Effect of the mortality on a density-dependent model with a predator-prey relationship

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ABSTRACT. In this work, we consider an inter-specific density-dependent model of two species competing on a single nutrient in a chemostat, taking into account the prey-predator relationship. With different dilution rates, we give a complete analysis of the existence and local stability of all the steady states. Indeed, under the joint effect of competition with the prey-predator relationship and mortality, we show that the positive steady state can be destabilized by a supercritical Hopf bifurcation with the appearance of a stable limit cycle. However, without mortality, there is a stable persistence of the coexistence steady state where there cannot be periodic orbits.

RÉSUMÉ. Dans ce travail, nous considérons un modèle densité-dépendant inter-spécifique de deux espèces en compétition sur un seul nutriment dans un chémostat, en tenant compte de la relation proie-prédateur. Avec des taux de dilution différents, nous donnons une analyse complète de l'existence et de la stabilité locale de tous les points d'équilibre. En effet, sous l'effet joint de la compétition avec la relation proie-prédateur et de la mortalité, nous montrons que l'équilibre positif peut se déstabiliser par une bifurcation de Hopf supercritiques avec l'apparition d'un cycle limite stable. Cependant, sans mortalité, il y a persistance stable de l'équilibre de coexistence où il ne peut pas y avoir des orbites périodiques.

KEYWORDS : Coexistence, Limit cycle, Predator-prey relationship, Supercritical Hopf bifurcation

MOTS-CLÉS : Coexistence, Cycle limite, Relation proie-prédateur, Bifurcation de Hopf super-critique

1. Introduction

In the chemostat, the coexistence of species could be explained through several mechanisms, such as the intra and interspecific competition between the species [2, 7], the flocculation of the species [5, 6], and the density-dependence of the growth functions [4, 9]. Also, predator-prey interaction can prove that species can coexist in the chemostat, see [1, 10]. Here, we will focus on the predator-prey relationship which is characterized by the fact that the one species (the prey) promotes the growth of the other species (the predator) which in turn inhibits the growth of the prey species. In this context, in [3, 11], it was considered an interspecific density-dependent model in the chemostat with the same dilution rate, taking into account the predator-prey relationship, when it was proved that the system may exhibit the coexistence and the bistability with a multiplicity of positive steady states. Moreover, in [11], the operating diagram according to the control parameters S_{in} and D shows all steady states that can appear or disappear only through saddle-node or transcritical bifurcations. In the present work, we proposed to study an extension of the model studied in [3, 11], considering the predator-prey relationship and distinct dilution rates. The model takes the form

$$\left\{\begin{array}{lcl} \dot{S} & = & D(S_{in}-S)-f_1(S,x_2)x_1-f_2(S,x_1)x_2, \\ \dot{x}_1 & = & (f_1(S,x_2)-D_1)x_1, \\ \dot{x}_2 & = & (f_2(S,x_1)-D_2)x_2, \end{array}\right. \tag{1}$$

where $S(t)$ is the concentration of the substrate at time t; $x_1(t)$ and $x_2(t)$ are, respectively, the concentrations of prey and predator at time t; D and S_{in} are, respectively, the dilution rate and the concentration of the substrate in the feed device; f_1 represents the growth rate of the prey which depends only on S and x_2 and f_2 represents the growth rate of the predator which depends only on S and x_1; D_i represents the removal rate of the species x_i and can be modeled by

$$D_i = D + a_i, \quad i = 1, 2$$

where a_i represents the nonnegative mortality rate parameter of species x_i. In the existing literature, it is well known that the addition of mortality terms of the species in a predator-prey model in the chemostat can cause destabilization of the system where stable limit cycles [1, 8] and multiple chaotic attractors [8] are found.

In our knowledge, model (1) has not yet been studied in the literature. Thus, our study, in this paper, is the first attempt to analyze the effect of the mortality on the behavior of a predator-prey model in the chemostat with interspecific density-dependent growth rates. Using the nullcline method, we present a geometric characterization that describes all steady states of the model (1) and shows the multiplicity of positive steady states. Considering specific growth rates, we succeeded in finding a set of parameters such that the coexistence can hold around a stable limit cycle, in contrast to the case without mortality where the coexistence may occur only around a positive steady state (see [3, 11]).

This paper is organized as follows. The next section presents general assumptions for the growth functions of the model (1) and the analysis of the existence of steady states. In Section 3, the asymptotic behavior analysis of model (1) was done. Considering specific growth rates, numerical simulations are presented in Section 4 to show the emergence of a limit cycle through a supercritical Hopf bifurcation. Finally, conclusion is drawn in Section 5. Most of the proofs are reported in Appendix A and the maximal number of solutions of an equation to determine the nullcline in this particular case with specific growth rates is given in Appendix B. Finally, all the parameter values used in simulations are provided in Appendix C.

