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FURTHER STUDIES OF A REACTION-DIFFUSION SYSTEM FOR AN UNSTIRRED CHEMOSTAT WITH INTERNAL STORAGE

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Dedicated to Professor Chris Cosner on the occasion of his 60th birthday

Abstract. The dynamics of a reaction-diffusion system for two species of microorganism in an unstirred chemostat with internal storage is studied. It is shown that the diffusion coefficient is a key parameter of determining the asymptotic dynamics, and there exists a threshold diffusion coefficient above which both species become extinct. On the other hand, for diffusion coefficient below the threshold, either one species or both species persist, and in the asymptotic limit, a steady state showing competition exclusion or coexistence is reached.

1. **Introduction.**

Chemostat is a simple bioreactor for continuous culture of microorganisms. Nutrient necessary for the microorganism growth is pumped into the vessel at a constant rate, while the mixture of the nutrient and microorganism is pumped out at the same rate so the volume is kept at a constant. Differential equation models have been set up for chemostats under various assumptions. One assumption is on the nutrient uptake rate: it is called constant yield if it is proportional to the microorganism per capita growth rate, and it is called variable yield if it also depends on the growth rate. In the constant yield case, it has been established that the competition exclusion principle holds so that only one species of microorganism survives in the long run [1, 9, 11].

For the variable yield case, Droop [3, 4] formulated the following "cell-quota" model for the phytoplankton growth with an internal storage of the nutrient:

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$$\begin{cases} S' = (S^{(0)} - S)D - f_1(S, Q_1)u - f_2(S, Q_2)v, \\ u' = (\mu_1(Q_1) - D)u, \\ Q_1' = f_1(S, Q_1) - \mu_1(Q_1)Q_1, \\ v' = (\mu_2(Q_2) - D)v, \\ Q_2' = f_2(S, Q_2) - \mu_2(Q_2)Q_2, \\ S(0) \ge 0,\ u(0) \ge 0,\ v(0) \ge 0,\ Q_1(0) \ge Q_{\min,1},\ Q_2(0) \ge Q_{\min,2}. \end{cases} \tag{1}$$

Here $S(t)$ is the substrate concentration, $u(t)$, $v(t)$ are the population concentrations for the two species of phytoplankton respectively, and $Q_i(t)$ $(i = 1, 2)$ is the average amount of stored nutrient per cell of the i-th population. The positive constants $S^{(0)}$ and D are the nutrient input rate and the washout rate respectively, $\mu_i(Q_i)$ is the growth rate of the i-th population as a function of cell quota Q_i, $f_i(S, Q_i)$ is the per capital nutrient uptake rate per cell of the i-th population as a function of nutrient concentration S and cell quota Q_i, and $Q_{\min,i}$ is the threshold cell quota below which no growth of the i-th population occurs. Typically the functions $\mu_i(Q_i)$ and $f_i(S, Q_i)$ satisfy the following assumptions: $(i = 1, 2)$

- $(H1)$ $\mu_i(Q_i)$ is continuously differentiable for $Q_i \ge Q_{\min,i}$, $\mu_i(Q_{\min,i}) = 0$, $\mu_i(Q_i) > 0$ and $\mu_i'(Q_i) > 0$ for $Q \ge Q_{\min,i}$.
- $(H2)$ $f_i(S, Q_i)$ is continuously differentiable for $S > 0$ and $Q \ge Q_{\min,i}$, $f_i(0, Q_i) = 0$, $f_i(S, Q_i) \ge 0$, $\frac{\partial f_i}{\partial S}(S, Q_i) > 0$ and $\frac{\partial f_i}{\partial Q_i}(S, Q_i) \le 0$ for $S > 0$ and $Q_i \ge Q_{\min,i}$.

Some specific functions $\mu_i(Q_i)$ and $f_i(S, Q_i)$ used in [2, 4] are

$$\mu_i(Q_i) = \mu_{i\infty}\left(1 - \frac{Q_{\min,i}}{Q_i}\right), \quad \mu_i(Q_i) = \mu_{i\infty}\frac{Q_i - Q_{\min,i}}{K_i + Q_i - Q_{\min,i}}, \tag{2}$$

where $\mu_{i\infty}$ is the maximal growth rate of the i-th population, and

$$\begin{aligned} & f_i(S, Q_i) = \rho_i(Q_i)\frac{S}{k_i + S}, \text{ where } \rho_i(Q_i) \text{ is defined by} \\ & \rho_i(Q_i) = \rho_{\max,i}^{\text{high}} - (\rho_{\max,i}^{\text{high}} - \rho_{\max,i}^{\text{low}})\frac{Q_i - Q_{\min,i}}{Q_{\max,i} - Q_{\min,i}}, \quad \text{or} \\ & \rho_i(Q_i) = \rho_{\max,i}\frac{Q_{\max,i} - Q_i}{Q_{\max,i} - Q_{\min,i}}, \quad \text{or} \\ & \rho_i(Q_i) = \rho_i^c, \quad (\text{constant}), \end{aligned} \tag{3}$$

where $Q_{\min,i} \le Q_i \le Q_{\max,i}$ (a maximal possible quota).

A complete mathematical analysis of (1) was carried out in [21]. It was shown that (1) possesses (i) a trivial steady state solution $E_0 = (\tilde{S}, 0, \tilde{Q}_1, 0, \tilde{Q}_2)$ for any positive parameters; (ii) a semi-trivial steady state solution $E_1 = (S^1, u^1, Q_1^1, 0, Q_2^1)$ if $\mu_1(Q_1^1) = D$ and $DQ_1^1 < f_1(S^{(0)}, Q_1^1)$ for some $Q_1^1 > Q_{min,1}$; and (iii) a semi-trivial steady state solution $E_2 = (S^2, 0, Q_1^2, v^2, Q_2^2)$ if $\mu_2(Q_2^2) = D$ and $DQ_2^2 < f_2(S^{(0)}, Q_2^2)$ for some $Q_2^2 > Q_{min,2}$. Moreover assuming that the steady state solutions are all non-degenerate, then a classification of the dynamics can be obtained as follows:

1. If E_1 and E_2 do not exist, then E_0 is globally asymptotically stable.
2. If E_1 exists but E_2 does not exist, then E_1 is globally asymptotically stable.
3. If E_2 exists but E_1 does not exist, then E_2 is globally asymptotically stable.

4. If E_1 and E_2 both exist, and $S^1 > S^2$, then E_2 is globally asymptotically stable.
5. If E_1 and E_2 both exist, and $S^1 < S^2$, then E_1 is globally asymptotically stable.
6. If E_1 and E_2 both exist, and $S^1 = S^2$, then there exists a family of positive steady states connecting E_1 and E_2, and each of these positive steady states can be an asymptotic limit.

In particular, positive coexistence steady states only exist in a very special parameter value, and for most cases, a competition exclusion holds for the two competing species. This result was extended to the n-species case in [10], and the time-periodic two-species case was considered in [20, 22]. More biological explanations of the Droop model (1) can be found in [5, 6].

On the other hand, the system (1) is based on the important assumption that the microorganism culture in the chemostat is well-stirred so the concentration functions are spatially uniform. In general this assumption is only approximately true and in reality nutrient and microorganism molecules move in the chemostat. Under the assumption that the molecular movement of nutrient and microorganism follows Fick's diffusion law, a reaction-diffusion model for an unstirred chemostat with an internal storage was proposed in [12] based on the Droop's model (1) and earlier work in [15] for the constant yield reaction-diffusion chemostat model. In this new model, the chemostat is assumed to have one-dimensional geometry so the domain is an interval $(0, 1)$, $S(x, t)$ is the nutrient concentration measured in units of mass per unit length, $u(x, t)$ and $v(x, t)$ are the microorganism cell concentration per unit length for species 1 and species 2, respectively. The instored nutrient per cell per unit length $Q_i(x, t)$ $(i = 1, 2)$ now also depends on the spatial variable x. We define $U(x, t) = u(x, t)Q_1(x, t)$, $V(x, t) = v(x, t)Q_2(x, t)$ to be the total amount of stored nutrient for species 1 and species 2, respectively. Then as the spatial movements of u and v satisfy the diffusion equation, U and V disperse with the same diffusion coefficient d. Therefore we have the following initial-boundary-value reaction-diffusion system for the variables (S, u, U, v, V):

$$\begin{cases} S_t = dS_{xx} - f_1\left(S, \frac{U}{u}\right)u - f_2\left(S, \frac{V}{v}\right)v, & x \in (0,1),\ t > 0, \\ u_t = du_{xx} + \mu_1\left(\frac{U}{u}\right)u, & x \in (0,1),\ t > 0, \\ U_t = dU_{xx} + f_1\left(S, \frac{U}{u}\right)u, & x \in (0,1),\ t > 0, \\ v_t = dv_{xx} + \mu_2\left(\frac{V}{v}\right)v, & x \in (0,1),\ t > 0, \\ V_t = dV_{xx} + f_2\left(S, \frac{V}{v}\right)v, & x \in (0,1),\ t > 0, \\ S_x(0,t) = -S^{(0)},\ S_x(1,t) + \gamma S(1,t) = 0, & \\ w_x(0,t) = 0,\ w_x(1,t) + \gamma w(1,t) = 0, & w = u, U, v, V, \\ w(x,0) = w^0(x) \geq (\not\equiv) 0, & w = S, u, U, v, V, \end{cases} \tag{4}$$

and the initial value functions $u^0(x)$, $U^0(x)$, $v^0(x)$, and $V^0(x)$ satisfy $\frac{U^0(x)}{u^0(x)} \geq Q_{\min,1}$, $\frac{V^0(x)}{v^0(x)} \geq Q_{\min,2}$. To understand the competition dynamics of (4) better, it is also useful to consider the internal storage model of one species consuming one nutrient from [12]:

$$\begin{cases} S_t = dS_{xx} - f\left(S, \frac{U}{u}\right) u, & x \in (0,1),\ t > 0, \\ u_t = du_{xx} + \mu\left(\frac{U}{u}\right) u, & x \in (0,1),\ t > 0, \\ U_t = dU_{xx} + f\left(S, \frac{U}{u}\right) u, & x \in (0,1),\ t > 0, \\ S_x(0,t) = -S^{(0)}, \quad S_x(1,t) + \gamma S(1,t) = 0, & \\ w_x(0,t) = 0,\ w_x(1,t) + \gamma w(1,t) = 0, & w = u, U, \\ w(x,0) = w^0(x) \geq (\not\equiv) 0, & w = S, u, U, \end{cases} \tag{5}$$

and we assume that $\mu(Q)$ and $f(S,Q)$ also satisfy $(H1)$ and $(H2)$.

