POLYTOPIC LYAPUNOV FUNCTIONS FOR PERSISTENCE ANALYSIS OF COMPETING SPECIES

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ABSTRACT. We show that stability of the equilibrium of a family of interconnected scalar systems can be proved by using a sum of monotonic $\mathcal{C}^0$ functions as Lyapunov function. We prove this result in the general framework of nonlinear systems and then in the special case of Kolmogorov systems. As an application, it is then used to show that intra-specific competition can explain coexistence of several species in a chemostat where they compete for a single substrate. This invalidates the Competitive Exclusion Principle, that states that in the classical case (without this intra-specific competition), it is indeed known that only one of the species will survive.

1. **INTRODUCTION.** In this paper, we present a tool for the stability analysis of interconnected scalar systems. This tool is simply the construction of a *polytopic* Lyapunov function, that is a Lyapunov function whose level sets are boundaries of polytopes (where we simply define a polytope as a a bounded intersection of a finite set of half-spaces). This Lyapunov function is built as the sum of monotonic $\mathcal{C}^0$ functions, that are not differentiable everywhere; however, because these functions are scalar, the use of advanced non-smooth analysis for the study of our system is not required.

The analysis of interconnected systems arises in many application fields because it often is a practical approach for the study of large systems. In control theory, the feedback or parallel interconnection of two *passive* systems results in a passive system, so that only the analysis of the smallest pieces of the puzzle is required [19]. Also, a general approach for the analysis of communication networks [9] and of metabolic or genetic network [5, 14] can be made by considering that the networks are made of interconnected compartments. One important step has been made in that line of work in [1], where the authors consider the interconnection of monotone systems. In this paper, we will concentrate on a system made of n scalar variables which are connected through a single link:

$$\dot{x}_i = f_i(x_i, u)$$

with $x_i, u \in \mathbb{R}$ where $u = -\sum_{j=1}^n g_j(x_j)$ is the interconnection and is common to all x_i subsystems. In a more particular framework we show that the stability result is retained when the interconnected systems are of the Kolomogorov type

$$\dot{x}_i = x_i f_i(x_i, u)$$

with $x_i \in \mathbb{R}_+$.

The analysis of this family of systems is interesting in itself because it shows how stability of the interconnected system is retained despite a common perturbation. However, we have shown that we could use this result in the stability analysis of the non-trivial equilibrium that arises in some mixed culture in competition for a single substrate.

It is well known that, when the growth rates of the different species only depend on the substrate, the generic equilibrium state for a given dilution rate consists in the survival of only one of the species [21], that is the species that requires the smallest substrate concentration to have a growth-rate equivalent to the dilution rate: it is the survival of the most efficient species at this rate. This observation has been validated through laboratory experiments [11], but it can also be seen that coexistence of the species is observed in real-world applications (such as the chemostat). This coexistence has been explained in different cases by a time-varying nutrient feed [22, 12, 10], multi-resource models [15, 13], non instantaneous growth [8], turbidity operating conditions [7], a crowding effect [6] or variable yield [18, 2]. In [4], the authors have shown that, in the context where the resource is growing according to a logistic growth, they could exhibit the stability of a single positive equilibrium when the different species are all subject to intraspecific competition (when the consumers feed on the resource following specific functional responses). It has been first shown in [16] that the coexistence of the different species and their convergence towards a positive equilibrium can also simply be explained by an intra-specific dependency of the growth functions, which represents an intra-specific competition, in the chemostat framework and without fixing a specific format for the growth-rate. The approach that was used for the proof made use of a multi-phase plane analysis. In this paper, we show that the Lyapunov function that we propose can be used for the proof.

This paper is structured as follows. In Section 2, we present the aforementioned Lyapunov function in a general nonlinear dynamical systems framework; it is then particularized to the Kolmogorov type positive systems in Section 3. In Section 4, we show how this tool can be used for the proof of stability of a single positive equilibrium in the chemostat framework that we just described. Finally, the existence of a single stable equilibrium among the non-negative equilibria is proved in Section 5 when no positive equilibrium exists in the chemostat. We then state the conclusion in Section 6.

2. **Interconnection of scalar systems through additive terms.** In this section, we will analyze the stability the interconnection of stable scalar systems through a perturbation that takes the form of a sum of increasing functions of the states. We will later see that, with the additional hypotheses, this could be interpreted as a competition between the elements of the system. However, we will not impose conditions on the signs of the partial derivatives of the considered functions, as is usually done in competitive contexts [20]; we will rather constrain the signs of the functions in some points:

Theorem 1. *Let the system of n equations*

$$\dot{x}_i = f_i(x_i, u)$$

with $x_i, u \in \mathbb{R}$ and $f_i(.,.)$ Lipschitz continuous in its arguments be such that

$$(A) \quad f_i(x_i, u) < 0 \text{ if } x_i > 0 \text{ and } u \leq 0$$
$$(B) \quad f_i(x_i, u) > 0 \text{ if } x_i < 0 \text{ and } u \geq 0$$

and a set of bijective increasing Lipschitz functions $g_j : \mathbb{R} \to \mathbb{R}$ such that $g_j(0) = 0$.

Then the system of n equations

$$\dot{x}_i = f_i(x_i, -\sum_{j=1}^{n} g_j(x_j)) \tag{1}$$

has a unique equilibrium at $(0, \cdots, 0)$, and it is globally asymptotically stable (GAS).

Proof. It is first clear that $f_i(0,0) = 0$ for all i. Indeed, we have $f_i(x_i, 0) > 0$ for $x_i < 0$ and $f_i(x_i, 0) < 0$ for $x_i > 0$, so that $f_i(0,0) = 0$ by continuity. System (1) then has an equilibrium at $(0, \cdots, 0)$.

We can show that system (1) cannot have an equilibrium with $\sum_{j=1}^{n} g_j(x_j) > 0$ (resp. < 0) by noting that there must then exist k such that $g_k(x_k) > 0$ (and $x_k > 0$), so that $\dot{x}_k = f(x_k, -\sum_{j=1}^{n} g_j(x_j)) < 0$ (because of assumption (B)). The same reasoning can be held for a potential equilibrium x such that $\sum_{j=1}^{n} g_j(x_j) = 0$ and some $g_k(x_k) > 0$. The origin is therefore the unique equilibrium of system (1).

In order to show stability, we will build a polytopic Lyapunov function that is built on the $g_j(.)$ functions. In order to do that, for any $x \in I\!\!R^n$, we define

$$S(x) = \sum_{j=1}^{n} g_j(x_j)$$

and the $\max$ functions

$$S_j^+(x_j) = \max(g_j(x_j), 0) \text{ for } j \in \{1, \cdots, n\}$$

$$S_j^-(x_j) = \max(-g_j(x_j), 0) \text{ for } j \in \{1, \cdots, n\}$$

which allow for the definitions of

$$S^+(x) = \sum_{j=1}^{n} S_j^+(x_j) \geq 0 \quad and \quad S^-(x) = \sum_{j=1}^{n} S_j^-(x_j) \geq 0$$

then $S(x) = S^+(x) - S^-(x)$ and the function

$$V(x) = \max(S^+(x), S^-(x)) \tag{2}$$

is positive definite, radially unbounded, has its unique minimum in $V(0) = 0$, and is a $\mathcal{C}^0$ polytopic function (as the maximum of continuous functions). Instead of checking $\dot{V} < 0$, as is usually done, and which is not applicable here because V is non-differentiable, we will verify, for each solution $x(.)$, that the composite map $t \rightarrow V(x(t))$ is decreasing everywhere except at $x = 0$, so that the equilibrium is attractive [3]. We then have two cases for the analysis of the evolution of $V(x(t))$:

$S^+(x) \geq S^-(x)$: In this region, our choice of V makes us consider the time evolution of $S^+(x(t))$. It is easily seen that, when some $x_j > 0$, we have $\dot{x}_j < 0$ because

$$\dot{x}_j = f_j(x_j, -\sum_{l=1}^{n} g_l(x_l)) = f_j(x_j, -S(x))$$

where

$$-S(x) = -S^+(x) + S^-(x) \leq 0$$

This implies that, as long as $S^+(x(t)) \geq S^-(x(t))$, the composite map $t \rightarrow S_j^+(x_j(t))$ is decreasing (because g_j is an increasing function of x_j and $\dot{x}_j < 0$). In the case where $x_j = 0$, a continuity argument applied to assumption (A) shows that $\dot{x}_j \leq 0$. The composite map $t \rightarrow S_j^+(x_j(t))$ is then non-increasing. Moreover, as long as $x(t) \neq 0$, there is always at least one k such that $x_k(t) > 0$ (otherwise, $S^+(x(t)) = 0$, which implies

that $S^-(x(t)) = 0$, and the considered $x(t)$ is the equilibrium). The composite map $t \rightarrow S_k^+(x_k(t))$ is therefore decreasing so that the composite map

$$t \rightarrow S^+(x(t))$$

is decreasing.

