Brazilian Journal of Probability and Statistics 2020, Vol. 34, No. 3, 613–628 https://doi.org/10.1214/19-BJPS434 © Brazilian Statistical Association, 2020

Galton–Watson processes in varying environment and accessibility percolation

Daniela Bertacchi^a, Pablo M. Rodriguez^b and Fabio Zucca^c

^aUniversità di Milano–Bicocca ^bUniversidade de São Paulo ^cPolitecnico di Milano

Abstract. This paper deals with branching processes in varying environment with selection, where the offspring distribution depends on the generation and every particle has a random fitness which can only increase along genealogical lineages (descendants with small fitness do not survive). We view the branching process in varying environment (BPVE) as a particular example of branching random walk. We obtain conditions for the survival or extinction of a BPVE (with or without selection), using fixed point techniques for branching random walks. These conditions rely only on the first and second moments of the offspring distributions. Our results can be interpreted in terms of accessibility percolation on Galton-Watson trees. In particular, we obtain that there is no accessibility percolation on almost every Galton-Watson tree where the expected number of offspring grows sublinearly in time, while superlinear growths allows percolation. This result is in agreement with what was found for deterministic trees in Nowak and Krug (*Europhysics Letters* **101** (2013) 66004).

1 Introduction

A branching process in varying environment (or *BPVE*), also called *time-inhomogeneous* branching process, is the generalization of the classical Galton-Watson process when the offspring distribution depends on the generation. The limit behaviour of these processes was firstly studied in Agresti (1975), Church (1971), Jagers (1974), Lindvall (1974), and later in Cohn and Jagers (1994), D'Souza and Biggins (1992), among others. Like the Galton-Watson process, the BPVE serves as a simple model for the growth of a biological population and to each of its realizations we can associate its Galton–Watson tree. We refer the reader to Jagers (1975) for a survey of earlier results about this topic and for biological motivations. See also Broman and Meester (2008) for a recent study on the survival properties of these processes and on their connection with percolation theory on trees.

Given a BPVE, we can assign a random label (say, a fitness) to each individual. We suppose that only the children with fitness higher than their parent's survive. A BPVE with this selection mechanism is called *branching Process in varying environment with selection* or *BPWS*. This process can be seen as a model for the evolution of species (for similar models see, for instance, Guiol, Machado and Schinazi (2011), Guiol, Machado and Schinazi (2013), Liggett and Schinazi (2009)). In particular, the BPWS is a generalization of the *accessibility percolation model* on regular trees, which was introduced in Nowak and Krug (2013), and recently studied on spherically symmetric trees in Coletti, Gava and Rodriguez (2018). In Nowak and Krug (2013), the authors have deterministic, finite rooted trees, where each vertex has a random label, assigned according to a non-atomic measure. The root is the ancestor of the population, vertices at distance *n* from the root represent individuals of generation *n*

Key words and phrases. Branching process, time inhomogeneous, varying environment, fitness, selection, accessibility percolation, generating function.

Received March 2018; accepted February 2019.

and each vertex in this generation has a fixed number h(n) of children in generation n + 1. For this model if h(n) grows sublinearly, then the probability that there is a path from the root, with increasing labels, reaching a vertex at distance n from the root, goes to 0 as n goes to infinity, if the growth is superlinear then the limit is 1.

The BPWS is thus a process where the existence of an infinite line of descendance is equivalent to the existence of an infinite accessibility path on the underlying (inhomogeneous) Galton–Watson tree. In this paper, we give conditions for survival (with positive probability there is an infinite population) and extinction (almost surely the process ends in finite time) for a BPWS. As a corollary, we obtain that, provided that a certain condition on the second moments is satisfied, if the expected number of children in generation n grows sublinearly then there is extinction, while if the growth is superlinear then there is survival.

