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# An SIS model in the Chemostat

Hayat Berhoune <sup>\*</sup>    Bachir Bar <sup>†</sup>    Mustapha Lakrib <sup>‡</sup>    Tewfik Sari<sup>§</sup>

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## Abstract

**Abstract.** We study a mathematical model of bacterial growth on a single limiting nutrient in a chemostat where a virus is present. The assumption is that the virus can infect the population, resulting in the emergence of two distinct populations: the susceptible and the infected, which are in competition. The model has the structure of an SIS epidemic model. We assume that the growth functions are general and not just linear or of the Monod type as in previous works in the literature. We analyze the local stability of both disease-free and endemic equilibria. The model can exhibit a multiplicity of endemic equilibria, as well as the appearance of periodic orbits by supercritical or subcritical Hopf bifurcations. Bistability between several equilibrium states or limit cycles is also possible. We present an explicit expression for the basic reproduction number of the epidemic in terms of biologically significant parameters. To better understand the richness of the model's behavior, a few bifurcation diagrams with respect to input nutrient concentration are examined.

**Keywords.** Chemostat; SIS epidemic model; Hopf bifurcation; Bi-stability; Multiple limit cycles.

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# 1 Introduction

The chemostat is a simple laboratory apparatus used for the continuous culture of microorganisms. It was introduced simultaneously by Novick and Szilard [25], and Monod [18]. For details and complements on continuous culture, the reader is referred to [13, 19]. The mathematical analysis of models of growth and competition in the chemostat can be found in [12, 30].

The *Competitive Exclusion Principle* predicts that in the basic chemostat model, operated at constant input and dilution rate, coexistence of two or more microbial populations competing for a single non-reproducing nutrient is not possible, see [12, 14, 27, 30, 32] and the references therein. However, the coexistence of competing population often occurs in natural ecosystems and, to explain this, several mechanisms of coexistence have been considered. For example temporal variability in the environment, may allow two or more species to coexist, see [30, Chapter 7] and [33, Chapter 5] and the references therein. Other hypotheses that explain the coexistence include the density dependence of growth function (see [1, 10, 20, 21, 22]), the consideration of inhibitory substances like antibiotic or pesticides (see [30, Chapter 4] and [2, 5, 6, 7, 17, 34]) and the incorporation of viruses (see [15, 23, 31]). Current research suggests that viruses have a significant impact on bacterial populations in aquatic environments and may play a role in regulating biodiversity [16]. Indeed, viral infection can be an important factor in the ecological control of planktonic micro-organisms,

and studying the role of viruses in aquatic environments is a major challenge [3]. In [23] the authors considered the model

$$\begin{cases} S' &= (S^0 - S)D - \frac{1}{\eta_s}\alpha_s Sx_s - \frac{1}{\eta_i}\alpha_i Sx_i - \frac{1}{\eta_y}\alpha_y Sy, \\ x'_s &= (\alpha_s S - D_s)x_s - \delta x_s x_i + \gamma x_i, \\ x'_i &= (\alpha_i S - D_i)x_i + \delta x_s x_i - \gamma x_i, \\ y' &= (\alpha_y S - D_y)y. \end{cases} \quad (1)$$

This model involves two species that compete for a single non-reproducing growth-limiting nutrient, in a well-stirred chemostat in the presence of a virus. The concentration of the nutrient at time  $t$  is denoted by  $S(t)$ . One species  $x$ , is susceptible to attack by the virus. This species is divided into two subpopulations, susceptible with concentration at time  $t$  denoted by  $x_s(t)$  and infective with concentration denoted by  $x_i(t)$ . The second species with concentration denoted by  $y(t)$ , is not susceptible to attack by the virus. Since the virus requires a host to replicate, it is not included in the model explicitly. The disease dynamics are therefore modeled in the form of an SIS epidemic model. In (1)  $S^0$  denotes the input concentration of the nutrient,  $D > 0$  is the dilution rate of the chemostat, and  $D_s, D_i, D_y$  are the removal rates of the bacteria, i.e.  $D_s = D + \epsilon_s$ ,  $D_i = D + \epsilon_i$  and  $D_y = D + \epsilon_y$ , denote the sum of the dilution rate  $D$  and the species-specific death rate. The parameters  $\eta_s, \eta_i$  and  $\eta_y$  are the growth yield coefficients, representing the conversion of nutrients to biomass. The rate of infection of susceptible bacteria in close proximity to infected bacteria is denoted by  $\delta$ , and  $\gamma$  denotes the rate of elimination of virus. The parameters  $\alpha_s, \alpha_i$  and  $\alpha_y$  denote the growth coefficients of susceptible, infected and non susceptible bacteria, respectively.

If  $x_i = 0$  then the system (1) reduces to the usual model of competition of species  $x_s$  and  $y$  in the chemostat for which competitive exclusion occurs. One of the main results of [23] is that coexistence of the competitors  $x_s, x_i$  and  $y$  is possible for the system (1). Therefore, while competitive exclusion occurs for (1) in the absence of the virus ( $x_i = 0$ ), coexistence of competitors becomes possible in its presence. These findings suggest that the presence of viruses could enhance bacterial diversity, potentially influencing bacterial species' survival.

Much of the analysis of (1) is based on understanding the particular subsystem of (1) obtained by letting  $y = 0$ :

$$\begin{cases} S' &= (S^0 - S)D - \frac{1}{\eta_s}\alpha_s Sx_s - \frac{1}{\eta_i}\alpha_i Sx_i, \\ x'_s &= (\alpha_s S - D_s)x_s - \delta x_s x_i + \gamma x_i, \\ x'_i &= (\alpha_i S - D_i)x_i + \delta x_s x_i - \gamma x_i. \end{cases} \quad (2)$$

Subsystem (2) was introduced in [31] who considered the existence and local stability of equilibria in the special case that  $D = D_s = D_i$ ,  $\eta_i < \eta_s$  and  $\alpha_i \approx \alpha_s$ . The global stability of equilibria of (2) was considered assuming  $D = D_s = D_i$  and  $\alpha_i = \alpha_s$  in [15]. The results of [15, 31] on the local and global analysis of the subsystem (2) were extended in [23] in the general case without the above mentioned restrictions on the removal rates, the yields coefficients and the growth rates. Relaxing the assumption that  $D = D_s = D_i$  requires more delicate analysis than previously done in [15, 31] and results in differences in the number of possible equilibria and the types of bifurcations that they can undergo. It is shown in [23] that the subsystem (2) has rich dynamics, including multiplicity of endemic equilibria, as well as the appearance of periodic orbits by supercritical or subcritical Hopf bifurcations. Bistability between several equilibrium points or limit cycles is also possible.

Our aim in this paper is to relax the hypotheses that the growth functions are linear and to extend the results of [23] on the existence and local stability of equilibria of (2) to general increasing growth functions. We also construct some bifurcation diagrams with respect to the nutrient input concentration  $S^0$ , when the dilution  $D$  and the biological parameters are fixed.

The organization of this paper is as follows. In Section 2, we present the model and assumptions that we would consider. In Section 3, we present our main result which gives the conditions of

existence and stability of the equilibrium points. In Section 4 we apply our result to the case where the growth rates are linear or Monod functions. In Section 5, we present some bifurcation diagrams as the input concentration varies. These diagrams show the system's behavior when the biological parameters are fixed and also the dilution rate. The paper concludes with a discussion. Technical proofs are given in A, and numerical experiments to support some of our proofs are given in B.

## 2 Mathematical model, notations and preliminary results

Following [23], we consider an SIS model in the chemostat taking the form

$$\begin{cases} S' &= (S^0 - S)D - \frac{1}{\eta_s} f_s(S)x_s - \frac{1}{\eta_i} f_i(S)x_i, \\ x'_s &= (f_s(S) - D_s)x_s - \delta x_s x_i + \gamma x_i, \\ x'_i &= (f_i(S) - D_i)x_i + \delta x_s x_i - \gamma x_i. \end{cases} \quad (3)$$

The variables and parameters in this model have the same meaning as in (2) except that the linear growth functions are replaced by general growth functions  $f_s(S)$  and  $f_i(S)$ . The removal rates  $D_s$  and  $D_i$  are given by

$$D_s = D + \epsilon_s, \quad D_i = D + \epsilon_i, \quad (4)$$

where  $D$  is the dilution rate and  $\epsilon_s, \epsilon_i$  the species-specific death rate of susceptible species  $x_s$  and infected species  $x_i$ , respectively. The functions  $f_s$  and  $f_i$ , represent the specific growth rates of the susceptible and infected bacteria, respectively. The system (2) corresponds to the particular case  $f_s(S) = \alpha_s S$  and  $f_i(S) = \alpha_i S$ . In this work, we do not assume that the growth functions have this specific form. We only assume that

**Hypothesis 1.**  $f_s(0) = f_i(0) = 0$  and, for all  $S > 0$ ,  $f'_s(S) > 0$  and  $f'_i(S) > 0$ .

It is assumed that infective bacteria have a higher death rate than susceptible bacteria, i.e.  $\epsilon_i \geq \epsilon_s$ . It is also assumed that the growth rate of infective bacteria is no better than that of susceptible bacteria. Therefore we add the following assumptions

**Hypothesis 2.** For all  $S \geq 0$ ,  $f_s(S) \geq f_i(S)$ .

**Hypothesis 3.**  $D_i \geq D_s$ .

We note that the positive cone is positively invariant and all solutions are positively bounded. The proof is classical and hence omitted. We define the break-even concentrations  $\lambda_s$  and  $\lambda_i$ :

$$\lambda_s = f_s^{-1}(D_s), \quad \lambda_i = f_i^{-1}(D_i). \quad (5)$$

When equation  $f_s(S) = D_s$  or  $f_i(S) = D_i$  has no solution, we put  $\lambda_s = \infty$  or  $\lambda_i = \infty$ .

**Lemma 1.** *If Hypotheses 1, 2 and 3 are satisfied, we have  $\lambda_i \geq \lambda_s$ .*

*Proof.* From Hypothesis 1 we deduce that  $f_i^{-1}$  is increasing. Using Hypothesis 3 we have  $\lambda_i = f_i^{-1}(D_i) \geq f_i^{-1}(D_s)$ . From Hypothesis 2 we deduce that  $f_i^{-1} \geq f_s^{-1}$ . Therefore,  $f_i^{-1}(D_s) \geq f_s^{-1}(D_s) = \lambda_s$ . Hence,  $\lambda_i \geq \lambda_s$ .  $\square$

In the rest of the paper, we will distinguish the two following cases:

$$\lambda_i > \lambda_s, \quad (6)$$

$$\lambda_i = \lambda_s. \quad (7)$$

Case (6) is more likely to occur. However, even if it is non generic, case (7) can occur, especially if  $f_s = f_i$  and  $\varepsilon_s = \varepsilon_i$ , which is biologically meaningful, since the species  $x_s$  and  $x_i$  are the same. We use the following notations

$$X_s := \frac{\gamma + D_i - f_i}{\delta}, \quad X_i := \frac{f_s - D_s}{D_i - f_i} X_s, \quad F := \frac{1}{\eta_s} f_s X_s + \frac{1}{\eta_i} f_i X_i. \quad (8)$$

**Remark 1.** In the case  $\lambda_s < \lambda_i$ , we denote by  $I := (\lambda_s, \lambda_i)$ . We have  $f_s(S) > D_s$  and  $f_i(S) < D_i$  for  $S \in I$ , and  $f_s(\lambda_s) = D_s$ ,  $f_i(\lambda_i) = D_i$ . Therefore the functions  $X_s$ ,  $X_i$  and  $F$  are non negative on  $I$  and we have  $X_s(\lambda_s) > 0$ ,  $X_i(\lambda_s) = 0$ ,  $X_s(\lambda_i) > 0$  and  $X_i(\lambda_i) = +\infty$ . Hence, we have  $F(\lambda_s) = \frac{D_s}{\eta_s} X_s(\lambda_s) > 0$ ,  $F(\lambda_i) = +\infty$  and  $F$  is positive on  $I$ . We use the following notation

$$G(S) := S + \frac{1}{D} F(S). \quad (9)$$

The function  $G$  is positive on  $I$  and has a vertical asymptote at  $S = \lambda_i$  (see Figs. 1, 4(a), 5, 7(a), 8(a), 9(a) and 10(a), for illustrative examples).

### 3 Results

#### 3.1 Existence of equilibria

The existence of equilibria of system (3) is stated by the following result.

**Proposition 2.** Assume that Hypothesis 1 is satisfied. System (3) has the following equilibria:

The washout equilibrium,  $E_0 = (S^0, 0, 0)$ , which always exists.

The disease free equilibrium (DFE),  $E_1 = (\bar{S}, \bar{x}_s, 0)$  of extinction of  $x_i$ , where

$$\bar{S} = \lambda_s, \quad \bar{x}_s = \frac{D\eta_s}{D_s} (S^0 - \lambda_s). \quad (10)$$

Here,  $\lambda_s$  is defined by (5). This equilibrium exists if and only if  $\lambda_s < S^0$ .

An endemic equilibrium, or coexistence equilibrium,  $E_2 = (S^*, x_s^*, x_i^*)$ , where the components are assumed to be positive. Two cases must be distinguished.

1. In the case  $\lambda_s < \lambda_i$ ,  $S^*$  is a solution of equation

$$S^0 = G(S), \quad (11)$$

where the function  $G$  is defined by (9), and  $x_s^*$ ,  $x_i^*$  are given by

$$x_s^* = X_s(S^*), \quad x_i^* = X_i(S^*), \quad (12)$$

where the functions  $X_s$  and  $X_i$  are defined by (8). This equilibrium exists if and only if equation (11) has a solution  $S = S^*$  such that  $\lambda_s < S^* < \lambda_i$ . Multiplicity of solution  $S^*$ , and hence of endemic equilibria  $E_2$ , can occur.

2. In the case  $\lambda_s = \lambda_i$ , we have  $S^* = \lambda_s$  and

$$x_s^* = \frac{\gamma}{\delta}, \quad x_i^* = \frac{\eta_i}{D_i} \left( D (S^0 - \lambda_s) - \frac{D_s \gamma}{\eta_s \delta} \right). \quad (13)$$

This equilibrium exists if and only if  $S^0 > \lambda_c := \lambda_s + \frac{D_s \gamma}{D \delta \eta_s}$ .

*Proof.* The proof is given in Appendix A.1.  $\square$

This proposition says that the washout equilibrium  $E_0$  always exists, while the DFE  $E_1$  is unique if it exists. Moreover, in the case (7), the positive equilibrium  $E_2$  is also unique if it exists. On the other hand, in the case (6), any solution  $S^* \in I$  of the equation (11) gives a positive equilibrium  $E_2$ . Therefore the number of positive equilibria depends on the number of solutions of the equation (11) belonging to  $I$ .

### 3.2 Multiplicity of positive equilibria in the case $\lambda_s < \lambda_i$

As stated in Remark 1, the function  $G$  is positive on interval  $I$  and tends to infinity when  $S$  tends to  $\lambda_i$ , see Fig. 1.

**Remark 2.** A positive equilibrium is given by a solution of the equation (11), belonging to  $I$ . A solution of this equation is the abscissa of a point of intersection of the horizontal line where  $S^0$  is fixed (in red in Fig. 1) and the curve  $\Gamma$  of equation  $S^0 = G(S)$  (in blue in Fig. 1).

Hence, existence of solutions of the equation (11) and their number is related to the monotonicity or not of the function  $G$ . Therefore, in the case (6), equation

$$G'(S) = 0 \quad (\text{or, equivalently, } F'(S) = -D), \quad (14)$$

plays a major role in the discussion of the uniqueness or multiplicity of the positive equilibria. Assume that equation (14) has solutions  $S_k^{SN}$  (depending on  $D$ ), where  $k = 1, 2, \dots$  is an integer. See Fig. 1(b) for an example with  $k = 1, 2$ .

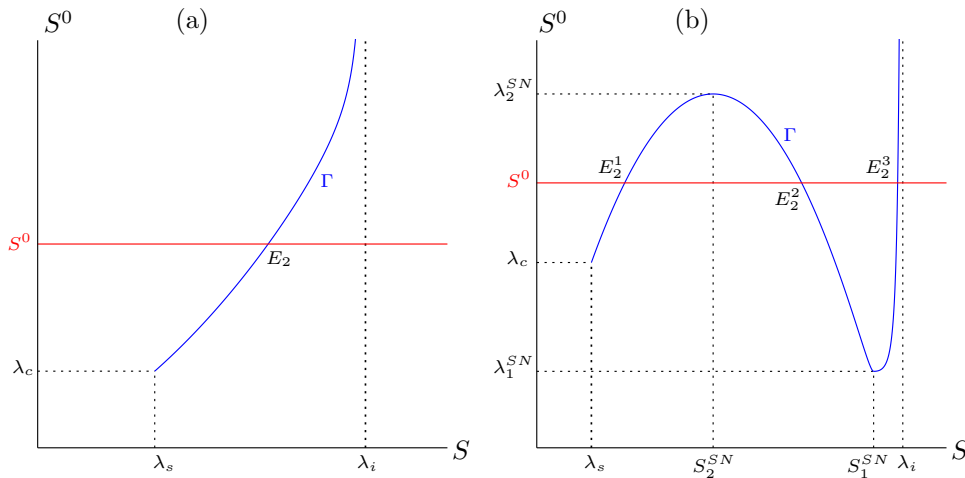


Figure 1: Illustration of the existence and multiplicity of positive equilibria. (a)  $G(S)$  is increasing. (b)  $G(S)$  is decreasing for  $S_2^{NS} < S < S_1^{NS}$  and increasing for  $\lambda_s < S < S_2^{NS}$  and  $S_1^{NS} < S < \lambda_i$ .

