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Association between competition and obligate mutualism in a chemostat

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In this paper, we consider a simple chemostat model involving two obligate mutualistic species feeding on a limiting substrate. Systems of differential equations are proposed as models of this association. A detailed qualitative analysis is carried out. We show the existence of a domain of coexistence, which is a set of initial conditions in which both species survive. We demonstrate, under certain supplementary assumptions, the uniqueness of the stable equilibrium point which corresponds to the coexistence of the two species.

Keywords: chemostat; competition; mutualism; asymptotic behaviour; coexistence; Dulac criterion; Thieme's result

1. Introduction

The study of the cooperation of living organisms has become of great interest over the last few decades because it is a common feature in nature [2,3]. Zientz *et al.* [27] emphasized that facultative or obligate intracellular bacteria can be found throughout the tree of life from protists to plants and animals, and that such biological relationships could have culminated with the stable integration of one cell into another as suggested in the endosymbiont theory [14,16]. In many cases, using lab experiments, it has been shown that mutualistic relationships were obligatory [4,5,10,17,18,24] and thus prevent competitive exclusion. Then, such interactions could be seen as a major factor of biodiversity. The study of this kind of biological interaction is not only relevant from a fundamental point of view but also from an engineering one. Indeed, in many practical situations, rendering the presence of a microorganism stable within a complex ecosystem presents important advantages. In particular, such obligatory relationships appear to be a possible way of maintaining a given species into a natural ecosystem while most attempts to maintain it by only playing with environmental conditions failed. Following this idea, a new class of synthetic cooperative system has recently been proposed. They are called CoSMO for cooperation that is synthetic and mutually obligatory [19]. In this paper, the yeast *Saccharomyces cerevisiae* was

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genetically modified to obtain two nonmating strains with different metabolic capabilities so that they behave essentially as two different species. More specifically they were made obligatory mutualists, the first one producing a protein necessary for the growth of the second one (while this synthesis was blocked within the metabolism of this second one) and conversely. Together, these two strains form a cooperative system that mimics two-species obligate mutualistic systems while being in competition on a single resource for their growth. The present paper aims at modelling such a complex system in a chemostat and at studying its theoretical properties.

The chemostat is an important laboratory apparatus used for the continuous culture of microorganisms. In ecology, it is often considered as a model of a simple lake system or of a wastewater treatment process. It is an excellent experimental venue in which one can study the effect of simple microbial interactions, including competition. Different mathematical models have been developed and analysed extensively by many different investigators (see, for example, the recent monograph by Smith and Waltman [21] and the references therein). Mathematical models of the chemostat are among the few predictive models in microbial ecology. The classical model of competition for a nonreproducing substrate in a well-stirred chemostat operated under constant input concentration and dilution predicts competitive exclusion. That is, it predicts that at most one competitor population avoids extinction [6,21,25,26]. However, the coexistence of competing populations is ubiquitous in nature. So, in order to explain this, it seems necessary to relax at least one of the assumptions in the above model. One natural approach is to introduce periodic coefficients to represent, for example, daily or seasonal variations in the environment. For this purpose, there has been some research on models of the chemostat involving either periodic nutrient input or periodic dilution rates [9,20,21]. An other natural approach is to make the hypothesis of a ratio-dependent growth rate [8,13,12,11,15] in the sense of [1]. As explained above, our approach in this paper is to consider obligate mutualism in the specific context of the competition of two species for a resource.

Freedman *et al.* [7] have proposed a particular model of two mutualistic predators. They assumed that the resource is governed by a logistic law and proved the existence of a locally stable equilibrium with both predators present. But the global behaviour is not described since it can be complex.

Our objective in this article is to reconsider the analysis of Freedman *et al.* [7] in the simpler case of a CoSMO system in the chemostat where, as it is well known, the presence of an attractive invariant set allows us to return the qualitative study to dimension 2. We prove the existence of two positive invariant domains such that one of them predicts the extinction and the other ensures the coexistence of the two species. We demonstrate, under certain supplementary assumptions, the uniqueness of a stable equilibrium point which corresponds to the coexistence of the two species. Finally, we illustrate the above results by numerical simulations.

2. Mathematical model and results

In this section we present our model and our results as Theorems 1–3 and their corollaries.

Let s , x_1 and x_2 denote, respectively, the concentration of substrate and the two microorganisms present in the chemostat at time t . We ignore all species-specific death rates and only consider the dilution rate. Our model is described by the following ordinary system of differential equations:

$$\begin{aligned}\dot{s} &= D(s_{in} - s) - f_1(s, x_2)x_1 - f_2(s, x_1)x_2, \\ \dot{x}_1 &= (f_1(s, x_2) - D)x_1, \\ \dot{x}_2 &= (f_2(s, x_1) - D)x_2,\end{aligned}\tag{1}$$

where s_{in} denotes the input concentration of nutrient and D is the dilution rate.

The functional response of each species $f_i : \mathbb{R}_+^2 \rightarrow \mathbb{R}_+$, $i = 1, 2$, satisfies:

H1: f_1 and f_2 are two $C^1(\mathbb{R}_+^2)$ functions.

H2: $f_1(0, x_2) = f_2(0, x_1) = 0, \forall (x_1, x_2) \in \mathbb{R}_+^2$.

