Long run coexistence in the chemostat with multiple species ☆

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ABSTRACT

In this work we analyze the transient behavior of the dynamics of multiple species competing in a chemostat for a single resource, presenting slow/fast characteristics. We prove that coexistence among a subset of species, with growth functions close to each other, can last for a substantially long time. For these cases, we also show that the proportion of non-dominant species can be increasing before decreasing, under certain conditions on the initial distribution.

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1. Introduction

A popular concept in microbial ecology is the competitive exclusion principle (CEP) which expresses the fact that when two or more microbial species grow on the same substrate in a chemostat, at most one species, i.e. the species that has the best affinity with the limiting substrate, will eventually survive. This concept has been first introduced by Hardin (1960) and has been widely mathematically studied in the literature since (e.g. Aris and Humphrey, 1977; Stephanopoulos et al., 1979; Armstrong and McGehee, 1980; Butler and Wolkowicz, 1985). However coexistence of multiple species in chemostat is largely encountered in practical situations. Many efforts have been done to emphasize mathematically such coexistence behavior, either via periodic inputs (e.g. Smith, 1981; Butler et al., 1985) or via model rewriting (e.g. Cenens et al., 2000 that considers the filamentous backbone theory to emphasize the coexistence of flocks and filaments, or Lobry et al., 2004; Lobry and Harmand, 2006; Lobry et al., 2006 where the specific growth rate models are also dependent on the biomass, via in particular ratio dependence).

One should have in mind that the CEP characterizes an asymptotic property of the system, but does not provide any information on the transient dynamics, that has not yet been thoroughly investigated, to our knowledge. In the present paper, we propose to study the transient dynamics of multiple species growing on the same substrate, depending on the initial species distribution. When some of the species have close growth functions, on may observe a *practical* coexistence in the following sense: even if the species with best affinity will finally be the only surviving one, the transient stage before the other species have almost disappeared may eventually be substantially long. It appears that the different species may coexist for a long time before the competitive exclusion practically applies. More precisely, some of species may be first increasing (before finally decreasing) depending on the initial distribution.

The motivation of considering many species with close growth functions comes from the observations made by recent molecular approaches. In microbial ecosystems, thousands of species are present whereas the number of functions is limited (Curtis and Sloan, 2004; Pace, 1997). Moreover, the structural instability of microbial communities shows that same function can be carried out by several different species (Zumstein et al., 2000). It is also well known that constant mutation rates lead to occurring new individuals with different traits and with different but close growth functions, that can be consider as new species from the modeling point of view. In chemostat-like systems, the main function under consideration is usually the degradation of a given substrate, which is measured by the growth functions of each species. But only about 1% of the overall micro-organisms observed in real ecosystems can be isolated and cultivated in laboratory (Amann et al., 1995). Thus micro-organisms whose growth functions can be clearly identified represent only a tip of the iceberg and it is most probable that among a huge number of species, many should have growth functions close to each other.

Our analysis is based on a slow–fast characterization of the system dynamics, and provides an estimation of bounds from below of the times at which each species stops increasing and therefore starts decreasing. The slow–fast technique consists in approximating the fast variables by "quasi-stationary" equilibria. Nevertheless, the validity of such an approximation has to be checked, proving the attractivity of the slow manifold (see for instance Tikhonov's theorem in Khalil, 1996), as we do in this paper. We believe that a slow–fast analysis of the chemostat model with many close growth functions has not yet been addressed in the literature, and brings a new message for biologists.

The paper is organized as follows. Section 2 is dedicated to some preliminaries about the system dynamics and the CEP. Section 3 concentrates on the slow–fast description of the system dynamics. A reduced order model is deduced from the slow–fast system characterization in Section 4, where the analysis provides elements for the practical coexistence of multiple species with closed growth functions. Finally the proposed results are illustrated via numerical simulations in Section 5.

2. Preliminaries

Let us consider the chemostat model with one limited resource and m species

$$\begin{cases} \dot{x}_i = \mu_i(s)x_i - Dx_i, \quad i = 1, \ldots, m, \\ \dot{s} = -\sum_{i=1}^{m} \frac{\mu_i(s)}{y_i}x_i + D(S_{in} - s). \end{cases} \quad (1)$$

The growth functions $\mu_i(\cdot)$ are assumed to be C^1 non-negative functions such that $\mu_i(0) = 0$.

Without any loss of generality, we shall assume in the following that all yield factors y_i have been taken equal to one (one can easily check that this amounts to replace x_i by x_i/y_i or to change the unit measuring each stock x_i). Let us first recall the following lemma.

Lemma 2.1. *The domain*

$$\mathscr{D} = \left\{ (x, s) \in \mathscr{R}_+^{m+1} \,\middle|\, \sum_{i=1}^{m} x_i + s \leqslant S_{in} \right\}$$

is invariant and attractive by dynamics (1) *in the non-negative cone* $\mathscr{R}_+^{m+1}$.

Proof. When $x_i = 0$, one has $\dot{x}_i = 0$. Consequently, the trajectories cannot cross the axes $x_i = 0$.

When $s = 0$, one has $\dot{s} = DS_{in} > 0$. The trajectories cannot approach the axis $s = 0$.

From these two facts, one concludes that $\mathscr{R}_+^{m+1}$ is an invariant domain. Consider now the variable

$$z = \sum_{i=1}^{m} x_i + s,$$

which is solution of the ordinary differential equation $\dot{z} = D(S_{in} - z)$. One immediately concludes that the domain $\mathscr{D} = \mathscr{R}_+^{m+1} \cap \{z \leqslant S_{in}\}$ is invariant and attractive. $\quad \square$

Let us now introduce the following assumption.

Assumption A0. Functions $\mu_i(\cdot)$ are increasing for any $i = 1, \ldots, m$.

Under Assumption A0, it is usual to define the break-even concentrations:

$$\lambda_i(D) = \begin{vmatrix} s_i & \text{such that } \mu_i(s_i) = D, \\ +\infty & \text{if } \mu_i(s) < D \text{ for any } s \geqslant 0 \end{vmatrix} \quad (2)$$

for each $i = 1, \ldots, m$. Let us recall the CEP (first proved for general response functions in Armstrong and McGehee, 1980; see also Smith and Waltman, 1985, Theorem 3.2), for which the following assumption is required.

