

Existence of traveling waves in a spatial model of bacteria quiescence

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Abstract

This work presents a reaction-diffusion model that captures the spatio-temporal evolution of a bacterial colony and takes into account the quiescent stage. Using the theory of monotone wavefronts for cooperative and partially degenerate reaction-diffusion systems, we establish the existence of traveling waves and show that the spreading speed coincides with the minimal wave speed. Furthermore, we show the existence of traveling waves using the method of constructing a pair of upper and lower solutions for a noncooperative partially degenerate differential system of equations. Results demonstrate that neglecting dormant cell dynamics overestimates the spreading speed of the colony. Numerical simulations are provided to illustrate our results.

Keywords: Microbial quiescence; traveling wave fronts; reaction-diffusion system; numerical computations.

1 Introduction

Mathematical models taking into account the consumption of a limiting nutrient in the presence of a chemo-attractant have been considered extensively in the literature. In particular, it has been observed in experiments that colonies of *Escherichia coli* (*E. coli*) and *Salmonella typhimurium* (*S. typhimurium*) strains inoculated in the center of plates form high-density aggregates arranged in striking regular patterns [13]. Although the geometry of the pattern varies significantly, authors in [17] reported that the pattern-forming process is the same. In [13], *S. typhimurium* pattern was described in the form of *bacterial lawn* while pattern forming mechanism exhibited by *E. coli* was referred to as a *swarm ring*. Their proposed mathematical semi-solid model assumes negligible nutrient consumption, which is supported by experiments. Turing patterns were predicted in the simplified two-component model that neglects the consumption of nutrient in the lawn.

While several mathematical and computational models have been constructed with the aim to provide an adequate explanation of these patterns [6, 17, 13, 14], not much has been done to predict the rate of spatial spread of these highly symmetric shapes or the precise structure of the traveling pulses. To name a few, in the work [13, 16], the authors presented a bacteria-chemoattractant-nutrient interaction chemotaxis model to simulate the experimentally observed

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pulse waves [18]. Numerical simulations are provided to support their findings. In particular, most of these models emphasised the motion of the cell population in response to the chemo-attractant concentration gradient - chemotaxis. For example, the work [12, 25] included the dynamics of the dormant cells in the absence of a chemo-attractant to investigate the asymptotic speed of the spread. An extensive literature survey on existing models incorporating the Patlak-Keller-Segel chemotaxis model with application to self-organisation phenomena is found in [14].

A distinct character of bacteria is the ability to adapt or survive significant changes in environmental conditions by transitioning from an active to a relatively inactive state but also exit the dormant state and be reactivated when supplied with sufficient chemo-attractant. In this work, we consider the existence of traveling waves in a bacteria-chemoattractant interaction model when the dynamics of the active cells are influenced by the change in chemo-attractant concentration, which may result in organisms transitioning to a quiescent state. The quiescent phase has been identified under different names in the literature, e.g., dormancy, resting phase, hibernation, and ecological refugee, to name a few [20]. In the case of constant switch rates, our approach follows the work of [2, 24, 26] and several earlier studies. Since the pioneering work in [3], extensive studies have been conducted on traveling wave solutions and asymptotic behavior in terms of spreading speeds for various evolution systems. Since then, the theory of spreading speeds and monotone traveling waves have been extended in such a way that they can be applied to invasion processes for cooperation or competition among multiple species [8], see for example [9, 10, 22, 23]. Using the theory of monotone wavefronts for cooperative and partially degenerate reaction-diffusion systems, we establish the existence of traveling waves and show that the spreading speed coincides with the minimal wave speed. Furthermore, we show the existence of traveling wave solutions for a noncooperative partially degenerate reaction-diffusion system in the case of variable conversion rates.

We begin by recalling the following reaction-diffusion system representing pattern-forming processes experimentally observed in both *E. coli* and *S. typhimurium*,

$$\begin{aligned}\frac{\partial u}{\partial t} &= D_u \nabla^2 u - \nabla [\chi(u, v) \nabla v] + k_3 u (k_4 h(n) - u), \\ \frac{\partial v}{\partial t} &= D_v \nabla^2 v + k_5 n g(u) - k_7 u f(v), \\ \frac{\partial n}{\partial t} &= D_n \nabla^2 n - k_8 k_4 h(n) u,\end{aligned}\quad x \in \Omega, t > 0, \quad (1.1)$$

see [17, 13] for further details. Under this setup, $x \in \Omega \subset \mathbb{R}^m$, ($m = 1, 2, 3$), is a simply connected bounded domain and $\partial\Omega$, the surface boundary enclosing Ω , $u(x, t)$ denotes bacterial cell density, $v(x, t)$ the aspartate (chemo-attractant) concentration and $n(x, t)$ the succinate (main nutrient) concentration. The chemotactic sensitivity function is given by $\chi(u, v)$, ∇^2 denoting the Laplacian operator with D_u , D_v and D_n representing diffusion coefficients of active bacteria, the chemo-attractant and nutrient, respectively. Consumption of succinate is proportional to population growth rate with proportionality constant k_8 . The cell growth rate is given by $k_3 u h(n)$ and the production of aspartate per cell is given by $k_5 n g(u)$. Furthermore, $k_7 f(v)$ represents the consumption of aspartate, where k_7 is the rate constant. Model (1.1) summarises a mechanism for *E. coli* in semi-solid medium experiments. The authors in [13]

assumed that non-motile cells are dead, and thus not considered in the dynamics of the model. Chemotaxis is taken into account to represent the directed or biased movement of organisms in response to the chemo-attractant concentration gradient.

Motivated by the reaction-diffusion system (1.1), we ignore chemotaxis, assume nutrient concentration is large compared to the concentration of cells (negligible nutrient consumption) - which is consistent with the work of [13, Section 5.5], and incorporate the dynamics of dormant cells. In addition, the response of bacteria to the availability of the chemoattractant is taken into account by tracking the dynamics of the dormant bacteria. Neglecting dormant cell mortality and assuming that they do not proliferate, the model considered takes the form

$$\begin{aligned}\frac{\partial w}{\partial t} &= k_1 q(v)u - k_2 p(v)w, \\ \frac{\partial u}{\partial t} &= D_u \nabla^2 u + k_3 u(k_4 - u) - k_1 q(v)u + k_2 p(v)w, \\ \frac{\partial v}{\partial t} &= D_v \nabla^2 v + k_5 g(u) - k_6 v - k_7 u f(v),\end{aligned}\tag{1.2}$$

where we introduce k_6 to denote the rate of natural degradation of the chemo-attractant. To the best of our knowledge, this is the first time the model and the related analysis have been studied. The model is rendered dimensionless by choosing the following scales

$$w \sim k_4, \quad u \sim k_4, \quad v \sim k_4, \quad x \sim \sqrt{\frac{D_u}{k_3}}, \quad t \sim \frac{1}{k_3 k_4},$$

to obtain

$$\begin{aligned}\frac{\partial w}{\partial t} &= r q(v)u - s p(v)w, \\ \frac{\partial u}{\partial t} &= \nabla^2 u + u(1 - u) - r q(v)u + s p(v)w, \\ \frac{\partial v}{\partial t} &= d_v \nabla^2 v + \alpha(\beta g(u) - v) - \gamma u f(v),\end{aligned}\tag{1.3}$$

where $d_v = D_v/D_u$, $r = k_1/(k_3 k_4)$, $s = k_2/(k_3 k_4)$, $\alpha = k_6/(k_3 k_4)$, $\beta = k_5/k_6$ and $\gamma = k_7/(k_3 k_4)$. From here forthwith, we assume $g(u) = 1 + g_1(u)$ with $g_1(0) = 0$. The assumption $g(0) > 0$ takes into account the background production of the chemo-attractant in the system.

Various types of response functions have been proposed in the literature, see for example [11, 13], and the literature therein. We generalise $f(v)$, and assume it satisfies the following hypotheses: $f(v) = 0$ iff $v = 0$ and $f'(v) \geq 0$, for all v . Furthermore, we invoke assumptions on the transition functions $p(v)$ and $q(v)$.

$$\mathcal{H}_1 : p : \mathbb{R}_+ \rightarrow (0, 1] \text{ is } C^1, p'(v) \geq 0 \text{ and } \lim_{v \rightarrow \infty} p(v) = 1 \text{ for all } v,$$

$$\mathcal{H}_2 : q : \mathbb{R}_+ \rightarrow (0, 1] \text{ is } C^1, q'(v) \leq 0 \text{ and } \lim_{v \rightarrow \infty} q(v) = 0 \text{ for all } v.$$

The reaction-diffusion model is partially degenerate in the sense that one of the diffusion coefficients is zero. We remark that the proposed model (1.3) is generic and can be adapted for, e.g., cancer models. Dormancy also has an important bearing in the treatment of infections, see for example [1, 15]. Since spores are highly resistant to disinfectants, they stay dormant in wounds for periods longer than the applied disinfectant. This normally accounts for the recurrence of infections.

In the construction of the traveling wave solution of degenerate reaction-diffusion equations, we consider the system of reaction-diffusion equations of the form

$$\mathbf{u}_t = D\mathbf{u}_{xx} + \mathbf{f}(\mathbf{u}), \quad x \in \mathbb{R}, t > 0, \quad (1.4)$$

with initial conditions $\mathbf{u}(x, 0) = \mathbf{u}^0(x)$ for $x \in \mathbb{R}$, where $\mathbf{u} = (u_i)$, $D = \text{diag}(d_1, d_2, \dots, d_N)$, $d_i \geq 0$ for $i = 1, 2, \dots, N$ and $\mathbf{f}(\mathbf{u}) = (f_1(\mathbf{u}), f_2(\mathbf{u}), \dots, f_N(\mathbf{u}))$. The system of equations generalised in (1.4) can be found in various sections of the applied sciences including mathematical epidemiology, chemical kinetics, and ecology, to name a few. A traveling wave solution of (1.4) is a solution of the form $\mathbf{u} = \mathbf{u}(\xi)$, with $\xi = x + ct$, such that if we substitute this solution into the system, we have the wave equation

$$D\mathbf{u}''(\xi) - c\mathbf{u}'(\xi) + \mathbf{f}(\mathbf{u}(\xi)) = 0, \quad \xi \in \mathbb{R}. \quad (1.5)$$

This will be discussed in detail in Section 2.1.

The novelty of this work is two-fold: first, a new mathematical model capturing the evolution of a bacteria colony with a quiescent phase is formulated. Secondly, we prove the existence of traveling waves for degenerate reaction-diffusion system of equations under different selection of switch functions. Furthermore, show that the spreading speed coincides with the minimal wave speed in the limit of constant switch rates.

This paper is organised as follows: we begin in Section 2 where we summarise the traveling wave results in the absence of the quiescent stage, while Section 3 provides the full analysis of the bacteria-chemoattractant interaction model when the dynamics of the active cells are influenced by a change in chemo-attractant concentration. We establish that there exists a traveling wave speed $c^* > 0$, such that for every $c > c^*$, the model admits a nontrivial traveling wave solution for both constant and variable switch functions. In the last section, we give concluding remarks.

2 Model without quiescence

Without quiescence, the model reduces to

$$\begin{aligned} \frac{\partial u}{\partial t} &= \nabla^2 u + u(1 - u), \\ \frac{\partial v}{\partial t} &= d_v \nabla^2 v + \alpha(\beta g(u) - v) - \gamma f(v)u. \end{aligned} \quad (2.1)$$

The uniform steady-state model has two equilibria: the bacteria-free equilibrium $E_0 = (0, \beta)$ and the co-existence equilibrium $E^* = (1, v^*)$, where v^* satisfies $H(v^*) = \alpha(\beta g(1) - v^*) - \gamma f(v^*) = 0$. We notice that $\lim_{v^* \rightarrow 0^+} H(v^*) = \alpha\beta g(1) > 0$ and $H'(v^*) = -\alpha - \gamma f'(v^*) < 0$. Hence, a unique co-existence equilibrium, E^* , exists. Using the linearisation method, it is straightforward to show that E_0 is unstable and E^* is locally asymptotically stable.

