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A branching model for intergenerational telomere length dynamics

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Abstract

We build and study an individual based model of the telomere length's evolution in a population across multiple generations. This model is a continuous time typed branching process, where the type of an individual includes its gamete mean telomere length and its age. We study its Malthusian's behaviour and provide numerical simulations to understand the influence of biologically relevant parameters.

Keywords: Telomeres dynamics; Population dynamics; Aged structured model; Branching processes; Quasi-stationary distributions.

MSC2020 Classification: 60K40; 60J80; 60J85; 60F99.

1 Introduction

Telomeres are specialized nucleoproteic structures that form protective caps at each end of eukaryotic chromosomes. They consist of non-coding repetitive nucleotide sequences associated with a family of proteins. These structures maintain genomic integrity through their capacity to prevent end-to-end chromosome fusions and chromosome extremity recognition as DNA breaks. With each cell division, part of the DNA located at telomeres' end is lost due to incomplete replication, a phenomenon known as the "end replication problem". Therefore, this leads to progressive telomere shortening in somatic cells, and in the end to critically short telomeres, which triggers replicative senescence, a state in which

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cells cease to divide Xu et al. (2013). We refer the reader to : Entringer et al. (2018) for an account on telomeres and on their length's dynamics with respect to the age of individuals, Whittemore et al. (2019) for a study of the relation between telomere length and life span across different species, and Laberthonnière et al. (2019) for a survey on the effect of telomere length on individuals health. In humans, it is acknowledged that short telomere lengths are determinants in the development of age-related diseases such as atherosclerosis Benetos et al. (2018). Telomere lengths also have a strong impact on the lifespan of an individual, but the statistical link remains unclear Gleib et al. (2016).

Somatic cells dysfunction is implicated in a large number of diseases that are suspected to arise from genomic instability or senescence, and thus potentially linked with telomere length. These cells show different phases of telomere length shortening Frenck et al. (1998). From embryonic phase up to childhood, the mean telomere length decreases strongly, while it decreases slowly in adulthood. The erosion speed is similar among adults, but the first phase is individual dependent and is influenced by many environmental factors (for instance intrauterine stress exposure Entringer et al. (2011), childhood obesity Buxton et al. (2011), exposure to violence during childhood Shalev et al. (2013)). But all these mechanisms reduce a starting length that is inherited from parents, and consequently from previous generations. Understanding the transmission of telomere lengths across generations within a population is therefore essential.

Telomere length is a highly heritable trait Hjelmberg et al. (2015); Broer et al. (2013); Honig et al. (2015) and is partially influenced by genetic factors. The telomere length of a child is strongly related to gametes' telomere lengths of the parents, particularly of the father Aviv and Susser (2013); De Meyer et al. (2007); Nordfjäll et al. (2005). Telomere lengths dynamics of male gametes are very different from those of somatic cells since they are subject to the activity of telomerase, an enzyme responsible for maintenance of the length of telomeres Zvereva et al. (2010). It results a tendency of telomere lengths in male gametes to increase with age Aviv and Susser (2013). The birth-rate as a function of age in a population is thus expected to have an influence over the evolution of telomere lengths distribution within a population. Therefore, knowing that parents in many countries are having children at an older age than half a century ago (see Figure 1), one might expect children to have longer telomeres on average. As explained in Aviv and Susser (2013), higher paternal age at conception has well-documented detrimental effects; these could be offset by beneficial effects due to telomere lengthening induced by paternity at later age. At the same time, the average length of telomeres in the population changes over relatively short time scales. A striking consequence of this fact is the difference in telomere shortening with age measured in longitudinal versus cross-sectional studies Holohan et al. (2015) and with potential implications for public health. This blurs the impact of heredity and prompts the development of models to better understand its real effect.

We propose a probabilistic process that models the evolution through generations of the size of a population as well as the average length of the telomeres of its individuals (see e.g. Bourgeron et al. (2015); Lee and Kimmel (2020); Mattarocci et al. (2021); Olofsson and Kimmel (1999) for models of telomere length's dynamic at the microscopic level). Each individual carries the telomere length of its gametes at breeding age, this does not detract

from the generality because it would be possible to obtain the average telomere length of an individual’s somatic cells at any age by applying a transfer function obtained by regression to the telomere length. The individuals are asexual; we can imagine that they are a reproductive couple of humans. This is a first model, and we do not want to introduce too much complexity. Age is the second characteristic of an individual since the length of the telomeres of the gametes depends on it. Individuals reproduce during a given period, in the context of a human couple it emulates the time between the formation of a couple, which is a sort of breeding age, and the menopause of the woman, and at a certain rate depending on age but not on the telomere length of gametes. Individuals also reproduce independently. Finally, the length of the telomeres at puberty is given by a transition function taking into account age and simulating the action of telomerase on the telomeres of gametes. We will specify its choice later.

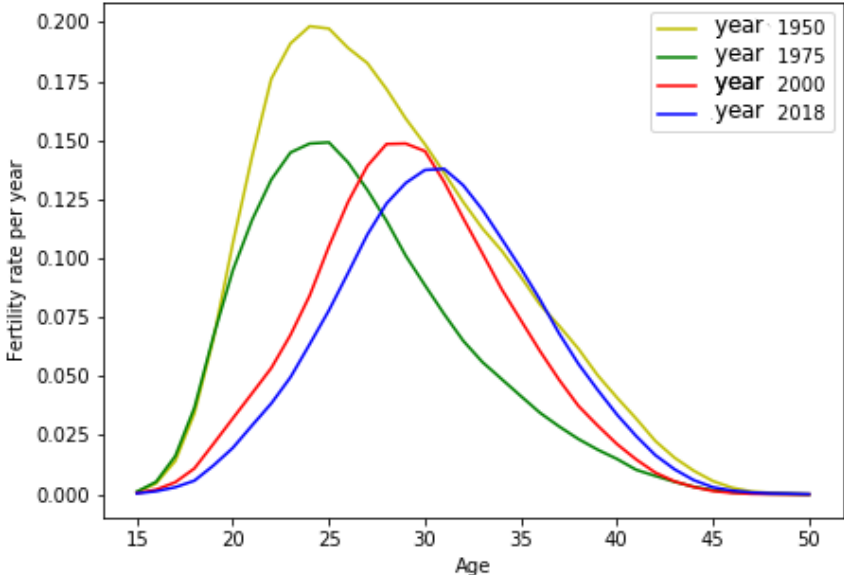


Figure 1: Birth-rate as a function of age in 1950, 1975, 2000 and 2018 (INSEE)

Mathematically speaking, the model is a Crump Mode Jagers typed branching process with age (abbreviated CMJ) which is a generalization of the age dependent branching processes described in (Harris, 1963, Chapter VI). We refer the reader to Jagers and Nerman (1984) (age structured branching processes without types) and Jagers (1989) (age structured branching processes with types) for an introduction; Olofsson (2009) provides refined convergence results and Bertoin (2017) a construction in a growth fragmentation setting. In these branching models, one considers the genealogy of the population, each individual being marked by its type (say s_i for individual i) and its birth time (say t_i), as represented in Figure 2. The age of an individual is denoted by $a \in [0, +\infty)$ and evolves linearly in time; the mean telomere length of its gametes, abbreviated by GTL, is designated

by $l \in [0, +\infty]$. The breeding age $a_p > 0$ is assumed to be fixed across the population. The birth rate is a function of age $b : [0, +\infty) \mapsto [0, +\infty)$ satisfying $b(a) = 0$ for $a < a_p$ (see Figure 1). With these notations, the dynamics describe right above reads as follows. Each alive individual in the population gives birth to one new individual at random times, independently from each others and from their GTL at puberty at rate $b(a)$ at age a . The GTL of an individual at age $a \geq a_p$ grows linearly with time, with a fixed slope $\alpha > 0$, so that it is given by $(a - a_p)\alpha$. When a newborn appears in the population, its initial age is 0 and its GTL at puberty parameter is chosen randomly, depending on the GTL of its parent at the time of birth, denoted by GTL_b . It follows a truncated Gaussian distribution with mean $GTL_b - \mu$, $\mu > 0$ being the mean erosion of telomeres during the pregnancy/childhood phase, and variance $\sigma^2 > 0$; truncation occurs in the interval $[l_{min}, l_{max}]$, where $l_{min} > 0$ and $l_{max} > 0$ are respectively the minimal and maximal length of any individual. Finally, we suppose that each individual dies at a same age $a_d > a_p$ (this last assumption could be weakened, at the expense of additional technicalities). Of course, one can represent the

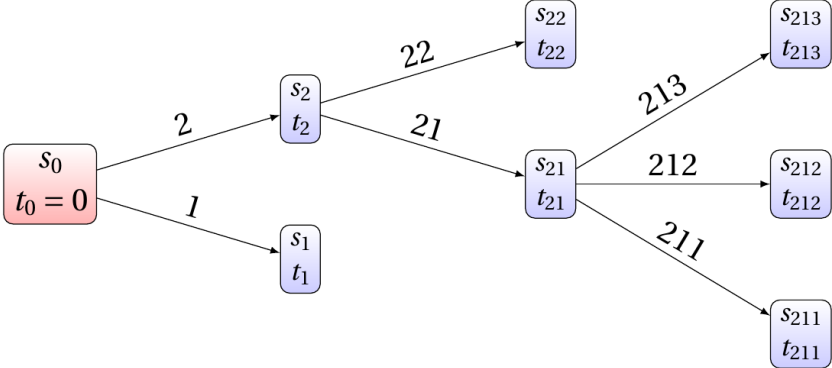


Figure 2: Example of a CMJ branching process.

process by unfolding the genealogy along the time dimension, as done in Figure 3.

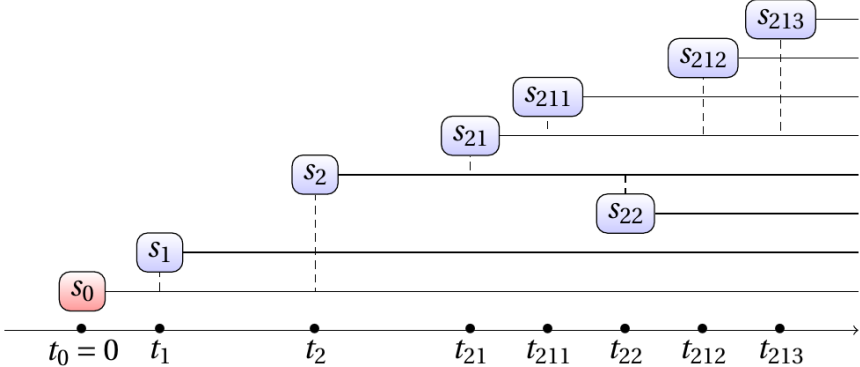


Figure 3: Same CMJ process but unfolded along a time axis.

We provide theoretical results and illustrative numerical experimentations. The first main theoretical result is a many-to-one formula for CMJ branching processes, where

we show that the potential kernel of those models can be represented via two different Feynman-Kac formulas whose equivalence relies on a simple and classical, yet powerful, argument : their associated semi-groups have the same infinitesimal generators Pazy (1983). The second relevant result concerns some spectral properties of the non-conservative semi-group involved : it converges exponentially fast to a ground state, thanks to some recent results on quasi-stationary distributions Champagnat and Villemonais (2016). At the end, it gives a representation of the Malthusian parameter of the model. These theoretical results are independent of the choices of the parameters b , α , μ , σ , l_{min} , l_{max} and a_d , and they apply to more general CMJ branching processes.

In numerical simulations, the birth-rate function b is chosen according to Figure 1, $\alpha = 0.017$ (a value justified in Aviv and Susser (2013)), $l_{min} = 5$ kb and $l_{max} = 25$ kbp (the quantity 1 kbp corresponds to a length of DNA of one thousand base pairs), and $\sigma = 0.1$ (this is chosen so that the standard deviation in the whole population is of the same order as in De Meyer et al. (2007) for the telomere length distribution in their cohort of male adults), although different measurements may be relevant. Different values of μ and shifted birth rate functions (corresponding to shifts in the parental reproduction age) are considered, and we observe qualitatively the changes implied by these perturbations on the equilibrium (long time) distribution of telomeres in the population, and on the relations between telomere length distribution, father age at birth and parental birth year.

In Section 2.1, we introduce the CMJ branching process that models the behavior of the GTL in a population. Then we state in Section 2.2 a Feynman-Kac representation (via a many-to-one formula) of the potential kernel of our branching process under a Poisson branching time assumption. Another many-to-one formula related to a different Feynman-Kac representation of the potential kernel is stated in Section 2.3. The exponential convergence of these non-conservative semi-groups is given in Section 3. Finally, we present numerical simulations to illustrate the effect of changes in μ and of the right shift of the birth-rate curves on the GTL distribution in a population (see Section 4).

Notations : \mathbb{R}_+ denotes the set of non-negative real numbers, $\mathcal{M}_P(E)$ the set of finite discrete measures on E , and $\|\cdot\|_{TV}$ the total variation distance between measures. As usual, for a mathematical object x belonging to a set X , δ_x stands for the Dirac mass at x .

2 Definition of the model and many-to-one formulas

2.1 Definition of the model

We define an age-dependent branching process with a type belonging to a Polish space \mathbb{S} . Each individual is represented by an atom $\delta_{s,t}$, where $s \in \mathbb{S}$ is the type of the individual and $t \in \mathbb{R}_+$ is the birth date of the individual. The n^{th} generation is a finite discrete measure on $\mathbb{S} \times \mathbb{R}_+$, denoted by $X_n \in \mathcal{M}_P(\mathbb{S} \times \mathbb{R}_+)$.

Remark 1. In the introduction and in our simulations section, $\mathbb{S} = [l_{min}, l_{max}]$. However, it may be desirable to include additional traits in the type space, that may be transmitted

from parents to childrens or shared among brotherhood, for instance the social environment, childhood exposition to violence, ethnicity or genetic diseases.

Let $b : \mathbb{S} \times \mathbb{R}_+ \rightarrow \mathbb{R}_+$ be a measurable, compactly supported and bounded function and γ a continuous probability kernel from $\mathbb{S} \times \mathbb{R}_+$ to \mathbb{S} . In our model, $b(s_0, a)$ represents the reproduction rate for an individual with type s_0 and age a , and $\gamma_{s_0, a}(ds)$ is the type's law of a child born from a father with type s_0 and age a . Said differently, we denote by P_{s_0} the law of a Poisson point process in $\mathbb{S} \times \mathbb{R}_+$, with intensity $b(s_0, a)\gamma_{s_0, a}(ds) da$, and assume that the progeny's distribution of an individual with type $s_0 \in \mathbb{S}$ at time 0 is given by P_{s_0} .

