



HAL
open science

Evolutionary attractors in the chemostat model

Ramsès Djidjou-Demasse, Ousmane Seydi, Alain Rapaport

► **To cite this version:**

Ramsès Djidjou-Demasse, Ousmane Seydi, Alain Rapaport. Evolutionary attractors in the chemostat model. 2024. hal-04734061

HAL Id: hal-04734061

<https://hal.science/hal-04734061v1>

Preprint submitted on 13 Oct 2024

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

Evolutionary attractors in the chemostat model

R. Djidjou-Demasse^{1,2}, O. Seydi² and A. Rapaport³

Abstract. We consider the evolutive chemostat model with a continuous phenotypic trait of the micro-organisms that impacts both the specific growth rate and the yield conversion, and whose evolution is driven by a mutation kernel. We study the evolutionary attractors (EAs) for a general class of non-linear growth functions, without assuming that the dynamics of the resource is fast compared to the growth. We generalize the well-known reproduction number as a function of the trait, and show a concentration of the asymptotic state on values of the trait that maximize the reproduction number. However, in the case of multiple maxima, we show that the system can have a unique globally stable EA, depending on a total order defined on the trait values.

Key-words. Chemostat model, mutations, evolutionary attractor, reproduction number.

AMS subject classifications. 92D15, 35R09, 35B40.

1 Introduction

Within the field of mathematical biology, competition modeling stands out as a particularly intricate area. There is a numerous of works for the mathematical analysis of dynamical systems related to populations competition and, in particular within the context of the microbial ecology and the "chemostat model" [20, 38]. This model describes the growth of one or several microbial species on a single limiting resource. Differently to more classical population models, this model couples the dynamics of the (biotic) populations with the one of the (abiotic) resource. Let us recall that the first experiments on species competition on a resource are attributed to Gause who conducted them on microbial populations [12]. Generally, one of the primary objective involves characterizing, among numerous competitors vying for a limited resource, which one (or ones) possess better competitive abilities. When there is a finite number of competitors for a single resource and no direct interaction among them, we often witness the manifestation of the Competitive Exclusion Principle (later popularized by Hardin as a general principle [19]). Put simply, one of the competitors will inevitably hold a slight advantage over the others, ultimately resulting in the extinction of all remaining contenders over the long term. Let us underline that environment is supposed to be (temporally and spatially) constant in this framework, as stressed in [2]. This principle has been proved on the mathematical model of the chemostat with several competitors on a single limited resource, under various assumptions [3, 21, 24, 36, 37, 43]. Interestingly, the possibility of changing the issue of the competition by modifying the operating conditions has been experimentally verified, as predicted by the mathematical analysis [18]. However, species mutation is known from a long time to occur in the chemostat [14, 30]. In [7], conditions for a mutant to invade in the chemostat model are studied, depending on the conversion efficiency parameter considered as the "trait" of micro-organisms. Trait substitution sequences can then be studied, converging to a global ESS (Evolutionarily Stable Strategy) trait. There is here an implicit assumption of a time scale separation between the (long) evolutionary time and the (relatively short) period of competitive interaction. However, when species have closed

¹MIVEGEC, Univ. Montpellier, IRD, CNRS, Montpellier, France. E-mail: ramses.djidjoudemasse@ird.fr

²CRISIN'2D, Ecole Polytechnique de Thiès, Senegal. E-mail: oseydi@ept.sn

³MISTEA, Univ. Montpellier, INRAE, Institut Agro, Montpellier, France. E-mail: alain.rapaport@inrae.fr

characteristics, the time for a better competitor to replace a resident species can be very long [35], and the assumption of time scale separation might be questionable. One may have then to consider a increasing number of competitors, which make the prediction of the composition of the ecosystem more challenging. Here, we consider a model of a chemostat with a continuum (or infinite) number of competitors, as in [9, 33] but with different hypotheses on the growth functions. The model proposed is subject to a dilution rate $d > 0$ with an input concentration of substrate s_{in} , assumed to be constant. The mortality rate of the biomass is considered to be negligible compared to the removal rate d (as in the classical chemostat model [20, 38]). We consider that the biomass is composed of a continuum of phenotypic traits represented by a scalar variable $x \in \mathbb{R}$. The variable x can be perceived as a taxonomic label for the competitors. Let $s(t)$ denote the concentration of substrate at time t and $v(t, x)$ the concentration of microorganisms at time t with phenotype $x \in \mathbb{R}$. The dynamics of s and v is given by the following set of equations

$$\begin{cases} \frac{ds(t)}{dt} = d(s_{\text{in}} - s(t)) - \int_{\mathbb{R}} \frac{\mu(s(t), y)}{\tau(y)} v(t, y) dy, \\ \frac{\partial v(t, x)}{\partial t} = \int_{\mathbb{R}} K(x, y) \mu(s(t), y) v(t, y) dy - d v(t, x), \end{cases} \quad (1.1)$$

where $\mu(\cdot, x)$ and $\tau(x)$ denote respectively the specific growth rate and yield coefficient of micro-organisms with trait x . The kernel function $K(x, y)$ represents the probability of mutation from phenotype y to phenotype x . Initial conditions are such that

$$s(0) = s_0 > 0 \quad \text{and} \quad v(0, \cdot) = v_0 \in L^1_+(\mathbb{R}). \quad (1.2)$$

In the works [9, 29, 33], similar models have been studied with one or several resources, but under the assumptions that i. the growth functions μ are linear with respect to s and ii. the dynamics of the resource s is fast compared to the ones of the micro-organisms v . Under these two assumptions, the quasi-static approximation gives an algebraic formula for s as function of v and the system (1.1) is replaced by the single p.d.e in v . The aim of the present work is to relax these two hypotheses and to study the whole system (1.1).

Note that Model (1.1) can be employed to retrieve the chemostat system with a finite number of consumers, as in [1]. Specifically, denote by $\{v_i\}_{i=1, \dots, n}$ the set of total densities for n competitors. Each competitor is labeled with a phenotypic trait x_i . Letting, $v(t, x) = \sum_{i=1}^n v_i(t) \delta_{x_i}(x)$, we can rewrite Model (1.1) as follows

$$\begin{cases} \frac{ds(t)}{dt} = d(s_{\text{in}} - s(t)) - \sum_{i=1}^n \frac{\mu_i(s(t))}{\tau_i} v_i(t), \\ \frac{dv_i(t)}{dt} = \sum_{j=1}^n K_{ij} \mu_j(s(t)) v_j(t) - d v_i(t), \end{cases} \quad (1.3)$$

where $\mu_j(s) = \mu(s, x_j)$, $\tau_j = \tau(x_j)$, $K_{ij} = K(x_i, x_j)$; with $\sum_{j=1}^n K_{ji} = 1$.

The primary objective of this study is to characterize the positive steady state of System (1.1). To achieve this, we will begin by presenting a result regarding the existence and uniqueness of such a steady state. In this investigation, we will focus on the concentration properties in the space of phenotypic values of the stationary state. Such a concentration properties of the steady state allows to characterize the most stronger phenotypic traits, or persistent phenotypic traits at the model steady state. Those stronger phenotypic traits will be refer as Evolutionary Attractors within the context of adaptive dynamics [9, 13, 28, 31]. Although the result concerning the existence and uniqueness of the steady state in Model (1.1) is derived under a relatively general assumption on the mutation kernel K , a more specific characterization of the steady state in terms of the phenotypic space necessitates a particular form of the mutation kernel K . More specifically, let us introduce a small positive parameter denoted ϵ (with

$0 < \epsilon \ll 1$) to represent the mutation variance in the phenotypic space. This dependence on ϵ can be characterized using the scaling form of the mutation kernel K , given by

$$K_\epsilon(x, y) = \frac{1}{\epsilon} K\left(\frac{x - y}{\epsilon}\right). \quad (1.4)$$

It is important to note that the specific form of the mutation kernel (1.4) does not imply that mutations are rare. On the contrary, mutations occur at each life cycle of the biological process. Depending on the properties of the growth rate function μ , we will demonstrate that a one-dimensional function defined in the phenotypic space is sufficient to fully characterize Evolutionary Attractors (EAs) of Model (1.1) in for some configuration. However, in certain configurations of the growth rate function μ , we will show that the Pairwise Invasibility Plot (PIP), a two-dimensional function used to study the spread of a new mutant strain in a resource already colonized by a resident strain, is necessary to accurately characterize the EAs.

Our approach is closely connected to the results previously developed in [10] within the context of steady-state concentration of integro-differential systems featuring non-local mutation terms. The work in [10] likely provides valuable insights and theoretical foundations that contribute to understanding and characterizing the concentration properties of Evolutionary Attractors in Model (1.1). However, in the past decade, there has been significant interest in the concentration properties of continuously structured models with slight mutations in evolutionary dynamics. For instance, in [9], the Hamilton-Jacobi approach is used to study concentration properties in the phenotypic values space for a resource-consumer problem, but under the assumptions of linearity of the growth function as mentioned previously. This approach has been successfully applied to understand concentration points in different scenarios involving small mutation parameters [6, 29, 34]. Other works, such as [4, 15], have also investigated the effects of small mutations on the phenotypic evolution of populations in different contexts.

The paper is organized as follows. Section 2 is dedicated to exploring several mathematical properties of Model (1.1). These properties encompass the examination of the system's existence, uniqueness, and positive solutions for System (1.1). Furthermore, we establish the existence and uniqueness of the positive steady state for System (1.1). Section 3 gives conditions for which the washed-out equilibrium (extinction of all the species) is globally attractive or on the contrary when there is persistence of the biomass. In Section 4 we focus on characterizing the EAs of Model (1.1) and in Section 5, we investigate the concentration property of the positive steady state and discuss it for a particular class of growth functions. We end by a conclusions section.

2 Mathematical properties of the model

System (1.1) is considered under the following general assumption.

Assumption 2.1 *We assume that*

(i) *The mutation kernel $K \in L^1(\mathbb{R}^2) \cap L^\infty(\mathbb{R}^2)$ is almost everywhere strictly positive, symmetric i.e. $K(x, y) = K(y, x)$ a.e. in \mathbb{R}^2 , and has a unit mass, i.e. $\int_{\mathbb{R}} K(x, y) dy = 1$, for all $x \in \mathbb{R}$.*

(ii) *There exist some constants $M_0 > 0$, $\eta_0 > 0$ and $\gamma_0 \in (0, 1)$ such that*

$$0 < K(x, y) \leq M_0 \exp(-\eta_0|x - y|^{\gamma_0}), \quad \text{a.e. } (x, y) \in \mathbb{R}^2.$$

(iii) *$d > 0$, $s_{in} > 0$.*

(iv) *$\tau = \tau(x)$ is positive, bounded function on \mathbb{R} , and there exists $\tau_0 > 0$ such that $\tau(x) \geq \tau_0$ for all $x \in \mathbb{R}$.*

(v) $\mu = \mu(s, x)$, with $(s, x) \in \mathbb{R}_+ \times \mathbb{R}$ is a bounded function such that, $\mu(0, \cdot) = 0$ and the map $s \rightarrow \mu(s, \cdot)$ is an increasing function.

(vi) For all $r > 0$ there exists $C_\mu(r) := C_\mu > 0$ such that

$$|\mu(s_1, x) - \mu(s_2, x)| \leq C_\mu |s_1 - s_2|, \quad \forall x \in \mathbb{R}, \quad 0 \leq s_1, s_2 \leq r.$$

Note that Assumption 2.1-(ii) is satisfied if K is positive almost everywhere and there exist some constants $\eta > 0$ and $\gamma > 0$ such that

$$\sup_{(x,y) \in \mathbb{R}^2} K(x, y) \exp(\eta|x - y|^\gamma) < +\infty.$$

To see that, let $\gamma_0 \in (0, \min(1, \gamma))$, then

$$\sup_{(x,y) \in \mathbb{R}^2} K(x, y) \exp(\eta|x - y|^{\gamma_0}) \leq \sup_{(x,y) \in \mathbb{R}^2} [K(x, y) \exp(\eta|x - y|^\gamma)] \sup_{(x,y) \in \mathbb{R}^2} \exp(-\eta|x - y|^\gamma + \eta|x - y|^{\gamma_0}) < +\infty.$$

Additionally, Assumption 2.1-(ii) is solely required to address the concentration properties of the steady state in Model (1.1).

2.1 Existence of non-negative of solution, and uniqueness

In this section, we will derive necessary and sufficient condition for the existence of steady state of (1.1). Let us introduce the linear operator \mathcal{H} defined, for all $\varphi \in L^1(\mathbb{R})$ and $s \in \mathbb{R}_+$, by

$$\mathcal{H}[s, \varphi](x) = \int_{\mathbb{R}} K(x, y) \mu(s, y) \varphi(y) dy, \quad \forall x \in \mathbb{R}. \quad (2.1)$$

Then, System (1.1) rewrites

$$\begin{cases} \frac{ds(t)}{dt} = d(s_{in} - s(t)) - \int_{\mathbb{R}} \frac{\mu(s(t), y)}{\tau(y)} v(t, y) dy, \\ \frac{\partial v(t, \cdot)}{\partial t} = -dv(t, \cdot) + \mathcal{H}[s(t), v(t, \cdot)], \\ s(0) = s_0 > 0, \quad v(0, \cdot) = v_0 \in L_+^1(\mathbb{R}). \end{cases} \quad (2.2)$$

The following result ensures the the well-posedness of System (2.2).

