



Local Analysis for a Mutual Inhibition in Presence of Two Viruses in a Chemostat

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Abstract: A competition with mutual inhibition is a form of direct competition between the populations of two species where each actively inhibits the other. In this paper, we consider a mathematical system of ordinary differential equations describing two species, with mutual inhibition, competing for a limiting substrate in the presence of two viruses. A detailed local qualitative analysis of the restriction of the system to the attractor set is carried out. We prove that for general nonlinear response functions, the Competitive Exclusion Principle is still fulfilled so that at most one species can survive. Initial species concentrations are important in determining which is the winning species. The results obtained were validated by numerical simulations using Matlab software.

Keywords: *chemostat; competition; reversible inhibition; virus; local analysis; competitive exclusion principle.*

Mathematics Subject Classification (2010): 34D20, 37C75, 65L07, 65L20, 92B05, 92B10, 93B18, 93D20.

1 Introduction

A chemostat is a laboratory device (bioreactor) in which organisms grow on the available nutrient in a controlled manner. In many applications, it is simply a vessel used as a wastewater treatment process [18]. In ecology, it refers to an artificial lake for the continuous culture of bacteria which allows us to analyse inter-specific interactions between bacteria. A large number of mathematical studies have been published [18]. The most used mathematical system modelling the bacterial competition for a single obligate limiting substrate predicts competitive exclusion [12], that is, at least one competitor bacteria loses the competition [18]. Hsu et al. [15] in 1977, were among the first to study the problem of competition in a chemostat. They considered n populations in competition for the same nutrient and showed that competitive exclusion was verified, namely, the competitor which is better at using the substrate in small quantities survives and the others are extinguished. In the case of nonmonotonic growth functions, Butler and Wolkowicz [2] in 1985, also verified the competitive exclusion principle. In 1992, Wolkowicz and Lu [19] used Lyapunov functions to also verify the competitive exclusion principle in the case of general shape-growth functions, but with different mortality rates. For each species, the competitive exclusion principle was further checked (the resulting equilibrium being globally stable). Li [16] recently extended this result to

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an even wider class of growth functions. In 1994, Smith and Waltman [17] verified this principle for the Droop model. Wolkowicz and Xia [20] and Wolkowicz et al. [21] studied competition in a chemostat with the recycling of dead organisms for different types of delays (discrete, distributed). This theoretical result (Competitive Exclusion Principle) was confirmed experimentally by Hansen and Hubbell [11].

In many cases, the competing bacteria can produce a plethora of secondary metabolites to increase their competitiveness against other bacteria. For example, the production of *Nisin* by a number of strains of *Lactococcus lactis*, which exert a high antibacterial activity against Gram-positive bacteria, has been widely studied [13,14]. This inter-specific interaction is classified as an inhibition relationship. Viruses are the most abundant and diverse form of life on the Earth. They can infect all types of organisms (*Vertebrates*, *Invertebrates*, *Plants*, *Fungi*, *Bacteria*, *Archaea*). Viruses that infect bacteria are called *bacteriophages* or *phages*.

In this work, we extend the chemostat model [18] to general growth rates taking into account the reversible inhibition between species as in [3,4,6], but in the presence of two viruses. As our study is qualitative, we assume that the two species are feeding on a nonreproducing limiting substrate that is essential for both species. We also assume that the chemostat is well-mixed so that environmental conditions are homogeneous. We neglect the natural mortality of the species and the viruses, compared to the removal rate D . We prove that with general nonlinear response functions, the mutual inhibitory relationship between two competing species confirms the competitive exclusion principle (CEP). We have shown that at least one of the species becomes extinct and that initial species concentrations are important in determining which is the winning species.

The rest of the paper is structured as follows. In Section 2, we propose a mathematical model for this association and we recall some useful results of the chemostat theory. In Section 3, we restrict the model to four dimensions since the conservation of the total biomass is fulfilled. In Sections 4, 5 and 6, three cases are considered, where the main results of the local stability are presented. Finally, in Section 7, some numerical examples are presented to illustrate the obtained results confirming the competitive exclusion principle.

2 Mathematical Model and Properties

The proposed normalised mathematical model is given by

$$\begin{cases} \dot{s} &= Ds^{in} - f_1(s, x_2) x_1 - f_2(s, x_1) x_2 - Ds, \\ \dot{x}_1 &= f_1(s, x_2)x_1 - \alpha_1 x_1 v_1 - Dx_1, \\ \dot{x}_2 &= f_2(s, x_1)x_2 - \alpha_2 x_2 v_2 - Dx_2, \\ \dot{v}_1 &= \alpha_1 x_1 v_1 - Dv_1, \\ \dot{v}_2 &= \alpha_2 x_2 v_2 - Dv_2, \end{cases} \quad (1)$$

where $s^{in} > 0$ is the input concentration of substrate into the chemostat, $D > 0$ is the dilution rate. $\alpha_i > 0$ is the rate of infection, $s(t)$ is the concentration of substrate in the chemostat at time t . $x_i(t)$ is the i^{th} species concentration in the chemostat at time t , $v_i(t)$ is the i^{th} virus concentration in the chemostat at time t , $f_i(s, x_j)$ is the species growth rate depending on substrate and the concentration of the other species. The functions $f_i : \mathbb{R}_+^2 \rightarrow \mathbb{R}_+$, $i = 1, 2$, are of class \mathcal{C}^1 , and satisfy

$$\mathbf{A1} \quad f_1(0, x_2) = f_2(0, x_1) = 0, \quad \forall x_1, x_2 \in \mathbb{R}_+.$$

$$\mathbf{A2} \quad \frac{\partial f_1}{\partial s}(s, x_2) > 0, \quad \forall (s, x_2) \in \mathbb{R}_+^2, \quad \frac{\partial f_2}{\partial s}(s, x_1) > 0, \quad \forall (s, x_1) \in \mathbb{R}_+^2.$$

$$\mathbf{A3} \quad \frac{\partial f_1}{\partial x_2}(s, x_2) < -\alpha_1 < 0, \quad \forall (s, x_2) \in \mathbb{R}_+^2, \quad \frac{\partial f_2}{\partial x_1}(s, x_1) < -\alpha_2 < 0, \quad \forall (s, x_1) \in \mathbb{R}_+^2.$$

Hypothesis **A1** states that the substrate is essential for the bacteria growth; hypothesis **A2** states that the growth rate increases with substrate. Hypothesis **A3** states that species inhibit each other and that each species is more sensitive to the other species than to the virus.

The system (1) plus **A1-A3** is not a realistic model for the biological system under consideration. To be more realistic, we should introduce two other variables describing intermediate

proteins. Each protein produced by species x_i inhibits the growth of species j , where $i, j = 1, 2$ and $i \neq j$. In this case, the model will be huge (\mathbb{R}^7) and then difficult to study.

El Hajji [3] considered two species feeding on limiting substrate in a chemostat assuming a mutual inhibitory relationship between both species. The proposed model is the same as the one we have proposed here, but with $\alpha_1 = \alpha_2 = 0$ (no viruses associated with both species). The author proved that at most one species can survive, which confirms the competitive exclusion principle. The author also proved that, in the case where there are two locally stable equilibrium points, the initial concentrations of species are of great importance in determining which species is the winner.

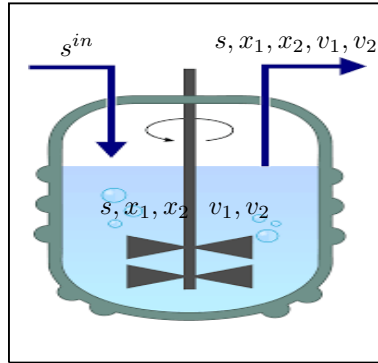


Figure 1: A simple chemostat schematic [3]: a continuous stirring mechanism at equal inflow and outflow rates (D), where two species (x_1, x_2) are competing for a limiting substrate (s) in the presence of two viruses (v_1, v_2), with an input concentration of substrate (s^{in}) and an output concentration of substrate (s), species concentrations (x_1, x_2) and virus concentrations (v_1, v_2).

Proposition 2.1 1. Let the initial condition $(s(0), x_1(0), x_2(0), v_1(0), v_2(0)) \in \mathbb{R}_+^5$, the solution of model (1) admit positive bounded components and then be definite for all $t \geq 0$.

2. $\Omega = \{(s, x_1, x_2, v_1, v_2) \in \mathbb{R}_+^5 / s + x_1 + x_2 + v_1 + v_2 = s^{in}\}$ is an invariant attractor set of all solutions of model (1).

Proof. The solutions' positivity can be proved as follows. If $s = 0$, then $\dot{s} = Ds^{in} > 0$, and if $x_i = 0$, then $\dot{x}_i = 0$ for $i = 1, 2$. If $v_i = 0$, then $\dot{v}_i = 0$ for $i = 1, 2$.

Next we prove the boundedness of solutions of model (1). Let $B(t) = s(t) + x_1(t) + x_2(t) + v_1(t) + v_2(t) - s^{in}$, then one obtains a single equation given by

$$\dot{B}(t) = \dot{s}(t) + \dot{x}_1(t) + \dot{x}_2(t) + \dot{v}_1(t) + \dot{v}_2(t) = D(s^{in} - s(t) - x_1(t) - x_2(t) - v_1(t) - v_2(t)) = -DB(t),$$

then $B(t) = B(0)e^{-Dt}$, which means that

$$s(t) + x_1(t) + x_2(t) + v_1(t) + v_2(t) = s^{in} + (s(0) + x_1(0) + x_2(0) + v_1(0) + v_2(0) - s^{in})e^{-Dt}. \tag{2}$$

Since s, x_1, x_2, v_1 and v_2 are positive, the solution of model (1) is bounded.

The invariance of the attractor Ω is a consequence of equation (2).

3 Restriction of System (1) to the Invariant Attractor Set Ω

The solutions of model (1) converge exponentially into Ω . Since we are studying the asymptotic behavior of (1), it is sufficient to restrict the study of model (1) to Ω . The projection of the restriction of model (1) to Ω on the plane (x_1, x_2, v_1, v_2) is given as follows:

$$\begin{cases} \dot{x}_1 &= f_1(s^{in} - (x_1 + x_2 + v_1 + v_2), x_2)x_1 - \alpha_1 x_1 v_1 - Dx_1, \\ \dot{x}_2 &= f_2(s^{in} - (x_1 + x_2 + v_1 + v_2), x_1)x_2 - \alpha_2 x_2 v_2 - Dx_2, \\ \dot{v}_1 &= \alpha_1 x_1 v_1 - Dv_1, \\ \dot{v}_2 &= \alpha_2 x_2 v_2 - Dv_2, \end{cases} \tag{3}$$

where the state vector (x_1, x_2, v_1, v_2) inside the sub-set is defined by

$$\mathcal{S} = \{(x_1, x_2, v_1, v_2) \in \mathbb{R}_+^4 : x_1 + x_2 + v_1 + v_2 \leq s^{in}\}.$$

In this section, the equilibria of system (3) are determined and their local stability properties are established. Define the parameters $\bar{x}_1, \bar{x}_2, \bar{v}_1, \bar{v}_2, \bar{\bar{x}}_1, \bar{\bar{x}}_2, \bar{\bar{v}}_1, \bar{\bar{v}}_2$, as follows:

- \bar{x}_1 is the solution of the equation $f_1(s^{in} - \bar{x}_1, 0) = D$.
- \bar{x}_2 is the solution of the equation $f_2(s^{in} - \bar{x}_2, 0) = D$.
- \bar{v}_1 is the solution of the equation $f_1(s^{in} - \frac{D}{\alpha_1} - \bar{v}_1, 0) = D + \alpha_1 \bar{v}_1$.
- \bar{v}_2 is the solution of the equation $f_2(s^{in} - \frac{D}{\alpha_2} - \bar{v}_2, 0) = D + \alpha_2 \bar{v}_2$.
- $(\bar{\bar{x}}_1, \bar{\bar{x}}_2)$ is the solution of the equations $f_1(s^{in} - \bar{\bar{x}}_1 - \bar{\bar{x}}_2, \bar{\bar{x}}_2) = f_2(s^{in} - \bar{\bar{x}}_1 - \bar{\bar{x}}_2, \bar{\bar{x}}_1) = D$.
- $(\bar{\bar{v}}_1, \bar{\bar{v}}_2)$ is the solution of the equations $f_1(s^{in} - \bar{\bar{x}}_1 - \frac{D}{\alpha_2} - \bar{\bar{v}}_2, \frac{D}{\alpha_2}) = D$ and $f_2(s^{in} - \bar{\bar{x}}_1 - \frac{D}{\alpha_2} - \bar{\bar{v}}_2, \bar{\bar{x}}_1) - \alpha_2 \bar{\bar{v}}_2 = D$.
- $(\bar{\bar{x}}_2, \bar{\bar{v}}_1)$ is the solution of the equations $f_1(s^{in} - \frac{D}{\alpha_1} - \bar{\bar{x}}_2 - \bar{\bar{v}}_1, \bar{\bar{x}}_2) - \alpha_1 \bar{\bar{v}}_1 = D$ and $f_2(s^{in} - \frac{D}{\alpha_1} - \bar{\bar{x}}_2 - \bar{\bar{v}}_1, \frac{D}{\alpha_1}) = D$.

Then the system (3) admits $F_0 = (0, 0, 0, 0), F_1 = (\bar{x}_1, 0, 0, 0), F_2 = (0, \bar{x}_2, 0, 0), F_3 = (\frac{D}{\alpha_1}, 0, \bar{v}_1, 0), F_4 = (0, \frac{D}{\alpha_2}, 0, \bar{v}_2), F_5 = (\bar{\bar{x}}_1, \bar{\bar{x}}_2, 0, 0), F_6 = (\bar{\bar{x}}_1, \frac{D}{\alpha_2}, 0, \bar{\bar{v}}_2)$ and $F_7 = (\frac{D}{\alpha_1}, \bar{\bar{x}}_2, \bar{\bar{v}}_1, 0)$ as equilibrium points.