The dynamics of Eq. (5) and Eq. (4) were studied in [12]. For the single species model (5), it was shown that either the population becomes extinct as $t \to \infty$, or the population approaches to a unique positive steady state as $t \to \infty$ regardless of initial conditions. The extinction and persistence of the population depends on the growth rate $\mu(Q)$, the uptake rate $f(S,Q)$ as well as the diffusion coefficient d. Similar results were also obtained for the competition model (4). But unlike the constant yield reaction-diffusion system in [15], the extinction or persistence of the population is not completely classified for all possible parameter ranges in [12], as the linearization techniques fail here because of the singular nonlinearities near $u = 0$ or $v = 0$ in (5) or (4).

In this article, we complete the studies of (5) to classify the dynamics for all possible parameter ranges, which also provides a more accurate description of the competition dynamics of (4). More precisely in Section 2, we show that there is a critical diffusion coefficient $d_0 > 0$ such that the population becomes extinct as $t \to \infty$ in (5) for any initial conditions if $d \geq d_0$, and the population tends to a unique positive steady state as $t \to \infty$ in (5) for any initial conditions if $0 < d < d_0$. The existence of a critical diffusion coefficient d_0 can be interpreted as a critical patch size. Indeed it is easy to verify that a system defined on an interval $(0,L)$ like

$$\begin{cases} \tilde{S}_t = \tilde{d}\tilde{S}_{yy} - f\left(\tilde{S}, \frac{U}{u}\right) u, & y \in (0,L),\ t > 0, \\ \tilde{u}_t = \tilde{d}\tilde{u}_{yy} + \mu\left(\frac{\tilde{U}}{\tilde{u}}\right) \tilde{u}, & y \in (0,L),\ t > 0, \\ \tilde{U}_t = \tilde{d}\tilde{U}_{yy} + f\left(\tilde{S}, \frac{\tilde{U}}{\tilde{u}}\right) \tilde{u}, & y \in (0,L),\ t > 0, \\ \tilde{S}_y(0,t) = -LS^{(0)}, \quad \tilde{S}_y(L,t) + \tilde{\gamma}\tilde{S}(L,t) = 0, & \\ w_y(0,t) = 0,\ w_y(1,t) + \tilde{\gamma} w(L,t) = 0, & w = \tilde{u}, \tilde{U}, \\ w(y,0) = w^0(y/L) \geq (\not\equiv) 0, & w = \tilde{S}, \tilde{u}, \tilde{U}, \end{cases} \tag{6}$$

can be converted to (5) via the change of variables $y = xL$, $\tilde{u}(y) = u(y/L)$, $\tilde{U}(y) = U(y/L)$ with the parameter change $\tilde{d} = dL^2$ and $\tilde{\gamma} = \gamma L$. Therefore the parameter d is equivalent to L^{-2}. Hence the result described above can be interpreted as: for a fixed diffusion coefficient $\tilde{d} > 0$, there exists an $L_0 > 0$, such that (6) has a unique positive steady state solution which is globally asymptotically stable when $L > L_0$, and all solutions of (6) tend to $(0,0)$ if $L < L_0$. So the critical domain size L_0 is a critical patch size for the persistence/extinction dynamics.

A complete description for the one species model (5) leads to a better understanding of the two species model (4). In Section 3, we obtain threshold diffusion coefficients for the existence of semi-trivial steady state solution which represents the competition exclusion in which a superior competitor prevails. We also provide criterion for the existence of coexistence steady state solutions. Some of our theoretical predictions are confirmed by numerical simulations in Section 2 (for one species model) and Section 3 (for two species model). In particular it is found that a coexistence steady state solution can be reached for small diffusion rate in the two species model.

We also comment that a different model was considered in [16] in which the rate of change of Q_i is local only. The model assumptions in [12] and this paper are more reasonable. Indeed one can show that $Q(x,t)$ satisfies an equation

$$Q_t = dQ_{xx} + 2d(\ln u)_x Q_x - \mu(Q)Q + f(S,Q), \quad x \in (0,1),$$

if (S,u,U) satisfies (5). Hence Q satisfies a diffusion rule $du^{-2}(u^2 Q_x)_x$ which depends on u. Another recent development based on the model (4) is the model of two species competing for two complementary resources with internal storage in [13]. Some other approaches were taken in [7, 8].

The remaining part of the paper is organized as follows. In Section 2, we consider the dynamics of the single species model and prove the existence of the critical diffusion coefficient $d_0 > 0$ for (7). In Section 3, we consider the two species competition model (4). Some concluding remarks are given in Section 4. For most places, we follow the notations in [12].

2. **Single species model.**

As shown in [12], the limiting system of (5) is

$$\begin{cases} u_t = du_{xx} + \mu\left(\frac{U}{u}\right)u, & x \in (0,1),\ t > 0, \\ U_t = dU_{xx} + f\left(z(x) - U, \frac{U}{u}\right)u, & x \in (0,1),\ t > 0, \\ w_x(0,t) = 0,\ w_x(1,t) + \gamma w(1,t) = 0, & w = u, U, \\ w(x,0) = w^0(x) \geq (\not\equiv) 0, & w = u, U. \end{cases} \tag{7}$$

where $z(x) = S^{(0)}\left(\frac{1+\gamma}{\gamma} - x\right)$. The steady states of (7) are the solutions of the following elliptic system:

$$\begin{cases} du'' + \mu\left(\frac{U}{u}\right)u = 0, & x \in (0,1), \\ dU'' + f\left(z(x) - U, \frac{U}{u}\right)u = 0, & x \in (0,1), \\ u'(0) = u'(1) + \gamma u(1) = 0, \\ U'(0) = U'(1) + \gamma U(1) = 0. \end{cases} \tag{8}$$

The biologically feasible domain for the system (7) is defined by

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

The eigenvalue problem

$$\begin{cases} d\phi_1''(x) + \eta_0 \phi_1(x) = 0, & x \in (0,1), \\ \phi_1'(0) = \phi_1'(1) + \gamma\phi_1(1) = 0 \end{cases} \tag{9}$$

has a principal eigenvalue $\eta_0(d) = k_0^2 d > 0$ with the corresponding positive eigenfunction $\phi_1(x) = \cos(k_0 x)$ uniquely determined by the normalization $\max_{x\in[0,1]} \phi_1(x) = \phi_1(0) = 1$, where $k_0 \in (0, \pi/2)$ is the smallest root of the equation $\tan(k) = \gamma/k$. Then from $(H1)$, for any $d > 0$, there is at most one constant $Q_{\mathrm{c}}(d) > Q_{\min}$ satisfying

$$\mu(Q_{\mathrm{c}}(d)) = \eta_0(d). \tag{10}$$

It is clear that such a $Q_{\mathrm{c}}(d)$ exists for small $d > 0$ since $\eta_0(d) = k_0^2 d \to 0$ as $d \to 0$, and from $(H1)$, $Q_{\mathrm{c}}(d)$ is strictly increasing in d with $\lim_{d\to 0^+} Q_{\mathrm{c}}(d) = Q_{min}$.

We recall the following results regarding (7) and (8) which were proved in [12] (see Lemmas 2.1, 2.2, 2.3 and Theorem 2.1 of [12]).

Proposition 2.1. *Suppose that $d > 0$, f, μ satisfy $(H1)$ and $(H2)$. Let Δ, $\eta_0(d)$, $Q_c(d)$ and $\phi_1(x)$ be defined as above. Then*

1. *The set Δ is positively invariant under the semiflow Φ_t generated by (7).*
2. *Suppose that $(u(x), U(x))$ is a nonnegative solution of (8) satisfying $u(x) \not\equiv 0$ and $U(x) \not\equiv 0$. Then $0 < u(x)Q_{\min} < U(x) < z(x)$ for $x \in [0,1]$.*
3. *Let $(\tilde{u}, \tilde{U}) := (\epsilon Q_c(d)^{-1}\phi_1, \epsilon\phi_1)$. Then for any $\epsilon > 0$, $(\tilde{u}, \tilde{U})$ is an upper solution for the system (8) if*
$$\max_{x\in[0,1]} f(z(x), Q_c(d)) \le \eta_0(d)Q_c(d); \tag{11}$$
and $(\tilde{u}, \tilde{U})$ is a lower solution for the system (8) if
$$\min_{x\in[0,1]} f(z(x), Q_c(d)) > \eta_0(d)Q_c(d), \tag{12}$$
where $0 < \epsilon < \min\{z(x)/\phi_1(x) : x \in [0,1]\}$ is sufficiently small.
4. *If (12) is satisfied, then (7) has a unique positive steady state solution which is globally asymptotically stable in Δ.*
5. *If (11) is satisfied, then there is no steady state solution in Δ, and every solution of (7) with initial conditions in Δ satisfies $(u(\cdot,t), U(\cdot,t)) \to (0,0)$ as $t \to \infty$.*
6. *For any parameter values, the system (7) has at most 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.*

