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Feedback control for nonmonotone competition models in the chemostat

Jean-Luc Gouzé*, Gonzalo Robledo

INRIA, Projet COMORE, 2004 Rte. des Lucioles, BP 93 - 06902 Sophia Antipolis Cedex, France

Abstract

This paper deals with the problem of feedback control of competition between two species with one substrate in the chemostat with nonmonotone growth functions. Without control, the generic behavior is competitive exclusion. The aim of this paper is to find a feedback control of the dilution rate, depending only on the total biomass, such that coexistence holds. We obtain a sufficient condition for the global asymptotic stability of a unique equilibrium point in the positive orthant for a three-dimensional differential system which arises from this controlled competition model. This paper generalizes the results obtained by De Leenheer and Smith in (J. Math. Biol. 46 (2003) 48).

Keywords: Chemostat; Nonmonotone growth functions; Competition model; Feedback control; Competitive dynamical systems; Global stability

1. Introduction

The model presented in this paper concerns the competition and coexistence of two species in a chemostat with a single substrate. Biological motivation for chemostat models can be found in [14]. Competition theory for chemostat models predicts that the *principle of competitive exclusion* holds, i.e., at most one species survives and the other one tends to extinction (see [3,14]).

In several chemostat models, control theory (see e.g., [10,16] for a general reference) obtains coexistence between species. While substrate and species are the state variables, the dilution rate and input substrate concentration can be used either or both of them as control

* Corresponding author. Tel.: +0033 492387875; fax: +0033 492387858.
E-mail addresses: gouze@sophia.inria.fr (J.-L. Gouzé), grobledo@sophia.inria.fr (G. Robledo).

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variables. *Open-loop control* (e.g., periodic input) and *Feedback control* are two control laws that give coexistence results. In this paper we are interested in the last control law.

De Leenheer and Smith [7] studied the linear feedback control for a well-known model of competition between two species and one substrate in a chemostat with monotone uptake functions, considering the dilution rate as a feedback control variable and keeping the input substrate concentration at a fixed value.

However, as it has been pointed out by several works (see e.g., [2,6,15]), the use of monotone uptake functions cannot be valid for substrates which are growth limiting at low concentrations but are inhibitory for the species at higher concentrations. Common examples of those cases are the inhibition of *Nitrobacter winogradskyi* and *Nitrosomas* by nitrite and ammonia, respectively, (see [2]), the inhibition of *Pseudomonas putida* and *Thricosporon cutaneum* by phenol (see [6,15]) and the inhibition of *Candida utilis* by ethanol (see [1]).

In the field of bioprocess, nonmonotone models are also widely used. The most common example is the so-called Haldane model, employed in the methanogenesis step of anaerobic digestion (see e.g., [4]).

The aim of the work presented in this paper is to extend the results obtained in [7] to nonmonotone uptake functions. We have obtained sufficient conditions for the coexistence of two species; to prove our main result, we will proceed in analogy to [7]. However, non-monotony properties of uptake functions make the study more complex than the monotone case, mainly because there are several types of nonlinearities to consider.

This paper is organized as follows: in Section 2 we have compiled some basic facts concerning the chemostat model with nonmonotone growth functions. In Section 3 we provide an exposition of the feedback control law and show the main result of coexistence. Section 4 presents some preliminary results related to the asymptotic behavior of the model with and without competition. The proof of the main result and some extensions are stated in Section 5; the robustness of the model is studied in Section 6.

2. Model of competition in the chemostat

The chemostat model with competition [14] is described by the differential equations:

$$\begin{cases} \dot{s} = D(s_{\text{in}} - s) - \dfrac{x_1}{y_1} f_1(s) - \dfrac{x_2}{y_2} f_2(s), \\ \dot{x}_1 = x_1(f_1(s) - D), \\ \dot{x}_2 = x_2(f_2(s) - D). \end{cases} \tag{1}$$

In model (1), s denotes the concentration of substrate at time t and x_i denotes the biomass density of the ith population of microorganisms at time t, $f_i(s)$ represents the per capita growth rate of nutrient of the ith population and so y_i is a growth yield constant; D and s_{in} denote, respectively, the dilution rate of the chemostat and the concentration of the input substrate.

We state the general assumptions on $f_i (i = 1, 2)$:

(F1). $f_i : \mathbb{R}_+ \mapsto \mathbb{R}_+$ and is $\mathscr{C}^1$.
(F2). $f_i(0) = 0$.

(F3). f_i is unimodal (i.e., there exists a number $s_i^* > 0$ such that f_i is increasing for $s \in [0, s_i^*)$ and decreasing for $s > s_i^*$) and moreover $\lim_{t\to+\infty} f_i(t) = c_i \geqslant 0$.

(F4). There is $s^* \in (0, s_{\text{in}})$ such that $f_1(s^*) = f_2(s^*) = D^*$; moreover,

$$\begin{cases} f_1(s) > f_2(s) & \text{if } s \in (0, s^*), \\ f_1(s) < f_2(s) & \text{if } s \in (s^*, +\infty). \end{cases}$$

Assumptions (F1)–(F2) state the general properties of population growth models; (F3) reflects the inhibition of growth of species x_1 and x_2 for high concentrations of substrate s.

An important function with properties (F1)–(F3) often found in the bioprocess literature is the Haldane function

$$f(s) = \frac{\mu^* s}{K_{\text{S}} + s + s^2/K_{\text{i}}}, \tag{2}$$

where μ^*, K_{S} and K_{i} are positive constants. Biological motivations for models with Haldane function can be found in [2].

Other examples are the functions proposed by Sokol and Howell in [15]:

$$f_1(s) = \frac{K_1 s}{K_2 + s^2}, \quad f_2(s) = \frac{K_1 s}{K_2 + s^{K_3}},$$

with K_1, $K_2 > 0$ and $K_3 > 1$.

Assumption (F4) involves a geometrical property on the graphs of f_1 and f_2; this implies several results about asymptotic behavior of solutions of (1) as we will see later on.

Remark 1. Clearly, $f_2'(s^*) \geqslant f_1'(s^*)$. Moreover, we have three possibilities for functions f_1 and f_2 satisfying (F1)–(F4), depending on the relative order of the intersection point s^* and the maximum points s_1^* and s_2^*. A graphical representation of all these cases is given in Figs. 1–3.

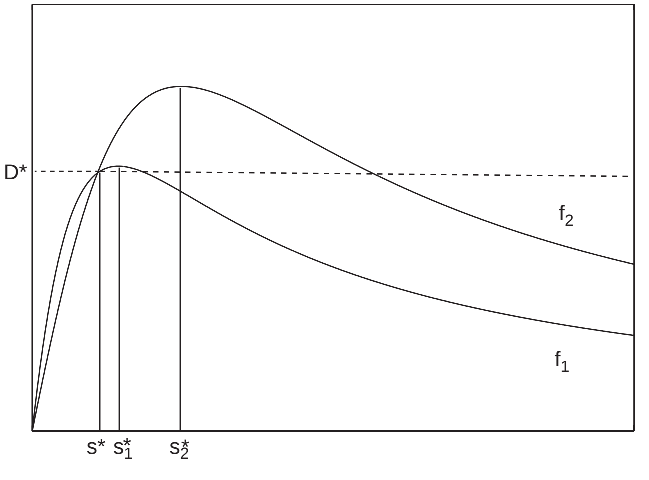

Fig. 1. Graph of f_1 and f_2. Case (a): $f_2'(s^*) > f_1'(s^*) \geqslant 0$, that is equivalent to $s^* < \min\{s_1^*, s_2^*\}$.

