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Spine for interacting populations and sampling

VINCENT BANSAYE[a]

CMAP, Ecole polytechnique, Palaiseau, France, [a]*vincent.bansaye@polytechnique.edu*

We consider some Markov jump processes which model structured populations with interactions via density dependence. We propose a Markov construction involving a distinguished individual (spine) which allows us to describe the random tree and random sample at a given time via a change of probability. This spine construction involves the extension of the type space of individuals to include the state of the population. The jump rates off the spine individual can also be modified. We exploit this approach to study issues concerning population dynamics. For single type populations, we derive the phase diagram of a growth fragmentation model with competition as well as the growth of the size of transient birth and death processes which permit multiple births. We also describe the ancestral lineages of a uniform sample in multitype populations.

Keywords: Interactions; jump Markov process; martingales; populations; positive semigroup; random tree; spine

1. Introduction

The aim of this paper is the study of the long time behavior and ancestral lineages of Markov jump processes describing density dependent populations. These models are used in population dynamics or genetics or epidemiology, see e.g. [6,18,30]. They allow to describe competition, mutualism, contamination, sexual reproduction or predation. The individual rate of birth, death or change of state then depends on the state of population, that is sizes and relevant characteristics. Density dependent models appear also in various other contexts, including chemistry, queueing systems or networks, see e.g. [2].

Each individual is characterized by a type x in a finite or denumerable type space $\mathcal{X}$. The type may represent e.g. a position, age, size, phenotype, genotype, species, sex. The population is then described by a vector $\mathbf{z} = (\mathbf{z}_x : x \in \mathcal{X})$, where $\mathbf{z}_x$ is the number of individuals with type x. Among a population $\mathbf{z}$, each individual with type x is replaced at rate $\tau_{\mathbf{k}}(x,\mathbf{z})$ by a finite set of individuals whose types are given by $\mathbf{k}$. The process $\mathbf{Z}$ counting the number of individuals of each type is thus a Markov jump process taking values in the space $\mathcal{Z}$ of compositions. This process jumps from $\mathbf{z}$ to $\mathbf{z} + \mathbf{k} - \mathbf{e}_x$ at rate $\mathbf{z}_x \tau_{\mathbf{k}}(x,\mathbf{z})$, where $\mathbf{e}_x$ is the vector representing one single individual with type x. For references on such processes, let us mention [19,30].

We study these density dependent processes by constructing another Markov process. It allows us to follow a typical individual, the spine, in a Markovian way. This spine construction involves a function ψ defined on the product space $\mathcal{X} \times \mathcal{Z}$ of space type and state space of the population. The construction is achieved for any positive function and the choice of ψ will depend on the question asked on the original process. In particular, harmonic functions will appear to simplify the construction and capture the behavior of a sample at fixed time.

Spine techniques have a long and fruitful story in branching processes. The main objective of this work is to provide an analogous construction when the branching property breaks down. At the same time, it complements the existing theory for branching processes in denumerable type space. Indeed, we allow a general function ψ and we can modify also the rates outside the spine. It gives the description of a uniform sample at fixed time in the original process, without considering a size biased tree.

Spine techniques and size biased trees have played a deep role in the analysis of branching Brownian motion and branching random walk from the works of Chauvin and Rouault [12] and Lyons [35]. Lyons, Peres and Pemantle [36] have given a conceptual approach of the famous $L \log L$ criterion involved

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in the asymptotic analysis of branching processes. Their spine construction provides an illuminating proof of the non-degeneracy of limiting martingale using branching processes with immigration. This Markov construction has been extended to multitype branching processes [29] and infinite dimension and we refer e.g. to [3,16,17]. We propose here an extension to density dependent process. Spine construction has allowed also to prove ergodic properties of type distribution among the population and shed light on sampling [37] for structured (multitype) branching processes. More generally, we refer to the description of reduced tree and backbone [15,21] and multispine construction [22]. It has finally proved to be a powerful way to analyse the first moment semigroup of branching processes, and more generally non-conservative semigroups or linear PDEs, see e.g. [4,10] and references therein.

Our original motivation for this work is the study of population models with competition. We use our spine construction for sampling in single type and multitype Markov processes with competition. For related motivations, let us mention the recent works [1] and [11]. In these models, some spine techniques for branching processes can be exploited. In the applications considered here, which motivates this work, our new construction is required to deal with the absence of branching property.

In recent decades, much attention has been paid to the study of genealogical structures of population and sampling. For branching processes, the contour (or exploration) process provides a full description of the genealogy, see e.g. [33]. The effect of competition as a pruning of trees has been introduced and studied in [7,34]. Spine construction offers a complementary insight by focusing on a *typical individual* in various senses. It can be extended to structured population and varying environment. The look-down construction also captures the genealogy. In this point of view, introduced by Kurtz and Donnelly, a level is added to individuals. The Poisson representation of this enlarged process allows in particular to build the genealogy of large population approximations and describe the longest branch in the tree. We refer to [31] for the look-down construction of branching processes and to [18] for a recent extension to interacting populations. The latter allows for a description of genealogy and samples by a tracing which follows the evolution of the levels back in time. We consider in this paper simpler models and propose a forward Markov consistent construction for samples.

The spine construction consists in a new process with a distinguished individual and all rates are modified using a positive function ψ on $\mathcal{X} \times \mathcal{Z}$. Roughly, the rate of the spine is first biased by the number of offsprings and types of descendants as for multitype branching process [29,36]. These rates are also modified following a Doob transform on the population sizes. We need to perform this second modification on the rates of non-distinguished individuals too. The last point differs from the classical construction for branching processes and allows in particular to get rid of the size bias in sampling on branching processes. The spine describes the lineage of a typical individual, which includes its time of branching, number of offsprings, types and so on. The construction contains more useful genealogical information than this ancestral path of a sample. Indeed the full tree seen from this lineage is described. It can be useful when tracing an infected individual in epidemiology or when looking at the subpopulation carrying a common mutation in population genetics. Among stimulating open questions is the way multisampling could be obtained, which will be just briefly evoked here and will be considered in forthcoming works.

We focus in this paper on the continuous time setting. Our spine construction has a counterpart in discrete time. As far as we see, the fact that in continuous time branching events are not simultaneous is more convenient for construction and analysis. Besides, models which motivate this work may be more classical in continuous time. For applications, we focus here on a finite type space $\mathcal{X}$ and we plan to deal with infinite state space in forthcoming works. The construction is achieved (only) in the denumerable case since it is a natural general setting. It requires less technicalities and a minimal number of assumptions. In particular no regularity conditions are necessary for now.

Example. To motivate this construction and illustrate it, we briefly present a result in the single type case and we refer to Section 3.1 for details. All the individuals are exchangeable. When the population

size is z, each individual branches and is replaced by k individuals at rate $\tau_k(z)$. In other words, an event occurs inside the population at rate $z\tau(z)$ and then one individual is chosen uniformly at random and is replaced by k individuals with probability $\tau_k(z)/\tau(z)$. For simplicity, we consider the case where the jump Markov process Z on $\mathbb{N}$ counting the number of individuals is well defined for any time (non-explosive) and does become extinct a.s. At a given fixed time, sample uniformly at random one individual alive. Then the times when the ancestral line of this sample has branched and its successive number of offsprings are given by the so called $1/z$-spine construction, which consists in realizing our construction for $\psi(z) = 1/z$. More precisely, the distinguished individual (the spine) is replaced by k individuals at rate $k\tau_k(z)z/(z+k-1)$ the other individuals branch independently and are replaced by k individuals at rate $\tau_k(z)z/(z+k-1)$. The joint law of the random tree of the original process and a uniform sample at this fixed time coincides with the law of the $1/z$-spine markovian construction. This result allows to specify how sampling bias the reproduction of individuals along time and the effect of population size. For Galton-Watson process in continuous time, it also complements the size biased construction [36] by describing the uniform sampling at fixed time. Finally, it allows us to classify the long time behavior of growth fragmentation process with density dependance of fragmentation, see forthcoming Corollary 1.

Outline of the paper. The paper is organized as follows. In the next section, we describe more precisely the original process and the so called ψ-spine construction associated to a positive function ψ on $\mathcal{X} \times \mathcal{Z}$. The main result provides a Girsanov type result (change of probability) to transform the original random tree with a randomly chosen individual at a give time into a new random tree with a distinguished individual, the spine. We complement this section by considering the associated semi-group and martingale, and a many-to-one formula, which focuses on the ancestral lineage of a typical individual. The two next sections are devoted to applications. In Section 3, we consider the single type case. In that case, computations can be achieved. It allows in particular to describe explicitly the uniform sampling at a given time when extinction does not occur. We exploit and illustrate this construction by considering a simple growth fragmentation process with competition and we determine the criterion of regulation of growth by competition and fragmentation. We also provide in this section a $L\log L$ criterion for the non-degeneracy of the natural positive martingale associated with the growth of the process, thus extending the criterion of Kesten-Stigum and the approach of [36]. In Section 4, we consider a population with a finite number of types. We describe the ancestral lineage of a uniform sample when the population size is bounded. Finally, we evoke sampling in large population approximation when the limiting process is a differential equation.

Notation. In the paper, we denote as $\mathbb{N} = \{1,2,\dots\}$, $\mathbb{N}_0 = \{0,1,2,\dots\} = \mathbb{N} \cup \{0\}$. The type space $\mathcal{X}$ is finite or denumerable. For two vectors $\mathbf{u} = (\mathbf{u}_x)_{x\in\mathcal{X}}$ and $\mathbf{v} = (\mathbf{v}_x)_{x\in\mathcal{X}}$, we denote as $\langle \mathbf{u}, \mathbf{v}\rangle = \sum_{x\in\mathcal{X}} \mathbf{u}_x\mathbf{v}_x$ the inner product.

We note $\|\mathbf{z}\|_1 = \sum_{x\in\mathcal{X}} \mathbf{z}_x$ the ℓ_1 norm of $\mathbf{z}$ and work with the associated normed and countable space

$$\mathcal{Z} = \{\mathbf{z} \in \mathbb{N}_0^{\mathcal{X}} : \|\mathbf{z}\|_1 < \infty\}.$$

It gives the state space of the population, by counting the number of individuals of each type. We do not only need the number of individuals of each type but also the genealogical links. For that purpose, we use the Ulam-Harris-Neveu notation to label the individuals of the population and each label will have a type and life length and offsprings (which may be empty). We thus introduce

$$\mathcal{U} = \cup_{k\geq 1}\mathbb{N}^k,$$

where $u = (u_1,\dots,u_k) \in \mathbb{N}^k$ means that u is an individual of the generation $k = |u|$ and the u_k-th child of $(u_1,\dots,u_{k-1})$. We denote as $v \preccurlyeq u$ (equivalently $u \succcurlyeq v$) when v is an ancestor of u (v is a descendant

of u). Finally, for several objects of the original process such as times, filtrations, rates.., we will use $\widehat{\bullet}$ for the corresponding object in the spine construction and $\widehat{\bullet}^\star$ for the spine individual.

2. Density dependent process and spine construction

2.1. The original Markov process and the associated tree

Let us construct the process $\mathbf{Z}$ and the corresponding tree $\mathcal{T}$ of individuals with their types, until any first explosion time. The population alive at time t is a random subset of $\mathcal{U}$, denoted by $\mathbb{G}(t)$, and the types of individuals at time t are $(Z^u, u \in \mathbb{G}(t))$. The vector counting the number of individuals of each type is $\mathbf{Z}(t) = (\mathbf{Z}_x(t), x \in \mathcal{X})$, where $\mathbf{Z}_x(t) = \#\{u \in \mathbb{G}(t) : Z^u = x\}$. We start with an initial population labeled by a non-empty, finite and deterministic subset $\mathfrak{g}$ of $\mathbb{N}$ together with their types are $(x^u, u \in \mathfrak{g})$. We denote as

$$\mathfrak{x} = \{(u, x^u), u \in \mathfrak{g}\}$$

this initial condition. We denote by $\mathbf{v} \in \mathcal{Z} = \{\mathbf{z} \in \mathbb{N}_0^{\mathcal{X}} : \|\mathbf{z}\|_1 < \infty\}$ the initial number of individuals of each type, that is $\mathbf{v} = (\mathbf{v}_x : x \in \mathcal{X})$ and $\mathbf{v}_x = \#\{u \in \mathfrak{g} : x^u = x\}$. Thus, $\mathbb{G}(0) = \mathfrak{g}$ and $\mathbf{Z}(0) = \mathbf{v}$.

Let us now construct the process for positive time, until any first explosion. The construction of the jump Markov process $\mathbf{Z}$ is classical [6,30]. It is achieved here together with labeling of individuals to keep track of the tree. We can proceed by iteration and use a sequence of independent exponential and uniform r.v. for times and choice of transition for the successive events, see [6].

Each individual u has a random life length $L^u \in (0, +\infty]$ and a type Z^u during all its life. Thus, u is born at time $\sum_{v \prec u} L^v$ and dies at time $\sum_{v \preccurlyeq u} L^v$. The life length L^u is given by the rate of replacement: each individual is replaced at rate $\tau(x, \mathbf{z}) = \sum_{\mathbf{k} \in \mathcal{Z}} \tau_{\mathbf{k}}(x, \mathbf{z})$ when its type is x and the population composition is $\mathbf{z}$. The types of its offsprings are then given by $\mathbf{k}$ with probability $\tau_{\mathbf{k}}(x, \mathbf{z})/\tau(x, \mathbf{z})$. In other words, each individual with type x is replaced by individuals with types $\mathbf{k}$ at rate $\tau_{\mathbf{k}}(x, \mathbf{z})$ when the population composition is $\mathbf{z}$. Then the composition of the population moves to $\mathbf{z} + \mathbf{k} - e(x)$. When an individual $u \in \mathcal{U}$ is replaced by $\mathbf{k}$, its offsprings are labeled by $(u, 1), \ldots, (u, \|\mathbf{k}\|_1)$. We need now to put labels and types together for these offsprings. The assignment of types will actually play no role but we will need do it in coherent way later in the spine construction. Thus, we consider a probability law $Q_{\mathbf{k}}$ on

$$\mathcal{X}_{\mathbf{k}} = \{\mathfrak{x} \in \mathcal{X}^{\|\mathbf{k}\|_1} : \forall x \in \mathcal{X}, \#\{i \geq 1 : \mathfrak{x}_i = x\} = \mathbf{k}_x\}$$

and $(Z_{(u,i)} : 1 \leq i \leq \|\mathbf{k}\|_1)$ is distributed as $Q_{\mathbf{k}}$. This assignment is achieved independently for each branching event and its law only depends on the type composition $\mathbf{k}$ of offsprings. A generic natural law is an exchangeable one, choosing successively the types of individuals uniformly at random among available choices, but models may suggest another one.

The process is then constructed iteratively. Writing T_n the successive events for $n \geq 0$, the process is constant in time intervals $[T_n, T_{n+1})$, where $T_0 = 0$ and $T_{n+1} = +\infty$ if no event occurs after T_n. At these times T_n, we may say *jump* or *branching event*, indifferently. Note that for any branching event, only one individual disappears. It may be replaced by a single individual with the same type (but a different label). The process is well defined until the limiting time of successive branching events $(T_n)_{n \geq 1}$:

$$T_{\mathrm{Exp}} = \lim_{n \to \infty} T_n \in \mathbb{R}_+ \cup \{+\infty\}.$$

This latter is finite if the sequence of branching events accumulate and as usual, we speak then of *explosion*. We denote as $\mathcal{T}$ the random tree obtained with this construction and $\mathcal{T}(t)$ the tree truncated

at time $t \geq 0$. Formally $\mathcal{T} = \{(u, L^u, Z^u) : u \in \mathcal{U}, \exists t \geq 0 \text{ s.t. } u \in \mathbb{G}(t)\}$ and $\mathcal{T}(t) = \{(u, L^u(t), Z^u) : u \in \mathcal{U}, \exists s \leq t \text{ s.t. } u \in \mathbb{G}(s)\}$ with $L^u(t)$ the life length of u, when u is killed at time t.