Let $D_1 = f_1(s^{in}, 0), D_2 = f_2(s^{in}, 0), D_3 = f_1(s^{in} - \frac{D}{\alpha_1}, 0), D_4 = f_2(s^{in} - \frac{D}{\alpha_2}, 0), D_5 = f_1(s^{in} - \frac{D}{\alpha_2} - \bar{v}_2, \frac{D}{\alpha_2}), D_6 = f_2(s^{in} - \frac{D}{\alpha_1} - \bar{v}_1, \frac{D}{\alpha_1}), D_7 = f_1(s^{in} - \bar{x}_2, \bar{x}_2), D_8 = f_2(s^{in} - \bar{x}_1, \bar{x}_1), D_9 = f_1(s^{in} - \bar{v}_1 - \frac{D}{\alpha_1}, \bar{v}_1)$ and $D_{10} = f_2(s^{in} - \bar{v}_2 - \frac{D}{\alpha_2}, \bar{v}_2)$. Note that $D_9 < D_3 < D_1, D_5 < D_1, D_7 < D_1, D_{10} < D_4 < D_2, D_6 < D_2$ and $D_8 < D_2$.

In the rest of the paper, for simplicity and without any loss of generality, we will assume that $\alpha_1 > \alpha_2$, then $\frac{D}{\alpha_1} < \frac{D}{\alpha_2}$ and we will consider only three situations, where $s^{in} < \frac{D}{\alpha_1}, \frac{D}{\alpha_1} < s^{in} < \frac{D}{\alpha_2}$ and $\frac{D}{\alpha_2} < s^{in} < \frac{D}{\alpha_1} + \frac{D}{\alpha_2}$.

4 First Case : $s^{in} < \frac{D}{\alpha_1}$

The system (3) admits F_0, F_1, F_2 and F_5 as equilibria with $\bar{x}_1, \bar{x}_2, \bar{\bar{x}}_1, \bar{\bar{x}}_2 < \frac{D}{\alpha_1} < \frac{D}{\alpha_2}$. The conditions of existence of the equilibria are given in the lemmas hereafter.

Lemma 4.1 *The trivial equilibrium point F_0 exists always. If $D < \max(D_1, D_2)$, then F_0 is a saddle point, however, if $D > \max(D_1, D_2)$, then F_0 is a stable node.*

Proof. The Jacobian matrix J_0 of system (3) on F_0 is then given by

$$J_0 = \begin{bmatrix} D_1 - D & 0 & 0 & 0 \\ 0 & D_2 - D & 0 & 0 \\ 0 & 0 & -D & 0 \\ 0 & 0 & 0 & -D \end{bmatrix}.$$

Its eigenvalues are given by $\lambda_1 = \lambda_2 = -D < 0, \lambda_3 = D_1 - D$ and $\lambda_4 = D_2 - D$. Therefore, if $D < \max(D_1, D_2)$, then F_0 is a saddle point, and if $D > \max(D_1, D_2)$, then F_0 is a stable node.

Lemma 4.2 *The equilibrium point F_1 exists if and only if $D < D_1$. If $D > D_8$, then F_1 is a stable node, however, if $D < D_8$, then F_1 is a saddle point.*

Proof. An equilibrium F_1 exists if and only if $\bar{x}_1 \in]0, s^{in}[$ is a solution of

$$f_1(s^{in} - \bar{x}_1, 0) = D. \tag{4}$$

Let $\psi_1(x_1) = f_1(s^{in} - x_1, 0) - D$. Since $\psi'_1(x_1) = -\frac{\partial f_1}{\partial s}(s^{in} - x_1, 0) < 0$, $\psi_1(0) = D_1 - D$ and $\psi_1(s^{in}) = -D < 0$, equation (4) admits a unique positive solution $\bar{x}_1 \in]0, s^{in}[$ if and only if $D < D_1$.

Assume that F_1 exists ($D < D_1$). The Jacobian matrix J_1 of model (3) at F_1 is given by

$$J_1 = \begin{bmatrix} -\bar{x}_1 \frac{\partial f_1}{\partial s} & \bar{x}_1 \frac{\partial f_1}{\partial x_2} - \bar{x}_1 \frac{\partial f_1}{\partial s} & -\alpha_1 \bar{x}_1 - \bar{x}_1 \frac{\partial f_1}{\partial s} & -\bar{x}_1 \frac{\partial f_1}{\partial s} \\ 0 & D_8 - D & 0 & 0 \\ 0 & 0 & \alpha_1 \bar{x}_1 - D & 0 \\ 0 & 0 & 0 & -D \end{bmatrix}.$$

J_1 admits four eigenvalues given by $\lambda_1 = -\bar{x}_1 \frac{\partial f_1}{\partial s}(s^{in} - \bar{x}_1, 0) < 0$, $\lambda_2 = -(D - D_8)$, $\lambda_3 = \alpha_1(\bar{x}_1 - \frac{D}{\alpha_1}) < 0$ and $\lambda_4 = -D < 0$. It follows that if $D > D_8$, then F_1 is a stable node, and if $D < D_8$, then F_1 is a saddle point.

Lemma 4.3 *The equilibrium point F_2 exists if and only if $D < D_2$. If $D > D_7$, then F_2 is a stable node, and if $D < D_7$, then F_2 is a saddle point.*

Proof. An equilibrium F_2 exists if and only if $\bar{x}_2 \in]0, s^{in}[$ is a solution of

$$f_2(s^{in} - \bar{x}_2, 0) = D. \tag{5}$$

Let $\psi_2(x_2) = f_2(s^{in} - x_2, 0) - D$. Since $\psi'_2(x_2) = -\frac{\partial f_2}{\partial s}(s^{in} - \bar{x}_2, 0) < 0$, $\psi_2(0) = D_2 - D$ and $\psi_2(s^{in}) = -D < 0$, equation (5) admits a unique positive solution $\bar{x}_2 \in]0, s^{in}[$ if and only if $D < D_2$.

Assume that F_2 exists ($D < D_2$). The Jacobian matrix J_2 of system (3) at F_2 is given by

$$J_2 = \begin{bmatrix} D_7 - D & 0 & 0 & 0 \\ x_2 \frac{\partial f_2}{\partial x_1} - x_2 \frac{\partial f_2}{\partial s} & -\bar{x}_2 \frac{\partial f_2}{\partial s} & -\bar{x}_2 \frac{\partial f_2}{\partial s} & -\alpha_2 \bar{x}_2 - \bar{x}_2 \frac{\partial f_2}{\partial s} \\ 0 & 0 & -D & 0 \\ 0 & 0 & 0 & \alpha_2 \bar{x}_2 - D \end{bmatrix}.$$

J_2 admits four eigenvalues given by $\lambda_1 = -\bar{x}_2 \frac{\partial f_2}{\partial s}(s^{in} - \bar{x}_2, 0) < 0$, $\lambda_2 = -(D - D_7)$, $\lambda_3 = \alpha_2(\bar{x}_2 - \frac{D}{\alpha_2}) < 0$ and $\lambda_4 = -D < 0$. It follows that if $D > D_7$, then F_2 is a stable node, however, if $D < D_7$, then F_2 is a saddle point.

Lemma 4.4 *The situation $D < \min(D_7, D_8)$ is impossible.*

Proof. Assume that $0 < D < \min(D_7, D_8)$. From Lemmas 4.2 and 4.3, F_1 and F_2 exist.

1. If $\bar{x}_1 \geq \bar{x}_2$, then $D = f_2(s^{in} - \bar{x}_2, 0) \geq f_2(s^{in} - \bar{x}_1, 0) > f_2(s^{in} - \bar{x}_1, \bar{x}_1) = D_8 > D$, which is impossible.
2. If $\bar{x}_1 \leq \bar{x}_2$, then $D = f_1(s^{in} - \bar{x}_1, 0) \geq f_1(s^{in} - \bar{x}_2, 0) > f_1(s^{in} - \bar{x}_2, \bar{x}_2) = D_7 > D$, which is impossible.

Lemma 4.5 *An equilibrium F_5 exists if and only if $\max(D_7, D_8) < D < \min(D_1, D_2)$. If it exists, then F_1 and F_2 exist and satisfy $\bar{x}_1 < \bar{x}_1$ and $\bar{x}_2 < \bar{x}_2$. F_5 is always a saddle point.*

Proof. Since the functions $x_2 \rightarrow f_1(s^{in} - x_1 - x_2, x_2)$ and $x_2 \rightarrow f_2(s^{in} - x_1 - x_2, x_1)$ are noncreasing, one deduces that the isoclines are the graphs of two functions $x_2 = \varphi_1(x_1)$ and $x_2 = \varphi_2(x_1)$ and then $0 = \varphi_1(\bar{x}_1)$ and $\bar{x}_2 = \varphi_2(0)$. \bar{x}_1 is a solution of $\psi_5(\bar{x}_1) = 0$, where $\psi_5(x_1) = \varphi_2(x_1) - \varphi_1(x_1)$. The derivatives of φ_1 and φ_2 are given by $\varphi_2'(x_1) = -1 + \frac{\partial f_2}{\partial x_1} / \frac{\partial f_2}{\partial s} < -1 < \varphi_1'(x_1) = -1 + \frac{\partial f_1}{\partial x_2} / (\frac{\partial f_1}{\partial x_2} - \frac{\partial f_1}{\partial s}) < 0$. One deduces that $\psi_5'(x_1) = \varphi_2'(x_1) - \varphi_1'(x_1) < 0$. $\psi_5(0) = \varphi_2(0) - \varphi_1(0) = \bar{x}_2 - \varphi_1(0)$ and $\psi_5(\bar{x}_1) = \varphi_2(\bar{x}_1)$, then \bar{x}_1 exists and is unique if and only if $\bar{x}_2 > \varphi_1(0)$ and $\varphi_2(\bar{x}_1) < 0$, and these are satisfied only if $D = f_1(s^{in} - \varphi_1(0), \varphi_1(0)) > f_1(s^{in} - \bar{x}_2, \bar{x}_2) = D_7$ and $D = f_2(s^{in} - \bar{x}_1 - \varphi_2(\bar{x}_1), \bar{x}_1) > f_2(s^{in} - \bar{x}_1, \bar{x}_1) = D_8$. The existence and the uniqueness of $\bar{x}_2 = \varphi_1(\bar{x}_1) = \varphi_2(\bar{x}_1)$ are easily deduced since the two functions $\varphi_1(\cdot)$ and $\varphi_2(\cdot)$ are decreasing.

Assume that F_5 exists. One has

$$\psi_3(\bar{x}_1) = 0 = f_1(s^{in} - \bar{x}_1, 0) - D > f_1(s^{in} - \bar{x}_1 - \bar{x}_2, \bar{x}_2) - D = 0 = \psi_3(\bar{x}_1),$$

then $\psi_3(\bar{x}_1) > \psi_3(\bar{x}_1)$ since the function $\psi_3(\cdot)$ is decreasing, $\bar{x}_1 > \bar{x}_1$.

$$\psi_4(\bar{x}_2) = f_2(s^{in} - \bar{x}_2, 0) - D > f_2(s^{in} - \bar{x}_1 - \bar{x}_2, \bar{x}_1) - D = 0 = \psi_4(\bar{x}_2),$$

then $\psi_4(\bar{x}_2) < \psi_4(\bar{x}_2)$ since the function $\psi_4(\cdot)$ is decreasing, $\bar{x}_2 > \bar{x}_2$.

Assume that F_5 exists. The Jacobian matrix J_5 of system (3) at $F_5 = (\bar{x}_1, \bar{x}_2, 0, 0)$ is given by

$$J_5 = \begin{bmatrix} -\bar{x}_1 \frac{\partial f_1}{\partial s} & \bar{x}_1 \frac{\partial f_1}{\partial x_2} - \bar{x}_1 \frac{\partial f_1}{\partial s} & -\alpha_1 \bar{x}_1 - \bar{x}_1 \frac{\partial f_1}{\partial s} & -\bar{x}_1 \frac{\partial f_1}{\partial s} \\ \bar{x}_2 \frac{\partial f_2}{\partial x_1} - \bar{x}_2 \frac{\partial f_2}{\partial s} & -\bar{x}_2 \frac{\partial f_2}{\partial s} & -\bar{x}_2 \frac{\partial f_2}{\partial s} & -\alpha_2 \bar{x}_2 - \bar{x}_2 \frac{\partial f_2}{\partial s} \\ 0 & 0 & \alpha_1 \bar{x}_1 - D & 0 \\ 0 & 0 & 0 & \alpha_2 \bar{x}_2 - D \end{bmatrix}.$$

J_5 admits four eigenvalues given by $\lambda_1 = \alpha_1(\bar{x}_1 - \frac{D}{\alpha_1}) < 0$, $\lambda_2 = \alpha_2(\bar{x}_2 - \frac{D}{\alpha_2}) < 0$ and two other eigenvalues of the solutions of

$$\lambda^2 + a\lambda + b = 0,$$

where

$$a = \bar{x}_1 \frac{\partial f_1}{\partial s} + \bar{x}_2 \frac{\partial f_2}{\partial s} > 0$$

and

$$b = \bar{x}_1 \bar{x}_2 \left[-\frac{\partial f_1}{\partial x_2} \frac{\partial f_2}{\partial x_1} + \frac{\partial f_1}{\partial x_2} \frac{\partial f_2}{\partial s} + \frac{\partial f_1}{\partial s} \frac{\partial f_2}{\partial x_1} \right] < 0.$$

It follows that F_5 is a saddle point.