The branching process is constructed recursively, generation after generation. Let $X_0 = \delta_{s_0, 0}$ be a fixed punctual measure representing the original state of the population at time 0, constituted of one individual with type s_0 and birth date 0. Assuming that $X_n = \sum_{i=1}^{\overline{X_n}} \delta_{s_i^n, t_i^n}$, where $\overline{X_n} := X_n(\mathbb{S} \times \mathbb{R}_+)$ is the number of individuals in generation n , we define

$$X_{n+1} = \sum_{i=1}^{\overline{X_n}} \theta_{t_i^n} \circ \xi_{s_i^n}^{n+1},$$

where the $\xi_{s_i^n}^{n+1}$, $1 \leq i \leq \overline{X_n}$, $i < \infty$, are random independent discrete measures with respective laws $P_{s_i^n}$, and where, for all $(s_1, t_1), \dots, (s_k, t_k) \in \mathbb{S}$ and all $t \in \mathbb{R}_+$,

$$\theta_t \circ \sum_{i=1}^k \delta_{s_i, t_i} := \sum_{i=1}^k \delta_{s_i, t_i + t}.$$

Informally, $X_n(A \times B)$ should be interpreted as the number of individuals of the n^{th} generation, with type in A and with birth date in B .

We emphasize that, since b has compact support and is bounded, each random measure X_n can be written under the form

$$X_n = \sum_{i=1}^{\overline{X_n}} \delta_{s_i^n, t_i^n},$$

where $\overline{X_n} < +\infty$ and $t_1^n < t_2^n < \dots$. Given $s_0 \in \mathbb{S}$, we denote by $\mathbb{P}_{(s_0, t_0)}$ the law of $(X_n)_{n \in \mathbb{Z}_+}$ when $X_0 = \delta_{(s_0, t_0)}$ almost surely, and by $\mathbb{E}_{(s_0, t_0)}$ the corresponding expectation.

Following (Jagers, 1989, Section 5), we define the *reproduction kernel* μ from $\mathbb{S} \times \mathbb{R}_+$ to $\mathbb{S} \times \mathbb{R}_+$ as

$$\mu(s, A \times B) = \int_{\mathcal{M}_P(\mathbb{S} \times \mathbb{R}_+)} \xi(A \times B) P_s(d\xi), \quad s \in \mathbb{S}, A \in \mathcal{B}(\mathbb{S}), B \in \mathcal{B}(\mathbb{R}_+).$$

Hence, given an individual with type $s \in \mathbb{S}$ at time 0, the quantity $\mu(s, A \times B)$ gives the mean number of its children whose type are in A and whose birth date is in B . We also define the iterates of μ as $\mu^0(s, \cdot) = \delta_{(s, 0)}$ and, by iteration,

$$\mu^{n+1}(s, A \times B) = \int_{\mathbb{S} \times \mathbb{R}_+} \mu(r, A \times (B - u)) \mu^n(s, dr \times du).$$

Since this is not stressed out in Jagers (1989), we give a short proposition giving the meaning of μ^n in terms of the composition X_n of the population at generation n : $\mu^n(s, A \times B)$ gives the mean number of individuals of the n^{th} generation whose type is in A and whose birth date is in B .

Proposition 1. *For all $n \in \mathbb{Z}_+$, all $s_0 \in \mathbb{S}$ and all measurable sets $A \subset \mathbb{S}$ and $B \subset \mathbb{R}_+$, we have*

$$\mathbb{E}_{(s_0,0)} [X_n(A \times B)] = \mu^n(s_0, A \times B).$$

Proof. We show this result by iteration over n . The cas $n = 0$ is immediate. Assume now that the property holds true for $n \in \mathbb{Z}_+$. Then, by definition of X_{n+1} ,

$$\mathbb{E} \left(X_{n+1}(A \times B) \mid X_n = \sum_{i=1}^{\overline{X_n}} \delta_{s_i^n, t_i^n} \right) = \sum_{i=1}^{\overline{X_n}} \int_{\mathcal{M}_P(\mathbb{S} \times \mathbb{R}_+)} \theta_{t_i^n} \circ \xi(A \times B) P_{s_i^n}(d\xi).$$

Taking the expectation and using the induction assumption, we obtain

$$\begin{aligned} \mathbb{E}(X_{n+1}(A \times B)) &= \int_{\mathbb{S} \times \mathbb{R}_+} \int_{\mathcal{M}_P(\mathbb{S} \times \mathbb{R}_+)} \theta_u \circ \xi(A \times B) P_r(d\xi) \mu^n(s_0, dr \times du) \\ &= \int_{\mathbb{S} \times \mathbb{R}_+} \int_{\mathcal{M}_P(\mathbb{S} \times \mathbb{R}_+)} \xi(A \times (B - u)) P_r(d\xi) \mu^n(s_0, dr \times du) \\ &= \int_{\mathbb{S} \times \mathbb{R}_+} \mu(r, A \times (B - u)) \mu^n(s_0, dr \times du) \\ &= \mu^{n+1}(s, A \times B). \end{aligned}$$

□

Similarly, for any $\lambda \in \mathbb{R}$, we define as in Jagers and Nerman (1984) the kernel μ_λ as

$$\mu_\lambda(r, ds \times du) = e^{-\lambda u} \mu(r, ds \times du),$$

$\mu_\lambda^0(s, \cdot) = \delta_{(s,0)}$ and, iteratively,

$$\mu_\lambda^{n+1}(s, A \times B) = \int_{\mathbb{S} \times \mathbb{R}_+} \mu_\lambda(r, A \times (B - u)) \mu_\lambda^n(s, dr \times du).$$

The proof of the following result is similar to the previous one and is thus left to the reader.

Proposition 2. *For all $\lambda \in \mathbb{R}$, $n \in \mathbb{Z}_+$, all $s_0 \in \mathbb{S}$ and all measurable sets $A \subset \mathbb{S}$ and $B \subset \mathbb{R}_+$, we have*

$$\mathbb{E}_{(s_0,0)} \left[\sum_{i=1}^{\overline{X_n}} \delta_{s_i^n, t_i^n} e^{-\lambda t_i^n} \right] = \mu_\lambda^n(s_0, A \times B).$$

2.2 Many-to-one formula for Poissonian reproduction times

The aim of this section is to provide a first many-to-one formula, which allows to express the potential kernel (which involves expectations over *many* individuals) as a Feynman-Kac type expression (which only involves *one* trajectory).

In order to do so, we consider the piecewise-deterministic Markov process $(Z_t)_{t \in [0, +\infty)}$ with values in $\mathbb{S} \times \mathbb{R}_+$, which evolves according to the flow $((s_0, a), t) \mapsto (s_0, a + t)$ and, at a rate $b(Z_t)$, jumps according to the probability measure $\gamma_{Z_t}(ds) \otimes \delta_0(da)$. We refer the reader to Davis (1984, 1993); Azaï s et al. (2014) for general aspects of the theory of piecewise-deterministic Markov processes. We denote respectively by $Z_t^{(s)}$ and by $Z_t^{(a)}$ the first and second component of Z_t , respectively in \mathbb{S} and \mathbb{R}_+ . The component $Z_t^{(a)}$ should be interpreted as the age of an individual (since the last jump), so that $t - Z_t^{(a)}$ is the birth date of the individual (that is the last jump time before time t). In what follows, the law of Z with initial position $(s, t) \in \mathbb{S} \times \mathbb{R}_+$ is denoted by $\mathbb{P}_{s,t}^Z$ and its associated expectation $\mathbb{E}_{s,t}^Z$.

Following Jagers (1989), we consider the potential kernel v , defined by

$$v(s, A \times B) = \sum_{n=0}^{\infty} \mu^n(s, A \times B),$$

for all $s \in \mathbb{S}$ and all measurable subsets $A \subset \mathbb{S}$ and $B \subset \mathbb{R}_+$. The following many-to-one formula is the main result of this section.

Proposition 3. *We have, for all $t \geq 0$, all $s_0 \in \mathbb{S}$ and all measurable sets $A \subset \mathbb{S}$ and $B \subset \mathbb{R}_+$,*

$$v(s_0, A \times (B \cap [0, t])) = \mathbb{E}_{s_0,0}^Z \left[\mathbf{1}_{Z_t^{(s)} \in A, t - Z_t^{(a)} \in B} \exp \left(\int_0^t b(Z_u) du \right) \right].$$

The proof of this proposition is postponed to Section A.3. Our proof's strategy is first to represent v as the expectation with respect to a process exploring a random branch of the model (see next section), and second to prove that both representations coincide.

We also define, for all $\lambda \in \mathbb{R}$, $v_\lambda = \sum_{n=0}^{\infty} \mu_\lambda^n$ and obtain the following corollary.

Corollary 1. *We have, for all $\lambda \in \mathbb{R}$, all $t \geq 0$ and all $s_0 \in \mathbb{S}$,*

$$v_\lambda(s_0, \mathbb{S} \times [0, t]) = e^{-\lambda t} \mathbb{E}_{s_0,0}^Z \left(e^{\lambda Z_t^{(a)}} e^{\int_0^t b(Z_u) du} \right)$$

2.3 Random exploration of a CMJ branch

We describe now a continuous time random process $(Y_t)_{t \in [0, +\infty)}$ which explores randomly a branch of the generation tree of a CMJ branching process. This process takes values in $\mathbb{X} := \mathbb{S} \times \mathbb{R}_+ \times \mathcal{M}_P(\mathbb{S} \times \mathbb{R}_+)$, the first component corresponding to the type of the current individual, the second component is the age of the current individual, and the third one is the total progeny of the current individual (starting at its birth time). Informally, the process Y starts at the ancestor position (which includes its type, its birth time, and its progeny) at time 0 and stays idle up to the first reproduction time. Then it either jumps

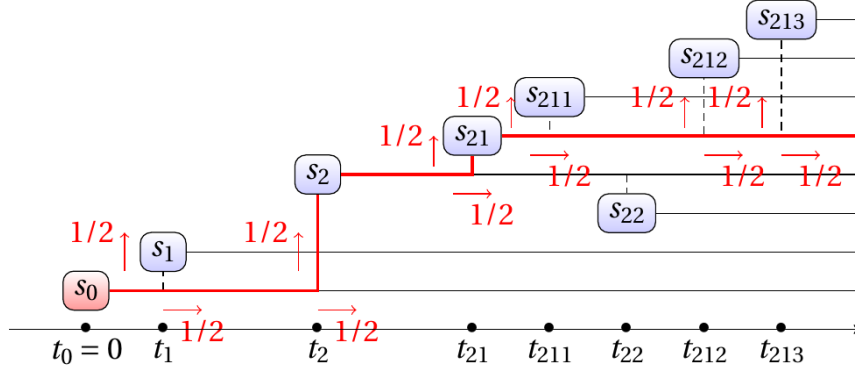


Figure 4: Example of a trajectory of the process Y : at each reproduction time, the process chooses one of the branches with probability $1/2$.

on the position of the newborn (with probability $1/2$), or it remains at its position (with probability $1/2$). Then it stays at the same position up to the next reproduction time and so on (see Figure 4).

Let us now define more formally the process Y . Let $\tau : \mathbb{X} \rightarrow \mathbb{R}_+$ and $\Lambda : \mathbb{X} \rightarrow \mathbb{S}$ be defined, for all $(s, a, \xi) \in \mathbb{X}$, by

$$\tau(s, a, \xi) = \inf\{t > 0, \xi(\mathbb{S} \times (a, a + t]) = 1\}$$

and

$$\Lambda(s, a, \xi) = l \text{ such that } \xi\{(l, \tau(s, a, \xi))\} = 1,$$

with the convention $\inf \emptyset = +\infty$ and, if $\tau(s, a, \xi) = +\infty$, $\Lambda(s, a, \xi) = s$. Informally, $\tau(s, a, \xi)$ gives the first reproduction time after time a , while $\Lambda(s, a, \xi)$ gives the type of the then born child. Now let Π_0 and Π_1 be two probability kernels defined by

$$\begin{aligned} \Pi_0 : \mathbb{X} \times \mathcal{X} &\rightarrow [0, 1] \\ ((s, a, \xi), A \times B \times C) &\mapsto \delta_{(s, a + \tau(s, a, \xi), \xi)}(A \times B \times C) \end{aligned}$$

and

$$\begin{aligned} \Pi_1 : \mathbb{X} \times \mathcal{X} &\rightarrow [0, 1] \\ ((s, a, \xi), A \times B \times C) &\mapsto \delta_{\Lambda(s, a, \xi), 0}(A \times B) P_{\Lambda(s, a, \xi)}(C), \end{aligned}$$

where \mathcal{X} is the product σ -field on \mathbb{X} and we recall that P_s is the law of the progeny of an individual with type $s \in \mathbb{S}$. On the one hand, given (s, a, ξ) , $\Pi_0(s, a, \xi)$ is a Dirac measure at $(s, a + \tau(s, a, \xi), \xi)$ and will be used as the jump kernel in the event where Y remains on the father's branch at the reproduction time $a + \tau(s, a, \xi)$. On the other hand, $\Pi_1(s, a, \xi)$ will be used as the jump kernel when Y jumps on the branch of the new-born, since $\Lambda(s, a, \xi)$ is the type of the child, 0 is its age at the time of birth, and $P_{\Lambda(s, a, \xi)}$ is the law of its progeny.

We first define the included chain of Y at jump times, denoted by $(\sigma_k, W_k)_{k \geq 0}$, where σ_k denotes the k^{th} jump time, while W_k denotes the k^{th} position after the jump (note that the size of a jump might be 0 if the process remains on the father's branch). Let $(\sigma_0, W_0) \in \mathbb{R}_+ \times \mathbb{X}$ and define the process iteratively as follows. Given (σ_k, W_k) , $k \geq 0$,

- we set $\sigma_{k+1} = \sigma_k + \tau(W_k)$,
- we choose W_{k+1} according to $\Pi_{\varepsilon_{k+1}}(W_k, \cdot)$, where ε_{k+1} is a Bernoulli random variable with parameter $1/2$ independent from the rest of the process.