H3: $(\partial f_1/\partial s)(s, x_2) > 0, \forall (s, x_2) \in \mathbb{R}_+^2$ and $(\partial f_2/\partial s)(s, x_1) > 0, \forall (s, x_1) \in \mathbb{R}_+^2$.

H4: $(\partial f_1/\partial x_2)(s, x_2) > 0, \forall (s, x_2) \in \mathbb{R}_+^2$ and $(\partial f_2/\partial x_1)(s, x_1) > 0, \forall (s, x_1) \in \mathbb{R}_+^2$.

H5: $f_1(s, 0) = f_2(s, 0) = 0, \forall s \in \mathbb{R}_+$.

Hypothesis *H2* expresses that no growth can take place without substrate; hypothesis *H3* means that the growth increases with substrate. Hypothesis *H4* expresses the mutualism between species and the hypothesis *H5* characterizes the obligate case where no nutrient uptake by one species occurs unless the other species is present.

We do not claim that Equation (1) plus *H1–H5* is a realistic model for the CoSMO system of bacteria. Actually it should be better to introduce in the model two supplementary state variables p_1 and p_2 representing the concentrations of the proteins produced, respectively, by species 1 and species 2, which are necessary for the growth of species 2 and species 1, respectively. But in this case the model would be in \mathbb{R}^5 and thus much more difficult to study. The model (1) is just a first step and its interest relies on the fact that it is completely tractable from the mathematical point of view.

Let us recall two fundamental well-known properties of the model of the chemostat [21].

PROPOSITION 1 (1) *For every initial condition in \mathbb{R}_+^3 , the solution of system (1) has positive components and is bounded and thus is defined for every positive t .*

(2) *The set $\Omega = \{(s, x_1, x_2) \in \mathbb{R}_+^3 / s + x_1 + x_2 = s_{in}\}$ is a positive invariant attractor of all solutions of system (1).*

For the convenience of the reader, we provide a proof.

(1) The invariance of \mathbb{R}_+^3 is guaranteed by the fact that if $s = 0$ then $\dot{s} = Ds_{in} > 0$ and if $x_i = 0$ then $\dot{x}_i = 0$ for $i = 1, 2$. Next we have to prove that the solution is bounded. If one adds the three equations of system (1), then one obtains, for $z = s + x_1 + x_2$, a single equation:

$$\dot{z} = \overbrace{(s + x_1 + x_2)}^{\dot{z}} = -D(s + x_1 + x_2 - s_{in}) = -D(z - s_{in});$$

then

$$z = s + x_1 + x_2 = s_{in} + Ke^{-Dt} \quad \text{where } K = z(0) = s(0) + x_1(0) + x_2(0) - s_{in}.$$

Since each term of the sum is positive, the solution is bounded.

(2) Point 2 is a direct consequence of the previous relation.

2.1. Restriction on the plane

We are interested in the asymptotic behaviour of the solutions of system (1). It is tempting to think that because the solutions of system (1) are exponentially convergent towards the set Ω , it is enough to restrict the study of the asymptotic behaviour of system (1) to Ω . In fact, this is false, in general, as shown by examples in [22,23]. However, fortunately, in our case, thanks to Thieme's results [22], the asymptotic behaviour of the solutions of the restriction of Equation (1) on Ω will be informative for the complete system. This justifies our study of the following reduced system.

Using the fact that $s = s_{in} - x_1 - x_2$, the projection, on the plane (x_1, x_2) , of the restriction of system (1) on Ω is given by

$$\begin{aligned}\dot{x}_1 &= x_1(f_1(s_{in} - (x_1 + x_2), x_2) - D) = g_1(x_1, x_2) x_1, \\ \dot{x}_2 &= x_2(f_2(s_{in} - (x_1 + x_2), x_1) - D) = g_2(x_1, x_2) x_2, \\ x_1, x_2 &\in T = \{(x_1, x_2) \in \mathbb{R}_+^2 / 0 \leq x_1 + x_2 \leq s_{in}\}.\end{aligned}\tag{2}$$

Let

$$\Gamma_1 = \{(x_1, x_2) \in T; g_1(x_1, x_2) = 0\} = \{(x_1, x_2) \in T; f_1(s_{in} - (x_1 + x_2), x_2) = D\}$$

and

$$\Gamma_2 = \{(x_1, x_2) \in T; g_2(x_1, x_2) = 0\} = \{(x_1, x_2) \in T; f_2(s_{in} - (x_1 + x_2), x_1) = D\}.$$

We remind that the nul-clines ($\dot{x}_1 = 0$ and $\dot{x}_2 = 0$) of system (2) are the sets:

$$C_1 = \Gamma_1 \cup \{(x_1, x_2) \in T; x_1 = 0\} \quad \text{and} \quad C_2 = \Gamma_2 \cup \{(x_1, x_2) \in T; x_2 = 0\}.$$

H6: Assume that the nul-clines are in ‘general position’, which means that Γ_1 and Γ_2 have a finite number of intersection points where Γ_1 and Γ_2 are transverse.