2.2. The ψ-spine construction associated to the original process

Recall that $\mathcal{Z} = \{\mathbf{z} \in \mathbb{N}_0^{\mathcal{X}} : \|\mathbf{z}\|_1 < \infty\}$ is denumerable and gives the state space of the composition of the population. We introduce the state space for the type of the spine and composition of the population:

$$\overline{\mathcal{Z}} = \{(x, \mathbf{z}) \in \mathcal{X} \times \mathcal{Z} : \mathbf{z}_x \geq 1\}.$$

We consider a (fixed) positive function $\psi : \overline{\mathcal{Z}} \to (0, \infty)$ which satisfies, for any $(x, \mathbf{z}) \in \overline{\mathcal{Z}}$,

$$\sum_{\mathbf{k} \in \mathcal{Z}} \tau_{\mathbf{k}}(x, \mathbf{z}) \langle \mathbf{k}, \psi(., \mathbf{z} + \mathbf{k} - \mathbf{e}(x)) \rangle < \infty. \tag{1}$$

Let us construct a new Markov process $\mathbf{V}^\psi = \mathbf{V}$ and the associated tree $\mathcal{A}^\psi = \mathcal{A}$. This construction contains a distinguished individual $E^\psi = E$ for any time. We follow the point of view of [29,36] for Galton-Watson processes. We denote now as $\mathbb{V}(t) \subset \mathcal{U}$ the random set of individuals alive at time $t \geq 0$. The types of individuals are given by $(V^u, u \in \mathbb{V}(t))$ and $\mathbf{V}_x(t) = \#\{u \in \mathbb{V}(t) : V^u = x\}$ is the number of individuals with type x at time t. Thus $E(t) \in \mathbb{V}(t)$ is the label of the spine at time t and the type of the spine is then $Y(t) = V^{E(t)}$.

The initial population $\mathfrak{x} = \{(u, x^u), u \in \mathfrak{g}\}$ is the same as the initial state of the original process $\mathfrak{X}(0)$ and types are also counted by $\mathbf{v}$ initially. Among this initial population, the distinguished individual $E(0)$ (the spine) is chosen randomly as follows

$$\mathbb{P}(E(0) = e) = \frac{\psi(x_e, \mathbf{v})}{\langle \mathbf{v}, \psi(., \mathbf{v}) \rangle} \qquad (e \in \mathfrak{g}).$$

The initial type $Y(0)$ of the spine is distributed as $\mathbb{P}(Y(0) = r) = \mathbf{v}_r \psi(r, \mathbf{v}) / \langle \mathbf{v}, \psi(., \mathbf{v}) \rangle$.

We can construct the process and the tree for positive time, in a similar way as the original process, writing now $\widehat{L}^u$ the life length of the individual u and $\widehat{Z}^u$ its type during its life. Among a population whose types are counted by $\mathbf{z}$, the spine E with type x branches and is replaced by offsprings of types $\mathbf{k}$ at rate

$$\widehat{\tau}^\star_{\mathbf{k}}(x, \mathbf{z}) = \tau_{\mathbf{k}}(x, \mathbf{z}) \frac{\langle \mathbf{k}, \psi(., \mathbf{z} - \mathbf{e}(x) + \mathbf{k}) \rangle}{\psi(x, \mathbf{z})}.$$

The total branching rate of the spine individual is then $\widehat{\tau}^\star(x, \mathbf{z}) = \sum_{\mathbf{k} \in \mathcal{Z}} \widehat{\tau}^\star_{\mathbf{k}}(x, \mathbf{z})$, which is finite by (1). Labels of offsprings are $(E(t-), 1), \ldots, (E(t-), \|\mathbf{k}\|_1)$ and their types are chosen using the probability law $Q_{\mathbf{k}}$ as above. Among these offsprings, each individual with type $y \in \mathcal{X}$ is chosen to be the new distinguished individual E with probability

$$q_y(\mathbf{k}, \mathbf{z}) = \frac{\psi(y, \mathbf{z} - \mathbf{e}(x) + \mathbf{k})}{\langle \mathbf{k}, \psi(., \mathbf{z} - \mathbf{e}(x) + \mathbf{k}) \rangle}.$$

Outside the spine, i.e. for individuals $u \in \mathbb{V}(t) - \{E(t)\}$ at time t, rates of jumps are modified as follows. Inside a population $\mathbf{z}$ with spine of type x, the individuals (except the spine) with type y branch and yield offsprings composed by $\mathbf{k}$ at rate

$$\widehat{\tau}_{\mathbf{k}}(y, x, \mathbf{z}) = \tau_{\mathbf{k}}(y, \mathbf{z}) \frac{\psi(x, \mathbf{z} - \mathbf{e}(y) + \mathbf{k})}{\psi(x, \mathbf{z})}.$$

This process with a distinguished individual is constant between successive jumps $\widehat{T}_n$ and $\widehat{T}_{n+1}$, where $\widehat{T}_0 = 0$ and $\widehat{T}_{n+1} = +\infty$ if no event occurs after $\widehat{T}_n$. This process is well defined by induction until explosion time

$$\widehat{T}_{\mathrm{Exp}} = \lim_{n\to\infty} \widehat{T}_n \in \mathbb{R}_+ \cup \{+\infty\},$$

which may be finite or not.

The Markovian construction achieved here provides the process $\mathbf{V}$ and the associated random tree $\mathcal{A}$, as for the original process, with an additional distinguished individual E. We can also define the tree $\mathcal{A}(t)$ truncated at time $t \geq 0$. This construction is associated to the original random process through the rates $(\tau_{\mathbf{k}}(x,\mathbf{z}) : x \in \mathcal{X}, \mathbf{k} \in \mathcal{Z}, \mathbf{z} \in \mathcal{Z})$ and the initial type composition $\mathbf{v}$. It then depends only on the choice of ψ, which will play a key role.

2.3. General result linking the original tree to the spine construction

We introduce now the linear operator $\mathcal{G}$ which will link the original process to the ψ-spine construction. For a function $f : \overline{\mathcal{Z}} \to \mathbb{R}$, we consider the function $\mathcal{G}f$ on $\overline{\mathcal{Z}}$ given by

$$\begin{aligned}\mathcal{G}f(x,\mathbf{z}) = &\sum_{\mathbf{k}\in\mathcal{Z}} \tau_{\mathbf{k}}(x,\mathbf{z})\,\langle \mathbf{k}, f(.,\mathbf{z}+\mathbf{k}-\mathbf{e}(x))\rangle \\ &+ \sum_{y\in\mathcal{X},\mathbf{k}\in\mathcal{Z}} \tau_{\mathbf{k}}(y,\mathbf{z})(\mathbf{z}_y - \delta_y^x) f(x,\mathbf{z}+\mathbf{k}-\mathbf{e}(y)) - \left(\sum_{y\in\mathcal{X}} \tau(y,\mathbf{z})\mathbf{z}_y\right) f(x,\mathbf{z}),\end{aligned} \tag{2}$$

where δ_y^x is the Kronecker symbol ($\delta_y^x = 1$ if $y = x$ and 0 otherwise). The first term corresponds to the contribution of the spine and the second of individuals outside the spine. This operator $\mathcal{G}$ is well defined on the set $\mathfrak{D}_{\mathcal{G}}$ of positive functions ψ on $\overline{\mathcal{Z}}$ which satisfy (1) and for any $(x,\mathbf{z}) \in \overline{\mathcal{Z}}$,

$$\sum_{y\in\mathcal{X},\mathbf{k}\in\mathcal{Z}} \tau_{\mathbf{k}}(y,\mathbf{z})\,\mathbf{z}_y\,\psi(x,\mathbf{z}+\mathbf{k}-\mathbf{e}(y)) < \infty.$$

In particular, $\mathfrak{D}_{\mathcal{G}}$ contains all the bounded positive functions on $\overline{\mathcal{Z}}$ which satisfy (1). By now, we assume that ψ belongs to $\mathfrak{D}_{\mathcal{G}}$ and we define the real valued function

$$\lambda = \frac{\mathcal{G}\psi}{\psi} \qquad \text{on } \overline{\mathcal{Z}}.$$

Observe that the ψ-transform $f \to \mathcal{G}(\psi f)/\psi - \lambda f$ yields the generator of $(Y(t),\mathbf{V}(t))_{t\geq 0}$. For any $t \geq 0$, we consider a random variable $U(t)$ by choosing an individual alive at time t among the original population process, when the population is alive. Its law is specified by the function p_e which yields the probability to choose e when the tree and times are given, i.e. for $t \geq 0$,

$$\mathbf{1}_{\mathbb{G}(t)\neq\varnothing, T_{\mathrm{Exp}}>t}\,\mathbb{P}(U(t) = e \,|\, \mathcal{T}(t)) = \mathbf{1}_{\mathbb{G}(t)\neq\varnothing, T_{\mathrm{Exp}}>t}\, p_e(\mathcal{T}(t)) \quad \text{a.s.}$$

and $\sum_{e\in\mathbb{G}(t)} p_e(\mathcal{T}(t)) = 1$ a.s. on the event $\{\mathbb{G}(t) \neq \varnothing, T_{\mathrm{Exp}} > t\}$. Our main interest in this paper is the uniform choice at time t, i.e. $p_e(\mathcal{T}(t)) = 1/\#\mathbb{G}(t) = 1/\|\mathbf{Z}(t)\|_1$. But sampling at a given time with a type bias may also be relevant, for instance. We introduce the process $\mathcal{W}$ associated to the spine construction

$(\mathcal{A}, E)$ and the sampling p:

$$\mathcal{W}(t) = \mathbf{1}_{\widehat{T}_{\mathrm{Exp}}>t} \frac{\exp\left(\int_0^t \lambda(Y(s), \mathbf{V}(s))ds\right)}{\psi(Y(t), \mathbf{V}(t))} p_{E(t)}(\mathcal{A}(t)).$$

We can now state the general result and link the random choice of an individual among our interacting population to the Markovian spine construction. It extends spine constructions of branching processes and allows to take into account density dependence. Let $\mathbb{T}$ be the space of finite trees where each node has a life length and an $\mathcal{X}$ valued type. Elements of $\mathbb{T}$ are identified to a finite collection of elements of $\mathcal{U} \times (\mathbb{R}_+ \cup \{+\infty\}) \times \mathcal{X}$ endowed with the product σ-algebra.

Theorem 1. *Let $\psi \in \mathfrak{D}_{\mathcal{G}}$. For any $t \geq 0$ and any measurable non-negative function $F : \mathbb{T} \times \mathcal{U} \to \mathbb{R}$,*

$$\mathbb{E}_{\mathfrak{x}}\left(\mathbf{1}_{\{T_{\mathrm{Exp}}>t,\, \mathbb{G}(t)\neq\varnothing\}} F(\mathcal{T}(t), U(t))\right) = \langle \mathbf{v}, \psi(.,\mathbf{v})\rangle\, \mathbb{E}_{\mathfrak{x}}\left(\mathcal{W}(t)\, F(\mathcal{A}(t), E(t))\right).$$

In particular, if $U(t)$ is a uniform choice among the set $\mathbb{G}(t)$ of individuals at time t,

$$\mathbb{E}_{\mathfrak{x}}\left(\mathbf{1}_{\{T_{\mathrm{Exp}}>t, \mathbb{G}(t)\neq\varnothing\}} F(\mathcal{T}(t), U(t))\right) = \langle \mathbf{v}, \psi(.,\mathbf{v})\rangle\, \mathbb{E}_{\mathfrak{x}}\left(\mathbf{1}_{\widehat{T}_{\mathrm{Exp}}>t} \frac{e^{\int_0^t \lambda(Y(s),\mathbf{V}(s))ds}}{\psi(Y(t), \mathbf{V}(t))\, \|\mathbf{V}(t)\|_1} F(\mathcal{A}(t), E(t))\right).$$

The proof is a consequence of the following lemma, where we specify the successive jumps. Recall that the successive branching times of the original process Z and of the spine process V are respectively denoted by $(T_i, 1 \leq i \leq N)$, with $N \in \mathbb{N} \cup \{+\infty\}$ and $(\widehat{T}_i,\ 1 \leq i \leq \widehat{N})$, with $\widehat{N} \in \mathbb{N} \cup \{+\infty\}$ and $T_0 = \widehat{T}_0 = 0$ a.s. The variable $N \in \mathbb{N} \cup \{+\infty\}$ yields the total number of branching events and $N = i < \infty$ means that the process does not branch after time T_i. The same holds for $\widehat{N}$.

For $1 \leq i \leq N$, we denote as U_i (respectively $\mathbf{K}_i$) the random label in $\mathcal{U}$ (respectively in $\mathcal{Z}$) which realizes the ith branching event in the original process (respectively the types of its offsprings at this event). We denote by $(X_{i,j}, j \leq \|\mathbf{K}_i\|_1)$ the types of the successive offsprings of U_i. At time T_i, the individual U_i is thus replaced by individuals (U_i, j), for $1 \leq j \leq \|\mathbf{K}_i\|_1$, whose types are $(X_{i,j}, 1 \leq j \leq \|\mathbf{K}_i\|_1)$. We denote similarly as $\widehat{U}_i$, $\widehat{\mathbf{K}}_i$ and $(\widehat{X}_{i,j}, j \leq \|\widehat{\mathbf{K}}_i\|_1)$ the variables involved in the ith branching event of the spine construction for $1 \leq i \leq \widehat{N}$. Besides, we denote as E_i the label of the distinguished individual just before the ith branching event occurs. Thus, if $E_i = \widehat{U}_i$, then $E_{i+1} \neq E_i$ and $E_{i+1} = (E_i, j)$ with $1 \leq j \leq \|\widehat{\mathbf{K}}_i\|_1$; otherwise $E_{i+1} = E_i$. For convenience we denote as

$$A_i = \left(U_i, \mathbf{K}_i, (X_{i,j})_{1\leq j\leq \|\mathbf{K}_i\|_1}\right), \qquad \widehat{A}_i = \left(\widehat{U}_i, \widehat{\mathbf{K}}_i, (\widehat{X}_{i,j})_{1\leq j\leq \|\widehat{\mathbf{K}}_i\|_1}\right)$$

the discrete variables describing these successive branching events.

Let $\mathfrak{A}_n^\star$ be the subset of non-extinct discrete trees with n internal nodes (i.e. n branching events), where a type in $\mathcal{X}$ each node. The roots of these tree are fixed and given by $\mathfrak{x} = \{(u, x^u), u \in \mathfrak{g}\}$. Each element of $a \in \mathfrak{A}_n^\star$ is thus a finite sequence $a = (a_i)_{1\leq i\leq n}$ which describes the successive branching events (forgetting the time). More precisely $a_i = (u_i, \mathbf{k}_i, (x_{i,j})_{1\leq j\leq \|\mathbf{k}_i\|_1}) \in \mathcal{U} \times \mathcal{Z} \times \cup_{k\geq 0}\mathcal{X}^k$ means that individual u_i has offsprings whose types are counted by $\mathbf{k}_i$ and successively given by $(x_{i,j})_{1\leq j\leq \|\mathbf{k}_i\|_1}$. For $0 \leq k \leq n$, we denote by $\mathfrak{g}_k(a) \subset \mathcal{U}$ the labels of individuals alive just after the k-th event (and before the $k+1$-th) and $\mathbf{z}_k(a) \in \mathcal{Z}$ the vector giving the type composition of the population. We also denote as $y_k(e)$ the type of the ancestor of e between these k-th and $k+1$-th branching event. The fact that the tree $a \in \mathfrak{A}_n^\star$ is non-extinct means that we require that $\mathfrak{g}_k(a) \neq \varnothing$ for $k \leq n$. Note also that $\mathfrak{g}_0(a) = \mathfrak{g}$ and see Figure 1.

