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# SPINE FOR INTERACTING POPULATIONS AND SAMPLING

VINCENT BANSAYE

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

*Key words:* Jump Markov process, random tree, spine, interactions, positive semigroup, martingales, population models.

## 1. INTRODUCTION

Spine techniques and size biased trees have a long and fruitful story in branching processes. They 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 [37]. More generally, spine construction provides a relevant point of view to tackle many issues related to the genealogy and long time behavior of branching processes. Lyons, Peres and Pemantle [38] have given a conceptual approach of the famous  $L \log L$  criterion involved in the asymptotic analysis of branching processes. Their construction provides an illuminating proof of the non degenerescence of limiting martingale using branching processes with immigration. This Markov construction has been extended to multitype branching process [31] and infinite dimension and we refer e.g. to [2, 17, 16]. It involves then either an eigenfunction or an exponential additive functional of trajectories corresponding to a Feynman Kac semigroup, both being linked by a change of probability. This construction is also involved in the fine estimate of the front of branching random walks, see Hu and Shi [23] and Roberts [41], thanks to a family of exponential eigenfunctions and Biggins martingale.

Spine constructions give a trajectorial and markovian sense to a typical individual alive at a given time. This allows to prove ergodic properties of type distribution among the population and shed light on sampling [36]. More generally, we refer to the description of reduced tree and backbone [21, 15] 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. [5, 7] and references therein.

These constructions exploit the branching property and independence of individuals. The aim of this paper is to propose a spine construction for dynamics taking into account

interactions, through density dependance of individual behaviors and associated *branching events*. Individuals may die or reproduce or move and individual branching events may depend on the state of the population. Such models are involved in population dynamics or genetics or epidemiology, see e.g. [30, 4, 18] and forthcoming examples. Indeed, for various models of competition, mutualism, contamination, sexual reproduction or predation, the individual rate of transition depends on the size of some species at a given location. Death or successive reproduction of asexual population may indeed depend on local competition and resources available, reproduction of females may depend on density of males, contaminations by infected individuals depends on the local number of susceptibles... Let us also mention that density dependent models appear in various other contexts, including chemistry, queueing systems or networks.

Our first motivation here is the study of population models with competition. The evolution of the distribution of traits among such a population is related to the distribution of a sample. They can both be tackled via a spine construction. Addario-Berry and Penington [1] have considered a competitive effect in a branching random walk. The authors obtain fine results on the front of propagation. They focus on a peculiar form of competition which enables them to link their model to branching brownian motion. In a large population approximation where a branching property can be recovered, Calvez, Henry, Méléard and Tran [11] describe the ancestral lineage of a sample in a context of competition and adaptation to a gradual environmental change. The examples considered in this work will involve different scalings.

In recent decades, lots of attention has been paid to the study of genealogical structures of population. For branching processes, the contour (or exploration) process provides a full description of the genealogy. From the work of Aldous and convergence to the continuum random tree, it has been generalized and used for instance for the description of mutations of splitting trees [34]. The effect of competition as a pruning of trees has been introduced and studied in [35, 6]. Spine construction offers a complementary insight in the structure by focusing on a *typical individual* in various senses. It allows for extension to structured population and varying environment. An other point of view enlightens genealogical structure of population models, the look-down construction introduced by Kurtz and Donnelly. In this construction, 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 [32] for the look-down construction of branching processes and to [18] for a recent extension to interacting populations. This 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 main objective is the study of structured populations : each individual has a type  $x \in \mathcal{X}$ , where  $\mathcal{X}$  is finite or countable here. The type can represent a size, a location, or any phenotypic or genotypic trait of the individual. The population is described by a vector  $\mathbf{z} = (\mathbf{z}_x : x \in \mathcal{X})$  where  $\mathbf{z}_x$  is the number of individuals with type  $x$ . We write  $\|\mathbf{z}\|_1 = \sum_{x \in \mathcal{X}} \mathbf{z}_x$  the  $\ell_1$  norm of  $\mathbf{z}$  and work with the associated normed and countable space

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

Informally, each individual of a population composed by  $\mathbf{z}$  branches independently and each individual with type  $x$  is replaced by an offspring  $\mathbf{k} \in \mathcal{Z}$  with rate  $\tau_{\mathbf{k}}(x, \mathbf{z})$ . In other words, an individual with type  $x$  branches at total rate

$$\tau(x, \mathbf{z}) = \sum_{\mathbf{k} \in \mathcal{Z}} \tau_{\mathbf{k}}(x, \mathbf{z}) < \infty$$

and is replaced by  $\mathbf{k}$  with probability  $p_{\mathbf{k}}(x, \mathbf{z}) = \tau_{\mathbf{k}}(x, \mathbf{z})/\tau(x, \mathbf{z})$ . The new composition of the population is then  $\mathbf{z} - \mathbf{e}(x) + \mathbf{k}$ , where  $\mathbf{e}(x)$  stands for one single individual with trait  $x$ , i.e.  $\mathbf{e}(x) = (\mathbf{e}_y(x), y \in \mathcal{X})$  and  $\mathbf{e}_x(x) = 1$  and  $\mathbf{e}_y(x) = 0$  for  $y \neq x$ . For a reference on density dependent Markov process, let us mention [19, 30].

The spine construction consists in a new process with a distinguished individual and rates are modified using a positive function  $\psi$  on  $\mathcal{X} \times \mathcal{Z}$ . Roughly, when the distinguished individual has type  $x$  and lives in population whose type composition is  $\mathbf{z}$ , this individual branches, yields  $\mathbf{k}$  offsprings and switches to type  $y$  with rate

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

This rate is biased by the size and type of offsprings as for branching structures. It is also corrected by the variation of the population composition through a  $\psi$  transform. The jump rates of individuals outside the spine are also modified and they branch at rate

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

when their type is  $y$  and the type of the spine is  $x$ . We observe that in the case when  $\psi$  is not dependent on the state  $\mathbf{z}$  of the population, we recover the construction for branching structures proposed in [38, 31].

In the applications considered here, the couple formed by the typical (or spine) individual and the composition of the population is involved. We will also consider the associated semigroup and martingale. The  $\psi$ -spine construction couples a size bias and a Doob transform on the product space  $\mathcal{X} \times \mathcal{Z}$ , which will provide a Feynman Kac representation of the semigroup. The spine will describe the lineage of a typical individual, which includes its time of branching, number of offsprings, types... More information on the underlying genealogy structure may be interesting. In particular, the tree associated to a sample is needed when tracing an infected individual in epidemiology or when looking at the subpopulation carrying a common mutation in population genetics. Our main result allows to describe the full tree around the spine. Among stimulating open questions is the way multisampling could be obtained, which will be just briefly evoked here.

We focus in this paper on the continuous time setting. The spine construction achieved has a counterpart in discrete time, for non-overlapping generations. As far as we see, the fact that in continuous time branching events are not simultaneous is actually more convenient for construction and analysis. Besides, models which motivate this work may be more classical or relevant in continuous time.

**Example.** To motivate this construction and illustrate it, let us briefly present the non-structured case and refer to Section 3.1 for details. In that case, individuals are exchangeable, i.e. each individual has a common type. 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  $\tau_k(z)/\tau(z)$ . Let us 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 not become extinct :  $\forall t \geq 0, Z(t) \in [1, \infty)$ . At a given time  $t$ , sample uniformly at random one individual alive. Then the times when the ancestral line has branched and the number of offsprings at these times is given (in law) by the  $1/z$ -spine construction. It means that it can be constructed in the forward sense by considering a Markov process with a distinguished individual (our sample) which is replaced by  $k$  individuals at rate  $k\tau_k(z)(z+k-1)/z$ , while the other individuals branch independently and are replaced by  $k$  individuals at rate  $\tau_k(z)(z+k-1)/z$ . In particular, this result allows to specify how sampling bias the reproduction of individuals along time and the effect of population size.

**Outline of the paper.** The paper is organized as follows. In the next section, we describe more precisely the  $\psi$ -spine construction associated to a positive function  $\psi$ . The main result provides then a Girsanov type result (change of probability) to transform the original random tree with a randomly chosen individual at a given time into a new random tree with a distinguished individual, the spine. We complement this section by considering the associated semigroup 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-degenerescence of the natural positive martingale associated with the growth of the process, thus extending the criterion of Kesten Stigum and the approach of [38]. In Section 4, we consider a population structured by a finite number of types. We describe the ancestral lineage of a uniform sample when the state space of the population is finite and the sampling in large population approximation when the limiting process is a differential equation.