System (2) admits $E_p^0 = (0, 0)$ as an equilibrium point. Hypothesis *H5* implies that there is no equilibrium point of the form $(\bar{x}_1, 0)$ nor $(0, \bar{x}_2)$ where $\bar{x}_1 > 0$ and $\bar{x}_2 > 0$. However, this system can have positive equilibrium points.

THEOREM 1 (1) *There cannot be periodic orbits nor polycycles inside Ω .*

(2) *E_p^0 is a locally asymptotically stable equilibrium point and if $\max_{\mathbb{R}_+ \times \mathbb{R}_+} f_i(s, x_j) \leq D$ for at least one of the two species, then E_p^0 is the only equilibrium point.*

(3) *If $\max_{\mathbb{R}_+ \times \mathbb{R}_+} f_1(s, x_2) > D$ and $\max_{\mathbb{R}_+ \times \mathbb{R}_+} f_2(s, x_1) > D$, there can exist positive equilibrium points of the form $E_p^* = (x_1^*, x_2^*)$ where $x_1^* > 0$ and $x_2^* > 0$. In this case, there exist two domains R^0 and R^* such that for every initial conditions in R^0 , the two species go to extinction and for every initial conditions in R^* , the two species persist.*

Proof of Theorem 1. (1) Let us make the change of variables $X_1 = Ln(x_1)$ and $X_2 = Ln(x_2)$, then system (2) becomes

$$\begin{aligned}\dot{X}_1 &= g_1(e^{X_1}, e^{X_2}), \\ \dot{X}_2 &= g_2(e^{X_1}, e^{X_2}).\end{aligned}$$

Let

$$G(X_1, X_2) = \begin{pmatrix} g_1(e^{X_1}, e^{X_2}) \\ g_2(e^{X_1}, e^{X_2}) \end{pmatrix}$$

The divergence of G is given by

$$\operatorname{div} G = - \left[e^{X_1} \frac{\partial f_1}{\partial s}(s_{in} - (e^{X_1} + e^{X_2}), e^{X_2}) + e^{X_2} \frac{\partial f_2}{\partial s}(s_{in} - (e^{X_1} + e^{X_2}), e^{X_1}) \right] < 0$$

and the Dulac criterion [23] allows us to conclude.

(2) As $f_1(s_{in}, 0) = f_2(s_{in}, 0) = 0$, then, there exists a neighbourhood V_1 of $(0, 0)$ such as $(f_1(s_{in} - (x_1 + x_2), x_2) - D)|_{V_1} < 0$ which implies that $\dot{x}_1 < 0$ and a neighbourhood V_2 of $(0, 0)$

such that $(f_2(s_{in} - (x_1 + x_2), x_1) - D)|_{V_2} < 0$, which implies that $\dot{x}_2 < 0$, then $\forall (x_1(0), x_2(0)) \in V_1 \cap V_2$, (x_1, x_2) converges to $(0, 0)$

We can also deduce the local stability of E_p^0 by computing the Jacobian matrix at $(0, 0)$.

If $\max_{\mathbb{R}_+ \times \mathbb{R}_+} f_i(s, x_j) \leq D$ for at least one of the two species, then there are no intersection points between the sets Γ_1 and Γ_2 , then E_p^0 is the only equilibrium point.

- (3) Using the fact that functions $x_1 \rightarrow f_1(s_{in} - (x_1 + x_2), x_2)$ and $x_2 \rightarrow f_2(s_{in} - (x_1 + x_2), x_1)$ are decreasing, we deduce immediately that the sets Γ_1 and Γ_2 are the graphs of two functions $x_1 = \gamma_1(x_2)$ and $x_2 = \gamma_2(x_1)$. If $\max_{\mathbb{R}_+ \times \mathbb{R}_+} f_1(s, x_2) > D$ and $\max_{\mathbb{R}_+ \times \mathbb{R}_+} f_2(s, x_1) > D$, then the graphs Γ_1 and Γ_2 (the D -level line of function f_1 and f_2) are non-empty. By (H6), these sets can intersect only at a finite number of equilibrium points of the form $E_p^* = (x_1^*, x_2^*)$, where $x_1^* > 0$ and $x_2^* > 0$, called positive equilibrium points.

Since E_p^0 is locally asymptotically stable, there exists an attraction domain R^0 to $(0, 0)$.

Assume that the sets Γ_1 and Γ_2 intersect at some points. Then $R^* = \Omega \setminus R^0$ is non-empty and is a persistence domain. Indeed, for every initial conditions in R^0 , all species vanish and for every initial conditions in R^* , (x_1, x_2) converges to a stable equilibrium point (x_1^*, x_2^*) where $x_1^* > 0$ and $x_2^* > 0$. ■

Remark 1 There exist two limit values $\sigma_1 > 0$ and $\sigma_2 > 0$ such that if $x_i(0) \leq \sigma_i$ and $0 \leq x_j(0) \leq s_{in}$ for $i, j = 1, 2, i \neq j$, then the two species vanish. This means that the rectangles $[0, \sigma_1] \times [0, s_{in}]$ and $[0, s_{in}] \times [0, \sigma_2]$ are contained in R^0 .