The number and the nature of equilibria of system (3) are summarized in the theorem below.

Theorem 4.1

A) If $\min(D_7, D_8) < D < \max(D_7, D_8)$, then

- (i) if $D_8 < D_7$ and $D_8 < D < \min(D_2, D_7)$, then system (3) admits three equilibria F_0, F_1 and F_2 . F_1 is a stable node, however, F_0 and F_2 are two saddle points.
- (ii) if $D_8 < D_7$ and $D_2 < D < D_7$, then system (3) admits two equilibria F_0 and F_1 . F_1 is a stable node and F_0 is a saddle point.
- (iii) if $D_7 < D_8$ and $D_7 < D < \min(D_8, D_1)$, then system (3) admits three equilibria F_0, F_1 and F_2 . F_2 is a stable node, however, F_0 and F_1 are two saddle points.
- (iv) if $D_7 < D_8$ and $D_1 < D < D_8$, then system (3) admits two equilibria F_0 and F_2 . F_2 is a stable node, however, F_0 is a saddle point.

B) If $\max(D_7, D_8) < D < \min(D_1, D_2)$, then system (3) admits four equilibria F_0, F_1, F_2 and F_5 . F_1 and F_2 are two stable nodes, however, F_0 and F_5 are two saddle points.

C) If $\min(D_1, D_2) < D < \max(D_1, D_2)$, then

(i) if $D_1 < D_2$, then system (3) admits two equilibria F_0 and F_2 . F_2 is a stable node, however, F_0 is a saddle point.

(ii) if $D_2 < D_1$, then system (3) admits two equilibria F_0 and F_1 . F_1 is a stable node, however, F_0 is a saddle point.

D) If $\max(D_1, D_2) < D$, then system (3) admits one stationary point F_0 . F_0 is a stable node.

5 Second Case : $\frac{D}{\alpha_1} < s^{in} < \frac{D}{\alpha_2}$

The system (3) admits F_0, F_1, F_2, F_3, F_5 and F_7 as equilibrium points with $\bar{x}_1, \bar{x}_2, \bar{\bar{x}}_1, \bar{\bar{x}}_2, \bar{v}_1 < \frac{D}{\alpha_2}$. The conditions of existence of the equilibria are stated in the lemmas hereafter.

Lemma 5.1 F_0 exists always. If $D < \max(D_1, D_2)$, then F_0 is a saddle point. If $D > \max(D_1, D_2)$, then F_0 is a stable node.

Proof. See the proof of Lemma 4.1.

Lemma 5.2 The equilibrium point F_2 exists if and only if $D < D_2$. If $D > D_7$, then F_2 is a stable node, however, if $D < D_7$, then F_2 is a saddle point.

Proof. See the proof of Lemma 4.3.

Lemma 5.3 The situation $D < \min(D_7, D_8)$ is impossible.

Proof. See the proof of Lemma 4.4.

Lemma 5.4 An equilibrium F_5 exists if and only if $\max(D_7, D_8) < D < \min(D_1, D_2)$. If it exists, then F_1 and F_2 exist and satisfy $\bar{\bar{x}}_1 < \bar{x}_1$ and $\bar{\bar{x}}_2 < \bar{x}_2$. F_5 is always a saddle point.

Proof. See the proof of Lemma 4.5.

Lemma 5.5 F_1 exists if and only if $D < D_1$. If $D > \max(D_3, D_8)$, then F_1 is a stable node, however, if $D < D_3$ or $D_3 < D < D_8$, then F_1 is a saddle point.

Proof. The proof of existence and uniqueness of F_1 is given in the proof of Lemma 4.2. Assume that F_1 exists ($D < D_1$). One has

- If $D < D_3$, then $f_1(s^{in} - \bar{x}_1, 0) = D < D_3 = f_1(s^{in} - \frac{D}{\alpha_1}, 0)$ and then $\bar{x}_1 > \frac{D}{\alpha_1}$.
- If $D > D_3$, then $f_1(s^{in} - \bar{x}_1, 0) = D > D_3 = f_1(s^{in} - \frac{D}{\alpha_1}, 0)$ and then $\bar{x}_1 < \frac{D}{\alpha_1}$.

The Jacobian matrix J_1 of system (3) at F_1 is given by

$$J_1 = \begin{bmatrix} -\bar{x}_1 \frac{\partial f_1}{\partial s} & \bar{x}_1 \frac{\partial f_1}{\partial x_2} - \bar{x}_1 \frac{\partial f_1}{\partial s} & -\alpha_1 \bar{x}_1 - \bar{x}_1 \frac{\partial f_1}{\partial s} & -\bar{x}_1 \frac{\partial f_1}{\partial s} \\ 0 & D_8 - D & 0 & 0 \\ 0 & 0 & \alpha_1 \bar{x}_1 - D & 0 \\ 0 & 0 & 0 & -D \end{bmatrix}.$$

J_1 admits four eigenvalues given by $\lambda_1 = -\bar{x}_1 \frac{\partial f_1}{\partial s}(s^{in} - \bar{x}_1, 0) < 0$, $\lambda_2 = -(D - D_8)$, $\lambda_3 = \alpha_1(\bar{x}_1 - \frac{D}{\alpha_1})$ and $\lambda_4 = -D < 0$. It follows that

- F_1 is a saddle point if $D < D_3$.
- F_1 is a stable node if $D > D_3$ and $D > D_8$.
- F_1 is a saddle point if $D > D_3$ and $D < D_8$.

Lemma 5.6 F_3 exists if and only if $D < D_3$. If $D_6 < D < D_3$, then F_3 is locally asymptotically stable. If $D < \min(D_3, D_6)$, then F_3 is unstable.

Proof. An equilibrium F_3 exists if and only if $\bar{v}_1 \in]0, s^{in} - \frac{D}{\alpha_1}[$ is a solution of

$$f_1(s^{in} - \frac{D}{\alpha_1} - \bar{v}_1, 0) = D + \alpha_1 \bar{v}_1. \tag{6}$$

Let $\psi_3(v_1) = f_1(s^{in} - \frac{D}{\alpha_1} - v_1, 0) - D - \alpha_1 v_1$. Since $\psi'_3(v_1) = -\frac{\partial f_1}{\partial s}(s^{in} - \frac{D}{\alpha_1} - v_1, 0) - \alpha_1 < 0$, $\psi_3(0) = D_3 - D$ and $\psi_3(s^{in} - \frac{D}{\alpha_1}) = -D - \alpha_1(s^{in} - \frac{D}{\alpha_1}) < 0$, equation (6) admits a unique positive solution $\bar{v}_1 \in]0, s^{in} - \frac{D}{\alpha_1}[$ if and only if $D < D_3$.

If F_3 exists, the Jacobian matrix J_1 of model (3) at F_3 is stated as follows:

$$J_3 = \begin{bmatrix} -\frac{D}{\alpha_1} \frac{\partial f_1}{\partial s} & \frac{D}{\alpha_1} \frac{\partial f_1}{\partial x_2} - \frac{D}{\alpha_1} \frac{\partial f_1}{\partial s} & -D - \frac{D}{\alpha_1} \frac{\partial f_1}{\partial s} & -\frac{D}{\alpha_1} \frac{\partial f_1}{\partial s} \\ 0 & D_6 - D & 0 & 0 \\ \alpha_1 \bar{v}_1 & 0 & 0 & 0 \\ 0 & 0 & 0 & -D \end{bmatrix}.$$

J_3 admits four eigenvalues given by $\lambda_1 = -D < 0$ and $\lambda_2 = -(D - D_6)$ and two other eigenvalues of the solution of the equation

$$\lambda^2 + a\lambda + b = 0,$$

where $a = \frac{D}{\alpha_1} \frac{\partial f_1}{\partial s}(s^{in} - \frac{D}{\alpha_1} - \bar{v}_1, 0) > 0$ and $b = \alpha_1 \bar{v}_1 (D + \frac{D}{\alpha_1} \frac{\partial f_1}{\partial s}(s^{in} - \frac{D}{\alpha_1} - \bar{v}_1, 0)) > 0$. It follows that

- If $D_6 < D < D_3$, then $\lambda_1 < 0, \lambda_2 < 0, \lambda_3 < 0, \lambda_4 < 0$ and F_3 is then locally asymptotically stable.
- If $D < \min(D_3, D_6)$, then F_3 is a saddle point.

Lemma 5.7 An equilibrium F_7 exists if and only if $\max(D_6, D_9) < D < D_3$. If F_7 exists, it follows that $\bar{\bar{v}}_1 < \bar{v}_1$ and F_7 is always unstable.

Proof. Since the functions $x_2 \rightarrow f_1(s^{in} - x_2 - \frac{D}{\alpha_1} - v_1, x_2) - \alpha_1 v_1$ and $x_2 \rightarrow f_2(s^{in} - x_2 - \frac{D}{\alpha_1} - v_1, \frac{D}{\alpha_1})$ are decreasing, one deduces that the isoclines are the graphs of two functions $x_2 = \varphi_5(v_1)$ and $x_2 = \varphi_6(v_1)$. $\bar{\bar{v}}_1$ is a solution of $\psi_7(\bar{\bar{v}}_1) = 0$, where $\psi_7(v_1) = \varphi_6(v_1) - \varphi_5(v_1)$. The derivatives of φ_5 and φ_6 are given by $\varphi'_6(v_1) = -1 < \varphi'_5(v_1) = -1 + \left(\frac{\partial f_1}{\partial x_2} + \alpha_1\right) / \left(\frac{\partial f_1}{\partial x_2} - \frac{\partial f_1}{\partial s}\right) < 0$. One deduces that $\psi'_7(v_1) = \varphi'_6(v_1) - \varphi'_5(v_1) < 0$. $\psi_7(0) = \varphi_6(0) - \varphi_5(0)$ and $\psi_7(\bar{v}_1) = \varphi_6(\bar{v}_1) - \varphi_5(\bar{v}_1)$, then $\bar{\bar{v}}_1$ exists and is unique if and only if $\varphi_5(0) < \varphi_6(0)$ and $\varphi_6(\bar{v}_1) < \varphi_5(\bar{v}_1)$. Note that $\varphi_5(\bar{v}_1) = 0$ and $\varphi_6(0) < \bar{v}_1$. Then the existence is satisfied only if $D = f_1(s^{in} - \varphi_5(0) - \frac{D}{\alpha_1}, \varphi_5(0)) > f_1(s^{in} - \bar{v}_1 - \frac{D}{\alpha_1}, \bar{v}_1) = D_9$ and $D = f_2(s^{in} - \varphi_6(\bar{v}_1) - \bar{v}_1 - \frac{D}{\alpha_1}, \frac{D}{\alpha_1}) > f_2(s^{in} - \bar{v}_1 - \frac{D}{\alpha_1}, \frac{D}{\alpha_1}) = D_6$.

Assume that F_7 exists. One has

$$\psi_4(\bar{\bar{x}}_2) = f_2(s^{in} - \bar{\bar{x}}_2, 0) - D \geq f_2(s^{in} - \bar{\bar{x}}_2 - \frac{D}{\alpha_1} - \bar{\bar{v}}_1, \frac{D}{\alpha_1}) - D = 0 = \psi_4(\bar{x}_2),$$

then $\psi_4(\bar{x}_2) < \psi_4(\bar{\bar{x}}_2)$ since the function $\psi_4(\cdot)$ is decreasing, $\bar{x}_2 > \bar{\bar{x}}_2$. The Jacobian matrix J_7 of system (3) at $F_7 = (\frac{D}{\alpha_1}, \bar{\bar{x}}_2, \bar{\bar{v}}_1, 0)$ is given by

$$J_7 = \begin{bmatrix} -\frac{D}{\alpha_1} \frac{\partial f_1}{\partial s} & \frac{D}{\alpha_1} \frac{\partial f_1}{\partial x_2} - \frac{D}{\alpha_1} \frac{\partial f_1}{\partial s} & -D - \frac{D}{\alpha_1} \frac{\partial f_1}{\partial s} & -\frac{D}{\alpha_1} \frac{\partial f_1}{\partial s} \\ \bar{\bar{x}}_2 \frac{\partial f_2}{\partial x_1} - \bar{\bar{x}}_2 \frac{\partial f_2}{\partial s} & -\bar{\bar{x}}_2 \frac{\partial f_2}{\partial s} & -\bar{\bar{x}}_2 \frac{\partial f_2}{\partial s} & -\alpha_2 \bar{\bar{x}}_2 - \bar{\bar{x}}_2 \frac{\partial f_2}{\partial s} \\ \alpha_1 \bar{\bar{v}}_1 & 0 & 0 & 0 \\ 0 & 0 & 0 & \alpha_2 \bar{\bar{x}}_2 - D \end{bmatrix}.$$

