COMPETITION FOR A SINGLE RESOURCE AND COEXISTENCE OF SEVERAL SPECIES IN THE CHEMOSTAT

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ABSTRACT. We study a model of the chemostat with several species in competition for 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 characteristics, we present a geometric characterization of the existence and stability of all equilibria. Moreover, we provide necessary and sufficient conditions on the control parameters of the system to have 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 coexistence region of the species.

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, [21]. The surviving species is the one with the smallest subsistence or break-even concentration of the limiting resource. The chemostat model describing the interactions between the microbial species has been used for different systems,

especially for wastewater treatment processes, biological reactors, etc. Nevertheless, for most of these systems, it is observed that many species can coexist 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 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, and or input nutrient concentration, see [8, 10, 22, 25] or with variable yields, [2, 18, 19, 20], see also [6, 7, 11, 12, 13, 14, 16, 23, 24] for other extensions.

Recently, within the framework of the classical chemostat model, Lobry et al. have introduced in [14, 15] growth functions that do not only depend on the resource concentration but also on the biomass concentration. In this model, they introduce the concept of the steady-state characteristic for each species. For several species in competition for a single 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. For the proposed model, they prove the existence of a globally asymptotically stable equilibrium of coexistence, see [12, 14]. 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 wastewater process engineering [9]. For instance, it has been proven that flocculation systems can be reduced, under certain assumptions, to systems with density-dependent growth rates where coexistence may occur through this mechanism, [3, 4, 7].

In order to explain coexistence, other approaches rely on taking into account, in the chemostat model, inter-specific interactions between populations of microorganisms or intra-specific interactions between individuals themselves. Wolkowicz and Lu [24] have considered two models, corresponding respectively to the case where only intra-specific interferences are permitted and to the case where only inter-specific interactions occur. In the case of intra-specific interactions in the dynamics of two species, there exists a coexistence equilibrium which is locally asymptotically stable. In the case of inter-specific interactions in the dynamics of two species, there exists a coexistence equilibrium, but it is unstable [24]. The case of both intra- and inter-specific interactions has been considered in [3, 5]. It has been shown that there can be one or more positive locally exponentially stable equilibria. In the case of more than one, bistability can occur, for certain values of the operating parameters.

De Leenheer et al. [11] have proposed a chemostat model where n species are competing for a single nutrient by considering that mortality rates are due to the crowding effects. The authors were interested only in the positive equilibrium. They require that the death rate parameters of all species are large enough to prove the existence of a positive equilibrium. They 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.

The goal of this paper is to give a quite comprehensive analysis of the model of De Leenheer et al. [11]. Using the concept of steady-state characteristics introduced by Lobry et al. [14, 15], we present a geometric characterization that describes all equilibria of the model and their stability, not only the positive equilibrium as

it is done in [11]. We give a necessary and sufficient condition for the existence of a positive equilibrium, not only a sufficient condition as it is done in [11]. In particular, we show that if the death rate parameters of all species are positive, then the existence of a stable positive equilibrium is possible for certain values of the operating parameters. Hence, the sufficient condition (the death rate parameters of all species are large enough) given by [11] is not necessary. These results were obtained in [3]. We generalize the Lyapunov function proposed by Wolkowicz and Lu [24], in the case of two species, to prove the global stability of the equilibrium, corresponding to the extinction of all species except the one with the lowest break-even concentration. Last but not least we determine the operating diagram of the model, that is to say, we determine the regions of the operating parameters (dilution rate and input concentration of the nutrient), which depict the existence and the stability of each equilibrium. This question was not considered in [11]. We show that the operating diagram is independent of the intra-specific competition parameter of the weaker species.

In this paper, we may allow that there is no intra-specific competition of the weaker species contrary to the literature where it is apparently always assumed that all intra-specific competition parameters are positive [3, 5, 6, 7, 11, 14, 15, 24]. Ruan et al. [17] considered the issue of the coexistence in a two-competitors/one-prey (biotic resource) model with a density-dependent mortality rate of only one of the competitors. Similarly to what is shown by [17] for a biotic resource, our findings demonstrate that in the case of an abiotic resource, two competitors can coexist when only one of the competitors exhibits intra-specific competition, namely the stronger one. The possible coexistence when the weaker species has no intra-specific competition is not surprising since the lack of intra-specific competition for the weaker species has a beneficial effect on this species' ability to survive. What is much more interesting is that, the operating diagram being independent of the intra-specific competition parameter of the weaker species, coexistence is possible. This occurs even for arbitrarily high levels of intra-specific competition of the weaker species and also for suitable given dilution rate and input concentration of the nutrient.

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 analyse this model in the case of two species. Using the concept of steady-state characteristics, 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. In Section 4, this approach is extended to the study of the multi-species model. In Section 5, we present the operating diagrams which depict the existence and the stability of each equilibrium according to control parameters. In Section 6, 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 7.

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.** We consider the chemostat model of n species competing for a single nutrient with intra-specific linear interactions, introduced by De Leenheer et al. [11]. This model reads:

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

where S denotes the concentration of the substrate; x_i denotes the concentration of the ith population of micro-organisms; 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 rate of species i and the dilution rate D, (D_i are not necessarily equal); a_i is a non-negative parameter giving rise to death rate $a_i x_i$ which is due to intra-specific interaction and $f_i(\cdot)$ denotes the per-capita growth rate of the ith population. We first make the following assumption on the growth functions:

H1: For $i = 1, \ldots, n$, $f_i(0) = 0$ 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 for any reasonable chemostat model.

