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Mathematical analysis of an interspecific density-dependent model with mutual inhibition and distinct removal rates

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Abstract

This paper deals with a complete analysis of a density-dependent model in a chemostat describing the competition of two species for a single nutrient with a mutual-inhibitory relationship. In the presence of species mortality and under general growth functions, we give a quite comprehensive analysis of the existence and local stability of all steady states of the three-dimensional system. The nullcline method permits us to show that if a positive steady state exists, then it is unique and unstable. In this case, the system exhibits a bi-stability where the behavior of the process depends on the initial condition. Our mathematical analysis proves that at most one species can survive which confirms the competitive exclusion principle. Comparing with the previous study of the inter and intraspecific model, we conclude that adding only interspecific competition in the classical chemostat model is not sufficient to show the coexistence of two species even considering mortality in the dynamics of two species.

Keywords

Chemostat; Coexistence; Competitive Exclusion Principle; Mortality; Mutual-inhibitory relationship

I INTRODUCTION

The Competitive Exclusion Principle (CEP) states that, in continuous culture and under specific assumptions, when two or more microbial species compete for the same limiting nutrient, only the species with the lowest “break-even concentration” survives while all other species are extinct, see for instance [2, 14]. Although this prediction has been corroborated by the experiences of Hansen and Hubbell [1], the biodiversity that is observed in microbial ecosystems as well as in wastewater treatment processes and bioreactors seems to contradict the CEP. Thus, the classical chemostat model is unable to reproduce reality and new assumptions should be considered in order to reconcile the theory and the experimental results.

In this vein, several mechanisms of coexistence of different species competing on a single limiting substrate in the chemostat were considered in the existing literature, such as the intraspecific competition [5, 11], the flocculation [8, 12, 17], the lethal external inhibitor [3, 18, 22], the predator-prey relationship between species [15, 19, 20, 23], the obligate mutualistic relationship [16]. Additionally, the intra and interspecific interference (see for instance [4, 6, 13]) can

explain the coexistence of species in the chemostat.

In [13], a model of two species in competition for a single nutrient was considered including general intra- and interspecific density-dependent growth rates with distinct removal rates for each species. For small enough interspecific interference terms with respect to intraspecific interference, it was shown the global convergence towards the coexistence steady state for any positive initial condition. However, when the interspecific interference pressure is large enough this system exhibits a bi-stability with the competitive exclusion of one species according to the initial condition. These results were numerically established by Lobry et al. [6, 9].

In this paper, we consider the particular case where only the interspecific interferences are present to understand if the coexistence of microbial species is due only to the intraspecific interference effect. Could this coexistence occur with only interspecific competitions?

Note that in the particular case with the same removal rates, El Hajji et al. [10, 16] have shown that the competition model of two species with only interspecific interference predicts the CEP although coexistence steady state may exist but it is always unstable where the system exhibits a bi-stability. Recently, the study of Alsaifi et al. [21] provides an extension of the model in [10, 16] to the case where a virus associated with the first species is present. They predict that the CEP is still fulfilled and the coexistence of species is impossible.

In our knowledge, in the existing literature it has not yet been studied the effect of mortality on the behavior of the model proposed in [10, 15], which is the matter of the present paper. Using the nullcline method [13, 19, 20, 23], we give a quite comprehensive analysis of the model and we present a geometric characterization that describes all steady states of the model and their stability. We show that the system can have at most four types of steady states: the washout of species, two boundary steady states and a positive steady state. These steady states are studied analytically by providing their necessary and sufficient conditions of existence and local stability, and showing their uniqueness.

The rest of this paper is organized in the following way. In the next Section II, we develop our model and we present general assumptions on the growth rates. Section III is devoted to the analysis of the model which describes the existence and stability conditions of steady states. Section IV deals with numerical simulations. The final Section V contains a brief conclusion of our results. Most of the proofs are reported in Appendix A. Finally, all the parameter values used in simulations are provided in Appendix B.

II MODEL DESCRIPTION AND ASSUMPTIONS

The system we focus on consists of two microbial species (x_1 and x_2), which are competitors for a single nutrient S . Additionally, each species inhibits the growth of the other species. This system can be modeled by the following set of differential equations

$$\dot{S} = D(S_{in} - S) - f_1(S, x_2)x_1 - f_2(S, x_1)x_2, \quad (1)$$

$$\dot{x}_1 = (f_1(S, x_2) - D_1)x_1, \quad (2)$$

$$\dot{x}_2 = (f_2(S, x_1) - D_2)x_2, \quad (3)$$

where D and S_{in} are, respectively, the dilution rate and the input substrate concentration in the chemostat. At time t , let $S(t)$ denote the substrate concentration and $x_i(t)$, $i = 1, 2$, the concentrations of species x_i . For $i = 1, 2$, f_i is the density-dependent growth rate of species x_i .