J_7 admits four eigenvalues given by $\lambda_1 = \alpha_2 \bar{\bar{x}}_2 - D$ and three other eigenvalues of the roots of the following characteristic polynomial:

$$P_7(X) = \begin{vmatrix} -X - \frac{D}{\alpha_1} \frac{\partial f_1}{\partial s} & \frac{D}{\alpha_1} \frac{\partial f_1}{\partial x_2} - \frac{D}{\alpha_1} \frac{\partial f_1}{\partial s} & -D - \frac{D}{\alpha_1} \frac{\partial f_1}{\partial s} \\ \bar{\bar{x}}_2 \frac{\partial f_2}{\partial x_1} - \bar{\bar{x}}_2 \frac{\partial f_2}{\partial s} & -X - \bar{\bar{x}}_2 \frac{\partial f_2}{\partial s} & -\bar{\bar{x}}_2 \frac{\partial f_2}{\partial s} \\ \alpha_1 \bar{\bar{v}}_1 & 0 & -X \end{vmatrix},$$

$$P_7(X) = -X \begin{vmatrix} -X - \frac{D}{\alpha_1} \frac{\partial f_1}{\partial s} & \frac{D}{\alpha_1} \frac{\partial f_1}{\partial x_2} - \frac{D}{\alpha_1} \frac{\partial f_1}{\partial s} \\ \bar{\bar{x}}_2 \frac{\partial f_2}{\partial x_1} - \bar{\bar{x}}_2 \frac{\partial f_2}{\partial s} & -X - \bar{\bar{x}}_2 \frac{\partial f_2}{\partial s} \end{vmatrix} + \alpha_1 \bar{\bar{v}}_1 \begin{vmatrix} \frac{D}{\alpha_1} \frac{\partial f_1}{\partial x_2} - \frac{D}{\alpha_1} \frac{\partial f_1}{\partial s} & -D - \frac{D}{\alpha_1} \frac{\partial f_1}{\partial s} \\ -X - \bar{\bar{x}}_2 \frac{\partial f_2}{\partial s} & -\bar{\bar{x}}_2 \frac{\partial f_2}{\partial s} \end{vmatrix},$$

$$P_7(X) = -X \left| \left(X + \frac{D}{\alpha_1} \frac{\partial f_1}{\partial s} \right) \left(X + \bar{\bar{x}}_2 \frac{\partial f_2}{\partial s} \right) - \left(\frac{D}{\alpha_1} \frac{\partial f_1}{\partial x_2} - \frac{D}{\alpha_1} \frac{\partial f_1}{\partial s} \right) \left(\bar{\bar{x}}_2 \frac{\partial f_2}{\partial x_1} - \bar{\bar{x}}_2 \frac{\partial f_2}{\partial s} \right) \right| + \alpha_1 \bar{\bar{v}}_1 \left| -\bar{\bar{x}}_2 \frac{\partial f_2}{\partial s} \left(\frac{D}{\alpha_1} \frac{\partial f_1}{\partial x_2} - \frac{D}{\alpha_1} \frac{\partial f_1}{\partial s} \right) - \left(D + \frac{D}{\alpha_1} \frac{\partial f_1}{\partial s} \right) \left(X + \bar{\bar{x}}_2 \frac{\partial f_2}{\partial s} \right) \right|,$$

$$P_7(X) = -X \left| X^2 + X \left(\frac{D}{\alpha_1} \frac{\partial f_1}{\partial s} + \bar{\bar{x}}_2 \frac{\partial f_2}{\partial s} \right) - \frac{D}{\alpha_1} \bar{\bar{x}}_2 \frac{\partial f_1}{\partial x_2} \frac{\partial f_2}{\partial x_1} + \frac{D}{\alpha_1} \bar{\bar{x}}_2 \frac{\partial f_1}{\partial x_2} \frac{\partial f_2}{\partial s} + \frac{D}{\alpha_1} \bar{\bar{x}}_2 \frac{\partial f_1}{\partial s} \frac{\partial f_2}{\partial x_1} \right| - \alpha_1 \bar{\bar{v}}_1 \left| \frac{D}{\alpha_1} \bar{\bar{x}}_2 \frac{\partial f_2}{\partial s} \frac{\partial f_1}{\partial x_2} + \left(D + \frac{D}{\alpha_1} \frac{\partial f_1}{\partial s} \right) X + D \bar{\bar{x}}_2 \frac{\partial f_2}{\partial s} \right|,$$

$$P_7(X) = -X^3 - X^2 \left(\frac{D}{\alpha_1} \frac{\partial f_1}{\partial s} + \bar{\bar{x}}_2 \frac{\partial f_2}{\partial s} \right) - X \left(-\frac{D}{\alpha_1} \bar{\bar{x}}_2 \frac{\partial f_1}{\partial x_2} \frac{\partial f_2}{\partial x_1} + \frac{D}{\alpha_1} \bar{\bar{x}}_2 \frac{\partial f_1}{\partial x_2} \frac{\partial f_2}{\partial s} + \frac{D}{\alpha_1} \bar{\bar{x}}_2 \frac{\partial f_1}{\partial s} \frac{\partial f_2}{\partial x_1} + \alpha_1 \bar{\bar{v}}_1 \left(D + \frac{D}{\alpha_1} \frac{\partial f_1}{\partial s} \right) \right) - \alpha_1 \bar{\bar{v}}_1 \left(\frac{D}{\alpha_1} \bar{\bar{x}}_2 \frac{\partial f_2}{\partial s} \frac{\partial f_1}{\partial x_2} + D \bar{\bar{x}}_2 \frac{\partial f_2}{\partial s} \right).$$

Then

$$P_7(X) = -(X^3 + b_1 X^2 + b_2 X + b_3)$$

with

$$b_1 = \left(\frac{D}{\alpha_1} \frac{\partial f_1}{\partial s} + \bar{\bar{x}}_2 \frac{\partial f_2}{\partial s} \right) > 0, \\ b_2 = \left(-\frac{D}{\alpha_1} \bar{\bar{x}}_2 \frac{\partial f_1}{\partial x_2} \frac{\partial f_2}{\partial x_1} + \frac{D}{\alpha_1} \bar{\bar{x}}_2 \frac{\partial f_1}{\partial x_2} \frac{\partial f_2}{\partial s} + \frac{D}{\alpha_1} \bar{\bar{x}}_2 \frac{\partial f_1}{\partial s} \frac{\partial f_2}{\partial x_1} + \alpha_1 \bar{\bar{v}}_1 \left(D + \frac{D}{\alpha_1} \frac{\partial f_1}{\partial s} \right) \right), \\ b_3 = \alpha_1 \bar{\bar{v}}_1 \left(\frac{D}{\alpha_1} \bar{\bar{x}}_2 \frac{\partial f_2}{\partial s} \frac{\partial f_1}{\partial x_2} + D \bar{\bar{x}}_2 \frac{\partial f_2}{\partial s} \right) = D \bar{\bar{v}}_1 \bar{\bar{x}}_2 \frac{\partial f_2}{\partial s} \left(\frac{\partial f_1}{\partial x_2} + \alpha_1 \right) < 0.$$

So, the conditions for the stability of F_7 are not satisfied, then F_7 is unstable.

The number and the nature of equilibria of model (3) are given in the theorem hereafter.

Theorem 5.1 A) If $\min(D_7, D_8) < D < \max(D_7, D_8)$, then

(i) if $D_8 < D_7$, then

1. if $\max(D_2, D_3) < D < D_7$, then system (3) admits two equilibria F_0 and F_1 . F_1 is a stable node, however, F_0 is a saddle point.
2. if $\max(D_2, D_9) < D < \min(D_3, D_7)$, then system (3) admits four equilibria F_0, F_1, F_3 and F_7 . F_0, F_1 and F_7 are three saddle points, however, F_3 is a stable node.
3. if $D_2 < D < \min(D_9, D_7)$, then system (3) admits three equilibria F_0, F_1 and F_3 . F_0 and F_1 are two saddle points, however, F_3 is a stable node.
4. if $\max(D_3, D_6, D_8) < D < \min(D_2, D_7)$, then system (3) admits three equilibria F_0, F_1 and F_2 . F_0 and F_2 are two saddle points, however, F_1 is a stable node.
5. if $\max(D_6, D_8, D_9) < D < \min(D_2, D_3, D_7)$, then system (3) admits five equilibria F_0, F_1, F_2, F_3 and F_7 . F_0, F_1, F_2 and F_7 are four saddle points, however, F_3 is a stable node.
6. if $\max(D_6, D_8) < D < \min(D_2, D_9, D_7)$, then system (3) admits four equilibria F_0, F_1, F_2 and F_3 . F_0, F_1 and F_2 are three saddle points, however, F_3 is a stable node.
7. if $\max(D_3, D_8) < D < \min(D_6, D_7)$, then system (3) admits three equilibria F_0, F_1 and F_2 . F_0 and F_2 are two saddle points, however, F_1 is a stable node.
8. if $D_8 < D < \min(D_3, D_6, D_7)$, then system (3) admits four equilibria F_0, F_1, F_2 and F_3 , all of them are saddle points.

(ii) if $D_7 < D_8$, then

1. if $D_7 < D < \min(D_9, D_6, D_8)$, then system (3) admits four equilibria F_0, F_1, F_2 and F_3 . F_0, F_1 and F_3 are three saddle points, however, F_2 is a stable node.
2. if $\max(D_9, D_7) < D < \min(D_3, D_6, D_8)$, then system (3) admits four equilibria F_0, F_1, F_2 and F_3 . F_0, F_1 and F_3 are three saddle points, however, F_2 is a stable node.
3. if $\max(D_3, D_7) < D < \min(D_1, D_6, D_8)$, then system (3) admits three equilibria F_0, F_1 and F_2 . F_0 and F_1 are two saddle points, however, F_2 is a stable node.
4. if $D_1 < D < \min(D_6, D_8)$, then system (3) admits two equilibria F_0 and F_2 . F_0 is a saddle point, however, F_2 is a stable node.
5. if $\max(D_6, D_7) < D < \min(D_8, D_9)$, then system (3) admits four equilibria F_0, F_1, F_2 and F_3 . F_0 and F_1 are two saddle points, however, F_2 and F_3 are two stable nodes.
6. if $\max(D_6, D_7, D_9) < D < \min(D_3, D_8)$, then system (3) admits five equilibria F_0, F_1, F_2, F_3 and F_7 . F_0, F_1 and F_7 are three saddle points, however, F_2 and F_3 are two stable nodes.
7. if $\max(D_6, D_7, D_3) < D < \min(D_1, D_8)$, then system (3) admits three equilibria F_0, F_1 and F_2 . F_0 and F_1 are two saddle points, however, F_2 is a stable node.
8. if $\max(D_6, D_1) < D < D_8$, then system (3) admits two equilibria F_0 and F_2 . F_0 is a saddle point, however, F_2 is a stable node.

B) If $\max(D_7, D_8) < D < \min(D_1, D_2)$, then

- (i) If $\max(D_3, D_6, D_7, D_8) < D < \min(D_1, D_2)$, then system (3) admits four equilibria F_0, F_1, F_2 and F_5 . F_0 and F_5 are saddle points, F_1 and F_2 are stable nodes.
- (ii) If $\max(D_6, D_7, D_8, D_9) < D < \min(D_2, D_3)$, then system (3) admits six equilibria F_0, F_1, F_2, F_3, F_5 and F_7 . F_0, F_1, F_5 and F_7 are saddle points, F_2 and F_3 are stable nodes.
- (iii) If $\max(D_3, D_7, D_8) < D < \min(D_1, D_6)$, then system (3) admits four equilibria F_0, F_1, F_2 and F_5 . F_0 and F_5 are saddle points, F_1 and F_2 are stable nodes.
- (iv) If $\max(D_7, D_8, D_9) < D < \min(D_3, D_6)$, then system (3) admits five equilibria F_0, F_1, F_2, F_3 and F_5 . F_0, F_1, F_3 and F_5 are saddle points, F_2 is a stable node.

(v) If $\max(D_7, D_8) < D < \min(D_6, D_9)$, then system (3) admits five equilibria F_0, F_1, F_2, F_3 and F_5 . F_0, F_1, F_3 and F_5 are saddle points, F_2 is a stable node.

(vi) If $\max(D_6, D_7, D_8) < D < \min(D_2, D_9)$, then system (3) admits five equilibria F_0, F_1, F_2, F_3 and F_5 . F_0, F_1 and F_5 are saddle points, F_2 and F_3 are stable nodes.

C) If $\min(D_1, D_2) < D < \max(D_1, D_2)$, then

(i) If $D_1 < D < D_2$, then system (3) admits two equilibria F_0 and F_2 . F_0 is a saddle point, however, F_2 is a stable node.

(ii) If $D_2 < D < D_1$, then

1. if $D_2 < D < D_9$, then system (3) admits three equilibria F_0, F_1 and F_3 . F_0 and F_1 are two saddle points, however, F_3 is a stable node.
2. if $\max(D_2, D_9) < D < D_3$, then system (3) admits four equilibria F_0, F_1, F_3 and F_7 . F_0, F_1 and F_7 are three saddle points, however, F_3 is a stable node.
3. if $\max(D_2, D_3) < D < D_1$, then system (3) admits two equilibria F_0 and F_1 . F_0 is a saddle point, however, F_1 is a stable node.

D) If $\max(D_1, D_2) < D$, then model (3) admits only F_0 as an equilibrium point. F_0 is a stable node.

6 Third Case : $\frac{D}{\alpha_2} < s^{in} < \frac{D}{\alpha_1} + \frac{D}{\alpha_2}$

The system (3) admits $F_0, F_1, F_2, F_3, F_4, F_5, F_6$ and F_7 as equilibrium points with

$$\bar{v}_1 < \min(s^{in} - \frac{D}{\alpha_1}, \frac{D}{\alpha_2}) \text{ and } \bar{v}_2 < \min(s^{in} - \frac{D}{\alpha_2}, \frac{D}{\alpha_1}).$$

The conditions of existence of the equilibria are stated in the lemmas hereafter.

Lemma 6.1 F_0 exists always. If $D < \max(D_1, D_2)$, then F_0 is a saddle point, however, if $D > \max(D_1, D_2)$, then F_0 is a stable node.

Proof. See the proof of Lemma 4.1.

Lemma 6.2 The equilibrium point F_1 exists if and only if $D < D_1$. If $D > \max(D_3, D_8)$, then F_1 is a stable node, however, if $D < D_3$ or $D_3 < D < D_8$, then F_1 is a saddle point.

Proof. See the proof of Lemma 5.5.

