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Competition model of n species for a single resource and coexistence in the chemostat

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Abstract

We study a model of the chemostat with several species in competition on a single resource. We take into account the intra-specific interactions between individuals of the same population of micro-organisms and we assume that the growth rates are increasing and the dilution rates are distinct. Using the concept of steady-state characteristic, we present a geometric characterization of the existence and stability of all equilibria. Moreover, we give the necessary and sufficient condition on the parameters such that the system has a positive equilibrium. Using a Lyapunov function, we give a global asymptotic stability result for the competition model of several species. The operating diagram describes the asymptotic behavior of this model with respect to control parameters and illustrates the effect of the intra-specific competition on the region of coexistence of several species.

Keywords: Chemostat, Coexistence, Competition, Intra-specific, Operating diagram

1. Introduction

The competitive exclusion principle (CEP) states that, in a chemostat and under specific assumptions, when microbial species compete for the same limiting nutrient in continuous culture, at most one species survives and all others perish, [18]. The surviving species is the one with the smallest subsistence or "break-even" concentration of the limiting resource. The chemostat model describing this interaction between the microbial species has been used for different systems specially for wastewater treatment processes and biological reactors... Nevertheless, for most of these systems, it is observed that many species can coexist together and the prediction given by the CEP is not in accordance with the reality. This has motivated a lot of recent research and a theory of microbial competition is now under development. The aim of these studies is to construct mathematical models in agreement with the observations and to predict the qualitative behavior of competition systems. By modifying the assumed operating conditions, many extensions of the classical chemostat model have been performed. Coexistence of several species has been proved when considering models with time-varying dilution rates, see [19], with time-varying input nutrient concentration, see [6, 8, 19] or with variable yields,

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[15, 17], see also [4, 5, 9–12, 14, 16, 20, 21] for other extensions. In particular, De Leenheer et al [9] have proposed a chemostat model where crowding effects are taken into consideration. In this model, n species compete for a single nutrient. The authors use the theory of monotone dynamical systems for an interconnection of two input/output systems to prove an almost-global stability result of the positive equilibrium, see Section 2 for the details.

Recently, Lobry and al. proposed in [13], to replace the classical functional responses that are only resource dependent, by growth functions that depend on both the resource and the consumers. In this model, they introduce the concept of steady-state characteristic for each species. For several species in competition on a resource, they show that the knowledge of the characteristics enables to give sufficient conditions for coexistence and to determine the asymptotic behavior of the system. They prove, for the proposed model, the existence of a locally exponentially stable equilibrium of coexistence, see [10, 12]. The consideration of density-dependent growth functions in the chemostat model, has been also introduced in the literature in the field of mathematical ecology [1] or waste-water process engineering [7]. It has been shown that flocculation systems, for example, can reduce, under certain assumptions, to systems with a single biomass compartment for each strain and a density-dependent growth rate, see [5], and that coexistence may arise through this mechanism, [2].

Other approaches, to explain coexistence, rely on taking into account, in the chemostat model, inter-specific interactions between populations of micro-organisms or intra-specific interactions between individuals themselves. In [21], two models, corresponding respectively to the case where only intra-specific interference is permitted and to the case of only inter-specific interactions, are considered. In the case of intra-specific interactions in the dynamics of two species, there exists a positive equilibrium of coexistence which is locally asymptotically stable. In the case of inter-specific interactions in the dynamics of two species, there exists a positive equilibrium of coexistence but which is unstable [21]. The case of both inter-specific interactions between two populations of micro-organisms and intra-specific interactions between individuals themselves has been considered in [3]. It has been shown the existence of one or many positive locally exponentially stable equilibria, according to the initial condition. The coexistence of both species occurs and for certain values of the operating parameters, bistability is proven.

This paper is organized as follows: in Section 2 we present an intra-specific competition model of n species and give some preliminary results. Section 3 is devoted to analyze this model in the case of two species. Using the concept of steady-state characteristic defined by Lobry et al. [12, 13], we give a geometric characterization of the existence and stability of all equilibria. We prove that only one equilibrium is stable. A global asymptotic stability result is given. At the end of the section, we present the operating diagrams which depict the existence and the stability of each equilibrium according to control parameters. In Section 4, this approach is extended to the study of the multi-species model. We generalize the Lyapunov function used in [21] in the case of two species, to prove the global stability of the equilibrium, corresponding to the extinction of all species except the one who has the lowest break-even. Numerical simulations with realistic growth functions (of Monod type) illustrate either the coexistence or the competitive exclusion in different cases. Finally, some conclusions are drawn in Section 5.

For convenience, we use the abbreviations LES for Locally Exponentially Stable equilibria and GAS for Globally Asymptotically Stable equilibria, in all what follows.

2. Mathematical model

In this paper, we consider a chemostat model of n species competing for a single nutrient with intra-specific linear interactions between species themselves. This model can be written as follows:

$$\begin{cases} \dot{S} &= D(S_{in} - S) - \sum_{i=1}^n f_i(S)x_i \\ \dot{x}_i &= [f_i(S) - a_i x_i - D_i]x_i, \quad i = 1, \dots, n \end{cases} \quad (1)$$

where S denotes the concentration of the substrate; x_i denotes the concentration of the i th population of microorganisms; S_{in} and D denote, respectively, the concentration of substrate in the feed bottle and the dilution rate of the chemostat; D_i denotes the removal rate of the species i which is the sum of the death rates of species i and the dilution rate D , (D_i are not necessarily equal); a_i is a positive parameter giving rise to death rate $a_i x_i$ which is due to intra-specific interactions and $f_i(\cdot)$ denotes the per-capita growth rate of the i th population.

Model (1) generalizes model (1.2) of [21] to multi-species populations, in the case of linear intra-specific interactions. De Leenheer et al., [9], have analyzed the model (1), considering that mortality rates are due to the crowding effects. The key idea of their analysis is the observation that system (1) can be interpreted as a negative feedback interconnection of monotone subsystems, see [9] and the references therein. They were interested only by positive equilibria and they proved, by applying a small-gain theorem developed for monotone systems and under certain conditions on the parameters a_i and on the functions f_i , $i = 1, \dots, n$, that system (1) possesses a positive equilibrium which is, with respect to positive initial conditions, *almost* GAS, (this means that the positive equilibrium point attracts all solutions that are not starting in a set of Lebesgue measure zero).

In this paper, we give a complete analysis of model (1). We describe all its equilibria and their stability, without assumptions on the parameters a_i . We give the necessary and sufficient condition on the parameters such that the system has a positive equilibrium. We first do the following assumption on the growth function:

H1: For $i = 1, \dots, n$, $f_i(0) = 0$ and for all $S > 0$, $f'_i(S) > 0$.

Hypothesis **H1** means that the growth can take place if and only if the substrate is present. Moreover, the growth rate of each species increases with the concentration of substrate. In the following, we prove that system (1) is behaving as well as one would expect from any reasonable model of the chemostat.

Proposition 2.1. *For any non-negative initial condition, the solution of (1) stay non-negative and is positively bounded.*

The set

$$\Omega = \left\{ (S, x_1, \dots, x_n) \in \mathbb{R}_+^{n+1} : Z = S + \sum_{i=1}^n x_i \leq \max\left(Z(0), \frac{D}{D^*} S_{in}\right) \right\}$$

is positively invariant and global attractor for (1), where $D^* = \min(D, D_1, \dots, D_n)$.

Proof. From (1), we have

$$\dot{Z} = DS_{in} - DS - \sum_{i=1}^n (D_i x_i + a_i x_i^2).$$

Hence,

$$\dot{Z} \leq D(S_{in} - \frac{D^*}{D}Z).$$

From Gronwall Lemma, we obtain

$$Z(t) \leq \frac{D}{D^*}S_{in} + \left(Z(0) - \frac{D}{D^*}S_{in}\right)e^{-D^*t}, \quad \text{for all } t \geq 0. \quad (2)$$

It is easy to see from (1) that the non-negative cone (S, x_1, \dots, x_n) is positively invariant. Thus solutions are non-negative for all $t \geq 0$ and from (2) we deduce that the solutions are bounded and the set Ω is invariant and attractor. ■

3. Analysis of the competition model with two species

For a better understanding of the qualitative behavior of solutions of model (1), we start by the case $n = 2$. In this particular case, we can describe precisely the solutions and provide operating diagrams illustrating the regions of equilibria stability according to the operating parameters S_{in} and D . System (1), in the case of two species competing for a single nutrient, reads

$$\begin{cases} \dot{S} &= D(S_{in} - S) - f_1(S)x_1 - f_2(S)x_2 \\ \dot{x}_1 &= [f_1(S) - a_1x_1 - D_1]x_1 \\ \dot{x}_2 &= [f_2(S) - a_2x_2 - D_2]x_2. \end{cases} \quad (3)$$

We assume that **H1** is verified for $n = 2$ and that the parameters a_1 and a_2 are positive. Now, we shall discuss the existence of the equilibria of system (3) and then their asymptotic stability.

