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Empirical distribution of ancestral lineages in populations with density-dependent interactions

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Abstract

We study a density-dependent Markov jump process describing a population where each individual is characterized by a type, and reproduces at rates depending both on its type and on the population type distribution. We are interested in the empirical distribution of ancestral lineages in the population process. First, we exhibit a time-inhomogeneous Markov process, which allows to capture the behavior of a sampled lineage in the population process. This is achieved through a many-to-one formula, which relates the expected value of a functional evaluated over the lineages in the population process to the expectation of the functional evaluated along this time-inhomogeneous process. This provides a direct interpretation of the underlying survivorship bias, as illustrated on a minimalistic population process. Second, we consider the large population regime, when the population size grows to infinity. Under classical assumptions, the population type distribution converges to a deterministic limit. Here, we focus on the empirical distribution of ancestral lineages in this large population limit, for which we establish a many-to-one formula. Using coupling arguments, we further quantify the approximation error which arises when sampling in this large population approximation instead of the finite-size population process.

Keywords. Interactions; Markov jump process; population process; many-to-one formula; large population limit.

1 Introduction

When considering population processes arising in various fields such as population genetics or epidemiology, the study of ancestral lineages may provide crucial information. For instance, such lineages yield insight on epidemic spread through contamination chains [15], or on the evolution of a trait of interest under selection [12]. As a consequence, several methods have been developed to finely characterize those lineages. On the one hand, a classical approach is to consider a backward-in-time process which reconstructs the genealogy by moving back from time t to time 0, and which is related to the initial population process by duality [9, 2, 21, 13, 15]. On the other hand, there also exists a forward-in-time approach which relies on a second population process, with one distinguished individual (the *spine*) whose lineage behaves as the lineage of a sampled individual in the original process.

More precisely, these *spinal constructions* have originally been introduced for branching processes, using an appropriate change in probability. The key to the construction of the spinal process is that the reproduction rates of the spine are biased towards leaving more numerous descendants than other individuals. This leads to the emergence of size-biased distributions,

which accurately depict the survivorship bias induced by sampling. Generally speaking, the obtained spinal construction has several strengths. Notably, it allows to establish *many-to-one* formulas (e.g. [20, 17, 18, 19]), which are closely related to Feynman-Kac path equations [14, Sections 1.3 and 1.4.4]. Many-to-one formulas translate the expected value of a functional evaluated over the lineages in the branching process, into the expectation of the functional evaluated along the spine, whose trajectories are exponentially weighted to capture the growth of the population. If the exponential weight is deterministic, this immediately implies a numerical advantage for computing such averages through Monte-Carlo simulations. Indeed, simulations of the spine are numerically affordable, whereas simulations of the whole genealogical tree in the original branching process can be numerically challenging due to exponential growth [24]. Also, spinal constructions have proven an effective way of establishing classical key results on branching processes, such as the Kesten Stigum theorem [20, 17]. More recently, the semi-group associated to the spinal construction has proven a successful tool in the analysis of non-conservative semi-groups, extending its applications beyond branching processes [5, 6].

While many models for population dynamics arising, for instance, in biology and epidemiology do not satisfy *per se* the branching approximation, a classical approach is to consider regimes in which the population process can be well approached by a branching process, using coupling arguments. For example, in epidemiology, it is well-known that at the beginning of an epidemic, the tree of infections can be captured by a branching process which neglects the depletion in susceptible individuals [3]. Similarly, in order to analyze the lineage of a uniformly sampled individual in a population which is subject to evolution under a changing environment, [12] consider the stationary regime. However, such branching approximations are restricted to specific parts of the dynamics of interest only; see for instance [8] and [7] for details in the case of epidemic models and invasion processes.

In order to address this limitation, there have been developments towards capturing the ancestral lineage of a sampled individual, as well as the whole genealogical tree, in populations with interactions. Recently, a spinal construction has been developed for this setting, focusing on multi-type processes with discrete type space [4]. The general idea consists in biasing the reproduction rates of the process, both along the spine and outside of it, according to a positive function ψ of the reproducing particle's trait x and the population's type composition \mathbf{z} . Intuitively, $\psi(x, \mathbf{z})$ can be regarded as the individual's reproductive value or long-term fertility. Hence, when the spine reproduces, offspring with higher values of ψ given the population state are favored, while the offspring of individuals outside of the spine are biased towards rendering the population more favorable for the spine. This spinal construction has since been extended to include more general type spaces [23]. It further has served to study the convergence of genealogies of density-dependent branching processes to the Kingman coalescent, establishing a connection with backward-in-time approaches [1].

In this paper, we focus on the empirical type distribution of ancestral lineages ($\psi = 1$), which arguably corresponds to the most natural and naive sampling strategy. In particular, we aim to capture the underlying survivorship bias. Notably, in the many-to-one formula associated to the aforementioned ψ -spine, spinal trajectories are penalized by an exponential weight which is generally stochastic. Thus the interpretation of the survivorship bias embodied by this spinal process is not straightforward, as this penalization needs to be taken into account. In addition, Monte-Carlo estimations of the many-to-one formula become delicate as rare trajectories may have a tremendous impact. As a consequence, we aim at proposing an alternative spinal construction, whose associated many-to-one formula does not require exponential weighting of trajectories. This is achieved by a time-inhomogeneous spinal process, inspired from a similar auxiliary process which captures the lineage of a uniformly sampled individual in a branching process with large initial population [22].

Further, a natural regime to consider is the large population limit $K \rightarrow +\infty$. Under classical

assumptions, several large population approximations can frequently be established. Indeed, these approximations may be more prone to mathematical analysis than the original population process. From a numerical point of view, simulating large population approximations is often less expensive than individual-based models for large population sizes, both in terms of computation time and memory. For instance, numerical evaluation of the ψ -spine many-to-one formula requires simulations of the spinal population process, which is computationally expensive for large population sizes. As a consequence, it is natural to develop approximate sampling strategies, which allow to sample directly in those large population approximations. Building on the large population approximation of the empirical distribution of ancestral lineages [4], we establish a many-to-one formula for sampling in the deterministic large population limit with our time-inhomogeneous spinal process. Finally, we quantify the approximation error which is made by sampling in the large population limit instead of the original population process.

This paper is structured as follows. The population process of interest is defined in Section 2. In Section 3, we introduce a new spinal construction, whereas Section 4 focuses on sampling in the large population limit. Finally, Section 5 presents a discussion on our results.

2 The population process

We consider a structured population, where each individual has a type $x \in \mathcal{X}$, and we assume for convenience that the type space \mathcal{X} is finite. The number of individuals of type x in the population is referred to as \mathbf{z}_x , and the corresponding vector \mathbf{z} describes the composition of the population. Here, we will assume that the population size cannot exceed K individuals (carrying capacity, absence of demographic births and deaths, etc.). Thus

$$\mathbf{z} \in \mathcal{Z}_K = \{\mathbf{z} \in (\mathbb{N} \cup \{0\})^{\mathcal{X}} : \|\mathbf{z}\|_1 \leq K\}.$$

Further, individuals will reproduce at rates depending on their type and the current population state. More precisely, an individual of type x may be replaced by an offspring $\mathbf{k} = (\mathbf{k}_y, y \in \mathcal{X}) \in \mathcal{Z}_K$, meaning that the individual dies and for any $y \in \mathcal{X}$, \mathbf{k}_y individuals of type y are born. This occurs at rate $\tau_{\mathbf{k}}(x, \mathbf{z})$. We suppose $\tau(x, \mathbf{z}) = \sum_{\mathbf{k}} \tau_{\mathbf{k}}(x, \mathbf{z}) < \infty$ for all $x \in \mathcal{X}$ and $\mathbf{z} \in \mathcal{Z}_K$. Further, let $(\mathbf{e}(x) : x \in \mathcal{X})$ be the canonical base of \mathcal{Z}_K , in the sense that for $x \in \mathcal{X}$, the only non-zero component of $\mathbf{e}(x)$ is its x component which equals one. Then, as the population size is bounded by K ,

$$\tau_{\mathbf{k}}(x, \mathbf{z}) = 0 \quad \text{if} \quad \|\mathbf{z} + \mathbf{k} - \mathbf{e}(x)\|_1 > K.$$

In order to keep track of the genealogy, we will make use of the Ulam-Harris-Neveu notations. Let $\mathcal{U} = \bigcup_{k \geq 1} \mathbb{N}^k$, then $u = (u_1, \dots, u_k) \in \mathcal{U}$ represents the u_k -th descendent of (u_1, \dots, u_{k-1}) and for $u, v \in \mathcal{U}$ we write $u \geq v$ if v is an ancestor of u . The type of $u \in \mathcal{U}$ will be called x_u . Hence when an individual u is replaced by its offspring \mathbf{k} , the new individuals are $(u, 1), \dots, (u, \|\mathbf{k}\|_1)$ and we need to decide the type of each descendent. We thus consider a probability distribution $\mathcal{Q}_{\mathbf{k}}$ on

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

and $(x_{(u,i)} : i \in \llbracket 1, \|\mathbf{k}\|_1 \rrbracket)$ is distributed as $\mathcal{Q}_{\mathbf{k}}$.

Let us now introduce the stochastic process of interest. Intuitively, it corresponds to describing the set of individuals alive and their types, at each time $t \geq 0$. We start from an initial set of individuals $\mathbb{G}(0) = \mathbf{g} \subset \mathbb{N}$, and the population will evolve as explained above. At each time t , let $\mathbb{G}(t) \subset \mathcal{U}$ be the set of individuals alive. The process of interest $(X(t), t \geq 0)$ is a Markov jump process with càdlàg trajectories, which for $t \geq 0$ tracks the individuals alive at time t , and their types. In particular, notice that there cannot be explosion, since there are at most K individuals reproducing at rate less than $\max_{x \in \mathcal{X}, \mathbf{z} \in \mathcal{Z}_K} \tau(x, \mathbf{z})$, which is a finite bound as \mathcal{X} and

\mathcal{Z}_K are finite sets. Finally, $Z(t) = \mathbf{z}(X(t))$ yields the composition of the population at time t , and for $u \in \mathbb{G}(t)$ and $s \leq t$, $x_u(s)$ stands for the type of the unique ancestor of u alive at time s .

Let us end this section by introducing some notation. Define the set

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

For any $\mathbf{z} \in \mathcal{Z}_K$, we consider an (arbitrary) labeling $\mathfrak{g}(\mathbf{z}) \subset \mathbb{N}$ of individuals, and for x such that $\mathbf{z}_x > 0$, we fix $u_x \in \mathfrak{g}(\mathbf{z})$ of type x . We designate the corresponding population state by $\mathfrak{X}(\mathbf{z})$. We let $\mathbb{E}_{\mathbf{z}}$ and $\mathbb{P}_{\mathbf{z}}$ designate the expectation and probability conditionally on $X(0) = \mathfrak{X}(\mathbf{z})$. With these notations,

$$M_t f(x, \mathbf{z}) = \mathbb{E}_{\mathbf{z}} \left[\sum_{u \in \mathbb{G}(t), u \geq u_x} f(x_u(t), Z(t)) \right]$$

is a semi-group whose generator G is defined by its action on functions $f : \mathcal{S}_K \rightarrow \mathbb{R}_+$:

$$\begin{aligned} \forall (x, \mathbf{z}) \in \mathcal{S}_K, \quad Gf(x, \mathbf{z}) = & \sum_{\mathbf{k} \in \mathcal{Z}_K} \tau_{\mathbf{k}}(x, \mathbf{z}) \left(\sum_{y \in \mathcal{X}} \mathbf{k}_y f(y, \mathbf{z} + \mathbf{k} - \mathbf{e}(x)) - f(x, \mathbf{z}) \right) \\ & + \sum_{\substack{y \in \mathcal{X} \\ \mathbf{k} \in \mathcal{Z}_K}} (\mathbf{z}_y - \mathbf{1}_{\{x=y\}}) \tau_{\mathbf{k}}(y, \mathbf{z}) (f(x, \mathbf{z} + \mathbf{k} - \mathbf{e}(y)) - f(x, \mathbf{z})). \end{aligned} \quad (1)$$

We are now ready to turn to the study of the empirical distribution of ancestral lineages.

3 Survivorship bias and the empirical distribution of ancestral lineages

In this section, our aim is to propose a many-to-one formula without stochastic penalization of spinal trajectories, in an effort to gain insight in on the survivorship bias. In order to do so, we will introduce a time inhomogeneous spinal construction. This approach is inspired by [22]. While we are particularly interested in the empirical distribution of ancestral lineages, the results obtained in this Section hold for a large class of sampling strategies, and are thus stated in a general setting.

3.1 A many-to-one formula

Consider a positive function ψ on $\mathcal{X} \times \mathcal{Z}_K$. As it is kept fixed, dependence on ψ is not explicit in our notations for readability. Define the following application m on $\mathcal{S}_K \times [0, t]$:

$$m(x, \mathbf{z}, t) = \mathbb{E}_{\mathbf{z}} \left[\sum_{\substack{u \in \mathbb{G}(t) \\ u \geq u_x}} \psi(x_u(t), Z(t)) \right]. \quad (2)$$

Notice that, by the Markov property, for $s \in [0, t]$,

$$m(x, \mathbf{z}, t - s) = \mathbb{E} \left[\sum_{\substack{u \in \mathbb{G}(t) \\ u \geq u_x}} \psi(x_u(t), Z(t)) \middle| X(s) = \mathfrak{X}(\mathbf{z}) \right].$$

In words, $m(x, \mathbf{z}, t - s)$ corresponds to the ψ -weighted average of the types of individuals alive at time t who descend from a given individual of type x at time s , given that at time s , the population was in state \mathbf{z} . For instance, if $\psi = 1$, this yields the average number of individuals

alive at time t , who descend from an individual of type x at time s when the population was in state \mathbf{z} .

Let us now introduce the time-inhomogeneous spinal process, which allows to capture the behavior of the ancestral lineage of a ψ -weighted sample of the population process. For $t \geq 0$ fixed, we will consider the time-inhomogeneous Markov process $(Y^{(t)}(s), \zeta^{(t)}(s))_{s \leq t}$ defined as follows. The main idea is to follow the type $Y^{(t)}$ of a distinguished individual, which will be referred to as *spine* in analogy to classical spinal constructions. At time $s \leq t$, when of type x in a population of state \mathbf{z} , the spine is replaced by offspring \mathbf{k} and switches to type y (*i.e.* among its offspring \mathbf{k} , one individual of type y is chosen to become the new spine) with rate

$$\rho_{y,\mathbf{k}}^{(t)}(s, x, \mathbf{z}) = \tau_{\mathbf{k}}(x, \mathbf{z}) \mathbf{k}_y \frac{m(y, \mathbf{z} + \mathbf{k} - \mathbf{e}(x), t - s)}{m(x, \mathbf{z}, t - s)}. \quad (3)$$

In other words, compared to the original process, at any time $s \leq t$, transitions along the distinguished lineage are biased in favor of those which lead to a larger ψ -average offspring at the final time t . However, due to the density-dependence of division rates, it is necessary to keep track of the population state $\zeta^{(t)}$. Again, transitions need to be biased, in order to account for the modified behavior of the distinguished individual when compared to the original process. As a consequence, when the population is in state \mathbf{z} and the spine is of type x at time $s \leq t$, individuals of type y other than the spine is replaced by offspring \mathbf{k} at rate

$$\hat{\rho}_{\mathbf{k}}^{(t)}(s, y, x, \mathbf{z}) = \tau_{\mathbf{k}}(y, \mathbf{z}) \frac{m(x, \mathbf{z} + \mathbf{k} - \mathbf{e}(y), t - s)}{m(x, \mathbf{z}, t - s)}. \quad (4)$$

Here, the bias favors those transitions which lead to a more favorable environment for the spine, *i.e.* a population composition in which the ψ -average of the spine's offspring is high.

