



**HAL**  
open science

# On the variations of the principal eigenvalue and the probability of survival with respect to a parameter in growth-fragmentation-death models

Fabien Campillo, Nicolas Champagnat, Coralie Fritsch

## ► To cite this version:

Fabien Campillo, Nicolas Champagnat, Coralie Fritsch. On the variations of the principal eigenvalue and the probability of survival with respect to a parameter in growth-fragmentation-death models. 2016. hal-01254053v2

**HAL Id: hal-01254053**

**<https://inria.hal.science/hal-01254053v2>**

Preprint submitted on 3 Feb 2016 (v2), last revised 23 Jan 2017 (v3)

**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.

# On the variations of the principal eigenvalue and the probability of survival with respect to a parameter in growth-fragmentation-death models

Fabien Campillo<sup>1,2</sup>      Nicolas Champagnat<sup>3,4,5</sup>      Coralie Fritsch<sup>3,4,5</sup>

Wednesday 3<sup>rd</sup> February, 2016

## Abstract

We study the variations of the principal eigenvalue associated to a growth-fragmentation-death equation with respect to a parameter. To this aim, we use the probabilistic individual-based interpretation of the model. We study the variations of the survival probability of the stochastic model, using a generation by generation approach. Then, making use of the link between the survival probability and the principal eigenvalue established in a previous work, we deduce the variations of the eigenvalue with respect to the parameter of the model.

**Keywords:** growth-fragmentation-death model, eigenproblem, integro-differential equation, invasion fitness, individual-based model, infinite dimensional branching process, piecewise-deterministic Markov process, bacterial population.

**Mathematics Subject Classification (MSC2010):** 35Q92, 45C05, 60J80, 60J85, 60J25, 92D25.

## 1 Introduction

In biology, microbiology and medicine, diverse models are used to describe structured population. For example the growth of a bacterial population or of tumor cells can be represented, in a constant environment, by the following growth-fragmentation-death equation (Doumic, 2007; Doumic Jauffret and Gabriel, 2010; Laurençot and Perthame, 2009; Fredrickson et al., 1967)

$$\frac{\partial}{\partial t} m_t(x) + \frac{\partial}{\partial x} (g(x) m_t(x)) + (b(x) + D) m_t(x) = 2 \int_0^M \frac{b(z)}{z} q\left(z, \frac{x}{z}\right) m_t(z) dz,$$

---

<sup>1</sup>Inria, LEMON, Montpellier, F-34095, France

<sup>2</sup>Institut Montpelliérain Alexander Grothendieck, Montpellier, F-34095, France

<sup>3</sup>Université de Lorraine, Institut Elie Cartan de Lorraine, UMR 7502, Vandœuvre-lès-Nancy, F-54506, France

<sup>4</sup>CNRS, Institut Elie Cartan de Lorraine, UMR 7502, Vandœuvre-lès-Nancy, F-54506, France

<sup>5</sup>Inria, TOSCA, Villers-lès-Nancy, F-54600, France

E-mail: fabien.campillo@inria.fr, nicolas.champagnat@inria.fr, coralie.fritsch@inria.fr

which describes the time evolution of the mass density  $m_t$  of the population of cells which is subject to growth at speed  $g$ , cell division at rate  $b$ , with daughter cells generated by a division kernel  $q$  and death at rate  $D$ . In order to study the asymptotic growth of the population, the eigenproblem associated to this equation is generally considered. The eigenvalue gives the asymptotic global growth rate of the population and allows to determine if the environment favors the development of the population.

Biologically, it is interesting to study the variation of this growth rate when its environment is changed (either by the action of an experimentalist or due to fluctuations of external conditions). In this article, we consider the model described previously, in which the growth function and the division rate depend on an environmental parameter  $S$  describing the constant environment. The death rate is assumed independent of  $S$  since we have in mind chemostat in which death is due to dilution at fixed rate. This parameter can, for example, represent an external resource or the influence of other populations supposed to be at equilibrium. The study of the influence of this parameter on the growth of the population is a question of biological interest for a better understanding of the model, but also of numerical interest, for example, for the study of mutant invasions in adaptive dynamics problems (Fritsch et al., 2016).

This new question seems to be difficult to approach with standard deterministic mathematical tools where, up to our knowledge, no result is available except a study of the influence of asymmetric division by Michel (2006, 2005) and an asymptotical study of the influence of the parameters by Calvez et al. (2012). The approach that we propose in this article uses the probabilistic interpretation of the growth-fragmentation-death equation under the form of a discrete stochastic individual-based model. This class of piecewise deterministic Markov processes is studied a lot, with a particular recent interest to the estimation of the parameters of the model (Doumic et al., 2015; Hoang, 2015; Hoffmann and Olivier, 2015). In this individual-based model, the growth of the population is determined by its growth rate, but also by its survival probability in some constant environment. The link between the eigenvalue of the deterministic model and the survival probability of the stochastic model, which correspond to two different definitions of the biological concept of invasion fitness (Metz et al., 1992; Metz, 2008), was established by Campillo et al. (2015). Our goal is to use this link to deduce variation properties of the eigenvalue with respect to the environmental parameter  $S$  from the variations on the survival probability. The probabilistic invasion fitness allows to use a generation by generation approach, which is more difficult to apply to the eigenproblem since generations overlap. Using this approach, the variations of the survival probability can be obtained by applying a coupling technique to the random process.

In an adaptive dynamics context, the variation of both invasion fitnesses are numerically very useful. For instance, considering the time evolution of a bacterial population in a chemostat, the invasion fitness determines if some mutant population can invade a resident one when a mutation occurs (Metz et al., 1996). This invasion fitness is the one of the mutant population in the environment at the equilibrium determined by the resident one. In this example, the environmental parameter  $S$  represents the substrate concentration at the equilibrium of the resident population. When the mutant population appears in the chemostat it appears in small size, hence its influence on the resident population and on

the resource concentration can be neglected, which allows to assume the substrate concentration  $S$  to be constant as long as the mutant population is small. Moreover, due to the small number of mutant individuals, it is essential to use a stochastic model (Fritsch et al., 2015; Campillo and Fritsch, 2015). However, the stochastic invasion fitness is numerically less straightforward to compute than the deterministic one. The mutual variations of both invasion fitnesses established in this article allow to considerably simplify the numerical analysis of a mutant invasion since the problem is reduced to the computation of a single eigenvalue in order to characterize the possibility of invasion of the mutant population (Fritsch et al., 2016).

In Section 2, we present the deterministic and the stochastic versions of our growth-fragmentation-death model. We give the definitions of invasion fitness in both cases : for the stochastic one, it is defined as the survival probability and for the deterministic one, it corresponds to the eigenvalue of an eigenproblem. We extend some results from Campillo et al. (2015), in particular Theorem 2.3 linking these two invasion fitnesses, to our more general context. Section 3.1 is devoted to the monotonicity properties of the survival probability of the stochastic model with respect to the initial mass and the death rate. In Section 3.2 we prove, under suitable assumptions, the monotonicity of the survival probability with respect to the environmental parameter  $S$ . In Section 3.3, we deduce from the previous results and from the link between the two invasion fitnesses, the monotonicity of the eigenvalue with respect to  $S$ . We extend this result assuming a particular form of the growth rate  $g$  and give a more general approach in Section 3.4.

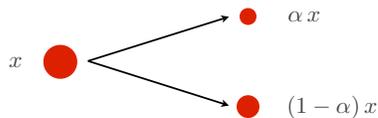
## 2 Models description

In this Section we present two descriptions of the growth-fragmentation-death model. This model is the one studied by Campillo et al. (2015), in which we add a dependence in a one-dimensional environmental parameter  $S$ , which is supposed to be fixed in time. In Section 3, we study the variation of the invasion possibility of the population (whose definition depends on the considered description) with respect to  $S$  for both descriptions.