It is assumed to be increasing in S and decreasing in x_j , $j \neq i$. For $i = 1, 2$, D_i is the removal rate of species x_i and can be modeled as in [17, 23] by

$$D_i = \alpha_i D + a_i, \quad (4)$$

where the coefficient α_i belongs to $[0, 1]$ and represents the fraction of species leaving the reactor to model a biomass reactor attached to the support or to decouple the residence time of solids and the hydraulic residence time ($1/D$); a_i is the nonnegative death rate of the species x_i .

We assume the following general assumptions on the given growth functions f_i , for $i = 1, 2$, $j = 1, 2$, $i \neq j$.

(H0) f_i belong to $C^1(\mathbb{R}_+, \mathbb{R}_+)$:

The functions must be sufficiently smooth so that existence, uniqueness and continuity of the solution for all nonnegative time and nonnegative initial condition are satisfied.

(H1) $f_i(0, x_j) = 0$ for all $x_j \geq 0$:

Growth rate of species x_i is take place if and only if the substrate S is present.

(H2) $\frac{\partial f_i}{\partial S}(S, x_j) > 0$ for all $S \geq 0$ and $x_j > 0$:

Growth rate of species x_i is favored by the substrate S .

(H3) $\frac{\partial f_i}{\partial x_j}(S, x_j) < 0$ for all $S > 0$ and $x_j \geq 0$:

Each species inhibits the growth of the other species, namely, by decreasing the growth of each by the other.

It is straightforward to show that all solutions of (1)-(3) are nonnegative and bounded. In fact, similar to [23], one can prove the following proposition.

Proposition 1:

Let $D_{\min} = \min(D, D_1, D_2)$ and $\Omega = \{(S, x_1, x_2) \in \mathbb{R}_+^3 : S + x_1 + x_2 \leq DS_{\text{in}}/D_{\min}\}$. Then, for any non-negative initial condition,

1. the solution of system (1)-(3) exists for all $t \geq 0$, remains nonnegative and is bounded.
2. Ω is positively invariant and is a global attractor for the dynamics (1)-(3).

III STEADY STATES: EXISTENCE AND LOCAL STABILITY

In this section, we discuss the existence and local stability conditions of all steady states of system (1)-(3). For convenience, we use the abbreviation LES for Locally Exponentially Stable steady state. In all figures, the straight line δ is defined by the equation $D_1x_1/D + D_2x_2/D = S_{\text{in}}$ and we have chosen the red color for LES steady state and the blue color for unstable steady state. In what follows, we need to define the set

$$M := \{(x_1, x_2) \in \mathbb{R}_+^2 : D_1x_1/D + D_2x_2/D \leq S_{\text{in}}\} \quad (5)$$

and the following notations:

$$E = \frac{\partial f_1}{\partial S}, \quad F = \frac{\partial f_2}{\partial S}, \quad G = -\frac{\partial f_1}{\partial x_2}, \quad H = -\frac{\partial f_2}{\partial x_1}. \quad (6)$$

We have used the opposite sign of the partial derivatives $G = -\frac{\partial f_1}{\partial x_2}$ and $H = -\frac{\partial f_2}{\partial x_1}$, such that all constants involved in the computation become positive.

3.1 Existence of steady states

First, under assumptions (H1) to (H3), we determine the steady states of (1)-(3) which are given by the solutions of the following equations with nonnegative components:

$$D(S_{in} - S) - f_1(S, x_2)x_1 - f_2(S, x_1)x_2 = 0 \quad (7)$$

$$(f_1(S, x_2) - D_1)x_1 = 0 \quad (8)$$

$$(f_2(S, x_1) - D_2)x_2 = 0. \quad (9)$$

System (1)-(3) predicts four steady states labeled as below:

- \mathcal{E}_0 ($x_1 = x_2 = 0$): the washout of two species.
- \mathcal{E}_1 ($x_1 > 0, x_2 = 0$): species x_1 survives while species x_2 is extinct.
- \mathcal{E}_2 ($x_1 = 0, x_2 > 0$): species x_1 is extinct while species x_2 survives.
- \mathcal{E}^* ($x_1 > 0, x_2 > 0$): the coexistence of two species.

If $x_1 = x_2 = 0$, from (7) one has $S = S_{in}$, then the washout $\mathcal{E}_0 = (S_{in}, 0, 0)$ always exists.