Assumption A1. There exists an unique $i^\star \in \{1, \ldots, m\}$ such that

$$\lambda_{i^\star}(D) = \min_{i=1,\ldots,m} \lambda_i(D).$$

Proposition 2.1 (*CEP*). *Under Assumptions* A0 *and* A1, *any trajectory of* (1) *with initial condition in the non-negative cone such that* $x_{i^\star}(0) > 0$ *fulfills the following properties*:

- *the substrate concentration* $s(\cdot)$ *converges asymptotically toward the steady state value*:

  $$s^\star = \min(\lambda_{i^\star}(D), S_{in}),$$
- *the species concentration* $x_{i^\star}(\cdot)$ *converges asymptotically toward* $S_{in} - s^\star$ *and*
- *any species concentration* $x_i(\cdot)$ *with* $i \neq i^\star$ *converges asymptotically toward zero*.

Corollary 2.1. *When* $s^\star < S_{in}$, *the convergence given by Proposition 2.1 is exponential*.

Proof. One can easily check the $m + 1$ eigenvalues of the Jacobian matrix at the non-null equilibrium are $-D < 0$, $-\mu'_{i^\star}(s^\star)(S_{in} - s^\star) < 0$ and $\mu_i(s^*) - D < 0$ for any $i \neq i^\star$. $\quad \square$

The CEP provides information about the asymptotic behavior of solutions of (1). In the present work, we rather focus on transient stages of the trajectories of system (1), when some of the functions $\mu_i(\cdot)$ are close to each other.

In the following, we shall assume that A0 and A1 are fulfilled with $s^\star < S_{in}$.

3. A slow–fast characterization

We assume that the m species are numbered such that the following assumption is fulfilled (see Fig. 1 for a graphical interpretation of this condition).

Assumption A2. There exists $n \in \{1, \ldots, m\}$ and positive numbers η, γ such that

$$\bar{\lambda}(D) \leqslant \lambda_i(D) - \eta, \quad \forall i > n, \quad (3)$$
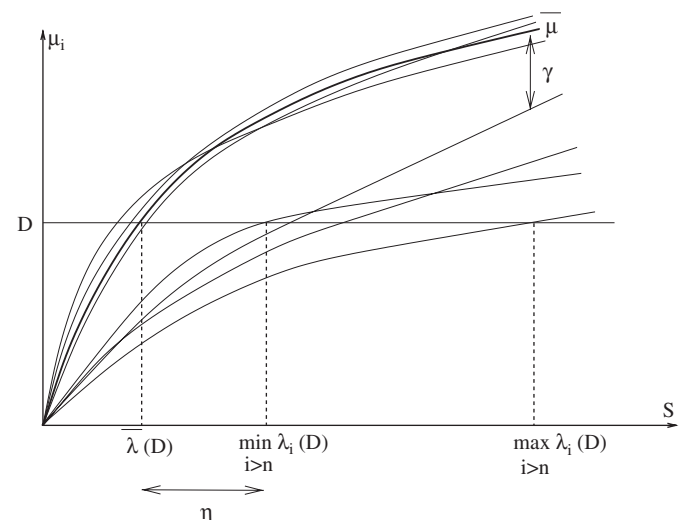

Fig. 1. Illustration of Assumption A2 and numbers η, γ.

and

$$\mu(s) > \max_i \mu_i(s) + \gamma, \quad \forall s \in \left[\bar{\lambda}(D), \max_{i>n} \lambda_i(D)\right], \tag{4}$$

where $\bar{\lambda}(D)$ is the break-even concentration associated to the average growth function $\bar{\mu}(\cdot)$:

$$\bar{\mu}(s) = \frac{1}{n}\sum_{i=1}^n \mu_i(s).$$

Under Assumption A2, define the number

$$\varepsilon = \max_{i \leqslant n} \max_{s \in [0, S_{in}]} |\mu_i(s) - \bar{\mu}(s)|. \tag{5}$$

Note that ε is positive under Assumption A1 with $s^\star < S_{in}$ (functions $\mu_i(\cdot)$ cannot coincide on the whole interval $[0, S_{in}]$). Then, consider the C^1 functions

$$v_i(s) = \frac{\mu_i(s) - \bar{\mu}(s)}{\varepsilon} \quad (i = 1, \dots, n). \tag{6}$$

Growth functions $\mu_i(\cdot)$ can then be expressed as follows:

$$\mu_i(s) = \bar{\mu}(s) + \varepsilon v_i(s) \quad (i = 1, \dots, n).$$

Let us now consider the total biomass b of the first n species, and their proportions p_i, defined as follows:

$$b = \sum_{i=1}^n x_i, \quad p_i = \frac{x_i}{b}.$$

Then the dynamics of the variables b, x_i $(i > n)$, s and p_i $(i \leqslant n)$ are given by the following equations:

$$\begin{cases} \dot{b} = \bar{\mu}(s)b - Db + \varepsilon\left(\sum_{i=1}^n v_i(s)p_i\right)b, \\ \dot{x}_i = \mu_i(s)x_i - Dx_i \quad (i > n), \\ \dot{s} = -\bar{\mu}(s)b - \sum_{i=n+1}^m \mu_i(s)x_i + D(S_{in} - s) - \varepsilon\left(\sum_{i=1}^n v_i(s)p_i\right)b, \\ \dot{p}_i = \varepsilon\left(\sum_{j=1}^n (v_i(s) - v_j(s))p_j\right)p_i \quad (i = 1, \dots, n). \end{cases} \tag{7}$$

Remark 3.1. If $n = m$, we simply omit, by writing convention, variables x_i in expression (7).

