

# Stability analysis of mathematical model of competition in a chain of chemostats in series with delay<sup>☆</sup>



Frédéric Mazenc<sup>a</sup>, Silviu-Iulian Niculescu<sup>a</sup>, Gonzalo Robledo<sup>b,\*</sup>

<sup>a</sup> EPI DISCO Inria-Saclay, Laboratoire des Signaux et Systèmes (UMR CNRS 8506), CNRS, CentraleSupélec, Université Paris-Sud, 3 rue Joliot Curie, Gif-sur-Yvette 91192, France

<sup>b</sup> Departamento de Matemáticas, Universidad de Chile, Casilla 653, Santiago, Chile

## ARTICLE INFO

### Article history:

Received 13 December 2018

Revised 7 June 2019

Accepted 10 June 2019

Available online 14 June 2019

### Keywords:

Competitive exclusion

Chemostat

Delay equations

Lyapunov functions,

## ABSTRACT

We study a nonlinear system of differential delay equations describing a model of a chain of two chemostats, where one contains two microbial species in competition for a single limiting nutrient and receives an external input of the less advantaged competitor, which is cultivated in an external chemostat. We obtain sufficient conditions ensuring coexistence of all the species in competition which consist in upper delay bounds.

© 2019 Elsevier Inc. All rights reserved.

## 1. Introduction

The chemostat [1,2] or continuous stirred-tank reactor (CSTR) is a continuous bioreactor whose operating parameters allow to reproduce the essential features of simple microbial ecosystems, namely, a spatially homogeneous and time invariant environment with a constant supply of limiting nutrients. In addition to its industrial applications, the chemostat has also a theoretical interest since is a remarkable tool employed to mimic a scenario of pure and simple competition between two or more microbial species inhabiting a common environment with a unique limiting nutrient whose availability affects the growth rate of the populations and the competition for this nutrient is the unique ecological interaction between the microbial populations.

The description of the population densities of the competing species and their evolution in time have several outcomes, one of the most usual ones being the competitive exclusion. This outcome contrasts sharply with the high levels of biodiversity observed in wild ecosystems, which has triggered illuminating debates and consequent progress in theoretical ecology [3,4] and mathematical modeling [5].

The classical model of competition in a stirred chemostat is described by the system of differential equations:

$$\begin{cases} \dot{s}(t) = D[s^0 - s(t)] - \sum_{i=1}^n \gamma_i^{-1} \mu_i(s(t)) x_i(t) \\ \dot{x}_j(t) = x_j(t) \mu_j(s(t)) - D x_j(t) \text{ for } j = 1, \dots, n, \end{cases} \quad (1.1)$$

<sup>☆</sup> This article is partially supported by MATHAMSUD regional cooperation program.

\* Corresponding author.

E-mail addresses: [frederic.mazenc@l2centralsupelec.fr](mailto:frederic.mazenc@l2centralsupelec.fr) (F. Mazenc), [silviu.niculescu@lss.supelec.fr](mailto:silviu.niculescu@lss.supelec.fr) (S. Niculescu), [grobledo@uchile.cl](mailto:grobledo@uchile.cl) (G. Robledo).

where  $n$  microbial species with densities denoted by  $x_1, \dots, x_n$  compete for a single nutrient, also called limiting substrate with concentration  $s$ . The positive constants  $s^0$  and  $D$  are called the input nutrient concentration and dilution rate, respectively. For any  $i = 1, \dots, n$ , the functions  $\mu_i : [0, +\infty) \rightarrow [0, +\infty)$  describe simultaneously the per-capita growth of the  $i$ th species and its consumption of nutrient. The constant  $\gamma_i > 0$  is a yield constant which relates the growth of the species with nutrient consumption.

The basic assumption of (1.1) is to consider that the consumption of nutrient has immediate effects on the growth rate of microbial biomass. In the present paper we will consider the existence of a time interval  $[t - \tau, t]$  that any microbial species takes to metabolize the nutrient.

After a change of variables and taking into in consideration the delays stated above, the system (1.1) can be transformed into

$$\begin{cases} \dot{s}(t) = D[s^0 - s(t)] - \sum_{i=1}^n \mu_i(s(t))x_i(t) \\ \dot{x}_j(t) = x_j(t)\mu_j(s(t - \tau)) - Dx_j(t) \text{ for } j = 1, \dots, n. \end{cases} \tag{1.2}$$

The model (1.2) with  $n = 1$  was introduced by Thingstad [6] which considers the experimental evidence of a time delay between a change in nutrient conditions and the resulting change in division rate of the cell population observed in [7]. A first generalization is made by Bush and Cook [8], where a more general uptake function is considered and the case  $n = 2$  was studied in [9]. The main focus of all these references is the existence of periodic orbits.

The case  $n = 1$  was revisited in [10–12], where existence and global stability of a positive equilibrium are studied. The general case, in which an arbitrary number of competing species was considered, has been studied in [13], where it is assumed that the functions  $\mu_i$  satisfy the following properties:

**(H1)** The functions have the Monod or Michaelis-Menten form:

$$\mu_i(s) = \frac{m_i s}{a_i + s} \text{ with } m_i > 0 \text{ and } a_i > 0. \tag{1.3}$$

**(H2)** For any  $i = 1, \dots, n$ , there exists  $\lambda_i \in (0, s^0)$  such that  $\mu_i(\lambda_i) = D$  and

$$0 < \lambda_n < \lambda_{n-1} < \dots < \lambda_2 < \lambda_1 < s^0. \tag{1.4}$$

The parameters  $m_i$  and  $a_i$  in **(H1)** are known as the *maximal growth rate* and the *half saturation constant* corresponding to the  $i$ th species. On the other hand, the assumption **(H2)** implies that  $D < \mu_n(s^0)$ . The constant  $\lambda_i$  is known as the *break-even concentration* corresponding to the  $i$ th species, namely, the minimal nutrient necessary to ensure the positive growth of the  $i$ th species.

The assumption **(H2)** implies that for a given dilution rate  $D$ , all the species can be ordered with respect to their competitive ability, the  $n$ th species being the most advantaged competitor due to the fact that it needs a lower concentration of nutrient to have a positive growth. In fact, the result in [13] states the long time consequences for this hierarchization of the competitive abilities: the most advantaged species converges to the  $n$ th break even concentration while the  $i$ th species ( $i = 1, \dots, n - 1$ ) converges to extinction.

**Proposition 1.** Assume that assumptions **(H1)** and **(H2)** are satisfied and let

$$\mathcal{M} = \max_{i \in \mathbb{N}_{n-1}} \{m_i\}, \quad \mathcal{C} = \max_{i \in \mathbb{N}_{n-1}} \{D - \mu_i(\lambda_n)\} \text{ and } \mathcal{T} = \max_{i \in \mathbb{N}_{n-1}} \left\{ \left( \frac{s^0}{a_i} + 3 \right) \frac{s^0 m_i}{a_i} \right\}$$

where  $\mathbb{N}_{n-1} = \{1, 2, \dots, n - 1\}$ . Then, there exists  $0 < \tau_0^* = \min_{i=1, \dots, 5} \{A_i\}$ , with

$$\begin{aligned} A_1 &= \frac{1}{D} \ln \left( \frac{6}{5} \right), \quad A_2 = \frac{1}{\mathcal{M} - D} \ln \left( \frac{4\mathcal{M}}{4\mathcal{M} - D} \right), \quad A_3 = \frac{a_n^2 \mathcal{C}}{8s^0(a_n + s^0)m_n \mathcal{M}} \\ A_4 &= \frac{\mathcal{C}}{8\mathcal{M}\mathcal{T}} \text{ and } A_5 = \frac{a_n^2 D}{2\sqrt{2}s^0 m_n (3a_n + s^0) \max \left\{ 1, \frac{s^0}{a_n}, \frac{\sqrt{D}}{\sqrt{\mathcal{C}}} \right\}}. \end{aligned}$$

such that, for any  $\tau \in [0, \tau_0^*)$  the solutions of system (1.2) verify:

$$\lim_{t \rightarrow +\infty} (s(t), x_1(t), \dots, x_n(t)) = (\lambda_n, 0, \dots, s^0 - \lambda_n).$$

**Proposition 1** can be seen as a chemostat's version of the *competitive exclusion principle*, which has been described by Hardin [14] for two species as follows: “(i) if two noninterbreeding populations “do the same thing”-that is, occupy precisely the same ecological niche in Elton's sense [15] and (ii) if they are “sympatric” that is, if they occupy the same geographic territory and (iii) if population A multiplies even the least bit faster than population B, then ultimately, A will completely displace B, which will become extinct”.

It is worth emphasizing that there exist other approaches describing the delay between consumption of nutrient and the corresponding growth of the microbial species. In particular, we highlight the model developed by Freedman et al. [16] and Ellermeyer [17], which has been extended in several directions [18,19] where the competitive exclusion is also verified.

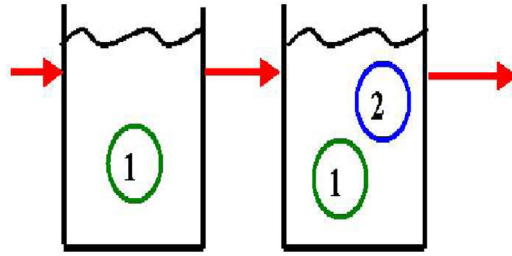


Fig. 1. The competitor  $x_1$  is cultivated in an external chemostat and pumped into a chemostat containing the two competitors.

The competitive exclusion has been the subject of several debates and controversies due to the difficulty to conciliate it with theoretical approaches devoted to biodiversity. For example, Darlington [3] recalls that the competitive exclusion is “only an hypothesis” and several misuses and misconceptions are pointed out. In addition, Keymer et al. [4] propose a unified framework to understand the emergence and maintaining of the biodiversity, where the competitive exclusion is considered as a particular regime. Now, with respect to the systems (1.1) and (1.2), several modifications are introduced in order to explain the coexistence of all the competing species by considering some decoupling between niche and territory in Hardin’s definition which can be induced by multiple factors such as environmental variability either stochastic [20–23] or deterministic [24–26], spatial heterogeneity of the liquid medium [5,27], intraspecific competition [28,29], multiple limiting nutrients [30,31], etc.

In spite of the above discussion, it is also important to emphasize that the competitive exclusion has been verified experimentally in microbial aquatic ecosystems described by (1.1) with  $n = 2$  in [32–34]. In this context, an idea is to introduce some inputs in the model as feedback control [35] or constant inputs of the weaker competitors [36] in order to obtain the coexistence of the competing species.

This article must be considered in the “input oriented” approach above described since it proposes a chain of chemostats interconnected in series, where the weaker competitor is cultivated in a first chemostat and, in order to promote the coexistence its output becomes the input of a second chemostat containing the two species in competition. We find a set of sufficient conditions in terms of upper delay bounds which ensure the coexistence of the species in competition.

This article is organized as follows. Section 2 introduces the chain of chemostat mentioned above, whose mathematical model consists in a system of differential delay equations. Section 3 is devoted to the study of the local asymptotic stability of the system via quasi-polynomials associated to the delay system linearized around the unique positive equilibrium. Section 4 introduces a set of conditions ensuring global asymptotical stability of the equilibrium and the corresponding proofs are given in Sections 5 and 6, respectively. The proofs are strongly inspired by the ideas and methods developed in [37,38]. The Section 7 provides an application of the model, namely, an improvement and complementary strategy to the feedback approach developed by De Leenher and Smith [35] in order to avoid the competitive exclusion. In addition, a numerical example of coexistence between *Saccharomyces cerevisiae* and *Candida utilis* is carried out. Some final comments are given in Section 8.

## 2. Problem statement

We will consider an idea developed by Contreras [39; Fig. 1] for the case without delay, where the competitive exclusion is verified and external inputs are introduced in order to promote coexistence. We will consider (1.2) with  $n = 2$  and then Proposition 1 ensures that  $x_1$  will not persist in the long term. In order to promote the coexistence of the two species, the first species, namely the less advantaged competitor, with concentration  $x_{11}$  is cultivated in a first chemostat, whose dynamics is described for any  $t \geq 0$  by the system

$$\begin{cases} \dot{s}_1(t) = D[s^0 - s_1(t)] - \mu_1(s_1(t))x_{11}(t), \\ \dot{x}_{11}(t) = x_{11}(t)\mu_1(s_1(t - \tau)) - Dx_{11}(t), \end{cases} \quad (2.1)$$

and by (H1)–(H2) it is easy to deduce that  $E_0^* = (\lambda_1, x_{11}^*)$  with  $x_{11}^* = s^0 - \lambda_1$  is the unique positive equilibrium.

Now, if the output of (2.1) becomes the input of (1.2) with  $n = 2$ , we obtain the coupled system:

$$\begin{cases} \dot{s}_1(t) = D[s^0 - s_1(t)] - \mu_1(s_1(t))x_{11}(t), \\ \dot{x}_{11}(t) = x_{11}(t)\mu_1(s_1(t - \tau)) - Dx_{11}(t), \\ \dot{s}_2(t) = D[s_1(t) - s_2(t)] - \mu_1(s_2(t))x_{12}(t) - \mu_2(s_2(t))x_{22}(t), \\ \dot{x}_{12}(t) = x_{12}(t)\mu_1(s_2(t - \tau)) + D[x_{11}(t) - x_{12}(t)], \\ \dot{x}_{22}(t) = x_{22}(t)\mu_2(s_2(t - \tau)) - Dx_{22}(t), \end{cases} \quad (2.2)$$

which emphasizes that  $x_{ij}$  is the concentration of the  $i$ th species in the  $j$ th chemostat, while  $s_i$  is the concentration of the same nutrient in the  $i$ th chemostat.