If $\sigma_{k+1} = +\infty$, then the Markov chain is stopped. We then formally define $(Y_t)_{t \in [0, +\infty)}$ as

$$Y_t = \sum_{k=0}^{+\infty} \mathbf{1}_{\sigma_k \leq t < \sigma_{k+1}} \vartheta_{t-\sigma_k} W_k,$$

where, for all $u \in \mathbb{R}_+$ and $(s, a, \xi) \in \mathbb{X}$, $\vartheta_u(s, a, \xi) = (s, a + u, \xi)$. Note that the first component of Y_t represents the current individual's type, the second component its age at time t , and the third component its progeny.

We also define the process $(N_t)_{t \geq 0}$ counting the number of jumps

$$N_t = \sum_{k=1}^{+\infty} \mathbf{1}_{\sigma_k \leq t}.$$

Note that, since b is assumed to be bounded, we have

$$\sigma_n \xrightarrow[n \rightarrow +\infty]{} +\infty \quad \text{almost surely.}$$

We define the filtration $(\mathcal{G}_t)_{t \geq 0}$ by

$$\mathcal{G}_t = \sigma((\sigma_k \leq t < \sigma_{k+1}) \cap A, \text{ where } k \geq 0 \text{ and } A \in \sigma(W_0, W_1, \dots, W_k)).$$

Proposition 4. *The process (N, Y) is a Markov process with respect to the filtration \mathcal{G} . More precisely, for all $f \in L^\infty(\mathbb{Z}_+ \times \mathbb{X})$ and all $t, u \geq 0$,*

$$\mathbb{E}(f(N_{t+u}, Y_{t+u}) \mid \mathcal{G}_t) = Q_u f(N_t, Y_t)$$

where Q is the semi-group¹ associated to the process (N, Y) , and is equal to

$$Q_u f(k, y) = \mathbf{1}_{u < \tau(Y_t)} f(N_t, \vartheta_u Y_t) + \sum_{j=0}^{+\infty} \int_{\mathbb{X}} \Pi(Y_t, dw) \mathbb{E}_{\tau(Y_t), w}^{\sigma, W} \left(\mathbf{1}_{\sigma_j \leq t+u < \sigma_{j+1}} f(N_t + 1 + j, \vartheta_{u-\sigma_j} W_j) \right),$$

with $\Pi = \frac{1}{2}\Pi_0 + \frac{1}{2}\Pi_1$ and where $\mathbb{E}_{\sigma_0, W_0}^{\sigma, W}$ denotes the expectation with respect to the law of $(\sigma_k, W_k)_k$ starting from (σ_0, W_0) .

The proof of Proposition 4 is detailed in Section A.1. We emphasize that it does not make direct use of the Poissonian nature of the jump mechanism.

In the construction of Y , and more precisely for the construction of (σ_k, W_k) , we use a sequence of independent Bernoulli random variables $(\varepsilon_k)_{k \geq 0}$, which encodes the choice of Y to remain on the father's branch ($\varepsilon_k = 0$) or to continue on the child's branch ($\varepsilon_k = 1$) at each time σ_k . The following result gives a representation of μ^n in terms of (N, Y) . In the following proposition, $Y_t^{(s)}$ and $Y_t^{(a)}$ denote respectively the first and second component of Y_t , with value in \mathbb{S} and \mathbb{R}_+ respectively. In particular, since $Y_t^{(a)}$ should be interpreted as the age of the individual chosen by Y at time t , the quantity $t - Y_t^{(a)}$ corresponds to its birth date.

¹by a semi-group, we mean that $Q_{s+t} = Q_s Q_t$ for all $s, t \geq 0$.

Proposition 5. For all measurable sets $A \subset \mathbb{S}$ and $B \subset \mathbb{R}_+$ and all $n \in \mathbb{Z}_+$, we have, for all $t \geq 0$ and all $s_0 \in \mathbb{S}$,

$$\mu^n(s_0, A \times (B \cap [0, t])) = \int_{\mathcal{M}_P(\mathbb{S} \times \mathbb{R}_+)} P_{s_0}(d\xi) \mathbb{E}_{s_0, 0, \xi}^Y \left(\mathbf{1}_{Y_t^{(s)} \in A, t - Y_t^{(a)} \in B} 2^{N_t} \mathbf{1}_{\sum_{i=1}^{N_t} \varepsilon_i = n} \right),$$

where $\mathbb{E}_{s_0, 0}^Y$ denotes the expectation with respect to the law of Y when the law of Y_0 is $\delta_{s_0} \otimes \delta_0 \otimes \mathbb{P}_{s_0}^J$. In particular,

$$v(s_0, A \times B) = \int_{\mathcal{M}_P(\mathbb{S} \times \mathbb{R}_+)} P_{s_0}(d\xi) \mathbb{E}_{s_0, 0, \xi}^Y \left(\mathbf{1}_{Y_t^{(s)} \in A, t - Y_t^{(a)} \in B} 2^{N_t} \right).$$

The proof of Proposition 5 is detailed in Section A.2. As the proof of Proposition 4, it does not make direct use of the Poissonian nature of the jump mechanism.

3 Malthusian properties of the associated semi-group of operators

In this section, we check that our model defines a *Malthusian process*, as coined by Olofsson Olofsson (2009). For the sake of simplicity, we assume in this section that \mathbb{S} is compact, and that there exists $b_m < b_M \in \mathbb{R}_+$ such that $b(s, a)$ is positive for all $(s, a) \in \mathbb{S} \times [b_m, b_M]$. We also assume that, for all $s_0, a_0 \in \mathbb{S} \times \mathbb{R}_+$, γ_{s_0, a_0} admits a positive density with respect to a reference measure π on \mathbb{S} , denoted by $g_{s_0, a_0}(s) \in (0, +\infty)$ at point s , and which is continuous with respect to $(s_0, s, a_0) \in \mathbb{S}^2 \times \mathbb{R}_+$.

The Malthusian parameter associated to the process X (see (Jagers, 1989, Section 5)) is given by

$$\alpha := \inf \{ \lambda \in \mathbb{R}, \text{ such that } v_\lambda(s, \mathbb{S} \times \mathbb{R}_+) < +\infty \text{ for some } s \in \mathbb{S} \}.$$

Defining the semi-group $(R_t)_{t \geq 0}$ by

$$\delta_{(s_0, a_0)} R_t := \mathbb{E}_{(s_0, a_0)} \left(\mathbf{1}_{Z_t \in \cdot} \exp \left(\int_0^t b(Z_u) du \right) \right), \quad \forall (s_0, a_0) \in \mathbb{S} \times \mathbb{R}_+,$$

we prove that α is equal to the leading eigenvalue $-\lambda_0$ of the semi-group $(R_t)_{t \geq 0}$ when λ_0 is negative. We first state some spectral properties of R , including the existence of λ_0 , related to the theory of quasi-stationary distributions (we refer the reader to Collet et al. (2013); van Doorn and Pollett (2013); Méléard and Villemonais (2012) for general references to quasi-stationary distributions). The proof of the following result is postponed to Section B.1.

Theorem 1. Under the above assumptions, there exists a non-negative measurable function $\eta : \mathbb{S} \times \mathbb{R}_+ \rightarrow \mathbb{R}_+$, constants $\lambda_0 \in \mathbb{R}$, $\lambda_1 \in (0, +\infty)$, $C > 0$ and a probability measure Υ on $\mathbb{S} \times \mathbb{R}_+$ such that, for all $t \geq 0$ and all $(s_0, a_0) \in \mathbb{S} \times \mathbb{R}_+$,

$$\left\| e^{\lambda_0 t} \delta_{(s_0, a_0)} R_t - \eta(s_0, a_0) \Upsilon \right\|_{TV} \leq C e^{-\lambda_1 t}.$$

Moreover, if $\lambda_0 < 0$, the Malthusian parameter α of the branching process X equals $-\lambda_0$.

Remark 2. The proof of Theorem 1 can be adapted to a more general setting (for instance with \mathbb{S} not compact, or $b(s, \cdot)$ positive on a segment that depends on s), at the expense of additional technicalities both in the presentation of the assumptions and in the proofs.

For any measurable function $f : \mathbb{S} \times \mathbb{R}_+ \rightarrow \mathbb{R}$ and all $t \geq 0$, we define the function

$$f_t(s_0, a_0) = \mathbf{1}_{a_0 \leq t} f(s_0, t - a_0),$$

so that, if s_0 and a_0 are respectively the type and the birth time of one individual, the number $f_t(s_0, a_0)$ is the function f of the type and age of the individual at time t . This is similar to the χ -counted population introduced in Section 7 of Jagers (1989). The next result thus describes the evolution of the expectation of the types and ages distribution across the population and is an immediate corollary of Theorem 1 and Proposition 3 (recall that X_n denotes the empirical measure of types and ages in the population at generation n). In particular, in this situation, it shows that the population size evolves exponentially fast with exponential parameter $-\lambda_0$ and that the telomere length distribution across the population converges to a limit which does not depend on the initial distribution of the population ages and telomere lengths.

Corollary 2. *For all bounded measurable function $f : \mathbb{S} \times \mathbb{R}_+ \rightarrow \mathbb{R}$ and all $t \geq 0$,*

$$\mathbb{E}_{(s_0, a_0)} \left(\sum_{n \geq 0} X_n(f_t) \right) = \delta_{(s_0, a_0)} R_t f.$$

In particular, for all $s_0 \in \mathbb{S}$,

$$\left| e^{\lambda_0 t} \mathbb{E}_{(s_0, a_0)} \left(\sum_{n \geq 0} X_n(f_t) \right) - \eta(s_0, a_0) Y(f) \right| \leq C e^{-\lambda_1' t} \|f\|_\infty,$$

where λ_0, Y are from Theorem 1 and for some constants $C, \lambda_1' > 0$.

We expect that $e^{-\lambda_0 t} \sum_{n \geq 0} X_n(f_t)$ converges almost surely toward $\eta(s_0, a_0) Y(f)$ times a non-negative random variable. This type of results is classical in the setting of multi-types branching processes and for branching processes with irreducible reproduction measure (see for instance Olofsson (2009)). The extension of these results to the situation at hand (where the reproduction measure is allowed to be reducible) is the subject of an ongoing work.

4 Numerical simulations

We analyze numerically the influence of the attrition parameter μ and the birth rate curve on the limit distribution Y , and on the dynamic of the telomere length distribution across the population. We set: $\mathbb{S} = [l_{\min}, l_{\max}]$, where $l_{\min} = 5$ kbp and $l_{\max} = 25$ kbp; $\alpha = 0.017$;

$$\gamma_{(s_0, a)}(ds) = c_\gamma \mathbf{1}_{s \in [l_{\min}, l_{\max}]} \exp \left(-\frac{(s - (s_0 + (a - a_p)\alpha - \mu))^2}{2\sigma^2} \right) ds, \quad \forall (s_0, a) \in \mathbb{S} \times \mathbb{R}_+ \rightarrow \mathbb{R}_+,$$

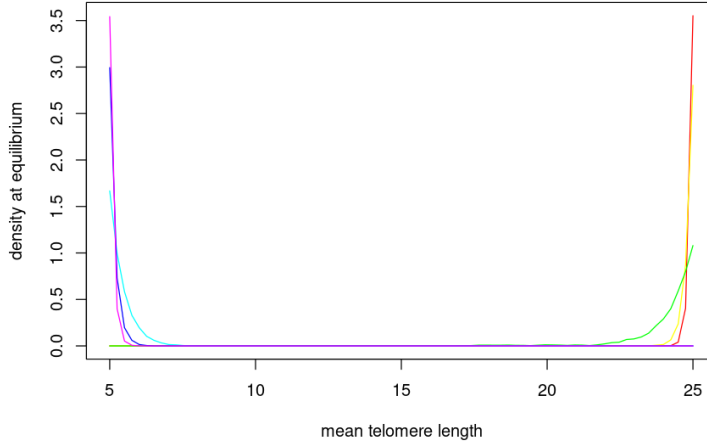


Figure 5: Density of the telomere's length distribution for values of μ in $\{8\alpha, 10\alpha, 12\alpha, 14\alpha, 16\alpha, 18\alpha\}$, where $\alpha = 0.017$ is fixed ($\mu = 8\alpha$ corresponds to the rightmost curve and $\mu = 18\alpha$ to the leftmost curve).

where $\sigma = 0.1$, $c_\gamma = 1 / \int_{l_{\min}}^{l_{\max}} e^{-\frac{(u-\mu)^2}{2\sigma^2}} du$ and $\mu = 20\alpha$ (different values of μ in $\{0, \dots, 25\alpha\}$ will also be considered); and

$$b(a) = b_0(a + s_f), \forall a \geq 0,$$

where b_0 is chosen according to the demographical empirical curve of year 1960 (see Figure 1) and $s_f = 0$ is a shift parameter (different values of s_f in $[-10, 10]$ will be considered).

We first investigate the influence of the parameters μ (see Figure 5) and s_f (see Figure 6) on the long time limiting distribution Y (see Theorem 1), which should be interpreted as the equilibrium telomere length distribution. As expected, a higher attrition before reproduction age (i.e. a higher parameter μ) leads to lower telomere lengths in the population at equilibrium, while a higher parental age at birth (i.e. a higher parameter s_f) entails higher telomere lengths in the population at equilibrium. An important feature of the model is that the equilibrium distribution is highly concentrated on the boundaries of the admissible limits. Figure 7 (resp. Figure 8) displays the influence of μ (resp. s_f) on the population's mean telomere length at equilibrium. We observe that the influences of μ and s_f are non-linear. Depending on the parameters value, even a slight decrease in the attrition parameter μ or an increase in the parental age at birth s_f can have drastically different effects; the model displays a transition phase phenomenon, with approximate critical values $\mu = 12.5$ and $s_f = 15$.

To investigate the time evolution of the telomere length in the population, we study the speed of convergence toward the equilibrium distribution Y (see Theorem 1) and the time evolution of the mean telomere length in the population. We display the total variation distance between the population telomere length distribution at time t and the telomere

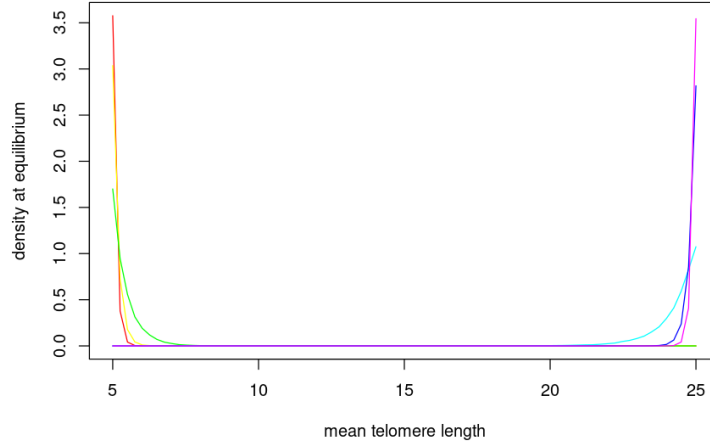


Figure 6: Density of the telomere's length distribution for values of s_f in $\{10, 12, 14, 16, 18, 20\}$ ($s_f = 10$ corresponds to the leftmost curve and $s_f = 20$ to the rightmost curve).