From assumption (H2), for $i = 1, 2$, the function $S \mapsto f_i(S, 0)$ is increasing, then the equation $f_i(S, 0) = \alpha_i D + a_i$ has a unique solution for all $0 < D < (f_i(+\infty, 0) - a_i)/\alpha_i$. This solution is called the *break-even concentration* and noted by

$$S = \lambda_i(D). \quad (10)$$

If $D > (f_i(+\infty, 0) - a_i)/\alpha_i$, we put $\lambda_i(D) = +\infty$. The following result gives the necessary and sufficient conditions for the existence of the boundary steady states $\mathcal{E}_1 = (\tilde{S}_1, \tilde{x}_1, 0)$ and $\mathcal{E}_2 = (\tilde{S}_2, 0, \tilde{x}_2)$ of system (1)-(3) according to the operating parameters D and S_{in} .

Proposition 2:

Assume that assumptions (H0)-(H3) hold. For $i = 1, 2, j = 1, 2, i \neq j$, let \mathcal{E}_i the boundary steady state of (1)-(3) with $x_i > 0$ and $x_j = 0$, where

$$\tilde{S}_i = \lambda_i(D) \quad \text{and} \quad \tilde{x}_i = \frac{D}{D_i}(S_{in} - \lambda_i(D)). \quad (11)$$

It exists if and only if

$$S_{in} > \lambda_i(D). \quad (12)$$

If it exists, then it is unique.

In the following, we will determine the existence condition of the coexistence steady state $\mathcal{E}^* = (S^*, x_1^*, x_2^*)$ where both populations survive, that is, $x_1 > 0$ and $x_2 > 0$. Therefore, its components must be the solutions of the set of equations

$$D(S_{in} - S) = D_1x_1 + D_2x_2, \quad (13)$$

$$f_1(S, x_2) = D_1, \quad (14)$$

$$f_2(S, x_1) = D_2. \quad (15)$$

From (13), we obtain

$$S^* = S_{in} - D_1x_1^*/D - D_2x_2^*/D. \quad (16)$$

By replacing the expression (16) in (14-15), we allow to say that $(x_1 = x_1^*, x_2 = x_2^*)$ is a solution of

$$\begin{cases} f_1(S_{\text{in}} - D_1x_1/D - D_2x_2/D, x_2) = D_1, \\ f_2(S_{\text{in}} - D_1x_1/D - D_2x_2/D, x_1) = D_2. \end{cases} \quad (17)$$

From (16), one see that S^* is positive if and only if $D_1x_1^*/D + D_2x_2^*/D < S_{\text{in}}$. Thus, (17) has a positive solution in the interior of the set M defined by (5).

Under assumptions (H0)-(H3), we need the following lemmas in order to solve (17) in the interior of M .

Lemma 1:

(1). Assume that $S_{\text{in}} > \lambda_1(D)$ and let \bar{x}_2 be the unique solution of the equation $f_1(S_{\text{in}} - D_2x_2/D, x_2) = D_1$. The equation $f_1(S_{\text{in}} - D_1x_1/D - D_2x_2/D, x_2) = D_1$ defines a decreasing function

$$\begin{aligned} F_1 &: [0, \tilde{x}_1] \longrightarrow [0, \bar{x}_2] \\ x_1 &\longmapsto F_1(x_1) = x_2, \end{aligned}$$

such that $F_1(\tilde{x}_1) = 0, F_1(0) = \bar{x}_2$ and

$$F_1'(x_1) = -\frac{D_1E}{D_2E+DG} < 0, \quad \text{for all } x_1 \in [0, \tilde{x}_1]. \quad (18)$$

Furthermore, the graph γ_1 of F_1 lies in the interior of M for all $x_1 \in (0, \tilde{x}_1)$ (see Figure 3 (a)).

(2). Assume that $S_{\text{in}} > \lambda_2(D)$ and let \bar{x}_1 be the unique solution of the equation $f_2(S_{\text{in}} - D_1x_1/D, x_1) = D_2$. The equation $f_2(S_{\text{in}} - D_1x_1/D - D_2x_2/D, x_1) = D_2$ defines a decreasing function

$$\begin{aligned} F_2 &: [0, \bar{x}_1] \longrightarrow [0, \tilde{x}_2] \\ x_1 &\longmapsto F_2(x_1) = x_2, \end{aligned}$$

such that $F_2(\bar{x}_1) = 0, F_2(0) = \tilde{x}_2$ and

$$F_2'(x_1) = -\frac{D_1F+DH}{D_2F} < 0, \quad \text{for all } x_1 \in [0, \bar{x}_1]. \quad (19)$$

In addition, the graph γ_2 of F_2 lies in the interior of M for all $x_1 \in (0, \bar{x}_1)$ (see Figure 3 (b)).

Using the derivatives (18) and (19) of functions F_1 and F_2 , respectively, we can state the following result.

