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Ergodic behaviour of a multi-type growth-fragmentation process modelling the mycelial network of a filamentous fungus

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Abstract

In this work, we introduce a stochastic growth-fragmentation model for the expansion of the network of filaments, or *mycelium*, of a filamentous fungus. In this model, each individual is described by a discrete type $\epsilon \in \{0, 1\}$ indicating whether the individual corresponds to an internal or terminal segment of filament, and a continuous trait $x \geq 0$ corresponding to the length of this segment. The length of internal segments cannot grow, while the length of terminal segments increases at a deterministic speed v . Both types of individuals/segment branch according to a type-dependent mechanism.

After constructing the stochastic bi-type growth-fragmentation process of interest, we analyse the corresponding mean measure (or first moment semigroup) and show a Harris-type ergodic theorem stating that, in the long run, the total mass of the mean measure increases exponentially fast while the type-dependent density in trait stabilises to an explicit distribution. In the particular model we consider, which depends on only 3 parameters, all the quantities needed to describe this asymptotic behaviour are explicit, which paves the way for parameter inference based on data collected in lab experiments.

Key words and phrases: *Branching processes, Growth-fragmentation systems.*

MSC2020 subject classification: 60J80, 35B40.

1 Introduction

Filamentous fungi are complex expanding organisms that are omnipresent in nature. They form filamentous structures known as *hyphae*. These filaments grow and branch to create potentially huge networks called *mycelia*, sometimes covering up to a few square kilometers. To feed the whole mycelium, hyphae tamper with their environment by decomposing the dead organic matter, making its chemical components available to the next generation of organisms (including the fungus itself). Thereby, filamentous fungi play a key role in the functioning of natural ecosystems. They are also able to quickly respond to local threats such as attacks by predators, physical obstacles, or noxious local conditions, through an

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efficient chemical communication along the hyphal network, leading to its partial reorganisation or to the reorientation of the growth capacity of the mycelium away from danger [7, 19]. All these characteristics made these species appealing to the biochemical (and in particular, pharmaceutical) industry, in which they are now routinely used to catalyse various reactions and produce different types of metabolites. See the review paper [5] for numerous examples and for a careful discussion of the relation between the extent of mycelial branching and metabolite production.

In this paper, we aim at understanding the basic growth properties of the mycelium in a given species of filamentous fungi, leaving aside the complex interactions with its environment and ecosystem mentioned above. More precisely, assuming that the fungus grows in homogeneous conditions and away from predators or pests (*e.g.*, on a Petri dish in a lab experiment), we want to identify simple descriptors that characterise the growth of the fungus and allow us to quantify the impact of various forms of stresses (nutrient depletion, pH, ...) on the mycelial growth and structure. These descriptors should be robust enough to allow the comparison of different fungus species.

The expansion of the hyphal network rests upon several biological processes. The first one is the growth of “primary” hyphae, in a more or less radial way. These hyphae extend the area already covered by the mycelium, exploring the environment in search for new sources of nutrients. They grow in numbers by branching in two at their tips (or *apexes* – we shall later speak of *apical* branching) at some rate. As in a spider web, these primary hyphae serve as a backbone for “secondary” hyphae, that branch off from the primary structure (approximately uniformly along the existing hyphae – we shall later speak of *lateral* branching). The secondary hyphae increase the density of the network by growing in different directions and by themselves branching both laterally and at their apexes. A third process is the fusion of two hyphae when they cross, called *anastomosis*. This phenomenon improves the connectivity of the mycelium, as it creates shortcuts for the diffusion of molecules along the network of filaments. Note that hyphae do not necessarily merge when they cross, even when they are constrained to evolve in two spatial dimensions as in lab conditions. Alternatively, they may simply bypass each other and keep growing in different directions; anastomosis represents only a fraction of the outcomes of the crossing events and these crossings may in fact occur less frequently in nature (in which fungi grow in three dimensions) than on the two dimensional surface of a Petri dish.

Understanding the basic growth properties and the branching structure of the network of hyphae that results from them will be the first step before engaging in a more detailed modelling of the fungal growth taking into account flows of nutrients and chemical signalling along the network, which will be the object of future work. These questions have already been the object of a lot of attention, and the current state of the art in models of mycelial growth is substantial. A significant part of it relies on graph theory and consists in the statistical analysis of experimental quantitative data (number of internal nodes, of apexes, hyphal length, ..., of mycelia grown in laboratory) [5, 15, 20]. The major difficulties in these approaches, on which progress is still being made, is to set up a high-quality recording of this multi-scale growth dynamics (starting from a spore of a few micrometres and ending when the mycelium covers the few square centimetres of a Petri dish), and to be able to extract the topological network information of interest thanks to semi- or fully automated post-processing tools able to resolve most of the ambiguities present in the images (note that the number of branch points observable in these images can reach 10^5 , rendering node identification “with the eye” clearly unfeasible). We refer to [15] for more details on current challenges in this area. More mechanistic approaches gave rise to a variety of

spatially explicit stochastic models for the spatial spread of fungal mycelia, either lattice-based or lattice-free, in which hyphae grow in length by colonising neighbouring (free) locations, branch at some rate to give birth to a new hypha colonising free locations in another direction, and sometimes merge with another hypha when they cross. See [8] for a review of such models and [17] and references therein for more recent work. Despite their clear mathematical formulation, to our knowledge no analytical results on the long-term growth properties of these stochastic networks have been derived, in particular due to the difficulty of handling spatial interactions such as anastomosis and self-avoidance. The analysis instead relies on intensive simulations, exploring the space of parameters to find families of parameters producing patterns that match the observations, or looking for phase transitions in the mycelial growth pattern.

On a much finer scale, most models zoom in on the tip of a single hypha to understand the mechanisms triggering its extension (see, *e.g.*, [2, 26]). In contrast, other models focus on much larger spatial and temporal scales and describe the interaction between filamentous fungi and their environments in natural conditions, mostly in an aggregated way : the whole mycelium is assimilated with a single scalar quantity, its biomass, and a system of ordinary differential equations describes the circulation of nutrients and chemical molecules between the fungus and the environment and its effect on the growth and degradation of the fungus biomass and on different characteristics of the environment (see, *e.g.*, [21]). More recently, spatially explicit models were introduced, based on reaction-diffusion partial differential equations [18] or based on a system of stochastic differential equations (encoding the behaviour of each hypha, including anastomosis and self-avoidance) and its mean-field deterministic limit [12]. These models are in the same vein as models of tumor-induced angiogenesis (see, *e.g.*, [11]) and allow in particular to study global quantities such as the stationary shape and speed of the invasion front formed by the whole mycelium on the spatial scale of observation with the naked eye.

In this work, we instead focus on an intermediate spatial scale, observable in lab experiments thanks to the previously mentioned technology for the automated recording and analysis of movies such as the one developed at LIED (University of Paris), which was used in [15] to measure several quantities (exponential growth rates of the number of free ends of filaments – “open” ends – and of the number of internal nodes in the network – “closed” ends – in particular) analogous to those which will naturally appear in our analysis below. Because we shall neglect anastomosis in order to keep a tractable model as a first exploration tool in what follows, some care will be needed when doing parameter inference based on the model developed below. This issue will be discussed in Section ??.

Let us now describe our approach. It is based on two strong assumptions which are mostly motivated by our aim to understand the exponential growth behaviour observed in [15] through a simple but informative half-mechanistic, half-statistical model :

- (i) In completely homogeneous conditions and over small space- and time-scales, the spatial organisation of the hyphae does not (really) matter. That is, since the mycelium naturally spreads over the available space, we shall make the approximation that every piece of filament evolves in the same conditions as the others. Here we neglect the depletion of food due to the high density of hyphae around the origin (or centre) of the mycelium, which is a reasonable choice when considering short timescales;
- (ii) Anastomosis (the fusion of crossing hyphae) does not need to be explicitly modelled and its impact can be incorporated via an appropriate statistical treatment of the data when doing parameter inference. See the section on *Apex, node and length*

growth dynamics in [15] and Section ?? below for more details on this point.

The second assumption may look like a surprising modelling choice, but it has the paramount advantage that distinct (pieces of) filaments will not interact with each other in the model, allowing us to encode the mycelium as a *branching process*.

Each individual in our branching process corresponds to a segment of filament lying between two branching points (internal, or *closed*, segment), or between a branching point and the extremity of the filament (terminal, or *open*, segment). See Figure ??. An individual is represented by a pair (\mathbf{e}, x) , where $x \geq 0$ is the current length of the corresponding segment and $\mathbf{e} \in \{0, 1\}$ encodes whether the segment is open ($\mathbf{e} = 1$) or closed ($\mathbf{e} = 0$). More precisely, the space in which the pairs (\mathbf{e}, x) take their values is

$$S := (\{0\} \times (0, \infty)) \cup (\{1\} \times [0, \infty)), \quad (1.1)$$

excluding closed segments of length 0 for mathematical convenience (in practice, the latter will never occur in the model). At every time $t \geq 0$, the set of all segments constituting the network is fully described by the following point measure on S

$$\mathcal{Z}_t := \sum_{u \in V_t} \delta_{(\mathbf{e}^u, x_t^u)}, \quad (1.2)$$

where V_t denotes the indexing set of the individuals alive at time t and $z_t^u = (\mathbf{e}^u, x_t^u)$ denotes the characteristics at time t of individual $u \in V_t$. Note that this representation of the population of segments at any given time does not allow us to infer who is hooked up with whom in the network, but it will be sufficient for our purposes (*cf.* Assumption (i)). We write $\mathcal{M}_p(S)$ for the space of all finite point measures on S and we endow it with the topology of weak convergence. We shall also use the standard notation, for $\nu = \sum_{i=1}^n \delta_{z_i}$ and φ a measurable function on S ,

$$\langle \nu, \varphi \rangle := \int_S \varphi(z) \nu(dz) = \sum_{i=1}^n \varphi(z_i).$$

Let us fix $v, b_1, b_2 \in (\mathbb{R}_+^*)^3$. The dynamics of the process $(\mathcal{Z}_t)_{t \geq 0}$ are as follows:

- (a) **Elongation.** Open segments elongate deterministically at speed v , while closed segments cannot grow. More precisely, for every $s, t \geq 0$ and $u \in V_s$, conditionally on individual u not being involved in a branching event during the time interval $[s, s+t)$, we have for all $r \in [0, t)$,

$$x_{s+r}^u = x_s^u + \mathbf{e}^u v r. \quad (1.3)$$

- (b) **Apical branching.** Each open segment branches “at its apex” at rate b_1 . That is, every extant individual u such that $\mathbf{e}^u = 1$, independently of each other and at rate b_1 , is removed from the population and replaced by three new individuals: one closed individual of the same length as the “parent”, therefore with characteristics $(0, x_{t-}^u)$ (where t is the time of the branching event), and two open individuals of length 0 (and thus both with characteristics $(1, 0)$). See Figure??

- (c) **Lateral branching.** Every segment (open or closed) of length $x > 0$ branches laterally at rate $b_2 x$ and the branching point is chosen uniformly at random along the segment. That is, for every $t \geq 0$ and every $u \in V_{t-}$ such that $x_{t-}^u > 0$, at the instantaneous rate $b_2 x_{t-}^u$ individual u is removed from the population and is replaced

by three new individuals: one closed individual of length $\alpha^u x_{t-}^u$, one individual with first characteristics \mathbf{e}^u (i.e., open if the parent was open, or closed if the parent was closed) and length $(1 - \alpha^u)x_{t-}^u$, and finally an open individual of length 0, where α^u is an independent draw from a uniform distribution over $[0, 1]$. See Figure ???. All individuals branch “laterally” independently of each other and independently of the apical branching events described in (b).

