Crowding effects promote coexistence in the chemostat*

Patrick De Leenheer[†], David Angeli[‡] and Eduardo D. Sontag[§]

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Abstract

This paper deals with an almost-global stability result for a particular chemostat model. It deviates from the classical chemostat because crowding effects are taken into consideration. This model can be rewritten as a negative feedback interconnection of two systems which are monotone (as input-output systems). Moreover, these subsystems behave nicely when subject to constant inputs. This allows the use of a particular small-gain theorem which has recently been developed for feedback interconnections of monotone systems. Application of this theorem requires -at least approximate- knowledge of two gain functions associated to the subsystems. It turns out that for the chemostat model proposed here, these approximations can be obtained explicitely and this leads to a sufficient condition for almost-global stability. In addition, we show that coexistence occurs in this model if the crowding effects are large enough.

1 Introduction

The chemostat model describes the interaction of microbial species which are competing for a single nutrient, see [15] for a review. It has been used for different systems such as lakes, waste-water treatment processes and biological reactors producing genetically altered organisms. The 'competitive exclusion principle' -probably the most important result for chemostat models- states roughly that the competition process yields at best a single winning species in the long run. In nature on the other hand, many species seem to coexist and this has triggered a lot of research

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[†]corresponding author: DIMACS, Rutgers University, 96 Frelinghuysen Rd, Piscataway, NJ 08854, email: leenheer@math.rutgers.edu, supported in part by NSF grant DMS 0342153, NSF grant EIA03-331486 and USAF grant F49620-01-1-0063

[‡]Dip. di Sistemi e Informatica Universitá di Firenze,Via di S. Marta 3, 50139 Firenze, Italy, email: angeli@dsi.unifi.it

[§]Supported in part by US Air Force Grant F49620-01-1-006, NIH grant P20 GM64375, and by NSF Grant CCR-0206789. Department of Mathematics, Rutgers University, New Brunswick, NJ 08903, http://www.math.rutgers.edu/~sontag, email:sontag@control.rutgers.edu

vestigations start from the assumption that the two natural operating parameters, the dilution rate and the input nutrient concentration, are time-varying rather than constant, see [18, 3] for time-varying dilution rates and [18, 10, 7] for time-varying input nutrient concentration. Other approaches rely on dropping the well-mixed hypothesis [17, 11]. Recently feedback control of the dilution rate has been used to *make* the chemostat coexistent [4].

Here we propose to modify the chemostat model in a different way:

$$\begin{aligned} \dot{S} &= 1 - S - \sum_{i=1}^{n} x_i f_i(S) \\ \dot{x}_i &= x_i(f_i(S) - D_i - a_i x_i) \end{aligned} \tag{1}$$

where $i = 1, 2, ..., n$, x_i is the concentration of species i (units mass/volume) and S is the nutrient concentration. The positive parameters D_i are the sum of the (natural) death rates of species i and the dilution rate, while the positive parameters a_i give rise to death rates $a_i x_i$ which are due to crowding effects. The D_i are not necessarily equal. Notice that (1) represents a *scaled* chemostat model; see [15] for more on the scaling procedure.

The following assumption for the uptake functions f_i is made throughout the paper:

$f_i : \mathbb{R}_+ \to \mathbb{R}_+$ is continuously differentiable [1], $f_i(0) = 0$ and $f_i' \geq 0$. Moreover the functions f_i are globally Lipschitz continuous on $\mathbb{R}_+$, i.e.

$$\forall i,\ \exists L_i > 0 : \ |f_i(S_1) - f_i(S_2)| \leq L_i |S_1 - S_2|,\ \forall S_1,\ S_2 \in \mathbb{R}_+.$$

For example, the often used Monod function $f(S) = MS/(b+S)$ where $b,\ M$ are given positive constants, satisfies these assumptions with a global Lipschitz constant M/b.

The monotonicity assumption ($f_i' \geq 0$) will be crucial in our approach. For work on chemostat models with uptake functions which are not necessarily monotone, we refer to [20].

Note that there is only a single difference between system (1) and the classical chemostat model in [15]: here, crowding effects are taken into consideration and they are quantified by the positive parameters a_i.

