

How the fractional-order improve and extend the well-known competitive exclusion principle in the chemostat model with n species competing for a single resource?

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Abstract

In this paper, a fractional-order mathematical model for n species competing, in a chemostat, for a single resource is proposed. The global dynamics was studied using Lyapunov theory, for any set of increasing growth functions. Obtained results generalize and improve the well-known competitive exclusion principle in the chemostat, that one species will eliminate all other species.

Keywords: Chemostat model; competitive exclusion; fractional order; Caputo fractional derivative; nonlinear growth rate; equilibrium points; local and global stability.

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1 Introduction

The chemostat is an experimental device used to analyze the growth of populations of microorganisms. It was introduced simultaneously by A. Novick and L. Szilard [24] in the 1936s and by J. Monod [23] in the 1950s. The mathematical growth of a species of bacteria in the chemostat is due to C. Spicer [32]. From this date there are many articles relating to the competition of several species. For the purpose of this introduction, let us say that it is a reactor (a container) crossed by a flow of liquid containing the nutritive substrate necessary for the growth of organisms. When the flow rate of liquid passing through the reactor is constant, a classic mathematical theory of the chemostat states that one species will eliminate all other species: this is the "competitive exclusion principle". This principle has been popularized by Hardin [19] and has since then been widely mathematically studied in the literature [1, 2, 33].

Different sophisticated tools were used, such as ω -limit sets [2], Lyapunov theory [20, 27, 29, 35], LaSalle Invariance Principle [16, 31] and more recently a proof using elementary analysis and comparing solutions of ordinary differential equations [26]. The theory of the competitive exclusion principle is established in parallel with numerous articles that show coexistence [11, 13, 12, 28]

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(obviously when the conditions of the exclusion theorems are violated). The book of H. Smith and P. Waltman [31] contains all the information and references concerning this subject.

Consider n species competing for a single resource in a chemostat (see Fig. 1). The most

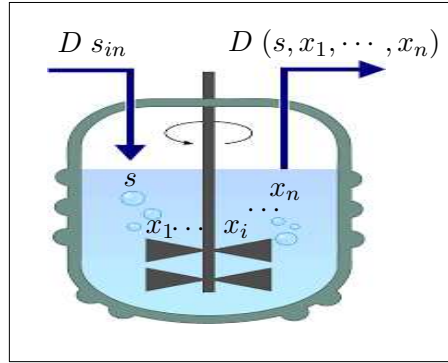


Fig. 1: Competition in a continuous reactor

classical model for the growth of n populations of different species [31] is

$$\begin{cases} \dot{s}(t) &= D [s_{in} - s(t)] - \sum_{i=1}^n \mu_i(s(t))x_i(t), \\ \dot{x}_i(t) &= [\mu_i(s(t)) - D]x_i(t) \end{cases} \quad (1.1)$$

The variables $s(t)$ and $x_i(t)$ are respectively the concentrations at time t of the resource and the concentration of the different populations of microorganisms. The growth rate of species i in the presence of a concentration s is:

$$\mu_i(s)$$

where the μ_i functions are of "Monod type", i.e. defined for s positive, continuous, equal zero at $s = 0$, increasing and bounded (Figure 2). Finally, D is the inflow and outflow (with constant volume) in the reactor. In general, for a given D , there exists a unique index $1 \leq i \leq n$ and a constant $\bar{\lambda}$ satisfying $\mu_i(\bar{\lambda}) = D$ such that, for any non-negative initial condition with $x_i(0) > 0$, the equilibrium:

$$(s = \bar{\lambda}, x_1 = 0, \dots, x_{i-1} = 0, x_i = s_{in} - \bar{\lambda}, x_{i+1} = 0, \dots, x_n = 0)$$

is globally asymptotically stable. Local stability is easily demonstrated by calculating the eigenvalues of the Jacobian, and the global stability using Lyapunov functions. This is the "competitive exclusion principle": all species disappear except the one having the best growth rate for $s = \bar{\lambda}$ (see Figure 2 where $\bar{\lambda} = \lambda_1$).

Fractional systems are appearing more and more frequently in the different fields of research. However, the progressive interest in these systems and applications in engineering sciences are still not well developed. Many biological phenomena (biological tissues) dependent on past history (memory) and therefore it is possible that careful modelling may lead to equations including fractional derivatives.

The present article is a contribution to the question of "competitive exclusion principle". More precisely, I revisit the classical mathematical model for the growth of n species competing for a single substrate in a chemostat but by considering the fractional-order time derivative instead of the classical ordinary differential equations (1.1).

