

On a reaction-diffusion-advection system modeling flocculation with mortality

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Abstract: In this paper, we are concerned with a diffusive flocculation model in heterogeneous environment. We proved global existence and coexistence of species in the medium. Stability of the washout steady state was shown by analyzing the sign of the principal eigenvalue corresponding to the trivial solution. And, by numerical simulations, we illustrate the convergence towards the washout steady state as diffusion becomes small or towards the coexistence of species as diffusion becomes large under some appropriate assumptions on mortality coefficients showing the effect of diffusion coefficient on the coexistence of microbial species. Our arguments rely on the invariant region method, the lower and upper solutions method and the spectral theory.

Keywords: flocculation, global solution, steady solution, microbial growth, spectral theory

I. INTRODUCTION

This paper studies a reaction-diffusion-advection system modeling bacterial flocculation in a non-homogeneous environment (e.g., a porous medium or unstirred chemostat). The system describes the interactions between a substrate S (nutrient), isolated bacteria u , and attached bacteria (flocs) v , with spatial diffusion and advection along a gradient (e.g., flow in a one-

dimensional domain $x \in [0, 1]$).

The system is governed by the following equations:

$$\begin{aligned} S_t &= d_0 S_{xx} - S_x - \frac{1}{y_u} f(S)u - \frac{1}{y_v} g(S)v, \\ u_t &= d_1 u_{xx} - u_x + f(S)u - \alpha(u, v)u \\ &\quad + \beta(u, v)v - m_u u, \\ v_t &= d_2 v_{xx} - v_x + g(S)v + \alpha(u, v)u \\ &\quad - \beta(u, v)v - m_v v, \end{aligned} \quad (1)$$

on $(0, 1) \times (0, T)$,

with Robin boundary conditions:

$$\begin{aligned} -d_0 S_x(0, t) + S(0, t) &= \gamma_S, S_x(1, t) = 0, \\ -d_1 u_x(0, t) + u(0, t) &= \gamma_u, u_x(1, t) = 0, \\ -d_2 v_x(0, t) + v(0, t) &= \gamma_v, v_x(1, t) = 0, \end{aligned}$$

and initial conditions:

$$\begin{aligned} S(x, 0) &= S_0(x), x \in [0, 1], \\ u(x, 0) &= u_0(x), x \in [0, 1], \\ v(x, 0) &= v_0(x), x \in [0, 1]. \end{aligned} \quad (2)$$

This model incorporates several key parameters and functions that govern the system dynamics. The diffusion coefficients d_0 , d_1 , and $d_2 > 0$ characterize

the random movement of substrate, isolated bacteria, and attached bacteria, respectively, the parameters $m_u, m_v > 0$ represent maintenance respiration losses in the planktonic and flocculated states, respectively. Boundary conditions are controlled by the influx parameters γ_S, γ_u , and $\gamma_v \geq 0$, which determine the substrate and bacterial inputs at the domain boundary.

The model incorporates spatial heterogeneity in bacterial distributions, reflecting the non-uniform colonization patterns observed in porous media and unstirred environments. It explicitly represents nutrient consumption and growth dynamics through the substrate-dependent functions $f(S)$ and $g(S)$, capturing how both planktonic and flocculated bacteria utilize available resources with yield coefficients $y_u, y_v > 0$ for the two bacterial populations. The attachment and detachment processes between planktonic and flocculated states are modeled through the rate functions $\alpha(u, v)$ and $\beta(u, v)$, capturing the reversible nature of bacterial aggregation.

Furthermore, the inclusion of both advection and diffusion terms allows the model to represent transport phenomena crucial in flowing systems, where both directed flow and random motion influence the spatial organization of microbial communities. This comprehensive approach provides valuable insights into the complex interplay between growth, aggregation, and transport in bacterial flocculation systems.

Before going further, let us recall some historical facts in relation to our work: Fekih-Salem et al. in [1] and [2], studied the following flocculation model:

$$\begin{aligned} S_t &= D(S_{in} - S) - f(S)u - g(S)v, \\ u_t &= (f(S) - D_0)u - \alpha(u, v)u + \beta(u, v)v, \\ v_t &= (g(S) - D_1)v + \alpha(u, v)u - \beta(u, v)v. \end{aligned}$$

Here $S(t)$ is the substrate concentration, $u(t)$ and $v(t)$ denote respectively the concentrations of isolated and attached bacteria at time t , $f(\cdot)$ and $g(\cdot)$ represent, respectively, the per-capita growth rates of the isolated and attached bacteria, S_{in} is the concentration of the input nutrient, D denotes the dilution rate, D_0 and D_1 denote the removal rate of isolated and attached bacteria which is the sum of dilution rate D and the death rate, $\alpha(\cdot)$ and $\beta(\cdot)$ denote, respectively, the flocculation and deflocculation rates.

The model in [1] and [2] is only driving by reaction systems representing instantaneous interactions in which spatial effects are considered negligible due to concentrations homogeneously distributed.

M. Ballyk and H. Smith in [3] studied a model of microbial growth in a plug flow reactor with wall

attachment described as follows:

$$\begin{aligned} S_t &= d_0 S_{xx} - S_x - f(S)u - \varepsilon g(S)W, \\ u_t &= d_1 u_{xx} - u_x + (f(S) - k)u \\ &\quad - \alpha u(1 - W)\varepsilon g(S)W(1 - G(W)) + \varepsilon \beta W, \\ W_t &= W(g(S)G(W) - k_w - \beta) \\ &\quad + \varepsilon^{-1} \alpha u(1 - W), \end{aligned} \quad (3)$$

with boundary conditions:

$$\begin{aligned} l - d_0 S_x(0, t) + S(0, t) &= 1, \quad S_x(1, t) = 0, \\ -d_1 u_x(0, t) + u(0, t) &= u_0, \quad u_x(1, t) = 0. \end{aligned} \quad (4)$$

M. Ballyk and H. Smith in [3] studied the effect of diffusion coefficients on the stability of trivial steady-state and coexistence steady-state solutions of system (3)-(4). A key feature of the model first formulated by Freter in [4] and [5], for the chemostat, is that attached bacteria u adhere to surfaces and form biofilms so the wall-attached bacteria W are assumed to be immobile, see also [3,6]. The mechanism of attachment to wall like biofilms or simply a formation of flocs or aggregates has been the subject of much research, both theoretical and experimental, see [1,7–9] and references therein.

Recently, authors in [9], considered a system modeling the fact that a fraction of isolated bacteria and flocs can stick together to form new flocs, with rate $\alpha(\cdot)u$. Reversibly, a fraction of flocs can split and liberate isolated bacteria with rate $\beta(\cdot)v$, under the assumption that the attached bacteria v are mobile and the cell death rates are ignored, described as follows:

$$\begin{aligned} S_t &= d_0 S_{xx} - S_x - f(S)u - g(S)v, \\ u_t &= d_1 u_{xx} - u_x + f(S)u - \frac{1}{\delta_u} \alpha(u, v)u + \beta(u, v)v, \\ v_t &= d_2 v_{xx} - v_x + g(S)v + \alpha(u, v)u - \frac{1}{\delta_v} \beta(u, v)v, \end{aligned}$$

on $(0, 1) \times (0, T)$,

with boundary conditions:

$$\begin{aligned} -d_0 S_x(0, t) + S(0, t) &= 1, \quad S_x(1, t) = 0, \\ -d_1 u_x(0, t) + u(0, t) &= 0, \quad u_x(1, t) = 0, \\ -d_2 v_x(0, t) + v(0, t) &= 0, \quad v_x(1, t) = 0. \end{aligned}$$

The authors in [9] established two global existence results for bounded flocculation rates where the per-capita growth rates are not monotone under some sufficient conditions. Then, reviewing the model in [9], J. Morgan et al. in [10] considered a more generalized model formulated on a one dimensional bounded domain with feed terms at one end of the interval and

shows existence of global classical positive solutions under general growth assumptions, with polynomial flocculation and deflocculation rates that guarantee uniform sup norm bounds for all time t obtained by an L^p –energy functional estimate.

However, under the hypothesis $\delta_u \delta_v < 1$, in the model studied in [9] and [10], there is different rates for outgoing and incoming flows between planktonic and flocculated population. In such model, floc never detaches entirely to release all its cells in the planktonic population, rather, only a part of cells are released, producing another smaller floc and planktonic bacteria.

Indeed, $\alpha(u, v)u$ and $\beta(u, v)v$ represent only exchanges between the two microbial compartments, they should not create or destroy biomass. The condition $\delta_u \delta_v < 1$ implies that these exchanges lead to a net loss of biomass-equivalent mass, which contradicts the mass conservation principle underlying the model. Mass conservation at the cellular level requires that no biomass is created or destroyed during flocculation and deflocculation, so the transfer rate from v to u and from u to v must be complementary. This requires $\delta_u = \delta_v = 1$.

With $\delta_u \delta_v < 1$, the outgoing flow from one population exceeds the incoming flow to the other, generating or destroying biomass, which is biologically inconsistent. Also assuming a yield coefficient of 1 between substrate and microbial population never happens. So, in this work, we take $\delta_u = \delta_v = 1$ and $y_u, y_v \leq 1$.

This work extends previous results in several significant directions. First, we establish global existence of componentwise nonnegative solutions under the biologically relevant condition $y_u, y_v \leq 1$. Second, we substantially generalize the admissible class of flocculation and deflocculation rates by allowing superlinear growth in these functions. Third, we develop a monotone method based on the construction of upper and lower solutions, inspired by techniques from [11] and [12], which enables the analysis of more complex nonlinearities. Finally, we prove the existence of nontrivial steady states for a wider class of rate functions than previously considered, removing the requirement of boundedness and monotonicity that limited earlier studies [3] and [9]. These extensions collectively provide a more comprehensive mathematical framework for analyzing bacterial flocculation processes in spatially heterogeneous environments.

In addition, we assume that $\gamma_u = \gamma_v = 0$, this homogenization is particularly useful because it removes the inhomogeneous boundary contributions. As a consequence, the associated linear operator becomes

dissipative and can be studied under homogeneous boundary conditions, which considerably simplifies the well-posedness and stability analysis.

