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Global stability in a chemostat with multiple nutrients

by

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ABSTRACT

We study a single species in a chemostat, limited by two nutrients, and separate nutrient uptake from growth. For a broad class of uptake and growth functions it is proved that a nontrivial equilibrium may exist. Moreover, if it exists it is unique and globally stable, generalizing a result in [9].

1 Introduction

In 1950, Monod [13] proposed his now classic model of the nutrient-limited growth of microorganisms. In this model, a single nutrient limits growth and growth is directly coupled to nutrient uptake. Two separate modifications of this model have been made. The first accounts for the observation that nutrient uptake and growth are often decoupled. Nutrient uptake increases the internal stores of nutrients upon which growth depends [1, 2]. The second extends the model to include multiple potentially limiting nutrients[10, 19]. When both nutrients are essential for growth, typically the nutrient in shortest supply limits growth [3], known as Liebig's law of the minimum [3, 14]. The mathematical theory and biological implications of both of these modifications of Monod's model have been studied extensively, both in terms of the growth of a single species and competition between two species (decoupling of uptake and growth: [4, 16]; multiple limiting nutrients: [10, 11, 12, 5, 19]).

Only recently have these two modifications of the Monod model been jointly examined. Legović and Cruzado [9] studied a chemostat model with Michaelis- Menten uptake functions, Droop's function relating growth rate to the internal store of the limiting nutrient, and Liebig's law of the minimum. They solved for equilibria and showed that if a nontrivial equilibrium exists, it is unique with a stable linearization. In [7] this model was further analyzed during the exponential growth phase and at equilibrium, and extensively related the model results to chemostat studies. This model has also been used as the basis of an evolutionary model determining the optimal chemical stoichiometry of phytoplankton [8].

Here, we further analyze a more general class of models of the nutrient- limited growth of microorganisms that includes the models studied by [9, 7]. Using techniques from monotone dynamic systems, we prove uniqueness and global stability of the nontrivial equilibrium for a broad class of uptake and growth functions. From mathematical point of view, the key idea is to transform the system into a monotone system by means of a nonlinear state transformation. A particular global stability result due to J.F. Jiang [6] is then used to prove the main result.

We will consider the following chemostat model which is operated at a constant dilution rate a:

$$\begin{aligned} \dot{R}_i &= a(R_{\text{in},i} - R_i) - f_i(R_i)B, \; i = 1,2 \\ \dot{Q}_i &= f_i(R_i) - Q_i \min_j \left(\mu_j(Q_j)\right), \; i = 1,2 \\ \dot{B} &= B[\min_j \left(\mu_j(Q_j)\right) - a] \end{aligned} \tag{1}$$

where R_i is the nutrient concentration of the i-th nutrient, Q_i is the cell quota of the i-th nutrient (this is the average amount of the i-th nutrient per cell) and B is the concentration of the organism (number of cells per unit volume), feeding on both nutrients. Note that loss of organism is only due to washout from the chemostat. Death of the organism inside the chemostat is neglected.

Nutrient uptake is governed by the nutrient uptake rate functions $f_i(R_i)$, both of which are assumed to satisfy the following hypotheses:

1. (*smoothness*) The functions $f_i : \mathbb{R}_+ \to \mathbb{R}$ are continuously differentiable and $f_i(0) = 0$.

2. (*strict monotonicity*) $f_i' > 0$ on $\mathbb{R}_+$.

A typical choice for f_i would be a Monod (or Michaelis-Menten) function:

$$f_i(R_i) = \frac{m_i R_i}{a_i + R_i}$$

for certain positive constants m_i and a_i.

Growth of the organism is assumed to follow 'the law of the minimum', a standard assumption in multiple nutrient models [3, 14]. This is reflected in the model by the presence of the minimum function, where the minimum is taken over both growth rate functions $\mu_j(Q_j)$, which are assumed to satisfy the following:

1. (*smoothness*) $\mu_j(Q_j) : [Q_{\min,j}, \infty) \to \mathbb{R}$ for some positive constant $Q_{\min,j}$, is continuously differentiable and $\mu_j(Q_{\min,j}) = 0$.

2. (*strict monotonicity*) $\mu_j' > 0$ on $[Q_{\min,j}, \infty)$.

A typical choice for μ_j has been proposed by Droop:

$$\mu_j(Q_j) = \mu_j(1 - \frac{Q_{\min,j}}{Q_j}) \text{ for } Q \in [Q_{\min,j}, \infty) \tag{2}$$

for certain positive constants μ_j and $Q_{\min,j}$.

The model studied in [9, 7] assumes that the uptake functions are Monod functions and that the growth functions take Droop's form.

Biologically meaningful initial conditions for system (1) are given by:

$$R_i(0) \geq 0,\ Q_i(0) \geq Q_{\min,i},\ B(0) > 0,\quad i = 1, 2$$

but we will analyze this system on the larger set

$$\mathcal{P} = \{(R_1, R_2, Q_1, Q_2, B) \in \mathbb{R}_+^5 \mid R_i \geq 0,\ Q_i \geq Q_{\min,i},\ B \geq 0,\ i = 1, 2\}$$

Note that $\mathcal{P}$ is a positively invariant set for (1).

We start the analysis by rescaling the system:

$$\bar{t} = at,\ \bar{R}_i = R_i/R_{\text{in},i}, \bar{Q}_i = Q_i/Q_i^*,\ \bar{B} = B/B^*,\ i = 1, 2$$

where Q_i^* and B^* are positive constants satisfying $B^* Q_i^* = R_{\text{in},i}$ for $i = 1, 2$. Defining new uptake functions and growth rate functions as follows:

$$\bar{f}_i(\bar{R}_i) = \frac{B^*}{aR_{\text{in},i}} f_i(R_{\text{in},i}\bar{R}_i),\ \bar{\mu}_i(\bar{Q}_i) = \frac{1}{a}\mu(Q_i^* Q_i)$$

noting that these functions satisfy the exact same hypotheses as their corresponding unbarred relatives, and dropping bars, leads to the following scaled system:

$$\begin{aligned}
\dot{R}_i &= 1 - R_i - f_i(R_i)B,\ i = 1, 2 \\
\dot{Q}_i &= f_i(R_i) - Q_i \min_j (\mu_j(Q_j)),\ i = 1, 2 \\
\dot{B} &= B[\min_j (\mu_j(Q_j)) - 1]
\end{aligned} \tag{3}$$

Notice that the state space $\mathcal{P}$ is unaffected by this rescaling operation (with $Q_{\min,i}$ now equal to $Q_{\min,i}/Q_i^*$).

