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SPINAL CONSTRUCTIONS FOR CONTINUOUS TYPE-SPACE BRANCHING PROCESSES WITH INTERACTIONS

CHARLES MEDOUS

ABSTRACT. We consider branching processes describing structured, interacting populations in continuous time. Dynamics of each individual's characteristics and branching properties can be influenced by the entire population. We propose a spinal construction, and establish a Girsanov-type result. By combining this result with the spinal decomposition, we derive a modified continuous-time version of the Kesten-Stigum theorem that incorporates interactions. Additionally, we propose an alternative simulation approach for stochastic size-dependent populations using appropriate spine constructions.

INTRODUCTION

Spine techniques and spinal trees are classical tools in the general context of branching processes since the work of Kallenberg [35], Chauvin and Rouault [11, 12], and later Kurtz, Lyons, Pemantle and Peres [44, 43, 37]. Spinal trees are constructed based on an original branching process by distinguishing a lineage, called the spine. Its only living representative—the spinal individual—follows a biased reproduction law compared to the other individuals in the process, ensuring that the spine does not die out. In the specific yet widely studied case of size-biased trees, the reproductive law $(\hat{p}_k, k \geq 0)$ of the spinal individual is defined by

$$\hat{p}_k = \frac{k p_k}{m}, \quad \text{for } k \geq 0,$$

where m is the mean value of the law of reproduction $(p_k, k \geq 0)$ in the branching process. This size-biased reproductive law of the spinal individual is closely related to the biased ancestral reproduction [12, 26]. In fact the spine was found to characterize the process of the trait of a uniformly sampled individual, in a large population approximation see *e.g.* [45]. The sampling of $k \geq 2$ distinct individuals from those living in a population at a time t is associated with a k -spines construction. For further literature on multiple-particles sampling we refer the reader to [30, 29, 34, 13] and the references herein.

Many-to-One formulas [31, 26] are prominent among classical spine results. Such formulas derive from a Girsanov-type result on the change of probability measure associated with the spine, which can be regarded as a Doob's transform, as described in references such as [14, 2]. These formulas give expectations of sums over particles in the branching process in terms of a Feynman-Kac path integral expectation related to the spinal individual. Consequently, the spinal individual is often referred to as a "typical individual" within the population. The connection to Feynman-Kac path integrals implies a shared foundation between these concepts. For a comprehensive overview on this subject, we refer to [18].

Another interesting property of spinal constructions is the "spinal decomposition" [11, 44]. It establishes that the spine process is equivalent to the initial branching process, with the removal of one individual and the addition of an immigration source. The introduction of new individuals into the population follows the biased reproductive law specific to the spine. In recent decades, the spinal decomposition has emerged as a highly valuable tool for investigating branching processes. One of its notable contributions is providing a new

proof of the $L \log L$ criteria, which were originally proved by Kesten and Stigum for Galton-Watson (GW) processes [36] and by Biggins for continuous-time branching processes [7] using analytical methods. These results give specific conditions on the reproductive law, ensuring the non-degeneracy of the martingale involved in the spinal change of measure at infinity. By combining the spinal decomposition with a previously known result from measure theory, Lyons, Pemantle, and Peres [44] provided a probabilistic "conceptual" proof of Kesten and Stigum's theorem for single-type GW processes. This method proved to be easily generalizable to continuous-time structured branching processes [2, 26, 8] as well as branching Brownian motions [38, 22, 27]. More recently Bertoin and Mallein extended this proof for general branching Levy processes [6]. For equivalent results on superprocesses we refer to [40, 41, 42, 21, 50]. Finally, we mention Hardy and Harris [28] who adapted the spinal decomposition to prove the \mathcal{L}^p -convergence of some key martingales, which was later used to establish strong laws of large numbers [23].

The fundamental assumption in the aforementioned works is the branching property, which assumes that the behavior of all particles in the process during their life is independent of one another. However, in various systems of population dynamics such as genetics, epidemiology, chemistry, and even queueing systems, interactions between individuals do occur and this fundamental hypothesis falls apart. Recently, Bansaye [3] established a spine construction and Many-to-One formulas for interacting branching populations, where the branching rates and reproductive laws depend on the traits of all individuals in the population. These traits belong to a finite set and are fixed during the life of the individuals. Using the spinal decomposition, Bansaye has found an $L \log L$ criterion for a single-type, density-dependent population. We also mention a recent work on spine processes for density-dependent individual-based models in a large population approximation [33].

In this article we consider a wide class of continuous-time structured branching processes with general interactions. These processes are used to model structured populations, where the behavior of each individual is influenced by the overall population state. Every individual in the population is characterized by its trait, taking values in a compact subset of \mathbb{R}^d . The lifespan of each individual is exponentially distributed with a time-inhomogeneous rate that depends on the traits of all individuals. Upon an individual's death, a random number of children are generated, each inheriting random traits at birth, that are influenced by the traits of all individuals in the population. Between these branching events, the evolution of the traits of all individuals in the population is deterministic and also influenced by the entire population's state. Notably, the branching parameters are determined by the traits of all individuals, thereby the branching property no longer holds in this framework. We introduce a comprehensive spinal construction for those processes, using a change of measure associated with a positive weight function ψ_ϕ that depends on the trait of the spinal individual and of those of every individual. For a fixed function ψ_ϕ both the spinal individual and those outside the spine are subject to a bias. We derive a Girsanov-type formula associated with this change of measure, taking the form of a path-integral formulation that involves a non-linear operator. A classical approach to establishing limiting results, such as the central limit theorem or large deviations, involves determining the eigenfunctions of such operators [8, 22, 15]. However, due to the presence of interactions, this operator is contingent on the entire population, necessitating the eigenfunctions to be dependent on the traits of all individuals. Thus, the weight function ψ_ϕ must rely on both the trait of the spinal individual and the traits of all individuals in order to account for this dependency. Under certain non-explosion assumptions regarding the branching parameters and the set of weight functions, we obtain a modified Many-to-One formula. Unlike the classical Many-to-One formula- that describes the behavior of the branching process using only the behavior of the spine- our formula relies on the whole spinal population.

Subsequently, we use this result in conjunction with the spinal decomposition to establish $L \log L$ criteria. More precisely, we exhibit both a sufficient condition and a necessary condition for the non-degeneracy at infinity of the additive martingale associated with the spinal change of measure. It is important to note that this result is only applicable when $\psi_\phi \equiv 1$, and therefore, we lack knowledge regarding the limit behavior of this derivative at infinity for more intricate weight functions.

Finally we study a particular case of structured Yule process with mass loss events happening at size-dependent rates. Yule processes are pure birth processes that are widely used in population genetics to model and reconstruct phylogenetic trees, see *e.g.* Aldous' review [1]. We use the spinal construction with a multiplicative weight function to retrieve a conditional branching property in the associated spine process, and propose an efficient algorithmic construction based on this property.

Notation

In the sequel $\mathbb{N}^* = \{1, 2, \dots\}$ will denote the set of positive integers, $\mathbb{R}_+ := [0, +\infty)$ the real line, $\overline{\mathbb{R}}_+ := \mathbb{R}_+ \cup \{+\infty\}$ and $\mathbb{R}_+^* := (0, +\infty)$. We will denote respectively by $\mathfrak{B}(A, B)$ (resp. $\mathcal{C}^1(A, B)$) the set of measurable (resp. continuously differentiable) B -valued functions on a set A . For every couple (f, g) of real-valued measurable functions on a set A , we denote for all x , $fg(x)$ the product $f(x)g(x)$. We denote by $\mathcal{M}_F(\mathcal{A})$ the set of finite non-negative measures on a set \mathcal{A} .

The set of trait \mathcal{X} is a compact subset of \mathbb{R}^d equipped with the ℓ_1 -norm on \mathbb{R}^d , that is denoted $|x|$ for all $x \in \mathcal{X}$. We denote \cdot the canonical scalar product on \mathbb{R}^d .

We use the Ulam-Harris-Neveu notations [47] to label these individuals. We introduce the set of labels:

$$\mathcal{U} := \{\emptyset\} \cup \bigcup_{k \geq 0} (\mathbb{N}^*)^{k+1}.$$

We consider branching processes starting from multiple initial individuals, thus the root \emptyset will be treated as a phantom individual and its direct descendants will be the ancestor generation. For two elements u, v of $\mathcal{U} \setminus \{\emptyset\}$, there exist two positive integers n, p such that $u = (u_1, \dots, u_n)$ and $v = (v_1, \dots, v_p)$ and we write $uv := (u_1, \dots, u_n, v_1, \dots, v_p)$ the concatenation of u and v . We identify both $\emptyset u$ and $u\emptyset$ with u . An individual $v \in \mathcal{U}$ is a descendant of u if there exists $w \in \mathcal{U}$ such that $v = uw$. In this case we denote $u \preceq v$ and we denote $u \prec v$ if $w \neq \emptyset$.

Let us introduce $\overline{\mathbb{V}}$ the subset of $\mathcal{M}_F(\mathcal{U} \times \mathcal{X})$ composed of all finite point measures on $\mathcal{U} \times \mathcal{X}$, that is

$$\overline{\mathbb{V}} := \left\{ \sum_{i=1}^N \delta_{(u^i, x^i)}, N \in \mathbb{N}, (u^i, 1 \leq i \leq N) \in \mathcal{U}^N, (x^i, 1 \leq i \leq N) \in \mathcal{X}^N \right\}.$$

We also define the set of marginal population measures, that is

$$\mathbb{V} := \left\{ \sum_{i=1}^N \delta_{x^i}, N \in \mathbb{N}, (x^i, 1 \leq i \leq N) \in \mathcal{X}^N \right\}.$$

For any measure $\bar{\nu} = \sum_{i=1}^N \delta_{(u^i, x^i)}$ in $\overline{\mathbb{V}}$, we will write $\nu := \sum_{i=1}^N \delta_{x^i}$ its projection on \mathbb{V} . By convention, if the number of points in the measure is $N = 0$, $\bar{\nu}$ and ν are the trivial zero measures on $\mathcal{U} \times \mathcal{X}$ and \mathcal{X} . We introduce for every $\bar{\nu} \in \overline{\mathbb{V}}$, every $g \in \mathfrak{B}(\mathcal{U} \times \mathcal{X}, \mathbb{R})$ and every $f \in \mathfrak{B}(\mathcal{X}, \mathbb{R})$

$$\langle \bar{\nu}, g \rangle := \int_{\mathcal{U} \times \mathcal{X}} g(u, x) \bar{\nu}(du, dx), \quad \text{and} \quad \langle \nu, f \rangle := \int_{\mathcal{X}} f(x) \nu(dx).$$

Finally, we denote by $\mathbb{D}(\mathcal{A}, \mathcal{M})$ the Skorohod space of càdlàg functions from a subset \mathcal{A} of \mathbb{R}_+ to a set \mathcal{M} . For every process $(X_t, t \in \mathcal{A}) \in \mathbb{D}(\mathcal{A}, \mathcal{M})$ and $x \in \mathcal{M}$, we will denote

$$\mathbb{E}_x[f(X_t)] := \mathbb{E}[f(X_t) | X_0 = x] \quad \text{and} \quad \mathbb{P}_x(f(X_t)) := \mathbb{P}(f(X_t) | X_0 = x).$$

1. DEFINITION OF THE POPULATION

In this section we describe informally the population process. Its rigorous definition as a strong solution of a stochastic differential equation (SDE) is presented in Section 5.1.

The population is described at any time $t \in \mathbb{R}_+$ by the finite point measure $\bar{\nu}_t \in \bar{\mathbb{V}}$ given by the sum of the Dirac masses at the pair composed of the label and the trait of every individual living in the population at this time. We write

$$\mathbb{G}(t) := \left\{ u \in \mathcal{U} : \int_{\mathcal{U} \times \mathcal{X}} \mathbb{1}_{\{v=u\}} \bar{\nu}_t(dv, dx) > 0 \right\}$$

the set of labels of living individuals at time t . For every individual labeled by $u \in \mathbb{G}(t)$ we denote X_t^u its trait, and with a slight abuse of notation, X_s^u will denote the trait of its unique ancestor living at time $s \in [0, t]$. The stochastic point process $(\bar{\nu}_t, t \geq 0) \in \mathbb{D}(\mathbb{R}_+, \bar{\mathbb{V}})$ describing the evolution of the population and its associated marginal process are given, for every $t \geq 0$, by

$$\bar{\nu}_t = \sum_{u \in \mathbb{G}(t)} \delta_{(u, X_t^u)} \quad \text{and} \quad \nu_t = \sum_{u \in \mathbb{G}(t)} \delta_{X_t^u}.$$

Let us remark that at all time t , $\bar{\nu}_t$ encodes the trait and lineage of every living individual, and the projection ν_t on \mathbb{V} keeps the information on the trait of each individual only.

The initial population is given by a measure $\bar{z} = \sum_{i=1}^N \delta_{(u^i, x^i)}$. During their lives, the traits of the individuals in the population evolve according to population-dependent dynamics. In a population $\bar{\nu}_t$ at time t , for all $u \in \mathbb{G}(t)$

$$\frac{dX_t^u}{dt} = \mu(X_t^u, \nu_t, t),$$

where μ is a measurable \mathcal{X} -valued function on $\mathcal{X} \times \mathbb{V} \times \mathbb{R}_+$.

An individual with trait x in a population ν_t at time t dies at an instantaneous rate $B(x, \nu_t, t)$, where B is a continuous function from $\mathcal{X} \times \mathbb{V} \times \mathbb{R}_+$ to \mathbb{R}_+ . It produces an offspring of n individuals, where n is randomly chosen with distribution $(p_k(x, \nu_t, t), k \in \mathbb{N})$ of first moment $m(x, \nu_t, t)$. Thus branching events that lead to n children happen at rate $B_n(\cdot) := B(\cdot) p_n(\cdot)$. If $n \geq 1$, the traits at birth of these n children are given by the vector $\mathbf{y} = (y^1, \dots, y^n)$ randomly chosen according to $K_n(x, \nu_t, t, \cdot)$, a probability measure on \mathcal{X}^n . The labeling choice for these children is arbitrary yet necessary to uniquely define a stochastic point process in $\mathbb{D}(\mathbb{R}_+, \bar{\mathbb{V}})$. Here, for a parent individual of label u , for all $1 \leq i \leq n$, the i -th child is labeled ui and its trait is y^i , the i -th coordinate of the vector \mathbf{y} .

We denote $T_{\text{Exp}} \in \bar{\mathbb{R}}_+$ the explosion time of the process $(\bar{\nu}_t, t \geq 0)$, defined as the limit of its jumps times $(T_k, k \geq 0)$. In order to ensure the non-explosion in finite time of such a process we introduce the following set of hypotheses.

Assumption A. *We consider the following assumptions:*

- (1) *There exists a positive continuous function μ_0 on \mathbb{R}_+ , such that for all $(x, \nu, t) \in \mathcal{X} \times \mathbb{V} \times \mathbb{R}_+$*

$$|\mu(x, \nu, t)| \leq \mu_0(t) \left(1 + |x| + \left| \frac{\langle \nu, I_d \rangle}{\langle \nu, 1 \rangle} \right| \right),$$

where I_d is the identity function on \mathcal{X} .

- (2) *For all $(x, \nu, t) \in \mathcal{X} \times \mathbb{V} \times \mathbb{R}_+$,*

$$B_1(x, \nu, t) < +\infty.$$

(3) There exists a positive continuous function b_0 on \mathbb{R}_+ , such that for all $(x, \nu, t) \in \mathcal{X} \times \mathbb{V} \times \mathbb{R}_+$

$$\sum_{n \neq 1} n B_n(x, \nu, t) \leq b_0(t) (1 + |x|).$$

(4) For all $(x, \nu, t, n) \in \mathcal{X} \times \mathbb{V} \times \mathbb{R}_+ \times \mathbb{N}^*$,

$$K_n(x, \nu, t, \mathcal{A}_n(x)) = 0, \quad \text{where } \mathcal{A}_n(x) := \left\{ (y^i, 1 \leq i \leq n) \in \mathcal{X}^n : \sum_{i=1}^n |y^i| > |x| \right\}.$$

The growth rate of the traits of individuals is bounded in the first hypothesis by an exponential growth rate controlled by the trait of each individual and the mean trait in the population. The second point ensures that events that do not change the number of individuals do not accumulate in finite populations. The third hypothesis uniformly controls the minimum lifetime of an individual. This hypothesis, together with the first one, ensures that the lifespan of each individual decreases exponentially at most with its trait. Note that this assumption does not constrain the function $B_1(\cdot)$. The last hypothesis restricts the framework under consideration to fragmentation processes that do not create matter or energy. This set of hypotheses is sufficiently large to cover a large portion of models in physics and ecology, exponential growth being a classical assumption in many stochastic models in ecology and evolution, see *e.g.* [49, 16].

Proposition 1.1. *Under Assumption A, the sequence $(T_k, k \geq 0)$ of jumps times of the process $(\bar{\nu}_t, t \geq 0)$ tends to infinity almost surely.*

We can thus conclude, following the proof of Theorem 2.1 in [45], that under this set of hypotheses, the process $(\bar{\nu}_t, t \geq 0)$ is uniquely defined on \mathbb{R}_+ . However, the spinal construction introduced in Section 2 can be established with less restrictive hypotheses. In this case, accumulation of jumps times may happen in finite time and the spinal construction holds until this explosion time.

2. RESULTS

In this section, we consider the law of a randomly sampled individual in the general branching population described in Section 1. Our main result gives the appropriate change of measure linking this distribution at time t to the trajectory of an auxiliary process until this time. We then explicit this auxiliary process as a spinal construction.

The spinal construction generates a $\bar{\mathbb{W}}$ -valued process along with the label of a distinguished individual that can change with time. For convenience, we will denote $\bar{\mathbb{W}}$ and \mathbb{W} the sets such that

$$\bar{\mathbb{W}} := \{(e, \bar{\nu}) \in \mathcal{U} \times \bar{\mathbb{V}} : \langle \bar{\nu}, \mathbb{1}_{\{e\} \times \mathcal{X}} \rangle \geq 1\}, \quad \text{and} \quad \mathbb{W} := \{(x, \nu) \in \mathcal{X} \times \mathbb{V} : \langle \nu, \mathbb{1}_{\{x\}} \rangle \geq 1\}.$$

Thus, the spine process is a $\bar{\mathbb{W}}$ -valued branching process and its marginal is a \mathbb{W} -valued branching process. We propose here a general spinal construction, where branching rates are biased with a weight function ψ_ϕ , that is an element of the set \mathcal{D} , defined by

$$\mathcal{D} := \{F_f \in \mathfrak{B}(\mathbb{W} \times \mathbb{R}_+, \mathbb{R}_+) \text{ s.t. } (f, F) \in \mathcal{C}^1(\mathcal{X} \times \mathbb{R}_+, \mathbb{R}) \times \mathcal{C}^1(\mathcal{X} \times \mathbb{R} \times \mathbb{R}_+, \mathbb{R}_+^*)\}, \quad (2.1)$$

where for every $(x, \nu, t) \in \mathbb{W} \times \mathbb{R}_+$, $F_f(x, \nu, t) := F(x, \langle \nu, f(\cdot, t) \rangle, t)$.