Lemma 6.3 The equilibrium point F_3 exists if and only if $D < D_3$. If $D_6 < D < D_3$, then F_3 is locally asymptotically stable. If $D < \min(D_3, D_6)$, then F_3 is unstable.

Proof. See the proof of Lemma 5.6.

Lemma 6.4 The situation $D < \min(D_7, D_8)$ is impossible.

Proof. See the proof of Lemma 4.4.

Lemma 6.5 An equilibrium F_5 exists if and only if $\max(D_7, D_8) < D < \min(D_1, D_2)$. If it exists, then F_1 and F_2 exist and satisfy $\bar{x}_1 < \bar{x}_1$ and $\bar{x}_2 < \bar{x}_2$. F_5 is always a saddle point.

Proof. See the proof of Lemma 4.5.

Lemma 6.6 An equilibrium F_7 exists if and only if $\max(D_6, D_9) < D < D_3$. Therefore, $\bar{v}_1 < \bar{v}_1$ and F_7 is always unstable.

Proof. See the proof of Lemma 5.7.

Lemma 6.7 The equilibrium point F_2 exists if and only if $D < D_2$. If $D > \max(D_4, D_7)$, then F_2 is a stable node, however, if $D < D_4$ or $D_4 < D < D_7$, then F_2 is a saddle point.

Proof. Existence and uniqueness of F_2 are given in the proof of Lemma 4.3. Assume that F_2 exists ($D < D_2$). One has

- If $D < D_4$, then $f_2(s^{in} - \bar{x}_2, 0) = D < D_4 = f_2(s^{in} - \frac{D}{\alpha_2}, 0)$ and then $\bar{x}_2 > \frac{D}{\alpha_2}$.
- If $D > D_4$, then $f_2(s^{in} - \bar{x}_2, 0) = D > D_4 = f_2(s^{in} - \frac{D}{\alpha_2}, 0)$ and then $\bar{x}_2 < \frac{D}{\alpha_2}$.

The Jacobian matrix J_2 of model (3) at F_2 is given as follows:

$$J_2 = \begin{bmatrix} D_7 - D & 0 & 0 & 0 \\ x_2 \frac{\partial f_2}{\partial x_1} - x_2 \frac{\partial f_2}{\partial s} & -\bar{x}_2 \frac{\partial f_2}{\partial s} & -\bar{x}_2 \frac{\partial f_2}{\partial s} & -\alpha_2 \bar{x}_2 - \bar{x}_2 \frac{\partial f_2}{\partial s} \\ 0 & 0 & -D & 0 \\ 0 & 0 & 0 & \alpha_2 \bar{x}_2 - D \end{bmatrix}.$$

J_2 admits four eigenvalues given by $\lambda_1 = -\bar{x}_2 \frac{\partial f_2}{\partial s}(s^{in} - \bar{x}_2, 0) < 0$, $\lambda_2 = -(D - D_7)$, $\lambda_3 = \alpha_2(\bar{x}_2 - \frac{D}{\alpha_2})$ and $\lambda_4 = -D < 0$. It follows that

- If $D < D_4$, then F_2 is a saddle point.
- If $D > D_4$ and $D > D_7$, then F_2 is a stable node.
- If $D > D_4$ and $D < D_7$, then F_2 is a saddle point.

Lemma 6.8 F_4 exists if and only if $D < D_4$. If $D_5 < D < D_4$, then F_4 is locally asymptotically stable. If $D < \min(D_4, D_5)$, then F_4 is unstable (saddle point).

Proof. An equilibrium F_4 exists if and only if $\bar{v}_2 \in]0, s^{in} - \frac{D}{\alpha_2}[$ is a solution of

$$f_2(s^{in} - \frac{D}{\alpha_2} - \bar{v}_2, 0) = D + \alpha_2 \bar{v}_2. \tag{7}$$

Let $\psi_4(v_2) = f_2(s^{in} - \frac{D}{\alpha_2} - v_2, 0) - D - \alpha_2 v_2$. Since $\psi_4'(v_2) = -\frac{\partial f_2}{\partial s}(s^{in} - \frac{D}{\alpha_2} - v_2, 0) - \alpha_2 < 0$, $\psi_4(0) = D_4 - D$, $\psi_4(s^{in} - \frac{D}{\alpha_2}) = -D - \alpha_2(s^{in} - \frac{D}{\alpha_2}) < 0$, equation (7) admits a unique positive solution $\bar{v}_2 \in]0, s^{in} - \frac{D}{\alpha_2}[$ if and only if $D < D_4$.

If F_4 exists, the Jacobian matrix J_4 of system (3) at F_4 is given by

$$J_4 = \begin{bmatrix} D_5 - D & 0 & 0 & 0 \\ \frac{D}{\alpha_2} \frac{\partial f_2}{\partial x_1} - \frac{D}{\alpha_2} \frac{\partial f_2}{\partial s} & -\frac{D}{\alpha_2} \frac{\partial f_2}{\partial s} & -\frac{D}{\alpha_2} \frac{\partial f_2}{\partial s} & -D - \frac{D}{\alpha_2} \frac{\partial f_2}{\partial s} \\ 0 & 0 & -D & 0 \\ 0 & \alpha_2 \bar{v}_2 & 0 & 0 \end{bmatrix}.$$

J_4 admits four eigenvalues given by $\lambda_1 = -D < 0$ and $\lambda_2 = -(D - D_5)$ and two other eigenvalues of the solution of the equation

$$\lambda^2 + a\lambda + b = 0,$$

where $a = \frac{D}{\alpha_2} \frac{\partial f_2}{\partial s}(s^{in} - \frac{D}{\alpha_2} - \bar{v}_2, 0) > 0$ and $b = \alpha_2 \bar{v}_2 \left(D + \frac{D}{\alpha_2} \frac{\partial f_2}{\partial s}(s^{in} - \frac{D}{\alpha_2} - \bar{v}_2, 0) \right) > 0$. It follows that

- If $D_5 < D < D_4$, then $\lambda_1 < 0, \lambda_2 < 0, \lambda_3 < 0, \lambda_4 < 0$ and F_4 is then locally asymptotically stable.
- If $D < \min(D_4, D_5)$, then F_4 is a saddle point.

Lemma 6.9 *An equilibrium F_6 exists if and only if $\max(D_5, D_{10}) < D < D_4$. Therefore, $\bar{v}_2 < \bar{v}_2$ and F_6 is always unstable.*

Proof. Since the functions $x_1 \rightarrow f_1(s^{in} - x_1 - \frac{D}{\alpha_2} - v_2, \frac{D}{\alpha_2})$ and $x_1 \rightarrow f_2(s^{in} - x_1 - \frac{D}{\alpha_2} - v_2, x_1) - \alpha_2 v_2$ are nonincreasing, one deduces that the isoclines are the graphs of two functions $x_1 = \varphi_3(v_2)$ and $x_1 = \varphi_4(v_2)$. \bar{v}_2 is the solution of $\psi_6(\bar{v}_2) = 0$, where $\psi_6(v_2) = \varphi_4(v_2) - \varphi_3(v_2)$. The derivatives of φ_3 and φ_4 are given by $\varphi'_3(v_2) = -1 < \varphi'_4(v_2) = -1 + \left(\frac{\partial f_2}{\partial x_1} + \alpha_2\right) / \left(\frac{\partial f_2}{\partial x_1} - \frac{\partial f_2}{\partial s}\right) < 0$. One deduces that $\psi'_6(v_2) = \varphi'_4(v_2) - \varphi'_3(v_2) > 0$. $\psi_6(0) = \varphi_4(0) - \varphi_3(0)$ and $\psi_6(\bar{v}_2) = \varphi_4(\bar{v}_2) - \varphi_3(\bar{v}_2)$, then \bar{v}_2 exists and is unique if and only if $\varphi_4(0) < \varphi_3(0)$ and $\varphi_3(\bar{v}_2) < \varphi_4(\bar{v}_2)$. Note that $\varphi_4(\bar{v}_2) = 0$ and $\varphi_3(0) < \bar{v}_2$. The existence is satisfied only if

$$D = f_2(s^{in} - \varphi_4(0) - \frac{D}{\alpha_2}, \varphi_4(0)) > f_2(s^{in} - \bar{v}_2 - \frac{D}{\alpha_2}, \bar{v}_2) = D_{10}$$

and

$$D = f_1(s^{in} - \varphi_3(\bar{v}_2) - \bar{v}_2 - \frac{D}{\alpha_2}, \frac{D}{\alpha_2}) > f_1(s^{in} - \bar{v}_2 - \frac{D}{\alpha_2}, \frac{D}{\alpha_2}) = D_5.$$

Assume that F_6 exists. One has

$$\psi_3(\bar{x}_1) = f_1(s^{in} - \bar{x}_1, 0) - D \geq f_1(s^{in} - \bar{x}_1 - \frac{D}{\alpha_2} - \bar{v}_2, \frac{D}{\alpha_2}) - D = 0 = \psi_3(\bar{x}_1),$$

then $\psi_3(\bar{x}_1) < \psi_3(\bar{x}_1)$ since the function $\psi_3(\cdot)$ is decreasing, $\bar{x}_1 > \bar{x}_1$. The Jacobian matrix J_6 of system (3) at $F_6 = (\bar{x}_1, \frac{D}{\alpha_2}, 0, \bar{v}_2)$ is given by

$$J_6 = \begin{bmatrix} -\bar{x}_1 \frac{\partial f_1}{\partial s} & \bar{x}_1 \frac{\partial f_1}{\partial x_2} - \bar{x}_1 \frac{\partial f_1}{\partial s} & -\alpha_1 \bar{x}_1 - \bar{x}_1 \frac{\partial f_1}{\partial s} & -\bar{x}_1 \frac{\partial f_1}{\partial s} \\ \frac{D}{\alpha_2} \frac{\partial f_2}{\partial x_1} - \frac{D}{\alpha_2} \frac{\partial f_2}{\partial s} & -\frac{D}{\alpha_2} \frac{\partial f_2}{\partial s} & -\frac{D}{\alpha_2} \frac{\partial f_2}{\partial s} & -D - \frac{D}{\alpha_2} \frac{\partial f_2}{\partial s} \\ 0 & 0 & \alpha_1 \bar{x}_1 - D & 0 \\ 0 & \alpha_2 \bar{v}_2 & 0 & 0 \end{bmatrix}.$$

J_6 admits four eigenvalues given by $\lambda_1 = \alpha_1 \bar{x}_1 - D$ and three other eigenvalues of the roots of the following characteristic polynomial:

$$P_6(X) = \begin{vmatrix} -X - \bar{x}_1 \frac{\partial f_1}{\partial s} & \bar{x}_1 \frac{\partial f_1}{\partial x_2} - \bar{x}_1 \frac{\partial f_1}{\partial s} & -\bar{x}_1 \frac{\partial f_1}{\partial s} \\ \frac{D}{\alpha_2} \frac{\partial f_2}{\partial x_1} - \frac{D}{\alpha_2} \frac{\partial f_2}{\partial s} & -X - \frac{D}{\alpha_2} \frac{\partial f_2}{\partial s} & -D - \frac{D}{\alpha_2} \frac{\partial f_2}{\partial s} \\ 0 & \alpha_2 \bar{v}_2 & -X \end{vmatrix},$$

$$P_6(X) = -X \begin{vmatrix} -X - \bar{x}_1 \frac{\partial f_1}{\partial s} & \bar{x}_1 \frac{\partial f_1}{\partial x_2} - \bar{x}_1 \frac{\partial f_1}{\partial s} \\ \frac{D}{\alpha_2} \frac{\partial f_2}{\partial x_1} - \frac{D}{\alpha_2} \frac{\partial f_2}{\partial s} & -X - \frac{D}{\alpha_2} \frac{\partial f_2}{\partial s} \end{vmatrix} - \alpha_2 \bar{v}_2 \begin{vmatrix} -X - \bar{x}_1 \frac{\partial f_1}{\partial s} & -\bar{x}_1 \frac{\partial f_1}{\partial s} \\ \frac{D}{\alpha_2} \frac{\partial f_2}{\partial x_1} - \frac{D}{\alpha_2} \frac{\partial f_2}{\partial s} & -D - \frac{D}{\alpha_2} \frac{\partial f_2}{\partial s} \end{vmatrix},$$

$$\begin{aligned} P_6(X) &= -X \left[\left(X + \bar{x}_1 \frac{\partial f_1}{\partial s}\right) \left(X + \frac{D}{\alpha_2} \frac{\partial f_2}{\partial s}\right) - \left(\bar{x}_1 \frac{\partial f_1}{\partial x_2} - \bar{x}_1 \frac{\partial f_1}{\partial s}\right) \left(\frac{D}{\alpha_2} \frac{\partial f_2}{\partial x_1} - \frac{D}{\alpha_2} \frac{\partial f_2}{\partial s}\right) \right] \\ &\quad - \alpha_2 \bar{v}_2 \left[\left(X + \bar{x}_1 \frac{\partial f_1}{\partial s}\right) \left(D + \frac{D}{\alpha_2} \frac{\partial f_2}{\partial s}\right) + \bar{x}_1 \frac{\partial f_1}{\partial s} \left(\frac{D}{\alpha_2} \frac{\partial f_2}{\partial x_1} - \frac{D}{\alpha_2} \frac{\partial f_2}{\partial s}\right) \right] \\ &= -X \left[X^2 + X \left(\bar{x}_1 \frac{\partial f_1}{\partial s} + \frac{D}{\alpha_2} \frac{\partial f_2}{\partial s}\right) - \bar{x}_1 \frac{D}{\alpha_2} \frac{\partial f_1}{\partial x_2} \frac{\partial f_2}{\partial x_1} + \bar{x}_1 \frac{D}{\alpha_2} \frac{\partial f_1}{\partial x_2} \frac{\partial f_2}{\partial s} + \bar{x}_1 \frac{D}{\alpha_2} \frac{\partial f_1}{\partial s} \frac{\partial f_2}{\partial x_1} \right] \\ &\quad - \alpha_2 \bar{v}_2 \left[X \left(D + \frac{D}{\alpha_2} \frac{\partial f_2}{\partial s}\right) + D \bar{x}_1 \frac{\partial f_1}{\partial s} + \bar{x}_1 \frac{D}{\alpha_2} \frac{\partial f_1}{\partial s} \frac{\partial f_2}{\partial x_1} \right] \\ &= -X^3 - X^2 \left(\bar{x}_1 \frac{\partial f_1}{\partial s} + \frac{D}{\alpha_2} \frac{\partial f_2}{\partial s}\right) \\ &\quad - X \left(-\bar{x}_1 \frac{D}{\alpha_2} \frac{\partial f_1}{\partial x_2} \frac{\partial f_2}{\partial x_1} + \bar{x}_1 \frac{D}{\alpha_2} \frac{\partial f_1}{\partial x_2} \frac{\partial f_2}{\partial s} + \bar{x}_1 \frac{D}{\alpha_2} \frac{\partial f_1}{\partial s} \frac{\partial f_2}{\partial x_1} + \alpha_2 \bar{v}_2 \left(D + \frac{D}{\alpha_2} \frac{\partial f_2}{\partial s}\right)\right) \\ &\quad - D \bar{v}_2 \bar{x}_1 \frac{\partial f_1}{\partial s} \left[\alpha_2 + \frac{\partial f_2}{\partial x_1}\right]. \end{aligned}$$

