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# Mathematical analysis of a competition model with mutualism

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## Abstract

In this work, we perform the analysis of a mathematical model describing the interaction of two species in a chemostat. This model involves competition (for the main source of carbon) and mutualism (due to cross-feeding), simultaneously. The model is a five-dimensional system of differential equations and involve nonlinear growth functions. In a previous study, this system has been studied only numerically, using growth functions of Monod type. Here, we describe in detail the dynamics of the system by determining analytically the existence and the local stability conditions of all steady-states, considering a large class of growth functions. We prove that there exists a unique stable coexistence steady state and we give the conditions under which bistability can occur. All conditions are given, with respect to the four operating parameters of the system, which are the dilution rate and the three substrate input concentrations. We give bifurcation diagrams and numerical simulations showing the rich behavior of the system.

**Keywords:** Chemostat, competition, mutualism, local stability, bistability, bifurcation diagrams.

## 1 Introduction

The chemostat is a laboratory apparatus invented simultaneously, by J. Monod and by A. Noviek, and L. Sziland in the 1950s, in which organisms grow in a controlled way, [21, 22]. This apparatus consists of an enclosure, containing the reaction volume, connected by input to feed the system with resources, and outlet through which microorganisms are removed. The chemostat model describes several ecological interactions (commensalism, syntrophy, competition, mutualism,...) and can capture complex relationships, such as the combination of mutualism and competition, [25, 12, 27]. Mutualism is a cooperative relationship between two or more species of organisms so that all parties benefit from this relationship. Mutualism can be described as reciprocal benefits interaction. Compared to competition and prey-predator relationship, this interaction had not received much attention from researchers until recent decades, where it had occupied an important area of attention and interest, [2], [20] and the references therein. The existence of a similar type of relationship between species is an important factor for biodiversity and deserves great interest, as it prevents the competitive exclusion. When several species are in

36 competition on a single nutrient, the competitive exclusion principle predicts that only one of  
 37 them can survive, [25]. The Lotka-Volterra equations are often used to describe population  
 38 dynamics. However, they fail to describe the dynamics when diverse interactions are involved.  
 39 Several authors have proposed different models of mutualism, [26, 11]. These models are a little  
 40 complicated, which made them difficult to study. Discrete models are common in the study of  
 41 population dynamics. For instance, in [3], a discrete model of mutualism was studied with the  
 42 aim of investigating the persistent property of the system. S. Vent et al. in [28], have studied a  
 43 model of two mutualistic species via cross-feeding in a chemostat. This model was reduced from  
 44 a six-dimensional system to a two-dimensional one. The obtained phase plane and the nullclines,  
 45 describing the dynamics of the species, are observed in different mutualistic models, [28] and  
 46 the references therein. The authors showed numerically that when the dilution is switched on,  
 47 the weak Allee effect turns into a strong Allee effect, which corresponds to bistability in the  
 48 system. In [30], one form of intraguild mutualism model with one resource and two consumers  
 49 is described. The authors prove numerically that the system exhibits a rich behavior. They  
 50 show that intraguild mutualism can enhance coexistence of consumers, induce cyclic dynamics,  
 51 give rise to a bistability or the washout of both consumer species. In [7], the authors consider  
 52 a three-dimensional chemostat model involving two obligate mutualistic species in competition  
 53 on a single resource. They performed the analytical analysis of the system and, considering  
 54 general growth functions, they showed the existence and the stability of coexistence steady states.  
 55 The unicity occurs in the case when the growth functions are of Monod type. Bistability has  
 56 been observed numerically in [27]. The model describes the dynamics of two species interacting  
 57 through mutualism as well as competition.

58 Competition is an interaction between two or more species in which all organisms are harmed.  
 59 There are two types of competition, intraspecific competition (between individuals of the same  
 60 species) and interspecific competition (between two or more different species). When competition  
 61 is exclusive in the system, the only case that the species can coexist at steady-state is when the  
 62 number of different nutrients they compete for is bigger than the number of these competing  
 63 species, [23]. The following equations describe the competition of  $n$  species on a single resource  
 64 (see [25]).

$$65 \quad \begin{cases} \dot{S} = D(S_{in} - S) - \sum_{i=1}^n \frac{\mu_i(S)}{y_i} x_i \\ \dot{x}_i = [\mu_i(S) - D_i] x_i, \quad i = 1, \dots, n \end{cases} \quad (1)$$

66 For  $i = 1, \dots, n$ ,  $x_i$  represents the concentration of species  $i$ .  $S$  is the concentration of the nutrient.  
 67 The parameters  $D_i$  are the sum of the dilution rate  $D$  and the death rates of species  $i$  (the death  
 68 rates are often neglected).  $S_{in}$  is the concentration of the substrate  $S$  in the feed.  $y_i$ ,  $i = 1, \dots, n$   
 69 are the yield coefficients.  $\mu_i(\cdot)$  is the growth rate of species  $i$ . When the growth rates depend  
 70 also on the species concentration  $x_i$ ,  $i = 1, \dots, n$ , we obtain a more general model, see for example  
 71 [12].

$$72 \quad \begin{cases} \dot{S} = D(S_{in} - S) - \sum_{i=1}^n \frac{\mu_i(S, x_1, \dots, x_n)}{y_i} x_i \\ \dot{x}_i = [\mu_i(S, x_1, \dots, x_n) - D_i] x_i, \quad i = 1, \dots, n \end{cases} \quad (2)$$

73 Table 1 and 2 summarize the modeling assumptions of the competition models (1) and (2)  
 74 studied in the literature, according to the number of competing species  $i$ ,  $S_{in}$ ,  $D_i$ , and the growth  
 75 rates  $\mu_i$ .

76

References	$i$	$S_{in}$	$D_i$	$\mu_i(S)$
Hsu, Hubbell and Waltman [15]	$1, \dots, n$	$> 0$	$D$	Monod
Hsu [14]	$1, \dots, n$	$> 0$	distinct	Monod
Wolkowicz and Lu [29]	$1, \dots, n$	$> 0$	$D + \varepsilon_i$	Linear, Monod, Nonmonotonic (inhibition)
Smith and Waltman [25]	2 $1, \dots, n$	$> 0$ 1	$D$ 1	Monod Increasing
Li [16]	$1, \dots, n$	$> 0$	distinct	Monotonic, Nonmonotonic
De Leenheer, Angeli and Sontag [6]	$1, \dots, n$	1	distinct	Increasing
Abdellatif, Fekih-Salem and Sari [1]	2 $1, \dots, n$	$> 0$ $> 0$	distinct distinct	Increasing Increasing

Table 1: Literature examples of competition relationship on one substrate model(1)

References	$i$	$S_{in}$	$D_i$	$\mu_i(S, x_1, \dots, x_n)$
Lobry, Mazenc and Rapaport [18]	$1, \dots, n$	$> 0$	$D$	depends only on $S$ and $x_i$ increasing in $S$ , decreasing in $x_i$
Lobry, Rapaport and Mazenc [19]	$1, \dots, n$	$> 0$	distinct	depends only on $S$ and $x_i$ increasing in $S$ , decreasing in $x_i$
Lobry and Mazenc [17]	$1, \dots, n$	$> 0$	distinct	depends only on $S$ and $x_i$ $f(S)g(x_i)$
Harmand, Rapaport, Dochain and Lobry [13]	$1, \dots, n$	$> 0$	$D$	depends only on $S$ and $x_i$ increasing in $S$ , decreasing in $x_i$
Fekih Salem, Harmand, Lobry, Rapaport and Sari [8]	$1, \dots, n$	$> 0$	$d_i(x_i)$	depends only on $S$ and $x_i$ increasing in $S$ , decreasing in $x_i$
Fekih Salem and Sari [10]	2	$> 0$	$D$	depends on both species increasing in $S$ , decreasing in $x_i$
Fekih Salem, Lobry and Sari [9]	2	$> 0$	$D_1 \neq D_2$	increasing in $S$ , decreasing in $x_1$ and $x_2$

Table 2: Literature examples of competition relationship model with density-dependant growth function (2)

77 In this paper, we are interested in studying the case of simultaneous mutualist and compet-  
78 itive relationship between two species, so that each of them gives the other a nutrient for its  
79 growth (cross-feeding) and at the same time they are competing for the main source of carbon,  
80 Fig.1. This phenomenon can be modeled by a chemostat system, with five variables. Two of  
81 them represent the species, and the others represent the substrates. The resulting system has  
82 been studied numerically in [27]. The authors carried out numerical simulations using random  
83 parameter values and Monod growth functions. They prove, by varying the values of the max-  
84 imal growth rates, that there could be two cases of bistability, bistability between extinction of  
85 both species and coexistence, and bistability between survival of the first species (without the  
86 second) and coexistence. For more information about the origin of the bistability, they reduced  
87 this complex system (due to the number of its equations and the nonlinearity of their growth

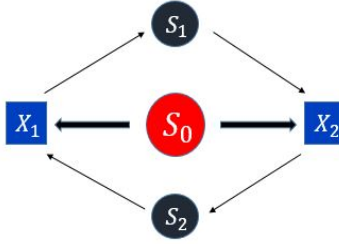


Figure 1: Interactions between the two species.  $X_1$  and  $X_2$  represent the microbial species, competing on the nutrient  $S_0$ .  $X_1$  (resp.  $X_2$ ) consumes the nutrient  $S_2$  (resp.  $S_1$ ) and produces  $S_1$  (resp.  $S_2$ ).

88 functions) into a set of two extended Lotka-Volterra equations. As the reduced model is a two-  
 89 dimensional system, they can illustrate its dynamics in the phase plane. Although it is observed,  
 90 by varying the growth rates, that both models have similar behavior, varying two of the oper-  
 91 ating parameters reveals a disparity between the stability regions of the chemostat model and  
 92 the extended Lotka-Volterra one. This disagreement can be explained by the elimination of high  
 93 order terms while reducing the model.

94 In this paper, we propose to give a comprehensive and analytical analysis of system (3) of [27].  
 95 We allow a large class of kinetics and we determine the existence and the local stability conditions  
 96 of the steady states, in this general case. In order to simplify the mathematical analysis, some  
 97 change of variables must be done in order to reduce the number of production (consumption)  
 98 constants. Three cases must be distinguished.

99 This paper is organized as follows. In Section 2, we provide a description of the model by  
 100 defining all variables and parameters and making some changes of variables. We present the  
 101 model assumptions and notations in Section 3. In Section 4, we determine the steady-states  
 102 of the model and their existence conditions according to the operating (or control) parameters.  
 103 We study the local stability of the steady-states in Section 5. In Section 6, we present some  
 104 bifurcation diagrams with respect to the limiting nutrient  $S_0$  and time simulations to illustrate  
 105 the different behaviors of the system.

## 2 The model

The model developed in [27] has five components: two biomasses and three substrates. This model is written as follows:

$$\begin{cases} \frac{dX_1}{dt} = (f_1(S_0, S_2) - D)X_1 \\ \frac{dX_2}{dt} = (f_2(S_0, S_1) - D)X_2 \\ \frac{dS_0}{dt} = D(S_0^{in} - S_0) - v_{01}f_1(S_0, S_2)X_1 - v_{02}f_2(S_0, S_1)X_2 \\ \frac{dS_1}{dt} = D(S_1^{in} - S_1) + v_{11}f_1(S_0, S_2)X_1 - v_{12}f_2(S_0, S_1)X_2 \\ \frac{dS_2}{dt} = D(S_2^{in} - S_2) - v_{21}f_1(S_0, S_2)X_1 + v_{22}f_2(S_0, S_1)X_2 \end{cases} \quad (3)$$

where for  $i = 1, 2$ ,  $X_i$  represents the bacterial population concentration,  $S_i$  represents the nutrient concentration,  $S_i^{in}$  is the inflow nutrient concentration,  $f_i$  is the growth rate of the bacteria.  $D$  is the dilution rate and  $v_{ij}$ ,  $i = 0, 1, 2$ ,  $j = 1, 2$  are the yield coefficients. These constants are preceded by a positive sign for production and by a negative one for consumption of nutrients. To facilitate the mathematical analysis and reduce the number of constants, we can rescale system and use the following change of biomass variables:

$$x_1 = v_{01}X_1, \quad x_2 = v_{02}X_2.$$

With this change of variables, we obtain the next system:

$$\begin{cases} \frac{dx_1}{dt} = (f_1(S_0, S_2) - D)x_1 & (4) \\ \frac{dx_2}{dt} = (f_2(S_0, S_1) - D)x_2 & (5) \\ \frac{dS_0}{dt} = D(S_0^{in} - S_0) - f_1(S_0, S_2)x_1 - f_2(S_0, S_1)x_2 & (6) \\ \frac{dS_1}{dt} = D(S_1^{in} - S_1) + \frac{v_{11}}{v_{01}}f_1(S_0, S_2)x_1 - \frac{v_{12}}{v_{02}}f_2(S_0, S_1)x_2 & (7) \\ \frac{dS_2}{dt} = D(S_2^{in} - S_2) - \frac{v_{21}}{v_{01}}f_1(S_0, S_2)x_1 + \frac{v_{22}}{v_{02}}f_2(S_0, S_1)x_2 & (8) \end{cases}$$