In the following, for every $(u, \bar{\nu}) \in \bar{\mathbb{W}}$ we denote x_u the trait of the individual of label u in the population $\bar{\nu}$, and for every $n \geq 0$ and every $\mathbf{y} = (y^i, 1 \leq i \leq n) \in \mathcal{X}^n$ we write

$$\bar{\nu}_+(u, \mathbf{y}) := \bar{\nu} - \delta_{(u, x_u)} + \sum_{i=1}^n \delta_{(u_i, y^i)}, \quad \text{and} \quad \nu_+(x, \mathbf{y}) := \nu - \delta_x + \sum_{i=1}^n \delta_{y^i}. \quad (2.2)$$

We introduce the key operator \mathcal{G} involved in the spinal construction. It is defined for all $F_f \in \mathcal{D}$ and $(x_e, \nu, t) \in \mathbb{W} \times \mathbb{R}_+$ by

$$\begin{aligned} \mathcal{G}F_f(x_e, \nu, t) &:= GF_f(x_e, \nu, t) \\ &+ \sum_{n \geq 0} \left\{ B_n(x_e, \nu, t) \int_{\mathcal{X}^n} \left[\sum_{i=1}^n F_f(y^i, \nu_+(x_e, \mathbf{y}), t) - F_f(x_e, \nu_+(x_e, \mathbf{y}), t) \right] K_n(x_e, \nu, t, d\mathbf{y}) \right. \\ &\quad \left. + \int_{\mathcal{X}} B_n(x, \nu, t) \int_{\mathcal{X}^n} [F_f(x_e, \nu_+(x, \mathbf{y}), t) - F_f(x_e, \nu, t)] K_n(x, \nu, t, d\mathbf{y}) \nu(dx) \right\}, \end{aligned} \quad (2.3)$$

where the operator G is the generator of the deterministic evolution of the traits between branching events, given for every $F_f \in \mathcal{D}$, and $(x_e, \nu, t) \in \mathbb{W} \times \mathbb{R}_+$ by

$$\begin{aligned} GF_f(x_e, \nu, t) &:= D_1 F(x_e, \langle \nu, f(\cdot, t) \rangle, t) \cdot \mu(x_e, \nu, t) + D_3 F(x_e, \langle \nu, f(\cdot, t) \rangle, t) \\ &\quad + D_2 F(x_e, \langle \nu, f(\cdot, t) \rangle, t) \int_{\mathcal{X}} \left[\frac{\partial f}{\partial x}(x, t) \cdot \mu(x, \nu, t) + \frac{\partial f}{\partial t}(x, t) \right] \nu(dx), \end{aligned} \quad (2.4)$$

where $D_i F(\cdot, \cdot)$ denotes the derivative of the function $F \in \mathcal{C}^1(\mathcal{X} \times \mathbb{R} \times \mathbb{R}_+, \mathbb{R}_+^*)$ with respect to i -th variable. Rigorously, the previously introduced objects are families of operators $(\mathcal{G}_{(x, \nu, t)}, (x, \nu, t) \in \mathcal{X} \times \mathbb{V} \times \mathbb{R}_+)$ and $(G_{(x, \nu, t)}, (x, \nu, t) \in \mathcal{X} \times \mathbb{V} \times \mathbb{R}_+)$. This abuse of notation will be used for the subsequently introduced operators in this work. The operator \mathcal{G} is generally not the generator of a conservative Markov process on \mathbb{W} . Indeed $\mathcal{G}1 = B(x_e, \nu, t)(m(x_e, \nu, t) - 1)$, which is non-zero if there exists a tuple (x_e, ν, t) such that the mean number of children $m(x_e, \nu, t) \neq 1$. We point out that these operators are the equivalents- for interacting, structured, branching populations- of the Schrödinger operator \mathcal{G} introduced in [15].

To ensure that for all $(x_e, \nu, t) \in \mathbb{W} \times \mathbb{R}_+$ the function $\mathcal{G}F_f(x_e, \nu, t)$ is finite we make an assumption on the functions $F_f \in \mathcal{D}$.

Assumption B. *Let $(p_n, n \in \mathbb{N})$ and $(K_n, n \in \mathbb{N})$ be the reproduction parameters of the original branching process and $\psi_\phi \in \mathcal{D}$ a weight-function. For all $(x, x_e, \nu, t) \in \mathcal{X} \times \mathbb{W} \times \mathbb{R}_+$,*

$$\sum_{n \in \mathbb{N}} p_n(\rho) \int_{\mathcal{X}^n} \left(\psi_\phi(x_e, \nu_+(x, \mathbf{y}), t) + \sum_{i=1}^n \psi_\phi(y^i, \nu_+(x, \mathbf{y}), t) \right) K_n(\rho, d\mathbf{y}) < +\infty.$$

Remark that for a chosen set of parameters of the original branching process $(\nu_s, s \geq 0)$, this assumption restricts the set of suitable weight functions.

We will establish in Proposition 2.4 that the operator \mathcal{G} constructs the generator $\widehat{\mathcal{L}}_{\psi_\phi}$ of the spine process associated with a function $\psi_\phi \in \mathcal{D}$ ensuring Assumption B, defined for functions F_f such that $(f, F) \in \mathcal{C}^1(\mathcal{U} \times \mathcal{X} \times \mathbb{R}_+, \mathbb{R}) \times \mathcal{C}^1(\mathcal{U} \times \mathbb{R} \times \mathbb{R}_+, \mathbb{R}_+^*)$ and for all $(e, \bar{\nu}, t) \in \overline{\mathbb{W}} \times \mathbb{R}_+$ by

$$\begin{aligned} \widehat{\mathcal{L}}_{\psi_\phi} F_f(e, \bar{\nu}, t) &:= \widehat{G}F_f(e, \bar{\nu}, t) \\ &+ \sum_{n \geq 0} \int_{\mathcal{U} \times \mathcal{X}} B_n(x, \nu, t) \int_{\mathcal{X}^n} \left\{ \mathbb{1}_{\{u=e\}} \sum_{i=1}^n [F_f(ei, \bar{\nu}_+(e, \mathbf{y}), t) - F_f(e, \bar{\nu}, t)] \frac{\psi_\phi(y^i, \nu_+(x_e, \mathbf{y}), t)}{\psi_\phi(x_e, \nu, t)} \right. \\ &\quad \left. + \mathbb{1}_{\{u \neq e\}} [F_f(e, \bar{\nu}_+(u, \mathbf{y}), t) - F_f(e, \bar{\nu}, t)] \frac{\psi_\phi(x_e, \nu_+(u, \mathbf{y}), t)}{\psi_\phi(x_e, \nu, t)} \right\} K_n(x, \nu, t, d\mathbf{y}) \bar{\nu}(du, dx), \end{aligned} \quad (2.5)$$

where

$$\begin{aligned} \widehat{G}F_f(e, \bar{\nu}, t) &:= D_2F(e, \langle \bar{\nu}, f(\cdot, t) \rangle, t) \int_{\mathcal{U} \times \mathcal{X}} \left[\frac{\partial f}{\partial x}(u, x, t) \cdot \mu(x, \nu, t) + \frac{\partial f}{\partial t}(u, x, t) \right] \bar{\nu}(du, dx) \\ &\quad + D_3F(e, \langle \bar{\nu}, f(\cdot, t) \rangle, t). \end{aligned}$$

Remark that branching rates of both spinal and non-spinal individuals are biased by the function ψ_ϕ . Assumption B ensures that the total branching rate is finite from every state of the spinal process, however it is not sufficient to avoid explosion of this process in finite time. Dynamics 2.2 and 2.3 below will provide a more intricate explanation of the spine process associated with this generator.

Finally, we introduce for all $t \geq 0$, the \mathcal{U} -valued random variable U_t that picks an individual alive at time t . Its law is characterized by the function $p_u(\bar{\nu}_t)$ which yields the probability to choose the individual of label u in the set $\mathbb{G}(t)$. We can now state our main result, that is a Girsanov-type formula for the spinal change of measure. It characterizes the joint probability distribution of $(U_t, (\bar{\nu}_s, s \leq t))$ - that is the randomly sampled individual in the population $\bar{\nu}_t$ at time t and the whole trajectory of the population until this time- and links it to the law of the spine process through a path-integral formula.

Theorem 2.1. *Let $\psi_\phi \in \mathcal{D}$ verifying Assumption B, $t \geq 0$, and $\bar{z} \in \bar{\mathbb{W}}$. Let $((E_t, \bar{\chi}_t), t \geq 0)$ be the time-inhomogeneous $\bar{\mathbb{W}}$ -valued branching process defined by the infinitesimal generator $\widehat{\mathcal{L}}_{\psi_\phi}$. Let \widehat{T}_{Exp} denote its explosion time and $((Y_t, \chi_t), t \geq 0)$ its projection on \mathbb{W} .*

Under Assumption B, for every measurable non-negative function H on $\mathcal{U} \times \mathbb{D}([0, t], \mathbb{V})$:

$$\begin{aligned} \mathbb{E}_{\bar{z}} \left[\mathbb{1}_{\{T_{Exp} > t, \mathbb{G}(t) \neq \emptyset\}} H(U_t, (\bar{\nu}_s, s \leq t)) \right] = \\ \langle z, \psi_\phi(\cdot, z) \rangle \mathbb{E}_{\bar{z}} \left[\mathbb{1}_{\{\widehat{T}_{Exp} > t\}} \xi(E_t, (\bar{\chi}_s, s \leq t)) H(E_t, (\bar{\chi}_s, s \leq t)) \right], \end{aligned}$$

where:

$$\xi(E_t, (\bar{\chi}_s, s \leq t)) := \frac{p_{E_t}(\bar{\chi}_t)}{\psi_\phi(Y_t, \chi_t, t)} \exp \left(\int_0^t \frac{\mathcal{G}\psi_\phi(Y_s, \chi_s, s)}{\psi_\phi(Y_s, \chi_s, s)} ds \right).$$

We take inspiration from the work of Bansaye [3] for the proof. The idea is to decompose both processes on their possible trajectories, then establish by induction on the successive jumps times the equality in law for the trajectories between these times.

The process $((E_t, \bar{\chi}_t), t \geq 0)$ gives at any time $t \geq 0$ the label of the spinal individual- that encodes the whole spine lineage- and the spinal population. Our result thus links, for every ψ_ϕ , the sampling of an individual and the trajectory of the population to the trajectory of the spine process. The path integral term that links these two terms is difficult to handle in general and finding eigenfunctions of \mathcal{G} may widely simplify the expression [15, 2, 3]. Finding such functions for single type, density-dependent populations is possible in models with simple interactions [3][Section 3]. Nevertheless, this becomes a challenging issue in the majority of scenarios. Subsequent sections of this work will explore applications of this formula where the path-integral component is tractable.

We first introduce additional notations concerning the dynamics of the spine process given by the generators introduced in (2.5). Following notations of Section 1, and disregarding the dependency on the chosen function $\psi_\phi \in \mathcal{D}$ ensuring Assumption B in the subsequent branching parameters, we introduce the dynamics of the traits in the spine process. As previously discussed, the construction distinguishes dynamics of the spine from the rest of the individuals. When there is no possible confusion, the label of the spinal individual at any time will be denoted e for convenience, and x_e its trait. We will also use for every $(x, (x_e, \nu), t) \in \mathcal{X} \times \mathbb{W} \times \mathbb{R}_+$ the notations

$$\rho_e := (x_e, \nu, t) \quad \text{and} \quad \rho := (x, \nu, t). \quad (2.6)$$

We first introduce the branching parameters of the individuals outside the spine in a spinal population.

Dynamics 2.2 (Individuals outside the spine). *For all $(n, x, (x_e, \nu), t)$ in $\mathbb{N}^* \times \mathcal{X} \times \mathbb{W} \times \mathbb{R}_+$*

- (i) $\widehat{K}_n(x_e, \rho, \cdot) \in \mathcal{M}_F(\mathcal{X}^n)$ is the kernel giving the traits at birth of the n children generated by a non-spinal individual of trait x at time t in a spinal population (x_e, ν) . For all $\mathcal{A} \subset \mathcal{X}^n$,

$$\widehat{K}_n(x_e, \rho, \mathcal{A}) := \frac{1}{\widehat{\Gamma}_n(x_e, \rho)} \int_{\mathcal{A}} \psi_\phi(x_e, \nu_+(x, \mathbf{y}), t) K_n(\rho, d\mathbf{y}), \quad (2.7)$$

where $\widehat{\Gamma}_n(\cdot)$ is the normalization function, defined as

$$\widehat{\Gamma}_n(x_e, \rho) := \int_{\mathcal{X}^n} \psi_\phi(x_e, \nu_+(x, \mathbf{y}), t) K_n(\rho, d\mathbf{y}),$$

and ν_+ is defined in (2.2).

- (ii) The law $(\widehat{p}_k(x_e, \rho), k \in \mathbb{N})$ of the number of children of an individual of trait x branching at time t in a spinal population (x_e, ν) , is defined for all $n \in \mathbb{N}$ as

$$\widehat{p}_n(x_e, \rho) := \frac{1}{\sum_{k \in \mathbb{N}} \widehat{\Gamma}_k(x_e, \rho) p_k(\rho)} \widehat{\Gamma}_n(x_e, \rho) p_n(\rho).$$

- (iii) Each individual of trait x outside the spine of trait x_e in a population ν at time t , branches to n children at rate $\widehat{B}_n(x_e, \rho)$, defined as

$$\widehat{B}_n(x_e, \rho) := \frac{\widehat{\Gamma}_n(x_e, \rho)}{\psi_\phi(x_e, \nu, t)} B_n(\rho).$$

The total branching rate outside the spine is defined, for all $(x_e, \nu, t) \in \mathbb{W} \times \mathbb{R}_+$ by

$$\widehat{\tau}(x_e, \nu, t) := \int_{\mathcal{X}} \sum_{n \geq 0} \widehat{B}_n(x_e, x, \nu, t) \nu(dx) - \sum_{n \geq 0} \widehat{B}_n(x_e, \rho_e).$$

We now introduce the branching parameters of the spine in a ψ_ϕ -spinal construction.

Dynamics 2.3 (Spinal individual). *For all $(n, x, (x_e, \nu), t)$ in $\mathbb{N}^* \times \mathcal{X} \times \mathbb{W} \times \mathbb{R}_+$*

- (i) $\widehat{K}_n^*(\rho_e, \cdot) \in \mathcal{M}_F(\mathcal{X}^n)$ is the kernel giving the traits at birth of the n children generated by the spinal individual of trait x_e at time t in a population ν . For all $\mathcal{A} \subset \mathcal{X}^n$,

$$\widehat{K}_n^*(\rho_e, \mathcal{A}) := \frac{1}{\widehat{\Gamma}_n^*(\rho_e)} \int_{\mathcal{A}} \sum_{i=1}^n \psi_\phi(y^i, \nu_+(x_e, \mathbf{y}), t) K_n(\rho_e, d\mathbf{y}), \quad (2.8)$$

where $\widehat{\Gamma}_n^*(\cdot)$ is the normalization function, defined as

$$\widehat{\Gamma}_n^*(\rho_e) := \int_{\mathcal{X}^n} \sum_{i=1}^n \psi_\phi(y^i, \nu_+(x_e, \mathbf{y}), t) K_n(\rho_e, d\mathbf{y}).$$

- (ii) The law $(\widehat{p}_k^*(\rho_e), k \in \mathbb{N})$ of the number of children of the spinal individual of trait x_e branching at time t in a population ν , is defined for all $k \in \mathbb{N}$ as

$$\widehat{p}_n^*(\rho_e) := \frac{1}{\sum_{k \in \mathbb{N}} \widehat{\Gamma}_k^*(\rho_e) p_k(\rho_e)} \widehat{\Gamma}_n^*(\rho_e) p_n(\rho_e).$$

- (iii) The spinal individual of trait x_e in a population ν at time t , branches to n children at a rate $\widehat{B}_n^*(\rho_e)$, defined as

$$\widehat{B}_n^*(\rho_e) := \frac{\widehat{\Gamma}_n^*(\rho_e)}{\psi_\phi(x_e, \nu, t)} B_n(\rho_e).$$

(iv) When the spinal individual of trait x_e branches at time t in a population ν and is replaced by n children with trait \mathbf{y} , the integer-valued random variable $J(\rho_e, \mathbf{y})$ choosing the new spinal individual after a spinal branching event is given, for all $1 \leq j \leq n$ by

$$\mathbb{P}(J(\rho_e, \mathbf{y}) = j) = \frac{\psi_\phi(y^j, \nu_+(x_e, \mathbf{y}), t)}{\sum_{i=1}^n \psi_\phi(y^i, \nu_+(x_e, \mathbf{y}), t)}. \quad (2.9)$$

The total branching rate from every trait ρ_e is denoted

$$\widehat{\tau}_{\text{tot}}(\rho_e) := \sum_{n \geq 0} \widehat{B}_n^*(\rho_e) + \widehat{\tau}(\rho_e). \quad (2.10)$$

Remark that $\widehat{K}_0^* = 0$, therefore the spinal individual cannot branch without children and the spinal population never goes extinct. Notice that for $\psi_\phi \equiv 1$, individuals outside the spine follow the same dynamics as the individuals in the population $(\nu_t, t \geq 0)$. In this case, the spinal individual of trait x_e branches at time t in a population ν with rate $m(\rho_e)B(\rho_e)$, where $m(\cdot)$ is the mean offspring number that is finite under Assumption B. The random number of children at a branching event thus follows the size-biased law $kp_k(\cdot)/m(\cdot)$ and the new spinal individual is chosen uniformly among the offspring.

Theorem 2.1 is verified until the first explosion time of both processes. We established in Proposition 1.1 that under Assumption A the branching process does not explode in finite time. To ensure the non explosion of the spine process, we have to consider an additional assumption on the weight function ψ_ϕ used for the construction.

Assumption C. *There exists a positive continuous function \widehat{b}_0 on \mathbb{R}_+ , such that for all $(x, \nu, t) \in \mathcal{X} \times \mathbb{V} \times \mathbb{R}_+$*

$$\sum_{n \neq 1} n \left(\widehat{B}_n(x, \nu, t) + \widehat{B}_n^*(x, \nu, t) \right) \leq \widehat{b}_0(t) (1 + |x|).$$

This assumption, involving both the branching parameters and the function ψ_ϕ , is stronger than Assumption B. The set of weight functions that can be used to construct a spine process that does not explode in finite time may differ from one model to another. However, one may rather use more restrictive conditions that are sufficient for every branching process under Assumption A. For example, in mass-conservative models, taking $\psi_\phi(x, \nu) = x$ ensures the non-explosion of the spine process regardless the initial branching process that satisfies Assumption A.

Proposition 2.4. *Under Assumption A, for every $\psi_\phi \in \mathcal{D}$ ensuring Assumption C, the spine process $((E_t, \bar{\chi}_t), t \geq 0)$ whose law is characterized by the generator $\widehat{\mathcal{L}}_{\psi_\phi}$ does not explode in finite time. Furthermore the generator \widehat{L}_{ψ_ϕ} of the marginal spine process $((Y_t, \chi_t), t \geq 0)$ given by Dynamics 2.2 and 2.3, is defined for all function $F_f \in \mathcal{D}$ and all $(x, \nu, t) \in \mathcal{X} \times \mathbb{V} \times \mathbb{R}_+$ by*

$$\widehat{L}_{\psi_\phi} F_f^t(x, \nu, t) := \frac{\mathcal{G}[\psi_\phi F_f](x, \nu, t)}{\psi_\phi(x, \nu, t)} - \frac{\mathcal{G}\psi_\phi(x, \nu, t)}{\psi_\phi(x, \nu, t)} F_f(x, \nu, t).$$

Proof. The proof of non-explosion is shown following the proof of Proposition 1.1. The expression of the generator of the marginal spine process is purely computational. Both of them are described in Appendix A. \square

It follows that the marginal law of the spine process is characterized by the operator \mathcal{G} and the weight function ψ_ϕ .