Let us consider the change of time variable $\tau = \varepsilon t$. System (7) can then be equivalently written as follows:

$$\begin{cases} \varepsilon\dfrac{db}{d\tau} = \bar{\mu}(s)b - Db + \varepsilon\left(\sum_{i=1}^n v_i(s)p_i\right)b, \\ \varepsilon\dfrac{dx_i}{d\tau} = \mu_i(s)x_i - Dx_i \quad (i > n), \\ \varepsilon\dfrac{ds}{d\tau} = -\bar{\mu}(s)b - \sum_{i=n+1}^m \mu_i(s)x_i + D(S_{in} - s) - \varepsilon\left(\sum_{i=1}^n v_i(s)p_i\right)b, \\ \dfrac{dp_i}{d\tau} = \left(\sum_{j=1}^n (v_i(s) - v_j(s))p_j\right)p_i \quad (i = 1, \dots, n). \end{cases} \tag{8}$$

When ε is small, i.e. the first n growth functions $\mu_i(\cdot)$ are all close to the average $\bar{\mu}(\cdot)$, system (8) is in the form of "slow–fast" dynamics. The vector

$$\xi = \begin{pmatrix} b \\ x_{n+1} \\ \vdots \\ x_m \\ s \end{pmatrix}$$

corresponds to the "fast" variables, and the "boundary-layer" dynamics is given by the system:

$$\begin{cases} \dot{\tilde{b}} = \bar{\mu}(\tilde{s})\tilde{b} - D\tilde{b}, \\ \dot{\tilde{x}}_i = \mu_i(\tilde{s})\tilde{x}_i - D\tilde{x}_i \quad (i > n), \\ \dot{\tilde{s}} = -\bar{\mu}(\tilde{s})\tilde{b} - \sum_{i>n} \mu_i(\tilde{s})\tilde{x}_i + D(S_{in} - \tilde{s}). \end{cases} \tag{9}$$

Note that system (9) has exactly the structure of (1) but in dimension $m - n + 2$. Denote $\bar{\lambda}(\cdot)$ the break-even concentration associated to function $\bar{\mu}(\cdot)$ and $\bar{s} = \bar{\lambda}(D)$.

Remark 3.2. Note that one has necessarily $\bar{s} \geqslant s^\star$, due to the monotonicity of the growth functions $\mu_i(\cdot)$.

Consider the following hypothesis.

Assumption A3. $\bar{s} < S_{in}$.

Under Assumptions A1–A3, dynamics (9) admits the equilibrium

$$\bar{E} = \begin{pmatrix} S_{in} - \bar{s} \\ 0 \\ \vdots \\ 0 \\ \bar{s} \end{pmatrix},$$

which is globally exponentially stable on $\mathscr{R}_+ \backslash \{0\} \times \mathscr{R}_+^{m-n+1}$ (see Corollary 2.1).

We show now that fixing an arbitrary small neighborhood $\mathscr{V}$ of $\bar{E}$ and an arbitrary small number τ, there exists $\bar{\varepsilon} > 0$ such that for any $\varepsilon < \bar{\varepsilon}$ the state vector $\xi(\cdot)$ enters and remains in $\mathscr{V}$ within the time τ.

Proposition 3.1. *Assume that* A1, A2 *and* A3 *are fulfilled. For any initial condition in $\mathscr{D}$ with $b(0) > 0$, there exist positive numbers α, κ and β such that for any $\varepsilon > 0$ sufficiently small, one has*

$$\|\xi(\tau) - \bar{E}\| \leqslant \alpha\varepsilon + \kappa\, e^{-\beta\tau/\varepsilon}, \quad \forall\tau \geqslant 0. \tag{10}$$

Proof. Let us fix an initial condition in $\mathscr{D}$ with $b(0) > 0$ and define

$$v(t) = \sum_{i=1}^n v_i(s(t))p_i(t)$$

along the solution of system (7). Recall from Lemma 2.1 that the solutions of (7) remain in the bounded domain $\mathscr{D}$, and from definition (6), one has

$$\max_{s \in [0, S_{in}]} |v_i(s)| \leqslant 1, \quad \forall i \leqslant n,$$

whatever the value of ε. Consequently $|v(\cdot)|$ is bounded by 1 uniformly in ε. Consider variables

$$m = b + \sum_{i>n} x_i \quad \text{and} \quad z = s + m,$$

whose time evolutions are solutions of the non-autonomous dynamics:

$$\begin{cases} \dot{m} = (\psi(t, z - m) - D)m, \\ \dot{z} = D(S_{in} - z), \end{cases} \tag{11}$$

where the function $\psi(\cdot)$ is defined as follows:

$$\psi(t, s) = (\bar{\mu}(s) + \varepsilon v(t))\frac{b(t)}{m(t)} + \sum_{i=n+1}^m \mu_i(s)\frac{x_i(t)}{m(t)}.$$

Note that $\psi(\cdot)$ is bounded by two autonomous functions

$$\psi_\varepsilon^-(s) \leqslant \psi(t, s) \leqslant \psi_\varepsilon^+(s), \quad \forall t \geqslant 0, \ \forall s \in [0, S_{in}]$$

with

$$\psi_\varepsilon^-(s) = \min\left(\bar{\mu}(s) - \varepsilon, \min_{i>n} \mu_i(s)\right),$$

$$\psi_\varepsilon^+(s) = \max\left(\bar{\mu}(s) + \varepsilon, \max_{i>n} \mu_i(s)\right).$$

Consider then $m^-(\cdot)$, $m^+(\cdot)$ solutions of the ordinary differential equations

$$\dot{m}^-(\cdot) = (\psi_\varepsilon^-(z(t) - m^-) - D)m^-, \quad m^-(0) = m(0),$$
$$\dot{m}^+(\cdot) = (\psi_\varepsilon^+(z(t) - m^+) - D)m^+, \quad m^+(0) = m(0),$$

from which one deduces bounds on $m(\cdot)$:

$$m^-(t) \leqslant m(t) \leqslant m^+(t), \quad \forall t \geqslant 0.$$

Denote $s^-(t) = z(t) - m^-(t)$ and $s^+(t) = z(t) - m^+(t)$ and note that variables (m^-, s^-) and (m^+, s^+) are solutions of the dynamical systems

$$\begin{cases} \dot{m}^- = (\psi_\varepsilon^-(s^-) - D)m^-, \\ \dot{s}^- = -\psi_\varepsilon^-(s^-)m^- + D(S_{in} - s^-), \end{cases} \tag{12}$$

$$\begin{cases} \dot{m}^+ = (\psi_\varepsilon^+(s^+) - D)m^+, \\ \dot{s}^+ = -\psi_\varepsilon^+(s^+)m^- + D(S_{in} - s^+). \end{cases} \tag{13}$$