When using the diffusion coefficient d as a bifurcation parameter, one can see that when d is large, then the condition (11) is satisfied since
$$\max_{x\in[0,1]} f(z(x), Q_c(d)) \le \max_{x\in[0,1]} f(z(x), Q_{min}), \quad \text{and} \quad \lim_{d\to d_*} \eta_0(d)Q_c(d) = \infty,$$
where $d_* = \infty$ if $\lim_{Q\to\infty} \mu(Q) = \infty$, or d_* satisfies $\eta(d_0) = \mu_\infty = \lim_{Q\to\infty} \mu(Q) < \infty$. On the other hand, when d is small, then the condition (12) is satisfied since
$$\lim_{d\to 0^+} \min_{x\in[0,1]} f(z(x), Q_c(d)) = \min_{x\in[0,1]} f(z(x), Q_{\min}) > 0, \quad \text{and} \quad \lim_{d\to 0^+} \eta_0(d)Q_c(d) = 0.$$
Indeed one can define $0 < d_{min} < d_{max}$ by
$$\begin{aligned} \eta_0(d_{max})Q_c(d_{max}) &= \max_{x\in[0,1]} f(z(x), Q_c(d_{max})), \\ \text{and} \quad \eta_0(d_{min})Q_c(d_{min}) &= \min_{x\in[0,1]} f(z(x), Q_c(d_{min})), \end{aligned} \tag{13}$$
then the extinction dynamics occurs when $d > d_{max}$ and the persistence (thus global stable steady state) dynamics occurs when $0 < d < d_{min}$. Note that such d_{max} and d_{min} can be uniquely determined since the functions
$$\begin{aligned} g^{max}(d) &= \max_{x\in[0,1]} f(z(x), Q_c(d)) - \eta_0(d)Q_c(d) \\ &= \max_{x\in[0,1]} f(z(x), Q_c(d)) - \mu(Q_c(d))Q_c(d), \\ g^{min}(d) &= \min_{x\in[0,1]} f(z(x), Q_c(d)) - \eta_0(d)Q_c(d) \\ &= \min_{x\in[0,1]} f(z(x), Q_c(d)) - \mu(Q_c(d))Q_c(d). \end{aligned} \tag{14}$$

are both strictly decreasing.

The analysis above based on previous results in [12] leaves a gap of $d_{min} \leq d \leq d_{max}$ for which the dynamics is not determined. In the following we show that a sharp threshold between the extinction and persistence dynamics exists. First we establish the following lemma.

Lemma 2.2. *Suppose that f, μ satisfy $(H1)$ and $(H2)$.*

1. *If (u_a, U_a) and (u_b, U_b) are positive solutions of (8) with $d = d_a$ and $d = d_b$ respectively, and $d_a > d_b > 0$, then $u_a(x) < u_b(x)$ and $U_a(x) < U_b(x)$ for $x \in [0,1]$.*
2. *If (u_d, U_d) is a positive solution of (8) for some $d > 0$, then (u_d, U_d) is linearly stable with respect to the dynamics of (7).*

Proof. 1. Since (u_a, U_a) is a positive solution of (8) with $d = d_a$, then

$$\begin{cases} d_b u_a'' + \mu\left(\frac{U_a}{u_a}\right) u_a = \frac{d_a - d_b}{d_b} \mu\left(\frac{U_a}{u_a}\right) u_a > 0, & x \in (0,1), \\ d_b U_a'' + f\left(z(x) - U_a, \frac{U_a}{u_a}\right) u_a = \frac{d_a - d_b}{d_b} f\left(z(x) - U_a, \frac{U_a}{u_a}\right) u_a > 0, & x \in (0,1), \\ u_a'(0) = u_a'(1) + \gamma u_a(1) = 0, \\ U_a'(0) = U_a'(1) + \gamma U_a(1) = 0. \end{cases}$$

Hence (u_a, U_a) is a lower solution of (8) with $d = d_b$. On the other hand, we can choose $d_c \in (0, d_{min})$ and $d_c < d_b$, where d_{min} is defined in (13), so that (8) has a positive solution (u_c, U_c) with $d = d_c$. By using the same argument as above, we can show that (u_c, U_c) is an upper solution of (8) with $d = d_b$. Therefore by applying the well-known upper-lower solution method, (8) has a positive solution $(\tilde{u_b}, \tilde{U_b})$ with $d = d_b$ satisfying

$$u_a \leq \tilde{u_b} \leq u_c, \quad \text{and} \quad U_a \leq \tilde{U_b} \leq U_c.$$

From part 6 of Proposition 2.1, the positive solution of (8) is unique if it exists. Hence $(\tilde{u_b}, \tilde{U_b}) = (u_b, U_b)$, which implies $u_a(x) \leq u_b(x)$ and $U_a(x) \leq U_b(x)$ for $x \in [0,1]$. By using the strong maximum principle, we obtain that $u_a(x) < u_b(x)$ and $U_a(x) < U_b(x)$ for $x \in [0,1]$.

2. Next we prove that (u_d, U_d) is linearly stable. It is standard to show that the mapping

$$F(d, u, U) = \begin{pmatrix} du'' + \mu\left(\frac{U}{u}\right) u \\ dU'' + f\left(z(x) - U, \frac{U}{u}\right) u \end{pmatrix}, \tag{15}$$

is continuously differentiable if $u > 0$, $U > 0$, where $d > 0$, $u, U \in X = \{v \in C^2([0,1]) : v(x) > 0, v'(0) = v'(1) + \gamma v(1) = 0\}$. Let $L = D_{(u,U)} F(d, u_d, U_d)$ be the Fréchet derivative of F with respect to (u, v) at a positive solution (u_d, U_d) of (8). Then

$$L(\phi, \psi) = \begin{pmatrix} d\phi'' + \left[\mu\left(\frac{U_d}{u_d}\right) - \frac{U_d}{u_d} \mu'\left(\frac{U_d}{u_d}\right)\right] \phi + \mu'\left(\frac{U_d}{u_d}\right) \psi \\ d\psi'' + f\phi - \frac{U_d}{u_d} f_Q \phi + [f_Q - f_S u_d] \psi \end{pmatrix},$$

where

$$f = f\left(z(x) - U_d, \frac{U_d}{u_d}\right), \; f_S = f_S\left(z(x) - U_d, \frac{U_d}{u_d}\right), \; f_Q = f_Q\left(z(x) - U_d, \frac{U_d}{u_d}\right).$$

Since

$$\mu'\left(\frac{U_d}{u_d}\right) > 0, \quad \text{and} \quad f\left(z(x) - U_d, \frac{U_d}{u_d}\right) - \frac{U_d}{u_d} f_Q\left(z(x) - U_d, \frac{U_d}{u_d}\right) \geq 0,$$

then the linear operator L is cooperative type. From [19], L and its adjoint operator L^* have a principal eigenvalue $\theta_1 \in R$ with positive principal eigenfunctions. We denote the principal eigenfunction associated with L^* by (ϕ_1, ψ_1). On the other hand, one can also show that the mapping $d \mapsto (u_d, U_d)$ is continuously differentiable, and the derivative $\left(\frac{\partial u_d}{\partial d}, \frac{\partial U_d}{\partial d}\right)$ satisfies

$$L\left(\frac{\partial u_d}{\partial d}, \frac{\partial U_d}{\partial d}\right) = -(u_d'', U_d'') = \left(\mu\left(\frac{U_d}{u_d}\right)u_d, f\left(z(x) - U_d, \frac{U_d}{u_d}\right)u_d\right).$$

Let $\langle \cdot, \cdot \rangle$ be the inner product of $L^2((0,1)) \times L^2((0,1))$. Then one obtain that $\theta_1 < 0$ by

$$\begin{aligned}
&\theta_1\left\langle\left(\frac{\partial u_d}{\partial d}, \frac{\partial U_d}{\partial d}\right), (\phi_1, \psi_1)\right\rangle = \left\langle\left(\frac{\partial u_d}{\partial d}, \frac{\partial U_d}{\partial d}\right), \theta_1(\phi_1, \psi_1)\right\rangle \\
=&\left\langle\left(\frac{\partial u_d}{\partial d}, \frac{\partial U_d}{\partial d}\right), L^*(\phi_1, \psi_1)\right\rangle = \left\langle L\left(\frac{\partial u_d}{\partial d}, \frac{\partial U_d}{\partial d}\right), (\phi_1, \psi_1)\right\rangle \\
=&\left\langle\left(\mu\left(\frac{U_d}{u_d}\right)u_d, f\left(z(x) - U_d, \frac{U_d}{u_d}\right)u_d\right), (\phi_1, \psi_1)\right\rangle > 0,
\end{aligned}$$

since $\frac{\partial u_d}{\partial d} < 0$, $\frac{\partial U_d}{\partial d} < 0$ from part 1, $\phi_1, \psi_1 > 0$ as (ϕ_1, ψ_1) is the principal eigenfunction, and $\mu\left(\frac{U_d}{u_d}\right)u_d > 0$, $f\left(z(x) - U_d, \frac{U_d}{u_d}\right)u_d > 0$ from $(H1)$ and $(H2)$. This implies that (u_d, U_d) is linearly stable (thus locally asymptotically stable) with respect to the dynamics of (7). □

Now we are ready to state the main result of this section about the existence of a threshold diffusion coefficient.

Theorem 2.3. *Suppose that $d > 0$, f, μ satisfy $(H1)$ and $(H2)$. Then there exists a $d_0 > 0$ such that*

1. *If $d \geq d_0$, then there is no steady state solution in Δ, and every solution of (7) with initial conditions in Δ satisfies $(u(\cdot,t), U(\cdot,t)) \to (0,0)$ as $t \to \infty$.*
2. *If $0 < d < d_0$, then (7) has a unique positive steady state solution (u_d, U_d) which is globally asymptotically stable in Δ. Moreover (u_d, U_d) is strictly decreasing in d such that*

$$\begin{aligned}
&\lim_{d \to d_0^-}(u_d(x), U_d(x)) = (0,0) \quad \textit{uniformly for } x \in [0,1], \textit{ and} \\
&\lim_{d \to 0^+}(u_d(x), U_d(x)) = (z(x)/Q_{\min}, z(x)) \quad \textit{uniformly for } x \in [0,1].
\end{aligned} \tag{16}$$

Proof. We define

$$d_0 = \sup_{d>0}\left\{(8) \text{ has a positive solution with this } d\right\}.$$

For any $d_a < d_0$, if (8) has a positive solution (u_a, U_a) with this $d = d_a$, then for any $d_b \in (0, d_a)$, (8) has a positive solution (u_b, U_b) for $d = d_b$ since we can use (u_a, U_a) as a lower solution, and (u_c, U_c) (a solution of (8) with $d = d_c \in (0, \min\{d_{min}, d_b\})$) as an upper solution to construct a solution for $d = d_b$ as in the proof of Lemma 2.2. Therefore for each $d < d_0$, (8) has a positive solution (u_d, U_d), and the solution is unique from part 6 of Proposition 2.1. For $d > d_0$, (8) has no positive solution from the definition of d_0.