Fractional calculus is a domain of mathematics whose purpose is to extend the definitions of traditional derivatives to non-integer orders. The fractional derivative represents the generalization to non-integer orders of the derivative [4], just like the real exponent power function which corresponds to the "extension" of the full exponent power function. Several definitions have been proposed for the non-integer derivation. It should be noted, however, that these definitions do not always lead to identical results but are globally equivalent for a large number of functions. In this paper, the Caputo derivative approach will be used due to its application advantages. The most important advantage is that the initial conditions for fractional order is the same as that of integer order, avoiding solvability issues.

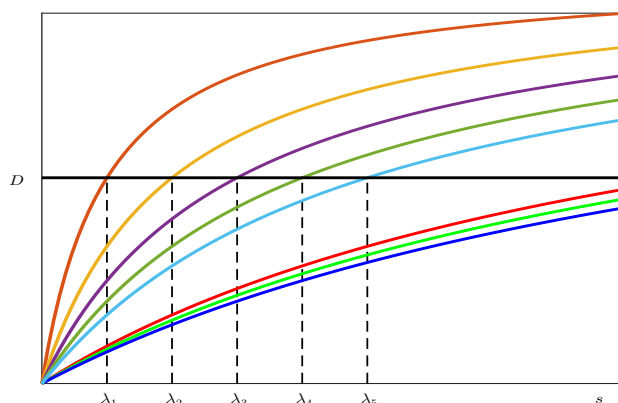


Fig. 2: Growth rates and their break-even concentrations.

2 Mathematical model and properties

First, let give some definitions that we use later in this paper. The definition of the Caputo fractional derivative is defined as follows

$$D_C^\alpha h(t) = J^{m-\alpha}[h^{(m)}(t)] = \frac{1}{\Gamma(n-\alpha)} \int_0^t (t-s)^{m-\alpha-1} h^{(m)}(s) ds \tag{2.1}$$

where m is the first integer greater than α .

The Laplace transform of the Caputo fractional derivative is given by

$$\mathcal{L}(D_C^\alpha h(t)) = \lambda^\alpha H(s) - \sum_{k=0}^{m-1} h^{(k)}(0) \lambda^{\alpha-k-1}. \tag{2.2}$$

Recall the Mittag-Leffler function defined by the following infinite power series:

$$E_{\alpha,\beta}(z) = \sum_{k=0}^{+\infty} \frac{z^k}{\Gamma(\alpha k + \beta)}. \tag{2.3}$$

The Laplace transform of the Mittag-Leffler function is given by

$$\mathcal{L}[t^{\beta-1}E_{\alpha,\beta}(\pm\alpha t^\alpha)] = \frac{s^{\alpha-\beta}}{s^\alpha \mp \alpha}. \tag{2.4}$$

Let $\alpha, \beta > 0$ and $z \in \mathbb{Z}$. The Mittag-Leffler functions satisfy the equality given by Theorem 4.2 in [3]

$$E_{\alpha,\beta}(z) = zE_{\alpha,\alpha+\beta}(z) + \frac{1}{\Gamma(\beta)}. \tag{2.5}$$

Here, D^α denotes the Caputo fractional derivative of order $0 < \alpha \leq 1$ defined for an arbitrary function $h(t)$ by [25] as follows:

$$D^\alpha h(t) = \frac{1}{\Gamma(1-\alpha)} \int_0^t (t-x)^{-\alpha} h'(x) dx.$$

Consider n populations of different species competing for a single resource in a chemostat. The proposed model for this competition is given by the following $n + 1$ -dimensional dynamical system of fractional differential equations:

$$\begin{cases} D^\alpha s(t) &= D [s_{in} - s(t)] - \sum_{i=1}^n \mu_i(s(t))x_i(t), \\ D^\alpha x_i(t) &= [\mu_i(s(t)) - D]x_i(t) \end{cases} \tag{2.6}$$

with positive initial condition $(s(0), x_1(0), \dots, x_n(0)) \in \mathbb{R}_+^{n+1}$. The operating parameters $D > 0$ and $s_{in} > 0$ are the inflow-outflow rate and the input resource density (substrate concentration). The variable $s(t)$ describes the substrate concentration at time t . For $1 \leq i \leq N$, $x_i(t)$ denote the concentration of the i -th species and $\mu_i(\cdot)$ is the specific growth rate function of species i . Without any loss of generality, assume that all yield coefficients are equal to 1.

Assumption 1. $\mu_i(\cdot)$ are non-negative $C^1(\mathbb{R}_+)$ increasing bounded functions such that $\mu_i(0) = 0$ and $\mu'_i(s) > 0$ for all $1 \leq i \leq n$.