**Definition 1.** We define the following numbers as relevant to the discussion of the existence and number of positive equilibria:

$$\lambda_c := G(\lambda_s) = \lambda_s + \frac{D_s}{D\delta\eta_s} (D_i - f_i(\lambda_s) + \gamma), \quad (15)$$

$$\lambda_k^{SN} := G(S_k^{SN}) = S_k^{SN} + \frac{1}{D} F(S_k^{SN}), \quad k = 1, 2, \dots \quad (16)$$

The number  $\lambda_c$  corresponds to a transcritical bifurcation of an endemic equilibrium  $E_2$  and the equilibrium  $E_1$ , while the numbers  $\lambda_k^{SN}$  correspond to saddle-node bifurcations of the positive equilibria.

For example, if  $G'(S) > 0$  for all  $S \in I$ , then equation (11) has at most one solution, see Fig. 1(a), where there is one solution if  $S^0 > \lambda_c$  and no solution if  $S^0 < \lambda_c$ . On the other hand, if  $G'(S) < 0$  for some  $S \in I$ , then equation (11) can have more than one solution. Assume for example that, as in Fig. 1(b), the equation (14) has two solutions  $S_1^{SN}$  and  $S_2^{SN}$  such that  $\lambda_i > S_1^{SN} > S_2^{SN} > \lambda_s$  and  $\lambda_1^{SN} < \lambda_c < \lambda_2^{SN}$ . Then, if  $S^0 < \lambda_1^{SN}$  there is no positive equilibrium point, if  $\lambda_1^{SN} < S^0 < \lambda_c$  there are two, if  $\lambda_c < S^0 < \lambda_2^{SN}$  there are three, and if  $S^0 > \lambda_2^{SN}$  the positive equilibrium point exists and is unique.

**Remark 3.** If  $\lambda_s = \lambda_i$  then  $D_i - f_i(\lambda_s) = 0$  and the number (15) becomes  $\lambda_c = \lambda_s + \frac{D_s\gamma}{D\delta\eta_s}$ , which is the number that appears in item (2) of Proposition 2. This is the reason why we have noted the two numbers by  $\lambda_c$ .

The following proposition gives the existence and uniqueness of the positive equilibrium of (3) in the case (6), when equation (14) has no solution in  $I$ .

**Proposition 3.** If equation (14) has no solution in  $I$ , then the positive equilibrium  $E_2 = (S^*, x_s^*, x_i^*)$  exists if and only if  $S^0 > \lambda_c$ , where  $\lambda_c$  is defined by (15). If it exists, it is unique.

*Proof.* As stated in Remark 2, a positive equilibrium corresponds to an intersection of the red and blue curves in Fig. 1. Since  $G$  is increasing, there exists at most one point of intersection. A point of intersection exists if and only if  $S^0 > \lambda_c$ , where  $\lambda_c$  is given by (15), see Fig. 1(a).  $\square$

When equation (14) has a solution in  $I$ , a multiplicity of positive equilibria is possible. More precisely, we have the following result.

**Proposition 4.** Assume that  $\lambda_s < \lambda_i$  and (14) has solutions  $S_k^{SN}$  in  $I$ . Let  $\lambda_c$  and  $\lambda_k^{SN}$  defined by (15) and (16).

(1) If  $S^0 > \lambda_c$ , then, generically, an odd number of positive equilibria exist (at least one).

(2) If  $S^0 < \lambda_c$ , then, generically, there is either no positive equilibrium or an even number of positive equilibria exist.

The values  $S^0 = \lambda_k^{SN}$  correspond to saddle node bifurcations of positive equilibria.

*Proof.* The curve  $\Gamma$  of equation  $S^0 = G(S)$  and an horizontal line of equation  $S^0$  kept constant have, generically, an odd number of points of intersection if  $S^0 > \lambda_c$  (at least one). If  $S^0 < \lambda_c$ , generically, an even number of points of intersection exist, with possibly no intersection point, see Fig. 1(b).  $\square$

**Lemma 5.** The equation  $S^0 = G(S)$  (or, equivalently,  $D(S^0 - S) = F(S)$ ) is equivalent to the equation  $f(S) = 0$  where  $f$  is defined by

$$f(S) := D\delta\eta_s\eta_i(D_i - f_i(S))(S^0 - S) - (D_i - f_i(S) + \gamma)(\eta_i(D_i - f_i(S))f_s(S) + \eta_s(f_s(S) - D_s)f_i(S)). \quad (17)$$



*Proof.* Using the definitions (8) of the functions  $X_s$ ,  $X_i$  and  $F$ , we see that the equation  $D(S^0 - S) = F(S)$  is equivalent to the equation  $f(S) = 0$ .  $\square$

Since we are looking for the solutions  $S^* \in (\lambda_s, \lambda_i)$  of this equation, it is useful to note that

$$\begin{aligned} f(\lambda_s) &= D\eta_s\eta_s\delta(D_i - f_i(\lambda_s))(S^0 - \lambda_c), \\ f(\lambda_i) &= D_i\eta_s\gamma(D_s - f_s(\lambda_i)) < 0, \end{aligned} \quad (18)$$

where  $\lambda_c$  is defined in (15). Since  $D_i > f_i(\lambda_s)$ ,  $f(\lambda_s, S^0, D)$  has the same sign as  $S^0 - \lambda_c$ . The number  $\lambda_c$  therefore plays an important role in the determination of the number of solutions of the solutions in the interval  $(\lambda_s, \lambda_i)$ , i.e. in the existence and number of positive equilibria. Indeed, we can make the following remark.

**Remark 4.** *Using the formulas (18) we can solve equation (17) on the interval  $(\lambda_s, \lambda_i)$  and deduce that*

- *If  $S^0 > \lambda_c$ , then  $f(\lambda_s) > 0$  and hence, generically, an odd number of positive equilibria exist (at least one).*
- *If  $S^0 < \lambda_c$ , then  $f(\lambda_s) < 0$  and hence, generically, there is either no positive equilibrium or an even number of positive equilibria exist.*

This is the result obtained in Proposition 4, by solving equation  $S^0 = G(S)$ . The advantage of the equation  $S^0 = G(S)$  over the equivalent equation  $f(S) = 0$  is that the function  $G(S)$  depends only on the parameter  $D$ , and the solutions have a clear geometric interpretation: they are the abscissas of the points of intersection of the horizontal line defined by  $S^0$  with the curve  $\Gamma$  defined as the graph of the function  $G(S)$ , see Remark 2 and Fig. 1. On the other hand, when we consider the equation  $f(S) = 0$ , the two parameters  $S^0$  and  $D$  are intertwined in the equation and the solutions do not have a nice graphical interpretation.

We now give a sufficient condition for  $F'(S) > 0$  for all  $S \in I$ , so that equation (14) has no solution in  $I$ , and the endemic equilibrium is unique, if it exists.

**Lemma 6.** *If  $\eta_s \geq \eta_i$  and  $f'_s(S) \geq f'_i(S)$  for all  $S \in I$ , then  $F'(S) > 0$  for all  $S \in I$ . Therefore, if it exists, the endemic equilibrium is unique.*

*Proof.* The proof is given in Appendix A.2  $\square$

Straightforward calculation gives

$$F' = \frac{\varphi_i(\varphi_i - \gamma)A_s f'_s + A_i f'_i}{\delta\eta_s\eta_i\varphi_i^2}, \quad (19)$$

where  $\varphi_s = f_s - D_s$ ,  $\varphi_i = f_i - D_i$  and

$$A_s = f_i(\eta_s - \eta_i) + \eta_i D_i, \quad A_i = \varphi_s \varphi_i^2 (\eta_s - \eta_i) - \eta_i \varphi_i^2 D_s + \gamma \eta_s \varphi_s D_i. \quad (20)$$

**Lemma 7.** *The equation  $G'(S) = 0$  (or, equivalently,  $F'(S) = -D$ ) is equivalent to the equation  $g(S) = 0$ , where  $g$  is defined by*

$$g := \varphi_i(\varphi_i - \gamma)A_s f'_s + A_i f'_i + D\delta\eta_s\eta_i\varphi_i^2, \quad (21)$$

and  $A_s$  and  $A_i$  are given by (20). Note that the condition  $G'(S) > 0$  (which is equivalent to the condition  $F'(S) > -D$ ) is satisfied if and only if  $g(S) > 0$ .

*Proof.* From (19) we deduce that the condition  $F'(S) = -D$  is equivalent to the equation  $g(S) = 0$ , where  $g$  is defined by (21).  $\square$

**Lemma 8.** *If it exists, the positive equilibrium is unique if and only if we have  $\min_{S \in I} g(S) \geq 0$ .*

*Proof.* From  $\varphi_i(\lambda_i) = 0$ , we deduce that

$$g(\lambda_i) = \gamma \eta_s D_i f'_i(\lambda_i) \varphi_s(\lambda_i), \quad g'(\lambda_i) = \gamma \eta_s D_i f''_i(\lambda_i) \varphi_s(\lambda_i). \quad (22)$$

Since  $\varphi_s(\lambda_i) > 0$  and  $f'_i(\lambda_i) > 0$ , we have  $g(\lambda_i) > 0$ . Therefore, the function  $g(S)$  does not change of sign on  $I$  if and only if  $\min_{S \in I} g(S) \geq 0$ .  $\square$

The sign of  $g(S)$  on  $I$  can be determined easily, for example by calculating the derivative  $g'(S)$  and studying its variations on the interval  $I$ . As nothing can be said in the general case, this study will be carried out in Section 4.1.3 for linear growth functions.

### 3.3 Basic reproduction number

Following [23], who considered the case of linear growth functions  $f_s(S) = \alpha_s S$  and  $f_i(S) = \alpha_i S$ , the *basic reproduction number*  $\mathcal{R}_0$  can be given by

$$\mathcal{R}_0 = \frac{f_i(\bar{S}) + \delta \bar{x}_s}{D_i + \gamma}, \quad (23)$$

where  $\bar{S} = \lambda_s$  and  $\bar{x}_s = \frac{D \eta_s}{D_s} (S^0 - \lambda_s)$  are the components of the DFE  $E_1 = (\bar{S}, \bar{x}_s, 0)$ , where the infective species  $x_i$  is extinct. The biological interpretation of this number is the following, see [23]: The numerator represents the mean number of infectives produced per unit time from both horizontal and vertical transmission resulting from the introduction of a single infective into an otherwise totally susceptible population at equilibrium, and  $\frac{1}{D_i + \gamma}$  represents the mean amount of time an infective individual remains in the chemostat as an infective. Using the expression

$$\mathcal{R}_0 = \frac{f_i(\lambda_s) + \delta \frac{D \eta_s}{D_s} (S^0 - \lambda_s)}{D_i + \gamma}, \quad (24)$$

a simple calculation shows that  $\mathcal{R}_0 > 1$  is equivalent to  $S^0 > \lambda_c$  and  $\mathcal{R}_0 < 1$  is equivalent to  $S^0 < \lambda_c$ , where  $\lambda_c$  is defined by (15). Therefore our results can be stated using the basic reproduction number. As a corollary of Propositions 3 and 4 we obtain the following result.

**Theorem 9.** *Assume that  $\mathcal{R}_0 > 1$  or equivalently  $S^0 > \lambda_c$ .*

1. *If equation (14) has no solution in  $I$ , then the positive equilibrium exists and is unique.*
2. *If equation (14) has a solution in  $I$ , then there exists at least one positive equilibrium and, generically, an odd number of positive equilibria exist.*

*Assume that  $\mathcal{R}_0 < 1$  or equivalently  $S^0 < \lambda_c$ .*

1. *If equation (14) has no solution in  $I$ , then no positive equilibrium exists.*
2. *If equation (14) has a solution in  $I$ , then, generically, there is either no positive equilibrium or an even number of positive equilibria exist.*

### 3.4 Local stability of equilibria

The local stability of the boundary equilibria  $E_0$  and  $E_1$  are given as follows.

**Proposition 10.**  $E_0$  is stable if and only if  $S^0 < \lambda_s$ , where  $\lambda_s$  is given by (5).  $E_1$  is stable if and only if  $S^0 < \lambda_c$  where  $\lambda_c$  is given by (15).

*Proof.* The proof is given in Appendix A.3 □

In what follows, we analyze the stability of a positive equilibrium  $E_2$ . The cases (6) and (7) must be distinguished.

**Proposition 11.** Assume that case (6) holds, i.e.  $\lambda_s < \lambda_i$ . An endemic equilibrium  $E_2 = (S^*, x_s^*, x_i^*)$  of (3), where  $S^*$  is a solution of (11), and  $x_s^*, x_i^*$  are given by (12), if it exists, is stable if and only if  $F'(S^*) > -D$  and  $a_1 a_2 - a_3 > 0$ , where  $a_1, a_2$  and  $a_3$  are given by

$$\begin{aligned} a_1 &= B + \gamma \frac{x_i^*}{x_s^*}, \\ a_2 &= \frac{1}{\eta_s} f_s(S^*) x_s^* f'_s(S^*) + \frac{1}{\eta_i} f_i(S^*) x_i^* f'_i(S^*) + \delta x_i^* C + B \frac{\gamma x_i^*}{x_s^*}, \\ a_3 &= \frac{1}{\eta_i} f_i(S^*) x_i^* \left( f'_s(S^*) \delta x_s^* + f'_i(S^*) \frac{\gamma x_i^*}{x_s^*} \right) + C \left( B \delta x_i^* - \frac{1}{\eta_s} f_s(S^*) x_i^* f'_i(S^*) \right), \end{aligned} \quad (25)$$

where  $B = D + \frac{x_s^*}{\eta_s} f'_s(S^*) + \frac{x_i^*}{\eta_i} f'_i(S^*)$  and  $C = \delta x_s^* - \gamma$ .

Assume that case (7) holds, i.e.  $\lambda_s = \lambda_i$ . If it exists, the equilibrium  $E_2 = (\lambda_s, x_s^*, x_i^*)$ , where  $x_s^*, x_i^*$  are given by (13), is stable if and only if  $b_1 b_2 - b_3 > 0$ , where  $b_1, b_2$  and  $b_3$  are given by

$$\begin{aligned} b_1 &= B + \delta x_i^*, \\ b_2 &= \frac{D_s}{\eta_s} x_s^* f'_s(\lambda_s) + \frac{D_i}{\eta_i} x_i^* f'_i(\lambda_s) + B \delta x_i^*, \\ b_3 &= \frac{D_i}{\eta_i} x_i^* (\gamma f'_s(\lambda_s) + f'_i(\lambda_s) \delta x_i^*), \end{aligned} \quad (26)$$

where  $B = D + \frac{x_s^*}{\eta_s} f'_s(\lambda_s) + \frac{x_i^*}{\eta_i} f'_i(\lambda_s)$ .

*Proof.* The proof is given in Appendix A.4 □

We now give a sufficient condition for the stability condition  $a_1 a_2 - a_3 > 0$  or  $b_1 b_2 - b_3 > 0$  to be satisfied.

**Lemma 12.** Assume that  $\lambda_s < \lambda_i$ . If

$$f'_s \geq f'_i \quad \text{and} \quad f'_s f'_i (f_s + f_i) \geq \delta (\eta_s f_i f'_s - \eta_i f_s f'_i) \quad (27)$$

for  $S = S^*$ , where  $S^* \in I$  is a solution of (11), then the corresponding equilibrium  $(S^*, x_s^*, x_i^*)$  satisfies  $a_1 a_2 - a_3 > 0$ . Therefore, it is stable if and only if  $G'(S^*) > 0$ .

Assume that  $\lambda_s = \lambda_i$ . If the conditions (27) are satisfied for  $S = \lambda_s$  then, if it exists,  $E_2$  satisfies  $b_1 b_2 - b_3 > 0$ . Therefore, it is stable.