Corollary 2.5. *Let $\psi_\phi \in \mathcal{D}$ ensuring Assumption C, $t \geq 0$ and $\bar{z} \in \bar{\mathbb{V}}$. Under Assumption A, for any f measurable non-negative function on $\mathcal{U} \times \mathbb{D}([0, t], \mathcal{X} \times \bar{\mathbb{V}})$,*

$$\begin{aligned} & \mathbb{E}_{\bar{z}} \left[\sum_{u \in \mathbb{G}(t)} \psi_\phi(X_t^u, \bar{\nu}_t, t) f(u, ((X_s^u, \bar{\nu}_s), 0 \leq s \leq t)) \right] \\ &= \langle z, \psi_\phi(\cdot, z, 0) \rangle \mathbb{E}_{\bar{z}} \left[\exp \left(\int_0^t \frac{\mathcal{G}\psi_\phi(Y_s, \chi_s, s)}{\psi_\phi(Y_s, \chi_s, s)} ds \right) f(E_t, ((Y_s, \bar{\chi}_s), 0 \leq s \leq t)) \right]. \end{aligned}$$

Proof. We use Assumptions A and C to ensure that T_{Exp} and \widehat{T}_{Exp} are almost surely infinite. Let f be measurable non-negative function on $\mathcal{U} \times \mathbb{D}([0, t], \mathcal{X} \times \bar{\mathbb{V}})$. We introduce H the measurable non-negative function defined for all $(u, \bar{z}_s, s \leq t) \in \mathcal{U} \times \mathbb{D}([0, t], \bar{\mathbb{V}})$ by

$$H(u, \bar{z}_s, s \leq t) := \psi_\phi(X_t^u, z_t, t) f(u, (X_s^u, \bar{z}_s), s \leq t) \langle z_t, 1 \rangle.$$

The corollary is thus a direct application of Theorem 2.1 to the function H with a uniformly sampled individual. \square

This formula gives a change of probability that involves the function $\mathcal{G}\psi_\phi/\psi_\phi$ with a path-integral formula. This study is related to Feynman-Kac path measures and semigroups. We refer to [18] for an overview on this subject. In the case of a branching process with interactions, the integral term depends on the trajectory of the whole spinal population. In general cases with interactions, the branching property is not verified and the so-called Many-to-One formula- see *e.g.* Proposition 9.3 in [5]- fall apart,. However, if ψ_ϕ is an eigenfunction of the operator \mathcal{G} , then we have the following Many-to-One formula for any non-negative measurable function g on $\mathbb{D}([0, t], \mathcal{X})$

$$\mathbb{E}_{\bar{z}} \left[\sum_{u \in \mathbb{G}(t)} \psi_\phi(X_t^u, \bar{\nu}_t, t) g(X_s^u, s \leq t) \right] = C_t \mathbb{E}_{\bar{z}} [g(Y_s, s \leq t)],$$

where C_t is a time-dependent positive constant. This formula, established in [15], reduces the empirical measure of the trajectories of all the individuals until time t to the law of the trajectory of a unique individual in the spinal construction, the spinal individual. The spinal individual in this case can be considered as a typical individual, reflecting the average behavior of the whole population.

Remark 2.6. *If we assume for all $(x, \nu, t) \in \mathcal{X} \times \mathbb{V} \times \mathbb{R}_+$, that $B(x, \nu, t) = B(t)$ and for all $k \geq 0$, $p_k(x, \nu, t) = p_k(t)$ in the considered branching process, taking $\psi_\phi \equiv 1$ gives the classical Many-to-One formula [4]:*

$$\mathbb{E}_{\bar{z}} \left[\sum_{u \in \mathbb{G}(t)} g(X_s^u, s \leq t) \right] = \mathbb{E}_{\bar{z}} [\langle \nu_t, 1 \rangle] \mathbb{E}_{\bar{z}} [g(Y_s, s \leq t)].$$

where the average number of individuals in the population is given at time t by

$$\mathbb{E}_{\bar{z}} [\langle \nu_t, 1 \rangle] = \langle z, 1 \rangle \exp \left(\int_0^t B(s)(m(s) - 1) ds \right).$$

3. KESTEN-STIGUM CRITERION

In this section, we present both a sufficient and a necessary Kesten-Stigum criterium for density-dependent branching processes with a continuous type space. Before stating the result, we introduce the limiting martingale that naturally follows from the spinal construction.

Proposition 3.1. *Under Assumption A, for every $\psi_\phi \in \mathcal{D}$ ensuring Assumption B,*

$$W_t(\psi_\phi) := \sum_{u \in \mathbb{G}(t)} \exp \left(- \int_0^t \frac{\mathcal{G}\psi_\phi(X_s^u, \nu_s, s)}{\psi_\phi(X_s^u, \nu_s, s)} ds \right) \psi_\phi(X_t^u, \nu_t, t) \quad (3.1)$$

is a non-negative martingale with respect to the filtration $(\mathcal{F}_t, t \geq 0)$ generated by the original process. It almost surely converges to a random variable $W(\psi_\phi) \in [0, \infty)$.

Note that if the process $(\nu_t, t \geq 0)$ goes extinct almost surely, then $W(\psi_\phi) = 0$ almost surely. However, even on the survival event, the martingale $(W_t(\psi_\phi), t \geq 0)$ may also almost surely degenerate to 0. The limit depends on the chosen ψ_ϕ function and we will focus here on the case $\psi_\phi \equiv 1$ (see [2] for the case without interactions). In this case the branching parameters of the original process must be such that $m(\cdot)$ is finite to ensure Assumption B. We denote

$$\mathcal{W}_t := W_t(1) = \sum_{u \in \mathbb{G}(t)} e^{-\int_0^t B(X_s^u, \nu_s, s)(m(X_s^u, \nu_s, s) - 1) ds} \quad \text{and} \quad \mathcal{W} := \limsup_{t \rightarrow \infty} \mathcal{W}_t. \quad (3.2)$$

We noticed in Remark 2.6 that if the branching rates do not depend on the trait nor the population then we have an expression of the mean size of the population. For non-structured branching processes the mean size $\mathbb{E}[N_t]$ of the population, where $N_t := \langle \nu_t, 1 \rangle$, is given by $\mathbb{E}[N_t] = N_0 \exp \left(\int_0^t B(s)(m(s) - 1) ds \right)$. One may ask under what conditions this exponential growth accurately reflects the rate of increase in the population size. In this particular case, $\mathcal{W}_t/N_0 = N_t/\mathbb{E}[N_t]$, thus finding conditions for the non-degeneracy of this martingale gives a direct answer to the question. In the general case with interactions, Corollary 2.5 gives

$$\mathcal{W}_t \frac{\mathbb{E}[N_t]}{N_0} = \sum_{u \in \mathbb{G}(t)} e^{-\int_0^t B(X_s^u, \nu_s, s)(m(X_s^u, \nu_s, s) - 1) ds} \mathbb{E}_{\bar{z}} \left[e^{\int_0^t B(Y_s, \chi_s, s)(m(Y_s, \chi_s, s) - 1) ds} \right],$$

that is close to N_t if the mean behavior of the spinal individual is not far from the averaging behavior of all the individuals in the branching process.

In the sequel we will suppose that the following hypothesis on the branching rates holds

Assumption D. *Assumptions A and C hold true and there exist $c, C, \bar{B} \in \mathbb{R}_+^*$ such that, for all $\rho \in \mathbb{W} \times \mathbb{R}_+$*

$$c \leq B(\rho)(m(\rho) - 1) \leq C \quad \text{and} \quad B(\rho) \leq \bar{B}.$$

This assumption ensures that the process is strongly supercritical- in a sense that the uniform lower bound of the reproductive law is strictly greater than 1- and that the only absorbing state for the branching process is the null measure $\nu \equiv 0$. This uniform hypothesis could be partially released under strong positivity assumptions on the generator of the branching process, see [37] in the discrete case and [32] Chapter 3 for continuous time. It also restricts the setting to branching processes with bounded branching rates. We can now express the result.

Theorem 3.2. *We assume Assumption D, and introduce for all $k \in \mathbb{N}$*

$$\bar{p}_k := \sup_{\rho \in \mathbb{W} \times \mathbb{R}_+} p_k(\rho), \quad \text{and} \quad \underline{p}_k := \inf_{\rho \in \mathbb{W} \times \mathbb{R}_+} p_k(\rho).$$

If $\sum_{k \geq 1} k \log(k) \bar{p}_k < +\infty$ then, for all initial measure $z \in \mathbb{V}$

$$\mathbb{E}_z[\mathcal{W}] = \langle z, 1 \rangle.$$

If $\sum_{k \geq 1} k \log(k) \underline{p}_k = +\infty$, then

$$\mathcal{W} = 0 \quad \text{almost surely.}$$

The idea of the proof, based on the conceptual proofs established in [44, 26, 3], is to consider the spinal process as a process with immigration: every individual outside the spine follows the same dynamics as the original process ($\nu_t, t \geq 0$) and the spinal individual provides new individuals at a biased rate. Note that the spinal construction also changes the branching rates of individuals outside the spine if ψ_ϕ depends on the population state.

Remark 3.3. *If $(\bar{p}_k, k \geq 0)$ and $(\underline{p}_k, k \geq 0)$ have finite first moment \bar{m} and \underline{m} , then we can introduce \bar{L} and \underline{L} the \mathbb{N} -valued random variables of law given respectively by $(\bar{p}_k/\bar{m}, k \in \mathbb{N})$ and $(\underline{p}_k/\underline{m}, k \in \mathbb{N})$. The conditions of Theorem 3.2 thus become $\mathbb{E}[\bar{L} \log(\bar{L})] < +\infty$ for the non-degeneracy and $\mathbb{E}[\underline{L} \log(\underline{L})] = +\infty$ for the degeneracy. Note that these conditions are similar to the conditions (16b) and (18b) in [2]. In the case of constant reproductive law, it is well known that these two conditions become a dichotomy. Athreya [2] showed that this dichotomy remains valid for multitype Galton-Watson processes with a finite set of traits and no interactions.*

4. A YULE PROCESS WITH COMPETITION

In this section, we introduce an alternative application of the spinal construction method that enables us to obtain a spine process with straightforward dynamics from a branching process with intricate interactions. As a toy model, we consider a time-inhomogeneous Yule process with competitive interactions between the individuals, affecting their traits. The individuals in the population are characterized by their trait $x \in \mathbb{R}_+^*$ that can be for example a mass or a size. An individual with trait x divides at an instantaneous rate $r(t)x$ where r is a measurable function on \mathbb{R}_+ , into two children of size Λx and $(1 - \Lambda)x$, where Λ is a $[0, 1]$ -valued random variable with probability density function (p.d.f) q . We assume that:

$$m_{\text{div}} := \mathbb{E}[\Lambda] \in (0, 1), \quad \text{and} \quad K_{\text{div}} := \mathbb{E} \left[\frac{1}{\Lambda(1 - \Lambda)} \right] < +\infty.$$

This mass-conservative mechanism of division is classical in cell modeling [25]. Moreover, each individual experiences the influence of the whole population, leading to a reduction of their trait. Consequently, at an instantaneous rate $d(t)N_t$ - where N_t is the population size at time t , and d is a positive measurable function on \mathbb{R}_+ - each individual loses a fraction $(1 - \Theta)$ of its size. Θ is a $[0, 1]$ -valued random variable with p its p.d.f and we assume that

$$m_{\text{loss}} := \mathbb{E}[\Theta] \in (0, 1) \quad \text{and} \quad K_{\text{loss}} := \mathbb{E} \left[\frac{1}{\Theta} \right] < +\infty.$$

These events can be interpreted as an inhibition of reproductive material in cells due to competitive interactions within the population. Finally, we consider that the trait of each individual grows exponentially at an instantaneous rate $\mu(t)$. The dependency in time of these parameters can represent an external control or the effect of a deterministic environment. This defines a branching process ($\nu_t, t \geq 0$), whose law is characterized by the infinitesimal generators ($\mathcal{J}^t, t \geq 0$). For all $t \geq 0$, \mathcal{J}^t is defined on the set \mathcal{D}_J , where

$\mathcal{D}_J := \{H_h \in \mathfrak{B}(\mathbb{R}_+), \exists (h, H) \in \mathcal{C}^1(\mathbb{R}_+, \mathbb{R}) \times \mathcal{C}^1(\mathbb{R}_+, \mathbb{R}_+^*) : \forall \nu \in \mathbb{W}, H_h(\nu) = H(\langle \nu, h \rangle)\}$
by

$$\begin{aligned} \mathcal{J}^t H_h(\nu) &= H'(\langle \nu, h \rangle) \int_{\mathbb{R}_+} h'(y) \mu(t) y \nu(dy) \\ &+ \int_{\mathbb{R}_+} r(t) y \int_0^1 [H_h(\nu - \delta_y + \delta_{\lambda y} + \delta_{(1-\lambda)y}) - H_h(\nu)] q(\lambda) d\lambda \nu(dy) \\ &+ d(t) \langle \nu, 1 \rangle \int_{\mathbb{R}_+} \int_0^1 [H_h(\nu - \delta_y + \delta_{\theta y}) - H_h(\nu)] p(\theta) d\theta \nu(dy). \end{aligned}$$

We remark that Assumption A is verified by the parameters of this branching process, and thus it does not explode in finite time almost surely. Note that in this population, the dynamics are correlated such that an increase in population size accelerates the rate of loss, while loss events slow the rate of division. The operator at the core of the spinal construction introduced in (2.3), defined for functions F_f in the set \mathcal{D} introduced in (2.1), is such that for all $(x, \nu, t) \in \mathbb{W} \times \mathbb{R}_+$

$$\begin{aligned} \mathcal{G}F_f(x, \nu, t) &= D_1 F(x, \langle \nu, f(\cdot, t) \rangle, t) \mu(t)x + D_3 F(x, \langle \nu, f(\cdot, t) \rangle, t) \\ &+ D_2 F(x, \langle \nu, f(\cdot, t) \rangle, t) \int_{\mathbb{R}_+} \left[\frac{\partial f}{\partial y}(y, t) \mu(t)y + \frac{\partial f}{\partial t}(y, t) \right] \nu(dy) \\ &+ r(t)x \int_0^1 [F_f(\lambda x, \nu - \delta_x + \delta_{\lambda x} + \delta_{(1-\lambda)x}, t) + F_f((1-\lambda)x, \nu - \delta_x + \delta_{\lambda x} + \delta_{(1-\lambda)x}, t) \\ &\quad - F_f(x, \nu - \delta_x + \delta_{\lambda x} + \delta_{(1-\lambda)x}, t)] q(\lambda) d\lambda \\ &+ d(t) \langle \nu, 1 \rangle \int_0^1 [F_f(\theta x, \nu - \delta_x + \delta_{\theta x}, t) - F_f(x, \nu - \delta_x + \delta_{\theta x}, t)] p(\theta) d\theta \\ &+ \int_{\mathbb{R}_+} r(t)y \int_0^1 [F_f(x, \nu - \delta_y + \delta_{\lambda y} + \delta_{(1-\lambda)y}, t) - F_f(x, \nu, t)] q(\lambda) d\lambda \nu(dy) \\ &+ d(t) \langle \nu, 1 \rangle \int_{\mathbb{R}_+} \int_0^1 [F_f(x, \nu - \delta_y + \delta_{\theta y}, t) - F_f(x, \nu, t)] p(\theta) d\theta \nu(dy). \end{aligned}$$

Notice that polynomial functions can not be eigenvalues of the operators \mathcal{G}^t for all t . Finding analytic expression of eigenfunctions for such non-local operator is complex, and the existence of such eigenfunctions is not guaranteed in general, see [9, 17]. Here we propose to use the change of measure associated with the spinal construction in order to decorrelate the dynamics within the spine process. We believe that this method can be generalized to different models. We choose $\psi \in \mathcal{C}^1(\mathbb{R}_+^* \times \mathbb{R} \times \mathbb{R}_+, \mathbb{R}_+^*)$ and $\phi \in \mathcal{C}^1(\mathbb{R}_+^* \times \mathbb{R}_+, \mathbb{R})$ such that for all $(x, y, t) \in \mathbb{R}_+^* \times \mathbb{R} \times \mathbb{R}_+$

$$\psi(x, y, t) := x e^{-y} \quad \text{and} \quad \phi(x, t) := \ln(xr(t)K_{\text{div}}). \quad (4.1)$$

Applied to a spinal state $(x_e, \chi, t) \in \mathbb{W}$ where $\chi := \sum_{u \in \mathbb{G}(t)} \delta_{x^u}$, this weight function verifies

$$\psi_\phi(x_e, \chi, t) = \frac{x_e}{\prod_{u \in \mathbb{G}(t)} (r(t)K_{\text{div}} x^u)}$$

and ensures Assumption B. We can now determine the parameters of the spinal process using this function ψ_ϕ . The behavior of the traits between branching events remains unchanged compared to the Yule process under consideration. The division events occur at rate 1 for both the spinal and the non-spinal individuals. The random variable $\widehat{\Lambda}$, which determines the distribution of mass during division in the spinal construction, has a density function \widehat{q} given by:

$$\widehat{q}(\lambda) := \frac{q(\lambda)}{\lambda(1-\lambda)K_{\text{div}}}. \quad (4.2)$$

As a result, in this ψ_ϕ -spinal process, division events are no longer dependent on the size of the individuals.

Individuals outside the spine lose a random fraction $1 - \widehat{\Theta}$ of their mass at a rate $\widehat{B}_1(x, \nu, t) := K_{\text{loss}} d(t) \langle \nu, 1 \rangle$ where $\widehat{\Theta}$ follows a probability density function \widehat{p} given by:

$$\widehat{p}(\theta) = \frac{p(\theta)}{\theta K_{\text{loss}}}. \quad (4.3)$$

The loss events for the spinal individual follow the same dynamics as those in the Yule process being considered. It is worth noting that Assumption C holds in this case, leading

to $\widehat{T}_{\text{Exp}} = \infty$ almost surely. Therefore, by using appropriate functions ψ and ϕ in the spinal construction, we can make division events independent of loss events, resulting in a conditional branching property. This property can be used to enhance the simulation complexity of the branching process.

A classical exact method to simulate non-homogeneous Poisson processes is the thinning algorithm, introduced by Lewis and Shedler [39]. It is used to simulate Poisson processes of intensity $c(t)$ on a window $[0, T]$ for a fixed $T > 0$. The idea is to generate possible jump times $(t_i, 1 \leq i \leq n)$ at a rate $\bar{c} := \sup_{[0, T]} c(t)$ and accept them with probability $c(t_i)/\bar{c}$. When the intensity $c(\cdot)$ depends not only on time t but also on the entire past of the point process, one can use Ogata's modified thinning algorithm [48]. Given the information of the first k points, $(t_i, 1 \leq i \leq k)$ the intensity $c(\cdot)$ is deterministic on $[t_k, T_{k+1}]$ with T_{k+1} the next time of jump. As a result, generating the next point in such processes can be considered as generating the first point in an inhomogeneous Poisson process. This idea has been more recently adapted for branching process, see *e.g.* [24, 10, 25]. The main limitation of this method is that \bar{c} can become excessively large even for small simulation windows T . This results in the rejection of most of the generated points. Another exact method, based on inverse transform sampling, consists in generating the arrival times of the process by sampling a uniform random variable U in $[0, 1]$, see *e.g.* [19]. The arrival times t_k are thus generated by inversion of the cumulative distribution function of the jumps times, such that $1 - \exp(-\int_0^{t_k} c(s)ds) = U$. However, an exact inversion is inaccessible in general cases, and in this model in particular.