2 Equilibria

We show that system (3) has at most 2 equilibria, one corresponding to extinction of the organism which always exists, and possibly a second one corresponding to the presence of the organism.

2.1 Unique extinction equilibrium point

Consider the following equations:

$$\begin{aligned} f_1(1) - Q_1 \min_j (\mu_j(Q_j)) &= 0 \\ f_2(1) - Q_2 \min_j (\mu_j(Q_j)) &= 0 \end{aligned} \tag{4}$$

Solutions of (4) determine the Q_1 and Q_2 values of extinction equilibria of system (3) for which $R_1 = R_2 = 1$ and $B = 0$.

There are two cases:

Case 1: $f_2(1)/f_1(1) \geq Q_{\min,2}/Q_{\min,1}$.

In this case we find that for every $Q_1 \geq Q_{\min,1}$, there holds that $[f_2(1)/f_1(1)]Q_1 \geq Q_{\min,2}$ and therefore (4) is equivalent to:

$$\begin{aligned} Q_1 \min\left(\mu_1(Q_1), \mu_2\left(\frac{f_2(1)}{f_1(1)}Q_1\right)\right) &= f_1(1) \\ Q_2 &= \frac{f_2(1)}{f_1(1)}Q_1 \end{aligned} \tag{5}$$

Now notice that the left hand side of the first equation in (5) is strictly increasing in Q_1, takes the value 0 at $Q_1 = Q_{\min,1}$ and has limit $+\infty$ as $Q_1 \to \infty$. Therefore there is a unique solution $\bar{Q}_1 \in (Q_{\min,1}, \infty)$ for the first equation in (5). Inserting $\bar{Q}_1$ in the second equation of (5) yields:

$$\bar{Q}_2 = \frac{f_2(1)}{f_1(1)}\bar{Q}_1 > Q_{\min,2},$$

proving uniqueness as well as existence of the equilibrium point.

Case 2: $f_2(1)/f_1(1) \leq Q_{\min,2}/Q_{\min,1}$.

In this case we find that for every $Q_2 \geq Q_{\min,2}$, there holds that $[f_1(1)/f_2(1)]Q_2 \geq Q_{\min,1}$ and therefore (4) is equivalent to:

$$\begin{aligned} Q_2 \min\left(\mu_1\left(\frac{f_1(1)}{f_2(1)}Q_2\right), \mu_2(Q_2)\right) &= f_2(1) \\ Q_1 &= \frac{f_1(1)}{f_2(1)}Q_2 \end{aligned} \tag{6}$$

A similar argument shows that the first equation has a unique solution $\bar{Q}_2 \in (Q_{\min,2}, \infty)$ which can then be inserted into the second to find $\bar{Q}_1 > Q_{\min,1}$, again proving uniqueness and existence of the equilibrium point.

Summarizing,

Proposition 1. *System* (3) *has a unique extinction equilibrium point:*

$$E_0 = (1, 1, \bar{Q}_1, \bar{Q}_2, 0) \in \mathcal{P}.$$

For the remainder of this paper we assume that $\mu_1(\bar{Q}_1) \neq \mu_2(\bar{Q}_2)$. Then without loss of generality (possibly after relabeling of indices), we assume that:

$$\mu_1(\bar{Q}_1) < \mu_2(\bar{Q}_2) \tag{7}$$

and therefore there holds by (4) that:

$$\begin{aligned} f_1(1) &= \bar{Q}_1\mu_1(\bar{Q}_1) \\ f_2(2) &= \bar{Q}_2\mu_1(\bar{Q}_1), \end{aligned} \tag{8}$$

a fact which will be used throughout the rest of this paper.

The local stability behavior of E_0 is determined by a single parameter as we show next.

Lemma 1. *The extinction equilibrium point E_0 is locally asymptotically stable if $\mu_1(\bar{Q}_1) < 1$ and unstable if $\mu_1(\bar{Q}_1) > 1$.*

Proof. Since $\mu_1(\bar{Q}_1) < \mu_2(\bar{Q}_1)$, we can linearize system (3) at E_0 and get the following Jacobian:

$$\begin{pmatrix} -1 & 0 & 0 & 0 & -f_1(1) \\ 0 & -1 & 0 & 0 & -f_2(1) \\ f_1'(1) & 0 & -\mu_1(\bar{Q}_1) - \bar{Q}_1\mu_1'(\bar{Q}_1) & 0 & 0 \\ 0 & f_2'(1) & -\bar{Q}_2\mu_1'(\bar{Q}_1) & -\mu_1(\bar{Q}_1) & 0 \\ 0 & 0 & 0 & 0 & \mu_1(\bar{Q}_1) - 1 \end{pmatrix}$$

Inspection of the Jacobian shows that four of its eigenvalues have negative real parts and that its fifth eigenvalue is $\mu_1(\bar{Q}_1) - 1$. This concludes the proof. □

2.2 Nontrivial equilibrium point

Nontrivial equilibria, i.e. equilibria with $B \neq 0$, correspond to solutions of:

$$\min_j (\mu_j(Q_j)) = 1$$
$$Q_1 = f_1(R_1),\ Q_2 = f_2(R_2)$$
$$B = (1 - R_1)/f_1(R_1) = (1 - R_2)/f_2(R_2)$$

with $R_i \in (0, 1)$.

