A new proof of the competitive exclusion principle in the chemostat

Alain Rapaport, Mario Veruete

Manuscript submitted to
AIMS' Journals
Volume **X**, Number **0X**, XX **200X**

doi:10.3934/xx.xx.xx.xx

pp. **X–XX**

A NEW PROOF OF THE COMPETITIVE EXCLUSION PRINCIPLE IN THE CHEMOSTAT

Alain Rapaport*

MISTEA, Univ. Montpellier, Inra, Montpellier SupAgro
2, place Pierre Viala
34060 Montpellier, France

and Mario Veruete

IMAG, Univ. Montpellier, CNRS
Place Eugène Bataillon
34090 Montpellier, France

(Communicated by the associate editor name)

Abstract. We give an new proof of the well-known competitive exclusion principle in the chemostat model with N species competing for a single resource, for any set of increasing growth functions. The proof is constructed by induction on the number of the species, after being ordered. It uses elementary analysis and comparisons of solutions of ordinary differential equations.

1. **Introduction.** The Competitive Exclusion Principle (CEP) has a long history in the scientific literature. Since the thirties, the Russian botanist Gause conducted experiments on the growth of yeasts and paramecia in mixed cultures, and reported that the most competitive species systematically eliminated the other [5]. In his book "The struggle for existence", he showed that competitive exclusion had indeed a more universal scope : two similar living organisms evolving in the same environment and competing for a shared resource cannot coexist for ever, one of them having always a slight advantage over the other one, or being more adapted to the ecosystem [6]. In the 1960s, this statement has become quite popular in ecology but also in economics : the CEP applies to many kinds of ecosystems, and not only for micro-organisms, since there are consumers and resources [7]. It is also commonly taught as "Gause's law" in theoretical ecology.

However, it was not until the 1970s that the first statement of a mathematical theorem was found in the literature, along with its proof [10], for the chemostat model. It refers to the mathematical result that establishes conditions under which almost all solutions converge toward a steady-state of the system having at most one species. The chemostat model is widely used in microbiology and ecology as a mathematical representation of growth of micro-organisms in ecosystems that are continuously fed with nutrients. Several textbooks on the mathematical analysis of

2010 *Mathematics Subject Classification.* 34K20, 92D25.

Key words and phrases. Chemostat model, competitive exclusion, global stability, comparison principle, induction.

* Corresponding author: Alain Rapaport.

this model with one and more species are available [17, 1, 8]. The chemostat model can be also considered as a quite general resource/consumers model [12]. The CEP has also a long history in the literature of bio-mathematics. Hsu, Hubbell and Waltman have proposed a first proof in 1977 for Monod's functions as particular growth rates [10]. Hsu generalized this result in 1978 for different removal rates [9]. These two contributions use explicit Lyapunov functions to demonstrate the overall convergence. In 1980, Armstrong and McGehee have given a simple proof for any monotonic growth functions but for particular initial conditions belonging to an invariant set [2]. In 1985, Butler and Wolkowicz proposed a proof for any monotonic growth function [3]. One of the difficulties to prove the global stability originates from the fact that the graphs of any growth function can intersect one another at several points. During the transients a species could dominate the competition without being the final winner of the competition on the long run. Finally, it was in 1992 that Wolkowicz and Lu proposed a proof, based on a Lyapunov function, for growth functions more general than Monod functions (but under additional technical assumptions) and different removal rates [18]. This result has been later extended or complemented [11, 14, 13, 16, 15]. However, the proof of global stability for any monotonic growth functions and removal rates remains today an open mathematical problem [4].

In the present paper, we propose a new proof of the CEP for any monotonic growth functions but under identical removal rates. The existing proofs rely on relatively sophisticated tools, such as ω-limit sets [3], Lyapunov functions and LaSalle Invariance Principle [10, 18] and the theory of asymptotically autonomous systems (e.g. Appendix F in [17]). We show here that it is possible to obtain a proof with elementary analysis, based on single comparisons of solutions of ordinary differential equations. While species are sorted in ascending break even concentrations, the key of the proof relies on the observation of the time evolution of the proportions r_i of the density of species i over the density of the first species. Whatever is the initial condition and how the transients could exhibit an alternation of dominance among species or not, there always exists a finite time at the end of which the proportion r_N is decreasing exponentially for any future time. We show that this property is due to the level of the resource that reaches in finite time an interval which is unfavourable for the N-th species, and belongs to this interval for ever. We show that these two properties hold for the other species by induction on the index set $\{N, N-1, \cdots, 2\}$: this is our main result (Proposition 2 given in Section 3.4). This proves that the only winner of the competition is the first species.