This manuscript is structured as follows. First, we establish fundamental a priori estimates demonstrating the existence of a finite upper bound for the total bacterial density, independent of diffusion coefficients. This crucial result enables us to prove the global existence of classical solutions to the reaction-diffusion-advection system under general conditions. Second, we employ topological methods and the technique of upper and lower solutions to investigate the existence of non-trivial steady states. We identify critical parameter ranges where spatially heterogeneous equilibrium solutions emerge, representing coexistence bacterial populations in the chemostat environment.

Finally, we complement our theoretical analysis with numerical simulations that illustrate the dynamic behavior of the system. These simulations validate our analytical results and provide additional insights into pattern formation, stability properties, and the relationship between diffusion coefficients and bacterial persistence.

II. MAIN RESULTS

This paper establishes three fundamental analytical results for the diffusion-advection flocculation system (1)-(2).

To investigate asymptotic behavior, we consider the eigenvalue problem:

$$(P_\lambda) \quad \begin{cases} \lambda \varphi = d\varphi'' - \varphi', \\ -d\varphi'(0) + \varphi(0) = 0, \\ \varphi'(1) = 0, \end{cases}$$

where $d > 0$. The monotonicity of the eigenvalues $\{\lambda_n\}_{n \geq 0}$ follows from the general theory of regular Sturm-Liouville problems, see [13, 14] and Lemma 9. Indeed, the eigenvalues $\{\lambda_n\}_{n \geq 0}$ satisfy $\lambda_{n+1} < \lambda_n$ for all $n \geq 0$ and $\lambda_0 < -1$.

Denote $\lambda_d := -\lambda_0$ and assume the following hypotheses:

- **(H₀)** $f, g : \mathbb{R}_+ \rightarrow \mathbb{R}_+$ and $\alpha, \beta : \mathbb{R}_+^2 \rightarrow \mathbb{R}_+$ are locally Lipschitzian functions satisfying $f(0) = g(0) = 0$ with $y_u \leq 1, y_v \leq 1$.
- **(H₁)** There exist positive constants $r, s < 2$ satisfying

$$\alpha(u, v) \approx (u + v)^r, \quad \beta(u, v) \approx (u + v)^s,$$

that is $\exists K > 1$ such that $\forall u, v \geq 0$,

$$\frac{1}{K}(u + v)^r \leq \alpha(u, v) \leq K(u + v)^r,$$

and

$$\frac{1}{K}(u+v)^s \leq \beta(u, v) \leq K(u+v)^s.$$

- **(H₂)** α and β are nondecreasing functions satisfying $\alpha(cu, cv) = c\alpha(u, v)$, $\forall c \geq 0$ and

$$\alpha(u, v) \approx \beta(u, v),$$

that is $\exists k > 1$ such that $\forall u, v \geq 0$,

$$\frac{1}{k}\beta(u, v) \leq \alpha(u, v) \leq k\beta(u, v).$$

The following result establishes the mathematical well-posedness of the model.

Theorem 1. Suppose **(H₀)** and **(H₁)** hold. If $1 \leq r, s < 2$, then for any non-negative, bounded initial data (S_0, u_0, v_0) , there exists a positive global solution (S, u, v) to (1)–(2) satisfying:

$$\sup_{t \geq 0} \|u + v\|_{L^\infty(0,1)} < +\infty.$$

The following results identify critical parameter thresholds governing bacterial persistence versus extinction.

Theorem 2. Assume **(H₀)** and **(H₂)** and let $d := d_0 = d_1 = d_2$. If

$$\lambda_d < (f(1) - m_u) \wedge (g(1) - m_v), \quad (5)$$

then there exists a positive non-trivial steady-state of (1)–(2).

Theorem 3. Assume **(H₀)** and **(H₂)** and let $d := d_0 = d_1 = d_2$. If

$$\lambda_d < (f(1) - m_u) \vee (g(1) - m_v) \quad (6)$$

and

$$(f(1) - m_u) \wedge (g(1) - m_v) \leq \lambda_d,$$

then there exists a nonnegative steady-state of (1)–(2) such that $(S, u, v) \neq (\gamma_S, 0, 0)$.

Finally, we prove stability of washout equilibrium.

Theorem 4. Assume **(H₀)**. Then,

- If $\lambda_d > (f(1) - m_u) \vee (g(1) - m_v)$, the washout steady-state $E_0 = (\gamma_S, 0, 0)$ is uniformly asymptotically stable.
- If $\lambda_d < (f(1) - m_u) \vee (g(1) - m_v)$, the washout steady-state is unstable.

III. A PRIORI ESTIMATES FOR BACTERIAL DENSITIES

In our study, we focus on dynamics in the region $S \geq 0$, $u \geq 0$ and $v \geq 0$ corresponding to biologically meaningful solutions. So first, using the invariant region method in [15], we show that solutions of system (1)–(2) are positive.

Lemma 1. Assume **(H₀)**. Then for any $d_0, d_1, d_2 > 0$ and any positive continuous functions S_0, u_0, v_0 , solutions of system (1)–(2) are positive.

Proof: We rewrite the system (1)–(2) in the vectorial form:

$$w_t = Dw_{xx} - w_x + F(w), \quad x \in (0, 1), \quad t > 0, \quad (7)$$

where

$$w = (S, u, v)^T, \quad D := \begin{pmatrix} d_0 & 0 & 0 \\ 0 & d_1 & 0 \\ 0 & 0 & d_2 \end{pmatrix},$$

and $F(w)$ is defined by:

$$\begin{pmatrix} -\frac{1}{y_u}f(S)u - \frac{1}{y_v}g(S)v \\ f(S)u - (\alpha(u, v) + m_u)u + \beta(u, v)v \\ g(S)v + \alpha(u, v)u - (\beta(u, v) + m_v)v \end{pmatrix}.$$

Let $1 \leq i \leq 3$ and

$$\Sigma = \{w = (S, u, v)^T \in (C[0, 1])^3 / G_i(w) \leq 0\},$$

where

$$G_1(w) = -S, \quad G_2(w) = -u, \quad G_3(w) = -v.$$

It is obvious that the initial data S_0, u_0, v_0 , belongs to the interior of Σ . If $w = (S, u, v)^T \in \partial\Sigma$, we have:

$$\nabla G_1 \cdot F|_{S=0} = \frac{1}{y_u}f(0)u + \frac{1}{y_v}g(0)v = 0,$$

$$\nabla G_2 \cdot F|_{u=0} = -\beta(0, v)v \leq 0,$$

$$\nabla G_3 \cdot F|_{v=0} = -\alpha(u, 0)u \leq 0.$$

By Theorem 14.14 of [15], it follows that Σ is invariant for (7), which ends the proof. ■

Our second result establishes a finite upper bound on the total bacterial density, independent of diffusion coefficients d_0, d_1 , and d_2 .

Lemma 2 (Uniform L^1 Bound). Suppose **(H₀)** holds. Then there exists $L > 0$ such that for all $t \geq 0$,

$$\int_0^1 (u(x, t) + v(x, t)) dx \leq L.$$

Proof: Integrating over $(0, 1)$ and summing yields to:

$$\begin{aligned} \frac{d}{dt} \int_0^1 (S + u + v) dx &\leq \gamma_S + \gamma_u + \gamma_v \\ &+ \int_0^1 \left(1 - \frac{1}{y_u}\right) f(S)u + \left(1 - \frac{1}{y_v}\right) g(S)v dx \\ &- \int_0^1 (m_u u + m_v v) dx. \end{aligned}$$

Since $y_u \leq 1$ and $y_v \leq 1$, then we obtain:

$$\begin{aligned} \frac{d}{dt} \int_0^1 (S + u + v) dx &\leq \gamma_S + \gamma_u + \gamma_v \\ &- \int_0^1 (m_u u + m_v v) dx. \end{aligned}$$

Let $\gamma := \gamma_S + \gamma_u + \gamma_v$, $m := m_u \wedge m_v$ and let us define:

$$z(t) := \int_0^1 (S + u + v) dx,$$

then we have:

$$z'(t) \leq \gamma - m \int_0^1 (u + v) dx.$$

By maximum principle, S is uniformly bounded,

$$\limsup_{t \rightarrow \infty} S(x, t) \leq \max\{\|S_0\|_\infty, \gamma_S\},$$

then there exists $M_S > 0$ such that for all $t \geq 0$,

$$\int_0^1 S(x, t) dx \leq M_S.$$

Let

$$w(t) := \int_0^1 (u + v) dx.$$

then for all $t \geq 0$, we have

$$z(t) \leq M_S + w(t).$$

Consequently,

$$w(t) \geq z(t) - M_S.$$

Using this estimate in

$$z'(t) \leq \gamma - mw(t),$$

we obtain

$$\begin{aligned} z'(t) &\leq \gamma - m(z(t) - M_S) \\ &= \gamma + mM_S - mz(t). \end{aligned}$$

Hence,

$$z'(t) + mz(t) \leq \gamma + mM_S.$$

Multiplying by e^{mt} and integrating yields:

$$z(t) \leq e^{-mt} z(0) + \frac{\gamma + mM_S}{m} (1 - e^{-mt}).$$

Therefore,

$$z(t) \leq \max\left\{z(0), M_S + \frac{\gamma}{m}\right\} \quad \text{for all } t \geq 0.$$

Since $S \geq 0$, it follows that:

$$w(t) \leq z(t),$$

and thus

$$w(t) \leq \max\left\{z(0), M_S + \frac{\gamma}{m}\right\}.$$

Setting

$$L := \max\left\{z(0), M_S + \frac{\gamma}{m}\right\},$$

which ends the proof. ■

Lemma 3 (Uniform L^p Estimates). *Suppose $(\mathbf{H}_0)$ and $(\mathbf{H}_1)$ hold. Let $\gamma_u = \gamma_v = 0$ and $p \geq 2$. Then there exists $C_p > 0$ such that for all $t \geq 0$,*

$$\int_0^1 (u^p(x, t) + v^p(x, t)) dx \leq C_p.$$

Proof: Define the energy functional:

$$\mathcal{L}_p(t) = \int_0^1 (u^p(x, t) + v^p(x, t)) dx.$$

Differentiating and using the equations of system (1)-(2), we have

$$\begin{aligned} \mathcal{L}'_p(t) &= p \int_0^1 u_t u^{p-1} + v_t v^{p-1} dx \\ &= p \int_0^1 u^{p-1} (d_1 u_{xx} - u_x + f(S)u \\ &\quad - \alpha(u, v)u + \beta(u, v)v - m_u u) dx \\ &\quad + p \int_0^1 v^{p-1} (d_2 v_{xx} - v_x + g(S)v \\ &\quad + \alpha(u, v)u - \beta(u, v)v - m_v v) dx \\ &\leq p \int_0^1 u^{p-1} (d_1 u_{xx} - u_x + f(S)u + \beta(u, v)v) dx \\ &\quad + p \int_0^1 v^{p-1} (d_2 v_{xx} - v_x + g(S)v + \alpha(u, v)u) dx. \end{aligned}$$