We will now characterize $(Y^{(t)}(s), \zeta^{(t)}(s))_{s \leq t}$ as the unique solution of a stochastic differential equation. In order to do so, we let $Y^{(t)}(s) \in \{\mathbf{e}(x) : x \in \mathcal{X}\}$ for any $s \in [0, t]$, where $Y^{(t)}(s) = \mathbf{e}(x)$ means that the spine is of type x . Define $E = \mathbb{R}_+ \times \mathcal{S}_K$, and consider two independent Poisson point processes Q and \hat{Q} on $\mathbb{R}_+ \times E$, of density $dr \otimes d\theta \otimes n(dy, d\mathbf{k})$ where $dr, d\theta$ designate the Lebesgue measure and n the counting measure on \mathcal{S}_K . Here, we assume that Q and \hat{Q} are defined on the same probability space as and independently from $(Y^{(t)}(0), \zeta^{(t)}(0))$, whose law is supposed to be given. Then, for any $s \in [0, t]$,

$$\begin{aligned} Y^{(t)}(s) &= Y^{(t)}(0) + \int_0^s \int_E \mathbf{1}_{\{\theta \leq \rho_{y,\mathbf{k}}^{(t)}(r, Y^{(t)}(r-), \zeta^{(t)}(r-))\}} (\mathbf{e}(y) - Y^{(t)}(r-)) Q(dr, d\theta, dy, d\mathbf{k}), \\ \zeta^{(t)}(s) &= \zeta^{(t)}(0) + \int_0^s \int_E \mathbf{1}_{\{\theta \leq \rho_{y,\mathbf{k}}^{(t)}(r, Y^{(t)}(r-), \zeta^{(t)}(r-))\}} (\mathbf{k} - Y^{(t)}(r-)) Q(dr, d\theta, dy, d\mathbf{k}) \\ &\quad + \int_0^s \int_E \mathbf{1}_{\{\theta \leq (\zeta_y^{(t)}(r-) - \mathbf{1}_{\{Y^{(t)}(r-)=y\}}) \hat{\rho}_{\mathbf{k}}^{(t)}(r, y, Y^{(t)}(r-), \zeta^{(t)}(r-))\}} (\mathbf{k} - \mathbf{e}(y)) \hat{Q}(dr, d\theta, dy, d\mathbf{k}). \end{aligned} \quad (5)$$

Remark 3.1. *Throughout the following, in order to simplify notations, we will make no distinction between the sets \mathcal{X} and $\{\mathbf{e}(x) : x \in \mathcal{X}\}$, based on the natural bijection between the two sets. For example, $Y^{(t)}(s) = x$ is equivalent to $Y^{(t)}(s) = \mathbf{e}(x)$. Similarly, to every real-valued function f on \mathcal{S}_K , we assign a function \hat{f} on $\{\mathbf{e}(x) : x \in \mathcal{X}\}$ by $\hat{f}(\mathbf{e}(x)) = f(x)$, the application $f \mapsto \hat{f}$ being a bijection between the sets of real-valued functions on \mathcal{S}_K and on $\{\mathbf{e}(x) : x \in \mathcal{X}\}$. Thus, we will always consider $Y^{(t)}$ to take values in the Skorokhod space $\mathbb{D}([0, t], \mathcal{X})$, unless mentioned otherwise.*

Our first result shows that the process $(Y^{(t)}(s), \zeta^{(t)}(s))_{s \leq t}$ is now well defined, and additionally provides its semi-group $R^{(t)} = (R_{r,s}^{(t)}, r \leq s \leq t)$. We recall that the latter is characterized by its action on non-negative functions f on \mathcal{S}_K : for $r \leq s \leq t$ and $(x, \mathbf{z}) \in \mathcal{S}_K$,

$$R_{r,s}^{(t)}(x, \mathbf{z}) = \mathbb{E}[f(Y^{(t)}(s), \zeta^{(t)}(s)) | (Y^{(t)}(r), \zeta^{(t)}(r)) = (x, \mathbf{z})].$$

Proposition 3.2. Equation (5) admits a unique strong solution $(Y^{(t)}, \zeta^{(t)})$ in the Skorokhod space $\mathbb{D}([0, t], \mathcal{S}_K)$. Its semi-group $R^{(t)}$ satisfies:

$$\forall 0 \leq r \leq s \leq t, \quad R_{r,s}^{(t)} = e^{\int_r^s A_\tau^{(t)} d\tau}, \quad (6)$$

where the operator $A^{(t)}$ is characterized by its action on non-negative functions f on \mathcal{S}_K . For any $s \in [0, t]$ and $(x, \mathbf{z}) \in \mathcal{S}_K$,

$$A_s^{(t)} f(x, \mathbf{z}) = m(x, \mathbf{z}, t - s)^{-1} (G(m(\cdot, t - s) f(\cdot))(x, \mathbf{z}) - G(m(\cdot, t - s))(x, \mathbf{z}) f(x, \mathbf{z})). \quad (7)$$

Notice that the operator $A^{(t)}$ corresponds to the generator of the semi-group $R^{(t)}$. As our state space \mathcal{S}_K is finite, $A_\tau^{(t)}$ can be represented as a matrix, whose elements correspond to the instantaneous transition rates at time τ which can be recovered by taking $f = \mathbf{1}_{\{(y, \mathbf{v})\}}$ for $(y, \mathbf{v}) \in \mathcal{S}_K$. In particular, this ensures that the generator $A^{(t)}$ uniquely characterizes the semi-group $R^{(t)}$, and thus the Markov process $(Y^{(t)}, \zeta^{(t)})$. The proof of the proposition is postponed to Section 3.2.

We are now ready to state our main result. With slight abuse of notation, $\mathbb{E}_{x, \mathbf{z}}$ will designate the expectation conditionally on the event $(Y^{(t)}(0), \zeta^{(t)}(0)) = (x, \mathbf{z})$.

Theorem 3.3. For any $t \geq 0$ and any measurable function $F : \mathbb{D}([0, t], \mathcal{S}_K) \rightarrow \mathbb{R}_+$, for any $\mathbf{z} \in \mathcal{Z}_K$,

$$\mathbb{E}_{\mathbf{z}} \left[\sum_{u \in \mathbb{G}(t)} \psi(x_u(t), Z(t)) F((x_u(s), Z(s))_{s \leq t}) \right] = \sum_{x \in \mathcal{X}} \mathbf{z}_x m(x, \mathbf{z}, t) \mathbb{E}_{x, \mathbf{z}} [F((Y^{(t)}(s), \zeta^{(t)}(s))_{s \leq t})]. \quad (8)$$

This result shows that the reproduction rates defined in Equations (3) and (4) yield the appropriate survivorship bias: reproduction events are favored if and only if they increase the ψ -average of the offspring at sampling time. In particular, the survivorship bias may thus be computed explicitly, giving access to a more precise interpretation. This will be illustrated in Section 3.3.

Remark 3.4. Before proceeding to the proof of Theorem 3.3, let us compare the obtained ψ -auxiliary process with the ψ -spine [4]. First, notice that both constructions are similar in spirit, as the former relies on the h -transform, whereas the latter may be regarded as a time-inhomogeneous m -transform. Second, in the special case where ψ is an eigenfunction of the generator G introduced above, a brief computation shows that as expected, Equation (8) amounts to the Feynman-Kac formula of [4, Proposition 1].

3.2 Proofs

The general idea is to proceed as follows. We start by establishing Proposition 3.2, and compute the generator $A^{(t)}$ of the time-inhomogeneous spinal process. Next, we introduce a time-inhomogeneous semi-group corresponding to the left-hand side of Equation (8) renormalized by m , and show that its generator is equal to $A^{(t)}$. As mentioned previously, the considered state space being finite, the generator uniquely characterizes the time-inhomogeneous semi-group. This finally allows to establish the many-to-one formula of Theorem 3.3.

3.2.1 Existence and uniqueness of the ψ -auxiliary process

We first establish Proposition 3.2, ensuring that the ψ -auxiliary process is well defined. We start with a technical lemma.

Lemma 3.5. For any $t \geq 0$, for any $(x, \mathbf{z}) \in \mathcal{S}_K$, the function $s \mapsto m(x, \mathbf{z}, t - s)$ is differentiable on $(0, t)$, and we have:

$$\partial_s m(x, \mathbf{z}, t - s) = -G(m(\cdot, t - s))(x, \mathbf{z}).$$

Proof. Let $(x, \mathbf{z}) \in \mathcal{S}_K$. Showing that $t \mapsto m(x, \mathbf{z}, t)$ is differentiable on \mathbb{R}_+ and computing its derivative is sufficient, as the desired result follows by composition. Let $t \geq 0$ and $h > 0$. The Markov property ensures that

$$m(x, \mathbf{z}, t + h) = \mathbb{E}_{\mathbf{z}} \left[\sum_{\substack{u \in \mathbb{G}(h) \\ u \geq u_x(0)}} m(x_u(h), Z(h), t) \right].$$

For $i \geq 1$, Let T_i be the time of the i -th jump of the population process. Then on the one hand, if $T_1 > h$, then the population at time h is identical to the population at time 0, and thus:

$$m(x, \mathbf{z}, t + h) = \mathbb{E}_{\mathbf{z}} \left[\sum_{\substack{u \in \mathbb{G}(h) \\ u \geq u_x(0)}} m(x_u(h), Z(h), t) \mathbf{1}_{\{T_1 < h\}} \right] + m(x, \mathbf{z}, t) \mathbb{P}_{\mathbf{z}}(T_1 > h).$$

Similarly, on the event $\{T_1 < h < T_2\}$, $Z(h) = Z(T_1)$ whence

$$\mathbb{E}_{\mathbf{z}} \left[\sum_{\substack{u \in \mathbb{G}(h) \\ u \geq u_x(0)}} m(x_u(h), Z(h), t) \mathbf{1}_{\{T_1 < h\}} \right] = a(h) + b(h),$$

where

$$\begin{aligned} a(h) &= \mathbb{E}_{\mathbf{z}} \left[\sum_{\substack{u \in \mathbb{G}(h) \\ u \geq u_x(0)}} m(x_u(T_1), Z(T_1), t) \mathbf{1}_{\{T_1 < h < T_2\}} \right], \\ b(h) &= \mathbb{E}_{\mathbf{z}} \left[\sum_{\substack{u \in \mathbb{G}(h) \\ u \geq u_x(0)}} m(x_u(h), Z(h), t) \mathbf{1}_{\{T_2 < h\}} \right]. \end{aligned}$$

As a consequence, we obtain that

$$m(x, \mathbf{z}, t + h) - m(x, \mathbf{z}, t) = A(h) + B(h), \quad (9)$$

with $A(h) = a(h) - m(x, \mathbf{z}, t) \mathbb{P}_{\mathbf{z}}(T_1 < h < T_2)$ and $B(h) = b(h) - m(x, \mathbf{z}, t) \mathbb{P}_{\mathbf{z}}(T_2 < h)$.

Let us first focus on $B(h)$. For any $t \geq 0$ and $(y, \mathbf{v}) \in \mathcal{S}_K$, it holds that $m(y, \mathbf{v}, t) \leq K \|\psi\|_{\infty}$. As \mathcal{S}_K is a finite set, it follows that there exists a constant $c > 0$ such that

$$B(h) \leq c \mathbb{P}_{\mathbf{z}}(T_2 < h).$$

For $\mathbf{v} \in \mathcal{Z}_K$, let us write $\Lambda(\mathbf{v}) = \sum_{y \in \mathcal{X}} \sum_{\mathbf{k} \in \mathcal{Z}_K} \mathbf{v}_y \tau_{\mathbf{k}}(y, \mathbf{v})$ for the total jump rate in a population whose type distribution is given by \mathbf{v} . In particular, Λ is bounded on \mathcal{Z}_K . Using the law of T_1 given $Z(0) = \mathbf{z}$ and the law of $T_2 - T_1$ given T_1 and $Z(T_1)$, we then obtain:

$$\mathbb{P}_{\mathbf{z}}(T_2 < h) = \int_0^h e^{-\Lambda(\mathbf{z})t_1} \sum_{\substack{y \in \mathcal{X} \\ \mathbf{k} \in \mathcal{Z}_K}} \mathbf{z}_y \tau_{\mathbf{k}}(y, \mathbf{z}) \int_0^{h-t_1} \Lambda(\mathbf{z} + \mathbf{k} - \mathbf{e}(y)) e^{-\Lambda(\mathbf{z} + \mathbf{k} - \mathbf{e}(y))t_2} dt_2 dt_1 \leq \frac{\|\Lambda\|_{\infty}^2}{2} h^2.$$

We deduce that

$$\frac{B(h)}{h} \xrightarrow{h \rightarrow 0^+} 0. \quad (10)$$

Let us now focus on $A(h)$. Proceeding in the same way, we have

$$\begin{aligned} A(h) &= \int_0^h e^{-\Lambda(\mathbf{z})t_1} e^{-\Lambda(\mathbf{z}+\mathbf{k}-\mathbf{e}(x))(h-t_1)} dt_1 \sum_{\mathbf{k} \in \mathcal{Z}_K} \tau_{\mathbf{k}}(x, \mathbf{z}) \sum_{y \in \mathcal{X}} \mathbf{k}_y (m(y, \mathbf{z} + \mathbf{k} - \mathbf{e}(x), t) - m(x, \mathbf{z}, t)) \\ &\quad + \sum_{\substack{y \in \mathcal{X} \\ \mathbf{k} \in \mathcal{Z}_K}} \int_0^h e^{-\Lambda(\mathbf{z})t_1} e^{-\Lambda(\mathbf{z}+\mathbf{k}-\mathbf{e}(y))(h-t_1)} dt_1 \tau_{\mathbf{k}}(y, \mathbf{z}) (m(x, \mathbf{z} + \mathbf{k} - \mathbf{e}(y), t) - m(x, \mathbf{z}, t)), \end{aligned}$$

from which it follows that

$$\begin{aligned} \frac{A(h)}{h} \xrightarrow{h \rightarrow 0^+} & \sum_{\mathbf{k} \in \mathcal{Z}_K} \tau_{\mathbf{k}}(x, \mathbf{z}) \left(\sum_{y \in \mathcal{X}} \mathbf{k}_y m(y, \mathbf{z} + \mathbf{k} - \mathbf{e}(x), t) - m(x, \mathbf{z}, t) \right) \\ & + \sum_{\substack{y \in \mathcal{X} \\ \mathbf{k} \in \mathcal{Z}_K}} (\mathbf{z}_y - \mathbf{1}_{\{x=y\}}) \tau_{\mathbf{k}}(y, \mathbf{z}) (m(x, \mathbf{z} + \mathbf{k} - \mathbf{e}(y), t) - m(x, \mathbf{z}, t)). \end{aligned} \quad (11)$$

As a consequence, right differentiability of $t \mapsto m(x, \mathbf{z}, t)$ is established by Equations (9), (10) and (11), and its right derivative is given by the right-hand side of Equation (11). As this corresponds to a continuous function on \mathbb{R}_+ , we deduce that $t \mapsto m(x, \mathbf{z}, t)$ is differentiable on \mathbb{R}_+ (see *e.g.* Corollary 1.2 of Chapter 2 in [26]) and

$$\begin{aligned} \frac{d}{dt} m(x, \mathbf{z}, t) &= \sum_{\mathbf{k} \in \mathcal{Z}_K} \tau_{\mathbf{k}}(x, \mathbf{z}) \left(\sum_{y \in \mathcal{X}} \mathbf{k}_y m(y, \mathbf{z} + \mathbf{k} - \mathbf{e}(x), t) - m(x, \mathbf{z}, t) \right) \\ &\quad + \sum_{\substack{y \in \mathcal{X} \\ \mathbf{k} \in \mathcal{Z}_K}} (\mathbf{z}_y - \mathbf{1}_{\{x=y\}}) \tau_{\mathbf{k}}(y, \mathbf{z}) (m(x, \mathbf{z} + \mathbf{k} - \mathbf{e}(y), t) - m(x, \mathbf{z}, t)). \end{aligned}$$

This concludes the proof. \square

We are now ready to establish the desired result.

Proof of Proposition 3.2. The proof is decomposed in three steps, establishing (i) existence and (ii) uniqueness of the solution to Equation (5) by classical arguments, before (iii) characterizing the associated semi-group $R^{(t)}$.

For ease of notation, throughout the proof, for $0 \leq s \leq t$ we let $\mathbb{Y}^{(t)}(s) = (Y^{(t)}(s), \zeta^{(t)}(s))$.

(i) *Existence.* First, notice that by assumption on $\tau(x, \mathbf{z})$ for $(x, \mathbf{z}) \in \mathcal{S}_K$ and continuity of m , both applications $\rho_{y, \mathbf{k}}^{(t)}$ and $\hat{\rho}_{\mathbf{k}}^{(t)}$ are bounded for any $y \in \mathcal{X}$ and $\mathbf{k} \in \mathcal{Z}_K$. As a consequence, existence of at least one solution to Equation (5) is ensured, as the associated sequence of jump times $(T_k)_{k \geq 0}$ cannot admit an accumulation point on \mathbb{R}_+ .

(ii) *Uniqueness.* Subsequently, in order to establish uniqueness, let us show by induction that for any $k \geq 0$ such that $T_k \leq t$, $(T_k, \mathbb{Y}^{(t)}(T_k))$ is entirely determined by $(\mathbb{Y}^{(t)}(0), Q, \hat{Q})$. As $T_0 = 0$, initialization of the induction argument is immediate. If the property holds for $k \geq 1$, then by construction, T_{k+1} only depends on $(T_k, \mathbb{Y}^{(t)}(T_k), Q, \hat{Q})$. Similarly, given T_{k+1} and the corresponding atoms A_{k+1} and \hat{A}_{k+1} of Q and \hat{Q} , it is clear that $\mathbb{Y}^{(t)}(T_{k+1})$ is fixed by $(T_{k+1}, A_{k+1}, \hat{A}_{k+1}, \mathbb{Y}^{(t)}(T_k))$. The desired conclusion thus is a consequence of the induction hypothesis.

(ii) *Characterization of $R^{(t)}$.* In order to establish Equation (6), it is sufficient to show that for any non-negative function f on \mathcal{S}_K and $(x, \mathbf{z}) \in \mathcal{S}_K$, the function

$$\tau \mapsto R_{s, \tau}^{(t)} f(x, \mathbf{z}) = \mathbb{E}[f(\mathbb{Y}^{(t)}(\tau)) | \mathbb{Y}^{(t)}(s) = (x, \mathbf{z})]$$

is right differentiable at $\tau = s$. Indeed, it then follows that Equation (6) holds with the operator $A^{(t)}$ defined by

$$\forall f : \mathcal{S}_K \rightarrow \mathbb{R}_+ \quad \forall (x, \mathbf{z}) \in \mathcal{S}_K, \quad A_s^{(t)} f(x, \mathbf{z}) = \lim_{h \rightarrow 0^+} \frac{1}{h} \left(R_{s, s+h}^{(t)} f(x, \mathbf{z}) - f(x, \mathbf{z}) \right). \quad (12)$$

As we will see, computing the right-hand side of Equation (12) leads to Equation (7).