2. Competitive exclusion principle for the chemostat.

The classical chemostat model for $N \in \mathbb{N}^*$ species competing for a single resource is given by the system of differential equations

$$\left\{ \begin{array}{ll} \dot{s} = & D(S_{\text{in}} - s) - \displaystyle\sum_{i=1}^{N} \mu_i(s) x_i \\ \dot{x}_i = & \mu_i(s) x_i - D x_i \quad (1 \leq i \leq N) \end{array} \right. , \tag{1}$$

where the operating parameters $D > 0$, $S_{\text{in}} > 0$ are the removal rate and the incoming density of resource (or input substrate concentration). The variable $s(t)$ denotes the density of resource (or substrate concentration) at time t. For $1 \leq i \leq N$, $x_i(t)$ represents the density of the i-th species and $\mu_i(\cdot)$ is the specific

growth rate function of species i. In this writing we have assumed, without any loss of generality, that the yield coefficients of resource s transformed in x_i are all identically equal to 1. In microbial ecology, the growth function μ_i often takes the form of a Monod's function $\mu(s) = \mu_{\max}\dfrac{s}{k+s}$, but we consider here more general ecosystems without particularizing the expression of the growth function. We make the following assumption.

Assumption 1 (Growth function)**.** *For each $1 \leq i \leq N$, we assume that*

1. $\mu_i \in C^1(\mathbb{R}^+)$.
2. $\mu_i(0) = 0$.
3. $\mu_i(\cdot)$ *is an increasing function.*

One can straightforwardly check that the positive orthant of $\mathbb{R}^{N+1}$ is invariant by the dynamics (1).

As often considered in the literature, we associate to each growth function the *break-even concentration* defined as follows.

Definition 1 (Break-even concentration)**.** *Under Assumption 1, for a given number $D > 0$, the break-even concentration $\lambda_i = \lambda_i(D)$ for the i-th species is defined as the unique solution of the equation $\mu_i(s) = D$, when it exists. When there is no solution to this equation, we set $\lambda_i = \infty$.*

On can notice that under Assumption 1, the growth functions are indeed more general than Monod type ones. They could for example change their concavity, be unbounded, or having isolated zeros for their derivatives, even for $s = \lambda_i$.

Assumption 2. *Species have distinct finite break-even concentrations, and without loss of generality are enumerated by indices such that*

$$\lambda_1 < \lambda_2 < \cdots < \lambda_N. \tag{2}$$

We dot not consider here species with $\lambda_i = \infty$, as one can straightforwardly check on equations (1) that this implies that the variable x_i converges to zero.

In Figure 1, we have represented several growth functions and the removal rate (in dashed line).

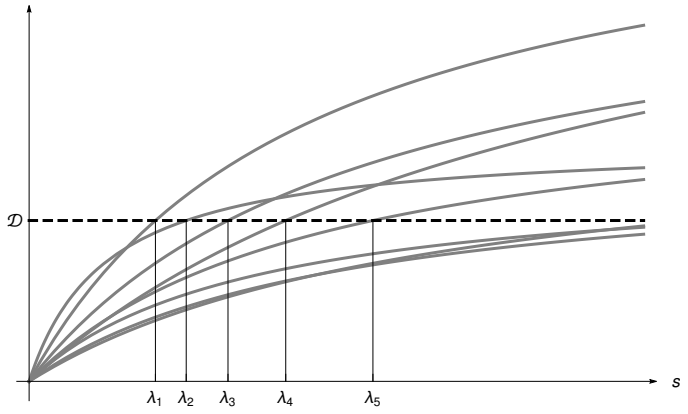

FIGURE 1. Growth functions and their break-even concentrations.

We shall see further how the particular cases when some numbers λ_i are identical can be tackled, packing the corresponding species (see Section 3.5 below). We first do not consider these non generic situations for sake of simplicity of the presentation.