*Proof.* The proof is given in Appendix A.5 □

We now propose a reformulation of the stability conditions that will be useful for the following applications. We begin with the case  $\lambda_s < \lambda_i$ . Let

$$A_4(S) = A_1(S) A_2(S) - A_3(S), \quad (28)$$

where  $A_1$ ,  $A_2$  and  $A_3$  are defined by

$$\begin{aligned} A_1 &= B + \gamma \frac{X_i}{X_s}, \\ A_2 &= \frac{1}{\eta_s} f_s X_s f'_s + \frac{1}{\eta_i} f_i X_i f'_i + \delta X_i C + B \frac{\gamma X_i}{X_s}, \\ A_3 &= \frac{1}{\eta_i} f_i X_i \left( f'_s \delta X_s + f'_i \frac{\gamma X_i}{X_s} \right) + C \left( B \delta X_i - \frac{1}{\eta_s} f_s X_i f'_i \right), \end{aligned}$$

where  $B = D + \frac{X_s}{\eta_s} f'_s + \frac{X_i}{\eta_i} f'_i$  and  $C = \delta X_s - \gamma$ . The coefficients  $A_i$  are defined by the same formulas as the coefficients  $a_i$ , see (25). The only difference is that  $S^*$  is replaced by  $S$  and  $x_s^*$  and  $x_i^*$  are replaced by  $X_s(S)$  and  $X_i(S)$ , defined by (8). Note that the coefficients  $A_i$  in (28) depend only on the operating parameter  $D$  and not on the operating parameter  $S^0$ , unlike the quantities  $a_i$  in (25), which also depend on it.

We fix  $D$ . To simplify the presentation, consider the case where there exist  $S_1^H$  and  $S_2^H$  (depending on  $D$ ) such that  $\lambda_s < S_1^H < S_2^H < \lambda_i$  and  $A_4(S, D) < 0$  for  $S \in (S_1^H, S_2^H)$ , and positive outside this interval. The more general case where there exist more than two solutions  $S_1^H$  and  $S_2^H$  can be studied similarly. We have the following result.

**Proposition 13.** *Assume that  $\lambda_s < \lambda_i$ . Let*

$$\lambda_k^H = G(S_k^H) := S_k^H + \frac{1}{D} F(S_k^H), \quad k = 1, 2. \quad (29)$$

*Then  $a_1 a_2 - a_3 < 0$  if and only if  $\lambda_1^H < S^0 < \lambda_2^H$ . The numbers  $\lambda_k^H$  correspond to Hopf bifurcations of a positive equilibrium.*

*Proof.* Using (12), we can write  $a_i = A_i(S^*(S^0))$  for  $i = 1, 2, 3$ , where  $S^*(S^0)$  is a solution of equation  $S^0 = G(S)$ . Hence,  $a_1 a_2 - a_3 < 0$  is equivalent to  $A_4(S^*(S^0)) < 0$ , that is to say  $S_1^H < S^*(S^0) < S_2^H$ , which is equivalent to  $\lambda_1^H < S^0 < \lambda_2^H$ .  $\square$

An illustrative example of how the numbers  $S_1^H$  and  $S_2^H$  are determined is given in Section 5.1.3, see Fig. 5.

We consider now the case  $\lambda_s = \lambda_i$ . Let  $b_4 = b_1 b_2 - b_3$ , where the coefficients  $b_1$ ,  $b_2$  and  $b_3$  are defined by (26). Note that  $b_4$  is a polynomial of degree 3 in  $x_i^*$ :

$$b_4 = aX^3 + bX^2 + cX + d \quad (30)$$

with  $X = x_i^*$  and

$$\begin{aligned} a &= \frac{\delta^2}{\eta_i} f'_i + \frac{\delta}{\eta_i^2} f_i'^2, & b &= \delta^2 D + \frac{\delta \gamma}{\eta_s} f'_s + \frac{2\delta D}{\eta_i} f'_i + \frac{1}{\eta_i^2} f_i f_i'^2 + \frac{2\gamma}{\eta_s \eta_i} f'_s f'_i, \\ c &= \delta D^2 + \frac{\gamma}{\eta_s} f_s f'_s + \frac{D}{\eta_i} f_i f'_i + \frac{2\gamma D}{\eta_s} f'_s + \frac{\gamma}{\delta \eta_s \eta_i} (f_s + f_i) f'_i f'_s + \frac{\gamma^2}{\delta \eta_s^2} f_s'^2 - \frac{\gamma}{\eta_i} f_i f'_s, \\ d &= \frac{D\gamma}{\delta \eta_s} f_s f'_s + \frac{\gamma^2}{\delta^2 \eta_s^2} f_s f_s'^2. \end{aligned}$$

The coefficients of  $b_4$  depend only on the parameter  $D$ , and not on  $S^0$ . This operating parameter appears in  $x_i^*$ , see (13). We need to consider the positive roots of  $b_4$ . Since  $a > 0$  and  $d > 0$ , the polynomial  $b_4$  has at least one negative real root. Therefore, the polynomial  $b_4$  can have a positive double root or two distinct positive real roots, or no positive real root. We have the following result

**Proposition 14.** *If  $b_4$  has no positive real root then  $E_2$  is stable whenever it exists, i.e. if and only if  $S^0 > \lambda_c$ . If  $b_4$  has two positive distinct real roots  $X_1^H < X_2^H$  (depending on  $D$ ), then  $E_2$  is unstable whenever  $\lambda_1^H < S^0 < \lambda_2^H$  and is stable if  $\lambda_c < S^0 < \lambda_1^H$  or  $S^0 > \lambda_2^H$ , where  $\lambda_k^H$ ,  $k = 1, 2$  are defined by*

$$\lambda_k^H = \lambda_c + \frac{D_i}{D\eta_i} X_k^H, \quad k = 1, 2. \quad (31)$$

*The numbers  $\lambda_1^H$  and  $\lambda_2^H$  correspond to Hopf bifurcations of the equilibrium  $E_2$ .*

*Proof.* If  $b_4$  has no positive root then  $b_4 > 0$  for any  $S^0 > \lambda_c$ . If  $b_4$  has two positive real roots  $X_1^H < X_2^H$  then it is negative if  $X_1^H < x_i^* < X_2^H$  and positive if  $x_i^* < X_1^H$  or  $x_i^* > X_2^H$ . Therefore using the definition (13) of  $x_i^*$ , we deduce that  $b_4$  is negative if  $\lambda_1^H < S^0 < \lambda_2^H$  and positive if  $\lambda_c < S^0 < \lambda_1^H$  or  $S^0 > \lambda_2^H$ , where  $\lambda_1^H$  and  $\lambda_2^H$  are defined by (31).  $\square$

An illustrative example of how the numbers  $X_1^H$  and  $X_2^H$  are determined is given in Section 5.1.1, see Fig. 3(a).

### 3.5 Summary of the conditions of existence and local stability

The results of Proposition 2 (existence of  $E_0$  and  $E_1$ ), Theorem 9 (existence of  $E_2$ ), Proposition 10 (stability of  $E_0$  and  $E_1$ ) and Proposition 11 (stability of  $E_2$ ) can be summarized in the following proposition.

Table 1: Existence and local asymptotic stability of equilibria of system (3) in the case where  $\lambda_s < \lambda_i$ . Here,  $\lambda_s$  is defined by (5),  $\lambda_c$  is defined by (3),  $S^*$  is a solution of equation (11) and  $a_1$ ,  $a_2$  and  $a_3$  are defined by (25). The multiplicity of endemic equilibria  $E_2$  can occur.

Equilibrium	Existence	Stability
$E_0$	Always exists	$S^0 < \lambda_s$
$E_1$	$S^0 > \lambda_s$	$S^0 < \lambda_c$
$E_2$	See Theorem 9	$F'(S^*) > -D$ and $a_1 a_2 - a_3 > 0$

Table 2: Existence and local asymptotic stability of equilibria of system (3) in the case where  $\lambda_s < \lambda_i$  and equation (14) has no solution in  $I$ . The numbers  $\lambda_s$ ,  $\lambda_c$ ,  $a_1$ ,  $a_2$  and  $a_3$  are defined as in Table 1. The equilibrium  $E_2$  is unique if it exists.

Equilibrium	Existence	Stability
$E_0$	Always exists	$S^0 < \lambda_s$
$E_1$	$S^0 > \lambda_s$	$S^0 < \lambda_c$
$E_2$	$S^0 > \lambda_c$	$a_1 a_2 - a_3 > 0$

Table 3: Existence and local asymptotic stability of equilibria of system (3) in the case where  $\lambda_s = \lambda_i$ . Here,  $\lambda_s$  is defined by (5),  $\lambda_c$  is defined by (3) and  $b_1$ ,  $b_2$  and  $b_3$  are defined by (26). The equilibrium  $E_2$  is unique if it exists.

Equilibrium	Existence	Stability
$E_0$	Always exists	$S^0 < \lambda_s$
$E_1$	$S^0 > \lambda_s$	$S^0 < \lambda_c$
$E_2$	$S^0 > \lambda_c$	$b_1 b_2 - b_3 > 0$

**Proposition 15.** *Assume that  $\lambda_s < \lambda_i$ . The necessary and sufficient conditions of existence and local stability of the equilibria  $E_0$ ,  $E_1$  and  $E_2$  of (3) are summarized in Table 1. In the case where  $F'(S) > -D$  for any  $S \in (\lambda_s, \lambda_i)$ , the conditions of existence and stability in Table 1 simplify as shown in Table 2.*

*Assume that  $\lambda_s = \lambda_i$ . The necessary and sufficient conditions of existence and local stability of the equilibria  $E_0$ ,  $E_1$  and  $E_2$  of (3) are summarized in Table 3.*

## 4 Applications

### 4.1 Linear growth functions

In this section we illustrate our results on (1) with linear growth functions

$$f_s(S) = \alpha_s S, \quad f_i(S) = \alpha_i S. \quad (32)$$

#### 4.1.1 Existence and stability of equilibria

For the growth functions (32), the break-even concentrations  $\lambda_s$ ,  $\lambda_i$  defined by (5) are given by

$$\lambda_s = \frac{D_s}{\alpha_s}, \quad \lambda_i = \frac{D_i}{\alpha_i}. \quad (33)$$

The threshold  $\lambda_c$  and the basic reproduction number  $\mathcal{R}_0$ , defined by (3) and (24) respectively, are given by

$$\lambda_c = \frac{D_s}{\alpha_s} + \frac{D_s}{\delta D \eta_s} \left( D_i - \alpha_i \frac{D_s}{\alpha_s} + \gamma \right), \quad \mathcal{R}_0 = \frac{\alpha_i \frac{D_s}{\alpha_s} + \delta \frac{D}{D_s} \eta_s (S^0 - \frac{D_s}{\alpha_s})}{D_i + \gamma}. \quad (34)$$

These formulas for  $\lambda_c$  and  $\mathcal{R}_0$  were given in [23, Eqs. (3.6) and (3.5)].

The condition  $f_s(S) \geq f_i(S)$  in Hypothesis 2 is equivalent to  $\alpha_s \geq \alpha_i$ . Therefore,  $f'_s(S) \geq f'_i(S)$ . Hence, Lemmas 6 and 12 can be applied. More precisely we have the following results which give sufficient conditions for the uniqueness of the positive equilibrium and for its stability. We start with the simplest case, (7).

**Proposition 16.** *Assume that  $\alpha_s \geq \alpha_i$  and  $\lambda_s = \lambda_i$ , then  $E_2$  is unique and exists if and only if  $S^0 > \lambda_c := \frac{D_s}{\alpha_s} + \frac{D_s \gamma}{\delta D \eta_s}$ . If  $\alpha_s + \alpha_i \geq \delta(\eta_s - \eta_i)$ , then it is stable if it exists. If  $\alpha_s + \alpha_i < \delta(\eta_s - \eta_i)$ ,  $E_2$  can be unstable. If  $E_2$  loses stability, it can only do so through a Hopf bifurcation.*

*Proof.* The necessary and sufficient condition of existence of  $E_2$  follows from Proposition 2. For stability, note that for linear growth functions the sufficient conditions of stability (27) become

$$\alpha_s \geq \alpha_i \quad \text{and} \quad (\alpha_s + \alpha_i) \geq \delta(\eta_s - \eta_i). \quad (35)$$

Hence, the result follows from Lemma 12. If  $E_2$  is unstable then  $b_1 b_2 - b_3 < 0$  and it is the only Routh-Hurwitz coefficient that changes sign. The stability of  $E_2$  can therefore only be lost by a Hopf bifurcation.  $\square$

We now consider the more complex case (6) where multiple endemic equilibria can occur.

**Proposition 17.** *Assume that  $\alpha_s \geq \alpha_i$  and  $\lambda_s < \lambda_i$ , then:*

1. *If  $\eta_s = \eta_i$ , then  $E_2$  is unique and stable, if it exists.*

2. If  $\eta_s > \eta_i$ , then  $E_2$  is unique, if it exists. If, in addition,  $\alpha_s + \alpha_i \geq \delta(\eta_s - \eta_i)$ , then  $E_2$  is stable. If  $\alpha_s + \alpha_i < \delta(\eta_s - \eta_i)$ , then  $E_2$  can be unstable. If  $E_2$  loses stability, it can only do so through a Hopf bifurcation.
3. If  $\eta_s < \eta_i$ , then the multiplicity of positive equilibria (and hence of saddle node bifurcation) is possible. However, no Hopf bifurcation is possible in this case.
4. If  $\alpha_s + \alpha_i \geq \delta(\eta_s - \eta_i)$ , then a positive equilibrium is stable if and only if  $G'(S^*) > 0$ .

*Proof.* The uniqueness of  $E_2$  in the first item follows from Lemma 6. Its stability can be deduced from Lemma 12 and the fact that (27) can be written as (35). Indeed, if  $\eta_s = \eta_i$ , the condition  $\alpha_s + \alpha_i \geq \delta(\eta_s - \eta_i)$  is satisfied. The uniqueness of  $E_2$  in the second item follows from Lemma 6. It is stable if  $\alpha_s + \alpha_i \geq \delta(\eta_s - \eta_i)$ . If  $E_2$  is unstable then  $a_1 a_2 - a_3 < 0$  and it is the only Routh-Hurwitz coefficient that changes sign. The stability of  $E_2$  can therefore only be lost by a Hopf bifurcation. To prove the third item, it suffices to note that if  $\eta_s < \eta_i$ , then condition  $\alpha_s + \alpha_i \geq \delta(\eta_s - \eta_i)$  is satisfied. From Lemma 12 we deduce that  $a_1 a_2 - a_3 > 0$ , so that no Hopf bifurcation is possible. Again using the fact that (27) is written as (35), the result of the fourth item can be deduced from Lemma 12.  $\square$

If  $\eta_s < \eta_i$ , an example showing the multiplicity of positive equilibria is given in Figs. 7, 8 and 9. If  $\alpha_s + \alpha_i < \delta(\eta_s - \eta_i)$ , examples showing the destabilization of  $E_2$  are given in Fig. 3, in the case  $\lambda_s = \lambda_i$  and in Fig. 6, in the case  $\lambda_s < \lambda_i$ .

If  $f_s$  and  $f_i$  are linear functions, then the equation  $f(S) = 0$ , defined in (17), is a cubic equation. Therefore there exist at most three positive equilibria, and Proposition 4 and Theorem 9 can be given more precisely, replacing *odd number* by *one or three* and *even number* by *two*. More precisely, using Proposition 17, we have the following result.