Here, we propose a new simulation method, based on the spinal construction, that is much faster than the Ogata's algorithm. The idea is to use the fact that the division events are independent from the mass in the spine process. Thus, we can generate a binary tree with unit rate, then spawn a Poisson point process indexed on this tree that distributes the loss events and chooses the spinal individual. Finally the trait of each individual at every time is computed using the deterministic growth and the encountered loss events. These three steps are illustrated in Figure 1 and a detailed algorithm can be found in Appendix D.

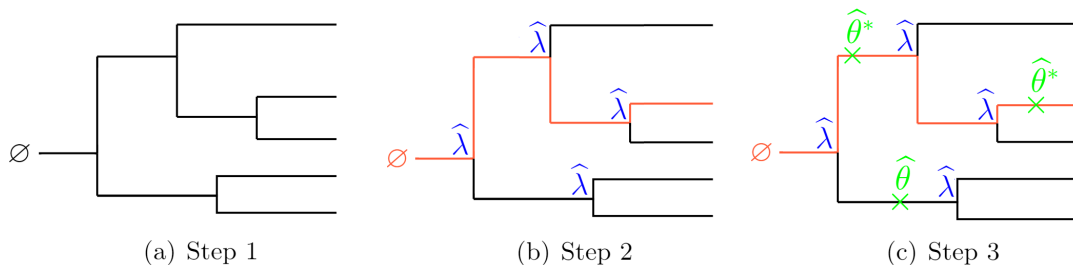


FIGURE 1. Algorithm description

We then use Theorem 2.1 to compute various statistics of the branching process based on the statistics obtained from the spine process. For all $(x, \nu, t) \in \mathbb{R}_+^* \times \mathbb{V} \times \mathbb{R}_+$, the expression of the operator \mathcal{G} applied to the chosen ψ_ϕ , defined in (4.1), is given by

$$\frac{\mathcal{G}\psi_\phi(x, \nu, t)}{\psi_\phi(x, \nu, t)} = \mu(t) + \left[\frac{\dot{r}(t)}{r(t)} - \mu(t) + d(t)(S - 1)(K_{\text{loss}} - 1) \right] S - r(t)B,$$

where for all $\nu \in \mathbb{V}$, $S := \langle \nu, 1 \rangle$ and $B := \int_{\mathbb{R}_+^*} x\nu(dx)$ denote respectively the size of the population ν and its total biomass.

Thus, any statistics on the branching process estimated by Monte Carlo methods can be alternatively estimated using trajectories of the spine process and the formula given by Theorem 2.1 applied to this spinal construction.

5. PROOFS

5.1. Proof of Section 1. In this section, we derive the result on the existence and uniqueness of the considered branching process.

Proof of Proposition 1.1. The description of the process $(\bar{\nu}_t, t \geq 0)$ introduced in Section 1 leads to a canonical SDE driven by the dynamics of the trait and a multivariate point process. This SDE is then used to show that the mean number of individuals in the population and the trait are bounded at any time $t \geq 0$. Using Assumption A.2 we conclude that there is no explosion in finite time of the population.

Following [4, 45], for convenience, we introduce a vector $\boldsymbol{\theta} := (\theta_i, i \in \mathbb{N}^*)$ of uniform independent random variables on $[0, 1]$ and a family $(F_{i,n}, i \leq n, n \in \mathbb{N}^*)$ of measurable maps from $\mathcal{X} \times \mathbb{V} \times \mathbb{R}_+ \times [0, 1]$ to \mathcal{X} such that for all $(n, x, \nu, t) \in \mathbb{N}^* \times \mathcal{X} \times \mathbb{V} \times \mathbb{R}_+$, the random vector $(F_{i,n}(x, \nu, t, \theta_i), i \leq n)$ is distributed as $K_n(x, \nu, t, \cdot)$. Note that taking a unique random variable θ uniform on $[0, 1]$ correlates the trait at birth between every child.

Let $E = \mathcal{U} \times \mathbb{R}_+ \times \mathbb{N} \times [0, 1]^{\mathbb{N}}$ and $Q(ds, du, dr, dk, d\boldsymbol{\theta})$ be a Poisson point measure on $\mathbb{R}_+ \times E$ with intensity q such that

$$q(ds, du, dr, dk, d\boldsymbol{\theta}) = ds \left(\sum_{v \in \mathcal{U}} \delta_v(du) \right) dr \left(\sum_{n \in \mathbb{N}} \delta_n(dk) \right) d\boldsymbol{\theta}.$$

We denote by $(\mathcal{F}_t, t \geq 0)$ the canonical filtration associated with this Poisson point measure and $(T_k, k \geq 0)$ the sequence of jumps times, that is the random sequence of times of arrivals given by the Poisson point measure Q .

Let $\bar{z} \in \bar{\mathbb{V}}$. For every function $g \in \mathcal{C}^1(\mathcal{U} \times \mathcal{X}, \mathbb{R})$ and $t \geq 0$, the process $(\bar{\nu}_t, t \geq 0)$ starting from \bar{z} verifies

$$\begin{aligned} \langle \bar{\nu}_t, g \rangle &:= \langle \bar{z}, g \rangle + \int_0^t \int_{\mathcal{U} \times \mathcal{X}} \frac{\partial g}{\partial x}(u, x) \cdot \mu(x, \nu_s, s) \bar{\nu}_s(du, dx) ds \\ &+ \int_{[0, t] \times E} \mathbb{1}_{\{u \in \mathbb{G}(\bar{\nu}_{s^-}), r \leq B_k(X_{s^-}^u, \nu_{s^-}, s)\}} \\ &\times \left[\sum_{i=1}^k g(ui, F_{i,k}(X_{s^-}^u, \nu_{s^-}, s, \theta_i)) - g(u, X_{s^-}^u) \right] Q(ds, du, dr, dk, d\boldsymbol{\theta}). \end{aligned} \quad (5.1)$$

Note that the dynamical construction of the marginal measure-valued process only does not ensure uniqueness: the individual for the next branching event is chosen according to its trait, and thus two individuals with the same trait can be indistinctly chosen to be the branching one. The labeling of individuals allows us to overcome this problem. However, any other labeling method could work, see e.g. [24].

The proof of uniqueness and existence of a solution is classical and has been first established for measure-valued process by Fournier and Meleard [24]. Here we consider non-bounded rates and we follow with small adaptations the proof of Lemma 2.5 in [45]. Let $T > 0$. We prove the non-accumulation of branching events on $[0, T]$. First we use equation (5.1) applied to the constant function equal to 1, that gives the number of individuals in the population, denoted $(N_t, t \geq 0)$. Using Assumption A.3, we have for all $t < T_k \wedge T$

$$\mathbb{E}_{\bar{z}}[N_t] \leq N_0 + \int_0^t b_0(s) \left(\mathbb{E}_{\bar{z}} \left[\sum_{u \in \mathbb{G}(t)} |X_s^u| \right] + \mathbb{E}_{\bar{z}}[N_s] \right) ds.$$

Next, we take a sequence of functions $(g_n, n \in \mathbb{N})$ in $\mathcal{C}^1(\mathcal{U} \times \mathcal{X}, \mathbb{R}_+)$ such that $\lim_{n \rightarrow \infty} g_n(u, x) = |x|$ and $\lim_{n \rightarrow \infty} \frac{\partial g_n}{\partial x}(u, x) \cdot \mu(x, \nu, s) \leq |\mu(x, \nu, s)|$ for all ν, s . Applying equation (5.1) to these

functions and using Assumptions A.1 and A.4, we have when $n \rightarrow +\infty$,

$$\mathbb{E}_{\bar{z}} \left[\sum_{u \in \mathbb{G}(t)} |X_t^u| \right] \leq \langle \bar{z}, |\cdot| \rangle + \int_0^t \mu_0(s) \left(\mathbb{E}_{\bar{z}} \left[\sum_{u \in \mathbb{G}(s)} |X_s^u| \right] + \mathbb{E}_{\bar{z}} \left[\sum_{u \in \mathbb{G}(s)} X_s^u \right] + \mathbb{E}_{\bar{z}} [N_s] \right) ds.$$

According to Grönwall's lemma, for all $t < T_k \wedge T$, we have

$$\mathbb{E}_{\bar{z}} [N_t] + \mathbb{E}_{\bar{z}} \left[\sum_{u \in \mathbb{G}(t)} |X_t^u| \right] \leq (N_0 + \langle \bar{z}, |\cdot| \rangle) e^{A(T)t} < \infty$$

where $A(T) = \sup_{s \leq T} b_0(s) + \mu_0(s)$. The number of individuals is thus almost surely finite at finite time as well as the trait of every individual. Assumption A.2 ensures that in finite time, there is no accumulation of branching events that does not change the size of the population. \square

5.2. Proof of Section 2. Theorem 2.1 is proved following the steps of the proof of Theorem 1 in [3]. Let $\psi_\phi \in \mathcal{D}$ ensuring Assumption B, and $((E_t, \bar{\chi}_t), t \geq 0)$ be the time-inhomogeneous $\bar{\mathbb{W}}$ -valued branching process of generators $(\hat{\mathcal{L}}_{\psi_\phi}^t, t \geq 0)$, defined in (2.5). We will first need to introduce some notations. We will denote $(U_k, k \geq 0)$ the sequence of \mathcal{U} -valued random variables giving the label of the branching individuals at the jumps times $(T_k, k \geq 0)$. Let $(N_k, k \geq 0)$ be the sequence of \mathbb{N} -valued random variables giving the number of children at each branching event and we denote for brevity $A_k := (U_k, N_k)$ for all $k \geq 0$. At the k -th branching time T_k , we denote \mathcal{Y}_k the \mathcal{X}^{N_k} -valued random variable giving the vector of offspring traits. Finally we introduce for all $k \geq 0$, $\mathcal{V}_k := (T_k, A_k, \mathcal{Y}_k)$. We similarly define $((\hat{T}_k, \hat{U}_k, \hat{N}_k, \hat{\mathcal{Y}}_k), k \geq 0)$, the sequence of jumps times, labels of the branching individual, number of children and trait of these children at birth in the spinal construction. Remark that the distribution of number of children and traits depend on whether the branching individual is the spinal one or not. We will also use for all $k \geq 0$, $\hat{\mathcal{V}}_k := (\hat{T}_k, \hat{A}_k, \hat{\mathcal{Y}}_k)$ where $\hat{A}_k := (\hat{U}_k, \hat{N}_k)$. At time $s \in [\hat{T}_{k-1}, \hat{T}_k)$, the label of the spinal individual is denoted E_k and its trait Y_k . For a given initial population $\bar{z} = \sum_{i=1}^n \delta_{(i, x^i)} \in \bar{\mathbb{V}}$, we use by convention $U_0 = \emptyset$, $N_0 = n$, $\mathcal{Y}_0 = (x^i, 1 \leq i \leq n)$ almost surely. The same convention holds for the spine process. For all $0 \leq k$, we introduce the associated filtrations

$$\mathcal{F}_k = \sigma(\mathcal{V}_i, 0 \leq i \leq k), \text{ and } \hat{\mathcal{F}}_k = \sigma(E_k, (\hat{\mathcal{V}}_i, 0 \leq i \leq k)).$$

Remark that these notations, summarized in Figure 2, are well-defined until the explosion time of the branching and spine processes and that the vectors $(\mathcal{V}_k, k \geq 0)$ where for all $k \geq 0$, $\mathcal{V}_k := (T_k, A_k, \mathcal{Y}_k)$ characterize the trajectories of $(\bar{\nu}_t, t \geq 0)$ until the explosion time.

For every initial population $\bar{z} \in \bar{\mathbb{V}}$ and every $k \geq 0$, we introduce the set of sequences of k branching events that lead to non-extinguished trajectories $\mathfrak{U}_k(\bar{z}) \subset (\mathcal{U} \times \mathbb{N})^k$, starting from \bar{z} . We also introduce for all $a \in \mathfrak{U}_k(\bar{z})$ and all $0 \leq i \leq k$, $\mathbb{G}_i(a)$ the set of labels of individuals living between the i -th and $(i+1)$ -th branching events in the population where all the branching events were given by a . By decomposing the branching process $(\bar{\nu}_t, t \geq 0)$ based on the sequences $a \in \mathfrak{U}_k(\bar{z})$ and sampling at time t an individual $e \in \mathbb{G}_k(a)$, we get that for every measurable non-negative function H on $\mathcal{U} \times \mathbb{D}([0, t], \mathbb{V})$

$$\begin{aligned} \mathbb{E}_{\bar{z}} \left[\mathbb{1}_{\{T_{\text{Exp}} > t, \mathbb{G}(t) \neq \emptyset\}} H(U_t, (\bar{\nu}_s, s \leq t)) \right] = \\ \sum_{k \geq 0} \sum_{a \in \mathfrak{U}_k(\bar{z})} \sum_{e \in \mathbb{G}_k(a)} \mathbb{E}_{\bar{z}} \left[H(e, (\bar{\nu}_s, s \leq t)) p_e(\bar{\nu}_t) \mathbb{1}_{\{T_k \leq t < T_{k+1}\}} \prod_{i=0}^k \mathbb{1}_{\{A_i = a_i\}} \right]. \end{aligned} \quad (5.2)$$

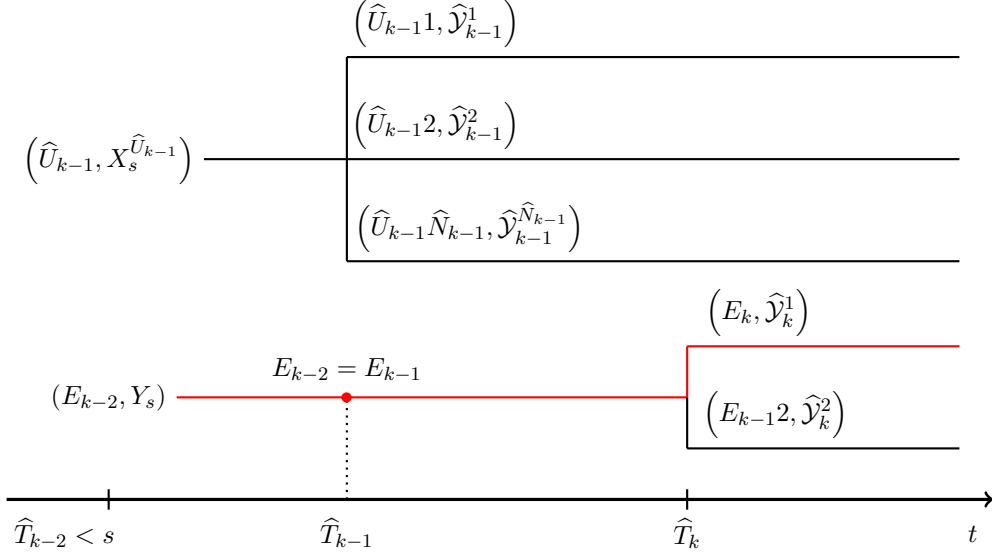


FIGURE 2. Sequential notations for the spine process.

The expectation on the right-hand side of (5.2) is linked by a Girsanov-type result to the spinal construction, as shown in Lemma 5.1. The difference with our proof and the proof of Theorem 1 in [3] lies essentially in the demonstration of this lemma.

Lemma 5.1.

For any $k > 0$, $\bar{z} \in \bar{\mathbb{V}}$ and $a = ((u_i, n_i), 0 \leq i \leq k) \in \mathfrak{A}_k(\bar{z})$, let F be a measurable non-negative function on $\prod_{i=1}^k (\mathbb{R}_+ \times \mathcal{U} \times \mathbb{N} \times \mathcal{X}^{n_i})$. For any $e \in \mathbb{G}_k(a)$,

$$\begin{aligned} \mathbb{E}_{\bar{z}} \left[F(\mathcal{V}_i, 0 \leq i \leq k) \prod_{i=0}^k \mathbb{1}_{\{A_i = a_i\}} \right] &= \langle z, \psi_\phi(\cdot, z, 0) \rangle \\ &\times \mathbb{E}_{\bar{z}} \left[\xi_k \left(E_k, (\hat{\mathcal{V}}_i, 0 \leq i \leq k) \right) F \left(\hat{\mathcal{V}}_i, 0 \leq i \leq k \right) \mathbb{1}_{\{E_k = e\}} \prod_{i=0}^k \mathbb{1}_{\{\hat{A}_i = a_i\}} \right], \end{aligned}$$

where

$$\xi_k \left(E_k, (\hat{\mathcal{V}}_i, 0 \leq i \leq k) \right) := \frac{1}{\psi_\phi \left(Y_{\hat{T}_k}, \chi_{\hat{T}_k}, \hat{T}_k \right)} \exp \left(\int_0^{\hat{T}_k} \frac{\mathcal{G}\psi_\phi(Y_s, \chi_s, s)}{\psi_\phi(Y_s, \chi_s, s)} ds \right).$$

We prove this lemma by induction on the number of branching events k . We will first state a technical lemma to avoid too long computations.

Lemma 5.2. For all $k > 0$, $\bar{z} \in \bar{\mathbb{V}}$ and $a = ((u_i, n_i), 0 \leq i \leq k) \in \mathfrak{A}_k(\bar{z})$,

$$\frac{\xi_k \left(E_k, (\hat{\mathcal{V}}_i, 0 \leq i \leq k) \right)}{\xi_{k-1} \left(E_{k-1}, (\hat{\mathcal{V}}_i, 0 \leq i \leq k-1) \right)} = \frac{\psi_\phi \left(Y_{\hat{T}_k}, \chi_{\hat{T}_k}, \hat{T}_k \right)}{\psi_\phi \left(Y_{\hat{T}_k}, \chi_{\hat{T}_k}, \hat{T}_k \right)} \exp \left(\int_{\hat{T}_{k-1}}^{\hat{T}_k} \lambda(Y_s, \chi_s, s) ds \right) \quad a.s.$$

where, for all $s \in [\hat{T}_{k-1}, \hat{T}_k)$,

$$\lambda(Y_s, \chi_s, s) := \hat{\tau}_{tot}(Y_s, \chi_s, s) - \int_{\mathcal{X}} B(x, \chi_s, s) \chi_s(dx). \quad (5.3)$$

We recall that $\hat{\tau}_{tot}$ is the total branching rate of the spine process defined in (2.10). The proof of this lemma is in Appendix B.