In the paper, we write  $\mathbb{N} = \{1, 2, \dots\}$ ,  $\mathbb{N}_0 = \{0, 1, 2, \dots\} = \mathbb{N} \cup \{0\}$ . For two vectors  $\mathbf{u} = (\mathbf{u}_x)_{x \in \mathcal{X}}$  and  $\mathbf{v} = (\mathbf{v}_x)_{x \in \mathcal{X}}$ , we write  $\langle \mathbf{u}, \mathbf{v} \rangle = \sum_{x \in \mathcal{X}} \mathbf{u}_x \mathbf{v}_x$  the inner product.

## 2. SPINE CONSTRUCTION

**2.1. Definition of the original process.** We construct the tree of individuals with their types, until the potential explosion time, as follows. We use the Ulam Harris Neveu notation to label the individuals of the population and each label has a type and life length. 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 consider now a random process  $Z$  and the associated random tree  $\mathcal{T}$  tree defined by iteration. We start with a population labeled by a non-empty and finite and deterministic subset  $\mathfrak{g}$  of  $\mathbb{N}$  and their types are  $(x_u, u \in \mathfrak{g})$ . We

write

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

this initial condition. We denote by  $\mathbf{v} \in \mathcal{Z}$  the vector counting the initial number of individuals of each type:  $\mathbf{v}_x = \#\{u \in \mathfrak{g} : x_u = x\}$ .

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  $\mathbf{Z}_x(t) = \#\{u \in \mathbb{G}(t) : Z_u = x\}$ . In particular,  $\mathbf{Z}(0) = \mathbf{v}$ .

The markovian construction by iteration is classical. Each individual  $u$  has a random life length  $L_u \in (0, +\infty]$  and a type  $Z_u$  during all its life. Each individual with type  $x$  is replaced by an offspring whose types are counted by  $\mathbf{k} \in \mathcal{Z}$  at rate  $\tau_{\mathbf{k}}(x, \mathbf{z})$  when the population composition is  $\mathbf{z}$ . When an individual  $u \in \mathcal{U}$  is replaced, the new individuals are labeled by  $(u, 1), \dots, (u, \|\mathbf{k}\|_1)$  and the population composition moves to  $\mathbf{z} + \mathbf{k} - e(x)$ . Each new individual has a type and the order of affectation of types will play no role. Let us prescribe a type  $Z_{(u,i)}$  to each new label  $(u, i)$ , for  $1 \leq i \leq \|\mathbf{k}\|_1$ , and will need do it in coherent way later in the spine construction. Thus, we consider a probability law  $Q_{\mathbf{k}}$  on

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

and  $(Z_{(u,i)} : 1 \leq i \leq \|\mathbf{k}\|_1)$  is distributed as  $Q_{\mathbf{k}}$ . This affectation is achieved independently for each event and its law only depends on the type composition  $\mathbf{k}$ . 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 constructed iteratively. Writing  $T_n$  the successive branching times, the process is constant in the 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 *event* or *branching event*, indifferently. Note that for any event, only one individual disappears. It may be replaced by a single individual with a same type (but a different label). The process is thus well defined until the limiting time of successive branching events  $(T_n)_{n \geq 1}$ :

$$T_{\text{Exp}} = \lim_{n \rightarrow \infty} T_n \in \mathbb{R} \cup \{+\infty\}.$$

This latter is finite if the sequence of branching events accumulate and as usual, we speak then of *explosion*. We write  $\mathcal{T}$  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  $u$  truncated at time  $t$ .

**2.2. The  $\psi$ -spine construction.** 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 now the state space for the type of the spine and composition of the population:

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

and consider a (fixed) positive function

$$\psi : \overline{\mathcal{Z}} \rightarrow (0, \infty).$$

We assume in the rest of the paper that for any  $(x, \mathbf{z}) \in \overline{\mathcal{Z}}$ ,

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

Let us construct a new process  $\Xi^\psi = \Xi$  and associated genealogical 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 [38, 31] for Galton-Watson processes. We write now  $\mathbb{V}(t)$  the random set of individuals alive at time  $t$  and the types of individuals are given by  $(\Xi_u, u \in \mathbb{V}(t))$ . Thus  $E(t) \in \mathbb{V}(t) \subset \mathcal{U}$  is the label of the spine at time  $t$  and the type of the spine is then  $Y(t) = \Xi_{E(t)}$ . Besides,  $\Xi_x(t) = \#\{u \in \mathbb{V}(t) : \Xi_u = x\}$ .

We start with the same population  $\mathbf{x} = \{(u, x_u), u \in \mathbf{g}\}$  as the original process, i.e. initial individuals are labeled by  $\mathbf{g}$  and have types  $(x_u : u \in \mathbf{g})$  counted by  $\mathbf{v}$ . The distribution of the initial label of the spine  $E(0)$  is

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

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

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

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

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

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

and provides the new label  $E(t)$  of the distinguished individual.

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 (but 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 particle 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  $\widehat{T}_n$ . It is thus also defined by induction until explosion time

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

which may be finite or not.

The Markovian construction achieved here provides a random tree  $\mathcal{A}$  with a distinguished individual  $E$ . It 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 the transform  $\psi$ , which will play a key role.

**2.3. General result.** We introduce the linear operator  $\mathcal{G}$  which arise in the spine construction. For a function  $f : \bar{\mathcal{Z}} \rightarrow \mathbb{R}$ , we consider the function  $\mathcal{G}f$  on  $\bar{\mathcal{Z}}$  given by

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

where  $\delta_y^x$  is the Kronecker symbol ( $\delta_y^x = 1$  if  $y = x$  and 0 otherwise). This operator  $\mathcal{G}$  is well defined and will be used on the set  $\mathfrak{D}_{\mathcal{G}}$  of positive functions  $\psi$  on  $\bar{\mathcal{Z}}$  which satisfy (1) and for any  $(x, \mathbf{z}) \in \bar{\mathcal{Z}}$ ,

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

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

$$\lambda = \frac{\mathcal{G}\psi}{\psi} \quad \text{on} \quad \bar{\mathcal{Z}}.$$

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

$$\mathbb{P}(U(t) = e | \mathcal{T}(t)) = p_e(\mathcal{T}(t))$$

and  $\sum_{e \in \mathbb{G}(t)} p_e(\mathcal{T}(t)) = 1$  a.s. on the event  $\mathbb{G}(t) \neq \emptyset$ . Our main interest in this paper is the uniform choice at time  $t$ , i.e.  $\mathbb{P}(U(t) = e | \mathcal{T}(t)) = p_e(\mathcal{T}(t)) = 1/\#\mathbb{G}(t) = 1/\|\mathbf{Z}(t)\|_1$ . But sampling at a given time with a type bias is also relevant for instance.

We introduce the random process  $\mathcal{W}$  associated with the spine construction  $(\mathcal{A}, E)$  and the choice  $p$ :

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

We can now state the result and link the random choice of an individual among our interacting population to the Markovian spine construction. Let  $\mathbb{T}$  be the space of finite trees where each nodd 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  $\sigma$ -algebra.

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

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

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

$$\begin{aligned} &\mathbb{E}_{\mathbf{x}} \left( \mathbf{1}_{\{T_{\text{Exp}} > t, \mathbb{G}(t) \neq \emptyset\}} F(\mathcal{T}(t), U(t)) \right) \\ &= \langle \mathbf{v}, \psi(\cdot, \mathbf{v}) \rangle \mathbb{E}_{\mathbf{x}} \left( \mathbf{1}_{\hat{T}_{\text{Exp}} > t} \frac{e^{\int_0^t \lambda(Y(s), \Xi(s)) ds}}{\psi(Y(t), \Xi(t)) \|\Xi(t)\|_1} F(\mathcal{A}(t), E(t)) \right). \end{aligned}$$



The proof is a consequence of the following lemma, which encodes the successive transitions. Recall that the successive branching times of the original process  $Z$  and of the spine process  $\Xi$  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 write  $U_i$  (resp.  $\mathbf{K}_i$ ) the random variable in  $\mathcal{U}$  (resp. in  $\mathcal{Z}$ ) which gives the label of the individual which realizes the  $i$ th branching events in the original process (resp. 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  $U_i$ . In other words, at time  $T_i$ , the individual  $U_i$  is 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 write similarly  $\widehat{U}_i$ ,  $\widehat{\mathbf{K}}_i$  and  $(\widehat{X}_{i,j}, j \leq \|\widehat{\mathbf{K}}_i\|_1)$  the variables involved in the  $i$ th branching event of the spine construction for  $1 \leq i \leq N$ . Besides, we write  $E_i$  the label of the distinguished individual when the  $i$ th 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 write

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

the discrete variables describing these successive branching events.