2. Assumptions on the model and steady states

In what follows, we study model (1) using the following general assumptions on the growth rates f_i, for $i = 1, 2, j = 1, 2, i \neq j$:

(H0) $f_i : \mathbb{R}_+^2 \longrightarrow \mathbb{R}_+$ is continuously differentiable.

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

(H2) $\dfrac{\partial f_i}{\partial S}(S, x_j) > 0$, for all $S \geq 0,\ x_1 > 0$ and $x_2 \geq 0$.

(H3) $\dfrac{\partial f_1}{\partial x_2}(S, x_2) < 0$ and $\dfrac{\partial f_2}{\partial x_1}(S, x_1) > 0$, for all $S > 0$, $x_1 \geq 0$ and $x_2 \geq 0$.

(H4) $f_2(S, 0) = 0$, for all $S > 0$.

Assumption (H1) means that the substrate is necessary for the growth of the two species. Assumption (H2) means that the growth rate of each species increases with the concentration of the substrate. Assumption (H3) means that the growth of the first species x_1 is inhibited by the second species x_2, while the growth of second species x_2 increases with the presence of first species x_1. Assumption (H4) means that the prey species x_1 is necessary for the growth of the predator species x_2. One has the following preliminary result on positivity and boundedness of solutions.

Proposition 2.1 *For any non-negative initial condition, the solutions of system (1) remain non-negative and positively bounded. In addition, the set*

$$\Omega = \left\{ (S, x_1, x_2) \in \mathbb{R}_+^3 : S + x_1 + x_2 \leq S_{in} \right\}$$

is positively invariant and is a global attractor for the dynamics (1).

The first step is to determine the steady states of (1). A steady state of (1) must be a solution of the system

$$\left\{ \begin{array}{lcl} 0 & = & D(S_{in} - S) - f_1(S, x_2)x_1 - f_2(S, x_1)x_2, \\ 0 & = & (f_1(S, x_2) - D_1)x_1, \\ 0 & = & (f_2(S, x_1) - D_2)x_2. \end{array} \right. \tag{2}$$

By (H4) and from the third equation of (2), when $x_1 = 0$, it follows that $x_2 = 0$, that is, system 1 cannot have a steady state where only the predator exists. Therefore, system (1) has the following types of steady states:

- the washout $\mathcal{E}_0 = (S_{in}, 0, 0)$, that always exists, where both populations are extinct.
- the extinction of the predator $\mathcal{E}_1 = (\tilde{S}, \tilde{x}_1, 0)$, where second population x_2 is extinct.
- the coexistence steady state $\mathcal{E}^* = (S^*, x_1^*, x_2^*)$, where both populations survive.

The components $S = \tilde{S}$ and $x_1 = \tilde{x}_1$ of a boundary steady state $\mathcal{E}_1$ are the solutions of (2) with $x_1 > 0$ and $x_2 = 0$. Therefore, $\tilde{S}$ and $\tilde{x}_1$ are the solutions of equations

$$D(S_{in} - \tilde{S}) = D_1 \tilde{x}_1, \tag{3}$$

$$f_1(\tilde{S}, 0) = D_1. \tag{4}$$

From (3), we obtain

$$\tilde{S} = S_{in} - \frac{D_1}{D}\tilde{x}_1. \tag{5}$$

Replacing $\tilde{S}$ by this expression in (4), we see that $x_1 = \tilde{x}_1$ must be a solution of

$$f_1\left(S_{in} - \frac{D_1}{D}x_1, 0\right) = D_1. \tag{6}$$

$\tilde{S}$ is positive if, and only if, $\tilde{x}_1 < DS_{in}/D_1$, that is to say, (6) has a solution in the interval $]0, DS_{in}/D_1[$. The function $x_1 \mapsto f_1\left(S_{in} - D_1x_1/D, 0\right)$ is decreasing from $f_1\left(S_{in}, 0\right)$ for $x_1 = 0$ to 0 for $x_1 = DS_{in}/D_1$. Thus, there exists a solution $x_1 = \tilde{x}_1 \in]0, DS_{in}/D_1[$ satisfying (6) if, and only if,

$$f_1(S_{in}, 0) > D_1. \tag{7}$$

If such an $\tilde{x}_1$ exists then it is unique. Therefore, we can state the following result:

Proposition 2.2 *Under assumptions (H0)-(H3), the boundary steady state $\mathcal{E}_1$ of (1) with $\tilde{x}_1 > 0$ and $x_2 = 0$ exists if, and only if, condition (7) holds where $\tilde{x}_1$ is the solution of (6) and $\tilde{S}$ is given by (5). If it exists, then it is unique.*

The components $S = S^*$, $x_1 = x_1^*$ and $x_2 = x_2^*$ of a positive steady state $\mathcal{E}^*$ must be the solutions of (2) with $x_1 > 0$ and $x_2 > 0$, that is, S^*, x_1^* and x_2^* are the solutions of the set of equations

$$D(S_{in} - S) = D_1x_1 + D_2x_2, \tag{8}$$
$$f_1(S, x_2) = D_1, \tag{9}$$
$$f_2(S, x_1) = D_2. \tag{10}$$