Assume that the sets Γ_1 and Γ_2 intersect at some points. Let us call $S_1, N_1, S_2, N_2, \dots, S_n$ and N_n the intersection points along Γ_2 where we increase x_1 from 0 (see Figure 1). The tangent vector to Γ_1 (respectively, Γ_2) at an intersection point is given by $T_1(x_1^*, x_2^*) = \begin{pmatrix} \gamma_1'(x_2^*) \\ 1 \end{pmatrix}$

(respectively, $T_2(x_1^*, x_2^*) = \begin{pmatrix} 1 \\ \gamma_2'(x_1^*) \end{pmatrix}$).

The nature of the positive equilibrium points is given in the following lemma.

- LEMMA 1 (1) If $\det(T_1, T_2) < 0$, the equilibrium is locally asymptotically stable and if $\det(T_1, T_2) > 0$ the equilibrium is a saddle point.
 (2) The equilibrium points $S_i, i = 1, n$, are saddle points and the equilibrium points $N_i, i = 1, n$, are locally asymptotically stable.

Proof The Jacobian matrix of system (2) at (x_1^*, x_2^*) is given by

$$A_p^* = \begin{bmatrix} -x_1^* \frac{\partial f_1}{\partial s} & x_1^* \frac{\partial f_1}{\partial x_2} - x_1^* \frac{\partial f_1}{\partial s} \\ x_2^* \frac{\partial f_2}{\partial x_1} - x_2^* \frac{\partial f_2}{\partial s} & -x_2^* \frac{\partial f_2}{\partial s} \end{bmatrix}$$

with characteristic equation for the eigenvalues:

$$P(\lambda) = \lambda^2 - \text{tr}(A_p^*)\lambda + \det(A_p^*) = 0.$$

The derivatives of γ_1 and γ_2 are given by

$$\gamma_1'(x_2) = -1 + \frac{\partial f_1 / \partial x_2}{\partial f_1 / \partial s} \quad \text{and} \quad \gamma_2'(x_1) = -1 + \frac{\partial f_2 / \partial x_1}{\partial f_2 / \partial s},$$

hence

$$\det(T_1, T_2) = \gamma'_1(x_2)\gamma'_2(x_1) - 1 = \left(\frac{\partial f_1}{\partial x_2} \frac{\partial f_2}{\partial x_1} - \frac{\partial f_1}{\partial s} \frac{\partial f_2}{\partial x_1} - \frac{\partial f_1}{\partial x_2} \frac{\partial f_2}{\partial s} \right) / \frac{\partial f_1}{\partial s} \frac{\partial f_2}{\partial s}.$$

We verify immediately that $\det(A_p^*) = -x_1^*x_2^*(\partial f_1/\partial s)(\partial f_2/\partial s) \det(T_1, T_2)$. Then:

- (1) If $\det(T_1, T_2) < 0$, then $\det(A_p^*) > 0$ and the equilibrium is locally asymptotically stable and if $\det(T_1, T_2) > 0$, then $\det(A_p^*) < 0$ and the equilibrium is a saddle point.
- (2) For the equilibrium points $N_i, i = 1, n$, $\det(T_1, T_2) < 0$, then $\det(A_p^*) > 0$, and they are locally asymptotically stable and for the equilibrium points $S_i, i = 1, n$, $\det(T_1, T_2) > 0$, then $\det(A_p^*) < 0$ and the points $S_i, i = 1, n$, are saddle points.

■

Remark 2 The nature of the positive equilibrium points depends on the location of the graph Γ_1 with regard to the graph Γ_2 at the intersection point. Assume that the orientation of Γ_1 is by increasing x_2 ; then if Γ_1 is going inwards in the region of the x_1x_2 -plane bounded by the graph Γ_2 and the x_1 -axis, then this point is a saddle point and if Γ_1 is going outwards, then this point is locally asymptotically stable. In particular, the first intersection is a saddle point.

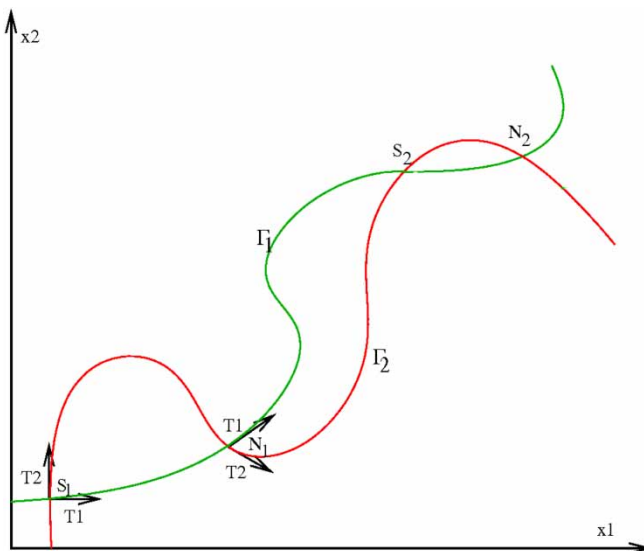


Figure 1. Location of graph Γ_1 with regard to the graph Γ_2 .