In order to obtain our results we see the BPVE as a particular case of a more general process, which is the branching random walk (or BRW) where each particle has a position inside a space X or, equivalently, the particle is assigned a type/label in X (the breeding law accounts for both the number of children and their position). We identify the BPVE with a BRW on the space \mathbb{N} (see Section 2 for details). We note that this identification allows us to consider these processes as BRWs on an at most countable space X, a case which is well-studied in both continuous time and discrete time: we refer the reader, for details and results on BRWs to Bertacchi and Zucca (2008, 2009b, 2015), Pemantle and Stacey (2001) (continuous time), Braunsteins, Decrouez and Hautphenne (2019), Bulinskaya (2015a, 2015b), Gantert et al. (2010), Hautphenne (2012), Hautphenne, Latouche and Nguyen (2013), Machado et al. (2001), Machado, Popov and Yu (2003) (discrete time); see also Bertacchi and Zucca (2012) for a survey on the topic. Examples of BRWs with countable space X (along with some variants) and their biological applications are presented in Kimmel and Axelrod (2002, Ch.7). Of course one could see the fitness of individuals in the BPWS as a position and thus use results for BRWs on uncountable spaces, but for the uncountable case, as well as cases with non-trivial interactions between particles, there is a lack of general tools (usually, different processes need different tools, see for instance Bertacchi, Posta and Zucca (2007)). As far as we know, only a small number of papers are devoted to BRWs where the space X is an uncountable set. One example of such a process is proposed in Biggins et al. (1991), where particles are labelled with a reproductive prowess and children who are too weak will not reproduce; the authors obtain conditions for survival on a family line. Another example of a model with uncountably many types is Cox and Schinazi (2014), where the type is the fitness of the individual. We stress here that the BPWS is not a particular case of a BPVE, because the number of surviving children of a particle depends on its generation and also on its fitness. In order to obtain conditions for survival of a BPWS, our strategy is to construct a stochastic coupling between the BPWS and a BPVE in such a way that the survival of the latter implies the survival of the former.

For the BPVE, we present conditions for survival (Proposition 2.5, Theorem 2.6 and Corollary 2.7) or extinction (Proposition 2.4). These results are related to other results in the literature: Proposition 2.4 is a consequence of Jagers (1974, Corollary 3) and Theorem 2.6 is essentially equivalent to the condition in Agresti (1975, Theorem 1). Nevertheless here we provide different and self-consistent proofs of these facts, which are based on fixed point techniques. These techniques are a well-established tool for branching processes and BRWs and are here applied to BPVEs and then to BPWSs. In particular, we exploit the fact that survival is equivalent to the existence of a nontrivial fixed point of the generating function of the process (Theorem 4.1). We note that while sufficient conditions for almost sure extinction involve only the sequence of the first moments of the reproduction laws, conditions for survival cannot rely only on the first moments. We show that given any sequence of first moments it is possible to construct a corresponding BPVE which dies out almost surely (see Example 2.10). We also provide a surviving BPVE in Example 2.9 where all the first moments are smaller than 1.

Here is the outline of the paper. In Section 2, we introduce the notions of BPVE, BRW, BPWS and define survival and extinction. We state the results for BPVEs and provide examples where the conditions for survival hold (Example 2.8). We also discuss the two aforementioned examples (Examples 2.10 and 2.9), which have a counterintuitive behaviour. Our main results are in Section 3, which is devoted to BPWSs: Proposition 3.1 and Theorem 3.2. As a corollary of these results, we provide some explicit examples of surviving BPWSs (Example 3.5) and show that on Galton–Watson trees there is a phase transition (from extinction to survival) where the threshold is the linear growth of the expected number of offspring of the reproduction laws (Proposition 3.3). In Section 4, the reader can find the proofs of the statements, along with the results on BRWs which are used to prove our main results.

2 BPVEs, BRWs and BPWSs

2.1 BPVE and BRW

We begin by defining a branching process in varying environment or BPVE. The process starts with one particle at time 0 (this is the 0th generation). The random number of particles generated by each particle in the *n*th generation has generating function $\Phi_n(z) := \sum_{i=0}^{+\infty} \rho_n(i) z^i$ and we define a sequence of random variables $\{W_n\}_{n\in\mathbb{N}}$ by $\mathbb{P}(W_n = i) := \rho_n(i)$. Note that $\mathbb{E}[W_n] = \Phi'_n(1)$; we denote by m_n this first moment. To avoid trivial situations, we assume henceforth that $m_n > 0$ for all $n \in \mathbb{N}$. The random variable W_n represents the "typical" random number of children of a particle in the *n*th generation; all the particles behave independently. More formally, the BPVE is the stochastic process $\{Z_n\}_{n\in\mathbb{N}}$ such that $Z_{n+1} := \sum_{j=1}^{Z_n} W_{n,j}$, where Z_n is the number of particles in the *n*th generation, Z_0 is the initial state ($Z_0 = 1$ in our case) and $\{W_{n,j}\}_{j\geq 1,n\geq 0}$ is a family of independent variables such that $\{W_{n,j}\}_{j\geq 1}$ are identically distributed copies of W_n .