Proof of Lemma 5.1. Following the proof of Theorem 1 in [3], the result is established by induction on the number k of branching events. The original branching process and its associated spine process may stop branching in finite time, in this case the total numbers of branching events, respectively N_{tot} and \widehat{N}_{tot} , are finite. For all k such that $k > N_{\text{tot}}$, the k -th branching event of the original construction arrives at $T_k = +\infty$. In this case we set $A_k = (\emptyset, 0)$ by convention. The same convention is used for the spinal construction. Let $\bar{z} := \sum_{i=1}^n \delta_{(i, x^i)} \in \bar{\mathbb{V}}$ be the initial population and let F be a measurable non-negative function on $\mathbb{R}_+ \times \mathcal{U} \times \mathbb{N} \times \mathcal{X}^n$. Then, by definition

$$\mathcal{V}_0 = \widehat{\mathcal{V}}_0 = (0, (\emptyset, n), (x^i, 1 \leq i \leq n)), \text{ a.s.}$$

Therefore, for all $e \in \mathbb{G}(0)$

$$\mathbb{E}_{\bar{z}} \left[\xi_0 \left(E_0, \widehat{\mathcal{V}}_0 \right) F \left(\widehat{\mathcal{V}}_0 \right) \mathbb{1}_{\{E_0=e\}} \mathbb{1}_{\{\widehat{A}_0=(\emptyset, n)\}} \right] = F(\mathcal{V}_0) \mathbb{1}_{\{A_0=(\emptyset, n)\}} \mathbb{E}_{\bar{z}} \left[\frac{\mathbb{1}_{\{E_0=e\}}}{\psi_\phi(Y_0, z, 0)} \right].$$

We recall that the individual $1 \leq i \leq n$ of trait x^i in the population \bar{z} is chosen to be the spinal individual with probability $\psi_\phi(x^i, z, 0) \langle z, \psi_\phi(\cdot, z, 0) \rangle^{-1}$. Then we have

$$\mathbb{E}_{\bar{z}} \left[\xi_0 \left(E_0, \widehat{\mathcal{V}}_0 \right) F \left(\widehat{\mathcal{V}}_0 \right) \mathbb{1}_{\{E_0=e\}} \mathbb{1}_{\{\widehat{A}_0=(\emptyset, n)\}} \right] = \frac{1}{\langle z, \psi_\phi(\cdot, z, 0) \rangle} \mathbb{E}_{\bar{z}} \left[\mathbb{1}_{\{A_0=(\emptyset, n)\}} F(0, A_0, \mathcal{Y}_0) \right].$$

Thus the result holds for $k = 0$. Now let $k \geq 1$ and assume that the following induction hypothesis holds at rank $k - 1$.

Induction Hypothesis. For every $a = (a_i, 0 \leq i \leq k - 1) \in (\mathcal{U} \times \mathbb{N})^{k-1}$ with $a_i = (u_i, n_i)$, every measurable non-negative function F on $\bigotimes_{i=1}^{k-1} (\mathbb{R}_+ \times \mathcal{U} \times \mathbb{N} \times \mathcal{X}^{n_i})$ and every $e \in \mathbb{G}_{k-1}(a)$:

$$\begin{aligned} \mathbb{E}_{\bar{z}} \left[F(\mathcal{V}_i, 0 \leq i \leq k - 1) \prod_{i=0}^{k-1} \mathbb{1}_{\{A_i=a_i\}} \right] &= \langle z, \psi_\phi(\cdot, z) \rangle \mathbb{E}_{\bar{z}} \left[\xi_{k-1} \left(E_{k-1}, \left(\widehat{\mathcal{V}}_i, 0 \leq i \leq k - 1 \right) \right) \right. \\ &\quad \left. \times F \left(\widehat{\mathcal{V}}_i, 0 \leq i \leq k - 1 \right) \mathbb{1}_{\{E_{k-1}=e\}} \prod_{i=0}^{k-1} \mathbb{1}_{\{A_i=a_i\}} \right]. \end{aligned} \quad (5.4)$$

Let $a = (a_i, 0 \leq i \leq k) \in (\mathcal{U} \times \mathbb{N})^n$ with $a_i = (u_i, n_i)$ and $e \in \mathbb{G}_k(a)$. We denote $a' = (a_i, 0 \leq i \leq k - 1)$ and take F_k^a a measurable non-negative function on $\bigotimes_{i=1}^k (\mathbb{R}_+ \times \mathcal{X}^{n_i})$ such that, for all $((t_i, y_i), 0 \leq i \leq k) \in \bigotimes_{i=1}^n (\mathbb{R}_+ \times \mathcal{X}^{n_i})$:

$$F_k^a((t_i, y_i), 0 \leq i \leq n) := F_{k-1}^{a'}((t_i, y_i), 0 \leq i \leq k - 1) I(t_k - t_{k-1}) F(y_k), \quad (5.5)$$

where $F_{k-1}^{a'}$, I and F are measurable non-negative and bounded, respectively on $\bigotimes_{i=1}^{k-1} (\mathbb{R}_+ \times \mathcal{X}^{n_i})$, \mathbb{R}_+ and \mathcal{X}^{n_k} . Let $e' \in \mathbb{G}_{k-1}(a')$, such that there exists $j \in \mathbb{N}^* \cup \{\emptyset\}$ verifying $e'j = e$. We introduce the $\mathbb{N}^* \cup \{\emptyset\}$ -valued random variable J_k choosing the label of the spinal individual at the k -th branching event, so that $E_k = E_{k-1} J_k$ almost surely.

Following the proof of Lemma 1 in [3], we express both sides of the equality (5.4) for $k \geq 1$ conditionally on the filtrations at the previous step $k - 1$. We recall that, for all $1 \leq j \leq k$

$$\mathcal{F}_j = \sigma(\mathcal{V}_i, 0 \leq i \leq j), \text{ and } \widehat{\mathcal{F}}_j = \sigma \left(E_j, \left(\widehat{\mathcal{V}}_i, 0 \leq i \leq j \right) \right).$$

Using (5.5) and conditioning on the filtration after the $(k-1)$ -th branching event, we have

$$\mathbb{E}_{\bar{z}} \left[F_k^a ((T_i, \mathcal{Y}_i), 0 \leq i \leq k) \prod_{i=0}^k \mathbb{1}_{\{A_i=a_i\}} \right] = \mathbb{E}_{\bar{z}} \left[F_{k-1}^{a'} ((T_i, \mathcal{Y}_i), 0 \leq i \leq k-1) C(\mathcal{V}_i, 0 \leq i \leq k-1) \prod_{i=0}^{k-1} \mathbb{1}_{\{A_i=a_i\}} \right], \quad (5.6)$$

where:

$$C(\mathcal{V}_i, 0 \leq i \leq k-1) := \mathbb{E} [I(T_k - T_{k-1}) F(\mathcal{Y}_k) \mathbb{1}_{\{A_k=a_k\}} | \mathcal{F}_{k-1}]. \quad (5.7)$$

We apply the induction hypothesis (5.4) in the previous equation (5.6) with H given by

$$H(\mathcal{V}_i, 0 \leq i \leq k-1) := F_{k-1}^{a'} ((T_i, \mathcal{Y}_i), 0 \leq i \leq k-1) C(\mathcal{V}_i, 0 \leq i \leq k-1).$$

Thus

$$\begin{aligned} \mathbb{E}_{\bar{z}} \left[F_k^a ((T_i, \mathcal{Y}_i), 0 \leq i \leq k) \prod_{i=0}^k \mathbb{1}_{\{A_i=a_i\}} \right] &= \langle z, \psi_\phi(\cdot, z, 0) \rangle \mathbb{E}_{\bar{z}} \left[\xi_{k-1} \left(E_{k-1}, (\widehat{\mathcal{V}}_i, 0 \leq i \leq k-1) \right) \right. \\ &\quad \left. \times F_{k-1}^{a'} \left((\widehat{T}_i, \widehat{\mathcal{Y}}_i), 0 \leq i \leq k-1 \right) C(\widehat{\mathcal{V}}_i, 0 \leq i \leq k-1) \mathbb{1}_{\{E_{k-1}=e'\}} \prod_{i=0}^{k-1} \mathbb{1}_{\{A_i=a_i\}} \right]. \end{aligned} \quad (5.8)$$

Similarly, we use (5.5) for the spine process. Conditioning on the filtration after the $(k-1)$ -th branching event, we have

$$\begin{aligned} \mathbb{E}_{\bar{z}} \left[\xi_k \left(E_k, (\widehat{\mathcal{V}}_i, 0 \leq i \leq k) \right) F_k^a \left((\widehat{T}_i, \widehat{\mathcal{Y}}_i), 0 \leq i \leq k \right) \mathbb{1}_{\{E_k=e\}} \prod_{i=0}^k \mathbb{1}_{\{\widehat{A}_i=a_i\}} \right] &= \\ \mathbb{E} \left[\xi_{k-1} \left(E_{k-1}, (\widehat{\mathcal{V}}_i, 0 \leq i \leq k-1) \right) F_{k-1}^{a'} \left((\widehat{T}_i, \widehat{\mathcal{Y}}_i), 0 \leq i \leq k-1 \right) \right. \\ &\quad \left. \times \widehat{C} \left(e', (\widehat{\mathcal{V}}_i, 0 \leq i \leq k-1) \right) \prod_{i=0}^{k-1} \mathbb{1}_{\{\widehat{A}_i=a_i\}} \right], \end{aligned} \quad (5.9)$$

where, using Lemma 5.2,

$$\begin{aligned} \widehat{C} \left(e', (\widehat{\mathcal{V}}_i, 0 \leq i \leq k-1) \right) &:= \mathbb{1}_{\{E_{k-1}=e'\}} \mathbb{E} \left[\frac{\psi_\phi \left(Y_{\widehat{T}_k}, \chi_{\widehat{T}_k}, \widehat{T}_k \right)}{\psi_\phi \left(Y_{\widehat{T}_k}, \chi_{\widehat{T}_k}, \widehat{T}_k \right)} \exp \left(\int_{\widehat{T}_{k-1}}^{\widehat{T}_k} \lambda(Y_s, \chi_s, s) ds \right) \right. \\ &\quad \left. \times \mathbb{1}_{\{J_k=j\}} I(\widehat{T}_k - \widehat{T}_{k-1}) F(\widehat{\mathcal{Y}}_k) \mathbb{1}_{\{\widehat{A}_k=a_k\}} \Big| \widehat{\mathcal{F}}_{k-1} \right]. \end{aligned} \quad (5.10)$$

If we can establish that

$$\widehat{C} \left(e', (\widehat{\mathcal{V}}_i, 0 \leq i \leq k-1) \right) = \mathbb{1}_{\{E_{k-1}=e'\}} C \left((\widehat{\mathcal{V}}_i, 0 \leq i \leq k-1) \right), \quad (5.11)$$

then the expectations in the right-hand sides of equations (5.8) and (5.9) are equal and we get

$$\begin{aligned} \mathbb{E}_{\bar{z}} \left[F_k^a ((T_i, \mathcal{Y}_i), 0 \leq i \leq k) \prod_{i=0}^k \mathbb{1}_{\{A_i=a_i\}} \right] &= \langle z, \psi_\phi(\cdot, z, 0) \rangle \\ &\quad \times \mathbb{E}_{\bar{z}} \left[\xi_k \left(E_k, (\widehat{\mathcal{V}}_i, 0 \leq i \leq k) \right) F_k^a \left((\widehat{T}_i, \widehat{\mathcal{Y}}_i), 0 \leq i \leq k \right) \mathbb{1}_{\{E_k=e\}} \prod_{i=0}^k \mathbb{1}_{\{\widehat{A}_i=a_i\}} \right]. \end{aligned}$$

From this equality and using a monotone class argument for the functions F_k^a defined in (5.5), we obtain (5.4) at rank k , that concludes the proof.

In the following we show (5.11), by describing the dynamics of both processes.

Computations for the branching process. Conditioning in chain the expression of C defined in (5.7), we get

$$C(\mathcal{V}_i, 0 \leq i \leq k-1) = \mathbb{E} \left[I(T_k - T_{k-1}) \mathbb{E} \left[\mathbb{1}_{\{A_k = a_k\}} \mathbb{E} [F(\mathcal{Y}_k) | \mathcal{F}_{k-1}, T_k, A_k] \middle| \mathcal{F}_{k-1}, T_k \right] \middle| \mathcal{F}_{k-1} \right].$$

Using the conditional distribution of \mathcal{Y}_n , we have

$$\mathbb{E} [F(\mathcal{Y}_k) | \mathcal{F}_{k-1}, T_k, A_k] = \int_{\mathcal{X}^{N_k}} F(\mathbf{y}) K_{N_k} \left(X_{T_k^-}^{U_k}, \nu_{T_k^-}, T_k, d\mathbf{y} \right).$$

Then we remark that for $a_k = (u_k, n_k)$,

$$\mathbb{E} [\mathbb{1}_{\{A_k = a_k\}} | \mathcal{F}_{k-1}, T_k] = \frac{B_{n_k} \left(X_{T_k^-}^{u_k}, \nu_{T_k^-}, T_k \right)}{\tau \left(\nu_{T_k^-}, T_k \right)},$$

where $\tau(\nu, s) := \int_{\mathcal{X}} B(x, \nu, s) \nu(dx)$ is the total branching rate. Finally, using that the time between two jumps follows an inhomogeneous exponential law of instantaneous rate $\tau(\cdot)$, we have

$$\begin{aligned} C(\mathcal{V}_i, 0 \leq i \leq k-1) &= \int_{\mathbb{R}_+} I(t) \exp \left(- \int_{T_{k-1}}^{t+T_{k-1}} \tau(\nu_s, s) ds \right) \\ &\quad \times B_{n_k} \left(X_{t+T_{k-1}}^{u_k}, \nu_{t+T_{k-1}}, t + T_{k-1} \right) \int_{\mathcal{X}^{n_k}} F(\mathbf{y}) K_{n_k} \left(X_{t+T_{k-1}}^{u_k}, \nu_{t+T_{k-1}}, t + T_{k-1}, d\mathbf{y} \right) dt. \end{aligned}$$

Computations for the spinal construction. We follow the computations for the branching process, and differentiate between whether the branching individual is the spinal one or not. Conditioning on the next jump time, \widehat{C} defined in (5.10), is such that

$$\begin{aligned} \widehat{C} \left(e', (\widehat{\mathcal{V}}_i, 0 \leq i \leq k-1) \right) &= \mathbb{1}_{\{E_{k-1} = e'\}} \mathbb{E} \left[\exp \left(\int_{\widehat{T}_{k-1}}^{\widehat{T}_k} \lambda(Y_s, \chi_s, s) ds \right) I \left(\widehat{T}_k - \widehat{T}_{k-1} \right) \right. \\ &\quad \left. \times \psi_\phi \left(Y_{\widehat{T}_k^-}, \chi_{\widehat{T}_k^-}, \widehat{T}_k \right) \mathbb{E} \left[\frac{F \left(\widehat{\mathcal{Y}}_k \right) \mathbb{1}_{\{J_k = j\}} \mathbb{1}_{\{\widehat{A}_k = a_k\}}}{\psi_\phi \left(Y_{\widehat{T}_k^-}, \chi_{\widehat{T}_k^-}, \widehat{T}_k \right)} \middle| \widehat{\mathcal{F}}_{k-1}, \widehat{T}_k \right] \middle| \widehat{\mathcal{F}}_{k-1} \right]. \end{aligned} \quad (5.12)$$

We handle this last equation by complete induction, on the event $\{j = \emptyset\} \cup \{j \neq \emptyset\}$, to show that

$$\begin{aligned} \psi_\phi \left(Y_{\widehat{T}_k^-}, \chi_{\widehat{T}_k^-}, \widehat{T}_k \right) \mathbb{E} \left[\frac{F \left(\widehat{\mathcal{Y}}_k \right) \mathbb{1}_{\{J_k = j\}} \mathbb{1}_{\{\widehat{A}_k = a_k\}}}{\psi_\phi \left(Y_{\widehat{T}_k^-}, \chi_{\widehat{T}_k^-}, \widehat{T}_k \right)} \middle| \widehat{\mathcal{F}}_{k-1}, \widehat{T}_k \right] &= \\ \frac{B_{n_k} \left(X_{T_k^-}^{u_k}, \chi_{T_k^-}, \widehat{T}_k \right)}{\widehat{\tau}_{\text{tot}} \left(\chi_{\widehat{T}_k^-}, \widehat{T}_k \right)} \int_{\mathcal{X}^{\widehat{N}_k}} F(\mathbf{y}) K_{\widehat{N}_k} \left(X_{\widehat{T}_k^-}^{\widehat{U}_k}, \chi_{\widehat{T}_k^-}, \widehat{T}_k, d\mathbf{y} \right). & \quad (5.13) \end{aligned}$$

Branching outside the spine. If $j = \emptyset$, then the branching individual is not the spinal one, and $e = e'j = e'$. We follow the same conditioning than for the branching process, and use the fact that on the event $\{j = \emptyset\}$ the trait of the spinal individual is $\widehat{\mathcal{F}}_{k-1}$ -measurable.

Using the expression of the ψ_ϕ -biased distribution \widehat{K} of $\widehat{\mathcal{Y}}_k$, defined in (2.7), we get

$$\begin{aligned} & \mathbb{E} \left[\frac{F(\widehat{\mathcal{Y}}_k) \mathbb{1}_{\{J_k=\emptyset\}} \mathbb{1}_{\{\widehat{A}_k=a_k\}}}{\psi_\phi(Y_{\widehat{T}_k}, \chi_{\widehat{T}_k}, \widehat{T}_k)} \middle| \widehat{\mathcal{F}}_{k-1}, \widehat{T}_k \right] = \\ & \mathbb{E} \left[\mathbb{1}_{\{\widehat{A}_k=a_k\}} \mathbb{1}_{\{J_k=\emptyset\}} \int_{\mathcal{X}^{\widehat{N}_k}} \frac{F(\mathbf{y})}{\widehat{\Gamma}_{n_k}(Y_{\widehat{T}_k}, X_{\widehat{T}_k}^{u_k}, \chi_{\widehat{T}_k}, \widehat{T}_k)} K_{n_k}(X_{\widehat{T}_k}, \chi_{\widehat{T}_k}, \widehat{T}_k, d\mathbf{y}) \middle| \widehat{\mathcal{F}}_{k-1}, \widehat{T}_k \right]. \end{aligned}$$

We then recall the distribution of \widehat{A}_k outside the spine, established in Dynamics 2.2 :

$$\mathbb{E} \left[\mathbb{1}_{\{\widehat{A}_k=a_k\}} \mathbb{1}_{\{J_k=\emptyset\}} \middle| \widehat{\mathcal{F}}_{k-1}, \widehat{T}_k \right] = \frac{\widehat{\Gamma}_{n_k}(Y_{\widehat{T}_k}, X_{\widehat{T}_k}^{u_k}, \chi_{\widehat{T}_k}, \widehat{T}_k) B_{n_k}(X_{\widehat{T}_k}^{u_k}, \chi_{\widehat{T}_k}, \widehat{T}_k)}{\psi_\phi(Y_{\widehat{T}_k}, \chi_{\widehat{T}_k}, \widehat{T}_k) \widehat{\tau}_{\text{tot}}(\chi_{\widehat{T}_k}, \widehat{T}_k)}.$$

This gives (5.13) on the event $\{j = \emptyset\}$.

