Persistent competition models on two complementary nutrients with density-dependent consumption rates

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Abstract We give a result of uniform persistence for a theoretical competition model of 3 species of microorganisms on 2 complementary nutrients in a chemostat with density-dependent growth functions. The proof consists of giving first sufficient conditions of persistence, which is by the way available for more than 3 species. Then, in the case of 2 species, we show under additional assumptions, and with the use of the so-called Hofbauer–Hutson theorem, that it is possible to obtain a uniform persistence around a positive equilibrium point. Finally, the main result is established from what preceeds and by means of Thieme–Zhao theorem. These results are illustrated by some numerical simulations.

Keywords Dynamical systems · Global stability · Uniform persistence · Chemostat · Complementary nutrients · Density dependence

Mathematics Subject Classifications 34C11 · 37N25 · 92B05

1 Introduction

The chemostat is a laboratory apparatus used for continuous cultivation of microorganisms in which the effect of limiting nutrient on the population of microorganisms can be investigated. A theoretical approach to the description of the competition of two or more populations of microorganisms on a limiting nutrient in a chemostat has been developed in the book of Smith and Waltman [18] (see also Harmand et al. [8], Ajbar and Alhumaizi [1] and the references therein). Our interest goes to models where growth functions are obtained by the combination of two limiting nutrients. The different classifications of limiting nutrients were

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introduced by Rapport [17] and Covich [6]. We mainly distinguish between two types, the so-called *complementary nutrients*, that is nutrients of different essential substances which are independently required for growth, and *substitutable nutrients*, that is alternative sources of an essential substance. Note that the first type is called complementary by Leon and Tumpson [12] and *essential* by Tilman [20]. Leon and Tumpson found the conditions of local stability of a positive equilibrium point and hence conditions of coexistence of the two populations. Hsu et al. [10] made a global study when the growth functions are of Michaelis–Menten type and obtained the classical results of the two dimensional Lotka–Volterra competition model. The same model with general monotonic and non-monotonic growth functions was studied by Butler and Wolkowicz [5]. Li [13] examined a model generalizing that of Butler and Wolkowicz with several populations of microorganisms and for a class of general growth functions. He proved global stability of a positive equilibrium point under some conditions. Mazenc and Malisoff [16] considered a more general model with M resources and N species and different removal rates. When $M = N$, they obtained a conditional existence of a positive equilibrium point by Brouwer degree theory. For particular families of the growth functions they proved the global asymptotic stability of such a point with the use of Lyapunov functions. Recently, Borsali and Yadi [4] studied the same model of two microorganisms where they added terms of interspecific interaction. They proved the permanence of the model and the existence of a positive equilibrium point under some conditions. On the other hand, many models where the growth function depends not only on the substrate but also on the microorganism, have been considered. In this context, Arditi and Ginzburg [2, 3] developed predator–prey models with functional responses depending on the prey and the predator. They suggested a class of functional responses which take into account the interference between the predators and depending on the amount of prey consumed by one predator that is on the ratio of the amount of consumed prey and the predator per unit time : the consumption rate decreases proportionally with the abundance of predators. The models with this type of functional response are called *ratio-dependent*. This approach has also been applied in competitive models in the chemostat. More exactly, in the following chemostat model of competition of n species “ x_i ” on a single nutrient “ s ”,

$$\begin{aligned}\dot{s} &= (s^\circ - s) D - \sum_{i=1}^n \frac{1}{y_i} \mu_i(s, x) x_i, \\ \dot{x}_i &= (\mu_i(s, x) - D) x_i, \quad i \in \{1, 2, \dots, n\},\end{aligned}\tag{1}$$

the growth function, denoted by $\mu_i(s, x)$, depends on the substrate and microorganisms. These models are rather called *density-dependent*.

Lobry and Mazenc [15] examined the following general density-dependent competition model called intra-specific competition model :

$$\begin{aligned}\dot{s} &= f(s) - \sum_{i=1}^n \frac{1}{y_i} \mu_i(s, x_i) x_i, \\ \dot{x}_i &= (\mu_i(s, x_i) - d_i) x_i, \quad i \in \{1, 2, \dots, n\}.\end{aligned}\tag{2}$$

Here, x_i is the biomass of the i^{th} population in the chemostat, s is the concentration of the nutrient, s° is the input concentration of the resource s , D is the dilution rate, y_i is the growth yield constant, and d_i is the removal rate of the i^{th} species. The function f is a positive function and of class C^1 . The growth function μ_i is supposed to vanish at $s = 0$, to be increasing with respect to s and decreasing with respect to x_i . This assumption is natural. It ensures that the growth function is zero in the absence of the nutrient, increases with

the amount of substrate, and decreases with the abundance of the microorganism. Under some assumptions, they showed that the model (2) has an interior equilibrium point globally asymptotically stable and therefore the coexistence of all the species of microorganisms. The demonstration is based on the construction of a Lyapunov function. Another study of the delay density-dependent model with the growth yield constants depending on the substrate was conducted by Xu and Li [14]. They also have the same result as that of Lobry and Mazenc [15].

The objective of the present paper is to study a density-dependent competition model of several microorganisms on two complementary nutrients. The model is written :

$$\begin{aligned}\dot{s} &= (s^\circ - s) D - \sum_{i=1}^n \frac{1}{y_{si}} \mu_i(s, r, x_i) x_i, \\ \dot{r} &= (r^\circ - r) D - \sum_{i=1}^n \frac{1}{y_{ri}} \mu_i(s, r, x_i) x_i, \\ \dot{x}_i &= (\mu_i(s, r, x_i) - D) x_i, \quad i \in \{1, 2, \dots, n\},\end{aligned}\tag{3}$$

where the functions $\mu_i(s, r, x_i) := \min(p_i(s, x_i), q_i(r, x_i))$ satisfy the following assumptions :

- H1.** The functions $s \mapsto p_i(s, x_i)$ and $r \mapsto q_i(r, x_i)$ are positive, continuously differentiable, increasing and such that $p_i(0, x_i) = q_i(0, x_i) = 0$.
- H2.** The functions $x_i \mapsto p_i(s, x_i)$ and $x_i \mapsto q_i(r, x_i)$ are positive, continuously differentiable and decreasing.

Since p_i and q_i are C^1 , the functions μ_i are locally Lipschitz. In particular, the assumptions H1 and H2 insure the existence and uniqueness property of solutions of (3) for prescribed initial conditions in $\mathbb{R}_+^{n+2}$. Moreover, the break-even concentrations will be defined as being the respective values λ_{s_i} and λ_{r_i} of s and r such that $p_i(\lambda_{s_i}, 0) = q_i(\lambda_{r_i}, 0) = D$.

This work should be seen as a contribution to the mathematical study of theoretical chemostat models in at least two aspects. The first one lies in the framework of multnutrients models, for which the references are less abundant. The second one concerns the density-dependence notion for which we believe that it will lead to new interesting questions. Even if this article is inspired by works in [15], the mathematical treatment turns to be more complex, except perhaps for the persistence result of Theorem 2.5 below. The aim of this work being theoretical, we do not give the connection with any realistic biological experiment.

In Sect. 2, we first show that the positive solutions of (3) are positively bounded and give conditions of washing out. We then prove the persistence of the model under some assumptions (Theorem 2.5). Section 3 is devoted to the study of the same model limited to two microorganisms and for which we obtain a uniform persistence result under some assumptions (Theorem 3.3). Moreover, we deduce that there exists a positive equilibrium point which is globally asymptotically stable (Theorem 3.4). Finally, in Sect. 4, thanks to the previous results we prove that our model (3) with three microorganisms is actually uniformly persistent and that there exists at least a positive equilibrium point (Theorem 4.1). Some numerical simulations are presented in this article to illustrate the results. Note that one can make the conjecture that the equilibrium point for the last case is unique and attractive.

2 Persistence in case of several species of microorganisms

2.1 Elementary properties

The first two propositions recall the usual properties of dissipativity (i.e. the solutions are positively bounded), invariance and conditions of washing out. The proof of the first proposition is classical and is omitted.

Proposition 2.1 *Under assumptions H1 and H2, the system (3) is dissipative and the positive orthant $\mathbb{R}_+^{n+2}$ is positively invariant. More exactly, there exists $t_0 > 0$ such for all $t > t_0$ one has $s(t) < s^\circ$, $r(t) < r^\circ$ and $x_i(t) < \min(y_{si}s^\circ, y_{ri}r^\circ)$, $i \in \{1, 2, \dots, n\}$.*

Proposition 2.2 *Suppose that H1 and H2 are satisfied. If $s^\circ < \lambda_{si}$ or $r^\circ < \lambda_{ri}$ then, for all positive initial conditions, one has*

$$\lim_{t \rightarrow +\infty} s(t) = s^\circ, \quad \lim_{t \rightarrow +\infty} r(t) = r^\circ \quad \text{and} \quad \lim_{t \rightarrow +\infty} x_i(t) = 0.$$

Proof If $s^\circ < \lambda_{si}$ or $r^\circ < \lambda_{ri}$ for all $i \in \{1, 2, \dots, n\}$, then there exists a real constant $\varepsilon > 0$ such that $s^\circ + \varepsilon < \lambda_{si}$ or $r^\circ + \varepsilon < \lambda_{ri}$.

