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EFFECT ON PERSISTENCE OF INTRA-SPECIFIC COMPETITION IN COMPETITION MODELS

CLAUDE LOBRY, FRÉDÉRIC MAZENC

Abstract. An ecological model describing the competition for a single substrate of an arbitrary number of species is considered. The mortality rates of the species are not supposed to have all the same value and the growth function of the substrate is not supposed to be linear or decreasing. Intra-specific competion is taken into account. Under additional technical assumptions, we establish that the model admits a globally asymptotically stable positive equilibrium point. This ensures persistence of the species. Our proof relies on a Lyapunov function.

1. Introduction

Current research efforts focus on the analysis of the solutions of models of chemostats with several species competing for one growth-limiting nutrient and undergoing an extra competition, which results from the difficulty of access to the substrate encountered by the micro-organisms. These models belong to a general class of systems of the form

$$\left\{\begin{array}{rcl} \dot{s} & = & f(s) - \displaystyle\sum_{i=1}^{n} \frac{h_i(s,x)}{Y_i} x_i, \\ \dot{x}_1 & = & \left[h_1(s,x) - d_1\right] x_1, \\ & \vdots & \\ \dot{x}_n & = & \left[h_n(s,x) - d_n\right] x_n, \end{array}\right. \tag{1.1}$$

evolving on $E = (0,+\infty)^{n+1}$. In these systems, s is the concentration of the nutrient, the x_i's are the concentrations of species of organisms, $x = (x_1, ..., x_n)^\top$ and the Y_i's are positive constants called yield coefficients. The functions h_i satisfy $h_i(0,x) = 0$ for all x because, no growth of the species is possible in the absence of substrate. In addition, the functions h_i are increasing with respect to s and decreasing with respect to each component x_j of the vector x to take into account the fact that the more there are micro-organisms, the more difficult is their access to the nutrient.

Recent works ([7], [11], [14], [12]) are devoted to stability analysis problems for (1.1) in the particular case where the functions h_i depend only on s and x_i. This property expresses the so-called intra-specific competition: the strongest the concentration of a species is, the smallest is its growth. In other words, the access of

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a micro-organism to the nutrient is supposed be hampered only by the presence of micro-organisms of its own species. The phenomenon of intra-specific competition can be explained by the flocculation process, which is of major importance in wastewater treatment plants: the presence of flocks limits the access of the biomass to the substrate. In [3] an effective way to include flocculation in existing models of chemostats, is proposed. It is shown that under certain conditions, this leads to density-dependent growth functions of the form $h_i(s, x_i)$. This establishes the link between the limited access to the substrate inside the flocks, and the growth characteristics of the biomass on the level of the bioreactor.

The works [7] and [11] present a study of the systems (1.1) in the particular case where only intra-specific competition occurs, where f is a linear function of the form $f(s) = D(s_{in} - s)$ and where the mortality can be neglected, which corresponds to the case where $d_1 = ... = d_n = D$. The main message conveyed by these works is that intra-specific competition may lead to the existence of a globally asymptotically stable positive equilibrium point and therefore can explain coexistence of the species. Hence, these works complement the literature (see for instance [2], [5], [4], [6]) devoted to the problem of explaining why coexistence is observed in real-world applications, in spite of the prediction of the Competitive Exclusion Principle, which, generally speaking, claims that when there is a single nutrient, asymptotically only one species survives and the others tend to extinction.

However, in more complex ecological contexts, the growth of the substrate is not linear, not necessarily decreasing, and the mortality terms cannot be neglected. First attempts to cope with the corresponding models are made in [9] and [14]. In [9], for a general model of chemostat with two species which takes into account intra-specific effects, the persitence of the two species is established. The technique of proof is based on a comparison principle. In [14], it is shown that a general system (1.1) with different removal rates d_i admits a globally asymptotically stable positive equilibrium point, provided that only intra-specific competition occurs and f is decreasing and its decay is sufficiently fast. The main advantage of this result is that it applies to systems (1.1) for which no explicit expression for the growth functions f and h_i is available. However, numerical simulations suggest that the stability property holds even when f is not decreasing.