In the above, removing (*resp.*, adding) an individual naturally translates into removing (*resp.*, adding) the corresponding atom in \mathcal{Z}_t at the time of the branching event. Inspired by this description, let us introduce the following operator \mathcal{G} , on which the martingale problem satisfied by $(\mathcal{Z}_t)_{t \geq 0}$ will be based. Let $C_b^1(\mathbb{R})$ stand for the set of all bounded functions on \mathbb{R} of class C^1 with bounded derivative, and let $C_b^1(S)$ stand for the set of all bounded continuous functions on S with bounded and continuous derivatives w.r.t. the variable x . For every $F \in C_b^1(\mathbb{R})$, $f \in C_b^1(S)$, let the function F_f be defined by

$$F_f(\nu) := F(\langle \nu, f \rangle), \quad \nu \in \mathcal{M}_p(S), \quad (1.4)$$

and define for all such functions F_f and all $\nu \in \mathcal{M}_p(S)$:

$$\begin{aligned} \mathcal{G}F_f(\nu) := & F'(\langle \nu, f \rangle) \int_S \mathbf{e} \nu \frac{\partial f}{\partial x}(\mathbf{e}, x) \nu(d\mathbf{e}, dx) \\ & + b_1 \int_S \mathbf{e} \left\{ F(\langle \nu, f \rangle) - f(\mathbf{e}, x) + f(0, x) + 2f(1, 0) \right\} \nu(d\mathbf{e}, dx) \\ & + b_2 \int_S x \int_0^1 \left\{ F(\langle \nu, f \rangle) - f(\mathbf{e}, x) + f(0, (1 - \alpha)x) + f(\mathbf{e}, \alpha x) + f(1, 0) \right. \\ & \quad \left. - F(\langle \nu, f \rangle) \right\} d\alpha \nu(d\mathbf{e}, dx). \end{aligned} \quad (1.5)$$

In Section 2, we follow the method developed in [22] and construct a process $(\bar{\mathcal{Z}}_t)_{t \geq 0}$ on a larger space in which the genealogical relationship between individuals is retained through the standard Ulam-Harris-Neveu encoding \mathcal{U} . This is the result of Theorem 2.1. If we then restrict our attention to its marginal over S and write $(\mathcal{Z}_t)_{t \geq 0}$ for the resulting $\mathcal{M}_p(S)$ -valued process (see Equation (2.6) for a more precise definition), we have the following property, also proved in Section 2. Let $p_l : S \rightarrow \mathbb{R}_+$ be the projector on the “length” coordinate, defined by $p_l(\mathbf{e}, x) = x$ for all $(\mathbf{e}, x) \in S$.

Proposition 1.1. *Let Z^0 be a random variable with values in $\mathcal{M}_p(S)$ such that*

$$\mathbb{E}[\langle Z^0, 1 \rangle] < \infty \quad \text{and} \quad \mathbb{E}[\langle Z^0, p_l \rangle] < \infty. \quad (1.6)$$

Let $(\mathcal{Z}_t)_{t \geq 0}$ be the càdlàg $\mathcal{M}_p(S)$ -valued process constructed in (2.5)-(2.6), starting at $\mathcal{Z}_0 = Z^0$. Then for every $F \in C_b^1(\mathbb{R})$ and $f \in C_b^1(S)$,

$$\left(F_f(\mathcal{Z}_t) - F_f(\mathcal{Z}_0) - \int_0^t \mathcal{G}F_f(\mathcal{Z}_s) ds \right)_{t \geq 0} \quad (1.7)$$

is a martingale.

To be more precise, we have tacitly assumed that $\bar{\mathcal{Z}}^0$ is constructed from Z^0 by giving a label 1, 2, ..., $\langle Z^0, 1 \rangle$ to the atoms of Z^0 to obtain a point measure on $\mathcal{U} \times S$. See Section 2 for more details.

Observe that it is implicitly assumed here that \mathcal{Z}_t is well-defined at any time $t \geq 0$, which is not obvious from the informal description of the process in terms of growth and branching events. Indeed, the total branching rate at time t is proportional to the number of open individuals $\langle \mathcal{Z}_t, \mathbb{1}_{\{\epsilon=1\}} \rangle$ and to the total length $\langle \mathcal{Z}_t, p_l \rangle$. Since the total length process itself increases between the branching times at a speed proportional to the number of open individuals, this may lead to an explosion in finite time of the number individuals in the population. It is one of the results of Theorem 2.1 that this explosion a.s. does not occur. We also derive useful bounds on the expectation of the total number of individuals and of the total length at time t in Lemma 2.2. From now on, we work with the process $(\mathcal{Z}_t)_{t \geq 0}$ of Proposition 1.1.

What we have just defined is a stochastic growth-fragmentation model, in which the growth term simply corresponds to the elongation of each open individual at a fixed linear speed while the branching of an individual corresponds to its fragmentation “into three pieces” (some of length 0) in such a way that the total length is conserved. Growth-fragmentation models are now common, in particular in the literature on partial differential equations where they have been extensively studied. See [25] for a classic and [3, 10, 16] for more recent examples covering different biological phenomena. Other approaches based on probabilistic representations of the solutions to growth-fragmentation equations appeared more recently, see in particular [4, 6] and references therein for the non-conservative case of which our model is an example. Potential applications include the evolution of age-structured populations (where age is the continuous individual trait that grows linearly and is “fragmented” into one individual with the same age and one individual with age 0 at the event of a birth), the growth of bacterial populations (in which the length, or another continuous individual trait of a bacterium, grows during its lifetime and is split between the two offspring bacteria resulting from a division event), as well as more general fragmentation phenomena (*e.g.*, of polymers) in which potentially more than two individuals come out of a fragmentation event and the sharing of the “parental” trait between the “offspring” may not be conservative (with the production of dust, for instance). Of particular interest is the long-term behaviour of the population size and trait distribution. A huge literature is devoted to this question, and we refer to the introduction of [23] for a comprehensive overview. In general, what is shown is that there exists an exponent $\lambda \in \mathbb{R}$ (called the *Malthusian exponent*) and a stationary profile N on the trait space such that the density $n_t(x)$ of individuals of trait x at time t behaves like

$$n_t(x) \approx e^{\lambda t} \langle n_0, \psi \rangle N(x) \quad \text{as } t \rightarrow \infty, \quad (1.8)$$

where ψ is a function characterising the impact of the initial condition. The approximation (1.8) is made rigorous by considering the appropriate function space and by proving the convergence of $e^{-\lambda t} n_t$ to $\langle n_0, \psi \rangle N$ in this space. Although multidimensional continuous traits (age and size, ...) are sometimes considered, the case of additional non-evolving discrete types that influence the individual growth and branching properties (like our type $\epsilon \in \{0, 1\}$) is less common and we could only find a few studies dealing with quiescent and proliferative cells in models for tumour growth (see, *e.g.*, Section 6 in [1], or [9]).

Such deterministic approaches apply when one considers very large populations, already distributed on the trait space according to some continuous density at the origin of time, for which we suspect that the stochasticity inherent to the branching or fragmentation dynamics only plays a minor role and the average behaviour of the population is sufficient to understand how the trait distribution evolves in time. To deal with initially very small populations, or to justify the growth-fragmentation equation at the population

level as being the large-population limit of a model at the microscopic level of individual dynamics, individual-based stochastic models are particularly appropriate tools. A further classical connection between the branching processes $(\mathcal{Z}_t)_{t \geq 0}$ and deterministic growth-fragmentation equations is made through the *mean measure* (or first moment semigroup) defined as follows. Let $\mathcal{M}_f(S)$ be the space of all finite measures on S (also endowed with the topology of weak convergence). For every $t \geq 0$, let $n_t \in \mathcal{M}_f(S)$ be defined by: for every bounded measurable function f on S ,

$$\langle n_t, f \rangle := \mathbb{E}[\langle \mathcal{Z}_t, f \rangle]. \quad (1.9)$$

Note that these quantities are well-defined for all t thanks to the bound on $\mathbb{E}[\langle \mathcal{Z}_t, 1 \rangle]$ obtained in Lemma 2.2. Note also that the definition of n_t depends on the distribution of \mathcal{Z}_0 , although for now we do not report this dependence in the notation for simplicity. To ease the statement of our next results, let us decompose each n_t as follows: for every bounded measurable $f : S \rightarrow \mathbb{R}$,

$$\langle n_t, f \rangle = \int_{\mathbb{R}_+} f(1, x) n_t^1(dx) + \int_{\mathbb{R}_+^*} f(0, x) n_t^0(dx), \quad (1.10)$$

where the measure n_t^1 on \mathbb{R}_+ (*resp.*, n_t^0 on \mathbb{R}_+^*) is uniquely defined by the set of equations (1.10) written for all f such that $f(\mathbf{e}, x) = 0$ whenever $\mathbf{e} = 0$ (*resp.*, $\mathbf{e} = 1$).

In Section 3, we use the martingale problem formulation (1.7) to show that if n_0^1 and n_0^0 both admit a density with respect to Lebesgue measure, then this property also holds true at any later time and, furthermore, these densities solve a system of growth-fragmentation equations. More precisely, we prove the following result.

Proposition 1.2. *Suppose that the assumptions of Proposition 1.1 are satisfied, and that the measures n_0^1 and n_0^0 defined by (1.10) (with $t = 0$) are absolutely continuous with respect to Lebesgue measure on \mathbb{R}_+ and \mathbb{R}_+^* , respectively. Then for every $t \geq 0$, n_t^1 and n_t^0 are also absolutely continuous with respect to Lebesgue measure. Furthermore, abusing notation and writing*

$$n_t^1(dx) = n_t^1(x) dx \quad \text{and} \quad n_t^0(dx) = n_t^0(x) dx, \quad (1.11)$$

then the densities $(n_t^0, n_t^1)_{t \geq 0}$ are weak solutions to the following system:

$$\begin{cases} \frac{\partial}{\partial t} n_t^1(x) + v \frac{\partial}{\partial x} n_t^1(x) + (b_1 + b_2 x) n_t^1(x) = b_2 \int_x^\infty n_t^1(y) dy, \\ v n_t^1(0) = 2b_1 \int_0^\infty n_t^1(y) dy + b_2 \int_0^\infty y (n_t^1(y) + n_t^0(y)) dy, \\ \frac{\partial}{\partial t} n_t^0(x) + b_2 x n_t^0(x) = b_1 n_t^1(x) + 2b_2 \int_x^\infty n_t^0(y) dy + b_2 \int_x^\infty n_t^1(y) dy. \end{cases} \quad (1.12)$$

Once this system has been derived, we may use it to understand the long-term behaviour of the mean measure (instead of the full stochastic process, to start with). To do so, let us first observe that if we scale time by a factor $1/v$ and consider $(n_{t/v})_{t \geq 0}$, then all the above remains true but elongation now happens at speed $\tilde{v} = 1$, apical branching at rate $\tilde{b}_1 = b_1/v$ and lateral branching at rate $\tilde{b}_2 x := (b_2/v)x$. Therefore, to ease the notation and without loss of generality, we now suppose that $v = 1$. Second, let us introduce the following functions, which will be needed for our convergence theorem below. Let $\lambda > 0$ be the unique positive solution to

$$b_1 + \frac{b_2}{\lambda} = \lambda. \quad (1.13)$$

Let $N_1 : \mathbb{R}_+ \rightarrow \mathbb{R}_+$ and $N_0 : \mathbb{R}_+^* \rightarrow \mathbb{R}_+$ be defined by

$$N_1(x) = (b_1 + b_2x + \lambda)e^{-\int_0^x (b_1 + b_2y + \lambda)dy}, \quad (1.14)$$

and

$$N_0(x) = \frac{N_1(x)}{(b_2x + \lambda)^2} (b_2 + b_1(b_2x + \lambda)) + \frac{b_2e^{-\int_0^x (b_1 + b_2y + \lambda)dy}}{(b_2x + \lambda)^3} (2b_2 + b_1(b_2x + \lambda)). \quad (1.15)$$

We shall show in Proposition 4.1 that N_1 and N_0 are probability densities (*i.e.*, they integrate to 1). Let us also define the functions ψ and V on S as follows:

$$\psi(\mathbf{e}, x) = \frac{\lambda^2}{\lambda^2 + b_2} \left(\mathbf{e} + \frac{b_2}{\lambda} x \right), \quad V(\mathbf{e}, x) = \psi(\mathbf{e}, x) + 1 + x^2. \quad (1.16)$$

Although these quantities look fairly mysterious at the moment, we shall see in Section 4.1 that they are eigenelements of the spectral problem associated with (1.12) and of the adjoint spectral problem (see Proposition 4.1). We can now formulate the following theorem.