Theorem 2.2 *Let Assumption 2.1 be satisfied.*

1. *There exists a global and unique solution $u(\cdot, s_0, v_0) : [0, \infty) \rightarrow \mathbb{R}_+ \times L_+^1(\mathbb{R})$ of (1.1) with $u(0, s_0, v_0) = (s_0, v_0)$ and $u(t, s_0, v_0) = (s(t), v(t, \cdot))$ for all $t > 0$.*
2. *The semi-flow defined by $\{u(t, s_0, v_0)\}_{t \in \mathbb{R}_+}$ is bounded dissipative and asymptotically smooth, and hence, it admits a global attractor in $\mathbb{R}_+ \times L_+^1(\mathbb{R})$.*

Bounded dissipative: there exists a bounded set $\mathcal{B} \subset \mathbb{R}_+ \times L_+^1(\mathbb{R})$ such that for any bounded set $U \subset \mathbb{R}_+ \times L_+^1(\mathbb{R})$, there exists $\eta = \eta(U, \mathcal{B}) \geq 0$ such that $u(t, U) \subset \mathcal{B}$ for $t \geq \eta$.

Asymptotically smooth: for any nonempty, closed, bounded set $U \subset \mathbb{R}_+ \times L_+^1(\mathbb{R})$, there exists a nonempty compact set $J = J(U)$ such that J attracts the set $\{\varphi \in U : u(t, \varphi) \in U, \forall t \geq 0\}$.

Moreover, we have

$$\limsup_{t \rightarrow +\infty} \left(s(t) + \frac{1}{\bar{\tau}} \int_{\mathbb{R}} v(t, x) dx \right) \leq s_{in} \quad (2.3)$$

with $\bar{\tau} = \sup_{x \in \mathbb{R}} \tau(x)$.

We recall that a nonempty set $J \subset \mathbb{R} \times L^1(\mathbb{R})$ is said to attract a nonempty set $B \subset \mathbb{R} \times L^1(\mathbb{R})$ if $\delta_{\mathbb{R} \times L^1(\mathbb{R})}(u(t, B), J) \rightarrow 0$ as $t \rightarrow +\infty$, where $\delta_{\mathbb{R} \times L^1(\mathbb{R})}(B, J) = \sup_{u \in B} \inf_{v \in J} |u - v|_{\mathbb{R} \times L^1(\mathbb{R})}$ is a semi-distance on $\mathbb{R} \times L^1(\mathbb{R})$. Moreover, it is worth noting that the term "asymptotically smooth" here is used within the terminology of Hale, Lasalle, and Slemrod [17]. However, this is strictly equivalent to the notion of "asymptotically compact" within the terminology of Ladyzhenskaya [23].

Proof. By setting $F(s, v) = \left(ds_{\text{in}} - \int_{\mathbb{R}} \frac{\mu(s, y)}{\tau(y)} v(y) dy, \mathcal{H}[s, v(\cdot)] \right)$, with $(s, v) \in \mathbb{R} \times L^1(\mathbb{R})$, System (2.2) becomes

$$\partial_t(s(t), v(t, x)) = -d(s(t), v(t, x)) + F(s(t), v(t, \cdot))(x). \quad (2.4)$$

By Assumption 2.1 on μ and τ , it comes that for each $r > 0$ there exists $\lambda = \lambda(r) > 0$ such that

$$\lambda v + \mathcal{H}[s, v] \in L^1_+(\mathbb{R}) \quad \text{and} \quad \lambda s + ds_{\text{in}} - \int_{\mathbb{R}} \frac{\mu(s, y)}{\tau(y)} v(y) dy \geq 0,$$

whenever $(s, v) \in \mathbb{R}_+ \times L^1_+(\mathbb{R})$ such that $0 \leq s \leq r$ and $0 \leq \int_{\mathbb{R}} v(y) dy \leq r$. Since $\lambda \cdot (s, v) + F(s, v)$ is locally Lipschitz, then for any $(s_0, v_0) \in \mathbb{R} \times L^1$, we can find $T_0 = T_0(s_0, v_0) > 0$ such that (2.2) has a unique solution $(s, v) \in \mathcal{C}([0, T_0] \times \mathbb{R}, \mathbb{R}_+ \times L^1_+) \cap \mathcal{C}^1([0, T_0] \times \mathbb{R}, \mathbb{R}_+ \times L^1_+)$. See, for *eg.*, [32] for classical results. The local well-posedness and positivity of (2.2) holds. To obtain the global existence of the solution we note that for any fixed x

$$\frac{d}{dt} \left(s(t) + \frac{1}{\bar{\tau}} \int_{\mathbb{R}} v(t, x) dx \right) \leq ds_{\text{in}} - d \left(s(t) + \frac{1}{\bar{\tau}} \int_{\mathbb{R}} v(t, x) dx \right), \quad t \geq 0$$

with $\bar{\tau} = \sup_{x \in \mathbb{R}} \tau(x)$. Therefore, the last inequality ensures that

$$\limsup_{t \rightarrow +\infty} \left(s(t) + \frac{1}{\bar{\tau}} \int_{\mathbb{R}} v(t, x) dx \right) \leq s_{\text{in}}. \quad (2.5)$$

We show that the semi-flow $\{u(t, \cdot, s_0, v_0)\}_t$ is asymptotically smooth, *ie.*, for any closed, bounded and positively invariant set $B \subset \mathbb{R}_+ \times L^1_+$, there exists a compact set $\Omega \subset \mathbb{R}_+ \times L^1_+$ such that $\gamma(u(t, K), \Omega) \rightarrow 0$ as $t \rightarrow \infty$, where γ is the Hausdorff semi-distance (*eg.*, see [16]). By (2.4) we have

$$(s(t), v(t, \cdot)) = e^{-dt}(s_0, v_0(\cdot)) + \int_0^t e^{-d(t-\eta)} F(s(\eta), v(\eta, \cdot)) d\eta, \quad \text{for } t \geq 0, s_0 \geq 0, v_0 \in L^1_+.$$

Then, the compactness of F gives that the semi-flow $\{u(t, \cdot)\}_t$ is asymptotically smooth [41]. Note that such a compactness of F comes from the compactness of the linear operator \mathcal{H} . Furthermore, the last item of Assumption 2.1 provides a condition on K to ensure the compactness of \mathcal{H} (see [10] for more details). ■

2.2 Steady states

Let $(s, v(\cdot)) \in \mathbb{R}_+ \times L^1(\mathbb{R})$ be a steady state of System (1.1). Then, by (2.2) we have

$$\begin{cases} d(s_{\text{in}} - s) = \int_{\mathbb{R}} \frac{\mu(s, y)}{\tau(y)} v(y) dy, \\ 0 = -dv + \mathcal{H}[s, v]. \end{cases} \quad (2.6)$$

First, it is easy to see that the washout steady state

$$E_0 = (s_{\text{in}}, 0_{L^1}) \quad (2.7)$$

is always a solution of (2.6).

In the following, we discuss the existence of a positive equilibrium $\bar{E} = (\bar{s}, \bar{v})$ with $\bar{s} > 0$ and $\bar{v} \in L_+^1(\mathbb{R}) \setminus \{0_{L^1}\}$. From the first equation of (2.6), note that a necessary condition for the existence of \bar{E} is that $\bar{s} \in (0, s_{\text{in}})$. Furthermore, the second equation of (2.6) rewrites

$$\frac{1}{d}\mathcal{H}[\bar{s}, \bar{v}] = \bar{v}. \quad (2.8)$$

Let us define the function

$$\mathcal{T}(s) := \frac{1}{d}r(\mathcal{H}[s, \cdot]), \quad s > 0 \quad (2.9)$$

where $r(\mathcal{H}[s, \cdot])$ denotes the spectral radius of the linear operator $\mathcal{H}[s, \cdot]$. In order to deal with the positive steady state \bar{E} , we define the *generalized break-even concentration* of the model (1.1) as the solution $s > 0$ such that

$$\mathcal{T}(s) = 1, \quad (2.10)$$

when it exists, and $+\infty$ otherwise.

Note that, since $\mathcal{H}[s, \cdot]$ is a positive bounded linear operator, we know from [40] that

$$\text{sign}(\mathcal{T}(s) - 1) = \text{sign}(b(\mathcal{H}[s, \cdot] - d\mathbf{I}_d)), \quad \forall s \in [0, s_{\text{in}}] \quad (2.11)$$

with \mathbf{I}_d the identity operator and $b(\mathcal{H}[s, \cdot] - d\mathbf{I}_d)$ the spectral bound of $\mathcal{H}[s, \cdot] - d\mathbf{I}_d$. We then introduce the following result (the proof is given later).

Lemma 2.3 *Let Assumption 2.1 be satisfied. Then $s \mapsto \mathcal{T}(s)$ is continuously increasing in $[0, s_{\text{in}}]$ and the equation (2.10) has a unique solution in $(0, s_{\text{in}})$ if and only if $\mathcal{T}(s_{\text{in}}) > 1$.*

Next, since for all $\bar{s} > 0$, $\frac{1}{d}\mathcal{H}[\bar{s}, \cdot]$ is compact and irreducible operator (eg., see [10]), by the equality (2.8) the Krein-Rutman's theorem gives that the spectral radius $\mathcal{T}(\bar{s})$ of $\frac{1}{d}\mathcal{H}[\bar{s}, \cdot]$ must satisfy $\mathcal{T}(\bar{s}) = 1$. Furthermore, \bar{v} is a multiple of the normalized positive eigenvector $\bar{\phi}(\bar{s}, \cdot) \in L_+^1(\mathbb{R})$ of $\frac{1}{d}\mathcal{H}[\bar{s}, \cdot]$ associated to the eigenvalue $\mathcal{T}(\bar{s})$. Thus, the positive steady state \bar{E} is such that

$$\begin{cases} \bar{v} = c\bar{\phi}(\bar{s}, \cdot), & \text{with } c > 0, \\ d(s_{\text{in}} - \bar{s}) = \int_{\mathbb{R}} \frac{\mu(\bar{s}, y)}{\tau(y)} \bar{v}(y) dy, \\ \mathcal{T}(\bar{s}) = 1. \end{cases} \quad (2.12)$$

Thanks to Lemma 2.3, we have the following result on the steady state of System (1.1)

Theorem 2.4 *Let Assumption 2.1 be satisfied.*

- i) *If $\mathcal{T}(s_{\text{in}}) \leq 1$, then System (1.1) has a unique steady state given by $E_0 = (s_{\text{in}}, 0)$.*
- ii) *If $\mathcal{T}(s_{\text{in}}) > 1$, then (1.1) has two steady states $E_0 = (s_{\text{in}}, 0)$ and $\bar{E} = (\bar{s}, \bar{v})$ with $\bar{s} \in (0, s_{\text{in}})$ the unique solution of $\mathcal{T}(\bar{s}) = 1$. Furthermore, $\bar{v} = c\bar{\phi}(\bar{s}, \cdot)$, where the function $\bar{\phi}(\bar{s}, \cdot) \in L_+^1(\mathbb{R})$ is the normalized principal eigenvector of $\frac{1}{d}\mathcal{H}[\bar{s}, \cdot]$ and $c = \frac{d^2(s_{\text{in}} - \bar{s})}{\int_{\mathbb{R}} \frac{\mu(\bar{s}, y)}{\tau(y)} \bar{\phi}(\bar{s}, y) dy} > 0$.*

We then complete this section by the proof of Lemma 2.3.

Proof of Lemma 2.3. We first note that the linear operator $\frac{1}{d}\mathcal{H}[s, \cdot]$ is a positive, bounded, compact, and irreducible linear operator for each $s > 0$, eg., see [10]. Therefore, the continuity of the spectral radius in the space of compact linear operators implies that the map $s \mapsto \mathcal{T}(s)$ is continuous in $s \geq 0$. Since $\frac{1}{d}\mathcal{H}[s, \cdot]$ converges to 0 as $s \rightarrow 0$ in the operator norm topology, it follows that $\mathcal{T}(s) \rightarrow 0$ when $s \rightarrow 0$. Next, Assumption 2.1 implies that for $s_1 > s_2 > 0$ and $v \in L_+^1(\mathbb{R}) \setminus \{0\}$

$$\frac{1}{d}(\mathcal{H}[s_1, \cdot] - \mathcal{H}[s_2, \cdot])v > 0.$$

Thus, by the compactness and the irreducibility of $\frac{1}{d}(\mathcal{H}[s, \cdot])$ it comes that $s \mapsto \mathcal{T}(s)$ is continuously increasing in $[0, +\infty)$ (see [22, Proposition 10.12]). The proof is completed by applying the intermediate values theorem. ■

3 Extinction and uniform persistence of biomass

In this section, our objective is to establish the global asymptotic stability of the washout steady state, specifically when $\mathcal{T}(s_{\text{in}}) \leq 1$. Furthermore, we will also show that the bacterium not only persists but achieves uniform persistence when $\mathcal{T}(s_{\text{in}}) > 1$. To do this, we first prove the following technical lemma.

