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MATHEMATICAL MODELLING AND ANALYSIS FOR A THREE-TIERED MICROBIAL FOOD WEB IN A CHEMOSTAT

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Abstract. In this article, we present a mathematical six-dimensional dynamical system involving a three-tiered microbial food web without maintenance. We give a qualitative analysis of the model, and an analysis of the local stability of equilibrium points. Under general assumptions of monotonicity, we prove the uniqueness and the local stability of the positive equilibrium point corresponding to the persistence of the three bacteria. Possibilities of periodic orbits are not excluded and asymptotic coexistence is satisfied.

1. Introduction

The anaerobic digestion model No. 1 (ADM1) is a sophisticated mathematical model developed by the international water association (IWA) modelling the anaerobic digestion processes created for full-scale industrial plants design, systems operational analysis and control [1]. This generic model permits to produce a platform for dynamic simulations of a variety of anaerobic processes. A way to facilitate the study of such a sophisticated model is by considering reduced models to better understand the biological phenomena of sub-processes while reducing the number of variables and parameters of the system in order to simplify the mathematical analysis.

It has been proved previously that simplifying or reducing the complexity of the model ADM1 can preserve biological significance while reducing the computational effort needed to find mathematical solutions to the equations of this model [9]. Note that when using gross simplification of a biological system, analytical techniques are unable to provide general solutions for the system and then numerical simulations must suffice.

In this work, we shall revisit the model proposed by Wade et al. [8] and analyzed by Sari and Wade [5] in considering two main changes relevant from an applied point of view. The contents of this paper is arranged as following. First, we present, in Section 2, a description of the model to be investigated, which is a reduction of the one given by [8]. Then existence, uniqueness and local stability of the 3D reduced system is analyzed in Section 3. Global stability of the reduced system is also

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discussed. In section 4, asymptotic behavior of the 6D-system is then deduced. Finally, in section 5, numerical simulations are given when using Monod's growth functions which are currently used in biotechnology

2. Mathematical model and results

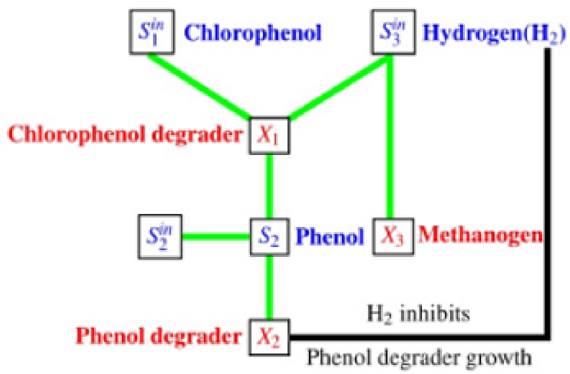

Figure 1. Three-tiered microbial food web

The model developed here has six components, three substrate and three biomass variables based on Anaerobic Digestion Model No. 1 (ADM1) (Batstone et al.[1]). The chlorophenol degrader (X_1) uses both chlorophenol (S_1) and hydrogen (S_3) for growth, producing phenol (S_2) as a product. Phenol (S_2) is consumed by the phenol degrader (X_2), which is inhibited by the hydrogen. The methanogen (X_3) growth on the hydrogen. In the actual paper, we revisit the model proposed by Wade et al. [8] and analyzed by Sari and Wade [5] in considering two main changes relevant from an applied point of view. First, we neglect all species specific mortality (maintenance) rates and take into account the dilution rate only. The second modification of the model is that we neglect the part of hydrogen produced by the phenol degrader. Chlorophenol, phenol and hydrogen are introduced into the reactor with a constant dilution rate D and an input concentration S_i^{in}, $i = 1, 2, 3$, respectively.

Biomass and substrate concentrations are then modelled by the following six-dimensional dynamical system of ODEs:

$$
\begin{gathered}
\dot{X}_1 = \big(\mu_1(S_3, S_1) - D\big) X_1 \,, \\
\dot{S}_1 = D(S_1^{in} - S_1) - \mu_1(S_3, S_1)\frac{X_1}{Y_1} \,, \\
\dot{X}_2 = \big(\mu_2(S_3, S_2) - D\big) X_2 \,, \\
\dot{S}_2 = D(S_2^{in} - S_2) + \mu_1(S_3, S_1)\frac{X_1}{Y_4} - \mu_2(S_3, S_2)\frac{X_2}{Y_2} \,, \\
\dot{X}_3 = \big(\mu_3(S_3) - D\big) X_3 \,, \\
\dot{S}_3 = D(S_3^{in} - S_3) - \mu_1(S_3, S_1)\frac{X_1}{Y_5} - \mu_3(S_3)\frac{X_3}{Y_3}.
\end{gathered} \tag{2.1}
$$

with initial conditions $\big(S_1(0), S_2(0), S_3(0), X_1(0), X_2(0), X_3(0)\big) \in \mathbb{R}_+^6$, where Y_i, $i = 1, 2, 3, 4$ are the yield coefficients.

Assume that the functional response of each species $\mu_1, \mu_2 : \mathbb{R}_+^2 \to \mathbb{R}_+$ and $\mu_3 : \mathbb{R}_+ \to \mathbb{R}_+$ satisfies

- (A1) $\mu_1, \mu_2 : \mathbb{R}_+^2 \to \mathbb{R}_+$ and $\mu_3 : \mathbb{R}_+ \to \mathbb{R}_+$ are of class $\mathcal{C}^1$,
- (A2) $\mu_1(0, S_1) = \mu_1(S_3, 0) = \mu_2(S_3, 0) = \mu_3(0) = 0$, for all $S_3, S_1 \in \mathbb{R}_+$,
- (A3) $\frac{\partial \mu_1}{\partial S_1}(S_3, S_1) > 0$, $\frac{\partial \mu_1}{\partial S_3}(S_3, S_1) > 0$, for all $S_1, S_3 \in \mathbb{R}_+$,
- (A4) $\frac{\partial \mu_2}{\partial S_2}(S_3, S_2) > 0$, $\frac{\partial \mu_2}{\partial S_3}(S_3, S_2) < 0$, for all $S_2, S_3 \in \mathbb{R}_+$,
- (A5) $\mu_3'(S_3) > 0$, for all $S_3 \in \mathbb{R}_+$.

