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# Long-time behaviour of a multidimensional age-dependent branching process with a singular jump kernel

Jules OLAYÉ<sup>\*,†</sup>

Milica TOMAŠEVIĆ<sup>\*</sup>

## Abstract

In this article, we investigate the ergodic behaviour of a multidimensional age-dependent branching process with a singular jump kernel, motivated by studying the phenomenon of telomere shortening in cell populations. Our model tracks individuals evolving within a continuous-time framework indexed by a binary tree, characterised by age and a multidimensional trait. Branching events occur with rates dependent on age, where offspring inherit traits from their parent with random increase or decrease in some coordinates, while the most of them are left unchanged. Exponential ergodicity is obtained at the cost of an exponential normalisation, despite the fact that we have an unbounded age-dependent birth rate that may depend on the multidimensional trait, and a non-compact transition kernel. These two difficulties are respectively treated by stochastically comparing our model to Bellman-Harris processes, and by using a weak form of a Harnack inequality. We conclude this study by giving examples where the assumptions of our main result are verified.

**Keywords**— Branching processes, ergodicity, long-time behaviour, jump Markov processes, telomere shortening

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# 1 Introduction

**Informal definition of the model.** In this work we consider a population of individuals evolving in continuous time indexed by a binary tree and characterised by their label in the tree, and a trait  $(x, a) \in (\mathbb{R}_+^{2k} \times \mathbb{R}_+) \cup \{(\partial, \partial)\}$ , where  $x$  is the trait that motivates our study,  $a$  is the age of the individual, and  $(\partial, \partial)$  is a cemetery state. Here,  $\partial$  is an arbitrary element outside of both  $\mathbb{R}_+^{2k}$  and  $\mathbb{R}_+$ , and we are interested in cases where  $k \in \mathbb{N}^*$  is large. The individuals branch with a rate depending on their age and at branching events the two daughters inherit the mother's trait  $x$  randomly perturbed as follows. We choose a random number of coordinates of  $x$  that go through a random elongation procedure according to a given distribution, and  $k$  coordinates of  $x$  that go to a shortening procedure according to another distribution, while the rest of the coordinates remains unchanged. Between these jump events, the trait remains also unchanged. The hack is that eventually, due to the shortening procedure, some coordinates of the individual traits will hit zero. When this happens, the individual is moved to the cemetery state  $(\partial, \partial)$ .

**Brief motivations and main result.** The goal of the paper is to study the long-time behaviour of the population trait distribution and prove that the first moment semigroup derived from our population model converges to a stationary profile at the cost of an exponential normalisation. Our main result is this long time behaviour of a jump process in a non-compact and branching setting. In particular, we extend the results of Velleret [54] to branching jump processes, with times between jumps depending both on the age and of the position of the particle, and which require Lyapunov functions to obtain the ergodic behaviour.

Furthermore, our careful and sometimes long computations when obtaining the long time behaviour enable us to directly get a density representation of the stationary profile with respect to the Lebesgue measure, without checking additional statements.

Finally, we present models for studying the biological phenomenon of telomere shortening (see the biological motivation below) with a continuous state space and non-exponential division times. In particular, we exhibit conditions for the parameters of these models which imply a convergence towards a stationary profile, and we compare them with the biological reality.

**Difficulties.** The main difficulty we face is that jumps occur in a continuous trait space, such that the jump kernel is not absolutely continuous with respect to the Lebesgue measure, due to the fact that certain coordinates of our trait stay fixed during jumps. This implies that the operator associated with the infinitesimal generator of our model is not compact. Hence, it is impossible to use methods based on Krein-Rutman theorem as for instance in Doumic [21] or Perthame [43], or even Bertoin [10]. In addition, for methods based on non-conservative versions of Harris' ergodic theorem as those presented in Champagnat and Villemonais [13, 16, 15, 14] or in Bansaye et al. [5], and applied for example in Tomašević, Bansaye, and Véber [49], the control of the asymptotic comparison of survival is not trivial. For more information, we refer to Section 4.4.

The second difficulty we face is the age structure of our model, and the fact that the birth rate is not bounded from above in the age variable, nor is it bounded away from 0. Therefore, obtaining fine exponential estimates for the growth of the total number of individuals or for the rate at which individuals come back to compact sets is arduous. The usual strategies of dominating the jump times with exponential random variables or of bounding the infinitesimal generator and then applying Gronwall's lemma fail. Moreover, even in the bounded rate case, these strategies do not give precise enough estimates necessary for our purpose. To circumvent the latter, we stochastically compare the number of individuals in our model by Bellman-Harris processes. This allows us to obtain very precise exponential estimates by using results from the renewal theory, see Athreya and Ney [3, Chap. IV.4]. We believe that this method can be applied in many other settings with an age structure. For more information, we refer to Sections 4.3.4, 4.3.5 and 4.4.4.

**Literature.** Studying long time behaviour of Markov processes has received considerable attention in the literature since the seminal work of Meyn and Tweedie [41]. Usually, the authors search for one criteria to verify in a general setting in order to obtain the ergodic behaviour with exponential speed of convergence in total variation norm, see e.g. [4, 5, 14, 15, 16, 19, 20, 23, 29, 30, 33, 40, 41, 52]. The

problem of the discontinuities with respect to the Lebesgue measure is very recent in the literature, and few articles have tackled it, either on the probability or PDE side. On the probability side, the only paper we have found dealing with this type of jump Markov process is [54]. This article is related to other works that we mention here [37, 51, 52, 53]. In these works, the author proposes to use stopping times to couple trajectories, with conditions on it allowing the control of the "rare events" that make the coupling of trajectories fails. This result can be understood as a weak form of Harnack inequality. As in the example presented in [54, Section 5], the rare events in our model are cases where the typical particle representing our branching process has not jumped in all the coordinates. On the PDE side, the recent and fine results obtained in Fonte Sanchez, Gabriel, and Mischler [24] also handle the issues we have linked to the discontinuities of our jump kernel with respect to the Lebesgue measure. In particular, we refer to [24, Section 12.2] where this type of model has been studied. In a forthcoming paper, an alternative proof from the PDE side combining regularisation approach and some ideas of the present work will be proposed.

Many studies about the ergodic behaviour of age-dependent models have been done in the recent years, see for example [4, 9, 18, 25, 27, 28, 35]. In most cases where the model is structured by a second trait, the birth/jump rate is bounded from above and/or below [9, 18, 25, 27, 35]. This condition, for example, enables one to use the infinitesimal and prove with ease that a Foster-Lyapunov criterion is satisfied when the Harris's ergodic theorem for conservative semigroups is used [25, 35]. We can identify at least two differences between our model and those of these studies. The first one is that as we use a non-conservative version of the Harris's ergodic theorem, we need to check additional assumptions for verifying the Lyapunov criterion, see the condition between  $\gamma_1$  and  $\gamma_2$  in [16, Assump.  $(F_2)$ ]. These additional assumptions correspond to the exponential estimates presented before. The second one is that we work with an unbounded birth rate. It is therefore not possible to compare birth/jump times with exponential random variables, and the computations with the infinitesimal generator are more difficult. This also means that we need to study a distorted version of the process in the age variable. We mention that in Bansaye, Cloez, and Gabriel [4, Section 3.3.2], a non-conservative version of the Harris's ergodic theorem is used to obtain the stationary profile of a model with an unbounded birth rate. However, Lyapunov techniques were not required for their model as there is no other trait than the age and as the speed of convergence does not depend on the initial condition. We also mention that in Gabriel and Martin [28], a stationary profile for a model with an unbounded birth rate is also obtained using operator theory and entropy methods. As entropy methods do not give information about the speed of convergence, there was no need to obtain exponential estimates as precise as we require here. To the best of our knowledge, our method based on stochastic comparisons by Bellman-Harris processes to obtain such exponential estimates has not yet been studied.

We finally point out that Benetos et al. [8] study the long-time behaviour of a model with a similar biological motivation to ours. The main difference from a mathematical point of view is that the model is in a discrete state space and without age structure.

**Proof strategy.** The result in [54] is stated for absorbing Markov processes with one particle. Moreover, in our model, the speed of convergence towards the stationary profile depends on the initial trait. To solve these issues, we first weight the first moment semigroup of our branching process with a Lyapunov function, then normalise it, and finally create an auxiliary particle representing this weighted-normalised semigroup. The creation of this auxiliary particle follows the ideas presented in [14]. Another way to represent our semigroup with an auxiliary particle is the one presented in [5]. However, it seems less adapted for a birth and death framework with jumps in a multidimensional space like ours. Once we have our auxiliary process, we verify the assumptions presented in [54] to get the ergodic behaviour of this auxiliary particle and then conclude by coming back to our population model.

During our proofs, we always juggle between the branching and the particle representation of our model. To be more precise, we return to the branching representation to do our stochastic comparisons to Bellman-Harris processes. For example, to obtain the accumulation of the mass of the semigroup on a compact set, we first bound from above or from below the (weighted) branching process by Bellman-Harris processes, and then we transmit the bounds we have obtained to the auxiliary process. This procedure is also used to obtain the weak form of Harnack inequality, where we also need exponential estimates. Going back and forth from the branching representation to the particle representation is an interesting way to verify the assumptions presented in [52, 54], or in [13, 14, 15, 16, 5].

**Biological motivation.** Motivated by studying telomere shortening in a cell population, our model aims to propose a mathematical framework for it, completing the different models of the phenomenon developed in the recent years [2, 8, 9, 34, 47, 55]. A telomere is a highly repetitive, and *a priori* non-coding, region of DNA situated at both ends of a chromosome. Its role is to protect the terminal regions of chromosomal DNA from progressive shortening and ensure the integrity of chromosomes. During DNA replication that precedes the cell division, enzymes essential for it fail to copy the last nucleotides on one end of each chromosome in the cell. Thus, the presence of telomeres at the ends of chromosomes prevents the rapid loss of genetic information crucial to the functioning of the cell. Instead of losing the nucleotides linked to the genetic information, it is the telomeres that are "shortened".

When the telomeres of a cell are not long enough to protect against the loss of coding DNA, the cell becomes senescent, which is characterised by an irreversible cell cycle arrest. It has been deduced experimentally and with the help of simulations that the shortest telomere of all the chromosomes is responsible for senescence onset in cell, see Abdallah et al. [1], Bourgeron et al. [11], Hemann et al. [31], Martin et al. [38] and Xu et al. [56]. To avoid the state of senescence, certain cells such as budding yeast cells have an enzyme, the telomerase, that regenerates telomere sequence by "lengthening". It acts just before the cell division, and it is yet unclear whether its action concerns both daughter cells or only one of them. Cells with sufficient telomerase activity are somehow considered immortal. On the level of human cells, this ability seems to be attributed to cancer cells, see Robinson and Schiemann [45].

**Organisation of the paper.** In Section 2, we present the main notions we use in the article, we give in detail the model under consideration, and we present the main result. In Section 3 we present the auxiliary processes we use to apply the result of [54]. In Section 4, we prove the main result of the article. Finally, in Section 5, we give conditions for which the assumptions necessary to use our theorem are satisfied, and present two models where they are verified. The appendices A-C are devoted to the proof of certain auxiliary statements given during this paper.

## 2 Notations, preliminaries and main result

Taking into account our biological motivation, from now on, the individuals in our population are called cells. Each cell has  $k$  chromosomes, and each extremity of each chromosome corresponds to one telomere, so the cell has  $2k$  telomeres. The traits  $(x, a) \in \mathbb{R}_+^{2k} \times \mathbb{R}_+$  of the cells that are not in the cemetery state are the lengths of their telomeres and their age. Branching events are called divisions, and at each division, certain telomere lengths are updated ("shortened" or "lengthened") with jumps in a continuous trait, while the others stay fixed. When the length of a telomere is below zero, we usually say that the cell becomes senescent, meaning that the individual is moved to the cemetery state.

The aim of this section is to present the main result of the paper: the exponential convergence of the first moment semigroup towards a stationary profile. To present this result, it is necessary to introduce a certain number of notions. Hence, the first part of this section is devoted to the presentation of the notations and the model that we use throughout the paper (Sections 2.1 and 2.2). We then present the assumptions and the main result in Section 2.3.

### 2.1 Notations and first definitions

Here are the notations and mathematical notions we use throughout the paper. In all the statements in this section,  $(\mathbb{X}, Top(\mathbb{X}))$  denotes an arbitrary topological space.

- i) We work on the probability space  $(\Omega, \mathcal{A}, \mathbb{P})$ .
- ii) We denote by  $\mathcal{B}(\mathbb{X})$  the  $\sigma$ -algebra of the Borel sets of  $(\mathbb{X}, Top(\mathbb{X}))$ .
- iii) For any random variable  $Z : (\Omega, \mathcal{A}, \mathbb{P}) \mapsto (\mathbb{X}, \mathcal{B}(\mathbb{X}))$ , we denote  $\mathbb{P}_Z$  the probability measure such that  $\mathbb{P}_Z = \mathbb{P} \circ Z^{-1}$ .
- iv) For all  $S \subset \mathbb{X}$ ,  $\text{int}(S)$  is the interior of  $S$ .
- v) Let  $\mathcal{U} = \bigcup_{n \in \mathbb{N}} \{\mathbb{N}^* \times \{1, 2\}^n\}$ . As we use a branching process, this set allows us to denote the individuals in the tree thanks to the classical Ulam-Harris-Neveu notation.

- vi) We consider  $\mathcal{X} = \mathbb{R}_+^{2k} \times \mathbb{R}_+$ , that we endow with the Euclidean topology. This space represents the trait space for non-senescent individuals.
- vii) We consider  $\partial$  an arbitrary element outside of  $\mathbb{R}^d$  for all  $d \in \mathbb{N}^*$ .
- viii) Let us denote for all  $n \in \mathbb{N}^*$  the tuple  $(\partial)_n := (\partial, \dots, \partial)$  where there is  $n$  times the term  $\partial$ . Each time it is used,  $(\partial)_n$  represents a cemetery for the cartesian product between  $n$  sets  $(A_i)_{1 \leq i \leq n}$ . We use the set  $(A_1 \times \dots \times A_n) \cup \{(\partial)_n\}$  instead of  $(A_1 \times \dots \times A_n) \cup \{\partial\}$  as it is meaningless to consider a tuple  $(a_1, \dots, a_n) \in \{\partial\}$ .
- ix) We consider  $\mathcal{X}_\partial = \mathcal{X} \cup \{(\partial)_2\}$ , such that  $(\partial)_2$  is an isolated point of  $\mathcal{X}_\partial$ . This space represents the trait space of individuals, and  $(\partial)_2$  represents the trait of senescent individuals.
- x) We use the convention that  $\prod_{\emptyset} = 1$  and  $\inf(\emptyset) = +\infty$  in all the paper.
- xi) We denote by  $\mathcal{M}(\mathbb{X})$  the set of positive measures on  $(\mathbb{X}, \mathcal{B}(\mathbb{X}))$ .
- xii) We denote by  $\mathcal{M}_1(\mathbb{X}) \subset \mathcal{M}(\mathbb{X})$  the set of probability measures on  $(\mathbb{X}, \mathcal{B}(\mathbb{X}))$ .
- xiii) We denote by  $\mathcal{M}_P(\mathbb{X})$  the set of all finite non-negative point measures on  $\mathbb{X}$ . We endow it with the topology of weak convergence.
- xiv) For every Borel measurable function  $f$  on  $(\mathbb{X}, \text{Top}(\mathbb{X}))$ , every  $\mu \in \mathcal{M}(\mathbb{X})$ , we write

$$\mu(f) := \int_{x \in \mathbb{X}} f(x) \mu(dx).$$

We also write  $\mu(1) := \int_{x \in \mathbb{X}} \mu(dx)$ .

- xv) Let  $(P_t)_{t \geq 0}$  a family of linear maps from the set of measurable function  $f : \mathbb{X} \rightarrow \mathbb{R}$  to itself. Then for all  $f : \mathbb{X} \mapsto \mathbb{R}$  measurable and  $\mu \in \mathcal{M}(\mathbb{X})$ , we write

$$\mu P_t(f) := \int_{z \in \mathbb{X}} P_t(f)(z) \mu(dz).$$

- xvi) For any stochastic process  $(X_t)_{t \geq 0}$  defined on  $\mathcal{X}$ , we write for all  $(x, a) \in \mathcal{X}$ ,  $f : \mathcal{X} \mapsto \mathbb{R}$  measurable,  $t \geq 0$

$$\mathbb{E}_{(x,a)} [f(X_t)] := \mathbb{E}_{(x,a)} [f(X_t) | Z_0 = (x, a)],$$

and for any  $\mu \in \mathcal{M}_1(\mathcal{X})$

$$\mathbb{E}_\mu [f(X_t)] := \int_{(x,a) \in \mathcal{X}} \mathbb{E}_{(x,a)} [f(X_t)] \mu(dx, da).$$

- xvii) Let  $(X_t)_{t \geq 0}$  a stochastic process defined on  $\mathcal{X}$ ,  $t \geq 0$ ,  $(x, a) \in \mathcal{X}$ . Then for any random variable  $W$ ,  $A$  a subset of the set where  $W$  takes its values, and  $f \in M_b(\mathcal{X})$ , we denote

$$\mathbb{E}_{(x,a)} [f(X_t); W \in A] := \mathbb{E}_{(x,a)} [f(X_t) \mathbf{1}_{\{W \in A\}}].$$

- xviii) We consider  $Y_0$  a  $\mathcal{M}_P(\mathcal{U} \times \mathcal{X}_\partial)$ -valued random variable. This random variable represents the initial distribution of the population. Its distribution will be specified when needed.
- xix) Let  $K \in \mathbb{N}^*$ . We consider  $N(ds, du, dz, d\theta)$  a Poisson point measure on  $\mathbb{R}_+ \times \mathcal{U} \times \mathbb{R}_+ \times [0, 1]^K$  with intensity measure  $ds \times (\sum_{u \in \mathcal{U}} \delta_u(du)) \times dz \times d\theta$ . This random measure allows us to describe the jumps that occur in our dynamics.  $K$  is the number of uniform random variables needed to update telomere lengths, and can be taken for example as  $K = 6k + 2$  (see the third point of the discussion about [\(S<sub>1</sub>\)](#), p.16).
- xx)  $(\mathcal{F}_t)_{t \geq 0}$  represents the canonical filtration generated by  $N(ds, du, dz, d\theta)$  and  $Y_0$ .
- xxi) We denote by  $\mathcal{C}_b^{m,1}(\mathcal{X}_\partial)$  the space of bounded Borel functions  $f : (x, a) \in \mathcal{X}_\partial \rightarrow \mathbb{R}$  verifying the following properties:

- $f$  is measurable in the first variable,
- The restriction of  $f$  on  $\mathcal{X}$  is continuously differentiable in the second variable, with bounded derivative in the second variable.

xxii) For all  $S \subset \mathcal{X}_\partial$  we denote by  $\mathcal{C}_b^{1,m,m,1}(\mathbb{R}_+ \times \mathcal{U} \times S)$  the space of bounded Borel functions  $f : (t, u, x, a) \in \mathbb{R}_+ \times \mathcal{U} \times S \rightarrow \mathbb{R}$ , verifying the following properties:

- $f$  is continuously differentiable in the first variable, with bounded derivative in the first variable.
- $f$  is measurable in the second and third variables.
- The restriction of  $f$  on  $\mathbb{R}_+ \times \mathcal{U} \times \mathcal{X}$  is continuously differentiable in the fourth variable, with bounded derivative in the fourth variable.

xxiii) We denote by  $M(\mathbb{X})$  the space of Borel functions  $f : \mathbb{X} \rightarrow \mathbb{R}$ , by  $M_b(\mathbb{X})$  the space of bounded Borel functions  $f : \mathbb{X} \rightarrow \mathbb{R}$ , and by  $M_b^{loc}(\mathbb{X})$  the space of locally bounded Borel functions  $f : \mathbb{X} \rightarrow \mathbb{R}$ .

xxiv) For any Borel function  $\psi : \mathbb{X} \rightarrow \mathbb{R}$ , we denote by  $\mathcal{B}(\psi)$  the space of the Borel functions  $f : \mathbb{X} \rightarrow \mathbb{R}$  such that

$$\sup_{x \in \mathbb{X}} \left| \frac{f(x)}{\psi(x)} \right| < +\infty.$$

We endow  $\mathcal{B}(\psi)$  with the norm  $\|f\|_{\mathcal{B}(\psi)} := \sup_{x \in \mathbb{X}} \left| \frac{f(x)}{\psi(x)} \right|$ .

xxv) For any Borel function  $\psi : \mathbb{X} \rightarrow \mathbb{R}$  such that  $\inf_{x \in \mathbb{X}} \psi(x) > 0$ , we denote by  $\mathcal{M}_+(\psi)$  the cone of the positive measures that integrate  $\psi$ , and  $\mathcal{M}(\psi) = \mathcal{M}_+(\psi) - \mathcal{M}_+(\psi)$  the set containing all the differences of measures in  $\mathcal{M}_+(\psi)$ . It is a subset of the signed measures space. We endow  $\mathcal{M}(\psi)$  with the norm  $\|\cdot\|_{\mathcal{M}(\psi)}$ , defined for all  $\mu = \mu_+ - \mu_- \in \mathcal{M}(\psi)$  as

$$\|\mu\|_{\mathcal{M}(\psi)} := \sup_{f \in \mathcal{B}(\psi), \|f\|_{\mathcal{B}(\psi)} \leq 1} |\mu(f)| = \mu_+(\psi) + \mu_-(\psi).$$

xxvi) We denote by  $L^1(\mathbb{X})$  the set of the functions  $f : \mathbb{X} \rightarrow \mathbb{R}$  that are integrable with respect to the Lebesgue measure. We also denote by  $L_{loc}^1(\mathbb{X})$  the space of the functions  $f : \mathbb{X} \rightarrow \mathbb{R}$  that are locally integrable with respect to the Lebesgue measure.

xxvii) For any Borel function  $\psi : \mathbb{R}_+^{2k} \times \mathbb{R}_+ \rightarrow \mathbb{R}$ , we denote

$$L^1(\psi) := \left\{ f : \mathbb{R}_+^{2k} \times \mathbb{R}_+ \rightarrow \mathbb{R} \mid \int_{\mathbb{R}_+^{2k} \times \mathbb{R}_+} |f(x, a) \psi(x, a)| dx da < +\infty \right\}.$$

xxviii) We denote by  $L_{p.d.f.}^1(\mathbb{X})$  the set of the measurable functions  $f : \mathbb{X} \rightarrow \mathbb{R}_+$  such that  $\int_{\mathbb{X}} f(x) dx = 1$ .

xxix) We denote by  $\mathcal{C}_c^\infty(\text{int}(\mathbb{X}))$  the space of  $\mathcal{C}^\infty$  functions defined on  $\text{int}(\mathbb{X})$ , taking values in  $\mathbb{R}$ , and with compact support.

xxx) For all  $d \in \mathbb{N}^*$ ,  $S \subset \mathbb{R}^d$ , we denote by  $\mathcal{C}_0(S)$  the space of continuous functions from  $S$  to  $\mathbb{R}$  that vanish at infinity.

xxxi)  $\|\cdot\|_{TV, \mathbb{X}}$  is the total variation norm on  $\mathcal{M}(\mathbb{X})$ . For any  $\mu \in \mathcal{M}(\mathbb{X})$ ,

$$\|\mu\|_{TV, \mathbb{X}} := \sup_{f : \mathbb{X} \rightarrow [-1, 1], f \text{ mes.}} |\mu(f)|.$$

xxxii) For all  $(a, b) \in \mathbb{Z}^2$  such that  $a < b$ , we denote

$$\llbracket a, b \rrbracket := \{a, a+1, \dots, b-1, b\}.$$

xxxiii) For any  $S \subset \mathbb{X}$ , we denote  $S^c = \mathbb{X} \setminus S$ .



xxxiv) For any finite set  $S \subset \mathbb{X}$ , we denote  $\#(S)$  the cardinal of  $S$ .

xxxv) For any set  $X$ , we denote by  $\mathcal{P}(X)$  the power set of  $X$  i.e. the set containing all subsets of  $X$ .

xxxvi) For any finite set  $X$ , and for any  $l \in \llbracket 0, \#X \rrbracket$ , we denote  $\mathcal{P}_l(X) = \{S \in \mathcal{P}(X) \mid \#S = l\}$  the set containing all subsets of  $X$  of size  $l$ .

xxxvii) Let  $n \in \mathbb{N}^*$ . For all  $i \in \llbracket 1, n \rrbracket$ ,  $e_i$  is the  $i$ -th vector in the canonical basis of  $\mathbb{R}^n$ .

xxxviii) We consider for all  $f : \mathbb{R}_+ \rightarrow \mathbb{R}$ ,  $g : \mathbb{R}_+ \rightarrow \mathbb{R}$ ,  $n \in \mathbb{N}$ , the operation  $f *^{(n)} g = f * f * \dots * f * g$ , where there is  $n$  times the function  $f$ . We use the convention that  $f *^{(0)} g = g$ .

xxxix) For any measurable function  $f : \mathbb{R}_+ \rightarrow \mathbb{R}$ , we denote by  $\mathcal{L}(f)$  its Laplace transform, defined such that  $\mathcal{L}(f)(p) = \int_0^{+\infty} e^{-pt} f(t) dt$  for all  $p \in \mathbb{C}$  such that the integral converges.

xl) For any probability density function  $F : \mathbb{R}_+ \rightarrow \mathbb{R}_+$ , we denote by  $\bar{F}$  its associated complementary cumulative distribution function.

## 2.2 Presentation of the model

We work in continuous time, and we use an individual-based approach where each individual is a cell. When a cell divides, it gives birth to two daughter cells  $A$  and  $B$  (the choice of which daughter cell is  $A$  or  $B$  is arbitrary). The traits of each individual are the lengths of its telomeres and its age, or  $(\partial)_2$  when it is a senescent cell. Each cell has  $2k$  telomeres, one per chromosome end. We associate each coordinate with the length of a telomere, such that for all  $i \in \llbracket 1, k \rrbracket$ , the coordinates  $i$  and  $i+k$  of a vector in  $\mathbb{R}_+^{2k}$  represent the lengths of the two telomeres of the same chromosome. Let us now introduce the following objects needed to construct our model.

- A division rate  $b : (x, a) \in \mathbb{R}_+^{2k} \times \mathbb{R}_+ \rightarrow \mathbb{R}_+$ , and constants  $\tilde{b} > 0$ ,  $d_b \in \mathbb{N}^*$ ,  $b_0 > 0$ ,  $a_0 \geq 0$ . We assume that the birth rate satisfies

$$\forall (x, a) \in \mathbb{R}_+^{2k} \times \mathbb{R}_+ : |b(x, a)| \leq \tilde{b}(1 + a^{d_b}), \quad \forall (x, a) \in \mathbb{R}_+^{2k} \times [a_0, +\infty[ : b(x, a) \geq b_0. \quad (2.2.1)$$

- A probability measure  $\mu^{(S)} \in \mathcal{M}_1(\mathbb{R}_+^{2k} \times \mathbb{R}_+^{2k})$  representing the distribution of telomere shortening at each cell division. It is assumed independent of telomere lengths. When we draw a pair  $(U, U')$  distributed according to  $\mu^{(S)}$ ,  $U$  corresponds to the shortening in the daughter cell  $A$ , and  $U'$  the shortening in the daughter cell  $B$ . The complete expression of this measure is given later, see (2.2.5).
- For all  $(s_1, s_2) \in \mathbb{R}^{2k} \times \mathbb{R}^{2k}$ , a probability measure  $\mu_{(s_1, s_2)}^{(E)} \in \mathcal{M}_1(\mathbb{R}_+^{2k} \times \mathbb{R}_+^{2k})$  which represents the distribution of telomere elongation by telomerase, when the two daughter cells  $A$  and  $B$  have respective telomere lengths  $s_1$  and  $s_2$  after shortening. When we draw a pair  $(V, V')$  distributed according to  $\mu_{(s_1, s_2)}^{(E)}$ ,  $V$  corresponds to the lengthening in the daughter cell  $A$ , and  $V'$  the lengthening in the daughter cell  $B$ . As for  $\mu^{(S)}$ , its complete expression is given later, see (2.2.7).
- For every  $x \in \mathbb{R}_+^{2k}$ , we define the measure  $\Pi_x$  such that  $\forall C \in \mathcal{B}((\mathbb{R}_+^{2k})^2)$

$$\Pi_x(C) := \int_{(y_1, y_2) \in (\mathbb{R}_+^{2k})^2} \left[ \int_{(z_1, z_2) \in (\mathbb{R}_+^{2k})^2} 1_C(-y_1 + z_1, -y_2 + z_2) d\mu_{(x-y_1, x-y_2)}^{(E)}(z_1, z_2) \right] d\mu^{(S)}(y_1, y_2). \quad (2.2.2)$$

This is the kernel used to represent the distribution of telomere lengths variation (shortening + lengthening), when a cell with telomere lengths  $x \in \mathbb{R}_+^{2k}$  divides.

- For all  $x \in \mathbb{R}_+^{2k}$ , we assume that we can define a measurable function  $R(x, \cdot) : [0, 1]^K \rightarrow (\mathbb{R}^{2k})^2$ , where  $K$  is defined in Notations [xix](#)), such that for all  $f : (\mathbb{R}^{2k})^2 \rightarrow \mathbb{R}$  bounded measurable

$$\int_{[0, 1]^K} f(R(x, \theta)) d\theta = \int_{(w_1, w_2) \in (\mathbb{R}^{2k})^2} f(w_1, w_2) d\Pi_x(w_1, w_2). \quad (2.2.3)$$

The latter represents a procedure to simulate random variables distributed according to  $\Pi_x$  with uniform random variables, see [\[36, p. 2655\]](#).

We now give the complete expression for the measures  $\mu^{(S)}$  and  $\left(\mu_{(s_1, s_2)}^{(E)}\right)_{(s_1, s_2) \in (\mathbb{R}^{2k})^2}$ . The expression of these measures comes from biological modelling.

- We start with  $\mu^{(S)}$ . At each cell division, for each chromosome  $i \in \llbracket 1, k \rrbracket$ , in view of [22, Fig.1] we have:
  - One of the daughter cells, which can be  $A$  or  $B$ , has the telomere represented by the coordinate  $i$  shortened (corresponds to one end of the chromosome  $i$ ), and the telomere represented by the coordinate  $i + k$  not shortened (corresponds to the other end of the chromosome  $i$ ).
  - The other daughter cell has the telomere represented by the coordinate  $i + k$  shortened, the telomere represented by the coordinate  $i$  not shortened.

Then, to write an explicit expression for  $\mu^{(S)}$ , we denote

$$\mathcal{I}_k := \left\{ I \in \mathcal{P}_k(\llbracket 1, 2k \rrbracket) \mid \forall (i, j) \in I^2 : i \neq j \implies (i \bmod k) \neq (j \bmod k) \right\}. \quad (2.2.4)$$

This corresponds to the set containing all the possible combinations of telomere coordinates that can be shortened at each division in one of the daughter cell (we refer to Example 2.1 for an expression of  $\mathcal{I}_k$  when  $k$  is small). Indeed, the condition " $\forall (i, j) \in I^2 : i \neq j \implies (i \bmod k) \neq (j \bmod k)$ " corresponds to the fact that for each chromosome  $i \in \llbracket 1, k \rrbracket$ , it is either the coordinate  $i$  or the coordinate  $i + k$  that is shortened during a cell division, but not both.

We also denote  $g \in L_{\text{p.d.f.}}^1(\mathbb{R}_+)$ , that corresponds to the probability density function of the shortening size. Then, we use the following expression for  $\mu^{(S)}$

$$\begin{aligned} d\mu^{(S)}(\alpha_1, \alpha_2) &= \frac{1}{\#(\mathcal{I}_k)} \sum_{I \in \mathcal{I}_k} \prod_{i \in I} [g((\alpha_1)_i) d(\alpha_1)_i \delta_0(d(\alpha_2)_i)] \\ &\times \prod_{i' \in \llbracket 1, 2k \rrbracket \setminus I} [g((\alpha_2)_{i'}) d(\alpha_2)_{i'} \delta_0(d(\alpha_1)_{i'})] =: \frac{1}{\#(\mathcal{I}_k)} \sum_{I \in \mathcal{I}_k} d\mu^{(S, I)}(\alpha_1, \alpha_2). \end{aligned} \quad (2.2.5)$$

Qualitatively, this expression means that at each division, we draw one set  $I \in \mathcal{I}_k$  uniformly. This set gives us which coordinates are shortened in the daughter cell  $A$  (terms  $g((\alpha_1)_i) d(\alpha_1)_i$ ), and that are not shortened in the daughter cell  $B$  (terms  $\delta_0(d(\alpha_2)_i)$ ). Considering now the set  $\llbracket 1, 2k \rrbracket \setminus I$ , we also have the coordinates that are shortened in the daughter cell  $B$  (terms  $g((\alpha_2)_{i'}) d(\alpha_2)_{i'}$ ), and not shortened in the daughter cell  $A$  (terms  $\delta_0(d(\alpha_1)_{i'})$ ).

**Example 2.1.** When  $k = 2$ , we have

$$\mathcal{I}_k = \{\{1, 2\}, \{1, 4\}, \{2, 3\}, \{3, 4\}\}.$$

If at a cell division we have drawn the set  $\{1, 4\} \in \mathcal{I}_k$ , then the coordinates where there is a shortening in the daughter cell  $A$  are 1 and 4, and the coordinates where there is a shortening in the daughter cell  $B$  are 2 and 3.

- Now, we deal with  $\left(\mu_{(s_1, s_2)}^{(E)}\right)_{(s_1, s_2) \in (\mathbb{R}^{2k})^2}$ . We denote

$$\mathcal{J}_k := \left\{ (J, M) \in \mathcal{P}_l(\llbracket 1, 2k \rrbracket) \times \mathcal{P}_m(\llbracket 1, 2k \rrbracket) \mid (l, m) \in \llbracket 1, 2k \rrbracket^2 \right\}.$$

This corresponds to the set containing all the possible combinations of telomere coordinates that can be lengthened at each division. For any pair  $(J, M) \in \mathcal{J}_k$ ,  $J$  corresponds to the coordinates that are lengthened in the daughter cell  $A$ , and  $M$  corresponds to the coordinates that are lengthened in the daughter cell  $B$ .

Short telomeres are more susceptible to be lengthened compared to large telomeres. Then, the choice of which coordinates are lengthened in the two daughter cells depends on the values of telomere lengths of the daughter cells after shortening. To take this into account, for any

$(s_1, s_2) \in (\mathbb{R}^{2k})^2$ , we introduce  $(p_{J,M}(s_1, s_2))_{(J,M) \in \mathcal{J}_k}$  a probability mass function on  $\mathcal{J}_k$  that corresponds to the distribution of the choice of which telomeres are lengthened at each division, when telomere lengths of the daughter cells  $A$  and  $B$  are respectively  $s_1$  and  $s_2$  after shortening. As the choice of which daughter cell is the daughter cell  $A$  or the daughter cell  $B$  is arbitrary, the distribution of elongation must be symmetric. Then, we assume that for all  $(J, M) \in \mathcal{J}_k$ ,  $(s_1, s_2) \in (\mathbb{R}^{2k})^2$  we have

$$p_{J,M}(s_1, s_2) = p_{M,J}(s_2, s_1). \quad (2.2.6)$$

We finally introduce for all  $x \in \mathbb{R}$  the function  $h(x, \cdot) \in L^1_{\text{p.d.f.}}(\mathbb{R}_+)$ . This function represents the distribution of the lengthening value, when the telomere that is lengthened has a length  $x$ . We are now able to write the expression we use for  $\mu_{(s_1, s_2)}^{(E)}$ . For all  $(s_1, s_2) \in (\mathbb{R}^{2k})^2$  (recall that  $\prod_{\emptyset} = 1$ ), we have

$$\begin{aligned} d\mu_{(s_1, s_2)}^{(E)}(\beta_1, \beta_2) &= \sum_{(J, M) \in \mathcal{J}_k} p_{J, M}(s_1, s_2) \left( \prod_{j \in J} h((s_1)_j, (\beta_1)_j) d(\beta_1)_j \right) \left( \prod_{j' \in [1, 2k] \setminus J} \delta_0(d(\beta_1)_{j'}) \right) \\ &\quad \times \left( \prod_{m \in M} h((s_2)_m, (\beta_2)_m) d(\beta_2)_m \right) \left( \prod_{m' \in [1, 2k] \setminus M} \delta_0(d(\beta_2)_{m'}) \right) \\ &=: \sum_{(J, M) \in \mathcal{J}_k} p_{J, M}(s_1, s_2) d\mu_{(s_1, s_2)}^{(E, J, M)}(\beta_1, \beta_2). \end{aligned} \quad (2.2.7)$$

Qualitatively, this expression means that at each division, just after shortening, if the telomere lengths of the daughter cells  $A$  and  $B$  are  $s_1$  and  $s_2$  respectively, we first draw a pair  $(J, M) \in \mathcal{J}_k$ , according to the distribution  $(p_{J', M'}(s_1, s_2))_{(J', M') \in \mathcal{J}_k}$  to know the coordinates that are lengthened in these daughter cells. Then, for any  $j \in J$ , the coordinate  $j$  of the daughter cell  $A$  is lengthened according to a distribution given by the density  $h((s_1)_j, \cdot)$ , and for any  $m \in M$ , the coordinate  $m$  of the daughter cell  $B$  is lengthened according to a distribution given by the density  $h((s_2)_m, \cdot)$ .

**Example 2.2.** We suppose that  $k = 1$ . If after the shortening we have drawn the pair of sets  $(\{1, 2\}, \{2\}) \in \mathcal{J}_k$ , then there is a lengthening in the coordinates 1 and 2 of the daughter cell  $A$ , and a lengthening in the coordinate 2 of the daughter cell  $B$ .

**Remark 2.3.** After telomere shortening and before telomere lengthening, the length of one of the telomeres in a daughter cell may be less than 0. This is because we have assumed that we determine whether a cell is senescent or not only after telomere lengthening. Therefore, if a cell has a negative telomere length after telomere shortening, it can still be saved by telomere lengthening. That is why the measures  $(\mu^{(E)})_{(s_1, s_2) \in (\mathbb{R}^{2k})^2}$  are defined for  $(s_1, s_2) \in (\mathbb{R}^{2k})^2$ , and not for  $(s_1, s_2) \in (\mathbb{R}_+^{2k})^2$ .

**Remark 2.4.** For all  $C \in \mathcal{B}(\mathbb{R}_+^{2k} \times \mathbb{R}_+^{2k})$ , we denote  $\underline{C} = \{(y_1, y_2) \in \mathbb{R}_+^{2k} \times \mathbb{R}_+^{2k} \mid (y_2, y_1) \in C\}$ . Eq. (2.2.6) and the fact that  $\{[1, 2k] \setminus I \mid I \in \mathcal{I}_k\} = \mathcal{I}_k$  imply that for all  $(s_1, s_2) \in (\mathbb{R}^{2k})^2$

$$\mu_{(s_1, s_2)}^{(E)}(C) = \mu_{(s_2, s_1)}^{(E)}(\underline{C}), \quad \text{and} \quad \mu^{(S)}(C) = \mu^{(S)}(\underline{C}). \quad (2.2.8)$$

Then, for all measurable function  $f : (\mathbb{R}_+^{2k})^2 \rightarrow \mathbb{R}$  and  $(s_1, s_2) \in (\mathbb{R}^{2k})^2$ , it holds

$$\begin{aligned} \int_{(\beta_1, \beta_2) \in (\mathbb{R}_+^{2k})^2} f(\beta_1, \beta_2) d\mu_{(s_1, s_2)}^{(E)}(\beta_1, \beta_2) &= \int_{(\beta_1, \beta_2) \in (\mathbb{R}_+^{2k})^2} f(\beta_2, \beta_1) d\mu_{(s_2, s_1)}^{(E)}(\beta_1, \beta_2), \\ \int_{(\beta_1, \beta_2) \in (\mathbb{R}_+^{2k})^2} f(\alpha_1, \alpha_2) d\mu^{(S)}(\alpha_1, \alpha_2) &= \int_{(\alpha_1, \alpha_2) \in (\mathbb{R}_+^{2k})^2} f(\alpha_2, \alpha_1) d\mu^{(S)}(\alpha_1, \alpha_2), \end{aligned}$$

which implies by (2.2.2) that for all  $f : (\mathbb{R}^{2k})^2 \rightarrow \mathbb{R}$  measurable and  $x \in \mathbb{R}^{2k}$

$$\int_{(w_1, w_2) \in (\mathbb{R}^{2k})^2} f(w_1, w_2) d\Pi_x(w_1, w_2) = \int_{(w_1, w_2) \in (\mathbb{R}^{2k})^2} f(w_2, w_1) d\Pi_x(w_1, w_2). \quad (2.2.9)$$

We now have everything we need to give the algorithm that builds our model. Recall that  $(\partial)_2$  represents the senescent state, and that the trait space is  $\mathcal{X}_\partial = (\mathbb{R}_+^{2k} \times \mathbb{R}_+) \cup \{(\partial)_2\}$ . Let  $(x, a) \in \mathcal{X}_\partial$  the trait of a cell, and  $u \in \mathcal{U}$  its label.

1. At a rate  $b(x, a)1_{\{(x,a) \neq (\partial, \partial)\}}$ , the cell divides.
2. At each division, we draw a pair of random variables  $(U, U') \in \mathbb{R}_+^{2k} \times \mathbb{R}_+^{2k}$  following a distribution given by  $\mu^{(S)}$ , and a pair of random variables  $(V, V') \in \mathbb{R}_+^{2k} \times \mathbb{R}_+^{2k}$  following a distribution given by  $\mu_{(x-U, x-U')}^{(E)}$ . The telomeres of the daughter cell  $A$  are shortened by  $U$ , lengthened by  $V$ . The telomeres of the daughter cell  $B$  are shortened by  $U'$ , lengthened by  $V'$ . Thus, the telomeres and the labels of the two daughter cells are updated as follows

$$x \longrightarrow \begin{cases} x - U + V, \\ x - U' + V', \end{cases} \quad u \longrightarrow \begin{cases} u1, \\ u2. \end{cases}$$

Let  $\theta = (\theta_1, \theta_2, \dots, \theta_K)$  a tuple of  $K$  independent uniform random variables on  $[0, 1]$ . As by (2.2.3) it holds  $R(x, \theta) \stackrel{d}{=} (-U + V, -U' + V')$ , we can rewrite the updating of the telomeres and the labels as

$$x \longrightarrow \begin{cases} x + (R(x, \theta))_1, \\ x + (R(x, \theta))_2, \end{cases} \quad u \longrightarrow \begin{cases} u1, \\ u2. \end{cases}$$

3. After the lengthening, if  $\min(x_i + (R(x, \theta))_i, i \in \llbracket 1, 2k \rrbracket) < 0$  for one of the daughter cells, the trait of this daughter cell at birth is  $(\partial)_2$ . Otherwise, the trait of this daughter cell is  $(x - U + V, 0)$  or  $(x - U' + V', 0)$ . Thus, 0 acts as a threshold to determine if a cell is senescent or not. It is also possible to use a rate to enter in senescence rather than a threshold. However, recent results coming from parameter calibration of telomere shortening models seem to support the fact that a deterministic threshold is a good approximation [44].

Assume that we start from  $Y_0$  defined in Notation xviii), and denote by  $(Y_t)_{t \geq 0}$  the  $\mathcal{M}_P(\mathcal{U} \times \mathcal{X}_\partial)$ -valued random process representing the dynamics described above. For all  $t \geq 0$ ,  $V_t \subset \mathcal{U}$  is the set that contains the labels of the individuals at time  $t$  with a trait different from  $(\partial)_2$ . For all  $u \in V_t$ , we denote by  $x^u$  the telomere lengths of  $u$ , by  $T_b(u)$  the birth time of  $u$ , and by  $a_t^u := t - T_b(u)$  the age of  $u$  at time  $t$ . Then  $(Y_t)_{t \geq 0}$  is a solution of the following equation for all  $f \in \mathcal{C}_b^{1,m,m,1}(\mathbb{R}_+ \times \mathcal{U} \times \mathcal{X}_\partial)$ ,  $t \geq 0$ ,

$$\begin{aligned} & \int_{\mathcal{U} \times \mathcal{X}_\partial} f(t, u, x, a) Y_t(du, dx, da) \\ &= \int_{\mathcal{U} \times \mathcal{X}_\partial} f(0, u, x, a) Y_0(du, dx, da) + \int_0^t \int_{\mathcal{U} \times \mathcal{X}_\partial} \left[ \frac{\partial f}{\partial s}(s, u, x, a) + \frac{\partial f}{\partial a}(s, u, x, a) 1_{\{u \in V_s\}} \right] Y_s(du, dx, da) ds \\ &+ \int_{[0,t] \times \mathcal{U} \times \mathbb{R}_+ \times [0,1]^K} 1_{\{u \in V_{s-}\}} 1_{\{z \leq b(x^u, a_{s-}^u)\}} \left[ \sum_{i=1}^2 \left[ f(s, ui, \partial, \partial) 1_{\{x^u + (R(x^u, \theta))_i \notin \mathbb{R}_+^{2k}\}} \right. \right. \\ & \left. \left. + f(s, ui, x^u + (R(x^u, \theta))_i, 0) 1_{\{x^u + (R(x^u, \theta))_i \in \mathbb{R}_+^{2k}\}} \right] - f(s, u, x^u, a_{s-}^u) \right] N(ds, du, dz, d\theta). \end{aligned} \quad (2.2.10)$$

The following theorem guarantees that the above model is well-posed, and that the number of individuals does not explode in finite time.

**Theorem 2.5** (Well-posedness and non-explosion). *Assume that (2.2.1) and (2.2.3) hold, and let  $Y_0$  defined in Notation xviii) such that  $\mathbb{E}[Y_0(1)] < +\infty$ . Then there exists a strongly unique  $(\mathcal{F}_t)_{t \geq 0}$ -adapted càdlàg process  $(Y_t)_{t \geq 0}$  taking values in  $\mathcal{M}_P(\mathcal{U} \times \mathcal{X}_\partial)$ , with initial condition  $Y_0$ , which is solution of (2.2.10).*

This type of result has been obtained as the starting point of many works in the literature, see for example Bansaye and Meleard [6], Bansaye and Tran [7], Champagnat, Ferrière, and Méléard [12], Fournier and Méléard [26], Marguet [36], Tran [50]. The proof has nowadays become standard and we

do not detail it here. We just present briefly the main steps of the proof. First, we adjust the proof of Marguet [36, Lemmas 2.1 and 2.3] to a setting where we need several uniform random variables to update offspring traits. Then, in view of (2.2.1), we bound from above  $\mathbb{E} \left[ \sup_{t \in [0, T]} (Y_t(1)) \right]$  for all  $T > 0$  by  $2\mathbb{E} [Y_0(1)]$  times the mean number of individuals of a dynamics of individuals that branches at a rate  $\tilde{b}(1 + a^{d_b})$  and gives birth to 2 offspring, as done in Bansaye, Cloez, and Gabriel [4, Corollary 3.10]. Finally, we use Athreya and Ney [3, Corollary 1, p.153] to justify that the latter is finite.

We end this subsection by presenting a deterministic representation of the model. We introduce  $(n_t(dx, da))_{t \geq 0}$  a family of measures such that for all  $t \geq 0$ ,  $f \in \mathcal{C}^{m,1}(\mathcal{X}_\partial)$

$$n_t(f) := \mathbb{E} \left[ \int_{\mathcal{U} \times \mathcal{X}_\partial} f(x, a) Y_t(du, dx, da) \right].$$

This measure is called the mean measure of  $(Y_t)_{t \geq 0}$ . For all  $C \in \mathcal{B}(\mathbb{R}_+^{2k})$ ,  $x \in \mathbb{R}_+^{2k}$ , we also introduce the following measure, that is frequently used in this paper

$$\begin{aligned} \mathcal{K}(C)(x) &:= \int_{(w_1, w_2) \in (\mathbb{R}_+^{2k})^2} 1_C((x + w_1)) 1_{\{x + w_1 \in \mathbb{R}_+^{2k}\}} d\Pi_x(w_1, w_2) \\ &+ \int_{(w_1, w_2) \in (\mathbb{R}_+^{2k})^2} 1_C((x + w_2)) 1_{\{x + w_2 \in \mathbb{R}_+^{2k}\}} d\Pi_x(w_1, w_2) \\ &= 2 \int_{(w_1, w_2) \in (\mathbb{R}_+^{2k})^2} 1_C((x + w_1)) 1_{\{x + w_1 \in \mathbb{R}_+^{2k}\}} d\Pi_x(w_1, w_2). \end{aligned} \quad (2.2.11)$$

The last equality is a consequence of (2.2.9). This measure represents the transition probability for telomere lengths of the daughter cells of a cell with telomere lengths  $x$  that divides. The following theorem gives a deterministic representation of (2.2.10). Again, we do not detail the proof of this result as it has become standard, see [6, 26, 49, 50].

**Theorem 2.6** (Deterministic representation). *Let us assume that the assumptions of Theorem 2.5 hold. Then the measure  $(n_t(dx, da))_{t \geq 0}$  is a weak solution of the following equation*

$$\begin{cases} \partial_t n(t, dx, da) + \partial_a n(t, dx, da) = -b(x, a) n(t, dx, da), & (x, a) \in \mathcal{X}, t \geq 0, \\ n(t, dx, a = 0) = \int_{(y, s) \in \mathcal{X}} \mathcal{K}(dx, y) b(y, s) n(t, dy, ds), & x \in \mathbb{R}_+^{2k}, t \geq 0, \\ \partial_t n(t, (\partial)_2) = \int_{(y, s) \in \mathcal{X}} (2 - \mathcal{K}(1)(y)) b(y, s) n(t, dy, ds), & t \geq 0. \end{cases} \quad (2.2.12)$$

In particular, we have the following infinitesimal generator for our model. For all  $f \in \mathcal{C}^{m,1}(\mathcal{X}_\partial)$

$$\frac{\partial}{\partial t} n_t(f)|_{t=0} = \frac{\partial}{\partial a} f(x, a) + b(x, a) (\mathcal{K}(f(x, 0))(x) - 1).$$

### 2.3 Assumptions and main result

Let us remind the reader that from now on,  $k$  is fixed. The main result of this article is the convergence of the first moment semigroup of a solution of (2.2.10) towards a stationary profile. To write the assumptions that we need to verify to obtain this convergence, we introduce the following notations related to the measures  $(\mathcal{K}(\cdot)(y))_{y \in \mathbb{R}_+^{2k}}$ .