We recall the statement of the Competitive Exclusion Principle.

Proposition 1 (Competitive Exclusion Principle)**.** *Assume one has* $\lambda_1 < S_{\rm in}$ *with Assumptions 1 and 2 fulfilled. For any non-negative initial condition with* $x_1(0) > 0$*, the solution of the system* (1) *converges to the equilibrium point* $(\lambda_1, S_{\rm in} - \lambda_1, 0, \dots, 0)$*.*

3. **Proof of Proposition 1.** The proof is based on a backward inductive argument : we show that the proportion, with respect to the density of the total biomass, of the density of each species goes to 0 when t tends to $+\infty$ excepted for the species with minimal break-even concentration.

3.1. **Change of coordinates.** We introduce the variable b, as the density of the total biomass, and the *proportion's vector* $p := (p_i)_{1 \le i \le N}$ where :

$$b := \sum_{i=1}^{N} x_i \quad \text{and} \quad p_i := \frac{x_i}{b}. \tag{3}$$

Additionally, we define the function $\bar\mu(s,p) := \sum_{i=1}^{N} p_i \mu_i(s)$. In those new variables, one can easily check that the system (1) writes :

$$\left\{ \begin{array}{rcll} \dot s & = & D(S_{\rm in} - s) - \bar\mu(s,p) b & \\ \dot b & = & \bar\mu(s,p) b - Db & \\ \dot p_i & = & p_i(\mu_i(s) - \bar\mu(s,p)) & (1 \le i \le N). \end{array} \right. \tag{4}$$

3.2. **Non extinction of the biomass.** We first give a necessary and sufficient condition for the persistence of the biomass, of interest in itself.

Lemma 1. *Consider that Assumptions 1 and 2 are fulfilled.*

1. *For any non-negative initial condition of* (1)*, the solution verifies*
$$\lim_{t \to +\infty} (b(t) + s(t)) = S_{\rm in}.$$
2. *Any species* j *with* $\lambda_j \ge S_{\rm in}$ *satisfies* $\lim_{t \to +\infty} x_j(t) = 0$*, whatever is the initial condition of* (1)*.*
3. *When* $\lambda_1 < S_{\rm in}$*, for any non-negative initial condition such that there exists* $i \in \{1, \cdots, N\}$ *with* $x_i(0) > 0$ *and* $\lambda_i < S_{\rm in}$*, the variable* $b(t)$ *is bounded from below by a positive number for any* $t > 0$*.*

Proof. 1. Consider the variable $m := b + s$. Then m solves the linear differential equation $\dot m = D(S_{\rm in} - m)$, which posses a unique equilibrium $m^\star = S_{\rm in}$, that is moreover globally asymptotically stable.

2. Consider first species j such that $\lambda_j \ge S_{\rm in}$ (if it exists). Fix $\epsilon > 0$. Then $\eta = D - \mu_j(S_{\rm in} - \epsilon/2)$ is a positive number. As $m(\cdot)$ converges to $S_{\rm in}$, there exists $T > 0$ such that $s(t) + x_j(t) \le m(t) < S_{\rm in} + \epsilon/2$ for any $t > T$. This implies that the dynamics of species j satisfies

$$\dot x_j(t) \le (\mu_j(S_{\rm in} - x_j(t) + \epsilon/2) - D)\, x_j(t) =: \phi_j(x_j(t))$$

for any $t > T$. The function ϕ_j has the property

$$x_j \geq \epsilon \;\Rightarrow\; \phi_j(x_j) \leq (\mu_j(S_{\text{in}} - \epsilon/2) - D)\, x_j \leq -\eta\epsilon < 0.$$

Therefore, the variable $x_j(t)$ exits the domain $\{x_j \geq \epsilon\}$ in finite time and stays outside for any future time, i.e. there exists $T' > T$ such that $x_j(t) < \epsilon$ for any $t > T'$. This statement is obtained for any arbitrary ϵ, which proves the convergence of the $x_j(\cdot)$ towards 0.