Integration by parts and using the boundary conditions of system (1)-(2) yields to

$$\begin{aligned}
 & \int_0^1 u^{p-1} (d_1 u_{xx} - u_x) dx \\
 &= \left(d_1 u^{p-1} u_x - \frac{u^p}{p} \right)_0^1 - (p-1) d_1 \int_0^1 u^{p-2} u_x^2 dx \\
 &= u^{p-1}(0) \left(-d_1 u_x(0, t) + \frac{u(0, t)}{p} \right) \\
 &\quad - \frac{u^p(1, t)}{p} - (p-1) d_1 \int_0^1 u_x^2 u^{p-2} dx \\
 &= - \int_0^1 (p-1) d_1 u_x^2 u^{p-2} dx \\
 &\quad + u^{p-1}(0) \left(-u(0, t) + \frac{u(0, t)}{p} \right) - \frac{u^p(1, t)}{p} \\
 &= - \int_0^1 (p-1) d_1 u_x^2 u^{p-2} dx \\
 &\quad + u^{p-1}(0, t) \left(\frac{(1-p)u(0, t)}{p} \right) - \frac{u^p(1, t)}{p} \\
 &= - \int_0^1 (p-1) d_1 u_x^2 u^{p-2} dx \\
 &\quad - \frac{(p-1)u^p(0, t)}{p} - \frac{u^p(1, t)}{p}.
 \end{aligned}$$

Here we used $u_x(1, t) = 0$ and

$$d_1 u_x(0, t) = u(0, t).$$

Thanks to the polynomial growth hypothesis ($\mathbf{H}_1$), we get

$$\begin{aligned}
 \mathcal{L}'_p(t) &\leq -p(p-1) \left(\int_0^1 d_1 u^{p-2} u_x^2 dx \right. \\
 &\quad \left. + \int_0^1 d_2 v^{p-2} v_x^2 dx \right) - u^p(1, t) - v^p(1, t) \\
 &\quad - (p-1)u^p(0, t) - (p-1)v^p(0, t) \\
 &\quad + p \int_0^1 f(S)u^p dx + pK \int_0^1 u^{p-1}(u+v)^s v dx \\
 &\quad + p \int_0^1 g(S)v^p dx + pK \int_0^1 v^{p-1}(u+v)^r u dx.
 \end{aligned}$$

Without loss of generality, we can assume that $r \geq s$, then

$$\begin{aligned}
 \mathcal{L}'_p(t) &\leq -p(p-1) \int_0^1 (d_1 u^{p-2} u_x^2 + d_2 v^{p-2} v_x^2) dx \\
 &\quad + p \int_0^1 (f(S)u^p + g(S)v^p) dx \\
 &\quad + 2pK \int_0^1 (1+u+v)^{p+r} dx.
 \end{aligned}$$

Let $d := \min(d_1, d_2)$, $\alpha_p := dp(p-1)$,

$$M_f := \max_{0 \leq S \leq \gamma_S} f(S), \quad M_g := \max_{0 \leq S \leq \gamma_S} g(S).$$

Using that for all $r \geq 0$, we have

$$u^p \leq 1 + u^{p+r},$$

and

$$(u+v)^{p+r} \leq 2^{p+r-1}(v^{p+r} + u^{p+r}).$$

Then, there exists a positive constant

$$C := C(M_f, M_g, p, r, K)$$

satisfying

$$\begin{aligned}
 \mathcal{L}'_p(t) + \alpha_p \int_0^1 (u^{p-2} u_x^2 + v^{p-2} v_x^2) dx \\
 \leq C \left(1 + \int_0^1 (u^{p+r} + v^{p+r}) dx \right).
 \end{aligned}$$

Since $\|u+v\|_{1,(0,1)}$ is uniformly bounded, then by above Gagliardo-Nirenberg inequality (8) with $\eta := r$, we conclude by induction that, for each $\varepsilon > 0$, there exists $C_{p,\varepsilon} > 0$, independent of u , so that

$$\int_0^1 |u(x)|^{p+r} dx \leq \varepsilon \int_0^1 \left| (u(x)^{p/2})_x \right|^2 dx + C_{p,\varepsilon}.$$

Adding $\int_0^1 (u^p + v^p) dx$ to both sides and choosing ε such that $0 < C_\varepsilon < \frac{4}{p^2} \alpha_p$, yields to

$$\mathcal{L}'_p(t) + \mathcal{L}_p(t) \leq C_p.$$

This Gronwall-type inequality implies

$$\sup_{t \geq 0} \mathcal{L}_p(t) \leq C_p.$$

■

IV. STEADY-STATE ANALYSIS VIA MONOTONE METHOD

In this section, we consider the special case $\gamma_S = 1$, $\gamma_u = \gamma_v = 0$, and $d_0 = d_1 = d_2$. The washout steady-state $E_0 = (1, 0, 0)$ is the unique constant solution of the system:

$$\begin{aligned}
 d_0 S_{xx} - S_x &= \frac{1}{y_u} f(S)u + \frac{1}{y_v} g(S)v, \\
 d_1 u_{xx} - u_x &= -f(S)u + \alpha(u, v)u \\
 &\quad - \beta(u, v)v + m_u u, \\
 d_2 v_{xx} - v_x &= -g(S)v - \alpha(u, v)u \\
 &\quad + \beta(u, v)v + m_v v, \\
 &\text{on } (0, 1),
 \end{aligned}$$

with boundary conditions:

$$\begin{aligned} -dS_x(0) + S(0) &= 1, \\ -du_x(0) + u(0) &= -dv_x(0) + v(0) = 0, \\ S_x(1) &= u_x(1) = v_x(1) = 0. \end{aligned}$$

Now, let $\tilde{S} = 1 - S$ (interpreted as $(1 - \tilde{S})_+$) and $d := d_0 = d_1 = d_2$. Then $\tilde{S}$ satisfies homogeneous boundary conditions, and the system becomes:

$$\begin{aligned} -d\tilde{S}_{xx} + \tilde{S}_x &= \frac{1}{y_u}f(1 - \tilde{S})u + \frac{1}{y_v}g(1 - \tilde{S})v, \\ -du_{xx} + u_x &= f(1 - \tilde{S})u + \beta(u, v)v \\ &\quad - \alpha(u, v)u - m_u u, \\ -dv_{xx} + v_x &= g(1 - \tilde{S})v + \alpha(u, v)u \\ &\quad - \beta(u, v)v - m_v v, \\ &\text{on } (0, 1), \end{aligned} \quad (8)$$

with boundary conditions:

$$\begin{aligned} -d\tilde{S}_x(0) + \tilde{S}(0) &= 0, \\ -du_x(0) + u(0) &= -dv_x(0) + v(0) = 0, \\ \tilde{S}_x(1) &= u_x(1) = v_x(1) = 0. \end{aligned} \quad (9)$$

Lemma 4. Assume that $(\mathbf{H}_0)$ holds. Let $(\tilde{S}, u, v) \in (C([0, 1], \mathbb{R}^+))^3$ satisfy (8)–(9). Then $0 \leq \tilde{S}(x) \leq 1$ for all $x \in [0, 1]$.

Proof: Multiply the first equation in system (8) by $\exp(-x/d)$ and integrate. Using boundary conditions:

$$\begin{aligned} \tilde{S}'(x) &= d^{-1} \int_x^1 \exp\left(\frac{x-t}{d}\right) \left(\frac{1}{y_u}f(1 - \tilde{S})u \right. \\ &\quad \left. + \frac{1}{y_v}g(1 - \tilde{S})v \right) dt. \end{aligned}$$

Then, we get

$$\begin{aligned} \tilde{S}(x) &= \int_0^1 \exp\left(\frac{\min(x, t) - t}{d}\right) \left(\frac{1}{y_u}f(1 - \tilde{S})u \right. \\ &\quad \left. + \frac{1}{y_v}g(1 - \tilde{S})v \right) dt. \end{aligned}$$

We proceed as in the proof of Lemma 1 in [9]. Indeed, if $\tilde{S}(x) > 1$ on an interval I , then the right-hand side vanishes, implying $\tilde{S} \equiv 0$, a contradiction. Maximality arguments at endpoints show no such interval can exist. Hence, $0 \leq \tilde{S}(x) \leq 1$. ■

We rewrite the system (8)–(9) in vector form:

$$\begin{aligned} Dw_{xx} - w_x + F(w) &= 0, \quad x \in (0, 1), \\ -dw_x(0) + w(0) &= 0, \quad w_x(1) = 0, \end{aligned} \quad (10)$$

where $w = (\tilde{S}, u, v)^T$, $D = dI_3$, and $F(w)$ is defined by:

$$\begin{pmatrix} \frac{1}{y_u}f(1 - \tilde{S})u + \frac{1}{y_v}g(1 - \tilde{S})v \\ f(1 - \tilde{S})u - (\alpha(u, v) + m_u)u + \beta(u, v)v \\ g(1 - \tilde{S})v + \alpha(u, v)u - (\beta(u, v) + m_v)v \end{pmatrix}. \quad (11)$$

A function $w \in C^1([0, 1])$ is called a *lower solution* of the system (10) if it satisfies

$$\begin{aligned} Dw_{xx} - w_x + F(w) &\geq 0, \quad x \in (0, 1), \\ -dw_x(0) + w(0) &\leq 0, \quad w_x(1) = 0. \end{aligned}$$

The vectorial inequality $U \leq V$ means that the component $U_i \leq V_i$, for each $i \in \{1, 2, 3\}$. If the inequality above is reversed, w is called an *upper solution*.