It will prove useful for future reference to notice that the last two equations and strict monotonicity of the f_i imply that B is a strictly decreasing function of $R_1 \in (0, 1)$ or of $R_2 \in (0, 1)$.

The solutions of the above equations are given by all solutions of:

$$\begin{aligned} \mu_1(Q_1) &= 1 \\ f_1(R_1) &= Q_1 \\ B &= (1 - R_1)/f_1(R_1) \\ 1 - R_2 - f_2(R_2)B &= 0 \\ Q_2 &= f_2(R_2) \end{aligned} \tag{9}$$

with the constraints $\mu_1(Q_1) \leq \mu_2(Q_2)$, $R_1, R_2 \in (0,1)$ and all solutions of

$$\begin{aligned} \mu_2(Q_2) &= 1 \\ f_2(R_2) &= Q_2 \\ B &= (1-R_2)/f_2(R_2) \\ 1 - R_1 - f_1(R_1)B &= 0 \\ Q_1 &= f_1(R_1) \end{aligned} \tag{10}$$

with the constraints $\mu_2(Q_2) \leq \mu_1(Q_1)$, $R_1, R_2 \in (0,1)$.

The following fact is useful:

Fact:

Each of the constrained equations (9), respectively (10) have at most one solution.

This follows immediately by an inspection of the equations: the first three equations of (9), (respectively (10)) may be solved for Q_1, R_1 and B (Q_2, R_2, B) which are unique by the strict monotonicity properties of f_1 and μ_1 (f_2 and μ_2). The fourth equation of (9) (respectively (10)) may then be solved for R_2 (R_1). Existence of this solution follows from the fact that the left hand side of this equation takes a positive value at $R_2 = 0$ $(R_1 = 0)$ and a negative value at $R_2 = 1$ (R_1=1), while uniqueness is inferred from strict monotonicity of the left hand side of this equation. Finally, the last equation may be solved to yield Q_2 (Q_1) which is unique by strict monotonicity of f_2 (f_1).

This fact implies that system (3) has at most two nontrivial equilibria, which are denoted

by[1]- if they exist:

$$\tilde{E}^1 = (\tilde{R}_1^1, \tilde{R}_2^1, \tilde{Q}_1^1, \tilde{Q}_2^1, \tilde{B}^1), \text{ respectively } \tilde{E}^2 = (\tilde{R}_1^2, \tilde{R}_2^2, \tilde{Q}_1^2, \tilde{Q}_2^2, \tilde{B}^2).$$

where $\tilde{E}^1$ $(\tilde{E}^2)$ corresponds to the solution of (9) (respectively (10)).

Proposition 2. *System* (3) *has at most one nontrivial equilibrium point.*

Proof. Suppose there are two different nontrivial equilibria $\tilde{E}^1$ and $\tilde{E}^2$. Then $\tilde{B}^1 \neq \tilde{B}^2$ (for if this would not be true, both equilibria would coincide). Assume that

$$\tilde{B}^1 < \tilde{B}^2$$

Recalling that B is strictly decreasing on R_1, this implies that:

$$\tilde{R}_1^1 > \tilde{R}_1^2.$$

Strict monotonicity of f_1 then implies that:

$$\tilde{Q}_1^1 = f_1(\tilde{R}_1^1) > f_1(\tilde{R}_1^2) = \tilde{Q}_1^2$$

Strict monotonicity of μ_1 then implies that:

$$1 = \mu_1(\tilde{Q}_1^1) > \mu_1(\tilde{Q}_1^2)$$

But this contradicts that $1 = \mu_2(\tilde{Q}_2^2) \leq \mu_1(\tilde{Q}_1^2)$.

If one assumes that $\tilde{B}^1 > \tilde{B}^2$, a similar proof also leads to a contradiction. □

[1]Superscripts 1 refer to solutions of (9) while superscripts 2 refer to solutions of (10).

The next result relates the existence of a (unique) nontrivial equilibrium point $\tilde{E}$ to the stability properties of E_0.

Lemma 2. *If system* (3) *has a nontrivial equilibrium point* $\tilde{E}$ *(which must be unique by proposition* 2*), then*

$$\mu_1(\bar{Q}_1) > 1.$$

It then follows (by lemma 1*) that the extinction equilibrium point* E_0 *is unstable.*

Proof. First assume that $\tilde{E} = \tilde{E}^1$. Then strict monotonicity of f_1 implies that:

$$\tilde{Q}_1^1 \mu_1(\tilde{Q}_1^1) = \tilde{Q}_1^1.1 = f_1(\tilde{R}_1^1) < f_1(1) = \bar{Q}_1 \mu_1(\bar{Q}_1),$$

where we have used that $\tilde{E}^1$ corresponds to a solution of (9) in the first two equalities, and (8) in the last equality. Now the function $Q_1\mu_1(Q_1)$ is strictly increasing because $\mu_1(Q_1)$ is. This implies that:

$$\tilde{Q}_1^1 < \bar{Q}_1$$

and hence, using monotonicity of μ_1 once more, that:

$$1 = \mu_1(\tilde{Q}_1^1) < \mu_1(\bar{Q}_1)$$

which concludes the proof for this case.

If $\tilde{E} = \tilde{E}^2$, we proceed by assuming that the lemma does not hold, i.e. that $\mu_1(\bar{Q}_1) \leq 1$. This implies that:

$$\bar{Q}_1 = \frac{f_1(1)}{\mu_1(\bar{Q}_1)} \geq f_1(1).$$

On the other hand we have that:

$$\tilde{Q}_1^2 = f_1(\tilde{R}_1^2) < f_1(1)$$

and thus upon combining inequalities that:

$$\tilde{Q}_1^2 < f_1(1) \leq \bar{Q}_1$$

Strict monotonicity of μ_1 and our initial assumption then imply that:

$$\mu_1(\tilde{Q}_1^2) < \mu_1(\bar{Q}_1) \leq 1$$

But this contradicts that $1 = \mu_2(\tilde{Q}_2^2) \leq \mu_1(\tilde{Q}_1^2)$. □

It is possible that there is no nontrivial equilibrium point. For example, if the μ_j are of the Droop form (2) with $\mu_j \leq 1$ for $j = 1, 2$, because then there is no solution to the equation $\min_j (\mu_j(Q_j)) = 1$. Thus, the interesting theoretical problem is when one assumes existence, uniqueness having already been proved. This justifies the following hypothesis, which we assume to hold throughout the remainder of this paper:

System (3) has a unique nontrivial equilibrium point $\tilde{E} \in \mathcal{P}$.