Our main result is the following:

Theorem 1. *If*

$$n.\max_i \left(\frac{L_i}{a_i}\right).\max_i \left(f_i(1)\right) \ < \ 1 \tag{2}$$

then there exists an equilibrium point $E^* \in \mathbb{R}_+^{n+1}$ *of system* (1) *such that almost every solution*

[1] This -and also other derivatives of functions which are defined on closures of open subsets of Euclidean spaces $\mathbb{R}^p$- should be understood as follows: There exist continuously differentiable extensions for the functions f_i, i.e. there exist functions F_i, defined on open sets $U_i \subset \mathbb{R}$ such that $\mathbb{R}_+ \subset U_i$, $F_i(S) = f_i(S)$ if $S \in \mathbb{R}_+$ and F_i is continuously differentiable on U_i. Then $f_i'(S) := F_i'(S)$ when $S \in \mathbb{R}_+$.

$$\lim_{t\to\infty} \xi(t) = E^*.$$

Remark 1. Under the hypotheses of theorem 1, it can be shown that the set $\mathcal{B}$ of initial conditions which give rise to solutions that do not converge to E^* (note that these solutions may converge to other equilibrium points) is a subset of $\mathcal{B}^*$ where:

$$\mathcal{B}^* := \{(S,\, x_1,\, ...,\, x_n)^T \in \mathbb{R}_+^{n+1} |\, \exists\, i : \, x_i = 0\}.$$

We will not prove this, but this follows from the proof of lemma 4 in the next section and the proof of Theorem 1 in [2].

The key idea to prove the main result is the observation that system (1) can be interpreted as a *negative feedback interconnection* of *monotone subsystems*. To see this, we introduce some notation first. Define $x = (x_1, x_2, ..., x_n)^T$, $f(S) = (f_1(S), f_2(S), ..., f_n(S))^T$, $D = (D_1, D_2, ..., D_n)^T$ and $a = (a_1, a_2, ..., a_n)^T$. System (1) can then be compactly rewritten as follows:

$$\begin{aligned} \dot{S} &= 1 - S + f^T(S)u_1, \; y_1 = S && (3) \\ \dot{x} &= \mathrm{diag}(x)(f(u_2) - D - \mathrm{diag}(a)x), \; y_2 = x && (4) \\ u_1 &= -y_2, \;\; u_2 = y_1 && (5) \end{aligned}$$

Notice that system (3) – (5) is a negative feedback system consisting of two input/output (I/O) subsystems (3) and (4) with inputs u_1, respectively u_2 and outputs y_1, respectively y_2. For this class of systems, a particular small-gain theorem is available to establish an almost-global stability result.

Recently, a theory for monotone I/O systems has been proposed in [1]. Its purpose is to generalize the rich theory of monotone dynamical systems developed by Hirsch [8], see [14] for a review. A monotone dynamical system is a dynamical system for which the flow preserves a partial order defined on the state space. It is known that a number of biological systems are monotone systems, see [14, 1, 6] for examples on the cellular level, both within and between cells. For an example of a monotone system in the context of epidemiological models, we refer to [13]. An attractive property of monotone dynamical systems is that they exhibit certain convergence properties. The extension of this class of systems to an I/O setting originates from the need to understand how they behave when interconnected (as cascades or feedback systems). It turns out that interconnections may possess desirable convergence properties as well. The main result of this paper illustrates this by applying a small-gain theorem developed for feedback interconnections of monotone systems [1, 2] to the chemostat model introduced before.

For an application of these ideas to predator-prey systems, see [5]. For an example of the use of small-gain ideas in a context with not necessarily monotone subsystems, see [16]. A good introduction to the classical, linear versions of small-gain theorems is provided in [19]. For nonlinear versions, see for instance [12].

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[2]This means that the result holds for all solutions starting in $\mathbb{R}_+^n$, except for those which start in a set $\mathcal{B}$ of (Lebesgue) measure zero.

2.1 Monotone I/O systems and a small-gain theorem

In this section we consider I/O systems described by differential equations. Several concepts (monotonicity, Input/State quasi characteristic) are reviewed which are needed for the statement of a particular small-gain theorem. Consider the following I/O system:

$$\dot{x} = f(x,u), \quad y = h(x) \tag{6}$$

where $x \in \mathbb{R}^n$ is the state, $u \in U \subset \mathbb{R}^m$ the input and $y \in Y \subset \mathbb{R}^p$ the output. It is assumed that f and g are smooth (say continuously differentiable) and that the input signals $u(t) : \mathbb{R} \to U$ are Lebesgue measurable functions and locally essentially bounded (i.e. for every compact time interval $[0,T]$, there is some compact set C such that $u(t) \in C$ for almost all $t \in [0,T]$). Then a solution with initial state $x_0 \in \mathbb{R}^n$ is defined and unique for every input $u(.)$. We denote this solution by $x(t, x_0, u(.))$, $t \in \mathcal{I}$ where $\mathcal{I}$ is the maximal interval of existence. From now on we also assume that a set $X \subset \mathbb{R}^n$ is given which is forward invariant, that is for all inputs $u(.)$ and for every $x_0 \in X$ it holds that $x(t, x_0, u(.)) \in X$, for all $t \in \mathcal{I} \cap \mathbb{R}_+$. From now on, initial conditions will be restricted to the set X. We assume that X is the closure of its interior.