3. Let k be the maximal index such that $\lambda_k < S_{\text{in}}$ (which exists by Assumption 2) and denote $b_0 := x_1 + \cdots + x_k$. For any $i \leq k$, notice that one has

$$\mu_i(s)x_i \geq \min_{1\leq j\leq k} \mu_j(s)x_i$$

for any s and x_i, and by simple addition,

$$\sum_{i=1}^{k} \mu_i(s)x_i \geq \left(\min_{1\leq i\leq k} \mu_i(s)\right)\left(\sum_{i=1}^{k} x_i\right) = \min_{1\leq i\leq k} \mu_i(s)b_0. \tag{5}$$

The dynamics of b_0 writes

$$\dot{b}_0 = \sum_{i=1}^{k} \dot{x}_i = \sum_{i=1}^{k} \mu_i(s)x_i - D\sum_{i=1}^{k} x_i$$

and by inequality (5), one has $\dot{b}_0(t) \geq \Psi(t, b_0(t))$ for any $t > 0$, where Ψ is defined as follows

$$\Psi(t, b_0) := \big(\min_{1\leq i\leq k} \mu_i(s(t)) - D\big)\, b_0. \tag{6}$$

As the inequality $\mu_i(S_{\text{in}}) > D$ is fulfilled for any $i \leq k$, and the functions μ_i are continuous, there exist $\epsilon > 0$ and $\eta > 0$ such that

$$\min_{1\leq i\leq k} \mu_i(\sigma) - D > \epsilon \text{ for any } \sigma > S_{\text{in}} - \eta. \tag{7}$$

Since $m(t)$ converges to S_{in} and $x_j(t)$ converges to 0 for any $j > k$, there is a time $T^\star \geq 0$ such that

$$s(t) = m(t) - b_0(t) - \sum_{j\geq k} x_j(t) > S_{\text{in}} - b_0(t) - \frac{\eta}{2} \text{ for any } t > T^\star.$$

Then, by inequality (7), the function Ψ defined in (6) fulfills the following property :

$$t > T^\star,\, b_0 \leq \tfrac{\eta}{2} \;\Rightarrow\; \Psi(t, b_0) \geq \big(\min_{1\leq i\leq k} \mu_i(S_{\text{in}} - \eta) - D\big)b_0 \geq \epsilon\, b_0.$$

As one has $b_0(0) > 0$ by hypothesis, $b_0(t)$ is strictly positive for any $t > T^\star$. Let us show that b_0 cannot stay into or enter the interval $[0, \frac{\eta}{2}]$ for times larger than $T^\star$. Notice first that for any $t > T^\star$ such that $b_0(t) = \frac{\eta}{2}$, one has $\dot{b}_0(t) > 0$. Therefore, if there exists $\bar{t} > T^\star$ such that $b(\bar{t}) = \frac{\eta}{2}$, one has $b(t) > \frac{\eta}{2}$ for any $t > \bar{t}$. If there exists $t_1 > T^\star$ such that $b(t_1) < \frac{\eta}{2}$, then one can use the comparison principle of scalar o.d.e. as follows. Let $\underline{b}_0(\cdot)$ be the solution of the Cauchy problem :

$$\dot{\underline{b}}_0 = \epsilon\underline{b}_0,\; \underline{b}_0(t_1) = b_0(t_1) > 0 \quad \Rightarrow \quad \underline{b}_0(t) = b_0(t_1)e^{\epsilon(t-t_1)}.$$

Then, one has $b_0(t) \geq \underline{b}_0(t)$ for any $t > t_1$ such that $b_0(t) < \frac{\eta}{2}$. As $\underline{b}_0$ reaches $\frac{\eta}{2}$ in finite time, we deduce that there exists $\bar{t} > t_1$ such that $b_0(\bar{t}) = \frac{\eta}{2}$ and one concludes as before. Finally, the variable $b(t) \geq b_0(t)$ is bounded from below by $\frac{\eta}{2}$ in finite time. □

3.3. **Frame on the substrate's dynamics.** By Assumption 2, growth functions are ordered on each interval $[\lambda_i, \lambda_{i+1}]$ (see Figure 1) in the sense that, for all $i \in \{1 \cdots N-1\}$, one has

$$\mu_i(s) > \mu_j(s), \quad \forall j > i, \quad \forall s \in [\lambda_i, \lambda_{i+1}].$$