### 2.1 Basic mechanisms

We consider models in which each individual is characterized by its mass  $x \in [0, M]$ , where  $M$  is the maximal mass of individuals, and is affected by the following mechanisms:

1. **Division:** each individual of mass  $x$  divides at rate  $b(S, x)$ , into two individuals with masses  $\alpha x$  and  $(1 - \alpha)x$ , where the proportion  $\alpha$  is distributed according to the probability distribution  $Q(x, d\alpha) = q(x, \alpha) d\alpha$  on  $[0, 1]$ .



2. **Death:** each individual dies at rate  $D$ .

3. **Growth:** between division and death times, the mass of an individual grows at speed  $g : \mathbb{R}_+ \times [0, M] \rightarrow \mathbb{R}_+$  depending on an environmental parameter  $S$ , i.e.

$$\frac{d}{dt}x_t = g(S, x_t). \quad (1)$$

In this model, individuals do not interact between themselves and the environmental parameter  $S$  is fixed in time. This means that the resource  $S$  is not limiting for the growth of the population, this is for example the case if the resource is continuously kept at the same level or the consumption of the resource is neglectable with respect to the resource quantity. This model is relevant for a population with few individuals in a given environment such that the resource consumption is low.

For any  $S > 0$ , let  $A_t(S, \cdot)$  be the flow associated to an individual's mass growth in the environment  $S$ , i.e. for any  $x \in (0, M)$  and  $t \geq 0$ ,

$$A_t(S, x) = x + \int_0^t g(S, A_u(S, x)) du. \quad (2)$$

Throughout this paper we assume the following set of assumptions.

**Assumptions 2.1.** 1. For any  $x \in [0, M]$ , the kernel  $q(x, \cdot)$  is symmetric with respect to 1/2:

$$q(x, \alpha) = q(x, 1 - \alpha), \quad \forall \alpha \in [0, 1]$$

such that  $\int_0^1 q(x, \alpha) d\alpha = 1$ .

2. For any  $\alpha \in [0, 1]$ , the function  $x \mapsto q(x, \alpha)$  is continuous on  $[0, M]$ .
3. There exists a function  $\bar{q} : [0, 1] \mapsto \mathbb{R}_+$  such that  $q(x, \alpha) \leq \bar{q}(\alpha)$  for any  $x \in (0, M)$  and  $\int_0^1 \bar{q}(\alpha) d\alpha < +\infty$ .
4.  $g(0) = g(M) = 0$  and  $g(x) > 0$  for any  $x \in (0, M)$ .
5.  $g \in C[0, M] \cap C^1(0, M)$ , where  $C[0, M]$  and  $C^1(0, M)$  respectively represent sets of continuous functions on  $[0, M]$  and continuously differentiable functions on  $(0, M)$ .
6.  $b(S, \cdot) \in C[0, M]$  and there exists  $m_{\text{div}} \in [0, M]$  and  $\bar{b} > 0$  such that

$$\begin{aligned} b(S, x) &= 0 \text{ if } x \leq m_{\text{div}}, \\ 0 &< b(S, x) \leq \bar{b} \text{ if } x \in (m_{\text{div}}, M). \end{aligned}$$

Assumptions 2.1-5 and 2.1-4 ensure existence and uniqueness of the growth flow defined by (2) for  $x \in (0, M)$  until the exit time  $T_{\text{exit}}(x)$  of  $(0, M)$  and that  $A \in C^1(\mathcal{D})$  with  $\mathcal{D} = \{(t, x), t < T_{\text{exit}}(x)\}$  (Demazure, 2000, Th. 6.8.1). We define this flow as constant when it starts from  $M$ .

## 2.2 Growth-fragmentation-death integro-differential model

The deterministic model associated to the previous mechanisms is given by the integro-differential equation

$$\frac{\partial}{\partial t} m_t^S(x) + \frac{\partial}{\partial x} (g(S, x) m_t^S(x)) + (b(S, x) + D) m_t^S(x) = 2 \int_0^M \frac{b(S, z)}{z} q\left(z, \frac{x}{z}\right) m_t^S(z) dz, \quad (3)$$

where  $m_t^S(x)$  represents the density of individuals with mass  $x$  at time  $t$  evolving in the environment determined by  $S$ , with a given initial condition  $m_0^S$ .

Let  $\mathcal{G}_S$  be the non local transport operator such that  $\partial_t m_t^S(x) = \mathcal{G}_S m_t^S(x)$ : for any  $f \in C^1(0, M)$ ,  $x \in (0, M)$ ,

$$\mathcal{G}_S f(x) \stackrel{\text{def}}{=} -\partial_x (g(S, x) f(x)) - (D + b(S, x)) f(x) + 2 \int_0^M \frac{b(S, z)}{z} q\left(z, \frac{x}{z}\right) f(z) dz, \quad (4)$$

and  $\mathcal{G}_S^*$  its adjoint operator defined for any  $f \in C^1(0, M)$ ,  $x \in (0, M)$  by

$$\mathcal{G}_S^* f(x) \stackrel{\text{def}}{=} -(D + b(S, x)) f(x) + g(S, x) \partial_x f(x) + 2 b(S, x) \int_0^1 q(x, \alpha) f(\alpha x) d\alpha. \quad (5)$$

We consider the eigenproblem

$$\mathcal{G}_S \hat{u}_S(x) = \Lambda_S \hat{u}_S(x), \quad (6a)$$

$$\lim_{x \rightarrow 0} g(S, x) \hat{u}_S(x) = 0, \quad D + \Lambda_S > 0, \quad \hat{u}_S(x) \geq 0, \quad \int_0^M \hat{u}_S(x) dx = 1 \quad (6b)$$

and the adjoint problem

$$\mathcal{G}_S^* \hat{v}_S(x) = \Lambda_S \hat{v}_S(x), \quad \hat{v}_S(x) \geq 0, \quad \int_0^M \hat{v}_S(x) \hat{u}_S(x) dx = 1. \quad (7)$$

The eigenvalue  $\Lambda_S$  is then interpreted as the exponential growth rate of the population.

In the rest of the paper, we will assume that the following assumption is satisfied. Campillo et al. (2015) have given some conditions under which this assumption holds (see also (Doumic, 2007) and (Doumic Jauffret and Gabriel, 2010) for slightly different models and (Perthame and Ryzhik, 2005) and (Laurençot and Perthame, 2009) for exponential stability of the eigenfunctions).

**Assumption 2.2.** *For any  $S > 0$ , the system (6)-(7) admits a solution  $(\hat{u}_S, \hat{v}_S, \Lambda_S)$  such that  $\hat{u}_S \in C^1(0, M)$  and  $\hat{v}_S \in C[0, M] \cap C^1(0, M)$ .*

### 2.3 Growth-fragmentation-death individual-based model

The mechanisms described in Section 2.1 can also be represented by a stochastic individual-based model, where the population at time  $t$  is represented by the counting measure

$$\eta_t^S(dx) \stackrel{\text{def}}{=} \sum_{i=1}^{N_t} \delta_{X_t^i}(dx), \quad (8)$$

where  $N_t = \int_0^M \eta_t^S(dx)$  is the number of individuals in the population at time  $t$  and  $(X_t^i, i = 1, \dots, N_t)$  are the masses of the  $N_t$  individuals (arbitrarily ordered).

The stochastic individual-based model is relevant for small population whereas the deterministic one is relevant for large population (Campillo and Fritsch, 2015).