Remark 1. The classical Monod function satisfies the assumption 1 (Fig. 2) and then can be used to express the growth rate.

$$\mu_i(s) = \frac{\bar{\mu}_i s}{k_i + s} \tag{2.7}$$

$\bar{\mu}_i$ represents the maximum specific growth rate. k_i is the Monod (half-velocity) constant.

\mathbb{R}_+^{n+1} , the closed non-negative cone in \mathbb{R}^{n+1} , is positively invariant [6, 7, 8, 9, 10, 11, 12, 13, 14, 15, 16, 17, 28, 31] by the system (2.6). More precisely,

Proposition 1.

1. For all initial condition $(s(0), x_1(0), \dots, x_n(0)) \in \mathbb{R}_+^{n+1}$, the solution of system (2.6) is bounded and has positive components and thus is defined for all $t > 0$.
2. System (2.6) admits a positive invariant attractor set of all solution given by $\Omega = \{(s, x_1, \dots, x_n) \in \mathbb{R}_+^{n+1} / s + \sum_{i=1}^n x_i = s_{in}\}$.

Proof. 1. The positivity of the solution is proved by the fact that :
 If $s = 0$ then $D^\alpha s = Ds_{in} > 0$ and if $x_i = 0$ then $D^\alpha x_i = 0$, for all $1 \leq i \leq n$.

Next we have to prove the boundedness of solution of (2.6). By adding all equations of system (2.6), one obtains, for $T = s + \sum_{i=1}^n x_i - s_{in}$, a single equation for the total density:

$$D^\alpha T(t) = D^\alpha s(t) + \sum_{i=1}^n D^\alpha x_i(t) = D(s_{in} - s - \sum_{i=1}^n x_i(t)) = -DT. \quad (2.8)$$

Solve Eq. (2.8) by applying the Laplace transform (2.2), one obtains

$$\lambda^\alpha \mathcal{L}(T(t)) - \lambda^{\alpha-1} T(0) = -D \mathcal{L}(T(t))$$

that can be written as below using the Laplace transform properties (2.4) and equality (2.5),

$$(\lambda^\alpha + D) \mathcal{L}(T(t)) = \lambda^{\alpha-1} T(0).$$

Then

$$\mathcal{L}(T(t)) = \frac{\lambda^{\alpha-1}}{(\lambda^\alpha + D)} T(0) = t^{\alpha-1} E_{\alpha,\alpha}(-Dt^\alpha) T(0)$$

where $0 < \alpha \leq 1$ and $E_{a,b}(z)$ is the two parameter Mittag-Leffler function with parameter a and b [6,18]. Since Mittag-Leffler function is an entire function, thus $E_{\alpha,\alpha}(-Dt^\alpha)$ is bounded for all $t > 0$. Therefore, I have

$$\lim_{t \rightarrow +\infty} T(t) = 0. \quad (2.9)$$

Thus, closed set Ω is positively invariant and attracting to the system (2.6).

Since all terms of the sum are positive, then the solution of system (2.6) is bounded.

2. The invariance of the attractor Ω is simply deduced from equality (2.9).

□

Definition 1. Assume that Assumption 1 is fulfilled. For a given constant dilution rate $D > 0$, the unique solution of the equation $\mu_i(s) = D$, when it exists, is denoted by $\lambda_i = \lambda_i(D)$ and is named the break-even concentration for the i -th species. If equation $\mu_i(s) = D$ has no solution, I set $\lambda_i = +\infty$.

Assumption 2. Assume that all species have different break-even concentrations and, in particular (without loss of generality), are arranged by indices as follows

$$\lambda_1 < \lambda_2 < \dots < \lambda_n. \quad (2.10)$$

In Fig. 2, a typical example is given where the growth rates with different break-even concentrations and the dilution rate were represented.

Let write the statement of the Competitive Exclusion Principle [31].

Proposition 2. Assume that Assumptions 1 and 2 are fulfilled.

- If $\lambda_1 > s_{in}$ then the system (2.6) admits a unique equilibrium point given by $E_0 = (s_{in}, 0, \dots, 0)$ and it is locally asymptotically stable.
- If $\lambda_1 < s_{in}$ then the system (2.6) admits two equilibrium points given by $E_0 = (s_{in}, 0, \dots, 0)$ and $E_1 = (\lambda_1, s_{in} - \lambda_1, 0, \dots, 0)$. The equilibrium point E_1 is locally asymptotically stable and the equilibrium point E_0 is unstable.