The objective of the present paper is to show that when f belongs to a family of functions which contains functions which have a positive, but small, first derivative and when the growth functions $h_i(s, x_i)$ admit a decomposition of the form $h_i(s, x_i) = \mu_i(s)\theta_i(x_i)$ where the functions θ_i are decreasing and where the functions μ_i belong to a family slightly larger than the family of the Michaelis-Menten functions, then global asymptotic stability of a positive equilibrium point can be established. Our technique of proof relies on a Lyapunov approach which is significantly different from the one used in [14] but is reminiscent of the one presented first in [8] and is incorporated in [16, Chapter 2]. This Lyapunov function allows to prove the Competitive Exclusion Principle in the particular case where the growth functions are $f(s) = D(s_{in} - s)$ and $h_i(s, x_i) = \mu_i(s) = \frac{K_i s}{L_i + s}$ and there are different removal rates d_i. The fact that the functions μ_i are of the Michaelis-Menten (or Monod) type is crucial in this Lyapunov approach. For general growth functions and distinct removal rates d_i, the Lyapunov function approach of [8] does not apply and the problem of proving the Competitive Exclusion Principle in that case is still open. To understand the difficulty of this problem, it is worth reading for instance the papers [17], [10], [18] where, through elegant and sophisticated proofs, partial solutions to this problem are established, in more general context.

Observe that, in contrast to the Lyapunov function proposed in [8], the Lyapunov function we exhibit is a strict Lyapunov function i.e. its derivative along the trajectories of the system is a negative definite function of the state variables. This property makes it possible to quantify the effect of disturbances or error of modeling (as illustrated for instance by [1], [15], [13]). In particular, it follows that the stability result we will establish still holds when, instead of being Michaelis-Menten functions, the growth functions are "almost" Michaelis-Menten functions, in a sense which can be made precise by means of the Lyapunov function. Finally, we wish to point out that we conjecture that the global stability result we will establish can be extended to systems with general growth functions, but we also presume that proving this extension is as difficult as proving the general version of the Competitive Exclusion Principle.

The paper is organized as follows. In Section 2, we introduce the family of systems we study as long as basic assumptions, accompanied with preliminary results. The main result is stated and proved in Section 3. Section 4 is dedicated to simple particular cases.

2. System description, preliminary results and comments

2.1. **Preliminaries.** • Throughout the paper, the functions are supposed to be of class C^1.

• The arguments of the functions will be omitted or simplified whenever no confusion can arise from the context.

• Consider a differential equation

$$\dot{x} = F(x) \tag{2.1}$$

with $x \in R^p$ where F is continuously differentiable on R^p. An equilibrium point of this system is called positive equilibrium point if all its components are positive.

Let G_c be closed and positively invariant for (2.1) and let us assume that the origin is an equilibrium point of (2.1). A function V is called a Lyapunov function for (2.1) on an open set $G \subset G_c$ if

(i) V is continuously differentiable on G,

(ii) For each $\overline{x} \in \overline{G}$, the closure of G, the limit $\lim\limits_{\substack{x \to \overline{x} \\ x \in G}} V(x)$ exists as either a real number or $+\infty$,

(iii) $\frac{\partial V}{\partial x}(x)F(x) \leq 0$ on G.

(iv) A function V is called a strict Lyapunov function for (2.1) if $\frac{\partial V}{\partial x}(x)F(x) < 0$ for all $x \in G$, $x \neq 0$.

(v) A function V is said to be proper if for each $x_b \in \overline{G} \backslash G$, the boundary of G, $\lim\limits_{\substack{x \to x_b \\ x \in G}} V(x) = +\infty$.

2.2. **The Model and the Basic assumptions.** We consider the system

$$\begin{cases} \dot{s} &= f(s) - \sum_{i=1}^{n} \mu_i(s)\theta_i(x_i)x_i, \\ \dot{x}_1 &= [\mu_1(s)\theta_1(x_1) - d_1]\, x_1, \\ &\vdots \\ \dot{x}_n &= [\mu_n(s)\theta_n(x_n) - d_n]\, x_n, \end{cases} \tag{2.2}$$

evolving on the state domain $D_f = [0, +\infty) \times [0, +\infty) \times ... \times [0, +\infty)$ where the d_i are positive constants.

We introduce the assumptions:

H1: The function f is such that $f(0) \geq 0$.

H2: The functions $\theta_i(x_i)$ are positive, decreasing and $\theta_i(0) = 1$. The functions $\theta_i(x_i)x_i$ are increasing.