From Proposition 2.1, we deduce that

$$\exists t_0 > 0 : \forall t > t_0 \quad s(t) < s^\circ + \varepsilon, \quad r(t) < r^\circ + \varepsilon.$$

On the other hand, from the constant variational formula, we have :

$$\begin{aligned} x_i(t) &= x_i(0) \exp \left(\int_0^t (\mu_i(s(\tau), r(\tau), x_i(\tau)) - D) d\tau \right), \\ &= x_i(0) \exp \left[\int_0^{t_0} (\mu_i(s(\tau), r(\tau), x_i(\tau)) - D) d\tau \right. \\ &\quad \left. + \int_{t_0}^t (\mu_i(s(\tau), r(\tau), x_i(\tau)) - D) d\tau \right]. \end{aligned}$$

Hence,

$$x_i(t) = C x_i(0) \exp \left(\int_{t_0}^t (\mu_i(s(\tau), r(\tau), x_i(\tau)) - D) d\tau \right),$$

where

$$C := \exp \left(\int_0^{t_0} (\mu_i(s(\tau), r(\tau), x_i(\tau)) - D) d\tau \right) > 0.$$

By assumption H2, we obtain :

$$\begin{aligned} x_i(t) &< C x_i(0) \exp \left(\int_{t_0}^t ((\mu_i(s^\circ + \varepsilon, r^\circ + \varepsilon, x_i(\tau)) - D)) d\tau \right) \\ &< C x_i(0) \exp \left(\int_{t_0}^t ((\mu_i(s^\circ + \varepsilon, r^\circ + \varepsilon, 0) - D)) d\tau \right). \end{aligned}$$

Finally, we have :

$$x_i(t) < C x_i(0) \exp(A_i(t - t_0)),$$

where $A_i := \mu_i (s^\circ + \varepsilon, r^\circ + \varepsilon, 0) - D$. The real constant A_i is negative since $s^\circ + \varepsilon < \lambda_{si}$ or $r^\circ + \varepsilon < \lambda_{ri}$ for all $i \in \{1, 2, \dots, n\}$. Finally, the solutions of the model (with positive initial conditions) are positive, then :

$$\lim_{t \rightarrow +\infty} x_i(t) = 0.$$

Now, let us set

$$\begin{aligned}\Sigma_1 &:= s + \sum_{i=1}^n \frac{1}{y_{si}} x_i, \\ \Sigma_2 &:= r + \sum_{i=1}^n \frac{1}{y_{ri}} x_i,\end{aligned}$$

which transforms the system (3) in :

$$\begin{aligned}\dot{\Sigma}_1 &= D(s^\circ - \Sigma_1), \\ \dot{\Sigma}_2 &= D(r^\circ - \Sigma_2), \\ \dot{x}_j &= \left(\mu_j \left(\Sigma_1 - \sum_{i=1}^n \frac{1}{y_{si}} x_i, \Sigma_2 - \sum_{i=1}^n \frac{1}{y_{ri}} x_i, x_j \right) - D \right) x_j, \quad j = 1..n.\end{aligned}\tag{4}$$

Hence, the solutions of the two first equations are simply :

$$\begin{aligned}\Sigma_1(t) &= s^\circ + (\Sigma_1(0) - s^\circ) e^{-Dt}, \\ \Sigma_2(t) &= r^\circ + (\Sigma_2(0) - r^\circ) e^{-Dt}.\end{aligned}$$

Finally, we deduce :

$$\lim_{t \rightarrow +\infty} s(t) = s^\circ \text{ and } \lim_{t \rightarrow +\infty} r(t) = r^\circ.$$

□

Remark 2.3 In what follows, we suppose that $\mu_i(s^\circ, r^\circ, 0) > D$ (i.e. $s^\circ > \lambda_{si}$ and $r^\circ > \lambda_{ri}$).

2.2 A persistence result

Let us additionally assume that, for all $i \in \{1, 2, \dots, n\}$,

H3. There exists a real number $h \in]0, 1]$ such that

$$\begin{aligned}p_i(s, x_i) &\leq p_i(s, 0) \frac{1}{(1 + x_i)^h}, \\ q_i(r, x_i) &\leq q_i(r, 0) \frac{1}{(1 + x_i)^h}.\end{aligned}$$

H4. The functions $s \mapsto p_i(s, 0)$ and $r \mapsto q_i(r, 0)$ are, respectively, bounded by two real constants $m_{si} > 0$ and $m_{ri} > 0$.

Note that, the functions p_i and q_i being C^1 , there exist two real constants $K_{si} > 0$ and $K_{ri} > 0$ such that

$$p_i(s, 0) \leq K_{si}s \quad \text{and} \quad q_i(r, 0) \leq K_{ri}r.$$

H5. The following inequalities, where $M_i := \min(m_{si}, m_{ri}) > D$, are satisfied :

$$s^\circ > D + \sum_{i=1}^n \frac{1}{y_{si}} K_{si} \left(\left(\frac{2M_i}{D} \right)^{\frac{1}{h}} - 1 \right),$$

$$r^\circ > D + \sum_{i=1}^n \frac{1}{y_{ri}} K_{ri} \left(\left(\frac{2M_i}{D} \right)^{\frac{1}{h}} - 1 \right).$$

H6. The functions μ_i satisfy $\mu_i(D, D, 0) > D$.

Note that the assumption $\mu_i(s^\circ, r^\circ, 0) := \min(p_i(s^\circ, 0), q_i(r^\circ, 0)) > D$ is a consequence of assumptions H5 and H6.

Remark 2.4 We give an example of a density-dependent growth function which is often used in biology and which satisfies the assumptions H3 and H4, namely the Beddington–DeAngelis type growth function :

$$p(s, x) = \frac{ms}{s + k + ax},$$

where m , k , and a are positive constants. Note that this function satisfies obviously the assumptions H1 and H2. One has :

$$p(s, 0) = \frac{ms}{s + k}.$$

Assumption H4 is clearly satisfied by $p(s, 0)$. We show that :

$$p(s, x) = p(s, 0) \frac{A(s)}{A(s) + x},$$

with $A(s) := \frac{s + k}{a}$. Now, if $A(s) \leq 1$, it is obvious that :

$$\frac{A(s)}{A(s) + x} \leq \frac{1}{1 + x}.$$

Hence, we obtain :

$$p(s, x) \leq p(s, 0) \frac{1}{1 + x},$$

which is the condition H3 with $h = 1$. On the other hand, knowing that $s < s^\circ$ we show that if $A(s) > 1$ then :

$$\frac{A(s)}{A(s) + x} \leq \frac{C}{1 + x},$$

where $C := A(s^\circ) > 1$. Hence,

$$p(s, x) \leq p(s, 0) \frac{C}{1 + x}.$$

Finally, since $C > 1$, the two inequalities imply :

$$p(s, x) \leq p(s, 0) \frac{1}{1 + x}.$$

Now, we can state and prove the main theorem of this section, which gives sufficient conditions of persistence of the model (3).

Theorem 2.5 *If assumptions H1 to H6 are satisfied, then the model (3) is persistent.*

Proof According to assumption H4, one has $\mu_i(s, r, 0) \leq M_i$. From the equations of x_i in (3) and assumption H3, one deduces that

$$\dot{x}_i \leq \left(\frac{M_i}{(1+x_i)^h} - D \right) x_i.$$

If $\frac{M_i}{(1+x_i)^h} \leq \frac{D}{2}$ then $\dot{x}_i \leq -\frac{D}{2}x_i < 0$. In other words, if $x_i \geq \left(\frac{2M_i}{D}\right)^{\frac{1}{h}} - 1$ then $\dot{x}_i < 0$. Hence,

$$\exists t_1 > 0 \text{ such that } \forall t \geq t_1 \ x_i(t) < \left(\frac{2M_i}{D}\right)^{\frac{1}{h}} - 1.$$

Note that $\left(\frac{2M_i}{D}\right)^{\frac{1}{h}} > 1$ since $M_i > D$. In the other hand, for all $t \geq t_1$, one has

$$\begin{aligned} \dot{s} &> (s^\circ - s) D - \sum_{i=1}^n \frac{1}{y_{si}} \mu_i(s, r, x_i) \left(\left(\frac{2M_i}{D}\right)^{\frac{1}{h}} - 1 \right), \\ \dot{r} &> (r^\circ - r) D - \sum_{i=1}^n \frac{1}{y_{ri}} \mu_i(s, r, x_i) \left(\left(\frac{2M_i}{D}\right)^{\frac{1}{h}} - 1 \right). \end{aligned}$$

According to assumption H2, one can see that $\mu_i(s, r, x_i) \leq \mu_i(s, r, 0)$. Hence,

$$\begin{aligned} \dot{s} &> (s^\circ - s) D - \sum_{i=1}^n \frac{1}{y_{si}} \mu_i(s, r, 0) \left(\left(\frac{2M_i}{D}\right)^{\frac{1}{h}} - 1 \right), \\ \dot{r} &> (r^\circ - r) D - \sum_{i=1}^n \frac{1}{y_{ri}} \mu_i(s, r, 0) \left(\left(\frac{2M_i}{D}\right)^{\frac{1}{h}} - 1 \right). \end{aligned}$$

Moreover, from H4, we know that

$$\begin{aligned} \mu_i(s, r, 0) &\leq p_i(s, 0) \leq K_{si}s, \\ \mu_i(s, r, 0) &\leq q_i(r, 0) \leq K_{ri}r. \end{aligned}$$

Therefore,

$$\begin{aligned} \dot{s} &> (s^\circ - s) D - \sum_{i=1}^n \frac{1}{y_{si}} K_{si} \left(\left(\frac{2M_i}{D}\right)^{\frac{1}{h}} - 1 \right) s, \\ \dot{r} &> (r^\circ - r) D - \sum_{i=1}^n \frac{1}{y_{ri}} K_{ri} \left(\left(\frac{2M_i}{D}\right)^{\frac{1}{h}} - 1 \right) r. \end{aligned}$$

If $s, r \in]0, D]$, then

$$\begin{aligned}\dot{s} &> \left[s^\circ - D - \sum_{i=1}^n \frac{1}{y_{si}} K_{si} \left(\left(\frac{2M_i}{D} \right)^{\frac{1}{h}} - 1 \right) \right] s, \\ \dot{r} &> \left[r^\circ - D - \sum_{i=1}^n \frac{1}{y_{ri}} K_{ri} \left(\left(\frac{2M_i}{D} \right)^{\frac{1}{h}} - 1 \right) \right] r.\end{aligned}$$

According to assumption H5, one concludes that $\dot{s} > 0$ and $\dot{r} > 0$ for all $s, r \in]0, D]$. Hence,

$$\exists t_2 > t_1 : \forall t \geq t_2, s(t) > D \quad \text{and} \quad \exists t'_2 > t_1 : \forall t \geq t'_2, r(t) > D,$$

then

$$\forall t \geq \max(t_2, t'_2), \dot{x}_i = (\mu_i(s, r, x_i) - D) x_i > (\mu_i(D, D, x_i) - D) x_i.$$

Now, by continuity of the function μ_i with respect to x_i , for all $\varepsilon_i > 0$, there exists $\delta > 0$ such that $|\mu_i(D, D, x_i) - \mu_i(D, D, 0)| \leq \varepsilon_i$ for all $x_i \leq \delta$. Hence, for all $x_i \leq \delta$ one has $\mu_i(D, D, x_i) - D \geq \mu_i(D, D, 0) - \varepsilon_i - D$.