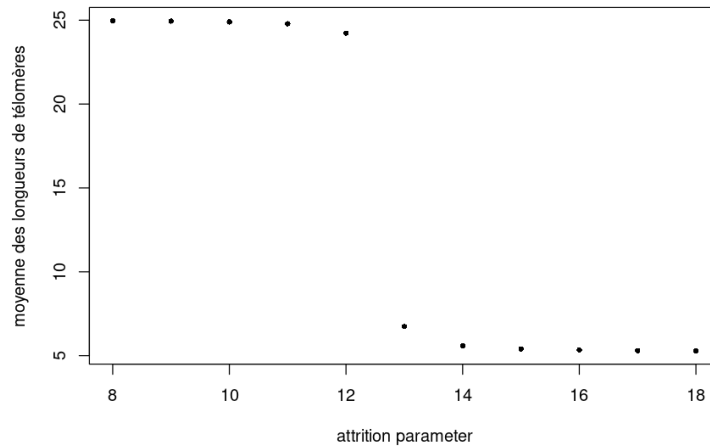


Figure 7: Population mean telomere length at equilibrium, as a function of μ/α , when μ ranges from $8 \times \alpha$ to $18 \times \alpha$, and $\alpha = 0.017$ is fixed.

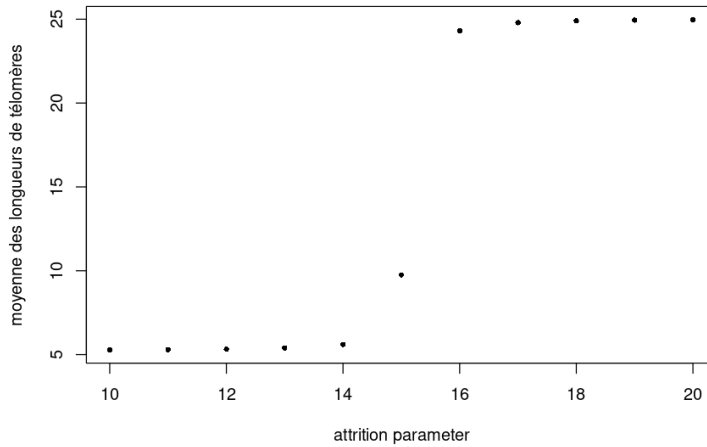


Figure 8: Population mean telomere length at equilibrium, as a function of s_f , when s_f ranges from 10 to 20.

length distribution at equilibrium, given an initial population of individuals with age 0 and telomere length 18 kbp. Figure 9 (resp. Figure 10) displays the evolution of this distance to equilibrium for different values of μ (resp. s_f). We observe that the speed of convergence to the equilibrium depends on the parameters, and that, in all cases, the convergence to equilibrium arises after several thousands years. Figure 11 (resp. Figure 12) displays the evolution of the population’s mean telomere length over time for several values of μ (resp. s_f). The mean also stabilises after several thousand years for most parameter choices, and a drift in the telomere length can be sustained for several thousand years. In such a time frame, mean attrition before reproduction and parental age at birth is subject to important changes, because of the demographic evolution.

As a result, our model suggests that the limiting distribution Υ does not materialize in a population where the parameters may change in a time window of less than one thousand year, so that, in empirical measures, the population is not observed at equilibrium, and that the drift in the population’s mean telomere length can be sustained during very long periods of time. This is coherent with the findings of Holohan et al. (2015).

Finally, we investigate the situation where the parameters μ or s_f undergo a change at some time point. Namely, we consider the situation where μ or s_f are constant for 5000 years and then shift to a new value for 1000 years. Our main focus is to study the impact of this evolution on the relations among individuals between telomere length at puberty (s_0), father age at birth (FAB), parental birth year (PBY) and birth date (BD), and to compare the behaviour of our model to the findings of Holohan et al. (2015). Figure 13 displays the evolution of the individual telomere length as a function of PBY adjusted for FAB, when $\mu = 13$ for individuals born in the time interval $[0, 5000]$ and $\mu = 16$ for individuals born in the time interval $(5000, 6000]$. Figure 14 displays the evolution of the individual telomere length as function of BD adjusted for PBY and FAB for individuals born after time 5000.

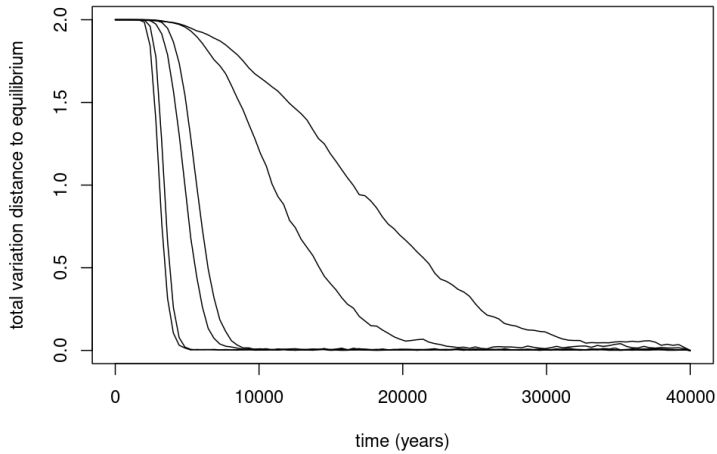


Figure 9: Total variation distance as a function of time between the population’s telomere distribution and telomere length distribution at equilibrium. Values of μ are in $\{8\alpha, 10\alpha, 12\alpha, 14\alpha, 16\alpha, 18\alpha\}$, with $\alpha = 0.017$.

Contrarily to the findings of Holohan et al. (2015), we do not observe a significant negative correlation in this last figure (different time frames do not change this fact). The negative impact of the change of μ at time 5000 does not materialize in this plot and thus our model can not support the hypothesis of Holohan et al. (2015) that an event negatively impacted the human population telomere length a century ago. This suggests that other mechanisms (either a statistical artefact or another type of demographical event) are the cause of the negative correlation found in the above cited study.

5 Conclusion

We constructed a probabilistic model representing the evolution of telomere length in a population across multiple generations. Various mathematical results, including many-to-one formulas and Perron-Frobenius type results, have allowed us to exhibit interesting properties concerning the asymptotic behaviour of the average telomere length in a population. These results were confirmed empirically by experiments in silico. In particular, we found the definite influence of the attrition parameter, as well as that of a particular modification of the reproduction rate using a time shift of the fertility curve.

We also studied the link between the length of the telomeres of individuals and the date of birth of their ancestor, adjusted by its age at the birth of the descendants. We were able to compare these numerical results with the literature. In particular, we could not confirm that an increase in the attrition parameter led to a negative correlation between telomere length and date of birth adjusted by FAB and PBY, as observed in Holohan et al. (2015). Understanding the discrepancy between the empirical and numerical datas will

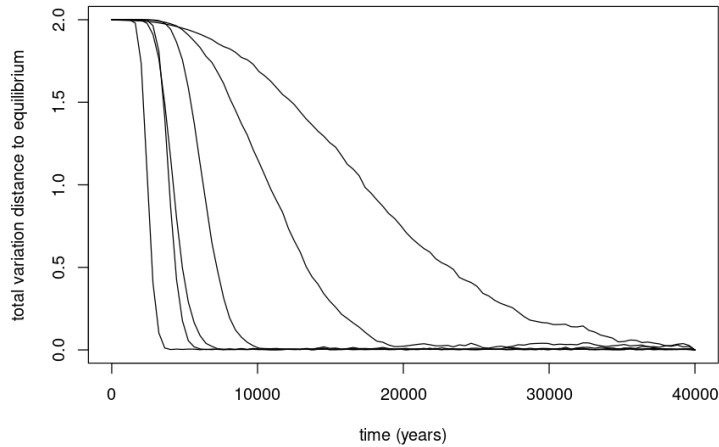


Figure 10: Total variation distance as function of time between the population's telomere length distribution and the telomere length distribution at equilibrium. Values of s_f are in $\{10, 12, 14, 16, 18, 20\}$.

require further investigations.

The proposed model contains important simplifications; it therefore appears necessary to study richer models. The integration of heterogeneity within the population with attrition factors depending on the geographical or societal environment would be more realistic, using a richer type space \mathbb{S} (see also Haccou et al. (2005) and references therein) or building a model using branching processes in random environment (see e.g. Bansaye (2009); Kaplan (1974); Keiding (1976); Kersting and Vatutin (2017); Smith and Wilkinson (1969)). Taking into account the influence of certain migratory phenomena would also be interesting (see for instance Bansaye and Méléard (2015); Kawazu and Watanabe (1971); Li (2006); Pakes (1971)). Finally, it seems essential to move towards the implementation of a bisexual model (see e.g. Daley (1968); Daley et al. (1986); Fritsch et al. (2022); González and Molina (1996); Hull (2003); Molina (2010)).

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Competing interest

The authors have no relevant financial or non-financial interests to disclose.

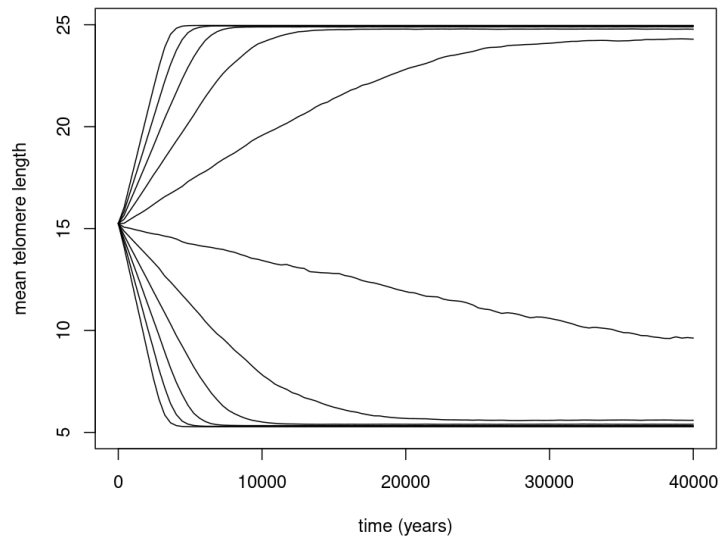


Figure 11: Population mean telomere length as a function of time, for different values of μ . The highest trajectory corresponds to $\mu = 8\alpha$ and the lowest trajectory to $\mu = 18\alpha$, with $\alpha = 0.017$.

Data availability statement

No datasets were generated or analysed during the current study.

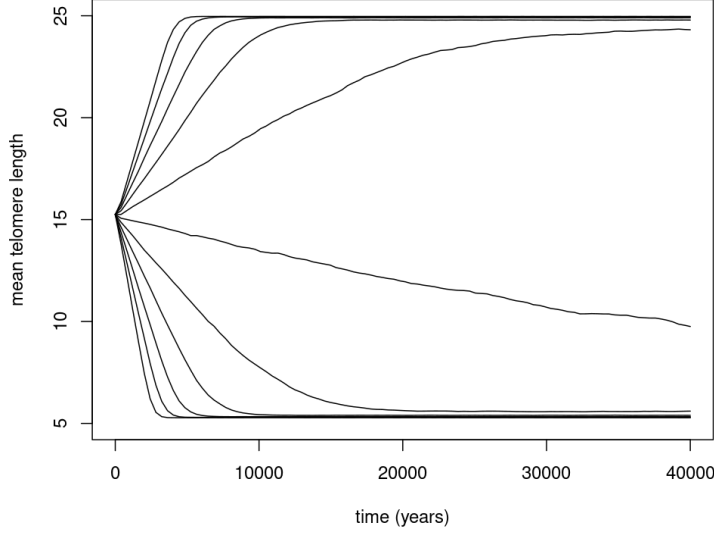


Figure 12: Population mean telomere length as a function of time, for different values of s_f . The highest trajectory corresponds to $s_f = 20$ and the lowest trajectory to $s_f = 10$.

A Proof of the results of Sections 2.2 and 2.3

We first prove Propositions 4 and 5 from Section 2.3 and conclude with Proposition 3 from Section 2.2.

A.1 Proof of Proposition 4

We have, setting $f = \mathbf{1}_{A \times B}$,

$$\mathbb{E}_{0, y_0} (f(N_{t+u}, Y_{t+u}) | \mathcal{G}_t) = \sum_{k=0}^{+\infty} \sum_{i=k}^{+\infty} \mathbb{E}_{0, y_0} (\mathbf{1}_{N_t=k} \mathbf{1}_{N_{t+u}=i} f(i, Y_{t+u}) | \mathcal{G}_t).$$

Fix $i, k \in \mathbb{Z}_+$. Assume first that $i \geq k + 1$, and set $j = i - (k + 1)$. We define the σ -algebra $\mathcal{F}_{k+1} = \sigma((\sigma_0, W_0), (\sigma_1, W_1), \dots, (\sigma_{k+1}, W_{k+1}))$. Then, for any \mathcal{G}_t -measurable non-negative random variable Z , the random variable $Z \mathbf{1}_{N_t=k}$ is \mathcal{F}_{k+1} -measurable and hence

$$\begin{aligned} & \mathbb{E}_{0, y_0} (Z \mathbf{1}_{N_t=k} \mathbf{1}_{N_{t+u}=i} f(i, Y_{t+u})) \\ &= \mathbb{E}_{0, y_0} [\mathbb{E} (Z \mathbf{1}_{N_t=k} \mathbf{1}_{N_{t+u}=i} f(i, Y_{t+u}) | \mathcal{F}_{k+1})] \\ &= \mathbb{E}_{0, y_0} [Z \mathbf{1}_{N_t=k} \mathbb{E} (\mathbf{1}_{\sigma_i \leq t+u < \sigma_{i+1}} f(i, \vartheta_{t+u-\sigma_i} W_i) | \mathcal{F}_{k+1})] \\ &= \mathbb{E}_{0, y_0} \left[Z \mathbf{1}_{N_t=k} \mathbb{E}_{\sigma_{k+1}, W_{k+1}}^W \left(\mathbf{1}_{\sigma_j \leq t+u < \sigma_{j+1}} f(i, \vartheta_{t+u-\sigma_j} W_j) \right) \right], \end{aligned}$$

where $\mathbb{E}_{u, w}^W$ is the expectation with respect to the law of $(\sigma_n, W_n)_{n \geq 0}$ when $\sigma_0 = u$ and $W_0 = w$.