From (8), it follows that S^* is given by

$$S^* = S_{in} - \frac{D_1}{D}x_1 - \frac{D_2}{D}x_2. \tag{11}$$

Replacing S^* by this expression in equations (9) and (10), we see that $(x_1 = x_1^*, x_2 = x_2^*)$ must be a solution of

$$\begin{cases} \widetilde{f_1}(x_1, x_2) = 0, \\ \widetilde{f_2}(x_1, x_2) = 0, \end{cases} \tag{12}$$

where

$$\widetilde{f_i}(x_1, x_2) := f_i(S_{in} - \frac{D_1}{D}x_1 - \frac{D_2}{D}x_2, x_j) - D_i, \quad i = 1, 2,\ j = 1, 2,\ i \neq j. \tag{13}$$

One see that S^* is positive if, and only if, $D_1x_1^*/D + D_2x_2^*/D < S_{in}$, that is to say, (12) has a positive solution in the set

$$M := \left\{(x_1, x_2) \in \mathbb{R}_+^2 : \frac{D_1}{D}x_1 + \frac{D_2}{D}x_2 < S_{in}\right\}.$$

To solve (12) in M, we need the following results:

Lemma 2.1 *Assume that (7) holds. The equation* $\widetilde{f}_1(x_1,x_2) = 0$ *defines a smooth decreasing function*

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

such that $F_1(\tilde{x}_1) = 0$, $F_1(0) = \tilde{x}_2$ *and* $-D_1/D_2 < F_1'(x_1) < 0$ *for all* $x_1 \in [0,\tilde{x}_1]$, *where* $\tilde{x}_1$ *is the solution of (6) defined by* $\widetilde{f}_1(x_1,0) = 0$ *and* $\tilde{x}_2$ *is the solution of the equation* $\widetilde{f}_1(0,x_2) = 0$*. Furthermore, the graph* γ_1 *of* F_1 *lies in* M *(see Fig. 1(b)). More precisely,* $(x_1, F_1(x_1)) \in M$ *for all* $x_1 \in [0,\tilde{x}_1]$.

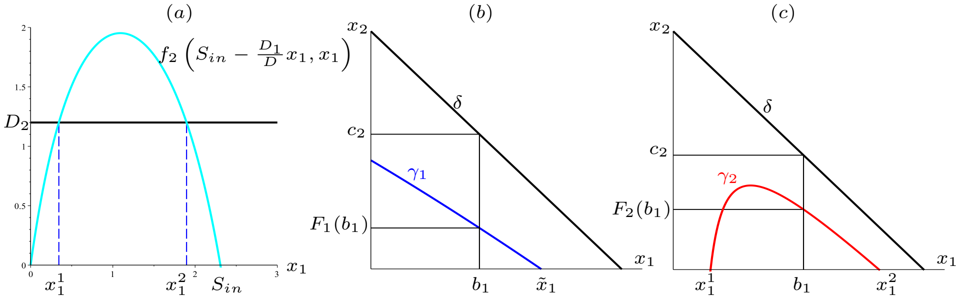

Figure 1. *With the specific growth functions (21):* (a) *Number of solutions of equation* $\widetilde{f}_2(x_1,0) = 0$, (b) *definition of* F_1, (c) *definition of* F_2.

To determine the function defined by the equation $\widetilde{f}_2(x_1,x_2) = 0$, we will see the number of solutions of the equation $\widetilde{f}_2(x_1,0) = 0$ in the following result.

Lemma 2.2 *The equation* $\widetilde{f}_2(x_1,0) = 0$ *has a solution in* $[0, DS_{in}/D_1]$ *if, and only if,*

$$\max_{x_1 \in [0, DS_{in}/D_1]} f_2\left(S_{in} - \frac{D_1}{D}x_1, x_1\right) \geq D_2. \tag{14}$$

Generically, this equation admits an even number of solutions in $[0, DS_{in}/D_1]$.

In what follows, without loss of generality, we can assume that the equation $\widetilde{f}_2(x_1,0) = 0$ admits two solutions x_1^1 and x_1^2 in $[0, DS_{in}/D_1]$ (see Fig. 1(a,c)). Appendix B shows that this property is fulfilled when the function $x_1 \mapsto \widetilde{f}_2(x_1,0)$ is deduced from the specific growth rate (21) satisfying our hypotheses. For more general multimodal functions, the study can be treated similarly. Then, we can state the following result:

Lemma 2.3 *Under condition (14), the equation* $\widetilde{f}_2(x_1,x_2) = 0$ *defines a function*

$$\begin{array}{rcccc} F_2 & : & [x_1^1, x_1^2] & \longrightarrow & [0, DS_{in}/D_2[\\ & & x_1 & \longmapsto & F_2(x_1) = x_2, \end{array}$$

such that $F_2(x_1^1) = F_2(x_1^2) = 0$ *and* $-D_1/D_2 < F_2'(x_1)$ *for all* $x_1 \in [x_1^1, x_1^2]$, *where* x_1^1 *and* x_1^2 *are the solutions of the equation* $\widetilde{f}_2(x_1,0) = 0$*. Moreover, the graph* γ_2 *of* F_2 *lies in* M *and* $(x_1, F_2(x_1)) \in M$ *for all* $x_1 \in [x_1^1, x_1^2]$ *(see Fig. 1(c)).*

The following result is a consequence of the previous lemmas.