Lemma 3.1 *Let Assumption 2.1 be satisfied and set $\lambda_0 := b(\mathcal{H}[s_{\text{in}}, \cdot] - d\mathbb{I}_d)$. Then there exists $\phi^* \in L_+^\infty(\mathbb{R})$ such that $\phi^*(x) > 0$ for almost every $x \in \mathbb{R}$ with the following properties*

$$\int_{\mathbb{R}} \phi^*(x)(\mathcal{H}[s_{\text{in}}, v](x) - dv(x))dx = \lambda_0 \int_{\mathbb{R}} \phi^*(x)v(x)dx, \quad \forall v \in L^1(\mathbb{R}) \quad (3.1)$$

and

$$\int_{\mathbb{R}} \phi^*(x)v(x)dx > 0, \quad \forall v \in L_+^1(\mathbb{R}) \setminus \{0_{L^1}\}. \quad (3.2)$$

Proof. Let $\{T(t)\}_{t \geq 0}$ denotes the semigroup generated by the bounded linear operator $\mathcal{H}[s_{\text{in}}, \cdot] - d$. Since $\mathcal{H}[s_{\text{in}}, \cdot] - d$ is a bounded linear operator, one has $\lambda_0 := b(\mathcal{H}[s_{\text{in}}, \cdot] - d\mathbb{I}_d) = \omega_0(\mathcal{H}[s_{\text{in}}, \cdot] - d\mathbb{I}_d)$ (see [11, Corollary 3.11]) where $\omega_0(\mathcal{H}[s_{\text{in}}, \cdot] - d\mathbb{I}_d)$ is the growth bound of $\{T(t)\}_{t \geq 0}$. Furthermore, $\mathcal{H}[s_{\text{in}}, \cdot]$ being, compact, and positive irreducible it follows that $\omega_{0, \text{ess}}(\mathcal{H}[s_{\text{in}}, \cdot] - d\mathbb{I}_d) \leq -d$ and $b(\mathcal{H}[s_{\text{in}}, \cdot]) > 0$. Consequently

$$\lambda_0 = \omega_0(\mathcal{H}[s_{\text{in}}, \cdot] - d\mathbb{I}_d) = b(\mathcal{H}[s_{\text{in}}, \cdot] - d\mathbb{I}_d) = b(\mathcal{H}[s_{\text{in}}, \cdot]) - d > -d \geq \omega_{0, \text{ess}}(\mathcal{H}[s_{\text{in}}, \cdot] - d\mathbb{I}_d).$$

Furthermore, one can prove by standard arguments that $\{T(t)\}_{t \geq 0}$ is positive irreducible. The result now follows from [42, Proposition 4.5] or [5, Theorem 8.10, Theorem 9.10, Theorem 9.11]. ■

Theorem 3.2 *Let Assumption 2.1 be satisfied. If $\mathcal{T}(s_{\text{in}}) \leq 1$ then the washout steady state $E_0 = (s_{\text{in}}, 0)$ is globally asymptotically stable in $[0, +\infty) \times L_+^1(\mathbb{R})$.*

Proof. Assume that $\mathcal{T}(s_{\text{in}}) \leq 1$. To prove that the washout equilibrium is globally asymptotically stable, we show that the global attractor \mathcal{A} of (1.1) is given by $\mathcal{A} = \{(s_{\text{in}}, 0_{L^1})\}$. To this end, let us first note that due to (2.11) we have $\lambda_0 := b(\mathcal{H}[s_{\text{in}}, \cdot] - d\mathbb{I}_d) \leq 0$. Let $t \in \mathbb{R} \mapsto (s(t), v(t, \cdot))$ be a complete orbit in the global attractor. Thanks to (2.3) we have

$$0 \leq s(t) \leq s_{\text{in}}, \quad \forall t \in \mathbb{R}. \quad (3.3)$$

Next, we note that using the v -equation in (1.1) and Lemma 3.1 one has

$$\frac{d}{dt} \int_{\mathbb{R}} \phi^*(x)v(t, x)dx = \lambda_0 \int_{\mathbb{R}} \phi^*(x)v(t, x)dx + \int_{\mathbb{R}} (\mathcal{H}[s(t), v(t, \cdot)] - \mathcal{H}[s_{\text{in}}, v(t, \cdot)]), \quad \forall t \in \mathbb{R}. \quad (3.4)$$

Recalling that for each $y \in \mathbb{R}$, the map $s \rightarrow \mu(s, y)$ is increasing, it follows from (3.3) and (3.4) that

$$\frac{d}{dt} \int_{\mathbb{R}} \phi^*(x)v(t, x)dx \leq 0, \quad \forall t \in \mathbb{R}. \quad (3.5)$$

If $\lambda_0 < 0$ then the equality (3.5) is achieved if and only if $s(t) \equiv s_{\text{in}}$ and $v(t, \cdot) \equiv 0_{L^1}$. If $\lambda_0 = 0$ then equality (3.5) is achieved if and only if $s(t) \equiv s_{\text{in}}$ so that $v(t, \cdot) \equiv 0_{L^1}$ for all $t \in \mathbb{R}$. This implies that the global attractor consists on the washout equilibrium $(s_{\text{in}}, 0_{L^1})$. ■

We now prove the uniform persistence of the bacteria when $\mathcal{T}(s_{\text{in}}) > 1$. To this end, we consider the following sets

$$\Gamma := \left\{ (s_0, v_0) \in \mathbb{R}_+ \times L_+^1(\mathbb{R}) : \int_{\mathbb{R}} v_0(x)dx > 0 \right\}$$

and

$$\partial\Gamma := \left\{ (s_0, v_0) \in \mathbb{R}_+ \times L_+^1(\mathbb{R}) : \int_{\mathbb{R}} v_0(x)dx = 0 \right\}.$$

The uniform persistence of the bacteria is precisely stated as follows.

Theorem 3.3 *Let Assumption 2.1 be satisfied, and assume $\mathcal{T}(s_{in}) > 1$. Then there exists $\xi_0 > 0$ such that for each $(s_0, v_0) \in \Gamma$ we have*

$$\liminf_{t \rightarrow +\infty} \int_{\mathbb{R}} v(t, x) dx \geq \xi_0.$$

Proof. Thanks to Assumption 2.1 and the form of (2.2), it can be easily proved that Γ and $\partial\Gamma$ are positively invariant with respect to the semi-flow generated by (2.2). Since the semi-flow generated by (2.2) has a compact global attractor, we infer from [27] that the uniform persistence of the bacteria is obtained from the ejectivity of $\partial\Gamma$. Before proceeding, we note that the continuity of the map $s \mapsto \mathcal{T}(s)$ in $[0, +\infty)$ and (2.11) imply that there exists $\eta \in (0, 1)$ small enough such that

$$\text{sign}(b(\mathcal{H}[s_{-\eta}, \cdot] - dI_d)) > 0, \quad \text{with } s_{-\eta} := (1 - \eta)s_{in}. \quad (3.6)$$

Next, we argue by contradiction to obtain the ejectivity of $\partial\Gamma$. To this end, let $\xi > 0$ be small enough such that

$$\frac{1}{1 + \xi} > 1 - \eta. \quad (3.7)$$

Let $(s_0, v_0) \in \Gamma$. Since $t \mapsto s(t)$ is bounded, we infer from items (iv), (v) and (vi) of Assumption 2.1 that there exists $C_0 > 0$ such that

$$0 \leq \frac{\mu(s(t), y)}{\tau(y)} \leq C_0 s(t), \quad \forall t \geq 0, \quad \forall y \in \mathbb{R}.$$

Next, assume that

$$\int_{\mathbb{R}} v(t, x) dx \leq \frac{1}{C_0} d \xi, \quad \forall t \geq 0 \quad (3.8)$$

so that

$$\int_{\mathbb{R}} \frac{\mu(s(t), y)}{\tau(y)} v(t, y) dy \leq d \xi s(t), \quad \forall t \geq 0.$$

As a consequence, the s -equation satisfies

$$\frac{ds(t)}{dt} \geq d(s_{in} - s(t)) - d \xi s(t), \quad \forall t \geq 0. \quad (3.9)$$

Recalling that $t \mapsto s(t)$ is bounded on $[0, +\infty)$, we infer from the method of fluctuation in [39, Proposition A.14] that there exists a sequence $t_n \rightarrow +\infty$ such that

$$\lim_{n \rightarrow +\infty} \frac{ds(t_n)}{dt} = 0 \quad \text{and} \quad \lim_{n \rightarrow +\infty} s(t_n) = \liminf_{t \rightarrow +\infty} s(t) := s_\infty. \quad (3.10)$$

Combining (3.7), (3.9), and (3.10) it comes

$$\liminf_{t \rightarrow +\infty} s(t) := s_\infty \geq \frac{s_{in}}{1 + \xi} > (1 - \eta)s_{in} = s_{-\eta}$$

from where we deduce that there exists $t_0 > 0$ such that

$$s(t) \geq s_{-\eta}, \quad \forall t \geq t_0.$$

Hence, using the v -equation of (2.2) and the monotony of $s \mapsto \mathcal{H}[s, \cdot]$ it follows that

$$\frac{dv(t, \cdot)}{dt} \geq -dv(t, \cdot) + \mathcal{H}[s_{-\eta}, v(t, \cdot)], \quad \forall t \geq t_0. \quad (3.11)$$

Next, noting that $\mathcal{H}[s_{-\eta}, \cdot] - dI_d$ is a bounded linear operator, one knows that the growth bound of the semigroup generated by $\mathcal{H}[s_{-\eta}, \cdot] - dI_d$ is $b(\mathcal{H}[s_{-\eta}, \cdot] - dI_d) > 0$ (see [11, Corollary 3.11]). Therefore, (3.11) and the comparison principles in [26] imply that

$$\lim_{t \rightarrow +\infty} \int_{\mathbb{R}} v(t, x) dx = +\infty$$

which contradicts (3.8). ■

4 Evolutionary attractors

In general, finding the Evolutionary Attractors (EAs) of dynamical systems is mostly based on properties of the invasion fitness on an adaptive landscape [9, 13, 28, 31]. The invasion fitness is a two dimensional function allowing to study the spread of a new mutant strain y in a resource already colonized by a resident strain x . Here, we show that in some situation, a one dimensional function is enough to completely characterize EAs of the system. Furthermore, from the classical Adaptive Dynamics point of view, several EAs may exist. We will show how the analysis presented here allow to go further steps by determining among EAs which one will persists.

Recall that by Theorem 2.4 the positive steady state \bar{E} of System (1.1) is primarily dependent on the principal eigenfunction of the linear operator $\mathcal{H}[\bar{s}, \cdot]$ when the given probability kernel K satisfies Assumption 2.1. However, if we introduce a small positive parameter (denoted as $0 < \epsilon \ll 1$) to represent the mutation variance in the phenotypic space, the profile of the endemic steady state \bar{E} with respect to $x \in \mathbb{R}$ can be precisely described. This dependence on ϵ can be characterized using the scaling form of the mutation kernel K , given by (1.4).

4.1 Invasion fitness

Taking formally the limit when $\epsilon \rightarrow 0$ in (1.1) it comes

$$\begin{cases} \frac{ds(t)}{dt} = d(s_{\text{in}} - s(t)) - \int_{\mathbb{R}} \frac{\mu(s(t), y)}{\tau(y)} v(t, y) dy \\ \frac{\partial v(t, x)}{\partial t} = -dv(t, x) + \mu(s(t), x)v(t, x), \quad x \in \mathbb{R}. \end{cases} \quad (4.1)$$

Assume that the population reaches a mono-morphic steady state E_x with trait x such that $E_x = (\bar{s}_x, \bar{v}_x \delta_x(\cdot))$. Since $\bar{v}_x > 0$, we have

$$d(s_{\text{in}} - \bar{s}_x) - \frac{\mu(\bar{s}_x, x)}{\tau(x)} \bar{v}_x = 0, \quad (4.2)$$

$$\frac{\mu(\bar{s}_x, x)}{d} = 1. \quad (4.3)$$

Let us posit the *generalized reproduction number* as a function of the trait

$$\mathcal{R}_0(x) = \frac{\mu(s_{\text{in}}, x)}{d}. \quad (4.4)$$

By Assumption 2.1 on the monotony of the function μ , it comes that the mono-morphic steady state E_x characterized by (4.2)-(4.3) exists (and is unique) if and only if $\mathcal{R}_0(x) > 1$. Indeed, the solution (4.2)-(4.3) can be interpreted as the intersection in the (s, v) plane of the lines $s + v/\tau(x) = s_{\text{in}}$ and $s = \bar{s}_x$ (where \bar{s}_x is the unique solution of $\mu(s, x) = d$). This intersection lies in the positive domain exactly when condition $\bar{s}_x < s_{\text{in}}$ is fulfilled, that is for $\mathcal{R}_0(x) > 1$. Next, assume that an invader with trait y introduces a perturbation in (1.1) where a resident population with trait x has reached a mono-morphic steady state E_x . The initial growth of the invader is then governed by the linearized system of (1.1) around E_x . Let $s(t) = \bar{s}_x + u(t)$ and $v(t, \cdot) = \bar{v}_x \delta_x(\cdot) + v_y(t) \delta_y(\cdot)$, then

$$v'_y(t) \delta_y(\cdot) = \mu(\bar{s}_x, y) K(\cdot, y) v_y(t) - d \delta_y(\cdot) v_y(t),$$

which gives by integration

$$v'_y(t) = \left[\mu(\bar{s}_x, y) \int_{\mathbb{R}} K(z, y) dz - d \right] v_y(t).$$

Since $\int_{\mathbb{R}} K(z, y) dz = 1$, it comes

$$v'_y(t) = \left[\frac{\mu(\bar{s}_x, y)}{d} - 1 \right] \mu_v(y) v_y(t). \quad (4.5)$$

By (4.5), the growth rate $f_x(y)$ of the initial invasion of mutant strategy y into a resident x -population is given by

$$f_x(y) = \frac{\mu(\bar{s}_x, y)}{d} - 1. \quad (4.6)$$

The growth rate $f_x(y)$ is the so-called *invasion fitness* (or *invasion exponent*) of the invader of trait y in the environment generated by the resident of trait x (eg., see [9, 13, 28]). Thus, the invader initiate an exponentially growing clan of y individuals if and only if $f_x(y) > 0$.