Then obviously, there holds that either $\tilde{E} = \tilde{E}^1$ or $\tilde{E} = \tilde{E}^2$.

Remark 1. Notice that we allow for the possibility that the values of μ_1 and μ_2 coincide at $\tilde{E}$, i.e. we allow that $\tilde{E}$ is a colimitation equilibrium point. Mathematically speaking, this may create some technical problems. For instance, it is not possible to linearize system (3) at a colimitation equilibrium point. However, as will become clear later, our approach to prove global stability does not require linearization arguments and hence avoids such problems.

3 Conservation principle

Consider the dynamics of the following quantities:

$$M_i = R_i + BQ_i,\ i = 1, 2$$

We interpret the M_i as the total concentration of nutrient i, both in free and stored form. These quantities satisfy:

$$\dot{M}_i = 1 - M_i$$

so $M_i(t) \to 1$ exponentially as $t \to \infty$. As a first step in the analysis of system (3), it seems therefore reasonable to replace R_i by $1 - BQ_i$ in the system equations which gives the following reduced system:

$$\begin{aligned} \dot{Q}_1 &= f_1(1 - BQ_1) - Q_1 \min_j (\mu_j(Q_j)), \\ \dot{Q}_2 &= f_2(1 - BQ_2) - Q_2 \min_j (\mu_j(Q_j)), \\ \dot{B} &= B[\min_j (\mu_j(Q_j)) - 1] \end{aligned} \tag{11}$$

We will later justify this reduction.

The state space of this system is:

$$\mathcal{P}^r = \{(Q_1, Q_2, B) \in \mathbb{R}^3_+ | Q_1 \geq Q_{\min,1},\ Q_2 \geq Q_{\min,2},\ BQ_1 \leq 1,\ BQ_2 \leq 1\}$$

which can be shown to be forward invariant. (A proof of this claim follows easily from the transformed version (20) of this system which we study later)

As before, biologically relevant initial conditions belong to $\mathcal{P}^r$ but also satisfy $B > 0$.

Next we show that all solutions of (11) eventually enter a compact set and remain in it forever after.

Proposition 3. *There is some constant $M > 0$ such that every solution $(Q_1(t), Q_2(t), B(t))$ satisfies:*

$$Q_1(t), Q_2(t), B(t) < M \textit{ for all sufficiently large } t.$$

Proof. First, we prove that solutions do not escape in finite time. To that end, consider the dynamics of the variable:

$$V := Q_1^2 + Q_2^2,$$

which obeys:

$$\dot{V} \leq 2\left(f_1(1)Q_1 + f_2(1)Q_2\right) \leq 2\left(f_1(1) + f_2(1)\right) + 2\max\left(f_1(1), f_2(1)\right) V$$

where we used monotonicity of f_i in the first inequality and the fact that $Q_i \leq 1 + Q_i^2$ in the second. The resulting inequality implies that V - and hence Q_1 and Q_2 - remains bounded in finite time intervals. Moreover, since $BQ_i \leq 1$, we also get a bound for $B(t)$ on finite time intervals.

Next, we introduce the following auxiliary variables:

$$z_i = BQ_i,\ i = 1, 2,$$

with dynamics given by:

$$\dot{z}_i = -z_i + Bf_i(1-z_i) = -z_i + \frac{z_i}{Q_i} f_i(1-z_i) \leq (-1 + \frac{f_i(1-z_i)}{Q_{\min,i}})z_i,\ i = 1,2. \quad (12)$$

Then we may pick a sufficiently small $\delta_i \in (0,1)$, $i = 1,2$, for which there holds that for all $z_i \in [1-\delta_i, 1]$:

$$\dot{z}_i \leq -c_i z_i < 0,\ i = 1,2$$

for some $c_i > 0$, $i = 1,2$, by continuity of the f_i. Then with $\Delta = \min\{\delta_1, \delta_2\}$, we obtain:

$$z_i(t) \leq 1 - \Delta \text{ for sufficiently large } t.$$

This bound and monotonicity of the f_i will yield a uniform lower bound for the $Q_i(t)$, $i = 1,2$. Indeed, first notice that:

$$\dot{Q}_i \geq f_i(\Delta) - Q_i \min_j (\mu_j(Q_j)) \text{ for sufficiently large } t.$$

So for sufficiently small $q > 0$, we find that whenever $Q_i \in [Q_{\min,i}, Q_{\min,i} + q]$:

$$\dot{Q}_i \geq f_i(\Delta) - cQ_i > 0,\ i = 1,2,$$

for some sufficiently small $c > 0$ by continuity of the μ_i, and thus that:

$$Q_i(t) \geq Q_{\min,i} + q,\ i = 1,2 \text{ for sufficiently large } t. \quad (13)$$

Finally, this lower bound leads to a uniform upper bound for the $Q_i(t)$:

$$\dot{Q}_i \leq f_i(1) - CQ_i,\ i = 1,2 \text{ for sufficiently large } t,$$

for some $C > 0$ (using that the f_i are strictly increasing and continuity of the μ_i). This implies that the statement of the proposition holds for the $Q_i(t)$, $i = 1,2$. To conclude this proof, notice that the statement is trivial for $B(t)$ since $B(t)Q_i(t) \leq 1$ and $Q_i(t) \geq Q_{\min,i}$ for $i = 1,2$, implying that $B(t) \leq 1/Q_{\min,i}$ for all $t \geq 0$. □