- For all  $x \in \mathbb{R}_+^{2k}$ ,  $n \in \mathbb{N}^*$ , for all measurable function  $f : \mathbb{R}_+^{2k} \rightarrow \mathbb{R}$ , we denote

$$\mathcal{K}^n(f)(x) := \underbrace{(\mathcal{K} \circ \dots \circ \mathcal{K})}_{n \text{ times}}(f)(x).$$

We use the convention that  $\mathcal{K}^0(f)(x) = 1$ .

- For all  $x \in \mathbb{R}_+^{2k}$ ,  $C \subset \mathbb{R}_+^{2k}$  a measurable set, and  $f : \mathbb{R}_+^{2k} \rightarrow \mathbb{R}$  a measurable function, we denote

$$\mathcal{K}_C(f)(x) := \mathcal{K}(f1_C)(x). \quad (2.3.1)$$

We now write the assumptions on our model that imply the main result of this paper. They will be discussed at the end of the section. We distinguish three sets of assumptions. The first set corresponds to lower/upper bounds and regularity assumptions on the different functions used to defined the model.

**(S<sub>1</sub>) : Lower/upper bounds and regularity.**

(S<sub>1.1</sub>) : The following four statements hold.

i) There exists  $\delta > 0$  such that

$$\text{supp}(g) := \{x \in \mathbb{R}_+, g(x) \neq 0\} = [0, \delta].$$

ii) There exists  $g_{\min} > 0$  such that for all  $x \in [0, \delta]$

$$g(x) \geq g_{\min}.$$

iii) There exist  $\Delta > 0$ , such that for all  $x \in \mathbb{R}$ , there exists  $\Delta_x \in [0, \Delta]$  such that

$$\text{supp}(h(x, \cdot)) := \{y \in \mathbb{R}_+, h(x, y) \neq 0\} = [0, \Delta_x].$$

Moreover, the function  $x \mapsto \Delta_x$  is bounded from below on compact sets.

iv) There exists  $h_{\min} > 0$  such that for all  $x \in \mathbb{R}$ ,  $y \in [0, \Delta_x]$

$$h(x, y) \geq h_{\min}.$$

(S<sub>1.2</sub>) : There exists  $m_0 \in \mathbb{N} \setminus \{0, 1\}$  a sequence of pairs  $(\mathbb{I}^n, \mathbb{J}^n, \mathbb{M}^n)_{n \in \llbracket 1, m_0 \rrbracket}$  taking values in  $\mathcal{I}_k \times \mathcal{J}_k$  verifying

$$\bigcup_{i=1}^{m_0} \mathbb{I}^i = \llbracket 1, 2k \rrbracket, \quad \forall i \in \llbracket 1, m_0 \rrbracket : \mathbb{I}^i \subset \mathbb{J}^i,$$

such that for all  $A > 0$ , there exists  $p_{\min} > 0$  verifying:

$$\inf_{\substack{i \in \llbracket 1, m_0 \rrbracket, \\ (s_1, s_2) \in [-\delta, A + m_0 \Delta]^2}} (p_{\mathbb{J}^i, \mathbb{M}^i}(s_1, s_2)) \geq p_{\min}.$$

(S<sub>1.3</sub>) : There exist  $\bar{g} > 0$  such that

$$\forall x \in \mathbb{R}_+ : g(x) \leq \bar{g}.$$

Moreover, the function  $h$  is bounded from above on compact sets.

(S<sub>1.4</sub>) : The function  $b$  and the functions  $(p_{J,M})_{(J,M) \in \mathcal{J}_k}$  are continuous. Moreover, for all  $x_0 \in \mathbb{R}$ , the set  $\{y \in [0, \Delta] \mid x \mapsto h(x, y) \text{ is not continuous in } x_0\}$  is negligible with respect to the Lebesgue measure.

Now, we need assumptions that allow us to justify the existence of a Lyapunov function.

**(S<sub>2</sub>) : Existence of a Lyapunov function.**

(S<sub>2.1</sub>) : There exist  $D \in \mathbb{N}^*$ ,  $\varepsilon_0 > 0$ ,  $B_{\max} > 0$ , and a set  $K_{\text{renew}} \subset [0, B_{\max}]^{2k}$  non-negligible with respect to the Lebesgue measure, such that for all  $x \in K_{\text{renew}}$

$$(\mathcal{K}_{[0, B_{\max}]^{2k}})^D (1_{\{K_{\text{renew}}\}})(x) \geq (1 + \varepsilon_0).$$

(S<sub>2.2</sub>) : There exist  $L_{\text{return}} \in \mathbb{N}^*$ ,  $\mathcal{V} : \mathbb{R}_+^{2k} \rightarrow (\mathbb{R}_+)^*$  a continuous function, and  $\varepsilon_1 > 0$  such that with  $B_{\max}$  defined above:

i) For all  $x \in \mathbb{R}_+^{2k}$

$$\mathcal{K}_{([0, B_{\max} L_{\text{return}}]^{2k})^c}(\mathcal{V})(x) \leq (1 + \varepsilon_1)\mathcal{V}(x).$$

ii) For all  $x \in \mathbb{R}_+^{2k}$ ,  $I \in \mathcal{I}_k$

$$\begin{aligned} & \sum_{(J,M) \in \mathcal{J}_k} \int_{(\alpha_1, \alpha_2) \in (\mathbb{R}_+^{2k})^2} p_{J,M}(x - \alpha_1, x - \alpha_2) \left[ \int_{(\beta_1, \beta_2) \in (\mathbb{R}_+^{2k})^2} \mathcal{V}(x - \alpha_1 + \beta_1) \right. \\ & \left. \times 1_{\{x - \alpha_1 + \beta_1 \in \mathbb{R}_+^{2k}\}} d\mu_{(x - \alpha_1, x - \alpha_2)}^{(E, J, M)}(\beta_1, \beta_2) \right] d\mu^{(S, I)}(\alpha_1, \alpha_2) \leq (1 + \varepsilon_1)\mathcal{V}(x). \end{aligned}$$

- iii)  $\mathcal{V}$  is bounded from above on compact sets and there exists  $\mathcal{V}_{\min} > 0$  such that for all  $x \in (\mathbb{R}_+)^{2k}$  it holds  $\mathcal{V}(x) \geq \mathcal{V}_{\min}$ .
- iv) There exists  $C_{\mathcal{V}} > 0$  such that

$$\sup_{x \in \mathbb{R}_+^{2k}} \left( \sup_{y \in \mathbb{R}_+^{2k} \text{ s.t. } \|y-x\|_{\infty} \leq \max(\delta, \Delta)} \frac{\mathcal{V}(y)}{\mathcal{V}(x)} \right) \leq C_{\mathcal{V}}.$$

Finally, we need assumptions to handle the age structure of our model.

**(S<sub>3</sub>) : From the generational level to the temporal level.**

(S<sub>3.1</sub>) : There exist  $\underline{b} : \mathbb{R}_+ \rightarrow \mathbb{R}_+$  and  $\bar{b} : \mathbb{R}_+ \rightarrow \mathbb{R}_+$ , such that for all  $(x, a) \in (\mathbb{R}_+)^{2k} \times \mathbb{R}_+$

$$\underline{b}(a) \leq b(x, a) \leq \bar{b}(a),$$

and such that  $\int_0^{+\infty} \underline{b}(a) da = +\infty$ .

(S<sub>3.2</sub>) : We denote for all  $a, s \geq 0$   $\mathcal{F}_a(s) := \underline{b}(a+s) \exp\left(-\int_a^{a+s} \underline{b}(u) du\right)$  and its associated cumulative distribution function  $\bar{\mathcal{F}}_a(s) := \exp\left(-\int_a^{a+s} \underline{b}(u) du\right)$ . Then there exists  $\alpha > 0$  such that

$$\mathcal{L}(\mathcal{F}_0)(\alpha) = \frac{1}{(1 + \varepsilon_0)^{\frac{1}{\alpha}}}, \quad \text{and} \quad \sup_{t \geq 0} \inf_{a \geq 0} \left( \int_0^t e^{-\alpha s} \mathcal{F}_a(s) ds \right) > 0.$$

(S<sub>3.3</sub>) : We denote for all  $a, s \geq 0$   $\mathcal{G}_a(s) := \bar{b}(a+s) \exp\left(-\int_a^{a+s} \bar{b}(u) du\right)$ , and its associated cumulative distribution function  $\bar{\mathcal{G}}_a(s) := \exp\left(-\int_a^{a+s} \bar{b}(u) du\right)$ . Then, there exists  $\beta \in (0, \alpha)$  such that

$$\mathcal{L}(\mathcal{G}_0)(\beta) = \frac{1}{1 + \varepsilon_1}.$$

In Section 5, we give criteria allowing to check (S<sub>2.2</sub>) and (S<sub>3</sub>), and present two models where all the above assumptions are verified. We now give the main result of the paper.

**Main result.** We consider the following semigroup, for all  $(x, a) \in \mathcal{X}$ ,  $f \in M(\mathcal{X})$  nonnegative,  $t \geq 0$

$$M_t(f)(x, a) = \mathbb{E} \left[ \sum_{u \in \mathcal{V}_t} f(x^u, a_t^u) \middle| Y_0 = \delta_{(1, x, a)} \right] \in [0, +\infty]. \quad (2.3.2)$$

We easily see that  $(M_t)_{t \geq 0}$  is similar to a solution of (2.2.12) starting from a Dirac measure, and without the individuals in the cemetery. Under Assumption (S<sub>2.2</sub>), we also consider the following space ( $\Psi$  is defined in Assumption (S<sub>2.2</sub>))

$$\Psi = \{ \psi \in M_b^{loc}(\mathcal{X}) \mid \exists d_{\psi} \in \mathbb{N}, d_{\psi} \geq d_b \text{ s.t. } \forall (x, a) \in \mathcal{X} : \psi(x, a) = (1 + a^{d_{\psi}}) \mathcal{V}(x) \}. \quad (2.3.3)$$

This space contains all the functions used to distort the space when we obtain our convergence result. We use several functions to distort the space to be able to obtain the convergence of the semigroup defined on a large space of functions. In Lemma 3.3, we prove that we can extend the definition of  $(M_t)_{t \geq 0}$  to functions in  $\cup_{\psi \in \Psi} \mathcal{B}(\psi)$ . We also denote  $\mathcal{B}(\Psi) = \cap_{\psi \in \Psi} \mathcal{B}(\psi)$  and  $L^1(\Psi) = \cap_{\psi \in \Psi} L^1(\psi)$ . We are ready to give the main result.

**Theorem 2.7** (Main result). *Let us assume that (2.2.1) and Assumptions (S<sub>1</sub>) – (S<sub>3</sub>) hold. Then, there exists a unique  $(N, \phi, \lambda) \in L^1(\Psi) \times \mathcal{B}(\Psi) \times [\alpha, +\infty[$  satisfying  $N \geq 0$ ,  $\phi > 0$  and*

$$\int_{(x, a) \in \mathcal{X}} N(x, a) dx da = \int_{(x, a) \in \mathcal{X}} N(x, a) \phi(x, a) dx da = 1,$$

such that for all  $\psi \in \Psi$ , there exist  $C, \omega > 0$  such that for all  $t > 0$ ,  $\mu \in \mathcal{M}(\psi)$

$$\sup_{f \in \mathcal{B}(\psi), \|f\|_{\mathcal{B}(\psi)} \leq 1} \left| e^{-\lambda t} \mu M_t(f) - \mu(\phi) \int_{(x,a) \in \mathcal{X}} f(x,a) N(x,a) dx da \right| \leq C \|\mu\|_{\mathcal{M}(\psi)} e^{-\omega t}.$$

Moreover, there exists  $N_0 \in L^1(\mathbb{R}_+^{2k})$  nonnegative such that for all  $(x,a) \in \mathcal{X}$  it holds

$$N(x,a) = N_0(x) \exp\left(-\int_0^a b(x,s) ds - \lambda a\right).$$

To prove this theorem, we first weight the space by  $\psi$  and study the weighted-normalised semigroup

$$M_t^{(\psi)}(f)(x,a) := e^{-\lambda_\psi t} \frac{M_t(f\psi)(x,a)}{\psi(x,a)}, \quad \forall t \geq 0, \forall f \in M_b(\mathcal{X}), \forall (x,a) \in \mathcal{X}, \quad (2.3.4)$$

where  $\lambda_\psi > 0$  is chosen in Lemma 3.4 such that for all  $(x,a) \in \mathcal{X}$ ,  $t \geq 0$  we have  $e^{-\lambda_\psi t} \frac{M_t^{(\psi)}(x,a)}{\psi(x,a)} \leq 1$ . This new semigroup satisfies the same equation as the first moment semigroup  $(P_t^\psi)_{t \geq 0}$  of a jump Markov process with an absorbing state. As this equation has a unique solution (Lemma 3.5), we can study the ergodic behaviour of  $(P_t^\psi)_{t \geq 0}$  to obtain the one of  $(M_t^{(\psi)})_{t \geq 0}$ . This kind of method has been presented in [14]. We then apply [54, Theorem 2.8] to obtain the convergence of  $(M_t^{(\psi)})_{t \geq 0}$  towards a stationary profile through  $(P_t^\psi)_{t \geq 0}$ . We conclude by the fact that the convergence of  $(M_t^{(\psi)})_{t \geq 0}$  to a stationary profile on  $\mathcal{M}(\mathcal{X})$  implies the convergence of  $(M_t)_{t \geq 0}$  on  $\mathcal{M}(\psi)$ . The delicate/most interesting points are the following.

- We need to handle the fact the age structure of our model. To do so, we stochastically compare our process with Bellman-Harris processes, which allows us to use results from the renewal theory [3, Chap. IV.4] to obtain exponential estimates where we need them (Sections 4.3.4, 4.3.5 and 4.4.4).
- As the birth rate depends on the multidimensional trait, we do not have independent identically distributed times between jumps, which is one of the main characteristics of Bellman-Harris processes. To retrieve independent identically distributed jumps, we use the fact that the jump rate is bounded (from above or from below) by another jump rate, independent of the multidimensional trait. Then, we control the times these jumps occur using the inverse transform sampling to simulate jumps (Section 4.3.3).
- We need to prove that when a renewal of the number of individuals in a set occurs in several generations, then we have exponential growth of the number of individuals, see Assumption (S<sub>2.1</sub>). To do so, we prove that it is not the number of individuals with telomere lengths in the set  $K_{\text{renew}}$  that grows exponentially, but the number of individuals with telomere lengths in the set  $[0, B_{\text{max}}]^{2k}$ , by connecting  $[0, B_{\text{max}}]^{2k}$  and  $K_{\text{renew}}$  using the Doeblin condition (Section 4.3.4).
- During the proof that a renewal in several generations implies an exponential growth, we also need to handle the fact that not only telomere lengths can renew, but also the age. This implies that we need to restrict ourselves to truncated versions of the distribution of jump times, such that jump times of this truncated version do not exceed a certain value. We prove that even for a truncated version of the distribution of jump times, we can still make a stochastic comparison of our process with a Bellman-Harris process by considering an alternative birth rate (Section 4.3.4).
- The irregularities of the jump kernel with respect to the Lebesgue measure make difficult the control of the asymptotic comparisons of survival needed to obtain the stationary profile of the auxiliary particle representing our branching process. To handle this, we use a weak form of a Harnack inequality (Section 4.4).

We finish this section with a discussion about the consequences of our assumptions, and why we made them.



## Discussion about the assumptions.

### Discussion about $(S_1)$ :

- $(S_1)$  : All the assumptions of this set are easy to verify, as they only correspond to lower/upper bounds and regularity assumptions.
- $(S_{1.1}) : 1)$  This assumption implies that the cumulative distribution functions of  $g$  and  $(h(x, \cdot))_{x \in \mathbb{R}^{2k}}$  are bijective on their support. Then, we can simulate shortening and lengthening values with the inverse transform sampling method, and then obtain that Eq. (2.2.3) is verified (the expression of the procedure  $R(\cdot, \cdot)$  is a bit complicated, so we do not make it explicit here). From the latter, we get that Theorem 2.5 holds, so that the model is well-posed and that the number of individuals does not explode in finite time.
- $(S_{1.1}) : 2)$  The lower bounds for  $g$  and  $h$  are useful to prove the Doeblin condition. This assumption is relatively strong, but any other hypothesis would imply more complicated calculations, which are not the main focus of this work. We prefer to focus on the intrinsic difficulties of the model.
- $(S_{1.1}) : 3)$  The constant  $\Delta > 0$  corresponds to the upper bound of the maximum value that can have the support of a function  $h(x, \cdot)$ , where  $x \in \mathbb{R}$ . Having this upper bound simplifies the computations when we obtain the weak form of the Harnack inequality.
- $(S_{1.1}) : 4)$  The fact that  $x \mapsto \Delta_x$  is bounded from below on compact sets, and the fact that  $g$  and  $h$  are bounded from below on their support simplify the computations when we obtain the Doeblin condition.
- $(S_{1.2}) : 1)$  This assumption means that the probability that every coordinate has been shortened and lengthened after  $m_0$  cell divisions is bounded from below on every compact set. It is useful to obtain the Doeblin condition.
- $(S_{1.2}) : 2)$  The assumption that for all  $i \in \llbracket 1, m_0 \rrbracket$  it holds  $\mathbb{I}^i \subset \mathbb{J}^i$  means that when a telomere is shortened at a cell division, it is also lengthened. This allows us to simplify a lot computations. For more complex models where this assumption is not verified, by slightly changing the assumption, the computations made in this paper can be adapted to obtain the existence of a stationary profile. However, it will be much more laborious.
- $(S_{1.3})$  : This assumption is useful to obtain the weak form of the Harnack inequality.
- $(S_{1.4})$  : This assumption is necessary to prove that the sample space we work with is of path type (see Sharpe [46, Def. (23.10)]). We refer to Section 4.1 to see what it is important to have such a sample space.

### Discussion about $(S_2)$ :

- $(S_{2.1})$  : This assumption means that there is a renewal of the number of individuals, with telomere lengths that stay in  $[0, B_{\max}]^{2k}$ , after  $D$  generations. In particular, if we study the dynamics at generations that are multiples of  $D$ , and starting from an initial condition in  $K_{\text{renew}}$ , the population grows exponentially. As we are in a multidimensional setting, there are cases where this is easier in practice to verify that a renewal occurs in several generations rather than in one generation. The simplest examples are cases where the procedure of lengthening acts on too many coordinates. In Section 5.2, this type of model is studied.
- $(S_{2.2}) : i)$  The first statement of this assumption means that for the space distortion defined with  $\mathcal{V}$ , a cell does not give birth to too many offspring with telomere lengths out of  $[0, B_{\max} L_{\text{return}}]^{2k}$ .
- $(S_{2.2}) : ii)$  This assumption means that the space distortion does not change too much the mean of the reproduction law of the branching process, uniformly in  $I \in \mathcal{I}_k$ . In particular, this implies that for all  $x \in \mathbb{R}_+^{2k}$  we have

$$\begin{aligned}
\frac{\mathcal{K}(\mathcal{V})(x)}{\mathcal{V}(x)} &= \frac{1}{\mathcal{V}(x)} \frac{2}{\#\mathcal{I}_k} \sum_{I \in \mathcal{I}_k} \sum_{(J,M) \in \mathcal{J}_k} \int_{(\alpha_1, \alpha_2) \in (\mathbb{R}_+^{2k})^2} p_{J,M}(x - \alpha_1, x - \alpha_2) \\
&\quad \left[ \int_{(\beta_1, \beta_2) \in (\mathbb{R}_+^{2k})^2} \mathcal{V}(x - \alpha_1 + \beta_1) 1_{\{x - \alpha_1 + \beta_1 \in \mathbb{R}_+^{2k}\}} d\mu_{(x - \alpha_1, x - \alpha_2)}^{(E, J, M)}(\beta_1, \beta_2) \right] d\mu^{(S, I)}(\alpha_1, \alpha_2) \\
&\leq 2(1 + \varepsilon_1).
\end{aligned} \tag{2.3.5}$$

It is important to have this condition uniformly in  $I \in \mathcal{I}_k$  to be able to apply the weak form of the Harnack inequality.

### Discussion about $(S_3)$ :

- $(S_{3.2}) : i)$  The first condition means that the frequency at which events of division occur implies an exponential growth of the number of individuals. This can be obtained for example by using the intermediate values theorem.
- $(S_{3.2}) : ii)$  If there exists  $a_1, b_1 > 0$  such that  $\underline{b}(a) \geq b_1$  when  $a \geq a_1$ , then the second condition is verified, see Section 5.1.1.
- $(S_{3.3})$  : This assumption means that the frequency at which events of division occur allows to observe the impact of the space distortion. This can be obtained for example by using the intermediate values theorem. When  $\underline{b} \equiv \bar{b} \equiv b$ , the condition  $\beta < \alpha$  is equivalent to  $1 + \varepsilon_1 < (1 + \varepsilon_0)^{\frac{1}{b}}$ , see Section 5.1.1.

## 3 Space distortion and auxiliary pure jump Markov processes

This section focuses on the introduction of the weighted-normalised semigroup  $(M_t^{(\psi)})_{t \geq 0}$ , and on its associated auxiliary process  $(Z_t^{(\psi)})_{t \geq 0}$ , for all  $\psi \in \Psi$ . First, in Section 3.1, we study the well-posedness of  $(M_t)_{t \geq 0}$  for functions in  $\cup_{\psi \in \Psi} \mathcal{B}(\psi)$ . Then, we introduce the weighted-normalised semigroup  $(M_t^{(\psi)})_{t \geq 0}$ , and prove that the equation satisfied by the latter has a unique solution in Section 3.2. Finally, we construct the auxiliary process  $(Z_t^{(\psi)})_{t \geq 0}$  thanks to the equation of  $(M_t^{(\psi)})_{t \geq 0}$  for all  $\psi \in \Psi$  in Section 3.3. Throughout this section, Assumptions  $(S_{1.1})$  and  $(S_{2.2})$  hold. We also assume for the rest of the paper that (2.2.1) holds. Until Lemma 3.3 is stated, the semigroup  $(M_t)_{t \geq 0}$  introduced in (2.3.2) is only defined for nonnegative measurable functions. Except Lemmas 3.10 and 3.11, all the statements given in this section are proved in Appendix A.

### 3.1 Well-posedness of weighted-normalised semigroups

To obtain the ergodic behaviour of our semigroup  $(M_t)_{t \geq 0}$ , a naive approach is to construct an absorbing Markov process with first moment semigroup  $(M_t e^{-\tilde{\lambda}t})_{t \geq 0}$  where  $\tilde{\lambda} > 0$ , then apply [54, Theorem 2.8] to this process, and finally conclude by multiplying by  $e^{\tilde{\lambda}t}$ . However, two problems occur with this approach.

- Let  $\tilde{\lambda} > 0$ . A necessary condition for the existence of an absorbing Markov process with first moment semigroup  $(e^{-\tilde{\lambda}t} M_t)_{t \geq 0}$ , is that for all  $t \geq 0$  and  $(x, a) \in \mathcal{X}$  it holds  $e^{-\tilde{\lambda}t} M_t(1)(x, a) \leq 1$ . Indeed, the latter means that the number of individuals is in average lower than 1 for any time. When the birth rate is unbounded, this last property is not verified. In fact, if we assume that  $M_t(1)(x, a) \leq e^{\tilde{\lambda}t}$ , then we have that  $\lim_{t \rightarrow 0} \frac{1}{t} (M_t(1)(x, a) - 1) \leq \tilde{\lambda}$ , so that  $\frac{d}{dt} (M_t(1)(x, a))$  at  $t = 0$  is bounded. However, in view of Theorem 2.6, the derivative in time of  $M_t(1)(x, a)$  at  $t = 0$  when  $\mathcal{K}(1)(x) = 2$  is  $b(x, a)$ , which is not bounded (we recall that  $M_t(1)$  is in fact  $n_t(1_{\mathcal{X}})$  starting from a Dirac measure). Then, we have a contradiction, implying that there is no absorbing Markov process allowing to represent  $(e^{-\tilde{\lambda}t} M_t)_{t \geq 0}$  for an unbounded birth rate.

- The speed of convergence of the semigroup  $(M_t)_{t \geq 0}$  towards a stationary profile depends on the initial condition. Indeed, it will take more time for dynamics starting from a cell with very large telomere lengths to converge towards a stationary distribution compared to starting from cells with smaller telomere lengths. Hence, we have an issue because [54, Theorem 2.8] only handle models with a speed of convergence independent of the initial condition.

In view of these issues, we weight the semigroup  $(M_t)_{t \geq 0}$  by a function  $\psi \in \Psi$ , which gives us the semigroup  $(M_t^{(\psi)})_{t \geq 0}$ . Studying  $(M_t^{(\psi)})_{t \geq 0}$  rather than  $(M_t)_{t \geq 0}$  allows us to manage the problems explained above for the following reasons (we recall that  $\psi(x, a) = (1 + a^{d_\psi})\mathcal{V}(x)$  with  $d_\psi \in \mathbb{N}^*$ ):

- In view of the definition of  $(M_t^{(\psi)})_{t \geq 0}$  (see (2.3.4)) and Theorem 2.6 (one need to extend the definition of  $(n_t)_{t \geq 0}$  to unbounded function as done below), the derivative of  $M_t^{(\psi)}(1)$  at  $t = 0$  is  $\frac{\partial}{\partial a} \psi(x, a) + b(x, a) \left( \frac{\mathcal{K}(\psi(\cdot, 0))(x)}{\psi(x, a)} - 1 \right)$ . As the latter is bounded, see Lemma 3.4, the first problem presented above is solved.
- In view of Assumptions  $(S_2) - (S_3)$ , weighting the space by  $\mathcal{V}$  implies that the time before returning to a cell with telomere lengths in  $[0, B_{\max} L_{\text{return}}]^{2k}$ , even starting from telomere lengths far from this set, is accelerated (for a typical particle conditioned to non-extinction). Therefore, we do not have issues linked to the speed of convergence with this weighting. In Theorem 2.7, the impact of the speed of convergence is seen by the term  $\|\mu\|_{m(\psi)}$ .

In order to use  $(M_t^{(\psi)})_{t \geq 0}$  to obtain the ergodic behaviour of  $(M_t)_{t \geq 0}$ , we first must be sure that  $(M_t)_{t \geq 0}$  is well-posed for functions in  $\cup_{\psi \in \Psi} \mathcal{B}(\psi)$ . For that purpose, let us give the following statement that is proved in Section A.1.

**Lemma 3.1** (Well-posedness of  $(M_t)_{t \geq 0}$ ). *Assume that  $(S_{1.1})$  and  $(S_{2.2})$  hold. Let us consider  $\psi_e(x, a) = e^a \mathcal{V}(x)$  with  $\mathcal{V}$  defined in  $(S_{2.2})$ . Then there exists  $c > 0$  such that for all  $T \geq 0$ ,  $(x, a) \in \mathcal{X}$ ,*

$$M_T(\psi_e)(x, a) \leq \psi_e(x, a) \exp(cT).$$

Thanks to the above statement, we are now able to extend the definition of  $(M_t)_{t \geq 0}$  to functions in  $\mathcal{B}(\psi)$ . Before extending the definition of  $(M_t)_{t \geq 0}$ , let us introduce some notations. First, we denote the set

$$\mathcal{Q}_k := \mathcal{I}_k \times \mathcal{P}(\llbracket 1, 2k \rrbracket).$$

Then, for all  $(I, J) \in \mathcal{Q}_k$ , we introduce the measure  $\pi_x^{I, J}$  defined for all  $C \in \mathcal{B}(\mathbb{R}^{2k})$  as

$$\begin{aligned} \pi_x^{I, J}(C) &:= \frac{1}{\#(\mathcal{I}_k)} \sum_{M \in \mathcal{P}(\llbracket 1, 2k \rrbracket)} \int_{(\alpha_1, \alpha_2) \in (\mathbb{R}_+^{2k})^2} p_{J, M}(x - \alpha_1, x - \alpha_2) \\ &\times \left[ \int_{(\beta_1, \beta_2) \in (\mathbb{R}_+^{2k})^2} 1_C(x - \alpha_1 + \beta_1) d\mu_{(x - \alpha_1, x - \alpha_2)}^{(E, J, M)}(\beta_1, \beta_2) \right] d\mu^{(S, I)}(\alpha_1, \alpha_2), \end{aligned} \quad (3.1.1)$$

where the measures  $\mu^{(S, I)}$  and  $\left( \mu_{(s_1, s_2)}^{(E, J, M)} \right)_{(s_1, s_2) \in \mathbb{R}^{2k}}$  are defined in (2.2.5) and (2.2.7). This measure represents the kernel for updating telomere lengths of the daughter cell  $A$ , when during the cell division, the indices of the coordinates that are shortened in this daughter cell are those in  $I$ , and the indices of the coordinates that are lengthened are those in  $J$ . All the measures introduced above are helpful to construct a particle  $(Z_t^{(\psi)})_{t \geq 0}$ , for which it is sufficient to only have information of what happens to the daughter cell  $A$ , and not to both daughter cells.

**Remark 3.2.** *Under  $(S_{1.1})$ , for all  $x \in \mathbb{R}_+^{2k}$ ,  $C \in \mathcal{B}(\mathbb{R}^{2k})$*

$$2 \sum_{(I, J) \in \mathcal{Q}_k} \int_{u \in \mathbb{R}^{2k}} 1_{\{x+u \in C\}} d\pi_x^{I, J} = 2 \int_{(w_1, w_2) \in (\mathbb{R}^{2k})^2} 1_{\{x+w_1 \in C\}} d\Pi_x(w_1, w_2) = \mathcal{K}(C).$$

We extend the definition of  $(M_t)_{t \geq 0}$  given in (2.3.2) to functions in  $\cup_{\psi \in \Psi} \mathcal{B}(\psi)$  with the following lemma that is proved in Section A.2.

**Lemma 3.3** (Extension of the definition of  $(M_t)_{t \geq 0}$ ). *Let us assume that (S1.1) and (S2.2) hold. Then*

1. *For any nonnegative  $f \in \cup_{\psi \in \Psi} \mathcal{B}(\psi)$ ,  $(x, a) \in \mathcal{X}$ ,  $t \geq 0$ ,  $M_t f(x, a)$  is finite. In particular, if we consider for all  $f \in \cup_{\psi \in \Psi} \mathcal{B}(\psi)$ :  $f_+$  its positive part and  $f_-$  its negative part, we can extend the definition of  $M$  to  $\cup_{\psi \in \Psi} \mathcal{B}(\psi)$  as follows*

$$M_t(f)(x, a) := M_t(f_+)(x, a) - M_t(f_-)(x, a).$$

2.  *$(M_t)_{t \geq 0}$  defined above is a positive semigroup which satisfies the following equation for every  $f \in \cup_{\psi \in \Psi} \mathcal{B}(\psi)$  and  $(x, a) \in \mathcal{X}$ :*

$$\begin{aligned} M_t(f)(x, a) &= f(x, a+t) \exp\left(-\int_a^{a+t} b(x, s) ds\right) + 2 \sum_{(I, J) \in \mathcal{Q}_k} \int_0^t b(x, a+s) \\ &\times \exp\left(-\int_a^{a+s} b(x, v) dv\right) \left[ \int_{u \in \mathbb{R}^{2k}} M_{t-s} f(x+u, 0) \mathbf{1}_{\{x+u \in \mathbb{R}_+^{2k}\}} d\pi_x^{I, J}(u) \right] ds. \end{aligned} \quad (3.1.2)$$

We are now able to study the long time behaviour of  $(M_t)_{t \geq 0}$  on  $\mathcal{M}(\psi)$ . We first choose the value of  $\lambda_\psi$  allowing to construct an auxiliary process and then apply [54, Theorem 2.8].

### 3.2 Choice of normalisations and equations of auxiliary semigroups

To be able to represent our weighted-renormalised semigroup  $(M_t^{(\psi)})_{t \geq 0}$  with a Markov process, we must choose  $\lambda_\psi > 0$  such that for all  $(x, a) \in \mathcal{X}$  and  $t \geq 0$  it holds  $M_t^{(\psi)}(1)(x, a) \leq 1$ . The following lemma allows us to do so, and is proved in Section A.3.

**Lemma 3.4** (Inequalities related to  $\psi$ ). *Let us assume that (S1.1) and (S2.2) hold. Then, for all  $\psi \in \Psi$ , there exist  $\lambda_\psi > 0$  and  $\bar{\psi} > 1$  such that for all  $(x, a) \in \mathcal{X}$*

- i)  $\frac{\partial}{\partial a} \frac{\psi(x, a)}{\psi(x, a)} + b(x, a) \frac{\mathcal{K}(\psi(\cdot, 0))(x)}{\psi(x, a)} - b(x, a) < \lambda_\psi$ ,
- ii)  $\frac{\partial}{\partial a} \frac{\psi(x, a)}{\psi(x, a)} + 2 \frac{b(x, a)}{\psi(x, a)} - b(x, a) < \lambda_\psi$ ,
- iii)  $\sup_{s \geq 0} \left| \frac{\psi(x, s+a)}{\psi(x, s)} \right| \leq \bar{\psi}(1 + a^{d_\psi})$ ,

where  $\mathcal{K}$  is defined by (2.2.11).

This lemma implies that the probabilities given later in Eq. (3.3.3) take indeed values in  $[0, 1]$ , which implies indirectly that  $e^{-\lambda_\psi t} \frac{M_t^{(\psi)}(x, a)}{\psi(x, a)} \leq 1$ . In the rest of the paper,  $\lambda_\psi$  and  $\bar{\psi}$  refers to the bounds of this lemma. In particular, for all,  $\psi \in \Psi$ , the semigroup  $(M_t^{(\psi)})_{t \geq 0}$  is defined with this  $\lambda_\psi$ . We now give preliminaries to obtain a representation of this semigroup through a process with a particle  $(Z_t^{(\psi)})_{t \geq 0}$ . In the rest of this section, we have fixed  $\psi \in \Psi$ . By (3.1.2),  $(M_t^{(\psi)})_{t \geq 0}$  satisfies for all  $t \geq 0$ ,  $f \in M_b(\mathcal{X})$ , and  $(x, a) \in \mathcal{X}$  ( $d\pi_x^{I, J}$  has been defined in (3.1.1))

$$\begin{aligned} M_t^{(\psi)}(f)(x, a) &= f(x, a+t) \frac{\psi(x, a+t)}{\psi(x, a)} \exp\left(-\int_a^{a+t} b(x, s) ds - \lambda_\psi t\right) + 2 \sum_{(I, J) \in \mathcal{Q}_k} \int_0^t \frac{b(x, a+s)}{\psi(x, a)} \\ &\times \exp\left(-\int_a^{a+s} b(x, v) dv - \lambda_\psi s\right) \left[ \int_{u \in \mathbb{R}^{2k}} M_{t-s}^{(\psi)}(f)(x+u, 0) \mathcal{V}(x+u) \mathbf{1}_{\{x+u \in \mathbb{R}_+^{2k}\}} d\pi_x^{I, J}(u) \right] ds. \end{aligned} \quad (3.2.1)$$

We can prove that this equation has a unique solution, and thus justify that we can use an auxiliary process  $(Z_t^{(\psi)})$  to study  $(M_t^{(\psi)})_{t \geq 0}$ . This gives us the following statement that is proved in Section A.4.

**Lemma 3.5** (Uniqueness and Feller property). *Let us assume that (S1.1) and (S2.2) hold. We consider  $T > 0$ , and denote  $\widehat{\mathcal{X}} = \mathcal{X} \times \mathbb{N} \times \mathcal{Q}_k$ . For all  $f \in M_b(\widehat{\mathcal{X}})$ , we also introduce the operator  $\Gamma_f$  from  $M_b([0, T] \times \widehat{\mathcal{X}})$  to itself, defined for all  $F \in M_b([0, T] \times \widehat{\mathcal{X}})$ , and  $z = (t, x, a, n, \tilde{I}, \tilde{J}) \in [0, T] \times \widehat{\mathcal{X}}$  as:*

$$\begin{aligned} \Gamma_f(F)(z) &= f(x, a + t, n, \tilde{I}, \tilde{J}) \frac{\psi(x, a + t)}{\psi(x, a)} \exp\left(-\int_a^{a+t} b(x, s) ds - \lambda_\psi t\right) + 2 \sum_{(I, J) \in \mathcal{Q}_k} \int_0^t \frac{b(x, a + s)}{\psi(x, a)} \\ &\times \exp\left(-\int_a^{a+s} b(x, v) dv - \lambda_\psi s\right) \left[ \int_{u \in \mathbb{R}^{2k}} F(t - s, x + u, 0, n + 1, I, J) \mathcal{V}(x + u) 1_{\{x+u \in \mathbb{R}_+^{2k}\}} d\pi_x^{I, J}(u) \right] ds. \end{aligned} \quad (3.2.2)$$

Then, there exists a unique  $\bar{f} \in M_b([0, T] \times \widehat{\mathcal{X}})$  that is solution to  $\Gamma_f(\bar{f}) = \bar{f}$ . In addition, if  $f \in \mathcal{C}_0(\widehat{\mathcal{X}})$ , then we have  $\bar{f} \in \mathcal{C}^0([0, T], \mathcal{C}_0(\widehat{\mathcal{X}}))$ , where  $\mathcal{C}^0([0, T], \mathcal{C}_0(\widehat{\mathcal{X}}))$  is the space of the continuous functions  $G : [0, T] \times \widehat{\mathcal{X}} \rightarrow \mathbb{R}$  verifying

$$\lim_{\|(x, a, n)\|_\infty \rightarrow +\infty} \left( \sup_{(t, I, J, u) \in [0, T] \times \mathcal{Q}_k \times [-\delta, \Delta]^{2k}} |G(t, x, a, n, I, J)| \right) = 0. \quad (3.2.3)$$

**Remark 3.6.** *Our result is stronger than what we need for the uniqueness of (3.2.1), as we have a result for  $\Gamma_f$  defined with  $f \in M_b(\widehat{\mathcal{X}})$  instead of  $f \in M_b(\mathcal{X})$ . This is because we need the result on the regularity of  $\bar{f}$  to prove that our sample space is of path type (see [46, Def. (23.10)]) later in Section 4.1.*

By Lemma 3.5, if we construct an auxiliary process such that its first moment semigroup satisfies (3.2.1), then the first moment semigroup of this auxiliary process and  $(M_t^{(\psi)})_{t \geq 0}$  have the same values. Obtaining the ergodic behaviour of this auxiliary process is then equivalent to obtaining the ergodic behaviour of  $(M_t^{(\psi)})_{t \geq 0}$ . Before doing the construction of our auxiliary process, we give a more suitable expression for (3.2.1). We denote for all  $(I, J) \in \mathcal{Q}_k$  and  $(x, a) \in \mathcal{X}$  the following

$$d^{I, J}(x) := \int_{u \in \mathbb{R}^{2k}} \mathcal{V}(x + u) 1_{\{x+u \in \mathbb{R}_+^{2k}\}} d\pi_x^{I, J}(u), \text{ and } q_\psi^{I, J}(x, a) = \frac{\frac{2d^{I, J}(x)b(x, a)}{\psi(x, a)}}{\lambda_\psi + b(x, a) - \frac{\partial_a \psi(x, a)}{\psi(x, a)}}. \quad (3.2.4)$$

Then, (3.2.1) can be rewritten as follows

$$\begin{aligned} M_t^{(\psi)}(f)(x, a) &= f(x, a + t) \exp\left(-\int_a^{a+t} b(x, s) ds - \lambda_\psi t + \int_a^{a+t} \frac{\partial_a \psi(x, s)}{\psi(x, s)} ds\right) \\ &+ \int_0^t \left( \lambda_\psi + b(x, a + s) - \frac{\partial_a \psi(x, a + s)}{\psi(x, a + s)} \right) \exp\left(-\int_a^{a+s} b(x, v) dv - \lambda_\psi s + \int_a^{a+s} \frac{\partial_a \psi(x, u)}{\psi(x, u)} du\right) \\ &\left( \sum_{(I, J) \in \mathcal{Q}_k} q_\psi^{I, J}(x, a + s) \left[ \frac{1}{d^{I, J}(x)} \int_{u \in \mathbb{R}^{2k}} M_{t-s}^{(\psi)}(f)(x + u, 0) \mathcal{V}(x + u) 1_{\{x+u \in \mathbb{R}_+^{2k}\}} d\pi_x^{I, J}(u) \right] \right) ds. \end{aligned} \quad (3.2.5)$$

This means that we can see (3.2.1) as the Duhamel's formula of a jump Markov process with an absorbing state such that:

- The process jumps at a rate  $\lambda_\psi + b(x, a) - \frac{\partial_a \psi(x, a)}{\psi(x, a)}$ ,
- At each jump, if we denote  $(x, a)$  is the trait of the particle at the jump, then:
  - For any  $(I, J) \in \mathcal{Q}_k$ , with probability  $q_\psi^{I, J}(x, a)$ , the trait of the particle is updated such that
$$(x, a) \longrightarrow (x + U, 0),$$
where  $U$  is distributed according the probability measure  $\frac{1}{d^{I, J}(x)} \mathcal{V}(x + u) 1_{\{x+u \in \mathbb{R}_+^{2k}\}} d\pi_x^{I, J}(u)$ .
  - With probability  $1 - \sum_{(I, J) \in \mathcal{Q}_k} q_\psi^{I, J}(x, a)$ , the jump Markov process jumps to a cemetery.

We now construct an auxiliary process that follows these dynamics.

### 3.3 Algorithmic construction of auxiliary processes associated to weighted-normalised semigroups

Let  $\psi \in \Psi$ . We keep the same  $\psi$  in all this subsection. Even if all the objects introduced in this subsection depends of  $\psi$ , we will drop the index to mark the dependence in  $\psi$  to simplify notations, except for  $(Z_t^{(\psi)})_{t \geq 0}$ . Our aim in this subsection is to construct an absorbing Markov process such that its first moment semigroup satisfies (3.2.5).

To construct our particle  $(Z_t^{(\psi)})_{t \geq 0}$ ,

- For all  $y \in \mathbb{R}_+^{2k}$ ,  $r, s \geq 0$  we define the following functions, that are the complementary cumulative distribution function and the probability density functions for times between jumps

$$\bar{\mathcal{H}}_s(y, r) = \exp \left( - \int_s^{s+r} b(y, u) du - \lambda_\psi r + \int_s^{s+r} \frac{\partial \psi}{\partial a}(y, u) \psi(y, u) du \right), \quad (3.3.1)$$

$$\mathcal{H}_s(y, r) = \left[ \lambda_\psi + b(y, s+r) - \frac{\partial \psi}{\partial a}(y, s+r) \right] \bar{\mathcal{H}}_s(y, r). \quad (3.3.2)$$

- For all  $(y, s) \in \mathcal{X}$ , we introduce  $(T_n(y, s))_{n \in \mathbb{N}}$  an i.i.d. sequence of random variables taking values in  $\mathbb{R}_+$  and distributed according to  $\mathcal{H}_s(y, \cdot)$ . This sequence of random variables is used to describe jump times of the auxiliary process.
- For  $(y, s) \in \mathcal{X}_\partial$ , we introduce  $((\tilde{I}_j, \tilde{J}_j)(y, s))_{j \geq 1}$  an i.i.d. sequence of random variables taking values in the set  $(\mathcal{Q}_k \cup \{(\partial)_2\})$ . For all  $(j, y, s) \in \mathbb{N}^* \times (\mathcal{X}_\partial)$ , the pair of random variables  $(\tilde{I}_j, \tilde{J}_j)(y, s)$  is independent of  $(T_n(x', a'))_{n \in \mathbb{N}, (x', a') \in \mathcal{X}}$ . Moreover, recalling that  $q_\psi^{I, J}$  is defined in (3.2.4):

$$\begin{aligned} \forall (y, s) \in \mathcal{X} : \quad \mathbb{P} [(\tilde{I}_j, \tilde{J}_j)(y, s) = (I, J)] &= \begin{cases} q_\psi^{I, J}, & \text{if } (I, J) \in \mathcal{Q}_k, \\ 1 - \sum_{(I, J) \in \mathcal{Q}_k} q_\psi^{I, J}(y, s), & \text{if } (I, J) = (\partial, \partial), \end{cases} \\ \mathbb{P} [(\tilde{I}_j, \tilde{J}_j)(\partial, \partial) = (I, J)] &= \begin{cases} 0, & \text{if } (I, J) \in \mathcal{Q}_k, \\ 1, & \text{if } (I, J) = (\partial, \partial). \end{cases} \end{aligned} \quad (3.3.3)$$

These random variables are used to describe the coordinates where there is a jump (shortening and/or lengthening), or if the particle jumps in the cemetery. Assume the trait of the particle at the  $j$ -th jump is  $(y, s)$ . If  $(\tilde{I}_j, \tilde{J}_j)(y, s) \neq (\partial)_2$ , then the coordinates where there is a shortening at the  $j$ -th jump are indexed by  $\tilde{I}_j(y, s)$ , and the coordinates where there is a lengthening are indexed by  $\tilde{J}_j(y, s)$ . Otherwise, we have  $(\tilde{I}_j, \tilde{J}_j)(y, s) = (\partial)_2$  and the particle jumps to the cemetery at the  $j$ -th jump.

- For all  $(I, J, y) \in \mathcal{Q}_k \times \mathbb{R}_+^{2k}$ , we introduce  $(\tilde{U}_{j, I, J}(y))_{\{j \geq 1\}}$  an i.i.d. sequence of random variables taking values in  $\mathbb{R}_+^{2k}$ . For all  $j \in \mathbb{N}^*$ , the random variable  $\tilde{U}_{j, I, J}(y)$  is independent of  $(T_n(x', a'))_{n \in \mathbb{N}, (x', a') \in \mathcal{X}}$  and  $((\tilde{I}_k, \tilde{J}_k)(x', a'))_{k \geq 1, (x', a') \in \mathcal{X}_\partial}$ , and is distributed according to the probability measure

$$d\mathbb{P}_{\tilde{U}_{j, I, J}(y)}(u) = \frac{1}{d_{I, J}(y)} \mathcal{V}(y+u) 1_{\{y+u \in \mathbb{R}_+^{2k}\}} d\pi_y^{I, J}(u). \quad (3.3.4)$$

These random variables are used to give the jump value at each jump of the auxiliary process.

- We consider the process  $(X_n, A_n, I_n, J_n, \mathcal{T}_n, U_n)_{n \in \mathbb{N}}$  taking values on  $(\mathcal{X} \times \mathcal{Q}_k \times \mathbb{R}_+ \times \mathbb{R}_+^{2k}) \cup \{(\partial)_6\}$  ( $\mathcal{X}$  and  $\mathcal{Q}_k$  are considered as the cartesian product between two sets), with initial condition

$(X_0, A_0, I_0, J_0, 0, 0)$ , and such that for all  $n \in \mathbb{N}$ :

$$\left\{ \begin{array}{l} (I_{n+1}, J_{n+1}) = (\tilde{I}_{n+1}, \tilde{J}_{n+1})(X_n, T_n(X_n, A_n)), \\ U_{n+1} = \begin{cases} \tilde{U}_{n+1, I_{n+1}, J_{n+1}}(X_n), & \text{if } (I_{n+1}, J_{n+1}) \neq (\partial, \partial), \\ \partial, & \text{otherwise,} \end{cases} \\ (X_{n+1}, A_{n+1}) = \begin{cases} (X_n + U_{n+1}, 0), & \text{if } (I_{n+1}, J_{n+1}) \neq \partial, \\ (\partial, \partial), & \text{otherwise,} \end{cases} \\ \mathcal{J}_{n+1} = \begin{cases} \mathcal{J}_n + T_n(X_n, A_n), & \text{if } (I_{n+1}, J_{n+1}) \neq (\partial, \partial), \\ \partial, & \text{otherwise.} \end{cases} \end{array} \right. \quad (3.3.5)$$

In the above,  $X_0, A_0, I_0, J_0$  are random variables, for which the distribution is given when needed (for example when we define semigroups). We also consider the random variables  $\mathcal{N}_\partial$  and  $\tau_\partial$  defined as

$$\mathcal{N}_\partial := \inf \{l \in \mathbb{N}, (I_l, J_l) = (\partial, \partial)\}, \quad \tau_\partial := \begin{cases} \mathcal{J}_{\mathcal{N}_\partial - 1} + T_n(X_{\mathcal{N}_\partial - 1}, A_{\mathcal{N}_\partial - 1}), & \text{if } \mathcal{N}_\partial \geq 1, \\ 0, & \text{otherwise,} \end{cases}$$

and the process  $(N_t)_{t \geq 0}$ , defined for all  $t \geq 0$  as

$$N_t := \begin{cases} \sup \{m \in \llbracket 0, \mathcal{N}_\partial - 1 \rrbracket \mid \mathcal{J}_m \leq t\}, & \text{if } t < \tau_\partial, \\ \mathcal{N}_\partial, & \text{otherwise.} \end{cases}$$

The random variables  $\mathcal{N}_\partial$  and  $\tau_\partial$  describe the number of jumps and the time before extinction of the dynamics, respectively. For all  $t \geq 0$ ,  $N_t$  describes the number of jumps that have occurred up to time  $t$ . For all  $n < \mathcal{N}_\partial$ ,  $X_n$  describes the values of telomere lengths after  $n$  jumps, and  $A_n$  is the age of the particle right after the  $n$ -th jump has occurred. For all  $n \in \mathbb{N}^*$ ,  $I_n$  is the random variable that describes where the coordinates of telomeres of the process  $(X_m)_{m \in \mathbb{N}}$  that are shortened at the  $n$ -th jump. Similarly,  $J_n$  describes the coordinates of the telomeres of  $(X_m)_{m \in \mathbb{N}}$  that are lengthened at the  $n$ -th jump.  $U_n$  describes the value of the jump that the process  $(X_m)_{m \in \mathbb{N}}$  make at the  $n$ -th jump.

In order to apply Lemma 3.5 later in the proof, see Section 4.1, we need to have a version of the process  $(N_t)_{t \geq 0}$  with an initial condition that can vary, and a cemetery state. Then, we finally introduce a variant to  $(N_t)_{t \geq 0}$  named  $(\tilde{N}_t)_{t \geq 0}$ , that is a process with initial condition  $\tilde{N}_0 \in \mathbb{N}$ , and such that for all  $t \geq 0$

$$\tilde{N}_t := \begin{cases} \tilde{N}_0 + N_t, & \text{if } t < \tau_\partial, \\ \partial, & \text{otherwise.} \end{cases}$$

This variant is only introduced to be more rigorous, and is not useful in practice.

**Remark 3.7.** One can easily see by (3.3.5) that if  $a \in \mathbb{R}_+$  is the initial condition of  $(A_n)_{n \in \mathbb{N}}$ , then for all  $n \in \mathbb{N}$  it holds  $A_n = a \mathbf{1}_{\{n=0\}} \mathbf{1}_{\{n < \mathcal{N}_\partial\}} + \partial \mathbf{1}_{\{n \geq \mathcal{N}_\partial\}}$ .