3.1. Existence of equilibria

We first denote $\lambda_i = f_i^{-1}(D_i)$, for $i = 1, 2$, if equation $f_i(S) = D_i$ has a solution. Otherwise, $\lambda_i = +\infty$. We assume that the populations x_i are labeled such that $\lambda_1 < \lambda_2$. The equilibria are solution of system (4):

$$\begin{cases} 0 &= D(S_{in} - S) - f_1(S)x_1 - f_2(S)x_2 \\ 0 &= [f_1(S) - a_1x_1 - D_1]x_1 \\ 0 &= [f_2(S) - a_2x_2 - D_2]x_2. \end{cases} \quad (4)$$

By solving system (4), we will prove the existence of four equilibria, according to the concentration S_{in} : a washout equilibrium, two equilibria corresponding to the extinction of respectively the first and the second species and a positive equilibrium corresponding to the coexistence of both species. Indeed, we first note that if $x_1 = x_2 = 0$, we obtain the washout equilibrium $E_0 = (S_{in}, 0, 0)$ which always exists. For the other equilibria, we have to define the functions

$$h_i(S) = \frac{f_i(S) - D_i}{a_i}f_i(S), \quad H_i(S) = D(S_{in} - S) - h_i(S), \quad i = 1, 2. \quad (5)$$

Let S_i be the solution of equation $H_i(S) = 0$ and let

$$\bar{x}_i = \frac{f_i(S_i) - D_i}{a_i}, \quad i = 1, 2. \quad (6)$$

Then, we can state:

Proposition 3.1.

1. The equilibrium $E_1 = (S_1, \bar{x}_1, 0)$, corresponding to the extinction of species x_2 , exists if and only if $S_{in} > \lambda_1$.
2. The equilibrium $E_2 = (S_2, 0, \bar{x}_2)$, corresponding to the extinction of species x_1 , exists if and only if $S_{in} > \lambda_2$.

Proof.

1. If $x_2 = 0$ and $x_1 \neq 0$, then from the second equation of (4), we deduce that

$$x_1 = \frac{f_1(S) - D_1}{a_1},$$

which is positive if and only if $S > \lambda_1$. From the first equation, we deduce that $H_1(S) = 0$. Since H_1 is decreasing on $[\lambda_1, +\infty[$,

$$H_1(\lambda_1) = D(S_{in} - \lambda_1) \quad \text{and} \quad H_1(S_{in}) = -h_1(S_{in}),$$

there exists a unique solution $S_1 > \lambda_1$ of equation $H_1(S) = 0$ if and only if $S_{in} > \lambda_1$.

2. If $x_1 = 0$ and $x_2 \neq 0$, in the same way, we prove that there exists a unique solution $S_2 > \lambda_2$ of equation $H_2(S) = 0$ if and only if $S_{in} > \lambda_2$. ■

We define, now, the function $H(\cdot)$ and the parameter $\bar{\lambda}_2$ by, respectively,

$$H(S) = D(S_{in} - S) - \sum_{i=1}^2 h_i(S) \quad \text{and} \quad \bar{\lambda}_2 = \lambda_2 + \frac{h_1(\lambda_2)}{D}.$$

Proposition 3.2. The positive equilibrium $E^* = (S^*, x_1^*, x_2^*)$ exists if and only if $S_{in} > \bar{\lambda}_2$ with S^* is solution of equation $H(S) = 0$ and

$$x_i^* = \frac{f_i(S^*) - D_i}{a_i}, \quad i = 1, 2.$$

Proof. If $x_1 \neq 0$ and $x_2 \neq 0$, then from the second and the third equation of (4), we obtain

$$x_i = \frac{f_i(S) - D_i}{a_i}, \quad i = 1, 2,$$

which is positive if and only if $S > \lambda_i$. From the first equation, we deduce that $H(S) = 0$. Since H is decreasing on $[\lambda_2, +\infty[$,

$$H(\lambda_2) = D(S_{in} - \lambda_2) - h_1(\lambda_2) \quad \text{and} \quad H(S_{in}) = - \sum_{i=1}^2 h_i(S_{in}),$$

there exists a unique solution $S^* > \lambda_2$ of equation $H(S) = 0$ if and only if $H(\lambda_2) > 0$, that is, $S_{in} > \bar{\lambda}_2$. ■

3.2. Stability of equilibria

To study the local asymptotic stability of equilibrium points of (3), we calculate the Jacobian matrix in (S, x_1, x_2) :

$$J = \begin{bmatrix} -D - f'_1(S)x_1 - f'_2(S)x_2 & -f_1(S) & -f_2(S) \\ f'_1(S)x_1 & f_1(S) - 2a_1x_1 - D_1 & 0 \\ f'_2(S)x_2 & 0 & f_2(S) - 2a_2x_2 - D_2 \end{bmatrix}.$$

In $E_0 = (S_{in}, 0, 0)$, we obtain the matrix

$$J_{E_0} = \begin{bmatrix} -D & -f_1(S_{in}) & -f_2(S_{in}) \\ 0 & f_1(S_{in}) - D_1 & 0 \\ 0 & 0 & f_2(S_{in}) - D_2 \end{bmatrix}.$$

The eigenvalues are on the diagonal. They are negative, that is, E_0 is a stable node if and only if $S_{in} < \lambda_i$, $i = 1, 2$. So, we can state

Proposition 3.3. E_0 is a stable node if and only if $S_{in} < \lambda_i$, for $i = 1, 2$.

Now, $E_1 = (S_1, \bar{x}_1, 0)$ exists if and only if $\lambda_1 < S_{in}$. The Jacobian matrix at E_1 is

$$J_{E_1} = \begin{bmatrix} -D - f'_1(S_1)\bar{x}_1 & -f_1(S_1) & -f_2(S_1) \\ f'_1(S_1)\bar{x}_1 & -a_1\bar{x}_1 & 0 \\ 0 & 0 & f_2(S_1) - D_2 \end{bmatrix}.$$

Thus, $f_2(S_1) - D_2$ is an eigenvalue of J_{E_1} . The other eigenvalues of J_{E_1} are the eigenvalues of the matrix

$$A_1 = \begin{bmatrix} -D - f'_1(S_1)\bar{x}_1 & -f_1(S_1) \\ f'_1(S_1)\bar{x}_1 & -a_1\bar{x}_1 \end{bmatrix}.$$

We can see that $\det(A_1) > 0$ and $\text{tr}(A_1) < 0$, then the two eigenvalues of A_1 have negative real part. The equilibrium E_1 is then LES if and only if $S_1 < \lambda_2$ or equivalently if $S_{in} < \bar{\lambda}_2$.

We use similar arguments to check the stability of $E_2 = (S_2, 0, \bar{x}_2)$, which exists if and only if $\lambda_2 < S_{in}$. Since the Jacobian matrix at E_2 is

$$J_{E_2} = \begin{bmatrix} -D - f'_2(S_2)\bar{x}_2 & -f_1(S_2) & -f_2(S_2) \\ 0 & f_1(S_2) - D_1 & 0 \\ f'_2(S_2)\bar{x}_2 & 0 & -a_2\bar{x}_2 \end{bmatrix}.$$

Then, $f_1(S_2) - D_1$ is an eigenvalue of J_{E_2} . The two other eigenvalues of J_{E_2} are the eigenvalues of the matrix

$$A_2 = \begin{bmatrix} -D - f'_2(S_2)\bar{x}_2 & -f_2(S_2) \\ f'_2(S_2)\bar{x}_2 & -a_2\bar{x}_2 \end{bmatrix}.$$

Since $\det(A_2) > 0$ and $\text{tr}(A_2) < 0$, the two eigenvalues of A_2 have negative real part. Consequently, E_2 is LES if and only if $S_2 < \lambda_1$. Since we have $S_2 > \lambda_2 > \lambda_1$, E_2 is a saddle point when it exists. Then,

Proposition 3.4.

1. E_1 is LES if and only if $\lambda_1 < S_{in} < \bar{\lambda}_2$.
2. When it exists, E_2 is a saddle point.

Now, by using a Routh-Hurwitz criterion, we can prove the local stability of the positive equilibrium E^* when it exists, that is, $S_{in} > \bar{\lambda}_2$.

Proposition 3.5. E^* is LES if and only if $S_{in} > \bar{\lambda}_2$.

Proof. We can write the Jacobian matrix at $E^* = (S^*, x_1^*, x_2^*)$ in the form:

$$J_{E^*} = \begin{bmatrix} -m_{11} & -m_{12} & -m_{13} \\ m_{21} & -m_{22} & 0 \\ m_{31} & 0 & -m_{33} \end{bmatrix}$$

where

$$\begin{aligned} m_{11} &= D + f'_1(S^*)x_1^* + f'_2(S^*)x_2^*, & m_{12} &= f_1(S^*), & m_{13} &= f_2(S^*), \\ m_{21} &= f'_1(S^*)x_1^*, & m_{22} &= a_1x_1^*, & m_{31} &= f'_2(S^*)x_2^*, & m_{33} &= a_2x_2^*, \end{aligned}$$

which are positive. The characteristic polynomial is given by

$$P(\lambda) = c_0\lambda^3 + c_1\lambda^2 + c_2\lambda + c_3,$$

where

$$c_0 = -1, \quad c_1 = -(m_{11} + m_{22} + m_{33}), \quad c_2 = -(m_{12}m_{21} + m_{13}m_{31} + m_{11}m_{22} + m_{11}m_{33} + m_{22}m_{33})$$

and

$$c_3 = -m_{22}m_{13}m_{31} - m_{11}m_{22}m_{33} - m_{12}m_{21}m_{33}.$$

According to Routh-Hurwitz criterion, E^* is LES if and only if

$$\begin{cases} c_i < 0, & i = 0, \dots, 3 \\ c_1c_2 - c_0c_3 > 0. \end{cases}$$

Since $m_{ij} \geq 0$, for all $i, j = 1, \dots, 3$, it follows that $c_i < 0$. Then, a straightforward calculation gives

$$c_1 c_2 - c_0 c_3 = -m_{11} c_2 + m_{22}(m_{12} m_{21} + m_{11} m_{22} + m_{22} m_{33}) + m_{33}(m_{13} m_{31} + m_{11} m_{22} + m_{11} m_{33} + m_{22} m_{33})$$

which is positive. Thus all the conditions of the Routh-Hurwitz criterion are satisfied and so E^* is LES when it exists. ■

Table 1 summarizes the previous results.