The process  $(\eta_t^S)_{t \geq 0}$  is defined by

$$\begin{aligned} \eta_t^S &= \sum_{j=1}^{N_0} \delta_{A_t^S(X_0^j)} \\ &+ \iiint_{[0,t] \times \mathbb{N}^* \times [0,1]^3} \mathbf{1}_{\{j \leq N_{u^-}\}} \mathbf{1}_{\{\theta_1 \leq b(S, X_{u^-}^j)/\bar{b}\}} \mathbf{1}_{\{\theta_2 \leq q(X_{u^-}^j, \alpha)/\bar{q}(\alpha)\}} \\ &\quad \left[ -\delta_{A_{t-u}^S(X_{u^-}^j)} + \delta_{A_{t-u}^S(\alpha X_{u^-}^j)} + \delta_{A_{t-u}^S((1-\alpha) X_{u^-}^j)} \right] \mathcal{N}_1(du, dj, d\alpha, d\theta_1, d\theta_2) \\ &- \iint_{[0,t] \times \mathbb{N}^*} \mathbf{1}_{\{j \leq N_{u^-}\}} \delta_{A_{t-u}^S(X_{u^-}^j)} \mathcal{N}_2(du, dj) \end{aligned} \quad (9)$$

where  $\mathcal{N}_1(du, dj, d\alpha, d\theta_1, d\theta_2)$  and  $\mathcal{N}_2(du, dj)$  are two independent Poisson random measures defined on  $\mathbb{R}_+ \times \mathbb{N}^* \times [0, 1] \times [0, 1] \times [0, 1]$  and  $\mathbb{R}_+ \times \mathbb{N}^*$ , corresponding respectively to the division and death mechanisms, with respective intensity measures

$$n_1(du, dj, d\alpha, d\theta) = \bar{b} du \left( \sum_{\ell \geq 1} \delta_\ell(dj) \right) \bar{q}(\alpha) d\alpha d\theta_1 d\theta_2, \quad (10)$$

$$n_2(du, dj) = D du \left( \sum_{\ell \geq 1} \delta_\ell(dj) \right), \quad (11)$$

(see Campillo and Fritsch (2015) and Campillo et al. (2015) for more details).

This population process can be seen as a multitype branching process with a continuum of types. We are interested in its survival probability.

We suppose that, at time  $t = 0$ , there is only one individual, with mass  $x_0$ , in the population, i.e.

$$\eta_0^S(dx) = \delta_{x_0}(dx).$$

The extinction probability of the population with initial mass  $x_0$  is

$$p^S(x_0) \stackrel{\text{def}}{=} \mathbb{P}_{\delta_{x_0}}^S(\exists t > 0, N_t = 0),$$

where  $\mathbb{P}_{\delta_{x_0}}^S$  is the law of the process  $(\eta_t^S)_{t \geq 0}$  under the initial condition  $\eta_0^S = \delta_{x_0}$ . The survival probability is then given by  $\mathbb{P}_{\delta_{x_0}}^S(\text{survival}) = 1 - p^S(x_0)$ .

We define the  $n$ -th generation as the set of individuals descended from a division of one individual of the  $(n - 1)$ -th generation. The generation 0 corresponds to the initial population. We denote by  $Z_n$  the number of individuals at the  $n$ -th generation and we define the extinction probability before the  $n$ -th generation as

$$p_n^S(x_0) \stackrel{\text{def}}{=} \mathbb{P}_{\delta_{x_0}}^S(Z_n = 0), \quad n \in \mathbb{N}. \quad (12)$$

It is obvious that

$$\lim_{n \rightarrow \infty} p_n^S(x_0) = p^S(x_0).$$

Let  $\tau$  be the stopping time of the first event (division or death). Then at time  $\tau$  the population is given by

$$\eta_\tau^S \stackrel{\text{def}}{=} \begin{cases} 0 & \text{if death,} \\ \delta_{X_1} + \delta_{X_2} & \text{if division,} \end{cases} \quad (13)$$

with  $X_1 = \alpha A_\tau^S(x_0)$  and  $X_2 = (1 - \alpha) A_\tau^S(x_0)$  where the proportion  $\alpha$  is distributed according to the kernel  $q(A_\tau^S(x_0), \alpha) d\alpha$ .

Applying the Markov property at time  $\tau$  and using the independence of particles, it is easy to prove (see Campillo et al. (2015)) that for any  $x \in [0, M]$  and  $n \in \mathbb{N}^*$

$$p_n^S(x) = D \int_0^\infty e^{-Dt} e^{-\int_0^t b(S, A_u^S(x)) du} dt + \int_0^\infty b(S, A_t^S(x)) e^{-\int_0^t b(S, A_u^S(x)) du - Dt} \int_0^1 q(A_t^S(x), \alpha) p_{n-1}^S(\alpha A_t^S(x)) p_{n-1}^S((1 - \alpha) A_t^S(x)) d\alpha dt.$$

with  $p_0^S(x) = 0$ . It can then be deduced (Campillo et al., 2015, Proposition 3.1) that  $p^S$  is the minimal non negative solution of

$$p^S(x) = \int_0^\infty D e^{-Dt} e^{-\int_0^t b(S, A_u^S(x)) du} dt + \int_0^\infty b(S, A_t^S(x)) e^{-\int_0^t b(S, A_u^S(x)) du - Dt} \int_0^1 q(A_t^S(x), \alpha) p^S(\alpha A_t^S(x)) p^S((1 - \alpha) A_t^S(x)) d\alpha dt, \quad (14)$$

in the sense that for any non negative solution  $\tilde{p}$  we have  $\tilde{p} \geq p^S$ .

For any  $x \in ]0, M[$  and  $y > 0$  such that  $x \leq y$ , let  $t_S(x, y)$  be the first hitting time of  $y$  by the flow  $A_t^S(x)$ , i.e.

$$t_S(x, y) \stackrel{\text{def}}{=} \inf\{t \geq 0, A_t^S(x) = y\} = \begin{cases} \tilde{A}_{S,x}^{-1}(y), & \text{if } x \leq y < M, \\ +\infty, & \text{if } y \geq M, \end{cases} \quad (15)$$

where  $\tilde{A}_{S,x}^{-1}$  is the inverse function of the  $C^1$ -diffeomorphism  $t \mapsto A_t^S(x)$ .

Campillo et al. (2015) have made the link between the survival probability of the stochastic process and the eigenvalue of the deterministic model, given by the theorem below. This result was proved for a kernel  $q(x, \cdot)$  which does not depend on  $x \in (0, M)$ , but it can easily be extended to our case where  $q(x, \cdot)$  depends on the mass  $x$  at the division time. The only difficulty concerns the third point of the proof of Theorem 4.11. of Campillo et al. (2015) in which the condition  $q([\varepsilon/(M - 2\varepsilon), 1/2]) > 0$  for some  $\varepsilon > 0$  must be replaced by the condition  $\inf_{\varepsilon \leq x \leq M - \varepsilon} q(x, [\varepsilon/(M - 2\varepsilon), 1/2]) > 0$  for some  $\varepsilon > 0$ . But as the function  $x \mapsto q(x, \alpha)$  is supposed to be continuous for any  $\alpha \in (0, 1)$ , we can prove that there exists  $\varepsilon > 0$  which satisfies this condition. Indeed, note that the infimum above is reached at some  $x_0(\varepsilon) \in [\varepsilon, M - \varepsilon]$ , by Assumptions 2.1-2 and 3. Therefore, we assume *ad absurdum* that there exists  $\varepsilon > 0$  such that  $q(x_0(\varepsilon), \alpha) = 0$  for almost all  $\alpha \in [\frac{\varepsilon}{M - 2\varepsilon}; \frac{1}{2}]$ . Then, from the sequence  $(x_0(\frac{1}{n}))_n$ , we can extract a subsequence which converges towards  $x_0^*$ . By continuity, we then get  $q(x_0^*, \alpha) = 0$  for almost all  $\alpha \in (0, 1)$ . Hence  $\int_0^1 q(x_0^*, \alpha) d\alpha = 0$ , which contradicts Assumption 2.1-1.