H3: There exists $(s_*, x_{1*}, ..., x_{n*}) \in (0, s_{in}) \times (0, +\infty) \times ... \times (0, +\infty)$ such that

$$f(s_*) = \sum_{j=1}^{n} d_j x_{j*} \tag{2.3}$$

and, for all $i \in \{1, ..., n\}$,

$$\mu_i(s_*)\theta_i(x_{i*}) = d_i \ . \tag{2.4}$$

H4: The functions μ_i are bounded, zero at zero, increasing and $\mu_i'(0) > 0$. There is a positive function Ω and positive constants c_i such that, for all $i \in \{1, ..., n\}$,

$$c_i \frac{\mu_i(s_*)}{\mu_i'(0)s_*} = \Omega(0) \tag{2.5}$$

and, for all $s > 0$, $s \neq s_*$,

$$c_i \frac{s}{\mu_i(s)} \frac{\mu_i(s) - \mu_i(s_*)}{s - s_*} = \Omega(s) \ . \tag{2.6}$$

Discussion of the assumptions

- Assumption H1 ensures that the domain D_f is positively invariant.
- In the system (2.2) the yield coefficients are equal to 1. Without loss of generality, this assumption can be made because these parameters can be eliminated by a simple linear change of coordinates.
- The function $f(s) = D(s_{in} - s)$ (which is present in models of chemostats) satisfies Assumption H1.
- Observe that the requirement (2.6) is equivalent to

$$\mu_i(s) = \frac{c_i \mu_i(s_*) s}{c_i s + (s_* - s)\Omega(s)} \ . \tag{2.7}$$

We shall see in Section 4.1 that this requirement is satisfied in the particular case where the functions μ_i are of Monod type. Moreover, observe that the function Ω is continuous on $[0, +\infty)$.

- The functions θ_i express the intra-specific competition: the growth of a species is inhibited by its own concentration. Assuming that the functions $\theta_i(x_i)x_i$ are increasing is relevant from a biological point of view.
- Assumption H3 is not restrictive: if a positive equilibrium point exists, then necessarily this assumption is satisfied.

2.3. **Equilibrium point.** Under the assumptions we have introduced, we can easily establish the existence and unicity of a positive equilibrium point for the system (2.2):

Lemma 2.1. *Assume that the system (2.2) satisfies Assumptions H1 to H4. Then the point $E = (s_*, x_{1*}, ..., x_{n*})$ is a positive equilibrium point.*

Proof. From Assumption H3, it follows that E is a positive equilibrium point of the system (2.2).

Lemma 2.1 allows us to introduce the assumption:

H5: The function

$$\Gamma(s) = -\frac{f(s) - f(s_*) + \sum_{i=1}^{n}[\mu_i(s_*) - \mu_i(s)]\theta_i(x_{i*})x_{i*}}{s - s_*} \tag{2.8}$$

is positive.

Remark. One can check that Assumption H5, in combination with Assumption H2 and the fact that the functions μ_i are increasing ensures that the system (2.2) admits only one positive equilibrium point.

3. Main result

In this section, we state and prove the main result of the work.

Theorem 3.1. *Assume that the system (2.2) satisfies Assumptions H1 to H5. Then the positive equilibrium $E = (s_*, x_{1*}, ..., x_{n*})$ is a globally asymptotically and a locally exponentially stable equilibrium point of the system (2.2) on $D_o = (0, +\infty) \times (0, +\infty) \times ... \times (0, +\infty)$.*

3.1. Proof of Theorem 3.1.

3.1.1. *Attractive invariant domain.*

Lemma 3.2. *The domains D_f and D_o are a positively invariant domains.*

Proof. The sign properties of the function f and the fact that each function μ_i is zero at zero imply that D_f and D_o are a positively invariant domains.

3.1.2. *Lyapunov construction.* Let us use the variables $\tilde{s} = s - s_*$, $\tilde{x}_i = x_i - x_i^*$. Then from Lemma 2.1, we deduce that

$$\begin{cases} \dot{\tilde{s}} &= f(s) - f(s_*) - \sum_{i=1}^{n} \mu_i(s)\theta_i(x_i)x_i + \sum_{i=1}^{n} \mu_i(s_*)\theta_i(x_{i*})x_{i*}, \\ \dot{\tilde{x}}_1 &= [\mu_1(s)\theta_1(x_1) - \mu_1(s_*)\theta_1(x_{1*})]\, x_1, \\ &\vdots \\ \dot{\tilde{x}}_n &= [\mu_n(s)\theta_n(x_{n*}) - \mu_n(s_*)\theta_n(x_{n*})]\, x_n. \end{cases} \tag{3.1}$$