Then, we multiply equation (7) by  $\frac{v_{02}}{v_{12}}$  and equation (8) by  $\frac{v_{01}}{v_{21}}$ , and we use the change of substrate variables:

$$s_0 = S_0, \quad s_1 = \frac{v_{02}}{v_{12}}S_1, \quad s_2 = \frac{v_{01}}{v_{21}}S_2. \quad (9)$$

The system writes in the following form:

$$\begin{cases} \frac{dx_1}{dt} = (\mu_1(s_0, s_2) - D)x_1 \\ \frac{dx_2}{dt} = (\mu_2(s_0, s_1) - D)x_2 \\ \frac{ds_0}{dt} = D(s_0^{in} - s_0) - \mu_1(s_0, s_2)x_1 - \mu_2(s_0, s_1)x_2 \\ \frac{ds_1}{dt} = D(s_1^{in} - s_1) + \omega_1\mu_1(s_0, s_2)x_1 - \mu_2(s_0, s_1)x_2 \\ \frac{ds_2}{dt} = D(s_2^{in} - s_2) - \mu_1(s_0, s_2)x_1 + \omega_2\mu_2(s_0, s_1)x_2 \end{cases} \quad (10)$$

115 where the growth functions  $\mu_i(\cdot, \cdot)$  are given by:

$$\begin{aligned}
 116 \quad \mu_1(s_0, s_2) &= f_1\left(s_0, \frac{v_{21}}{v_{01}}s_2\right), \\
 \mu_2(s_0, s_1) &= f_2\left(s_0, \frac{v_{12}}{v_{02}}s_1\right),
 \end{aligned}
 \tag{11}$$

117 the input concentrations are :

$$118 \quad s_0^{in} = S_0^{in}, \quad s_1^{in} = \frac{v_{02}}{v_{12}}S_1^{in}, \quad s_2^{in} = \frac{v_{01}}{v_{21}}S_2^{in}.
 \tag{12}$$

and the constants  $\omega_i$ ,  $i = 1, 2$  are defined by:

$$\omega_1 = \frac{v_{02}v_{11}}{v_{01}v_{12}}, \quad \omega_2 = \frac{v_{01}v_{22}}{v_{02}v_{21}}.$$

119 System (10) has the benefit of involving only two constants (instead of six), according to which  
 120 we'll discuss the existence and the stability of steady states.

### 121 3 Assumptions on the model and notations

122 We assume that the growth rates are of class  $C^1$  on  $\mathbb{R}_+^2$  and satisfy:

123 **H1**  $\forall s_0 > 0$  and  $s_2 > 0$ ,  $0 < \mu_1(s_0, s_2) < +\infty$  and  $\mu_1(0, s_2) = \mu_1(s_0, 0) = 0$ .

124 This assumes that there is no growth of species  $x_1$  in the absence of the substrate  $s_0$  or the  
 125 substrate  $s_2$ .

126 **H2**  $\forall s_0 > 0$  and  $s_1 > 0$ ,  $0 < \mu_2(s_0, s_1) < +\infty$  and  $\mu_2(0, s_1) = \mu_2(s_0, 0) = 0$ .

127 This assumes that there is no growth of species  $x_2$  in the absence of the substrate  $s_0$  or the  
 128 substrate  $s_1$ .

129 **H3**  $\forall s_0 > 0$  and  $s_2 > 0$ ,  $\frac{\partial \mu_1}{\partial s_0}(s_0, s_2) > 0$  and  $\frac{\partial \mu_1}{\partial s_2}(s_0, s_2) > 0$ ,

130 which means that the growth rate of species  $x_1$  increases with both substrates  $s_0$  and  $s_2$ .

131 **H4**  $\forall s_0 > 0$  and  $s_1 > 0$ ,  $\frac{\partial \mu_2}{\partial s_0}(s_0, s_1) > 0$  and  $\frac{\partial \mu_2}{\partial s_1}(s_0, s_1) > 0$ ,

132 which means that the growth rate of species  $x_2$  increases with both substrates  $s_0$  and  $s_1$ .

133 **H5** The functions  $s_0 \rightarrow \mu_1(s_0, +\infty)$  and  $s_0 \rightarrow \mu_2(s_0, +\infty)$  are monotonically increasing.

134 Hypothesis (**H5**) means that there is a direct relationship between the growth of species  $x_1, x_2$   
 135 and the concentration of  $s_0$ .

136 Solutions of system (10) verify the following result. Its proof uses classical tools, see for  
 137 example [4] or [9].

**Proposition 3.1.** *For positive initial conditions, solutions of the system (10) are bounded and remain positive, for all  $t \geq 0$ . In addition, the set*

$$\Omega = \{(x_1, x_2, s_0, s_1, s_2) \in \mathbb{R}_+^5 / \omega_1 x_1 + \omega_2 x_2 + \omega_1 \omega_2 s_0 + \omega_2 s_1 + \omega_1 s_2 = s_{in}\},$$

where

$$s_{in} = \omega_1 \omega_2 s_0^{in} + \omega_2 s_1^{in} + \omega_1 s_2^{in},$$

144 is a positive invariant attractor for all solutions of system (10).

145  
146

In the following table, we provide some notations and definitions that we will use later.

Definition	
$s_i = M_j(s_0, y),$ $i = 1, 2, j = 1, 2, i \neq j$	Let $s_0 \geq 0, s_i = M_j(s_0, y)$ is the unique solution of $\mu_j(s_0, s_i) = y$ , for all $0 \leq y < \mu_j(s_0, +\infty)$ .
$s_0^i = s_0^i(D), i = 1, 2$	$s_0^i = s_0^i(D)$ is the unique solution of $\mu_i(s_0^i, +\infty) = D$ , for all $D < \mu_i(+\infty, +\infty)$ .
$\tilde{s}_0$	$\tilde{s}_0 = \max(s_0^1, s_0^2)$
$I$	$I = ]\tilde{s}_0, +\infty[$
$H(s_0, D)$	$H(s_0, D) = (\omega_1\omega_2 - 1)s_0 + (\omega_1 + 1)M_1(s_0, D) + (\omega_2 + 1)M_2(s_0, D)$ , for all $s_0 \in I$ and $D \in [0, \min(\mu_1(s_0, +\infty), \mu_2(s_0, +\infty))]$ .
$M(D)$	$M(D) = (\omega_1 + 1)M_1(+\infty, D) + (\omega_2 + 1)M_2(+\infty, D)$ .
$F_1(D)$	$F_1(D) = \inf_{s_0 \in (\tilde{s}_0, +\infty)} H(s_0, D)$ .

Table 3: Definition of auxiliary functions, interval  $I$ , and some notations.

147  
148  
149

Fig 2 illustrates the graphs of functions  $\mu_1(., +\infty), \mu_2(., +\infty)$ .  $s_0^1$  and  $s_0^2$ , are the intersection of these graphs with the line  $y = D$ , respectively.

From the definition of  $M_1, M_2, s_0^1$  and  $s_0^2$  provided in Table 3, we can deduce that:

$$M_1(s_0^1, D) = +\infty, \quad M_2(s_0^2, D) = +\infty.$$

Therefore, we have:

$$\lim_{s_0 \rightarrow s_0^+} H(s_0, D) = +\infty,$$

and

$$\lim_{s_0 \rightarrow +\infty} H(s_0, D) = \begin{cases} -\infty & \text{si } \omega_1\omega_2 < 1 \\ M(D) & \text{si } \omega_1\omega_2 = 1 \\ +\infty & \text{si } \omega_1\omega_2 > 1 \end{cases}$$

150 where  
151

$$M(D) = (\omega_1 + 1)M_1(+\infty, D) + (\omega_2 + 1)M_2(+\infty, D). \quad (13)$$

Fig 3 illustrates the graph of function  $H$  according to the position of  $\omega_1\omega_2$  to 1. Therefore, when  $\omega_1\omega_2 > 1$ , the positive function  $s_0 \rightarrow H(s_0, D)$  tends to  $+\infty$  at the extremities of  $I$  and has a minimum value on this interval. So, we can add the following assumption:

**H6** The function  $s_0 \rightarrow H(s_0, D)$  has a unique minimum at  $\bar{s}_0 := \bar{s}_0(D)$  in the interval  $I$  such that:

$$\forall s_0 \in (\tilde{s}_0, \bar{s}_0), \frac{\partial H}{\partial s_0}(s_0, D) < 0 \quad \text{and} \quad \forall s_0 \in (\bar{s}_0, +\infty), \frac{\partial H}{\partial s_0}(s_0, D) > 0.$$

Consequently, we have

$$F_1(D) = H(\bar{s}_0, D).$$

152



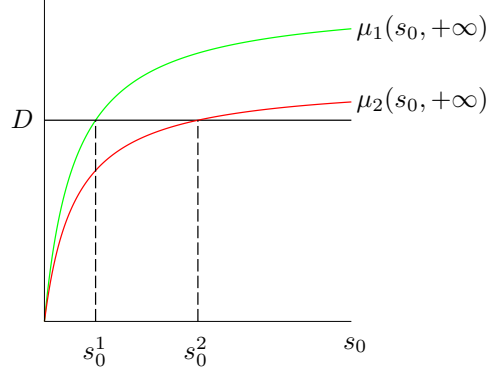


Figure 2: Graphs of the functions  $\mu_1(\cdot, +\infty)$ ,  $\mu_2(\cdot, +\infty)$  and definition of the values  $s_0^1$  and  $s_0^2$ .

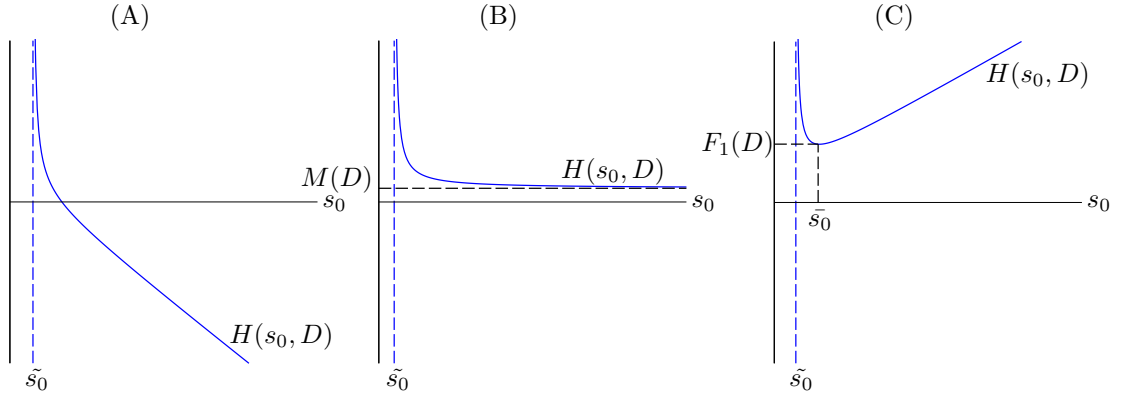


Figure 3: Graph of  $H$ : (A) the case  $\omega_1\omega_2 < 1$ , (B) the case  $\omega_1\omega_2 = 1$ , (C) the case  $\omega_1\omega_2 > 1$  and definition of  $\tilde{s}_0$  and  $F_1(D)$ .

## 153 4 Existence of steady-states

We get the steady-states by setting the right-hand side of equations of (10) equal to zero:

$$(\mu_1(s_0, s_2) - D)x_1 = 0 \quad (14)$$

$$(\mu_2(s_0, s_1) - D)x_2 = 0 \quad (15)$$

$$D(s_0^{in} - s_0) - \mu_1(s_0, s_2)x_1 - \mu_2(s_0, s_1)x_2 = 0 \quad (16)$$

$$D(s_1^{in} - s_1) + \omega_1\mu_1(s_0, s_2)x_1 - \mu_2(s_0, s_1)x_2 = 0 \quad (17)$$

$$D(s_2^{in} - s_2) - \mu_1(s_0, s_2)x_1 + \omega_2\mu_2(s_0, s_1)x_2 = 0 \quad (18)$$

A steady-state exists if and only if all its components are nonnegative. Equation (14) induces that:

$$x_1 = 0 \quad \text{or} \quad \mu_1(s_0, s_2) = D,$$

and from (15), we deduce that:

$$x_2 = 0 \quad \text{or} \quad \mu_2(s_0, s_1) = D.$$

154 Then, we can have four types of steady-states:

155  $E_0$ :  $x_1 = 0, x_2 = 0$  where both species are extinct.