**Theorem 18.** *Assume that  $\lambda_s < \lambda_i$ .*

1. *Assume that  $\mathcal{R}_o > 1$  or equivalently  $S^0 > \lambda_c$ .*
  - (i) *If  $\eta_s = \eta_i$ , then  $E_2$  exists, is unique and is stable.*
  - (ii) *If  $\eta_s > \eta_i$ , then  $E_2$  exists and is unique. It is stable if  $\alpha_s + \alpha_i \geq \delta(\eta_s - \eta_i)$ . If it loses its stability, it can only do so through a Hopf bifurcation.*
  - (iii) *If  $\eta_s < \eta_i$ , then at least one and at most three positive equilibria exist. Saddle node bifurcations of positive equilibria are possible but Hopf bifurcation is not.*
2. *Assume that  $\mathcal{R}_o < 1$  or equivalently  $S^0 < \lambda_c$ .*
  - (i) *If  $\eta_s \geq \eta_i$ , then no positive equilibrium exists.*
  - (ii) *If  $\eta_s < \eta_i$ , then there is either no positive equilibrium point or generically two positive equilibria. Saddle node bifurcation of positive equilibria are possible, but Hopf bifurcation is not.*

*Proof.* The result of item (1i) follows from Theorem 9 and item (1) of Proposition 17. The result of item (1ii) follows from Theorem 9 and item (2) of Proposition 17. The result of item (1iii) follows from Theorem 9 and item (3) of Proposition 17. The result of item (2i) follows from Theorem 9. The result of item (2ii) follows from Theorem 9 and item (3) of Proposition 17.  $\square$

#### 4.1.2 Comparison with previous results in the literature

We recover in Theorem 18 all results given in [23, Theorem 3.4], except for the sufficient conditions of uniqueness of the positive equilibrium [23, (3.7) and (3.8)]. However, in the next section, we give a necessary and sufficient condition for the uniqueness of the positive equilibrium. Before stating this result, it's worth comparing our proof of Theorem 18 with that of [23]. In their proof, these authors consider the cubic equation  $f(S) = 0$ , which is written

$$f(S) := c_0 + c_1 S + c_2 S^2 + c_3 S^3 = 0, \quad (36)$$

where

$$\begin{aligned} c_0 &= DD_i \delta \eta_s \eta_i S^0, \\ c_1 &= -D \delta \eta_s \eta_i S^0 \alpha_i - DD_i \delta \eta_s \eta_i - \alpha_s \eta_i \gamma D_i - \alpha_s \eta_i D_i^2 + \alpha_i \eta_s D_s \gamma + \alpha_i \eta_s D_s D_i, \\ c_2 &= \alpha_i (D \delta \eta_s \eta_i + \alpha_s (\eta_i - \eta_s) \gamma + \alpha_s (\eta_i - \eta_s) D_i + \alpha_s \eta_i D_i - \alpha_i \eta_s D_s), \\ c_3 &= \alpha_s \alpha_i^2 (\eta_s - \eta_i). \end{aligned}$$

Note that  $f(0) = D \delta \eta_s \eta_i D_i S^0 > 0$  and our formulas (18) become

$$\begin{aligned} f(\lambda_s) &= D \eta_s \eta_s \delta (D_i - \alpha_i \lambda_s) (S^0 - \lambda_c), \\ f(\lambda_i) &= D_i \eta_s \gamma (D_s - \alpha_s \lambda_i) < 0. \end{aligned} \quad (37)$$

The cubic equation (36) is the same as [23, Eq. (B.1)] and the formulas (37) are the same as [23, Eqs. (B.3, B.4)]. As mentioned in Remark 4, the results on the existence and number of equilibria can be obtained by solving equation (37) directly. This is the method used in [23]. These authors proceed by considering the cases  $\eta_s = \eta_i$ ,  $\eta_s > \eta_i$  and  $\eta_s < \eta_i$  separately. We give the details of their argument in the  $\eta_s = \eta_i$  case and refer the reader to [23, Page 1068] for the  $\eta_s < \eta_i$  and  $\eta_s > \eta_i$  cases. Assume that  $\eta_s = \eta_i$ . Then  $c_3 = 0$  and since  $\alpha_s \geq \alpha_i$  and  $D_i \geq D_s$ , we have  $c_2 > 0$  in (36). Therefore  $f(S)$  is quadratic,  $f(0) > 0$ ,  $f(\lambda_i) < 0$  and the coefficient of  $S^2$  is positive. Therefore both roots are real and positive, and one root lies to the right of  $\lambda_i$ . If  $f(\lambda_s) > 0$  or equivalently  $S^0 > \lambda_c$ , there is a unique positive root  $S^* \in (\lambda_s, \lambda_i)$  and hence the equilibrium  $E_2$  exists and is unique. If  $S^0 < \lambda_c$ , no positive equilibrium exists. This proves the existence condition in item (1i) of Theorem 18. For the stability condition, they proceeded as we did, of course, by calculating the Jacobian matrices. They also obtained the sufficient condition (35) to have  $a_1 a_2 - a_3 > 0$ , see [23, Eq. (B.6)]. However, in our approach, this condition is obtained as a special case of the more general condition (27).

#### 4.1.3 A necessary and sufficient condition for the uniqueness of the positive equilibrium

Lemma 8 gives a necessary and sufficient condition so that, if it exists, the endemic equilibrium is unique. In the case of linear growth functions, the function  $g(S)$ , given by (21), is a cubic polynomial function whose sign on  $I$  can be determined. Indeed, its derivative  $g'(S)$  is a quadratic function and, since  $f_i'' = 0$ , from (22) we have  $g'(\lambda_i) = 0$ . Consequently, the derivative cancels out only for a second value,  $\bar{S}$ . A direct calculation shows that

$$g'(S) = 2\alpha_i^2 (\lambda_i - S) (3\alpha_s \alpha_i (\eta_i - \eta_s) S - B),$$

where  $B = \alpha_s (\eta_i - \eta_s) (D_i + \gamma) + \alpha_s \eta_i D_i - \alpha_i \eta_s D_s + D \delta \eta_s \eta_i$ . Therefore,

$$\bar{S} = \frac{\alpha_s (\eta_i - \eta_s) (D_i + \gamma) + \alpha_s \eta_i D_i - \alpha_i \eta_s D_s + D \delta \eta_s \eta_i}{3\alpha_s \alpha_i (\eta_i - \eta_s)}. \quad (38)$$

We have the following result.



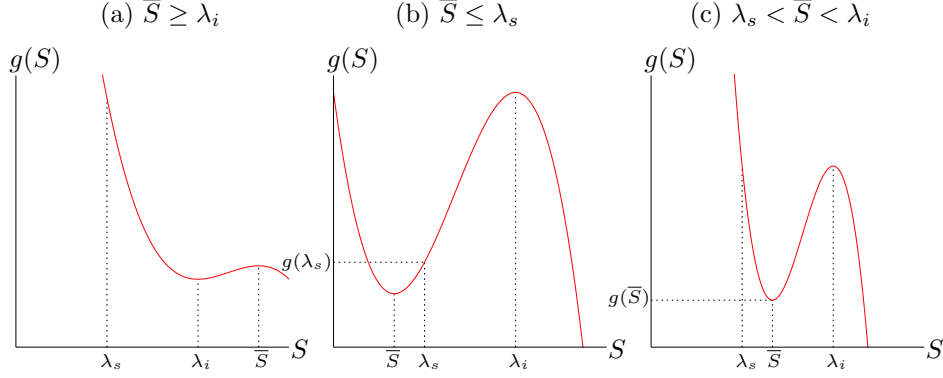


Figure 2: Case of uniqueness of the endemic equilibrium when the growth functions are linear.

**Proposition 19.** *Assume that the growth functions are linear,  $f_s(S) = \alpha_s S$  and  $f_i(S) = \alpha_i S$ , with  $\alpha_s \geq \alpha_i$ . Let  $\bar{S}$  be defined by (38). The endemic equilibrium  $E_2$  is unique, if and only if  $\eta_s \geq \eta_i$  or  $\eta_s < \eta_i$  and one of the following conditions holds*

1.  $\bar{S} \geq \lambda_i$ ,
2.  $\bar{S} \leq \lambda_s$  and  $g(\lambda_s) \geq 0$ ,
3.  $\bar{S} \in I$  and  $g(\bar{S}) \geq 0$ .

*Proof.* Using items (1) and (2) of Proposition 17, if  $\eta_s \geq \eta_i$  then, if it exists, the endemic equilibrium  $E_2$  is unique. Assume that  $\eta_s < \eta_i$ . Since  $g'(S)$  is quadratic and the coefficient of  $S^2$  is negative,  $g'(S)$  is positive for  $S$  between the  $\lambda_i$  and  $\bar{S}$  roots and negative outside them. Therefore,  $g(S)$  is increasing for  $S$  between  $\lambda_i$  and  $\bar{S}$  and decreasing outside them. Therefore  $g(S)$  does not cancel in  $I$  if and only if  $\bar{S} \geq \lambda_i$ , see Fig. 2(a),  $\bar{S} \leq \lambda_s$  and  $g(\lambda_s) \geq 0$ , see Fig. 2(b), or  $\bar{S} \in I$  and  $g(\bar{S}) \geq 0$ , see Fig. 2(c).  $\square$

Note that using (4),  $\lambda_s$ ,  $\lambda_i$  and  $\bar{S}$  are linear in  $D$ . Therefore,  $g(\lambda_s)$  and  $g(\bar{S})$  are cubic in  $D$ . It is therefore possible to determine  $D$ , as a function of the biological parameters, such that the conditions of Proposition 19 are satisfied. We won't attempt to do this in the general case, as the conditions obtained are rather cumbersome to write and have no biological interpretation. However, when the biological parameters are fixed, it is very easy to determine whether the conditions of Proposition 19 are satisfied or not, see Appendix B.1.

## 4.2 Monod growth functions

In this section we show how our results can be applied to Monod growth functions:

$$f_s(S) = \frac{m_s S}{K_s + S}, \quad f_i(S) = \frac{m_i S}{K_i + S}. \quad (39)$$

If condition  $f_s(S) \geq f_i(S)$  in Hypothesis 2 is satisfied we do not necessarily have  $f'_s(S) \geq f'_i(S)$  as for linear growth functions. Therefore Lemma 6 cannot be applied and the multiplicity of positive equilibria can occur. We have the following result.

**Lemma 20.** *Assume that  $f_s$  and  $f_i$  are given by (39). The condition  $f_s(S) \geq f_i(S)$  in Hypothesis 2 is equivalent to  $m_s \geq m_i$  and  $m_s K_s \geq m_i K_i$ . Moreover, the condition  $f'_s(S) \geq f'_i(S)$  in Lemmas*

6 or 12 is satisfied if and only if, in addition,  $m_s K_i \geq m_i K_s$ . The second condition in (27) is equivalent to

$$\frac{m_s}{K_s+S} + \frac{m_i}{K_i+S} \geq \delta \left( \eta_s - \eta_i + S \left( \frac{\eta_s}{K_i} - \frac{\eta_i}{K_s} \right) \right). \quad (40)$$

*Proof.* We have

$$f_s(S) - f_i(S) = \frac{(m_s - m_i)S + m_s K_i - m_i K_s}{(K_s + S)(K_i + S)} S.$$

Therefore, for all  $S \geq 0$ ,  $f_s(S) \geq f_i(S)$  if and only if  $m_s \geq m_i$  and  $m_s K_i \geq m_i K_s$ . On the other hand, we have

$$f'_s(S) - f'_i(S) = \frac{(m_s K_s - m_i K_i)S^2 + 2K_s K_i (m_s - m_i)S + K_s K_i (m_s K_i - m_i K_s)}{(K_s + S)^2 (K_i + S)^2}.$$

Therefore, for all  $S \geq 0$ ,  $f'_s(S) \geq f'_i(S)$  if and only if  $m_s K_s \geq m_i K_i$ ,  $m_s \geq m_i$  and  $m_s K_i \geq m_i K_s$ . The condition  $f'_s f'_i (f_s + f_i) \geq \delta(\eta_s f_i f'_s - \eta_i f_s f'_i)$  in (27) becomes

$$\frac{m_s K_s m_i K_i}{(K_s + S)^2 (K_i + S)^2} \left( \frac{m_s S}{K_s + S} + \frac{m_i S}{K_i + S} \right) \geq \frac{\delta m_s K_s m_i K_i S}{(K_s + S)^2 (K_i + S)^2} \left( \eta_s \frac{K_i + S}{K_i} - \eta_i \frac{K_s + S}{K_s} \right)$$

which is the same as (40).  $\square$

Note that in the limit  $m_s = \alpha_s K_s$ ,  $m_i = \alpha_i K_i$  and  $K_s = K_i = \infty$ , the Monod growth functions (39) tend to the linear growth functions (32) and the condition (40) reduces to the condition  $\alpha_s + \alpha_i \geq \delta(\eta_s - \eta_i)$  obtained in (35). Section 5.2 shows an example where  $\eta_s > \eta_i$ , and yet the system does not admit the uniqueness of the endemic equilibrium. Consequently, the case of Monod functions is more complicated than the case of linear functions, and presents more situations than those encountered in Theorem 18. This case will be the subject of a forthcoming work.

## 5 Bifurcation diagrams

### 5.1 Linear growth functions

In this section we consider the model (2), where  $D_s$  and  $D_i$  are given by (4). We fix the biological parameters, i.e. the specific death rates  $\epsilon_s$  and  $\epsilon_i$  of the species, the rates of infection  $\delta$  and the rate of elimination of viruses  $\gamma$ , the growth yield coefficients  $\eta_s$  and  $\eta_i$  and the growth rates  $\alpha_s$  and  $\alpha_i$  of the species. We also fix the dilution rate  $D$  and we study the behavior of the model with respect to the input concentration of the nutrient  $S^0$ .

**Remark 5.** *With the exception of Figs. 10 and 11 (made with Monod growth functions), all the figures illustrating our results were made with linear growth functions  $f_s(S) = \alpha_s S$  and  $f_i(S) = \alpha_i S$ . The biological parameter values are depicted in Table 4. These values have no biological meaning. We chose them only to illustrate our findings and compare them with the results of [23]. In all figures an equilibrium or a cycle is drawn in red when it is stable and in blue when it is unstable.*

#### 5.1.1 A case where $\lambda_s = \lambda_i$ and $E_2$ is unique and can be unstable

We consider (2) with the biological parameter values depicted in row 1 of Table 4. For these biological parameter values the sufficient condition of stability  $\alpha_s + \alpha_i \geq \delta(\eta_s - \eta_i)$  in Proposition 16 is not satisfied. Therefore,  $E_2$  can be unstable. Let us illustrate this for  $D = 0.5$ . The plot of the third degree polynomial  $b_4$ , defined by (30), is depicted in Fig. 3(a). This polynomial is negative for  $X_1^H < X < X_2^H$  and positive for  $0 < X < X_1^H$  or  $X > X_2^H$ .

Table 4: Biological parameter values for the system (2), where  $D_s$  and  $D_i$  are given by (4).

Figures	$\epsilon_s$	$\epsilon_i$	$\eta_s$	$\eta_i$	$\alpha_s$	$\alpha_i$	$\delta$	$\gamma$	Figures of [23]
Fig. 3	0.2	0.2	10	0.01	3.0	3.0	2	5.5	
Fig. 4	2	12	10	5	7	5	0.7	0.2	Figs. 1, 3
Figs. 5, 6	2	192	55	0.5	7	6.5	2	0.01	Fig. 4
Figs. 7, 8, 9	0.01	0.81	0.01	1	0.5	0.4	1	0.02	Fig. 5

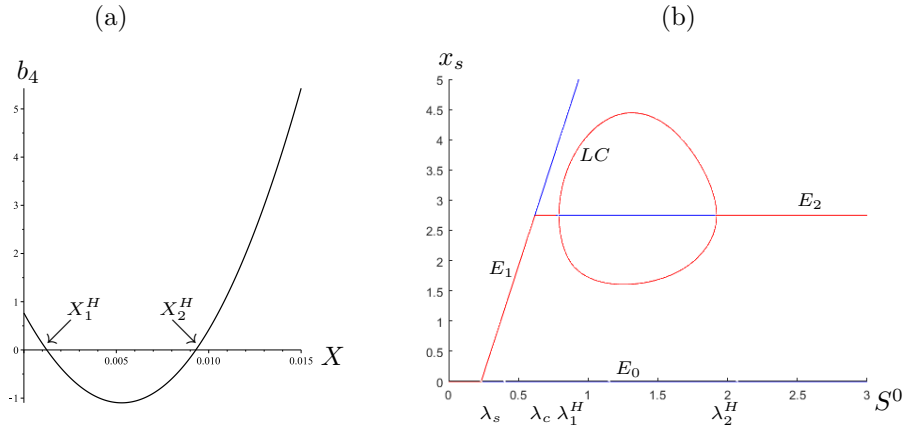


Figure 3: The biological parameter values are given Table 4 and  $D = 0.5$ . (a) The plot of the polynomial  $b_4$  for  $X > 0$  showing its positive roots  $X_1^H \approx 0.0012$  and  $X_2^H \approx 0.0093$ . (b) Bifurcation diagram showing the  $x_s$  components of the equilibria or limit cycle of (3) with respect of  $S_0$ . We have  $\lambda_s = 0.7/3$ ,  $\lambda_c = 1.855/3$ ,  $\lambda_1^H \approx 0.791$  and  $\lambda_2^H \approx 1.921$ .

The theoretical results in Table 3 predict that for  $S^0 \in (0, \lambda_s)$ ,  $E_0$  is stable and coalesces with  $E_1$  when  $S^0 = \lambda_s$  and then stability is transferred to  $E_1$ . For  $S^0 \in (\lambda_s, \lambda_c)$ ,  $E_1$  is stable and coalesces with  $E_2$  when  $S^0 = \lambda_c$  and then stability is transferred to  $E_2$ .  $E_2$  is stable for  $\lambda_c < S_0 < \lambda_1^H$  or  $S_0 > \lambda_2^H$  and unstable for  $\lambda_1^H < S_0 < \lambda_2^H$ , where  $\lambda_1^H$  and  $\lambda_2^H$  are given by (31). These theoretical predictions are confirmed by the bifurcation diagram shown in Fig. 3(b) and obtained with the software MATCONT [8]. This diagram shows that a stable limit cycle appears at  $\lambda_1^H$  and disappears at  $\lambda_2^H$ .