Next we consider the limiting behavior of (u_d, U_d) as $d \to d_0^-$. Since (u_d, U_d) is strictly decreasing in d from the proof above, then

$$(u_0(x), U_0(x)) = \lim_{d \to d_0^-} (u_d(x), U_d(x))$$

exists. We prove that $u_0(x) \equiv 0$ and $U_0(x) \equiv 0$ for $x \in [0,1]$. Suppose this is not true. Define $\delta_d = ||u_d||_\infty$. Then $\lim_{d \to d_0^-} \delta_d = \delta_0 > 0$. Let $w_d = u_d/\delta_d$ and $W_d = U_d/\delta_d$, then (w_d, W_d) satisfies

$$\begin{cases} dw_d'' + \mu\left(\frac{W_d}{w_d}\right) w_d = 0, & x \in (0,1), \\ dW_d'' + f\left(z(x) - \delta_d W_d, \frac{W_d}{w_d}\right) w_d = 0, & x \in (0,1), \\ w_d'(0) = w_d'(1) + \gamma w_d(1) = 0, \\ W_d'(0) = W_d'(1) + \gamma W_d(1) = 0. \end{cases} \tag{17}$$

Since $\{(u_d, U_d) : d_0 - \epsilon < d < d_0\}$ and $\{Q_d = U_d/u_d = W_d/w_d : d_0 - \epsilon < d < d_0\}$ are uniformly bounded from part 2 of Proposition 2.1, and f, g are continuously differentiable, then (w_d, W_d) is bounded in $C^3([0,1])$. Then from Ascoli-Arzela Theorem, there exists a sequence $\{d^i : i \geq 1\}$ such that $d^{i+1} > d^i$ and $\lim_{i\to\infty} d^i = d_0$, and

$$(w_{d^i}, W_{d^i}) \to (w_0, W_0), \qquad \text{in } \ C^2([0,1]), \quad \text{as } \ i \to \infty.$$

Then (w_0, W_0) satisfies

$$\begin{cases} d_0 w_0'' + \mu\left(\frac{W_0}{w_0}\right) w_0 = 0, & x \in (0,1), \\ d_0 W_0'' + f\left(z(x) - \delta_0 W_0, \frac{W_0}{w_0}\right) w_0 = 0, & x \in (0,1), \\ w_0'(0) = w_0'(1) + \gamma w_0(1) = 0, \\ W_0'(0) = W_0'(1) + \gamma W_0(1) = 0. \end{cases} \tag{18}$$

Since $||w_d||_\infty = 1$, then $||w_0||_\infty = 1$ and $||W_0||_\infty \geq Q_{min}||w_0||_\infty > 0$. Since $h_1 = \mu(W_0/w_0) > 0$ on $[0,1]$, then w_0 must be positive for $x \in [0,1]$. This implies that $u_0(x) = \delta_0 w_0(x) > 0$, $U_0(x) \geq Q_{min} u_0(x) > 0$ for $x \in [0,1]$, and (u_0, U_0) is a positive solution of (8) with $d = d_0$.

Since $u_0 > 0$ and $U_0 > 0$, then from Lemma 2.2 we know that (u_0, U_0) is linearly stable thus a non-degenerate solution of (8). By applying the implicit function theorem to F defined in (15), we obtain that for $d \in (d_0 - \varepsilon, d_0 + \varepsilon)$ for some $\varepsilon > 0$, (8) has a unique solution $(\tilde{u}_d, \tilde{U}_d)$ near (u_0, U_0). Apparently $\tilde{u}_d > 0$ and $\tilde{U}_d > 0$ for d close to d_0 since $u_0 > 0$ and $U_0 > 0$. This contradicts with the definition of d_0 as the supremum of d for the existence of positive solutions to (8). Therefore $u_0 \equiv 0$ and $U_0 \equiv 0$.

Finally we prove the limiting behavior of (u_d, U_d) as $d \to 0^+$. Since (u_d, U_d) is decreasing in d and $0 < U_d(x) < z(x)$, then for $d \in (0, \delta)$, there exists $C > 0$ such that $0 < C < U_d(x) < z(x)$ and $0 < C < u_d(x) < z(x)/Q_{\min}$. Since both u_d and U_d are monotone in d and uniformly bounded, then there exists a measurable $\tilde{Q}$ such that $U_d/u_d \to \tilde{Q}$ pointwisely as $d \to 0^+$. Since μ is continuous, then we also have $\mu(U_d/u_d) \to \mu(\tilde{Q})$ pointwisely as $d \to 0^+$. Integrating the equation of u in (8) and applying the boundary conditions, we obtain

$$-d\gamma u_d(1) + \int_0^1 \mu\left(\frac{U_d}{u_d}\right) u_d dx = 0. \tag{19}$$

Since $u_d(1)$ is bounded as $d \to 0^+$, and $0 < C < u_d(x) < z(x)/Q_{\min}$, then

$$\lim_{d\to 0^+} \int_0^1 \mu\left(\frac{U_d}{u_d}\right) u_d dx = \lim_{d\to 0^+} \int_0^1 \mu\left(\frac{U_d}{u_d}\right) dx = 0.$$

From Lebesgue's Dominated Convergence Theorem, we have

$$\int_0^1 \mu\left(\tilde{Q}\right) dx = \lim_{d\to 0^+} \int_0^1 \mu\left(\frac{U_d}{u_d}\right) dx = 0.$$

From the condition $(H1)$ and $\tilde{Q} \geq Q_{min}$, we must have $\tilde{Q}(x) \equiv Q_{min}$. By integrating the equation of U in (8) and applying the boundary conditions, we obtain

$$-d\gamma U_d(1) + \int_0^1 f\left(z(x) - U_d, \frac{U_d}{u_d}\right) u_d dx = 0. \tag{20}$$

Hence

$$\lim_{d\to 0^+} \int_0^1 f\left(z(x) - U_d, \frac{U_d}{u_d}\right) u_d dx = 0.$$

Then similar to the argument above, $z(x) - U_d(x) \to 0$ pointwisely as $d \to 0^+$, and since $U_d/u_d \to Q_{\min}$ as $d \to 0^+$, then $u_d \to z(x)/Q_{\min}$. This proves that $(u_d, U_d) \to (z(x)/Q_{min}, z(x))$ uniformly as $d \to 0^+$. The dynamical behavior in the statement of the theorem follows form part 6 of Proposition 2.1. $\square$

We remark that the curve of positive steady state solutions $\Gamma_1 = \{(d, u_d, U_d) : 0 < d < d_0\}$ connects to the line $\Gamma_0 = \{(d, 0, 0) : d > 0\}$, so in some sense the curve Γ_1 bifurcates from Γ_0 at $d = d_0$. It is not a bifurcation in the classical sense since $(0, 0)$ is not a classical steady state of the system and the system (7) is not defined for $(u, U) = (0, 0)$. On the other hand, as $d \to d_0$, although u_d and U_d both approach to zero, their quotient $Q_d(x) = U_d(x)/u_d(x)$ (or equivalently the stored nutrient per cell) approaches to a fixed profile. Indeed we define a change of variable

$$U(x) = u(x)Q(x), \tag{21}$$

then one can calculate that the steady state (u, Q) satisfies the equation

$$\begin{cases} du'' + \mu(Q)u = 0, & x \in (0,1), \\ dQ'' + 2d(\ln u)'Q' - \mu(Q)Q + f(z(x) - uQ, Q) = 0, & x \in (0,1), \\ u'(0) = u'(1) + \gamma u(1) = 0, \\ Q'(0) = Q'(1) = 0. \end{cases} \tag{22}$$

Let $w = u/||u||_\infty$, then (w, Q) satisfies

$$\begin{cases} dw'' + \mu(Q)w = 0, & x \in (0,1), \\ dQ'' + 2d(\ln w)'Q' - \mu(Q)Q + f(z(x) - ||u||_\infty wQ, Q) = 0, & x \in (0,1), \\ w'(0) = w'(1) + \gamma w(1) = 0, \\ Q'(0) = Q'(1) = 0. \end{cases} \tag{23}$$

Because of the boundedness of $(w_d, Q_d) = (u_d/||u_d||_\infty, U_d/u_d)$ in as $d \to d_0$, then $\lim_{d\to d_0}(w_d, Q_d) = (w_0, Q_0)$ exists and satisfies

$$\begin{cases} d_0 w_0'' + \mu(Q_0)w_0 = 0, & x \in (0,1), \\ d_0 Q_0'' + 2d_0(\ln w_0)'Q_0' - \mu(Q_0)Q_0 + f(z(x), Q_0) = 0, & x \in (0,1), \\ w_0'(0) = w_0'(1) + \gamma w_0(1) = 0, \\ Q_0'(0) = Q_0'(1) = 0. \end{cases} \tag{24}$$

Note that in Theorem 2.3, an explicit characterization of the threshold diffusion coefficient d_0 is not obtained, but (24) provides a nonlinear eigenvalue equation satisfied by (d_0, w_0, Q_0). For the ODE Droop model (1), the threshold dilution rate D_0 can be explicitly solved by algebraic equations $\mu(Q_0) = D_0$ and $D_0 Q_0 = f(S^{(0)}, Q_0)$ (see [21]). In the following proposition the monotonicity of the solutions $u_d(x)$, $U_d(x)$ as well as $Q_d(x)$ with respect to the spatial variable x is shown.