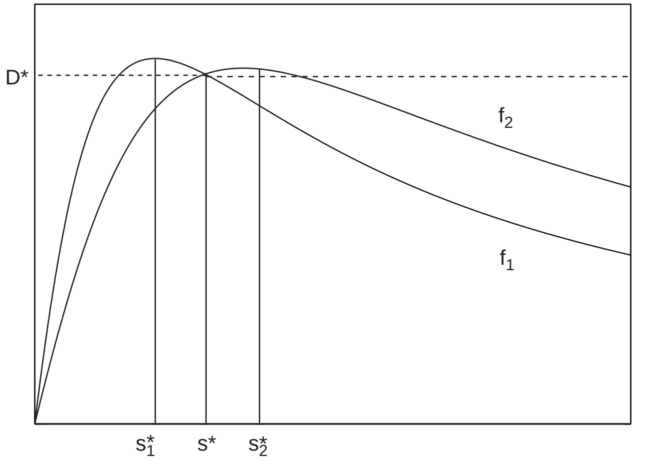

Fig. 2. Graph of f_1 and f_2. Case (b): $f_1'(s^*) < 0 < f_2'(s^*)$, that is equivalent to $s_1^* < s^* < s_2^*$.

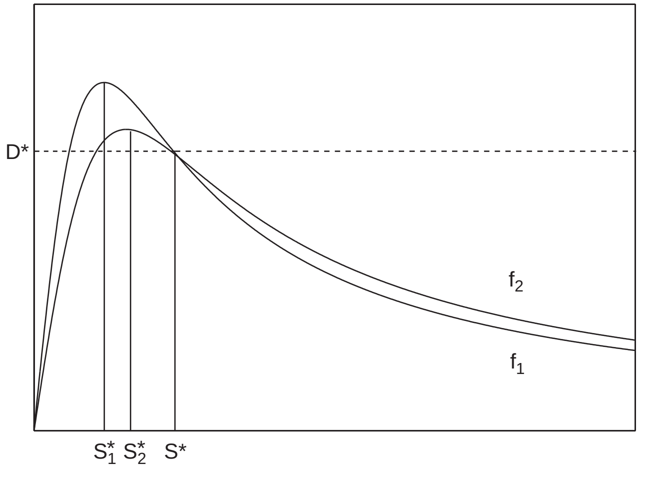

Fig. 3. Graph of f_1 and f_2. Case (c): $f_1'(s^*) < f_2'(s^*) \leqslant 0$, that is equivalent to $s^* > \max\{s_1^*, s_2^*\}$.

This model has been studied in [5] for n species. Next, we consider its main result tailored for $n = 2$ and functions that verify (F1)–(F4).

If $D \neq D^*$, there exist uniquely two defined positive real numbers η_i and μ_i such that $\eta_i < \mu_i \leqslant +\infty$ $(i = 1, 2)$ and

$$\begin{cases} f_i(s) < D & \text{if} \quad s \notin [\eta_i, \mu_i], \\ f_i(s) \geqslant D & \text{if} \quad s \in [\eta_i, \mu_i]. \end{cases}$$

Without loss of generality we will suppose that $\max\{\mu_1, \mu_2\} < s_{\mathrm{in}}$. Other cases can be studied similarly.

The results in [6] can be summarized coupling the relative order of numbers $\{s^*, s_1^*, s_2^*\}$ stated in Remark 1 and $\{D, D^*\}$:

Proposition 1 (*Butler and Wolkowicz [6]*). *With the exception of a set of initial conditions of Lebesgue measure zero, all solutions of* (1) *are initial condition dependent and satisfy*:

If $D < D^*$ or $D > D^*$ and $s^* > \max\{s_1^*, s_2^*\}$:

$$\lim_{t\to+\infty} (s(t), x_1(t), x_2(t)) = (\eta_1, y_1[s_{\mathrm{in}} - \eta_1], 0)$$

or

$$\lim_{t\to+\infty} (s(t), x_1(t), x_2(t)) = (s_{\mathrm{in}}, 0, 0).$$

If $D > D^*$ and $s_1^* < s^* < s_2^*$:

$$\lim_{t\to+\infty} (s(t), x_1(t), x_2(t)) = (\eta_1, y_1[s_{\mathrm{in}} - \eta_1], 0),$$
$$\lim_{t\to+\infty} (s(t), x_1(t), x_2(t)) = (\eta_2, 0, y_2[s_{\mathrm{in}} - \eta_2])$$

or

$$\lim_{t\to+\infty} (s(t), x_1(t), x_2(t)) = (s_{\mathrm{in}}, 0, 0).$$

If $D > D^*$ and $s^* < \min\{s_1^*, s_2^*\}$:

$$\lim_{t\to+\infty} (s(t), x_1(t), x_2(t)) = (\eta_2, 0, y_2[s_{\mathrm{in}} - \eta_2])$$

or

$$\lim_{t\to+\infty} (s(t), x_1(t), x_2(t)) = (s_{\mathrm{in}}, 0, 0).$$

Note that Proposition 1 is a result qualitatively different from the model with functions f_i strictly increasing: the novelty is that extinction of the two species can be expected because $(s_{\mathrm{in}}, 0, 0)$ is a locally asymptotically stable solution (see e.g., [6,14] for details).

In the remainder of this paper we assume that $y_1 \neq y_2$. In the sequel $y_{\min}$,$y_{\max}$ denote $\min\{y_1, y_2\}$ and $\max\{y_1, y_2\}$, respectively.

3. The uniform persistence in a control setting

Until now, we have used the term coexistence as the survival of the two species. Henceforth, we will use the concepts of *persistence* and *uniform persistence*. We recall the definitions given by Butler et al. in [5]:

Definition 1. A component $x_i(t)$ of a given ODE system is said to be persistent if for any $x_i(0) > 0$ it follows that $x_i(t) > 0$ for all $t > 0$ and $\liminf_{t\to+\infty} x_i(t) > 0$.

If there exists $\delta > 0$ independent of $x_i(0)$ such that component $x_i(t)$ is persistent and $\liminf_{t\to+\infty} x_i(t) > \delta$, then $x_i(t)$ is uniformly persistent.

Uniform persistence of the species is usually observed as the existence of a globally attracting periodic solution or a globally asymptotically stable solution. As we have seen in Proposition 1, persistence of two species is not possible in system (1).

3.1. The feedback control problem

In several works (see e.g., [14]), uniform persistence of competition models in chemostat has been obtained considering the input s_{in} or the dilution rate D as periodic functions. In this paper we will follow another approach, using control theory and feedback control with dilution rate D. Our goal is to obtain sufficient conditions for uniform persistence considering the following hypotheses:

Hypothesis 1 (*Control Hypothesis*). *Dilution rate D is the feedback control variable.*

Hypothesis 2 (*Output Hypothesis*). *The only output available is*

$$y = x_1 + x_2.$$

Output hypothesis is considered because in several cases, technical difficulties do not allow to measure x_1 and x_2 independently and it is necessary to consider total biomass. For example, the measurement is done often by photometric methods (see [15] and the references given there) that do not allow to distinguish between the two species.