**(H3)** The constants  $\lambda_1$  and  $\lambda_2$  are such that the following inequality is satisfied

$$\lambda_2 + \frac{\mu_1(\lambda_2)(s^0 - \lambda_1)}{D - \mu_1(\lambda_2)} < \lambda_1. \tag{2.3}$$

One can prove that this assumption implies that (2.2) has a unique positive equilibrium  $E^* = (s_1^*, x_{11}^*, s_2^*, x_{11}^*, x_{12}^*)$  whose components are:

$$\begin{cases} s_1^* = \lambda_1, & s_2^* = \lambda_2, & x_{11}^* = s^0 - \lambda_1 \\ x_{12}^* = \frac{Dx_{11}^*}{D - \mu_1(\lambda_2)}, & x_{22}^* = \lambda_1 - \lambda_2 - \frac{\mu_1(\lambda_2)x_{11}^*}{D - \mu_1(\lambda_2)}. \end{cases} \tag{2.4}$$

The assumption **(H3)** is equivalent to

$$s^0 < \lambda_1 + (\lambda_1 - \lambda_2) \left( \frac{D - \mu_1(\lambda_2)}{\mu_1(\lambda_2)} \right), \tag{2.5}$$

which suggests an interesting ecological interpretation: there is a threshold for the concentration of the limiting substrate  $s^0$  that must be pumped into the first chemostat in order to ensure the existence of the two species equilibrium  $E^*$ . Indeed, in [39], the system (2.2) is studied when  $\tau = 0$  and it was proved that  $E^*$  is globally attractive for any componentwise positive initial condition if and only if (2.5) is verified. On the other hand, if (2.5) is not satisfied the species  $x_2$ , the strongest competitor in the previous context, cannot persist while  $x_1$ , the weakest competitor, is the only survival species. This is a counterintuitive fact: *the excess of nutrient does not promote the coexistence of the species*.

In this article, we obtain sufficient conditions ensuring the global stability of  $E^*$  for some delay margin  $[0, \tau^*)$ . While in [39] the proof is made by using monotone dynamical systems combined with some asymptotic properties of triangular systems, our proof will be made by constructing a Lyapunov-like function. Indeed, the Lyapunov functions have been used in several ecological and bioprocesses models as in [40–42] and several techniques of [37,38] can be adapted in order to carry out a stability study of (2.1) and (2.2).

### 3. Local stability results

#### 3.1. Linearization of (2.1) around $E_0^*$

After the simple change of coordinates  $u_1 = s_1 - \lambda_1$ ,  $u_2 = x_{11} - x_{11}^*$ , one can easily check that the linearization of the system (2.1) around the equilibrium  $(\lambda_1, x_{11}^*)$  is given by

$$\dot{u}(t) = A_0 u(t) + B_0 u(t - \tau), \tag{3.1}$$

where the matrices  $A_0$  and  $B_0$  are

$$A_0 = \begin{bmatrix} -(D + \mu_1'(\lambda_1)x_{11}^*) & -D \\ 0 & 0 \end{bmatrix}, \quad \text{and} \quad B_0 = \begin{bmatrix} 0 & 0 \\ \mu_1'(\lambda_1)x_{11}^* & 0 \end{bmatrix}.$$

The asymptotic stability analysis of (3.1) has been carried out in several works as for instance [10,11,43]. Nevertheless, the following result is included for the sake of completeness.

**Lemma 3.1.** *There exists a delay margin*

$$\tau_0 = \frac{1}{\omega_0} \arccos \left( \frac{\omega_0^2}{B} \right) \quad \text{with} \quad \omega_0 = \sqrt{\frac{-A^2 + \sqrt{A^4 + 4B^2}}{2}}, \tag{3.2}$$

where the constants  $A$  and  $B$  are defined by

$$A = D + \mu_1'(\lambda_1)x_{11}^* \quad \text{and} \quad B = D\mu_1'(\lambda_1)x_{11}^*, \tag{3.3}$$

such that if  $\tau \in [0, \tau_0)$  then the origin is an asymptotically stable equilibrium of (3.1).

**Proof.** The characteristic equation of (3.1) is

$$p_1(s, e^{-\tau s}) = \det(sI - A_0 - B_0 e^{-\tau s}) = s^2 + As + B e^{-\tau s}. \tag{3.4}$$

Thus the origin is a uniformly asymptotically stable solution of (3.1) if and only if all the roots of (3.4) have a negative real part. Moreover, it is well known (see e.g. [44] for details) that the function  $\Omega : \mathbb{R}_+ \rightarrow \mathbb{C}$  defined by  $\Omega(\tau) = \sup\{Re s : p_1(s, \tau) = 0\}$  is continuous.

As  $A_0 + B_0$  is a Hurwitz matrix, the system (3.1) is asymptotically stable when  $\tau = 0$ . On the other hand, the characteristic equation (3.4) is a polynomial when  $\tau = 0$  but becomes a quasipolynomial as  $\tau$  increases and the number of roots becomes infinite and vary continuously with respect to  $\tau$ . In addition, there exists a delay margin  $\tau_0$  such that the origin of (3.1) is asymptotically stable for any  $\tau \in [0, \tau_0)$  and  $p_1(i\omega, e^{-i\tau_0\omega}) = 0$ .

The equation  $|p_1(i\omega, e^{-i\tau_0\omega})|^2 = 0$  is equivalent to

$$\omega^4 + \mathcal{A}^2\omega^2 - \mathcal{B}^2 = 0, \tag{3.5}$$

whose real roots (also called crossover frequencies) are  $\pm\omega_0$ , which are defined in (3.2). Now, note that  $p_1(i\omega_0, e^{-i\omega_0\tau_0}) = 0$  is also equivalent to

$$\omega_0^2 - \mathcal{B} \cos(\omega_0\tau) = 0 \quad \text{and} \quad \mathcal{A}\omega_0 + \mathcal{B} \sin(\omega_0\tau) = 0$$

and (3.2) follows by the left above identity. □

### 3.2. Linearization of (2.2) around $E^*$

Using the additional change of variables  $u_3 = \lambda_2 - s_2, u_4 = x_{12} - x_{12}^*$  and  $u_5 = x_{22} - x_{22}^*$ , we deduce that the linearization around the equilibrium  $E^*$  is

$$\dot{u} = \begin{bmatrix} A_0 & 0 \\ A_1 & A_2 \end{bmatrix} u(t) + \begin{bmatrix} B_0 & 0 \\ 0 & B_2 \end{bmatrix} u(t - \tau), \tag{3.6}$$

where  $A_0$  and  $B_0$  are defined above while  $A_1, A_2$  and  $B_2$  are

$$A_1 = \begin{bmatrix} D & 0 \\ 0 & D \\ 0 & 0 \end{bmatrix}, \quad A_2 = \begin{bmatrix} -\{D + \mu'_1(\lambda_2)x_{12}^* + \mu'_2(\lambda_2)x_{22}^*\} & -\mu_1(\lambda_2) & -D \\ 0 & \mu_1(\lambda_2) - D & 0 \\ 0 & 0 & 0 \end{bmatrix},$$

and

$$B_2 = \begin{bmatrix} 0 & 0 & 0 \\ \mu'_1(\lambda_2)x_{12}^* & 0 & 0 \\ \mu'_2(\lambda_2)x_{22}^* & 0 & 0 \end{bmatrix}.$$

As the determinant of a block triangular matrix is the product of the determinants of its diagonal blocks, the characteristic quasipolynomial of (3.6) is

$$p(s, e^{-\tau s}) = p_1(s, e^{-\tau s})p_2(s, e^{-\tau s}),$$

where  $p_1(s, e^{-\tau s})$  was stated in (3.4) and  $p_2(s, e^{-\tau s})$  is

$$p_2(s, e^{-\tau s}) = \det(sI - A_2 - B_2e^{-\tau s}) = Q_0(s) + Q_1(s)e^{-\tau s}$$

where  $Q_0$  and  $Q_1$  are the polynomials

$$Q_0(s) = s^3 + as^2 + bs, \quad \text{and} \quad Q_1(s) = cs + d,$$

with the coefficients

$$a = 2D - \mu_1(\lambda_2) + \sum_{i=1}^2 \mu'_i(\lambda_2)x_{i2}^*, \quad b = -(D + \sum_{i=1}^2 \mu'_i(\lambda_2)x_{i2}^*)(\mu'_1(\lambda_2) - D)$$

$$c = \sum_{i=1}^2 \mu_i(\lambda_2)\mu'_i(\lambda_2)x_{i2}^*, \quad d = -\mu'_2(\lambda_2)x_{22}^*D[\mu_1(\lambda_2) - D].$$

**Lemma 3.2.** *The equilibrium  $E^*$  is an asymptotically stable solution of (3.6) if  $\tau \in [0, \min\{\tau_0, \widehat{\tau}_0\})$ , with  $\widehat{\tau}_0 = u_0$  or  $\widehat{\tau}_0 = \min\{u_1, u_2, u_3\}$ , where*

$$u_j = \frac{1}{\omega_j} \arccos\left(\frac{\{bc - ad\}\omega_j^2 - ac\omega_j^4}{d^2 + c^2\omega_j^2}\right) \quad \text{with } j = 0 \text{ or } j = 1, 2, 3,$$

and the  $\omega_j$ s are positive roots of the polynomial

$$Q_2(\omega) = -d^2 + (b^2 - c^2)\omega^2 - (a^2 - 2b)\omega^4 + \omega^6. \tag{3.7}$$

**Proof.** In order to find the crossover frequencies, the identity  $p_2(i\omega, e^{-i\tau\omega}) = 0$  leads to  $|Q_0(i\omega)| = |Q_1(i\omega)|$ , which is equivalent to the equation  $Q_2(\omega) = 0$ .

Notice that, the polynomial (3.7) has either two roots  $\pm\omega_0$  or six roots  $\pm\omega_j$  with  $j = 1, 2, 3$ . Without loss of generality, we will consider the last case and consider the identities  $Q_0(i\omega_j)/Q_1(i\omega_j) = e^{i\tau\omega_j}$ , which give, by taking the real parts,

$$\cos(\tau\omega_j) = \frac{(bc - ad)\omega_j^2 - ac\omega_j^4}{d^2 + c^2\omega_j^2}$$

and the lemma follows. □

**4. Global stability results**

In order to state our first global stability result, let us introduce the constants

$$d_0 = \frac{2s^0 \mu_1(s^0) e^{\tau[\mu_1(s^0) - D]} a_1 m_1}{a_1 + \lambda_1} \quad \text{and} \quad a_0 = \sqrt{\frac{s^0}{a_1 + s^0}}, \tag{4.1}$$

$$\bar{\Gamma} = D + \frac{a_1 m_1 x_{11}^*}{(a_1 + \lambda_1)(a_1 + s^0)} \quad \text{and} \quad \underline{s}_1 = \frac{Ds^0}{D + 2s^0 \frac{m_1}{a_1} e^{\tau D}}. \tag{4.2}$$

**Theorem 1.** *If the assumptions (H1) and (H2) are satisfied for  $n = 1$  and the delay  $\tau$  is such that the inequalities*

$$0 < \tau < \bar{\tau}_1 = \begin{cases} \frac{1}{D - \mu_1(s^0)} \ln \left( 1 - \frac{D}{2\mu_1(s^0)} \right) & \text{if } 2\mu_1(s^0) > D, \\ +\infty & \text{if } 2\mu_1(s^0) \leq D \end{cases} \tag{4.3}$$

and

$$\tau^2 (d_0 a_0)^2 < \bar{\Gamma}^2 (\underline{s}_1 + \lambda_1), \tag{4.4}$$

are verified, then the equilibrium  $(\lambda_1, s^0 - \lambda_1)$  of (2.1) is globally asymptotically stable for any positive initial condition.

The global stability of (2.1) has been previously studied in [12], where the authors introduce sufficient conditions for the global asymptotic stability of  $E_0^*$ . We point out that these conditions are not directly comparable with those of Theorem 1. In addition, we will see that our method can be easily extended to other systems of delay equations.

In order to state our main result for (2.2), let us introduce the constants:

$$\bar{\Theta} = D + \sum_{i=1}^2 \frac{a_i m_i x_{i2}^*}{(a_i + \lambda_2)(a_i + \lambda_1)}, \quad C = \lambda_1 + x_{11}^* e^{\tau[\mu_1(s^0) - \mu_1(\lambda_2)]}, \tag{4.5}$$

$$\underline{s} = \frac{D\lambda_1}{D + 2C \sum_{i=1}^2 \frac{m_i}{a_i} e^{\mu_i(\lambda_2)\tau}}, \quad B_i = \mu_i(\lambda_1) - \mu_i(\lambda_2), \quad c_i = \frac{a_i}{a_i + \lambda_2} \tag{4.6}$$

$$\underline{\xi}_1 = \frac{x_{11}^*}{e^{\tau\mu_1(\lambda_2)}}, \quad q = \frac{B_1}{c_1}, \quad b = Dx_{11}^* m_1 e^{\tau B_1} \quad d_i = 4Cm_i c_i \mu_i(\lambda_1) e^{\tau B_i}, \tag{4.7}$$

where  $i \in \{1, 2\}$ .