We assume there exist lower and upper solutions $\underline{w} \leq \bar{w}$ on $[0, 1]$, and let $\lambda > 0$ be large enough such that $\forall i \in \{1, 2, 3\}$ and $\underline{w}_i \leq x_i \leq y_i \leq \bar{w}_i$,

$$\lambda x_i + F_i(\cdot, x_i, \cdot) \leq \lambda y_i + F_i(\cdot, y_i, \cdot).$$

Define the operator T on $(C^1([0, 1]))^3$ by $Tw = z$, where z solves:

$$\begin{aligned} Dz_{xx} - z_x - \lambda z &= -\lambda w - F(w), \quad x \in (0, 1), \\ -dz_x(0) + z(0) &= 0, \quad z_x(1) = 0. \end{aligned}$$

Then

$$z(x) = Tw(x) = \int_0^1 G(x, t) (\lambda w(t) + F(w(t))) dt,$$

where the Green's function G is positive (see e.g. Theorem 4.2 of [13]). Furthermore, T is a nondecreasing operator on $[\underline{w}, \bar{w}]$, and w is a solution of (10) if and only if $Tw = w$.

Lemma 5. If U and V are lower and upper solutions for (10) in $[\underline{w}, \bar{w}]$, then TU is a lower solution with $U \leq TU$, and TV is an upper solution with $TV \leq V$.

Proof: Let U be a lower solution for the problem (10) such that

$$\underline{w} \leq U \leq \bar{w}.$$

Set $w = TU - U$, then we have:

$$\begin{aligned} Dw_{xx} - w_x - \lambda w &= -F(U) - DU_{xx} + U_x \leq 0, \\ -dw_x(0) + w(0) &= 0, \quad x \in (0, 1), \quad w_x(1) = 0. \end{aligned}$$

Which yields that $w \geq 0$ on $[0, 1]$. That is, $U \leq TU$ on $[0, 1]$, and similarly, we prove that $TV \leq V$ on $[0, 1]$.

Now, since we have:

$$\underline{w} \leq U \leq TU \leq T\bar{w} \leq \bar{w},$$

then TU satisfies:

$$\begin{aligned} D(TU)_{xx} - (TU)_x + F(TU) &= F(TU) + \lambda TU \\ &\quad - \lambda U - F(U) \geq 0, \\ -d(TU)_x(0) + TU(0) &= 0, \\ (TU)_x(1) &= 0, \quad x \in (0, 1). \end{aligned}$$

Which implies that TU is a lower solution for the problem (10) and similarly, we prove that TV is an upper solution for the problem (10). ■

In what follows, by a monotone method, we prove existence solutions to the problem (10).

Lemma 6. Let $\underline{w} = (\underline{S}, \underline{u}, \underline{v})$ and $\overline{w} = (\overline{S}, \overline{u}, \overline{v})$ be, respectively, a lower solution and an upper solution for the problem (10), such that $\underline{S} \leq \overline{S}$, $\underline{u} \leq \overline{u}$, $\underline{v} \leq \overline{v}$ on $[0, 1]$. Then, there exist two extremal solutions in $[\underline{w}, \overline{w}]$ of the problem (10).

Proof: We define $(\underline{w}_n)_{n \in \mathbb{N}}$ and $(\overline{w}_n)_{n \in \mathbb{N}}$ as follows $\underline{w}_0 = \underline{w}$, $\overline{w}_0 = \overline{w}$,

$$\underline{w}_{n+1} = T\underline{w}_n \quad \text{and} \quad \overline{w}_{n+1} = T\overline{w}_n.$$

Using the previous lemma, we obtain that

$$\begin{aligned} \underline{w}_0 &\leq \dots \leq \underline{w}_n \leq \underline{w}_{n+1} \\ &\leq \overline{w}_{n+1} \leq \overline{w}_n \leq \dots \leq \overline{w}_0. \end{aligned}$$

Hence, the sequences $(\underline{w}_n)_{n \in \mathbb{N}}$ and $(\overline{w}_n)_{n \in \mathbb{N}}$ converge, respectively, to functions $\underline{W}$ and $\overline{W}$ such that $\underline{w} \leq \underline{W} \leq \overline{W} \leq \overline{w}$. It follows that

$$\begin{aligned} \lambda \underline{w} + F(\underline{w}) &\leq \lambda \underline{W} + F(\underline{W}) \\ &\leq \lambda \overline{W} + F(\overline{W}) \leq \lambda \overline{w} + F(\overline{w}). \end{aligned}$$

So, by dominated convergence theorem, we obtain that $\underline{W} = T\underline{W}$ and $\overline{W} = T\overline{W}$. Which ends the proof. ■

If w is solution of the problem (10) such that $\underline{w} \leq w \leq \overline{w}$, then we have for every $n \in \mathbb{N}$ that $T^n \underline{w} \leq T^n w \leq T^n \overline{w}$, which implies $\underline{w}_n \leq w \leq \overline{w}_n$. Thus, $\underline{W} \leq w \leq \overline{W}$. That is $\underline{W}$ and $\overline{W}$ are extremal solutions of the problem (10).

V. PROOFS OF MAIN THEOREMS

A. Proof of Theorem 1

Let $\varphi: \mathbb{R} \rightarrow [0, 1]$ be a smooth cutoff function such that $\varphi(t) = 0$ for $t \leq 0$, $\varphi(t) = 1$ for $t \geq 1$, and $0 \leq \varphi'(t) \leq 2$ for all $t \in \mathbb{R}$.

Define the shifted function $\varphi_\tau(\cdot) = \varphi(\cdot - \tau)$. Then, for each $x \in (0, 1)$, $t \in (\tau, \tau + 2)$ we have $\varphi_\tau(t)u(x, t)$,

which satisfies:

$$\begin{aligned} (\varphi_\tau u)_t - d_1(\varphi_\tau u)_{xx} + (\varphi_\tau u)_x &= F_\tau(S, u, v), \\ -d_1(\varphi_\tau u)_x(0, t) + (\varphi_\tau u)(0, t) &= 0, \\ (\varphi_\tau u)_x(1, t) &= 0, \\ (\varphi_\tau u)(x, \tau) &= 0, \end{aligned}$$

where

$$\begin{aligned} F_\tau(S, u, v) &:= \varphi_\tau(t)(f(S)u - \alpha(u, v)u \\ &\quad + \beta(u, v)v - m_u u) + \varphi'_\tau(t)u. \end{aligned}$$

By hypothesis (H_1) , we have the polynomial bound:

$$|F_\tau(S, u, v)| \leq C(1 + u + v)^\mu,$$

where $\mu := (\max(r, s) + 1)$. So, by using Lemmas 2 and 3, for any $1 \leq p < \infty$, there exists $C_p > 0$ such that:

$$\int_\tau^{\tau+2} \int_0^1 |F_\tau(S, u, v)|^p dx dt \leq C_p.$$

By comparison principles for parabolic equations, this implies:

$$\|\varphi_\tau u\|_{L^\infty((0,1) \times (\tau, \tau+2))} \leq C,$$

where C is independent of $\tau \in \mathbb{N}$. Since $\varphi_\tau(t) = 1$ for $t \in (\tau + 1, \tau + 2)$, we obtain:

$$\|u\|_{L^\infty((0,1) \times (\tau, \tau+2))} \leq C.$$

Similarly, we prove $\|v\|_{L^\infty((0,1) \times (\tau, \tau+2))} \leq C$. Thus, the solution is globally defined and uniformly bounded.

B. Proof of Theorem 2

Since $k > 1$ we have $1 - 1/k > 0$ and $k - 1 > 0$. We choose $l > 0$ small enough so that

$$\begin{aligned} \alpha(l, l) &< \frac{m_u + \lambda_d}{k - 1} \wedge \frac{m_v + \lambda_d}{1 - \frac{1}{k}} \\ \alpha(l, l) &< \left(\frac{g(1) - m_v - \lambda_d}{k - 1} \right) \wedge \left(\frac{f(1) - m_u - \lambda_d}{1 - \frac{1}{k}} \right). \end{aligned} \quad (12)$$

which is possible because $\alpha(0, 0) = 0$ and both right-hand sides are strictly positive under assumption (5). We then choose $c > 1$ satisfying:

$$\frac{\alpha(l, l)(k - 1)}{m_u + \lambda_d} < \frac{1}{c} < \frac{f(1) - m_u - \lambda_d}{\alpha(l, l)(1 - 1/k)} \quad (13)$$

and

$$\frac{\alpha(l, l)(1 - \frac{1}{k})}{m_v + \lambda_d} < \frac{1}{c} < \frac{g(1) - m_v - \lambda_d}{\alpha(l, l)(k - 1)}. \quad (14)$$

The existence of such c follows from (12).

Now, let $\phi := \phi_d$ be the principal eigenfunction associated to λ_d with:

$$\|\phi\|_\infty = l, \quad (15)$$

and denote:

$$\underline{w} = \left(0, \frac{\phi}{c}, \frac{\phi}{c}\right).$$

Let

$$G(w) := Dw_{xx} - w_x + F(w),$$

where F is defined as in (11). Then, we get:

$$G(\underline{w}) = \begin{pmatrix} G_1(\underline{w}) \\ G_2(\underline{w}) \\ G_3(\underline{w}) \end{pmatrix},$$

such that

$$G_1(\underline{w}) = \frac{1}{y_u} f(1) \frac{\phi}{c} + \frac{1}{y_v} g(1) \frac{\phi}{c},$$

$$G_2(\underline{w}) = \left(-\lambda_d - m_u + f(1) - \alpha\left(\frac{\phi}{c}, \frac{\phi}{c}\right) + \beta\left(\frac{\phi}{c}, \frac{\phi}{c}\right) \right) \frac{\phi}{c},$$

$$G_3(\underline{w}) = \left(-\lambda_d - m_v + g(1) + \alpha\left(\frac{\phi}{c}, \frac{\phi}{c}\right) - \beta\left(\frac{\phi}{c}, \frac{\phi}{c}\right) \right) \frac{\phi}{c}.$$

Using (H_2) , we get:

$$\begin{aligned} \beta\left(\frac{\phi}{c}, \frac{\phi}{c}\right) - \alpha\left(\frac{\phi}{c}, \frac{\phi}{c}\right) &\geq \left(\frac{1}{k} - 1\right) \alpha\left(\frac{\phi}{c}, \frac{\phi}{c}\right) \\ &= \left(\frac{1}{k} - 1\right) \frac{1}{c} \alpha(\phi, \phi), \end{aligned}$$

and by (15), we obtain:

$$\alpha(\phi, \phi) \leq \alpha(l, l).$$

Now, since $k > 1$, then we get:

$$\beta\left(\frac{\phi}{c}, \frac{\phi}{c}\right) - \alpha\left(\frac{\phi}{c}, \frac{\phi}{c}\right) \geq \left(\frac{1}{k} - 1\right) \frac{1}{c} \alpha(l, l).$$

This yields to:

$$\begin{aligned} G_2(\underline{w}) &\geq \left(-\lambda_d - m_u + f(1) + \left(\frac{1}{k} - 1\right) \frac{1}{c} \alpha(l, l) \right) \frac{\phi}{c}. \end{aligned}$$

So, using (13) leads to:

$$G_2(\underline{w}) \geq 0.$$

Using again (H_2) , we obtain:

$$\begin{aligned} \alpha\left(\frac{\phi}{c}, \frac{\phi}{c}\right) - \beta\left(\frac{\phi}{c}, \frac{\phi}{c}\right) &\geq (1 - k) \alpha\left(\frac{\phi}{c}, \frac{\phi}{c}\right) \\ &\geq (1 - k) \frac{1}{c} \alpha(l, l). \end{aligned}$$

A parallel argument, using (14), leads to:

$$\begin{aligned} G_3(\underline{w}) &\geq \left(-\lambda_d - m_v + g(1) + (1 - k) \frac{1}{c} \alpha(l, l) \right) \frac{\phi}{c} \geq 0. \end{aligned}$$

Thus, $\underline{w}$ is a lower solution.