We define the feedback control law $D : \mathbb{R}_+^2 \mapsto \mathbb{R}_+$ by

$$D(x_1, x_2) = g(x_1 + x_2). \tag{3}$$

We also make the following assumptions on the function g:

(G1). $g : \mathbb{R}_+ \mapsto \mathbb{R}_+$ is $\mathscr{C}^1$ and globally Lipschitz.
(G2). $g(0) \in [0, f_1(s_{\text{in}}))$, g is strictly increasing and there is $s_c > 0$ such that $g(s_c) = D^*$.

Replacing D by the feedback control law (3), system (1) becomes

$$\begin{cases} \dot{s} = g(x_1 + x_2)(s_{\text{in}} - s) - \dfrac{x_1}{y_1} f_1(s) - \dfrac{x_2}{y_2} f_2(s), \\ \dot{x}_1 = x_1(f_1(s) - g(x_1 + x_2)), \\ \dot{x}_2 = x_2(f_2(s) - g(x_1 + x_2)). \end{cases} \tag{4}$$

Remark 2. Nonnegativity of function g is supposed because dilution rate D cannot be negative. Assumption (G1) ensures the existence and uniqueness of the initial value problem and (G2) implies the existence of a new critical point.

3.2. Choice of the control

Our goal is to obtain sufficient conditions on the function g and its relations with f_1 and f_2 to have existence and global asymptotic stability of the interior critical point.

First, let us define the following equations that will be used to study the asymptotic behavior of system (4):

$$f_1(s) - g(y_1[s_{\text{in}} - s]) = 0, \tag{5}$$

$$f_2(s) - g(y_2[s_{\text{in}} - s]) = 0. \tag{6}$$

We will make the assumptions

(H1). $g(y_{\max}[s_{\text{in}} - s^*]) > D^* > g(y_{\min}[s_{\text{in}} - s^*])$.
(H2). Eqs. (5) and (6) have one positive solution λ_1 and λ_2, respectively. Moreover, if $y_1 > y_2$ we have that $\lambda_1 \in (s^*, s_{\text{in}})$ and $\lambda_2 \in (0, s^*)$.
(H3). $y_{\min} g'(x_1 + x_2) > -f_1'\left(s_{\text{in}} - \dfrac{x_1}{y_1} - \dfrac{x_2}{y_2}\right)$ for all $(x_1, x_2) \in \mathcal{O}$,
(H4). $y_{\min} g'(x_1 + x_2) > -f_2'\left(s_{\text{in}} - \dfrac{x_1}{y_1} - \dfrac{x_2}{y_2}\right)$ for all $(x_1, x_2) \in \mathcal{O}$,

where

$$\mathcal{O} = \left\{ (x_1, x_2) \in \mathbb{R}_+^2 : 0 \leqslant \frac{x_1}{y_1} + \frac{x_2}{y_2} \leqslant s_{\text{in}} \right\}.$$

Remark 3. As we can choose the strictly increasing function g, assumptions (H1)–(H2) are always satisfied with reasonable choices. In fact, these assumptions can be interpreted geometrically with the graph of functions defined in Eqs. (5) and (6) (see Fig. 4).

Note that, in some cases it can be difficult to find a function g checking assumptions (H3)–(H4). Otherwise, if $s_1^* \geqslant s_{\text{in}}$ (respectively $s_2^* \geqslant s_{\text{in}}$) then assumption (H3) (respectively (H4)) is always verified.

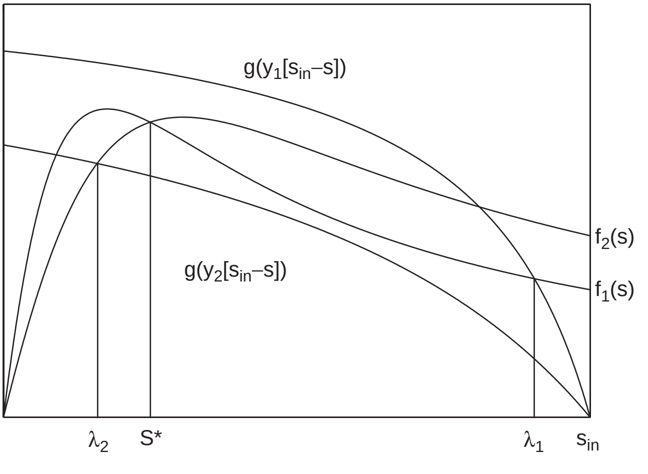

Fig. 4. Geometrical interpretation of (H1)–(H2).

Inequality $y_1 \neq y_2$ implies that system (4) has a critical point (s^*, x_1^*, x_2^*) defined by

$$x_1^* = \frac{y_1[y_2(s_{\text{in}} - s^*) - g^{-1}(D^*)]}{y_2 - y_1}, \quad x_2^* = \frac{y_2[g^{-1}(D^*) - y_1(s_{\text{in}} - s^*)]}{y_2 - y_1}.$$

Assumption (H1) implies that $(s^*, x_1^*, x_2^*) \in \text{int}\mathbb{R}_+^3$, (H2) implies that there are two hyperbolic critical points of system (4) in the boundary of $\mathbb{R}_+^3$ defined by

$$E_1 = (\lambda_1, y_1[s_{\text{in}} - \lambda_1], 0) \quad \text{and} \quad E_2 = (\lambda_2, 0, y_2[s_{\text{in}} - \lambda_2]).$$

Finally, note that if $g(0) = 0$, then

$$\Lambda = \{(s, x_1, x_2) \in \mathbb{R}_+^3 : \ s \geqslant 0, \ x_1 = x_2 = 0\}$$

is a set of nonhyperbolic critical points of system (4). In the remainder of this paper we assume that the initial conditions of system (4) are in $\mathbb{R}_+^3 \backslash \Lambda$.

3.3. Main result

The main result of this paper provides a sufficient condition for the global asymptotic stability of the critical point (s^*, x_1^*, x_2^*).

Theorem 1. *Let* $y_{\max} = y_1$, *if at least one of the following conditions is verified*:

(i) *Assumptions* (H1)–(H4) *hold*.
(ii) *Assumptions* (H1)–(H3) *hold and inequalities* $s^* < \min\{s_1^*, s_2^*\}$ *or* $s^* \in (s_1^*, s_2^*)$ *are verified*.
(iii) *Assumptions* (H1)–(H2) *hold and* $s^* < \min\{s_1^*, s_2^*\}$.

Then, the critical point (s^*, x_1^*, x_2^*) *is a globally asymptotically stable solution of system* (4) *for all initial conditions in* $\text{int}\mathbb{R}_+^3$.