Lemma 2:

If a positive intersection point (x_1, x_2) of γ_1 and γ_2 exists, then the tangent of γ_1 at point (x_1, x_2) is always above the tangent of γ_2 at point (x_1, x_2) . In addition,

$$F_1'(x_1) - F_2'(x_1) = \frac{D(DGH+D_1FG+D_2EH)}{D_2F(D_2E+DG)} > 0.$$

Recall that, for $i = 1, 2, j = 1, 2, i \neq j, \tilde{x}_i$ and \bar{x}_i are respectively the solutions of

$$f_i(S_{\text{in}} - D_ix_i/D, 0) = D_i \quad \text{and} \quad f_j(S_{\text{in}} - D_ix_i/D, x_i) = D_j.$$

These quantities represent the coordinates of the intersections of the curves γ_1 and γ_2 with the coordinates axes. The relative positions of \tilde{x}_i and $\bar{x}_i, i = 1, 2$, play a major role in the behavior

of the system. Thus, from Lemma 2, there exists three cases that must be distinguished (see Figure 1):

$$\begin{aligned}
\text{Case 1 : } & \bar{x}_1 < \tilde{x}_1 \quad \text{and} \quad \tilde{x}_2 < \bar{x}_2. \\
\text{Case 2 : } & \bar{x}_1 < \tilde{x}_1 \quad \text{and} \quad \bar{x}_2 < \tilde{x}_2. \\
\text{Case 3 : } & \tilde{x}_1 < \bar{x}_1 \quad \text{and} \quad \bar{x}_2 < \tilde{x}_2.
\end{aligned} \tag{20}$$

All these previous results lead us to the following proposition which gives the necessary and sufficient condition for the existence and uniqueness of positive steady state \mathcal{E}^* .

Proposition 3:

Assume that assumptions (H0)-(H3) and condition (12) hold for $i = 1, 2$. A positive steady state \mathcal{E}^* exists if and only if the curves γ_1 and γ_2 have a positive intersection in the interior of M . More precisely, $(x_1 = x_1^*, x_2 = x_2^*)$ is a positive solution of equation

$$x_2 = F_1(x_1) \quad \text{and} \quad x_2 = F_2(x_1). \tag{21}$$

and S^* is given by (16). Furthermore, \mathcal{E}^* exists if and only if Case 2 of (20) holds. If it exists, then it is unique.

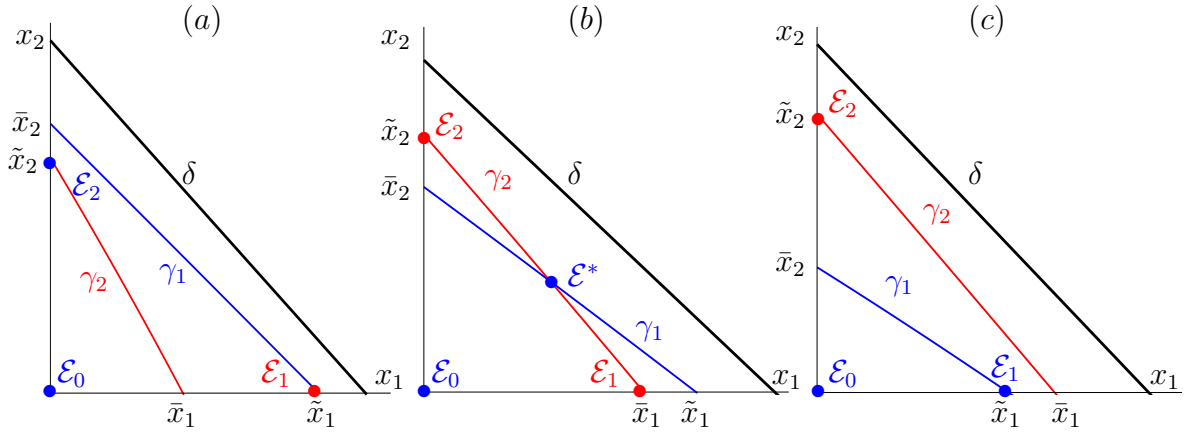


Figure 1: Cases of (20): (a) Case 1, (b) Case 2, (c) Case 3.

3.2 Local stability

In the following, we will investigate the local stability of all steady states of system (1)–(3). Let computing the Jacobian matrix of (1)–(3) at (S, x_1, x_2) which takes the form

$$J = \begin{pmatrix} -D - x_1E - x_2F & -f_1(S, x_2) + x_2H & x_1G - f_2(S, x_1) \\ x_1E & f_1(S, x_2) - D_1 & -x_1G \\ x_2F & -x_2H & f_2(S, x_1) - D_2 \end{pmatrix}$$

where E, F, G and H are given by (6). The following proposition determines the local stability conditions of the boundary steady states.