$\underline{S^+(x) \leq S^-(x)}$: Through a similar reasoning, we can show that the composite map

$$t \rightarrow S^-(x(t))$$

is decreasing in this region.

If we now consider the composite map

$$t \rightarrow V(x(t)) = \max(S^+(x(t)), S^-(x(t)))$$

we see that it is always decreasing when $x(t) \neq 0$ and $S^+(x(t)) \neq S^-(x(t))$ because, in this case, it is equivalent to only one of the functions S^+ or S^- at a time. If $x \neq 0$ and $S^+(x(t)) = S^-(x(t))$, both composite functions decrease, so that $t \rightarrow V(x(t)) = \max(S^+(x(t)), S^-(x(t)))$ also decreases, which implies that the origin is GAS.   □

Example: The shape of the level sets of this Lyapunov function is illustrated on Figure 1 in the case where $g_j(x_j) = x_j$: they are centered at the origin and have a polytopic form. We have also added simulations of the system

$$\begin{cases} \dot{x}_1 & = & -x_1(1.01 - \sin(10x_1)) + u(1.01 - \sin(7u)) \\ \dot{x}_2 & = & -x_2(1.01 - \sin(10x_2)) + 2u(1.01 - \sin(7u)) \end{cases} \tag{3}$$

with $u = -x_1 - x_2$ which satisfies the hypotheses of Theorem 1, so that along the solutions of this system, the Lyapunov function decreases. This system does not satisfy monotonicity hypotheses as classical models of competition do, but it satisfies the sign hypothesis.
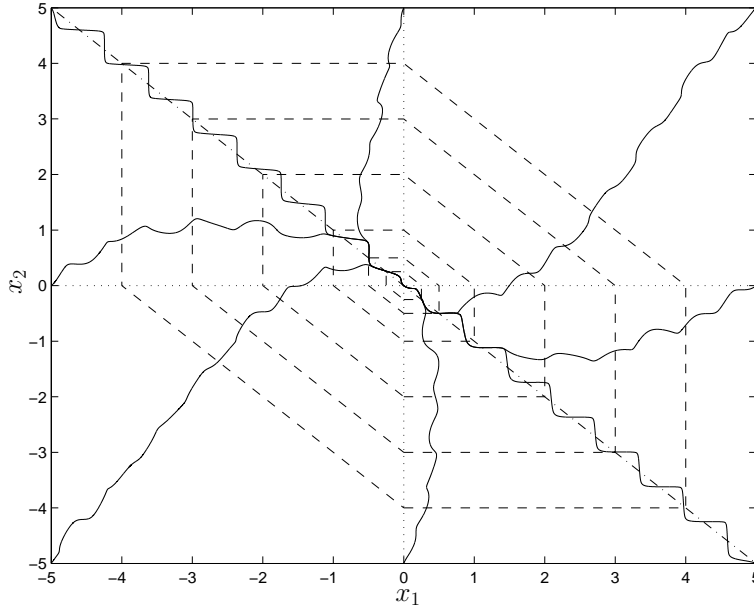

FIGURE 1. Level sets of the polytopic Lyapunov functions for the 2D system (1) (dashed lines) and simulations of system (3) (solid lines)

Counter-example: In our proof, we see the importance of the bijectivity of the g_j functions. This is the property that ensures the radial unboundedness of the Lyapunov function, so that global stability is proved. To underline this property, we will now show that, if it is not satisfied, global stability is not always guaranteed. Let us consider the system

$$\begin{aligned} \dot{x}_1 &= -x_1 + x_1^2(-\sigma(x_1) - x_2) \\ \dot{x}_2 &= -x_2 \end{aligned}$$

where $\sigma(s) = \frac{s}{\max(1,|s|)}$. This system fits into the family of systems that are defined in Theorem 1 by taking $f_1(x_1, u) = -x_1 + x_1^2 u$, $f_2(x_2, u) = -x_2$, $g_1(x_1) = \sigma(x_1)$, and $g_2(x_2) = x_2$, except that $g_1(x_1)$ is bounded, and therefore not a bijection from $\mathbb{R}$ to $\mathbb{R}$.

For a given initial condition for the x_2 state $(x_2(0))$, x_1 then evolves according to

$$\dot{x}_1 = -x_1 + x_1^2(-\sigma(x_1) - x_2(0)e^{-t})$$

We then see that, if $x_2(0)$ was taken positive and very large, and $x_1(0)$ negative large, this systems presents a finite escape time, that is $x_1(t)$ goes to $-\infty$ in finite time, because the right-hand side of this equation is dominated by the $-x_2(0)e^{-t}x_1^2$ term. This shows that, in the absence of the bijectivity assumption, the origin is not guaranteed to be globally asymptotically stable.

3. **Interconnection of positive Kolmogorov systems.** We have stated, in the first part of this paper, that the family of systems that we consider can be linked to competition between different species (and we will further evidence that in Section 4). Two key aspects of systems representing the evolution of living species are that the states need to be non-negative and, if some species is not present in the considered system, no matter the resource feeding the system is given, this species will not appear. The classical way of representing this property consists in writing the evolution of a single species as a system of Kolmogorov:

$$\dot{x}_i = x_i f_i(x), \quad x_i \geq 0$$

which satisfies both properties that we have just stated. In order to simply consider systems that are linked to the ones that were presented in the previous section, we will rather consider that the evolution of a single species follows

$$\dot{x}_i = x_i h_i(x_i, u), \quad x_i \geq 0 \tag{4}$$

with $u = -\sum_{j=1}^{n} g_j(x_j)$. Obviously, the equilibrium that we will consider is not the origin anymore, because it is of little interest in the framework of ecosystems. We will therefore suppose that there exists an equilibrium $\bar{x} = (\bar{x}_1, \cdots, \bar{x}_n) > 0$ to system (4). The following theorem is then proven

Theorem 2. *Let the system of n equations*

$$\dot{x}_i = x_i h_i(x_i, u)$$

with $x_i \in \mathbb{R}_+, u \in \mathbb{R}$ and $h_i(.,.)$ Lipschitz continuous in its arguments and a set of increasing Lipschitz functions $g_j; \mathbb{R}_+ \to \mathbb{R}$ such that $\lim_{x_j \to +\infty} g_j(x_j) = +\infty$ be such that the system of equations

$$h_i\left(x_i, -\sum_{j=1}^{n} g_j(x_j)\right) = 0$$

has an equilibrium at $\bar{x} = (\bar{x}_1, \cdots, \bar{x}_n) > 0$. If, moreover,

$$\begin{aligned} &(A) \quad h_i(x_i, u) < 0 \text{ if } x_i > \bar{x}_i \text{ and } u \leq -\sum_{j=1}^{n} g_j(\bar{x}_j) \\ &(B) \quad h_i(x_i, u) > 0 \text{ if } x_i < \bar{x}_i \text{ and } u \geq -\sum_{j=1}^{n} g_j(\bar{x}_j) \end{aligned}$$

Then the system of n equations

$$\dot{x}_i = x_i h_i(x_i, -\sum_{j=1}^{n} g_j(x_j)) \tag{5}$$

has a unique positive equilibrium at $\bar{x}$, and it is asymptotically stable with the positive orthant as its region of attraction.

Remark 1. *The first temptation for proving this result consists in changing coordinates:*

$$y_i = \ln(\frac{x_i}{\bar{x}_i})$$

so that system (5) takes the form of (1):

$$\dot{y}_i = \frac{\bar{x}_i}{x_i} x_i h_i(\bar{x}_i e^{y_i}, -\sum_{j=1}^{n} g_j(\bar{x}_j e^{y_j})) = \bar{x}_i h_i(\bar{x}_i e^{y_i}, -\sum_{j=1}^{n} g_j(\bar{x}_j e^{y_j}))$$

The function $f_i(y_i, u) = \bar{x}_i h_i(\bar{x}_i e^{y_i}, u)$ indeed satisfies conditions (A) and (B) of Theorem 1. However, the role of the g_j functions of Theorem 1 is taken by $g_j(\bar{x}_j e^{y_j})$ functions; those are indeed increasing in y_j, but they are not guaranteed to be bijective from $\mathbb{R}$ to $\mathbb{R}$, so that Theorem 1 cannot be directly applied.

Proof. The proof of stability that was used in Theorem 1 is adapted to the considered case. We first show uniqueness of the positive equilibrium (there are other equilibria were some $x_j = 0$): It is first clear that $h_i(\bar{x}_i, -\sum_{j=1}^{n} g_j(\bar{x}_j)) = 0$ for all i. Indeed, we have $h_i(x_i, -\sum_{j=1}^{n} g_j(\bar{x}_j)) > 0$ for $x_i < \bar{x}_i$ and $h_i(x_i, -\sum_{j=1}^{n} g_j(\bar{x}_j)) < 0$ for $x_i > \bar{x}_i$, so that $h_i(\bar{x}_i, -\sum_{j=1}^{n} g_j(\bar{x}_j)) = 0$ by continuity. System (1) then has an equilibrium at $\bar{x}$.