Note that the relative order of points s^*, s_1^* and s_2^* summarized in Remark 1 implies different requirements on assumptions (H1)–(H4); in fact, the functions depicted in Fig. 1—case (a)—satisfy (H1)–(H2). Secondly, the functions depicted in Fig. 2—case (b)—satisfy (H1)–(H3). Finally, the functions depicted in Fig. 3—case (c)— satisfy (H1)–(H4). This is important because assumption (H4) is unnecessarily restrictive for case (ii) and assumptions (H3)–(H4) are unnecessarily restrictive for case (iii). Furthermore, as we have pointed out in Remark 3, there are some cases where checking assumptions (H3)–(H4) can be rather complicated.

4. Preliminary results

In the following results, we establish some properties related to the asymptotic behavior of solutions which are needed in the proof of Theorem 1.

Lemma 1. *Let* $(s(t), x_1(t), x_2(t))$ *be a solution of system* (4) *with initial condition in* $\operatorname{int}\mathbb{R}^3_+$. *Then this solution is bounded and verifies*

$$\lim_{t\to+\infty} s + \frac{x_1}{y_1} + \frac{x_2}{y_2} = s_{\text{in}}. \tag{7}$$

Proof. The main idea of the proof is taken from [11]. Let $V : \mathbb{R}_+ \mapsto \mathbb{R}$ be defined by

$$V(t) = \left(s(t) + \frac{x_1(t)}{y_1} + \frac{x_2(t)}{y_2} - s_{\text{in}} \right).$$

Clearly, $V' = -g(x_1 + x_2)V$; the lemma follows if $V(t)$ is convergent to 0 when $t \to +\infty$.

Case (i): If $g(0) > 0$ the result is a consequence of LaSalle invariance principle.

Case (ii): If $g(0) = 0$; clearly, Eq. (7) follows if and only if

$$\lim_{t\to+\infty} \int_0^t g(x_1(s) + x_2(s))\,\mathrm{d}s = +\infty.$$

Conversely, if we suppose that

$$\lim_{t\to+\infty} \int_0^t g(x_1(s) + x_2(s))\,\mathrm{d}s < +\infty,$$

it is easily seen that the function $t \mapsto g(x_1(t) + x_2(t))$ is nonnegative and integrable. Moreover, we can prove that every solution of system (4) is bounded: In fact, if $V(0) \leqslant 0$ it follows that $V(t) \leqslant 0$ for any $t \geqslant 0$ and every solution is bounded by the plane

$$\Sigma = \left\{ (s, x_1, x_2 | s + \frac{x_1}{y_1} + \frac{x_2}{y_2} = s_{\text{in}} \right\},$$

if $V(0) > 0$ it follows that $V(t) > 0$ and $V'(t)$ is negative; hence, the boundedness follows.

Using this fact, combined with the mean value theorem implies that every solution of system (4) is uniformly continuous on $[0, \infty)$ and finally we conclude that the function $t \mapsto g(x_1(t) + x_2(t))$ is uniformly continuous; therefore, Barbălat's lemma (see e.g. [10]) yields

$$\lim_{t\to+\infty} g(x_1(t) + x_2(t)) = 0.$$

As $g(0) = 0$ and g is strictly increasing, we obtain that $\lim_{t\to+\infty} x_i(t) = 0$. On the other hand, by continuity of g we have that

$$\lim_{t\to+\infty} \frac{\exp[\int_0^t f_i(s(u))\,\mathrm{d}u]}{\exp[\int_0^t g(x_1(u) + x_2(u))\,\mathrm{d}u]} = \lim_{t\to+\infty} x_i(t) = 0$$

and it follows that

$$\lim_{t\to+\infty} \exp\left(\int_0^t f_i(s(u))\,\mathrm{d}u \right) = 0,$$

but this is not possible, hence (7) holds, which completes the proof. □

If $g(0)=0$, it follows by Lemma 1 that critical points in $\Lambda\backslash\{(s_{\mathrm{in}},0,0)\}$ are not attractive. We will denote by U_1 and U_2 the positively invariant sets:

$$U_1=\{(s,x_1,x_2)\in\mathbb{R}^3_+ : s\geqslant 0, x_1>0 \quad \text{and } x_2=0\},$$

$$U_2=\{(s,x_1,x_2)\in\mathbb{R}^3_+ : s\geqslant 0, x_2>0 \quad \text{and } x_1=0\}.$$

As we are interested in persistence of species x_1 and x_2, it is important to know if each species is persistent in the chemostat without competition. Each species must be able to survive alone in the chemostat if it is to be able to survive with a competitor. The following result gives an affirmative answer.

Lemma 2. *Let* $(s(t),x_1(t),x_2(t))$ *be a solution of system* (4) *with initial condition in* U_i $(i=1,2)$. *Then this solution is bounded and verifies*:

$$\lim_{t\to+\infty} s+\frac{x_i}{y_i}=s_{\mathrm{in}}, \tag{8}$$

$$\lim_{t\to+\infty} x_i(t)=y_i[s_{\mathrm{in}}-\lambda_i] \quad \textit{and} \quad \lim_{t\to+\infty} s(t)=\lambda_i. \tag{9}$$

Proof. We give the proof for the case $i=1$; the other case is similar. Eq. (8) is an immediate consequence of Lemma 1. Clearly, $x_2(t)=0$ for $t\geqslant 0$. We consider the second equation of system (4) and insert the solution $s(t)$ initiated at $s(0)$. Then we obtain the following nonautonomous differential equation:

$$\dot{x}_1=x_1(f_1(s(t))-g(x_1)). \tag{10}$$

By (8), it follows that for each initial condition $s(0)$, Eq. (10) is asymptotically autonomous (see e.g., [17] for details) with limit equation

$$\dot{z}_1=z_1\left(f_1\left(s_{\mathrm{in}}-\frac{z_1}{y_1}\right)-g(z_1)\right). \tag{11}$$

Assumption (H2) implies that the solution $z_1(t)$ of Eq. (11) satisfies

$$\lim_{t\to+\infty} z_1(t)=y_1[s_{\mathrm{in}}-\lambda_1].$$

Applying corollary 4.3 from [17], it follows that each solution of Eq. (10) converges to $y_1[s_{\mathrm{in}}-\lambda_1]$ and (8) makes it obvious that $\lim_{t\to+\infty} s(t)=s^*$, which proves the Lemma. □

Lemma 3. *If* $y_{\max}=y_1$, *then every component* $x_i(t)$ *of a solution of system* (4) *with initial condition in* $\mathrm{int}\mathbb{R}^3_+$ *is uniformly persistent.*

Proof. Let $\mathrm{X}=\{(s,x_1,x_2)\in\mathbb{R}^3_+ : s\leqslant s_{\mathrm{in}},\ x_1+x_2\leqslant L\}$, where $L>y_1 s_{\mathrm{in}}$ and $g(L)>\max\{f_1(s_1^*),\ f_2(s_2^*)\}$. Lemma 1 implies that X is positively invariant and every solution of system (4) reaches X in finite time and cannot leave it. Hence, we can consider only the initial conditions in X.