Let $f : \mathcal{S}_K \rightarrow \mathbb{R}_+$ and $(x, \mathbf{z}) \in \mathcal{S}_K$. We introduce the following notations. For any $(y, \mathbf{k}) \in \mathcal{S}_K$ such that $\tau_{\mathbf{k}}(x, \mathbf{z}) > 0$,

$$\mathfrak{d}_{y, \mathbf{k}} f(x, \mathbf{z}) = f(y, \mathbf{z} + \mathbf{k} - \mathbf{e}(x)) - f(x, \mathbf{z}).$$

Further, for any $y \in \mathcal{X}$ such that $\mathbf{z}_y > 0$ and $\mathbf{k} \in \mathcal{Z}_K$ such that $\tau_{\mathbf{k}}(y, \mathbf{z}) > 0$, let

$$\widehat{\mathfrak{d}}_{y, \mathbf{k}} f(x, \mathbf{z}) = f(x, \mathbf{z} + \mathbf{k} - \mathbf{e}(y)) - f(x, \mathbf{z}).$$

Equation (5) then ensures that, on the event $\mathbb{Y}^{(t)}(s) = (x, \mathbf{z})$, we have for any $h \in [0, t - s]$:

$$\begin{aligned} f(\mathbb{Y}^{(t)}(s+h)) - f(x, \mathbf{z}) &= \int_s^{s+h} \int_E \mathbf{1}_{\{\theta \leq \rho_{y, \mathbf{k}}^{(t)}(r, \mathbb{Y}^{(t)}(r-))\}} \mathfrak{d}_{y, \mathbf{k}} f(\mathbb{Y}^{(t)}(r-)) Q(dr, d\theta, n(dy, d\mathbf{k})) \\ &\quad + \int_s^{s+h} \int_E \mathbf{1}_{\{\theta \leq (\zeta_y^{(t)}(r-) - \mathbf{1}_{\{Y^{(t)}(r-)=y\}}) \widehat{\rho}_{\mathbf{k}}^{(t)}(r, y, \mathbb{Y}^{(t)}(r-))\}} \widehat{\mathfrak{d}}_{y, \mathbf{k}} f(\mathbb{Y}^{(t)}(r-)) \widehat{Q}(dr, d\theta, n(dy, d\mathbf{k})). \end{aligned}$$

Notice that, for instance,

$$\begin{aligned} \mathbb{E} \left[\int_s^{s+h} \int_E \mathbf{1}_{\{\theta \leq \rho_{y, \mathbf{k}}^{(t)}(r, \mathbb{Y}^{(t)}(r-))\}} \mathfrak{d}_{y, \mathbf{k}} f(\mathbb{Y}^{(t)}(r-)) Q(dr, d\theta, n(dy, d\mathbf{k})) \mid \mathbb{Y}^{(t)}(s) = (x, \mathbf{z}) \right] \\ = \mathbb{E} \left[\int_s^{s+h} \sum_{(y, \mathbf{k}) \in \mathcal{S}_K} \rho_{y, \mathbf{k}}^{(t)}(r, \mathbb{Y}^{(t)}(r)) \mathfrak{d}_{y, \mathbf{k}} f(\mathbb{Y}^{(t)}(r)) dr \mid \mathbb{Y}^{(t)}(s) = (x, \mathbf{z}) \right]. \end{aligned}$$

On the one hand, almost surely,

$$\lim_{h \rightarrow 0^+} \frac{1}{h} \int_s^{s+h} \sum_{(y, \mathbf{k}) \in \mathcal{S}_K} \rho_{y, \mathbf{k}}^{(t)}(r, \mathbb{Y}^{(t)}(r)) \mathfrak{d}_{y, \mathbf{k}} f(\mathbb{Y}^{(t)}(r)) dr = \sum_{(y, \mathbf{k}) \in \mathcal{S}_K} \rho_{y, \mathbf{k}}^{(t)}(s, \mathbb{Y}^{(t)}(s)) \mathfrak{d}_{y, \mathbf{k}} f(\mathbb{Y}^{(t)}(s)).$$

On the other hand, as mentioned at the beginning of the proof,

$$\|\rho^{(t)}\|_\infty = \max_{s \in [0, t], (y, \mathbf{k}) \in \mathcal{S}, (x, \mathbf{z}) \in \mathcal{S}_K} \rho_{y, \mathbf{k}}^{(t)}(s, x, \mathbf{z}) < \infty.$$

Further, as \mathcal{S}_K is a finite set, $\|f\|_\infty = \max_{(x, \mathbf{z}) \in \mathcal{S}_K} f(x, \mathbf{z}) < \infty$. Thus, for any $h \in [0, t - s]$,

$$\frac{1}{h} \int_s^{s+h} \left| \sum_{(y, \mathbf{k}) \in \mathcal{S}_K} \rho_{y, \mathbf{k}}^{(t)}(r, \mathbb{Y}^{(t)}(r)) \mathfrak{d}_{y, \mathbf{k}} f(\mathbb{Y}^{(t)}(r)) \right| dr \leq 2 \text{Card}(\mathcal{S}_K) \|\rho^{(t)}\|_\infty \|f\|_\infty < \infty.$$

Taken together, we obtain by dominated convergence:

$$\begin{aligned} \frac{1}{h} \mathbb{E} \left[\int_s^{s+h} \int_E \mathbf{1}_{\{\theta \leq \rho_{y, \mathbf{k}}^{(t)}(r, \mathbb{Y}^{(t)}(r-))\}} \mathfrak{d}_{y, \mathbf{k}} f(\mathbb{Y}^{(t)}(r-)) Q(dr, d\theta, n(dy, d\mathbf{k})) \mid \mathbb{Y}^{(t)}(s) = (x, \mathbf{z}) \right] \\ \xrightarrow{h \rightarrow 0^+} \sum_{(y, \mathbf{k}) \in \mathcal{S}_K} \rho_{y, \mathbf{k}}^{(t)}(s, x, \mathbf{z}) \mathfrak{d}_{y, \mathbf{k}} f(x, \mathbf{z}). \end{aligned}$$

The other terms arising on the right-hand side of Equation (12) can be treated analogously. This leads to the desired result. \square

3.2.2 Proof of the many-to-one formula

We are now ready to turn to the proof of Theorem 3.3, which comprises several steps. Let $t \geq 0$, and start by introducing the time-inhomogeneous semi-group of interest $P^{(t)} = (P_{r,s}^{(t)}, r \leq s \leq t)$ through its action on applications $f : \mathcal{S}_K \rightarrow \mathbb{R}_+$. For $s \leq t$, $u_x(s)$ will designate a chosen individual of type x in $\mathbb{G}(s)$, if it exists. For any $(x, \mathbf{z}) \in \mathcal{S}_K$ and $0 \leq r \leq s \leq t$,

$$P_{r,s}^{(t)} f(x, \mathbf{z}) = m(x, \mathbf{z}, t - r)^{-1} \mathbb{E} \left[\sum_{\substack{u \in \mathbb{G}(t) \\ u \geq u_x(r)}} \psi(x_u(t), Z(t)) f(x_u(s), Z(s)) | X(r) = \mathfrak{X}(\mathbf{z}) \right]. \quad (13)$$

Lemma 3.6. $(P_{r,s}^{(t)}, r \leq s \leq t)$ defines a conservative, time-inhomogeneous semi-group acting on the set of functions $\{f : \mathcal{S}_K \rightarrow \mathbb{R}_+\}$.

Proof. The conservativity of $P^{(t)}$ follows directly from Equation (13) applied to $f \equiv 1$, which shows that $P^{(t)}1 \equiv 1$.

Let us now turn to the inhomogeneous semi-group property. Let $r \leq \tau \leq s \leq t$, and consider $f : \mathcal{S}_K \rightarrow \mathbb{R}_+$ and $(x, \mathbf{z}) \in \mathcal{S}_K$. Throughout the proof, we let $\mathfrak{X}_0 = \mathfrak{X}(\mathbf{z})$. By definition of the semi-group,

$$\begin{aligned} P_{r,s}^{(t)} f(x, \mathbf{z}) &= m(x, \mathbf{z}, t - r)^{-1} \mathbb{E} \left[\sum_{\substack{u \in \mathbb{G}(t) \\ u \geq u_x(r)}} \psi(x_u(t), Z(t)) f(x_u(s), Z(s)) | X(r) = \mathfrak{X}_0 \right] \\ &= m(x, \mathbf{z}, t - r)^{-1} \mathbb{E} \left[\sum_{\substack{v \in \mathbb{G}(\tau) \\ v \geq u_x(r)}} \sum_{\substack{u \in \mathbb{G}(t) \\ u \geq v}} \psi(x_u(t), Z(t)) f(x_u(s), Z(s)) | X(r) = \mathfrak{X}_0 \right] \end{aligned} \quad (14)$$

$$P_{r,s}^{(t)} f(x, \mathbf{z}) = m(x, \mathbf{z}, t - r)^{-1} \mathbb{E} \left[\sum_{\substack{v \in \mathbb{G}(\tau) \\ v \geq u_x(r)}} g(x_v(\tau), Z(\tau)) | X(r) = \mathfrak{X}_0 \right],$$

where we define the function $g : \mathcal{S}_K \rightarrow \mathbb{R}_+$ by

$$g(x, \mathbf{z}) = \mathbb{E} \left[\sum_{\substack{u \in \mathbb{G}(t) \\ u \geq u_x(\tau)}} \psi(x_u(t), Z(t)) f(x_u(s), Z(s)) | X(\tau) = \mathfrak{X}_0 \right].$$

Notice that, for any measurable function $G : \mathbb{D}([0, \tau], \mathcal{S}_K) \rightarrow \mathbb{R}_+$,

$$\begin{aligned} &\mathbb{E} \left[\sum_{\substack{u \in \mathbb{G}(t) \\ u \geq u_x(r)}} \psi(x_u(t), Z(t)) m(x_u(\tau), Z(\tau), t - \tau)^{-1} G((x_u(\sigma), Z(\sigma))_{\sigma \leq \tau}) | X(r) = \mathfrak{X}_0 \right] \\ &= \mathbb{E} \left[\sum_{\substack{v \in \mathbb{G}(\tau) \\ v \geq u_x(r)}} \mathbb{E} \left[\sum_{\substack{u \in \mathbb{G}(t) \\ u \geq v}} \psi(x_u(t), Z(t)) | X(\tau) \right] m(x_v(\tau), Z(\tau), t - \tau)^{-1} G((x_v(\sigma), Z(\sigma))_{\sigma \leq \tau}) | X(r) = \mathfrak{X}_0 \right] \\ &= \mathbb{E} \left[\sum_{\substack{v \in \mathbb{G}(\tau) \\ v \geq u_x(r)}} G((x_v(\sigma), Z(\sigma))_{\sigma \leq \tau}) | X(r) = \mathfrak{X}_0 \right]. \end{aligned} \quad (15)$$

Applying this equality to $G((x_v(s), Z(s))_{s \leq \tau}) = g(x(\tau), Z(\tau))$ finally yields the desired semi-group property:

$$P_{r,s}^{(t)} f(x, \mathbf{z}) = P_{r,\tau}^{(t)} P_{\tau,s}^{(t)} f(x, \mathbf{z}).$$

This concludes the proof. □

Let us now compute the generator of $(P_{r,s}^{(t)}, r \leq s \leq t)$.

Lemma 3.7. Let $t \geq 0$. The generator of the semi-group $(P_{r,s}^{(t)}, r \leq s \leq t)$ is $(A_s^{(t)}, s \leq t)$.

Proof. Consider $f : \mathcal{S}_K \rightarrow \mathbb{R}_+$. Let $(x, \mathbf{z}) \in \mathcal{S}_K$ and $t \geq 0$. For any $0 \leq s \leq t$ and $h > 0$ such that $s + h \leq t$, it follows from Equation (15) and the Markov property that

$$P_{s,s+h}^{(t)} f(x, \mathbf{z}) = m(x, \mathbf{z}, t - s)^{-1} \mathbb{E}_{\mathbf{z}} \left[\sum_{\substack{u \in \mathbb{G}(h) \\ u \geq u_x(0)}} m(x_u(h), Z(h), t - (s + h)) f(x_u(h), Z(h)) \right].$$

Using Lemma 3.5 as well as the fact that \mathcal{S}_K is a finite set, we obtain the following Taylor expansion:

$$\begin{aligned} m(x, \mathbf{z}, t - s) P_{s,s+h}^{(t)} f(x, \mathbf{z}) &= \mathbb{E}_{\mathbf{z}} \left[\sum_{\substack{u \in \mathbb{G}(h) \\ u \geq u_x(0)}} m(x_u(h), Z(h), t - s) f(x_u(h), Z(h)) \right] \\ &\quad + h \mathbb{E}_{\mathbf{z}} \left[\sum_{\substack{u \in \mathbb{G}(h) \\ u \geq u_x(0)}} \partial_s m(x_u(h), Z(h), t - s) f(x_u(h), Z(h)) \right] + o(h). \end{aligned}$$

As a consequence,

$$\begin{aligned} m(x, \mathbf{z}, t - s) \frac{P_{s,s+h}^{(t)} f(x, \mathbf{z}) - f(x, \mathbf{z})}{h} &= \mathbb{E}_{\mathbf{z}} \left[\sum_{\substack{u \in \mathbb{G}(h) \\ u \geq u_x(0)}} \partial_s m(x_u(h), Z(h), t - s) f(x_u(h), Z(h)) \right] \\ &\quad + h^{-1} \left(\mathbb{E}_{\mathbf{z}} \left[\sum_{\substack{u \in \mathbb{G}(h) \\ u \geq u_x(0)}} m(x_u(h), Z(h), t - s) f(x_u(h), Z(h)) \right] - m(x, \mathbf{z}, t - s) f(x, \mathbf{z}) \right) + \epsilon(h), \end{aligned}$$

where $\epsilon(h)$ is such that $\lim_{h \rightarrow 0^+} \epsilon(h) = 0$. We thus obtain that

$$\lim_{h \rightarrow 0^+} \frac{P_{s,s+h}^{(t)} f(x, \mathbf{z}) - f(x, \mathbf{z})}{h} = m(x, \mathbf{z}, t - s)^{-1} (G(m(\cdot, t - s) f(\cdot))(x, \mathbf{z}) + \partial_s m(x, \mathbf{z}, t - s) f(x, \mathbf{z})),$$

where we recall that G is defined by (1). Lemma 3.5 yields the desired result. \square

We finally are ready to establish Theorem 3.3. The proof follows the lines of [22], it is thus only outlined here and we refer to Appendix A for detail.

Proof of Theorem 3.3. Lemma 3.7 implies that the semi-groups $P^{(t)}$ and $R^{(t)}$ are identical. Using an induction argument, it follows that Equation (8) holds for

$$F((x(s), \mathbf{z}(s))_{s \leq t}) = \prod_{j=1}^k f_j(x(s_j), \mathbf{z}(s_j)),$$

where $k \geq 1$, $0 \leq s_1 \leq \dots \leq s_k \leq t$ and $f_1, \dots, f_k : \mathcal{S}_K \rightarrow \mathbb{R}_+$. A monotone class argument finally allows to extend the result to any measurable function $F : \mathbb{D}([0, t], \mathcal{S}_K) \rightarrow \mathbb{R}_+$. \square

3.3 An application to the empirical distribution of ancestral lineages in a density-dependent population

Let us end this section by illustrating how the time-inhomogeneous spinal process may be used to gain insight on survivorship bias.

Generally speaking, in order to make use of the time-inhomogeneous spinal process, the key is the computation of m . The set \mathcal{S}_K being of finite dimension d , Lemma 3.5 implies that m is characterized as the unique solution of a linear system of ODEs. More precisely, with slight abuse of notation, let G designate the matrix form of generator G defined by Equation (1). It

then follows from Lemma 3.5 that for $t \geq 0$, the vector $m(t) = (m(x, \mathbf{z}, t) : (x, \mathbf{z}) \in \mathcal{S}_K)$ is given by

$$m(t) = e^{Gt}\psi.$$

While this implies that m can always be computed numerically, there are cases for which an analytical expression of m is achievable. In particular, assume that G is diagonalizable, with linearly independent eigenvectors v_1, \dots, v_d associated to eigenvalues $\lambda_1, \dots, \lambda_d$. Then

$$m(t) = \sum_{k=1}^d c_k e^{\lambda_k t} v_k,$$

where the constants c_1, \dots, c_d are such that $m(0) = \psi$. Throughout the following, we will make use of this observation in order to compute the reproduction rates of the time-inhomogeneous spinal process.

Let us illustrate the computation of the time-inhomogeneous spinal process on a toy model describing a population of at most two particles, which at each time are either of type A or B . Indeed, while computations are achievable for larger populations and state spaces, we restrict ourselves to this minimalistic population in order to keep \mathcal{S}_K small, so that we can exhibit and comment all transition rates of the time-inhomogeneous spinal process. Our population is thus described by $\mathbf{z} = (\mathbf{z}_A, \mathbf{z}_B)$, where \mathbf{z}_x counts the number of particles in state x .