Assumption (A2) means that species X_1 cannot grow without substrates S_1 and S_3 and that the intermediate product S_2 is obligate for the growth of species X_2 and that the substrate S_3 is obligate for the growth of species X_3. Hypothesis (A3) expresses that the growth of species X_1 increases with the substrate S_1 and the substrate S_3. Hypothesis (A4) expresses that the species X_2 growth increases with intermediate product S_2 produced by species X_1 whereas X_2 is inhibited by the substrate S_3. Hypothesis (A5) expresses that the growth of species X_3 increases with the substrate S_3.

This proposed mathematical six-dimensional dynamical system describe a three-tiered microbial food web without maintenance. Previous works on two-tier ecological systems gave complete stability analysis, locally and globally (El Hajji et al. [3]; Sari et al. [4], Weedermann et al. [9]).

To scale the system (2.1) consider the following change of variables and parameters:

$$
\begin{gathered}
s_1 = S_1, \quad s_2 = \frac{Y_4}{Y_1} S_2, \quad s_3 = \frac{Y_5}{Y_1} S_3, \quad x_1 = \frac{X_1}{Y_1}, \quad x_2 = \frac{Y_4}{Y_1 Y_2} X_2, \\
x_3 = \frac{Y_5}{Y_1 Y_3} X_3, \quad s_1^{in} = S_1^{in}, \quad s_2^{in} = \frac{Y_4}{Y_1} S_2^{in}, \quad s_3^{in} = \frac{Y_5}{Y_1} S_3^{in}.
\end{gathered}
$$

The dimensionless equations thus obtained are :

$$
\begin{gathered}
\dot{x}_1 = \big(f_1(s_3, s_1) - D\big) x_1 , \\
\dot{s}_1 = D\big(s_1^{in} - s_1\big) - f_1(s_3, s_1) x_1 , \\
\dot{x}_2 = \big(f_2(s_3, s_2) - D\big) x_2 , \\
\dot{s}_2 = D(s_2^{in} - s_2) + f_1(s_3, s_1) x_1 - f_2(s_3, s_2) x_2 , \\
\dot{x}_3 = \big(f_3(s_3) - D\big) x_3 , \\
\dot{s}_3 = D(s_3^{in} - s_3) - f_1(s_3, s_1) x_1 - f_3(s_3) x_3 .
\end{gathered} \tag{2.2}
$$

Here, functions $f_1, f_2 : \mathbb{R}_+^2 \to \mathbb{R}_+$ and $f_3 : \mathbb{R}_+ \to \mathbb{R}_+$ are given by

$$
f_1(s_3, s_1) = \mu_1(\frac{Y_1}{Y_5} s_3, s_1), \quad f_2(s_3, s_2) = \mu_1(\frac{Y_1}{Y_5} s_3, \frac{Y_1}{Y_4} s_2), \quad f_3(s_3) = \mu_3(\frac{Y_1}{Y_5} s_3).
$$

Then the Assumptions (A1)–(A5) satisfied by the functions μ_1, μ_2 and μ_3 are translated to the following assumptions on the functions f_1, f_2 and f_3:

- (A6) $f_1, f_2 : \mathbb{R}_+^2 \to \mathbb{R}_+$ and $f_3 : \mathbb{R}_+ \to \mathbb{R}_+$ are of class $\mathcal{C}^1$,
- (A7) $f_1(0, s_1) = f_1(s_3, 0) = f_2(s_3, 0) = f_3(0) = 0$, for all $s_1, s_3 \in \mathbb{R}_+$,
- (A8) $\frac{\partial f_1}{\partial s_1}(s_3, s_1) > 0$, $\frac{\partial f_1}{\partial s_3}(s_3, s_1) > 0$, for all $s_1, s_3 \in \mathbb{R}_+$,
- (A9) $\frac{\partial f_2}{\partial s_2}(s_3, s_2) > 0$, $\frac{\partial f_2}{\partial s_3}(s_3, s_2) < 0$, for all $s_2, s_3 \in \mathbb{R}_+$,
- (A10) $f_3'(s_3) > 0$, for all $s_3 \in \mathbb{R}_+$.

The closed non-negative cone $\mathbb{R}^6_+$, in $\mathbb{R}^6$, is positively invariant by the system (2.2). More precisely we have the following result.

Proposition 2.1. *(1) For all initial condition in $\mathbb{R}^6_+$, the solution of system* (2.2) *is bounded and has positive components and thus is defined for all $t > 0$.*

(2) System (2.2) *admits a positive invariant attractor set of all solution given by* $\Omega = \{(s_1, s_2, s_3, x_1, x_2, x_3) \in \mathbb{R}^6_+ / s_1 + x_1 = s_1^{in},\ x_1 + s_3 + x_3 = s_3^{in},\ s_2 + x_2 + s_3 + x_3 = s_2^{in} + s_3^{in}\}$.

Proof. (1) The positivity of the solution is proved by the fact that: If $s_i = 0$ then $\dot{s}_i = Ds_i^{in} > 0$ for $i = 1, 3$, and if $x_i = 0$ then $\dot{x}_i = 0$ for $i = 1, 2, 3$. Now, if $s_2 = 0$ then $\dot{s}_2 = Ds_2^{in} + f_1(s_3, s_1)x_1 > 0$. Next we have to prove the boundedness of solutions of (2.2). By adding the two first equations of system (2.2), one obtains, for $z_1 = s_1 + x_1 - s_1^{in}$, a single equation: $\dot{z}_1 = -Dz_1$ then

$$s_1(t) + x_1(t) = s_1^{in} + \big(s_1(0) + x_1(0) - s_1^{in}\big)e^{-Dt} \tag{2.3}$$

Similarly, by adding the first and the two last equations of system (2.2), one obtains, for $z_2 = x_1 + s_3 + x_3 - s_3^{in}$, a single equation: $\dot{z}_2 = -Dz_2$ then

$$x_1(t) + s_3(t) + x_3(t) = s_3^{in} + \big(x_1(0) + s_3(0) + x_3(0) - s_3^{in}\big)e^{-Dt} \tag{2.4}$$

Finally, by adding the last four equations of system (2.2), one obtains, for $z_3 = s_2 + x_2 + s_3 + x_3 - s_2^{in} - s_3^{in}$, a single equation: $\dot{z}_3 = -Dz_3$ then

$$\begin{aligned} &s_2(t) + x_2(t) + s_3(t) + x_3(t)\\ &= s_2^{in} + s_3^{in} + (s_2(0) + x_2(0) + s_3(0) + x_3(0) - s_2^{in} - s_3^{in})e^{-Dt} \end{aligned} \tag{2.5}$$

Since all terms of the two sums are positive, then the solution is bounded.