Theorem 1.3. *There exist $C, w > 0$ such that for any solution $(n_t^0, n_t^1)_{t \geq 0}$ of (1.12) satisfying $\langle n_0, V \rangle < \infty$, we have for all $t \geq 0$*

$$\|e^{-\lambda t} n_t^1 - \langle n_0, \psi \rangle N_1\|_{L^1(\mathbb{R}_+)} + \|e^{-\lambda t} n_t^0 - \langle n_0, \psi \rangle N_0\|_{L^1(\mathbb{R}_+^*)} \leq C e^{-wt} \langle n_0, V \rangle. \quad (1.17)$$

Theorem 1.3 is in fact a corollary of the finer convergence theorem formulated in Section 4.2, namely Theorem 4.3, in which the convergence is shown to occur in weighted total variation norm in the appropriate functional space. Since its statement requires another round of heavy notation, we only provide here a more reader-friendly version. The proof of Theorem 4.3 uses an analogue of Harris' ergodic theorem for non-conservative semigroups (*i.e.*, whose total mass is not conserved through time) derived from growth-fragmentation equations. More precisely, we use Theorem 1.1 in [4] and most of Section 4.2 will be devoted to proving that the assumptions of this theorem are satisfied by $(n_t)_{t \geq 0}$.

This approach was also used in the recent paper [14] in which individuals (bacteria) can be of two types with different growth parameters: for both types of individuals, the trait considered grows exponentially fast but at two different rates $\alpha_0, \alpha_1 > 0$, and the branching/fragmentation rate is common to all individuals and is trait-dependent. During each fragmentation event, the length of the "parent" is split between the two offspring in fixed proportions $\theta_0, \theta_1 = 1 - \theta_0$. Because of the very quick elongation of both types of individuals, together with the assumption that the (positive) branching rate tends to infinity as the individual length goes to infinity, it is natural (although not easy to prove) that the same form of convergence (1.8) as in similar systems with only one type of individuals should occur in their framework, and indeed this constitutes the main results of [14]. In contrast, in our case closed individuals do not elongate at all and the length of open individuals increases rather slowly (linearly with time). Since the branching rate of closed individuals is proportional to their lengths, it is not at all obvious that the subpopulation of closed individuals will develop quickly enough that the whole population size increases exponentially fast. Furthermore, smaller and smaller closed individuals may accumulate, preventing the length distribution within the population from stabilising. Therefore, the convergence stated in Theorem 1.3 is a somehow more surprising example of the robustness of the asymptotic behaviour of growth-fragmentation equations.

Finally, note that the theorems from [22] and [4] on which our existence and long-term convergence results hinge are very general and would allow us to consider various generalisations of our type-dependent growth and fragmentation mechanisms. However, in the particular case considered here all the quantities and functions of interest are explicit (a nice property which is bound to fail in most generalisations) and in future work we intend to apply this precise model to experimental data, in collaboration with our colleagues from the NEMATIC¹ research project. We shall therefore stick to this particular model, which should be seen as a simple but characteristic example of what may be done with other multi-type growth-fragmentation dynamics.

The rest of the paper is organised as follows. In Section 2 we construct the $\mathcal{M}_p(S)$ -valued process of interest, $(\mathcal{Z}_t)_{t \geq 0}$, and provide useful bounds on the expected total size $\langle \mathcal{Z}_t, 1 \rangle$ and total length $\langle \mathcal{Z}_t, p_l \rangle$ of the system at any time $t \geq 0$. In Section 3, we prove Proposition 1.2. In Section 4 we analyse the long time behaviour of the mean measure. First, we state the spectral problem associated to the system (1.12) and its adjoint and provide explicit solutions to both problems (Section 4.1). Second, in Section 4.2, we prove the finer convergence Theorem 4.3, of which Theorem 1.3 is a consequence. Finally, in Appendix A.1 we obtain that the eigen values of the above mentioned spectral problem satisfy the equation (1.13). In Appendix A.2 we check that the explicit values we provided as the solutions of the spectral problem indeed satisfy it.

2 Construction of the process $(\mathcal{Z}_t)_{t \geq 0}$

We work on a probability space $(\Omega, \mathcal{F}, \mathbb{P})$ rich enough to accommodate all the objects we use below. Following the method used in [22], we first construct a process $(\bar{Z}_t)_{t \geq 0}$ keeping track of the different lines of descent. To do so, we use the standard Ulam notation to identify each individual:

$$\mathcal{U} = \cup_{n \in \mathbb{N}} \{ \mathbb{N} \times (\{1, 2, 3\})^n \}. \quad (2.1)$$

For a given initial state of the population Z_0 with I_0 individuals (or atoms in Z_0), we label its atom by $1, \dots, I_0$. The offspring of an individual $u \in \mathcal{U}$ are denoted by $u1, u2, u3$.

We now proceed as in Section 2 of [22], with a few simplifications due to our particular framework. First, the growth and branching dynamics are homogeneous in time and consequently, in their notation we may take $\mathcal{X} = \mathcal{Y} = S$ (we do not need to add a last coordinate to keep track of the current value of time as they do in their definition of \mathcal{X}). The flow Φ describing the deterministic growth process is simply given for any $(\mathbf{e}, x) \in S$ and $0 \leq s \leq t$ by

$$\Phi((\mathbf{e}, x), s, t) := (\mathbf{e}, x + \mathbf{e}(t - s)v). \quad (2.2)$$

The instantaneous rate at which a division (or reproduction) event happens to an individual with trait (\mathbf{e}, x) is given by

$$B(\mathbf{e}, x) := b_1 \mathbf{e} + b_2 x. \quad (2.3)$$

The function B is continuous on S . Each reproducing individual is replaced by exactly 3 offspring, and so in the notation of [22] we have $p_k(\mathbf{e}, x) = \mathbb{1}_{\{k=3\}}$ for all $(\mathbf{e}, x) \in S$. The traits at birth of the 3 offspring of an individual of trait $z = (\mathbf{e}, x)$ are given by a triplet $(F_1(z, \Theta), F_2(z, \Theta), F_3(z, \Theta))$, where Θ is an independent draw from a uniform random

¹Growing and branching networks: Analysis, modelling and simulation of multi-scale spatial exploration, spreading and morphogenesis under constraints. Confrontation with experimental data obtained from mycelial thalli of *Podospora anserina*.

variable on $[0, 1)$ and the functions $F_1, F_2, F_3 : S \times [0, 1) \rightarrow S$ are given by: for every $(\mathbf{e}, x) \in S$ and $\theta \in [0, 1)$,

$$\begin{aligned} & (F_1(\mathbf{e}, x, \theta), F_2(\mathbf{e}, x, \theta), F_3(\mathbf{e}, x, \theta)) \\ & := \begin{cases} \left(\left(0, x \frac{\theta(b_1\mathbf{e} + b_2x)}{b_2x} \right), \left(\mathbf{e}, x \left(1 - \frac{\theta(b_1\mathbf{e} + b_2x)}{b_2x} \right) \right), (1, 0) \right) & \text{if } \theta < \frac{b_2x}{b_1\mathbf{e} + b_2x}, \\ ((0, x), (1, 0), (1, 0)) & \text{if } \theta \geq \frac{b_2x}{b_1\mathbf{e} + b_2x}. \end{cases} \end{aligned} \quad (2.4)$$

In words, assuming that Θ follows a uniform distribution on $[0, 1)$ we see that the branching of an open individual ($\mathbf{e} = 1$) is “lateral” (first line above) with probability $b_2x/(b_1 + b_2x)$, or “apical” with probability $b_1/(b_1 + b_2x)$. Conditionally on $\Theta < b_2x/(b_1 + b_2x)$, the first offspring inherits a fraction $\Theta/[b_2x/(b_1 + b_2x)]$ of the parental length, which indeed corresponds to a uniformly distributed split. If we now consider closed individuals ($\mathbf{e} = 0$), we have $b_2x/(b_1\mathbf{e} + b_2x) = 1$ and since we have excluded the case $\theta = 1$, only “lateral” branching can occur and during such an event, the parental length x is split uniformly at random between the first two offspring.

On top of the individuals’ traits, we follow their labels in \mathcal{U} indicating the genealogical relationship between them. Let thus $\mathcal{M}_p(\mathcal{U} \times S)$ be the space of all finite point measures on $\mathcal{U} \times S$, equipped with the topology of weak convergence. The state of the population at any time t will take the form

$$\bar{Z}_t := \sum_{u \in V_t} \delta_{(u, \mathbf{e}^u, x_t^u)}, \quad (2.5)$$

where V_t is the index set of all individuals alive at time t (*i.e.*, of all atoms of \bar{Z}_t). Restricting our attention to the marginal on S of \bar{Z}_t , we shall then obtain the following measure $\mathcal{Z}_t \in \mathcal{M}_p(S)$:

$$\mathcal{Z}_t := \sum_{u \in V_t} \delta_{(\mathbf{e}^u, x_t^u)}. \quad (2.6)$$

The main result of this section is the following theorem. Let M be a Poisson point measure on $\mathbb{R}_+ \times \mathcal{U} \times \mathbb{R}_+ \times [0, 1)$ with intensity $ds \otimes \nu(du) \otimes dz \otimes d\theta$, where $\nu(du)$ denotes the counting measure on \mathcal{U} . Let $(\mathcal{F}_t)_{t \geq 0}$ denote the natural filtration associated to M . Finally, let $C_b^1(\mathcal{U} \times S)$ stand for the space of all measurable functions on $\mathcal{U} \times S$ that are bounded, continuously differentiable with respect to the variable x and whose first derivatives w.r.t. x are bounded uniformly in u, \mathbf{e} .

Theorem 2.1. *Let $\bar{Z}^0 \in \mathcal{M}_p(\mathcal{U} \times S)$. Then, there exists a strongly unique $(\mathcal{F}_t)_{t \geq 0}$ -adapted càdlàg process $(\bar{Z}_t)_{t \geq 0}$ with values in $\mathcal{M}_p(\mathcal{U} \times S)$ such that $\bar{Z}_0 = \bar{Z}^0$ a.s., and for all $f \in C_b^1(\mathcal{U} \times S)$ and all $t \geq 0$,*

$$\begin{aligned} \langle \bar{Z}_t, f \rangle &= \langle \bar{Z}_0, f \rangle + \int_0^t \int_{\mathcal{U} \times S} v\mathbf{e} \frac{\partial f}{\partial x}(u, \mathbf{e}, x) \bar{Z}_s(du, d\mathbf{e}, dx) ds \\ &+ \int_0^t \int_{\mathcal{U} \times \mathbb{R}_+ \times [0, 1)} \mathbb{1}_{\{u \in V_{s-}, z \leq B(\mathbf{e}^u, x_{s-}^u)\}} \left[\sum_{i=1}^3 f(ui, F_i(\mathbf{e}^u, x_{s-}^u, \theta)) - f(u, \mathbf{e}^u, x_{s-}^u) \right] \\ &M(ds, du, dz, d\theta). \end{aligned} \quad (2.7)$$

We prove Theorem 2.1 and then show that it implies Proposition 1.1.

Proof. (Proof of Theorem 2.1) We only have to check that Assumptions **A** and **B** of Theorem 2.2 in [22] are satisfied.

Concerning **A.1**, we have for all $(\mathbf{e}, x) \in S$

$$B(\mathbf{e}, x) \leq (b_1 \vee b_2)(|\mathbf{e}| + |x|),$$

and so Assumption **A.1** is satisfied with $\gamma = 1$.

Assumption **A.2** is trivially satisfied since for all $(\mathbf{e}, x) \in S$ and $\theta \in [0, 1)$, we have

$$\sum_{i=1}^3 F_i(\mathbf{e}, x, \theta) \leq (2, x) \quad \text{componentwise.}$$

Assumption **A.3** is satisfied since the offspring number is a.s. equal to 3, independently of the parental trait.

As concerns Assumption **A.4**, the branching rate of open individuals is bounded from below by $b_1 > 0$, which yields the result in this case. Since elements of S of the form $(0, x)$ satisfy that $x > 0$ by construction, we can write

$$\int_s^t B(\Phi((0, x), s, r)) dr = b_2 x(t - s) \rightarrow +\infty \quad \text{a.s. as } t \rightarrow \infty,$$

which is the desired condition.