The particles behave as follows. If the population corresponds to a single particle of type A , the latter may give birth to another particle of the same type at rate b . Whenever there are two particles of type A , each may die due to competition at rate a , or escape competition by switching to state B at rate c_A . Finally, a particle of type B can only switch back to state A , at rate c_B . Throughout the following, we assume that $b = a$ and $c_A = c_B$, for ease of computation. In other words, the state space of the population with a distinguished particle is described by the ordered set $\{(A, 1, 0), (A, 2, 0), (A, 1, 1), (B, 1, 1)\}$, and the dynamics are characterized by four reproduction rates :

$$\tau_{(2,0)}(A, 1, 0) = \tau_{(0,0)}(A, 2, 0) = b, \text{ and } \tau_{(0,1)}(A, 2, 0) = \tau_{(1,0)}(B, 1, 1) = c.$$

In this case, the generator G takes the matrix form

$$G = \begin{pmatrix} -b & 2b & 0 & 0 \\ b & -2(b+c) & c & c \\ 0 & c & -c & 0 \\ 0 & c & 0 & -c \end{pmatrix}.$$

In particular, G is diagonalizable, with non-positive eigenvalues as the population size is bounded. Hence m can be computed as mentioned previously. For instance, in the case $\psi = \mathbf{1} = (1, 1, 1, 1)$, we obtain that

$$m(t) = \frac{4}{5} \begin{pmatrix} 2 \\ 1 \\ 1 \\ 1 \end{pmatrix} - \frac{\lambda_-}{10\sqrt{\Delta}} e^{-\frac{\lambda_+ t}{2}} \begin{pmatrix} \frac{-3b+3c-\sqrt{\Delta}}{2c} \\ \frac{-3b+c+\sqrt{\Delta}}{2c} \\ 1 \\ 1 \end{pmatrix} + \frac{\lambda_+}{10\sqrt{\Delta}} e^{-\frac{\lambda_- t}{2}} \begin{pmatrix} \frac{-3b+3c+\sqrt{\Delta}}{2c} \\ \frac{-3b+c-\sqrt{\Delta}}{2c} \\ 1 \\ 1 \end{pmatrix},$$

with $\Delta = 9b^2 + 9c^2 - 2bc$ and $\lambda_{\pm} = 3b + 3c \pm \sqrt{\Delta}$.

It thus is possible to explicitly compute the reproduction rates of the time-inhomogeneous spinal process by Equations (3) and (4). For example, assume that sampling occurs at time t .

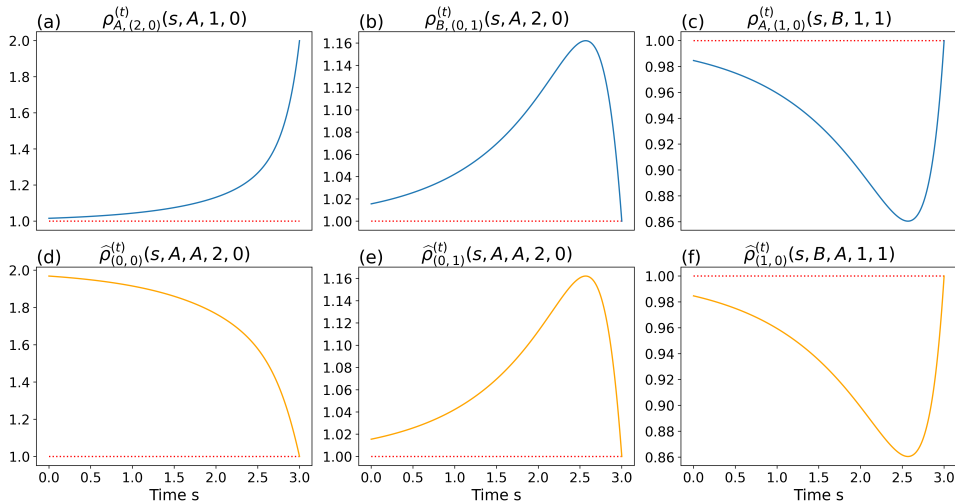


Figure 1: Time-inhomogeneous reproduction rates of the spine (blue, top) and outside of the spine (orange, bottom). Red dotted lines indicate the unbiased transition rates. Parameters: $t = 3$, $b = 1$, $c = 2$.

If at time s , the spine is the sole particle alive and of type A , it gives birth to a second particle of type A at rate

$$\begin{aligned} \rho_{A,(2,0)}^{(t)}(s, A, 1, 0) &= 2b \frac{m(A, 2, 0, t-s)}{m(A, 1, 0, t-s)} \\ &= 2b \frac{16c\sqrt{\Delta} + \lambda_-(3b + c + \sqrt{\Delta})e^{-\frac{\lambda_+(t-s)}{2}} - \lambda_+(3b + c - \sqrt{\Delta})e^{-\frac{\lambda_-(t-s)}{2}}}{32c\sqrt{\Delta} + \lambda_-(-3b + 3c - \sqrt{\Delta})e^{-\frac{\lambda_+(t-s)}{2}} - \lambda_+(-3b + 3c + \sqrt{\Delta})e^{-\frac{\lambda_-(t-s)}{2}}}. \end{aligned}$$

The other reproduction rates of the time-inhomogeneous spinal process process can be computed analogously.

Figure 1 illustrates the reproduction rates of the ψ -auxiliary process for the (arbitrary) parameter choice $t = 3$, $b = 1$ and $c = 2$. Recall that in the original process, the sum of the weights ψ of the descendants of a given particle is maximal if the latter has two descendants alive at time t , when sampling occurs. Hence, both the birth rate of the spine (panel a) and the death rate of the other particle (panel d) are inflated, as the latter needs to die for the spine to be able to give birth. In addition, whenever there are two particles, transitions from state A to state B are favored (panels b, e), whereas transitions from state B to state A are repressed (panels c, f). In other words, when the population is of size two, the auxiliary process favors the population state $(1, 1)$, thus limiting the competitive pressure exerted on the spine.

This illustrates our contributions on capturing the survivorship bias associated to (uniform) sampling in density-dependent populations of bounded size.

4 Empirical distribution of ancestral lineages in large populations

In this section, we are interested in empirical distribution of ancestral lineages in large populations, corresponding to the case $\psi = 1$. Indeed, when the population size K grows to infinity, the population trait distribution converges under classical assumptions to a deterministic limit z , characterized as the unique solution of a dynamical system. Here, we show that it is possible to sample in the limit z with a time-inhomogeneous spine construction, analogously to Theorem

3.3. In addition, we quantify the approximation error made by sampling in the large population limit instead of the original finite-size population process.

4.1 Many-to-one formula and speed of convergence

We first consider the large population limit of the population process. Let $D = \text{Card}(\mathcal{X})$ and

$$\mathcal{Z} = \{\mathbf{z} \in [0, 1]^D : \|\mathbf{z}\|_1 \leq 1\}.$$

Let $(\tau_{\mathbf{k}}, \mathbf{k} \in \mathbb{N}^D)$ be a family of continuous bounded functions $\tau_{\mathbf{k}} : \mathcal{X} \times \mathcal{Z} \rightarrow \mathbb{R}_+$ such that the set $J = \{(x, \mathbf{k}) \in \mathcal{X} \times \mathbb{N}^D : \tau_{\mathbf{k}}(x, \cdot) \neq 0\}$ is finite.

For $K \geq 1$, consider the population process X^K where an individual of type x in a population of composition $\mathbf{z} \in \mathcal{Z}_K$ is replaced by offspring \mathbf{k} at rate $\tau_{\mathbf{k}}(x, \mathbf{z}/K)$. For the population size to be bounded by K , this imposes the following condition:

$$\forall K \geq 1, \forall (x, \mathbf{k}) \in J, \forall \mathbf{z} \in \mathcal{Z}_K, \quad \tau_{\mathbf{k}}(x, \mathbf{z}/K) = 0 \text{ if } \|\mathbf{z} + \mathbf{k} - \mathbf{e}(x)\|_1 \geq K. \quad (16)$$

Notice that for instance, classical epidemic models satisfy this condition, as population size is often kept constant. Letting $Z^K = Z(X^K)/K$ then ensures that $Z^K(t) \in \mathcal{Z}$ almost surely, for every $t \geq 0$.

Introducing the large population limit of the population process requires some notations. Consider a given sequence of initial conditions $(x, \mathbf{z}^K)_{K \geq 1}$ such that for any K , $\mathbf{z}^K \in \mathcal{Z}_K/K$, $\mathbf{z}_x^K \geq 1/K$ and $\lim_{K \rightarrow \infty} \mathbf{z}^K = \mathbf{z} \in \mathcal{Z}$. Define $A(\mathbf{z}) = (A_{x,y}(\mathbf{z}))_{x,y \in \mathcal{X}}$ for $\mathbf{z} \in \mathcal{Z}$ by $A_{x,y}(\mathbf{z}) = \sum_{\mathbf{k}} (\mathbf{k}_y - \mathbf{1}_{\{x=y\}}) \tau_{\mathbf{k}}(x, \mathbf{z})$. Throughout the section, we work under the following assumption.

Assumption 4.1. For every $(x, \mathbf{k}) \in J$, $\tau_{\mathbf{k}}(x, \cdot)$ is Lipschitz continuous on \mathcal{Z} .

In particular, $\mathbf{z} \mapsto A(\mathbf{z})$ is Lipschitz continuous on \mathcal{Z} and there exists a unique solution z to the differential equation

$$z'(t) = z(t)A(z(t)), \quad z(0) = \mathbf{z}. \quad (17)$$

Then Z^K converges uniformly in probability to z on finite time intervals [16, Theorem 3.1, Chapter 11].

Let us turn to sampling in the large population limit with the inhomogeneous spinal construction. Generally speaking, the idea is that the impact of the spine on the spinal population becomes negligible in the large population limit, so that in large populations, $\zeta^{(t)}$ is well approximated by z . As a consequence, only the dynamics of the spinal individual need to be described.

Let $\mathcal{S} = \mathcal{X} \times \mathcal{Z}$, and define the following operator \mathcal{G} acting on differentiable functions $f : \mathcal{S} \rightarrow \mathbb{R}$. For any $(x, \mathbf{z}) \in \mathcal{S}$,

$$\mathcal{G}f(x, \mathbf{z}) = \sum_{\mathbf{k}} \tau_{\mathbf{k}}(x, \mathbf{z}) \langle \mathbf{k} - \mathbf{e}(x), f(\cdot, \mathbf{z}) \rangle + \sum_{\mathbf{k}, y} \mathbf{z}_y \tau_{\mathbf{k}}(y, \mathbf{z}) \langle \mathbf{k} - \mathbf{e}(y), \nabla_{\mathbf{z}} f(x, \mathbf{z}) \rangle.$$

Consider a family of functions $\mathbf{m} : \mathcal{X} \times \mathcal{Z} \times \mathbb{R}_+ \rightarrow \mathbb{R}_+$ characterized by the following system of partial differential equations.

$$\begin{aligned} &\text{For all } x \in \mathcal{X}, \text{ for almost every } t \geq 0 \text{ and } \mathbf{z} \in \mathcal{Z}, \\ &\quad \partial_t \mathbf{m}(x, \mathbf{z}, t) = \mathcal{G}(\mathbf{m}(\cdot, t))(x, \mathbf{z}), \\ &\text{and for any } (x, \mathbf{z}) \in \mathcal{S}, \quad \mathbf{m}(x, \mathbf{z}, t = 0) = 1. \end{aligned} \quad (18)$$

While existence of at least one solution will be established below, we require some additional Assumptions on the solutions to Equation (18).

Assumption 4.2. *The system of partial differential equations given by Equation (18) admits a unique positive solution, which further is differentiable on $\mathcal{X} \times \mathcal{Z} \times \mathbb{R}_+$.*

We are now ready to define the inhomogeneous spinal process. We want to sample at time $t > 0$ in a population of initial condition $\mathbf{z} \in \mathcal{Z}$. At time $s \leq t$, the population is of composition $z(s)$, and the spine behaves as follows. Given its type x , it is replaced by offspring \mathbf{k} and become of type y at rate

$$\rho_{\mathbf{k},y}^{(t)}(x, z(s), s) = \tau_{\mathbf{k}}(x, z(s)) \mathbf{k}_y \frac{\mathbf{m}(y, z(s), t-s)}{\mathbf{m}(x, z(s), t-s)}.$$

We designate by $\Upsilon^{(t)}$ the time-inhomogeneous Markov process which keeps track of the type along the spine. It can be characterized as the unique strong solution to an SDE, analogously to Equation (5). Consider a family of independent Poisson Point Processes $(Q_j, j \in J)$ of intensity the Lebesgue measure on \mathbb{R}_+^2 . The process $(\Upsilon^{(t)}, z)$ then is characterized as follows: for any $s \in [0, t]$, for any initial condition $(x, \mathbf{z}) \in \mathcal{S}$,

$$\begin{aligned} z'(s) &= z(s)A(z(s)), \quad z(0) = \mathbf{z}, \\ \Upsilon^{(t)}(s) &= \mathbf{e}(x) + \sum_{\mathbf{k}, y \in J} \int_0^t \int_0^{+\infty} \mathbf{1}_{\{\theta \leq \rho_{\mathbf{k},y}^{(t)}(\Upsilon^{(t)}(u-), z(u), u)\}} (\mathbf{e}(y) - \mathbf{e}(\Upsilon^{(t)}(u-))) Q_{\mathbf{k},y}(du, d\theta). \end{aligned} \quad (19)$$

Further, the semi-group associated to the process $(\Upsilon^{(t)}, z)$ is defined by its action on functions $f \in L^\infty(\mathcal{S})$: for $r \leq s \leq t$ and $(x, \mathbf{z}) \in \mathcal{S}$,

$$\mathcal{R}_{r,s}^{(t)} f(x, \mathbf{z}) = \mathbb{E}[f(\Upsilon^{(t)}(s), z(s)) | (\Upsilon^{(t)}(r), z(r)) = (x, \mathbf{z})].$$

The following Proposition ensures that $(\Upsilon^{(t)}, z)$ is well defined, and characterizes the generator of its semi-group.

Proposition 4.3. *Consider Assumptions 4.1 and 4.2. Equation (19) admits a unique strong solution $(\Upsilon^{(t)}, z)$ in $\mathbb{D}([0, t], \mathcal{X}) \times \mathcal{C}^1([0, t], \mathcal{Z})$. In addition, its semi-group $\mathcal{R}^{(t)}$ is a time-inhomogeneous semi-group of bounded linear operators on $L^\infty(\mathcal{S})$, whose generator $\mathcal{A}^{(t)}$ is characterized by its action on functions $f \in \mathcal{C}^1(\mathcal{S})$ as follows. For $s \leq t$ and $(x, \mathbf{z}) \in \mathcal{S}$,*

$$\mathcal{A}_s^{(t)} f(x, \mathbf{z}) = \mathbf{m}(x, \mathbf{z}, t-s)^{-1} (\mathcal{G}(\mathbf{m}(\cdot, t-s)f(\cdot))(x, \mathbf{z}) - \mathcal{G}\mathbf{m}(\cdot, t-s)(x, \mathbf{z})f(x, \mathbf{z})). \quad (20)$$

The proof of Proposition 4.3 follows the same steps as the proof of Proposition 3.2. We refer to Appendix B for detail.

Our main contribution lies in upcoming Theorem 4.5, which provides a many-to-one formula for sampling in the large population limit and quantifies the associated speed of convergence. It relies on the following Assumption.

Assumption 4.4. *The generator $\mathcal{A}^{(t)}$ characterizes a unique time-inhomogeneous semi-group of bounded linear operators on $L^\infty(\mathcal{S})$.*

For example, this assumption is satisfied in the case of strongly continuous semi-groups [26, Chapter 1].

Throughout the following, we let $\mathbb{E}_{x,\mathbf{z}}$ denote the expectation conditionally on $(\Upsilon^{(t)}(0), z(0)) = (x, \mathbf{z})$. Finally, we introduce the function set

$$\begin{aligned} \mathfrak{L} &= \left\{ F : \mathbb{D}([0, t], \mathcal{X}) \times \mathbb{D}([0, t], \mathcal{Z}) \rightarrow \mathbb{R} \text{ bounded s.t. } \exists L : \forall x \in \mathbb{D}([0, t], \mathcal{X}), \forall \mathbf{z}_1, \mathbf{z}_2 \in \mathbb{D}([0, t], \mathcal{Z}), \right. \\ &\quad \left. |F((x(s), \mathbf{z}_1(s))_{s \leq t}) - F((x(s), \mathbf{z}_2(s))_{s \leq t})| \leq L \sup_{s \in [0, t]} \|\mathbf{z}_1(s) - \mathbf{z}_2(s)\|_1 \right\}. \end{aligned}$$

We are now ready to state the main result of this Section.

Theorem 4.5. Consider Assumptions 4.1, 4.2 and 4.4. Let $t > 0$ and $F \in \mathfrak{L}$. For any $\mathbf{z} \in \mathcal{Z}$, there exists $C > 0$ such that for any $K \geq 1$,

$$\left| \frac{1}{K} E_{\mathbf{z}^K} \left[\sum_{u \in \mathbb{G}(t)} F((x_u(s), Z^K(s))_{s \leq t}) \right] - \sum_{x \in \mathcal{X}} \mathbf{z}_x \mathbf{m}(x, \mathbf{z}, t) \mathbb{E}_{x, \mathbf{z}} \left[F((\Upsilon^{(t)}(s), z(s))_{s \leq t}) \right] \right| \leq \frac{C}{K^{1/4}}.$$

This theorem shows that the spinal process $(\Upsilon^{(t)}, z)$ indeed captures the typical lineage of a sampled particle in the large population limit z . Further, if one samples in the large population limit instead of a population whose size is of order K , the approximation error is at most of order $K^{-1/4}$.

4.2 Proofs

In order to establish Theorem 4.5, we proceed in two steps. First, we show that $(\Upsilon^{(t)}, z)$ indeed provides a many-to-one formula for sampling in the large population limit. Analogously to the proof of Theorem 3.3, we identify $\mathcal{R}^{(t)}$ with an appropriate time-inhomogeneous semi-group derived from the large population limit of the homogeneous spine construction, which is well established [4]. In particular, this step relies on Assumptions 4.2 and 4.4. Second, we couple the homogeneous spine with its large population limit, and control the approximation error of the spinal population by its deterministic limit. If this error is small with high probability, then the homogeneous spine and its large population approximation are likely to coincide over finite time intervals. This finally allows to control the approximation error in the many-to-one formula, both of the homogeneous and inhomogeneous spinal constructions.