(2) The second point is simply a direct consequence of equalities (2.3)-(2.4)-(2.5). □

3. Restriction to $\mathbb{R}^3_+$

Trajectories of the 6D-system (2.2) converge exponentially inside the set Ω and our aim is to study the asymptotic behavior of these trajectories. The idea is to restrict the study of the asymptotic behavior of the system (2.2) onto the attractive set Ω. Using Theme's results [7], the asymptotic behavior of the solutions of the reduced system will be informative for the complete system (2.2) (cf. EL Hajji et al. [2] and Sari et al. [4]). Note that in our case, periodic orbits are not excluded.

The projection on the three-dimensional space (x_1, x_2, x_3) of the restriction of system (2.2) on Ω is given by the following reduced system.

$$\begin{gathered} \dot{x}_1 = \Big(f_1(s_3^{in} - x_1 - x_3, s_1^{in} - x_1) - D\Big)x_1\,,\\ \dot{x}_2 = \Big(f_2(s_3^{in} - x_1 - x_3, s_2^{in} + x_1 - x_2) - D\Big)x_2\,,\\ \dot{x}_3 = \Big(f_3(s_3^{in} - x_1 - x_3) - D\Big)x_3\,. \end{gathered} \tag{3.1}$$

Thus, for (3.1) the state-vector (x_1, x_2, x_3) belongs to the following subset of $\mathbb{R}^3_+$:

$$\mathcal{S} = \big\{(x_1, x_2, x_3) \in \mathbb{R}^3_+ : 0 \le x_1 \le s_1^{in},\ 0 \le x_2 \le x_1 + s_2^{in},\ 0 \le x_1 + x_3 \le s_3^{in}\big\}.$$

3.1. **Local analysis.**

3.1.1. *Equilibrium points.* The system can have the following eight types of equilibrium points.

- Trivial equilibria $F^0 = (0, 0, 0)$.
- Boundary equilibria $F^1 = (\bar{x}_1, 0, 0)$, where $x_1 = \bar{x}_1$ is solution, if it exists, of equation
$$f_1(s_3^{in} - x_1, s_1^{in} - x_1) = D. \tag{3.2}$$
- Boundary equilibria $F^2 = (0, \bar{x}_2, 0)$, where $x_2 = \bar{x}_2$ is a solution, if it exists, of equation
$$f_2(s_3^{in}, s_2^{in} - x_2) = D. \tag{3.3}$$
- Boundary equilibria $F^3 = (0, 0, s_3^{in} - s^*)$, where $s^* = f_3^{-1}(D)$.
- Boundary equilibria $F^{13} = (x_1^*, 0, s_3^{in} - s^* - x_1^*)$, where $x_1 = x_1^*$ is solution, if it exists, of equation
$$f_1(s^*, s_1^{in} - x_1) = D. \tag{3.4}$$
- Boundary equilibria $F^{23} = (0, \bar{\bar{x}}_2, s_3^{in} - s^*)$, where $x_2 = \bar{\bar{x}}_2$ is solution, if it exists, of equation
$$f_2(s^*, s_2^{in} - x_2) = D. \tag{3.5}$$
- Boundary equilibria $F^{12} = (\bar{x}_1, \bar{\bar{\bar{x}}}_2, 0)$, where $x_2 = \bar{\bar{\bar{x}}}_2$ is solution, if it exists, of equation
$$f_2(s_3^{in} - \bar{x}_1, s_2^{in} + \bar{x}_1 - x_2) = D. \tag{3.6}$$
- Positive equilibria $F^* = (x_1^*, x_2^*, s_3^{in} - s^* - x_1^*)$, where $x_2 = x_2^*$ is solution, if it exists, of equation
$$f_2(s^*, s_2^{in} + x_1^* - x_2) = D. \tag{3.7}$$

Existence and uniqueness. For a given D, let $s^* = f_3^{-1}(D)$, x_1^* the unique solution, if it exists, of $f_1(s^*, s_1^{in} - x_1) = D$ and $\bar{x}_1$ the unique solution, if it exists, of $f_1(s_3^{in} - x_1, s_1^{in} - x_1) = D$. We use the following notation
$$D_1 = f_1(s_3^{in}, s_1^{in}), \quad D_2 = f_2(s_3^{in}, s_2^{in}), \quad D_3 = f_3(s_3^{in}),$$
$$D_4 = f_1(s^*, s_1^{in}), \quad D_5 = f_2(s^*, s_2^{in}), \quad D_6 = f_2(s^*, s_2^{in} + x_1^*),$$
$$D_7 = f_2(s_3^{in} - \bar{x}_1, s_2^{in} + \bar{x}_1), \quad D_8 = f_3(s_3^{in} - \bar{x}_1).$$

Remark 3.1. By assumptions (A6)–(A10), one can easily verify that
$$D_2 < D_5 < D_6, \quad D_2 < D_7, \quad D_4 < D_1, \quad D_8 < D_3\,.$$

Existence and uniqueness conditions of the equilibrium points F^0, F^1, F^2, F^3, F^{12}, F^{13}, F^{23} and F^* are given in the following theorem.

Theorem 3.2.

- $F^0 = (0, 0, 0)$ *exists always and is unique,*
- F^1 *exists and is unique if and only if* $D < D_1$*,*
- F^2 *exists and is unique if and only if* $D < D_2$*,*
- F^3 *exists and is unique if and only if* $D < D_3$*,*
- F^{13} *exists and is unique if and only if* $D < \min(D_3, D_4)$*,*
- F^{23} *exists and is unique if and only if* $D < \min(D_3, D_5)$*,*
- F^{12} *exists and is unique if and only if* $D < \min(D_1, D_7)$*,*
- F^* *exists and is unique if and only if* $D < \min(D_3, D_4, D_6)$*.*

Proof.

- $F^0 = (0, 0, 0)$ exists always.