Let  $\mathfrak{A}_n^*$  be the subset of non-extincted discrete trees with types in  $\mathcal{X}$  and  $n$  internal nodes (i.e.  $n$  branching events) and initial population  $\mathbf{x} = \{(u, x_u), u \in \mathfrak{g}\}$ . Each element of  $a \in \mathfrak{A}_n^*$  is 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 corresponding type composition. We also write  $y_k(e)$  the type of the ancestor of  $e$  between these  $k$ -th and  $k+1$ -th branching event. The fact that the tree  $a \in \mathfrak{A}_n^*$  is non-extincted means that we require that  $\mathfrak{g}_k(a) \neq \emptyset$  for  $k \leq n$ . Note also that  $\mathfrak{g}_0(a) = \mathfrak{g}$ .

**Lemma 1.** *Let  $n \geq 0$  and  $G$  be a measurable non-negative function from  $\mathbb{R}_+^n$ . For any  $a \in \mathfrak{A}_n^*$  and any  $e \in \mathfrak{g}_n(a)$ ,*

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

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  $\mathbf{x}$  is fixed and notation is omitted in this proof. For convenience, we also write  $\mathbf{z}_n = \mathbf{z}_n(a)$  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  $e \in \mathfrak{g}_0 = \mathfrak{g}$ ,

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

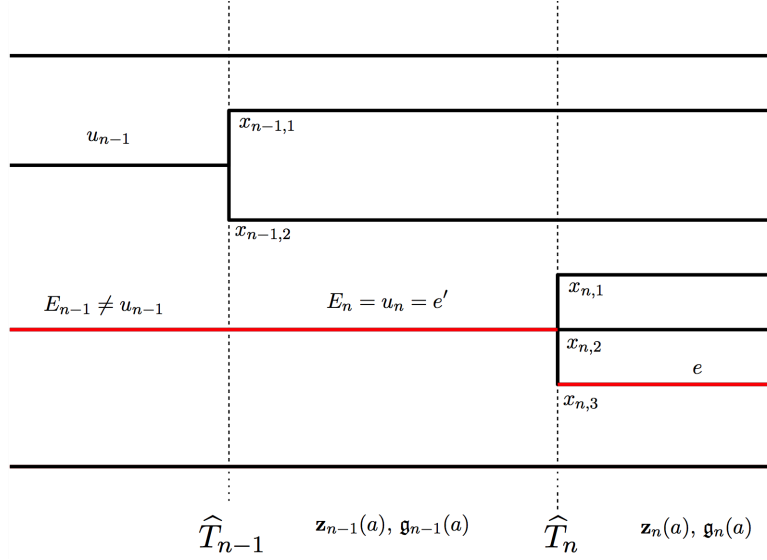


FIGURE 1. Illustration of the construction and notation. The lines correspond to individuals and their label is indicated just above the line. Below the line we give types for these individuals. The spine is represented in red.

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  $a = (a_i)_{1 \leq i \leq n} \in \mathfrak{A}_n^*$  and first observe that

$$(2) \quad \mathbb{E} \left( \mathbf{1}_{\{N \geq n\}} G_n(T_i, 1 \leq i \leq n) \mathbf{1}_{\{A_i = a_i : 1 \leq i \leq n\}} \mid \mathcal{F}_{T_{n-1}} \right) = \mathbf{1}_{\{N \geq n-1\}} G(T_i, 1 \leq i \leq n-1) \mathbf{1}_{\{A_i = a_i : 1 \leq i \leq n-1\}} B_n,$$

where

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

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

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

Considering  $a_n$ , the label  $u_n$  branches and this latter 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 write

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

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

$$(3) \quad B_n = \mathbf{1}_{\{\tau_n \neq 0\}} \tau_{\mathbf{k}_n}(x_{u_n}, \mathbf{z}_{n-1}) Q_n \int_{\mathbb{R}_+} H(t) e^{-\tau_n t} dt.$$

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

$$(4) \quad \mathbb{E} \left( \mathbf{1}_{\{\widehat{N} \geq n, E_{n+1}=e\}} \mathcal{W}_n^{((a_i:i \leq n), e)} G_n(\widehat{T}_i, 1 \leq i \leq n) \mathbf{1}_{\{\widehat{A}_i=a_i: 1 \leq i \leq n\}} \mid \widehat{\mathcal{F}}_{T_{n-1}} \right) \\ = \mathbf{1}_{\{\widehat{N} \geq n-1, E_n=e'\}} \mathcal{W}_{n-1}^{((a_i:i \leq n-1), e')} G(\widehat{T}_i, 1 \leq i \leq n-1) \mathbf{1}_{\{\widehat{A}_i=a_i: 1 \leq i \leq n-1\}} \frac{\psi(y', \mathbf{z}_{n-1})}{\psi(y, \mathbf{z}_n)} \widehat{B}_n,$$

where

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

and  $y$  (resp.  $y'$ ) is the type of the spinal individual  $e$  (resp.  $e'$ ) after (resp. before) the  $n$ th branching event. We write respectively

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

the total branching rates of the population outside 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 write

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

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,

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

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  $y$  is

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

We distinguish two cases, corresponding to the fact that the  $n$ th 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  $\widehat{\tau}_n + \widehat{\tau}_n^*$  and we get

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

Adding that by definition of  $\lambda$ ,

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

we obtain from (4)

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

Using (2) and (3) and the fact that  $\widehat{\tau}_n + \widehat{\tau}_n^* = 0$  is equivalent to  $\tau_n = 0$ , the induction hypothesis ensures

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

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.  $\square$

*Proof of Theorem 1.* The result is a consequence of the previous lemma. On the event  $\{N < \infty\}$ , we set  $T_n = +\infty$  for  $n > N$ . 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  $\mathbb{R}_+^n \times \mathfrak{A}_n^*$  such that, on the event  $\{T_n \leq t < T_{n+1}, N \geq n\}$  we have

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

Then

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

where

$$F_n^{t,e}(a) = \mathbb{E}_{\mathbf{x}} \left( G_n^{t,e}(T_1, \dots, T_n, a_1, \dots, a_n) f_t(T_n, a_1, \dots, a_n) \mathbf{1}_{\{A_i=a_i: 1 \leq i \leq n, T_n \leq t, N \geq n\}} \right)$$

and

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

To end the proof, we apply Lemma 1 to express  $F_n^{t,e}(a)$  in terms of the spine construction and writing  $y_n(e)$  the type of the spine at the  $n$ th event, we use that

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

This latter identity is proved following the last lines as in the proof of Lemma 1.  $\square$

**2.4. Positive semigroup and martingale.** For each  $(r, \mathbf{v}) \in \bar{\mathcal{Z}}$ , we associate an initial labeling  $\mathbf{x} = x(\mathbf{v}) = ((u, x_u) : u \in \mathfrak{g})$ , where  $x_u$  is the type of  $u \in \mathfrak{g}$  and  $\#\{u \in \mathfrak{g} : x_u = x\} = \mathbf{v}_x$ . Since  $\mathbf{v}_r \geq 1$ , we can also associate a label  $u_r \in \mathfrak{g}$  such that  $x_{u_r} = r$ . For any  $t \geq 0$  and  $f$  function from  $\bar{\mathcal{Z}}$  to  $\mathbb{R}_+ \cup \{+\infty\}$ , we define for any  $(r, \mathbf{v}) \in \bar{\mathcal{Z}}$ ,

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

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

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

where  $\mathbf{Z}_x^{(u)}(t) = \#\{v \in \mathbb{G}(t) : v \succcurlyeq u, Z_v(t) = x\}$  is the number of individuals with type  $x$  at time  $t$  who are descendant of  $u$ .