Proof. The Jacobian matrix of system (2.6) at a point $(s, x_1, x_2, \dots, x_n)$ is given by:

$$J = \begin{pmatrix} -D - \sum_{i=1}^n \mu'_i(s)x_i & -\mu_1(s) & \cdots & -\mu_{n-1}(s) & -\mu_n(s) \\ \mu'_1(s)x_1 & \mu_1(s) - D & 0 & \cdots & 0 \\ \mu'_2(s)x_2 & 0 & \mu_2(s) - D & 0 & 0 \\ \vdots & \vdots & \vdots & \vdots & \vdots \\ \mu'_{n-1}(s)x_{n-1} & 0 & \cdots & \mu_{n-1}(s) - D & 0 \\ \mu'_n(s)x_n & 0 & \cdots & 0 & \mu_n(s) - D \end{pmatrix}.$$

The Jacobian matrix of system (2.6) evaluated at $E_0 = (s_{in}, 0, \dots, 0)$ is then given by:

$$J_0 = \begin{pmatrix} -D & -\mu_1(s) & \cdots & -\mu_{n-1}(s_{in}) & -\mu_n(s_{in}) \\ 0 & \mu_1(s_{in}) - D & 0 & \cdots & 0 \\ 0 & 0 & \mu_2(s_{in}) - D & 0 & 0 \\ \vdots & \vdots & \vdots & \vdots & \vdots \\ 0 & 0 & \cdots & \mu_{n-1}(s_{in}) - D & 0 \\ 0 & 0 & \cdots & 0 & \mu_n(s_{in}) - D \end{pmatrix}.$$

- If $\lambda_1 > s_{in}$ then $\mu_i(s_{in}) < D$ for all $i = 1, \dots, n$, therefore J_0 admits $n + 1$ nonpositive eigenvalues given by $-D < 0$ and $\mu_i(s_{in}) - D < 0$ for all $i = 1, \dots, n$. It follows that E_0 is then locally asymptotically stable.
- If $\lambda_1 < s_{in}$ then $\mu_i(s_{in}) > D$ and then J_0 admits at least one nonnegative eigenvalue. It follows that E_0 is then unstable.

The Jacobian matrix of system (2.6) evaluated at $E_1 = (\lambda_1, s_{in} - \lambda_1, 0, \dots, 0)$ is then given by:

$$J_1 = \begin{pmatrix} -D - \mu'_1(\lambda_1)(s_{in} - \lambda_1) & -\mu_1(\lambda_1) & \cdots & -\mu_{n-1}(\lambda_1) & -\mu_n(\lambda_1) \\ \mu'_1(\lambda_1)(s_{in} - \lambda_1) & 0 & 0 & \cdots & 0 \\ 0 & 0 & \mu_2(\lambda_1) - D & 0 & 0 \\ \vdots & \vdots & \vdots & \vdots & \vdots \\ 0 & 0 & \cdots & \mu_{n-1}(\lambda_1) - D & 0 \\ 0 & 0 & \cdots & 0 & \mu_n(\lambda_1) - D \end{pmatrix}.$$

- If $\lambda_1 > s_{in}$ then there is no equilibrium point E_1 .
- If $\lambda_1 < s_{in}$ then $\mu_i(\lambda_1) < D$ for all $i = 2, \dots, n$, therefore J_1 admits $n - 1$ nonpositive eigenvalues given by $\mu_i(\lambda_1) - D < 0$ for all $i = 2, \dots, n$. J_1 admits also two other eigenvalues solution of

$$\lambda^2 + A_1\lambda + A_0 = 0,$$

where $A_0 = \mu'_1(\lambda_1)\mu_1(\lambda_1)(s_{in} - \lambda_1) > 0$ and $A_1 = D + \mu'_1(\lambda_1)(s_{in} - \lambda_1) > 0$ and thus using Routh-Hurwitz criterion, both eigenvalues have negative real parts. It follows that E_1 is then locally asymptotically stable.

□

Define the functions

$$g_i(s) = \frac{\mu_i(s)(\mu_1(s) - D)(s_{in} - \lambda_1)}{D(s_{in} - s)[\mu_i(s) - D]}, \quad i = 2, \dots, n.$$

Assumption 3. It is possible to find constants $c_i > 0$, for each $i \geq 2$ satisfying $\lambda_i < s_{in}$ such that

$$\max_{0 < s < \lambda_1} g_i(s) \leq c_i \leq \min_{\lambda_i < s < s_{in}} g_i(s)$$

The global stability of the equilibrium E_0 and the equilibrium E_1 are given in the following theorem.

Theorem 1. Assume that Assumptions 1, 2 and 3 are fulfilled.