Definition 2.1. The BPVE becomes extinct (almost surely) if $p_e := \mathbb{P}(\bigcup_{n \ge 1} \{Z_n = 0\}) = 1$; otherwise, we say that it survives (with positive probability).

If we define $H_0(z) := z$ for all $z \in [0, 1]$ and, recursively, $H_{n+1} := H_n \circ \Phi_n$, it is not difficult to show that $H_n(0)$ is the probability that the population is extinct at time n; in particular $H_n(0) \uparrow p_e$ as $n \to +\infty$. The probability of extinction is monotone with respect to $\{\Phi_n\}_{n \in \mathbb{N}}$, meaning that, if $\Phi_n \ge \overline{\Phi}_n$ (where $\{\overline{\Phi}_n\}_{n \in \mathbb{N}}$ is the sequence of generating functions related to another BPVE with extinction probability \overline{p}_e), then by induction $H_n \ge \overline{H}_n$ and thus $p_e \ge \overline{p}_e$.

In order to avoid trivial situations we require that $\Phi_n(0) < 1$ for all $n \in \mathbb{N}$, that is, there is always a nonzero probability of having at least one child for a particle in any generation. This implies that there is always a positive probability of finding descendants in the *n*th generation for any given *n*, that is, $H_n(0) < 1$ for all $n \in \mathbb{N}$.

The main idea behind our results is the interpretation of a BPVE as a particular case of a branching random walk. In a branching process all the particles are indistinguishable. In a branching random walk, on the other hand, particles live on a spatial structure and are thus characterized by their position (which can also be interpreted as their *type*).

A discrete-time BRW on an at most countable set X is a stochastic process $\{\eta_n\}_{n \in \mathbb{N}}$, where $\eta_n(x)$ represents the number of particles alive at $x \in X$ at time n. More formally, consider a family $\nu = \{\nu_x\}_{x \in X}$ of probability measures on the (countable) measurable space $(S_X, 2^{S_X})$

where $S_X := \{f : X \to \mathbb{N} : \sum_{y \in X} f(y) < +\infty\}$. To obtain generation n + 1 from generation n, we proceed as follows: a particle at site $x \in X$ lives one unit of time, then a function $f \in S_X$ is chosen at random according to the law v_x and the original particle is replaced by f(y) particles at y, for all $y \in X$; this is done independently for all particles of generation n. Note that the choice of f simultaneously assigns the total number of children and the location where they will live.

We consider initial configurations with only one particle placed at a fixed site x: let \mathbb{P}^{δ_x} be the law of this process.

Definition 2.2. The BRW survives (globally) starting from x if $\bar{\mathbf{q}}(x) := 1 - \mathbb{P}^{\delta_x}(\sum_{w \in X} \eta_n(w) > 0, \forall n \in \mathbb{N}) < 1$. There is (global) extinction if $\bar{\mathbf{q}}(x) = 1$.

We remark here that a globally surviving BRW can also survive locally, meaning that with positive probability there will be infinitely many returns to the starting location. Since here we are just interested in the global survival, we refer the reader to Bertacchi and Zucca (2009a), Zucca (2011) for details.

Given a BPVE, with its sequence $\{\Phi_n\}_{n\in\mathbb{N}}$ of generating functions, we call *associated BRW* the process on \mathbb{N} where each particle at $n \in \mathbb{N}$ has a random number of offsprings at n + 1 according to the distribution ρ_n . This is a reducible BRW whose generating function $G:[0,1]^{\mathbb{N}} \to [0,1]^{\mathbb{N}}$ satisfies

$$G(\mathbf{q}|n) := \Phi_n(\mathbf{q}(n+1)), \quad \forall \mathbf{q} \in [0,1]^{\mathbb{N}}$$

$$(2.1)$$

(note that the same identification holds in general for a BRW in varying environment (that is, time-inhomogeneous BRW) on X and a time-homogeneous BRW on $X \times \mathbb{N}$). A BPVE starting with one particle survives if and only if the associated BRW does (starting with one particle at 0).