**Remark 3.8.** In view of (3.3.5), one can easily see that the values of the initial conditions  $I_0$  and  $J_0$  do not influence the values of  $(X_n, A_n, I_n, J_n, \mathcal{J}_n, U_n)_{n \in \mathbb{N}}$ . However, as for  $(\tilde{N}_t)_{t \geq 0}$ , we do not fix an initial condition for these two random variables to be able to define rigorously the first moment semigroup of a process that will be introduced later in Section 4.1, see (4.1.1).

Now, we define  $(Z_t^{(\psi)})_{t \geq 0}$  a process taking values in  $\mathcal{X}_\partial$ , such that for all  $t \geq 0$

$$Z_t^{(\psi)} = \left( X_{N_t}, A_{N_t} + (t - \mathcal{J}_{N_t}) \mathbf{1}_{\{A_{N_t} \neq \partial\}} \right). \quad (3.3.6)$$

One can observe that  $(X_0, A_0)$  is the initial condition of  $(Z_t^{(\psi)})_{t \geq 0}$ . We also consider the following notations, that are very useful for the proof of the main theorem.



**Notation 3.9.** For all Borel set  $A \subset \mathcal{X}$ , we denote in the rest of the paper

$$\tau_A := \inf \{t > 0 \mid Z_t^{(\psi)} \in A\}, \text{ and } T_A := \inf \{t > 0 \mid Z_t^{(\psi)} \notin A\}.$$

We finally introduce the semigroup  $(P_t^{(\psi)})_{t \geq 0}$  such that for all  $f \in M_b(\mathcal{X})$ ,  $t \geq 0$ ,  $(x, a) \in \mathcal{X}$

$$P_t^{(\psi)}(f)(x, a) = \mathbb{E} \left[ f(Z_t^{(\psi)}) 1_{\{t < \tau_\partial\}} \mid (X_0, A_0) = (x, a) \right]. \quad (3.3.7)$$

If we condition the expectation with respect to the first jump time, we obtain that this semigroup satisfies (3.2.5). Then, as (3.2.1) is equivalent to (3.2.5), Lemma 3.5 implies that for all  $f \in M_b(\mathcal{X})$ ,  $t \geq 0$ ,  $(x, a) \in \mathcal{X}$

$$P_t^{(\psi)}(f)(x, a) = M_t^{(\psi)}(f)(x, a). \quad (3.3.8)$$

We now give statements that facilitate the computation of the distribution of the auxiliary process during the proof of Theorem 2.7. First, we introduce the following function that is essential to simplify notations during the proof of the main theorem. For all  $(x, a, t) \in \mathcal{X} \times \mathbb{R}_+$

$$\begin{aligned} \mathcal{G}_a(x, t) &= 2 \frac{b(x, a+t)}{\psi(x, a+t)} \exp \left( - \int_a^{a+t} b(x, u) du - \lambda_\psi t + \int_a^{a+t} \frac{\partial_a \psi(x, u)}{\psi(x, u)} du \right) \\ &= 2 \frac{b(x, a+t)}{\psi(x, a)} \exp \left( - \int_a^{a+t} b(x, u) du - \lambda_\psi t \right). \end{aligned} \quad (3.3.9)$$

Then, we have the following equality, that we easily prove.

**Lemma 3.10** (Distribution at one jump). *Let us assume that (S1.1) and (S2.2) hold. We consider  $t \geq 0$ ,  $B \in \mathcal{B}(\mathbb{R}_+^{2k})$ ,  $(i, j) \in \mathcal{Q}_k$  and  $C \in \mathcal{B}([0, t])$ . Then for any  $f \in M_b(\mathcal{X})$  nonnegative,  $(x, a) \in \mathcal{X}$ , we have*

$$\begin{aligned} &\mathbb{E}_{(x, a)} \left[ f(Z_t^{(\psi)}); X_1 \in B, N_t = 1, (I_1, J_1) = (i, j), \mathcal{T}_1 - \mathcal{T}_0 \in C \right] \\ &= \int_{s \in \mathbb{R}_+} \int_{u \in \mathbb{R}^{2k}} f(x+u, t-s) 1_{\{x+u \in B\}} 1_{\{s \in C\}} \mathcal{V}(x+u) \mathcal{G}_a(x, s) \overline{\mathcal{H}}_0(x+u, t-s) ds d\pi_x^{i, j}(u). \end{aligned}$$

*Proof.* We denote  $\mathcal{E} = \mathbb{E}_{(x, a)} \left[ f(Z_t^{(\psi)}); X_1 \in B, N_t = 1, (I_1, J_1) = (i, j), \mathcal{T}_1 - \mathcal{T}_0 \in C \right]$  in this proof. First, by Eq. (3.3.5) and Eq. (3.3.6), we have on the event  $\{N_t = 1, (I_1, J_1) = (i, j)\}$  that it holds  $Z_t^{(\psi)} = (x + \tilde{U}_{1, I_1, J_1}, t - T_0(x, a))$ . Second, we know by the construction of the particle that  $T_0(x, a) = \mathcal{T}_1 - \mathcal{T}_0$  is the time before the first jump occurs and is distributed according to the density  $\mathcal{H}_a(x, \cdot)$ . Finally, on the event  $\{N_t = 1\}$ , the second jump has not yet occurred at time  $t$ , implying that  $\mathcal{T}_2 - \mathcal{T}_1 = T_1(x + \tilde{U}_{1, I_1, J_1}, 0) > t - T_0(x, a)$ . From these three points, it comes

$$\begin{aligned} \mathcal{E} &= \int_{s \in \mathbb{R}_+} \mathbb{P}_{(x, a)}[(\tilde{I}_1, \tilde{J}_1)(x, a+s) = (i, j)] \left[ \int_{u \in \mathbb{R}^{2k}} f(x+u, t-s) 1_{\{x+u \in B\}} \right. \\ &\quad \left. \times 1_{\{s \in C\}} \mathbb{P}[T_1(x+u, 0) > t-s] d\mathbb{P}_{\tilde{U}_{j, i, j}(y)}(u) \right] \mathcal{H}_a(x, s) ds. \end{aligned} \quad (3.3.10)$$

In addition, one can easily develop the expression of the following mathematical objects, using (3.3.2), (3.3.3) combined with (3.2.4), and (3.3.4), to obtain

$$\mathcal{H}_a(x, s) \mathbb{P}_{(x, a)}[(\tilde{I}_1, \tilde{J}_1)(x, a+s) = (i, j)] d\mathbb{P}_{\tilde{U}_{j, i, j}(y)}(u) = \mathcal{V}(x+u) \mathcal{G}_a(x, s) 1_{\{x+u \in \mathbb{R}_+^{2k}\}} d\pi_x^{i, j}(u).$$

Plugging the latter in (3.3.10), and using the fact that  $\mathbb{P}[T_1(x+u, 0) > t-s] = \overline{\mathcal{H}}_0(x+u, t-s)$  allows us to conclude that the lemma is true.  $\square$

This statement can be extended to the event  $\{N_t = n\}$ , where  $n \in \mathbb{N} \setminus \{0, 1\}$ , by iterating what we have done to obtain Lemma 3.10:



**Lemma 3.11** (Distribution at  $n$  jumps). *Let us assume that (S1.1) and (S2.2) hold. Let  $t \geq 0$  and  $n \in \mathbb{N} \setminus \{0, 1\}$ . We consider  $(B_1, \dots, B_n) \in (\mathcal{B}(\mathbb{R}_+^{2k}))^n$ ,  $((i_1, j_1), \dots, (i_n, j_n)) \in (\mathcal{Q}_k)^n$  and  $(C_1, \dots, C_n) \in (\mathcal{B}([0, t]))^n$ . Then for any  $f \in M_b(\mathcal{X})$  nonnegative,  $(x, a) \in \mathcal{X}$ , we have*

$$\begin{aligned} & \mathbb{E}_{(x,a)} \left[ f(Z_t^{(\psi)}); N_t = n, \forall p \in \llbracket 1, n \rrbracket : X_p \in B_p, (I_p, J_p) = (i_p, j_p), \mathcal{F}_p - \mathcal{F}_{p-1} \in C_p \right] \\ &= \int_{s_1 \in [0, t]} \int_{s_2 \in [0, t-s_1]} \cdots \int_{s_n \in [0, t-\sum_{i=1}^{n-1} s_i]} \int_{u_1 \in \mathbb{R}^{2k}} \cdots \int_{u_n \in \mathbb{R}^{2k}} f \left( x + \sum_{i=1}^n u_i, t - \sum_{i=1}^n s_i \right) \mathcal{V}(x + u_1) \cdots \\ & \times \mathcal{V} \left( x + \sum_{i=1}^n u_i \right) \mathcal{G}_a(x, s_1) \mathcal{G}_0(x + u_1, s_2) \cdots \mathcal{G}_0 \left( x + \sum_{i=1}^{n-1} u_i, s_n \right) \overline{\mathcal{H}}_0 \left( x + \sum_{i=1}^n u_i, t - \sum_{i=1}^n s_i \right) \\ & \times \mathbb{1}_{\{\forall p \in \llbracket 1, n \rrbracket : x + \sum_{i=1}^p u_i \in B_p, s_p \in C_p\}} (ds_1 ds_2 \cdots ds_n) \left( d\pi_x^{i_1, j_1}(u_1) \cdots d\pi_{x + \sum_{i=1}^{n-1} u_i}^{i_n, j_n}(u_n) \right). \end{aligned}$$

## 4 Long time behaviour: Proof of the main theorem

To obtain the ergodic behaviour of our model, we apply [54, Theorem 2.8] to the auxiliary processes constructed in Section 3.3. For the reader's convenience, we give it below slightly rewritten to fit our framework and notations.

**Theorem 4.1** (Theorem 2.8 in [54]). *Let  $\Omega$  be of path type (see [46, Def. (23.10)]),  $\mathcal{X}$  a Polish space,  $\partial$  an element outside of  $\mathcal{X}$ , and  $(Z_t)_{t \geq 0}$  a strong Markov process for a complete and right-continuous filtration  $(\overline{\mathcal{F}}_t)_{t \geq 0}$ , taking values in  $\mathcal{X} \cup \{\partial\}$  and absorbed at  $\partial$ . Let us assume that there exist  $(D_l)_{l \in \mathbb{N}^*}$  a sequence of closed subsets of  $\mathcal{X}$ , a probability measure  $\nu$  on  $\mathcal{X}$ , a closed measurable set  $E \subset \cup_{l \geq 1} D_l$  and a constant  $\rho > 0$  such that*

- $(A_0)$  : For any  $l \in \mathbb{N}^*$ ,  $D_l \subset \text{int}(D_{l+1})$ .
- $(A_1)$  : For any  $l \in \mathbb{N}^*$ , there exist  $L > l$ ,  $c, t > 0$  such that for all  $z \in D_l$

$$\mathbb{P}_z [Z_t \in dz', t < \min(\tau_\partial, T_{D_L})] \geq c\nu(dz'),$$

where  $\tau_\partial$  is the extinction time of  $(Z_t)_{t \geq 0}$  and  $T_{D_L}$  the first time it exits  $D_L$ .

- $(A_2)$  : It holds

$$\rho > \sup \left\{ \gamma \in \mathbb{R} \mid \sup_{L \geq 1} \inf_{t > 0} e^{\gamma t} \mathbb{P}_\nu [t < \min(\tau_\partial, T_{D_L})] = 0 \right\} =: \rho_S,$$

and

$$\sup_{z \in \mathcal{X}} [\mathbb{E}_z [\exp(\rho \min(\tau_\partial, \tau_E))] ] < +\infty.$$

- $(A_3)_F$  : For all  $\varepsilon \in (0, 1)$ , there exist  $t_F, c' > 0$  such that for any  $z \in E$  there exist two stopping times  $U_H$  and  $V$  such that

$$\mathbb{P}_z [Z_{U_H} \in dz'; U_H < \tau_\partial] \leq c' \mathbb{P}_\nu [Z_V \in dz'; V < \tau_\partial], \quad (4.0.1)$$

and

$$\{\min(\tau_\partial, t_F) < U_H\} = \{U_H = \infty\}, \quad (4.0.2)$$

$$\mathbb{P}_x [U_H = \infty, t_F < \tau_\partial] \leq \varepsilon \exp(-\rho t_F). \quad (4.0.3)$$

Then, there exist a unique  $(\tilde{\gamma}, \tilde{\phi}, \tilde{\lambda}) \in \mathcal{M}_1(\mathbb{X}) \times M_b(\mathbb{X}) \times \mathbb{R}_+$ , and  $C, \omega > 0$ , such that for all  $t > 0$ , and for all  $\tilde{\mu} \in \mathcal{M}(\mathbb{X})$  with  $\|\tilde{\mu}\|_{TV, \mathbb{X}} \leq 1$

$$\|e^{\tilde{\lambda}t} \tilde{\mu} P_t - \tilde{\mu}(\tilde{\phi}) \tilde{\gamma}\|_{TV, \mathbb{X}} \leq C e^{-\omega t},$$

where  $\tilde{\mu} P_t(dy) = \mathbb{P}_{\tilde{\mu}}(Z_t \in dy, t < \tau_{\partial})$ .

Now, we prove Theorem 2.7. Let us start with preliminaries where we first give the framework we use (Polish space, process, filtration), then prove that we have a sample space of path type and (A<sub>0</sub>), and finally present the plan of the rest of the proof.

## 4.1 Preliminaries

**Space, process and filtration.** We work with  $\mathbb{X} = \mathcal{X}$  endowed with the Euclidean topology. It is well-known that this is a Polish space. Let  $\psi \in \Psi$  and  $(Z_t^{(\psi)})_{t \geq 0}$  its associated auxiliary process constructed in Section 3.3. From now on, to simplify the notations, we drop the index  $\psi$  in  $(Z_t^{(\psi)})_{t \geq 0}$ . We keep in mind that  $\psi$  is fixed up to Section 4.6.  $(Z_t)_{t \geq 0}$  is the process we are interested in. We work with the filtration  $(\mathcal{G}_t)_{t \geq 0}$ , defined as the augmented filtration generated by the process  $(\bar{Z}_t)_{t \geq 0} := (Z_t, \tilde{N}_t, I_{N_t}, J_{N_t})_{t \geq 0}$ , see [46, Def. (6.1) - (ii)]. This filtration is complete by construction, and right-continuous by [17, p.62]. It is essential to use this filtration because it is on it that hitting times are stopping times [46, Section 10]. It is also essential to consider a filtration induced by  $(\bar{Z}_t)_{t \geq 0}$  instead of only  $(Z_t)_{t \geq 0}$  because we use information coming from the others random variables in the proof. We point out that the random variables  $(\mathcal{J}_n)_{0 \leq n \leq N_t}$ , are induced by  $(\tilde{N}_t)_{t \geq 0}$  because they are hitting times for the process  $(N_t)_{t \geq 0}$ . We also point out that the random variables  $(U_n)_{1 \leq n \leq N_t}$  are induced by the process  $(X_{N_t})_{t \geq 0}$ , as for all  $n \in \mathbb{N}^*$  it holds  $U_n = (X_n - X_{n-1})_{n \in \mathbb{N}}$  on the event  $\{N_t = n\}$  (we do not have information for  $U_0$ , but we do not need it).

**Sample space of path type.** Having a sample space  $\Omega$  of path type is necessary to prove that the stopping time  $U_H$  presented in Theorem 4.1 is regular with respect to the Markov property, see [54, Prop. 2.2]. In [54, Sect. A.3], it is suggested to use [32, Prop. 8.8] to justify this. The problem is that this criteria does not apply when we work with the augmented filtration. Let us present an alternative way to justify that we work on a sample space of path type.

We recall that  $\hat{\mathcal{X}} = \mathcal{X} \times \mathbb{N} \times \mathcal{Q}_k$  and denote  $\hat{\mathcal{X}}_{\partial} = \hat{\mathcal{X}} \cup \{(\partial)_5\}$  the Alexandroff one-point compactification of  $\hat{\mathcal{X}}$ . This compactification means that the neighborhoods of  $(\partial)_5$  are the complement of all the compact sets, see [17, p.48]. We also denote by  $\mathbb{W}(\mathbb{R}_+, \hat{\mathcal{X}}_{\partial})$  the space of the right-continuous functions from  $\mathbb{R}_+$  to  $\hat{\mathcal{X}}_{\partial}$ . As the process  $(\bar{Z}_t)_{t \geq 0}$  is right-continuous and takes its values on  $\hat{\mathcal{X}}_{\partial}$ , without loss of generality, we assume that we work with the canonical sample space  $\Omega = \mathbb{W}(\mathbb{R}_+, \hat{\mathcal{X}}_{\partial})$ . The latter is defined as the sample space such that for all  $\omega = (\omega_t)_{t \geq 0} \in \Omega$  and  $t \geq 0$ , we have  $(\bar{Z})(\omega) = \omega_t$ . We now prove that this sample space verifies [46, Def. (23.10)]. First, [46, Def. (23.10) - (ii), (vi), (vii)] are directly satisfied for a sample space corresponding to right-continuous maps. In addition, [46, Def. (23.10) - (iii), (v)] are also almost direct to check in view of [46, p.45, p.63, p.110]. To verify the last statement, namely [46, Def. (23.10) - (i)], we need to prove that the process  $(\bar{Z}_t)_{t \geq 0}$  is right-continuous in the Ray topology, and have left-limits in a Ray compactification of  $\hat{\mathcal{X}}$ . We refer to [46, p. 91] where these two notions are presented in detail. In view of [17, Theorems 8.30 and 8.32], the latter is true for a Feller process. Let us thus prove that  $(\bar{Z}_t)_{t \geq 0}$  is a Feller process to obtain that  $\Omega$  is of path type.

We denote  $(\bar{P}_t)_{t \geq 0}$  the semigroup defined for all  $t \geq 0$ ,  $f \in M_b(\hat{\mathcal{X}}_{\partial})$ , and  $(x, a, n, I, J) \in \hat{\mathcal{X}}_{\partial}$  as

$$\bar{P}_t(f)(x, a, n, I, J) = \mathbb{E}[\bar{Z}_t | (X_0, A_0, \tilde{N}_0, I_0, J_0) = (x, a, n, I, J)]. \quad (4.1.1)$$

In view of [17, p.49], we need to prove that for all  $f \in \mathcal{C}_0(\hat{\mathcal{X}}_{\partial})$  we have:

$$\forall t \geq 0 : \bar{P}_t(f) \in \mathcal{C}_0(\hat{\mathcal{X}}_{\partial}) \quad \text{and} \quad \forall z \in \hat{\mathcal{X}}_{\partial} : \lim_{t \rightarrow 0} \bar{P}_t(f)(z) = f(z). \quad (4.1.2)$$

We denote for all  $f \in M_b(\widehat{\mathcal{X}}_\partial)$ ,  $(t, z) \in \mathbb{R}_+ \times \widehat{\mathcal{X}}$ , the function  $\overline{P}_f(t, z) = \overline{P}_t(f)(z)$ , and write  $\overline{P}_1$  this function for  $f \equiv 1$ . We also recall that we have introduced in (3.2.2) the operator  $\Gamma_f$ , and denote by  $\Gamma_1$  this operator for  $f \equiv 1$ . By conditioning with respect to the first jump of  $(\overline{Z})_{t \geq 0}$ , and then applying the strong Markov property, one can easily obtain that for all  $t \geq 0$ ,  $f \in M_b(\widehat{\mathcal{X}})$  and  $z \in \widehat{\mathcal{X}}_\partial$  it holds

$$\overline{P}_t(f)(z) = \begin{cases} \Gamma_f(\overline{P}_f)(t, z) + (1 - \Gamma_1(\overline{P}_1)(t, z)) f((\partial)_5), & \text{if } z \neq ((\partial)_5), \\ f((\partial)_5), & \text{otherwise.} \end{cases} \quad (4.1.3)$$

Moreover, as for all  $f \in \mathcal{C}_0(\widehat{\mathcal{X}}_\partial)$  it holds  $\lim_{z \rightarrow ((\partial)_5)} f(z) = 0$  (function that vanishes at infinity + one point-compactification), we have by continuity that  $f((\partial)_5) = 0$ . Combining these two results, we obtain that for all  $(t, z) \in \mathbb{R}_+ \times \widehat{\mathcal{X}}$ ,  $f \in \mathcal{C}_0(\widehat{\mathcal{X}}_\partial)$ , it holds  $\overline{P}_f(t, z) = \Gamma_f(\overline{P}_f)(t, z)$ . Then, by Lemma 3.5, for all  $T > 0$ , the restriction of  $\overline{P}_f$  on  $[0, T] \times \widehat{\mathcal{X}}$  is in  $\mathcal{C}^0([0, T], \mathcal{C}_0(\widehat{\mathcal{X}}))$ . By continuity of  $\overline{P}_f$  on this restriction, and the second line of (4.1.3), the right-hand side of (4.1.2) is verified. By (3.2.3) and the fact that the neighborhood of  $(\partial)_5$  is the complement of all compact of  $\widehat{\mathcal{X}}$ , the left-hand side of (4.1.2) is also verified. Then,  $(\overline{Z}_t)_{t \geq 0}$  is a Feller process, which implies that  $\Omega$  is of path type.

**Assumption (A<sub>0</sub>).** As this is short, we now give the sequence  $(D_l)_{l \geq 1}$  we use and verify (A<sub>0</sub>). To simplify the future computations, we need that the marginal over telomere lengths in  $D_1$  is a subset of  $[0, B_{\max} l]^{2k}$ , defined in (S<sub>2.2</sub>). For the same reason, we also need to be able to compare the age variable to  $a_0$ , defined above (2.2.1). That is why we take for all  $l \geq 1$

$$D_l = [0, B_{\max} l]^{2k} \times [0, a_0 l], \quad \mathcal{D}_l = [0, B_{\max} l]^{2k}. \quad (4.1.4)$$

The set  $\mathcal{D}_l$  corresponds to the marginal of  $D_l$  over telomere lengths, and is frequently used in this paper. It is trivial to see that this is a sequence of closed subsets such that for all  $l \geq 1$ :  $D_l \subset \text{int}(D_{l+1})$ . Thus, (A<sub>0</sub>) is verified for this choice of  $(D_l)_{l \geq 1}$ .

**Plan of the proof.** We now verify Assumptions (A<sub>1</sub>) – (A<sub>2</sub>) – (A<sub>3</sub>)<sub>F</sub>, which require more computations, in Sections 4.2, 4.3, and 4.4 respectively. Then, in Section 4.5 we prove that the latter implies the existence of a stationary profile for  $(M_t)_{t \geq 0}$  on  $\mathcal{M}(\psi)$ . In Section 4.6, we prove that this stationary profile is the same for all the functions in  $\Psi$ . Finally, in Section 4.7, we obtain a representation of the stationary profile by a function.

## 4.2 Assumption (A<sub>1</sub>) : Doeblin condition on the event $\{t < T_{D_L}\}$

Assumption (A<sub>1</sub>) corresponds to a Doeblin condition on the event  $\{t < T_{D_L}\}$ . Our aim is to show that such a condition is verified, for any initial condition supported on one of the sets  $(D_l)_{l \geq 1}$ . The following proposition implies (A<sub>1</sub>) with  $\nu$  defined by

$$\nu(dx, da) := \frac{1}{C_{\text{renorm}}} \left( \prod_{i=1}^{2k} (x_i)^{m_0} \right) 1_{D_1}(x, a) dx da,$$

where  $C_{\text{renorm}} = \int_{(u,v) \in D_1} \left( \prod_{i=1}^{2k} (u_i)^{m_0} \right) dudv$  and  $m_0$  has been introduced in (S<sub>1.2</sub>).

**Proposition 4.2** (Doeblin condition). *Assume that (S<sub>1.1</sub>), (S<sub>1.2</sub>) and (S<sub>2.2</sub>) hold. Then for all  $l \geq 1$  there exist  $L \geq l + 2$ , and  $t, c_F > 0$ , such that for all  $(x, a) \in D_l$*

$$\mathbb{P}_{(x,a)} [Z_t \in dx' da'; t < \min(\tau_\partial, T_{D_L})] \geq c_F \left( \prod_{i=1}^{2k} (x'_i)^{m_0} \right) 1_{D_l}(x', a') dx' da'.$$

The above statement is stronger than what we need to have (A<sub>1</sub>), as we have  $1_{D_l}$  instead of  $1_{D_1}$  in the right-hand side term. This is because we need it later when we prove (A<sub>3</sub>)<sub>F</sub>, see Section 4.4. Our aim in the current section is to prove Proposition 4.2.

Let us denote for all  $x \in \mathbb{R}_+^{2k}$ ,  $r > 0$ ,

$$B(x, r) = \{u \in \mathbb{R}_+^{2k} \mid \|u - x\|_\infty < r\}.$$

Let us define the notions of  $(r, l, L, t, c)$ - and  $(r, l, L)$ -local Doeblin conditions. We remind that  $\mathcal{D}_l$ , defined in (4.1.4), corresponds to the marginal of  $D_l$  over telomere lengths.

**Definition 4.3** (Local Doeblin condition). *Let  $l, L \geq 1$ ,  $r > 0$ .*

- *For all  $t > 0$ ,  $c > 0$ , we say that a  $(r, l, L, t, c)$ -local Doeblin condition holds from  $x_I \in \mathcal{D}_l$  to  $x_F \in \mathcal{D}_l$  when for all  $(x, a) \in [B(x_I, r) \cap \mathcal{D}_l] \times [0, a_0 l]$  we have*

$$\mathbb{P}_{(x,a)} [Z_t \in dyds; t < \min(\tau_\partial, T_{D_L})] \geq c \left( \prod_{i=1}^{2k} (y_i)^{m_0} \right) 1_{\{(y,s) \in B(x_F, r) \cap \mathcal{D}_l \times [0, a_0 l]\}} dyds.$$

- *We say that a  $(r, l, L)$ -local Doeblin condition holds from  $x_I \in \mathcal{D}_l$  to  $x_F \in \mathcal{D}_l$ , if there exists  $t > 0$ ,  $c > 0$ , such that a  $(r, l, L, t, c)$ -local Doeblin condition holds from  $x_I$  to  $x_F$ .*

As  $\mathcal{D}_l$  is a compact set, for all  $r > 0$  we can find  $N \in \mathbb{N}^*$  and  $(x_j)_{j \in [1, N]} \in (\mathcal{D}_l)^N$  such that  $\mathcal{D}_l = \cup_{j \in [1, N]} [B(x_j, r) \cap \mathcal{D}_l]$ . Then, obtaining  $(r, l, L)$ -local Doeblin conditions from  $x_j$  to  $x_{j'}$  for all  $(j, j') \in ([1, N])^2$  implies Proposition 4.2.

We fix  $r = \min\left(\frac{B_{\max}}{2}, \frac{|\min_{x \in \mathcal{D}_l}(\Delta x) - \delta|}{10}\right)$  for the radius of the balls we use to recover  $\mathcal{D}_l$ . The constants in the definition of  $r$  have been introduced in (S1.1) and (S2.1). We also introduce for all  $l \geq 1$ ,  $x \in \mathcal{D}_l$ ,  $L \geq l$ ,  $c > 0$  the following set, that allows us to know where there are  $(r, l, L, t, c)$ -local Doeblin conditions

$$R_{l,L}^x(c) := \{(t, y) \in \mathbb{R}_+ \times \mathbb{R}_+^{2k} \mid \text{a } (r, l, L, t, c)\text{-local Doeblin condition holds from } x \text{ to } y\}.$$

We now give the steps of the proof.

**Steps of the proof.** To obtain Proposition 4.2, we follow [54, Section 4]. The detail of the proof is given in Appendix B. Here are the steps of the proof.

1. We prove that if two points are contained in a same ball or radius  $r$ , then a  $(r, l, L)$ -local Doeblin condition holds between them. This gives us at the end Lemma B.1, stated and proved in Appendix B.1.
2. We use Lemma B.1 to prove that if a  $(r, l, L)$ -local Doeblin condition holds from  $x_I \in \mathcal{D}_l$  to  $x_F \in \mathcal{D}_l$ , then for all  $y \in (B(x_F, r) \cap \mathcal{D}_l)$ , a  $(r, l, L)$ -local Doeblin condition also holds from  $x_I$  to  $y$ , with a smaller Doeblin coefficient. This gives us at the end Lemma B.2, stated and proved in Appendix B.2.
3. From the latter, we prove that a  $(r, l, L)$ -local Doeblin condition holds for each pair of points of the set  $\mathcal{D}_l$ , even if the points are far apart. Then, as  $\mathcal{D}_l$  can be covered by a finite union of balls of radius  $r$ , the proposition is proved. This step corresponds to the proof of Proposition 4.2, and is detailed in Appendix B.3.

### 4.3 Assumption (A<sub>2</sub>) : Concentration of the mass of the semigroup conditioned to the non-extinction on one of the $D_l$

As the set  $\mathcal{X}$  is not compact, we need to prove that the mass of the semigroup accumulates on a compact set. The latter can be proved by obtaining exponential estimates that we present in Section 4.3.1. The usual ways to obtain these estimates is to bound from below/above stopping times involved in the dynamics by exponential variables, as done in [52, 54, 16, 39], or to bound the infinitesimal generator and then apply Gronwall's lemma, as presented in [5]. However, as mentioned in the introduction, these strategies fail for our model. This is due to the fact that the birth rate is neither bounded from above nor bounded away from 0, and due to the fact that the renewal of individuals in a compact set may occur in

several generations (when (S<sub>2.1</sub>) holds with  $D > 1$ ). Moreover, even when the birth rate is bounded and  $D = 1$ , the estimates obtained with these methods are not precise enough to verify the condition  $\rho_S < \rho$  in (A<sub>2</sub>). Indeed, checking this condition comes down to imposing a restriction on  $\varepsilon_0$  and  $\varepsilon_1$  ( $\varepsilon_1$  and  $\varepsilon_0$  are introduced in (S<sub>2.1</sub>)). This restriction is not optimal due to the loss of information that occurs when the birth rate, which depends on the age, is compared with age-independent rates.

We present here a method to handle these issues based on Bellman-Harris processes, which are the most classical age-dependent branching processes [3, Chap. IV]. In our method, the birth rate only needs to be bounded from below/above by other age-dependent rates (see (S<sub>3.1</sub>)). The restriction on  $\varepsilon_0$  and  $\varepsilon_1$  is also better optimised, as information on the evolution of the birth rate with age is used (see (S<sub>3.2</sub>)-(S<sub>3.3</sub>)). We are therefore able to manage more cases than when the strategies above are used.

First, we present a simplification of Assumption (A<sub>2</sub>) and the notion of Bellman-Harris process in Section 4.3.1. The simplification of the assumption corresponds to a condition that we give to verify (A<sub>2</sub>) that is easy to prove in this context. Then, we present auxiliary statements that allow to verify our simplified version of (A<sub>2</sub>) and check (A<sub>2</sub>) in Section 4.3.2. Finally, we prove all these auxiliary statements in Sections 4.3.3, 4.3.4 and 4.3.5.

### 4.3.1 Simplification of the assumption and Bellman-Harris processes

Qualitatively, Assumption (A<sub>2</sub>) combined with Assumption (A<sub>1</sub>) implies that there exists  $l_o \in \mathbb{N}^*$  such that the mass of the semigroup (conditioned to the non-extinction) is concentrated on  $D_{l_o}$  after a certain time [52, Theorem 5.1]. A condition that seems to imply this is when there exists  $L_1 \in \mathbb{N}^*$ , such that the rate at which the particle leaves  $(D_{L_1})^c$  is greater than the rate the particle renews in  $D_{L_1}$ . Rigorously, this occurs for example when there exist  $\alpha', \beta' \in \mathbb{R}$  such that  $\alpha' > \beta'$ ,  $t_1, t_2 > 0$ , a set  $A \subset D_1$  non negligible with respect to  $\nu$ , and  $L_1 \in \mathbb{N}^*$  such that

$$\forall (x, a) \in A : \quad \mathbb{P}_{(x,a)} [X_{t_1} \in A, \min(\tau_\partial, T_{D_{L_1}}) > t_1] \geq e^{\alpha' t_1}, \quad (4.3.1)$$

$$\forall (x, a) \in (D_{L_1})^c, \forall t \geq t_2 : \quad \mathbb{P}_{(x,a)} [\min(\tau_{D_{L_1}}, \tau_\partial) > t] \leq e^{\beta' t}. \quad (4.3.2)$$

Indeed, as  $A \subset D_1 \subset D_{L_1}$ , the rate at which the particle leaves in  $(D_{L_1})^c$  is strictly greater than the rate at which the particle renews in the set  $D_{L_1}$ . Let us prove that (4.3.1) and (4.3.2) imply Assumption (A<sub>2</sub>).

**Proposition 4.4** (Simplification of (A<sub>2</sub>)). *We suppose that there exist  $\alpha', \beta' \in \mathbb{R}$  such that  $\alpha' > \beta'$ ,  $t_1, t_2 > 0$ , a set  $A \subset D_1$  non negligible with respect to  $\nu$ , and  $L_1 \in \mathbb{N}^*$  such that (4.3.1) and (4.3.2) are satisfied. Then, (A<sub>2</sub>) is verified with  $E = D_{L_1}$  and for any  $\rho \in (-\alpha', -\beta')$ . Moreover, we have  $\rho_S \leq -\alpha'$ .*

*Proof.* First, in view of (4.3.1) and [52, Lemma 3.0.2], we have

$$\rho_S \leq -\frac{\ln(e^{\alpha' t})}{t} = -\alpha'.$$

Now, changing the order of integration we have for all  $\rho \in (-\alpha', -\beta')$ ,  $(x, a) \in (D_{L_1})^c$

$$\begin{aligned} \mathbb{E}_{(x,a)} [\exp(\rho \min(\tau_\partial, \tau_E))] &= \int_0^{+\infty} e^{\rho u} d\mathbb{P}_{\min(\tau_\partial, \tau_E)}(u) = \int_0^{+\infty} \left[ \int_0^u \rho \exp(\rho s) ds + 1 \right] d\mathbb{P}_{\min(\tau_\partial, \tau_E)}(u) \\ &= \rho \int_0^{+\infty} \mathbb{P}_{(x,a)} [\min(\tau_\partial, \tau_E) > s] \exp(\rho s) ds + 1. \end{aligned}$$

This implies in particular using (4.3.2) that for all  $\rho \in (-\alpha', -\beta')$ ,  $(x, a) \in (D_{L_1})^c$

$$\mathbb{E}_{(x,a)} [\exp(\rho \min(\tau_\partial, \tau_E))] \leq \rho \int_0^{t_2} \exp(\rho s) ds + \rho \int_{t_2}^{+\infty} e^{(\rho+\beta')s} ds + 1 < +\infty.$$

Finally, for all  $(x, a) \in D_{L_1}$  we have  $\tau_{D_{L_1}} = 0$  a.s., implying that  $\mathbb{E}_{(x,a)} [\exp(\rho \min(\tau_\partial, \tau_E))] = 1$ . The latter and the above equation imply that Assumption (A<sub>2</sub>) is verified with  $E = D_{L_1}$  and for any  $\rho \in (-\alpha', -\beta')$ .  $\square$

We underline the fact that (4.3.1) and (4.3.2) correspond more or less to [14, Assump. (G<sub>2</sub>)] in continuous time, and with  $\psi_1 = 1$ ,  $\psi_2 = 1_{K_{\text{renew}}}$ . Our aim is to obtain (4.3.1) and (4.3.2), and then apply Proposition 4.4 to verify (A<sub>2</sub>).

To obtain (4.3.1) and (4.3.2), we use Bellman-Harris processes [3, Chap. IV]. These correspond to branching processes defined as follows.

- Lifetimes of individuals are independent and identically distributed.
- At the end of its life, an individual gives birth to a certain number of new individuals. The number of new individuals is distributed according to a reproduction law  $(p_k)_{k \in \mathbb{N}}$ .

The property we exploit to get (4.3.1) and (4.3.2) is that the average number of such a process grows exponentially. Indeed, let us consider an arbitrary Bellman-Harris process. We denote by  $f$  the probability density function of individual lifetimes, by  $\bar{f}$  its associated complementary cumulative distribution function, and by  $\gamma = \sum_{k \geq 0} k p_k$  the mean of its reproduction law. We also denote by  $m(t)$  the mean number of individuals of this Bellman-Harris process at time  $t > 0$ . If there exists  $\alpha' > 0$  such that  $\mathcal{L}(f)(\alpha') = \frac{1}{\gamma}$ , then by and [3, Eq. (12), p.143] and [3, Theorem 3.A, p.152], there exists  $n_1 > 0$  such that

$$m(t) = \sum_{n \geq 0} \gamma^n [f *^{(n)} \bar{f}](t) \underset{t \rightarrow +\infty}{\sim} n_1 e^{\alpha' t}, \quad (4.3.3)$$

where the operation  $*^{(n)}$  is defined in Notation xxxviii).

Let us explain how we get (4.3.1) and (4.3.2) from (4.3.3). We recall that  $(M_t)_{t \geq 0}$ , defined in (2.3.2), is the first moment semigroup of the branching process introduced in Section 2.2. From now on, we call "distorted branching process" the branching process that has for first moment semigroup  $\frac{M_t(f\psi)(x,a)}{\psi(x,a)}$ , for all  $t \geq 0$ ,  $f \in M_b(\mathcal{X})$ ,  $(x, a) \in \mathcal{X}$ . By (2.3.4) and (3.3.8), the semigroup of the particle  $(Z_t)_{t \geq 0}$  is the same as the one of the distorted branching process multiplied by  $e^{-\lambda_\psi t}$ . Thus, below is the intuition of what we need to do to obtain (4.3.1) and (4.3.2).

- We consider a Bellman-Harris process with individual lifetimes distributed according to the density  $\mathcal{F}_0 *^{(D-1)} \mathcal{F}_0$  and a reproduction law with mean  $1 + \varepsilon_0$ . We also recall that the Laplace transform of the convolution of two functions is the product of their Laplace transforms. Then, in view of (4.3.3) and (S<sub>3.2</sub>), we need to bound from below the average number of individuals of the distorted branching process that renews in  $D_{L_1}$  using the mean of this Bellman-Harris process. Indeed, if we transmit the bound obtained for the distorted branching process to  $(Z_t)_{t \geq 0}$  by multiplying by  $e^{-\lambda_\psi t}$ , then we will have (4.3.1).
- We consider a Bellman-Harris process with individual lifetimes distributed according to the density  $\mathcal{G}_0$ , and a reproduction law with mean  $1 + \varepsilon_1$ . Then, in view of (4.3.3) and (S<sub>3.3</sub>), we need to bound from above the average number of individuals of the distorted branching process that stays in  $(D_{L_1})^c$  using the mean of this Bellman-Harris process. Again, if we transmit the bound obtained for the distorted branching process to  $(Z_t)_{t \geq 0}$  by multiplying by  $e^{-\lambda_\psi t}$ , then we will have (4.3.2).

We are going to put this intuition into practice. For the first case, we need to handle the fact that the age of the particle stays in a compact set during renewal. Thus, we do not use exactly the Bellman-Harris presented above to obtain our lower bound. We rather use all the Bellman-Harris processes such that lifetimes are distributed according to  $\mathcal{F}_0 *^{(D-1)} \mathcal{F}_0$ , and such that the reproduction law has a mean in  $(1, 1 + \varepsilon_0)$ , see Section 4.3.4. We now present statements that imply (4.3.1) and (4.3.2), and use them to verify (A<sub>2</sub>).

### 4.3.2 Auxiliary statements and proof that (A<sub>2</sub>) is verified

We first present the following statement, essential for obtaining (4.3.1) and (4.3.2). The proof of this statement is given in Section 4.3.3.

**Lemma 4.5** (Transfer of means). *Let  $m \in \mathbb{N}^*$ ,  $(q(x, dw_1, \dots, dw_m))_{x \in \mathbb{R}_+^{2k}}$  a family of probability measures on  $(\mathbb{R}_+^{2k})^m$ ,  $(A_1, A_2) \in [0, +\infty]^2$  such that  $A_1 \geq A_2$ , and two functions  $b_1 : \mathbb{R}_+^{2k} \times [0, A_1] \mapsto \mathbb{R}_+$  and  $b_2 : \mathbb{R}_+^{2k} \times [0, A_2] \mapsto \mathbb{R}_+$  such that*

$$\begin{aligned} \forall (x, a) \in \mathbb{R}_+^{2k} \times [0, A_2] : & \quad b_1(x, a) \leq b_2(x, a), \\ \forall i \in \{1, 2\}, \forall (x, a) \in \mathbb{R}_+^{2k} \times [0, A_i] : & \quad \lim_{t \rightarrow A_i} \int_a^t b_i(x, s) ds = +\infty. \end{aligned}$$

We denote for all  $i \in \{1, 2\}$ ,  $(x, a, t) \in \mathbb{R}_+^{2k} \times [0, A_i] \times \mathbb{R}_+$

$$\begin{aligned} F_i(x, a, t) &= b_i(x, a) \exp\left(-\int_a^{a+t} b_i(x, u) du\right) \mathbf{1}_{t \in [0, A_i - a]}, \\ \bar{F}_i(x, a, t) &= \exp\left(-\int_a^{a+t} b_i(x, u) du\right) \mathbf{1}_{t \in [0, A_i - a]}, \end{aligned}$$

and for all  $c > 1$

$$\begin{aligned} E_i(x, a, t, c) &= \bar{F}_i(x, a, t) + \sum_{\substack{(n,r) \in \mathbb{N} \times \llbracket 0, m-1 \rrbracket \\ (n,r) \neq (0,0)}} c^n \int_{[0,t]} \cdots \int_{[0, t - \sum_{i=1}^{nm+r-1} s_i]} \int_{(\mathbb{R}_+^{2k})^m} \cdots \int_{(\mathbb{R}_+^{2k})^m} \\ &\times [F_i(x, a, s_1) F_i(w_1, 0, s_2) \cdots F_i(w_{nm+r-1}, 0, s_{nm+r})] \bar{F}_i\left(w_{nm+r}, 0, t - \sum_{j=1}^{nm+r} s_j\right) \\ &\times (ds_1 \dots ds_{nm+r}) (q(x, dw_1, \dots, dw_m) \dots q(w_{nm}, dw_{nm+1}, \dots, dw_{(n+1)m})). \end{aligned} \quad (4.3.4)$$

Then for all  $(x, a, t, c) \in \mathbb{R}_+^{2k} \times [0, A_2] \times \mathbb{R}_+ \times ]1, +\infty[$ , we have

$$E_1(x, a, t, c) \leq E_2(x, a, t, c).$$

**Remark 4.6.** *When for  $i \in \{1, 2\}$ ,  $b_i(x, a) = b_i(a)$  i.e. does not depend on  $x$ , we can integrate all the measures  $q$  in (4.3.4) to obtain, using Notation [xxxviii](#)),*

$$E_i(x, a, t, c) = \bar{F}_i(a, t) + \sum_{\substack{(n,r) \in \mathbb{N} \times \llbracket 0, m-1 \rrbracket \\ (n,r) \neq (0,0)}} c^n (F_i(a, \cdot)) * (F_i(0, \cdot))^{*(nm+r-1)} \bar{F}_i(0, \cdot)(t).$$

In the above, for all  $i \in \{1, 2\}$  and  $(x, a, t, c) \in \mathbb{R}_+^{2k} \times [0, A_2] \times \mathbb{R}_+ \times ]1, +\infty[$ ,  $E_i(x, a, t, c)$  represents the mean number of individuals of a branching process structured by a trait in  $\mathbb{R}_+^{2k} \times [0, A_i]$  at time  $t$ . This branching process starts from an individual with trait  $(x, a) \in \mathbb{R}_+^{2k} \times [0, A_i]$ . The age of each individual grows with a transport term. Each individual branches at a rate  $b_i(x', a')$ , where  $(x', a') \in \mathbb{R}_+ \times [0, A_i]$  is the trait of the individual. At each generation that is a multiple of  $m$ , lengths of the offspring of the  $m$  next generations are updated thanks to the kernel  $q(x', dw_1, \dots, dw_m)$ , where  $x'$  is the trait in space of the individual that branches. In addition, for all  $n \in \mathbb{N}$  and  $r \in \llbracket 0, m-1 \rrbracket$ , the mean number of individuals at the  $(nm+r)$ -th generation is  $c^n$ .

Qualitatively, this lemma states that when  $b_2 \geq b_1$  and  $c > 1$ , the branching process presented above with branching rate  $b_2$  has on average more individuals than the one with branching rate  $b_1$ . We use this property to transfer bounds that we have obtained for a branching process with branching rate  $\bar{b}(a)$  or  $\underline{b}(a)$  to a branching process with branching rate  $b(x, a)$ , using Assumption [\(S3.1\)](#). In particular, this allows us to handle the fact that the branching rate may depend on  $x$  in our case.

In view of the above statement, we obtain [\(4.3.1\)](#) as a direct consequence of the following proposition, whose proof is given in Section [4.3.4](#).

**Proposition 4.7** (Renewal). *Assume that [\(S1.1\)](#), [\(S1.2\)](#), [\(S2\)](#) and [\(S3\)](#) hold. Then for all  $\eta > 0$ , there exist  $l \geq 1$ ,  $L' \geq l + 2m_0$  and  $t_1 > 0$  such that for all  $L \geq \max(t_1/a_0, L')$ ,  $(x, a) \in [0, B_{\max}]^{2k} \times [0, a_0(l+1)]$ , we have*

$$\mathbb{P}_{(x,a)} \left[ Z_{t_1} \in [0, B_{\max}]^{2k} \times [0, a_0(l+1)]; \min(\tau_{\partial}, T_{D_L}) > t_1 \right] \geq e^{(\alpha - \lambda_{\psi} - \eta)t_1}. \quad (4.3.5)$$



As explained in the paragraph about Bellman-Harris processes, the proof of this proposition is based on the fact that in view of (S<sub>2.1</sub>) and (S<sub>3.1</sub>), we can bound from below the left-hand side term of (4.3.5) by the expectations of Bellman-Harris processes (multiplied by  $e^{-\lambda_\psi t}$ ). We use Lemma 4.5 to obtain these lower bounds.

Similarly, (4.3.2) is obtained as a consequence of the following proposition which is proved in Section 4.3.5.

**Proposition 4.8** (Return in a compact set). *Assume that (S<sub>1.1</sub>) and (S<sub>2</sub>) – (S<sub>3</sub>) hold. Then for all  $L_1 \geq L_{\text{return}}$ ,  $\eta > 0$ , there exists  $t_2 > 0$ , such that for all  $t \geq t_2$ ,  $(x, a) \in \mathcal{X}$*

$$\mathbb{P}_{(x,a)} [\min(\tau_{D_{L_1}}, \tau_\partial) > t] \leq e^{(\beta - \lambda_\psi + \eta)t}. \quad (4.3.6)$$

We prove this proposition by bounding from above  $\mathbb{P}_{(x,a)} [\min(\tau_E, \tau_\partial) > t]$  by the mean of a Bellman-Harris process (translated by  $e^{-\lambda_\psi t}$ ), using Lemma 4.5 to obtain the upper bound.

In view of Propositions 4.7 and 4.8, we now use Proposition 4.4 to obtain that there exists  $L_1 \in \mathbb{N}^*$  such that (A<sub>2</sub>) is verified with  $E = D_{L_1}$  and for any  $\rho \in (\lambda_\psi - \alpha, \lambda_\psi - \beta)$  ( $\eta > 0$  of Propositions 4.7 and 4.8 can be taken as small as possible). In particular, we also have by Proposition 4.4 that

$$\rho_S \leq \lambda_\psi - \alpha. \quad (4.3.7)$$

In the rest of the proof, we take arbitrarily  $\rho = \lambda_\psi - \frac{\alpha + \beta}{2} \in (\lambda_\psi - \alpha, \lambda_\psi - \beta)$ . We now prove all the statements presented above.

### 4.3.3 Proof of Lemma 4.5

Before starting to prove this lemma, we need to introduce random variables. The random variables introduced here are only useful for this proof. Let  $(x, a) \in \mathbb{R}_+^{2k} \times [0, A_2)$ . We consider  $(W_l)_{l \in \mathbb{N}}$  a stochastic process taking values in  $\mathbb{R}_+^{2k}$ , such that:

- The initial term is  $W_0 = x$ .
- For all  $n \in \mathbb{N}$ , the distribution of  $(W_{nm+1}, \dots, W_{(n+1)m})$ , knowing  $W_{nm}$ , is given by the measure  $q(W_{nm}, dw_1, \dots, w_m)$ .

Let  $(V_n)_{n \in \mathbb{N}}$  a sequence of independent uniform random variables on  $[0, 1]$ . We also define for  $i \in \{1, 2\}$  the sequence of random variables  $(T_n^{(i)})_{n \in \mathbb{N}}$ , such that  $T_0^{(i)} = 0$  a.s. and:

- For all  $\omega \in \Omega$ :  $T_1^{(i)}(\omega) = (1 - \bar{F}_i)^{-1}(x, a, V_0(\omega))$ , where for all  $(x', a', u) \in \mathbb{R}_+^{2k} \times [0, A_i) \times (0, 1)$

$$(1 - \bar{F}_i)^{-1}(x', a', u) = \inf \{y \in [0, A_i - a') \mid 1 - \bar{F}_i(x', a', y) \geq u\}.$$

The function  $(1 - \bar{F}_i)(x, a, \cdot)$  can be seen as the cumulative distribution function linked to the probability density function  $F_i(x, a, \cdot)$ . Thus, in view of the inverse transform sampling, the distribution of  $T_1^{(i)}$  is given by the probability density function  $F_i(x, a, \cdot)$ .

- For all  $n \in \mathbb{N}^*$ ,  $\omega \in \Omega$ :  $T_{n+1}^{(i)}(\omega) = T_n^{(i)}(\omega) + (1 - \bar{F}_i)^{-1}(W_n(\omega), 0, V_n(\omega))$ . Thus, in view of the inverse transform sampling, the distribution of  $T_{n+1}^{(i)} - T_n^{(i)}$ , knowing  $W_n$  is given by the probability density function  $F_i(W_n, 0, \cdot)$ .

Let  $c > 1$ . We finally define for all  $t \geq 0$ ,  $i \in \{1, 2\}$ ,  $\omega \in \Omega$

$$S_t^{(i)}(\omega) = \sum_{n \geq 0} \sum_{j=0}^{m-1} c^n \mathbf{1}_{\{T_{nm+j}^{(i)}(\omega) \leq t < T_{nm+j+1}^{(i)}(\omega)\}}.$$

One can notice that for all  $t \geq 0$  we have  $E_i(x, a, t, c) = \mathbb{E} [S_t^{(i)}]$ . Thus, if we prove that almost surely it holds  $S_t^{(1)} \leq S_t^{(2)}$ , then the lemma is proved. As  $c > 1$ , the sequence  $(c^n)_{n \in \mathbb{N}}$  increases. Then, we only have to prove that  $T_l^{(1)} \geq T_l^{(2)}$  a.s. for all  $l \in \mathbb{N}$ , to obtain that  $S_t^{(1)} \leq S_t^{(2)}$  a.s..