- If $\lambda_1 \geq s_{in}$ then the equilibrium point $E_0 = (s_{in}, 0, \dots, 0)$ is globally asymptotically stable.
- If $\lambda_1 < s_{in}$ then for any non-negative initial condition with $x_1(0) > 0$, the equilibrium point $E_1 = (\lambda_1, s_{in} - \lambda_1, 0, \dots, 0)$ is globally asymptotically stable and the equilibrium point $E_0 = (s_{in}, 0, \dots, 0)$ is unstable.

Proof. • Assume that $\lambda_1 \geq s_{in}$ and let (s, x_1, \dots, x_n) to be a solution of the system (2.6). Since Ω is an attractor of all solution of system (2.6) then consider the system (2.6) restricted to the invariant hyperplane Ω and then by using the fact that $s = s_{in} - \sum_{i=1}^n x_i$, I obtain the following reduced system

$$D^\alpha x_i(t) = [\mu_i(s_{in} - \sum_{i=1}^n x_i) - D]x_i(t), \quad i = 1, \dots, n. \tag{2.11}$$

The relevant domain for (2.11) is the set $\Gamma = \{(x_1, \dots, x_n) \in \mathbb{R}_+^n / \sum_{i=1}^n x_i \leq s_{in}\}$.

Define the Lyapunov function

$$V_0(t) = \sum_{i=1}^n x_i.$$

The equilibrium point E_0 is the only stationary point and minimum point of $V_0(t)$, and $V_0(t) \mapsto +\infty$ at the boundary of the positive quadrant. Consequently, E_0 is the global minimum point, and the function is bounded from below.

The Caputo fractional derivative of $V_0(t)$ along solution of system (2.6) is given by

$$\begin{aligned}
 D^\alpha V_0(x_1, \dots, x_n) &= \sum_{i=1}^n D^\alpha x_i \\
 &= \sum_{i=2}^n [\mu_i(s_{in} - \sum_{i=1}^n x_i) - D]x_i \\
 &\leq \sum_{i=2}^n [\mu_i(s_{in}) - D]x_i \\
 &\leq 0
 \end{aligned}$$

in Γ . If $\lambda_1 > s_{in}$ then

$$E = \{(x_1, \dots, x_n) \in \Gamma; D^\alpha V_0(x_1, \dots, x_n) = 0\} = \{(x_1, \dots, x_n) \in \Gamma; x_1 = \dots = x_n = 0\},$$

whereas if $\lambda_1 = s_{in}$ then

$$E = \{(x_1, \dots, x_n) \in \Gamma; x_1 = \dots = x_n = 0 \text{ or } \sum_{i=1}^n x_i = s_{in}\}.$$

As Ω is an attractor of all solution of system (2.6) it follows that the largest invariant set M in E is

$$\{(x_1, \dots, x_n) \in \Gamma; x_1 = \dots = x_n = 0\}.$$

Therefore using the LaSalle corollary [21, 35], E_0 is globally asymptotically stable (for other applications, see [11, 16, 28]).

- Assume that $\lambda_1 < s_{in}$ and let (s, x_1, \dots, x_n) to be a solution of the system (2.6) and define the Lyapunov function [35]

$$V_1(t) = \frac{(s_{in} - \lambda_1)}{D} \int_{\lambda_1}^s \frac{\mu_1(\eta) - D}{s_{in} - \eta} d\eta + x_1 - x_1^* - x_1^* \ln \left(\frac{x_1}{x_1^*} \right) + \sum_{i=1}^n c_i x_i.$$

The equilibrium E_1 is the only internal stationary point and minimum point of $V_1(t)$, and $V_1(t) \mapsto +\infty$ at the boundary of the positive quadrant. Consequently, E_1 is the global minimum point, and the function is bounded from below.

The Caputo fractional derivative of $V_1(t)$ along solution of system (2.6) is given by