Example 1 In order to show that the number of positive equilibria could be greater than 2, we have constructed two functions that satisfy the necessary conditions of Theorem 1 for the existence of positive equilibrium points:

$$\begin{aligned} f_1(s, x_2) &= \frac{2}{\pi} \operatorname{arctg}(50x_2)s + \frac{2}{\pi} [\beta_1x_2 + \alpha_1 \sin(\omega_1x_2)] \operatorname{arctg}(50s), \\ f_2(s, x_1) &= \frac{2}{\pi} \operatorname{arctg}(50x_1)s + \frac{2}{\pi} [\beta_2x_1 + \alpha_2 \sin(\omega_2x_1)] \operatorname{arctg}(50s), \end{aligned} \tag{3}$$

where the constants α_i, β_i and ω_i are strictly positive, such that $\alpha_i\omega_i < \beta_i, i = 1, 2$. We present here the cases of four and six positive equilibrium points (see Figures 2 and 3).

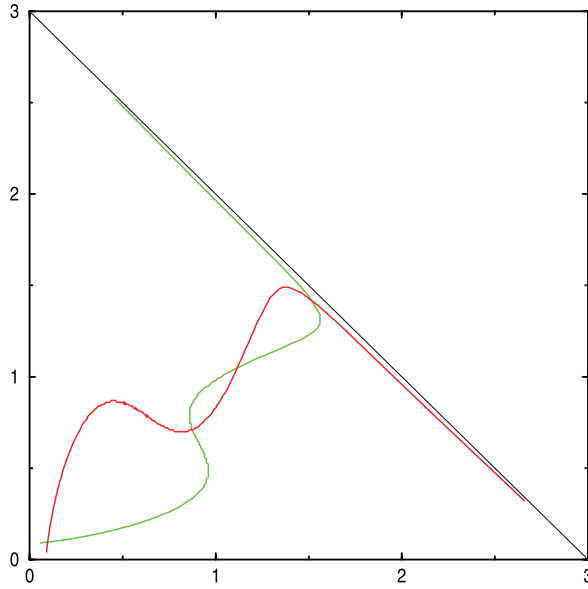


Figure 2. $\beta_1 = 2.2, \beta_2 = 2, \alpha_1 = \alpha_2 = 0.35, \omega_1 = \omega_2 = 5$.

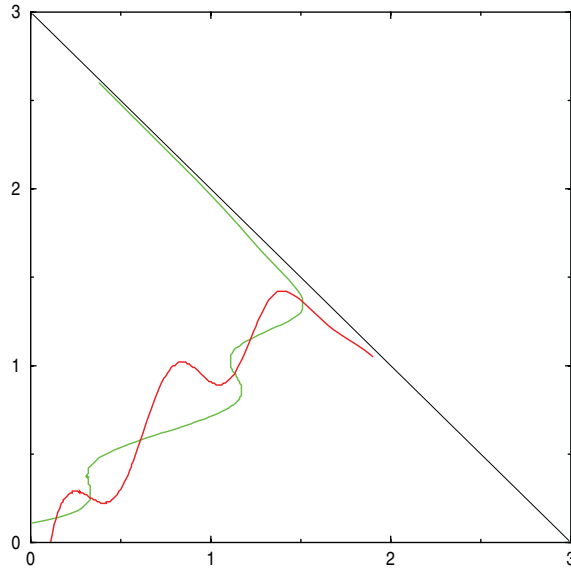


Figure 3. $\beta_1 = 2, \beta_2 = 2.2, \alpha_1 = 0.195, \alpha_2 = 0.18, \omega_1 = \omega_2 = 10$.

COROLLARY 1 *If E_p^0 is the only equilibrium point, then it is globally asymptotically stable and $R^0 = \Omega$.*

Proof We assume that E_p^0 is the only equilibrium point. Since the omega limit set of any trajectory is contained in the two-dimensional compact and positively invariant set Ω , and E_p^0 lies on the boundary of Ω , E_p^0 must be globally asymptotically stable by the Poincaré–Bendixson theorem. ■

2.2. Uniqueness of the stable equilibrium point

Next, we present some constraints on the response functional for which we have at most one stable positive equilibrium point.

THEOREM 2 *If Γ_1 and Γ_2 are concave, then system (2) has at most two positive equilibrium points. There exists a value D_0 such that*

- (1) *If $D < D_0$, system (2) has exactly two equilibrium points in the interior of Ω ; one of them is locally asymptotically stable and the second is a saddle point.*
- (2) *If $D > D_0$, then there are no equilibrium points in the interior of Ω .*

Proof of Theorem 2. Assume that Γ_1 and Γ_2 intersect. Let A and B be two consecutive intersection points. Let Δ_{AB} be the straight line joining A and B , let Δ_A be the parallel to the second bissectrice passing through A and Δ_B the one passing through B . These three lines define six regions $1A, 1AB, 1B$ and $2A, 2AB, 2B$ in the plane (see Figure 4). Since the function $(x_1, x_2) \mapsto f_1(s_{in} - (x_1 + x_2), x_2)$ is monotone along any line $x_1 + x_2 = k$, it turns out that the lines Δ_A and Δ_B must not intersect Γ_1 except in A and B . Γ_1 is a graph of a concave function of x_2 , and the position of Γ_1 between A and B must belong to $2AB$. This proves that Γ_1 must belong to $1A$ and $1B$. For the same reasons, Γ_2 must belong to $1AB, 2A$ and $2B$ and by the way $\Gamma_1 \cap \Gamma_2$ is reduced to A and B .