From the definition of Γ in (2.8) and the equality

$$\begin{aligned} \mu_i(s)\theta_i(x_i) - \mu_i(s_*)\theta_i(x_{i*}) &= \mu_i(s_*)[\theta_i(x_i) - \theta_i(x_{i*})] \\ &\quad +[\mu_i(s) - \mu_i(s_*)]\theta_i(x_i) \end{aligned} \tag{3.2}$$

it follows that

$$\begin{cases} \frac{\dot{\tilde{s}}}{s} &= \frac{-\Gamma(s)\tilde{s}}{s} + \sum_{i=1}^{n} \frac{\mu_i(s)}{s}[\theta_i(x_{i*})x_{i*} - \theta_i(x_i)x_i], \\ \frac{\dot{\tilde{x}}_1}{x_1} &= \mu_1(s_*)[\theta_1(x_1) - \theta_1(x_{1*})] + [\mu_1(s) - \mu_1(s_*)]\theta_1(x_1), \\ &\vdots \\ \frac{\dot{\tilde{x}}_n}{x_n} &= \mu_n(s_*)[\theta_n(x_n) - \theta_n(x_{n*})] + [\mu_n(s) - \mu_n(s_*)]\theta_n(x_n). \end{cases} \tag{3.3}$$

Let us introduce simplifying notations:

$$\alpha_i(x_i) = -\mu_i(s_*)\frac{\theta_i(x_i) - \theta_i(x_{i*})}{x_i - x_{i*}}\ ,\ \beta_i(x_i) = \frac{\theta_i(x_i)x_i - \theta_i(x_{i*})x_{i*}}{x_i - x_{i*}}\ . \tag{3.4}$$

Assumption H2 ensures that the functions α_i and β_i are positive. The system (3.3) rewrites

$$\begin{cases} \frac{\dot{\tilde{s}}}{s} &= \frac{-\Gamma(s)\tilde{s}}{s} - \sum_{i=1}^{n} \frac{\mu_i(s)}{s}\beta_i(x_i)\tilde{x}_i, \\ \frac{\dot{\tilde{x}}_1}{x_1} &= -\alpha_1(x_1)\tilde{x}_1 + [\mu_1(s) - \mu_1(s_*)]\theta_1(x_1), \\ &\vdots \\ \frac{\dot{\tilde{x}}_n}{x_n} &= -\alpha_n(x_n)\tilde{x}_n + [\mu_n(s) - \mu_n(s_*)]\theta_n(x_n). \end{cases} \tag{3.5}$$

From Assumption H4, we deduce that

$$\begin{cases} \Omega(s)\tilde{s}\frac{\dot{\tilde{s}}}{s} &= -\frac{\Omega(s)\Gamma(s)\tilde{s}^2}{s} - \sum_{i=1}^{n} c_i[\mu_i(s) - \mu_i(s_*)]\beta_i(x_i)\tilde{x}_i, \\ c_1\frac{\beta_1(x_1)}{\theta_1(x_1)x_1}\tilde{x}_1\dot{\tilde{x}}_1 &= -c_1\frac{\alpha_1(x_1)\beta_1(x_1)}{\theta_1(x_1)}\tilde{x}_1^2 + c_1[\mu_1(s) - \mu_1(s_*)]\beta_1(x_1)\tilde{x}_1, \\ &\vdots \\ c_n\frac{\beta_n(x_n)}{\theta_n(x_n)x_n}\tilde{x}_n\dot{\tilde{x}}_n &= -c_n\frac{\alpha_n(x_n)\beta_n(x_n)}{\theta_n(x_n)}\tilde{x}_n^2 + c_n[\mu_n(s) - \mu_n(s_*)]\beta_n(x_n)\tilde{x}_n. \end{cases} \tag{3.6}$$