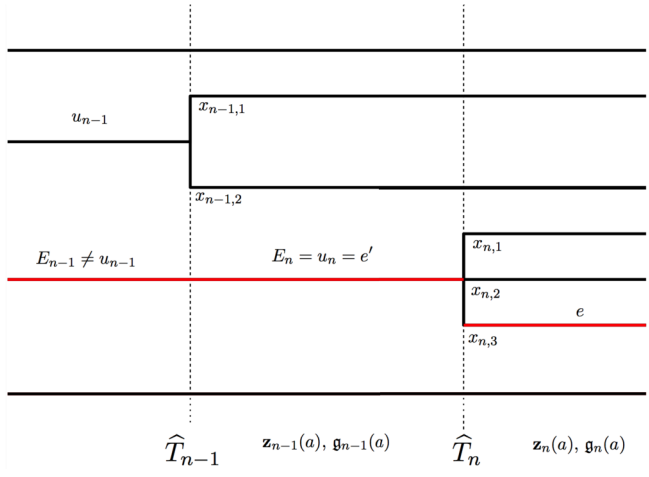

Figure 1. Illustration of the construction and notation for Lemma 1 and its proof. The label u_n realizes the nth branching. The lines correspond to individuals and their label is indicated just above the line. Below the line we give the types of these individuals. The spine is represented in red. At time $\widehat{T}_{n-1}$, an individual outside the spine branches and at $\widehat{T}_n$, the spines branches. They are replaced respectively by 2 and 3 individuals. The spine keeps the same label e' at the first event $\widehat{T}_{n-1}$ but move from label e' to label e at time $\widehat{T}_n$.

Lemma 1. *Let $n \geq 0$ and G be a measurable non-negative function from $\mathbb{R}_+^n$. Then*

$$\begin{aligned}&\mathbb{E}_{\mathfrak{x}}\left(\mathbf{1}_{\{N\geq n\}}G(T_1,\dots,T_n)\,\mathbf{1}_{\{A_i=a_i:\,1\leq i\leq n\}}\right)\\&\qquad=\langle\mathbf{v},\psi(.,\mathbf{v})\rangle\,\mathbb{E}_{\mathfrak{x}}\left(\mathbf{1}_{\{\widehat{N}\geq n,\,E_{n+1}=e\}}\,\mathcal{W}_n^{(a,e)}\,G(\widehat{T}_1,\dots,\widehat{T}_n)\mathbf{1}_{\{\widehat{A}_i=a_i:\,1\leq i\leq n\}}\right),\end{aligned}$$

for any $a=(a_i)_{1\leq i\leq n}\in\mathfrak{A}_n^\star$ and any $e\in\mathfrak{g}_n(a)$, where

$$\mathcal{W}_n^{(a,e)}=\frac{\exp\left(\sum_{k=0}^{n-1}(\widehat{T}_{k+1}-\widehat{T}_k)\lambda(y_k(e),\mathbf{z}_k(a))\right)}{\psi(y_n(e),\mathbf{z}_n(a))}.$$

Proof. The initial population $\mathfrak{x}$ is fixed and notation is omitted in this proof. For convenience, we also denote as $\mathbf{z}_n=\mathbf{z}_n(a)$ the composition of the population between the n-th and $(n+1)$-th branching event and $\mathfrak{g}_n=\mathfrak{g}_n(a)$ the set of labels alive at this time.

We proceed by induction and start with $n=0$. For any $e\in\mathfrak{g}_0=\mathfrak{g}$,

$$\langle\mathbf{v},\psi(.,\mathbf{v})\rangle\mathbb{E}(\mathbf{1}_{\{E_1=e\}}\,\mathcal{W}_0^{(\varnothing,e)})=\mathbb{E}\left(\mathbf{1}_{\{E_1=e\}}\,\frac{\langle\mathbf{v},\psi(.,\mathbf{v})\rangle}{\psi(x_e,\mathbf{v})}\right)=1.$$

Let us now consider $n\geq 1$ and assume that the identity holds for $n-1$. We consider $G_n(t_i:1\leq i\leq n)=G(t_i:1\leq i\leq n-1)H(t_n-t_{n-1})$, where G and H are measurable and non-negative and bounded respectively on $\mathbb{R}_+^{n-1}$ and $\mathbb{R}_+$. We fix also $a=(a_i)_{1\leq i\leq n}\in\mathfrak{A}_n^\star$ and first observe that

$$\begin{aligned}&\mathbb{E}\left(\mathbf{1}_{\{N\geq n\}}\,G_n(T_i,\,1\leq i\leq n)\,\mathbf{1}_{\{A_i=a_i:\,1\leq i\leq n\}}\,\middle|\,\mathcal{F}_{T_{n-1}}\right)\\&\qquad=\mathbf{1}_{\{N\geq n-1\}}\,G(T_i,\,1\leq i\leq n-1)\,\mathbf{1}_{\{A_i=a_i:\,1\leq i\leq n-1\}}\,B_n,\end{aligned}\tag{3}$$

where

$$B_n = \mathbb{E}\left(\mathbf{1}_{\{N\geq n\}}\, H(T_n - T_{n-1})\, \mathbf{1}_{\{A_n = a_n\}} \,\middle|\, \mathcal{F}_{T_{n-1}}\right)$$

and $\mathcal{F}_{T_{n-1}} = \sigma(T_i, A_i : i \leq n-1)$ is the filtration generated until time T_{n-1} in the original construction. Conditionally on $\mathcal{F}_{T_{n-1}}$, on the event $\{A_i = a_i : 1 \leq i \leq n-1\}$ the random variable $T_n - T_{n-1}$ is exponentially distributed with parameter

$$\tau_n = \sum_{u\in\mathfrak{g}_{n-1}} \tau(x^u, \mathbf{z}_{n-1}).$$

When the label u_n branches, it is replaced by individual with types $(x_{n,j})_{1\leq j\leq \|\mathbf{k}_n\|_1}$ and composition $\mathbf{k}_n$. For convenience, we also denote as

$$Q_n = Q_{\mathbf{k}_n}(x_{n,j}, 1 \leq j \leq \|\mathbf{k}_n\|_1),$$

the probability to choose the types $(x_{n,j}, 1 \leq j \leq \|\mathbf{k}_n\|_1)$. On the event $\{N \geq n-1\} \cap \{A_i = a_i : 1 \leq i \leq n-1\}$, we get

$$B_n = \mathbf{1}_{\{\tau_n \neq 0\}}\, \tau_{\mathbf{k}_n}(x_{u_n}, \mathbf{z}_{n-1})\, Q_n \int_{\mathbb{R}_+} H(t)\, e^{-\tau_n t}\, dt. \tag{4}$$

Similarly for $e \in \mathfrak{g}_n$, with direct ancestor $e' \in \mathfrak{g}_{n-1}$ before the last branching event,

$$\begin{aligned}
&\mathbb{E}\left(\mathbf{1}_{\{\widehat{N}\geq n,\, E_{n+1}=e\}}\, \mathcal{W}_n^{((a_i:i\leq n),e)}\, G_n(\widehat{T}_i,\, 1\leq i\leq n)\mathbf{1}_{\{\widehat{A}_i=a_i:\,1\leq i\leq n\}} \,\middle|\, \widehat{\mathcal{F}}_{T_{n-1}}\right)\\
&\qquad = \mathbf{1}_{\{\widehat{N}\geq n-1,\, E_n=e'\}}\, \mathcal{W}_{n-1}^{((a_i:i\leq n-1),e')}\, G(\widehat{T}_i,\, 1\leq i\leq n-1)\mathbf{1}_{\{\widehat{A}_i=a_i:\,1\leq i\leq n-1\}}\, \frac{\psi(y', \mathbf{z}_{n-1})}{\psi(y, \mathbf{z}_n)}\, \widehat{B}_n,
\end{aligned} \tag{5}$$

where

$$\widehat{B}_n = \mathbb{E}\left(\mathbf{1}_{\{\widehat{N}\geq n,\, E_{n+1}=e\}}\, e^{(T_n - T_{n-1})\lambda(y', \mathbf{z}_{n-1})}\, H(\widehat{T}_n - \widehat{T}_{n-1})\mathbf{1}_{\{\widehat{A}_n = a_n\}} \,\middle|\, \widehat{\mathcal{F}}_{T_{n-1}}\right)$$

and y (respectively y') is the type of the spinal individual e (respectively e') after (respectively before) the nth branching event. We denote respectively as

$$\widehat{\tau}_n = \sum_{u\in\mathfrak{g}_{n-1}-\{e'\}} \widehat{\tau}(x^u, y', \mathbf{z}_{n-1}), \qquad \widehat{\tau}_n^\star = \widehat{\tau}^\star(y', \mathbf{z}_{n-1}),$$

the total branching rates of the population oustide the spine and of the spine. Recalling that $\mathbf{z}_n = \mathbf{z}_{n-1} - \mathbf{e}(x_{u_n}) + \mathbf{k}_n$, we also denote as

$$\widehat{\tau}_{n,\mathbf{k}_n} = \tau_{\mathbf{k}_n}(x_{u_n}, \mathbf{z}_{n-1}) \frac{\psi(y, \mathbf{z}_n)}{\psi(y', \mathbf{z}_{n-1})}$$

the rate at which an individual outside the spine is replaced by $\mathbf{k}_n$. If the branching indeed occurs outside the spine, $y' = y$ and this rate $\widehat{\tau}_{n,\mathbf{k}_n}$ coincides with $\widehat{\tau}_{\mathbf{k}_n}(x_{u_n}, y', \mathbf{z}_{n-1})$. Besides,

$$\widehat{\tau}^\star_{n,\mathbf{k}_n} = \widehat{\tau}^\star_{\mathbf{k}_n}(y', \mathbf{z}_{n-1}) = \tau_{\mathbf{k}_n}(y', \mathbf{z}_{n-1}) \frac{\langle \mathbf{k}_n, \psi(., \mathbf{z}_n)\rangle}{\psi(y', \mathbf{z}_{n-1})}$$

yields the branching rates for the spine. If the branching event indeed concerns the spine, $y' = x_{u_n}$ may differ from y. Similarly, the probability to choose a spine with type y at step n is

$$q_n = q_y(\mathbf{k}_n, \mathbf{z}_n) = \frac{\psi(y, \mathbf{z}_n)}{\langle \mathbf{k}_n, \psi(., \mathbf{z}_n)\rangle}.$$

We distinguish two cases, corresponding to the fact that the nth branching event concerns the spine or not, i.e. either $u_n = e'$ or ($u_n \neq e'$ and $y = y'$). On the event $\{\widehat{N} \geq n-1, E_{n-1} = e'\} \cap \{\widehat{A}_i = a_i : 1 \leq i \leq n-1\}$, the time $\widehat{T}_n - \widehat{T}_{n-1}$ is exponentially distributed with parameter $\widehat{\tau}_n + \widehat{\tau}_n^\star$ and we get

$$\begin{aligned}
\widehat{B}_n &= \mathbf{1}_{\{\widehat{\tau}_n + \widehat{\tau}_n^\star \neq 0,\, u_n \neq e'\}} \int_{\mathbb{R}_+} H(t) e^{t(\lambda(y', \mathbf{z}_{n-1}) - (\widehat{\tau}_n + \widehat{\tau}_n^\star))}\, \widehat{\tau}_{n,\mathbf{k}_n}\, Q_n\, dt \\
&\quad + \mathbf{1}_{\{\widehat{\tau}_n + \widehat{\tau}_n^\star \neq 0,\, u_n = e'\}} \int_{\mathbb{R}_+} H(t) e^{t(\lambda(y', \mathbf{z}_{n-1}) - (\widehat{\tau}_n + \widehat{\tau}_n^\star))} \widehat{\tau}^\star_{n,\mathbf{k}_n}\, q_n Q_n\, dt \\
&= \mathbf{1}_{\{\widehat{\tau}_n + \widehat{\tau}_n^\star \neq 0\}} \frac{\psi(y, \mathbf{z}_n)}{\psi(y', \mathbf{z}_{n-1})}\, \tau_{\mathbf{k}_n}(x_{u_n}, \mathbf{z}_{n-1})\, Q_n \int_{\mathbb{R}_+} H(t) e^{t(\lambda(y', \mathbf{z}_{n-1}) - (\widehat{\tau}_n + \widehat{\tau}_n^\star))}\, dt.
\end{aligned}$$

Recalling Definition (2) of $\mathcal{G}$ and the definition $\lambda = \mathcal{G}\psi/\psi$, we observe that

$$\widehat{\tau}_n + \widehat{\tau}_n^\star - \lambda(y', \mathbf{z}_{n-1}) = \tau_n.$$

Then we obtain from (5)

$$\begin{aligned}
&\mathbb{E}\left(\mathbf{1}_{\{\widehat{N} \geq n,\, E_{n+1} = e\}} \mathcal{W}_n^{((a_i : i \leq n), e)}\, G_n(\widehat{T}_i, 1 \leq i \leq n) \mathbf{1}_{\{\widehat{A}_i = a_i : 1 \leq i \leq n\}} \,\middle|\, \widehat{\mathcal{F}}_{T_{n-1}}\right) \\
&\quad = \mathbf{1}_{\{\widehat{N} \geq n-1,\, E_n = e'\}} \mathcal{W}_{n-1}^{((a_i : i \leq n-1), e')}\, G(\widehat{T}_i, 1 \leq i \leq n-1) \mathbf{1}_{\{\widehat{A}_i = a_i : 1 \leq i \leq n-1,\, \widehat{\tau}_n + \widehat{\tau}_n^\star \neq 0\}} \\
&\qquad \times \int_{\mathbb{R}_+} H(t) e^{-\tau_n t}\, dt \times \tau_{\mathbf{k}_n}(x_{u_n}, \mathbf{z}_{n-1})\, Q_n.
\end{aligned}$$

Using (3) and (4) and the fact that $\widehat{\tau}_n + \widehat{\tau}_n^\star = 0$ is equivalent to $\tau_n = 0$, the induction hypothesis ensures

$$\begin{aligned}
&\mathbb{E}\left(\mathbf{1}_{\{N \geq n\}}\, G_n(T_i, 1 \leq i \leq n)\, \mathbf{1}_{\{A_i = a_i : 1 \leq i \leq n\}}\right) \\
&\quad = \langle \mathbf{v}, \psi(., \mathbf{v})\rangle\, \mathbb{E}\left(\mathbf{1}_{\{\widehat{N} \geq n,\, E_{n+1} = e\}} \mathcal{W}_n^{((a_i : i \leq n), e)}\, G_n(\widehat{T}_i, 1 \leq i \leq n) \mathbf{1}_{\{\widehat{A}_i = a_i : 1 \leq i \leq n\}}\right)
\end{aligned}$$

by conditioning both sides with respect to their filtration until the $(n+1)$th branching event. It ends the proof by a monotone class argument. □

Proof of Theorem 1. The result is a consequence of the previous lemma. For each $t \geq 0$ and $n \geq 0$ and $e \in \mathcal{U}$, we introduce a measurable non-negative function $G_n^{t,e}$ from $\mathbb{R}_+^n \times \mathfrak{A}_n^\star$ such that, on the event $\{T_n \leq t < T_{n+1}, N \geq n\}$ we have

$$F(\mathcal{T}(t), e) p_e(\mathcal{T}(t)) = G_n^{t,e}(T_1, \ldots, T_n, A_1, \ldots, A_n) \quad \text{a.s,}$$

recalling that $T_{n+1} = \infty$ if $n + 1 > N$. Then

$$\begin{aligned}
&\mathbb{E}_{\mathfrak{x}}\left(\mathbf{1}_{\{T_{\mathrm{Exp}} > t,\, \mathbb{G}(t) \neq \varnothing\}} F(\mathcal{T}(t), U(t))\right) \\
&\quad = \sum_{\substack{n \geq 0, \\ a \in \mathfrak{A}_n^\star,\, e \in \mathfrak{g}_n(a)}} \mathbb{E}_{\mathfrak{x}}\left(F(\mathcal{T}(t), e) p_e(\mathcal{T}(t)) \mathbf{1}_{A_i = a_i : 1 \leq i \leq n,\, T_n \leq t < T_{n+1},\, N \geq n}\right) = \sum_{\substack{n \geq 0, \\ a \in \mathfrak{A}_n^\star,\, e \in \mathfrak{g}_n(a)}} F_n^{t,e}(a),
\end{aligned}$$

where for $n \geq 0$, $a = (a_i)_{1 \leq i \leq n} \in \mathfrak{A}_n^\star$ and $e \in \mathfrak{g}_n(a)$,

$$F_n^{t,e}(a) = \mathbb{E}_{\mathfrak{x}} \left(\mathbf{1}_{\{N \geq n, T_n \leq t\}} G_n^{t,e}(T_1, \ldots, T_n, a) f_t(T_n, a) \mathbf{1}_{\{A_i = a_i : 1 \leq i \leq n\}} \right)$$

and

$$f_t(T_n, a) = \mathbb{P}(T_{n+1} > t | T_n, A_n = a_n, \ldots, A_1 = a_1).$$

W apply Lemma 1 which yields an express $F_n^{t,e}(a)$ in terms of the spine construction:

$$F_n^{t,e}(a) = \mathbb{E}_{\mathfrak{x}} \left(\mathbf{1}_{\{\hat{N} \geq n, \widehat{T}_n \leq t\}} G_n^{t,e}(\widehat{T}_1, \ldots, \widehat{T}_n, a) f_t(\widehat{T}_n, a) \mathbf{1}_{\{A_i = a_i : 1 \leq i \leq n\}} \mathcal{W}_n^{(a,e)} \right).$$

Recalling that $y_n(e)$ the type of the spine e at the nth event and following the last lines of the proof of Lemma 1, we observe also that

$$\mathbf{1}_{\{E_{n+1} = e\}} f_t(\widehat{T}_n, a) = \mathbf{1}_{\{E_{n+1} = e\}} e^{(t - \widehat{T}_n)\lambda(y_n(e), \mathbf{z}_n(a))} \mathbb{P}(\widehat{T}_{n+1} > t | \widehat{T}_n, \widehat{A}_n = a_n, \ldots, \widehat{A}_1 = a_1).$$

This ends the proof. □

2.4. Positive semigroup and martingale

For each $(r, \mathbf{v}) \in \overline{\mathcal{Z}}$, we associate an initial labeling $\mathfrak{x} = \mathfrak{x}(\mathbf{v}) = ((u, x^u) : u \in \mathfrak{g})$, where x^u is the type of $u \in \mathfrak{g}$ and $\#\{u \in \mathfrak{g} : x^u = x\} = \mathbf{v}_x$ for any $x \in \mathcal{X}$. Since $\mathbf{v}_r \geq 1$, there exists at initial time a label whose type is r. Let us choose one (for instance the smallest one) and note it u_r: $u_r \in \mathfrak{g}$ and $x_{u_r} = r$.