- The mapping $x_1 \mapsto f_1(s_3^{in} - x_1, s_1^{in} - x_1)$ is decreasing. Hence, there exists a unique $\bar{x}_1$ such that $f_1(s_3^{in} - \bar{x}_1, s_1^{in} - \bar{x}_1) = D$ if and only if $D < D_1 = f_1(s_3^{in}, s_1^{in})$. Then, F^1 exists and is unique if and only if $D < D_1$.
- The mapping $x_2 \mapsto f_2(s_3^{in}, s_2^{in} - x_2)$ is decreasing. Hence, there exists a unique $\bar{x}_2$ such that $f_2(s_3^{in}, s_2^{in} - \bar{x}_2) = D$ if and only if $D < D_2 = f_2(s_3^{in}, s_2^{in})$. Then, F^2 exists and is unique if and only if $D < D_2$
- The mapping $s_3 \mapsto f_3(s_3)$ is increasing. Hence, there exists a unique s^* such that $f_3(s^*) = D$ if and only if $D < D_3 = f_3(s_3^{in})$. Then, F^3 exists and is unique if and only if $D < D_3$.
- s^* exists if and only if $D < D_3$. The mapping $x_1 \mapsto f_1(s^*, s_1^{in} - x_1)$ is decreasing. Hence, there exists a unique x_1^* such that $f_1(s^*, s_1^{in} - x_1^*) = D$ if and only if $D < D_4 = f_1(s^*, s_1^{in})$. Then, F^{13} exists and is unique if and only if $D < \min(D_3, D_4)$.
- Similarly, the mapping $x_2 \mapsto f_2(s^*, s_2^{in} - x_2)$ is decreasing. Hence, there exists a unique $\bar{\bar{x}}_2$ such that $f_2(s^*, s_2^{in} - \bar{\bar{x}}_2) = D$ if and only if $D < D_5 = f_2(s^*, s_2^{in})$. Then, F^{23} exists and is unique if and only if $D < \min(D_3, D_5)$.
- $\bar{x}_1$ exists and is unique if and only if $D < D_1$. For $D < D_1$, the mapping $x_2 \mapsto f_2(s_3^{in} - \bar{x}_1, s_2^{in} + \bar{x}_1 - x_2)$ is decreasing. Hence, there exists a unique $\bar{\bar{\bar{x}}}_2$ such that $f_2(s_3^{in} - \bar{x}_1, s_2^{in} + \bar{x}_1 - \bar{\bar{\bar{x}}}_2) = D$ if and only if $D < D_7 = f_2(s_3^{in} - \bar{x}_1, s_2^{in} + \bar{x}_1)$. One deduce that F^{12} exists and is unique if and only if $D < \min(D_1, D_7)$.
- $s^* = f_3^{-1}(D)$ exists and is unique if and only if $D < D_3$. x_1^* exists and is unique if and only if $D < D_4$. For $D < \min(D_3, D_4)$, the mapping $x_2 \mapsto f_2(s^*, s_2^{in} + x_1^* - x_2)$ is decreasing. Hence, there exists a unique x_2^* such that $f_2(s^*, s_2^{in} + x_1^* - x_2^*) = D$ if and only if $D < D_6$. One deduce that F^* exists and is unique if and only if $D < \min(D_3, D_4, D_6)$.

$\square$

Local stability. The Jacobian matrix of (3.1), at point (x_1, x_2, x_3), is

$$J = \begin{bmatrix} f_1 - D - \frac{\partial f_1}{\partial s_3} x_1 - \frac{\partial f_1}{\partial s_1} x_1 & 0 & -\frac{\partial f_1}{\partial s_3} x_1 \\ -\frac{\partial f_2}{\partial s_3} x_2 + \frac{\partial f_2}{\partial s_2} x_2 & f_2 - D - \frac{\partial f_2}{\partial s_2} x_2 & -\frac{\partial f_2}{\partial s_3} x_2 \\ -f_3' x_3 & 0 & f_3 - D - f_3' x_3 \end{bmatrix}$$

where the function f_1 is evaluated at $(s_3^{in} - x_1 - x_3, s_1^{in} - x_1)$, f_2 is evaluated at $(s_3^{in} - x_1 - x_3, s_2^{in} + x_1 - x_2)$ and f_3 is evaluated at $s_3^{in} - x_1 - x_3$. In the following lemma, the nature of the equilibrium point F^0 is given.

Lemma 3.3. *If $D > \max(D_1, D_2, D_3)$ then F^0 is a stable node.*
If $\min(D_1, D_2, D_3) < D < \max(D_1, D_2, D_3)$ then F^0 is a saddle point.
If $D < \min(D_1, D_2, D_3)$ then F^0 is an unstable node.

Proof. The Jacobian matrix at F^0 is

$$J^0 = \begin{bmatrix} D_1 - D & 0 & 0 \\ 0 & D_2 - D & 0 \\ 0 & 0 & D_3 - D \end{bmatrix}$$

The eigenvalues are $D_1 - D$, $D_2 - D$ and $D_3 - D$. Thus, if $D > \max(D_1, D_2, D_3)$ then F^0 is a stable node. If $\min(D_1, D_2, D_3) < D < \max(D_1, D_2, D_3)$ then F^0 is a saddle point. If $D < \min(D_1, D_2, D_3)$ then F^0 is an unstable node. $\square$

In the following lemmas, the nature of the boundary equilibrium points F^1, F^2, F^3, F^{12}, F^{13} and F^{23} is given.

Lemma 3.4. *F^1 is a stable node if $D > \max(D_7, D_8)$. F^1 is a saddle point if $D < \max(D_7, D_8)$.*

Proof. The Jacobian matrix at F^1 is

$$J^1 = \begin{bmatrix} -\frac{\partial f_1}{\partial s_3}\bar{x}_1 - \frac{\partial f_1}{\partial s_1}\bar{x}_1 & 0 & -\frac{\partial f_1}{\partial s_3}\bar{x}_1 \\ 0 & D_7 - D & 0 \\ 0 & 0 & D_8 - D \end{bmatrix}$$

where f_1 is evaluated at $(s_3^{in} - \bar{x}_1, s_3^{in} - \bar{x}_1)$. The eigenvalues are given by

$$-\frac{\partial f_1}{\partial s_3}\bar{x}_1 - \frac{\partial f_1}{\partial s_1}\bar{x}_1 < 0, \quad D_7 - D, \quad D_8 - D.$$

Thus F^1 is a stable node if $D > \max(D_7, D_8)$. F^1 is a saddle point if $D < \max(D_7, D_8)$. □

Lemma 3.5. *F^2 is a stable node if $D > \max(D_1, D_3)$. It is a saddle point if $D < \max(D_1, D_3)$.*