These equalities lead us to consider the function

$$U(\tilde{s}, \tilde{x}_1, ..., \tilde{x}_n) = \int_0^{\tilde{s}} \Omega(l + s_*)\frac{l}{l + s_*}dl + \sum_{i=1}^{n} c_i \int_0^{\tilde{x}_i} \frac{\beta_i(x_{i*} + l)}{\theta_i(x_{i*} + l)(x_{i*} + l)}ldl \tag{3.7}$$

which is positive definite on $D_t = (-s_*, +\infty) \times (-x_{1*}, +\infty) \times ... \times (-x_{n*}, +\infty)$ because the constants c_i and the functions Ω, β_i, θ_i are positive. From (3.6), we deduce that its derivative along the trajectories of (3.1) satisfies

$$\dot{U} = -W(\tilde{s}, \tilde{x}_1, ..., \tilde{x}_n) \tag{3.8}$$

with

$$W(\tilde{s}, \tilde{x}_1, ..., \tilde{x}_n) = \frac{\Omega(s)\Gamma(s)\tilde{s}^2}{s} + \sum_{i=1}^{n} c_i\frac{\alpha_i(x_i)\beta_i(x_i)}{\theta_i(x_i)}\tilde{x}_i^2\ . \tag{3.9}$$

3.1.3. *Stability analysis.* Let us first prove the following result

Lemma 3.3. *The function U defined in (3.7) is positive definite and proper on D_t.*

Proof. We have already shown that U is positive definite. Next, observe that

$$\begin{aligned} \Omega(s) &= c_1\frac{s}{\mu_1(s)}\frac{\mu_1(s)-\mu_1(s_*)}{s-s_*} \\ &= c_1\frac{s}{s-s_*}\left(1 - \frac{\mu_1(s_*)}{\mu_1(s)}\right)\ . \end{aligned} \tag{3.10}$$

Therefore, since μ_1 is increasing, for all $s \geq 2s_*$,

$$\Omega(s) \geq c_1 \left(1 - \frac{\mu_1(s_*)}{\mu_1(2s_*)}\right) > 0 \ . \tag{3.11}$$

We deduce easily that

$$\lim_{\tilde{s} \to +\infty} \int_0^{\tilde{s}} \Omega(l + s_*) \frac{l}{l + s_*} dl = +\infty \ . \tag{3.12}$$

Since the function Ω is positive and continuous on $[0, +\infty)$, we deduce that

$$\lim_{\tilde{s} \to -s_*} \int_0^{\tilde{s}} \Omega(l + s_*) \frac{l}{l + s_*} dl = +\infty \ . \tag{3.13}$$

Next, observe that

$$\begin{aligned} \frac{\beta_i(x_i)}{\theta_i(x_i)} &= \frac{\theta_i(x_i)x_i - \theta_i(x_{i*})x_{i*}}{\theta_i(x_i)(x_i - x_{i*})} \\ &= \frac{1 - \frac{\theta_i(x_{i*})x_{i*}}{\theta_i(x_i)x_i}}{1 - \frac{x_{i*}}{x_i}} \ . \end{aligned} \tag{3.14}$$

According to Assumption H2, θ_i is decreasing and $\theta_i(x_i)x_i$ is increasing. We deduce that, for all $x_i \geq 2x_{i*}$,

$$\frac{\beta_i(x_i)}{\theta_i(x_i)} \geq 1 - \frac{\theta_i(x_{i*})x_{i*}}{\theta_i(2x_{i*})2x_{i*}} > 0 \ . \tag{3.15}$$

It follows that

$$\lim_{\tilde{x}_i \to +\infty} \int_0^{\tilde{x}_i} \frac{\beta_i(x_{i*} + l)}{\theta_i(x_{i*} + l)(x_{i*} + l)} l dl = +\infty \ . \tag{3.16}$$

Since the functions β_i and θ_i are positive and continuous on $[0, +\infty)$, we deduce that

$$\lim_{\tilde{x}_i \to -x_{i*}} \int_0^{\tilde{x}_i} \frac{\beta_i(x_{i*} + l)}{\theta_i(x_{i*} + l)(x_{i*} + l)} l dl = +\infty \ . \tag{3.17}$$

At last, from (3.13), (3.16), (3.17) we deduce that U is proper.

Next, by taking advantage of Assumption H5, one can easily prove that the function W is positive definite on D_t. This property and the result of Lemma 3.3 ensure that the Lyapunov theorem applies and therefore

$$\lim_{t \to +\infty} \tilde{s}(t) = 0 \ , \ \lim_{t \to +\infty} \tilde{x}_i(t) = 0 \ , \ \forall i = 1, ..., n \ . \tag{3.18}$$

Moreover, the local exponential stability of the origin of the system (3.1) can be proved by verifying that both U and W are, on a neighborhood of the origin, lower bounded by a positive definite quadratic function.

