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► **To cite this version:**

Vincent Bansaye. Ancestral lineages and limit theorems for branching Markov chains. 2013. hal-00851284v2

**HAL Id: hal-00851284**

**<https://hal.science/hal-00851284v2>**

Submitted on 24 Nov 2013 (v2), last revised 10 Nov 2014 (v4)

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# Ancestral lineages and limit theorems for branching Markov chains

Vincent Bansaye \*

November 24, 2013

## Abstract

We consider a multitype branching model in discrete time, where the type of each individual is a trait, which belongs to some general state space. Both the reproduction law and the trait inherited by the offsprings may depend on the trait of the mother and the environment. We study the long time behavior of the population and the ancestral lineage of typical individuals under general assumptions. We focus on the growth rate, the trait distribution among the population for large time, so as local densities and the position of extremal individuals. A key role is played by well chosen (possibly non-homogeneous) Markov chains. It relies in particular on an extension of many-to-one formula [G07, BDMT11] and spine decomposition in the vein of [LPP95, KLPP97, GB03]. The applications use properties of the underlying genealogy and sufficient conditions for the ergodic convergence of Markov chains.

**Key words.** Branching processes, Markov chains, Varying environment, Genealogies.

**A.M.S. Classification.** 60J80, 60J05, 60F05, 60F10

## 1 Introduction

We are interested in a branching Markov chain, which means a multitype branching process whose number of types may be infinite. The environment may evolve (randomly) but when the environment, each individual evolves independently and the (quenched branching property hold).

Let  $(E, T)$  be a pair consisting of a set  $E$  of environments and an invertible map  $T$  on  $E$ . One can keep in mind the case when the environment is  $\mathbf{e} = (e_i : i \in \mathbb{Z})$  and  $T\mathbf{e} = (e_{i+1} : i \in \mathbb{Z})$ .

Let  $(\mathcal{X}, \mathcal{B}_{\mathcal{X}})$  be a measurable space which gives the state space of the branching Markov

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\*CMAP, Ecole Polytechnique, CNRS, route de Saclay, 91128 Palaiseau Cedex-France; E-mail: [vincent.bansaye@polytechnique.edu](mailto:vincent.bansaye@polytechnique.edu)

chain. The example  $\mathcal{X} \subset \mathbb{R}^d$  will be relevant for the applications.

For each  $k \in \mathbb{N}$  and  $\mathbf{e} \in E$ , let  $P^{(k)}(\cdot, \mathbf{e}, \cdot)$  be a function from  $\mathcal{X} \times \mathcal{B}_{\mathcal{X}^k}$  into  $[0, 1]$  which satisfies

a) For each  $x \in \mathcal{X}$ ,  $P^{(k)}(x, \mathbf{e}, \cdot)$  is a probability measure on  $(\mathcal{X}, \mathcal{B}_{\mathcal{X}^k})$ .

b) For each  $A \in \mathcal{B}_{\mathcal{X}^k}$ ,  $P^{(k)}(\cdot, \mathbf{e}, A)$  is a  $\mathcal{B}_{\mathcal{X}}$  measurable function.

In the whole paper, we use the classical notation  $u = u_1 u_2 \dots u_n$  with  $u_i \in \mathbb{N}^*$  to identify each individual in the population. We denote by  $|u| = n$  the generation of the individual  $u$ , by  $N(u)$  the number of offsprings of the individual  $u$  and by  $X(u) \in \mathcal{X}$  the trait (or position) of the individual  $u$ .

For any generation, each individual with trait  $x \in \mathcal{X}$  which lives in environment  $\mathbf{e} \in E$  gives birth independently to a random number of offsprings, whose law both depend on  $x$  and  $\mathbf{e}$ . This number of offsprings is distributed as a r.v.  $N(x, \mathbf{e})$  whose mean is denoted by

$$m(x, \mathbf{e}) = \mathbb{E}(N(x, \mathbf{e})).$$

In the whole paper, we assume that  $m(x, \mathbf{e}) > 0$  for each  $x \in \mathcal{X}, \mathbf{e} \in E$  for convenience. A natural framework for our models will be given  $\mathbf{e} = (e_i : i \in \mathbb{Z})$  and  $N(x, \mathbf{e})$  depends only on  $x$  and  $e_0$ , so that  $e_i$  yields the environment in generation  $i$  and the reproduction law in generation  $i$  just depends on  $e_i$ .

If the environment is  $\mathbf{e}$ , we denote by  $\mathbb{P}_{\mathbf{e}}$  the associated probability. The distribution of the traits of the offsprings of the individual  $u$  living in generation  $n$  ( $|u| = n$ ) is given by

$$\begin{aligned} \mathbb{P}_{\mathbf{e}}(X_{u1} \in dx_1, \dots, X_{uk} \in dx_k \mid (X(v) : |v| \leq n), N(u) = k) \\ = P^{(k)}(X(u), T^n \mathbf{e}, dx_1 \dots, dx_k). \end{aligned}$$

In other words, one individual with trait  $x$  living in environment  $\mathbf{e}$  gives birth to a set of individuals  $(X_1, \dots, X_{N(x, \mathbf{e})})$  whose trait are specified by  $(P^{(k)}(\mathbf{e}, x, \cdot) : k \in \mathbb{N}, \mathbf{e} \in E)$ .

This process is a multitype branching process in varying environment where the types take value in  $\mathcal{X}$ . They have been largely studied for finite number of types, whereas much less is known or understood in the infinite case, but some results due to Seneta, Vere Jones, Moy, Kesten for countable types.

The case of branching random walk has attracted lots of attention from the pioneering works of Biggins. Then  $\mathcal{X} = \mathbb{R}^d$  and the transitions  $P^{(k)}$  are invariant by translation, i.e.  $P^{(k)}(x, \mathbf{e}, x + dx_1 \dots, x + dx_k)$  does not depend on  $x \in \mathcal{X}$ . Recently, fine results have been obtained about the extremal individuals and their genealogy for such models, see e.g. [HS09, AS10]. Such questions have also been investigated for branching random walk in random environment. In particular the recurrence property [M08, CP07a], the survival and the growth rate [GMPV10, CP07b, CY11], central limit theorems [Y08, N11] and large deviations results [HL11] have been obtained.

As far as I see, the methods used for such models and in particular the spectral methods and the martingale arguments are not easily adaptable to the general case we consider. We are motivated by applications to models for biology and ecology such as cell division models for cellular aging [G07] or parasite infection [B08] and reproduction-dispersion models in non-homogeneous environment [BL12]. Thus, we are here (also) inspired by the utilization of auxiliary Markov chains, branching decomposition and  $L^2$  computations, in the vein of the works of Athreya and Khang [AK98a, AK98b] and Guyon [G07]. The

applications and references will be given along the paper.

We are interested here in the evolution of the measure associated to the traits of the individuals:

$$Z_n := \sum_{|u|=n} \delta_{X(u)}$$

and more specifically by  $Z_n(A_n) = \#\{u : |u| = n, X(u) \in A_n\}$ . We also define

$$Z_n(f) = \sum_{|u|=n} f(X(u)), \quad f_n \cdot Z_n = \sum_{|u|=n} \delta_{f_n(X(u))}.$$

First, we want to know if the process may survive globally and how it would grow. Thus, Section 2 yields an expression of the mean growth rate of the population relying on the dynamic of the trait and the offspring laws, in the same vein as [BL12] for metapopulations with a finite number of patches and fixed environment. Then (Section 3), we study the repartition of the population and focus on the asymptotic behavior of the proportions of individuals whose trait belongs to  $A$ , i.e.  $Z_n(\mathcal{X})/Z_n(A)$ . It is inspired by [AK98a, G07, BH13] and extends the law of large numbers to both varying environment and trait dependent reproduction. We add that we take into account some possible renormalization of the traits via a function  $f_n$  to cover non recurrent positive cases. Finally, in Section 4, we provide some asymptotic results about  $Z_n(A_n)$ , outside the range of law of large numbers. It relies on the large deviations of the auxiliary process and the trajectory associated with. As an application we can derive the position of the extremal particles in some monotone models motivated by biology, where new behaviors appear.

Let us also mention that the probabilistic approach we follow suggests a way to simulate the long time distribution of the population and will be applied to some biological models motivated by cell division or reproduction-dispersion dynamics.

We end up the introduction with recalling some classical notations. If  $u = u_1 \cdots u_n$  and  $v = v_1 \cdots v_m$ , then  $uv = u_1 \cdots u_n v_1 \cdots v_m$ . For two different individuals  $u, v$  of a tree, write  $u < v$  if  $u$  is an ancestor of  $v$ , and denote by  $u \wedge v$  the nearest common ancestor of  $u$  and  $v$  in the means that  $|w| \leq |u \wedge v|$  if  $w < u$  and  $w < v$ .

## 2 Growth rate of the population

We denote by  $\rho_{\mathbf{e}} = \lim_{n \rightarrow \infty} n^{-1} \log \mathbb{E}_{\mathbf{e}}(Z_n(\mathcal{X}))$  the growth rate of the population in the environment  $\mathbf{e}$ , when it exists.

We are giving an expression of this growth rate in terms of a Markov chain associated with a random lineage. Its transition kernel is defined by

$$P(x, \mathbf{e}, dy) := \frac{1}{m(x, \mathbf{e})} \sum_{k \geq 1} \mathbb{P}(N(x, \mathbf{e}) = k) \sum_{i=1}^k P^{(k)}(x, \mathbf{e}, \mathcal{X}^{i-1} dy \mathcal{X}^{k-i})$$

so that the auxiliary Markov chain  $X$  is given by

$$\mathbb{P}_{\mathbf{e}}(X_{n+1} \in dy | X_n = x) = P(x, T^n \mathbf{e}, dy).$$

It means that we follow a lineage by choosing uniformly at random one of the offsprings at each generation, biased by the number of children.

We assume now that  $\mathcal{X}$  is a locally compact polish space endowed with a complete metric and its Borel  $\sigma$  field. Moreover  $E$  is a Polish Space and  $T$  is an homomorphism. In the rest of the paper, we endow  $\mathcal{M}_1(\mathcal{X} \times E)$  with the weak topology, where  $\mathcal{M}_1(\mathcal{X} \times E)$  is the space of probabilities on  $\mathcal{X} \times E$ . It is the smallest topology such that  $\mu \in \mathcal{M}_1(\mathcal{X} \times E) \rightarrow \int_{\mathcal{X} \times E} f(z)\mu(dz)$  is continuous as soon as  $f$  is continuous and bounded.

**Definition 1.** We say that  $X$  satisfies a Large Deviation Principle (LDP) with good rate function  $I_{\mathbf{e}}$  in environment  $\mathbf{e}$  when there exists a lower semi continuous function  $I : \mathcal{X} \times E \rightarrow \mathbb{R}$  with compact level subsets<sup>1</sup> for the weak topology such that

$$L_n^{\mathbf{e}} = \frac{1}{n+1} \sum_{k=0}^n \delta_{X_k, T^k \mathbf{e}}$$

satisfies for every  $x \in \mathcal{X}$

$$\limsup_{n \rightarrow \infty} \frac{1}{n} \log \mathbb{P}_{\mathbf{e}, x}(L_n \in F) \leq - \inf_{z \in F} I_{\mathbf{e}}(z)$$

for every closed set  $F$  of  $\mathcal{M}_1(\mathcal{X} \times E)$ , and

$$\liminf_{n \rightarrow \infty} \frac{1}{n} \log \mathbb{P}_{\mathbf{e}, x}(L_n \in O) \geq - \inf_{z \in O} I_{\mathbf{e}}(z)$$

for every open set  $O$  of  $\mathcal{M}_1(\mathcal{X} \times E)$ .

The existence of such a principle is classical for fixed environment  $E = \{\mathbf{e}\}$ , finite  $\mathcal{X}$ , under irreducibility assumption. We refer to Sanov's theorem, see e.g. chapter 6.2 in [DZ98]. We note that the principle can be extended to periodic environments, taking care of the irreducibility. Besides, we are using an analogous result for stationary random environment to get forthcoming Corollary 2, under Doeblin type conditions, which is due to [S94].

The first question that we tackle now is the mean growth rate of the population. The branching property yields the linearity of the operator  $\mu \rightarrow m(\mu) = \mathbb{E}_{\mathbf{e}, \mu}(Z_1(\cdot))$  for some measurable set  $A$ .

In the case of fixed environment,  $P$  and  $N$  do not depend on  $\mathbf{e}$ , so  $m$  is also fixed and the mean growth rate of the process  $Z$  is the limit of  $\log \| m^n \| / n$ , with  $\| \cdot \|$  an operator norm. If  $\mathcal{X}$  is finite, it yields the Perron-Frobenius eigenvalue under strong irreducibility assumption, with a min max representation due to Collatz-Wielandt. Krein-Rutman theorem gives an extension to infinite dimension space requiring compactness of the operator  $m$  and strict positivity.

In the random environment case, it corresponds to the Lyapounov exponent and quenched asymptotic results can be obtained in the case  $\mathcal{X}$  is finite [FK60]. Then, the process is a branching process in random environment and we refer to [AK71, K74] for extinction criteria and [C89, T88] for its growth rate.

To go beyond these assumptions and get an interpretation of the growth rate in terms of reproduction-dispersion dynamics, we provide here an other characterization.

This is a functional large deviation principle relying on Varadhan's lemma. It allows to

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<sup>1</sup>It means that  $\{\mu \in \mathcal{M}_1(\mathcal{X} \times E) : I(\mu) \leq l\}$  is compact for the weak topology

decouple the reproduction and dispersion in the dynamic. Thus, it yields an extension of Theorem 5.3 in [BL12] both for varying environment and infinite state space  $\mathcal{X}$ . We refer to this latter article for motivations in ecology, more specifically for metapopulations. The next Corollary then puts in light the dispersion strategy followed by typical individuals of the population for large times.