For any $t \geq 0$ and f function from $\overline{\mathcal{Z}}$ to $\mathbb{R}_+ \cup \{+\infty\}$, we define for any $(r, \mathbf{v}) \in \overline{\mathcal{Z}}$,

$$M_t f(r, \mathbf{v}) = \mathbb{E}_{\mathfrak{x}(\mathbf{v})} \left(\mathbf{1}_{\{T_{\mathrm{Exp}} > t\}} \sum_{u \in \mathbb{G}(t),\, u \succcurlyeq u_r} f(Z^u(t), \mathbf{Z}(t)) \right),$$

where Z and $\mathbf{Z}$ are defined in Section 2.1 with initial condition $\mathfrak{x}(\mathbf{v})$. This corresponds to the first moment associated to the empirical measure of the descendance of a specific initial individual, together with the composition of the population. We observe that this definition does not depend on the assignments of types and labels, and in particular it does not depend on the choice of u_r. We observe that

$$M_t f(r, \mathbf{v}) = \mathbb{E}_{\mathfrak{x}(\mathbf{v})} \left(\mathbf{1}_{\{T_{\mathrm{Exp}} > t\}} \langle \mathbf{Z}^{\succcurlyeq u_r}(t), f(., \mathbf{Z}(t)) \rangle \right),$$

where $\mathbf{Z}_x^{\succcurlyeq u}(t) = \#\{w \in \mathbb{G}(t) : w \succcurlyeq u, Z^w(t) = x\}$ is the number of individuals with type x at time t who are descendant of u and we recall that $\langle \mathbf{u}, \mathbf{v} \rangle = \sum_{x \in \mathcal{X}} \mathbf{u}_x \mathbf{v}_x$ is the inner product. Let us first observe that the generator of the semigroup M is the linear operator $\mathcal{G}$ introduced in (2). This will be made explicit in applications.

Recall that ψ is positive and $\lambda = \mathcal{G}\psi / \psi$ on $\overline{\mathcal{Z}}$. Recall also that $\mathbf{V}$ is the process counting types in the ψ-spine construction and $Y(t) = V^{E(t)}(t)$ is the type of the spine at time t. Observe that $(Y, \mathbf{V})$ is a jump Markov process whose jump rates are given by $\widehat{\tau}_{\mathbf{k}}(y, x, \mathbf{z})$ and $\widehat{\tau}_{\mathbf{k}}^\star(x, \mathbf{z})$ for $\mathbf{k}, \mathbf{z} \in \mathcal{Z}$ and $y, x \in \mathcal{X}$. It starts from $(Y(0), \mathbf{V}(0)) = (r, \mathbf{v})$.

Proposition 1. *Let $\psi \in \mathfrak{D}_{\mathcal{G}}$. The family $(M_t)_{t\geq 0}$ is a positive semigroup on the set of functions from $\overline{\mathcal{Z}}$ to $\mathbb{R}_+ \cup \{+\infty\}$. Besides, for any $t \geq 0$, for any non-negative function f on $\overline{\mathcal{Z}}$ and $(r,\mathbf{v}) \in \overline{\mathcal{Z}}$,*

$$M_t f(r,\mathbf{v}) = \psi(r,\mathbf{v})\,\mathbb{E}_{(r,\mathbf{v})}\left(\mathbf{1}_{\{\widehat{T}_{\mathrm{Exp}}>t\}}\,\frac{e^{\int_0^t \lambda(Y(s),\mathbf{V}(s))ds}}{\psi(Y(t),\mathbf{V}(t))}\,f(Y(t),\mathbf{V}(t))\right).$$

Furthermore, for any G measurable function from $\mathbb{D}([0,t],\mathcal{X}\times\mathcal{Z})$ to $\mathbb{R}_+$,

$$\begin{aligned}\mathbb{E}_{\mathfrak{x}(\mathbf{v})}&\left(\mathbf{1}_{\{T_{\mathrm{Exp}}>t\}}\sum_{u\in\mathbb{G}(t)}\psi(Z^u(t),\mathbf{Z}(t))G((Z^u(s),\mathbf{Z}(s))_{s\leq t})\right)\\ &= \langle \mathbf{v},\psi(.,\mathbf{v})\rangle\mathbb{E}_{(r,\mathbf{v})}\left(\mathbf{1}_{\{\widehat{T}_{\mathrm{Exp}}>t\}}\,e^{\int_0^t\lambda(Y(s),\mathbf{V}(s))ds}\,G((Y(s),\mathbf{V}(s))_{s\leq t})\right),\end{aligned}$$

where for $u\in\mathbb{G}(t)$, $Z^u(s)$ is the type of the (unique) ancestor of u at time $s\leq t$

This result provides a Feynman-Kac representation of the semigroup and a so-called many-to-one formula for the population. We refer to [14] for a general reference on Feynman-Kac formulae. For similar representations for structured branching processes and in particular for fragmentations or growth fragmentations, we mention the works of Bertoin [8,9] and Cloez [13] and Marguet [37]. We note that the event $\{\widehat{T}_{\mathrm{Exp}} > t\}$ is measurable with respect to filtration associated to $\mathbf{V}$ since it corresponds to the absence of accumulation of jumps for $\mathbf{V}$ before time t.

Proof. For convenience, we omit the initial condition in the notation. To prove that M is a semigroup, we condition by the filtration $\mathcal{F}_t$ generated by the original process until time t. For any $u\in\mathcal{U}$ and non-negative function f,

$$\mathbb{E}\left(\mathbf{1}_{\{T_{\mathrm{Exp}}>t+s,\,u\in\mathbb{G}(t)\}}\langle\mathbf{Z}^{\succcurlyeq u}(t+s),\,f(.,\mathbf{Z}(t+s))\rangle\,\middle|\,\mathcal{F}_t\right) = \mathbf{1}_{\{T_{\mathrm{Exp}}>t,\,u\in\mathbb{G}(t)\}}M_s f(Z^u(t),\mathbf{Z}(t)).$$

We get

$$\begin{aligned}M_{t+s}f &= \mathbb{E}\Big(\mathbf{1}_{\{T_{\mathrm{Exp}}>t\}}\sum_{u\in\mathbb{G}(t),\,u\succcurlyeq u_r}\mathbb{E}\left(\mathbf{1}_{\{T_{\mathrm{Exp}}>t+s,\,u\in\mathbb{G}(t)\}}\langle\mathbf{Z}^{\succcurlyeq u}(t+s),\,f(.,\mathbf{Z}(t+s))\rangle\,\middle|\,\mathcal{F}_t\right)\Big)\\ &= \mathbb{E}\left(\mathbf{1}_{\{T_{\mathrm{Exp}}>t\}}\langle\mathbf{Z}^{\succcurlyeq u_r}(t),\,M_s f(.,\mathbf{Z}(t))\rangle\right) = M_t(M_s f).\end{aligned}$$

To prove the Feynmac Kac representation of the semigroup M and get the ancestral lineage of a typical individual, we prove that for $t\geq 0$,

$$\begin{aligned}\mathbb{E}&\Big(\mathbf{1}_{\{T_{\mathrm{Exp}}>t\}}\sum_{u\in\mathbb{G}(t),\,u\succcurlyeq u_r}\psi(Z^u(t),\mathbf{Z}(t))G((Z^u(s),\mathbf{Z}(s))_{s\leq t})\Big)\\ &= \psi(r,\mathbf{v})\mathbb{E}\left(\mathbf{1}_{\{\widehat{T}_{\mathrm{Exp}}>t\}}\,e^{\int_0^t\lambda(Y(s),\mathbf{V}(s))ds}\,G((Y(s),\mathbf{V}(s))_{s\leq t})\right).\end{aligned}\tag{6}$$

Indeed, we can apply Theorem 1 to

$$F(\mathrm{tree}_t,u) = \#\{v\in\mathfrak{g}(t):\,v\succcurlyeq u_r\}\,\psi(z^u(t),\mathbf{z}(t))\,G((z^u(s),\mathbf{z}(s))_{s\leq t}),\quad p_u(\mathfrak{t}) = \frac{\mathbf{1}_{u\in\mathfrak{g}(t),\,u\succcurlyeq u_r}}{\#\{v\in\mathfrak{g}(t):\,v\succcurlyeq u_r\}},$$

where tree_t is a tree with life length $t \geq 0$, $\mathfrak{g}(t)$ is the set of labels alive at time t in this tree, $\mathbf{z}(s)$ is the type composition at time $s \leq t$ of the population and $z^u(s)$ the type of the ancestor of individual u alive at time $s \leq t$. We observe that $\mathbb{E}\left(\mathbf{1}_{T_{\text{Exp}}>t,\, \mathbb{G}(t)\neq\varnothing}\, F(\mathcal{T}(t), U(t))\right)$ gives the left hand side of (6) by exploiting the law $p(\mathcal{T}(t))$ of $U(t)$ conditionally on $\mathcal{T}(t)$, while $\mathbb{E}\left(\mathcal{W}(t)\, F(\mathcal{A}(t), E(t))\right)$ yields the right hand side of (6) by conditioning by $E(0) = u_r$. Identity (6) proves the first identity of the proposition by considering marginal functions at time t and dividing by ψ. It also yields the second one by summation over initial individuals, which ends the proof. □

Let us remark that (6) amounts to a spine construction with initial condition $E(0) = e, Y(0) = r$, which focuses on the lineages of individuals whose initial ancestor is u_r. This would provide an alternative proof of the previous proposition. We complement this result by the following one:

Proposition 2. *Let $\psi \in \mathfrak{D}_{\mathcal{G}}$. If $T_{\text{Exp}} = +\infty$ p.s. and $\widehat{T}_{\text{Exp}} = +\infty$ p.s., then*

$$M(t) = \sum_{u\in\mathbb{G}(t)} e^{-\int_0^t \lambda(Z^u(s),\mathbf{Z}(s))\, ds}\, \psi(Z^u(t), \mathbf{Z}(t))$$

is a non-negative martingale with respect to the filtration $(\mathcal{F}_t)_{t\geq 0}$ generated by the original process Z. Furthermore, it converges a.s. to $W \in [0, \infty)$.

The case when the semigroup M has a positive eigenfunction (harmonic function) allows to simplify the exponential term, since λ is then constant. It is of particular interest and will be exploited in applications of the next sections. We refer to [4,38] and references therein for general results ensuring existence and/or uniqueness of eigenelements of positive semigroup in related contexts.

Proof. The initial condition $\mathfrak{x}$ is fixed and omitted in notation. The fact $T_{\text{Exp}} = +\infty$ p.s and Proposition 1 applied to

$$G((Z^u(s), \mathbf{Z}(s))_{s\leq t}) = e^{-\int_0^t \lambda(Z^u(s),\mathbf{Z}(s))ds}\psi(Z^u(t), \mathbf{Z}(t))$$

ensure that

$$\langle \mathbf{v}, \psi(., \mathbf{v})\rangle \mathbb{P}\left(\widehat{T}_{\text{Exp}} > t\right) = \mathbb{E}\left(\sum_{u\in\mathbb{G}(t)} e^{-\int_0^t \lambda(Z^u(s),\mathbf{Z}(s))ds}\psi(Z^u(t), \mathbf{Z}(t))\right) \tag{7}$$

for any $t \geq 0$. This identity guarantees the integrability of M. Similarly Markov property and (6) yield for u, t fixed, on the event $u \in \mathbb{G}(t)$,

$$\mathbb{E}\left(\sum_{v\in\mathbb{G}(t+s),\, v\succcurlyeq u} e^{-\int_t^{t+s} \lambda(Z^u(\tau),\mathbf{Z}(\tau))d\tau}\psi(Z_v(t+s), \mathbf{Z}(t+s)) \,\middle|\, \mathcal{F}_t\right) = \psi(Z^u(t), \mathbf{Z}(t))$$

since $\widehat{T}_{\text{Exp}} = \infty$ a.s. We get

$$\mathbb{E}(M(t+s)|\mathcal{F}_t) = \sum_{u\in\mathbb{G}(t)} e^{-\int_0^t \lambda(Z^u(\tau),\mathbf{Z}(\tau))d\tau}\psi(Z^u(t), \mathbf{Z}(t)) = M(t),$$

which proves the proposition. □

Let us observe from (7) that under the condition $T_{\mathrm{Exp}} = +\infty$ p.s, the fact that M is a martingale (and not only a local martingale) is equivalent to $\widehat{T}_{\mathrm{Exp}} = +\infty$ a.s. Besides, the limit W may degenerate to 0. In the case of branching processes, the criterion for non-degeneracy is the $L \log L$ condition for reproduction law, coming from Kesten and Stigum theorem. In Section 3.2, we deal with a counterpart with interactions.

3. Single type density dependent Markov process and neutral evolution

In this section, we consider single type populations and some issues which have originally motivated this work. In that case, when the size of the population is $z \in \mathbb{N}$, each individual branches and is replaced by k individuals with rate $\tau_k(z)$, for $k \in \mathbb{N}_0$. We do not use bold letters in this section since there is a single type and $(Z(t))_{t\geq 0}$ is the jump Markov process on $\mathbb{N}_0$ giving the population size along time. It jumps from z to $z + k - 1$ at rate $z\tau_k(z)$.