System (5) cannot have an equilibrium with $\sum_{j=1}^{n} g_j(x_j) > \sum_{j=1}^{n} g_j(\bar{x}_j)$ (resp. $<$) because there would then exist k such that $g_k(x_k) > g_k(\bar{x}_k)$ (and $x_k > \bar{x}_k$), so that $\dot{x}_k = x_k h_k(x_k, -\sum_{j=1}^{n} g_j(x_j)) < 0$ (because of assumption (A)). The same reasoning can be held for a potential equilibrium x such that $\sum_{j=1}^{n} g_j(x_j) = \sum_{j=1}^{n} g_j(\bar{x}_j)$ and some $g_k(x_k) > g_k(\bar{x}_k)$. $\bar{x}$ is therefore the unique positive equilibrium of system (5).

In order to show stability, we will build a polytopic Lyapunov function that is built on the $g_j(.)$ functions. In order to do that, for any $x \in \mathbb{R}^n_+$, we define

$$S(x) = \sum_{j=1}^{n} g_j(x_j) - g_j(\bar{x}_j)$$

and the max functions

$$S_j^+(x_j) = \max(g_j(x_j) - g_j(\bar{x}_j), 0) \text{ for } j \in \{1, \cdots, n\}$$

$$S_j^-(x_j) = \max(-g_j(x_j) + g_j(\bar{x}_j), 0) \text{ for } j \in \{1, \cdots, n\}$$

which allow for the definitions of

$$S^+(x) = \sum_{j=1}^{n} S_j^+(x_j) \geq 0 \quad and \quad S^-(x) = \sum_{j=1}^{n} S_j^-(x_j) \geq 0$$

then $S(x) = S^+(x) - S^-(x)$ and the function

$$V(x) = \max(S^+(x), S^-(x)) \tag{6}$$

is positive definite, has its unique minimum in $V(\bar{x}) = 0$, and is a $\mathcal{C}^0$ polytopic function (as the maximum of continuous functions). It tends to infinity when $|x| \to +\infty$. We then

have two cases for the analysis of the evolution of $V(x(t))$ inside the positive orthant (all $x_i > 0$):

$S^+(x) \geq S^-(x)$: In this region, our choice of V makes us consider the time evolution of $S^+(x(t))$. We have

$$\dot{x}_j = x_j h_j(x_j, -\sum_{k=1}^{n} g_k(x_k)) = x_j h_j(x_j, -S(x) - \sum_{k=1}^{n} g_k(\bar{x}_k))$$

where

$$-S(x) = -S^+(x) + S^-(x) \leq 0$$

and the fact that

$$h_j\left(\bar{x}_j, -\sum_{k=1}^{n} g_k(\bar{x}_k)\right) = 0$$

so that we can use Assumption (A) to see that for all $x_j > \bar{x}_j$

$$h_j\left(x_j, -S(x) - \sum_{k=1}^{n} g_k(\bar{x}_k)\right) < 0 \tag{7}$$

so that $\dot{x}_j < 0$. This implies that, as long as $S^+(x(t)) \geq S^-(x(t))$ and $x_j(t) > \bar{x}_j$, the composite map $t \to S_j^+(x_j(t))$ is decreasing (because g_j is an increasing function of x_j and $\dot{x}_j < 0$). In the case where $x_j(t) = \bar{x}_j$, a continuity argument applied to assumption (A) shows that $\dot{x}_j \leq 0$. The composite map $t \to S_j^+(x_j(t))$ is then non-increasing everywhere (it stays constant when $x_j(t) < \bar{x}_j$). Moreover, as long as $x(t) \neq \bar{x}$, there is always at least one k such that $x_k(t) > \bar{x}_k$ (otherwise, $S^+(x(t)) = 0$, which implies that $S^-(x(t)) = 0$, and the considered $x(t)$ is the equilibrium). The composite map $t \to S_k^+(x_k(t))$ is therefore decreasing so that the composite map

$$t \to S^+(x(t))$$

is decreasing.

$S^+(x) \leq S^-(x)$: Through a similar reasoning, we can show that, in this region, the composite map

$$t \to S^-(x(t))$$

is decreasing through the use of

$$-S(x) = -S^+(x) + S^-(x) \geq 0$$

and the fact that

$$h_j\left(\bar{x}_j, -\sum_{k=1}^{n} g_k(\bar{x}_k)\right) = 0$$

so that we can use Assumption (A) to see that for all $x_j < \bar{x}_j$

$$h_j\left(x_j, -S(x) - \sum_{k=1}^{n} g_k(\bar{x}_k)\right) > 0 \tag{8}$$

Note, however, that troubles could arise when some of the x_js are equal to zero, so that $\dot{x}_j = 0$.

If we now consider the composite map

$$t \to V(x(t)) = \max(S^+(x(t)), S^-(x(t)))$$

we see that it is always decreasing when $x(t) \neq \bar{x}$ and $S^+(x(t)) \neq S^-(x(t))$ because, in this case, it is equivalent to only one of the functions S^+ or S^- at a time. If $x(t) \neq \bar{x}$

and $S^+(x(t)) = S^-(x(t))$, both composite functions decrease, so that $t \rightarrow V(x(t)) = \max(S^+(x(t)), S^-(x(t)))$ also decreases.

The analysis is not completed here yet. Indeed, we can wonder if convergence can take place towards one of the faces of $\mathbb{R}_+^n$ (extinction of one or several of the species)? We have indeed only shown that V is strictly decreasing inside the positive orthant, and not on the border of the orthant. Moreover, the Lyapunov function is not radially unbounded in the usual sense when considering positive systems; indeed, it is usually considered that V grows unbounded as x approaches the boundary of the orthant, which is not the case here.

Looking at Figure 2, we see that the solid level sets are within the positive orthant and that the dash-dotted level set touches the border of the orthant. It is clear that the level corresponding to the dash-dotted line is $\bar{V} = \min_j(g_j(\bar{x}_j) - g_j(0))$; indeed, as long as $V(x) < \bar{V}$, we can easily see that no x_j can be equal to 0 while, for $x = (\bar{x}_1, \cdots, \bar{x}_{j-1}, 0, \bar{x}_{j+1}, \cdots, \bar{x}_n)$ (for the j given by the minimum), we have $V(x) = \bar{V}$.
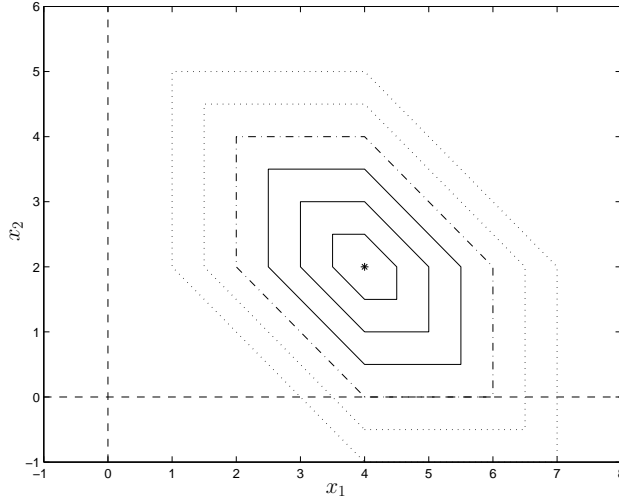

FIGURE 2. Level sets of the polytopic Lyapunov functions for a 2D system having its equilibrium at $(x_1, x_2) = (4, 2)$, and $g_j(x_j) = x_j$.

Any solution with initial condition satisfying $V(x) < \bar{V}$ then converges to the equilibrium. On the other hand, the dotted level sets cross the border of the orthant, so that a solution having its initial condition within them could very well go to the border. A more detailed analysis is necessary.

It can be shown that a solution with initial condition outside the level set defined by $V(x) = \bar{V}$, and that is such that

$$\liminf_{t \to +\infty} x_i(t) > 0$$

for all i must reach the set in finite time. Indeed, there exists $\delta > 0$ such that, when $S(x(t)) \geq 0$, there exists k such that $g_k(x_k(t)) \geq g_k(\bar{x}_k) + \frac{\bar{V}}{n}$ and, as long as $g_k(x_k(s)) \geq g_k(\bar{x}_k) + \frac{\bar{V}}{2n}$ and $S(x(s)) \geq 0$ (for $s > t$), we have $g_k(x_k(s)) - g_k(x_k(t)) \leq -\delta(s-t)$. The same thing can be written when $S(x(t)) \leq 0$: we have $g_k(x_k(s)) - g_k(x_k(t)) \geq \delta(s - t)$ for $g_k(\inf_r(x_k(r))) \leq g_k(x_k(t)) \leq g_k(\bar{x}_k) - \frac{\bar{V}}{n}$ and $g_k(\inf_r(x_k(r))) \leq g_k(x_k(s)) \leq g_k(\bar{x}_k) - \frac{\bar{V}}{2n}$.