$$\begin{aligned}
 D^\alpha V_1 &= \frac{(s_{in} - \lambda_1) \mu_1(s) - D}{D} D^\alpha s + (D^\alpha x_1 - x_1^* \frac{D^\alpha x_1}{x_1}) + \sum_{i=2}^n \alpha_i D^\alpha x_i \\
 &= \frac{(s_{in} - \lambda_1) \mu_1(s) - D}{D} \left(D [s_{in} - s] - \sum_{i=1}^n \mu_i(s) x_i \right) \\
 &\quad + \left(1 - \frac{x_1^*}{x_1} \right) [\mu_1(s) - D] x_1 + \sum_{i=2}^n \alpha_i [\mu_i(s) - D] x_i \\
 &= (\mu_1(s) - D) \left[\frac{(s_{in} - \lambda_1)}{D(s_{in} - s)} \left(D [s_{in} - s] - \mu_1(s) x_1 \right) + \left(1 - \frac{x_1^*}{x_1} \right) x_1 \right] \\
 &\quad - \frac{(s_{in} - \lambda_1) \mu_1(s) - D}{D} \sum_{i=2}^n \mu_i(s) x_i + \sum_{i=2}^n \alpha_i [\mu_i(s) - D] x_i \\
 &= (\mu_1(s) - D) \left[(s_{in} - \lambda_1) - \frac{(s_{in} - \lambda_1)}{D(s_{in} - s)} \mu_1(s) x_1 + (x_1 - x_1^*) \right] \\
 &\quad + \sum_{i=2}^n \left(- \frac{(s_{in} - \lambda_1) \mu_1(s) - D}{D} \frac{\mu_1(s) - D}{s_{in} - s} \mu_i(s) + \alpha_i [\mu_i(s) - D] \right) x_i
 \end{aligned}$$

Then

$$\begin{aligned}
 D^\alpha V_1 &= (\mu_1(s) - D) \left[1 - \frac{(s_{in} - \lambda_1) \mu_1(s)}{(s_{in} - s) D} \right] x_1 \\
 &\quad + \sum_{i=2}^n \left(- \frac{(s_{in} - \lambda_1) \mu_1(s) - D}{D} \frac{\mu_1(s) - D}{s_{in} - s} \mu_i(s) + \alpha_i [\mu_i(s) - D] \right) x_i \\
 &= (\mu_1(s) - D) \left[1 - \frac{(s_{in} - \lambda_1) \mu_1(s)}{(s_{in} - s) D} \right] x_1 + \sum_{i=2}^n (\alpha_i - g_i(s)) [\mu_i(s) - D] x_i.
 \end{aligned}$$

The first term of the above sum is non-positive for $0 < s < s_{in}$ and equals 0 if and only if $s = \lambda_1$ or $x_1 = 0$. Since Assumption 3 is fulfilled, the second term is nonpositive for $0 < s < s_{in}$ and equal to zero if and only if $x_i = 0$ for $i = 2, \dots, n$. Since all parameters of the model are non-negative, it follows that $D^\alpha V_1 \leq 0$. $D^\alpha V_1 = 0$ if and only if $x_i = 0$ for $i = 1, \dots, n$ or $s = \lambda_1$ and $x_i = 0$ for $i = 2, \dots, n$. Using the Krasovskii-LaSalle extension theorem, the ω -limit set of the trajectory is E_1 . This completes the proof. □

3 Numerical Simulations

The system (2.6) has the following form

$$D_C^\alpha y(t) = f(t, y(t)), \quad y(0) = y_0 \tag{3.1}$$

There are several analytical and numerical methods have been proposed to solve such systems (3.1). Diethelm and Freed [5] proposed the well-known algorithm called FracPECE, using the classical predict, evaluate, correct, evaluate (PECE) type approach, but modified in order to solve

fractional order derivative equations [18]. This approach combines fractional Adams-Bashforth-Moulton methods.

Suppose that the time interval $[0, T]$ is discretized uniformly into N sub-intervals; define $t_j = j dt, n = 0, 1, \dots, N$, where $dt = T/N$ is the time step. Let y_j be the exact value of a function $y(t)$ at time step t_j .

Firstly, **let calculate** the predictor y_{n+1}^P according to

$$y_{n+1}^P = y_0 + \frac{1}{\Gamma(\alpha)} \sum_{j=0}^n b_{j,n+1} f(t_j, y_j) \quad (3.2)$$

where

$$b_{j,n+1} = \frac{dt^\alpha}{\alpha} \left((n+1-j)^\alpha - (n-j)^\alpha \right). \quad (3.3)$$

Then $f(t_{n+1}, y_{n+1}^P)$ was evaluated, and use this to determine the corrector y_{n+1} by means of equation

$$y_{n+1} = y_0 + \frac{1}{\Gamma(\alpha)} \left(\sum_{j=0}^n a_{j,n+1} f(t_j, y_j) + a_{n+1,n+1} f(t_{n+1}, y_{n+1}^P) \right) \quad (3.4)$$

where

$$a_{j,n+1} = \frac{dt^\alpha}{\alpha(\alpha+1)} \left((n+2-j)^{\alpha+1} - 2(n+1-j)^{\alpha+1} + (n-j)^{\alpha+1} \right). \quad (3.5)$$

Finally $f(t_{n+1}, y_{n+1})$ **was evaluated** which is then used in the next integration step.