Systems (12) and (13) are chemostat models of form (1) for a single fictitious species with monotonic growth function $\psi_\varepsilon^-(\cdot)$ and $\psi_\varepsilon^+(\cdot)$, respectively. Denote $\lambda_\varepsilon^-(\cdot)$, resp. $\lambda_\varepsilon^+(\cdot)$ the break-even concentrations associated to $\psi_\varepsilon^-(\cdot)$, resp. $\psi_\varepsilon^+(\cdot)$ (see Definition 2). One has clearly $\lambda_\varepsilon^+(D) < \lambda_\varepsilon^-(D)$ and when ε is small enough, one ensures $\lambda_\varepsilon^+(D) < \lambda_\varepsilon^-(D) < S_{in}$. Then Proposition 2.1 gives the asymptotic convergence of $s^-(\cdot)$, resp. $s^+(\cdot)$ toward $\lambda_\varepsilon^+(D)$, resp. $\lambda_\varepsilon^-(D)$, from any initial condition with $m(0) > 0$. Corollary 2.1 gives also the exponential convergence and one can easily check that an exponential decay is guaranteed uniformly in ε sufficiently small. So, there exist numbers $k_0 > 0$ and $\beta_0 > 0$ such that the property

$$s(t) \in I_\varepsilon(t) = [\lambda_\varepsilon^+(D) - k_0 e^{-\beta_0 t}, \lambda_\varepsilon^-(D) + k_0 e^{-\beta_0 t}], \quad \forall t \geqslant 0 \tag{14}$$

is fulfilled for any ε small enough. Note that Assumption A2 gives the equalities

$$\lambda_\varepsilon^+(D) = \bar{\lambda}(D - \varepsilon), \quad \lambda_\varepsilon^-(D) = \max_{i>n} \lambda_i(D), \tag{15}$$

when ε is small enough, and the existence of $T_0 < +\infty$ such that the property

$$s \in I_\varepsilon(t) \Longrightarrow \bar{\mu}(s) \geqslant \max_{i>n} \mu_i(s) + \varepsilon + \gamma/2 \tag{16}$$

is satisfied for any $t > T_0$ and any $\varepsilon < \gamma/2$ small enough.

From equations (7), the dynamics of the proportion variable $q = b/m$ can be written as follows:

$$\dot{q} = q(1-q)\left(\bar{\mu}(s(t)) + \varepsilon v(t) - \sum_{i>n} \mu_i(s(t))\frac{x_i(t)}{\sum_{j>n} x_j(t)}\right).$$

Then, from (16) one obtains the inequality

$$\dot{q}(t) \geqslant \frac{\gamma}{2} q(t)(1 - q(t)), \quad \forall t \geqslant T_0$$

for any ε small enough. Note that the hypothesis $b(0) > 0$ implies $q(0) > 0$ and consequently $q(t) > 0$ for any time t. We then deduce the exponential convergence of the variable q toward 1, or equivalently the exponential convergence of the concentrations x_i toward 0 for any $i > n$, i.e. there exists $k_x > 0$, $\beta_x > 0$ such that

$$x_i(t) \leqslant k_x e^{-\beta_x t}, \quad \forall t \geqslant T_0, \ \forall i > n \tag{17}$$

for any $\varepsilon > 0$ small enough. We also deduce the existence of a finite time $T_1 \geqslant T_0$ such that

$$\bar{\mu}(s)q(t) + \min_{i>n} \mu_i(s)(1 - q(t)) \geqslant \bar{\mu}(s) - \varepsilon, \quad \forall s \in I_\varepsilon(t), \ \forall t \geqslant T_1$$

for any ε small enough, which implies the inequality

$$\psi(t,s) \geqslant (\bar{\mu}(s) - \varepsilon)q(t) + \min_{i>n} \mu_i(s)(1 - q(t)) \geqslant \bar{\mu}(s) - 2\varepsilon,$$
$$\forall s \in I_\varepsilon(t), \ \forall t \geqslant T_1$$

to be fulfilled. Then, the following upper bound on the derivative of s is obtained, for any $t > T_1$ (and $\varepsilon > 0$ small enough):

$$\dot{s} = -\psi(t,s)(z(t) - s) + D(S_{in} - s) \leqslant -(\bar{\mu}(s) - 2\varepsilon)(z(t) - s) + D(S_{in} - s).$$

Recall now from equations (11) that $z(\cdot)$ is solution of the differential equation $\dot{z} = D(S_{in} - z)$, independently of the functions $\mu_i(\cdot)$, whose solution is

$$z(t) = S_{in} + (z(0) - S_{in}) e^{-Dt}, \quad \forall t \geqslant 0. \tag{18}$$

Consequently, one has

$$\dot{s} \leqslant (D - \bar{\mu}(s) + 2\varepsilon)(S_{in} - s) - (\bar{\mu}(s) - 2\varepsilon)(z(0) - S_{in}) e^{-Dt}, \quad \forall t \geqslant T_1,$$

from which one deduces the existence of $k_1 > 0$ and $\beta_1 > 0$ such that

$$s(t) \leqslant \bar{\lambda}(D + 2\varepsilon) + k_1 e^{-\beta_1 t}, \quad \forall t \geqslant T_1.$$

With (14) and (15), one obtains more precise bounds on the variable s

$$\bar{\lambda}(D - \varepsilon) - k_0 e^{-\beta_0 t} \leqslant s(t) \leqslant \bar{\lambda}(D + 2\varepsilon) + k_1 e^{-\beta_1 t}, \quad \forall t \geqslant T_1. \tag{19}$$