Now, let us denote

$$\bar{w} := (1, c\phi, c\phi).$$

Then:

$$G(\bar{w}) := D\bar{w}_{xx} - \bar{w}_x + F(\bar{w}),$$

where

$$G(\bar{w}) = \begin{pmatrix} G_1(\bar{w}) \\ G_2(\bar{w}) \\ G_3(\bar{w}) \end{pmatrix},$$

such that

$$\begin{aligned} G_1(\bar{w}) &= \frac{1}{y_u} f(0) c\phi + \frac{1}{y_v} g(0) c\phi, \\ G_2(\bar{w}) &= \left(-\lambda_d - m_u + f(0) - \alpha(c\phi, c\phi) + \beta(c\phi, c\phi) \right) c\phi, \\ G_3(\bar{w}) &= \left(-\lambda_d - m_v + g(0) + \alpha(c\phi, c\phi) - \beta(c\phi, c\phi) \right) c\phi. \end{aligned}$$

Using (H_2) , (13) and (14), we get:

$$\begin{aligned} -\lambda_d - m_u - \alpha(c\phi, c\phi) + \beta(c\phi, c\phi) &\leq -\lambda_d - m_u + (k - 1) \alpha(c\phi, c\phi) \\ &\leq -\lambda_d - m_u + (k - 1) c \alpha(l, l) \leq 0, \\ -\lambda_d - m_v + \alpha(c\phi, c\phi) - \beta(c\phi, c\phi) &\leq -\lambda_d - m_v + \left(1 - \frac{1}{k}\right) \alpha(c\phi, c\phi) \\ &\leq -\lambda_d - m_v + \left(1 - \frac{1}{k}\right) c \alpha(l, l) \leq 0. \end{aligned}$$

And, since $f(0) = g(0) = 0$, then we obtain

$$G_1(\bar{w}) \leq 0, \quad G_2(\bar{w}) \leq 0 \quad \text{and} \quad G_3(\bar{w}) \leq 0.$$

Thus, $\bar{w}$ is an upper solution. Since F is continuously differentiable on $[\underline{w}, \bar{w}] \subset (C([0, 1]))^3$, and for large λ the map $w_i \mapsto \lambda w_i + F_i(\cdot, w_i, \cdot)$ is nondecreasing on $[\underline{w}_i, \bar{w}_i]$ for $i \in \{1, 2, 3\}$, therefore Lemma 6 implies

the existence of solutions in $[\underline{w}, \bar{w}]$. Hence, there exists a non-trivial steady state (S, u, v) with

$$\frac{1}{c}\phi(x) \leq u(x), v(x) \leq c\phi(x), \quad x \in [0, 1],$$

i.e., $u(x) \approx v(x) \approx \phi(x)$.

C. Proof of Theorem 3

We assume that

$$g(1) - m_v < f(1) - m_u.$$

We proceed as in the previous proof. Indeed, by (6), there exists $l > 0$ satisfying

$$\alpha(l, l) < f(1) - m_u - \lambda_d \quad (16)$$

and

$$\alpha(l, l) < \frac{m_u + \lambda_d}{k - 1} \wedge \frac{m_v + \lambda_d}{1 - \frac{1}{k}}.$$

Then, let $\phi := \phi_d$ be the principal eigenfunction associated to λ_d with

$$\|\phi\|_\infty = l.$$

Choose $c > 1$ sufficiently large and denote

$$\underline{w} = \left(0, \frac{\phi}{c}, 0\right).$$

Let

$$G(w) := Dw_{xx} - w_x + F(w),$$

where F is defined as in (11). Then, we get

$$G(\underline{w}) = \begin{pmatrix} G_1(\underline{w}) \\ G_2(\underline{w}) \\ G_3(\underline{w}) \end{pmatrix},$$

such that

$$\begin{aligned} G_1(\underline{w}) &= \frac{1}{y_u} f(1) \frac{\phi}{c}, \\ G_2(\underline{w}) &= \left(-\lambda_d - m_u + f(1) - \alpha\left(\frac{\phi}{c}, 0\right) \right) \frac{\phi}{c}, \\ G_3(\underline{w}) &= \alpha\left(\frac{\phi}{c}, 0\right) \frac{\phi}{c}. \end{aligned}$$

It is clear that

$$G_1(\underline{w}) \geq 0 \quad \text{and} \quad G_3(\underline{w}) \geq 0.$$

Now, using $(\mathbf{H}_2)$, we get

$$\alpha\left(\frac{\phi}{c}, 0\right) \leq \alpha(l, l).$$

Using (16) yields to

$$G_2(\underline{w}) \geq \left(-\lambda_d - m_u + f(1) - \frac{1}{c}\alpha(l, l) \right) \frac{\phi}{c} \geq 0.$$

Thus, $\underline{w}$ is a lower solution.

Now, as in the proof of Theorem 2, we show that

$$\bar{w} := (1, c\phi, c\phi)$$

is an upper solution. Hence, there exists a non-trivial steady state (S, u, v) with

$$\frac{1}{c}\phi(x) \leq u(x) \leq c\phi(x),$$

and $0 \leq v(x) \leq \phi(x)$, $x \in [0, 1]$.

In the case

$$f(1) - m_u < g(1) - m_v,$$

we proceed in a similar manner and prove the existence of a non-trivial steady state (S, u, v) with

$$0 \leq u(x) \leq \phi(x),$$

and $\frac{1}{c}\phi(x) \leq v(x) \leq c\phi(x)$, $x \in [0, 1]$.

D. Proof of Theorem 4

The linearization of (1) at the washout state $E_0 = (1, 0, 0)$ is:

$$\begin{aligned} S_t &= dS_{xx} - S_x - \frac{1}{y_u} f(1)u - \frac{1}{y_v} g(1)v, \\ u_t &= du_{xx} - u_x + f(1)u - m_u u, \\ v_t &= dv_{xx} - v_x + g(1)v - m_v v. \end{aligned}$$

Let $\tilde{S} = 1 - S$. The eigenvalue problem for stability is:

$$(E_\lambda) \quad \begin{cases} \lambda \tilde{S} = d\tilde{S}'' - \tilde{S}' + \frac{1}{y_u} f(1)u + \frac{1}{y_v} g(1)v, \\ \lambda u = du'' - u' + (f(1) - m_u)u, \\ \lambda v = dv'' - v' + (g(1) - m_v)v, \end{cases}$$

with homogeneous boundary conditions:

$$\begin{cases} -d\tilde{S}'(0) + \tilde{S}(0) = 0, & \tilde{S}'(1) = 0, \\ -du'(0) + u(0) = 0, & u'(1) = 0, \\ -dv'(0) + v(0) = 0, & v'(1) = 0. \end{cases}$$

The eigenvalues λ of (E_λ) correspond to the eigenvalues λ_n of (P_λ) or $\lambda_n + f(1) - m_u$ or $\lambda_n + g(1) - m_v$.

Then, λ verifies the following inequalities:

$$\begin{aligned} \lambda &\leq -\lambda_d \quad \text{or} \\ \lambda &\leq -\lambda_d + g(1) - m_v \quad \text{or} \\ \lambda &\leq -\lambda_d + f(1) - m_u. \end{aligned}$$

The stability assertions of the Theorem 4 follow from Theorem 4.2 in [16].

Indeed, if $\lambda_d > g(1) - m_v$ and $\lambda_d > f(1) - m_u$, then $\lambda < 0$ and the washout steady-state is stable.

If $\lambda_d < g(1) - m_v$ or $\lambda_d < f(1) - m_u$, then there exists a positive eigenvalue, so E_0 is unstable, which ends the proof.

VI. NUMERICAL SIMULATIONS

In this section, we present numerical simulations that illustrate the asymptotic behavior of solutions of the system (1)-(2) as a function of two variables x and t and show the transition between washout and coexistence as diffusion and mortality vary.

In what follows, the flocculation and deflocculation rates are given by:

$$\alpha(u, v) = u + v \quad \text{and} \quad \beta(u, v) = 2(u + v).$$

And the yield coefficients are set to:

$$y_u = y_v = 1.$$

First, we consider the growth functions f and g following Monod kinetics:

$$f(S) = \frac{3S}{1+S}, \quad g(S) = \frac{5S}{1+S}.$$

The initial conditions are set to:

$$S(x, 0) = 1, \quad u(x, 0) = v(x, 0) = 0.1.$$

Fig. 1 demonstrates the system's behavior for large diffusion coefficient $d = 1000$ and $m_u = 3$, $m_v = 5$, showing convergence to the washout steady-state $E_0 = (1, 0, 0)$, indicating microbial extinction. In fact, since $m_u = 3 > f(1) = 1.5$ and $m_v = 5 > g(1) = 2.5$, we have $\lambda_d > (f(1) - m_u) \vee (g(1) - m_v)$, so washout is indeed stable.

Fig. 2 demonstrates the system's behavior with $d = 1000$, $m_u = 1$, $m_v = 1$, then $f(1) - m_u = 0.5 > 0$ and $g(1) - m_v = 1.5 > 0$, showing convergence to a steady state where at least one bacterial populations persists. For $d = 1000$, λ_d is small, close to 1, see Table 1, so $(f(1) - m_u) < \lambda_d < (g(1) - m_v)$, and persistence of attached bacteria is predicted.