Then $P_6(X) = -(X^3 + b_1X^2 + b_2X + b_3)$ with

$$\begin{aligned} b_1 &= \left(\bar{x}_1 \frac{\partial f_1}{\partial s} + \frac{D}{\alpha_2} \frac{\partial f_2}{\partial s} \right) > 0, \\ b_2 &= \left(-\bar{x}_1 \frac{D}{\alpha_2} \frac{\partial f_1}{\partial x_2} \frac{\partial f_2}{\partial x_1} + \bar{x}_1 \frac{D}{\alpha_2} \frac{\partial f_1}{\partial x_2} \frac{\partial f_2}{\partial s} + \bar{x}_1 \frac{D}{\alpha_2} \frac{\partial f_1}{\partial s} \frac{\partial f_2}{\partial x_1} + \alpha_2 \bar{v}_2 \left(D + \frac{D}{\alpha_2} \frac{\partial f_2}{\partial s} \right) \right), \\ b_3 &= D \bar{v}_2 \bar{x}_1 \frac{\partial f_1}{\partial s} \left[\alpha_2 + \frac{\partial f_2}{\partial x_1} \right] < 0. \end{aligned}$$

So, the conditions for the stability of F_6 are not satisfied, then F_6 is unstable.

The number and the nature of equilibrium points of model (3) are stated in the following theorem.

Theorem 6.1 *A) If $\min(D_7, D_8) < D < \max(D_7, D_8)$, then*

(i) if $D_8 < D_7$, then

1. *if $\max(D_2, D_3) < D < D_7$, then system (3) admits two equilibria F_0 and F_1 . F_0 is a saddle point, however, F_1 is a stable node.*
2. *if $\max(D_2, D_9) < D < \min(D_3, D_7)$, then system (3) admits four equilibria F_0, F_1, F_3 and F_7 . F_0, F_1 and F_7 are three saddle points, however, F_3 is a stable node.*
3. *if $D_2 < D < \min(D_7, D_9)$, then system (3) admits three equilibria F_0, F_1 and F_3 . F_0 and F_1 are two saddle points, however, F_3 is a stable node.*
4. *if $\max(D_3, D_4, D_6, D_8) < D < \min(D_2, D_7)$, then system (3) admits three equilibria F_0, F_1 and F_2 . F_0 and F_2 are two saddle points, however, F_1 is a stable node.*
5. *if $\max(D_3, D_5, D_6, D_8, D_{10}) < D < \min(D_4, D_7)$, then system (3) admits five equilibria F_0, F_1, F_2, F_4 and F_6 . F_0, F_2 and F_6 are three saddle points, however, F_1 and F_4 are two stable nodes.*
6. *if $\max(D_3, D_5, D_6, D_8) < D < \min(D_7, D_{10})$, then system (3) admits four equilibria F_0, F_1, F_2 and F_4 . F_0 and F_2 are saddle points, however, F_1 and F_4 are two stable nodes.*
7. *if $\max(D_3, D_6, D_8) < D < \min(D_4, D_5, D_7)$, then system (3) admits four equilibria F_0, F_1, F_2 and F_4 . F_0, F_2 and F_4 are three saddle points, however, F_1 is a stable node.*
8. *if $\max(D_4, D_6, D_8, D_9) < D < \min(D_2, D_3, D_7)$, then system (3) admits five equilibria F_0, F_1, F_2, F_3 and F_7 . F_0, F_1, F_2 and F_7 are four saddle points, however, F_3 is a stable node.*
9. *if $\max(D_5, D_6, D_8, D_9, D_{10}) < D < \min(D_3, D_4, D_7)$, then system (3) admits seven equilibria $F_0, F_1, F_2, F_3, F_4, F_6$ and F_7 . F_0, F_1, F_2, F_6 and F_7 are five saddle points, however, F_3 and F_4 are two stable nodes.*
10. *if $\max(D_5, D_6, D_8, D_9) < D < \min(D_3, D_7, D_{10})$, then system (3) admits six equilibria F_0, F_1, F_2, F_3, F_4 and F_7 . F_0, F_1, F_2 and F_7 are four saddle points, however, F_3 and F_4 are two stable nodes.*
11. *if $\max(D_6, D_8, D_9) < D < \min(D_3, D_4, D_5, D_7)$, then system (3) admits six equilibria F_0, F_1, F_2, F_3, F_4 and F_7 . F_0, F_1, F_2, F_4 and F_7 are five saddle points, however, F_3 is a stable node.*
12. *if $\max(D_4, D_6, D_8) < D < \min(D_2, D_7, D_9)$, then system (3) admits four equilibria F_0, F_1, F_2 and F_3 . F_0, F_1 and F_2 are three saddle points, however, F_3 is a stable node.*
13. *if $\max(D_5, D_6, D_8, D_{10}) < D < \min(D_4, D_7, D_9)$, then system (3) admits six equilibria F_0, F_1, F_2, F_3, F_4 and F_6 . F_0, F_1, F_2 and F_6 are four saddle points, however, F_3 and F_4 are stable nodes.*
14. *if $\max(D_5, D_6, D_8) < D < \min(D_7, D_9, D_{10})$, then system (3) admits five equilibria F_0, F_1, F_2, F_3 and F_4 . F_0, F_1 and F_2 are three saddle points, however, F_3 and F_4 are stable nodes.*

15. if $\max(D_6, D_8) < D < \min(D_4, D_5, D_7, D_9)$, then system (3) admits five equilibria F_0, F_1, F_2, F_3 and F_4 . F_0, F_1, F_2 and F_4 are four saddle points, however, F_3 is a stable node.
 16. if $\max(D_3, D_4, D_8) < D < \min(D_6, D_7)$, then system (3) admits three equilibria F_0, F_1 and F_2 . F_0 and F_2 are two saddle points, however, F_1 is a stable node.
 17. if $\max(D_3, D_5, D_8, D_{10}) < D < \min(D_4, D_6, D_7)$, then system (3) admits five equilibria F_0, F_1, F_2, F_4 and F_6 . F_0, F_1, F_2 and F_6 are three saddle points, however, F_1 and F_4 are stable nodes.
 18. if $\max(D_3, D_5, D_8) < D < \min(D_6, D_7, D_{10})$, then system (3) admits four equilibria F_0, F_1, F_2 and F_4 . F_0 and F_2 are two saddle points, however, F_1 and F_4 are stable nodes.
 19. if $\max(D_3, D_8) < D < \min(D_4, D_5, D_6, D_7)$, then system (3) admits four equilibria F_0, F_1, F_2 and F_4 . F_0, F_2 and F_4 are three saddle points, however, F_1 is a stable node.
 20. if $\max(D_4, D_8, D_9) < D < \min(D_3, D_6, D_7)$, then system (3) admits four equilibria F_0, F_1, F_2 and F_3 , all of them are saddle points.
 21. if $\max(D_5, D_8, D_9, D_{10}) < D < \min(D_3, D_4, D_6, D_7)$, then system (3) admits six equilibria F_0, F_1, F_2, F_3, F_4 and F_6 . F_0, F_1, F_2, F_3 and F_6 are five saddle points, however, F_4 is a stable node.
 22. if $\max(D_5, D_8, D_9) < D < \min(D_3, D_6, D_7, D_{10})$, then system (3) admits five equilibria F_0, F_1, F_2, F_3 and F_4 . F_0, F_1, F_2 and F_3 are four saddle points, however, F_4 is a stable node.
 23. if $\max(D_8, D_9) < D < \min(D_3, D_4, D_5, D_6, D_7)$, then system (3) admits five equilibria F_0, F_1, F_2, F_3 and F_4 , all of them are saddle points.
 24. if $\max(D_4, D_8) < D < \min(D_6, D_7, D_9)$, then system (3) admits four equilibria F_0, F_1, F_2 and F_3 , all of them are saddle points.
 25. if $\max(D_5, D_8, D_{10}) < D < \min(D_4, D_6, D_7, D_9)$, then system (3) admits six equilibria F_0, F_1, F_2, F_3, F_4 and F_6 . F_0, F_1, F_2, F_3 and F_6 are five saddle points, however, F_4 is a stable node.
 26. if $\max(D_5, D_8) < D < \min(D_6, D_7, D_9, D_{10})$, then system (3) admits five equilibria F_0, F_1, F_2, F_3 and F_4 . F_0, F_1, F_2 and F_3 are four saddle points, however, F_4 is a stable node.
 27. if $D_8 < D < \min(D_4, D_5, D_6, D_7, D_9)$, then system (3) admits five equilibria F_0, F_1, F_2, F_3 and F_4 , all of them are saddle points.
- (ii) if $D_7 < D_8$, then
1. if $\max(D_4, D_7) < D < \min(D_6, D_8, D_9)$, then system (3) admits four equilibria F_0, F_1, F_2 and F_3 . F_0, F_1 and F_3 are three saddle points, however, F_2 is a stable node.
 2. if $\max(D_5, D_7, D_{10}) < D < \min(D_4, D_6, D_8, D_9)$, then system (3) admits six equilibria F_0, F_1, F_2, F_3, F_4 and F_6 . F_0, F_1, F_2, F_3 and F_6 are five saddle points, however, F_4 is a stable node.
 3. if $\max(D_5, D_7) < D < \min(D_6, D_8, D_9, D_{10})$, then system (3) admits five equilibria F_0, F_1, F_2, F_3 and F_4 . F_0, F_1, F_2 and F_3 are four saddle points, however, F_4 is a stable node.
 4. if $D_7 < D < \min(D_4, D_5, D_6, D_8, D_9)$, then system (3) admits five equilibria F_0, F_1, F_2, F_3 and F_4 , all of them are saddle points.
 5. if $\max(D_4, D_7, D_9) < D < \min(D_3, D_6, D_8)$, then system (3) admits four equilibria F_0, F_1, F_2 and F_3 . F_0, F_1 and F_3 are three saddle points, however, F_2 is a stable node.
 6. if $\max(D_5, D_7, D_9, D_{10}) < D < \min(D_3, D_4, D_6, D_8)$, then system (3) admits six equilibria F_0, F_1, F_2, F_3, F_4 and F_6 . F_0, F_1, F_2, F_3 and F_6 are five saddle points, however, F_4 is a stable node.