Let us prove that  $T_l^{(1)} \geq T_l^{(2)}$  a.s. for all  $l \in \mathbb{N}$  by induction. The base case is trivial. We detail the induction step. We suppose that the assertion is true for  $l \in \mathbb{N}$ . Let  $\omega \in \Omega$ . As  $b_1(x', a') \leq b_2(x', a')$  for all  $(x', a') \in \mathbb{R}_+^{2k} \times [0, A_2)$ , we have for all  $s \in [0, A_2)$

$$\begin{aligned} (1 - \bar{F}_1)(W_l(\omega), 0, s) &= 1 - \exp\left(-\int_0^s b_1(W_l(\omega), u) du\right) \\ &\leq 1 - \exp\left(-\int_0^s b_2(W_l(\omega), u) du\right) = (1 - \bar{F}_2)(W_l(\omega), 0, s). \end{aligned}$$

This implies that

$$(1 - \bar{F}_1)^{-1}(W_l(\omega), 0, V_l(\omega)) \geq (1 - \bar{F}_2)^{-1}(W_l(\omega), 0, V_l(\omega)).$$

The induction assumption and the latter imply that when  $l \geq 1$

$$\begin{aligned} T_{l+1}^{(1)}(\omega) &= T_l^{(1)}(\omega) + (1 - \bar{F}_1)^{-1}(W_l(\omega), 0, V_l(\omega)) \\ &\geq T_l^{(2)}(\omega) + (1 - \bar{F}_2)^{-1}(W_l(\omega), 0, V_l(\omega)) = T_{l+1}^{(2)}(\omega). \end{aligned}$$

By the same reasoning, when  $l = 0$ , we also have  $T_{l+1}^{(1)}(\omega) \geq T_{l+1}^{(2)}(\omega)$ . Hence, we obtain that  $T_l^{(1)} \geq T_l^{(2)}$  almost surely, so that the lemma is proved.  $\square$

#### 4.3.4 Proof of Proposition 4.7

The objects we use in this proof are mostly introduced in (S<sub>2</sub>), (S<sub>3.1</sub>), and (S<sub>3.2</sub>). We first notice that, if for all  $\tilde{\alpha} \in (0, \alpha)$  Eq. (4.3.5) is true with  $\tilde{\alpha}$  instead of  $\alpha$  in the equation, then the proposition will be true because  $\tilde{\alpha}$  can be taken as close as possible to  $\alpha$ . Thus, we need to prove that for all  $\tilde{\alpha} \in (0, \alpha)$ , Eq. (4.3.5) is true, replacing  $\alpha$  by  $\tilde{\alpha}$  in the latter.

Let  $\tilde{\alpha} \in (0, \alpha)$ . The function  $\mathcal{L}(\mathcal{F}_0)(x) = \int_0^{+\infty} e^{-sx} \mathcal{F}_0(s) ds$  strictly decreases on  $[0, \alpha]$ , with  $\mathcal{L}(\mathcal{F}_0)(0) = 1$  and  $\mathcal{L}(\mathcal{F}_0)(\alpha) = \frac{1}{(1+\varepsilon_0)^{\frac{1}{D}}}$  in view of (S<sub>3.2</sub>). In addition, by (S<sub>3.1</sub>), we have  $\lim_{x \rightarrow +\infty} \exp(-\int_0^x \underline{b}(s) ds) = 0$ . Then, there exists  $\tilde{\varepsilon}_0 \in (0, \varepsilon_0)$  and  $\tilde{l} \in \mathbb{N}^*$  such that

$$\mathcal{L}(\mathcal{F}_0)(\tilde{\alpha}) = \frac{1}{(1 + \tilde{\varepsilon}_0)^{\frac{1}{D}}}, \quad 1 - \exp\left(-\int_0^{a_0(\tilde{l}+1)} \underline{b}(s) ds\right) \geq \left(\frac{1 + \tilde{\varepsilon}_0}{1 + \varepsilon_0}\right)^{\frac{1}{D}}. \quad (4.3.8)$$

The proof that (4.3.5) is true with  $\tilde{\alpha}$  instead of  $\alpha$  is done in three steps. In Step 1, we prove that there exists  $C > 0$  such that for all  $t \geq 0$ ,  $(x, a) \in K_{\text{renew}} \times [0, a_0\tilde{l}]$ ,  $L \geq t/a_0 + \tilde{l}$ , we have

$$\begin{aligned} \mathbb{P}_{(x,a)}[Z_t \in [0, B_{\max}]^{2k} \times [0, a_0(\tilde{l}+1)]; \min(\tau_{\partial}, T_{D_L}) > t] \\ \geq C e^{-\lambda_{\psi} t} \sum_{\substack{(j,r) \in \mathbb{N} \times \llbracket 0, D-1 \rrbracket \\ (j,r) \neq (0,0)}} (1 + \tilde{\varepsilon}_0)^j \left(\mathcal{F}_a * \mathcal{F}_0^{*(jD+r-1)} \bar{\mathcal{F}}_0\right)(t). \end{aligned} \quad (4.3.9)$$

Then, we prove in Step 2 that for all  $\eta' > 0$ , there exists  $t_{\eta'} > 0$  such that for all  $t \geq t_{\eta'}$

$$F(t) = \sum_{j' \geq 0} \sum_{r'=0}^{D-1} [(1 + \tilde{\varepsilon}_0)]^{j'} \left[(\mathcal{F}_0)^{*(j'D+r')} \bar{\mathcal{F}}_0\right](t) \geq e^{(\tilde{\alpha}-\eta')t}. \quad (4.3.10)$$

Finally, using (4.3.9) and (4.3.10), we conclude the proof of the proposition in Step 3.

**Step 1:** To shorten the number of lines of our equations, we denote in this proof for all  $t \geq 0$ ,  $(x, a) \in \mathcal{X}$ , and  $(l, L) \in (\mathbb{N}^*)^2$

$$I_B = [0, B_{\max}]^{2k} \text{ and } P_B(t, x, a, l, L) = \mathbb{P}_{(x,a)}\left[Z_t \in I_B \times [0, a_0(l+1)]; \min(\tau_{\partial}, T_{D_L}) > t\right].$$

Recall from Section 3.3 that  $N_t$  is the number of jumps of the particle up to time  $t$ , and that on the event  $\{N_t = n, t < \tau_\partial\}$ , we have  $Z_t = (X_n, a1_{\{n=0\}} + t - \mathcal{T}_n)$ , where  $a \geq 0$  is the initial age of the particle. Recall also that  $\overline{\mathcal{H}}_a(x, s) = \frac{\psi(x, a+s)}{\psi(x, a)} \exp(-\lambda_\psi s - \int_a^{a+s} b(u) du)$  is the complementary cumulative distribution function for the time of the first jump when the initial condition is  $(x, a)$ . Using these notations, we have for all  $t \geq 0$ ,  $(x, a) \in K_{\text{renew}} \times [0, a_0\tilde{l}]$ ,  $L \geq t/a_0 + \tilde{l}$

$$P_B(t, x, a, \tilde{l}, L) = \overline{\mathcal{H}}_a(x, t) + \sum_{n \geq 1} \mathbb{P}_{(x, a)} [(X_n, t - \mathcal{T}_n) \in I_B \times [0, a_0(\tilde{l} + 1)], t < \tau_\partial, N_t = n, \forall i \in \llbracket 1, n \rrbracket : X_i \in \mathcal{D}_L]. \quad (4.3.11)$$

Now, we develop the right-hand side term of (4.3.11) in order to exhibit a lower bound. Recall that for all  $x \in \mathbb{R}_+^{2k}$ ,  $a, s \geq 0$ , we have introduced the function  $\mathcal{G}_a(x, s) = 2 \frac{b(x, a+s)}{\psi(x, a)} \exp(-\int_a^{a+s} b(x, u) du - \lambda_\psi s)$ , and that for all  $w \in \mathbb{R}_+^{2k}$  and  $f \in M_b(\mathcal{X})$  we write  $\mathcal{K}_{\mathcal{D}_L}(f)(w) = \mathcal{K}(f1_{\mathcal{D}_L})(w)$ . In view of Lemmas 3.10 and 3.11, Remark 3.2 we have

$$\begin{aligned} P_B(t, x, a, \tilde{l}, L) &= \overline{\mathcal{H}}_a(x, t) + \sum_{n \geq 1} \frac{1}{2^n} \int_{[0, t] \times \mathbb{R}^{2k}} \int_{[0, t-s_1] \times \mathbb{R}^{2k}} \cdots \int_{[0, t-\sum_{i=1}^{n-1} s_i] \times \mathbb{R}^{2k}} \\ &\times \mathcal{V}(w_1) \dots \mathcal{V}(w_n) \mathcal{G}_a(x, s_1) \mathcal{G}_0(w_1, s_2) \dots \mathcal{G}_0(w_{n-1}, s_n) \overline{\mathcal{H}}_0 \left( w_n, t - \sum_{i=1}^n s_i \right) \\ &\times 1_{\{w_n \in I_B\}} 1_{\{t - \sum_{i=1}^n s_i \leq a_0(\tilde{l}+1)\}} (ds_1 \mathcal{K}_{\mathcal{D}_L}(x, dw_1)) \dots (ds_n \mathcal{K}_{\mathcal{D}_L}(w_{n-1}, dw_n)). \end{aligned} \quad (4.3.12)$$

To continue our development, we need to introduce new functions, and obtain intermediate equalities and inequalities. We denote for all  $x \in \mathbb{R}_+^{2k}$ ,  $a, s \geq 0$

$$\mathcal{Y}_a(x, s) = b(x, a+s) \exp\left(-\int_a^{a+s} b(x, u) du\right), \quad \overline{\mathcal{Y}}_a(s) = \exp\left(-\int_a^{a+s} b(x, u) du\right). \quad (4.3.13)$$

These correspond respectively to the probability density function and the complementary cumulative distribution function for times between events that occur at a rate  $b(x, a)$  (for example, the division time of a cell in the branching process introduced in Section 2.2). We also introduce the truncated versions on the interval  $[0, a_0(\tilde{l} + 1))$  of the functions introduced above

$$\begin{aligned} \mathcal{Y}_a^{\tilde{l}}(x, s) &= \frac{\mathcal{Y}_a(x, s)}{1 - \overline{\mathcal{Y}}_a(x, a_0(\tilde{l} + 1) - a)} 1_{s \in [0, a_0(\tilde{l} + 1) - a)}, \\ \overline{\mathcal{Y}}_a^{\tilde{l}}(x, s) &= \frac{\overline{\mathcal{Y}}_a(x, s) - \overline{\mathcal{Y}}_a(x, a_0(\tilde{l} + 1) - a)}{1 - \overline{\mathcal{Y}}_a(x, a_0(\tilde{l} + 1) - a)} 1_{s \in [0, a_0(\tilde{l} + 1) - a)}. \end{aligned}$$

We now obtain the intermediate equalities and inequalities needed to develop (4.3.12). First, in the upper term of the equation below, the terms  $\exp(-\lambda_\psi s_i)$  in  $\mathcal{G}_a(w_0, s_1)$  and  $\mathcal{G}_0(w_i, s_{i+1})$  ( $i \in \llbracket 1, n-1 \rrbracket$ ) can be multiplied with the term  $\exp(-\lambda_\psi (t - \sum_{i=1}^n s_i))$  in  $\overline{\mathcal{H}}_0(w_n, t - \sum_{i=1}^n s_i)$  to give a term  $\exp(-\lambda_\psi t)$ . In addition, for any  $i \in \llbracket 1, n-1 \rrbracket$ , the term  $1/\psi(w_i, 0) = 1/\mathcal{V}(w_i)$  in  $\mathcal{G}_0(w_i, \cdot)$  can be simplified with the term  $\mathcal{V}(w_i)$ . Hence, it comes for all  $n \in \mathbb{N}^*$ ,  $t \in \mathbb{R}_+$ ,  $a \geq 0$ ,  $w = (w_0, \dots, w_n) \in (\mathbb{R}_+^{2k})^{n+1}$ ,  $f \in M_b(\mathbb{R}_+^{n+1})$

$$\begin{aligned} &\int_{[0, t]} \int_{[0, t-s_1]} \cdots \int_{[0, t-\sum_{i=1}^{n-1} s_i]} f(t, s_1, \dots, s_n) \mathcal{G}_a(w_0, s_1) \mathcal{G}_0(w_1, s_2) \dots \mathcal{G}_0(w_{n-1}, s_n) \\ &\times \mathcal{V}(w_1) \dots \mathcal{V}(w_n) \overline{\mathcal{H}}_0 \left( w_n, t - \sum_{i=1}^n s_i \right) ds_1 \dots ds_n \\ &= \frac{2^n \mathcal{V}(w_n) \exp(-\lambda_\psi t)}{\psi(w_0, a)} \int_{[0, t]} \int_{[0, t-s_1]} \cdots \int_{[0, t-\sum_{i=1}^{n-1} s_i]} f(t, s_1, \dots, s_n) \mathcal{Y}_a(w_0, s_1) \mathcal{Y}_0(w_1, s_2) \dots \\ &\times \mathcal{Y}_0(w_{n-1}, s_n) \overline{\mathcal{Y}}_0 \left( w_n, t - \sum_{i=1}^n s_i \right) \left[ 1 + \left( t - \sum_{j=1}^n s_j \right)^{d_\psi} \right] ds_1 \dots ds_n. \end{aligned} \quad (4.3.14)$$

Moreover, we easily have by restricting the integration on the interval  $[a_0\tilde{l}, a_0(\tilde{l} + 1)]$ , and then applying (2.2.1), that for all  $(x, a, s) \in \mathbb{R}_+^{2k} \times [0, a_0\tilde{l}] \times \mathbb{R}_+$

$$\mathcal{Y}_a(x, s) \geq \left(1 - \exp\left(-\int_a^{a_0(\tilde{l}+1)} b(x, s) ds\right)\right) \mathcal{Y}_a^{\tilde{l}}(x, s) \geq (1 - e^{-b_0 a_0}) \mathcal{Y}_a^{\tilde{l}}(x, s). \quad (4.3.15)$$

One can also obtain by similar computations, (S3.1) and (4.3.8) that

$$\mathcal{Y}_0(x, s) \geq \left(\frac{1 + \tilde{\varepsilon}_0}{1 + \varepsilon_0}\right)^{\frac{1}{D}} \mathcal{Y}_0^{\tilde{l}}(x, s) \quad \text{and} \quad \overline{\mathcal{Y}}_0(x, s) \geq \left(\frac{1 + \tilde{\varepsilon}_0}{1 + \varepsilon_0}\right)^{\frac{1}{D}} \overline{\mathcal{Y}}_0^{\tilde{l}}(x, s). \quad (4.3.16)$$

Finally, we have as  $\psi(x, a) = \mathcal{V}(x)(1 + a^{d_\psi})$

$$\overline{\mathcal{H}}_a(x, s) = \frac{\psi(x, a + s)}{\psi(x, a)} \exp\left(-\lambda_\psi s - \int_a^{a+s} b(x, u) du\right) \geq e^{-\lambda_\psi s} \overline{\mathcal{Y}}_a(x, s). \quad (4.3.17)$$

We are now able to develop (4.3.12). First, we apply Eq. (4.3.14) and (4.3.17), to transform functions  $\mathcal{G}_a, \mathcal{G}_0, \overline{\mathcal{H}}_a$  and  $\overline{\mathcal{H}}_0$  into functions  $\mathcal{Y}_a, \mathcal{Y}_0, \overline{\mathcal{Y}}_a$  and  $\overline{\mathcal{Y}}_0$ . Then, we use (4.3.15) and (4.3.16) to display the truncated versions of  $\mathcal{Y}_0, \mathcal{Y}_a, \overline{\mathcal{Y}}_0$  and  $\overline{\mathcal{Y}}_a$ . Thereafter, we use the fact that  $1 + (t - \sum_{i=1}^n y_i)^{d_\psi} \geq 1$  and the fact that  $\mathcal{V}(w_n) \geq \mathcal{V}_{\min}$  by the third statement of (S2.2). Finally, we group indices in the sum according to their remainder for the Euclidean division by  $D$ . It comes for all  $t \geq 0, (x, a) \in K_{\text{renew}} \times [0, a_0\tilde{l}]$ ,  $L \geq t/a_0 + \tilde{l}$

$$\begin{aligned} P_B(t, x, a, \tilde{l}, L) &\geq e^{-\lambda_\psi t} \overline{\mathcal{Y}}_a^{\tilde{l}}(x, t) + (1 - e^{-b_0 a_0}) \frac{\mathcal{V}_{\min} e^{-\lambda_\psi t}}{\psi(x, a)} \sum_{\substack{(j,r) \in \mathbb{N} \times \llbracket 0, D-1 \rrbracket \\ (j,r) \neq (0,0)}} \left[ \left(\frac{1 + \tilde{\varepsilon}_0}{1 + \varepsilon_0}\right)^{\frac{1}{D}} \right]^{jD+r} \\ &\times \int_{[0,t] \times \mathbb{R}^{2k}} \cdots \int_{[0,t - \sum_{i=1}^{jD+r-1} s_i] \times \mathbb{R}^{2k}} \mathcal{Y}_a^{\tilde{l}}(x, s_1) \mathcal{Y}_0^{\tilde{l}}(w_1, s_2) \cdots \mathcal{Y}_0^{\tilde{l}}(w_{jD+r-1}, s_{jD+r}) \\ &\times \overline{\mathcal{Y}}_0^{\tilde{l}} \left( w_{jD+r}, t - \sum_{j=1}^{jD+r} s_j \right) \mathbf{1}_{\{w_{jD+r} \in I_B\}} (ds_1 \mathcal{K}_{\mathcal{D}_L}(x, dw_1)) \cdots (ds_{jD+r} \mathcal{K}_{\mathcal{D}_L}(w_{jD+r-1}, dw_{jD+r})). \end{aligned} \quad (4.3.18)$$

We denote the family of probability measures  $(q(y, dw_1, \dots, dw_D))_{y \in \mathbb{R}_+^{2k}}$  on  $(\mathbb{R}_+^{2k})^D$ , defined for all  $y \in \mathbb{R}_+^{2k}$  in the following way

$$q(y, dw_1, \dots, dw_D) = \frac{\mathbf{1}_{\{w_D \in K_{\text{renew}}\}}}{(\mathcal{K}_{I_B})^D (\mathbf{1}_{\{K_{\text{renew}}\}})(y)} \mathcal{K}_{I_B}(y, dw_1) \mathcal{K}_{I_B}(w_1, dw_2) \cdots \mathcal{K}_{I_B}(w_{D-1}, dw_D).$$

Our aim now is to bound from below the measures  $(\mathcal{K}_{\mathcal{D}_L}(w_{i-1}, dw_i))_{i \in \llbracket 1, jD+r+1 \rrbracket}$  in (4.3.18), using the measure introduced above. To do so, we first need an auxiliary inequality. Let  $i \in \llbracket 1, D-1 \rrbracket$  and  $y \in I_B$ . As at each generation, we have at most 2 offspring, it comes  $(\mathcal{K}_{I_B})^{D-i} (\mathbf{1}_{\{K_{\text{renew}}\}})(y) \leq 2^{D-i} \leq 2^D$ . Then, one can easily obtain from this inequality, (S2.1), and the fact that  $\frac{1}{1+\varepsilon_0} \leq 1$ , that for all  $f \in M_b(\mathbb{R}_+^i)$  nonnegative

$$\begin{aligned} &\int_{w_1 \in \mathbb{R}_+^{2k}} \cdots \int_{w_D \in \mathbb{R}_+^{2k}} f(w_1, \dots, w_i) q(y, dw_1, \dots, dw_D) \\ &\leq 2^D \int_{w_1 \in \mathbb{R}_+^{2k}} \cdots \int_{w_i \in \mathbb{R}_+^{2k}} f(w_1, \dots, w_i) \mathcal{K}_{I_B}(w_1, dw_2) \cdots \mathcal{K}_{I_B}(w_{i-1}, dw_i). \end{aligned} \quad (4.3.19)$$

We are now able to bound from below the measures  $(\mathcal{K}_{\mathcal{D}_L}(w_{i-1}, dw_i))_{i \in \llbracket 1, jD+r+1 \rrbracket}$  in (4.3.18). For all  $(j, r) \in \mathbb{N} \times \llbracket 0, D-1 \rrbracket$  such that  $(j, r) \neq (0, 0)$ :

- When  $r \neq 0$ , in view of (4.3.19) and the fact that  $I_B \subset \mathcal{D}_L$ , we bound from below the measure  $\mathcal{K}_{\mathcal{D}_L}(w_{jD}, dw_{jD+1}) \times \cdots \times \mathcal{K}_{\mathcal{D}_L}(w_{jD+r-1}, dw_{jD+r})$  in (4.3.18) by the measure

$$\frac{1}{2^D} \int_{w_{jD+r+2} \in I_B} \cdots \int_{w_{jD+D-1} \in I_B} \int_{w_{(j+1)D} \in K_{\text{renew}}} q(w_{jD}, dw_{jD+1}, \dots, dw_{j(D+1)}).$$

- Then, in view of Assumption (S<sub>2.1</sub>), we bound from below all the measures of the form  $\mathcal{K}_{\mathcal{D}_L}(w_{(i-1)D}, dw_{(i-1)D+1}) \times \dots \times \mathcal{K}_{\mathcal{D}_L}(w_{(i-1)D+D-1}, dw_{iD})$  in (4.3.18), where  $i \in \llbracket 1, j \rrbracket$ , by the measure

$$(1 + \varepsilon_0)q(w_{(i-1)D}, dw_{(i-1)D+1}, \dots, dw_{iD}).$$

- In view of the fact that  $\left(\frac{1+\tilde{\varepsilon}_0}{1+\varepsilon_0}\right)^{\frac{1}{D}} \leq 1$ , we bound from below the term  $\left[\left(\frac{1+\tilde{\varepsilon}_0}{1+\varepsilon_0}\right)^{\frac{1}{D}}\right]^{jD+r}$  in (4.3.18) by the term  $\left(\frac{1+\tilde{\varepsilon}_0}{1+\varepsilon_0}\right)^{\frac{D-1}{D}} \left(\frac{1+\tilde{\varepsilon}_0}{1+\varepsilon_0}\right)^j$ .
- Finally, in view of the fact that  $\tilde{\varepsilon}_0 < \varepsilon_0$  and the fact that  $\frac{\mathcal{V}_{\min}}{\psi(x,a)} \leq \frac{\mathcal{V}(x)}{\psi(x,a)} \leq 1$ , we bound from below the term  $e^{-\lambda_\psi t} \overline{\mathcal{Y}}_a^{\tilde{l}}(x, s)$  in (4.3.18) by the term  $\left(\frac{1+\tilde{\varepsilon}_0}{1+\varepsilon_0}\right)^{\frac{D-1}{D}} (1 - e^{-b_0 a_0}) \frac{\mathcal{V}_{\min} e^{-\lambda_\psi t}}{\psi(x,a)} \overline{\mathcal{Y}}_a^{\tilde{l}}(x, s)$ .

At the end, we obtain that for all  $t \geq 0$ ,  $(x, a) \in K_{\text{renew}} \times [0, a_0 \tilde{l}]$ ,  $L \geq t/a_0 + \tilde{l}$

$$\begin{aligned} P_B(t, x, a, \tilde{l}, L) &\geq \left(\frac{1+\tilde{\varepsilon}_0}{1+\varepsilon_0}\right)^{\frac{D-1}{D}} (1 - e^{-b_0 a_0}) \frac{\mathcal{V}_{\min} e^{-\lambda_\psi t}}{2^D \psi(x, a)} \left( \overline{\mathcal{Y}}_a^{\tilde{l}}(x, t) + \sum_{\substack{(j,r) \in \mathbb{N} \times \llbracket 0, D-1 \rrbracket \\ (j,r) \neq (0,0)}} (1 + \tilde{\varepsilon}_0)^j \right. \\ &\times \int_{[0,t]} \dots \int_{[0, t - \sum_{i=1}^{jD+r-1} s_i]} \int_{(\mathbb{R}_+^{2k})^D} \dots \int_{(\mathbb{R}_+^{2k})^D} \mathcal{Y}_a^{\tilde{l}}(x, s_1) \mathcal{Y}_0^{\tilde{l}}(w_1, s_2) \dots \mathcal{Y}_0^{\tilde{l}}(w_{jD+r-1}, s_{jD+r}) \\ &\times \overline{\mathcal{Y}}_0^{\tilde{l}} \left( w_{jD+r}, t - \sum_{j=1}^{jD+r} s_j \right) (ds_1 \dots ds_{jD+r}) (q(x, dw_1, \dots, dw_D) \dots q(w_{jD}, dw_{jD+1}, \dots, dw_{(j+1)D})) \Big). \end{aligned}$$

The functions  $\mathcal{Y}_0^{\tilde{l}}$  and  $\overline{\mathcal{Y}}_0^{\tilde{l}}$  correspond to the probability density function and the complementary cumulative distribution function of times between events that occur at a rate  $b_{\tilde{l}}: \mathbb{R}_+^{2k} \times [0, a_0(\tilde{l}+1)] \mapsto \mathbb{R}_+$ , defined such that for all  $(x, a) \in \mathbb{R}_+^{2k} \times [0, a_0(\tilde{l}+1)]$

$$b_{\tilde{l}}(x, a) = -\frac{d}{da} \left( \ln \left( \overline{\mathcal{Y}}_0^{\tilde{l}}(x, a) \right) \right) = \frac{b(x, a) \exp \left( -\int_0^a b(x, s) ds \right)}{\exp \left( -\int_0^a b(x, s) ds \right) - \exp \left( -\int_0^{a_0(\tilde{l}+1)} b(x, s) ds \right)}.$$

We have  $b_{\tilde{l}} \geq \underline{b}$  on  $\mathbb{R}_+^{2k} \times [0, a_0(\tilde{l}+1)]$  by (S<sub>3.1</sub>). Hence, we can apply Lemma 4.5 with  $b_1(x, a) = \underline{b}(a)$ ,  $b_2(x, a) = b_{\tilde{l}}(x, a)$ , and the probability measures  $(q(y, w_1, \dots, w_D))_{y \in \mathbb{R}_+^{2k}}$  (see Remark 4.6 for the simplification when the birth rate does not depend on telomere lengths), to obtain for all  $t \geq 0$ ,  $(x, a) \in K_{\text{renew}} \times [0, a_0 \tilde{l}]$ ,  $L \geq t/a_0 + \tilde{l}$  the following

$$\begin{aligned} P_B(t, x, a, \tilde{l}, L) &\geq \left(\frac{1+\tilde{\varepsilon}_0}{1+\varepsilon_0}\right)^{\frac{D-1}{D}} (1 - e^{-b_0 a_0}) \frac{\mathcal{V}_{\min} e^{-\lambda_\psi t}}{2^D \psi(x, a)} \left( \overline{\mathcal{F}}_a(t) + \sum_{\substack{(j,r) \in \mathbb{N} \times \llbracket 0, D-1 \rrbracket \\ (j,r) \neq (0,0)}} (1 + \varepsilon_0)^j \right) \\ &\times \left( (\overline{\mathcal{F}}_a) * (\overline{\mathcal{F}}_0) *^{(jD+r-1)} (\overline{\mathcal{F}}_0) \right) (t). \end{aligned}$$

Now, in the above equation, we use the fact that  $\overline{\mathcal{F}}_a(t) \geq 0$ . Then, we use the fact that in view of (S<sub>2.2</sub>), it holds for all  $(x, a) \in (K_{\text{renew}} \times [0, a_0 \tilde{l}]) \subset (\mathcal{D}_1 \times [0, a_0 \tilde{l}])$

$$\frac{1}{\psi(x, a)} = \frac{1}{\mathcal{V}(x)(1 + a^{d_\psi})} \geq \frac{1}{\sup_{y \in \mathcal{D}_1} (\mathcal{V}(y)) (1 + (a_0 \tilde{l})^{d_\psi})}.$$

It comes that (4.3.9) is true.

**Step 2:** We first prove by induction that for all  $n \in \mathbb{N}^*$ ,  $t \geq 0$

$$\sum_{r'=0}^{n-1} [\mathcal{F}_0 *^{(r')} \overline{\mathcal{F}}_0] (t) = \int_t^{+\infty} (\mathcal{F}_0 *^{(n-1)} \mathcal{F}_0) (s) ds. \quad (4.3.20)$$

The base case is trivial with the convention that  $(f *^{(0)} g)(t) = g(t)$  (see Notation xxxviii), and the fact that  $\int_t^{+\infty} \mathcal{F}_0(s) ds = \overline{\mathcal{F}}_0(t)$ . For the induction step, we first observe by developing the convolution that

$$\begin{aligned} \int_t^{+\infty} (\mathcal{F}_0 *^{(n)} \mathcal{F}_0) (s) ds &= \int_t^{+\infty} \left[ \int_0^t (\mathcal{F}_0 *^{(n-1)} \mathcal{F}_0) (r) \mathcal{F}_0(s-r) dr \right] ds \\ &\quad + \int_t^{+\infty} \left[ \int_t^s (\mathcal{F}_0 *^{(n-1)} \mathcal{F}_0) (r) \mathcal{F}_0(s-r) dr \right] ds. \end{aligned}$$

Then, we switch  $\int_t^{+\infty}$  and  $\int_0^t$  in the first term, and  $\int_t^{+\infty}$  and  $\int_t^s$  in the second term, and use the fact that  $\int_t^{+\infty} \mathcal{F}_0(s-r) ds = \overline{\mathcal{F}}_0(t-r)$  and  $\int_r^{+\infty} \mathcal{F}_0(s-r) ds = 1$ , to obtain

$$\int_t^{+\infty} (\mathcal{F}_0 *^{(n)} \mathcal{F}_0) (s) ds = (\mathcal{F}_0 *^{(n)} \overline{\mathcal{F}}_0) (t) + \int_t^{+\infty} (\mathcal{F}_0 *^{(n-1)} \mathcal{F}_0) (r) dr.$$

Finally, we apply the induction hypothesis on the above equation. It comes that the induction step is done, and thus that (4.3.20) holds.

Now, we denote for all  $t \geq 0$  the function  $\mathcal{F}_{0,D}(t) = (\mathcal{F}_0 *^{(D-1)} \mathcal{F}_0) (t)$ , that can be seen as a probability density function with complementary cumulative function  $\overline{\mathcal{F}}_{0,D}(t) = \int_t^{+\infty} (\mathcal{F}_0 *^{(D-1)} \mathcal{F}_0) (s) ds$ . Using (4.3.20), the function  $F$  defined in (4.3.10) becomes

$$F(t) = \sum_{j' \geq 0} (1 + \varepsilon_0)^{j'} (\mathcal{F}_{0,D} *^{(j')} \overline{\mathcal{F}}_{0,D}) (t).$$

In particular,  $F$  is the mean of a Bellman-Harris process with lifetimes distributed according to  $\mathcal{F}_{0,D}$  and a reproduction law with mean  $1 + \varepsilon_0$ , see [3, Eq. (12), p.143]. In addition, as the Laplace transform of the convolution of two functions is the product of their Laplace transform, for all  $x \in \mathbb{R}$  such that the Laplace transform of  $\mathcal{F}_0$  is defined, we have  $\mathcal{L}(\mathcal{F}_{0,D})(x) = (\mathcal{L}(\mathcal{F}_0)(x))^D$ . Then, in view of the first equality in (4.3.8) and (4.3.3), there exists  $n_1 > 0$  such that  $F(t) \sim n_1 e^{\tilde{\alpha}t}$  when  $t \rightarrow +\infty$ . We easily deduce Eq. (4.3.10) from the latter.

**Step 3:** Let  $\eta' > 0$  and  $t_{\eta'}$  such that (4.3.10) holds for  $\eta'$  previously fixed. A consequence of the second condition in (S3.2) and the fact that  $\tilde{\alpha} < \alpha$  is that there exists  $t_c, c > 0$  such that for all  $t \geq t_c$ ,  $a \geq 0$ , we have

$$\int_0^t e^{-\tilde{\alpha}s} \mathcal{F}_a(s) ds \geq c. \quad (4.3.21)$$

We use this inequality and (4.3.9) to bound from below  $P_B(t, x, a, \tilde{l}, L)$  by an exponential term. First, in view of Tonelli's theorem, we put the convolution by  $\mathcal{F}_a$  in (4.3.9) outside the sum. Then, we bound from below what remains in the sum by  $F$  defined in (4.3.10). The bound appears when we change the indices in the sum, and take  $r' = r - 1$ , and  $j' = j + 1$  when  $r' = -1$ . Finally, we plug the inequality given in (4.3.10) and (4.3.21) in the lower bound we have obtained. This gives us that for all  $t \geq t_{\eta'} + t_c$ ,  $(x, a) \in K_{\text{renew}} \times [0, a_0 \tilde{l}]$ ,  $L \geq t/a_0 + \tilde{l}$

$$P_B(t, x, a, l, L) \geq C e^{-\lambda_\psi t} \int_0^t F(t-s) \mathcal{F}_a(s) ds \geq C e^{-\lambda_\psi t} \int_0^{t-t_{\eta'}} F(t-s) \mathcal{F}_a(s) ds \geq c.C.e^{(\tilde{\alpha}-\lambda_\psi-\eta')t}. \quad (4.3.22)$$

Using now the Markov property, Proposition 4.2, and finally (4.3.22), we can find  $t'_1 > 0$ ,  $c_1 > 0$ ,  $L' \geq (\tilde{l}+1) + 2m_0$ , such that for all  $t \geq t_{\eta'} + t_c$ ,  $(x, a) \in [0, B_{\text{max}}]^{2k} \times [0, a_0(\tilde{l}+1)]$ ,  $L \geq \max(t/a_0 + \tilde{l}, L')$

$$\begin{aligned} P_B(t + t'_1, x, a, l, L) &\geq c_1 \int_{(x', a') \in K_{\text{renew}} \times [0, a_0 \tilde{l}]} P_B(t, x', a', l, L) dx' da' \\ &\geq c_1 \cdot \text{Leb}(K_{\text{renew}}) \cdot (a_0 \tilde{l}) \cdot c.C.e^{(\tilde{\alpha}-\lambda_\psi-\eta')t}, \end{aligned} \quad (4.3.23)$$

where Leb is the Lebesgue measure on  $\mathbb{R}_+^{2k}$ .

Let  $\eta > \eta'$ . The ratio between the right-hand side term of (4.3.23) and  $t \mapsto e^{(\tilde{\alpha} - \lambda_\psi - \eta)(t+t'_1)}$  tends to infinity when  $t \rightarrow +\infty$ . Therefore, as  $\eta'$  can be taken as small as possible, we easily obtain that (4.3.5) is true replacing  $\alpha$  by  $\tilde{\alpha}$ , for any  $\tilde{\alpha} \in (0, \alpha)$ . As stated at the beginning of the proof, this yields that the proposition is true.  $\square$

### 4.3.5 Proof of Proposition 4.8

Let  $L_1 \geq L_{\text{return}}$ . By the definition of  $\tau_{D_{L_1}}$ , for all  $(x, a) \in D_{L_1}$ , we have

$$\mathbb{P}_{(x,a)} [\min(\tau_{D_{L_1}}, \tau_\partial) > t] = 0.$$

Thus, we just need to prove (4.3.6) for all  $(x, a) \in (D_{L_1})^c$ . The proof that (4.3.6) holds for all  $(x, a) \in (D_{L_1})^c$  is done in two steps. First, in Step 1, we prove that for all  $t \geq 0$ ,  $(x, a) \notin D_{L_1}$

$$\mathbb{P}_{(x,a)} [\min(\tau_{D_{L_1}}, \tau_\partial) > t] \leq \bar{\psi}(1 + t^{d_\psi}) e^{-\lambda_\psi t} \left( \bar{\mathcal{G}}_a(t) + \sum_{n \geq 1} (1 + \varepsilon_1)^n (\mathcal{G}_a * \mathcal{G}_0 *^{(n-1)} \mathcal{G}_0)(t) \right), \quad (4.3.24)$$

where  $\bar{\psi}$  is defined by Lemma 3.4,  $d_\psi$  in (2.3.3), and  $\mathcal{G}_a$  in (S3.3). The conclusion is then given in Step 2.

**Step 1:** Let  $(x, a) \in (D_{L_1})^c$ ,  $t \geq 0$ . Recall from Section 3.3 that  $\mathcal{T}_1$  is the waiting time for the first jump of  $(Z_t)_{t \geq 0}$ ,  $N_t$  is the total number of jumps  $(Z_t)_{t \geq 0}$  has made up to time  $t > 0$ , and  $(X_n)_{n \in \mathbb{N}}$  is the evolution of telomere lengths of  $(Z_t)_{t \geq 0}$  jump by jump. In view of the latter, we have

$$\mathbb{P}_{(x,a)} [\min(\tau_{D_{L_1}}, \tau_\partial) > t] = \mathbb{P}_{(x,a)} [\mathcal{T}_1 > t] + \sum_{n \geq 1} \mathbb{P}_{(x,a)} [\forall i \in \llbracket 1, n \rrbracket : X_i \in (D_{L_1})^c, N_t = n, \tau_\partial > t]. \quad (4.3.25)$$

First, we bound from above the first term on the right-hand side. Using the equality  $\int_a^{a+t} \frac{\partial \psi}{\partial a}(x, u) du = \ln \left( \frac{\psi(x, a+t)}{\psi(x, a)} \right)$  and the third statement of Lemma 3.4, we obtain

$$\begin{aligned} \mathbb{P}_{(x,a)} [\mathcal{T}_1 > t] &= \bar{\mathcal{H}}_a(x, t) = \exp \left( - \int_a^{a+t} b(x, u) du - \lambda_\psi t + \int_a^{a+t} \frac{\partial \psi}{\partial a}(x, u) du \right) \\ &\leq \bar{\psi}(1 + t^{d_\psi}) \exp \left( - \int_a^{a+t} b(x, u) du - \lambda_\psi t \right). \end{aligned} \quad (4.3.26)$$

Now, we bound from above the second term in (4.3.25). Let  $n \in \mathbb{N}^*$ . Recall (2.3.1) for the definition of  $\mathcal{K}_{(D_L)^c}$ . In view of Lemmas 3.10 and 3.11, Remark 3.2, and Eq. (4.3.14), we have

$$\begin{aligned} \mathbb{P}_{(x,a)} [\forall i \in \llbracket 1, n \rrbracket : X_i \in (D_{L_1})^c, N_t = n, \tau_\partial > t] &= \frac{e^{-\lambda_\psi t}}{\psi(x, a)} \int_{[0, t] \times \mathbb{R}_+^{2k}} \int_{[0, t-s_1] \times \mathbb{R}_+^{2k}} \cdots \int_{[0, t-\sum_{i=1}^{n-1} s_i] \times \mathbb{R}_+^{2k}} \\ &\times \mathcal{Y}_{a_1}(x, s_1) \mathcal{Y}_0(w_1, s_2) \cdots \mathcal{Y}_0(w_{n-1}, s_n) \bar{\mathcal{Y}}_0 \left( w_n, t - \sum_{j=1}^n s_j \right) \left[ 1 + \left( t - \sum_{j=1}^n s_j \right)^{d_\psi} \right] \mathcal{V}(w_n) \\ &\times (ds_1 \mathcal{K}_{(D_{L_1})^c}(x, dw_1)) \cdots (ds_n \mathcal{K}_{(D_{L_1})^c}(w_{n-1}, dw_n)). \end{aligned} \quad (4.3.27)$$

Let us introduce a family of probability measure  $(q(w, dw'))_{w \in \mathbb{R}_+^{2k}}$  such that for all  $w \in \mathcal{X}$

$$q(w, dw') = \frac{\mathcal{V}(w') \mathcal{K}_{(D_{L_1})^c}(w, dw')}{\mathcal{K}_{(D_{L_1})^c}(\mathcal{V})(w)}.$$

Our aim is to bound from above the measures  $(\mathcal{K}_{(D_{L_1})^c}(w_{i-1}, dw_i))_{i \in \llbracket 1, n \rrbracket}$  in (4.3.27) (convention that  $w_0 = x$ ), using the measures introduced above. To do so, we use the first statement of (S2.2) to bound

from above the measure  $\mathcal{V}(w_n)\mathcal{K}_{(\mathcal{D}_{L_1})^c}(w_{n-1}, dw_n)$  by  $(1 + \varepsilon_1)\mathcal{V}(w_{n-1})q(w_{n-1}, dw_n)$ . Then, iterate this procedure  $n - 1$  times, such that at the end we bound from above  $(1 + \varepsilon_1)^{n-1}\mathcal{V}(w_1)\mathcal{K}_{(\mathcal{D}_{L_1})^c}(x, dw_1)$  by  $(1 + \varepsilon_1)^n\mathcal{V}(x)q(x, dw_1)$ . This gives us an upper bound for (4.3.27). We plug in (4.3.25) the upper bound obtained and (4.3.26), and bound from above the term  $1 + (t - \sum_{j=1}^n s_j)^{d_\psi}$  in (4.3.25) by  $1 + t^{d_\psi}$ . We obtain after these steps

$$\begin{aligned} \mathbb{P}_{(x,a)}[\min(\tau_{D_{L_1}}, \tau_\partial) > t] &\leq e^{-\lambda_\psi t}(1 + t^{d_\psi}) \left[ \bar{\psi} \bar{\mathcal{Y}}_a(t) + \frac{\mathcal{V}(x)}{\psi(x,a)} \sum_{n \geq 1} (1 + \varepsilon_1)^n \int_{[0,t] \times \mathbb{R}_+^{2k}} \cdots \int_{\left[0, t - \sum_{i=1}^{n-1} s_i\right] \times \mathbb{R}_+^{2k}} \right. \\ &\times \mathcal{Y}_a(x, s_1) \mathcal{Y}_0(w_1, s_2) \cdots \mathcal{Y}_0(w_{n-1}, s_n) \bar{\mathcal{Y}}_0 \left( w_n, t - \sum_{j=1}^n s_j \right) (ds_1 q(x, dw_1)) \cdots (ds_n q(w_{n-1}, dw_n)) \left. \right]. \end{aligned}$$

As  $\bar{\psi} > 1$ , we bound from above the term  $\frac{\mathcal{V}(x)}{\psi(x,a)} = \frac{\mathcal{V}(x)}{(1+a^{d_\psi})\mathcal{V}(x)}$  by  $\bar{\psi}$ . Then, recalling that  $\mathcal{G}_a(s) = \bar{b}(a+s) \exp\left(-\int_a^{a+s} \bar{b}(u) du\right)$ , we obtain (4.3.24) by applying Lemma 4.5 with  $b_1 = b$ ,  $b_2 = \bar{b}$  and the probability measures  $(q(w, dw'))_{w \in \mathcal{X}}$  (we have  $b_1 \leq b_2$  by (S3.1) and see Remark 4.6 for the simplification of the notations when one of the birth rate does not depend on telomere lengths).

**Step 2:** Let us denote for all  $t \geq 0$

$$m(t) = \sum_{n \geq 0} (1 + \varepsilon_1)^n \left[ \mathcal{G}_0 *^{(n)} \bar{\mathcal{G}}_0 \right](t).$$

This function is the mean of a Bellman-Harris process with lifetimes distributed according to  $\mathcal{G}_0$ , and a reproduction law with mean  $1 + \varepsilon_1$ , see [3, Eq. (12), p.143]. To have a reproduction law with mean  $1 + \varepsilon_1$ , we take for reproduction law  $(p_l)_{l \in \mathbb{N}^*}$  such that  $p_1 + r p_r = 1 + \varepsilon_1$  and  $p_1 + p_r = 1$ , where  $r \in \mathbb{N} \setminus \{0, 1\}$  is taken sufficiently large. By (4.3.3) and (S3.3), there exists  $n_1 > 0$  such that  $m(t) \underset{t \rightarrow +\infty}{\sim} n_1 e^{\beta t}$ . Then, for all  $\eta' > 0$ , there exists  $t'_2 > 0$  such that for all  $t \geq t'_2$

$$m(t) \leq e^{(\beta + \eta')t}. \quad (4.3.28)$$

In addition, as  $p_0 = 0$ , the number of individuals of such a Bellman-Harris increases with time. Then,  $m$  is an increasing function.

Let us fix  $\eta' > 0$ . Using the bound in (4.3.28), the fact that  $m$  is increasing and that  $\int_0^\infty \mathcal{G}_a(s') ds' = 1$ , Eq. (4.3.24) becomes for all  $t \geq t'_2$

$$\begin{aligned} \mathbb{P}_{(x,a)}[\min(\tau_{D_{L_1}}, \tau_\partial) > t] &\leq \bar{\psi}(1 + t^{d_\psi}) e^{-\lambda_\psi t} \left( \bar{\mathcal{G}}_a(t) + (1 + \varepsilon_1)(\mathcal{G}_a * m)(t) \right) \\ &\leq \bar{\psi}(1 + t^{d_\psi}) e^{-\lambda_\psi t} \left( 1 + (1 + \varepsilon_1)e^{(\beta + \eta')t} \right). \end{aligned} \quad (4.3.29)$$

For any  $\eta > \eta'$ , the ratio between the right-hand-side term of (4.3.29) and  $e^{(\beta - \lambda_\psi + \eta)t}$  goes to 0 when  $t$  goes to infinity. The latter and the fact that  $\eta'$  can be taken as small as possible imply that the proposition is proved.  $\square$

#### 4.4 Assumption $(A_3)_F$ : Asymptotic comparison of survival with a weak form of a Harnack inequality

To verify  $(A_3)_F$ , we need to construct a stopping time  $U_H$  such that (4.0.1), (4.0.2) and (4.0.3) are true. For the stopping time that we present in this section, the fact that (4.0.2) is true is trivial by its definition. To check (4.0.1), the only difficulty is that the calculations are cumbersome. That is why, we postpone a large part of the proof of them in Appendix C, and only sketch why this is true in Section 4.4.6. The most interesting part, that we detail in this section, is the proof of (4.0.3). Again, we need to handle the fact that we have an age-dependent process, with a birth rate that depends both on the age and on telomere lengths of the particle. Hence, a stochastic comparison of the distorted branching



process by a Bellman-Harris process is done to verify (4.0.3). We believe that the proof presented here allows to handle more general cases than the one presented in [54], in particular models where the age is involved.

Let us proceed as follows. First, we explain the assumption, and construct the stopping time  $U_H$  in Section 4.4.1. Then, we give the auxiliary statements that allow us to get (4.0.3) in Section 4.4.2, and prove these statements in Sections 4.4.3, 4.4.4 and 4.4.5. Finally, we obtain (4.0.1) and (4.0.3) in Section 4.4.6. The latter allows us to conclude that  $(A_3)_F$  is verified.

#### 4.4.1 Context and construction of the stopping time $U_H$

**Context.** It is well-known since [13] that a Doeblin condition, combined with the fact that the probability of non-extinction starting from  $\nu$  is not too small compared to the probability of non-extinction starting from elsewhere, implies the existence of a stationary profile. In the setting of [52], this last criteria is called "asymptotic comparison of survival" and is stated as

$$\limsup_{t \rightarrow +\infty} \sup_{x \in E} \frac{\mathbb{P}_x [t < \tau_\partial]}{\mathbb{P}_\nu [t < \tau_\partial]} < +\infty. \quad (4.4.1)$$

One of the methods to compare the probability of non-extinction starting from  $\nu$ , and starting from elsewhere, is to use a Harnack inequality. The latter corresponds to the fact that there exist  $t_0, t_1 > 0$  and  $C > 0$  such that for all  $z \in E$

$$\mathbb{P}_z [Z_{t_0} \in dz', t < \tau_\partial] \leq C \cdot \mathbb{P}_\nu [Z_{t_1} \in dz', t < \tau_\partial]. \quad (4.4.2)$$

By Proposition 4.2, we know that the right-hand side term of (4.4.2) is bounded from below, up to a constant, by the Lebesgue measure restricted on intervals of the form  $[\eta, A]^{2k}$ , where  $\eta > 0, A > 0$ . Thus, if we prove that the left-hand side term of (4.4.2) is bounded from above, up to a constant, by the restriction of the Lebesgue measure on one of these intervals, then we will have (4.4.2). However, the particle  $(Z_t)_{t \geq 0}$  has a jump kernel that is discontinuous with respect to the Lebesgue measure: there are Dirac measures in the coordinates where the particle does not jump. In addition, for all  $t > 0, \eta > 0, A > 0$ , the probability that the particle has telomere lengths out of  $[\eta, A]^{2k}$  at time  $t$  is strictly larger than 0. Hence, the above tactics does not work.

Assumption  $(A_3)_F$  allows us to handle these problems by considering events where a Harnack inequality holds, and events where it fails. The latter are called "rare events". When the probability to have a rare event is "sufficiently" small, then we have (4.4.1), see [54, Theorem 2.3]. This can be seen as a "weak form of a Harnack inequality".

**Construction of the stopping time.** The first thing we do is to construct the stopping time  $U_H$  involved in this assumption. The above rare events are the following:

- The particle has not jumped in all the coordinates,
- The number of jumps is too large,
- The particle has a telomere with a length too close to 0.

To write them rigorously, we need to introduce some notions. We recall from Section 3.3 that for all  $l \geq 1$ , the random variables  $I_l$  and  $J_l$  correspond respectively to the sets of "shortened coordinates", and of "lengthened coordinates", at the  $l$ -th jump. We also recall that  $\mathcal{N}_\partial$  is the random variable that describes the number of jumps of the particle before extinction. For all  $j \in \llbracket 1, 2k \rrbracket$ , we introduce  $\mathcal{N}_j$  the number of jumps before the first jump in the  $j$ -th coordinate, defined as

$$\mathcal{N}_j := \inf \{l \in \llbracket 1, \mathcal{N}_\partial \rrbracket, j \in I_l \cup J_l\}.$$

We also introduce  $T_{all}$  the time before the particle  $(Z_t)_{t \geq 0}$  has jumped in all coordinates, defined as

$$T_{all} := \max_{j \in \llbracket 1, 2k \rrbracket} \mathcal{J}_{\mathcal{N}_j}.$$



Let  $\varepsilon \in (0, 1)$ . In view of the above list of "rare events", our aim is to find  $t_F > 0$ ,  $n_J \in \mathbb{N}^*$  and  $\eta_0 > 0$  such that the statements of  $(A_3)_F$  are satisfied for  $\varepsilon$  and  $U_H$  of the form

$$U_H := \begin{cases} t_F, & \text{if } t_F < \tau_\partial \text{ and } T_{all} \leq t_F \text{ and } N_{t_F} \leq n_J \text{ and } X_{N_{t_F}} \in [\eta_0, B_{\max} L_1 + n_J \Delta]^{2k}, \\ +\infty, & \text{otherwise.} \end{cases} \quad (4.4.3)$$

Eq. (4.0.2) is trivially verified. Thus, we focus on proving that there exists  $t_F > 0$ ,  $n_J \in \mathbb{N}^*$  and  $\eta_0 > 0$  such that (4.0.1) and (4.0.3) are verified. In particular, we now present auxiliary statements that allows us to obtain (4.0.3).