**Theorem 1.** *Assume that  $X$  satisfies a LDP with good rate function  $I_{\mathbf{e}}$  in environment  $\mathbf{e}$  and  $\log m : \mathcal{X} \times E \rightarrow (-\infty, \infty)$  is continuous and bounded. Then, for every  $x \in \mathcal{X}$ ,*

$$\lim_{n \rightarrow \infty} \frac{1}{n} \log \mathbb{E}_{\mathbf{e}, \delta_x}(Z_n(\mathcal{X})) = \sup_{\mu \in \mathcal{M}_1(\mathcal{X} \times E)} \left\{ \int_{\mathcal{X} \times E} \log(m(x, e)) \mu(dxde) - I_{\mathbf{e}}(\mu) \right\} := \varrho_{\mathbf{e}}$$

and

$$M_{\mathbf{e}} := \left\{ \mu \in \mathcal{M}_1(\mathcal{X} \times E) : \int \log(m(x, e)) \mu(dxde) - I_{\mathbf{e}}(\mu) = \varrho_{\mathbf{e}} \right\}$$

is compact and non empty.

In particular,  $\limsup_{n \rightarrow \infty} \frac{1}{n} \log Z_n(\mathcal{X}) \leq \varrho_{\mathbf{e}}$  a.s. The limit can hold only on the survival event. It is the case under classical  $N \log N$  moment assumption for finite state space  $\mathcal{X}$ , see e.g. [LPP95] for one type of individual and fixed environment and [AK71] in random environment. But it is a rather delicate problem when the number of types is infinite.

We introduce now the event

$$\mathcal{S} := \left\{ \liminf_{n \rightarrow \infty} \frac{1}{n} \log Z_n(\mathcal{X}) \geq \varrho_{\mathbf{e}} \right\}.$$

Conditionally on  $\mathcal{S}$ , we let  $U_n$  be an individual uniformly chosen at random in generation  $n$ . Let us then focus on its trait frequency up to time  $n$  and the associated environment :

$$\nu_n(A) := \frac{1}{n+1} \#\{0 \leq i \leq n : (X_i(U_n), T^i \mathbf{e}) \in A\} \quad (A \in \mathcal{B}_{\mathcal{X} \times E}).$$

where  $X_i(u)$  is the trait of the ancestor of  $u$  in generation  $i$ . We prove that the support of  $\nu_n$  converges in probability to  $M_{\mathbf{e}}$  on the event  $\mathcal{S}$ .

**Corollary 1.** *Under the assumptions of Theorem 1, we further suppose that  $\varrho_{\mathbf{e}} > 0$  and  $\mathcal{S}$  has positive probability. Then, for every  $x \in \mathcal{X}$ ,*

$$\mathbb{P}_{\mathbf{e}, \delta_x}(\nu_n \in F | \mathcal{S}) \xrightarrow{n \rightarrow \infty} 0$$

for every closed set  $F$  of  $\mathcal{M}_1(\mathcal{X} \times E)$  which is disjoint of  $M_{\mathbf{e}}$ .

This result yields an information on the pedigree [JN96, NJ84] or ancestral lineage of a typical individual. It ensures that the trait frequency along the lineage of a typical individual converges to one of the argmax of  $\varrho_{\mathbf{e}}$ . We are going a bit farther in the next Section, with a description of this ancestral lineage via size biased random choice, see in particular Lemma 2.

Let us now specify the theorem for stationary ergodic environment  $\mathcal{E} \in E$ , under Doeblin type assumptions. Following [S94], we let  $\pi$  be a  $T$  invariant ergodic probability, i.e.  $\pi \circ T^{-1} = \pi$  and if  $A \in \mathcal{B}_E$  satisfies  $T^{-1}A = A$ , then  $\pi(A) \in \{0, 1\}$ . Then we need :

**Assumption A.** There exist a positive integer  $b$ , a  $T$  invariant subset  $E'$  of  $E$  and a measurable function  $M : E \rightarrow [1, \infty)$  such that  $\log M \in L^1(\pi)$ ,  $\pi(E') = 1$  and for all  $x, y \in \mathcal{X}$ ,  $A \in \mathcal{B}_{\mathcal{X}}$  and  $\mathbf{e} \in E'$ ,

$$P^b(x, \mathbf{e}, A) \leq M(\mathbf{e})P^b(y, \mathbf{e}, A).$$

We denote by  $V_b(\mathcal{X} \times E)$  the set of bounded continuous functions that map  $\mathcal{X} \times E$  into  $[1, \infty)$  to state the result.

**Corollary 2.** *Under Assumption A, we further suppose that  $\log m(\cdot, \mathcal{E})$  is  $\pi$  a.s. bounded and continuous. Then  $\pi$  a.s., for every  $x \in \mathcal{X}$ ,*

$$\lim_{n \rightarrow \infty} \frac{1}{n} \log \mathbb{E}_{\mathcal{E}, \delta_x}(Z_n(\mathcal{X})) = \sup_{\mu \in \mathcal{M}_1(\mathcal{X} \times E)} \left\{ \int \log(m(x, e)) \mu(dx, de) - I(\mu) \right\},$$

where  $I$  is defined by

$$I(\mu) := \sup \left\{ \int_{\mathcal{X} \times E} \log \left( \frac{u(x, e)}{\int_{\mathcal{X}} P(x, e, dy) u(y, T e)} \right) \mu(dx, de) : u \in V_b(\mathcal{X} \times E) \right\}.$$

To prove these results, we need the following lemma, where  $\mathcal{B}_b(\mathcal{X})$  is the set of bounded measurable functions on  $\mathcal{X}$ .

**Lemma 1.** *Let  $F \in \mathcal{B}(\mathcal{X}^k)$  non-negative. Then, for every  $\nu \in \mathcal{M}_1(\mathcal{X})$ ,*

$$\mathbb{E}_{\mathbf{e}, \nu} \left( \sum_{|u|=n} F(X_0(u), \dots, X_n(u)) \right) = \mathbb{E}_{\mathbf{e}, \nu} \left( F(X_0, \dots, X_n) \prod_{i=0}^{n-1} m(X_i, T^i \mathbf{e}) \right)$$

where we recall that  $X_i(u)$  is the trait of the ancestor of  $u$  in generation  $n$ .

*Proof.* For every  $f_0, \dots, f_n \in \mathcal{B}(\mathcal{X})$  non-negative, by branching property

$$\begin{aligned} & \mathbb{E}_{\mathbf{e}, \nu} \left( \sum_{|u|=n} f_0(X_0(u)) \cdots f_n(X_n(u)) \right) \\ &= \int \nu(dx_0) f_0(x_0) \int m_1(x_0, \mathbf{e}, dx_1) \mathbb{E}_{T\mathbf{e}, \delta_{x_1}} \left( \sum_{|u|=n-1} f_1(X_0(u)) \cdots f_n(X_{n-1}(u)) \right). \end{aligned}$$

where

$$m_1(x_0, \mathbf{e}, dx_1) = \mathbb{E}_{\mathbf{e}, x_0} (\#\{|u|=1 : X(u) \in dx_1\}) = m(x_0, \mathbf{e})P(x_0, \mathbf{e}, dx_1).$$

So by induction

$$\begin{aligned} & \mathbb{E}_{\mathbf{e}, \nu} \left( \sum_{|u|=n} f_0(X_0(u)) \cdots f_n(X_n(u)) \right) \\ &= \int_{\mathcal{X}^n \times A} \nu(dx_0) f(x_0) \prod_{i=0}^{n-1} m(x_i, T^i \mathbf{e}) P(x_i, T^i \mathbf{e}, dx_{i+1}) f(x_{i+1}) \end{aligned}$$

It completes the proof.  $\square$

*Proof of Theorem 1.* The previous lemma applied to  $F = 1$  ensures that

$$\mathbb{E}_{\mathbf{e}, \nu}(Z_n(\mathcal{X})) = \mathbb{E}_{\mathbf{e}, \nu} \left( \prod_{i=0}^{n-1} m(X_i, T^i \mathbf{e}) \right).$$

Thus

$$\mathbb{E}_{\mathbf{e}, \nu}(Z_n(\mathcal{X})) = \mathbb{E}_{\mathbf{e}, \nu} \left( \exp \left( n \int_{\mathcal{X} \times E} \log(m(x, e)) L_{n-1}^{\mathbf{e}}(dx, de) \right) \right)$$

As  $\log m$  is bounded and continuous by assumption, so is

$$\mu \in \mathcal{M}_1(\mathcal{X} \times E) \rightarrow \phi(\mu) = \int_{\mathcal{X} \times E} \log(m(x, e)) \mu(dx, de).$$

Using the LDP principle satisfied by  $L_n^{\mathbf{e}}$ , we can apply Varadhan's lemma (see [DZ98] Theorem 4.3.1) to the previous function to get the first part of the Theorem.

Let us now consider a sequence  $\mu_n$  such that

$$\int_{\mathcal{X} \times E} \log(m(x, e)) \mu_n(dx, de) - I_{\mathbf{e}}(\mu_n) \xrightarrow{n \rightarrow \infty} \varrho_{\mathbf{e}}.$$

Then  $I_{\mathbf{e}}(\mu_n)$  is upper bounded, which ensures that  $\mu_n$  belongs to a sublevel set. By Definition 1, such a set is compact so can extract a subsequence  $\mu_{n_k}$  which converges weakly in  $\mathcal{M}(\mathcal{X}, E)$ . As  $I_{\mathbf{e}}$  is lower semicontinuous, the limit  $\mu$  of this subsequence satisfies

$$\liminf_{k \rightarrow \infty} I_{\mathbf{e}}(\mu_{n_k}) \geq I_{\mathbf{e}}(\mu).$$

Recalling that  $\phi$  is continuous, we get

$$\varrho_{\mathbf{e}} = \lim_{n \rightarrow \infty} \left\{ \int_{\mathcal{X} \times E} \log(m(x, e)) \mu_{\phi(n)}(dx, de) - I_{\mathbf{e}}(\mu_{\phi(n)}) \right\} \leq \int \log(m(x, e)) \mu(dx, de) - I_{\mathbf{e}}(\mu)$$

and  $\mu$  is a maximizer. That ensures that  $M_{\mathbf{e}}$  is compact and non empty.  $\square$

*Proof of Corollary 1.* We define for any individual  $u$  in generation  $n$

$$\nu_n(u)(A) = \frac{1}{n+1} \sum_{0 \leq i \leq n} \delta_{X_i(u)}.$$

Using Lemma 1 with  $F(x_0, \dots, x_n) = 1(\frac{1}{n+1} \sum_{0 \leq i \leq n} \delta_{x_i} \in F)$ , we have

$$\mathbb{E}_{\mathbf{e}, \nu}(\#\{u : |u| = n, \nu_n(u) \in F\}) = \mathbb{E}_{\nu} \left( \exp \left( n \int_{\mathcal{X} \times E} \log(m(x, e)) L_{n-1}^{\mathbf{e}}(dx, de) \right) 1_{L_n^{\mathbf{e}} \in F} \right)$$

Applying again Varadhan's to any bounded continuous function  $\phi : \mathcal{M}_1(\mathcal{X} \times E) \rightarrow \mathbb{R}$  such that, for every  $\mu \in F$ ,

$$\phi(\mu) \leq \int_{\mathcal{X} \times E} \log(m(x, e)) \mu(dx, de) \tag{1}$$

we get,

$$\limsup_{n \rightarrow \infty} \frac{1}{n} \log \mathbb{E}_{\mathbf{e}, \nu}(\#\{u : |u| = n, \nu_n(u) \in F\}) \leq \sup\{\phi(\mu) - I_{\mathbf{e}}(\mu) : \mu \in \mathcal{M}_1(\mathcal{X} \times E)\}.$$



Let us now check that we can find  $\phi$  such that the right hand side is strictly less than  $\varrho_{\mathbf{e}}$ . We proceed by contradiction and assume that for every  $\phi$  continuous and bounded which satisfies (1), we have  $\sup\{\phi(\mu) - I_{\mathbf{e}}(\mu) : \mu \in \mathcal{M}_1(\mathcal{X} \times E)\} = \varrho_{\mathbf{e}}$ . Then using the fact  $I_{\mathbf{e}}$  is a good rate function, we obtain that there exists  $\mu(\phi)$  such that  $\phi(\mu(\phi)) - I_{\mathbf{e}}(\mu(\phi)) = \varrho_{\mathbf{e}}$ , thanks to the same arguments as the end of the previous proof. Recalling that  $\mathcal{M}_1(\mathcal{X} \times E)$  can be metrizable by a distance  $d$ , we define now  $\phi_n(\mu) := -nd(\mu, F) + \int_{\mathcal{X} \times E} \log(m(x, e))\mu(dx, de)$ . We use again the compactness of sub-level sets of  $I_{\mathbf{e}}$  to extract a sequence  $\mu(\phi_{n_k})$  which converges to  $\mu_0$ . Then  $\mu_0 \in F \cap M_{\mathbf{e}}$ , which yields the contradiction.

Thus we can choose  $\rho'$  such that

$$\limsup_{n \rightarrow \infty} \frac{1}{n} \log \mathbb{E}_{\mathbf{e}, \nu} (\#\{u : |u| = n, F_n(u) \in F\}) < \varrho' < \varrho_{\mathbf{e}}.$$

Adding that

$$\begin{aligned} \mathbb{P}(\nu_n(U_n) \in F | \mathcal{S}) &\leq \mathbb{E}(\#\{u : |u| = n, \nu_n(u) \in F\} / Z_n(\mathcal{X}) | \mathcal{S}) \\ &\leq e^{-\varrho' n} \mathbb{E}(\#\{u : |u| = n, \nu_n(u) \in F\}) / \mathbb{P}(\mathcal{S}) \end{aligned}$$

for  $n$  large enough by definition of  $\mathcal{S}$  and that the left hand side goes to 0 ends up the proof.  $\square$

*Proof of Corollary 2.* Under Assumption A, Theorem 3.3 [S94] ensures that there exists a function  $I$  which satisfies  $\pi$  a.s. the Definition 1 (uniformly with respect to  $x \in \mathcal{X}$ ). The result is then a direct application of Theorem 1.  $\square$

We have given above an expression of the mean growth rate and specified the ancestral lineage of surviving individuals. It leaves several open questions and we are considering the following ones in the next Section, which are linked :

Does the process grows like its mean when it survives ?