The assumptions made before imply that system (11) has precisely two equilibria. First, there is an extinction equilibrium

$$E_0^r = (\bar{Q}_1, \bar{Q}_2, 0),$$

see proposition 1. Secondly, there is a nontrivial equilibrium point $\tilde{E}^r$ given by:

$$\tilde{E}^r = (\tilde{Q}_1^1, \tilde{Q}_2^1, \tilde{B}^1) \quad \text{or} \ (\tilde{Q}_1^2, \tilde{Q}_1^2, \tilde{B}^2).$$

Notice that the set $\mathcal{B}_0 = \{(Q_1, Q_2, B) \in \mathcal{P}^r \mid B = 0\}$ is forward invariant for system (11) and that the dynamics on this set are given by the following planar system:

$$\begin{aligned} \dot{Q}_1 &= f_1(1) - Q_1 \min_j (\mu_j(Q_j)), \\ \dot{Q}_2 &= f_2(1) - Q_2 \min_j (\mu_j(Q_j)), \end{aligned} \quad (14)$$

defined on $\mathcal{Q} = \{(Q_1, Q_2) \in \mathbb{R}_+^2 \mid Q_i \geq Q_{\min,i}\}$. The asymptotic behavior of this system (both in forward and backward time) will later prove to play an important role and is investigated next.

Proposition 4. *System* (14) *has a globally asymptotically stable equilibrium point in* $E_0^{r,0} = (\bar{Q}_1, \bar{Q}_1)$. *Every backward solution, except for the equilibrium* $E_0^{r,0}$, *leaves* $\mathcal{Q}$ *in finite time or is unbounded.*

Proof. First notice that (forward) solutions are bounded by proposition 3. Next consider:

$$V = (\frac{f_2(1)}{f_1(1)}Q_1 - Q_2)^2.$$

Taking the time derivative of V along solutions of (14) shows that:

$$\dot{V} = -2[\frac{f_2(1)}{f_1(1)}Q_1 - Q_2]^2 \min_j (\mu_j(Q_j)) \leq 0.$$

Lasalle's invariance principle implies that solutions converge to the largest invariant set in the set where $\dot{V} = 0$. The latter consists of three straight lines given by the equations $Q_1 = Q_{\min,1}$, $Q_2 = Q_{\min,2}$ and $Q_2 = [f_2(1)/f_1(1)]Q_1$.

From the system equations (14), it follows that the vector field is transversal to the first two lines, implying that solutions starting here leave the lines instantaneously. The third line is invariant for (14) and contains the unique equilibrium point $E_0^{r,0}$. Suppose that a point l on this line different from $E_0^{r,0}$ is an ω limit point. Then by backward invariance of ω limit sets, the ω limit set is unbounded or contains a point outside the state space. But this is impossible by proposition 3 and hence $E_0^{r,0}$ is the only possible ω limit point.

To prove the statement regarding the backward solutions we consider the backward time system:

$$\begin{aligned} \dot{Q}_1 &= -f_1(1) + Q_1 \min_j (\mu_j(Q_j)), \\ \dot{Q}_2 &= -f_2(1) + Q_2 \min_j (\mu_j(Q_j)), \end{aligned} \tag{15}$$

defined on $\mathcal{Q}$. Let us suppose that the statement does not hold. Then there is a solution $(Q_1(t), Q_2(t))$ of system (15) which is in $\mathcal{Q}$ and bounded for all $t \geq 0$. Thus there is some $M > 0$ such that:

$$Q_{\min,i} \leq Q_i(t) \leq M, \ i = 1, \ 2, \ \forall t \geq 0. \tag{16}$$

Pick $\epsilon > 0$ small enough such that for $i = 1, 2$ there holds:

$$-f_i(1) + Q_i \min_j(\mu_j(Q_j)) \leq -\alpha < 0, \ \forall Q_i \in [Q_{\min,i}, Q_{\min,i} + \epsilon]. \tag{17}$$

for some $\alpha > 0$.

Then we claim that the lower bound in (16) can be strengthened to:

$$Q_{\min,i} + \epsilon < Q_i(t), \ i = 1, \ 2, \ \forall t \geq 0. \tag{18}$$

If this were not the case, then there would exist a time $t^* \geq 0$ and some index i^* such that $Q_{i^*}(t^*) \in [Q_{\min,i^*}, Q_{\min,i^*} + \epsilon]$. Then by (17) we obtain:

$$\dot{Q}_{i^*} = -f_{i^*}(1) + Q_{i^*} \min_j (\mu_j(Q_j)) \leq -\alpha$$

implying that there exists some time $T > t^*$ such that $Q_{i^*}(T) < Q_{\min,i^*}$, contradicting (16).

Let us now introduce the following auxiliary variable:

$$q_2 = Q_2 - \frac{f_2(1)}{f_1(1)} Q_1$$

Along the solution $(Q_1(t), Q_2(t))$ this variable obeys the following equation:

$$\dot{q}_2 = q_2 \min_j (\mu_j(Q_j(t))) \geq c q_2$$

for some $c > 0$, using (18). There are two cases to consider. If $q_2(0) \neq 0$, then $q_2(t)$ will diverge, which contradicts boundedness of the solution $(Q_1(t), Q_2(t))$. If $q_2(0) = 0$, then $q_2(t) = 0$ for all $t \geq 0$. In other words, the solution $(Q_1(t), Q_2(t))$ evolves on the invariant line given by the equation $Q_2 = [f_2(1)/f_1(1)]Q_1$. But it is easy to see from the system equations (15) that a solution on this line (and different from the solution at the equilibrium $E_0^{r,0}$) either leaves $\mathcal{Q}$ in finite time or diverges. This concludes the proof. $\square$