#### 4.4.2 Statements useful to obtain (4.0.3)

To obtain (4.0.3), we need to control the probability that  $U_H = \infty$  on  $\{t_F < \tau_\partial\}$ . From the definition of  $U_H$ , the three cases that correspond to this situation are cases where  $T_{all}$  is too large, cases where  $N_{t_F}$  is too large, and cases where  $X_{N_{t_F}} \in ([\eta_0, +\infty]^{2k})^c$ . The third case is directly handled by the statement allowing to obtain (4.0.1), see Section 4.4.6. For the two other cases, we introduce for each one statements allowing to control their probability and briefly explain how they are obtained. Then, in Sections 4.4.3, 4.4.4 and 4.4.5 we give all the proofs.

**Statements to control the probability that  $T_{all}$  is too large.** Inspired by what we have done in Section 4.3, we propose to use Bellman-Harris processes to control this probability. To be more precise, we need to stochastically compare the distorted branching process presented in Section 4.3.1, by the Bellman-Harris process used to prove Proposition 4.8. This will give us that the probability that  $\min(T_{all}, \tau_\partial) > t$  tends to 0 faster than  $e^{(\beta - \lambda_\psi + \eta)t}$ , for all  $\eta > 0$ .

To do so, we first obtain an upper bound for the probability that a coordinate is not shortened at one event of division. As the choice of which telomeres are shortened is uniform, we only have to control for all  $i \in \llbracket 1, 2k \rrbracket$  the cardinal of  $\{I \in \mathcal{I}_k \mid i \notin I\}$  (we recall that  $\mathcal{I}_k$  is defined in (2.2.4), and is the set that contains all the possible combinations of indices of telomeres that can be shortened). The following lemma, which is proved in Section 4.4.3, deals with the latter.

**Lemma 4.9** (Number of combinations for the shortening). *Let us consider  $i \in \llbracket 1, 2k \rrbracket$ . Then, the functions  $f_1 : \{0, 1\}^k \rightarrow \mathcal{I}_k$  and  $f_2 : \{0, 1\}^{k-1} \rightarrow \{I \in \mathcal{I}_k, i \notin I\}$  defined such that*

$$f_1(x) = \{1 + kx_1, \dots, k + kx_k\}, \quad f_2(x) = \begin{cases} \{j + kx_j \mid j \in \llbracket 1, k \rrbracket, j \neq i\} \cup \{i + k\}, & \text{if } i \leq k, \\ \{j + kx_j \mid j \in \llbracket 1, k \rrbracket, j \neq i\} \cup \{i - k\}, & \text{otherwise,} \end{cases}$$

are bijective. In particular,  $\#\{I \in \mathcal{I}_k, i \notin I\} = 2^{k-1}$ ,  $\#(\mathcal{I}_k) = 2^k$  and  $\frac{\#\{I \in \mathcal{I}_k, i \notin I\}}{\#(\mathcal{I}_k)} = \frac{1}{2}$ .

From here, we use a Bellman-Harris process to bound from above the probability that  $\min(T_{all}, \tau_\partial) > t$ . This gives us the following lemma, which is proved in Section 4.4.4.

**Lemma 4.10** (Control of the discontinuities). *Assume that  $(S_{1.1})$ ,  $(S_2)$  and  $(S_3)$  hold. Then, for all  $\varepsilon > 0$ , we can find  $t_0 > 0$  such that for all  $t \geq t_0$*

$$\sup_{(x,a) \in E} (\mathbb{P}_{(x,a)}[\min(T_{all}, \tau_\partial) > t]) \leq \frac{\varepsilon}{3} \exp(-\rho t), \quad (4.4.4)$$

where  $\rho = \lambda_\psi - \frac{\alpha + \beta}{2}$  is defined in Section 4.3.2, under (4.3.7).

**Statement to control the probability that  $N_{t_F}$  is too large.** To control the probability that  $N_{t_F}$  is too large, we only use the following statement, that we prove in Section 4.4.5. Briefly, we obtain this using the fact that  $(\mathbb{P}[\mathcal{N}_\partial > n])_{n \geq 0}$  decreases exponentially fast.

**Lemma 4.11** (Control of the number of jumps). *Assume that  $(S_{1.1})$ ,  $(S_2)$  and  $(S_3)$  hold. Then for all  $\varepsilon > 0$ , there exists an increasing function  $n : \mathbb{R}_+ \rightarrow \mathbb{N}^*$  such that for all  $t \geq 0$*

$$\sup_{(x,a) \in E} (\mathbb{P}_{(x,a)} [N_t > n(t), t < \tau_\partial]) \leq \frac{\varepsilon}{3} \exp(-\rho t), \quad (4.4.5)$$

where  $\rho = \lambda_\psi - \frac{\alpha+\beta}{2}$  is defined in Section 4.3.2, under (4.3.7).

Let us prove now all the statements given above, and then obtain (4.0.1) and (4.0.3).

#### 4.4.3 Proof of Lemma 4.9

The injectivity of each of these functions is trivial. We prove the surjectivity for  $f_1$  (this is very similar for  $f_2$ ). Let  $I \in \mathcal{I}_k$ . As  $I \subset \{1, 2, \dots, 2k\}$ , for all  $i \in I$  we have  $i - 1 \in \{0, 1, \dots, 2k - 1\}$ . Then, for all  $i \in I$  there exists  $(q_i, r_i) \in \{0, 1\} \times \llbracket 0, k - 1 \rrbracket$  such that  $i - 1 = q_i k + r_i$ . By the definition of  $\mathcal{I}_k$ , for all  $(i, j) \in I^2$  such that  $i \neq j$  we have that  $r_i \neq r_j$ . In addition, we know that  $\#(I) = k$ . Combining these two statements yields that the set  $\{r_i, i \in I\}$  is a set with  $k$  different elements. Then, necessarily

$$\{r_i, i \in I\} = \{0, \dots, k - 1\}.$$

We can now define  $\sigma : I \rightarrow \llbracket 1, k \rrbracket$  as  $\sigma(i) = r_i + 1$  for all  $i \in I$ . We obtain a new expression for  $I$  using  $\sigma$

$$I = \{q_i k + r_i + 1 \mid i \in I\} = \{q_{\sigma^{-1}(j)} k + j \mid j \in \llbracket 1, k \rrbracket\}.$$

Thus, if we take  $x = (q_{\sigma^{-1}(1)}, q_{\sigma^{-1}(2)}, \dots, q_{\sigma^{-1}(k)})$  we have  $f_1(x) = I$ . This implies that  $f_1$  is surjective.  $\square$

#### 4.4.4 Proof of Lemma 4.10

Let  $(x, a) \in E$  be the initial condition of the process  $(Z_t)_{t \geq 0}$ . Recall that  $\mathcal{N}_\partial$  is the random variable that describes the number of jumps before extinction, and for all  $j \in \llbracket 1, 2k \rrbracket$ ,  $\mathcal{N}_j$  is the random variable used to describe the number of jumps before having a jump in the  $j$ -th coordinate. For every  $j \in \llbracket 1, 2k \rrbracket$  we also define

$$\mathbb{N}_j := \inf \{l \in \llbracket 1, \mathcal{N}_\partial \rrbracket, j \in I_l\},$$

the number of jumps before having a shortening in the  $j$ -th coordinate. We easily see that  $\mathcal{T}_{\mathbb{N}_j}$  is a random variable that describes the time of the first jump in the  $j$ -th coordinate, and  $\mathcal{T}_{\mathbb{N}_j}$  is a random variable that describes the time of the first shortening in the  $j$ -th coordinate. As  $N_t = l$  is equivalent to  $\mathcal{T}_{l+1} > t \geq \mathcal{T}_l$  and  $T_{all} = \max_{j \in \llbracket 1, 2k \rrbracket} \mathcal{T}_{\mathbb{N}_j}$ , we have for all  $t \geq 0$

$$\begin{aligned} \mathbb{P}_{(x,a)} [\min(T_{all}, \tau_\partial) > t] &= \sum_{l \geq 0} \mathbb{P}_{(x,a)} [\min(T_{all}, \tau_\partial) > t, N_t = l] \\ &\leq \sum_{l \geq 0} \sum_{j \in \llbracket 1, 2k \rrbracket} \mathbb{P}_{(x,a)} [\min(\mathcal{T}_{\mathbb{N}_j}, \tau_\partial, \mathcal{T}_{l+1}) > t \geq \mathcal{T}_l]. \end{aligned}$$

Recall that in (4.3.26), we bounded from above the tail of the time of the first event. Then, rewriting the previous equation with the latter implies

$$\begin{aligned} \mathbb{P}_{(x,a)} [\min(T_{all}, \tau_\partial) > t] &\leq 2k\bar{\psi}(1 + t^{d_\psi}) \exp\left(-\int_a^{a+t} b(x, u) du - \lambda_\psi t\right) \\ &\quad + \sum_{l \geq 1} \sum_{j \in \llbracket 1, 2k \rrbracket} \mathbb{P}_{(x,a)} [\min(\mathcal{T}_{\mathbb{N}_j}, \tau_\partial, \mathcal{T}_{l+1}) > t \geq \mathcal{T}_l] \\ &=: 2k\bar{\psi}(1 + t^{d_\psi}) \exp\left(-\int_a^{a+t} b(x, u) du - \lambda_\psi t\right) + \sum_{l \geq 1} \sum_{j \in \llbracket 1, 2k \rrbracket} L(j, l). \end{aligned} \quad (4.4.6)$$

We now bound from above  $L(j, l)$ . Notice first that for all  $i \in \llbracket 1, 2k \rrbracket$  it holds  $\mathcal{I}_{N_i} \geq \mathcal{I}_{N_i}$  a.s.. In addition, on the event  $\{\min(\mathcal{I}_{N_j}, \tau_\partial, \mathcal{I}_{l+1}) > t \geq \mathcal{I}_l\}$ , we know that there has been exactly  $l$  jumps without visiting  $\partial$  and that the coordinate  $j$  has not been shortened yet. This yields the following

$$L(j, l) \leq \mathbb{P}_{(x,a)} [\mathcal{I}_{l+1} > t \geq \mathcal{I}_l, \forall i \in \llbracket 1, l \rrbracket : (I_i, J_i) \neq (\partial, \partial) \text{ and } j \notin I_i]. \quad (4.4.7)$$

We consider for all  $C \in \mathcal{B}(\mathbb{R}_+^{2k})$

$$\mathcal{K}_j(C)(x) = 2 \sum_{\substack{(I,J) \in \mathcal{Q}_k, \\ j \notin I}} \int_{u \in \mathbb{R}^{2k}} \mathbb{1}_{\{x+u \in C\}} d\pi_x^{I,J}(u), \quad (4.4.8)$$

where  $\pi_x^{I,J}$  is the measure given in (3.1.1). We use Lemmas 3.10 and 3.11 in (4.4.7), then (4.3.14) and (4.4.8), and finally the fact that  $\left[1 + \left(t - \sum_{j=1}^n y_j\right)^{d_\psi}\right] \leq 1 + t^{d_\psi}$ . We obtain (recalling the notation (4.3.13))

$$\begin{aligned} L(j, l) &\leq \frac{\exp(-\lambda_\psi t)}{\psi(x, a)} (1 + t^{d_\psi}) \int_{[0,t] \times \mathbb{R}_+^{2k}} \int_{[0,t-s_1] \times \mathbb{R}_+^{2k}} \cdots \int_{[0,t-\sum_{i=1}^{l-1} s_i] \times \mathbb{R}_+^{2k}} \mathcal{Y}_a(x, s_1) \mathcal{Y}_0(w_1, s_2) \cdots \\ &\quad \times \mathcal{Y}_0(w_{l-1}, s_l) \overline{\mathcal{Y}}_0 \left( w_l, t - \sum_{j=1}^l s_j \right) \mathcal{V}(w_l) (ds_1 \mathcal{K}_j(x, dw_1)) \cdots (ds_l \mathcal{K}_j(w_{l-1}, dw_l)). \end{aligned} \quad (4.4.9)$$

Now that  $L(j, l)$  is upper-bounded, we need a last auxiliary inequality in order to bound from above  $\mathbb{P}_{(x,a)} [\min(T_{all}, \tau_\partial) > t]$ . First, use the definition of  $\pi_x^{I,J}$  given in (3.1.1) and the second statement of (S2.2) to bound from above  $\mathcal{K}_j(\mathcal{V})(x)$ . Then, use Lemma 4.9 to write the bound obtained in a more convenient way. It comes

$$\mathcal{K}_j(\mathcal{V})(x) \leq \frac{2}{\#(\mathcal{I}_k)} \sum_{I \in \mathcal{I}_k, j \notin I} (1 + \varepsilon_1) \mathcal{V}(x) = (1 + \varepsilon_1) \mathcal{V}(x). \quad (4.4.10)$$

We now bound from above  $\mathbb{P}_{(x,a)} [\min(T_{all}, \tau_\partial) > t]$ . Using (4.4.9) and (4.4.10), we proceed exactly as we did to obtain (4.3.24) from the first statement of (S2.2). First, we introduce a family of probability measures  $(q(w, dw'))_{w \in \mathbb{R}_+^{2k}}$  defined such that for all  $w \in \mathbb{R}_+^{2k}$

$$q(w, dw') = \frac{\mathcal{V}(w') \mathcal{K}_j(w, dw')}{\mathcal{K}_j(\mathcal{V})(w)}.$$

Then, we iterate (4.4.10) to successively bound from above the measures of the form  $\mathcal{V}(w_i) \mathcal{K}_j(w_{i-1}, dw_i)$  in (4.4.9), where  $i \in \llbracket 1, l \rrbracket$ , by the measure  $(1 + \varepsilon_1) \mathcal{V}(w_{i-1}) q(w_{i-1}, dw_i)$ . Thereafter, we plug the upper bound we have obtained for (4.4.9) in (4.4.6). Finally, in view of (S3.1), we use Lemma 4.5 for  $b_1 = b$ ,  $b_2 = \bar{b}$  and the kernel  $(q(w, dw'))_{w \in \mathcal{X}}$ . We get (recalling that  $\bar{\psi} > 1$ )

$$\mathbb{P}_{(x,a)} [\min(T_{all}, \tau_\partial) > t] \leq 2k \bar{\psi} (1 + t^{d_\psi}) e^{-\lambda_\psi t} \left( \bar{\mathcal{G}}_a(t) + \sum_{n \geq 1} (1 + \varepsilon_1)^n (\mathcal{G}_a * \mathcal{G}_0^{*(n-1)} \mathcal{G}_0)(t) \right).$$

We finally do exactly what we did to obtain (4.3.29) from (4.3.24) to conclude the proof of the lemma from the above equation.  $\square$

#### 4.4.5 Proof of Lemma 4.11

Let  $\varepsilon > 0$ ,  $n \geq 1$ , and let  $(x, a) \in E$  be the initial condition of the process  $(Z_t)_{t \geq 0}$ . Recall that  $\mathcal{N}_\partial$  is the random variable that describes the number of jumps before extinction. We have for all  $t \geq 0$ ,

$$\mathbb{P}_{(x,a)} [N_t > n, t < \tau_\partial] \leq \mathbb{P}_{(x,a)} [\mathcal{N}_\partial > n] = \mathbb{P}_{(x,a)} [\forall i \in \llbracket 1, n \rrbracket : (I_i, J_i) \neq (\partial, \partial)]. \quad (4.4.11)$$

Our aim is to bound from above  $\mathbb{P}_{(x,a)}[\mathcal{N}_\partial > n]$ . Lemma 3.11 can be slightly readapted, so that the time is no longer taken into account (we do not have a term  $\overline{\mathcal{H}}_0$ , as we do not have a condition for  $\mathcal{F}_2 - \mathcal{F}_1$ ). Readapting this lemma, and using Remark 3.2, we develop the right-hand side term of (4.4.11) to obtain

$$\begin{aligned} \mathbb{P}_{(x,a)}[\mathcal{N}_\partial > n] &= \frac{1}{2^n} \int_{\mathbb{R}_+ \times \mathbb{R}_+^{2k}} \cdots \int_{\mathbb{R}_+ \times \mathbb{R}_+^{2k}} \mathcal{V}(w_1) \cdots \mathcal{V}(w_n) \mathcal{G}_a(x, s_1) \mathcal{G}_0(w_1, s_2) \cdots \\ &\quad \times \mathcal{G}_0(w_{n-1}, s_n) (ds_1 d\mathcal{K}(x, dw_1)) \cdots (ds_n d\mathcal{K}(w_{n-1}, dw_n)). \end{aligned} \quad (4.4.12)$$

For all  $(a', x', s') \in [0, a_0 L_1] \times \mathbb{R}_+^{2k} \times \mathbb{R}_+$ , it is easy to notice from Eq. (2.2.1) and the expression  $\psi(x', a') = \mathcal{V}(x')(1 + (a')^{d_\psi})$  that

$$\mathcal{G}_{a'}(x', s') = 2 \frac{b(x', a' + s')}{\psi(x', a')} \exp\left(-\int_{a'}^{a'+s'} b(x', u) du - \lambda_\psi s'\right) \leq 2 \frac{\tilde{b}(1 + (a_0 L_1 + s')^{d_b})}{\mathcal{V}(x')} \exp(-\lambda_\psi s').$$

In addition, as  $(x, a) \in E = D_{L_1}$ , we know that  $a \leq a_0 L_1$ . The latter, combined with (4.4.12), the above equation, and the fact that  $\frac{(\mathcal{K})^n(\mathcal{V})(x)}{\mathcal{V}(x)} \leq 2^n(1 + \varepsilon_1)^n$  by iterating (2.3.5), yields

$$\mathbb{P}_{(x,a)}[\mathcal{N}_\partial > n] \leq \left(2\tilde{b}(1 + \varepsilon_1) \int_{\mathbb{R}_+} (1 + (a_0 L_1 + s)^{d_b}) \exp(-\lambda_\psi s) ds\right)^n =: (c_{\lambda_\psi})^n.$$

One can notice that if  $n \geq \frac{\ln(\frac{\varepsilon}{3}) - \rho t}{\ln(c_{\lambda_\psi})}$  and  $c_{\lambda_\psi} < 1$ , then it holds  $(c_{\lambda_\psi})^n \leq \frac{\varepsilon}{3} \exp(-\rho t)$ . Thus, if  $\lambda_\psi$  is large enough to satisfy  $c_{\lambda_\psi} < 1$ , then the function

$$n(t) = \begin{cases} \left\lceil \frac{\ln(\frac{\varepsilon}{3}) - \rho t}{\ln(c_{\lambda_\psi})} \right\rceil, & \text{if } t > \frac{\ln(\frac{\varepsilon}{3})}{\rho}, \\ 1, & \text{if } t \leq \frac{\ln(\frac{\varepsilon}{3})}{\rho}, \end{cases}$$

will verify the statements of Lemma 4.11.

Now, recall that  $\lambda_\psi$  was chosen to verify the first two statements of Lemma 3.4. If the chosen value is not large enough to verify  $c(\lambda_\psi) < 1$ , then we choose another  $\bar{\lambda}_\psi > \lambda_\psi$ .  $\square$

#### 4.4.6 Proof of (4.0.1) and (4.0.3)

**Proof of (4.0.1).** We consider  $t_F > 0$ ,  $n_J = n(t_F) \in \mathbb{N}^*$  and  $\eta_0 > 0$ , and a stopping time  $U_H$  defined as in (4.4.3) with these constants. Let us prove that (4.0.1) holds for this stopping time. We consider  $L_2 \in \mathbb{N}^*$  such that  $L_2 \geq L_1$ ,  $L_2 B_{\max} > L_1 B_{\max} + n_J \Delta$  and  $a_0 L_2 \geq t_F$ . With this choice, one can see that  $D_{L_1} \subset D_{L_2}$  and  $([\eta_0, L_1 B_{\max} + n_J \Delta]^{2k} \times [0, t_F]) \subset D_{L_2}$ . We also fix  $V = t(L_2)$ , where  $t(L_2) > 0$  is a time such that there exists  $C_{L_2} > 0$  satisfying

$$\forall (x, a) \in E = D_{L_1} : \mathbb{P}_{(x,a)}[Z_{t(L_2)} \in dx' da'; t(L_2) < \tau_\partial] \geq C_{L_2} 1_{[\eta_0, B_{\max} L_2]^{2k} \times [0, a_0 L_2]}(x', a') dx' da'.$$

Such a time exists by Proposition 4.2. In view of the above, the fact that on the event  $\{U_H < \tau_\partial\}$  it holds  $X_{N_{t_F}} \in [\eta_0, B_{\max} L_1 + n_J \Delta]^{2k}$  (see (4.4.3)), and the fact that  $(X_{N_t})_{t \geq 0}$  is the marginal of  $(Z_t)_{t \geq 0}$  over telomere lengths, if the following statement is true, then we will have that (4.0.1) is true with  $U_H$  defined above and  $V = t(L_2)$ .

**Proposition 4.12** (Upper bound on non-rare events). *Assume (S<sub>1.1</sub>), (S<sub>1.3</sub>), and (S<sub>2.2</sub>) hold. Then for all  $t \geq 0$ , there exists  $\overline{C}(t) > 0$  such that for every  $(x, a) \in E = D_{L_1}$*

$$\mathbb{P}_{(x,a)}[Z_t \in dx' da'; T_{all} \leq t < \tau_\partial, N_t \leq n(t)] \leq \overline{C}(t) \cdot 1_{[0, B_{\max} L_1 + n(t) \Delta]^{2k} \times [0, t]}(x', a') dx' da'. \quad (4.4.13)$$

Moreover,  $\overline{C}(t)$  increases with  $t$ .

We point out here that the increasing character of  $\bar{C}(t)$  is only useful to obtain the density representation of the stationary profile in Section 4.7, and is not used here.

The proof of Proposition 4.12 is long, computational and requires a lot of notations to be introduced. However, there is no real interesting technical point in it, so we leave the detailed proof of the proposition in Appendix C. Below are given briefly the main arguments of this proof.

- In view of  $(S_{1.1})$ , the probability density function  $g$  representing the distribution of shortening values is bounded on  $\mathbb{R}_+$ , and the probability density function  $h$  representing the distribution of lengthening values is bounded on the set  $[-\delta, B_{\max}L_1 + n(t)\Delta] \times [0, \Delta]$ .
- Proposition 4.12 concerns initial conditions  $(x, a) \in D_{L_1}$ . Hence, the initial age is bounded by  $a_0L_1$ , and before the time  $t$ , the age of the particle is bounded by  $[0, a_0L_1 + t]$ . This implies by (2.2.1) that the rate at which a jump occurs stays bounded.
- All coordinates have been mixed at least once by the Lebesgue measure, and the number of mixing is bounded by  $n(t)$ .

Since "everything is bounded" and since each coordinate has been mixed at least one time by the Lebesgue measure, the left-hand side term of (4.4.13) is bounded by the Lebesgue measure multiplied by a constant  $\bar{C}(t)$ . The function  $\bar{C}$  increases because  $n$  increases by Lemma 4.11. For telomere lengths, the Lebesgue measure is restricted on the set  $[0, B_{\max}L_1 + n(t)\Delta]^{2k}$  for the following reason: the initial condition is  $x \in [0, B_{\max}L_1]^{2k}$ , we have at most  $n(t)$  jumps, and the maximum lengthening value is  $\Delta$ . For the age, we have a restriction of the Lebesgue measure on  $[0, t]$  because on the event  $\{T_{all} \leq t\}$ , at least one jump occurs before time  $t$ . At this jump the age is reset to 0, so we necessarily have that the age of the particle is at most  $t$  at time  $t$ .

From these points, Proposition 4.12 is true, which implies that Eq. (4.0.1) is verified for  $U_H$  defined as above.

**Proof of (4.0.3).** Now, we prove that for all  $\varepsilon > 0$ , there exists  $t_F > 0$ , and  $\eta_0 > 0$  such that (4.0.3) is verified for  $U_H$  defined with  $t_F$ ,  $n_J = n(t_F)$  and  $\eta_0$ . Before proving (4.0.3), we need to control the probability that the particle has a telomere with a length too close to 0. Let us fix  $\varepsilon > 0$ , and  $t_F > 0$  and  $n_J = n(t_F) \in \mathbb{N}^*$  such that (4.4.4) and (4.4.5) are satisfied. In view of the fact that  $(X_{N_t})_{t \geq 0}$  is the marginal of  $(Z_t)_{t \geq 0}$  over telomere lengths, first apply Proposition 4.12 to bound from above  $\mathbb{P}_{(x,a)}[X_{N_{t_F}} \in ([\eta, +n_J\Delta]^{2k})^c; T_{all} \leq t_F < \tau_\partial, N_t \leq n_J]$ . Then, use the fact that

$$[0, B_{\max}L_1 + n(t_F)\Delta]^{2k} \setminus ([\eta, B_{\max}L_1 + n(t_F)\Delta]^{2k}) \subset \bigcup_{i=1}^{2k} \{x \in [0, B_{\max}L_1 + n(t_F)\Delta]^{2k} \mid x_i \leq \eta\}$$

to bound from above the marginal of the Lebesgue measure over telomere lengths in the bound we have obtained (the measure of the set on the right is bounded from above by  $2k\eta(B_{\max}L_1 + n_J\Delta)^{2k-1}$ ). It comes that for all  $\eta > 0$ ,  $(x, a) \in E$

$$\mathbb{P}_{(x,a)}[X_{N_{t_F}} \in ([\eta, +n_J\Delta]^{2k})^c; T_{all} \leq t_F < \tau_\partial, N_{t_F} \leq n_J] \leq \bar{C}(t_F)2k\eta(B_{\max}L_1 + n_J\Delta)^{2k-1}t_F.$$

The latter implies that there exists  $\eta_0 > 0$  such that

$$\mathbb{P}_{(x,a)}[X_{N_{t_F}} \in ([\eta_0, +n_J\Delta]^{2k})^c; T_{all} \leq t_F < \tau_\partial, N_{t_F} \leq n_J] \leq \frac{\varepsilon}{3} \exp(-\rho t_F). \quad (4.4.14)$$

Now, let us consider  $U_H$  defined as in (4.4.3) with  $t_F$ ,  $n_J$  and  $\eta_0$  of the previous paragraph. Combining (4.4.4), (4.4.5) and (4.4.14) yields that for all  $(x, a) \in E$ ,

$$\begin{aligned} \mathbb{P}_{(x,a)}[U_H = \infty, t_F < \tau_\partial] &= \mathbb{P}_{(x,a)}[\min(T_{all}, \tau_\partial) > t_F] + \mathbb{P}_{(x,a)}[N_{t_F} > n_J, T_{all} \leq t_F, t_F < \tau_\partial] \\ &\quad + \mathbb{P}_{(x,a)}[X_{N_{t_F}} \in ([\eta_0, +n_J\Delta]^{2k})^c; T_{all} \leq t_F < \tau_\partial, N_{t_F} \leq n_J] \\ &\leq \varepsilon \exp(-\rho t_F). \end{aligned}$$

Then, (4.0.3) is satisfied, which ends the proof of Assumption  $(A_3)_F$ .

## 4.5 Existence of the stationary profile

We recall here Notations **xxiv**-**xxv**), and refer to (2.3.2), (2.3.4) and (3.3.7) for the definitions of the semigroups  $(M_t)_{t \geq 0}$ ,  $(M_t^{(\psi)})_{t \geq 0}$  and  $(P_t^{(\psi)})_{t \geq 0}$  used in this section. We also recall that the index  $\psi$  was dropped in the process  $(Z_t^{(\psi)})_{t \geq 0}$ . We now prove that there exists a stationary profile for the semigroup  $(M_t)_{t \geq 0}$  using what we did in the previous sections.

First, as  $(A_1)$ ,  $(A_2)$  and  $(A_3)_F$  are verified for the process  $(Z_t^{(\psi)})_{t \geq 0}$ , by (3.3.8) and Theorem 4.1 there exists a triplet of eigenelements  $(\tilde{\gamma}, \tilde{\phi}, \tilde{\lambda}) \in \mathcal{M}_1(\mathcal{X}) \times M_b(\mathcal{X}) \times \mathbb{R}_+$  s.t.  $\tilde{\gamma}(\tilde{\phi}) = 1$ , and two constants  $C, \omega > 0$ , such that for all  $t > 0$ ,  $\tilde{\mu} \in \mathcal{M}_1(\mathcal{X})$

$$\sup_{\tilde{f} \in M_b(\mathcal{X}), \|\tilde{f}\|_\infty \leq 1} \left| e^{(\tilde{\lambda} - \lambda_\psi)t} \tilde{\mu} \left( \frac{M_t(\psi \tilde{f})}{\psi}(\cdot) \right) - \tilde{\mu}(\tilde{\phi}) \tilde{\gamma}(\tilde{f}) \right| = \left\| e^{\tilde{\lambda}t} \tilde{\mu} P_t^{(\psi)} - \tilde{\mu}(\tilde{\phi}) \tilde{\gamma} \right\|_{TV, \mathcal{X}} \leq C e^{-\omega t}. \quad (4.5.1)$$

From [54, Prop. 2.10], we also have  $\tilde{\phi} > 0$ .

Second, recalling Notations **xxiv**-**xxv**), the following equalities hold:

$$\{\tilde{f}\psi \text{ s.t. } \tilde{f} \in M_b(\mathcal{X}), \|\tilde{f}\|_\infty \leq 1\} = \{f \in \mathcal{B}(\psi) \text{ s.t. } \|f\|_{\mathcal{B}(\psi)} \leq 1\}, \quad (4.5.2)$$

$$\left\{ \mu \in \mathcal{M}_+(\psi) \mid \exists \tilde{\mu} \in \mathcal{M}_1(\mathcal{X}) \text{ s.t. } \mu(\cdot) = \tilde{\mu} \left( \frac{\cdot}{\psi} \right) \right\} = \{ \mu \in \mathcal{M}_+(\psi) \mid \|\mu\|_{m(\psi)} = 1 \}. \quad (4.5.3)$$

Finally, we consider  $\phi = \tilde{\gamma}(\frac{1}{\psi}) \cdot \tilde{\phi}\psi \in \mathcal{B}(\psi)$  and  $\gamma(\cdot) = \frac{1}{\tilde{\gamma}(\frac{1}{\psi})} \tilde{\gamma}(\frac{\cdot}{\psi}) \in [\mathcal{M}_+(\psi) \cap \mathcal{M}_1(\mathcal{X})]$ . As  $\tilde{\gamma}(\tilde{\phi}) = 1$ , we easily see that  $\gamma(\psi) = 1$ . We also introduce  $\lambda = \lambda_\psi - \tilde{\lambda}$ , that belongs to  $[\alpha, +\infty[$  by Proposition 4.4 and the fact that  $\rho_S = \tilde{\lambda}$  (see [54, Theorem 2.8]).

We can use these three results to conclude on the convergence towards a stationary profile, starting from measures in  $\mathcal{M}_+(\psi)$  s.t.  $\|\mu\|_{m(\psi)} = 1$ . First, we replace the terms  $\tilde{\gamma}$ ,  $\tilde{\phi}$  and  $\tilde{\lambda} - \lambda_\psi$  in (4.5.1) by the terms  $\gamma$ ,  $\phi$  and  $\lambda$  respectively, using the definitions of the latter. Then, we use (4.5.2) to change functions  $\tilde{f}\psi$  in (4.5.1) into functions  $f \in \mathcal{B}(\psi)$ . Finally, we use (4.5.3) to change measures  $\tilde{\mu}(\frac{\cdot}{\psi})$  into measures  $\mu \in \mathcal{M}(\psi)$ . We obtain that for all  $\mu \in \mathcal{M}_+(\psi)$  such that  $\|\mu\|_{m(\psi)} = 1$

$$\forall \mu \in \mathcal{M}_+(\psi) \text{ s.t. } \|\mu\|_{m(\psi)} = 1 : \sup_{f \in \mathcal{B}(\psi), \|f\|_{\mathcal{B}(\psi)} \leq 1} \left| e^{-\lambda t} \mu M_t(f) - \mu(\phi) \gamma(f) \right| \leq C e^{-\omega t}. \quad (4.5.4)$$

Now, we extend the result above to measures in  $\mathcal{M}(\psi)$ . Let us consider  $\mu \in \mathcal{M}(\psi)$ . By definition of  $\mathcal{M}(\psi)$  (Notation **xxv**), there exists a couple  $(\mu_+, \mu_-) \in \mathcal{M}_+(\psi) \times \mathcal{M}_+(\psi)$  such that  $\mu = \mu_+ - \mu_-$ . First, we take for initial measures  $\frac{\mu_+}{\|\mu_+\|_{m(\psi)}} = \frac{\mu_+}{\mu_+(\psi)}$  (or  $\frac{\mu_-}{\|\mu_-\|_{m(\psi)}}$ ). Then, we apply (4.5.4) and multiply by  $\mu_+(\psi)$  (or  $\mu_-(\psi)$ ). Finally in view of the equality  $\mu = \mu_+ - \mu_-$ , we use the triangular inequality. We obtain at the end the desired result.

## 4.6 Uniqueness of the stationary profile

We recall that the set  $\Psi$ , that contains all the functions used to distort the space, was defined in (2.3.3). The function  $\psi \in \Psi$  that we have fixed at the beginning of the proof is no more fixed from this subsection. By Section 4.5, we have that for all  $\psi \in \Psi$ , the first moment semigroup converges towards a stationary profile in  $\mathcal{M}(\psi)$  endowed with  $\|\cdot\|_{m(\psi)}$ . We now prove that this stationary profile is the same whatever the function  $\psi \in \Psi$ .

Let  $(\psi_1, \psi_2) \in \Psi^2$ . For all  $i \in \{1, 2\}$ , we denote by  $(\gamma_i, \phi_i, \lambda_i) \in \mathcal{M}(\psi_i) \times \mathcal{B}(\psi_i) \times \mathbb{R}_+^*$  the triplet of eigenelements of  $(M_t)_{t \geq 0}$  obtained by a distortion of the space by  $\psi_i$ . These eigenelements also verify the following properties:  $\gamma_i \in \mathcal{M}_1(\mathcal{X})$ ,  $\phi_i > 0$  and  $\gamma_i(\phi_i) = 1$ . We suppose without loss of generality that  $d_{\psi_1} \leq d_{\psi_2}$  (see (2.3.3)). Before proving that  $(\gamma_1, \phi_1, \lambda_1) = (\gamma_2, \phi_2, \lambda_2)$ , let us do some preliminaries. First, as for all  $i \in \{1, 2\}$ :  $\psi_i(x, a) = \mathcal{V}(x)(1 + a^{d_{\psi_i}})$ , as  $1 + a^{d_{\psi_1}} \leq 2$  when  $a \leq 1$ , and as  $d_{\psi_1} \leq d_{\psi_2}$ , one can easily check that for all  $f \in \mathcal{B}(\psi_1)$  and  $(x, a) \in \mathbb{R}_+^{2k} \times \mathbb{R}_+$  we have

$$\begin{aligned} \text{If } a \in [0, 1] : & \quad \psi_1(x, a) \leq 2\mathcal{V}(x) \leq 2\psi_2(x, a), \\ \text{If } a \in [1, +\infty) : & \quad \psi_1(x, a) \leq \psi_2(x, a). \end{aligned}$$

Thus, it comes

$$\left\{ f \in \mathcal{B}(\psi_1) \mid \|f\|_{\mathcal{B}(\psi_1)} \leq \frac{1}{2} \right\} \subset \left\{ f \in \mathcal{B}(\psi_2) \mid \|f\|_{\mathcal{B}(\psi_2)} \leq 1 \right\} \text{ and } \mathcal{M}(\psi_2) \subset \mathcal{M}(\psi_1). \quad (4.6.1)$$

In addition, for  $i \in \{1, 2\}$ , there exists  $C_i, \omega_i > 0$  such that for all  $t \geq 0$  and  $\mu \in \mathcal{M}(\psi_i)$

$$\sup_{f \in \mathcal{B}(\psi_i), \|f\|_{\mathcal{B}(\psi_i)} \leq 1} \left| e^{-\lambda_i t} \mu M_t(f) - \mu(\phi_i) \gamma_i(f) \right| \leq C_i \|\mu\|_{\mathcal{M}(\psi_i)} e^{-\omega_i t}. \quad (4.6.2)$$

Then, combining (4.6.1) and (4.6.2) yields for all  $\mu \in \mathcal{M}(\psi_2)$  and  $t \geq 0$

$$\sup_{f \in \mathcal{B}(\psi_1), \|f\|_{\mathcal{B}(\psi_1)} \leq 1} \left| e^{-\lambda_2 t} \mu M_t(f) - \mu(\phi_2) \gamma_2(f) \right| \leq 2C_2 \|\mu\|_{\mathcal{M}(\psi_2)} e^{-\omega_2 t}. \quad (4.6.3)$$

Now, we prove that  $\lambda_1 = \lambda_2$ . We suppose by contradiction that  $\lambda_1 > \lambda_2$ . Let  $z_0 \in \mathcal{X}$ . Eq. (4.6.2) and (4.6.3) for  $\mu = \delta_{z_0}$  and  $f = \psi_1$  imply that for all  $t \geq 0$ ,  $i \in \{1, 2\}$

$$\lim_{t \rightarrow +\infty} e^{-\lambda_i t} M_t(\psi_1)(z_0) = \phi_i(z_0) \gamma_i(\psi_1). \quad (4.6.4)$$

As  $\gamma_1 \in \mathcal{M}_1(\mathcal{X})$  and  $\psi_1 \geq \mathcal{V}_{\min}$  (see the third statement of (S2.2)), we also have  $\phi_1(z_0) \gamma_1(\psi_1) > 0$ . Then, taking the ratio between (4.6.4) for  $i = 2$  and (4.6.4) for  $i = 1$  yields

$$\lim_{t \rightarrow +\infty} e^{(\lambda_1 - \lambda_2)t} = \frac{\phi_2(z_0) \gamma_2(\psi_1)}{\phi_1(z_0) \gamma_1(\psi_1)}.$$

This is in contradiction with  $\lambda_1 > \lambda_2$ . By exactly the same reasoning, we also obtain a contradiction when  $\lambda_2 > \lambda_1$ .

Let us prove now that  $\phi_1 = \phi_2$ . In view of (4.6.2), (4.6.3), we have that for all  $z \in \mathcal{X}$ ,  $\phi_1(z)$  and  $\phi_2(z)$  are respectively limit of  $e^{-\lambda_1 t} M_t(1)(z)$  and  $e^{-\lambda_2 t} M_t(1)(z)$  (we take  $\mu = \delta_z$  and  $f = \frac{1}{\|1\|_{\mathcal{B}(\psi_1)}}$  to obtain this). As  $\lambda_1 = \lambda_2$ , this implies by uniqueness of the limit that  $\phi_1 = \phi_2$ .

Finally, we prove that  $\gamma_1 = \gamma_2$ . We fix  $z_0 \in \mathcal{X}$ . In view of (4.6.2), (4.6.3), and the fact that  $\lambda_1 = \lambda_2$ , by the triangular inequality we have for all  $t \geq 0$

$$\sup_{f \in \mathcal{B}(\psi_1), \|f\|_{\mathcal{B}(\psi_1)} \leq 1} |\phi_2(z_0) \gamma_2(f) - \phi_1(z_0) \gamma_1(f)| \leq C_1 \psi_1(z_0) e^{-\omega_1 t} + 2C_2 \psi_2(z_0) e^{-\omega_2 t}.$$

As  $\phi_1(z_0) = \phi_2(z_0) > 0$ , letting  $t$  goes to infinity yields  $\|\gamma_2 - \gamma_1\|_{\mathcal{M}(\psi_1)} = 0$ . Then, as  $\|\cdot\|_{\mathcal{M}(\psi_1)}$  is a norm, we obtain that  $\gamma_1 = \gamma_2$ .

## 4.7 Density representation of the stationary profile

Now that we know that there exists a stationary profile which is the same for all  $\psi \in \Psi$ , we prove that the latter can be represented by a function. In particular, we emphasize the fact that the density representation of the stationary profile can be obtained as a consequence of the statements and the arguments given to prove Assumption (A3)<sub>F</sub>. We believe that this proof can be adapted to many other models for which the discontinuities with respect to the Lebesgue of the model can be controlled over the time, as for example the models given in [53, 54].

First, we prove in Section 4.7.1 that the stationary profile admits a density with respect to the Lebesgue measure thanks to the results obtained in Section 4.4. Then, we prove in Section 4.7.2 that the function representing our stationary profile can be seen as the product of two functions, one linked to telomere lengths, and the other linked to the age.

### 4.7.1 Absolute continuity of the stationary profile with respect to the Lebesgue measure

Let  $\psi \in \Psi$ . In view of Section 4.5, we have the equivalence between obtaining the absolute continuity of the stationary profile of  $(M_t)_{t \geq 0}$  with respect to  $\psi(x, a) dx da$ , and obtaining the absolute continuity of



the stationary profile of  $(P_t^{(\psi)})_{t \geq 0}$  with respect to  $dx da$ . We will hence prove that the stationary profile of  $(P_t^{(\psi)})_{t \geq 0}$ , denoted  $\tilde{\gamma}$ , has a density with respect to the Lebesgue measure.

Let  $\tilde{\lambda} \in \mathbb{R}_+$  the absorbing rate of  $(P_t^{(\psi)})_{t \geq 0}$ . As  $\tilde{\gamma}$  is a quasi-stationary distribution for  $(P_t^{(\psi)})_{t \geq 0}$ , we easily obtain by [52, Eq. (2.3)] that for all  $t \geq 0$ ,  $A \in \mathcal{B}(\mathcal{X})$ ,

$$\tilde{\gamma}(A) = e^{\tilde{\lambda}t} \int_{(x,a) \in \mathcal{X}} P_t^{(\psi)}(1_A)(x,a) \tilde{\gamma}(dx, da). \quad (4.7.1)$$

We use this equality to get the absolute continuity of the stationary profile. Two difficulties arise:

- As explained in Section 4.4,  $(P_t^{(\psi)})_{t \geq 0}$  has a part absolutely continuous with respect to the Lebesgue measure, and another part discontinuous with respect to the Lebesgue measure. We need to handle the discontinuous part. For that, we use the results obtained in Section 4.4.
- The results we have obtained in Section 4.4 are only true for measures starting from  $E = D_{L_1}$ , where  $L_1 \in \mathbb{N}^*$  is large and has been fixed in the last paragraph of Section 4.3.2. In (4.7.1), the relation between  $\tilde{\gamma}$  and  $(P_t^{(\psi)})_{t \geq 0}$  involves initial conditions in the set  $E^c$ . Thus, we need to handle such initial conditions.

Let us first control the time we need to return to  $E$ . As  $\rho = \lambda_\psi - \frac{\alpha + \beta}{2}$  and  $\beta < \alpha$ , Proposition 4.8 ( $L_1$  is chosen sufficiently large to have  $L_1 \geq L_0$ ) implies the following statement.

**Lemma 4.13** (Control of the time to return to  $E$ ). *Assume that (S<sub>1.1</sub>), (S<sub>2</sub>) and (S<sub>3</sub>) hold. Then there exists  $t_1 > 0$  such that for all  $t \geq t_1$*

$$\sup_{(x,a) \in \mathcal{X}} (\mathbb{P}_{(x,a)} [\min(\tau_E, \tau_\partial) > t]) \leq \frac{\varepsilon}{3} \exp(-\rho t).$$

Now that we have Lemma 4.13, using the constant  $t_0$  introduced in Lemma 4.10, we control  $P_t^{(\psi)}$  starting from the restriction of  $\tilde{\gamma}$  on  $E^c$  for  $t \geq t_0 + t_1$ . This implies the following statement, that is proved at the end of the subsection.

**Lemma 4.14** (Control of the discontinuities starting from  $E^c$ ). *Assume that (S<sub>1.1</sub>), (S<sub>2</sub>) and (S<sub>3</sub>) hold. Let  $t_0, t_1 > 0$  the two constants introduced in Lemmas 4.10 and 4.13. Then for all  $t \geq t_0 + t_1$ ,  $A \in \mathcal{B}(\mathcal{X})$ , the following holds*

$$\int_{(x,a) \in E^c} P_t^{(\psi)}(1_A)(x,a) \tilde{\gamma}(dx, da) \leq \bar{C}(t) \text{Leb}(A) + \frac{2\varepsilon}{3} e_{\mathcal{T}} e^{-\rho t} + \frac{\varepsilon}{3} e^{-\rho(t-t_0)}, \quad (4.7.2)$$

where  $e_{\mathcal{T}} := \sup_{(x,a) \in \mathcal{X}} [\mathbb{E}_{(x,a)} [\exp(\rho \min(\tau_\partial, \tau_E))]]$  (finite by (A<sub>2</sub>)), and  $\bar{C}(t)$  is the constant introduced in Proposition 4.12.

For the restriction of  $\tilde{\gamma}$  on  $E$ , a similar upper bound can be obtained with the same arguments. The only slight difference is that we do not need to handle the fact that we need to return to  $E$ . Here is the statement that corresponds to this upper bound. As the proof of this statement consists of applying exactly the same arguments as those used to obtain (4.7.2) without handling the return to  $E$ , we do not detail it.

**Lemma 4.15** (Control of the discontinuities starting from  $E$ ). *Assume that (S<sub>1.1</sub>), (S<sub>2</sub>) and (S<sub>3</sub>) hold. Let  $t_0 > 0$  the constant introduced in Lemma 4.10. Then for all  $t \geq t_0$ ,  $A \in \mathcal{B}(\mathcal{X})$ , the following holds*

$$\int_{(x,a) \in E} P_t^{(\psi)}(1_A)(x,a) \tilde{\gamma}(dx, da) \leq \bar{C}(t) \text{Leb}(A) + \frac{2\varepsilon}{3} e^{-\rho t}, \quad (4.7.3)$$

where  $\bar{C}(t)$  is the constant introduced in Proposition 4.12.

Now, we obtain that  $\tilde{\gamma}$  can be represented by a function. Plugging (4.7.2) and (4.7.3) in (4.7.1), we get for all  $t \geq t_0 + t_1$

$$\tilde{\gamma}(A) \leq 2e^{\tilde{\lambda}t}\overline{C}(t)\text{Leb}(A) + \frac{2\varepsilon}{3}.e_{\mathcal{T}}.e^{-\rho t + \tilde{\lambda}t} + \frac{2\varepsilon}{3}e^{-\rho(t-t_0) + \tilde{\lambda}t} + \frac{\varepsilon}{3}e^{-\rho t + \tilde{\lambda}t}.$$

As  $\rho = \lambda_\psi - \frac{\alpha + \beta}{2} > \tilde{\lambda}$  (by (4.3.7) and the fact that  $\tilde{\lambda} = \rho_S$ , see [54, Theorem 2.8]), there exists  $t_2 \geq t_0 + t_1$  such that  $e^{-\rho t_2 + \tilde{\lambda}t_2} \leq \min\left(1, \frac{1}{e_{\mathcal{T}}}, e^{-\rho t_0}\right)$ . Then, take  $t = t_2$  in the above equation to obtain

$$\tilde{\gamma}(A) \leq 2e^{\tilde{\lambda}t_2}\overline{C}(t_2)\text{Leb}(A) + \frac{5\varepsilon}{3}.$$

From the above and [42, Prop. 15.5.b],  $\tilde{\gamma}$  is absolutely continuous with respect to the Lebesgue measure.

We now denote  $\gamma$  the stationary profile of  $(M_t)_{t \geq 0}$  that is equal to  $\gamma(\cdot) = \frac{1}{\tilde{\gamma}(\frac{\cdot}{\psi})}\tilde{\gamma}\left(\frac{\cdot}{\psi}\right)$  by Section 4.5. We prove that it can be represented by a function in  $L^1(\Psi)$ . As  $\tilde{\gamma}$  is absolutely continuous with respect to the Lebesgue measure, the relation between  $\gamma$  and  $\tilde{\gamma}$  implies that there exists  $N \in L^1_{p.d.f.}(\mathcal{X}) \cap L^1(\psi)$  (see Notation xxviii)) such that for all  $A \in \mathcal{B}(\mathcal{X})$

$$\gamma(A) = \int_A N(x, a) dx da. \quad (4.7.4)$$

Thus, as  $\psi \in \Psi$  was chosen arbitrarily, and as the stationary profile is the same whatever the function  $\psi \in \Psi$ , we have  $N \in \bigcap_{\psi \in \Psi} L^1(\psi) = L^1(\Psi)$ . It remains to prove Lemma 4.14.