Recall that  $\psi \in \mathfrak{D}_G$  is positive on  $\bar{\mathcal{Z}}$  and satisfies (1) and that  $\lambda = \mathcal{G}\psi/\psi$  on  $\bar{\mathcal{Z}}$ . Recall also that  $\Xi$  is the process counting types in the  $\psi$ -spine construction and  $Y(t) = \Xi_{E(t)}(t)$  is the type of the spine at time  $t$ . Observe that  $(Y, \Xi)$  is a jump Markov process whose jump rates are determined by  $\hat{\tau}_{\mathbf{k}}$  and  $\hat{\tau}_{\mathbf{k}}^*$  for  $\mathbf{k} \in \mathcal{Z}$ . It starts from  $(Y(0), \Xi(0)) = (r, \mathbf{v})$ . For  $u \in \mathbb{G}(t)$ , we write  $Z_u(s)$  the type of the (unique) ancestor of  $u$  at time  $s \leq t$ .

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

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

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

$$\begin{aligned} \mathbb{E}_{x(\mathbf{v})} \left( \mathbf{1}_{\{T_{\text{Exp}} > t\}} \sum_{u \in \mathbb{G}(t)} \psi(Z_u(t), \mathbf{Z}(t)) G((Z_u(s), \mathbf{Z}(s))_{s \leq t}) \right) \\ = \langle \mathbf{v}, \psi(\cdot, \mathbf{v}) \rangle \mathbb{E}_{x(\mathbf{v})} \left( \mathbf{1}_{\{\hat{T}_{\text{Exp}} > t\}} e^{\int_0^t \lambda(Y(s), \Xi(s)) ds} G((Y(s), \Xi(s))_{s \leq t}) \right). \end{aligned}$$

We first observe that the generator of the semigroup  $M$  is the linear operator  $\mathcal{G}$  introduced above. This will be made explicit in applications. This proposition 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 and Biggins and Kyprianou [10] for related works on multiplicative martingales. For such representations in the context of structured branching processes and in particular for fragmentations or growth fragmentations, we mention the works of Bertoin [9, 8] and Cloez [13] and Marguet [36]. We note that the event  $\{\hat{T}_{\text{Exp}} > t\}$  is measurable with respect to filtration associated to the process  $\Xi$  since this event is characterized by the absence of accumulation of jumps for  $\Xi$  before time  $t$ .

*Proof.* We omit initial condition in 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  $f$ ,

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

We get

$$\begin{aligned} & M_{t+s} f(r, \mathbf{v}) \\ &= \mathbb{E} \left( \mathbf{1}_{\{T_{\text{Exp}} > t\}} \sum_{u \in \mathbb{G}(t), u \succ u_r} \mathbb{E} \left( \mathbf{1}_{\{T_{\text{Exp}} > t+s, u \in \mathbb{G}(t)\}} \langle \mathbf{Z}^{(u)}(t+s), f(\cdot, \mathbf{Z}(t+s)) \rangle \mid \mathcal{F}_t \right) \right) \\ &= \mathbb{E} \left( \mathbf{1}_{\{T_{\text{Exp}} > t\}} \langle \mathbf{Z}^{(u_r)}(t), M_s f(\cdot, \mathbf{Z}(t)) \rangle \right) = M_t(M_s f)(r, \mathbf{v}). \end{aligned}$$

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

$$\begin{aligned} & \mathbb{E} \left( \mathbf{1}_{\{T_{\text{Exp}} > t\}} \sum_{u \in \mathbb{G}(t), u \succ u_r} \psi(Z_u(t), \mathbf{Z}(t)) G((Z_u(s), \mathbf{Z}(s))_{s \leq t}) \right) \\ (5) \quad &= \psi(r, \mathbf{v}) \mathbb{E}_{(r, \mathbf{v})} \left( \mathbf{1}_{\{\widehat{T}_{\text{Exp}} > t\}} e^{\int_0^t \lambda(Y(s), \Xi(s)) ds} G((Y(s), \Xi(s))_{s \leq t}) \right). \end{aligned}$$

Indeed, we can apply Theorem 1 to

$$\begin{aligned} F(\mathbf{t}, u) &= \#\{v \in \mathbf{g}(t) : v \succ u_r\} \psi(z_u(t), \mathbf{z}(t)) G((z_u(s), \mathbf{z}(s))_{s \leq t}), \\ p_u(\mathbf{t}) &= \frac{\mathbf{1}_{u \in \mathbf{g}(t), u \succ u_r}}{\#\{v \in \mathbf{g}(t) : v \succ u_r\}}, \end{aligned}$$

where  $\mathbf{g}(t)$  is the set of labels of  $\mathbf{t}$  alive at time  $t$ ,  $\mathbf{z}(t)$  is the type composition at time  $t$  of the population and  $z_u(t)$  the type of individual  $u$  at time  $t$ . We observe that  $\mathbb{E}(\mathbf{1}_{T_{\text{Exp}} > t, \mathbb{G}(t) \neq \emptyset} F(\mathcal{T}(t), U(t)))$  gives the left hand side of (5) by exploiting the law  $p(\mathcal{T}(t))$  of  $U(t)$  conditionally on  $\mathcal{T}(t)$ , while  $\mathbb{E}(\mathcal{W}(t) F(\mathcal{A}(t), E(t)))$  yields the right hand side of (5) by conditioning by  $E(0) = u_r$ . We can also remark that (5) 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. Identity (5) proves the first expected expression of semigroup  $M$  by considering marginal functions at time  $t$ . It also yields the second one by summation over initial individuals, which ends the proof.  $\square$

**Proposition 2.** *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 proof of the martingale property uses  $\widehat{T}_{\text{Exp}} = +\infty$ . Indeed, otherwise mass decays and in the case of jump process, we do not have a direct compensation via a killing rate. Observe from (6) below that under the condition  $T_{\text{Exp}} = +\infty$  p.s., the fact that  $M$  is a martingale (and not only a local martingale) is equivalent to  $\widehat{T}_{\text{Exp}} = +\infty$  a.s.

Besides, the limit  $W$  may degenerate to 0. In the case of branching processes, the criterion for non-degenerescence 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 in the single type case, following the spinal approach of [38] for Galton Watson processes. It corresponds to the case  $\psi = 1$ . Then  $\lambda(x, \mathbf{z}) = \sum_{\mathbf{k} \in \mathcal{Z}} \tau_{\mathbf{k}}(x, \mathbf{z}) \|\mathbf{k}\|_1 - \tau(x, \mathbf{z})$  yields the growth rate induced by individuals of type  $x$  among population  $\mathbf{z}$ .

Finally, we stress that the case when the semigroup  $M$  has a positive eigenfunction (harmonic function) allows to simplify the exponential term, since  $\lambda$  is then constant. It is of particular interest and will be exploited in applications of the next sections. In population dynamics and genetics, this eigenfunction corresponds to the notion of *reproductive value*, giving the long term impact in terms of population size of a given individual (depending on its trait). We refer to [39, 5] and references therein for general results ensuring existence and/or uniqueness of eigenelements of positive semigroup in related contexts.

*Proof.* The initial condition  $\mathbf{x}$  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

$$(6) \quad \langle \mathbf{v}, \psi(\cdot, \mathbf{v}) \rangle \mathbb{P}(\widehat{T}_{\text{Exp}} > t) = \mathbb{E} \left( \sum_{u \in \mathbb{G}(t)} e^{-\int_0^t \lambda(Z_u(s), \mathbf{Z}(s)) ds} \psi(Z_u(t), \mathbf{Z}(t)) \right)$$

for any  $t \geq 0$ . This identity guarantees the integrability of  $M$ . Similarly Markov property and (5) allow to write for  $u, t$  fixed, on the event  $u \in \mathbb{G}(t)$ ,

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

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.  $\square$

### 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 forget bold letters in this section for single type case and  $(Z(t))_{t \geq 0}$  is the jump Markov process on  $\mathbb{N}_0$  giving the population size along time.

We consider  $\psi : \mathbb{N} \rightarrow (0, \infty)$  and the  $\psi$ -spine construction is as follows. The distinguished individual is replaced by  $k \in \mathbb{N}$  individuals at rate

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

Among these offsprings, each individual is chosen to be the new label of the spine with probability  $1/k$ .