156  $E_1$ :  $x_1 > 0$  and  $x_2 = 0$ , where species  $x_1$  survives while species  $x_2$  is extinct.

157  $E_2$ :  $x_1 = 0$  and  $x_2 > 0$ , where species  $x_1$  is extinct while  $x_2$  survives.

158  $E^*$ :  $x_1 > 0$  and  $x_2 > 0$ , where both species are maintained.

159

160 In the following result we give the steady-states of (10) and the necessary and sufficient con-  
161 ditions of their existence.

162 **Theorem 1.** *Under hypotheses **H1-H4**, the system (10) has the following steady-states*

163  $E_0 = (0, 0, s_0^{in}, s_1^{in}, s_2^{in})$ , which always exists.

164  $E_1 = (x_1^*, 0, s_0^*, s_1^*, s_2^*)$ , where  $s_2^*$  is the unique solution in the interval  $]max(s_2^{in} - s_0^{in}, 0), s_2^{in}[$  of  
165 equation

$$166 \mu_1(s_0^{in} - s_2^{in} + s_2, s_2) = D, \quad (19)$$

167

$$168 x_1^* = s_2^{in} - s_2^*, \quad s_0^* = s_0^{in} - s_2^{in} + s_2^* \quad \text{and} \quad s_1^* = s_1^{in} + \omega_1(s_2^{in} - s_2^*). \quad (20)$$

169 *This steady-state exists if and only if  $\mu_1(s_0^{in}, s_2^{in}) > D$ .*

170  $E_2 = (0, x_2^*, s_0^*, s_1^*, s_2^*)$ , where  $s_1^*$  is the unique solution in the interval  $]max(s_1^{in} - s_0^{in}, 0), s_1^{in}[$  of  
171 the equation

$$172 \mu_2(s_0^{in} - s_1^{in} + s_1, s_1) = D, \quad (21)$$

173

$$174 x_2^* = s_1^{in} - s_1^*, \quad s_0^* = s_0^{in} - s_1^{in} + s_1^* \quad \text{and} \quad s_2^* = s_2^{in} + \omega_2(s_1^{in} - s_1^*). \quad (22)$$

175 *It exists if and only if  $\mu_2(s_0^{in}, s_1^{in}) > D$ .*

176  $E^* = (x_1^*, x_2^*, s_0^*, s_1^*, s_2^*)$ , where  $s_0^*$  is a solution of the equation :

$$177 H(s_0, D) = s^{in}, \quad (23)$$

178

$$179 \begin{aligned} & s_1^* = M_2(s_0^*, D), \quad s_2^* = M_1(s_0^*, D), \\ & x_1^* = \frac{s_0^{in} - s_1^{in} + M_2(s_0^*, D) - s_0^*}{\omega_1 + 1} \quad \text{and} \quad x_2^* = \frac{s_0^{in} - s_2^{in} + M_1(s_0^*, D) - s_0^*}{\omega_2 + 1}, \end{aligned} \quad (24)$$

180 with :  $s^{in} = (\omega_1\omega_2 - 1)s_0^{in} + (\omega_2 + 1)s_1^{in} + (\omega_1 + 1)s_2^{in}$ .

181 • If  $\omega_1\omega_2 < 1$ ,  $E^*$  exists if and only if  $s_0^{in} - s_1^{in} > s_0 - M_2(s_0, D)$  and  $s_0^{in} - s_2^{in} > s_0 - M_1(s_0, D)$ .

182 • If  $\omega_1\omega_2 = 1$ ,  $E^*$  exists if and only if  $s_0^{in} - s_1^{in} > s_0 - M_2(s_0, D)$ ,  $s_0^{in} - s_2^{in} > s_0 - M_1(s_0, D)$   
183 and  $M(D) < s^{in}$ .

184 • If  $\omega_1\omega_2 > 1$ ,  $E^*$  exists if and only if  $s_0^{in} - s_1^{in} > s_0 - M_2(s_0, D)$ ,  $s_0^{in} - s_2^{in} > s_0 - M_1(s_0, D)$   
185 and  $F_1(D) \leq s^{in}$ .

186 The proof of Theorem 1 is given in the Appendix.

187 **Remark 1.** *Under hypothesis **H6**, if  $F_1(D) < s^{in}$  then (23) has two solutions, we denote them*  
188 *by  $s_0^1$  and  $s_0^2$  such that  $\bar{s}_0 < s_0^1 < \bar{s}_0 < s_0^2 < +\infty$ , see Fig 4.*

189 *If  $F_1(D) = s^{in}$  then  $\bar{s}_0 < s_0^1 = \bar{s}_0 = s_0^2 < +\infty$ .*

190 *The two solutions  $s_0^1$  and  $s_0^2$  give rise to two steady-states, we denote them by  $E_1^*$  and  $E_2^*$ ,*  
191 *respectively. When  $F_1(D) = s^{in}$ , these steady-states coalesce.*

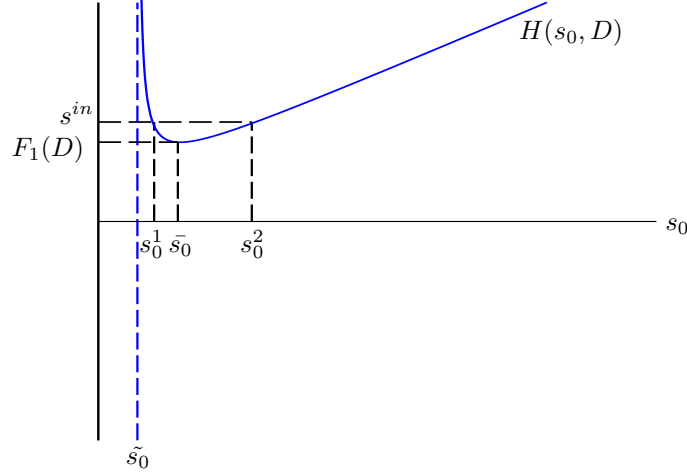


Figure 4: The values  $s_0^1$  and  $s_0^2$  in the case  $\omega_1\omega_2 > 1$ .

## 5 Local stability of steady-states

In this section, we will study the local stability of the steady-states by calculating the Jacobian matrices. We use the abbreviation LES for local exponentially stable.

**Theorem 2.** Under hypotheses **H1-H6**,

- $E_0$  is LES if and only if  $\mu_1(s_0^{in}, s_2^{in}) < D$  and  $\mu_2(s_0^{in}, s_1^{in}) < D$ .

- $E_1$  is LES if and only if  $\mu_2(s_0^{in} - s_2^{in} + s_2^*, s_1^{in} + \omega_1(s_2^{in} - s_2^*)) < D$ , where  $s_2^*$  is a solution of equation (19).

- $E_2$  is LES if and only if  $\mu_1(s_0^{in} - s_1^{in} + s_1^*, s_2^{in} + \omega_2(s_1^{in} - s_1^*)) < D$ , where  $s_1^*$  is a solution of equation (21).

-If  $\omega_1\omega_2 \leq 1$ , the steady-state  $E^*$  is LES when it exists. If  $\omega_1\omega_2 > 1$  the steady-state  $E^*$  is LES if and only if  $\frac{\partial H}{\partial s_0}(s_0^*, D) < 0$ , where  $s_0^*$  is solution in  $I$  of equation (23) and  $D \in [0, \min(\mu_1(s_0, +\infty), \mu_2(s_0, +\infty))]$ .

We summarize in Table 4 the existence and local stability conditions of steady-states of model (10).

Steady-state	Existence conditions	Stability conditions
$E_0$	Always exists	$\mu_1(s_0^{in}, s_2^{in}) < D$ $\mu_2(s_0^{in}, s_1^{in}) < D$
$E_1$	$\mu_1(s_0^{in}, s_2^{in}) > D$	$\mu_2(s_0^{in} - s_2^{in} + s_2^*, s_1^{in} + \omega_1(s_2^{in} - s_2^*)) < D$
$E_2$	$\mu_2(s_0^{in}, s_1^{in}) > D$	$\mu_1(s_0^{in} - s_1^{in} + s_1^*, s_2^{in} + \omega_2(s_1^{in} - s_1^*)) < D$
$E^*$	$s_0^{in} - s_1^{in} > s_0^* - M_2(s_0^*, D)$ $s_0^{in} - s_2^{in} > s_0^* - M_1(s_0^*, D)$ $s^{in} > F_1(D)$	$\frac{\partial H}{\partial s_0}(s_0^*, D) < 0$

Table 4: Existence and local stability of steady-states of (10). Functions  $M_1, M_2, H$  and  $F_1$  are defined in Table 3

206 **Remark 2.** • When  $\omega_1\omega_2 < 1$ , the condition  $s^{in} > F_1(D)$  of existence of  $E^*$ , and its stability  
207 condition  $\frac{\partial H}{\partial s_0}(s_0^*, D) < 0$  are always satisfied.

208 • When  $\omega_1\omega_2 = 1$ , we have  $F_1(D) = M(D)$ , then, the condition  $s^{in} > F_1(D)$  of existence of  $E^*$   
209 becomes  $s^{in} > M(D)$ . And its stability condition is always satisfied.

210 • When  $\omega_1\omega_2 > 1$ , the stability condition is always satisfied for the steady-state  $E_1^*$ , and it is not  
211 satisfied for  $E_2^*$ .

212 Let's notice, from Table 4, that if  $E_1$  or  $E_2$  exists then, the washout steady-state becomes  
213 unstable.

## 214 6 Bifurcation diagrams and time simulations

In this section, we illustrate our theoretical results by bifurcation diagrams with the input concentration  $S_0^{in}$ , for model (3) considered in [27]. The growth rates are of double-Monod type and are given by the following functions:

$$f_1(S_0, S_2) = \bar{\mu}_1 \frac{S_0}{K_{10} + S_0} \frac{S_2}{K_{12} + S_2},$$

$$f_2(S_0, S_1) = \bar{\mu}_2 \frac{S_0}{K_{20} + S_0} \frac{S_1}{K_{21} + S_1},$$

215  $\bar{\mu}_i, i = 1, 2$  are the maximal growth rate and  $K_{ij}, i, j = 0, 1, 2$ , are the half saturation constants.

216 These parameters depend on the organisms and substrates considered and are fixed. The biological  
217 parameters values used in this section are given in Table 5. In order to compare our results  
218 to those of [27], we use the same values of biological parameters.

Parameter	$\bar{\mu}_1$	$\bar{\mu}_2$	$K_{10}$	$K_{20}$	$K_{12}$	$K_{21}$
Value	1600	800	200	200	200	200

Table 5: Biological parameter values. The unit of the maximal growth rates  $\bar{\mu}_i, i = 1, 2$  is 1/time and the unit of the half-saturation constants  $K_{ij}$  is mass/volume.