Fig. 3 demonstrates the system's behavior for a small diffusion coefficient $d = 0.1$ and $m_u = 1$, $m_v = 1$, showing convergence to the washout steady-state $E_0 = (1, 0, 0)$. Indeed, $\lambda_d \simeq 3.02$, then $\lambda_d > (f(1) - m_u) \vee (g(1) - m_v)$, and microbial extinction is predicted.

Fig. 4 illustrates the system dynamics for diffusion coefficient $d = 10$ and $m_u = 1 < f(1)$, $m_v = 5 > g(1)$. The solutions converge to the washout steady-state $E_0 = (1, 0, 0)$, implying the extinction of both microbial populations. This agrees with the theoretical results, since $\lambda_d \simeq 1.017$ satisfies $\lambda_d > (f(1) - m_u) \vee (g(1) - m_v) = 0.5$.

However, keeping the same diffusion coefficient $d = 10$ as in Fig. 4, Fig. 5 illustrates that, when $m_u = 3 > f(1)$ and $m_v = 1 < g(1)$, the system converges to persistence of the attached bacteria.

Fig. 6 demonstrates the system's behavior with $d = 100$, $m_u = m_v = 0.2$, then $f(1) - m_u = 1.3$ and $g(1) - m_v = 2.3$, showing convergence to a steady state where both bacterial populations persist. For $d = 100$, $\lambda_d \approx 1.0017$, see Table 1, so $\lambda_d < (f(1) - m_u) \wedge (g(1) - m_v)$, and coexistence is predicted.

Now, let us consider a growth function f following Haldane kinetics and g following Monod kinetics:

$$f(S) = \frac{3S}{1+S+S^2}, \quad g(S) = \frac{5S}{1+S},$$

with nonhomogenous initial conditions:

$$S(x, 0) = x(1-x)^2, \quad u(x, 0) = v(x, 0) = x^2(1-x)^2.$$

Fig. 7 illustrates the system dynamics for Haldane type growth with mortality coefficients satisfying $m_u = 3 > f(1)$ and $m_v = 1 < g(1)$. In this case, coexistence is sustained by the attached bacteria population.

We now consider smaller diffusion coefficients than those used in Fig. 7, while keeping Haldane type growth and the same mortality coefficients, namely $m_u = 3 > f(1)$ and $m_v = 1 < g(1)$. Fig. 8 shows that, for $d = 0.5$, the solution converges to a steady state characterized by the persistence of the attached bacteria and the extinction of the free bacteria. For an even smaller diffusion coefficient, $d = 0.1$, Fig. 9 shows convergence to the washout steady state.

Fig. 10 illustrates the non-washout regime predicted by Theorem 3. For the parameter values $d = 100$, $m_u = 0.01$, and $m_v = 0.1$, we have $f(1) - m_u = 0.99$, $g(1) - m_v = 2.4$ and $\lambda_d \approx 1.0017$, see Table 1, so $f(1) - m_u < \lambda_d < g(1) - m_v$. The numerical simulations show convergence to a positive steady state, indicating the persistence of both bacterial populations. Thus, both species are observed to coexist numerically, in agreement with the theoretical prediction of the non-washout regime.

These results highlight the critical role of diffusion in determining population persistence, with higher diffusivity promoting coexistence and lower diffusivity leading to washout. Moreover, the model admits parameter regimes in which only one species survives, leading to competitive exclusion of the other species. In addition, by numerical simulations above, if $m_u \geq f(1)$ and $m_v \geq g(1)$ the convergence is towards washout steady state even for higher diffusivity. The numerical findings align perfectly with our theoretical stability analysis presented in Theorem 4.

The numerical simulations were performed using the pdepe function in MATLAB to solve the system of reaction-diffusion equations. The spatial domain $[0, 1]$

d	0.1	0.5	1	10	100	1000
λ_d	3.02	1.35	1.17	1.017	1.0017	1.0002

Table 1: Computed values of the principal eigenvalue λ_d for the diffusion coefficients used in the numerical simulations.

was discretized into 100 equally spaced points, while the temporal domain $[0, 300]$ was discretized into 600 equally spaced points. The pdepe function employs an implicit time-stepping method, which is known for its stability.

To support the interpretation of the numerical results, we report in Table 1 the computed values of the principal eigenvalue λ_d corresponding to the diffusion coefficients used in the simulations. To compute λ_d , we discretize the operator $L = d \frac{d^2}{dx^2} - \frac{d}{dx}$ on a uniform grid defined by $x_i = ih$ with $h = \frac{1}{N}$. The operator is approximated using second order centered differences for interior nodes, leading to the formulation of $L_h \phi_i$. Boundary conditions are applied to eliminate ϕ_0 and ϕ_N , with specific formulas derived for the left Robin and right Neumann boundaries. This substitution results in a reduced matrix A_c of size $(N-1) \times (N-1)$, whose eigenvalues are real due to the operator's self-adjoint nature. The principal eigenvalue λ_0 is obtained by computing the largest eigenvalue of A_c using MATLAB's $\text{eig}(A_c)$, with a focus on convergence for values of N between 50 and 2000.

To verify the robustness of our solutions, we also performed simulations with the temporal step size reduced by a factor of 10. The comparison showed that the solutions did not change drastically, affirming that our original time step was adequate.

VII. CONCLUSION

In this paper, we were concerned with a reaction-diffusion-advection system on the one-dimensional domain $(0, 1)$ modeling bacterial flocculation in a heterogeneous environment. Under sufficient conditions on the growth functions and the flocculation rates, we showed the global existence of positive solutions. We proved the existence and the stability of the washout steady-state by analyzing the sign of the principal eigenvalue corresponding to the trivial solution.

Furthermore, we showed the existence of non-trivial steady state solutions. Because the nonlinearity of the growth functions and the flocculation rates, there is some difficulty in the analysis of the asymptotic behaviour of the positive steady-state solution. The stability of the coexistence steady-state is under consideration.

Our simulations results demonstrate that diffusion is a key factor governing population persistence. While sufficiently large diffusion coefficients, with mortality does not exceed the growth, favor the coexistence of both species, small diffusion coefficients may result in washout. Moreover, the model admits parameter regimes in which only one species survives, leading to competitive exclusion of the other species. The intermediate regime in which exactly one of the quantities $f(1) - m_u$ and $g(1) - m_v$ exceeds λ_d is also treated numerically, showing different scenario.

To clarify the dynamics, it is necessary to analyze the corresponding ω -limit sets and investigate the long-time convergence properties of the system. This challenging problem is currently under investigation and will be addressed in future work.

VIII. APPENDIX

Lemma 7 (Gagliardo-Nirenberg inequality). *Let $a \in [0, 1]$, $1 \leq p, q, r \leq \infty$, and $u \in W^{1,r}(\mathbb{R}) \cap L^q(\mathbb{R})$,*

$$\|u\|_{L^p} \leq C \|u'\|_{L^r}^a \cdot \|u\|_{L^q}^{1-a}$$

with

$$\frac{1}{p} = a \left(\frac{1}{r} - 1 \right) + \frac{1-a}{q}.$$

Lemma 8. *Suppose $p \geq 2$ and $w^{p/2} \in H^1(0, 1)$. If $\|w\|_{p/2, (0,1)} \leq M$, $0 \leq \eta < 2$ and $\varepsilon > 0$, there exists $C_{p,\varepsilon,M} > 0$, independent of w , so that:*

$$\int_0^1 |w(x)|^{p+\eta} dx \leq \varepsilon \int_0^1 \left| \left(w(x)^{p/2} \right)_x \right|^2 dx + C_{p,\varepsilon,M}.$$

Proof: Let $z = w^{p/2}$. From the Gagliardo-Nirenberg inequality, if $2 \leq q < 4$ and $q = \frac{2}{2-3\theta}$, then $\frac{1}{3} \leq \theta < \frac{1}{2}$, and there exists $C_q > 0$ so that

$$\begin{aligned} \int_0^1 |z(x)|^q dx &\leq C_q \left(\int_0^1 |z_x(x)|^2 dx \right)^{q \frac{\theta}{2}} \\ &\quad \times \left(\int_0^1 |z(x)| dx \right)^{q(1-\theta)}. \end{aligned}$$

Also, $0 < q \frac{\theta}{2} < 1$. Young's inequality implies that there exists $C_{q,\varepsilon} > 0$, so that from above:

$$\begin{aligned} \int_0^1 |z(x)|^q dx &\leq \varepsilon \int_0^1 |z_x(x)|^2 dx \\ &\quad + C_{q,\varepsilon} \left(\int_0^1 |z(x)| dx \right)^{\frac{2q(1-\theta)}{2-q\theta}}. \end{aligned}$$

The result follows by choosing $q = 2 + \frac{2\eta}{p}$. ■

Since our work relies heavily on principal eigenvalues and eigenvectors, to improve readability, we include

a brief introduction on the principal eigenvalue theory associated with our proposed model.

Let $L\varphi := d\varphi'' - \varphi'$ with boundary conditions $-d\varphi'(0) + \varphi(0) = 0$, $\varphi'(1) = 0$.

Consider the eigenvalue problem $L\varphi = \lambda\varphi$. To study the spectrum, we rewrite the equation in self-adjoint form. Multiplying the equation by the integrating factor $e^{-x/d}$, we obtain:

$$d \left(e^{-x/d} \varphi' \right)' = \lambda e^{-x/d} \varphi.$$

Hence, the problem is a regular Sturm-Liouville problem with weight $w(x) = e^{-x/d} > 0$.

Lemma 9. Consider the eigenvalue problem

$$(P_\lambda) \quad \begin{cases} \lambda\varphi = d\varphi'' - \varphi', & x \in (0, 1), \\ -d\varphi'(0) + \varphi(0) = 0, \\ \varphi'(1) = 0, \end{cases}$$

where $d > 0$. Then, the spectrum of (P_λ) consists of a sequence of simple real eigenvalues

$$\lambda_0 > \lambda_1 > \lambda_2 > \dots, \quad \lambda_n \rightarrow -\infty \text{ as } n \rightarrow \infty.$$

In particular, $\lambda_{n+1} < \lambda_n$ for all $n \geq 0$, and the principal eigenvalue satisfies $\lambda_0 < -1$.