Numerical simulations **were performed** for system (2.6) using FracPECE algorithm. **Five species were considered.** Classical Monod functions were used to express the growth rates $\mu_i(s) = \frac{\bar{\mu}_i s}{(k_i + s)}$ with $\bar{\mu}_i, k_i > 0$ which satisfy Assumption 1 and such that $\lambda_1 < \lambda_2 < \lambda_3 < \lambda_4 < \lambda_5$ (Assumption 2). α is chosen to be 0.8.

Two cases were considered. The first one (Fig. 3, left) performing the global stability of the equilibrium E_0 when $\lambda_1 \geq s_{in}$. The other test (Fig. 3, right) perform the global stability of the equilibrium E_1 when $\lambda_1 < s_{in}$.

4 Conclusion

A fractional-order mathematical model for n species competing, in a chemostat, for a single resource is proposed. The global dynamics was carried out, for any set of increasing growth rates. Obtained results generalize and improve the well-known competitive exclusion principle in the chemostat, that is at most one competitor population avoids extinction [31].

References

- [1] Aris R, Humphrey A E. Dynamics of a chemostat in which two organisms compete for a common substrate. *Biotech. Bioeng.* 1977;19:1375-1386.
- [2] Butler, G J, Wolkowicz G S K. A mathematical model of the chemostat with a general class of functions describing nutrient uptake. *SIAM J. Appl. Math.* 1985;45:137-151.
- [3] Diethelm K. The analysis of fractional differential equations: an application-oriented exposition using operators of caputo type. Springer. 2004.

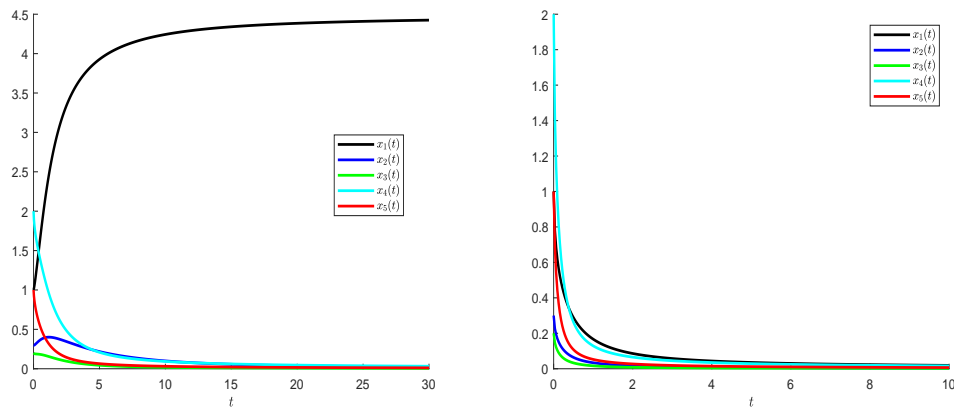


Fig. 3: Left, $s_{in} = 5, D = 2, \bar{\mu}_1 = 6, k_1 = 1, \bar{\mu}_2 = 5, k_2 = 1, \bar{\mu}_3 = 4, k_3 = 1, \bar{\mu}_4 = 3, k_4 = 1, \bar{\mu}_5 = 2, k_5 = 1$ and right $s_{in} = 5, D = 7, \bar{\mu}_1 = 6, k_1 = 1, \bar{\mu}_2 = 5, k_2 = 1, \bar{\mu}_3 = 4, k_3 = 1, \bar{\mu}_4 = 3, k_4 = 1, \bar{\mu}_5 = 2, k_5 = 1$. As it can be seen on the figure on the left, all components vanish, except the first one. The solution converge to E_1 . For the figure on the right, all species go extinct and the solution converge to E_0 .

[4] Diethelm K, Ford N J. Analysis of fractional differential equations. J. Math. Anal. Appl. 2002;260(2):229-48.

[5] Diethelm K, Freed A D. The fracPECE subroutine for the numerical solution of differential equations of fractional order. Forschung Wiss Rechnen. 1998;57-71.

[6] El Hajji M. Global analysis of an epidemic mathematical model in a chemostat. J. Comp. Sys. Bio. 2019;2(1):105.

[7] El Hajji M. Mathematical analysis of a fractional-order "SIR" epidemic model with a general nonlinear saturated incidence rate in a chemostat. Asian Research J. Math. 2019.

[8] El Hajji M. Optimal control of an "SIR" epidemic model in a chemostat using some suitable protein doses. J. Adv. Math. Computer Sci. 2019.