How is the population spread for large times ?

### 3 Law of large numbers

We consider the mean measure under the environment  $\mathbf{e}$  :

$$m_n(x, \mathbf{e}, A) := \mathbb{E}_{\mathbf{e}, \delta_x} (Z_n(A)) = \mathbb{E}_{\mathbf{e}, \delta_x} (\#\{u : |u| = n, X(u) \in A\}) \quad (A \in \mathcal{B}_{\mathcal{X}}).$$

It yields the mean number of descendant in generation  $n$ , whose trait belongs  $A$ , of an initial individual with trait  $x$ . Similarly we consider its mean number of descendants in generation  $n$ . We define a new family of Markov kernel  $Q_n$  by

$$Q_n(x, \mathbf{e}, dy) := m_1(x, \mathbf{e}, dy) \frac{m_{n-1}(y, T\mathbf{e}, \mathcal{X})}{m_n(x, \mathbf{e}, \mathcal{X})}.$$

The fact that  $Q_n(x, \mathbf{e}, \mathcal{X}) = 1$  for all  $n \in \mathbb{N}, x \in \mathcal{X}, \mathbf{e} \in E$  comes directly from the branching property. We introduce the associated semigroup, more precisely the successive composition of  $Q_j$  between the generations  $i$  and  $n$  :

$$Q_{i,n}(x, \mathbf{e}, A) = Q_{n-i}(x, T^i \mathbf{e}, \cdot) * Q_{n-i-1}(\cdot, T^{i+1} \mathbf{e}, \cdot) * \dots * Q_1(\cdot, T^{n-1} \mathbf{e}, \cdot)(A),$$

where we recall the notation  $Q(x, \cdot) * Q'(\cdot, \cdot)(A) = \int_{\mathcal{X}} Q(x, dy) Q'(y, A)$ . The next section links the semigroups  $m_n$  and  $Q_{0,n}$ .

### 3.1 The auxiliary process and the many-to-one formula

The following many-to-one formula links the expectation of the number of individuals whose trait belongs to  $A$  to the probability that the Markov chain associated to the kernel  $Q_n$  belongs to  $A$ .

**Lemma 2.** *For all  $n \in \mathbb{N}, x \in \mathcal{X}$  and  $F \in \mathcal{B}(\mathcal{X}^{n+1})$  non-negative, we have*

$$\mathbb{E}_{\mathbf{e}, \delta_x} \left( \sum_{|u|=n} F(X_0(u), \dots, X_n(u)) \right) = m_n(x, \mathbf{e}, \mathcal{X}) \mathbb{E}_{\mathbf{e}, x}(F(Y_0^{(n)}, \dots, Y_n^{(n)})),$$

where  $(Y_i^{(n)} : i = 0, \dots, n)$  is a non-homogeneous Markov chain with kernels  $(Q_{i,n}(\cdot, \mathbf{e}, \cdot) : i = 0, \dots, n-1)$ . In particular for each  $f \in \mathcal{B}(\mathcal{X})$  non-negative,

$$m_n(x, \mathbf{e}, f) = m_n(x, \mathbf{e}, \mathcal{X}) Q_{0,n}(x, \mathbf{e}, f),$$

where we recall the notation  $\nu(f) = \int_{\mathcal{X}} f(y) \nu(dy)$ .

We note that  $m_n(x, \mathbf{e}, \mathcal{X})$  is the mean number of individuals in generation  $n$  considered in the previous Section. Here, combining the branching property and the lemma above yields an other expression of the growth rate:

$$\frac{m_{n+1}(x, \mathbf{e}, \mathcal{X})}{m_n(x, \mathbf{e}, \mathcal{X})} = \int_{\mathcal{X}} m(y, T^n \mathbf{e}) Q_{0,n}(x, \mathbf{e}, dy).$$

The many-to-one formula yields a spine decomposition of the size-biased tree : the dynamic of the trait along the spine follows the non-homogeneous Markov chain  $Y$ . Going further and describing the whole process seen from the spine requires additional work. The reproduction of the individuals along the spine is a size biased law and independent process then grow following the original distribution. Such a decomposition has been firstly achieved for Galton-Watson processes in [LPP95]. We refer to [KLPP97] for an extension to multitype Galton-Watson processes, when the bias among the population relies on the eigenvector of the mean operator, [GB03] for continuous time and [G99] for related results in varying environment.

The second part of the Lemma is an extension of the many one-to-one formula for binary tree [G07], Galton-Watson trees [DM10] and Galton-Watson trees in stationary random environments [BH13]. In continuous time, many-to-one formula and formula for forks can be found in [BDMT11]. But these later do not let the reproduction depend on the trait. We refer to [C11, HR12, HR13] for other many-to-one formulas and asymptotic results when reproduction law depend on the trait in some particular cases.

For branching random walk in random environment, let us mention the use of induced random walk eliminating the branching, see e.g. [CP07a].

*Proof.* By a telescopic argument :

$$\prod_{i=0}^{n-1} Q_{n-i}(x_i, T^i \mathbf{e}, dx_{i+1}) = \frac{m_0(x_n, \mathbf{e}, \mathcal{X})}{m_n(x_0, \mathbf{e}, \mathcal{X})} \prod_{i=0}^{n-1} m_1(x_i, T^i \mathbf{e}, dx_{i+1}).$$

Adding that  $m_1(x_i, T^i \mathbf{e}, dx_{i+1}) = m(x_i, T^i \mathbf{e}) P(x_i, T^i \mathbf{e}, dx_{i+1})$ , the first part of the lemma is a consequence of Lemma 1. We then deduce the second part by applying the identity obtained to  $F(x_0, \dots, x_n) = f(x_n)$ .  $\square$

Our aim is now to get ride of the expectation and obtain the repartition of the population for large times. We want to derive it from the asymptotic distribution of this auxiliary Markov chain with kernel  $Q_n$  and prove a law of large number on the proportions of individuals whose trait belongs to  $A$ . One approach would be to find a martingale via maximal eigenvalue and eigenvector, as for finite type and fixed environment. It has been extended to branching processes with infinite number of types in [A00] but the assumptions required are not easily fulfilled, at least regarding the motivations from biology and ecology we give in this work. Moreover the generalization to varying environment seems more adapted to the technicals described here. Thus, we are here inspired by ideas and technics developed in [AK98a, AK98b] using the branching property or that in [G07] relying on  $L^2$  computations.

### 3.2 Branching decomposition

In this part, we focus on the particular case when extinction does not occur and actually assume that the population has a positive growth rate. We have then the following strong law of large numbers, on the following event ensuring geometric growth :

$$\mathcal{T} := \left\{ \forall n, Z_n(\mathcal{X}) > 0; \liminf_{n \rightarrow \infty} \frac{Z_{n+1}(\mathcal{X})}{Z_n(\mathcal{X})} > 1 \right\}.$$

**Theorem 2.** *Let us fix  $\mathbf{e} \in E$  and  $\mathcal{F}$  a bounded subset of  $\mathcal{B}(\mathcal{X})$ . We assume that there exists a measure  $Q$  with finite first moment such that for all  $x \in \mathcal{X}, k, l \geq 0$ ,*

$$\mathbb{P}(N(x, T^k \mathbf{e}) \geq l) \leq Q[l, \infty). \quad (2)$$

*Assume also that there exists a sequence of probability measure  $\mu_n$  such that*

$$\sup_{\lambda \in \mathcal{M}_1(\mathcal{X})} |Q_{i,n}(\lambda, T^i \mathbf{e}, f \circ f_n) - \mu_n(f)| \rightarrow 0, \quad (3)$$

*uniformly for  $n - i \rightarrow \infty$  and  $f \in \mathcal{F}$ . Then,*

$$\frac{f_n \cdot Z_n(f)}{Z_n(\mathcal{X})} - \mu_n(f) \xrightarrow{n \rightarrow \infty} 0 \quad \mathbb{P}_{\mathbf{e}} \text{ a.s. on the event } \mathcal{T}. \quad (4)$$

This result extends [AK98a, AK98b] to the case when the reproduction law may depend on the trait and to time varying environment. Moreover, here the Markov kernel  $P^{(k)}$  is not forced to be a direct product of the same kernel. It yields a strong law of large numbers relying on the uniform ergodicity of the auxiliary Markov chain  $Q_{i,n}$ . The assumption of a.s. survival and positive growth rate will be relaxed in the next part using  $L^2$  assumptions.

We first state a result on the sum of independent random variables, which is being used several time. It is an easy extension of Lemma 1 in [AK98a], which itself is proved using [K72].

**Lemma 3.** *Let  $\{\mathcal{F}\}_0^\infty$  be a filtration contained in  $(\Omega, \mathcal{B}, \mathbb{P})$ . Let  $\{X_{n,i} : n, i \geq 1\}$  be r.v. such that for each  $n$ ,  $\mathcal{F}_n \{X_{n,i} : i \geq 1\}$  are centered independent r.v. Let  $\{N_n : n \geq 1\}$  be non-negative integer valued r.v. such that for each  $n$ ,  $N_n$  is  $\mathcal{F}_n$  measurable.*

*We assume that there exists a random measure  $Q$  with finite first moment such,*

$$\forall t > 0, \quad \sup_{i, n \geq 1} \mathbb{P}(|X_{n,i}| > t | \mathcal{F}_n) \leq Q(t, \infty) \quad \text{a.s.}$$

Then for each  $n_0 \geq 1$  and  $l > 1$ ,

$$\frac{1}{N_n} \sum_{i=1}^{N_n} X_{n,i} \xrightarrow{n \rightarrow \infty} 0$$

a.s. on the event  $\{\forall n \geq n_0 : N_n > 0; N_{n+1}/N_n \geq l\}$ .

*Proof.* The proof can be simply adapted from the proof of Lemma 1 in [AK98a]. For any  $\delta > 0$  and  $l > 1$ , we define

$$A_n := \left\{ \left| \frac{1}{N_n} \sum_{i=1}^{N_n} X_{n,i} \right| > \delta; \forall k = n_0, \dots, n : \frac{N_k}{N_{k-1}} \geq l \right\}$$

and prove similarly that  $\sum_{n \geq n_0} \mathbb{P}(A_n | \mathcal{F}_n) < \infty$ .  $\square$

We use first this lemma to prove the following result, with

$$A_{n_0, l} := \{\forall n \geq n_0 : N_n > 0; Z_{n+1}(\mathcal{X})/Z_n(\mathcal{X}) \geq l\}.$$

**Lemma 4.** For each  $n_0 \geq 0$  and  $l > 1$ ,

$$\frac{1}{Z_{n+p}(\mathcal{X})} \sum_{|u|=n} m_p(X(u), T^n \mathbf{e}, \mathcal{X}) \rightarrow 1 \quad \text{as } n \rightarrow \infty. \quad (5)$$

a.s on the event  $A_{n_0, l}$ .

*Proof.* The branching property gives a natural decomposition of the population in generation  $n + p$ , as already used in [AK98b] :

$$Z_{n+p}(\mathcal{X}) = \sum_{|u|=n} Z_p^{(u)}(\mathcal{X}),$$

where  $Z^{(u)}$  is the branching Markov chain whose root is the individual  $u$  and whose environment is  $T^n \mathbf{e}$ . First, we check that Indeed,

$$Z_{n+p}(\mathcal{X}) - \sum_{|u|=n} m_p(X(u), T^n \mathbf{e}, \mathcal{X}) = \sum_{|u|=n} \left[ Z_p^{(u)}(\mathcal{X}) - m_p(X(u), T^n \mathbf{e}, \mathcal{X}) \right] = Z_n(\mathcal{X}) \epsilon_{n,p},$$

where

$$\epsilon_{n,p} := \frac{1}{Z_n(\mathcal{X})} \sum_{|u|=n} X_{p,u}^{(n)}, \quad X_{p,u}^{(n)} := Z_p^{(u)}(\mathcal{X}) - m_p(X(u), T^n \mathbf{e}, \mathcal{X}).$$

We note that  $(X_{p,u}^{(n)} : |u| = n)$  are independent conditionally on  $\mathcal{F}_n = \sigma(X(v) : |v| \leq n)$ ,  $\mathbb{E}(X_{p,u}^{(n)}) = 0$  and  $|X_{p,u}^{(n)}| \leq |Z_p^{(u)}(\mathcal{X})| + m_p(X(u), T^n \mathbf{e}, \mathcal{X})$ , so that the stochastic domination assumption (2) ensures that there exists a measure with finite first moment  $Q'$  such that

$$\sup_{u \in \mathbb{T}} \mathbb{P}_{\mathbf{e}}(|X_{p,u}^{(n)}| > t | \mathcal{F}_{|u|}) \leq Q'(t, \infty),$$

where we recall that  $\mathbb{T}$  is the set of all individuals. We can then apply the law of large number of Lemma 4 to get that for every  $p \geq 0$ ,  $\epsilon_{n,p} \rightarrow 0$   $\mathbb{P}_{\mathbf{e}}$  a.s. on the event  $A_{n_0, l}$ , as  $n \rightarrow \infty$ . Recalling that  $Z_{n+p}(\mathcal{X}) \geq Z_n(\mathcal{X})$  for  $n$  large enough, we obtain (5).  $\square$

We can now prove the Theorem.