The usual partial order on $\mathbb{R}^n$ is denoted by $\preceq$: $x \preceq y$ iff $y - x \in \mathbb{R}^n_+$ for x, $y \in \mathbb{R}^n$. Given that the state space X (input space U, output space Y) is a subset of $\mathbb{R}^n$ ($\mathbb{R}^m$, $\mathbb{R}^p$), it inherits this partial order of $\mathbb{R}^n$. Similarly, the set of input signals can be partially ordered in the following, natural way: $u(.) \preceq v(.)$ if $u(t) \preceq v(t)$ for almost all $t \geq 0$.

Next we provide a definition for the concept of a monotone I/O system, which generalizes the concept of a monotone dynamical system (without inputs or outputs) in a straightforward fashion.

Definition 1. *The I/O system* (6) *is monotone (with respect to the usual partial orders) if the following conditions hold:*

$$x_1 \preceq x_2 \text{ and } u(.) \preceq v(.) \Rightarrow x(t, x_1, u(.)) \preceq x(t, x_2, v(.)) \text{ for all } t \in (\mathcal{I}_1 \cap \mathcal{I}_2) \cap \mathbb{R}_+ \tag{7}$$

and

$$h \text{ is a monotone map, i.e. } x_1 \preceq x_2 \Rightarrow h(x_1) \preceq h(x_2). \tag{8}$$

In Proposition 3.3 in [1] a sufficient condition is provided to determine whether a given I/O system is monotone.

Later it will prove useful to consider monotone I/O systems which behave nicely when supplied with constant inputs. The following notion [2], makes this precise.

Definition 2. *Assume that X has positive (Lebesgue) measure. The I/O system* (6) *possesses an Input/State (I/S) quasi-characteristic $k : U \to X$ if for every constant input $u \in U$, there exists a set of Lebesgue measure zero $\mathcal{B}_u$ such that:*

$$\forall x_0 \in X \setminus \mathcal{B}_u : \lim_{t \to +\infty} x(t, x_0, u) = k(u). \tag{9}$$

If system (6) *possesses an I/S quasi-characteristic k, then one can also associate an Input/Output (I/O) quasi-characteristic $g : U \to Y$ to it, defined as $g := h \circ k$.*

chemostat model. It is a special case of a more general result proved in [1]. Below we use the notion of an *almost-globally attractive equilibrium point* of an autonomous system to designate an equilibrium point which attracts all solutions that are not starting in a set of (Lebesgue) measure zero. Input, state and output spaces of the subsystems are assumed to satisfy all conditions introduced so far.

Theorem 2. *Consider the following two I/O systems:*

$$\dot{x}_1 = f_1(x_1, u_1), \quad y_1 = h_1(x_1) \tag{10}$$

$$\dot{x}_2 = f_2(x_2, u_2), \quad y_2 = h_2(x_2) \tag{11}$$

where $x_i \in X_i \subset \mathbb{R}^{n_i}$, $u_i \in U_i \subset \mathbb{R}^{m_i}$ and $y_i \in Y_i \subset \mathbb{R}^{p_i}$ for $i = 1, 2$. Suppose that $Y_1 = U_2$ and $Y_2 = -U_1$ and that the I/O systems are interconnected through a (negative) feedback loop:

$$u_2 = y_1, \quad u_1 = -y_2 \tag{12}$$

Assume that:

1. *Both I/O systems* (10) *and* (11) *are monotone.*
2. *Both I/O systems* (10) *and* (11) *possess* **continuous** *I/S quasi-characteristics k_1 and k_2 respectively (and thus also continuous I/O quasi-characteristics g_1 and g_2).*
3. *All forward solutions of the feedback system* (10) – (12) *are bounded.*

Then the feedback system possesses an almost-globally attractive equilibrium point $(\bar{x}_1, \bar{x}_2) \in X_1 \times X_2$ if the following discrete-time system, defined on U_2:

$$u_{k+1} = (g_1 \circ (-g_2))(u_k) \tag{13}$$

possesses a globally attractive fixed point $\bar{u} \in U_2$. In that case $(\bar{x}_1, \bar{x}_2) = ((k_1 \circ (-k_2))(\bar{u}),\ k_2(\bar{u}))$.

This result is usually referred to as a *small-gain theorem*. The attractivity condition for system (13) is often referred to as a *small-gain condition*. We will use this terminology in the sequel.

2.2 Invariance and boundedness for the full system

We will first show that system (1) leaves $\mathbb{R}_+^{n+1}$ forward invariant and that solutions remain uniformly ultimately bounded.