Proof: Introduce the change of variables $\varphi(x) = e^{\frac{x}{2d}}\psi(x)$. Then

$$\begin{aligned} \varphi' &= e^{\frac{x}{2d}} \left(\psi' + \frac{1}{2d} \psi \right), \\ \varphi'' &= e^{\frac{x}{2d}} \left(\psi'' + \frac{1}{d} \psi' + \frac{1}{4d^2} \psi \right). \end{aligned}$$

Substituting into $\lambda\varphi = d\varphi'' - \varphi'$ yields $-d\psi'' + \frac{1}{4d}\psi = \mu\psi$, where $\mu = -\lambda$. The boundary conditions become

$$\begin{aligned} -d\psi'(0) + \frac{1}{2}\psi(0) &= 0, \\ \psi'(1) + \frac{1}{2d}\psi(1) &= 0. \end{aligned}$$

By the classical spectral theory of regular Sturm-Liouville problems, the spectrum consists of a sequence of simple real eigenvalues

$$\mu_0 < \mu_1 < \mu_2 < \dots, \quad \mu_n \rightarrow +\infty.$$

Since $\mu_n = -\lambda_n$ and $d > 0$, it follows that

$$\lambda_0 > \lambda_1 > \lambda_2 > \dots, \quad \lambda_n \rightarrow -\infty.$$

It remains to prove that $\lambda_0 < -1$. By the Rayleigh-quotient argument from the transformed problem, μ is

defined by

$$\left(d \int_0^1 |\psi'|^2 dx + \frac{1}{2} (\psi(0)^2 + \psi(1)^2) + \frac{1}{4d} \int_0^1 \psi^2 dx \right) / \left(\int_0^1 \psi^2 dx \right),$$

whose minimum exceeds 1, so $\mu_0 = -\lambda_0 > 1$.

This completes the proof. $\blacksquare$

The presence of the advection term $-\varphi'$ does not destroy the variational structure of the problem (P_λ) .

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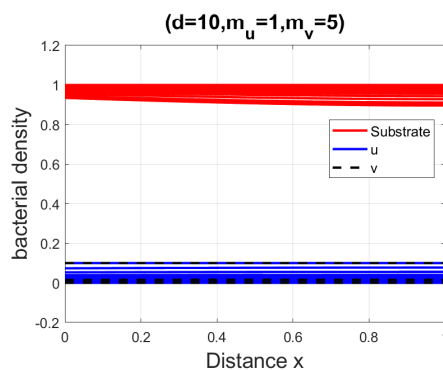
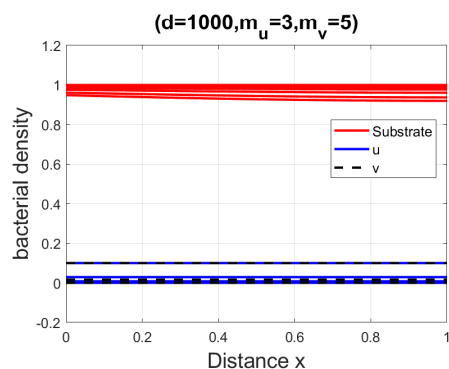


Fig. 1: The solution (S, u, v) of system (1)-(2) as a function of two variables x and t , in the case $d = 1000$ and $m_u = 3 > f(1)$, $m_v = 5 > g(1)$. Convergence towards the washout steady-state.

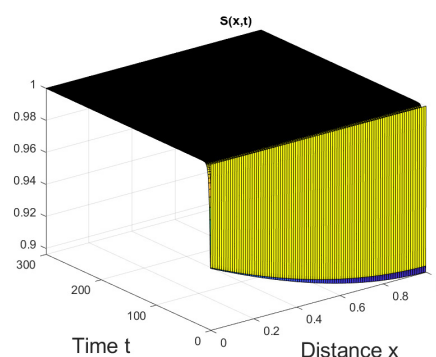
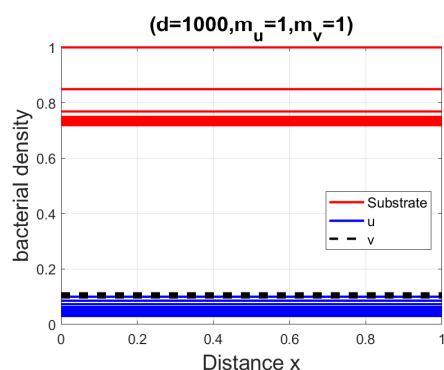


Fig. 2: The solution (S, u, v) of system (1)-(2) as a function of two variables x and t , in the case $d = 1000$, $m_u = m_v = 1$, $f(S) = \frac{3S}{1+S}$ and $g(S) = \frac{5S}{1+S}$. Convergence towards the persistence steady-state.

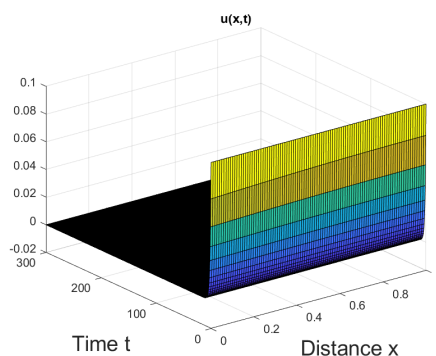
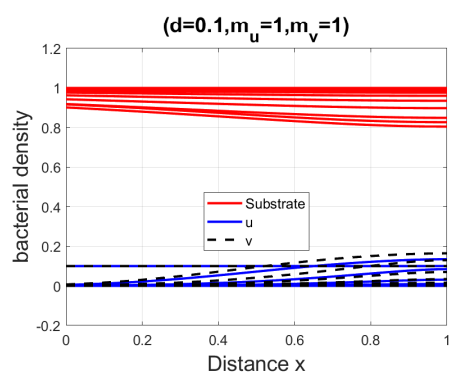


Fig. 3: The solution (S, u, v) of system (1)-(2) as a function of two variables x and t , in the case $d = 0.1$, $m_u = m_v = 1$, $f(S) = \frac{3S}{1+S}$ and $g(S) = \frac{5S}{1+S}$. Convergence towards the washout steady-state.

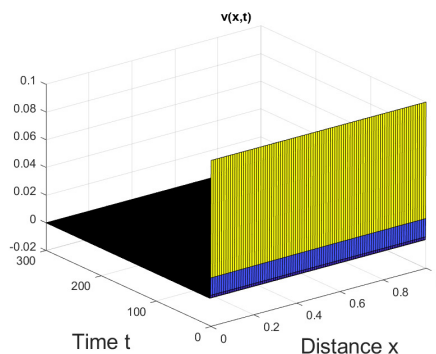


Fig. 4: The solution (S, u, v) of system (1)-(2) as a function of two variables x and t , in the case $d = 10$, $m_u = 1$, $m_v = 5$, $f(S) = \frac{3S}{1+S}$ and $g(S) = \frac{5S}{1+S}$. Convergence towards the washout steady-state.

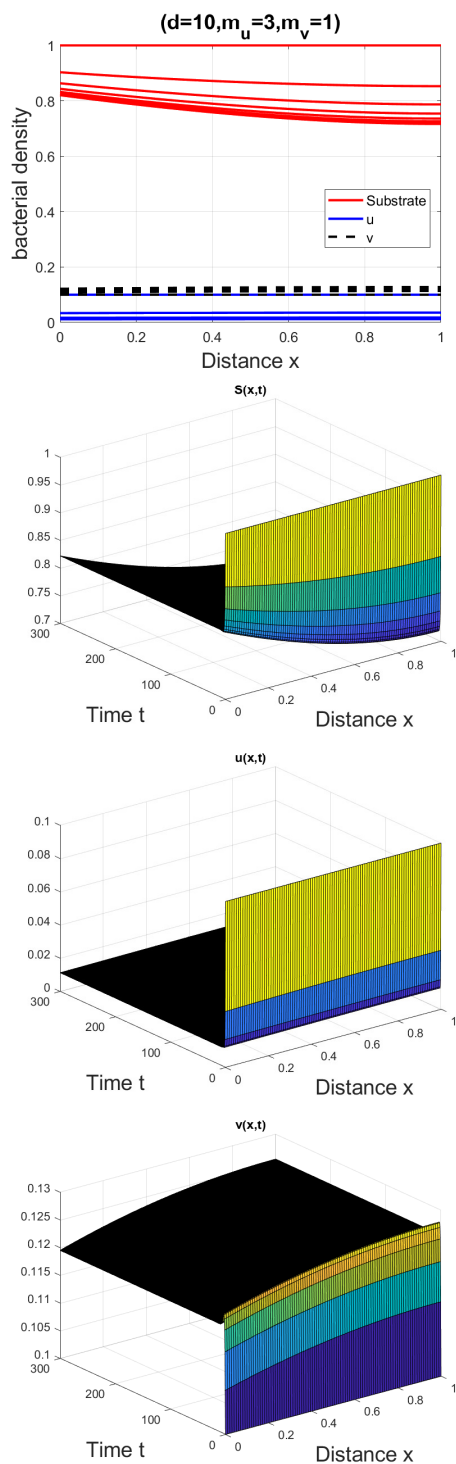


Fig. 5: The solution (S, u, v) of system (1)-(2) as a function of two variables x and t , in the case $d = 10, m_u = 3, m_v = 1, f(S) = \frac{3S}{1+S}$ and $g(S) = \frac{5S}{1+S}$. Convergence towards the persistence of attached bacteria.