**Theorem 2.3** (Campillo, Champagnat, Fritsch (2015)). *We have the following relation between the two invasion criteria*

$$\Lambda_S > 0 \iff \mathbb{P}_{\delta_x}^S(\text{survival}) > 0, \forall x \in (0, M).$$

### 3 Variations of the invasion fitnesses with respect to the environmental variable

Our goal is to study the variation of  $\Lambda_S$  w.r.t  $S$ . For this, we start by studying the monotonicity properties of the survival probability in the stochastic model.

#### 3.1 Monotony properties w.r.t. the initial mass and the death rate on the stochastic model

For any  $x \in (0, 1)$ , let  $F_x : [0, 1] \rightarrow [0, 1]$  be the cumulative distribution function associated to the law  $q(x, \alpha) d\alpha$ , that is for any  $u \in [0, 1]$

$$F_x(u) = \int_0^u q(x, \alpha) d\alpha$$

and let  $F_x^{-1}$  be its inverse function defined by

$$F_x^{-1}(v) = \inf_{u \in [0, 1]} \{F_x(u) \geq v\}.$$

**Assumption 3.1.** *The cumulative distribution function  $F_x$  satisfies, for any  $u \in (0, 1)$  and any  $x \leq y$ ,*

$$x F_x^{-1}(u) \leq y F_y^{-1}(u) \quad \text{and} \quad (1 - x) F_x^{-1}(u) \leq (1 - y) F_y^{-1}(u).$$

As we will see in Lemma 3.4 below, this assumption corresponds to a coupling condition on the mass of offsprings born from individuals of different sizes. We need this condition because our method can be seen as a construction of a coupling of the masses of individuals at each generation in two stochastic processes starting from different initial masses (see our comments on Proposition 3.12 below).

**Remark 3.2.** *If  $F_x^{-1}$  is such that for any  $u \in (0, 1)$ ,  $x \mapsto F_x^{-1}(u) \in C^1([0, M])$  and satisfies for any  $x \in (0, M)$ ,*

$$x \partial_x F_x^{-1}(u) \in [-F_x^{-1}(u), 1 - F_x^{-1}(u)],$$

then

$$\partial_x (x F_x^{-1}(u)) = F_x^{-1}(u) + x \partial_x F_x^{-1}(u) \geq 0.$$

Hence  $x F_x^{-1}(u)$  is non decreasing. In the same way,  $(1 - x) F_x^{-1}(u)$  is non decreasing too. Therefore, Assumption 3.1 holds.

**Examples 3.3.** *We give some examples which satisfy Assumption 3.1.*

1. *We consider the following division kernel,*

$$q(x, \alpha) = \frac{\mathbf{1}_{\{l(x) \leq \alpha \leq 1 - l(x)\}}}{1 - 2l(x)}. \quad (16)$$

where  $l \in C^1([0, M], (0, 1/2))$ . Then for  $u \in (0, 1)$ ,

$$F_x^{-1}(u) = (1 - 2u) l(x) + u$$

and, by Remarks 3.2, Assumption 3.1 holds if for any  $x$ ,  $0 \leq x l'(x) + l(x) \leq 1$ .

2. *We can extend the previous example considering the following function  $q$ ,*

$$q(x, \alpha) = \frac{(\alpha - l(x))^{\beta(x)}}{C(x)} \mathbf{1}_{\{l(x) \leq \alpha \leq 1/2\}} + \frac{(1 - \alpha - l(x))^{\beta(x)}}{C(x)} \mathbf{1}_{\{1/2 \leq \alpha \leq 1 - l(x)\}}$$

where  $C(x) = 2 (1/2 - l(x))^{\beta(x)+1} / (\beta(x) + 1)$  is a normalizing constant. The previous example corresponds to  $\beta(x) = 0$  for any  $x \in [0, M]$ . Then

$$F_x(u) = \frac{1}{2} \left( \frac{u - l(x)}{\frac{1}{2} - l(x)} \right)^{\beta(x)+1} \mathbf{1}_{\{l(x) \leq \alpha \leq 1/2\}} + \left( 1 - \frac{1}{2} \left( \frac{1 - u - l(x)}{\frac{1}{2} - l(x)} \right)^{\beta(x)+1} \right) \mathbf{1}_{\{1/2 < \alpha \leq 1 - l(x)\}} + \mathbf{1}_{\{1 - l(x) < \alpha\}} \quad (17)$$

and for any  $u \in (0, 1)$

$$F_x^{-1}(u) = \left( \left( \frac{1}{2} - l(x) \right) (2u)^{1/(\beta(x)+1)} + l(x) \right) \mathbf{1}_{\{0 < u \leq 1/2\}} + \left( 1 - l(x) - \left( \frac{1}{2} - l(x) \right) (2(1 - u))^{1/(\beta(x)+1)} \right) \mathbf{1}_{\{1/2 < u < 1\}}. \quad (18)$$

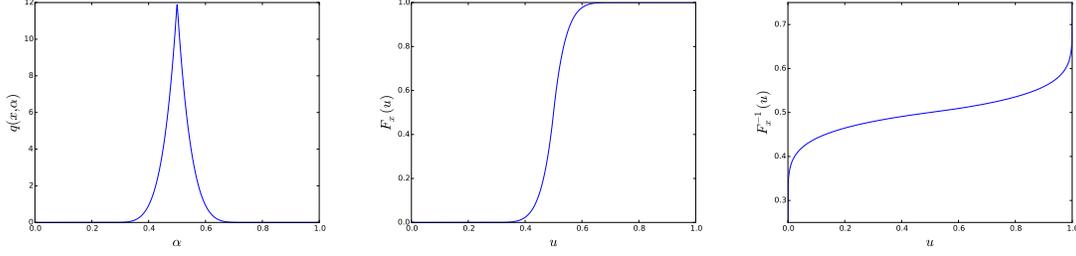


Figure 1: Representation of the function  $q$  (left),  $F_x$  (center) and  $F_x^{-1}$  (right) respectively defined by Equations (16), (17) and (18) with  $l(x) = 0.25$  and  $\beta(x) = 5$ .

An example of such functions is given in Figure 1.

For  $u \in (0, 1/2]$ ,

$$\partial_x F_x^{-1}(u) = \left( -l'(x) - \left( \frac{1}{2} - l(x) \right) \frac{\beta'(x)}{(\beta(x) + 1)^2} \ln(2u) \right) (2u)^{1/(\beta(x)+1)} + l'(x)$$

and for  $u \in [1/2, 1)$ ,

$$\partial_x F_x^{-1}(u) = \left( l'(x) + \left( \frac{1}{2} - l(x) \right) \frac{\beta'(x)}{(\beta(x) + 1)^2} \ln(2(1-u)) \right) (2(1-u))^{1/(\beta(x)+1)} - l'(x)$$

Assumption 3.1 holds if  $0 \leq x \partial_x F_x^{-1}(u) + F_x^{-1}(u) \leq 1$  for any  $u \in (0, 1)$ , for example if  $\beta$  is a constant function and if  $0 \leq l(x) + x l'(x) \leq 1$  for any  $x \in (0, M)$ .

**Lemma 3.4.** Let  $f$  be a non-increasing function on  $[0, M]$ . Then, under Assumption 3.1, the function

$$x \mapsto \int_0^1 q(x, \alpha) f(\alpha x) f((1-\alpha)x) d\alpha$$

is non-increasing.

