_2(Q_2) - D\big)v, \\
\frac{dQ_2}{dt} = f_2(S, Q_2) - \mu_2(Q_2)Q_2, \\
S(0) \geqslant 0, \qquad u(0) \geqslant 0, \qquad v(0) \geqslant 0, \qquad Q_1(0) \geqslant Q_{\min,1}, \qquad Q_2(0) \geqslant Q_{\min,2}.
\end{gathered} \tag{1.1}
$$

For $i = 1, 2$, $Q_i(t)$ represents the average amount of stored nutrient per cell of i-th population at time t, $\mu_i(Q_i)$ is the growth rate of species i as a function of cell quota Q_i, $f_i(S, Q_i)$ is the per capita nutrient uptake rate, per cell of species i as a function of nutrient concentration S and cell quota Q_i, $Q_{\min,i}$ denotes the threshold cell quota below which no growth of species i occurs.

The growth rate $\mu_i(Q_i)$ takes the forms [2–4]:

$$
\begin{gathered}
\mu_i(Q_i) = \mu_{i\infty}\left(1 - \frac{Q_{\min,i}}{Q_i}\right), \\
\mu_i(Q_i) = \mu_{i\infty}\frac{(Q_i - Q_{\min,i})_+}{K_i + (Q_i - Q_{\min,i})_+},
\end{gathered} \tag{1.2}
$$

where $Q_{\min,i}$ is the minimum cell quota necessary to allow cell division and $(Q_i - Q_{\min,i})_+$ is the positive part of $(Q_i - Q_{\min,i})$ and $\mu_{i\infty}$ is the maximal growth rate of the species.

According to Grover [5], the uptake rate $f_i(S, Q_i)$ takes the form:

$$
\begin{gathered}
f_i(S, Q_i) = \rho_i(Q_i)\frac{S}{k_i + S}, \quad \text{where } \rho_i(Q_i) \text{ is defined as follows} \\
\rho_i(Q_i) = \rho^{\text{high}}_{\max,i} - \big(\rho^{\text{high}}_{\max,i} - \rho^{\text{low}}_{\max,i}\big)\frac{Q_i - Q_{\min,i}}{Q_{\max,i} - Q_{\min,i}}, \quad \text{or} \\
\rho_i(Q_i) = \rho_{\max,i}\frac{Q_{\max,i} - Q_i}{Q_{\max,i} - Q_{\min,i}},
\end{gathered} \tag{1.3}
$$

where $Q_{\min,i} \leqslant Q_i \leqslant Q_{\max,i}$. Cunningham and Nisbet [2,3] took $\rho_i(Q_i)$ to be a constant.

Motivated by these examples, we assume that $\mu_i(Q_i)$ is defined and continuously differentiable for $Q_i \geqslant Q_{\min,i} > 0$ and satisfies

(H_1) $\mu_i(Q_i) \geqslant 0$, $\mu_i'(Q_i) > 0$ and is continuous for $Q_i \geqslant Q_{\min,i}$, $\mu_i(Q_{\min,i}) = 0$.

We assume that $f_i(S, Q_i) \geqslant 0$ is continuously differentiable for $S > 0$ and $Q_i \geqslant Q_{\min,i}$ and satisfies

$$f_i(0, Q_i) = 0, \qquad \frac{\partial f_i}{\partial S} > 0, \qquad \frac{\partial f_i}{\partial Q_i} \leqslant 0. \tag{H_2}$$

Let $U = uQ_1$, $V = vQ_2$ be the total amount of stored nutrient at time t for the species 1 and species 2, respectively. Then we have the conservation property:

$$S + U + V = S^{(0)} + O\left(e^{-Dt}\right) \quad \text{as } t \to \infty. \tag{1.4}$$

In [20,21], Smith and Waltman used the method of monotone dynamical system to prove the competitive exclusion principle also holds for internal storage model.

Since coexistence of competing species is obvious in the nature, a candidate for an explanation is to remove the “well-mixed” hypothesis. In [12] a system of reaction–diffusion equation was constructed as follows:

$$\begin{aligned} S_t &= dS_{xx} - \frac{1}{y_1} f_1(S)u - \frac{1}{y_2} f_2(S)v, \\ u_t &= du_{xx} + f_1(S)u, \quad 0 < x < 1,\ t > 0, \\ v_t &= dv_{xx} + f_2(S)v, \end{aligned} \tag{1.5}$$

with boundary conditions

$$\begin{aligned} &S_x(0,t) = -S^{(0)}, \qquad S_x(1,t) + \gamma S(1,t) = 0, \\ &u_x(0,t) = v_x(0,t) = 0, \\ &u_x(1,t) + \gamma u(1,t) = v_x(1,t) + \gamma v(1,t) = 0, \end{aligned} \tag{1.6}$$

and initial conditions

$$\begin{aligned} &S(x,0) = S^0(x) \geqslant 0, \\ &u(x,0) = u^0(x) \geqslant 0, \qquad u^0(x) \not\equiv 0, \\ &v(x,0) = v^0(x) \geqslant 0, \qquad v^0(x) \not\equiv 0. \end{aligned} \tag{1.7}$$

In (1.5) we assume that nutrient $S(x,t)$ and microbial species $u(x,t)$ and $v(x,t)$ have the same diffusion coefficient d. $S^{(0)}$ is the nutrient flux and y_i is the yield constant. The Monod functions $f_i(S) := \frac{m_i S}{k_i + S}$ describe the nutrient uptake and growth rates of species i at nutrient concentration S. The constant γ in (1.6) represents the washout constant. The system (1.5)–(1.7) has conservation property:

$$\left\| S(\cdot,t) + u(\cdot,t) + v(\cdot,t) - z(\cdot) \right\|_\infty = O\left(e^{-\alpha t}\right) \quad \text{as } t \to \infty, \tag{1.8}$$

for some $\alpha > 0$, where $z(x) = S^{(0)}(\frac{1+\gamma}{\gamma} - x)$, $0 < x < 1$.

We note that we may assume $y_1 = y_2 = 1$ in (1.5) by scaling $u \to u/y_1$, $v \to v/y_2$. Hsu and Waltman [12] showed that under the spatial effect two competing species u and v coexist under certain parameter range in contrary to the competitive exclusion in the constant-yield model. Now we intend to combine the well-mixed internal storage model (1.1) and the fixed-yield unstirred chemostat model (1.5)–(1.7) into a new model of competition for a single nutrient with internal storage in an unstirred chemostat. Following [12], $S(x,t)$ represents a nutrient density measured in units of mass per unit length; $u(x,t)$ and $v(x,t)$ are the number of cells per unit length. Since $U(x,t) = u(x,t)Q_1(x,t)$, $V(x,t) = v(x,t)Q_2(x,t)$ are the total amount of stored nutrient for species 1 and species 2, respectively. Obviously when the species u and v diffuse, U and V also diffuse with the same diffusion coefficient. In this paper, we consider the following system of reaction–diffusion equations with internal storage in an unstirred chemostat:

$$
\begin{aligned}
S_t &= dS_{xx} - f_1\left(S, \frac{U}{u}\right)u - f_2\left(S, \frac{V}{v}\right)v, \\
u_t &= du_{xx} + \mu_1\left(\frac{U}{u}\right)u, \\
U_t &= dU_{xx} + f_1\left(S, \frac{U}{u}\right)u, \quad x \in (0,1),\ t > 0, \\
v_t &= dv_{xx} + \mu_2\left(\frac{V}{v}\right)v, \\
V_t &= dV_{xx} + f_2\left(S, \frac{V}{v}\right)v,
\end{aligned}
\tag{1.9}
$$

with boundary conditions

$$
\begin{aligned}
&S_x(0,t) = -S^{(0)}, &&S_x(1,t) + \gamma S(1,t) = 0, \\
&u_x(0,t) = 0, &&u_x(1,t) + \gamma u(1,t) = 0, \\
&U_x(0,t) = 0, &&U_x(1,t) + \gamma U(1,t) = 0, \\
&v_x(0,t) = 0, &&v_x(1,t) + \gamma v(1,t) = 0, \\
&V_x(0,t) = 0, &&V_x(1,t) + \gamma V(1,t) = 0,
\end{aligned}
\tag{1.10}
$$

and initial conditions

$$
\begin{aligned}
&S(x,0) = S^0(x) \geqslant 0, \\
&u(x,0) = u^0(x) \geqslant 0, \qquad u^0(x) \not\equiv 0, \\
&U(x,0) = U^0(x) \geqslant 0, \qquad U^0(x) \not\equiv 0, \\
&v(x,0) = v^0(x) \geqslant 0, \qquad v^0(x) \not\equiv 0, \\
&V(x,0) = V^0(x) \geqslant 0, \qquad V^0(x) \not\equiv 0,
\end{aligned}
\tag{1.11}
$$

where the initial value functions $u^0(x)$, $U^0(x)$, $v^0(x)$, and $V^0(x)$ satisfy $\frac{U^0(x)}{u^0(x)} \geqslant Q_{\min,1}$, $\frac{V^0(x)}{v^0(x)} \geqslant Q_{\min,2}$. We note that $Q_1(x,t) = \frac{U(x,t)}{u(x,t)}$, $Q_2(x,t) = \frac{V(x,t)}{v(x,t)}$ are the instored nutrient per cell per unit length. The nutrient uptake rates $f_1(S, Q_1)$, $f_2(S, Q_2)$ satisfy (H_2) and the growth rate $\mu_i(Q_i)$ satisfies (H_1).

The problem of understanding competition for resources in spatially variable habitats is a challenging and very significant one for theoretical ecology. The specific question of how storage of nutrient resources affects competition in spatially variable habitats is virtually unknown from a theoretical perspective. Recently Grover [6] used a Lagrangian modelling approach to study the competition of phytoplankton for a single nutrient resource. Each competitor population is divided into many subpopulations that move through two model habitats with gradient in nutrient availability: an unstirred chemostat and a partially-mixed water column. By numerical simulations, he concludes some interesting results. However his mathematical model cannot be formally formulated and his results are numerical, not analytic.

The rest of this paper is organized as follows. In Section 2, we study the single population growth and extinction. We establish the global stability of a steady state. In Section 3, we study the competition of two populations. It is determined when neither, one or both competing populations survive.

2. Population dynamics of single species

Consider the following internal storage model of one species consuming one nutrient:

$$\begin{aligned} S_t &= dS_{xx} - f\left(S, \frac{U}{u}\right)u, \\ u_t &= du_{xx} + \mu\left(\frac{U}{u}\right)u, \quad x \in (0,1),\ t > 0, \\ U_t &= dU_{xx} + f\left(S, \frac{U}{u}\right)u, \end{aligned} \tag{2.1}$$

with boundary conditions

$$\begin{aligned} S_x(0,t) &= -S^{(0)}, \qquad S_x(1,t) + \gamma S(1,t) = 0, \\ u_x(0,t) &= 0, \qquad u_x(1,t) + \gamma u(1,t) = 0, \\ U_x(0,t) &= 0, \qquad U_x(1,t) + \gamma U(1,t) = 0, \end{aligned} \tag{2.2}$$

and initial conditions

$$\begin{aligned} &S(x,0) = S^0(x) \geqslant 0, \\ &u(x,0) = u^0(x) \geqslant 0, \qquad u^0(x) \not\equiv 0, \\ &U(x,0) = U^0(x) \geqslant 0, \qquad U^0(x) \not\equiv 0, \\ &\frac{U^0(x)}{u^0(x)} \geqslant Q_{\min}, \end{aligned} \tag{2.3}$$

where the functions $\mu(Q)$ and $f(S,Q)$ satisfy (H_1) and (H_2), respectively.