4 Transformation to a monotone system

This section contains the key step in the global analysis of the reduced system (11). We will show that by means of a nonlinear state transformation, the reduced system can be transformed in a monotone system. Consider new state variables for system (11):

$$z_1 = BQ_1, \; z_2 = BQ_2, \; B = B \tag{19}$$

The interpretation for z_i is the concentration of nutrient i stored in the organism. In terms of the variables (z_1, z_2, B) we get:

$$\begin{aligned} \dot{z}_i &= -z_i + Bf_i(1 - z_i), \; i = 1, 2, \\ \dot{B} &= B[\min_j (\mu_j(z_j/B)) - 1]. \end{aligned} \tag{20}$$

Some caution should be taken in defining the state space for this system. First, notice that the state transformation (19) is not one-to-one since every point $(Q_1, Q_2, 0) \in \mathcal{P}^r$ is mapped to $(0, 0, 0)$. On the other hand, biologically relevant initial conditions correspond to $B \neq 0$ and for these points the transformation *is* one-to-one (in fact, the transformation is even invertible here by the inverse function theorem). The state space for the transformed system is:

$$\mathcal{P}^t = \{(z_1, z_2, B) \in \mathbb{R}^3_+ \mid z_i \in [0, 1], Q_{\min,i} B \leq z_i, \; i = 1, 2, \; B > 0\} \cup \{(0, 0, 0)\}$$

Notice that system (20) has 2 equilibria, one at $(0, 0, 0)$ and a second one at $\tilde{E}^t$ which is the image of $\tilde{E}^r$ under the state transformation (19).

We show next that this system is monotone [15]. First recall that a system $\dot{x} = f(x)$, defined on some forward invariant subset $X \subset \mathbb{R}^n$, is called monotone (with respect to the standard order $\leq$ on $\mathbb{R}^n$, generated by the nonnegative orthant

$\mathbb{R}^n_+$) if for any two solutions $x(t)$ and $y(t)$ with $x(0) \leq y(0)$, defined on some interval $[0,T]$ for some $T > 0$, there holds that $x(t) \leq y(t)$ for all $t \in [0,T]$. It is well-known that if the state space X is p-convex (meaning that whenever $x, y \in X$ with $x \leq y$, then the line segment connecting x and y is also contained in X), a sufficient condition for this to happen is that the system is of type K, see e.g. chapter 3, proposition 1.1 in [15]. A system $\dot{x} = f(x)$ is of type K if whenever $x \leq y$, and $x_i = y_i$ for some i, then $f_i(x) \leq f_i(y)$.

Lemma 3. *System* (20) *is of type K on the p-convex set $\mathcal{P}^t$ and hence monotone.*

Proof. It is easily checked that $\mathcal{P}^t$ is p-convex. Denote the vector field of system (20) by $F(z_1, z_2, B)$ and pick two states $(z_1^a, z_2^a, B^a) \leq (z_1^b, z_2^b, B^b)$ with $B^a = B^b$. (The proof is trivial when $z_1^a = z_1^b$ or $z_2^a = z_2^b$) Then

$$\begin{aligned} F_3(z_1^a, z_2^a, B^a) &= B^a[\min_j \left(\mu_j(z_j^a/B^a)\right) - 1] \\ &\leq B^a[\min_j \left(\mu_j(z_j^b/B^a)\right) - 1] \\ &= B^b[\min_j \left(\mu_j(z_j^b/B^b)\right) - 1] = F_3(z_1^b, z_2^b, B^b) \end{aligned}$$

where the middle inequality holds because the functions μ_j are increasing. □

We will need the following result from the theory of monotone systems. The result is due to J.F. Jiang [6] and stated next.

Theorem 1. *Suppose that a system $\dot{x} = f(x)$ is monotone on the state space $X = \Pi_{i=1}^n I_i \subset \mathbb{R}^n$ where I_i are intervals (i.e. $I_i = (a_i, b_i)$, $[a_i, b_i]$, $[a_i, b_i)$ or $(a_i, b_i]$ for - possibly extended - real numbers $a_i < b_i$). Assume that*

1. *Every forward orbit has compact closure in X.*
2. *The system has a unique equilibrium point $\bar{x} \in X$.*

Then, $\bar{x}$ is globally asymptotically stable.

The main result of this section is the following.

Theorem 2. *The equilibrium point $\tilde{E}^t$ of system* (20) *is globally asymptotically state with respect to initial conditions in $\mathcal{P}^t \backslash \{(0,0,0)\}$. Equivalently, the equilibrium point $\tilde{E}^r$ of system* (11) *is globally asymptotically stable with respect to initial conditions in $\mathcal{P}^r$ for which $B \neq 0$.*

Proof. The idea of the proof is to extend the state space of system (20) and delete the equilibrium at the origin, in such a way that theorem 1 is applicable. First, for $i = 1, 2$ pick arbitrary continuously differentiable extensions μ_i^e of the μ_i functions such that:

$$\mu_i^e : \mathbb{R}_+ \to \mathbb{R},\ \ \mu_i^e(Q_i) < 0 \text{ for } Q_i \in [0, Q_{\min,i}),\ \mu_i^e(Q_i) = \mu_i(Q_i) \text{ for } Q_i \geq Q_{\min,i},\ \mu_i' > 0 \text{ on } \mathbb{R}_+.$$

For example, we may pick $\mu_i^e(Q_i) = \mu_i(Q_i)$ when $Q_i \geq Q_{\min,i}$, and $\mu_i^e(Q_i) = (Q_i - Q_{\min,i})\mu_i'(Q_{\min,i})$ for $Q_i < Q_{\min,i}$.