Proposition 2.1. *The uniform steady state system (2.1) has no periodic orbits.*

Proof. To prove this result, we apply the Dulac-Bendixon criterion. Let $Z \subset X$ be open and simply connected in the first quadrant. Let $h_u(u, v) = u(1 - u)$ and $h_v(u, v) = \alpha(\beta g(u) - v) -$

$\gamma f(v)u$. We need to show that there exists a function $\psi : Z \rightarrow \mathbb{R}$, continuously differentiable on Z , such that

$$\frac{\partial(\psi h_u)}{\partial u} + \frac{\partial(\psi h_v)}{\partial v},$$

is either strictly negative or strictly positive everywhere on Z . Let $\psi(u, v) = \frac{1}{u^2}$. Taking Z to be open in the first quadrant, clearly, ψ is continuously differentiable in Z . Furthermore,

$$\frac{\partial(\psi h_u)}{\partial u} + \frac{\partial(\psi h_v)}{\partial v} = -\frac{1}{u^2} (1 + \alpha + \gamma f'(v)u) < 0.$$

Hence, the system has no periodic orbits in the open first quadrant. \square

Remark 2.1. *In the next section, we investigate the existence of traveling waves for model (2.1). It is straightforward to observe that the bacteria population follows the well-known Fisher's reaction-diffusion equation which admits a mono-stable traveling wave solution $u(x, t) = u(x + ct) = u(\xi)$. Assuming boundary conditions $u(-\infty) = 0$ and $u(+\infty) = 1$ for the Fisher's equation, we have the traveling wave speed $c \geq 2$.*

2.1 Traveling waves

We investigate the existence of traveling waves for system (1.4) in the setting where it is cooperative and partially degenerate. The system is cooperative on the interval if $\mathbf{f}(\mathbf{u})$ is non-decreasing in \mathbf{u} on this interval. Consider system (1.4). We begin by recalling some useful results from [2]. We denote the stability modulus of the square matrix A by

$$z(A) := \max\{Re\lambda : \det(\lambda I - A) = 0\}.$$

Let $A(\mu) = \mu^2 D + \mathbf{f}'(\mathbf{0})$ for any $\mu > 0$, and $\lambda(\mu) = z(A)$ be a simple eigenvalue of $A(\mu)$. Given that $\mathbf{f}'(\mathbf{0})$ is cooperative and irreducible, then $\lambda(\mu) > 0$ for all $\mu > 0$ such that $\Phi(\mu) = \frac{\lambda(\mu)}{\mu}$ can be defined. Then, by [2, Lemma 2.1] we define $\bar{c} = \inf_{\mu > 0} \Phi(\mu) \geq 0$. Following [2], we can prove the existence of monostable traveling waves for system (1.4) by verifying the following conditions, denoted here as assumption \mathcal{J} .

1. $\mathbf{f}(\mathbf{0}) = \mathbf{f}(\mathbf{1}) = \mathbf{0}$ and there is no ν other than $\mathbf{0}$ and $\mathbf{1}$ such that $\mathbf{f}(\nu) = \mathbf{0}$ and $\mathbf{0} \leq \nu \leq \mathbf{1}$.
2. System (1.4) is cooperative.
3. $\mathbf{f}(\mathbf{u})$ is piecewise continuous differentiable in \mathbf{u} for $\mathbf{0} \leq \mathbf{u} \leq \mathbf{1}$ and differentiable at $\mathbf{0}$, and the matrix $\mathbf{f}'(\mathbf{0})$ is irreducible with $z(\mathbf{f}'(\mathbf{0})) > 0$.

Assume assumption \mathcal{J} holds. Let $\phi \in \mathcal{C}_1$ and $\mathbf{u}(t, x; \phi)$ be the unique solution of (the integral form) (1.4) through ϕ . Then, there exists a real number $c^* \geq \bar{c} > 0$ such that the following statements are valid (see [2, Lemma 2.3]):

- (i) If ϕ has a compact support, then $\lim_{t \rightarrow \infty, |x| \geq ct} \mathbf{u}(t, x; \phi) = \mathbf{0}$, for all $c > c^*$.
- (ii) For any $c \in (0, c^*)$ and $\tau^* > 0$, there is a positive number R_{τ^*} such that for any $\phi \in \mathcal{C}_1$ with $\phi \geq \tau^*$ on an interval of length $2R_{\tau^*}$, there holds $\lim_{t \rightarrow \infty, |x| \leq ct} \mathbf{u}(t, x; \phi) = \mathbf{1}$.

(iii) If, in addition, $\mathbf{f}(\min\{\rho v(\mu^*), \mathbf{1}\}) \leq \rho \mathbf{f}'(\mathbf{0})v(\mu^*)$, $\forall \rho > 0$, then $c^* = \bar{c}$.

Further, in [2], the authors obtained the minimal wave speed and its coincidence with the spreading speed through the following assumptions, denoted here as assumption \mathcal{K} .

1. $\mathbf{f}(\mathbf{0}) = \mathbf{f}(\mathbf{1}) = \mathbf{0}$ and there is no ν other than $\mathbf{0}$ and $\mathbf{1}$ such that $\mathbf{f}(\nu) = \mathbf{0}$ and $\mathbf{0} \leq \nu \leq \mathbf{1}$.
2. System (1.4) is cooperative.
3. $\mathbf{f}(\mathbf{u})$ is piecewise continuous differentiable in \mathbf{u} for $\mathbf{0} \leq \mathbf{u} \leq \mathbf{1}$ and differentiable at $\mathbf{0}$ and the matrix $\mathbf{f}'(\mathbf{0})$ is irreducible with $z(\mathbf{f}'(\mathbf{0})) > 0$.
4. There exists $\kappa > 0$, $\sigma > 1$ and $\tau^* > 0$ such that $\mathbf{f}(\mathbf{u}) \geq \mathbf{f}'(\mathbf{0})\mathbf{u} - \kappa\|\mathbf{u}\|^\sigma \mathbf{1}$ for all $\mathbf{0} \leq \mathbf{u} \leq \tau^*$.
5. For any $\rho > 0$, $\mathbf{f}(\min\{\rho v(\mu), \mathbf{1}\}) \leq \rho \mathbf{f}'(\mathbf{0})v(\mu)$, $\forall \mu \in (0, \mu^*]$, where μ^* is the value of μ at which $\Phi(\mu)$ attains its infimum.

We recall the reaction-diffusion equation model (2.1), which we restate in the form (1.4) where

$$\mathbf{u} = (u, v)^T, \quad D = \text{diag}(1, d_v), \quad \mathbf{f}(\mathbf{u}) = \begin{pmatrix} u(1-u) \\ \alpha(\beta-v) - \gamma f(v)u \end{pmatrix}, \quad (2.2)$$

and have assumed $g(u) = \text{constant}$. Without loss of generality, we take $g(u) = 1$. For mathematical convenience, we make the change of variable $h = \beta - v$ which converts the system of equations (2.2) to

$$\mathbf{u} = (u, h)^T, \quad D = \text{diag}(1, d_v), \quad \mathbf{f}(\mathbf{u}) = \begin{pmatrix} u(1-u) \\ -\alpha h + \gamma f(v^* - h)u \end{pmatrix}. \quad (2.3)$$

For this system, the only equilibria are: $\mathbf{0} = (0, 0)^T$ and $\mathbf{1} = (1, \beta - v^*)^T$. We aim to find a traveling wave that can be viewed as a heteroclinic orbit connecting the two equilibria, $\mathbf{0}$ and $\mathbf{1}$.

Theorem 2.1. *The reaction diffusion system (2.2) with (2.3) admits a traveling wave solution $\mathbf{u}(x + ct)$ for all $c \geq \bar{c}$ connecting $\mathbf{0}$ and $\mathbf{1}$.*

Proof. To prove this result, we need to verify that the reaction-diffusion equation (2.2) with (2.3) satisfies assumption \mathcal{J} , or equivalently assumptions \mathcal{K}_{1-3} . The Jacobian matrix for $\mathbf{f}(\mathbf{u})$ is given by

$$\mathbf{f}'(\mathbf{u}) = \begin{pmatrix} (1-2u) & 0 \\ \gamma f(\beta-h) & -\alpha - \gamma u f'(\beta-h) \end{pmatrix},$$

so that

$$\mathbf{f}'(\mathbf{0}) = \begin{pmatrix} 1 & 0 \\ \gamma f(\beta) & -\alpha \end{pmatrix}.$$

We can deduce that system (2.2) with (2.3) is monotone cooperative since $\mathbf{f}(\mathbf{u})$ is differentiable and all off-diagonal entries of the Jacobian matrix, $\mathbf{f}'(\mathbf{u})$, are non-negative. It is clear that the solution \mathbf{u} verifies $\mathbf{0} \leq \mathbf{u} \leq \mathbf{1}$, such that there are no other points other than $\mathbf{0}$ and $\mathbf{1}$ that verify

$\mathbf{f}(\mathbf{0}) = \mathbf{f}(\mathbf{1}) = \mathbf{0}$. Moreover, the characteristic equation of $\mathbf{f}'(\mathbf{0})$ has one of the eigenvalues equal to 1. Hence, the stability modulus of $\mathbf{f}'(\mathbf{0})$, $z(\mathbf{f}'(\mathbf{0}))$, is strictly positive. Consequently, $\mathbf{f}'(\mathbf{0})$ is irreducible. \square

Theorem 2.2. *Consider system (2.2) with (2.3). For each $c \geq c^* = \bar{c}$, the system has a non-decreasing traveling wave solution $\mathbf{u}(x + ct)$ connecting $\mathbf{0}$ and $\mathbf{1}$, while for $c < c^*$ there is no traveling wave solution connecting $\mathbf{0}$ and $\mathbf{1}$.*

Proof. Since assumptions \mathcal{K}_{1-3} are already satisfied, we need to verify assumptions \mathcal{K}_4 and \mathcal{K}_5 to deduce that the spreading speed, c^* , coincides with the minimal wave speed, \bar{c} . In particular, we aim to find the minimal wave speed of the growing population. We assume f to be a linear such that, $f(\beta - h) = \beta - h$.

Using the fact that $-hu \geq -\frac{1}{2}(h^2 + u^2) = -\frac{1}{2}\|\mathbf{u}\|_2^2$ and $-u^2 \geq -\|\mathbf{u}\|_2^2$, we deduce that

$$\mathbf{f}(\mathbf{u}) = \mathbf{f}'(\mathbf{0})\mathbf{u} - \begin{pmatrix} u^2 \\ \gamma uh \end{pmatrix} \geq \mathbf{f}'(\mathbf{0})\mathbf{u} - \kappa\|\mathbf{u}\|_2^2\mathbf{1},$$

with $\kappa = \max\{1, \frac{1}{2}\gamma\} > 0$, $\sigma = 2$, for $\mathbf{0} < \mathbf{u} < \boldsymbol{\tau}^* = \mathbf{1}$. Thus, \mathcal{K}_4 holds. For $\mu > 0$, let us define

$$A(\mu) = \mu^2 D + \mathbf{f}'(\mathbf{0}) = \begin{pmatrix} \mu^2 + 1 & 0 \\ \gamma\beta & \mu^2 d_v - \alpha \end{pmatrix}. \quad (2.4)$$

Clearly, the eigenvalues of $A(\mu)$ are $\lambda_1 = \mu^2 + 1$ and $\lambda_2 = \mu^2 d_v - \alpha$ which are positive and negative, respectively.

The positive eigenvector corresponding to the largest eigenvalue, λ_1 , is

$$v_0 = \begin{pmatrix} \lambda_1 - \lambda_2 \\ \gamma\beta \end{pmatrix} > \mathbf{0},$$

and we set $v(\mu) = \frac{v_0}{\|v_0\|}$ such that $\|v(\mu)\| = 1$. Now, let us consider the function $\Phi(\mu) = \frac{\lambda_1(\mu)}{\mu} > 0$ for $\mu > 0$, and set $\bar{c} = \inf_{\mu > 0} \Phi(\mu)$. We aim to show that the infimum \bar{c} is reached for a positive value of μ^* . Since we have that $\Phi(\mu) > \mu$, therefore, $\lim_{\mu \rightarrow \infty} \Phi(\mu) = +\infty$. Moreover, since $\lim_{\mu \rightarrow 0} \lambda_1(\mu) > 0$, thus, we obtain $\lim_{\mu \rightarrow 0^+} \Phi(\mu) = +\infty$. Furthermore,

$$\Phi'(\mu) = \frac{\lambda_1'(\mu)\mu - \lambda_1(\mu)}{\mu^2}, \text{ then } \Phi'(\mu) = 0 \text{ whenever } \lambda_1'(\mu)\mu - \lambda_1(\mu) = 0.$$

We have that

$$\Phi'(\mu) = \frac{\mu^2 - 1}{\mu^2}.$$

Solving for $\Phi'(\mu) = 0$, we deduce that there exists $\mu^* = 1$ at which $\Phi(\mu)$ attains its infimum,

i.e., $\bar{c} = \frac{\lambda_1(\mu^*)}{\mu^*} = 2$. We compute

$$\begin{aligned} \mathbf{f}(\rho v(\mu)) &= \begin{pmatrix} \rho v_1(1 - \rho v_1) \\ -\alpha \rho v_2 + \gamma(\beta - \rho v_2)\rho v_1 \end{pmatrix} \\ &= \rho \begin{pmatrix} 1 & 0 \\ \gamma\beta & -\alpha \end{pmatrix} v(\mu) + \rho \begin{pmatrix} -\rho v_1 & 0 \\ -\rho\gamma v_1 & 0 \end{pmatrix} v(\mu) \leq \rho \mathbf{f}'(\mathbf{0})v(\mu). \end{aligned}$$

This completes the proof. \square

We remark from the above result that the minimal speed for model (2.1) is given by $\bar{c} = 2\sqrt{k_3 k_4 D_u}$ (in dimensional form) which describes the spatial rate of spread of bacteria. Numerical simulations will be provided to support these results in the next section.