Introducing the new variable

$$\Theta(x,t) = S + U \tag{2.4}$$

into (2.1)–(2.3), one shall have the following relation:

$$\begin{aligned} &\Theta_t = d\Theta_{xx}, \quad x \in (0,1),\ t > 0, \\ &\Theta_x(0,t) = -S^{(0)}, \qquad \Theta_x(1,t) + \gamma\Theta(1,t) = 0. \end{aligned} \tag{2.5}$$

Thus $\Theta(x,t)$ satisfies $\lim_{t\to\infty}\Theta(x,t)=z(x)$ uniformly in $x\in[0,1]$, where $z(x)=S^{(0)}(\frac{1+\gamma}{\gamma}-x)$. Then one can use the standard argument as in [12,16,22] to conclude that the limiting system of (2.1)–(2.3) is as follows:

$$\begin{aligned} u_t &= du_{xx}+\mu\left(\frac{U}{u}\right)u,\\ U_t &= dU_{xx}+f\left(z(x)-U,\frac{U}{u}\right)u, \end{aligned} \tag{2.6}$$

in $(0,1)\times(0,\infty)$, with boundary conditions

$$\begin{aligned} u_x(0,t)&=0, \qquad u_x(1,t)+\gamma u(1,t)=0,\\ U_x(0,t)&=0, \qquad U_x(1,t)+\gamma U(1,t)=0, \end{aligned} \tag{2.7}$$

and initial conditions

$$\begin{aligned} u(x,0)&=u^0(x)\geqslant 0, \qquad u^0(x)\not\equiv 0,\\ U(x,0)&=U^0(x)\geqslant 0, \qquad U^0(x)\not\equiv 0. \end{aligned} \tag{2.8}$$

From the biological view of point, the feasible domain for initial value functions corresponding to (2.6)–(2.8) should be

$$\Delta=\left\{\left(u^0,U^0\right)\in\left(C\left([0,1]\right)\right)^2 \,\middle|\, u^0(x)>0,\ 0<U^0(x)\leqslant z(x),\ \frac{U^0(x)}{u^0(x)}\geqslant Q_{\min}\text{ on }[0,1]\right\}.$$

In the following subsection, we first determine the dynamics of the limiting system (2.6)–(2.8). Then we will lift the results for the limiting system dynamics to the dynamics of the original system (2.1)–(2.3).

2.1. Positive invariance on feasible domain

It is not difficult to check by definition that Δ is convex. In order to prove the positive invariance of the set Δ under the semi-flow Φ_t generated by (2.6)–(2.8), we need to extend the functions $f(S,Q)$, $\mu(Q)$ in a natural way as follows

$$F(S,Q)=\begin{cases} f(S,Q) & \text{for } S\geqslant 0,\ Q\geqslant Q_{\min},\\ -f(|S|,Q) & \text{for } S<0,\ Q\geqslant Q_{\min},\\ f(S,Q_{\min}) & \text{for } S>0,\ Q<Q_{\min},\\ -f(|S|,Q_{\min}) & \text{for } S<0,\ Q<Q_{\min}, \end{cases} \tag{2.9}$$

and

$$\tilde{\mu}(Q)=\begin{cases} \mu(Q) & \text{for } Q\geqslant Q_{\min},\\ \mu'(Q_{\min})(Q-Q_{\min}) & \text{for } Q<Q_{\min}. \end{cases} \tag{2.10}$$

It is easy to see that $\tilde{\mu}'(Q)>0$ for all Q and $F(S,Q)$ is increasing with respect to S. Hence,

$$\tilde{\mu}(Q)=G(Q)(Q-Q_{\min}), \quad \text{where } G(Q)=\int_0^1 \tilde{\mu}'\left(\tau Q+(1-\tau)Q_{\min}\right)d\tau>0. \tag{2.11}$$

Introducing

$$W = U - Q_{\min} u,$$

we get that

$$\tilde{\mu}\left(\frac{U}{u}\right) = G\left(\frac{U}{u}\right)\frac{W}{u}.$$

Now, we consider the extended system corresponding to (2.6)–(2.8)

$$\begin{aligned} u_t &= du_{xx} + \tilde{\mu}\left(\frac{U}{u}\right)u, \\ U_t &= dU_{xx} + F\left(z(x) - U, \frac{U}{u}\right)u, \end{aligned} \tag{2.12}$$

in $(0,1) \times (0,\infty)$, with boundary conditions (2.7) and initial conditions (2.8).

Without causing confusion, we drop the notation tilde in the following. Furthermore, we introduce

$$Y = z(x) - U.$$

The following lemma shows that the system (2.6)–(2.8) is as in "well-behaved" as one intuits from the biological problem.

Lemma 2.1. *The set Δ is positively invariant under the semi-flow Φ_t generated by* (2.6)–(2.8)*.*

Proof. It suffices to show that the set Δ is positively invariant under the semi-flow Φ_t generated by (2.12). By the theory of semi-linear parabolic differential equations (see [8]), it follows that for every initial value function $(u^0, U^0) \in \Delta$, (2.12) has a unique regular solution $(u(x,t,u^0,U^0), U(x,t,u^0,U^0))$ with the maximal interval of existence $[0, \tau(u^0,U^0))$ and $\tau(u^0,U^0) = \infty$ provided $(u(x,t,u^0,U^0), U(x,t,u^0,U^0))$ has an L^∞-bound on $[0,\tau(u^0,U^0))$. The solution semi-flow is defined by

$$\Phi_t\big(u^0,U^0\big) = \big(u\big(\cdot,t,u^0,U^0\big), U\big(\cdot,t,u^0,U^0\big)\big).$$

Fix any pair of initial value functions (u^0, U^0) in Δ, by the continuity of the solutions with respect to initial value functions, we may assume that $U^0(x) < z(x)$ and $\frac{U^0(x)}{u^0(x)} > Q_{\min}$ on $[0,1]$. Thus $\Phi_t(u^0,U^0) \in \Delta$ for all sufficiently small t.

Suppose that the lemma is false. Let

$$t^* = \sup\big\{\tau \;\big|\; \Phi_t\big(u^0,U^0\big) \in \Delta \text{ on } [0,\tau]\big\}.$$

Then $0 < t^* < \tau(u^0,U^0)$. This implies that one of the following four cases (see Fig. 1) must occur.

(I) $U(x,t) > 0$ for all $0 \leqslant x \leqslant 1$, $0 \leqslant t < t^*$, and $U(x^*,t^*) = 0$ for some x^* in $[0,1]$, and $u(x,t) \geqslant 0$, $W(x,t) \geqslant 0$, $Y(x,t) \geqslant 0$ on $[0,1] \times [0,t^*]$;

(II) $u(x,t) > 0$ for all $0 \leqslant x \leqslant 1$, $0 \leqslant t < t^*$, $u(x^*,t^*) = 0$ for some x^* in $[0,1]$, and $W(x,t) \geqslant 0$, $Y(x,t) \geqslant 0$, $U(x,t) > 0$ on $[0,1] \times [0,t^*]$;

(III) $Y(x,t) > 0$ for all $0 \leqslant x \leqslant 1$, $0 \leqslant t < t^*$, for any $t > t^*$ sufficiently close to t^* there is a point $(\bar{x},\bar{t}) \in [0,1] \times (t^*,t)$ such that $Y(\bar{x},\bar{t}) < 0$, and $W(x,t) \geqslant 0$, $u(x,t) > 0$, $U(x,t) > 0$ on $[0,1] \times [0,t^*]$;

(IV) $W(x,t) > 0$ for all $0 \leqslant x \leqslant 1$, $0 \leqslant t < t^*$, for any $t > t^*$ sufficiently close to t^* there is a point $(\bar{x},\bar{t}) \in [0,1] \times (t^*,t)$ such that $W(\bar{x},\bar{t}) < 0$, and $Y(x,t) > 0$, $u(x,t) > 0$, $U(x,t) > 0$ on $[0,1] \times [0,t^*]$.

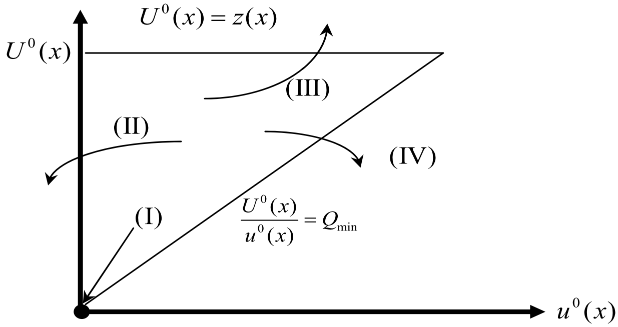

Fig. 1. One of four cases must occur if Δ is not positively invariant under Φ_t.

Let $\Omega_t = (0,1)\times(0,t]$. In each case, we shall deduce a contradiction as follows.

Suppose that the case I occurs. Then

$$Y(x,t) = z(x) - U(x,t) \geqslant 0 \quad \text{in } \bar{\Omega}_{t^*},$$

$$dU_{xx} - U_t = -F\left(z(x) - U(x,t), \frac{U}{u}\right)u(x,t) = -F\left(Y(x,t), \frac{U(x,t)}{u(x,t)}\right)u(x,t) \leqslant 0 \quad \text{on } \Omega_{t^*}$$

by the assumptions of the case I, and $U(x,t) \geqslant 0$ on $\bar{\Omega}_{t^*}$, $U(x^*,t^*) = 0$. Applying the strong maximum principle (see [17, pp. 168–169, Theorem 2]), we obtain that $U(x,t) \equiv 0$ on $\bar{\Omega}_{t^*}$ if $0 < x^* < 1$, which is impossible because $U(x,0) = U^0(x) > 0$ on $[0,1]$. Thus $x^* = 0$ or 1. Assume that $x^* = 0$. Then by [17, p. 170, Theorem 3], $U_x(0,t^*) > 0$, contradicting the boundary condition. Assume $x^* = 1$, that is, $U(1,t^*) = 0$. Then $U_x(1,t^*) < 0$ by the same theorem in [17]. However, from the boundary condition $U_x(1,t^*) + \gamma U(1,t^*) = 0$, we deduce that $U_x(1,t^*) = 0$, a contradiction. Case II can be treated analogously.

Suppose case III occurs. Then

$$dY_{xx} - Y_t = -dU_{xx} + U_t = F\left(Y(x,t), \frac{U(x,t)}{u(x,t)}\right)u(x,t) = u\left[\int_0^1 \frac{\partial F}{\partial S}\left(\tau Y, \frac{U}{u}\right)d\tau\right]Y \quad \text{on } \Omega_{\bar{t}}.$$

Let $h(x,t) \triangleq u\int_0^1 \frac{\partial F}{\partial S}(\tau Y, \frac{U}{u})\,d\tau$. Then $h(x,t) \geqslant 0$ on $\Omega_{\bar{t}}$ and $Y(x,t)$ satisfies

$$dY_{xx} - Y_t - h(x,t)Y = 0 \quad \text{on } \Omega_{\bar{t}}.$$

Suppose that $Y(x,t)$ get the minimum at the point $\tilde{P} = (\tilde{x},\tilde{t})$ on $\bar{\Omega}_{\bar{t}}$. By assumption, $Y(\tilde{P}) \leqslant Y(\bar{x},\bar{t}) < 0$. The maximal principle in [17, p. 172, Theorem 4] implies that $Y(x,t) \equiv Y(\tilde{P})$ for $t \leqslant \tilde{t}$ in the case $0 < \tilde{x} < 1$, which contradicts to the boundary condition with respect to U at $x = 0$. If $\tilde{x} = 0$, then $Y_x(0,\tilde{t}) = -S^{(0)} - U_x(0,\tilde{t}) = -S^{(0)}$ by the boundary condition. Therefore, $Y(x,\tilde{t})$ is strictly decreasing as $0 < x \ll 1$, contradicting that Y attains a minimum at $(0,\tilde{t})$. Assume that $\tilde{x} = 1$. Then $Y_x(1,\tilde{t}) = -S^{(0)} - U_x(1,\tilde{t}) = -S^{(0)} + \gamma U(1,\tilde{t}) \leqslant 0$. But $0 > Y(1,\tilde{t}) = \frac{S^{(0)}}{\gamma} - U(1,\tilde{t})$, equivalently, $-S^{(0)} + \gamma U(1,\tilde{t}) > 0$, a contradiction.

