

Mathematical Investigation for Two-Bacteria Competition in Presence of a Pathogen With Leachate Recirculation

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Abstract. This paper provides a thorough exploration of two-species competition in a continuous bioreactor when adding a pathogen that affects only one species and with leachate recirculation inside the reactor. The dynamics is modelled by a well-constructed system of nonlinear differential equations extending the classical model of the chemostat by adding more realism, enhancing its applicability. The nonnegativity and boundedness of trajectories, the determination of steady states and their local stability strengthens the credibility of the proposed system. The global stability analysis was conducted using uniform persistence theory. The coexistence of both species under somewhat natural assumptions is a key finding, contradicting the well-known competitive exclusion principle. Several numerical examples offer a practical demonstration of the theoretical concepts.

1. INTRODUCTION

In recent years, a new waste treatment system has appeared: the bioreactor (Figure 1). This concept consists of accelerating the decomposition and therefore the stabilization of waste thanks to a controlled supply of humidity within the waste mass. To do this, leachate collected at the bottom of the bin is injected into the waste mass. This recirculation is done by vertical wells or horizontal drains. The advantages of bioreactors are multiple: an acceleration of the degradation of waste, a reduction in the stabilization time of waste and therefore a reduction in the post-operation period as well as long-term environmental risks (pollution of groundwater or release of gases with greenhouse), finally increased and accelerated biogas production, which allows it to be better exploited [1]. The technological challenge of the bioreactor is to find a way to control and quantify the diffusion of the injected leachate in order to obtain optimal humidity

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throughout the waste. It is generally accepted that the recirculation of leachate in household waste storage centers promotes bacterial activity by providing moisture and nutrients and thus makes it possible to reduce the stabilization time of the landfill and its operating costs [2]. In addition, by activating the biodegradation of waste, the pollutant load of recirculated leachate is reduced and the production of energy-recoverable biogas is increased [3].

In this study, we consider a bacterial competition of two different bacteria growing on an essential nutriment. This competition is modelled by the classical chemostat model which predicts the competitive exclusion principle predicting the survive of at most one bacteria species. In our case, we consider the necessary assumption such that bacteria 1 will be the winner. The main contribution in this study is to add both, a pathogen that affects only bacteria 1 and we assume that the nutriment is present into two forms, insoluble nutriment (N_1) and soluble nutriment (N_2) and by considering the leachate recirculation, a part of the insoluble nutriment is transformed into soluble one as given in [4]. The proposed mathematical model is constructed of five-dimensional system of nonlinear ordinary differential equations where the growth, solubilization and hydrolysis rates are all of them general increasing functions. The system was reduced to a one of three ordinary differential equations. We calculated the steady states and we discussed their local stability. The global stability analysis for both reduced and original systems was conducted using uniform persistence theory. The main finding in this study is the coexistence of both bacteria under somewhat natural general assumptions. This finding contradicts the well-known competitive exclusion principle.

2. MATHEMATICAL MODEL

Leachate recirculation is an effective methods increasing organic matter conversion and improve bioprocess stability in a bioreactor [5,6]. The rate of microbial degradation increases with the organic solution leading to high methane production. In this section we construct the mathematical model predicting a two-bacterial competition influenced by leachate recirculation in the presence of a pathogen affecting only one bacteria. Assume that the nutriment is present into two forms, namely insoluble nutriment (N_1) and soluble nutriment (N_2) and that due to leachate recirculation, the insoluble nutriment is transformed to soluble one. Both forms of nutriment were added to the reactor at the same rate, D at a concentrations N_1^{in} and N_2^{in} , respectively. The two types of bacteria (B_1 and B_2) compete inside the reactor for the nutriment in the presence of a pathogen (P) affecting only the first bacteria (B_1). The culture (N_1, N_2, B_1, B_2, P) inside the bio-reactor is well mixed and continuously removed at a rate D . Note that the role of the leachate recirculation is to transform a major part of the insoluble nutriment (N_1) into a soluble nutriment (N_2).

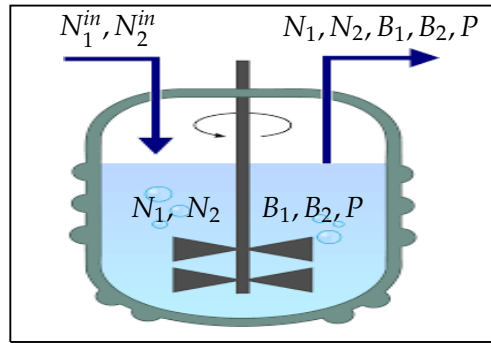


FIGURE 1. A continuous bioreactor to which a nutriment is continuously added at a flow rate D . The nutriment is present in two forms (insoluble nutriment N_1 and soluble nutriment N_2).

The mathematical model that we studied in this article is an extension of previous model studied in [7, 8] by including the influence of leachate recirculation which is already considered in [4, 9–11] with generalised bacteria growth rates. Let $N_1(t)$, $N_2(t)$, $B_1(t)$, $B_2(t)$ and $P(t)$ express the concentrations of insoluble nutriment, soluble nutriment, bacteria 1, bacteria 2 and the pathogen in the reactor at time t .

$$\begin{cases} \dot{N}_1 &= D(N_1^{in} - N_1) - h(u)g(N_1), \\ \dot{N}_2 &= D(N_2^{in} - N_2) + h(u)g(N_1) - \frac{f_1(N_2)}{Y_1}B_1 - \frac{f_2(N_2)}{Y_2}B_2, \\ \dot{B}_1 &= f_1(N_2)B_1 - DB_1 - \alpha PB_1, \\ \dot{B}_2 &= f_2(N_2)B_2 - DB_2, \\ \dot{P} &= k\alpha PB_1 - DP. \end{cases} \quad (2.1)$$

Here initial conditions satisfy $N_1(0) \geq 0$, $N_2(0) \geq 0$ while $B_1(0) > 0$, $B_2(0) > 0$ and $P(0) > 0$. D is the dilution rate and N_1^{in} and N_2^{in} are the input concentrations, which are positive constants. Y_1 and Y_2 denote the soluble nutriment-to-bacteria 1 and soluble nutriment-to-bacteria 2 yields, respectively. f_1 and f_2 are the growth rates of bacteria 1 and bacteria 2, respectively.

A diagram explaining the interactions between components of the proposed mathematical model is given in Figure 2. A part of the insoluble nutriment N_1 is transformed into soluble one at a rate of solubilization given by $h(u)g(N_1)$ where u is the leachate recirculation rate. Both forms of nutriment are added continuously with a same rate, D . The soluble nutriment N_2 was consumed by both type of bacteria B_1 and B_2 with growth rates $f_1(N_2)$ and $f_2(N_2)$, respectively. The pathogen P affects only the bacteria B_1 with an incidence rate αPB_1 . All compartment are removed from the chemostat at the same dilution rate, D . Note that natural mortality rates were neglected with respect to the dilution rate.

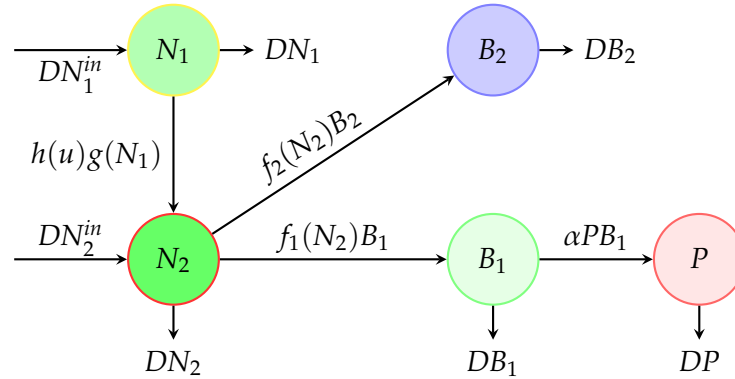


FIGURE 2. Two bacterial competition in a continuous bioreactor in presence of a one bacteria pathogen under the influence of leachate recirculation [12].