Proposition 1. *For any non-negative initial condition, the solutions of (1) remain non-negative and are positively bounded. The set*

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

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

Proof. From (1), we have

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

Hence,

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

From Gronwall's Lemma, we obtain

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

It is easy to see from (1) that the cone $\mathbb{R}_+^{n+1}$ is positively invariant. Thus solutions are non-negative for all $t \geqslant 0$ and from (2) we deduce that solutions are positively bounded and that the set Ω is positively invariant and is a global attractor for (1). $\qquad \square$

3. **Analysis of the competition model with two species.** For a better understanding of the qualitative behavior of solutions of the model (1), we begin with the case $n = 2$. In this particular case, we can describe precisely the solutions and give stability results for all equilibria. Moreover, we can show that a necessary and sufficient condition of coexistence of both species is the inhibition of the strongest

species by intra-specific competition. System (1), in the case of two species competing for a single nutrient, reads

$$
\begin{cases}
\dot{S} & = & D(S_{in} - S) - f_1(S)x_1 - f_2(S)x_2 \\
\dot{x}_1 & = & [f_1(S) - a_1 x_1 - D_1]x_1 \\
\dot{x}_2 & = & [f_2(S) - a_2 x_2 - D_2]x_2.
\end{cases}
\tag{3}
$$

We assume that **H1** is satisfied for $n = 2$. Now, we shall discuss the existence of equilibria of system (3) and then their asymptotic stability for $a_1 > 0$ and $a_2 \geqslant 0$.

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

$$
\begin{cases}
0 & = & D(S_{in} - S) - f_1(S)x_1 - f_2(S)x_2 \\
0 & = & [f_1(S) - a_1 x_1 - D_1]x_1 \\
0 & = & [f_2(S) - a_2 x_2 - D_2]x_2.
\end{cases}
\tag{4}
$$

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 the first and the second species, respectively, and a positive equilibrium corresponding to the coexistence of both species. For the description of the equilibria, we need the following notations

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

and

$$
\bar{\lambda}_2 = \lambda_2 + \frac{h_1(\lambda_2)}{D}.
\tag{6}
$$

Notice that the function $h_2(\cdot)$ is defined only when $a_2 > 0$. In this case, we define the function $H(\cdot)$ by

$$
H(S) = D(S_{in} - S) - \sum_{i=1}^{2} h_i(S).
$$

Then, we can state:

Proposition 2. *System (3) admits the following equilibria:*

1. *The washout equilibrium $E_0 = (S_{in}, 0, 0)$, that always exists.*
2. *The equilibrium $E_1 = (S_1, \bar{x}_1, 0)$, of extinction of species x_2, where S_1 is the unique solution of $H_1(S) = 0$, and $\bar{x}_1 = \dfrac{f_1(S_1) - D_1}{a_1}$. E_1 exists if and only if $S_{in} > \lambda_1$.*
3. *The equilibrium $E_2 = (S_2, 0, \bar{x}_2)$, of extinction of species x_1, where $S_2 = \lambda_2$ and $\bar{x}_2 = \dfrac{D(S_{in} - \lambda_2)}{D_2}$ if $a_2 = 0$ and S_2 is the unique solution of $H_2(S) = 0$, and $\bar{x}_2 = \dfrac{f_2(S_2) - D_2}{a_2}$ if $a_2 > 0$. E_2 exists if and only if $S_{in} > \lambda_2$.*
4. *The positive equilibrium $E^* = (S^*, x_1^*, x_2^*)$, where $S^* = \lambda_2$, $x_1^* = \dfrac{f_1(\lambda_2) - D_1}{a_1}$, $x_2^* = H_1(\lambda_2)/D_2$ if $a_2 = 0$ and S^* is the unique solution of equation $H(S) = 0$, $x_i^* = \dfrac{f_i(S^*) - D_i}{a_i}$, $i = 1, 2$, if $a_2 > 0$. E^* exists if and only if $S_{in} > \bar{\lambda}_2$.*

Proof. 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 proof of item 2, 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 $[\lambda_1, +\infty[$, and we have

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

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

For the proof of item 3, if $x_1 = 0$ and $x_2 \neq 0$, two cases must be distinguished.

If $a_2 > 0$ then, in the same way as the previous item, we prove that there exists a unique solution $S_2 > \lambda_2$ of equation $H_2(S) = 0$ if and only if $S_{in} > \lambda_2$.

If $a_2 = 0$ then $f_2(S) = D_2$ which implies that $S_2 = \lambda_2$ and then $x_2 = D(S_{in} - \lambda_2)/D_2$ which is positive if and only if $S_{in} > \lambda_2$.

For the proof of item 4, if $x_1 \neq 0$ and $x_2 \neq 0$, then two cases must be distinguished.

If $a_2 > 0$ 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, $S_{in} > \bar{\lambda}_2$.

If $a_2 = 0$ then the third equation of system (4) implies that $S^* = \lambda_2$ and from the second one we have $x_1^* = (f_1(S) - D_1)/a_1$. The first equation leads to

$$x_2^* = \frac{D(S_{in} - S) - h_1(\lambda_2)}{D_2} = \frac{H_1(\lambda_2)}{D_2}.$$

$\square$

In the next section, we will show that the positive equilibrium E^* is stable as long as it exists. We explain here what are the consequences of the existence of this equilibrium on the coexistence of the species. More precisely, we justify the claim of the introduction that coexistence may be possible, even though the weaker competitor exhibits arbitrarily high levels of intra-specific competition. According to Proposition 2, the existence of a positive equilibrium holds if $S_{in} > \bar{\lambda}_2$ or equivalently, using (5) and (6), if

$$S_{in} > \lambda_2 + \frac{f_1(\lambda_2) - D_1}{a_1 D} f_1(\lambda_2). \tag{7}$$

This is the necessary and sufficient condition for the existence of the positive equilibrium. This condition does not involve the intra-specific competition parameter

a_2 of the weaker competitor. In particular, the weaker competitor may exhibit arbitrarily high levels of intra-specific competition a_2. However, since the density of the weaker competitor at the equilibrium is given by

$$x_2^* = \frac{f_2(S^*) - D_2}{a_2},$$

it tends to 0 as a_2 tends to $+\infty$. There is another interesting observation which can be obtained from (7). If for example $S_{in} > \lambda_2$ (which expresses that species 2 could survive in the absence of the stronger competitor 1, and the absence of intra-specific competition with itself), then (7) holds for all sufficiently large a_1, i.e. for all sufficiently large levels of intra-specific competition of the stronger competitor 1. This relates to the findings of De Leenheer et al. [11] who established the existence of a positive equilibrium if the parameters a_1 and a_2 are large enough.