Lemma 1. $\mathbb{R}_+^{n+1}$ *is a forward invariant set for system* (1) *and the solutions starting in this set are uniformly ultimately bounded.*

The second claim can be proved by considering the function $V : \mathbb{R}_+^{n+1} \to \mathbb{R}_+$

$$V(S,\, x) = S + \sum_{i=1}^{n} x_i$$

and observing that along a solution of (1) this function obeys

$$\dot{V} = 1 - S - \sum_{i=1}^{n} x_i(D_i + a_i x_i)$$

Defining $D^* = \min(1,\, D_1,\, D_2,\, ...,\, D_n)$ this implies that

$$\dot{V} \leq 1 - D^* V$$

and thus by a comparison argument that

$$V(t) \leq V(0)\, \mathrm{e}^{-D^* t} + \frac{1}{D^*}$$

Since V is proper in $\mathbb{R}_+^{n+1}$ (i.e. the sets $\{(S,\, x) \in \mathbb{R}_+^{n+1} |\ a \leq V(S,\, x) \leq b\}$ are compact for any choice of $a \leq b$) the desired result is obtained. In fact, a slightly stronger conclusion is reached since the last inequality for $V(t)$ implies that $\limsup_{t\to\infty} V(t) \leq 1/D^*$ and thus solutions are uniformly ultimately bounded (i.e. there exists a compact set $K \subset \mathbb{R}_+^{n+1}$ such that every solution eventually enters K and remains there for ever after) □

2.3 Invariance and I/S characteristics for the subsystems

Next we will focus on the feedback representation (3) – (5) of system (1). In particular we will investigate the I/O-properties of the subsystems (3) and (4). Let us be more precise on the input, state and output space of these subsystems first. The nutrient subsystem is given by:

$$\begin{aligned} \dot{S} &= 1 - S + f^T(S) u_1 \\ y_1 &= S \end{aligned} \tag{14}$$

where $S \in X_1 := \mathbb{R}_+$ denotes the state, $u_1 \in U_1 := -\mathbb{R}_+^n$ denotes the input and $y_1 \in Y_1 := \mathbb{R}_+$ denotes the output. The input signals $u_1(t) : \mathbb{R} \to U_1$ are assumed to be Lebesgue measurable and essentially locally bounded, ensuring existence and uniqueness of solutions as discussed in the previous subsection.

Similarly consider the subsystem describing the dynamics of the species:

$$\begin{aligned} \dot{x} &= \mathrm{diag}(x)(f(u_2) - D - \mathrm{diag}(a)x) \\ y_2 &= x \end{aligned} \tag{15}$$

where $x \in X_2 := \mathbb{R}_+^n$ denotes the state, $u_2 \in U_2 := \mathbb{R}_+$ denotes the input and $y_2 \in Y_2 := \mathbb{R}_+^n$ denotes the output. The input signals $u_2(t) : \mathbb{R} \to U_2$ are also assumed to be Lebesgue measurable and essentially locally bounded. An obvious question is whether the respective state spaces X_1 and X_2 are invariant for the subsystems.

system (15).

Proof. The proof is based on Theorem 3 in [1]. We will only sketch it for system (14) since it is completely analogous for system (15).

Denoting the right-hand side of (14) by $F_1(S, u_1)$ it is easily checked that F_1 is locally Lipschitz in S, locally uniformly in u_1. Moreover, denoting $F_{1,D}(S) = \{F_1(S,\, u_1)|\ u_1 \in D\}$ for an arbitrary compact subset D of U_1, it can be easily verified that

$$\forall S \in X_1 :\ F_{1,D} \subset T_S X_1$$

where $T_S X_1 = T_S \mathbb{R}_+$ is the tangent cone to $\mathbb{R}_+$ at $S \in \mathbb{R}_+$. □

Lemma 3. *Systems* (14) *and* (15) *are monotone.*

Proof. This is based on Proposition 3.3 in [1]. Denoting the right-hand side of system (14) and (15) by $F_1(S, u_1)$, respectively $F_2(x, u_2)$ we need to check whether the following holds:

1. The matrices
$$\frac{\partial F_1}{\partial S}(S,\, u_1) \text{ and } \frac{\partial F_2}{\partial x}(x,\, u_2)$$
are Metzler (i.e. have non-negative off-diagonal entries) for all $(S,\, u_1) \in X_1 \times U_1$, respectively $(x,\, u_2) \in X_2 \times U_2$.

2. The matrices
$$\frac{\partial F_1}{\partial u_1}(S,\, u_1) \text{ and } \frac{\partial F_2}{\partial u_2}(x,\, u_2)$$
have non-negative entries for all $(S,\, u_1) \in X_1 \times U_1$, respectively $(x,\, u_2) \in X_2 \times U_2$.

It is easily checked that both conditions are satisfied. □

The next result is the key to proving the main theorem and reveals that both subsystems possess I/S quasi-characteristics with certain smoothness properties. We denote the Euclidean norm on $\mathbb{R}^n$ by $|.|$.