219 Using the change of variables (12) and (11), the growth rates  $\mu_i(\cdot, \cdot), i = 1, 2$  of model (10)  
 220 are given by

$$\mu_1(s_0, s_2) = \frac{\bar{\mu}_1 s_0}{K_{10} + s_0} \frac{s_2}{\left(\frac{v_{01}}{v_{21}}\right) K_{12} + s_2},$$

$$\mu_2(s_0, s_1) = \frac{\bar{\mu}_2 s_0}{K_{20} + s_0} \frac{s_1}{\left(\frac{v_{02}}{v_{12}}\right) K_{21} + s_1}.$$
(25)

Assumptions **(H1)**-**(H5)** are satisfied by the functions defined in (25). The inverse functions  $M_1(s_0, D)$  and  $M_2(s_0, D)$  of functions (25), are given respectively by:  
 for  $y \in [0, \mu_1(s_0, +\infty))$ ,

$$M_1(s_0, y) = \frac{\left(\frac{v_{01}}{v_{21}}\right) K_{12} y}{\frac{\bar{\mu}_1 s_0}{K_{10} + s_0} - y},$$

for  $y \in [0, \mu_2(s_0, +\infty))$ ,

$$M_2(s_0, y) = \frac{\left(\frac{v_{02}}{v_{12}}\right) K_{21} y}{\frac{\bar{\mu}_2 s_0}{K_{20} + s_0} - y}$$

and

$$\mu_1(s_0, +\infty) = \frac{\bar{\mu}_1 s_0}{K_{10} + s_0}, \quad \mu_2(s_0, +\infty) = \frac{\bar{\mu}_2 s_0}{K_{20} + s_0}.$$

In addition,

$$s_0^1(D) = \frac{DK_{10}}{\bar{\mu}_1 - D}, \quad s_0^2(D) = \frac{DK_{20}}{\bar{\mu}_2 - D}.$$

The function  $H$  is given by:

$$H(s_0, D) = (\omega_1 \omega_2 - 1) s_0 + (\omega_1 + 1) \frac{\left(\frac{v_{01}}{v_{21}}\right) K_{12} y}{\frac{\bar{\mu}_1 s_0}{K_{10} + s_0} - y} + (\omega_2 + 1) \frac{\left(\frac{v_{02}}{v_{12}}\right) K_{21} y}{\frac{\bar{\mu}_2 s_0}{K_{20} + s_0} - y}.$$

Notice that

$$\frac{\partial^2 H}{\partial s_0^2}(s_0, D) = (\omega_1 + 1) \frac{\partial^2 M_1}{\partial s_0^2}(s_0, D) + (\omega_2 + 1) \frac{\partial^2 M_2}{\partial s_0^2}(s_0, D),$$

with, for all  $s_0 \in I$  and  $D \in [0, \mu_1(s_0, +\infty)[$ ,

$$\frac{\partial^2 M_1}{\partial s_0^2}(s_0, D) = \frac{2 \frac{v_{01}}{v_{21}} \bar{\mu}_1 K_{10} K_{12} D [(s_0 + K_{10}) \left(\frac{\bar{\mu}_1 - s_0}{K_{10} + s_0} - D\right)^2 + (s_0 + K_{10})^2 \left(\frac{\bar{\mu}_1 s_0}{K_{10} + s_0} - D\right) \frac{\bar{\mu}_1 K_{10}}{(K_{10} + s_0)^2}]}{[(K_{10} + s_0)^2 \left(\frac{\bar{\mu}_1 s_0}{K_{10} + s_0} - D\right)^2]^2},$$

222 since  $D \in [0, \mu_1(s_0, +\infty)[$ , we have  $\frac{\bar{\mu}_1 s_0}{K_{10} + s_0} - D > 0$ , which proves that  $\frac{\partial^2 M_1}{\partial s_0^2}(s_0, D) > 0$ .

223 In the same way, we can prove that  $\frac{\partial^2 M_2}{\partial s_0^2}(s_0, D) > 0$ , for  $s_0 \in I, D \in [0, \mu_2(s_0, +\infty)[$ .

224 Therefore,  $\frac{\partial^2 H}{\partial s_0^2}(s_0, D) > 0$ , for all  $s_0 \in I$  and  $D \in [0, \min(\mu_1(s_0, +\infty), \mu_2(s_0, +\infty))]$ . So the

225 function  $s_0 \rightarrow H(s_0, D)$  is convex and satisfies hypothesis **H6**.

226 In the following, we give the bifurcation diagrams with respect to  $S_0^{in}$  in the three cases:  
 227  $\omega_1 \omega_2 > 1$ ,  $\omega_1 \omega_2 = 1$  and  $\omega_1 \omega_2 < 1$ . Therefore, we fix the values of the input concentrations  
 228  $S_1^{in}, S_2^{in}$  and the dilution rate  $D$ . Assume that  $S_1^{in} = S_2^{in} = 1, D = 2$ , for all cases and the  
 229 biological parameters of (3) given by Table 5.

230 We consider the yield coefficients defined in Table 6. The bifurcation values  $\sigma_i, i = 1, \dots, 4$  are  
 231 defined in Table 7, and provided in Table 8.

Case	$v_{01}$	$v_{02}$	$v_{11}$	$v_{12}$	$v_{21}$	$v_{22}$
$\omega_1\omega_2 > 1$	1	1	0.2	0.1	0.1	0.2
$\omega_1\omega_2 = 1$	1	1	0.1	0.1	0.1	0.1
$\omega_1\omega_2 < 1$	1	1	0.2	1	0.1	0.2

Table 6: Values of yield coefficients, for the three cases.

$S_0^{in}$	Definition
$\sigma_1$	the solution of equation $\mu_1(S_0^{in}, \frac{v_{01}}{v_{21}} S_2^{in}) = D$
$\sigma_2$	the solution of equation $\mu_2(S_0^{in}, \frac{v_{02}}{v_{12}} S_1^{in}) = D$
$\sigma_3$	the solution of equation $\mu_2(S_0^{in} - \frac{v_{01}}{v_{21}} S_2^{in} + s_2^*, \frac{v_{02}}{v_{12}} S_1^{in} + \omega_1(\frac{v_{01}}{v_{21}} S_2^{in} - s_2^*)) = D$
$\sigma_4$	the solution of equation $F_1(D) = S^{in}$

Table 7: Definitions of the critical values of  $\sigma_i, i = 1, \dots, 4$

Case	$\sigma_1$	$\sigma_2$	$\sigma_3$	$\sigma_4$
$\omega_1\omega_2 > 1$	67.1118530885	202.0100502513	103.3607227	65.55518440
$\omega_1\omega_2 = 1$	67.11185309	202.0100503	124.4188425	-
$\omega_1\omega_2 < 1$	67.11185309	202.0100502513	103.3607227	-

Table 8: Values of  $\sigma_i$ , in the three cases.

We then give the next result, corresponding to the case  $\omega_1\omega_2 > 1$ :

**Proposition 6.1.** *Assume that  $\omega_1\omega_2 > 1$ . The existence and stability of steady-states of (3), with respect to the input concentration  $S_0^{in}$  is given in Table 9.*

Interval of $S_0^{in}$	$E_0$	$E_1$	$E_2$	$E_1^*$	$E_2^*$
$(0, \sigma_4)$	S				
$(\sigma_4, \sigma_1)$	S			S	U
$(\sigma_1, \sigma_3)$	U	S		S	U
$(\sigma_3, \sigma_2)$	U	U		S	
$(\sigma_2, +\infty)$	U	U	U	S	

Table 9: Existence and stability of steady-states, with respect to  $S_0^{in}$ , in the case  $\omega_1\omega_2 > 1$ . The letter S (resp. U) means that the corresponding steady-states is LES (resp. unstable). No letter means that the steady-state does not exist. The values of  $\sigma_i, i = 1, \dots, 4$  are provided in Table 8.

232 Notice that, in this case, bistability occurs between  $E_0$  and  $E_1^*$ , for  $S_0^{in} \in (\sigma_4, \sigma_1)$  and between  
 233  $E_1$  and  $E_1^*$ , for  $S_0^{in} \in (\sigma_1, \sigma_3)$ . Bifurcations at the values  $\sigma_i, i = 1, \dots, 4$ , when  $\omega_1\omega_2 > 1$ , are

described in Table 10.

	Type of the bifurcation
$\sigma_1$	Transcritical bifurcation of $E_0$ and $E_1$
$\sigma_2$	Transcritical bifurcation of $E_0$ and $E_2$
$\sigma_3$	Transcritical bifurcation of $E_1$ and $E_2^*$
$\sigma_4$	Saddle-node bifurcation of $E_1^*$ and $E_2^*$

Table 10: Type of bifurcations corresponding to the critical values  $\sigma_i, i = 1, \dots, 4$ , when  $\omega_1\omega_2 > 1$ .

234

235 Now, we consider the case  $\omega_1\omega_2 \leq 1$ . Notice that, in this case, there is a unique positive  
 236 steady state, so  $\sigma_4$  doesn't exist. The corresponding values of  $\sigma_i, i = 1, 2, 3$  are given in Table 8.  
 237 Despite the difference between the bifurcation values in the case  $\omega_1\omega_2 = 1$  and the case  $\omega_1\omega_2 < 1$ ,  
 238 the existence and the behavior of the steady states in both cases are similar. We then have,

239 **Proposition 6.2.** *When  $\omega_1\omega_2 \leq 1$ , the existence and stability of steady-states of (3), with respect*  
 240 *to the input concentration  $S_0^{in}$  is given in Table 11.*

Interval of $S_0^{in}$	$E_0$	$E_1$	$E_2$	$E^*$
$(0, \sigma_1)$	S			
$(\sigma_1, \sigma_3)$	U	S		
$(\sigma_3, \sigma_2)$	U	U		S
$(\sigma_2, +\infty)$	U	U	U	S

Table 11: Existence and stability of steady-states, with respect to  $S_0^{in}$ , in the case  $\omega_1\omega_2 \leq 1$ . The values of  $\sigma_i, i = 1, \dots, 3$  are provided in Table 8.

241 In this case, there are only transcritical bifurcations between the steady states. When  $S_0^{in}$   
 242 crosses the value  $\sigma_1$ , a transcritical bifurcation occurs between the washout  $E_0$  and  $E_1$ .  $E_0$   
 243 bifurcate with  $E_2$  at  $\sigma_2$  and at  $\sigma_3$ , there is a transcritical bifurcation between the steady state  
 244  $E_1$  of extinction of the second species and the coexistence steady state  $E^*$ .

245  
 246 Figs 5, 6 and 7 show the bifurcation diagrams of (3) in the different cases, according to  
 247  $\omega_1\omega_2$ . We represent the components  $X_1$  and  $X_2$  of the steady states, as a function of the input  
 248 concentration  $S_0^{in}$ . We use a specific color for each steady state. The colors used in Figs 5, 6 and  
 7, are given in Table 12. Figs. 5 and 6 show, in the case  $\omega_1\omega_2 \leq 1$ , the transcritical bifurcations

$E_0$	$E_1$	$E_2$	$E^*$
Magenta	Green	Cyan	Red

Table 12: Colors used in Figs 5, 6 and 7. (In fig 7, we use the red color for  $E_1^*$ , and the blue color for  $E_2^*$ ). The solid (resp. dashed) lines means that the steady-state is LES (resp. unstable).

249

250 at  $\sigma_1, \sigma_2$ , and  $\sigma_3$ . The steady-state  $E_0$  loses its stability when  $E_1$  appears,  $E_1$  also loses its  
 251 stability when the positive steady-state  $E^*$  appears. Fig 7 illustrates the case  $\omega_1\omega_2 > 1$ , where  
 252 a saddle-node bifurcation of  $E_1^*$  and  $E_2^*$  appears at  $\sigma_4$ . These two steady-states appear at the

253 same time,  $E_1^*$  is always stable, while  $E_2^*$  is always unstable and disappears at  $\sigma_3$ , which is the  
 254 value where  $E_1$  loses its stability.

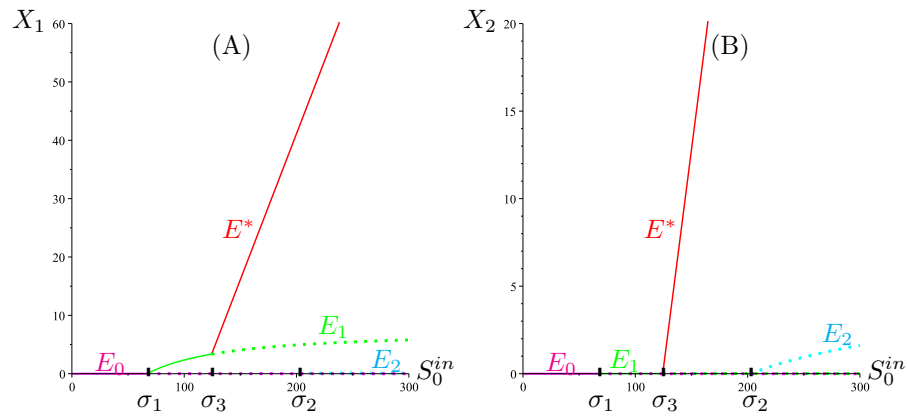


Figure 5: Bifurcation diagram in the case  $\omega_1\omega_2 = 1$  (A) The component  $X_1$  with respect to  $S_0^{in}$   
 (B) The component  $X_2$  with respect to  $S_0^{in}$ .

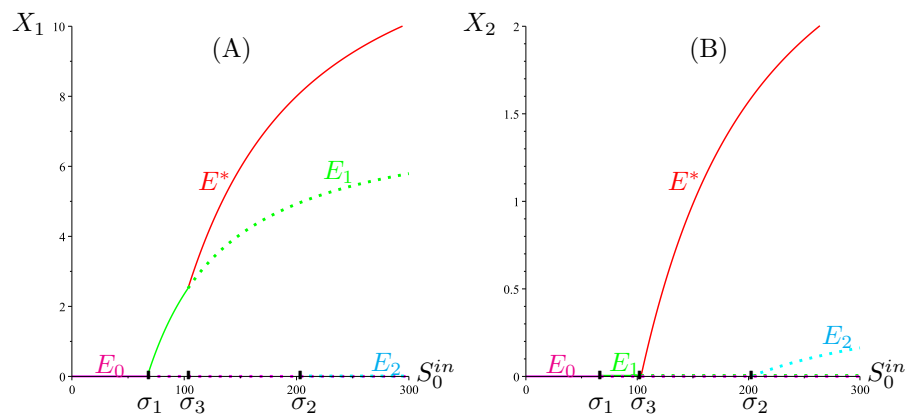


Figure 6: Bifurcation diagram in the case  $\omega_1\omega_2 < 1$  (A) The component  $X_1$  with respect to  $S_0^{in}$   
 (B) The component  $X_2$  with respect to  $S_0^{in}$ .