Let $A_i := \mu_i(D, D, 0) - D$ which is positive according to H6. If we chose $\varepsilon_i = \frac{A_i}{2}$, then there exists $\delta > 0$ such that, for all $x_i \leq \delta$,

$$\mu_i(D, D, x_i) - D \geq \frac{A_i}{2},$$

which implies that

$$\forall x_i \leq \delta, \dot{x}_i > \frac{A_i}{2} x_i > 0.$$

Finally,

$$\exists t_3 > \max(t_2, t'_2) : \forall t \geq t_3, x_i(t) > \delta,$$

which establishes the persistence of the model (3). $\square$

3 Global asymptotic stability in case of two species

Consider the model

$$\begin{aligned}\dot{s} &= (s^\circ - s) D - \sum_{i=1}^2 \frac{1}{y_{si}} \mu_i(s, r, x_i) x_i, \\ \dot{r} &= (r^\circ - r) D - \sum_{i=1}^2 \frac{1}{y_{ri}} \mu_i(s, r, x_i) x_i, \\ \dot{x}_1 &= (\mu_1(s, r, x_1) - D) x_1, \\ \dot{x}_2 &= (\mu_2(s, r, x_2) - D) x_2,\end{aligned} \tag{5}$$

which is the system (3) with $n = 2$ and suppose that assumptions H1 and H2 are still satisfied.

3.1 Uniform persistence

In the following Lemma, we omit the subscribe i for convenience.

Lemma 3.1 *The equation $\mu\left(s^\circ - \frac{1}{y_s}x, r^\circ - \frac{1}{y_r}x, x\right) - D = 0$ has a unique solution in $]0, \min(y_s s^\circ, y_r r^\circ)[$.*

Proof Define :

$$F(x) := \mu\left(s^\circ - \frac{1}{y_s}x, r^\circ - \frac{1}{y_r}x, x\right) - D.$$

One has :

$$F(0) = \mu(s^\circ, r^\circ, 0) - D > 0 \text{ and } F(\min(y_s s^\circ, y_r r^\circ)) = -D < 0.$$

We check now that the function F is decreasing. Recall that both functions p and q are increasing with respect to their first argument and decreasing with respect to the second one. Let $x_1 < x_2$.

$$\begin{aligned} p\left(s^\circ - \frac{1}{y_s}x_1, x_1\right) &> p\left(s^\circ - \frac{1}{y_s}x_2, x_1\right) > p\left(s^\circ - \frac{1}{y_s}x_2, x_2\right) \\ &\geq \min\left(p\left(s^\circ - \frac{1}{y_s}x_2, x_2\right), q\left(r^\circ - \frac{1}{y_r}x_2, x_2\right)\right), \end{aligned}$$

then

$$p\left(s^\circ - \frac{1}{y_s}x_1, x_1\right) > \mu\left(s^\circ - \frac{1}{y_s}x_2, r^\circ - \frac{1}{y_r}x_2, x_2\right).$$

Likewise,

$$\begin{aligned} q\left(r^\circ - \frac{1}{y_r}x_1, x_1\right) &> q\left(r^\circ - \frac{1}{y_r}x_2, x_1\right) > q\left(r^\circ - \frac{1}{y_r}x_2, x_2\right) \\ &\geq \min\left(p\left(s^\circ - \frac{1}{y_s}x_2, x_2\right), q\left(r^\circ - \frac{1}{y_r}x_2, x_2\right)\right), \end{aligned}$$

then

$$q\left(r^\circ - \frac{1}{y_r}x_1, x_1\right) > \mu\left(s^\circ - \frac{1}{y_s}x_2, r^\circ - \frac{1}{y_r}x_2, x_2\right).$$

These two inequalities imply

$$\mu\left(s^\circ - \frac{1}{y_s}x_1, r^\circ - \frac{1}{y_r}x_1, x_1\right) > \mu\left(s^\circ - \frac{1}{y_s}x_2, r^\circ - \frac{1}{y_r}x_2, x_2\right).$$

We deduce that $F(x_1) > F(x_2)$. Hence, the equation $F(x) = 0$ has a unique solution in $]0, \min(y_s s^\circ, y_r r^\circ)[$. $\square$

We can make the additional following assumption :

H7. The unique solution $\tilde{x}_i$ of the equation $\mu_i \left(s^\circ - \frac{1}{y_{si}} x_i, r^\circ - \frac{1}{y_{ri}} x_i, x_i \right) - D = 0$ in $]0, \min(y_{si}s^\circ, y_{ri}r^\circ)[$ verifies :

$$\begin{aligned} \mu_1 \left(s^\circ - \frac{\tilde{x}_2}{y_{s2}}, r^\circ - \frac{\tilde{x}_2}{y_{r2}}, 0 \right) - D &> 0, \\ \mu_2 \left(s^\circ - \frac{\tilde{x}_1}{y_{s1}}, r^\circ - \frac{\tilde{x}_1}{y_{r1}}, 0 \right) - D &> 0. \end{aligned}$$

Remark 3.2 The assumption $\mu_i(s^\circ, r^\circ, 0) := \min(p_i(s^\circ, 0), q_i(r^\circ, 0)) > D$ is a consequence of the assumption H7 (see Remark 2.3).

Concerning the function μ_i satisfying hypothesis H7, we reconsider here the example of Beddington–DeAngelis growth function and show that the solutions $\tilde{x}_i$ can be explicitly determined. This can be done also for the so-called Contois growth function $p(s, x) = ms/(s + kx)$, where $m, k > 0$, but, unfortunately, assumption H4 is not satisfied in this case. For convenience, we will consider the equation :

$$\mu(s^\circ - \alpha x, r^\circ - \beta x, x) - D = 0,$$

where $\alpha = 1/y_s$ and $\beta = 1/y_r$.

Let us set :

$$F(x) := \mu(s^\circ - \alpha x, r^\circ - \beta x, x) - D,$$

with

$$\mu(s, r, x) := \min(p(s, x), q(r, x)).$$

Consider then

$$p(s, x) = \frac{ms}{s + k + ax}, \quad q(r, x) = \frac{m'r}{r + k' + a'x},$$

where m, m', k, k', a and a' are positive constants. If $F(x) = p(s^\circ - \alpha x, x) - D$, then :

$$\begin{aligned} F(x) = 0 &\Leftrightarrow (\alpha(m - D) + aD)x = (m - D)s^\circ - kD \\ &\Leftrightarrow x = \frac{(m - D)s^\circ - kD}{\alpha(m - D) + aD} > 0. \end{aligned}$$

The positiveness of x is a consequence of the condition of non-washing out (Remark 2.3). The case $F(x) = q(r^\circ - \beta x, x) - D$ is similar.

We can state the following result giving sufficient conditions of permanence of the system (5). The proof will use a corollary 2 of the paper [7] cited in the appendix. This corollary is a consequence of Hofbauer's and Hutson's theorem [9, 11].

Theorem 3.3 *If assumptions H1, H2 and H7 are satisfied, then the model (5) is permanent.*

Proof According to Proposition 2.1, the system (5) is dissipative and the following bounded set

$$C := \left\{ (s, r, x_1, x_2) \in \mathbb{R}_+^4 : s \leq s^\circ, r \leq r^\circ, x_i \leq \min(y_{si}s^\circ, y_{ri}r^\circ) \right\}$$

is an *attracting* one, in the sense that all trajectories eventually lie in it. By setting :

$$\begin{aligned}\Sigma_1 &:= s + \sum_{i=1}^2 \frac{1}{y_{si}} x_i, \\ \Sigma_2 &:= r + \sum_{i=1}^2 \frac{1}{y_{ri}} x_i,\end{aligned}$$

the system (5) becomes :

$$\begin{aligned}\dot{\Sigma}_1 &= D(s^\circ - \Sigma_1), \\ \dot{\Sigma}_2 &= D(r^\circ - \Sigma_2), \\ \dot{x}_1 &= \left(\mu_1 \left(\Sigma_1 - \sum_{i=1}^2 \frac{1}{y_{si}} x_i, \Sigma_2 - \sum_{i=1}^2 \frac{1}{y_{ri}} x_i, x_1 \right) - D \right) x_1, \\ \dot{x}_2 &= \left(\mu_2 \left(\Sigma_1 - \sum_{i=1}^2 \frac{1}{y_{si}} x_i, \Sigma_2 - \sum_{i=1}^2 \frac{1}{y_{ri}} x_i, x_2 \right) - D \right) x_2.\end{aligned}\tag{6}$$

The solutions of the two first equations are :

$$\begin{aligned}\Sigma_1(t) &= s^\circ + (\Sigma_1(0) - s^\circ) e^{-Dt}, \\ \Sigma_2(t) &= r^\circ + (\Sigma_2(0) - r^\circ) e^{-Dt}.\end{aligned}$$

The couple $(\Sigma_1(t), \Sigma_2(t))$ converges exponentially to (s°, r°) . Hence, the ω -limit set of all positive trajectories of the model (5) lies in the simplex :

$$\Lambda := \left\{ (s, r, x_1, x_2) \in C : s + \sum_{i=1}^2 \frac{1}{y_{si}} x_i = s^\circ, r + \sum_{i=1}^2 \frac{1}{y_{ri}} x_i = r^\circ \right\}.$$

The system (6) reduced on Λ is given by :

$$\begin{aligned}\dot{x}_1 &= \left(\mu_1 \left(s^\circ - \sum_{i=1}^2 \frac{1}{y_{si}} x_i, r^\circ - \sum_{i=1}^2 \frac{1}{y_{ri}} x_i, x_1 \right) - D \right) x_1, \\ \dot{x}_2 &= \left(\mu_2 \left(s^\circ - \sum_{i=1}^2 \frac{1}{y_{si}} x_i, r^\circ - \sum_{i=1}^2 \frac{1}{y_{ri}} x_i, x_2 \right) - D \right) x_2,\end{aligned}\tag{7}$$

and is defined on :

$$X := \left\{ (x_1, x_2) \in \mathbb{R}_+^2 : \sum_{i=1}^2 \frac{1}{y_{si}} x_i \leq s^\circ \text{ and } \sum_{i=1}^2 \frac{1}{y_{ri}} x_i \leq r^\circ \right\}.$$