[9] El Hajji M. Analysis of a fractional-order "SVEIR" epidemic model with a general nonlinear saturated incidence rate in a continuous reactor. Asian Research J. Math. 2019.

[10] El Hajji M. Boundedness and asymptotic stability of nonlinear Volterra integro-differential equations using Lyapunov functional. J. King Saud Univ. Sci. 2018.

[11] El Hajji M. How can inter-specific interferences explain coexistence or confirm the competitive exclusion principle in a chemostat. Int. J. Biomath. 2018;11(8):1850111.

[12] El Hajji M, Chorfi N, Jleli M. Mathematical modelling and analysis for a three-tiered microbial food web in a chemostat. Electron. J. Diff. Eqns. 2017;2017(255):1-13.

[13] El Hajji M, Chorfi N, Jleli M. Mathematical model for a membrane bioreactor process, Electron. J. Diff. Eqns. 2015;2015(315):1-7.

[14] El Hajji M, Rapaport A. Design of a cascade observer for a model of bacterial batch culture with nutrient recycling. IFAC Proceedings Volumes. 2010;43(6):203-208.

[15] El Hajji M, Mazenc F, Harmand J. A mathematical study of a syntrophic relationship of a model of anaerobic digestion process. Math. Biosci. Eng. 2010;7(3):641-656.

- [16] El Hajji M, Rapaport A. Practical coexistence of two species in the chemostat - A slow-fast characterization. *Math. Biosci.* 2009;218(1):33-39.
- [17] El Hajji M, Harmand J, Chaker H, Lobry C. Association between competition and obligate mutualism in a chemostat. *J. Biol. Dynamics.* 2009;3(6):635-647.
- [18] Garrappa R. Trapezoidal methods for fractional differential equations: theoretical and computational aspects. *Math. Comput. Simul.* 2015;11:96-112.
- [19] Hardin G. The competition exclusion principle. *Science.* 1960;131:1292-1298.
- [20] Hsu S B, Hubbell S, Waltman P. A mathematical theory for single-nutrient competition in continuous cultures of micro-organisms. *SIAM J. APPL. MATH.* 1977;32(2):366-383.
- [21] LaSalle J P. *The Stability of Dynamical Systems.* SIAM. 1976;25.
- [22] Lin Y, Xu C. Finite difference/spectral approximations for the time-fractional diffusion equation. *J. Comput. Phys.* 2007;225(2):1533-1552.
- [23] Monod J. La technique de culture continue. *Ann. Inst. Pasteur.* 1950;79:390-410.
- [24] Novick A, Szilard L. Experiments with the chemostat on spontaneous mutations of bacteria. *Proc. Nat. Acad. Sci.* 1936;36:708-719.
- [25] Pinho S T R, Ferreira C P, Esteva L, Barreto F R, Morato E, Silva V C, Teixeira M G L. Modelling the dynamics of dengue real epidemics. *Philos. TransR. Soc.* 2006;368:5679-93.
- [26] Rapaport A, Veruete M. A new proof of the competitive exclusion principle in the chemostat. *Disc. Cont. Dyn. Syst. B.* 2017.
- [27] Sari T, Mazenc F. Global dynamics of the chemostat with different removal rates and variable yields. *Math. Biosci. Engng.* 2011;8(3):827-840.
- [28] Sari T, El Hajji M, Harmand J. The mathematical analysis of a syntrophic relationship between two microbial species in a chemostat. *Math. Biosci. Engng.* 2012;9(1):627-645.
- [29] Sari T. Competitive exclusion for chemostat equations with variable yields. *Acta Appl. Math.* 2013;123(1):201-219.
- [30] Smith H L, Thieme H R. Chemostat and Epidemics: competition for nutrients/hosts. *Math. Biosci. Eng.* 2013;10(5&6):1635-1650.
- [31] Smith H L, Waltman P. *The theory of the chemostat, Dynamics of microbial competition.* Cambridge Studies in Mathematical Biology, Cambridge University Press. 1995.
- [32] Spicer C. *The theory of constant growth apparatus.* Biometrics. 1995.
- [33] Stephanopoulos G, Aris R, Frederickson A G. A stochastic analysis of the growth of competing microbial populations in a continuous biochemical reactor. *Math. Biosci.* 1979;45:99-135.
- [34] Thieme H R. Convergence results and a Poincaré-Bendixson trichotomy for asymptotically autonomous differential equations. *J. Math. Biol.* 1992;30(7):755-763.
- [35] Wolkowicz G S K, Lu Z. Global dynamics of a mathematical model of competition in the chemostat : general response functions and differential death rates. *SIAM J. Appl. Math.* 1992;52(1):222-233.