4.2.1 Many-to-one formula in the large population limit

Now that $(\Upsilon^{(t)}, z)$ is well defined, our aim is to establish a many-to-one formula connecting it to sampling in the large population limit. In order to achieve this, we make use of the homogeneous spine construction introduced by [4], as it will allow us to properly characterize the inhomogeneous semi-group associated to a uniform sample in the large population limit.

The homogeneous spine construction. In this paragraph, we briefly introduce the homogeneous spine construction [4], as the proof of Theorem 4.5 builds on it. We first focus on populations of finite size. For $\psi = 1$, individuals other than the spine behave exactly as in the original population process. Whenever the spine is of type x in a population of type distribution $\mathbf{z} \in \mathcal{Z}$ such that $\mathbf{z}_x > 0$, it is replaced by offspring \mathbf{k} and becomes of type y at rate $\mathbf{k}_y \tau_{\mathbf{k}}(x, \mathbf{z})$.

For convenience, we introduce a slight change in the type space allowing us to derive an equation for the spinal population which does not depend on Y^K . More precisely, the type space now becomes $\mathcal{X}^* = \{0, 1\} \times \mathcal{X}$. An individual of type $(0, x) \in \mathcal{X}^*$ corresponds to an individual of type x which is not the spine, whereas an individual is of type $(1, x) \in \mathcal{X}^*$ if it is the spine and of type x . We let $\zeta^K = (\zeta_{i,x}^K, (i, x) \in \mathcal{X}^*)$ designate the corresponding type distribution of the spinal population. Finally, we define $\zeta^K|_{\mathcal{X}} = ((\zeta^K|_{\mathcal{X}})_x, x \in \mathcal{X})$ by

$$(\zeta^K|_{\mathcal{X}})_x = \zeta_{1,x}^K + \zeta_{0,x}^K \quad \forall x \in \mathcal{X}.$$

Throughout the following, with slight abuse of notation, we write $\tau_{\mathbf{k}}(x, \mathbf{z})$ instead of $\tau_{\mathbf{k}}(x, \mathbf{z}|_{\mathcal{X}})$ for clarity.

For $(x, \mathbf{k}) \in J$ and $(x, \mathbf{k}, y) \in J^* = \{(x, \mathbf{k}, y) : (x, \mathbf{k}) \in J, \mathbf{k}_y > 0\}$, we let

$$h_0(x, \mathbf{k}) = \sum_{y \in \mathcal{X}} (\mathbf{k}_y - \delta_y^x) \mathbf{e}(0, y) \text{ and } h_1(x, \mathbf{k}, y) = \sum_{w \in \mathcal{X}} (\mathbf{k}_w - \mathbf{1}_{\{y=w\}}) \mathbf{e}(0, w) + \mathbf{e}(1, y) - \mathbf{e}(1, x).$$

Finally, any initial condition $(y, \mathbf{z}^K) \in \mathcal{X} \times \mathcal{Z}_K/K$ becomes $(y, \bar{\mathbf{z}}_0^K)$ with

$$\bar{\mathbf{z}}_0^K = \frac{1}{K} \mathbf{e}(1, y) + \sum_{x \in \mathcal{X}} \left((\mathbf{z}^K)_x - \frac{1}{K} \mathbf{1}_{\{x=y\}} \right) \mathbf{e}(0, x).$$

Given a family of independent Poisson Point Processes $(Q_j, j \in J \cup J^*)$ of intensity the Lebesgue measure on \mathbb{R}_+^2 , the process (Y^K, ζ^K) can then be defined as follows:

$$\begin{aligned} Y^K(t) &= \mathbf{e}(y_0) + \sum_{(x, \mathbf{k}, y) \in J^*} \int_0^t \int_0^{+\infty} \mathbf{1}_{\{Y^K(s-) = x, \theta \leq \mathbf{k}_y \tau_{\mathbf{k}}(x, \zeta^K(s-))\}} (\mathbf{e}(y) - \mathbf{e}(x)) Q_{x, \mathbf{k}, y}(ds, d\theta), \\ \zeta^K(t) &= \bar{\mathbf{z}}_0^K + \frac{1}{K} \sum_{(x, \mathbf{k}, y) \in J^*} h_1(x, \mathbf{k}, y) \int_0^t \int_0^{+\infty} \mathbf{1}_{\{\theta \leq K \zeta_{1, x}^K(s-) \mathbf{k}_y \tau_{\mathbf{k}}(x, \zeta^K(s-))\}} Q_{x, \mathbf{k}, y}(ds, d\theta) \\ &\quad + \frac{1}{K} \sum_{(x, \mathbf{k}) \in J} h_0(x, \mathbf{k}) \int_0^t \int_0^{+\infty} \mathbf{1}_{\{\theta \leq K \zeta_{0, x}^K(s-) \tau_{\mathbf{k}}(x, \zeta^K(s-))\}} Q_{x, \mathbf{k}}(ds, d\theta). \end{aligned} \quad (21)$$

The large population limit of the homogeneous spinal process is derived as follows. Let (Y^K, ζ^K) be the spine construction with initial condition $(x, [K\mathbf{z}]/K)$ in a population of size K . Then [4, Proposition 7] ensures that $(Y^K, \zeta^K)_{K \geq 1}$ converges in law, on finite time intervals, to (Υ, z) where z is the unique solution to (17), and Υ is a time-inhomogeneous \mathcal{X} -valued Markov jump process which, at time t , transitions from x to y at rate

$$\sum_{\mathbf{k}} \tau_{\mathbf{k}}(x, z(t)) \mathbf{k}_y \frac{\psi(y, z(t))}{\psi(x, z(t))}.$$

In particular, the many-to-one formula associated to sampling in the large population limit relies on an exponential weighting of spinal trajectories, as expected. For $(x, \mathbf{z}) \in \mathcal{X} \times \mathcal{Z}$, let

$$\lambda(x, \mathbf{z}) = \sum_{\mathbf{k}: (x, \mathbf{k}) \in J} (\|\mathbf{k}\|_1 - 1) \tau_{\mathbf{k}}(x, \mathbf{z}).$$

For $t \geq 0$, define

$$\mathcal{W}(t) = \exp \left(\int_0^t \lambda(\Upsilon(s), z(s)) ds \right).$$

With these notations, [4, Proposition 7] provides the following many-to-one formula:

$$\left| \frac{1}{K} \mathbb{E}_{\mathbf{z}^K} \left[\sum_{u \in \mathbb{G}(t)} F((x_u(s), Z^K(s))_{s \leq t}) \right] - \sum_{x \in \mathcal{X}} \mathbf{z}_x \mathbb{E}_{x, \mathbf{z}} [\mathcal{W}(t) F((\Upsilon(s), z(s))_{s \leq t})] \right| \xrightarrow{K \rightarrow \infty} 0. \quad (22)$$

We will now make use of the homogeneous spinal process and its large population limit to establish Theorem 4.5.

Outline of the proof of Theorem 4.5. The connection between the homogeneous spine construction and Theorem 4.5 is the following. Define the time-inhomogeneous semi-group $\mathcal{P}^{(t)}$ acting on functions $f \in L^\infty(\mathcal{S})$ by: for any $0 \leq r \leq s \leq t$ and $(x, \mathbf{z}) \in \mathcal{S}$,

$$\mathcal{P}_{r, s}^{(t)} f(x, \mathbf{z}) = \mathbf{m}(x, \mathbf{z}, t - s)^{-1} \mathbb{E} \left[e^{-\int_r^t \lambda(\Upsilon(u), z(u)) du} f(\Upsilon(s), z(s)) \middle| \Upsilon(r) = x, z(r) = \mathbf{z} \right].$$

We start by showing that the semi-groups $\mathcal{P}^{(t)}$ and $\mathcal{R}^{(t)}$ are identical, which relies on Assumptions 4.2 and 4.4, leading to the following proposition.

Proposition 4.6. For any $t \geq 0$ and any measurable function $F : \mathbb{D}([0, t], \mathcal{X}) \times \mathcal{C}^1([0, t], \mathcal{Z}) \rightarrow \mathbb{R}_+$, for any $\mathbf{z} \in \mathcal{Z}_K$,

$$\mathbb{E}_{x, \mathbf{z}}[\mathcal{W}(t)F((\Upsilon(s), z(s))_{s \leq t})] = \mathbf{m}(x, \mathbf{z}, t)\mathbb{E}_{x, \mathbf{z}}[F((\Upsilon^{(t)}(s), z(s))_{s \leq t})]. \quad (23)$$

In particular, Equation (22) thus implies

$$\left| \frac{1}{K} \mathbb{E}_{\mathbf{z}^K} \left[\sum_{u \in \mathbb{G}(t)} F((x_u(s), Z^K(s))_{s \leq t}) \right] - \sum_{x \in \mathcal{X}} \mathbf{z}_x \mathbf{m}(x, \mathbf{z}, t) \mathbb{E}_{x, \mathbf{z}}[F((\Upsilon^{(t)}(s), z(s))_{s \leq t})] \right| \xrightarrow{K \rightarrow \infty} 0. \quad (24)$$

It then remains to quantify the speed of convergence, which will be achieved in Section 4.2.2.

Preliminaries. We start by establishing some preliminary results, which will be useful throughout the remainder of the proofs.

Let us define $\mathbf{m}_\Upsilon : \mathcal{S} \times \mathbb{R}_+$ as follows:

$$\mathbf{m}_\Upsilon(x, \mathbf{z}, t) = \mathbb{E}_{x, \mathbf{z}}[\mathcal{W}(t)].$$

Notice that choosing $F = 1$ shows that for Proposition 4.6 to hold, \mathbf{m}_Υ must satisfy Equation (18), as the desired equality then follows by Assumption 4.2. In order to proof this, we proceed in two steps. First, we will show that for any $x \in \mathcal{X}$ and $t \geq 0$, $\mathbf{z} \mapsto \mathbf{m}_\Upsilon(x, \mathbf{z}, t)$ is Lipschitz continuous. Rademacher's theorem then ensures that this application is differentiable almost everywhere. Second, we compute $\partial_t \mathbf{m}_\Upsilon(x, \mathbf{z}, t)$ to show that \mathbf{m}_Υ indeed solves Equation (18).

In order to achieve Lipschitz continuity of $\mathbf{z} \mapsto \mathbf{m}_\Upsilon(x, \mathbf{z}, t)$, we want to control the difference between trajectories of (Υ, z) whose population composition starts in different initial conditions. We thus first control the distance between two solutions of dynamical system (17). Throughout the following, we write $\phi(t, \mathbf{z})$ for the solution to Equation (17) evaluated at time t .

Lemma 4.7. Let $t \geq 0$. Under Assumption 4.1, there exists $C(t) > 0$ such that

$$\forall \mathbf{z}_1, \mathbf{z}_2 \in \mathcal{Z}, \quad \sup_{s \in [0, t]} \|\phi(s, \mathbf{z}_1) - \phi(s, \mathbf{z}_2)\|_1 \leq C(t) \|\mathbf{z}_1 - \mathbf{z}_2\|.$$

The result is classical for dynamical systems, and is included in Appendix C for completeness.

We next want to show that controlling the difference in population composition is actually sufficient to control the probability that the spinal processes grow apart, in final time. This is achieved by a coupling argument.

Let ζ_1 and ζ_2 be two population processes in $\mathbb{D}([0, t], \mathcal{Z})$ defined on the same probability space $(\Omega, \mathcal{F}, \mathbb{P})$. Consider a family of independent Poisson Point Processes $(Q_j, j \in J^*)$ of intensity the Lebesgue measure on \mathbb{R}_+^2 , which is also defined on Ω , and for $y_0 \in \mathcal{X}$ let

$$Y_1(t) = \mathbf{e}(y_0) + \sum_{(x, \mathbf{k}, y) \in J^*} \int_0^t \int_0^{+\infty} \mathbf{1}_{\{Y_1(s-) = x, \theta \leq \mathbf{k}_y \tau_{\mathbf{k}}(x, \zeta_1(s-))\}} (\mathbf{e}(y) - \mathbf{e}(x)) Q_{x, \mathbf{k}, y}(ds, d\theta),$$

$$Y_2(t) = \mathbf{e}(y_0) + \sum_{(x, \mathbf{k}, y) \in J^*} \int_0^t \int_0^{+\infty} \mathbf{1}_{\{Y_2(s-) = x, \theta \leq \mathbf{k}_y \tau_{\mathbf{k}}(x, \zeta_2(s-))\}} (\mathbf{e}(y) - \mathbf{e}(x)) Q_{x, \mathbf{k}, y}(ds, d\theta).$$

Notice that $Y_j(t)$ corresponds to the dynamics of the spine, given that the population composition is provided by ζ_j , for $j \in \{1, 2\}$. For instance, if $\zeta_1 = \phi(\cdot, \mathbf{z}_1)$, we have $(Y_1, \zeta_1) = (\Upsilon, z)$ with initial condition (y_0, \mathbf{z}_1) .

Lemma 4.8. *Let $t > 0$, and assume that there exist two positive sequences (ε_K) and (α_K) such that for every $K \geq 1$,*

$$\mathbb{P} \left(\sup_{s \in [0, t]} \|\zeta_1(s) - \zeta_2(s)\|_1 \geq \varepsilon_K \right) \leq \alpha_K. \quad (25)$$

Under Assumption 4.1, there exists a constant $C(t) > 0$ such that for every $K \geq 1$,

$$\mathbb{P}(\forall s \in [0, t], Y_1(s) = Y_2(s)) \geq 1 - C(t)(\alpha_K + \varepsilon_K).$$

Proof. We are interested in the first instant T_K at which Y_1 differs from Y_2 :

$$T_K = \inf\{t \geq 0 : Y_1(t) \neq Y_2(t)\}.$$

Let $K \geq 1$. For two sets A and B , we let $A \Delta B$ designate their symmetric difference. For $(x, \mathbf{k}, y) \in J^*$, $(x', \mathbf{z}) \in \mathcal{S}$ and $\theta > 0$, define the event

$$\mathcal{E}_{x, \mathbf{k}, y}(\theta, y, \mathbf{z}) = \{x' = x, \theta \leq \mathbf{k}_y \tau_{\mathbf{k}}(x, \mathbf{z})\}$$

Notice that, by the coupling of Y_1 and Y_2 ,

$$\begin{aligned} \{T_K \geq t\} &\supseteq \left\{ T_K \geq t, \sum_{(x, \mathbf{k}, y) \in J^*} \int_0^t \int_0^{+\infty} \mathbf{1}_{\{\mathcal{E}_{x, \mathbf{k}, y}(\theta, Y_1(s-), \zeta_1(s-)) \Delta \mathcal{E}_{x, \mathbf{k}, y}(\theta, Y_2(s-), \zeta_2(s-))\}} Q_{x, \mathbf{k}, y}(ds, d\theta) = 0 \right\} \\ &\supseteq \left\{ T_K \geq t, \sum_{(x, \mathbf{k}, y) \in J^*} \int_0^t \int_0^{+\infty} \mathbf{1}_{\{\mathcal{E}_{x, \mathbf{k}, y}(\theta, Y_1(s-), \zeta_1(s-)) \Delta \mathcal{E}_{x, \mathbf{k}, y}(\theta, Y_1(s-), \zeta_2(s-))\}} Q_{x, \mathbf{k}, y}(ds, d\theta) = 0 \right\} \\ \{T_K \geq t\} &\supseteq \left\{ \sum_{(x, \mathbf{k}, y) \in J^*} \int_0^t \int_0^{+\infty} \mathbf{1}_{\{\mathcal{E}_{x, \mathbf{k}, y}(\theta, Y_1(s-), \zeta_1(s-)) \Delta \mathcal{E}_{x, \mathbf{k}, y}(\theta, Y_1(s-), \zeta_2(s-))\}} Q_{x, \mathbf{k}, y}(ds, d\theta) = 0 \right\}. \end{aligned}$$

Let $\mathcal{D} = \{(y, \mathbf{k}) : \exists x \in \mathcal{X} \text{ s.t. } (x, \mathbf{k}) \in J, \mathbf{k}_y > 0\}$. Recall from Assumption 4.1 that for any $(x, \mathbf{k}) \in J$, $\tau_{\mathbf{k}}(x, \cdot)$ is $L_{x, \mathbf{k}}$ -Lipschitz continuous. Let $L = \max_{(x, \mathbf{k}) \in J} \|k\|_1 L_{x, \mathbf{k}}$. We introduce the event

$$A_K = \left\{ \max_{(y, \mathbf{k}) \in \mathcal{D}} \sup_{s \in [0, t]} \mathbf{k}_y |\tau_{y, \mathbf{k}}(Y_1(s), \zeta_1(s)) - \tau_{y, \mathbf{k}}(Y_1(s), \zeta_2(s))| < L \varepsilon_K \right\}.$$

It follows that

$$\begin{aligned} \mathbb{P}(T_K \leq t) &\leq \mathbb{P}(A_K, \sum_{(x, \mathbf{k}, y) \in J^*} \int_0^t \int_0^{+\infty} \mathbf{1}_{\{\mathcal{E}_{x, \mathbf{k}, y}(\theta, Y_1(s-), \zeta_1(s-)) \Delta \mathcal{E}_{x, \mathbf{k}, y}(\theta, Y_1(s-), \zeta_2(s-))\}} Q_{x, \mathbf{k}, y}(ds, d\theta) \geq 1) \\ &\quad + \mathbb{P}(A_K^C). \end{aligned} \quad (26)$$