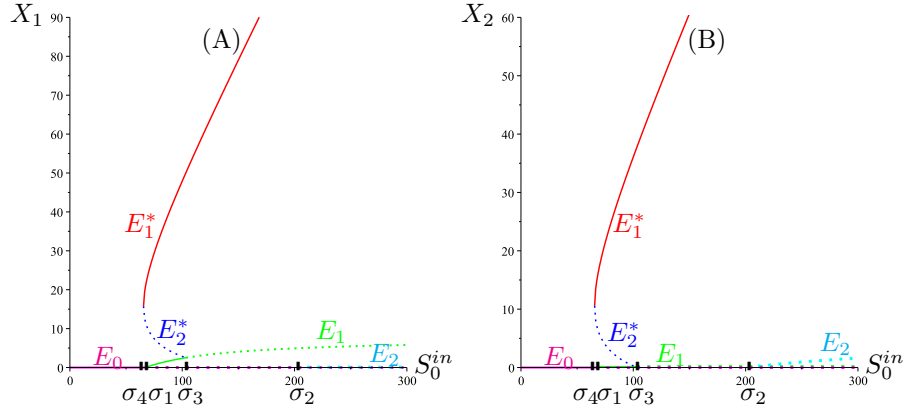


Figure 7: Bifurcation diagram in the case  $\omega_1\omega_2 > 1$  (A) The component  $X_1$  with respect to  $S_0^{in}$  (B) The component  $X_2$  with respect to  $S_0^{in}$ .

255 Bistability between  $E_0$  and  $E_1^*$  and between  $E_1$  and  $E_1^*$  can be observed also by time sim-  
 256 ulations. The simulations presented in Figs 8 and 9 show the bistability behavior, in the case  
 257  $\omega_1\omega_2 > 1$ . Values of  $S_0^{in}$ , and initial conditions used in Figs 8 and 9 are given in Table 13.

$S_0^{in}$	Interval of $S_0^{in}$	$(X_1(0), X_2(0), S_0(0), S_1(0), S_2(0))$	Figure
66	$(\sigma_4, \sigma_1)$	$(10, 10, 10, 3, 3)$	8 (A)
66	$(\sigma_4, \sigma_1)$	$(10, 10, 30, 3, 3)$	8 (B)
90	$(\sigma_1, \sigma_3)$	$(10, 0.1, 10, 3, 3)$	9 (A)
90	$(\sigma_1, \sigma_3)$	$(10, 0.1, 10, 15, 15)$	9 (B)

Table 13: Values, intervals of  $S_0^{in}$ , and initial conditions for Figs 8 and 9.

258 According to the initial conditions, the solutions converge either to  $E_0$  or to  $E_1^*$ , for  $S_0^{in} =$   
 259  $66 \in (\sigma_4, \sigma_1)$ . In Fig 8 (A), the solutions of (3) converge to the steady-state  $E_0$ . Fig 8 (B)  
 260 shows that the solutions converge to the steady-state  $E_1^*$ . This proves the existence of bistability  
 261 between  $E_0$  and  $E_1^*$  when  $S_0^{in} \in (\sigma_4, \sigma_1)$ . In Fig 9 (A), the solutions of (3) converge to  $E_1$  and in  
 262 Fig 9 (B) the solutions converge to  $E_1^*$ . From here, we conclude that there is bistability between  
 263  $E_1$  and  $E_1^*$  when  $S_0^{in} = 90 \in (\sigma_1, \sigma_3)$ . These numerical simulations confirms the results obtained  
 264 by the analytical analysis and observed in the bifurcation diagrams.

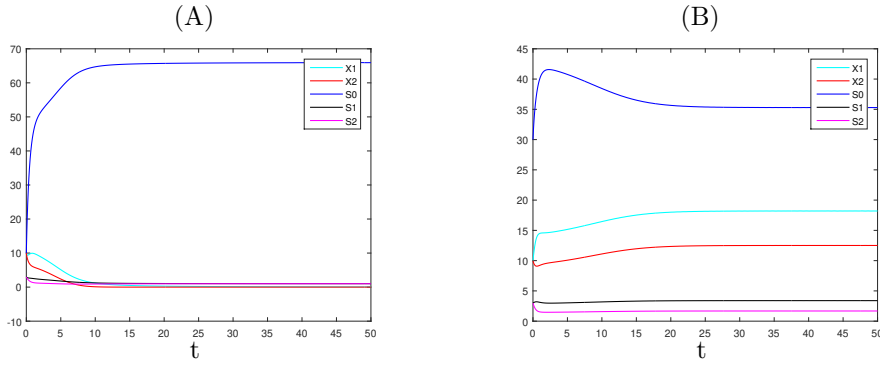


Figure 8: Time simulations for  $S_0^{in} = 66 \in (\sigma_4, \sigma_1)$ : (A) Convergence to  $E_0$ , washout of the species. (B) Convergence to  $E_1^*$ , coexistence of both species.

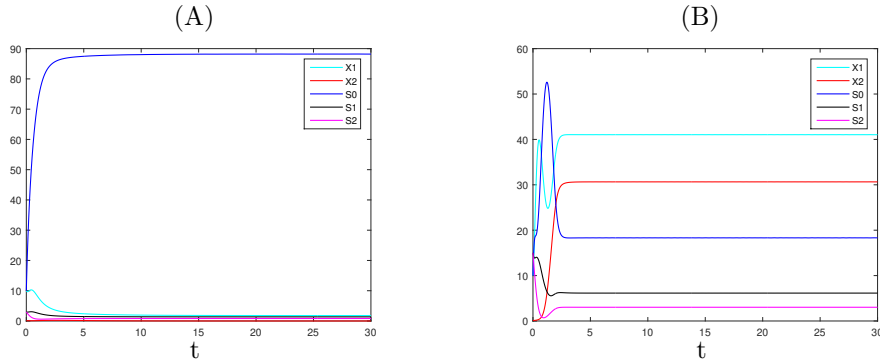


Figure 9: Time simulations for  $S_0^{in} = 90 \in (\sigma_1, \sigma_3)$ : (A) Convergence to  $E_1$ , extinction of the second species. (B) Convergence to  $E_1^*$ , coexistence of the species.

## 7 Conclusion

265

266 In this work, we performed the mathematical analysis of model (3), which was proposed in [27]  
 267 and studied only numerically. The model consider the phenomenon of a simultaneous competi-  
 268 tive and mutualist relationship between two microbial species in a chemostat. This interesting  
 269 phenomenon occurs when bacterial species cross-feed essential nutrients and in parallel compete  
 270 for the main source of carbon, which occurs in several situations.

271 Our first step, after transforming the model in order to reduce the number of the yield coefficients,  
 272 was to determine the steady-states and to provide the conditions of their existence with respect  
 273 to the operating parameters, which are the dilution rate and the input concentrations. We used  
 274 a general class of growth functions and we give an exhaustive study of the behavior of the system  
 275 (independently of the values of the parameters). We distinguished three different cases according  
 276 to the value of  $\omega_1\omega_2$ . The numerical study of [27] corresponds to the case  $\omega_1\omega_2 > 1$ . Model (10)  
 277 can have four types of steady-states, the washout steady-state, two steady-states of extinction of  
 278 one of species, and a coexistence steady-state, where the two species survive at the same time.  
 279 All types of steady-states are unique, except in the case  $\omega_1\omega_2 > 1$ , where we prove that there are  
 280 two positive steady-states. Next, we discussed the local stability of the steady-states, which can  
 281 be asymptotically stable, according to the operating parameters. The positive steady state is

282 always stable, when it is unique. In the case,  $\omega_1\omega_2 > 1$ , one of the steady state is asymptotically  
 283 stable and the other is unstable. The existence of an unstable steady state can not be ob-  
 284 served by a numerical study, as in [27]. Finally, we have drawn the bifurcation diagrams of model  
 285 (3) that show how the system behaves when we vary the input concentration  $S_0^{in}$ . In the case  
 286  $\omega_1\omega_2 > 1$ , the bifurcation diagrams show that the system exhibits bistability, once between the  
 287 washout steady-state  $E_0$  and the steady-state of coexistence  $E_1^*$  and once between the extinction  
 288 of the second species steady-state  $E_1$  and the positive steady-state  $E_1^*$ . This behavior is already  
 289 detected by the numerical study in [27]. Our results are confirmed by time simulations.

290 In [27], operating diagrams with respect to the input concentration  $S_0^{in}$  and the flow rate are  
 291 presented. These diagrams are bifurcation diagrams that indicate how stability of the steady  
 292 states changes as function of the operating parameters and show the stability (or the bistability)  
 293 regions of the different steady states. Since there are four operating parameters in the system  
 294 (the three input concentrations and the dilution (or the flow) rate), one must fix two of them  
 295 to have planar diagrams. The comparison between the operating diagrams corresponding to the  
 296 chemostat equations and the extended Lotka-Volterra, see Fig 5 of [27], reveals that there is  
 297 a discrepancy between the two models. As observed numerically in [27], our analytical study  
 298 proves that there is a unique stable coexistence steady state, although that the Lotka-Volterra  
 299 model predicts the possibility of existence of two positive steady states. We aim in a future work  
 300 to use our analytical results to perform the operating diagrams and compare them to those of  
 301 [27]. On another hand, it was shown that in a two-tiered food chain describing a syntrophic  
 302 interaction, [24], introducing maintenance (or decay) terms in the model preserves the stability  
 303 of the system, for all parameters values and for a large class of growth functions. Our next aim is  
 304 to take into account maintenance terms in the competitive mutualistic model and to investigate  
 305 if they have effects on the asymptotic behavior of the system. If stability and bistability are  
 306 not affected, determining operating diagrams in both cases, with and without maintenance, will  
 307 allow to investigate if regions of stability (or bistability) change.

## 308 Appendix. Proofs.

### 309 Proof of Theorem 1.

When  $x_1 = 0, x_2 = 0$ , from (16), (17) and (18) respectively, we deduce that  $s_0 = s_0^{in}, s_1 = s_1^{in},$   
 $s_2 = s_2^{in}$ . So,  $E_0 = (0, 0, s_0^{in}, s_1^{in}, s_2^{in})$ , it always exists.

For the steady-state  $E_1$ ,  $x_1 \neq 0$  and  $x_2 = 0$ . From (14), we deduce that

$$\mu_1(s_0, s_2) = D.$$

From (18), we have:

$$D(s_2^{in} - s_2) = \mu_1(s_0, s_2)x_1,$$

then,  $x_1 = s_2^{in} - s_2$ , which is positive if and only if  $s_2 < s_2^{in}$ .

From (17), we can deduce that:

$$D(s_1 - s_1^{in}) = \omega_1\mu_1(s_0, s_2)x_1,$$

which gives,  $s_1 = s_1^{in} + \omega_1(s_2^{in} - s_2)$ . Under the condition  $s_2 < s_2^{in}$ ,  $s_1$  is positive.

From (16), we obtain

$$D(s_0^{in} - s_0) = \mu_1(s_0, s_2)x_1,$$

and as a result  $s_0 = s_0^{in} - s_2^{in} + s_2$ , which is positive if and only if  $s_2 > s_2^{in} - s_0^{in}$ .

We deduce that  $s_2^*$  is a solution of the equation (19).

$E_1$  exists if and only if equation (19) admits a positive solution that guarantees the positivity of the components  $x_1, s_0$  and  $s_1$ . So we conclude that  $s_2^* \in ]\max(s_2^{in} - s_0^{in}, 0), s_2^{in}[$ .

We define the function:

$$s_2 \rightarrow g(s_2) = \mu_1(s_0^{in} - s_2^{in} + s_2, s_2).$$

The function  $g$  is strictly increasing on  $]\max(s_2^{in} - s_0^{in}, 0), s_2^{in}[$  since its derivative

$$g'(s_2) = \frac{\partial \mu_1}{\partial s_0}(s_0^{in} - s_2^{in} + s_2, s_2) + \frac{\partial \mu_1}{\partial s_2}(s_0^{in} - s_2^{in} + s_2, s_2),$$

is positive for  $s_2 > 0$ .