2.2 Numerical simulations

We present one-dimensional numerical results for the reduced system (2.1) to support the results summarised in Theorems 2.1 and 2.2. We note that the proposed model is generic and can be used for other modeling scenarios, hence the selection of parameters is for illustration of the theoretical results only. All numerical simulations are obtained using MatLab's solver, PDEPE. We assume the production function to be given by

$$g(u) = 1 + \frac{u}{\delta + u}, \quad (2.5)$$

and the response function, $f(v) = v$. With this selection, $E_0 = (0, \beta)^T$ and $E^* = (1, v^*)^T$ where $v^* = \frac{\alpha\beta g(1)}{\gamma + \alpha}$. Unless stated differently under the figure caption, we choose $\gamma = 1$, $d_v = 0.05$, $\beta = 1$ and $\alpha = 0.5$. Fig. 1 illustrates the results in Theorems 2.1 and 2.2. Clearly, a comparison of Figs. 1 and 2 show that the wave speed is independent of the model parameters α, β and γ . This is supported by calculations of the wave speed in Fig. 3.

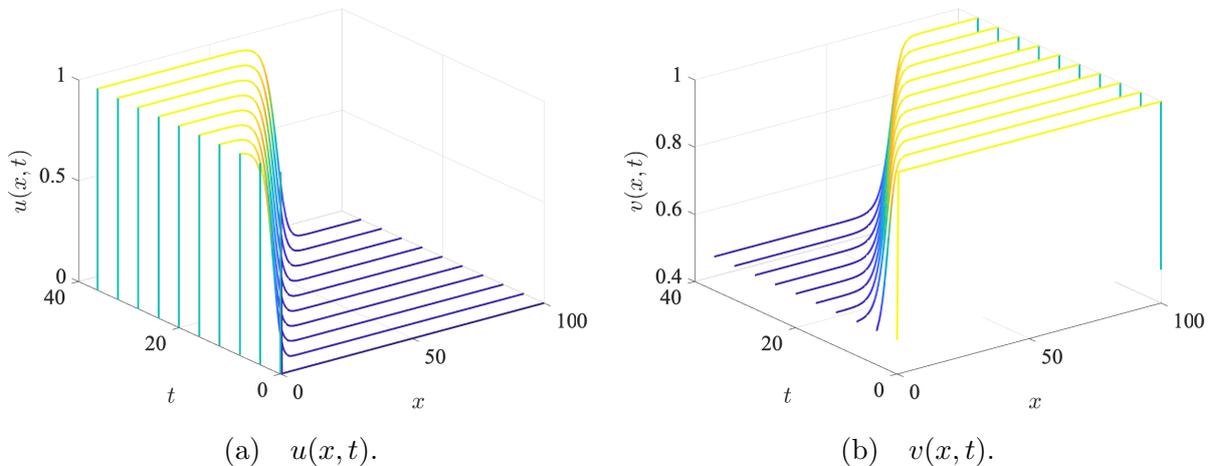


Figure 1: Stable traveling wave profiles for $u(x, t)$ and $v(x, t)$ with $g(u) = 1$ in support of results in Theorems 2.1 and 2.2.

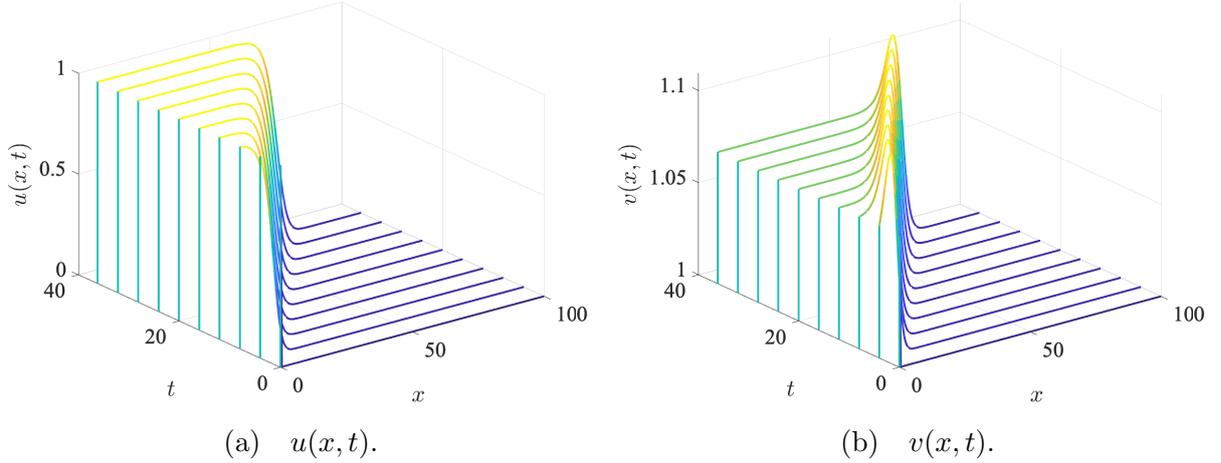


Figure 2: Stable traveling wave profiles for $u(x, t)$ and $v(x, t)$ with $g(u)$ as given in (2.5). The parameters are modified to $\alpha = 2.5$ and $\delta = 1$.

Initially, we assume a bacteria-free domain and background concentration $v(x, 0) = \beta$. Bacteria cells are introduced at $x = 0$ and the reduction in aspartate (chemo-attractant) concentration is a result of aspartate consumption. This is supported by both Figs. 1 and 2. In Fig. 2, non-monotonic traveling waves are observed in the chemo-attractant concentration profiles. The solution behaves like a stable oscillatory wave-front traveling from right to left. However, the noticeable difference comes from the condition that $\beta > v^* = 0.5$ in Fig. 1 and $\beta < v^* = 1.07$ in Fig. 2 due to the production of aspartate by the cells. In the case where $v^* > \beta$ (in Fig. 2), we see the excess production of aspartate appearing as humps in their concentration profiles. The predicted wave speed is calculated from Fig. 3 by using the slope of the contour lines. A comparison of theoretical and numerical wave speed supports the good convergence properties of the proposed method.

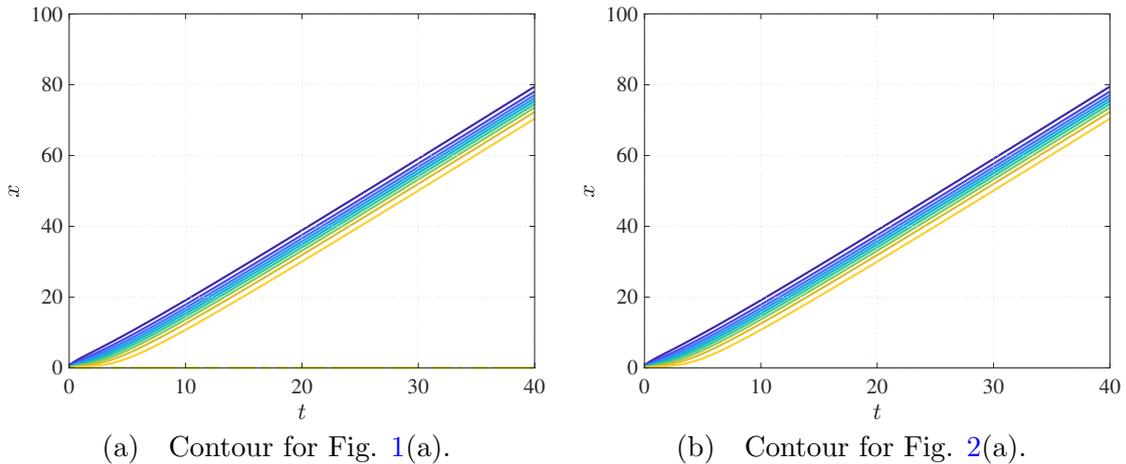


Figure 3: Contour plots corresponding to Fig. 1 and Fig. 2. The slope of the contour plot gives the wave speed, $\bar{c} \approx 2$ for each case.

3 Existence of traveling waves

We are now interested in the case where bacteria switch states depending on the chemo-attractant concentration in the system. We begin by recalling the partial differential system of equations (1.2), which we restate as follows

$$\mathbf{u}_t = D\mathbf{u}_{xx} + \mathbf{f}(\mathbf{u}), \quad x \in \mathbb{R}, t > 0, \quad (3.1)$$

where

$$\mathbf{u} = (w, u, v)^T, \quad D = \text{diag}(0, 1, d_v), \quad \mathbf{f}(\mathbf{u}) = \begin{pmatrix} rq(v)u - sp(v)w \\ u(1-u) - rq(v)u + sp(v)w \\ \alpha(\beta g(u) - v) - \gamma u f(v) \end{pmatrix}. \quad (3.2)$$

We aim to investigate and observe the dynamics of the model when the microbial population transition from one state to another is a direct consequence of the change in chemo-attractant concentration. We restrict our work to switch functions satisfying \mathcal{H}_1 and \mathcal{H}_2 . First, we consider the uniform steady-state model, i.e., ignore diffusion. We have the following result.

Proposition 3.1. *System (3.1) admits the following equilibria:*

- the microbial-free state $P^0 = (0, 0, \beta)$, and
- a unique co-existence state $P^* = (w^*, u^*, v^*)$, where $u^* = 1$, $w^* = \frac{rq(v^*)}{sp(v^*)}u^*$ and v^* satisfies $\alpha(\beta g(1) - v^*) - \gamma f(v^*) = 0$.

Proof. First, setting the right-hand side of the homogeneous system of (3.1) to zero, we obtain P^0 and P^* as the only equilibria points where v^* satisfies $\alpha(\beta g(1) - v^*) - \gamma f(v^*) = 0$. Defining $H(v^*) = \alpha(\beta g(1) - v^*) - \gamma f(v^*)$, then $H(v^*)$ is a monotonically decreasing function since $H'(v^*) = -\alpha - \gamma f'(v^*) < 0$, where we have used the properties of functions f and g . Furthermore, $\lim_{v^* \rightarrow 0^+} H(v^*) = \alpha\beta g(1) > 0$, hence, a unique solution v^* satisfying $H(v^*) = \alpha(\beta g(1) - v^*) - \gamma f(v^*) = 0$ exists. \square

To study the local stability of equilibria, we consider the general Jacobian matrix of system (3.1) given by

$$J(w, u, v) = \begin{pmatrix} -sp(v) & rq(v) & rq'(v)u - sp'(v)w \\ sp(v) & (1-u) - u - rq(v) & -rq'(v)u + sp'(v)w \\ 0 & \alpha\beta g'(u) - \gamma f(v) & -\alpha - \gamma u f'(v) \end{pmatrix}.$$

At the microbial-free state, P^0 , we have

$$J(P^0) = \begin{pmatrix} -sp(\beta) & rq(\beta) & 0 \\ sp(\beta) & 1 - rq\beta & 0 \\ 0 & \alpha\beta g'(0) - \gamma f(\beta) & -\alpha \end{pmatrix}.$$

Clearly, $-\alpha$ is one of the eigenvalues of $J(P^0)$. The remaining eigenvalues are obtained from the reduced matrix

$$\begin{pmatrix} -sp(\beta) & rq(\beta) \\ sp(\beta) & 1 - rq(\beta) \end{pmatrix},$$

whose trace is $1 - (rq(\beta) + sp(\beta))$ and the determinant given by $-sp(\beta)$. Under the hypotheses \mathcal{H}_1 and \mathcal{H}_2 , the microbial-free equilibrium state is unstable.