3.2. **Stability of equilibria.** For $a_2 \geqslant 0$, the local asymptotic stability of equilibria of (3) is given in the following result:

Proposition 3.

1. E_0 is LES if and only if $S_{in} < \lambda_i$, for $i = 1, 2$.
2. E_1 is LES if and only if $\lambda_1 < S_{in} < \bar{\lambda}_2$.
3. E_2 is a saddle point when it exists.
4. E^* is LES if and only if $S_{in} > \bar{\lambda}_2$.

Proof. Let J be the Jacobian matrix of (3) at (S, x_1, x_2), that is given by

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

At $E_0 = (S_{in}, 0, 0)$, we have

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

The eigenvalues are on the diagonal. They are negative, that is, E_0 is LES if and only if $S_{in} < \lambda_i$, $i = 1, 2$. For the proof of item 2, the Jacobian matrix of (3) at $E_1 = (S_1, \bar{x}_1, 0)$, is given by:

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

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 $\operatorname{tr}(A_1) < 0$, then the two eigenvalues of A_1 have negative real parts. The equilibrium E_1 is then LES if and only if $S_1 < \lambda_2$ or equivalently $S_{in} < \bar{\lambda}_2$.

For item 3, 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 parts. 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.

For the proof of item 4, 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

$$m_{11} = D + f_1'(S^*)x_1^* + f_2'(S^*)x_2^*, \quad m_{12} = f_1(S^*), \quad m_{13} = f_2(S^*),$$

$$m_{21} = f_1'(S^*)x_1^*, \quad m_{22} = a_1 x_1^*, \quad m_{31} = f_2'(S^*)x_2^*, \quad m_{33} = a_2 x_2^*,$$

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

$$c_0 = -1, \quad c_1 = -(m_{11} + m_{22} + m_{33}),$$

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

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

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

$$\begin{cases} c_i < 0, & i = 0, \ldots, 3 \\ c_1 c_2 - c_0 c_3 > 0. \end{cases}$$

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

$$\begin{aligned} c_1 c_2 - c_0 c_3 &= -m_{11}c_2 + m_{22}(m_{12}m_{21} + m_{11}m_{22} + m_{22}m_{33}) \\ &\quad + m_{33}(m_{13}m_{31} + m_{11}m_{22} + m_{11}m_{33} + m_{22}m_{33}) \end{aligned}$$

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. Fig. 1 shows that the stable equilibrium is the one on the red arc and all other equilibria (in blue) are unstable. More precisely, 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. 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

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^*	$S_{in} > \bar{\lambda}_2$	Stable whenever it exists

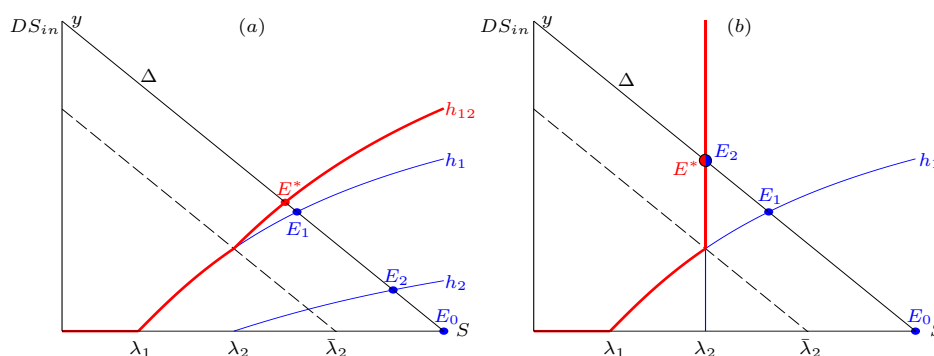TABLE 1. Existence and local stability of equilibria of system (3).

FIGURE 1. Steady-state characteristics with $S_{in} > \bar{\lambda}_2$: (a) equilibria of (3) when $a_2 > 0$, (b) equilibria of (3) when $a_2 = 0$. We use red color for LES equilibria and blue color for unstable equilibria.

E^*. If $\lambda_2 < S_{in} < \bar{\lambda}_2$, there exist three equilibria E_1, E_2 and E_0 given by the intersection between the line Δ and either the function $h_i(\cdot)$, $i = 1, 2$, respectively, or the line of equation $y = 0$. If $\lambda_1 < S_{in} < \lambda_2$, there exist two equilibria E_1 and E_0 given by the intersection between the line Δ and either the function $h_1(\cdot)$ or the line of equation $y = 0$. If $S_{in} < \lambda_1$, there exists one equilibrium E_0 given by the intersection between the line Δ and the line of equation $y = 0$.

Notice that when $S_{in} = \bar{\lambda}_2$, E_1 coalesces with E^* where E_1 is a saddle-node equilibrium since it has a zero eigenvalue and it is due to a saddle-node bifurcation of E_1 (saddle point) and E^* (stable node), (see Fig. 1(a)). Similarly, when $S_{in} = \lambda_2$, E_0 coalesces with E_2 and when $S_{in} = \lambda_1$, E_0 coalesces with E_1.