Finally, we consider case IV. From the assumptions of the case IV, we may assume that $Y(x,t) > 0$ on $[0,1]\times[0,t^*+\epsilon]$ with $\epsilon > 0$ sufficiently small. We fix $t^* < t < t^* + \epsilon$. By calculation,

$$dW_{xx} - W_t - Q_{\min}G\left(\frac{U}{u}\right)W = -F\left(Y(x,t), \frac{U(x,t)}{u(x,t)}\right)u(x,t) \leqslant 0 \quad \text{on } \Omega_{\bar{t}}$$

with the boundary conditions

$$W_x(0,t)=0, \qquad W_x(1,t)+\gamma W(1,t)=0.$$

The assumptions for case IV imply that $W(x,t)$ attains a negative minimum at a point $\tilde{P}=(\tilde{x},\tilde{t})$ on $\bar{\Omega}_{\tilde{t}}$. Due to $h=-Q_{\min}G(\frac{U}{u})<0$ by assumptions in case IV, a maximum principle in [17, p. 174, Theorem 7] is applied to this case to conclude that

$$W(x,t)\equiv W(\tilde{P})<0 \quad \text{on } \bar{\Omega}_{\tilde{t}}$$

if $0<\tilde{x}<1$. This contradicts to that

$$W(x,0)=U^0(x)-Q_{\min}u^0(x)>0 \quad \text{on } [0,1].$$

If $\tilde{x}=0$, then we have $W_x(0,\tilde{t})>0$, contradicting to boundary condition $W_x(0,t)=0$. If $\tilde{x}=1$, then $W_x(1,\tilde{t})<0$. From the boundary condition for W,

$$W_x(1,\tilde{t})=-\gamma W(1,\tilde{t})>0,$$

we obtain a contradiction. Thus, we complete the proof of Lemma 2.1. □

From now on, we restrict our attention on the system (2.6)–(2.8) whose initial value functions lie on Δ. It is easy to see that system (2.6)–(2.8) is monotone. Then its solutions generate a monotone semi-flow Φ_t in the interior of Δ. Furthermore, such a semi-flow is strongly monotone.

2.2. *Steady states of single species population*

We focus on the nonnegative steady states to the following elliptic system corresponding to (2.6)–(2.8):

$$\begin{aligned} &du''+\mu\left(\frac{U}{u}\right)u=0,\\ &dU''+f\left(z(x)-U,\frac{U}{u}\right)u=0, \end{aligned} \tag{2.13}$$

in $(0,1)$, with boundary conditions

$$\begin{aligned} &u'(0)=u'(1)+\gamma u(1)=0,\\ &U'(0)=U'(1)+\gamma U(1)=0. \end{aligned} \tag{2.14}$$

Recall in the proof of Lemma 2.1, we assume that all initial value functions are in the feasible domain Δ. However we cannot assert that all nonnegative steady states of (2.6)–(2.8) lie in Δ. Thus it is necessary to show that all nonnegative steady states of (2.6)–(2.8) are in Δ. The next a priori estimates give the proof.

Lemma 2.2. *Suppose (u,U) is a nonnegative solution of* (2.13)–(2.14) *with $u\not\equiv 0$ and $U\not\equiv 0$. Then*

(1) $u>0$, $0<U<z$ *on* $[0,1]$;
(2) $U>uQ_{\min}$ *on* $[0,1]$.

Proof. Firstly, we prove the positivity for U and u. Since (u, U) is a nonnegative solution of (2.13)–(2.14), one has that $c(x) := \mu(\frac{U}{u})$ is well defined for all $x \in (0,1)$. We can rewrite $c(x) = c^+(x) - c^-(x)$, where $c^+(x)$, $c^-(x)$ are the positive part and negative part of $c(x)$. Hence, the first equation of (2.13) becomes

$$du'' - c^-(x)u = -c^+(x)u \leqslant 0 \quad \text{for all } x \in (0,1).$$

Suppose that $u(x_0) = 0$, for some $x_0 \in [0,1]$. If $x_0 \in (0,1)$, by the strong maximum principle, one has that $u \equiv 0$, a contradiction. If $x_0 = 0$, by the Hopf boundary lemma, one has $u'(0) > 0$, this is a contradiction. Similarly, $x_0 = 1$ is impossible. Thus, $u > 0$ on $[0,1]$.

We claim that $U < z$ on $[0,1]$. Let $y(x) = z(x) - U(x)$. Then y satisfies

$$dy'' - u\left[\int_0^1 \frac{\partial F}{\partial S}\left(\tau y, \frac{U}{u}\right) d\tau\right] y = 0, \quad x \in (0,1), \qquad y'(0) = -S^{(0)}, \qquad y'(1) + \gamma y(1) = 0.$$

Suppose y attains a minimum $y(\hat{x}) \leqslant 0$ at some point $\hat{x} \in [0,1]$. If $\hat{x} \in (0,1)$, then by the strong maximum principle (see [17, p. 64, Theorem 6]), one has that $y \equiv y(\hat{x})$, a contradiction to its boundary condition at $x = 0$. If $\hat{x} = 0$, by the Hopf boundary lemma, one has $y'(0) > 0$, this is a contradiction. Similarly, $\hat{x} = 1$ is impossible. Hence, $U < z$ on $[0,1]$. Similarly, $U > 0$ on $[0,1]$.

Now we are in a position to show that $U > uQ_{\min}$ on $[0,1]$. Let $w(x) = U - uQ_{\min}$. Then w satisfies

$$\begin{aligned} dw'' - Q_{\min} G\left(\frac{U}{u}\right) w = -f\left(z - U, \frac{U}{u}\right) u \leqslant 0 \quad \text{on } (0,1), \\ w'(0) = 0, \qquad w'(1) + \gamma w(1) = 0. \end{aligned} \tag{2.15}$$

Suppose $\inf_{0 \leqslant x \leqslant 1} w(x) = w(x_0) \leqslant 0$, for some $x_0 \in [0,1]$. If $x_0 \in (0,1)$, then one has $w(x) \equiv w(x_0)$ by the same maximal principle as before. It follows from the boundary condition with respect to w at $x = 1$ that $w(x) \equiv 0$. Thus $U = Q_{\min} u$. From the first equation of (2.13) and (H_1), it follows that $u'' \equiv 0$. Together with its boundary condition, we conclude that $u \equiv 0$, a contradiction to the assumption for $u \not\equiv 0$. If $x_0 = 0$, then the Hopf boundary lemma implies that $w'(0) > 0$, contradicting to $w'(0) = 0$. Similarly, $x_0 = 1$ is impossible. Hence, $U > uQ_{\min}$ on $[0,1]$. This completes the proof. □

Let $\eta_0 > 0$ be the principal eigenvalue of the problem

$$\begin{aligned} d\phi_1''(x) + \eta_0 \phi_1(x) = 0, \quad x \in (0,1), \\ \phi_1'(0) = \phi_1'(1) + \gamma \phi_1(1) = 0 \end{aligned} \tag{2.16}$$

with the corresponding positive eigenfunction $\phi_1(x)$ uniquely determined by the normalization $\max_{[0,1]} \phi_1(x) = 1$. Suppose that there exists a unique constant number $Q_c \geqslant Q_{\min}$ satisfying

$$\mu(Q_c) = \eta_0. \tag{2.17}$$

Remark 2.1. When we choose the following functions $\mu(Q) = \mu_\infty(1 - \frac{Q_{\min}}{Q})$, it is easy to see that (2.17) holds provided that the asymptotic growth rate μ_∞ is large enough.

Lemma 2.3. *Let $(\tilde{u}, \tilde{U}) \triangleq (\epsilon \frac{1}{Q_c}\phi_1, \epsilon\phi_1)$. Then $(\tilde{u}, \tilde{U})$ is an upper solution for the system* (2.13)–(2.14) *if $\max_{x\in[0,1]} f(z(x), Q_c) \leqslant \eta_0 Q_c$; and a lower solution if $\min_{x\in[0,1]} f(z(x), Q_c) > \eta_0 Q_c$, where $\epsilon < \min\{\frac{z(x)}{\phi_1(x)} \mid x \in [0,1]\}$ is sufficiently small and $\phi_1(x)$ is defined in* (2.16)*.*

Proof. Obviously, $(\tilde{u}, \tilde{U}) \in \Delta$ satisfies the boundary conditions for the system (2.13)–(2.14). It is not hard to show the following relations:

$$d\tilde{u}'' + \mu\left(\frac{\tilde{U}}{\tilde{u}}\right)\tilde{u} = \frac{\epsilon}{Q_c}\left[d\phi_1''(x) + \mu(Q_c)\phi_1(x)\right] = \frac{\epsilon}{Q_c}\left[d\phi_1''(x) + \eta_0\phi_1(x)\right] = 0$$

and

$$\begin{aligned} d\tilde{U}'' + f\left(z(x) - \tilde{U}, \frac{\tilde{U}}{\tilde{u}}\right)\tilde{u} &= \frac{\epsilon}{Q_c}\left[d\phi_1''(x)Q_c + f\big(z(x) - \epsilon\phi_1(x), Q_c\big)\phi_1\right] \\ &= \frac{\epsilon}{Q_c}\left[-\eta_0 Q_c + f\big(z(x) - \epsilon\phi_1(x), Q_c\big)\right]\phi_1. \end{aligned}$$

Thus

$$d\tilde{U}'' + f\left(z(x) - \tilde{U}, \frac{\tilde{U}}{\tilde{u}}\right)\tilde{u} < \frac{\epsilon}{Q_c}\Big[-\eta_0 Q_c + \max_{x\in[0,1]} f\big(z(x), Q_c\big)\Big]\phi_1 \leqslant 0$$

if $\max_{x\in[0,1]} f(z(x), Q_c) \leqslant \eta_0 Q_c$; and

$$d\tilde{U}'' + f\left(z(x) - \tilde{U}, \frac{\tilde{U}}{\tilde{u}}\right)\tilde{u} = \frac{\epsilon}{Q_c}\left[-\eta_0 Q_c + f\big(z(x) - \epsilon\phi_1(x), Q_c\big)\right]\phi_1 > 0,$$

provided that $\min_{x\in[0,1]} f(z(x), Q_c) > \eta_0 Q_c$ and $\epsilon > 0$ is small enough. The proof is complete. □

2.3. Global stability of the limiting system for single species

In this subsection, the following results concerning the global behavior of (2.6)–(2.8) are proved.

We first introduce some notations which will be used in our proof later. Let $X = (C([0,1]))^2$ and (X, X^+) be an ordered Banach space with positive cone X^+ having nonempty interior $\operatorname{Int} X^+$. Let $a, b \in X$, we define two order intervals as follows: $[[a, b] = \{x \in X \mid a \ll x \leqslant b\}$ (provided that $a \ll b$) and $[a, \infty]] = \{x \in X^+ \mid a \leqslant x\}$.

Theorem 2.1. *The system* (2.6)–(2.8) *has at least one positive steady state in its feasible set Δ. If such a positive steady state exists, then it is globally asymptotically stable in the feasible set Δ, otherwise, the origin is globally attractive. Furthermore,*

(i) *if $\min_{x\in[0,1]} f(z(x), Q_c) > \eta_0 Q_c$, then system* (2.6)–(2.8) *has a unique steady state which is globally asymptotically stable in Δ;*
(ii) *if $\max_{x\in[0,1]} f(z(x), Q_c) \leqslant \eta_0 Q_c$, then there is no steady state in Δ and every solution of the system* (2.6)–(2.8) *with initial conditions in Δ satisfies $(u(\cdot,t), U(\cdot,t)) \to (0,0)$ as $t \to \infty$.*

Proof. Rewrite the system (2.6)–(2.8) in vector form. Let $V = (u, U)$ and

$$G(V) = \left(\mu\left(\frac{U}{u}\right)u, f\left(z(x) - U, \frac{U}{u}\right)u\right).$$

Then (2.6)–(2.8) takes the form

$$V_t = dV_{xx} + G(V), \quad 0 < x < 1,\ t > 0,$$
$$V_x(0,t) = 0, \qquad V_x(1,t) + \gamma V(1,t) = 0.$$

It is easy to verify the following sublinear property of G: for any $0 < \alpha < 1$,

$$G(\alpha V) > \alpha G(V).$$

If $V(x,0) = \alpha P \in \Delta$ then $V(x,t) = \Phi_t(\alpha P)$. Let $Y(x,t) = \alpha \Phi_t(P)$. Then

$$\begin{aligned} Y_t &= \alpha\big[d\big(\Phi_t(P)\big)_{xx} + G\big(\Phi_t(P)\big)\big] \\ &= d\big(\alpha\Phi_t(P)\big)_{xx} + \alpha G\big(\Phi_t(P)\big) \\ &< d\big(\alpha\Phi_t(P)\big)_{xx} + G\big(\alpha\Phi_t(P)\big) \\ &= dY_{xx} + G(Y). \end{aligned}$$

Since Φ_t is strongly monotone in the interior of Δ, from comparison principle, it follows that

$$\alpha\Phi_t(P) = Y(x,t) < V(x,t) = \Phi_t(\alpha P).$$

Hence the system (2.6)–(2.8) is sublinear. Such kind of systems have been studied extensively (see [9,14,19]). Therefore, the solution semi-flow has the property:

$$\Phi_t(\alpha P) > \alpha\Phi_t(P) \quad \text{for } 0 < \alpha < 1 \text{ and } P := \big(u^0, U^0\big) \in \Delta. \tag{2.18}$$

Suppose that $P^* = (u^*, U^*)$ is a positive steady state for the system (2.6)–(2.8), that is, $P^* \gg 0$. Thus $\alpha P^* \in \Delta$ for each $0 < \alpha < 1$. We claim that P^* is globally asymptotically stable. In fact, by (2.18),

$$\Phi_t\big(\alpha P^*\big) > \alpha P^* \quad \text{for } 0 < \alpha < 1 \text{ and } t > 0.$$

Since the solution semi-flow is strongly monotone in the interior of Δ,

$$\Phi_t\big(\alpha P^*\big) \gg \alpha P^* \quad \text{for } 0 < \alpha < 1 \text{ and } t > 0. \tag{2.19}$$

Thus by Convergence Criterion for monotone semi-flow (see [18, p. 3, Theorem 2.1]), $\Phi_t(\alpha P^*)$ converges to a steady state of (2.6)–(2.8) for each $0 < \alpha < 1$.