*Proof of Lemma 4.14.* Let us consider  $t \geq t_0 + t_1$ , and  $A \in \mathcal{B}(\mathcal{X})$ . We have

$$\begin{aligned} \int_{(x,a) \in E^c} P_t^{(\psi)}(1_A)(x, a) \gamma(dx, da) &= \int_{(x,a) \in E^c} \mathbb{P}_{(x,a)} \left[ Z_t^{(\psi)} \in A; \tau_E \leq t - t_0, t < \tau_\partial \right] \gamma(dx, da) \\ &+ \int_{(x,a) \in E^c} \mathbb{P}_{(x,a)} \left[ Z_t^{(\psi)} \in A; \tau_E > t - t_0, t < \tau_\partial \right] \gamma(dx, da). \end{aligned}$$

One can easily see that if  $\tau_E > t - t_0$  and  $\tau_\partial > t$ , then  $\min(\tau_E, \tau_\partial) > t - t_0 \geq t_1$ . The latter combined with Lemma 4.13 yields

$$\int_{(x,a) \in E^c} P_t^{(\psi)}(1_A)(x, a) \gamma(dx, da) \leq \int_{(x,a) \in E^c} \mathbb{P}_{(x,a)} \left[ Z_t^{(\psi)} \in A; \tau_E \leq t - t_0, t < \tau_\partial \right] \gamma(dx, da) + \frac{\varepsilon}{3} e^{-\rho(t-t_0)}. \quad (4.7.5)$$

We now obtain an upper bound for the first term on the right-hand side term of (4.7.5). With the strong Markov property (and an abuse of notations), we have for all  $(x, a) \in E^c$

$$\mathbb{P}_{(x,a)} \left[ Z_t^{(\psi)} \in A; \tau_E \leq t - t_0, t < \tau_\partial \right] = \mathbb{E}_{(x,a)} \left[ \mathbb{P}_{Z_{\tau_E}^{(\psi)}} \left[ \tilde{Z}_{t-\tau_E}^{(\psi)} \in A, t - \tau_E < \tilde{\tau}_\partial \right], \tau_E \leq t - t_0, \tau_E < \tau_\partial \right], \quad (4.7.6)$$

where  $(\tilde{Z}_t^{(\psi)})_{t \geq 0}$  is an independent copy of  $(Z_t^{(\psi)})_{t \geq 0}$  that has the same distribution and  $\tilde{\tau}_\partial$  is the equivalent of  $\tau_\partial$  for  $(\tilde{Z}_t^{(\psi)})_{t \geq 0}$ . One can decompose the probability in the right-hand side term as follows

$$\begin{aligned} \mathbb{P}_{Z_{\tau_E}^{(\psi)}} \left[ \tilde{Z}_{t-\tau_E}^{(\psi)} \in A, t - \tau_E < \tilde{\tau}_\partial \right] &= \mathbb{P}_{Z_{\tau_E}^{(\psi)}} \left[ \tilde{Z}_{t-\tau_E}^{(\psi)} \in A, \tilde{T}_{all} \leq t - \tau_E < \tilde{\tau}_\partial, \tilde{N}_{t-\tau_E} \leq n(t - \tau_E) \right] \\ &+ \mathbb{P}_{Z_{\tau_E}^{(\psi)}} \left[ \tilde{Z}_{t-\tau_E}^{(\psi)} \in A, \tilde{T}_{all} \leq t - \tau_E < \tilde{\tau}_\partial, \tilde{N}_{t-\tau_E} > n(t - \tau_E) \right] \\ &+ \mathbb{P}_{Z_{\tau_E}^{(\psi)}} \left[ \tilde{Z}_{t-\tau_E}^{(\psi)} \in A, \tilde{T}_{all} > t - \tau_E, t - \tau_E < \tilde{\tau}_\partial \right], \end{aligned}$$

where  $\tilde{T}_{all}$  and  $\tilde{N}_t$  are the equivalents of  $T_{all}$  and  $N_t$  for  $(\tilde{Z}_t^{(\psi)})_{t \geq 0}$ . Then, in view of Proposition 4.12 for the first term, Lemma 4.11 for the second term, and Lemma 4.10 for the last term, it holds on the event  $\{\tau_E \leq t - t_0, \tau_E < \tau_\partial\}$

$$\mathbb{P}_{Z_{\tau_E}^{(\psi)}} \left[ \tilde{Z}_{t-\tau_E}^{(\psi)} \in A, t - \tau_E < \tilde{\tau}_\partial \right] \leq \bar{C}(t - \tau_E) \text{Leb}(A) + \frac{2\varepsilon}{3} \exp(-\rho(t - \tau_E)).$$

Plugging this in (4.7.6), then using the fact that  $\bar{C}$  increases (see Prop. 4.12), and finally noticing that  $\tau_E = \min(\tau_E, \tau_\partial)$  on the event  $\{\tau_E < \tau_\partial\}$  yields ( $e_{\mathcal{T}}$  is defined in the statement of the lemma)

$$\mathbb{P}_{(x,a)} \left[ Z_t^{(\psi)} \in A; \tau_E \leq t - t_0, t < \tau_\partial \right] \leq \bar{C}(t) \text{Leb}(A) + \frac{2\varepsilon}{3} \cdot e^{-\rho t} \cdot e_{\mathcal{T}}.$$

Then, plugging the latter in (4.7.5) implies that the lemma is proved.  $\square$

## 4.7.2 Separation of the space and age

Here, we prove that there exists  $N_0 \in L^1(\mathbb{R}_+^{2k})$  nonnegative, such that for all  $(x, a) \in \mathcal{X}$

$$N(x, a) = N_0(x) \exp \left( -\lambda a - \int_0^a b(x, s) ds \right). \quad (4.7.7)$$

Let  $g \in C_c^\infty(\text{int}(\mathcal{X}))$  and  $s \geq 0$ . First, we use (4.5.4) with  $\mu = \gamma$  and  $f = M_s(g)$  (one can  $f$  normalise to have  $\|f\|_{\mathcal{B}(\psi)} \leq 1$ ) to obtain that  $\lim_{t \rightarrow +\infty} e^{-\lambda t} \gamma M_{t+s}(g) = \gamma(M_s(g))$ . Then, we apply again (4.5.4) with  $\mu = \gamma$  and  $f = g$  to obtain that  $\lim_{t \rightarrow +\infty} e^{-\lambda t} \gamma M_t(g) = \gamma(g)$ . It comes from these two equalities and (4.7.4) that

$$e^{\lambda s} \int_{(x,a) \in \text{int}(\mathcal{X})} g(x, a) N(x, a) dx da = \int_{(x,a) \in \text{int}(\mathcal{X})} M_s(g)(x, a) N(x, a) dx da.$$

Now, we take the derivative of the two terms of this equality in  $s = 0$ , using Theorem 2.6 for the second term. This yields (noticing that  $g(x, 0) = 0$  as  $g \in C_c^\infty(\text{int}(\mathcal{X}))$ )

$$\begin{aligned} \lambda \int_{(x,a) \in \text{int}(\mathcal{X})} g(x, a) N(x, a) dx da &= \int_{(x,a) \in \text{int}(\mathcal{X})} \frac{\partial g}{\partial a}(x, a) N(x, a) dx da \\ &\quad - \int_{(x,a) \in \text{int}(\mathcal{X})} g(x, a) b(x, a) N(x, a) dx da. \end{aligned}$$

In particular,  $N$  is the solution of the following equation (in the weak sense)

$$\frac{\partial}{\partial a} N(x, a) + (\lambda + b(x, a)) N(x, a) = 0.$$

From this equation, we have that the weak derivative of  $\tilde{N}(x, a) = \exp(\lambda a + \int_0^a b(x, s) ds) N(x, a)$  in the variable  $a$  is zero. Then, there exists  $N_0 \in L_{\text{loc}}^1(\mathbb{R}_+^{2k})$  such that  $N(x, a) = N_0(x) \exp(-\lambda a - \int_0^a b(x, s) ds)$  for all  $(x, a) \in \text{int}(\mathcal{X})$ . As  $N$  is nonnegative, we have that  $N_0$  is nonnegative. By (2.2.1), we also have

$$\left( \int_{x \in \mathbb{R}_+^{2k}} N_0(x) dx \right) \left( \int_{a \in \mathbb{R}_+} \exp \left( -\lambda a - \int_0^a (1 + s^{d_b}) ds \right) da \right) \leq \int_{(x,a) \in \mathcal{X}} N(x, a) dx da < +\infty,$$

which implies that  $N_0 \in L^1(\mathbb{R}_+^{2k})$ . Thus, (4.7.7) holds and we have obtained that the stationary profile is the product of two functions, one linked to the variable  $x$ , the other linked to the variable  $a$ .

## 5 Sufficient criteria for Lyapunov functions and two toy models

Now that we have proved Theorem 2.7, we give conditions and models for which Assumptions (S<sub>1</sub>) – (S<sub>3</sub>) are verified. First, we present in Section 5.1 conditions implying Assumptions (S<sub>2.2</sub>) and (S<sub>3</sub>). Then, we present in Sections 5.2 and 5.3 two models where all the assumptions are verified. The first one is a model for which all coordinates are lengthened at each division. The second one is a model for which for each telomere, its probability to be lengthened is independent of the other telomeres. For each of these models, we devote a large part of their study to check (S<sub>2.1</sub>), which is the most difficult assumption to verify.

## 5.1 The Lyapunov function

We first present in Section 5.1.1 the key statement of this subsection that allows us to check (S<sub>2.2</sub>). We also discuss about the relation between  $\varepsilon_1$  and  $\varepsilon_0$  that must occur to check (S<sub>3</sub>) from this statement. Then, in Section 5.1.2, we give two criteria useful in practice to prove that (S<sub>2.2</sub>) and (S<sub>3</sub>) hold. Finally, in Section 5.1.3, we prove the key statement.

### 5.1.1 Statement implying (S<sub>2.2</sub>) and its link with (S<sub>3</sub>)

The function  $\mathcal{V}$  that we need to find to verify (S<sub>2.2</sub>) corresponds to a Lyapunov function. Qualitatively, this is a function that measures the impact of the initial condition of the semigroup on the speed of convergence towards the stationary profile. We thus need to think about how the speed of convergence varies when telomere lengths vary to obtain our Lyapunov function. In our case, the speed of convergence increases exponentially when telomere lengths increase. Hence, the Lyapunov function must have an exponential form. Until the next proposition is stated, we assume that  $\mathcal{V}$  has an exponential form.

By the first statement of (S<sub>2.2</sub>), our aim is to bound from above  $\frac{\mathcal{K}(\mathcal{V})(x)}{\mathcal{V}(x)}$  when  $\max_{i \in \llbracket 1, 2k \rrbracket} (x_i)$  is "large". To do so, under (S<sub>1.1</sub>) and (S<sub>2.1</sub>), we first introduce for all  $x \in \mathbb{R}^{2k}$ ,  $L \in \mathbb{N}^*$  the following set

$$\mathcal{E}_L(x) := \{i \in \llbracket 1, 2k \rrbracket \mid x_i > B_{\max}L - 2\Delta - \delta\}.$$

This set is used to represent the coordinates of  $x$  which are considered to be "large". We also consider the following function, for all  $\lambda \geq 0$ ,  $L \in \mathbb{N}^*$

$$\Lambda(\lambda, L) := \sup_{(r,s) \in (\mathbb{R}^{2k})^2} \left[ \sum_{(J,M) \in \mathcal{J}_k} p_{J,M}(r,s) \left( \prod_{i \in J \cap \mathcal{E}_L(r)} \mathcal{L}(h(r_i, \cdot))(-\lambda) \right) \right], \quad (5.1.1)$$

where for all  $y > 0$ ,  $\mathcal{L}(h(y, \cdot))$  denotes the Laplace transform of  $h(y, \cdot)$ . As  $\mathcal{V}$  has an exponential form, the Laplace transform term gives information about the integral of the marginals of  $\mathcal{V}$  with respect to the measures  $(h(x_i, y)dy)_{i \in \mathcal{E}_L(x)}$ . Then, as  $h$  is the probability density function for lengthening values, the function  $\Lambda$  allows us to bound from above how the lengthening impacts the value of  $\frac{\mathcal{K}(\mathcal{V})(x)}{\mathcal{V}(x)}$ .

To bound from above how the shortening impacts the value of  $\frac{\mathcal{K}(\mathcal{V})(x)}{\mathcal{V}(x)}$ , we use the function  $1 + \mathcal{L}(g)$ , where  $\mathcal{L}(g)$  is the Laplace transform of the shortening density  $g$ . To be more precise, it is possible to bound from above  $\frac{\mathcal{K}(\mathcal{V})(x)}{\mathcal{V}(x)}$  when  $\max_{i \in \llbracket 1, 2k \rrbracket} (x_i)$  is large by the product between  $\Lambda$  and  $1 + \mathcal{L}(g)$ . This gives us the following key statement, that allows us to verify (S<sub>2.2</sub>), and that is proved in Section 5.1.3.

**Proposition 5.1** (Existence of a Lyapunov function). *Let us assume that (S<sub>1.1</sub>), (S<sub>1.3</sub>) and (S<sub>2.1</sub>) hold with  $B_{\max} > \Delta + \delta$ . Then for all  $\lambda_0 > 0$ ,  $L \in \mathbb{N}^*$ , Assumption (S<sub>2.2</sub>) is verified with  $L_{\text{return}} = L$  and the following function  $\mathcal{V}$  and constant  $\varepsilon_1$ :*

$$\forall x \in \mathbb{R}_+^{2k} : \mathcal{V}(x) = \exp \left[ \lambda_0 \cdot \sum_{i=1}^{2k} \max(x_i - B_{\max}L + \Delta + \delta, 0) \right], \quad \varepsilon_1 = (1 + \mathcal{L}(g)(\lambda_0)) \Lambda(\lambda_0, L) - 1. \quad (5.1.2)$$

However, the main difficulty is not to verify (S<sub>2.2</sub>), but to verify both (S<sub>2.2</sub>) and (S<sub>3</sub>). Indeed, the values of the constants  $\alpha$  and  $\beta$  in (S<sub>3</sub>) depend on the value of  $\varepsilon_0$  and  $\varepsilon_1$  and we must have  $\beta < \alpha$ . Thus, we need to have a suitable relation between  $\varepsilon_1$  and  $\varepsilon_0$  to verify these assumptions. When the birth rate does not depend on  $x$ , this relation is  $1 + \varepsilon_1 < (1 + \varepsilon_0)^{\frac{1}{D}}$ . We illustrate this by proving the following statement.

**Corollary 5.2.** *Let us assume that the assumptions of Proposition 5.1 hold. Assume also that the birth rate  $b$  is independent of  $x$ , and that there exists  $\lambda_0 > 0$ ,  $L \in \mathbb{N}^*$  such that*

$$(1 + \mathcal{L}(g)(\lambda_0)) \Lambda(\lambda_0, L) < (1 + \varepsilon_0)^{\frac{1}{D}}. \quad (5.1.3)$$

*Then, Assumptions (S<sub>2.2</sub>) and (S<sub>3</sub>) are verified.*

*Proof.* One can easily apply Proposition 5.1 to verify (S2.2) with  $\varepsilon_1 = (1 + \mathcal{L}(g)(\lambda_0)) \Lambda(\lambda_0, L) - 1$ , and then verify (S3.1) with  $\underline{b} \equiv b \equiv \bar{b}$ . We then focus on verifying (S3.2) and (S3.3). We define for all  $x \geq 0$  the function  $f(x) = \int_0^{+\infty} b(s) \exp(-\int_0^s b(u) du) e^{-xs} ds$ . We observe by (2.2.1) that for all  $x > 0$

$$f(x) \leq \tilde{b} \int_0^{+\infty} (1 + s^{d_b}) e^{-xs} ds.$$

Thus, it holds  $\lim_{x \rightarrow +\infty} f(x) = 0$ . We also have by classic computations that  $f(0) = 1$  and that  $f$  is a continuous decreasing function. Then, by the intermediate values theorem and the fact that  $1 + \varepsilon_1 < (1 + \varepsilon_0)^{\frac{1}{\underline{b}}}$ , there exist  $0 < \beta < \alpha$  such that  $f(\alpha) = \frac{1}{(1 + \varepsilon_0)^{\frac{1}{\underline{b}}}}$  and  $f(\beta) = \frac{1}{1 + \varepsilon_1}$ . These correspond to the equalities we need to verify (S3.2) and (S3.3). Thus, it only remains to prove the second condition of (S3.2) and the corollary will be proved.

We notice that for all  $a, s \geq 0$ , we have that  $\mathcal{F}_a(s) = b(a + s) \exp(-\int_a^{a+s} b(u) du)$  and  $\bar{\mathcal{F}}_a(s) = \exp(-\int_a^{a+s} b(u) du)$ . Let us bound from below  $\int_0^t \mathcal{F}_a(s) e^{-\alpha s} ds$  for all  $(a, t) \in \mathbb{R}_+ \times [a_0, +\infty)$ . First, after an integration by parts, use the fact that  $\bar{\mathcal{F}}_a(s) \leq 1$  for  $a, s \geq 0$ , and the fact that  $\bar{\mathcal{F}}_a(s) \leq \exp(-b_0(s - a_0))$  when  $s \geq a_0$  by (2.2.1). Then, integrate in  $s$ . It comes for all  $t \geq a_0, a \geq 0$

$$\int_0^t \mathcal{F}_a(s) e^{-\alpha s} ds = [-\bar{\mathcal{F}}_a(s) e^{-\alpha s}]_0^t - \alpha \int_0^t e^{-\alpha s} \bar{\mathcal{F}}_a(s) ds \geq e^{-\alpha a_0} - e^{-\alpha t} - \frac{\alpha}{\alpha + b_0} e^{-\alpha a_0}.$$

We easily deduce that the second condition of (S3.2) is verified from the above equation by taking  $t$  sufficiently large.  $\square$

When the birth rate depends on  $x$ , a stronger inequality needs to be verified to check (S3). This inequality depends on the gap between  $\underline{b}$  and  $\bar{b}$ . For example, when the birth rate is bounded from above and from below by a positive constant, the inequality is the following.

**Corollary 5.3.** *Let us assume that the assumptions of Proposition 5.1 hold. Assume also that there exists  $b_1, b_2 > 0$  such that for all  $(x, a) \in \mathcal{X}$  it holds  $b_1 \leq b(x, a) \leq b_2$ , and  $\lambda_0 > 0, L \in \mathbb{N}^*$  such that*

$$(1 + \mathcal{L}(g)(\lambda_0)) \Lambda(\lambda_0, L) < \frac{b_1}{b_2} \left( (1 + \varepsilon_0)^{\frac{1}{\underline{b}}} - 1 \right) + 1. \quad (5.1.4)$$

*Then, Assumptions (S2.2) and (S3) are verified.*

**Remark 5.4.** *This result shows that more the birth rate varies with respect to telomere lengths, more it is difficult to ensure the existence of a stationary profile.*

*Proof.* One can easily apply Proposition 5.1 to verify (S2.2) with  $\varepsilon_1 = (1 + \mathcal{L}(g)(\lambda_0)) \Lambda(\lambda_0, L) - 1$ , and then verify (S3.1) with  $\underline{b} \equiv b_1$  and  $\bar{b} \equiv b_2$ . We then focus on verifying (S3.2) and (S3.3). First, we have by easy computations that for all  $y \in \mathbb{R}_+$

$$\int_0^{+\infty} e^{-ys} \mathcal{F}_0(s) ds = b_1 \int_0^{+\infty} e^{-(y+b_1)s} ds = \frac{b_1}{y + b_1}.$$

From the above, the equality on the left in (S3.2) is verified for  $\alpha = b_1 \left( (1 + \varepsilon_0)^{\frac{1}{\underline{b}}} - 1 \right)$ . The inequality on the right is then trivially verified because with similar computations as the above, we have for all  $t \geq 0, a \geq 0$ :  $\int_0^t e^{-\alpha s} \mathcal{F}_a(s) ds = \frac{b_1}{\alpha + b_1} (1 - e^{-\alpha t})$ .

To verify (S3.3), we first observe that for all  $y \geq 0$ :  $\int_0^{+\infty} e^{-ys} \mathcal{G}_0(s) ds = \frac{b_2}{y + b_2}$ . Then, for  $\beta = b_2 \varepsilon_1$ , the equality stated in (S3.3) holds. The fact that  $\beta < \alpha$  easily comes from (5.1.4).  $\square$

In practice, verifying formally inequalities as the one presented in (5.1.3) or (5.1.4) is quite difficult (but it can be easily done numerically). In addition, this requires conditions quite restrictive on the birth rate, see assumptions of Corollaries 5.2 and 5.3. To solve these issues, we now present two conditions on the lengthening densities  $(h(x, \cdot))_{x \in \mathbb{R}}$  or the probability mass functions  $(p_{J,M}(r, s))_{(J,M) \in \mathcal{J}_k, (r,s) \in \mathbb{R}^2}$ , that allow to check (S2.2) and (S3) in practice.

### 5.1.2 Practical criteria to verify $(S_{2.2})$ and $(S_3)$

In view of Proposition 5.1, we need to control the value of  $(1 + \mathcal{L}(g))\Lambda$ . Indeed, if the latter can be taken as small as we want, then by the intermediate values theorem it will always be possible to find  $\varepsilon_1 > 0$  and  $\alpha > \beta > 0$  such that  $(S_{2.2})$  and  $(S_3)$  are verified. In fact,  $\mathcal{L}(g)$  can be taken as small as we want. Thus, if for all  $\lambda > 0$  we can control the value of  $\Lambda(\lambda, \cdot)$ , then we will be able to verify the assumptions. We illustrate this by proving the following statement.

**Proposition 5.5** (Criterion to check  $(S_{2.2})$  and  $(S_3)$ ). *Let us assume that  $(S_{1.1})$ ,  $(S_{1.3})$ ,  $(S_{2.1})$  and  $(S_{3.1})$  hold with  $B_{\max} > \Delta + \delta$ , and that*

$$\forall \lambda > 0, \varepsilon > 0, \exists L \in \mathbb{N}^* \text{ s.t. } \Lambda(\lambda, L) \leq 1 + \varepsilon, \quad (5.1.5)$$

$$\exists b_1 > 0, d_1 \in \mathbb{N} \text{ s.t. } \forall (x, a) \in \mathbb{R}_+^{2k} \times [a_1, +\infty) : \bar{b}(x, a) \leq b_1(1 + a^{d_1}), \quad (5.1.6)$$

$$\exists b_2 > 0, a_2 \geq 0 \text{ s.t. } \forall (x, a) \in \mathbb{R}_+^{2k} \times [a_2, +\infty) : \underline{b}(x, a) \geq b_2. \quad (5.1.7)$$

Then,  $(S_{2.2})$  and  $(S_3)$  are verified.

*Proof.* First, proceeding as in the proof of Corollary 5.2, one can easily obtain from the intermediate values theorem, (5.1.6) and (5.1.7) that there exists  $\alpha > 0$  such that  $(S_{3.2})$  is verified. Then, we focus on proving  $(S_{2.2})$  and  $(S_{3.3})$ .

Let  $\beta \in (0, \alpha)$  and  $\varepsilon_1 = \frac{1}{\mathcal{L}(g_0)(\beta)} - 1$ . First, by  $(S_{1.1})$ , it holds for all  $x \in \mathbb{R}_+^*$ :  $\mathcal{L}(g)(x) \leq \frac{\bar{g}}{x}$ . The latter, the fact that  $\mathcal{L}(g)(0) = 1$  and  $\varepsilon_1 < 1$ , and the continuity of  $\mathcal{L}(g)$ , imply that there exists  $\lambda_0 > 0$  such that

$$\mathcal{L}(g)(\lambda_0) < (1 + \varepsilon_1)^{\frac{1}{2}} - 1. \quad (5.1.8)$$

Second, in view of (5.1.5), there exists  $L > 0$  such that

$$\Lambda(\lambda_0, L) < (1 + \varepsilon_1)^{\frac{1}{2}}.$$

Combining (5.1.8) and the above equation yields that  $(1 + \mathcal{L}(g)(\lambda_0))\Lambda(\lambda_0, L) < 1 + \varepsilon_1$ . In view of Proposition 5.1 and the fact that  $\varepsilon_1 = \frac{1}{\mathcal{L}(g_0)(\beta)} - 1$ , we then obtain that Assumption  $(S_{2.2})$  and  $(S_{3.3})$  are verified.  $\square$

The most difficult assumption of Proposition 5.5 to check is (5.1.5). Let us fix  $\lambda > 0$ . The quantities that can be large in the expression of  $\Lambda(\lambda, \cdot)$  are the Laplace transforms of the functions  $(h(x, \cdot))_{x \in \mathbb{R}}$ . Here are two ways to control them.

- By finding conditions implying that these Laplace transforms are very small for large coordinates.
- By finding  $L \in \mathbb{N}^*$  such that for all  $(r, s) \in \mathbb{R}_+^{2k}$ , the probabilities  $(p_{J,M}(r, s))_{(J,M) \in \mathcal{J}_k, J \cap \mathcal{E}_L(x) \neq \emptyset}$  are very small. Indeed, according to (5.1.1), if these probabilities are small, then they will compensate for the Laplace transforms of the functions  $(h(x, \cdot))_{x \in \mathbb{R}}$ .

Let us now give two statements, each corresponding one of the above points, implying (5.1.5). We begin with the following statement, providing a condition allowing to directly control the values of the Laplace transforms. Its qualitative interpretation is that the longer a telomere is, the smaller its lengthening value becomes.

**Proposition 5.6** (Control of the Laplace transforms). *Let us assume that  $(S_{1.1})$  and  $(S_{2.1})$  hold with  $B_{\max} > \Delta + \delta$ , and that*

$$\lim_{x \rightarrow +\infty} \Delta_x = 0. \quad (5.1.9)$$

Then, Eq. (5.1.5) holds.

*Proof.* Let  $\lambda > 0$ . First, as the functions  $(h(x, \cdot))_{x \in \mathbb{R}}$  are probability density functions, one has for all  $x \in \mathbb{R}$  that

$$1 \leq \mathcal{L}(h(x, \cdot))(-\lambda) = \int_0^{\Delta_x} \exp(\lambda u) h(x, u) du \leq \exp(\lambda \Delta_x). \quad (5.1.10)$$

Then, by (5.1.9) we have  $\lim_{x \rightarrow +\infty} \mathcal{L}(h(x, \cdot))(-\lambda) = 1$ , implying that for all  $\varepsilon > 0$ , there exists  $C_\varepsilon > 0$  such that for all  $x > C_\varepsilon$

$$1 \leq \mathcal{L}(h(x, \cdot))(-\lambda) \leq (1 + \varepsilon)^{\frac{1}{2k}}. \quad (5.1.11)$$

We now use the latter to prove the proposition. Let  $\varepsilon > 0$ , and  $L \in \mathbb{N}^*$  such that  $L > \frac{C_\varepsilon + \Delta + \delta}{B_{\max}}$ . First, we use (5.1.11) to bound from above the term  $\prod_{i \in J \cap \mathcal{E}_L(r)} \mathcal{L}(h(r_i, \cdot))(-\lambda)$  by  $(1 + \varepsilon)$ . Then, we use the fact that for all  $(r, s) \in (\mathbb{R}^{2k})^2$ , the sum of the probabilities  $(p_{J,M}(r, s))_{(J,M) \in \mathcal{J}_k}$  is 1. It comes that  $\Lambda(\lambda, L) \leq 1 + \varepsilon$ , which ends the proof of the proposition.  $\square$

Now, we provide a condition allowing to control the values of the probabilities  $(p_{J,M}(r, s))_{(J,M) \in \mathcal{J}_k}$ , for all  $(r, s) \in \mathbb{R}^{2k}$ . Its qualitative interpretation is that the longer a telomere is, the smaller its probability to be lengthened becomes.

**Proposition 5.7** (Control of the lengthening probabilities). *Let us assume that (S1.1), (S1.3) and (S2.1) hold with  $B_{\max} > \Delta + \delta$ , and that for all  $(J, M) \in \mathcal{J}_k$*

$$\lim_{\substack{\max_{j \in J}(x_j) \rightarrow +\infty \\ j \in J}} \left( \sup_{y \in \mathbb{R}^{2k}} (p_{J,M}(x, y)) \right) = 0. \quad (5.1.12)$$

Then, Eq. (5.1.5) holds.

**Remark 5.8.** *In view of (2.2.6), Proposition (5.7) is still true if we replace in Eq. (5.1.12) the terms  $\sup_{y \in \mathbb{R}^{2k}}$  and  $\max_{j \in J}(x_j) \rightarrow +\infty$  by  $\sup_{x \in \mathbb{R}^{2k}}$  and  $\max_{m \in M}(y_m) \rightarrow +\infty$  respectively.*

*Proof.* Let  $\lambda > 0$ . By (5.1.12) and the fact that  $\#(\mathcal{J}_k) < +\infty$ , for all  $\varepsilon > 0$  there exists  $C_\varepsilon > 0$  such that for all  $(x, y) \in (\mathbb{R}_+^{2k})^2$  and  $(J, M) \in \mathcal{J}_k$  verifying  $\max_{j \in J}(x_j) \geq C_\varepsilon$ , we have

$$p_{J,M}(x, y) < \frac{1}{\sup_{r \in \mathbb{R}} (\mathcal{L}(h(r, \cdot))(-\lambda_0))^{2k}} \frac{\varepsilon}{\#(\mathcal{J}_k)} =: p_0. \quad (5.1.13)$$

The fact that  $\sup_{x \in \mathbb{R}} (\mathcal{L}(h(x, \cdot))(-\lambda_0)) < +\infty$  is a consequence of (5.1.10) and the fact that  $\Delta_x \leq \Delta$  for all  $x \in \mathbb{R}$ , see (S1.1).

Let us now use (5.1.13) to get (5.1.5). We fix  $\varepsilon > 0$  and  $L \in \mathbb{N}^*$  such that  $L > \frac{C_\varepsilon + \Delta + \delta}{B_{\max}}$ . First, in (5.1.1), we use (5.1.13) to bound from above  $p_{J,M}(r, s)$  when  $J \cap \mathcal{E}_L(r) \neq \emptyset$  by  $p_0$ . Then, for all  $(r, s) \in \mathbb{R}^{2k} \times \mathbb{R}^{2k}$ , we bound from above the sum of the probabilities  $(p_{J,M}(r, s))_{(J,M) \in \mathcal{J}_k \text{ s.t. } J \cap \mathcal{E}_L(r) = \emptyset}$  by 1. Finally, using the definition of  $p_0$  (see (5.1.13)), we bound from above the other sum by  $\varepsilon$ , and sum this bound with the bound obtained for the first sum. It comes that  $\Lambda(\lambda, L) \leq 1 + \varepsilon$ , which ends the proof of the proposition.  $\square$

We present in Sections 5.2 and 5.3 models where the criteria given in this section are used. We now conclude this subsection by proving Proposition 5.1.

### 5.1.3 Proof of Proposition 5.1

Let  $\lambda_0 > 0$  and  $L \in \mathbb{N}^*$ . We first define for all  $y \in \mathbb{R}$

$$v(y) := \exp[\lambda_0 \cdot \max(y - B_{\max}L + \Delta + \delta, 0)].$$

We also define for all  $x \in \mathbb{R}_+^{2k}$ ,  $(I, J, M) \in \mathcal{I}_k \times \mathcal{J}_k$

$$\begin{aligned} A(x, I, J, M) &:= \int_{(\alpha_1, \alpha_2) \in ([0, \delta]^{2k})^2} p_{J,M}(x - \alpha_1, x - \alpha_2) \left[ \int_{(\beta_1, \beta_2) \in ([0, \Delta]^{2k})^2} v(x - \alpha_1 + \beta_1) \right. \\ &\quad \left. \times \mathbf{1}_{\{x - \alpha_1 + \beta_1 \in \mathbb{R}_+^{2k}\}} d\mu_{(x - \alpha_1, x - \alpha_2)}^{(E, J, M)}(\beta_1, \beta_2) \right] d\mu^{(S, I)}(\alpha_1, \alpha_2). \end{aligned}$$

This represents the kernel for telomere lengths updating for the branching process when the sets that index which telomeres are shortened and lengthened in the daughter cell  $A$  are respectively  $I$  and  $J$ , and in the daughter cell  $B$  are respectively  $I^c$  and  $M$ . We finally notice that for all  $x \in \mathbb{R}_+^{2k}$  we have

$$V(x) = \prod_{i \in [1, 2k]} v(x_i), \quad \text{and} \quad \mathcal{K}(V)(x) = \frac{2}{\#(\mathcal{I}_k)} \sum_{(I, J, M) \in \mathcal{I}_k \times \mathcal{J}_k} A(x, I, J, M). \quad (5.1.14)$$



In this proof, we extend the definition of  $\mathcal{V}$  to  $(\mathbb{R}_+^{2k})^c$ , by writing for all  $y \in (\mathbb{R}_+^{2k})^c$ :  $\mathcal{V}(y) = \prod_{i \in \llbracket 1, 2k \rrbracket} v(y_i)$ .

The proof of Proposition 5.1 is done in three steps. In Step 1, we prove the following auxiliary inequality. For all  $x \in \mathbb{R}_+^{2k}$  and  $(\alpha_1, \alpha_2) \in ([0, \delta]^{2k})^2$

$$\sum_{(J, M) \in \mathcal{J}_k} p_{J, M}(x, y) \int_{(\beta_1, \beta_2) \in ([0, \Delta]^{2k})^2} \mathcal{V}(x - \alpha_1 + \beta_1) d\mu_{(x - \alpha_1, x - \alpha_2)}^{(E, J, M)}(\beta_1, \beta_2) \leq \mathcal{V}(x - \alpha_1) \Lambda(\lambda_0, L). \quad (5.1.15)$$

Then, we prove in Step 2 a second auxiliary inequality. For all  $x \in \mathbb{R}_+^{2k}$ ,  $I \in \mathcal{I}_k$

$$\begin{aligned} & \int_{(\alpha_1, \alpha_2) \in ([0, \delta]^{2k})^2} \mathcal{V}(x - \alpha_1) d\mu^{(S, I)}(\alpha_1, \alpha_2) \\ & \leq \left( \mathbf{1}_{\{\forall i \in I \text{ s.t. } x_i \leq B_{\max} L - \Delta\}} + \mathcal{L}(g)(\lambda_0) \mathbf{1}_{\{\exists i_0 \in I \text{ s.t. } x_{i_0} > B_{\max} L - \Delta\}} \right) \mathcal{V}(x). \end{aligned} \quad (5.1.16)$$

Finally, in Step 3 we verify (S2.2) using the previous inequalities.

**Step 1:** Let  $x \in \mathbb{R}_+^{2k}$ ,  $(\alpha_1, \alpha_2) \in ([0, \delta]^{2k})^2$ ,  $(\beta_1, \beta_2) \in [0, \Delta]^{2k}$ , and  $(J, M) \in \mathcal{J}_k$ . For all  $i \in (\mathcal{E}_L(x))^c$ , we have by definition of  $\mathcal{E}_L(x)$  that  $x_i - (\alpha_1)_i + (\beta_1)_i \leq B_{\max} L - \Delta - \delta$ . This implies

$$v(x_i - (\alpha_1)_i + (\beta_1)_i) = 1 = v(x_i - (\alpha_1)_i). \quad (5.1.17)$$

In addition, by (2.2.7), the measure  $\mu_{(x - \alpha_1, x - \alpha_2)}^{(E, J, M)}$  is a Dirac measure in 0 for the coordinates that are not in  $J$ , and is the measure  $h(x_i - (\alpha_1)_i, u) du$  for the coordinates  $i \in J$ . By the equality on the left in (5.1.14), Eq. (5.1.17) and the latter, we thus have

$$\begin{aligned} & \int_{(\beta_1, \beta_2) \in ([0, \Delta]^{2k})^2} \mathcal{V}(x - \alpha_1 + \beta_1) d\mu_{(x - \alpha_1, x - \alpha_2)}^{(E, J, M)}(\beta_1, \beta_2) \\ & = \left[ \prod_{\substack{i \in \llbracket 1, 2k \rrbracket \\ i \notin \mathcal{E}_L(x) \text{ or } i \notin J}} v(x_i - (\alpha_1)_i) \right] \left[ \prod_{\substack{i \in \llbracket 1, 2k \rrbracket \\ i \in J \cap \mathcal{E}(x)}} \left( \int_{u \in [0, \Delta]} v(x_i - (\alpha_1)_i + u) h(x_i - (\alpha_1)_i, u) du \right) \right]. \end{aligned} \quad (5.1.18)$$

We now obtain Eq. (5.1.15) from the above equality. First, notice that for all  $u \in [0, \Delta]$  we have  $v(x_i - (\alpha_1)_i + u) \leq v(x_i - (\alpha_1)_i) \exp(\lambda_0 u)$ , and apply this inequality to the right-hand side term of (5.1.18). Then, integrate in  $u$  to obtain for all  $i \in J \cap \mathcal{E}(x)$  the Laplace transform of  $h(x_i - (\alpha_1)_i, \cdot)$  in  $-\lambda_0$  and group all the  $(v(x_i - (\alpha_1)_i))_{i \in \llbracket 1, 2k \rrbracket}$  into one product to get  $\mathcal{V}(x - \alpha_1)$ . Finally, multiply both sides of the inequality by  $p_{J, M}(x, y)$ , sum with respect to the indices  $(J, M) \in \mathcal{J}_k$ , and take the supremum for the right-hand side term. This gives (5.1.15).

**Step 2:** Let  $x \in \mathbb{R}_+^{2k}$  and  $I \in \mathcal{I}_k$ . Assume first that for all  $i \in I$ :  $x_i \leq B_{\max} L - \Delta$ . Notice that the function  $v$  increases. Then, by the form of  $\mathcal{V}$  given in (5.1.14) we have for all  $\alpha_1 \in \mathbb{R}_+^{2k}$ :  $\mathcal{V}(x - \alpha_1) \leq \mathcal{V}(x)$ . Plugging this in the left-hand side term of (5.1.16) and then using the fact that  $\mu^{(S, I)}$  is a probability measure yields that (5.1.16) is true when for all  $i \in I$ :  $x_i \leq B_{\max} L - \Delta$ .

Now, assume that there exists  $i_0 \in I$  such that  $x_{i_0} > B_{\max} L - \Delta$ . Recall that  $v$  increases. Then, by the form of  $\mathcal{V}$  given in (5.1.14) and the fact that  $x_{i_0} > B_{\max} L - \Delta$ , we have for all  $\alpha_1 \in [0, \delta]^{2k}$

$$\mathcal{V}(x - \alpha_1) \leq v(x_{i_0} - (\alpha_1)_{i_0}) \prod_{\substack{i \in \llbracket 1, 2k \rrbracket \\ i \neq i_0}} v(x_i) = \exp(-\lambda_0 (\alpha_1)_{i_0}) \mathcal{V}(x). \quad (5.1.19)$$

In addition, for all  $I \in \mathcal{I}_k$ , the measure  $\mu^{(S, I)}$  is the measure  $g(u) du$  for the coordinates in  $I$ , and is a probability measure for the other coordinates (see (2.2.5)). Then, we obtain that (5.1.16) is true by integrating both sides of (5.1.19) with respect to  $\mu^{(S, I)}$ .

**Step 3:** We now verify (S2.2). The third statement is easy to verify. We begin with the first statement. Let  $x \in [0, B_{\max}L - \Delta]^{2k}$ . As the maximum lengthening value is  $\Delta$ , we have that the offspring of a cell that has telomere length  $x$  necessarily have telomere length in  $[0, B_{\max}L]^{2k}$  after one division. Then it holds  $\mathcal{K}_{([0, B_{\max}L]^{2k})^c}(\mathcal{V})(x) = 0$  and the first statement is verified for  $x \in [0, B_{\max}L - \Delta]^{2k}$ . Now, let  $x \in ([0, B_{\max}L - \Delta]^{2k})^c$  and  $i_0 \in \llbracket 1, 2k \rrbracket$  satisfying  $x_{i_0} > B_{\max}L - \Delta$ . As it holds  $\mathcal{K}_{([0, B_{\max}L]^{2k})^c}(\mathcal{V})(x) \leq \mathcal{K}(\mathcal{V})(x)$ , we prove the inequality for  $\mathcal{K}(\mathcal{V})(x)$  instead of  $\mathcal{K}_{([0, B_{\max}L]^{2k})^c}(\mathcal{V})(x)$ . First, develop  $\mathcal{K}(\mathcal{V})(x)$  as in (5.1.14) and bound from above for all  $(I, J, M) \in \mathcal{I}_k \times \mathcal{J}_k$  the term  $A(x, I, J, M)$  by applying (5.1.15). Then, split the new sum in two sums, grouping the sets  $(I, J, M) \in \mathcal{I}_k \times \mathcal{J}_k$  such that  $i_0 \in I$  in one sum, and the other sets in a second sum. Finally, apply (5.1.16) to bound from above the terms that are summed in the first sum by  $\mathcal{L}(g)(\lambda_0)\mathcal{V}(x)$ , and the terms that are summed in the second sum by  $\mathcal{V}(x)$ . We mention that by the fact that  $\mathcal{L}(g)(\lambda_0) \leq 1$ , we can bound from above all the terms such that  $i_0 \notin I$  by  $\mathcal{V}(x)$ , even when there exists  $i_1 \in I$  such that  $x_{i_1} > B_{\max}L - \Delta$ . It comes

$$\mathcal{K}(\mathcal{V})(x) \leq \frac{2}{\#(\mathcal{I}_k)} \sum_{\substack{I \in \mathcal{I}_k \\ i_0 \in I}} \Lambda(\lambda_0, L) \mathcal{L}(g)(\lambda_0) \mathcal{V}(x) + \frac{2}{\#(\mathcal{I}_k)} \sum_{\substack{I \in \mathcal{I}_k \\ i_0 \notin I}} \Lambda(\lambda_0, L) \mathcal{V}(x).$$

Now, we use Lemma 4.9 above to get that  $\frac{2}{\#(\mathcal{I}_k)} \sum_{I \in \mathcal{I}_k, i_0 \in I} = \frac{2}{\#(\mathcal{I}_k)} \sum_{I \in \mathcal{I}_k, i_0 \notin I} = 1$ . We obtain that the first statement of (S2.2) is verified.

To verify the second statement of (S2.2), first notice that as  $v$  is increasing and as  $\Lambda(\lambda_0, L) \leq 1 + \varepsilon_1$ , it holds  $\mathcal{V}(x - \alpha_1) \Lambda(\lambda_0, L) \leq \mathcal{V}(x)(1 + \varepsilon_1)$ . Then, plug this in the right-hand side term of (5.1.15), and integrate both sides of the new inequality with respect to the measure  $\mu^{(S, I)}$ . As this is a probability measure, the right-hand side term stays equal to  $\mathcal{V}(x)(1 + \varepsilon_1)$ . It comes that the second statement of (S2.2) is verified.

We finally prove the fourth statement of (S2.2). We consider  $(x, y) \in (\mathbb{R}_+^{2k})^2$  verifying the inequality  $\|y - x\|_\infty \leq \max(\delta, \Delta)$ . As  $v$  is an increasing function we have from the last inequality

$$\mathcal{V}(y) \leq \exp \left[ \lambda_0 \cdot \sum_{i=1}^{2k} \max(x_i + \max(\delta, \Delta) - B_{\max}L + \Delta + \delta, 0) \right] \leq \mathcal{V}(x) \exp(2k \lambda_0 \max(\delta, \Delta)).$$

Then, the fourth statement of (S2.2) comes from the above inequality by taking the ratio between the left and right-hand side terms.  $\square$

## 5.2 A model where all telomeres are lengthened

We now present toy models for telomere shortening for which all the assumptions of Theorem 2.7 are verified. The first model is a model for which at each cell division, every telomere is lengthened. This is a concrete example of model for which this is easier to verify (S2.1) with  $D > 1$ . Let two constants  $\Delta > \delta > 0$  verifying

$$\left( \frac{\Delta - \delta}{\Delta} \right)^{2k^2 + 4k} > \frac{1}{4}. \quad (5.2.1)$$

This condition means that  $\delta$  must be sufficiently small in comparison to  $\Delta$ . Our model is the branching process introduced in Section 2.2 defined in the following way:

- For all  $(x, a) \in \mathbb{R}_+^{2k} \times \mathbb{R}_+$ :  $b(x, a) = a$ .
- For all  $y \in \mathbb{R}_+$ :  $g(y) = \frac{1}{\delta} 1_{[0, \delta]}(y)$ .
- For all  $(x, y) \in \mathbb{R} \times \mathbb{R}_+$ :  $h(x, y) = \frac{1}{\Delta} 1_{[0, \Delta]}(y) 1_{\{x < 0\}} + \frac{x+1}{\Delta} 1_{[0, \frac{\Delta}{x+1}]}(y) 1_{\{x \geq 0\}}$ .
- For all  $(s_1, s_2) \in (\mathbb{R}^{2k})^2$ ,  $(J, M) \in \mathcal{J}_k$ ,

$$p_{J, M}(s_1, s_2) = \begin{cases} 1 & \text{if } (J, M) = (\{1, \dots, 2k\}, \{1, \dots, 2k\}), \\ 0, & \text{otherwise.} \end{cases}$$

As  $p_{J, M}(s_1, s_2)$  does not depend on  $s_1$  and  $s_2$ , we drop  $(s_1, s_2)$  in the notation. We also denote  $(J_0, M_0) = (\{1, \dots, 2k\}, \{1, \dots, 2k\})$ .

We easily see that Assumption  $(S_1)$  is verified for this model. We also easily verify  $(S_{3.1})$  with  $\underline{b} \equiv b \equiv \bar{b}$ . Therefore, by Propositions 5.5 and 5.6, if  $(S_{2.1})$  is satisfied, then all the other assumptions are verified. We thus focus on verifying  $(S_{2.1})$ . We first explain why we do not verify  $(S_{2.1})$  with  $D = 1$  and then we verify it with  $D = 2$ .

**Problem for  $D = 1$ .** A natural candidate for the set is a set of the form  $[0, L]^{2k}$ , where  $L > 0$ . The reason is that these sets have a very simple form, and thus computations are easier. However, we cannot verify  $(S_{2.1})$  with  $K_{\text{renew}}$  of this form and  $D = 1$  as all the telomeres of a cell are lengthened at each division. Let us formalise it. We fix  $L > 0$ , and then consider  $x = \sum_{i=1}^{2k} L e_i$ , where  $(e_i)_{i \in \llbracket 1, 2k \rrbracket}$  are the vectors of the canonical basis. We study a cell with telomere lengths  $x$  that divides. By Eq. (2.2.5), each of its daughter cells has at least  $k$  telomeres that stay unchanged after shortening. In addition, as all telomeres are lengthened in this model (because the probability to draw  $(J_0, M_0)$  is 1), the  $k$  telomeres that stayed unchanged during the shortening are lengthened. We then necessarily have at least  $k$  telomeres with a length strictly larger than  $L$  after lengthening. In particular, daughter cells of the cell that divides necessarily have telomere lengths out of  $[0, L]^{2k}$ . As  $\mathcal{K}(\cdot)(x)$  is the transition probability for telomere lengths of the daughter cells, the latter yields that

$$\mathcal{K}(1_{[0, L]^{2k}})(x) = 0.$$

Thus, the inequality presented in  $(S_{2.1})$  fails for  $x = \sum_{i=1}^{2k} L e_i$  and it is impossible to have a renewal in one generation for a set of the form  $[0, L]^{2k}$ , where  $L > 0$ . We thus have two options to verify  $(S_{2.1})$ : either we should consider a set for the renewal with a more complex form, or we should verify  $(S_{2.1})$  with  $D > 1$ . The problem with the first option is that due to the multidimensional trait space and the fact that the expression of the jump kernel is complicated, exhibiting the good set is not trivial. We then choose the second option. Let us begin with some preliminaries.

**Preliminaries.** In view of (5.2.1), we first introduce  $\gamma \in (0, 1)$  such that

$$(1 - \gamma)^{2k} \left( \frac{\Delta - \delta}{\Delta} \right)^{2k^2 + 4k} > \frac{1}{4}. \quad (5.2.2)$$

We use  $\gamma$  in order to write the quantity  $\gamma\delta$ , which is a minimum shortening value for the cells we are interested in later in the proof. The above condition implies that  $\gamma$  must be sufficiently small so that we can control the number of non-senescent offspring of a cell for which telomeres are shortened by at least  $\gamma\delta$ .