*Proof.* For any  $x \in (0, 1)$ , let  $\theta_x$  defined by  $\theta_x = F_x^{-1}(U)$  where  $U$  is uniformly distributed on  $[0, 1]$ . Therefore the law of the variable  $\theta_x$  is  $q(x, \alpha) d\alpha$ . By Assumption 3.1,

$$\partial_x(x \theta_x) = \theta_x + x \partial_x F_x^{-1}(U) \geq \theta_x - F_x^{-1}(U) = 0 \quad \text{a.s.}$$

and

$$\partial_x(x(1-\theta_x)) = 1 - \theta_x - x \partial_x F_x^{-1}(U) \geq 1 - \theta_x - (1 - F_x^{-1}(U)) = 0.$$

Therefore, for any  $x < y$  we have  $x \theta_x \leq y \theta_y$  a.s. and  $x(1-\theta_x) \leq y(1-\theta_y)$  a.s. Hence,

$$\begin{aligned} \int_0^1 q(x, \alpha) f(\alpha x) f((1-\alpha)x) d\alpha &= \mathbb{E}(f(\theta_x x) f((1-\theta_x)x)) \\ &\leq \mathbb{E}(f(\theta_y y) f((1-\theta_y)y)) \\ &= \int_0^1 q(y, \alpha) f(\alpha y) f((1-\alpha)y) d\alpha. \quad \square \end{aligned}$$

**Proposition 3.5.** *Under Assumption 3.1, if the division rate  $b(S, \cdot)$  is non decreasing then the extinction probability  $p^S : x \mapsto p^S(x)$  is non increasing.*

*Proof.* We prove by induction that the function  $p_n^S$  is non increasing for any  $n \in \mathbb{N}^*$ , where  $p_n^S$  is defined by (12). Let  $0 < x < y < M$ . As  $A_u^S(x) < A_u^S(y)$ , for any  $u \geq 0$ ,

$$p_1^S(x) = D \int_0^\infty e^{-\int_0^t b(S, A_u^S(x)) du - Dt} dt \geq D \int_0^\infty e^{-\int_0^t b(S, A_u^S(y)) du - Dt} dt = p_1^S(y).$$

Then the function  $p_1^S$  is non increasing. Let  $n \in \mathbb{N}^*$ , we assume that the function  $p_n^S$  is non increasing.

We can write  $p_{n+1}^S(x)$  as

$$p_{n+1}^S(x) = p_1^S(x) + \mathbb{P}_{\delta_x}^S (\{\text{extinction before the } (n+1)\text{-th generation}\} \cap \{\eta_\tau^S \neq 0\}),$$

with

$$\begin{aligned} & \mathbb{P}_{\delta_x}^S (\{\text{extinction before the } (n+1)\text{-th generation}\} \cap \{\eta_\tau^S \neq 0\}) \\ &= \int_0^\infty b(S, A_t^S(x)) e^{-\int_0^t b(S, A_u^S(x)) du - Dt} \int_0^1 q(A_t^S(x), \alpha) p_n^S(\alpha A_t^S(x)) p_n^S((1-\alpha) A_t^S(x)) d\alpha dt. \end{aligned}$$

The following relation holds

$$p_{n+1}^S(x) = p_1^S(x) + p_{n+1}^S(x | \eta_\tau^S \neq 0) (1 - p_1^S(x))$$

with

$$p_{n+1}^S(x | \eta_\tau^S \neq 0) = \mathbb{P}_{\delta_x}^S (\text{extinction before the } (n+1)\text{-th generation} | \eta_\tau^S \neq 0).$$

Since for any  $t \geq 0$ ,  $A_{t(x,y)+t}^S(x) = A_t^S(y)$ , then, by a change of variable,

$$\begin{aligned} & \int_{t_S(x,y)}^\infty b(S, A_t^S(x)) e^{-\int_0^t b(S, A_u^S(x)) du - Dt} \int_0^1 q(A_t^S(x), \alpha) p_n^S(\alpha A_t^S(x)) p_n^S((1-\alpha) A_t^S(x)) d\alpha dt \\ &= e^{-\int_0^{t_S(x,y)} b(S, A_u^S(x)) du - Dt_S(x,y)} \int_0^\infty b(S, A_t^S(y)) e^{-\int_0^t b(S, A_u^S(y)) du - Dt} \\ & \quad \int_0^1 q(A_t^S(y), \alpha) p_n^S(\alpha A_t^S(y)) p_n^S((1-\alpha) A_t^S(y)) d\alpha dt \\ &= e^{-\int_0^{t_S(x,y)} b(S, A_u^S(x)) du - Dt_S(x,y)} p_{n+1}^S(y | \eta_\tau^S \neq 0) (1 - p_1^S(y)). \end{aligned} \quad (19)$$

For any  $t \in [0, t_S(x, y)]$  we have  $A_t^S(x) \leq y$ . Since we assume that the function  $p_n^S$  is non increasing, from Lemma 3.4, we then get

$$\begin{aligned} & \int_0^{t_S(x,y)} b(S, A_t^S(x)) e^{-\int_0^t b(S, A_u^S(x)) du - Dt} \int_0^1 q(A_t^S(x), \alpha) p_n^S(\alpha A_t^S(x)) p_n^S((1-\alpha) A_t^S(x)) d\alpha dt \\ & \geq \int_0^{t_S(x,y)} b(S, A_t^S(x)) e^{-\int_0^t b(S, A_u^S(x)) du - Dt} dt \int_0^1 q(y, \alpha) p_n^S(\alpha y) p_n^S((1-\alpha) y) d\alpha \\ &= \left( 1 - e^{-\int_0^{t_S(x,y)} b(S, A_u^S(x)) du - Dt(x,y)} - D \int_0^{t_S(x,y)} e^{-\int_0^t b(S, A_u^S(x)) du - Dt} dt \right) \\ & \quad \times \int_0^1 q(y, \alpha) p_n^S(\alpha y) p_n^S((1-\alpha) y) d\alpha. \end{aligned} \quad (20)$$

Still because the function  $p_n^S$  is non increasing and from Lemma 3.4,

$$\begin{aligned} \mathbb{P}_{\delta_y}^S (\{\text{extinction before the } (n+1)\text{-th generation}\} \cap \{\eta_\tau^S \neq 0\}) \\ \leq \int_0^\infty b(S, A_t^S(y)) e^{-\int_0^t b(S, A_u^S(y)) du - Dt} dt \int_0^1 q(y, \alpha) p_n^S(\alpha y) p_n^S((1-\alpha)y) d\alpha \\ = (1 - p_1^S(y)) \int_0^1 q(y, \alpha) p_n^S(\alpha y) p_n^S((1-\alpha)y) d\alpha. \end{aligned}$$

Hence

$$\int_0^1 q(y, \alpha) p_n^S(\alpha y) p_n^S((1-\alpha)y) d\alpha \geq p_{n+1}^S(y | \eta_\tau^S \neq 0).$$

Adding (19) and (20), and using the last inequality, we then get

$$\begin{aligned} p_{n+1}^S(x | \eta_\tau^S \neq 0) \geq \left[ \frac{1 - D \int_0^{t_S(x,y)} e^{-\int_0^t b(S, A_u^S(x)) du - Dt} dt}{1 - p_1^S(x)} \right. \\ \left. - e^{-\int_0^{t_S(x,y)} b(S, A_u^S(x)) du - Dt_S(x,y)} \frac{p_1^S(y)}{1 - p_1^S(x)} \right] p_{n+1}^S(y | \eta_\tau^S \neq 0). \end{aligned}$$

Moreover,

$$p_1^S(x) = D \int_0^{t_S(x,y)} e^{-\int_0^t b(S, A_u^S(x)) du - Dt} dt + e^{-\int_0^{t_S(x,y)} b(S, A_u^S(x)) du - Dt_S(x,y)} p_1^S(y).$$

Hence,

$$p_{n+1}^S(x | \eta_\tau^S \neq 0) \geq p_{n+1}^S(y | \eta_\tau^S \neq 0).$$

Thus,

$$\begin{aligned} p_{n+1}^S(x) - p_{n+1}^S(y) &= p_1^S(x) + p_{n+1}^S(x | \eta_\tau^S \neq 0) (1 - p_1^S(x)) \\ &\quad - p_1^S(y) - p_{n+1}^S(y | \eta_\tau^S \neq 0) (1 - p_1^S(y)) \\ &\geq (p_1^S(x) - p_1^S(y)) (1 - p_{n+1}^S(y | \eta_\tau^S \neq 0)) \geq 0. \end{aligned}$$

This ends the induction. Passing to the limit, we finally get

$$p^S(x) - p^S(y) = \lim_{n \rightarrow \infty} (p_n^S(x) - p_n^S(y)) \geq 0. \quad \square$$

We extend the notation of the extinction probability with a dependence in  $D$  : let  $p^{S,D}(x)$  be the extinction probability of the population evolving in the environment determined by  $S$ , with a death rate  $D$  and a initial individual with mass  $x$ .