**Theorem 2.** *If assumptions (H1)–(H3) are satisfied, the delay  $\tau$  satisfies the inequalities stated in Proposition 1 and Lemma 3.2 together with*

$$0 < \tau < \bar{\tau}_{2_i} = \begin{cases} \frac{1}{\mu_i(\lambda_2) - \mu_i(\lambda_1)} \ln \left( 1 - \frac{D}{2\mu_i(\lambda_1)} \right) & \text{if } 2\mu_i(\lambda_1) > D, \\ +\infty & \text{if } 2\mu_i(\lambda_1) \leq D, \end{cases} \tag{4.8}$$

for  $i = 1, 2$

$$\tau \lambda_1 \left( \frac{1}{2\bar{\Theta}\underline{s}} \max_{1 \leq i \leq 2} \left\{ \frac{d_i^2}{(\underline{s} + a_i)(a_i + \lambda_1)} \right\} + \frac{b^2}{4q\underline{\xi}_1(a_1 + \underline{s})(a_1 + \lambda_1)} \right) < \bar{\Theta}, \tag{4.9}$$

holds, then the equilibrium  $E^*$  is a globally asymptotically stable solution of (2.2) for any positive initial condition.

Note that (2.2) has hierarchical structure, namely the behavior of (2.1) is independent of the other equations. This prompts us to consider the subsystem

$$\begin{cases} \dot{s}_2(t) = D[s_1(t) - s_2(t)] - \mu_1(s_2(t))x_{12}(t) - \mu_2(s_2(t))x_{22}(t), \\ \dot{x}_{12}(t) = x_{12}(t)\mu_1(s_2(t - \tau)) + D[x_{11}(t) - x_{12}(t)], \\ \dot{x}_{22}(t) = x_{22}(t)\mu_2(s_2(t - \tau)) - Dx_{22}(t), \end{cases} \tag{4.10}$$

where  $t \rightarrow s_1(t)$  and  $t \rightarrow x_{11}(t)$  are solutions of (2.1). Now, under the assumptions of Theorem 1, we can verify that (4.10) is asymptotically autonomous to

$$\begin{cases} \dot{s}_2(t) = D[\lambda_1 - s_2(t)] - \mu_1(s_2(t))x_{12}(t) - \mu_2(s_2(t))x_{22}(t), \\ \dot{x}_{12}(t) = x_{12}(t)\mu_1(s_2(t - \tau)) + D[x_{11}^* - x_{12}(t)], \\ \dot{x}_{22}(t) = x_{22}(t)\mu_2(s_2(t - \tau)) - Dx_{22}(t), \end{cases} \tag{4.11}$$

for any positive initial condition. This system has been studied in a more general context but without delays in [36].

On the other hand, (4.10) is also equivalent to the perturbed system

$$\begin{cases} \dot{s}_2(t) = D[\lambda_1 - s_2(t)] - \mu_1(s_2(t))x_{12}(t) - \mu_2(s_2(t))x_{22}(t) + \delta_0(t), \\ \dot{x}_{12}(t) = x_{12}(t)\mu_1(s_2(t - \tau)) + D[x_{11}^* - x_{12}(t)] + \delta_1(t), \\ \dot{x}_{22}(t) = x_{22}(t)\mu_2(s_2(t - \tau)) - Dx_{22}(t), \end{cases} \tag{4.12}$$

where the perturbations  $t \mapsto \delta_i(t)$  ( $i = 0, 1$ ) are defined by

$$\delta_0(t) = D[s_1(t) - \lambda_1] \quad \text{and} \quad \delta_1(t) = D[x_{11}(t) - x_{11}^*].$$

We can see that (4.12) has similar structure to the system studied in [38], where general bounded and measurable perturbations  $\delta_i$  are considered and sufficient conditions ensuring input–to–state stability (ISS) are obtained with respect to the disturbances  $\delta_i$ . We point out that under the assumptions of Theorem 1 it follows that  $\lim_{t \rightarrow +\infty} \delta_i(t) = 0$  and this case has not been considered in [37,38].

### 5. Proof of Theorem 1

The proof will be decomposed in several steps.

*Step 1: A priori estimations.* As in [38], we introduce the operators

$$\alpha_1(t) = x_{11}(t)e^{\int_{t-\tau}^t [\mu_1(s_1(\ell)) - D] d\ell}, \tag{5.1}$$

and the system (2.1) gives

$$\begin{cases} \dot{s}_1(t) = D[s^0 - s_1(t)] - \mu_1(s_1(t))\alpha_1(t)e^{\int_{t-\tau}^t [D - \mu_1(s_1(\ell))] d\ell}, \\ \dot{\alpha}_1(t) = \alpha_1(t)[\mu_1(s_1(t)) - D]. \end{cases} \tag{5.2}$$

Now, we use the following lemma:

**Lemma 5.1.** *There is a constant  $T_c > 0$  such that  $s(t) < s^0$  for all  $t \geq T_c$ .*

**Proof.** Let us observe that if the initial conditions are in the interior of the positive cone, then  $s_1(t)$  and  $\alpha_1(t)$  are positive for any  $t \geq 0$ . Now, let us distinguish between 2 cases.

(Case i): There is  $t_l \geq 0$  such that  $s_1(t_l) \leq s^0$ . Then it is easy to prove that  $s_1(t) < s^0$  for all  $t > t_l$ .

(Case ii):  $s_1(0) > s^0$ . Let us proceed by contradiction. Assume that for all  $t \geq 0$ , we have  $s_1(t) \geq s^0$ . Then for all  $t \geq 0$ , we also have  $\dot{s}_1(t) < 0$ . Therefore, there is a constant  $s_\infty \geq s^0$  such that  $\lim_{t \rightarrow +\infty} s_1(t) = s_\infty$ . From  $\mu_1(s^0) > D$ , we deduce that  $\alpha_1$  is increasing and  $\lim_{t \rightarrow +\infty} \alpha_1(t) = +\infty$ . Also,

$$\int_0^t \mu_1(s^0)\alpha_1(\ell) d\ell \leq s_1(0) - s_1(t) \leq s_1(0) - s_\infty \tag{5.3}$$

for all  $t \geq 0$ . It follows that  $t \mapsto \int_0^t \alpha_1(\ell) d\ell$  is bounded, which yields a contradiction with the fact that  $\alpha_1$  is increasing and  $\lim_{t \rightarrow +\infty} \alpha_1(t) = +\infty$ .  $\square$

In order to state the next result, let us define

$$\sigma_1(t) = s_1(t) + \alpha_1(t).$$

**Lemma 5.2.** *If Assumptions (H1) and (H2) hold, then for any  $\theta_1 > 1$  arbitrarily close to 1, there is a constant  $T_d \geq T_c + \tau$  such that  $\sigma_1(t) \leq 2s^0\theta_1$  for all  $t \geq T_d$ .*

**Proof.** It follows from (5.2) that

$$\dot{\sigma}_1(t) = D[s^0 - \sigma_1(t)] + \mu_1(s_1(t))\alpha_1(t)[1 - e^{\int_{t-\tau}^t [D - \mu_1(s_1(\ell))] d\ell}]. \tag{5.4}$$

From the fact that  $s(t) \leq s^0$  when  $t \geq T_c$  combined with the upper bound  $\bar{\tau}_1$  for the delay from (4.3), we can deduce

$$\begin{aligned} \dot{\sigma}_1(t) &\leq Ds^0 - D\sigma_1(t) + \mu_1(s^0)[1 - e^{\tau[D - \mu_1(s^0)]}]\sigma_1(t) \\ &\leq Ds^0 - \frac{D}{2}\sigma_1(t) \quad \text{for any } t \geq T_c + \tau. \end{aligned}$$

By using comparison results for scalar differential inequalities, for example the Theorem 3.4.1 from [45], we can deduce that  $\sigma_1(t) \leq u(t)$  for any  $t \geq T_c + \tau$ , where  $u(\cdot)$  is solution of

$$\dot{u}(t) = Ds^0 - \frac{D}{2}u(t) \quad \text{with } u(T_c + \tau) = \sigma_1(T_c + \tau).$$

Now, letting  $t \rightarrow +\infty$ , we have that

$$\limsup_{t \rightarrow +\infty} \sigma_1(t) \leq 2s^0,$$

which implies that for any  $\theta_1 > 1$  close enough to 1, there exists  $T_d > T_c$  such that  $\sigma_1(t) \leq 2s^0\theta_1$  for all  $t \geq T_d$ . □

The following result provides a useful positive lower bound for  $s(t)$  for sufficiently large values of the time.

**Lemma 5.3.** *If assumptions (H1)–(H2) hold, then for any couple  $(\theta_1, \theta_2)$  with  $\theta_2 < 1 < \theta_1$  and  $\theta_i$  arbitrarily close to 1, there is a constant  $T_e \geq T_d + \tau$  such that*

$$s_1(t) \geq s_\theta = \frac{D\theta_2 s^0}{D + 2\theta_1 s^0 \frac{m_1}{a_1} e^{\tau D}} \quad \text{for any } t \geq T_e. \tag{5.5}$$

**Proof.** For any  $\theta_1 > 1$  (arbitrarily close to 1), Lemma 5.2 ensures the existence of  $T_d > T_c$  such that  $\alpha_1(t) \leq 2s^0\theta_1$  for any  $t \geq T_d + \tau$  and we can deduce that

$$\dot{s}_1(t) \geq D[s^0 - s_1(t)] - 2s^0\theta_1 \frac{m_1}{a_1} e^{\tau D} s_1(t)$$

for any  $t \geq T_d + \tau$ . Now, we can consider the differential equation

$$\dot{w}(t) = D[s^0 - w(t)] - 2s^0\theta_1 \frac{m_1}{a_1} e^{\tau D} w(t) \quad \text{with } s_1(T_d + \tau) = w(T_d + \tau).$$

By using again comparison results of differential inequalities we have that  $s_1(t) \geq w(t)$  for any  $t \geq T_d + \tau$ , which implies

$$\liminf_{t \rightarrow +\infty} s_1(t) \geq \frac{Ds^0}{D + 2\theta_1 s^0 \frac{m_1}{a_1} e^{\tau D}}.$$

Then, for any  $\theta_2 < 1$ , there exists  $T_e > T_d$  such that (5.5) is satisfied. □

*Step 2: Error dynamics.* From now on, we will assume that  $t \geq T_e + \tau$  and introduce the new functions

$$\tilde{s}_1(t) = s_1(t) - \lambda_1 \quad \text{and} \quad \tilde{\alpha}_1(t) = \alpha_1(t) - x_{11}^*. \tag{5.6}$$

From the identities

$$D[s^0 - \lambda_1] = Dx_{11}^* \quad \text{and} \quad \frac{\mu_1(\lambda_1) - \mu_1(s_1(t))}{\lambda_1 - s_1(t)} = \frac{a_1}{\lambda_1 + a_1} \frac{m_1}{s_1(t) + a_1},$$

we can verify that (5.2) becomes

$$\begin{cases} \dot{\tilde{s}}_1(t) = -\Gamma(s_1(t))\tilde{s}_1(t) - \mu_1(s_1(t))\tilde{\alpha}_1(t) + \mu_1(s_1(t))\alpha_1(t) \{1 - e^{\int_{t-\tau}^t [D - \mu_1(s_1(\ell))] d\ell}\} \\ \dot{\tilde{\alpha}}_1(t) = \frac{a_1}{a_1 + \lambda_1} \mu_1(s_1(t)) \frac{\tilde{s}_1(t)}{s_1(t)} \alpha_1(t), \end{cases} \tag{5.7}$$

with  $\Gamma$  defined as follows

$$\Gamma(s_1) = D + \frac{a_1 m_1 x_{11}^*}{(a_1 + \lambda_1)(a_1 + s_1)}$$

*Step 3: Construction of a Lyapunov-like function.* Let us consider the function

$$V_1(\tilde{s}_1(t), \tilde{\alpha}_1(t)) := V_1(t) = \nu(\tilde{s}_1(t)) + \frac{a_1 + \lambda_1}{a_1} \Psi_1(\tilde{\alpha}_1(t)),$$

where  $\nu(\tilde{s}_1)$  and  $\Psi_1(\tilde{\alpha}_1)$  are defined by

$$\nu(\tilde{s}_1) = \tilde{s}_1 - \lambda_1 \ln\left(\frac{\tilde{s}_1 + \lambda_1}{\lambda_1}\right) \quad \text{and} \quad \Psi_1(\tilde{\alpha}_1) = \tilde{\alpha}_1 - x_{11}^* \ln\left(\frac{\tilde{\alpha}_1 + x_{11}^*}{x_{11}^*}\right),$$

which are nonnegative and of class  $C^1$  on  $(-\lambda_1, +\infty)$  and  $(-x_{11}^*, +\infty)$  respectively.