### 5.1.2 A case where $\lambda_s < \lambda_i$ and $E_2$ is unique and stable

We consider (2) with the biological parameter values in row 2 of Table 4. Since  $\eta_s > \eta_i$  and  $\alpha_s + \alpha_i > \delta(\eta_s - \eta_i)$  we deduce from item (2) of Proposition 17 (see also [23, Theorem 3.4]) that the positive equilibrium  $E_2$  is stable and unique if it exists. The bifurcation diagram depicted in [23, Fig. 3] corresponds to the behaviour of the system for  $D = 8$ . The graph  $\Gamma$  of the function  $G$ , for  $D = 8$ , is depicted in Fig. 4(a). This figure illustrates why  $E_2$  is unique if it exists. For example, if  $S^0 = 2 < \lambda_c$ , there is no positive equilibrium and if  $S^0 = 10 > \lambda_c$ ,  $E_2$  exists.

The theoretical results in Table 2 predict that  $E_0$  loses its stability by a transcritical bifurcation with  $E_1$  for  $S^0 = \lambda_s$  and  $E_1$  loses its stability by a transcritical bifurcation with  $E_2$  for  $S^0 = \lambda_c$ .

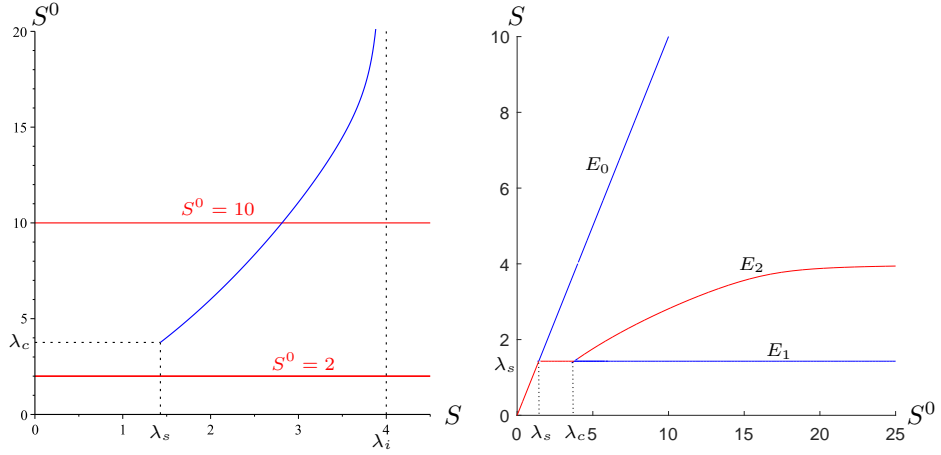


Figure 4: (a) The function  $S^0 = G(S)$  for the biological parameter values given in Table 4 and  $D = 8$ . We have  $\lambda_s \approx 1.43$  and  $\lambda_c \approx 3.76$ . (b) Bifurcation diagram showing the  $S$  component of the equilibria as  $S^0$  varies.

The corresponding bifurcation diagram showing the  $S$  components of the equilibria or limit cycle of (2) with respect of  $S_0$  is depicted in Fig. 4(b). Actually, the results of [23] concern the coexistence of species  $x_s$  and  $x_i$  with a third species  $y$ . Hence, if we compare our Fig. 4 with [23, Fig. 3] we should notice that our equilibria  $E_0$ ,  $E_1$  and  $E_2$  correspond to the equilibria  $E_0$ ,  $E_{1x}$  and  $E_2$  of [23, Fig. 3]. In this figure, we see that there are also equilibria  $E_{1y}$  and  $E_3$  which correspond to the presence of the species  $y$ .

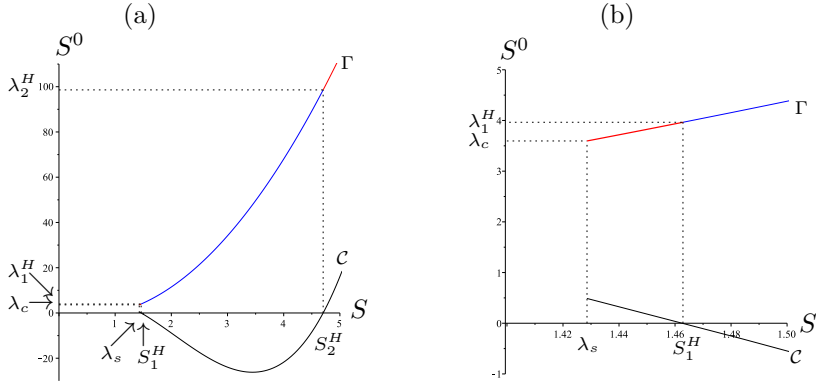


Figure 5: (a) The curve  $\Gamma$  of  $G$  and the curve  $C$  of the function  $A_4(S)$ , defined by (28), for the biological parameter values given in Table 4 and  $D = 8$ . We have  $A_4(S) < 0$  for  $S_1^H < S < S_2^H$ . (b) Magnification showing the values  $\lambda_s$ ,  $S_1^H$ ,  $\lambda_c$  and  $\lambda_1^H$ . We have  $\lambda_s = 10/7$ ,  $S_1^H \approx 1.463$ ,  $S_2^H \approx 4.702$ ,  $\lambda_c \approx 3.59$ ,  $\lambda_1^H \approx 3.96$  and  $\lambda_2^H \approx 98.59$ .

### 5.1.3 A case where $\lambda_s < \lambda_i$ and $E_2$ is unique and can be unstable

We consider (2) with the biological parameter values depicted in row 3 of Table 4. For these biological parameter values the sufficient condition of stability  $\alpha_s + \alpha_i \geq \delta(\eta_s - \eta_i)$  in Proposition 16 is not

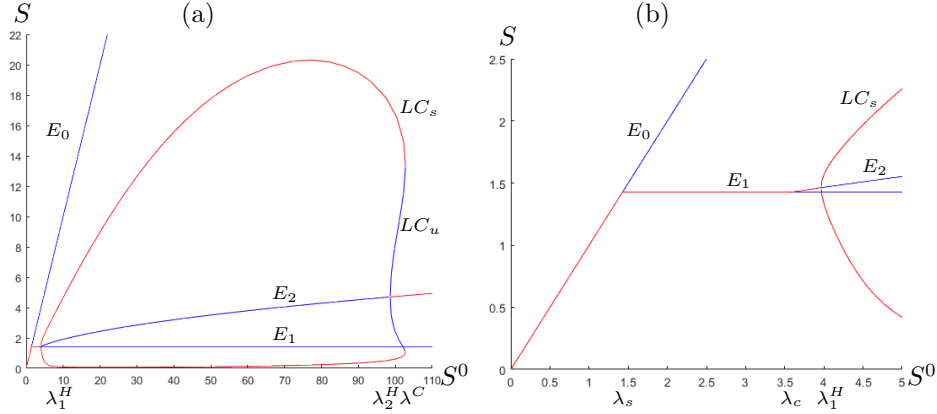


Figure 6: (a) Bifurcation diagram of (2) corresponding to Fig. 5, showing the  $S$  component of equilibria and limit cycles. There is a supercritical Hopf bifurcation of  $E_2$  at  $\lambda_1^H$  giving rise to a stable limit cycle  $LC_s$  and a subcritical Hopf bifurcation of  $E_2$  at  $\lambda_2^H$ , giving rise to an unstable limit cycle  $LC_u$ . In addition, there is a confluence of  $LC_s$  and  $LC_u$  at  $\lambda^C \approx 102.73$ . (b) Magnification showing the values  $\lambda_s$ ,  $\lambda_c$  and  $\lambda_1^H$ .

satisfied. Therefore,  $E_2$  can be unstable. These parameter values were used in [23, Fig. 4], with  $S^0 = 100$ ,  $D = 8$  and  $\eta_s \in (0, 150)$  to illustrate the bifurcation diagram when all parameters are fixed except  $\eta_s$  which is varying. They proved that there is a range of the parameter  $\eta_s$  for which there are two limit cycles, the one with larger amplitude orbitally asymptotically stable and the other one unstable. More precisely, as the parameter  $\eta_s$  is increased from zero, there is a saddle-node bifurcation of limit cycles resulting in two periodic orbits. As  $\eta_s$  is increased further, the unstable periodic orbit disappears in a subcritical Hopf bifurcation at  $E_2$ . Although the demonstration of this type of bifurcation is very interesting from the point of view of the mathematical understanding of the model, it is questionable whether it can be encountered in a real situation, since the bifurcation parameter  $\eta_s$  is a biological parameter. Our aim is to show that these types of bifurcations also occur when the operating parameter  $S^0$  is varying. Therefore, they can be encountered in real life situations.

Let us construct the bifurcation diagram of (3) when  $D = 8$  and  $S^0$  is varying. The curve  $\mathcal{C}$  of the function  $S \mapsto A_4(S)$  depicted in Fig. 5 shows that this function change sign at  $S_1^H$  and  $S_2^H$ . Recall that this function is defined for  $\lambda_s < S < \lambda_i$ . The curve  $\Gamma$  of the function  $S \mapsto G(S)$  is colored in blue if  $S \in (S_1^H, S_2^H)$  and in red if not. This choice of the red and blue color indicates the stability of  $E_2$  (in red) and its instability (in blue). Note that  $A_4(S)$  takes very large values. This is the reason why in Fig. 5, the  $\mathcal{C}$  curve is actually the graph of the function  $A_4/5000$ , not the graph of  $A_4$ .

The theoretical results in Table 3 predict that for  $S^0 \in (0, \lambda_s)$ ,  $E_0$  is stable and coalesces with  $E_1$  when  $S^0 = \lambda_s$  and then stability is transferred to  $E_1$ . For  $S^0 \in (\lambda_s, \lambda_c)$ ,  $E_1$  is stable and coalesces with  $E_2$  when  $S^0 = \lambda_c$  and then stability is transferred to  $E_2$ .  $E_2$  is stable for  $\lambda_c < S_0 < \lambda_1^H$  or  $S_0 > \lambda_2^H$  and unstable for  $\lambda_1^H < S_0 < \lambda_2^H$ , where  $\lambda_1^H$  and  $\lambda_2^H$  are given by (29). The values  $\lambda_1^H$  and  $\lambda_2^H$  correspond to Hopf bifurcations of  $E_2$ , see Appendix B.2 for the numerical evidence of a Hopf bifurcation. These theoretical predictions are confirmed by the bifurcation diagram depicted in Fig. 6 and obtained with the software MATCONT [8]. This diagram shows that, as  $S^0$  is decreased from 110 at  $S^0 = \lambda^C$ , there is a confluence of limit cycles resulting in two periodic orbits, the one with

larger amplitude is orbitally asymptotically stable and the other one unstable. As  $S^0$  is decreased further the unstable periodic orbit disappears in a subcritical Hopf bifurcation of  $E_2$  at  $S^0 = \lambda_2^H$ . Note that the stable limit cycle exists for all  $S^0 \in (\lambda_1^H, \lambda^C)$ . Moreover, as  $S^0$  is decreased further, the stable periodic orbit disappears in a supercritical Hopf bifurcation of  $E_2$  at  $S^0 = \lambda_1^H$ .

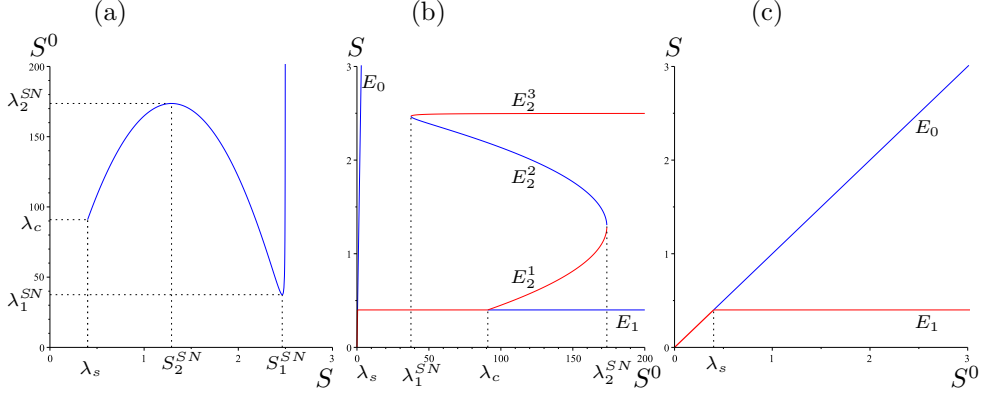


Figure 7: (a) The function  $S^0 = G(S)$  for the biological parameter values Table 4 and  $D = 0.19$ . We have  $\lambda_s = 0.4$ ,  $S_2^{SN} \approx 1.29$ ,  $S_1^{SN} \approx 2.47$ ,  $\lambda_i = 2.5$ ,  $\lambda_c \approx 90.93$ ,  $\lambda_1^{SN} \approx 37.52$ , and  $\lambda_2^{SN} \approx 173.64$ . (b) Bifurcation diagram showing the  $S$  component of the equilibria as  $S^0$  varies. (c) Magnification showing  $\lambda_s$  and the transcritical bifurcation involving  $E_0$  and  $E_1$ .

#### 5.1.4 Multiplicity of positive equilibria

Let us consider the biological parameter values depicted in row 4 of Table 4. These values were used in [23, Fig. 5], with  $S^0 \in [0, 200]$  and  $D = 0.19$ , to illustrate the multiplicity of coexistence equilibria of  $x_s$  and  $x_i$  and show their bifurcation diagram as  $S^0$  varies. Since we have a necessary and sufficient condition for the existence of a positive equilibrium, we can determine the values of  $D$  for which multiplicity can occur. We have the following result.

**Proposition 21.** *For the biological parameter values depicted in row 4 of Table 4 there exists two critical values  $D_1 \approx 0.05993$  and  $D_2 \approx 1.42359$ , such that, if  $D = D_1$  then  $\lambda_1^{SN} = \lambda_c$ , if  $D = D_2$ , then  $\lambda_2^{SN} = \lambda_c$  and we have*

$$\begin{aligned}
0 < D < D_1 &\implies \lambda_c < \lambda_1^{SN} < \lambda_2^{SN}, \\
D_1 < D < D_2 &\implies \lambda_1^{SN} < \lambda_c < \lambda_2^{SN}, \\
D_2 < D &\implies \lambda_1^{SN} < \lambda_c \text{ and } \lambda_2^{SN} \text{ does not exist.}
\end{aligned} \tag{41}$$

*Proof.* The proof is given in Appendix B.1. □

The bifurcation diagram depicted in [23, Fig. 5] corresponds to the behaviour of the system for  $D = 0.19$ . This value satisfies the condition  $D_1 < D < D_2$ . The graph  $\Gamma$  of function  $G$  is shown in Fig. 7(a). We see that multiplicity of positive equilibria occurs when  $\lambda_1^{SN} < S^0 < \lambda_2^{SN}$ . The theoretical results in Table 1 predict that for  $S^0 \in (0, \lambda_s)$ ,  $E_0$  is stable and coalesces with  $E_1$  when  $S^0 = \lambda_s$  and then stability is transferred to  $E_1$ . For  $S^0 \in (\lambda_s, \lambda_c)$ ,  $E_1$  is stable and coalesces with  $E_2^1$  when  $S^0 = \lambda_c$  and then stability is transferred to  $E_2^1$ , see Fig. 7(b,c). Besides these transcritical bifurcations, a saddle node bifurcation of  $E_2^2$  and  $E_2^3$  occurs at  $\lambda_1^{SN}$  and a saddle node bifurcation of  $E_2^1$  and  $E_2^2$  occurs at  $\lambda_2^{SN}$ .  $E_2^1$  is stable for  $\lambda_c < S_0 < \lambda_2^{SN}$ ,  $E_2^3$  is stable for  $S_0 > \lambda_1^{SN}$  and  $E_2^2$  is

unstable for  $\lambda_1^{SN} < S^0 < \lambda_2^{SN}$ , see Fig. 7(b). Proposition 21 shows that the behavior described in Fig. 7 is not specific to the  $D = 0.19$  value. Indeed, for any  $D \in (D_1, D_2)$ , we will have the same behavior since  $\lambda_s < \lambda_1^{SN} < \lambda_c < \lambda_2^{SN}$ . Note that if  $\lambda_1^{SN} < S^0 < \lambda_c$ ,  $E_1$  and  $E_2^3$  are both stable and, if  $\lambda_c < S^0 < \lambda_2^{SN}$ ,  $E_2^1$  and  $E_2^3$  are both stable.

If  $D \in (0, D_1)$  or  $D > D_2$ , the bifurcation diagram when  $S^0$  varies does not have the same behavior, as shown in Figs. 8 and 9, respectively.