X is obviously a closed set. Let us show that it is positively invariant. Suppose that $\sum_{i=1}^2 \frac{1}{y_{si}} x_i(0) = s^\circ$ and $\sum_{i=1}^2 \frac{1}{y_{ri}} x_i(0) = r^\circ$. One can see that :

$$\left. \frac{d}{dt} \left(\sum_{i=1}^2 \frac{1}{y_{si}} x_i(t) \right) \right|_{t=0} = -Ds^\circ < 0, \quad \left. \frac{d}{dt} \left(\sum_{i=1}^2 \frac{1}{y_{ri}} x_i(t) \right) \right|_{t=0} = -Dr^\circ < 0.$$

Hence, for all $t > 0$:

$$\sum_{i=1}^2 \frac{1}{y_{si}} x_i(t) < s^\circ \quad \text{and} \quad \sum_{i=1}^2 \frac{1}{y_{ri}} x_i(t) < r^\circ.$$

On the other hand, one has :

$$x_i(t) = x_i(0) \exp \left[\int_0^t \left(\mu_i \left(s^\circ - \sum_{i=1}^2 \frac{1}{y_{si}} x_i(\tau), r^\circ - \sum_{i=1}^2 \frac{1}{y_{ri}} x_i(\tau), x_i(\tau) \right) - D \right) d\tau \right].$$

Hence, $x_i(t) \geq 0$ when $x_i(0) \geq 0$.

Now, let set $S := \partial R_+^2 \cap X = [0, \min(y_{s1}s^\circ, y_{r1}r^\circ)] \cup [0, \min(y_{s2}s^\circ, y_{r2}r^\circ)]$. The set S is obviously compact and positively invariant. Define the function $P : X \rightarrow \mathbb{R}_+$ by $P(x_1, x_2) := x_1 x_2$, which clearly vanishes on S . We compute the derivative of P at $(x_1, x_2) \in X \setminus S$ in the direction of the field F defined by the reduced system (7).

$$\begin{aligned} \dot{P}(x_1, x_2) &:= \langle \text{grad} P(x_1, x_2), F(x_1, x_2) \rangle = \sum_{j=1}^2 \frac{\partial P(x_1, x_2)}{\partial x_j} F_j(x_1, x_2) \\ &= x_1 x_2 \left[\sum_{i=1}^2 \mu_i \left(s^\circ - \sum_{i=1}^2 \frac{1}{y_{si}} x_i, r^\circ - \sum_{i=1}^2 \frac{1}{y_{ri}} x_i, x_i \right) - 2D \right]. \end{aligned}$$

Let $\psi : X \rightarrow \mathbb{R}$ defined by :

$$\psi(x_1, x_2) := \sum_{i=1}^2 \mu_i \left(s^\circ - \sum_{i=1}^2 \frac{1}{y_{si}} x_i, r^\circ - \sum_{i=1}^2 \frac{1}{y_{ri}} x_i, x_i \right) - 2D.$$

One has :

$$\dot{P}(x_1, x_2) = P(x_1, x_2) \psi(x_1, x_2) \quad \forall (x_1, x_2) \in X \setminus S.$$

The function ψ is bounded below by $-2D$. The condition (i) of Corollary A.1 of the appendix is then verified. For the condition (ii), it is sufficient to check that $\psi(E_k) > 0$ where E_k is an equilibrium point in S . Indeed, the unidimensional set S is positively invariant and its ω -limit set, denoted by $\Omega(S)$, is formed by the equilibrium points E_k in S . Let us determine these equilibrium points.

If $(x_1(0), x_2(0)) \in S$ such that $x_1(0) > 0$ and $x_2(0) = 0$, then $x_2(t) \equiv 0$ and the system (7) is written :

$$\dot{x}_1 = \left(g_1 \left(s^\circ - \frac{1}{y_{s1}} x_1, r^\circ - \frac{1}{y_{r1}} x_1, x_1 \right) - D \right) x_1.$$

The nullclines are $g_1 \left(s^\circ - \frac{1}{y_{s1}} x_1, r^\circ - \frac{1}{y_{r1}} x_1, x_1 \right) - D = 0$ or $x_1 = 0$. If $x_1 = 0$, then $E_0(0, 0)$ is an equilibrium point in S . If $x_1 \neq 0$, then according to assumption H7, the first equation has a unique solution $\tilde{x}_1$ in $]0, \min(y_{s1}s^\circ, y_{r1}r^\circ)[$. Hence, $E_1(\tilde{x}_1, 0)$ is an equilibrium point in S . Analogously, if $(x_1(0), x_2(0)) \in S$ such that $x_1(0) = 0$ and $x_2(0) > 0$, then there exists another equilibrium point $E_2(0, \tilde{x}_2)$ for $\tilde{x}_2 \in]0, \min(y_{s2}s^\circ, y_{r2}r^\circ)$. Hence, $\Omega(S) = \{E_0, E_1, E_2\}$. From assumption H7, one has :

$$\begin{aligned}\psi(E_0) &= \sum_{i=1}^2 \mu_i(s^\circ, r^\circ, 0) - 2D > 0, \\ \psi(E_1) &= \mu_2\left(s^\circ - \frac{\tilde{x}_1}{y_{s1}}, r^\circ - \frac{\tilde{x}_1}{y_{r1}}, 0\right) - D > 0, \\ \psi(E_2) &= \mu_1\left(s^\circ - \frac{\tilde{x}_2}{y_{s2}}, r^\circ - \frac{\tilde{x}_2}{y_{r2}}, 0\right) - D > 0.\end{aligned}$$

The condition (ii) of Corollary A.1 is then satisfied which implies that S is a uniform repeller and that the model (7) is uniformly persistent. Finally, since $\lim_{t \rightarrow +\infty} \Sigma_1(t) = s^\circ$ and $\lim_{t \rightarrow +\infty} \Sigma_2(t) = r^\circ$, the whole system (5) is uniformly persistent. $\square$

3.2 Global asymptotic stability

Uniform persistence and properties of the planar systems lead to the following result of existence of a G.A.S. equilibrium point.

Theorem 3.4 *Under assumptions H1, H2 and H7, the system (5) has a positive G.A.S. equilibrium point.*

Proof First, we determine the trivial equilibrium points of the reduced system (7) and their nature. The Jacobian matrix at an arbitrary point $E(x_1, x_2)$ is given by :

$$J(E) = \begin{bmatrix} \mu_1 - D + x_1 a_1 & x_1 b_{12} \\ x_2 b_{21} & \mu_2 - D + x_2 a_2 \end{bmatrix},$$

with the following notations :

$$\begin{aligned}\mu_j &:= \mu_j\left(s^\circ - \sum_{i=1}^2 \frac{1}{y_{si}} x_i, r^\circ - \sum_{i=1}^2 \frac{1}{y_{ri}} x_i, x_j\right), \\ a_j &:= -\frac{1}{y_{sj}} \frac{\partial p_j}{\partial s}\left(s^\circ - \sum_{i=1}^2 \frac{1}{y_{si}} x_i, x_j\right) + \frac{\partial p_j}{\partial x_j}\left(s^\circ - \sum_{i=1}^2 \frac{1}{y_{si}} x_i, x_j\right) \text{ or} \\ a_j &:= -\frac{1}{y_{rj}} \frac{\partial q_j}{\partial r}\left(r^\circ - \sum_{i=1}^2 \frac{1}{y_{si}} x_i, x_j\right) + \frac{\partial q_j}{\partial x_j}\left(r^\circ - \sum_{i=1}^2 \frac{1}{y_{si}} x_i, x_j\right), \\ b_{jk} &:= -\frac{1}{y_{sk}} \frac{\partial p_j}{\partial s}\left(s^\circ - \sum_{i=1}^2 \frac{1}{y_{si}} x_i, x_j\right) \text{ or} \\ b_{jk} &:= -\frac{1}{y_{rk}} \frac{\partial q_j}{\partial r}\left(r^\circ - \sum_{i=1}^2 \frac{1}{y_{si}} x_i, x_j\right) \text{ with } k \in \{1, 2\}, k \neq j.\end{aligned}$$

The nullclines equations are given by :

$$\begin{aligned}\left(\mu_1\left(s^\circ - \sum_{i=1}^2 \frac{1}{y_{si}} x_i, r^\circ - \sum_{i=1}^2 \frac{1}{y_{ri}} x_i, x_1\right) - D\right) x_1 &= 0, \\ \left(\mu_2\left(s^\circ - \sum_{i=1}^2 \frac{1}{y_{si}} x_i, r^\circ - \sum_{i=1}^2 \frac{1}{y_{ri}} x_i, x_2\right) - D\right) x_2 &= 0.\end{aligned}$$

1st case : $x_1 = x_2 = 0$. The Jacobian matrix at the equilibrium point $E_0(0, 0)$ is simply :

$$J(E_0) = \begin{bmatrix} \mu_1(s^\circ, r^\circ, 0) - D & 0 \\ 0 & \mu_2(s^\circ, r^\circ, 0) - D \end{bmatrix},$$

the eigenvalues of which are $v_i^0 := \mu_i(s^\circ, r^\circ, 0) - D$, $i \in \{1, 2\}$. The origin E_0 unstable, since $\mu_i(s^\circ, r^\circ) > D$.