Proposition 4:

- (1). \mathcal{E}_0 is LES if and only if $S_{\text{in}} < \lambda_i(D)$, for $i = 1, 2$.
- (2). For $i = 1, 2$, \mathcal{E}_i is LES if and only if $\bar{x}_i < \tilde{x}_i$.

Now if a positive steady state \mathcal{E}^* exists, we analytically characterize their stability by using the Routh–Hurwitz stability criterion. For \mathcal{E}^* , the characteristic polynomial is

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

where the coefficients $c_i, i = 1, 2, 3$ are given in Table 1.

Table 1: Routh–Hurwitz coefficients for \mathcal{E}^* where E, F, G and H are given by (6) and evaluated at \mathcal{E}^* .

$$\begin{aligned} c_1 &= D + Ex_1^* + Fx_2^* \\ c_2 &= D_1Ex_1^* + D_2Fx_2^* - (GH + FG + EH)x_1^*x_2^* \\ c_3 &= -(DGH + D_1FG + D_2EH)x_1^*x_2^* \\ \hline c_4 &= c_1c_2 - c_3 \end{aligned}$$

From Table 1, one can see that the coefficient c_3 is always negative. According to the Routh–Hurwitz criterion, \mathcal{E}^* is unstable. Thus, we can state the following result.

Proposition 5:

If a positive steady state \mathcal{E}^* exists, then it is always unstable.

The necessary and sufficient conditions of existence and local stability of all steady states of (1)–(3) are summarized in the following Table 2.

Table 2: Existence and stability conditions of steady states of (1)–(3).

	Existence	Local stability
\mathcal{E}_0	Always exists	$S_{\text{in}} < \lambda_i(D), i = 1, 2$
\mathcal{E}_1	$S_{\text{in}} > \lambda_1(D)$	$\bar{x}_1 < \tilde{x}_1$
\mathcal{E}_2	$S_{\text{in}} > \lambda_2(D)$	$\bar{x}_2 < \tilde{x}_2$
\mathcal{E}^*	Case 2 of (20) holds	unstable whenever it exists

From Table 2, we can deduce the following result.

Proposition 6:

- \mathcal{E}_0 is LES if and only if \mathcal{E}_1 and \mathcal{E}_2 do not exist.
- A positive steady state \mathcal{E}^* exists if and only if \mathcal{E}_1 and \mathcal{E}_2 are LES.

IV NUMERICAL SIMULATIONS

This section is dedicated to present some numerical simulations which illustrate our findings. To this end, we use the following growth rates satisfying assumptions (H0)–(H3):

$$f_1(S, x_2) = \frac{m_1S}{K_1+S} \frac{1}{1+x_2/L_1}, \quad f_2(S, x_1) = \frac{m_2S}{K_2+S} \frac{1}{1+x_1/L_2}, \quad (22)$$

where m_1, m_2 denote the maximum growth rates; K_1 and K_2 denote the Michaelis-Menten constants; L_1 (respectively L_2) represents the inhibition factor due to x_2 (respectively x_1) for the growth of the species x_1 (respectively the species x_2). The parameter values used for numerical simulations are provided in Table 3.

Figure 2 illustrates the trajectories over time in three-dimensional space (S, x_1, x_2) for several positive initial conditions in the three cases of (20). In Case 1 of (20), Figure 2 (a) shows

the convergence towards the steady state $\mathcal{E}_1 \simeq (0.14835, 0.94627, 0)$ for any initial positive condition in the interior of M . In Case 3 of (20) (see Figure 1 (c)), the solutions of model (1)-(3) converges toward the extinction of the first species $\mathcal{E}_2 \simeq (0.2, 0, 0.8)$ for several positive initial conditions as shown in Figure 2 (c).

In the Case 2 of (20) (see Figure 1 (b)), from Table 2 and Proposition 6, system (1)–(3) exhibits a bi-stability where at most one species wins the competition according to the initial condition. In Figure 2 (b), we show the bi-stability with two basins of attraction, with either convergence to $\mathcal{E}_1 \simeq (0.22413, 0.59681, 0)$ or $\mathcal{E}_2 \simeq (0.22448, 0, 0.705)$. These two basins are separated by the stable manifold of saddle point \mathcal{E}^* .