Lemma 4. *System* (14) *has a continuously differentiable I/S quasi-characteristic* $k_1 : U_1 \to X_1$. *Moreover,* k_1 *is globally Lipschitz with Lipschitz constant* $L_1^* := \sqrt{n} \max_{i=1,\dots,n} f_i(1)$, *i.e.*

$$\forall u_1^a,\, u_1^b \in U_1 :\ |k_1(u_1^a) - k_1(u_1^b)| \le L_1^* |u_1^a - u_1^b|. \tag{16}$$

System (15) *possesses a globally Lipschitz continuous I/S quasi-characteristic* $k_2 : U_2 \to X_2$ *with Lipschitz constant* $L_2^* := \sqrt{n} \max_{i=1,\dots,n} L_i/a_i$, *i.e.*

$$\forall u_2^a,\, u_2^b \in U_2 :\ |k_2(u_2^a) - k_2(u_2^b)| \le L_2^* |u_2^a - u_2^b| \tag{17}$$

$g_{u_1} : X_1 = \mathbb{R}_+ \to \mathbb{R}$ as follows:

$$g_{u_1}(S) = 1 - S + f^T(S)u_1$$

Then by continuity of g_{u_1}, $g_{u_1}(0) = 1 > 0$ and $g_{u_1}(1) = f^T(1)u_1 \leq 0$ we have that g_{u_1} possesses at least one root $S_{u_1} \in (0,\, 1]$. Moreover g_{u_1} is strictly decreasing since $g'_{u_1}(S) < 0$ for all $S \in X_1$, so this root is unique in X_1. For every $u_1 \in U_1$ we denote S_{u_1} by $k_1(u_1)$, yielding a map $k_1 : U_1 \to X_1$. In fact, the above arguments show that the range of k_1 is a subset of $(0,\, 1]$. Using the fact that $g'_{u_1}(S) < 0$ for all $S \in X_1$ once more, an application of the implicit function theorem shows that k_1 is continuously differentiable in X_1. To find $\partial k_1/\partial u_1$, it suffices to consider the following equality

$$1 - k_1(u_1) + f^T(k_1(u_1))u_1 = 0$$

and take derivatives with respect to u_1. Using the chain rule, the product rule for derivatives and after some simple algebraic manipulations, one obtains -using the notation f'^T for the row vector $(f'_1,\ f'_2,\ ...,\ f'_n)$

$$\frac{\partial k_1}{\partial u_1} = \frac{1}{1 - f'^T(.)u_1} f^T(.) \tag{18}$$

where $(.) \equiv (k_1(u_1))$. Since k_1 maps to $(0,\, 1]$, $U_1 = -\mathbb{R}^n_+$ and every f_i is non-decreasing it follows that:

$$\left| \frac{\partial k_1}{\partial u_1} \right| \leq \sqrt{n} |f(1)|_{\max}. \tag{19}$$

where $|.|_{\max}$ denotes the max-norm on $\mathbb{R}^n$. An application of the mean value theorem to the function k_1, followed by the Cauchy-Schwartz inequality and invoking (19) results is (16).

Finally, we claim that k_1 is the I/S quasi-characteristic for system (14). From the previous discussion it is clear that for every $u_1 \in U_1$, $k_1(u_1)$ is the unique equilibrium point of system (14) (of course we assume that the input signal is the constant u_1). Since solutions are bounded (by noticing that $\dot{S} < 0$ for $S > 1$) the equilibrium point is globally attractive with respect to initial conditions in X_1. In particular, the set of non-converging initial conditions $\mathcal{B}_{u_1}$ is empty for every $u_1 \in U_1$. This proves our claim.

Next we consider system (15). For every $u_2 \in U_2 = \mathbb{R}_+$, system (15) subject to the constant input signal u_2 possesses a -not necessarily unique- equilibrium point $x_{u_2} \in X_2$ with components given by

$$\forall i = 1, ..., n: \ (x_{u_2})_i = \max\left(0,\ \frac{f_i(u_2) - D_i}{a_i}\right). \tag{20}$$

This allows us to construct a map $k_2 : U_2 \to X_2$, defined as $k_2(u_2) := x_{u_2}$. Let us

$$
\begin{aligned}
|k_2(u_2^a) - k_2(u_2^b)| &\leq \sqrt{n}|k_2(u_2^a) - k_2(u_2^b)|_{\max} \\
&= \sqrt{n} \max_{i=1,\ldots,n} \left[\left| \max\left(0, \frac{f_i(u_2^a) - D_i}{a_i}\right) - \max\left(0, \frac{f_i(u_2^b) - D_i}{a_i}\right) \right| \right] \\
&\leq \sqrt{n} \max_{i=1,\ldots,n} \left[\left| \frac{f_i(u_2^a) - f_i(u_2^b)}{a_i} \right| \right] \\
&\leq \sqrt{n} \max_{i=1,\ldots,n} \left[\left| \frac{L_i(u_2^a - u_2^b)}{a_i} \right| \right] \\
&= \sqrt{n} \left(\max_{i=1,\ldots,n} \frac{L_i}{a_i} \right) .|u_2^a - u_2^b|.
\end{aligned}
$$

where we have used global Lipschitz properties (of the scalar function $h(r) = \max(0, r)$ in the second step and of the functions f_i in the third step).