First, we may notice that Assumption 4.1 ensures that

$$A_K^C \subseteq \left\{ \sup_{s \in [0, t]} \|\zeta_1(s) - \zeta_2(s)\|_1 \geq \varepsilon_K \right\},$$

from which we deduce by Equation (25) that

$$\mathbb{P}(A_K^C) \leq \alpha_K. \quad (27)$$

Second, on the event A_K , it holds that for any $\theta \geq 0$ and $(x, \mathbf{k}, y) \in J^*$,

$$\begin{aligned} &\mathcal{E}_{x, \mathbf{k}, y}(\theta, Y_1(s-), \zeta_1(s-)) \Delta \mathcal{E}_{x, \mathbf{k}, y}(\theta, Y_1(s-), \zeta_2(s-)) \\ &\subseteq \{\theta \in [\mathbf{k}_y \tau_{\mathbf{k}}(Y_1(s-), \zeta_1(s-)) - L \varepsilon_K, \mathbf{k}_y \tau_{\mathbf{k}}(Y_1(s-), \zeta_1(s-)) + L \varepsilon_K]\}. \end{aligned}$$

As a consequence,

$$\begin{aligned} & \left\{ A_K, \sum_{(x,\mathbf{k},y) \in J^*} \int_0^t \int_0^{+\infty} \mathbf{1}_{\{\mathcal{E}_{x,\mathbf{k},y}(\theta, Y_1(s-), \zeta_1(s-)) \Delta \mathcal{E}_{x,\mathbf{k},y}(\theta, Y_1(s-), \zeta_2(s-))\}} Q_{x,\mathbf{k},y}(ds, d\theta) \geq 1 \right\} \\ & \subseteq \left\{ \sum_{(x,\mathbf{k},y) \in J^*} \int_0^t \int_0^{+\infty} \mathbf{1}_{\{\theta \in [\mathbf{k}_y \tau_{\mathbf{k}}(Y_1(s-), \zeta_1(s-)) - L\varepsilon_K, \mathbf{k}_y \tau_{\mathbf{k}}(Y_1(s-), \zeta_1(s-)) + L\varepsilon_K]\}} Q_{x,\mathbf{k},y}(ds, d\theta) \geq 1 \right\}. \end{aligned}$$

Hence, Markov's inequality leads to

$$\begin{aligned} & \mathbb{P}(A_K, \sum_{(x,\mathbf{k},y) \in J^*} \int_0^t \int_0^{+\infty} \mathbf{1}_{\{\mathcal{E}_{x,\mathbf{k},y}(\theta, Y_1(s-), \zeta_1(s-)) \Delta \mathcal{E}_{x,\mathbf{k},y}(\theta, Y_1(s-), \zeta_1(s-))\}} Q_{x,\mathbf{k},y}(ds, d\theta) \geq 1) \\ & \leq \mathbb{E} \left[\sum_{(x,\mathbf{k},y) \in J^*} \int_0^t \int_0^{+\infty} \mathbf{1}_{\{\theta \in [\mathbf{k}_y \tau_{\mathbf{k}}(Y_1(s-), \zeta_1(s-)) - L\varepsilon_K, \mathbf{k}_y \tau_{\mathbf{k}}(Y_1(s-), \zeta_1(s-)) + L\varepsilon_K]\}} Q_{x,\mathbf{k},y}(ds, d\theta) \right] \quad (28) \\ & \leq Ct\varepsilon_K, \end{aligned}$$

with $C = 2L\text{Card}(J^*)$. Injecting Inequalities (27) and (28) into Equation (26) concludes. \square

We are now ready to establish Lipschitz continuity of \mathbf{m}_Υ .

Lemma 4.9. *For any $T \geq 0$, for any $x \in \mathcal{X}$, the application $(\mathbf{z}, t) \mapsto \mathbf{m}_\Upsilon(x, \mathbf{z}, t)$ is Lipschitz continuous on $\mathcal{Z} \times [0, T]$.*

Proof. Let $T > 0$, $x \in \mathcal{X}$ and $\mathbf{z}_1, \mathbf{z}_2 \in \mathcal{Z}$. We apply Lemma 4.8 to $\zeta_1 = \phi(\cdot, \mathbf{z}_1)$ and $\zeta_2 = \phi(\cdot, \mathbf{z}_2)$ which according to Lemma 4.7 satisfy Equation (25) with $\varepsilon_K = C(t)\|\mathbf{z}_1 - \mathbf{z}_2\|$ and $\alpha_K = 0$. In this case, for $j \in \{1, 2\}$, $(Y_j, \zeta_j) = (\Upsilon, z)$ with initial condition $\Upsilon(0) = y_0$ and $z(0) = \mathbf{z}_j$. For clarity, for $j \in \{1, 2\}$, we thus write (Υ_j, z_j) for the spinal constructions with initial condition (x, \mathbf{z}_j) defined on the same probability space such that

$$\mathbb{P}(\exists s \in [0, t], \Upsilon_1(s) \neq \Upsilon_2(s)) \leq C(t)\|\mathbf{z}_1 - \mathbf{z}_2\|_1.$$

Throughout the following, $C(t)$ designates a positive constant whose value may vary from line to line, but which only depends on t . For $t_1, t_2 \in [0, T]$ and $\mathbf{z}_1, \mathbf{z}_2 \in \mathcal{Z}$, we thus obtain:

$$\begin{aligned} |\mathbf{m}_\Upsilon(x, \mathbf{z}_1, t_1) - \mathbf{m}_\Upsilon(x, \mathbf{z}_2, t_2)| &= \left| \mathbb{E} \left[e^{\int_0^{t_1} \lambda(\Upsilon_1(s), z_1(s)) ds} - e^{\int_0^{t_2} \lambda(\Upsilon_2(s), z_2(s)) ds} \right] \right| \\ &\leq \left| \mathbb{E} \left[e^{\int_0^{t_1} \lambda(\Upsilon_1(s), z_1(s)) ds} - e^{\int_0^{t_2} \lambda(\Upsilon_1(s), z_2(s)) ds} \right] \right| \\ &\quad + C(t)\mathbb{P}(\exists s \in [0, t], \Upsilon_1(s) \neq \Upsilon_2(s)) \\ &\leq \mathbb{E} \left[\left| e^{\int_0^{t_1} \lambda(\Upsilon_1(s), z_1(s)) ds} - e^{\int_0^{t_2} \lambda(\Upsilon_1(s), z_1(s)) ds} \right| \right] \\ &\quad + \mathbb{E} \left[\left| e^{\int_0^{t_2} \lambda(\Upsilon_1(s), z_1(s)) ds} - e^{\int_0^{t_2} \lambda(\Upsilon_1(s), z_2(s)) ds} \right| \right] \\ &\quad + C(T)\|\mathbf{z}_1 - \mathbf{z}_2\|_1. \end{aligned}$$

where the last inequality follows from Lemma 4.7. Recall that λ is bounded. Thus $t \mapsto \exp\left(\int_0^t \lambda(\Upsilon_1(s), z_1(s)) ds\right)$ is Lipschitz continuous on $[0, T]$, for a Lipschitz constant which can be chosen to be independent of x and \mathbf{z} . Hence

$$\mathbb{E} \left[\left| \exp\left(\int_0^{t_1} \lambda(\Upsilon_1(s), z_1(s)) ds\right) - \exp\left(\int_0^{t_2} \lambda(\Upsilon_1(s), z_1(s)) ds\right) \right| \right] \leq C(T)|t_2 - t_1|.$$

Further, by Lipschitz continuity of λ , the following inequality holds almost surely:

$$\begin{aligned}
& \left| e^{\int_0^{t_2} \lambda(\Upsilon_1(s), z_1(s)) ds} - e^{\int_0^{t_2} \lambda(\Upsilon_1(s), z_2(s)) ds} \right| \\
& \leq C(T) \left| \int_0^{t_2} \lambda(\Upsilon_1(s), z_1(s)) ds - \int_0^{t_2} \lambda(\Upsilon_1(s), z_2(s)) ds \right| \\
& \leq C(T) \sup_{s \in [0, T]} \|z_1(s) - z_2(s)\|_1 \\
& \leq C(T) \|\mathbf{z}_1 - \mathbf{z}_2\|.
\end{aligned}$$

This concludes the proof. \square

We are now ready to establish the desired result.

Lemma 4.10. \mathbf{m}_Υ is a solution to Equation (18).

Proof. Lemma 4.9 ensures by Rademacher's theorem that for any $x \in \mathcal{X}$, the application $\mathbf{z} \mapsto \mathbf{m}_\Upsilon(x, \mathbf{z}, t)$ is differentiable for almost every $t \geq 0$ and $\mathbf{z} \in \mathcal{Z}$. We thus consider t, \mathbf{z} such that \mathbf{m}_Υ is differentiable at (x, \mathbf{z}, t) , for any $x \in \mathcal{X}$.

Start by noticing that for $h > 0$,

$$\mathbf{m}_\Upsilon(x, \mathbf{z}, t + h) = \mathbb{E}_{x, \mathbf{z}} [\mathcal{W}(h) \mathbf{m}(\Upsilon(h), z(h), t)].$$

Let T_1 and T_2 designate the times of the first and second reproduction event, respectively. Then

$$\begin{aligned}
\mathbf{m}_\Upsilon(x, \mathbf{z}, t + h) &= \mathbb{E}_{x, \mathbf{z}} [\mathcal{W}(h) \mathbf{1}_{\{T_1 > h\}}] \mathbf{m}(x, z(h), t) \\
&\quad + \mathbb{E}_{x, \mathbf{z}} [\mathcal{W}(h) \mathbf{m}(\Upsilon(h), z(h), t) \mathbf{1}_{\{T_1 \leq h < T_2\}}] \\
&\quad + \mathbb{E}_{x, \mathbf{z}} [\mathcal{W}(h) \mathbf{m}(\Upsilon(h), z(h), t) \mathbf{1}_{\{T_2 \leq h\}}].
\end{aligned}$$

Since \mathbf{m}_Υ is differentiable in \mathbf{z} at (t, \mathbf{z}) , we may now proceed as in the Proof of Proposition 4.3 to show that

$$\lim_{h \rightarrow 0^+} \frac{1}{h} (\mathbf{m}_\Upsilon(x, \mathbf{z}, t + h) - \mathbf{m}_\Upsilon(x, \mathbf{z}, t)) = \mathcal{G}(\mathbf{m}_\Upsilon(\cdot, t))(x, \mathbf{z}).$$

This concludes the proof. \square

Many-to-one formula. Let us now focus on the characterization of $\mathcal{P}^{(t)}$.

Proposition 4.11. $\mathcal{P}^{(t)}$ is a time-inhomogeneous, conservative semi-group of bounded linear operators on $L^\infty(\mathcal{S})$ whose generator is $\mathcal{A}^{(t)}$, as defined in Equation (20).

Proof. Start by noticing that it follows from Assumption 4.2 and Lemma 4.10 that for any $0 \leq r \leq s \leq t$, for any $(x, \mathbf{z}) \in \mathcal{S}$,

$$\mathcal{P}_{r,s}^{(t)} \mathbf{1}(x, \mathbf{z}) = \frac{\mathbf{m}_\Upsilon(x, \mathbf{z}, t - r)}{\mathbf{m}(x, \mathbf{z}, t - r)} = 1.$$

In addition, it is clear that $\mathcal{P}_{r,s}^{(t)}$ is a linear operator on $L^\infty(\mathcal{S})$ such that $\|\mathcal{P}_{r,s}^{(t)} f\| \leq \|f\|_\infty$.

Let us establish the semi-group property, i.e. we want to show that for any $0 \leq r \leq \tau \leq s \leq t$,

$$\mathcal{P}_{r,\tau}^{(t)} \mathcal{P}_{\tau,s}^{(t)} = \mathcal{P}_{r,s}^{(t)}.$$

Throughout the proof, we write $\mathbb{Y} = (\Upsilon, z)$. Let $f \in L^\infty(\mathcal{S})$. For $t_1 \geq t_2$, define

$$\mathcal{W}(t_1, t_2) = \exp \left(\int_{t_1}^{t_2} \lambda(\mathbb{Y}(u)) du \right).$$

Be definition, we have for $(x, \mathbf{z}) \in \mathcal{S}$,

$$\begin{aligned} \mathbf{m}(x, \mathbf{z}, t - r) \mathcal{P}_{r,\tau}^{(t)} \mathcal{P}_{\tau,s}^{(t)} f(x, \mathbf{z}) &= \mathbb{E}[\mathcal{W}(r, t) \mathcal{P}_{\tau,s}^{(t)} f(\mathbb{Y}(\tau)) | \mathbb{Y}(r) = (x, \mathbf{z})] \\ &= \mathbb{E}[\mathcal{W}(r, t) \mathbf{m}(\mathbb{Y}(\tau), t - \tau)^{-1} \mathbb{E}[\mathcal{W}(\tau, t) f(\mathbb{Y}(s)) | \mathbb{Y}(\tau)] | \mathbb{Y}(r) = (x, \mathbf{z})]. \end{aligned}$$

Notice that

$$\mathcal{W}(r, t) = \mathcal{W}(r, \tau) \mathcal{W}(\tau, t).$$

Designate by $(\mathcal{F}_s, s \geq 0)$ the natural filtration associated to \mathbb{Y} . As $\mathcal{W}(r, \tau)$ is \mathcal{F}_τ -measurable, we obtain that

$$\mathbf{m}(x, \mathbf{z}, t - r) \mathcal{P}_{r,\tau}^{(t)} \mathcal{P}_{\tau,s}^{(t)} f(x, \mathbf{z}) = \mathbb{E}[\mathcal{W}(\tau, t) \mathbf{m}(\mathbb{Y}(\tau), t - \tau)^{-1} \mathbb{E}[\mathcal{W}(r, t) f(\mathbb{Y}(s)) | \mathbb{Y}(\tau)] | \mathbb{Y}(r) = (x, \mathbf{z})].$$

Further, it follows from Lemma 4.10 that $E[\mathcal{W}(\tau, t) | \mathbb{Y}(\tau)] = \mathbf{m}(\mathbb{Y}(\tau), t - \tau)$. Since $\mathcal{F}_r \subseteq \mathcal{F}_\tau$, this finally leads to

$$\mathbf{m}(x, \mathbf{z}, t - r) \mathcal{P}_{r,\tau}^{(t)} \mathcal{P}_{\tau,s}^{(t)} f(x, \mathbf{z}) = \mathbb{E}[\mathcal{W}(r, t) f(\mathbb{Y}(s)) | \mathbb{Y}(r) = (x, \mathbf{z})],$$

as desired.

It remains to compute the generator of $\mathcal{P}^{(t)}$. Let $0 \leq s \leq s + h \leq t$ and $(x, \mathbf{z}) \in \mathcal{S}$. As $\mathcal{F}_s \subseteq \mathcal{F}_{s+h}$, we have

$$\begin{aligned} \mathbf{m}(x, \mathbf{z}, t - s) \mathcal{P}_{s,s+h}^{(t)} f(x, \mathbf{z}) &= \mathbb{E}[\mathcal{W}(s, t) f(\mathbb{Y}(s + h)) | \mathbb{Y}(s) = (x, \mathbf{z})] \\ &= \mathbb{E}[\mathcal{W}(s, s + h) \mathbf{m}(\mathbb{Y}(s + h), t - s - h) f(\mathbb{Y}(s + h)) | \mathbb{Y}(s) = (x, \mathbf{z})]. \end{aligned}$$

Let $g(x, \mathbf{z}, s) = f(x, \mathbf{z}) \mathbf{m}(x, \mathbf{z}, t - s)$. With this notation, we have

$$\begin{aligned} \mathbf{m}(x, \mathbf{z}, t - s) (\mathcal{P}_{s,s+h}^{(t)} f(x, \mathbf{z}) - f(x, \mathbf{z})) \\ = \mathbb{E}[\mathcal{W}(s, s + h) g(\mathbb{Y}(s + h), s + h) | \mathbb{Y}(s) = (x, \mathbf{z})] - g(x, \mathbf{z}, s). \end{aligned}$$

By Assumption 4.2, the application $(\mathbf{z}, s) \mapsto g(x, \mathbf{z}, t - s)$ is differentiable on $\mathcal{Z} \times [0, t]$. As a consequence, we may proceed as in the proof of Proposition 4.3 to show that

$$\lim_{h \rightarrow 0^+} \mathbf{m}(x, \mathbf{z}, t - s) (\mathcal{P}_{s,s+h}^{(t)} f(x, \mathbf{z}) - f(x, \mathbf{z})) = \mathcal{G}(\mathbf{m}(\cdot, t - s) f(\cdot))(x, \mathbf{z}) - \mathcal{G}(\mathbf{m}(\cdot, t - s))(x, \mathbf{z}) f(x, \mathbf{z}).$$

This concludes the proof. \square

We are finally ready to establish Proposition 4.6.

Proof of Proposition 4.6. Propositions 4.3 and 4.11 ensure thanks to Assumption 4.4 that the semi-groups $\mathcal{P}^{(t)}$ and $\mathcal{R}^{(t)}$ are identical. Hence Equation (23) holds for

$$\begin{aligned} F : \mathbb{D}([0, t], \mathcal{X}) \times \mathcal{C}^1([0, t], \mathcal{Z}) &\rightarrow \mathbb{R} \\ (y(s), z(s))_{s \leq t} &\mapsto f(Y(s), z(s)), \end{aligned}$$

with $s \in [0, t]$ and $f \in L^\infty(\mathcal{S})$ given. As in the Proof of Theorem 3.3, this suffices to conclude by induction and using a monotone class argument. \square

4.2.2 Speed of convergence

It remains to quantify the speed of convergence in Equation (24). Notice that according to Proposition 4.6, is identical to the speed of convergence in Equation (22). By coupling the homogeneous spine in a population of size K to its large population limit, we are able to provide the following result.