The system (2.1) can be simplified by using the change of variable given by $n_1 = N_1, n_2 = N_2, n_1^{in} = N_1^{in}, n_2^{in} = N_2^{in}, b_1 = \frac{B_1}{Y_1}, b_2 = \frac{B_2}{Y_2}, p = \alpha P$, and $\eta = k\alpha Y_1$. Therefore, the simplified system is given by

$$\begin{cases} \dot{n}_1 = -h(u)g(n_1) + D(n_1^{in} - n_1), \\ \dot{n}_2 = h(u)g(n_1) - f_1(n_2)b_1 - f_2(n_2)b_2 + D(n_2^{in} - n_2), \\ \dot{b}_1 = f_1(n_2)b_1 - Db_1 - pb_1, \\ \dot{b}_2 = f_2(n_2)b_2 - Db_2, \\ \dot{p} = \eta pb_1 - Dp. \end{cases} \quad (2.2)$$

f_1, f_2, g and h are non-negative C^1 functions satisfying the following assumption.

Assumption 2.1. $f_1, f_2, g, h : \mathbb{R}_+ \rightarrow \mathbb{R}_+$ C^1 functions such that

- f_1 and f_2 are increasing functions such that $f_1(0) = f_2(0) = 0$ and $f_1(n_2) > f_2(n_2)$ for all $n_2 \in (0, n_1^{in} + n_2^{in})$. A typical example is given in Figure 3.
- g and h are increasing functions such that $g(0) = h(0) = 0$.

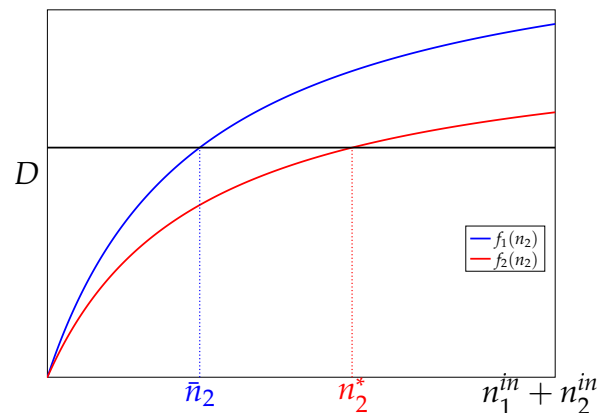


FIGURE 3. Bacterial growth rates with $\bar{n}_2 < n_2^* < n_1^{in} + n_2^{in}$.

3. PRELIMINARY RESULTS

We start by giving some basic results for the dynamics (2.2) which are useful for the rest of the analysis.

Lemma 3.1. *Under Assumption 2.1, then there exists a unique $n_1^* \in (0, n_1^{in})$ satisfying*

$$h(u)g(n_1^*) = D(n_1^{in} - n_1^*) . \tag{3.1}$$

Proof. Let $\psi(n_1) = D(n_1^{in} - n_1) - h(u)g(n_1)$ then $\psi'(n_1) = -D - h(u)g'(n_1) < 0$, $\psi(0) = Dn_1^{in} > 0$, $\psi(n_1^{in}) = -h(u)g(n_1^{in}) < 0$ and the continuous function ψ is increasing. Thus, there exists a unique $n_1^* \in (0, n_1^{in})$ satisfying (3.1). \square

Assumption 3.1. *The function f_2 satisfies $f_2(n_1^{in} + n_2^{in} - n_1^*) > D$.*

Lemma 3.2. *Under Assumptions 2.1 and 3.1, then there exist a unique $\tilde{n}_2 \in (0, n_1^{in} + n_2^{in} - n_1^*)$ satisfying*

$$f_1(\tilde{n}_2) = D . \tag{3.2}$$

Proof. It is evident since $f_1(0) = 0$, $f_1(n_1^{in} + n_2^{in} - n_1^*) > f_2(n_1^{in} + n_2^{in} - n_1^*) > D$ and f_1 is a continuous increasing function. \square

Lemma 3.3. *Under Assumptions 2.1 and 3.1, then there exists a unique $\tilde{n}_2 \in (0, n_1^{in} + n_2^{in} - n_1^*)$ satisfying*

$$f_1(\tilde{n}_2) + \eta(n_1^* + \tilde{n}_2 - n_1^{in} - n_2^{in}) = 0 . \tag{3.3}$$

Proof. Let the function $f(n_2) = f_1(n_2) + \eta(n_1^* + n_2 - n_1^{in} - n_2^{in})$. Then $f(0) = -\eta(n_1^{in} + n_2^{in} - n_1^*) < 0$, $f(n_1^{in} + n_2^{in} - n_1^*) = f_1(n_1^{in} + n_2^{in} - n_1^*) > 0$ and $f'(n_2) = f_1'(n_2) + \eta > 0$. Thus, there exists a unique $\tilde{n}_2 \in (0, n_1^{in} + n_2^{in} - n_1^*)$ such that $f(\tilde{n}_2) = 0$. \square

Lemma 3.4. *Under Assumptions 2.1 and 3.1, then there exist a unique $n_2^* \in (0, n_1^{in} + n_2^{in} - n_1^*)$ satisfying*

$$f_2(n_2^*) = D . \tag{3.4}$$

Proof. It is evident since $f_2(0) = 0$, $f_2(n_1^{in} + n_2^{in} - n_1^*) > D$ and f_2 is a continuous increasing function. \square

Let us define some parameters as follows: $b_2^* = n_1^{in} + n_2^{in} - n_1^* - n_2^* - \frac{f_1(n_2^*)}{\eta} > 0$, $\tilde{p} = f_1(\tilde{n}_2) - D > 0$ and $p^* = f_1(n_2^*) - D > 0$.

Lemma 3.5. $\tilde{n}_2 < n_2^* < \tilde{n}_2$.

Proof. Since $f_1(\tilde{n}_2) = D + \tilde{p} > D = f_1(\tilde{n}_2)$ then $\tilde{n}_2 < \tilde{n}_2$. Since $D = f_1(\tilde{n}_2) = f_2(n_2^*) < f_1(n_2^*)$ therefore $\tilde{n}_2 < n_2^*$. Since n_2^* satisfies $f_1(n_2^*) + \eta b_2^* = \eta(n_1^{in} + n_2^{in} - n_1^* - n_2^*)$ then $f(n_2^*) = f_1(n_2^*) + \eta(n_1^* + n_2^* - n_1^{in} - n_2^{in}) < 0 = f(\tilde{n}_2)$ then $n_2^* < \tilde{n}_2$. Thus, we conclude that $\tilde{n}_2 < n_2^* < \tilde{n}_2$. \square

Lemma 3.6. $D < f_1(n_2^*) < \eta(n_1^{in} + n_2^{in} - n_1^* - \tilde{n}_2)$.

Proof. Since $\bar{n}_2 < n_2^* < \tilde{n}_2 < n_1^{in} + n_2^{in} - n_1^*$ and by Assumption 2.1, we obtain $D = f_1(\bar{n}_2) < f_1(n_2^*)$ and $f_1(n_2^*) < f_1(\tilde{n}_2) = \eta(n_1^{in} + n_2^{in} - n_1^* - \tilde{n}_2) < \eta(n_1^{in} + n_2^{in} - n_1^* - n_2^*) < \eta(n_1^{in} + n_2^{in} - n_1^* - \bar{n}_2)$. \square

The dynamics (2.2) is defined on the non-negative cone, thus, we give some classical properties (see other examples in [13–20]).