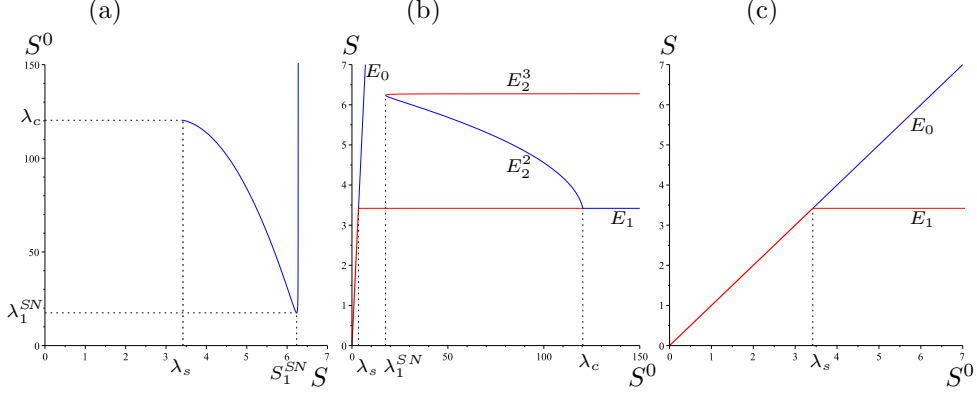


Figure 8: (a) The function  $S^0 = G(S)$  for the biological parameter values in Table 4 and  $D = 1.7$ . We have  $\lambda_s = 3.42$ ,  $S_1^{SN} \approx 6.236$ ,  $\lambda_i = 6.275$ ,  $\lambda_c \approx 120.30$  and  $\lambda_1^{SN} \approx 17.48$ . (b) Bifurcation diagram showing the  $S$  component of the equilibria as  $S^0$  varies. (c) Magnification showing  $\lambda_s$  and the transcritical bifurcation involving  $E_0$  and  $E_1$ .

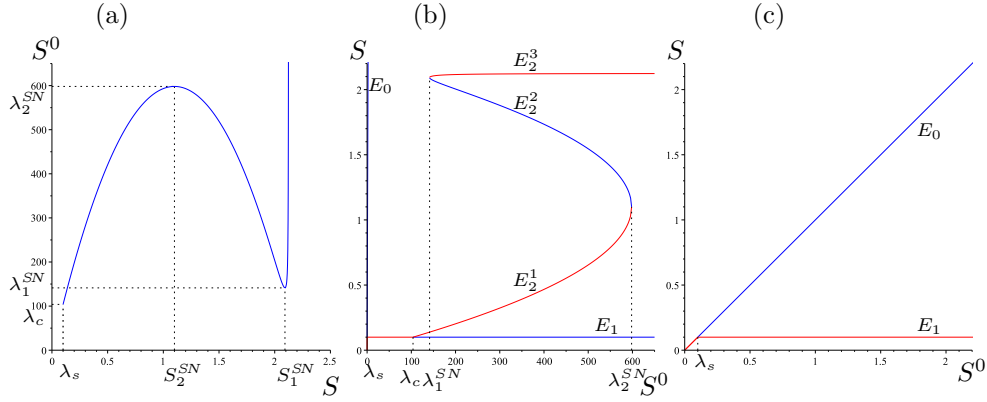


Figure 9: (a) The function  $S^0 = G(S)$  for the biological parameter values in Table 4 and  $D = 0.04$ . We have  $\lambda_s = 0.1$ ,  $S_2^{SN} \approx 1.10$ ,  $S_1^{SN} \approx 2.09$ ,  $\lambda_i = 2.125$ ,  $\lambda_c = 103.85$ ,  $\lambda_1^{SN} \approx 141.32$ , and  $\lambda_2^{SN} \approx 598.12$ . (b) Bifurcation diagram showing the  $S$  component of the equilibria as  $S^0$  varies. (c) Magnification showing  $\lambda_1$  and the transcritical bifurcation involving  $E_0$  and  $E_1$ .

If  $D = 1.7 > D_2$ , the graph  $\Gamma$  of function  $G$  is shown in Fig. 8(a). The theoretical results in Table 1 predict that for  $S^0 \in (0, \lambda_s)$ ,  $E_0$  is stable and coalesces with  $E_1$  when  $S^0 = \lambda_s$  and then stability is transferred to  $E_1$ . For  $S^0 \in (\lambda_s, \lambda_c)$ ,  $E_1$  is stable and coalesces with  $E_2^2$  when  $S^0 = \lambda_c$  and loses its stability when  $S^0 > \lambda_c$ , see Fig. 8(b,c). Besides these transcritical bifurcations, a

saddle node bifurcation of  $E_2^2$  and  $E_2^3$  occurs at  $\lambda_1^{SN}$ .  $E_2^3$  is stable for  $S_0 > \lambda_1^{SN}$  and  $E_2^2$  is unstable for  $\lambda_1^{SN} < S_0 < \lambda_c$ , see Fig. 8(b). Proposition 21 shows that the behavior described in Fig. 8 is not specific to the  $D = 1.7$  value. Indeed, for any  $D > D_2$ , we will have the same behavior since  $\lambda_s < \lambda_1^{SN} < \lambda_c$  and  $\lambda_2^{SN}$  does not exist. Note that if  $\lambda_1^{SN} < S^0 < \lambda_c$ ,  $E_1$  and  $E_2^3$  are both stable.

If  $D = 0.04 \in (D_1, D_2)$ , the graph  $\Gamma$  of function  $G$  is shown in Fig. 9(a). The theoretical results in Table 1 predict that for  $S^0 \in (0, \lambda_s)$ ,  $E_0$  is stable and coalesces with  $E_1$  when  $S^0 = \lambda_s$  and then stability is transferred to  $E_1$ . For  $S^0 \in (\lambda_s, \lambda_c)$ ,  $E_1$  is stable and coalesces with  $E_2^1$  when  $S^0 = \lambda_c$  and then stability is transferred to  $E_2^1$ , see Fig. 9(b,c). Besides these transcritical bifurcations, a saddle node bifurcation of  $E_2^2$  and  $E_2^3$  occurs at  $\lambda_1^{SN}$  and a saddle node bifurcation of  $E_2^1$  and  $E_2^2$  occurs at  $\lambda_2^{SN}$ .  $E_2^1$  is stable for  $\lambda_c < S_0 < \lambda_2^{SN}$ ,  $E_2^3$  is stable for  $S_0 > \lambda_1^{SN}$  and  $E_2^2$  is unstable for  $\lambda_1^{SN} < S_0 < \lambda_2^{SN}$ , see Fig. 9(b). Proposition 21 shows that the behavior described in Fig. 7 is not specific to the  $D = 0.04$  value. Indeed, for any  $D \in (0, D_1)$ , we will have the same behavior since  $\lambda_s < \lambda_c < \lambda_1^{SN} < \lambda_2^{SN}$ . Note that if  $\lambda_1^{SN} < S^0 < \lambda_2^{SN}$ ,  $E_2^1$  and  $E_2^3$  are both stable. The difference with the behavior of the bifurcation diagram of Fig. 7 lies in the absence of the interval  $(\lambda_1^{SN}, \lambda_c)$  in which  $E_1$  and  $E_2^3$  are both stable.

## 5.2 Monod growth functions

Our aim is to illustrate our findings for (1), with Monod growth functions (39). We plot in Fig. 10(a) the graph of the function  $G$  with the parameter values given in the caption of the figure. Note that for these parameter values we have  $\eta_s > \eta_i$  and yet there is a multiplicity of positive equilibria, contrary to what happens for linear growth functions (see item 2 of Proposition 17).

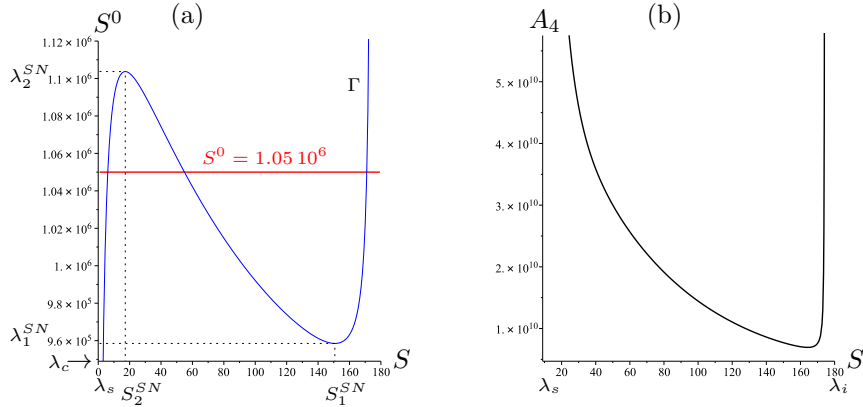


Figure 10: Multiplicity of positive equilibria of (1) with the Monod growth functions (39) and parameter values:  $D = 2$ ,  $\epsilon_s = 291.2$ ,  $\epsilon_i = 310.6$ ,  $m_s = 575$ ,  $m_i = 515$ ,  $\eta_s = 4.560$ ,  $\eta_i = 2.943$ ,  $\delta = 0.016$ ,  $\gamma = 0.313$ ,  $K_s = 0.85$  and  $K_i = 112.9$ . (a) The curve  $\Gamma$  of the function  $G(S)$  showing that equation  $S^0 = G(S)$  has three solutions when  $\lambda_1^{SN} < S^0 < \lambda_2^{SN}$ . We have  $\lambda_s \approx 0.8843$ ,  $\lambda_i = 174.3703$ ,  $S_1^{SN} \approx 150.686$ ,  $S_2^{SN} \approx 17.238$ ,  $\lambda_c \approx 6.207 \times 10^5$ ,  $\lambda_1^{SN} \approx 9.5851 \times 10^5$ ,  $\lambda_2^{SN} \approx 1.1037 \times 10^6$ . (b) The graph of the function  $A_4(S)$  showing that  $A_4(S) > 0$  for  $S \in I$ .

Note that the sufficient condition of stability (40) is satisfied in this case but not the condition  $m_s K_i \geq m_i K_s$ . However, the plot of the graph of the function  $A_4(S)$  defined by (28) shows that this function is always positive, see Fig. 10(b). Therefore the positive equilibria  $E_2^1$  and  $E_2^3$  are stable whenever they exist while  $E_2^2$  is unstable if it exist. The theoretical results in Table 1 predict that for



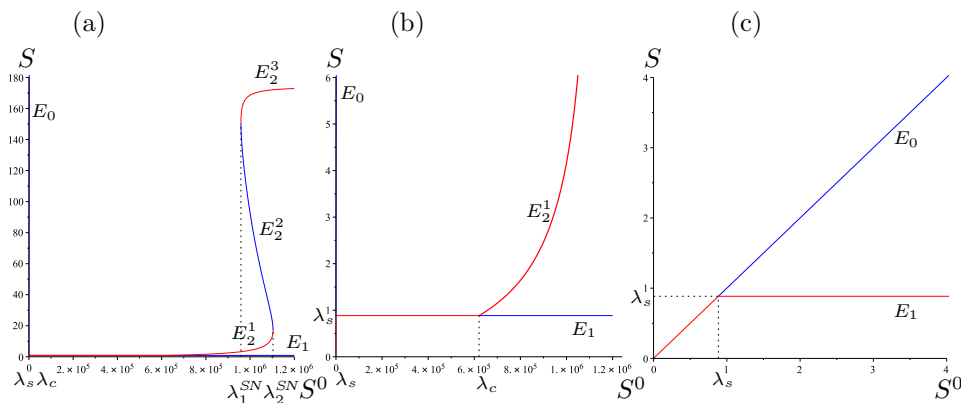


Figure 11: (a) Bifurcation diagram showing the  $S$  component of the equilibria as  $S^0$  varies for the parameter values considered in Fig. 10. (b) Magnification showing the transcritical bifurcation of  $E_1$  and  $E_2^1$  at  $S^0 = \lambda_c$ . (c) Magnification showing  $\lambda_s$  and the transcritical bifurcation involving  $E_0$  and  $E_1$ .

$S^0 \in (0, \lambda_s)$ ,  $E_0$  is stable and coalesces with  $E_1$  when  $S^0 = \lambda_s$  and then stability is transferred to  $E_1$ . For  $S^0 \in (\lambda_s, \lambda_c)$ ,  $E_1$  is stable and coalesces with  $E_2^1$  when  $S^0 = \lambda_c$  and then stability is transferred to  $E_2^1$ , see Fig. 11(b,c). Besides these transcritical bifurcations, a saddle node bifurcation of  $E_2^2$  and  $E_2^3$  occurs at  $\lambda_1^{SN}$  and a saddle node bifurcation of  $E_2^1$  and  $E_2^2$  occurs at  $\lambda_2^{SN}$ .  $E_2^1$  is stable for  $\lambda_c < S^0 < \lambda_2^{SN}$ ,  $E_2^3$  is stable for  $S^0 > \lambda_1^{SN}$  and  $E_2^2$  is unstable for  $\lambda_1^{SN} < S^0 < \lambda_2^{SN}$ , see Fig. 9(b). Note that if  $\lambda_1^{SN} < S^0 < \lambda_2^{SN}$ ,  $E_2^1$  and  $E_2^3$  are both stable.

## 6 Discussion

This article studies the impact of a virus on two competing populations - one susceptible and the other resistant - using an SIS epidemic model in a chemostat-like environment. We extend the SIS model (2) of competition between susceptible and infected bacteria in the chemostat studied in [15, 23, 31]. Our extension involves considering the model (3) with general growth rate functions for competitors. Our mathematical analysis highlights various potential behaviors. Proposition 2 provides a complete theoretical description of the outcomes of this competition. Beyond to the washout equilibrium, where susceptible and infected bacteria disappear, the system may exhibit a DFE equilibrium, where infected bacteria vanish while susceptible bacteria persist, and endemic positive equilibria, where both infected and susceptible bacteria coexist. The conditions of the existence of the DFE and the conditions of existence and uniqueness of the endemic equilibria, and the stability conditions of all equilibria are established in Section 3. As expected the basic reproduction number, as given in (23), plays a crucial role in predicting which populations survive, as discussed in Section 3.3.

Our results apply to the case where the growth functions are linear (see Section 4.1), allowing us to recover the results of [23] (see Section 4.1.2). We also obtain a necessary and sufficient condition for the uniqueness of endemic equilibrium, whereas [23] proposed only sufficient conditions. Our methods contribute significantly in terms of mathematical methodology for addressing a broad class of growth functions. For example, the examination of model (3) with Monod functions is outlined in this article (see Section 4.2). We demonstrate that new behaviors can emerge in this case compared to model (2), where the growth functions are linear. A thorough investigation of the case with

Monod growth functions demands further exploration and will be the focus of a forthcoming article.

The full competition model (1), which incorporates general growth rates, will be the subject of future work. Examining this model with the competitor  $y$  holds ecological significance. In the case of linear growth rates, previous studies, such as in [23], have indicated that while competitive exclusion occurs in the absence of a virus, coexistence of competitors becomes possible in the presence of a virus. These findings suggest that the presence of viruses could enhance bacterial diversity, potentially influencing bacterial species' survival. A critical question remains: do these outcomes hold true for more general growth functions?

To better understand the richness of the model's behavior, a few bifurcation diagrams with respect to input nutrient concentration are examined, see Section 5. We find some of the bifurcation diagrams described in [23]. Since we have a necessary and sufficient condition of uniqueness of the endemic equilibrium, we can show that the bifurcation diagram that was given in [23] to illustrate the multiplicity of equilibria retains the same qualitative behavior when we change the rate  $D$  (see Section 5.1.4). For practical utility, a description of the system in terms of both operating parameters  $D$  and  $S^0$  is essential, giving their significance in the model and ease of experimental manipulation. This diagram, known as the operating diagram is very useful to understand the model from both the mathematical and biological points of view [12]. It is often constructed both in the biological literature [17, 26, 28] and in the mathematical literature [1, 2, 4, 5, 6, 7, 9, 10, 20, 21, 24, 29, 34]. The construction of the operating diagram for the SIS model in the chemostat is the subject of a forthcoming publication.

## A Proofs

### A.1 Proof of Proposition 2

Equilibria of (3) are the solutions of the set of equations

$$0 = D(S^0 - S) - \frac{1}{\eta_s} f_s(S)x_s - \frac{1}{\eta_i} f_i(S)x_i, \quad (42)$$

$$0 = (f_s(S) - D_s)x_s - (\delta x_s - \gamma)x_i, \quad (43)$$

$$0 = (f_i(S) - D_i + \delta x_s - \gamma)x_i. \quad (44)$$

If  $x_s = 0$ , then from (43) we have  $x_i = 0$ , and hence, from (42) we have  $S = S^0$ . One obtains the washout equilibrium  $E_0 = (S^0, 0, 0)$ , which always exists.

Assume now that  $x_s > 0$ . If  $x_i = 0$  then from (43) we have  $f_s(S) = D_s$ , so that  $S = \lambda_s$ , where  $\lambda_s$  is given by (5). Therefore, using (42) we have  $x_s = \frac{D\eta_s}{D_s}(S^0 - \lambda_s)$ , which is the expression of  $\bar{x}_s$  given in (10). One obtains the DFE. This equilibrium exists if and only if  $x_s > 0$ , that is,  $\lambda_s < S^0$ .