Similarly, we can prove that

$$\Phi_t\big(\alpha P^*\big) \ll \alpha P^* \quad \text{for } \alpha > 1 \text{ such that } \alpha P^* \in \Delta \text{ and } t > 0. \tag{2.20}$$

Thus $\Phi_t(\alpha P^*)$ converges to a steady state of (2.6)–(2.8) for each $\alpha > 1$. Now we assert that the steady state in Δ is unique. If not, then there exists another positive steady state $Q^* \in \Delta$. It is easy to see that $[[0, P^*] \cap \Delta$ and $[P^*, \infty]] \cap \Delta$ are positively invariant. We may assume that there is a unique number $0 < \beta < 1$ such that βQ^* lies on the boundary of $[[0, P^*] \cap \Delta$. The above equation (2.19) shows that

$$\Phi_t\big(\beta Q^*\big) \gg \beta Q^* \quad \text{for any } t > 0.$$

This contradicts the invariance for $[[0, P^*] \cap \Delta$. Similarly, we may assume that there is a unique number $\beta > 1$ such that βQ^* lies on the boundary of $[P^*, \infty]] \cap \Delta$. The above equation (2.20) shows that

$$\Phi_t\big(\beta Q^*\big) \ll \beta Q^* \quad \text{for any } t > 0.$$

This contradicts the invariance for $[P^*, \infty]] \cap \Delta$. Hence, the steady state P^* is unique.

For a monotone dynamical system, the unique steady state is globally asymptotically stable if and only if every forward orbit has compact closure (see [13, Theorem D]). Thus, if positive steady state exists, then it is globally asymptotically stable in Δ. Suppose that there is no steady state in Δ. Then we claim that every omega set from initial point in Δ is the origin. Let $P \in \Delta$ and $\omega(P)$ be its ω-limit set. Suppose that $\omega(P) \neq \{0\}$. Then since Δ is convex, $\omega(P)$ has the least upper bound $Q \in \Delta$. Then $\Phi_t(\omega(P)) \leqslant \Phi_t(Q)$ for all t and $\omega(P) \leqslant \Phi_t(Q)$ by the invariance of ω-limit set. Thus $Q \leqslant \Phi_t(Q)$. Therefore, by Convergence Criterion (see [18, p. 3, Theorem 2.1]), $\Phi_t(Q)$ converges to a steady state $P^* \gg 0$, contradicting that there is no steady state in Δ.

Suppose that $\min_{x\in[0,1]} f(z(x), Q_c) > \eta_0 Q_c$. Then by Lemma 2.3, the system (2.6)–(2.8) has a lower solution $P(\epsilon) = (\tilde{u}, \tilde{U}) = (\frac{1}{Q_c}\epsilon\phi_1(x), \epsilon\phi_1(x))$ for sufficiently small ϵ. Thus $\Phi_t(P(\epsilon))$ increasingly tends to a (unique) steady state P^* for (2.6)–(2.8).

Suppose that $\max_{x\in[0,1]} f(z(x), Q_c) \leqslant \eta_0 Q_c$. Then by Lemma 2.3, $P(\epsilon) = (\tilde{u}, \tilde{U}) = (\frac{1}{Q_c}\epsilon\phi_1(x), \epsilon\phi_1(x))$ is an upper solution of system (2.6)–(2.8) for ϵ sufficiently small. Thus $\Phi_t(P(\epsilon))$ is decreasing as t increases. It is not difficult to see that $u(\cdot, t, P(\epsilon))$ tends to zero as $t \to \infty$. From the second equation of (2.6)–(2.8), $U(\cdot, t, P(\epsilon))$ also converges to zero. This completes the proof. $\square$

We notice that the origin $(0, 0)$ is a singularity for the system (2.6)–(2.8). But if $\max_{x\in[0,1]} f(z(x), Q_c) \leqslant \eta_0 Q_c$, then all solutions originating from Δ converge to this singularity. Thus we may define that the origin $(0, 0)$ is an equilibrium. In this way, it is convenient to state some results and make an explanation in the sequel. Observing the previous proof, we conclude that the system (2.6)–(2.8) has a unique steady state which is globally asymptotically stable iff there is a lower solution, and the singularity $(0, 0)$ is globally attractive iff there is an upper solution such that it is close to $(0, 0)$ as much as one wishes.

Remark 2.2. Since $z(x) = S^{(0)}(\frac{1+\gamma}{\gamma} - x)$ and $f(S, Q)$ satisfies (H_2), it follows that $\min_{x\in[0,1]} f(z(x), Q_c) = f(z(1), Q_c)$ and $\max_{x\in[0,1]} f(z(x), Q_c) = f(z(0), Q_c)$.

Remark 2.3 *(Biological interpretation for Theorem 2.1).* It is easy to calculate

$$\eta_0 = \eta_0(d, \gamma) = dR^2(\gamma), \qquad \phi_1(x) = \cos\sqrt{\frac{\eta_0}{d}}x \quad \text{on } [0, 1], \tag{2.21}$$

where $R(\gamma)$ is the unique root for the equation

$$\cot u = \frac{1}{\gamma}u \quad \text{on } \left(0, \frac{\pi}{2}\right).$$

It is not hard to see that $\eta_0(d, \gamma)$ is increasing in d and γ respectively and $\eta_0(d, \gamma) \to 0$ as $d \to 0$ or $\gamma \to 0$. From (1.3), we assume $f(S, Q)$ takes the form

$$f\big(z(x), Q\big) = \rho_{\max}\frac{Q_{\max} - Q}{Q_{\max} - Q_{\min}}\frac{z(x)}{k + z(x)}.$$

Since $z(x) = S^{(0)}(\frac{1+\gamma}{\gamma} - x)$, by Remark 2.2, it follows that

$$\min_{x\in[0,1]} f\big(z(x), Q_c\big) = \rho_{\max}\frac{Q_{\max} - Q_c}{Q_{\max} - Q_{\min}}\frac{\frac{S^{(0)}}{\gamma}}{k + \frac{S^{(0)}}{\gamma}}$$

and

$$\max_{x\in[0,1]} f\big(z(x), Q_c\big) = \rho_{\max}\frac{Q_{\max}-Q_c}{Q_{\max}-Q_{\min}}\frac{S^{(0)}\frac{1+\gamma}{\gamma}}{k+S^{(0)}\frac{1+\gamma}{\gamma}}.$$

Theorem 2.1(i) is equivalent to

$$\rho_{\max}\frac{Q_{\max}-Q_c}{Q_{\max}-Q_{\min}}\frac{\frac{S^{(0)}}{\gamma}}{k+\frac{S^{(0)}}{\gamma}} > \eta_0(d,\gamma)Q_c,$$

it means that if the maximal uptake rate $\rho_{\max}$ is larger, the diffusion coefficient d is smaller, the washout constant γ is smaller then the species survives.

Theorem 2.1(ii) is equivalent to

$$\rho_{\max}\frac{Q_{\max}-Q_c}{Q_{\max}-Q_{\min}}\frac{S^{(0)}\frac{1+\gamma}{\gamma}}{k+S^{(0)}\frac{1+\gamma}{\gamma}} \leqslant \eta_0(d,\gamma)Q_c,$$

it means that if the maximal uptake rate $\rho_{\max}$ is smaller, the nutrient flux $S^{(0)}$ is smaller, the half-saturation constant k is larger then the species goes to extinction.

2.4. Dynamics of the full system (2.1)–(2.3)

In this subsection, we present the global dynamics of the full system (2.1)–(2.3).

Theorem 2.2. *The system* (2.1)–(2.3) *has at least one positive steady state in its feasible domain. If such a positive steady state exists, then it is globally asymptotically stable in its feasible domain, otherwise,* $(z(x), 0, 0)$ *is globally attractive. Furthermore,*

(i) *if* $\min_{x\in[0,1]} f(z(x), Q_c) > \eta_0 Q_c$*, then system* (2.1)–(2.3) *has a unique steady state which is globally asymptotically stable in its feasible domain*;
(ii) *if* $\max_{x\in[0,1]} f(z(x), Q_c) \leqslant \eta_0 Q_c$*, then every solution of the system* (2.1)–(2.3) *with initial conditions in its feasible domain satisfies* $(S(\cdot,t), u(\cdot,t), U(\cdot,t)) \to (z(x), 0, 0)$ *as* $t\to\infty$.

Proof. Consider

$$\begin{aligned} u_t &= du_{xx} + \mu\left(\frac{U}{u}\right)u,\\ U_t &= dU_{xx} + f\left(\Theta(x,t) - U, \frac{U}{u}\right)u, \end{aligned} \tag{2.22}$$

in $(0,1)\times(0,\infty)$, with boundary conditions

$$\begin{aligned} &u_x(0,t)=0, \qquad u_x(1,t)+\gamma u(1,t)=0,\\ &U_x(0,t)=0, \qquad U_x(1,t)+\gamma U(1,t)=0, \end{aligned} \tag{2.23}$$

and initial conditions

$$\begin{aligned} &u(x,0)=u^0(x)\geqslant 0, \qquad u^0(x)\not\equiv 0,\\ &U(x,0)=U^0(x)\geqslant 0, \qquad U^0(x)\not\equiv 0,\\ &\frac{U^0(x)}{u^0(x)}\geqslant Q_{\min}, \end{aligned} \tag{2.24}$$

where

$$\Theta(x,t) = S + U, \tag{2.25}$$

and

$$\begin{aligned} &\Theta_t = d\Theta_{xx}, \quad x \in (0,1),\ t > 0, \\ &\Theta_x(0,t) = -S^{(0)}, \qquad \Theta_x(1,t) + \gamma\Theta(1,t) = 0. \end{aligned} \tag{2.26}$$

Thus $\Theta(x,t)$ satisfies $\lim_{t\to\infty}\Theta(x,t) = z(x)$ uniformly in $x \in [0,1]$, where $z(x) = S^{(0)}(\frac{1+\gamma}{\gamma} - x)$.

The system (2.22)–(2.24) is asymptotically autonomous (see [15]) and its limiting system is (2.6)–(2.8). According to Theorem 1.8 in [15], every forward limit set for an asymptotically autonomous system is a chain recurrent set for its limiting system. However, from Theorem 2.1, we know that any chain recurrent set for the limiting system (2.6)–(2.8) is either a positive steady state, or the origin. Thus every solution of (2.22)–(2.24) is convergent. From the relation (2.25) and Theorem 2.1, Theorem 2.2 follows immediately. □

We note that one can also use Lemma 2.1′ in [11] to lift the dynamics of the limiting system (2.6)–(2.8) to the full system (2.1)–(2.3).

Remark 2.4. Due to the singularity produced in $\frac{U}{u}$ with $U = 0$ and $u = 0$, we are unable to do the bifurcation analysis from the extinction to the survival for the single species.