Proposition 2.3 *A positive steady state* $\mathcal{E}^* = (S^*, x_1^*, x_2^*)$ *of (1) exists if, and only if, the curves* γ_1 *and* γ_2 *have a positive intersection, where* S^* *is given by (11) and* (x_1^*, x_2^*) *is a positive solution of equations*

$$x_2 = F_1(x_1) \quad \textit{and} \quad x_2 = F_2(x_1). \tag{15}$$

Note that $\tilde{x}_1$, x_1^1 and x_1^2 represent the coordinates of the intersections of the curves γ_1 and γ_2 with the axis $x_2 = 0$. To determine the number of positive steady states, three cases must be distinguished according to their relative positions:

$$\text{Case 1 : } \tilde{x}_1 < x_1^1 < x_1^2, \text{ Case 2 : } x_1^1 < \tilde{x}_1 < x_1^2, \text{ Case 3 : } x_1^1 < x_1^2 < \tilde{x}_1. \tag{16}$$

Note that Case 1 or Case 3 is equivalent to the condition $\widetilde{f_2}(\tilde{x}_1, 0) < 0$, while Case 2 is equivalent to $\widetilde{f_2}(\tilde{x}_1, 0) > 0$ (see Fig. 1(a)). The number of positive steady states of (1) is given by the following proposition.

Proposition 2.4 *Assume that (7) and (14) hold.*

- *If Case 1 holds, then the system (1) can have no positive steady state.*
- *If Case 2 holds, then there exists at least one positive steady state. Generically, there is an odd number of positive steady states.*
- *If Case 3 holds, then the system can have no positive steady state or generically an even number of positive steady states.*

3. Local stability of steady states

In this section, we focus on the study of local asymptotic stability of each steady state of system (1). For convenience, we shall use the abbreviation LES for Locally Exponentially Stable steady state. It is useful to use the change of variables $z = S + x_1 + x_2$. Using the variables (z, x_1, x_2), system (1) can be written

$$\left\{\begin{array}{lcl} \dot{z} & = & D(S_{in} - z) - a_1 x_1 - a_2 x_2, \\ \dot{x}_1 & = & (f_1(z - x_1 - x_2, x_2) - D_1) x_1, \\ \dot{x}_2 & = & (f_2(z - x_1 - x_2, x_1) - D_2) x_2. \end{array}\right. \tag{17}$$

Let J denote the Jacobian matrix of (17) evaluated at (z, x_1, x_2):

$$J = \begin{bmatrix} -D & -a_1 & -a_2 \\ Ex_1 & f_1 - D_1 - Ex_1 & -(E+G)x_1 \\ Fx_2 & (H-F)x_2 & f_2 - D_2 - Fx_2 \end{bmatrix} \tag{18}$$

where

$$E = \frac{\partial f_1}{\partial S}, \quad F = \frac{\partial f_2}{\partial S}, \quad G = -\frac{\partial f_1}{\partial x_2}, \quad H = \frac{\partial f_2}{\partial x_1}. \tag{19}$$

which are nonnegative. The stability of the boundary steady states $\mathcal{E}_0$ and $\mathcal{E}_1$ is given as follows.

Proposition 3.1

- *$\mathcal{E}_0$ is LES if, and only if, $f_1(S_{in}, 0) < D_1$.*
- *$\mathcal{E}_1$ is LES if, and only if, $f_2\left(S_{in} - \frac{D_1}{D}\tilde{x}_1, \tilde{x}_1\right) < D_2$, that is, Case 1 or Case 3 holds.*

In what follows, we analyze the stability of positive steady state $\mathcal{E}^*$. The Jacobian matrix at $\mathcal{E}^* = (S^*, x_1^*, x_2^*)$ is given by

$$J^* = \begin{bmatrix} -D & -a_1 & -a_2 \\ Ex_1^* & -Ex_1^* & -(E+G)x_1^* \\ Fx_2^* & (H-F)x_2^* & -Fx_2^* \end{bmatrix}$$

where E, F, G and H are given by (19) and evaluated at $\mathcal{E}^*$. The characteristic polynomial is given by:

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

where

$$c_1 = -(D + Ex_1^* + Fx_2^*), \quad c_2 = -D_1Ex_1^* - D_2Fx_2^* + (FG - GH - EH)x_1^*x_2^*,$$
$$c_3 = (D_1GF - DGH - D_2EH)x_1^*x_2^*.$$

Since $c_1 < 0$, according to the Routh-Hurwitz criterion, $\mathcal{E}^*$ is LES if, and only if,

$$c_3 < 0 \quad \text{and} \quad c_4 = c_1c_2 + c_3 > 0. \tag{20}$$

In the next proposition, we will show that the sign of c_3 is given by the position of curves of functions $F_1(\cdot)$ and $F_2(\cdot)$.