By returning to the original coordinates, we deduce that E is a globally asymptotically and a locally exponentially stable equilibrium point of the system (2.2) on D_o.

4. Particular cases, example

4.1. **Families of functions μ_i satisfying Assumption H4.** In this section, we exhibit families of functions which fullfill Assumption H4.

Lemma 4.1. *Let us consider n linear functions:*

$$\mu_i(s) = K_i s \tag{4.1}$$

with $K_i > 0$. These functions satisfy Assumption H4 with $\Omega(s) = 1$ and, for $i = 1, ..., n$, $c_i = 1$.

Proof. The trivial proof of this result is omitted.

Lemma 4.2. *Let us consider n functions:*

$$\mu_i(s) = \frac{K_i A(s)}{L_i B(s) + A(s)} \tag{4.2}$$

with $K_i > 0, L_i > 0$ and where A is increasing and satisfies $A(0) = 0$, $A'(0) > 0$ and B is positive and nondecreasing. These functions satisfy Assumption H4 with $\Omega(s) = \frac{s}{A(s)} \frac{A(s)B(s_*) - A(s_*)B(s)}{s - s_*}$ and, for $i = 1, ..., n$, $c_i = \frac{L_i B(s_*) + A(s_*)}{L_i}$.

Remark. When $A(s) = s$ and $B(s) = 1$, the functions (4.2) belong to the family of the Michaelis-Menten functions and the corresponding function Ω and constants c_i are $\Omega(s) = 1$, $c_i = \frac{L_i + s_*}{L_i}$.

Proof The result is a consequence of the simple calculations:

$$\begin{aligned} \frac{s}{\mu_i(s)} \frac{\mu_i(s) - \mu_i(s_*)}{s - s_*} &= s \frac{L_i B(s) + A(s)}{K_i A(s)} \frac{1}{s - s_*} \left[\frac{K_i A(s)}{L_i B(s) + A(s)} - \frac{K_i A(s_*)}{L_i B(s_*) + A(s_*)} \right] \\ &= \frac{s}{A(s)} \frac{1}{s - s_*} \left[\frac{A(s)(L_i B(s_*) + A(s_*))}{L_i B(s_*) + A(s_*)} - \frac{A(s_*)(L_i B(s) + A(s))}{L_i B(s_*) + A(s_*)} \right] \\ &= \frac{s}{A(s)} \frac{1}{s - s_*} \left[\frac{A(s)(L_i B(s_*) + A(s_*)) - A(s_*)(L_i B(s) + A(s))}{L_i B(s_*) + A(s_*)} \right] \\ &= \frac{L_i}{L_i B(s_*) + A(s_*)} \frac{s}{A(s)} \frac{A(s)B(s_*) - A(s_*)B(s)}{s - s_*} . \end{aligned} \tag{4.3}$$

Since A is increasing, satisfies $A(0) = 0$, $A'(0) > 0$ and B is positive and nondecreasing, it follows that the function $\Omega(s) = \frac{s}{A(s)} \frac{A(s)B(s_*) - A(s_*)B(s)}{s - s_*}$ is well-defined and positive on $[0, +\infty)$.

4.2. **Families of functions θ_i satisfying Assumption H2.** In this section, we exhibit families of functions which fullfill Assumption H2.

Lemma 4.3. *Consider a function*

$$\theta(x) = \frac{a}{(a + x)^\nu} \tag{4.4}$$

with $a > 0$ and $\nu \in (0, 1]$. Then this function is positive, decreasing and $x\theta(x)$ is increasing.

Proof. One can check easily that θ is positive with a negative first derivative. Moreover,

$$\frac{d[\theta(x)x]}{dx} = a \frac{(a + x)^\nu - \nu x(a + x)^{\nu - 1}}{(a + x)^{2\nu}} = a \frac{a + (1 - \nu)x}{(a + x)^{\nu + 1}} > 0 \tag{4.5}$$

and therefore $x\theta(x)$ is increasing.