*Proof of Theorem 2.* Using again the branching decomposition,

$$\frac{f_{n+p} \cdot Z_{n+p}(f)}{Z_{n+p}(\mathcal{X})} - \mu_{n+p}(f) = \frac{1}{Z_n(\mathcal{X})} \sum_{|u|=n} \frac{Z_n(\mathcal{X})}{Z_{n+p}(\mathcal{X})} f_{n+p} \cdot Z_p^{(u)}(f) - \mu_{n+p}(f) \quad \text{a.s.} \quad (6)$$

and we are proving that the right hand side goes to 0 as  $n \rightarrow \infty$  on  $A_{n_0, l}$ , for each  $n_0 \geq 0, l > 1$ . For that purpose, we split this expression and use the many-to-one formula (Lemma 2)

$$\begin{aligned} & \left| \frac{1}{Z_n(\mathcal{X})} \sum_{|u|=n} \frac{Z_n(\mathcal{X})}{f_{n+p} \cdot Z_{n+p}(\mathcal{X})} Z_p^{(u)}(f) - \mu_{n+p}(f) \right| \\ & \leq \frac{1}{Z_n(\mathcal{X})} \left| \sum_{|u|=n} \frac{Z_n(\mathcal{X})}{Z_{n+p}(\mathcal{X})} \left[ f_{n+p} \cdot Z_p^{(u)}(f) - m_p(X(u), T^n \mathbf{e}, f \circ f_{n+p}) \right] \right| \\ & \quad + \frac{1}{Z_{n+p}(\mathcal{X})} \left| \sum_{|u|=n} m_p(X(u), T^n \mathbf{e}, \mathcal{X}) [Q_p(X(u), T^n \mathbf{e}, f) - \mu_{n+p}(f)] \right| \\ & \quad + \mu_{n+p}(f) \left| \sum_{|u|=n} \frac{m_p(X(u), T^n \mathbf{e}, \mathcal{X})}{Z_{n+p}(\mathcal{X})} - 1 \right|. \end{aligned}$$

To prove that the first term of this sum goes to zero a.s. on the event  $A_{n_0, l}$  as  $n \rightarrow \infty$ , we use again the law of large numbers of Lemma 4 with now

$$X_{u,n} = \frac{Z_n(\mathcal{X})}{f_{n+p} \cdot Z_{n+p}(\mathcal{X})} \left[ Z_p^{(u)}(f) - m_p(X(u), T^n \mathbf{e}, f \circ f_{n+p}) \right].$$

We note that

$$X_{u,n} \leq f_{n+p} \cdot Z_p^{(u)}(f) + m_p(X(u), T^n \mathbf{e}, f \circ f_{n+p}) \leq M [Z_p^{(u)}(\mathcal{X}) + m_p(X(u), T^n \mathbf{e}, \mathcal{X})],$$

where  $M := \sup_{f \in \mathcal{F}} \|f\|_\infty$ . Then, noting

$$M_p := \sup_{n \in \mathbb{N}} \left| \frac{1}{Z_n(\mathcal{X})} \sum_{|u|=n} \frac{Z_n(\mathcal{X})}{Z_{n+p}(\mathcal{X})} Z_p^{(u)}(f) - \mu_{n+p}(f) \right|$$

and recalling (5), we get

$$\begin{aligned} & \limsup_{n \rightarrow \infty} \left| \frac{1}{Z_n(\mathcal{X})} \sum_{u \in \mathbb{G}_n} \frac{Z_n(\mathcal{X})}{Z_{n+p}(\mathcal{X})} Z_p^{(u)}(f) - \mu_{n+p}(f) \right| \\ & \leq M_p \limsup_{n \rightarrow \infty} \frac{1}{Z_n(\mathcal{X})} \sum_{|u|=n} \frac{m_p(X(u), T^n \mathbf{e}, \mathcal{X})}{Z_{n+p}(\mathcal{X})} \\ & \quad + M \limsup_{n \rightarrow \infty} \left| \sum_{|u|=n} \frac{m_p(X(u), T^n \mathbf{e}, \mathcal{X})}{Z_{n+p}(\mathcal{X})} - 1 \right| \leq M(p). \end{aligned}$$

Using now (3), we have  $M_p \rightarrow 0$  as  $p \rightarrow \infty$ , so that (6) yields

$$\limsup_{p \rightarrow \infty} \limsup_{n \rightarrow \infty} \left| \frac{Z_{n+p}(f)}{f_{n+p} \cdot Z_{n+p}(\mathcal{X})} - \mu_{n+p}(f) \right| = 0.$$

It ends up the proof.  $\square$

### 3.3 $L^2$ convergence

In this section, we state weak and strong law of large numbers by combining  $L^2$  computations, the ergodicity of the auxiliary Markov chain  $Y$  and the position of the most recent common ancestor of the individuals.

We recall the notations  $Q(\lambda, \mathbf{e}, f)(x) = \int_{\mathcal{X}^2} \lambda(dx) Q(x, \mathbf{e}, dy) f(y)$  and  $\mathcal{B}(\mathcal{X})$  for the set of measurable functions from  $\mathcal{X}$  to  $\mathbb{R}$ . We note  $\mathcal{B}_b(\mathcal{X})$  the set of measurable functions from  $\mathcal{X}$  to  $\mathbb{R}$ , which are bounded by a same constant  $b \geq 0$ .

The main assumption we are using concern the ergodic behavior of the time non-homogeneous auxiliary Markov chain  $Y$  associated with the transitions kernels  $Q_{i,n}$ .

**Assumption 1.** Let  $\mathbf{e}_n \in E$ ,  $\mathcal{F} \subset \mathcal{B}(\mathcal{X})$ ,  $f_n \in \mathcal{B}(\mathcal{X})$  and  $\mu_n \in \mathcal{M}_1(\mathcal{X})$  for each  $n \in \mathbb{N}$ .

(a) For all  $\lambda \in \mathcal{M}(\mathcal{X})$  and  $i \in \mathbb{N}$ ,

$$\sup_{f \in \mathcal{F}} |Q_{i,n}(\lambda, \mathbf{e}_n, f \circ f_n) - \mu_n(f)| \xrightarrow{n \rightarrow \infty} 0.$$

(b) For every  $k_n \leq n$  such that  $n - k_n \rightarrow \infty$ ,

$$\sup_{\lambda \in \mathcal{M}(\mathcal{X}), f \in \mathcal{F}} |Q_{k_n, n}(\lambda, \mathbf{e}_n, f \circ f_n) - \mu_n(f)| \xrightarrow{n \rightarrow \infty} 0.$$

The second assumption (uniform ergodicity) clearly implies the first one. Sufficient conditions will be given in the applications. In particular, they are linked to Harris ergodic theorem and more specifically they will be formulated in terms of Doeblin and Lyapounov type conditions. The function  $f_n$  is bound to make the process ergodic if it is not originally. We have for example in mind the case when the auxiliary Markov chain  $X_n$  satisfies a central limit theorem, i.e.  $f_n(x) = (x - a_n)/b_n$  and  $f(X_n)$  converges to the same distribution whatever the initial value  $X_0$  is. Such convergence hold for example for branching random walks.

We consider now the genealogy of the population and the time of the most recent common ancestor of two individuals chosen uniformly.

**Assumption 2.** (a) For every  $\epsilon > 0$ , there exists  $K \in \mathbb{N}$ , such that for  $n$  large enough,

$$\frac{\mathbb{E}_{\mathbf{e}_n, \delta_x} (\#\{u, v : |u| = |v| = n, u \wedge v \geq K\})}{m_n(x, \mathbf{e}_n, \mathcal{X})^2} \leq \epsilon. \quad (7)$$

Moreover there exists  $C_i \in \mathcal{B}(\mathcal{X}^2)$  such that for all  $i \in \mathbb{N}, x, y \in \mathcal{X}$ ,

$$\sup_{n \geq i} \frac{m_{n-i}(y, T^i \mathbf{e}_n, \mathcal{X})}{m_n(x, \mathbf{e}_n, \mathcal{X})} \leq C_i(x, y), \quad \text{with } \mathbb{E} (\max\{C_i(x, X(w))^2 : |w| = i + 1\}) < \infty.$$

(b) For every  $K \in \mathbb{N}$ ,

$$\frac{\mathbb{E}_{\mathbf{e}_n, \delta_x} (\#\{u, v : |u| = |v| = n, u \wedge v \geq n - K\})}{m_n(x, \mathbf{e}_n, \mathcal{X})^2} \xrightarrow{n \rightarrow \infty} 0. \quad (8)$$

Moreover,

$$\sup_{n \in \mathbb{N}} \mathbb{E}(Z_n(\mathcal{X})^2)/m_n(x, \mathbf{e}_n, \mathcal{X})^2 < \infty.$$

These expressions can be rewritten in terms of normalized variance of  $Z_n(\mathcal{X})$  and more tractable sufficient assumptions can be specified, see the applications. We also observe that these assumptions require that  $Z_n(\mathcal{X})$  has a finite second moment, so each reproduction law involved in the dynamic has a finite second moment. Moreover  $m_n(x, \mathbf{e}_n, \mathcal{X})$  has to go to  $\infty$ .

The assumption (7) says that the common ancestor is at the beginning of the genealogy. It is the case for Galton-Watson trees, branching processes in random environment and many others “regular trees”. The assumption (8) says that the common ancestor is not at the end of the genealogy, so it is weaker. For a simple example where (7) is fulfilled but (8) is not, one can consider the tree  $T_n$  which is composed by a single individual until generation  $n - k_n$  and equal to the binary tree between the generations  $n - k_n$  and  $n$ , with  $k_n \rightarrow \infty$ . One can also construct examples of branching Markov chain with time homogeneous reproduction. As an hint, we mention the degenerated case when the tree is formed by a spine where in each generation, the individual of the spine has one child outside the spine which gives exactly one child in each generation. More generally, such genealogy may arise by considering increasing Markov chains and increasing mean reproduction (which may be deterministic) with respect to  $x \in \mathcal{X}$ .

**Theorem 3** (Weak LLN). *Let  $\mathbf{e}_n \in E^n$ ,  $x \in \mathcal{X}$ ,  $f_n : \mathcal{X} \rightarrow \mathcal{X}$  and  $\mathcal{F} \subset \mathcal{B}_b(\mathcal{X})$ .*

*We assume either that Assumptions 1(a) and 2(a) hold or that Assumptions 1(b) and 2(b) hold. Then, uniformly for  $f \in \mathcal{F}$ ,*

$$\frac{f_n \cdot Z_n(f) - \mu_n(f) Z_n(\mathcal{X})}{m_n(x, \mathbf{e}_n, \mathcal{X})} \xrightarrow{n \rightarrow \infty} 0 \quad (9)$$

in  $L^2_{\mathbf{e}_n, \delta_x}$  and for all  $\epsilon, \eta > 0$ ,

$$\mathbb{P}_{\mathbf{e}_n, \delta_x} \left( \left| \frac{f_n \cdot Z_n(f)}{Z_n(\mathcal{X})} - \mu_n(f) \right| \geq \eta ; Z_n(\mathcal{X})/m_n(x, \mathbf{e}_n, \mathcal{X}) \geq \epsilon \right) \xrightarrow{n \rightarrow \infty} 0.$$

We first note that  $f_n \cdot Z_n(\mathbb{1}(A))/Z_n(\mathcal{X})$  is the proportion of individuals in generation  $n$  whose trait belongs to  $f_n^{-1}(A)$ . The assumptions require either weak ergodicity and early separation of lineages or strong ergodicity and non-late separation of lineages.

We refer to the next section for various applications, in particular we recover in Section 3.4.1 the classical weak law of large numbers for Markov chains along Galton-Watson trees [DM10] and branching processes in random environment [BH13].

We also mention that the Theorem holds also if  $f_n : \mathcal{X} \rightarrow \mathcal{X}'$  and can be extended to unbounded  $f$  with domination assumptions following [G07]. Finally, let us mention that the a.s. convergence may fail in the theorem above, even in the field of applications we can have in mind. One can think for example of an underlying genealogical tree growing very slowly and each individual is attached with i.i.d. random variable, as appears e.g. in tree indexed random walks.