Proposition 3.2 *One has* $c_3 = D_2F\left(\frac{D_2}{D}E + G\right)(F_1'(x_1^*) - F_2'(x_1^*))x_1^*x_2^*$.

Since the condition $c_4 > 0$ of the Routh-Hurwitz criterion (20) could be unfulfilled where c_4 can change its sign by varying the control parameter S_{in}, the next section is devoted to show numerically how the positive steady state $\mathcal{E}^*$ could be destabilized with the emergence of stable limit cycles.

4. Numerical simulations

In order to show that the condition $c_4 > 0$ evaluated at $\mathcal{E}^* = (S^*, x_1^*, x_2^*)$ could be unfulfilled, all biological parameters were fixed. Then, the control parameter S_{in} was varied. To see the change of sign of the function $S_{in} \mapsto c_4(S_{in})$ evaluated at $\mathcal{E}^*$, it is useful to illustrate the curve of this function. To this end, we assumed that the growth functions satisfying the assumptions (H0)-(H4) are given by :

$$f_1(S, x_2) = \frac{m_1S}{K_1 + S}\frac{1}{1 + \frac{x_2}{K_i}}, \quad f_2(S, x_1) = \frac{m_2S}{K_2 + S}\frac{x_1}{L_2 + x_1}, \tag{21}$$

where m_i, K_i, $i = 1, 2$, and L_2 are the maximum growth rates and the Michaelis-Menten constants, respectively, while K_i is the inhibition factor due to x_2 for the growth of the species x_1. Indeed, we succeeded in finding a set of parameters (see Table 1) such that c_4 can change its sign as S_{in} increases (see Fig. 2(a)). In fact, the solution $S_{in}^{cr} \simeq 6.265$ of equation $c_4(S_{in}) = 0$ represents the critical value of S_{in} for which the positive steady state loses its stability.

To understand and analyze this change of local behavior of $\mathcal{E}^*$ in S_{in}^{cr} without any bifurcation with other steady states, we determine numerically the eigenvalues of the Jacobian matrix J^* at the positive steady state $\mathcal{E}^*$. Indeed, this Jacobian matrix J^* has one negative eigenvalue and one pair of complex-conjugate eigenvalues :

$$\bar{\lambda}_j = \mu(S_{in}) \pm i\nu(S_{in}), \quad j = 1, 2.$$

Increasing the control parameter S_{in}, Fig. 2(b) shows that this pair crosses the imaginary axis at the critical value $S_{in} = S_{in}^{cr}$ from negative half plane to positive half plane, that is, it becomes purely imaginary for S_{in}^{cr} such that $\mu(S_{in}^{cr}) = 0$, with $\nu(S_{in}^{cr}) \neq 0$. Thus, $\mathcal{E}^*$ becomes unstable with occurrence of stable limit cycle via a supercritical Hopf

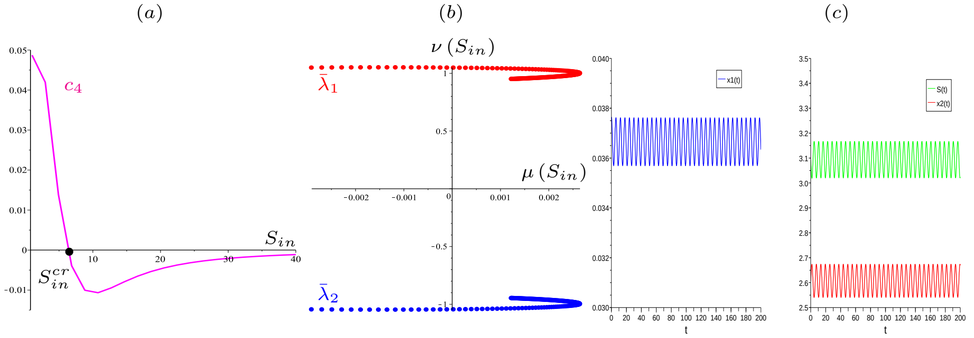

Figure 2. *(a) Change of sign of $c_4(S_{in})$. (b) Variation of a pair of complex-conjugate eigenvalues as S_{in} increases. (c) Stable limit cycle when the oscillations are sustained.*

bifurcation. For $S_{in} \simeq 6.27 > S_{in}^{cr}$, the numerical simulations (see Fig. 2(c)) show the occurrence of limit cycle when the oscillations are sustained.