Equilibria	Existence condition	Stability condition
E_0	Always exists	$S_{in} < \lambda_i, i = 1, 2$
E_1	$S_{in} > \lambda_1$	$S_{in} < \bar{\lambda}_2$
E_2	$S_{in} > \lambda_2$	Unstable whenever it exists
E^*	$S_{in} > \bar{\lambda}_2$	Whenever it exists

Table 1: Existence and local stability of equilibria in system (3).

Fig. 1(a) shows the number of equilibria according to the concentration of substrate in the feed bottle S_{in} . The equilibria are given by the intersection between the line Δ of equation $y = D(S_{in} - S)$ and either the curve of the function $h_{12}(\cdot) = h_1(\cdot) + h_2(\cdot)$ defined for $S > \lambda_2$, or the curve of the function $h_i(\cdot)$ defined respectively for $S > \lambda_i, i = 1, 2$, or the line of equation $y = 0$ which represents the washout equilibrium E_0 .

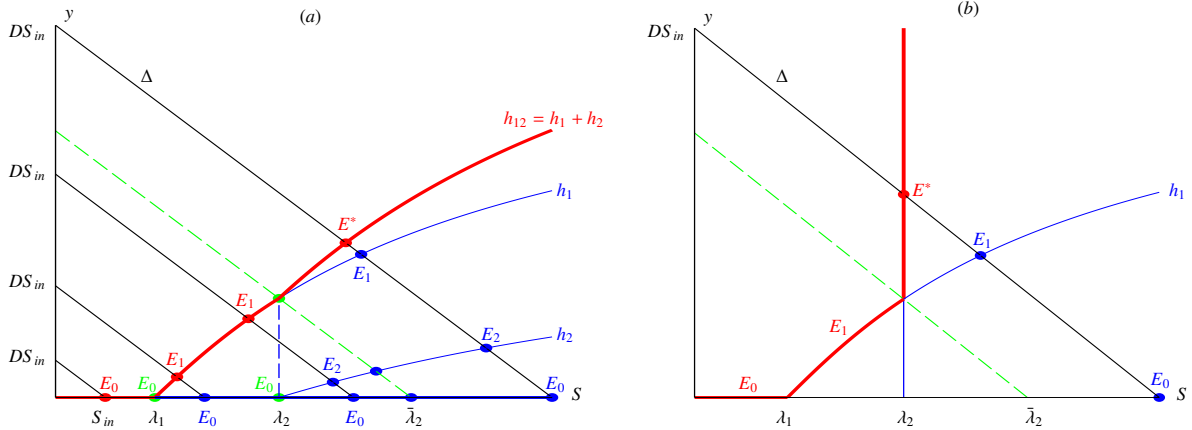


Figure 1: Steady-state characteristic: (a) equilibria of (3) according to S_{in} for $a_2 > 0$ and (b) existence of the positive equilibrium E^* for $a_2 = 0$.

If $S_{in} > \bar{\lambda}_2$, the intersection between the line Δ and the curve of the function $h_{12}(\cdot)$ represents the solution S^* of the equation $H(S) = 0$ satisfying $S^* > \lambda_2$. Therefore, the condition $x_i^* > 0, i = 1, 2$, is satisfied, and there exists a unique positive equilibrium E^* . We choose the red color for GAS equilibrium, the green color for saddle-node equilibrium and blue color for unstable equilibrium. Notice that when $S_{in} = \lambda_1$, E_0 coalesces with E_1 , when $S_{in} = \lambda_2$, E_0 coalesces with E_2 and when $S_{in} = \bar{\lambda}_2$, E_1 coalesces with E^* .

From previous results, Lemma 1.1 and Theorem 2.2 of [21], we can derive the global asymptotic behavior of (3) according to S_{in} . More specifically, we have the following result:

Proposition 3.6. *Under assumption H1 in the case $n = 2$ and for $a_i > 0$, $i = 1, 2$, the following cases occur:*

1. *If $S_{in} < \lambda_1$, there exists a unique equilibrium $E_0 = (S_{in}, 0, 0)$ which is GAS.*
2. *If $\lambda_1 < S_{in} < \lambda_2$, then there exists two equilibria: E_0 is unstable and $E_1 = (S_1, \bar{x}_1, 0)$ is GAS.*
3. *If $\lambda_2 < S_{in} < \bar{\lambda}_2$, then there exists three equilibria: E_0 and $E_2 = (S_2, 0, \bar{x}_2)$ are unstable while E_1 is LES. Moreover, if it exists a constant $\alpha > 0$ which satisfies:*

$$\max_{0 < S < S_1} g(S) \leq \alpha \leq \min_{\lambda_2 < S < S_{in}} g(S) \quad \text{where} \quad g(S) = \frac{f_2(S)}{f_1(S_1)} \frac{f_1(S) - f_1(S_1)}{f_2(S) - D_2} \frac{S_{in} - S_1}{S_{in} - S},$$

then E_1 is GAS with respect to all solutions with $x_1(0) > 0$, (see Fig. 4(a)).

4. *If $S_{in} > \bar{\lambda}_2$, then there exists four equilibria: E_0 , E_1 and E_2 are unstable while $E^* = (S^*, x_1^*, x_2^*)$ is LES (see Fig. 4(b)).*

In the following, we consider the case $a_2 = 0$ where the system might yet have a positive equilibrium and we show that the hypothesis $a_2 > 0$ is not necessary for coexistence. The model can be rewritten as

$$\begin{cases} \dot{S} &= D(S_{in} - S) - f_1(S)x_1 - f_2(S)x_2 \\ \dot{x}_1 &= [f_1(S) - a_1x_1 - D_1]x_1 \\ \dot{x}_2 &= [f_2(S) - D_2]x_2. \end{cases} \quad (7)$$

Using the same manner as the proof of Propositions 3.1 and 3.2, we have proved the following result:

Proposition 3.7. *The system (7) admits the following equilibria:*

1. *The washout equilibrium $E_0 = (S_{in}, 0, 0)$, that always exists.*
2. *The equilibrium $E_2 = (\lambda_2, 0, D(S_{in} - \lambda_2)/D_2)$ of extinction of species x_1 , that exists if and only if $S_{in} > \lambda_2$.*
3. *The equilibrium $E_1 = (S_1, \bar{x}_1, 0)$, of extinction of species x_2 , with S_1 is solution of $H_1(S) = 0$, that exists if and only if $S_{in} > \lambda_1$.*
4. *The positive equilibrium $E^* = (\lambda_2, x_1^*, x_2^*)$, with $x_1^* = (f_1(\lambda_2) - D_1)/a_1$, $x_2^* = H_1(\lambda_2)/D_2$, that exists if and only if $S_{in} > \bar{\lambda}_2$,*

where the function $H_1(\cdot)$ and \bar{x}_1 are defined in (5) and (6).

In the particular case $a_2 = 0$, the local and global stability of the equilibria can be determined as previously. Thus, we obtain the same result of existence and stability as in Table 1 and Prop. 3.6. Fig. 1(b) illustrates the steady-state characteristic and the same condition of existence of the positive equilibrium E^* in this case. This means that the intra-specific competition of the most competitive species inhibits its growth and allow then the coexistence even if the least competitive species has a zero inhibition term.

Thus, if $\lambda_1 < \lambda_2$ then the first species has a competitive advantage over the second species and so this second species need not to inhibit its growth in order to coexist with the other species. Hence, the coexistence is due to the fact that the most efficient species sees its growth inhibited by the intra-specific competition when the other species has no reason to be inhibited.

3.3. Operating diagram

The operating diagram describes the system behavior when the concentration of the substrate in the feed bottle S_{in} and the dilution rate D vary. In model (3), each parameter D_i , $i = 1, 2$, can be written as $D_i = D + A_i$, $A_i \geq 0$ where A_i can be interpreted as the specific natural death rate of species i .

We first denote $\bar{m}_i = \sup_{S \geq 0} f_i(S) - A_i$ and we assume that $\bar{m}_i > 0$. For the description of the steady-states and their stability, with respect to control parameters S_{in} and D , we define the inverse function F_i of the increasing functions f_i , $i = 1, 2$, so that:

$$S = F_i(D) \Leftrightarrow f_i(S) = D + A_i, \text{ for all } S \in [0, +\infty[\text{ and } D \in [0, \bar{m}_i[.$$

Note that the inverse functions F_1 and F_2 can be calculated explicitly in the case of the Monod growth functions considered in Section 3.4. Let Γ_1 be the curve of equation $S_{in} = F_1(D)$ and Γ_2 that of equation $S_{in} = F_2(D)$.