Proposition 2.4. *Suppose that $d > 0$, f, μ satisfy $(H1)$ and $(H2)$. Let $(u_d(x), U_d(x))$ be the unique positive solution of (8) for $0 < d < d_0$. Then*

1. *The functions $u_d(x)$ and $U_d(x)$ are strictly decreasing in x,*
2. *The functions $Q_d(x) = U_d(x)/u_d(x)$ and $S_d(x) = z(x) - U_d(x)$ are strictly decreasing in x.*

Proof. The monotonicity of u_d and U_d follows easily from the equations and boundary conditions in (8). Since μ and f are positive, then each of u_d and U_d is concave. Combining that $u_d'(0) = U_d'(0) = 0$, we obtain that each of u_d and U_d is strictly decreasing in x.

We notice that $S_d(x) = z(x) - U_d(x)$ is indeed the steady state resource function. That is, (S_d, u_d, U_d) is a steady state solution of the (5). Hence from $S_d''(x) = f(S_d, U_d/u_d)u_d > 0$, $S_d'(0) = -S^{(0)} < 0$ and $S_d'(1) = -\gamma S_d(1) < 0$, we conclude that $S_d(x)$ is strictly decreasing in x. To prove that $Q_d(x)$ is decreasing, we prove by contradiction. Suppose that $Q_d(x)$ is not strictly decreasing, then there exist $0 \le x_1 < x_2 \le 1$ such that $Q_1 = Q_d(x_1) < Q_d(x_2) = Q_2$, $Q_d'(x) > 0$ for $x \in (x_1, x_2)$, and $Q_d'(x_1) = Q_d'(x_2) = 0$. Then from the equation of Q_d in (22), we obtain that

$$-\mu(Q_1)Q_1 + f(S_d(x_1), Q_1) \le 0 \le -\mu(Q_2)Q_2 + f(S_d(x_2), Q_2).$$

By using $(H1)$ and $(H2)$, we obtain that $S_d(x_1) < S_d(x_2)$, which contradicts with that $S_d(x)$ is strictly decreasing. Hence $Q_d(x)$ must be strictly decreasing in x. □

We comment that the fact of u_d, U_d and S_d are all decreasing in x is not surprising as $x = 0$ is the source of the nutrient. But the decreasing property of the quota function $Q_d(x)$ is not obvious. Hence the monotonicity of $Q_d(x)$ in x proved in Proposition 2.4 shows that the microorganism in the chemostat tends to store more nutrient near the source.

Some numerical simulations of (u_d, U_d) and Q_d are shown in Fig. 1-2 with the growth function and uptake function given by

$$\mu(Q) = 1 - \frac{Q_{\min}}{Q}, \quad f(S, Q) = \frac{\rho_{\max}(Q_{\max} - Q)}{Q_{\max} - Q_{\min}} \cdot \frac{S}{k + S}, \tag{25}$$

with

$$\rho_{max} = 1,\ Q_{min} = 2,\ Q_{max} = 4,\ k = 1,\ \gamma = 1,\ S^{(0)} = 1. \tag{26}$$

For this set of growth, uptake functions and parameters, one can observe (through numerical simulation) that the critical diffusion coefficient $d_0 \approx 0.27$. The left panel of Fig. 1 shows the profile of (u_d, U_d) for $d = 0.26$, while the right panel shows the profile of Q_d. Since it is close to the bifurcation point, the amplitude of the steady state is small ($\max u_d \approx 0.009$ and $\max U_d \approx 0.022$). Fig. 2 shows the profiles of (u_d, U_d) and Q_d for $d = 0.1$.

In Fig. 3, the profile of functions $U_d(x)$ and $Q_d(x)$ for various d-values is plotted. We have proved in Theorem 2.3 that $U_d(x)$ is strictly decreasing in d and $U_d(x) \to z(x) = 2 - x$ as $d \to 0$. On the other hand it appears that $Q_d(x)$ is strictly increasing in d with $\lim_{d\to 0^+} Q_d(x) = Q_{min}$.

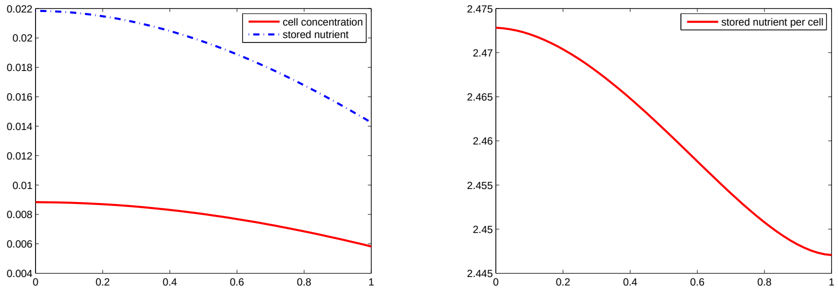

FIGURE 1. Profile of the functions $u_d(x)$, $U_d(x)$ and $Q_d(x)$ with growth and uptake functions as in (25) and (26). Here $d = 0.26$. Left: graph of $u_d(x)$ and $U_d(x)$; Right: graph of $Q_d(x)$. The horizontal axis is x $(0 \le x \le 1)$, and the vertical axis is the value of functions.

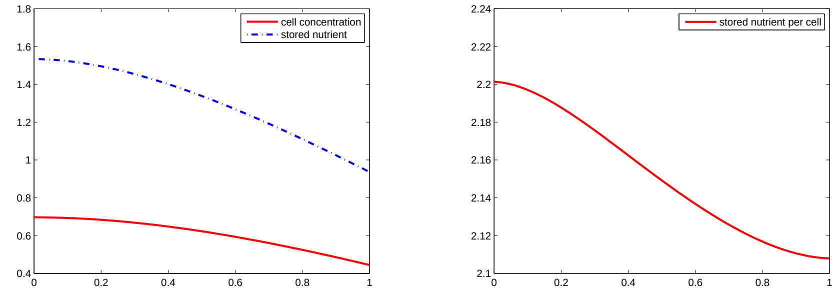

FIGURE 2. Profile of the functions $u_d(x)$, $U_d(x)$ and $Q_d(x)$ with growth and uptake functions as in (25) and (26). Here $d = 0.1$. Left: graph of $u_d(x)$ and $U_d(x)$; Right: graph of $Q_d(x)$. The horizontal axis is x $(0 \le x \le 1)$, and the vertical axis is the value of functions.

3. Competition model.

In this section we consider the dynamics of the two species competition model (4) with f_i, μ_i satisfying $(H1)$ and $(H2)$. Similar to the single species model, the dynamics of (4) can be reduced to the one of the limiting system:

$$\begin{cases} u_t = du_{xx} + \mu_1\left(\frac{U}{u}\right)u, & x \in (0,1),\ t > 0, \\ U_t = dU_{xx} + f_1\left(z(x) - U - V, \frac{U}{u}\right)u, & x \in (0,1),\ t > 0, \\ v_t = dv_{xx} + \mu_2\left(\frac{V}{v}\right)v, & x \in (0,1),\ t > 0, \\ V_t = dV_{xx} + f_2\left(z(x) - U - V, \frac{V}{v}\right)v, & x \in (0,1),\ t > 0, \\ w_x(0,t) = 0, w_x(1,t) + \gamma w(1,t) = 0, & w = u, U, v, V, \\ w(x,0) = w^0(x) \ge (\not\equiv) 0, & w = u, U, v, V. \end{cases} \tag{27}$$

As shown in [12], the feasible domain for initial value functions of (27) is

$$\Sigma = \Big\{(u^0, U^0, v^0, V^0) \in (C([0,1]))^4 : u^0(x) > 0,\ U^0(x) > 0,\ v^0(x) > 0,\ V^0(x) > 0,$$

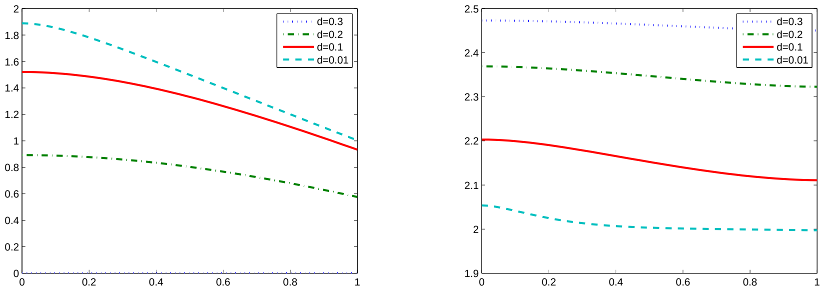

FIGURE 3. Profile of the function $U_d(x)$ and $Q_d(x)$ with growth and uptake functions as in (25) and (26). Here d takes the values $0.3, 0.2, 0.1$ and 0.01. Left: graph of $U_d(x)$; Right: graph of $Q_d(x)$. The horizontal axis is x $(0 \le x \le 1)$, and the vertical axis is the value of functions.

$$U^0(x) + V^0(x) \le z(x),\ \frac{U^0(x)}{u^0(x)} \ge Q_{\min,1},\ \frac{V^0(x)}{v^0(x)} \ge Q_{\min,2} \text{ on } [0,1]\Big\}.$$

The steady state equation of (27) is given by

$$\begin{cases} du'' + \mu_1\left(\frac{U}{u}\right)u = 0, & x \in (0,1), \\ dU'' + f_1\left(z(x) - U - V, \frac{U}{u}\right)u = 0, & x \in (0,1), \\ dv'' + \mu_2\left(\frac{V}{v}\right)v = 0, & x \in (0,1), \\ dV'' + f_2\left(z(x) - U - V, \frac{V}{v}\right)v = 0, & x \in (0,1), \\ u'(0) = u'(1) + \gamma u(1) = 0,\ U'(0) = U'(1) + \gamma U(1) = 0, & \\ v'(0) = v'(1) + \gamma v(1) = 0,\ V'(0) = V'(1) + \gamma V(1) = 0. & \end{cases} \tag{28}$$