Even though the time-derivative $\dot{V}$ is not always defined, we deduce from this that $V(x(t))$ decreases at a rate that is faster than $-\delta$, so that

$$V(x(t)) - V(x(0)) \leq -\delta t$$

The level $V(x(t)) = \bar{V}$ is then reached in finite time, which implies convergence to the equilibrium.

Let us now suppose that we have a solution $x(t)$ such that

$$\liminf_{t \to +\infty} x_i(t) = 0$$

for some $i \in \{1, \cdots, n\}$, so that it does not converge towards the equilibrium.

We can then build a sequence $(T_q)_{q \in \mathbb{N}}$ such that $T_q \to +\infty$ and

$$lim_{q \to +\infty} x_i(T_q) = 0$$

while $x_i(T_q)$ is a decreasing sequence, satisfying $\dot{x}_i(T_q) \leq 0$

Because every solution lies in a compact set, we can then extract a subsequence $t_q \to +\infty$ from the T_q sequence such that

$$lim_{q \to +\infty} x(t_q) = x^*$$

where, obviously, $x_i^* = 0$.

When q is large, we necessarily have that $x_i(t_q) < \bar{x}_i$. Using hypothesis (B), we see that the only way for having $x_i(t_q) < \bar{x}_i$ and $\dot{x}_i(t_q) \leq 0$ (so that $h_i(.,.) \leq 0$) consists in having $u < -\sum_{k=1}^n g_k(\bar{x}_k)$, that is $-\sum_{k=1}^n g_k(x_k(t_q)) < -\sum_{k=1}^n g_k(\bar{x}_k)$, that is

$$S(x(t_q)) > 0$$

We then conclude that $S(x^*) \geq 0$, so that $V(x^*) = S^+(x^*)$. Because $x^* \neq \bar{x}$, we have that $V(x^*) > 0$, so that $S^+(x^*) > 0$. Therefore, there exists $l \neq i$ such that $x_l^* > \bar{x}_l$.

We will now show that we must have $S(x^*) > 0$. First suppose that $S(x^*) = 0$. We will then study what happens to $\dot{x}_i$ when x_i and $S(x)$ both are small and positive.

Because $lim_{q \to +\infty} x_i(t_q) = 0$, there exists Q_1 large enough such that $x_i(t_q) \leq \epsilon$ for all $q \geq Q_1$ and a given ϵ. From Hypothesis (B), it is clear that, when $0 \leq x_i \leq \epsilon$ and $S(x) = 0$, we have that $h_i(x_i, -S(x) - \sum_{k=1}^n g_k(\bar{x}_k)) > 0$; in fact, on this compact set, $h_i(x_i, -S(x) - \sum_{k=1}^n g_k(\bar{x}_k))$ is lower bounded with a positive constant H. Therefore, there exists a small constant δ such that $h_i(x_i, -S(x) - \sum_{k=1}^n g_k(\bar{x}_k))$ is lower-bounded with $\frac{H}{2}$ inside the compact set where $0 \leq x_i \leq \epsilon$ and $0 \leq S(x) \leq \delta$. Moreover, because $lim_{q \to +\infty} S(x(t_q)) = 0$, there exists Q_2 large enough such that $S(x(t_q)) \leq \delta$ for all $q \geq Q_2$. Therefore, when $q > \max(Q_1, Q_2)$, we have that $\dot{x}_i(t_q) > 0$, which is in contradiction with the construction of the sequence $x_i(t_q)$. This shows that $S(x^*) > 0$.

We have shown earlier that there exists $l \neq i$ such that $x_l^* > \bar{x}_l$. For Q large enough, there must then exist $\nu > 0$ such that $x_l(t_q) > \bar{x}_l + \nu$ for all $q > Q$. We will then be able to write

$$\dot{x}_l = x_l h_l(x_l, -S(x) - \sum_{k=1}^n g_k(\bar{x}_k)) \leq -\bar{x}_l \eta$$

at the times t_q (with $q > Q$). Indeed, $x_l(t_q)$ is a bounded sequence staying in an interval $[\bar{x}_l + \nu, x_{l,max}]$ and $-S(x(t_q)) - \sum_{k=1}^n g_k(\bar{x}_k))$ is a bounded sequence staying in an interval $[-U, -\sum_{k=1}^n g_k(\bar{x}_k))]$ (for some positive U). The continuous function $h_i(x, u)$, on the compact set $[\bar{x}_l + \nu, x_{l,max}] \times [-U, -\sum_{k=1}^n g_k(\bar{x}_k))]$, has a maximum (which is negative because of (A)), that we will denote $-\eta$ (with $\eta > 0$).

Because $S(x^*) > 0$, the function S is uniformly continuous, and the application $t \to x(t)$ is uniformly continuous, there exists Q large enough and $\beta > 0$ such that $S(x(t)) > 0$

and $x_l(t) > \bar{x}_l$ for all $t \in [t_q, t_q + \beta]$ (for all $q \geq Q$). We conclude from there that $V(x(t)) = S^+(x(t))$ in those intervals.

Therefore, for all j that are such that $x_j(t_q) > \bar{x}_j$, we have that $S_j^+(x_j(t))$ is non-increasing in the interval $t \in [t_q, t_q + \beta]$ (it is decreasing until $x_j(t)$ reaches $\bar{x}$, and then stays constant at 0); for all those j, we then have that $S_j^+(x(t)) - S_j^+(x(t_q)) \leq 0$. We can then write that

$$
\begin{aligned}
V(x(t)) - V(x(t_q)) &= S^+(x(t)) - S^+(x(t_q)) \\
&\leq S_l^+(x_l(t)) - S_l^+(x_l(t_q)) \\
&= g_l(x_l(t)) - g_l(x_l(t_q))
\end{aligned}
$$

Because $x(t)$ is $\mathcal{C}^1$, there exists $s_q \in [t_q, t]$ such that $x_l(t) = x_l(t_q) + (t - t_q)\dot{x}_l(s_q)$. Also, because $x(t)$ is bounded, and the Lipschitz functions $h(.,.)$ and $g(.)$ only depend on $x(t)$, the application

$$
t \to \dot{x}_l(t) = x_l(t)h_l(x_l(t), -S(x(t)) - \sum_{k=1}^{n} g_k(\bar{x}_k))
$$

is globally Lipschitz with a Lipschitz constant $\frac{C}{2}$, so that

$$
\dot{x}_l(s_q) \leq \dot{x}_l(t_q) + (s_q - t_q)\frac{C}{2} \leq \dot{x}_l(t_q) + (t - t_q)\frac{C}{2}
$$

We then have that

$$
x_l(t) - x_l(t_q) \leq (t - t_q)\dot{x}_l(t_q) + (t - t_q)^2\frac{C}{2} \leq -(t - t_q)\eta\bar{x}_l + (t - t_q)^2\frac{C}{2}
$$

We can then pick $r_q = t_q + \min(\beta, \frac{\eta\bar{x}_l}{C})$, so that

$$
x_l(r_q) - x_l(t_q) \leq -\min\left(\frac{\beta\eta\bar{x}_l}{2}, \frac{(\eta\bar{x}_l)^2 C}{2}\right) = -\Gamma
$$

We then have that

$$
g_l(x_l(r_q)) - g_l(x_l(t_q)) \leq g_l(x_l(t_q) - \Gamma) - g_l(x_l(t_q)) \triangleq G_l(x_l(t_q))
$$

Because $g_l(x_l)$ is an increasing function, $G_l(x_l)$ is a negative function defined on the interval inside which $x_l(t_q)$ can be, that is $[\bar{x}_l, g_l^{-1}(V(x(0) + g_l(\bar{x}_l)))]$. Therefore, G_l has a maximum on this interval, that we will denote $-M$ (with $M > 0$). We then have that

$$
V(x(r_q)) \leq V(x(t_q)) + g_l(x_l(r_q)) - g_l(x_l(t_q)) \leq V(x(t_q)) - M
$$

and $V(x(t_q))$ goes to $-\infty$, which is a contradiction.

The solutions do not go to the boundary of the positive orthant, so that they reach the level $V(x) = \bar{V}$ in finite time, before converging to the equilibrium $\bar{x}$

$\square$

In the following section, we will apply this result for the stability analysis of a model of evolution of competing species for a single substrate.

4. **Single-nutrient competition in the chemostat.** The classical model of a mixed culture in competition for a single substrate in a chemostat is given by the following equations:

$$
\begin{cases}
\dot{s} &= -\sum_{j=1}^{n} \frac{\mu_j(s)}{k_j}x_j + D(s_{in} - s) \\
\dot{x}_i &= x_i(\mu_i(s) - D)
\end{cases}
\tag{9}
$$

where $s \in \mathbb{R}_+$ represents the substrate, $s_{in} > 0$ the substrate concentration in the input, $k_j > 0$ the yield, $x_i \in \mathbb{R}_+$ a competing species ($i \in \{1, \cdots, n\}$), $\mu_i(s)$ the growth-rate of the species x_i on the substrate s and $D \in \mathbb{R}_+$ the constant dilution rate.