It remains to check Assumption **B**. Recall from **A.1** that $\gamma = 1$. The infinitesimal generator of the individual trait dynamics corresponding to the flow Φ is simply given by: for all $f \in C_b^1(S)$ and $(\mathbf{e}, x) \in S$,

$$\mathcal{H}f(\mathbf{e}, x) := v\mathbf{e} \frac{\partial f}{\partial x}(\mathbf{e}, x).$$

The function $h : (\mathbf{e}, x) \mapsto (|\mathbf{e}| + |x|)^\gamma = \mathbf{e} + x$ does not belong to the domain of \mathcal{H} since it is not bounded. However, it is easy to construct a sequence $(h_n)_{n \geq 1}$ of functions on S such that for every $n \geq 1$, h_n and h coincide on the set $\{(\mathbf{e}, x) \in S : x \leq n\}$, $h_n \in C_b^1(S)$ and there exists $c_1, c_2 \geq 0$ such that for all $n \geq 1$ and $(\mathbf{e}, x) \in S$,

$$\lim_{n \rightarrow \infty} \mathcal{H}h_n(\mathbf{e}, x) \leq c_1(\mathbf{e} + x) + c_2.$$

For instance, define $h_n(\mathbf{e}, x) = h(\mathbf{e}, x)$ if $x \leq n$, $h_n(\mathbf{e}, x) = \mathbf{e} + (n + 1)$ if $x \geq n + 1$ and define $h_n(\mathbf{e}, x)$ for $x \in (n, n + 1)$ in such a way that h_n is differentiable with respect to x and its derivative is bounded by 2 on $[n, n + 1]$.

Theorem 2.2 in [22] then yields the result (observing that their martingales $M_{0,\cdot}^f(x)$ are identically equal to 0 in our case since the individual growth process is deterministic). \square

Let us now allow the initial condition \bar{Z}^0 to be random (recall that we supposed that $(\Omega, \mathcal{F}, \mathbb{P})$ could be as large as needed), and assume from now on that \bar{Z}^0 is such that

$$\mathbb{E}[\langle \bar{Z}^0, 1 \rangle] < \infty \quad \text{and} \quad \mathbb{E}[\langle \bar{Z}^0, p_l \rangle] < \infty, \quad (2.8)$$

where we have used again the notation p_l (introduced just before Proposition 1.1) for the projector $(u, \mathbf{e}, x) \mapsto x$ on the length coordinate.

If we restrict our attention to functions f that are independent of the \mathcal{U} -coordinate, Equation (2.7) reads

$$\begin{aligned} \langle \mathcal{Z}_t, f \rangle &= \langle \mathcal{Z}_0, f \rangle + \int_0^t \int_S v \mathbf{e} \frac{\partial f}{\partial x}(\mathbf{e}, x) \mathcal{Z}_s(d\mathbf{e}, dx) ds \\ &\quad + \int_0^t \int_{\mathcal{U} \times \mathbb{R}_+ \times [0,1]} \mathbb{1}_{\{u \in V_{s-}, z \leq B(\mathbf{e}^u, x_{s-}^u)\}} \left[\sum_{i=1}^3 f(F_i(\mathbf{e}^u, x_{s-}^u, \theta)) - f(\mathbf{e}^u, x_{s-}^u) \right] \\ &\quad M(ds, du, dz, d\theta). \end{aligned} \quad (2.9)$$

For $f \equiv 1$, this yields for all $t \geq 0$

$$\langle \mathcal{Z}_t, 1 \rangle = \langle \mathcal{Z}_0, 1 \rangle + 2 \int_0^t \int_{\mathcal{U} \times \mathbb{R}_+ \times [0,1]} \mathbb{1}_{\{u \in V_{s-}, z \leq B(\mathbf{e}^u, x_{s-}^u)\}} M(ds, du, dz, d\theta). \quad (2.10)$$

Taking expectations in the above and using that $B(\mathbf{e}, x) \leq b_1 + b_2 x$ for all $(\mathbf{e}, x) \in S$ and Fubini's theorem, we obtain

$$\begin{aligned} \mathbb{E}[\langle \mathcal{Z}_t, 1 \rangle] &= \mathbb{E}[\langle \mathcal{Z}_0, 1 \rangle] + 2 \int_0^t \mathbb{E}[\langle \mathcal{Z}_s, B \rangle] ds \\ &\leq \mathbb{E}[\langle \mathcal{Z}_0, 1 \rangle] + 2b_1 \int_0^t \mathbb{E}[\langle \mathcal{Z}_s, 1 \rangle] ds + 2b_2 \int_0^t \mathbb{E}[\langle \mathcal{Z}_s, p_l \rangle] ds \\ &\leq \mathbb{E}[\langle \mathcal{Z}_0, 1 \rangle] + 2b_2 t \mathbb{E}[\langle \mathcal{Z}_0, p_l \rangle] + (2b_1 + 2b_2 vt) \int_0^t \mathbb{E}[\langle \mathcal{Z}_s, 1 \rangle] ds, \end{aligned} \quad (2.11)$$

where on the last line we have used the fact $(\langle \mathcal{Z}_s, 1 \rangle)_{s \geq 0}$ is a non-decreasing process and therefore

$$\mathbb{E}[\langle \mathcal{Z}_t, p_l \rangle] \leq \mathbb{E}[\langle \mathcal{Z}_0, p_l \rangle] + vt \mathbb{E}[\langle \mathcal{Z}_t, 1 \rangle]. \quad (2.12)$$

Combining (2.11), Gronwall's lemma and (2.12), we obtain the following bounds.

Lemma 2.2. *There exists $C_1 > 0$ such that for all $t \geq 0$, we have*

$$\mathbb{E}[\langle \mathcal{Z}_t, 1 \rangle] \leq (\mathbb{E}[\langle \mathcal{Z}_0, 1 \rangle] + 2b_2 t \mathbb{E}[\langle \mathcal{Z}_0, p_l \rangle]) e^{C_1 t^2}$$

and

$$\mathbb{E}[\langle \mathcal{Z}_t, p_l \rangle] \leq \mathbb{E}[\langle \mathcal{Z}_0, p_l \rangle] + (\mathbb{E}[\langle \mathcal{Z}_0, 1 \rangle] + 2b_2 t \mathbb{E}[\langle \mathcal{Z}_0, p_l \rangle]) v t e^{C_1 t^2}.$$

Lemma 2.2 gives rather crude bounds on the expectations of the two quantities that control the total branching rate of $(\bar{\mathcal{Z}}_t)_{t \geq 0}$ (or equivalently, of $(\mathcal{Z}_t)_{t \geq 0}$). Its main point is that these expectations are finite at all times. It will be used in the proof of Proposition 1.1.

Proof. (Proof of Proposition 1.1) The proof is rather standard. Recall the notation F_f from (1.4). Conditioning on the value of $\bar{\mathcal{Z}}^0$ and using the construction of $(\bar{\mathcal{Z}}_t)_{t \geq 0}$ given in Theorem 2.1, we can write that for every $F \in C_b^1(\mathbb{R})$ and $f \in C_b^1(S)$ (abusing notation and seeing f as a function in $C_b^1(\mathcal{U} \times S)$ independent of the first coordinate), and every $0 \leq t \leq t'$,

$$\begin{aligned} &F(\langle \mathcal{Z}_{t'}, f \rangle) - F(\langle \mathcal{Z}_t, f \rangle) - \int_t^{t'} \int_S v \mathbf{e} F'(\langle \mathcal{Z}_s, f \rangle) \frac{\partial f}{\partial x}(\mathbf{e}, x) \mathcal{Z}_s(d\mathbf{e}, dx) ds \\ &= \int_t^{t'} \int_{\mathcal{U} \times \mathbb{R}_+ \times [0,1]} \mathbb{1}_{\{u \in V_{s-}, z \leq B(\mathbf{e}^u, x_{s-}^u)\}} \left[F(\langle \mathcal{Z}_{s-}, f \rangle + \sum_{i=1}^3 f(F_i(\mathbf{e}^u, x_{s-}^u, \theta)) - f(\mathbf{e}^u, x_{s-}^u)) \right. \\ &\quad \left. - F(\langle \mathcal{Z}_{s-}, f \rangle) \right] M(ds, du, dz, d\theta), \end{aligned}$$

so that

$$\begin{aligned}
& F(\langle \mathcal{Z}_{t'}, f \rangle) - F(\langle \mathcal{Z}_t, f \rangle) - \int_t^{t'} \mathcal{G}F_f(\mathcal{Z}_s) ds \tag{2.13} \\
&= \int_t^{t'} \int_{\mathcal{U} \times \mathbb{R}_+ \times [0,1]} \mathbb{1}_{\{u \in V_{s-}, z \leq B(\mathbf{e}^u, x_{s-}^u)\}} \left[F(\langle \mathcal{Z}_{s-}, f \rangle + \sum_{i=1}^3 f(F_i(\mathbf{e}^u, x_{s-}^u, \theta)) - f(\mathbf{e}^u, x_{s-}^u)) \right. \\
&\quad \left. - F(\langle \mathcal{Z}_{s-}, f \rangle) \right] M(ds, du, dz, d\theta) \\
&\quad - b_1 \int_t^{t'} \int_S \mathbf{e} \left\{ F(\langle \mathcal{Z}_{s-}, f \rangle - f(\mathbf{e}, x) + f(0, x) + 2f(1, 0)) - F(\langle \mathcal{Z}_{s-}, f \rangle) \right\} \mathcal{Z}_{s-}(d\mathbf{e}, dx) \\
&\quad - b_2 \int_t^{t'} \int_S x \int_0^1 \left\{ F(\langle \mathcal{Z}_{s-}, f \rangle - f(\mathbf{e}, x) + f(0, (1-\alpha)x) + f(\mathbf{e}, \alpha x) + f(1, 0)) \right. \\
&\quad \left. - F(\langle \mathcal{Z}_{s-}, f \rangle) \right\} d\alpha \mathcal{Z}_{s-}(d\mathbf{e}, dx).
\end{aligned}$$

Consequently, using Fubini's theorem we obtain that

$$\begin{aligned}
& \mathbb{E} \left[\left| F(\langle \mathcal{Z}_{t'}, f \rangle) - F(\langle \mathcal{Z}_t, f \rangle) - \int_t^{t'} \mathcal{G}F_f(\mathcal{Z}_s) ds \right| \right] \\
& \leq 2\|F\|_\infty \int_t^{t'} \mathbb{E}[\langle \mathcal{Z}_{s-}, B \rangle] ds + 2b_1\|F\|_\infty \int_t^{t'} \mathbb{E}[\langle \mathcal{Z}_{s-}, 1 \rangle] ds \\
& \quad + 2b_2\|F\|_\infty \int_t^{t'} \mathbb{E}[\langle \mathcal{Z}_{s-}, p_l \rangle] ds.
\end{aligned}$$

By Lemma 2.2, this quantity is finite and so the quantity on the l.h.s. of (2.13) is integrable for all $0 \leq t \leq t'$. The martingale property of

$$\left(F(\langle \mathcal{Z}_t, f \rangle) - F(\langle \mathcal{Z}_0, f \rangle) - \int_0^t \mathcal{G}F_f(\mathcal{Z}_s) ds \right)_{t \geq 0}$$

is then easy to show using the expression given on the r.h.s. of (2.13). Proposition 1.1 is proved. \square

3 Growth-fragmentation system

In this section we analyse the mean measure $(n_t)_{t \geq 0}$ related to our process $(Z_t)_{t \geq 0}$ and defined in (1.9). Namely, we prove Proposition 1.2 about the absolute continuity of the marginals $(n_t^0)_{t \geq 0}$ and $(n_t^1)_{t \geq 0}$ of $(n_t)_{t \geq 0}$ w.r.t. the type variable (provided that initially these quantities are absolutely continuous) and we derive the growth-fragmentation system (1.12).

Let $T > 0$ and $t \leq T$. In view of Proposition 1.1, one has for all $f \in C_b^1(S)$ that

$$\frac{\partial}{\partial t} \mathbb{E}[\langle Z_t, f \rangle] = \mathbb{E}[\mathcal{G}\langle Z_t, f \rangle]. \tag{3.1}$$

Using the decomposition in (1.10), one rewrites (3.1) in the following way:

$$\begin{aligned}
& \int_0^\infty f(1, x)n_t^1(dx) + \int_0^\infty f(0, x)n_t^0(dx) = \int_0^\infty (f(1, x)n_0^1(dx) + f(0, x)n_0^0(dx)) \\
& + v \int_0^t \int_0^\infty \frac{\partial}{\partial x} f(1, x)n_s^1(dx) ds \\
& + 2b_1 f(1, 0) \int_0^t \int_0^\infty n_s^1(dx) ds + b_1 \int_0^t \int_0^\infty (f(0, x) - f(1, x))n_s^1(dx) ds \tag{3.2} \\
& + b_2 f(1, 0) \int_0^t \int_0^\infty x(n_s^1(dx) + n_s^0(dx)) ds - b_2 \int_0^t \int_0^\infty x(f(1, x)n_s^1(dx) + f(0, x)n_s^0(dx)) ds \\
& + b_2 \int_0^t \int_0^\infty \int_0^x (f(1, y) + f(0, y)) dy n_s^1(dx) ds + 2b_2 \int_0^t \int_0^\infty \int_0^x f(0, y) dy n_s^0(dx) ds.
\end{aligned}$$

This is particularly useful for the following section.