By elementary calculations along the solutions of (5.7) it is easy to see that

$$\begin{aligned} \dot{V}_1(t) &= -\Gamma(s_1(t)) \frac{\tilde{s}_1^2(t)}{s_1(t)} - \mu_1(s_1(t)) \tilde{\alpha}_1(t) \frac{\tilde{s}_1(t)}{s_1(t)} \\ &\quad + \mu_1(s_1(t)) \alpha_1(t) \frac{\tilde{s}_1(t)}{s_1(t)} \left[ 1 - e^{\int_{t-\tau}^t [\mu_1(\lambda_1) - \mu_1(s_1(\ell))] d\ell} \right], \\ \dot{\Psi}_1(\tilde{\alpha}_1(t)) &= \frac{a_1}{a_1 + \lambda_1} \mu_1(s_1(t)) \tilde{\alpha}_1(t) \frac{\tilde{s}_1(t)}{s_1(t)}. \end{aligned}$$

The time derivative of  $V_1$  along the solutions of the system (5.7) satisfies

$$\dot{V}_1(t) = -\Gamma(s_1(t)) \frac{\tilde{s}_1^2(t)}{s_1(t)} + \mu_1(s_1(t)) \alpha_1(t) \frac{\tilde{s}_1(t)}{s_1(t)} \left[ 1 - e^{\int_{t-\tau}^t [\mu_1(\lambda_1) - \mu_1(s_1(\ell))] d\ell} \right].$$



By Lemma 5.1, we have that for any  $t \geq T_c + \tau$ ,

$$\dot{V}_1(t) \leq -\bar{\Gamma} \frac{\tilde{s}_1^2(t)}{s_1(t)} + \mu_1(s^0) \alpha_1(t) \frac{|\tilde{s}_1(t)|}{s_1(t)} \left| 1 - e^{\Delta\mu_1(s_1(t))} \right|,$$

where  $\bar{\Gamma} = \Gamma(s^0)$  was defined in (4.2) and  $\Delta\mu_1(s_1(t))$  is defined by

$$\Delta\mu_1(s_{1,t}) = \left| \int_{t-\tau}^t [\mu_1(\lambda_1) - \mu_1(s_1(\ell))] d\ell \right| = \left| \int_{t-\tau}^t \frac{a_1}{a_1 + \lambda_1} \frac{m_1 \tilde{s}_1(\ell)}{a_1 + s_1(\ell)} d\ell \right|.$$

The mean value theorem ensures that

$$|1 - e^\xi| \leq |\xi| e^{|\xi|}$$

for any  $\xi \in \mathbb{R}$ . This fact combined with Lemma 5.2 allows to deduce that for any  $t \geq T_d + \tau$ ,

$$\begin{aligned} \dot{V}_1(t) &\leq -\bar{\Gamma} \frac{\tilde{s}_1^2(t)}{s_1(t)} + 2s^0 \mu_1(s^0) \theta_1 \frac{|\tilde{s}_1(t)|}{s_1(t)} \Delta\mu_1(s_1(t)) e^{\Delta\mu_1(s_1(t))}, \\ &\leq -\bar{\Gamma} \frac{\tilde{s}_1^2(t)}{s_1(t)} + 2s^0 \mu_1(s^0) \theta_1 \frac{|\tilde{s}_1(t)|}{s_1(t)} \Delta\mu_1(s_1(t)) e^{\tau|\mu_1(s^0) - \mu_1(\lambda_1)|} \\ &\leq -\bar{\Gamma} \frac{\tilde{s}_1^2(t)}{s_1(t)} + \theta_1 r_0 \left| \int_{t-\tau}^t \frac{a_1}{a_1 + \lambda_1} \frac{m_1 \tilde{s}_1(\ell)}{a_1 + s_1(\ell)} d\ell \right| \frac{|\tilde{s}_1(t)|}{s_1(t)} \\ &\leq -\bar{\Gamma} \frac{\tilde{s}_1^2(t)}{s_1(t)} + \int_{t-\tau}^t \frac{\theta_1 d_0 |\tilde{s}_1(\ell)|}{a_1 + s_1(\ell)} d\ell \frac{|\tilde{s}_1(t)|}{s_1(t)}, \end{aligned} \tag{5.8}$$

where  $d_0$  is defined in (4.1) and  $r_0$  is defined by

$$r_0 = \frac{d_0(a_1 + \lambda_1)}{a_1 m_1} = 2s^0 \mu_1(s^0) e^{\tau|\mu_1(s^0) - D|}.$$

Now we use (4.1) and (4.2) and recall that Lemmas 5.1, 5.2 and 5.3 guarantee that  $s_\theta \leq s_1(t) \leq s^0$  for any  $t \geq T_e$ . We deduce that

$$\begin{aligned} \int_{t-\tau}^t \frac{\theta_1 d_0 |\tilde{s}_1(\ell)|}{a_1 + s_1(\ell)} d\ell \frac{|\tilde{s}_1(t)|}{s_1(t)} &\leq \left\{ \frac{\theta_1 d_0 a_0}{\sqrt{\bar{\Gamma} s_\theta (s_\theta + a_1)}} \int_{t-\tau}^t \frac{|\tilde{s}_1(\ell)|}{\sqrt{s_1(\ell)}} d\ell \right\} \left\{ \frac{\sqrt{\bar{\Gamma}} |\tilde{s}_1(t)|}{\sqrt{s_1(t)}} \right\} \\ &\leq \frac{(\theta_1 d a_0)^2}{2\bar{\Gamma} s_\theta (s_\theta + a_1)} \left( \int_{t-\tau}^t \frac{|\tilde{s}_1(\ell)|}{\sqrt{s_1(\ell)}} d\ell \right)^2 + \frac{\bar{\Gamma}}{2} \frac{|\tilde{s}_1(t)|^2}{s_1(t)}, \end{aligned}$$

for any  $t \geq T_e + \tau$ . Moreover, the Jensen integral inequality implies

$$\int_{t-\tau}^t \frac{\theta_1 d |\tilde{s}_1(\ell)|}{a_1 + s_1(\ell)} d\ell \frac{|\tilde{s}_1(t)|}{s_1(t)} \leq \frac{\tau (\theta_1 d a_0)^2}{2\bar{\Gamma} s_\theta (s_\theta + a_1)} \int_{t-\tau}^t \frac{\tilde{s}_1^2(\ell)}{s_1(\ell)} d\ell + \frac{\bar{\Gamma}}{2} \frac{|\tilde{s}_1(t)|^2}{s_1(t)}$$

and the above estimation together with (5.8) imply

$$\dot{V}_1(t) \leq -\frac{\bar{\Gamma}}{2} \frac{\tilde{s}_1^2(t)}{s_1(t)} + \frac{\tau (\theta_1 d a_0)^2}{2\bar{\Gamma} s_\theta (s_\theta + a_1)} \int_{t-\tau}^t \frac{\tilde{s}_1^2(\ell)}{s_1(\ell)} d\ell \quad \text{for any } t \geq T_e + \tau. \tag{5.9}$$

By the Leibniz rule, we know that

$$\frac{d}{dt} \left( \int_{t-\tau}^t \int_{\ell}^t \frac{\tilde{s}_1^2(r)}{s_1(r)} dr d\ell \right) = \tau \frac{\tilde{s}_1^2(t)}{s_1(t)} - \int_{t-\tau}^t \frac{\tilde{s}_1^2(\ell)}{s_1(\ell)} d\ell.$$

Then we deduce that, for any  $t \geq T_e + \tau$  the derivative along the trajectories of (5.7) of function

$$V(\tilde{s}_{1,t}, \tilde{\alpha}_{1,t}) = V_1(t) + \mathcal{M}_\theta(\tau) \int_{t-\tau}^t \frac{\tilde{s}_1^2(\ell)}{s_1(\ell)} d\ell \quad \text{with } \mathcal{M}_\theta(\tau) = \frac{\tau (\theta_1 d a_0)^2}{2\bar{\Gamma} s_\theta (s_\theta + a_1)}$$

satisfies

$$\dot{V}(t) \leq \left( -\frac{\bar{\Gamma}}{2} + \tau \mathcal{M}_\theta(\tau) \right) \frac{|\tilde{s}_1(t)|^2}{s_1(t)}.$$

Since the inequality (4.4) is strict, we can chose  $\theta_1$  and  $\theta_2$  close enough to 1 such that  $\tau \mathcal{M}_\theta(\tau) < \bar{\Gamma}/2$  and there exists  $c_0 > 0$  such that

$$\dot{V}(t) \leq -c_0 \frac{|\tilde{s}_1(t)|^2}{s_1(t)}. \tag{5.10}$$

*Step 4: Convergence towards the equilibrium.* Recall from Lemmas 5.1, 5.2 and 5.3 that all the solutions enter (in finite time) a compact set which is independent of the initial conditions. It follows that all the solutions are uniformly continuous and  $t \mapsto \tilde{s}_1(t)$  is a uniformly continuous function. Moreover (5.10), combined with the nonnegativeness of  $V$ , implies that

$$\int_0^{+\infty} \frac{\tilde{s}_1^2(\ell)}{s_1(\ell)} d\ell < +\infty. \tag{5.11}$$

By Barbălat's Lemma (see e.g. Lemma 8.2 from [46] for details) combined with the strict positiveness and boundedness of  $s_1(t)$ , we deduce that  $\lim_{t \rightarrow +\infty} \tilde{s}_1(t) = 0$  and consequently

$$\lim_{t \rightarrow +\infty} s_1(t) = \lambda_1. \tag{5.12}$$

As  $\lim_{t \rightarrow +\infty} \mu_1(s_1(t)) = D$ , it follows that (5.4) is of type

$$\dot{\sigma}_1(t) = D[s^0 - \sigma_1(t)] + \Delta(t) \tag{5.13}$$

where  $\Delta(t) = \mu_1(s_1(t))\alpha_1(t)\{1 - e^{\int_{t-\tau}^t [D - \mu_1(s_1(\ell))] d\ell}\}$  verifies  $\lim_{t \rightarrow +\infty} \Delta(t) = 0$ .

The following result is a direct consequence of  $D > 0$  and  $\lim_{t \rightarrow +\infty} \Delta(t) = 0$ :

**Lemma 5.4.** *The solutions of Eq. (5.13) verify  $\lim_{t \rightarrow +\infty} \sigma_1(t) = s^0$ .*

Hence, by using our definition of  $\sigma_1(t)$  and (5.12) we obtain

$$\lim_{t \rightarrow +\infty} \alpha_1(t) = s^0 - \lim_{t \rightarrow +\infty} s_1(t) = s^0 - \lambda_1 = x_{11}^*.$$

Finally, by using the above limit combined with (5.1) and (5.12), we have

$$\lim_{t \rightarrow +\infty} x_{11}(t) = \lim_{t \rightarrow +\infty} \alpha_1(t) e^{\int_{t-\tau}^t [D - \mu_1(s_1(\ell))] d\ell} = x_{11}^*.$$

This concludes the proof.

**Remark 1.** Lemma 5.4 can be generalized: if  $\delta : [t_0, +\infty) \rightarrow \mathbb{R}$  is continuous and such that  $\lim_{t \rightarrow +\infty} \delta(t) = 0$ , then the scalar differential equations

$$\dot{u}(t) = a - bu(t) + \delta(t) \quad \text{and} \quad \dot{v}(t) = a - bv(t) \quad \text{with } a, b > 0$$

are asymptotically equivalent, namely,  $\lim_{t \rightarrow +\infty} u(t) = \lim_{t \rightarrow +\infty} v(t) = a/b$ . This property will be useful in the next section.

**Corollary 1.** *For any solution  $t \mapsto x(t, \varphi)$  of (2.1) such that  $x(\theta) = \varphi(\theta) > 0$  for any  $\theta \in [-\tau, 0]$ , there exists  $\tilde{T}(\varphi) > 0$  and  $K(\varphi) > 1$  such that*

$$|x(t, \varphi)| \leq Ke^{-\lambda t} \quad \text{for any } t > \tilde{T} + \tau$$

**Proof.** The system (2.1) with the above initial condition can be written as

$$\dot{x}(t) = g(x(t), x(t - \tau)) \tag{5.14}$$

and  $u(t) = x(t) - E^*$  leads to

$$\dot{u}(t) = A_0u(t) + B_0u(t - \tau) + f(u(t), u(t - \tau)), \tag{5.15}$$

where  $A_0u(t) + B_0u(t - \tau)$  is the right part of (3.1) and

$$f(u(t), u(t - \tau)) = g(u(t) + E^*, u(t - \tau) + E^*) - A_0u(t) - B_0u(t - \tau).$$

As the global asymptotic stability of  $E^*$  implies the existence of  $T_2(\varphi) > \max\{T_e, T_1\}$  such that  $|(s_1(t), x_{11}(t)) - E^*| < \varepsilon$  or equivalently  $|u(t)| < \varepsilon$  for any  $t > T_2 + \tau$ , the mean value theorem for functions on convex sets combined with  $f(0, 0) = 0$  and the definition of  $A_0$  and  $B_0$  implies that  $|f(u(t), u(t - \tau))| \leq \gamma(\varepsilon)\{|u(t)| + |u(t - \tau)|\}$ , where  $\gamma(\varepsilon)$  converges to zero when  $\varepsilon \rightarrow 0$ .

By Lemma 3.1 we know that the origin is an asymptotically stable solution of (3.1). In addition, as the system is autonomous, the stability is indeed uniform and Theorem 4.6 from [47] ensures that the origin is a uniformly asymptotically stable solution of (5.14). Moreover, a careful reading of the end of the proof in [47] makes it possible to conclude that the origin is in fact exponentially stable. □

**6. Proof of Theorem 2**

The proof has a similar structure and uses similar methods as the previous one: Firstly we obtain upper and lower bounds for some variables (Lemmas 6.1, 6.2 and 6.3). Secondly, we define the error dynamics described by (6.6) and finish by constructing a Lyapunov-like function and studying the convergence to the equilibrium. As it was stated at Section 3, we will only study the system (4.10).

