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PERSISTENCE IN RATIO-DEPENDENT MODELS OF CONSUMER-RESOURCE DYNAMICS

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Abstract. In a recent work Cantrell, Cosner and Ruan show that intraspecific interference is responsible for coexistence of many consumers for one resource with a logistic like growth rate. Recently, we have established a similar result for the case of a chemostat using a rather different technique. In the present note, we complement these two works to the case of an unknown nonlinear growth rate for the resource satisfying mild assumptions.

1. Introduction

The classical model of a mixed culture in competition for a single substrate in a chemostat is given by the following equations (see [21, 20, 9]).

$$\begin{aligned} \dot{s} &= -\sum_{j=1}^{n} \frac{\mu_j(s)}{k_j} x_j + D(s_{in} - s)\,, \\ \dot{x}_i &= (\mu_i(s) - D)x_i\,. \quad (i = 1, \dots, n) \end{aligned} \tag{1.1}$$

The variables s and x_i are, respectively, the substrate and the i-th micro-organism concentrations. D is the dilution rate of the input flow of feed concentration s_{in}. The activity of the i-th micro-organism on the substrate is characterized by the growth function $\mu_i(\cdot)$ and the yield factor k_i. A typical instance of functions $\mu_i(\cdot)$ is given by the Monod law $\mu_i(s) = \overline{\mu_i}\frac{s}{s+K_i}$. In absence of competition, i.e. for a pure culture of species i, the condition of persistence is given by the inequality

$$\mu_i(s_{in}) > D\,. \tag{1.2}$$

The concentration of micro-organism β_i at equilibrium is then given by $\mu_i(\beta_i) = D$. For a mixed culture when condition (1.2) is fulfilled for any i, the "Competitive Exclusion Principle" states the following property: If there exists i^* such that $\beta_{i^*} < \beta_j$ for all $j \neq i^*$, then $x_j(t) \to 0$ as $t \to +\infty$, for any $j \neq i^*$, and $x_{i^*}(t) \to \beta_{i^*}$, as soon as $x_{i^*}(0) > 0$. This principle, originally proposed by Hardin in 1960 [12], has been proved mathematically under different kinds of hypotheses [16, 13, 2, 4, 18]. Although this principle has been validated on laboratory experiments [10], coexistence of several species is observed in complex or real world applications (such

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as continuously stirred bioreactors). Later on, several extensions of this model have been proposed in the literature, exhibiting the existence of a strictly positive asymptotically stable equilibrium. Among them, let us mention time-varying nutrient feed [22, 14, 11, 3], multi-resource models [17, 15] turbidity operating conditions [7] or crowding effects [6]. In [19], it is shown that the single consideration of an intra-specific dependency of the growth functions is enough to explain a possible coexistence in a chemostat. In [5], sufficient conditions ensuring coexistence for species described by systems of the form

$$\begin{aligned} \dot{s} &= rs(1-\frac{s}{K}) - \sum_{j=1}^{n} \frac{A_j s x_j}{1+B_j s + C_j x_j}\,, \\ \dot{x}_i &= \Big(-D + \frac{E_i s}{1+B_i s + C_i x_i}\Big) x_i \quad (i=1,\dots,n)\,, \end{aligned} \tag{1.3}$$

are given.

In [19], we have replaced in the basic model (1.1) the functions $\mu_i(s)$ by functions $h_i(s, x_i)$ which results in the system

$$\begin{aligned} \dot{s} &= -\sum_{j=1}^{n} \frac{h_j(s,x_j)}{k_j} x_j + D(s_{in} - s)\,, \\ \dot{x}_i &= (h_i(s,x_i) - D)x_i \quad (i=1,\dots,n)\,. \end{aligned} \tag{1.4}$$

We have imposed the following hypotheses.