2.2 BPWS and accessibility percolation

Given a BPVE, each individual can be assigned a label; this label can be interpreted as a position, a type or a fitness. We assume that the label is assigned at birth independently for each individual, according to a non-atomic measure μ on \mathbb{R} (that is, $x \mapsto \mu(-\infty, x)$ is a continuous map).

By using this label, we define a selection mechanism as follows: all children of a particle with fitness $x \in \mathbb{R}$ survive if and only if their fitness belong to the interval $[x, +\infty)$. This is a Bernoulli-type selection, meaning that every child survives (independently) with probability $\mu(x, +\infty)$. Hence, elementary computations show that the generating function of the number of children of a particle with fitness x of generation n, after selection, is $G_{n,x}(z) :=$ $\Phi_n(z\mu(x, +\infty) + 1 - \mu(x, +\infty))$. If we call m_n the expected number of children, before selection, of a particle in generation n, then $G'_{n,x}(1) = \Phi'_n(1)\mu(x, +\infty) = m_n\mu(x, +\infty)$. We call this process branching Process in varying environment with selection or BPWS.

One graphical way to construct the BPWS is to generate the Galton–Watson tree of the progeny of the BPVE before selection (starting with one individual represented by the root of the tree) and to associate independently to every vertex v a random variable $X_v \sim \mu$. The BPWS erases all the subtrees branching from a vertex v' such that $X_{v'} < X_v$, where v is the parent of v'. There is survival whenever the pruned tree is infinite with positive probability.

Survival of a BPWS is thus equivalent to the presence of accessibility percolation on the Galton–Watson tree of the associated BPVE. Indeed in the the *accessibility percolation model* (introduced in Nowak and Krug (2013)), one considers a graph $G = (\mathcal{V}, \mathcal{E})$, and an independent identically distributed sequence of continuous random variables $\{X_v\}_{v \in \mathcal{V}}$. The main question of interest is the existence of self-avoiding paths of vertices $\{v_i\}_{i \in \mathbb{N}}$, starting from

the root to the border of the graph (that is, an infinite path when \mathcal{V} is infinite), such that $X_{v_i} \leq X_{v_{i+1}}$ for all $i \in \mathbb{N}$. Such a path is called *accessibility path* and the existence of at least one of them, with positive probability, is called *accessibility percolation*. This question has been addressed mainly on regular trees and hypercubes in Berestycki, Brunet and Shi (2016), Nowak and Krug (2013), Roberts and Zhao (2013), Schmiegelt and Krug (2014).

In order to study the behaviour of a BPWS, we denote by A_n the random set of fitness of the particles of generation *n*; hence, the size of the population is $N_n := #A_n$ (# represents the cardinality of a set) almost surely. From now on, whenever the ancestor has fitness *x*, we say that the process starts from *x*.

Definition 2.3.

- 1. We define the probability of *local extinction* in $I \subseteq \mathbb{R}$ starting from x by $\mathbb{P}(\liminf_{n \to +\infty} \{A_n \cap I = \emptyset\} | A_0 = \{x\})$. We say that there is *local extinction* when this probability is equal to 1 and that there is *local survival* otherwise.
- 2. We say that there is *global survival* starting from x if and only if there is local survival in \mathbb{R} starting from x.

Note that there is global survival starting from x if and only if $\mathbb{P}(A_n \neq \emptyset, \forall n \in \mathbb{N} | A_0 = \{x\}) \equiv \mathbb{P}(N_n > 0, \forall n \in \mathbb{N} | A_0 = \{x\}) > 0$. It is clear from the definition that local survival implies global survival. We note that the progeny of a particle with fitness x has fitness in $[x, +\infty)$; moreover, if we are interested in *local survival*, that is, the survival of the progeny in a fitness interval (a, b), we can disregard (or "kill") all particles with fitness outside this interval. Moreover, by using a coupling argument, it is easy to see that the probability of local extinction is nondecreasing with respect to $x \in \mathbb{R}$.