5. Conclusion

In this work, we have analyzed the effect of the mortality of species on the behavior of an interspecific density-dependent model with a predator-prey relationship. We give a complete analysis of the existence and local stability of all steady states where we have shown the multiplicity of positive steady states by using the nullcline method. Considering specific growth rates, we succeeded in finding a set of parameters such that a condition of the Routh Hurwitz criterion (20) can change its sign as S_{in} increases. More precisely, the positive steady state $\mathcal{E}^*$ can destabilize through a supercritical Hopf bifurcation with the occurrence of a stable limit cycle. This feature cannot occur without mortality, where generically the coexistence can be only around a positive steady state.

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A. Proofs

Proof of Proposition 2.1. If $S = 0$ then $\dot{S} = DS_{in} > 0$. Thus no trajectory can leave the positive octant $\mathbb{R}^3_+$ by crossing the boundary face $S = 0$. In addition, if $x_1 = 0$ and $x_2 = 0$ then $\dot{x}_1 = 0$ and $\dot{x}_2 = 0$ and the set

$$\Gamma_0 = \left\{(S, x_1, x_2) \in \mathbb{R}^3_+ : S > 0,\ x_1 = 0,\ x_2 = 0\right\}$$

is invariant under the system (1) because the function

$$t \longmapsto (S(t), x_1(t), x_2(t)) = \left(S_{in} + (S(0) - S_{in})e^{-Dt}, 0, 0\right)$$

is a solution (1). By uniqueness of solutions, the set Γ_0 cannot be reached in finite time by trajectories for which $x_1(0) > 0$ or $x_2(0) > 0$. Furthermore, for $i = 1, 2$, if $x_i = 0$ then $\dot{x}_i = 0$ and the set

$$\Gamma_i = \left\{(S, x_1, x_2) \in \mathbb{R}^3_+ : S \geq 0,\ x_i = 0,\ x_j \geq 0\right\}, \quad j = 1, 2,\ i \neq j$$

is invariant under the system (1) because the function

$$t \longmapsto \left(S_{in} + (S(0) - S_{in})e^{-Dt}, 0, x_2(0)e^{-D_2 t}\right) \quad (resp.\ t \longmapsto (S(t), x_1(t), 0))$$

is a solution of (1). By uniqueness of solutions, the set Γ_i cannot be reached in finite time by trajectories for $x_i(0) > 0$. Therefore, the solutions remain non-negative. Let $z = S + x_1 + x_2$. From system (1), we have

$$\dot{z} = D(S_{in} - z) - a_1 x_1 - a_2 x_2.$$

Consequently,

$$\dot{z} \leq D(S_{in} - z).$$

Using Gronwall's lemma, we obtain

$$z(t) \leq S_{in} + (z(0) - S_{in})e^{-Dt} \quad \text{for all} \quad t \geq 0. \tag{22}$$

We deduce that

$$z(t) \leq \max(z(0), S_{in}) \quad \text{for all} \quad t \geq 0.$$

Therefore, the solutions of (1) are positively bounded and are defined for all $t \geq 0$. From (22), we deduce that the set Ω is positively invariant and is a global attractor for (1). ■

Proof of Lemma 2.1. Let l_1 be a fixed line defined by $x_1 = b_1$ that intersects the line δ defined by

$$\frac{D_1}{D}x_1 + \frac{D_2}{D}x_2 = S_{in}, \quad \text{at point} \quad x_2 = c_2 = \frac{D}{D_2}S_{in} - \frac{D_1}{D_2}b_1,$$

(see Fig. 1(b)). From hypotheses (H1)-(H3), it follows that the function $x_2 \mapsto \widetilde{f}_1(b_1, x_2)$ is decreasing from $f_1(S_{in} - D_1 b_1/D, 0) - D_1$ for $x_2 = 0$ to $-D_1$ for $x_2 = c_2$. Therefore, there exists a unique $b_2 \in [0, c_2[$ such that $\widetilde{f}_1(b_1, b_2) = 0$ if, and only if,

$$f_1\left(S_{in} - \frac{D_1}{D}b_1, 0\right) \geq D_1,$$

which is equivalent to $b_1 \leq \tilde{x}_1$ since the function $x_1 \mapsto f_1\left(S_{in} - D_1 x_1/D, 0\right)$ is decreasing and $\tilde{x}_1$ is a solution of (6). Thus, we have shown that for all $b_1 \in [0, \tilde{x}_1]$ there exists a unique $b_2 \in [0, c_2[$ such that $\widetilde{f}_1(b_1, b_2) = 0$, that is, each line l_1 meets the set $\widetilde{f}_1(x_1, x_2) = 0$ exactly once if $0 \leqslant b_1 \leqslant \tilde{x}_1$. Thus, we define the function F_1 by $b_2 = F_1(b_1)$. The graph γ_1 of this function lies in M (see Fig. 1(b)). Using the implicit function theorem and from (H2)-(H3), the function F_1 is smooth and decreasing since

$$-\frac{D_1}{D_2} < F_1'(x_1) = -\frac{\frac{\partial \widetilde{f}_1}{\partial x_1}}{\frac{\partial \widetilde{f}_1}{\partial x_2}} = \frac{\frac{D_1}{D}\frac{\partial f_1}{\partial S}}{-\frac{D_2}{D}\frac{\partial f_1}{\partial S} + \frac{\partial f_1}{\partial x_2}} < 0. \tag{23}$$