The individuals but the spine branch and are replaced by  $k \in \mathbb{N}_0$  individuals at rate

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

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

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

Thus,  $\Xi$  is a population process with individual branching rates  $\tau_k(z)\psi(z+k)/\psi(z)$ , plus additional size depend immigration, where  $k \geq 1$  immigrants arrive in the population of size  $z \geq 1$  at rate  $k\tau_k(z)\psi(z-1+k)/\psi(z)$ .

Generator  $\mathcal{G}$  is now defined for real valued functions  $f$  on  $\mathbb{N}$  and writes for  $z \geq 1$  as

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

Function  $\lambda = \mathcal{G}\psi/\psi$  becomes for  $z \geq 1$ ,

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

**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 eigenfunction associated with the eigenvalue  $\lambda = 0$  when the process cannot reach (and be absorbed) in 0, i.e. in the case  $\tau_0(1) = 0$ . Let us then consider a uniform choice  $U(t)$  among individuals alive at time  $t$ . Conditionally on  $\mathbb{G}(t)$ , we assume that this variable is independent of  $\mathcal{T}(t)$  and uniformly distributed  $\mathbb{G}(t)$ , when this latter is non empty. Since here  $\lambda = 0$ , we get  $\mathcal{W}(t) = \mathbf{1}_{T_{\text{Exp}} > t}$  a.s. and Theorem 1 yields:

**Proposition 3.** *Assume  $\tau_0(1) = 0$ . Then, for any  $t \geq 0$ ,  $\mathbf{1}_{T_{\text{Exp}} > t}(\mathcal{T}(t), U(t))$  is distributed as  $\mathbf{1}_{\widehat{T}_{\text{Exp}} > t}(\mathcal{A}(t), E(t))$ , where  $(\mathcal{A}, E)$  is the  $1/z$ -spine construction.*

This  $1/z$ -spine construction consists in a single type density dependent Markov process with a distinguished individual and individual jump rates

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

for  $z \geq 1, k \geq 0$ . We recover the fact that the process  $\Xi$  counting the size of the population in the  $1/z$ -spine construction is distributed as the original process  $Z$ . We give a consequence about ancestral lineage of samples, which will be useful. We consider the case when the size of the population of the spine construction  $\#\mathbb{V}(t)$  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

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

Before applying this result, 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  $\psi$  is then non-explicit in general, but can be written as  $h(z)/z$  for  $z \geq 1$ , where  $h$  is the harmonic function of the killed process. It allows in particular to describe sampling in



the quasistationary regime, i.e. when the process conditioned to survive at a given time converges in law. In that case the process  $\Xi$  survives a.s. but the original process dies out.

**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 [5, 7, 8, 13, 36] and references therein. We assume for this example that cells divide in two daughter cells

$$(7) \quad b_z = \tau_2(z), \quad d_z = \tau_0(z), \quad \tau_1(z) = \tau_k(z) = 0 \quad \text{for } z \geq 1, k \geq 3.$$

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

$$(8) \quad \sup_{z \geq 1} b_z \leq \bar{b}, \quad d_1 = 0.$$

So process  $Z$  is well defined and positive for any time and we are exploiting the  $1/z$  spine construction. Each cell is now equipped with a size, which 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 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 offsprings 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  $1 - F$ , i.e. the law of  $F$  is symmetric with respect to one half. Let us refer to [3, 36] 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. For that purpose and convenience, we use a Poisson representation for constructing the original birth and death process  $Z$ , given by a Poisson point measure and use the same measure for the spine construction. More precisely, we define the process  $(Z(t), \zeta^*(t))_{t \geq 0}$  as the unique strong solution of the following stochastic differential equation

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

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

where  $\mathcal{N}$  is a Poisson point measure on  $\mathbb{R}_+^2 \times (0, 1)$  with intensity  $ds du \mathbb{P}(F \in df)$ . Existence and strong uniqueness are classical and we refer e.g. to [24, 4]. In words,  $\zeta^*$  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  $Z$ . Since explosion is here excluded by assumption, Proposition 3 yields:

**Proposition 4.** *Assume that (7) and (8) hold. Let  $t \geq 0$  and  $U(t)$  be a uniform choice among  $\mathbb{G}(t)$ , which is independent of  $(\zeta_u(s))_{s \geq 0, u \in \mathbb{G}(s)}$  conditionally on  $\mathbb{G}(t)$ . Then,  $(Z(t), \zeta_{U(t)}(t))$  is distributed as  $(Z(t), \zeta^*(t))$ .*

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. Thus we also assume now that the Markov process  $Z$  is irreducible and positive recurrent on  $\mathbb{N}$  (see [26, 27] for explicit conditions). Then  $Z(t)$  converges in law to the unique stationary distribution  $\pi = (\pi_z)_{z \geq 1}$  as  $t$  tends to infinity and we set

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

Finally, we make the following moment assumption:

$$(9) \quad \mathbb{E}(\log(F)^2) < \infty$$

and we get under these conditions the following classification for this model.

**Corollary 1.** *Assume that (7)-(8)-(9) hold and that  $Z$  is irreducible and positive recurrent. i) If  $r < \mathbb{E}(\log(1/F)) \hat{\pi}$ , then  $\zeta^*(t)$  tends a.s. to 0 as  $t \rightarrow \infty$  and*

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

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

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

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

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

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

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

where

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

and  $\tilde{\mathcal{N}}$  is the compensated measure of  $\mathcal{N}$ . Birkhoff theorem for continuous time Markov processes [40] ensures that

$$\frac{1}{t} \int_0^t h(Z(s)) ds \xrightarrow{t \rightarrow \infty} \sum_{z \geq 1} h(z) \pi_z \quad \text{a.s.}$$

since  $h$  is bounded by Assumption (8). Besides  $(M(t))_{t \geq 0}$  is a martingale with bounded quadratic variation on finite time intervals by Assumption (9). We deduce that

$$\frac{1}{t}M(t) \xrightarrow{t \rightarrow \infty} 0 \quad \text{a.s.}$$

and we can conclude that  $\log(\zeta^*(t))$  tends to  $+\infty$  or  $-\infty$  depending on the fact that  $r + \alpha \sum_{k \geq 0} h(z)\pi_z$  is positive or negative.

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

$$\mathbb{P}(\max\{\zeta_u(t) : u \in \mathbb{G}(t)\} \geq \varepsilon, \#\mathbb{G}(t) \leq A) \leq A\mathbb{P}(\zeta_{U(t)}(t) \geq \varepsilon) = A\mathbb{P}(\zeta^*(t) \geq \varepsilon)$$

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

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  $\zeta^*$  oscillates a.s. and that for any  $\varepsilon > 0$ ,

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

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 with other cells is  $c > 0$ :

$$b_z = b, \quad d_z = c(z - 1) \quad (z \geq 1).$$

The stationary probability  $\pi$  of the population size is

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

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):

$$r < 2b \left(1 - \frac{c}{b} + \frac{1}{e^{b/c} - 1}\right) \mathbb{E}(\log(1/F)).$$

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. [4]. Both division (by splitting) and competition (by killing) participate to the regulation of the growth of the cell mass. The threshold above (so as the mass growth rate, see the proof) makes appear the function  $f(b, b/c)$ , where  $f(b, y) = b(1 - 1/y + 1/(e^y - 1))$  is increasing with respect to  $b$  and  $y$ . The value of  $b/c$  is linked to a carrying capacity, i.e. a value above which the population size tend to decrease. Competition destructs cells and could help for regulation but its also make the carrying capacity decrease and at end it plays against the regulation of the trait.

**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-degenerescence of the limiting martingale [38]. For a Galton-Watson process  $Z$  with reproduction r.v.  $L$ ,  $W = \lim_{n \rightarrow \infty} Z_n / \mathbb{E}(L)^n$  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 work in the case when the original process and the spine construction do not explode.

We follow the ideas of [38]. We recall that  $\tau_0(z) < \infty$  for any  $z \geq 1$  and assume in this section that for any  $z \geq 1$ ,

$$(10) \quad \sum_{k \geq 1} k \tau_k(z) < \infty.$$

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.

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

Similarly, we write

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

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

**Lemma 2.** *Assume (10) and that  $T_{\text{Exp}} = +\infty$  and  $\widehat{T}_{\text{Exp}} = +\infty$  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,  $\Xi - 1$  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  $\Xi - 1$  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  $\lambda$  and  $\tau$  are constant and  $M(t) = \exp(-\lambda t) Z(t)$ .