Sometimes it is useful to consider the fitness of the least-fit individual which we denote by $l_n := \min A_n$ (where $\min(\emptyset) := +\infty$). By the nature of the selection process and the fact that μ is non-atomic, $\{l_n\}_{n\in\mathbb{N}}$ is a strictly increasing random sequence almost surely. Given any measurable set *I*, if $\mu(I) = 0$ there is local extinction in *I*. In general there is local survival in *I* starting from *x* if and only if $\mathbb{P}(\mu((\lim_{n \in \mathbb{N}} l_n, +\infty) \cap \operatorname{co}(I)) > 0) > 0$ (where $\operatorname{co}(I)$ is the *essential* convex hull of *I*, that is the smallest interval *J* such that $\mu(I \setminus J) = 0$). Indeed no contribution to $\operatorname{co}(I)$ can come from its right since particles cannot have a smaller fitness than their parent's and, by definition of l_n , there are no individuals of generation *n* with fitness in $(-\infty, l_n)$. Once there is survival in $\operatorname{co}(I)$ then if is easy to show, by using a Borel-Cantelli argument, that there is survival in *I*.

2.3 Preliminary results for BPVEs

We consider a BPVE: although the paper is focused mainly on conditions for survival, nevertheless, there is a simple condition for extinction which involves only the sequence of first moments $\{m_n\}_{n \in \mathbb{N}}$ (see Example 2.9 for an application).

Proposition 2.4. Given a BPVE such that if $\inf_{n \in \mathbb{N}} \prod_{i=0}^{n} m_i = 0$, then there is extinction.

The following characterization of surviving BPVEs comes from a result on BRWs (see Theorem 4.1).

Proposition 2.5. Consider a BPVE and its sequence $\{\Phi_n\}_{n\in\mathbb{N}}$ of generating functions. There is survival for the process if and only if there exists $\mathbf{q} \in [0, 1]^{\mathbb{N}}$, $n_0 \in \mathbb{N}$ such that $\mathbf{q}(n_0) < 1$ and $\Phi_n(\mathbf{q}(n+1)) \leq \mathbf{q}(n)$ for all $n \geq n_0$.

Although this proposition is very useful from a theoretical point of view, it is sometimes difficult to find the sequence \mathbf{q} . Thus, it is natural to look for different (sufficient) conditions

for survival which can be derived from Proposition 2.5. To this aim, we denote by $m_n^{(2)}$ the second moment $\mathbb{E}[W_n^2]$ of the reproduction law of the *n*th generation; henceforth we suppose that this moment is finite for every sufficiently large *n*. Note that $m_n^{(2)} = \Phi_n''(1) + m_n$. Theorem 2.6 and Corollary 2.7 provide sufficient conditions for survival (see Example 2.10 for an application). The strategy to prove survival is to show that, to find a good sequence **q**, it suffices to control the ratio between the second moment and the product of the first moments of the reproduction laws.

Theorem 2.6. Consider a BPVE such that $m_n^{(2)} < +\infty$ for every sufficiently large *n*. Then, for every $n \in \mathbb{N}$, the following statements are equivalent:

$$\begin{cases} \sum_{j=n}^{+\infty} \frac{m_j^{(2)} - m_j}{m_j} \left(\prod_{i=n}^j m_i\right)^{-1} < +\infty, \\ \inf_{j \in \mathbb{N}} \prod_{i=0}^j m_i > 0, \end{cases}$$

2.

$$\lim_{k \to +\infty} \left[\left(\prod_{i=n}^{n+k} m_i \right)^{-1} + \sum_{j=n}^{n+k} \frac{m_j^{(2)} - m_j}{m_j} \left(\prod_{i=n}^j m_i \right)^{-1} \right] < +\infty.$$

Moreover, if one of these conditions holds for some n then the BPVE survives.

Note that if (1) (resp. (2)) holds for some $n = n_0$ then it holds for every $n \ge n_0$. The conditions in Theorem 2.6 are implied by other conditions which are easier to check, as the following corollary shows.