As stated in the introduction, when the growth-rates are different, such that $\mu_i(0) = 0$, non-decreasing and upper-bounded, the generic globally asymptotically stable equilibrium of this system only presents one persisting species (the others being washed-out). We indeed see, from the analysis of the $\dot{x}_i = 0$ equation that, if two species (i_1 and i_2) are to be present at the same time at the equilibrium, the equations

$$\begin{aligned} \mu_{i_1}(\bar{s}) &= D \\ \mu_{i_2}(\bar{s}) &= D \end{aligned}$$

should both be satisfied. As we can see on Figure 3, this is generically not the case for two arbitrary Monod functions and an arbitrary dilution rate. A local stability analysis shows that only one equilibrium where a singles species survives is stable: the one having the population that requires the smallest substrate value for having $\mu_i(s) = D$.
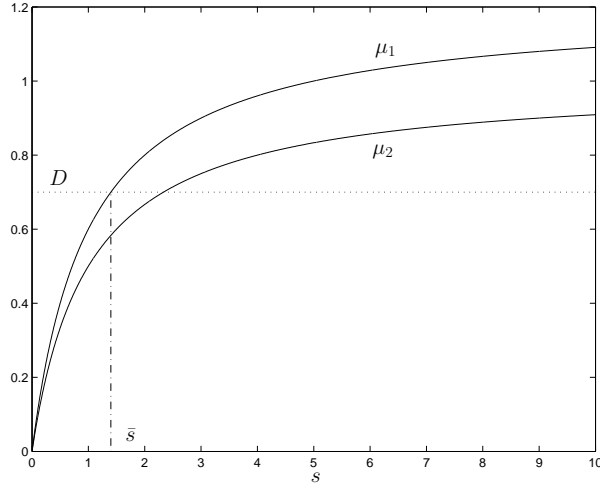

FIGURE 3. Graphic representation of the $\mu_i(s) = D$ equations, with the value $\bar{s}$ of the substrate at the stable equilibrium

We have seen that this wash-out was not always observed in real-life, and that several explanations have been given for such a phenomenon: time-varying nutrient feed, multi-resource models, turbidity operating conditions or a crowding effect. In this paper, we show that intra-specific competition is sufficient for creating such an equilibrium that presents more than one subsisting species. In order to express this intra-specific competition, we simply replace the $\mu_i(.)$ functions with functions h_i of s and x_i:

$$\begin{cases} \dot{s} &= -\sum_{j=1}^{n} \frac{h_j(s,x_j)}{k_j} x_j + D(s_{in} - s) \\ \dot{x}_i &= x_i(h_i(s, x_i) - D) \end{cases} \tag{10}$$

where h_i satisfies

Assumption 1. *The functions $h_i : \mathbb{R}_+^2 \to \mathbb{R}_+$ of class $\mathcal{C}^1$ satisfy*

(i) $h_i(0,.) = 0$

(ii) $\frac{\partial h_i}{\partial s}(.,.) > 0$ *(for all $s \geq 0$, $x \geq 0$) and* $\frac{\partial h_i}{\partial x_i}(.,.) < 0$ *(for all $s > 0$, $x \geq 0$).*

(iii) *The inequality $h_i(s_{in}, 0) > D$ holds and, for all fixed $s > 0$, we have*

$$lim_{x_i \to +\infty} h_i(s, x_i) = 0$$

(iv) *For the maximal value $\tilde{s}$ of s such that there exists some k such that $h_k(\tilde{s}, 0) = D$, the $\dot{x}_i = 0$ equations yield non-trivial solutions $\tilde{x}_i > 0$ (except for k) such that*

$$\sum_{\substack{j=1 \\ j \neq k}}^{n} \frac{\tilde{x}_j}{k_j} < s_{in} - \tilde{s}$$

Point (i) ensures that no growth can take place without substrate; point (ii) shows that the growth of the x_i species is improved by the increase of substrate concentration and is inhibited by its own concentration (intra-specific competition); $h_i(s_{in}, 0) > D$ is necessary because, if it is not satisfied for one of the species, this species is necessarily washed out; with the addition of the rest of (iii) and (iv) the existence of an equilibrium where all species are present is guaranteed.

Remark 2. *It might look difficult to check when Assumption (iv) is satisfied. However, we can always make sure that it is the case by eliminating some species. Indeed, let us suppose that (iv) is not satisfied for a given system. We will then eliminate x_k from the system (where k is defined as in (iv)). This will enable us to consider a smaller value of $\tilde{s}$, which is now the largest value of s such that there exists some l such that $h_l(\tilde{s}, 0) = D$. Because $\tilde{s}$ is now smaller, the solutions $\tilde{x}_i$ of the $\dot{x}_i = 0$ equations are now smaller also (because of (ii)), so that*

$$\sum_{\substack{j=1 \\ j \neq k, l}}^{n} \frac{\tilde{x}_j}{k_j} < s_{in} - \tilde{s}$$

stands a better chance of being correct. Indeed, the left-hand-side has been reduced and the right-hand-side has been increased. If it is not verified, we should keep apply this procedure until the inequality is satisfied. In the worst case, the whole system will be trimmed except one species. The left-hand-side then becomes 0 and the right hand side is positive, so that the inequality is satisfied. The reduced system now has Assumption (iv) satisfied.

The uniqueness of the equilibrium is shown as follows; first make the following change of coordinates:

$$(s, x_1, \cdots, x_n) \to (z, x_1, \cdots, x_n) = (s + \sum_{j=1}^{n} \frac{x_j}{k_j}, x_1, \cdots, x_n)$$

so that the system (10) becomes

$$\begin{cases} \dot{z} &= D(s_{in} - z) \\ \dot{x}_i &= x_i \left(h_i \left(z - \sum_{j=1}^n \frac{x_j}{k_j}, x_i \right) - D \right) \end{cases} \tag{11}$$

We directly see that $\bar{z} = s_{in}$, so that, at a positive equilibrium, $\bar{x}_i$ must satisfy

$$h_i \left(s_{in} - \sum_{j=1}^{n} \frac{\bar{x}_j}{k_j}, \bar{x}_i \right) = D$$

Let us now replace $\sum_{j=1}^{n} \frac{\bar{x}_j}{k_j}$ with a constant u. The equilibrium value of x_i is then a function of u that we will denote $\tilde{x}_i(u)$ and that satisfies

$$h_i\left(s_{in} - u, \tilde{x}_i(u)\right) = D \text{ for } u < s_{in}$$

These functions $\tilde{x}_i(u)$ are identical to the "equilibrium characteristics of species i" that were defined in [16]. For $u = 0$, point (iii) of Assumption 1 ensures that, for each i, there exists a single value $\tilde{x}_i(0) > 0$ such that $h_i\left(s_{in}, \tilde{x}_i(0)\right) = D$; the sum of all these $\frac{\tilde{x}_i(0)}{k_j}$ is then larger than $u = 0$. Differentiating $h_i\left(s_{in} - u, \tilde{x}_i(u)\right) - D = 0$ with respect to u yields

$$-\frac{\partial h_i}{\partial s} + \frac{\partial h_i}{\partial x_i}\frac{d\tilde{x}_i}{du} = 0$$

so that point (ii) implies that

$$\frac{d\tilde{x}_i}{du} < 0$$

For increasing values of u, the value of the sum $\sum_{j=1}^{n} \frac{\tilde{x}_j(u)}{k_j}$ then decreases until $u = s_{in} - \tilde{s}$. At this moment, point (iv) shows that the sum is smaller than $u = s_{in} - \tilde{s}$. There exists therefore a single value $\bar{u}$ of u (that belongs to the open interval $(0, s_{in} - \tilde{s})$) such that we have

$$\bar{u} = \sum_{j=1}^{n} \frac{\tilde{x}_j(\bar{u})}{k_j}$$

There is therefore a single equilibrium to system (11) inside the positive orthant, and it is defined by:

$$(\bar{z}, \bar{x}_1, \cdots, \bar{x}_n) = (s_{in}, \tilde{x}_1(\bar{u}), \cdots, \tilde{x}_n(\bar{u}))$$

We can then state the main theorem of this section:

Theorem 3. *The single positive equilibrium of system (10) is asymptotically stable with a basin of attraction containing the positive orthant.*

Proof. In order to prove the stability of this equilibrium, we will first study the system on the attractive manifold defined by $z = s_{in}$. Indeed, we directly see from (11) that z exponentially converges towards s_{in}. We will study the stability of the interconnected system afterwards. The system that we need to analyze therefore has the form

$$\dot{x}_i = x_i\left(h_i\left(s_{in} - \sum_{j=1}^{n}\frac{x_j}{k_j}, x_i\right) - D\right) \tag{12}$$

which is defined in the set

$$\mathcal{D} = \{x \in I\!R^n | x_i \geq 0 \text{ for } i \in \{1, \cdots, n\}, \sum_{j=1}^{n}\frac{x_j}{k_j} \leq s_{in}\}$$