- (A1) The functions $h_i(.,.)$ are C^1 with $\frac{\partial h_i}{\partial s}(., x_i) > 0$ and $\frac{\partial h_i}{\partial x_i}(s, .) < 0$ for $s > 0$, $h_i(0, .) = 0$.
- (A2) $h_i(s_{in}, 0) > D$.
- (A3) For any $s > 0$, $\lim_{x_i \to +\infty} h_i(s, x_i) = 0$.

For instance, h_i could be of the form $h_i(s, x_i) = \mu_i(s)g_i(x_i)$, where g_i is a decreasing positive function with $g_i(0) = 1$. These correction terms aim at taking into account that for a small concentration x_i the dynamics of the i-th species is close to the one in (1.1), while the intra-specific competition for food makes decreasing the effective growth for large density x_i.

In [5], the analytical forms of the growth rates are supposed to be known and in [19], the analytical form of the growth rate for s is supposed to be known. However, in practice determining an accurate expression for these growth rates is a difficult task. This motivates the present work. We replace the linear term $D(s_{in} - s)$ in (1.4) by a possibly nonlinear function $f(s)$ (possibly zero at zero) for which only a few data are available and determine two families of systems which describe ecosystems for which coexistence occur. In the first case we consider, we assume that the functions $x_i \to h_i(s, x_i)x_i$ are increasing and in the second case, we assume that the functions $x_i \to h_i(s, x_i)x_i$ are decreasing.

The paper is organized as follows. In Section 2, we present the family of systems we study. In Section 3, two technical lemmas are established. In Section 4, we analyze persistence in the case when the functions $x_i \to h_i(s, x_i)x_i$ are increasing. In Section 5, we analyze persistence in the case when the functions $x_i \to h_i(s, x_i)x_i$ are decreasing. Section 6 is devoted to illustrations of the main results. Concluding remarks are given in Section 7.

2. The system studied

Throughout the paper, we consider systems with the following structure

$$\begin{aligned}\dot{s} &= f(s) - \sum_{j=1}^{n} h_j(s, x_j)x_j \,, \\ \dot{x}_i &= (h_i(s, x_i) - d_i)x_i \quad (i = 1, \dots, n)\,.\end{aligned} \tag{2.1}$$

To simplify, we introduce the notation $x = (x_1, \dots, x_n)^\top$. All the constants d_i are positive. Without loss of generality, we have chosen to consider the case where each yield factor is equal to 1.

At last, we introduce the following assumptions:

- (B1) For any $i = 1, \dots, n$, the functions h_i are of class C^1 with $\frac{\partial h_i}{\partial s}(., x_i) > 0$.
- (B2) The function $f(\cdot)$ is of class C^1 and for some constant $\kappa > 0$, $f(l) > 0$ for all $l \in]0, \kappa)$ and $f(l) < 0$ for all $l > \kappa$.

3. Preliminary lemmas

In this section, we establish technical lemmas which are instrumental in establishing the main results of our paper.

Lemma 3.1. *Assume that the system* (2.1) *satisfies the assumptions (B1) and (B2). Consider any solution* $(s(t), x(t))$ *of the system* (2.1) *with initial condition* (s_0, x_0) *satisfying for* $i = 1, \dots, n$, $s_0 > 0, x_{i0} > 0$. *Then, for all* $t \geq 0$, *the solution* $(s(t), x(t))$ *exists and for* $i = 1, \dots, n$, $s(t) > 0, x_i(t) > 0$.