Corollary 2.7. Consider a BPVE such that $m_n^{(2)} < +\infty$ for every sufficiently large n. If one of the following holds:

1. $\sum_{j=n}^{+\infty} \frac{m_j^{(2)}}{m_j} (\prod_{i=n}^j m_i)^{-1} < +\infty \text{ for some } n \in \mathbb{N};$

2. $\limsup_{n \to +\infty} \sqrt[n]{m_n^{(2)}/m_n^2} < \liminf_{n \to +\infty} \sqrt[n]{\prod_{i=0}^{n-1} m_i};$

- 3. there exists a function $g : \mathbb{N} \to [1, +\infty)$ such that $m_n^{(2)}/m_n^2 \le g(n)$ for every sufficiently large n and such that $\limsup_{n \to +\infty} g(n+1)/g(n) < \liminf_{n \to +\infty} \sqrt[n]{\prod_{i=0}^{n-1} m_i}$;
- 4. $\lim_{n \to +\infty} m_n = +\infty$ and there exists $M, k \ge 1$ such that $m_n^{(2)}/m_n^2 \le kM^n$ for all sufficiently large $n \in \mathbb{N}$;

then the BPVE survives.

Theorem 2.6 is essentially contained in Agresti (1975) but here we make use of a different, self-consistent proof. To compare with other results in the literature, we note that the sufficient condition for a.s. extinction in Broman and Meester (2008, Proposition 1.1) is a consequence of Proposition 2.4. On the other hand, the sufficient condition for survival in Broman and Meester (2008, Proposition 1.1) follows from Corollary 2.7(3) by taking $g(n) := \sup_{j \in \mathbb{N}} m_j^{(2)} / \inf_{j \in \mathbb{N}} m_j^2 > 0$. Another sufficient condition for survival of a BPVE is given by D'Souza and Biggins (1992, Theorem 1) which, in general, is not comparable with Theorem 2.6.

In the following example, we consider some relevant reproduction laws which satisfy the conditions of Theorem 2.6.

Example 2.8. Consider the following sequences of reproduction laws ρ_n .

- 1. Let the law be geometric: $\rho_n(i) = m_n^i/(1+m_n)^{i+1}$. The BPVE survives provided $\sum_{n=0}^{+\infty} (\prod_{j=0}^n m_j)^{-1} < +\infty$. As a partial converse, when $\sum_{n=0}^{+\infty} (\prod_{j=0}^n m_j)^{-1} = +\infty$, we have that it is enough $\inf_{n \in \mathbb{N}} \prod_{i=0}^n m_i = 0$ or $\inf_{n \in \mathbb{N}} m_n > 0$ to get extinction.
- 2. Let the law be Poisson: $\rho_n \sim \mathcal{P}(m_n)$. If $\sum_{n=0}^{+\infty} (\prod_{j=0}^n m_j)^{-1} < +\infty$, then the BPVE survives; when $\sum_{n=0}^{+\infty} (\prod_{j=0}^n m_j)^{-1} = +\infty$, we have that it is enough that $\inf_{n \in \mathbb{N}} \prod_{i=0}^n m_i = 0$ or $\inf_{n \in \mathbb{N}} m_n > 0$ to get extinction.
- 3. Let the law be binomial: $\rho_n \sim \mathcal{B}(k_n, r_n)$. If $\sum_{n=0}^{+\infty} (\prod_{j=0}^n k_j r_j)^{-1} < +\infty$, then there is survival. Noting that $m_n = k_n r_n$, the same above conditions for extinction apply.

Note that the geometric law is particularly relevant since it appears as the total number of children of a particle in a continuous-time branching process with breeding rate m_n and death rate 1. Survival follows from Theorem 2.6, noting that the generating function is $\Phi_n(z) := 1/(1 + m_n(1 - z))$, whence the average number of children is $\frac{d}{dz}\Phi_n(z)|_{z=1} = m_n$ and $m_n^{(2)} - m_n = \frac{d^2}{dz}\Phi_n(z)|_{z=1} = 2m_n^2$ which implies $(m_n^{(2)} - m_n)/m_n^2 = 2$ for all *n*. Extinction is a consequence of Proposition 2.4 for the first condition, and of Agresti (1975, Theorem 2) for the second one. The other two cases are analogously obtained.

The following two examples show that a BPVE can survive even if $m_n < 1$ for all n, while it can die out whatever the sequence $\{m_n\}_{n \in \mathbb{N}}$ (even if $\inf_{n \in \mathbb{N}} m_n > 1$ or $m_n \to \infty$).