Using Lemma 1, A is a saddle point and B is a stable equilibrium point.

Γ_1 and Γ_2 are the D -level line of functions $(x_1, x_2) \mapsto f_1(s_{in} - (x_1 + x_2), x_2)$ and $(x_1, x_2) \mapsto f_2(s_{in} - (x_1 + x_2), x_1)$; hence there exists a value D_0 such that if $D < D_0$, system (2) has two equilibrium points inside Ω and if $D > D_0$, there are no intersection points. ■

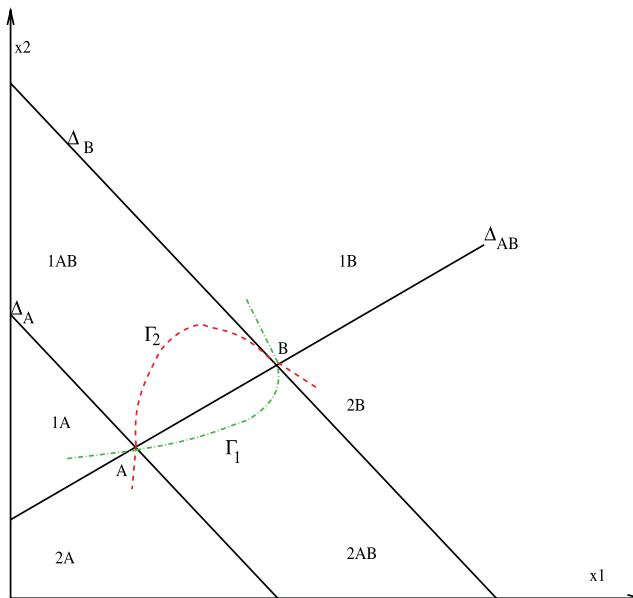


Figure 4. Γ_1 and Γ_2 are concave.

We present in the next corollary two particular cases for which the conditions of Theorem 2 are satisfied and by the way the uniqueness of the stable equilibrium point inside Ω .

COROLLARY 2 Let f_1 and f_2 be two $C^2(\mathbb{R}_+^2)$ functions. If one of the next conditions is satisfied,

- (1) f_1 and f_2 are concave functions,
- (2) $f_1(s, x_2) = g_1(s)h_1(x_2)$ and $f_2(s, x_1) = g_2(s)h_2(x_1)$ where g_1, g_2, h_1 and h_2 are four concave functions,

then system (2) has at most two equilibrium points inside Ω of which only one is locally asymptotically stable.

Proof (1) If the functions f_1 and f_2 are concave then their Hessians H_1 and H_2 are negative semidefinite matrix. In particular,

$$\gamma_1''(x_2) = \frac{\langle H_1 v_1, v_1 \rangle}{\partial f_1 / \partial s} < 0 \quad \text{and} \quad \gamma_2''(x_1) = \frac{\langle H_2 v_2, v_2 \rangle}{\partial f_2 / \partial s} < 0,$$

where $v_1 = (\gamma_1'(x_2) + 1, -1)^T$ and $v_2 = (\gamma_2'(x_1) + 1, -1)^T$.

Hence the graphs Γ_1 and Γ_2 are concave and the result is deduced from Theorem 2.

- (2) If $f_1(s, x_2) = g_1(s)h_1(x_2)$ and $f_2(s, x_1) = g_2(s)h_2(x_1)$ where g_1, g_2, h_1 and h_2 are concave functions, then

$$\gamma_1''(x_2) = \frac{-2(\gamma_1'(x_2) + 1)g_1'(s)h_1'(x_2) + g_1(s)h_1''(x_2) + (\gamma_1'(x_2) + 1)^2g_1''(s)h_1(x_2)}{g_1'(s)h_1(x_2)} < 0$$

and

$$\gamma_2''(x_1) = \frac{-2(\gamma_2'(x_1) + 1)g_2'(s)h_2'(x_1) + g_2(s)h_2''(x_1) + (\gamma_2'(x_1) + 1)^2g_2''(s)h_2(x_1)}{g_2'(s)h_2(x_1)} < 0$$

then graphs Γ_1 and Γ_2 are concave and the result is deduced from Theorem 2. ■

Remark 3 If $f_1(s, x_2) = a_1 x_2 g(s)$ and $f_2(s, x_1) = a_2 x_1 g(s)$, we can verify immediatly that:

$$a_2 x_1 - a_1 x_2 = (a_2 x_1(0) - a_1 x_2(0))e^{-Dt}$$

then the qualitative study can be reduced to one dimensional.

2.3. Reconstruction of the asymptotic behaviour of system (1)

It turns out that the phase portrait of system reduced to Ω (2) contains only locally stable equilibria, saddle points and no trajectory joining two saddle points. Thus we can apply Thieme's results [22] and conclude that the asymptotic behaviour of the solution of the complete system (1) is similar to the asymptotic behaviour described for the reduced system (2).

Let $E^0 = (0, 0, 0)$ and $E^* = (s^*, x_1^*, x_2^*)$ be the equilibrium points of system (1) such that its projection in the plane (x_1, x_2) are the equilibrium points $E_p^0 = (0, 0)$ and $E_p^* = (x_1^*, x_2^*)$ of system (2).