We consider $\psi : \mathbb{N} \to (0, \infty)$ and specify the ψ-spine construction in this single type setting. The distinguished individual is replaced by $k \in \mathbb{N}$ individuals at rate

$$\widehat{\tau}_k^{\star}(z) = k\tau_k(z)\frac{\psi(z-1+k)}{\psi(z)} \qquad (z \geq 1).$$

Among these k offsprings, each individual may become the new spine with probability $1/k$. The individuals but the spine branch and are replaced by $k \in \mathbb{N}_0$ individuals at rate

$$\widehat{\tau}_k(z) = \tau_k(z)\frac{\psi(z-1+k)}{\psi(z)} \qquad (z \geq 2).$$

We observe that the size V of the population in the ψ-spine construction is a density dependent Markov process with transition rates from z to $z + k - 1$ equal to

$$(k+z-1)\tau_k(z)\frac{\psi(z-1+k)}{\psi(z)} \qquad (z \geq 1).$$

Thus, the population size V evolve with individual branching rates $\tau_k(z)\psi(z-1+k)/\psi(z)$, plus additional size depend immigration, where $k \geq 2$ immigrants arrive in the population of size $z \geq 1$ at rate $(k-1)\,\tau_k(z)\,\psi(z-1+k)/\psi(z)$. Generator $\mathcal{G}$ is now defined for real valued functions f on $\mathbb{N}$ and for $z \geq 1$

$$\mathcal{G}f(z) = \sum_{k\in\mathbb{N}_0} \tau_k(z)(z+k-1)f(z+k-1) - z\tau(z)f(z).$$

Consequently, for single type population the function $\lambda = \mathcal{G}\psi/\psi$ becomes for $z \geq 1$,

$$\lambda(z) = \frac{\mathcal{G}\psi(z)}{\psi(z)} = \sum_{k\in\mathbb{N}_0} \tau_k(z)(z+k-1)\frac{\psi(z+k-1)}{\psi(z)} - z\tau(z).$$

3.1. Harmonic function

Exchangeability in the single type case suggests the choice $\psi(z) = 1/z$ for $z \geq 1$. We get $\lambda(z) = 0$ if $z \geq 2$ and $\lambda(1) = -\tau_0(1)$. In particular the inverse function is an eigenelement of $\mathcal{G}$ when the process

cannot reach (and be absorbed) in 0. More precisely, if $\tau_0(1) = 0$ we obtain that the function λ is null and $\mathcal{W}(t) = \mathbf{1}_{T_{\mathrm{Exp}}>t}$ a.s. Theorem 1 becomes, for uniform sampling $U(t)$ at time t:

Proposition 3. *Let $\tau_k(z) \in \mathbb{R}_+$ for $z \geq 1$ and $k \geq 0$ with $\tau_0(1) = 0$. Consider the Markov process Z on $\mathbb{N}$ whose jump rate from z to $z + k - 1$ is equal to $z\tau_k(z)$ for $z \geq 1$ and $k \geq 0$. Let $\mathcal{T}$ be the associated tree and $(\mathcal{A}, E)$ be the $1/z$-spine construction associated to these rates as defined in Section 2. Let $t \geq 0$ and $U(t)$ a random variable in $\mathcal{U}$ such that $\mathbb{P}(U(t) = e|\mathcal{T}(t)) = 1/Z(t)$ a.s. for any $e \in \mathbb{G}(t)$.*

Then, $\mathbf{1}_{T_{\mathrm{Exp}}>t}(\mathcal{T}(t), U(t))$ is distributed as $\mathbf{1}_{\widehat{T}_{\mathrm{Exp}}>t}(\mathcal{A}(t), E(t))$.

This $1/z$-spine construction consists here in a single type density dependent Markov process with a distinguished individual. Individual jump rates given respectively for the spine and off the spine by

$$\widehat{\tau}_k^\star(z) = k\,\tau_k(z)\frac{z}{z-1+k}, \qquad \widehat{\tau}_k(z) = \tau_k(z)\,\frac{z}{z-1+k}$$

for $z \geq 1, k \geq 0$. We can observe here that Z and V are identically distributed, since $\widehat{\tau}_k^\star(z) + (z-1)\widehat{\tau}_k(z) = z\tau_k(z)$. The last proposition goes beyond that by describing a uniform sample.

We give now a useful consequence of the previous proposition about ancestral lineage of samples. We consider the case when the size of the population of the spine construction $V(t) =_{law} Z(t)$ converges in law to a stationary distribution $\pi = (\pi_z)_{z\geq 1}$. Then, the number of branching events with k offsprings along the ancestral lineage of a uniform sample in $\mathbb{G}(t)$ grows linearly with rate

$$\widehat{\pi}_k = k \sum_{z\geq 1} \pi_z\,\tau_k(z)\,\frac{z}{z-1+k}.$$

A growth fragmentation model with competition. We consider a neutral model of dividing cells including competition, which induces death of cells. The mass of the cell grows during its life at a fixed exponential speed, and two mechanisms may regulate this mass: division (random splitting of the mass) and death (with individual death rate of cells increasing with total number of cells). Without interactions, for branching structures, such processes have received lots of attention, including deterministic, random and structured frameworks. We refer e.g. to [4,9,10,13,37] and references therein. In our model here, we assume that cells divide in two daughter cells or die, i.e. for $z \geq 1$:

$$b_z = \tau_2(z), \quad d_z = \tau_0(z), \quad \tau_1(z) = \tau_k(z) = 0 \quad \text{for } k \geq 3. \tag{8}$$

We assume also that the individual birth rate is bounded and death is only caused by competition:

$$\sup_{z\geq 1} b_z \leq \overline{b}, \qquad d_1 = 0. \tag{9}$$

So Z is a birth and death process and well defined on $\mathbb{R}_+$ (no explosion a.s.) and positive for any time.

Each cell is now characterized by a size in $\mathbb{R}_+$ and grows at exponential rate $r > 0$. Let us denote by $(\zeta_u(t))_{u\in\mathbb{G}(t)}$ the process giving the size of each cell alive at time t. Thus, between two jumps (division or death) of the cell population,

$$\zeta_u'(t) = r\zeta_u(t).$$

When the cell dies, its mass is lost. When it divides, it is shared randomly between each daughter cell, using a random fraction $F \in (0,1)$ a.s. More precisely, we draw an i.i.d. family of r.v. $(F_u)_{u\in\mathcal{U}}$ distributed as F and when cell u divides at time t with mass $\zeta_u(t-)$, its two daugthers get masses

$$(\zeta_{(u,1)}(t), \zeta_{(u,2)}(t)) = (F_u\zeta_u(t-), (1-F_u)\zeta_u(t-)).$$

Without loss of generality, we assume that F is distributed as $1-F$. We refer to [5,37] for similar constructions in general context of branching processes. We start for simplicity from a single cell with size $\zeta_0 > 0$: $Z(0) = 1$, $\zeta_1(0) = \zeta_0$. Let us give a trajectorial description of the population process together with the spine individual. We use a Poisson representation for constructing the original birth and death process Z, given by a Poisson point measure $\mathcal{N}$ on $\mathbb{R}_+^2 \times (0,1)$ with intensity $dsdu\mathbb{P}(F \in df)$. For convenience, we use the same measure for the $1/z$-spine construction. More precisely, we define the process $(Z(t), \zeta^\star(t))_{t\geq 0}$ as the unique strong solution of the following stochastic differential equation

$$Z(t) = 1 + \int_0^t \int_{\mathbb{R}_+^2} \left(\mathbf{1}_{u \leq Z(s-)b_{Z(s-)}} - \mathbf{1}_{Z(s-)b_{Z(s-)} < u \leq Z(s-)(b_{Z(s-)}+d_{Z(s-)})} \right) \mathcal{N}(ds, du, df),$$

$$\zeta^\star(t) = \zeta_0 + \int_0^t r\zeta^\star(s)\, ds - \int_0^t \int_{\mathbb{R}_+\times(0,1)} (1-f)\zeta^\star(s) \mathbf{1}_{u \leq 2b_{Z(s-)}Z(s-)/(Z(s-)+1)} \mathcal{N}(ds, du, df).$$

Existence and strong uniqueness are classical and we refer e.g. to [6,23]. In words, $\zeta^\star$ is a Markov process growing exponentially at speed r, which undergoes multiplicative jumps distributed as F. These jumps occur at the birth rate along the spine, which itself lives under population Z. Non explosion and survival of the original process are guaranteed by (8)-(9) and Proposition 3 yields the following result. We let again $U(t)$ be a uniform choice among $\mathbb{G}(t)$, which is here also independent of $(\zeta_u(s))_{s\geq 0, u\in\mathbb{G}(s)}$ conditionally on $\mathbb{G}(t)$.

Proposition 4. *Under Conditions* (8)-(9)*, for any* $t \geq 0$*,* $(Z(t), \zeta_{U(t)}(t))$ *is distributed as* $(Z(t), \zeta^\star(t))$*.*

We stress that this identity in law holds (only) for fixed time t, not for the full processes. This result allows to use Markov techniques to study the regulation of the size of cells through a typical (uniformly chosen) lineage. In particular, we can state here a new transition phase exploiting Birkhoff ergodic theorem, when the number of cells is regulated by competition.

Corollary 1. *Assume that* (8)-(9) *hold and that the Markov process* Z *is irreducible and positive recurrent on* $\mathbb{N}$*. Then* $Z(t)$ *converges in law to the unique stationary distribution* $\pi = (\pi_z)_{z\geq 1}$ *as* t *tends to infinity. We set*

$$\widehat{\pi} = 2\sum_{z\geq 1} \pi_z b_z \frac{z}{z+1}$$

and assume also

$$\mathbb{E}(\log(F)^2) < \infty. \tag{10}$$

i) If $r < \mathbb{E}(\log(1/F))\widehat{\pi}$*, then* $\zeta^\star(t)$ *tends a.s. to* 0 *as* $t \to \infty$ *and*

$$\lim_{t\to\infty} \max\{\zeta_u(t) : u \in \mathbb{G}(t)\} = 0 \quad \textit{in probability.}$$

ii) If $r > \mathbb{E}(\log(1/F))\widehat{\pi}$*, then* $\zeta^\star(t)$ *tends a.s. to infinity as* $t \to \infty$ *and*

$$\lim_{t\to\infty} \min\{\zeta_u(t) : u \in \mathbb{G}(t)\} = +\infty \quad \textit{in probability.}$$

We refer to [25,26] for explicit conditions for positive recurrence of birth and death processes.

Proof. Recalling the SDE representation of $\zeta^\star$ given above, we have

$$\log(\zeta^\star(t)) = \log(\zeta_0) + rt + \int_0^t \int_{\mathbb{R}_+\times(0,1)} \log(f)\mathbf{1}_{u\le g(Z(s-))}\,\mathcal{N}(ds,du,df),$$

where $g(z) = 2b_z z/(z+1)$. The classification and asymptotic behavior of $\zeta^\star$ is inherited from ergodic averaging of Birkhoff theorem. Indeed, writing $\alpha = \mathbb{E}(\log(F))$,

$$\log(\zeta^\star(t)) = \log(\zeta_0) + rt + \alpha\int_0^t g(Z(s))ds + M(t),$$

where, by denoting $\widetilde{\mathcal{N}}$ the compensated measure of $\mathcal{N}$,

$$M(t) = \int_0^t \int_{\mathbb{R}_+\times(0,1)} \log(f)\mathbf{1}_{u\le g(Z(s-))}\,\widetilde{\mathcal{N}}(ds,du,df).$$

Birkhoff theorem for continuous time Markov processes [39] ensures that

$$\frac{1}{t}\int_0^t g(Z(s))ds \overset{t\to\infty}{\longrightarrow} \sum_{z\ge1} g(z)\pi_z \qquad \text{a.s.}$$

since g is bounded by Assumption (9). Besides $(M(t))_{t\ge0}$ is a martingale with bounded quadratic variation on finite time intervals by Assumption (10). We deduce that $M(t)/t \overset{t\to\infty}{\longrightarrow} 0$ a.s. and we can conclude that $\log(\zeta^\star(t))$ tends to $+\infty$ or $-\infty$ depending on the fact that $r + \alpha\sum_{z\ge1} g(z)\pi_z$ is positive or negative.

We conclude on the original process by using Proposition 4. Indeed, let $\varepsilon > 0$ and $A > 0$,

$$\mathbb{P}\left(\max\{\zeta_u(t) : u\in\mathbb{G}(t)\}\ge\varepsilon, \#\mathbb{G}(t)\le A\right) \le A\mathbb{P}\left(\zeta_{U(t)}(t)\ge\varepsilon\right) = A\mathbb{P}\left(\zeta^\star(t)\ge\varepsilon\right)$$

and the right hand tends to 0 if $r < \mathbb{E}(\log(1/F))\widehat{\pi}$. We conclude for i) by letting A go to infinity and ε go to 0 and by using that $\#\mathbb{G}(t) = Z(t)$ is stochastically bounded. The other case is treated similarly. □

Let us comment briefly this result and the proof. The assumptions of boundedness of the individual birth rate b_z and the second moment of $\log F$ could be probably relaxed using finer ergodic techniques. The critical case is interesting. We expect that in general $\zeta^\star$ oscillates a.s. and that for any $\varepsilon > 0$,

$$\limsup_{t\to\infty}\mathbb{P}(\max\{\zeta_u(t) : u\in\mathbb{G}(t)\}\le\varepsilon) = 1, \quad \limsup_{t\to\infty}\mathbb{P}(\min\{\zeta_u(t) : u\in\mathbb{G}(t)\}\ge 1/\varepsilon) = 1.$$

We illustrate now Corollary 1 with a classical logistic competition model and the criterion becomes explicit. The individual birth rate is fixed and equals to $b > 0$ and the competition coefficient is $c > 0$:

$$b_z = b, \qquad d_z = c(z-1) \qquad (z\ge1).$$

The stationary probability π of the population size is

$$\pi_z = \frac{1}{e^{b/c}-1}\left(\frac{b}{c}\right)^z\frac{1}{z!} \qquad (z\ge1).$$

The criterion for the regulation of the growth of mass can be given in terms of the parameters b (birth) and c (competition) and r (growth) and F (random repartition at division):

$$r < 2b\,f(b/c)\,\mathbb{E}(\log(1/F)), \quad \text{with } f(y) = (1 - 1/y + 1/(e^y-1)).$$

Letting c tend to 0 allows to recover the expected criterion for branching process, with classical accelerated rate of branching $2b$ along a typical lineage, see e.g. [6]. Both division (by splitting) and competition (by killing) participate to the regulation of the growth of the cell mass. The value b/c is linked to a carrying capacity, i.e. a value above which the population size tend to decrease. Besides f is increasing with respect to y. Competition destroys cells and could help with regulation but its also makes the carrying capacity decrease and at end it plays against the regulation of the size.

Allowing extinction. We mention that in the case when $\tau_0(1) \neq 0$, an analogous result can be stated conditionally on the survival of the process. The eigenfunction h is then non-explicit in general, but can be written as $h_0(z)/z$ for $z \geq 1$, where h_0 is the harmonic function of the killed process. It allows to describe sampling in the quasi-stionnary regime, i.e. when the process conditioned to survive at a given time converges in law. In that case the process V survives a.s. but the original process dies out.

3.2. $L \log L$ criterion for branching processes with interactions

For branching processes, spine construction yields a conceptual approach for the Kesten-Stigum criterion of non-degeneracy of the limiting martingale [36]. For a Galton-Watson process Z with reproduction r.v. L, $W = \lim_{n\to\infty} Z_n/\mathbb{E}(L)^n$ is a.s. positive on the survival event iff $\mathbb{E}(L\log(L)) < \infty$. The same criterion holds for continuous time Galton-Watson, with similar approaches. We are interested in the counterpart of this criterion and approach when reproduction is density dependent. We follow the ideas of [36]. We recall that $\tau_0(z) < \infty$ for any $z \geq 1$ and consider the following first moment assumption:

$$\sum_{k\geq 1} k\tau_k(z) < \infty \quad (z \geq 1). \tag{11}$$

We can thus achieve the spine construction with $\psi = 1$ and set for $z \geq 1$,

$$\lambda(z) = \sum_{k\geq 0}(k-1)\tau_k(z).$$

We first get from Proposition 2 or could directly check that

$$M(t) = \exp\left(-\int_0^t \lambda(Z(s))ds\right) Z(t)$$

is a non-negative martingale which converges a.s. to a finite non-negative r.v.

$$W = \lim_{t\to\infty} M(t).$$

Similarly, we introduce

$$N(t) = \exp\left(-\int_0^t \lambda(V(s))ds\right) V(t),$$

where V is the size of the population in the **1**-spine construction. Theorem 1 yields the following expression of $\mathbb{E}(W)$ and a way to know when W is degenerate:

Lemma 2. *Assume* (11) *and that* $T_{\mathrm{Exp}} = +\infty$ *and* $\widehat{T}_{\mathrm{Exp}} = +\infty$ *a.s. Then, for any* $z \geq 1$,

$$\mathbb{E}_z(W) = z\,\mathbb{P}_z\left(\sup_{t\in[0,\infty)} N(t) < \infty\right).$$

Besides, $V-1$ is a Markov jump process on $\mathbb{N}_0$ whose transition rate from z to $z+k-1$ is equal to $k\tau_k(z+1)+z\tau_k(z+1)$ for $z\geq 0, k\geq 0$.