Let $M = \mathrm{X} \cap (U_1 \cup U_2)$; following the method developed in [9], we will prove that M is a repeller set that is equivalent to uniform persistence. Next, we build the *average Lyapunov function* $P : \mathrm{X} \mapsto \mathbb{R}$, defined by

$$P(x_1, x_2) = x_1 x_2.$$

Clearly, $P(x_1, x_2)=0$ for $(x_1, x_2) \in M$ and $P(x_1, x_2) > 0$ for $(x_1, x_2) \in \mathrm{X}\backslash M$. Moreover, $\dot{P}(x_1, x_2) = \Psi(s, x_1, x_2)P(x_1, x_2)$ where $\Psi : \mathrm{X} \mapsto \mathbb{R}$ is the continuous function

$$\Psi(s, x_1, x_2) = f_1(s) + f_2(s) - 2g(x_1 + x_2).$$

Let $W^s(E_i)$ and $W^u(E_i)$ be the stable and unstable manifold, respectively, of critical points E_i. By $y_{\max} = y_1$ and Lemma 2, we have that U_i are included in $W^s(E_i)$; moreover, (H2) implies that E_i are saddle-points and $\Psi(E_i) > 0$. Finally, theorem 12.2.2 from [9] (see also corollaries 1 and 2 from [8]) implies that M is a repeller set and the proof is complete. □

5. Proof of main result

Let us return to system (4) in equations $\dot{x}_1$ and $\dot{x}_2$ and insert the solution $s(t)$ initiated at $s(0)$. Then, for each initial condition $s(0)$ we obtain the nonautonomous system:

$$\begin{cases} \dot{x}_1 = x_1(f_1(s(t)) - g(x_1 + x_2)), \\ \dot{x}_2 = x_2(f_2(s(t)) - g(x_1 + x_2)). \end{cases} \tag{12}$$

Note that Lemma 1 implies that for each initial condition $s(0)$, system (12) is asymptotically autonomous with limit system

$$\begin{cases} \dot{z}_1 = z_1 \left(f_1 \left(s_{\text{in}} - \dfrac{z_1}{y_1} - \dfrac{z_2}{y_2} \right) - g(z_1 + z_2) \right), \\ \dot{z}_2 = z_2 \left(f_2 \left(s_{\text{in}} - \dfrac{z_1}{y_1} - \dfrac{z_2}{y_2} \right) - g(z_1 + z_2) \right). \end{cases} \tag{13}$$

Moreover, system (13) defines a dynamical system in the set $\mathcal{O} \subset \mathbb{R}^2_+$ and the relation between asymptotic behavior of both systems is summarized by the following result:

Proposition 2 (*Thieme [17]*). *Let ω be the ω-limit of a forward bounded solution of* (12). *Assume that there exists a neighborhood of ω which contains at most finitely many equilibria of* (13). *Then the following trichotomy holds*:

(a′) *ω consists of an equilibrium of* (13).
(b′) *ω is the union of periodic orbits of* (13) *and possibly of centers of* (13) *that are surrounded by periodic orbits living in ω.*
(c′) *ω contains equilibria of* (13) *that are cyclically chained to each other in ω by orbits of* (13).

The critical points of system (13) are the projections in the set $\mathcal{O}$ of the hyperbolic critical points stated in the previous section beside $(s_{\text{in}}, 0, 0) \in \Lambda$:

$$E_0^p = (0, 0),$$
$$E_1^p = (y_1[s_{\text{in}} - \lambda_1], 0),$$
$$E_2^p = (0, y_2[s_{\text{in}} - \lambda_2]),$$
$$E_s^p = (x_1^*, x_2^*).$$

The local properties of critical points of (13) are summarized in the following Lemma:

Lemma 4. *Let assumptions* (H1)–(H2) *and* $y_{\max} = y_1$ *hold. Then all the critical points of* (13) *are hyperbolic, moreover*:

(a) *Critical point* E_0^p *is a repeller*.
(b) *Critical points* E_i^p *are saddle-points,* $W^u(E_i^p)$ *are in* $\text{int}\mathbb{R}_+^2$ $(i = 1, 2)$ *and*

$$W^s(E_1^p) = \{(z_1, z_2) \in \mathcal{O} : 0 < z_1 < y_1 s_{\text{in}} \quad \textit{and} \quad z_2 = 0\},$$

$$W^s(E_2^p) = \{(z_1, z_2) \in \mathcal{O} : 0 < z_2 < y_2 s_{\text{in}} \quad \textit{and} \quad z_1 = 0\}.$$

Moreover, E_1^p *and* E_2^p *cannot belong to* $\omega(\vec{z}(0))$ *when* $\vec{z}(0) \in \text{int}\mathcal{O}$.
(c) *Local asymptotic stability of critical point* E_s^p *is always verified when* $s^* < \min\{s_1^*, s_2^*\}$, *is verified by assumption* (H3) *when* $s^* \in (s_1^*, s_2^*)$ *and by assumptions* (H3) *and* (H4) *when* $s^* > \max\{s_1^*, s_2^*\}$.

Proof. Result (a) is obtained from the standard linearization procedure and (G2). Result (b) is obtained following the lines of the proof of Lemma 3. Finally, as $y_{\max} = y_1$ a necessary and sufficient condition for local stability of E_s^p is

$$s^* g'(s^*) > -\frac{x_1^*}{y_1} f_1'(s^*) + \frac{x_2^*}{y_2} f_2'(s^*). \tag{14}$$

Now, the proof of result (c) is straightforward. $\square$

The proof of the theorem will be divided into three steps:

(1) Let $\vec{x}(0) \in \text{int}\mathbb{R}_+^2$ be an initial condition of system (12). We will prove that system (13) cannot have periodic orbits or a cycle of critical points. A consequence of Proposition 2 is that the set $\omega(\vec{x}(0))$ is a critical point of system (13).
(2) Lemma 3 implies that this critical point cannot be in $\partial\mathcal{O}$, hence, $\omega(\vec{x}(0)) = (x_1^*, x_2^*)$.
(3) Finally, Eq. (7) makes it obvious that $\lim_{t\to+\infty} s(t) = s^*$, which proves the theorem.

We will prove all the cases (i)–(iii) in the statement of Theorem 1.

5.1. Proof of case (i)

Let $\vec{z}(0) \in \text{int}\mathcal{O}$ be an initial condition of (13). The asymptotic behavior of a solution with this initial condition is described by the following Lemma:

Lemma 5. *Let $\vec{z}(t)$ be a solution of* (13) *with initial condition $\vec{z}(0)$, then there exists a real number $T > 0$ such that the solutions $z_i(t)$ are monotone on $t > T$. In particular we know that $\omega(\vec{z}(0))$ is a critical point.*

Proof. By (H3)–(H4) we have that system (13) is *competitive* on $\mathcal{O}$ (i.e., the off-diagonal entries of the Jacobian matrix on $\mathcal{O}$ are negative or zero). As the forward orbit of $\vec{z}(0)$ is a relatively compact set, we apply Theorem 3.2.2 from [12] and the Lemma follows. □

A consequence of Lemma 5 is that system (13) cannot have periodic orbits or a cycle of critical points, which proves the theorem.

Assume now that $s^* < \min\{s_1^*, s_2^*\}$ or $s^* \in (s_1^*, s_2^*)$ and (H4) is not verified. Note that in this case, system (13) is not necessary competitive and Lemma 5 cannot be applied.

As before, let $\vec{z}(t)$ be a solution of system (13) with initial condition $\vec{z}(0) \in \text{int}\mathcal{O}$. We will prove that $\vec{z}(t)$ cannot be a periodic orbit and that $\omega(\vec{z}(0))$ cannot be a cycle of critical points.