If  $s_2^{in} - s_0^{in} > 0$ ,  $g(s_2^{in} - s_0^{in}) = \mu_1(0, s_2^{in} - s_0^{in}) = 0$  and  $g(s_2^{in}) = \mu_1(s_0^{in}, s_2^{in})$ , the equation  $g(s_2) = D$  admits a solution in the interval  $]s_2^{in} - s_0^{in}, s_2^{in}[$  if and only if  $g(s_2^{in}) = \mu_1(s_0^{in}, s_2^{in}) > D$ . If  $s_2^{in} - s_0^{in} < 0$ , we have  $g(0) = \mu_1(s_0^{in} - s_2^{in}, 0) = 0$  and  $g(s_2^{in}) = \mu_1(s_0^{in}, s_2^{in})$ , the equation  $g(s_2) = D$  admits a solution in the interval  $]0, s_2^{in}[$  if and only if  $g(s_2^{in}) = \mu_1(s_0^{in}, s_2^{in}) > D$ . If  $s_2$  exists, it is unique.

For the steady-state  $E_2$ ,  $x_1 = 0$  and  $x_2 \neq 0$ . From (15) we deduce that

$$\mu_2(s_0, s_1) = D.$$

From (17), we have:

$$D(s_1^{in} - s_1) = \mu_2(s_0, s_1)x_2,$$

then,  $x_2 = s_1^{in} - s_1$ , which is positive if and only if  $s_1 < s_1^{in}$ .

From (16), we deduce:

$$D(s_0^{in} - s_0) = \mu_2(s_0, s_1)x_2,$$

as a consequence, we have  $s_0 = s_0^{in} - s_1^{in} + s_1$ , which is positive if and only if  $s_1 > s_1^{in} - s_0^{in}$ .

From (18), we obtain that:

$$D(s_2^{in} - s_2) = -\omega_2 \mu_2(s_0, s_1)x_2,$$

that gives  $s_2 = s_2^{in} + \omega_2(s_1^{in} - s_1)$ , which is positive if  $s_1 < s_1^{in}$ .

We deduce that  $s_1$  is a solution of equation (21).

The steady-state  $E_2$  exists if and only if equation (21) admits a positive solution that guarantees the positivity of the components  $x_2, s_0, s_2$ . Then, we conclude that  $s_1^* \in ]\max(s_1^{in} - s_0^{in}, 0), s_1^{in}[$ .

We define the function

$$s_1 \rightarrow j(s_1) = \mu_2(s_0^{in} - s_1^{in} + s_1, s_1).$$

The derivative of the function  $j$  is given by:

$$j'(s_1) = \frac{\partial \mu_2}{\partial s_0}(s_0^{in} - s_1^{in} + s_1, s_1) + \frac{\partial \mu_2}{\partial s_1}(s_0^{in} - s_1^{in} + s_1, s_1),$$

which is positive for  $s_1 > 0$ . Then, the function  $j$  is strictly increasing on  $]\max(s_1^{in} - s_0^{in}, 0), s_1^{in}[$ .

If  $s_1^{in} - s_0^{in} > 0$ , we have  $j(s_1^{in} - s_0^{in}) = \mu_2(0, s_1^{in} - s_0^{in}) = 0$  and  $j(s_1^{in}) = \mu_2(s_0^{in}, s_1^{in})$ . The equation  $j(s_1) = D$  admits a solution in the interval  $]s_1^{in} - s_0^{in}, s_1^{in}[$  if and only if  $j(s_1^{in}) = \mu_2(s_0^{in}, s_1^{in}) > D$ . If  $s_1^{in} - s_0^{in} < 0$ , we have  $j(0) = \mu_2(s_0^{in} - s_1^{in}, 0) = 0$  and  $j(s_1^{in}) = \mu_2(s_0^{in}, s_1^{in})$ , then the equation  $j(s_1) = D$  admits a solution in the interval  $]0, s_1^{in}[$  if and only if  $j(s_1^{in}) = \mu_2(s_0^{in}, s_1^{in}) > D$ .

Finally, for the steady-state  $E^*$ , when  $x_1 \neq 0$  and  $x_2 \neq 0$ . From (14) and (15), we deduce that  $\mu_1(s_0, s_2) = D$  and  $\mu_2(s_0, s_1) = D$ , which give  $s_2 = M_1(s_0, D)$  and  $s_1 = M_2(s_0, D)$ .

By subtracting equation (16) from equation (17), we obtain  $x_1 = \frac{s_0^{in} - s_1^{in} + s_1 - s_0}{\omega_1 + 1}$ . Then,

$$x_1 = \frac{s_0^{in} - s_1^{in} + M_2(s_0, D) - s_0}{\omega_1 + 1}.$$

And by subtraction of equation (16) from equation (18), we have  $x_2 = \frac{s_0^{in} - s_2^{in} + s_2 - s_0}{\omega_2 + 1}$  which gives

$$x_2 = \frac{s_0^{in} - s_2^{in} + M_1(s_0, D) - s_0}{\omega_2 + 1}.$$

As a consequence of equation (16),  $s_0$  is a solution of the following equation:

$$(\omega_1\omega_2 - 1)s_0 + (\omega_2 + 1)M_2(s_0, D) + (\omega_1 + 1)M_1(s_0, D) = (\omega_1\omega_2 - 1)s_0^{in} + (\omega_2 + 1)s_1^{in} + (\omega_1 + 1)s_2^{in}.$$

310 The component  $x_1 > 0$  if and only if  $s_0^{in} - s_1^{in} > s_0 - M_2(s_0, D)$  and  $x_2 > 0$  if and only if

311  $s_0^{in} - s_2^{in} > s_0 - M_1(s_0, D).$

312 Moreover, we have:

313 
$$s_0 \rightarrow \frac{\partial H}{\partial s_0}(s_0, D) = (\omega_1\omega_2 - 1) + (\omega_1 + 1)\frac{\partial M_1}{\partial s_0}(s_0, D) + (\omega_2 + 1)\frac{\partial M_2}{\partial s_0}(s_0, D). \quad (26)$$

314 Noticing that, from definition of  $M_1$  given in Table 3, we have:

315 
$$\mu_1(s_0, M_1(s_0, D)) = D, \quad \text{for all } D \in [0, \mu_1(s_0, +\infty)[ \quad (27)$$

calculating the derivative of (27) with respect to  $s_0$ , we can prove that

$$\frac{\partial M_1}{\partial s_0}(s_0, D) = - \left( \frac{\partial \mu_1}{\partial s_0}(s_0, M_1(s_0, D)) \right) \left( \frac{\partial \mu_1}{\partial s_2}(s_0, M_1(s_0, D)) \right)^{-1} < 0,$$

316 thanks to **H3**.

317 In a similar way, we prove that  $\frac{\partial M_2}{\partial s_0}(s_0, D) < 0$ .

318

319 According to the value of  $\omega_1\omega_2$ , we have to distinguish 3 cases:

320 If  $\omega_1\omega_2 < 1$ ,  $\frac{\partial H}{\partial s_0}(s_0, D)$  is negative on the interval  $I$ , then the equation  $H(s_0, D) = s^{in}$  admits a

321 unique solution in the interval  $I$  (see Fig 3 (A)).

322 If  $\omega_1\omega_2 = 1$ ,  $\frac{\partial H}{\partial s_0}(s_0, D)$  is strictly negative on the interval  $I$ , then the equation  $H(s_0, D) = s^{in}$

323 admits a solution in the interval  $I$  if and only if  $M(D) < s^{in}$ , where  $M(D)$  is given by (13) (see

324 Fig 3 (B)).

325 If  $\omega_1\omega_2 > 1$ , from hypothesis **H6**, equation  $H(s_0, D) = s^{in}$  admits a solution on the interval  $I$  if

326 and only if  $F_1(D) \leq s^{in}$  (see Fig 3 (C)).

327

□

## 328 Proof of Theorem 2.

To simplify the study of the local stability of the steady-states, we use the following change of variables:

$$z_0 = s_0 + x_1 + x_2, \quad z_1 = s_1 - \omega_1 x_1 + x_2, \quad z_2 = s_2 + x_1 - \omega_2 x_2.$$

329 Therefore, system (10) writes:

330 
$$\begin{cases} \frac{dx_1}{dt} = (\mu_1(z_0 - x_1 - x_2, z_2 - x_1 + \omega_2 x_2) - D)x_1 \\ \frac{dx_2}{dt} = (\mu_2(z_0 - x_1 - x_2, z_1 + \omega_1 x_1 - x_2) - D)x_2 \\ \frac{dz_0}{dt} = D(s_0^{in} - z_0) \\ \frac{dz_1}{dt} = D(s_1^{in} - z_1) \\ \frac{dz_2}{dt} = D(s_2^{in} - z_2) \end{cases} \quad (28)$$

A steady-state of (28) is of type  $(x_1, x_2, z_0, z_1, z_2)$ . Then, the four steady-states  $E_0, E_1, E_2, E^*$  write as:

$$-E_0 = (0, 0, s_0^{in}, s_1^{in}, s_2^{in}).$$

$$-E_1 = (x_1^*, 0, s_0^{in}, s_1^{in}, s_2^{in}), \text{ where } x_1^* \text{ is given by (20).}$$

$$-E_2 = (0, x_2^*, s_0^{in}, s_1^{in}, s_2^{in}), \text{ where } x_2^* \text{ is given by (22).}$$

$$-E^* = (x_1^*, x_2^*, s_0^{in}, s_1^{in}, s_2^{in}), \text{ where } x_1^*, x_2^* \text{ are given by (24).}$$

The Jacobian matrix of (28) has a block triangular form:

$$J = \begin{bmatrix} J_1 & J_2 \\ 0 & J_3 \end{bmatrix},$$

where:

$$J_1 = \begin{bmatrix} \mu_1 - D - (E + F)x_1 & (-E + \omega_2 F)x_1 \\ (-G + \omega_1 K)x_2 & \mu_2 - D - (G + K)x_2 \end{bmatrix}, \quad J_2 = \begin{bmatrix} Ex_1 & 0 & Fx_1 \\ Gx_2 & Kx_2 & 0 \end{bmatrix} \text{ and}$$

$$J_3 = \begin{bmatrix} -D & 0 & 0 \\ 0 & -D & 0 \\ 0 & 0 & -D \end{bmatrix}$$

with

$$\begin{aligned} \mu_1 &= \mu_1(s_0, s_2), & \mu_2 &= \mu_2(s_0, s_1), \\ E &= \frac{\partial \mu_1}{\partial s_0}(s_0, s_2), & F &= \frac{\partial \mu_1}{\partial s_2}(s_0, s_2), & G &= \frac{\partial \mu_2}{\partial s_0}(s_0, s_1), & K &= \frac{\partial \mu_2}{\partial s_1}(s_0, s_1). \end{aligned}$$

Notice that all these derivatives are positive.

The eigenvalues of  $J$  which is a block triangular matrix are  $-D$  (with multiplicity 3) and the eigenvalues of the matrix  $J_1$ .

At the steady-state  $E_0$ , the matrix  $J_1$  is given by:

$$J_1 = \begin{bmatrix} \mu_1(s_0^{in}, s_2^{in}) - D & 0 \\ 0 & \mu_2(s_0^{in}, s_1^{in}) - D \end{bmatrix}$$

The eigenvalues of  $J_1$  are  $\lambda_1 = \mu_1(s_0^{in}, s_2^{in}) - D$ ,  $\lambda_2 = \mu_2(s_0^{in}, s_1^{in}) - D$ . Then,  $E_0$  is stable if and only if  $\lambda_1$  negative and  $\lambda_2$  negative which equivalent to  $\mu_1(s_0^{in}, s_2^{in}) < D$  and  $\mu_2(s_0^{in}, s_1^{in}) < D$ .