Spine branching. We follow the same computations when $j \neq \emptyset$, that corresponds to the case when the branching individual is the spinal one, i.e $u_k = e'$. In this case, the distribution of $Y_{\widehat{T}_k}$ now depends on the traits $\widehat{\mathcal{Y}}_k$. Thus conditioning on $\widehat{\mathcal{Y}}_k$ and using the distribution of the next spinal individual, defined in (2.9), we have

$$\begin{aligned} & \mathbb{1}_{\{j \neq \emptyset\}} \mathbb{E} \left[\frac{F(\widehat{\mathcal{Y}}_k) \mathbb{1}_{\{J_k=j\}} \mathbb{1}_{\{\widehat{A}_k=a_k\}}}{\psi_\phi(Y_{\widehat{T}_k}, \chi_{\widehat{T}_k}, \widehat{T}_k)} \middle| \widehat{\mathcal{F}}_{k-1}, \widehat{T}_k \right] = \\ & \mathbb{E} \left[\mathbb{1}_{\{\widehat{A}_k=(e', n_k)\}} \mathbb{E} \left[\frac{F(\widehat{\mathcal{Y}}_k)}{\sum_{i=1}^{\widehat{N}_k} \psi_\phi(\widehat{\mathcal{Y}}_k^i, \chi_{\widehat{T}_k} - \delta_{Y_{\widehat{T}_k}} + \sum_{l=1}^{\widehat{N}_k} \delta_{\widehat{\mathcal{Y}}_k^l}, \widehat{T}_k)} \middle| \widehat{\mathcal{F}}_{k-1}, \widehat{T}_k, \widehat{A}_k \right] \middle| \widehat{\mathcal{F}}_{k-1}, \widehat{T}_k \right]. \end{aligned}$$

We then use the distribution \widehat{K}^* of $\widehat{\mathcal{Y}}_k$, defined in (2.8) when the branching individual is the spinal one, conditioning on \widehat{A}_k , defined in Dynamics 2.3.

$$\begin{aligned} & \mathbb{1}_{\{\widehat{A}_k=(e', n_k)\}} \mathbb{E} \left[\frac{F(\widehat{\mathcal{Y}}_k)}{\sum_{i=1}^{\widehat{N}_k} \psi_\phi(\widehat{\mathcal{Y}}_k^i, \chi_{\widehat{T}_k} - \delta_{Y_{\widehat{T}_k}} + \sum_{l=1}^{\widehat{N}_k} \delta_{\widehat{\mathcal{Y}}_k^l}, \widehat{T}_k)} \middle| \widehat{\mathcal{F}}_{k-1}, \widehat{T}_k, \widehat{A}_k \right] = \\ & \mathbb{1}_{\{\widehat{A}_k=(e', n_k)\}} \int_{\mathcal{X}^{n_k}} \frac{F(\mathbf{y})}{\widehat{\Gamma}_{n_k}^*(Y_{\widehat{T}_k}, \chi_{\widehat{T}_k}, \widehat{T}_k)} K_{n_k}(Y_{\widehat{T}_k}, \chi_{\widehat{T}_k}, \widehat{T}_k, d\mathbf{y}). \end{aligned}$$

Finally we use the distribution of \widehat{A}_k when the branching individual is the spinal one, defined in Dynamics 2.3.

$$\mathbb{E} \left[\mathbb{1}_{\{\widehat{A}_k=(e', n_k)\}} \middle| \widehat{\mathcal{F}}_{k-1}, \widehat{T}_k \right] = \frac{\widehat{\Gamma}_{n_k}^*(Y_{\widehat{T}_k}, \chi_{\widehat{T}_k}, \widehat{T}_k) B_{n_k}(Y_{\widehat{T}_k}, \chi_{\widehat{T}_k}, \widehat{T}_k)}{\psi_\phi(Y_{\widehat{T}_k}, \chi_{\widehat{T}_k}, \widehat{T}_k) \widehat{\tau}_{\text{tot}}(\chi_{\widehat{T}_k}, \widehat{T}_k)}.$$

This gives (5.13) on the event $\{j \neq \emptyset\}$. Now, combining (5.12) and (5.13), we get

$$\begin{aligned} \widehat{C} \left(e', \left(\widehat{\mathcal{V}}_i, 0 \leq i \leq k-1 \right) \right) &= \mathbb{1}_{\{E_{k-1}=e'\}} \mathbb{E} \left[\exp \left(\int_{\widehat{T}_{k-1}}^{\widehat{T}_k} \lambda(Y_s, \chi_s, s) ds \right) I \left(\widehat{T}_k - \widehat{T}_{k-1} \right) \right. \\ &\quad \left. \times \frac{B_{n_k} \left(X_{\widehat{T}_k}^{u_k}, \chi_{\widehat{T}_k}, \widehat{T}_k \right)}{\widehat{\tau}_{\text{tot}} \left(\chi_{\widehat{T}_k}, \widehat{T}_k \right)} \int_{\mathcal{X}^{n_k}} F(\mathbf{y}) K_{n_k} \left(X_{\widehat{T}_k}^{u_k}, \chi_{\widehat{T}_k}, \widehat{T}_k, d\mathbf{y} \right) \Big| \widehat{\mathcal{F}}_{k-1} \right]. \end{aligned}$$

Using that the time between two jump follows an inhomogeneous exponential law of instantaneous rate $\widehat{\tau}_{\text{tot}}$, we have

$$\begin{aligned} \widehat{C} \left(e', \left(\widehat{\mathcal{V}}_i, 0 \leq i \leq k-1 \right) \right) &= \mathbb{1}_{\{E_{k-1}=e'\}} \int_{\mathbb{R}_+} I(t) \exp \left(\int_{\widehat{T}_{k-1}}^{\widehat{T}_k} \lambda(Y_s, \chi_s, s) - \widehat{\tau}_{\text{tot}}(Y_s, \chi_s, s) ds \right) \\ &\quad \times B_{n_k} \left(X_{t+\widehat{T}_{k-1}}^{u_k}, \nu_{t+\widehat{T}_{k-1}}, t + \widehat{T}_{k-1} \right) \int_{\mathcal{X}^{n_k}} F(\mathbf{y}) K_{n_k} \left(X_{t+\widehat{T}_{k-1}}^{u_k}, \nu_{t+\widehat{T}_{k-1}}, t + \widehat{T}_{k-1}, d\mathbf{y} \right) dt. \end{aligned} \quad (5.14)$$

Finally, using in (5.14) the fact that λ , defined in (5.3), is the difference of branching rates between the branching process and the spine process, we get (5.11) and it concludes the proof. \square

Proof of Theorem 2.1. Let $\psi_\phi \in \mathcal{D}$, $t \geq 0$, and $\bar{z} \in \bar{\mathbb{W}}$. Let $((E_t, \bar{\chi}_t), t \geq 0)$ be the time-inhomogeneous $\bar{\mathbb{W}}$ -valued branching process of generators $(\widehat{\mathcal{L}}_{\psi_\phi}^t, t \geq 0)$ defined in (2.5). Let \widehat{T}_{Exp} denote its explosion time and $((Y_t, \chi_t), t \geq 0)$ its projection on \mathbb{W} . For every $t < T_{\text{Exp}}$, there exists $k \in \mathbb{N}$ such that $\{T_k \leq t < T_{k+1}\}$ where $T_{k+1} = +\infty$ if there is no more jumps after T_k . Thus we can write

$$\mathbb{E}_{\bar{z}} \left[\mathbb{1}_{\{T_{\text{Exp}} > t, \mathbb{G}(t) \neq \emptyset\}} H(U_t, (\bar{\nu}_s, s \leq t)) \right] = \sum_{k \geq 0} \mathbb{E}_{\bar{z}} \left[\mathbb{1}_{\{T_k \leq t < T_{k+1}, \mathbb{G}(t) \neq \emptyset\}} H(U_t, (\bar{\nu}_s, s \leq t)) \right].$$

For every $t \geq 0$, $k \in \mathbb{N}$, every non-extinguished sequence $a = (a_i, 1 \leq i \leq k) \in \mathfrak{A}_k(\bar{z})$ with $a_i = (u_i, n_i)$ and every $e \in \mathbb{G}_k(a)$, there exists a measurable non-negative function $F_{k,a}^{t,e}$ on $\bigotimes_{i=1}^k (\mathbb{R}_+ \times \mathcal{U} \times \mathbb{N} \times \mathcal{X}^{n_i})$, such that

$$\begin{aligned} \mathbb{E}_{\bar{z}} \left[\mathbb{1}_{\{T_{\text{Exp}} > t, \mathbb{G}(t) \neq \emptyset\}} H(U_t, (\bar{\nu}_s, s \leq t)) \right] &= \\ &= \sum_{k \geq 0} \sum_{a \in \mathfrak{A}_k(\bar{z})} \sum_{e \in \mathbb{G}_k(a)} \mathbb{E}_{\bar{z}} \left[\mathbb{E} \left[\mathbb{1}_{\{T_{k+1} > t\}} | \mathcal{F}_k \right] \mathbb{1}_{\{T_k \leq t\}} F_{k,a}^{t,e}(\mathcal{V}_i, 0 \leq i \leq k) \prod_{i=0}^k \mathbb{1}_{\{A_i = a_i\}} \right]. \end{aligned}$$

We apply Lemma 5.1 with the non-negative measurable function F defined for all sequence $(v_i, 0 \leq i \leq k) \in \bigotimes_{i=1}^k (\mathbb{R}_+ \times \mathcal{U} \times \mathbb{N} \times \mathcal{X}^{n_i})$, where for all $0 \leq i \leq k$, $v_i := (t_i, a_i, y_i)$, by

$$F(v_i, 0 \leq i \leq k) := \mathbb{P} \left(S_{k+1} > t - t_k \Big| \bigcap_{0 \leq i \leq k} \{\mathcal{V}_i = v_i\} \right) \mathbb{1}_{t_k \leq t} F_{k,a}^{t,e}(v_i, 0 \leq i \leq k),$$

where S_{k+1} is the random variable giving the $(k+1)$ -th inter-arrival time of jumps in the original process. Note that S_{k+1} follows the same probability law as $T_{k+1} - T_k$. We thus get,

for all $e \in \mathbb{G}_k(a)$

$$\begin{aligned} \mathbb{E}_{\bar{z}} \left[\mathbb{1}_{\{\mathbb{G}(t) \neq \emptyset\} \cap \{T_{\text{Exp}} > t\}} H(U_t, (\bar{\nu}_s, s \leq t)) \right] &= \langle z, \psi_\phi(\cdot, z, 0) \rangle \sum_{k \geq 0} \sum_{a \in \mathfrak{A}_k(\bar{z})} \sum_{e \in \mathbb{G}_k(a)} \mathbb{E}_{\bar{z}} \left[\mathbb{1}_{\{E_k = e\}} \right. \\ &\quad \left. \times \xi_k \left(E_k, \left(\widehat{\nu}_i, 0 \leq i \leq k \right) \right) F \left(\widehat{\nu}_i, 0 \leq i \leq k \right) \prod_{i=0}^k \mathbb{1}_{\{\widehat{A}_i = a_i\}} \right]. \end{aligned} \quad (5.15)$$

Then, using that λ introduced in (5.3) verifies $\lambda := \widehat{\tau}_{\text{tot}} - \tau$,

$$\begin{aligned} \mathbb{P} \left(S_{k+1} > t - \widehat{T}_k \mid \bigcap_{0 \leq i \leq k} \left\{ \widehat{\nu}_i = v_i \right\} \right) \mathbb{1}_{\{\widehat{T}_k \leq t\}} &= e^{\int_{\widehat{T}_k}^t \lambda(Y_s, \chi_s, s) ds} e^{-\int_{\widehat{T}_k}^t \widehat{\tau}_{\text{tot}}(Y_s, \chi_s, s) ds} \mathbb{1}_{\{\widehat{T}_k \leq t\}} \\ &= e^{\int_{\widehat{T}_k}^t \lambda(Y_s, \chi_s, s) ds} \mathbb{E} \left[\mathbb{1}_{\{\widehat{T}_{k+1} > t\}} \mid \widehat{\mathcal{F}}_k \right] \mathbb{1}_{\{\widehat{T}_k \leq t\}}. \end{aligned}$$

We recall that on the event $\{\widehat{T}_{k+1} > t\}$, there is no jump in the interval $(\widehat{T}_k, t]$, thus, applying Lemma 5.2 on this interval we get

$$\begin{aligned} \xi_k \left(E_k, \left(\widehat{\nu}_i, 0 \leq i \leq k \right) \right) \mathbb{P} \left(S_k > t - \widehat{T}_k \mid \bigcap_{0 \leq i \leq k} \left\{ \widehat{\nu}_i = v_i \right\} \right) \mathbb{1}_{\{\widehat{T}_k \leq t\}} &= \\ \frac{1}{\psi_\phi(Y_t, \chi_t, t)} \exp \left(\int_0^t \frac{\mathcal{G}\psi_\phi(Y_s, \chi_s, s)}{\psi_\phi(Y_s, \chi_s, s)} ds \right) \mathbb{E} \left[\mathbb{1}_{\{\widehat{T}_k \leq t < \widehat{T}_{k+1}\}} \mid \widehat{\mathcal{F}}_k \right]. \end{aligned} \quad (5.16)$$

On the event $\{\widehat{T}_k \leq t < \widehat{T}_{k+1}\}$, $E_k = E(t)$ almost surely, then using (5.15) and (5.16) gives

$$\begin{aligned} \mathbb{E}_{\bar{z}} \left[\mathbb{1}_{\{T_{\text{Exp}} > t, \mathbb{G}(t) \neq \emptyset\}} H(U_t, (\bar{\nu}_s, s \leq t)) \right] &= \langle z, \psi_\phi(\cdot, z) \rangle \sum_{k \geq 0} \sum_{a \in \mathfrak{A}_k(\bar{z})} \sum_{e \in \mathbb{G}_k(a)} \mathbb{E}_{\bar{z}} \left[\mathbb{1}_{\{E(t) = e\}} \right. \\ &\quad \left. \times \frac{\mathbb{1}_{\{\widehat{T}_k \leq t < \widehat{T}_{k+1}\}}}{\psi_\phi(Y_t, \chi_t, t)} \exp \left(\int_0^t \frac{\mathcal{G}\psi_\phi(Y_s, \chi_s, s)}{\psi_\phi(Y_s, \chi_s, s)} ds \right) F_{k,a}^{t,e} \left(\widehat{\nu}_i, 0 \leq i \leq k \right) \prod_{i=0}^k \mathbb{1}_{\{\widehat{A}_i = a_i\}} \right]. \end{aligned}$$

Reconstructing the right-hand side and using the fact that the spine process does not extinct, we have

$$\begin{aligned} \mathbb{E}_{\bar{z}} \left[\mathbb{1}_{\{T_{\text{Exp}} > t, \mathbb{G}(t) \neq \emptyset\}} H(U_t, (\bar{\nu}_s, s \leq t)) \right] &= \\ \langle z, \psi_\phi(\cdot, z, 0) \rangle \mathbb{E}_{\bar{z}} \left[\mathbb{1}_{\{\widehat{T}_{\text{Exp}} > t\}} \frac{p_{E_t}(\bar{\chi}_t)}{\psi_\phi(Y_t, \chi_t, t)} \exp \left(\int_0^t \frac{\mathcal{G}\psi_\phi(Y_s, \chi_s, s)}{\psi_\phi(Y_s, \chi_s, s)} ds \right) H(E_t, (\bar{\chi}_s, s \leq t)) \right], \end{aligned}$$

that concludes the proof. \square

5.3. Proofs of Section 3. In this section we derive the results on the limiting martingale and a $L \log L$ criterion.

Proof of Proposition 3.1. Let $\psi_\phi \in \mathcal{D}$ ensuring Assumption B, we first show for all $t \geq 0$, the integrability of the random variable $W_t(\psi_\phi)$ introduced in (3.1). As Assumption A is satisfied, we can apply Corollary 2.5 for any $t \geq 0$ to the positive function f on $\mathbb{D}([0, t], \mathcal{X} \times \bar{\mathbb{V}})$, such that for all $u \in \mathbb{G}(t)$,

$$f((X_s^u, \bar{\nu}_s), 0 \leq s \leq t) := \exp \left(- \int_0^t \frac{\mathcal{G}\psi_\phi(X_s^u, \nu_s, s)}{\psi_\phi(X_s^u, \nu_s, s)} ds \right).$$

Theorem 2.1 applied to the function f , ensures that for any initial condition \bar{z} ,

$$\mathbb{E}_{\bar{z}} \left[\sum_{u \in \mathbb{G}(t)} \exp \left(- \int_0^t \frac{\mathcal{G}\psi_\phi(X_s^u, \nu_s, s)}{\psi_\phi(X_s^u, \nu_s, s)} ds \right) \psi_\phi(X_t^u, \nu_t, t) \right] = \langle z, \psi_\phi(\cdot, z, 0) \rangle. \quad (5.17)$$

This last identity guarantees the integrability of $W_t(\psi_\phi)$.

Now, for all $r, t \in \mathbb{R}_+^*$, such that $t \geq r$, we decompose the population at time t according to their ancestors at time r . We then have

$$\begin{aligned} \mathbb{E}_{\bar{z}} [W_t(\psi_\phi) | \mathcal{F}_r] &= \sum_{v \in \mathbb{G}(r)} \exp \left(- \int_0^r \frac{\mathcal{G}\psi_\phi(X_s^u, \nu_s, s)}{\psi_\phi(X_s^u, \nu_s, s)} ds \right) \\ &\quad \times \mathbb{E}_{\bar{z}} \left[\sum_{u \in \mathbb{G}(t), s.t. v \preceq u} \exp \left(- \int_r^t \frac{\mathcal{G}\psi_\phi(X_s^u, \nu_s, s)}{\psi_\phi(X_s^u, \nu_s, s)} ds \right) \psi_\phi(X_t^u, \nu_t, t) \middle| \mathcal{F}_r \right]. \end{aligned}$$

Now, in order to establish that the conditional expectation is equal to $\psi_\phi(X_r^v, \nu_r)$ for all $v \in \mathbb{G}(r)$, we apply Corollary 2.5 to the positive functions f_v on $\mathcal{U} \times \mathbb{D}([0, t], \bar{\nu})$, such that

$$f_v(u, (\bar{\nu}_s, 0 \leq s \leq t)) := \mathbb{1}_{v \preceq u} \exp \left(- \int_r^t \frac{\mathcal{G}\psi_\phi(X_s^u, \nu_s, s)}{\psi_\phi(X_s^u, \nu_s, s)} ds \right)$$

and use the Markov property. We get that for all $v \in \mathbb{G}(r)$

$$\begin{aligned} \mathbb{E} \left[\sum_{\substack{u \in \mathbb{G}(t), \\ s.t. v \preceq u}} \exp \left(- \int_r^t \frac{\mathcal{G}\psi_\phi(X_s^u, \nu_s, s)}{\psi_\phi(X_s^u, \nu_s, s)} ds \right) \psi_\phi(X_t^u, \nu_t, t) \middle| \mathcal{F}_r \right] &= \\ &= \langle \nu_r, \psi_\phi(\cdot, \nu_r, r) \rangle \mathbb{E} [\mathbb{1}_{\{v \preceq E_t\}} | v \in \mathbb{G}(r)]. \end{aligned}$$

Finally using the new spinal individual distribution (2.9), we get

$$\mathbb{E} [W_t(\psi_\phi) | \mathcal{F}_r] = \sum_{v \in \mathbb{G}(r)} \exp \left(- \int_0^r \frac{\mathcal{G}\psi_\phi(X_s^u, \nu_s, s)}{\psi_\phi(X_s^u, \nu_s, s)} ds \right) \psi_\phi(X_r^v, \nu_r, r).$$

That concludes the proof. \square

To establish Theorem 3.2, we need the following lemma from measure theory.