Proof. The properties of the x-subsystem of (2.1) ensure that the real-valued functions $x_i(t)$ cannot take nonpositive values. Assumption (B1) ensures that $h_i(0, \cdot) = 0$. One can deduce from these properties and the existence and uniqueness of the solutions of an ordinary differential equation with a C^1 vector field that $s(t)$ cannot take nonpositive values. We prove now that the solutions exist for all $t \geq 0$. Consider now the function

$$\Lambda = s + \sum_{j=1}^{n} x_j \,. \tag{3.1}$$

Then, for all $t \geq 0$, its derivative along the trajectories of (2.1) is

$$\dot{\Lambda}(t) = f(s(t)) - \sum_{j=1}^{n} d_j x_j(t)\,. \tag{3.2}$$

Assumption (B2) ensures that $\max_{s \geq 0}\{f(s)\}$ is a finite positive real number. Moreover, for all $t \geq 0$, the term $-\sum_{j=1}^{n} d_j x_j(t)$ is nonpositive. Therefore, for all $t \geq 0$, the inequality

$$\dot{\Lambda}(t) \leq \max_{s \geq 0}\{f(s)\} \tag{3.3}$$

is satisfied. It follows that $\Lambda(t)$ is bounded on any finite interval $[0, A]$. This fact and the sign property of $s(t)$ and the $x_i(t)$'s imply that the finite escape time phenomenon does not occur and thereby the solutions are defined on $[0, +\infty)$. $\square$

Lemma 3.2. *Assume that the system* (2.1) *satisfies the assumptions (B1) and (B2). Let* ν *be a positive real number. Consider any solution* $(s(t), x(t))$ *of the system* (2.1) *with initial condition* (s_0, x_0) *satisfying, for* $i = 1, \dots, n$, $s_0 > 0, x_{i0} > 0$. *Then there exists* $T_1 \geq 0$ *such that, for all* $t \geq T_1$, $s(t) \leq \kappa + \nu$.

Proof. For all $t \geq 0$, the term $-\sum_{j=1}^{n} h_j(s(t), x_j(t))x_j(t)$ is nonpositive. We deduce that, for all $t \geq 0$,

$$\dot{s}(t) \leq f(s(t)) . \tag{3.4}$$

From Assumption (B2), it follows readily that there exists $T_1 \geq 0$ such that, for all $t \geq T_1$, $s(t) \leq \kappa + \nu$. □

4. First case of persistence

This section is devoted to the case when the functions $x_i \to h_i(s, x_i)x_i$ are increasing. We introduce extra assumptions

(C1) There exist two real numbers $\gamma > 0$ and $p \in (0, 1]$ such that, for all $s > 0, x_j > 0$,

$$h_j(s, x_j) \leq \frac{\gamma s}{(1 + x_j)^p(1 + s)} , \tag{4.1}$$

$$\gamma > \max_{i=1,\dots,n} \{\frac{d_i}{2}\} . \tag{4.2}$$

(C2) The function f is such that there exist $\varepsilon > 0$ and $D > 0$ such that

$$f(s) - \gamma \sum_{i=1}^{n} \left[\left(\frac{2\gamma}{d_i}\right)^{1/p} - 1\right]^{1-p} \frac{s}{1+s} > \varepsilon s , \quad \forall s \in [0, D] . \tag{4.3}$$

(C3) For each $i = 1, \dots, n$, the inequality $h_i(D, 0) > d_i$ is satisfied.

Remark. Observe that if f belongs to the family $f(s) = rs(1 - \frac{s}{K})$ (resp. to the family $f(s) = D(s_{in} - s)$), one can determine families of parameters K, r (resp. families of parameters D, s_{in}) such that the corresponding functions f satisfies (4.3).

We are ready to state the main result of this section.

Theorem 4.1. *Assume that the system* (2.1) *satisfies Assumptions (B1), (B2) and (C1)–(C3). Consider any solution of* (2.1) *with initial condition* (s_0, x_0) *satisfying for* $i = 1, \dots, n$, $s_0 > 0, x_{i0} > 0$. *Then, for* $i = 1, \dots, n$,

$$\inf_{t \in [0,+\infty)} x_i(t) > 0 . \tag{4.4}$$

Proof. According to Lemma 3.1, for all $t \geq 0$, the solution $(s(t), x(t))$ exists and for $i = 1, \dots, n$, $s(t) > 0, x_i(t) > 0$. These inequalities and Assumption (C1) imply that, for $i = 1, \dots, n$, and for all $t \geq 0$,

$$\dot{x}_i(t) \leq \Big[\frac{\gamma s(t)}{(1 + x_i(t))^p(1 + s(t))} - d_i\Big]x_i(t) \leq \Big[\frac{\gamma}{(1 + x_i(t))^p} - d_i\Big]x_i(t) . \tag{4.5}$$