By continuity of $\mu_i(\cdot)$, there are numbers $\nu > 0$, $s_i^- < \lambda_i$ and $s_i^+ > \lambda_{i+1}$ such that

$$\mu_i(s) > \mu_j(s) + \nu, \quad \forall s \in [s_i^-, s_i^+], \quad \forall j > i. \tag{8}$$

By monotonicity of μ_i, we have $\mu_i(s_i^-) < D$ and $\mu_i(s_i^+) > D$. Moreover, one has

$$\begin{array}{rcl} j < i & \Rightarrow & \mu_j(s_i^+) > \mu_j(\lambda_i) > \mu_j(\lambda_j) = D \\ s_i^+ > \lambda_{i+1} & \Rightarrow & \mu_{i+1}(s_i^+) > D \end{array}$$

Therefore, the numbers

$$\left\{ \begin{array}{rcl} \gamma^- & := & D - \mu_1(s_1^-) \\ \gamma^+ & := & \min\limits_{2 \le i \le N} \min\limits_{j<i} \mu_j(s_{i-1}^+) - D \end{array} \right. \tag{9}$$

are positive. We define also the following numbers :

$$D^- := D - \frac{\gamma^-}{2}, \quad D^+ := D + \frac{\gamma^+}{2}\ . \tag{10}$$

Lemma 2. *Assume one has $\lambda_1 < S_{\rm in}$ with Assumptions 1 and 2. For any non-negative initial condition with $x_1(0) > 0$, there exists $T > 0$ such that $\dot{s}(t) \in [\Phi^-(t, s(t)), \Phi^+(t, s(t))]$ for any $t > T$, where*

$$\left\{ \begin{array}{rcl} \Phi^-(t,s) & := & [D^- - \bar{\mu}(s, p(t))]\, b(t) \\ \Phi^+(t,s) & := & [D^+ - \bar{\mu}(s, p(t))]\, b(t). \end{array} \right. \tag{11}$$

Proof. From Lemma 1, we know that $b(\cdot)$ is bounded from below by a positive number. Consider the function

$$z := \frac{S_{\rm in} - s}{b} = 1 + \frac{S_{\rm in} - m}{b}.$$

Since $m(\cdot)$ converges to $S_{\rm in}$ and $b(\cdot)$ is bounded from below by a positive number (see Lemma 1), $z(t)$ converges to 1 when t tends to $+\infty$. Furthermore, for $t > T$ with T large enough, one has $Dz(t) \in [D^-, D^+]$. Remark that the substrate dynamics can be written as follows

$$\dot{s} = \Phi(t,s) := b(t)\left[Dz(t) - \bar{\mu}(s, p(t))\right]\ ,$$

and one then obtains the inequalities $\Phi^-(t,s) \le \Phi(t,s) \le \Phi^+(t,s)$ for any $t > T$. □

3.4. **Extinction of the species by induction.**

Proposition 2. *Assume one has $\lambda_1 < S_{\rm in}$ with Assumptions 1 and 2. For any non-negative initial condition with $x_1(0) > 0$, the solution of system (1) satisfies*

i. *There exists $T_1 > 0$ s.t. $s(t) \in [s_1^-, s_1^+]$, $\forall t > T_1$*
ii. $\lim\limits_{t \to +\infty} p_j(t) = 0$, $\forall j > 1$.

Proof. We shall proceed by backward induction. Let us define the property

$$(\mathcal{P}_i): \quad \left\{ \begin{array}{ll} i. & \text{There exists } T_i > 0 \text{ s.t. } s(t) \in I_i := [s_1^-, s_i^+],\ \forall t > T_i \\ ii. & \lim\limits_{t \to +\infty} p_j(t) = 0,\ \forall j > i. \end{array} \right.$$

for $i \in \{1, \ldots, N-1\}$.