Proposition 3.1. *One has*

- (1) *Solutions of system (2.2) are defined for any positive time and stay non-negative and bounded.*
- (2) *The attractor set $\Sigma = \{(n_1, n_2, b_1, b_2, p) \in \mathbb{R}_+^5 \mid n_1 + n_2 + b_1 + b_2 + \frac{p}{\eta} = n_1^{in} + n_2^{in}\}$ is a positively invariant of all trajectory of the dynamics (2.2) inside the non-negative cone.*

Proof. (1) \mathbb{R}_+^5 is invariant since we have: $n_1(t) = 0 \Rightarrow \dot{n}_1(t) = Dn_1^{in} > 0$, $n_2(t) = 0 \Rightarrow \dot{n}_2(t) = h(u)g(n_1) + Dn_2^{in} > 0$, $b_i(t) = 0 \Rightarrow \dot{b}_i(t) = 0$ for $i = 1, 2$ and $p(t) = 0 \Rightarrow \dot{p}(t) = 0$.

Consider the variable $T(t) = n_1(t) + n_2(t) + b_1(t) + b_2(t) + \frac{p(t)}{\eta} - n_1^{in} - n_2^{in}$. By summing the five equations of system (2.2), we obtain a single equation:

$$\dot{T}(t) = -DT(t), \quad (3.5)$$

from which one deduces

$$n_1(t) + n_2(t) + b_1(t) + b_2(t) + \frac{p(t)}{\eta} = n_1^{in} + n_2^{in} + T_0 e^{-Dt}$$

with

$$T_0 = n_1(0) + n_2(0) + b_1(0) + b_2(0) + \frac{p(0)}{\eta} - n_1^{in} - n_2^{in}.$$

Since all terms of T are non-negative, we conclude that the trajectory is bounded.

- (2) It is a direct consequence of equation (3.5). \square

We use the same notation of the steady states as the ones given in [7, 21]. Formally, let E, E_1, E_2, E_1^1 and $E_{1,2}^1$ be the five equilibria of the dynamics (2.2) on Σ :

$$\begin{aligned} E &= (n_1^*, n_1^{in} + n_2^{in} - n_1^*, 0, 0, 0), \quad E_1 = (n_1^*, \bar{n}_2, n_1^{in} + n_2^{in} - n_1^* - \bar{n}_2, 0, 0), \\ E_2 &= (n_1^*, n_2^*, 0, n_1^{in} + n_2^{in} - n_1^* - n_2^*, 0), \quad E_1^1 = \left(n_1^*, \bar{n}_2, \frac{D}{\eta}, 0, \bar{p}\right), \quad E_{1,2}^1 = \left(n_1^*, n_2^*, \frac{D}{\eta}, b_2^*, p^*\right). \end{aligned}$$

4. REDUCTION TO A THIRD DIMENSIONAL DYNAMICS

Lemma 4.1. *Consider a solution (n_1, n_2, b_1, b_2, p) of dynamics (2.2). Let*

$$\beta_1 = n_1 - n_1^*, \quad \beta_2 = n_1^{in} + n_2^{in} - n_1 - n_2 - b_1 - b_2 - \frac{p}{\eta} = n_1^{in} + n_2^{in} - n_1^* - n_2 - b_1 - b_2 - \frac{p}{\eta} - \beta_1. \quad (4.1)$$

Then, we obtain

$$\begin{cases} \dot{\beta}_1 & \leq -D\beta_1, \\ \dot{\beta}_2 & = -D\beta_2, \end{cases} \quad (4.2)$$

and

$$\begin{cases} \dot{b}_1 &= f_1(n_1^{in} + n_2^{in} - n_1^* - b_1 - b_2 - \frac{p}{\eta} - \beta_1 - \beta_2)b_1 - Db_1 - pb_1, \\ \dot{b}_2 &= f_2(n_1^{in} + n_2^{in} - n_1^* - b_1 - b_2 - \frac{p}{\eta} - \beta_1 - \beta_2)b_2 - Db_2, \\ \dot{p} &= \eta pb_1 - Dp. \end{cases} \quad (4.3)$$

Proof. We omit the prove of lemma 4.1 since it is evident. □

Solutions of the five-dimensional dynamics (2.2) converge toward Σ . Therefore, it is sufficient to restrict the analysis of the system (2.2) to Σ which will be informative for the dynamics (2.2) on \mathbb{R}_+^5 according to [22] (see [14,23] for other examples). The reduced model of (2.2) on Σ is

$$\begin{cases} \dot{b}_1 &= f_1(n_1^{in} + n_2^{in} - n_1^* - b_1 - b_2 - \frac{p}{\eta})b_1 - Db_1 - pb_1, \\ \dot{b}_2 &= f_2(n_1^{in} + n_2^{in} - n_1^* - b_1 - b_2 - \frac{p}{\eta})b_2 - Db_2, \\ \dot{p} &= \eta pb_1 - Dp, \end{cases} \quad (4.4)$$

where the variable (b_1, b_2, p) belongs to the three-dimensional set, \mathcal{S} , given hereafter:

$$\mathcal{S} = \left\{ (b_1, b_2, p) \in \mathbb{R}_+^3 : b_1 + b_2 + \frac{p}{\eta} \leq n_1^{in} + n_2^{in} - n_1^* \right\}.$$

Observe that the system (4.4) is obtained by considering the system (4.3) with $\beta_1 = 0$ and $\beta_2 = 0$. Formally, let F, F_1, F_2, F_1^1 and $F_{1,2}^1$ be the five equilibria of the reduced dynamics (4.4) on \mathcal{S} : $F = (0, 0, 0)$, $F_1 = (n_1^{in} + n_2^{in} - n_1^* - \bar{n}_2, 0, 0)$, $F_2 = (0, n_1^{in} + n_2^{in} - n_1^* - n_2^*, 0)$, $F_1^1 = \left(\frac{D}{\eta}, 0, \bar{p}\right)$, and $F_{1,2}^1 = \left(\frac{D}{\eta}, b_2^*, p^*\right)$. Then, one has the following results based on the linearization around the equilibria.

Theorem 4.1. *Under assumptions 2.1 and 3.1, F, F_1, F_2, F_1^1 and $F_{1,2}^1$ exist and are unique. F, F_1, F_2 and F_1^1 are saddle points and $F_{1,2}^1$ is a stable node.*

Proof. The Jacobian matrix of (4.4) at a state (b_1, b_2, p) is

$$J = \begin{bmatrix} -f_1' b_1 + f_1 - D - p & -f_1' b_1 & -\frac{1}{\eta} f_1' b_1 - b_1 \\ -f_2' b_2 & -f_2' b_2 + f_2 - D & -\frac{1}{\eta} f_2' b_2 \\ \eta p & 0 & \eta b_1 - D \end{bmatrix}.$$

where f_1 and f_2 are expressed at $(n_1^{in} + n_2^{in} - n_1^* - b_1 - b_2 - \frac{p}{\eta})$.

(1) The Jacobian matrix of (4.4) at the equilibrium F is

$$J_0 = \begin{bmatrix} f_1(n_1^{in} + n_2^{in} - n_1^*) - D & 0 & 0 \\ 0 & f_2(n_1^{in} + n_2^{in} - n_1^*) - D & 0 \\ 0 & 0 & -D \end{bmatrix}.$$

The eigenvalues are $X_1 = f_1(n_1^{in} + n_2^{in} - n_1^*) - D > 0$, $X_2 = f_2(n_1^{in} + n_2^{in} - n_1^*) - D > 0$ and $X_3 = -D < 0$. Thus, F is a saddle point.

(2) The Jacobian matrix of (4.4) at the equilibrium F_1 is

$$J_1 = \begin{bmatrix} -f_1'(\bar{n}_2)(n_1^{in} + n_2^{in} - n_1^* - \bar{n}_2) & -f_1'(\bar{n}_2)(n_1^{in} + n_2^{in} - n_1^* - \bar{n}_2) & -\left(\frac{f_1'(\bar{n}_2)}{\eta} + 1\right)(n_1^{in} + n_2^{in} - n_1^* - \bar{n}_2) \\ 0 & f_2(\bar{n}_2) - D & 0 \\ 0 & 0 & \eta(n_1^{in} + n_2^{in} - n_1^* - \bar{n}_2) - D \end{bmatrix}.$$

The eigenvalues are given by $X_1 = -f_1'(\bar{n}_2)(n_1^{in} + n_2^{in} - n_1^* - \bar{n}_2) < 0$, $X_2 = f_2(\bar{n}_2) - D < 0$ and $X_3 = \eta(n_1^{in} + n_2^{in} - n_1^* - \bar{n}_2) - D > f_1(\bar{n}_2) - D > 0$. Thus, F_1 is a saddle point.