3. The competition model

Now we consider our model equations (1.9) with boundary conditions (1.10) and initial conditions (1.11). Introduce the new variable

$$\tilde{\Theta}(x,t) = S + U + V \tag{3.1}$$

in (1.9) yields $\lim_{t\to\infty}[\tilde{\Theta}(x,t) - z(x)] = 0$ uniformly in $x \in [0,1]$, where $z(x) = S^{(0)}(\frac{1+\gamma}{\gamma} - x)$. Thus we obtain the limiting system of (1.9)–(1.11) as follows:

$$\begin{aligned} u_t &= du_{xx} + \mu_1\left(\frac{U}{u}\right)u, \\ U_t &= dU_{xx} + f_1\left(z(x) - U - V, \frac{U}{u}\right)u, \\ v_t &= dv_{xx} + \mu_2\left(\frac{V}{v}\right)v, \\ V_t &= dV_{xx} + f_2\left(z(x) - U - V, \frac{V}{v}\right)v, \end{aligned} \tag{3.2}$$

in $(0,1)\times(0,\infty)$, with boundary conditions

$$\begin{aligned} u_x(0,t) &= 0, \qquad u_x(1,t) + \gamma u(1,t) = 0, \\ U_x(0,t) &= 0, \qquad U_x(1,t) + \gamma U(1,t) = 0, \\ v_x(0,t) &= 0, \qquad v_x(1,t) + \gamma v(1,t) = 0, \end{aligned}$$

$$V_x(0,t)=0, \qquad V_x(1,t)+\gamma V(1,t)=0, \tag{3.3}$$

and initial conditions

$$\begin{aligned} u(x,0)&=u^0(x)\geqslant 0, \qquad u^0(x)\not\equiv 0,\\ U(x,0)&=U^0(x)\geqslant 0, \qquad U^0(x)\not\equiv 0,\\ v(x,0)&=v^0(x)\geqslant 0, \qquad v^0(x)\not\equiv 0,\\ V(x,0)&=V^0(x)\geqslant 0, \qquad V^0(x)\not\equiv 0. \end{aligned} \tag{3.4}$$

From the biological viewpoint, the feasible domain for initial value functions should be

$$\Sigma=\Bigg\{\big(u^0,U^0,v^0,V^0\big)\in\big(C\big([0,1]\big)\big)^4 \;\Big|\; u^0(x)>0,\ U^0(x)>0,\ v^0(x)>0,\ V^0(x)>0,$$
$$U^0(x)+V^0(x)\leqslant z(x),\ \frac{U^0(x)}{u^0(x)}\geqslant Q_{\min,1},\ \frac{V^0(x)}{v^0(x)}\geqslant Q_{\min,2} \text{ on } [0,1]\Bigg\}.$$

In the following subsection, we first determine the dynamics of the limiting system (3.2)–(3.4). Then we will use the similar arguments in Section 2 to lift the results for the limiting system dynamics to the dynamics of the original system (1.9)–(1.11).

3.1. The positive invariance on feasible domain

In order to prove Σ is positively invariant under the semi-flow Ψ_t generated by (3.2)–(3.4), we need to extend the functions involving in (3.2)–(3.4). We extend $f_j(S,Q)$, $\mu_j(Q)$, $j=1,2$, in a natural way as follows

$$F_j(S,Q)=\begin{cases} f_j(S,Q) & \text{for } S\geqslant 0,\ Q\geqslant Q_{\min,j},\\ -f_j(|S|,Q) & \text{for } S<0,\ Q\geqslant Q_{\min,j},\\ f_j(S,Q_{\min,j}) & \text{for } S>0,\ Q<Q_{\min,j},\\ -f_j(|S|,Q_{\min,j}) & \text{for } S<0,\ Q<Q_{\min,j} \end{cases} \tag{3.5}$$

and

$$\tilde{\mu}_j(Q)=\begin{cases} \mu_j(Q) & \text{for } Q\geqslant Q_{\min,j},\\ \mu_j'(Q_{\min,j})(Q-Q_{\min,j}) & \text{for } Q<Q_{\min,j}. \end{cases} \tag{3.6}$$

Hence,

$$\tilde{\mu}_j(Q)=G_j(Q)(Q-Q_{\min,j}), \quad \text{where } G_j(Q)=\int_0^1 \tilde{\mu}_j'\big(\tau Q+(1-\tau)Q_{\min,j}\big)\,d\tau>0. \tag{3.7}$$

Introducing

$$W_1=U-Q_{\min,1}u, \qquad W_2=V-Q_{\min,2}v,$$

we get that

$$\tilde{\mu}_1\left(\frac{U}{u}\right) = G_1\left(\frac{U}{u}\right)\frac{W_1}{u}, \qquad \tilde{\mu}_2\left(\frac{V}{v}\right) = G_2\left(\frac{V}{v}\right)\frac{W_2}{v}.$$

Now, we consider the extended system

$$\begin{aligned} u_t &= du_{xx} + \tilde{\mu}_1\left(\frac{U}{u}\right)u, \\ U_t &= dU_{xx} + F_1\left(z(x) - U - V, \frac{U}{u}\right)u, \\ v_t &= dv_{xx} + \tilde{\mu}_2\left(\frac{V}{v}\right)v, \\ V_t &= dV_{xx} + F_2\left(z(x) - U - V, \frac{V}{v}\right)v, \end{aligned} \tag{3.8}$$

in $(0,1)\times(0,\infty)$, with the usual boundary conditions (3.3) and initial conditions (3.4).

Without causing confusion, we drop the notation tilde in the following. Furthermore, we introduce

$$Y = z(x) - U - V.$$

Lemma 3.1. *Σ is positively invariant under the semi-flow Ψ_t generated by the system* (3.2)–(3.4).

Proof. It suffices to show that the set Σ is positively invariant under the semi-flow Ψ_t generated by (3.8). By the theory of semi-linear parabolic differential equations (see [8]), it follows that for every initial data $P_0 = (u^0, U^0, v^0, V^0) \in \Sigma$, the system (3.8) has a unique regular solution

$$\big(u(x,t,P_0), U(x,t,P_0), v(x,t,P_0), V(x,t,P_0)\big)$$

with the maximal interval of existence $[0, \tau(P_0))$ and $\tau(P_0) = \infty$ provided

$$\big(u(x,t,P_0), U(x,t,P_0), v(x,t,P_0), V(x,t,P_0)\big)$$

has an L^∞-bound on $[0, \tau(P_0))$. The solution semi-flow is defined by

$$\Psi_t(P_0) = \big(u(\cdot,t,P_0), U(\cdot,t,P_0), v(\cdot,t,P_0), V(\cdot,t,P_0)\big).$$

Fix any initial data $P_0 = (u^0, U^0, v^0, V^0)$ in Σ. From the continuity of the solutions with respect to initial data, we may assume that $U^0(x) + V^0(x) < z(x)$, $\frac{U^0(x)}{u^0(x)} > Q_{\min,1}$ and $\frac{V^0(x)}{v^0(x)} > Q_{\min,2}$ for $0 \leqslant x \leqslant 1$. Thus $\Psi_t(u^0, U^0, v^0, V^0) \in \Sigma$ for all sufficiently small t.

Suppose that the lemma is false. Let

$$t^* = \sup\big\{\tau \;\big|\; \Psi_t\big(u^0, U^0, v^0, V^0\big) \in \Sigma \text{ on } [0,\tau]\big\}.$$

Then $0 < t^* < \tau(u^0, U^0, v^0, V^0)$. This implies that one of the following seven cases must occur.

(I) $U(x,t) > 0$ for all $0 \leqslant x \leqslant 1$, $0 \leqslant t < t^*$ with $U(x^*, t^*) = 0$ for some x^* in $[0,1]$, and $u(x,t) \geqslant 0$, $V(x,t) \geqslant 0$, $v(x,t) \geqslant 0$, $Y(x,t) \geqslant 0$, $W_1(x,t) \geqslant 0$, $W_2(x,t) \geqslant 0$ on $[0,1]\times[0,t^*]$;

(II) $u(x,t) > 0$ for all $0 \leqslant x \leqslant 1$, $0 \leqslant t < t^*$, $u(x^*, t^*) = 0$ for some x^* in $[0,1]$, and $U(x,t) > 0$, $V(x,t) \geqslant 0$, $v(x,t) \geqslant 0$, $Y(x,t) \geqslant 0$, $W_1(x,t) \geqslant 0$, $W_2(x,t) \geqslant 0$ on $[0,1]\times[0,t^*]$;

(III) $V(x,t) > 0$ for all $0 \leqslant x \leqslant 1$, $0 \leqslant t < t^*$, and $V(x^*, t^*) = 0$ for some x^* in $[0,1]$, and $U(x,t) > 0$, $u(x,t) > 0$, $v(x,t) \geqslant 0$, $Y(x,t) \geqslant 0$, $W_1(x,t) \geqslant 0$, $W_2(x,t) \geqslant 0$ on $[0,1] \times [0,t^*]$;

(IV) $v(x,t) > 0$ for all $0 \leqslant x \leqslant 1$, $0 \leqslant t < t^*$, $v(x^*, t^*) = 0$ for some x^* in $[0,1]$, and $U(x,t) > 0$, $u(x,t) > 0$, $V(x,t) > 0$, $Y(x,t) \geqslant 0$, $W_1(x,t) \geqslant 0$, $W_2(x,t) \geqslant 0$ on $[0,1] \times [0,t^*]$;

(V) $Y(x,t) > 0$ for all $0 \leqslant x \leqslant 1$, $0 \leqslant t < t^*$, for any $t > t^*$ sufficiently close to t^* there is a point $(\bar{x}, \bar{t}) \in [0,1] \times (t^*, t)$ such that $Y(\bar{x}, \bar{t}) < 0$, and $U(x,t) > 0$, $u(x,t) > 0$, $V(x,t) > 0$, $v(x,t) > 0$, $W_1(x,t) \geqslant 0$, $W_2(x,t) \geqslant 0$ on $[0,1] \times [0,t^*]$;

(VI) $W_1(x,t) > 0$ for all $0 \leqslant x \leqslant 1$, $0 \leqslant t < t^*$, for any $t > t^*$ sufficiently close to t^* there is a point $(\bar{x}, \bar{t}) \in [0,1] \times (t^*, t)$ such that $W_1(\bar{x}, \bar{t}) < 0$, and $U(x,t) > 0$, $u(x,t) > 0$, $V(x,t) > 0$, $v(x,t) > 0$, $Y(x,t) > 0$, $W_2(x,t) \geqslant 0$ on $[0,1] \times [0,t^*]$;

(VII) $W_2(x,t) > 0$ for all $0 \leqslant x \leqslant 1$, $0 \leqslant t < t^*$, for any $t > t^*$ sufficiently close to t^* there is a point $(\bar{x}, \bar{t}) \in [0,1] \times (t^*, t)$ such that $W_2(\bar{x}, \bar{t}) < 0$, and $U(x,t) > 0$, $u(x,t) > 0$, $V(x,t) > 0$, $v(x,t) > 0$, $Y(x,t) > 0$, $W_1(x,t) > 0$ on $[0,1] \times [0,t^*]$.

Let $\Omega_t = (0,1) \times (0,t]$. In each case, we shall deduce a contradiction as follows.

Suppose that the case I occurs. Then

$$Y(x,t) = z(x) - U(x,t) - V(x,t) \geqslant 0 \quad \text{in } \bar{\Omega}_{t^*},$$

and

$$\begin{aligned} dU_{xx} - U_t &= -F_1\left(z(x) - U(x,t) - V(x,t), \frac{U}{u}\right)u(x,t) \\ &= -F_1\left(Y(x,t), \frac{U(x,t)}{u(x,t)}\right)u(x,t) \leqslant 0 \quad \text{on } \Omega_{t^*}. \end{aligned}$$

If $0 < x^* < 1$, then from the strong maximum principle (see [17, pp. 168–169, Theorem 2]), we obtain that $U(x,t) \equiv 0$ on $\bar{\Omega}_{t^*}$ which is impossible because $U(x,0) = U^0(x) > 0$ on $[0,1]$. Thus $x^* = 0$ or 1. If $x^* = 0$, then $U_x(0,t^*) > 0$ by [17, p. 170, Theorem 3], contradicting to the boundary condition (3.3). If $x^* = 1$, that is, $U(1,t^*) = 0$, then $U_x(1,t^*) < 0$ by the same theorem in [17]. However, from the boundary condition $U_x(1,t^*) + \gamma U(1,t^*) = 0$, we deduce that $U_x(1,t^*) = 0$, a contradiction. Cases II, III, IV can be treated analogously.