THEOREM 3 (1) E^0 is locally asymptotically stable.

(2) E_p^* and E^* have the same type of stability.

(3) The ω -limit set of a solution of Equation (1) is reduced to one of the equilibria of Equation (1).

- (4) If the persistence domain is non-empty for the reduced system (2), then the persistence domain of the full system (1) is non-empty. Any trajectory of initial condition in this domain converges to an interior equilibrium point in Ω .

Proof of Theorem 3. Let us recall that $z = s + x_1 + x_2$. We verify immediately that system (1) is equivalent to the system below:

$$\begin{aligned} \dot{z} &= -Dz, \\ \dot{x}_1 &= x_1(f_1(z - (x_1 + x_2), x_2) - D), \\ \dot{x}_2 &= x_2(f_2(z - (x_1 + x_2), x_1) - D). \end{aligned}$$

- (1) The Jacobian matrix at E^0 is $-DI_3$, then E^0 is locally asymptotically stable.
 (2) The Jacobian matrix at E^* is given by

$$A^* = \begin{bmatrix} -D & 0 & 0 \\ x_1^* \frac{\partial f_1}{\partial s} & -x_1^* \frac{\partial f_1}{\partial s} & x_1^* \frac{\partial f_1}{\partial x_2} - x_1^* \frac{\partial f_1}{\partial s} \\ x_2^* \frac{\partial f_2}{\partial s} & x_2^* \frac{\partial f_2}{\partial x_1} - x_2^* \frac{\partial f_2}{\partial s} & -x_2^* \frac{\partial f_2}{\partial s} \end{bmatrix}.$$

Thus $-D$ is an eigenvalue and the two other eigenvalues are the same as those of A_p^* associated to system (2), then the positive equilibrium points E^* and E_p^* have the same nature.

- (3) Let (s, x_1, x_2) some bounded solution of system (1) then its ω -limit, called ω , set is not empty. We have seen that $s = s_{in} - x_1 - x_2 + Ke^{-Dt}$ and (x_1, x_2) is solution of

$$\begin{aligned} \dot{x}_1 &= x_1(f_1(s_{in} - (x_1 + x_2) + Ke^{-Dt}, x_2) - D), \\ \dot{x}_2 &= x_2(f_2(s_{in} - (x_1 + x_2) + Ke^{-Dt}, x_1) - D). \end{aligned} \tag{4}$$

For every value of $s(0)$, we have a non-autonomous system (4) in which the right-hand side converges to the right-hand side of system (2). The set ω is contained in Ω , which contains only a finite number of equilibrium points. On the other hand, we saw that the reduced system (2) does not admit periodic orbits nor cyclic chains. From [22, Theorem 1.6], we deduce that the ω -limit set consists of an equilibrium of Equation (2).

- (4) Using Thieme’s results [22], we conclude that if systems (1) and (2) have the same asymptotic behaviour, then the persistence domain of the full system (1) is non-empty. ■

3. Numerical simulations

We performed numerical simulations on the two systems. The first uses classical Monod functions to express growth rates, and the second is somewhat artificial and uses the two functions we used in example 1 to show that the number of interior equilibria could be greater than 2.

In both cases, we compare two different values of the dilution rate D showing the bifurcation phenomenon (see Figures 5 and 6).

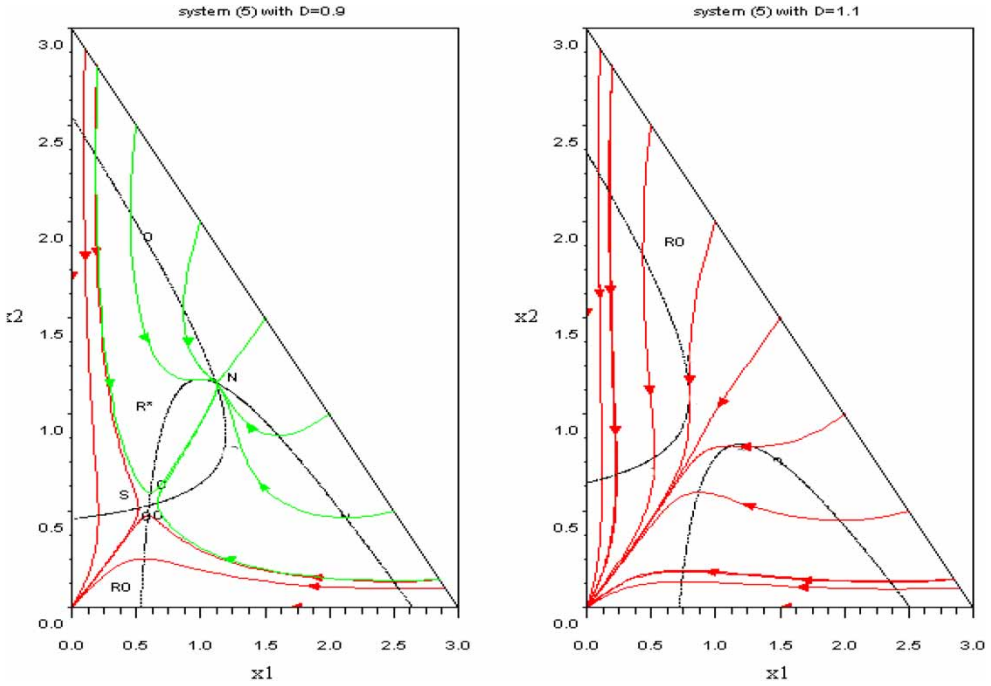


Figure 5. Left: the green trajectories are filling the domain R^* of coexistence and converging to the equilibrium N . The red trajectories converge to $(0, 0)$ and fill the domain R^0 . The boundary of R^0 and R^* consists in the two stable trajectories of the saddle point S . Right: the domain R^0 is the whole domain Ω . Available in colour online.