5.2. Proof of case (ii)

Let $\hat{s} \in (s^*, s_2^*)$. We define an increasing $\mathscr{C}^1$-function $e_2 \colon [\hat{s}, +\infty) \mapsto \mathbb{R}$ such that $e_2^{(k)}(\hat{s}) = f_2^{(k)}(\hat{s})$ for $k = 0, 1$. Let us denote by m_2 the *increasing envelope* of f_2 as the function

$$m_2(s) = \begin{cases} f_2(s) & \text{if} \quad s \in [0, \hat{s}], \\ e_2(s) & \text{if} \quad s \geqslant \hat{s}. \end{cases} \tag{15}$$

Let us consider the system:

$$\begin{cases} \dot{u}_1 = u_1 \left(f_1 \left(s_{\text{in}} - \dfrac{u_1}{y_1} - \dfrac{u_2}{y_2} \right) - g(u_1 + u_2) \right), \\ \dot{u}_2 = u_2 \left(m_2 \left(s_{\text{in}} - \dfrac{u_1}{y_1} - \dfrac{u_2}{y_2} \right) - g(u_1 + u_2) \right), \\ u_1(0) = z_1(0) > 0, u_2(0) = z_2(0) > 0. \end{cases} \tag{16}$$

Notice that system (16) has the same critical points as system (13) with the same local properties summarized by Lemma 4. Assumption (H3) implies that system (16) is competitive and replacing f_2 by m_2 in the case (i) of Theorem 1 we have that

$$\lim_{t \to +\infty} (u_1(t), u_2(t)) = (x_1^*, x_2^*).$$

Using the order $K_{(0,1)}$ and Proposition 3 (see Appendix) we have the inequalities

$$(z_1(0), z_2(0)) \geqslant_{K_{(0,1)}} (u_1(0), u_2(0)) \geqslant_{K_{(0,1)}} (0, u_2(0))$$

and

$$(z_1(t), z_2(t)) \geqslant_{K_{(0,1)}} (u_1(t), u_2(t)) \geqslant_{K_{(0,1)}} (0, u_2(t))$$

for all $t \geqslant 0$. Letting $t \to +\infty$, we have that:

$$\liminf_{t\to+\infty} z_1(t) \geqslant x_1^* \quad \text{and} \quad \limsup_{t\to+\infty} z_2(t) \leqslant x_2^* \leqslant y_2[s_{\text{in}} - \lambda_2]. \tag{17}$$

This gives that $\omega(\vec{z}(0))$ is a subset of $\{(x_1, x_2) \in \mathcal{O} | x_1 \geqslant x_1^*,\ 0 < x_2 \leqslant x_2^*\}$; hence, $\vec{z}(t)$ cannot be a periodic orbit. Indeed, otherwise we would have a periodic orbit parametrized by $\vec{\psi}$ and by Poincaré–Bendixson theorem, the critical point (x_1^*, x_2^*) would be inside $\vec{\psi}$, obtaining a contradiction.

It remains to prove that there is no cycle of critical points. If we suppose the existence of one, Lemma 4 implies that E_0^p is a repeller and E_s^p is locally asymptotically stable; hence, they cannot belong to this cycle. Moreover, Eq. (17) implies that E_2^p cannot belong to this cycle, so only E_1^p could possibly belong to it.

But Lemma 4 implies that $W^s(E_1^p) \cap W^u(E_1^p) \backslash E_1^p = \emptyset$; hence, E_1^p cannot belong to this cycle, which proves the Theorem.

5.3. *Proof of case (iii)*

Let $\hat{s} \in (s^*, \max\{s_1^*, s_2^*\})$. We define a couple of continuous increasing functions e_1,e_2 : $[\hat{s}, +\infty) \mapsto \mathbb{R}$ such that $e_i^{(k)}(\hat{s}) = f_i^{(k)}(\hat{s})$ for $k = 0, 1$ and $e_2(s) > e_1(s)$ for all $s > \hat{s}$. Let us denote by m_i the *increasing envelope* of f_i as the functions

$$m_i(s) = \begin{cases} f_i(s) & \text{if} \quad s \in [0, \hat{s}], \\ e_i(s) & \text{if} \quad s \geqslant \hat{s}. \end{cases} \tag{18}$$

Let us consider the system:

$$\begin{cases} \dot{u}_1 = u_1 \left(m_1 \left(s_{\text{in}} - \dfrac{u_1}{y_1} - \dfrac{u_2}{y_2} \right) - g(u_1 + u_2) \right), \\ \dot{u}_2 = u_2 \left(m_2 \left(s_{\text{in}} - \dfrac{u_1}{y_1} - \dfrac{u_2}{y_2} \right) - g(u_1 + u_2) \right), \\ u_1(0) > 0, u_2(0) > 0. \end{cases} \tag{19}$$

Note that system (19) is competitive and has the same interior critical point as (13). Now, we will prove that system (13) cannot have periodic orbits. Indeed, if we suppose that there is a solution of system that is a nontrivial periodic orbit parametrized by $\vec{\psi}(t)$ with (x_1^*, x_2^*) inside, we shall arrive at a contradiction by considering the backward orbits of systems (13) and (19), note that this orbit is a solution of reversed time cooperative system:

$$\begin{cases} \dot{v}_1 = -v_1 \left(m_1 \left(s_{\text{in}} - \dfrac{v_1}{y_1} - \dfrac{v_2}{y_2} \right) - \alpha g(v_1 + v_2) \right), \\ \dot{v}_2 = -v_2 \left(m_2 \left(s_{\text{in}} - \dfrac{v_1}{y_1} - \dfrac{v_2}{y_2} \right) - \alpha g(v_1 + v_2) \right), \\ v_1(0) = u_1(0) > 0, v_2(0) = u_2(0) > 0. \end{cases} \tag{20}$$

We choose the initial conditions of systems such that

$$z_1(0) = \psi_1(0) > v_1(0) = x_1^*, \quad z_2(0) = \psi_2(0) > v_2(0) = x_2^*.$$

Applying Theorem B.1 from [14], it follows that

$$\psi_1(t) > x_1^* \quad \text{and} \quad \psi_2(t) > x_2^* \quad \text{for all } t < 0,$$

it follows that the critical point (x_1^*, x_2^*) is not inside $\vec{\psi}$ obtaining a contradiction with Poincaré–Bendixson theorem.

It remains to prove that there is no cycle of critical points. If we suppose the existence of one, as in the proof of case (ii) Lemma 4 implies that E_0^p and E_s^p cannot belong to this cycle, so only E_1^s and/or E_2^s could possibly belong to it.

By Lemma 4 we have that $W^u(E_1^p) \cap W^s(E_2^p) = \emptyset$ and $W^u(E_2^p) \cap W^s(E_1^p) = \emptyset$, then there is no cycle connecting E_1^p and E_2^p.

Finally, as in the proof of case (ii), the existence of a cycle connecting E_i^p $(i = 1, 2)$ to itself is not possible, which proves the theorem.

6. Robustness of model

We consider the case when the uptake functions f_i of system (4) are, in some sense, *unknown*. Usually, the formulation of uptake functions is based on experimental evidence with measurement error (see e.g., [15]). Thus, we are not able to obtain an analytic form of the functions, but only some qualitative properties and quantitative bounds. Our goal is to obtain sufficient conditions for the uniform persistence in such cases.