4.2 Singular points

Based on above notations, the evolution of a trait x is then governed by the selection gradient defined by

$$r(x) = \left. \frac{\partial f_x}{\partial y} \right|_{y=x}.$$

Steady states of the adaptive dynamics (also called singular strategies or singular points) are trait x at which the selection gradient vanishes, *i.e.*, $r(x) = 0$. The classification of singular points is the corner stone of Adaptive Dynamics theory as much information about the dynamics can be derived once all singular points and their character are known [9, 13, 28]. This classification involves second-order derivatives of the invasion fitness, namely, we have to compute below coefficients:

$$c_{22} := \left. \frac{\partial^2 f_x}{\partial y^2} \right|_{y=x}, \quad c_{12} = c_{21} := \left. \frac{\partial^2 f_x}{\partial x \partial y} \right|_{y=x}, \quad c_{11} := \left. \frac{\partial^2 f_x}{\partial x^2} \right|_{y=x}.$$

According to [8, 13, 28], a singular point x is called *Evolutionary Stable Strategy* (ESS) if $c_{22} < 0$ and *Convergent Stable Strategy* (CSS) if $c_{12} + c_{22} < 0$. *Evolutionary Attractor* (EA) is then a strategy that is both ESS and CSS. Finally, a *branching point* is a CSS which satisfies $c_{12} < 0$.

Returning to Model (1.1), we can demonstrate that computing the invasion fitness and the coefficients c_{ij} s is not always essential for fully characterizing singular points. More precisely, by (4.4) and (4.3), we have $\mathcal{R}_0(y) = \frac{\mu(s_{\text{in}}, y)}{d}$ and $\frac{\mu(\bar{s}_x, x)}{d} = 1$. Therefore, the invasion fitness $f_x(y)$ defined by (4.6) rewrites

$$f_x(y) = \frac{\mu(\bar{s}_x, y)}{\mu(s_{\text{in}}, y)} \mathcal{R}_0(y) - \frac{\mu(\bar{s}_x, x)}{d} = \frac{\mu(\bar{s}_x, y)}{\mu(s_{\text{in}}, y)} \mathcal{R}_0(y) - \frac{\mu(\bar{s}_x, x)}{\mu(s_{\text{in}}, x)} \mathcal{R}_0(x).$$

Hence, assume that for all x and y , we can find a constant $c = c(x, y)$ such that

$$\mu(\cdot, x) = c(x, y) \mu(\cdot, y). \quad (4.7)$$

Therefore, under (4.7) we have

$$\frac{\mu(\bar{s}_x, y)}{\mu(s_{\text{in}}, y)} = \frac{c(x, y) \mu(\bar{s}_x, x)}{c(x, y) \mu(s_{\text{in}}, x)} = \frac{\mu(\bar{s}_x, x)}{\mu(s_{\text{in}}, x)}.$$

Consequently, under (4.7), let us introduce the function χ such that

$$\chi(s) := \frac{\mu(s, x)}{\mu(s_{\text{in}}, x)}, \text{ for all } (s, x) \in \mathbb{R}_+ \times \mathbb{R}, \quad (4.8)$$

then one has

$$f_x(y) = \chi(\bar{s}_x) (\mathcal{R}_0(y) - \mathcal{R}_0(x)). \quad (4.9)$$

Note that in this case the dynamics of v simply writes

$$\frac{\partial v(t, x)}{\partial t} = dv(t, x) \left(\chi(s) \mathcal{R}_0(x) - 1 \right), \quad x \in \mathbb{R}. \quad (4.10)$$

In such a case, an optimization principle based on the function \mathcal{R}_0 holds and the model's evolutionary attractors coincide with the local maximum points of \mathcal{R}_0 (eg., see [25] for more discussion). Indeed, by (4.9), a straightforward computation gives

$$r(x) = \chi(\bar{s}_x)\mathcal{R}'_0(x), \quad c_{22} = \chi(\bar{s}_x)\mathcal{R}''_0(x), \quad c_{12} = \mathcal{R}'_0(x)\frac{\partial}{\partial x}(\chi(\bar{s}_x)).$$

From this, we deduce the properties

- i. a singular point x is a ESS if and only if x is a local maximum of the map r . A sufficient condition is to have $\mathcal{R}'_0(x) = 0$ and $\mathcal{R}''_0(x) < 0$.
- ii. a singular point x is a CSS if and only if the map $x \mapsto \frac{\partial f_x}{\partial y}(y)$ is decreasing at $y = x$. A sufficient condition is to have $\mathcal{R}'_0(x) = 0$ and $\chi(\bar{s}_x)\mathcal{R}''_0(x) + \frac{\partial}{\partial x}[\chi(\bar{s}_x)]\mathcal{R}'_0(x) < 0$, that is $\mathcal{R}'_0(x) = 0$ and $\mathcal{R}''_0(x) < 0$.
- iii. model (1.1) has no branching points, because $c_{12} = 0$.

As a result, EAs of Model (1.1) correspond to local maximum points of \mathcal{R}_0 when condition (4.8) is satisfied. An example of a such condition is when the growth functions take the well-known Monod expression

$$\mu(s, x) = \mu_{max}(x)\frac{s}{\nu + s}, \quad (4.11)$$

where ν is the half-saturation constant for uptake, which is assumed to be independent of the trait x . In such a configuration, as an optimization principle based on the function \mathcal{R}_0 holds, the population always becomes mono-morphic around an evolutionary attractor corresponding to the global maximum of the function \mathcal{R}_0 (Figure 1).

However, when the half saturation constant for uptake depends on the phenotypic trait

$$\mu(s, x) = \mu_{max}(x)\frac{s}{\nu(x) + s}, \quad (4.12)$$

the optimization principle based on the function \mathcal{R}_0 does not apply (compared to the previous scenario) and EAs could not be always characterized by the shape the function \mathcal{R}_0 . Accordingly, the Pairwise Invasibility Plot (PIP) based on the calculation of invasion fitness using equation (4.6) becomes necessary to characterize model's EAs at the evolutionary steady state. Usually, the EA selected at steady state may not correspond to the global maximum of the function \mathcal{R}_0 (Figure 2).

5 Globally stable EA and concentration phenomenon

In the context of this work, several EAs may exist. Classifying these EAs among themselves can then be of significant use, *i.e.* by characterizing which one is persistent at the evolutionary steady state. We only deal with the case where the growth function $\mu = \mu(s, x)$ satisfies the condition (4.8). In such a case and when the scaling parameter ϵ introduced in (1.4) is small enough, we shall show that only one EA persists at the evolutionary steady state. The persistent EA (among several EAs) will be referred to as the Globally Stable Evolutionary Attractor (GSEA for short). Furthermore, we shall show that the positive steady state of Model (1.1) concentrates on the GSEA (when ϵ is small enough).

We now denote by $\mathcal{H}_\epsilon \equiv \mathcal{H}$ the linear operator defined by (2.1) with $K_\epsilon \equiv K$. Then, by Theorem 2.4, we recall that the positive steady state $\bar{E}_\epsilon = (\bar{s}_\epsilon, \bar{v}_\epsilon)$ of System (1.1) is characterized by (2.8), *i.e.* by the eigenvalue equation

$$\frac{1}{d}\mathcal{H}[\bar{s}_\epsilon, \bar{\phi}(\bar{s}_\epsilon, \cdot)] = \bar{\phi}(\bar{s}_\epsilon, \cdot),$$

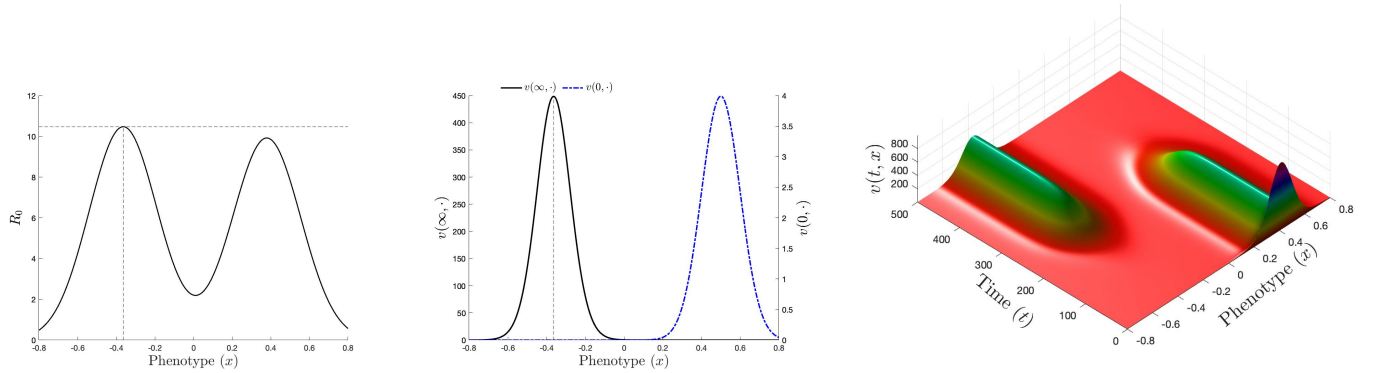


Figure 1: The function \mathcal{R}_0 is bimodal, with both a global and a local maximum (left panel). At $t = 0$, the v -population is concentrated around the local maximum (central and right panels). The evolutionary dynamics and phenotypic composition of the v -population are shown in the central panel. The distribution of the v -population with respect to the phenotypic space x at $t = 0$ and at steady state is depicted in the central and right panels, respectively. Here we fix, $d = 1$, $s_{\text{in}} = 100$, $\tau(\cdot) \equiv 1$, $K(x) = \exp\left(-\frac{|x|}{2}\right)$, $\epsilon = 0.03$, $\nu(\cdot) \equiv 10$, and $\mu_{\text{max}}(x) = \mathcal{N}(x, -0.47, 0.2) + \mathcal{N}(x, 0.49, 0.2)$, where $\mathcal{N}(x, a, b)$ stand for the normalized density function of the Gaussian distribution.

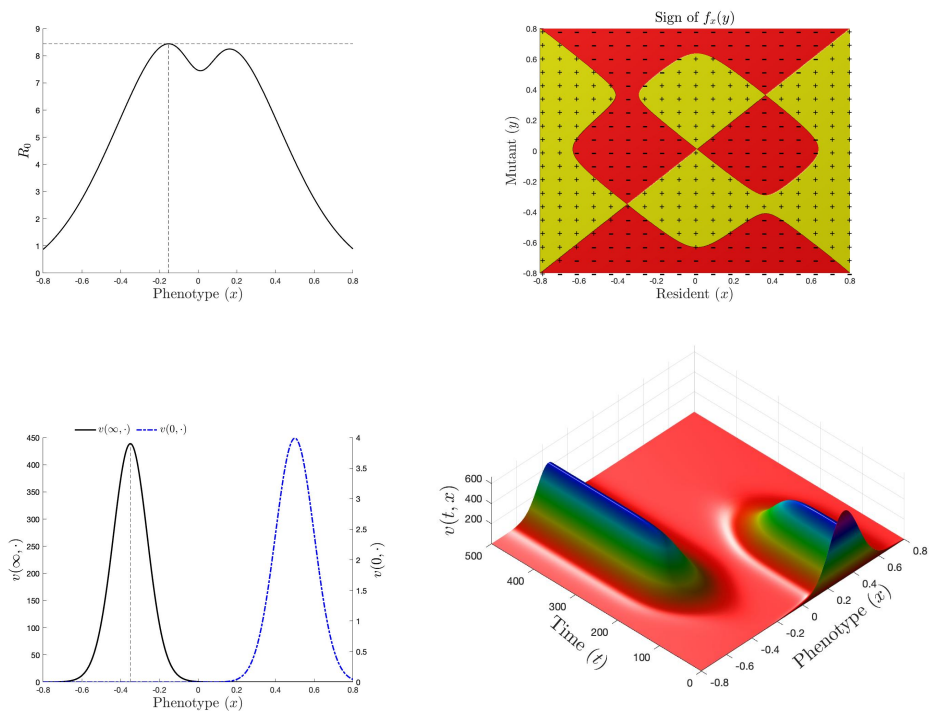


Figure 2: An illustration the evolutionary attractor selected at the steady state, $x^* \approx -0.38$ (line 2), does not correspond to either the global maximum, $x \approx -0.18$, or a local maximum, $x \approx +0.2$, of the function \mathcal{R}_0 (line 1, left panel). The pairwise invasibility plot (PIP) visualize the sign of invasion fitness $f_x(y)$ (line 1, right panel). As a mutant strain y will invade the resident population x if and only if $f_x(y) > 0$, the PIP reveals a single evolutionary attractor $x^* \approx -0.38$ (the vertical line through x^* is completely contained within a region marked "-"). Here we have $\nu(x) = 10(\mathcal{N}(x, -0.47, 0.2) + \mathcal{N}(x, 0.49, 0.2))^{-1}$, $\mu_{\text{max}}(\cdot) \equiv 1$ and the other parameters are as in Figure 1.

which, under condition (4.8), is equivalent to

$$\mathcal{L}^\epsilon[\phi(\bar{s}_\epsilon, \cdot)] = \frac{1}{\chi(\bar{s}_\epsilon)} \phi(\bar{s}_\epsilon, \cdot),$$

where \mathcal{L}^ϵ is the linear operator defined on $L^1(\mathbb{R})$ by

$$\mathcal{L}^\epsilon[w](x) = \int_{\mathbb{R}} K_\epsilon(x, y) \Theta^2(y) w(y) dy, \quad (5.1)$$

and the function $\Theta : \mathbb{R} \rightarrow \mathbb{R}_+$ by

$$\Theta(y) = \sqrt{\frac{\mu(s_{\text{in}}, y)}{d}} = \sqrt{\mathcal{R}_0(y)}. \quad (5.2)$$

Note that the square function Θ^2 is introduced here in anticipation of later facilitating the reformulation of the non self-adjoint operator \mathcal{L}^ϵ into a self-adjoint operator on the Hilbert space $L^2(\mathbb{R}, \mathbb{R})$.