*Proof.* Let us prove the first part of the Theorem under Assumptions 1(a) and 2(a). In the whole proof,  $x$  is fixed and we omit  $\delta_x$  in the notation of the probability and of the expectation. For convenience, we also write  $m(x, \mathbf{e}_n) := m(x, \mathbf{e}_n, \mathcal{X})$  and denote

$$g_n(x) := f(f_n(x)) - \mu_n(f).$$

Let us compute for  $K \geq 1$ ,

$$\begin{aligned} & \mathbb{E}_{\mathbf{e}_n} (Z_n(g_n)^2) \\ &= \mathbb{E}_{\mathbf{e}_n} \left( \sum_{|u|=|v|=n} g_n(X(u))g_n(X(v)) \right) \\ &= \mathbb{E}_{\mathbf{e}_n} \left( \sum_{\substack{|u|=|v|=n \\ |u \wedge v| < K}} g_n(X(u))g_n(X(v)) \right) + \mathbb{E}_{\mathbf{e}_n} \left( \sum_{\substack{|u|=|v|=n \\ |u \wedge v| \geq K}} g_n(X(u))g_n(X(v)) \right) \end{aligned}$$

The second term of the right hand side is smaller than

$$2 \|f\|_\infty^2 \mathbb{E}(\#\{|u|=|v|=n : |u \wedge v| > K\}) \leq 2b^2 m(x, \mathbf{e}_n)^2 \cdot \epsilon_{K,n},$$

where  $\limsup_{n \rightarrow \infty} \epsilon_{K,n} \rightarrow 0$  as  $K \rightarrow \infty$  using the first part of Assumption 2(a). So we just deal with the first term and consider  $i = 1, \dots, K$ . Thanks to the branching property,

$$\begin{aligned} & \mathbb{E}_{\mathbf{e}_n} \left( \sum_{\substack{|u|=|v|=n \\ |u \wedge v|=i-1}} g_n(X(u))g_n(X(v)) \right) \\ &= \mathbb{E}_{\mathbf{e}_n} \left( \sum_{\substack{|w|=i-1 \\ |wa|=|wb|=i}} \sum_{\substack{|u|=n \\ u \geq wa}} \sum_{\substack{|v|=n \\ v \geq wb}} g_n(X(u))g_n(X(v)) \right) \\ &= \mathbb{E}_{\mathbf{e}_n} \left( \sum_{\substack{|w|=i-1 \\ |wa|=|wb|=i}} R_{i,n}(X(wa))R_{i,n}(X(wb)) \right), \end{aligned}$$

where the many-to-one formula of Lemma 2 allows us to write

$$R_{i,n}(x) := \mathbb{E}_{T^i \mathbf{e}_n, \delta_x} \left( \sum_{|u|=n-i} g_n(X(u)) \right) = m_{n-i}(x, T^i \mathbf{e}_n) Q_{n-i}(x, T^i \mathbf{e}_n, g_n). \quad (10)$$

Then Assumption 1(a) ensures that

$$F_{i,n}(u) := R_{i,n}(X(u))/m_{n-i}(X(u), T^i \mathbf{e}_n)$$

goes to 0 a.s. for each  $i \in \mathbb{N}$ ,  $|u| = i$  uniformly for  $f \in \mathcal{F}$ . We also note that this quantity is bounded by  $b$ . Then,

$$\begin{aligned} & m(x, \mathbf{e}_n, \mathcal{X})^{-2} \mathbb{E}_{\mathbf{e}_n} \left( \sum_{\substack{|u|=|v|=n \\ |u \wedge v| \leq K}} g_n(X(u))g_n(X(v)) \right) \\ &= \mathbb{E}_{\mathbf{e}_n} \left( \sum_{\substack{i \leq K, |w|=i-1 \\ |wa|=|wb|=i}} F_{i,n}(wa)F_{i,n}(wb) \frac{m_{n-i}(X(wa), T^i \mathbf{e}_n)m_{n-i}(X(wb), T^i \mathbf{e}_n, \mathcal{X})}{m_n(x, \mathbf{e}_n)^2} \right). \end{aligned}$$



Adding that

$$\begin{aligned} F_{i,n}(wa)F_{i,n}(wb) \frac{m_{n-i}(X(wa), T^i \mathbf{e}_n) m_{n-i}(X(wb), T^i \mathbf{e}_n)}{m_n(x, \mathbf{e}_n)^2} \\ \leq b^2 \sup_n \frac{m_{n-i}(X(wa), T^i \mathbf{e}_n)}{m_n(x, \mathbf{e}_n)} \cdot \sup_n \frac{m_{n-i}(X(wb), T^i \mathbf{e}_n)}{m_n(x, \mathbf{e}_n)}, \end{aligned}$$

the second part of Assumption 2(a) ensures the  $L_{\mathbf{e}_n}^2$  convergence (9), uniformly for  $f \in \mathcal{F}$ .

The proof of (9) under Assumptions 1(b) and 2(b) is almost the same, replacing  $K$  by  $n - k_n$  with  $k_n \rightarrow \infty$ . Indeed, Assumption 1(b) ensures that there exists  $k_n \rightarrow \infty$  such that

$$\frac{\mathbb{E}_{\mathbf{e}_n, \delta_x} (\#\{|u| = |v| = n : u \wedge v > n - k_n\})}{m_n(x, \mathbf{e}_n)^2} \xrightarrow{n \rightarrow \infty} 0,$$

whereas

$$\begin{aligned} \mathbb{E}_{\mathbf{e}_n} \left( \sum_{\substack{i \leq n - k_n, |w| = i - 1 \\ |wa| = |wb| = i}} F_{i,n}(wa)F_{i,n}(wb) \frac{m_{n-i}(X(wa), T^i \mathbf{e}_n) m_{n-i}(X(wb), T^i \mathbf{e}_n)}{m_n(x, \mathbf{e}_n)^2} \right) \\ \leq \left( \sup_{n-i \geq k_n, x \in \mathcal{X}} F_{i,n}(x) \right)^2 \frac{\mathbb{E}(Z_n(\mathcal{X})^2)}{m_n(x, \mathbf{e}_n)^2}. \end{aligned}$$

Assumption 1(b) ensures that  $\sup_{n-i \geq k_n, x \in \mathcal{X}} F_{i,n}(x) \rightarrow 0$  as  $k_n \rightarrow \infty$  and the second part of Assumption 2(b) ensures that  $\mathbb{E}_{\mathbf{e}_n}(Z_n(\mathcal{X})^2)/m_n(x, \mathbf{e}_n)$  is bounded. The conclusion is thus the same.

The proof of the last part of the Theorem comes simply from Cauchy-Schwarz inequality :

$$\begin{aligned} \mathbb{E}_{\mathbf{e}_n} \left( \mathbb{1}_{Z_n(\mathcal{X})/m_n(x, \mathbf{e}_n) \geq \epsilon} \left[ \frac{f_n \cdot Z_n(f)}{Z_n(\mathcal{X})} - \mu_n(f) \right] \right)^2 \\ \leq \mathbb{E}_{\mathbf{e}_n} \left( \frac{m_n(x, \mathbf{e}_n)^2}{Z_n(\mathcal{X})^2} \mathbb{1}_{Z_n(\mathcal{X})/m_n(x, \mathbf{e}_n) \geq \epsilon} \right) \mathbb{E}_{\mathbf{e}_n} \left( \left[ \frac{f_n \cdot Z_n(f) - Z_n(\mathcal{X}) \mu_n(f)}{m_n(x, \mathbf{e}_n)} \right]^2 \right). \end{aligned}$$

The first term of the right-hand side is bounded with respect to  $n$ . So applying the first part of the theorem to the second term and using Markov inequality ends up the proof.  $\square$

We give now a strong law of large numbers. For that purpose, we define

$$V_i(x_0, x_1) = \sup_{k \geq 0} \frac{m_k(x_0, T^i \mathbf{e}, \mathcal{X}) m_k(x_1, T^i \mathbf{e}, \mathcal{X})}{m_{i+k}(x, \mathbf{e}, \mathcal{X})^2}.$$

**Lemma 5.** *Let  $\mathbf{e} \in E$ ,  $x \in \mathcal{X}$  and assume that*

$$\sum_{n \geq 0} m_n(x, \mathbf{e}, \mathcal{X})^{-1} < \infty; \quad \sum_{i \geq 1} \mathbb{E}_{\mathbf{e}, \delta_x} \left( \sum_{\substack{|w| = i - 1 \\ |wa| = |wb| = i}} V_i(X(wa), X(wb)) \right) < \infty, \quad (11)$$

then  $Z_n(\mathcal{X})/m_n(x, \mathbf{e}, \mathcal{X})$  is bounded in  $L_{\mathbf{e}, \delta_x}^2$ .

The proof of this Lemma is given after the following main result.

**Theorem 4** (Strong LLN). *Let  $\mathbf{e} \in E$ ,  $x \in \mathcal{X}$  and  $f \in \mathcal{B}_b(\mathcal{X})$ .*

*Assume that (11) hold and that there exists a sequence of probability measure  $\mu_n$  on  $\mathcal{X}$  such that*

$$\sup_{i \in \mathbb{N}, f \in \mathcal{F}} \sum_{n \geq i} \sup_{\lambda \in \mathcal{M}_1} |Q_{i,n}(\lambda, T^i \mathbf{e}, f \circ f_n) - \mu_n(f)|^2 < \infty. \quad (12)$$

*Then,*

$$\frac{f_n \cdot Z_n(f) - \mu_n(f) Z_n(\mathcal{X})}{m_n(x, \mathbf{e}_n, \mathcal{X})} \xrightarrow{n \rightarrow \infty} 0 \quad \mathbb{P}_{\mathbf{e}, \delta_x} \text{ a.s.}$$

The first assumption is related to the genealogy of the population and the second one is linked to the ergodic property of the auxiliary Markov chain  $Y$ . Both assumptions are stronger than their counterpart of the previous theorem.

We refer to [G07] for more general conditions on the functions  $f \in \mathcal{F}$  in the fixed environment case, when the reproduction law does not depend on the position.

We note that under the Assumptions of the Theorem,  $Z_n(\mathcal{X})/m_n(x, \mathbf{e}, \mathcal{X})$  is bounded in  $L^2_{\mathbf{e}}$  thanks to the previous Lemma. It entails that the probability of the event  $\{Z_n(\mathcal{X})/m_n(x, \mathbf{e}, \mathcal{X}) \geq \epsilon\}$  is positive for  $\epsilon$  small enough and every  $n \geq 1$ . On this event, we get  $f_n \cdot Z_n(f)/Z_n(\mathcal{X}) - \mu_n(f) \rightarrow 0$  a.s. as  $n \rightarrow \infty$ .

*Proof of Lemma 5.* We again omit the initial state  $\delta_x$  in the notations and write  $m_n(x, \mathbf{e})$  for  $m_n(x, \mathbf{e}, \mathcal{X})$ . Using the branching property and distinguishing if the common ancestor of two individuals lives before generation  $n$  or in generation  $n$ , we have

$$\begin{aligned} \mathbb{E}_{\mathbf{e}}(Z_n(\mathcal{X})^2) &= \mathbb{E}_{\mathbf{e}} \left( \sum_{|u|=|v|=n} 1 \right) \\ &= \mathbb{E}_{\mathbf{e}}(Z_n(\mathcal{X})) + \mathbb{E}_{\mathbf{e}} \left( \sum_{i \leq n} \sum_{\substack{|w|=i-1 \\ |wa|=|wb|=i}} \sum_{\substack{|u|=n:u>wa \\ |v|=n:v>wb}} 1 \right) \\ &= m_n(x, \mathbf{e}) + \sum_{i \leq n} \mathbb{E}_{\mathbf{e}} \left( \sum_{\substack{|w|=i-1 \\ |wa|=|wb|=i}} m_{n-i}(X(wa), T^i \mathbf{e}) m_{n-i}(X(wb), T^i \mathbf{e}) \right). \end{aligned}$$

Then,

$$\frac{\mathbb{E}_{\mathbf{e}}(Z_n(\mathcal{X})^2)}{m_n(x, \mathbf{e})^2} \leq \frac{1}{m_n(x, \mathbf{e})} + \sum_{i \leq n} \mathbb{E}_{\mathbf{e}} \left( \sum_{\substack{|w|=i-1 \\ |wa|=|wb|=i}} V_i(X(wa), X(wb)) \right),$$

which ends up the proof.  $\square$

*Proof of Theorem 4.* To get the a.s. convergence, we prove that

$$\mathbb{E}_{\mathbf{e}} \left( \sum_{n \geq 1} \left[ \frac{f_n \cdot Z_n(f) - \mu(f) Z_n(\mathcal{X})}{m_n(x, \mathbf{e})} \right]^2 \right) < \infty.$$

For that purpose, we use the notations of the proof of the previous Theorem, in particular

$$g_n(x) := f(f_n(x)) - \mu_n(f)$$

and we are inspired by [G07]. Using Fubini inversion, the branching property and (10), we have

$$\begin{aligned} & \sum_{n \geq 0} m_n(x, \mathbf{e})^{-2} \mathbb{E}_{\mathbf{e}}(Z_n(g_n)^2) \\ &= \mathbb{E}_{\mathbf{e}} \left( \sum_{n \in \mathbb{N}} \sum_{|u|=|v|=n} m_n(x, \mathbf{e})^{-2} g_n(X(u)) g_n(X(v)) \right) \\ &= \mathbb{E}_{\mathbf{e}} \left( \sum_{n \in \mathbb{N}} \sum_{i \leq n} \sum_{\substack{|u|=|v|=n \\ |u \wedge v|=i}} m_n(x, \mathbf{e})^{-2} g_n(X(u)) g_n(X(v)) \right) \\ &= \mathbb{E}_{\mathbf{e}} \left( \sum_{i \leq n} \sum_{\substack{|w|=i-1 \\ |wa|=|wb|=i}} \sum_{\substack{|u|=n: u \geq wa \\ |v|=n: v \geq wb}} m_n(x, \mathbf{e})^{-2} g_n(X(u)) g_n(X(v)) \right) \\ &\quad + \mathbb{E}_{\mathbf{e}} \left( \sum_{n \in \mathbb{N}, |u|=n} m_n(x, \mathbf{e})^{-2} g_n(X(u))^2 \right) \\ &\leq \mathbb{E}_{\mathbf{e}} \left( \sum_{i \leq n} \sum_{\substack{|w|=i-1 \\ |wa|=|wb|=i}} \frac{m_{n-i}(X(wa), T^i \mathbf{e}) m_{n-i}(X(wb), T^i \mathbf{e})}{m_n(x, \mathbf{e})^2} R_{i,n}(X(wa)) R_{i,n}(X(wb)) \right) \\ &\quad + 2 \|g_n\|_{\infty} \mathbb{E}_{\mathbf{e}} \left( \sum_{n \in \mathbb{N}} m_n(x, \mathbf{e})^{-2} Z_n(\mathcal{X}) \right) \\ &\leq \mathbb{E}_{\mathbf{e}} \left( \sum_{\substack{i \in \mathbb{N}, |w|=i-1 \\ |wa|=|wb|=i}} V_i(X(wa), X(wb)) H_i \right) + b \sum_{n \in \mathbb{N}} m_n(x, \mathbf{e})^{-1}, \end{aligned}$$

where  $b := (2 \|f\|_{\infty})^2$  and

$$H_i = \sup_{y, z} \sum_{n \geq i} R_{i,n}(y) R_{i,n}(z), \quad V_i(x_0, x_1) = \sup_{n \geq i} \frac{m_{n-i}(x_0, T^i \mathbf{e}) m_{n-i}(x_1, T^i \mathbf{e})}{m_n(x, \mathbf{e})^2}.$$

Then, the assumptions ensure that

$$\begin{aligned} \sum_{n \geq 0} m_n(x, \mathbf{e}, \mathcal{X})^{-2} \mathbb{E}_{\mathbf{e}}(Z_n(g_n)^2) &\leq b \sum_{n \geq 0} m_n(x, \mathbf{e})^{-1} \\ &\quad + \sup_{i \in \mathbb{N}} H_i \cdot \sum_{i \in \mathbb{N}} \mathbb{E} \left( \sum_{\substack{|w|=i-1 \\ |wa|=|wb|=i}} V_i(X(wa), X(wb)) \right) < \infty. \end{aligned}$$

Then,  $Z_n(g_n)/m_n(x, \mathbf{e}) \rightarrow 0$  a.s., which completes the proof.  $\square$

### 3.4 Applications

We now provide some applications of the previous results.