**Proposition 3.6.** *For any  $x \in [0, M]$ , the function  $D \mapsto p^{S,D}(x)$  is non-decreasing.*

*Proof.* Let  $D' > D$ .

$$\begin{aligned} p_1^{S,D}(x) &= D \int_0^\infty e^{-\int_0^t b(A_u^S(x)) du - Dt} = 1 - \int_0^\infty b(A_u^S(x)) e^{-\int_0^t b(A_u^S(x)) du - Dt} \\ &\leq 1 - \int_0^\infty b(A_u^S(x)) e^{-\int_0^t b(A_u^S(x)) du - D't} = p_1^{S,D'}(x). \end{aligned}$$

Hence  $D \mapsto p_1^{S,D}(x)$  is non-decreasing. For  $n \in \mathbb{N}^*$ , let assume that  $D \mapsto p_n^{S,D}(x)$  is non-decreasing, then

$$\begin{aligned} p_{n+1}^{S,D}(x) &= 1 - \int_0^\infty b(A_u^S(x)) e^{-\int_0^t b(A_u^S(x)) du - Dt} \\ &\quad \left[ 1 - \int_0^1 q(A_t^S(x), \alpha) p_n^{D,S}(\alpha A_t^S(x)) p_n^{D,S}((1-\alpha) A_t^S(x)) d\alpha \right] dt \\ &\leq 1 - \int_0^\infty b(A_u^S(x)) e^{-\int_0^t b(A_u^S(x)) du - D't} \\ &\quad \left[ 1 - \int_0^1 q(A_t^S(x), \alpha) p_n^{D',S}(\alpha A_t^S(x)) p_n^{D',S}((1-\alpha) A_t^S(x)) d\alpha \right] dt \\ &= p_{n+1}^{S,D'}(x) \end{aligned}$$

Then for any  $n$ ,  $p_n^{S,D}(x) \leq p_n^{S,D'}(x)$ . Passing to the limit,

$$p^{S,D}(x) = \lim_{n \rightarrow \infty} p_n^{S,D}(x) \leq \lim_{n \rightarrow \infty} p_n^{S,D'}(x) = p^{S,D'}(x). \quad \square$$

### 3.2 Monotony properties w.r.t. $S$ on the stochastic model

We now study the variations of the survival probability w.r.t. the environmental parameter  $S$ . We need additional assumptions.

**Assumptions 3.7.** 1. The division rate function  $b$  is non decreasing in the two variables  $S$  and  $x$ .

2. The growth speed  $g$  is non decreasing in  $S$ :

$$g(S^1, x) \leq g(S^2, x), \quad \forall x \in [0, M], 0 < S^1 < S^2.$$

3. For any  $x \in (0, M)$

$$\partial_x \left( \frac{g(S^1, x) b(S^2, x)}{g(S^2, x) b(S^1, x)} \right) \geq 0.$$

4. For any  $x \in (0, M)$ , the function  $S \mapsto \frac{b(S, x)}{g(S, x)}$  is non increasing.

5. For any  $S > 0$ , we have  $g(S, 0) = g(S, M) = 0$  et  $g(S, x) > 0$  for any  $x \in (0, M)$ .

These assumptions are satisfied, for instance, if  $b$  does not depends on the variable  $S$  and if  $g$  is of the form:  $g(S, x) = \mu(S) \tilde{g}(x)$ , where  $\mu$  is an non decreasing function, for example a Monod kinetics  $\mu(S) = \mu_{\max} \frac{S}{K+S}$  where  $\mu_{\max}$  and  $K$  are constants, and  $\tilde{g}$  is such that  $\tilde{g}(0) = \tilde{g}(M) = 0$  and  $\tilde{g}(x) > 0$  for any  $x \in (0, M)$ .

**Theorem 3.8.** *Under Assumptions 3.1 and 3.7, we have for any  $x \in (0, M)$*

$$\mathbb{P}_x^{S^1}(\text{survival}) \leq \mathbb{P}_x^{S^2}(\text{survival}), \quad \forall 0 < S^1 \leq S^2.$$

In other words, for the chemostat model, under the assumptions of the previous theorem, the higher the substrate concentration in the chemostat at the mutation time is, the higher the survival probability is.

*Proof.* For any  $y \in (0, M)$  the function  $S \mapsto g(S, y)$  is non decreasing then  $A_u^{S^1}(x) \leq A_u^{S^2}(x)$  for any  $u \geq 0$ . Moreover the function  $(S, x) \mapsto b(S, x)$  is non decreasing in the two variables  $S$  and  $x$ , then we have

$$p_1^{S^1}(x) - p_1^{S^2}(x) = D \int_0^\infty e^{-Dt} \left[ e^{-\int_0^t b(S^1, A_u^{S^1}(x)) du} - e^{-\int_0^t b(S^2, A_u^{S^2}(x)) du} \right] dt \geq 0.$$

The function  $S \mapsto p_1^S(x)$  is then non increasing for any  $x \in (0, M)$ . Let  $n \in \mathbb{N}^*$ , we assume that the function  $S \mapsto p_n^S(x)$  is non increasing for any  $x \in (0, M)$ . In the same way as in the proof of Proposition 3.5, we use the following decomposition

$$p_{n+1}^S(x) = p_1^S(x) + p_{n+1}^S(x | \eta_\tau^S \neq 0) (1 - p_1^S(x))$$

where

$$p_{n+1}^S(x | \eta_\tau^S \neq 0) = \frac{1}{1 - p_1^S(x)} \int_0^\infty \left( b(S, A_t^S(x)) e^{-\int_0^t b(S, A_u^S(x)) du - Dt} \right. \\ \left. \times \int_0^1 q(A_t^S(x), \alpha) p_n^S(\alpha A_t^S(x)) p_n^S((1 - \alpha) A_t^S(x)) d\alpha \right) dt$$

represents the probability of extinction before the  $(n+1)$ -th generation, in the environment  $S$ , given the initial mass is  $x$  and the first event is a division.

Using the change of variable  $y = A_t^S(x)$ , we get

$$p_{n+1}^S(x | \eta_\tau^S \neq 0) = \frac{1}{(1 - p_1^S(x))} \int_x^M \frac{b(S, y)}{g(S, y)} e^{-\int_x^y \frac{b(S, z) + D}{g(S, z)} dz} \\ \int_0^1 q(y, \alpha) p_n^S(\alpha y) p_n^S((1 - \alpha) y) d\alpha dy. \quad (21)$$

This new formulation allows to focus on mass-dependence rather than time. In particular, it will allow to use the result of Proposition 3.5 later in the proof.