Suppose case V occurs. Then

$$\begin{aligned} dY_{xx} - Y_t &= (-dU_{xx} + U_t) + (-dV_{xx} + V_t) \\ &= F_1\left(Y(x,t), \frac{U(x,t)}{u(x,t)}\right)u(x,t) + F_2\left(Y(x,t), \frac{V(x,t)}{v(x,t)}\right)v(x,t) \quad \text{on } \Omega_{\bar{t}}. \end{aligned}$$

Denote

$$h(x,t) = u\int_0^1 \frac{\partial F_1}{\partial S}\left(\tau Y, \frac{U}{u}\right)d\tau + v\int_0^1 \frac{\partial F_2}{\partial S}\left(\tau Y, \frac{V}{v}\right)d\tau.$$

Then $h(x,t) \geqslant 0$ and $Y(x,t)$ satisfies that

$$dY_{xx} - Y_t - h(x,t)Y = 0 \quad \text{on } \Omega_{\bar{t}}.$$

Let $Y(x,t)$ get the minimum at the point $\tilde{P} = (\tilde{x}, \tilde{t})$ on $\bar{\Omega}_{\bar{t}}$. By assumption, $Y(\tilde{P}) \leqslant Y(\bar{x}, \bar{t}) < 0$. The maximal principle implies that $Y(x,t) \equiv \text{const}$ for $t \leqslant \tilde{t}$ if $\tilde{x} \in (0,1)$, contradicting to the boundary conditions (3.3). If $\tilde{x} = 0$, then $Y_x(0,\tilde{t}) = -S^{(0)} - U_x(0,\tilde{t}) - V_x(0,\tilde{t}) = -S^{(0)} < 0$, which implies that

$Y(x,0)$ is decreasing in a neighborhood of $x=0$, contradicting the minimality for Y to attain at $(0,\tilde{t})$. If $\tilde{x}=1$, then $Y_x(1,\tilde{t})=-S^{(0)}-U_x(1,\tilde{t})-V_x(1,\tilde{t})=-S^{(0)}+\gamma U(1,\tilde{t})+\gamma V(1,\tilde{t})\leqslant 0$. But $0>Y(1,\tilde{t})=\frac{S^{(0)}}{\gamma}-U(1,\tilde{t})-V(1,\tilde{t})$, equivalently, $-S^{(0)}+\gamma U(1,\tilde{t})+\gamma V(1,\tilde{t})>0$, a contradiction to the above inequality.

We consider case VI. From the assumptions of case VI, we may assume that $Y(x,t)>0$ on $[0,1]\times[0,t^*+\epsilon]$ with $\epsilon>0$ sufficiently small. We fix $t^*<t<t^*+\epsilon$. By calculation,

$$d(W_1)_{xx}-(W_1)_t-Q_{\min,1}G_1\left(\frac{U}{u}\right)W_1=-F_1\left(Y(x,t),\frac{U(x,t)}{u(x,t)}\right)u(x,t)\leqslant 0\quad\text{on }\Omega_{\bar{t}}$$

with the boundary conditions

$$(W_1)_x(0,t)=0,\qquad (W_1)_x(1,t)+\gamma W_1(1,t)=0.$$

The assumptions for case VI imply that $W_1(x,t)$ attains a negative minimum at a point $\tilde{P}=(\tilde{x},\tilde{t})$ on $\bar{\Omega}_{\tilde{t}}$. If $0<\tilde{x}<1$, then due to $h=-Q_{\min,1}G_1(\frac{U}{u})<0$ by assumptions in case VI, a maximum principle in [17, p. 174, Theorem 7] is applied to this case to conclude that

$$W_1(x,t)\equiv W_1(\tilde{P})<0\quad\text{on }\bar{\Omega}_{\tilde{t}}$$

which leads to a contradiction that

$$W_1(x,0)=U^0(x)-Q_{\min,1}u^0(x)>0\quad\text{on }[0,1].$$

If $\tilde{x}=0$, then again using [17, p. 174, Theorem 7], we have $(W_1)_x(0,\tilde{t})>0$, contradicting to the boundary condition $(W_1)_x(0,t)=0$. If $\tilde{x}=1$, then [17, p. 174, Theorem 7] implies that $(W_1)_x(1,\tilde{t})<0$. But $W_1(1,\tilde{t})<0$, it follows from the boundary condition for W_1 that

$$(W_1)_x(1,\tilde{t})=-\gamma W_1(1,\tilde{t})>0,$$

a contradiction. The case VII can be treated analogously. Thus we complete the proof of Lemma 3.1. $\square$

From now on, we restrict our attention to the system (3.2)–(3.4) with initial conditions in the feasible set Σ. The Jacobian of reaction terms in (3.2) with respect to (u,U,v,V) at points $(u,U,v,V)\in\Sigma$, has the form

$$J=\begin{pmatrix} * & + & 0 & 0\\ a_{21} & * & 0 & -\\ 0 & 0 & * & +\\ 0 & - & a_{43} & * \end{pmatrix},$$

where

$$a_{21}=f_1\left(z(x)-U-V,\frac{U}{u}\right)-\frac{U}{u}\frac{\partial f_1}{\partial Q_1}\left(z(x)-U-V,\frac{U}{u}\right)\geqq f_1\left(z(x)-U-V,\frac{U}{u}\right)\geqq 0,$$
$$a_{43}=f_2\left(z(x)-U-V,\frac{V}{v}\right)-\frac{V}{v}\frac{\partial f_2}{\partial Q_2}\left(z(x)-U-V,\frac{V}{v}\right)\geqq f_2\left(z(x)-U-V,\frac{V}{v}\right)\geqq 0.$$

Obviously, J has the block structure characteristic of type K monotone system [18], consisting of diagonal 2×2 blocks with nonnegative off-diagonal entries and off-diagonal 2×2 non-positive blocks, where $K = \{(u^0, U^0, v^0, V^0) \in (C([0,1]))^4 \mid u^0 \geqslant 0,\ U^0 \geqslant 0;\ v^0 \leqslant 0,\ V^0 \leqslant 0\}$. Thus, the semi-flow generated by the system (3.2)–(3.4) is monotone [18] under the partial order $\leqslant_K$. Furthermore, if

$$U + V < z(x) \quad \text{for } x \in [0,1],$$

then J is irreducible, which implies that such a semi-flow is strongly monotone in the interior of Σ. However, we can go beyond this.

Lemma 3.2. *Σ is convex, and $\Psi_t : \Sigma \to \Sigma$ is strongly monotone in the K-order.*

Proof. From the above discussion, it suffices to show that for any initial data $P = (u^0, U^0, v^0, V^0) \in \Sigma$ with $U^0(x_0) + V^0(x_0) = z(x_0)$ for some $x_0 \in [0,1]$, we have

$$U(x,t,P) + V(x,t,P) < z(x) \quad \text{for any } x \in [0,1].$$

If not, then there are a $\bar{t} > 0$ and $\bar{x} \in [0,1]$ such that

$$U(\bar{x}, \bar{t}, P) + V(\bar{x}, \bar{t}, P) = z(\bar{x}).$$

Let $Y(x,t) = z(x) - U(x,t,P) - V(x,t,P)$. Then

$$dY_{xx} - Y_t = F_1\left(Y(x,t), \frac{U(x,t)}{u(x,t)}\right)u(x,t) + F_2\left(Y(x,t), \frac{V(x,t)}{v(x,t)}\right)v(x,t) \quad \text{on } \Omega_{\bar{t}}.$$

Denote

$$h(x,t) = u\int_0^1 \frac{\partial F_1}{\partial S}\left(\tau Y, \frac{U}{u}\right)d\tau + v\int_0^1 \frac{\partial F_2}{\partial S}\left(\tau Y, \frac{V}{v}\right)d\tau.$$

Then $h(x,t) \geqslant 0$ and zero is the minimum value for $Y(x,t)$ on $\bar{\Omega}_{\bar{t}}$ at $(\bar{x}, \bar{t})$, and

$$dY_{xx} - Y_t - h(x,t)Y = 0 \quad \text{on } \Omega_{\bar{t}}.$$

Applying maximal principle, we obtain a contradiction. Thus we conclude that $\Psi_t : \Sigma \to \Sigma$ is strongly monotone. □

3.2. Steady states for the system (3.2)–(3.4)

We focus on the nonnegative steady-state solutions to the following elliptic system corresponding to the system (3.2)–(3.4):

$$\begin{aligned}
du_{xx} + \mu_1\left(\frac{U}{u}\right)u &= 0, \\
dU_{xx} + f_1\left(z(x) - U - V, \frac{U}{u}\right)u &= 0, \\
dv_{xx} + \mu_2\left(\frac{V}{v}\right)v &= 0, \\
dV_{xx} + f_2\left(z(x) - U - V, \frac{V}{v}\right)v &= 0,
\end{aligned} \tag{3.9}$$

in $(0,1)$, with boundary conditions

$$\begin{aligned} &u'(0)=u'(1)+\gamma u(1)=0, \qquad U'(0)=U'(1)+\gamma U(1)=0,\\ &v'(0)=v'(1)+\gamma v(1)=0, \qquad V'(0)=V'(1)+\gamma V(1)=0, \end{aligned} \tag{3.10}$$

where $z(x)=S^{(0)}(\frac{1+\gamma}{\gamma}-x)$.

The next lemma gives a priori estimates for positive solution of the system (3.9)–(3.10).

Lemma 3.3. *Let (u,U,v,V) be a nonnegative solution of the system* (3.9)–(3.10) *with $u\not\equiv 0$, $U\not\equiv 0$, $v\not\equiv 0$, and $V\not\equiv 0$. Then*

(1) $u>0$, $U>0$, $v>0$, $V>0$ *on* $[0,1]$;
(2) $U+V<z$;
(3) $U>uQ_{\min,1}$, $V>vQ_{\min,2}$ *on* $[0,1]$.

Proof. The positivity for U, u, V and v and (3) can be proved in a similar way as in Lemma 2.2.

Let $y(x)=z(x)-U(x)-V(x)$ on $[0,1]$. Then y satisfies

$$dy''-\left[u\int_0^1\frac{\partial F_1}{\partial S}\left(\tau y,\frac{U}{u}\right)d\tau+v\int_0^1\frac{\partial F_2}{\partial S}\left(\tau y,\frac{V}{v}\right)d\tau\right]y=0,\quad x\in(0,1),$$

$$y'(0)=-S^{(0)},\qquad y'(1)+\gamma y(1)=0.$$

By assumption, bracket in the above equation is nonnegative. Thus, the rest of the proof is exactly the same as that in Lemma 2.2. □

3.3. The asymptotic behavior for system (3.2)–(3.4)

Now we are ready to state and prove our main results in this section. Suppose that there exists a unique constant number $Q_{c,i}\geqslant Q_{\min,i}$ satisfying

$$\mu_i(Q_{c,i})=\eta_0,\quad i=1,2, \tag{3.11}$$

where η_0 is defined in (2.21).

Remark 3.1. Choose the following functions $\mu_i(Q)=\mu_{i,\infty}(1-\frac{Q_{\min,i}}{Q_i})$, it is easy to see that (3.11) holds provided that the asymptotic growth rate $\mu_{i,\infty}$ is large enough for $i=1,2$.

The following theorem states the conditions for which both of species go to extinction; one species survives and the other goes to extinction.