4.3. **Example.** We illustrate Theorem 3.1 by applying it to the system

$$\begin{cases} \dot{s} &= \frac{7}{6} - \frac{s}{1+s} \frac{x_1}{1+x_1} - \frac{4s}{2+s} \frac{x_2}{1+x_2}, \\ \dot{x}_1 &= \left[\frac{s}{1+s} \frac{1}{1+x_1} - \frac{1}{2} \right] x_1, \\ \dot{x}_2 &= \left[\frac{4s}{2+s} \frac{1}{1+x_2} - 1 \right] x_2. \end{cases} \tag{4.6}$$

With our general notations, we have $f(s) = \frac{7}{6}$, $\mu_1(s) = \frac{s}{1+s}$, $\mu_2(s) = \frac{4s}{2+s}$, $\theta_1(x_1) = \frac{1}{1+x_1}$, $\theta_2(x_2) = \frac{1}{1+x_2}$. Observe that the growth function of the substrate $f(s) = \frac{7}{6}$ is a constant. Therefore the results of [11], [7] or [14] cannot be used to establish the global asymptotic stability of an equilibrium point of (4.6). Let us verify that the system (4.6) satisfies the assumptions H1 to H5.

1) Since $f(0) = \frac{7}{6} > 0$, Assumption H1 is satisfied.
2) We deduce from Lemma 4.3 that Assumption H2 is satisfied.
3) Assumption H3 is satisfied: the positive point $E = (2, \frac{1}{3}, 1)$ is an equilibrium point of (4.6).
4) We deduce from Lemma 4.2 that Assumption H4 is satisfied. Since μ_1 and μ_2 are Monod functions, one can choose $\Omega(s) = 1$, $c_1 = 3$, $c_2 = 2$.
5) Simple calculations yield

$$\begin{aligned}\Gamma(s) &= -\frac{\frac{7}{6}-\frac{7}{6}+\left[\frac{2}{3}-\frac{s}{1+s}\right]\frac{\frac{1}{3}}{1+\frac{1}{3}}+\left[2-\frac{4s}{2+s}\right]\frac{1}{2}}{s-2} \\ &= \frac{1}{12(1+s)}+\frac{1}{2+s}\,.\end{aligned}$$

Therefore the function Γ is positive and Assumption H5 is satisfied.

We conclude that Theorem 3.1 applies. It follows that E is a globally asymptotically and a locally exponentially stable equilibrium point of (4.6). Moreover, the derivative of the Lyapunov function

$$\begin{aligned}U(\tilde{s},\tilde{x}_1,\tilde{x}_2) &= \int_0^{\tilde{s}}\frac{l}{l+s_*}dl + c_1\int_0^{\tilde{x}_1}\frac{\beta_1(x_{1*}+l)}{\theta_1(x_{1*}+l)(x_{1*}+l)}ldl \\ &\quad + c_2\int_0^{\tilde{x}_2}\frac{\beta_2(x_{2*}+l)}{\theta_2(x_{2*}+l)(x_{2*}+l)}ldl \\ &= \tilde{s} - s_*\ln\left(1+\frac{\tilde{s}}{s_*}\right) + \frac{c_1}{1+x_{1*}}\int_0^{\tilde{x}_1}\frac{l}{x_{1*}+l}dl \\ &\quad + \frac{c_2}{1+x_{2*}}\int_0^{\tilde{x}_2}\frac{l}{x_{2*}+l}dl \\ &= \tilde{s} - s_*\ln\left(1+\frac{\tilde{s}}{s_*}\right) + \frac{9}{4}\left[\tilde{x}_1 - x_{1*}\ln\left(1+\frac{\tilde{x}_1}{x_{1*}}\right)\right] \\ &\quad + \tilde{x}_2 - x_{2*}\ln\left(1+\frac{\tilde{x}_2}{x_{2*}}\right)\end{aligned} \tag{4.7}$$

along the trajectories of (4.6) satisfies

$$\dot{U} = -W(\tilde{s},\tilde{x}_1,\tilde{x}_2) \tag{4.8}$$

with

$$W(\tilde{s},\tilde{x}_1,\tilde{x}_2) = \left(\frac{1}{12(1+s)}+\frac{1}{2+s}\right)\frac{\tilde{s}^2}{s} + \frac{9}{8(1+x_1)}\tilde{x}_1^2 + \frac{1}{(1+x_2)}\tilde{x}_2^2\,. \tag{4.9}$$

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Claude Lobry, Frédéric Mazenc

Projet MERE INRIA-INRA, UMR Analyse des Systèmes et Biométrie, INRA 2, pl. Viala, 34060 Montpellier, France.

E-mail address: claude.lobry@inria.fr

E-mail address: mazenc@supagro.inra.fr