Then bounds on the variable b are obtained from (17), (18), for any $t \geqslant T_1$ and any ε small enough

$$S_{in} - \bar{\lambda}(D + 2\varepsilon) - \zeta^-(t) \leqslant b(t) \leqslant S_{in} - \bar{\lambda}(D - \varepsilon) + \zeta^+(t) \tag{20}$$

with

$$\begin{cases} \zeta^-(t) = k_1 e^{-\beta_1 t} + (m-n)k_x e^{-\beta_x t} - (z(0) - S_{in}) e^{-Dt}, \\ \zeta^+(t) = k_0 e^{-\beta_0 t} + (z(0) - S_{in}) e^{-Dt}. \end{cases}$$

Finally, continuity of $\bar{\lambda}(\cdot)$ and inequalities (17), (19) and (20) give together the conclusion (10). □

Let $p = (p_i)_{i=1,\dots,n}$ be the vector of the "slow" variables (i.e. the distribution among the first n species) and consider the reduced dynamics:

$$\frac{dp_i}{d\tau} = \left(\sum_{j=1}^n (v_i(\bar{s}) - v_j(\bar{s}))p_j\right) p_i \quad (i = 1, \dots, n). \tag{21}$$

In the next section, we shall study the solutions of system (21) and compare them with the solutions of the original system (8).

4. The reduced dynamics

The reduced dynamical equations (21) of the "slow" part is given by the bilinear dynamical equation

$$\frac{dp_i}{d\tau} = \sum_{j=1}^n A_{ij} p_j p_i, \tag{22}$$

where $A = [A_{ij}]$ is a skew symmetric matrix with $A_{ij} = v_i(\bar{s}) - v_j(\bar{s})$.

Let us consider the generic case with the following assumption.

Assumption A4. For any $i \neq j$, one has $v_i(\bar{s}) \neq v_j(\bar{s})$.

Without any loss of generality, we can assume that the n species are numbered such that

$$v_n(\bar{s}) > v_{n-1}(\bar{s}) > \cdots > v_1(\bar{s}).$$

Let us then define numbers $B_i = A_{ni}$, where

$$B_1 > B_2 > \cdots > B_{n-1} > B_n = 0. \tag{23}$$

Since $\sum_j p_j = 1$, one has

$$\sum_j A_{ij} p_j = \sum_j (v_i - v_j) p_j = -v_n + v_i + \sum_j (v_n - v_j) p_j = -B_i + \sum_j B_j p_j,$$

and one can write equivalently the dynamical equations (22) as follows:

$$\frac{\mathrm{d}p_i}{\mathrm{d}\tau} = \left(-B_i + \sum_{j=1}^n B_j p_j \right) p_i, \quad i = 1, \ldots, n. \tag{24}$$

Remark 4.1. Under Assumptions A3 and A4, one has $\lambda_n(D) = s^\star$ for ε small enough. In accordance with the CEP, the n-th species asymptotically wins the competition because it has the (unique) smallest break-even concentration.

Under Assumption A4, system (24) admits exactly n distinct equilibria, which are exactly the vertexes of the simplex:

$$\mathscr{S} = \left\{ p \in \mathscr{R}_+^n \left| \sum_{i=1}^n p_i = 1 \right. \right\}.$$

One can easily check that $\mathscr{S}$ is invariant by dynamics (24) and the eigenvalues of the Jacobian matrix at an equilibrium $\bar{p} \in \mathscr{S}$ such that $\bar{p}_i = 1$ are B_i and $B_j - B_i$ for $j \neq i$. Consequently one obtains immediately the following properties for the dynamics defined on $\mathscr{S}$:

- when $\bar{p}_1 = 1$, $\bar{p}$ is a source,
- when $\bar{p}_n = 1$, $\bar{p}$ is a sink and
- when $\bar{p}_i = 1$ with $i \in 2, \ldots, n-1$, $\bar{p}$ is a saddle point with a stable manifold of dimension $i - 1$ contained in the face:

$$\mathscr{F}_i = \left\{ p \in \mathscr{S} \left| \sum_{j=1}^i p_j = 1 \right. \right\}.$$

Note that solutions $q_i(\cdot)$ of dynamics $\dot{q}_i = -B_i q_i$ $(i = 1, \ldots, n)$ fulfill $(\mathrm{d}/\mathrm{d}t)\bar{q}_i = (-B_i + \sum_j B_j \bar{q}_j)\bar{q}_i$ with $\bar{q}_i = q_i/\sum_j q_j$. We deduce that the solutions of system (24) are given by the analytical formula:

$$p_i(\tau) = \frac{p_i(0)\, \mathrm{e}^{-B_i \tau}}{\sum_{j=1}^n p_j(0)\, \mathrm{e}^{-B_j \tau}}, \quad i = 1, \ldots, n. \tag{25}$$

Let $p^\star$ be the equilibrium $(0, \ldots, 0, 1)' \in \mathscr{S}$. Its stability property is given by the lemma.

Lemma 4.1. *For any initial condition $p(0) \in \mathscr{S}$ with $p_n(0) > 0$, the solution $p(\cdot)$ of the reduced dynamics (24) converges exponentially toward the equilibrium $p^\star$.*

Proof. From equations (25), one has $p_n(\tau) \to 1$ and $p_i(\tau) \to 0$ for any $i = 1, \ldots, n-1$, when $\tau \to +\infty$. The linearized dynamics of (22) about $p^\star$ is simply $\dot{p}_i = -B_i p_i$ $(i = 1, \ldots, n)$. Consequently, each component p_i for $i < n$ converges exponentially toward 0 and $p_n = 1 - \sum_{i<n} p_i$ converges exponentially toward 1. $\square$

Let us now compare the distribution $p(\cdot)$ of the reduced dynamics (22) with $p_\varepsilon(\cdot)$ of the original dynamics (8), when ε is small. When $x_n(0) > 0$, we already know from Corollary 2.1 and Lemma 4.1 that both $p(\cdot)$ and $p_\varepsilon(\cdot)$ converge exponentially toward $p^\star$. We give now a result that compares these distributions during their transient stage.