2nd case : $x_1 \neq 0, x_2 = 0$. According to assumption H7, the equation :

$$\mu_1\left(s^\circ - \frac{1}{y_{s1}}x_1, r^\circ - \frac{1}{y_{r1}}x_1, x_1\right) - D = 0,$$

has a unique solution $\tilde{x}_1$ in $]0, \min(y_{s1}s^\circ, y_{r1}r^\circ)[$. The Jacobian matrix evaluated at the equilibrium point $E_1(\tilde{x}_1, 0)$ is given by :

$$J(E_1) = \begin{bmatrix} \tilde{x}_1 \tilde{a}_1 & \tilde{x}_1 \tilde{b}_{12} \\ 0 & \tilde{\mu}_2 - D \end{bmatrix},$$

where

$$\begin{aligned} \tilde{\mu}_2 &:= \mu_2\left(s^\circ - \frac{1}{y_{s1}}\tilde{x}_1, r^\circ - \frac{1}{y_{r1}}\tilde{x}_1, 0\right), \\ \tilde{a}_1 &:= -\frac{1}{y_{s1}}\frac{\partial p_1}{\partial s}\left(s^\circ - \frac{1}{y_{s1}}\tilde{x}_1, \tilde{x}_1\right) + \frac{\partial p_1}{\partial x_1}\left(s^\circ - \frac{1}{y_{s1}}\tilde{x}_1, \tilde{x}_1\right) \text{ or} \\ \tilde{a}_1 &:= -\frac{1}{y_{r1}}\frac{\partial q_1}{\partial r}\left(r^\circ - \frac{1}{y_{r1}}\tilde{x}_1, \tilde{x}_1\right) + \frac{\partial q_1}{\partial x_1}\left(r^\circ - \frac{1}{y_{r1}}\tilde{x}_1, \tilde{x}_1\right), \\ \tilde{b}_{12} &:= -\frac{1}{y_{s2}}\frac{\partial p_1}{\partial s}\left(s^\circ - \frac{1}{y_{s1}}\tilde{x}_1, \tilde{x}_1\right) \text{ or} \\ \tilde{b}_{12} &:= -\frac{1}{y_{r2}}\frac{\partial q_1}{\partial r}\left(r^\circ - \frac{1}{y_{r1}}\tilde{x}_1, \tilde{x}_1\right). \end{aligned}$$

The eigenvalues of $J(E_1)$ are $v_1^1 := \tilde{x}_1 \tilde{a}_1$ and $v_2^1 := \tilde{\mu}_2 - D$. According to assumption H2, the value v_1^1 is negative while, according to assumption H7, the value v_2^1 is positive. The equilibrium point E_1 is unstable (saddle point).

3rd case : $x_1 = 0, x_2 \neq 0$. This case is analogous to the second one. The obtained equilibrium point, also a saddle point, is $E_2(0, \tilde{x}_2)$ where $\tilde{x}_2$ is the unique solution of :

$$\mu_2\left(s^\circ - \frac{1}{y_{s2}}x_2, r^\circ - \frac{1}{y_{r2}}x_2, x_2\right) - D = 0,$$

in $]0, \min(y_{s2}s^\circ, y_{r2}r^\circ)[$.

Now, let us show that the model (7) has no limit cycle with the use of Dulac–Bendixson Criterion [18]. Let A be the simply connected attracting domain of the system (7):

$$A := \left\{ (x_1, x_2) \in \mathbb{R}_+^2 : \varepsilon \leq x_i \leq \min(y_{si}s^\circ, y_{ri}r^\circ) \right\},$$

where ε is a positive real number such that $\liminf_{t \rightarrow +\infty} x_i(t) > \varepsilon$. Such a uniform bound exists according the Theorem 3.3. Let $B : A \rightarrow \mathbb{R}$ the C^1 function defined by $B(x_1, x_2) := 1/x_1 x_2$ and denote by $F := (F_1, F_2)$ the vector field of (7) :

$$F_1(x_1, x_2) := \left(\mu_1 \left(s^\circ - \sum_{i=1}^2 \frac{1}{y_{si}} x_i, r^\circ - \sum_{i=1}^2 \frac{1}{y_{ri}} x_i, x_1 \right) - D \right) x_1,$$

$$F_2(x_1, x_2) := \left(\mu_2 \left(s^\circ - \sum_{i=1}^2 \frac{1}{y_{si}} x_i, r^\circ - \sum_{i=1}^2 \frac{1}{y_{ri}} x_i, x_2 \right) - D \right) x_2.$$

The divergence of the field $B.F$ is then given by :

$$\operatorname{div}((B.F)(x_1, x_2)) := \frac{\partial}{\partial x_1} (B(x_1, x_2) F_1(x_1, x_2)) + \frac{\partial}{\partial x_2} (B(x_1, x_2) F_2(x_1, x_2)).$$

Simple calculations lead to

$$\frac{\partial}{\partial x_1} (B(x_1, x_2) F_1(x_1, x_2)) = \frac{1}{x_2} a_1 \text{ and } \frac{\partial}{\partial x_2} (B(x_1, x_2) F_2(x_1, x_2)) = \frac{1}{x_1} a_2,$$

where

$$a_j := -\frac{1}{y_{sj}} \frac{\partial p_j}{\partial s} \left(s^\circ - \sum_{i=1}^2 \frac{1}{y_{si}} x_i, x_j \right) + \frac{\partial p_j}{\partial x_j} \left(s^\circ - \sum_{i=1}^2 \frac{1}{y_{si}} x_i, x_j \right) \text{ or}$$

$$a_j := -\frac{1}{y_{rj}} \frac{\partial q_j}{\partial r} \left(r^\circ - \sum_{i=1}^2 \frac{1}{y_{si}} x_i, x_j \right) + \frac{\partial q_j}{\partial x_j} \left(r^\circ - \sum_{i=1}^2 \frac{1}{y_{si}} x_i, x_j \right).$$

Finally,

$$\operatorname{div}((B.F)(x_1, x_2)) = \frac{1}{x_2} a_1 + \frac{1}{x_1} a_2.$$

According to assumption H2, the quantity $\operatorname{div}((B.F)(x_1, x_2))$ is negative for all (x_1, x_2) in A . Hence, according to Dulac–Bendixson Criterion and Poincaré–Bendixson theorem, the model (7) has no limit cycle and admits at least a positive equilibrium point in A . Let $E(x_1^*, x_2^*)$ be such a point and let us evaluate the Jacobian matrix at it :

$$J(E) = \begin{bmatrix} x_1^* a_1^* & x_1^* b_{12}^* \\ x_2^* b_{21}^* & x_2^* a_2^* \end{bmatrix},$$

where :

$$a_j^* := -\frac{1}{y_{sj}} \frac{\partial p_j}{\partial s} \left(s^\circ - \sum_{i=1}^2 \frac{1}{y_{si}} x_i^*, x_j^* \right) + \frac{\partial p_j}{\partial x_j} \left(s^\circ - \sum_{i=1}^2 \frac{1}{y_{si}} x_i^*, x_j^* \right) \text{ or}$$

$$a_j^* := -\frac{1}{y_{rj}} \frac{\partial q_j}{\partial r} \left(r^\circ - \sum_{i=1}^2 \frac{1}{y_{si}} x_i^*, x_j^* \right) + \frac{\partial q_j}{\partial x_j} \left(r^\circ - \sum_{i=1}^2 \frac{1}{y_{si}} x_i^*, x_j^* \right),$$

$$b_{jk}^* := -\frac{1}{y_{sk}} \frac{\partial p_j}{\partial s} \left(s^\circ - \sum_{i=1}^2 \frac{1}{y_{si}} x_i^*, x_j^* \right) \text{ or}$$

$$b_{jk}^* := -\frac{1}{y_{rk}} \frac{\partial q_j}{\partial r} \left(r^\circ - \sum_{i=1}^2 \frac{1}{y_{si}} x_i^*, x_j^* \right) \text{ with } k \in \{1, 2\}, k \neq j.$$

The trace $\operatorname{Tr}(J(E)) = x_1^* a_1^* + x_2^* a_2^*$ of $J(E)$ is clearly negative. The determinant is given by $\det(J(E)) = x_1^* x_2^* (a_1^* a_2^* - b_{12}^* b_{21}^*)$. If, for example, at the equilibrium point, $\mu_j = p_j$ (the case $\mu_j = q_j$ is similar), one has :

$$\det(J(E)) = \frac{\partial p_1}{\partial x_1} \frac{\partial p_2}{\partial x_2} - \frac{1}{y_{s1}} \frac{\partial p_1}{\partial s} \frac{\partial p_2}{\partial x_2} - \frac{1}{y_{s2}} \frac{\partial p_2}{\partial s} \frac{\partial p_1}{\partial x_1} > 0.$$

The equilibrium point E is then locally asymptotically stable. Therefore, knowing that there is no limit cycle, and that the equilibrium E is an arbitrary one, which is locally asymptotically stable, one can conclude that E is unique and G.A.S..

Return back to the whole system (6). In the proof of Theorem 3.3, we showed that the equilibrium point $E_{sr}(s^\circ, r^\circ)$ is G.A.S. for the first two equations of the model (6). Moreover, the solutions of (6) are positively bounded. Then, one can use the Separation Principle Lemma [21] to conclude that the positive equilibrium point $E^*(s^\circ, r^\circ, x_1^*, x_2^*)$ of the model (6), then also the positive equilibrium point $\left(s^\circ - \sum_{i=1}^2 \frac{1}{y_{si}} x_i^*, r^\circ - \sum_{i=1}^2 \frac{1}{y_{ri}} x_i^*, x_1^*, x_2^*\right)$ of the initial model (5), is G.A.S. $\square$

4 Uniform persistence of three species of microorganisms

Reconsider the model (3) with $n = 3$.

$$\begin{aligned} \dot{s} &= (s^\circ - s) D - \sum_{i=1}^3 \frac{1}{y_{si}} \mu_i(s, r, x_i) x_i, \\ \dot{r} &= (r^\circ - r) D - \sum_{i=1}^3 \frac{1}{y_{ri}} \mu_i(s, r, x_i) x_i, \\ \dot{x}_i &= (\mu_i(s, r, x_i) - D) x_i, \quad i \in \{1, 2, 3\}. \end{aligned} \quad (8)$$

We show in this section that we are able to say more than for the general case even if we do not prove the existence of a G.A.S. point. We assume that hypotheses H1 to H7 for all $i \in \{1, 2, 3\}$ are fulfilled, where H7 should be understood as follows : the unique solution $\tilde{x}_i$ of the equation $\mu_i\left(s^\circ - \frac{1}{y_{si}} x_i, r^\circ - \frac{1}{y_{ri}} x_i, x_i\right) - D = 0$ in $]0, \min(y_{si}s^\circ, y_{ri}r^\circ)[$ satisfies :

$$\mu_i\left(s^\circ - \frac{\tilde{x}_j}{y_{sj}}, r^\circ - \frac{\tilde{x}_j}{y_{rj}}, 0\right) - D > 0, \quad i, j \in \{1, 2, 3\}, \quad i \neq j.$$