We now obtain auxiliary results useful to choose the value  $L > 0$  of the set  $K_{\text{renew}} = [0, L]^{2k}$ . Let us consider for all  $x \geq 0$ :  $f(x) = x - \gamma\delta + \frac{\Delta}{x+1} + \frac{\Delta}{\max(x-\delta+1, 1)}$ . We first easily have that it holds  $\lim_{x \rightarrow +\infty} f(x) - (x - \frac{\gamma}{2}\delta) = -\frac{\gamma}{2}\delta < 0$ , so that  $f$  is smaller than the function  $\text{Id} - \frac{\gamma}{2}\delta$  after a certain value  $L_0 > 0$ . In addition, we have that  $f$  is differentiable on  $(\delta, +\infty)$  and  $\lim_{x \rightarrow +\infty} f'(x) = 1$ , which implies that there exists  $L_1 > 0$  such that  $f$  strictly increases on  $[L_1, +\infty)$ . As  $\lim_{x \rightarrow +\infty} f(x) = +\infty$ , we finally have that there exists  $L_2 > 0$  such that for all  $x \geq L_2$ :  $f(x) \geq \max_{y \in [0, L_1]} f(y)$ . These three results respectively imply that

$$\begin{aligned} \forall x \geq \max(L_0, L_1, L_2) : & \quad f(x) \leq x - \frac{\gamma}{2}, \\ \forall x \in [L_1, \max(L_0, L_1, L_2)] : & \quad f(x) \leq f(\max(L_0, L_1, L_2)), \\ \forall x \in [0, L_1] : & \quad f(x) \leq \max_{y \in [0, L_1]} f(y) \leq f(\max(L_0, L_1, L_2)). \end{aligned} \quad (5.2.3)$$

By combining the first inequality in (5.2.3) with the second one, and then the first with the third one, we obtain that for all  $x \in [0, \max(L_0, L_1, L_2)]$ :  $f(x) \leq \max(L_0, L_1, L_2) - \frac{\gamma}{2}$ . From the latter and the first inequality in (5.2.3), it comes the following, which is the auxiliary inequality we need:

$$\forall L \geq \max(L_0, L_1, L_2), \forall x \in [0, L] : \quad f(x) \leq L - \frac{\gamma}{2}. \quad (5.2.4)$$

We now introduce the set and constants for which we verify (S<sub>2.1</sub>). We first fix an arbitrary  $L > \max(\Delta, L_0, L_1, L_2)$  verifying

$$\frac{k\Delta}{L - \frac{\gamma}{2}\delta + 1} \leq \frac{\gamma}{2}\delta, \quad (5.2.5)$$

We also consider  $\varepsilon_0 = 4(1 - \gamma)^{2k} \left(\frac{\Delta - \delta}{\Delta}\right)^{2k^2 + 4k} - 1$ ,  $D = k + 2$ ,  $B_{\max} = L + D\Delta$ , and  $K_{\text{renew}} = [0, L]^{2k}$ . To verify (S<sub>2.1</sub>), we proceed in two steps. We first prove in Step 1 that for all  $x \in [0, L - \frac{\gamma}{2}\delta]^{2k}$  we have

$$(\mathcal{K})^k (1_{K_{\text{renew}}})(x) \geq 2^k \left(\frac{\Delta - \delta}{\Delta}\right)^{2k^2}. \quad (5.2.6)$$

Then, we conclude in Step 2. We start with the following remark:

**Remark 5.9.** *As we start from  $x \in K_{\text{renew}} = [0, L]^{2k}$ , as the maximum lengthening value is  $\Delta$ , and as  $B_{\max} = L + D\Delta$ , the offspring of  $x$  from the first to the  $D$ -th generations stays in  $[0, B_{\max}]^{2k}$ . Therefore, if the inequality presented in (S<sub>2.1</sub>) is obtained for  $\mathcal{K}$ , then it will be also obtained for  $\mathcal{K}_{[0, B_{\max}]^{2k}}$  (see (2.3.1) for the definition of  $\mathcal{K}_{[0, B_{\max}]^{2k}}$ ). Hence, in the rest of the subsection, we omit the term  $[0, B_{\max}]^{2k}$  in  $\mathcal{K}_{[0, B_{\max}]^{2k}}$  and rather study  $\mathcal{K}$ .*

**Step 1:** Let us fix  $x \in [0, L - \frac{\gamma}{2}\delta]^{2k}$ . We also consider  $y \in [0, L - \frac{\Delta}{L - \frac{\gamma}{2}\delta + 1}]^{2k}$  and the set

$$I_y := \left\{ w \in [0, L]^{2k} \mid w_i \leq \max\left(y_i + \frac{\Delta}{L - \frac{\gamma}{2}\delta + 1}, \Delta\right) \right\}.$$

We first bound from below  $\mathcal{K}(1_{I_y})(y)$ . To do so, we use the following inequalities, that easily come from the expression of  $h$  and the fact that the maximum of  $j(x) = x + \frac{\Delta}{x+1}$  on  $[0, L - \frac{\gamma}{2}\delta]$  is in  $x = 0$  or  $x = L - \frac{\gamma}{2}\delta$ :

$$\begin{aligned} \forall s \in [0, L - \frac{\gamma}{2}\delta] : & \int_0^{\frac{\Delta}{s+1}} \mathbb{1}_{\{s+u \in [0, \max(s + \frac{\Delta}{L - \frac{\gamma}{2}\delta + 1}, \Delta)]\}} h(s, u) du = 1 \geq \frac{\Delta - \delta}{\Delta}, \\ \forall s \in [-\delta, 0) : & \frac{1}{\Delta} \int_0^{\Delta} \mathbb{1}_{\{s+u \in [0, \max(s + \frac{\Delta}{L - \frac{\gamma}{2}\delta + 1}, \Delta)]\}} h(s, u) du \geq \frac{1}{\Delta} \int_{\delta}^{\Delta} du = \frac{\Delta - \delta}{\Delta}. \end{aligned} \quad (5.2.7)$$

First, develop  $\mathcal{K}(1_{I_y})(y)$  and only keep the pair of sets  $(J_0, M_0)$  in the sum of the elements over  $\mathcal{J}_k$  (as the other probabilities are 0). Then, noticing that for all  $(s_1, s_2) \in (\mathbb{R}^{2k})^2$  the marginal of the measure  $\mu_{(s_1, s_2)}^{(E, J_0, M_0)}$  over each coordinate is the Lebesgue measure weighted by the function  $h$  (see (2.2.7)), use Eq. (5.2.7) to bound from below the integral with respect to  $d\mu_{(x - \alpha_1, x - \alpha_2)}^{(E, J_0, M_0)}$  by  $\left(\frac{\Delta - \delta}{\Delta}\right)^{2k}$ . Finally, integrate with respect to the probability measure  $\mu^{(S, I)}$ , and simplify  $\frac{1}{\#(\mathcal{I}_k)}$  by  $\sum_{I \in \mathcal{I}_k}$ . It comes

$$\begin{aligned} \mathcal{K}(1_{I_y})(y) &= \frac{2}{\#(\mathcal{I}_k)} \sum_{I \in \mathcal{I}_k} \int_{(\alpha_1, \alpha_2) \in (\mathbb{R}_+^2)^{2k}} \left[ \int_{(\beta_1, \beta_2) \in (\mathbb{R}_+^2)^{2k}} \mathbb{1}_{\{x - \alpha_1 + \beta_1 \in [0, L]^{2k}\}} \right. \\ &\quad \left. \times d\mu_{(x - \alpha_1, x - \alpha_2)}^{(E, J_0, M_0)}(\beta_1, \beta_2) \right] d\mu^{(S, I)}(\alpha_1, \alpha_2) \geq 2 \left(\frac{\Delta - \delta}{\Delta}\right)^{2k}. \end{aligned} \quad (5.2.8)$$

Now, let us consider  $(w^{(1)}, \dots, w^{(k)}) \in (\mathbb{R}_+^{2k})^k$  such that  $w^{(1)} \in I_x$  and such that for all  $i \in \llbracket 1, k-1 \rrbracket$ :  $w^{(i+1)} \in I_{w^{(i)}}$ . First, iterate the condition in the definition of the sets  $(I_y)_{y \in \mathbb{R}_+^{2k}}$ . Then, use Eq. (5.2.5), the fact that  $x \in [0, L - \frac{\gamma}{2}\delta]^{2k}$ , and the fact that  $L > \Delta$ . We obtain that for all  $i \in \llbracket 1, 2k \rrbracket$

$$(w^{(k)})_i \leq \max\left(\left(w^{(k-1)}\right)_i + \frac{\Delta}{L - \frac{\gamma}{2}\delta + 1}, \Delta\right) \leq \dots \leq \max\left(x + \frac{k\Delta}{L - \frac{\gamma}{2}\delta + 1}, \Delta\right) \leq L.$$

In particular, we have  $w^{(k)} \in K_{\text{renew}}$ . Using the latter and (5.2.8), we get the following inequality, which ends the first step:

$$(\mathcal{K})^k (1_{K_{\text{renew}}})(x) \geq \int_{w^{(1)} \in I_x} \dots \int_{w^{(k)} \in I_{w^{(k)}}} \mathcal{K}(x, dw^{(1)}) \dots \mathcal{K}(w^{(k-1)}, dw^{(k)}) \geq \left( 2 \left( \frac{\Delta - \delta}{\Delta} \right)^{2k} \right)^k.$$

**Step 2:** Now, we fix  $x \in K_{\text{renew}} = [0, L]^{2k}$ . Our aim is to bound from below  $(\mathcal{K})^2 \left( 1_{[0, L - \frac{\gamma}{2}\delta]^{2k}} \right) (x)$ . Let  $(\alpha_1, \alpha'_1) \in ([0, \delta]^{2k})^2$  and  $(\beta_1, \beta'_1) \in ([0, \Delta]^{2k})^2$ . Assume that for all  $i \in \llbracket 1, 2k \rrbracket$  either  $(\alpha_1)_i \geq \gamma\delta$  and  $(\alpha'_1)_i = 0$ , or  $(\alpha_1)_i = 0$  and  $(\alpha'_1)_i \geq \gamma\delta$ . Assume also that

- If  $x_i - (\alpha_1)_i < 0$ , then  $\delta \leq (\beta_1)_i \leq \Delta$ .
- If  $x_i - (\alpha_1)_i \geq 0$ , then  $0 \leq (\beta_1)_i \leq \frac{\Delta}{x_i + 1}$ .
- If  $x_i - (\alpha_1)_i + (\beta_1)_i - (\alpha'_1)_i < 0$ , then  $\delta \leq (\beta'_1)_i \leq \Delta$ .
- If  $x_i - (\alpha_1)_i + (\beta_1)_i - (\alpha'_1)_i \geq 0$ , then  $0 \leq (\beta'_1)_i \leq \frac{\Delta}{x_i - (\alpha_1)_i + (\beta_1)_i - (\alpha'_1)_i + 1}$ . This implies by the conditions on  $\alpha_1, \alpha'_1$  and  $\beta_1$  that  $(\beta'_1)_i \leq \frac{\Delta}{x_i - \delta + 1}$  when  $x_i \geq \delta$ , so that  $(\beta'_1)_i \leq \frac{\Delta}{\max(x_i - \delta + 1, 1)}$  whatever the value of  $x_i$  (as  $(\beta'_1)_i \leq \Delta$ ).

The above statements correspond to the conditions we have on  $\alpha_1, \alpha'_1, \beta_1$  and  $\beta'_1$  in the integrals used to develop  $(\mathcal{K})^2 \left( 1_{[0, L - \frac{\gamma}{2}\delta]^{2k}} \right) (x)$ , see (5.2.8) for the development of  $\mathcal{K}$ . In view of the above, and Eq. (5.2.4) combined with the fact that  $L \geq \max(L_0, L_1, L_2)$ , we have for all  $i \in \llbracket 1, 2k \rrbracket$  that

$$0 \leq x_i - (\alpha_1)_i + (\beta_1)_i - (\alpha'_1)_i + (\beta'_1)_i \leq x_i - \gamma\delta + \frac{\Delta}{x_i + 1} + \frac{\Delta}{\max(x_i - \delta + 1, 1)} \leq L - \frac{\gamma}{2}.$$

Then, it holds  $x - \alpha_1 + \beta - \alpha'_1 + \beta'_1 \in [0, L - \frac{\gamma}{2}\delta]^{2k}$  when the above conditions are verified. Now, we use the latter to bound from below  $(\mathcal{K})^2 \left( 1_{[0, L - \frac{\gamma}{2}\delta]^{2k}} \right) (x)$ . First, we develop the measure  $\mathcal{K}$  two times, using the expression in the first line of (5.2.8), and only keep the pair of sets  $(J_0, M_0)$  in the sum of the elements over  $\mathcal{I}_k$ . This gives us a sum of elements over  $(I, I') \in (\mathcal{I}_k)^2$ . Then, we only keep the indices  $(I, I^c)$  where  $I \in \mathcal{I}_k$  in this sum. Finally, we add indicators to restrict the domain of integration, such that the conditions implying that  $x - \alpha_1 + \beta - \alpha'_1 + \beta'_1 \in [0, L - \frac{\gamma}{2}\delta]^{2k}$  hold. We get

$$\begin{aligned} (\mathcal{K})^2 \left( 1_{[0, L - \frac{\gamma}{2}\delta]^{2k}} \right) (x) &\geq \left( \frac{2}{\#(\mathcal{I}_k)} \right)^2 \sum_{I \in \mathcal{I}_k} \int_{(\alpha_1, \alpha_2) \in ([0, \delta]^{2k})^2} \int_{(\beta_1, \beta_2) \in ([0, \Delta]^{2k})^2} \left[ \int_{(\alpha'_1, \alpha'_2) \in ([0, \delta]^{2k})^2} \right. \\ &\times \int_{(\beta'_1, \beta'_2) \in ([0, \Delta]^{2k})^2} \mathbf{1}_{\{\forall i \in I: (\alpha_1)_i \geq \gamma\delta, \forall j \in I^c: (\alpha'_1)_j \geq \gamma\delta\}} \mathbf{1}_{\{\forall i \in \llbracket 1, 2k \rrbracket \text{ s.t. } x_i - (\alpha_1)_i + (\beta_1)_i - (\alpha'_1)_i < 0: (\beta'_1)_i \geq \delta\}} \\ &\times d\mu^{(S, I^c)}(\alpha'_1, \alpha'_2) d\mu_{(x - \alpha_1 + \beta_1 - \alpha'_1, x - \alpha_1 + \beta_1 - \alpha'_2)}^{(E, J_0, M_0)}(\beta'_1, \beta'_2) \left. \right] d\mu^{(S, I)}(\alpha_1, \alpha_2) d\mu_{(x - \alpha_1, x - \alpha_2)}^{(E, J_0, M_0)}(\beta_1, \beta_2). \end{aligned} \quad (5.2.9)$$

Now, as the measure  $\mu_{(s_1, s_2)}^{(E, J_0, M_0)}$  over each coordinate is the Lebesgue measure weighted by the function  $h$  (see (2.2.7)), use Eq. (5.2.7) to bound from below the integrals with respect to the measures  $\left( \mu_{(s_1, s_2)}^{(E, J_0, M_0)} \right)_{(s_1, s_2) \in \mathbb{R}_+^{2k}}$  in (5.2.9) by  $\left( \frac{\Delta - \delta}{\Delta} \right)^{2k}$ . Then, integrate with respect to the measures  $\mu^{(S, I)}$  and  $\mu^{(S, I^c)}$ . Each integral is equal to  $(1 - \gamma)^k$ . It comes in view of Lemma 4.9

$$(\mathcal{K})^2 \left( 1_{[0, L - \frac{\gamma}{2}\delta]^{2k}} \right) (x) \geq \left( \frac{2}{\#(\mathcal{I}_k)} \right)^2 \sum_{I \in \mathcal{I}_k} \left( (1 - \gamma)^k \left( \frac{\Delta - \delta}{\Delta} \right)^{2k} \right)^2 = \frac{4}{2^k} (1 - \gamma)^{2k} \left( \frac{\Delta - \delta}{\Delta} \right)^{4k}.$$

The latter implies in view of (5.2.6) that

$$\begin{aligned} (\mathcal{K})^D (1_{K_{\text{renew}}})(x) &\geq (\mathcal{K})^2 \left( 1_{[0, L - \frac{\gamma}{2}\delta]^{2k}} (\cdot) (\mathcal{K})^k (1_{K_{\text{renew}}})(\cdot) \right) (x) \\ &\geq 4 (1 - \gamma)^{2k} \left( \frac{\Delta - \delta}{\Delta} \right)^{2k^2 + 4k} = 1 + \varepsilon_0. \end{aligned}$$

Thus, (S<sub>2.1</sub>) is verified and the model admits a stationary profile.

### 5.3 A model with mutually independent lengthening probabilities

We now present a second toy model for telomere shortening. Contrary to previous model, the maximum lengthening values  $(\Delta_x)_{x \in \mathbb{R}}$  are all equal in this model, while the lengthening probabilities  $(p_{J,M})_{(J,M) \in \mathcal{J}_k}$  depend on telomere lengths of the two daughter cells after shortening. Let us consider two constants  $\Delta > \delta > 0$  satisfying

$$\left(\frac{\Delta - \delta}{\Delta}\right)^{2k} > \frac{1}{2}. \quad (5.3.1)$$

We also introduce a continuous function  $q : \mathbb{R} \mapsto (0, 1]$  such that  $\lim_{x \rightarrow +\infty} q(x) = 0$  and

$$\inf_{x \in [-\delta, 0)} q(x) \geq \left(\frac{\left(\frac{\Delta - \delta}{\Delta}\right)^{2k} + \frac{1}{2}}{2 \left(\frac{\Delta - \delta}{\Delta}\right)^{2k}}\right)^{\frac{1}{8k}}. \quad (5.3.2)$$

Our model in this section is the branching process constructed in Section 2.2, with:

- For all  $(x, a) \in \mathcal{X}$ :  $b(x, a) = a$ ,
- For all  $y \in \mathbb{R}_+$ :  $g(y) = \frac{1}{\delta} 1_{[0, \delta]}(y)$ ,
- For all  $(x, y) \in \mathbb{R} \times \mathbb{R}_+$ :  $h(x, y) = \frac{1}{\Delta} 1_{[0, \Delta]}(y)$ ,
- For all  $(x, y) \in (\mathbb{R}^{2k})^2$ ,  $(J, M) \in \mathcal{J}_k$ ,

$$p_{J,M}(x, y) = \left(\prod_{j \in J} q(x_j)\right) \left(\prod_{m \in M} q(y_m)\right) \left(\prod_{j \notin J} (1 - q(x_j))\right) \left(\prod_{m \notin M} (1 - q(y_m))\right).$$

Qualitatively, this choice for the function  $p_{J,M}$  means that at each division, for each telomere of each daughter cell, if its length after shortening is  $y \in \mathbb{R}$  (see Remark 2.3), then the probability that it is lengthened is  $q(y)$ . Conversely, the probability that it is not lengthened is  $1 - q(y)$ . In other words, the lengthening of each telomere is independent from the other telomeres. This way to model lengthening is used for example in [8].

The condition stated in (5.3.1) implies a significant difference between the maximum lengthening and shortening values. It has been experimentally deduced that this is the case see [48], which is encouraging. For example, in the case of budding yeast cells, the maximum shortening value can be set as  $\delta = 10$  and we have  $k = 16$  chromosomes. Thus, according to (5.3.1), we require  $\Delta > 10 / (1 - (\frac{1}{2})^{\frac{1}{32}}) \simeq 466.68$  to be sure to observe a convergence towards a stationary profile. This a little too much, but not totally absurd as telomeres can be lengthened by more than 100 nucleotides at a cell division, see [48]. To compare, in the model presented in Section 5.2, for the same  $k$  and  $\delta$  we must have  $\Delta > 10 / (1 - (\frac{1}{4})^{\frac{1}{576}}) \simeq 4159.96$ , which is much less realistic.

The condition stated in (5.3.2) means that the probability that small telomeres are lengthened must be sufficiently large. When we have a large number of chromosomes, the condition implies that the probability must be very close to 1. Again, the condition is not optimal, and can be refined by being more meticulous in our computations, or by choosing other distributions than uniform distributions for  $g$  and  $h$ .

Assumption (S<sub>1</sub>) and (S<sub>3.1</sub>) are trivially verified for this model (we take  $\underline{b} \equiv b \equiv \bar{b}$  for (S<sub>3.1</sub>)). Assumption (S<sub>2.1</sub>) is also verified, and the proof is given in the paragraph below. Using finally Propositions 5.5 and 5.7, we conclude that all the assumptions of Theorem 2.7 are verified, so that there exists a stationary profile for this model.

**Proof that (S<sub>2.1</sub>) is verified.** We begin with a preliminary result. As  $\lim_{y \rightarrow +\infty} q(y) = 0$ , and as  $1 > \frac{(\frac{\Delta - \delta}{\Delta})^{2k} + \frac{1}{2}}{2(\frac{\Delta - \delta}{\Delta})^{2k}}$  by (5.3.1), there exists  $B_{\max} > 2\Delta$  such that

$$\forall y > B_{\max} - \Delta : 1 - q(y) \geq \left(\frac{\left(\frac{\Delta - \delta}{\Delta}\right)^{2k} + \frac{1}{2}}{2 \left(\frac{\Delta - \delta}{\Delta}\right)^{2k}}\right)^{\frac{1}{8k}}. \quad (5.3.3)$$

Our aim is to prove that (S2.1) is verified with  $K_{\text{renew}} = [0, B_{\text{max}}]^{2k}$ . To do so, we first obtain an auxiliary inequality. For all  $(x, y) \in ([-\delta, B_{\text{max}}]^{2k})^2$ , we consider  $\mathcal{A}(x, y) \subset \mathcal{J}_k$  such that

$$\begin{aligned} \mathcal{A}(x, y) = & \left\{ (J, M) \in \mathcal{J}_k \mid \{i \in \llbracket 1, 2k \rrbracket \mid x_i \in [-\delta, 0)\} \subset J \text{ and } \{i \in \llbracket 1, 2k \rrbracket \mid y_i \in [-\delta, 0)\} \subset M, \right. \\ & \left. \{i \in \llbracket 1, 2k \rrbracket \mid x_i \in (B_{\text{max}} - \Delta, B_{\text{max}}]\} \cap J = \emptyset \text{ and } \{i \in \llbracket 1, 2k \rrbracket \mid y_i \in (B_{\text{max}} - \Delta, B_{\text{max}}]\} \cap M = \emptyset \right\}. \end{aligned} \quad (5.3.4)$$

When  $k = 1$ , if we denote  $(x^*, y^*) = ((-\frac{\delta}{2}, \frac{B_{\text{max}}}{2}), (B_{\text{max}} - \frac{\Delta}{2}, B_{\text{max}} - \frac{\Delta}{2}))$ , then we have

$$\mathcal{A}(x^*, y^*) = \{(\{1, 2\}, \emptyset), (\{1\}, \emptyset)\}.$$

In particular, from the definition of  $p_{J,M}$ , the following holds:

$$\begin{aligned} \sum_{(J,M) \in \mathcal{A}(x^*, y^*)} p_{J,M}(x^*, y^*) &= q(x_1^*)q(x_2^*)(1 - q(y_1^*))(1 - q(y_2^*)) + q(x_1^*)(1 - q(x_2^*))(1 - q(y_1^*))(1 - q(y_2^*)) \\ &= q(x_1^*)(1 - q(y_1^*))(1 - q(y_2^*)). \end{aligned}$$

In other terms,  $\sum_{(J,M) \in \mathcal{A}(x^*, y^*)} p_{J,M}(x^*, y^*)$  can be seen as a product of functions  $q$  for the coordinates in  $[-\delta, 0)$ , and functions  $1 - q$  for the coordinates in  $(B_{\text{max}} - \Delta, B_{\text{max}}]$ . In fact, this equality can be generalised for all  $k \in \mathbb{N}^*$  and  $(x, y) \in ([-\delta, B_{\text{max}}]^{2k})^2$ . The reason is that in view of the conditions given in (5.3.4), for all  $(J, M) \in \mathcal{A}(x, y)$ , the following holds:

- For all  $i \in \llbracket 1, 2k \rrbracket$  such that  $x_i \in [0, B_{\text{max}} - \Delta]$ , if  $i \in J$ , then  $(J \setminus \{i\}, M) \in \mathcal{A}(x, y)$ . Conversely, if  $i \notin J$ , then  $(J \cup \{i\}, M) \in \mathcal{A}(x, y)$ .
- For all  $i \in \llbracket 1, 2k \rrbracket$  such that  $y_i \in [0, B_{\text{max}} - \Delta]$ , if  $i \in M$ , then  $(J, M \setminus \{i\}) \in \mathcal{A}(x, y)$ . Conversely, if  $i \notin M$ , then  $(J, M \cup \{i\}) \in \mathcal{A}(x, y)$ .

Hence, if we sum all the  $(J, M) \in \mathcal{A}(x, y)$ , then we will always have a term  $q$  and  $1 - q$  that will sum to give 1 for the coordinates in  $[0, B_{\text{max}} - \Delta]$ . The latter, combined with the inequalities given in (5.3.2) and (5.3.3) yields for all  $(x, y) \in ([-\delta, B_{\text{max}}]^{2k})^2$  that

$$\begin{aligned} \sum_{(J,M) \in \mathcal{A}(x,y)} p_{J,M}(x, y) &= \left( \prod_{\substack{i \in \llbracket 1, 2k \rrbracket \\ x_i \in [-\delta, 0)}} q(x_i) \right) \left( \prod_{\substack{i \in \llbracket 1, 2k \rrbracket \\ x_i \in (B_{\text{max}} - \Delta, B_{\text{max}}]}} (1 - q(x_j)) \right) \\ &\times \left( \prod_{\substack{i \in \llbracket 1, 2k \rrbracket \\ y_i \in [-\delta, 0)}} q(y_i) \right) \left( \prod_{\substack{i \in \llbracket 1, 2k \rrbracket \\ y_i \in (B_{\text{max}} - \Delta, B_{\text{max}}]}} (1 - q(y_j)) \right) \geq \frac{(\frac{\Delta - \delta}{\Delta})^{2k} + \frac{1}{2}}{2 \left(\frac{\Delta - \delta}{\Delta}\right)^{2k}}. \end{aligned} \quad (5.3.5)$$

Now, we are able to verify (S2.1). We denote  $(x, y) \in ([-\delta, B_{\text{max}}]^{2k})^2$  the telomere lengths, after shortening but before lengthening, of two daughter cells of a cell that divides. If the two following hold:

- The coordinates where there is a lengthening are indexed by a pair of sets  $(J, M) \in \mathcal{A}(x, y)$ ,
- The coordinates  $i \in \llbracket 1, 2k \rrbracket$  such that  $x_i < 0$  or  $y_i < 0$ , are lengthened by a value greater than  $\delta$ ,

we easily have that the telomere lengths of the daughter cells stay in  $[0, B_{\text{max}}]^{2k} = K_{\text{renew}}$  after lengthening. In view of the two points above, in (5.3.6), we do the following steps:

1. We bound from below the sum of the pairs  $(J, M)$  over  $\mathcal{J}_k$  by a sum of  $(J, M)$  over  $\mathcal{A}(x - \alpha_1, y - \alpha_1)$ , and apply (5.3.5).
2. We restrict the integrals for the measures  $h((\beta_1)_i)d(\beta_1)_i$  or  $h((\beta_2)_i)d(\beta_2)_i$  (see (2.2.7)) on the interval  $[\delta, \Delta]$  for the coordinates where there is a shortening. The function  $1_{\{x - \alpha_1 + \beta_1 \in K_{\text{renew}}\}}$  is equal to 1 on this domain of integration by the two points presented above.



3. We integrate in  $\beta$ . As there are  $2k$  coordinates in the two daughter cells that are shortened at each division, see (2.2.4) and (2.2.5), and as  $h$  is the uniform distribution, the integral is bounded from below by  $\left(\frac{\Delta-\delta}{\Delta}\right)^{2k}$ .
4. We integrate in  $\alpha$ , using the fact that the measures  $(\mu^{(S,I)})_{I \in \mathcal{I}_k}$  are probability measures, and simplify  $\frac{1}{\#\mathcal{I}_k}$  by  $\sum_{I \in \mathcal{I}_k}$ .

It comes

$$\begin{aligned} \mathcal{K}(1_{K_{\text{renew}}})(x) &= \frac{2}{\#\mathcal{I}_k} \sum_{I \in \mathcal{I}_k} \sum_{(J,M) \in \mathcal{J}_k} \int_{(\alpha_1, \alpha_2) \in (\mathbb{R}_+^{2k})^2} p_{J,M}(x - \alpha_1, x - \alpha_2) \\ &\quad \left[ \int_{(\beta_1, \beta_2) \in (\mathbb{R}_+^{2k})^2} 1_{\{x - \alpha_1 + \beta_1 \in K_{\text{renew}}\}} d\mu_{(x - \alpha_1, x - \alpha_2)}^{(E,J,M)}(\beta_1, \beta_2) \right] d\mu^{(S,I)}(\alpha_1, \alpha_2) \quad (5.3.6) \\ &\geq 2 \left(\frac{\Delta - \delta}{\Delta}\right)^{2k} \frac{\left(\frac{\Delta - \delta}{\Delta}\right)^{2k} + \frac{1}{2}}{2 \left(\frac{\Delta - \delta}{\Delta}\right)^{2k}} = \left(\frac{\Delta - \delta}{\Delta}\right)^{2k} + \frac{1}{2}. \end{aligned}$$

Then, as  $\left(\frac{\Delta - \delta}{\Delta}\right)^{2k} + \frac{1}{2} > 1$  by (5.3.1), we obtain that  $(S_{2.1})$  is verified with  $D = 1$  and  $\varepsilon_0 = \left(\frac{\Delta - \delta}{\Delta}\right)^{2k} - \frac{1}{2}$ .

**Some biological perspectives.** Our study has provided theoretical guarantees for the existence of a stationary profile. Thus, it helps to improve the rigour of the previous study of this phenomenon [56], which developed a simplified model and carried out numerical simulations to obtain the stationary profile without proving its existence in more general cases. This is all the more important that this stationary profile is used as a preliminary step for the models of senescence further developed in [11, 38, 44]. To continue this study, a new question can be raised: Under which conditions the marginals of the stationary profile of our model over each coordinate are, at least approximately, independent and identically distributed? In other words, recalling the function  $N_0 \in L^1(\Psi)$  in the expression of the stationary profile, see Theorem 2.7, under which condition we have the existence of  $n_0 \in L^1(\mathbb{R}_+)$ , such that for all  $x \in \mathbb{R}_+^{2k}$

$$N_0(x) \approx \prod_{i=1}^{2k} n_0(x_i).$$

This approximation was made in the previous studies of this phenomenon, so obtaining theoretical guarantees for it will further improve the rigour behind these studies. However, it should be noted that telomeres on the same chromosome (at coordinates  $i$  and  $i + k$ ) are not independent during shortening: both telomeres cannot be shortened simultaneously. Consequently, it seems not trivial to justify that such an approximation is possible, and further numerical/mathematical studies must be done to obtain a good justification. This question is the subject of a future work

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## A Proof of the statements given in Section 3

### A.1 Proof of Lemma 3.1

Let  $T > 0$ , and  $(x, a) \in \mathcal{X}$ . We suppose that  $Y_0 = \delta_{(1,x,a)}$ . For all  $p \in \mathbb{N}^*$  we consider  $h_p \in \mathcal{C}_b^{1,m,m,1}(\mathbb{R}_+ \times \mathcal{U} \times \mathcal{X})$  such that for all  $(s, u, x, a) \in \mathbb{R}_+ \times \mathcal{U} \times \mathcal{X}$

$$h_p(s, u, x, a) = \left[ \mathcal{V}(x) 1_{\{x \in [0,p]^{2k}\}} + \mathcal{V}_{\min} 1_{\{x \notin [0,p]^{2k}\}} \right] \\ \times \left[ e^a 1_{\{a \in [0,p]\}} + \left( e^p + e^p \frac{2 \sin\left(\frac{\pi}{2}(a-p)\right)}{\pi} \right) 1_{\{a \in (p,p+1)\}} + \left( e^p + \frac{2e^p}{\pi} \right) 1_{a \geq p+1} \right].$$

It is easy to check that  $h_p$  and  $\frac{\partial h_p}{\partial a}$  are bounded by  $\psi_e$ , and that  $(h_p)_{p \geq 0}$  is an increasing sequence of functions which converges pointwise to  $e^a \mathcal{V}$ . First, we apply (2.2.10), (2.2.3), (2.2.11), and (2.3.5) to obtain

$$\mathbb{E} \left[ \sum_{u \in V_T} h_p(s, u, x^u, a_s^u) \right] \leq \psi_e(x, a) + \mathbb{E} \left[ \int_{s \in [0,T]} \sum_{u \in V_s} \frac{\partial h_p}{\partial a}(s, u, x^u, a_s^u) ds \right] \\ + 2(1 + \varepsilon_1) \mathbb{E} \left[ \int_{s \in [0,T]} \sum_{u \in V_{s-}} b(x^u, a_{s-}^u) \mathcal{V}(x^u) ds \right].$$

Then, we use inequality  $\left| \frac{\partial h_p}{\partial a} \right| \leq \psi_e$ , Eq. (2.2.1), and Tonelli’s theorem to have

$$\mathbb{E} \left[ \sum_{u \in V_T} h_p(s, u, x^u, a_s^u) \right] \leq \psi_e(x, a) + \int_{s \in [0,T]} \mathbb{E} \left[ \sum_{u \in V_s} \psi_e(x^u, a_s^u) \right] ds \\ + 2(1 + \varepsilon_1) \tilde{b} \int_{s \in [0,T]} \mathbb{E} \left[ \sum_{u \in V_{s-}} \mathcal{V}(x^u) (1 + (a_{s-}^u)^{d_b}) \right] ds.$$

Finally, we use the fact that there exists  $C_{d_b} > 0$  such that  $1 + a^{d_b} \leq C_{d_b} e^a$ , and we let  $p$  go to infinity by using the monotone convergence theorem to get

$$M_T(\psi_e)(x, a) \leq \psi_e(x, a) + (1 + 2\tilde{b}(1 + \varepsilon_1)C_{d_b}) \int_{s \in [0,T]} M_s(\psi_e(x, a)) ds.$$

Apply Gronwall’s lemma to conclude the proof.  $\square$

### A.2 Proof of Lemma 3.3

1. This statement is immediate thanks to Lemma 3.1 and the fact that for every function  $f \in \cup_{\psi \in \Psi} \mathcal{B}(\psi)$ , there exists  $C_f > 0$  such that for all  $(x, a) \in \mathcal{X}$  it holds  $|f(x, a)| \leq C_f \mathcal{V}(x) e^a$ .
2. The semigroup property is a direct consequence of the branching Markov property. The positivity of this semigroup is trivial. To obtain the equation of the semigroup, first condition with respect to the first event of division in Eq. (2.2.10) and use the strong Markov property. Then, apply (2.2.3) and (2.2.9). It comes for all  $t \geq 0$ ,  $(x, a) \in \mathcal{X}$  and  $f \in \cup_{\psi \in \Psi} \mathcal{B}(\psi)$

$$\begin{aligned}
M_t f(x, a) &= f(x, a + t) \exp\left(-\int_a^{a+t} b(x, u) du\right) + 2 \int_0^t b(x, a + s) \exp\left(-\int_a^{a+s} b(x, u) du\right) \\
&\quad \times \left[ \int_{(w_1, w_2) \in (\mathbb{R}^{2k})^2} M_{t-s} f(x + w_1, 0) 1_{\{x+w_1 \in \mathbb{R}_+^{2k}\}} d\Pi_x(w_1, w_2) \right] ds.
\end{aligned}$$

In view of Remark 3.2, it follows directly that the lemma is proved from the above equation.  $\square$

### A.3 Proof of Lemma 3.4

Let  $\psi \in \Psi$ . We prove each inequality one by one.

i) First, as for all  $(x, a) \in \mathcal{X}$ :  $\psi(x, a) = \mathcal{V}(x)(1 + d^\psi)$ , we easily have that

$$\frac{\frac{\partial}{\partial a} \psi(x, a)}{\psi(x, a)} + b(x, a) \frac{\mathcal{K}(\psi(\cdot, 0))(x)}{\psi(x, a)} - b(x, a) = \frac{d_\psi a^{d_\psi - 1}}{1 + a^{d_\psi}} + b(x, a) \left[ \frac{\mathcal{K}(\mathcal{V})(x)}{\mathcal{V}(x)(1 + a^{d_\psi})} - 1 \right].$$

It is well-known that there exists a constant  $C_\psi > 0$  such that for all  $a \in \mathbb{R}_+$  it holds  $\frac{d_\psi a^{d_\psi - 1}}{1 + a^{d_\psi}} \leq C_\psi$ . Then, using the latter, (2.3.5) and (2.2.1), we obtain

$$\frac{\frac{\partial}{\partial a} \psi(x, a)}{\psi(x, a)} + b(x, a) \frac{\mathcal{K}(\psi(\cdot, 0))(x)}{\psi(x, a)} - b(x, a) \leq C_\psi + 2\tilde{b}(1 + \varepsilon_1) \frac{1 + a^{d_b}}{1 + a^{d_\psi}}.$$

As  $d_\psi \geq d_b$  (see (2.3.3)), there exists  $C'_\psi$  such that for all  $a \geq 0$  it holds  $\frac{1 + a^{d_b}}{1 + a^{d_\psi}} \leq C'_\psi$ . Thus, the first inequality of the lemma is proved for  $\lambda_\psi > C_\psi + 2\tilde{b}(1 + \varepsilon_1)C'_\psi$ .

ii) The proof of the second statement is very similar to the proof of the first one. Let  $(x, a) \in \mathcal{X}$ . First, use the inequality  $\frac{d_\psi a^{d_\psi - 1}}{1 + a^{d_\psi}} \leq C_\psi$  and Eq. (2.2.1). Then, use the inequality  $\frac{1 + a^{d_b}}{1 + a^{d_\psi}} \leq C'_\psi$ . It comes

$$\frac{\frac{\partial}{\partial a} \psi(x, a)}{\psi(x, a)} + 2 \frac{b(x, a)}{\psi(x, a)} - b(x, a) \leq C_\psi + \frac{2\tilde{b}(1 + a^{d_b})}{\mathcal{V}(x)(1 + a^{d_\psi})} \leq C_\psi + \frac{2\tilde{b}C'_\psi}{\mathcal{V}(x)}.$$

Using the third statement of (S2.2), we now conclude that the first and second statements of this lemma are true for  $\lambda_\psi > \max\left(C_\psi + 2\tilde{b}C'_\psi(1 + \varepsilon_1), C_\psi + \frac{2\tilde{b}C'_\psi}{\mathcal{V}_{\min}}\right)$ .

iii) For all  $(x, a) \in \mathcal{X}$ ,  $s \geq 0$

$$\frac{\psi(x, s + a)}{\psi(x, s)} = \frac{1 + (a + s)^{d_\psi}}{1 + s^{d_\psi}} = 1 + \frac{(a + s)^{d_\psi} - s^{d_\psi}}{1 + s^{d_\psi}} \leq 1 + \sum_{j=1}^{d_\psi} \binom{d_\psi}{j} \frac{s^{d_\psi - j}}{1 + s^{d_\psi}} a^j.$$

As  $s \mapsto \frac{s^{d_\psi - j}}{1 + s^{d_\psi}}$  is bounded when  $j \in \llbracket 1, d_\psi \rrbracket$ , we easily obtain from this inequality that the third statement of the lemma is true, which concludes the proof of the lemma.  $\square$

### A.4 Proof of Lemma 3.5

The proof is based on a fixed point argument. Let  $\tilde{T} > 0$ . We endow  $M_b([0, \tilde{T}] \times \widehat{\mathcal{X}})$  with the supremum norm. By Remark 3.2 and (2.3.5), we have that for all  $z = (t, x, a, n, \tilde{I}, \tilde{J}) \in [0, \tilde{T}] \times \widehat{\mathcal{X}}$ , and  $(g_1, g_2) \in \left(M_b([0, \tilde{T}] \times \widehat{\mathcal{X}})\right)^2$

$$|\Gamma_f(g_1 - g_2)(z)| \leq 2(1 + \varepsilon_1) \|g_1 - g_2\|_\infty \mathcal{V}(x) \left[ \int_0^t \frac{b(x, a + s)}{\psi(x, a)} \exp\left(-\int_a^{a+s} b(x, u) du - \lambda_\psi s\right) ds \right]. \quad (\text{A.4.1})$$

In addition, by (2.2.1), the fact that  $d_\psi \geq d_b$  and then the third statement of Lemma 3.4, there exists  $C_\psi > 0$  such that for all  $(x, a, s) \in \mathcal{X} \times \mathbb{R}_+$  it holds  $\frac{b(x, a+s)}{\psi(x, a)} \leq \frac{\tilde{b}C_\psi(1+(a+s))^{d_\psi}}{\mathcal{V}(x)(1+a^{d_\psi})} \leq \frac{\tilde{b}C_\psi\bar{\psi}(1+s^{d_\psi})}{\mathcal{V}(x)}$ . Plugging this inequality in (A.4.1) yields

$$\|\Gamma_f(g_1) - \Gamma_f(g_2)\|_\infty \leq 2\tilde{b}C_\psi\bar{\psi}(1 + \varepsilon_1)\|g_1 - g_2\|_\infty \int_0^{\tilde{T}} (1 + s^{d_\psi})ds.$$

Choosing  $\tilde{T}$  such that  $\int_0^{\tilde{T}} (1 + s^{d_\psi})ds < \frac{1}{2\tilde{b}C_\psi\bar{\psi}(1 + \varepsilon_1)}$ , by the Banach fixed point theorem we have that there exists a unique solution  $\bar{f}$  to the equation  $\Gamma_f(\bar{f}) = \bar{f}$ . Then, as usual, iterating this procedure on  $[\tilde{T}, 2\tilde{T}]$ ,  $[2\tilde{T}, 3\tilde{T}]$  etc... yields that for all  $T > 0$ , we have a unique solution to  $\Gamma(\bar{f}) = \bar{f}$  in  $M_b([0, T] \times \widehat{\mathcal{X}})$ .

To obtain that this solution is in  $\mathcal{S} := \mathcal{C}^0([0, T], \mathcal{C}_0(\widehat{\mathcal{X}}))$  when  $f \in \mathcal{C}_0(\widehat{\mathcal{X}})$ , we only have to do the same steps as above with  $\Gamma_f$  defined on  $\mathcal{S}$  instead of  $M_b([0, T] \times \widehat{\mathcal{X}})$  and conclude by uniqueness. To do these steps, we need to verify that for all  $F \in \mathcal{S}$  and  $f \in \mathcal{C}_0(\widehat{\mathcal{X}})$  it holds  $\Gamma_f(F) \in \mathcal{S}$ . Let us do it. We fix  $f \in \mathcal{C}_0(\widehat{\mathcal{X}})$  and  $F \in \mathcal{S}$ . We first sketch that the  $\Gamma_f(F)$  is continuous. Let  $(\tilde{t}, \tilde{x}, \tilde{a}, \tilde{n}) \in [0, T] \times \mathcal{X} \times \mathbb{N}$ . We denote for all  $r \in \mathbb{R}$  the set  $A(r) = \{y \in [0, \Delta] \mid x \mapsto h(x, y) \text{ is continuous in } r\}$ . Let  $(I, J, M) \in \mathcal{I}_k \times \mathcal{J}_k$ ,  $s \in \mathbb{R}_+ \setminus \{t_1\}$ ,  $(\alpha_1, \alpha_2) \in ([0, \delta]^{2k})^2$  and  $\beta_1 \in [0, \Delta]^{2k}$  verifying that

$$\#\{i \in \llbracket 1, 2k \rrbracket \mid \tilde{x}_i - (\alpha_1)_i + (\beta_1)_i = 0 \text{ or } (i \in J \text{ and } (\beta_1)_i \notin A(\tilde{x}_i - (\alpha_1)_i))\} = 0,$$

when  $(I, J) \neq (\emptyset, \emptyset)$ , and verifying that  $\alpha_1 = \beta_1 = 0$  when  $(I, J) = (\emptyset, \emptyset)$ . By (S1.4) and the fact that  $F$  is continuous, we have that the function defined for all  $(t, x, a, n) \in \mathcal{X} \times \mathbb{R}_+ \times \mathbb{N}$  as

$$\begin{aligned} g_{s, \alpha_1, \beta_1}(x, a, t, n) &= b(x, a + s) \exp\left(-\int_a^{a+s} b(x, v)dv\right) F(t - s, x - \alpha_1 + \beta_1, 0, n + 1, I, J) \\ &\times \mathcal{V}(x - \alpha_1 + \beta_1) p_{J, M}(x - \alpha_1, x - \alpha_2) \left(\prod_{i \in I} g((\alpha_1)_i)\right) \left(\prod_{j \in J} h(x_j - (\alpha_1)_j, (\beta_1)_j)\right) \mathbf{1}_{\{s \leq t\}} \mathbf{1}_{\{x - \alpha_1 + \beta_1 \in \mathbb{R}_+^{2k}\}} \end{aligned}$$

is continuous in  $(\tilde{t}, \tilde{x}, \tilde{a}, \tilde{n})$ . Therefore, by the condition on  $h$  given in (S1.4), the set

$$\{(s, \alpha_1, \alpha_2, \beta_1) \mid g_{s, \alpha_1, \alpha_2, \beta_1} \text{ is discontinuous at } (\tilde{t}, \tilde{x}, \tilde{a}, \tilde{n})\}$$

is negligible with respect to the measure  $ds d\mu^{(S, I)}(\alpha_1, \alpha_2) \left(\prod_{j \in J} d(\beta_1)_j\right) \left(\prod_{j \notin J} \delta_0(d(\beta_1)_j)\right)$ . In addition, in view of (S1.3) and (S2.2), the function  $g_{s, \alpha_1, \alpha_2, \beta_1}$  is bounded from above on every compact set. Then, by a domination argument and by summing over  $(I, J, M) \in \mathcal{I}_k \times \mathcal{J}_k$ , we have that the second term of  $\Gamma_f(F)$  is continuous. One can also obtain by the continuity of  $f$ ,  $\psi$  and  $b$  that the first term of  $\Gamma_f(F)$  is continuous. Then, the function  $\Gamma_f(F)$  is continuous.

Now, it remains to prove that Eq. (3.2.3) is true for  $G = \Gamma_f(F)$ . Let us prove it by bounding from above  $\Gamma_f(F)$ . We fix  $z = (t, x, a, n, \tilde{I}, \tilde{J}) \in [0, T] \times \widehat{\mathcal{X}}$ . First, by Lemma 3.4, we bound from above the first term of  $\Gamma_f(F)(z)$  by  $|f(x, a + t, n, \tilde{I}, \tilde{J})| (1 + t^{d_\psi})$ . Then, in view of the fact that the maximum shortening and lengthening values are respectively  $\delta$  and  $\Delta$ , we use the fourth statement of (S2.2) to bound from above the ratio  $\mathcal{V}(x + u)\psi(x, a)$  in the second term of  $\Gamma_f(F)(z)$  by  $\frac{C_V}{1 + a^{d_\psi}}$ . Finally, we take the supremum in the first variable of  $F$  in the second term of  $\Gamma_f(F)(z)$ , and use the fact that  $\int_0^t b(x, a + s) \exp\left(-\int_a^{a+s} b(x, u)du\right) ds \leq 1$ . It comes

$$\begin{aligned} |\Gamma_f(F)(z)| &\leq |f(x, a + t, n, \tilde{I}, \tilde{J})| (1 + t^{d_\psi}) \\ &+ \frac{2C_V}{1 + a^{d_\psi}} \sum_{(I, J) \in \mathcal{Q}_k} \int_{u \in \mathbb{R}^{2k}} \sup_{r \in [0, t], (i, j) \in \mathcal{Q}_k} (F(r, x + u, 0, n + 1, i, j)) \mathbf{1}_{\{x + u \in \mathbb{R}_+^{2k}\}} d\pi_x^{I, J}(u). \end{aligned}$$

We recall that as  $F \in \mathcal{S}$ , Eq. (3.2.3) is true with  $G = F$ . We also recall that as  $\delta$  is the maximum shortening value, for all  $(I, J) \in \mathcal{Q}_k$  it holds  $\pi_x^{I, J}(\{u \in \mathbb{R}_+^{2k} \mid \exists i \in \llbracket 1, 2k \rrbracket \text{ s.t. } u_i \leq -\delta\}) = 0$ . Combining



these two results, we obtain that the second term of the above vanishes when  $\|(x, n)\|_\infty \rightarrow +\infty$ . As  $F$  is bounded, as  $(\pi^{I,J})_{I,J \in \mathcal{Q}_k}$  are probability measures, and as  $1 + a^{d_\psi}$  goes to infinity when  $a \rightarrow +\infty$ , the second term also vanishes when  $a \rightarrow +\infty$ . Then, we have that the second term vanishes when  $\|(x, a, n)\|_\infty \rightarrow +\infty$ . The latter and the fact that  $f \in \mathcal{C}_0(\mathcal{X} \times \mathcal{Q}_k)$  yields that  $\Gamma_f(F)$  verifies (3.2.3). Then, we have that  $\Gamma_f(F) \in \mathcal{S}$  which concludes the proof of the lemma.  $\square$

## B Proof of Proposition 4.2

This section is devoted to the of the proof of the Doeblin conditon presented in Section 4.2. First, in Sections B.1 and B.2, we prove the two following statements. They correspond to the first two steps of the proof of (A<sub>1</sub>), see Section 4.2. Then, we prove Proposition 4.2 in Section B.3.

**Lemma B.1** (Local Doeblin conditions in balls of radius  $r$ ). *Assume that (S<sub>1.1</sub>), (S<sub>1.2</sub>), and (S<sub>2.2</sub>) hold. Let us fix  $l \geq 1$ . Then, there exists  $L \geq l + 2m_0$ , such that for all  $t \in [(l + 2(m_0 - 1) + 1)a_0, (l + 2m_0)a_0]$ , there exists  $C(t) > 0$  such that for all  $x_I \in \mathcal{D}_l$  and  $x' \in B(x_I, r) \cap \mathcal{D}_l$ , a  $(r, l, L, t, C(t))$ -Doeblin condition holds from  $x_I$  to  $x'$ .*

**Lemma B.2** (Transfer of local Doeblin conditions). *Assume that (S<sub>1.1</sub>), (S<sub>1.2</sub>) and (S<sub>2.2</sub>) hold. Let us fix  $l \geq 1$ . Then, there exist  $L \geq l + 2m_0$  and  $t_a, c_a > 0$ , such that for all  $(x_I, x_F) \in (\mathcal{D}_l)^2$ ,  $t > 0$ , if  $(t, x_F) \in R_{l,L}^{x_I}(c)$ , then*

$$\{t + t_a\} \times (B(x_F, r) \cap \mathcal{D}_l) \subset R_{l,L}^{x_I}(c.c_a).$$

### B.1 Proof of Lemma B.1

In this proof, we mostly use the objects introduced in Assumption (S<sub>1</sub>). We use the convention that for all sequence  $(u_n)_{n \in \mathbb{N}}$  and  $(n_1, n_2) \in \mathbb{N}^2$  such that  $n_2 < n_1$ , we have  $\sum_{n_1}^{n_2} u_n = 0$ . We also use the convention that  $[0, \delta]^0 = \{\emptyset\}$  and that for all  $n \in \mathbb{N}^*$ ,  $C \in \mathcal{B}(\mathbb{R}^n)$  and  $f : [0, \delta]^0 \times \mathbb{R}^n \rightarrow \mathbb{R}$  measurable:

$$\int_{\tilde{u} \in [0, \delta]^0} \int_{\tilde{v} \in C} f(\tilde{u}, \tilde{v}) d\tilde{u} d\tilde{v} = \int_{\tilde{v} \in C} f(\tilde{u}, \tilde{v}) d\tilde{v}.$$

To simplify notations, we finally denote  $\kappa = \min_{x \in \mathcal{D}_l}(\Delta_x)$ , and notice that with this notation we have  $r = \min\left(\frac{B_{\max}}{2}, \frac{\min(\delta, \kappa)}{10}\right)$ .