Corollary 4.1. *Assume that A3 and A4 are fulfilled. For any initial condition of (1) in $\mathscr{D}$ with $x_n(0) > 0$ and any $T > 0$, there exists $\bar{\varepsilon} > 0$ such that*

$$\varepsilon < \bar{\varepsilon} \Rightarrow p(\tau) - p_\varepsilon(\tau) = O(\varepsilon) \quad \text{uniformly for } \tau > T. \tag{26}$$

Proof. Recalling the facts:

1. the equilibrium $\bar{E}$ of the boundary layer dynamics (9) is exponentially stable (Corollary 2.1) and
2. the equilibrium $p^\star$ of the reduced dynamics (22) is exponentially stable (Lemma 4.1),

the Tikhonov's theorem (see for instance Khalil, 1996, Theorem 9.4) gives the conclusion (26) for any initial condition close to $(\bar{E}, p^\star)$ in $\mathscr{R}_+^{m-n} \times \mathscr{S}$, and then extended to larger initial conditions by Proposition 3.1. $\square$

Consider now the time function:

$$\pi(\tau) = \sum_{j=1}^n B_j p_j(\tau).$$

The transient behavior of the solutions of (7) can be characterized by $\pi(0)$, as described by the following result.

Proposition 4.1. *Under Assumption A4, for any initial condition $p(0)$ in $\mathscr{S}$, the solution $p(\cdot)$ of (7) fulfills the following properties:*

- *for indexes i such that $\pi(0) \leqslant B_i$, $p_i(\cdot)$ is decreasing and*
- *for indexes i such that $\pi(0) > B_i$, $p_i(\cdot)$ is increasing up to T_i such that $p_i(T_i) = B_i$ and is then decreasing. Furthermore, one has*

$$T_i \geqslant \underline{T}_i = \frac{1}{B_1} \log \frac{\pi(0)(B_1 - B_i)}{B_i(B_1 - \pi(0))}. \tag{27}$$

Proof. One has immediately

$$\frac{\mathrm{d}\pi}{\mathrm{d}\tau} = -\sum_{j=1}^n B_j^2 p_j + \left(\sum_{j=1}^n B_j p_j \right)^2 = -\sum_{j=1}^n \phi(B_j) p_j + \phi\left(\sum_{j=1}^n B_j p_j \right), \tag{28}$$

where $\phi(\cdot)$ is the square function. $\phi(\cdot)$ being a convex function, one deduces that $\mathrm{d}\pi/\mathrm{d}\tau \leqslant 0$. The function $\tau \mapsto \pi(\tau)$ is non-increasing. Note that one has also

$$\frac{\mathrm{d}p_i}{\mathrm{d}\tau} = (-B_i + \pi(\tau))p_i.$$

Consequently, the function $\tau \to p_i(\tau)$ is always decreasing when $\pi(0) \leqslant B_i$. Otherwise, $\tau \to p_i(\tau)$ is increasing up to T_i such that $\pi(T_i) = B_i$ and then decreasing.

From (28), one can derive the inequality:

$$\frac{\mathrm{d}\pi}{\mathrm{d}\tau} = \pi^2 - B_1 \pi + \sum_{j=1}^n B_j p_j(B_1 - B_j) \geqslant \pi^2 - B_1 \pi,$$

and deduce an estimation from below of the function $\pi(\cdot)$:

$$\pi(\tau) \geqslant \pi^-(\tau), \quad \tau \geqslant 0,$$

where $\pi^-(\cdot)$ is solution of the differential equation:

$$\frac{\mathrm{d}\pi^-}{\mathrm{d}\tau} = \pi^{-2} - B_1 \pi^-, \quad \pi^-(0) = \pi(0).$$

It is straightforward to check that $\pi^-(\cdot)$ is given by the following expression:

$$\pi^-(\tau) = \frac{\pi(0)B_1}{\pi(0) + (B_1 - \pi(0))\, \mathrm{e}^{B_1 \tau}}. \tag{29}$$

Let us fix an initial condition $p_1(0), \ldots, p_n(0)$ and consider i_0 the smallest index $i = 1, \ldots, n$ such that $B_i < \pi(0)$. Note that inequality $B_1 > \pi(0)$ is fulfilled exactly when $i_0 \leqslant n - 1$. For $i_0 \leqslant n - 1$, the

following bound from below of time T_i is obtained from (29):

$$T_i \geqslant \frac{1}{B_1} \log \frac{\pi(0)(B_1 - B_i)}{B_i(B_1 - \pi(0))}. \qquad \square$$

Remark 4.2. Note that $\tau \mapsto p_1(\tau)$ is always a non-increasing function, and the function $\tau \mapsto p_n(\tau)$ is always non-decreasing.

Let i_0 be the smallest index in $1, \ldots, n$ such that $B_i < \pi(0)$. One has necessarily $T_{i_0} < T_{i_0+1} < \cdots < T_{n-1}$. From expression (27), one can deduce the following qualitative properties:

(i) when $\pi(0)$ is close to B_1 (i.e. species 1 is majority at initial time), all the species concentrations, except for the species 1, are increasing for a long time and

(ii) when $\pi(0)$ is close to B_i with $i > 1$, the concentrations of species j for $j \leqslant i$ are rapidly decreasing.

5. Simulation results

Numerical simulations have been performed in order to illustrate the concepts developed here above. We have considered 10 species (i.e. $m = 10$) among two families, whose specific growth rates are depicted in Fig. 2. For each family, specific growth rates are been chosen closed to each other, in terms of Monod analytic functions

$$\mu_i = \frac{\mu_{\max,i} s}{K_{s,i} + s}, \tag{30}$$

where $\mu_{\max,i}$ and $K_{s,i}$ are the maximum specific rate (h^{-1}) and the affinity constant (g/l) associated to each species x_i, respectively. Numerical values of the parameters are given in the following table.