7. if $\max(D_5, D_7, D_9) < D < \min(D_3, D_6, D_8, D_{10})$, then system (3) admits five equilibria F_0, F_1, F_2, F_3 and F_4 . F_0, F_1, F_2 and F_3 are four saddle points, however, F_4 is a stable node.
8. if $\max(D_7, D_9) < D < \min(D_3, D_4, D_5, D_6, D_8)$, then system (3) admits five equilibria F_0, F_1, F_2, F_3 and F_4 , all of them are saddle points.
9. if $\max(D_3, D_4, D_7) < D < \min(D_1, D_6, D_8)$, then system (3) admits three equilibria F_0, F_1 and F_2 . F_0 and F_1 are two saddle points, however, F_2 is a stable node.
10. if $\max(D_3, D_5, D_7, D_{10}) < D < \min(D_1, D_4, D_6, D_8)$, then system (3) admits five equilibria F_0, F_1, F_2, F_4 and F_6 . F_0, F_1, F_2 and F_6 are four saddle points, however, F_4 is a stable node.
11. if $\max(D_3, D_5, D_7) < D < \min(D_1, D_6, D_8, D_{10})$, then system (3) admits four equilibria F_0, F_1, F_2 and F_4 . F_0, F_1 and F_2 are three saddle points, however, F_4 is a stable node.
12. if $\max(D_3, D_7) < D < \min(D_4, D_5, D_6, D_8)$, then system (3) admits four equilibria F_0, F_1, F_2 and F_4 , all of them are saddle points.
13. if $\max(D_4, D_1) < D < \min(D_6, D_8)$, then system (3) admits two equilibria F_0 and F_2 . F_0 is a saddle point, however, F_2 is a stable node.
14. if $\max(D_{10}, D_1) < D < \min(D_4, D_6, D_8)$, then system (3) admits four equilibria F_0, F_2, F_4 and F_6 . F_0, F_2 and F_6 are three saddle points, however, F_4 is a stable node.
15. if $D_1 < D < \min(D_6, D_8, D_{10})$, then system (3) admits three equilibria F_0, F_2 and F_4 . F_0 and F_2 are two saddle points, however, F_4 is a stable node.
16. if $\max(D_4, D_6, D_7) < D < \min(D_8, D_9)$, then system (3) admits four equilibria F_0, F_1, F_2 and F_3 . F_0 and F_1 are two saddle points, however, F_2 and F_3 are two stable nodes.
17. if $\max(D_5, D_6, D_7, D_{10}) < D < \min(D_4, D_8, D_9)$, then system (3) admits six equilibria F_0, F_1, F_2, F_3, F_4 and F_6 . F_0, F_1, F_2 and F_6 are four saddle points, however, F_3 and F_4 are two stable nodes.
18. if $\max(D_5, D_6, D_7) < D < \min(D_8, D_9, D_{10})$, then system (3) admits five equilibria F_0, F_1, F_2, F_3 and F_4 . F_0, F_1 and F_2 are three saddle points, however, F_3 and F_4 are stable nodes.
19. if $\max(D_6, D_7) < D < \min(D_4, D_5, D_8, D_9)$, then system (3) admits five equilibria F_0, F_1, F_2, F_3 and F_4 . F_0, F_1, F_2 and F_4 are four saddle points, however, F_3 is a stable node.
20. if $\max(D_4, D_6, D_7, D_9) < D < \min(D_3, D_8)$, then system (3) admits five equilibria F_0, F_1, F_2, F_3 and F_7 . F_0, F_1 and F_7 are three saddle points, however, F_2 and F_3 are two stable nodes.
21. if $\max(D_5, D_6, D_7, D_9, D_{10}) < D < \min(D_3, D_4, D_8)$, then system (3) admits seven equilibria $F_0, F_1, F_2, F_3, F_4, F_6$ and F_7 . F_0, F_1, F_2, F_6 and F_7 are five saddle points, however, F_3 and F_4 are two stable nodes.
22. if $\max(D_5, D_6, D_7, D_9) < D < \min(D_3, D_8, D_{10})$, then system (3) admits six equilibria F_0, F_1, F_2, F_3, F_4 and F_7 . F_0, F_1, F_2 and F_7 are four saddle points, however, F_3 and F_4 are two stable nodes.
23. if $\max(D_6, D_7, D_9) < D < \min(D_3, D_4, D_5, D_8)$, then system (3) admits six equilibria F_0, F_1, F_2, F_3, F_4 and F_7 . F_0, F_1, F_2, F_4 and F_7 are five saddle points, however, F_3 is a stable node.
24. if $\max(D_3, D_4, D_6, D_7) < D < \min(D_1, D_8)$, then system (3) admits three equilibria F_0, F_1 and F_2 . F_0 and F_1 are two saddle points, however, F_2 is a stable node.
25. if $\max(D_3, D_5, D_6, D_7, D_{10}) < D < \min(D_1, D_4, D_8)$, then system (3) admits five equilibria F_0, F_1, F_2, F_4 and F_6 . F_0, F_1, F_2 and F_6 are four saddle points, however, F_4 is a stable node.
26. if $\max(D_3, D_5, D_6, D_7) < D < \min(D_1, D_8, D_{10})$, then system (3) admits four equilibria F_0, F_1, F_2 and F_4 . F_0, F_1 and F_2 are three saddle points, however, F_4 is a stable node.

27. if $\max(D_3, D_6, D_7) < D < \min(D_4, D_5, D_8)$, then system (3) admits four equilibria F_0, F_1, F_2 and F_4 , all of them are saddle points.
28. if $\max(D_6, D_4, D_1) < D < D_8$, then system (3) admits two equilibria F_0 and F_2 . F_0 is a saddle point, however, F_2 is a stable node.
29. if $\max(D_{10}, D_6, D_1) < D < \min(D_4, D_8)$, then system (3) admits four equilibria F_0, F_2, F_4 and F_6 . F_0, F_2 and F_6 are three saddle points, however, F_4 is a stable node.
30. if $\max(D_6, D_1) < D < \min(D_{10}, D_8)$, then system (3) admits three equilibria F_0, F_2 and F_4 . F_0 and F_2 are two saddle points, however, F_4 is a stable node.

B) If $\max(D_7, D_8) < D < \min(D_1, D_2)$, then

1. If $\max(D_3, D_6, D_7, D_8, D_4) < D < \min(D_1, D_2)$, then system (3) admits four equilibria F_0, F_1, F_2 and F_5 . F_0 and F_5 are saddle points, F_1 and F_2 are stable nodes.
2. If $\max(D_3, D_5, D_6, D_7, D_8, D_{10}) < D < \min(D_1, D_4)$, then system (3) admits six equilibria F_0, F_1, F_2, F_4, F_5 and F_6 . F_0, F_2, F_5 and F_6 are saddle points, F_1 and F_4 are stable nodes.
3. If $\max(D_3, D_5, D_6, D_7, D_8) < D < \min(D_1, D_{10})$, then system (3) admits five equilibria F_0, F_1, F_2, F_4 and F_5 . F_0, F_2 and F_5 are saddle points, F_1 and F_4 are stable nodes.
4. If $\max(D_3, D_6, D_7, D_8) < D < \min(D_4, D_5)$, then system (3) admits five equilibria F_0, F_1, F_2, F_4 and F_5 . F_0, F_2, F_4 and F_5 are saddle points, F_1 is a stable node.
5. If $\max(D_4, D_6, D_7, D_8, D_9) < D < \min(D_2, D_3)$, then system (3) admits six equilibria F_0, F_1, F_2, F_3, F_5 and F_7 . F_0, F_1, F_5 and F_7 are saddle points, F_2 and F_3 are stable nodes.
6. If $\max(D_5, D_6, D_7, D_8, D_9, D_{10}) < D < \min(D_3, D_4)$, then system (3) admits eight equilibria $F_0, F_1, F_2, F_3, F_4, F_5, F_6$ and F_7 . F_0, F_1, F_2, F_5, F_6 and F_7 are saddle points, F_3 and F_4 are stable nodes.
7. If $\max(D_5, D_6, D_7, D_8, D_9) < D < \min(D_3, D_{10})$, then system (3) admits seven equilibria $F_0, F_1, F_2, F_3, F_4, F_5$ and F_7 . F_0, F_1, F_2, F_5 and F_7 are saddle points, F_3 and F_4 are stable nodes.
8. If $\max(D_6, D_7, D_8, D_9) < D < \min(D_3, D_4, D_5)$, then system (3) admits seven equilibria $F_0, F_1, F_2, F_3, F_4, F_5$ and F_7 . F_0, F_1, F_2, F_4, F_5 and F_7 are saddle points, F_3 is a stable node.
9. If $\max(D_3, D_4, D_7, D_8) < D < \min(D_1, D_6)$, then system (3) admits four equilibria F_0, F_1, F_2 and F_5 . F_0 and F_5 are saddle points, F_1 and F_2 are stable nodes.
10. If $\max(D_3, D_5, D_7, D_8, D_{10}) < D < \min(D_1, D_4, D_6)$, then system (3) admits six equilibria F_0, F_1, F_2, F_4, F_5 and F_6 . F_0, F_2, F_5 and F_6 are saddle points, F_1 and F_4 are stable nodes.
11. If $\max(D_3, D_5, D_7, D_8) < D < \min(D_1, D_6, D_{10})$, then system (3) admits five equilibria F_0, F_1, F_2, F_4 and F_5 . F_0, F_2 and F_5 are saddle points, F_1 and F_4 are stable nodes.
12. If $\max(D_3, D_7, D_8) < D < \min(D_4, D_5, D_6)$, then system (3) admits five equilibria F_0, F_1, F_2, F_4 and F_5 . F_0, F_2, F_4 and F_5 are saddle points, F_1 is a stable node.
13. If $\max(D_4, D_7, D_8, D_9) < D < \min(D_3, D_6)$, then system (3) admits five equilibria F_0, F_1, F_2, F_3 and F_5 . F_0, F_1, F_3 and F_5 are saddle points, F_2 is a stable node.
14. If $\max(D_5, D_7, D_8, D_9, D_{10}) < D < \min(D_3, D_4, D_6)$, then system (3) admits seven equilibria $F_0, F_1, F_2, F_3, F_4, F_5$ and F_6 . F_0, F_1, F_2, F_3, F_5 and F_6 are saddle points, F_4 is a stable node.
15. If $\max(D_5, D_7, D_8, D_9) < D < \min(D_3, D_6, D_{10})$, then system (3) admits six equilibria F_0, F_1, F_2, F_3, F_4 and F_5 . F_0, F_1, F_2, F_3 and F_5 are saddle points, F_4 is a stable node.
16. If $\max(D_7, D_8, D_9) < D < \min(D_3, D_4, D_5, D_6)$, then system (3) admits six equilibria F_0, F_1, F_2, F_3, F_4 and F_5 , all of them are saddle points.

17. If $\max(D_4, D_7, D_8) < D < \min(D_6, D_9)$, then system (3) admits five equilibria F_0, F_1, F_2, F_3 and F_5 . F_0, F_1, F_3 and F_5 are saddle points, F_2 is a stable node.
18. If $\max(D_5, D_7, D_8, D_{10}) < D < \min(D_4, D_6, D_9)$, then system (3) admits seven equilibria $F_0, F_1, F_2, F_3, F_4, F_5$ and F_6 . F_0, F_1, F_2, F_3, F_5 and F_6 are saddle points, F_4 is a stable node.
19. If $\max(D_5, D_7, D_8) < D < \min(D_6, D_9, D_{10})$, then system (3) admits six equilibria F_0, F_1, F_2, F_3, F_4 and F_5 . F_0, F_1, F_2, F_3 and F_5 are saddle points, F_4 is a stable node.
20. If $\max(D_7, D_8) < D < \min(D_4, D_5, D_6, D_9)$, then system (3) admits six equilibria F_0, F_1, F_2, F_3, F_4 and F_5 , all of them are saddle points.
21. If $\max(D_4, D_6, D_7, D_8) < D < \min(D_2, D_9)$, then system (3) admits five equilibria F_0, F_1, F_2, F_3 and F_5 . F_0, F_1 and F_5 are saddle points, F_2 and F_3 are stable nodes.
22. If $\max(D_5, D_6, D_7, D_8, D_{10}) < D < \min(D_4, D_9)$, then system (3) admits seven equilibria $F_0, F_1, F_2, F_3, F_4, F_5$ and F_6 . F_0, F_1, F_2, F_5 and F_6 are saddle points, F_3 and F_4 are stable nodes.
23. If $\max(D_5, D_6, D_7, D_8) < D < \min(D_9, D_{10})$, then system (3) admits six equilibria F_0, F_1, F_2, F_3, F_4 and F_5 . F_0, F_1, F_2 and F_5 are saddle points, F_3 and F_4 are stable nodes.
24. If $\max(D_6, D_7, D_8) < D < \min(D_4, D_5, D_9)$, then system (3) admits six equilibria F_0, F_1, F_2, F_3, F_4 and F_5 . F_0, F_1, F_2, F_4 and F_5 are saddle points, F_3 is a stable node.

C) If $\min(D_1, D_2) < D < \max(D_1, D_2)$, then

(i) If $D_1 < D < D_2$, then

1. if $D_1 < D < D_{10}$, then system (3) admits three equilibria F_0, F_2 and F_4 . F_0 and F_2 are two saddle points, however, F_4 is a stable node.
2. if $\max(D_1, D_{10}) < D < D_4$, then system (3) admits four equilibria F_0, F_2, F_4 and F_6 . F_0, F_2 and F_6 are three saddle points, however, F_4 is a stable node.
3. if $\max(D_1, D_4) < D < D_2$, then system (3) admits two equilibria F_0 and F_2 . F_0 is a saddle point, however, F_2 is a stable node.

(ii) If $D_2 < D < D_1$, then

1. if $D_2 < D < D_9$, then system (3) admits three equilibria F_0, F_1 and F_3 . F_0 and F_1 are two saddle points, however, F_3 is a stable node.
2. if $\max(D_2, D_9) < D < D_3$, then system (3) admits four equilibria F_0, F_1, F_3 and F_7 . F_0, F_1 and F_7 are three saddle points, however, F_3 is a stable node.
3. if $\max(D_2, D_3) < D < D_1$, then system (3) admits two equilibria F_0 and F_1 . F_0 is a saddle point, however, F_1 is a stable node.

D) If $\max(D_1, D_2) < D$, then model (3) admits only F_0 as an equilibrium point. F_0 is a stable node.

7 Numerical Simulations

We validated the obtained results by some numerical simulations on a system that uses Monod growth rates and takes into account the reversible inhibition between species:

$$\begin{cases} \dot{s} = D(s^{in} - s) - \frac{4s x_1}{(1+s)(1+x_2)} - \frac{4s x_2}{(2+s)(1.5+x_1)}, \\ \dot{x}_1 = \left(\frac{4s}{(1+s)(1+x_2)} - D - 0.2v_1 \right) x_1, \\ \dot{x}_2 = \left(\frac{4s}{(2+s)(1.5+x_1)} - D - 0.1v_2 \right) x_2, \\ \dot{v}_1 = (0.2x_1 - D)v_1, \\ \dot{v}_2 = (0.1x_2 - D)v_2. \end{cases} \quad (8)$$

One can readily check that the functional responses satisfy Assumptions **A1** to **A3**.