We will suppose that the following properties are satisfied:

(R1). f_1 and f_2 are functionally bounded, i.e., there exist a couple of well-known maps l_i and u_i (see Fig. 5), such that they satisfy assumptions (F1)–(F4) (with maximums noted by s_{i-}^* and s_{i+}^*, respectively) and verify

$$l_i(s) \leqslant f_i(s) \leqslant u_i(s), \quad s \geqslant 0, \quad i = 1, 2. \tag{21}$$

Let us denote by s^- and s^+ (see Fig. 6) the points in $(0, s_{\text{in}})$ such that $s^- < s^+$ and

$$l_1(s^-) = u_2(s^-) = D^- > 0,$$

$$u_1(s^+) = l_2(s^+) = D^+ > 0.$$

(R2). $u_1(s) < l_2(s)$ for all $s \in (s^+, s_{\text{in}})$.

(R3). We have that $D^+ > D^-$ or $y_{\min} > \frac{g^{-1}(D^-) - g^{-1}(D^+)}{s^+ - s^-}$ if $D^- > D^+$.

Let us build system $(4)^-$ substituting f_1, f_2 by l_1, u_2 in system (4). Analogously, we build system $(4)^+$ substituting f_1, f_2 by u_1, l_2 in system (4).

Let us denote by (5^-) and (5^+) Eq. (5) with f_1 replaced by l_1 and u_1, respectively. Analogously we denote by (6^-) and (6^+) Eq. (6) with f_2 replaced by l_2 and u_2, respectively.

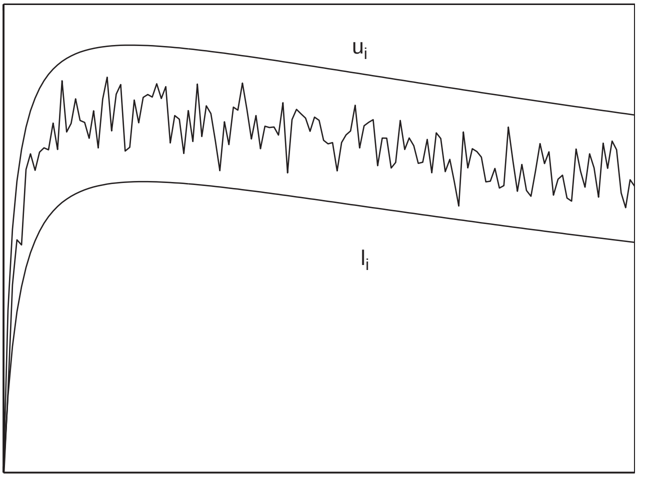

Fig. 5. Geometrical interpretation of (R1): Graphs of upper envelope u_i and lower envelope l_i for f_i.

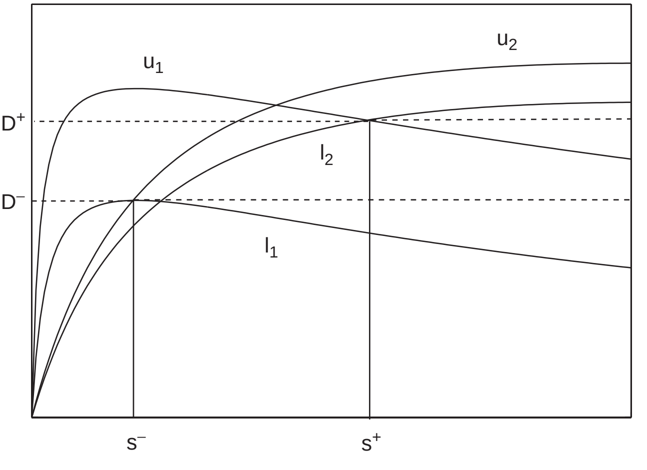

Fig. 6. Location of points D^-, D^+, s^- and s^+.

We will make the assumptions for systems (4^-) and (4^+):

(H1*). The following inequalities hold:

$$g(y_1[s_{\text{in}} - s^-]) > D^- > g(y_2[s_{\text{in}} - s^-]),$$

$$g(y_1[s_{\text{in}} - s^+]) > D^+ > g(y_2[s_{\text{in}} - s^+]).$$

(H2*). Eqs. (5^-) and (6^+) have one positive solution λ_1^- and λ_2^+, respectively. Eqs. (5^+) and (6^-) have one positive solution λ_1^+ and λ_2^-, respectively. Moreover, if $y_1 > y_2$, then λ_1^-,λ_1^+ are in (s^*, s_{in}) and λ_2^-,λ_2^+ are in $(0, s^*)$.

(H3*). $$\begin{cases} y_{\min} g'(x_1+x_2) > -\,l_1'\left(s_{\rm in} - \dfrac{x_1}{y_1} - \dfrac{x_2}{y_2}\right) & \text{for all } (x_1,x_2)\in\mathcal{O}, \\ y_{\min} g'(x_1+x_2) > -\,u_1'\left(s_{\rm in} - \dfrac{x_1}{y_1} - \dfrac{x_2}{y_2}\right) & \text{for all } (x_1,x_2)\in\mathcal{O}. \end{cases}$$

(H4*). $$\begin{cases} y_{\min} g'(x_1+x_2) > -\,u_2'\left(s_{\rm in} - \dfrac{x_1}{y_1} - \dfrac{x_2}{y_2}\right) & \text{for all } (x_1,x_2)\in\mathcal{O}, \\ y_{\min} g'(x_1+x_2) > -\,l_2'\left(s_{\rm in} - \dfrac{x_1}{y_1} - \dfrac{x_2}{y_2}\right) & \text{for all } (x_1,x_2)\in\mathcal{O}. \end{cases}$$

Theorem 1 implies that (s^-, x_1^-, x_2^-) and (s^+, x_1^+, x_2^+) are solutions globally asymptotically stable of $(4)^-$ and $(4)^+$, respectively. Moreover, x_i^- and x_i^+ are defined by:

$$x_1^- = \frac{y_1[y_2(s_{\rm in}-s^-) - g^{-1}(D^-)]}{y_2-y_1}, \quad x_2^- = \frac{y_2[g^{-1}(D^-) - y_1(s_{\rm in}-s^-)]}{y_2-y_1},$$
$$x_1^+ = \frac{y_1[y_2(s_{\rm in}-s^+) - g^{-1}(D^+)]}{y_2-y_1}, \quad x_2^+ = \frac{y_2[g^{-1}(D^+) - y_1(s_{\rm in}-s^+)]}{y_2-y_1}.$$

By assumption (R2) we have that $x_1^- < x_1^+$ and $x_2^+ < x_2^-$.