Species	1	2	3	4	5	6	7	8	9	10
$\mu_{\max,i}$	0.5	0.5	0.5	0.5	0.5	0.5	0.5	0.5	0.5	0.5
$K_{s,i}$	1.02	1.01	1	0.99	0.98	2.04	2.02	2	1.98	1.96

The operating conditions of the chemostat have been selected as follows:

$$D = 0.1\,\text{h}^{-1}, \quad s_{in} = 5\,\text{g/l}. \tag{31}$$
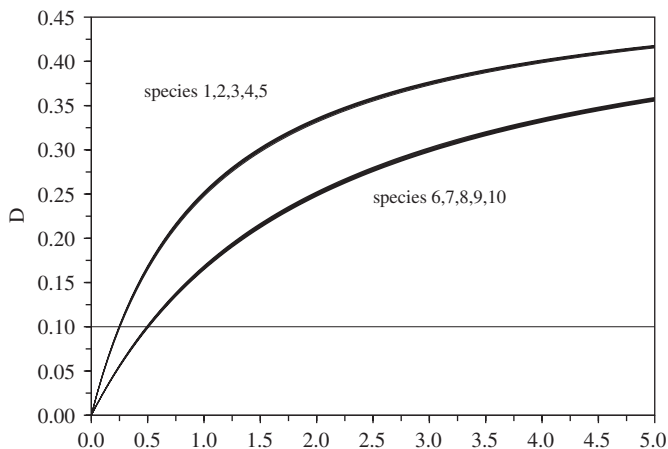

Fig. 2. Specific growth rates.

Moreover, we have considered, for the sake of simplicity, yield coefficients y_i equal to 1. The next table gives the numerical values of the break-even concentrations defined in (2).

Species	1	2	3	4	5	6	7	8	9	10
$\lambda_i(D)$	0.2550	0.2525	0.2500	0.2475	0.2450	0.5100	0.5050	0.5000	0.4950	0.4900

The CEP (Proposition 2.1) tells us that species 5 asymptotically wins the competition. Let us consider the following non-uniform initial distribution of the biomass (see Fig. 3).

Species	1	2	3	4	5	6	7	8	9	10
$x_i(0)$	0.1015	0.0068	0.0076	0.0081	0.0085	0.0087	2.4357	2.0298	0.0091	0.0092

The simulation given in Fig. 4 shows that the total biomass b and the substrate s get very close to their steady state in about 100 time steps. If one looks at the biomass distribution between both families, one faces the classical CEP situation. The first family wins
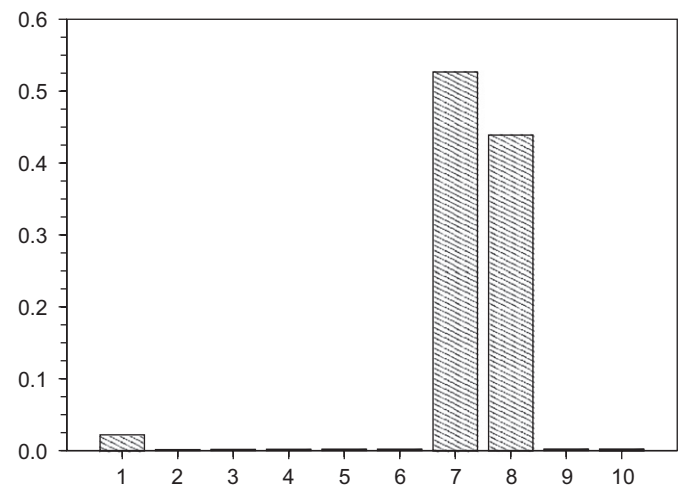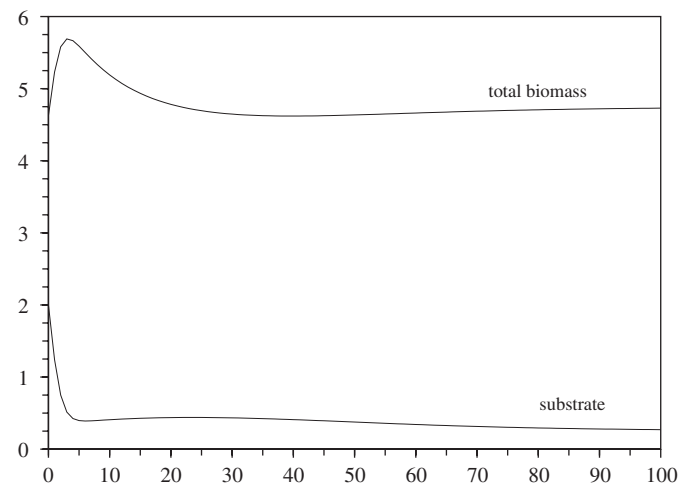

Fig. 3. Initial distribution of the biomass.
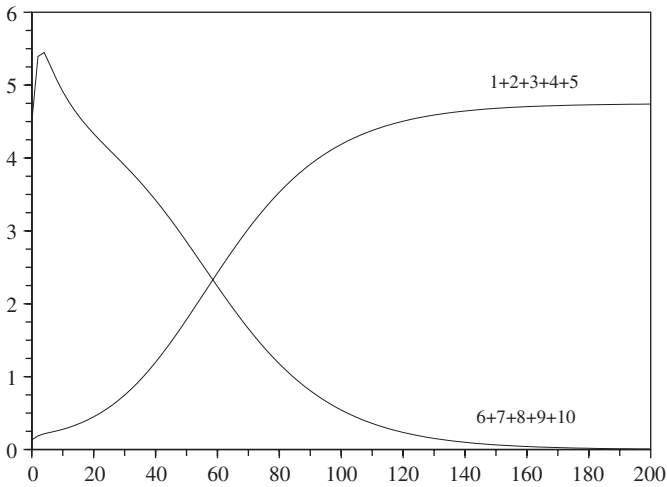

Fig. 4. Short run simulation.