Next, we consider the local stability of the co-existence equilibrium, P^* . The Jacobian matrix at the co-existence equilibrium is

$$J(P^*) = \begin{pmatrix} -sp(v^*) & rq(v^*) & rq'(v^*) - sp'(v^*)w^* \\ sp(v^*) & -1 - rq(v^*) & -rq'(v^*) + sp'(v^*)w^* \\ 0 & \alpha\beta g'(1) - \gamma f(v^*) & -\alpha - \gamma f'(v^*) \end{pmatrix},$$

and the characteristic equation of the Jacobian is given by

$$Q(\lambda) = \lambda^3 + s_1\lambda^2 + s_2\lambda + s_3,$$

where the coefficients are given by

$$\begin{aligned} s_1 &= 1 + sp(v^*) + rq(v^*) + (\alpha + \gamma f'(v^*)), \\ s_2 &= (\alpha + \gamma f'(v^*))(1 + rq(v^*) + sp(v^*)) + (\gamma f(v^*) - \alpha\beta g'(1))(sp'(v^*)w^* - rq'(v^*)) + sp(v^*), \\ s_3 &= sp(v^*) (\alpha + \gamma f'(v^*)). \end{aligned}$$

Clearly, s_1 and s_3 are unconditionally positive and s_2 is positive provided $\gamma f(v^*) - \alpha\beta g'(1) \geq 0$. It remains to check if Δ_2 is positive. The second Hurwitz determinant is given by

$$\begin{aligned} \Delta_2 &= s_1 s_2 - s_3 \\ &= sp(v^*) (sp(v^*) + rq(v^*)) (\alpha + \gamma f'(v^*)) + (1 + rq(v^*) + (\alpha + \gamma f'(v^*))) \times s_2 \\ &\quad + sp(v^*) (sp(v^*) + (\gamma f(v^*) - \alpha\beta g'(1))(sp'(v^*)w^* - rq'(v^*))), \end{aligned}$$

and it is unclear if the complete expression is positive. However, assuming $\gamma f(v^*) - \alpha\beta g'(1) \geq 0$, then the coefficients $s_i > 0$ for $i = 1, 2, 3$ and the second-Hurwitz determinant, $\Delta_2 > 0$, as a result, P^* becomes locally asymptotically stable. When $\gamma f(v^*) - \alpha\beta g'(1) < 0$, the expression is not mathematically tractable and we will proceed numerically, see for example Fig. 4.

We now study the existence of traveling waves for the full system (3.1). A traveling-wave solution is a nonnegative and bounded solution in the form of $\mathbf{u}(x, t) = (w(x, t), u(x, t), v(x, t))^T = (w(z), u(z), v(z))^T$, $z = x + ct$, where $c > 0$ is referred to as traveling-wave speed. We seek to find a traveling wave that can be viewed as a heteroclinic orbit connecting the two equilibria, $\mathbf{1}$ and $\mathbf{0}$.

3.1 Constant switch rates

In this section, we study the existence of traveling waves for the full system (3.1) under the simplifying assumption that the transition functions are constants. Here, the theory of cooper-

ative systems is applicable. Furthermore, we focus on the monostable case since P^* is locally asymptotically stable. As before, we assume $g(u) = \text{constant}$, and make the change of variable $h = \beta - v$ to rewrite the system (3.1) as

$$\mathbf{u} = (w, u, h)^T, \quad D = \text{diag}(0, 1, d_v), \quad \mathbf{f}(\mathbf{u}) = \begin{pmatrix} r^*u - s^*w \\ u(1-u) - r^*u + s^*w \\ -\alpha h + \gamma f(\beta - h)u \end{pmatrix}. \quad (3.3)$$

For this system, the only equilibria are: $\mathbf{0} = (0, 0, 0)^T$ and $\mathbf{1} = (w^*, 1, \beta - v^*)^T$. Now we have the following result.

Theorem 3.1. *Consider system (3.1) with (3.3). Assuming $r^* \leq 1$, for each $c \geq c^* = \bar{c}$, the system has a non-decreasing traveling wave solution $\mathbf{u}(x + ct)$ connecting $\mathbf{0}$ and $\mathbf{1}$, while for $c < c^*$ there is no traveling wave solution connecting $\mathbf{0}$ and $\mathbf{1}$.*

Proof. First, we need to verify that the reaction-diffusion equation (3.1) satisfies assumption \mathcal{J} , or equivalently assumptions \mathcal{K}_{1-3} . The Jacobian matrix for $\mathbf{f}(\mathbf{u})$ is given by

$$\mathbf{f}'(\mathbf{u}) = \begin{pmatrix} -s^* & r^* & 0 \\ s^* & (1-2u) - r^* & 0 \\ 0 & \gamma f(\beta - h) & -\alpha - \gamma u f'(\beta - h) \end{pmatrix},$$

so that

$$\mathbf{f}'(\mathbf{0}) = \begin{pmatrix} -s^* & r^* & 0 \\ s^* & 1 - r^* & 0 \\ 0 & \gamma f(\beta) & -\alpha \end{pmatrix}.$$

We can deduce that system (3.1) with (3.3) is monotone cooperative since $\mathbf{f}(\mathbf{u})$ is differentiable and all off-diagonal entries of the Jacobian matrix, $\mathbf{f}'(\mathbf{u})$, are non-negative. It is clear that the solution \mathbf{u} verifies $\mathbf{0} \leq \mathbf{u} \leq \mathbf{1}$, such that there are no other points other than $\mathbf{0}$ and $\mathbf{1}$ that verify $\mathbf{f}(\mathbf{0}) = \mathbf{f}(\mathbf{1}) = \mathbf{0}$. Moreover, the characteristic equation of $\mathbf{f}'(\mathbf{0})$ has one of the eigenvalues equal to $-\alpha$. The remaining two eigenvalues are from the following submatrix

$$\begin{pmatrix} -s^* & r^* \\ s^* & 1 - r^* \end{pmatrix}.$$

The trace and determinant of the submatrix are given by $1 - (s^* + r^*)$ and $-s^*$, respectively, which implies that one eigenvalue is real and positive. Hence, the stability modulus of $\mathbf{f}'(\mathbf{0})$, $z(\mathbf{f}'(\mathbf{0}))$, is strictly positive. Consequently, $\mathbf{f}'(\mathbf{0})$ is irreducible.

Next, we need to verify assumptions \mathcal{K}_4 and \mathcal{K}_5 to deduce that the spreading speed \bar{c} coincides with the minimal wave speed c^* . In particular, we aim to find the minimal wave speed of the growing population. We take $f(v) = v$, that is, $f(\beta - h) = \beta - h$.

Using the fact that $-uh \geq -\frac{1}{2}(h^2 + u^2) = -\frac{1}{2}\|\mathbf{u}\|_2^2$ and $-u^2 \geq -\|\mathbf{u}\|_2^2$, we deduce that

$$\mathbf{f}(\mathbf{u}) = \mathbf{f}'(\mathbf{0})\mathbf{u} - \begin{pmatrix} 0 \\ u^2 \\ \gamma uh \end{pmatrix} \geq \mathbf{f}'(\mathbf{0})\mathbf{u} - \kappa\|\mathbf{u}\|_2^2\mathbf{1},$$

with $\kappa = \max\{1, \frac{1}{2}\gamma\} > 0$, $\sigma = 2$, for $\mathbf{0} < \mathbf{u} < \boldsymbol{\tau}^* = \mathbf{1}$. Thus, \mathcal{K}_4 holds.

For $\mu > 0$, let us define

$$A(\mu) = \mu^2 D + \mathbf{f}'(\mathbf{0}) = \begin{pmatrix} -s^* & r^* & 0 \\ s^* & \mu^2 + 1 - r^* & 0 \\ 0 & \gamma\beta & d_v\mu^2 - \alpha \end{pmatrix}. \quad (3.4)$$

Clearly, the first eigenvalue of $A(\mu)$ is $\lambda_1 = d_v\mu^2 - \alpha$ and the other eigenvalues can be obtained from the characteristic equation

$$\lambda^2 + [s^* + r^* - 1 - \mu^2] \lambda - s^* [1 + \mu^2] = 0.$$

From the polynomial equation, we have the discriminant given by $\Delta = (s^* + r^* - 1 - \mu^2)^2 + 4s^*(1 + \mu^2) > 0$. Consequently,

$$\lambda_2 = \frac{\sqrt{\Delta} - (s^* + r^* - 1 - \mu^2)}{2} > 0,$$

and

$$\lambda_3 = \frac{-\sqrt{\Delta} - (s^* + r^* - 1 - \mu^2)}{2} < 0.$$

Clearly, $\lambda_2 > \lambda_3$. Additionally, assuming $d_v \leq 1$, we have

$$\begin{aligned} \lambda_2 - \lambda_1 &= \frac{\sqrt{\Delta} - (s^* + r^* - 1 - \mu^2)}{2} - (d_v\mu^2 - \alpha) \\ &\geq \frac{\sqrt{\Delta} - (s^* + r^* - 1) + \mu^2(1 - 2d_v)}{2} \\ &\geq \frac{\sqrt{\Delta} - (s^* + r^* - 1 + \mu^2)}{2}, \text{ since } \mu^2(1 - 2d_v) \geq -\mu^2, \\ &= \frac{\Delta - (s^* + r^* - 1 + \mu^2)^2}{2[\sqrt{\Delta} + (s^* + r^* - 1 + \mu^2)]} \\ &= \frac{2[s^* + \mu^2(1 - r^*)]}{[\sqrt{\Delta} + (s^* + r^* - 1 + \mu^2)]} \\ &= \frac{s^* + \mu^2(1 - r^*)}{\mu^2 - \lambda_3} > 0, \end{aligned}$$

with $\lambda_3 < 0$ and $r^* \leq 1$ such that $\lambda_2 > \max\{\lambda_1, \lambda_3\}$. The positive eigenvector corresponding to the largest eigenvalue, λ_2 , is

$$\mathbf{v}_0 = \left(\frac{r^*(\lambda_2 - \lambda_1)}{\gamma\beta(s^* + \lambda_2)}, \frac{\lambda_2 - \lambda_1}{\gamma\beta}, 1 \right)^T > \mathbf{0},$$

and we set $\mathbf{v}(\mu) = \frac{\mathbf{v}_0}{\|\mathbf{v}_0\|}$ such that $\|\mathbf{v}(\mu)\| = 1$. Now, let us consider the function $\Phi(\mu) = \frac{\lambda_2(\mu)}{\mu} > 0$ for $\mu > 0$, and set $\bar{c} = \inf_{\mu > 0} \Phi(\mu)$. We aim to show that the infimum \bar{c} is reached for a positive value of μ^* . Since we have that $\Phi(\mu) > \mu - \frac{s^* + r^*}{\mu}$, therefore, $\lim_{\mu \rightarrow \infty} \Phi(\mu) = +\infty$.

Moreover, since $\lim_{\mu \rightarrow 0} \lambda_2(\mu) > 0$, thus, we obtain $\lim_{\mu \rightarrow 0^+} \Phi(\mu) = +\infty$. Furthermore,

$$\Phi'(\mu) = \frac{\lambda_2'(\mu)\mu - \lambda_2(\mu)}{\mu^2}, \text{ then } \Phi'(\mu) = 0 \text{ whenever } \lambda_2'(\mu)\mu - \lambda_2(\mu) = 0.$$

We have

$$\Phi'(\mu) = \mu \left(\frac{2\mu s^* - \mu(s^* + r^* - (1 + \mu^2))}{\sqrt{\Delta}} + \mu \right) - \frac{\sqrt{\Delta} - (s^* + r^* - (1 + \mu^2))}{2},$$

and after some algebra, solving for $\Phi'(\mu) = 0$ is equivalent to finding the roots of the following third-order polynomial,

$$x^3 + a_2x^2 + a_1x + a_0 = 0, \quad (3.5)$$

with $x = \mu^2$. The coefficients are given by

$$\begin{aligned} a_0 &= -(s^*)^2 - 2s^*(1 + r^*) - (r^* - 1)^2, \\ a_1 &= (s^* + r^*)^2 - 1, \\ a_2 &= 2(s^* + r^*) + 1. \end{aligned} \quad (3.6)$$

Coefficients a_2 and a_0 are strictly positive and negative, respectively. In addition, we have that a_1 is negative if $r^* \leq 1$. For any value of s^* and r^* this ensures $\Phi'(\mu) = 0$ changes sign only once on $(0, \infty)$. Hence, by Descartes's rule of signs, it follows that there is a unique positive root $\mu^* \in (0, \infty)$ at which $\Phi(\mu)$ attains its infimum, i.e., $\bar{c} = \frac{\lambda_2(\mu^*)}{\mu^*}$ provided $r^* \leq 1$.