If the curves Γ_1 and Γ_2 do not intersect, we assume, without loss of generality, that for all $D \in]0, \bar{m}_2[$, $F_1(D) < F_2(D)$, (see Fig. 2(a)). To express the stability condition $S_{in} > \bar{\lambda}_2$, we define the function:

$$\begin{aligned} F_{12} :]0, \bar{m}_2[&\longrightarrow]0, +\infty[\\ D &\longrightarrow F_2(D) + \frac{h_1(F_2(D))}{D}. \end{aligned}$$

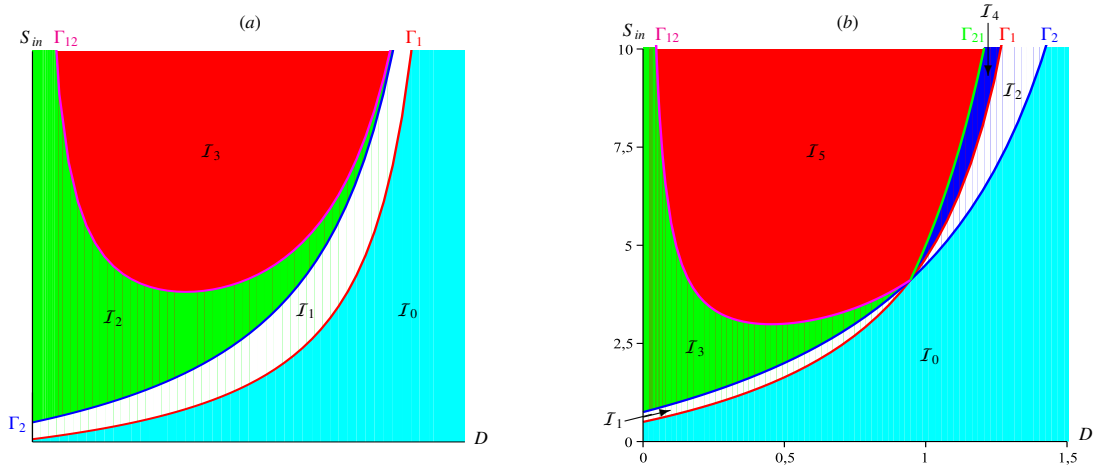


Figure 2: Operating diagram of (3) : (a) Curves Γ_i do not intersect. (b) Curves Γ_i intersect.

In Figure 2, the curve of equation $S_{in} = F_{12}(D)$ is labeled as Γ_{12} . Notice that if $A_i > 0$, then

$$\lim_{D \rightarrow 0^+} F_{12}(D) = +\infty,$$

and since $h_1(F_2(D)) > 0$, we have $F_2(D) < F_{12}(D)$ for all $D \in]0, \bar{m}_2[$.

The curves Γ_i , $i = 1, 2$ and Γ_{12} separate the operating plane (D, S_{in}) in four regions, as shown in Fig. 2(a), labeled as I_k , $k = 0, \dots, 3$. The transition from the region I_0 to the region I_1 by the curve Γ_1 (the red curve) corresponds to a saddle-node bifurcation making the equilibrium E_0 unstable (saddle point) with the appearance of a LES equilibrium

E_1 . The transition from the region \mathcal{I}_1 to the region \mathcal{I}_2 by the curve Γ_2 (the blue curve) corresponds to the appearance of a saddle point E_2 by a bifurcation with a saddle point E_0 . The transition from the region \mathcal{I}_2 to the region \mathcal{I}_3 by the curve Γ_{12} (the magenta curve) corresponds to a saddle-node bifurcation making the equilibrium E_1 unstable (saddle point) with the appearance of a LES equilibrium E^* .

Notice that the function $F_i(\cdot)$ is not defined if $\sup_{S \geq 0} f_i(S) \leq A_i$ and we let $F_i(0) = +\infty$. In this case, the regions \mathcal{I}_1 , \mathcal{I}_2 and \mathcal{I}_3 are empty. Table 2 summarizes the results of Prop. 3.6 and shows the existence and stability of equilibria E_0 , E_1 , E_2 and E^* in the regions \mathcal{I}_k , $k = 0, \dots, 3$, of the operating diagram, in the case where Γ_1 and Γ_2 do not intersect and $F_1(D) < F_2(D)$. The letter S (resp. U) means stable (resp. unstable). No letter means that the corresponding equilibrium does not exist.

Region	E_0	E_1	E_2	E^*
$(D, S_{in}) \in \mathcal{I}_0$	S			
$(D, S_{in}) \in \mathcal{I}_1$	U	S		
$(D, S_{in}) \in \mathcal{I}_2$	U	S	U	
$(D, S_{in}) \in \mathcal{I}_3$	U	U	U	S

Table 2: Existence and local stability of steady states according to (D, S_{in}) , in the case $\Gamma_1 \cap \Gamma_2 = \emptyset$.

Now, we assume that the curves Γ_1 and Γ_2 intersect in D^* . The cases $D < D^*$ and $D > D^*$ have to be distinguished. When $D < D^*$, we assume for example that $F_1(D) < F_2(D)$, for all $D \in]0, D^*[$ (see Fig. 2(b)). Hence,

$$F_2(D) < F_{12}(D) \quad \text{for all } D \in]0, D^*[$$

since $h_1(F_2(D)) > 0$. In this case, the result is similar to that when the curves Γ_1 and Γ_2 do not intersect.

When $D > D^*$, $F_2(D) < F_1(D)$ for all $D \in]D^*, \bar{m}_1[$. In this case, E^* is stable if $S_{in} > \bar{\lambda}_1 := \lambda_1 + h_2(\lambda_1)/D$. We then define the function:

$$F_{21} : [D^*, \bar{m}_1[\longrightarrow]F_1(D^*), +\infty[$$

$$D \longrightarrow F_1(D) + \frac{h_2(F_1(D))}{D}.$$

The curve of equation $S_{in} = F_{21}(D)$ is labeled as Γ_{21} . Since $h_2(F_1(D)) > 0$, it follows that

$$F_1(D) < F_{21}(D) \quad \text{for all } D \in]D^*, \bar{m}_1[.$$

For $D > D^*$, the curves Γ_2 , Γ_1 and $\Gamma_{21}(D)$ separate the operating plane (D, S_{in}) in four regions, as shown in Fig. 2(b), labeled \mathcal{I}_0 , \mathcal{I}_2 , \mathcal{I}_4 and \mathcal{I}_5 . The curve Γ_2 (the blue curve) is the border which makes E_0 a saddle point and at the same time E_2 exists and is a LES equilibrium. The curve Γ_1 (the red curve) is the border which makes E_1 exists but it is a saddle point. The curve Γ_{21} (the green curve) is the border which makes E_2 a saddle point and at the same time E^* exists and is a LES equilibrium.

Table 3 shows the existence and local stability of equilibria in the regions \mathcal{I}_k , $k = 0, \dots, 5$, of the operating diagram, when the curves Γ_1 and Γ_2 intersect.

Region	E_0	E_1	E_2	E^*
$(D, S_{in}) \in \mathcal{I}_0$	S			
$(D, S_{in}) \in \mathcal{I}_1$	U	S		
$(D, S_{in}) \in \mathcal{I}_2$	U		S	
$(D, S_{in}) \in \mathcal{I}_3$	U	S	U	
$(D, S_{in}) \in \mathcal{I}_4$	U	U	S	
$(D, S_{in}) \in \mathcal{I}_5$	U	U	U	S

Table 3: Existence and local stability of steady states according to (D, S_{in}) , in the case Γ_i intersect.

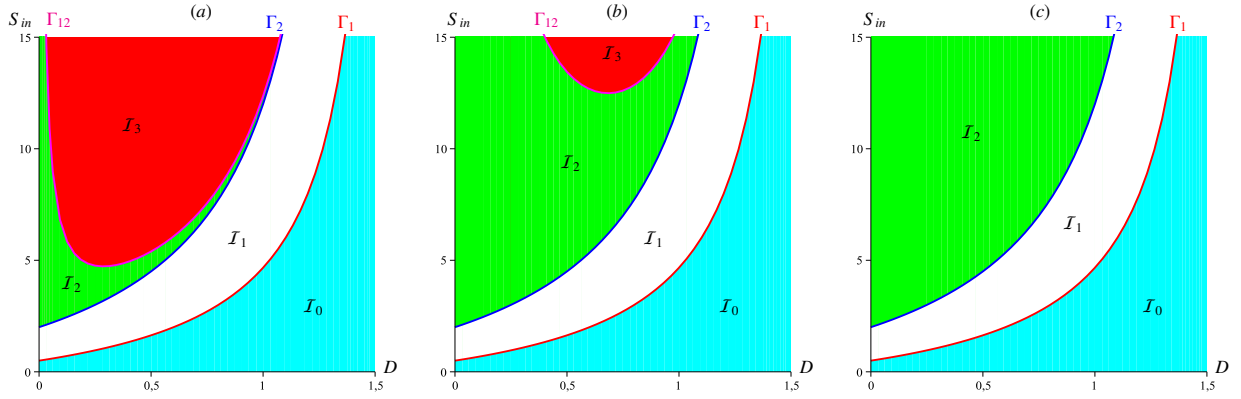


Figure 3: Reduction and disappearance of the region \mathcal{I}_3 of coexistence as a_1 decreases: (a) $a_1 = 1.5$, (b) $a_1 = 0.15$ and (c) $a_1 = 0.1$.