As $x_1(0) > 0$, the variable x_1 stays positive for any time and one can consider variables $r_i := \frac{x_i}{x_1}$ for $i \in \{2, \cdots, N\}$, whose dynamics is

$$\dot{r}_i = [\mu_i(s(t)) - \mu_1(s(t))]r_i. \tag{12}$$

By monotonicity of functions $\mu_i(\cdot)$ and property (8), we can write

$$s < s_1^- \Rightarrow \max_i \mu_i(s) < \max_i \mu_i(s_1^-) = \mu_1(s_1^-) \leq D^- - \frac{\gamma^-}{2} \tag{13}$$

where γ^-, D^- are defined in (9), (10). Similarly, one has

$$s > s_{N-1}^+ \Rightarrow \min_i \mu_i(s) > \min_i \mu_i(s_{N-1}^+) \geq D^+ + \frac{\gamma^+}{2} \tag{14}$$

where γ^+, D^+ are defined in (9), (10).

Consider a number $T > 0$ given by Lemma 2. From Lemma 1, there exists a number $\eta > 0$ such that $b(t) \geq \frac{\eta}{2}$ for any $t > T$. It then follows from (13) and (14) that the functions $\Phi^{\pm}$ defined in (11) fulfill the following inequalities :

$$\begin{aligned} s < s_1^-,\ t > T \quad &\Rightarrow \quad \Phi^-(t,s) \geq b(t)\left(D^- - \max_i \mu_i(s)\right) > \frac{\eta\,\gamma^-}{4} > 0 \\ s > s_{n-1}^+,\ t > T \quad &\Rightarrow \quad \Phi^+(t,s) \leq b(t)\left(D^+ - \min_i \mu_i(s)\right) < -\frac{\eta\,\gamma^+}{4} < 0. \end{aligned}$$

Therefore the variable s enters the interval I_{N-1} in a finite time $T_{N-1} > T$ and belongs to it for any future time. Furthermore, the inequalities (8) ensure to have $\mu_N(s) - \mu_1(s) < -\nu$ for any s in the interval I_{N-1}, and then the dynamics of r_N satisfies $\dot{r}_N \leq -\nu r_N$ for $t > T_{N-1}$. Thus r_N converges to 0, and x_N converges as well. Property $\mathcal{P}_{N-1}$ is then satisfied.

Assume that $\mathcal{P}_i$ is satisfied for an index $i \in \{2, \cdots, N-1\}$ and let us show that $\mathcal{P}_{i-1}$ is fulfilled. Figure 2 illustrates the sets I_i. Since the functions p_j converge to

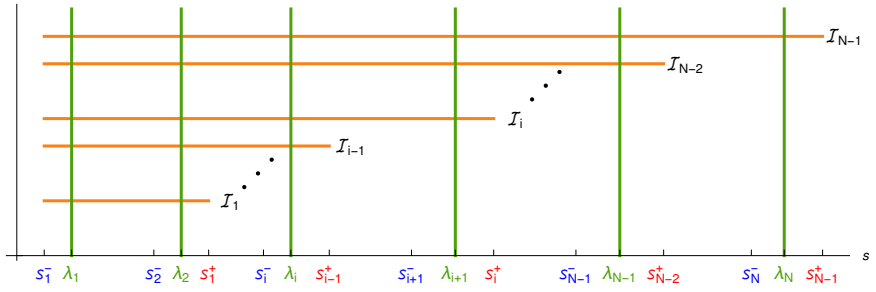

FIGURE 2. Illustration of the intervals $I_i = [s_1^-, s_i^+]$ for $i \in \{1, \cdots, N-1\}$ (in green, the values of the break-even concentrations λ_i, in orange, the nested intervals I_i)

.

0 for all $j > i$, there is $T' > T_i$ such that

$$\sum_{j>i} p_j(t) < \varepsilon := \frac{\gamma^+/4}{D^+ + \gamma^+/2}, \quad \forall t > T'.$$

Then, for $s > s_{i-1}^+$ and $t > T'$, the following inequality holds

$$\begin{aligned}\bar\mu(s,p(t)) &\geq \sum_{j\leq i}\mu_j(s)p_j(t)\\ &\geq \min_{j\leq i}\mu_j(s_{i-1}^+)(1-\varepsilon)\\ &\geq (D^+ + \tfrac{\gamma^+}{2})(1-\varepsilon) = D^+ + \frac{\gamma^+}{4}\end{aligned}$$

which provides the property of the function Φ^+:

$$s > s_{i-1}^+,\ t > T' \ \Rightarrow\ \Phi^+(t,s) \leq -\frac{\eta\,\gamma^+}{8} < 0.$$

Thus, in a finite time $T_{i-1} > T'$, s enters into the interval I_{i-1} and stays inside it for any future time. Furthermore, inequalities (8) lead to write $\dot r_i \leq -\nu r_i$ for $t > T_{i-1}$, which shows that x_i converges to zero. Property $\mathcal{P}_{i-1}$ is then satisfied. □

3.5. **The case of identical break-even concentration.** We relax Assumption 2 allowing some λ_i with $i > 1$ to be identical and show that Proposition 1 is also satisfied.