Assume now that  $x_s > 0$  and  $x_i > 0$ . Adding (43) and (44) one obtains

$$(f_s(S) - D_s)x_s + (f_i(S) - D_i)x_i = 0.$$

This equation implies that

$$f_s(S) - D_s \quad \text{and} \quad f_i(S) - D_i \quad \text{are of opposite signs,} \quad (45)$$

or

$$f_s(S) - D_s = f_i(S) - D_i = 0. \quad (46)$$

The condition (45) is satisfied in the case (6), and, as stated in Remark 1, we must have  $\lambda_s < S < \lambda_i$ . Using (44), we have

$$f_i(S) - D_i + \delta x_s - \gamma = 0,$$

from which we deduce that  $x_s = \frac{\gamma + D_i - f_i(S)}{\delta} = X_s(S)$ , where  $X_s$  is the function given in (8). Using (43) and the relation  $\delta x_s - \gamma = D_i - f_i(S)$ , which is deduced from the above equation, we have

$$(f_s(S) - D_s)x_s = (\delta x_s - \gamma)x_i = (D_i - f_i(S))x_i.$$

Therefore  $x_i = \frac{f_s(S) - D_s}{D_i - f_i(S)}x_s = X_i(S)$ , where  $X_i$  is the function given in (8). By replacing  $x_s$  and  $x_i$  in (42), we obtain

$$D(S^0 - S) = \frac{1}{\eta_s}f_s(S)X_s(S) + \frac{1}{\eta_i}f_i(S)X_i(S) =: F(S),$$

where  $F$  is the function given in (8). Hence, we proved that  $S$  must be a solution of equation (11), such that  $\lambda_s < S < \lambda_i$ , and  $x_s = X_s(S)$ ,  $x_i = X_i(S)$ , which proves (12).

The condition (46) is satisfied in the case (7) and  $S = \lambda_s = \lambda_i$ . From (43) we have  $x_s = \frac{\gamma}{\delta}$ . By replacing  $S$  and  $x_s$  in (42), we obtain  $x_i = \frac{\eta_i}{D_i} \left( D(S^0 - \lambda_s) - \frac{D_s \gamma}{\eta_s \delta} \right)$ , which proves (13). This equilibrium exists if and only if  $x_i > 0$ , that is to say,  $S^0 > \lambda_c := \lambda_s + \frac{D_s \gamma}{D \delta \eta_s}$ .

## A.2 Proof of Lemma 6

Note that  $\varphi_s > 0$  and  $\varphi_i < 0$  on  $I$ . Therefore  $\varphi_i(\varphi_i - \gamma)$  is positive. Let  $N$  be the numerator of (19). Assuming  $f'_s \geq f'_i$ , we have

$$N = \varphi_i(\varphi_i - \gamma)A_s f'_s + A_i f'_i \geq [\varphi_i(\varphi_i - \gamma)A_s + A_i]f'_i.$$

Using the expression of  $A_i$  we have

$$\varphi_i(\varphi_i - \gamma)A_s + A_i = \varphi_i(\varphi_i - \gamma)A_s + \varphi_s \varphi_i^2 (\eta_s - \eta_i) - \eta_i \varphi_i^2 D_s + \gamma \eta_s \varphi_s D_i.$$

Assume that  $\eta_s \geq \eta_i$ . All the terms are positive except  $-\eta_i \varphi_i^2 D_s$ . From the definition of  $A_s$  we have  $A_s \geq D_i \eta_i$ . Therefore

$$\varphi_i(\varphi_i - \gamma)A_s \geq \varphi_i(\varphi_i - \gamma)\eta_i D_i > \varphi_i^2 \eta_i D_i \geq \varphi_i^2 \eta_i D_s.$$

Hence,  $\varphi_i(\varphi_i - \gamma)A_s + A_i > 0$ , so that  $N > 0$ . Therefore  $F'(S) > 0$  for  $S \in I$ . This proves that equation (14) cannot have a solution.

## A.3 Proof of Proposition 10

Let  $J$  be the Jacobian matrix of (3) at an equilibrium  $(S, x_s, x_i)$ . We have

$$J = \begin{pmatrix} -D - \frac{x_s}{\eta_s} f'_s(S) - \frac{x_i}{\eta_i} f'_i(S) & -\frac{1}{\eta_s} f_s(S) & -\frac{1}{\eta_i} f_i(S) \\ x_s f'_s(S) & f_s(S) - D_s - \delta x_i & -\delta x_s + \gamma \\ x_i f'_i(S) & \delta x_i & f_i(S) - D_i + \delta x_s - \gamma \end{pmatrix}. \quad (47)$$

At  $E_0 = (S^0, 0, 0)$ , the Jacobian matrix (47) becomes

$$J_0 = \begin{pmatrix} -D & -\frac{1}{\eta_s} f_s(S^0) & -\frac{1}{\eta_i} f_i(S^0) \\ 0 & f_s(S^0) - D_s & \gamma \\ 0 & 0 & f_i(S^0) - D_i - \gamma \end{pmatrix}.$$

The eigenvalues of  $J_0$  are given by the diagonal elements. They are all negative when  $f_s(S^0) < D_s$  and  $f_i(S^0) < D_i + \gamma$ , i.e.  $S^0 < \lambda_s$ , where  $\lambda_s = f_s^{-1}(D_s)$  and  $S^0 < \lambda_\gamma$ , where  $\lambda_\gamma = f_i^{-1}(D_i + \gamma)$ . Using Lemma 1 and  $f'_i(S) > 0$ , we have  $\lambda_s \leq \lambda_i < \lambda_\gamma$ . Hence  $E_0$  is stable if and only if  $S^0 < \lambda_s$ .

At  $E_1 = (\lambda_s, \bar{x}_s, 0)$ , the Jacobian matrix (47) becomes

$$J_1 = \begin{pmatrix} -D - \frac{\bar{x}_s}{\eta_s} f'_s(\lambda_s) & -\frac{1}{\eta_s} f_s(\lambda_s) & -\frac{1}{\eta_i} f_i(\lambda_s) \\ \bar{x}_s f'_s(\lambda_s) & 0 & -\delta \bar{x}_s + \gamma \\ 0 & 0 & f_i(\lambda_s) - D_i + \delta \bar{x}_s - \gamma \end{pmatrix}. \quad (48)$$

The characteristic polynomial is given by

$$P(\lambda) = (f_i(\lambda_s) - D_i + \delta \bar{x}_s - \gamma - \lambda) (\lambda^2 + c_1 \lambda + c_2),$$

where  $c_1 = \frac{\bar{x}_s}{\eta_s} f'_s(\lambda_s)$  and  $c_2 = \frac{\bar{x}_s}{\eta_s} f_s(\lambda_s) f'_s(\lambda_s)$ . Since  $c_1 > 0$  and  $c_2 > 0$ , the eigenvalues corresponding to the quadratic term have negative real parts. The eigenvalue from the linear term is

$$\lambda = f_i(\lambda_s) - D_i + \delta \bar{x}_s - \gamma = f_i(\lambda_s) - D_i - \gamma + \frac{\delta D \eta_s}{D_s} (S^0 - \lambda_s).$$

It is negative if and only if  $S^0 < \lambda_s + \frac{D_s}{\delta D \eta_s} (D_i - f_i(\lambda_s) + \gamma)$ . Therefore  $E_1$  is stable if and only if  $S^0 < \lambda_c$ , where  $\lambda_c$  is defined by (15).

#### A.4 Proof of Proposition 11

Let  $E_2 = (S^*, x_s^*, x_i^*)$  be a positive equilibrium of (3). The Jacobian matrix (47) becomes

$$J_2 = \begin{pmatrix} -D - \frac{x_s^*}{\eta_s} f'_s(S^*) - \frac{x_i^*}{\eta_i} f'_i(S^*) & -\frac{1}{\eta_s} f_s(S^*) & -\frac{1}{\eta_i} f_i(S^*) \\ x_s^* f'_s(S^*) & f_s(S^*) - D_s - \delta x_i^* & -\delta x_s^* + \gamma \\ x_i^* f'_i(S^*) & \delta x_i^* & f_i(S^*) - D_i + \delta x_s^* - \gamma \end{pmatrix}.$$

Since  $(S^*, x_s^*, x_i^*)$  satisfies (43), we have  $(f_s(S^*) - D_s - \delta x_i^*) x_s^* = -\gamma x_i^*$ . Thus,

$$f_s(S^*) - D_s - \delta x_i^* = -\gamma \frac{x_i^*}{x_s^*}.$$

Similarly, since  $(S^*, x_s^*, x_i^*)$  satisfies (44), we have

$$f_i(S^*) - D_i + \delta x_s^* - \gamma = 0.$$

Therefore, at  $E_2$ , the Jacobian matrix  $J_2$  can be written

$$J_2 = \begin{pmatrix} -m_{11} & -m_{12} & -m_{13} \\ m_{21} & -m_{22} & m_{23} \\ m_{31} & m_{32} & 0 \end{pmatrix} \quad (49)$$

where  $m_{ij}$  are given by

$$\begin{aligned} m_{11} &= D + \frac{x_s^*}{\eta_s} f'_s(S^*) + \frac{x_i^*}{\eta_i} f'_i(S^*), & m_{12} &= \frac{1}{\eta_s} f_s(S^*), & m_{13} &= \frac{1}{\eta_i} f_i(S^*), \\ m_{21} &= x_s^* f'_s(S^*), & m_{22} &= \gamma \frac{x_i^*}{x_s^*}, & m_{23} &= \gamma - \delta x_s^*, \\ m_{31} &= x_i^* f'_i(S^*), & m_{32} &= \delta x_i^*. \end{aligned} \quad (50)$$

The characteristic polynomial is given by

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

with  $c_1$ ,  $c_2$  and  $c_3$  are defined by

$$\begin{aligned} c_1 &= m_{11} + m_{22}, \\ c_2 &= m_{12}m_{21} + m_{13}m_{31} - m_{32}m_{23} + m_{11}m_{22}, \\ c_3 &= m_{13}(m_{21}m_{32} + m_{31}m_{22}) + m_{23}(m_{31}m_{12} - m_{11}m_{32}), \end{aligned} \quad (51)$$

where  $m_{ij}$  are given by (50). According to the Routh-Hurwitz criteria,  $E_2$  is stable if and only if

$$c_1 > 0, \quad c_3 > 0 \quad \text{and} \quad c_1c_2 - c_3 > 0. \quad (52)$$

From the definition of  $c_1$ , we see that  $c_1 > 0$ . We distinguish now the cases (6) and (7).

In the case (6), i.e.  $\lambda_s < \lambda_i$ ,  $S^*$  is a solution of (11), such that  $S^* \in J$ , and  $x_s^*$ ,  $x_i^*$  are given by (12). Therefore the coefficients  $c_1$ ,  $c_2$  and  $c_3$  given by (51), where the  $m_{ij}$  are defined by (50), are the same as the coefficients  $a_1$ ,  $a_2$  and  $a_3$  given by (25). Now, using the definitions (8) of  $X_s$  and  $X_i$ , we can write

$$\begin{aligned} m_{32}m_{23} &= \delta x_i^*(\gamma - \delta x_s^*) = -\delta \frac{\varphi_s}{\varphi_i} \frac{\gamma - \varphi_i}{\delta} (\gamma - \delta \frac{\gamma - \varphi_i}{\delta}) \Big|_{S=S^*} \\ &= \varphi_s(S^*)(\varphi_i(S^*) - \gamma). \end{aligned}$$

Since  $S^* \in J$ , we have  $\varphi_s(S^*) > 0$  and  $\varphi_i(S^*) < 0$ . Therefore  $m_{23}m_{32} \neq 0$ . Hence, using the Lemma A.1. in [11], we have

$$\det(J_2) = -F'(S^*)m_{23}m_{32} = F'(S^*)\varphi_s(S^*)(\gamma - \varphi_i(S^*)), \quad (53)$$

where,

$$h(S) = D(S^0 - S) - f_s(S) \frac{X_s(S)}{\eta_s} - f_i(S) \frac{X_i(S)}{\eta_i} = D(S^0 - S) - F(S). \quad (54)$$

The development of the determinant of  $J_2$ , given by (49), with respect to its third column, shows that  $c_3 = -\det(J_2)$ . From (54), we have  $F'(S) = -D - F'(S)$ . Therefore, from (53) we deduce that

$$c_3 = -\det(J_2) = \varphi_s(S^*)(\gamma - \varphi_i(S^*))(F'(S^*) + D).$$

Since  $\varphi_s(S^*) > 0$  and  $\varphi_i(S^*) < 0$  we deduce that  $c_3 > 0$  if and only if  $F'(S^*) > -D$ . Replacing  $m_{ij}$  by their expressions (50) shows that for  $i = 1, 2, 3$ ,  $c_i = a_i$ , where  $a_i$  are given by (25). From (52) we obtain that  $E_2$  is stable if and only if  $F'(S^*) > -D$  and  $a_1a_2 - a_3 > 0$ .

In the case (7), i.e.  $\lambda_s = \lambda_i$ ,  $S^* = \lambda_s$  and  $x_s^*$ ,  $x_i^*$  are given by (13). Hence  $m_{23} = 0$ , so that the coefficients  $c_2$  and  $c_3$  given by (51) can be written now

$$\begin{aligned} c_2 &= m_{12}m_{21} + m_{13}m_{31} + m_{11}m_{22}, \\ c_3 &= m_{13}(m_{21}m_{32} + m_{31}m_{22}), \end{aligned}$$

where the  $m_{ij}$  are defined by (50). Note that  $c_3 > 0$ . Using  $m_{22} = \delta x_i^*$ ,  $f_s(S^*) = D_s$  and  $f_i(S^*) = D_i$ , one sees that for  $i = 1, 2, 3$ ,  $c_i = b_i$ , where  $b_i$  are given by (26). From (52) we obtain that  $E_2$  is stable if and only if  $b_1b_2 - b_3 > 0$ .

## A.5 Proof of Lemma 12

Assume that  $\lambda_s < \lambda_i$ . Recall that

$$\begin{aligned} a_1 &= B + \frac{\gamma x_i^*}{x_s^*}, \\ a_2 &= \frac{x_s^*}{\eta_s} f_s f'_s + \frac{x_i^*}{\eta_i} f_i f'_i + \delta x_i^* C + B \frac{\gamma x_i^*}{x_s^*}, \\ a_3 &= \frac{x_i^*}{\eta_i} f_i \left( f'_s \delta x_s^* + f'_i \frac{\gamma x_i^*}{x_s^*} \right) + C \left( B \delta x_i^* - \frac{x_i^*}{\eta_s} f_s f'_i \right), \end{aligned}$$

where  $B = D + \frac{x_s^*}{\eta_s} f'_s + \frac{x_i^*}{\eta_i} f'_i$ ,  $C = \delta x_s^* - \gamma$ , and the functions  $f_s, f'_s, f_i, f'_i$  are evaluated at  $S^*$ . We have

$$a_1 a_2 = \left( B + \frac{\gamma x_i^*}{x_s^*} \right) \left( \frac{x_s^*}{\eta_s} f_s f'_s + B \frac{\gamma x_i^*}{x_s^*} \right) + \frac{B x_i^*}{\eta_i} f_i f'_i + BC \delta x_i^* + \frac{\gamma x_i^{*2}}{\eta_i x_s^*} f_i f'_i + \delta C \frac{\gamma x_i^{*2}}{x_s^*}.$$

The terms  $BC \delta x_i^*$  and  $\frac{\gamma x_i^{*2}}{\eta_i x_s^*} f_i f'_i$  in  $a_1 a_2$  and  $a_3$  are simplified and we obtain

$$a_1 a_2 - a_3 = \left( B + \frac{\gamma x_i^*}{x_s^*} \right) \left( \frac{x_s^*}{\eta_s} f_s f'_s + B \frac{\gamma x_i^*}{x_s^*} \right) + \frac{B x_i^*}{\eta_i} f_i f'_i + \delta C \frac{\gamma x_i^{*2}}{x_s^*} + \frac{C x_i^*}{\eta_s} f_s f'_i - \frac{\delta x_s^* x_i^*}{\eta_i} f_i f'_s.$$

Hence,

$$a_1 a_2 - a_3 > \left( B + \frac{\gamma x_i^*}{x_s^*} \right) \frac{x_s^*}{\eta_s} f_s f'_s + \frac{B x_i^*}{\eta_i} f_i f'_i + \frac{C x_i^*}{\eta_s} f_s f'_i - \frac{\delta x_s^* x_i^*}{\eta_i} f_i f'_s. \quad (55)$$

From the definition of  $B$  we deduce that

$$\left( B + \frac{\gamma x_i^*}{x_s^*} \right) \frac{x_s^*}{\eta_s} f_s f'_s > \frac{x_s^* x_i^*}{\eta_s \eta_i} f_s f'_s f'_i + \frac{\gamma x_i^*}{\eta_s} f_s f'_s, \quad \frac{B x_i^*}{\eta_i} f_i f'_i > \frac{x_s^* x_i^*}{\eta_s \eta_i} f'_s f_i f'_i.$$

Using these inequalities and replacing  $C = \delta x_s^* - \gamma$  in (55) gives

$$\begin{aligned} a_1 a_2 - a_3 &> \frac{x_s^* x_i^*}{\eta_s \eta_i} f'_s f'_i (f_s + f_i) + \frac{\gamma x_i^*}{\eta_s} f_s f'_s + \frac{\delta x_s^* x_i^*}{\eta_s} f_s f'_i - \frac{\gamma x_i^*}{\eta_s} f_s f'_i - \frac{\delta x_s^* x_i^*}{\eta_i} f_i f'_s \\ &= \frac{\gamma x_i^*}{\eta_s} f_s (f'_s - f'_i) + \frac{x_s^* x_i^*}{\eta_s \eta_i} [f'_s f'_i (f_s + f_i) + \delta (\eta_i f_s f'_i - \eta_s f_i f'_s)]. \end{aligned}$$

Therefore  $a_1 a_2 - a_3 > 0$  if the condition (27) is satisfied for  $S = S^*$ .