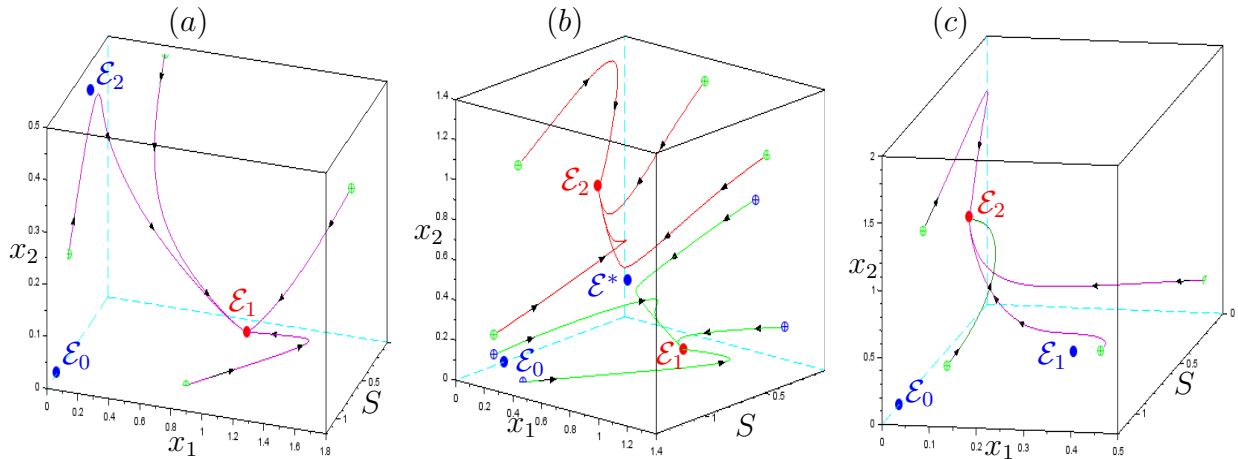


Figure 2: The trajectories of system (1)-(3) in three-dimensional space (S, x_1, x_2) : (a) Convergence to \mathcal{E}_1 , (b) bi-stability of \mathcal{E}_1 and \mathcal{E}_2 , (c) convergence to \mathcal{E}_2 .

V CONCLUSION

In this work, we have considered the mathematical model describing the competition of two species for a single growth-limiting resource in a chemostat with a reversible inhibition relationship between species and different removal rates. For general interspecific density-dependent growth functions and different dilution rates, our mathematical analysis proves that the outcome of competition satisfies the CEP which predicts that only one species can exist. More precisely, using the nullcline method [13, 20, 23], we present a geometric characterization describing all steady states of the model and their stability. We prove that the positive steady state is unique and unstable, if it exists. In addition, the positive steady state exists if and only if both boundary steady states are LES. Therefore, the model exhibits a bi-stability where the outcome of competition depends on the initial condition.

In the existing literature [13], it was proved that the simultaneous presence of the inter- and intraspecific interference can explain the coexistence of species. Furthermore, for small enough interspecific interference terms, there is a stable persistence of two species that can coexist for any positive initial condition. However, if these terms are large enough, the system exhibits bi-stability with the competitive exclusion of one species according to the initial condition. These results are numerically shown in the paper of Lobry et al. [6, 9]. Considering only intraspecific interference, the coexistence between several species was shown in [7].

In the absence of mortality of species, that is, with the same removal rates, it was proved in [10, 15] that the system predicts the CEP. Thus, even adding the species mortality terms in the

interspecific density-dependent model of two species with a mutual inhibitory relationship, the CEP is still fulfilled. Hence, the intraspecific interference is necessary to ensure the coexistence of species in the competition models. Moreover, it has a significant impact to explain the coexistence around a stable positive steady state.

Our study is the first attempt to highlight the effect of species mortality on the behavior of a two-species interspecific density-dependent model in the chemostat. Our theoretical message explains that the addition of mortality with only interspecific interference could not lead to the coexistence around a stable positive steady state.

To make our theoretical results useful in practice, it would be interesting to analyze in future work the operating diagram of this model in order to describe the behavior of the system according to the control parameters D and S_{in} .

VI ACKNOWLEDGEMENTS

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A PROOFS

Proof of Proposition 2: For $i = 1, 2, j = 1, 2, i \neq j$, a boundary steady state \mathcal{E}_i is a solution of (7)–(9) with $\tilde{x}_i > 0$ and $x_j = 0$. That is, the components \tilde{S}_i and \tilde{x}_i are the solutions of equations

$$D(S_{\text{in}} - \tilde{S}_i) = D_i \tilde{x}_i \quad (23)$$

$$f_i(\tilde{S}_i, 0) = D_i. \quad (24)$$

Using definition (10) of λ_i , from (24) we have $\tilde{S}_i = \lambda_i(D)$. Thus, by replacing the expression of \tilde{S}_i in (23), we obtain $\tilde{x}_i = \frac{D}{D_i}(S_{\text{in}} - \lambda_i(D))$ which is positive if and only if (12) holds. This completes the proof. \square