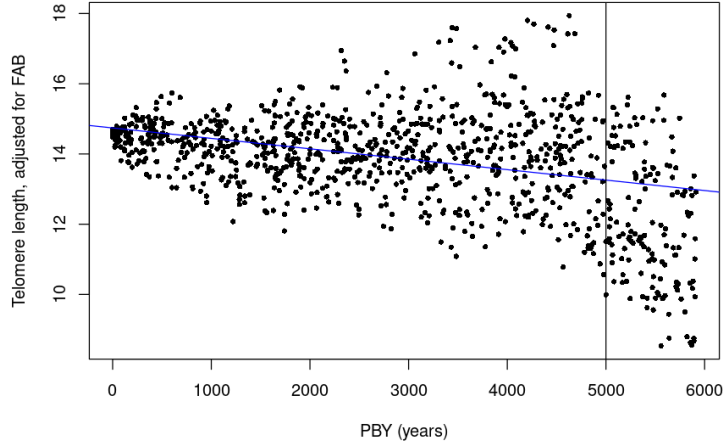


Figure 13: Sample of the population and linear regression lines for s_0 as a function of PBY adjusted for FAB, when $\mu = 13$ for individuals born in the time interval $[0, 5000]$ and $\mu = 16$ for individuals born in the time interval $(5000, 6000]$. The regression line has coefficient -2.97×10^{-4} .

w . Now, since $\sigma_{k+1} = t + \tau(Y_t)$, we have

$$\begin{aligned} & \mathbb{E}_{0, y_0} \left(Z \mathbf{1}_{N_t=k} \mathbf{1}_{N_{t+u}=i} f(i, Y_{t+u}) \right) \\ &= \mathbb{E}_{0, y_0} \left[Z \mathbf{1}_{N_t=k} \mathbb{E}_{t+\tau(Y_t), W_{k+1}}^W \left(\mathbf{1}_{\sigma_j \leq t+u < \sigma_{j+1}} f(i, \vartheta_{t+u-\sigma_j} W_j) \right) \right] \\ &= \mathbb{E}_{0, y_0} \left[Z \mathbf{1}_{N_t=k} \mathbb{E}_{\tau(Y_t), W_{k+1}}^W \left(\mathbf{1}_{\sigma_j \leq t+u < \sigma_{j+1}} f(i, \vartheta_{u-\sigma_j} W_j) \right) \right]. \end{aligned}$$

Using the fact that $W_{k+1} \sim \Pi(Y_t, \cdot)$, we deduce that

$$\mathbf{1}_{N_t=k} \mathbb{E} \left(\mathbf{1}_{N_{t+u}=i} f(i, Y_{t+u}) \mid \mathcal{G}_t \right) = \mathbf{1}_{N_t=k} \int_{\mathbb{X}} \Pi(Y_t, dw) \mathbb{E}_{\tau(Y_t), w}^W \left(\mathbf{1}_{\sigma_j \leq t+u < \sigma_{j+1}} f(i, \vartheta_{u-\sigma_j} W_j) \right).$$

Assume now that $i = k \in \mathbb{Z}_+$, so that

$$\mathbb{E} \left[\mathbf{1}_{N_t=k} \mathbf{1}_{\sigma_i \leq t+u < \sigma_{i+1}} f(i, Y_{t+u}) \mid \mathcal{G}_t \right] = \mathbf{1}_{N_t=k} \mathbf{1}_{u < \tau(Y_t)} f(k, \vartheta_u Y_t)$$

Using the last two equations, we deduce that, for all $k \geq 0$,

$$\begin{aligned} \mathbb{E} \left(\mathbf{1}_{N_t=k} f(i, Y_{t+u}) \mid \mathcal{G}_t \right) &= \mathbf{1}_{N_t=k} \left[\mathbf{1}_{u < \tau(Y_t)} f(k, \vartheta_u Y_t) \right. \\ &\quad \left. + \sum_{j=0}^{+\infty} \int_{\mathbb{X}} \Pi(Y_t, dw) \mathbb{E}_{\tau(Y_t), w}^W \left(\mathbf{1}_{\sigma_j \leq t+u < \sigma_{j+1}} f(N_t + 1 + j, \vartheta_{u-\sigma_j} W_j) \right) \right] \end{aligned}$$

Summing over $k \geq 0$, we finally obtain

$$\begin{aligned} \mathbb{E} \left(f(Y_{t+u}) \mid \mathcal{G}_t \right) &= \mathbf{1}_{u < \tau(Y_t)} f(N_t, \vartheta_u Y_t) \\ &\quad + \sum_{j=0}^{+\infty} \int_{\mathbb{X}} \Pi(Y_t, dw) \mathbb{E}_{\tau(Y_t), w}^W \left(\mathbf{1}_{\sigma_j \leq t+u < \sigma_{j+1}} f(N_t + 1 + j, \vartheta_{u-\sigma_j} W_j) \right), \end{aligned}$$

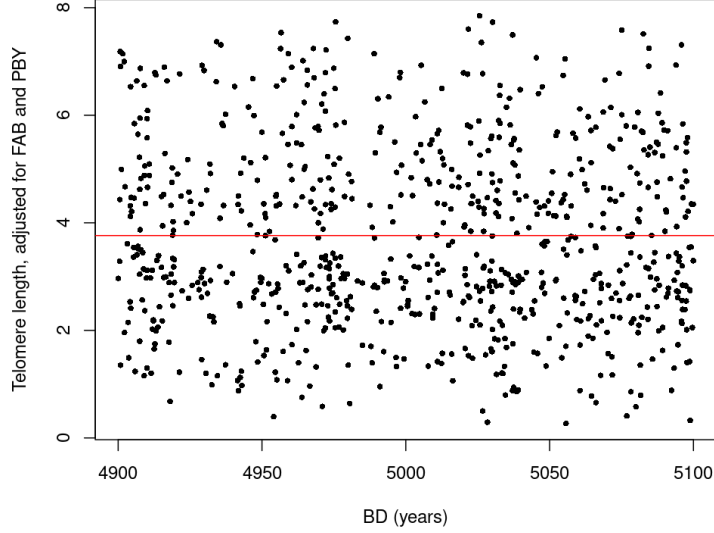


Figure 14: Sample of the population and linear regression lines for s_0 as a function of BD adjusted for FAB and PBV, when $\mu = 13$ for individuals born in the time interval $[0, 5000]$ and $\mu = 16$ for individuals born in the time interval $(5000, 6000]$. The regression line has coefficient -2.97×10^{-4} .

which concludes the proof.

A.2 Proof of Proposition 5

Let us introduce the sequence of random indices $(I_n)_{n \geq 1}$, defined inductively by $I_0 = 0$ and, for all $n \geq 0$,

$$I_{n+1} = \inf\{k \geq I_n + 1, \text{ such that } \varepsilon_k = 1\}.$$

One easily checks that, with this notation, $W_{I_n}^{(a)} = 0$ for all $n \geq 1$ almost surely and that, for all $t \geq 0$,

$$(Y_t^{(s)}, Y_t^{(a)}) = \sum_{n \geq 0} \mathbf{1}_{\tau_n \leq t < \tau_{n+1}} (V_n^{(s)}, t - \tau_n), \quad (1)$$

where $\tau_n := \sigma_{I_n}$ and $V_s = W_{I_n}$ (so that $V_n^{(s)} := W_{I_n}^{(s)}$). We prove the result by induction on n .

Step 1. Initialization of the inductive procedure.

For all $w_0 = (s_0, 0, \xi_0) \in \mathbb{X}$, we have, setting $f = \mathbf{1}_{A \times B}$,

$$\mathbb{E}_{0, w_0}^{\sigma, W} \left[f(V_0^{(s)}, \tau_0) 2^{N_t} \mathbf{1}_{\tau_0 \leq t < \tau_1} \right] = f(w_0, 0) \mathbb{E}_{0, w_0}^{\sigma, W} \left[2^{N_t} \mathbf{1}_{\tau_0 \leq t < \tau_1} \right] = f(w_0, 0).$$

Then, for all $w_0 = (s_0, 0, \xi_0) \in \mathbb{X}$, we have, setting $f = \mathbf{1}_{A \times B}$,

$$\begin{aligned}
\mathbb{E}_{0, w_0}^W \left[f(V_1^{(s)}, \tau_1) 2^{N_t} \mathbf{1}_{\tau_1 \leq t < \tau_2} \right] &= \mathbb{E}_{0, w_0}^W \left[f(V_1^{(s)}, \tau_1) 2^{N_{\tau_1}} \mathbf{1}_{\tau_1 \leq t} \mathbb{E}_{\tau_1, V_1}^W \left(2^{N_{t-u}} \mathbf{1}_{t-u < \tau_1} \right) \Big|_{u=\tau_1} \right] \\
&= \mathbb{E}_{0, w_0}^W \left[f(V_1^{(s)}, \tau_1) 2^{N_{\tau_1}} \mathbf{1}_{\tau_1 \leq t} \right] \\
&= \sum_{k \geq 0} \mathbb{E}_{0, w_0}^W \left[\mathbf{1}_{I_1=k} f(\xi_0^{(s)}(k), \xi_0^{(a)}(k)) 2^k \mathbf{1}_{\xi_0^{(a)}(k) \leq t} \right] \\
&= \sum_{k \geq 0} f(\xi_0^{(s)}(k), \xi_0^{(a)}(k)) \mathbf{1}_{\xi_0^{(a)}(k) \leq t} 2^k \mathbb{P}_{0, w_0}^W (I_1 = k) \\
&= \sum_{k \geq 0} f(\xi_0^{(s)}(k), \xi_0^{(a)}(k)) \mathbf{1}_{\xi_0^{(a)}(k) \leq t}.
\end{aligned}$$

Integrating with respect to $\mathbb{P}_{s_0}^J$ and using (1), we deduce that

$$\int_{\mathcal{M}_P(\mathbb{S} \times \mathbb{R}_+)} \mathbb{P}_{s_0}^J(d\xi_0) \mathbb{E}_{(s_0, 0, \xi_0)}^Y \left[f(Y_t^{(s)}, t - Y_t^{(s)}) 2^{N_t} \mathbf{1}_{\tau_1 \leq t < \tau_2} \right] = \mu(s_0, A \times B \cap [0, t]).$$

This concludes the first step, since $\sum_{k=0}^{N_t} \varepsilon_k = 1$ is equivalent to $\tau_1 \leq t < \tau_2$.

Step 2. Induction.

Fix $n \geq 1$ and assume that the property holds true for this value of n . For all $w_0 = (s_0, 0, \xi_0) \in \mathbb{X}$, we have

$$\begin{aligned}
\mathbb{E}_{0, w_0}^W \left[f(V_{n+1}^{(s)}, \tau_{n+1}) \mathbf{1}_{\tau_{n+1} \leq t < \tau_{n+2}} 2^{N_t} \right] \\
&= \mathbb{E}_{0, w_0}^W \left[\mathbf{1}_{\tau_1 \leq t} 2^{N_{\tau_1}} \mathbb{E}_{\tau_1, V_1}^W \left(f(V_n^{(s)}, \tau_n) \mathbf{1}_{\tau_n \leq t < \tau_{n+1}} 2^{N_{t-u}} \right) \Big|_{u=\tau_1} \right] \\
&= \mathbb{E}_{0, w_0}^W \left[\mathbf{1}_{\tau_1 \leq t} 2^{N_{\tau_1}} \mathbb{E}_{0, V_1}^W \left(f(V_n^{(s)}, \tau_n + u) \mathbf{1}_{\tau_n \leq t-u < \tau_{n+1}} 2^{N_{t-u}} \right) \Big|_{u=\tau_1} \right] \\
&= \mathbb{E}_{0, w_0}^W \left[\mathbf{1}_{\tau_1 \leq t} 2^{N_{\tau_1}} \mu^n(V_1^{(s)}, A \times ((B - \tau_1) \cap [0, t - \tau_1])) \right],
\end{aligned}$$

where we used the law of V_1 conditionally to $V_1^{(s)}$ and the induction assumption. Similarly as in Step 1, we now decompose over the possible values of I_1 and obtain

$$\begin{aligned}
\mathbb{E}_{0, w_0}^W \left[f(V_{n+1}^{(s)}, \tau_{n+1}) \mathbf{1}_{\tau_{n+1} \leq t < \tau_{n+2}} 2^{N_t} \right] \\
&= \sum_{k \geq 0} \mu^n(\xi_0^{(s)}(k), A \times ((B - \xi_0^{(a)}(k)) \cap [0, t - \xi_0^{(a)}(k)])) \mathbf{1}_{\xi_0^{(a)}(k) \leq t}.
\end{aligned}$$

Using (1) and integrating with respect to $\mathbb{P}_{s_0}^J$, we obtain

$$\begin{aligned}
\int_{\mathcal{M}_P(\mathbb{S} \times \mathbb{R}_+)} \mathbb{P}_{s_0}^J(d\xi_0) \mathbb{E}_{(s_0, 0, \xi_0)}^Y \left[f(Y_t^{(s)}, t - Y_t^{(s)}) 2^{N_t} \mathbf{1}_{\tau_{n+1} \leq t < \tau_{n+2}} \right] \\
&= \int_{\mathbb{S} \times \mathbb{R}_+} \mu(s_0, ds \times du) \mu^n(s, A \times ((B - u) \cap [0, t - u])) \mathbf{1}_{u \leq t} \\
&= \int_{\mathbb{S} \times \mathbb{R}_+} \mu(s_0, ds \times du) \mu^n(s, A \times (B \cap [0, t] - u)) \\
&= \mu^{n+1}(s_0, A \times (B \cap [0, t])).
\end{aligned}$$

This concludes the proof.