Observe that the inequality

$$\frac{\gamma}{(1 + x_i)^p} \leq \frac{d_i}{2} \tag{4.6}$$

is equivalent to

$$x_i \geq \Big(\frac{2\gamma}{d_i}\Big)^{1/p} - 1 . \tag{4.7}$$

Therefore,

$$\dot{x}_i(t) \leq -\frac{1}{2}d_i x_i(t) \quad \text{whenever} \quad x_i(t) \geq \Big(\frac{2\gamma}{d_i}\Big)^{1/p} - 1 . \tag{4.8}$$

Since Assumption (C1) ensures that, for any $i = 1, \dots, n$, $(\frac{2\gamma}{d_i})^{1/p} - 1 > 0$, one can deduce that there exists $T_1 \geq 0$ such that, for all $t \geq T_1$, the inequality

$$x_i(t) < \Big(\frac{2\gamma}{d_i}\Big)^{1/p} - 1 \tag{4.9}$$

is satisfied. On the other hand, Assumption (C1) implies that, for all $t \geq 0$,

$$\begin{aligned} \dot{s}(t) &\geq f(s(t)) - \gamma \sum_{j=1}^{n} \frac{s(t)}{(1 + x_j(t))^p (1 + s(t))} x_j(t)\,, \\ &\geq f(s(t)) - \gamma \frac{s(t)}{1 + s(t)} \sum_{j=1}^{n} x_j(t)^{1-p}\,. \end{aligned} \tag{4.10}$$

Combining (4.9) and (4.10), we obtain

$$\dot{s}(t) \geq f(s(t)) - \gamma \frac{s(t)}{1 + s(t)} \sum_{j=1}^{n} \Big[\Big(\frac{2\gamma}{d_i}\Big)^{1/p} - 1\Big]^{1-p}\,. \tag{4.11}$$

From Assumption (C2), we deduce that,

$$\dot{s}(t) > \varepsilon s(t)\,, \quad \text{whenever} \quad s(t) \in (0, D]\,. \tag{4.12}$$

Since $s(t) > 0$ for all $t \geq 0$, we deduce that there exists $T_2 \geq T_1$ such that, for all $t \geq T_2$,

$$s(t) > D \tag{4.13}$$

According to Assumption (B1), the functions h_i are increasing with respect to s. It follows that for all $t \geq T_2$,

$$\dot{x}_i(t) \geq (h_i(D, x_i(t)) - d_i) x_i(t) \quad (i = 1, \dots, n)\,. \tag{4.14}$$

Since each function h_i is continuous, there exist $\delta_1 > 0$ and $\delta_2 > 0$ such that, for all $i = 1, \dots, n$,

$$h_i(D, x_i) - d_i \geq \delta_2\,, \quad \forall x_i \in [0, \delta_1]\,. \tag{4.15}$$

We deduce easily that there exists $T_3 \geq T_2$ such that, for all $i = 1, \dots, n$, and for all $t \geq T_3$,

$$x_i(t) \geq \frac{1}{2}\delta_1\,. \tag{4.16}$$

This concludes the proof. □

5. Second case of persistence

This section is devoted to the case when the functions $x_i \to h_i(s, x_i)x_i$ are decreasing. We introduce extra assumptions:

- (D1) For each $i = 1, \dots, n$, the function $x_i \to h_i(s, x_i)x_i$ is decreasing.
- (D2) For any $i = 1, \dots, n$, the function h_i is such that, for any fixed $s \geq 0$, $\lim_{x_i \to +\infty} h_i(s, x_i) = 0$.
- (D3) The function f is such that, $f(0) > 0$.