Lemma 5.3. *Let $(\Omega, \mathcal{F}, \mu)$ be a probability space and let $\hat{\mu}$ be a finite non negative measure on Ω . Let $(\mathcal{F}_t, 0 \leq t)$ be increasing σ -fields such that $\sigma \left(\bigcup_{0 \leq t} \mathcal{F}_t \right) = \mathcal{F}$, and $\hat{\mu}_t, \mu_t$ be the restrictions of $\hat{\mu}$ and μ to \mathcal{F}_t . Suppose that there exists a non-negative \mathcal{F}_t -martingale $(W_t, 0 \leq t)$ such that for all $t \geq 0$*

$$\frac{d\hat{\mu}_t}{d\mu_t} = W_t.$$

Then, denoting $W := \limsup_{t \rightarrow +\infty} W_t$, we have the following dichotomy:

- (1) $\int W d\mu = \int W_0 d\mu$ if and only if $W < +\infty$ $\hat{\mu}$ -a.s.
- (2) $W = 0$ μ -a.s. if and only if $W = +\infty$ $\hat{\mu}$ -a.s.

Proof. We refer to Athreya [2] for the proof of this result in discrete time. The extension to continuous time changes of measure uses Kolmogorov's extension theorem, see Durrett Appendix A [20] for further details. \square

We now state the following lemma, that is the dual proposition of Theorem 3.2.

Lemma 5.4. *Under Assumption D, let $(\widehat{W}_t, t \leq \widehat{T}_{Exp})$ be the $\widehat{\mathcal{F}}_t$ -adapted process such that, for all $t \leq \widehat{T}_{Exp}$*

$$\widehat{W}_t := \sum_{u \in \widehat{\mathbb{G}}(t)} e^{-\int_0^t B(X_s^u, \chi_s, s)(m(X_s^u, \chi_s, s) - 1) ds}, \quad (5.18)$$

where $\widehat{\mathbb{G}}(t)$ is the set of labels of individuals living in the spinal population at time t .

If $\sum_{k \geq 1} k \log(k) \bar{p}_k < +\infty$ then $\widehat{T}_{Exp} = \infty$ a.s. and $\limsup_{t \rightarrow +\infty} \widehat{\mathcal{W}}_t < +\infty$ a.s.

if $\sum_{k \geq 1} k \log(k) \underline{p}_k = +\infty$, then $\limsup_{t \rightarrow +\infty} \widehat{\mathcal{W}}_t = +\infty$ a.s.

The proof of this lemma is technical and is given in Appendix C. It involves the decomposition of the spine process as an immigration process along a line, as well as stochastic calculus tools.

Proof of Theorem 3.2. Theorem 2.1 applied with $\psi_\phi \equiv 1$ exhibits the martingale \mathcal{W}_t as a Radon-Nikodym derivative. We can thus apply Lemma 5.3 to the spinal change of measure. The martingale \mathcal{W}_t and its limit \mathcal{W} , introduced in (3.2), verify the following dichotomy:

(1) $\mathbb{E}_{\bar{z}}[\mathcal{W}] = \mathbb{E}_{\bar{z}}[\mathcal{W}_0]$ if and only if $\limsup_{t \rightarrow +\infty} \widehat{\mathcal{W}}_t < +\infty$ a.s.

(2) $\mathcal{W} = 0$ a.s. if and only if $\limsup_{t \rightarrow +\infty} \widehat{\mathcal{W}}_t = +\infty$ a.s.

We use (5.17) with $\psi_\phi \equiv 1$ to obtain that

$$\mathbb{E}_{\bar{z}}[\mathcal{W}_0] = \langle \nu_0, 1 \rangle,$$

and a direct application of Lemma 5.4 concludes the proof. \square

APPENDIX A. PROOF OF PROPOSITION 2.4

The spine process $((E_t, \bar{\chi}_t), t \geq 0)$ defined by Dynamics 2.2 and 2.3 can be rigorously expressed as the solution of a SDE driven by a multivariate point measure.

We introduce $\widehat{\theta} := (\widehat{\theta}_i, i \in \mathbb{N}^*)$ and $\widehat{\theta}^* := (\widehat{\theta}_i^*, i \in \mathbb{N}^*)$ two vectors of independent uniform random variables on $[0, 1]$. The random vectors giving the traits of the offspring of size n are denoted $(\widehat{F}_{i,n}(x, x_e, \chi, t, \widehat{\theta}_i), i \leq n)$ outside the spine and $(\widehat{F}_{i,n}^*(x_e, \chi, t, \widehat{\theta}_i^*), i \leq n)$ for the spinal individual of trait x_e .

Let $\widehat{E} = \mathcal{U} \times \mathbb{R}_+ \times \mathbb{N} \times [0, 1]^{\mathbb{N}}$ and $\widehat{E}^* = \mathbb{R}_+ \times \mathbb{N} \times [0, 1]^{\mathbb{N}}$. Let $\widehat{Q}(ds, du, dr, dk, d\theta)$ and $\widehat{Q}^*(ds, dr, dk, d\theta, dj)$ be two independent Poisson point measures on $\mathbb{R}_+ \times \widehat{E}$ and $\mathbb{R}_+ \times \widehat{E}^*$ with respective intensity $ds(\sum_{v \in \mathcal{U}} \delta_v(du))dr(\sum_{n \in \mathbb{N}} \delta_n(dk))d\widehat{\theta}$ outside the spine and $dsdr(\sum_{n \in \mathbb{N}} \delta_n(dk))d\widehat{\theta}^*(\sum_{n \in \mathbb{N}} \delta_n(dj))$ for the spine. We denote by $(\widehat{\mathcal{F}}_t, t \geq 0)$ the canonical filtration associated with these Poisson point measures. The $\widehat{\mathcal{F}}_t$ -adapted set of labels of the living individuals in the population outside the spine is denoted $\widehat{\mathbb{G}}(t)$.

Let $(e, \bar{z}) \in \overline{\mathbb{W}}$. Under Assumptions A and C, the process $((E_t, \bar{\chi}_t), t \geq 0)$ is the unique $\widehat{\mathcal{F}}_t$ -adapted solution, for every function $g \in \mathcal{C}^1(\mathcal{U} \times \mathcal{U} \times \mathcal{X}, \mathbb{R})$ and $t \geq 0$, of the following equation

$$\begin{aligned} \langle \bar{\chi}_t, g(E_t, \cdot) \rangle &:= \langle \bar{z}, g(e, \cdot) \rangle + \int_0^t \int_{\mathcal{U} \times \mathcal{X}} \frac{\partial g}{\partial x}(E_s, u, x) \cdot \mu(x, \chi_s, s) \bar{\chi}_s(du, dx) ds \\ &+ \int_{[0, t] \times \widehat{E}} \left[\sum_{i=1}^k g(E_{s-}, ui, \widehat{F}_{i,k}(X_{s-}^u, Y_{s-}, \chi_{s-}, s, \widehat{\theta}_i)) - g(E_{s-}, u, X_{s-}^u) \right] \\ &\quad \times \mathbb{1}_{\{u \in \widehat{\mathbb{G}}_{s-}\}} \mathbb{1}_{\{r \leq \widehat{B}_k(X_{s-}^u, Y_{s-}, \chi_{s-}, s)\}} \widehat{Q}(ds, du, dr, dk, d\widehat{\theta}) \\ &+ \int_{[0, t] \times \widehat{E}^*} \left[\sum_{i=1}^k g(E_{s-}, E_{s-}, Y_{s-}, \widehat{F}_{i,k}^*(Y_{s-}, \chi_{s-}, s, \widehat{\theta}_i^*)) - g(E_{s-}, E_{s-}, Y_{s-}) \right] \\ &\quad \times \mathbb{1}_{\{r \leq \widehat{B}_k^*(Y_{s-}, \chi_{s-}, s)\}} \widehat{Q}^*(ds, dr, dk, d\widehat{\theta}^*, dj). \end{aligned} \quad (\text{A.1})$$

This assertion is shown following the same computations than for proof of Proposition 1.1 and [45], using the positivity of the ψ_ϕ function. Assumption C leads to the same bound as Assumption A.3 in the case of a spine process.

Now we establish the expression of the generator of the marginal spine process. We recall the notations $\nu_+(x, \mathbf{y}) := \nu + \sum_{i=1}^n \delta_{y^i} - \delta_x$, $\rho := (x, \nu, t)$ and $\rho_e := (x_e, \nu, t)$ introduced in (2.6). Taking expectations of (A.1) for the marginal process on \mathbb{W} , we derive the non-homogeneous infinitesimal operator of $((Y_t, \chi_t), t \geq 0)$, following steps in [24]. It is given by the operator \widehat{L}_{ψ_ϕ} , defined for every $F_f \in \mathcal{D}$, introduced in (2.1), and $(x_e, \nu, t) \in \mathbb{W} \times \mathbb{R}_+$, by

$$\begin{aligned} \widehat{L}_{\psi_\phi} F_f(x_e, \nu, t) &:= G F_f(x_e, \nu, t) \\ &+ \sum_{n \geq 0} \left\{ \widehat{B}_n^*(\rho_e) \int_{\mathcal{X}^n} \left[\frac{\sum_{i=1}^n F_f \psi_\phi(y^i, \nu_+(x_e, \mathbf{y}), t)}{\sum_{j=1}^n \psi_\phi(y^j, \nu_+(x_e, \mathbf{y}), t)} - F_f(x_e, \nu, t) \right] \widehat{K}_n^*(\rho_e, d\mathbf{y}) \right. \\ &+ \int_{\mathcal{X}} \widehat{B}_n(\rho) \int_{\mathcal{X}^n} \left[F_f(x_e, \nu_+(x, \mathbf{y}), t) - F_f(x_e, \nu, t) \right] \widehat{K}_n(\rho, d\mathbf{y}) \nu(dx) \\ &\left. - \widehat{B}_n(\rho_e) \int_{\mathcal{X}^n} \left[F_f(x_e, \nu_+(x_e, \mathbf{y})) - F_f(x_e, \nu) \right] \widehat{K}_n(\rho_e, d\mathbf{y}) \right\}. \end{aligned}$$

The first line gives the dynamical evolution between branching events. The second is related to spinal branching events and the choice of a new spinal individual among the offspring population. The last two lines describe the branching events outside the spine, for all individuals but the spinal one. Using that

$$\frac{G[\psi_\phi F_f]}{\psi_\phi}(\cdot) = \frac{G\psi_\phi}{\psi_\phi} F_f(\cdot) + G F_f(\cdot),$$

we get

$$\frac{\mathcal{G}[\psi_\phi F_f]}{\psi_\phi}(\cdot) - \frac{G\psi_\phi}{\psi_\phi} F_f(\cdot) = G F_f(\cdot) + \sum_{n \geq 0} \frac{B(\cdot)}{\psi_\phi(\cdot)} \widehat{\mathcal{T}}_n(\cdot),$$

where the jump part $\widehat{\mathcal{T}}_n$ is defined for all $(x_e, \nu, t) \in \mathbb{W} \times \mathbb{R}_+$ by

$$\begin{aligned} \widehat{\mathcal{T}}_n(\rho_e) &:= p_n(\rho_e) \int_{\mathcal{X}^n} \sum_{i=1}^n \psi_\phi F_f(y_i, \nu_+(x_e, \mathbf{y}), t) - \psi_\phi F_f(x_e, \nu_+(x_e, \mathbf{y}), t) K_n(\rho_e, d\mathbf{y}) \\ &+ \int_{\mathcal{X}} p_n(\rho) \int_{\mathcal{X}^n} [\psi_\phi F_f(x_e, \nu_+(x, \mathbf{y}), t) - \psi_\phi F_f(x_e, \nu, t)] K_n(\rho, d\mathbf{y}) \nu(dx) \\ &- p_n(\rho_e) \int_{\mathcal{X}^n} \left[\sum_{i=1}^n \psi_\phi(y_i, \nu_+(x_e, \mathbf{y}), t) - \psi_\phi(x_e, \nu_+(x_e, \mathbf{y}), t) \right] F_f(x_e, \nu, t) K_n(\rho_e, d\mathbf{y}) \\ &- \int_{\mathcal{X}} p_n(\rho) \int_{\mathcal{X}^n} [\psi_\phi(x_e, \nu_+(x, \mathbf{y}), t) - \psi_\phi(x_e, \nu, t)] F_f(x_e, \nu, t) K_n(\rho, d\mathbf{y}) \nu(dx). \quad (\text{A.2}) \end{aligned}$$

Rearranging the terms in (A.2) we get

$$\begin{aligned} \widehat{\mathcal{T}}_n(\rho_e) &:= p_n(\rho_e) \int_{\mathcal{X}^n} \sum_{i=1}^n \psi_\phi(y_i, \nu_+(x_e, \mathbf{y})) [F_f(y_i, \nu_+(x_e, \mathbf{y})) - F_f(x_e, \nu)] K_n(\rho_e, d\mathbf{y}) \\ &+ \int_{\mathcal{X}} p_n(\rho) \int_{\mathcal{X}^n} [F_f(x_e, \nu_+(x, \mathbf{y})) - F_f(x_e, \nu)] \psi_\phi(x_e, \nu_+(x, \mathbf{y})) K_n(\rho, d\mathbf{y}) \nu(dx) \\ &- p_n(\rho_e) \int_{\mathcal{X}^n} [F_f(x_e, \nu_+(x_e, \mathbf{y})) - F_f(x_e, \nu)] \psi_\phi(x_e, \nu_+(x_e, \mathbf{y})) K_n(\rho_e, d\mathbf{y}). \end{aligned}$$

We conclude the proof using the branching rates introduced in Dynamics 2.2 and 2.3.

APPENDIX B. PROOF OF LEMMA 5.2

The recursive equality for ξ_n derives from the fundamental theorem of calculus. Let $n \geq 1$,

$$\frac{\xi_n \left(E_n, \left(\widehat{\nu}_i, 0 \leq i \leq n \right) \right)}{\xi_{n-1} \left(E_{n-1}, \left(\widehat{\nu}_i, 0 \leq i \leq n-1 \right) \right)} = \frac{\psi_\phi \left(Y_{\widehat{T}_{n-1}}, \chi_{\widehat{T}_{n-1}} \right)}{\psi_\phi \left(Y_{\widehat{T}_n}, \chi_{\widehat{T}_n} \right)} \exp \left(\int_{\widehat{T}_{n-1}}^{\widehat{T}_n} \frac{\mathcal{G} \psi_\phi (Y_s, \chi_s)}{\psi_\phi (Y_s, \chi_s)} ds \right).$$

We remark that \mathcal{G} and G introduced in (2.3) and (2.4), verify for all $(x_e, \nu, t) \in \mathbb{W} \times \mathbb{R}_+$

$$\frac{[\mathcal{G} - G] \psi_\phi (x_e, \nu, t)}{\psi_\phi (x_e, \nu, t)} = \widehat{\tau}_{\text{tot}} (x_e, \nu, t) - \int_{\mathcal{X}} B(x, \nu, t) \nu(dx),$$

where $\widehat{\tau}_{\text{tot}}$ is defined in (2.10). Then, using derivative chain rule we get that

$$G (\ln \circ \psi_\phi) (x_e, \nu, t) = \frac{G \psi_\phi (x_e, \nu, t)}{\psi_\phi (x_e, \nu, t)}.$$

Between successive branching events, the evolution of the process is purely deterministic and we can apply the fundamental theorem of calculus:

$$\int_{\widehat{T}_{n-1}}^{\widehat{T}_n} G (\ln \circ \psi_\phi) (Y_s, \chi_s, s) ds = \ln \left(\psi_\phi \left(Y_{\widehat{T}_n}, \chi_{\widehat{T}_n}, \widehat{T}_n \right) \right) - \ln \left(\psi_\phi \left(Y_{\widehat{T}_{n-1}}, \chi_{\widehat{T}_{n-1}}, \widehat{T}_{n-1} \right) \right).$$

We thus have

$$\exp \left(\int_{\widehat{T}_{n-1}}^{\widehat{T}_n} \frac{\mathcal{G} \psi_\phi (Y_s, \chi_s, s)}{\psi_\phi (Y_s, \chi_s, s)} ds \right) = \frac{\psi_\phi \left(Y_{\widehat{T}_n}, \chi_{\widehat{T}_n}, \widehat{T}_n \right)}{\psi_\phi \left(Y_{\widehat{T}_{n-1}}, \chi_{\widehat{T}_{n-1}}, \widehat{T}_{n-1} \right)} \exp \left(\int_{\widehat{T}_{n-1}}^{\widehat{T}_n} \lambda (Y_s, \chi_s, s) ds \right),$$

that concludes the proof.

APPENDIX C. PROOF OF LEMMA 5.4

To establish this lemma, we follow the conceptual decomposition of the spine process, first introduced by Lyons, Pemantle and Peres [44]. In the following, $\psi_\phi \equiv 1$. We consider the process $(\dot{\chi}_t, t \geq 0)$ describing all the individuals outside the spine and its associated marginal process $\dot{\chi}_t$, defined for all $t \geq 0$ by:

$$\dot{\chi}_t := \bar{\chi}_t - \delta_{(E_t, Y_t)}, \quad \text{and} \quad \dot{\chi}_t := \chi_t - \delta_{Y_t}.$$

The random set $\mathring{\mathbb{G}}(t)$ of labels of individuals outside the spine living at time t is defined by

$$\mathring{\mathbb{G}}(t) = \left\{ u \in \mathcal{U} \setminus \{E_t\} : \int_{\mathcal{U} \times \mathcal{X}} \mathbb{1}_{\{v=u\}} \bar{\chi}_t(dv, dx) > 0 \right\}.$$

We also introduce for all $t \geq 0$,

$$\dot{\mathcal{W}}_t := \sum_{u \in \mathring{\mathbb{G}}(t)} \exp \left(- \int_0^t \Lambda (X_s^u, \dot{\chi}_s + \delta_{Y_s}, s) ds \right),$$

where for all $(x, \nu, t) \in \mathbb{W} \times \mathbb{R}_+$, $\Lambda(x, \nu, t) := B(x, \nu, t)(m(x, \nu, t) - 1)$.

We remark that, under Assumption D, for all $t \geq 0$

$$\dot{\mathcal{W}}_t \leq \widehat{\mathcal{W}}_t \leq \dot{\mathcal{W}}_t + 1, \tag{C.1}$$

where $\widehat{\mathcal{W}}_t$ is the process introduced in (5.18).

We first establish the non-degenerate case, and suppose that $\sum_{k \geq 1} k \log(k) \bar{p}_k < +\infty$. We show that the process $(\dot{\mathcal{W}}_t, t \geq 0)$ does not explode and is almost surely bounded at infinity, following proof of Proposition 5 in [3]. To this end, we express it as a solution of a SDE, where we distinguish the contribution of the spinal individual from that of the other individuals.