A.3 Proof of Proposition 3

We denote by $(R_t)_{t \geq 0}$ the semi-group associated to the Feynman-Kac expression of the proposition. Namely, for all $f \in L^\infty(\mathbb{S} \times \mathbb{R}_+)$ and all $(s_0, t_0) \in \mathbb{S} \times \mathbb{R}_+$, we set

$$R_t f(s_0, t_0) = \mathbb{E}_{s_0, t_0}^Z \left[f(Z_t) \exp \left(\int_0^t b(Z_u) du \right) \right].$$

In the setting of Poissonian reproduction mechanism of Section 2.2, it is also clear that $\mathbf{Z} := (Y^{(s)}, Y^{(a)})$ is a continuous time pure jump Markov process, with jump rate $b(\mathbf{Z})$ and jump distribution $\frac{1}{2}(\delta_{\mathbf{Z}_t} + \gamma_{\mathbf{Z}} \otimes \delta_0)$. We denote by T the semi-group of defined by

$$T_t f(s_0, t_0) = \mathbb{E}_{s_0, t_0}^Z (f(\mathbf{Z}_t) 2^{N_t}),$$

where N_t is the number of jumps of \mathbf{Z} before time t . Of course, this coincides with the last expression of Proposition 5.

Our aim is to show that R and T coincide when they are considered as semi-group over the set of uniformly continuous functions \mathcal{UC}_b^0 . This will imply that they coincide on bounded measurable functions and hence, using Proposition 5, that the equality of Proposition 3 holds true.

We first show that both semi-groups can be restricted to \mathcal{UC}_b^0 .

Lemma 1. *For all $f \in \mathcal{UC}_b^0$ and all $t \geq 0$, $R_t f \in \mathcal{UC}_b^0$ and $T_t f \in \mathcal{UC}_b^0$.*

Proof. The process $(Z_t, \int_0^t b(Z_u) du)_{t \geq 0}$ is a PDMP which satisfies the conditions of (Davis, 1993, Theorem 27.6). Hence, for any value of $m > 0$, the application

$$g_m : (s_0, t_0) \mapsto \mathbb{E}_{s_0, t_0}^Z \left[f(Z_t) \exp \left(m \wedge \int_0^t b(Z_u) du \right) \right]$$

is bounded and continuous. But $\int_0^t b(Z_u) du$ is uniformly bounded by $t \|b\|_\infty$, which implies that, choosing m large enough, $R_t f$ is continuous and bounded. Moreover, b has compact support, say K . Hence, for all $(s_0, t_0) \notin K$, $(Z_t)_{t \geq 0}$ starting from (s_0, t_0) is equal to $(s_0, t_0 + t)$ almost surely and hence $R_t f(s_0, t_0) = f(s_0, t_0 + t)$ which is uniformly compact over $(s_0, t_0) \notin K$. Since $R_t f$ is continuous over K , it is also uniformly continuous over K , and we deduce that $R_t f \in \mathcal{UC}_b^0$.

Similarly, the process $(\mathbf{Z}_t, N_t)_{t \geq 0}$ is a PDMP which satisfies the conditions of (Davis, 1993, Theorem 27.6). Hence, for any value of $m > 0$, the application

$$h_m : (s_0, t_0) \mapsto \mathbb{E}_{s_0, t_0}^Z [f(\mathbf{Z}_t) 2^{m \wedge N_t}]$$

is bounded and continuous. But

$$\left| \mathbb{E}_{s_0, t_0}^Z [f(\mathbf{Z}_t) 2^{N_t}] - \mathbb{E}_{s_0, t_0}^Z [f(\mathbf{Z}_t) 2^{m \wedge N_t}] \right| \leq \|f\|_\infty \mathbb{E}_{(s_0, t_0)}^Z [2^{N_t} \mathbf{1}_{N_t > m}],$$

where the right hand side converges to 0 uniformly in $(s_0, t_0) \in \mathbb{S} \times \mathbb{R}_+$ since b is bounded. This implies that $T_t f$ is the uniform limit of a sequence of bounded continuous functions, and hence that it is itself bounded continuous. As in the case of $R_t f$, we deduce that $T_t f \in \mathcal{UC}_b^0$. \square

We then obtain the strong continuity (see (Pazy, 1983, Definition 2.1)) of the semi-groups when they are defined over \mathcal{UC}_b^0 .

Lemma 2. *The semi-groups R and T are strongly continuous semi-groups on \mathcal{UC}_b^0 , which means that*

$$\|R_t f - f\|_\infty \xrightarrow{t \rightarrow 0} 0,$$

and similarly for T .

Proof. Since the proof is similar for both semi-group, we only detail it for T . Let $f \in \mathcal{UC}_b^0$, $\varepsilon > 0$ and $\delta > 0$ such that

$$\forall z_1, z_2, d(z_1, z_2) < \delta \Rightarrow |f(z_1) - f(z_2)| < \varepsilon.$$

For any $z_0 = (s_0, a_0) \in \mathbb{S} \times \mathbb{R}$ and $t < \delta$, we have

$$\begin{aligned} |T_t f(s_0, a_0) - f(s_0, a_0)| &= |\mathbb{E}_{s_0, a_0} (f(Z_t) 2^{N_t} \mathbf{1}_{N_t=0}) + \mathbb{E}_{s_0, a_0} (f(Z_t) 2^{N_t} \mathbf{1}_{N_t \geq 1}) - f(s_0, a_0)| \\ &\leq |f(s_0, a_0 + t) \mathbb{P}(N_t = 0) - f(s_0, a_0)| + \|f\|_\infty \mathbb{E}_{s_0, a_0} (2^{N_t} \mathbf{1}_{N_t \geq 1}) \\ &\leq |f(s_0, a_0 + t) - f(s_0, a_0)| + \|f\|_\infty \mathbb{P}(N_t \geq 1) + \|f\|_\infty \mathbb{E}_{s_0, a_0} (2^{N_t} \mathbf{1}_{N_t \geq 1}). \end{aligned}$$

The term $|f(s_0, a_0 + t) - f(s_0, a_0)|$ goes to 0 when $t \rightarrow 0$, uniformly in (s_0, a_0) , since f is uniformly continuous. Moreover, $\mathbb{E}_{s_0, a_0} (2^{N_t} \mathbf{1}_{N_t \geq 1})$ is bounded (since N_t is stochastically dominated by a Poisson random variable) and goes to 0 since N_t is non-decreasing right continuous at time 0, with $N_0 = 0$.

This concludes the proof of Lemma 2. \square

We now use the characterization of strongly continuous semi-groups by their infinitesimal generators (see Pazy (1983) Definition 1.1 and Theorem 2.6).

Lemma 3. *Fix $f \in \mathcal{UC}_b^0$. Then there exists a constant $C > 0$ such that*

$$\left\| \frac{R_t f - f}{t} - \frac{T_t f - f}{t} \right\|_\infty \leq C t.$$

In particular, R and T have the same infinitesimal generator over \mathcal{UC}_b^0 and hence they coincide.

Proof. Let $z_0 = (s_0, a_0) \in \mathbb{S} \times \mathbb{R}_+$. We have

$$\begin{aligned} R_t f(z_0) &= \mathbb{E}_{z_0}^Z \left(f(Z_t) \mathbf{1}_{\overline{N}_t=0} e^{\int_0^t b(Z_u) du} \right) \\ &\quad + \mathbb{E}_{z_0}^Z \left(f(Z_t) 2 \mathbf{1}_{\overline{N}_t=1} e^{\int_0^t b(Z_u) du} \right) \\ &\quad + \mathbb{E}_{z_0}^Z \left(f(Z_t) 2^{N_t} \mathbf{1}_{\overline{N}_t \geq 2} e^{\int_0^t b(Z_u) du} \right) \\ &= f(s_0, a_0 + t) e^{\int_0^t b(s_0, a_0 + u) du} e^{-\int_0^t b(s_0, a_0 + u) du} \\ &\quad + \int_0^t du b(s_0, a_0 + u) e^{-\int_0^u b(s_0, a_0 + v) dv} \\ &\quad \times \int_{\mathbb{S}} \gamma_{s_0, a_0 + u}(ds) f(s, t - u) e^{\int_0^u b(s_0, a_0 + v) dv} + \int_0^{t-u} b(s, v) dv \\ &\quad + \mathcal{O}(t^2), \end{aligned}$$

with $\mathcal{O}(t^2)$ uniform in the initial position $z_0 \in \mathbb{S} \times \mathbb{R}_+$, where the first term is obtained from the definition of the process Z before its first jump-time, the second term from the jump rate of the process and its jump measure, and the third one from the fact that b is uniformly bounded and N_t is stochastically dominated by a Poisson random variable with intensity $\|b\|_\infty$ (hence uniformly in $z_0 \in \mathbb{S} \times \mathbb{R}_+$).

Similarly,

$$\begin{aligned} T_t f(z_0) &= \mathbb{E}_{z_0}^Z (f(Z_t) 2^{N_t} \mathbf{1}_{N_t=0}) + \mathbb{E}_{z_0}^Z (f(Z_t) 2^{N_t} \mathbf{1}_{N_t=1}) + \mathbb{E}_{z_0} (f(Z_t) 2^{N_t} \mathbf{1}_{N_t \geq 2}) \\ &= f(s_0, a_0 + t) + \int_0^t du b(s_0, a_0 + u) e^{-\int_0^u b(s_0, a_0 + v) dv} \int_{\mathbb{S}} \gamma_{s_0, a_0 + u}(ds) f(s, t - u) + \mathcal{O}(t^2), \end{aligned}$$

where $\mathcal{O}(t^2)$ is uniform in (s_0, a_0) (since the increment rate of N_t is uniformly bounded, the probability that 2 or more jump occur in time t is of order t^2).

Hence we obtain

$$\begin{aligned} |R_t f(z_0) - T_t f(z_0)| &= \int_0^t du b(s_0, a_0 + u) e^{-\int_0^u b(s_0, a_0 + v) dv} \int_{\mathbb{S}} \gamma_{s_0, a_0 + u}(ds) |f(s, t - u)| \\ &\quad \times \left| e^{\int_0^u b(s_0, a_0 + v) dv + \int_0^{t-u} b(s, v) dv} - 1 \right| + \mathcal{O}(t^2). \end{aligned}$$

But the term $\left| e^{\int_0^u b(s_0, a_0 + v) dv + \int_0^{t-u} b(s, v) dv} - 1 \right|$ is of smaller than $2\|b\|_\infty t$ for t small enough (uniformly in $z_0 \in \mathbb{S} \times \mathbb{R}_+$), and we then deduce that

$$\|R_t f(z_0) - T_t f(z_0)\| = \mathcal{O}(t^2),$$

which concludes the proof of the first assertion.

The fact that R and T have the same infinitesimal generator is a direct consequence of its definition (see (Pazy, 1983, Definition 1.1)). Since they are strongly continuous semi-group, we deduce from (Pazy, 1983, Theorem 2.6) that they are equal. \square

We have proved that, for all fixed $t \geq 0$, $T_t f = R_t f$ for all functions $f \in \mathcal{UC}_b^0$. Since $\mathbb{S} \times \mathbb{R}_+$ is a metric space, this implies that $T_t f = R_t f$ for all bounded Borel function f (see for instance (Varadarajan, 1958, Lemma 2.3)). This and Proposition 5 conclude the proof of Proposition 3.

B Proof of the results of Sections 3

This section is devoted to the proof of Theorem 1 and Corollary 2.

B.1 Proof of Theorem 1

Let R^M be the sub-Markov semi-group defined as

$$\begin{aligned}\delta_{(s_0, a_0)} R_t^M &:= e^{-\|b\|_\infty t} \mathbb{E}_{a_0, s_0}^Z \left[\exp \left(\int_0^t b(Z_u) du \right) \mathbf{1}_{Z_t \in \cdot} \mathbf{1}_{t < \tau_M} \right] \\ &= \mathbb{E}_{a_0, s_0}^Z \left[\exp \left(\int_0^t -\kappa(Z_u) du \right) \mathbf{1}_{Z_t \in \cdot} \mathbf{1}_{t < \tau_M} \right],\end{aligned}$$

where $\tau_M = \inf\{t \geq 0, Z_t^{(a)} \geq b_M\}$ and $\kappa(z) = \|b\|_\infty - b(z)$ for all $z \in \mathbb{S} \times \mathbb{R}_+$. The semi-group R^M is the semi-group of the process Y^M , defined as follows : it evolves as Z but with an additional killing rate κ and killed when its age reaches τ_M . By *killed*, we mean as usual that the process is sent to a cemetery point $\partial \notin \mathbb{S} \times \mathbb{R}_+$ at the killing time, in a càdlàg way. We denote by $\tau_\partial^M := \inf\{t \geq 0, Y_t^M \in \partial\}$ its killing time, and by \mathbb{E}^M (resp. \mathbb{P}^M) the expectation (resp. the probability) associated to the law of Y^M , so that

$$\delta_{(s_0, a_0)} R_t^M = \mathbb{E}_{s_0, a_0}^M \left[\mathbf{1}_{Y_t^M \in \cdot} \mathbf{1}_{t < \tau_\partial^M} \right], \quad \forall (s_0, a_0) \in \mathbb{S} \times [0, b_M).$$

Lemma 4. *There exists positive constants $\lambda_0^M \in (0, \|b\|_\infty)$, $\lambda_1 > 0$, $C > 0$, $t_0 \geq 0$, a probability measure Υ_M on $\mathbb{S} \times [0, b_M)$ and a bounded function $\eta : [0, b_M) \rightarrow (0, +\infty)$ such that, for all $t \geq t_0$ and all $(a_0, s_0) \in [0, b_M) \times \mathbb{S}$,*

$$\left\| e^{\lambda_0^M t} \delta_{(s_0, a_0)} R_t^M - \eta(s_0, a_0) \Upsilon_M \right\|_{TV} \leq C e^{-\lambda_1 t} \eta(s_0, a_0).$$

Proof. Our strategy is to check that Assumption A from Champagnat and Villemonais (2016) is satisfied by the process Y^M . Once this is done, Theorem 1.1 in this reference states that

$$\left\| e^{\lambda_0^M t} \delta_{(s_0, a_0)} R_t^M - \delta_{(s_0, a_0)} R_t^M \mathbf{1}_{\mathbb{S} \times [0, b_M)} \Upsilon_M \right\|_{TV} \leq C e^{-\lambda_1 t} \delta_{(s_0, a_0)} R_t^M \mathbf{1}_{\mathbb{S} \times [0, b_M)}.$$

Now, using Theorem 2.1 and Equation (3.2) in Champagnat and Villemonais (2017), we deduce that there exists $t_0 > 0$ such that, for all $t \geq t_0$,

$$\left| e^{\lambda_0^M t} \delta_{(s_0, a_0)} R_t^M \mathbf{1}_{\mathbb{S} \times [0, b_M)} - \eta(s_0, a_0) \right| \leq C \eta(s_0, a_0) e^{-\lambda_1 t},$$

up to a change in the constant C , and for some positive bounded function $\eta : \mathbb{S} \times [0, b_M) \rightarrow \mathbb{R}_+$. The last two equations allow to conclude the proof of Lemma 4 (the fact that $0 < \lambda_0^M < \|b\|_\infty$ is a consequence of the fact that $\kappa \leq \|b\|_\infty$ and $0 < \Upsilon_M(\kappa) < \|b\|_\infty$).