Fig. 1(b) illustrates the steady-state characteristics for $a_2 = 0$ and the existence of the positive equilibrium E^* which is obtained by the intersection between the line Δ and the vertical line that corresponds to the curve of function $h_{12}(\cdot)$. Since E^* and E_2 have the same S component, $S = \lambda_2$, they appear at the same point of the (S, y) plane. However, these equilibria do not coincide, since they have distinct x_1 and x_2 components.

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. The absence of intra-specific inhibition for the weaker species may allow it to survive. Hence, the coexistence is due to the fact that the most efficient species sees its growth inhibited by its own intra-specific competition.

We can derive, now, the global asymptotic behavior of (3) according to S_{in}. More specifically, we have the following result:

Proposition 4. *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 exist 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 exist three equilibria: E_0 and $E_2 = (S_2, 0, \bar{x}_2)$ are unstable while E_1 is LES. Moreover, if there exists a constant $\alpha > 0$ which satisfies:*

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

then E_1 is GAS with respect to all solutions with $x_1(0) > 0$.
4. *If $S_{in} > \bar{\lambda}_2$, then there exist four equilibria: E_0, E_1 and E_2 are unstable while $E^* = (S^*, x_1^*, x_2^*)$ is LES.*

Proof. First, the global stability of the washout equilibrium follows from part 5. of Lemma 1.1 of [24]. For item 2, the global stability of E_1 derives from part 4. of Theorem 2.2 of [24]. For item 3, it derives from part 5. of Theorem 2.2 of [24]. We conclude by using Proposition 3. Item 4 is a consequence of Proposition 3. $\square$

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 specify the asymptotic stability according to the control parameter S_{in}. For that, we use the concept of steady-state characteristics, to describe geometrically the equilibria. The steady-state characteristic is a curve which is associated with 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.

4.1. **Existence of equilibria.** In the following, we study the existence of equilibria of system (1) under assumption **H1** and for all $a_i > 0$, $i = 1, \ldots, n$. 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

$$\lambda_1 < \lambda_2 < \cdots < \lambda_n.$$

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

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

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

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

and

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

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

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

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 $[\lambda_n, +\infty[$ and $h_n(\lambda_n) = 0$,

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

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 5. *System (1) admits a unique positive equilibrium $E^* = (S^*, x_1^*, \ldots, x_n^*)$ if and only if*

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

In order to identify the other equilibria corresponding to the extinction of one or many species, we first introduce the following definition:

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

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

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

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 $y = h_J(S)$, $J \subset \{1, \ldots, n\}$, (see Fig. 2, for $n = 3$). We can deduce that:

- If $S_{in} > \bar{\lambda}_n$, there exist 2^n equilibria:
    1. A washout equilibrium E_0.
    2. C_n^1 equilibria $E_1, \ldots, E_n$, where one species survives, which are given by the intersections of Δ and the curves of h_i, $i = 1, \ldots, n$.
    3. C_n^2 equilibria E_{ij}, with $i, j = 1, \ldots, n$ and $i < j$, where two species coexist and the other species are excluded. They are given by the intersections of Δ and the curves $h_{ij} = h_i + h_j$.
    4. C_n^m equilibria where m species coexist, for any $1 \leqslant m \leqslant n$.
    5. A positive equilibrium E^*, where all species coexist, which is given by the intersection of Δ and the curve $h_{12\ldots n} = \sum_{i=1}^{n} h_i$.
    The total number of equilibria is, then, $\sum_{k=0}^{n} C_n^k = 2^n$.
- If $\lambda_1 < S_{in} \leqslant \bar{\lambda}_n$, we can extend the last reasoning to see that according to the position of S_{in}, the intersections of Δ with the steady-state characteristics $y = h_J$, $J = \{1, 2, \ldots, j\}$, $j \leqslant n$ are composed of the intersections with the curve $y = 0$ (which corresponds to the washout equilibrium), the curves $y = h_i$, $i = 1, \ldots, j$, the curves $y = h_i + h_k$, $i, k = 1, \ldots, j$, $i \neq k$, ... and

the curve $y = h_1 + h_2 + \ldots + h_j$ (which corresponds to the coexistence of j species).

- If $S_{in} \leqslant \lambda_1$, the only intersection point of the characteristics with Δ is on the curve $y = 0$ and it corresponds to the washout equilibrium E_0.
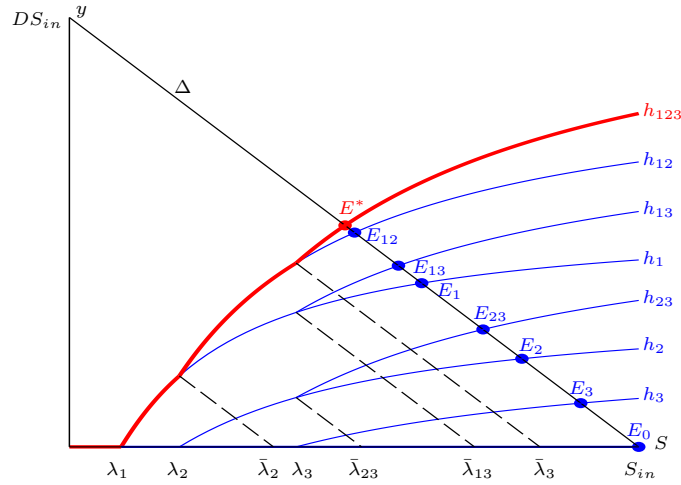

FIGURE 2. Steady-state characteristics for $n = 3$. The equilibrium E^* (in red) is the only stable equilibrium. It has the smallest S component. All other equilibria (in blue) are unstable.