Similar to the definition in (10), for $d > 0$, we define $Q_{c,i}(d) \ge Q_{\min,i}$ to be the unique number such that

$$\mu_i(Q_{c,i}(d)) = \eta_0(d), \quad i = 1, 2, \tag{29}$$

where $\eta_0(d)$ is the principal eigenvalue of (9). Furthermore for $i = 1, 2$, we define functions

$$\begin{aligned} g_i^{max}(d) &= \max_{x\in[0,1]} f_i(z(x), Q_{c,i}(d)) - \eta_0(d)Q_{c,i}(d) \\ &= \max_{x\in[0,1]} f_i(z(x), Q_{c,i}(d)) - \mu_i(Q_{c,i}(d))Q_{c,i}(d), \\ g_i^{min}(d) &= \min_{x\in[0,1]} f_i(z(x), Q_{c,i}(d)) - \eta_0(d)Q_{c,i}(d) \\ &= \min_{x\in[0,1]} f_i(z(x), Q_{c,i}(d)) - \mu_i(Q_{c,i}(d))Q_{c,i}(d). \end{aligned} \tag{30}$$

It is easy to verify that $g_i^*(d)$ is strictly decreasing in d for $* = max, min$. Indeed, for example, observing that $g_i^{max}(d) = f_i(z(1), Q_{c,i}(d)) - \mu_i(Q_{c,i}(d))Q_{c,i}(d)$, and

$$(g_i^{max})'(d) = [(f_i)_Q(z(1), Q_{c,i}(d)) - \mu_i'(Q_{c,i}(d))Q_{c,i}(d) - \mu_i(Q_{c,i}(d))]Q_{c,i}'(d) < 0,$$

since $(f_i)_Q < 0$, $\mu_i'(Q) > 0$, and $Q_{c,i}'(d) > 0$. Thus for each of $i = 1, 2$, there exist unique $d_{max,i}$ and $d_{min,i}$ such that

$$0 < d_{min,i} < d_{max,i},\quad g_i^{max}(d_{max,i}) = 0,\quad g_i^{min}(d_{min,i}) = 0. \tag{31}$$

From the results in Section 2, for each of $i = 1, 2$, there exists $d_{0,i}$ satisfying $d_{min,i} < d_{0,i} < d_{max,i}$, such that the population of the species i persists when $0 < d < d_{0,i}$, and it becomes extinct when $d > d_{0,i}$. In the following we assume that

$$d_{max,2} \leq d_{min,1}. \tag{32}$$

The assumption (32) implies that

$$0 < d_{min,2} < d_{0,2} < d_{max,2} \leq d_{min,1} < d_{0,1} < d_{max,1}. \tag{33}$$

Hence the species 2 requires a smaller threshold diffusion coefficient $d_{0,2}$ than the one $d_{0,1}$ for the species 1, or equivalently, the species 2 requires a larger critical patch size $L_{0,2}$ than the one $L_{0,1}$ for the species 1. This suggests that the species 1 is a superior competitor than the species 2. Indeed the assumption (32) holds if we assume that

$$\max_{x\in[0,1]} f_2(z(x), Q) \leq \min_{x\in[0,1]} f_1(z(x), Q), \quad \text{and } \mu_2(Q) < \mu_1(Q), \quad Q \geq Q_{min}, \tag{34}$$

where $Q_{min} = Q_{min,1} = Q_{min,2}$, as (34) implies that $Q_{c,1}(d) < Q_{c,2}(d)$ and

$$\max_{x\in[0,1]} f_2(z(x), Q_{c,2}) \leq \max_{x\in[0,1]} f_2(z(x), Q_{c,1}) \leq \min_{x\in[0,1]} f_1(z(x), Q_{c,1}).$$

Biologically (34) means that the species 1 has larger per capita nutrient uptake rate and larger growth rate than the species 2, which makes the species 1 a superior competitor.

By using the results in Section 2, for $d > 0$, the system (28) has a trivial generalized steady state solution $(0, 0, 0, 0)$, and possibly two semi-trivial generalized steady state solutions $(u_d, U_d, 0, 0)$ and $(0, 0, v_d, V_d)$. We assume that (32) is satisfied, then the trivial and semi-trivial generalized steady state solutions are on three curves in the space $\mathbb{R}^+ \times \Sigma$:

$$\begin{aligned} \Gamma_0 &= \{(d, 0, 0, 0, 0) : d > 0\}, \\ \Gamma_1 &= \{(d, u_d, U_d, 0, 0) : d_{0,1} > d > 0\}, \\ \Gamma_2 &= \{(d, 0, 0, v_d, V_d) : d_{0,2} > d > 0\}. \end{aligned} \tag{35}$$

For a generalized steady state solution of (27) with either $u = 0$ or $v = 0$, linear stability cannot be defined through linearized equation because of the singularity in the equations. Nevertheless we define that a generalized steady state solution (u_*, U_*, v_*, V_*) of (27) is locally asymptotically stable, if there exists a $\delta > 0$ such that when the initial condition satisfies $||(u_0, U_0, v_0, V_0) - (u_*, U_*, v_*, V_*)|| < \delta$, then $||(u(\cdot, t), U(\cdot, t), v(\cdot, t), V(\cdot, t)) - (u_*, U_*, v_*, V_*)|| < \delta$ for all $t > 0$ and

$$\lim_{t\to\infty} ||(u(\cdot, t), U(\cdot, t), v(\cdot, t), V(\cdot, t)) - (u_*, U_*, v_*, V_*)|| = 0,$$

and we define that (u_*, U_*, v_*, V_*) of (27) is globally asymptotically stable if the convergence holds for all $(u_0, U_0, v_0, V_0) \in \Sigma$.

Now we can prove the following global stability result following the results in Section 2.

Theorem 3.1. *Suppose that $d > 0$, f_i, μ_i satisfy $(H1)$ and $(H2)$ for $i = 1, 2$, and the condition (32) is satisfied. Then*

1. *If $d \geq d_{0,1}$, then $(0, 0, 0, 0)$ is globally asymptotically stable, and every solution of (27) with initial conditions in Σ satisfies*

$$\lim_{t\to\infty} (u(\cdot, t), U(\cdot, t), v(\cdot, t), V(\cdot, t)) = (0, 0, 0, 0).$$

2. *If* $d_{0,2} \le d < d_{0,1}$, *then* $(u_d, U_d, 0, 0)$ *is globally asymptotically stable, and every solution of* (27) *with initial conditions in* Σ *satisfies*

$$\lim_{t\to\infty}(u(\cdot,t),U(\cdot,t),v(\cdot,t),V(\cdot,t)) = (u_d,U_d,0,0).$$

Proof. (i) If $d \ge d_{0,1}$, then from (27), $(v(x,t),V(x,t))$ satisfies inequalities

$$\begin{aligned} v_t &= dv_{xx} + \mu_2\left(\frac{V}{v}\right)v,\\ V_t &= dV_{xx} + f_2\left(z(x) - U - V, \frac{V}{v}\right)v \le dV_{xx} + f_2\left(z(x) - V, \frac{V}{v}\right)v. \end{aligned}$$

Then by the comparison theorem and part 1 of Theorem 2.3, $\lim_{t\to\infty}(v(x,t),V(x,t)) = (0,0)$ uniformly in $x \in [0,1]$ since $d \ge d_{0,1} > d_{0,2}$. Similarly $\lim_{t\to\infty}(u(x,t),U(x,t)) = 0$ uniformly in $x\in[0,1]$.

(ii) If $d_{0,2} \le d < d_{0,1}$, then with the same proof, we have $\lim_{t\to\infty}(v(x,t),V(x,t)) = (0,0)$ uniformly in $x \in [0,1]$ since $d \ge d_{0,2}$. Then the limiting equations of the first two equations in (27) become

$$u_t = du_{xx} + \mu_1\left(\frac{U}{u}\right)u,\ \ U_t = dU_{xx} + f_1\left(z(x) - U, \frac{U}{u}\right)u,$$

with the same boundary conditions. Then $(u(\cdot,t),U(\cdot,t))$ converges to (u_d,U_d) as $t\to\infty$ from the part 2 of Theorem 2.3. □

We remark that Theorem 3.1 makes the result in Theorem 3.1 in [12] complete, since the result in [12] is equivalent to

1. If $d \ge d_{max,1}$, then the result in Theorem 3.1 part 1 holds.
2. If $d_{max,2} \le d < d_{min,1}$, then the result in Theorem 3.1 part 2 holds.

The results in Theorem 3.1 is more complete from the relations in (33).

To further consider the stability of the semi-trivial generalized steady state solutions $(u_d,U_d,0,0)$ and $(0,0,v_d,V_d)$ for $0 < d < d_{0,2}$, we define

$$\begin{aligned} \widetilde{g}_1^{max}(d) &= \max_{x\in[0,1]} f_1(z(x) - V_d(x), Q_{c,1}(d)) - \eta_0(d)Q_{c,1}(d)\\ &= \max_{x\in[0,1]} f_1(z(x) - V_d(x), Q_{c,1}(d)) - \mu_1(Q_{c,1}(d))Q_{c,1}(d),\\ \widetilde{g}_1^{min}(d) &= \min_{x\in[0,1]} f_1(z(x) - V_d(x), Q_{c,1}(d)) - \eta_0(d)Q_{c,1}(d)\\ &= \min_{x\in[0,1]} f_1(z(x) - V_d(x), Q_{c,1}(d)) - \mu_1(Q_{c,1}(d))Q_{c,1}(d), \end{aligned} \tag{36}$$

where $d\in(0,d_{0,2})$ and

$$\begin{aligned} \widetilde{g}_2^{max}(d) &= \max_{x\in[0,1]} f_2(z(x) - U_d(x), Q_{c,2}(d)) - \eta_0(d)Q_{c,2}(d)\\ &= \max_{x\in[0,1]} f_2(z(x) - U_d(x), Q_{c,2}(d)) - \mu_2(Q_{c,2}(d))Q_{c,2}(d),\\ \widetilde{g}_2^{min}(d) &= \min_{x\in[0,1]} f_2(z(x) - U_d(x), Q_{c,2}(d)) - \eta_0(d)Q_{c,2}(d)\\ &= \min_{x\in[0,1]} f_2(z(x) - U_d(x), Q_{c,2}(d)) - \mu_2(Q_{c,2}(d))Q_{c,2}(d), \end{aligned} \tag{37}$$

where $d\in(0,d_{0,1})$.