Proposition 4.12. *Let $t > 0$ and $F \in \mathfrak{L}$. There exists $C > 0$ such that for any sequence $(\varepsilon_K)_{K \geq 0}$ of positive real numbers, for any $K \geq 1$, letting $\delta_K = C(\varepsilon_K + K^{-1/2}\varepsilon_K^{-1})$,*

$$\left| \mathbb{E}_{\mathbf{z}^K} \left[\sum_{u \in \mathbb{G}(t)} F((x_u(s), Z^K(s))_{s \leq t}) \right] - \sum_{x \in \mathcal{X}} \mathbf{z}_x \mathbb{E}_{x, \mathbf{z}} [\mathcal{W}(t) F((\Upsilon(s), z(s))_{s \leq t})] \right| \leq \delta_K.$$

Combining Equation (22) with Proposition 4.6 and 4.12 for $\varepsilon_K = K^{-1/4}$ finally yields Theorem 4.5.

Let us start by establishing the following Lemma which quantifies the approximation error of the spinal population process by its large population limit.

Lemma 4.13. *Let $t > 0$. Under Assumption 4.1, there exists $C(t) > 0$ such that for every $K \geq 1$ and $\varepsilon_K > 0$,*

$$\mathbb{P} \left(\sup_{s \in [0, t]} \|\zeta^K(s) - z(s)\|_1 \geq \varepsilon_K \right) \leq \frac{C(t)}{\sqrt{K} \varepsilon_K}.$$

Proof. Let us define the large population limit z on the same state space \mathcal{X}^* as ζ^K . For any $t \geq 0$,

$$z(t) = \bar{\mathbf{z}}_0 + \sum_{(x, \mathbf{k}) \in J} h_0(x, \mathbf{k}) \int_0^t z_{0,x}(s) \tau_{\mathbf{k}}(x, z(s)) ds, \quad (29)$$

with $\bar{\mathbf{z}}_0 = \sum_{x \in \mathcal{X}} \mathbf{z}_x \mathbf{e}(0, x)$ and \mathbf{z} the initial condition in Equation (17). In particular, $\mathbf{z}_{1,x}(t) = 0$ for any $x \in \mathcal{X}$ and $t \geq 0$, as expected since the spine becomes negligible as population size grows large.

In order to control our quantity of interest $\|\zeta^K - z\|_1$, we introduce some notation. For $(x, \mathbf{k}) \in J$, let

$$\tilde{Q}_{x, \mathbf{k}}(ds, d\theta) = Q_{x, \mathbf{k}}(ds, d\theta) - ds d\theta$$

be the compensated martingale-measure associated to $Q_{x, \mathbf{k}}$, and consider the following martingale:

$$M_{x, \mathbf{k}}^K(t) = \frac{\|h_0(x, \mathbf{k})\|_1}{K} \int_0^t \int_0^{+\infty} \mathbf{1}_{\{\theta \leq K \zeta_{0,x}^K(s-) \tau_{\mathbf{k}}(x, \zeta^K(s-))\}} \tilde{Q}_{x, \mathbf{k}}(ds, d\theta).$$

Finally, let

$$M^K(t) = \sum_{(x, \mathbf{k}) \in J} M_{x, \mathbf{k}}^K(t),$$

$$A^K(t) = \left\| \bar{\mathbf{z}}_0^K - \bar{\mathbf{z}}_0 + \sum_{(x, \mathbf{k}) \in J} h_0(x, \mathbf{k}) \int_0^t (\zeta_{0,x}^K(s) \tau_{\mathbf{k}}(x, \zeta^K(s)) - z_{0,x}(s) \tau_{\mathbf{k}}(x, z(s))) ds \right\|_1,$$

$$B^K(t) = \left\| \frac{1}{K} \sum_{(x, \mathbf{k}, y) \in J^*} h_1(x, \mathbf{k}, y) \int_0^t \int_0^{+\infty} \mathbf{1}_{\{\theta \leq K \zeta_{1,x}^K(s-) \mathbf{k}_y \tau_{\mathbf{k}}(x, \zeta^K(s-))\}} Q_{x, \mathbf{k}, y}(ds, d\theta) \right\|_1.$$

With these notations, Equations (21) and (29) ensure that, for any $t \geq 0$

$$\|\zeta^K(t) - z(t)\|_1 \leq M^K(t) + A^K(t) + B^K(t).$$

We thus turn to controlling M^K , A^K and B^K over any given interval $[0, t]$.

Start by noticing that, for any $(x, \mathbf{k}) \in J$, $M_{x, \mathbf{k}}^K$ is square integrable. Indeed, as $\tau_{\mathbf{k}}$ is bounded and $\|\zeta^K\|_1 \leq 1$ by definition, there exists a positive constant $c(x, \mathbf{k})$ such that, for any $K \geq 1$,

$$\mathbb{E} \left[\int_0^t \int_0^{+\infty} \left(\frac{\|h_0(x, \mathbf{k})\|_1}{K} \mathbf{1}_{\{\theta \leq K \zeta_{0,x}^K(s) \tau_{\mathbf{k}}(x, \zeta^K(s))\}} \right)^2 d\theta ds \right] \leq \frac{tc(x, \mathbf{k})}{K}.$$

It follows that its quadratic variation is given by

$$\langle M_{x, \mathbf{k}}^K \rangle(t) = \int_0^t \frac{\|h_0(x, \mathbf{k})\|_1^2}{K} \zeta_{0,x}^K(s) \tau_{\mathbf{k}}(x, \zeta^K(s)) ds.$$

M^K thus is itself a square integrable martingale, and Doob's inequality shows that there exists a positive constant κ such that

$$\mathbb{E} \left[\sup_{s \in [0, t]} (M^K(s))^2 \right] \leq \kappa \sum_{(x, \mathbf{k}) \in J} \mathbb{E}[\langle M_{x, \mathbf{k}}^K \rangle(t)]. \quad (30)$$

Since J is a finite set, it follows that there exists a positive, finite constant $c = \kappa \sum_{x, \mathbf{k}} c(x, \mathbf{k})$ such that, for any $K \geq 1$,

$$\mathbb{E} \left[\sup_{s \in [0, t]} (M^K(s))^2 \right] \leq \frac{tc}{K}.$$

Noticing that $M^K \geq 0$ almost surely, Cauchy-Schwarz inequality finally leads to

$$\mathbb{E} \left[\sup_{s \in [0, t]} M^K(s) \right] \leq \sqrt{\frac{tc}{K}}.$$

Let us now turn to A^K . By definition, there exists a finite constant $c > 0$ such that, for any $K \geq 1$,

$$\|\bar{z}_0^K - \bar{z}_0\|_1 \leq \frac{c}{K}.$$

Since further the set J is finite and $\tau_{\mathbf{k}}(x, \cdot)$ is Lipschitz-continuous according to Assumption 4.1, there exists $c' > 0$ such that, for any $K \geq 1$,

$$\begin{aligned} \sup_{s \in [0, t]} A^K(s) &\leq \frac{c}{K} + \sum_{(x, \mathbf{k}) \in J} \|h_0(x, \mathbf{k})\|_1 \int_0^t |\zeta_{0,x}^K(s) \tau_{\mathbf{k}}(x, \zeta^K(s)) - z_{0,x}(s) \tau_{\mathbf{k}}(x, z(s))| ds \\ &\leq \frac{c}{K} + c' \int_0^t \|\zeta^K(s) - z(s)\|_1 ds. \end{aligned}$$

In particular, we obtain that for any $K \geq 1$,

$$\mathbb{E} \left[\sup_{s \in [0, t]} A^K(s) \right] \leq \frac{c}{K} + c' \int_0^t \mathbb{E} \left[\sup_{u \in [0, s]} \|\zeta^K(u) - z(u)\| ds \right]. \quad (31)$$

Finally, notice that it follows from Equation (21) that for any $t \geq 0$ and $x \in \mathcal{X}$, we have $\zeta_{1,x}^K \leq K^{-1}$ almost surely. As further the set J^* is finite and the reproduction rates bounded, there exists a finite, non-negative constant c such that, for any $K \geq 1$,

$$\mathbb{E} \left[\sup_{s \in [0, t]} B^K(s) \right] \leq \sum_{(x, \mathbf{k}, y) \in J^*} \|h_1(x, \mathbf{k}, y)\|_1 \mathbb{E} \left[\int_0^t \zeta_{1,x}^K(s) \mathbf{k}_y \tau_{\mathbf{k}}(x, \zeta^K(s)) ds \right] \leq \frac{tc}{K}. \quad (32)$$

Combining Equations (30), (31) and (32) yields the existence of finite, non-negative constants $c_1(t)$ and c_2 such that, for any $K \geq 1$,

$$\mathbb{E} \left[\sup_{s \in [0, t]} \|\zeta^K(s) - z(s)\|_1 \right] \leq \frac{c_1(t)}{\sqrt{K}} + c_2 \int_0^t \mathbb{E} \left[\sup_{u \in [0, s]} \|\zeta^K(u) - z(u)\|_1 \right] ds.$$

Hence, by Gronwall's Lemma, there exists $C(t)$ such that, for any $K \geq 1$,

$$\mathbb{E} \left[\sup_{s \in [0, t]} \|\zeta^K(s) - z(s)\|_1 \right] \leq \frac{C(t)}{\sqrt{K}}.$$

The conclusion follows from Markov's inequality. \square

Next, we focus on quantifying how well Υ approaches Y^K , yielding the approximation error associated to replacing (Y^K, ζ^K) by (Υ, z) on finite time intervals. In order to achieve this, we couple Υ and Y^K , by defining Υ as the unique strong solution to an SDE driven by the same family of Poisson Point Processes $(Q_{x, \mathbf{k}, y}, (x, \mathbf{k}, y) \in J^*)$ as in Equation (21):

$$\Upsilon(t) = \mathbf{e}(y_0) + \sum_{(x, \mathbf{k}, y) \in J^*} \int_0^t \int_0^{+\infty} \mathbf{1}_{\{\Upsilon(s-) = x, \theta \leq \mathbf{k}_y \tau_{\mathbf{k}}(x, z(s))\}} (\mathbf{e}(y) - \mathbf{e}(x)) Q_{x, \mathbf{k}, y}(ds, d\theta).$$

We are now ready to state our result.

Lemma 4.14. *Let $t > 0$. Under Assumption 4.1, there exists a constant $C(t) > 0$ such that for every $K \geq 1$ and $\varepsilon_K > 0$, letting $\alpha_K = (\sqrt{K} \varepsilon_K)^{-1}$,*

$$\mathbb{P}(\forall s \in [0, t], Y^K(s) = \Upsilon(s) \text{ and } \|\zeta^K(s) - z(s)\|_1 \leq \varepsilon_K) \geq 1 - C(t)(\alpha_K + \varepsilon_K).$$

Proof. Consider Lemma 4.8 with $\zeta_1 = \zeta^K$ and $\zeta_2 = z$, i.e. $(Y_1, \zeta_1) = (Y^K, \zeta^K)$ and $(Y_2, \zeta_2) = (\Upsilon, z)$. Thanks to Lemma 4.13, we thus obtain that

$$\mathbb{P}(\exists t \leq t : Y^K(t) \neq \Upsilon(t)) \leq c(t)\alpha_K + Ct\varepsilon_K. \quad (33)$$

The conclusion follows by combining Lemma 4.13 and Equation (33). \square

In order to simplify notations, for any function $G : \mathbb{D}([0, t], \mathcal{X}) \times \mathbb{D}([0, t], \mathcal{Z}) \rightarrow \mathbb{R}$ as well as càdlàg trajectories $(x(s))_{s \leq t}$ in \mathcal{X} and $(\mathbf{z}(s))_{s \leq t} = (\mathbf{z}_{i, x}(s))_{(i, x) \in \mathcal{X}^*, s \leq t}$ in \mathcal{Z}^2 , we let

$$G((x(s), \mathbf{z}(s))_{s \leq t}) := G((x(s), \mathbf{z}|_{\mathcal{X}}(s))_{s \leq t}).$$

We are now ready to establish the main result.

Proof of Proposition 4.12. Throughout the proof, we write $\mathbb{Y}^K = (Y^K, \zeta^K)$ for the spinal construction in the initial population process, and $\mathbb{Y} = (\Upsilon, z)$ for the spinal process in the large population limit.

Let $t \geq 0$ and $F \in \mathfrak{L}$. It follows from Theorem 1 in [4] that

$$\mathbb{E}_{\mathbf{z}^K} \left[\sum_{\substack{u \in \mathbb{G}(t), \\ u \geq u_x}} F((x_u(s), Z^K(s))_{s \leq t}) \right] = \mathbb{E} [H((\mathbb{Y}^K(s))_{s \leq t})],$$

where

$$H((\mathbb{Y}^K(s))_{s \leq t}) = e^{\int_0^t \lambda(\mathbb{Y}^K(s)) ds} F((\mathbb{Y}^K(s))_{s \leq t}).$$

As J is a finite set, Equation (16) and Assumption 4.1 imply that $H \in \mathfrak{L}$. In other words, there exists a constant M depending on t and F such that for any $x \in \mathbb{D}([0, t], \mathcal{X})$,

$$|H((x(s), \zeta^K(s))_{s \leq t}) - H((x(s), z(s))_{s \leq t})| \leq M \sup_{s \in [0, t]} \|\zeta^K(s) - z(s)\|_1. \quad (34)$$

Consider the event

$$A_K = \{\forall s \in [0, t], Y^K(s) = \Upsilon(s) \text{ and } \|\zeta^K(s) - z(s)\|_1 \leq \varepsilon_K\}.$$

We have

$$\begin{aligned} \mathbb{E}[|H((\mathbb{Y}^K(s))_{s \leq t}) - H((\mathbb{Y}(s))_{s \leq t})|] &\leq \mathbb{E}[|H((\mathbb{Y}^K(s))_{s \leq t}) - H((\mathbb{Y}(s))_{s \leq t})| \mathbf{1}_{A_K}] \\ &\quad + \mathbb{E}[|H((\mathbb{Y}^K(s))_{s \leq t}) - H((\mathbb{Y}(s))_{s \leq t})| \mathbf{1}_{A_K^c}] \end{aligned}$$

On the one hand, it follows from the definition of A_K and Equation (34) that

$$\mathbb{E}[|H((\mathbb{Y}^K(s))_{s \leq t}) - H((\mathbb{Y}(s))_{s \leq t})| \mathbf{1}_{A_K}] \leq M\varepsilon_K.$$

On the other hand, the boundedness of H and Lemma 4.14 imply the existence of a constant c such that

$$\mathbb{E}[|H((\mathbb{Y}^K(s))_{s \leq t}) - H((\mathbb{Y}(s))_{s \leq t})| \mathbf{1}_{A_K^c}] \leq c(\alpha_K + \varepsilon_K).$$

Taken together, we thus obtain existence of a constant C such that

$$\mathbb{E}[|H((\mathbb{Y}^K(s))_{s \leq t}) - H((\mathbb{Y}(s))_{s \leq t})|] \leq C(\alpha_K + \varepsilon_K).$$

This concludes the proof. \square

5 Discussion

First, we have introduced a time-inhomogeneous spinal process allowing to gain insight on the survivorship bias associated to any sampling weight ψ .

Indeed, the corresponding many-to-one formula does not require stochastic weighting of trajectories. This implies that the bias of reproduction rates relying on the application m defined in Equation (2) accurately depicts the survivorship bias. In addition, the stochastic exponential weight associated to the many-to-one formula for the homogeneous spinal process implies that rare trajectories may have tremendous impact, making Monte-Carlo estimations delicate. As a consequence, the time-inhomogeneous spinal process may facilitate the numerical evaluation of the many-to-one formula. However, due to the time-inhomogeneity, simulating trajectories of the time-inhomogeneous spinal process through standard algorithms may be expensive in terms of computation time [28].

A desirable extension of Theorem 3.3 consists in capturing the whole tree, instead of being restricted to the type evolution along sampled lineages. We expect this to be achievable, using a classical induction argument [4][Theorem 1]. In addition, one may be interested in sampling more than one individual, in the spirit of many-to-one formulas for forks in branching processes [22]. A possible strategy for achieving this would be a double spine construction. More precisely, one may augment the type space of the spinal process to distinguish spinal and non-spinal individuals, and then consider the spinal process associated to (re-)sampling in this population process.

Second, under appropriate assumptions, we have focused on sampling in the deterministic large population limit, and quantified the associated approximation error. In particular, the process describing the spine's offspring then corresponds to a time-inhomogeneous multi-type

branching process whose reproduction rates depend on a changing environment, given by z . If we assume that z admits a stable equilibrium, then starting from this equilibrium, the offspring is described by a classical multi-type branching process [12].

A natural perspective of our work is to extend our results on the empirical distribution of ancestral lineages in the large population limit over longer time scales. In order to achieve this, we need some control of the form:

$$\mathbb{P} \left(\sup_{s \in [0, t_K]} \|\zeta^K(s) - z(s)\|_1 \geq \varepsilon_K \right) \leq \alpha_K,$$

with ε_K and α_K converging to zero and t_K growing to infinity, as K grows large. We consider expecting such control to be reasonable. Indeed, it corresponds to understanding and controlling the fluctuations of the finite-population process ζ^K around its deterministic limit, which is a well studied question with several classical regimes: Gaussian fluctuations for $\varepsilon_K = O(K^{-1/2})$, which are related to the diffusion approximation, moderate deviations with $\varepsilon_K = O(K^{-p})$ for $p \in (0, 1/2)$ and large deviations where $\varepsilon_K = O(1)$ [11, 25, 27]. In particular, moderate and large deviations appear to be interesting regimes, as they allow to consider longer time scales. Nevertheless, in the case of the spinal population process, they are not immediate, due to a boundary problem arising from the fact that the spinal individual becomes negligible in large populations. As a consequence, these considerations are left for a futur work.