We can state and show that :

Theorem 4.1 *Under assumptions H1–H7, the model (8) is permanent.*

Proof 1. Reduction : According to Proposition 2.1, the system (3) is dissipative and the following set in an attracting one :

$$C := \left\{ (s, r, x_1, x_2, x_3) \in \mathbb{R}_+^5 : s \leq s^\circ, \quad r \leq r^\circ, \quad x_i \leq \min(y_{si}s^\circ, y_{ri}r^\circ) \right\}.$$

If we set $\Sigma_1 := s + \sum_{i=1}^3 \frac{1}{y_{si}} x_i$ and $\Sigma_2 := r + \sum_{i=1}^3 \frac{1}{y_{ri}} x_i$, the system (8) becomes :

$$\begin{aligned}
 \dot{\Sigma}_1 &= D(s^\circ - \Sigma_1), \\
 \dot{\Sigma}_2 &= D(r^\circ - \Sigma_2), \\
 \dot{x}_1 &= \left(\mu_1 \left(\Sigma_1 - \sum_{i=1}^3 \frac{1}{y_{si}} x_i, \Sigma_2 - \sum_{i=1}^3 \frac{1}{y_{ri}} x_i, x_1 \right) - D \right) x_1, \\
 \dot{x}_2 &= \left(\mu_2 \left(\Sigma_1 - \sum_{i=1}^3 \frac{1}{y_{si}} x_i, \Sigma_2 - \sum_{i=1}^3 \frac{1}{y_{ri}} x_i, x_2 \right) - D \right) x_2, \\
 \dot{x}_3 &= \left(\mu_3 \left(\Sigma_1 - \sum_{i=1}^3 \frac{1}{y_{si}} x_i, \Sigma_2 - \sum_{i=1}^3 \frac{1}{y_{ri}} x_i, x_3 \right) - D \right) x_3,
 \end{aligned} \tag{9}$$

the ω -limit set of which lies in the simplex :

$$\Lambda := \left\{ (s, r, x_1, x_2, x_3) \in C : s + \sum_{i=1}^3 \frac{1}{y_{si}} x_i = s^\circ, r + \sum_{i=1}^3 \frac{1}{y_{ri}} x_i = r^\circ \right\}.$$

On Λ the system (9) is reduced to :

$$\begin{aligned}
 \dot{x}_1 &= \left(\mu_1 \left(s^\circ - \sum_{i=1}^3 \frac{1}{y_{si}} x_i, r^\circ - \sum_{i=1}^3 \frac{1}{y_{ri}} x_i, x_1 \right) - D \right) x_1, \\
 \dot{x}_2 &= \left(\mu_2 \left(s^\circ - \sum_{i=1}^3 \frac{1}{y_{si}} x_i, r^\circ - \sum_{i=1}^3 \frac{1}{y_{ri}} x_i, x_2 \right) - D \right) x_2, \\
 \dot{x}_3 &= \left(\mu_3 \left(s^\circ - \sum_{i=1}^3 \frac{1}{y_{si}} x_i, r^\circ - \sum_{i=1}^3 \frac{1}{y_{ri}} x_i, x_3 \right) - D \right) x_3.
 \end{aligned} \tag{10}$$

The system (10) is defined on :

$$X := \left\{ (x_1, x_2, x_3) \in \mathbb{R}_+^3 : \sum_{i=1}^3 \frac{1}{y_{si}} x_i \leq s^\circ \text{ and } \sum_{i=1}^3 \frac{1}{y_{ri}} x_i \leq r^\circ \right\}.$$

2. Boundary equilibria: In order to use Thieme–Zhao’s theorem, we set $X_1 := \text{int } X$ and $X_2 := \partial X$. Hence $X = X_1 \cup X_2$, $X_1 \cap X_2 = \emptyset$. The set X_2 is a closed subset of X . Moreover, X_1 is positively invariant for (10) since, for all positive initial condition, one has :

$$x_i(t) = x_i(0) \exp \left[\int_0^t \left(\mu_i \left(s^\circ - \sum_{i=1}^3 \frac{1}{y_{si}} x_i(\tau), r^\circ - \sum_{i=1}^3 \frac{1}{y_{ri}} x_i(\tau), x_i(\tau) \right) - D \right) d\tau \right] > 0.$$

Now, let us determine the set M of the equilibria of the system (10) in X_2 . First, we claim that any solution of this system starting in X_1 converges to a point of M . Indeed, in the proof of Theorem 2.5, we have already showed that, under assumptions H1–H6, there exists a positive real number δ and a positive instant t_0 such that, for all $t \geq t_0$ and all $i \in \{1, 2, \dots, n\}$, one has $x_i(t) > \delta$. Hence, $\liminf_{t \rightarrow +\infty} x_i(t) > 0$ for all component $x_i(t)$ of a positive solution of the system (10). Now, the jacobian matrix of (10) at an arbitrary point $E(x_1, x_2, x_3)$ is given by :

$$J(E) = \begin{bmatrix} \mu_1 - D + x_1 a_1 & x_1 b_{12} & x_1 b_{13} \\ x_2 b_{21} & \mu_2 - D + x_2 a_2 & x_2 b_{23} \\ x_3 b_{31} & x_3 b_{32} & \mu_3 - D + x_3 a_3 \end{bmatrix},$$

where :

$$\begin{aligned} \mu_j &:= \mu_j \left(s^\circ - \sum_{i=1}^3 \frac{1}{y_{si}} x_i, r^\circ - \sum_{i=1}^3 \frac{1}{y_{ri}} x_i, x_j \right), \\ a_j &:= -\frac{1}{y_{sj}} \frac{\partial p_j}{\partial s} \left(s^\circ - \sum_{i=1}^3 \frac{1}{y_{si}} x_i, x_j \right) + \frac{\partial p_j}{\partial x_j} \left(s^\circ - \sum_{i=1}^3 \frac{1}{y_{si}} x_i, x_j \right) \text{ or} \\ a_j &:= -\frac{1}{y_{rj}} \frac{\partial q_j}{\partial r} \left(r^\circ - \sum_{i=1}^3 \frac{1}{y_{si}} x_i, x_j \right) + \frac{\partial q_j}{\partial x_j} \left(r^\circ - \sum_{i=1}^3 \frac{1}{y_{si}} x_i, x_j \right), \\ b_{jk} &:= -\frac{1}{y_{sk}} \frac{\partial p_j}{\partial s} \left(s^\circ - \sum_{i=1}^3 \frac{1}{y_{si}} x_i, x_j \right) \text{ or} \\ b_{jk} &:= -\frac{1}{y_{rk}} \frac{\partial q_j}{\partial r} \left(r^\circ - \sum_{i=1}^3 \frac{1}{y_{si}} x_i, x_j \right) \text{ with } k \in \{1, 2, 3\}, k \neq j. \end{aligned}$$

The nullclines being :

$$\begin{aligned} \left(\mu_1 \left(s^\circ - \sum_{i=1}^3 \frac{1}{y_{si}} x_i, r^\circ - \sum_{i=1}^3 \frac{1}{y_{ri}} x_i, x_1 \right) - D \right) x_1 &= 0, \\ \left(\mu_2 \left(s^\circ - \sum_{i=1}^3 \frac{1}{y_{si}} x_i, r^\circ - \sum_{i=1}^3 \frac{1}{y_{ri}} x_i, x_2 \right) - D \right) x_2 &= 0, \\ \left(\mu_3 \left(s^\circ - \sum_{i=1}^3 \frac{1}{y_{si}} x_i, r^\circ - \sum_{i=1}^3 \frac{1}{y_{ri}} x_i, x_3 \right) - D \right) x_3 &= 0, \end{aligned}$$

we distinguish the following cases :

If $x_1 = x_2 = x_3 = 0$, the origin $E_0(0, 0, 0) \in X_2$ is an equilibrium point at which the jacobian matrix is :

$$J(E_0) = \begin{bmatrix} \mu_1(s^\circ, r^\circ, 0) - D & 0 & 0 \\ 0 & \mu_2(s^\circ, r^\circ, 0) - D & 0 \\ 0 & 0 & \mu_3(s^\circ, r^\circ, 0) - D \end{bmatrix}.$$

Since the eigenvalues are all positive, E_0 is unstable.

If $x_1 \neq 0$, $x_2 = x_3 = 0$, according to assumption H7, the nullcline

$$\mu_1 \left(s^\circ - \frac{1}{y_{s1}} x_1, r^\circ - \frac{1}{y_{r1}} x_1, x_1 \right) - D = 0,$$

has a unique solution $\tilde{x}_1$ in $]0, \min(y_{s1}s^\circ, y_{r1}r^\circ)[$. The jacobian matrix of the system (10) at the boundary equilibrium point $E_1(\tilde{x}_1, 0, 0) \in X_2$ is :

$$J(E_1) = \begin{bmatrix} \tilde{x}_1 \tilde{a}_1 & \tilde{x}_1 \tilde{b}_{12} & \tilde{x}_1 \tilde{b}_{13} \\ 0 & \tilde{\mu}_2 - D & 0 \\ 0 & 0 & \tilde{\mu}_3 - D \end{bmatrix},$$

where

$$\begin{aligned}\tilde{\mu}_j &:= \mu_j \left(s^\circ - \frac{1}{y_{s1}} \tilde{x}_1, r^\circ - \frac{1}{y_{r1}} \tilde{x}_1, 0 \right), \quad j \in \{2, 3\}, \\ \tilde{a}_1 &:= -\frac{1}{y_{s1}} \frac{\partial p_1}{\partial s} \left(s^\circ - \frac{1}{y_{s1}} \tilde{x}_1, \tilde{x}_1 \right) + \frac{\partial p_1}{\partial x_1} \left(s^\circ - \frac{1}{y_{s1}} \tilde{x}_1, \tilde{x}_1 \right) \text{ or} \\ \tilde{a}_1 &:= -\frac{1}{y_{r1}} \frac{\partial q_1}{\partial r} \left(r^\circ - \frac{1}{y_{r1}} \tilde{x}_1, \tilde{x}_1 \right) + \frac{\partial q_1}{\partial x_1} \left(r^\circ - \frac{1}{y_{r1}} \tilde{x}_1, \tilde{x}_1 \right), \\ \tilde{b}_{1k} &:= -\frac{1}{y_{sk}} \frac{\partial p_1}{\partial s} \left(s^\circ - \frac{1}{y_{s1}} \tilde{x}_1, \tilde{x}_1 \right) \text{ or} \\ \tilde{b}_{1k} &:= -\frac{1}{y_{rk}} \frac{\partial q_1}{\partial r} \left(r^\circ - \frac{1}{y_{r1}} \tilde{x}_1, \tilde{x}_1 \right), \quad k \in \{2, 3\}.\end{aligned}$$

The eigenvalues of $J(E_1)$ are $v_1^1 := \tilde{x}_1 \tilde{a}_1$, $v_2^1 := \tilde{\mu}_2 - D$ and $v_3^1 := \tilde{\mu}_3 - D$. The first one is negative according to H2, the others are positives according to H7. The equilibrium E_1 is then a saddle point. The stable separatrix lies on the x_1 -axis. The other two cases where either $x_2 \neq 0$ or $x_3 \neq 0$ is analogous and determines two other saddle points $E_2(0, \tilde{x}_2, 0)$ and $E_3(0, 0, \tilde{x}_3)$ in X_2 for which the stable separatrices are, respectively, the x_2 -axis and the x_3 -axis.