Proof. The Jacobian matrix at F^2 is

$$J^2 = \begin{bmatrix} D_1 - D & 0 & 0 \\ -\frac{\partial f_2}{\partial s_3}\bar{x}_2 + \frac{\partial f_2}{\partial s_2}\bar{x}_2 & -\frac{\partial f_2}{\partial s_2}\bar{x}_2 & -\frac{\partial f_2}{\partial s_3}\bar{x}_2 \\ 0 & 0 & D_3 - D \end{bmatrix}$$

where the function f_2 is evaluated at $(s_3^{in}, s_2^{in} - \bar{x}_2)$. The eigenvalues are

$$-\frac{\partial f_2}{\partial s_2}\bar{x}_2 < 0, \quad D_1 - D, \quad D_3 - D.$$

Thus F^2 is a stable node if $D > \max(D_1, D_3)$. It is a saddle point if $D < \max(D_1, D_3)$. □

Lemma 3.6. *F^3 is a stable node if $D > \max(D_4, D_5)$. F^3 is a saddle point if $D < \max(D_4, D_5)$.*

Proof. The Jacobian matrix at F^3 is

$$J^3 = \begin{bmatrix} D_4 - D & 0 & 0 \\ 0 & D_5 - D & 0 \\ -f_3'(s^*)(s_3^{in} - s^*) & 0 & -f_3'(s^*)(s_3^{in} - s^*) \end{bmatrix}$$

The eigenvalues are

$$-f_3'(s^*)(s_3^{in} - s^*) < 0, \quad D_4 - D, \quad D_5 - D.$$

Thus F^3 is a stable node if $D > \max(D_4, D_5)$. F^3 is a saddle point if $D < \max(D_4, D_5)$. □

Lemma 3.7. *F^{12} is a stable node if $D > D_8$. F^{12} is a saddle point if $D < D_8$.*

Proof. The Jacobian matrix at F^{12} is

$$J^{12} = \begin{bmatrix} -\frac{\partial f_1}{\partial s_3}\bar{x}_1 - \frac{\partial f_1}{\partial s_1}\bar{x}_1 & 0 & -\frac{\partial f_1}{\partial s_3}\bar{x}_1 \\ (-\frac{\partial f_2}{\partial s_3} + \frac{\partial f_2}{\partial s_2})\bar{\bar{\bar{x}}}_2 & -\frac{\partial f_2}{\partial s_2}\bar{\bar{\bar{x}}}_2 & -\frac{\partial f_2}{\partial s_3}\bar{\bar{\bar{x}}}_2 \\ 0 & 0 & D_8 - D \end{bmatrix},$$

where the function f_1 is evaluated at $(s_3^{in} - \bar{x}_1, s_1^{in} - \bar{x}_1)$, f_2 is evaluated at $(s_3^{in} - \bar{x}_1, s_2^{in} + \bar{x}_1 - \bar{\bar{\bar{x}}}_2)$. Then eigenvalues are $\lambda_1 = D_8 - D$, $\lambda_2 = -\frac{\partial f_2}{\partial s_2}\bar{\bar{\bar{x}}}_2 < 0$ and $\lambda_3 = -(\frac{\partial f_1}{\partial s_3}\bar{x}_1 + \frac{\partial f_1}{\partial s_1}\bar{x}_1) < 0$. Thus F^{12} is a stable node if $D > D_8$. F^{12} is a saddle point if $D < D_8$. □

Lemma 3.8. *F^{13} is a stable node if $D > D_6$. F^{13} is a saddle point if $D < D_6$.*

Proof. The Jacobian matrix at F^{13} is

$$J^{13} = \begin{bmatrix} -\frac{\partial f_1}{\partial s_3}x_1^* - \frac{\partial f_1}{\partial s_1}x_1^* & 0 & -\frac{\partial f_1}{\partial s_3}x_1^* \\ & 0 & D_6 - D & 0 \\ -(s_3^{in} - s^* - x_1^*)f_3'(s^*) & 0 & -(s_3^{in} - s^* - x_1^*)f_3'(s^*) \end{bmatrix}$$

where the function f_1 is evaluated at $(s^*, s_1^{in} - x_1^*)$ and f_2 is evaluated at $(s^*, s_2^{in} + x_1^*)$.

The characteristic polynomial is

$$(D_6 - D - \lambda)\Big[\lambda^2 + \lambda(\frac{\partial f_1}{\partial s_3}x_1^* + \frac{\partial f_1}{\partial s_1}x_1^* + (s_3^{in} - s^* - x_1^*)f_3'(s^*)) + \frac{\partial f_1}{\partial s_1}f_3'(s^*)(s_3^{in} - s^* - x_1^*)x_1^*\Big]$$

Eigenvalues are then $\lambda_1 = D_6 - D$ and two other negative eigenvalues (by Routh's Stability Criterion). Thus F^{13} is a stable node if $D > D_6$. F^{13} is a saddle point if $D < D_6$. □

Lemma 3.9. *F^{23} is a stable node if $D > D_4$ and it is a saddle point if $D < D_4$.*

Proof. The Jacobian matrix at F^{23} is

$$J^{23} = \begin{bmatrix} D_4 - D & 0 & 0 \\ -\frac{\partial f_2}{\partial s_3}\bar{\bar{x}}_2 + \frac{\partial f_2}{\partial s_3}\bar{\bar{x}}_2 & -\frac{\partial f_2}{\partial s_2}\bar{\bar{x}}_2 & -\frac{\partial f_2}{\partial s_3}\bar{\bar{x}}_2 \\ -(s_3^{in} - s^*)f_3'(s^*) & 0 & -(s_3^{in} - s^*)f_3'(s^*) \end{bmatrix},$$

where the function f_2 is evaluated at $(s^*, s_2^{in} - \bar{\bar{x}}_2)$. The eigenvalues are

$$D_4 - D, \quad -\frac{\partial f_2}{\partial s_2}\bar{\bar{x}}_2 < 0, \quad -(s_3^{in} - s^*)f_3'(s^*) < 0.$$

Thus F^{23} is a stable node if $D > D_4$ and it is a saddle point if $D < D_4$. □

Let us discuss now the local stability of the positive equilibria $F^* = (x_1^*, x_2^*, x_3^*)$ where $x_1^* > 0, x_2^* > 0$ and $x_3^* > 0$.