Example 2.9. Let us consider a sequence $\{a_n\}_{n \in \mathbb{N}}$ such that $a_n \in (0, 1)$ for all *n*. Define W_n as a Bernoulli variable with parameter $1 - a_n$. Clearly $m_n^{(2)} = m_n = 1 - a_n < 1$ for all *n*: the corresponding BPVE survives with positive probability if and only if and $\sum_{n \in \mathbb{N}} a_n < +\infty$.

It is well known that, since $a_n < 1$ for all $n \in \mathbb{N}$ then $\sum_{n \in \mathbb{N}} a_n < +\infty$ if and only if $\prod_{n \in \mathbb{N}} (1-a_n) > 0$. If $\sum_{n \in \mathbb{N}} a_n = +\infty$ then $\prod_{n \in \mathbb{N}} m_n = \prod_{n \in \mathbb{N}} (1-a_n) = 0$ and the BPVE dies out according to Proposition 2.4. Survival would follow analogously when $\sum_{n \in \mathbb{N}} a_n < +\infty$ by applying Theorem 2.6; indeed the sum in the first condition of the theorem is 0 (since $m_n^{(2)} = m_n$) and $\inf_j \prod_{i=0}^j m_i = \prod_{n \in \mathbb{N}} (1-a_n) > 0$.

Example 2.10. Consider a nonnegative sequence $\{m_n\}_{n \in \mathbb{N}}$. Define W_n by

$$\mathbb{P}(W_n = i) = \begin{cases} m_n/k_n & \text{if } i = k_n, \\ 1 - m_n/k_n & \text{if } i = 0, \end{cases}$$

where the sequence $\{k_n\}_{n \in \mathbb{N}}$ of integers satisfies

$$\sum_{n \in \mathbb{N}} (1 - m_n / k_n)^{\prod_{i=0}^{n-1} k_i} = +\infty.$$

Note that $m_n = \mathbb{E}[W_n]$. We show recursively that such a sequence $\{k_n\}_{n \in \mathbb{N}}$ exists and we claim that the corresponding BPVE dies out almost surely.

Indeed, consider any sequence $\{a_n\}_{n\in\mathbb{N}}$ such that $a_n \in (0, 1)$ and $\sum_{n\in\mathbb{N}} a_n = +\infty$ (take for instance $a_n := \varepsilon > 0$ for all n). The idea is to find $\{k_n\}_{n\in\mathbb{N}}$ in such a way that $(1 - m_n/k_n)^{\prod_{i=0}^{n-1} k_i} \ge a_n$. Fix $k_0 \in \mathbb{N}$ such that $1 - m_0/k_0 \ge a_0$. Suppose we already defined k_i for all $i \le n-1$; since $(1 - m_n/x)^{\prod_{i=0}^{n-1} k_i} \to 1$ as $x \to +\infty$, there exists $k_n \in \mathbb{N}$ such that $(1 - m_n/k_n)^{\prod_{i=0}^{n-1} k_i} \ge a_n$.

Now denote as before by A_n the event "the BPVE survives up to time *n*". Since the maximum number of individuals alive at time *n* is $\prod_{i=0}^{n-1} k_i$ we have $\mathbb{P}(A_n^c | \bigcap_{j=1}^{n-1} A_j) \ge 1$

 $(1 - m_{n-1}/k_{n-1})^{\prod_{i=0}^{n-2} k_i} \ge a_{n-1}$ for all $n \ge 1$ (where $\prod_{i=0}^{-1} k_i := 1$). The result follows this equivalence:

$$\mathbb{P}\left(\bigcap_{i=0}^{+\infty} A_{i}\right) > 0 \quad \Longleftrightarrow \quad \begin{cases} \mathbb{P}\left(A_{i}^{c} \Big| \bigcap_{j=0}^{i-1} A_{j}\right) < 1, \quad \forall i \geq 0, \\ \sum_{i=0}^{+\infty} \mathbb{P}\left(A_{i}^{c} \Big| \bigcap_{j=0}^{i-1} A_{j}\right) < +\infty, \end{cases}$$
(2.2)