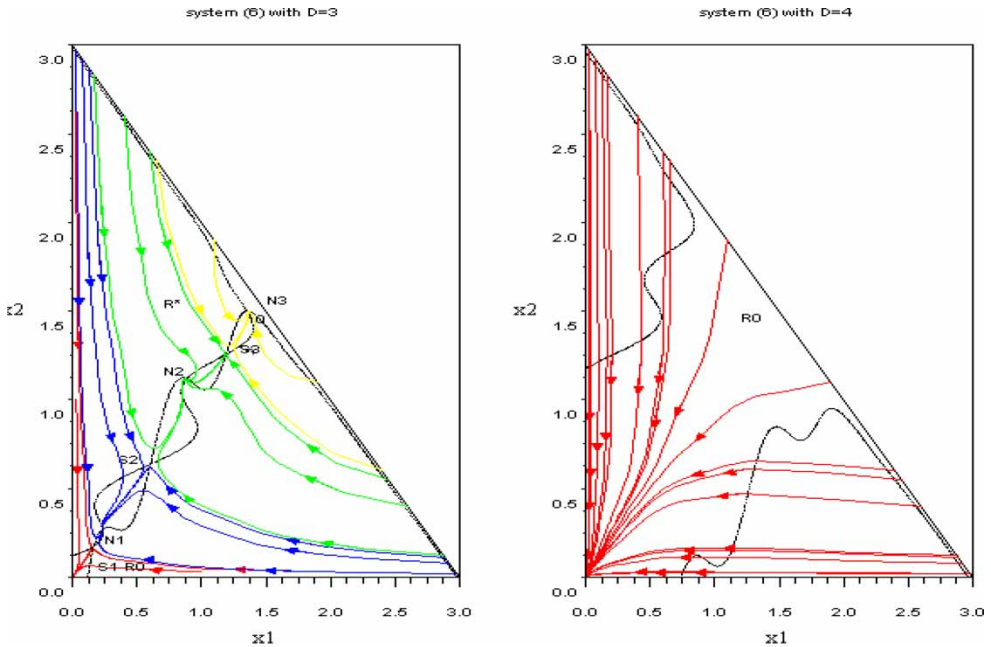


Figure 6. Left: the red trajectories fills the domain R^0 . The blue, green and yellow trajectories are filling the coexistence domain R^* . Blue trajectories converges to N_1 , green ones to N_2 and yellow ones to N_3 ; the reached equilibrium depends on initial conditions. Right: the domain R^0 is the whole domain Ω . Available in colour online.

3.1. Numerical test 1

$$\begin{aligned}\dot{s} &= D(3-s) - 4\frac{s}{1+s}\frac{x_2}{1+x_2}x_1 - 6\frac{s}{1+s}\frac{x_1}{2+x_1}x_2, \\ \dot{x}_1 &= \left(4\frac{s}{1+s}\frac{x_2}{1+x_2} - D\right)x_1, \\ \dot{x}_2 &= \left(6\frac{s}{1+s}\frac{x_1}{2+x_1} - D\right)x_2.\end{aligned}\tag{5}$$

3.2. Numerical test 2

$$\begin{aligned}\dot{s} &= D(3-s) - \left(\frac{2}{\pi}\arctg(50x_2)s + \frac{2}{\pi}[2x_2 + 0.195\sin(10x_2)]\arctg(50s)\right)x_1 \\ &\quad - \left(\frac{2}{\pi}\arctg(50x_1)s + \frac{2}{\pi}[2.2x_1 + 0.18\sin(10x_1)]\arctg(50s)\right)x_2, \\ \dot{x}_1 &= \left(\frac{2}{\pi}\arctg(50x_2)s + \frac{2}{\pi}[2x_2 + 0.195\sin(10x_2)]\arctg(50s) - D\right)x_1, \\ \dot{x}_2 &= \left(\frac{2}{\pi}\arctg(50x_1)s + \frac{2}{\pi}[2.2x_1 + 0.18\sin(10x_1)]\arctg(50s) - D\right)x_2.\end{aligned}\tag{6}$$

4. Conclusion

We have considered the mathematical model (1) of competition for one resource with obligate mutualism. We proved, under general and natural assumptions of monotony on f_1 and f_2 , the existence of a domain of extinction and a domain of persistence. Under these general assumptions the persistence equilibrium is not necessary unique as we showed with a somewhat artificial example (6). If we restrict to functions f_1 and f_2 , which are the products of Monod functions as it is often the case in more specific biological models, the equilibrium is unique.

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