Lemma 3.10. *F^*, if it exists, is always a stable node.*

Proof. The Jacobian matrix at F^* is

$$J^* = \begin{bmatrix} -\frac{\partial f_1}{\partial s_3}x_1^* - \frac{\partial f_1}{\partial s_1}x_1^* & 0 & -\frac{\partial f_1}{\partial s_3}x_1^* \\ (-\frac{\partial f_2}{\partial s_3} + \frac{\partial f_2}{\partial s_2})x_2^* & -\frac{\partial f_2}{\partial s_2}x_2^* & -\frac{\partial f_2}{\partial s_3}x_2^* \\ -f_3'(s^*)x_3^* & 0 & -f_3'(s^*)x_3^* \end{bmatrix},$$

where the function f_1 is evaluated at $(s^*, s_1^{in} - x_1^*)$ and f_2 is evaluated at $(s^*, s_2^{in} + x_1^* - x_2^*)$. The eigenvalues are

$$-f_3'(s^*)x_3^* < 0, \quad -\frac{\partial f_2}{\partial s_2}x_2^* < 0, \quad -\frac{\partial f_1}{\partial s_3}x_1^* - \frac{\partial f_1}{\partial s_1}x_1^* < 0.$$

Thus F^*, if it exists, is always a stable node. □

3.2. **Summary.** Conditions of existence and uniqueness and the nature of equilibrium points are summarized in Table 1.

Table 1. Condition of existence and uniqueness and the nature of equilibrium points.

Equil.	Existence/uniqueness	Stable node	Saddle point
F^0	always	$D > \max(D_1, D_2, D_3)$	$\min(D_i) < D < \max(D_i)$, $i = 1, 2, 3$
F^1	$D < D_1$	$D > \max(D_7, D_8)$	$D < \max(D_7, D_8)$
F^2	$D < D_2$	$D > \max(D_1, D_3)$	$D < \max(D_1, D_3)$
F^3	$D < D_3$	$D > \max(D_4, D_5)$	$D < \max(D_4, D_5)$
F^{13}	$D < \min(D_3, D_4)$	$D > D_6$	$D < D_6$
F^{23}	$D < \min(D_3, D_5)$	$D > D_4$	$D < D_4$
F^{12}	$D < \min(D_1, D_7)$	$D > D_8$	$D < D_8$
F^*	$D < \min(D_3, D_4, D_6)$	always	

3.3. **Global analysis.** In the following, we consider only the case when

(A11) $D < \min(D_2, D_4, D_8)$

This hypothesis guarantees that $D < \min(D_1, D_2, D_3, D_4, D_5, D_6, D_7, D_8)$ which ensure the existence of F^*, the only stable node for the system (3.1). F^1, F^2, F^3, F^{12}, F^{13} and F^{23} are saddle points. F^0 is an unstable node.

Remark 3.11. Consider a solution of system (2.2) belonging to Ω. Consider the transformation of the system (2.2) through the change of variables $\eta_i = \ln(x_i)$, $i = 1, 2, 3$. Then one gets the new system

$$\begin{gathered}
\dot\eta_1 = h_1(\eta_1, \eta_2, \eta_3) := f_1(s_3^{in} - e^{\eta_1} - e^{\eta_3}, s_1^{in} - e^{\eta_1}) - D\,, \\
\dot\eta_2 = h_2(\eta_1, \eta_2, \eta_3) := f_2(s_3^{in} - e^{\eta_1} - e^{\eta_3}, s_2^{in} + e^{\eta_1} - e^{\eta_2}) - D\,, \\
\dot\eta_3 = h_3(\eta_1, \eta_2, \eta_3) := f_3(s_3^{in} - e^{\eta_1} - e^{\eta_3}) - D\,.
\end{gathered} \tag{3.8}$$

We have

$$\frac{\partial h_1}{\partial \eta_1} + \frac{\partial h_2}{\partial \eta_2} + \frac{\partial h_3}{\partial \eta_3} = -\Big(\frac{\partial f_1}{\partial s_3} e^{\eta_1} + \frac{\partial f_1}{\partial s_1} e^{\eta_1} + \frac{\partial f_2}{\partial s_2} e^{\eta_2} + f_3' e^{\eta_3}\Big) < 0.$$

From Dulac criterion [6], the system (3.8) has no invariant sets (including tori) with no-zero volume wholly inside Ω. If there is a strange attractor it must be (typically) a fractal set with zero volume. Note that periodic orbits (of zeros volume) are not excluded.

- $\frac{\partial h_1}{\partial \eta_1} + \frac{\partial h_2}{\partial \eta_2} = -\big(\frac{\partial f_1}{\partial s_3} e^{\eta_1} + \frac{\partial f_1}{\partial s_1} e^{\eta_1} + \frac{\partial f_2}{\partial s_2} e^{\eta_2}\big) < 0$. From Dulac criterion [6], then the system (2.2) has no periodic trajectory in the plane x_1x_2 ($x_3 = 0$).
- $\frac{\partial h_1}{\partial \eta_1} + \frac{\partial h_3}{\partial \eta_3} = -\big(\frac{\partial f_1}{\partial s_3} e^{\eta_1} + \frac{\partial f_1}{\partial s_1} e^{\eta_1} + f_3' e^{\eta_3}\big) < 0$. From Dulac criterion [6], then the system (2.2) has no periodic trajectory in the plane x_1x_3 ($x_2 = 0$).
- $\frac{\partial h_2}{\partial \eta_2} + \frac{\partial h_3}{\partial \eta_3} = -\big(\frac{\partial f_2}{\partial s_2} e^{\eta_2} + f_3' e^{\eta_3}\big) < 0$. From Dulac criterion [6], then the system (2.2) has no periodic trajectory in the plane x_2x_3 ($x_1 = 0$).