In Fig. 2, we illustrate the case of three species competing for a single nutrient. It shows the number of equilibria of (1) according to S_{in}. We use the following notations

$$\bar{\lambda}_k = \lambda_k + \frac{1}{D} \sum_{i=1}^{k-1} h_i(\lambda_k), \qquad k = 1, \ldots, n \tag{10}$$

and

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

Then, we can see that

- If $S_{in} > \bar{\lambda}_3$, there exist 2^3 equilibria: A washout equilibrium E_0, a positive equilibrium E^*, which is the intersection of 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 there exist 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 there exist six equilibria: $E_0, E_1, E_2, E_3, E_{12}$ and E_{23}.
- If $\lambda_3 < S_{in} < \bar{\lambda}_{23}$, then there exist five equilibria: E_0, E_1, E_2, E_3 and E_{12}.
- If $\bar{\lambda}_2 < S_{in} < \lambda_3$, then there exist four equilibria: E_0, E_1, E_2 and E_{12}.
- If $\lambda_2 < S_{in} < \bar{\lambda}_2$, then there exist three equilibria: E_0, E_1 and E_2.
- If $\lambda_1 < S_{in} < \lambda_2$, then there exist two equilibria E_0 and E_1.
- If $S_{in} < \lambda_1$, then there exists a unique equilibrium E_0.

4.2. **Stability of equilibria.** We are interested, now, in the asymptotic behavior of (1). As explained in the previous section, the system can have at most 2^n equilibria obtained by taking the intersections of the line Δ with the steady-state characteristics. We show that in each case, only one equilibrium is stable, namely the leftmost one (with the smallest S component), corresponding to the intersection of Δ with the red steady-state characteristic $y = \sum_{i=1}^{k} h_i(S)$. All other equilibria corresponding to the intersections of Δ with the blue steady-state characteristics are unstable. In order to do this, we calculate the Jacobian matrix and we use mainly Lemma 6.3 of [4], which we recall here:

Lemma 4.2. *Consider the matrix*

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

Assume that $D > 0$ and for $i = 1, \ldots, n$, $\alpha_i \geqslant 0$, $b_i > 0$ and $c_i \leqslant b_i$. Then, all the eigenvalues of A have negative real parts.

We have the following result:

Proposition 6. *Let D and S_{in} be fixed. The equilibrium with the smallest S component is LES. All other equilibria are unstable.*

Proof. Let $E = (S, x_1, \ldots, x_n)$ an equilibrium. The Jacobian matrix at E has the form (11) with

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

From (10), we easily see that $\lambda_1 = \bar{\lambda}_1 < \bar{\lambda}_2 < \cdots < \bar{\lambda}_n$. Assume first that $S_{in} > \bar{\lambda}_n$. The leftmost equilibrium is the positive equilibrium $E^* = (S^*, x_1^*, \ldots, x_n^*)$, which satisfies $f_i(S^*) - a_i x_i^* - D_i = 0$. Therefore 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 4.2, we conclude that E^* is LES.

If we denote by $\bar{E} = (\bar{S}, x_1, \ldots, x_n)$ an equilibrium point corresponding to the intersection of Δ with the blue steady-state characteristic, we have $x_k = 0$ for at least one $k = 1, \ldots, n$. The Jacobian matrix at $\bar{E}$ has the form (11) with $\alpha_k = 0$ and has $-b_k = f_k(\bar{S}) - D_k$ as an eigenvalue. Because $S_{in} > \bar{\lambda}_n$, we have $\bar{S} > \lambda_n \geqslant \lambda_k$ and the eigenvalue $-b_k$ is positive. Thus $\bar{E}$ is unstable.

Assume now that $S_{in} < \lambda_1$. Then the washout $E_0 = (S_{in}, 0, \ldots, 0)$ is the only equilibrium. It corresponds to the intersection of Δ with the red steady-state characteristic $y = 0$. The Jacobian matrix at E_0 has the form (11) with $\alpha_k = 0$ for all $k = 1, \ldots, n$ and has $-D$ and $-b_k = f_k(S_{in}) - D_k$, $k = 1, \ldots, n$, as eigenvalues. Because $S_{in} < \lambda_1$, all eigenvalues $-b_k$ are negative. Therefore E_0 is LES.

Assume now that $\bar{\lambda}_k < S_{in} < \bar{\lambda}_{k+1}$ for some $k = 1, \ldots, n-1$. We denote by $E^k = (S^k, x_1^k, \ldots, x_n^k)$ the leftmost equilibrium, that is to say, the intersection of Δ with the steady-state characteristic $y = \sum_{i=1}^{k} h_i(S)$. Then we have $\lambda_k < S^k < \lambda_{k+1}$.

From definition ([9](#)) we see that,

$$h_{k+1}(S) = \ldots = h_n(S) = 0, \quad \text{for} \quad \lambda_k < S < \lambda_{k+1}$$

and then $x_{k+1}^k = \ldots = x_n^k = 0$. The Jacobian matrix at E^k has the form ([11](#)) with $\alpha_j = 0$ for $j = k+1, \ldots, n$. We deduce that $-b_j = f_j(S^k) - D_j$, $j = k+1, \ldots, n$ are eigenvalues of the Jacobian matrix at E^k. Because $S^k < \lambda_{k+1}$, these eigenvalues are negative. The upper-left $k \times k$ square matrix of the Jacobian matrix has also the form ([11](#)) with

$$\alpha_i = f_i'(S^k)x_i^k, \quad b_i = a_i x_i^k \quad \text{and} \quad c_i = -f_i(S^k), \quad i = 1, \ldots, k.$$

Using Lemma [4.2](#), the eigenvalues of this matrix have negative real parts. Therefore, the equilibrium E^k is LES.