We will also define

$$\mathcal{D}_+ = \{x \in I\!R^n | x_i > 0 \text{ for } i \in \{1, \cdots, n\}, \sum_{j=1}^{n}\frac{x_j}{k_j} \leq s_{in}\}$$

The result of the previous section has been given for the case where the domain of definition was $I\!R_+^n$. In order to be able to use it here, we first note that, on the face where $\sum_{j=1}^{n}\frac{x_j}{k_j} = s_{in}$ the dynamics are defined as

$$\dot{x}_i = -Dx_i$$

We simply use these dynamics inside the region where $\sum_{j=1}^{n} \frac{x_j}{k_j} > s_{in}$, which is equivalent to stating that $\mu(s) = 0$ for $s < 0$, and we analyze the full system. If we now put (12) into the format of (5), we write the system

$$\dot{x}_i = x_i \left(h_i \left(s_{in} - u, x_i \right) - D \right)$$

and it is easily seen, from hypothesis (ii), that points (A) and (B) of Theorem 2 are satisfied by these equations with $g_j(x_j) = \frac{x_j}{k_j}$. The unique equilibrium of (12) is therefore attractive in the whole positive orthant (in $\mathcal{D}_+$, in fact).

The analysis of the interconnected system is concluded by noting that a solution of the interconnected system (11) either goes to the equilibrium, goes to the boundary of the positive orthant or goes unbounded. This last option is clearly not possible because we can easily see that $z(t)$ is upper-bounded with $\max(s_{in}, z(0))$ and $\sum_{j=1}^{n} \frac{x_j}{k_j}$ is upper-bounded with $z(t)$ because of the way z was defined through a change of coordinates. We will show that no solution can go to the boundary of the positive orthant.

In order to do that, it suffices to use a theorem that was given by Thieme [23] and Markus [17], in a version that can be found in [21] about triangular systems

$$
\begin{array}{llll}
\dot{y} & = & Ay & y \in D_y \in I\!\!R^m \\
\dot{x} & = & f(x, y) & x \in D_x \in I\!\!R_+^n
\end{array}
\tag{13}
$$

where $D_y \times D_x$ is positively invariant for this system, which is dissipative (all solution converge to a compact subset of $D_y \times D_x$) and has A Hurwitz. This theorem states that

Theorem 4 (Thieme & Markus). *If the reduced system*

$$\dot{x} = f(x, 0)$$

- **(I):** *has isolated hyperbolic equilibria x^i ($i \in \{1, \cdots, p\}$) and all of its solutions converge towards one of these equilibria.*
- **(II):** *has the dimension of its stable manifold $\mathcal{M}^+(x^i)$ equal to n for $i \in \{1, \cdots, r\}$ and less than n for $i \in \{r+1, \cdots, p\}$.*
- **(III):** *does not have a cycle of equilibria.*

then every solution of (13) converges towards one of the equilibria $(0, x^i)$ and

$$dim(\Lambda^+(0, x^i)) = m + dim(\mathcal{M}^+(x^i))$$

where $\Lambda^+(0, x^i)$ is the stable manifold of $(0, x^i)$. Also $\cup_{i=r+1}^{p} \Lambda^+(x_i, 0)$ has Lebesgue measure zero.

In our case, $m = 1$, $y = z - s_{in}$ and $\dot{x} = f(x, 0)$ represents system (12). We will directly consider system (11) in our analysis instead of doing the (unnecessary) change of coordinates from z to y.

We will now check if Assumptions (I)-(III) of Theorem 4 are satisfied for (12) in $\mathcal{D}$.

We have seen that it has a single equilibrium in $\mathcal{D}_+$. If we now consider faces of $\mathcal{D}$, we see that the same holds. Indeed, let us consider a face where $x_i = 0$ for $i \in \mathcal{I}$ ($\mathcal{I}$ is a subset of $\{1, \cdots, n\}$), that we will denote

$$\mathcal{D}_+^{\mathcal{I}} = \{x \in \mathcal{D}_+ | \forall i \in \mathcal{I} : x_i = 0 \text{ and } \forall i \notin \mathcal{I} : x_i \neq 0\}$$

(we will also write $\mathcal{D}^{\mathcal{I}} = \{x \in \mathcal{D}_+ | \forall i \in \mathcal{I} : x_i = 0\}$).

We now see that the reduced system $\Sigma^{\mathcal{I}}$ (where we have eliminated the indices belonging to $\mathcal{I}$, which can be seen to correspond to locally unstable dynamics) indicates the behavior of (12) on $\mathcal{D}_+^{\mathcal{I}}$. Because $\Sigma^{\mathcal{I}}$ satisfies Assumptions (i)-(iv), it has a single positive equilibrium, so that (12) has a single equilibrium in the face $\mathcal{D}_+^{\mathcal{I}}$. System (12) then has a

single equilibrium $\bar{x}^{\mathcal{I}}$ in each face $\mathcal{D}_+^{\mathcal{I}}$, for all combinations $\mathcal{I}$ of indices of $\{1, \cdots, n\}$. Moreover, the satisfaction of Assumptions (i)-(iv) by $\Sigma^{\mathcal{I}}$ implies that all solutions with initial condition inside $\mathcal{D}_+^{\mathcal{I}}$ converge to $\bar{x}^{\mathcal{I}}$, while they go elsewhere if they start outside $\mathcal{D}_+^{\mathcal{I}}$. The stable manifold $M^+(\bar{x}^{\mathcal{I}})$ therefore is equal to $\mathcal{D}_+^{\mathcal{I}}$, and its dimension is $n - \sharp\mathcal{I}$. Consequently, every solution of (12) converges towards an equilibrium, so that (I) and (II) are satisfied (with $r = 1$).

The absence of a cycle of equilibria is seen as follows. Let us suppose that a cycle of equilibria goes through an equilibrium $\bar{x}^{\mathcal{I}}$ such that $x_i = 0$ for exactly q indices i. Because the stable manifold of this equilibrium is the whole q-dimensional face $\mathcal{D}_+^{\mathcal{I}}$ it belongs to, the cycle arrives at the equilibrium through a solution belonging to that face. While leaving $\bar{x}^{\mathcal{I}}$, the cycle then has to leave $\mathcal{D}_+^{\mathcal{I}}$, so that at least one of the x_i, which was equal to zero, becomes positive. The solution now belongs to a face where, at most, $q - 1$ indices satisfy $x_i = 0$, and converges to the corresponding equilibrium where at most, $q - 1$ indices satisfy $x_i = 0$. Recursively applying this reasoning, we see that the cycle of equilibria must eventually reach the region where 0 indices are such that $x_i = 0$, that is $\mathcal{D}_+$. Convergence then takes place towards $\bar{x}$, which cannot be part of a cycle because it is asymptotically stable. No cycle of equilibria then exists, and (iii) is satisfied.

We then conclude from Theorem 4 that all the solutions of system (11) converge towards one of its equilibria. Moreover, the set of initial conditions that do not converge towards $(0, \bar{x})$ has Lebesgue measure zero, so that it is already clear that almost all solutions with initial condition in the set $\mathbb{R}_+ \times \mathcal{D}$ will converge towards the interesting equilibrium. Because any system $\Sigma_z^{\mathcal{I}}$ (which is defined by setting $x_i = 0$ and eliminating the $\dot{x}_i$ equations in system (11) for all $i \in \mathcal{I}$) satisfies Assumptions (i)-(iv), we know that almost all solutions of (11) with initial condition in $\mathbb{R}_+ \times \mathcal{D}^{\mathcal{I}}$ converge to $(0, \bar{x}^{\mathcal{I}})$. Therefore the dimension of the part of the stable manifold of $(0, \bar{x}^{\mathcal{I}})$ that is nested in $\mathbb{R}_+ \times \mathcal{D}^{\mathcal{I}}$ is $n - \sharp\mathcal{I} + 1$ and is equal to almost the whole face $\mathbb{R}_+ \times \mathcal{D}^{\mathcal{I}}$. Theorem 4 states that the dimension of the whole stable manifold of $(0, \bar{x}^{\mathcal{I}})$ is also equal to $n - \sharp\mathcal{I} + 1$, so that it cannot reach out of $\mathbb{R}_+ \times \mathcal{D}^{\mathcal{I}}$. No stable manifold of the equilibria (other than $(0, \bar{x})$) can therefore go into the positive orthant, so that all solutions of (11) with initial condition inside $\mathbb{R}_+ \times \mathcal{D}_+$ converge towards $(0, \bar{x})$.