7.1 First case

In Fig. 2, if the dilution rate $D = 4$ satisfying $D_2 = 2.42 < D_1 = 3.8 < D = 4$, each solution with the initial condition inside the whole domain converges to the equilibrium F_0 , from where the extinction of the two species. However, in Fig. 3, for $D = 2.5$ satisfying $D_2 = 2.3 < D < D_1 = 3.7$,

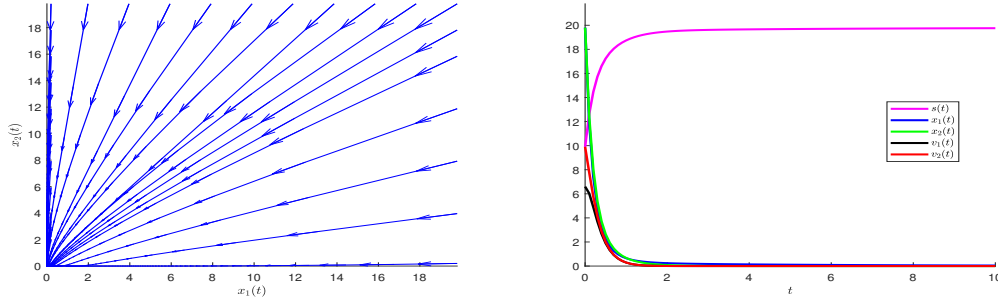


Figure 2: $x_1 - x_2$ behaviour for $D = 4, s^{in} = 19.8$.

each solution with the initial condition inside the whole domain is converging to the equilibrium F_1 , from where only species 1 can survive.

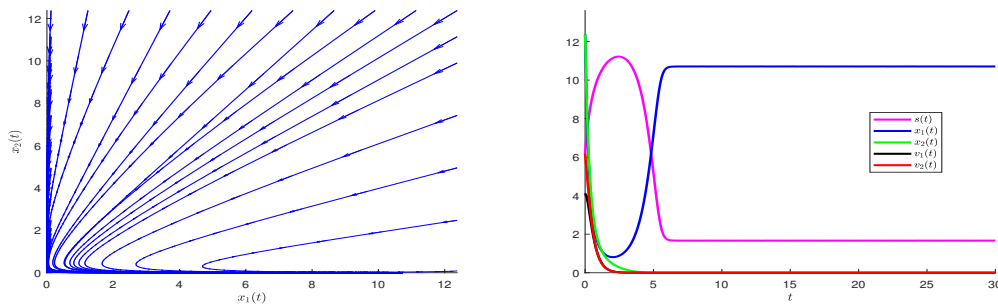


Figure 3: $x_1 - x_2$ behaviour for $D = 2.5, s^{in} = 12.38$.

In Fig. 4, for $D = 1.2$ satisfying then $D = 1.2 < D_2 = 2 < D_1 = 3.42$, each solution with the initial condition inside the red domain converges to the equilibrium F_2 and each solution with the initial condition inside the blue domain converges to the equilibrium F_1 . The competitive exclusion principle is fulfilled here since at least one species goes extinct. As seen in Fig. 4, initial species concentrations are important in determining which is the winning species.

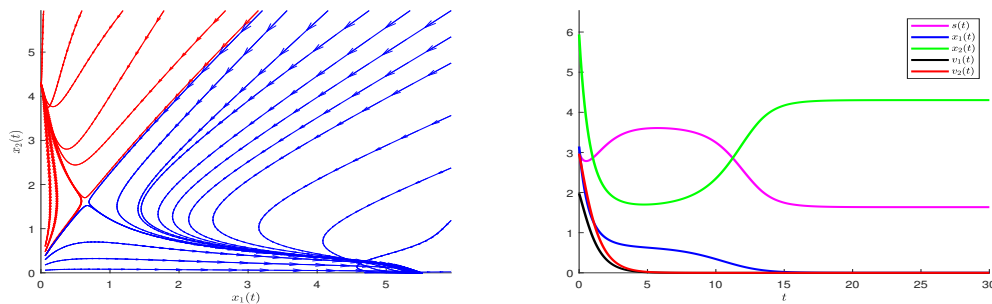


Figure 4: $x_1 - x_2$ behaviour for $D = 1.2, s^{in} = 5.94$.

7.2 Second case

In Fig. 5, if $D = 4$, which satisfies $D_2 = 2.5 < D_1 = 3.87 < D = 4$, each solution with the initial condition inside the whole domain is converging to the equilibrium F_0 , from where the extinction of the two species.

However, in Fig. 6, if $D = 2.5$, which satisfies $D_9 = 0.16 < D_7 = 0.36 < D_2 = 2.41 < D <$

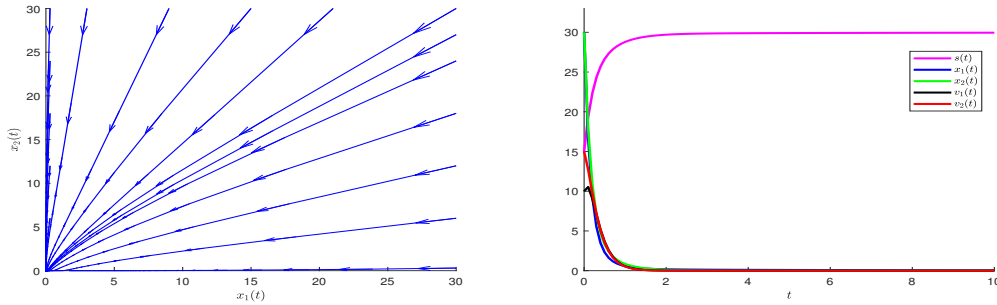


Figure 5: $x_1 - x_2$ behaviour for $D = 4, s^{in} = 30$.

$D_1 = 3.8$, each solution with the initial condition inside the whole domain is converging to the equilibrium F_1 , from where only species 1 can survive.

In Fig. 7, if $D = 2$, which satisfies $D_8 = 0.09 < D_9 = 0.2 < D_7 = 0.34 < D = 2 < D_3 = 3.33 <$

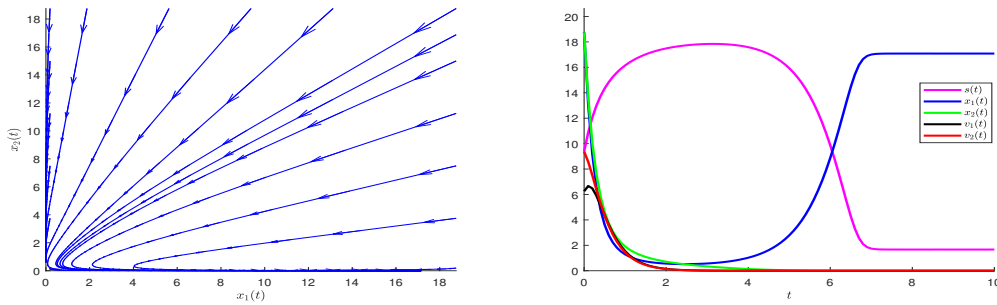


Figure 6: $x_1 - x_2$ behaviour for $D = 2.5, s^{in} = 18.75$.

$D_2 = 2.35 < D_1 = 3.75$, each solution with the initial condition inside the red domain converges to the equilibrium F_2 and each solution with the initial condition inside the blue domain converges to the equilibrium F_3 . The competitive exclusion principle is fulfilled here since at least one species goes extinct.

7.3 Third case

In Fig. 8, if $D = 4$, which satisfies $D_2 = 2.55 < D_1 = 3.91 < D = 4$, each solution with the initial condition inside the whole domain is converging to the equilibrium F_0 , from where the extinction of the two species.

However, in Fig. 9, if $D = 2.5$, which satisfies $D_2 = 2.49 < D < D_1 = 3.86$, each solution with the initial condition inside the whole domain is converging to the equilibrium F_3 , from where only species 1 can survive.

In Fig. 10, if $D = 1.2$, which satisfies $D_6 = 0.23 < D = 1.2 < D_2 = 2.32 < D_3 = 3.53 < D_1 = 3.72$, each solution with the initial condition inside the red domain converges to the equilibrium F_2 and each solution with the initial condition inside the blue domain converges to the equilibrium F_3 . The competitive exclusion principle is fulfilled here since at least one species goes extinct.

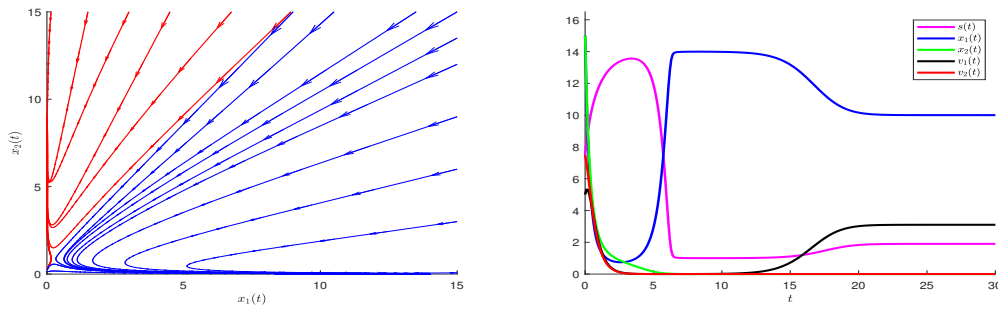


Figure 7: $x_1 - x_2$ behaviour for $D = 2, s^{in} = 15$.

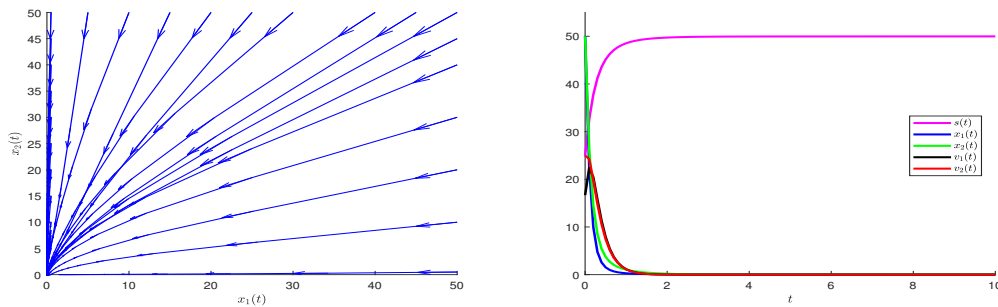


Figure 8: $x_1 - x_2$ behaviour for $D = 4, s^{in} = 45$.

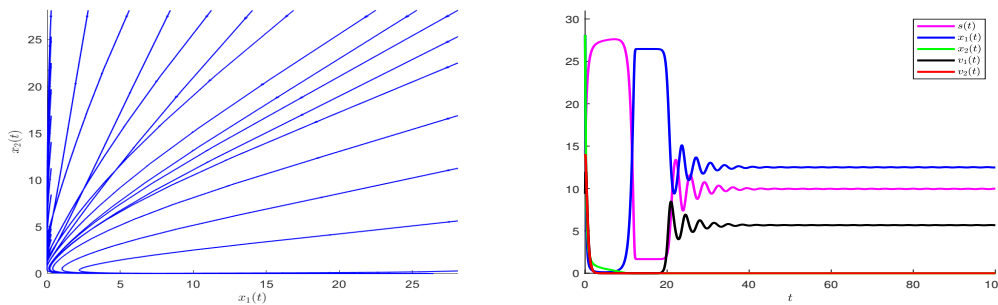


Figure 9: $x_1 - x_2$ behaviour for $D = 2.5, s^{in} = 31.25$.

In the case where we have two equilibrium points which are locally stable (Figures 4,7 and 10), the initial concentrations of species are important in determining which species is the winner. If the initial concentration is inside the attraction domain of the equilibrium point corresponding to the persistence of species 1, then species 2 becomes extinct, and if the initial concentration is inside the attraction domain of the equilibrium point corresponding to the persistence of species 2, then species 1 becomes extinct.

8 Conclusion

The CEP has been widely studied in the scientific literature. In 1932, Gause conducted experiments on the growth of yeasts and paramecia [10]. He deduced that the most competitive species consistently wins the competition. In 1960, this principle became quite popular in ecology. In fact, the CEP is still valid for many kinds of ecosystems [12]. Hsu et al. [15] in 1977, were among the first to study the problem of competition in a chemostat. They considered n populations in com-

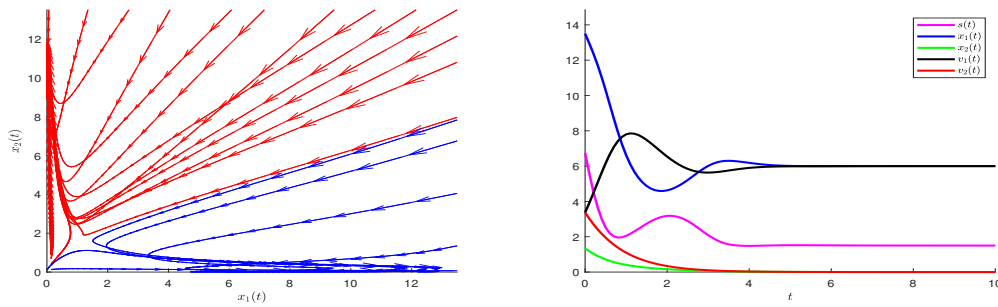


Figure 10: $x_1 - x_2$ behaviour for $D = 1.2, s^{in} = 13.5$.

petition for the same nutrient and verified the competitive exclusion, namely, that the competitor which better uses the substrate in small quantities survives, whereas the others are extinguished.

In this paper, we proposed a mathematical model (1) describing a reversible inhibition relationship between two competing bacteria for one resource in the presence of two viruses. We locally analysed the restriction of system (1) to the attractor set Ω . We proved that in a continuous reactor and under nonlinear general functional responses f_1 and f_2 , the competitive exclusion principle is still fulfilled with at least one species becoming extinct. Initial species concentrations are important in determining which is the winning species.

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