Theorem 3.1. *The following statements hold*:

(i) *If* $\max_{x\in[0,1]}f_1(z(x),Q_{c,1})\leqslant\eta_0Q_{c,1}$ *and* $\max_{x\in[0,1]}f_2(z(x),Q_{c,2})\leqslant\eta_0Q_{c,2}$, *then every solution* (u,U,v,V) *for system* (3.2)–(3.4) *with initial data in Σ satisfies that* $\lim_{t\to\infty}(u(x,t),U(x,t),v(x,t),V(x,t))=0$ *uniformly in* $x\in[0,1]$.
(ii) *If* $\min_{x\in[0,1]}f_1(z(x),Q_{c,1})>\eta_0Q_{c,1}$ *and* $\max_{x\in[0,1]}f_2(z(x),Q_{c,2})\leqslant\eta_0Q_{c,2}$, *then there is a semi-trivial solution* $(u^*(x),U^*(x),0,0)$ *for system* (3.2)–(3.4) *which is globally attractive in Σ.*

(iii) *If* $\max_{x\in[0,1]} f_1(z(x), Q_{c,1}) \leqslant \eta_0 Q_{c,1}$ *and* $\min_{x\in[0,1]} f_2(z(x), Q_{c,2}) > \eta_0 Q_{c,2}$*, then there is a semi-trivial solution* $(0, 0, v^*(x), V^*(x))$ *for system* (3.2)–(3.4) *which is globally attractive in* Σ*.*

Proof. (i) From (3.2), we have the following inequalities

$$v_t = dv_{xx} + \mu_2\left(\frac{V}{v}\right)v,$$

$$V_t = dV_{xx} + f_2\left(z(x) - U - V, \frac{V}{v}\right)v \leqslant dV_{xx} + f_2\left(z(x) - V, \frac{V}{v}\right)v.$$

By comparison theorem and (ii) of Theorem 2.1, $\lim_{t\to\infty}(v(x,t), V(x,t)) = 0$ uniformly in $x \in [0, 1]$. Similarly, (u, U) satisfies $\lim_{t\to\infty}(u(x,t), U(x,t)) = 0$ uniformly in $x \in [0, 1]$.

(ii) Obviously, from the proof of (i), (v, V) goes to extinction, and therefore, the limiting equations for the first two equations in (3.2) become

$$u_t = du_{xx} + \mu_1\left(\frac{U}{u}\right)u,$$

$$U_t = dU_{xx} + f_1\left(z(x) - U, \frac{U}{u}\right)u,$$

in $(0, 1) \times (0, \infty)$, with the usual boundary conditions and initial conditions. By (i) of Theorem 2.1, (u, U) will tend to a positive steady-state solution for (2.6)–(2.8).

(iii) The proof for (iii) is similar. □

In order to prove our final result on coexistence or persistence, we need some notations and preliminary results. Set $C := (C([0, 1]))^4$. For $P, Q \in C$ with $P \ll_K Q$, define type-K order intervals

$$[P, Q]_K = \{R \in C \mid P \leqslant_K R \leqslant_K Q\} \quad \text{and}$$

$$[[P, Q]]_K = \{R \in C \mid P \ll_K R \ll_K Q\}.$$

Let $\min_{x\in[0,1]} f_1(z(x), Q_{c,1}) > \eta_0 Q_{c,1}$. Then from Theorem 2.1,

$$\begin{aligned}
u_t &= du_{xx} + \mu_1\left(\frac{U}{u}\right)u, \quad x \in (0, 1),\ t > 0,\\
U_t &= dU_{xx} + f_1\left(z(x) - U, \frac{U}{u}\right)u, \quad x \in (0, 1),\ t > 0,\\
u_x(0, t) &= 0, \qquad u_x(1, t) + \gamma u(1, t) = 0,\\
U_x(0, t) &= 0, \qquad U_x(1, t) + \gamma U(1, t) = 0
\end{aligned} \tag{3.12}$$

has a unique positive steady state $(u^*(x), U^*(x))$ which is globally asymptotically stable in its feasible region.

Similarly, if $\min_{x\in[0,1]} f_2(z(x), Q_{c,2}) > \eta_0 Q_{c,2}$, then the system

$$v_t = dv_{xx} + \mu_2\left(\frac{V}{v}\right)v, \quad x \in (0, 1),\ t > 0,$$

$$V_t = dV_{xx} + f_2\left(z(x) - V, \frac{V}{v}\right)v, \quad x \in (0, 1),\ t > 0,$$

$$\begin{aligned} &v_x(0,t)=0, \qquad v_x(1,t)+\gamma v(1,t)=0,\\ &V_x(0,t)=0, \qquad V_x(1,t)+\gamma V(1,t)=0 \end{aligned} \tag{3.13}$$

has a unique positive steady state $(v^*(x), V^*(x))$ which is globally asymptotically stable in its feasible region.

The proof of Theorem 3.2 (the coexistence results) will depend on the following lemmas:

Lemma 3.4. *Let $P^* = (0, 0, v^*(x), V^*(x))$ and $Q^* = (u^*(x), U^*(x), 0, 0)$. Then $\omega(P) \subset [P^*, Q^*]_K$ for any $P \in \Sigma$.*

Proof. Fix a point $P = (u^0, U^0, v^0, V^0) \in \Sigma$. Let

$$\Psi_t(P) = \big(u(\cdot,t,P), U(\cdot,t,P), v(\cdot,t,P), V(\cdot,t,P)\big)$$

be the solution with initial data P. Then $(u(\cdot,t,P), U(\cdot,t,P))$ satisfies

$$\begin{gathered} u_t = du_{xx} + \mu_1\left(\frac{U}{u}\right)u, \quad x \in (0,1),\ t>0,\\ U_t \leqslant dU_{xx} + f_1\left(z(x)-U, \frac{U}{u}\right)u, \quad x \in (0,1),\ t>0,\\ u_x(0,t)=0, \qquad u_x(1,t)+\gamma u(1,t)=0,\\ U_x(0,t)=0, \qquad U_x(1,t)+\gamma U(1,t)=0,\\ u(\cdot,0)=u^0, \qquad U(\cdot,0)=U^0, \end{gathered}$$

and $(v(\cdot,t,P), V(\cdot,t,P))$ satisfies

$$\begin{gathered} v_t = dv_{xx} + \mu_2\left(\frac{V}{v}\right)v, \quad x \in (0,1),\ t>0,\\ V_t \leqslant dV_{xx} + f_2\left(z(x)-V, \frac{V}{v}\right)v, \quad x \in (0,1),\ t>0,\\ v_x(0,t)=0, \qquad v_x(1,t)+\gamma v(1,t)=0,\\ V_x(0,t)=0, \qquad V_x(1,t)+\gamma V(1,t)=0,\\ v(\cdot,0)=v^0, \qquad V(\cdot,0)=V^0. \end{gathered}$$

From [18, p. 130, Theorem 3.4] it follows that for any $t>0$

$$\begin{gathered} \big(u(\cdot,t,P), U(\cdot,t,P)\big) \leqslant \Psi_t^u\big(u^0, U^0\big) \quad \text{and}\\ \big(v(\cdot,t,P), V(\cdot,t,P)\big) \leqslant \Psi_t^v\big(v^0, V^0\big), \end{gathered}$$

where $\Psi_t^u(u^0, U^0)$ and $\Psi_t^v(v^0, V^0)$ are the solutions for (3.12) and (3.13), respectively. Thus, applying Theorem 2.1, we obtain that

$$\begin{gathered} P^u\omega(P) \leqslant \big(u^*(x), U^*(x)\big) \quad \text{and}\\ P^v\omega(P) \leqslant \big(v^*(x), V^*(x)\big), \end{gathered}$$

where

$$P^u\big(u^0, U^0, v^0, V^0\big) = \big(u^0, U^0\big) \quad \text{and}$$
$$P^v\big(u^0, U^0, v^0, V^0\big) = \big(v^0, V^0\big)$$

are projection mappings, that is,

$$\omega(P) \subset \big[P^*, Q^*\big]_K. \qquad \square$$

Lemma 3.5. *The following statements hold.*

(i) *Let* $\min_{x\in[0,1]} f_1(z(x), Q_{c,1}) > \eta_0 Q_{c,1}$ *and* $\min_{x\in[0,1]} f_2(z(x) - U^*(x), Q_{c,2}) > \eta_0 Q_{c,2}$. *Then for* $\varepsilon > 0$ *sufficiently small,*

$$\bar{Q}(\epsilon) := (\bar{u}, \bar{U}, \underline{v}, \underline{V}) = \left(u^*(x), U^*(x), \epsilon\frac{1}{Q_{c,2}}\phi_1, \epsilon\phi_1\right)$$

is a strict upper solution for the system (3.9)–(3.10) (*or* (3.2)–(3.4)) *in the type* K*-order, where* $(u^*(x), U^*(x))$ *is a positive solution of* (3.12) *and* ϕ_1 *is defined in* (2.21).

(ii) *Let* $\min_{x\in[0,1]} f_2(z(x), Q_{c,2}) > \eta_0 Q_{c,2}$ *and* $\min_{x\in[0,1]} f_1(z(x) - V^*(x), Q_{c,1}) > \eta_0 Q_{c,1}$. *Then for* $\varepsilon > 0$ *sufficiently small,*

$$\underline{P}(\epsilon) := (\underline{u}, \underline{U}, \bar{v}, \bar{V}) = \left(\epsilon\frac{1}{Q_{c,1}}\phi_1, \epsilon\phi_1, v^*(x), V^*(x)\right)$$

is a strict lower solution for the system (3.9)–(3.10) (*or* (3.2)–(3.4)) *in the type* K*-order, where* $(v^*(x), V^*(x))$ *is a positive solution of* (3.13) *and* ϕ_1 *is defined in* (2.21).

Proof. It is not difficult to show that $\bar{Q}(\epsilon)$, $\underline{P}(\epsilon) \in \Sigma$, for $\varepsilon > 0$ sufficiently small. Clearly,

$$\begin{aligned}
-\bar{u}'(0) &= \bar{u}'(1) + \gamma\bar{u}(1) = 0, & -\bar{U}'(0) &= \bar{U}'(1) + \gamma\bar{U}(1) = 0,\\
-\bar{v}'(0) &= \bar{v}'(1) + \gamma\bar{v}(1) = 0, & -\bar{V}'(0) &= \bar{V}'(1) + \gamma\bar{V}(1) = 0,\\
-\underline{u}'(0) &= \underline{u}'(1) + \gamma\underline{u}(1) = 0, & -\underline{U}'(0) &= \underline{U}'(1) + \gamma\underline{U}(1) = 0,\\
-\underline{v}'(0) &= \underline{v}'(1) + \gamma\underline{v}(1) = 0, & -\underline{V}'(0) &= \underline{V}'(1) + \gamma\underline{V}(1) = 0.
\end{aligned}$$

It is straightforward to show the following inequalities:

$$d\bar{u}_{xx} + \mu_1\left(\frac{\bar{U}}{\bar{u}}\right)\bar{u} = du^*_{xx} + \mu_1\left(\frac{U^*}{u^*}\right)u^* = 0 \leqslant 0,$$
$$\begin{aligned}
d\bar{U}_{xx} + f_1\left(z(x) - \bar{U} - \underline{V}, \frac{\bar{U}}{\bar{u}}\right)\bar{u} &= dU^*_{xx} + f_1\left(z(x) - U^* - \epsilon\phi_1, \frac{U^*}{u^*}\right)u^*\\
&< dU^*_{xx} + f_1\left(z(x) - U^*, \frac{U^*}{u^*}\right)u^* = 0,
\end{aligned}$$
$$d\underline{v}_{xx} + \mu_2\left(\frac{\underline{V}}{\underline{v}}\right)\underline{v} = \frac{\epsilon}{Q_{c,2}}\big[d\phi_1''(x) + \mu_2(Q_{c,2})\phi_1(x)\big] = \frac{\epsilon}{Q_{c,2}}\big[d\phi_1''(x) + \eta_0\phi_1(x)\big] = 0 \geqslant 0,$$

$$d\underline{V}_{xx} + f_2\left(z(x) - \bar{U} - \underline{V}, \frac{\underline{V}}{\underline{v}}\right)\underline{v} = \frac{\epsilon}{Q_{c,2}}\left[d\phi_1''(x)Q_{c,2} + f_2\big(z(x) - U^* - \epsilon\phi_1(x), Q_{c,2}\big)\phi_1\right]$$
$$= \frac{\epsilon}{Q_{c,2}}\left[-\eta_0 Q_{c,2} + f_2\big(z(x) - U^* - \epsilon\phi_1(x), Q_{c,2}\big)\right]\phi_1 > 0,$$

provided that $\min_{x\in[0,1]} f_2(z(x) - U^*(x), Q_{c,2}) > \eta_0 Q_{c,2}$ and $\epsilon > 0$ is small enough. Thus, $(\bar{u}, \bar{U}, \underline{v}, \underline{V})$ is a strict upper solution of (3.9)–(3.10) or (3.2)–(3.4) in the type K-order.