By the induction assumption, we have for  $0 < S^1 < S^2$ ,

$$p_{n+1}^{S^1}(x | \eta_\tau^{S^1} \neq 0) - p_{n+1}^{S^2}(x | \eta_\tau^{S^2} \neq 0) \geq \int_x^M h_x(y) \int_0^1 q(y, \alpha) p_n^{S^2}(\alpha y) p_n^{S^2}((1 - \alpha) y) d\alpha dy,$$

where  $h_x$  is defined for any  $y \in [x, M)$  by

$$h_x(y) \stackrel{\text{def}}{=} \frac{1}{1 - p_1^{S^1}(x)} \frac{b(S^1, y)}{g(S^1, y)} e^{-\int_x^y \frac{b(S^1, z) + D}{g(S^1, z)} dz} - \frac{1}{1 - p_1^{S^2}(x)} \frac{b(S^2, y)}{g(S^2, y)} e^{-\int_x^y \frac{b(S^2, z) + D}{g(S^2, z)} dz}$$

and represents the difference of the two probability density functions of the mass of division given the first event is a division. By the same change of variable as previously, we get for  $i = 1, 2$ ,

$$\int_x^M \frac{b(S^i, y)}{g(S^i, y)} e^{-\int_x^y \frac{b(S^i, z) + D}{g(S^i, z)} dz} dy = \int_0^\infty b(S^i, A_t^{S^i}(x)) e^{-\int_0^t b(S^i, A_u^{S^i}(x)) du - Dt} dt = 1 - p_1^{S^i}(x).$$

Hence,  $h_x$  satisfies

$$\int_x^M h_x(y) dy = 0.$$

Moreover

$$h_x(y) = \frac{1}{1 - p_1^{S^1}(x)} \frac{b(S^1, y)}{g(S^1, y)} \exp\left(-\int_x^y \frac{b(S^1, z) + D}{g(S^1, z)} dz\right) f_x(y)$$

with

$$f_x(y) \stackrel{\text{def}}{=} 1 - \frac{1 - p_1^{S^1}(x)}{1 - p_1^{S^2}(x)} \frac{g(S^1, y)}{g(S^2, y)} \frac{b(S^2, y)}{b(S^1, y)} \exp\left(\int_x^y \left(\frac{b(S^1, z) + D}{g(S^1, z)} - \frac{b(S^2, z) + D}{g(S^2, z)}\right) dz\right).$$

From Assumptions 3.7-3 and 4, for any  $y \in [x, M)$ ,

$$\begin{aligned} f_x'(y) &= -\frac{1 - p_1^{S^1}(x)}{1 - p_1^{S^2}(x)} \left[ \partial_y \left( \frac{g(S^1, y)}{g(S^2, y)} \frac{b(S^2, y)}{b(S^1, y)} \right) + \frac{g(S^1, y)}{g(S^2, y)} \frac{b(S^2, y)}{b(S^1, y)} \left( \frac{b(S^1, y) + D}{g(S^1, y)} - \frac{b(S^2, y) + D}{g(S^2, y)} \right) \right] \\ &\quad \times \exp\left(\int_x^y \left(\frac{b(S^1, z) + D}{g(S^1, z)} - \frac{b(S^2, z) + D}{g(S^2, z)}\right) dz\right) \\ &\leq 0. \end{aligned}$$

Moreover, by Assumption 3.7-4

$$f_x(x) = 1 - \frac{1 - p_1^{S^1}(x)}{1 - p_1^{S^2}(x)} \frac{g(S^1, x)}{g(S^2, x)} \frac{b(S^2, x)}{b(S^1, x)} \geq 0.$$

Thus  $h_x(x) \geq 0$ ,  $h_x$  and  $f_x$  have the same sign,  $f_x$  is non increasing and  $\int_x^M h_x(y) dy = 0$ . Therefore, there exists  $y^* \in [x, M)$  such that

- $h_x(y) \geq 0$  for any  $y \leq y^*$
- $h_x(y) \leq 0$  for any  $y \geq y^*$ .

From Proposition 3.5 the function  $y \mapsto p_n^{S^2}(y)$  is non increasing. Moreover  $h_x$  is non negative on  $[x, y^*]$ , so from Lemma 3.4

$$\begin{aligned} \int_x^{y^*} h_x(y) \int_0^1 q(y, \alpha) p_n^{S^2}(\alpha y) p_n^{S^2}((1 - \alpha)y) d\alpha dy, \\ \geq \int_0^1 q(y^*, \alpha) p_n^{S^2}(\alpha y^*) p_n^{S^2}((1 - \alpha)y^*) d\alpha \int_x^{y^*} h_x(y) dy. \end{aligned}$$

In the same way,  $h_x$  is non positive on  $[y^*, M]$  and so

$$\begin{aligned} & \int_{y^*}^M h_x(y) \int_0^1 q(y, \alpha) p_n^{S^2}(\alpha y) p_n^{S^2}((1-\alpha)y) d\alpha dy \\ & \geq \int_0^1 q(y^*, \alpha) p_n^{S^2}(\alpha y^*) p_n^{S^2}((1-\alpha)y^*) d\alpha \int_{y^*}^M h_x(y) dy. \end{aligned}$$

Hence,

$$\begin{aligned} & p_{n+1}^{S^1}(x | \eta_\tau^{S^1} \neq 0) - p_{n+1}^{S^2}(x | \eta_\tau^{S^2} \neq 0) \\ & \geq \int_0^1 q(\alpha) p_n^{S^2}(\alpha y^*) p_n^{S^2}((1-\alpha)y^*) d\alpha \int_x^M h_x(y) dy = 0 \end{aligned}$$

and

$$\begin{aligned} p_{n+1}^{S^1}(x) - p_{n+1}^{S^2}(x) &= p_1^{S^1}(x) + p_{n+1}^{S^1}(x | \eta_\tau^{S^1} \neq 0) (1 - p_1^{S^1}(x)) \\ &\quad - p_1^{S^2}(x) - p_{n+1}^{S^2}(x | \eta_\tau^{S^2} \neq 0) (1 - p_1^{S^2}(x)) \\ &\geq (p_1^{S^1}(x) - p_1^{S^2}(x)) \left(1 - p_{n+1}^{S^2}(x | \eta_\tau^{S^2} \neq 0)\right) \\ &\geq 0. \end{aligned}$$

Finally, passing to the limit, we get

$$p^{S^1}(x) - p^{S^2}(x) = \lim_{n \rightarrow \infty} (p_n^{S^1}(x) - p_n^{S^2}(x)) \geq 0. \quad \square$$

### 3.3 Properties on the variations of the eigenvalue

From Theorems 2.3 and 3.8, we directly obtain the following result.

**Corollary 3.9.** *Under Assumptions 3.1 and 3.7,*

1. *if there exists  $S_1 > 0$  such that  $\Lambda_{S_1} > 0$ , then  $\Lambda_{S_2} > 0$  for any  $S_2 > S_1$ ;*
2. *if there exists  $S_1 > 0$  such that  $\Lambda_{S_1} \leq 0$ , then  $\Lambda_{S_2} \leq 0$  for any  $S_2 < S_1$ .*

This Corollary allows to deduce the following result about variation of the eigenvalue with respect to  $S$ .

**Corollary 3.10.** *Under Assumptions 3.7, the function  $S \mapsto \Lambda_S$  is non decreasing.*

*Proof.* Let  $S^* > 0$  be fixed. We set  $D' = D + \Lambda_{S^*} > 0$ . Let  $\Lambda'_S$  be the eigenvalue of the following eigenproblem:

$$\partial_x(g(S, x) \hat{u}'_S(x)) + (b(S, x) + D' + \Lambda'_S) \hat{u}'_S(x) = 2 \int_0^M \frac{b(S, z)}{z} q\left(z, \frac{x}{z}\right) \hat{u}'_S(z) dz.$$

For  $S = S^*$ , we have  $\Lambda'_{S^*} = 0$ , then from Corollary 3.9, for any  $S \leq S^*$ ,  $\Lambda'_S \leq 0$ . Moreover

$$\Lambda'_S = \Lambda_S + D - D' = \Lambda_S - \Lambda_{S^*}.$$

Hence  $\Lambda_S \leq \Lambda_{S^*}$ . □

### 3.4 Extensions and concluding remarks

The previous method can be applied for more general  $g$ , for which the growth in one environment is larger than the growth in the other one for all masses. A particular case is given in the following corollary.