The process $V-1$ can thus be seen as the original density dependent Markov process plus a density dependent immigration of $k-1$ individuals with rate $k\,\tau_k(z)$. This extends the result for branching processes when λ and τ are constant and $M(t)=\exp(-\lambda t)Z(t)$.

Proof. We let $t\geq 0$ and $K>0$. We apply Theorem 1 with $\psi=1$ to function F defined by

$$F(\mathrm{tree}_t,e)=F(\mathrm{tree}_t)=\#\mathfrak{g}(t)\,e^{-\int_0^t\lambda(\#\mathfrak{g}(s))ds}\,\mathbf{1}_{\left\{\sup_{s\leq t}\left\{\#\mathfrak{g}(s)\,\exp\left(-\int_0^s\lambda(\#\mathfrak{g}(v))dv\right)\right\}\leq K\right\}}$$

where tree_t is a tree of life lenght t; or we can apply (7) as well and get

$$\mathbb{E}\left(\mathbf{1}_{\{\sup_{u\in[0,t]}M(u)\leq K\}}\,M(t)\right)=\mathbb{P}\left(\sup_{u\in[0,t]}N(u)\leq K\right).$$

Bounded and monotone limit as $t\to\infty$ ensure

$$\mathbb{E}\left(\mathbf{1}_{\{\sup_{u\in[0,\infty)}M(u)\leq K\}}\,W\right)=\mathbb{P}\left(\sup_{u\in[0,\infty)}N(u)\leq K\right).$$

We conclude the proof of the first part by monotone limit letting K go to infinity. For the second part, we observe that V jumps from z to $z+k-1$ with rate $\widehat{\tau}_k^\star(z)+(z-1)\widehat{\tau}_k(z)=k\tau_k(z)+(z-1)\tau_k(z)$. □

Let us derive moment conditions which guarantee that the limiting martingale is non-degenerate. It has been largely studied for Galton-Watson processes, even for infinite number of types and we refer to [3]. For interactions, it has been also studied at least in the discrete framework, for controlled Galton-Watson processes, and we refer to [27,32]. In these works, a monotonicity assumption or regularity and convexity assumptions are required. Such assumptions seem to be partially relaxed here. Besides, the method can be extended to multitype setting. We focus here on the case where the process grows exponentially but density dependence affects the growth rate. Competition can make it decrease and cooperation may make it increase, while non monotone behavior appear in particular with Allee effect.

Proposition 5. *Assume that*

$$\inf_{z\geq 1}\lambda(z)>0,\qquad \sum_{k\geq 1}k(\log(k)+1)\sup_{z\geq 1}\tau_k(z)<\infty. \tag{12}$$

Then $T_{\mathrm{Exp}}=+\infty$ and $\widehat{T}_{\mathrm{Exp}}=+\infty$ a.s. and for any for $z\geq 1$, $\mathbb{E}_z(W)=z$.

The second assumption is stronger than (11). The uniformity assumptions can be partially relaxed and required only for z large enough under some irreducibility condition. The $L\log L$ moment condition is known to be necessary for positivity of $\mathbb{E}(W)$ in some cases including branching processes.

Proof. We notice that the finiteness of $\sum_{k\geq 1}k\,\sup_{z\geq 1}\tau_k(z)$ yields an upperbound of the growth rate of the population size the original process Z. It guarantees that $T_{\mathrm{Exp}}=\infty$ a.s. Let us deal with the **1**-spine construction and localize the process by considering the stopping times $T^m=\inf\{t\geq 0: V_t\geq m\}$ for

$m \geq 1$. We separate the component coming from immigration and give a trajectorial representation of $\Xi = V - 1$. For $t \leq T^m$, it is defined as the unique strong solution of the following SDE

$$\Xi(t) = \Xi(0) + \int_0^t \int_{\mathbb{R}_+ \times \mathbb{N}} \mathbf{1}_{\{u \leq \Xi(s-)\tau_k(\Xi(s-)+1)\}} (k-1) \mathcal{N}(ds, du, dk) + \int_0^t \int_{\mathbb{R}_+ \times \mathbb{N}} \mathbf{1}_{\{u \leq k\tau_k(\Xi(s-)+1)\}} (k-1) \mathcal{N}_I(ds, du, dk),$$

where we use two independent Poisson point measures, $\mathcal{N}$ and $\mathcal{N}_I$, with intensity $ds\, du\, \mathfrak{n}(dk)$ on $\mathbb{R}_+^2 \times \mathbb{N}$, where $\mathfrak{n} = \sum_{k \in \mathbb{N}_0} \delta_k$ is the counting measure, see e.g. [6]. Defining

$$Q(t) = \Xi(t) e^{-\int_0^t \lambda(\Xi(s))ds} = N(t) - e^{-\int_0^t \lambda(\Xi(s))ds},$$

we get for $t \leq T^m$,

$$Q(t) = Q(0) + \int_0^t \int_{\mathbb{R}_+ \times \mathbb{N}} \mathbf{1}_{\{u \leq \Xi(s-)\tau_k(\Xi(s-))\}} (k-1) e^{-\int_0^s \lambda(\Xi(v))dv} \widetilde{\mathcal{N}}(ds, du, dk) + \int_0^t \int_{\mathbb{R}_+ \times \mathbb{N}} \mathbf{1}_{\{u \leq k\tau_k(\Xi(s-))\}} (k-1) e^{-\int_0^s \lambda(\Xi(v))dv} \mathcal{N}_I(ds, du, dk),$$

where $\widetilde{\mathcal{N}}$ is the compensated measure of $\mathcal{N}$. Thus, conditionally on $\mathcal{N}_I$, $N_1(. \wedge T_m)$ is a submartingale. Besides, writing $c = \inf \lambda > 0$ and $\overline{\tau}_k = \sup_{z \geq 1} \tau_k(z) < \infty$, we get for any $m \geq 1$ and $t \geq 0$

$$\mathbb{E}_z(Q(t \wedge T^m) \,|\, \mathcal{N}_I) \leq z - 1 + \int_0^t \int_{\mathbb{R}_+ \times \mathbb{N}} 1_{u \leq k\overline{\tau}_k} (k-1) e^{-cs} \mathcal{N}_I(ds, du, dk).$$

Let us check now that the right hand side is a.s. bounded with respect to t. Indeed

$$\int_0^\infty \int_{\mathbb{R}_+ \times \mathbb{N}} 1_{u \leq kp_k} (k-1) e^{-cs} \mathcal{N}_I(ds, du, dk) = \sum_{i \geq 0} \widehat{L}_i e^{-cS_i} \tag{13}$$

is a compound Poisson process, where $(S_{i+1} - S_i : i \geq 0)$ are i.i.d. exponential random variables with parameters $\mu = \sum_{k \geq 2} k\overline{\tau}_k \in [0, \infty)$ and $(\widehat{L}_i : i \geq 0)$ are i.i.d random variables with the size bias distribution $\mathbb{P}(\widehat{L} = k-1) = k\overline{\tau}_k/\mu$ for $k \geq 2$. By Borel Cantelli lemma, assumption $\sum_{k \geq 2} \log(k) k\overline{\tau}_k < \infty$ ensures that $\limsup_{n \to \infty} \log(\widehat{L}_n)/n = 0$ p.s. Adding that $c > 0$ and that S_i grows linearly a.s. to infinity as i tends to infinity, the series in (13) are a.s. finite.

We get then that V is not explosive by using that λ is upper bounded and letting $m \to \infty$. By Fatou's lemma, we obtain that $\sup_{t \geq 0} \mathbb{E}_z(Q(t) \,|\, \mathcal{N}_I) < \infty$ a.s. Thus, the quenched submatingale $(Q(t))_{t \geq 0}$ converges to a finite random variable a.s. as $t \to \infty$. So does $N(t)$, towards the same limit, since $\inf \lambda > 0$. Lemma 2 allows then to conclude. □

In particular, we can describe the growth of the process Z. When the growth rate $\lambda(z)$ tends to b as $z \to \infty$ fast enough, the robustness of exponential growth of Galton-Watson process is expected. It has already been studied in the discrete setting and needs in general some technical conditions, see the works mentioned above and also Klebaner [28] for the counterpart in discrete time.

Corollary 2. *Assume* (12) *and* $\lim_{z\to\infty}\lambda(z) = b > 0$. *Then*

$$\mathbb{P}\left(\lim_{t\to\infty}\frac{\log(Z_t)}{t} = b\right) > 0.$$

Assuming further that there exists $a > 1$ *such that* $|\lambda(z) - b| \le C\log(z+1)^{-a}$ *for any* $z > 0$, *then*

$$\mathbb{P}\left(\lim_{z\to\infty} e^{-bt}\, Z(t) \in (0,\infty)\right) > 0.$$

A natural question now is to know if the limiting martingale is a.s. positive on the survival event. It is well known for branching processes. We expect extensions to similar processes with interactions but size dependence may make the classification more delicate.

Proof. Recall that $W = \lim_{t\to\infty} Z(t)\exp(-\int_0^t \lambda(Z(s))ds)$ a.s. and the previous proposition ensures that $\mathbb{P}(W > 0) > 0$. Then Z survives with positive probability and then goes to infinity. On this event $\{W > 0\}$, $\lambda(Z_t)$ tends to b and $\lim_{t\to\infty}\log(Z_t)/t = b$. Besides writing $r(z) = \lambda(z) - b$, $\int_0^\infty |r(Z_t)|dt < \infty$ a.s. since $|r(Z_t)| \le C\log(\exp(bt/2)+1)^{-a}$ for t large enough. It ensures that $\exp(\int_0^t \lambda(Z_s)ds)$ is equivalent to $\exp(bt)$ on $\{W > 0\}$ and ends the proof. □

4. Applications to multitype processes

Let us turn to structured populations with a finite number of types. Explicit computations of eigenelements seem to be more delicate in general than in the single type considered above. We consider two simple relevant regimes for population models. First, random but bounded population size, where conditions for existence and uniqueness of positive eigenelement are well known from Perron-Frobenius theory. Second, we consider sampling in the large population approximation.

4.1. Finite irreducible case

We consider a simple case relevant for applications: the number of types is finite and the size of the population is bounded. More explicitly, we assume that $\#\mathcal{X} < \infty$ and that there exists $\bar{z} > 0$ such that

$$(\mathbf{A}) \qquad \text{For all } (\mathbf{z}, x, \mathbf{k}) \in \mathcal{Z}\times\mathcal{X}\times\mathcal{Z} \text{ such that } \|\mathbf{z}+\mathbf{k}-\mathbf{e}(x)\|_1 > \bar{z}, \quad \tau_{\mathbf{k}}(x,\mathbf{z}) = 0.$$

In words, the total size of the population can not go beyond $\bar{z}$. This quantity may correspond to a carrying (or biological) capacity of the environment where population lives. The corresponding state space with a distinguished individual is denoted by $\mathcal{S}$ defined by

$$\mathcal{S} = \{(r,\mathbf{v}) \in \mathcal{X}\times\mathbb{N}_0^{\mathcal{X}} : \mathbf{v}_r \ge 1, \|\mathbf{v}\|_1 \le \bar{z}\} \subset \overline{\mathcal{Z}}.$$

We assume that the initial condition is a deterministic vector $\mathbf{Z}(0) = \mathbf{v}$ of $\mathbb{N}^{\mathcal{X}}$ such that $\|\mathbf{v}\|_1 \le \bar{z}$. We observe that boundedness ensures that the process a.s. does not explode. We recall that $\mathfrak{x} = \mathfrak{x}(\mathbf{v})$ is the finite initial population whose types are counted by $\mathbf{v}$ and u_r a label of the population with type r. Besides, the positive semigroup M is defined by

$$M_t f(a) = M_t f(r,\mathbf{v}) = \mathbb{E}_{\mathfrak{x}(\mathbf{v})}\left(\sum_{y\in\mathcal{X}} \mathbf{Z}_y^{(u_r)}(t) f(y,\mathbf{Z}(t))\right)$$

for any non-negative function f on $\mathcal{S}$ and $a=(r,\mathbf{v})\in\mathcal{S}$. Similarly, the operator $\mathcal{G}$ is restricted to real functions f defined on $\mathcal{S}$ and defined for any $a=(x,\mathbf{z})\in\mathcal{S}$

$$\mathcal{G}f(a)=\sum_{\substack{\mathbf{k}\in\mathcal{Z}\\ \|\mathbf{z}+\mathbf{k}-\mathbf{e}(x)\|_1\le\bar{z}}}\tau_{\mathbf{k}}(x,\mathbf{z})\,\langle\mathbf{k},f(.,\mathbf{z}+\mathbf{k}-\mathbf{e}(x))\rangle$$

$$+\sum_{\substack{y\in\mathcal{X},\mathbf{k}\in\mathcal{Z}\\ \|\mathbf{z}+\mathbf{k}-\mathbf{e}(y)\|_1\le\bar{z}}}\tau_{\mathbf{k}}(y,\mathbf{z})(\mathbf{z}_y-\delta_y^x)f(x,\mathbf{z}+\mathbf{k}-\mathbf{e}(y))-\left(\sum_{y\in\mathcal{X}}\tau(y,\mathbf{z})\mathbf{z}_y\right)f(x,\mathbf{z}).$$

Functions on $\mathcal{S}$ can be identified to vectors indexed by $\mathcal{S}$, which is finite. The operator $\mathcal{G}$ is a positive linear operator on the finite dimensional space $\mathbb{R}^{\mathcal{S}}$ and can be identified to a finite square matrix. Under irreducibility conditions, Perron-Frobenius theorem ensures the existence (and uniqueness up to a positive constant) of a positive eigenfunction h for the semigroup M and its generator $\mathcal{G}$. Using the corresponding h-spine construction, we obtain a characterization of the ancestral lineage (or pedigree) of a typical individual, and in particular the ancestral types. We refer to [20,24] and references therein for similar results for branching processes using the eigenelements of the first moment semigroup. Function h corresponds to *reproductive value* in population dynamics or genetics.

We can now state and prove the result. Let us consider $t\ge 0$ and again a uniform choice $U(t)$ in $\mathbb{G}(t)$. We set for $a\in\mathcal{S}$ and $\mathbf{k}\in\mathcal{Z}$,

$$P_a(t)=\int_0^t\mathbf{1}_{(Z^{U(t)}(s),Z(s))=a}\,ds,\qquad N_{a,\mathbf{k}}(t)=\#\{u\preccurlyeq U(t):(Z^u,\mathbf{Z}^{u+})=a,\,\mathbf{K}^u=\mathbf{k}\},$$

where $Z_u(s)$ is the type of the unique ancestor of u at time s, $\mathbf{Z}^{u+}$ (respectively $\mathbf{K}^u$) is the composition of the population (respectively of offsprings of u) when u branches. In words, P_a records the time spent in state a by the ancestral lineage and $N_{a,\mathbf{k}}$ the number of branching events with offsprings $\mathbf{k}$.