Assume that  $\lambda_s = \lambda_i$ . Recall that

$$\begin{aligned} b_1 &= B + \delta x_i^*, \\ b_2 &= \frac{x_s^*}{\eta_s} f_s f'_s + \frac{x_i^*}{\eta_i} f_i f'_i + B \delta x_i^*, \\ b_3 &= \frac{x_i^*}{\eta_i} f_i (\gamma f'_s + \delta x_i^* f'_i), \end{aligned}$$

where  $B = D + \frac{x_s^*}{\eta_s} f'_s + \frac{x_i^*}{\eta_i} f'_i$ , and the functions  $f_s, f'_s, f_i, f'_i$  are evaluated at  $\lambda_s$ . We have

$$b_1 b_2 = (B + \delta x_i^*) \left( \frac{x_s^*}{\eta_s} f_s f'_s + B \delta x_i^* \right) + \frac{B x_i^*}{\eta_i} f_i f'_i + \frac{\delta x_i^{*2}}{\eta_i} f_i f'_i.$$

The term  $\frac{\delta x_i^{*2}}{\eta_i} f_i f'_i$  in  $b_1 b_2$  and  $b_3$  is simplified and we obtain

$$b_1 b_2 - b_3 = (B + \delta x_i^*) \left( \frac{x_s^*}{\eta_s} f_s f'_s + B \delta x_i^* \right) + \frac{B x_i^*}{\eta_i} f_i f'_i - \frac{\gamma x_i^*}{\eta_i} f_i f'_s.$$

Hence,

$$b_1 b_2 - b_3 > (B + \delta x_i^*) \frac{x_s^*}{\eta_s} f_s f'_s + \frac{B x_i^*}{\eta_i} f_i f'_i - \frac{\gamma x_i^*}{\eta_i} f_i f'_s. \quad (56)$$

From the definition of  $B$  and using  $\delta x_s^* = \gamma$  we deduce that

$$(B + \delta x_i^*) \frac{x_s^*}{\eta_s} f_s f'_s > \frac{\gamma x_i^*}{\delta \eta_s \eta_i} f_s f'_s f'_i + \frac{\gamma x_i^*}{\eta_s} f_s f'_s, \quad \frac{B x_i^*}{\eta_i} f_i f'_i > \frac{\gamma x_i^*}{\delta \eta_s \eta_i} f'_s f_i f'_i.$$

Using these inequalities and adding and subtracting  $\frac{\gamma x_i^*}{\eta_s} f_s f'_i$  in (56) gives

$$\begin{aligned} b_1 b_2 - b_3 &> \frac{\gamma x_i^*}{\delta \eta_s \eta_i} f'_s f'_i (f_s + f_i) + \frac{\gamma x_i^*}{\eta_s} f_s f'_s + \frac{\gamma x_i^*}{\eta_s} f_s f'_i - \frac{\gamma x_i^*}{\eta_s} f_s f'_i - \frac{\gamma x_i^*}{\eta_i} f_i f'_s \\ &= \frac{\gamma x_i^*}{\eta_s} f_s (f'_s - f'_i) + \frac{\gamma x_i^*}{\delta \eta_s \eta_i} [f'_s f'_i (f_s + f_i) + \delta (\eta_i f_s f'_i - \eta_s f_i f'_s)]. \end{aligned}$$

Therefore  $b_1 b_2 - b_3 > 0$  if the condition (27) is satisfied for  $S = \lambda_s$ .

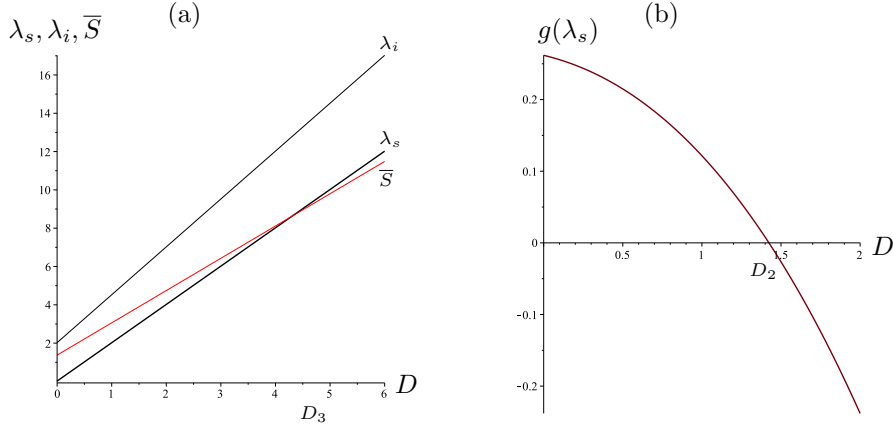


Figure 12: (a) The functions  $D \mapsto \lambda_s$ ,  $D \mapsto \lambda_i$  (in black) and  $D \mapsto \bar{S}$  (in red) for the biological parameters used in Proposition 21. (b) The function  $D \mapsto g(\lambda_s)$ .

## B Numerical experimentation

### B.1 Proof of Proposition 21

For the biological parameter values used in Proposition 21, we have

$$\lambda_s = 2D + 0.02, \quad \lambda_i = 2.5D + 2.025, \quad \bar{S} = 1.6852D + 1.3734,$$

$$g(\lambda_s) = -0.0114D^3 - 0.0755D^2 - 0.0533D + 0.2618,$$

$$g(\bar{S}) = -0.0171D^3 - 0.0411D^2 - 0.0328D - 0.0087.$$

We have  $\lambda_s < \bar{S} < \lambda_i$  for  $0 < D < D_3$  where  $D_3 \approx 4.2991$  and  $\bar{S} < \lambda_s$  for  $D > D_3$ , see Fig. 12(a). Moreover,  $g(\bar{S}) < 0$  and, since there is one change of sign in the sequence of polynomial coefficients, Descartes' rule of signs asserts that the number of positive roots of  $g(\lambda_s)$  is 1. Numerical computation shows that  $g(\lambda_s)$  admits the root  $D_2$ , where  $D_2 \approx 1.4236$ . We have  $g(\lambda_s) > 0$  for  $0 \leq D < D_2$ , while  $g(\lambda_s) < 0$  for  $D > D_2$ , see Fig. 12(b). Therefore, using Proposition 19, for  $0 < D < D_2$ , equation  $g(S) = 0$  admits two solutions  $S_2^{SN} < S_1^{SN}$  in  $I$  and there is only one solution  $S_1^{SN}$  if  $D > D_2$ . In addition, there is a unique value  $D_1$  such that  $\lambda_c < \lambda_1^{SN}$  for  $D < D_1$ , while  $\lambda_1^{SN} < \lambda_c$  for  $D > D_1$ . This proves the properties depicted in (41).

### B.2 Numerical evidence for a Hopf bifurcation

We numerically calculate the eigenvalues of the Jacobian matrix (49) at  $E_2$  and plot them as  $S^0$  varies. Actually, the Jacobian matrix has one real negative eigenvalue and two complexes that are depicted in Fig. 13. The real part of the conjugate pair of eigenvalues is negative as the operating parameter  $S^0 < \lambda_1^H$  or  $S^0 > \lambda_2^H$  and positive when  $\lambda_1^H < S^0 < \lambda_2^H$ . The transversality condition  $\frac{d\alpha}{dS^0}(\lambda_{1,2}^H) \neq 0$  is checked numerically. Therefore according to the Hopf theorem a limit cycle appears at  $S^0 = \lambda_1^H$  and  $S^0 = \lambda_2^H$ .

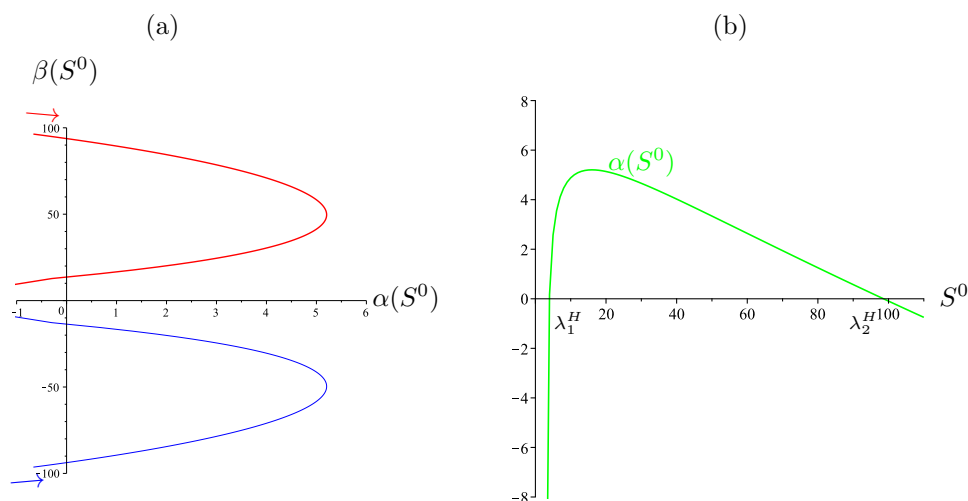


Figure 13: The dilution rate  $D = 8$  is fixed together with all biological parameters, as in Fig. 6. (a) Variation of the conjugate eigenvalues  $\alpha(S^0) \pm i\beta(S^0)$  of the Jacobian matrix of  $E_2$  as a function of  $S^0 \in (2, 110)$ . (b) Numerical evidence for a Hopf bifurcation at  $S^0 = \lambda_1^H$  and  $S^0 = \lambda_2^H$ .

### B.3 Numerical illustrations

The aim of this section is to provide the trajectories over time in various interesting situations to illustrate our findings. We consider the biological parameter values used in Fig. 6,  $D = 8$  and various values of  $S^0$ . If  $\lambda_c < S^0 < \lambda_1^H$  or  $S^0 > \lambda^C$ , all numerical simulations show the global convergence of (3) toward  $E_2$  or toward the limit cycle, as depicted in Fig. 14. However, as predicted by Fig. 6, since the Hopf bifurcation at  $S^0 = \lambda_2^H$  is sub-critical when  $\lambda_2^H < S^0 < \lambda^C$ , the solutions converge to  $E_2$  or to the stable limit cycle, depending on the initial condition, showing the bistability of the system, see Fig. 15. The convergence to  $E_2$  is very slow. If we perform the numerical simulation until  $t = 100$  we see clearly that the solution depicted in red in the figure tends to  $E_2$ .

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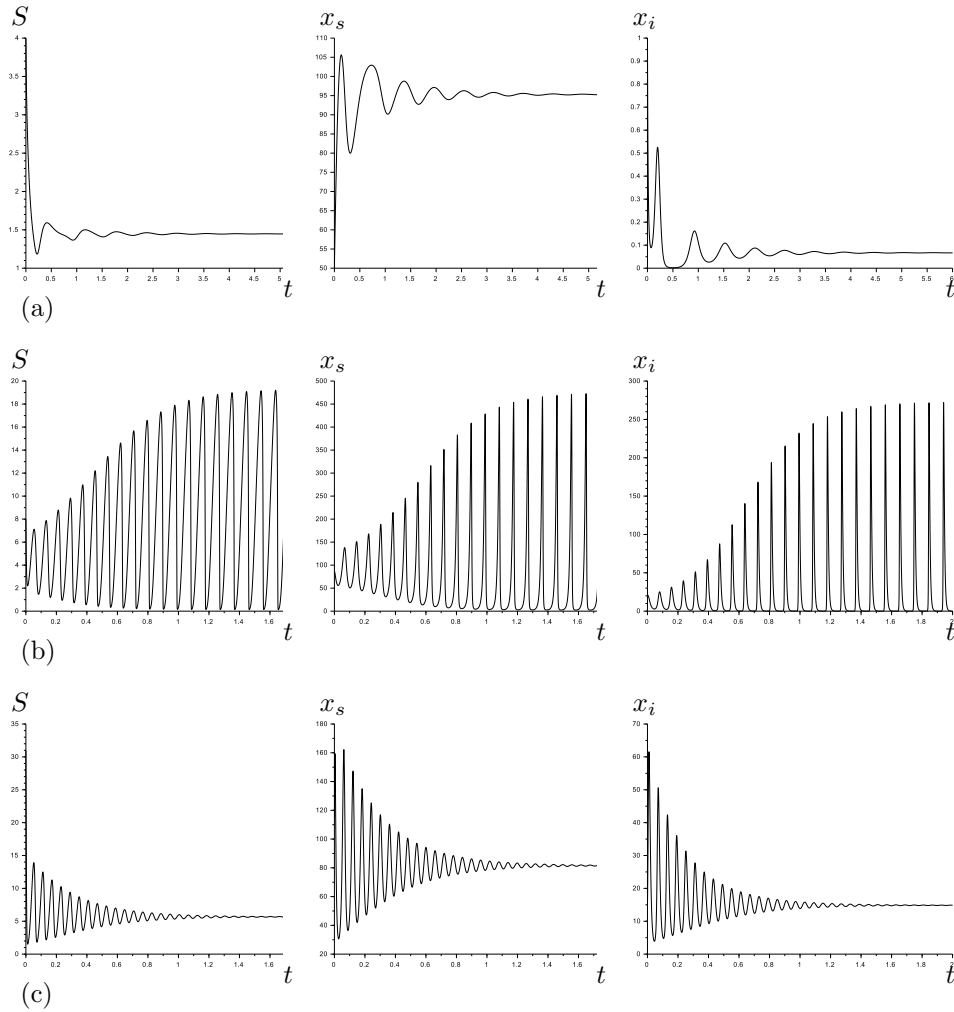


Figure 14: Numerical illustration of the global convergence of (3) toward  $E_2$  or toward the limit cycle, for the biological parameter values used in Fig. 6 and  $D = 8$ . (a)  $S^0 = 3.8 \in (\lambda_c, \lambda_1^H)$  with initial condition  $(S(0), x_s(0), x_i(0)) = (4, 50, 1)$  : global convergence to  $E_2$ . (b)  $S^0 = 60 \in (\lambda_1^H, \lambda_2^H)$  with initial condition  $(S(0), x_s(0), x_i(0)) = (8, 86, 20)$  : global convergence to the limit cycle. (c)  $S^0 = 150 > \lambda^C$  with initial condition  $(S(0), x_s(0), x_i(0)) = (31, 115, 15)$  : global convergence to  $E_2$ .

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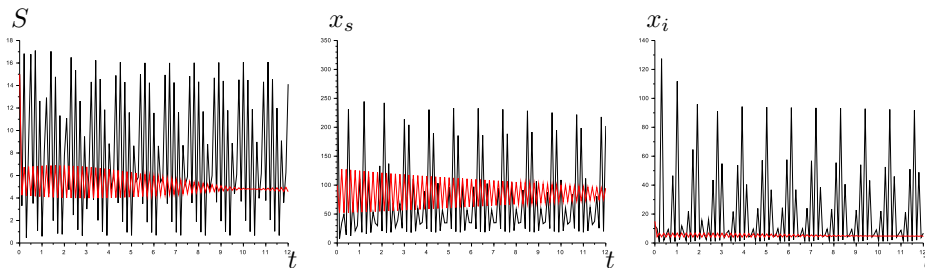


Figure 15: Numerical illustration of the bistability of (3), for the biological parameter values used in Fig. 6 and  $D = 8$ ,  $S^0 = 101 \in (\lambda_2^H, \lambda^C)$ . With initial condition (in black)  $(S(0), x_s(0), x_i(0)) = (15, 350, 12)$ , convergence to the limit cycle; with initial condition (in red)  $(S(0), x_s(0), x_i(0)) = (15, 100, 12)$ , convergence to  $E_2$ .

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