If we denote by $\bar{E} = (\bar{S}, x_1, \ldots, x_n)$ an equilibrium point corresponding to the intersection of Δ with a blue steady-state characteristic, we have $x_i = 0$ for at least one $i = 1, \ldots, k$. The Jacobian matrix at $\bar{E}$ has the form ([11](#)) with $\alpha_i = 0$ and hence $-b_i = f_i(\bar{S}) - D_i$ is an eigenvalue. Because $S_{in} > \bar{\lambda}_k$, we have $\bar{S} > \lambda_k \geqslant \lambda_i$ and then, the eigenvalue $-b_i$ is positive. Thus $\bar{E}$ is unstable. $\qquad\square$

In Fig. [2](#), we stained in red the part of the characteristics which correspond to LES equilibria, and in blue the unstable equilibria. Table [2](#) summarizes the previous results where the letter S (resp. U) means stable (resp. unstable). The absence of letter means that the corresponding equilibrium does not exist.

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 2. Existence and local stability of equilibria of ([1](#)) with $n = 3$.

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

Proposition 7. *Assume that $\lambda_1 < S_{in} < \bar{\lambda}_2$ and that there exist constants $\alpha_i > 0$, for each $i \geqslant 2$ satisfying $\lambda_i < S_{in}$ such that*

$$\max_{0 < S < \lambda_1} g_i(S) \leqslant \alpha_i \leqslant \min_{\lambda_i < S < S_{in}} g_i(S) \tag{12}$$

where

$$g_i(S) = \frac{f_i(S)}{f_1(S_1)} \frac{f_1(S) - f_1(S_1)}{f_i(S) - D_i} \frac{S_{in} - S_1}{S_{in} - S}.$$

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 $V = V(S, x_1, \ldots, x_n)$ 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 $x_i > 0$, $i = 1, \ldots, n$ 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:

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

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 $i = 2, \ldots, n$. Finally, the last term of the above sum is always non-positive for every $S \in]0, S_{in}[$ and is equal to zero if and only if $x_i = 0$ for $i = 2, \ldots, n$. Then, $\dot{V} \leqslant 0$ and $V = 0$ if and only if $S = S_1$, $x_1 = \bar{x}_1$ and $x_i = 0$ for $i = 2, \ldots, n$. Hence, the result follows by applying the LaSalle extension theorem (see [21]).   □

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

We first denote $\bar{m}_i = \sup_{S \geqslant 0} f_i(S) - A_i$ 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, $i = 1, \cdots, n$, 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 function F_i can be calculated explicitly in the case of the Monod growth functions considered in Section 6. In the following, we assume, without loss of generality, that:

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

To illustrate the operating diagram, we also define the following functions:

$$\begin{aligned} F_J :]0, \quad \bar{m}_{\bar{j}}[\quad &\longrightarrow \quad]0, +\infty[\\ D \quad &\longrightarrow \quad F_{\bar{j}}(D) + \frac{1}{D} \sum_{j \in J} h_j(F_{\bar{j}}(D)), \end{aligned}$$

where J is a non-empty subset of $\{1, \ldots, n\}$, and $\bar{j} = \max\{j : j \in J\}$.

Let Γ_J be the curve of equation $S_{in} = F_J(D)$. Thus, there exist 2^{n-1} curves that separate the plane (D, S_{in}) into regions of existence and stability of the different equilibria. Since the functions F_J depend only on $a_1, \ldots, a_{n-1}$, the regions of the operating diagram are independent of a_n. Hence, the intra-specific competition of the least competitive species has no effect on the coexistence region. For a better

understanding, we illustrate the previous results in the cases $n = 2$ and 3, with the parameter values provided in Table 5.

In the case $n = 2$, the curves Γ_i, $i = 1, 2$ and Γ_{12} separate the operating plane (D, S_{in}) in four regions, as shown in Fig. 3(b-c), labeled as $\mathcal{I}_k$, $k = 0, \ldots, 3$.

Table 3 shows the existence and local stability of equilibria in the regions $\mathcal{I}_k$, $k = 0, \ldots, 3$, when the curves Γ_1 and Γ_2 do not intersect. Note that the case where the curves Γ_i intersect can be treated similarly.

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

The transition from the region $\mathcal{I}_0$ to the region $\mathcal{I}_1$ 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 an 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 an LES equilibrium E^*.
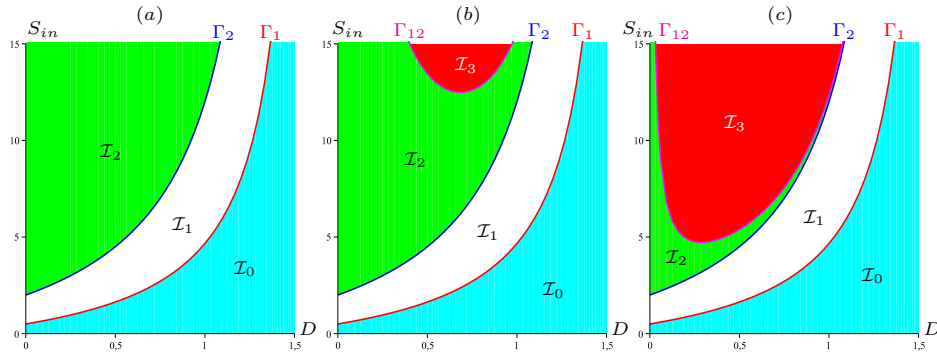

FIGURE 3. Emergence of the coexistence region $\mathcal{I}_3$ (a) $a_1 = 0$, (b) $a_1 = 0.15$ and (c) $a_1 = 1.5$.