Theorem 3.12. *For every initial conditions $x_1(0) > 0, x_2(0) > 0, x_3(0) > 0$ in $\mathcal{S}$, three species coexist i.e.*

$$\lim_{t\to+\infty} x_1(t) > 0, \quad \lim_{t\to+\infty} x_2(t) > 0, \quad \lim_{t\to+\infty} x_3(t) > 0.$$

Proof. Let $x_1(0) > 0$, $x_2(0) > 0$, $x_3(0) > 0$, and let ω the ω-limit set of $(x_1(0), x_2(0), x_3(0))$ which is compact and invariant such that $\omega \subset \bar{\mathcal{S}}$. Suppose that ω contains a point M on the boundary of the positive cone $\mathbb{R}^3_+$ then:

- As F^0 is an unstable node then F^0 can't be a part of the ω-limit set of $(x_1(0), x_2(0), x_3(0))$, and thus M can not be F^0.
- If $M \in]\bar{x}_1, s_1^{in}] \times \{0\} \times \{0\}$ (similarly $M \in \{0\} \times]\bar{x}_2, s_2^{in}] \times \{0\}$ or $M \in \{0\} \times \{0\} \times]s_3^{in} - s^*, s_3^{in}]$). As ω is invariant then $\gamma(M) \subset \omega$ and this is impossible because ω is bounded and $\gamma(M) =]\bar{x}_1, +\infty[\times \{0\} \times \{0\}$ (similarly $\gamma(M) = \{0\} \times]\bar{x}_2, +\infty[\times \{0\}$ or $\gamma(M) = \{0\} \times \{0\} \times]s_3^{in} - s^*, +\infty[$).
- If $M \in]0, \bar{x}_1[\times \{0\} \times \{0\}$ (similarly $M \in \{0\} \times]0, \bar{x}_2[\times \{0\}$ or $M \in \{0\} \times \{0\} \times]0, s_3^{in} - s^*[$). ω contains $\gamma(M) =]0, \bar{x}_1[\times \{0\} \times \{0\}$ (similarly $\gamma(M) = \{0\} \times]0, \bar{x}_2[\times \{0\}$ or $\gamma(M) = \{0\} \times \{0\} \times]0, s_3^{in} - s^*[$). As ω is a compact, then it contains the adherence of $\gamma(M)$, $[0, \bar{x}_1] \times \{0\} \times \{0\}$ (similarly $\{0\} \times [0, \bar{x}_2] \times \{0\}$ or $\{0\} \times \{0\} \times [0, s_3^{in} - s^*]$). In particular, ω contains F^0 and this is impossible.
- If $M = F^1$ (similarly $M = F^2$ or $M = F^3$). ω is not reduced to F^1 (similarly to F^2 or to F^3). By Butler-McGehee theorem, ω contains a point P of $(0, +\infty) \times \{0\} \times \{0\}$ other that F^1 (similarly of $\{0\} \times (0, +\infty) \times \{0\}$ other that F^2 or $\{0\} \times \{0\} \times (0, +\infty)$ other that F^3) and this is impossible.
- If $M \in]\bar{x}_1, s_1^{in}] \times \{0\} \times]s_3^{in} - s^*, s_3^{in}]$ (similarly $M \in \{0\} \times]\bar{x}_2, s_2^{in}] \times]s_3^{in} - s^*, s_3^{in}]$ or $M \in]\bar{x}_1, s_1^{in}] \times]\bar{x}_2, s_2^{in}] \times \{0\}$). As ω is invariant then $\gamma(M) \subset \omega$ and this is impossible because ω is bounded and $\gamma(M) =]\bar{x}_1, +\infty[\times \{0\} \times]s_3^{in} - s^*, +\infty[$ (similarly $\gamma(M) = \{0\} \times]\bar{x}_2, +\infty[\times]s_3^{in} - s^*, +\infty[$ or $\gamma(M) =]\bar{x}_1, +\infty[\times]\bar{x}_2, +\infty[\times \{0\}$).
- If $M \in]\bar{x}_1, s_1^{in}] \times \{0\} \times]0, s_3^{in} - s^*[$ (similarly $M \in]0, \bar{x}_1[\times \{0\} \times]s_3^{in} - s^*, s_3^{in}]$ or $M \in \{0\} \times]\bar{x}_2, s_2^{in}] \times]0, s_3^{in} - s^*[$ or $M \in \{0\} \times]0, \bar{x}_2[\times]s_3^{in} - s^*, s_3^{in}]$ or $M \in]\bar{x}_1, s_1^{in}] \times]0, \bar{x}_2[\times \{0\}$ or $M \in]0, \bar{x}_1[\times]\bar{x}_2, s_2^{in}] \times \{0\}$). As ω is invariant then $\gamma(M) \subset \omega$ which is impossible because ω is bounded and $\gamma(M) =]\bar{x}_1, +\infty[\times \{0\} \times]0, s_3^{in} - s^*[$ (similarly $\gamma(M) =]0, \bar{x}_1[\times \{0\} \times]s_3^{in} - s^*, +\infty[$ or $\gamma(M) = \{0\} \times]\bar{x}_2, +\infty[\times]0, s_3^{in} - s^*[$ or $\gamma(M) = \{0\} \times]0, \bar{x}_2[\times]s_3^{in} - s^*, +\infty[$ or $\gamma(M) =]\bar{x}_1, +\infty[\times]0, \bar{x}_2[\times \{0\}$ or $\gamma(M) =]0, \bar{x}_1[\times]\bar{x}_2, +\infty[\times \{0\}$).
- If $M \in]0, \bar{x}_1[\times \{0\} \times]0, s_3^{in} - s^*[$ (similarly $M \in \{0\} \times]0, \bar{x}_2[\times]0, s_3^{in} - s^*[$ or $M \in]0, \bar{x}_1[\times]0, \bar{x}_2[\times \{0\}$). ω contains $\gamma(M) =]0, \bar{x}_1[\times \{0\} \times]0, s_3^{in} - s^*[$ (similarly $\gamma(M) = \{0\} \times]0, \bar{x}_2[\times]0, s_3^{in} - s^*[$ or $\gamma(M) =]0, \bar{x}_1[\times]0, \bar{x}_2[\times \{0\}$). As ω is a compact, then it contains the adherence of $\gamma(M)$, $[0, \bar{x}_1] \times \{0\} \times [0, s_3^{in} - s^*]$ (similarly $\{0\} \times [0, \bar{x}_2] \times [0, s_3^{in} - s^*]$ or $[0, \bar{x}_1] \times [0, \bar{x}_2] \times \{0\}$). In particular, ω contains F^0 and this is impossible.

If $M = F^{13}$ (similarly $M = F^{23}$ or $M = F^{12}$). ω is not reduced to F^{13} (similarly to F^{23} or to F^{12}). By Butler-McGehee theorem, ω contains a point P of $(0, +\infty) \times \{0\} \times (0, +\infty)$ other that F^{13} (similarly of $\{0\} \times (0, +\infty) \times (0, +\infty)$ other that F^{23} or $(0, +\infty) \times (0, +\infty) \times \{0\}$ other that F^{12}) and this is impossible.