It remains to check Assumption A, which is stated as follows.

Assumption A. There exists a probability measure β on $\mathbb{S} \times [0, b_M)$ and positive constants t_A, c_A, c'_A , such that

A1. for all $x \in \mathbb{S} \times [0, b_M)$,

$$\mathbb{P}^M (Y_{t_A}^M \in \cdot \mid t_A < \tau_\partial^M) \geq c_A \beta,$$

A2. for all $x \in \mathbb{S} \times [0, b_M)$ and all $t \geq 0$,

$$\mathbb{P}_\beta^M(t < \tau_\partial^M) \geq c'_A \mathbb{P}_x^M(t < \tau_\partial^M).$$

The end of the proof, divided in two steps, is dedicated to checking A1 and A2 respectively.

Step 1. Checking A1. We denote by $\tau_1 \leq \dots \leq \tau_n \leq \dots$ the successive jump times of Y^M , with $\tau_n = +\infty$ if there are less than n jumps. Using the definition of Y^M and the strong Markov property at time τ_n , we obtain that, for all $s_0 \in \mathbb{S}$ and all $n \geq 0$,

$$\begin{aligned} & \mathbb{P}_{(s_0,0)}^M \left(Y_{\tau_{n+1}}^M \in ds_{n+1} \times \{0\}, \tau_{n+1} \in da_{n+1} \right) \\ &= \int_{\mathbb{S} \times \mathbb{R}_+} \mathbb{P}_{(s_0,0)}^M \left(Y_{\tau_n}^M \in ds_n \times \{0\}, \tau_n \in da_n \right) \mathbb{P}_{(s_n,0)}^M \left(Y_{\tau_1}^M \in ds_{n+1}, \tau_1 \in da_{n+1} - a_n \right) \\ &\geq \int_{\mathbb{S} \times \mathbb{R}_+} \mathbb{P}_{(s_0,0)}^M \left(Y_{\tau_n}^M \in ds_n \times \{0\}, \tau_n \in da_n \right) \mathbf{1}_{a_n \leq a_{n+1} \leq a_n + b_M} e^{-2\|b\|_\infty b_M} \\ &\quad \times b(s_n, a_{n+1} - a_n) g_{s_n, a_{n+1} - a_n}(s_{n+1}) \pi(ds_{n+1}) \lambda(da_{n+1}) \\ &\geq \int_{\mathbb{S} \times \mathbb{R}_+} \mathbb{P}_{(s_0,0)}^M \left(Y_{\tau_n}^M \in ds_n \times \{0\}, \tau_n \in da_n \right) \underline{b} \underline{g} \pi(ds_{n+1}) \lambda_{|[a_n + b_M, a_n + b_M]}(da_{n+1}), \end{aligned}$$

where λ denotes the Lebesgue measure on \mathbb{R} , and where $\underline{b} := e^{-2\|b\|_\infty b_M} \inf_{s \in \mathbb{S}, a \in [b_m, b_M]} b(s, a)$ and $\underline{g} := \inf_{s_0, s \in \mathbb{S}, a \in [b_m, b_M]} g_{s_0, a}(s)$ are positive (by continuity of b and g and by the compactness of \mathbb{S}). Using an iterative procedure, we deduce that, for all $n \geq 1$,

$$\mathbb{P}_{(s_0,0)}^M \left(Y_{\tau_n}^M \in ds_n \times \{0\}, \tau_n \in da_n \right) \geq \underline{b}^n \underline{g}^n \pi(ds_n) \left(\lambda_{|[b_m, b_M]} \right)^{\otimes n}(da_n).$$

But $\left(\lambda_{|[b_m, b_M]} \right)^{\otimes n}$ admits a positive continuous density on (nb_m, nb_M) , hence there exist $n \geq 1$, $c > 0$ and $d > b_M$ such that

$$\left(\lambda_{|[b_m, b_M]} \right)^{\otimes n}(da_n) \geq c \lambda_{|[d - b_M, d + b_m]}(da_n),$$

so that

$$\mathbb{P}_{(s_0,0)}^M \left(Y_{\tau_n}^M \in ds_n \times \{0\}, \tau_n \in da_n \right) \geq c \underline{b}^n \underline{g}^n \pi(ds_n) \lambda_{|[d - b_M, d + b_m]}(da_n). \quad (2)$$

Now, let $s_0 \in \mathbb{S}$ and $a_0 \in (0, b_M)$. We have, for all measurable $A \subset \mathbb{S}$ and all $\ell < \ell' \in [0, b_m]$,

$$\begin{aligned} & \mathbb{P}_{(s_0, a_0)}^M \left(Y_{d+b_m}^M \in A \times [\ell, \ell'] \right) \geq \mathbb{P}_{(s_0, a_0)}^M \left(Y_{d+b_m}^M \in A \times [\ell, \ell'], \tau_{n+1} \in [d, d + b_m] \right) \\ & \geq \mathbb{P}_{(s_0, a_0)}^M \left(Y_{\tau_{n+1}}^M \in A \times \{0\}, d + b_m - \tau_{n+1} \in [0, b_m] \cap [\ell, \ell'], \tau_{n+2} > \tau_{n+1} + b_m \right) \\ & \geq \mathbb{P}_{(s_0, a_0)}^M \left(Y_{\tau_{n+1}}^M \in A \times \{0\}, d + b_m - \tau_{n+1} \in [\ell, \ell'] \right) e^{-2\|b\|_\infty b_m}, \end{aligned}$$

where we used the strong Markov property at time τ_{n+1} and the fact that the total jump rate of Y^M (including the killing rate) is uniformly bounded by $2\|b\|_\infty$. Using the strong Markov

inequality at time τ_1 , we deduce that, for all measurable $A \subset \mathbb{S}$ and all $\ell < \ell' \in [0, b_m)$,

$$\begin{aligned}
\mathbb{P}_{(s_0, a_0)}^M \left(Y_{d+b_m}^M \in A \times [\ell, \ell'] \right) &\geq e^{-2\|b\|_\infty b_m} \int_{[a_0, b_M]} \lambda(da_1) e^{-2\|b\|_\infty b_M} b(s_0, a_1) \int_{\mathbb{S}} \gamma_{s_0, a_1}(ds_1) \\
&\quad \times \mathbb{P}_{(s_1, 0)}^M \left(Y_{\tau_n}^M \in A \times \{0\}, d + b_m - \tau_n - a_1 \in [\ell, \ell'] \right) \\
&\geq e^{-4\|b\|_\infty b_M} \int_{[a_0, b_M]} \lambda(da_1) b(s_0, a_1) \int_{\mathbb{S}} \gamma_{s_0, a_1}(ds_1) c \underline{b}^n \underline{g}^n \pi(A) \\
&\quad \times \lambda_{|[d-2b_M, d+b_m]}([d + b_m - a_1 + \ell, d + b_m - a_1 + \ell']) \\
&= e^{-4\|b\|_\infty b_M} \int_{[a_0, b_M]} \lambda(da_1) b(s_0, a_1) c \underline{b}^n \underline{g}^n \pi(A) \lambda([l, l']),
\end{aligned}$$

where we used (2) for the second inequality. Since $\{d + b_m < \tau_\partial\} \subset \{\tau_1 \in [a_0, b_M]\}$, we also have

$$\mathbb{P}_{(s_0, a_0)}^M (d + b_m < \tau_\partial) \leq \int_{[a_0, b_M]} \lambda(da_1) b(s_0, a_1),$$

so that Assumption A1 holds true with $t_A = d + b_m$, $c_A = e^{-4\|b\|_\infty b_M} c \underline{b}^n \underline{g}^n b_m$, and

$$\beta(ds \times da) = \pi(ds) \lambda_{|[0, b_m]}(da) / b_m.$$

Step 2. Checking A2. On the one hand, for all $(s_0, a_0) \in \mathbb{S} \times [0, b_M)$ and all $t \geq b_m + b_M$, we obtain, using the strong Markov property at time τ_1 ,

$$\begin{aligned}
\mathbb{P}_{(s_0, a_0)}(t < \tau_\partial) &\leq \bar{g} \int_{\mathbb{S}} \pi(ds) \mathbb{P}_{(s, 0)}(t - a_0 < \tau_\partial) \\
&\leq \bar{g} \int_{\mathbb{S}} \pi(ds) \int_{[0, b_m]} \frac{da}{b_m} \mathbb{P}_{(s, a)}(t - a_0 - a < \tau_\partial) \\
&\leq \bar{g} \int_{\mathbb{S}} \pi(ds) \int_{[0, b_m]} \frac{da}{b_m} \mathbb{P}_{(s, a)}(t - b_M - b_m < \tau_\partial), \tag{3}
\end{aligned}$$

where we used the fact that $\mathbb{P}_{(s, a)}(u < \tau_\partial)$ decreases with u , and where $\bar{g} := \sup_{(s_0, a, s) \in \mathbb{S} \times [0, b_M] \times \mathbb{S}}$, which is finite by continuity of g and compactness of \mathbb{S} . On the other hand, using Step 1 (where we can and do assume without loss of generality that $t_A \geq b_m + b_M$),

$$\mathbb{P}_\beta(X_{t_A} \in \cdot) \geq \mathbb{P}_\beta(t_A < \tau_\partial) c_A \beta,$$

so that, using the Markov property at time t_A ,

$$\mathbb{P}_\beta(t < \tau_\partial) \geq \mathbb{P}_\beta(t_A < \tau_\partial) c_A \mathbb{P}_\beta(t - t_A < \tau_\partial) \geq \mathbb{P}_\beta(t_A < \tau_\partial) c_A \mathbb{P}_\beta(t - b_m - b_M < \tau_\partial). \tag{4}$$

Since $\mathbb{P}_\beta(t_A < \tau_\partial) > 0$, we deduce from (3) and (4) that Assumption A2 holds true with

$$c'_A = \frac{\mathbb{P}_\beta(t_A < \tau_\partial) c_A}{\bar{g}}.$$

This concludes the proof of Lemma 4. □

We introduce now the semi-group R^∞ defined by

$$\delta_{(s_0, a_0)} R_t^\infty := e^{-\|b\|_\infty t} \delta_{(s_0, a_0)} R_t = \mathbb{E}_{a_0, s_0}^Z \left[\exp \left(\int_0^t -\kappa(Z_u) du \right) \mathbf{1}_{Z_t \in \cdot} \right],$$

which is the semi-group of the Markov process Y^∞ defined as follows : it evolves as Z but with an additional killing κ (without killing when at time τ_M , contrarily to Y^M). Then we have, denoting by \mathbb{E}^∞ the expectation associated to the law of Y^∞ , for all $(s_0, a_0) \in \mathbb{S} \times [0, b_M)$ and all bounded measurable function $f : \mathbb{S} \times \mathbb{R}_+ \cup \{\partial\} \rightarrow \mathbb{R}$ such that $f(\partial) = 0$,

$$\mathbb{E}_{(s_0, a_0)}^\infty (f(Y_t^\infty) \mathbf{1}_{t < \tau_\partial}) = \mathbb{E}_{(s_0, a_0)}^M (f(Y_t^M) \mathbf{1}_{t < \tau_\partial}) + \mathbb{E}_{(s_0, a_0)}^\infty (f(Y_t^\infty) \mathbf{1}_{\tau_M \leq t < \tau_\partial}). \quad (5)$$

We will need the following technical result to exhibit the limiting behavior of R_t^∞ , when $t \rightarrow +\infty$. Our strategy can be used in general when a reducible process satisfies Assumption A in a given communication class, and can go into another set where the killing rate is strictly larger than the parameter λ_0^M associated to the process restricted to the initial communication class.

Lemma 5. *There exists a constant $C > 0$ such that, for all $t \geq 0$ and all $(s, a) \in \mathbb{S} \times \mathbb{R}_+$,*

$$\mathbb{P}_{(s, a)}^\infty (\tau_M \leq t < \tau_\partial) \leq C e^{-\lambda_0^M t}.$$

Proof. We have, using the Markov property at time τ_M ,

$$\begin{aligned} \mathbb{P}_{(s, a)}^\infty (\tau_M \leq u < \tau_\partial) &\leq \int_0^t \mathbb{P}_{(s, a)}^M (\tau_\partial \in du) e^{-\|b\|_\infty (t-u)} \\ &\leq \|b\|_\infty e^{-\|b\|_\infty t} \int_0^t dv \mathbb{P}_{(s, a)}^M (v < \tau_\partial) e^{\|b\|_\infty v} \\ &\leq \|b\|_\infty e^{-\|b\|_\infty t} \int_0^t dv c e^{-\lambda_0^M v} e^{\|b\|_\infty v}, \end{aligned}$$

where $c > 0$ is a constant (see Equation (2.4) of Champagnat and Villemonais (2016)). The computation of the right hand term concludes the proof. \square

We denote by Y_{exit} the law of $Y_{\tau_\partial^M}^M$ under $\mathbb{P}_{Y_M}^M$.