Finally we claim that the map k_2 is an I/S quasi-characteristic for system (15). For every $u_2 \in U_2$, we define the support set of $k_2(u_2)$:

$$
\text{supp}(k_2(u_2)) = \{x \in X_1 = \mathbb{R}^n_+ |\ x_i > 0 \text{ if } (k_2(u_2))_i > 0\}
$$

and then define the set $\mathcal{B}_{u_2}$ as follows

$$
\mathcal{B}_{u_2} = X_1 \setminus \text{supp}(k_2(u_2)).
$$

Clearly $\mathcal{B}_{u_2}$ is a set of measure zero in $X_1 = \mathbb{R}^n_+$ since it is a subset of the boundary of $\mathbb{R}^n_+$. Now pick an initial condition $x_0 \in X_1 \setminus \mathcal{B}_{u_2} = \text{supp}(k_2(u_2))$. Denoting the solution of system (15) starting in x_0 and with constant input u_2 by $x(t, x_0)$ we will show that

$$
\forall x_0 \in X_1 \setminus \mathcal{B}_{u_2} = \text{supp}(k_2(u_2)) \ : \ \lim_{t \to \infty} x(t, x_0) = k_2(u_2). \tag{21}
$$

Notice that system (15) consists of n decoupled scalar differential equations. Each equation has exactly one or two equilibrium points. The i-th equation has only one equilibrium point at 0 if $(k_2(u_2))_i = 0$ and two equilibria if $(k_2(u_2))_i > 0$ (one equilibrium is again at 0, the other at $(k_2(u_2))_i$). If the i-th equation has only one equilibrium point at 0, then all solutions converge to it. If on the other hand there are two equilibrium points, then all solutions with a positive initial condition converge to the positive equilibrium point (of course, the solution starting in 0 remains there forever after). These facts imply that (21) holds, which concludes the proof.

□

Remark 2. Notice that the output spaces Y_1, Y_2 of systems (14) and (15) are identical to their respective state spaces X_1, X_2 and that the output mappings h_1 and h_2 are just the identity mappings. Therefore the I/O quasi-characteristics g_1 and g_2 of these systems equal their respective I/S quasi-characteristics k_1 and k_2 and of course g_1 and g_2 possesses the same properties as k_1 and k_2. In particular both mappings are globally Lipschitz with Lipschitz constants L_1^*, respectively L_2^*.

In this section we will prove Theorem 1, based on a contraction mapping principle.

Proof of Theorem 1

Consider system (1) or its equivalent feedback representation (3) – (5). We will show that under the conditions of theorem 1, the three conditions of theorem 2 together with the small-gain condition are satisfied. The first, second and third conditions follow from respectively lemma 3, lemma 4 and lemma 1. To see that small-gain condition is satisfied, recall from lemma 4 and remark 2 that $g_1 = k_1$ and $g_2 = k_2$ are globally Lipschitz with Lipschitz constants L_1^*, respectively L_2^*. Then the composition $g := g_1 \circ (-g_2)$ satisfies the following

$$\forall u^a,\, u^b \in U_2 : \; |g(u^a) - g(u^b)| \leq L_1^* L_2^* |u^a - u^b|$$

which by condition (2) shows that g is a contraction mapping on $U_2 = \mathbb{R}_+$. In turn this implies that the small-gain condition is satisfied, which concludes the proof of this theorem.

4 Coexistence

In this section we investigate whether system (1) can be coexistent. Let us first be precise about the term coexistence.

Definition 3. *System* (1) *is coexistent if there exists some* $\epsilon > 0$ *such that for* $i = 1, ..., n$ *holds:*

$$\liminf_{t \to \infty} x_i(t) > \epsilon \textit{ whenever } x_j(0) > 0, \; \forall j = 1, ..., n$$

where $(S(t), x_1(t), ..., x_n(t))^T$ *denotes the solution of system* (1) *with initial condition* $(S(0), x_1(0), ..., x_n(0))^T \in \mathbb{R}_+^{n+1}$.