Proof of Lemma 1: We will prove item 1 of Proposition and item 2 will be obtained in the same fashion. Let l_1 be a fixed line defined by $x_1 = b_1$ that intersects the line δ at point $x_2 = c_2 = DS_{\text{in}}/D_2 - D_1b_1/D_2$ (see Fig. 3 (a)). From assumptions (H1)–(H2), we see that the function $x_2 \mapsto f_1(S_{\text{in}} - D_1b_1/D - D_2x_2/D, x_2)$ is decreasing from $f_1(S_{\text{in}} - D_1b_1/D, 0)$ for $x_2 = 0$ to 0 for $x_2 = c_2$. Therefore, there exists a unique $b_2 \in [0, c_2)$ such that $f_1(S_{\text{in}} - D_1b_1/D - D_2b_2/D, b_2) = D_1$ if and only if

$$f_1(S_{\text{in}} - D_1b_1/D, 0) \geq D_1,$$

which is equivalent to $b_1 \leq \tilde{x}_1$. Indeed, for $i = 1$ from (23), one has $S = S_{\text{in}} - D_1x_1/D$. By replacing this expression in (24), one can see that \tilde{x}_1 is the unique solution of $f_1(S_{\text{in}} - D_1x_1/D, 0) = D_1$ since the function $x_1 \mapsto f_1(S_{\text{in}} - D_1x_1/D, 0)$ is decreasing from $f_1(S_{\text{in}}, 0)$ for $x_1 = 0$ to 0 for $x_1 = DS_{\text{in}}/D_1$.

Therefore, we have shown that for all $b_1 \in [0, \tilde{x}_1]$ there exists a unique $b_2 \in [0, c_2)$ such that $f_1(S_{\text{in}} - D_1b_1/D - D_2b_2/D, b_2) = D_1$, that is, each line l_1 meets the set $f_1(S_{\text{in}} - D_1x_1/D - D_2x_2/D, x_2) = D_1$ exactly once if $0 \leq b_1 \leq \tilde{x}_1$ and not at all if $b_1 > \tilde{x}_1$. Thus, we define the function F_1 by $b_2 = F_1(b_1)$. The graph γ_1 of this function lies in M (see Fig. 3 (a)).

By the implicit function theorem, the function F_1 is decreasing. Indeed, using assumptions (H2) and (H3) and notations (6), it follows that

$$F_1'(x_1) = -\frac{\frac{\partial f_1}{\partial x_1}(x_1, F_1(x_1))}{\frac{\partial f_1}{\partial x_2}(x_1, F_1(x_1))} = \frac{\frac{D_1}{D} \frac{\partial f_1}{\partial S}}{-\frac{D_2}{D} \frac{\partial f_1}{\partial S} + \frac{\partial f_1}{\partial x_2}} = \frac{-D_1E}{D_2E + DG} < 0$$

Furthermore, if $x_2 = 0$ then $F_1(x_1) = 0$ which equivalent to solve the equation $f_1(S_{\text{in}} - D_1x_1/D, 0) = D_1$, that is, $x_1 = \tilde{x}_1$ the unique solution as it was shown above. Moreover, if $x_1 = 0$, then

$$F_1(0) = x_2 \Leftrightarrow f_1(S_{\text{in}} - D_2x_2/D, x_2) = D_1.$$

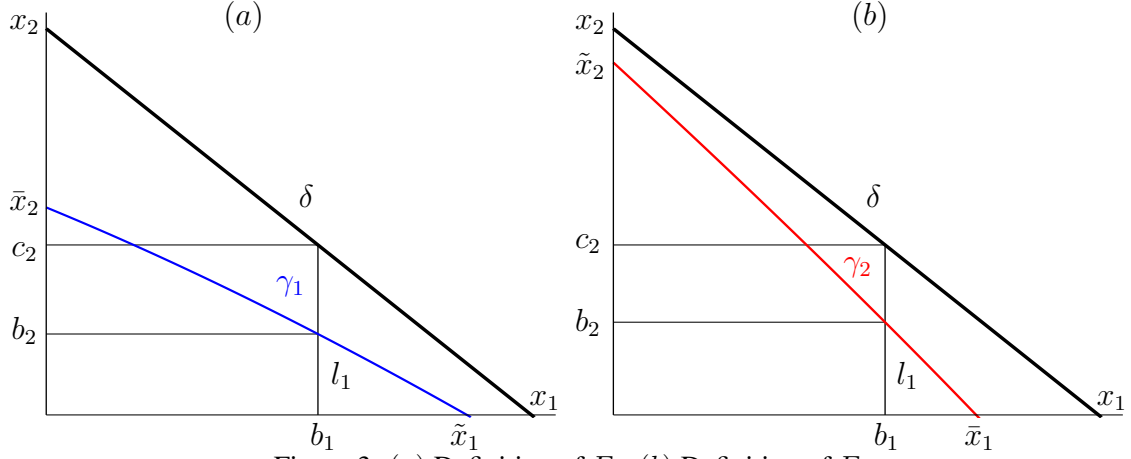


Figure 3: (a) Definition of F_1 . (b) Definition of F_2 .