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

$$F(\mathbf{t}, e) = F(\mathbf{t}) = \#\mathbf{g}(t) e^{-\int_0^t \lambda(\#\mathbf{g}(s)) ds} \mathbf{1}_{\{\sup_{s \leq t} \#\mathbf{g}(s) \cdot e^{-\int_0^s \lambda(\#\mathbf{g}(v)) dv} \leq K\}}$$

or can apply (6) 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  $t \rightarrow \infty$  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 of the proposition by monotone limit letting  $K$  go to infinity. For the second part, we observe that  $\Xi$  jumps from  $z$  to  $z + k - 1$  with rate  $\widehat{\tau}_k^*(z) + (z - 1)\widehat{\tau}_k(z) = k\tau_k(z) + (z - 1)\tau_k(z)$ .  $\square$

Let us derive moment conditions which guarantee that the limiting martingale is non degenerated. These issues have already been considered, at least in the discrete framework, motivated by controlled Galton-Watson processes [33, 29]. 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. The case where the process becomes critical asymptotically has received lots of attention and is often called *near or almost critical*. We focus in the application here on the case where the process grows exponentially but density depend 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*

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

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

The uniformity assumptions can be partially relaxed. For instance, with some irreducibility condition one can only assume that  $\lambda$  is lower bounded by a positive constant for  $z$  large enough. The  $L \log L$  moment condition is necessary for positivity of  $\mathbb{E}(W)$  in some cases including branching processes or perturbation of them.

*Proof.* We first notice that the fact  $\sum_{k \geq 1} k \sup_{z \geq 1} \tau_k(z)$  is finite provides an upperbound of the growth rate of the size of the population of the original process  $Z$ . It guarantees that  $T_{\text{Exp}} = \infty$  a.s. Let us deal with the 1-spine construction and localize the process by considering the stopping times  $T^m = \inf\{t \geq 0 : \Xi_t \geq m\}$  for  $m \geq 1$ . We separate the component coming from immigration and give a trajectorial representation of  $\Xi - 1$ . Let us consider  $V = \Xi - 1$ . For  $t \leq T^m$ , it is defined as the unique strong solution of the following SDE

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

where we use two independent Poisson point measures,  $\mathcal{N}$  and  $\mathcal{N}_I$ , with intensity  $ds du \mathbf{n}(dk)$  on  $\mathbb{R}_+^2 \times \mathbb{N}$ , where  $\mathbf{n} = \sum_{k \in \mathbb{N}_0} \delta_k$  is the counting measure, see e.g. [4]. Defining

$$N_1(t) = V(t)e^{-\int_0^t \lambda(\Xi(s))ds} = N(t) - e^{-\int_0^t \lambda(\Xi(s))ds},$$

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

$$\begin{aligned} N_1(t) &= N_1(0) - \int_0^t \lambda(\Xi(s))V(s)ds \\ &\quad + \int_0^t \int_{\mathbb{R}_+ \times \mathbb{N}} \mathbf{1}_{\{u \leq V(s-) \tau_k(\Xi(s-))\}} (k-1) e^{-\int_0^s \lambda(\Xi(v))dv} \mathcal{N}(ds, du, dk) \\ &\quad + \int_0^t \int_{\mathbb{R}_+ \times \mathbb{N}} \mathbf{1}_{\{u \leq k \tau_k(\Xi(s-))\}} (k-1) e^{-\int_0^s \lambda(\Xi(v))dv} \mathcal{N}_I(ds, du, dk) \end{aligned}$$

Then

$$\begin{aligned} N_1(t) &= N_1(0) + \int_0^t \int_{\mathbb{R}_+ \times \mathbb{N}} \mathbf{1}_{\{u \leq \Xi(s-) \tau_k(\Xi(s-))\}} (k-1) e^{-\int_0^s \lambda(\Xi(v))dv} \tilde{\mathcal{N}}(ds, du, dk) \\ &\quad + \int_0^t \int_{\mathbb{R}_+ \times \mathbb{N}} \mathbf{1}_{\{u \leq k \tau_k(\Xi(s-))\}} (k-1) e^{-\int_0^s \lambda(\Xi(v))dv} \mathcal{N}_I(ds, du, dk), \end{aligned}$$

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

$$\mathbb{E}_z(N_1(t \wedge T^m) | \mathcal{N}_I) \leq z - 1 + \int_0^t \mathbf{1}_{u \leq k p_k} (k-1) e^{-cs} \mathcal{N}_I(ds, du, dk).$$

Let us show that the  $L \log L$  assumption ensures that the right hand side is a.s. bounded with respect to  $t$ . Indeed

$$(11) \quad \int_0^\infty \mathbf{1}_{u \leq k p_k} (k-1) e^{-cs} \mathcal{N}_I(ds, du, dk) = \sum_{i \geq 0} \widehat{L}_i e^{-cS_i}$$

is a compound Poisson process, where  $(S_{i+1} - S_i : i \geq 0)$  are i.i.d. exponential random variables with parameters  $\mu = \sum_{k \geq 2} k p_k \in [0, \infty)$  and  $(\widehat{L}_i : i \geq 0)$  are i.i.d random variables with the size bias distribution  $\mathbb{P}(\widehat{L} = k-1) = k p_k / \mu$  for  $k \geq 2$ . By Borel Cantelli lemma, the fact that  $\sum_{k \geq 2} \log(k) k p_k < \infty$  ensures that  $\limsup_{n \rightarrow \infty} \log(\widehat{L}_n)/n = 0$  p.s. Adding that  $c > 0$  and that  $S_i$  grows linearly a.s. to infinity as  $i$  tends to infinity, the series in (11) are a.s. finite.

We get then that  $\Xi$  is not explosive by using that  $\lambda$  is upper bounded and letting  $m \rightarrow \infty$ . By Fatou's lemma, we obtain that  $\sup_{t \geq 0} \mathbb{E}_z(N_1(t) | \mathcal{N}_I) < \infty$  a.s. Thus, the quenched submartingale  $(N_1(t))_{t \geq 0}$  converges to a finite random variable a.s. as  $t \rightarrow \infty$ . So does  $N(t)$ , towards the same limit, since  $\inf \lambda > 0$ . Lemma 2 allows then to conclude.  $\square$

In particular, we can describe the growth of the process  $Z$ . When  $\tau(z)$  tends to  $b$  as  $z \rightarrow \infty$  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].

**Corollary 2.** *Under assumptions of Proposition 5, assume further that  $\lim_{z \rightarrow \infty} \lambda(z) = b > 0$ . Then*

$$\lim_{t \rightarrow \infty} \log(Z_t)/t = b \quad \text{with positive probability.}$$

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

$$\lim_{z \rightarrow \infty} e^{-bt} Z(t) = W \in (0, \infty) \quad \text{with positive probability.}$$

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 and a direct consequence of the branching property. We expect extensions to similar processes with interactions. The papers mentioned above in discrete time contain interesting results in this direction. Finding relevant general conditions seems a delicate and interesting problem. Extension to multiple dimension is also natural. In infinite dimension, for the case of branching processes, we refer to [2] for a similar point of view and sufficient conditions of non-degenerescence.

*Proof.* Using monotonicity of  $Z$  or the previous proposition, we first observe that  $Z_t$  goes to infinity a.s. as  $t \rightarrow \infty$ . Then  $\lambda(Z_t)$  tends to  $b$  a.s. and the previous proposition ensures  $\lim_{t \rightarrow \infty} \log(Z_t)/t = b$  with positive probability.

Besides writing  $r(z) = \lambda(z) - b$ ,  $\int_0^\infty |r(Z_t)| dt < \infty$  a.s. since  $|r(Z_t)| \leq C \log(\exp(bt/2) + 1)^{-a}$  for  $t$  large enough. It ensures that  $\exp(\int_0^t \lambda(Z_s) ds)$  is a.s. equivalent to  $\exp(bt)$ , which ends the proof.  $\square$

#### 4. APPLICATIONS TO MULTITYPE PROCESSES

Let us turn to structured populations with a finite number of types, i.e.  $\#\mathcal{X} < \infty$ . 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 of dynamical systems.