#### 3.4.1 Weak law of large numbers along branching trees

First, we consider the neutral case, which means that the reproduction law of the individuals to do not depend on their trait. So the underlying genealogy is simply a branching process (possibly non-homogeneous) and Assumption 2(a) can be easily checked. We also note that  $m_n := m_n(x, \mathbf{e}, \mathcal{X}) = \prod_{j=0}^{n-1} m(x, T^j \mathbf{e})$  does not depend on  $x$ . Thanks to Theorem 3, we only require weak ergodicity of the auxiliary Markov chain, whose kernel transition simplifies as

$$Q_n(x, \mathbf{e}, dy) := m_1(x, \mathbf{e}, dy) \frac{1}{m_1(x, \mathbf{e}, \mathcal{X})} = P(x, \mathbf{e}, dy).$$

Moreover  $W_n = Z_n/m_n$  is (a.s. with respect to the environment) a martingale which converges to a positive limit on the non extinction event thanks to  $L^2$  assumptions, so that we obtain

$$\mathbb{P}_{\mathbf{e}} \left( \left| \frac{f_n \cdot Z_n(f)}{Z_n(\mathcal{X})} - \mu_n(f) \right| \geq \eta ; \forall n \in \mathbb{N}, Z_n(\mathcal{X}) > 0 \right) \xrightarrow{n \rightarrow \infty} 0.$$

We recover here classical weak law of large numbers for proportions of individuals with a given trait for Markov chains along trees, such as Galton-Watson trees [G07] (Section 2.2), [DM10] (Theorem 1.3) and branching processes in random environment [BH13] (Theorem 3.2).

#### 3.4.2 Under Doeblin type conditions

For convenience, we assume here strong Doeblin type conditions on the mean measure, in the same vein as Section 2.

**Assumption 3.** There exist  $M : E \rightarrow [1, \infty)$  such that for all  $x \in \mathcal{X}, \mathbf{e} \in E$ ,

$$m_1(x, \mathbf{e}, A) \leq M(\mathbf{e})m_1(y, \mathbf{e}, A).$$

We could relax this assumption, for example by requiring such an inequality for  $m_b$  instead of  $m$ , for some  $b \geq 1$ . We note that this assumption hold if both  $m(x, \mathbf{e})$  and  $P(x, \mathbf{e}, \cdot)$  satisfy the analogous condition. We refer to the next part and to [M13] for more general conditions in the-non homogeneous framework.

Let us denote

$$\sigma(\mathbf{e}) := \sup_{x \in \mathcal{X}} \mathbb{E}(N(x, \mathbf{e})^2), \quad D(\mathbf{e}) := \frac{\sigma(\mathbf{e})M(\mathbf{e})M(T\mathbf{e})^2}{m(x, T\mathbf{e})}$$

to state the result.

**Corollary 3.** Let  $\mathbf{e} \in E, x \in \mathcal{X}$  and  $f \in \mathcal{B}_b(\mathcal{X})$ . We assume that Assumption 3 holds with

$$\sum_{n \geq 1} \frac{1 + D(T^{n-1}\mathbf{e})}{m_n(x, \mathbf{e}, \mathcal{X})} < \infty, \quad \sum_{n \geq 0} \prod_{k=0}^n (1 - 1/M(T^k \mathbf{e})^2) < \infty. \quad (13)$$

Then,  $Z_n(\mathcal{X})/m_n(x, \mathbf{e}, \mathcal{X})$  is bounded in  $L_{\mathbf{e}, \delta_x}^2$  and

$$\frac{Z_n(f) - Z_n(\mathcal{X})Q_{0,n}(x, \mathbf{e}, f)}{m_n(x, \mathbf{e}, \mathcal{X})} \xrightarrow{n \rightarrow \infty} 0 \quad \mathbb{P}_{\mathbf{e}, \delta_x} \quad a.s.$$

The assumptions above ensure that  $m_n(x, \mathbf{e}, \mathcal{X})$  goes to  $\infty$  (supercriticality). The assumptions are fulfilled for example if  $m_n$  tends fast enough to  $\infty$  and both  $\sigma, M, m$  are bounded.

The proof here uses Theorem 4 and some additional lemma allowing to check the assumptions required. We may derive an application of this result to the random environment framework directly or relax the assumptions to get only convergence in probability.

The fact that  $Z_n(\mathcal{X})/m_n(x, \mathbf{e}, \mathcal{X})$  is bounded in  $L_{\mathbf{e}, \delta_x}^2$  ensures that  $Z_n(\mathcal{X}) \rightarrow \infty$  with positive probability. Using Paley-Sigmund inequality and a stronger assumption in the first part of (13) to ensure the uniformity with respect to the initial environment, one can prove that  $\liminf_{n \rightarrow \infty} Z_n(\mathcal{X})/m_n(x, \mathbf{e}, \mathcal{X}) > 0$  on the event  $\{Z_n(\mathcal{X}) \rightarrow \infty\}$ . Then,  $\mathbb{P}_{\mathbf{e}, \delta_x}$  a.s on the event  $\{Z_n(\mathcal{X}) \rightarrow \infty\}$ , we have  $Z_n(f)/Z_n(\mathcal{X}) - Q_{0,n}(x, \mathbf{e}, f) \rightarrow 0$  as  $n \rightarrow \infty$ .

**Lemma 6.** *Under Assumption 3, for all  $x, y \in \mathcal{X}, \mathbf{e} \in E, n \geq 0, A \in \mathcal{B}_{\mathcal{X}}$ ,*

$$\frac{m_n(x, \mathbf{e})}{m_n(y, \mathbf{e})} \in [M(\mathbf{e})^{-1}, M(\mathbf{e})], \quad Q_n(x, \mathbf{e}, A) \leq M(\mathbf{e})^2 Q_n(y, \mathbf{e}, A).$$

*Proof.* We have

$$\begin{aligned} m_n(x, \mathbf{e}) &= \int_{\mathcal{X}} m_1(x, \mathbf{e}, dz) m_{n-1}(z, T\mathbf{e}) \leq M(\mathbf{e}) \int_{\mathcal{X}} m_1(y, \mathbf{e}, dz) m_{n-1}(z, T\mathbf{e}) \\ &\leq M(\mathbf{e}) m_n(y, \mathbf{e}). \end{aligned}$$

It yields the first part of the lemma. We then write

$$\begin{aligned} Q_n(x, \mathbf{e}, A) &= \int_{\mathcal{X}} \frac{m_1(x, \mathbf{e}, dz)}{m_n(x, \mathbf{e})} m_{n-1}(z, T\mathbf{e}, A) \\ &\leq M(\mathbf{e})^2 \int_{\mathcal{X}} \frac{m_1(y, \mathbf{e}, dz)}{m_n(y, \mathbf{e})} m_{n-1}(z, T\mathbf{e}, A) \leq M(\mathbf{e})^2 Q_n(y, \mathbf{e}, A) \end{aligned}$$

to get the second part of the lemma.  $\square$

*Proof of Corollary 3.* Using the branching property in generation  $i$  and the first part of Lemma 6, we have for all  $x, y \in \mathcal{X}$ ,

$$m_{i+k}(x, \mathbf{e}) \geq m_i(x, \mathbf{e}) M(T^i \mathbf{e})^{-1} m_k(y, T^i \mathbf{e}).$$

Then, letting  $y = x_0, x_1$ ,

$$V_i(x_0, x_1) = \sup_{k \geq 0} \frac{m_k(x_0, T^i \mathbf{e}) m_k(x_1, T^i \mathbf{e})}{m_{k+i}(x, \mathbf{e})^2} \leq \frac{M(T^i \mathbf{e})^2}{m_i(x, \mathbf{e})^2}.$$

Moreover  $m_i(x, \mathbf{e}) \geq m_{i-1}(x, \mathbf{e}) M(T^{i-1} \mathbf{e}) m(x, T^{i-1} \mathbf{e})$  and

$$\begin{aligned} \sum_{i \geq 1} \mathbb{E}_{\mathbf{e}, \delta_x} \left( \sum_{|w|=i-1} \sum_{|wa|=|wb|=i} V_i(X(wa), X(wb)) \right) &\leq \sum_{i \geq 1} \mathbb{E}_{\mathbf{e}, \delta_x} (Z_{i-1}(\mathcal{X})) \sigma(T^{i-1} \mathbf{e}) \frac{M(T^i \mathbf{e})^2}{m_i(x, \mathbf{e})^2} \\ &\leq \sum_{i \geq 1} \sigma(T^{i-1} \mathbf{e}) \frac{M(T^{i-1} \mathbf{e}) M(T^i \mathbf{e})^2}{m(x, T^{i-1} \mathbf{e}) m_i(x, \mathbf{e})}. \end{aligned}$$

So the first part of (13) ensures that (11) is fulfilled and Lemma 5 ensures that  $Z_n(\mathcal{X})/m_n(x, \mathbf{e})$  is bounded in  $L^2_{\mathbf{e}, \delta_x}$ . The first part of the Theorem is proved and we prove now the a.s. convergence.

Using the second part of Lemma 6, we first get the geometric ergodicity of  $Q_{i,n}$ . Indeed, a simple induction leads to

$$|Q_{i,n}(\lambda, \mathbf{e}, f) - Q_{i,n}(\mu, \mathbf{e}, f)| \leq \|f\|_\infty \prod_{j=i}^{n-1} (1 - 1/M(T^j \mathbf{e})^2)$$

and the second part of (13) ensures that (12) hold. Then Theorem 4 yields the expected a.s. convergence.  $\square$

### 3.4.3 Under Lyapounov type conditions

One can relax the conditions of Section 3.4.2 and still get the geometric ergodicity of  $Q_{i,n}$  via Harris ergodic theorems. A well known method relies on the use of Lyapounov function outside a compact set, see e.g. [MT09, HM08]. The results can be easily adapted to the non-homogeneous setting required here to get sufficient conditions for (3), Assumption 1(b) or (12).

But one also need to control the underlying genealogy to get a law of large numbers. The additional work required to apply finely Theorem 4 seems beyond the scope of this paper and could be a future work. Let us note that Theorem 2 can be more easily applied and yields to first interesting results.

### 3.4.4 Comments on multitype branching processes

When the state space  $\mathcal{X}$  is finite, the process  $Z$  is a multitype branching process and much finer results can be obtained. In particular, the limit behavior of  $Z_n/m_n(x, \mathbf{e}, \mathcal{X})$  is known, see e.g. [KLPP97] in fixed environment and [C89] in random environment. Let us still mention that we provide in Lemma 2 a slightly different spine decomposition than [KLPP97], without projection with respect to the eigenvector associated to the mean operator. It might be of interest. Finally, we note that Corollary 3 may be applied easily to get new results in varying environment.

In the two next applications, we consider the case when the reproduction law does not depend on the trait, so  $Q_{i,n}$  just depends on  $i$  and the auxiliary Markov chain with kernel  $Q_i$  is denoted by  $Y$ . We focus in these two examples on the functions  $f_n$  one can use to derive relevant results.

### 3.4.5 Comments on branching random walks and random environment

Branching random walks have been largely studied from the pioneering works of Biggins (see e.g. [B77]) and central limit theorems have been obtained to describe the repartition of the population for large times [B90].

For branching random walks (possibly in varying environment in time and space), the auxiliary Markov chain  $Y$  is a random walk (possibly in varying environment in time and space). To get law of large numbers for  $Z_n$ , one can then check that some convergence in law

$$(Y_n - a_n)/b_n \Rightarrow W$$

where the limit  $W$  does not depend on the initial state  $x \in \mathcal{X}$ . Then we can use Theorem 3 with  $f_n(x) = (x - a_n)/b_n$  to obtain the asymptotic proportion of individuals whose trait  $x$  satisfies  $f_n(x) \in [a, b]$ . It is given by  $\mathbb{P}(W \in [a, b])$  soon as  $\mathbb{P}(W \in \{a, b\}) = 0$ .

Thus it can be used when the auxiliary process satisfies a central limit theorem. We refer to [BH13] Section 3.4 for some examples in the case when the reproduction law does not depend on the trait  $x \in \mathcal{X}$  and the environment is stationary ergodic in time.

One can actually directly derive some (rougher) law of large numbers directly from the speed of random walk (in environment), i.e. use  $Y_n/a_n \Rightarrow v$ . As an example, we recall that in dimension 1 the random walk in random environment  $Y$  may be subalistic and  $b_n = n^\gamma$  with  $\gamma \in (0, 1)$ .

We finally mention [N11] when the offspring distribution is chosen in an i.i.d. manner for each time  $n$  and location  $x \in \mathbb{Z}$ .