If $x_1 \neq 0$, $x_2 \neq 0$, $x_3 = 0$, the nontrivial nullclines are :

$$\begin{aligned}\mu_1 \left(s^\circ - \sum_{i=1}^2 \frac{1}{y_{si}} x_i, r^\circ - \sum_{i=1}^2 \frac{1}{y_{ri}} x_i, x_1 \right) - D &= 0, \\ \mu_2 \left(s^\circ - \sum_{i=1}^2 \frac{1}{y_{si}} x_i, r^\circ - \sum_{i=1}^2 \frac{1}{y_{ri}} x_i, x_2 \right) - D &= 0.\end{aligned}$$

In the proof of Theorem 3.4 we showed that the model (7) has a unique positive equilibrium which is globally asymptotically stable. Hence, the system (10) has an equilibrium point $E_{12}(\bar{x}_1, \bar{x}_2, 0)$ in X_2 , at which the jacobian matrix is :

$$J(E_{12}) = \begin{bmatrix} \bar{x}_1 \bar{a}_1 & \bar{x}_1 \bar{b}_{12} & \bar{x}_1 \bar{b}_{13} \\ \bar{x}_2 \bar{b}_{21} & \bar{x}_2 \bar{a}_2 & \bar{x}_2 \bar{b}_{23} \\ 0 & 0 & \bar{\mu}_3 - D \end{bmatrix},$$

where :

$$\begin{aligned}\bar{\mu}_j &:= \mu_j \left(s^\circ - \sum_{i=1}^2 \frac{1}{y_{si}} \bar{x}_i, r^\circ - \sum_{i=1}^2 \frac{1}{y_{ri}} \bar{x}_i, \bar{x}_j \right), \\ \bar{a}_j &:= -\frac{1}{y_{sj}} \frac{\partial p_j}{\partial s} \left(s^\circ - \sum_{i=1}^2 \frac{1}{y_{si}} \bar{x}_i, \bar{x}_j \right) + \frac{\partial p_j}{\partial x_j} \left(s^\circ - \sum_{i=1}^2 \frac{1}{y_{si}} \bar{x}_i, \bar{x}_j \right) \text{ or} \\ \bar{a}_j &:= -\frac{1}{y_{rj}} \frac{\partial q_j}{\partial r} \left(r^\circ - \sum_{i=1}^2 \frac{1}{y_{si}} \bar{x}_i, \bar{x}_j \right) + \frac{\partial q_j}{\partial x_j} \left(r^\circ - \sum_{i=1}^2 \frac{1}{y_{si}} \bar{x}_i, \bar{x}_j \right), \\ \bar{b}_{jk} &:= -\frac{1}{y_{sk}} \frac{\partial p_j}{\partial s} \left(s^\circ - \sum_{i=1}^2 \frac{1}{y_{si}} \bar{x}_i, \bar{x}_j \right) \text{ or} \\ \bar{b}_{jk} &:= -\frac{1}{y_{rk}} \frac{\partial q_j}{\partial r} \left(r^\circ - \sum_{i=1}^2 \frac{1}{y_{si}} \bar{x}_i, \bar{x}_j \right) \text{ with } k \in \{1, 2, 3\}, \quad k \neq j.\end{aligned}$$

The characteristic equation of $J(E_{12})$ is given by :

$$(\bar{\mu}_3 - D - v)(v^2 + Av + B) = 0,$$

where

$$\begin{aligned} A &:= -\bar{x}_1\bar{a}_1 - \bar{x}_2\bar{a}_2, \\ B &:= \bar{x}_1\bar{x}_2(\bar{a}_1\bar{a}_2 - \bar{b}_{12}\bar{b}_{21}). \end{aligned}$$

One has :

$$\begin{aligned} \bar{a}_1\bar{a}_2 - \bar{b}_{12}\bar{b}_{21} &= \frac{1}{y_{s1}y_{s2}} \frac{\partial p_1}{\partial s} \frac{\partial p_2}{\partial s} + \frac{\partial p_1}{\partial x_1} \frac{\partial p_2}{\partial x_2} - \frac{1}{y_{s1}} \frac{\partial p_1}{\partial s} \frac{\partial p_2}{\partial x_2} \\ &\quad - \frac{1}{y_{s2}} \frac{\partial p_2}{\partial s} \frac{\partial p_1}{\partial x_1} - \frac{1}{y_{s2}} \frac{\partial p_1}{\partial s} \frac{1}{y_{s1}} \frac{\partial p_2}{\partial s} > 0, \end{aligned}$$

or

$$\begin{aligned} \bar{a}_1\bar{a}_2 - \bar{b}_{12}\bar{b}_{21} &= \frac{1}{y_{r1}y_{r2}} \frac{\partial q_1}{\partial r} \frac{\partial q_2}{\partial r} + \frac{\partial q_1}{\partial x_1} \frac{\partial q_2}{\partial x_2} - \frac{1}{y_{r1}} \frac{\partial q_1}{\partial r} \frac{\partial q_2}{\partial x_2} \\ &\quad - \frac{1}{y_{r2}} \frac{\partial q_2}{\partial r} \frac{\partial q_1}{\partial x_1} - \frac{1}{y_{r2}} \frac{\partial q_1}{\partial r} \frac{1}{y_{r1}} \frac{\partial q_2}{\partial r} > 0. \end{aligned}$$

Hence, the coefficients A and B are positive. According to Routh Criterion (see for example [18]), the equation $v^2 + Av + B = 0$ has two eigenvalues with negative real parts. The persistence result of Theorem 2.5 implies that the other eigenvalue $\bar{\mu}_3 - D$ must be positive. Hence, E_{12} is a saddle point in X_2 . The stable manifold is the x_1x_2 -plane.

If $x_1 \neq 0$, $x_3 \neq 0$, $x_2 = 0$, or $x_2 \neq 0$, $x_3 \neq 0$, $x_1 = 0$, one obtains two other saddle points E_{13} and E_{23} in X_2 the stable manifolds of which are, respectively, the x_1x_3 -plane and the x_2x_3 -plane.

3. Thieme–Zhao’s conditions: Now, having the set of the equilibria of the system (10) in X , namely

$$M = \{E_0, E_1, E_2, E_3, E_{12}, E_{13}, E_{23}\},$$

we begin to show that the three hypotheses of Thieme–Zhao’s theorem ([19, 22], see also the Appendix) are verified.

Condition T1 : If $(x_1(0), x_2(0), x_3(0)) \neq E_0 \in M$, we distinguish the following cases :

If $x_1(0) \neq 0$, $x_2(0) = x_3(0) = 0$, since $x_i(t) \equiv 0$ for $i \in \{2, 3\}$, the system (10) simply becomes :

$$\dot{x}_1 = \left(\mu_1 \left(s^\circ - \frac{1}{y_{s1}}x_1, r^\circ - \frac{1}{y_{r1}}x_1, x_1 \right) - D \right) x_1.$$

It admits two equilibria, namely the origin which is clearly unstable and $\tilde{x}_1$ in $]0, \min(y_{s1}s^\circ, y_{r1}r^\circ)[$ for which the global asymptotic stability is obvious according to what precedes and corresponds to the point E_1 . The cases $x_1(0) = 0$, $x_2(0) \neq 0$, $x_3(0) = 0$ and $x_1(0) = 0$, $x_2(0) = 0$, $x_3(0) \neq 0$ are similar. It means that all solutions starting in X_2 stay in X_2 and converge to E_1, E_2 or E_3 .

If $x_1(0) \neq 0$, $x_2(0) \neq 0$, $x_3(0) = 0$, the system (10) becomes :

$$\begin{aligned}\dot{x}_1 &= \left(\mu_1 \left(s^\circ - \sum_{i=1}^2 \frac{1}{y_{si}} x_i, r^\circ - \sum_{i=1}^2 \frac{1}{y_{ri}} x_i, x_1 \right) - D \right) x_1, \\ \dot{x}_2 &= \left(\mu_2 \left(s^\circ - \sum_{i=1}^2 \frac{1}{y_{si}} x_i, r^\circ - \sum_{i=1}^2 \frac{1}{y_{ri}} x_i, x_2 \right) - D \right) x_2.\end{aligned}$$

In the proof of Theorem 3.4, we already showed that this system has a unique positive equilibrium point which is G.A.S. and denoted by $(\bar{x}_1, \bar{x}_2)$. Hence, the solutions of (10) such that $x_1(0) \neq 0$, $x_2(0) \neq 0$, $x_3(0) = 0$ converge to the corresponding equilibria $E_{12}(\bar{x}_1, \bar{x}_2, 0) \in M$. The cases $x_1(0) \neq 0$, $x_3(0) \neq 0$, $x_2(0) = 0$ and $x_2(0) \neq 0$, $x_3(0) \neq 0$, $x_1(0) = 0$ are analogous and the considered solutions converge, respectively, to E_{13} and E_{23} .