The following result connects the local stability of the semi-trivial steady state solutions to the functions $\widetilde{g}_i^*$ ($i = 1,2$, and $* = min, max$).

Proposition 3.2. *Let* $\widetilde{g}_i^*(d)$ *($i = 1, 2$, and $* = min, max$) be defined as above.*

1. *Suppose that $0 < d < d_{0,1}$. If $\widetilde{g}_2^{min}(d) > 0$, then the semi-trivial steady state solution $(u_d, U_d, 0, 0)$ is unstable; and if $\widetilde{g}_2^{max}(d) < 0$, then $(u_d, U_d, 0, 0)$ is locally asymptotically stable.*
2. *Suppose that $0 < d < d_{0,2}$. If $\widetilde{g}_1^{min}(d) > 0$, then the semi-trivial steady state solution $(0, 0, v_d, V_d)$ is unstable; and if $\widetilde{g}_1^{max}(d) < 0$, then $(0, 0, v_d, V_d)$ is locally asymptotically stable.*

Proof. The instability part is proved in Lemma 3.5 of [12], so we only prove the local stability part. For that purpose, we construct a different lower solution for the case $0 < d < d_{0,1}$ and $\widetilde{g}_2^{max}(d) < 0$. Since u_d and U_d are strictly positive, then there exists $\xi > 0$ such that $U_d(x) > \xi\phi_1(x)$, where ϕ_1 is the normalized positive principal eigenfunction defined in (9). For small $\epsilon > 0$, we define

$$\underline{Q}(\epsilon) := (\underline{u}, \underline{U}, \overline{v}, \overline{V}) = \left((1-\epsilon)u_d(x), (1-\epsilon)U_d(x), \frac{\epsilon\xi}{Q_{c,2}}\phi_1(x), \epsilon\xi\phi_1(x)\right).$$

It is easy to verify that that $\underline{Q}(\epsilon) \in \Sigma$, for $\varepsilon > 0$ sufficiently small, and $\underline{Q}(\epsilon)$ satisfies all boundary conditions. The following calculation verifies that $\underline{Q}(\epsilon)$ is a strict lower solution:

$$\begin{aligned}
&d\underline{u}_{xx} + \mu_1\left(\frac{\underline{U}}{\underline{u}}\right)\underline{u} = (1-\epsilon)\left[d(u_d)_{xx} + \mu_1\left(\frac{U_d}{u_d}\right)u_d\right] = 0 \geq 0,\\
&d\underline{U}_{xx} + f_1\left(z - \underline{U} - \overline{V}, \frac{\underline{U}}{\underline{u}}\right)\underline{u}\\
=&(1-\epsilon)\left[d(U_d)_{xx} + f_1\left(z - (1-\epsilon)U_d - \epsilon\xi\phi_1, \frac{U_d}{u_d}\right)u_d\right]\\
>&(1-\epsilon)\left[d(U_d)_{xx} + f_1\left(z - U_d, \frac{U_d}{u_d}\right)u_d\right] = 0,
\end{aligned}$$

and

$$\begin{aligned}
&d\overline{v}_{xx} + \mu_2\left(\frac{\overline{V}}{\overline{v}}\right)\overline{v} = \frac{\epsilon\xi}{Q_{c,2}}[d\phi_1'' + \mu_2(Q_{c,2})\phi_1]\\
=&\frac{\epsilon\xi}{Q_{c,2}}[d\phi_1'' + \eta_0(d)\phi_1] = 0 \leq 0,\\
&d\overline{V}_{xx} + f_2\left(z(x) - \underline{U} - \overline{V}, \frac{\overline{V}}{\overline{v}}\right)\overline{v}\\
=&\frac{\epsilon\xi}{Q_{c,2}}[dQ_{c,2}\phi_1'' + f_2(z - (1-\epsilon)U_d - \epsilon\xi\phi_1, Q_{c,2})\phi_1]\\
=&\frac{\epsilon\xi}{Q_{c,2}}[-\eta_0(d)Q_{c,2} + f_2(z - (1-\epsilon)U_d - \epsilon\xi\phi_1, Q_{c,2})]\phi_1 < 0,
\end{aligned}$$

provided that $\widetilde{g}_2^{max}(d) < 0$ and $\epsilon > 0$ is small enough. Hence $\underline{Q}(\epsilon)$ is a strict lower solution of (27) in the type-K order. For initial condition P in Σ, we can choose P sufficiently close to $(u_d, U_d, 0, 0)$ so that $\underline{Q}(\epsilon) \ll_K \Psi_t(P)$, then $\omega(P) = Q^* = (u_d, U_d, 0, 0)$. □

From Proposition 3.2, we obtain the following criterion on the existence of coexistence equilibria:

Theorem 3.3. *Suppose that* f_i, μ_i *satisfy* $(H1)$ *and* $(H2)$ *for* $i = 1, 2$, *and the condition* (32) *is satisfied. Assume that* $0 < d < d_{0,2}$, *and let* $\widetilde{g}_i^*(d)$ ($i = 1, 2$, *and* $* = min, max$) *be defined as* (36) *and* (37).

1. *If* $\widetilde{g}_1^{min}(d) > 0$ *and* $\widetilde{g}_2^{min}(d) > 0$, *then there is 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*
$$\omega(P) \subset [E^-, E^+]_K \cap \Sigma \quad \text{for any } P \in \Sigma.$$
The system (27) *is uniformly persistent and* $\Psi_t(P)$ *tends to a steady state for* P *in an open and dense subset in* Σ.
2. *If* $\widetilde{g}_1^{max}(d) < 0$ *and* $\widetilde{g}_2^{max}(d) < 0$, *then each of* $P^* = (0, 0, v_d, V_d)$ *and* $Q^* = (u_d, U_d, 0, 0)$ *is locally asymptotically stable in* Σ, *and there exists at least one positive steady state solution of* (27) *in* Σ.

Proof. The first part is proved in Theorem 3.2 of [12]. The second part follows from the result in [14]. ☐

We comment that if we assume that

$$f_2(S,Q) \le f_1(S,Q), \quad \text{and } \mu_2(Q) < \mu_1(Q), \quad S \ge 0, \quad Q \ge Q_{min}, \tag{38}$$

then the species 1 is a superior competitor than the species 2. Note that the condition for f_i in (38) is pointwisely defined while the one in (34) is not. The condition (38) is easily satisfied if we assume, for example

$$\mu_{1\infty} > \mu_{2\infty}, \; K_1 = K_2, \; Q_{min,1} = Q_{min,2}, \tag{39}$$

in (2), and

$$\rho_{max,1} \ge \rho_{max,2}, \; k_1 < k_2, \;\; Q_{min,1} = Q_{min,2}, \; Q_{max,1} = Q_{max,2}, \tag{40}$$

in (3). Under the condition (38), one can prove that for $0 < d < d_{0,2}$, for the semi-trivial solutions $P^* = (0, 0, v_d, V_d)$ and $Q^* = (u_d, U_d, 0, 0)$, we have $v_d(x) < u_d(x)$ and $V_d(x) < U_d(x)$. Hence $\widetilde{g}_2^*(d) \le \widetilde{g}_1^*(d)$ for $d \in (0, d_{0,2})$ and $* = min, max$. This suggests that three scenarios are possible for $d \in (0, d_{0,2})$ (following [14]):

1. $Q^* = (u_d, U_d, 0, 0)$ is locally asymptotically stable, and $P^* = (0, 0, v_d, V_d)$ is unstable.
2. Both of Q^* and P^* are locally asymptotically stable, and there exists at least one positive steady state solution.
3. Both of Q^* and P^* are unstable, the system is persistent, and there exists at least one positive steady state solution.

From the monotonicity of the steady state (u, U) (and also (Q, S)) of (5) in spatial variable x proved in Proposition 2.4, we can also obtain these properties for components of the semi-trivial steady state Q^* and P^*. Here we point out that such monotonicity also holds for a coexistence steady state. Let $(u_*(x), U_*(x), v_*(x), V_*(x))$ be a positive steady state of (4). Define $Q_1(x) = U_*(x)/u_*(x)$ and $Q_2(x) = V_*(x)/v_*(x)$. Then Q_1 and Q_2 satisfy

$$\begin{cases} dQ_1'' + 2d(\ln u_*)'Q_1' - \mu_1(Q_1)Q_1 + f_1(z(x) - u_*Q_1 - v_*Q_2, Q_1) = 0, & x \in (0,1), \\ dQ_2'' + 2d(\ln v_*)'Q_2' - \mu_2(Q_1)Q_2 + f_2(z(x) - u_*Q_1 - v_*Q_2, Q_2) = 0, & x \in (0,1), \\ Q_1'(0) = Q_1'(1) = Q_2'(0) = Q_2'(1) = 0. \end{cases}$$

Then by using the same proof as in Proposition 2.4, we can prove the following result about the monotonicity of the coexistence steady state with respect to x.