We assume that (B2) and (D3) are satisfied by the system (2.1). Then one can determine a positive real number $s_{in} > 0$ and two arbitrarily small positive real numbers $\nu_1 > 0$ and $\nu_2 > 0$ such that

$$D(s_{in} - l) < f(l)\,, \quad \forall l \in [0, \kappa + \nu_2] \tag{5.1}$$

with $D = \max_{i=1,\dots,n}\{d_i\} + \nu_1$. Consider now the system

$$\begin{aligned} \dot u &= D(s_{in} - u) - \sum_{j=1}^{n} h_j(u, y_j) y_j \,, \\ \dot y_i &= (h_i(u, y_i) - D) y_i \quad (i = 1, \dots, n)\,, \end{aligned} \tag{5.2}$$

and introduce the assumption:

(D4) The system (5.2) satisfies the assumptions (A1)–(A3).

We are ready to state the main result of this section.

Theorem 5.1. *Assume that the system* (2.1) *satisfies the assumptions (B1), (B2) and (D1) to (D4). Let* (s_0, x_0) *be initial conditions of* (2.1) *such that for* $i = 1, \dots, n$, $s_0 > 0, x_{i0} > 0$. *Then, for* $i = 1, \dots, n$,

$$\inf_{t \in [0,+\infty)} x_i(t) > 0\,. \tag{5.3}$$

Proof. Consider a solution $(s(t), x(t))$ of (2.1) with an initial condition (x_0, x_0) satisfying, for all $i = 1, \dots, n$, $x_0 > 0$, $x_{i0} > 0$. From Lemma 3.2, we deduce that, without loss of generality, we may assume that $s_0 \le \kappa + \nu_2$ and therefore $s(t) \le \kappa + \nu_2$ for all $t \ge 0$. We select the trajectory of (5.2) with initial condition $u_0 = \frac{s_0}{2}, y_{i0} = \frac{x_{i0}}{2}$. Let us prove that, for such a choice, for all $t \ge 0$, the inequalities

$$u(t) < s(t)\,, \quad y_i(t) < x_i(t)\,, \quad (i = 1, \dots, n)\,, \tag{5.4}$$

are satisfied. To prove this result, we proceed by contradiction. We distinguish between the two cases which necessarily occur if (5.4) is not satisfied.

First case. Assume that there exists $t_\alpha > 0$ such that $s(t_\alpha) = u(t_\alpha)$ and for all $t \in [0, t_\alpha)$, $s(t) > u(t), x_i(t) > y_i(t)$. Then

$$\begin{aligned} \dot s(t_\alpha) &= f(s(t_\alpha)) - \sum_{j=1}^{n} h_j(s(t_\alpha), x_j(t_\alpha)) x_j(t_\alpha) \\ &= f(u(t_\alpha)) - \sum_{j=1}^{n} h_j(u(t_\alpha), x_j(t_\alpha)) x_j(t_\alpha)\,. \end{aligned} \tag{5.5}$$

Thanks to Assumption (D1), we obtain

$$\dot s(t_\alpha) \ge f(u(t_\alpha)) - \sum_{j=1}^{n} h_j(u(t_\alpha), y_j(t_\alpha)) y_j(t_\alpha)\,. \tag{5.6}$$

We know that $s(t) \le \kappa + \nu_2$ for all $t \ge 0$. This property and (5.1) imply that

$$\dot s(t_\alpha) > D(s_{in} - u(t_\alpha)) - \sum_{j=1}^{n} h_j(u(t_\alpha), y_j(t_\alpha)) y_j(t_\alpha) = \dot u(t_\alpha)\,. \tag{5.7}$$

It follows that there exists $\xi > 0$ such that $s(t) < u(t)$ for all $t \in [t_\alpha - \xi, t_\alpha)$. This yields a contradiction.