No points on the boundary of the positive cone $\mathbb{R}^3_+$ can be inside the ω-limit set. System (3.1) has possible "positive" periodic orbit inside $\mathcal{S}$. Using the Poincaré-Bendixon Theorem [6], the solution of system (3.1) converge asymptotically either to the unique stable node F^* or to a "positive" periodic orbit (if it exists) such that

$$\lim_{t \to +\infty} x_1(t) > 0, \quad \lim_{t \to +\infty} x_2(t) > 0, \quad \lim_{t \to +\infty} x_3(t) > 0.$$

□

4. Back to $\mathbb{R}^6_+$

Theorem 4.1. *Consider the system* (2.2) *under Assumptions* (A6)–(A11). *For every initial conditions* $s_1(0) > 0$, $s_2(0) > 0$, $s_3(0) > 0$, $x_1(0) > 0$, $x_2(0) > 0$, $x_3(0) > 0$ *in* $\mathbb{R}^6_+$, *three species coexist i.e.*

$$\lim_{t\to+\infty} x_1(t) > 0, \quad \lim_{t\to+\infty} x_2(t) > 0, \quad \lim_{t\to+\infty} x_3(t) > 0.$$

Proof. Let $(s_1(t), x_1(t), s_2(t), x_2(t), s_3(t), x_3(t))$ be a solution of (2.2). From (2.3), (2.4) and (2.5) we deduce that

$$\begin{gathered} s_1(t) = s_1^{in} - x_1(t) + K_1 e^{-Dt}, \\ s_2(t) = s_2^{in} + x_1(t) - x_2(t) + K_3 e^{-Dt}, \\ s_3(t) = s_3^{in} - x_1(t) - x_3(t) + K_2 e^{-Dt}, \end{gathered} \tag{4.1}$$

where $K_1 = s_1(0) + x_1(0) - s_1^{in}$, $K_2 = x_1(0) + x_3(0) - s_3^{in}$ and $K_3 = -s_3^{in} - x_1(0) + x_2(0)$. Hence $(x_1(t), x_2(t), x_3(t))$ is a solution of the non-autonomous system of three differential equations:

$$\begin{gathered} \dot{x}_1 = \Big(f_1(s_3^{in} - x_1 - x_3 + K_2 e^{-Dt}, s_1^{in} - x_1 + K_1 e^{-Dt}) - D\Big)x_1\,, \\ \dot{x}_2 = \Big(f_2(s_3^{in} - x_1 - x_3 + K_2 e^{-Dt}, s_2^{in} + x_1 - x_2 + K_3 e^{-Dt}) - D\Big)x_2\,, \\ \dot{x}_3 = \Big(f_3(s_3^{in} - x_1 - x_3 + K_2 e^{-Dt}) - D\Big)x_3\,. \end{gathered} \tag{4.2}$$

This system is an asymptotically autonomous differential system converging to the autonomous system (3.1). Note that Ω is an attractor of all trajectories in $\mathbb{R}^6_+$ and that the phase portrait of the reduced (to Ω) system (3.1) contains only one locally stable node, one unstable node, and six saddle points and possible "positive" periodic trajectory. Thus applying Themes's results [7] and concluding that the asymptotic behavior of solution of system (4.2) is the same as the one of solution of the reduced system (3.1). The result is then deduced. □

5. Numerical example

In this section we consider growth functions

$$\begin{gathered} f_1(s_3, s_1) = \frac{m_1 s_1 s_3}{(K_1 + s_1)(L_1 + s_3)}, \quad f_2(s_3, s_2) = \frac{m_2 s_2}{(K_2 + s_2)(L_2 + s_3)}, \\ f_3(s_3) = \frac{m_3 s_3}{L_3 + s_3}. \end{gathered} \tag{5.1}$$

These functions are currently used in biotechnology where the growth of a species is limited by one or more than one substrates. One can easily check that (5.1) satisfy the given Assumptions (A6) to (A10).

Table 2. Parameters for (5.1)

Parameter	D	m_1	K_1	L_1	m_2	K_2	L_2	m_3	L_3	s_1^{in}	s_2^{in}	s_3^{in}
Value	1	3	1	1	12	1	1	4	3	5	5	5

D_1	D_2	D_3	D_4	D_5	D_6	D_7	D_8
$\frac{75}{36}$	$\frac{60}{36}$	$\frac{20}{8}$	$\frac{15}{12}$	15	$\frac{16}{3}$	4.545	1.251

Note that $D = 1 < \min(D_2, D_4, D_8)$. As it is shown in Figure 1, all trajectories inside the whole positive cone $\mathbb{R}_+^3$ converge to the positive equilibrium point $(x_1^*, x_2^*, x_3^*) = (3, 7.8, 1)$ corresponding to the persistence of the three bacteria.

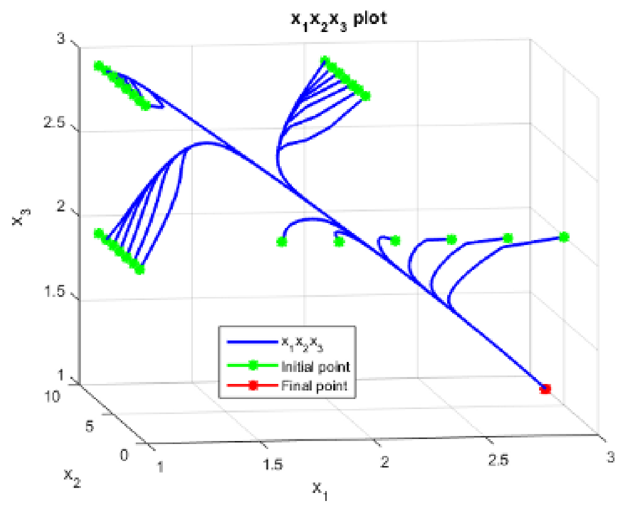

Figure 2. The $x_1x_2x_3$ behavior.

Conclusion. A mathematical model involving a three-tiered microbial food web without maintenance was proposed. A detailed qualitative analysis is carried out. The local stability analysis of the equilibria are performed. It is concluded from this study that, under general and natural assumptions of monotonicity on the growth rates, the asymptotic persistence of the three bacteria is guaranteed.

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