(3) The Jacobian matrix of (4.4) at the equilibrium F_2 is

$$J_2 = \begin{bmatrix} p^* & 0 & 0 \\ -f_2'(n_2^*)(n_1^{in} + n_2^{in} - n_1^* - n_2^*) & -f_2'(n_2^*)(n_1^{in} + n_2^{in} - n_1^* - n_2^*) & -\frac{1}{\eta}f_2'(n_2^*)(n_1^{in} + n_2^{in} - n_1^* - n_2^*) \\ 0 & 0 & -D \end{bmatrix}.$$

The eigenvalues are given by $X_1 = p^* > 0$, $X_2 = -f_2'(n_2^*)(n_1^{in} + n_2^{in} - n_1^* - n_2^*) < 0$ and $X_3 = -D < 0$. Thus, F_2 is a saddle point.

(4) The Jacobian matrix of (4.4) at the equilibrium F_1^1 is

$$J_3 = \begin{bmatrix} -f_1'(\tilde{n}_2)\frac{D}{\eta} & -f_1'(\tilde{n}_2)\frac{D}{\eta} & -\frac{1}{\eta}f_1'(\tilde{n}_2)\frac{D}{\eta} - \frac{D}{\eta} \\ 0 & f_2(\tilde{n}_2) - D & 0 \\ \eta\tilde{p} & 0 & 0 \end{bmatrix},$$

with a characteristic polynomial

$$\begin{aligned} P_3(X) &= \begin{vmatrix} -f_1'\frac{D}{\eta} - X & -f_1'(\tilde{n}_2)\frac{D}{\eta} & -\frac{1}{\eta}f_1'(\tilde{n}_2)\frac{D}{\eta} - \frac{D}{\eta} \\ 0 & f_2(\tilde{n}_2) - D - X & 0 \\ \eta\tilde{p} & 0 & -X \end{vmatrix} \\ &= \left(f_1'(\tilde{n}_2)\frac{D}{\eta} + X\right)(f_2(\tilde{n}_2) - D - X)X + \eta\tilde{p}(f_2(\tilde{n}_2) - D - X)\left(\frac{f_1'(\tilde{n}_2)}{\eta} + 1\right)\frac{D}{\eta} \\ &= (f_2(\tilde{n}_2) - D - X)\left[\left(f_1'(\tilde{n}_2)\frac{D}{\eta} + X\right)X + \eta\tilde{p}\left(\frac{f_1'(\tilde{n}_2)}{\eta} + 1\right)\frac{D}{\eta}\right]. \end{aligned}$$

The first eigenvalue is given by $X_1 = f_2(\tilde{n}_2) - D > 0$. The remained eigenvalues are roots of

$$X^2 + f_1'(\tilde{n}_2)\frac{D}{\eta}X + D\tilde{p} + \tilde{p}f_1'(\tilde{n}_2)\frac{D}{\eta} = 0.$$

Since $f_1'(\tilde{n}_2)\frac{D}{\eta} > 0$ and $D\tilde{p} + \tilde{p}f_1'(\tilde{n}_2)\frac{D}{\eta} > 0$, thus, F_1^1 is a saddle point.

(5) The Jacobian matrix of (4.4) at the equilibrium $F_{1,2}^1$ is

$$J_4 = \begin{bmatrix} -D \frac{f_1'(n_2^*)}{\eta} & -D \frac{f_1'(n_2^*)}{\eta} & -\left(\frac{f_1'(n_2^*)}{\eta} + 1\right) \frac{D}{\eta} \\ -f_2'(n_2^*)b_2^* & -f_2'(n_2^*)b_2^* & -\frac{f_2'(n_2^*)}{\eta} b_2^* \\ \eta p^* & 0 & 0 \end{bmatrix},$$

with a characteristic polynomial

$$\begin{aligned} P_4(X) &= \begin{vmatrix} -D \frac{f_1'(n_2^*)}{\eta} - X & -D \frac{f_1'(n_2^*)}{\eta} & -\left(\frac{f_1'(n_2^*)}{\eta} + 1\right) \frac{D}{\eta} \\ -f_2'(n_2^*)b_2^* & -f_2'(n_2^*)b_2^* - X & -\frac{f_2'(n_2^*)}{\eta} b_2^* \\ \eta p^* & 0 & -X \end{vmatrix} \\ &= \eta p^* \begin{vmatrix} -D \frac{f_1'(n_2^*)}{\eta} & -\left(\frac{f_1'(n_2^*)}{\eta} + 1\right) \frac{D}{\eta} \\ -f_2'(n_2^*)b_2^* - X & -\frac{f_2'(n_2^*)}{\eta} b_2^* \end{vmatrix} - X \begin{vmatrix} -D \frac{f_1'(n_2^*)}{\eta} - X & -D \frac{f_1'(n_2^*)}{\eta} \\ -f_2'(n_2^*)b_2^* & -f_2'(n_2^*)b_2^* - X \end{vmatrix} \\ &= \eta p^* \left[D b_2^* \frac{f_1'(n_2^*)}{\eta} \frac{f_2'(n_2^*)}{\eta} - (f_2'(n_2^*)b_2^* + X) \left(\frac{f_1'(n_2^*)}{\eta} + 1\right) \frac{D}{\eta} \right] \\ &\quad - X \left[\left(D \frac{f_1'(n_2^*)}{\eta} + X\right) (f_2'(n_2^*)b_2^* + X) - f_1'(n_2^*)f_2'(n_2^*)b_2^* \frac{D}{\eta} \right] \\ &= - \left[X^3 + \left(D \frac{f_1'(n_2^*)}{\eta} + f_2'(n_2^*)b_2^*\right) X^2 + D p^* \left(\frac{f_1'(n_2^*)}{\eta} + 1\right) X + D p^* f_2'(n_2^*)b_2^* \right] \\ &= - \left[X^3 + a_2 X^2 + a_1 X + a_0 \right] \end{aligned}$$

where

$$\begin{cases} a_2 = \left(D \frac{f_1'(n_2^*)}{\eta} + f_2'(n_2^*)b_2^*\right) > 0, \\ a_1 = D p^* \frac{f_1'(n_2^*)}{\eta} + D p^* > 0, \\ a_0 = D p^* f_2'(n_2^*)b_2^* > 0. \end{cases}$$

The conditions of the stability are written as following:

$$a_2 > 0, a_2 a_1 - a_0 > 0, a_0 > 0.$$

Since we have

$$\begin{aligned} a_2 a_1 - a_0 &= \left(D \frac{f_1'(n_2^*)}{\eta} + f_2'(n_2^*)b_2^*\right) \left(D p^* \frac{f_1'(n_2^*)}{\eta} + D p^*\right) - D p^* f_2'(n_2^*)b_2^* \\ &= D p^* f_1'(n_2^*) \frac{D}{\eta} \left(1 + \frac{f_1'(n_2^*)}{\eta}\right) + D p^* f_2'(n_2^*)b_2^* \frac{f_1'(n_2^*)}{\eta} > 0, \end{aligned}$$

Therefore, the steady state $F_{1,2}^1$ is always locally asymptotically stable.

□

5. NON PERIODIC ORBITS ON FACES OF \mathcal{S}

In this section, we aim to prove that there is no possible periodic solution of (4.4) on the faces of \mathcal{S} .