Let $\widehat{E} = \mathcal{U} \times \mathbb{R}_+ \times \mathbb{N} \times [0, 1]^{\mathbb{N}}$ and $\widehat{E}^* = \mathbb{R}_+ \times \mathbb{N} \times [0, 1]^{\mathbb{N}} \times \mathbb{N}$. Let $\widehat{Q} (ds, du, dr, dk, d\theta)$ and $\widehat{Q}^* (ds, dr, dk, d\theta, dj)$ be two independent Poisson point measures on $\mathbb{R}_+ \times \widehat{E}$ and $\mathbb{R}_+ \times \widehat{E}^*$ with respective intensity $dsC_{\mathcal{U}}(du)drC_{\mathbb{N}}(dk)d\widehat{\theta}$ and $dsC_{\mathcal{U}}(du)drC_{\mathbb{N}}(dk)d\widehat{\theta}^*C_{\mathbb{N}}(dj)$, where $C_{\mathcal{U}}(du)$ and $C_{\mathbb{N}}(dk)$ denote the counting measures respectively on \mathcal{U} and \mathbb{N} . We denote by $(\widehat{\mathcal{F}}_t^*, t \geq 0)$ the canonical filtration associated with \widehat{Q}^* . We introduce $\widehat{\theta} := (\widehat{\theta}_i, i \in \mathbb{N}^*)$ and $\widehat{\theta}^* := (\widehat{\theta}_i^*, i \in \mathbb{N}^*)$ two vectors of independent uniform random variables on $[0, 1]$. The random vectors giving the traits of the offspring are denoted $(\widehat{F}_{i,n} (x, \chi, t, \widehat{\theta}_i), i \leq n)$ outside the spine and $(\widehat{F}_{i,n}^* (x, \chi, t, \widehat{\theta}_i^*), i \leq n)$ for the spinal individual.

We localize the process $(\dot{\mathcal{W}}_t, t \geq 0)$ to avoid explosion. Let $T^m := \inf\{t \geq 0 : \text{Card}(\dot{\mathbb{G}}(t)) \geq m\}$ be the first time at which the population outside the spine includes more than m individuals for $m \geq 1$. We remark that the branching events impact the process $(\dot{\mathcal{W}}_t, t \leq T^m)$ only through the change in the number of individuals. Furthermore, as $\psi_\phi \equiv 1$, every individual in $\dot{\mathbb{G}}(t)$ behaves like the individuals in the original branching process. Then, for all $t \leq T^m$

$$\begin{aligned} \dot{\mathcal{W}}_t &= \dot{\mathcal{W}}_0 - \int_0^t \sum_{u \in \dot{\mathbb{G}}(s)} \Lambda(X_s^u, \chi_s, s) e^{-\int_0^s \Lambda(X_w^u, \chi_w, w) dw} ds \\ &\quad + \int_0^t \int_{\widehat{E}} \mathbb{1}_{\{u \in \dot{\mathbb{G}}(s)\}} \mathbb{1}_{\{r \leq B_k(X_{s^-}^u, \chi_{s^-}, s)\}} (k-1) e^{-\int_0^s \Lambda(X_w^u, \chi_w, w) dw} \widehat{Q} (ds, du, dr, dk, d\widehat{\theta}) \\ &\quad + \int_0^t \int_{\widehat{E}^*} \mathbb{1}_{\{r \leq k B_k(X_{s^-}^u, \chi_{s^-}, s)\}} (k-1) e^{-\int_0^s \Lambda(Y_w, \chi_w, w) dw} \widehat{Q}^* (ds, dr, dk, d\widehat{\theta}, dj). \end{aligned}$$

The first line describes the dynamics of the function between branching events. The second line describes the branching events outside the spine. The last one is associated with the contribution of the spinal individual that is here a source of immigration, where the individual chosen to be the new spinal individual is removed from the process. Introducing $\widetilde{Q} (ds, du, dr, dk, d\widehat{\theta})$ the compensated measure of $\widehat{Q} (ds, du, dr, dk, d\widehat{\theta})$, we get

$$\begin{aligned} \dot{\mathcal{W}}_t &= \dot{\mathcal{W}}_0 + \int_0^t \int_{\widehat{E}} \mathbb{1}_{\{u \in \dot{\mathbb{G}}(s)\}} \mathbb{1}_{\{r \leq B_k(X_{s^-}^u, \chi_{s^-}, s)\}} (k-1) e^{-\int_0^s \Lambda(X_w^u, \chi_w, w) dw} \widetilde{Q} (ds, du, dr, dk, d\widehat{\theta}) \\ &\quad + \int_0^t \int_{\widehat{E}^*} \mathbb{1}_{\{r \leq k B_k(X_{s^-}^u, \chi_{s^-}, s)\}} (k-1) e^{-\int_0^s \Lambda(Y_w, \chi_w, w) dw} \widehat{Q}^* (ds, dr, dk, d\widehat{\theta}). \end{aligned}$$

Remark that this last equality only holds for constant ψ_ϕ . Then, conditionally on $\widehat{\mathcal{F}}_\infty^*$, $(\dot{\mathcal{W}}_{t \wedge T^m}, t \geq 0)$ is a submartingale and we have, for all $t \leq T^m$

$$\mathbb{E}_{\bar{z}} \left[\dot{\mathcal{W}}_t | \widehat{\mathcal{F}}_t^* \right] = \mathbb{E}_{\bar{z}} \left[\dot{\mathcal{W}}_0 \right] + \int_0^t \int_{\widehat{E}^*} \mathbb{1}_{\{r \leq k B_k(X_{s^-}^u, \chi_{s^-}, s)\}} (k-1) e^{-\int_0^s \Lambda(Y_w, \chi_w, w) dw} \widehat{Q}^* (ds, dr, dk, d\widehat{\theta}). \quad (\text{C.2})$$

Using that $\mathbb{E}_{\bar{z}} \left[\dot{\mathcal{W}}_0 \right] = \langle z, 1 \rangle - 1$, along with bounds in Assumption D and in (C.2), we get

$$\mathbb{E}_{\bar{z}} \left[\dot{\mathcal{W}}_{t \wedge T^m} | \widehat{\mathcal{F}}_\infty^* \right] \leq \langle z, 1 \rangle + \int_0^t \int_{\widehat{E}^*} \mathbb{1}_{\{r \leq k \bar{B} \bar{p}_k\}} (k-1) e^{-cs} \widehat{Q}^* (ds, dr, dk, d\widehat{\theta}),$$

where $\bar{B} = \sup_{\rho \in \mathbb{W} \times \mathbb{R}_+} B(\rho) < +\infty$. Then there exist two independent families of random variables $(\bar{S}_i, i \geq 0)$ and $(\bar{N}_i, i \geq 0)$, where the S_i are independent exponential random variables of parameter \bar{B} , and the \bar{N}_i are independent random variables distributed as

$\mathbb{P}(\bar{N}_i = k - 1) = k\bar{p}_k / (\sum_{k \geq 0} k\bar{p}_k)$, such that

$$\mathbb{E}_{\bar{z}} \left[\dot{\mathcal{W}}_{t \wedge T^m} | \hat{\mathcal{F}}_{\infty}^* \right] \leq \langle z, 1 \rangle + \sum_{i \geq 0} \bar{N}_i e^{-c\bar{T}_i},$$

where $\bar{T}_i := \sum_{k=0}^i \bar{S}_k$. Note that the assumption $\sum_{k \geq 1} k \log(k) \bar{p}_k < +\infty$ ensures that the law of the random variables \bar{N}_i is well defined. The conclusion follows the steps from proof of Proposition 5 in [3]: using the Borel Cantelli lemma, $\sum_{k \geq 1} k \log(k) \bar{p}_k < +\infty$, ensures that $\limsup_{i \rightarrow \infty} \ln(\bar{N}_i)/i = 0$ a.s.. Thus the series $(\sum_{i \geq 0} \bar{N}_i e^{-c\bar{T}_i})$ is almost surely finite. Letting $m \rightarrow \infty$ and using the upper bound of Assumption D, we get that $T^m \rightarrow \infty$ almost surely. By Fatou's lemma, we then have $\sup_{t \geq 0} \mathbb{E}_{\bar{z}} \left[\dot{\mathcal{W}}_t | \hat{\mathcal{F}}_{\infty}^* \right] < \infty$. The quenched submartingale $(\dot{\mathcal{W}}_{t \wedge T^m}, t \geq 0)$ converges a.s. to a finite random variable. Thus $\limsup_{t \rightarrow +\infty} \dot{\mathcal{W}}_t < +\infty$ almost surely and we conclude the proof using (C.1).

We handle now the degenerated case, and suppose that $\sum_{k \geq 1} k \log(k) \underline{p}_k = +\infty$. We denote $(\hat{T}_n^*, n \geq 0)$ the sequence of jumps times of the spinal individual, given by the measure \hat{Q}^* , and $(\hat{N}_n^*, n \geq 0)$ the sequence giving the number of children at each branching event of the spine. For all $n \geq 0$, we remark that

$$\dot{\mathcal{W}}_{\hat{T}_n^*} = \dot{\mathcal{W}}_{\hat{T}_n^* -} + \left(\hat{N}_n^* - 1 \right) \exp \left(- \int_0^{\hat{T}_n^*} \Lambda(Y_s, \chi_s, s) ds \right).$$

Using that $\dot{\mathcal{W}}$ is almost surely non-negative, and using the upper bound in Assumption D, we obtain

$$\dot{\mathcal{W}}_{\hat{T}_n^*} \geq \left(\hat{N}_n^* - 1 \right) \exp \left(-C\hat{T}_n^* \right). \quad (\text{C.3})$$

Assumption C with $\psi_{\phi} \equiv 1$ implies that for all $\rho \in \mathcal{X} \times \mathbb{V} \times \mathbb{R}_+$, $\sum_{k \geq 1} k p_k(\rho) < +\infty$. Thus $\sum_{k \geq 1} k \underline{p}_k < +\infty$ and we introduce \underline{N} the random variable of law $(k \underline{p}_k / (\sum_{k \geq 1} k \underline{p}_k), k \geq 0)$. The criterion $\sum_{k \geq 1} k \log(k) \underline{p}_k = +\infty$ thus ensures that for all $K > 0$

$$\frac{\mathbb{E}[\log(\underline{N})]}{K} = +\infty.$$

Thus, we get for all $K > 0$,

$$\sum_{n \geq 1} \mathbb{P} \left(\frac{\log(\hat{N}_n^*)}{n} \geq K \mid \hat{\mathcal{F}}_{\hat{T}_n^*}^* \right) \geq \sum_{n \geq 1} \mathbb{P} \left(\frac{\log(\underline{N})}{K} \geq n \right) = +\infty.$$

We can apply the conditional second Borel-Cantelli lemma, see Theorem 4.3.4 in [20]. For all $K > 0$,

$$\limsup_{n \rightarrow \infty} \hat{N}_n^* e^{-Kn} = +\infty \quad \text{a.s.} \quad (\text{C.4})$$

Then using Markov's inequality we get

$$\mathbb{P} \left(\hat{T}_n^* \geq nK \right) \leq \frac{\mathbb{E} \left[\sum_{i=1}^n \hat{T}_i^* - \hat{T}_{i-1}^* \right]}{nK}.$$

The upper bound in Assumption D ensures that the rate of every inter-arrival time of jumps is lower than \bar{B} . Thus we obtain for all $K > 0$,

$$\mathbb{P} \left(\hat{T}_n^* \geq nK \right) \leq \frac{\bar{B}}{K}. \quad (\text{C.5})$$

Thus, combining (C.4) and (C.5) into (C.3), we get that $\limsup_{n \rightarrow \infty} \dot{\mathcal{W}}_{\hat{T}_n^*} = +\infty$ almost surely. Notice that Assumption D ensures that the jumps times $(\hat{T}_n^*, n \geq 0)$ almost surely degenerate at infinity, thus $\limsup_{t \rightarrow \infty} \dot{\mathcal{W}}_t = +\infty$ and relation (C.1) concludes the proof.

APPENDIX D. ALGORITHMIC CONSTRUCTION

We propose the efficient algorithm that generates trajectories of the spine process constructed with the ψ_ϕ function introduced in (4.1). We introduce F_{div}^{-1} , F_{loss}^{-1} and F_{loss}^{*-1} the generalized inverse of the cumulative distribution functions of the random variables $\hat{\Lambda}$, $\hat{\Theta}$ and Θ , defined in (4.2) and (4.3). Using the deterministic evolution of the traits and knowing the branching events, it is easy to recover the traits at all time of the individuals.

We first generate a realization of a Poisson point process of intensity 1 on the interval $[t_1, t_2]$, starting from n roots following classical algorithms [46]. It returns a list $T_{\text{div}} = [t_1, T_1, T_2, \dots]$ of increasing times, a list $I_{\text{div}} = [i_1, i_2, \dots]$ containing the numbering of the individuals that branched at these times, a list $L_{\text{div}} = [\lambda_1, \lambda_2, \dots]$ of fractions of mass at birth, and the numbering E of the spinal individual. The numbering choice is arbitrary and we chose to add every new individuals at the end of the hidden list. This computation is handled by the following function `Tree`, where i_0 is the initial numbering of the spinal individual.

```

function ( $T_{\text{div}}, I_{\text{div}}, E, L_{\text{div}}$ ) = Tree( $t_1, t_2, n, i_0, F_{\text{div}}^{-1}$ )
  ( $T_{\text{div}}, N$ ) = ( $[t_1], n$ )
  % Step 1; generating the division times
  while  $T_{\text{div}}[\text{end}] < t_2$  do
    Generate  $u \sim \text{uniform}(0, 1)$ 
    append  $T_{\text{div}}[\text{end}] - \ln(u)/N$  to  $T_{\text{div}}$                                 ▷ Branching time
     $N \leftarrow N + 1$                                                     ▷ New population size
  end while
  if  $T_{\text{div}}[\text{end}] > t_2$  then pop  $T_{\text{div}}$ 
  % Step 2; generating the fractions at birth and choosing the spinal individual
  ( $I_{\text{div}}, E$ ) = ( $[0, \dots, 0], i_0$ )                                    ▷  $I_{\text{div}}$  of size length( $T_{\text{div}}$ )
  for  $i \in \{1, \dots, \text{length}(T_{\text{div}}) - 1\}$  do
    Generate  $I \sim \text{uniform}(\{1, \dots, n + i - 1\})$                     ▷ Branching individual
     $I_{\text{div}}[i] \leftarrow I$ 
    Generate  $v, q \sim \text{uniform}(0, 1)$ 
    append  $F_{\text{div}}^{-1}(u)$  to  $L_{\text{div}}$                                        ▷ Fraction  $\lambda$  at birth
    if  $E = i$  and  $p > F_{\text{div}}^{-1}(u)$  then  $E \leftarrow n + i$            ▷ New spinal individual position
  end for
end function

```

From the list I_{div} , it is possible to retrieve the lineage of all individuals using any chosen labeling method. In our case we used the Ulam-Harris-Neveu notations and we propose the following algorithm to generate the list U of labels from the list I previously obtained and the initial size of the population n .

```

function  $U = \text{Labels}(I_{\text{div}}, n)$ 
   $N_{\text{div}} = \text{length}(I_{\text{div}})$ 
   $U = [1, \dots, n, 0, \dots, 0]$                                        ▷  $U$  is of size  $n + N_{\text{div}}$ 
  for  $i \in \{1, \dots, N_{\text{div}}\}$  do
    ( $U[I_{\text{div}}[i]], U[n + i]$ )  $\leftarrow$  ( $U[I_{\text{div}}[i]]1, U[I_{\text{div}}[i]]2$ )    ▷  $U[I_{\text{div}}[i]] \in \mathcal{U}$ 
  end for
   $U \leftarrow \text{QuickSort}(U)$                                            ▷ sorting algorithm in  $O((N_{\text{div}} + n) \log(N_{\text{div}} + n))$ 
end function

```

The last line of this algorithm lists the labels of individuals in increasing order, grouping siblings together. The label of the spinal individual is thus $U[E]$. To compute a trajectory of the spinal process on the interval $[0, T]$, we need to establish the time of jumps and their outcomes. Using the deterministic evolution of the traits and knowing the branching events, it is easy to recover the traits at all time for the individuals. Furthermore, depending on the statistics that one want to evaluate on the system, it might not be necessary to compute the traits of all individuals. For that reason we propose an algorithmic construction of a trajectory of the spinal process, returning the list of jumps times, events and labels of the individuals living at time T . This algorithm also distinguishes the spinal individual in the population by returning the label of the spinal individual in the living ones at time T . To simplify we will denote $\text{PPP}_{[t_1, t_2]}(c(\cdot))$ the list of times given by a Poisson point process of intensity $c(\cdot)$ on the interval $[t_1, t_2]$, computed using Lewis' thinning algorithm [39].

Algorithm 1 Simulation algorithm of the jumps times until time T

Input: model parameters: $d, F_{\text{div}}^{-1}, F_{\text{loss}}^{-1}, F_{\text{loss}}^{*-1}, T$, initial condition: $z = [x^1, \dots, x^n]$.
Output: $(T_{\text{div}}, I_{\text{div}}, E, L_{\text{div}}, T_{\text{loss}}, T_{\text{loss}}^*, I_{\text{loss}}, L_{\text{loss}}, L_{\text{loss}}^*)$

```

% Initializing the spine
Generate  $u \sim \text{uniform}(0, 1)$ 
 $i_0 = 1$ 
while  $\sum_{i=1}^{i_0} x^i / (\sum_{i=1}^n x^i) < u$  do
     $i_0 \leftarrow i_0 + 1$ 
end while
% Generating binary spinal tree on division events
 $(T_{\text{div}}, I_{\text{div}}, E, L_{\text{div}}) = \text{Tree}(0, T, n, i_0, F_{\text{div}}^{-1})$ 
% Generating loss events for the spine and individuals outside the spine
 $(T_{\text{loss}}, T_{\text{loss}}^*, I_{\text{loss}}) = ([\cdot], [\cdot], [\cdot])$ 
for  $i \in \{1, \dots, \text{length}(T_{\text{div}})\}$  do
    % For the individuals outside the spine
    Generate  $P \sim \text{PPP}_{[T_{\text{div}}[i-1], T_{\text{div}}[i]]}(K_{\text{loss}}(n+i-1)^2 d(\cdot))$  ▷ Times of loss events
    append  $P$  to  $T_{\text{loss}}$ 
    Generate  $I_u \sim (\text{uniform}(\{1, \dots, n+i-1\})^{\text{length}(T_{\text{loss}}[i])})$  ▷ Distributing loss events
    append  $I_u$  to  $I_{\text{loss}}$ 
    % For the spine
    Generate  $P^* \sim \text{PPP}_{[T_{\text{div}}[i-1], T_{\text{div}}[i]]}((n+i-1)d(\cdot))$  ▷ Times of loss events
    append  $P^*$  to  $T_{\text{loss}}^*$ 
end for
Generate  $L_u \sim (\text{uniform}(0, 1))^{\text{length}(T_{\text{loss}})}$  ▷ Generating fractions lost
 $L_{\text{loss}} = F_{\text{loss}}^{-1}(L_u)$ 
Generate  $L_u^* \sim (\text{uniform}(0, 1))^{\text{length}(T_{\text{loss}}^*)}$  ▷ Generating fractions lost
 $L_{\text{loss}}^* = F_{\text{loss}}^{*-1}(L_u^*)$ 

```

The output tuple $(T_{\text{div}}, I_{\text{div}}, E, L_{\text{div}}, T_{\text{loss}}, T_{\text{loss}}^*, I_{\text{loss}}, L_{\text{loss}}, L_{\text{loss}}^*)$ is the minimal information needed to construct the spinal process introduced in Section 4. The list U of labels of the individuals can be computed with the function $\text{Labels}(I_{\text{div}}, n)$. Notice that a lot of operations can be parallelized in this algorithm, unlike in the classical Lewis' algorithm. Moreover, depending on the statistic that one wants to compute on this process, the algorithm can be further simplified. For example, if one takes interest in the total biomass of the population, the indexes of the individuals that branched are not necessary.

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