3.1 Proof of Proposition 1.2

We first prove that the measures n_t^1 and n_t^0 admit density functions. To do so, we follow the strategy of [27].

Notice that one can rewrite Eq. (3.2) for test functions $f(t, \mathbf{e}, x) = f_t(\mathbf{e}, x)$ defined on $\mathbb{R}_+ \times S$ and of class $C_b^{1,0,1}(\mathbb{R}_+ \times S)$. One has

$$\begin{aligned}
& \int_0^\infty f_t(1, x)n_t^1(dx) + \int_0^\infty f_t(0, x)n_t^0(dx) = \int_0^\infty (f_0(1, x)n_0^1(dx) + f_0(0, x)n_0^0(dx)) \\
& + \int_0^t \int_0^\infty \left(\frac{\partial}{\partial s} f_s(1, x)n_s^1(dx) + \frac{\partial}{\partial s} f_s(0, x)n_s^0(dx) \right) ds + v \int_0^t \int_0^\infty \frac{\partial}{\partial x} f_s(1, x)n_s^1(dx) ds \\
& + 2b_1 \int_0^t f_s(1, 0) \int_0^\infty n_s^1(dx) ds + b_1 \int_0^t \int_0^\infty (f_s(0, x) - f_s(1, x))n_s^1(dx) ds \tag{3.3} \\
& + b_2 \int_0^t f_s(1, 0) \int_0^\infty x(n_s^1(dx) + n_s^0(dx)) ds - b_2 \int_0^t \int_0^\infty x(f_s(1, x)n_s^1(dx) + f_s(0, x)n_s^0(dx)) ds \\
& + b_2 \int_0^t \int_0^\infty \int_0^x (f_s(1, y) + f_s(0, y)) dy n_s^1(dx) ds + 2b_2 \int_0^t \int_0^\infty \int_0^x f_s(0, y) dy n_s^0(dx) ds.
\end{aligned}$$

We will first show that n_t^1 is absolutely continuous w.r.t. Lebesgue measure on \mathbb{R}_+ . Let $\phi \in C_K^1(\mathbb{R}_+)$ a non-negative function. Consider for $s \leq t$ the function $f_s(x) := \phi(v(t-s) + x)$. It is obvious that f_s satisfies the following equation

$$\begin{cases} \frac{\partial}{\partial s} f_s(x) + v \frac{\partial}{\partial x} f_s(x) = 0, & s < t, \\ f_t(x) = \phi(x). \end{cases} \tag{3.4}$$

Define a test function $\varphi_s(\mathbf{e}, x) = \mathbf{e} f_s(x)$. According to (3.3), when one neglects the negative terms and uses the relation in (3.4), we have

$$\begin{aligned}
& \int_0^\infty \phi(x)n_t^1(dx) \leq \int_0^\infty \phi(tv + x)n_0^1(dx) + 2b_1 \int_0^t \phi(v(t-s)) \int_0^\infty n_s^1(dx) ds \tag{3.5} \\
& + b_2 \int_0^t \phi(v(t-s)) \int_0^\infty x(n_s^1(dx) + n_s^0(dx)) ds + b_2 \int_0^t \int_0^\infty \int_0^x (\phi(v(t-s) + y)) dy n_s^1(dx) ds.
\end{aligned}$$

Rewrite the right hand side as

$$\begin{aligned} \int_0^\infty \phi(x)n_t^1(dx) &\leq \int_{tv}^\infty \phi(y)n_0^1(y-tv)dy + \frac{2b_1}{v} \int_0^{tv} \phi(y) \int_0^\infty n_{t-\frac{y}{v}}^1(dx) dy \\ &+ \frac{b_2}{v} \int_0^{tv} \phi(y) \int_0^\infty x(n_{t-\frac{y}{v}}^1(dx) + n_{t-\frac{y}{v}}^0(dx)) ds + \frac{b_2}{v} \int_0^{tv} \int_0^\infty \int_0^x \phi(\alpha+y) dy n_{t-\frac{y}{v}}^1(dx) d\alpha. \end{aligned} \quad (3.6)$$

Notice that by Fubini-Tonelli theorem, one has

$$\int_0^{tv} \int_0^\infty \int_0^x \phi(\alpha+y) dy n_{t-\frac{y}{v}}^1(dx) ds = \int_0^\infty \phi(\alpha+y) \int_0^{tv} \int_y^\infty n_{t-\frac{y}{v}}^1(dx) d\alpha dy.$$

Finally, plugging the previous expression into (3.6), we get

$$\int_0^\infty \phi(x)n_t^1(dx) \leq \int_0^\infty \phi(y)H(t,y)dy,$$

where

$$\begin{aligned} H(t,y) &:= \mathbb{1}\{tv \leq y\}n_0^1(y-tv) + \frac{2b_1}{v} \mathbb{1}\{y \leq tv\} \int_0^\infty n_{t-\frac{y}{v}}^1(dx) \\ &+ \frac{b_2}{v} \mathbb{1}\{y \leq tv\} \int_0^\infty x(n_{t-\frac{y}{v}}^1(dx) + n_{t-\frac{y}{v}}^0(dx)) + \frac{b_2}{v} \int_0^{tv} \int_{y-\alpha}^\infty n_{t-\frac{y}{v}}^1(dx) d\alpha. \end{aligned}$$

Obviously, H is a non-negative function. In addition, as $\int_0^\infty \phi(y)H(t,y)dy$ is exactly equal to the r.h.s. of (3.5) and this quantity is finite (due to the fact that $\mathbb{E}(I_T) + \mathbb{E}(S_T) < \infty$, see Lemma 2.2). Thus, we conclude that $H(t, \cdot)$ is integrable on \mathbb{R}_+ . That is to say, the measure n_t^1 is dominated by an absolutely continuous measure for regular test functions. A classical density argument allows us to conclude the absolute continuity of n_t^1 .

Now we turn to n_t^0 and let $\phi \in C_K^1(\mathbb{R}_+^*)$. Define the test function $f(\epsilon, x) = (1 - \epsilon)\phi(x)$. According to (3.2) when we neglect the negative terms, one has

$$\begin{aligned} \int_0^\infty \phi(x)n_t^0(dx) &\leq \int_0^\infty \phi(x)n_0^0(x)dx + \int_0^t \int_0^\infty \phi(x)n_s^1(dx) ds \\ &+ 2b_2 \int_0^t \int_0^\infty \int_0^x \phi(y) dy n_s^0(dx) ds. \end{aligned}$$

Use the fact that n_t^1 admits a density (still denoted by n_t^1) and Fubini-Tonelli theorem. It comes,

$$\begin{aligned} \int_0^\infty \phi(x)n_t^0(dx) &\leq \int_0^\infty \phi(x) \left(n_0^0(x) + \int_0^t n_s^1(x) ds + 2b_2 \int_0^t \int_x^\infty n_s^0(dy) ds \right) dx \\ &=: \int_0^\infty \phi(x)G(t,x) dx. \end{aligned}$$

As $G(t, \cdot)$ is positive and integrable we use the same arguments as above to conclude that n_t^0 is absolutely continuous.

Now, we are ready to prove that the families of densities $(n_t^1)_{t \in [0, T]}$ and $(n_t^0)_{t \in [0, T]}$ satisfy (1.12) in the weak sense. Let us take a test function $\phi \in C_K^1(\mathbb{R}_+^*)$, bounded with

compact support. Let $f(\boldsymbol{\epsilon}, x) = \boldsymbol{\epsilon}\phi(x)$. In particular, this means that $f(\boldsymbol{\epsilon}, 0) = 0$ and $f(0, x) = 0$.

In view of (3.2) and the definition of f , one has

$$\begin{aligned} \frac{\partial}{\partial t} \int_0^\infty \phi(x) n_t^1(x) dx &= \int \frac{\partial}{\partial x} \phi(x) n_t^1(x) dx - \int_0^\infty (b_1 + b_2 x) \phi(x) n_t^1(x) dx \\ &\quad + b_2 \int_0^\infty \int_0^x \phi(y) dy n_t^1(x) dx. \end{aligned}$$

The integration by parts and Fubini's Theorem lead to

$$\begin{aligned} \frac{\partial}{\partial t} \int_0^\infty \phi(x) n_t^1(x) dx &= - \int \phi(x) \frac{\partial}{\partial x} n_t^1(x) dx - \int_0^\infty (b_1 + b_2 x) \phi(x) n_t^1(x) dx \\ &\quad + b_2 \int_0^\infty \int_x^\infty n_t^1(y) dy \phi(x) dx. \quad (3.7) \end{aligned}$$

Now, take any test function $\phi \in C_b^1(\mathbb{R}_+)$, define $f(\boldsymbol{\epsilon}, x) = \boldsymbol{\epsilon}\phi(x)$ and read for it the equation (3.2). Notice that for any $t > 0$, n_t^1 is a finite measure and as such it satisfies $\lim_{x \rightarrow \infty} n_t^1(x) = 0$. As above, we apply the integration by parts and Fubini's theorem. It comes

$$\begin{aligned} \frac{\partial}{\partial t} \int_0^\infty \phi(x) g_t(x) dx &= -g_t(0)\phi(0) - \int \phi(x) \frac{\partial}{\partial x} g_t(x) dx \\ &\quad - \int_0^\infty (b_1 + b_2 x) \phi(x) g_t(x) dx + 2b_1 \phi(0) \int_0^\infty g_t(x) dx \\ &\quad + b_2 \phi(0) \int_0^\infty x(g_t(x) + h_t(x)) dx + b_2 \int_0^\infty \int_x^\infty g_t(y) dy \phi(x) dx. \end{aligned}$$

In view of (3.7), the above expression leads to the boundary condition

$$g_t(0) = 2b_1 \int_0^\infty g_t(x) dx + b_2 \int_0^\infty x(g_t(x) + h_t(x)) dx.$$

It remains to derive the equation for h_t . To do so, take $\phi \in C_b^1(\mathbb{R}_+^*)$ and define $f(\boldsymbol{\epsilon}, x) = (1 - \boldsymbol{\epsilon})\phi(x)$. The procedure is analogous to the above one without the integration by parts as there is no growth term in this case.

4 Long time behaviour

In this section we formulate the spectral problems related to the operator in (1.12) and its adjoint (Section 4.1). Then, we provide the explicit solutions for these problems, the stationary profiles N_1 and N_0 . Then, we prove in Section 4.2 that the mean measures n_t^1 and n_t^0 converge, as $t \rightarrow \infty$, towards these profiles.

4.1 Stationary profiles

For $t > 0$, plug $e^{\lambda t} N_1$ and $e^{\lambda t} N_0$ in (1.12) instead of n_t^1 and n_t^0 . One obtains the formulation of the following spectral problem related to the operator in (1.12), which captures the

stationary profile of the mean measure:

$$\begin{cases} (N_1)'(x) + (b_1 + b_2x + \lambda)N_1(x) = b_2 \int_x^\infty N_1(y) dy & x \in \mathbb{R}_+, & (4.1a) \\ N_1(0) = 2b_1 \int_0^\infty N_1(y)dy + b_2 \int_0^\infty y(N_1(y) + N_0(y))dy, & & (4.1b) \\ (b_2x + \lambda)N_0(x) = b_1N_1(x) + 2b_2 \int_x^\infty N_0(y)dy + b_2 \int_x^\infty N_1(y)dy, & x > 0. & (4.1c) \end{cases}$$

We observe that we can solve this system, by first computing N_1 and then N_0 . Indeed, if one looks at the equation satisfied by $\widehat{N}_1(x) = e^{\int_0^x (b_1+b_2y+\lambda)dy} N_1(x)$, one obtains that its solution is exactly the linear function $b_1 + b_2x + \lambda$.