When $a_1 = 0$, the operating diagram corresponds to the classical chemostat model (see Fig. 3(a)). Increasing a_1 leads to the emergence of the coexistence region $\mathcal{I}_3$ and to the reduction of the region $\mathcal{I}_2$ corresponding to the competitive exclusion of the second species (see Fig. 3(b-c)). Thus, the intra-specific competition of the most competitive species leads to changes in the size and emergence of coexistence regions.

Notice that the function $F_i(\cdot)$ is not defined if $\sup_{S \geqslant 0} f_i(S) \leqslant A_i$ and we let $F_i(0) = +\infty$. In this case, the regions $\mathcal{I}_1$, $\mathcal{I}_2$ and $\mathcal{I}_3$ are empty. In addition, if

$A_i > 0$, then

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

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

For $n = 3$, the seven curves Γ_i, Γ_{ij}, $i, j = 1, 2, 3$ with $i < j$ and Γ_{123} determine the regions where various equilibria exist, and indicate their stability properties. These curves separate the operating plane (D, S_{in}) in ten regions, as shown in Fig. 4(a), labeled $\mathcal{I}_k$, $k = 0, \ldots, 9$. Table 4 shows the existence and local stability of equilibria in the regions $\mathcal{I}_k$, $k = 0, \ldots, 9$, when the curves Γ_i, $i = 1, 2, 3$, do not intersect.

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 4. Existence and local stability of steady states of three species model.

The curve Γ_{12} does intersect the curves Γ_{23} and Γ_3 in D_1^* and D_2^*, respectively. According to the value of dilution rate D with respect to D_1^* and D_2^*, we obtain the three steady-state characteristics illustrated in Figs. 4(b) and 5(a-b).
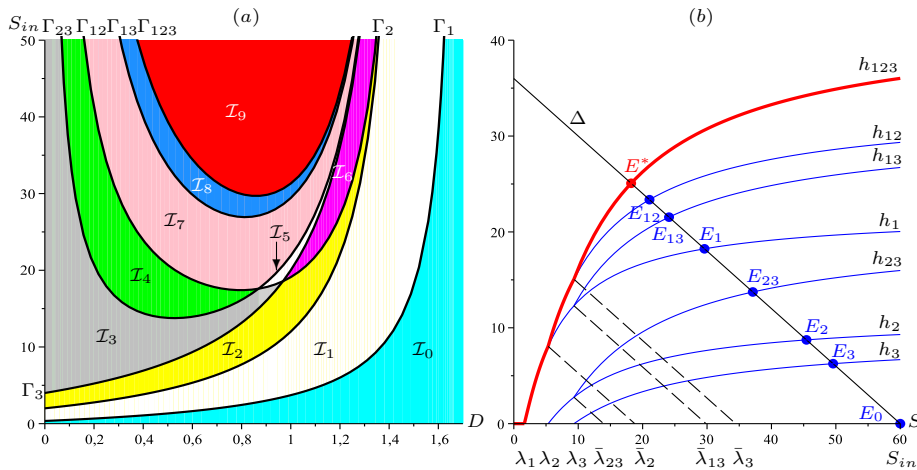

FIGURE 4. (a) Operating diagram of (1) in the case $n = 3$. (b) Steady-state characteristics for $D < D_1^*$.
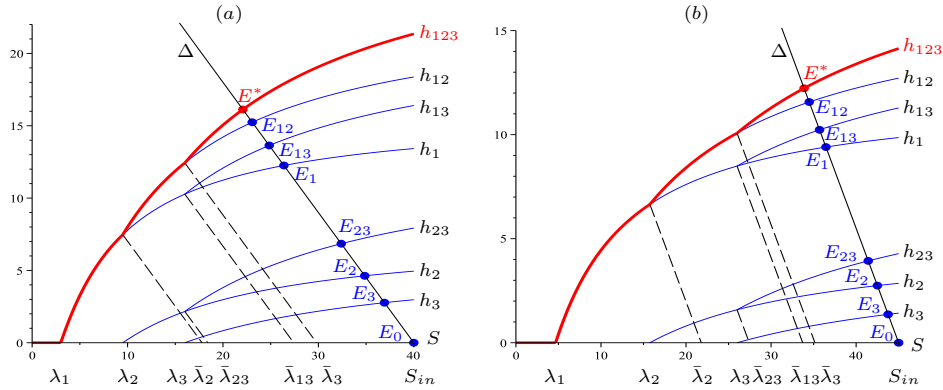
FIGURE 5. Steady-state characteristics for (a) $D_1^* < D < D_2^*$ and (b) $D_2^* < D$.

In fact, Fig. 4(b) illustrates the case $D < D_1^*$ where

$$\lambda_1 < \lambda_2 < \lambda_3 < \bar{\lambda}_{23} < \bar{\lambda}_2 < \bar{\lambda}_{13} < \bar{\lambda}_3.$$

Fig. 5(a) illustrates the case $D_1^* < D < D_2^*$ where

$$\lambda_1 < \lambda_2 < \lambda_3 < \bar{\lambda}_2 < \bar{\lambda}_{23} < \bar{\lambda}_{13} < \bar{\lambda}_3.$$

Fig. 5(b) illustrates the case $D_2^* < D$ where

$$\lambda_1 < \lambda_2 < \bar{\lambda}_2 < \lambda_3 < \bar{\lambda}_{23} < \bar{\lambda}_{13} < \bar{\lambda}_3.$$

6. **Simulations.** In the following, we illustrate the results obtained for system (1) in the case $n = 3$ and the functions $f_i(\cdot)$ are of Monod-type, defined by:

$$f_i(S) = \frac{m_i S}{K_i + S}, \quad i = 1, 2, 3, \tag{13}$$

where m_i is the maximum specific growth rate and K_i is the Michaelis-Menten (or half-saturation) constant. Straightforward calculation shows that

$$F_i(D) = \frac{K_i(D + A_i)}{m_i - D - A_i}, \quad i = 1, 2, 3.$$

For the numerical simulations, we use the parameters provided in Table 5.