If there exist i and $\ell \geq 1$ such that $\lambda_1 < \lambda_{i-\ell} = \cdots = \lambda_i < S_{\rm in}$, at step i in the induction of the proof, we replace species i by the sum of species $i-\ell,\dots,i$ and show property $\mathcal{P}_i$, that is $\lim_{t\to+\infty} p_j(t) = 0$ for all $j > i-\ell+1$.

This can be done considering $\overline{r}_i := \sum_{j=i-\ell}^{i} r_j$ instead of r_i, and remark that we have also $s_{i-1}^+ = \cdots = s_{i-1-\ell}^+$. Then, one has

$$\dot{\overline{r}}_i = \left[\sum_{j=i-\ell}^{i}\alpha_j(t)\mu_j(s(t)) - \mu_1(s(t))\right] r_i$$

where $\alpha_j(t) = \dfrac{r_j(t)}{\overline{r}_i(t)} > 0$ with $\sum_{j=i-1}^{i}\alpha_j(t) = 1$. By (8), we have

$$\sum_{j=i-1}^{i}\alpha_j(t)\mu_j(s) < \mu_1(s) - \nu, \quad \forall s \in [s_1^-, s_i^+]$$

and then $\dot{\overline{r}}_i(t) < -\eta\overline{r}_i(t)$. Thus $\dot{\overline{r}}_i \leq \eta\,\overline{r}_i$ for $t > T$ which shows that $\overline{r}_i$ converges to zero as well as every x_j with $i \leq j \leq i+\ell$. The rest of the proof is identical.

3.6. **Conclusion.** Now that we know that the variables x_j converge to 0 for any $j > 1$, we can easily show that s tends to λ_1 as follows.

Accordingly to Proposition 2, there exists $T_1 > 0$ such that $s(t) \in [s_1^-, s_1^+]$ for any $t > T_1$. By Lemma 1, $b(t) + s(t)$ tends to $S_{\rm in}$ and the variable b is bounded from below by a positive number, say $\zeta > 0$. Then, there exists $\overline{T}_1 > T_1$ such that $s(t) \in [s_1^-, S_{in} - \frac{\zeta}{2}]$ for any $t > \overline{T}_1$. We then consider the variable

$$r(t) = \frac{\bar\mu(s(t),p(t))b(t)}{\mu_1(s(t))(S_{\rm in}-s(t))}, \quad t > \overline{T}_1$$

which tends to 1 when t tends to $+\infty$, and write the dynamics of s as

$$\dot s = \Gamma(t,s) := (S_{\rm in}-s)(D - \mu_1(s)r(t)) \tag{15}$$

Take any $\epsilon > 0$ sufficiently small to have $[\lambda_1 - \epsilon, \lambda_1 + \epsilon] \subset (s_1^-, S_{\rm in} - \frac{\zeta}{2})$. Define then $\eta = 2\min(\mu_1(\lambda_1 + \epsilon) - D, D - \mu_1(\lambda_1 - \epsilon))$. The function $\mu_1(\cdot)$ being increasing such that $\mu_1(\lambda_1) = D$, one has $\eta > 0$ and can write

$$s > \lambda_1 + \epsilon \Rightarrow \mu_1(s) > D + \tfrac{\eta}{2}\ ,\ s < \lambda_1 - \epsilon \Rightarrow \mu_1(s) < D - \tfrac{\eta}{2}.$$

As r tends to 1, there exists $T_2 > \overline{T}_1$ such that

$$\begin{array}{l} t > T_2,\ s > \lambda_1 + \epsilon \Rightarrow \mu_1(s) r(t) > D + \eta \\ t > T_2,\ s < \lambda_1 - \epsilon \Rightarrow \mu_1(s) r(t) < D - \eta \end{array}$$