Second case. Assume that there exist $t_\alpha > 0$ and $j \in \{1, \dots, n\}$ such that $x_j(t_\alpha) = y_j(t_\alpha)$ and, for all $t \in [0, t_\alpha)$, $s(t) > u(t)$, $x_i(t) > y_i(t)$ and $s(t_\alpha) > u(t_\alpha)$. Then

$$\begin{aligned} \dot x_j(t_\alpha) &= (h_j(s(t_\alpha), x_j(t_\alpha)) - d_j) x_j(t_\alpha) \\ &= (h_j(s(t_\alpha), y_j(t_\alpha)) - d_j) y_j(t_\alpha)\,. \end{aligned} \tag{5.8}$$

The function $s \to h_j(s, x_j)$ is increasing and $s(t_\alpha) > u(t_\alpha)$. These properties and the definition of D imply

$$\begin{aligned} \dot{x}_j(t_\alpha) &> (h_j(u(t_\alpha), y_j(t_\alpha)) - d_j)y_j(t_\alpha) \\ &> (h_j(u(t_\alpha), y_j(t_\alpha)) - D)y_j(t_\alpha) = \dot{y}_j(t_\alpha)\,. \end{aligned} \tag{5.9}$$

The reasoning used in the previous case leads again to a contradiction. Therefore (5.4) is satisfied.

The system (5.2) satisfies the Assumptions (A1)–(A3). Therefore, according to [19], there exist constants $y_i^* > 0$ such that

$$\lim_{t \to +\infty} y_i(t) = y_i^* \quad (i = 1, \dots, n)\,. \tag{5.10}$$

Combining (5.8) and (5.4), it straightforwardly follows that (5.3) is satisfied. This concludes the proof. $\square$

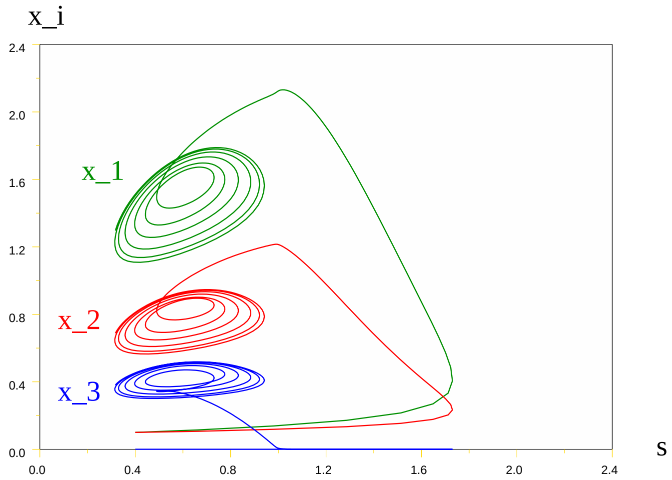

FIGURE 1. Species w.r.t. substrate concentrations in Example 6.1.

6. ILLUSTRATION

In this part, we illustrate our main results via two simple systems whose stability property can be established by applying respectively Theorem 4.1 and Theorem 5.1.

Example 6.1. We first consider a system with three species, where $f(\cdot)$ is a logistic function and the functions $h_i(\cdot)$ are of Mickaelis-Menten form. One can readily check that the system with the following characteristics

$$
\begin{aligned}
f(s) &= 2s\big(1-\frac{s}{2}\big),\\
h_1(s,x_1) &= \frac{7}{5}\frac{s}{(1+s/2)(1+x_1)}, \quad d_1 = 0.3\,,\\
h_2(s,x_2) &= \frac{6}{5}\frac{s}{(1+s/2)(1+x_2)}, \quad d_2 = 0.3\,,\\
h_3(s,x_3) &= \frac{s}{(1+s/2)(1+x_3)}, \quad d_3 = 0.3\,,
\end{aligned}
\tag{6.1}
$$

satisfies assumptions (B1), (B2) and (C1) to (C3). Simulations are depicted on Figure 1. In place of plotting the x_i's against the time, we plotted on the same plane all the x_i's against s. Notice that this is no longer a "phase portrait" but the superposition of projections on the (s,x_i) planes. Different color is used for each projection. Simulations show that the solutions converge to a positive limit-cycle, in accordance with the persistence property proved by Theorem 4.1.