Finally, we let $\mu \in (0, \mu^*]$ and $\rho > 0$. We compute

$$\begin{aligned} \mathbf{f}(\rho v(\mu)) &= \begin{pmatrix} r^* \rho v_2 - s^* \rho v_1 \\ \rho v_2(1 - \rho v_2) - r^* \rho v_2 + s^* \rho v_1 \\ -\alpha \rho v_3 + \gamma(\beta - \rho v_3) \rho v_2 \end{pmatrix} \\ &= \rho \begin{pmatrix} -s^* & r^* & 0 \\ s^* & 1 - r^* & 0 \\ 0 & \gamma\beta & -\alpha \end{pmatrix} v(\mu) + \rho \begin{pmatrix} 0 & 0 & 0 \\ 0 & -\rho v_2 & 0 \\ 0 & -\rho\gamma v_2 & 0 \end{pmatrix} v(\mu) \leq \rho \mathbf{f}'(\mathbf{0})v(\mu). \end{aligned}$$

Hence, we deduce the existence of a wave-front $\mathbf{u}(x + ct)$ for each $c \geq \bar{c}$ connecting $\mathbf{0}$ and $\mathbf{1}$. We also note that the asymptotic speed of population spread is identical to the minimal wave speed of traveling wave solutions connecting equilibria $\mathbf{0}$ and $\mathbf{1}$. \square

Remarks concerning the above result will be meaningful. First, we note that the existence of the traveling wave was established for constant switch functions and constant production function $g(u)$. Secondly, to establish the minimal wave speed, we needed to make a specific choice for the response function $f(v)$, otherwise, the analysis is not mathematically tractable.

In the case of the variable switch function, the system is non-cooperative, therefore, the theory on cooperative systems is not applicable. Most of the existing theoretical literature in this direction assumes cooperative, nondegenerate systems. In the case of competitive systems,

a simple change of variables will change a competition into a cooperative system. See for example [7]. Recent results for non-cooperative systems can be found, for example, in [19] and [5]. However, [19]'s work is not applicable to non-degenerate systems, while the work by [5] on non-cooperative degenerate time-periodic systems is also not applicable as it is impossible to construct the upper and lower cooperative subsystems. Thus, in the next section, we study the existence of traveling waves for general variable conversion rates, $p(v)$, $q(v)$.

3.2 Variable switch rates

In this section, we study the existence of traveling waves for the full system (3.1). Thus, substituting $\mathbf{u}(x, t) = (w(z), u(z), v(z))^T$ into (3.1) we obtain

$$\begin{cases} cw' = rq(v)u - sp(v)w, \\ cu' = u'' + (1 - u)u - rq(v)u + sp(v)w, \\ cv' = d_v v'' + \alpha(\beta g(u) - v) - \gamma u f(v), \end{cases} \quad (3.7)$$

where prime denotes differentiation with respect to z . The asymptotic conditions for (3.7) are given as follows

$$\begin{cases} w(-\infty) = w^*, & w(\infty) = 0, \\ u(-\infty) = u^*, & u(\infty) = 0, \\ v(-\infty) = v^*, & v(\infty) = \beta. \end{cases} \quad (3.8)$$

To show the existence of traveling wave solutions of system (3.1), we will adopt the technique of constructing a pair of upper and lower solutions. However, it is challenging to directly construct a pair of upper and lower solutions for system (3.1). Following the work [26], we will introduce an auxiliary system from which a pair of upper and lower solutions can be obtained. Using the auxiliary system, we can establish the existence of traveling waves for system (3.1). Below, we describe the needed results.

First, we study the eigenvalue problem of the wave profile at the bacteria-free state $\mathbf{0} = (0, 0, \beta)^T$. Linearising the equations at the bacteria-free state yields

$$\begin{cases} cw' = rq(\beta)u - sp(\beta)w, \\ cu' = u'' + u - rq(\beta)u + sp(\beta)w, \\ cv' = d_v v'' + \alpha(u\beta g'(0) - v) - \gamma u f(\beta). \end{cases} \quad (3.9)$$

We further reduce the number of equations in system (3.9) to two. Indeed, together with boundary conditions (3.8) we use equation (3.9)₁ to express $w(z)$ in terms of $u(z)$, i.e.,

$$w(z) = \frac{rq(\beta)}{c} \int_{-\infty}^z u(\xi) e^{\frac{-sp(\beta)}{c}(z-\xi)} d\xi. \quad (3.10)$$

Substituting (3.10) into (3.9) leads to

$$\begin{aligned} cu' &= u'' + (1 - rq(\beta))u + \frac{sp(\beta)rq(\beta)}{c} \int_{-\infty}^z u(\xi) e^{-\frac{sp(\beta)}{c}(z-\xi)} d\xi, \\ cv' &= d_v v'' + \alpha(u\beta g'(0) - v) - \gamma u f(\beta). \end{aligned} \quad (3.11)$$

By substituting $v(z) = e^{\lambda z}$ into (3.11)₁, we have the characteristic equation

$$\lambda^2 - c\lambda + (1 - rq(\beta))u + \frac{sp(\beta)rq(\beta)}{c(\lambda + sp(\beta)/c)} = 0, \quad (3.12)$$

or

$$P(\lambda) = \lambda^3 + e_2\lambda^2 + e_1\lambda + e_0, \quad (3.13)$$

with

$$e_2 = \frac{sp(\beta)}{c} - c, \quad e_1 = 1 - sp(\beta) - rq(\beta), \quad \text{and} \quad e_0 = \frac{sp(\beta)}{c}.$$

Now, we have two cases depending on the sign of e_1 : $1 < sp(\beta) + rq(\beta)$ or $1 \geq sp(\beta) + rq(\beta)$. As we will see later in the discussion of Lemma 3.1, the case $1 > sp(\beta) + rq(\beta)$ does not guarantee the existence of $c^* > 0$, and will not be considered further.

Lemma 3.1. *There exists $c^* > 0$ and $\lambda^* > 0$ such that*

$$P(\lambda^*) = 0, \quad \text{and} \quad \left. \frac{\partial P}{\partial \lambda} \right|_{\lambda=\lambda^*} = 0. \quad (3.14)$$

The result in Lemma 3.1 is similar to the discussion in [27, Section 3]. For completeness, we will provide an outline of the proof here. We see that (3.14) has one negative root and two roots with positive real parts. By calculation, to identify the conditions under which these two roots are positive real numbers, we have

$$\begin{aligned} P(0, c) &= \frac{sp(\beta)}{c} > 0, \\ P_1(\lambda) &:= \frac{1}{3} \frac{\partial P}{\partial \lambda} = \lambda^2 + \frac{2}{3} \left(\frac{sp(\beta)}{c} - c \right) \lambda + \frac{1}{3} (1 - sp(\beta) - rq(\beta)). \end{aligned}$$

We see that $P_1(\lambda)$ has a unique positive root

$$\lambda^* = \frac{1}{3} \frac{c^2 - sp(\beta) + \sqrt{c^4 + sp(\beta)[c^2 + sp(\beta)] + 3c^2[rq(\beta) - 1]}}{c}, \quad (3.15)$$

provided $rq(\beta) \geq 1$. Since $P(0, c)$ is positive, then equation (3.13) has two positive roots if and only if $P(\lambda^*) < 0$, otherwise, there exists two complex roots with positive real parts if $P(\lambda^*) > 0$.

To obtain an equation for the minimal wave speed, c , we transform (3.13) to get an expression giving its discriminant, i.e., an expression in terms of the parameters. Suppose

$$\begin{aligned} P(\lambda) &= P_1(\lambda)Q_1(\lambda) + R_1(\lambda), \\ P_1(\lambda) &= R_1(\lambda)Q_2(\lambda) + R_2(c, \beta), \end{aligned}$$

where $Q_1(\lambda)$, $R_1(\lambda)$ are the quotient and remainder terms when $P(\lambda)$ is divided by $P_1(\lambda)$, respectively. Similarly, $Q_2(\lambda)$, $R_2(c, \beta)$ are the quotient and remainder terms of $P_1(\lambda)$ divided by $R_1(\lambda)$. Obviously, when $R_2(c, \beta) = 0$, then $P(\lambda^*) = P_1(\lambda^*) = 0$. The sign of $-R_2(c, \beta)$ is determined by

$$\Delta(c, \beta) = b_0c^6 + b_1c^4 + b_2c^2 + b_3, \quad (3.16)$$

where

$$\begin{aligned} b_0 &= (sp(\beta))^2 + 2sp(\beta)(1 + rq(\beta)) + (rq(\beta) - 1)^2, \\ b_1 &= 2(sp(\beta))^3 + 2(sp(\beta))^2(4rq(\beta) - 1) + 2sp(\beta)(5rq(\beta) + 4)(rq(\beta) - 1) + 4(rq(\beta) - 1)^3, \\ b_2 &= (sp(\beta))^4 + 2(sp(\beta))^3(rq(\beta) - 4) + (sp(\beta))^2((rq(\beta))^2 - 20rq(\beta) - 8), \\ b_3 &= -4(sp(\beta))^4. \end{aligned}$$

From the above equation (3.16), we have the following result.

Lemma 3.2. *Assume $rq(\beta) \geq 1$. Then there exist a constant $c^* > 0$ which is a unique root of (3.16) such that*

- (i) *if $0 < c < c^*$, (3.13) has a negative real root and two complex conjugate roots with positive real parts;*
- (ii) *if $c = c^*$, (3.13) has a negative real root and a positive real multiple roots;*
- (iii) *if $c > c^*$, (3.13) has a negative real root and two different positive real roots.*

Proof. From equation (3.16), we notice that $b_3 < 0$, $b_0 > 0$ and $b_1 > 0$ provided $rq(\beta) \geq 1$. Using Descarte's rule of signs, it follows that there is a unique $c^* > 0$ such that $\Delta(c^*, \beta) = 0$, and this implies

$$\Delta(c, \beta) \begin{cases} < 0 & \text{if } c \in (0, c^*), \\ = 0 & \text{if } c = c^*, \\ > 0 & \text{if } c > c^*. \end{cases} \quad (3.17)$$

Direct calculations show that $P(\lambda^*) = P_1(\lambda^*) = 0$ is valid when $c = c^*$ and $P(\lambda)$ is a decreasing function of c . Hence, we conclude that for $c > c^*$, $P(\lambda^*) < 0$ (we have two positive roots), for $c \in (0, c^*)$, $P(\lambda^*) > 0$ (we have two complex roots), and we obtain only one positive root if $c = c^*$. It follows from Lemma 3.1 and Descarte's rule of signs that conditions (i)–(ii) hold. \square

By the method of linearization, we have shown that system (3.7) admits a minimal wave speed, c^* , which is the unique root of (3.16). Thus, it remains to show the existence of a traveling wave solution for system (3.7). We now state the main result for the existence of traveling wave solutions of system (3.1).

Theorem 3.2. *Assume $rq(\beta) \geq 1$. Then there exists a minimal wave speed $c^* > 0$, which is a unique positive root of equation (3.16). When $c \geq c^*$, system (3.1) has a traveling wave solution satisfying boundary conditions (3.8). When $0 < c < c^*$, system (3.1) has no traveling wave solution satisfying conditions (3.8).*

Theorem 3.2 will be proved through several lemmas, see for example [27, 26, 21]. We will construct a pair of upper and lower solutions for system (3.11) to show the existence of traveling wave solutions using an auxiliary system.

In order to use the method of constructing lower and upper solutions, we begin with the following result.

Lemma 3.3. *Suppose that $y \in C^2(\mathbb{R}, \mathbb{R})$ and y, y' and y'' are bounded on \mathbb{R} . If*

$$cy'(z) \geq y''(z) + (1 - rq(\beta))y(z), \quad \forall z \in \mathbb{R},$$

then $y(z) \geq 0, \forall z \in \mathbb{R}$.

Proof. Let

$$x(z) = cy'(z) - y''(z) - (1 - rq(\beta))y(z), \quad z \in \mathbb{R}.$$

Then $x(z)$ is a nonnegative, continuous and bounded function on \mathbb{R} , and we have that $x(z)$ satisfies the linear equation

$$y''(z) - cy'(z) + (1 - rq(\beta))y(z) + x(z) = 0, \quad z \in \mathbb{R}. \quad (3.18)$$

Using the theory of second-order linear ordinary differential equations, we obtain

$$y(z) = c_1 e^{\gamma_1 z} + c_2 e^{\gamma_2 z} + \frac{1}{\gamma_2 - \gamma_1} \left(\int_{-\infty}^z e^{\gamma_1(z-\xi)} x(\xi) d\xi + \int_z^{\infty} e^{\gamma_2(z-\xi)} x(\xi) d\xi \right), \quad (3.19)$$

where

$$\gamma_1 = \frac{c - \sqrt{c^2 - 4(1 - rq(\beta))}}{2} < 0, \quad \gamma_2 = \frac{c + \sqrt{c^2 - 4(1 - rq(\beta))}}{2} > 0$$

provided $rq(\beta) \geq 1$.