- Let us restrict the dynamics (4.4) on the side of \mathcal{S} where $p = 0$

$$\begin{cases} \dot{b}_1 &= f_1(n_1^{in} + n_2^{in} - n_1^* - b_1 - b_2)b_1 - Db_1, \\ \dot{b}_2 &= f_2(n_1^{in} + n_2^{in} - n_1^* - b_1 - b_2)b_2 - Db_2. \end{cases} \quad (5.1)$$

defined on $\mathcal{S}_{b_1b_2}$ given by

$$\mathcal{S}_{b_1b_2} = \left\{ (b_1, b_2) \in \mathbb{R}_+^2 : b_1 + b_2 \leq n_1^{in} + n_2^{in} - n_1^* \right\}.$$

The axes $b_1 = 0$ and $b_2 = 0$ are invariant. By using the transformation $x_1 = \ln(b_1)$ and $x_2 = \ln(b_2)$ for $b_1, b_2 > 0$, one obtains the following model:

$$\begin{cases} \dot{x}_1 &= h_1(x_1, x_2) := f_1(n_1^{in} + n_2^{in} - n_1^* - e^{x_1} - e^{x_2}) - D, \\ \dot{x}_2 &= h_2(x_1, x_2) := f_2(n_1^{in} + n_2^{in} - n_1^* - e^{x_1} - e^{x_2}) - D. \end{cases} \quad (5.2)$$

We have $\frac{\partial h_1}{\partial x_1} + \frac{\partial h_2}{\partial x_2} = -\left(f_1'(n_1^{in} + n_2^{in} - n_1^* - e^{x_1} - e^{x_2})e^{x_1} + f_2'(n_1^{in} + n_2^{in} - n_1^* - e^{x_1} - e^{x_2})e^{x_2}\right) < 0$. Using the criterion of Dulac [13], dynamics (5.2) (and dynamics (5.1)) has no periodic trajectory. Thus, the system (4.4) has no periodic trajectory in b_1b_2 -face ($p = 0$).

- Let us restrict the dynamics (4.4) on the side of \mathcal{S} where $b_2 = 0$:

$$\begin{cases} \dot{b}_1 &= f_1(n_1^{in} + n_2^{in} - n_1^* - b_1 - \frac{p}{\eta})b_1 - Db_1 - pb_1, \\ \dot{p} &= \eta pb_1 - Dp. \end{cases} \quad (5.3)$$

defined on \mathcal{S}_{b_1p} given by

$$\mathcal{S}_{b_1p} = \left\{ (b_1, p) \in \mathbb{R}_+^2 : b_1 + \frac{p}{\eta} \leq n_1^{in} + n_2^{in} - n_1^* \right\}.$$

The axes $b_1 = 0$ and $p = 0$ are invariant. By using the transformation $x_1 = \ln(b_1)$ and $x_3 = \ln(p)$ for $b_1, p > 0$, one obtains the following model :

$$\begin{cases} \dot{x}_1 &= h_1(x_1, x_3) := f_1(n_1^{in} + n_2^{in} - n_1^* - e^{x_1} - \frac{e^{x_3}}{\eta}) - D - e^{x_3}, \\ \dot{x}_3 &= h_3(x_1, x_3) := \eta e^{x_1} - D. \end{cases} \quad (5.4)$$

We have $\frac{\partial h_1}{\partial x_1} + \frac{\partial h_3}{\partial x_3} = -f_1'(n_1^{in} + n_2^{in} - n_1^* - e^{x_1} - \frac{e^{x_3}}{\eta})e^{x_1} < 0$. Using Dulac criterion [13], the dynamics (5.4) (and dynamics (5.3)) has no periodic trajectory. Thus, the system (4.4) has no periodic trajectory in b_1p -face ($b_2 = 0$).

- Let us restrict the dynamics (4.4) on the side of \mathcal{S} where $b_1 = 0$

$$\begin{cases} \dot{b}_2 &= f_2(n_1^{in} + n_2^{in} - n_1^* - b_2 - \frac{p}{\eta})b_2 - Db_2, \\ \dot{p} &= -Dp. \end{cases} \quad (5.5)$$

defined on \mathcal{S}_{b_2p} given by

$$\mathcal{S}_{b_2p} = \left\{ (b_2, p) \in \mathbb{R}_+^2 : b_2 + \frac{p}{\eta} \leq n_1^{in} + n_2^{in} - n_1^* \right\}.$$

The axes $b_2 = 0$ and $p = 0$ are invariant. By using the transformation $x_2 = \ln(b_2)$ and $x_3 = \ln(p)$ for $b_2, p > 0$, one obtains the following model :

$$\begin{cases} \dot{x}_2 = h_2(x_2, x_3) := f_2(n_1^{in} + n_2^{in} - n_1^* - e^{x_2} - \frac{e^{x_3}}{\eta}) - D, \\ \dot{x}_3 = h_3(x_2, x_3) := -D. \end{cases} \quad (5.6)$$

We have $\frac{\partial h_2}{\partial x_2} + \frac{\partial h_3}{\partial x_3} = -f_2'(n_1^{in} + n_2^{in} - n_1^* - e^{x_2} - \frac{e^{x_3}}{\eta})e^{x_2} < 0$. Using the criterion of Dulac [13], dynamics (5.6) (and dynamics (5.5)) has no periodic trajectory. Thus, dynamics (4.4) has no periodic trajectory in b_2p -face ($b_1 = 0$).

6. UNIFORM PERSISTENCE

In this section, we aim to prove the persistence of both bacteria using the uniform persistence theory when applied to the dynamics (4.4). Since all boundary equilibria of dynamics (4.4) are saddle points, then, we apply a prove given in [24] by using the Butler–McGehee Lemma [13] several times. We start by giving a necessary definition for the uniform persistence [24] and we recall the Butler–McGehee Lemma [13].

Definition 6.1. Let a dynamics $\dot{x} = g(x)$ with $x(0) = x_0$ where $x \in \mathbb{R}^m$ and $g : \mathbb{R}^m \rightarrow \mathbb{R}^m$. The dynamics is called weakly persistent if it satisfies $\limsup_{t \rightarrow +\infty} x(t) > 0$ for all solution having positive initial condition. The dynamics is called persistent if $\liminf_{t \rightarrow +\infty} x(t) > 0$ for all solution having positive initial condition. The dynamics is called uniformly persistent if $\exists \eta$ satisfying $\liminf_{t \rightarrow +\infty} x(t) > \eta$ for all solution having positive initial condition.

Lemma 6.1. (Butler–McGehee Lemma [13]) Consider a continuously differentiable function $g : \mathbb{R}^m \rightarrow \mathbb{R}^m$ and x^* an hyperbolic equilibrium point of the dynamics $\dot{x} = g(x)$ such that $x(0) = x_0 \in \mathbb{R}^m$. Let the positive semi-orbit $\gamma^+(x_0)$ through x_0 and the omega limit set $\omega(x_0)$ of $\gamma^+(x_0)$. Assume that x^* is not the entire omega limit set but it is in $\omega(x_0)$. Then, $\omega(x_0)$ should intersect stable and unstable manifolds of x^* .

Theorem 6.1. Dynamics (4.4) is persistent.

Proof. Faces b_1b_2 , b_1p , and b_2p are invariant. Stable and unstable manifolds of the equilibria on the boundary are identified and are given in Figure 4. Let $\vec{x} = (b_1(t), b_2(t), p(t))$ be a solution with initial condition $\vec{x}(0) = (b_1(0), b_2(0), p(0))$ with $b_1(0), b_2(0)$ and $p(0) > 0$. We aim to prove that the omega limit set has no point on the boundary (with zero coordinate). We a contradiction process:

- Suppose that the omega limit set of $\gamma^+(\vec{x}(0))$ denoted by $\omega(\gamma^+(\vec{x}(0)))$ contains the steady state F . F is a saddle point and its stable manifold $W^s(F)$ is the p -axis of dimension one. Therefore, the entire omega limit set $\omega(\gamma^+(\vec{x}(0)))$ is not reduced to F . By applying Butler–McGehee lemma [13], there exists a point $x^* \neq F$ in $\omega(\gamma^+(\vec{x}(0))) \cap W^s(F)$. $W^s(F)$ is the

p -axis, but the p -axis is unbounded and because all orbits of dynamics (4.4) are bounded with bounded omega limit set, this is a contradiction of the existence of x^* . Therefore, $F \notin \omega(\gamma^+(\vec{x}(0)))$.