Then the eigenvalue λ has to satisfy

$$b_1 + \frac{b_2}{\lambda} = \lambda. \quad (4.2)$$

and we refer to Appendix A.1 for details. By now, we consider the maximal eigenvalue, which is the unique positive solution of the previous equation. It is given by

$$\lambda = \frac{b_1 + \sqrt{b_1^2 + 4b_2}}{2}.$$

Let us introduce now the dual problem. We consider the the eigenvectors (ψ_1, ψ_0) related to the adjoint operator in (1.12) for the maximal eigenvalue λ . They will provide the influence of initial condition on the growth of the population size:

$$\begin{cases} -\psi_1'(x) + (b_1 + b_2x + \lambda)\psi_1(x) = b_1\psi_0(x) + b_2 \int_0^x \psi_0(y)dy + & (4.3a) \\ & b_2 \int_0^x \psi_1(y) dy + \psi_1(0)[2b_1 + b_2x], \\ (b_2x + \lambda)\psi_0(x) = 2b_2 \int_0^x \psi_0(y)dy + b_2x\psi_1(0), & x \in \mathbb{R}_+, & (4.3b) \end{cases}$$

Here again, we can solve the spectral problem and compute ψ_0 and ψ_1 . That leads the following statement.

Proposition 4.1. *The following quadruplet of non-negative functions $(N_0, N_1, \psi_0, \psi_1)$ is a solution of the spectral problem (4.1)- (4.3) :*

$$\begin{aligned} N_1(x) &= (b_1 + b_2x + \lambda)e^{-\int_0^x (b_1+b_2y+\lambda) dy}, \\ N_0(x) &= \frac{N_1(x)}{(b_2x + \lambda)^2}(b_2 + b_1(b_2x + \lambda)) + \frac{b_2e^{-\int_0^x (b_1+b_2y+\lambda) dy}}{(b_2x + \lambda)^3}(2b_2 + b_1(b_2x + \lambda)). \\ \psi_1(x) &= c_0(1 + \frac{b_2}{\lambda}x) \\ \psi_0(x) &= c_0 \frac{b_2x}{\lambda}, \end{aligned}$$

where $c_0 = \frac{\lambda^2}{\lambda^2+b_2}$. Besides, this solution satisfies

$$\int_0^\infty (N_1(x) + N_0(x)) dx = 2, \quad \int_0^\infty (\psi_1(y)N_1(y) + \psi_0(y)N_0(y)) dy = 1. \quad (4.4)$$

For the proof, one can use the expressions above and check that these elements are solution of the spectral problem. We refer to Appendix A.2 for details.

This quadruplet provides the unique solution of the spectral problem associated to the maximal eigenvalue λ under the normalizing conditions (4.4). Uniqueness in the weighted space related to our Lyapounov function V_γ will be obtained in the next section, see Theorem 4.3.

4.2 Convergence of the mean measure

In this section we prove Theorem 1.3 about the longtime convergence of the mean density of external and internal filaments. Actually, we will prove a more general statement involving the semigroup associated to the process $(Z_t)_{t \geq 0}$ that will automatically yield Theorem 1.3. Before we present this result, we need some notational preparation. The approach we will adopt is the semi-group approach of [4].

For $(\mathbf{e}, x) \in S$ and $\gamma \geq 2$ we define

$$\psi(\mathbf{e}, x) = c_0 \left(e + \frac{b_2}{\lambda} x \right), \quad V_\gamma(\mathbf{e}, x) = \psi(\mathbf{e}, x) + x^\gamma + 1. \quad (4.5)$$

Here $c_0 = \frac{\lambda^2}{\lambda^2 + b_2}$ so that $\psi(1, x)$ and $\psi(0, x)$ satisfy the adjoint spectral problem (4.3).

One denotes by $\mathcal{B}(V_\gamma)$ the set of all measurable functions $f : S \rightarrow \mathbb{R}$ such that the following quantity is finite:

$$\|f\|_{\mathcal{B}(V_\gamma)} = \sup_{z \in S} \frac{|f(z)|}{V_\gamma(z)}.$$

Now, $\mathcal{M}(V_\gamma)$ denotes the set of weighted signed measures on S that integrate V_γ . $\mathcal{M}(V_\gamma)$ is endowed with the weighted total variation norm

$$\|\mu\|_{\mathcal{M}(V_\gamma)} = \sup_{\|f\|_{\mathcal{B}(V_\gamma)} \leq 1} \left| \int_S f(z) \mu(dz) \right|$$

We recall that Z is a well defined measure-valued process for any initial condition restricted to one particle with type $z = (\mathbf{e}, x) \in S$. We can then define for any positive and measurable function f on S :

$$M_t f(z) = \mathbb{E}(\langle Z_t, f \rangle | Z_0 = \delta_z) \in [0, +\infty].$$

Let us set

$$\mathfrak{B} = \cup_{\gamma \geq 2} \mathcal{B}(V_\gamma)$$

We extend M to this set and prove that it is finite and satisfies the semigroup property.

Lemma 4.2. (i) For any $\gamma \geq 2$, There exists $C_\gamma > 0$ such that for any $t \geq 0$,

$$M_t V_\gamma \leq e^{C_\gamma t} V_\gamma.$$

(ii) For any $f \in \mathfrak{B}$ which is non-negative, $M_t f(z)$ is finite for any $z \in S$ and we can extend the definition of M to \mathfrak{B} as follows. For any $\gamma \geq 2$ and any $f \in \mathcal{B}(V_\gamma)$, we set

$$M_t f = \mathbb{E}(\langle Z_t, f \rangle) = M_t f_+ - M_t f_- \in \mathcal{B}(V_\gamma),$$

where f_+ (resp. f_-) is the positive (resp. negative part) of f .

(iii) M_t is a positive semigroup on \mathfrak{B} and satisfies

$$\begin{aligned} M_t f(\mathbf{e}, x) &= f(\mathbf{e}, x + \mathbf{e}t) e^{-\int_0^t (b_1 \mathbf{e} + b_2(x + \mathbf{e}s)) ds} \\ &\quad + \int_0^t e^{-\int_0^s (b_1 \mathbf{e} + b_2(x + \mathbf{e}s')) ds'} \int_S M_{t-s} f(\bar{\mathbf{e}}, \bar{x}) Q(\mathbf{e}, x + \mathbf{e}s, d\bar{\mathbf{e}}, d\bar{x}) ds, \end{aligned}$$

where for $(\mathbf{e}, x) \in S$, one has

$$Q(\mathbf{e}, x, d\bar{e}, d\bar{x}) = \mathbb{1}\{\bar{x} \leq x\} \left[b_1 \mathbf{e} [2\delta_1(d\bar{e}) \otimes \delta_0(d\bar{x}) + \delta_0(d\bar{e}) \otimes \delta_x(d\bar{x})] \right. \\ \left. + b_2 x [\delta_1(d\bar{e}) \otimes \delta_0(d\bar{x}) + \delta_0(d\bar{e}) \otimes \frac{d\bar{x}}{x} + \delta_{\mathbf{e}}(d\bar{e}) \otimes \frac{d\bar{x}}{x}] \right].$$

Proof. To prove i), we notice that for $(\mathbf{e}, x) \in S$,

$$\mathcal{L}V_\gamma(\mathbf{e}, x) = \lambda\psi(\mathbf{e}, x) + \mathbf{e}\gamma x^{\gamma-1} - b_2 \frac{\gamma-1}{\gamma+1} x^{\gamma+1} + 2b_1 \mathbf{e} + 2b_2 x \\ \leq \frac{\lambda}{c_0} \left(1 + \frac{\gamma x_0}{b_2} + 2\right) \psi(\mathbf{e}, x) + \frac{2b_1}{c_0} \psi(\mathbf{e}, x),$$

where $x_0 = \left(\frac{\gamma(\gamma+1)}{b_2(\gamma-1)}\right)^{\frac{\gamma-1}{2}}$. Therefore, using a standard monotone convergence in Kolmogorov equation (3.1) and Gronwall lemma, one has for any $z \in S$ and any $t \leq T$,

$$M_t V_\gamma(z) \leq e^{\frac{\lambda}{c_0}(1+\frac{\gamma x_0}{b_2}+2)t + \frac{2b_1}{c_0}t} V_\gamma(z). \quad (4.6)$$

ii) is a direct consequence of i) noticing that the definition of M on the embedded sets $\mathcal{B}(V_\gamma)$ is compatible since it coincide with $\mathbb{E}(\langle Z_t, f \rangle | Z_0 = \delta_z)$. The semigroup property is classical : it is a consequence of the branching Markov property of Z . Finally, the proof of Duhamel formula in iii) comes as usual by conditioning by the first jump of Z and using the strong Markov property. \square

We are ready to state the convergence result in its generality. For every bounded measurable $f : S \rightarrow \mathbb{R}$, we define the measure N on S in the spirit of the decomposition (1.10):

$$\langle N, f \rangle = \int_{\mathbb{R}_+} f(1, x) N_1(dx) + \int_{\mathbb{R}_+^*} f(0, x) N_0(dx). \quad (4.7)$$

The fact that we know (explicitly here) an eigenfunction ψ allows to invoke a Doob h transform. This method is powerful for the study of non-conservative semigroups [24] and in particular for the study of the first moment of branching processes. We can then derive ergodic estimates of our semigroup M from Harris ergodic theorem applied to the associated conservative semigroup, as recently achieved in [13] for growth fragmentation PDE's. We obtain here directly these results by applying [4, Thm 1.1]. It is equivalent and convenient in our framework. It also allows the extension of the results to models where the positive eigenfunction is not known a priori.

Theorem 4.3. *Let $\gamma \geq 2$. There exists $C, w > 0$ such that for $t \geq 0$ and $\mu \in \mathcal{M}(V_\gamma)$,*

$$\|e^{-\lambda t} \mu M_t - \langle \mu, \psi \rangle N\|_{\mathcal{M}(V_\gamma)} \leq C e^{-wt} \|\mu\|_{\mathcal{M}(V_\gamma)}.$$

Let us also mention that combining the proof below and [4] allow to obtain a lowerbound of the spectral gap and speed of convergence w in terms of the parameters of the model of growth fragmentation.

Proof. We write \lesssim to mean that an inequality holds up to some constants, which does not depend on the variables of the semigroup, i.e. neither on time $t \geq 0$ nor on $x \in S$. We define

$$K = \{z \in S : V(z) \leq R\psi(z)\}$$

and first observe that $\psi \leq V$ on S and $V \lesssim \psi$ on K . Second, using (4.6) and that ψ is an eigenfunction,

$$MV_\gamma \lesssim V_\gamma \quad \text{and} \quad M\psi \gtrsim \psi \quad \text{on} \quad [0, T] \times S.$$

To apply [4, Thm 1.1] and obtain the expected estimate, we need to check the following assumption.

Assumption A. *There exist $\tau, T > 0$, $\beta > \alpha > 0$, $\theta \geq 0$, $(c, d) \in (0, 1]^2$, $K \subset S$ and ν a probability measure on S supported by K such that*

$$(A1) \quad M_\tau V_\gamma \leq \alpha V_\gamma + \theta \mathbb{1}_K \psi,$$

$$(A2) \quad M_\tau \psi \geq \beta \psi,$$

$$(A3) \quad \text{For all } z \in K \text{ and } f \in \mathcal{B}_+(V_\gamma/\psi),$$

$$M_\tau(f\psi)(z) \geq c \nu(f) M_\tau \psi(z),$$

$$(A4) \quad \text{For any integer } n,$$

$$d \sup_{z \in K} \frac{M_{n\tau} \psi(z)}{\psi(z)} \leq \nu \left(\frac{M_{n\tau} \psi}{\psi} \right).$$

Let us recall that in view of (3.1), one has

$$\frac{\partial}{\partial t} M_t f = M_t \mathcal{L} f, \tag{4.8}$$

where

$$\mathcal{L} f(\mathbf{e}, x) = \mathbf{e} \frac{\partial}{\partial x} f(\mathbf{e}, x) - (b_1 \mathbf{e} + b_2 x) f(\mathbf{e}, x) + \int_S f(\bar{\mathbf{e}}, \bar{x}) Q(\mathbf{e}, x, d\bar{\mathbf{e}}, d\bar{x}).$$

We first observe that for any $\tau > 0$, (A2) and (A4) are obviously satisfied with $\beta = e^{\lambda\tau}$ and $d = 1$. Indeed, ψ is an eigenfunction of the adjoint operator and $\mathcal{L}\psi = \lambda\psi$ one has that for any $t > 0$ $M_t \psi = e^{\lambda t} \psi$. The proof is now separated into two steps. In **Step 1** we check (A1), while **Step 2** is devoted to checking (A3) holds true.