Lemma 6. *There exist positive constants C, λ'' such that, for all bounded measurable function f and all*

$$\left| e^{\lambda_0^M t} \mathbb{E}_{Y_M}^\infty (f(Y_t^\infty) \mathbf{1}_{\tau_M \leq t < \tau_\partial}) - \lambda_0 \int_0^\infty du e^{\lambda_0^M u} \int_{\mathbb{S} \times \{b_M\}} Y_{\text{exit}}(ds, da) \mathbb{E}_{(s, a)}^\infty (f(Y_u^\infty) \mathbf{1}_{u < \tau_\partial}) \right| \leq \|f\|_\infty C e^{-\lambda'' t}.$$

Proof. Under $\mathbb{P}_{Y_M}^M$, τ_∂^M is independent from $Y_{\tau_\partial^M}^M$ and is an exponential random variable with parameter λ_0^M (these are well known results from the theory of quasi-stationary distributions, see for instance Collet et al. (2013)). Hence, using the strong Markov property

at time τ_M for Y^∞ and using the facts that $Y_{\tau_M}^\infty = Y_{\tau_M-}^\infty$ and that, up to time $\tau_M \wedge \tau_\delta$ (excluded), Y^M and Y^∞ have the same law, we obtain

$$\mathbb{E}_{Y_M}^\infty (f(Y_t^\infty) \mathbf{1}_{\tau_M \leq t < \tau_\delta}) = \mathbb{E}_{Y_M}^M \left(\mathbf{1}_{\tau_\delta^M \leq t, Y_{\tau_\delta^M-}^M \in \mathbb{S} \times \{b_M\}} \mathbb{E}_{Y_{\tau_\delta^M-}^M}^\infty (f(Y_{t-\nu}) \mathbf{1}_{t-\nu < \tau_\delta}) \Big|_{\nu=\tau_M} \right).$$

Then

$$\begin{aligned} e^{\lambda_0^M t} \mathbb{E}_{Y_M}^\infty (f(Y_t^\infty) \mathbf{1}_{\tau_M \leq t < \tau_\delta}) &= \int_0^t d\nu \lambda_0^M e^{\lambda_0^M (t-\nu)} \int_{\mathbb{S} \times \{b_M\}} \Upsilon_{\text{exit}}(ds, da) \mathbb{E}_{(s,a)}^\infty (f(Y_{t-\nu}^\infty) \mathbf{1}_{t-\nu < \tau_\delta}) \\ &= \lambda_0 \int_0^t du \lambda_0^M e^{\lambda_0^M u} \int_{\mathbb{S} \times \{b_M\}} \Upsilon_{\text{exit}}(ds, da) \mathbb{E}_{(s,a)}^\infty (f(Y_u^\infty) \mathbf{1}_{u < \tau_\delta}). \end{aligned}$$

Now, since $a = b_M$ entails that $\mathbb{E}_{(s,a)}^\infty (f(Y_u^\infty) \mathbf{1}_{u < \tau_\delta}) \leq \|f\|_\infty e^{-\|b\|_\infty u}$ with $\|b\|_\infty > \lambda_0^M$, one obtains

$$\int_t^{+\infty} du \lambda_0^M e^{\lambda_0^M u} \int_{\mathbb{S} \times \{b_M\}} \Upsilon_{\text{exit}}(ds, da) \mathbb{E}_{(s,a)}^\infty (f(Y_u) \mathbf{1}_{u < \tau_\delta}) \leq \|f\|_\infty \frac{e^{-(\|b\|_\infty - \lambda_0^M)t}}{\|b\|_\infty - \lambda_0^M},$$

which concludes the proof. \square

The first term on the right hand side of (5) multiplied by $e^{\lambda_0^M t}$ converges, according to Lemma 4. Let us focus on the second term. We fix $\epsilon > 0$ such that $(1 - \epsilon)\|b\|_\infty > \lambda_0^M$ and obtain

$$\mathbb{E}_{(s_0, a_0)}^\infty (f(Y_t) \mathbf{1}_{\tau_M \leq t < \tau_\delta}) = \mathbb{E}_{(s_0, a_0)}^\infty \left[\mathbf{1}_{\epsilon t < \tau_M \leq t} \mathbb{E}_{Y_{\tau_M}}^\infty (f(Y_{t-u}) \mathbf{1}_{t-u < \tau_\delta}) \Big|_{u=\tau_M} \right] \quad (6)$$

$$+ \mathbb{E}_{(s_0, a_0)}^\infty \left(\mathbf{1}_{\tau_M \leq \epsilon t} \mathbb{E}_{Y_{\tau_M}}^\infty (f(Y_{t-u}) \mathbf{1}_{t-u < \tau_\delta}) \Big|_{u=\tau_M} \right). \quad (7)$$

On the one hand, the term (7) is bounded by $\|f\|_\infty e^{-\|b\|_\infty (1-\epsilon)t}$. On the other hand, setting $g(y, u) = \mathbb{E}_y (f(Y_{t-u}) \mathbf{1}_{t-u < \tau_\delta})$, we have

$$\begin{aligned} \mathbb{E}_{(s_0, a_0)}^\infty \left[\mathbf{1}_{\epsilon t < \tau_M \leq t} g(Y_{\tau_M}, \tau_M) \right] &= \mathbb{E}_{(s_0, a_0)}^M \left[\mathbf{1}_{\epsilon t < \tau_M} \mathbb{E}_{Y_{\tau_M}}^\infty (g(Y_{\tau_M}, \tau_M + \epsilon t) \mathbf{1}_{\tau_M \leq (1-\epsilon)t}) \right] \\ &= e^{-\epsilon t \lambda_0^M} \eta(s_0, a_0) \mathbb{E}_{Y_M}^\infty (g(Y_{\tau_M}, \tau_M + \epsilon t) \mathbf{1}_{\tau_M \leq (1-\epsilon)t}) \\ &\quad + \mathcal{O}(e^{-(\lambda_0^M + \lambda_1)\epsilon t}) \sup_{(s,a) \in \mathbb{S} \times \mathbb{R}_+} \mathbb{E}_{(s,a)}^\infty (g(Y_{\tau_M}, \tau_M + \epsilon t) \mathbf{1}_{\tau_M \leq (1-\epsilon)t}), \end{aligned}$$

where $\mathcal{O}(e^{-\lambda_1 t})$ is uniform in (s_0, a_0) by Lemma 4. We note that, according to Lemma 5,

$$\mathbb{E}_{(s,a)}^\infty (g(Y_{\tau_M}, \tau_M + \epsilon t) \mathbf{1}_{\tau_M \leq (1-\epsilon)t}) \leq \|f\|_\infty \mathbb{P}_{(s,a)}^\infty (\tau_M \leq (1-\epsilon)t < \tau_\delta) \leq C \|f\|_\infty e^{-(1-\epsilon)\lambda_0^M t}.$$

As a consequence (using also the bound on (7)), there exists a constant $\lambda' > 0$ such that

$$\mathbb{E}_{(s_0, a_0)}^\infty (f(Y_t) \mathbf{1}_{\tau_M \leq t < \tau_\delta}) = e^{-\epsilon t \lambda_0^M} \eta(s_0, a_0) \mathbb{E}_{Y_M}^\infty (g(Y_{\tau_M}, \tau_M + \epsilon t) \mathbf{1}_{\tau_M \leq (1-\epsilon)t}) + \mathcal{O}(e^{-(\lambda_0^M + \lambda')t}), \quad (8)$$

$$= e^{-\epsilon t \lambda_0^M} \eta(s_0, a_0) \mathbb{E}_{Y_M}^M (g(Y_{\tau_M-}, \tau_M + \epsilon t) \mathbf{1}_{\tau_M \leq (1-\epsilon)t}) + \mathcal{O}(e^{-(\lambda_0^M + \lambda')t}), \quad (9)$$

uniformly in $(s_0, a_0) \in \mathbb{S} \times [0, b_M)$. But the same procedure as in the proof of Lemma 6 shows that

$$\begin{aligned} \mathbb{E}_{Y_M}^M (g(Y_{\tau_M-}, \tau_M + \epsilon t) \mathbf{1}_{\tau_M \leq (1-\epsilon)t}) &= \int_0^{(1-\epsilon)t} du \lambda_0^M e^{-\lambda_0^M u} \int_{\mathbb{S} \times \{b_M\}} \Upsilon_{\text{exit}}(dy) g(y, u + \epsilon t) \\ &= e^{\epsilon \lambda_0^M t} \int_{\epsilon t}^t dv \lambda_0^M e^{-\lambda_0^M v} \int_{\mathbb{S} \times \{b_M\}} \Upsilon_{\text{exit}}(dy) g(y, v). \end{aligned}$$

Since, $\Upsilon_{\text{exit}}(dy)$ -almost surely, $g(y, v)$ is bounded by $\|f\|_\infty e^{-\|b\|_\infty(t-v)}$, we have

$$\begin{aligned} &\left| e^{-\epsilon \lambda_0^M t} \mathbb{E}_{Y_M}^M (g(Y_{\tau_M-}, \tau_M + \epsilon t) \mathbf{1}_{\tau_M \leq (1-\epsilon)t}) - \mathbb{E}_{Y_0}^M (g(Y_{\tau_M}, \tau_M) \mathbf{1}_{\tau_M \leq t}) \right| \\ &\leq \|f\|_\infty \int_0^{\epsilon t} dv \lambda_0^M e^{-\lambda_0^M v} e^{-\|b\|_\infty(t-v)} \\ &= \|f\|_\infty \lambda_0^M e^{-\|b\|_\infty t} \frac{e^{\epsilon(\|b\|_\infty - \lambda_0^M)t} - 1}{\|b\|_\infty - \lambda_0^M} \\ &= e^{-\lambda_0^M t} \mathcal{O}(e^{-(1-\epsilon)(\|b\|_\infty - \lambda_0^M)t}). \end{aligned}$$

Using the last inequality, combined with (9), (5) and Lemma 6, we deduce that

$$\left| e^{\lambda_0^M t} \mathbb{E}_{(s_0, a_0)}^\infty (f(Y_t) \mathbf{1}_{t < \tau_\delta}) - \eta(s_0, a_0) \Upsilon(f) \right| \leq C \|f\|_\infty e^{-\lambda t},$$

for some positive constants $C > 0$ and $\lambda > 0$, where

$$\Upsilon(f) = \Upsilon_M(f) + \lambda_0 \int_0^\infty du e^{\lambda_0^M u} \int_{\mathbb{S} \times \{b_M\}} \Upsilon_{\text{exit}}(ds, da) \mathbb{E}_{(s, a)}^\infty (f(Y_u) \mathbf{1}_{u < \tau_\delta}). \quad (10)$$

The previous analysis was valid for $(s_0, a_0) \in \mathbb{S} \times [0, b_M)$. When $(s_0, a_0) \in \mathbb{S} \times [b_M, +\infty)$, then the killing rate of the process is $\|b\|_\infty$, so that the last inequality holds true (up to a modification of C and λ) with $\eta(s_0, a_0) = 0$.

Taking $\lambda_0 = \lambda_0^M - \|b\|_\infty$, this concludes the proof of the first part of Theorem 1.

Let us now prove the last assertion of the theorem. Fix $\lambda > -\lambda_0$. From Corollary 1, we now that, for all $s_0 \in \mathbb{S}$ and all $t \geq 0$,

$$v_\lambda(s_0, \mathbb{S} \times [0, t]) = e^{-\lambda t} \mathbb{E}_{s_0, 0}^Z \left(e^{\lambda Z_t^{(a)}} e^{\int_0^t b(Z_u) du} \right) = e^{(\|b\|_\infty - \lambda)t} \mathbb{E}_{(s_0, 0)}^\infty \left(e^{\lambda Y_t^{(a)}} \mathbf{1}_{t < \tau_\delta} \right)$$

where Z is the process described in Section 2.2. Note that $Y_t^{(a)} \leq b_M$ for all $t \leq \tau_M$ and since $Y_t^{(a)} = t - \tau_M$ for all $t \in [\tau_M, \tau_\delta)$. Hence, on the one hand,

$$\mathbb{E}_{(s_0, 0)}^\infty \left(e^{\lambda Y_t^{(a)}} \mathbf{1}_{t < \tau_\delta \wedge \tau_M} \right) \leq e^{\lambda b_M} \mathbb{P}_{s_0, 0}^\infty (t < \tau_\delta \wedge \tau_M).$$

But $\|b\|_\infty - \lambda < \|b\|_\infty + \lambda_0 = \lambda_0^M$, so that, according to (10),

$$e^{(\|b\|_\infty - \lambda)t} \mathbb{E}_{(s_0, 0)}^\infty \left(e^{\lambda Y_t^{(a)}} \mathbf{1}_{t < \tau_\delta \wedge \tau_M} \right) \xrightarrow[t \rightarrow +\infty]{} 0. \quad (11)$$

On the other hand, we have

$$\begin{aligned}\mathbb{E}_{(s_0,0)}^\infty \left(e^{\lambda Y_t^{(a)}} \mathbf{1}_{\tau_M \leq t < \tau_\delta} \right) &= e^{\lambda t} \mathbb{E}_{(s_0,0)}^\infty \left(e^{-\lambda \tau_M} \mathbf{1}_{\tau_M \leq t < \tau_\delta} \right) \\ &\leq e^{\lambda t} \mathbb{E}_{(s_0,0)}^M \left(e^{-\lambda \tau_M} \mathbf{1}_{\tau_M = \tau_\delta} \right) \\ &\leq e^{\lambda t} \mathbb{E}_{(s_0,0)}^M \left(e^{-\lambda \tau_\delta} \right).\end{aligned}$$

But the killing time τ_δ under $\mathbb{P}_{(s_0,a_0)}^M$ has an exponential queue with parameter λ_0^M (see for instance Proposition 2.3 in Champagnat and Villemonais (2016)), so that there exists a constant $C > 0$ such that

$$\mathbb{E}_{(s_0,0)}^\infty \left(e^{\lambda Y_t^{(a)}} \mathbf{1}_{\tau_M \leq t < \tau_\delta} \right) \leq C e^{\lambda t} \int_0^t e^{-\lambda u} e^{-\lambda_0^M u} du = C \exp(\lambda t) \frac{e^{-(\lambda + \lambda_0^M)t} - 1}{\lambda + \lambda_0^M}$$

Hence, using the fact that $\|b\|_\infty - \lambda_0^M = -\lambda_0 < \lambda$,

$$\mathbb{E}_{(s_0,0)}^\infty \left(e^{\lambda Y_t^{(a)}} \mathbf{1}_{\tau_M \leq t < \tau_\delta} \right) \leq C \frac{e^{(\|b\|_\infty - \lambda - \lambda_0^M)t}}{\lambda + \lambda_0^M} \xrightarrow{t \rightarrow +\infty} 0.$$

Finally, we have proved that, for all $\lambda > -\lambda_0$,

$$v_\lambda(s_0, \mathbb{S} \times \mathbb{R}_+) = \lim_{t \rightarrow +\infty} v_\lambda(s_0, \mathbb{S} \times [0, t]) = 0,$$

so that $\alpha \leq -\lambda_0$.

Finally, one observes that, according to the already proved first part of Theorem 1,

$$v_{-\lambda_0}(s_0, \mathbb{S} \times [0, t]) \geq e^{\lambda_0 t} \delta_{s_0,0} R_t \xrightarrow{t \rightarrow +\infty} \eta(s_0, a_0) Y(\mathbf{1}_{\mathbb{S} \times \mathbb{R}_+}) > 0,$$

so that $\alpha \geq -\lambda_0$. This concludes the proof of Theorem 1.

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