Then, the function Γ fulfills the following properties

$$\begin{array}{l} t > T_2,\ s \in [\lambda_1 + \epsilon, S_{\rm in} - \frac{\zeta}{2}] \Rightarrow \Gamma(t,s) < -\eta\frac{\zeta}{2} < 0 \\ t > T_2,\ s \in [s_1^-, \lambda_1 - \epsilon] \Rightarrow \Gamma(t,s) > \eta(S_{\rm in} - s_1^-) > 0 \end{array}$$

which allows to conclude that the variable s converges to the interval $[\lambda_1 - \epsilon, \lambda_1 + \epsilon]$, and this can be obtained for any arbitrarily small $\epsilon > 0$.

Acknowledgments. The authors are thankful for having fruitful exchanges with Tewfik Sari, Claude Lobry, Jérôme Harmand, Kevin Cauvin and Romaric Condé about the chemostat model. Mario Veruete is grateful for the support of the National Council For Science and Technology of Mexico and to his Ph.D. supervisor, Dr. Matthieu Alfaro, for his permanent encouragement.

REFERENCES

[1] A. Ajbar and K. Alhumaizi. *Dynamics of the Chemostat: a Bifurcation Theory Approach*. Chapman and Hall, 2011.
[2] R.A. Armstrong and R. McGehee. Competitive exclusion. *American Naturalist*, 115:l51–170, 1980.
[3] G.J. Butler, , and G. Wolkowicz. A mathematical model of the chemostat with a general class of functions describing nutrient uptake. *SIAM Journal on Applied Mathematics*, 45:137–151, 1985.
[4] P. de Leenheer, B. Li, and H.L. Smith. Competition in the chemostat: Some remarks. *Canadian Applied Mathematics Quarterly*, 11(3):229–248, 2003.
[5] G.F. Gause. Experimental studies on the struggle for existence. *Journal of Experimental Biology*, 9:389–402, 1932.
[6] G.F. Gause. *The struggle for existence*. Dover, 1934. translated from Russian in 1971.
[7] G. Hardin. The competitive exclusion principle. *Science*, 131:1292–1297, 1960.
[8] J. Harmand, C. Lobry, A. Rapaport, and T. Sari. *The Chemostat: Mathematical Theory of Microorganism Cultures*. ISTE-Wiley, 2017.
[9] S. Hsu. Limiting behavior for competing species. *SIAM Journal on Applied Mathematics*, 34:760–763, 1978.
[10] S. Hsu, S. Hubbell, and P. Waltman. A mathematical theory for single-nutrient competition in continuous cultures of microorganisms. *SIAM Journal on Applied Mathematics*, 32:366–383, 1977.
[11] B. Li. Global asymptotic behavior of the chemostat: General response functions and differential removal rates. *SIAM Journal on Applied Mathematics*, 59:411–422, 1998.
[12] W. Murdoch, C. Briggs, and R. Nisbet. *Consumer-Resource Dynamics*. Princeton University Press, 2003.
[13] A. Rapaport and J. Dochain, D. Harmand. Long run coexistence in the chemostat with multiple species. *J. Theoretical Biology*, 257(2):252–259, 2009.
[14] A. Rapaport and J. Harmand. Biological control of the chemostat with nonmonotonic response and different removal rates. *Mathematical Biosciences & Engineering*, 5(3):539–547, 2008.
[15] T. Sari. Competitive exclusion for chemostat equations with variable yields. *Acta Applicandae Mathematicae*, 123(1):201–219, 2013.
[16] T. Sari and F. Mazenc. Global dynamics of the chemostat with different removal rates and variable yields. *Math. Biosci. Eng.*, 8:827–840, 2011.

[17] H. Smith and P. Waltman. *The Theory of the Chemostat: Dynamics of Microbial Competition*. Cambridge, 1995.

[18] G. Wolkowicz and Z. Lu. Global dynamics of a mathematical model of competition in the chemostat: General response functions and differential death rates. *SIAM Journal on Applied Mathematics*, 52:222–233, 1992.

E-mail address: alain.rapaport@inra.fr

E-mail address: mario.veruete@umontpellier.fr