At  $E_1$ , the matrix  $J_1$  is:

$$J_1 = \begin{bmatrix} -(E + F)x_1^* & (-E + \omega_2 F)x_1^* \\ 0 & \mu_2(s_0^{in} - x_1^*, s_1^{in} + \omega_1 x_1^*) - D \end{bmatrix}$$

The eigenvalues of  $J_1$  are  $\lambda_1 = -(E + F)x_1^*$  and  $\lambda_2 = \mu_2(s_0^{in} - x_1^*, s_1^{in} + \omega_1 x_1^*) - D$ .  $\lambda_1$  is always negative, then  $E_1$  is stable if and only if  $\mu_2(s_0^{in} - x_1^*, s_1^{in} + \omega_1 x_1^*) < D$ , which means that

$$\mu_2(s_0^{in} + s_2^* - s_2^{in}, s_1^{in} + \omega_1(s_2^{in} - s_2^*)) < D.$$

The matrix  $J_1$  at  $E_2$  is:

$$J_1 = \begin{bmatrix} \mu_1(s_0^{in} - x_2^*, s_2^{in} + \omega_2 x_2^*) - D & 0 \\ (-G + \omega_1 K)x_2^* & -(G + K)x_2^* \end{bmatrix}$$

The eigenvalues of  $J_1$  are  $\lambda_1 = \mu_1(s_0^{in} - x_2^*, s_2^{in} + \omega_2 x_2^*) - D$  and  $\lambda_2 = -(G + K)x_2^*$ .  $\lambda_2$  is always negative, then  $E_2$  is stable if and only if  $\mu_1(s_0^{in} - x_2^*, s_2^{in} + \omega_2 x_2^*) < D$ , which means that

$$\mu_1(s_0^{in} - s_1^{in} + s_1^*, s_2^{in} + \omega_2(s_1^{in} - s_1^*)) < D.$$

Finally, the matrix  $J_1$  at  $E^*$  is:

$$J_1 = \begin{bmatrix} -(E+F)x_1^* & (-E+\omega_2 F)x_1^* \\ (-G+\omega_1 K)x_2^* & -(G+K)x_2^* \end{bmatrix}$$

The trace of this matrix is negative so its eigenvalues are of negative real part if and only if its determinant is positive which means that:

$$(E+F)(G+K)x_1^*x_2^* - (-E+\omega_2 F)(-G+\omega_1 K)x_1^*x_2^* > 0,$$

leading to:

$$[(1+\omega_1)EK + (1+\omega_2)FG + (1-\omega_1\omega_2)FK]x_1^*x_2^* > 0.$$

331 Therefore, since  $x_1^* > 0$  and  $x_2^* > 0$ ,

$$332 \quad (1+\omega_1)EK + (1+\omega_2)FG + (1-\omega_1\omega_2)FK > 0. \quad (29)$$

Notice that

$$\begin{aligned} \frac{\partial M_1}{\partial s_0}(s_0, y) &= -\frac{\partial \mu_1}{\partial s_0}(s_0, s_2) \left[ \frac{\partial \mu_1}{\partial s_2}(s_0, s_2) \right]^{-1} = -E/F. \\ \frac{\partial M_2}{\partial s_0}(s_0, y) &= -\frac{\partial \mu_2}{\partial s_0}(s_0, s_1) \left[ \frac{\partial \mu_2}{\partial s_1}(s_0, s_1) \right]^{-1} = -G/K. \end{aligned}$$

From (26), we deduce that:

$$\frac{\partial H}{\partial s_0}(s_0, D) = (\omega_1\omega_2 - 1) + (\omega_2 + 1)\left(-\frac{G}{K}\right) + (\omega_1 + 1)\left(-\frac{E}{F}\right).$$

Then,

$$\frac{\partial H}{\partial s_0}(s_0, D) = -\frac{(1-\omega_1\omega_2)FK + (\omega_1 + 1)EK + (\omega_2 + 1)GF}{FK}.$$

333 As a consequence, condition (29) is equivalent to  $\frac{\partial H}{\partial s_0}(s_0^*, D) < 0$ . This condition is always  
334 satisfied when  $\omega_1\omega_2 \leq 1$ .

335

□

## 336 Proof of Propositions 6.1 and 6.2.

337 From Table 4, and by using the change of variables (12), we obtain the conditions of existence  
338 and stability of (3), see Table 14,

Steady-state	Existence conditions	Stability conditions
$E_0$	Always exists	$\mu_1(S_0^{in}, \frac{v_{01}}{v_{21}} S_2^{in}) < D$ $\mu_2(S_0^{in}, \frac{v_{02}}{v_{12}} S_1^{in}) < D$
$E_1$	$\mu_1(S_0^{in}, \frac{v_{01}}{v_{21}} S_2^{in}) > D$	$\mu_2(S_0^{in} - \frac{v_{01}}{v_{21}} S_2^{in} + s_2^*,$ $\frac{v_{02}}{v_{12}} S_1^{in} + \omega_1(\frac{v_{01}}{v_{21}} S_2^{in} - s_2^*)) < D$
$E_2$	$\mu_2(S_0^{in}, \frac{v_{02}}{v_{12}} S_1^{in}) > D$	$\mu_1(S_0^{in} - \frac{v_{02}}{v_{12}} S_1^{in} + s_1^*,$ $\frac{v_{01}}{v_{21}} S_2^{in} + \omega_2(\frac{v_{02}}{v_{12}} S_1^{in} - s_1^*)) < D$
$E^*$	$S_0^{in} - \frac{v_{02}}{v_{12}} S_1^{in} > s_0^* - M_2(s_0^*, D)$ $S_0^{in} - \frac{v_{01}}{v_{21}} S_2^{in} > s_0^* - M_1(s_0^*, D)$ $S_1^{in} > F_1(D)$	$\frac{\partial H}{\partial S_0}(s_0^*, D) < 0$

Table 14: Existence and local stability of steady-states of (3)

with,

$$S^{in} = (\omega_1 \omega_2 - 1) S_0^{in} + (\omega_2 + 1) \frac{v_{02}}{v_{12}} S_1^{in} + (\omega_1 + 1) \frac{v_{01}}{v_{21}} S_2^{in}.$$

Using Table 14, we can see that:

- The steady-state  $E_0$  always exists and is stable for  $S_0^{in} < \sigma_1$ , since  $\mu_1(\sigma_1, \frac{v_{01}}{v_{21}} S_2^{in}) = 2 = D$ , and  $\mu_2(\sigma_1, \frac{v_{02}}{v_{12}} S_1^{in}) = 1 < D = 2$ . The first condition of stability of  $E_0$  becomes unfulfilled, for  $S_0^{in} > \sigma_1$ .
- $E_1$  exists for  $S_0^{in} > \sigma_1$ . Fig 10 shows that this steady-state is LES if and only if

$$S_0^{in} < \sigma_3,$$

$\sigma_3$  is the value of  $S_0^{in}$  such that

$$\mu_2(\sigma_3 - \frac{v_{01}}{v_{21}} S_2^{in} + s_2^*, \frac{v_{02}}{v_{12}} S_1^{in} + \omega_1(\frac{v_{01}}{v_{21}} S_2^{in} - s_2^*)) = D.$$



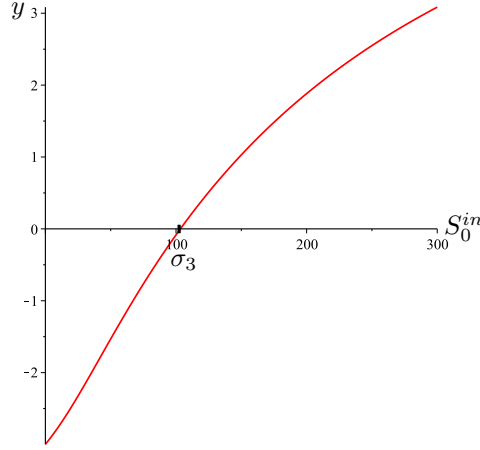


Figure 10: Curve of the function  $y = \mu_2(S_0^{in} - \frac{v_{01}}{v_{21}}S_2^{in} + s_2^*, \frac{v_{02}}{v_{12}}S_1^{in} + \omega_1(\frac{v_{01}}{v_{21}}S_2^{in} - s_2^*)) - D$ , in the case  $\omega_1\omega_2 < 1$ .

339 We have a similar figure for the case  $\omega_1\omega_2 \geq 1$ .

340 •  $E_2$  exists if and only if

$$341 \quad \mu_2(S_0^{in}, \frac{v_{02}}{v_{12}}S_1^{in}) > D. \quad (30)$$

Since  $\mu_2(\sigma_2, \frac{v_{02}}{v_{12}}S_1^{in}) = D$ , condition (30) is fulfilled when

$$S_0^{in} > \sigma_2.$$

342 From Fig 11 the steady-state  $E_2$  is unstable, because the condition of its stability is not satisfied  
343 for  $S_0^{in} > \sigma_2$ .

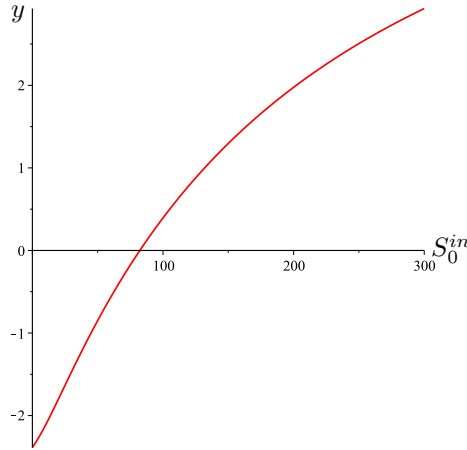


Figure 11: Curve of the function  $y = \mu_1(S_0^{in} - \frac{v_{02}}{v_{12}}S_1^{in} + s_1^*, \frac{v_{01}}{v_{21}}S_2^{in} + \omega_2(\frac{v_{02}}{v_{12}}S_1^{in} - s_1^*)) - D$ , in the case  $\omega_1\omega_2 < 1$ .

We can prove in a similar way that, in the case  $\omega_1\omega_2 \geq 1$ ,  $E_2$  is unstable for  $S_0^{in} > \sigma_2$ . Now, in the case  $\omega_1\omega_2 \leq 1$ , the positive steady-state  $E^*$  exists, for

$$S_0^{in} > \sigma_3.$$

344 This condition is obtained from the second condition of existence of  $E^*$  in Table 14. It guarantees  
345 the fulfillment of the first condition (see Fig. 12). From remark 2,  $E^*$  is always stable.

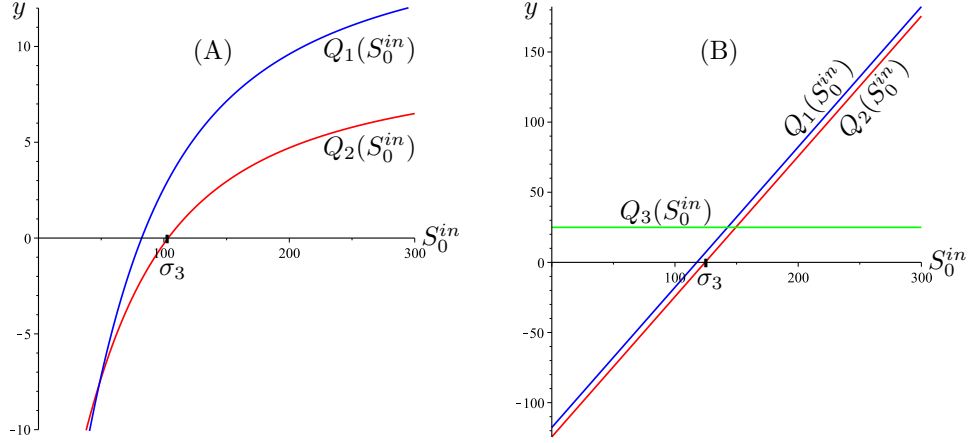


Figure 12: Curves of functions  $Q_1(S_0^{in}) = S_0^{in} - \frac{v_{02}}{v_{12}}S_1^{in} - s_0^* + M_2(s_0^*, D)$ ,  $Q_2(S_0^{in}) = S_0^{in} - \frac{v_{01}}{v_{21}}S_2^{in} - s_0^* + M_1(s_0^*, D)$  and  $Q_3(S_0^{in}) = S_0^{in} - M(D)$ . (A) In the case  $\omega_1\omega_2 < 1$ . (B) In the case  $\omega_1\omega_2 = 1$ .

For  $\omega_1\omega_2 > 1$ , from Table 14, the third condition of existence of positive steady-states is satisfied for

$$S_0^{in} > \frac{1}{\omega_1\omega_2 - 1} (F_1(D) - (\omega_2 + 1) \frac{v_{02}}{v_{12}} S_1^{in} - (\omega_1 + 1) \frac{v_{01}}{v_{21}} S_2^{in}) =: \sigma_4.$$

This is what Fig 13 (A) shows. Fig 13 (B) and Fig 13 (C) show that the first and the second existence condition of the positive steady state are always satisfied for  $E_1^*$  when  $S_0^{in} > \sigma_4$ .

For  $E_2^*$ , the first condition of existence is satisfied only when  $S_0^{in} \in [\sigma_4, \alpha]$ ,  $\alpha \simeq 142$ , and the second condition is satisfied when  $S_0^{in} \in [\sigma_4, \sigma_3]$ ,  $\sigma_3 \simeq 103.36$ . Then we deduce that the steady-state  $E_2^*$  exists for

$$S_0^{in} \in [\sigma_4, \alpha] \cap [\sigma_4, \sigma_3] = [\sigma_4, \sigma_3].$$

346 This is what explains that the steady state  $E_2^*$  disappears for  $S_0^{in} > \sigma_3$ . From Remark 2, the  
347 steady-states  $E_1^*$  is always stable, because the stability condition is always satisfied, and  $E_2^*$  is  
348 always unstable. Therefore, at  $S_0^{in} = \sigma_4$  there is a saddle-node bifurcation of  $E_1^*$  and  $E_2^*$  and a  
349 transcritical bifurcation of  $E_1$  and  $E_2^*$ , at  $S_0^{in} = \sigma_3$ .