Theorem 2. *Let* $y_{\max} = y_1$, *if the functions* f_1 *and* f_2 *are unknown but verify assumptions* (R1)–(R3) *and the functions* g, u_i, l_i $(i=1,2)$ *satisfy assumptions* (H1*)–(H4*), *then the solutions of system* (4) *verify*:

$$x_1^- \leqslant \liminf_{t\to+\infty} x_1(t) \leqslant \limsup_{t\to+\infty} x_1(t) \leqslant x_1^+,$$
$$x_2^+ \leqslant \liminf_{t\to+\infty} x_2(t) \leqslant \limsup_{t\to+\infty} x_2(t) \leqslant x_2^-,$$
$$s^- \leqslant \liminf_{t\to+\infty} s(t) \leqslant \limsup_{t\to+\infty} s(t) \leqslant s^+. \tag{22}$$

In particular, *system* (4) *is uniformly persistent*.

Proof. Note that, even if f_1 and f_2 are unknown, the asymptotic behavior stated by Lemma 1 is still valid. Then we can proceed as in the proof of Theorem 1 and we need study only the ω-limit set of the planar system (13). Moreover, we consider the restricted competitive systems associated to $(4)^-$ and $(4)^+$, respectively:

$$\begin{cases} \dot v_1 = v_1\left(l_1\left(s_{\rm in} - \dfrac{v_1}{y_1} - \dfrac{v_2}{y_2}\right) - g(v_1+v_2)\right), \\ \dot v_2 = v_2\left(u_2\left(s_{\rm in} - \dfrac{v_1}{y_1} - \dfrac{v_2}{y_2}\right) - g(v_1+v_2)\right). \end{cases} \tag{23}$$

$$\begin{cases} \dot w_1 = w_1\left(u_1\left(s_{\rm in} - \dfrac{w_1}{y_1} - \dfrac{w_2}{y_2}\right) - g(w_1+w_2)\right), \\ \dot w_2 = w_2\left(l_2\left(s_{\rm in} - \dfrac{w_1}{y_1} - \dfrac{w_2}{y_2}\right) - g(w_1+w_2)\right). \end{cases} \tag{24}$$

Replacing (4) by $(4)^-$ and $(4)^+$ in Theorem 1 we obtain that

$$\lim_{t\to+\infty}(v_1(t), v_2(t)) = (x_1^-, x_2^-) \quad \text{and} \quad \lim_{t\to+\infty}(w_1(t), w_2(t)) = (x_1^+, x_2^+).$$

Let (z_1, z_2) be a solution of system (13) such that $z_i(0) = v_i(0) = w_i(0)$, Proposition 3 (see Appendix) implies that

$$v_1(t) \leqslant z_1(t) \leqslant w_1(t) \quad \text{and} \quad w_2(t) \leqslant z_2(t) \leqslant v_2(t) \quad \text{for all} \quad t \geqslant 0.$$

Letting $t \to +\infty$, Proposition 2 implies (22) and the proof is complete. □

Remark 4. Let s_{1l}^* and s_{1u}^* (s_{2l}^* and s_{2u}^*) be the maximum of l_1 and u_1 (l_2 and u_2), respectively. In some cases, the relative order of these points allows us to drop some statements of assumptions (H3*)–(H4*):

If $s^+ < \min\{s_{2l}^*, s_{2u}^*\}$, we can replace the function u_2 by an envelope m_2 as in the proof of case (ii) of Theorem 1, hence the first inequality in (H4*) is unnecessary and the proof of Theorem 2 runs as before.

If $s^+ < \min\{s_{1l}^*, s_{1u}^*, s_{2l}^*, s_{2u}^*\}$ we can replace the functions u_i by envelopes m_i as in the proof of case (iii) of Theorem 1. Moreover, if we can build an envelope m_1 that does not intersects l_2 before s_{in}, hence the second inequality in (H3*) and first inequality in (H4*) are unnecessary and the proof of Theorem 2 runs as before.

7. Discussion

We have analyzed a model of the chemostat with competition such that the only output available is the total biomass. The main result is that, considering the dilution rate D as a feedback control, one has—under some hypotheses—the uniform persistence of competing species in contrast to competitive exclusion in the classical chemostat. The novelty of this work is to consider nonmonotone uptake functions, generalizing in some way the result presented in [7].

The model takes the form of a system of differential equations such that its asymptotic behavior is equivalent to a competitive planar differential system. The theory of asymptotically autonomous dynamical systems and the theory of competitive dynamical systems played a prominent role.

If we consider ε_i to be the specific death rate of species x_i and we substitute D by $D_i = D + \varepsilon_i$ in Eq. (1), the tools mentioned above cannot be used because we cannot eliminate one variable (the substrate) to study the asymptotic behavior of the model. Handling different death rates remains an open question, worth further study.

Moreover, from an experimental point of view, it would be very interesting to study the same problem considering s_{in} as the feedback control variable and the substrate s as the output available.

One of the strongest assumptions in our model is $y_{\max} = y_1$. It is clear that we must consider other feedback control laws for the cases $y_{\max} = y_2$ and $y_1 = y_2$.

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Appendix A.

In this section we state a result of comparison for competitive dynamical systems that is essential in the proof of Theorems 1 and 2 (see [12,13] for more details).

Let the convex cone $K_{(0,1)}$ be defined as

$$K_{(0,1)} = \{(u_1, u_2) \in \mathbb{R}^2 : u_1 \geqslant 0 \quad \text{and} \quad u_2 \leqslant 0\}$$

and define an order in $\mathbb{R}^2$ by $\vec{y} \leqslant_{K_{(0,1)}} \vec{x}$ if $\vec{x} - \vec{y} \in K_{(0,1)}$, that means $y_1 \leqslant x_1$ and $y_2 \geqslant x_2$.

Let a continuous function $F : \Omega \mapsto \mathbb{R}^2$ where Ω is an open set in $\mathbb{R}^2$. $F = (F_1, F_2)$ is said to be of type $K_{(0,1)}$ if for each i, $(-1)^{m_i} F_i(\vec{a}) < (-1)^{m_i} F_i(\vec{b})$ for any two points $\vec{a}$ and $\vec{b}$ in Ω satisfying $\vec{a} \leqslant_{K_{(0,1)}} \vec{b}$, $(m_1, m_2) = (0, 1)$ and $a_i = b_i$.

The object is to compare solutions of the system of differential equations

$$x' = F(x), \tag{A1}$$

with solutions of the systems of differential equations

$$z' = G(z), \tag{A2}$$

$$y' = H(y), \tag{A3}$$

such that the continuous functions $G, H\colon \Omega \mapsto \mathbb{R}^2$ verify $H \leqslant_{K_{(0,1)}} F \leqslant_{K_{(0,1)}} G$.

Proposition 3 (*Comparison Theorem*). *Let F be continuous on Ω and of type $K_{(0,1)}$. Let $x(t)$ be a solution of* (A1) *defined on $[a, b]$. If $z(t)$ is a continuous function on $[a, b]$ satisfying* (A2) *on (a, b) with $z(a) \leqslant_{K_{(0,1)}} x(a)$, then $z(t) \leqslant_{K_{(0,1)}} x(t)$ for all t in $[a, b]$. If $y(t)$ is a continuous function on $[a, b]$ satisfying* (A3) *on (a, b) with $y(a) \geqslant_{K_{(0,1)}} x(a)$, then $y(t) \geqslant_{K_{(0,1)}} x(t)$ for all t in $[a, b]$.*

Proof. See Lemma 2 from [13].

Note that, if system (A1) is competitive and Ω is convex, then F is of type $K_{(0,1)}$.

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