Therefore, by Theorem 2.4, the positive steady state \bar{E} of Model (1.1) strongly relies on the spectral properties of the linear operator \mathcal{L}^ϵ . Moreover, note that spectral radius $r(\mathcal{H}_\epsilon)$ and $r(\mathcal{L}^\epsilon)$ of operators \mathcal{H}_ϵ and \mathcal{L}^ϵ are such that

$$\mathcal{T}(s) = \frac{1}{d} r(\mathcal{H}_\epsilon[s, \cdot]) = \chi(s) r(\mathcal{L}^\epsilon), \text{ for all } s > 0. \quad (5.3)$$

5.1 Preliminaries

In this section, we introduce some results on the principal eigenpair of the linear operator \mathcal{L}^ϵ . By Assumption 2.1, the function Θ is such that $\Theta \in C^\infty(\mathbb{R}, \mathbb{R})$ and $\Theta(x) > 0$ for all $x \in \mathbb{R}$. Moreover, we assume that the function Θ satisfies

Assumption 5.1 *There exists a finite number of local maximum points, at $\{x_k\}_{k=1, \dots, n} \subset \mathbb{R}$, to the function Θ . That is,*

$$\Theta'(x_k) = 0 \text{ and } \Theta''(x_k) < 0, \text{ for all } k = 1, \dots, n.$$

Note that the above assumption is a sufficient condition to have a local maximum; we could have zero derivatives up to a higher order.

Under Assumptions 5.1 and 2.1, we are able to derive the following spectral properties of the linear operator \mathcal{L}^ϵ .

Theorem 5.2 *Let Assumptions 2.1 and 5.1 be satisfied, and let $\epsilon > 0$,*

1. *For each $p \geq 1$, the linear operator \mathcal{L}^ϵ is compact, positive, and irreducible on $L^p(\mathbb{R}, \mathbb{R})$ and its spectral radius, $r(\mathcal{L}^\epsilon)$ is positive. Furthermore, there exists a function $\phi^\epsilon \in L^1(\mathbb{R}, \mathbb{R})$ such that $\phi^\epsilon > 0$ a.e. and $\mathcal{L}^\epsilon[\phi^\epsilon] = r(\mathcal{L}^\epsilon)\phi^\epsilon$.*
2. *For each $k \in \{1, \dots, n\}$, such that $\Theta(x_k) = \|\Theta\|_\infty$, we can find a unique sequence $\{\lambda_{j,k}\}_{j \geq 0} \subset \mathbb{R}$ such that for any $N \geq 0$, $r(\mathcal{L}^\epsilon)$ writes:*

$$r(\mathcal{L}^\epsilon) = \sum_{j=0}^N \epsilon^{2j} \lambda_{j,k} + \mathcal{O}(\epsilon^{N+1}).$$

The first three components of the above expansion are explicitly given by

$$\lambda_{0,k} = \Theta^2(x_k), \quad \lambda_{1,k} = 0, \quad \lambda_{2,k} = -\frac{\Theta^2(x_k)}{2} \sqrt{-2m_2[K] \frac{\Theta''(x_k)}{\Theta(x_k)}}, \quad (5.4)$$

where $m_2[K] = \int_{\mathbb{R}} z^2 K(z) dz$.

Details on the proof of Theorem 5.2 are provided by [10]. Here, we give some comments on above results. Under Assumptions 5.1 and 2.1, for any $p \geq 1$ and $w \in L^p(\mathbb{R}, \mathbb{R})$, we have $\mathcal{L}^\epsilon[w] \in L^p(\mathbb{R}, \mathbb{R})$, such that \mathcal{L}^ϵ can be viewed as a linear operator from $L^p(\mathbb{R}, \mathbb{R})$ to $L^p(\mathbb{R}, \mathbb{R})$ as appropriate. However, \mathcal{L}^ϵ is not a self-adjoint operator on the Hilbert space $L^2(\mathbb{R}, \mathbb{R})$. We then introduce the following linear operator defined on $L^2(\mathbb{R}, \mathbb{R})$ by

$$\mathcal{M}^\epsilon[w](x) = \Theta(x) \int_{\mathbb{R}} K_\epsilon(x, y) \Theta(y) w(y) dy. \quad (5.5)$$

Then, \mathcal{M}^ϵ is compact, irreducible and self-adjoint operator on the Hilbert space $L^2(\mathbb{R}, \mathbb{R})$. Furthermore, spectral radius of \mathcal{M}^ϵ and \mathcal{L}^ϵ coincide, *i.e.*,

$$r(\mathcal{M}^\epsilon) = r(\mathcal{L}^\epsilon). \quad (5.6)$$

Basically, for any $k \in \{1, \dots, n\}$, the sequence $\{\lambda_{k,j}\}_{k \geq 0}$ specified in Theorem 5.2 is obtained by a construction of a suitable quasi-modes for the operator \mathcal{M}^ϵ around each local maximum point x_k of the function Θ . More specifically, we introduce the unitary operators \mathcal{U}_k^ϵ defined on $L^2(\mathbb{R}, \mathbb{R})$ by

$$\mathcal{U}_k^\epsilon[u](x) = \epsilon^{-\frac{1}{4}} u \left(\epsilon^{-\frac{1}{2}} (x - x_k) \right).$$

and define the following linear operator

$$\mathcal{M}_k^\epsilon[u](x) = \left((\mathcal{U}_k^\epsilon)^{-1} \circ \mathcal{M}^\epsilon \circ \mathcal{U}_k^\epsilon \right) [u](x). \quad (5.7)$$

The sequence $\{\lambda_{k,j}\}_{k \geq 0}$ then comes from the fact that, the principal eigenvalue λ_k^ϵ of the linear operator \mathcal{M}_k^ϵ has an asymptotic series, such that $\lambda_k^\epsilon = \sum_{j=0}^{\infty} \epsilon^{\frac{j}{2}} \lambda_{k,j}$. In Appendix A, we give more details on the derivation of \mathcal{M}_k^ϵ and the first three terms of the asymptotic series given by (5.4).

5.2 Globally stable evolutionary attractor

By Section 4.2, recall that, under condition (4.8), each maximum point x_j of the function Θ is an EA of Model (1.1). Moreover, for any maximum point $x_j \in \{x_1, \dots, x_n\}$ of the function Θ , we are able to define a sequence $\{\lambda_{j,k}\}_{k \geq 0} \subset \mathbb{R}$ (Theorem 5.2). Consequently, we can define an order relation on the set $\{x_1, \dots, x_n\}$. For that purpose, recall that the set of real sequences $\mathbb{R}^{\mathbb{N}}$ can be endowed by the usual (total) lexicographical order, denoted by \preceq , and defined as follows: for any pair of sequences, $\{a_j\}_{j \geq 0}$ and $\{b_j\}_{j \geq 0}$, one has

$$\{a_j\}_{j \geq 0} \preceq \{b_j\}_{j \geq 0} \Leftrightarrow \begin{cases} \text{either } a_0 < b_0, \\ \text{either } \exists p \geq 0, a_j = b_j, \forall j = 0, \dots, p \text{ and } a_{p+1} < b_{p+1}, \\ \text{or } a_j = b_j, \forall j \geq 0. \end{cases}$$

This total order for real sequences allows us to define the following total order \trianglelefteq on the set $\{x_1, \dots, x_n\}$ as follows: for any $x_k, x_l \in \{x_1, \dots, x_n\}$ we define

$$x_k \trianglelefteq x_l \Leftrightarrow \{\lambda_{j,k}\}_{j \geq 0} \preceq \{\lambda_{j,l}\}_{j \geq 0}. \quad (5.8)$$

Next, we now introduce the set $\mathcal{M}_{max} \subset \{x_1, \dots, x_n\}$ defined by

$$\mathcal{M}_{max} = \max(\{x_1, \dots, x_n\}, \trianglelefteq). \quad (5.9)$$

In other words, $x_i \in \mathcal{M}_{max}$ if and only if $x_p \trianglelefteq x_i$ for each $p \in \{1, \dots, n\}$. Observe that $\mathcal{M}_{max} \neq \emptyset$ because $\{x_1, \dots, x_n\}$ is finite and \mathcal{M}_{max} is not necessarily reduced to a single point. Furthermore, if $x_i \neq x_j$ belongs to \mathcal{M}_{max} , then $\lambda_{i,k} = \lambda_{j,k}$ for all $k \geq 0$, that is $\Theta^{(k)}(x_i) = \Theta^{(k)}(x_j)$ for all $k \geq 0$. We then introduce the following definition.

Definition 5.3 *The globally stable evolutionary attractor (GSEA) is the evolutionary attractor (EA) x_{i_0} , when $\mathcal{M}_{max} = \{x_{i_0}\}$.*

To better explain this result, let x_1 and x_2 be two local maximum points of the basic reproduction number \mathcal{R}_0 introduced by (4.4), or equivalently of the function Θ introduced by (5.2). By above results, both x_1 and x_2 are EAs of Model (1.1). By Theorem 5.2, the spectral radius $r(\mathcal{L}^\epsilon)$ of the operator \mathcal{L}^ϵ can be written as an asymptotic expansion of two sequences $\{a_j\}_{j \geq 0}$ and $\{b_j\}_{j \geq 0}$ defined about x_1 and x_2 respectively. More precisely we have,

$$r(\mathcal{L}^\epsilon) = \begin{cases} a_0 + a_1\epsilon^{1/2} + a_2\epsilon + \mathcal{O}(\epsilon^{3/2}); & \text{about } x_1, \\ b_0 + b_1\epsilon^{1/2} + b_2\epsilon + \mathcal{O}(\epsilon^{3/2}); & \text{about } x_2. \end{cases} \quad (5.10)$$

Since $\Theta(x) = (\mathcal{R}_0(x))^{1/2}$, by (5.4), we find that

$$a_0 = \mathcal{R}_0(x_1), \quad a_1 = 0, \quad a_2 = -\frac{a_0}{2} \sqrt{-m_2[K] \frac{\mathcal{R}_0''(x_1)}{2\mathcal{R}_0(x_1)}},$$

and

$$b_0 = \mathcal{R}_0(x_2), \quad b_1 = 0, \quad b_2 = -\frac{a_0}{2} \sqrt{-m_2[K] \frac{\mathcal{R}_0''(x_2)}{2\mathcal{R}_0(x_2)}}.$$

Using the total order \leq (defined by (5.8)) on the set $\{x_1, x_2\}$, we can then determine among both EAs x_1 and x_2 which one is persistent as follows:

- if $\mathcal{R}_0(x_1) \neq \mathcal{R}_0(x_2)$, then the GSEA is x_1 when $\mathcal{R}_0(x_1) > \mathcal{R}_0(x_2)$ and x_2 when $\mathcal{R}_0(x_1) < \mathcal{R}_0(x_2)$.
- if $\mathcal{R}_0(x_1) = \mathcal{R}_0(x_2)$, then the GSEA is x_1 when $\mathcal{R}_0''(x_1) > \mathcal{R}_0''(x_2)$ and x_2 when $\mathcal{R}_0''(x_1) < \mathcal{R}_0''(x_2)$.
- if $\mathcal{R}_0(x_1) = \mathcal{R}_0(x_2)$ and $\mathcal{R}_0''(x_1) = \mathcal{R}_0''(x_2)$, then we need to determine higher-order terms in the asymptotic expansion (5.10) to characterize \mathcal{M}_{max} and possibly the GSEA.