In fact we will prove the much stronger result that under certain conditions there exists an equilibrium point in $\text{int}(\mathbb{R}_+^{n+1})$ which is globally asymptotically stable with respect to initial conditions in

$$\mathcal{P} := \{(S, x_1, ..., x_n) \in \mathbb{R}_+^{n+1} \mid x_i > 0, \forall i = 1, ..., n\}. \tag{22}$$

This contrasts the competitive exclusion principle which holds for the classical chemostat model. Since crowding effects are the only difference between the classical chemostat and the chemostat model presented here, this suggests they may be responsible for the observed coexistence of several species competing for a single nutrient.

Recall the assumptions made for system (1) in the introduction. Then according to lemma 1, $\mathbb{R}_+^{n+1}$ is a forward invariant set of system (1) and solutions are uniformly ultimately bounded. We will always restrict initial conditions for system (1) to $\mathbb{R}_+^{n+1}$.

Lemma 5. *Suppose that* $a_i > 0$ *for all* $i = 1, ..., n$. *If system* (1) *has an equilibrium point in* $\text{int}(\mathbb{R}_+^{n+1})$, *then it is locally asymptotically stable.*

of system (1), evaluated at $\bar{E}$:

$$J(\bar{E}) = \begin{pmatrix} -1-\sum_{i=1}^n \bar{x}_i f_i'(\bar{S}) & -f_1(\bar{S}) & -f_2(\bar{S}) & \dots & -f_n(\bar{S}) \\ \bar{x}_1 f_1'(\bar{S}) & -a_1\bar{x}_1 & 0 & \dots & 0 \\ \bar{x}_2 f_2'(\bar{S}) & 0 & -a_2\bar{x}_2 & \dots & 0 \\ \vdots & \vdots & \ddots & \vdots & \vdots \\ \bar{x}_n f_n'(\bar{S}) & 0 & 0 & \dots & -a_n\bar{x}_n \end{pmatrix}$$

Notice that necessarily $f_i(\bar{S}) > 0$ for all i (for otherwise $\bar{x}_i = -D_i/a_i$ would be negative, a contradiction).

All we need to show is that $J(\bar{E})$ is a Hurwitz matrix. In fact, all that matters in determining local stability of $\bar{E}$ is the sign structure of the entries of $J(\bar{E})$. We claim that every matrix with the following sign structure (negative diagonal entries, negative entries in the first row, nonnegative entries in the first column -except for the first entry, which is negative- and zeros elsewhere), is Hurwitz:

$$J = \begin{pmatrix} -j_{11} & -j_{12} & -j_{13} & \dots & -j_{1N} \\ +j_{21} & -j_{22} & 0 & \dots & 0 \\ +j_{31} & 0 & -j_{33} & \dots & 0 \\ \vdots & \vdots & \ddots & \vdots & \vdots \\ +j_{N1} & 0 & 0 & \dots & -j_{NN} \end{pmatrix}$$

where $j_{kk} > 0$, $j_{1k} > 0$ for $k = 1, ..., N$ and $j_{l1} \geq 0$ for $l = 2, ..., N$. The claim follows from Theorem 15.5.3 in [9]. To apply this result we first introduce some terminology. To an arbitrary $N \times N$ matrix A we can associate a *directed graph* $G(A)$ consisting of N nodes and directed arrows from node i to j whenever $a_{ji} \neq 0$. A cycle of length k occurs in $G(A)$ whenever there is a nonvanishing product $a_{i_1i_2}a_{i_2i_3}...a_{i_ki_1}$ for a sequence of pairwise distinct indices i_1, ..., i_k. Theorem 15.5.3 now states that if there are no cycles of length $k \geq 3$ in $G(A)$, if $a_{ii} < 0$ for all $i = 1$, ..., N and if $a_{ij}a_{ji} \leq 0$ for all pairwise distinct i, $j = 1$, ..., N, then A is a Hurwitz matrix. It is easily verified that all these conditions hold for J.

Alternatively, we can show that there exists a quadratic Lyapunov function for the linear system $\dot{z} = Jz$. Define:

$$V(z) = z_1^2/2 + \sum_{i=2}^N \alpha_i z_i^2/2$$

where the α_i are positive constants, to be determined later. Then along solutions of $\dot{z} = Jz$ we find that:

$$\dot{V} = -j_{11}z_1^2 - \sum_{i=2}^N j_{ii}\alpha_i z_i^2 + z_1(\sum_{k=2}^N (-j_{1k} + \alpha_k j_{k1})z_k)$$

So by setting:

$$\alpha_k = j_{1k}/j_{k1},\ k = 2, ..., N$$

we find that $\dot{V} = -j_{11}z_1^2 - \sum_{i=2}^N j_{ii}j_{1i}z_i^2$ and thus that $\dot{V} < 0$ whenever $z \neq 0$, proving our claim. □

indeed have an equilibrium point in int($\mathbb{R}_+^{n+1}$). Before doing so, we introduce an additional assumption:

H For each $i \in \{1, ..., n\}$ there exists a unique number $\lambda_i \in (0, 1)$ such that
$$f_i(\lambda_i) - D_i = 0.$$

Lemma 6. *Suppose that $a_i > 0$ for all i and that* **H** *holds. There exists some $\bar{a} > 0$ such that if $a_i > \bar{a}$ for all i, then system* (1) *has an equilibrium point $\bar{E} \in \mathrm{int}(\mathbb{R}_+^{n+1})$.*

Proof. System (1) has an equilibrium point $\bar{E} \in \mathrm{int}(\mathbb{R}_+^{n+1})$ if the following set of equations is solvable in $\mathrm{int}(\mathbb{R}_+^{n+1})$:

$$\begin{aligned} 1 - S - \sum_{i=1}^{n} \frac{f_i(S) - D_i}{a_i} f_i(S) &= 0 \\ x_i = \frac{f_i(S) - D_i}{a_i},\ i = 1, ..., n & \end{aligned} \qquad (23)$$

Obviously, for this to be the case, we should try to solve the first equation for S to obtain $\tilde{S} > 0$ and then check if $f_i(\tilde{S}) - D_i > 0$ for all i.

Setting:

$$\epsilon_i = 1/a_i,\ i = 1, ..., n$$

and defining

$$\epsilon = (\epsilon_1 ... \epsilon_n)^T,\ g(S) = (f_1(S)(f_1(S) - D_1) ... f_n(S)(f_n(S) - D_n))$$

we can compactly rewrite the first equation as follows:

$$F(S, \epsilon) := 1 - S - \epsilon^T g(S) = 0$$

The function F is C^1 in $(S, \epsilon) \in \mathbb{R}_+ \times \mathbb{R}^n$ (note that we allow the components of ϵ to be negative) and satisfies:

$$F(1, 0) = 0,\ \frac{\partial F}{\partial S}|_{(1,0)} = -1 \neq 0.$$

Therefore, by the implicit function theorem, there exists a C^1 function $S(\epsilon)$, defined on some open neighborhood of $\epsilon = 0$, such that $S(0) = 1$ and:

$$F(S(\epsilon), \epsilon) = 0.$$

Then by continuity of $S(\epsilon)$ and in view of **H** (which in particular implies that $\max_i(\lambda_i) < 1$), there is some $\bar{\epsilon} > 0$ such that:

$$\max_i(\lambda_i) < S(\epsilon) \text{ if } |\epsilon|_{\max} < \bar{\epsilon}$$

Then by uniqueness of the λ_i and monotonicity of the f_i, there holds for all i that:

$$f_i(S(\epsilon)) - D_i > 0 \text{ if } |\epsilon|_{\max} < \bar{\epsilon}$$

In terms of the a_i, this implies that there is some $0 < \bar{a} = 1/\bar{\epsilon}$ such that (23) is solvable in $\mathrm{int}(\mathbb{R}_+^{n+1})$, provided $a_i > \bar{a}$ for all i. This concludes the proof. □

gain condition (2) holds and such that $a_i > \bar{a}$ for all i where $\bar{a}$ is the bound from lemma 6.

Then lemmas 5 and 6 guarantee the existence of a locally asymptotically stable equilibrium point $\bar{E} \in \text{int}(\mathbb{R}_+^{n+1})$, while Theorem 1 ensures the existence of an equilibrium point $E^* \in \mathbb{R}_+^{n+1}$ which attracts almost every solutin starting in $\mathbb{R}_+^{n+1}$. Then obviously $E^* = \bar{E}$. In remark 1 we have seen that the set $\mathcal{B}$ of initial conditions corresponding to solutions which are not converging to E^* form a subset of $\mathcal{B}^*$. In fact, it is not hard to see that $\mathcal{B} = \mathcal{B}^*$, since the set $\mathcal{B}^*$ is invariant and disjoint from $\text{int}(\mathbb{R}_+^{n+1})$, which contains E^*. Notice also that $\mathbb{R}_+^{n+1} \setminus \mathcal{B} = \mathcal{P}$ and this implies in particular that all solutions starting in $\mathcal{P}$ converge to E^* and consequently that system (1) is coexistent.

We summarize this coexistence result next.

Theorem 3. *Assume that* **H** *holds. Consider system* (1) *and interpret the* a_i, $i = 1, ..., n$ *as positive parameters. If these parameters* a_i *are chosen large enough, then system* (1) *possesses an equilibrium point* $\bar{E} \in \text{int}(\mathbb{R}_+^{n+1})$ *which is almost-globally asymptotically stable with respect to initial conditions in* $\mathbb{R}_+^{n+1}$. *Moreover, every solution starting in* $\mathcal{P}$ *converges to* $\bar{E}$, *implying in particular that system* (1) *is coexistent.*

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