**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

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

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

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

We assume that the initial condition  $\mathbf{Z}(0)$  is a random vector of  $\mathbb{N}^{\mathcal{X}}$  such that  $\|\mathbf{Z}(0)\|_1 \leq \bar{z}$  a.s. We observe that boundedness ensures that the process a.s. does not explode. We recall that  $x(\mathbf{v})$  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

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

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 for any  $(x, \mathbf{z}) \in \mathcal{S}$

$$\begin{aligned}
\mathcal{G}f(x, \mathbf{z}) &= \sum_{\substack{\mathbf{k} \in \mathcal{Z} \\ \|\mathbf{z} + \mathbf{k} - \mathbf{e}(x)\|_1 \leq \bar{z}}} \tau_{\mathbf{k}}(x, \mathbf{z}) \langle \mathbf{k}, f(\cdot, \mathbf{z} + \mathbf{k} - \mathbf{e}(x)) \rangle \\
&+ \sum_{\substack{y \in \mathcal{X}, \mathbf{k} \in \mathcal{Z} \\ \|\mathbf{z} + \mathbf{k} - \mathbf{e}(y)\|_1 \leq \bar{z}}} \tau_{\mathbf{k}}(y, \mathbf{z}) (\mathbf{z}_y - \delta_y^x) f(x, \mathbf{z} + \mathbf{k} - \mathbf{e}(y)) - \left( \sum_{y \in \mathcal{X}} \tau(y, \mathbf{z}) \mathbf{z}_y \right) f(x, \mathbf{z}).
\end{aligned}$$

Functions on  $\mathcal{S}$  can be identified to real vectors indexed by  $\mathcal{S}$ , which is finite. The operator  $\mathcal{G}$  is thus 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 (or eigenvector)  $h$  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 [25, 20] and references therein for similar issues for multitype branching processes and the description of ancestral lineage using the eigenelements of the first moment semigroup. This description will involve the stationary law of the Markov process  $(Y(t), \Xi(t))_{t \geq 0}$ . Finally, Perron Frobenius theorem also ensures the existence of a left eigenvector  $\gamma$  of matrix  $\mathcal{G}$  (or right eigenvector for the dual operator  $\mathcal{G}^*$ ), for the same eigenvalue as  $h$ .

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

$$P_a(t) = \int_0^t \mathbf{1}_{(Z_{U(t)}(s), Z_s) = a} ds, \quad N_{a, \mathbf{k}}(t) = \#\{u \preceq U(t) : (Z_u, \mathbf{Z}^u) = a, \mathbf{K}_u = \mathbf{k}\},$$

where  $Z_u(s)$  is the type of the unique ancestor of  $u$  at time  $s$ ,  $\mathbf{Z}^u$  (resp.  $\mathbf{K}_u$ ) is the type composition of the population (resp. of offsprings of individual  $u$ ) 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 that for any  $a, b \in \mathcal{S}$ ,  $M_1 \mathbf{1}_b(a) > 0$ .*

*Then, there exists a unique triplet  $(\lambda, h, \gamma)$  where  $\lambda \in (-\infty, 0]$  and  $h, \gamma \in (0, \infty)^{\mathcal{S}}$  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  $t \geq 0$  and any measurable non-negative function  $F : \mathbb{T} \times \mathcal{U} \rightarrow \mathbb{R}$ , we have for any non-empty initial condition  $\mathbf{x}$ ,*

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

Assumption  $M_1 \mathbf{1}_b(a) > 0$  amounts to an irreducibility property of the population process  $\mathbf{Z}$ , with a distinguished particle, excluding the state when the whole population is extinct. 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, each individual gives birth to one offsprings with a 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 is a direct consequence of Perron Frobenius theorem. The fact that the eigenvalue  $\lambda$  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  $\lambda$  is constant since  $h$  is an eigenfunction.  $\square$

The Markov process  $(Y, \Xi)$  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  $\mathbf{x}$  (omitted in notation).

**Corollary 3.** *Under conditions of Proposition 6,  $(Y(t), \Xi(t))$  converges in law to  $\pi = (\pi_a)_{a \in \mathcal{S}}$  as  $t \rightarrow \infty$ , 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  $\|\mathbf{z} + \mathbf{k} - \mathbf{e}(x)\|_1 \leq \bar{z}$ ,*

$$\left( \frac{P_a(t)}{t}, \frac{N_{a,\mathbf{k}}(t)}{t} \right)_{|\mathbb{G}(t) \neq \emptyset} \Rightarrow (\pi_a, \gamma_a \tau_{\mathbf{k}}(a) \langle \mathbf{k}, h(\cdot, \mathbf{z} + \mathbf{k} - \mathbf{e}(x)) \rangle)$$

*as  $t \rightarrow \infty$ , where the convergence of the couple holds in law conditionally on the event  $\mathbb{G}(t) \neq \emptyset$ .*

*Proof.* First, we recall that the generator of  $(Y, \Xi)$  is the  $h$ -Doob-transform of  $\mathcal{G}$ , i.e.  $f \rightarrow \mathcal{G}(hf)/h - \lambda f$ . We can then check that  $(h_a \gamma_a)_{a \in \mathcal{S}}$  is a stationary law, using that  $\gamma \mathcal{G} = 0$ . Uniqueness of stationary law holds by irreducibility and the first part is proved. We consider the  $h$ -spine construction  $(\mathcal{A}, E)$  and we write for  $a = (x, \mathbf{z}) \in \mathcal{S}$  and  $\mathbf{k} \in \mathcal{Z}$ ,

$$N_{a,\mathbf{k}}^*(t) = \#\{u \preceq E(t) : (\Xi_u, \Xi^u) = a, \widehat{\mathbf{K}}_u^* = \mathbf{k}\},$$

where  $\widehat{\mathbf{K}}_u^*$  is the type composition of the offsprings of the spine  $u$  when it branches and  $\Xi^u$  the state of the population when it branches. Then ergodic theorem ensures the a.s. convergence:

$$(12) \quad \lim_{t \rightarrow \infty} \frac{N_{a,\mathbf{k}}^*(t)}{t} = \pi_a \tau_{\mathbf{k}}(a) \frac{\langle \mathbf{k}, h(\cdot, \mathbf{z} + \mathbf{k} - \mathbf{e}(x)) \rangle}{h(a)} =: \tilde{\pi}_{a,\mathbf{k}}.$$

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  $t \geq 0$  and  $F$  measurable and positive, we get

$$\mathbb{E}(\mathbf{1}_{\mathbb{G}(t) \neq \emptyset} F(N_{a,\mathbf{k}}(t))) = e^{\lambda t} \langle \mathbf{v}, h(\cdot, \mathbf{v}) \rangle \mathbb{E} \left( \frac{1}{h(Y(t), \Xi(t)) \|\Xi(t)\|_1} F(N_{a,\mathbf{k}}^*(t)) \right)$$

and

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

Considering  $F(n) = \mathbf{1}_{|n/t - \tilde{\pi}_{a,\mathbf{k}}| \geq \varepsilon}$  for  $\varepsilon > 0$  and using that  $h$  and  $\Xi$  are bounded and taking the ratio of the two expectations, (12) yields

$$\mathbb{P}(|N_{a,\mathbf{k}}(t)/t - \tilde{\pi}_{a,\mathbf{k}}| \geq \varepsilon | \mathbb{G}(t) \neq \emptyset) \xrightarrow{t \rightarrow \infty} 0.$$

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

To get finer results on ancestral lineages with a spinal approach, one may be inspired from e.g. [20, 11, 41]. In particular, see [20] for a control of deviation of ancestral type frequency using large deviation theory for multitype branching processes. Such existence and uniqueness results can be extended to infinite type space  $\mathcal{X}$ . In particular, Krein Rutman theorem extends this setting with a compactness assumption. This result can itself be extended with perturbation of dissipative operator [39]. Irreducibility assumption can also be coupled with Lyapunov control to obtain uniqueness of eigenvalue, see [5] for a statement useful in our context. That may be the object of future interesting investigations.