Remark 3.1. For small or large parameter values of D and S_{in} , we see that there is either the washout of two species or the exclusion of one species. In the case $F_1(D) < F_2(D)$ for all $D \in]0, \bar{m}_2[$, making the parameter a_2 varying, the regions of operating diagram are identical since the functions $F_i(\cdot)$, $i = 1, 2$, and $F_{12}(\cdot)$ are independent of a_2 . Hence, the intra-specific competition of the least competitive species has no effect on the region of coexistence.

In the other hand, decreasing a_1 reduces the region \mathcal{I}_3 of coexistence and increases the region \mathcal{I}_2 of competitive exclusion of the second species (see Fig. 3(a-b)). Then, the region \mathcal{I}_3 tends to disappear as a_1 tends to zero and we find the operating diagram of the classical chemostat model with $a_1 = 0$ (see Fig. 3(c)). Thus, the intra-specific competition of the most competitive species leads to changes in the size and presence of regions of coexistence.

3.4. Simulations

To illustrate our results, we consider model (3) when the functions $f_i(\cdot)$ are of Monod type, defined by:

$$f_i(S) = \frac{m_i S}{K_i + S}, \quad i = 1, 2,$$

where m_i is the maximum specific growth rate and K_i is the Michaelis-Menten (or half-saturation) constant. Straightforward calculation shows that the inverse functions F_i , $i = 1, 2$ are given by:

$$F_i(D) = \frac{K_i(D + A_i)}{m_i - D - A_i}$$

and

$$F_{ij}(D) = F_j(D) + \frac{1}{a_i D} \left[\frac{m_i F_j(D)}{K_i + F_j(D)} - D - A_i \right] \frac{m_i F_j(D)}{K_i + F_j(D)}, \quad i, j = 1, 2, \quad \text{with } i \neq j.$$

Note that if $A_i = 0$, $i = 1, 2$, then

$$\lim_{D \rightarrow 0} F_{ij}(D) = 0, \quad \text{for } i \neq j \quad \text{and } j = 1, 2.$$

For the numerical simulations, we use the values of the parameters given in Table 4: see Figs. 2(b) and 4.

Parameters	m_1	m_2	K_1	K_2	a_1	a_2	A_1	A_2
Values	2	2.5	2	3	0.2	0.1	0.4	0.5

Table 4: Parameter values for model (3) with a Monod growth function.

For Fig. 3, we considered successively the cases $a_1 = 1.5, 0.15$ and 0.1 , while $A_2 = 1$. The other parameters remain unchanged.

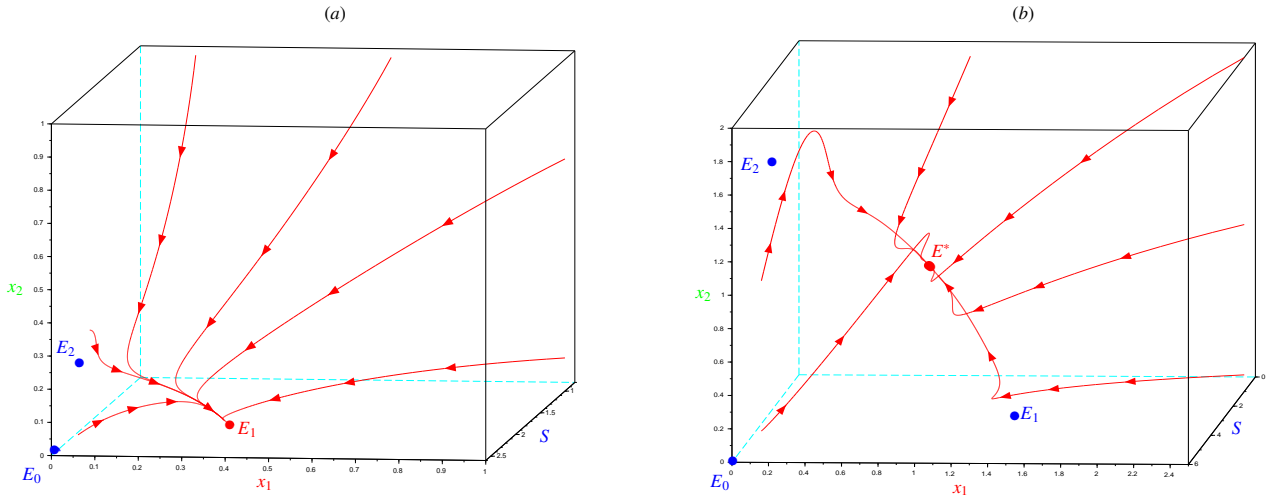


Figure 4: The case $D < D^*$: (a) Global convergence to the equilibrium E_1 for $(D, S_{in}) \in I_3$. (b) Global convergence to the coexistence equilibrium E^* for $(D, S_{in}) \in I_5$.

Fig. 2(b) illustrates the case where the curves $S_{in} = F_i(D)$ intersect once. For example, we choose the case $D = 0.5 < D^* \simeq 0.945$. For $(D, S_{in}) = (0.5, 2.5) \in I_3$, Fig. 4(a) shows the global convergence towards the competitive exclusion of the second species for any positive initial condition. In this case, the break even concentrations are given

by: $\lambda_1 \approx 1.636$, $\lambda_2 = 2$. Moreover, $\lambda_2 < S_{in} < \bar{\lambda}_2 = 3$ and the equilibria are given by

$$E_0 = (2.5, 0, 0), \quad E_1 \approx (1.867, 0.328, 0) \quad \text{and} \quad E_2 \approx (2.071, 0, 0.21),$$

where E_1 is GAS in the interior of the positive quadrant and all other equilibria are unstable.

For $(D, S_{in}) = (0.5, 6) \in \mathcal{I}_5$, Fig. 4(b) shows the global convergence to the coexistence equilibrium E^* for any positive initial conditions. In this case, $S_{in} > \bar{\lambda}_2$ and the equilibria are given by

$$E_0 = (6, 0, 0), \quad E_1 \approx (2.826, 1.355, 0), \quad E_2 \approx (2.555, 0, 1.498) \quad \text{and} \quad E^* \approx (2.304, 0.853, 0.860).$$

4. Study of the competition model with several species

Now, we consider the case of n species competing for a same limiting resource, we determine the equilibria of (1) under assumption **H1** and we precise their asymptotic stability according to the control parameter S_{in} . For that, we use the concept of steady-state characteristic introduced by Lobry and al., [12, 13], to describe geometrically the equilibria. The steady-state characteristic is a curve which is associated to each species. It permits, if the dynamic of the renewal of the resource is known to give sufficient conditions for coexistence and to predict the issue of the competition. These curves are determined empirically.

4.1. Existence of equilibria

In the following, we study the existence of the equilibria of the system (1) under assumption **H1** and for all $a_i > 0$, $i = 1, \dots, n$. If equation $f_i(S) = D_i$ has a solution, then we denote $\lambda_i = f_i^{-1}(D_i)$. Otherwise, $\lambda_i = +\infty$. We assume that the populations x_i are labeled such that

$$\lambda_1 < \lambda_2 < \dots < \lambda_n.$$

To find the equilibria of (1), we solve the following system:

$$\begin{cases} 0 &= D(S_{in} - S) - \sum_{i=1}^n f_i(S)x_i \\ 0 &= [f_i(S) - a_i x_i - D_i]x_i, \quad i = 1, \dots, n. \end{cases} \quad (8)$$

For convenience, we introduce the following functions, for $i = 1, \dots, n$:

$$h_i(S) = \begin{cases} \frac{f_i(S) - D_i}{a_i} f_i(S) & \text{if } S > \lambda_i \\ 0, & \text{else} \end{cases} \quad (9)$$

and

$$H(S) = D(S_{in} - S) - \sum_{i=1}^n h_i(S).$$

If $x_i = 0$ for all $i = 1, \dots, n$, then $S = S_{in}$ from the first equation of (8). This corresponds to the washout equilibrium $E_0 = (S_{in}, 0, \dots, 0)$, which always exists. If $x_i \neq 0$, for all $i = 1, \dots, n$, we deduce from equation $i + 1$ of (8) that,

$$x_i = \frac{f_i(S) - D_i}{a_i}, \quad (10)$$

which is positive if and only if $S > \lambda_i$. From the first equation of (8), we deduce that $H(S) = 0$. Since H is decreasing on $[\lambda_n, +\infty[$,

$$H(\lambda_n) = D(S_{in} - \lambda_n) - \sum_{k=1}^{n-1} h_k(\lambda_n) \quad \text{and} \quad H(S_{in}) = - \sum_{i=1}^n h_i(S_{in}),$$

there exists a unique solution $S^* > \lambda_n$ of equation $H(S) = 0$ if and only if $H(\lambda_n) > 0$, that is,

$$S_{in} > \bar{\lambda}_n \quad \text{with} \quad \bar{\lambda}_n = \lambda_n + \frac{1}{D} \sum_{k=1}^{n-1} h_k(\lambda_n).$$

Hence, one has the following result.