Next define the following system:

$$\begin{aligned} \dot{z}_i &= -z_i + Bf_i(1-z_i),\ i=1,2, \\ \dot{B} &= B[\min_j \left(\mu_j^e(z_j/B)\right) - 1] \end{aligned} \qquad (21)$$

with state space

$$X = \{(z_1, z_2, B) \in \mathbb{R}^3_+ \mid z_i \in [0,1], i=1,2,\ B \in (0,\infty)\}$$

Notice that system (21) is monotone since it is of type K on X (the same proof as in lemma 3 holds for system (21)), that it has a *unique* equilibrium point at $\tilde{E}^t$ and that the state space is of the form described in theorem 1. Clearly, if we can prove that forward orbits have compact closure in X, then it follows from theorem 1 that $\tilde{E}^t$ is globally asymptotically stable for system (21) and hence also for system (20) provided initial conditions are in in $\mathcal{P}^t \setminus \{(0,0,0)\}$, so we are done.

Before doing just that, we introduce one more system, namely an extended version of system (11):

$$\begin{aligned} \dot{Q}_i &= f_i(1-BQ_i) - Q_i \min_j \left(\mu_j^e(Q_j)\right),\ \ i=1,2, \\ \dot{B} &= B[\min_j \left(\mu_j^e(Q_j)\right) - 1] \end{aligned} \qquad (22)$$

with state space $\mathcal{P}^{r,e} = \{(Q_1, Q_2, B) \in \mathbb{R}^3_+ \mid Q_i \geq 0, BQ_i \leq 1,\ i=1,2\}$. Notice that this system has two equilibria, one at E_0^r and a second one at $\tilde{E}^r$. A careful inspection of the proofs of proposition 3 and proposition 4, reveals that both propositions remain valid for this extended system. Let us start by re-examining the proof of proposition 3. First, we show that there are no finite escape times for solutions of system (22). To that end we introduce -without loss of generality- the following additional assumption for the μ_i^e: there exists some $\beta > 0$ such that $\mu_i^e(Q_i) \geq -\beta$ for $Q_i \in \mathbb{R}_+$. Now re-consider the dynamics of the variable $V = Q_1^2 + Q_2^2$ along solutions of system (22):

$$\dot{V} \leq 2\left(f_1(1)Q_1 + f_2(1)Q_2\right) + 2\beta V \leq 2\left(f_1(1) + f_2(1)\right) + \beta^* V$$

for some $\beta^* > 0$. This shows that $V(t)$ and hence $Q_1(t)$ and $Q_2(t)$ remain bounded on bounded time intervals. Then the equation for B in (22) shows that on bounded time intervals $\dot{B} \leq B(c-1)$ for some $c > 0$ and hence the same conclusion holds for $B(t)$ as well.

Next we prove that solutions of (22) are bounded. First notice that the system equations imply that $Q_i(t) > 0$ for all $t > 0$ and $i = 1,2$. Now there exists $\epsilon > 0$ small enough such that for all $Q_i \in (0, \epsilon]$ holds that:

$$\dot{Q}_i \geq \alpha Q_i,\ \ i=1,2,$$

for some $\alpha > 0$, implying that for all sufficiently large t, we have that:

$$Q_i(t) \geq \epsilon,\ \ i=1,2.$$

This and the fact that $BQ_i \leq 1$, imply in particular that for all sufficiently large t, $B(t) \leq 1/\epsilon$, which establishes a lower bound for the B-component of solutions of (22). The whole argument in the proof of proposition 3 involving the variables $z_i = BQ_i$ for $i = 1, 2$ can now be repeated if one replaces $Q_{\min,i}$ by ϵ in the inequality (12). Then as before, there exists some $\Delta > 0$ such that $z_i(t) \leq 1 - \Delta$ for $i = 1, 2$ and all sufficiently large t. Moreover, one obtains a uniform lower bound for the $Q_i(t)$ by noticing that for all sufficiently large t, there holds that:

$$\dot{Q}_i \geq f_i(\Delta) - Q_i \min_j \mu_j^e(Q_j), \quad i = 1, 2.$$

But then there is some sufficiently small $q > 0$, such that whenever $Q_i \in [0, Q_{\min,i} + q]$, we have that:

$$\dot{Q}_i \geq +\alpha^*, \quad i = 1, 2,$$

for some $\alpha^* > 0$ and hence that (13) holds for all sufficiently large t and $i = 1, 2$. Then the same argument as in the proof of proposition 3 leads to a uniform upper bound for the $Q_i(t)$. The lower bound (13) also plays a significant role in showing the validity of proposition 4. Indeed, it implies that the ω limit set of every solution of system (22) starting in the invariant set $\{(Q_1, Q_2, B) \in \mathcal{P}^{r,e} \,|\, B = 0\}$, must belong to the state space $\mathcal{Q}$ of system (14). But proposition 4 shows that there is only one possible ω limit set, namely the equilibrium point $E_0^{r,0}$.

Finally, the assertion regarding backward solutions of system (22), restricted to the invariant set $\{(Q_1, Q_2, B) \in \mathcal{P}^{r,e} \,|\, B = 0\}$ (except for the unique equilibrium point $\tilde{E}^t$) is proved using a similar argument as in the proof of proposition 4. Reconsider system (15), but replace μ_j by μ_j^e and the state space $\mathcal{Q}$ by the (extended) state space $\mathbb{R}^2_+$. It is clear from the proof of proposition 4 that a possibly bounded solution of the extended version of system (15) enters the subset of $\mathbb{R}^2_+$ where for at least one i, $Q_i \in [0, Q_{\min,i})$. But then $\dot{Q}_i < -f_i(1)$, so there exists some time T such that $Q_i(T) < 0$, implying that the solution has left the state space, a contradiction.