If $x_2 = 0$, then the equation $F_1(x_1) = 0$ is equivalent to $\widetilde{f}_1(x_1, 0) = 0$ which has a unique solution $x_1 = \tilde{x}_1$ using Proposition 2.2 when condition (7) holds. Similarly, if $x_1 = 0$, then the equation $F_1(0) = x_2$ is equivalent to $\widetilde{f}_1(0, x_2) = 0$ which has a unique solution $x_2 = \tilde{x}_2 \in]0, DS_{in}/D_2[$ when condition (7) holds, since the function $x_2 \mapsto \widetilde{f}_1(0, x_2)$ is decreasing from $f_1(S_{in}, 0) - D_1$ for $x_2 = 0$ to $-D_1$ for $x_2 = DS_{in}/D_2$. ■

Proof of Lemma 2.2. Under hypothesis (H0), the function $x_1 \mapsto \widetilde{f}_2(x_1, 0)$ is continuous on $[0, DS_{in}/D_1]$ with $\widetilde{f}_2(0, 0) = \widetilde{f}_2(DS_{in}/D_1, 0) = -D_2$. Then, the equation $\widetilde{f}_2(x_1, 0) = 0$ has a solution in $[0, DS_{in}/D_1]$ if, and only if,

$$\max_{x_1 \in [0, DS_{in}/D_1]} \widetilde{f}_2(x_1, 0) \geq 0,$$

that is, condition (14) holds. ■

Proof of Lemma 2.3. Let l_1 be a fixed line defined by $x_1 = b_1$ that intersects the line δ defined by

$$\frac{D_1}{D} x_1 + \frac{D_2}{D} x_2 = S_{in}, \quad \text{at point} \quad x_2 = c_2 = \frac{D}{D_2} S_{in} - \frac{D_1}{D_2} b_1,$$

(see Fig. 1(c)). From hypotheses (H1)-(H2), the function $x_2 \mapsto \widetilde{f}_2(b_1, x_2)$ is decreasing from $f_2(S_{in} - D_1 b_1/D, b_1) - D_2$ for $x_2 = 0$ to $-D_2$ for $x_2 = c_2$. Hence, there exists a unique $b_2 \in [0, c_2[$ such that $\widetilde{f}_2(b_1, b_2) = 0$ if, and only if,

$$f_2\left(S_{in} - \frac{D_1}{D} b_1, b_1\right) \geq D_2,$$

which is equivalent to $b_1 \in [x_1^1, x_1^2]$ in the particular case where the equation $\widetilde{f}_2(x_1, 0) = 0$ admits only two solutions x_1^1 and x_1^2 (see Fig. 1(a,c)). Thus, we have shown that for all $b_1 \in [x_1^1, x_1^2]$ there exists a unique $b_2 \in [0, c_2[$ such that $\widetilde{f}_2(b_1, b_2) = 0$. Hence, we define the function F_2 by $b_2 = F_2(b_1)$ where the graph γ_2 of this function lies in M. Using the implicit function theorem and assumptions (H2)-(H3), we obtain

$$-\frac{D_1}{D_2} < F_2'(x_1) = -\frac{\frac{\partial \widetilde{f}_2}{\partial x_1}}{\frac{\partial \widetilde{f}_2}{\partial x_2}} = -\frac{D_1}{D_2} + \frac{D}{D_2} \frac{\frac{\partial f_2}{\partial x_1}}{\frac{\partial f_2}{\partial S}}. \tag{24}$$

When $x_2 = 0$, we have $F_2(x_1) = 0$, that is, $\widetilde{f}_2(x_1, 0) = 0$. From Lemma 2.2, this equation has two solutions x_1^1 and x_1^2 in $[0, DS_{in}/D_1]$ since condition (14) holds. ■

Proof of Proposition 3.1. At $\mathcal{E}_0$, the Jacobian matrix J defined by (18) is written as follows:

$$J_0 = \begin{bmatrix} -D & -a_1 & -a_2 \\ 0 & f_1(S_{in}, 0) - D_1 & 0 \\ 0 & 0 & -D_2 \end{bmatrix}.$$