### 3.4.6 Comments on Kimmel's cell infection model and non-ergodicity

In the Kimmel's branching model [B08] for cell division with parasite infection, the auxiliary Markov chain  $Y_n$  is a Galton-Watson in (stationary ergodic) random environment. For example, in the case when no extinction is possible, i.e.  $\mathbb{P}_1(Y_1 > 0) = 1$ , under the usual integrability assumption we have

$$Y_n / \prod_{i=0}^{n-1} m_i \xrightarrow{n \rightarrow \infty} W \in (0, \infty) \quad \text{a.s.}$$

where  $m_i$  is the mean number of offsprings for each parasite in generation  $i$ . We note that the distribution of  $W$  depends on the initial value of  $Y$ . But

$$\log(Y_n)/n \xrightarrow{n \rightarrow \infty} \mathbb{E}(\log m_0) \quad \text{a.s.}$$

and the limit here does not depend on  $Y_0$  anymore. So we get the ergodic property required to use Theorem 3 with  $f_n(x) = \log(x)/n$ . We obtain that the proportion of cells in generation whose number of parasites is between  $\exp([\mathbb{E}(\log m_0) - \epsilon]n)$  and  $\exp([\mathbb{E}(\log m_0) + \epsilon]n)$  goes to 1 in probability, for every  $\epsilon > 0$ . This yields some first new result on the infection propagation, which could be improved by additional work.

Soon as the number of parasites in a cell can be equal to zero, i.e.  $\mathbb{P}_1(Y_1 = 0) > 0$ , ergodicity is failing and some additional work is needed. Using monotonicity argument, one may still conclude, see [B08] for an example.

## 4 Local densities and extremal particles.

We deal now with local densities and the associated ancestral lineages. More precisely, we focus on the number of individuals whose trait belongs to some set  $A_n$  in generation  $n$ , when  $n \rightarrow \infty$ .

We have proved the many-to-one formula

$$\mathbb{E}(Z_n(A_n)) = m_n(x, \mathbf{e}, \mathcal{X}) Q_{0,n}(x, \mathbf{e}, A_n)$$

in the previous section. We have then checked that the ergodicity of  $Q_{0,n}$  ensures that  $Z_n(A)/m_n(x, \mathbf{e}, \mathcal{X}) - Q_{0,n}(x, \mathbf{e}, A)$  goes to zero under some conditions.

Now we wish to compare the asymptotic behaviors of  $Z_n(A_n)$  and

$m_n(x, \mathbf{e}, \mathcal{X})Q_{0,n}(x, \mathbf{e}, A_n)$ , when  $Q_{0,n}(x, \mathbf{e}, A_n) \rightarrow 0$  as  $n \rightarrow \infty$ . In particular, we are studying the links between the local densities  $Z_n(A_n)$  for large times and the large deviations events of  $Q_{0,n}$ , i.e. the asymptotic behavior of  $Q_{0,n}(x, \mathbf{e}, A_n)$ .

Such questions have been well studied for branching random walks from the pioneering work of Biggins [B77], and we refer to [R93, HS09] for related results and to [R00, S08] for reviews on the topic. We also mention [CP07b, N12] for the random environment framework and [DMS05] for large deviations Markov chain along tree with  $n$  vertices.

The upper bound for such results comes directly from Markov inequality and we are working on the lower bound. As usual, we could then derive the rough asymptotic behavior of the extremal (minimal or maximal position) individual. It covers classical results for branching random walks on the speed of the extremal individual at the log scale. We provide some other examples motivated by cell's infection model, where the associated deviation strategy is more subtle. We mention also that  $Z_n(A_n)$  may be negligible compared to  $m_n(x, \mathbf{e}, \mathcal{X})Q_{0,n}(x, \mathbf{e}, A_n)$ .

**Definition 2.** For all  $0 \leq i \leq n$ ,  $A, B \in \mathcal{B}_{\mathcal{X}}$ , we define the measure

$$\mu_{i,n}(A, \mathbf{e}, B)[l, \infty) := \inf_{x \in A} \mathbb{P}_{\delta_x, T^i \mathbf{e}}(Z_{n-i}(B) \geq l)$$

We note  $\bar{\mu}$  the mean of  $\mu$  and  $\hat{\mu}$  the variance of  $\mu/\bar{\mu}$ , so that

$$\bar{\mu}_{i,n}(A, \mathbf{e}, B) = \sum_{l \geq 1} \mu_{i,n}(A, \mathbf{e}, B)[l, \infty), \quad \hat{\mu}_{i,n}(A, \mathbf{e}, B) = \frac{\sum_{l \geq 1} l^2 \mu_{i,n}(A, \mathbf{e}, B)\{l\}}{\bar{\mu}_{i,n}(A, \mathbf{e}, B)^2} - 1.$$

We start by coupling our process in the first stages by a particular branching process in varying environment to use both the convergence of the associated martingale during these first steps ( $i = 0, \dots, \phi(n)$ ) and a law of large number argument on the remaining time ( $i = 0, \dots, \psi(n)$ ).

**Lemma 7.** Let  $\mathbf{e}$  and  $x \in \mathcal{X}$ . We assume that there exists a non-decreasing sequence  $k_i$  of integers and a sequence  $B_i$  of subsets of  $\mathcal{X}$  such that

$$x \in B_0, \quad \liminf_{i \rightarrow \infty} \bar{\mu}_{k_i, k_{i+1}}(B_i, \mathbf{e}, B_{i+1}) > 1, \quad \sum_{i \geq 0} \frac{\hat{\mu}_{k_i, k_{i+1}}(B_i, \mathbf{e}, B_{i+1})}{\prod_{i=0}^{n-1} \bar{\mu}_{k_i, k_{i+1}}(B_i, \mathbf{e}, B_{i+1})} < \infty.$$

Then there exists an event  $A$  whose probability is positive, such that for any non-decreasing sequence of integers  $\phi_n, \psi_n$  and  $k_{i,n}$  and any sequence  $B_{i,n}$  of subsets of  $\mathcal{X}$  which satisfy

$$k_{0,n} = k_{\phi_n}, \quad \phi_n \rightarrow \infty, \quad \sup_n \sum_{i=0}^{\psi_n-1} \frac{\hat{\mu}_{k_{i,n}, k_{i+1,n}}(B_{i,n}, \mathbf{e}, B_{i+1,n})}{\prod_{i=0}^{n-1} \bar{\mu}_{k_{i,n}, k_{i+1,n}}(B_{i,n}, \mathbf{e}, B_{i+1,n})} < \infty,$$

we have

$$\left\{ \liminf_{n \rightarrow \infty} \frac{Z_n(B_{n, \psi_n})}{P_n} > 0 \right\} \supset A,$$

where

$$P_n := \prod_{i=0}^{\phi_n-1} \bar{\mu}_{k_i, k_{i+1}}(B_i, \mathbf{e}, B_{i+1}) \cdot \prod_{i=0}^{\psi_n-1} \bar{\mu}_{k_{i,n}, k_{i+1,n}}(B_{i,n}, \mathbf{e}, B_{i+1,n})$$



*Proof.* We use a coupling of the branching Markov chain  $Z$  with a supercritical Branching Process in Varying Environment (BPVE). Roughly speaking, it is obtained by selecting the individuals whose lineage lives in the tube  $(B_i : i \leq \phi(n), B_{j,n} : j \leq \psi_n)$ . More precisely, we consider the subpopulation of  $Z$  constructed recursively by keeping the descendance of the population in generation  $k_i$  whose trait belongs to  $B_i$  for  $i \leq \phi_n$  and then belongs to  $B_{j,n}$  for  $j \leq \psi_n$ . The size of the population obtained by this construction in generation  $k_i$  is a.s. larger than a branching process  $N_i$  whose reproduction law in generation  $i$  is  $\mu_i := \mu_{k_i, k_{i+1}}(B_i, \mathbf{e}, B_{i+1})$ . Similarly, the size of the population in generation  $k_{\psi_n, n}$  is larger than a branching process in varying environment, with initial value equal to  $N_{\phi_n}$  and successive reproduction laws  $\mu_{j,n} := \mu_{k_{j,n}, k_{j+1,n}}(B_{j,n}, \mathbf{e}, B_{j+1,n})$  for  $j = 0, \dots, \psi_n$ . Thus,

$$Z_n(B_{n, \psi(n)}) \geq \sum_{j=1}^{N_{\phi_n}} U_{j,n},$$

where  $U_{j,n}$  is distributed as a BPVE in generation  $\psi_n$ , denoted by  $U_n$ , whose successive reproduction laws are  $\mu_{k_i, n, k_{i+1, n}}(B_{i,n}, \mathbf{e}, B_{i+1, n})$  for  $i = 0, \dots, \psi_n - 1$ . Moreover  $(U_{j,n} : j = 0, \dots, \psi_n)$  are independent by branching property.

Using the assumption

$$\sum_{i \geq 0} \frac{\text{Var}(\mu_i / \bar{\mu}_i)}{\prod_{j=0}^{i-1} \bar{\mu}_j} < \infty,$$

we know by orthogonality that the martingale

$$\frac{N_i}{\prod_{j=0}^{i-1} \bar{\mu}_j}$$

converges in  $L_{\mathbf{e}}^2$  and has a finite positive limit  $W$  on the survival event  $A := \{\forall n \geq 0 : N_n > 0\}$ . Recalling that  $\liminf_{i \rightarrow \infty} \bar{\mu}_i > 1$  by assumption,  $A$  has positive probability and conditionally on that event, we have a.s.

$$\liminf_{i \rightarrow \infty} \frac{N_{i+1}}{N_i} > 1.$$

Similarly  $U_{j,n} / \mathbb{E}(U_{j,n})$  is bounded by the moment assumptions and

$$X_{j,n} \stackrel{d}{=} \frac{U_{j,n} - \mathbb{E}(U_{j,n})}{\mathbb{E}(U_{j,n})}$$

are independent random variables, which are independent of  $(N_i : i = 0, \dots, \phi_n)$  and bounded in  $L_{\mathbf{e}}^2$ . Thanks to Lemma 3,

$$\frac{1}{N_{k_{\phi_n}}} \sum_{j=1}^{N_{k_{\phi(n)}}} X_{j,n}$$

goes to 0 as  $n \rightarrow \infty$  a.s. on the event  $A$ . Then

$$Z_n(B_{n, \psi(n)}) \geq N_{k_{\phi_n}} \mathbb{E}(U_n) \cdot [1 + \epsilon_n]$$

where  $\epsilon_n \rightarrow 0$ . Finally, we use

$$\mathbb{E}(N_{k_{\phi_n}}) = \prod_{i=0}^{\phi_n-1} \bar{\mu}_{k_i, k_{i+1}}(B_i, \mathbf{e}, B_{i+1}), \quad \mathbb{E}(U_n) = \prod_{i=0}^{\psi_n-1} \bar{\mu}_{k_i, n, k_{i+1, n}}(B_{i,n}, \mathbf{e}, B_{i+1, n})$$

to get

$$\liminf_{n \rightarrow \infty} \frac{Z_n(B_{n,\psi_n})}{P_n} \geq \liminf_{n \rightarrow \infty} \frac{N_{\phi_n}}{\mathbb{E}(N_{\phi_n})} (1 + \epsilon_n) \geq W.$$

Recalling that  $A = \{W > 0\}$  and it has positive probability ends up the proof.  $\square$

#### 4.1 Monotone Branching Markov chain

Our aim is to see the local densities in terms of the large deviations of the auxiliary process and the way this large deviation event is achieved. First, let us derive from the previous lemma the number of individuals in  $A_n = [a_n, \infty) := \{x \in \mathcal{X} : x \geq a_n\}$  in the monotone case, which yields the applications for the cell models and branching random walks which initially motivated these questions.

Thus, by now, we assume that  $\mathcal{X}$  is totally ordered by  $\leq$  and the branching Markov chain satisfies the following condition.

**Assumption 4** (Monotonicity). For all  $x \leq y$ ,  $\mathbf{e} \in E$  and  $a \in \mathcal{X}$ , we have

$$\mathbb{P}_{\delta_x, \mathbf{e}}(Z_1([a, \infty)) \geq l) \leq \mathbb{P}_{\delta_y, \mathbf{e}}(Z_1([a, \infty)) \geq l) \quad (l \geq 0).$$

**Assumption 5** (Mean growth rate). Let  $\rho > 0$  such that

$$\lim_{n \rightarrow \infty} \frac{1}{n} \log m_n(x, \mathbf{e}, [a_n, \infty)) = \rho.$$

We also assume that there exist  $p \geq 1$  and  $b_i \in \mathcal{X}$  such that  $x \geq b_0$  and

$$\liminf_{i \rightarrow \infty} m_p(b_i, T^{ip} \mathbf{e}, [b_{i+1}, \infty)) > 1.$$

Finally, for every  $\epsilon > 0$ , there exist  $q = q(\epsilon)$ ,  $\phi(n) \rightarrow \infty$  and  $(b_{j,n} : j, n \geq 0)$  such that

$$\liminf_{n \rightarrow \infty} \frac{1}{n} \sum_{j < (n - \phi(n)p)/q} \log m_q(b_{j,n}, T^{i\phi(n) + jq} \mathbf{e}, [b_{j+1,n}, \infty)) \geq \rho - \epsilon.$$

The values  $(b_i : i \leq \phi(n), b_{j,n} : j \leq \psi(n))$  correspond to the (lower) curve which yields the trait of the subpopulation which realizes the main contribution to the population size  $Z_n([a_n, \infty))$  in generation  $n$ . This curve is a (straight) line for branching random walk or for  $a_n = 1$  in the Kimmel's branching model [B08], see below. But this curve is not straight for the other quantities of interest in Kimmel's branching model, such as the large deviations associated to  $a_n \rightarrow \infty$ . Other motivating examples when the curve are not a straight are given by large deviation events which are realized in one step of the process. It can be the case for random walks with heavy tails or autoregressive processes.

**Theorem 5.** Let  $\mathbf{e} \in E$  and  $x \in \mathcal{X}$ . Under the Assumptions 4, 5 and

$$\sup \{ \mathbb{E}(N(z, T^k \mathbf{e})^2) : z \in \mathcal{X}, k \geq 0 \} < \infty,$$

then

$$\mathbb{P}_{\mathbf{e}, \delta_x} \left( \frac{1}{n} \log Z_n([a_n, \infty)) \xrightarrow{n \rightarrow \infty} \rho \right) > 0.$$

The upper bound of the convergence above is actually a.s. Letting the initial population go to infinity in this statement allows to get the convergence a.s. by branching property. Getting the result a.s. on the survival event seems to require additional assumptions.