Example 6.2. We consider now a system with two species, where $f(\cdot)$ is no longer concave and the functions $h_i(\cdot)$ have ratio-dependant terms. One can readily check that the following functions

$$
\begin{aligned}
f(s) &= \frac{3}{10} + \frac{4}{5}s^2\big(1-\frac{s}{5}\big),\\
h_1(s,x_1) &= \frac{s/x_1}{1/2+s+x_1}, \quad d_1 = \frac{1}{2}\,,\\
h_2(s,x_2) &= \frac{3}{2}\frac{s/x_2}{1+s+x_2/2}, \quad d_2 = \frac{1}{5}\,,
\end{aligned}
\tag{6.2}
$$

satisfy Assumptions (B1), (B2) and (D1) to (D4). Of course, the relevance of such models from a biological point of view need to be investigated deeper. Simulations are depicted on Figure 2, using a "multi-phase" representation. It shows that the solutions converge to one of two positive equilibria, in accordance with the persistence property proved by Theorem 5.1.

7. Conclusion

We established persistence for broad families of models of a mixed culture in competition for a single substrate when there is intra-specific competition. We modelized intra-specific competition by replacing the usual growth functions (also called uptake functions) by growth functions which depend on the substrate and the micro-organism concentrations. Our main results are general in the sense that they apply to systems whose functions do not belong to any specific family of functions like, for instance, linear, or logistic, or Monod functions and different from those obtained in [19], [8], where, for more restictive families of systems, existence and global attractivity of an equilibrium point where all the species are present is established.

Our work complements the literature devoted to the problem of understanding coexistence of species in situations where the classical "competitive exclusion principle", which predicts extinction, does not hold.

In particular, our work owes a great deal to the pioneer paper [2], where Armstrong and McGehee made the important observation that, even in the absence

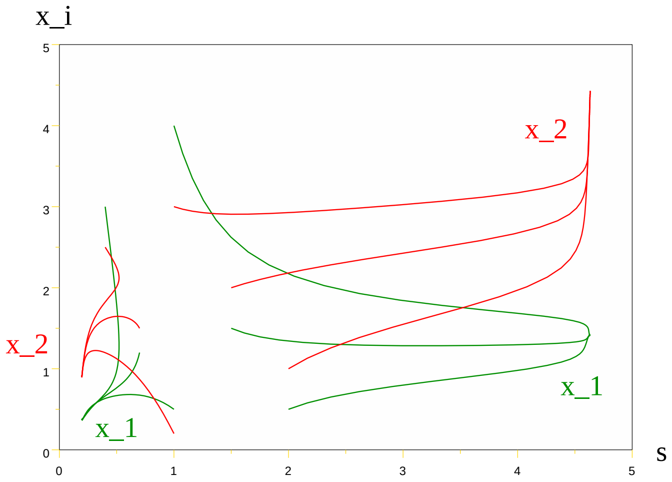

FIGURE 2. Species w.r.t. substrate concentrations in Example 6.2.

of a locally stable equilibrium point i.e. of an equilibrium point corresponding to a case where all the species are present, coexistence may occur, due to sustained oscillations, and exhibited systems which indeed admit non-trivial limit cycles. It also owes a great deal (and perhaps even more) to the notion of ratio-dependency introduced by Arditi and Ginzburg in [1], in a slightly different context. This notion arises from the fact that in the case of a one consumer-one resource relation, a model with ratio-dependent growth function i.e. where the growth function depends on the ratio of the resource density by the consumer density, is frequently a better model than the traditional one.

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