Condition T2 : The equilibrium points of M are hyperbolic. The origin is unstable, and the others are saddle points. Therefore, the singleton of each point of M is an isolated invariant set. Moreover, the persistence of the system (3) as showed in Sect. 2 means that the set M is a repeller for X_1 .

Condition T3 : Recall that the stable manifolds of E_0 , E_i ($i \in \{1, 2, 3\}$) and E_{ij} ($i, j \in \{1, 2, 3\}$ with $i < j$) are, respectively, $\{E_0\}$, the axes (Ox_i) and the planes $P_{ij} := \{(x_i, x_j) \in \mathbb{R}_+^2 : x_i \neq 0 \text{ and } x_j \neq 0\}$. Thus, the only chains occurring in X_2 are :

$$\begin{aligned}E_0 &\rightarrow E_i, \quad E_1 \rightarrow E_{12}, \quad E_2 \rightarrow E_{23}, \quad E_3 \rightarrow E_{13}, \\ E_0 &\rightarrow E_{ij}, \quad E_1 \rightarrow E_{13}, \quad E_2 \rightarrow E_{12}, \quad E_3 \rightarrow E_{23}.\end{aligned}$$

There is no cycle (closed chain) in X_2 . In virtue of Theorem [19] and [22], X_2 is a uniform repeller for X_1 . Actually, X_1 being a convex set, there exists at least an equilibrium point in X_1 . Hence, the system (10) is uniformly persistent. $\square$

5 Numerical simulations

We give some examples of a model of two and three microorganisms in competition on two complementary nutrients. First, the growth functions p_i , q_i are of Beddington–DeAngelis type, then we present a case where the growth functions are of the form $p_i(s)\theta_i(x_i)$, $q_i(s)\theta_i(x_i)$, where p_i and q_i are increasing and θ_i is decreasing¹. The parameters used in these examples do not necessarily have a biological meaning and the simulations are given just as an illustration of the result.

Simulation 1 Let the right-hand side functions of the model (5) be given by :

$$\begin{aligned}p_1(s, x_1) &= \frac{4s}{2x_1 + s + 2}, \quad q_1(r, x_1) = \frac{5r}{2x_1 + r + 1}, \\ p_2(s, x_2) &= \frac{5s}{x_2 + s + 2}, \quad q_2(r, x_2) = \frac{6r}{2x_2 + r + 4},\end{aligned}$$

while the parameters are $s^\circ = 10$, $r^\circ = 20$, $D = 1$, $y_{s1} = 2$, $y_{s2} = 3$, $y_{r1} = 1$ and $y_{r2} = 7$. One can check that the assumptions of the theorem are all satisfied. The numerical simulations have been performed with the use of Maple 18. In

¹ This multiplicative form is justified for example by Zwietering et al. [23].

Fig. 1 Eight trajectories of Simulation 1 in the space (x_1, x_2) with the initial data given in the text

Fig. 1, we represent eight trajectories with initial conditions $(s(0), r(0), x_1(0), x_2(0)) = (2.5, 3.5, 15, 25), (2.5, 3.5, 20, 10), (2.5, 3.5, 0.1, 15), (2.5, 3.5, 6, 27), (2.5, 3.5, 15, 0.1), (2.5, 3.5, 1.75, 0.1), (2.5, 3.5, 0.1, 0.1)$ and $(2.5, 3.5, 0.1, 30)$ in the phase space (x_1, x_2) . These numerical simulations show that the solutions converge to the positive equilibrium point, in accordance with the uniform persistence and the global asymptotic stability property of Theorems 3.3 and 3.4.

Simulation 2 We make the following choice of the functions and the parameters occurring in the model (8)

$$\begin{aligned} p_1(s, x_1) &= \frac{4s}{2x_1 + s + 2}, & q_1(r, x_1) &= \frac{5r}{2x_1 + r + 1}, \\ p_2(s, x_2) &= \frac{5s}{x_2 + s + 2}, & q_2(r, x_2) &= \frac{6r}{2x_2 + r + 4}, \\ p_3(s, x_3) &= \frac{4s}{x_3 + s + 2}, & q_3(r, x_3) &= \frac{7r}{x_3 + r + 2}, \end{aligned}$$

and $s^\circ = 30, r^\circ = 35, D = 1, y_{s_1} = 5, y_{s_2} = 8, y_{s_3} = 5, y_{r_1} = 8, y_{r_2} = 4$ and $y_{r_3} = 9$. Six trajectories are represented in Fig. 2, namely those with initial conditions $(s(0), r(0), x_1(0), x_2(0), x_3(0)) = (2.5, 3.5, 30, 85, 1), (2.5, 3.5, 30, 5, 80), (2.5, 3.5, 30, 30, 25), (2.5, 3.5, 0.5, 0.5, 0.5), (2.5, 3.5, 5, 30, 70)$ and $(2.5, 3.5, 10, 90, 30)$. The uniform persistence of the three species of microorganisms is confirmed, and the solutions seem to converge to a positive equilibrium point.

Simulation 3 Now, the right-hand side functions of (5) are given by :

$$\begin{aligned} p_1(s) &= \frac{4s}{2 + s}, & q_1(r) &= \frac{5r}{2 + r}, & \theta_1(x_1) &= \frac{1}{1 + 1.5x_1}, \\ p_2(s) &= \frac{5s}{1 + s}, & q_2(r) &= \frac{6r}{2 + r}, & \theta_2(x_2) &= \frac{1}{1 + 2x_2}, \end{aligned}$$

Fig. 2 Six trajectories of Simulation 2 in the space (x_1, x_2, x_3) with the initial data given in the text

Fig. 3 Eight trajectories of Simulation 3 in the space (x_1, x_2) with the initial data given in the text

with $s^\circ = 10$, $r^\circ = 20$, $D = 1$, $y_{s1} = 2$, $y_{s2} = 3$, $y_{r1} = 1$ and $y_{r2} = 7$. In Fig. 3, we represent eight trajectories with initial conditions $(s(0), r(0), x_1(0), x_2(0)) = (2.5, 3.5, 5, 5)$, $(2.5, 3.5, 5, 15)$, $(2.5, 3.5, 0.1, 15)$, $(2.5, 3.5, 2.5, 15)$, $(2.5, 3.5, 5, 0.1)$, $(2.5, 3.5, 1.75, 0.1)$, $(2.5, 3.5, 0.1, 0.1)$ and $(2.5, 3.5, 0.1, 6)$ in the phase space (x_1, x_2) .

Simulation 4 We consider the model (8) with the following functions :

$$\begin{aligned} p_1(s) &= \frac{4s}{2+s}, & q_1(r) &= \frac{5r}{2+r}, & \theta_1(x_1) &= \frac{1}{1+x_1}, \\ p_2(s) &= \frac{5s}{1+s}, & q_2(r) &= \frac{6r}{2+r}, & \theta_2(x_2) &= \frac{1}{1+x_2}, \\ p_3(s) &= \frac{4s}{1+s}, & q_3(r) &= \frac{7r}{1+r}, & \theta_3(x_3) &= \frac{1}{1+x_3}. \end{aligned}$$

Fig. 4 Six trajectories of Simulation 4 in the space (x_1, x_2, x_3) with the initial data given in the text

The numerical simulation is performed with the parameters $s^\circ = 30$, $r^\circ = 35$, $D = 1$, $y_{s1} = 5$, $y_{s2} = 8$, $y_{s3} = 5$, $y_{r1} = 8$, $y_{r2} = 4$ and $y_{r3} = 9$. Six trajectories are represented in Fig. 4, namely those with initial conditions $(s(0), r(0), x_1(0), x_2(0), x_3(0)) = (2.5, 3.5, 5, 0.5, 1)$, $(2.5, 3.5, 5, 5, 11)$, $(2.5, 3.5, 5, 1, 5)$, $(2.5, 3.5, 0.5, 15, 3)$, $(2.5, 3.5, 0.5, 5, 7)$ and $(2.5, 3.5, 0.5, 15, 10)$.

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A Appendix

Corollary A.1 (Hofbauer–Hutson theorem) [7] *Let $X \subseteq \mathbb{R}_+^n$ be closed, $F : X \rightarrow \mathbb{R}^n$ be locally Lipschitz and consider the ordinary differential system*

$$\dot{x} = F(x) \quad (11)$$

Assume that X is positively invariant for the system (12). Let S be a compact set and $P \in C(X, \mathbb{R}_+) \cap C^1(X \setminus S, \mathbb{R})$ be such that $P(x) = 0 \Leftrightarrow x \in S$. Moreover, suppose that there exist a lower semicontinuous function $\psi : X \rightarrow \mathbb{R}$, bounded below, and an $\alpha \in [0, 1]$ such that :

- (i) $\dot{P}(x) \geq [P(x)]^\alpha \psi(x) \forall x \in X \setminus S$,
- (ii) $\forall x \in \Sigma \sup_{T \geq 0} \int_0^T \psi(x(t)) dt > 0$,

where Σ denotes S or, whenever S is positively invariant, $\bar{\Omega}(S)$. Then S is a uniform repeller. By $\Omega(S)$ we denote the whole ω -limit of the orbits on S .

Theorem A.2 (Thieme–Zhao) [19, 22] *Let $X \subseteq \mathbb{R}_+^n$ be closed, $F : X \rightarrow \mathbb{R}^n$ be locally Lipschitz and consider the ordinary differential system*

$$\dot{x} = F(x) \quad (12)$$

Assume that X is positively invariant for the system (12) which is supposed to be dissipative on X . Let $X = X_1 \cup X_2$, $X_1 \cap X_2 = \emptyset$, with X_2 being a closed subset of $\mathbb{R}^n$ and X_1 positively invariant. Let M be a finite set of equilibria of (12) in X_2 . Assume that :

- T1. Every solution that starts in X_2 and stays in X_2 for all forward times converges to one of the equilibria in M ,
- T2. Every equilibrium in M is an isolated invariant set in X and a weak repeller for X_1 ,
- T3. M is acyclic in X_2 .

Then X_2 is a uniform strong repeller for X_1 . Moreover, if X_1 is convex, there exists at least one equilibrium point in X_1 .

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