Proposition 6. *Assume* (**A**) *and that for any $a,b\in\mathcal{S}$, $M_1\mathbf{1}_b(a)>0$. Then, there exists a unique triplet (λ,h,γ) such that $\lambda\in(-\infty,0]$ and $h,\gamma:\mathcal{S}\to(0,\infty)$ and $\sum_{a\in\mathcal{S}}\gamma(a)=\sum_{a\in\mathcal{S}}h(a)\gamma(a)=1$ and*

$$\mathcal{G}h=\lambda\,h,\quad \gamma\mathcal{G}=\lambda\,\gamma.$$

Moreover, writing $(\mathcal{A},E)$ the corresponding h-spine construction, for any $t\ge 0$ and any measurable non-negative function $F:\mathbb{T}\times\mathcal{U}\to\mathbb{R}$, we have for any non-empty initial condition $\mathfrak{x}$,

$$\mathbb{E}_{\mathfrak{x}}\left(\mathbf{1}_{\{\mathbb{G}(t)\neq\varnothing\}}F(\mathcal{T}(t),U(t))\right)=\langle\mathbf{v},h(.,\mathbf{v})\rangle e^{\lambda t}\,\mathbb{E}_{\mathfrak{x}}\left(\frac{1}{h(Y(t),\mathbf{V}(t))\,\|\mathbf{V}(t)\|_1}F(\mathcal{A}(t),E(t))\right).$$

Note that $\gamma\mathcal{G}=\lambda\,\gamma$ means that for any $b\in\mathcal{S}$, $\sum_{a\in S}\gamma(a)\mathcal{G}\mathbf{1}_b(a)=\lambda\gamma(b)$. Assumption $M_1\mathbf{1}_b(a)>0$ guarantees irreducibility of the population process $\mathbf{Z}$, with a distinguished particle. It is equivalent to

$$\forall(r,\mathbf{v})\in\mathcal{S},\,\forall(x,\mathbf{z})\in\mathcal{S},\quad \mathbb{P}_{\mathfrak{x}(\mathbf{v})}\left(\mathbf{Z}_x^{(u_r)}(1)>0,\,\mathbf{Z}(1)=\mathbf{z}\right)>0.$$

This irreducibility condition concerns the states where the population is alive (i.e. $\mathbf{z}\neq\mathbf{0}$). Let us illustrate this condition on the following spatial model with competition. Consider a finite number of sites with finite carrying capacities. On each site, the individuals give birth with positive rate, when it has not reached the carrying capacity, and dies with a positive rate. These individual rates may be dependent of the local and global density of individuals. Besides, each individual may move from one

site to another. This model satisfies the assumptions of the previous statement as soon as the motion of individuals (including their offsprings) is irreducible, i.e. when the graph of nodes whose oriented edges correspond to positive probability of transition at branching events is strongly connected.

Proof. The first point (uniqueness of normalized positive eigenelements, associated with the maximal eigenvalue) is guaranteed by Perron-Frobenius theorem. The fact that the eigenvalue λ is not positive is due to the fact that the process is bounded. The second part is then a consequence of Theorem 1, recalling that there is no explosion and that $\lambda = \mathcal{G}h/h$ is constant since h is an eigenvector of $\mathcal{G}$. □

The Markov process $(Y, \mathbf{V})$ takes values in a finite state space and the assumption and the positivity of h ensures that it is irreducible. We derive the following ergodic behavior, where the limiting law does not depend on the initial (non empty) condition $\mathfrak{x}$ (omitted in notation).

Corollary 3. *Under conditions of Proposition 6, $(Y(t), \mathbf{V}(t))$ converges in law to $\pi = (\pi(a))_{a\in\mathcal{S}}$ as $t \to \infty$, where $\pi(a) = h(a)\gamma(a)$ for $a \in \mathcal{S}$. Besides for any $a = (x, \mathbf{z}) \in \mathcal{S}$ and $\mathbf{k} \in \mathcal{Z}$ such that $\|\mathbf{z} + \mathbf{k} - \mathbf{e}(x)\|_1 \le \bar{z}$,*

$$\left(\frac{P_a(t)}{t}, \frac{N_{a,\mathbf{k}}(t)}{t}\right)_{|\mathbb{G}(t)\neq\varnothing} \longrightarrow (\pi(a)\,,\, \gamma(a)\,\tau_{\mathbf{k}}(a)\,\langle \mathbf{k}\,,\, h(.,\mathbf{z}+\mathbf{k}-\mathbf{e}(x))\rangle)$$

as $t \to \infty$, where the convergence of the couple holds in probability conditionally on the event $\mathbb{G}(t) \neq \varnothing$.

Proof. First, we recall that the generator of $(Y, \mathbf{V})$ is the h-Doob-transform of $\mathcal{G}$, i.e. $f \to \mathcal{G}(hf)/h - \lambda f$. We can then check that $(h(a)\gamma(a))_{a\in\mathcal{S}}$ is a stationary law, using that $\gamma\mathcal{G} = \lambda\gamma$. Uniqueness of stationary law holds by irreducibility and the first part is proved.

We consider now the h-spine construction $(\mathcal{A}, E)$ and we consider for $a = (x, \mathbf{z}) \in \mathcal{S}$ and $k \in \mathcal{Z}$,

$$N^{\star}_{a,\mathbf{k}}(t) = \#\{u \preccurlyeq E(t) : (V^u, \mathbf{V}^{u+}) = a, \widehat{\mathbf{K}}^u = \mathbf{k}\},$$

where $\widehat{\mathbf{K}}^u$ (respectively $\mathbf{V}^{u+}$) is the composition of the offsprings of the spine u (respectively the state of the population) when u branches. Then ergodic theorem ensures the a.s. convergence:

$$\lim_{t\to\infty} \frac{N^{\star}_{a,\mathbf{k}}(t)}{t} = \pi(a)\,\tau_{\mathbf{k}}(a)\,\frac{\langle \mathbf{k}, h(.,\mathbf{z}+\mathbf{k}-\mathbf{e}(x))\rangle}{h(a)} =: \widetilde{\pi}(a, \mathbf{k}). \tag{14}$$

We did not find the appropriate reference in continuous time but the proof can be achieved for instance by standard renewal argument (strong renewal theorem) using that the successive times when a Markov jump process is in a given state and make a given jump forms a renewal process, here with finite expected mean. The result is then a consequence of the previous proposition. Indeed for any $t \ge 0$ and F measurable and positive, we get

$$\mathbb{E}\left(\mathbf{1}_{\mathbb{G}(t)\neq\varnothing} F(N_{a,\mathbf{k}}(t))\right) = e^{\lambda t}\,\langle \mathbf{v}, h(.,\mathbf{v})\rangle \mathbb{E}\left(\frac{1}{h(Y(t), \mathbf{V}(t))\|\mathbf{V}(t)\|_1} F(N^{\star}_{a,\mathbf{k}}(t))\right)$$

and

$$\mathbb{E}\left(\mathbf{1}_{\mathbb{G}(t)\neq\varnothing}\right) = e^{\lambda t}\,\langle \mathbf{v}, h(.,\mathbf{v})\rangle \mathbb{E}\left(\frac{1}{h(Y(t), \mathbf{V}(t))\,\|\mathbf{V}(t)\|_1}\right).$$

Considering $F(n) = \mathbf{1}_{|n/t - \widetilde{\pi}(a,\mathbf{k})| \geq \varepsilon}$ for $\varepsilon > 0$ and using that h and $\mathbf{V}$ are bounded and taking the ratio of the two expectations, (14) yields

$$\mathbb{P}\left(|N_{a,\mathbf{k}}(t)/t - \widetilde{\pi}(a,\mathbf{k})| \geq \varepsilon \,\middle|\, \mathbb{G}(t) \neq \varnothing\right) \overset{t\to\infty}{\longrightarrow} 0.$$

The proof is analogous for the limit of $P_a(t)/t$ when $t \to \infty$. □

To get finer results on ancestral lineages with a spinal approach, one may be inspired from e.g. [11,20]. We also expect to extend results to infinite type space $\mathcal{X}$, using for instance [4,38].

4.2. Large population approximation

We consider in this section the deterministic regime appearing when the initial population is large and the process renormalized. The set of types $\mathcal{X}$ is still finite but the size of the population is not bounded. Our aim is to describe uniform sampling in classical dynamical systems for some macroscopic evolution of populations. The scaling parameter is denoted by $N \geq 1$ and corresponds to the order of magnitude of the size of the population, see [6,19,30] for general references. The space of types $\mathcal{X}$ is finite and the types of the initial population are given by

$$[N\mathbf{v}] = ([N\mathbf{v}_x], x \in \mathcal{X}),$$

for some fixed positive $\mathbf{v} \in (0,\infty)^{\mathcal{X}}$. Each individual with type $x \in \mathcal{X}$ living in a population $\mathbf{z} \in \mathbb{N}_0^{\mathcal{X}}$ is replaced by $\mathbf{k}$ offsprings at rate

$$\tau_{\mathbf{k}}^N(x,\mathbf{z}) = \tau_{\mathbf{k}}(x,\mathbf{z}/N),$$

where $\mathbf{z} \in \mathbb{R}_+^{\mathcal{X}} \to \tau_{\mathbf{k}}(x,\mathbf{z})$ is a continuous function. Let us denote as

$$\mathbf{x}_N = \{(u, x_u), u \in \mathfrak{g}_N\}$$

the labels and types of the initial population with type composition $[N\mathbf{v}]$.

Following the rest of the paper, we denote as $\mathbf{Z}^N$ the vector counting types in the population and $\mathcal{T}^N$ the tree associated to this process. For sake of simplicity and regarding our motivations from population models, we assume that

$$\textbf{(A1)} \qquad \sup_{x\in\mathcal{X},\,\mathbf{z}\in\mathbb{R}_+^{\mathcal{X}}} \sum_{\mathbf{k}\in\mathcal{Z},\,\|\mathbf{k}\|_1>1} \|\mathbf{k}\|_1^2\, \tau_{\mathbf{k}}(x,\mathbf{z}) < \infty,$$

$$\textbf{(A2)} \qquad \forall K > 0, \quad \sup_{x\in\mathcal{X},\,\mathbf{z}\in\mathcal{Z}_K} \tau(x,\mathbf{z}) < \infty,$$

where $\mathcal{Z}_K = \{\mathbf{z} \in \mathbb{R}_+^{\mathcal{X}} : \|\mathbf{z}\|_1 \leq K\}$ and $\tau(x,\mathbf{z}) = \sum_{\mathbf{k}\in\mathcal{Z}} \tau_{\mathbf{k}}(x,\mathbf{z})$. The ℓ^2 uniform condition in **(A1)** will guarantee that the contribution of the spine in the growth of the population size is vanishing as $N \to \infty$. **(A1)** and **(A2)** also ensure uniform bound on the growth rate and guarantee non explosion of the processes Z^N and V^N for fixed N. To ensure that $T_{\mathrm{Exp}}^N = \infty$ a.s., a ℓ^1 uniform bound in **(A1)** would have been enough. We observe that these assumptions allow non bounded individual death or motion rate. For instance, the death rate may tend to infinity with respect to the size of the population due to competition. These assumptions also ensure that the following size dependent growth matrix $A(\mathbf{z}) =$

$(A_{x,y}(\mathbf{z}))_{x,y\in\mathcal{X}}$ is well defined:

$$A_{x,y}(\mathbf{z}) = \sum_{\mathbf{k}\in\mathcal{Z}} \tau_{\mathbf{k}}(x,\mathbf{z})\mathbf{k}_y - \tau(x,\mathbf{z})$$

for $\mathbf{z} \in \mathbb{R}_+^{\mathcal{X}}$ and $x, y \in \mathcal{X}$.

We also assume that A is locally Lipschitz: for any $K > 0$, there exists M such that

$$\textbf{(A3)} \qquad \forall x, y \in \mathcal{X}, \quad \forall \mathbf{z}_1, \mathbf{z}_2 \in \mathcal{Z}_K, \qquad |A_{x,y}(\mathbf{z}_1) - A_{x,y}(\mathbf{z}_2)| \le M\|\mathbf{z}_1 - \mathbf{z}_2\|_1.$$

Thus $\mathbf{z} \to \mathbf{z}\,A(\mathbf{z})$ is locally Lipschitz on $\mathbb{R}_+^{\mathcal{X}}$. Using (**A1**) guarantees the non explosivity of the dynamical system associated to this vector filed. Cauchy Lipschitz theorem then ensures the existence and uniqueness of the solution $(\mathbf{z}(t,\mathbf{v}))_{t\ge 0}$ of the following ordinary differential equation on $\mathbb{R}_+$

$$\mathbf{z}'(t,\mathbf{v}) = \mathbf{z}(t,\mathbf{v})\,A(\mathbf{z}(t,\mathbf{v})), \quad \mathbf{z}(0,\mathbf{v}) = \mathbf{v}.$$

Under these assumptions, we know that $\mathbf{Z}^N/N$ converges in law in $\mathbb{D}(\mathbb{R}_+, \mathbb{R}_+^{\mathcal{X}})$ to the non-random process $\mathbf{z}(.,\mathbf{v})$ and refer to Theorem 2 in Chapter 11 of [19]. We are actually needing in the proof a counterpart for the spine construction, see below. Finally, we assume that the limiting dynamical system does not come too close to the extinction boundary in finite time:

$$\textbf{(A4)} \qquad \forall T > 0, \qquad \inf_{x\in\mathcal{X}, t\in[0,T]} \mathbf{z}_x(t,\mathbf{v}) > 0.$$

This assumption holds for many classical population models and allows us to consider functions ψ which go to infinity on the boundary.

We are interested in the limiting ψ-spine construction and consider a function ψ from $\mathcal{X} \times [0,\infty)^{\mathcal{X}}$ to $(0,\infty)$, such that for any $x \in \mathcal{X}$, $\psi_x : \mathbf{z} \in (0,\infty)^{\mathcal{X}} \to \psi(x,\mathbf{z})$ is continuously differentiable. Besides, we assume that for any $\varepsilon > 0$, there exists L such that for any $x \in \mathcal{X}$ and $\mathbf{z} \in (\varepsilon, 1/\varepsilon)^{\mathcal{X}}$ and $\mathbf{k} \in \mathbb{R}_+^{\mathcal{X}}$,

$$\| \psi(x,\mathbf{z}+\mathbf{k}) - \psi(x,\mathbf{z}) \|_1 \le L \| \mathbf{k} \|_1 . \tag{15}$$

The ψ-spine construction is initiated with a single individual, the root $E(0) = \varnothing$, whose type $Y(0)$ is chosen as follows:

$$\mathbb{P}(Y(0) = x) = \frac{\psi(x,\mathbf{v})}{\langle \mathbf{v}, \psi(.,\mathbf{v})\rangle} \qquad (x \in \mathcal{X}).$$

Let us explain informally why in this section the spine construction is restricted to one single initial individual. Indeed, the density dependance reduces to a deterministic effect when the size of the population goes to infinity, since the normalized process converges to the $\mathbf{z}(.,\mathbf{v})$. Like for propagation of chaos, in the large population approximation, the individuals behave independently and a (time inhomogeneous) branching property holds. Besides, when the limiting object $\mathbf{z}(.,\mathbf{v})$ converges to an equilibrium when times goes to infinity, this non-homogeneity actually vanishes, as discussed below.