- Suppose that the omega limit set $\omega(\gamma^+(\vec{x}(0)))$ contains F_2 . F_2 is a saddle point and its stable manifold $W^s(F_2)$ is the b_2p -plane of dimension two. Therefore, the entire omega limit set $\omega(\gamma^+(\vec{x}(0)))$ is not reduced to $\{F_2\}$. By applying Butler–McGehee lemma [13], there exists a point $x^* \neq F_2$ in $\omega(\gamma^+(\vec{x}(0))) \cap W^s(F_2) \setminus \{F_2\}$. $W^s(F_2)$ lies in the b_2p -plane, and the entire orbit through x^* is inside $\omega(\gamma^+(\vec{x}(0)))$ which is unbounded, this is a contradiction to that F_2 is in $\omega(\gamma^+(\vec{x}(0)))$.
- Suppose that the omega limit set $\omega(\gamma^+(\vec{x}(0)))$ contains F_1 . Similarly as in the cases of F and F_2 , there exists a point $x^* \neq F_1$ in $\omega(\gamma^+(\vec{x}(0))) \cap W^s(F_1) \setminus \{F_1\}$. The stable manifold $W^s(F_1)$ lies entirely in the b_1b_2 -face and it is dimension 2. Then, the entire orbit through x^* in $\omega(\gamma^+(\vec{x}(0)))$ is unbounded and its closure contains F_1 , this is a contradiction to the fact that F_1 is in $\omega(\gamma^+(\vec{x}(0)))$.
- Suppose that the omega limit set $\omega(\gamma^+(\vec{x}(0)))$ contains F_1^1 . Similarly as in the cases of F , F_1 and F_2 , the entire omega limit set $\omega(\gamma^+(\vec{x}(0)))$ should not be reduced to $\{F_1^1\}$; thus, there exists a point $x^* \neq F_1^1$ in $\omega(\gamma^+(\vec{x}(0))) \cap W^s(F_1^1) \setminus \{F_1^1\}$. This point will be in the b_1p -face, and $W^s(F_1^1)$ is of dimension 2 and contained in the b_1p -face. The entire orbit passing through x^* will be in $\omega(\gamma^+(\vec{x}(0)))$. Note that according to Section 5, there is no periodic orbits in the b_1p -face, and since $\{F_1^1\} \notin \omega(\gamma^+(\vec{x}(0)))$, the orbit is unbounded, this is a contradiction to the fact that F_1^1 is in $\omega(\gamma^+(\vec{x}(0)))$.

Let $\hat{x} = (\hat{b}_1(t), \hat{b}_2(t), \hat{p}(t))$ such that at least one components $\hat{b}_1(t)$, $\hat{b}_2(t)$ or $\hat{p}(t)$ is zero and $\hat{x} \in \omega(\gamma^+(\vec{x}(0)))$. Therefore, the entire orbit through \hat{x} will be in $\omega(\gamma^+(\vec{x}(0)))$. Note that the orbit lies entirely in either b_1b_2 , b_2p , or b_1p face, and then it will converge to one of the boundary equilibria. Thus, this equilibrium is in $\omega(\gamma^+(\vec{x}(0)))$, and this is a contradiction to the fact that all boundary equilibria are saddle points. Thus, components of the solution should be greater than zero, and then we obtain

$$\liminf_{t \rightarrow \infty} b_1(t) > 0, \quad \liminf_{t \rightarrow \infty} b_2(t) > 0 \quad \text{and} \quad \liminf_{t \rightarrow \infty} p(t) > 0,$$

and the dynamics (4.4) is persistent (see [24] (Section 4.3) for another application). \square

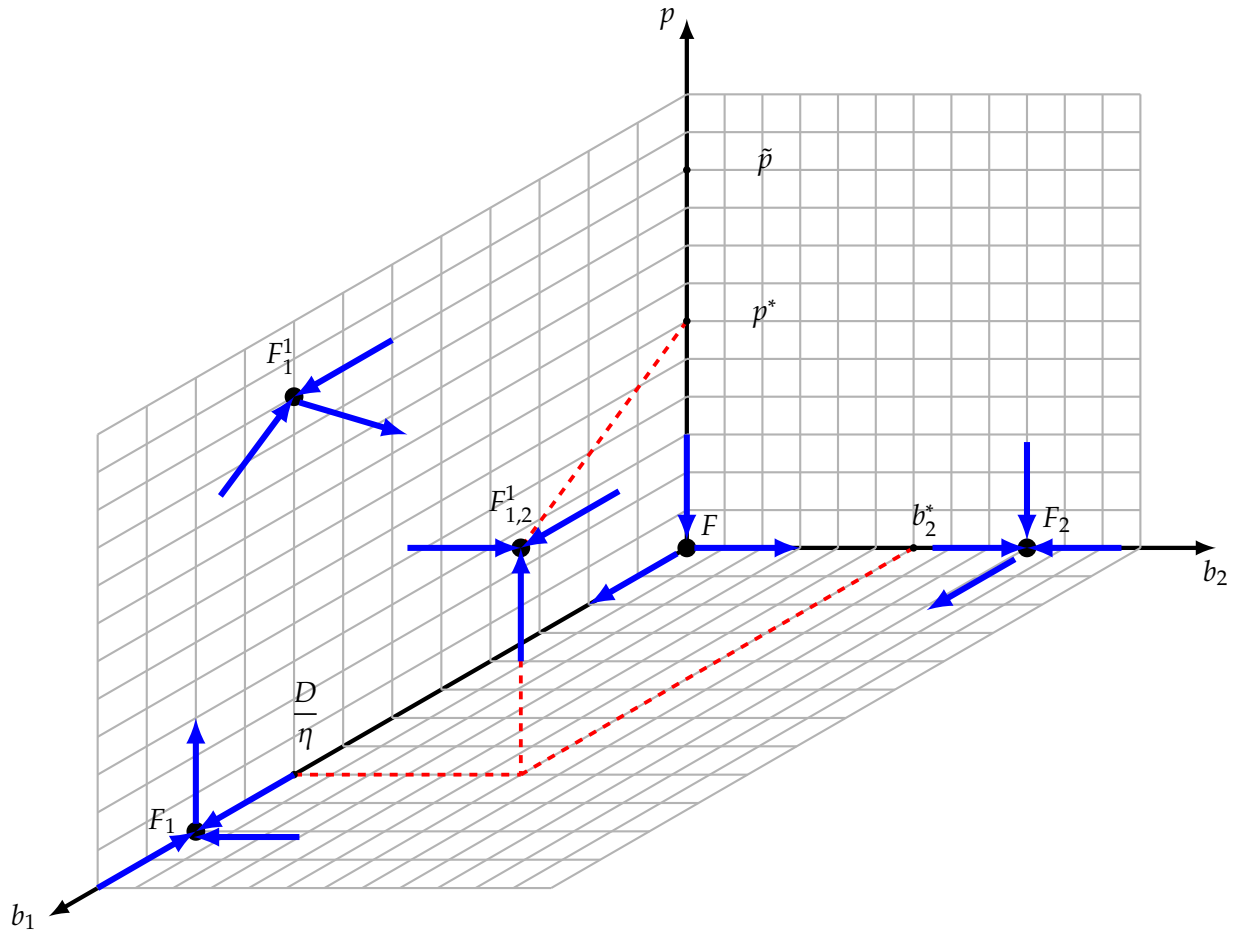


FIGURE 4. Steady states configuration. F, F_1, F_2 , and F_1^1 are saddle points, however, $F_{1,2}^1$ is an asymptotically stable steady state.