The uniform bound on the second moment assumption can be relaxed (see the proof), in particular the bound can depend on the environment to capture some branching models in random environment.

*Proof.* As for branching random walks, the upper bound comes directly from Markov inequality. For every  $\eta > 0$ ,

$$\mathbb{P}_{x,\mathbf{e}}(Z_n([a_n, \infty)) \geq \exp((\rho + \eta)n)) \leq \exp(-(\rho + \eta)n)m_n(x, \mathbf{e}, [a_n, \infty)),$$

so that the first part of the Assumption 5 ensures that the right hand side is summable. Then Borel-Cantelli lemma yields the a.s. upper bound.

The lower bound comes from the previous Lemma with

$$k_i = ip, \quad k_{n,j} = \phi_n p + jq, \quad B_j = [b_j, \infty), \quad B_{j,n} = [b_{j,n}, \infty), \quad \psi_n = [(n - \phi_n p)/q],$$

where  $i = 0, \dots, \phi_n$ ,  $j = 0, \dots, \psi_n$  and  $[x]$  is the smallest integer larger or equal to  $x$ . By Assumption 4 (monotonicity),

$$\mu_{k_j, k_{j+1}}(B_j, \mathbf{e}, B_{j+1})(\cdot) := \mathbb{P}_{\delta_{b_j}, T^{k_j} \mathbf{e}}(Z_{k_{j+1}-k_j}([b_{j+1}, \infty)) = \cdot)$$

and the definition of  $\mu_{k_j, n, k_{j+1}, n}(B_{j,n}, \mathbf{e}, B_{j+1, n})(\cdot)$  is analogous. So

$$\bar{\mu}_{k_j, k_{j+1}}(B_j, \mathbf{e}, B_{j+1}) = m_{k_{j+1}-k_j}(b_j, T^{k_j} \mathbf{e}, [b_{j+1}, \infty)) = m_p(b_j, T^{jp} \mathbf{e}, [b_{j+1}, \infty)).$$

and the analogous identity hold for  $\bar{\mu}_{k_j, n, k_{j+1}, n}(B_{j,n}, \mathbf{e}, B_{j+1, n})$ . By Assumption 5, we have for  $\epsilon \in (0, \rho)$ ,

$$\liminf_{j \rightarrow \infty} \bar{\mu}_{k_j, k_{j+1}}(B_j, \mathbf{e}, B_{j+1}) > 1, \quad \liminf_{n \rightarrow \infty} \frac{1}{n} \log(\prod_{j=0}^{\psi_n-1} \bar{\mu}_{k_j, n, k_{j+1}, n}(B_{j,n}, \mathbf{e}, B_{j+1, n})) \geq \rho - \epsilon > 0.$$

Recalling that  $\sup\{\mathbb{E}(N(x, T^k \mathbf{e})^2) : x \in \mathcal{X}, k \geq 0\} < \infty$  is assumed, we get

$$\sum_{i \geq 0} \frac{\hat{\mu}_{k_i, k_{i+1}}(B_i, \mathbf{e}, B_{i+1})}{\prod_{j=0}^{i-1} \bar{\mu}_{k_j, k_{j+1}}(B_j, \mathbf{e}, B_{j+1})} < \infty; \quad \sup_n \sum_{i=0}^{\psi_n-1} \frac{\hat{\mu}_{k_i, n, k_{i+1}, n}(B_{i,n}, \mathbf{e}, B_{i+1, n})}{\prod_{j=0}^{i-1} \bar{\mu}_{k_j, n, k_{j+1}, n}(B_{j,n}, \mathbf{e}, B_{j+1, n})} < \infty.$$

Thus, we can apply Lemma 7 and get

$$A \subset \left\{ \liminf_{n \rightarrow \infty} \frac{Z_n([a_n, \infty))}{\prod_{i=1}^{\psi_n} \bar{\mu}_{k_i, n, k_{i+1}, n}(B_{i,n}, \mathbf{e}, B_{i+1, n})} > 0 \right\} \subset \left\{ \liminf_{n \rightarrow \infty} \frac{1}{n} \log Z_n([a_n, \infty)) \geq \rho - \epsilon \right\}$$

Noting that  $A$  is fixed when  $\epsilon \rightarrow 0$  and  $\mathbb{P}(A) > 0$  ends up the proof.  $\square$

As expected, we can now precise the asymptotic behavior of the extremal individuals. If  $a_n(x)$  satisfies the assumptions of Theorem 5 with some rate  $\rho(x)$ , then, for every  $x$  such that  $\rho(x) > \log m$ ,

$$\limsup_{n \rightarrow \infty} \frac{\max\{X(u) : |u| = n\}}{a_n(x)} \leq 1 \quad \mathbb{P}_{\delta_x, \mathbf{e}} \text{ a.s.}$$

and for every  $x$  such that  $\rho(x) < \log m$ ,

$$\liminf_{n \rightarrow \infty} \frac{\max\{X(u) : |u| = n\}}{a_n(x)} \geq 1 \quad \mathbb{P}_{\delta_x, \mathbf{e}} \text{ a.s.}$$

on some event whose probability is positive.

The proof is standard. The first part comes directly from Borel-Cantelli Lemma, recalling that

$$\mathbb{P}_{\delta_x, \mathbf{e}}(\max\{X(u) : |u| = n\} \geq a_n(x)) \leq \mathbb{E}_{\delta_x, \mathbf{e}}(Z_n([a_n(x), \infty))) = m(x, \mathbf{e}, [a_n(x), \infty))$$

decreases exponentially with rate  $\rho - \rho(x)$ . The second part comes from the Theorem 5 which ensures that there are many particles beyond  $a_n(x)$ .

## 4.2 Monotone Markov chain indexed by branching trees

Let us specify in a simpler framework the results above, more precisely the link between the local densities and the large deviations of the auxiliary chain. We assume here that the reproduction law does not depend on the trait of the individual, so that

$$N(\mathbf{e}) := N(x, \mathbf{e}), \quad m(\mathbf{e}) := m(x, \mathbf{e}), \quad m_n(\mathbf{e}) := m_n(x, \mathbf{e}, \mathcal{X}) = \prod_{i=0}^{n-1} m(T^i \mathbf{e}). \quad (14)$$

As above, we require the monotonicity of the trait distribution : assume :

**Assumption 6** (Monotonicity of  $P$ ). For all  $x \leq y$ ,  $\mathbf{e} \in E$  and  $a \in \mathcal{X}$ , we have

$$P(x, \mathbf{e}, [a, \infty)) \leq P(y, \mathbf{e}, [a, \infty)).$$

We assume also that the large deviations of  $Q_{i,n}$  beyond  $a_n$  occur with rate  $\alpha > 0$  and that the beginning of the associated trajectory is supercritical, i.e.

**Assumption 7** (Large deviations of the auxiliary process  $Q$ ). There exists  $\alpha \geq 0$  such that

$$\lim_{n \rightarrow \infty} \frac{1}{n} \log Q_{0,n}(x, \mathbf{e}, [a_n, \infty)) = -\alpha$$

Moreover, we assume that there exist  $p \geq 1$  and  $b_i \in \mathcal{X}$  such that

$$\liminf_{i \rightarrow \infty} m_p(T^{ip} \mathbf{e}) Q_p(b_i, T^{ip} \mathbf{e}, [b_{i+1}, \infty)) > 1$$

and that for every  $\epsilon > 0$ , there exist  $q = q(\epsilon)$ ,  $\phi(n) \rightarrow \infty$  and  $(b_{j,n} : j, n \geq 0)$  such that

$$\liminf_{n \rightarrow \infty} \frac{1}{n} \sum_{j < (n - \phi(n)p)/q} \log Q_q(b_{j,n}, T^{i\phi(n) + jq} \mathbf{e}, [b_{j+1,n}, \infty)) \geq -\alpha - \epsilon.$$

These assumptions are satisfied for the applications we have in mind. For an example of large deviations following Assumption 7, a sufficient condition is  $P_{a_n}(Y_n \geq a_n + b_n) \sim \mathbb{P}_0(Y_n \geq b_n)$ . The trajectory associated to the large deviation event is then straight and we can choose  $k_{i,n} = k_i$ . It holds for random walks and more generally for random walks in random environment under general moment assumptions.

**Corollary 4.** *Let  $\mathbf{e} \in E$  and  $x \in \mathcal{X}$ . If (14),  $\sup\{\mathbb{E}(N(T^k \mathbf{e})^2) : k \geq 0\} < \infty$  and Assumptions 6 and 7 hold, we have*

$$\mathbb{P}_{\mathbf{e}, \delta_x} \left( \frac{1}{n} \log (Z_n([a_n, \infty)) / m_n(\mathbf{e})) \xrightarrow{n \rightarrow \infty} -\alpha \right) > 0.$$

As expected, the large deviation of the auxiliary Markov chain quantifies the lost of growth  $\alpha$  of the size of the population beyond  $a_n$ ,  $Z_n([a_n, \infty))$ , compared to the whole growth of the population given by  $m_n(\mathbf{e})$ . In the case of fixed environment, let us mention a related work on critical branching Markov chain [GM05], where the recurrence property is investigated.

### 4.3 Applications

We first give some details on a motivating example for which straight and non straight curve for large deviations appear. We then give some first comments on a new possible challenging questions.

#### 4.3.1 Kimmel's branching model

We refer to [B08] for a complete description of the model and the motivations. The population of individuals is a binary tree of cells and the trait is the number of parasites of the cell. The auxiliary Markov process  $Y$  is then a branching process in random environment. Monotonicity (Assumption 6) is a direct consequence of the branching property of  $Y$ . Tackling the local densities and the trait of extremal individuals thanks to the previous Corollary (only) requires to check Assumption 7.

One of the motivating question in [B08] is to count the number of infected cells in the subcritical case, which means that  $Y$  is a.s. absorbed in finite time. Three regimes appear in the subcritical case [GKV03] and in particular in the weak subcritical case

$$\mathbb{P}(Y_n > 0) \sim cn^{-3/2} \gamma^n,$$

where  $\gamma < \mathbb{E}_1(Y_1)$ . The mean number of infected cells is equal to  $2^n \mathbb{P}(Y_n > 0)$  and obtaining a.s. results was left open in this regime. Corollary 4 ensures that if  $2\gamma > 0$ , the number  $N_n^*$  of infected cells in generation  $n$  satisfies

$$\frac{1}{n} \log(N_n^*) \xrightarrow{n \rightarrow \infty} \log(2\gamma) \quad \text{a.s.}$$

on the event when the whole population of parasites survives. Indeed, this result is applied for  $p$  large enough such that  $2^p \mathbb{P}_1(Y_p > 0) > 1$ ,  $a_n = [1, \infty]$ ,  $b_i = 1, b_{j,n} = 1$ ,  $\phi(n) = o(n)$  and  $q$  is chosen such that

$$\log \mathbb{P}_1(Y_q > 0) \geq q \log(\gamma) - \epsilon.$$

Second, when counting the number of cells infected less than the typical cell in the supercritical regime, the problem is now linked to the lower large deviation of branching processes in random environment  $Y_n$ , i.e. to

$$\mathbb{P}(1 \leq Y_n \leq \exp(n\theta)), \quad \text{where } \theta < \mathbb{E}(\log m(\mathcal{E}))$$

and the way this large deviation event is realized. We refer to [BB12] for the results. Here again Corollary 4 allows to determine the a.s. behavior of the number of cells whose number of parasites is between 1 and  $\exp(\theta n)$ . It is worth noting that for this question the associated trajectory is not straight and  $k_{i,n}$  depends on  $n$ .

### 4.3.2 Comments on branching random walks and random environment

We can recover here the classical result on the asymptotic behavior of

$$\frac{1}{n} \log Z_n[an, \infty)$$

for a branching random walk with random increment  $X$ . It converges a.s. to

$$\log(m) - \Lambda(a)$$

soon as  $a \geq \mathbb{E}(X)$  and  $\log(m) > \Lambda(a)$ , where  $\Lambda$  is the rate function associated to the random walk  $S = \sum_{i=0}^{n-1} X_i$ , see e.g. [R00, S08].

One can extend this result to offsprings distribution in time varying environment and random walks in varying environment using the last Corollary and large deviations of random walks in varying environment. Here  $b_i = aip$ ,  $b_{j,n} = ajp + b_{\phi(n)}$ ,  $\phi(n) = o(n)$ . We refer in particular to [Z04] for results on quenched and annealed large deviations of random walk in random environment.

The uniform bound of the second moment of the reproduction in Theorem 5 can be relaxed and depend on the environment. Similarly, Assumption 5 can be extended to

$$\liminf_{i \rightarrow \infty} m_p(b_i, T^{ip_i(\mathbf{e})} \mathbf{e}, [b_{i+1}, \infty)) > 1.$$

Thus, using still Lemma 7, one can get an analogous result in stationary random environment.

### 4.3.3 Perspectives

A main motivation for this work is the control of local densities in cell division models for aging [G07, DM10], for damages [ES07] or infection such as Kimmel's branching model already mentioned. An other motivation comes from spatial models in ecology with time and/or space inhomogeneity. We aim at investigating further these questions and determine the behavior of extremal particles in these models, which seem to show different large deviation's curves.

**Acknowledgement.** This work was partially funded by Chair Modelisation Mathématique et Biodiversité VEOLIA-Ecole Polytechnique-MNHN-F.X., the professorial chair Jean Marjoulet, the project MANEGE 'Modèles Aléatoires en Écologie, Génétique et Évolution' 09-BLAN-0215 of ANR (French national research agency).

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