Proposition 4.1. *The system (1) admits a unique positive equilibrium $E^* = (S^*, x_1^*, \dots, x_n^*)$ if and only if*

$$S_{in} > \bar{\lambda}_n.$$

To get the other equilibria corresponding to the extinction of one or many species, we first define the steady-state characteristic: in order to identify these equilibria.

Definition 4.1. *We define the steady-state characteristic by the set of the curves $y = 0$ and $y = h_J(S)$ where*

$$h_J = \sum_{i \in J} h_i,$$

with J is a subset of $\{1, \dots, n\}$, defined for $S \geq \max\{\lambda_j : j \in J\}$.

From the first equation of (8), for any fixed value of S_{in} , the equilibria are obtained by taking the intersections of the line Δ of equation $y = D(S_{in} - S)$ with the steady-state characteristics $y = 0$ and $y = h_J(S)$, $J \subset \{1, \dots, n\}$, (see Fig. 5, for $n = 3$). We can see then that:

- If $S_{in} > \bar{\lambda}_n$, it exists 2^n equilibria:
 1. A washout equilibrium E_0 .
 2. C_n^1 equilibria E_1, \dots, E_n , where one species survives, and given by the intersection of Δ and the curves of h_i , $i = 1, \dots, n$.
 3. C_n^2 equilibria E_{ij} , with $i, j = 1, \dots, n$ and $i < j$, where two species coexist and the other species are excluded. They are given by the intersection of Δ and the curves $h_{ij} = h_i + h_j$.
 4. C_n^m equilibria where m species coexist, for any $1 \leq m \leq n$.

5. A positive equilibrium E^* where all species coexist, which is the intersection of the line Δ and the curve $h_{12\dots n} = \sum_{i=1}^n h_i$.

The total number of equilibria is, then, $\sum_{k=0}^n C_n^k = 2^n$.

- If $\lambda_1 < S_{in} \leq \bar{\lambda}_n$, we can extend the last reasoning to see that according to the position of S_{in} , the intersection of the line Δ with the steady-state characteristics $y = h_j$, $J = \{1, 2, \dots, j\}$, $j \leq n$ is composed of the intersection with the curve $y = 0$ (which corresponds to the washout equilibrium), the curves $y = h_i$, $i = 1, \dots, j$, the curves $y = h_i + h_k$, $i, k = 1, \dots, j$, $i \neq k, \dots$ and the curve $y = h_1 + h_2 + \dots + h_j$ (which corresponds to the coexistence of j species).
- If $S_{in} \leq \lambda_1$, the only intersection point of the characteristics with Δ is on the curve $y = 0$ and it corresponds to the washout equilibrium E_0 .

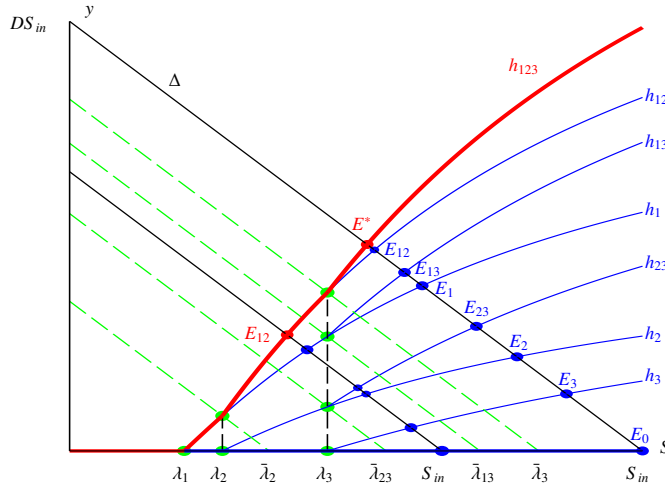


Figure 5: Steady-state characteristic for $n = 3$.

In Fig. 5, we illustrate the case of three species competing for a nutriment. It shows the number of equilibria of (1) according to S_{in} . We denote by

$$\bar{\lambda}_{13} = \lambda_3 + \frac{h_1(\lambda_3)}{D} \quad \text{and} \quad \bar{\lambda}_{23} = \lambda_3 + \frac{h_2(\lambda_3)}{D}.$$

Then, we can see that

- If $S_{in} > \bar{\lambda}_3$, it exists 2^3 equilibria: A washout equilibrium E_0 , a positive equilibrium E^* , which is the intersection of the line Δ and the curve $h_{123} := \sum_{i=1}^3 h_i$. Three equilibria E_1, E_2 and E_3 , where one species survives, three equilibria E_{12}, E_{13} and E_{23} , where two species coexist while the third species is excluded.
- If $\bar{\lambda}_{13} < S_{in} < \bar{\lambda}_3$, then it exists seven equilibria: $E_0, E_1, E_2, E_3, E_{12}, E_{13}$ and E_{23} .
- If $\bar{\lambda}_{23} < S_{in} < \bar{\lambda}_{13}$, then it exists six equilibria: $E_0, E_1, E_2, E_3, E_{12}$ and E_{23} .
- If $\lambda_3 < S_{in} < \bar{\lambda}_{23}$, then it exists five equilibria: E_0, E_1, E_2, E_3 and E_{12} .
- If $\bar{\lambda}_2 < S_{in} < \lambda_3$, then it exists four equilibria: E_0, E_1, E_2 and E_{12} .

- If $\lambda_2 < S_{in} < \bar{\lambda}_2$, then it exists three equilibria: E_0, E_1 and E_2 .
- If $\lambda_1 < S_{in} < \lambda_2$, then it exists two equilibria E_0 and E_1 .
- If $S_{in} < \lambda_1$, then it exists a unique equilibrium E_0 .

4.2. Stability of equilibria

We are interested, now, in the asymptotic behavior of (1). We show that in each case, only one equilibrium can be stable. To do so, we calculate the Jacobian matrix and we use mainly Lemma 6.3 of [2], what we recall here:

Lemma 4.1. *Consider the matrix*

$$A = \begin{bmatrix} -D - \sum_{i=1}^n \alpha_i & c_1 & c_2 & \cdots & c_n \\ \alpha_1 & -b_1 & 0 & \cdots & 0 \\ \alpha_2 & 0 & -b_2 & \cdots & 0 \\ \vdots & \vdots & \vdots & \ddots & \vdots \\ \alpha_n & 0 & 0 & \cdots & -b_n \end{bmatrix}. \quad (11)$$

Assume that $D > 0$ and for $i = 1, \dots, n$, $\alpha_i \geq 0$, $b_i > 0$ and $c_i \leq b_i$. Then, all the eigenvalues of A have negative real part.

We first prove the next result:

Proposition 4.2. *If $S_{in} > \bar{\lambda}_n$, the positive equilibrium $E^* = (S^*, x_1^*, \dots, x_n^*)$ is LES and all other equilibria are unstable.*

Proof. The Jacobian matrix at (S, x_1, \dots, x_n) is in the form (11) with

$$\alpha_i = f'_i(S)x_i, \quad b_i = -[f_i(S) - 2a_i x_i - D_i] \quad \text{and} \quad c_i = -f_i(S).$$

If $S_{in} > \bar{\lambda}_n$, then the positive equilibrium $E^* = (S^*, x_1^*, \dots, x_n^*)$ satisfies $f_i(S^*) - a_i x_i^* - D_i = 0$ and the Jacobian matrix terms at E^* satisfy:

$$\alpha_i = f'_i(S^*)x_i^*, \quad b_i = a_i x_i^* \quad \text{and} \quad c_i = -f_i(S^*).$$

Using **H1**, the positivity of the coefficients a_i and Lemma 4.1, we conclude that E^* is LES.

Now, denoting by $\bar{E} = (\bar{S}, x_1, \dots, x_n)$ the equilibrium point which has at least one component $x_k = 0$, for $k = 1, \dots, n$. The Jacobian matrix at \bar{E} is in the form (11) with

$$\alpha_i = f'_i(\bar{S})x_i, \quad b_i = a_i x_i, \quad c_i = -f_i(\bar{S}) \quad \text{for all } i \neq k$$

and

$$\alpha_k = f'_k(\bar{S})x_k = 0, \quad b_k = D_k - f_k(\bar{S}).$$

If $S_{in} > \bar{\lambda}_n$, then $\bar{S} > \lambda_n \geq \lambda_k$ and the eigenvalue $f_k(\bar{S}) - D_k$ is positive. Thus, all equilibria that admit at least one zero component are unstable. \blacksquare

One can extend this result for any value of S_{in} . We can prove that the equilibrium corresponding to the intersection of the line Δ with the curve of the function $h_{1\dots n} := \sum_{i=1}^n h_i$, is LES and all other equilibria are unstable. Indeed, when $S \in]\lambda_k, \lambda_{k+1}]$, $k = 1, \dots, n-1$, we denote by $E^k = (S^k, x_1^k, \dots, x_n^k)$, $k = 1, \dots, n-1$, the intersection of the line Δ with the steady-state characteristic $y = \sum_{i=1}^k h_i(S)$. From definition (9) of h_i , $i = 1, \dots, n$ we see that, for $S \in]\lambda_k, \lambda_{k+1}]$, $h_{k+1}(S) = \dots = h_n(S) = 0$ and then, from (10), $x_{k+1}^k = \dots = x_n^k = 0$. We deduce that $f_{k+1}(S^k) - D_{k+1}, \dots, f_n(S^k) - D_n$ are eigenvalues of the Jacobian matrix at E^k . Since $S^k < \lambda_{k+1} < \dots < \lambda_n$, these eigenvalues are negative. Using Lemma (4.1), the other eigenvalues have negative real parts. The equilibrium E^k is then LES. Now, the other equilibria with $S \in]\lambda_k, \lambda_{k+1}]$ have at least a null component among the first $k+1$ ones. The corresponding eigenvalue of the Jacobian matrix associated to such component is then positive. Hence, such equilibria are unstable.