Let us be more specific. The spine with type x branches with the following rate at time t

$$\widehat{\tau}_{\mathbf{k}}^{\star}(x,t,\mathbf{v}) = \tau_{\mathbf{k}}(x,\mathbf{z}(t,\mathbf{v})))\frac{\langle \mathbf{k}, \psi(.,\mathbf{z}(t,\mathbf{v}))\rangle}{\psi(x,\mathbf{z}(t,\mathbf{v}))},$$

while individuals with type x but the spine branch at time t with rate

$$\widehat{\tau}_{\mathbf{k}}(x,t,\mathbf{v}) = \tau_{\mathbf{k}}(x,\mathbf{z}(t,\mathbf{v})).$$

We use again the Ulam Harris Neveu notation to label individuals and denote by $\mathcal{A}_\star(t)$ the tree rooted in the spine. Observe also that (**A4**) and regularity of ψ ensure that $\psi(.,\mathbf{z}(t,\mathbf{v}))$ is bounded on finite time intervals. Using (**A1** – **A2**) then ensures that this spine construction is not explosive. Recall that $E(t)$ is the label of the spine at time t and set

$$\mathcal{G}f(x,\mathbf{z}) = \sum_{\mathbf{k}\in\mathcal{Z}} \tau_{\mathbf{k}}(x,\mathbf{z})\,\langle \mathbf{k}-\mathbf{e}(x), f(.,\mathbf{z})\rangle + \mathcal{L}f_x(\mathbf{z})$$

for $\mathbf{z}\in(0,\infty)^{\mathcal{X}}$ and $x,y\in\mathcal{X}$, where $\mathcal{L}$ is the adjoint operator associated to $\mathbf{z}A(\mathbf{z})$:

$$\mathcal{L}g(\mathbf{z}) = \sum_{y,x\in\mathcal{X},\mathbf{k}\in\mathcal{Z}} \mathbf{z}_y\tau_{\mathbf{k}}(y,\mathbf{z})(\mathbf{k}_x-\delta_x^y)\frac{\partial g}{\partial \mathbf{z}_x}(\mathbf{z}),$$

where $\delta_x^y=1$ if $y=x$ and 0 otherwise. Using (**A1**) and differentiability of ψ, ψ is in the domain of $\mathcal{G}$ and we define λ as

$$\lambda(x,\mathbf{z}) = \frac{\mathcal{G}\psi(x,\mathbf{z})}{\psi(x,\mathbf{z})}$$

for $x\in\mathcal{X}$ and $\mathbf{z}\in\mathbb{R}_+^{\mathcal{X}}$ and can state the result on the subtree containing the sample. More precisely, recall that L_v^N is the life length of individual v in the original process Z^N, $L_v^N(t)$ this life length when the process is stopped at time t, and Z_v^N the type of individual v. Writing u_0 the ancestor of u at time 0, we set

$$\mathcal{T}_u^N(t) = \{(v,L_v^N(t),Z_v^N) : \exists s\le t, (u_0,v)\in\mathbb{G}^N(s)\},$$

where $\mathbb{G}^N(s)$ is the set of labels alive in $\mathcal{T}^N$ at time s. The random tree $\mathcal{T}_u^N(t)$ is the tree associated with the ancestral lineage of u and their descendants, rooted in $\varnothing$. We endow the space $\mathbb{T}\times\mathcal{X}$ with a ℓ_1 topology on the collection of labels together with their life lengths and types, defined as follows. Recall that a finite tree $\mathrm{t}=\{(v,\ell_v,z_v) : v\in\mathcal{U}(\mathrm{t})\}$ of $\mathbb{T}$ is a collection $\mathcal{U}(\mathrm{t})\subset\mathcal{U}$ of labels corresponding to individuals $v\in\mathcal{U}(\mathrm{t})$ of the population with time lenght ℓ_v and type z_v. For two trees $\mathrm{t}=\{(v,\ell_v,z_v) : v\in\mathcal{U}(\mathrm{t})\}$ and $\mathrm{t}'=\{(v,\ell_v',z_v') : v\in\mathcal{U}(\mathrm{t}')\}$. We denote as $\mathrm{t}\Delta\mathrm{t}' := \mathcal{U}(\mathrm{t})\,\Delta\,\mathcal{U}(\mathrm{t}')$ the set of labels of $\mathcal{U}$ in one tree but not in the other and $\mathrm{t}\cap\mathrm{t}' := \mathcal{U}(\mathrm{t})\cap\mathcal{U}(\mathrm{t}')$ the set of labels in both. We consider the following distance on trees

$$d(\mathrm{t},\mathrm{t}') = \#(\mathrm{t}\Delta\mathrm{t}') + \sum_{u\in\mathrm{t}\cap\mathrm{t}'} (|\ell_u-\ell_u'| + |\mathbf{k}_u-\mathbf{k}_u'|)$$

and endow $\mathbb{T}$ with this distance and $\mathbb{T}\times\mathcal{X}$ with the product topology.

Proposition 7. *Assume that* **(A1-2-3-4)** *hold. Let $t\ge 0$ and $U^N(t)$ be a uniform choice among individuals of $\mathcal{T}^N(t)$ alive at time t. Then for any F continuous and positive from $\mathbb{T}\times\mathcal{X}$ to $\mathbb{R}_+$,*

$$\lim_{N\to\infty} \mathbb{E}_{\mathbf{x}_N}\left(F(\mathcal{T}_{U^N(t)}^N(t),U^N(t))\right) = \langle \mathbf{v},\psi(.,\mathbf{v})\rangle\,\mathbb{E}\left(\frac{\exp\left(\int_0^t \lambda(Y(s),\mathbf{z}(s,\mathbf{v}))\,ds\right)}{\psi(Y(t),\mathbf{z}(t,\mathbf{v}))\,\|\mathbf{z}(t,\mathbf{v})\|_1}\,F(\mathcal{A}_\star(t),E(t))\right).$$

This result can be extended to finite multiple sampling at time t with independent construction started at initial time. Indeed, in this large population approximation and finite time horizon, the different samples at time t come from different original individuals and behave independently. We can more generally consider a finite number of initial individuals in the description. Considering an infinite number of

initial individuals should lead to change the topology for convergence. Besides, relaxing the ℓ^2 uniform bound of (**A1**) should be interesting. Keeping the ℓ^1 uniform bound would give a continuous limiting population process with potential infinite rate of branching along the spine (and the uniform sampling). Considering even larger jumps would give a stochastic limit and more complex spinal constructions. It is another interesting direction.

Let us prepare the proof of Proposition 7. We denote as $(\mathcal{A}^N, E^N)$ the ψ_N-spine construction associated to $\mathcal{T}^N$, with

$$\psi_N(x,\mathbf{z}) = \psi(x,\mathbf{z}/N)$$

for $x \in \mathcal{X}$ and $\mathbf{z} \in (0,\infty)^{\mathcal{X}}$ and initial condition $\mathbf{x}_N$. Function ψ_N is extended to the space $\mathcal{X} \times \mathbb{R}_+^{\mathcal{X}}$ by setting $\psi_N = 1$ on the boundary of $\mathcal{X} \times \mathbb{R}_+^{\mathcal{X}}$. We introduce

$$\lambda^N(x,\mathbf{z}) = \frac{\mathcal{G}^N \psi_N(x,\mathbf{z})}{\psi_N(x,\mathbf{z})}$$

on $\mathcal{X} \times \mathbb{R}_+^{\mathcal{X}}$, where

$$\mathcal{L}^N g(\mathbf{z}) = \sum_{y \in \mathcal{X}, \mathbf{k} \in \mathcal{Z}} \mathbf{z}_y \tau_{\mathbf{k}}(y,\mathbf{z}/N)\,(g(\mathbf{z}+\mathbf{k}-\mathbf{e}(y)) - g(\mathbf{z}))$$

and

$$\mathcal{G}^N f(x,\mathbf{z}) = \sum_{\mathbf{k} \in \mathcal{Z}} \tau_{\mathbf{k}}(x,\mathbf{z}/N)\,\langle \mathbf{k}-\mathbf{e}(x), f(.,\mathbf{z}+\mathbf{k}-\mathbf{e}(x))\rangle + \mathcal{L}^N f_x(\mathbf{z}).$$

The spine construction (Theorem 1) yields

$$\mathbb{E}_{\mathbf{x}_N}\left(\mathbf{1}_{\{\mathbb{G}^N(t)\neq\varnothing\}} F(\mathcal{T}^N(t), U^N(t))\right) = \langle [N\mathbf{v}]/N, \psi(.,[N\mathbf{v}]/N)\rangle\, \mathbb{E}_{\mathbf{x}_N}\left(G_N(\mathcal{A}^N(t), E^N(t))\right), \tag{16}$$

where

$$G_N(\mathcal{A}^N(t), E^N(t)) = \frac{e^{\int_0^t \lambda^N(Y^N(s),\mathbf{V}^N(s))ds}}{\psi(Y^N(t),\mathbf{V}^N(t)/N)\,\|\mathbf{V}^N(t)/N\|_1} F(\mathcal{A}^N(t), E^N(t)).$$

Roughly speaking, all the quantities involved converge as $N \to \infty$. The process $\mathbf{V}^N$ which counts the types of individuals in the ψ_N-spine construction converges to the same limit as $\mathbf{Z}^N$. Indeed, when N goes to infinity, Assumption (**A1**) guarantees that there is no jump of order N and the regularity of ψ ensures that

$$\lim_{N\to\infty} \frac{\psi(x,([N\mathbf{z}]-\mathbf{k}+1)/N)}{\psi(x,[N\mathbf{z}]/N)} = 1.$$

Thus the contribution of the spine vanishes in the large population limit, despite the biased rate. Besides, at a macroscopic level, the other individuals behave as in the original process. We can now turn to the proof.

Proof of Proposition 7. First, following the proof of Theorem 2 in Chapter 11 of [18], we obtain that the sequence of process $(\mathbf{V}^N)_N$ converges in law in $\mathbb{D}(\mathbb{R}_+, \mathbb{R}_+^{\mathcal{X}})$ to $(\mathbf{z}(t,\mathbf{v}))_{t\geq 0}$ as N tends to infinity.

To adapt the proof, we note that $\mathbf{V}^N$ alone is not a Markov process. One has to consider the couple $(Y^N, \mathbf{V}^N)_N$ but the influence of the type of the spine Y^N is vanishing in computations using ℓ^2 bound (**A1**) and the fact the population is renormalized by N. Assumptions **(A1,A2,A3)** thus allow us to get the counterpart of conditions (2.6), (2.7), (2.8) of Theorem 2 in Chapter 11 of [19], while the initial condition converges in law by definition of the model.

Now, we check that $(x,\mathbf{z}) \to \lambda_N(x, N\mathbf{z})$ converges uniformly on compact sets of $\mathcal{X} \times (0,\infty)^{\mathcal{X}}$ and use a localization procedure to get the convergence in (16) as $N \to \infty$. Indeed,

$$\mathcal{L}^N(\psi_N)_x(N\mathbf{z}) = N \sum_{y\in\mathcal{X},\mathbf{k}\in\mathcal{Z}} \mathbf{z}_y \tau_{\mathbf{k}}(y,\mathbf{z}) \left(\psi(x,\mathbf{z} + (\mathbf{k} - \mathbf{e}(y))/N) - \psi(x,\mathbf{z})\right).$$

Since ψ_x is continuously differentiable on $(0,\infty)^{\mathcal{X}}$ and using (**A1**) – (**A2**),

$$N \sum_{y\in\mathcal{X},\, \|\mathbf{k}\|_1 \le \sqrt{N}} \mathbf{z}_y \tau_{\mathbf{k}}(y,\mathbf{z}) \left| \psi\left(x, \mathbf{z} + \frac{\mathbf{k} - \mathbf{e}(y)}{N}\right) - \psi(x,\mathbf{z}) - \sum_{y'\in\mathcal{X}} \frac{\mathbf{k}_{y'} - \delta_y^{y'}}{N} \frac{\partial \psi_x}{\partial \mathbf{z}_{y'}}(\mathbf{z}) \right|$$

tends to 0 as $N \to \infty$, uniformly for $\mathbf{z} \in (\varepsilon, 1/\varepsilon)^{\mathcal{X}}$, where $\varepsilon \in (0,1)$ is fixed. Besides, using (15) and (**A1**),

$$N \sum_{y\in\mathcal{X},\, \|\mathbf{k}\|_1 > \sqrt{N}} \mathbf{z}_y \tau_{\mathbf{k}}(y,\mathbf{z}) \left| \psi\left(x, \mathbf{z} + \frac{\mathbf{k} - \mathbf{e}(y)}{N}\right) - \psi(x,\mathbf{z}) \right|$$
$$\le L\varepsilon^{-1} \sum_{y\in\mathcal{X},\, \|\mathbf{k}\|_1 > \sqrt{N}} (\|\mathbf{k}\|_1 + 1)\tau_{\mathbf{k}}(y,\mathbf{z}) \overset{N\to\infty}{\longrightarrow} 0,$$

uniformly for $\mathbf{z} \in (\varepsilon, 1/\varepsilon)^{\mathcal{X}}$. Recalling the definition of λ and controlling the terms for $\|\mathbf{k}\|_1 > \sqrt{N}$ in λ as above with (**A1**) ensures that for any $\varepsilon > 0$,

$$\sup_{x\in\mathcal{X},\mathbf{z}\in(\varepsilon,1/\varepsilon)^{\mathcal{X}}} |\lambda^N(x,N\mathbf{z}) - \lambda(x,\mathbf{z})| \overset{N\to\infty}{\longrightarrow} 0.$$

Using the convergence of $\mathbf{V}^N$ to $\mathbf{z}(.,\mathbf{v})$ in $\mathbb{D}(\mathbb{R}_+, \mathbb{R}_+^{\mathcal{X}})$ and (**A4**), (16) yields

$$\lim_{N\to\infty} \Big| \mathbb{E}_{\mathbf{x}_N} \left(\mathbf{1}_{\{\mathbb{G}^N(t)\neq\varnothing\}} F(\mathcal{T}^N_{U^N(t)}(t), U^N(t)) \right)$$
$$- \langle [N\mathbf{v}]/N, \psi(., [N\mathbf{v}]/N) \rangle \, \mathbb{E}_{\mathbf{x}_N} \left(H(\mathcal{A}^N(t), E^N(t)) \right) \Big| = 0,$$

for F continuous, positive and bounded, where

$$H(\mathcal{A}^N(t), E^N(t)) = \frac{e^{\int_0^t \lambda(Y^N(s),\mathbf{z}(t,\mathbf{v})))ds}}{\psi(Y^N(t), \mathbf{z}(t,\mathbf{v}))\, \|\mathbf{z}(t,\mathbf{v})\|_1} F(\mathcal{A}^N_\star(t), E^N(t))$$

and $\mathcal{A}^N_\star$ is the tree $\mathcal{A}^N$ where we only keep the tree rooted in the initial spine individual. The conclusion can be achieved by a coupling argument, since the first time when one individual of $\mathcal{A}^N_\star$ has an offspring of size greater than $\sqrt{N}$ tends to infinity. Thus the individual branching rates of $\mathcal{A}^N_\star$ converge uniformly to the rates of $\mathcal{A}_\star$, using the same localization as above to keep the process $\mathbf{V}^N$ in compact sets excluding boundaries. □

In general and as in the previous subsection, one may expect to solve the limit eigenproblem:

$$\sum_{\mathbf{k}\in\mathcal{Z}} \tau_{\mathbf{k}}(x,\mathbf{z})\,\langle \mathbf{k}-\mathbf{e}(x),\psi(.,\mathbf{z})\rangle + \sum_{y,x\in\mathcal{X},\mathbf{k}\in\mathcal{Z}} \mathbf{z}_y\tau_{\mathbf{k}}(y,\mathbf{z})(\mathbf{k}_x-\delta_x^y)\frac{\partial\psi_x}{\partial\mathbf{z}_x}(\mathbf{z}) = \lambda(x,\mathbf{z})\psi(x,\mathbf{z})$$

for any $x\in\mathcal{X}$ and $\mathbf{z}\in\mathbb{R}_+^{\mathcal{X}}$ such that $\mathbf{z}_x>0$. One also expects that uniqueness of positive normalized solution holds under irreducibility conditions. We only illustrate the result with two simple and more explicit examples. First, in one dimension $\mathcal{X}=\{x_1\}$, taking $\psi(z)=1/z$ is reminiscent from the previous section for single type models. It yields $\lambda=0$ and as $N\to\infty$, $(\mathcal{T}^N_{U(t)}(t),U^N(t))$ initiated in $\mathbf{x}_N$ converges in law to $(\mathcal{A}(t),E(t)))$ as $N\to\infty$.

Second, when the population process is at equilibrium, we can also be more explicit. More precisely, assume that there exists $\mathbf{z}_*\in\mathbb{R}_+^{\mathcal{X}}$ such that

$$\mathbf{z}_*A(\mathbf{z}_*)=0.$$

Then $\mathcal{L}f_x(\mathbf{z}_*)=0$ for any f and $x\in\mathcal{X}$. The spectral problem $\mathcal{G}\psi=0$ simplifies since the influence of the population on the spinal tree is constant. The solution of the problem is then given by $\psi(x,\mathbf{z})=\varphi(x)$ where $\varphi:\mathcal{X}\to(0,\infty)$ is solution of

$$\forall x\in\mathcal{X},\qquad \sum_{\mathbf{k}\in\mathcal{Z}}\tau_{\mathbf{k},*}(x)\,\langle\mathbf{k}-\mathbf{e}(x),\varphi\rangle=0,$$

and

$$\tau_{\mathbf{k},*}(x)=\tau_{\mathbf{k}}(x,\mathbf{z}_*)\frac{\langle\mathbf{k},\varphi(.)\rangle}{\varphi(x)}.$$

It means that

$$\forall x\in\mathcal{X},\qquad \sum_{y\in\mathcal{X}}\varphi(y)A_{y,x}(\mathbf{z}_*)=0.$$

Existence and uniqueness of positive ϕ under irreducibility assumption is then again a consequence of Perron Frobenius theorem and we recover in that case the spine construction for critical multitype Galton Watson process proposed in [20,29]. In this vein, let us refer to [11], for a more complex model in infinite dimension motivated by adaptation to environmental change, which uses the branching limiting structure and also describes the backward process appearing in sampling.

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