Since $y(z)$ and $x(z)$ are bounded on \mathbb{R} , we have that $c_1 = c_2 = 0$. As a result, $y(z) \geq 0, \forall z \in \mathbb{R}$ since $x(z)$ is nonnegative on \mathbb{R} . \square

Let $X = BUC(\mathbb{R}, \mathbb{R})$ be the *Banach* space of the functions that are uniformly continuous and bounded from \mathbb{R} to \mathbb{R} . We define a continuous mapping $B(\phi)(z)$ as follows

$$B(\phi)(z) = \frac{sp(\beta)rq(\beta)}{c(\gamma_2 - \gamma_1)} \left\{ \int_{-\infty}^z e^{\gamma_1(z-\xi)} d\xi \int_{-\infty}^{\xi} e^{-\frac{sp(\beta)}{c}(\xi-\theta)} \phi(\theta) d\theta + \int_z^{\infty} e^{\gamma_2(z-\xi)} d\xi \int_{-\infty}^{\xi} e^{-\frac{sp(\beta)}{c}(\xi-\theta)} \phi(\theta) d\theta \right\}. \quad (3.20)$$

We see that the first and second order derivatives of $B(\phi)(z)$ with respect to z are bounded on \mathbb{R} , moreover, $B(\phi)(z)$ is the unique bounded solution \mathbb{R} to the linear ordinary differential equation

$$cy'(z) = y''(z) + y(z)(1 - rq(\beta)) + \frac{sp(\beta)rq(\beta)}{c} \int_{-\infty}^z \phi(\xi) e^{-\frac{sp(\beta)}{c}(z-\xi)} d\xi.$$

Clearly, any fixed point of B in X is a solution of equation (3.11)₁, [27].

Since it is challenging to construct upper and lower solutions for system (3.11), the authors in [26] proposed and constructed an auxiliary system to overcome the problem. As a result, we propose the auxiliary system given as

$$\begin{aligned} cu' &= u'' + (1 - rq(\beta))u + \frac{sp(\beta)rq(\beta)}{c} \int_{-\infty}^z u(\xi) e^{-\frac{sp(\beta)}{c}(z-\xi)} d\xi - \alpha_2 u^2, \\ cv' &= d_v v'' + \alpha(u\beta g'(0) - v) - \gamma u f(\beta), \end{aligned} \quad (3.21)$$

and assume $rq(\beta) \geq 1$.

Consider the case where $c > c^*$. To construct the upper and lower solutions, we let $\lambda_1 < \lambda_2$ be two positive roots of equation (3.13) and define

$$\begin{aligned} \underline{v}(\xi) &= \max\{v^0 - \sigma e^{\alpha_1 \xi}, 0\}, \\ \bar{u}(\xi) &= \min\{e^{\lambda_1 \xi}, u^0\}, \\ \underline{u}(\xi) &= \max\{e^{\lambda_1 \xi} (1 - E e^{\varepsilon \xi}), 0\}, \end{aligned}$$

where $u^0 > \max\{1, 1/\alpha_2\}$. The positive constants $\alpha_1, \sigma, \varepsilon, v^0, u^0$ and E will be determined in the lemmas that follow.

Lemma 3.4. *Function $\bar{u}(\xi)$ satisfies the inequality*

$$c\bar{u}' \geq \bar{u}'' + (1 - rq(\beta))\bar{u} + \frac{sp(\beta)rq(\beta)}{c} \int_{-\infty}^z \bar{u}(\xi) e^{-\frac{sp(\beta)}{c}(z-\xi)} d\xi - \alpha_2 \bar{u}^2,$$

for any $\xi \neq \ln u^0 / \lambda_1$.

Proof. First, we assume that $\xi < \ln u^0 / \lambda_1$. Then $\bar{u}(\xi) = e^{\lambda_1 \xi}$. Since $\bar{u}(\xi)$ satisfies equation (3.21)₁, we have

$$\begin{aligned} c\bar{u}' - \bar{u}'' - (1 - rq(\beta))\bar{u} - \frac{sp(\beta)rq(\beta)}{c} \int_{-\infty}^z \bar{u}(\xi) e^{-\frac{sp(\beta)}{c}(z-\xi)} d\xi + \alpha_2 \bar{u}^2 \\ = e^{\lambda_1 \xi} \left(c\lambda_1 - \lambda_1^2 - (1 - rq(\beta)) - \frac{sp(\beta)rq(\beta)}{c} \int_{-\infty}^z e^{\lambda_1 \xi} e^{-\frac{sp(\beta)}{c}(z-\xi)} d\xi \right) + \alpha_2 (e^{\lambda_1 \xi})^2 \\ = e^{\lambda_1 \xi} P(\lambda_1) + \alpha_2 \bar{u}^2 \\ = \alpha_2 \bar{u}^2 \geq 0. \end{aligned}$$

Secondly, we suppose that $\xi > \ln u^0 / \lambda_1$ implying that $\bar{u}(\xi) = u^0$. Then we have

$$\begin{aligned} c\bar{u}' - \bar{u}'' - (1 - rq(\beta))\bar{u} - \frac{sp(\beta)rq(\beta)}{c} \int_{-\infty}^z \bar{u}(\xi) e^{-\frac{sp(\beta)}{c}(z-\xi)} d\xi + \alpha_2 \bar{u}^2 \\ = -u^0(1 - rq(\beta)) - \frac{sp(\beta)rq(\beta)}{c} \int_{-\infty}^z u^0 e^{-\frac{sp(\beta)}{c}(z-\xi)} d\xi + \alpha_2 (u^0)^2 \\ = -u^0 + \alpha_2 (u^0)^2 \\ = u^0 (\alpha_2 u^0 - 1) > 0. \end{aligned}$$

That concludes the proof. \square

Lemma 3.5. For $0 < \alpha_1 < \min\{c/d_v, \lambda_1\}$ and $\sigma > \max\{v^0, \alpha v^0/(c - d_v \alpha_1)\alpha_1\}$, the function $\underline{v}(\xi)$ satisfies

$$c\underline{v}' \leq d_v \underline{v}'' + \alpha(\bar{u}\beta g'(0) - \underline{v}) - \gamma \bar{u}f(\beta),$$

for any $\xi \neq 1/\alpha_1 \ln(u^0/\sigma)$.

Proof. Since $u^0 > 1$, we have that $1/\alpha_1 \ln(u^0/\sigma) < 0 < \ln u^0/\lambda_1$. When $v^0 - \sigma e^{\alpha_1 \xi} < 0$, that is, if $\xi > 1/\alpha_1 \ln(v^0/\sigma)$, then we have $\underline{v}(\xi) = 0$. Hence, we have that

$$\begin{aligned} & -c\underline{v}' + d_v \underline{v}'' + \alpha(\bar{u}\beta g'(0) - \underline{v}) - \gamma \bar{u}f(\beta). \\ & = \bar{u}(\alpha\beta g'(0) - \gamma f(\beta)) \geq 0, \end{aligned}$$

provided $\alpha\beta g'(0) - \gamma f(\beta) \geq 0$. Thus, the lemma is true. Now, we consider the case where $\xi < 1/\alpha_1 \ln(v^0/\sigma)$. Then $\underline{v}(\xi) = v^0 - \sigma e^{\alpha_1 \xi}$, which leads to

$$\begin{aligned} & -c\underline{v}' + d_v \underline{v}'' + \alpha(\bar{u}\beta g'(0) - \underline{v}) - \gamma \bar{u}f(\beta) \\ & = c(\sigma\alpha_1 e^{\alpha_1 \xi}) - d_v(\sigma\alpha_1^2 e^{\alpha_1 \xi}) + \alpha(e^{\lambda_1 \xi} \beta g'(0) - v^0 + \sigma e^{\alpha_1 \xi}) - \gamma e^{\lambda_1 \xi} f(\beta) \\ & = \left[c\sigma\alpha_1 - d_v\sigma\alpha_1^2 + \alpha\beta g'(0)e^{(\lambda_1 - \alpha_1)\xi} - \alpha v^0 e^{-\alpha_1 \xi} + \alpha\sigma - \gamma f(\beta)e^{(\lambda_1 - \alpha_1)\xi} \right] e^{\alpha_1 \xi} \\ & = \left[(c - d_v\alpha_1)\sigma\alpha_1 + (\alpha\beta g'(0) - \gamma f(\beta))e^{(\lambda_1 - \alpha_1)\xi} + \alpha\sigma - \alpha v^0 e^{-\alpha_1 \xi} \right] e^{\alpha_1 \xi} \\ & \geq \left[(c - d_v\alpha_1)\sigma\alpha_1 - \alpha v^0 e^{-\alpha_1 \xi} \right] e^{\alpha_1 \xi} \\ & \geq \left[(c - d_v\alpha_1)\sigma\alpha_1 - \alpha v^0 \right] e^{\alpha_1 \xi} \geq 0. \end{aligned}$$

\square

Lemma 3.6. Let $\varepsilon < \alpha_1 < \min\{\lambda_1, \lambda_2 - \lambda_1\}/2$. Then for $E > 0$ sufficiently large, the function $\underline{u}(\xi)$ satisfies

$$c\underline{u}' \leq \underline{u}'' + \underline{u}(1 - rq(\beta)) + \frac{sp(\beta)rq(\beta)}{c} \int_{-\infty}^z \underline{u}(\xi) e^{-\frac{sp(\beta)}{c}(z-\xi)} d\xi - \alpha_2 \underline{u}^2,$$

for any $\xi \neq 1/\varepsilon \ln(1/E)$.

Proof. Clearly, $\underline{v}(\xi) = 0$ if and only if $\xi \geq 1/\alpha_1 \ln(v^0/\sigma)$, $\underline{u}(\xi) = 0$ if and only if $\xi \geq 1/\varepsilon \ln(1/E)$, and $1/\varepsilon \ln(1/E) < 1/\alpha_1 \ln(v^0/\sigma)$ if and only if $E > (\sigma/v^0)e^{\alpha_1/\varepsilon}$. Assume $E > \max\{1, (\sigma/v^0)e^{\alpha_1/\varepsilon}\}$. When $\xi > 1/\varepsilon \ln(1/E)$, we have that $e^{\lambda_1 \xi} (1 - Ee^{\varepsilon \xi}) < 0$ and $\underline{u}(\xi) = 0$, moreover, the inequality in Lemma 3.6 holds.

Now, we look at the case where $\xi < 1/\varepsilon \ln(1/E)$ which implies that $\xi < 0$ since $E > 1$. Then $\xi < 1/\alpha_1 \ln(v^0/\sigma)$, $\underline{v}(\xi) = v^0 - \sigma e^{\alpha_1 \xi} > 0$ and $\underline{u}(\xi) = e^{\lambda_1 \xi} (1 - Ee^{\varepsilon \xi}) > 0$. Let L and H be two linear operators defined by

$$L(\varphi)(z) := \varphi'' - c\varphi' + \varphi(1 - rq(\beta)), \quad \text{and} \quad H(\varphi)(z) := \frac{sp(\beta)rq(\beta)}{c} \int_{-\infty}^z \varphi(\xi) e^{-\frac{sp(\beta)}{c}(z-\xi)} d\xi.$$

It then follows that

$$\begin{aligned} L(e^{\lambda \cdot})(z) &= \lambda^2 - c\lambda + (1 - rq(\beta)), \quad \forall z \in \mathbb{R}; \\ L(e^{\lambda \cdot})(z) + H(e^{\lambda \cdot})(z) &= \frac{P(\lambda)}{c(\lambda + sp(\beta)/c)} e^{\lambda z}, \quad \forall z \in \mathbb{R}, \quad \lambda \geq 0. \end{aligned}$$