Similarly, under the conditions $\min_{x\in[0,1]} f_1(z(x)-V^*(x), Q_{c,1}) > \eta_0 Q_{c,1}$ and $\epsilon > 0$ is small enough we can show the following inequalities hold:

$$d\underline{u}_{xx} + \mu_1\left(\frac{\underline{U}}{\underline{u}}\right)\underline{u} = 0 \geqslant 0,$$

$$d\underline{U}_{xx} + f_1\left(z(x) - \underline{U} - \bar{V}, \frac{\underline{U}}{\underline{u}}\right)\underline{u} > 0,$$

$$d\bar{v}_{xx} + \mu_2\left(\frac{\bar{V}}{\bar{v}}\right)\bar{v} = 0 \leqslant 0,$$

$$d\bar{V}_{xx} + f_2\left(z(x) - \underline{U} - \bar{V}, \frac{\bar{V}}{\bar{v}}\right)\bar{v} < 0.$$

Thus $(\underline{u}, \underline{U}, \bar{v}, \bar{V})$ is a strict lower solution of (3.9)–(3.10) or (3.2)–(3.4) in the type K-order. □

The following is the coexistence result.

Theorem 3.2. *Let $\min_{x\in[0,1]} f_1(z(x) - V^*(x), Q_{c,1}) > \eta_0 Q_{c,1}$ and $\min_{x\in[0,1]} f_2(z(x) - U^*(x), Q_{c,2}) > \eta_0 Q_{c,2}$, where $U^*(x)$ and $V^*(x)$ are defined in Theorem 3.1. Then there are a minimal positive steady state $E^- \in \Sigma$ which is lower asymptotically stable and a maximal positive steady state $E^+ \in \Sigma$ which is upper asymptotically stable such that*

$$\omega(P) \subset \left[E^-, E^+\right]_K \cap \Sigma \quad \text{for any } P \in \Sigma.$$

The system (3.2)–(3.4) is uniformly persistent and $\Psi_t(P)$ tends to a steady state for P in an open and dense subset in Σ.

Proof. Combining Lemma 3.5, Theorem 3.4 in [18, p. 130] and strong monotonicity for Ψ_t, we get that for any $t > 0$

$$\underline{P}(\epsilon) \ll_K \Psi_t\big(\underline{P}(\epsilon)\big) \ll_K \Psi_t\big(\bar{Q}(\epsilon)\big) \ll_K \bar{Q}(\epsilon).$$

The Convergence Criterion in [18, p. 3, Theorem 2.1] deduces that $\Psi_t(\underline{P}(\epsilon))$ converges to a lower asymptotically stable steady state $E^-(\epsilon) \gg_K \underline{P}(\epsilon)$, and $\Psi_t(\bar{Q}(\epsilon))$ tends to an upper asymptotically stable steady state $E^+(\epsilon) \ll_K \bar{Q}(\epsilon)$. Since $E^+(\epsilon)$ attracts $\bar{Q}(\delta)$ for an open neighborhood of ϵ, $E^+(\epsilon)$ is independent of ϵ for $\epsilon > 0$ sufficiently small, similarly for $E^-(\epsilon)$.

By Lemma 3.4,

$$\omega(P) \subset \left[P^*, Q^*\right]_K \quad \text{for any fixed } P \in \Sigma.$$

Thus for t sufficiently large, say $t \geqslant t_0$,

$$\Psi_t(P) \in \left[\!\left[\big(0, 0, v^*(x), V^*(x)\big), \big(u^*(x), U^*(x), 0, 0\big)\right]\!\right]_K.$$

This implies that for $\epsilon > 0$ sufficiently small,

$$\underline{P}(\epsilon) \ll_K \Psi_t(P) \ll_K \bar{Q}(\epsilon),$$

that is,

$$E^- \leqslant_K \omega(P) \leqslant_K E^+.$$

The remaining results follow from the theory of strongly monotone dynamical systems (see [18]). $\square$

Remark 3.2 *(Biological interpretation for Theorem 3.2).* The condition $\min_{x\in[0,1]} f_1(z(x) - V^*(x), Q_{c,1}) > \eta_0 Q_{c,1}$ says that species u is able to invade the community with species v alone. Similarly, the condition $\min_{x\in[0,1]} f_2(z(x) - U^*(x), Q_{c,2}) > \eta_0 Q_{c,2}$ says that species v is able to invade the community with species u alone. Thus Theorem 3.2 states that coexistence is possible provided that mutual invasibility occurs. We note that from (H$_2$), $\min_{x\in[0,1]} f_1(z(x), Q_{c,1}) > \min_{x\in[0,1]} f_1(z(x) - V^*(x), Q_{c,1})$. Thus invasion condition for species u: $\min_{x\in[0,1]} f_1(z(x) - V^*(x), Q_{c,1}) > \eta_0 Q_{c,1}$ implies the survival condition for species u: $\min_{x\in[0,1]} f_1(z(x), Q_{c,1}) > \eta_0 Q_{c,1}$. Similarly, invasion condition for species v: $\min_{x\in[0,1]} f_2(z(x) - U^*(x), Q_{c,2}) > \eta_0 Q_{c,2}$ implies the survival condition of species v: $\min_{x\in[0,1]} f_2(z(x), Q_{c,2}) > \eta_0 Q_{c,2}$.

3.4. Dynamics of (1.9)–(1.11)

In this subsection, we use the similar arguments in Section 2.4 to discuss the dynamics of the original system (1.9)–(1.11).

Theorem 3.3. *Let* $\min_{x\in[0,1]} f_1(z(x) - V^*(x), Q_{c,1}) > \eta_0 Q_{c,1}$ *and* $\min_{x\in[0,1]} f_2(z(x) - U^*(x), Q_{c,2}) > \eta_0 Q_{c,2}$*, where* $U^*(x)$ *and* $V^*(x)$ *are defined in Theorem* 3.1. *Then the system* (1.9)–(1.11) *is uniformly persistent and the semi-flow generated by* (1.9)–(1.11) *tends to a steady state for its initial condition in an open and dense subset of its feasible domain.*

Proof. Rewrite (1.9)–(1.11) as

$$\begin{aligned}
u_t &= du_{xx} + \mu_1\left(\frac{U}{u}\right)u, \\
U_t &= dU_{xx} + f_1\left(\tilde{\Theta}(x,t) - U - V, \frac{U}{u}\right)u, \\
v_t &= dv_{xx} + \mu_2\left(\frac{V}{v}\right)v, \\
V_t &= dV_{xx} + f_2\left(\tilde{\Theta}(x,t) - U - V, \frac{V}{v}\right)v,
\end{aligned} \tag{3.14}$$

in $(0,1)\times(0,\infty)$, with boundary conditions

$$\begin{aligned}
u_x(0,t) &= 0, \qquad u_x(1,t) + \gamma u(1,t) = 0, \\
U_x(0,t) &= 0, \qquad U_x(1,t) + \gamma U(1,t) = 0, \\
v_x(0,t) &= 0, \qquad v_x(1,t) + \gamma v(1,t) = 0, \\
V_x(0,t) &= 0, \qquad V_x(1,t) + \gamma V(1,t) = 0,
\end{aligned} \tag{3.15}$$

and initial conditions, where $\tilde{\Theta}(x,t)$ is defined in (3.1) which satisfies (2.26) and $\lim_{t\to\infty}\tilde{\Theta}(x,t) = z(x)$ uniformly in $x \in [0,1]$, where $z(x) = S^{(0)}(\frac{1+\gamma}{\gamma} - x)$. This shows that system (3.14)–(3.15) with usual initial conditions is asymptotically autonomous and its limiting system is (3.2)–(3.4). From Theorem 3.2 we conclude that any chain recurrent set for the limiting system (3.2)–(3.4) is contained in $[E^-, E^+]_K \cap \Sigma$. Again using Theorem 1.8 in [15], we get uniform persistence. Almost convergence result follows from Theorem 3.2. The proof is complete. $\square$

We note that one can also use the results in [11] to lift the dynamics of the limiting system (3.2)–(3.4) to the full system (1.9)–(1.11).

Remark 3.3. In Theorem 3.3, we give sufficient conditions for the coexistence of two species. We conjecture that competitive exclusion (i.e. only one species survives) is possible and our numerical simulations confirm it. It is still an open problem.

Remark 3.4. In the near future, we shall investigate a similar mathematical model of two species competing for two complementary resources with internal storage.

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References

[1] R.A. Armstorng, R. McGehee, Competitive exclusion, American Naturalist 115 (1980) 151–170.
[2] A. Cunningham, R.M. Nisbet, Time lag and co-operativity in the transient growth dynamics of microalgae, J. Theoret. Biol. 84 (1980) 189–203.
[3] A. Cunningham, R.M. Nisbet, Transient and Oscillation in Continuous Culture, in: M.J. Bazin (Ed.), Mathematics in Microbiology, Academic Press, New York, 1983.
[4] M. Droop, Some thoughts on nutrient limitation in algae, J. Phycol. 9 (1973) 264–272.
[5] J.P. Grover, Constant- and variable-yield models of population growth: Responses to environmental variability and implications for competition, J. Theoret. Biol. 158 (1992) 409–428.
[6] J.P. Grover, Is storage an adaptation to spatial variation in resource availability?, American Naturalist 173 (2009) E44–E61.
[7] S.B. Hsu, Limiting behavior for competing species, SIAM J. Appl. Math. 34 (1978) 760–763.
[8] P. Hess, Periodic-Parabolic Boundary Value Problem and Positivity, Pitman Res. Notes Math., vol. 247, Longman Scientific and Technical, 1991.
[9] M.W. Hirsch, The dynamical systems approach to differential equations, Bull. Amer. Math. Soc. 11 (1984) 1–64.
[10] S.B. Hsu, S. Hubbell, P. Waltman, Mathematical theory for single nutrient competition in continuous cultures of microorganisms, SIAM J. Appl. Math. 32 (1977) 366–383.
[11] W.M. Hirsch, H.L. Smith, X.Q. Zhao, Chain transitivity, attractivity, and strong repellers for semidynamical systems, J. Dynam. Differential Equations 13 (2001) 107–131.
[12] S.B. Hsu, P. Waltman, On a system of reaction–diffusion equations arising from competition in an unstirred chemostat, SIAM J. Appl. Math. 53 (1993) 1026–1044.
[13] J. Jiang, On the global stability of cooperative systems, Bull. Lond. Math. Soc. 26 (1994) 455–458.
[14] J. Jiang, Sublinear discrete-time order-preserving dynamical systems, Math. Proc. Cambridge Philos. Soc. 119 (1996) 561–574.
[15] K. Mischaikow, H.L. Smith, H. Thieme, Asymptotically autonomous semiflows: Chain recurrence and Liapunov functions, Trans. Amer. Math. Soc. 347 (1995) 1669–1685.
[16] H. Nie, J. Wu, G.S.K. Wolkowicz, The effect of inhibitor on the plasmid-bearing and plasmid-free model in the unstirred chemostat, SIAM J. Appl. Math. 38 (2007) 1860–1885.
[17] M.H. Protter, H.F. Weinberger, Maximum Principles in Differential Equations, Springer-Verlag, 1984.
[18] H.L. Smith, Monotone Dynamical Systems: An Introduction to the Theory of Competitive and Cooperative Systems, Math. Surveys Monogr., vol. 41, American Mathematical Society, Providence, RI, 1995.
[19] H.L. Smith, Cooperative systems of differential equations with concave nonlinearities, Nonlinear Anal. 10 (1986) 1037–1052.
[20] H.L. Smith, P.E. Waltman, Competition for a single limiting resource in continuous culture: The variable-yield model, SIAM J. Appl. Math. 34 (1994) 1113–1131.
[21] H.L. Smith, P.E. Waltman, The Theory of the Chemostat, Cambridge Univ. Press, 1995.
[22] J. Wu, G.S.K. Wolkowicz, A system of resource-based growth models with two resources in the unstirred chemostat, J. Differential Equations 172 (2001) 300–332.