To end this part on the finite case, let us consider a classical epidemiological model, SIR model. In this case irreducibility fails since *Recovered* is an absorbing state. Positive eigenfunctions exist but uniqueness does not hold. More precisely, consider  $\mathcal{X} = \{i, r\}$  and the Markov process  $\mathbf{Z} = (\mathbf{Z}_i, \mathbf{Z}_r)$  taking values in  $\{0, \dots, N\}^2$ . The processes  $\mathbf{Z}_i(t)$  and  $\mathbf{Z}_r(t)$  count respectively the number of infected and recovered individuals at time  $t$  in a fixed population  $N$ . The branching rates are

$$\tau_{(2,0)}(i, \mathbf{z}) = \beta(N - (\mathbf{z}_i + \mathbf{z}_r)), \quad \tau_{(0,1)}(i, \mathbf{z}) = \gamma,$$

where  $\beta$  is the infection rate and  $\gamma$  the remission rate. The other rates are 0. For such an example, not only the ancestral lineage of the random sample and the associated population size may be relevant for applications. When considering tracing of infected individuals, the tree of infection associated with the sample is involved. For this point, the  $\psi$ -construction should help. It is left for a future work. We could also see a counterpart in the large population approximation in the next section.

**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 [19, 30, 4] 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  $\mathbf{z} \in \mathbb{R}_+^{\mathcal{X}} \rightarrow \tau_{\mathbf{k}}(x, \mathbf{z})$  is a continuous function. Let us write

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

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

Following the rest of the paper, we write  $\mathbf{Z}^N$  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

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

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

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  $\ell^2$  uniform condition in (A1) will guarantee that the contribution of the spine in the growth of the population size is vanishing as  $N \rightarrow \infty$ . (A1) and (A2) also ensure uniform bound on the growth rate and guarantee non explosion of the processes  $Z^N$  and  $\Xi^N$  for fixed  $N$ . To ensure that  $T_{\text{Exp}}^N = \infty$  a.s., a  $\ell^1$  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

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

Thus  $\mathbf{z} \rightarrow \mathbf{z} A(\mathbf{z})$  is locally Lipschitz on  $\mathbb{R}_+^{\mathcal{X}}$ . Using (A1) guarantees the non explosivity of the dynamical system associated to this vector field. Cauchy Lipschitz theorem then ensures the existence and uniqueness of the solution  $(\mathbf{z}(t, \mathbf{v}))_{t \geq 0}$  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  $\mathbf{z}(\cdot, \mathbf{v})$  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 :

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

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

We are interested in the limiting  $\psi$ -spine construction and consider a function  $\psi$  from  $\mathcal{X} \times [0, \infty)^{\mathcal{X}}$  to  $(0, \infty)$ , such that for any  $x \in \mathcal{X}$ ,  $\psi_x : \mathbf{z} \in (0, \infty)^{\mathcal{X}} \rightarrow \psi(x, \mathbf{z})$  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  $\mathbf{k} \in \mathbb{R}_+^{\mathcal{X}}$ ,

$$(13) \quad \|\psi(x, \mathbf{z} + \mathbf{k}) - \psi(x, \mathbf{z})\|_1 \leq L \|\mathbf{k}\|_1.$$

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

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

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  $\mathbf{z}(\cdot, \mathbf{v})$ . 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  $\mathbf{z}(\cdot, \mathbf{v})$  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  $t$

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

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 as in Section 2 the Ulam Harris Neveu notation to label individuals and denote by  $\mathcal{A}_*(t)$  the tree rooted in the spine. Observe also that **(A4)** and regularity of  $\psi$  ensure that  $\psi(\cdot, \mathbf{z}(t, \mathbf{v}))$  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

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

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  $\psi$ ,  $\psi$  is in the domain of  $\mathcal{G}$  and we define  $\lambda$  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

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

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  $\emptyset$ . We endow the space  $\mathbb{T} \times \mathcal{X}$  with a  $\ell_1$  topology on the collection of labels together with their life lengths and types, defined as follows. Recall that a finite tree  $\mathbf{t} = \{(v, \ell_v, z_v) : v \in \mathcal{U}(\mathbf{t})\}$  of  $\mathbb{T}$  is a collection  $\mathcal{U}(\mathbf{t}) \subset \mathcal{U}$  of labels corresponding to individuals  $v \in \mathcal{U}(\mathbf{t})$  of the population with time length  $\ell_v$  and type  $z_v$ . For two trees  $\mathbf{t} = \{(v, \ell_v, z_v) : v \in \mathcal{U}(\mathbf{t})\}$  and

$\mathfrak{t}' = \{(v, \ell'_v, z'_v) : v \in \mathcal{U}(\mathfrak{t}')\}$ . We write  $\mathfrak{t}\Delta\mathfrak{t}' := \mathcal{U}(\mathfrak{t}) \Delta \mathcal{U}(\mathfrak{t}')$  the set of labels of  $\mathcal{U}$  in one tree but not in the other and  $\mathfrak{t} \cap \mathfrak{t}' := \mathcal{U}(\mathfrak{t}) \cap \mathcal{U}(\mathfrak{t}')$  the set of labels in both. We consider the following distance on trees

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

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  $t \geq 0$  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  $\mathbb{R}_+$ ,*

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

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  $\ell^2$  uniform bound of (A1) should be interesting. Keeping the  $\ell^1$  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. Following Section 2, we write  $(\mathcal{A}^N, E^N)$  the  $\psi_N$ -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  $\psi_N$  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

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

Theorem 1 yields

$$(14) \quad \mathbb{E}_{\mathbf{x}_N} \left( \mathbf{1}_{\{\mathbb{G}^N(t) \neq \emptyset\}} F(\mathcal{T}^N(t), U^N(t)) \right) = \langle [N\mathbf{v}]/N, \psi(\cdot, [N\mathbf{v}]/N) \rangle \mathbb{E}_{\mathbf{x}_N} (G_N(\mathcal{A}^N(t), E^N(t))),$$

where

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

Roughly speaking, all the quantities involved converge as  $N \rightarrow \infty$ . The process  $\Xi^N$  which counts the types of individuals in the  $\psi_N$ -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  $\psi$  ensures that

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

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  $(\Xi^N)_N$  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  $\Xi^N$  alone is not a Markov process. One has to consider the couple  $(Y^N, \Xi^N)_N$  but the influence of the type of the spine  $Y^N$  is vanishing in computations using  $\ell^2$  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  $(x, \mathbf{z}) \rightarrow \lambda_N(x, N\mathbf{z})$  converges uniformly on compact sets of  $\mathcal{X} \times (0, \infty)^{\mathcal{X}}$  and use a localization procedure to get the convergence in (14) as  $N \rightarrow \infty$ . Indeed,

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

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

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

tends to 0 as  $N \rightarrow \infty$ , uniformly for  $\mathbf{z} \in (\varepsilon, 1/\varepsilon)^{\mathcal{X}}$ , where  $\varepsilon \in (0, 1)$  is fixed. Besides, using (13) and **(A1)**,

$$\begin{aligned} N \sum_{y \in \mathcal{X}, \|\mathbf{k}\|_1 > \sqrt{N}} \mathbf{z}_y \tau_{\mathbf{k}}(y, \mathbf{z}) \left| \psi \left( x, \mathbf{z} + \frac{\mathbf{k} - \mathbf{e}(y)}{N} \right) - \psi(x, \mathbf{z}) \right| \\ \leq L\varepsilon^{-1} \sum_{y \in \mathcal{X}, \|\mathbf{k}\|_1 > \sqrt{N}} (\|\mathbf{k}\|_1 + 1) \tau_{\mathbf{k}}(y, \mathbf{z}) \xrightarrow{N \rightarrow \infty} 0, \end{aligned}$$

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

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

Using the convergence of  $\Xi^N$  to  $\mathbf{z}(\cdot, \mathbf{v})$  in  $\mathbb{D}(\mathbb{R}_+, \mathbb{R}_+^{\mathcal{X}})$  and **(A4)**, (14) yields

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

for  $F$  continuous, positive and bounded, where

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

and  $\mathcal{A}_*^N$  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  $\mathcal{A}_*^N$  has an offspring of size greater than  $\sqrt{N}$  tends to infinity. Thus the individual branching rates of  $\mathcal{A}_*^N$  converge uniformly to the rates of  $\mathcal{A}_*$ , using the same localization as above to keep the process  $\Xi^N$  in compact sets excluding boundaries.  $\square$

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

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

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. 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  $N \rightarrow \infty$ ,  $(\mathcal{T}_{U^N(t)}^N(t), U^N(t))$  initiated in  $\mathbf{x}_N$  converges in law to  $(\mathcal{A}(t), E(t))$  as  $N \rightarrow \infty$ .

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  $\varphi : \mathcal{X} \rightarrow (0, \infty)$  is solution of

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

and

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

It means that

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

Existence and uniqueness of positive  $\phi$  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 [31, 20]. 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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