Let  $l \geq 1$  and  $L \geq l + 2m_0$  such that  $B_{\max}L \geq B_{\max}l + m_0\Delta$ . We begin with some preliminaries. We first consider  $p_{\min} > 0$  that verifies the statement of (S<sub>1.2</sub>) with  $A = B_{\max}L$ , and the following constants, for all  $t \geq 0$ :

$$\begin{aligned} C_1(t) &= \left[ \frac{2b_0 V_{\min}}{(\sup_{y \in \mathcal{D}_L} \mathcal{V}(y)) (1 + (a_0 L)^{d_\psi})} \right]^{m_0} \exp\left(- (m_0 + 1)(\lambda_\psi + \tilde{b}(1 + (a_0 L)^{d_b}))t\right), \quad \forall t \geq 0, \\ C_2 &= \left[ \frac{p_{\min}(g_{\min})^k (h_{\min})^{2k}}{\#(\mathcal{I}_k)} \right]^{m_0}. \end{aligned} \tag{B.1.1}$$

These constants are useful to obtain lower bounds. In view of (S<sub>1.2</sub>), we then define for all  $j \in \llbracket 1, 2k \rrbracket$

$$\gamma_j := \# \{n \in \llbracket 1, m_0 \rrbracket \mid j \in \mathbb{I}^n\}, \quad \omega_j := \# \{n \in \llbracket 1, m_0 \rrbracket \mid j \in \mathbb{J}^n\}.$$

They correspond respectively to the number of times the telomere associated to the coordinate  $j$  is shortened and the number of times it is lengthened on the event  $\{(I_l, J_l)_{l \in \llbracket 1, m_0 \rrbracket} = (\mathbb{I}^l, \mathbb{J}^l)_{l \in \llbracket 1, m_0 \rrbracket}\}$ . By (S<sub>1.2</sub>), it holds  $\omega_j \geq \gamma_j \geq 1$ . We finally define for all  $j \in \llbracket 1, 2k \rrbracket$ ,  $(y, s) \in \mathbb{R}_+ \times \mathbb{R}$ ,  $(u, v) \in [0, \delta]^{\gamma_j - 1} \times [0, \kappa]^{\omega_j}$  the following:

$$\begin{aligned} g_{j,1}(y, s, u, v) &= \mathbb{1}_{\left\{s \in \left[-\delta + \sum_{i=1}^{\gamma_j-1} (v_i - u_i) + \sum_{i=\gamma_j}^{\omega_j} v_i, \sum_{i=1}^{\gamma_j-1} (v_i - u_i) + \sum_{i=\gamma_j}^{\omega_j} v_i\right]\right\}}, \\ g_{j,2}(y, s, u, v) &= \left( \mathbb{1}_{\{\forall l \in \llbracket 1, \gamma_j - 1 \rrbracket: y + \sum_{i=1}^l (v_i - u_i) \geq 0\}} \mathbb{1}_{\{\gamma_j \geq 2\}} + \mathbb{1}_{\{\gamma_j = 1\}} \right) \mathbb{1}_{\left\{y + s - \sum_{i=\gamma_j+1}^{\omega_j} v_i \geq 0\right\}}, \\ F_j(y, s) &= \int_{\tilde{u} \in [0, \delta]^{\gamma_j - 1}} \int_{\tilde{v} \in [0, \kappa]^{\omega_j}} g_{j,1}(y, s, \tilde{u}, \tilde{v}) g_{j,2}(y, s, \tilde{u}, \tilde{v}) d\tilde{u} d\tilde{v}. \end{aligned} \tag{B.1.2}$$



The function  $F_j(y, \cdot)$  is a lower bound for the density of telomere length variation in the  $j$ -th coordinate of the particle  $(Z_t)_{t \geq 0}$  on the event  $\left\{N_t = m_0, (I_l, J_l)_{l \in \llbracket 1, m_0 \rrbracket} = (\mathbb{I}^l, \mathbb{J}^l)_{l \in \llbracket 1, m_0 \rrbracket}\right\}$  when the initial length of the telomere is  $y$ . Let us explain why. First, we notice that the integral  $\int_{\tilde{u} \in [0, \delta]^{\gamma_j - 1}} \int_{\tilde{v} \in [0, \kappa]^{\omega_j}} g_{j,1}(y, s, \tilde{u}, \tilde{v}) d\tilde{u} d\tilde{v}$  corresponds to the convolution between  $\omega_j$  times the function  $1_{[0, \kappa]}(s)$  and  $\gamma_j$  times the function  $1_{[0, \delta]}(-s)$ . Second, we have by (S1.2) that the probability density functions for the shortening and lengthening values, namely  $g$  and  $(h(x, \cdot))_{x \in \mathbb{R}}$ , are bounded from below on  $[0, \delta]$  and  $[0, \kappa]$  respectively. Finally, we recall that the probability density function of the sum of random variables is given by the convolution of their densities. By these three results, we obtain that  $\int_{\tilde{u} \in [0, \delta]^{\gamma_j - 1}} \int_{\tilde{v} \in [0, \kappa]^{\omega_j}} g_{j,1}(y, s, \tilde{u}, \tilde{v}) d\tilde{u} d\tilde{v}$  is, up to a constant, a lower bound for the probability density function of the sum of  $\gamma_j$  random variables of shortening and  $\omega_j$  random variables of lengthening.

However, there is another constraint that we need to take into account: during the first  $m_0$  jumps, the length of this telomere must remain nonnegative (otherwise there is extinction of the particle). The conditions for the variables  $y, u$  and  $v$  in the indicators of the function  $g_{j,2}$  allow to handle this. Indeed, they mean that the length of the telomere must remain nonnegative when one of the  $\gamma_j$  events where there is a shortening occurs (there is also a lengthening at these events as for all  $i \in \llbracket 1, m_0 \rrbracket$  it holds  $\mathbb{I}^i \subset \mathbb{J}^i$ ). We do not need any condition for the other events because the length of the telomere cannot become negative when they occur (as there is no shortening). The latter, the above paragraph, and the fact that  $F_j$  is the integral of  $g_{j,1}g_{j,2}$  yield that  $F_j(y, \cdot)$  corresponds to the lower bound stated above.

Now, let  $t \in [(l + 2(m_0 - 1) + 1)a_0, (l + 2m_0)a_0]$ ,  $x_I \in \mathcal{D}_l$ ,  $(x, x') \in (B(x_I, r) \cap \mathcal{D}_l)^2$ ,  $a \in [0, a_0]$ , and  $f$  a bounded measurable function such that  $f \geq 0$ . We know that it holds  $L \geq l + 2m_0$ ,  $t \leq (l + 2m_0)a_0$ ,  $B_{\max}L \geq B_{\max}l + m_0\Delta$ , and that  $\Delta$  is the maximum lengthening value. Thus, if  $m_0$  jumps have occurred during the interval of time  $[0, t]$ , if the time before the first jumps is smaller than  $2a_0$ , and if the particle has not jumped to the cemetery, then the particle  $(Z_t)_{t \geq 0}$  stays in  $D_L$  during all the interval of time  $[0, t]$ . In particular, the following holds

$$\begin{aligned} \mathbb{E}_{(x,a)} [f(Z_t); t < \min(\tau_\partial, T_{D_L})] &\geq \mathbb{E}_{(x,a)} \left[ f(X_{m_0}, t - \mathcal{J}_{m_0}); N_t = m_0, \forall i \in \llbracket 1, m_0 \rrbracket : (I_i, J_i) = (\mathbb{I}^i, \mathbb{J}^i) \right. \\ &\quad \left. \forall i \in \llbracket 1, m_0 - 1 \rrbracket : \mathcal{J}_i - \mathcal{J}_{i-1} \in [a_0, 2a_0], \mathcal{J}_{m_0} - \mathcal{J}_{m_0-1} \in [a_0, t - \mathcal{J}_1] \right]. \end{aligned} \quad (\text{B.1.3})$$

Now, we use Lemma 3.11 to develop the right-hand side term of the above equation and obtain

$$\begin{aligned} \mathbb{E}_{(x,a)} [f(Z_t); t < \min(\tau_\partial, T_{D_L})] &\geq \int_{[a_0, 2a_0] \times \mathbb{R}^{2k}} \cdots \int_{[a_0, 2a_0] \times \mathbb{R}^{2k}} \int_{[a_0, t - \sum_{i=1}^{m_0-1} s_i] \times \mathbb{R}_+^{2k}} \\ &\times f \left( x + \sum_{i=1}^{m_0} u_i, t - \sum_{i=1}^{m_0} s_i \right) \mathcal{G}_a(x, s_1) \mathcal{G}_0(x + u_1, s_2) \cdots \mathcal{G}_0 \left( x + \sum_{i=1}^{m_0-1} u_i, s_m \right) \overline{\mathcal{H}}_0 \left( x + \sum_{j=1}^{m_0} u_j, t - \sum_{j=1}^{m_0} s_j \right) \\ &\times 1_{\{\forall j \in \llbracket 1, m_0 \rrbracket : x + \sum_{i=1}^j u_i \in \mathcal{D}_i\}} \left( \mathcal{V}(x + u_1) ds_1 d\pi_x^{\mathbb{I}^1, \mathbb{J}^1}(u_1) \right) \cdots \left( \mathcal{V} \left( x + \sum_{i=1}^{m_0} u_i \right) ds_{m_0} d\pi_{x + \sum_{i=1}^{m_0-1} u_i}^{\mathbb{I}^{m_0}, \mathbb{J}^{m_0}}(u_{m_0}) \right). \end{aligned} \quad (\text{B.1.4})$$

By (2.2.1), Assumption (S2.2) and the definition of  $\psi \in \Psi$  given in (2.3.3), we know that for all  $(w, s) \in D_L$

$$b(w, s) \leq \tilde{b}(1 + (a_0L)^{d_b}), \quad \psi(w, s) \leq \sup_{y \in \mathcal{D}_L} (\mathcal{V}(y)) (1 + (a_0L)^{d_\psi}), \quad \text{and } \mathcal{V}(w) \geq \mathcal{V}_{\min}.$$

Thus, in view of the expression of  $\mathcal{G}_a$  and  $\mathcal{G}_0$  given in (3.3.9), the expression of  $\overline{\mathcal{H}}_0$  given in (3.3.1), and the definition of the constant  $C_1(t)$  introduced in (B.1.1), one can bound from below (B.1.4) to get

$$\begin{aligned} \mathbb{E}_{(x,a)} [f(Z_t); t < \min(\tau_\partial, T_{D_L})] &\geq C_1(t) \int_{[a_0, 2a_0] \times \mathbb{R}^{2k}} \cdots \int_{[a_0, 2a_0] \times \mathbb{R}^{2k}} \int_{[a_0, t - \sum_{i=1}^{m_0-1} s_i] \times \mathbb{R}_+^{2k}} \\ &\times f \left( x + \sum_{i=1}^{m_0} u_i, t - \sum_{i=1}^{m_0} s_i \right) 1_{\{\forall j \in \llbracket 1, m_0 \rrbracket : x + \sum_{i=1}^j u_i \in \mathcal{D}_i\}} \left( ds_1 d\pi_x^{\mathbb{I}^1, \mathbb{J}^1}(u_1) \right) \cdots \left( ds_{m_0} d\pi_{x + \sum_{i=1}^{m_0-1} u_i}^{\mathbb{I}^{m_0}, \mathbb{J}^{m_0}}(u_{m_0}) \right). \end{aligned} \quad (\text{B.1.5})$$

We recall that the definition of  $(\pi_{y,J}^{I,J})_{y \in \mathbb{R}_+^{2k}, (I,J) \in \mathcal{Q}_k}$  is given in (3.1.1), and that the measures used to define it are given in (2.2.5) and (2.2.7). We continue to bound from below the left-hand side term of (B.1.5). First, we use (S1.1) (without loss of generality, we can assume that  $h_{\min} < 1$ ) and the second statement of (S1.2), and do the change of variables  $v = \sum_{i=1}^{2k} u_i$  to bound from below the measures  $\left( \pi_{x+\sum_{i=1}^{p-1} u_i}^{[p], [p]}(u_p) \right)_{p \in [1, m_0]}$  in the right-hand side term of (B.1.5) by the measure  $C_2 \cdot \prod_{i=1}^{2k} F_i(v_i) dv_i$  (see (B.1.1) and (B.1.2)). Then, we do the change of variables  $w = v + x - x'$ . Finally, we restrict the domain of integration on  $[-r, r]^{2k}$ . It comes

$$\begin{aligned} \mathbb{E}_{(x,a)} [f(Z_t); t < \min(\tau_\partial, T_{D_L})] &\geq C_1(t) C_2 \int_{w \in [-r, r]^{2k}} \int_{[a_0, 2a_0]} \cdots \int_{[a_0, 2a_0]} \int_{[a_0, t - \sum_{i=1}^{m_0-1} s_i]} \\ &\times f \left( x' + w, t - \sum_{i=1}^{m_0} s_i \right) 1_{\{x'+w \in \mathbb{R}_+^{2k}\}} F_1(x_1, (w+x'-x)_1) \dots F_{2k}(x_{2k}, (w+x'-x)_{2k}) dw ds. \end{aligned} \quad (\text{B.1.6})$$

To continue our computations, we now obtain lower bounds for the functions  $(F_j)_{j \in [1, 2k]}$ . Let us consider  $j \in [1, 2k]$ ,  $y \in [0, B_{\max} l]$ ,  $s \in [\max(-3r, -y), 3r]$ ,  $u \in [0, \delta]^{\gamma_j-1}$  and  $v \in [0, \kappa]^{\omega_j}$ . Assume that  $\sum_{i=1}^{\gamma_j-1} (v_i - u_i) \in [0, \frac{\min(\delta, \kappa)}{20}]$ , that  $v_{\gamma_j} \in [\frac{3 \min(\delta, \kappa)}{10}, \frac{6 \min(\delta, \kappa)}{10}]$  and that  $\sum_{\gamma_j+1}^{\omega_j} v_i \leq \frac{\min(\delta, \kappa)}{20}$ . Then, one can easily obtain that the lower bound of the interval in the indicator function used to define  $g_{j,1}$  (see (B.1.2)) is bounded from above by  $-\delta + \frac{\min(\delta, \kappa)}{20} + \frac{6 \min(\delta, \kappa)}{10} + \frac{\min(\delta, \kappa)}{20} \leq -\frac{3 \min(\delta, \kappa)}{10}$ . With similar computations, we also have that the upper bound of this interval is bounded from below by  $\frac{3 \min(\delta, \kappa)}{10}$ . Then, as  $|s| \leq 3r \leq \frac{3 \min(\delta, \kappa)}{10}$ , we get that  $g_{j,1}(y, s, u, v) = 1$ . Combining this with the fact that  $y \geq 0$  (to bound from below the first indicator in  $g_{j,2}$ ), we obtain

$$\begin{aligned} F_j(y, s) &\geq \int_{\tilde{u} \in [0, \delta]^{\gamma_j-1}} \int_{\tilde{v} \in [0, \kappa]^{\omega_j}} \left( 1_{\{\forall l \in [1, \gamma_j-1]: \sum_{i=1}^l (\tilde{v}_i - \tilde{u}_i) \in [0, \frac{\min(\delta, \kappa)}{20}]\}} 1_{\{\gamma_j \geq 2\}} + 1_{\{\gamma_j=1\}} \right) \\ &\times 1_{\{\tilde{v}_{\gamma_j} \in [\frac{3 \min(\delta, \kappa)}{10}, \frac{6 \min(\delta, \kappa)}{10}]\}} 1_{\{\sum_{i=\gamma_j+1}^{\omega_j} \tilde{v}_i \leq \min(y+s, \frac{\min(\delta, \kappa)}{20})\}} d\tilde{u} d\tilde{v}. \end{aligned}$$

Now, first observe that

$$\int_{\tilde{u} \in [0, \delta]^{\gamma_j-1}} \int_{\tilde{v} \in [0, \kappa]^{\omega_j}} \left( 1_{\{\forall l \in [1, \gamma_j-1]: \sum_{i=1}^l (\tilde{v}_i - \tilde{u}_i) \in [0, \frac{\min(\delta, \kappa)}{20}]\}} 1_{\{\gamma_j \geq 2\}} + 1_{\{\gamma_j=1\}} \right) d\tilde{u} d\tilde{v} > 0$$

because it is the integral of a nonnegative function, positive on a non negligible set. Thereafter, notice that  $\int_{\tilde{v}_{\gamma_j} \in [\frac{3 \min(\delta, \kappa)}{10}, \frac{6 \min(\delta, \kappa)}{10}]} d\tilde{v}_{\gamma_j} > 0$  for the same reason. Finally, notice that if  $\omega_j - \gamma_j \geq 1$  and for all  $i \in [\gamma_j + 1, \omega_j]$  we have  $\tilde{v}_i \leq \frac{1}{\omega_j - \gamma_j} \min(y + s, \frac{\min(\delta, \kappa)}{20})$ , then it holds that  $\sum_{i=\gamma_j+1}^{\omega_j} \tilde{v}_i \leq \min(y + s, \frac{\min(\delta, \kappa)}{20})$ . We get from these two results that there exists  $c_{j,1} > 0$ , independent of  $y$  and  $s$ , such that

$$F_j(y, s) \geq c_{j,1} \left( \left( \int_0^{\frac{1}{\omega_j - \gamma_j} \min(y+s, \frac{\min(\delta, \kappa)}{20})} du \right)^{\omega_j - \gamma_j} 1_{\{\omega_j - \gamma_j \geq 1\}} + 1_{\{\omega_j - \gamma_j = 0\}} \right). \quad (\text{B.1.7})$$

In addition, as  $y + s \in [0, B_{\max} l + 3r]$ , we have that  $\min(y + s, \frac{\min(\delta, \kappa)}{20}) \geq (y + s) \min(1, \frac{\min(\delta, \kappa)}{20(B_{\max} l + 3r)})$ . We also have by classic computations that as  $\omega_j - \gamma_j \leq m_0$ , there exists  $c_{j,2} > 0$  such that for all  $x \in [0, B_{\max} l + 3r]$  it holds  $x^{\omega_j - \gamma_j} \geq c_{j,2} x^{m_0}$ . Combining these two results with (B.1.7), we finally obtain that there exists  $c_{j,3} > 0$  such that for all  $y \in [0, B_{\max} l]$  and  $s \in [\max(-3r, y), 3r]$  we have  $F_j(y, s) \geq c_{j,3} (y + s)^{m_0}$ .

We now conclude. Let us denote  $C(t) = C_1(t) C_2 \left( \prod_{i=1}^{2k} c_{j,3} \right) (a_0)^{m-1}$ . First, we bound from below the functions  $(F_j)_{j \in [1, 2k]}$  in (B.1.6) by the bounds obtained above. Then, we do the changes of variables  $w' = x' + w$  and  $s' = t - \sum_{i=1}^{m_0} s_i$ . Finally, we use the fact that  $t - 2(m_0 - 1)a_0 - a_0 \geq la_0$ . The following comes to end the proof:

$$\begin{aligned}
\mathbb{E}_{(x,a)}[f(Z_t); t < \min(\tau_\partial, T_{D_L})] &\geq C_1(t)C_2 \left( \prod_{j=1}^{2k} c_{j,3} \right) \int_{w' \in B(x',r)} \int_{[a_0, 2a_0]} \cdots \int_{[a_0, 2a_0]} \int_{[0, t - \sum_{i=1}^{m_0-1} s_i - a_0]} \\
&\times f(w', s') \left( \prod_{j=1}^{2k} (w'_j)^{m_0} \right) dw' ds_1 \dots ds_{m_0-1} ds' \\
&\geq C(t) \int_{w' \in B(x',r)} \int_0^{la_0} f(w', s') \left( \prod_{j=1}^{2k} (w'_j)^{m_0} \right) dw' ds'.
\end{aligned}$$

□

## B.2 Proof of Lemma B.2

Let  $l \geq 1$ ,  $t_a = (l + 2(m_0 - 1) + 1)a_0$ , and  $C(t_a)$  its associated constant obtained by Lemma B.1 (also associated to a certain  $L \geq l$ ). We consider the constant

$$c_a = a_0 \cdot l \cdot C(t_a) \inf_{y \in \mathcal{D}_l} \left[ \int_{u \in B(y,r) \cap \mathcal{D}_l} \left( \prod_{i=1}^{2k} (u_i)^{m_0} \right) du \right]. \quad (\text{B.2.1})$$

Let  $x_I \in \mathcal{D}_l$ ,  $c > 0$ ,  $(t, x_F) \in \mathbb{R}_+^* \times \mathcal{D}_l$  such that  $(t, x_F) \in R_{l,L}^{x_I}(c)$ . By the Markov property and the definition of  $R_{l,L}^{x_I}(c)$ , we have for all  $(x, a) \in (B(x_I, r) \cap \mathcal{D}_l) \times [0, a_0 l]$

$$\begin{aligned}
\mathbb{E}_{(x,a)}[f(Z_{t+t_a}); t + t_a < \min(\tau_\partial, T_{D_L})] &\geq c \int_{u \in B(x_F, r) \cap \mathcal{D}_l} \int_0^{a_0 l} \\
&\times \left[ \int_{z \in \mathcal{X}} f(z) \mathbb{P}_{(u,s)}[Z_{t_a} \in dz; t_a \leq \min(\tau_\partial, T_{D_L})] \right] \left( \prod_{i=1}^{2k} (u_i)^{m_0} \right) dudS.
\end{aligned}$$

Now, first apply Lemma B.1 with  $x_I = u$  and  $x' = x_F$ . Then, integrate in  $du$  and  $dS$ . Finally, take the infimum. It comes

$$\mathbb{E}_{(x,a)}[f(Z_{t+t_a}); t + t_a < \min(\tau_\partial, T_{D_L})] \geq c \cdot c_a \int_{w \in B(x_F, r) \cap \mathcal{D}_l} \int_0^{a_0 l} f(w, S) \left( \prod_{i=1}^{2k} (w_i)^{m_0} \right) dw dS.$$

It remains to prove that  $c_a > 0$  to end the proof. Let  $y \in \mathcal{D}_l$ . For all  $i \in [1, 2k]$ , we consider  $u_i \in [0, r]$ . When  $y_i \leq \frac{B_{\max}}{2}l$ , as  $r \leq \frac{B_{\max}}{2}$ , we have

$$y_i \leq y_i + u_i \leq \frac{B_{\max}}{2}l + r \leq lB_{\max}.$$

Conversely, when  $y_i > \frac{B_{\max}}{2}l$ , as  $r \leq \frac{B_{\max}}{2}$ , we have

$$y_i - u_i \geq y_i - r \geq \frac{B_{\max}}{2}l - r \geq 0.$$

Hence, as  $\mathcal{D}_l = [0, B_{\max}l]^{2k}$ , one can easily obtain

$$\begin{aligned}
\int_{u \in B(y,r) \cap \mathcal{D}_l} \left( \prod_{i=1}^{2k} (u_i)^{m_0} \right) du &\geq \prod_{\substack{i \in [1, 2k], \\ y_i \in [0, \frac{B_{\max}}{2}l]}} \left[ \int_{y_i}^{y_i+r} (u_i)^{m_0} du_i \right] \prod_{\substack{j \in [1, 2k], \\ y_j \in (\frac{B_{\max}}{2}l, l]}} \left[ \int_{y_j-r}^{y_j} (u_j)^{m_0} du_j \right] \\
&\geq \left( \int_0^r v^{m_0} dv \right)^{2k} = \left( \frac{r^{m_0}}{m_0} \right)^{2k} > 0.
\end{aligned}$$

Then, in view of (B.2.1), we have that  $c_a \geq a_0 l C(t_a) \left( \frac{r^{m_0}}{m_0} \right)^{2k} > 0$ , which concludes the proof of this lemma. □

### B.3 Proof of Proposition 4.2

Let  $l \in \mathbb{N}^*$  and  $L \geq l$  sufficiently large to apply Lemma B.2. We begin with two preliminary results. First, by compactness, there exist  $J \in \mathbb{N}^*$  and  $(x^j)_{1 \leq j \leq J} \in (\mathcal{D}_l)^J$  such that

$$\bigcup_{j \in \llbracket 1, J \rrbracket} [B(x^j, r) \cap \mathcal{D}_l] = \mathcal{D}_l.$$

Second, by Lemma B.1, there exists  $(t_I, c_I) \in (\mathbb{R}_+^*)^2$  such that for all  $j \in \llbracket 1, J \rrbracket$  it holds  $(t_I, x^j) \in R_{l,L}^{x^j}(c_I)$ .

Now, we fix  $(j, j') \in \llbracket 1, J \rrbracket^2$  such that  $j \neq j'$ . As  $(t_I, x^j) \in R_{l,L}^{x^j}(c_I)$ , we need to successively apply Lemma B.2 to obtain that there exist  $t_F, c_F > 0$  such that  $(t_F, x^{j'}) \in R_{l,L}^{x^{j'}}(c_F)$ . Let  $N \in \mathbb{N}^*$  satisfying  $N > \max_{(j, j') \in \llbracket 1, J \rrbracket^2} \frac{\|x^{j'} - x^j\|_\infty}{r}$ , and  $(u_k)_{k \in \llbracket 0, N \rrbracket}$  a sequence defined as

$$\begin{cases} u_0 = x^j, \\ u_{k+1} = u_k + \frac{1}{N}(x^{j'} - x^j), \quad \forall k \in \llbracket 0, N-1 \rrbracket. \end{cases}$$

One can easily see that as  $(u_k)_{k \in \llbracket 0, N \rrbracket}$  is an arithmetic sequence:  $u_N = x^{j'}$ .

For all  $k \in \llbracket 0, N-1 \rrbracket$ , we successively apply Lemma B.2 with  $x_I = u_k$  and  $x_F = u_{k+1}$ . At each iteration, as  $u_k \in R_{l,L}^{x^j}(c_I(c_a)^k)$  and  $u_{k+1} \in (B(u_k, r) \cap \mathcal{D}_l)$ , we have

$$(t_0 + (k+1)t_a, u_{k+1}) \in R_{l,L}^{x^j}(c_I(c_a)^{k+1}).$$

As  $u_N = x^{j'}$ , we finally obtain that  $(t_0 + Nt_a, x^{j'}) \in R_{l,L}^{x^j}(c_I(c_a)^N)$ . Hence, there exist two positive constants  $t_F = t_I + Nt_a$  and  $c_F = c_I(c_a)^N$  such that for all  $(j, j') \in \llbracket 1, J \rrbracket^2$  it holds  $(t_F, x^{j'}) \in R_{l,L}^{x^{j'}}(c_F)$ . In particular, for all  $(j, j') \in \llbracket 1, J \rrbracket^2$  and  $(x, a) \in (B(x^j, r) \cap \mathcal{D}_l) \times [0, a_0 l]$ , we have

$$\mathbb{P}_{(x,a)} [Z_{t_F} \in dx' da'; \min(\tau_\partial, T_{D_L})] \geq c_F \left( \prod_{i=1}^{2k} (x'_i)^{m_0} \right) \mathbb{1}_{\{B(x^{j'}, r) \cap \mathcal{D}_l \times [0, a_0 l]\}}(x', a') dx' da'.$$

As  $\bigcup_{j' \in \llbracket 1, J \rrbracket} [B(x^{j'}, r) \cap \mathcal{D}_l] = \mathcal{D}_l$ , summing in  $j'$  in the above equation yields that Proposition 4.2 is proved.  $\square$

## C Proof of Proposition 4.12

We consider in this section  $(\mathcal{H}_n)_{n \geq 0}$  the filtration that corresponds to the augmented filtration generated by the process  $(X_n, A_n, \mathcal{F}_n, \bar{I}_n, J_n)_{n \in \mathbb{N}}$ . It contains all the information we have at the  $n$ -th generation. Each time we condition with respect to this filtration in this section, we work on an event of the form  $\{\mathcal{T}_l \leq t\}$ , where  $l \in \mathbb{N}$  and  $t > 0$ , that belongs to  $\mathcal{G}_t$ . Then, this conditioning does not pose any issues with the fact that we work with the filtration  $(\mathcal{G}_t)_{t \geq 0}$ .

The proof of Proposition 4.12 requires auxiliary statements to be introduced. In Section C.1, we present these auxiliary statements and prove the proposition. Then, we prove all the auxiliary statements in Section C.2.

### C.1 Auxiliary statements and proof of Proposition 4.12

#### C.1.1 Auxiliary statements

##### 1. Decomposition of the measure

To obtain Proposition 4.12, we first use the following statement, that allows us to decompose the measure on the left-hand side term of (4.4.13). We prove this statement in Section C.2.1.

**Lemma C.1** (Decomposition of the measure). *Assume that (S1.1) and (S1.3) hold. Then the following statement holds for all nonnegative function  $f \in M_b(\mathcal{X})$ ,  $t > 0$ ,  $(x, a) \in E$*

$$\begin{aligned} \mathbb{E}_{(x,a)} [f(Z_t); T_{all} \leq t < \tau_\partial, N_t \leq n(t)] &\leq \sum_{l=1}^{n(t)} \sum_{(i_1, i_2, \dots, i_{2k}) \in \llbracket 1, l \rrbracket^{2k}} \mathbb{E}_{(x,a)} \left[ f(X_l, t - \mathcal{I}_l); \right. \\ &\quad X_l \in [0, B_{\max} L_1 + l\Delta]^{2k}, \mathcal{I}_l \leq t, \\ &\quad \forall p \in \llbracket 1, l \rrbracket : (I_p, J_p) \neq (\partial, \partial), \\ &\quad \left. \forall j \in \llbracket 1, 2k \rrbracket : j \in I_{i_j} \cup J_{i_j} \right]. \end{aligned} \quad (\text{C.1.1})$$

We now give statements allowing to bound from above the right-hand side term of (C.1.1).

2. *Bound from above jump by jump*

Let  $t \geq 0$ . Bounding from above the right-hand side term of (C.1.1) can be done by successively conditioning with respect to  $\mathcal{H}_{n-1}$ , for all  $n \in \llbracket 1, n(t) \rrbracket$ . This reduces the problem to obtaining an upper bound jump by jump. Let  $l \in \llbracket 1, n(t) \rrbracket$  and  $i = (i_1, \dots, i_{2k}) \in \llbracket 1, l \rrbracket^{2k}$  that we keep fixed until the end of the subsection. We introduce:

- The following set for all  $m \in \llbracket 1, l \rrbracket$

$$\mathcal{C}_{m,i} := \{j \in \llbracket 1, 2k \rrbracket, i_j = m\}.$$

This set gives information about which coordinates are modified at the  $m$ -th jump.

- For all  $(I, J, p) \in \mathcal{Q}_k \times \llbracket 1, 2k \rrbracket$ , the measure  $\nu_{I,J,p}$ , defined for all  $A \in \mathcal{B}(\mathbb{R})$  as

$$\nu_{I,J,p}(A) := \begin{cases} \delta_0(A), & \text{if } p \notin I \cup J, \\ \int_{u \in [-\delta, \Delta]} 1_A(u) du, & \text{otherwise.} \end{cases}$$

This measure partially composes the measure we use to bound from above the right-hand side term of (C.1.1).

- For all  $m \in \llbracket 1, l \rrbracket$ , the measures  $\mu_{m,i}^1$ ,  $\mu_m^2$  and  $\mu_{m,i}$ , defined such that for all  $A \in \mathcal{B}(\mathbb{R}_+^{2k})$

$$\begin{aligned} \mu_{m,i}^1(A) &:= \sum_{\substack{(I,J) \in \mathcal{Q}_k, \\ \forall p \in \mathcal{C}_{m,i} : p \in I \cup J}} \left[ \int_A \left( \prod_{p \in \mathcal{C}_{m,i}} d\omega_j \right) \left( \prod_{p \notin \mathcal{C}_{m,i}} d\nu_{I,J,p}(w_p) \right) \right], \\ \mu_m^2(A) &:= \sum_{(I,J) \in \mathcal{Q}_k} \int_A \prod_{p \in \llbracket 1, 2k \rrbracket} d\nu_{I,J,p}(w_p), \end{aligned} \quad (\text{C.1.2})$$

and

$$\mu_{m,i}(A) := \begin{cases} \mu_{m,i}^1(A), & \text{if } \mathcal{C}_{m,i} \neq \emptyset, \\ \mu_m^2(A), & \text{otherwise.} \end{cases}$$

These measures are used to bound from above the right-hand side term of (C.1.1).

The following two lemmas are useful to show how we obtain an upper bound at one jump. The proof of Lemma C.2 is given in Section C.2.2. The proof of Lemma C.3 is not given as it follows the same lines of proof.

**Lemma C.2** (Upper bound when  $\mathcal{C}_{m,i} \neq \emptyset$ ). *Assume that (S1.1) and (S1.3) hold. Then for all  $l \in \mathbb{N}^*$ , there exists  $\overline{C}_1(l) > 0$  such that for all  $t \geq 0$ ,  $(m, i) \in \llbracket 1, l \rrbracket \times \llbracket 1, l \rrbracket^{2k}$  verifying  $\mathcal{C}_{m,i} \neq \emptyset$ ,  $v \in [-\delta l, \Delta l]^{2k}$ , and  $f \in M_b(\mathcal{X})$  nonnegative*

$$\begin{aligned}
& \mathbb{E}_{(x,a)} \left[ f(X_m + v, t - \mathcal{J}_m); X_m + v \in [0, B_{\max}L_1 + l\Delta]^{2k}, \mathcal{J}_m \leq t, \right. \\
& \left. (I_m, J_m) \neq (\partial, \partial), \mathcal{C}_{m,i} \subset (I_m \cup J_m) \mid \mathcal{H}_{m-1} \right] \\
& \leq \overline{C}_1(l) \int_{u \in [-\delta, \Delta]^{2k}} \int_{s \in [0, t - \mathcal{J}_{m-1}]} f(X_{m-1} + u + v, t - s - \mathcal{J}_{m-1}) \\
& \quad \times \mathbf{1}_{\{X_{m-1} + u + v \in [0, B_{\max}L_1 + l\Delta]^{2k}\}} d\mu_{m,i}^1(u) ds.
\end{aligned}$$

**Lemma C.3** (Upper bound when  $\mathcal{C}_{m,i} = \emptyset$ ). *Assume that (S1.1) and (S1.3) hold. Then for all  $l \in \mathbb{N}^*$ , there exists  $\overline{C}_2(l) > 0$  such that for all  $t \geq 0$ ,  $(m, i) \in \llbracket 1, l \rrbracket \times \llbracket 1, l \rrbracket^{2k}$  verifying  $\mathcal{C}_{m,i} = \emptyset$ ,  $v \in [-\delta l, \Delta l]^{2k}$ , and  $f \in M_b(\mathcal{X})$  nonnegative*

$$\begin{aligned}
& \mathbb{E} \left[ f(X_m + v, t - \mathcal{J}_m); X_m + v \in [0, B_{\max}L_1 + l\Delta]^{2k}, \mathcal{J}_m \leq t, (I_m, J_m) \neq (\partial, \partial) \mid \mathcal{H}_{m-1} \right] \\
& \leq \overline{C}_2(l) \int_{u \in [-\delta, \Delta]^{2k}} \int_{s \in [0, t - \mathcal{J}_{m-1}]} f(X_{m-1} + u + v, t - s - \mathcal{J}_{m-1}) \\
& \quad \times \mathbf{1}_{\{X_{m-1} + u + v \in [0, B_{\max}L_1 + l\Delta]^{2k}\}} d\mu_m^2(u) ds.
\end{aligned}$$

We now have all the auxiliary statements required to prove Proposition 4.12.

### C.1.2 Proof of Proposition 4.12

Let  $t \geq 0$ ,  $l \in \llbracket 1, n(t) \rrbracket$ ,  $i = (i_1, \dots, i_{2k}) \in \llbracket 1, l \rrbracket^{2k}$ . To obtain an upper bound for the right-hand side term of (C.1.1), we successively condition with respect to  $\mathcal{H}_{n-1}$  ( $n \in \llbracket 1, l \rrbracket$ ). At each conditioning, we apply Lemma C.2 or Lemma C.3. When  $\mathcal{C}_{n,i} \neq \emptyset$ , we apply Lemma C.2, and when  $\mathcal{C}_{n,i} = \emptyset$ , we apply Lemma C.3. For example, if we suppose that  $\mathcal{C}_{l,i} \neq \emptyset$ , then applying Lemma C.2 and using Tonelli's theorem yields

$$\begin{aligned}
& \mathbb{E}_{(x,a)} \left[ f(X_l, t - \mathcal{J}_l); X_l \in [0, B_{\max}L_1 + l\Delta]^{2k}, \mathcal{J}_l \leq t, \forall i \in \llbracket 1, l \rrbracket : (I_i, J_i) \neq (\partial, \partial), \right. \\
& \left. \forall j \in \llbracket 1, 2k \rrbracket : j \in I_{i_j} \cup J_{i_j} \right] \leq \overline{C}_1(l) \int_{(u,s) \in [-\delta, \Delta]^{2k} \times \mathbb{R}_+} \\
& \quad \times \mathbb{E}_{(x,a)} \left[ f(X_{l-1} + u, t - s - \mathcal{J}_{l-1}) \mathbf{1}_{\{X_{l-1} + u \in [0, B_{\max}L_1 + l\Delta]^{2k}\}}; s + \mathcal{J}_{l-1} \leq t, \right. \\
& \left. \forall i \in \llbracket 1, l-1 \rrbracket : (I_i, J_i) \neq (\partial, \partial), \forall j \in \llbracket 1, 2k \rrbracket \text{ s.t. } i_j \leq l-1 : j \in I_{i_j} \cup J_{i_j} \right] d\mu_{1,i}^1(u) ds. \quad (\text{C.1.3})
\end{aligned}$$

We continue to iterate this for  $X_{l-1}, X_{l-2} \dots$ . We obtain at the end an upper bound for the left-hand side term of (C.1.3). We plug this upper bound in (C.1.1). We get

$$\begin{aligned}
& \mathbb{E}_{(x,a)} \left[ f(Z_t); T_{all} < t < \tau_{\partial}, N_t \leq n(t) \right] \leq \sum_{l=1}^{n(t)} \sum_{i \in \llbracket 1, l \rrbracket^{2k}} \left( \max_{m_1, m_2 \in \llbracket 1, l \rrbracket} \overline{C}_1(l)^{m_1} \overline{C}_2(l)^{m_2} \right) \\
& \quad \times \int_{u_1 \in [-\delta, \Delta]^{2k}} \dots \int_{u_l \in [-\delta, \Delta]^{2k}} \int_{s_1 \in [0, t]} \dots \int_{s_l \in [t - \sum_{r=1}^{l-1} s_r]} f \left( x + \sum_{r=1}^l u_r, t - \sum_{r=1}^l s_r \right) \\
& \quad \times \mathbf{1}_{\{x + \sum_{r=1}^l u_r \in [0, B_{\max}L_1 + l\Delta]^{2k}\}} d\mu_{1,i}(u_1) \dots d\mu_{l,i}(u_l) ds_1 \dots ds_l.
\end{aligned}$$

For each coordinate, we have, up to a constant, the convolution of Dirac measures and Lebesgue measures with at least one Lebesgue measure. A convolution of this type has a bounded density with respect to the Lebesgue measure. The number of possible combinations we have for these convolutions is finite. Therefore, we take the maximum among all the bounds of these convolutions with respect to the Lebesgue

measure. We obtain that there exists  $\underline{C}(n(t)) > 0$  such that

$$\begin{aligned} \mathbb{E}_{(x,a)}[f(Z_t); T_{all} < t < \tau_{\partial}, N_t \leq n(t)] &\leq \underline{C}(n(t)) \sum_{l=1}^{n(t)} \sum_{i \in \llbracket 1, l \rrbracket^{2k}} \left( \max_{m_1, m_2 \in \llbracket 1, l \rrbracket} \overline{C}_1(l)^{m_1} \overline{C}_2(l)^{m_2} \right) \\ &\times \int_{v \in [-n(t)\delta, n(t)\Delta]^{2k}} \int_{s_1 \in [0, t]} \cdots \int_{s_l \in [t - \sum_{r=1}^{l-1} s_r]} \\ &\times f \left( x + v, t - \sum_{r=1}^l s_r \right) \mathbf{1}_{\{x+v \in [0, B_{\max} L_1 + l\Delta]^{2k}\}} dv ds. \end{aligned} \quad (\text{C.1.4})$$

The value of  $\underline{C}(n(t))$  increases with the value of  $n(t)$ , as the cardinal of the set of all the possible cases increases when  $n(t)$  increases. We now first denote

$$\overline{C}(n(t)) = \underline{C}(n(t))(n(t))^{2k} \left( \max_{l \in \llbracket 1, n(t) \rrbracket} \max_{m_1, m_2 \in \llbracket 1, l \rrbracket} \overline{C}_1(l)^{m_1} \overline{C}_2(l)^{m_2} \right),$$

that increases when  $n(t)$  increases, and bound from above the constants and sums before the integrals in (C.1.4) by  $\sum_{l=1}^{n(t)} \overline{C}(n(t))$ . Then, we do the changes of variables  $w = x + v$  and  $s' = t - \sum_{r=1}^l s_r$  (for the variable  $s_l$ ), and extend every domain of integration of the integral with respect to the variables  $(s_i)_{i \in \llbracket 1, l-1 \rrbracket}$  to  $[0, t]$ . Finally, we compute the integrals with respect to the measures  $(ds_i)_{i \in \llbracket 1, l-1 \rrbracket}$ . It comes, denoting the constant  $C(t) = \overline{C}(n(t)) \left( \sum_{l=1}^{n(t)} t^{l-1} \right)$ ,

$$\mathbb{E}_{(x,a)}[f(Z_t); T_{all} < t < \tau_{\partial}, N_t \leq n(t)] \leq C(t) \int_{[0, B_{\max} L_1 + n(t)\Delta]^{2k}} \int_{[0, t]} f(w, s') dw ds'.$$

From the above, the proposition is proved because  $C(t)$  increases when  $t$  increases (classic result combined with Lemma 4.11).  $\square$

## C.2 Proof of the auxiliary statements

### C.2.1 Proof of Lemma C.1

Let  $t > 0$ ,  $(x, a) \in E = D_{L_1}$  the initial condition of our process and let  $f$  a nonnegative measurable function. In the left-hand side term of (C.1.1), first use the representation of  $Z_t$  presented in (3.3.6). Then use the fact that

$$t < \tau_{\partial} \iff \forall p \in \llbracket 1, N_t \rrbracket : (I_p, J_p) \neq (\partial, \partial).$$

Finally develop all the values that  $N_t$  can take (necessarily,  $N_t \geq 1$  on the event  $\{T_{all} \leq t\}$ ). It comes

$$\begin{aligned} \mathbb{E}_{(x,a)} \left[ f(Z_t); T_{all} \leq t < \tau_{\partial}, N_t \leq n(t) \right] &= \sum_{l=1}^{n(t)} \mathbb{E}_{(x,a)} \left[ f(X_l, t - \mathcal{J}_l); T_{all} \leq t, N_t = l, \right. \\ &\quad \left. \forall p \in \llbracket 1, l \rrbracket : (I_p, J_p) \neq (\partial, \partial) \right]. \end{aligned}$$

On the event  $\{T_{all} \leq t\}$ , we introduce for every  $j \in \llbracket 1, 2k \rrbracket$  the random variable  $\mathcal{W}_{t,j}$  that represents the last event where a jump has occurred in the coordinate  $j$  during the first  $N_t$  jumps. Formally, we define it as

$$\mathcal{W}_{t,j} = \max \{ p \in \llbracket 1, N_t \rrbracket, j \in I_p \cup J_p \}.$$

By decomposing all the possible values that  $(\mathcal{W}_{t,j})_{j \in \llbracket 1, 2k \rrbracket}$  can take, we have

$$\begin{aligned} \mathbb{E}_{(x,a)} \left[ f(Z_t); T_{all} \leq t < \tau_{\partial}, N_t \leq n(t) \right] &= \sum_{l=1}^{n(t)} \sum_{(i_1, i_2, \dots, i_{2k}) \in \llbracket 1, l \rrbracket^{2k}} \mathbb{E}_{(x,a)} \left[ f(X_l, t - \mathcal{J}_l); T_{all} \leq t, N_t = l, \right. \\ &\quad \left. \forall p \in \llbracket 1, l \rrbracket : (I_p, J_p) \neq (\partial, \partial), \forall j \in \llbracket 1, 2k \rrbracket : \mathcal{W}_{t,j} = i_j \right]. \end{aligned} \quad (\text{C.2.1})$$



We need to prove the following inclusion for all  $l \in \llbracket 1, n(t) \rrbracket$ ,  $(i_1, i_2, \dots, i_{2k}) \in \llbracket 1, l \rrbracket^{2k}$ :

$$\begin{aligned} & \{T_{all} \leq t, N_t = l, \forall p \in \llbracket 1, l \rrbracket : (I_p, J_p) \neq (\partial, \partial), \forall j \in \llbracket 1, 2k \rrbracket : \mathcal{W}_{t,j} = i_j\} \\ & \subset \{X_l \in [0, B_{\max}L_1 + l\Delta]^{2k}, \mathcal{F}_l \leq t, \forall p \in \llbracket 1, l \rrbracket : (I_p, J_p) \neq (\partial, \partial), \forall j \in \llbracket 1, 2k \rrbracket : j \in (I_{i_j} \cup J_{i_j})\}. \end{aligned}$$

Indeed, the latter allows us to easily bound from above the second term in (C.2.1) to obtain (C.1.1).

Let us say why the inclusion is true. First, as the initial condition for telomere length is  $x \in [0, B_{\max}L_1]^{2k}$  and as the maximum lengthening value is  $\Delta$ , we have  $X_l \in [0, B_{\max}L_1 + l\Delta]^{2k}$ . Second, as  $N_t = l$ , we easily have that  $\mathcal{F}_l \leq t$ . Finally, as  $\mathcal{W}_{t,j}$  corresponds to the last jump in the  $j$ -th coordinate, we necessarily have a jump in the  $j$ -th coordinate on the event  $\{\mathcal{W}_{t,j} = i_j\}$  (or formally,  $\mathcal{W}_{t,j} = i_j \implies j \in (I_{i_j} \cup J_{i_j})$ ). From these three points, it comes that the inclusion is true, and the lemma is proved.  $\square$

## C.2.2 Proof of Lemma C.2

Let  $m \leq l \in \mathbb{N}^*$ ,  $i = (i_1, i_2, \dots, i_{2k}) \in \llbracket 1, 2k \rrbracket^l$  such that  $\mathcal{C}_{m,i} = \{j \in \llbracket 1, 2k \rrbracket, i_j = m\}$  is not empty. Throughout the proof,  $f$  is a nonnegative measurable function. We consider  $(\tilde{Z}_t)_{t \geq 0}$  a process with the same distribution as  $(Z_t)_{t \geq 0}$ , and independent of it. We also introduce the random variables  $\tilde{X}_1, \tilde{\mathcal{F}}_1$  and  $(\tilde{I}_1, \tilde{J}_1)$ , that are the equivalents of  $X_1, \mathcal{F}_1$  and  $(I_1, J_1)$  for the process  $(\tilde{Z}_t)_{t \geq 0}$ . We finally define for all  $(x, w) \in \mathbb{R}_+^{2k} \times \mathbb{R}_+$

$$\begin{aligned} h_{\text{cond}}(x, w) &= \mathbb{E}_{(x, 1_{m=1}a)} [f(\tilde{X}_1 + v, t - w - \tilde{\mathcal{F}}_1); \tilde{X}_1 + v \in [0, B_{\max}L_1 + l\Delta]^{2k}, \\ & w + \tilde{\mathcal{F}}_1 \leq t, (I_1, J_1) \neq (\partial, \partial), \mathcal{C}_{m,i} \subset (I_1 \cup J_1)]. \end{aligned}$$

Thanks to the Markov property we have

$$\begin{aligned} & \mathbb{E}_{(x,a)} [f(X_m + v, t - \mathcal{F}_m); X_m + v \in [0, B_{\max}L_1 + l\Delta]^{2k}, \mathcal{F}_m \leq t, (I_m, J_m) \neq (\partial, \partial), \\ & \forall j \in \llbracket 1, 2k \rrbracket \text{ s.t. } i_j = m : j \in I_m \cup J_m \mid \mathcal{H}_{m-1}] = h_{\text{cond}}(X_{m-1}, \mathcal{F}_{m-1}). \end{aligned} \quad (\text{C.2.2})$$

Thus, our goal is to obtain an upper bound for  $h_{\text{cond}}$ . By summing the different events that can occur, we first have

$$\begin{aligned} h_{\text{cond}}(x, w) &= \sum_{\substack{(I,J) \in \mathcal{Q}_k, \\ \forall p \in \mathcal{C}_{m,i} : p \in I \cup J}} \mathbb{E}_{(x, 1_{m=1}a)} [f(\tilde{X}_1 + v, t - w - \tilde{\mathcal{F}}_1); \\ & \tilde{X}_1 + v \in [0, B_{\max}L_1 + l\Delta]^{2k}, w + \tilde{\mathcal{F}}_1 \leq t, (\tilde{I}_1, \tilde{J}_1) = (I, J)]. \end{aligned}$$

Now, we develop the expectation by slightly reajusting Lemma 3.10 (we do not have a term  $\bar{\mathcal{H}}_0$ , as we do not have a condition for  $\tilde{\mathcal{F}}_2 - \tilde{\mathcal{F}}_1$ ). Then, we use the second statement of Lemma 3.4 to bound from above  $\mathcal{G}_a$  by  $\mathcal{H}_a$ . It comes

$$\begin{aligned} h_{\text{cond}}(x, w) &\leq \sum_{\substack{(I,J) \in \mathcal{Q}_k, \\ \forall p \in \mathcal{C}_{m,i} : p \in I \cup J}} \int_{u \in \mathbb{R}^{2k}} \int_{s \in [0, t-w]} f(x + u + v, t - w - s) \\ & \times \mathbf{1}_{\{x+u+v \in [0, B_{\max}L_1 + l\Delta]^{2k}\}} \mathcal{V}(x + u) d\pi_x^{I,J}(u) \mathcal{H}_{1_{m=1}a}(x, s) ds. \end{aligned}$$

In view of (3.3.2), (2.2.1), the fact that  $\frac{\partial \psi}{\partial a}(x, 1_{m=1}a+s) \geq 0$ , the fact that  $a \leq a_0L_1$ , the fact that  $\int_0^t \frac{\partial \psi}{\partial a}(x, 1_{m=1}a+s) ds = \ln \left( \frac{\psi(x, 1_{m=1}a+t)}{\psi(x, 1_{m=1}a)} \right)$  and the third statement of Lemma 3.4 we have

$$\mathcal{H}_{1_{m=1}a}(x, s) \leq [\lambda_\psi + \tilde{b}(1 + (a_0L_1 + s)^{d_b})] [\bar{\psi}(1 + s^{d_\psi})] \exp(-\lambda_\psi s).$$

Thus, there exists a constant  $C > 0$  such that  $\mathcal{H}_{1_{m=1}a}(x, s) \leq C$  and

$$\begin{aligned} h_{\text{cond}}(x, w) &\leq C \sum_{\substack{(I,J) \in \mathcal{Q}_k, \\ \forall p \in \mathcal{C}_{m,i} : p \in I \cup J}} \int_{u \in \mathbb{R}^{2k}} \int_{s \in [0, t-w]} f(x + u + v, t - w - s) \\ & \times \mathbf{1}_{\{x+u+v \in [0, B_{\max}L_1 + l\Delta]^{2k}\}} \mathcal{V}(x + u) d\pi_x^{I,J}(u) ds. \end{aligned} \quad (\text{C.2.3})$$

First, we bound from above the term  $\mathcal{V}(x+u)$  in (C.2.3) using the third statement of (S2.2). Second, we use the fact that by the definition of  $\pi_x^{I,J}$  given in (3.1.1) and Assumption (S1.3), we have in each coordinate of the measure  $\pi_x^{I,J}$  either the Dirac measure or, up to a constant, the Lebesgue measure. Finally, we use the fact that for all  $p \in \mathcal{C}_{m,i}$ ,  $(I, J) \in \mathcal{Q}_k$  such that  $p \in I \cup J$ , we are sure that we have a jump in the coordinate  $p$ , so we are sure that the measure  $\pi_x^{I,J}$  in the coordinate  $p$  is, up to a constant, the Lebesgue measure. Hence, in view of the definition of  $\mu_{m,i}^1$  given in (C.1.2), there exists  $C' > 0$  such that

$$h_{\text{cond}}(x, w) \leq C' \sum_{\substack{(I, J) \in \mathcal{Q}_k, \\ \forall p \in \mathcal{C}_{m,i} : p \in I \cup J}} \int_{u \in \mathbb{R}^{2k}} \int_{s \in [0, t-w]} f(x+u+v, t-w-s) 1_{\{x+u+v \in [0, B_{\max} L_1 + l\Delta]^{2k}\}} d\mu_{m,i}^1(u) ds.$$

Plugging the above equation in (C.2.2) ends the proof.  $\square$