**Corollary 3.11.** *We assume that the division rate function  $b$  does not depend on the variable  $S$  and is non decreasing in the variable  $x$  and that the growth speed  $g$  is of the form  $g(S, x) = \mu(S) \tilde{g}(x)$ , where  $g(S, x) > 0$  for any  $x \in (0, M)$  and  $\tilde{g} \in C[0, M] \cap C^1(0, M)$  is such that  $\tilde{g}(0) = \tilde{g}(M) = 0$ . Then, we have*

$$\mathbb{P}_x^{S^1}(\text{survival}) \leq \mathbb{P}_x^{S^2}(\text{survival}) \iff \mu(S^1) \leq \mu(S^2)$$

and

$$\Lambda_{S^1} \leq \Lambda_{S^2} \iff \mu(S^1) \leq \mu(S^2).$$

More generally, the following result states the link between the comparison of the survival probability and the comparison of the eigenvalue.

We extend the notations of the survival probability  $\mathbb{P}_{\delta_x}^{S,D}(\text{survival})$  and the eigenvalue  $\Lambda_S^D$  with a dependence to the death rate  $D$ .

**Proposition 3.12.** *Let  $S_1, S_2 > 0$ . If for any  $x \in [0, M]$  and for any  $D > 0$ , we have  $\mathbb{P}_{\delta_x}^{S_1, D}(\text{survival}) \geq \mathbb{P}_{\delta_x}^{S_2, D}(\text{survival})$ , then*

$$\forall D > 0, \quad \Lambda_{S_1}^D \geq \Lambda_{S_2}^D.$$

The condition on the survival probability stated in the previous theorem can be obtained, for example using a more probabilistic method, by a coupling of random variables. For example, it is possible to check by induction that under Assumptions 3.1 and 3.7, the stochastic models started from  $\delta_x$  and  $\delta_y$  with  $x < y$  can be coupled in such a way that the masses of individuals at their birth at each generation started from  $\delta_x$  are smaller than the masses of individuals at the same generation started from  $\delta_y$  (with possibly more individuals alive at this generation). This property implies the condition of Proposition 3.12 and allows to give a probabilistic view of our results and our assumptions.

This method could be applied for example to the case where the division distribution  $q$  depends on the variable  $S$ . The results of Section 3.1 hold as, for this section, the substrate concentration is fixed. The difficulties are in the control of the variation in  $S$  of the terms which integrate  $q$  with respect to the extinction probability  $p_n^S$ , as in (21).

*Proof.* Let  $S_1 > 0$ . We set  $D' = D + \Lambda_{S_1}^D > 0$ . Let  $\Lambda'_S$  be the eigenvalue associated to the eigenproblem

$$\partial_x(g(S, x) \hat{u}'_S(x)) + (b(S, x) + D' + \Lambda'_S) \hat{u}'_S(x) = 2 \int_0^M \frac{b(S, z)}{z} q\left(\frac{x}{z}\right) \hat{u}'_S(z) dz.$$

For  $S = S_1$ ,  $\Lambda'_{S_1} = 0$ , we then deduce, from Theorem 2.3, that  $\mathbb{P}_{\delta_x}^{S_1, D'}(\text{survival}) = 0$  and then, by assumption, that  $\mathbb{P}_{\delta_x}^{S_2, D'}(\text{survival}) = 0$ . From Theorem 2.3  $\Lambda'_{S_2} \leq 0$ . Moreover

$$\Lambda'_{S_2} = \Lambda_{S_2}^D + D - D' = \Lambda_{S_2}^D - \Lambda_{S_1}^D$$

hence

$$\Lambda_{S_2}^D \leq \Lambda_{S_1}^D . \quad \square$$

## References

- Calvez, V., Doumic, M., and Gabriel, P. (2012). Self-similarity in a general aggregation-fragmentation problem ; application to fitness analysis. *Journal de Mathématiques Pures et Appliquées*, 98(1):1–27.
- Campillo, F., Champagnat, N., and Fritsch, C. (2015). Links between deterministic and stochastic approaches for invasion in growth-fragmentation-death models. *ArXiv Mathematics e-prints*. arXiv/1509.0819 [math.PR].
- Campillo, F. and Fritsch, C. (2015). Weak convergence of a mass-structured individual-based model. *Applied Mathematics & Optimization*, 72(1):37–73.
- Demazure, M. (2000). *Bifurcations and catastrophes : geometry of solutions to nonlinear problems*. Springer, New York.
- Doumic, M. (2007). Analysis of a population model structured by the cells molecular content. *Mathematical Modelling of Natural Phenomena*, 2:121–152.
- Doumic, M., Hoffmann, M., Krell, N., and Robert, L. (2015). Statistical estimation of a growth-fragmentation model observed on a genealogical tree. *Bernoulli*, 21(3):1760–1799.
- Doumic Jauffret, M. and Gabriel, P. (2010). Eigenelements of a general aggregation-fragmentation model. *Mathematical Models and Methods in Applied Sciences*, 20(05):757–783.
- Fredrickson, A. G., Ramkrishna, D., and Tsuchiya, H. M. (1967). Statistics and dynamics of procaryotic cell populations. *Mathematical Biosciences*, 1(3):327–374.
- Fritsch, C., Campillo, F., and Ovaskainen, O. (2016). Numerical analysis of invasion in a chemostat. In preparation.
- Fritsch, C., Harmand, J., and Campillo, F. (2015). A modeling approach of the chemostat. *Ecological Modelling*, 299:1–13.
- Hoang, V. H. (2015). Estimating the division kernel of a size-structured population. *ArXiv Mathematics e-prints*. arXiv/1509.02872 [math.ST].
- Hoffmann, M. and Olivier, A. (2015). Nonparametric estimation of the division rate of an age dependent branching process. *ArXiv Mathematics e-prints*. arXiv/1412.5936v2 [stat.OT].
- Laurençot, P. and Perthame, B. (2009). Exponential decay for the growth-fragmentation/cell-division equations, *Communications in Mathematical Sciences*, 7(2):503–510.

- Metz, J. (2008). Fitness. In Fath, S. E. J. D., editor, *Encyclopedia of Ecology*, pages 1599–1612. Academic Press, Oxford.
- Metz, J. A., Nisbet, R. M., and Geritz, S. A. (1992). How should we define ‘fitness’ for general ecological scenarios? *Trends in Ecology & Evolution*, 7(6):198–202.
- Metz, J. A. J., Geritz, S. A. H., Meszéna, G., Jacobs, F. J. A., and van Heerwaarden, J. S. (1996). Adaptive dynamics: A geometric study of the consequences of nearly faithful reproduction. In van Strien, S. J. and Verduyn-Lunel, S. M., editors, *Stochastic and spatial structures of dynamical systems (Amsterdam, 1995)*, pages 183–231. North-Holland.
- Michel, P. (2005). Fitness optimization in a cell division model, *Comptes Rendus Mathématique*, 341(12):731–736.
- Michel, P. (2006). Optimal proliferation rate in a cell division model, *Mathematical Modelling of Natural Phenomena*, 1(2):23–44.
- Perthame, B. and Ryzhik, L. (2005). Exponential decay for the fragmentation or cell-division equation. *Journal of Differential Equations*, 210(1):155–177.