Consequently, we can state:

Proposition 4.3. *For any value of S_{in} , there is only one LES equilibrium. All other equilibria are unstable.*

In Fig. 5, we stained in red the part of the characteristic which corresponds to LES equilibria, and in blue the unstable equilibria. Table 5 summarizes the previous results:

Condition	E_0	E_1	E_2	E_{12}	E_3	E_{23}	E_{13}	E^*
$S_{in} < \lambda_1$	S							
$\lambda_1 < S_{in} < \lambda_2$	U	S						
$\lambda_2 < S_{in} < \bar{\lambda}_2$	U	S	U					
$\bar{\lambda}_2 < S_{in} < \lambda_3$	U	U	U	S				
$\lambda_3 < S_{in} < \bar{\lambda}_{23}$	U	U	U	S	U			
$\bar{\lambda}_{23} < S_{in} < \bar{\lambda}_{13}$	U	U	U	S	U	U		
$\bar{\lambda}_{13} < S_{in} < \bar{\lambda}_3$	U	U	U	S	U	U	U	
$S_{in} > \bar{\lambda}_3$	U	U	U	U	U	U	U	S

Table 5: Existence and local stability of equilibria of (1) with $n = 3$.

We aim now, to prove in the case of multi-species model the global stability of the equilibrium $E_1 = (S_1, \bar{x}_1, 0, \dots, 0)$ corresponding to the extinction of all species except the one who has the lowest break-even concentration.

Proposition 4.4. *Assume that $\lambda_1 < S_{in} < \bar{\lambda}_2$ and that there exist constants $\alpha_i > 0$, for each $i \geq 2$ satisfying $\lambda_i < S_{in}$ such that*

$$\max_{0 < S < \lambda_1} g_i(S) \leq \alpha_i \leq \min_{\lambda_i < S < S_{in}} g_i(S) \quad \text{where} \quad g_i(S) = \frac{f_i(S)}{f_i(S_1)} \frac{f_1(S) - f_1(S_1)}{f_1(S) - D_i} \frac{S_{in} - S_1}{S_{in} - S}, \quad (12)$$

Then, the equilibrium E_1 is GAS for system (1) with respect to all solutions with $x_1(0) > 0$.

Proof. Consider the Lyapunov function $V = V(S, x_1, \dots, x_n)$ defined as follows:

$$V = \frac{S_{in} - S_1}{f_1(S_1)} \int_{S_1}^S \frac{f_1(\sigma) - f_1(S_1)}{S_{in} - \sigma} d\sigma + \int_{\bar{x}_1}^{x_1} \frac{\xi - \bar{x}_1}{\xi} d\xi + \sum_{i=2}^n \alpha_i x_i,$$

where $\alpha_i > 0$ are the positive constants satisfying (12) if $S < S_{in}$ and $\alpha_i > 0$ are arbitrary if $S > S_{in}$. The function V is continuously differentiable for $0 < S < S_{in}$ and $x_i > 0$, $i = 1, \dots, n$ and positive except at the point E_1 , where it is equal to 0. The time derivative of V computed along the trajectories of (1) is given by:

$$V' = x_1(f_1(S) - f_1(S_1)) \left[1 - \frac{f_1(S)}{S_{in} - S} \frac{S_{in} - S_1}{f_1(S_1)} \right] - a_1(x_1 - \bar{x}_1)^2 - \sum_{i=2}^n \alpha_i a_i x_i^2 + \sum_{i=2}^n x_i(f_i(S) - D_i)(\alpha_i - g_i(S))$$

First, note that, the first term of the above sum is always non-positive for $0 < S < S_{in}$ and equals 0 for $S \in]0, S_{in}[$ if and only if $S = S_1$ or $x_1 = 0$. The second and the third term are obviously non-positive and vanish only if $x_1 = \bar{x}_1$ and $x_i = 0$ for $i = 2, \dots, n$. Finally, the last term of the above sum is always non-positive for every $S \in]0, S_{in}[$ and equal to zero if and only if $x_i = 0$ for $i = 2, \dots, n$. Then, $V \leq 0$ and $V = 0$ if and only if $S = S_1$, $x_1 = \bar{x}_1$ and $x_i = 0$ for $i = 2, \dots, n$. Hence, the result follows by applying the LaSalle extension theorem (see [18]). ■

4.3. Operating diagram with three species

In the following, we analyse the operating diagram of model (1) with $n = 3$ in the case $A_i \geq 0$, with respect to control parameters S_{in} and D . The function f_3 has an increasing inverse function that we denote by F_3 . We set $\bar{m}_3 = \sup_{S \geq 0} f_3(S) - A_3$ and we assume that $\bar{m}_3 > 0$ and for example that

$$F_1(D) < F_2(D) < F_3(D), \quad \text{for all } D \in]0, \bar{m}_3[.$$

To illustrate the stability conditions given by Table 5, we also define the functions:

$$\begin{aligned} F_{23} :]0, \bar{m}_3[&\longrightarrow]0, +\infty[\\ D &\longrightarrow F_3(D) + \frac{h_2(F_3(D))}{D}, \end{aligned}$$

$$\begin{aligned} F_{13} :]0, \bar{m}_3[&\longrightarrow]0, +\infty[\\ D &\longrightarrow F_3(D) + \frac{h_1(F_3(D))}{D} \end{aligned}$$

and

$$\begin{aligned} F_{123} :]0, \bar{m}_3[&\longrightarrow]0, +\infty[\\ D &\longrightarrow F_3(D) + \frac{1}{D} [h_1(F_3(D)) + h_2(F_3(D))]. \end{aligned}$$

Note that if $A_i > 0$, $i = 1, \dots, 3$, then

$$\lim_{D \rightarrow 0^+} F_{23}(D) = \lim_{D \rightarrow 0^+} F_{13}(D) = \lim_{D \rightarrow 0^+} F_{123}(D) = +\infty.$$

By the definition of F_{23} and since $h_2(F_3(D)) > 0$, it follows that

$$F_3(D) < F_{23}(D) \quad \text{for all } D \in]0, \bar{m}_3[$$

and for similar reasons that

$$F_{12}(D) < F_{13}(D) < F_{123}(D) \quad \text{for all } D \in]0, \bar{m}_3[.$$

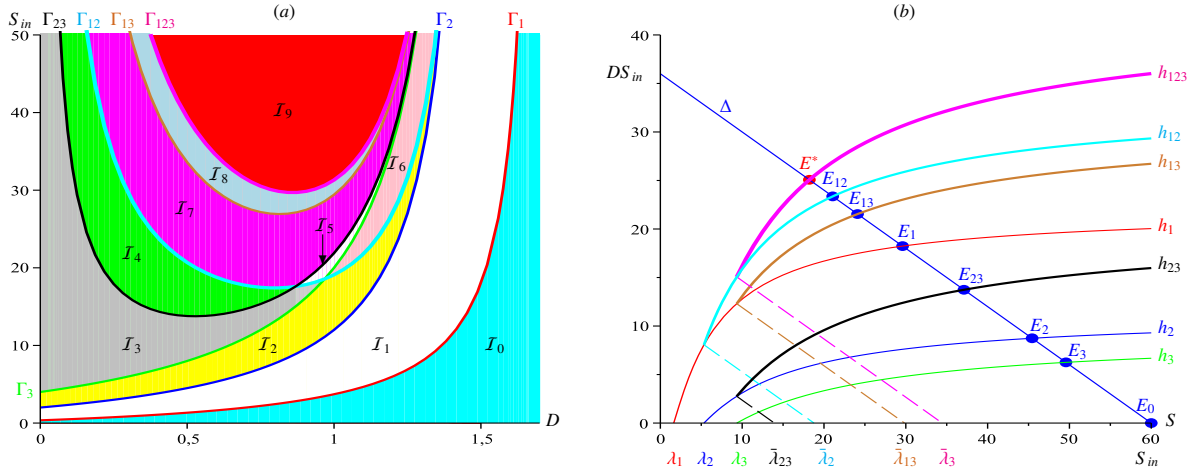


Figure 6: (a) Operating diagram of (1) with $n = 3$. (b) Steady-state characteristic for $(D, S_{in}) \in \mathcal{I}_9$ with $D < D_1^*$.