Step 1. Notice that

$$\begin{aligned} M_t V_\gamma(\mathbf{e}, x) &= 1 + x^\gamma + \left(\frac{\lambda}{c_0} \left(\frac{\gamma}{b_2} + 2 \right) + \frac{2b_1}{c_0} \right) \int_0^t M_s \psi \, ds + e^{\lambda t} \psi \\ &\leq V_\gamma(\mathbf{e}, x) + \left(\frac{\lambda}{c_0} \left(\frac{\gamma}{b_2} + 2 \right) + \frac{2b_1}{c_0} \right) (e^{\lambda t} - 1) \psi + e^{\lambda t} \psi \end{aligned}$$

Now, using that on K^c one has $\psi \leq \frac{1}{R} V_\gamma$, one has

$$\begin{aligned} M_t V_\gamma(\mathbf{e}, x) &\leq V_\gamma + \left(\left(\frac{\lambda}{c_0} \left(\frac{2}{b_2} + 2 \right) + \frac{2b_1}{c_0} \right) (e^{\lambda t} - 1) + e^{\lambda t} \right) \frac{1}{R} V_\gamma \\ &\quad + \left(\left(\frac{\lambda}{c_0} \left(\frac{2}{b_2} + 2 \right) + \frac{2b_1}{c_0} \right) (e^{\lambda t} - 1) + e^{\lambda t} \right) \psi \mathbb{1}_K \end{aligned}$$

Now, if t was fixed, we would define $\alpha := 1 + \left(\left(\frac{\lambda}{c_0} \left(\frac{\gamma}{b_2} + 2 \right) + \frac{2b_1}{c_0} \right) (e^{\lambda t} - 1) + e^{\lambda t} \right) \frac{1}{R}$ and $\theta := \left(\frac{\lambda}{c_0} \left(\frac{\gamma}{b_2} + 2 \right) + \frac{2b_1}{c_0} + e^{\lambda t} \right)$. To obtain that $\alpha < \beta$, we just need to take R large enough. Indeed, it should hold

$$\left(\left(\frac{\lambda}{c_0} \left(\frac{\gamma}{b_2} + 2 \right) + \frac{2b_1}{c_0} \right) (e^{\lambda t} - 1) + e^{\lambda t} \right) \frac{1}{R} < e^{\lambda t} - 1,$$

which is obviously true for R large enough. Of course, implicitly R depends on the $t > 0$ that we will fix when checking Assumption (A3).

Finally, with our choice of R we should justify why K is non empty and bounded. As we can choose $R > 1 + \frac{1}{c_0} \left(1 + \frac{\lambda}{b_2} \right)$, the set K is non-empty (it contains all $(1, x)$ such that $0 \leq x \leq 1$). However, as for any $e \in \{0, 1\}$ we have $\lim_{x \rightarrow \infty} \frac{\psi(e, x)}{x^\gamma} = 0$, the values of x for which (e, x) belongs to K must be bounded. As a consequence, there exist k_0, K_0 and K_1 such that

$$K = (\{0\} \times (k_0, K_0]) \cup (\{1\} \times [0, K_1]).$$

Filaments $(0, x)$ where x is arbitrary small do not belong to K as $V_\gamma(0, x) \geq 1$ while $\psi(0, x)$ may be arbitrary small.

Step 2. With our choice of ψ , we can reformulate Assumption (A3) in the following way: There exist $\tau > 0$, $c \in (0, 1]$, and ν a probability measure on S supported by K such that for all $z \in K$ and $f \in \mathcal{B}_+(V_\gamma/\psi)$, one has

$$\frac{M_\tau(f\psi)(z)}{e^{\lambda\tau}\psi(z)} \geq c\nu(f).$$

Notice that until now, there was no constraint on τ . This is where a constraint on it will appear.

Now, for $z \in S$, $t > 0$ and $f \in \mathcal{B}_+(V_\gamma/\psi)$, define the semigroup $P_t f(z) = \frac{M_t(\psi f)(z)}{e^{\lambda t}\psi(z)}$. Notice that P is a conservative semigroup. The above condition reads: There exist $\tau > 0$, $c \in (0, 1]$, and ν a probability measure on S supported by K such that for all $z \in K$ and $f \in \mathcal{B}_+(V_\gamma/\psi)$, one has

$$P_\tau(f) \geq c \int_K f(z)\nu(dz). \quad (4.9)$$

In order to prove the above statement, we will first analyse the generator \mathcal{A} related to P . For a test function f , we compute

$$\mathcal{A}f(\mathbf{e}, x) = \frac{\partial}{\partial t} P_t(f) \Big|_{t=0}.$$

Using the fact that $M_t\psi = e^{\lambda t}\psi$, one gets

$$\mathcal{A}f(\mathbf{e}, x) = \mathbf{e} \frac{\partial}{\partial x} f(\mathbf{e}, x) + \int_S (f(\mathbf{e}', x') - f(\mathbf{e}, x)) \frac{\psi(\mathbf{e}', x')}{\psi(\mathbf{e}, x)} Q(\mathbf{e}, x; d\mathbf{e}', dx').$$

Define

$$B(\mathbf{e}, x) = \int_S \frac{\psi(\mathbf{e}', x')}{\psi(\mathbf{e}, x)} Q(\mathbf{e}, x; d\mathbf{e}', dx').$$

Then, as before, the semi-group $(P_t)_{t \geq 0}$ admits the following representation:

$$(P_t f)(\mathbf{e}, x) = f(\mathbf{e}, x + et) e^{-\int_0^t B(\mathbf{e}, x + es) ds} \quad (4.10)$$

$$+ \int_0^t e^{-\int_0^s B(\mathbf{e}, x + es') ds'} \int_S (P_{t-s} f)(\mathbf{e}', x') \bar{Q}(\mathbf{e}, x + \mathbf{e}s, d\mathbf{e}', dx') ds, \quad (4.11)$$

where for $(\mathbf{e}, x) \in S$, one has

$$\bar{Q}(\mathbf{e}, x + \mathbf{e}s, d\mathbf{e}', dx') = \frac{\psi(\mathbf{e}', x')}{\psi(\mathbf{e}, x)} Q(\mathbf{e}, x; d\mathbf{e}', dx').$$

Here, $\psi(\mathbf{e}', x')$ should be understood as a weight function.

Before we start building the measure ν , we will first compute the death rate B . For $(\mathbf{e}, x) \in S$, one has

$$B(\mathbf{e}, x) = \frac{1}{\psi(\mathbf{e}, x)} \left((\lambda + b_1 \mathbf{e} + b_2 x) \psi(\mathbf{e}, x) - \mathbf{e} c_0 \frac{b_2}{\lambda} \right) = (\lambda + b_1 \mathbf{e} + b_2 x) - \mathbf{e} \frac{\frac{b_2}{\lambda}}{\mathbf{e} + \frac{b_2}{\lambda} x}.$$

We remark that $B(\mathbf{e}, x) > 0$. Indeed, $B(0, x) = \lambda + b_2 x > 0$ and using the relationship $\lambda = b_1 + \frac{b_2}{\lambda}$ one has

$$B(1, x) = \lambda + b_1 + b_2 x - \frac{b_2}{\lambda} + \left(\frac{b_2}{\lambda} \right)^2 \frac{1}{1 + \frac{b_2}{\lambda} x} = 2b_1 + b_2 x + \left(\frac{b_2}{\lambda} \right)^2 \frac{1}{1 + \frac{b_2}{\lambda} x} > 0.$$

In addition, one has that

$$\sup_{\mathbf{e} \in \{0,1\}, x \leq A} B(\mathbf{e}, x) \leq \lambda + b_1 + b_2 A + \left(\frac{b_2}{\lambda} \right)^2 \quad (4.12)$$

The latter will be very useful when proving (4.9) as for $x \leq K_0 \vee K_1$ we will have

$$e^{-\int_0^t B(\mathbf{e}, x + \mathbf{e}s') ds'} \geq e^{-\lambda t} e^{-t \left(b_1 + b_2(t + K_0 \vee K_1) + \left(\frac{b_2}{\lambda} \right)^2 \right)}.$$

Let us now start from an individual $(1, x) \in K$ and fix $t > 2(K_0 \vee K_1)$. From (4.11) keeping only the two open filaments of size zero coming from the apical branching, we have

$$P_t(1, x) \geq \int_0^t e^{-\int_0^s B(1, x + s') ds'} 2(P_{t-s} f)(1, 0) \frac{1}{1 + \frac{b_2}{\lambda}(x + s)} ds.$$

Now, for one of the terms of the form $(P_{t-s} f)(1, 0)$, we only keep the growth term (4.10). For the other one, we only keep the apical branching and a filament of type 0 coming from it. Hence, we get

$$\begin{aligned} P_t(1, x) &\geq b_1 \int_0^t e^{-\int_0^s B(1, x + s') ds'} e^{-\int_0^{t-s} B(1, s') ds'} f(1, s) \frac{1}{1 + \frac{b_2}{\lambda}(x + s)} ds \\ &+ b_1^2 \int_0^t e^{-\int_0^s B(1, x + s') ds'} \frac{1}{1 + \frac{b_2}{\lambda}(x + s)} \int_0^{t-s} e^{-\int_0^u B(1, u') du'} P_{t-s-u} f(0, u) \frac{\psi(0, u)}{\psi(1, u)} du ds \\ &=: I + II. \quad (4.13) \end{aligned}$$

Now, for the first term use that $x \leq K_1$ and $t \geq K_1$. It comes

$$I \geq \frac{b_1 e^{-t \max_{e \in \{0,1\}; y \leq K_1+t} B(e,x)}}{1 + \frac{b_2}{\lambda}(K_1+t)} \int_0^{K_1} f(1,s) ds$$

For the second term, do again one more minoration keeping only the growth term (4.10) and apply Fubini's theorem. It comes after using that $x \geq K_1$ and $t \geq 2K_0$,

$$\begin{aligned} II &\geq \frac{b_1^2}{1 + \frac{b_2}{\lambda}(K_1+t)} \int_0^t e^{-\int_0^s B(1,x+s')} ds' \int_0^{t-s} e^{-\int_0^u B(1,u') du'} e^{-(t-s-u)B(0,u)} f(0,u) \frac{\frac{b_2}{\lambda} u}{1 + \frac{b_2}{\lambda} u} du ds \\ &\geq C_1(t) \int_0^t \int_0^{t-s} u f(0,u) du ds \geq C_1(t) \int_0^t u f(0,u) (t-u) du \\ &\geq C_1(t) \int_0^{K_0} u f(0,u) (2K_0 - K_0) du. \end{aligned}$$

Here $C_1(t) := \frac{b_1^2 \frac{b_2}{\lambda} e^{-\lambda t} e^{-\left(b_1 + b_2(K_1+t) + \left(\frac{b_2}{\lambda}\right)^2\right)t}}{\left(1 + \frac{b_2}{\lambda}(K_1+t)\right)\left(1 + \frac{b_2}{\lambda}t\right)}$. Plug the bounds for I and II into (4.13) to obtain

$$P_t(1,x) \geq C_2(t) \int_0^{K_1} f(1,s) ds + K_0 C_1(t) \int_0^{K_0} u f(0,u) du \quad (4.14)$$

where $C_2(t) := \frac{b_1 e^{-\lambda t} e^{-\left(b_1 + b_2(K_1+t) + \left(\frac{b_2}{\lambda}\right)^2\right)t}}{1 + \frac{b_2}{\lambda}(K_1+t)}$. Hence

$$P_t(1,x) \geq C_2(t) \int_0^{K_1} f(1,s) ds + K_0 C_1(t) k_0 \int_{k_0}^{K_0} f(0,u) du. \quad (4.15)$$

Now, we will start from $(0,x) \in K$. Lateral branching in (4.11) leads us to

$$P_t f(0,x) \geq \int_0^t e^{-B(0,x)s} P_{t-s} f(1,0) \frac{\psi(1,0)}{\psi(0,x)} b_2 x ds = \lambda \int_0^t e^{-B(0,x)s} P_{t-s} f(1,0) ds.$$

Now, using (4.14) for $t = t - s$ and $x = 0$ we get

$$\begin{aligned} P_t f(0,x) &\geq \lambda \int_0^t e^{-B(0,x)s} \left(C_2(t-s) \int_0^{K_1} f(1,u) du \right. \\ &\quad \left. + K_0 C_1(t-s) \int_0^{K_0} u f(0,u) du \right) ds \end{aligned}$$

In view of (4.12), we obtain

$$\begin{aligned} P_t f(0,x) &\geq \lambda \frac{b_1 e^{-\lambda t} e^{-\left(b_1 + b_2(K_0 \vee K_1 + t) + \left(\frac{b_2}{\lambda}\right)^2\right)t}}{1 + \frac{b_2}{\lambda}(K_1+t)} \int_0^t \int_0^{K_1} f(1,u) du ds \\ &\quad + \frac{K_0 b_1^2 \frac{b_2}{\lambda} e^{-\lambda t} e^{-\left(b_1 + b_2(K_0 \vee K_1 + t) + \left(\frac{b_2}{\lambda}\right)^2\right)t}}{\left(1 + \frac{b_2}{\lambda}(K_1+t)\right)\left(1 + \frac{b_2}{\lambda}t\right)} \lambda \int_0^t \int_0^{K_0} u f(0,u) du ds \end{aligned}$$

Hence, we obtain

$$P_t f(0,x) \geq C_3(t) \int_0^{K_1} f(1,u) du + C_4(t) \int_{k_0}^{K_0} f(0,u) du, \quad (4.16)$$

where $C_3(t) := \lambda t \frac{b_1 e^{-\lambda t} e^{-\left(b_1 + b_2(K_0 \vee K_1 + t) + \left(\frac{b_2}{\lambda}\right)^2\right)t}}{1 + \frac{b_2}{\lambda}(K_1 + t)}$ and $C_4(t) := \frac{k_0 K_0 b_1^2 \frac{b_2}{\lambda} e^{-\lambda t} e^{-\left(b_1 + b_2(K_0 \vee K_1 + t) + \left(\frac{b_2}{\lambda}\right)^2\right)t}}{\left(1 + \frac{b_2}{\lambda}(K_1 + t)\right)\left(1 + \frac{b_2}{\lambda}t\right)} \lambda t$.