From (H3), we see that the function $x_2 \mapsto f_1(S_{\text{in}} - D_2 x_2/D, x_2)$ is decreasing from $f_1(S_{\text{in}}, 0)$ for $x_2 = 0$ to 0 for $x_2 = DS_{\text{in}}/D_2$. Consequently, the equation $f_1(S_{\text{in}} - D_2 x_2/D, x_2) = D_1$ has a solution $\bar{x}_2 \in (0, S_{\text{in}})$ if and only if $f_1(S_{\text{in}}, 0) > D_1$, that is, condition (12) hold for $i = 1$. If such an \bar{x}_2 exists then it is unique. \square

Proof of Proposition 3:

By (17) and Lemma 1, a positive steady state exists if and only if the curves γ_1 and γ_2 have a positive intersection (x_1^*, x_2^*) . If the intersection exists, then it lies in the interior of M . Consequently, the component S^* which defined by (16), is positive.

The necessary and sufficient condition of the intersection given by Case 2 of 20, and the uniqueness of the positive steady state are illustrated in Figure 1 (b). \square

Proof of Proposition 4: (1). At $\mathcal{E}_0 = (S_{\text{in}}, 0, 0)$, the characteristic polynomial is

$$P(\lambda) = (-D - \lambda)(f_1(S_{\text{in}}, 0) - D_1 - \lambda)(f_2(S_{\text{in}}, 0) - D_2 - \lambda)$$

Therefore, \mathcal{E}_0 is LES if and only if $f_i(S_{\text{in}}, 0) < D_i$, for $i = 1, 2$, that is, $S_{\text{in}} < \lambda_i(D)$. Using Proposition 2, we deduce that these conditions hold if and only if the boundary steady states \mathcal{E}_i , $i = 1, 2$ do not exist.

(2). At $\mathcal{E}_1 = (\lambda_1(D), \tilde{x}_1, 0)$, the characteristic polynomial is

$$P(\lambda) = (f_2(S_{\text{in}} - D_1 \tilde{x}_1/D, \tilde{x}_1) - D_2 - \lambda)(\lambda^2 + \beta_1 \lambda + \beta_2)$$

where $\beta_1 = D + \tilde{x}_1 E$ and $\beta_2 = D_1 \tilde{x}_1 E$. Since $\beta_1 > 0$ and $\beta_2 > 0$, the real parts of the roots of the quadratic factor are negative. Therefore, \mathcal{E}_1 is LES if and only if $f_2(S_{\text{in}} - D_1 \tilde{x}_1/D, \tilde{x}_1) < D_2$, that is, $\bar{x}_1 < \tilde{x}_1$.

Similarly, at $\mathcal{E}_2 = (\lambda_2(D), 0, \tilde{x}_2)$, the characteristic polynomial is

$$P(\lambda) = (f_1(S_{\text{in}} - D_2 \tilde{x}_2/D, \tilde{x}_2) - D_1 - \lambda)(\lambda^2 + \delta_1 \lambda + \delta_2)$$

where $\delta_1 = D + \tilde{x}_2 F$ and $\delta_2 = D_2 \tilde{x}_2 F$. Since $\delta_1 > 0$ and $\delta_2 > 0$, the real parts of the roots of the quadratic factor are negative. Therefore, \mathcal{E}_2 is LES if and only if $f_1(S_{\text{in}} - D_2 \tilde{x}_2/D, \tilde{x}_2) < D_1$, that is, $\bar{x}_2 < \tilde{x}_2$. \square

B PARAMETER VALUES USED FOR NUMERICAL SIMULATIONS

All the values of the parameters used in the numerical simulations are provided in Table 3.

Table 3: Parameter values used for model (1)-(3) when the growth rates f_1 and f_2 are given by (22).

Parameter	m_1	K_1	L_1	m_2	K_2	L_2	D	S_{in}	α_1	α_2	a_1	a_2
Fig. 3								3	0.5	0.25	0.8	0.5
Figs. 1(a) and 2(a)								1	0.1	0.5	0.4	0.5
Figs. 1(b) and 2(b)	5	1.5	1	3	1	1	0.5	1	0.1	0.7	0.6	0.2
Figs. 1(c) and 2(c)								1	0.6	0.1	0.8	0.45

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