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A Detail on the proof of Theorem 3.3

Throughout this proof, for readability, we will make use of the following notations. On the one hand, for $t \geq 0$ and u such that there exists $v \in \mathbb{G}(t)$ satisfying $u \geq v$, let

$$\mathbb{X}_u(t) = (x_u(t), Z(t)).$$

Similarly, for $0 \leq s \leq t$, we let

$$\mathbb{Y}^{(t)}(s) = (Y^{(t)}(s), \zeta^{(t)}(s)).$$

Let us start by showing that Equation (8) holds for $F((x(s), \mathbf{z}(s))_{s \leq t}) = \prod_{j=1}^k f_j(x(s_j), \mathbf{z}(s_j))$ where $k \geq 1$, $0 \leq s_1 \leq \dots \leq s_k \leq t$ and $f_1, \dots, f_k : \mathcal{S}_K \rightarrow \mathbb{R}_+$.

This part of the proof proceeds by induction. For $k \geq 1$, let H_k be the property that for any $0 \leq s_1 \leq \dots \leq s_k \leq t$ and $f_1, \dots, f_k : \mathcal{S}_K \rightarrow \mathbb{R}_+$,

$$\mathbb{E}_{\mathbf{z}} \left[\sum_{u \in \mathbb{G}(t), u \geq u_x(0)} \psi(\mathbb{X}_u(t)) \prod_{j=1}^k f_j(\mathbb{X}_u(s_j)) \right] = m(x, \mathbf{z}, t) \mathbb{E}_{x, \mathbf{z}} \left[\prod_{j=1}^k f_j(\mathbb{Y}^{(t)}(s_j)) \right].$$

Let us turn our attention to the initialization step. As \mathcal{S}_K is a finite set, a semi-group acting on non-negative functions on \mathcal{S}_K is uniquely characterized by its generator. Thus Lemma 3.7 implies that the semi-groups $P^{(t)}$ and $R^{(t)}$ are identical. Hence for any $s \in [0, t]$ and $f : \mathcal{S}_K \rightarrow \mathbb{R}_+$, Equation (13) becomes

$$\mathbb{E}_{\mathbf{z}} \left[\sum_{u \in \mathbb{G}(t), u \geq u_x(0)} \psi(\mathbb{X}_u(t)) f(\mathbb{X}_u(s)) \right] = m(x, \mathbf{z}, t) R_{0,s}^{(t)} f(x, \mathbf{z}).$$

This exactly corresponds to H_1 by definition of $R^{(t)}$.

Suppose now that H_{k-1} is true for $k > 1$, and let us show that H_k follows. Consider functions $f_1, \dots, f_k : \mathcal{S}_K \rightarrow \mathbb{R}_+$ and $0 \leq s_1 \leq \dots \leq s_k \leq t$. Notice that

$$\begin{aligned} \mathbb{E}_{\mathbf{z}} \left[\sum_{\substack{u \in \mathbb{G}(t) \\ u \geq u_x(0)}} \psi(\mathbb{X}_u(t)) \prod_{j=1}^k f_j(\mathbb{X}_u(s_j)) \right] &= \\ \mathbb{E}_{\mathbf{z}} \left[\sum_{\substack{u \in \mathbb{G}(s_{k-1}) \\ u \geq u_x(0)}} \prod_{j=1}^{k-1} f_j(\mathbb{X}_u(s_j)) \mathbb{E} \left[\sum_{\substack{v \in \mathbb{G}(t) \\ v \geq u_{x_u(s_{k-1})}}} \psi(\mathbb{X}_v(t)) f_k(\mathbb{X}_v(s_k)) \middle| X(s_{k-1}) = \mathfrak{X}(\mathbb{X}_u(s_{k-1})) \right] \right] &= \end{aligned}$$

As for H_1 , equality of $P^{(t)}$ and $R^{(t)}$ leads to:

$$\begin{aligned} \mathbb{E}_{\mathbf{z}} \left[\sum_{\substack{u \in \mathbb{G}(t) \\ u \geq u_x(0)}} \psi(\mathbb{X}_u(t)) \prod_{j=1}^k f_j(\mathbb{X}_u(s_j)) \right] = \\ \mathbb{E}_{\mathbf{z}} \left[\sum_{\substack{u \in \mathbb{G}(s_{k-1}) \\ u \geq u_x(0)}} m(\mathbb{X}_u(s_{k-1}), t - s_{k-1}) \prod_{j=1}^{k-1} f_j(\mathbb{X}_u(s_j)) \mathbb{E}[f_k(\mathbb{Y}^{(t)}(s_k)) | \mathbb{Y}^{(t)}(s_{k-1}) = \mathbb{X}_u(s_{k-1})] \right]. \end{aligned}$$

Equation (15) allows to rewrite this as:

$$\begin{aligned} \mathbb{E}_{\mathbf{z}} \left[\sum_{\substack{u \in \mathbb{G}(t) \\ u \geq u_x(0)}} \psi(\mathbb{X}_u(t)) \prod_{j=1}^k f_j(\mathbb{X}_u(s_j)) \right] = \\ \mathbb{E}_{\mathbf{z}} \left[\sum_{\substack{u \in \mathbb{G}(t) \\ u \geq u_x(0)}} \psi(\mathbb{X}_u(t)) \prod_{j=1}^{k-1} f_j(\mathbb{X}_u(s_j)) \mathbb{E}[f_k(\mathbb{Y}^{(t)}(s_k)) | \mathbb{Y}^{(t)}(s_{k-1}) = \mathbb{X}_u(s_{k-1})] \right]. \end{aligned}$$

Finally, H_{k-1} yields:

$$\begin{aligned} \mathbb{E}_{\mathbf{z}} \left[\sum_{\substack{u \in \mathbb{G}(t) \\ u \geq u_x(0)}} \psi(\mathbb{X}_u(t)) \prod_{j=1}^k f_j(\mathbb{X}_u(s_j)) \right] \\ = m(x, \mathbf{z}, t) \mathbb{E}_{x, \mathbf{z}} \left[\prod_{j=1}^{k-1} f_j(\mathbb{Y}^{(t)}(s_j)) \mathbb{E}[f_k(\mathbb{Y}^{(t)}(s_k)) | \mathbb{Y}^{(t)}(s_{k-1})] \right] \\ = m(x, \mathbf{z}, t) \mathbb{E}_{x, \mathbf{z}} \left[\prod_{j=1}^k f_j(\mathbb{Y}^{(t)}(s_j)) \right]. \end{aligned}$$

This concludes the induction argument.

In order to obtain the desired result, we will reason using the monotone class theorem. Let us introduce the set

$$I = \left\{ \bigcap_{j=1}^k \{x \in \mathbb{D}([0, t], \mathcal{S}_K) : x(s_j) \in B_j\}, k \in \mathbb{N}, s_j \in [0, t], B_j \in \mathcal{P}(\mathcal{S}_K) \right\}$$

where $\mathcal{P}(\mathcal{S}_K)$ is the set of subsets of \mathcal{S}_K . The set I is a π -system, which induces the Borel σ -algebra $\mathcal{B}(\mathbb{D}([0, t], \mathcal{S}_K))$ on the Skorokhod space $\mathbb{D}([0, t], \mathcal{S}_K)$ (Theorem 12.5 in [10]). Further, define

$$M = \{\mathbf{B} \in \mathcal{B}(\mathbb{D}([0, t], \mathcal{S}_K)) : \text{Equation (8) is satisfied for } F = \mathbf{1}_{\mathbf{B}}\}.$$

M is a monotone class which contains I according to our induction argument. It thus follows from the monotone class theorem that $M = \mathcal{B}(\mathbb{D}([0, t], \mathcal{S}_K))$. In other words, for any $\mathbf{B} \in \mathcal{B}(\mathbb{D}([0, t], \mathcal{S}_K))$, Equation (8) is satisfied for $F = \mathbf{1}_{\mathbf{B}}$. As a consequence, Equation (8) holds for any positive measurable function $F : \mathbb{D}([0, t], \mathcal{S}_K) \rightarrow \mathbb{R}_+$ as there exists an increasing sequence of simple functions converging pointwise to F , from which the result follows by monotone convergence.

B Proof of Proposition 4.3

In order to see that the process $(\Upsilon^{(t)}, z)$ is well defined on $[0, t]$, start by noticing that existence and uniqueness of $z \in \mathcal{C}^1(\mathbb{R}_+)$ follows from the Cauchy-Lipschitz theorem and Assumption 4.1.

Further, Equation (16) implies that System (17) is positively invariant in \mathcal{Z} : $z(0) \in \mathcal{Z}$ implies that $z(s) \in \mathcal{Z}$ for any $s \geq 0$.

It remains to focus on existence and uniqueness of $\Upsilon^{(t)}$, given z . This can be achieved through similar arguments as for steps (i) and (ii) in the proof of Proposition 3.2. Indeed, notice that Assumption 4.2 ensures that for any $x \in \mathcal{X}$, $\mathfrak{m}(x, \cdot)$ is positive and continuous on $\mathcal{Z} \times [0, t]$. It thus is bounded from below by a positive constant, and the reproduction rates $\rho_{\mathbf{k}, y}^{(t)}$ are also bounded.

We now turn to characterizing the associated semi-group $\mathcal{R}^{(t)}$. It is clear that for any $0 \leq r \leq s \leq t$, $\mathcal{R}_{r,s}^{(t)}$ is a linear operator on $L^\infty(\mathcal{S})$. Further,

$$\forall f \in L^\infty(\mathcal{S}), \quad \|\mathcal{R}_{r,s}^{(t)} f\|_\infty \leq \|f\|_\infty.$$

Thus, $\mathcal{R}_{r,s}^{(t)} : L^\infty(\mathcal{S}) \rightarrow L^\infty(\mathcal{S})$ and its operator norm equals one, as $\mathcal{R}_{r,s}^{(t)} 1 = 1$.

Let us finally compute the generator of $\mathcal{R}^{(t)}$: we want to show that for any $f \in C^1(\mathcal{S})$, $s \leq t$ and $(x, \mathbf{z}) \in \mathcal{S}$,

$$\lim_{h \rightarrow 0^+} \frac{1}{h} \left(\mathcal{R}_{s,s+h}^{(t)} f(x, \mathbf{z}) - f(x, \mathbf{z}) \right) = \mathcal{A}_s^{(t)} f(x, \mathbf{z}).$$

Fix s and define T_1 and T_2 as the times of the first and second reproduction events after time s . By definition, we have

$$\mathcal{R}_{s,s+h}^{(t)} f(x, \mathbf{z}) = A(h) + B(h) + C(h),$$

where

$$\begin{aligned} A(h) &= \mathbb{E}[f(\Upsilon^{(t)}(s+h), z(s+h)) \mathbf{1}_{\{T_1 > h\}} | \Upsilon^{(t)}(s) = x, z(s) = \mathbf{z}], \\ B(h) &= \mathbb{E}[f(\Upsilon^{(t)}(s+h), z(s+h)) \mathbf{1}_{\{T_1 \leq h < T_2\}} | \Upsilon^{(t)}(s) = x, z(s) = \mathbf{z}], \\ C(h) &= \mathbb{E}[f(\Upsilon^{(t)}(s+h), z(s+h)) \mathbf{1}_{\{T_2 \leq h\}} | \Upsilon^{(t)}(s) = x, z(s) = \mathbf{z}]. \end{aligned}$$

On the event $\{T_1 > h\}$, it holds that $\Upsilon^{(t)}(s+h) = x$. Further, for $(x, \mathbf{z}) \in \mathcal{S}$ and $s \in [0, t]$, let $\Lambda^{(t)}(x, \mathbf{z}, s) = \sum_{\mathbf{k}, y} \rho_{\mathbf{k}, y}^{(t)}(x, \mathbf{z}, s)$. It follows that

$$\begin{aligned} \mathbb{P}(T_1 > h | \Upsilon^{(t)}(s) = x, z(s) = \mathbf{z}) &= \int_h^{+\infty} \Lambda^{(t)}(x, z(s+t_1), s+t_1) e^{-\int_0^{t_1} \Lambda^{(t)}(x, z(s+u), s+u) du} dt_1 \\ &= e^{-\int_0^h \Lambda^{(t)}(x, z(s+u), s+u) du}, \end{aligned}$$

from which it follows by the chain rule that

$$\begin{aligned} \lim_{h \rightarrow 0^+} \frac{1}{h} (A(h) - \mathbb{P}(T_1 > h | \Upsilon^{(t)}(s) = x, z(s) = \mathbf{z}) f(x, \mathbf{z})) \\ &= \lim_{h \rightarrow 0^+} \mathbb{P}(T_1 > h | \Upsilon^{(t)}(s) = x, z(s) = \mathbf{z}) (f(x, z(s+h)) - f(x, z(s))) \\ &= \sum_{\mathbf{k}, y} \mathbf{z}_y \tau_{\mathbf{k}}(y, \mathbf{z}) \langle \nabla_{\mathbf{z}} f(x, \mathbf{z}), \mathbf{k} - e(y) \rangle. \end{aligned}$$

Let us turn to the case $\{T_1 \leq h < T_2\}$. For $\mathbf{k} \in \mathbb{N}^d$ and $y \in \mathcal{X}$, we can compute the probability that the spine is replaced by offspring \mathbf{k} and becomes of type y at T_1 , and does not reproduce anymore until time $s+h$:

$$P_{\mathbf{k}, y}^{(t)}(h) = \int_0^h \rho^{(t)}(x, z(s+t_1), s+t_1) e^{-\int_0^{t_1} \Lambda^{(t)}(x, z(s+u), s+u) du} e^{-\int_{t_1}^h \Lambda^{(t)}(y, z(s+u), s+u) du} dt_1.$$

Hence

$$\mathbb{P}(T_1 \leq h < T_2 | \Upsilon^{(t)}(s) = x, z(s) = \mathbf{z}) = \sum_{\mathbf{k}, y} P_{\mathbf{k}, y}^{(t)}(h),$$

and

$$B(h) = \sum_{\mathbf{k}, y} P_{\mathbf{k}, y}^{(t)}(h) f(y, z(s+h)).$$

In particular, $P_{\mathbf{k}, y}^{(t)}$ satisfies

$$\lim_{h \rightarrow 0^+} \frac{1}{h} P_{\mathbf{k}, y}^{(t)}(h) = \rho_{\mathbf{k}, y}^{(t)}(x, \mathbf{z}, s).$$

Thus, by continuity of z ,

$$\lim_{h \rightarrow 0^+} \frac{1}{h} (B(h) - \mathbb{P}(T_1 \leq h < T_2 | \Upsilon^{(t)}(s) = x, z(s) = \mathbf{z}) f(x, \mathbf{z})) = \sum_{\mathbf{k}, y} \rho_{\mathbf{k}, y}^{(t)}(x, \mathbf{z}, s) (f(y, \mathbf{z}) - f(x, \mathbf{z})).$$

Finally, a similar computation yields that there exists $C > 0$ such that

$$\mathbb{P}(T_2 \leq h | \Upsilon^{(t)}(s) = x, z(s) = \mathbf{z}) \leq Ch^2.$$

As $f \in \mathcal{C}^1(\mathcal{S})$ and \mathcal{S} is a closed set, f is bounded, which implies

$$\begin{aligned} |C(h) - \mathbb{P}(T_2 \leq h | \Upsilon^{(t)}(s) = x, z(s) = \mathbf{z}) f(x, \mathbf{z})| &\leq 2\|f\|_\infty \mathbb{P}(T_2 \leq h | \Upsilon^{(t)}(s) = x, z(s) = \mathbf{z}) \\ &\leq 2\|f\|_\infty Ch^2 \xrightarrow{h \rightarrow 0^+} 0. \end{aligned}$$

This concludes the proof.

C Proof of Lemma 4.7

By definition, for any $\mathbf{z} \in \mathcal{Z}$,

$$\phi(t, \mathbf{z}) = \mathbf{z} + \int_0^t \phi(\mathbf{z}, s) A(\phi(\mathbf{z}, s)) ds.$$

As $\|\mathbf{z}\|_1 \leq 1$ and A is Lipschitz continuous on \mathcal{Z} according to Assumption 4.1, it follows that $\mathbf{z} \mapsto \mathbf{z}A(\mathbf{z})$ is Lipschitz continuous as well. Thus, there exists $L > 0$ such that

$$\|\phi(s, \mathbf{z}_1) - \phi(s, \mathbf{z}_2)\|_1 \leq \|\mathbf{z}_1 - \mathbf{z}_2\|_1 + L \int_0^s \|\phi(u, \mathbf{z}_1) - \phi(u, \mathbf{z}_2)\|_1 du.$$

Hence

$$\sup_{s \in [0, t]} \|\phi(s, \mathbf{z}_1) - \phi(s, \mathbf{z}_2)\|_1 \leq \|\mathbf{z}_1 - \mathbf{z}_2\|_1 + L \int_0^t \sup_{\sigma \in [0, u]} \|\phi(\sigma, \mathbf{z}_1) - \phi(\sigma, \mathbf{z}_2)\|_1 du.$$

The conclusion follows from Gronwall's lemma.