Fig. 5. Mid-run simulation.
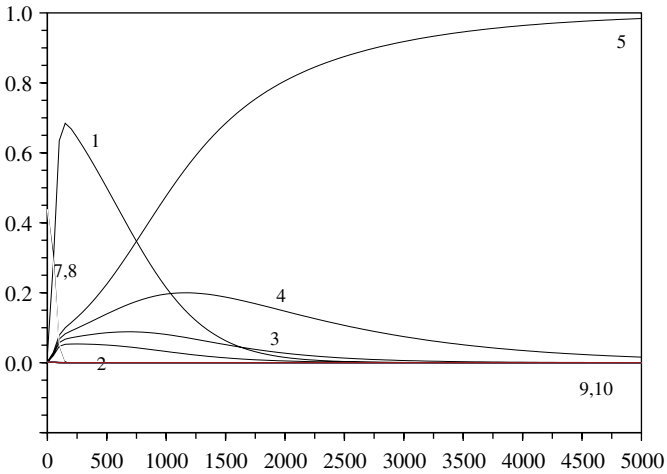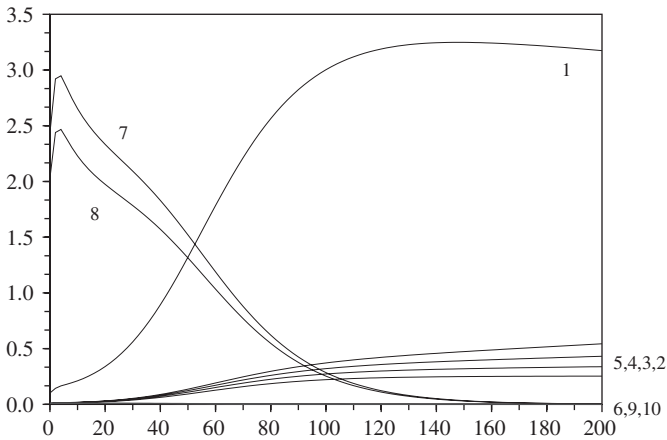

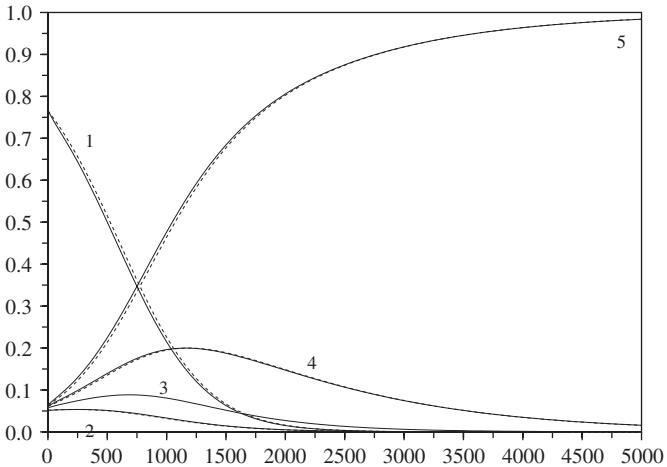**Fig. 7.** Long run simulation.

Fig. 6. Mid-run simulation.

Fig. 8. Species distribution among the first family (reduced dynamics in dashed line).

the competition over the second one (see Fig. 5), and less than 200 time steps is required for both biomass to reach an almost stationary state. If one looks now at the individual concentrations of each species on the same time interval, one might believe that species 1 is the winner (see Fig. 6). But it turns out that more than 10 times of this interval length is necessary for the species 5 to significantly takes the leadership over all the other species (see Fig. 7).

For $n = 5$, one can easily compute $\bar{\lambda} = 0.24996$ and check that Assumption A2 is fulfilled with $\eta = 0.24$. Furthermore, one has

$$\varepsilon = 2.5 \times 10^{-3}.$$

We illustrate in Fig. 8 that reduced dynamics whose solution given by the explicit formula (25) is a good approximation of the dynamics of the species distribution among the first family.

As predicted by the theory, the proportions $p_i(\cdot)$ are increasing and then decreasing, or monotonic with respect to time. The next table shows that the lower estimates on times T_i, provided by formula (27), give a relevant information, to be compared to the times that maximizes the proportions of each species (computed on the original dynamics (7)).
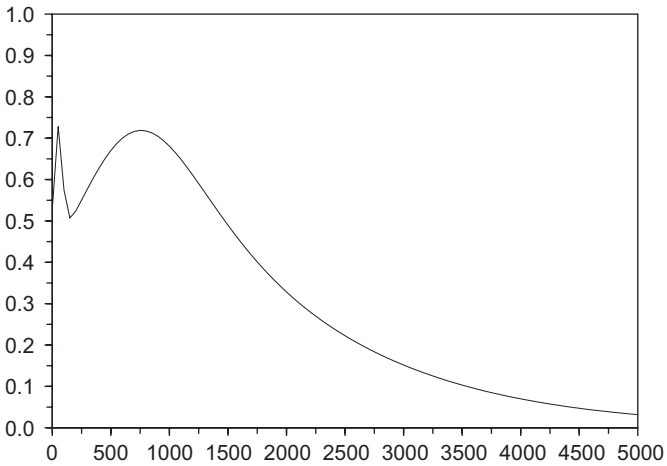

Fig. 9. Time evolution of the Simpson's index.

Finally, we have represented the time evolution of the Simpson's diversity index

$$\sigma(t) = 1 - \sum_{i=1}^{10} p_i^2(t),$$

Species	1	2	3	4	5
$\underline{T}_i$	$-\infty$	188	531	874	$+\infty$
$\mathrm{argmax}_t\, p_i(t)$	0	231	684	1161	$+\infty$

which is commonly used to measure the diversity of an ecosystem. Fig. 9 shows its non-monotonic behavior, that can be explained in the present situation by the exchange of leadership between species 5 and 1 that increases temporarily the diversity, and the relatively long time before approaching zero.

6. Conclusions

In this paper we have studied the behavior of multiple species competing for the same substrate in a chemostat, when initial conditions can substantially modify the transient behavior of the system. We have shown in particular by considering slow–fast dynamics that intermediate species can survive for a substantially long time before starting to decrease and leave the room for the species that has the best affinity with the nutrient. Moreover, we give the explicit solution of a reduced dynamics, that can be easily computed even when the size of the system is too large to be solved numerically, and that gives a good prediction of the time evolution of the distribution between species. This formalizes the practical situation when coexistence of multiple species can last for long time before substantial decrease of the non-dominant species takes place. The results have been illustrated in numerical simulation.

Acknowledgments

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