Let us return now to the issue of proving that forward orbits of system (21) have compact closure in X. First of all, we have shown above that $B(t)$ is bounded for solutions of system (22), and hence also for solutions of system (21). This proves boundedness of solutions of system (21). So, what remains to be shown is that for all $x \in X$, the omega limit set $\omega(x)$ does not meet the set $\{(z_1, z_2, B) \in \mathbb{R}^3_+ \mid B = 0\}$. Now, from proposition 3 applied to system (22), it follows that solutions of system (21) will reside in a wedge-shaped region:

$$Q_i(t) = z_i(t)/B(t) < M \text{ for all large } t. \tag{23}$$

This implies that the only possible ω limit point with $B = 0$ for solutions of system (21) is $(0, 0, 0)$ (for if $(\bar{z}_1, \bar{z}_2, 0)$ would be another limit point with $\bar{z}_i \neq 0$ for at least one i, then there would be a sequence of times $\{t_k\} \to \infty$ such that $B(t_k) \to 0$ and $z_i(t_k) \to \bar{z}_i$; but then for at least one i the inequality (23) would be violated) and we are left with proving that it is *not* an ω limit point.[2] In terms of system (22), this means that we need to show that no ω limit point of a solution starting in the subset of $\mathcal{P}^{r,e}$ where $B \neq 0$, belongs to $\mathcal{B}_0 = \{(Q_1, Q_2, B) \in \mathcal{P}^{r,e} \mid B = 0\}$. (recall that the single point $(0, 0, 0)$ is the image of the set $\mathcal{B}_0$ under transformation (19)) Suppose this is not true, then for some $x \in \mathcal{P}^{r,e}$ with nonzero B-value, we have

[2]Strictly speaking we should *add* the point $(0, 0, 0)$ to the state space X of system (21), if it were *to be* an ω limit point.

that $p \in \omega(x)$ for some $p \in \mathcal{B}_0$. If $p \neq E_0^r$, then the backward solution through p also belongs to $\omega(x)$ (by backward invariance of ω limit sets). But this backward solution leaves the state space in some finite time, or is unbounded by proposition 4, applied to system (22). So we should only consider the case that $p = E_0^r$. But this case can be reduced to the previous one by means of the Butler-McGehee lemma, see e.g. [16] p. 12.

Indeed, a simple linearization argument shows that E_0^r is a hyperbolic equilibrium point with 2-dimensional stable and 1-dimensional unstable manifold (see lemmas 1 and 2). Then the Butler-McGehee lemma implies that $\omega(x)$ should contain some point $q \in W^s(E_0^r)$, the stable manifold of E_0^r, such that $q \neq E_0^r$. Since $W^s(E_0^r)$ is 2-dimensional and in view of the stability result in proposition 4, applied to the 2-dimensional system (22), we conclude that $q \in \mathcal{B}_0$. So we have reduced this case to the previous one and therefore the proof is finished. □

5 Global stability for the original system

In this section we justify why the global stability result for the reduced system (11) implies a global stability result for the original system. In turn, this leads to the main result of this paper.

Theorem 3. *The nontrivial equilibrium point $\tilde{E}$ of system* (3) *is globally asymptotically stable with respect to all initial conditions in $\mathcal{P}$ for which $B \neq 0$.*

Proof. The proof relies on a global stability result for cascaded systems. First, notice that by introducing the new variables:

$$M_i = R_i + BQ_i, \quad i = 1, 2,$$

system (3) can be rewritten as a cascaded system:

$$\begin{aligned} \dot{M}_i &= 1 - M_i \\ \dot{Q}_i &= f_i(M_i - BQ_i) - Q_i \min_j (\mu_j(Q_j)) \\ \dot{B} &= B[\min_j (\mu_j(Q_j)) - 1] \end{aligned} \tag{24}$$

with state space $\mathcal{P}^c = \{(M_1, M_2, Q_1, Q_2, B) \in \mathbb{R}_+^5 \mid M_i \geq 0,\ Q_i \geq Q_{\min,i},\ B \geq 0,\ i = 1, 2\}$. Here we are only interested in solutions with initial conditions satisfying $B \neq 0$.

If solutions of (24) are bounded, then the global asymptotically stable equilibrium point of the first subsystem $\dot{M}_i = 1 - M_i$, $i = 1, 2$ at (1, 1), and theorem 2, imply that system (24) has a global asymptotically stable equilibrium point, see e.g. Appendix F in [16] or [17, 18]. From this we conclude that the theorem is proved.

So we are left with proving that solutions of (24) are bounded. We will show the equivalent statement that solutions of (3) are bounded instead. First, notice that the definition and the dynamics of the auxiliary variables M_i imply in particular that there is an arbitrarily small $\epsilon > 0$ such that:

$$R_i(t),\ B(t)Q_i(t) \leq 1 + \epsilon \text{ for all sufficiently large } t \text{ and } i = 1, 2.$$

which already establishes a bound for $R_i(t)$. Now, since $Q_i(t) \geq Q_{\min,i} > 0$ for $i = 1, 2$ and all $t \geq 0$, this implies that:

$$B(t) \leq \alpha \text{ for all sufficiently large } t$$

for some $\alpha > 0$. This establishes the bound on B. Then for all sufficiently large t we have that:

$$\dot{R}_i = 1 - R_i - B(t) f_i(R_i) \geq 1 - R_i - \alpha f_i(R_i), \ i = 1, 2$$

and then continuity of the f_i implies that there exists some $\delta > 0$ such that if $R_i \in [0, \delta]$, then $\dot{R}_i \geq \rho$ for some $\rho > 0$ and thus we infer that:

$$R_i(t) > \delta \text{ for all sufficiently large } t \text{ and } i = 1, 2.$$

This, and strict monotonicity of the f_i, imply that for sufficiently large t:

$$\dot{Q}_i \geq f_i(\delta) - Q_i \min_j \left(\mu_j(Q_j) \right), \ i = 1, 2$$

which by a similar argument as in the proof of proposition 3 results in a uniform lower bound for the $Q_i(t)$, see (13).

Finally we find a uniform upper bound for the $Q_i(t)$ as follows. First notice that for all sufficiently large t:

$$\dot{Q}_i \leq f_i(1 + \epsilon) - C Q_i, \ i = 1, 2$$

for some $C > 0$. This can be inferred using strict monotonicity of the f_i, the bound $R_i(t) \leq 1 + \epsilon$ given above, the lower bound (13) and continuity of the μ_j. Then there is some $M > 0$ such that for all sufficiently large t and $i = 1, 2$, there holds that $Q_i(t) < M$. □

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