350

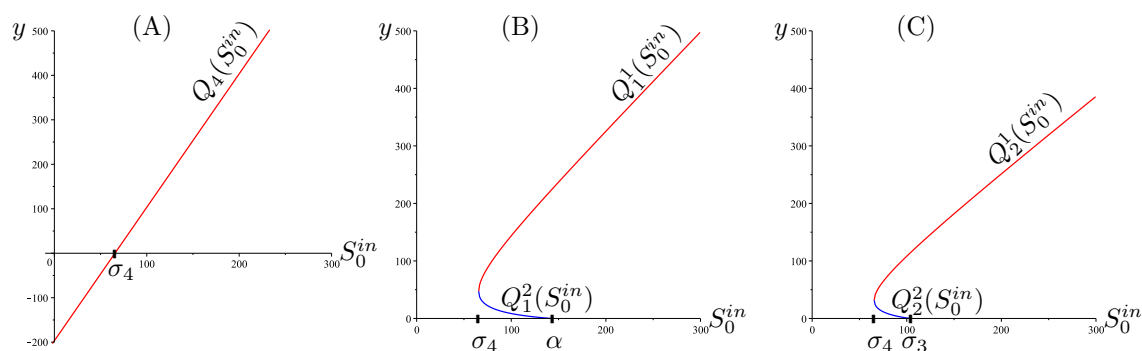


Figure 13: (A) Curve of the function  $Q_4(S_0^{in}) = S_0^{in} - F_1(D)$ . (B) Curves of the functions  $Q_1^1(S_0^{in}) = S_0^{in} - \frac{v_{02}}{v_{12}}S_1^{in} - s_0^1 + M_2(s_0^1, D)$  corresponding to  $E_1^*$  and  $Q_1^2(S_0^{in}) = S_0^{in} - \frac{v_{02}}{v_{12}}S_1^{in} - s_0^2 + M_2(s_0^2, D)$  corresponding to  $E_2^*$ . (C) Curves of the functions  $Q_2^1(S_0^{in}) = S_0^{in} - \frac{v_{01}}{v_{21}}S_2^{in} - s_0^1 + M_1(s_0^1, D)$  and  $Q_2^2(S_0^{in}) = S_0^{in} - \frac{v_{01}}{v_{21}}S_2^{in} - s_0^2 + M_1(s_0^2, D)$  corresponding to  $E_1^*$  and  $E_2^*$ , respectively.

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□

## References

352

- 353 [1] N. Abdellatif, R. Fekih-Salem and T. Sari, Competition for a single resource and coexistence  
 354 of several species in the chemostat, *Mathematical Bioscience and Engineering*, **13** (2016),  
 355 631–652, <https://doi.org/10.3934/mbe.2016012>.
- 356 [2] C. T. Bergstrom, J. L. Bronstein, R. Bshary, R. C. Connor, M. Daly, S. A. Frank, H.  
 357 Gintis, L. Keller, O. Leimar, R. Noë and D. C. Queller, Interspecific mutualism: puzzles and  
 358 predictions, *Genetic and Cultural Evolution of Cooperation*, P. Hammerstein, ed., MIT Press,  
 359 Cambridge, MA, (2003), 241–256.
- 360 [3] F. Chen, Permanance for the discrete mutualism model with time delays, *Mathematical and*  
 361 *Computer Modelling*, **47** (2008), 431–435, <https://doi.org/10.1016/j.mcm.2007.02.023>.
- 362 [4] Y. Daoud, N. Abdellatif, J. Harmand, Modèles mathématiques de digestion anaérobie: effet  
 363 de l’hydrolyse sur la production du biogaz, *Revue Africaine de la Recherche en Informatique et*  
 364 *Mathématiques Appliquées*, **28**, Mathematics for Biology and the Environment (2019), 25–59,  
 365 <https://doi.org/10.46298/arima.4440>.
- 366 [5] Y. Daoud, N. Abdellatif, T. Sari, and J. Harmand, Steady state analysis of a syntrophic  
 367 model: The effect of a new input substrate concentration, *Math. Model. Nat. Phenom.*, **13**  
 368 (2018), 1–22, <https://doi.org/10.1051/mmnp/2018037>.
- 369 [6] P. De Leenheer, D. Angeli and E. D. Sontag, Crowding effects promote coexistence in the  
 370 chemostat, *J. Math. Anal. Appl.*, **319** (2006), 48–60, <https://doi.org/10.1016/j.jmaa.2006.02.036>.  
 371
- 372 [7] M. Elhajji, J. Harmand, H. Chaker, C. Lobry, Assiation between competition and obligate  
 373 mutualism in a chemostat, *Journal of biological dynamics*, **3**, (6) (2009), 635–647, <http://dx.doi.org/10.1080/17513750902915978>.  
 374

- 375 [8] R. Fekih-Salem, J. Harmand, C. Lobry, A. Rapaport and T. Sari, Extensions of the chemostat  
376 model with flocculation, *J. Math. Anal. Appl.*, **397** (2013), 292–306, [https://doi.org/10.](https://doi.org/10.1016/j.jmaa.2012.07.055)  
377 [1016/j.jmaa.2012.07.055](https://doi.org/10.1016/j.jmaa.2012.07.055).
- 378 [9] R. Fekih-Salem, C. Lobry, T. Sari, A density-dependent model of competition for one  
379 resource in the chemostat, *Mathematical Biosciences*, **286** (2017), 104–122, [https://doi.](https://doi.org/10.1016/j.mbs.2017.02.007)  
380 [org/10.1016/j.mbs.2017.02.007](https://doi.org/10.1016/j.mbs.2017.02.007).
- 381 [10] R. Fekih-Salem and T. Sari, On the global stability of the coexistence equilibrium of a  
382 density dependent model of competition for one resource, *Proceedings of the 12th African*  
383 *Conference on Research in Computer Science and Applied Mathematics*, INRIA (2014), 19–  
384 30, <https://hal.archives-ouvertes.fr/hal-01128594>.
- 385 [11] B. S. Goh, Stability in models of mutualism, *The American Naturalist*, **113** (1979),  
386 261–276, <https://doi.org/10.1086/283384>.
- 387 [12] J. Harmand, C. Lobry, A. Rapaport, and T. Sari, The Chemostat: Mathematical Theory  
388 of Microorganism Cultures, *Chemical Eng. Ser.*, ISTE-Wiley, New York, 2017.
- 389 [13] J. Harmand, A. Rapaport, D. Dochain and C. Lobry, Microbial ecology and bioprocess  
390 control: Opportunities and challenges, *Journal of Process Control*, **18** (2008), 865–875, [https:](https://doi.org/10.1016/j.jprocont.2008.06.017)  
391 [//doi.org/10.1016/j.jprocont.2008.06.017](https://doi.org/10.1016/j.jprocont.2008.06.017).
- 392 [14] S. B. Hsu, Limiting behavior for competing species, *SIAM J. Appl. Math.*, **34** (1978),  
393 760–763, <https://doi.org/10.1137/0134064>.
- 394 [15] S. B. Hsu, S. P. Hubbell and P. Waltman, A mathematical theory for single-nutrient  
395 competition in continuous cultures of micro-organisms, *SIAM J. Appl. Math.*, **32** (1977),  
396 366–383, <https://doi.org/10.1137/0132030>.
- 397 [16] B. Li, Global asymptotic behavior of the chemostat: general response functions and dif-  
398 ferent removal rates, *SIAM J. Appl. Math.*, **59** (1998), 411–422, [https://doi.org/10.1137/](https://doi.org/10.1137/S003613999631100X)  
399 [S003613999631100X](https://doi.org/10.1137/S003613999631100X).
- 400 [17] C. Lobry and F. Mazenc, Effect on persistence of intra-specific competition in competi-  
401 tion models, *Electron. J. Diff. Eqns.*, **125** (2007), 1–10, [https://ejde.math.txstate.edu/](https://ejde.math.txstate.edu/Volumes/2007/125/lobry.pdf)  
402 [Volumes/2007/125/lobry.pdf](https://ejde.math.txstate.edu/Volumes/2007/125/lobry.pdf).
- 403 [18] C. Lobry, F. Mazenc and A. Rapaport, Persistence in ecological models of competition for  
404 a single resource, *C. R. Acad. Sci. Paris, Ser. I*, **340** (2005), 199–204, [https://doi.org/10.](https://doi.org/10.1016/j.crma.2004.12.021)  
405 [1016/j.crma.2004.12.021](https://doi.org/10.1016/j.crma.2004.12.021).
- 406 [19] C. Lobry, A. Rapaport and F. Mazenc, Sur un modèle densité-dépendant de compétition  
407 pour une ressource, *C. R. Biol.*, **329** (2006), 63–70, [https://doi.org/10.1016/j.crvi.](https://doi.org/10.1016/j.crvi.2005.11.004)  
408 [2005.11.004](https://doi.org/10.1016/j.crvi.2005.11.004).
- 409 [20] R. D. Megee III, J. F. Drake, A. G. Fredrickson and H. M. Tsuchiya, Studies in inter-  
410 microbial symbiosis. *Saccharomyces cerevisiae* and *Lactobacillus casei*, *Canadian Journal of*  
411 *Microbiology*, **18** (1972), 1733–1742, <https://doi.org/10.1139/m72-269>.
- 412 [21] J. Monod, La technique de culture continue: Théorie et applications, *Ann. Inst. Pasteur*,  
413 **79** (1950), 390–410.

- 414 [22] A. Novick, L. Szilard, Experiments with the chemostat on spontaneous mutations of  
415 bacteria, *Proceedings of the National Academy of Sciences*, **36**, no.12 (1950), 708–719,  
416 <https://dx.doi.org/10.1073/pnas.36.12.708>.
- 417 [23] S. Pavlou, Microbial competition in bioreactors, *Chemical Industry and Chemical Engi-*  
418 *neering Quarterly.*, **12** (2006), 71–81, <https://doi.org/10.2298/CICEQ0601071P>.
- 419 [24] T. Sari and J. Harmand, A model of a syntrophic relationship between two microbial species  
420 in a chemostat including maintenance, *Math. Biosci.*, **275** (2016), 1–9, [https://doi.org/](https://doi.org/10.1016/j.mbs.2016.02.008)  
421 [10.1016/j.mbs.2016.02.008](https://doi.org/10.1016/j.mbs.2016.02.008).
- 422 [25] H. L. Smith and P. Waltman, The Theory of the Chemostat: Dynamics of Microbial  
423 Competition, *Cambridge University Press*, 1995.
- 424 [26] J. H. Vandermeer, D. H. Boucher, Varieties of mutualistic interaction in population  
425 models, *Journal of Theoretical Biology*, **74** (1978), 549–558, [https://doi.org/10.1016/](https://doi.org/10.1016/0022-5193(78)90241-2)  
426 [0022-5193\(78\)90241-2](https://doi.org/10.1016/0022-5193(78)90241-2).
- 427 [27] S. Vet, S. De Buyl, K. Faust, J. Danckaert, D. Gonze, L. Gelens, Bistability in a sys-  
428 tem of two species interacting through mutualism as well as competition: Chemostat vs.  
429 Lotka-Volterra equations, *Plos One*, **13** (2018), [https://doi.org/10.1371/journal.pone.](https://doi.org/10.1371/journal.pone.0197462)  
430 [0197462](https://doi.org/10.1371/journal.pone.0197462).
- 431 [28] S. Vet, L. Gelens, D. Gonze, Mutualistic cross-feeding in microbial systems generates  
432 bistability via an Allee effect, *Scientific Reports*, **10** (2020), [https://doi.org/10.1038/](https://doi.org/10.1038/s41598-020-63772-4)  
433 [s41598-020-63772-4](https://doi.org/10.1038/s41598-020-63772-4).
- 434 [29] G. S. K. Wolkowicz and Z. Lu, Global dynamics of a mathematical model of competition in  
435 the chemostat: general response functions and differential death rates, *SIAM J. Appl. Math.*,  
436 **52** (1992), 222–233, <https://doi.org/10.1137/0152012>.
- 437 [30] Z. Zhang, Mutualism or cooperation among competitors promotes coexistence and compet-  
438 itive ability, *Ecological modelling*, **164**, (2-3) (2003), 271–282, [https://doi.org/10.1016/](https://doi.org/10.1016/S0304-3800(03)00069-3)  
439 [S0304-3800\(03\)00069-3](https://doi.org/10.1016/S0304-3800(03)00069-3).