Now, as in the previous section, we introduce the operators

$$\xi_i(t) = x_{i2}(t)e^{\int_{t-\tau}^t [\mu_i(s_2(\ell)) - \mu_i(\lambda_2)] d\ell}, \tag{6.1}$$

and the system (4.10) gives

$$\begin{cases} \dot{s}_2(t) = D[\lambda_1 - s_2(t)] - \sum_{i=1}^2 \mu_i(s_2(t))e^{\int_{t-\tau}^t [\mu_i(\lambda_2) - \mu_i(s_2(\ell))] d\ell} \xi_i(t) + D\tilde{s}_1(t) \\ \dot{\xi}_1(t) = [\mu_1(s_2(t)) - D]\xi_1(t) + Dx_{11}^* e^{\int_{t-\tau}^t [\mu_1(s_2(\ell)) - \mu_1(\lambda_2)] d\ell} + D\tilde{\alpha}_1(t)e^{\int_{t-\tau}^t [\mu_1(s_2(\ell)) - \mu_1(\lambda_2)] d\ell} \\ \dot{\xi}_2(t) = [\mu_2(s_2(t)) - D]\xi_2(t). \end{cases} \tag{6.2}$$

**Lemma 6.1.** For any  $\hat{\theta}_0 > 1$ , there exists a constant  $\hat{T}_c \geq 0$  such that  $s_2(t) \leq \hat{\theta}_0 \lambda_1$  for any  $t > \hat{T}_c$ .

**Proof.** Notice that

$$\dot{s}_2(t) \leq D[\lambda_1 - s_2(t)] + D\tilde{s}_1(t)$$

and consider the equations

$$\dot{u}(t) = D[\lambda_1 - u(t)] + D\tilde{s}_1(t) \quad \text{and} \quad \dot{v}(t) = D[\lambda_1 - v(t)] \quad \text{with} \quad u(0) = s_2(0).$$

By using the previous comparison result for scalar differential inequalities, we can deduce easily that  $s_2(t) \leq u(t)$  for any  $t \geq 0$ . On the other hand, as  $\tilde{s}_1(t) \rightarrow 0$  when  $t \rightarrow +\infty$ , we can prove as in Lemma 5.4, that  $u$  and  $v$  are asymptotically equivalent, which implies that  $\limsup_{t \rightarrow +\infty} s_2(t) \leq \lambda_1$  and the lemma follows.  $\square$

**Lemma 6.2.** For any  $\hat{\theta}_1 > 1$  there exists  $\hat{T}_d > \hat{T}_c$  such that

$$\sigma_2(t) = s_2(t) + \xi_1(t) + \xi_2(t) < 2\hat{\theta}_1 C_\theta \quad \text{where} \quad C_\theta = \lambda_1 + x_{11}^* e^{\tau[\mu_1(\lambda_1 \hat{\theta}_0) - \mu_1(\lambda_2)]}.$$

for any  $t > \hat{T}_d + \tau$ .

**Proof.** Notice that  $\sigma_2(t)$  satisfies

$$\begin{aligned} \dot{\sigma}_2(t) &= D[\lambda_1 + x_{11}^* - \sigma_2(t)] + Dx_{11}^* (e^{\int_{t-\tau}^t [\mu_1(s_2(\ell)) - \mu_1(\lambda_2)] d\ell} - 1) \\ &\quad + \sum_{i=1}^2 \mu_i(s_2(t)) \xi_i(t) \left\{ 1 - e^{\int_{t-\tau}^t [\mu_i(\lambda_2) - \mu_i(s_2(\ell))] d\ell} \right\} \\ &\quad + D(\tilde{s}_1(t) + \tilde{\alpha}_1(t)e^{\int_{t-\tau}^t [\mu_1(s_2(\ell)) - \mu_1(\lambda_2)] d\ell}). \end{aligned} \tag{6.3}$$

If  $t \geq \hat{T}_c + \tau$ , it follows that

$$\begin{aligned} \dot{\sigma}_2(t) &\leq D[\lambda_1 - \sigma_2(t)] + \sum_{i=1}^2 \mu_i(\hat{\theta}_0 \lambda_1) \xi_i(t) \left\{ 1 - e^{\tau[\mu_i(s_2(\hat{\theta}_0 \lambda_1)) - \mu_i(\lambda_2)]} \right\} \\ &\quad + Dx_{11}^* e^{\tau[\mu_1(s_2(\hat{\theta}_0 \lambda_1)) - \mu_1(\lambda_2)]} + D(\tilde{s}_1(t) + \tilde{\alpha}_1(t)e^{\tau[\mu_1(\hat{\theta}_0 \lambda_1) - \mu_1(\lambda_2)]}). \end{aligned}$$

By (4.8), we know that if

$$\mu_i(\lambda_1) \left\{ 1 - e^{\tau[\mu_i(\lambda_2) - \mu_i(\lambda_1)]} \right\} < \frac{D}{2},$$

this inequality is still valid when  $e^{-\tau \mu_1(\lambda_1)}$  is replaced by  $e^{-\tau \mu_1(\hat{\theta}_0 \lambda_1)}$  with  $\hat{\theta}_0$  arbitrarily close to 1. Now, in this case we can deduce that  $\sigma_2$  satisfies the differential inequality

$$\dot{\sigma}_2(t) \leq D \left[ \lambda_1 - \frac{1}{2} \sigma_2(t) \right] + Dx_{11}^* e^{\tau[\mu_1(s_2(\hat{\theta}_0 \lambda_1)) - \mu_1(\lambda_2)]} + \delta(t),$$

where  $\delta(t) = D(\tilde{s}_1(t) + \tilde{\alpha}_1(t)e^{\tau[\mu_1(\hat{\theta}_0 \lambda_1) - \mu_1(\lambda_2)]})$  converges to zero when  $t \rightarrow +\infty$ . Now, let us consider the differential equations

$$\dot{u}(t) = D \left[ \lambda_1 - \frac{1}{2} u(t) \right] + Dx_{11}^* e^{\tau[\mu_1(s_2(\hat{\theta}_0 \lambda_1)) - \mu_1(\lambda_2)]} + \delta(t) \quad \text{with} \quad \sigma_2(\hat{T}_c) = u(\hat{T}_c),$$

and

$$\dot{v}(t) = D \left[ \lambda_1 - \frac{1}{2} v(t) \right] + D x_{11}^* e^{\tau [\mu_1 (s_2(\hat{\theta}_0 \lambda_1) - \mu_1(\lambda_2))]}.$$

By standard results of differential inequalities, we can deduce that  $\sigma_2(t) \leq u(t)$  for any  $t \geq \hat{T}_e$ . In addition, we know that  $v(t)$  converges to  $2C_\theta$  when  $t \rightarrow +\infty$ . Now, by Remark 1 we can prove that the two above equations are asymptotically equivalent, which implies that  $\limsup_{t \rightarrow +\infty} \sigma_2(t) \leq 2C_\theta$  and the lemma follows.  $\square$

**Remark 2.** Note that (6.3) can be written as

$$\dot{\sigma}_2(t) = D[\lambda_1 + x_{11}^* - \sigma_2(t)] + \Delta(s_2(t)) \tag{6.4}$$

with  $\Delta$  such that  $\lim_{t \rightarrow +\infty} \Delta(s_2(t)) = 0$  if  $\lim_{t \rightarrow +\infty} s_2(t) = \lambda_2$ . We shall return to this fact at the end of the proof.

**Lemma 6.3.** For any  $\hat{\theta}_2 < 1$ , there exists  $\hat{T}_e > \hat{T}_d + \tau$  such that

$$s_2(t) \geq \hat{\theta}_2 \underline{s}_\theta = \frac{D \lambda_1 \hat{\theta}_2}{D + 2 \hat{\theta}_1 C_\theta \sum_{i=1}^2 \frac{m_i}{a_i} e^{\mu_i(\lambda_2)\tau}} \quad \text{and} \quad \xi_1(t) \geq \underline{\xi}_{1\theta} = \hat{\theta}_2 x_{11}^* e^{-\mu_1(\lambda_2)\tau}$$

for any  $t \geq \hat{T}_e$ .

**Proof.** By Lemma 6.2, we can verify that  $s_2(t)$  satisfies the differential inequality for any  $t > \hat{T}_d$

$$\dot{s}_2(t) \geq D \lambda_1 - \left( D + 2 \hat{\theta}_1 C_\theta \sum_{i=1}^2 \frac{m_i}{a_i} e^{\mu_i(\lambda_2)\tau} \right) s_2(t) + D \tilde{s}_1(t).$$

As before, let us consider the differential equations

$$\begin{aligned} \dot{u}(t) &= D \lambda_1 - \left( D + 2 \hat{\theta}_1 C_\theta \sum_{i=1}^2 \frac{m_i}{a_i} e^{\mu_i(\lambda_2)\tau} \right) u(t) + D \tilde{s}_1(t), \\ \dot{v}(t) &= D \lambda_1 - \left( D + 2 \hat{\theta}_1 C_\theta \sum_{i=1}^2 \frac{m_i}{a_i} e^{\mu_i(\lambda_2)\tau} \right) v(t), \end{aligned}$$

where  $u(\hat{T}_d + \tau) = s_2(\hat{T}_d + \tau)$ . Now, by the previous results of differential inequalities, we can deduce that  $s_2(t) \geq u(t)$  for any  $t \geq \hat{T}_d$ . Moreover, we know that  $v(t)$  converges to  $\underline{s}_\theta$  when  $t \rightarrow +\infty$ . Now, by Remark 1 we can prove that the two above equations are asymptotically equivalent, which implies that  $\limsup_{t \rightarrow +\infty} s_2(t) \geq \underline{s}_\theta$  and the first inequality follows.

The second inequality can be proved similarly by considering the differential inequality and the differential equations with  $v(\hat{T}_d + \tau) = \xi_1(\hat{T}_d + \tau)$

$$\begin{aligned} \dot{\xi}_1(t) &\geq -D \xi_1(t) + D x_{11}^* e^{-\mu_1(\lambda_2)\tau} + D \tilde{\alpha}_1(t) e^{\int_{t-\tau}^t [\mu_1(s_2(\ell)) - \mu_1(\lambda_2)] d\ell} \\ \dot{v}(t) &= -D v(t) + D x_{11}^* e^{-\mu_1(\lambda_2)\tau} + D \tilde{\alpha}_1(t) e^{\int_{t-\tau}^t [\mu_1(s_2(\ell)) - \mu_1(\lambda_2)] d\ell} \\ \dot{u}(t) &= -D u(t) + D x_{11}^* e^{-\mu_1(\lambda_2)\tau}. \end{aligned}$$

$\square$

Let us introduce the change of variables

$$\tilde{s}_2(t) = s_2(t) - \lambda_2 \quad \text{and} \quad \tilde{\xi}_i(t) = \xi_i(t) - x_{i2}^* \quad (i = 1, 2). \tag{6.5}$$

By (6.5) combined with the identities

$$D(\lambda_1 - \lambda_2) = \mu_1(\lambda_2) x_{12}^* + \mu_2(\lambda_2) x_{22}^* \quad \text{and} \quad \mu_i(\lambda_2) - \mu_i(s_2(t)) = \frac{a_i}{a_i + \lambda_2} \mu_i(s_2(t)) \frac{\tilde{s}_2(t)}{s_2(t)}$$

the system (6.2) becomes

$$\begin{cases} \dot{\tilde{s}}_2(t) = -\Theta(s_2(t))\tilde{s}_2(t) - \sum_{i=1}^2 \mu_i(s_2(t))\tilde{\xi}_i(t) + D\tilde{s}_1(t) \\ \quad + \sum_{i=1}^2 \mu_i(s_2(t))\xi_i(t) \left\{ 1 - e^{\int_{t-\tau}^t [\mu_i(s_2(\ell)) - \mu_i(s_2(t))] d\ell} \right\} \\ \dot{\tilde{\xi}}_1(t) = c_1 \xi_1(t) \mu_1(s_2(t)) \frac{\tilde{s}_2(t)}{s_2(t)} + D\alpha_{11}^* \left\{ e^{\int_{t-\tau}^t [\mu_1(s_2(\ell)) - \mu_1(s_2(t))] d\ell} - 1 \right\} \\ \quad - p\tilde{\xi}_1(t) + D\tilde{\alpha}_1(t) e^{\int_{t-\tau}^t [\mu_1(s_2(\ell)) - \mu_1(s_2(t))] d\ell} \\ \dot{\tilde{\xi}}_2(t) = c_2 \xi_2(t) \mu_2(s_2(t)) \frac{\tilde{s}_2(t)}{s_2(t)}, \end{cases} \tag{6.6}$$

where  $\Theta$  is defined by

$$\Theta(s_2) = D + \sum_{i=1}^2 \frac{\mu_i(s_2) - \mu_i(\lambda_2)}{s_2 - \lambda_2} x_{i2}^* = D + \sum_{i=1}^2 \frac{m_i a_i x_{i2}^*}{(a_i + s_2)(a_i + \lambda_2)}$$

while  $c_i$  ( $i = 1, 2$ ) are defined in (4.6) and  $p$  is defined by

$$p = D - \mu_1(\lambda_2) > 0. \tag{6.7}$$

Now let us define the function

$$W_1(t) = \nu_2(\tilde{s}_2(t)) + \sum_{i=1}^2 \frac{1}{c_i} \Psi_i(\tilde{\xi}_i(t)),$$

with

$$\nu(\tilde{s}_2) = \tilde{s}_2 - \lambda_2 \ln\left(\frac{\tilde{s}_2 + \lambda_2}{\lambda_2}\right) \text{ and } \Psi_i(\tilde{\xi}_i) = \tilde{\xi}_i - x_{2i}^* \ln\left(\frac{\tilde{\xi}_i + x_{2i}^*}{x_{2i}^*}\right),$$

which are nonnegative and of class  $C^1$  on their domain of definition.