□

Subsequently, it is sufficient to show that

$$\begin{aligned} & \underline{u}'' - c\underline{u}' + \underline{u}(1 - rq(\beta)) + \frac{sp(\beta)rq(\beta)}{c} \int_{-\infty}^z \underline{u}(\xi) e^{-\frac{sp(\beta)}{c}(z-\xi)} d\xi - \alpha_2 \underline{u}^2 \\ &= e^{\lambda_1 \xi} \left[\lambda_1^2 - c\lambda_1 - E(\lambda_1 + \varepsilon)^2 e^{\varepsilon \xi} + cE(\lambda_1 + \varepsilon) e^{\varepsilon \xi} + (1 - Ee^{\varepsilon \xi})(1 - rq(\beta)) \right] \\ &+ e^{\lambda_1 \xi} \left[\frac{sp(\beta)rq(\beta)}{c} e^{-\lambda_1 \xi} \int_{-\infty}^z e^{\lambda_1 \xi} (1 - Ee^{\varepsilon \xi}) e^{-\frac{sp(\beta)}{c}(z-\xi)} d\xi - \alpha_2 e^{\lambda_1 \xi} (1 - Ee^{\varepsilon \xi})^2 \right] \\ &= e^{\lambda_1 \xi} \left[\lambda_1^2 - c\lambda_1 + (1 - rq(\beta)) + \frac{sp(\beta)rq(\beta)}{c} e^{-\lambda_1 \xi} \int_{-\infty}^z e^{\lambda_1 \xi} e^{-\frac{sp(\beta)}{c}(z-\xi)} d\xi \right] \\ &+ e^{\lambda_1 \xi} Ee^{\varepsilon \xi} \left[-(\lambda_1 + \varepsilon)^2 + c(\lambda_1 + \varepsilon) - (1 - rq(\beta)) - \frac{sp(\beta)rq(\beta)}{c} e^{-\lambda_1 \xi} \int_{-\infty}^z e^{\lambda_1 \xi} e^{-\frac{sp(\beta)}{c}(z-\xi)} d\xi \right] \\ &- \alpha_2 e^{\lambda_1 \xi} (1 - Ee^{\varepsilon \xi})^2 \\ &= e^{\lambda_1 \xi} \left[-E(\lambda_1 + \varepsilon)^2 + Ec(\lambda_1 + \varepsilon) - E(1 - rq(\beta)) - \alpha_2 e^{(\lambda_1 - \varepsilon)\xi} (1 - Ee^{\varepsilon \xi})^2 \right] e^{\varepsilon \xi} \\ &- Ee^{\lambda_1 \xi} \left[\frac{sp(\beta)rq(\beta)}{c} \int_{-\infty}^z e^{\lambda_1 \xi} e^{-\frac{sp(\beta)}{c}(z-\xi)} d\xi \right] e^{\varepsilon \xi} \\ &= e^{\lambda_1 \xi} \left[-EL(e^{(\lambda_1 + \varepsilon)\cdot})(z) - \alpha_2 e^{(\lambda_1 - \varepsilon)\xi} (1 - Ee^{\varepsilon \xi})^2 \right] e^{\varepsilon \xi} - Ee^{(\lambda_1 + \varepsilon)\xi} H(e^{(\lambda_1 + \varepsilon)\cdot})(z) \\ &= -e^{(\lambda_1 + \varepsilon)\xi} \left[EL(e^{(\lambda_1 + \varepsilon)\cdot})(z) + EH(e^{(\lambda_1 + \varepsilon)\cdot})(z) + \alpha_2 e^{(\lambda_1 - \varepsilon)\xi} (1 - Ee^{\varepsilon \xi})^2 \right] \\ &= -e^{(\lambda_1 + \varepsilon)\xi} \left[E \frac{P(\lambda_1 + \varepsilon)}{c(\lambda_1 + \varepsilon + sp(\beta)/c)} + \alpha_2 e^{(\lambda_1 - \varepsilon)\xi} (1 - Ee^{\varepsilon \xi})^2 \right] \geq 0, \end{aligned} \tag{3.22}$$

where we need to show that

$$-E \frac{P(\lambda_1 + \varepsilon)}{c(\lambda_1 + \varepsilon + sp(\beta)/c)} \geq \alpha_2 e^{(\lambda_1 - \varepsilon)\xi} (1 - Ee^{\varepsilon \xi})^2. \tag{3.23}$$

Since $\xi < 0$ and $\lambda_1 - \varepsilon > 0$, we have

$$\alpha_2 \geq \alpha_2 (1 - Ee^{\varepsilon \xi})^2 e^{(\lambda_1 - \varepsilon)\xi}.$$

Using the fact that $P(\lambda_1) = 0$ and $P(\lambda_1 + \varepsilon) < 0$, inequality (3.23) is satisfied if

$$E > -\frac{c(\lambda_1 + \varepsilon + sp(\beta)/c)}{P(\lambda_1 + \varepsilon)}.$$

Remark 3.1. We can choose positive constants $\alpha_1, \sigma, \varepsilon, v^0, u^0$ and E such that $\underline{v}(\xi), \bar{u}(\xi)$ and $\underline{u}(\xi)$ satisfy Lemmas 3.4-3.6.

In the case where $c = c^*$, we choose a sequence $\{c_m\}$ such that $c_m \in (c^*, c^* + 1]$ and $\lim_{m \rightarrow \infty} c_m = c^*$ in system (3.11). By similar arguments to those in the case $c > c^*$, see [27, 26], we can conclude the existence of traveling wave solution connecting $(0, 0, \beta)$ and (w^*, u^*, v^*) .

For $0 < c < c^*$, system (3.21) has no non-negative traveling wave solution $(w(z), u(z), v(z))$ satisfying boundary conditions (3.8). If we assume $0 < c < c^*$, then the characteristic equation (3.13) has one negative root and a pair of conjugate roots with positive real parts. Thus, there is a two-dimensional unstable manifold at $(0, 0, \beta)$. The critical point $(0, 0, \beta)$ is a spiral on the unstable manifold, hence a trajectory approaching $(0, 0, \beta)$ has $(w(\xi), u(\xi), v(\xi)) < 0$ for some ξ . However, this violates the requirement that traveling waves are non-negative, thus, system (3.7) with (3.8) admits no monotone traveling wave solution if $0 < c < c^*$.

3.3 Numerical simulations

We have proved in the previous section that the reaction-diffusion system admits a non-negative heteroclinic orbit connecting P^0 and P^* when $rq(\beta) \geq 1$. Numerical simulations to support the results and the effect of parameters will be investigated in this section. The system of equations (3.1) is integrated using MatLab's PDEPE solver. For all simulations, and to ensure convergence, we choose 300 cells in space with both relative and absolute error tolerances set at 10^{-8} . We remark that the model was also solved for different parameters to ensure that the wave solution is not unstable relative to their small changes. Similar to the simulations for the reduced model, we choose $f(v) = v$ and $g(u)$ as given in equation (2.5). Following [4], the hibernation function takes the form

$$q(v) = \frac{1}{1 + v^m}, \quad (3.24)$$

while the arousal function takes the modified version

$$p(v) = \frac{\sigma + v^m}{1 + v^m}, \quad (3.25)$$

where m is a positive integer. The modified arousal function is important since no activation is possible using the simple Hill function $v^m/(1 + v^m)$. In this context, σ , taken to be $\sigma = 0.1$, defines the minimum concentration or density at which the switch can take place. Unless stated otherwise under the figure caption, we choose the baseline parameter values as follows

$$r = 1, \quad s = 1, \quad \beta = 2, \quad \alpha = 1.$$

We begin with the numerical results for the uniform steady state with a focus on the nonzero equilibrium point P^* , see Fig. 4. Using the baseline parameters, then $\gamma f(v^*) - \alpha \beta g'(1) = 1 > 0$ for $\gamma = 1$ and clearly $P^* = (0.128, 1.00, 1.50)^T$ is locally asymptotically stable. On the other hand, choosing $\gamma = 0.1$, then $\gamma f(v^*) - \alpha \beta g'(1) = -0.227 < 0$, and $P^* = (0.0066, 1.00, 2.72)^T$ remains locally asymptotically stable. The simulations in Fig. 4 were obtained using MatLab's ode15s solver.

Next, we consider the numerical solution of the reaction-diffusion system (3.1). Since we are

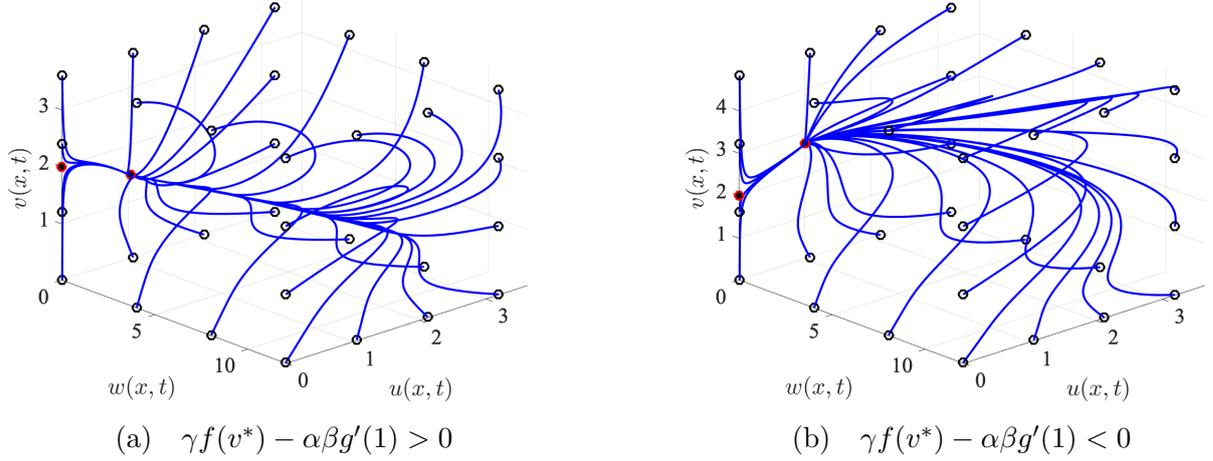


Figure 4: Illustration of the local stability of P^* . The open circles indicate the initial conditions and the solid circles indicate the equilibria.

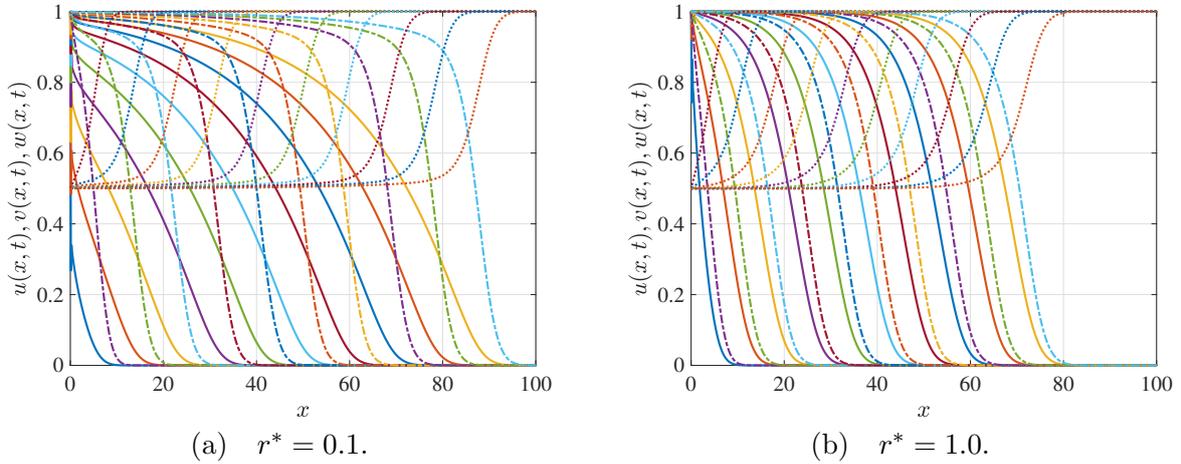


Figure 5: Illustration of the existence of traveling wave for $r^* \leq 1$ with constant switch functions. The solid line is $w(x, t)$, the dash-dot line is $v(x, t)$, and the dotted line is $u(x, t)$ at equally spaced time intervals.

interested in traveling waves, the asymptotic conditions are

$$\begin{aligned}
 w(-\infty, t) &= 0, & u(-\infty, t) &= 0, & v(-\infty, t) &= \beta, \\
 w(\infty, t) &= w^* = \frac{rq(v^*)}{sp(v^*)}, & u(\infty, t) &= u^* = 1, & v(\infty, t) &= v^* = \frac{\alpha\beta g(1)}{\gamma + \alpha}.
 \end{aligned}$$

The numerical simulations are performed on the truncated domain $x \in [0, 100]$, with the above asymptotic conditions at the endpoints. The asymptotic conditions as $x \rightarrow -\infty$ are taken as initial data for all values of x .

In Figs. 5 - 7 we support the results on the existence of the traveling waves for model (3.1). In particular, we illustrate the existence of the wave solution connecting $\mathbf{0} = (0, 0, \beta)^T$ and $\mathbf{1} = (w^*, u^*, v^*)^T$ through profiles at equally spaced time intervals. From numerical results in Fig. 5, we see the system has a traveling wave solution $\mathbf{u}(x + ct)$ connecting $\mathbf{0}$ and $\mathbf{1}$. The monotone traveling wave exists and the spreading speed coincides with the minimal wave speed

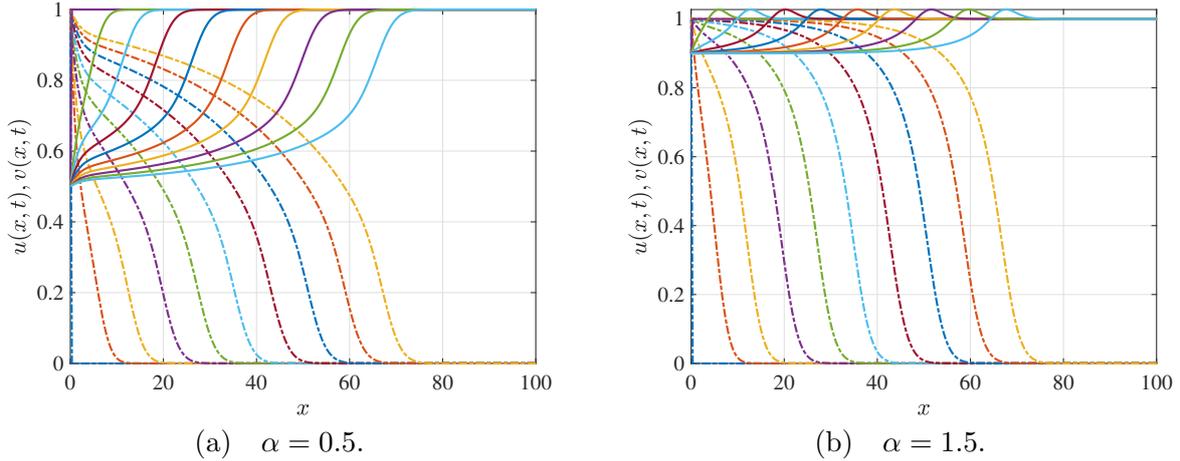


Figure 6: Illustration of the existence of traveling wave for variable switch functions ($p = p(v)$, $q = q(v)$) as given in equations (3.24) and (3.25). The broken line is $u(x, t)$ and the solid line is $v(x, t)$.

provided that $r^* \leq 1$ with constant switch functions, in addition to a constant production function, $g(u)$.