7. UNIFORM PERSISTENCE OF THE REDUCED SYSTEM

In this section. we aim to prove that the dynamics (4.4) is uniformly persistent. We used an essential theory given in [25] that consider a dynamics \mathcal{D} such that \mathbb{R}_+^3 and $\partial\mathbb{R}_+^3$ are invariant. Let $\partial\mathcal{D}$ be the restriction of \mathcal{D} to $\partial\mathbb{R}_+^3$. Therefore, \mathcal{D} is uniformly persistent under constraints [25]. Let \mathcal{D} be the dynamics on Σ defined in Proposition 3.1. $\partial\Sigma$ is not invariant, however, the result in [25], as used in [24,26], could be used when $\partial\Sigma = \Sigma_1 \cup \Sigma_2$ and \mathcal{D} is invariant on Σ_1 but repelling into the interior of Σ on Σ_2 , provided that both conditions 3 and 4 of [25] are satisfied by the restriction of \mathcal{D} on Σ_1 . In our case, the invariant set Σ is bounded. Therefore, condition 1 is verified. As for any biological system, the persistence leads to the weak persistence and then condition 2 holds by Theorem 6.1. Moreover, condition 3 is satisfied since all boundary equilibria are hyperbolic and then each one of them form the maximal invariant set in its neighbourhood, and their union forms a covering of all omega limit sets of Σ_1 . Condition 4 is the satisfied since all

boundary equilibria are not linked cyclically. Thus, we conclude on the uniform persistence of the dynamics (4.4) as follows :

Theorem 7.1. *Dynamics (4.4) is uniformly persistent, i.e., there exists $\zeta > 0$, independent of the initial condition, such that*

$$\liminf_{t \rightarrow \infty} b_1(t) > \zeta, \liminf_{t \rightarrow \infty} b_2(t) > \zeta, \liminf_{t \rightarrow \infty} p(t) > \zeta.$$

8. UNIFORM PERSISTENCE OF MAIN SYSTEM

In this section, we aim to prove the uniform persistence of the dynamics (2.2).

Let $\vec{z}_0 = (n_1(0), n_2(0), b_1(0), b_2(0), p(0))$ where $n_1(0) \geq 0, n_2(0) \geq 0, b_1(0) \geq 0, b_2(0) \geq 0$ and $p(0) \geq 0$, then necessarily $\omega(\vec{z}_0) \in \Sigma$. Moreover, there exist a point $\vec{r} \in \mathbb{R}_+^5 \setminus \Sigma$ and a time sequence (t_n) converging to ∞ , such that the associated solution converges to \vec{r} which means that Σ is not globally attracting and this is false according to proposition 3.1. Assume that $\omega(\vec{z}_0)$ contains a boundary point where at least one of the components b_1, b_2 or p is zero, thus, necessarily the entire orbit into and out of this point will be in $\omega(\vec{z}_0)$ and the omega limit set $\omega(\vec{z}_0)$ will be entirely included in Σ . We conclude the following main finding.

Theorem 8.1. *Dynamics (2.2) is uniformly persistent.*

9. NUMERICAL INVESTIGATION

We validate the theoretical findings using Monod functions to model growth rates, solubilization rate and hydrolysis rate as follows :

$$f_1(n_2) = \frac{f_1^{max} n_2}{\kappa_1 + n_2}, f_2(n_2) = \frac{f_2^{max} n_2}{\kappa_2 + n_2}, g(n_1) = \frac{g^{max} n_1}{\kappa_3 + n_1} \text{ and } h(u) = \frac{h^{max} u}{\kappa_4 + u}$$

where $\kappa_1, \kappa_2, \kappa_3$ and κ_4 are Monod constants, however, $f_1^{max}, f_2^{max}, g^{max}$ and h^{max} are the maximum growth rates of bacteria 1 and bacteria 2, the maximum solubilization rate and the maximum hydrolysis rate, respectively. It is easy to see that the functions f_1, f_2, g and h satisfy Assumption 2.1. We used the parameters data presented in Table 1.

TABLE 1. Used parameters for the numerical approach with no biological meaning.

Parameter	f_1^{max}	f_2^{max}	g^{max}	h^{max}	κ_1	κ_2	κ_3	κ_4	η	n_1^{in}	n_2^{in}	u
Value	4	3	3	3	6	6	2	2	2	2	4	

We present several numerical examples hereafter confirming the theoretical results. For example, in Figure 5, the trajectory of dynamics (2.2) converges to the steady state $E_{1,2}^1$, where both bacteria coexist, which contradicts the competitive exclusion principle which predict that only one bacteria can survive asymptotically, while the other bacteria should disappear.

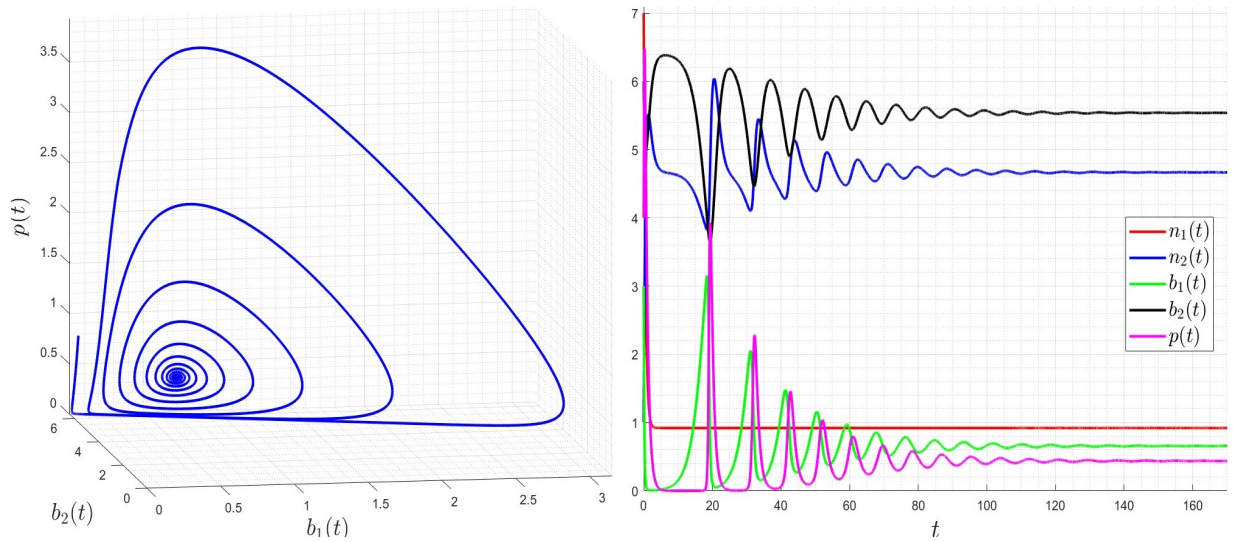


FIGURE 5. For $D = 1.3125$, Assumptions 2.1 and 3.1 are satisfied, and the trajectory of dynamics (2.2) converges to the steady state E_1^1 , where both bacteria persist with the pathogen.

In Figure 6, the trajectory of dynamics (2.2) converges to the steady state E_1^1 , where only bacteria 1 persists with the pathogen, confirming in this case the competitive exclusion principle. In Figure 7, the trajectory of dynamics (2.2) converges to the steady state E_1 , where only bacteria 1 persists. Finally, in Figure 8, the trajectory of dynamics (2.2) converges to the steady state E , where both bacteria go extinct. We can conclude from Figures 6, 7 and 8 that no coexistence of both bacteria (b_1 and b_2) is possible without the presence of the pathogen (p) and the satisfaction of Assumptions 2.1 and 3.1 which contradicts the competitive exclusion principle.