Now, we need to normalize the measures appearing in (4.15) and (4.16) and choose τ large enough so that the constants appearing become smaller than 1 (see (4.9)). After the renormalization, we should choose τ such that $\tau \geq 2(K_0 \vee K_1)$ and

$$C_4(\tau)(K_0 - k_0) \leq 1, \quad C_3(\tau)K_1 \leq 1, \quad C_2(\tau)K_1 \leq 1, \quad C_1(\tau)k_0K_0(K_0 - k_0) \leq 1.$$

This is obviously possible as the exponential decay dominates in all the conditions. Hence, for τ large enough, there exists $c \in (0, 1]$ such that for all $(\mathbf{e}, x) \in K$

$$P_\tau f(\mathbf{e}, x) \geq c \left(\int_{k_0}^{K_0} f(0, u) \frac{du}{K_0 - k_0} + \int_0^{K_1} f(0, u) \frac{du}{K_1} \right).$$

Hence, Assumption (A3) is satisfied for the probability measure ν defined as

$$\nu(d\mathbf{e}, dx) = \delta_0(d\mathbf{e}) \times \left(\mathbb{1}_{k_0 \leq x \leq K_0} \frac{dx}{K_0 - k_0} \right) + \delta_1(d\mathbf{e}) \times \left(\mathbb{1}_{x \leq K_1} \frac{dx}{K_1} \right).$$

Conclusion As Assumption **A** is verified, we are now in the position to apply [4, Thm 1.1] to conclude the proof. □

Appendix

A.1 Characterisation of eigen values

In this section we consider the spectral problem (4.1) with eigenfunctions N_1 and N_0 satisfying the following conditions:

$$\int (1+x)|N_0(x)|dx < \infty, \quad \int (1+x)|N_1(x)|dx < \infty, \quad \lim_{x \rightarrow \infty} N_1(x) = 0 \quad \text{and} \quad \lim_{x \rightarrow \infty} xN_1(x) = 0.$$

We prove that the associated eigenvalues satisfy (4.2).

First, notice that for N_1 and N_0 one has

$$\int_0^\infty N_1(x)dx = \int_0^\infty N_0(x)dx. \tag{A.1}$$

Namely, integrate (4.1a) and (4.1c) over \mathbb{R}_+ and then subtract the two expressions. Since $\lim_{x \rightarrow \infty} N_1(x) = 0$, one has

$$(b_1 + \lambda) \int_0^\infty N_1(x)dx - \lambda \int_0^\infty N_0(x)dx = N_1(0) - b_1 \int_0^\infty N_1(x)dx - b_2 \int_0^\infty x(N_1(x) + N_0(x))dx.$$

In view of the value prescribed for $N_1(0)$ in (4.1b), one concludes that (A.1) holds true.

Now, integrate (4.1a) and (4.1c) over \mathbb{R}_+ and then sum up the two expressions. It comes

$$\lim_{x \rightarrow \infty} N_1(x) - N_1(0) + \lambda \int_0^\infty (N_1(x) + N_0(x)) dx = b_2 \int_0^\infty x(N_1(x) + N_0(x)) dx.$$

In view of (4.1b), one has

$$\lambda \int_0^\infty (N_1(x) + N_0(x)) dx = 2b_1 \int_0^\infty N_1(x) dx + 2b_2 \int_0^\infty x(N_1(x) + N_0(x)) dx. \quad (\text{A.2})$$

Now, multiply both (4.1a) and (4.1c) by x , integrate over \mathbb{R}_+ and then sum up the two expressions. Then, integrate by parts and use Fubini's theorem. It comes,

$$[xN_1(x)]_0^\infty - \int_0^\infty N_1(x) dx + \lambda \int_0^\infty x(N_1(x) + N_0(x)) dx = 0.$$

Using that $\lim_{x \rightarrow \infty} xN_1(x) = 0$, one has

$$\lambda \int_0^\infty x(N_1(x) + N_0(x)) dx = \int_0^\infty N_1(x) dx. \quad (\text{A.3})$$

Plug (A.3) into (A.2) and use (A.1) It comes that λ satisfies the desired equation

$$\lambda = b_1 + \frac{b_2}{\lambda}.$$

A.2 Proof of Proposition 4.1

We first deal with N . Let $N_1(x) = (b_1 + b_2x + \lambda)e^{-\int_0^x (b_1 + b_2y + \lambda) dy}$. Notice that

$$N_1'(x) = (b_2 - (b_1 + b_2x + \lambda)^2)e^{-\int_0^x (b_1 + b_2y + \lambda) dy}$$

and

$$\int_x^\infty N_1(y) dy = e^{-\int_0^x (b_1 + b_2y + \lambda) dy}.$$

Hence, N_1 obviously satisfies (4.1a). Moreover, N_1 is a probability density function on \mathbb{R}_+ as it is non-negative and $\int_0^\infty N_1(x) dx = 1$. Hence, from (4.4), we have that

$$\int_0^\infty N_0(x) dx = 1.$$

From the expression for N_1 , one has $N_1(0) = b_1 + \lambda$. We are going to see that this value matches the one prescribed in (4.1b) thanks to (4.2). Namely, combining (4.1b) with the relationship in (A.3), one has that

$$N_1(0) = \left(2b_1 + \frac{b_2}{\lambda}\right) \int_0^\infty N_1(x) dx.$$

In view of (4.2), one indeed has $N_1(0) = b_1 + \lambda$.

Now, we turn to our expression for N_0 . The equation for N_0 can be solved by variation of constants. Notice that from the constraint in (4.4) and from (4.1c), one gets that $\lim_{x \rightarrow 0} N_0(x) = \frac{b_1 N_1(0) + 3b_2}{\lambda}$. Thus, we should solve

$$\begin{cases} (b_2x + \lambda)N_0'(x) = b_1N_1'(x) - 3b_2N_0(x) - b_2N_1(x), & t > 0, \quad x > 0, \\ N_0(0) = \frac{b_1 N_1(0) + 3b_2}{\lambda}. \end{cases} \quad (\text{A.4})$$

The solution is of the form $N_0(x) = C(x) \frac{\lambda^3}{(b_2x + \lambda)^3}$, where

$$C(x) = N_0(0) + \frac{1}{\lambda^3} \int_0^x (b_2y + \lambda)^2 (b_1N_1'(y) - b_2N_1(y)) dy.$$

Integrating by parts the first integral in the expression for $C(x)$, one has

$$N_0(x) = \frac{N_0(0)\lambda^3}{(b_2x + \lambda)^3} + \frac{b_1N_1(x)}{b_2x + \lambda} - \frac{\lambda^2b_1N_1(0)}{(b_2x + \lambda)^3} - \frac{2b_1b_2}{(b_2x + \lambda)^3} \int_0^x N_1(y)(b_2y + \lambda) dy - \frac{b_2}{(b_2x + \lambda)^3} \int_0^x (b_2y + \lambda)^2 N_1(y) dy.$$

Using the value $N_0(0)$, one cancels out the term involving $N_1(0)$ in the above expression to obtain

$$N_0(x) = \frac{3\lambda^2b_2}{(b_2x + \lambda)^3} + \frac{b_1N_1(x)}{b_2x + \lambda} - \frac{2b_1b_2}{(b_2x + \lambda)^3} \int_0^x (b_2y + \lambda)N_1(y) dy - \frac{b_2}{(b_2x + \lambda)^3} \int_0^x (b_2y + \lambda)^2 N_1(y) dy. \quad (\text{A.5})$$

It remains to simplify the above expression by integrating by parts the last two integrals. Denote the last two terms in (A.5) by T_1 and T_2 , respectively.

Using that $N_1(y) = \frac{\partial}{\partial y} \left[-e^{-\int_0^y (b_1+b_2z+\lambda)dz} \right]$, one gets after integrating by parts that

$$T_1 = \frac{2b_1b_2}{(b_2x + \lambda)^2} e^{-\int_0^x (b_1+b_2z+\lambda)dz} - \frac{2b_1b_2\lambda}{(b_2x + \lambda)^3} - \frac{2b_1b_2^2}{(b_2x + \lambda)^3} \int_0^x e^{-\int_0^y (b_1+b_2z+\lambda)dz} dy,$$

and

$$T_2 = \frac{b_2}{b_2x + \lambda} e^{-\int_0^x (b_1+b_2z+\lambda)dz} - \frac{b_2\lambda^2}{(b_2x + \lambda)^3} - \frac{2b_2^2}{(b_2x + \lambda)^3} \int_0^x (b_2y + \lambda) e^{-\int_0^y (b_1+b_2z+\lambda)dz} dy.$$

Now, plug T_1 and T_2 in (A.5), use that $b_1\lambda = \lambda^2 - b_2$ and use the expression for N_1 . It comes

$$\begin{aligned} N_0(x) &= \frac{b_1N_1(x)}{b_2x + \lambda} + \frac{b_2(2b_1 + b_2x + \lambda)}{(b_2x + \lambda)^2} e^{-\int_0^x (b_1+b_2z+\lambda)dz} \\ &\quad + \frac{3\lambda^2b_2 - 2b_1b_2\lambda - b_2\lambda^2 - 2b_2^2 \int_0^x (b_1 + b_2y + \lambda) e^{-\int_0^y (b_1+b_2z+\lambda)dz} dy}{(b_2x + \lambda)^3} \\ &= \frac{b_1N_1(x)}{b_2x + \lambda} + \frac{b_2N_1(x)}{(b_2x + \lambda)^2} + \frac{b_2b_1}{(b_2x + \lambda)^2} e^{-\int_0^x (b_1+b_2z+\lambda)dz} \\ &\quad + \frac{2b_2^2 - 2b_2^2 \left(1 - \int_x^\infty (b_1 + b_2y + \lambda) e^{-\int_0^y (b_1+b_2z+\lambda)dz} dy \right)}{(b_2x + \lambda)^3} \end{aligned}$$

Finally, we obtain

$$N_0(x) = \frac{N_1(x)}{(b_2x + \lambda)^2} (b_2 + b_1(b_2x + \lambda)) + \frac{b_2 \int_x^\infty N_1(y) dy}{(b_2x + \lambda)^3} (2b_2 + b_1(b_2x + \lambda))$$

We now proceed with ψ . Plugging $\psi_1(x) = c_0(1 + \frac{b_2}{\lambda}x)$ and $\psi_0(x) = c_0\frac{b_2x}{\lambda}$ in (4.3a) and (4.3b), one easily gets that these functions satisfy the system.

In order to compute c_0 one should use the relation in (4.4) that reads

$$c_0 \left(1 + \frac{b_2}{\lambda} \int x(N_1(x) + N_0(y))dx \right) = 1.$$

From (A.3), we get that $c_0 = \frac{\lambda^2}{\lambda^2 + b_2}$.

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