Parameters	m_1	K_1	A_1	m_2	K_2	A_2	m_3	K_3	A_3
Fig. 3	2	2	0.4	2.5	3	1			
Figs. 4, 5 and 6	2	2	0.3	2.5	3	1	3	4	1.5

TABLE 5. Parameter values of model (1) with the Monod function (13) for $n = 2$ and $n = 3$.

For these parameter values, the curves $S_{in} = F_i(D)$ do not intersect and we obtain the operating diagram in Fig. 4(a). Note that

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

The steady-state characteristics are depicted in Fig. 4(b) for $D < D_1^*$,

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

where there exist 2^3 equilibria for system (1). In this case, Fig. 6(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. Fig. 6(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 $E_{12} \simeq (8.583, 7.220, 1.262, 0)$.
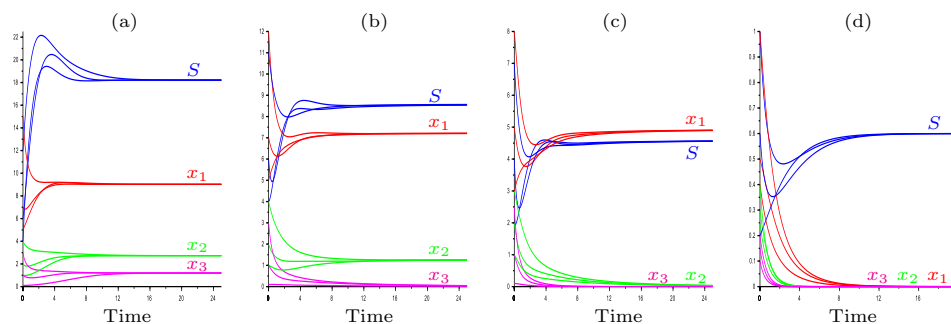
FIGURE 6. (a) Coexistence of the three species for $(D, S_{in}) \in \mathcal{I}_9$. (b) Competitive exclusion of the third species for $(D, S_{in}) \in \mathcal{I}_8$. (c) Competitive exclusion of the third and the second species for $(D, S_{in}) \in \mathcal{I}_4$. (d) Washout of all species for $(D, S_{in}) \in \mathcal{I}_0$.

Fig. 6(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. 6(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 $E_0 \simeq (0.6, 0, 0, 0)$.

7. **Conclusion.** In this paper, we considered the mathematical model describing multi-species competition for a single growth-limiting resource in a chemostat proposed by De Leenheer et al. [11]. For monotonic growth functions and different dilution rates, we proved that the outcome of competition does not always satisfy the CEP which predicts that only one species can exist in the long term. Indeed, we proved that according to the operating parameters (D the dilution rate and S_{in} the concentration of substrate in the feed bottle) several species can coexist: the system has one and only one LES equilibrium for which a certain number $p \leqslant n$ of the species are present. In the other equilibria, the present species are less than p and all these equilibria are unstable.

If the intra-specific parameters values of all species are positive, we proved the existence of a stable positive equilibrium for certain values of the operating parameters. We determined precisely the region of the operating parameters for which the coexistence of all species holds. This region is one of the regions of the operating diagram which depicts the existence and the stability of each equilibrium. We generalize the Lyapunov function proposed by Wolkowicz and Lu [24], in the

case of two species, to prove the global stability of the unique LES equilibrium, corresponding to the extinction of all species except the one with the lowest break-even concentration. This result shows that even if the species exhibits intra-specific competition, then the CEP may hold. Indeed, if $\lambda_1 < S_{in} < \bar{\lambda}_2$ then all species except the one with the lowest break-even concentration are excluded. Moreover, if $S_{in} < \lambda_1$ then as in the classical chemostat, all species are washed out. If $S_{in} > \bar{\lambda}_2$ then the coexistence of two species or more is possible.

The GAS result of the equilibrium where only one species is present, in the case where it is LES, imposes some assumptions on the growth functions, which do not necessarily hold for all monotone growth functions. We conjecture that the result is true for all monotone growth function. The problem is certainly as difficult as the similar classical one with no intra-specific competition which is still open. Another interesting and challenging open problem for further work is to find Lyapunov functions showing the global stability of the coexistence equilibrium under some assumptions on the growth functions.

In the case of two species, we showed that coexistence occurs also if the death rate parameter of the weaker (less competitive) species is non-negative (the zero value is allowed) and the death rate parameter of the stronger species is positive. The coexistence is not unexpected, since the lack of intra-specific competition for the weaker species has a beneficial effect on its ability to survive. What is much more interesting is that coexistence may be possible, even though the weaker competitor exhibits arbitrarily high levels of intra-specific competition. A surprising and unexpected result is that the operating diagram does not depend on the intra-specific competition parameter a_n of the weaker species. Obviously, the values of some equilibrium components will depend on a_n, but the conditions of existence and stability of all equilibria do not involve the parameter a_n.

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 parameter values of D and S_{in} should be chosen in the coexistence region, not in the other regions where exclusion of at least one species occurs. The operating diagram is of great importance in the applied literature since it permits to determine critical limits for the good functioning of the chemostat and the protection of the weaker competing species in the microbial ecosystems. We have showed how the intra-specific competition of the $n-1$ most efficient species introduces a coexistence region of n species, while the death rate parameter of the least competitive species has no effects on the regions of the operating diagram. When the intra-specific competition terms of the $n-1$ stronger species are zero, we find the operating diagram of the classical chemostat model. Increasing these terms reduces the regions of competitive exclusion and increases the region of coexistence. The simulations illustrate the mathematical results demonstrated in the case where the growth rates are of Monod-type.

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