The equilibrium $(z, x) = (s_{in}, \bar{x})$ is then asymptotically stable with $\mathbb{R}_+ \times \mathcal{D}_+$ as region of attraction.

$\square$

Remark 3. *It is clear that Assumptions (i)-(iv) are tailored so that system (12) satisfies Assumptions (A) and (B) of Theorem 2. They are however natural (except maybe point (iv)), as they ensure uniqueness of the positive equilibrium and point (ii) and (iii) accurately represent the intra-specific competition. Point (ii) concentrates on the sign of the derivatives, while point (A) and (B) are only concerned with the signs of the functions.*

In this section, we have shown how intra-specific competition could prevent inter-specific competition from resulting in extinction of all but one of the species competing for the same nutrient. This idea is in fact quite intuitive: if one of the species starts growing and eliminating the others, the intra-specific competition will limit its growth rate, so that the other species stand a chance of survival.

The polytopic Lyapunov function that has been used is also quite intuitive: while working on the manifold $z = s_{in}$, the growth-rate is not limited by the actual $s(t)$, but rather by the crowding of the bioreactor: the crowding of the bioreactor is equivalent to the possibility of accessing the substrate for each species. If the reactor is very crowded, the species that are above their target equilibrium have a limited growth-rate because of this crowding

that limit their access and by the intra-specific competition, so that their concentrations are guaranteed to decrease; if the bioreactor is lightly populated, the species that are under their target equilibrium have an important growth-rate because they have an easy access to the substrate and because they have little competition with their own peers. The polytopic Lyapunov function simply expresses this observation in mathematical terms.

5. **Competitive exclusion despite intra-specific competition.** In this section, we will stick with the family of models (10), but we will check what happens when more species are present than what the chemostat can sustain. This is translated in mathematical term by considering models where no positive equilibrium exists. In order to do that, we consider system (10) with points (i)-(iii) of Assumption 1, but without point (iv). We remember that point (iv) was crucial in proving the existence of an equilibrium in the positive orthant. Without it, many equilibria still exist, but they are on the faces of the orthant, so that at least one of the species will disappear if there is convergence to an equilibrium point.

We will illustrate this on a simple case: let us assume that we have a system with n coexisting species, that feed on a single substrate. Let us now introduce a new species; three things can occur:

1. The species can simply join the existing species, and the system can go to a new positive equilibrium, where all species are present. It can be seen that the equilibrium value of the substrate is reduced with respect to the previous equilibrium, as well as the equilibrium values of the early species. This is quite intuitive.
2. There exists no equilibrium where all species are present, and the new species is the weakest of all (in a sense that will be evidenced later). This new species is eliminated and the system goes back to its previous equilibrium.
3. There exists no equilibrium where all species are present, but the new species is fitter than previously present species. Some of the early species are eliminated (the weakest), and the new species grows to an equilibrium.

In order to check what can happen in those scenarios, we will analyze the equilibria of system (11) when Assumption (iv) is not satisfied:

$$\begin{cases} \dot{z} & = & D(s_{in} - z) \\ \dot{x}_i & = & x_i \left(h_i \left(z - \sum_{j=1}^n \frac{x_j}{k_j}, x_i \right) - D \right) \end{cases} \tag{14}$$

where the equilibrium value of z is s_{in}, so that an equilibrium of (14) must satisfy:

$$\bar{x}_i \left(h_i \left(s_{in} - \sum_{j=1}^n \frac{\bar{x}_j}{k_j}, \bar{x}_i \right) - D \right) = 0$$

Following the same procedure as in our proof of uniqueness of a positive equilibrium before Theorem 3, we replace $\sum_{j=1}^n \frac{x_j}{k_j}$ with a constant u. To begin with, we will be interested in an equilibrium where, if a given species could survive for the given dilution D and the given substrate level $s_{in} - u$, it is present in the system. The equilibrium value of x_i is then a function of u that we will denote $\tilde{x}_i(u)$, the largest value of x_i that satisfies

$$\tilde{x}_i(u)(h_i \left(s_{in} - u, \tilde{x}_i(u) \right) - D) = 0 \text{ for } u < s_{in} \tag{15}$$

This means that, if

$$h_i \left(s_{in} - u, \tilde{x}_i(u) \right) - D = 0$$

has a solution, we take this solution. Otherwise, we take $\tilde{x}_i(u) = 0$. We can easily see that $\tilde{x}_i(u)$ is a decreasing function of u as long as $\tilde{x}_i(u) > 0$ (as we had shown before Theorem

3), and that it is equal to zero for $u \geq \tilde{u}_i$, where $\tilde{u}_i$ is the solution of

$$h_i\left(s_{in} - \tilde{u}_i, 0\right) - D = 0$$

For $u = 0$, point (iii) of Assumption 1 ensures that, for each i, there exists a single value $\tilde{x}_i(0) > 0$ such that $h_i\left(s_{in}, \tilde{x}_i(0)\right) = D$; the sum of all these $\frac{\tilde{x}_i(0)}{k_j}$ is then larger than $u = 0$. For increasing values of u, the value of the sum $\sum_{j=1}^{n} \frac{\tilde{x}_j(u)}{k_j}$ then decreases until $\sum_{j=1}^{n} \frac{\tilde{x}_j(u)}{k_j} = 0$ (in fact, this happens at the value of $u = \max_i(\tilde{u}_i)$). There exists therefore a single value $\bar{u}$ of u (that belongs to the open interval $(0, \max_i(\tilde{u}_i))$) such that we have

$$\bar{u} = \sum_{j=1}^{n} \frac{\tilde{x}_j(\bar{u})}{k_j}$$

We will denote this equilibrium $\bar{x} = \tilde{x}(\bar{u})$; it is given by the solution of

$$\begin{aligned} h_i\left(s_{in} - \bar{u}, \bar{x}_i\right) - D = 0 & \qquad \text{if } \bar{u} < \tilde{u}_i \\ \bar{x}_i = 0 & \qquad \text{if } \bar{u} \geq \tilde{u}_i \end{aligned}$$

It is interesting to note that the $\tilde{u}_i$ values are indicators of the ability of the species to resist to competition at the dilution rate D: the largest $\tilde{u}_i$, the stronger the species x_i.

Because we set ourselves in the case where Assumption (iv) is not satisfied, there is some i such that $\bar{u} > \tilde{u}_i$. We can now define two sets of indices:

$$\begin{aligned} \mathcal{I}_+ &= \{i \in \{1, \cdots, n\} | \bar{x}_i > 0\} \\ \mathcal{I}_0 &= \{i \in \{1, \cdots, n\} | \bar{x}_i = 0\} \end{aligned}$$

Our assumptions imply that neither is empty.

We can now show that this equilibrium is asymptotically stable because the linearization of the x_i dynamics for $i \in \mathcal{I}_0$ is in the form

$$\begin{aligned} \dot{X}_i &= \left(h_i\left(s_{in} - \sum_{j \in \mathcal{I}_+} \frac{\bar{x}_j}{k_j}, 0\right) - D\right) X_i \\ &= \left(h_i\left(s_{in} - \bar{u}, 0\right) - D\right) X_i \end{aligned}$$

Because $i \in \mathcal{I}_0$, we have that, for $\tilde{u}_i < \bar{u}$, $h_i\left(s_{in} - \tilde{u}_i, 0\right) = D$; this induces that

$$h_i\left(s_{in} - \bar{u}, 0\right) - D < 0$$

so that the X_i dynamics are stable. We can then focus on the stability analysis of the reduced system (where we have eliminated all $i \in \mathcal{I}_0$ and replaced those x_i by 0 in the rest of the system). This reduced system is exactly system (12), with Assumptions (i)-(iv) satisfied, so that the positive equilibrium is stable. The analysis of this reduced system also shows that no other equilibrium x^* has $x_i^* > 0$ for all $i \in \mathcal{I}_+$ and $x_i^* = 0$ for all $i \in \mathcal{I}_0$.

Other equilibria are then either characterized by $x_i > 0$ for some $i \in \mathcal{I}_0$ or $x_i = 0$ for some $i \in \mathcal{I}_+$. We will detail those two cases in the following and analyze their stability.