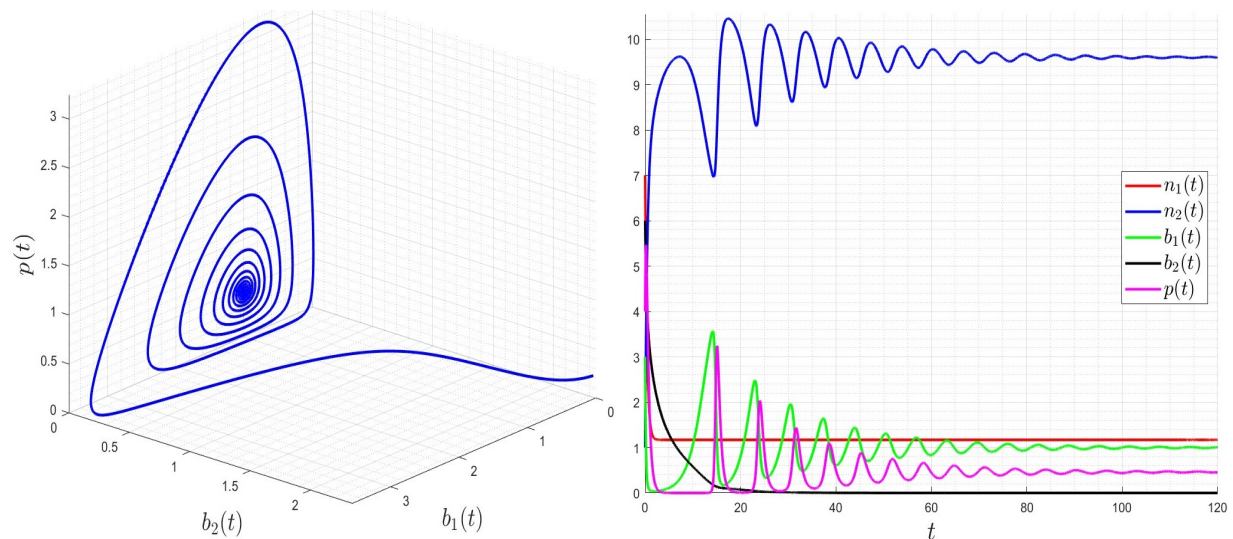


FIGURE 6. For $D = 2$, the trajectory of dynamics (2.2) converges to the steady state E_1^1 , where bacteria 1 persists with the pathogen however bacteria 2 goes extinct.

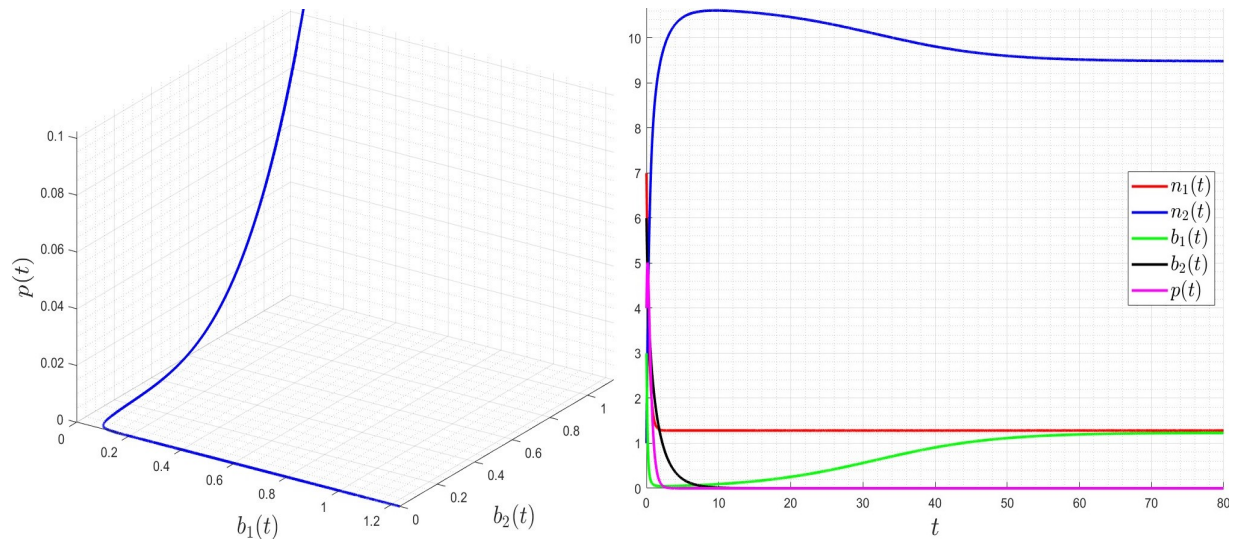


FIGURE 7. For $D = 2.45$, and the trajectory of dynamics (2.2) converges to the steady state E_1 , where only bacteria 1 persist.

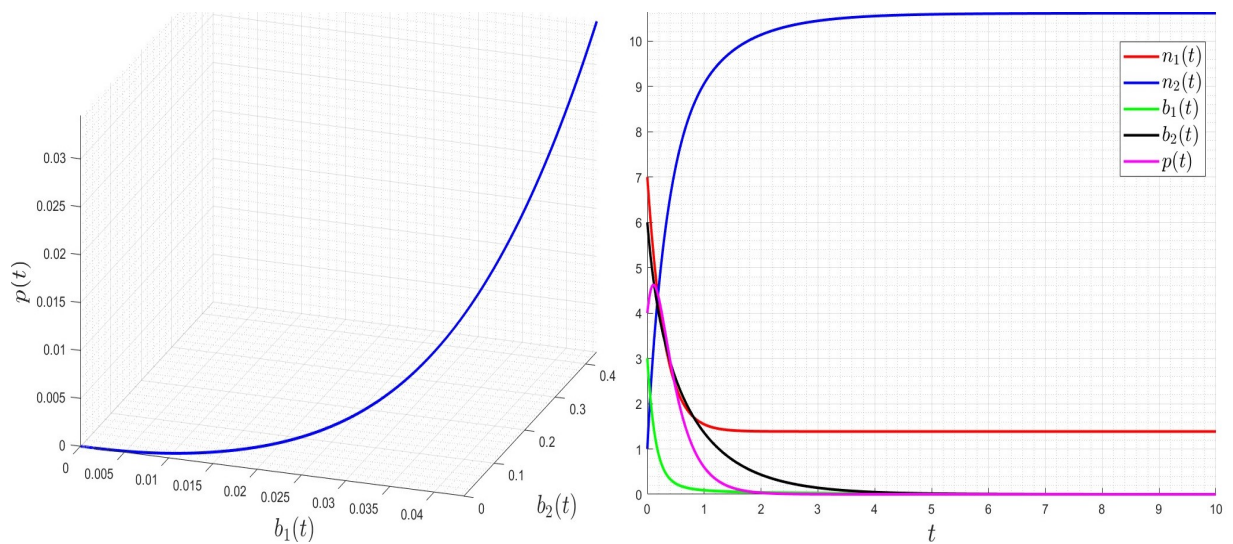


FIGURE 8. For $D = 3$, and the solution of dynamics (2.2) converges to the equilibrium E , where both bacteria go extinct.

10. CONCLUSIONS

By considering a two-bacterial competition for an essential limited nutrient, one can conjure the competitive exclusion principle that at most one bacteria can avoid extinction and the other bacteria goes to extinction. However, if we include an additional mechanism to the competition, as in our case, the coexistence of both bacteria will be possible. In this paper, we presented the interesting and theoretically significant to add a pathogen to a classical model for bacterial competition when bacteria cannot coexist in the absence of the pathogen. The influence of leachate recirculation

was also included since nutriment are generally present into forms, insoluble and soluble. We proposed a mathematical model for a two-bacterial competition for an essential growth-limiting nutriment influenced by both the presence of a pathogen affecting only the bacteria who should win the competition in its absence and the leachate recirculation. The model is composed of five nonlinear ordinary differential equations with general increasing growth rates, solubilization rate and hydrolysis rate. The neglect natural mortality rates allows us to reduce the dynamics to a three-dimensional system. Since all boundary equilibria are unstable, we used the Butler–McGehee theory [13] and the uniform persistence theory [24] to prove the persistence of both bacteria with the pathogen contradicting the competitive exclusion principle. All obtained theoretical results were supported by some numerical example using classical Monod function to express growth, solubilization and hydrolysis rates.

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