One can verify that

$$\begin{aligned} \dot{\nu}_2(t) &= -\Theta(\tilde{s}_2(t)) \frac{\tilde{s}_2^2(t)}{s_2(t)} - \sum_{i=1}^2 \mu_i(s_2(t)) \tilde{\xi}_i(t) \frac{\tilde{s}_2(t)}{s_2(t)} + D\tilde{s}_1(t) \frac{\tilde{s}_2(t)}{s_2(t)} \\ &\quad + \sum_{i=1}^2 \mu_i(s_2(t)) \xi_i(t) \left\{ 1 - e^{\int_{t-\tau}^t [\mu_i(s_2(\ell)) - \mu_i(s_2(t))] d\ell} \right\} \frac{\tilde{s}_2(t)}{s_2(t)}, \\ \dot{\Psi}_1(t) &= -p \frac{\tilde{\xi}_1^2(t)}{\tilde{\xi}_1(t)} + c_1 \mu_1(s_2(t)) \tilde{\xi}_1(t) \frac{\tilde{s}_2(t)}{s_2(t)} + D\tilde{\alpha}_1(t) e^{\int_{t-\tau}^t [\mu_1(s_2(\ell)) - \mu_1(s_2(t))] d\ell} \frac{\tilde{\xi}_1(t)}{\tilde{\xi}_1(t)} \\ &\quad + D\alpha_{11}^* \left\{ e^{\int_{t-\tau}^t [\mu_1(s_2(\ell)) - \mu_1(s_2(t))] d\ell} - 1 \right\} \frac{\tilde{\xi}_1(t)}{\tilde{\xi}_1(t)}, \\ \dot{\Psi}_2(t) &= c_2 \mu_2(s_2(t)) \tilde{\xi}_2(t) \frac{\tilde{s}_2(t)}{s_2(t)} \end{aligned}$$

and deduce the identity

$$\begin{aligned} \dot{W}_1(t) &= -\Theta(\tilde{s}_2(t)) \frac{\tilde{s}_2^2(t)}{s_2(t)} + \frac{D}{c_1} x_{11}^* \left\{ e^{\int_{t-\tau}^t [\mu_1(s_2(\ell)) - \mu_1(s_2(t))] d\ell} - 1 \right\} \frac{\tilde{\xi}_1(t)}{\tilde{\xi}_1(t)} \\ &\quad + \sum_{i=1}^2 \mu_i(s_2(t)) \xi_i(t) \left\{ 1 - e^{\int_{t-\tau}^t [\mu_i(s_2(\ell)) - \mu_i(s_2(t))] d\ell} \right\} \frac{\tilde{s}_2(t)}{s_2(t)} \\ &\quad - \frac{p}{c_1} \frac{\tilde{\xi}_1^2(t)}{\tilde{\xi}_1(t)} + D\tilde{s}_1(t) \frac{\tilde{s}_2(t)}{s_2(t)} + \frac{D}{c_1} \tilde{\alpha}_1(t) e^{\int_{t-\tau}^t [\mu_1(s_2(\ell)) - \mu_1(s_2(t))] d\ell} \frac{\tilde{\xi}_1(t)}{\tilde{\xi}_1(t)}. \end{aligned}$$

By Lemmas 6.1 and 6.2 we know that for any  $t > \hat{T}_d + \tau$ ,

$$\begin{aligned} \dot{W}_1(t) &\leq -\mathcal{N}(\tilde{s}_2(t), \tilde{\xi}_1(t)) + \frac{D}{c_1} x_{11}^* \left\{ e^{\int_{t-\tau}^t [\mu_1(s_2(\ell)) - \mu_1(s_2(t))] d\ell} - 1 \right\} \frac{\tilde{\xi}_1(t)}{\tilde{\xi}_1(t)} \\ &\quad + 4\hat{\theta}_1 C_\theta \max_{i=1,2} \left\{ \mu_i(\hat{\theta}_0 \lambda_1) \left| 1 - e^{\int_{t-\tau}^t [\mu_i(s_2(\ell)) - \mu_i(s_2(t))] d\ell} \right| \right\} \frac{|\tilde{s}_2(t)|}{s_2(t)} + o(1), \end{aligned}$$

where  $\mathcal{N}_2$  is defined by

$$\mathcal{N}(\tilde{s}_2, \tilde{\xi}_1) = \Theta(\tilde{s}_2) \frac{\tilde{s}_2^2}{s_2} + \frac{p}{c_1} \frac{\tilde{\xi}_1^2}{\xi_1}$$

and  $o(1)$  denotes the function

$$o(1) = D\tilde{s}_1(t) \frac{\tilde{s}_2(t)}{s_2(t)} + \frac{D}{c_1} \tilde{\alpha}_1(t) e^{\int_{t-\tau}^t [\mu_1(s_2(\ell)) - \mu_1(\lambda_2)]} \frac{\tilde{\xi}_1(t)}{\xi_1(t)},$$

which converges to zero when  $t \rightarrow +\infty$ .

By using again the inequality (5), we can deduce that when  $t \geq \hat{T}_e + \tau$ ,

$$\begin{aligned} \dot{W}_1(t) \leq & -\mathcal{N}(\tilde{s}_2(t), \tilde{\xi}_1(t)) + \frac{Dx_{11}^*}{c_1} \frac{|\tilde{\xi}_1(t)|}{\xi_1(t)} |\Delta\mu_1(s_{2,t})| e^{\Delta\mu_1(s_{2,t})} \\ & + 4\hat{\theta}_1 \max_{i \in \{1,2\}} \left\{ C_\theta \mu_i(\hat{\theta}_0 \lambda_1) |\Delta\mu_i(s_2(t))| e^{\Delta\mu_i(s_2(t))} \right\} \frac{|\tilde{s}_2(t)|}{s_2(t)} + o(1), \end{aligned}$$

with

$$\Delta\mu_i(s_{2,t}) = \left| \int_{t-\tau}^t [\mu_i(s_2(\ell)) - \mu_i(\lambda_2)] d\ell \right| = \left| \int_{t-\tau}^t \frac{c_i m_i \tilde{s}_2(\ell)}{a_i + s_2(\ell)} d\ell \right|.$$

From Lemma 6.1 we deduce

$$\Delta\mu_i(s_2(t)) \leq \tau [\mu_i(\hat{\theta}_0 \lambda_1) - \mu_i(\lambda_2)] = B_{i,\theta} \tau$$

and it follows that for  $t \geq \hat{T}_e + \tau$ , we have

$$\begin{aligned} \dot{W}_1(t) \leq & -\frac{p}{c_1} \frac{\tilde{\xi}_1^2(t)}{\xi_1(t)} + \hat{\theta}_1 \max_{i=1,2} \left\{ \int_{t-\tau}^t \frac{d_{i,\theta} |\tilde{s}_2(\ell)|}{a_i + s_2(\ell)} d\ell \right\} \frac{|\tilde{s}_2(t)|}{s_2(t)} \\ & - \Theta(\hat{\theta}_0 \lambda_1) \frac{\tilde{s}_2^2(t)}{s_2(t)} + \frac{|\tilde{\xi}_1(t)|}{\xi_1(t)} \int_{t-\tau}^t \frac{b_\theta |\tilde{s}_2(\ell)|}{a_1 + s_2(\ell)} d\ell + o(1), \end{aligned} \tag{6.8}$$

where  $d_{i,\theta}$  (with  $i = 1, 2$ ) and  $b_\theta$  are defined by

$$d_{i,\theta} = 4C_\theta m_i c_i \mu_i(\hat{\theta}_0 \lambda_1) e^{\tau B_{i,\theta}} \quad \text{and} \quad b_\theta = Dx_{11}^* m_1 e^{\tau B_{1,\theta}}.$$

By using the inequalities

$$s_\theta \leq s_2(t) \leq \hat{\theta}_0 \lambda_1 \quad \text{and} \quad \underline{\xi}_{1\theta} \leq \xi_1(t) \quad \text{for} \quad t \geq \tau + \hat{T}_e$$

and defining  $a_i^* = \sqrt{s^0/(a_i + s^0)}$ , it follows that

$$\int_{t-\tau}^t \frac{|\tilde{s}_2(\ell)|}{a_i + s_2(\ell)} d\ell \leq \frac{a_i^*}{\sqrt{a_i + \underline{s}_\theta}} \int_{t-\tau}^t \frac{|\tilde{s}_2(\ell)|}{\sqrt{s_2(\ell)}} d\ell \quad \text{for any } i = 1, 2.$$

This inequality combined with the well known inequality  $ab \leq \frac{a^2}{2\varepsilon} + \frac{\varepsilon b^2}{2}$  with  $\varepsilon = 1$  and  $\varepsilon = 2$  and the Jensen integral inequality, allows to prove that

$$\begin{aligned} \hat{\theta}_1 d_{i,\theta} \int_{t-\tau}^t \frac{|\tilde{s}_2(\ell)|}{a_i + s_2(\ell)} d\ell \frac{|\tilde{s}_2(t)|}{s_2(t)} & \leq \left\{ \frac{\hat{\theta}_1 d_{i,\theta} a_i^*}{\sqrt{\Theta_\theta \underline{s}_\theta} (a_i + \underline{s}_\theta)} \int_{t-\tau}^t \frac{|\tilde{s}_2(\ell)|}{\sqrt{s_2(\ell)}} d\ell \right\} \left\{ \frac{\sqrt{\Theta_\theta} |\tilde{s}_2(t)|}{\sqrt{s_2(t)}} \right\} \\ & \leq \frac{\tau \hat{\theta}_1^2 d_{i,\theta}^2}{2\Theta_\theta \underline{s}_\theta (a_i + \underline{s}_\theta)} \frac{\hat{\theta}_0 \lambda_1}{\hat{\theta}_0 \lambda_1 + a_i} \int_{t-\tau}^t \frac{\tilde{s}_2^2(\ell)}{s_2(\ell)} d\ell + \frac{\Theta_\theta \tilde{s}_2^2(t)}{2s_2(t)}, \end{aligned}$$

and

$$\begin{aligned} b_\theta \frac{|\tilde{\xi}_1(t)|}{\xi_1(t)} \int_{t-\tau}^t \frac{|\tilde{s}_2(\ell)|}{a_1 + s_2(\ell)} d\ell & \leq \left\{ \frac{b_\theta a_1^*}{\sqrt{\hat{\theta}_2 q \underline{\xi}_{1\theta}} (a_1 + \underline{s}_\theta)} \int_{t-\tau}^t \frac{|\tilde{s}_2(\ell)|}{\sqrt{s_2(\ell)}} d\ell \right\} \left\{ \frac{\sqrt{q \hat{\theta}_2} |\tilde{\xi}_1(t)|}{\sqrt{\xi_1(t)}} \right\} \\ & \leq \frac{\tau b_\theta^2}{4\hat{\theta}_2 q \underline{\xi}_{1\theta} (a_1 + \underline{s}_\theta)} \frac{\hat{\theta}_0 \lambda_1}{\hat{\theta}_0 \lambda_1 + a_1} \int_{t-\tau}^t \frac{\tilde{s}_2^2(\ell)}{s_2(\ell)} d\ell + \frac{\hat{\theta}_2 q \tilde{\xi}_1^2(t)}{\xi_1(t)}, \end{aligned}$$

where  $\bar{\Theta}_\theta = \Theta(\hat{\theta}_0 \lambda_1)$  and  $q = p/c_1$ , see also (4.7) for details.