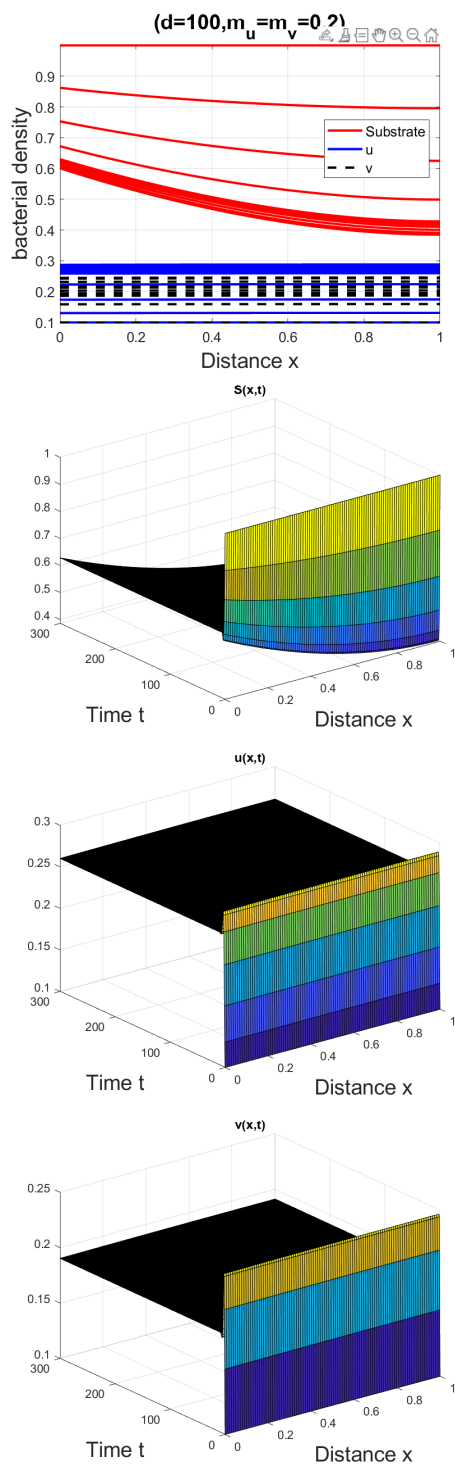


Fig. 6: The solution (S, u, v) of system (1)-(2) as a function of two variables x and t , in the case $d = 100, m_u = m_v = 0.2, f(S) = \frac{3S}{1+S}$ and $g(S) = \frac{5S}{1+S}$. Convergence towards coexistence steady state.

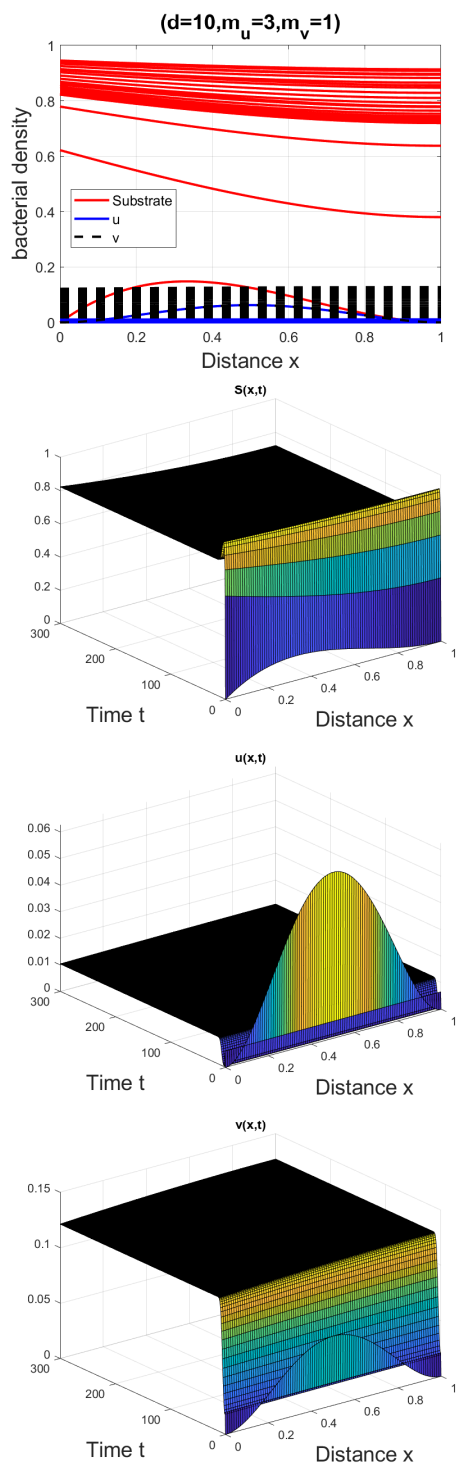


Fig. 7: The solution (S, u, v) of system (1)-(2) as a function of two variables x and t , in the case $d = 10$, $m_u = 3$, $m_v = 1$, $f(S) = \frac{3S}{1+S+S^2}$ and $g(S) = \frac{5S}{1+S}$. Convergence towards persistence of attached bacteria.

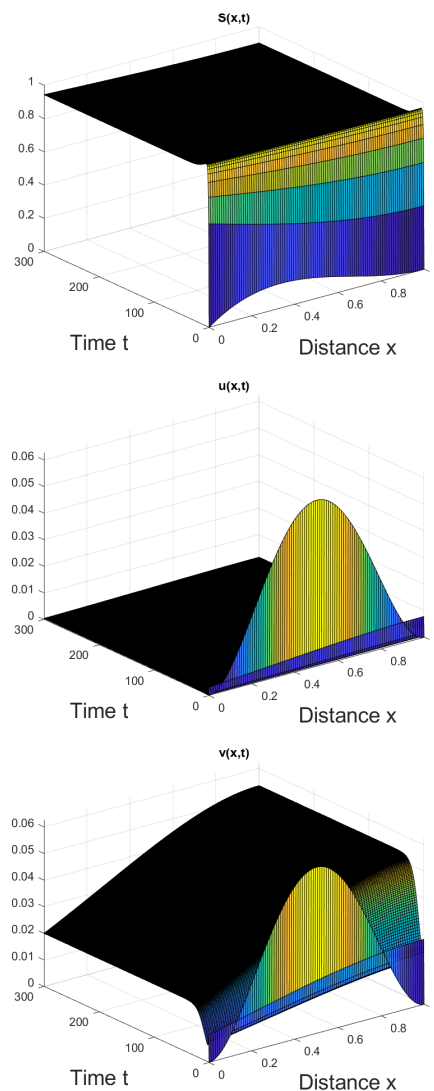


Fig. 8: The solution (S, u, v) of system (1)-(2) as a function of two variables x and t , in the case $d = 0.5$, $m_u = 3$, $m_v = 1$, $f(S) = \frac{3S}{1+S+S^2}$ and $g(S) = \frac{5S}{1+S}$. Convergence towards persistence of attached bacteria.

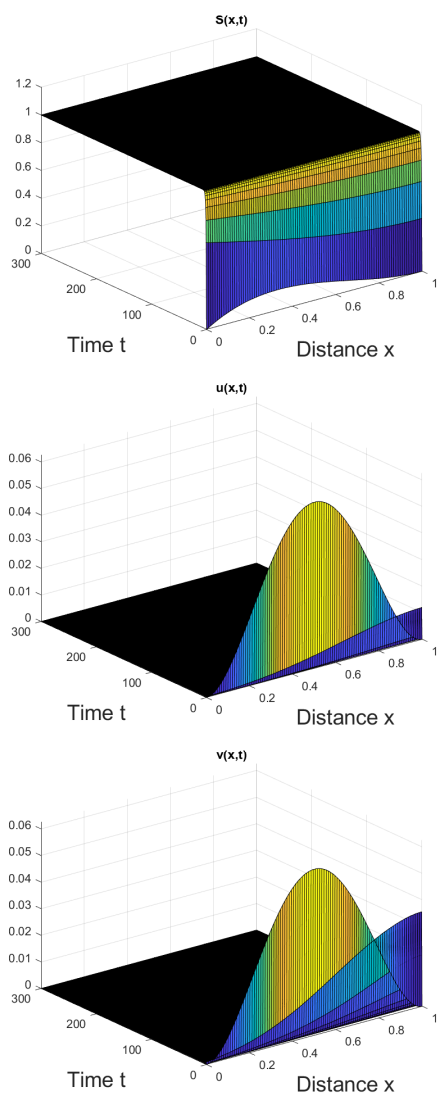


Fig. 9: The solution (S, u, v) of system (1)-(2) as a function of two variables x and t , in the case $d = 0.1$, $m_u = 3$, $m_v = 1$, $f(S) = \frac{3S}{1+S+S^2}$ and $g(S) = \frac{5S}{1+S}$. Convergence towards washout steady state.

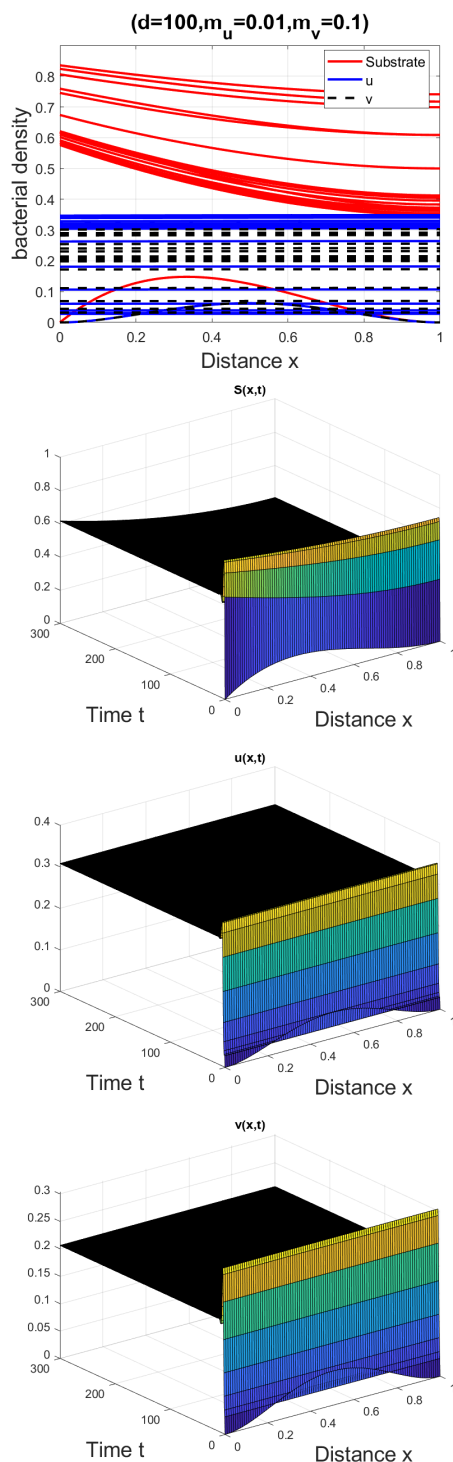


Fig. 10: The solution (S, u, v) of system (1)-(2) as a function of two variables x and t , in the case $d = 100$, $m_u = 0.01$, $m_v = 0.1$, $f(S) = \frac{3S}{1+S+S^2}$ and $g(S) = \frac{5S}{1+S}$. Convergence towards coexistence steady state.