5.3 Concentration of the evolutionary steady state

Recall that, by Theorem 2.4, Model (1.1) has a unique positive steady state $\bar{E}^\epsilon = (\bar{s}^\epsilon, \bar{v}^\epsilon)$ if and only if the spectral radius $\mathcal{T}(s_{in}) = \mathcal{T}^\epsilon(s_{in})$ of the operator $\frac{1}{d}\mathcal{H}_\epsilon[s_{in}, \cdot]$, is such that $\mathcal{T}^\epsilon(s_{in}) > 1$. Moreover, by (5.3), we know that $\mathcal{T}^\epsilon(s_{in}) = \chi(s_{in})r(\mathcal{L}^\epsilon) = r(\mathcal{L}^\epsilon)$, because by (4.8) $\chi(s_{in}) = 1$. Since $r(\mathcal{L}^\epsilon) = r(\mathcal{M}^\epsilon)$, see (5.6), and \mathcal{M}^ϵ is a self-adjoint operator, the Rayleigh quotient gives

$$r(\mathcal{L}^\epsilon) = \sup_{\substack{\varphi \in L^2(\mathbb{R}) \\ \|\varphi\|_{L^2(\mathbb{R})} = 1}} \iint_{\mathbb{R} \times \mathbb{R}} \Theta(x)\Theta(y)K_\epsilon(x, y)\varphi(x)\varphi(y)dx dy. \quad (5.11)$$

Even with an explicit formula of $r(\mathcal{L}^\epsilon)$ given by (5.11), the threshold $\mathcal{T}^\epsilon(s_{in})$ remains quite difficult to obtain (except through numerical computations). However, when the kernel parameter ϵ is small, we can go further steps by giving a simple approximation of $\mathcal{T}^\epsilon(s_{in})$. Indeed, let $\bar{x} \in \mathbb{R}$ be any point maximizing of the function Θ , *i.e.*, $\Theta(\bar{x}) = \|\Theta\|_\infty$ (by Assumption 5.1, such a point is known to exist). Furthermore, Theorem 5.2 ensures the existence of a sequence $\{\lambda_j\}_j$ such that $r(\mathcal{L}^\epsilon) = \sum_{j=0}^{+\infty} \epsilon^{\frac{j}{2}} \lambda_j$, with $\lambda_0 = \|\Theta\|_\infty^2$, see (5.4). From where,

$$\mathcal{T}^\epsilon(s_{in}) = \|\Theta\|_\infty^2 + \mathcal{O}(\epsilon),$$

such that for ϵ small enough, condition $\|\Theta\|_\infty > 1$ guarantees the existence of a unique positive steady state \bar{E}^ϵ of Model (1.1).

Another interesting property of the positive steady state $\bar{E}^\epsilon = (\bar{s}^\epsilon, \bar{v}^\epsilon(\cdot))$ is the concentration phenomenon. Indeed, when the kernel parameter ϵ is small and condition (4.8) is satisfied, the v^ϵ -component of the steady state \bar{E}^ϵ elusively concentrates around some points in the phenotypic space \mathbb{R} . This concentration phenomenon is a consequence of the below theorem concerning the normalized eigenvector ϕ^ϵ of the linear operator \mathcal{L}^ϵ (see [10]).

Theorem 5.4 *Let Assumptions 2.1 and 5.1 be satisfied, and assume $\mathcal{M}_{max} = \{x_i\}$. Consider the principal eigenvector ϕ^ϵ of \mathcal{L}^ϵ normalized so that $\|\phi^\epsilon\|_{L^1(\mathbb{R})} = 1$. Then for each $\gamma \in (0, \gamma_0)$ there exists $\eta > 0$ such that the following concentration property holds*

$$\int_{\mathbb{R} \setminus]x_i - \epsilon^\gamma, x_i + \epsilon^\gamma[} \phi^\epsilon(x) dx = \mathcal{O}(\exp(-\eta \epsilon^{-\gamma})) \text{ as } \epsilon \rightarrow 0.$$

In particular, one gets $\phi^\epsilon \rightarrow \delta_{x_i}$ as $\epsilon \rightarrow 0$ for the narrow topology, that is, for any continuous function $f \in \mathcal{C}(\mathbb{R})$ one has

$$\lim_{\epsilon \rightarrow 0} \int_{\mathbb{R}} f(x) \phi^\epsilon(x) dx = \int_{\mathbb{R}} f(x) \delta_{x_i}(x) dx = f(x_i).$$

Consequently (by Theorems 2.4 and 5.4) and) the concentration of the evolutionary steady state $\bar{E}^\epsilon = (\bar{s}_\epsilon, \bar{v}_\epsilon)$ of Model (1.1) reads as

Corollary 5.5 *Let Assumptions 2.1 and 5.1 be satisfied, and $\|\Theta\|_\infty > 1$. Assume one has $\mathcal{M}_{max} = \{x_i\}$. Then, there exist $\gamma > 0$ and $\eta > 0$ such that the following concentration property holds*

$$\int_{\mathbb{R} \setminus]x_i - \epsilon^\gamma, x_i + \epsilon^\gamma[} \bar{v}^\epsilon(x) dx = \mathcal{O}(\exp(-\eta \epsilon^{-\gamma})) \text{ as } \epsilon \rightarrow 0.$$

Furthermore, one has

$$\lim_{\epsilon \rightarrow 0} \bar{s}_\epsilon = \chi^{-1} \left(\frac{1}{\|\Theta\|_\infty^2} \right),$$

and

$$\lim_{\epsilon \rightarrow 0} \int_{\mathbb{R}^N} f(x) v^\epsilon(x) dx = \frac{d\tau(x_i)}{\mu(s_{in}, x_i)} \left[s_{in} - \chi^{-1} \left(\frac{1}{\|\Theta\|_\infty^2} \right) \right] f(x_i).$$

In other words, Corollary 5.5 says that, under condition 4.8, when $\mathcal{M}_{max} = \{x_i\}$ and the dispersal in the phenotypic space is small, namely $\epsilon \ll 1$, the unique positive steady state of Model (1.1) concentrates on a single trait x_i , *i.e.*, the steady state of the biomass population is essentially mono-morphic.

For instance, if the growth function μ follows the Monod-type expression (4.11), the proportionality condition (4.7) is met, and \mathcal{R}_0 writes

$$\mathcal{R}_0(x) = \frac{s_{in}}{d(\nu + s_{in})} \mu_{max}(x).$$

Hence, there will be an asymptotic concentration around a singular trait even if the function μ_{max} exhibits multiple maxima. Another intriguing scenario involves a linear combination of separable growth functions μ as $\mu(s, x) = \sum_{j=1}^n \alpha_j(x) \mu_j(s)$, with $\alpha_{j,s}$ and $\mu_{j,s}$ non-negative functions. Hence, for all x and y ,

$$\mu(s, x) = \sum_{j=1}^n \frac{\alpha_j(x)}{\alpha_j(y)} \alpha_j(y) \mu_j(s),$$

and the proportionality condition (4.7), which leads to the optimization principle for \mathcal{R}_0 , holds when the functions $\alpha_{j,s}$ do not depend on the index j .

6 Conclusion

In this work, we have developed an integro-differential model that extends classical chemostat models. The model proposed here incorporates a continuum of different consumer phenotypic traits represented by a scalar variable, each consumer competing for a single common resource. The micro-organisms quantitative factors given by the specific growth rate and the yield coefficient are assumed to depend on the phenotypic trait. The evolution in the space of phenotypic values is modeled with an integral operator with a kernel describing mutations from a micro-organisms with a phenotypic value to another one. In our investigation, we have established the model's mathematical well-posedness through the classical semi-groups theory, along with demonstrating the existence and uniqueness of a positive steady state.

We have also investigated concentration properties in the space of phenotypic values at stationary state. Such properties enable us to characterize the most dominant or persistent phenotypic traits at the model steady state, which are referred to as Evolutionary Attractors (EAs). Under the assumption of the proportionality of the growth rate functions associated to each phenotypic trait, we have demonstrated that the EAs of the model correspond to local maximum points of a generalized reproduction number \mathcal{R}_0 , defined as a function of the trait. Indeed, this is facilitated by the application of an optimization principle that holds under this configuration condition.

Furthermore, when the set of maximum points of the function \mathcal{R}_0 admits an unique maximizer for an order defined from the expansion of the principal eigenvalues of a linear operator, we have shown the concentration property of the population towards a single trait. Let us underline that having an unique maximizer in this sense is possible even when the generalized reproduction number admits several maximum points. Importantly, even under the condition of proportionality of the growth functions of each trait, their proportionality coefficient can have multiple maxima as a function of the trait, while the asymptotic concentration is with a single trait.

Finally, when the optimization principle is not satisfied, the characterization of EAs relies on a Pairwise Invasibility Plot (PIP) of the invasion fitness. The PIP is a two-dimensional function that facilitates the study of the spread of a new mutant strain in a resource already colonized by a resident strain.

A Asymptotic estimates of the principal eigenpair

The objective of this section is to provide a step by step computations of the asymptotic expansion (up to order 2) of the principal eigenvalue λ^ϵ of \mathcal{L}^ϵ . Let us mention that we do not intend to give a proof different from the one in [10] but present the computations in dimension 1 for completeness. Let $\mathcal{L}^\epsilon : L^1(\mathbb{R}) \rightarrow L^1(\mathbb{R})$ be defined by

$$\mathcal{L}^\epsilon[w](x) = \int_{\mathbb{R}} \frac{1}{\epsilon} K\left(\frac{x-y}{\epsilon}\right) \Theta(y)^2 w(y) dy, \quad \forall x \in \mathbb{R}, \quad \forall w \in L^1(\mathbb{R})$$

with K and Θ satisfying Assumptions 2.1 and 5.1. We introduce the following self-adjoint linear operator

$$\mathcal{M}^\epsilon[w](x) = \Theta(x) \int_{\mathbb{R}} \frac{1}{\epsilon} K\left(\frac{x-y}{\epsilon}\right) \Theta(y) w(y) dy, \quad \forall x \in \mathbb{R}, \quad \forall w \in L^1(\mathbb{R})$$

which is related to \mathcal{L}^ϵ by the following formula

$$\mathcal{M}^\epsilon[\Theta w] = \Theta \mathcal{L}^\epsilon[w], \quad \forall w \in L^1(\mathbb{R}).$$

Let $(\lambda^\epsilon, \phi^\epsilon)$ be the principal eigenpair of \mathcal{L}^ϵ with $\|\phi^\epsilon\|_{L^1} = 1$. Observe that

$$\mathcal{M}^\epsilon[\Theta \phi^\epsilon] = \Theta \mathcal{L}^\epsilon[\phi^\epsilon] = \lambda^\epsilon \Theta \phi^\epsilon \tag{A.1}$$

so that λ^ϵ is also the principal eigenvalue of \mathcal{M}^ϵ . Therefore, in what follows we will manipulate the operator \mathcal{M}^ϵ instead of \mathcal{L}^ϵ .

Reformulation of \mathcal{M}^ϵ . In the next steps we will rewrite \mathcal{M}^ϵ in a more convenient form. Let $w \in L^1(\mathbb{R})$ and $x \in \mathbb{R}$ be given. We first we make the change of variable $z = \frac{x-y}{\epsilon}$ to obtain

$$\mathcal{M}^\epsilon[w](x) = \Theta(x) \int_{\mathbb{R}} K(z) \Theta(x - \epsilon z) w(x - \epsilon z) dz \tag{A.2}$$

and secondly the change of variable $z = -\frac{x-y}{\epsilon}$ to obtain

$$\mathcal{M}^\epsilon[w](x) = \Theta(x) \int_{\mathbb{R}} K(z) \Theta(x + \epsilon z) w(x + \epsilon z) dz. \tag{A.3}$$

Therefore summing up (A.2) and (A.3) we obtain

$$\mathcal{M}^\epsilon[w](x) = \frac{\Theta(x)}{2} \int_{\mathbb{R}} K(z) \Theta(x + \epsilon z) w(x + \epsilon z) dz + \frac{\Theta(x)}{2} \int_{\mathbb{R}} K(z) \Theta(x - \epsilon z) w(x - \epsilon z) dz$$

or equivalently

$$\begin{aligned} \mathcal{M}^\epsilon[w](x) &= \frac{\Theta(x)}{2} \int_{\mathbb{R}} K(z) \Theta(x + \epsilon z) [w(x + \epsilon z) - w(x)] dz \\ &\quad + \frac{\Theta(x)}{2} \int_{\mathbb{R}} K(z) \Theta(x - \epsilon z) [w(x - \epsilon z) - w(x)] dz \\ &\quad + \frac{\Theta(x)}{2} \int_{\mathbb{R}} K(z) w(x) [\Theta(x - \epsilon z) + \Theta(x + \epsilon z)] dz. \end{aligned} \tag{A.4}$$

To get the desired form of the operator \mathcal{M}^ϵ we note that up to a change of variables we have

$$\frac{\Theta(x)}{2} \int_{\mathbb{R}} K(z) \Theta(x - \epsilon z) [w(x - \epsilon z) - w(x)] dz = \frac{\Theta(x)}{2} \int_{\mathbb{R}} K(z) \Theta(x + \epsilon z) [w(x + \epsilon z) - w(x)] dz \tag{A.5}$$

and we infer from (A.4) and (A.5) that

$$\begin{aligned} \mathcal{M}^\epsilon[w](x) &= \Theta(x) \int_{\mathbb{R}} K(z) \Theta(x + \epsilon z) [w(x + \epsilon z) - w(x)] dz \\ &\quad + w(x) \frac{\Theta(x)}{2} \int_{\mathbb{R}} K(z) [\Theta(x - \epsilon z) + \Theta(x + \epsilon z)] dz. \end{aligned} \quad (\text{A.6})$$

Asymptotic expansion around a local maximum. Let $x_1 \in \mathbb{R}$ be such that $\Theta(x_1) = \|\Theta\|_\infty$. In what follows, will show how to obtain the three first terms of the sequence $\{\lambda_{j,k}\}$ defined in Theorem 5.2. Following [10], we first localize the operator \mathcal{M}^ϵ around x_1 by means of the operator $\mathcal{U}_1^\epsilon : L^1(\mathbb{R}) \rightarrow L^1(\mathbb{R})$, $\epsilon > 0$

$$\mathcal{U}_1^\epsilon[w] = w \left(\frac{\cdot - x_1}{\sqrt{\epsilon}} \right), \quad \forall w \in L^1(\mathbb{R}) \Leftrightarrow (\mathcal{U}_1^\epsilon)^{-1}[w] = w(x_1 + \sqrt{\epsilon} \cdot), \quad \forall w \in L^1(\mathbb{R}).$$