By using Corollary 1, it is tedious but not difficult to prove the existence of positive constants  $K, \eta_1, \eta_2$  and  $\hat{T} > \hat{T}_e$  (dependent of the initial condition) such that

$$|\tilde{s}_1(t)| \leq Ke^{-\eta_1 t} \quad \text{and} \quad |\tilde{\alpha}_1(t)| \leq Ke^{-\eta_2 t} \quad \text{for any } t > \hat{T} + \tau. \tag{6.9}$$

The previous inequalities lead to

$$\begin{aligned} \dot{W}_1(t) \leq & -\frac{\bar{\Theta}_\theta}{2} \frac{\tilde{s}_2^2(t)}{s_2(t)} - q(1 - \hat{\theta}_2) \frac{\tilde{\xi}_1^2(t)}{\xi_1(t)} + \tau \mathcal{M}_\theta(\tau) \int_{t-\tau}^t \frac{\tilde{s}_1^2(\ell)}{s_1(\ell)} d\ell \\ & + DK e^{-\eta_1 t} \frac{\tilde{s}_2(t)}{s_2(t)} + \frac{D}{c_1} K e^{-\eta_2 t} |\Delta\mu_1(s_2(t))| e^{\Delta\mu_1(s_2(t))} \frac{|\tilde{\xi}_1(t)|}{\xi_1(t)}, \end{aligned}$$

where

$$\mathcal{M}_\theta(\tau) = \frac{\hat{\theta}_0 \lambda_1}{2} \left( \frac{\hat{\theta}_1^2}{\bar{\Theta}_\theta s_\theta} \max_{1 \leq i \leq 2} \left\{ \frac{d_i^2}{(s_\theta + a_i)(a_i + \hat{\theta}_0 \lambda_1)} \right\} + \frac{b_\theta^2}{2 \hat{\theta}_2 q \xi_{1\theta} (a_1 + s_\theta)(a_1 + \hat{\theta}_0 \lambda_1)} \right).$$

Now, we define the function

$$\begin{aligned} W_2(t) = & W_1(t) + \tau \mathcal{M}_\theta(\tau) \int_{t-\tau}^t \int_\ell^t \frac{\tilde{s}_2^2(r)}{s_2(r)} dr d\ell + \int_t^\infty K D e^{-\eta_1 \ell} \frac{\tilde{s}_2(\ell)}{s_2(\ell)} d\ell \\ & + \frac{KD}{c_1} \int_t^\infty e^{-\eta_2 \ell} |\Delta\mu_1(s_2(\ell))| e^{\Delta\mu_1(s_2(\ell))} \frac{|\tilde{\xi}_1(\ell)|}{\xi_1(\ell)} d\ell \end{aligned} \tag{6.10}$$

for any  $t > \hat{T} + \tau$ . We notice that  $\dot{W}_2(t)$  satisfies

$$\dot{W}_2(t) \leq -\left( \frac{\bar{\Theta}_\theta}{2} - \tau \mathcal{M}_\theta(\tau) \right) \frac{|\tilde{s}_2(t)|^2}{s_2(t)} - q(1 - \hat{\theta}_2) \frac{|\tilde{\xi}_1(t)|^2}{\xi_1(t)}.$$

As the inequality (4.9) is strict, we can choose  $\hat{\theta}_2 < 1 < \hat{\theta}_i$  ( $i = 0, 1$ ) arbitrarily close to 1, such that  $\tau \mathcal{M}_\theta(\tau) < \bar{\Theta}_\theta/2$ . In addition, we can prove the existence of  $c_1 > 0$  such that

$$\dot{W}_2(t) \leq -c_1 \left( \frac{|\tilde{s}_2(t)|^2}{s_2(t)} + \frac{|\tilde{\xi}_1(t)|^2}{\xi_1(t)} \right).$$

Lemmas 6.1, 6.2 and 6.3 imply that any solution enters a compact set in a finite time (independent of the initial conditions), which also implies that the solutions  $t \mapsto \tilde{s}_2(t)$  and  $t \mapsto \tilde{\xi}_1(t)$  are uniformly continuous. Then, proceeding as in the previous section we can prove by Barbālat’s lemma that  $\lim_{t \rightarrow +\infty} \tilde{s}_2(t) = 0$  and  $\lim_{t \rightarrow +\infty} \tilde{\xi}_1(t) = 0$ . This fact combined with (6.1) and (6.5) allows us to verify that

$$\lim_{t \rightarrow +\infty} s_2(t) = \lambda_2 \quad \text{and} \quad \lim_{t \rightarrow +\infty} x_{12}(t) = x_{12}^*. \tag{6.11}$$

By using the above property together with Remark 2, we can verify that (6.3) is of type

$$\dot{\sigma}_2(t) = D[\lambda_1 + x_{11}^* - \sigma_2(t)] + \Delta(t) \quad \text{where} \quad \lim_{t \rightarrow +\infty} \Delta(t) = 0.$$

Now, by following the lines of Lemma 5.4, we can prove that

$$\lim_{t \rightarrow +\infty} \sigma_2(t) = \lim_{t \rightarrow +\infty} [s_2(t) + \xi_1(t) + \xi_2(t)] = \lambda_1 + x_{11}^*,$$

which, combined with (2.4), (6.1), (6.5) and (6.11), imply that

$$\begin{aligned} \lim_{t \rightarrow +\infty} x_{22}(t) &= \lambda_1 - \lambda_2 + x_{11}^* - x_{12}^* \\ &= \lambda_1 - \lambda_2 - \frac{\mu_1(\lambda_2)}{D - \mu_1(\lambda_2)} x_{11}^* = x_{22}^*. \end{aligned}$$

This allows us to conclude.

**Remark 3.** A basic assumption of our model was that both species have similar delay  $\tau > 0$  between consumption of nutrient and growth of biomass. When dropping this assumption, the model becomes

$$\begin{cases} \dot{s}_1(t) = D[s^0 - s_1(t)] - \mu_1(s_1(t))x_{11}(t), \\ \dot{x}_{11}(t) = x_{11}(t)\mu_1(s_1(t - \tau_1)) - D x_{11}(t), \\ \dot{s}_2(t) = D[s_1(t) - s_2(t)] - \mu_1(s_2(t))x_{12}(t) - \mu_2(s_2(t))x_{22}(t), \\ \dot{x}_{12}(t) = x_{12}(t)\mu_1(s_2(t - \tau_1)) + D[x_{11}(t) - x_{12}(t)], \\ \dot{x}_{22}(t) = x_{22}(t)\mu_2(s_2(t - \tau_2)) - D x_{22}(t). \end{cases}$$

Nevertheless, a careful reading of the proofs of Theorems 1 and 2 shows that the upper bounds for the delays  $\tau_1$  and  $\tau_2$  can be obtained in a similar procedure.

**Table 1**  
Parameters.

| Competitor            | Maximal growth rate                           | Half saturation constant                 |
|-----------------------|---|--|
| <i>S. cerevisiae</i>  | $m_1 = 0.49 \pm 0.01 \text{ (h}^{-1}\text{)}$ | $a_1 = 110 \pm 10 \text{ (}\mu\text{M)}$ |
| <i>Candida utilis</i> | $m_2 = 0.59 \pm 0.01 \text{ (h}^{-1}\text{)}$ | $a_2 = 15 \pm 2 \text{ (}\mu\text{M)}$   |

**7. An illustrative application**

As an application, we will show that our global stability result can be seen as a complement or an alternative to the feedback control strategy developed by Smith and de Leenheer [35] in order to avoid the competitive exclusion in a chemostat with two species. These authors assume that the competitive exclusion is verified in the model (1.2) with  $n = 2$  and  $\tau = 0$  while the uptake functions  $\mu_i(\cdot)$  satisfy (H2) combined with the additional property:

(H4) There exists a unique  $s^* \in (0, s^0)$  such that  $\mu_1(s) = \mu_2(s)$ .

In [35] it is also assumed that each microbial species can be measured online while the dilution rate  $D$  can be implemented as a feedback control variable depending on the output  $y(t) = (x_1(t) \ x_2(t))$ . Under these assumptions, the feedback model becomes the system:

$$\begin{cases} \dot{s}(t) = D(x_1(t), x_2(t))[s^0 - s(t)] - \sum_{i=1}^2 \mu_i(s(t))x_i(t) \\ \dot{x}_1(t) = x_1(t)\mu_1(s(t)) - D(x_1(t), x_2(t))x_1(t) \\ \dot{x}_2(t) = x_2(t)\mu_2(s(t)) - D(x_1(t), x_2(t))x_2(t), \end{cases} \tag{7.1}$$

where the dilution is now depending of the output and defined by

$$D(x_1(t), x_2(t)) = k_1x_1(t) + k_2x_2 + \varepsilon \quad \text{with } k_1 > 0, k_2 > 0 \text{ and } \varepsilon \geq 0.$$

The assumption (H4) plays a key role in the main result of [35], which states conditions on the parameters  $k_i$  and  $\varepsilon$  ensuring the existence of a globally asymptotically stable equilibrium  $E^* = (s^*, x_1^*, x_2^*)$ , where  $s^*$  is stated in (H4) and  $x_i^* > 0$  with  $i = 1, 2$ .

When considering a delay between consumption of biomass and growth of species, the above system becomes:

$$\begin{cases} \dot{s}(t) = D(x_1(t), x_2(t))[s^0 - s(t)] - \sum_{i=1}^2 \mu_i(s(t))x_i(t) \\ \dot{x}_1(t) = x_1(t)\mu_1(s(t - \tau)) - D(x_1(t), x_2(t))x_1(t) \\ \dot{x}_2(t) = x_2(t)\mu_2(s(t - \tau)) - D(x_1(t), x_2(t))x_2(t). \end{cases} \tag{7.2}$$

It is worth emphasizing that (7.2) has not been studied previously in the literature but the robustness of (7.1) for small delays can be easily verified numerically which allow us to conjecture that the positive equilibrium  $E^*$  for (7.2) is globally asymptotically stable for small delays.

Now, let us observe that the assumption (H4) is not verified when considering a couple of functions satisfying the following property:

$$\mu_1(s) < \mu_2(s) \quad \text{for any } s \in (0, s^0). \tag{7.3}$$

Notice that when the property (7.3) is verified, the feedback control strategy described by (7.2) cannot achieve the coexistence of the two species in competition because (H4) is not satisfied. Nevertheless, as the chain of two chemostats (2.2) is not affected by (7.3), the coexistence can be obtained for a wide range of parameters satisfying (H3). This crucial fact shows a practical advantage of our model.

In order to illustrate this application, we will consider a liquid medium where two species, namely, *Candida utilis* and *Saccharomyces cerevisiae* are in competition for glucose. The growth of these species is described by the Monod’s functions (1.3) considered by Potsma et al. [33, p.3215] and described in the Table 1.

It is easy to see that  $\mu_1(s) < \mu_2(s)$  for any  $s > 0$ . Then, the assumption (H4) is not satisfied and the coexistence between the two species cannot be obtained by the feedback control strategy described by (7.2).

From now on, we will take the values  $m_i$  and  $a_i$  ( $i = 1, 2$ ) without considering uncertainties. When the dilution is  $D = 0.01 \text{ (h}^{-1}\text{)}$  we obtain the break even concentrations  $\lambda_1 = 2.291666$  and  $\lambda_2 = 0.258620$ . Proposition 1 ensures that the competitive exclusion is verified for some  $\tau \in [0, \tau_0^*)$  and *C. utilis* will be always the advantaged competitor. On the other hand, by (2.5) we can see that (H3) is verified for any  $s^0 < 15.889 \text{ (g/liter)}$ .

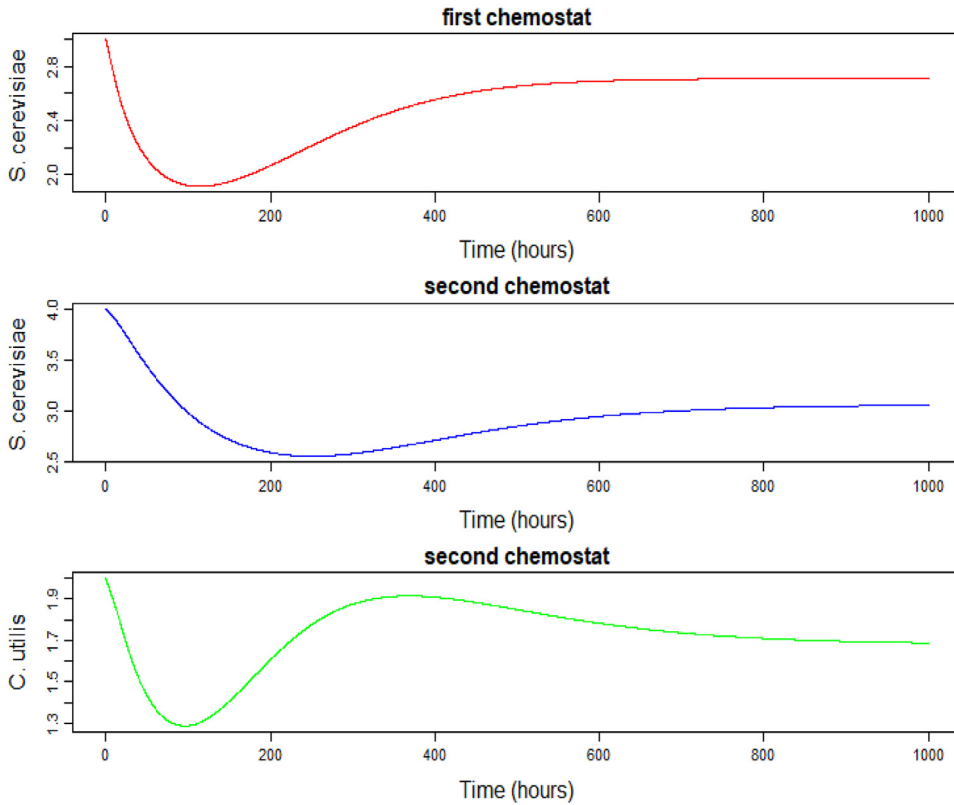
We made a numerical simulation considering  $s^0 = 5$ , which leads to

$$s_1^* = \lambda_1, \ x_{11}^* = 2.7083, \ s_2^* = \lambda_2, \ x_{12}^* = 3.06 \text{ and } x_{22}^* = 1.6813.$$

In order to study the local stability of  $E_0^*$  in the system (2.1), we have that the constants  $\mathcal{A}$  and  $\mathcal{B}$  defined in (3.3) and the crossover frequency are

$$\mathcal{A} = 0.021884, \ \mathcal{B} = 0.000119 \quad \text{and} \quad \omega_0 = 0.9650485,$$





**Fig. 2.** Time evolution of  $x_{11}$  (red),  $x_{12}$  (blue) and  $x_{22}$  (green). The species converge to  $x_{11}^*$ ,  $x_{12}^*$  and  $x_{22}^*$ . (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

which leads to a delay margin  $\tau_0 = 117.2399$ .