In Fig. 6 we use switch functions as given in (3.24) and (3.25) with $g(u)$ as given by expression (2.5). It is clear that changing parameters, see in Fig. 6(b), the wave profiles may be non-monotonic under this setup. In particular, we see the appearance of a hump in the profiles, see also Fig. 2.

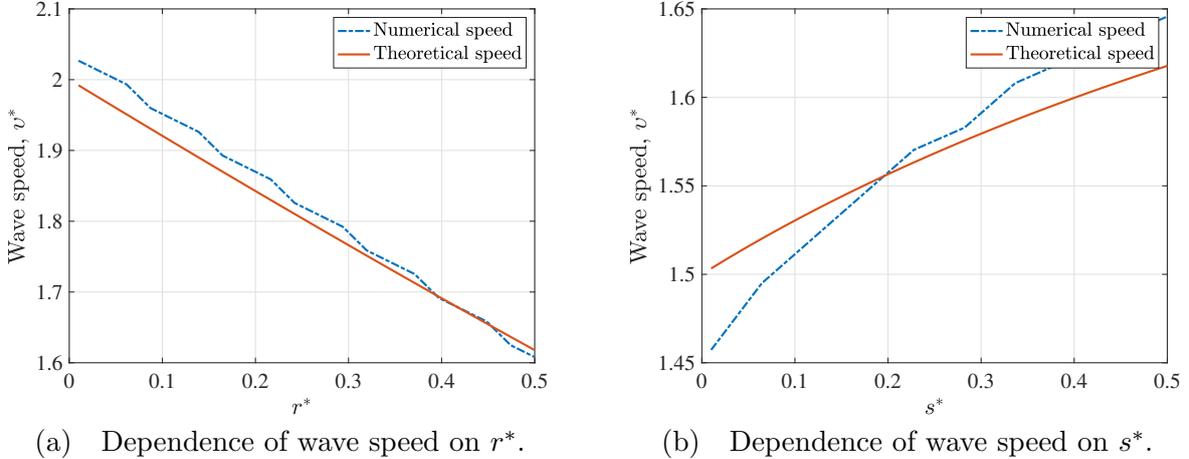


Figure 7: Comparison of theoretical and numerical wave speeds under the setup of Theorem 3.1. Throughout, we choose $r^* \leq 1$.

In order to illustrate theoretical results in comparison to numerical results, in Figs. 7 and 8 we present simulations comparing the wave speeds by varying the switch rates s and r . Results in Fig. 7 for the model with quiescence, in comparison with model results without quiescence, clearly show that ignoring dormant cells overestimates the wave speed. In particular, the wave speed for the model without quiescence is identically 2 which is above the wave speed in Fig. 7. In Fig. 8, the theoretical wave speed is obtained from the roots of the discriminant polynomial (3.13). Moreover, we observe that increasing the rate of hibernation, reduces the spreading speed, and increasing the rate of activation, increases the spreading speed.

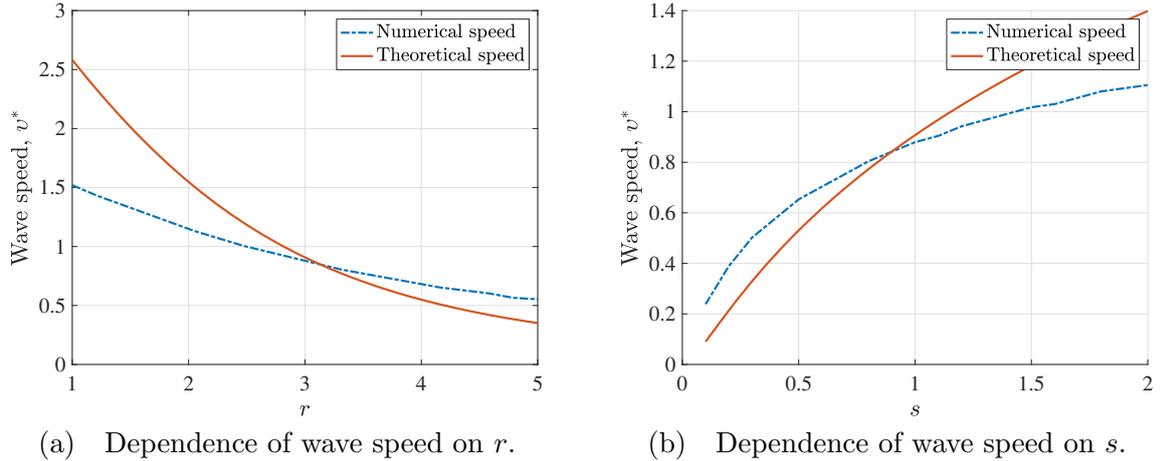


Figure 8: Comparison of theoretical and numerical wave speeds under the setup of Theorem 3.2. Throughout, we choose $rq(\beta) \geq 1$.

4 Conclusions

Mathematical models can provide insights into the dynamics of the biology they represent. In this paper, we considered the dynamics of a reaction-diffusion model describing the evolution of a bacterial colony with both active and dormant cells. We show that the solution of the model converges to a traveling wave with a speed strongly dependent on the switching rates. By using the theory of monotone wavefronts for cooperative and partially degenerate reaction-diffusion systems, the minimal wave speed is established for the model. Without quiescence, a closed form expression for the minimal wave speed was obtained to be: $\bar{c} = 2\sqrt{k_3 k_4 D_u}$. Theoretically, an implicit expression related to the solution of the eigenvalue problem is obtained in the case of constant switch functions. The wave speed is $\bar{c} = \frac{\lambda_2(\mu^*)}{\mu^*}$, where μ^* is a positive root of (3.5) under the restriction that $r^* \leq 1$. Finally, the full model with variable switch functions is investigated by linearising the eigenvalue problem around the bacteria-free state (Section 3.2). As in the case of constant switch functions, an implicit expression related to the growth rate of cells and the switch rates is obtained theoretically, i.e., the positive root of the polynomial (3.16) under the restriction that $rq(\beta) \geq 1$. In the case of variable switch functions, we established the existence of traveling waves using the method of constructing a pair of upper and lower solutions for a noncooperative partially degenerate differential system of equations. In particular, the minimal wave speed plays a crucial role in the spread of the bacterial lawn.

By reverting to the physical parameters and the above summary, the wave speed is a function of model parameters k_1, k_2, k_3, k_4 and D_u . This is consistent with the fact that the cells are producing their own food source, hence the rate of spread is not limited by the availability of aspartate. Numerical results indicate the importance of the quiescent stage in the speed of spread.

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References

- [1] V. Burke, A. Sprague, and L. Barnes. Dormancy in bacteria. *The Journal of Infectious Diseases*, pages 555–560, 1925.
- [2] J. Fang and X. Zhao. Monotone wavefronts for partially degenerate reaction-diffusion systems. *Journal of Dynamics and Differential Equations*, 21(4):663–680, 2009.
- [3] R. A. Fisher. The wave of advance of advantageous genes. *Annals of Eugenics*, 7(4):355–369, 1937.
- [4] A. Fowler and H. Winstanley. Microbial dormancy and boom-and-bust population dynamics under starvation stress. *Theoretical Population Biology*, 120:114–120, 2018.
- [5] M. Huang, S.-L. Wu, and X.-Q. Zhao. Propagation dynamics for time-periodic and partially degenerate reaction-diffusion systems. *SIAM Journal on Mathematical Analysis*, 54(2):1860–1897, 2022.
- [6] I. R. Lapidus and R. Schiller. A model for traveling bands of chemotactic bacteria. *Biophysical Journal*, 22(1):1–13, 1978.
- [7] B. Li, H. Weinberger, and M. Lewis. Spreading speeds as slowest wave speeds for cooperative systems. *Mathematical Biosciences*, 196(1):82–98, 2005.
- [8] X. Liang and X.-Q. Zhao. Asymptotic speeds of spread and traveling waves for monotone semiflows with applications. *Communications on Pure and Applied Mathematics: A Journal Issued by the Courant Institute of Mathematical Sciences*, 60(1):1–40, 2007.
- [9] R. Lui. Biological growth and spread modeled by systems of recursions. i. mathematical theory. *Mathematical Biosciences*, 93(2):269–295, 1989.
- [10] R. Lui. Biological growth and spread modeled by systems of recursions. ii. biological theory. *Mathematical Biosciences*, 93(2):297–311, 1989.
- [11] T. Malik and H. Smith. A resource-based model of microbial quiescence. *Journal of Mathematical Biology*, 53(2):231–252, 2006.
- [12] M. Mimura, H. Sakaguchi, and M. Matsushita. Reaction–diffusion modelling of bacterial colony patterns. *Physica A: Statistical Mechanics and its Applications*, 282(1-2):283–303, 2000.
- [13] J. Murray. *Mathematical biology II: Spatial models and biomedical applications*, volume 3. Springer-Verlag, Berlin Heidelberg, 2001.
- [14] K. J. Painter. Mathematical models for chemotaxis and their applications in self-organisation phenomena. *Journal of Theoretical Biology*, 481:162–182, 2019.

- [15] E. S. Rittershaus, S.-H. Baek, and C. M. Sasseti. The normalcy of dormancy: common themes in microbial quiescence. *Cell Host & Microbe*, 13(6):643–651, 2013.
- [16] J. Saragosti, V. Calvez, N. Bournaveas, A. Buguin, P. Silberzan, and B. Perthame. Mathematical description of bacterial traveling pulses. *PLoS Computational Biology*, 6(8):e1000890, 2010.
- [17] R. Tyson, S. Lubkin, and J. D. Murray. A minimal mechanism for bacterial pattern formation. *Proceedings of the Royal Society of London B: Biological Sciences*, 266(1416):299–304, 1999.
- [18] J. Y. Wakano, A. Komoto, and Y. Yamaguchi. Phase transition of traveling waves in bacterial colony pattern. *Physical Review E*, 69(5):051904, 2004.
- [19] H. Wang. Spreading speeds and traveling waves for non-cooperative reaction–diffusion systems. *Journal of Nonlinear Science*, 21(5):747–783, 2011.
- [20] J. Wang. Dynamics of a reaction–diffusion–ode system with quiescence. *Nonlinear Analysis: Real World Applications*, 58:103229, 2021.
- [21] K. Wang and W. Wang. Propagation of HBV with spatial dependence. *Mathematical Biosciences*, 210(1):78–95, 2007.
- [22] H. F. Weinberger. Long-time behavior of a class of biological models. *SIAM Journal on Mathematical Analysis*, 13(3):353–396, 1982.
- [23] H. F. Weinberger. On spreading speeds and traveling waves for growth and migration models in a periodic habitat. *Journal of Mathematical Biology*, 45(6):511–548, 2002.
- [24] S.-L. Wu and H. Wang. Front-like entire solutions for monostable reaction-diffusion systems. *Journal of Dynamics and Differential Equations*, 25(2):505–533, 2013.
- [25] K. Zhang and X. Zhao. Asymptotic behaviour of a reaction diffusion model with a quiescent stage. *Proceedings of the Royal Society A: Mathematical, Physical and Engineering Sciences*, 463(2080):1029–1043, 2007.
- [26] T. Zhang, W. Wang, and K. Wang. Minimal wave speed of a bacterial colony model. *Applied Mathematical Modelling*, 40(23-24):10419–10436, 2016.
- [27] X.-Q. Zhao and W. Wang. Fisher waves in an epidemic model. *Discrete & Continuous Dynamical Systems-B*, 4(4):1117, 2004.