More precisely we set

$$\mathcal{M}_1^\epsilon := (\mathcal{U}_1^\epsilon)^{-1} \circ \mathcal{M}^\epsilon \circ \mathcal{U}_1^\epsilon, \quad \forall \epsilon > 0$$

so that for each $w \in L^1(\mathbb{R})$ we have

$$\mathcal{M}_1^\epsilon[w](x) = \mathcal{M}^\epsilon \left[w \left(\frac{\cdot - x_1}{\sqrt{\epsilon}} \right) \right] (x_1 + \sqrt{\epsilon}x), \quad \forall x \in \mathbb{R}. \quad (\text{A.7})$$

Thus from (A.6) and (A.7) we deduce that

$$\begin{aligned} \mathcal{M}_1^\epsilon[w](x) &= \Theta(x_1 + \sqrt{\epsilon}x) \int_{\mathbb{R}} K(z) \Theta(x_1 + \sqrt{\epsilon}x + \epsilon z) [w(x + \sqrt{\epsilon}z) - w(x)] dz \\ &\quad + w(x) \frac{\Theta(x_1 + \sqrt{\epsilon}x)}{2} \int_{\mathbb{R}} K(z) [\Theta(x_1 + \sqrt{\epsilon}x - \epsilon z) + \Theta(x_1 + \sqrt{\epsilon}x + \epsilon z)] dz. \end{aligned} \quad (\text{A.8})$$

Remark A.1 Since $\Theta(x_1)$ is a global maximum of Θ , λ^ϵ , the principal eigenvalue of \mathcal{L}^ϵ , is also the principal eigenvalue of \mathcal{M}_1^ϵ (eg., see [10]).

In the following we give an formal asymptotic expansion in terms of ϵ which is fully justified in [10]. More precisely we have for each $x, z \in \mathbb{R}$ and $\epsilon > 0$

$$w(x + \sqrt{\epsilon}z) - w(x) = \sqrt{\epsilon}zw'(x) + \epsilon \frac{z^2}{2}w''(x) + \epsilon\sqrt{\epsilon} \frac{z^3}{6}w'''(x) + \dots \quad (\text{A.9})$$

Recalling that $\Theta'(x_1) = 0$ we have for $x \in \mathbb{R}$ and $\epsilon > 0$

$$\Theta(x_1 + \sqrt{\epsilon}x) = \Theta(x_1) + \epsilon \frac{x^2}{2}\Theta''(x_1) + \epsilon\sqrt{\epsilon} \frac{x^3}{6}\Theta'''(x_1) + \dots \quad (\text{A.10})$$

Next we also note that for each $x, z \in \mathbb{R}$ and $\epsilon > 0$

$$\begin{aligned} \Theta(x_1 + \sqrt{\epsilon}x + \epsilon z) &= \Theta(x_1) + \frac{(\sqrt{\epsilon}x + \epsilon z)^2}{2}\Theta''(x_1) + \frac{(\sqrt{\epsilon}x + \epsilon z)^3}{6}\Theta'''(x_1) + \dots \\ &= \Theta(x_1) + \frac{\epsilon x^2 + 2\epsilon\sqrt{\epsilon}xz}{2}\Theta''(x_1) + \frac{\epsilon\sqrt{\epsilon}x^3}{6}\Theta'''(x_1) + \dots \end{aligned} \quad (\text{A.11})$$

and

$$\begin{aligned} \Theta(x_1 + \sqrt{\epsilon}x - \epsilon z) &= \Theta(x_1) + \frac{(\sqrt{\epsilon}x - \epsilon z)^2}{2}\Theta''(x_1) + \frac{(\sqrt{\epsilon}x - \epsilon z)^3}{6}\Theta'''(x_1) + \dots \\ &= \Theta(x_1) + \frac{\epsilon x^2 - 2\epsilon\sqrt{\epsilon}xz}{2}\Theta''(x_1) + \frac{\epsilon\sqrt{\epsilon}x^3}{6}\Theta'''(x_1) + \dots \end{aligned}$$

so that

$$\Theta(x_1 + \sqrt{\epsilon}x + \epsilon z) + \Theta(x_1 + \sqrt{\epsilon}x - \epsilon z) = 2\Theta(x_1) + \epsilon x^2\Theta''(x_1) + \epsilon\sqrt{\epsilon} \frac{x^3}{3}\Theta'''(x_1) + \dots \quad (\text{A.12})$$

From (A.10) and (A.12), keeping only the term of order at most $\epsilon\sqrt{\epsilon}$ we obtain

$$\begin{aligned} \frac{\Theta(x_1 + \sqrt{\epsilon}x)}{2} [\Theta(x_1 + \sqrt{\epsilon}x + \epsilon z) + \Theta(x_1 + \sqrt{\epsilon}x - \epsilon z)] &= \Theta(x_1)^2 + \epsilon x^2 \Theta(x_1) \Theta''(x_1) \\ &\quad + \epsilon\sqrt{\epsilon} \frac{x^3}{3} \Theta(x_1) \Theta'''(x_1) + \dots \end{aligned} \quad (\text{A.13})$$

From (A.9) and (A.11), keeping only the term of order at most $\epsilon\sqrt{\epsilon}$ we obtain

$$\begin{aligned} \Theta(x_1 + \sqrt{\epsilon}x + \epsilon z) [w(x + \sqrt{\epsilon}z) - w(x)] &= \sqrt{\epsilon}z \Theta(x_1) w'(x) + \epsilon \frac{z^2}{2} \Theta(x_1) w''(x) \\ &\quad + \epsilon\sqrt{\epsilon} \frac{z^3}{6} w'''(x) \Theta(x_1) + \epsilon\sqrt{\epsilon} \frac{x^2 z}{2} w'(x) \Theta''(x_1) + \dots \end{aligned} \quad (\text{A.14})$$

and we deduce from (A.14) and (A.10) that

$$\begin{aligned} \Theta(x_1 + \sqrt{\epsilon}x) \Theta(x_1 + \sqrt{\epsilon}x + \epsilon z) [w(x + \sqrt{\epsilon}z) - w(x)] &= \sqrt{\epsilon}z \Theta(x_1)^2 w'(x) + \epsilon \frac{z^2}{2} \Theta(x_1)^2 w''(x) \\ &\quad + \epsilon\sqrt{\epsilon} \left[\frac{z^3}{6} w'''(x) \Theta(x_1)^2 + x^2 z w'(x) \Theta''(x_1) \Theta(x_1) \right] + \dots \end{aligned} \quad (\text{A.15})$$

Next observing that

$$\int_{\mathbb{R}} K(z) z^n dz = 0, \quad n = 2k + 1, \quad k \in \mathbb{N}$$

it follows from (A.8) together with (A.13) and (A.15) that

$$\begin{aligned} \mathcal{M}_1^\epsilon[w](x) &= \epsilon \frac{\Theta(x_1)^2}{2} w''(x) \int_{\mathbb{R}} K(z) z^2 dz + \Theta(x_1)^2 w(x) \int_{\mathbb{R}} K(z) dz \\ &\quad + \epsilon \Theta(x_1) \Theta''(x_1) w(x) \int_{\mathbb{R}} x^2 K(z) dz + \epsilon\sqrt{\epsilon} \Theta(x_1) \Theta'''(x_1) w(x) \int_{\mathbb{R}} \frac{x^3}{3} K(z) dz + \dots \end{aligned} \quad (\text{A.16})$$

Let $\widehat{\phi}^\epsilon$ be the eigenvector associated with the eigenvalue λ^ϵ of \mathcal{M}_1^ϵ . Then (A.16) implies that

$$\begin{aligned} \lambda^\epsilon \widehat{\phi}^\epsilon(x) &= \epsilon \frac{\Theta(x_1)^2}{2} \frac{d^2 \widehat{\phi}^\epsilon(x)}{dx^2} \int_{\mathbb{R}} K(z) z^2 dz + \Theta(x_1)^2 \widehat{\phi}^\epsilon(x) \int_{\mathbb{R}} K(z) dz \\ &\quad + \epsilon \Theta(x_1) \Theta''(x_1) \widehat{\phi}^\epsilon(x) \int_{\mathbb{R}} x^2 K(z) dz + \epsilon\sqrt{\epsilon} \Theta(x_1) \Theta'''(x_1) \widehat{\phi}^\epsilon(x) \int_{\mathbb{R}} \frac{x^3}{3} K(z) dz + \dots \end{aligned} \quad (\text{A.17})$$

Thanks to [10] one knows that

$$\lambda^\epsilon = \sum_{k=0}^n \epsilon^{\frac{k}{2}} \lambda_k \quad \text{and} \quad \widehat{\phi}^\epsilon = \sum_{k=0}^n \epsilon^{\frac{k}{2}} \varphi_k \quad (\text{A.18})$$

Hence we have on the one hand

$$\begin{aligned} \lambda^\epsilon \widehat{\phi}^\epsilon &= \lambda_0 [\varphi_0 + \sqrt{\epsilon} \varphi_1 + \epsilon \varphi_2 + \epsilon\sqrt{\epsilon} \varphi_3] + \sqrt{\epsilon} \lambda_1 [\varphi_0 + \sqrt{\epsilon} \varphi_1 + \epsilon \varphi_2] + \epsilon \lambda_2 [\varphi_0 + \sqrt{\epsilon} \varphi_1] + \epsilon\sqrt{\epsilon} \lambda_3 \varphi_0 + \dots \\ &= \lambda_0 \varphi_0 + \sqrt{\epsilon} [\lambda_0 \varphi_1 + \lambda_1 \varphi_0] + \epsilon [\lambda_0 \varphi_2 + \lambda_1 \varphi_1 + \lambda_2 \varphi_0] + \epsilon\sqrt{\epsilon} [\lambda_0 \varphi_3 + \lambda_1 \varphi_2 + \lambda_2 \varphi_1 + \lambda_3 \varphi_0] + \dots, \end{aligned} \quad (\text{A.19})$$

and on the other hand, plugging (A.18) into (A.19) yields

$$\begin{aligned} \lambda^\epsilon \widehat{\phi}^\epsilon(x) &= \sum_{k=0}^n \epsilon \frac{\Theta(x_1)^2}{2} \epsilon^{\frac{k}{2}} \varphi_k''(x) \int_{\mathbb{R}} K(z) z^2 dz \\ &\quad + \sum_{k=0}^n \Theta(x_1)^2 \epsilon^{\frac{k}{2}} \varphi_k(x) \int_{\mathbb{R}} K(z) dz \\ &\quad + \sum_{k=0}^n \epsilon \Theta(x_1) \Theta''(x_1) \epsilon^{\frac{k}{2}} \varphi_k(x) \int_{\mathbb{R}} x^2 K(z) dz \\ &\quad + \sum_{k=0}^n \epsilon\sqrt{\epsilon} \Theta(x_1) \Theta'''(x_1) \epsilon^{\frac{k}{2}} \varphi_k(x) \int_{\mathbb{R}} \frac{x^3}{3} K(z) dz + \dots \end{aligned} \quad (\text{A.20})$$

By keeping only the terms of order at most $\epsilon\sqrt{\epsilon}$ in (A.20) we obtain

$$\begin{aligned}
\lambda^\epsilon \widehat{\phi}^\epsilon(x) &= \epsilon \frac{\Theta(x_1)^2}{2} \varphi_0''(x) \int_{\mathbb{R}} K(z) z^2 dz + \epsilon\sqrt{\epsilon} \frac{\Theta(x_1)^2}{2} \varphi_1''(x) \int_{\mathbb{R}} K(z) z^2 dz \\
&\quad + \Theta(x_1)^2 \varphi_0(x) \int_{\mathbb{R}} K(z) dz + \sqrt{\epsilon} \Theta(x_1)^2 \varphi_1(x) \int_{\mathbb{R}} K(z) dz \\
&\quad + \epsilon \Theta(x_1)^2 \varphi_2(x) \int_{\mathbb{R}} K(z) dz + \epsilon\sqrt{\epsilon} \Theta(x_1)^2 \varphi_3(x) \int_{\mathbb{R}} K(z) dz \\
&\quad + \epsilon \Theta(x_1) \Theta''(x_1) \varphi_0(x) \int_{\mathbb{R}} x^2 K(z) dz + \epsilon\sqrt{\epsilon} \Theta(x_1) \Theta''(x_1) \varphi_1(x) \int_{\mathbb{R}} x^2 K(z) dz \\
&\quad + \epsilon\sqrt{\epsilon} \Theta(x_1) \Theta'''(x_1) \varphi_0(x) \int_{\mathbb{R}} \frac{x^3}{3} K(z) dz + \dots
\end{aligned}$$

and rearranging the terms with respect to the order of ϵ it follows that

$$\begin{aligned}
\lambda^\epsilon \widehat{\phi}^\epsilon(x) &= \Theta(x_1)^2 \varphi_0(x) \int_{\mathbb{R}} K(z) dz + \sqrt{\epsilon} \Theta(x_1)^2 \varphi_1(x) \int_{\mathbb{R}} K(z) dz \\
&\quad + \epsilon \frac{\Theta(x_1)^2}{2} \varphi_0''(x) \int_{\mathbb{R}} K(z) z^2 dz + \epsilon \Theta(x_1)^2 \varphi_2(x) \int_{\mathbb{R}} K(z) dz + \epsilon \Theta(x_1) \Theta''(x_1) \varphi_0(x) \int_{\mathbb{R}} x^2 K(z) dz \\
&\quad + \epsilon\sqrt{\epsilon} \Theta(x_1)^2 \varphi_3(x) \int_{\mathbb{R}} K(z) dz + \epsilon\sqrt{\epsilon} \frac{\Theta(x_1)^2}{2} \varphi_1''(x) \int_{\mathbb{R}} K(z) z^2 dz \\
&\quad + \epsilon\sqrt{\epsilon} \Theta(x_1) \Theta''(x_1) \varphi_1(x) \int_{\mathbb{R}} x^2 K(z) dz + \epsilon\sqrt{\epsilon} \Theta(x_1) \Theta'''(x_1) \varphi_0(x) \int_{\mathbb{R}} \frac{x^3}{3} K(z) dz + \dots
\end{aligned} \tag{A.21}$$