In order to study the global asymptotic stability of  $E_0^*$  in (2.1), we observe that

$$\bar{\Gamma} = 0.021304, \quad a_0 = 0.208514, \quad \mu_1(s^0) = 0.021304$$

and

$$d_0 = 0.102261e^{0.011304\tau} \quad \text{and} \quad s_1 = \frac{0.05}{0.01 + 0.044545e^\tau}.$$

We can verify that the inequalities (4.3) and (4.4) are satisfied for any  $\tau \in [0, 10.276118)$  and  $\tau \in [0, 0.021)$  respectively.

In order to study the global asymptotic stability of  $E^*$  in (2.2), one can easily verify that the inequality (4.8) is satisfied with  $\tau_{21} = 78.315834$  and  $\tau_{22} = 0.420841$ . The constants stated in (4.5)–(4.7) are  $\bar{\Theta} = 0.079717$ ,  $B_1 = 0.088851$ ,  $B_2 = 0.068192$ ,  $c_1 = 0.997654$ ,  $c_2 = 0.983051$  and  $q = 0.0872$ . The  $\tau$ -dependent parameters are

$$d_1 = d_{11}e^{d_{12}\tau} + d_{13}e^{d_{14}\tau}, \quad d_2 = d_{21}e^{d_{22}\tau} + d_{23}e^{d_{24}\tau}, \quad \xi_1 = \xi_{11}e^{-\xi_{12}\tau},$$

$$\underline{s} = \frac{s_1}{D + (s_2 + s_3e^{s_4\tau})(s_5e^{s_6\tau} + s_7e^\tau)}, \quad C = c_{11} + c_{12}e^{c_{12}\tau}, \quad b = b_{11}e^{b_{12}\tau},$$

and the parameters are  $d_{11} = 0.044811$ ,  $d_{12} = 0.008151$ ,  $d_{13} = 0.052958$ ,  $d_{14} = 0.028305$ ,  $d_{21} = 0.415719$ ,  $d_{22} = 0.068192$ ,  $d_{23} = 0.491305$ ,  $d_{24} = 0.088739$ ,  $\xi_1 = 2.708333$ ,  $\xi_2 = 0.001149$ ,  $s_1 = 0.022916$ ,  $s_2 = 4.58332$ ,  $s_3 = 5.41666$ ,  $s_4 = 0.0201547$ ,  $s_5 = 0.004455$ ,  $s_6 = 0.001149$ ,  $s_7 = 0.039$ ,  $s_8 = 0.01$ ,  $c_{11} = 2.291666$ ,  $c_{12} = 2.708333$ ,  $c_{13} = 0.0201547$ ,  $b_{11} = 0.013217$  and  $b_{12} = 0.008851$ . We can verify that the inequality (4.9) is verified for any  $\tau \in [0, 0.088)$  approximately.

Finally, Fig. 2 shows a numerical solution of (2.2) with constant initial conditions  $s_1(0) = 0.1$ ,  $x_{11}(0) = 3$ ,  $s_2(0) = 0.1$ ,  $x_{12}(0) = 4$  and delay  $\tau = 10$ , which shows the conservativeness of our results.

### 8. Discussion

This work generalizes the result of Contreras [39] by taking into account the delays between the consumption of the nutrient and its effects on the species growth. We point out that the model can be generalized in several ways.

For example: (i) we can consider three species in competition and construct a chain of three chemostats. Certainly, our methods could be applied for this case but the positiveness of the resulting equilibrium will impose more restrictions on the break-even concentrations and the parameter  $s^0$ . This fact provides an additional advantage over the feedback model from [35]. (ii) another extension of this work would be to replace  $D$  and  $s^0$  in the systems (2.1) and (2.2) by positive  $\omega$ -periodic inputs. In spite that there exists an impressive literature devoted to this topic for undelayed chemostat models, there are few works where delays are taken into account. Recently, some nonlinear topological methods combined with fixed point results have been successfully employed to study the existence of a periodic solution for (2.1) and we expect to adapt the Lyapunov-like functions approach in order to obtain sufficient conditions for its attractiveness.

Finally, It is also important to emphasize the conservativeness of our delay margins of stability compared with the linear stability analysis. In spite that this fact is quite usual in the study of nonlinear delay systems arising from population dynamics, we think that our Lyapunov-like approach could be improved in order to obtain less conservative results.

## References

- [1] J. Monod, La technique de culture continue, théorie et applications, *Ann. l'Inst. Pasteur* 79 (1950) 390–410.
- [2] A. Novick, L. Slizard, Description of the chemostat, *Science* 112 (1950) 715–716.
- [3] P.J. Darlington, Competition, competitive repulsion, and coexistence, *Proc. Natl. Acad. Sci. USA* 69 (1972) 3151–3155.
- [4] J.E. Keymer, M.A. Fuentes, P.A. Marquet, Diversity emerging: from competitive exclusion to neutral coexistence in ecosystems, *Theor. Ecol.* 5 (2012) 457–463.
- [5] H.L. Smith, P. Waltman, *The Theory of the Chemostat. Dynamics of Microbial Competition*, first ed, Cambridge University Press, Cambridge, 1995.
- [6] T.F. Thingstad, Dynamics of chemostat culture: the effect of a delay in cell response, *J. Theor. Biol.* 48 (1974) 149–159.
- [7] C. Helmstetter, S. Copper, O. Pierucci, E. Revelas, On the bacterial life sequence, *Cold Spring Harb. Symp. Quant. Biol.* 33 (1968) 809–822.
- [8] A.W. Bush, A.E. Cook, The effect of time delay and growth inhibition in the bacterial treatment of wastewater, *J. Theor. Biol.* 63 (1975) 385–395.
- [9] H.I. Freedman, J.W.H. So, P. Waltman, Coexistence in a model of competition in the chemostat incorporating discrete delays, *SIAM J. Appl. Math.* 49 (1989) 859–870.
- [10] J. Pan, Parameter analysis of a chemostat equation with delay, *Funkcialaj Ekvacioj* 41 (1998) 347–361.
- [11] J. Kato, J. Pan, Stability domain of a chemostat system with delay, *Fields Inst. Commun.* 21 (1999) 307–315.
- [12] E. Beretta, Y. Kuang, Global stability in a well known delayed chemostat model, *Commun. Appl. Anal.* 4 (2000) 147–155.
- [13] P. Gajardo, F. Mazenc, H. Ramirez, Competitive exclusion principle in a model of chemostat with delays, *Dynam. Contin. Dis. Ser. A* 16 (2009) 253–272.
- [14] G. Hardin, Competitive exclusion principle, *Science* 131 (1960) 1292–1297.
- [15] C.S. Elton, *Animal Ecology*, Sidgwick & Jackson, London, 1927.
- [16] H.I. Freedman, J.W.H. So, P. Waltman, R.V. Paris, P. Borne, J. Vignes, Chemostat competition with time delays, in: *Proceedings of the IMACS 1988: Twelfth World Congress on Scientific Computation: Modelling and Simulation of Systems*, Gerfidn Cite Scientifique, France, 1988, pp. 102–104.
- [17] S.F. Ellermeyer, *Delayed Growth Response in Models of Microbial Growth and Competition in Continuous Culture*, Dept. of Math. and Comput. Sci., Emory University, Atlanta, GA, 1991 Ph.d. thesis.
- [18] L. Wang, G.S.K. Wolkowicz, A delayed chemostat model with general nonmonotone response functions and differential removal rates, *J. Math. Anal. Appl.* 321 (2006) 452–468.
- [19] S. Liu, X. Wang, L. Wang, H. Song, Competitive exclusion in delayed chemostat models with differential removal rates, *SIAM J. Appl. Math.* 74 (2014) 634–648.
- [20] F. Campillo, M. Joannides, I. Larramendi-Valverde, Stochastic modeling of the chemostat, *Ecol. Model.* 222 (2011) 2676–2689.
- [21] T. Caraballo, X. Han, P.E. Kloeden, Chemostats with random inputs and wall growth, *Math. Meth. Appl. Sci.* 38 (2015) 3538–3550.
- [22] C. Xu, S. Yuan, Competition in the chemostat: a stochastic multi-species model and its asymptotic behavior, *Math. Biosci.* 280 (2016) 1–9.
- [23] S. Sun, Y. Sun, G. Zhang, X. Liu, Dynamical behavior of a stochastic two-species Monod competition chemostat model, *Appl. Math. Comp.* 298 (2017) 153–170.
- [24] I. Aviram, A. Rabinovitch, Bacteria and lytic phage coexistence in a chemostat with periodic nutrient supply, *Bull. Math. Biol.* 76 (2014) 225–244.
- [25] T. Caraballo, X. Han, P.E. Kloeden, A. Rapaport, Dynamics of nonautonomous chemostat models, in: V.A. Sadovnichiy, M.Z. Zgurovsky (Eds.), *Continuous and Distributed Systems II Theory and Applications*, Springer, 2015. 103–120
- [26] G. Fan, H.L. Smith, H.R. Thieme, Competition in the chemostat with time-dependent differential removal rates, *Vietnam. J. Math.* 45 (2017) 153–178.
- [27] S. Pavlou, Microbial competition in bioreactors, *Chem. Ind. Chem. Eng. Q.* 12 (2006) 71–81.
- [28] F. Grogard, F. Mazenc, A. Rapaport, Polytopic Lyapunov functions for persistence analysis of competing species, *Discrete Contin. Dyn. Syst. Ser. B* 8 (2007) 73–93.
- [29] R. Fekih-Salem, C. Lobry, T. Sari, A density-dependent model of competition for one resource in the chemostat, *Math. Biosci.* 286 (2017) 104–122.
- [30] P. De Leenheer, S. Levin, E. Sontag, C. Klausmeier, Global stability in a chemostat with multiple nutrients, *J. Math. Biol.* 52 (2006) 419–438.
- [31] M.M. Ballyk, G.S.K. Wolkowicz, Classical and resource-based competition: a unifying graphical approach, *J. Math. Biol.* 62 (2011) 81–109.
- [32] S. Hansen, S. Hubell, Single nutrient microbial competition: agreement between experimental and forecast outcomes, *Science* 207 (1980) 1491–1493.
- [33] E. Pottsma, A. Kuiper, W. tomasow, W. Scheffers, J.V. Dijken, Competition for glucose between the yeasts *saccharomyces cerevisiae* and *candida utilis*, *Appl. Environ. Microbiol.* 55 (1989) 3124–3220.
- [34] S. Dikshitulu, B. Baltzis, G. Lewandowski, S. Pavlou, Competition between two microbial populations in a sequencing fed-batch reactor: theory, experimental verification, and implications for waste treatment applications, *Biotechnol. Bioeng.* 42 (2004) 643–656.
- [35] P. De Leenheer, H.L. Smith, Feedback control for chemostat models, *J. Math. Biol.* 46 (2004) 48–70.
- [36] G. Robledo, F. Grogard, J.L. Gouzé, Global stability for a model of competition in the chemostat with microbial inputs, *Nonlinear Anal. Real World Appl.* 13 (2012) 582–598.
- [37] F. Mazenc, M. Malisoff, G. Robledo, Stability and robustness analysis for a multi-species chemostat model with uncertainties, in: *Proceedings of the 2017 American Control Conference*, 2017, pp. 2130–2134. Seattle, WA, 24–26 May
- [38] F. Mazenc, M. Malisoff, G. Robledo, Stability and robustness analysis for a multispecies chemostat model with delays in the growth rates and uncertainties, *Discr. Contin. Dyn. Syst. Ser. B* 23 (2018) 1851–1872.
- [39] G. Contreras, *Mathematical Model of Competition in a Chain of Chemostats: Some Results About Coexistence and Exclusion*, Universidad de Chile, 2013 Master thesis.
- [40] M. Malisoff, F. Mazenc, *Constructions of Strict Lyapunov Functions*, first ed, Springer-Verlag, London, 2009.
- [41] F. Mazenc, Z.P. Jiang, Global output feedback stabilization of a chemostat with an arbitrary number of species, *IEEE Trans. Aut. Control* 55 (2010) 2570–2575.
- [42] F. Mazenc, J. Harmand, M. Malisoff, Stabilization in a chemostat with sampled and delayed measurements, in: *Proceedings of the 2016 American Control Conference* (Boston, MA, 6–8 July, 2016, pp. 1857–1862.
- [43] E. Malakhovsky, L. Mirkin, On stability of second-order quasi-polynomials with a single delay, *Automatica* 42 (2006) 1041–1047.

- [44] R. Datko, A procedure for determination of the exponential stability of certain differential–difference equations, *Q. Appl. Math.* 36 (1978) 279–292.
- [45] P. Hartman, *Ordinary Differential Equations*, second ed, SIAM, Philadelphia, 2002.
- [46] H. Khalil, *Nonlinear Systems*, third ed., Prentice Hall, Upper Saddle River, 2000.
- [47] A. Halanay, *Differential Equations: Stability, Oscillations, Time Lags*, first ed, Academic Press, New York, 1966.