Let Γ_3 be the curve of equation $S_{in} = F_3(D)$, Γ_{23} that of $S_{in} = F_{23}(D)$, Γ_{13} that of $S_{in} = F_{13}(D)$ and Γ_{123} that of $S_{in} = F_{123}(D)$. The curves Γ_i , $i = 1, 2, 3, \Gamma_{23}, \Gamma_{12}, \Gamma_{13}$ and Γ_{123} separate the operating plane (D, S_{in}) in ten regions, as shown in Fig. 6(a), labeled \mathcal{I}_k , $k = 0, \dots, 9$. The curve Γ_1 (the red curve) is the border which makes E_0 a saddle point and at the same time E_1 exists and is a LES equilibrium. The curve Γ_2 (the blue curve) is the border which makes E_2 exists but it is a saddle point. The curve Γ_3 (the green curve) is the border which makes E_3 exists but it is a saddle point. The curve Γ_{12} (the cyan curve) is the border which makes E_1 a saddle point and at the same time E_{12} exists and is a LES equilibrium. The curve Γ_{23} (the black curve) is the border which makes E_{23} exists but it is a saddle point. The curve Γ_{13} (the gold curve) is the border which makes E_{13} exists but it is a saddle point. The curve Γ_{123} (the magenta curve) is the border which makes E_{12} a saddle point and at the same time E^* exists and is a LES equilibrium. The curve Γ_{12} does intersect with the curves Γ_{23} and Γ_3 in D_1^* and D_2^* , respectively.

Table 6 shows the existence and local stability of equilibria in the regions \mathcal{I}_k , $k = 0, \dots, 9$, when the curves Γ_i , $i = 1, 2, 3$, do not intersect. Note that in the case where the curves Γ_i intersect, the study can be treated similarly.

In the case $n > 2$, we remark that if there are two zeros parameters a_i then the positive equilibrium E^* does not exist. Thus, a necessary condition of existence of E^* is that at most one a_i is zero. Furthermore, E^* can be stable if all the

Region	E_0	E_1	E_2	E_3	E_{23}	E_{12}	E_{13}	E^*
$(D, S_{in}) \in \mathcal{I}_0$	S							
$(D, S_{in}) \in \mathcal{I}_1$	U	S						
$(D, S_{in}) \in \mathcal{I}_2$	U	S	U					
$(D, S_{in}) \in \mathcal{I}_3$	U	S	U	U				
$(D, S_{in}) \in \mathcal{I}_4$	U	S	U	U	U			
$(D, S_{in}) \in \mathcal{I}_5$	U	U	U	U		S		
$(D, S_{in}) \in \mathcal{I}_6$	U	U	U			S		
$(D, S_{in}) \in \mathcal{I}_7$	U	U	U	U	U	S		
$(D, S_{in}) \in \mathcal{I}_8$	U	U	U	U	U	S	U	
$(D, S_{in}) \in \mathcal{I}_9$	U	U	U	U	U	U	U	S

Table 6: Existence and local stability of steady states of three species model.

species are inhibited (namely, $a_i \neq 0$) except the least competitive species.

4.4. Simulations

In the following, we illustrate the results obtained for system (1) with $n = 3$ and the functions $f_i(\cdot)$ are of Monod type, defined by:

$$f_i(S) = \frac{m_i S}{K_i + S}, \quad i = 1, 2, 3.$$

For the numerical simulations, we use the parameters shown in Table 7 and Table 8.

Parameters	m_1	m_2	m_3	K_1	K_2	K_3
Values	2	2.5	3	2	3	4

Table 7: Parameter values for Monod functions.

Parameters	a_1	a_2	a_3	A_1	A_2	A_3
Values	0.1	0.2	0.3	0.3	1	1.5

Table 8: Parameter values for model (1) with $n = 3$.

Note that

$$D_1^* \simeq 0.869 \quad \text{and} \quad D_2^* \simeq 0.968.$$

For these parameter values, the curves $S_{in} = F_i(D)$ do not intersect and we obtain the operating diagram in Fig. 6(a). The steady-state characteristic is depicted in Fig. 6(b) for

$$(D, S_{in}) = (0.6, 60) \in \mathcal{I}_9 \quad \text{or even} \quad S_{in} > \bar{\lambda}_3 \simeq 34.443,$$

where there exist 2^3 equilibria for system (1). In this case, Fig. 7(a) shows the coexistence of the three species and the convergence towards the positive equilibrium $E^* \simeq (18.214, 9.021, 2.732, 1.199)$ for several positive initial conditions.

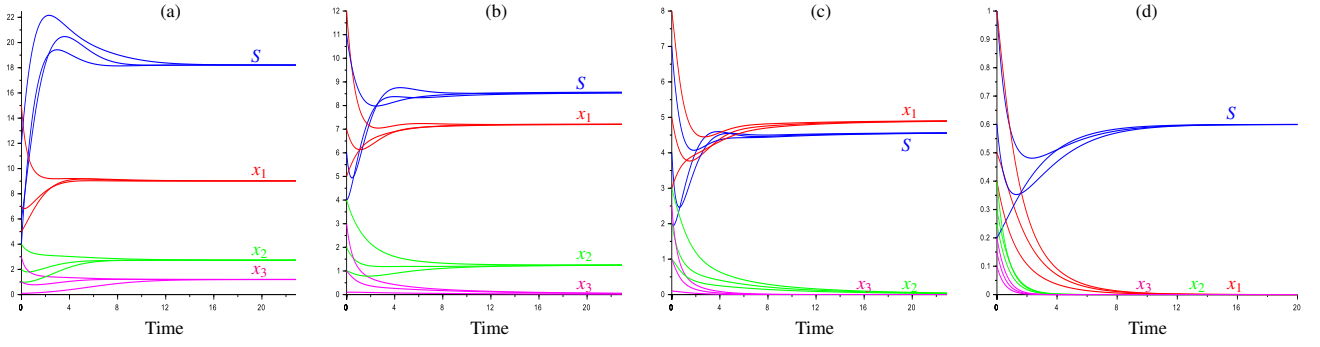


Figure 7: (a) Coexistence of the three species for $(D, S_{in}) \in \mathcal{I}_9$. (b) Competitive exclusion of the third species for $(D, S_{in}) \in \mathcal{I}_8$. (c) Competitive exclusion of the third and the second species for $(D, S_{in}) \in \mathcal{I}_4$. (d) Washout of all species for $(D, S_{in}) \in \mathcal{I}_0$.

Fig. 7(b) shows the competitive exclusion of the third species for

$$(D, S_{in}) = (0.6, 32) \in \mathcal{I}_8 \quad \text{or even} \quad \bar{\lambda}_{13} \simeq 29.840 < S_{in} < \bar{\lambda}_3.$$

For several positive initial conditions, the solutions of (1) converge towards the equilibrium $E_{12} \simeq (8.583, 7.220, 1.262, 0)$.

Fig. 7(c) shows the competitive exclusion of the third and the second species for

$$(D, S_{in}) = (0.6, 16) \in \mathcal{I}_4 \quad \text{or even} \quad \bar{\lambda}_{23} \simeq 13.935 < S_{in} < \bar{\lambda}_2 \simeq 18.777.$$

For several positive initial conditions, the solutions of (1) converge towards the equilibrium $E_1 \simeq (4.581, 4.922, 0, 0)$.

Fig. 7(d) shows the washout of all species for

$$(D, S_{in}) = (0.6, 0.6) \in \mathcal{I}_0 \quad \text{or even} \quad S_{in} < \lambda_1 \simeq 1.636.$$

For several positive initial conditions, the solutions of (1) converge towards the equilibrium $E_0 \simeq (0.6, 0, 0, 0)$.

5. Conclusion

In this paper, we considered a mathematical model describing multi-species competition for a single growth-limiting resource in a chemostat. For monotonic growth functions and different dilution rates, we proved that the outcome of competition contrasts the competitive exclusion principle which predicts that only one species can exist in the long term. Indeed, we proved that according to the concentration S_{in} of the substrate in the chemostat, several species can coexist. If S_{in} is large enough, there exists a unique coexistence equilibrium which is LES while all other equilibria are unstable. This proves that intra-specific interactions, between individuals of the same species, may be responsible for the observed coexistence, since they are the only difference between the classical chemostat model [18] and the model presented here.

The operating diagram depicts regions in the (D, S_{in}) plane in which the various outcomes occur. To maintain the coexistence of species in the chemostat, the ideally parameter values of D and S_{in} should be chosen in the red region of

coexistence but not in the cyan region of washout or in the other regions of exclusion of one species (see Figs. 2, 3 and 6). Hence, the importance of the main control parameters D and S_{in} on the maintenance of species coexistence and the protection of the least relevant species among microbial ecosystems.

The intra-specific competition of the $n - 1$ most efficient species introduces a region of coexistence of n species while the least competitive species has no reason to be inhibited in order to coexist with all other species. Decreasing the values of intra-specific competition terms reduces the region of coexistence and increases the regions of competitive exclusion. When these terms tends to zero, the region of coexistence tends to disappear and we find the same result than for the classical chemostat model. The simulations illustrate the mathematical results demonstrated in the case where the growth rates are of Monod type.

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