The eigenvalues are negative if, and only if, $f_1(S_{in}, 0) < D_1$. The Jacobian matrix at $\mathcal{E}_1$ is given by

$$J_1 = \begin{bmatrix} -D & -a_1 & -a_2 \\ E\tilde{x}_1 & -E\tilde{x}_1 & -(E+G)\tilde{x}_1 \\ 0 & 0 & f_2(S_{in} - \frac{D_1}{D}\tilde{x}_1, \tilde{x}_1) - D_2 \end{bmatrix}$$

where E and G are evaluated at $\mathcal{E}_1$. The eigenvalues are

$$f_2\left(S_{in} - \frac{D_1}{D}\tilde{x}_1, \tilde{x}_1\right) - D_2$$

which is negative if, and only if, $\tilde{x}_1 < x_1^1$ or $\tilde{x}_1 > x_1^2$, together with the eigenvalues of the upper left square matrix

$$A = \begin{bmatrix} -D & -a_1 \\ E\tilde{x}_1 & -E\tilde{x}_1 \end{bmatrix}.$$

Since

$$\text{tr}\, A = -(D + E\tilde{x}_1) < 0 \quad \text{and} \quad \det A = DE\tilde{x}_1 + a_1 E\tilde{x}_1 > 0,$$

the real part of the eigenvalues of A are negative. Therefore, $\mathcal{E}_1$ is LES if, and only if, Case 1 or Case 3 holds. ■

Proof of Lemma 3.2. Using definition (19) and the expressions of $F_1'(x_1)$ and $F_2'(x_1)$ in (23) and (24), it follows that

$$F_1'(x_1) = \frac{\frac{D_1}{D}E}{-\frac{D_2}{D}E - G} \quad \text{and} \quad F_2'(x_1) = -\frac{D_1}{D_2} + \frac{D}{D_2}\frac{H}{F}.$$

Then, we obtain

$$F_1'(x_1) - F_2'(x_1) = \frac{D_1 FG - D_2 EH - DGH}{D_2 F\left(\frac{D_2}{D}E + G\right)}.$$

Consequently, at $\mathcal{E}^*$, we have

$$c_3 = D_2 F\left(\frac{D_2}{D}E + G\right)(F_1'(x_1^*) - F_2'(x_1^*))x_1^* x_2^*.$$

■

B. The particular case for growth functions (21)

In this particular case with the specific growth rates (21), we determine the maximal number of solutions of the equation $\widetilde{f}_2(x_1, 0) = 0$ in the following lemma :

Lemma B.1 *Consider the specific growth functions (21) and assume that (14) holds. Then, the equation* $\widetilde{f}_2(x_1, 0) = 0$ *has exactly two solutions* x_1^1 *and* x_1^2 *on* $[0, DS_{in}/D_1]$.

Proof of Lemma B.1. Assume that the growth functions are given by (21). Let ϕ be the function defined by

$$\phi(x_1) := f_2\left(S_{in} - \frac{D_1}{D}x_1, x_1\right). \tag{25}$$

Straightforward calculation shows that

$$\begin{aligned} \phi'(x_1) &= \frac{m_2(-DD_1K_2 + D_1^2L_2)x_1^2 - 2DD_1L_2m_2(S_{in} + K_2)x_1}{(K_2D + S_{in}D - D_1x_1)^2(x_1 + L_2)^2} \\ &+ \frac{m_2D^2L_2S_{in}(S_{in} + K_2)}{(K_2D + S_{in}D - D_1x_1)^2(x_1 + L_2)^2}. \end{aligned}$$

Hence, the solutions of $\phi'(x_1) = 0$ are given by those of the following equation

$$m_2(-DD_1K_2 + D_1^2L_2)x_1^2 - 2DD_1L_2m_2(S_{in} + K_2)x_1 + m_2D^2L_2S_{in}(S_{in} + K_2) = 0$$

which has at most two solutions on $]0, DS_{in}/D_1[$ since it is an algebraic equation of degree two in x_1. Moreover, under (H0)-(H4), ϕ is positive, continuous and $\phi(0) = \phi(DS_{in}/D_1) = 0$. Consequently, ϕ must has a unique positive extremum on $]0, DS_{in}/D_1[$. Therefore, when (14) holds, the equation $\widetilde{f}_2(x_1, 0) = 0$ has exactly two solutions x_1^1 and x_1^2 on $[0, DS_{in}/D_1]$ (see Fig. 1(a)). ■

C. Parameters used in numerical simulations

Table 1. *Parameter values used for (1) when the growth rates f_1 and f_2 are given by (21).*

Parameter	m_1	K_1	K_i	m_2	K_2	L_2	a_1	a_2	D	S_{in}
Figure 1	4	2	3	8	1.8	1	0.3	0.2	1	3
Figure 2(a,b)	4	2	3	8	0.1	0.2	0.3	0.2	1	variable
Figure 2(c)	4	2	3	8	0.1	0.2	0.3	0.2	1	6.27

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