Next making an identification between (A.19) and (A.21) it follows that

$$\left\{ \begin{aligned}
\lambda_0 \varphi_0(x) &= \Theta(x_1)^2 \varphi_0(x) \int_{\mathbb{R}} K(z) dz \\
\lambda_0 \varphi_1(x) + \lambda_1 \varphi_0(x) &= \Theta(x_1)^2 \varphi_1(x) \int_{\mathbb{R}} K(z) dz \\
\lambda_0 \varphi_2(x) + \lambda_1 \varphi_1(x) + \lambda_2 \varphi_0(x) &= \frac{\Theta(x_1)^2}{2} \varphi_0''(x) \int_{\mathbb{R}} K(z) z^2 dz \\
&\quad + \Theta(x_1) \Theta''(x_1) \varphi_0(x) \int_{\mathbb{R}} x^2 K(z) dz \\
&\quad + \Theta(x_1)^2 \varphi_2(x) \int_{\mathbb{R}} K(z) dz \\
\lambda_0 \varphi_3(x) + \lambda_1 \varphi_2(x) + \lambda_2 \varphi_1(x) + \lambda_3 \varphi_0(x) &= \Theta(x_1)^2 \varphi_3(x) \int_{\mathbb{R}} K(z) dz + \frac{\Theta(x_1)^2}{2} \varphi_1''(x) \int_{\mathbb{R}} K(z) z^2 dz \\
&\quad + \Theta(x_1) \Theta''(x_1) \varphi_1(x) \int_{\mathbb{R}} x^2 K(z) dz \\
&\quad + \Theta(x_1) \Theta'''(x_1) \varphi_0(x) \int_{\mathbb{R}} \frac{x^3}{3} K(z) dz
\end{aligned} \right. \tag{A.22}$$

The first equation of (A.22) implies that

$$\lambda_0 = \Theta(x_1)^2 \int_{\mathbb{R}} K(z) dz. \tag{A.23}$$

Hence the second equation of (A.22) rewrites as

$$\lambda_0 \varphi_1(x) + \lambda_1 \varphi_0(x) = \lambda_0 \varphi_1(x), \quad \forall x \in \mathbb{R} \Rightarrow \lambda_1 = 0. \tag{A.24}$$

Using (A.23) and (A.24) together with the third equation of (A.22) we obtain

$$\lambda_2 \varphi_0(x) = \frac{\Theta(x_1)^2}{2} \varphi_0''(x) \int_{\mathbb{R}} K(z) z^2 dz + \Theta(x_1) \Theta''(x_1) \varphi_0(x) \int_{\mathbb{R}} x^2 K(z) dz, \quad \forall x \in \mathbb{R}. \tag{A.25}$$

Set

$$m_i[K] := \int_{\mathbb{R}} K(z) z^i dz, \quad \forall i \in \mathbb{N}$$

so that (A.25) rewrites as

$$\lambda_2 \varphi_0(x) = \frac{\Theta(x_1)^2}{2} \varphi_0''(x) m_2[K] + \Theta(x_1) \Theta''(x_1) \varphi_0(x) x^2 m_0[K], \quad \forall x \in \mathbb{R} \quad (\text{A.26})$$

or equivalently

$$\varphi_0''(x) - \sqrt{-\frac{2\Theta''(x_1) m_0[K]}{\Theta(x_1) m_2[K]}}^2 x^2 \varphi_0(x) = \frac{2}{\Theta(x_1)^2} \frac{\lambda_2}{m_2[K]} \varphi_0(x), \quad \forall x \in \mathbb{R}. \quad (\text{A.27})$$

Thus,

$$-\frac{2}{\Theta(x_1)^2} \frac{\lambda_2}{m_2[K]} = \sqrt{-\frac{2\Theta''(x_1) m_0[K]}{\Theta(x_1) m_2[K]}} \Leftrightarrow \lambda_2 = -m_2[K] \frac{\Theta(x_1)^2}{2} \sqrt{-\frac{2\Theta''(x_1) m_0[K]}{\Theta(x_1) m_2[K]}}.$$

References

- [1] S. Arkin. *Microbial Evolution in the Chemostat*. Phd thesis, Imperial College, London, U.K., 01 2010.
- [2] R. A. Armstrong and R. McGehee. Competitive exclusion. *The American Naturalist*, 115(2):151–170, 1980.
- [3] G. J. Butler and G. S. K. Wolkowicz. A mathematical model of the chemostat with a general class of functions describing nutrient uptake. *SIAM Journal on Applied Mathematics*, 45(1):138–151, 1985.
- [4] À. Calsina, S. Cuadrado, L. Desvillettes, and G. Raoul. Asymptotics of steady states of a selection–mutation equation for small mutation rate. *Proceedings of the Royal Society of Edinburgh Section A: Mathematics*, 143(6):1123–1146, Dec. 2013.
- [5] P. Clément, H. Heijmans, S. Angenent, H. van Duijn, and B. de Pagter. *One-Parameter Semigroups*. CWI Monographs. North-Holland Publishing Company, Amsterdam, 1987.
- [6] L. Desvillettes, P. E. Jabin, S. Mischler, and G. Raoul. On selection dynamics for continuous structured populations. *Communications in Mathematical Sciences*, 6(3):729–747, Sept. 2008.
- [7] O. Diekmann. A beginners guide to adaptive dynamics. *Banach Center Publications*, 63:47–86, 01 2003.
- [8] O. Diekmann. A beginner’s guide to adaptive dynamics. *Banach Center Publications*, 63(1):47–86, 2003.
- [9] O. Diekmann, P.-E. Jabin, S. Mischler, and B. Perthame. The dynamics of adaptation: An illuminating example and a Hamilton-Jacobi approach. *Theoretical Population Biology*, 67(4):257–271, June 2005.
- [10] R. Djidjou-Demasse, A. Ducrot, and F. Fabre. Steady state concentration for a phenotypic structured problem modeling the evolutionary epidemiology of spore producing pathogens. *Mathematical Models and Methods in Applied Sciences*, Feb. 2017.
- [11] K.-J. Engel, R. Nagel, S. Brendle, M. Campiti, T. Hahn, G. Metafuno, G. Nickel, D. Pallara, C. Perazzoli, A. Rhandi, S. Romanelli, and R. Schnaubelt. *One-Parameter Semigroups for Linear Evolution Equations*. Springer, New York, 2000th edition edition, Oct. 1999.

- [12] G. Gause. Experimental studies on the struggle for existence: 1. Mixed population of two species of yeast. *Journal of Experimental Biology*, 9(4):389–402, 1932.
- [13] S. Geritz, J. Metz, É. Kisdi, and G. Meszéna. Dynamics of Adaptation and Evolutionary Branching. *Physical Review Letters*, 78(10):2024–2027, Mar. 1997.
- [14] D. Gresham and J. Hong. The functional basis of adaptive evolution in chemostats. *FEMS Microbiology Reviews*, 39(1):2–16, 11 2014.
- [15] I. Gudelj, C. D. Coman, and R. E. Beardmore. Classifying the role of trade-offs in the evolutionary diversity of pathogens. *Proceedings of the Royal Society A: Mathematical, Physical and Engineering Sciences*, 462(2065):97–116, Nov. 2005.
- [16] J. K. Hale. *Asymptotic Behavior of Dissipative Systems*. American Mathematical Society, 1988.
- [17] J. K. Hale, J. P. Lasalle, and M. Slemrod. Theory of a general class of dissipative processes. *Journal of Mathematical Analysis and Applications*, 39, July 1972.
- [18] S. R. Hansen and S. P. Hubbell. Single-nutrient microbial competition: qualitative agreement between experimental and theoretically forecast outcomes. *Science*, 1980.
- [19] G. Hardin. The Competitive Exclusion Principle. *Science*, 131:1292–1297, 1960.
- [20] J. Harmand, C. Lobry, A. Rapaport, and T. Sari. *The Chemostat*. John Wiley & Sons, Ltd, 2017.
- [21] S. B. Hsu, S. Hubbell, and P. Waltman. A mathematical theory for single-nutrient competition in continuous cultures of micro-organisms. *SIAM Journal on Applied Mathematics*, 32(2):366–383, 1977.
- [22] H. Inaba. *Age-Structured Population Dynamics in Demography and Epidemiology*. Springer, 1st ed. 2017 édition edition, Mar. 2017.
- [23] O. A. Ladyzhenskaya. On the determination of minimal global attractors for the Navier-Stokes and other partial differential equations. *Russian Mathematical Surveys*, 42(6):27–73, Dec. 1987.
- [24] B. Li. Global asymptotic behavior of the chemostat: General response functions and different removal rates. *SIAM Journal on Applied Mathematics*, 59(2):411–422, 1998.
- [25] S. Lion and J. A. J. Metz. Beyond R_0 Maximisation: On Pathogen Evolution and Environmental Dimensions. *Trends in Ecology & Evolution*, 33(6):458–473, June 2018.
- [26] P. Magal, O. Seydi, and F.-B. Wang. Monotone abstract non-densely defined Cauchy problems applied to age structured population dynamic models. *Journal of Mathematical Analysis and Applications*, 479(1):450–481, Nov. 2019.
- [27] P. Magal and X.-Q. Zhao. Global attractors and steady states for uniformly persistent dynamical systems. *SIAM Journal on Mathematical Analysis*, 37(1):251–275, 2005.
- [28] J. Metz, S. Geritz, G. Meszena, F. Jacobs, and J. van Heerwaarden. Adaptive Dynamics: A Geometrical Study of the Consequences of Nearly Faithful Reproduction. <http://pure.iiasa.ac.at/id/eprint/4497/>, Sept. 1995.
- [29] S. Mirrahimi, B. Perthame, and J. Y. Wakano. Evolution of species trait through resource competition. *Journal of Mathematical Biology*, 64(7):1189–1223, June 2012.

- [30] A. Novick and L. Szilard. Experiments with the chemostat on spontaneous mutations of bacteria. *Proceedings of the National Academy of Sciences of the United States of America*, 36(12):708–19, Dec 1950.
- [31] M. A. Nowak and K. Sigmund. Evolutionary dynamics of biological games. *Science (New York, N.Y.)*, 303(5659):793–799, Feb. 2004.
- [32] A. Pazy. Semigroups of linear operators and applications to partial differential equations. *Semigroups of linear operators and applications to partial differential equations*, 44:VIII–279 p, 1983.
- [33] B. Perthame. *Transport equations in biology*. Springer, Series Frontiers in Mathematics, 2006.
- [34] B. Perthame and G. Barles. Dirac Concentrations in Lotka-Volterra Parabolic PDEs. *Indiana University Mathematics Journal*, 57(7):3275–3301, 2008.
- [35] A. Rapaport, D. Dochain, and J. Harmand. Long run coexistence in the chemostat with multiple species. *Journal of theoretical biology*, 257(2):252–9, Mar 2009.
- [36] A. Rapaport and M. Veruete. A new proof of the competitive exclusion principle in the chemostat. *Discrete and Continuous Dynamical Systems-series B*, 2019.
- [37] T. Sari. Competitive exclusion for chemostat equations with variable yields. *Acta Applicandae Mathematicae*, 2013.
- [38] H. L. Smith and W. Paul. The theory of the chemostat. *Cambridge University Press*, 01 1995.
- [39] H. L. Smith and H. Thieme. *Dynamical Systems And Population Persistence*. American Mathematical Society, 2010.
- [40] H. R. Thieme. Spectral Bound and Reproduction Number for Infinite-Dimensional Population Structure and Time Heterogeneity. *SIAM Journal on Applied Mathematics*, 70(1):188–211, Jan. 2009.
- [41] G. F. Webb. Compactness of bounded trajectories of dynamical systems in infinite dimensional spaces†. *Proceedings of the Royal Society of Edinburgh Section A: Mathematics*, 84(1-2):19–33, 1979/ed.
- [42] G. F. Webb. An operator-theoretic formulation of asynchronous exponential growth. *Transactions of the American Mathematical Society*, 303(2):751–763, 1987.
- [43] G. S. K. Wolkowicz and Z. Lu. Global dynamics of a mathematical model of competition in the chemostat: General response functions and differential death rates. *SIAM Journal on Applied Mathematics*, 52(1):222–233, 1992.