Proposition 3.4. *Suppose that* $d > 0$*,* f_i, μ_i *satisfy* $(H1)$ *and* $(H2)$ *for* $i = 1, 2$. *Let* $(u_*(x), U_*(x), v_*(x), V_*(x))$ *be a positive steady state of* (4)*. Then*

1. *The functions* $u_*(x)$*,* $U_d(x)$*,* $v_*(x)$ *and* $V_*(x)$ *are strictly decreasing in* x*,*
2. *The functions* $Q_1(x) = U_*(x)/u_*(x)$*,* $Q_2(x) = V_*(x)/v_*(x)$ *and* $S_*(x) = z(x) - U_*(x) - V_*(x)$ *are strictly decreasing in* x*.*

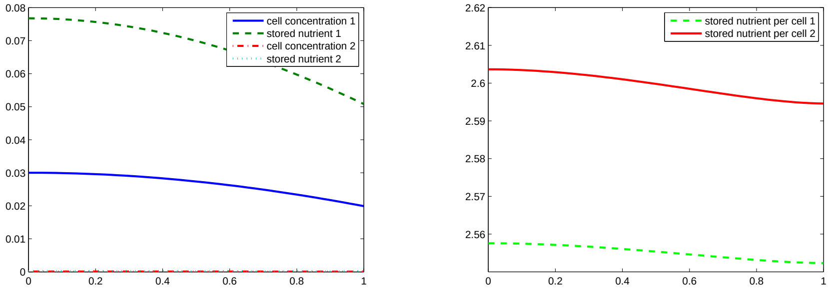

FIGURE 4. Profile of the competition exclusion steady state (left) and $Q_1(x)$, $Q_2(x)$ (right) with growth and uptake functions as in (41) and (42). Here $d = 0.38$. The horizontal axis is x $(0 \leq x \leq 1)$, and the vertical axis is the value of functions.

Finally some numerical simulations of steady state solutions to (27) are shown in Fig. 4-5 with

$$\mu_i(Q_i) = \mu_{i\infty}\left(1 - \frac{Q_{\min,i}}{Q_i}\right), \quad f_i(S, Q_i) = \frac{\rho_{\max,i}(Q_{\max,i} - Q_i)}{Q_{\max,i} - Q_{\min,i}} \cdot \frac{S}{k_i + S}, \tag{41}$$

with

$$\begin{aligned} &\rho_{max,1} = \rho_{max,2} = 1,\ Q_{min,1} = Q_{min,2} = 2,\ Q_{max,1} = Q_{max,2} = 4,\ \gamma = 1,\\ &\mu_{1\infty} = 1.2,\ \mu_{2\infty} = 1,\ k_1 = 1,\ k_2 = 2,\ S^{(0)} = 8. \end{aligned} \tag{42}$$

Note that the growth, uptake functions and parameters are chosen in (41)-(42) so that (39) and (40) are satisfied, which implies that species 1 is a superior competitor than species 2. In this case, $d_{0,1} \approx 0.4$. In Fig. 4, a competition exclusion is achieved when d is slightly smaller than $d_{0,1}$ with species 2 becoming extinct. We notice that the asymptotic limit of $Q_2(x,t) = V(x,t)/v(x,t)$ is higher than that of $Q_1(x,t) = U(x,t)/u(x,t)$ (see the right panel of Fig. 4). When d is smaller, it appears that a coexistence steady state becomes the asymptotic limit of the solution. Fig. 5 shows the profile of a coexistence steady state for $d = 0.1$. In the coexistence steady state $C = (u_*, U_*, v_*, V_*)$, u_* is much larger than v_* and U_* is much larger than V_*, but (v_*, V_*) is not zero (see the lower panel of Fig. 5). Hence it is likely that a branch of coexistence steady state solutions “bifurcate” from the branch of semi-trivial solutions $(d, u_d, V_d, 0, 0)$ near $d = 0.1$. Indeed the (stable) coexistence steady state is observed for all $d \in (0, 0.1)$. The profile of a coexistence steady state for very small d $(d = 0.01)$ is shown in Fig. 6. In this case, again $U_*(x) + V_*(x) \approx z(x)$ (this can be analytically proved using similar proof as in Section 2), and Q_1, Q_2 are both near $Q_{min} = Q_{min,1} = Q_{min,2} = 2$. However while (v_*, V_*) is still smaller than (u_*, U_*), the share of the resource taken by species 2 is much larger than the one for larger d. This shows a quite robust coexistence is

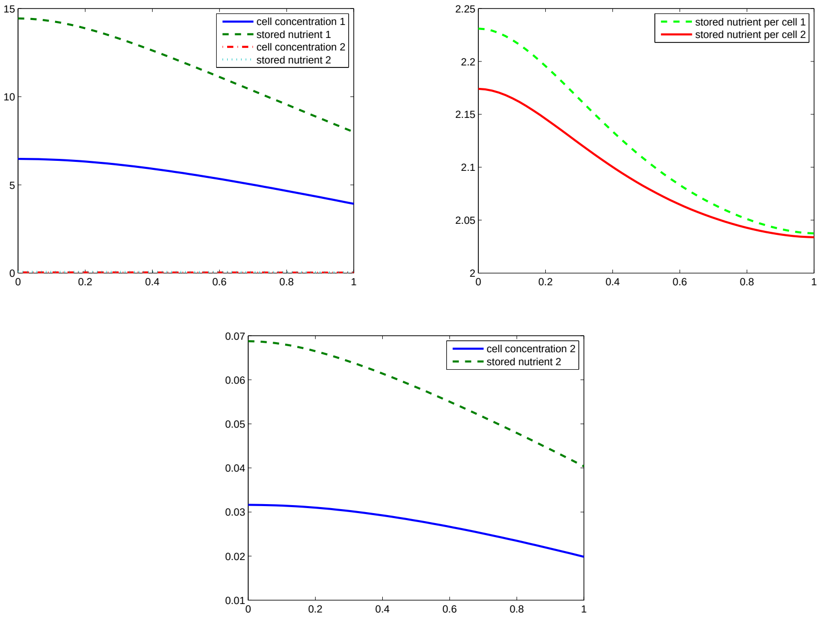

FIGURE 5. Profile of the coexistence steady state (upper left) and $Q_1(x)$, $Q_2(x)$ (upper right) with growth and uptake functions as in (41) and (42). The lower panel shows the profile of steady state (v, V) in a different scale. Here $d = 0.10$. The horizontal axis is x $(0 \le x \le 1)$, and the vertical axis is the value of functions.

achieved for small diffusion rate or a large spatial domain even though species 1 is a superior competitor.

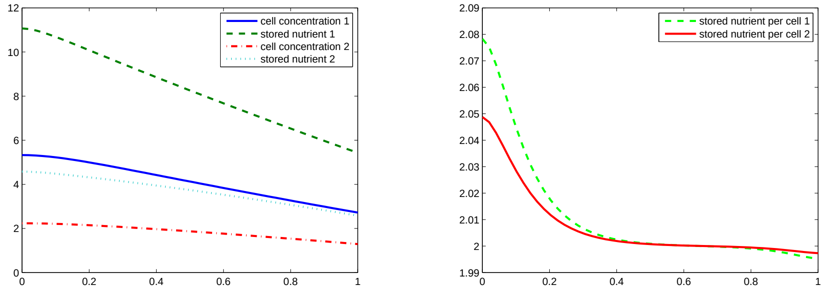

FIGURE 6. Profile of the coexistence steady state (left) and $Q_1(x)$, $Q_2(x)$ (right) with growth and uptake functions as in (41) and (42). Here $d = 0.01$. The horizontal axis is x $(0 \le x \le 1)$, and the vertical axis is the value of functions.

4. **Conclusions.** The dynamics of a reaction-diffusion two-species competitive system for an unstirred chemostat with internal storage is completed. A first threshold

diffusion coefficient $d_{0,1}$ exists so that when the system diffusion coefficient d is above $d_{0,1}$, both species become extinct. There is a second threshold diffusion coefficient $d_{0,2}$ so that species 1 always wipes out species 2 for $d_{0,2} < d < d_{0,1}$, assuming that species 1 is a superior competitor. When $0 < d < d_{0,2}$, the two competing species may reach a coexistence steady state. The conditions on parameters for the coexistence is not quite explicit, but coexistence has been observed for all small diffusion coefficient values. These findings are compatible with early studies for Monod type chemostat models with fixed yields. It is known that for the well-mixed fixed yield (ODE) model, competition exclusion holds for most cases so that only one species can survive in the chemostat [9, 11], while for the unstirred fixed yield (reaction-diffusion) model, coexistence is possible for certain parameter ranges [15]. Together with earlier work in [12], here we establish a qualitative picture for the unstirred variable yield (reaction-diffusion) Droop model in which coexistence can be achieved at small diffusion rate, which is not likely for the well-stirred (ODE) Droop model [21]. While the two parallel classes of models show some similarity in qualitative behavior, the Droop cell-quota model is known to have several advantages over the Monod model [17, 18].

A richer structure for the quota function $Q(x)$ is also revealed through our qualitative analysis. While the quota Q is a constant in well-stirred ODE model, the spatial heterogeneity in the unstirred model makes the quota function to be spatially heterogenous as well. Moreover we prove that the $Q(x)$ is always a decreasing function of x from the nutrient influx point towards the outflux point, and numerical simulations show that $Q(x)$ is increasing in d so that when d is very small, the quota is close to the minimum.

From a mathematical point of view, the analysis for the Droop type model (4) is more difficult due to the singularity caused by the ratio U/u at the extinction steady state. This makes standard techniques such as linearization and bifurcation hard to be applied at the extinction steady state. This difficulty does not occur in ODE Droop model as one can analyze the equations of the population u and the quota Q, which do not have a singularity. In this paper and [12], we avoid to use linearization and bifurcation near the extinction steady state, but use monotone method and continuation method for the analysis. The disadvantage for such approach is that we cannot obtain an explicit expression for the threshold diffusion coefficient d_0, which was expressed as a principal eigenvalue for the diffusive Monod model. Another unanswered question for both diffusive Droop model and Monod model is the parameter ranges for the two semi-trivial steady state solutions to be both stable or both unstable. When such conditions are met, then the abstract theory for general competition models in [14] can be applied to ensure the existence of coexistence steady states.

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