• Let us first consider (s_{in}, x^*), an equilibrium of (14) that is such that $x_i^* > 0$ for all i in $\mathcal{K}$, a subset of $\mathcal{I}_0$. We will first show that there exists some $j \in \mathcal{I}_+$ that is such that $x_j^* = 0$. Indeed, if it were not the case, the equilibrium would be the solution of the equations

$$h_k\left(s_{in} - \sum_{l \in \mathcal{I}_+ \cup \mathcal{K}} \frac{x_l^*}{k_l}, x_k^*\right) - D = 0 \quad \forall k \in \mathcal{I}_+ \cup \mathcal{K} \tag{16}$$

We will redo the previous procedure, except that we will now only concentrate on those equations. Replacing $\sum_{l \in \mathcal{I}_+ \cup \mathcal{K}} \frac{x_l^*}{k_l}$ with the constant u, we now look at

$$h_k\left(s_{in} - u, \tilde{x}_k(u)\right) - D = 0 \quad \forall k \in \mathcal{I}_+ \cup \mathcal{K} \tag{17}$$

This system has no solution as we have seen while looking for $\bar{x}$. Indeed, we have seen that, before u reaches $\bar{u}$, all solutions of (15) go to zero for $j \in \mathcal{K}$, so that there exists $0 < \tilde{u} < \bar{u}$ such that the set of equations (17) has no solution for $u > \tilde{u}$. At that point, we have $\tilde{x}_k(\tilde{u}) > \tilde{x}_k(\bar{u})$, so that

$$\sum_{l \in \mathcal{I}_+ \cup \mathcal{K}} \frac{\tilde{x}_l(\tilde{u})}{k_l} > \sum_{l \in \mathcal{I}_+} \frac{\tilde{x}_l(\bar{u})}{k_l} = \bar{u} > \tilde{u}$$

No solution of the set of equations (17) can then be found for u inside $(0, \tilde{u}]$ because

$$\sum_{l \in \mathcal{I}_+ \cup \mathcal{K}} \frac{\tilde{x}_l(u)}{k_l} > u$$

for all u inside this interval.

Therefore, we are in the presence of an equilibrium x^* that is such that $x_i^* > 0$ for all $i \in \mathcal{K}$, a subset of $\mathcal{I}_0$ and $x_i^* = 0$ for all $i \in \mathcal{J}$, a subset of $\mathcal{I}_+$. Let us now consider some $i \in \mathcal{K}$. We have seen that

$$h_i(s_{in} - \bar{u}, x_i) = D$$

has no solution. Therefore, we see that $u^* < \bar{u}$, so that

$$h_i(s_{in} - u^*, x_i^*) = D$$

can have a solution. This solution is such that $x_i^* > \bar{x}_i$ for all $i \in \mathcal{I}_+ \setminus \mathcal{J}$ and $s^* > \bar{s}$.

• Let us now consider (s_{in}, x^*), an equilibrium of (14) that is such that $x_i^* = 0$ for all $i \in \mathcal{I}_0$ ($\mathcal{K}$ is empty) and there exists a non-empty subset $\mathcal{J}$ of $\mathcal{I}_+$ that contains all indices j of $\mathcal{I}_+$ that are such that $x_j^* = 0$. The equilibrium x^* must then satisfy

$$h_k \left(s_{in} - \sum_{l \in \mathcal{I}_+ \setminus \mathcal{J}} \frac{x_l^*}{k_l}, x_k^* \right) - D = 0 \quad \forall k \in \mathcal{I}_+ \setminus \mathcal{J}$$

Let us replace $\sum_{l \in \mathcal{I}_+ \setminus \mathcal{J}} \frac{x_l^*}{k_l}$ with a constant u and analyze the solutions of

$$h_k(s_{in} - u, \tilde{x}_k(u)) - D = 0 \quad \forall k \in \mathcal{I}_+ \setminus \mathcal{J}$$

The functions $\tilde{x}_k(u)$ still are decreasing functions of u that start in $\tilde{x}_k(0) > 0$ (so that $\sum_{l \in \mathcal{I}_+ \setminus \mathcal{J}} \frac{\tilde{x}_l(0)}{k_l} > u = 0$). When u reaches $\bar{u}$, we obviously have

$$\begin{aligned} \sum_{l \in \mathcal{I}_+ \setminus \mathcal{J}} \frac{\tilde{x}_l(\bar{u})}{k_l} &= \sum_{l \in \mathcal{I}_+ \setminus \mathcal{J}} \frac{\bar{x}_l}{k_l} \\ &< \sum_{l \in \mathcal{I}_+} \frac{\bar{x}_l}{k_l} \\ &= \bar{u} \end{aligned}$$

The solution u^* of the equation $u = \sum_{l \in \mathcal{I}_+ \setminus \mathcal{J}} \frac{\tilde{x}_l(u)}{k_l}$ therefore belongs to the interior of the interval $(0, \bar{u})$. For all $l \in \mathcal{I}_+ \setminus \mathcal{J}$, we therefore have

$$x_l^* > \bar{x}_l$$

and $s^* > \bar{s}$. This is quite intuitive: if less species are present, they can grow more, while keeping more substrate.

With that, we have covered all the possible equilibria. We can now study their stability by noting what they have in common: $u^* < \bar{u}$ and there exists some $i \in \mathcal{I}_+$ such that $x_i^* = 0$. Let us concentrate on the dynamics of this x_i near x^*:

$$\dot{x}_i = x_i \left(h_i \left(z - \sum_{j=1}^n \frac{x_j}{k_j}, x_i \right) - D \right)$$

The linearization of this equation near the equilibrium x^* yields

$$\begin{aligned}
\dot{X}_i &= \left(h_i \left(s_{in} - \sum_{j \in (\mathcal{I}_+ \setminus \mathcal{J}) \cup \mathcal{K}} \frac{x_j^*}{k_j}, 0 \right) - D \right) X_i \\
&= \left(h_i \left(s_{in} - u^*, 0 \right) - D \right) X_i
\end{aligned}$$

Remembering that

$$h_i \left(s_{in} - \bar{u}, \bar{x}_i \right) - D = 0$$

we have that

$$h_i \left(s_{in} - u^*, 0 \right) - D > 0$$

because $\frac{\partial h_i}{\partial s} > 0$ and $s_{in} - u^* > s_{in} - \bar{u}$, while $\frac{\partial h_i}{\partial x_i} < 0$ with $0 < \bar{x}_i$. The X_i dynamics are unstable, so that every equilibrium $x_i^* \neq \bar{x}$ is unstable.

From this analysis, we can derive the following proposition:

Proposition 1. *The only stable equilibrium of system (14) satisfying points (i)-(iii) of Assumption 1 is the one with the minimal substrate level with respect to all other equilibria*

Indeed, we have seen that $\bar{u} > u^*$ for any equilibrium $x^* \neq \bar{x}$ so that

$$\sum_{j=1}^{n} \frac{\bar{x}_j}{k_j} > \sum_{j=1}^{n} \frac{x_j^*}{k_j} \tag{18}$$

Since we have $\sum_{j=1}^{n} \frac{x_j^*}{k_j} + s^* = s_{in}$ for all equilibria, we then have $\bar{s} < s^*$ for all equilibria $x^* \neq \bar{x}$, and the proposition follows. It is interesting to note that this result is classically also valid for the original competition model (9).

If we go back to the three scenarios that we described, about a new species x_{n+1} invading an ecosystem where n species are already present (at the equilibrium value $x^{\{n\}}$), we have

1. If there exists a positive equilibrium $\bar{x}^{\{n+1\}}$, all the species survive, and the value of $\sum_{j=1}^{n+1} \frac{\bar{x}_j^{\{n+1\}}}{k_j} > \sum_{j=1}^{n} \frac{\bar{x}_j^{\{n\}}}{k_j}$. This is because $(\bar{x}^n, 0)$ is also an equilibrium x^* of the $n + 1$-dimensional system, so that (18) holds.
2. If no positive equilibrium exists, and the arriving species is eliminated, this is because $(\bar{x}^n, 0)$ is the equilibrium which maximizes the weighted sum. The species x_{n+1} is the weakest of the species, in the sense that it is the species that cannot survive for the largest value of the substrate concentration ($\tilde{u}_{n+1}$ is the minimum of all species, so that $s_{in} - \tilde{u}_{n+1}$ is maximum)
3. If no positive equilibrium exists, and the equilibrium $(\bar{x}^n, 0)$ does not maximize the weighted sum, some species are eliminated, but not x_{n+1}. A number of those, which have the smallest value of $\tilde{u}_i$ do not survive.

In all those cases, the transition is made to minimize the equilibrium substrate (or maximize the substrate consumption). In the slightly different case where $\bar{x}^n$ (the pre-existing equilibrium) had some vanishing species, the conclusions are unchanged with respect to the previous discussion: either all non-zero species survive while accepting or rejecting x_{n+1}, or some of them disappear (and x_{n+1} joins the equilibrium); no competitor mediated coexistence, as presented in [2], can occur.

In this section, the analysis has solely concentrated on the local aspects in order to infer global conclusions. However, our Lyapunov approach of the previous sections could certainly be extended to encompass equilibria on the border of the orthant.

6. **Conclusion.** In this paper, we have shown global stability of the equilibrium of interconnected scalar systems through the use of a non-smooth Lyapunov function. This result is valid in the general nonlinear case, and in the case of Kolmogorov systems. We have then used this result to show that persistence of all the species in a chemostat where all species are in competition for the same nutrient, can be explained through intra-specific competition. Finally, we have proved that, if all species cannot survive, there still exists a single stable equilibrium in the chemostat, the one that maximizes the total weighted biomass and minimizes the substrate; some exclusion is again present because of the competition.

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