where $\mathbb{P}(A_0^c | \bigcap_{j=0}^{-1} A_j) := \mathbb{P}(A_0^c).$

For an explicit example, take $m_n := 2$ for all $n, k_0 > 2$ and $k_n := k_0^{2^{n-1}}$ for all $n \ge 1$. Clearly $\prod_{i=0}^{n-1} k_i = k_0^{2^{n-1}} = k_n$ hence $0 < (1 - m_n/k_n)^{\prod_{i=0}^{n-1} k_i} = (1 - 2/k_n)^{k_n} \to e^{-2}$ which implies $\min_n (1 - m_n/k_n)^{\prod_{i=0}^{n-1} k_i} > 0$; thus $\sum_{n \in \mathbb{N}} (1 - m_n/k_n)^{\prod_{i=0}^{n-1} k_i} = +\infty$.

3 BPWS: Main results

Throughout this section, we consider a BPWS with fitness measure μ ; we denote by $\{m_n\}_{n\in\mathbb{N}}$ and $\{m_n^{(2)}\}_{n\in\mathbb{N}}$ the first and second moment of the offspring distribution of the process before selection. The generating functions before selection are denoted by $\{\Phi_n\}_{n\in\mathbb{N}}$.

In the following proposition, we give a condition for extinction of a BPWS by proving the absence of an admissible infinite path from the root in the associated accessibility percolation model on the Galton–Watson tree. This generalizes what was already noted in Coletti, Gava and Rodriguez (2018).

Proposition 3.1. *Given a BPWS, if there exists* $n_0 \ge 0$ *such that*

$$\liminf_{n \to +\infty} \frac{\prod_{i=0}^{n-1} m_i}{(n+n_0+1)!} = 0,$$

then there is global extinction for every starting fitness $x \in \mathbb{R}$.

In particular, Proposition 3.1 applies to Galton–Watson trees associated to time-homogeneous branching processes (or in any case where $\{m_n\}_{n \in \mathbb{N}}$ is a constant sequence or simply sublinear): on these trees there is no accessibility percolation. The following theorem gives a sufficient condition for survival of a BPWS (by definition $\prod_{i=n}^{n-1} c_i := 1$).

Theorem 3.2. Suppose that there exists a sequence $\{c_i\}_{i\geq 0}$ of positive real numbers such that $\sum_{i=0}^{+\infty} c_i/m_i < +\infty$ and

$$\begin{cases} \sum_{j=n}^{+\infty} \frac{m_j^{(2)} - m_j}{m_j^2} \left(C^j \prod_{i=n}^{j-1} c_i \right)^{-1} < +\infty, \\ \inf_{n \in \mathbb{N}} C^n \prod_{j=0}^n c_i > 0 \end{cases}$$
(3.1)

for some $n \in \mathbb{N}$ and C > 0. Then the BPWS starting with one particle with fitness \bar{x} such that $\mu(\bar{x}, +\infty) > 0$ survives locally in every $I \subseteq [\bar{x}, +\infty)$ such that $\mu(I) > 0$.

As an application of Proposition 3.1 and Theorem 3.2, we have that, on almost every Galton–Watson tree with the expected number of offspring growing as n^{α} , there is a phase transition at the critical exponent $\alpha = 1$. The proof is very easy and we omit it.

Proposition 3.3. Consider a BPWS such that $m_n \sim \beta n^{\alpha}$, $\beta > 0$.

- 1. If $\alpha < 1$, there is extinction.
- 2. If $\alpha > 1$ and equation (3.1) is satisfied, then there is survival.

More generally, (1) if $m_n/(n+\bar{n}) \leq 1$ for all sufficiently large n (and some $\bar{n} \in \mathbb{N}$) then there is extinction, (2) if $\liminf m_n/n^{\alpha} > 0$ for some $\alpha > 1$ (and equation (3.1) is satisfied) then there is survival.

The following corollary, as Corollary 2.7, gives more explicit conditions for survival. We omit its proof.

Corollary 3.4. Suppose that there exists a sequence $\{c_i\}_{i>0}$ of positive real numbers such that $\sum_{i=0}^{+\infty} c_i/m_i < +\infty$ and one of the following conditions holds for some C > 0:

- 1. $\sum_{j=n}^{+\infty} \frac{m_j^{(2)}}{m_i^2} (C^j \prod_{i=n}^{j-1} c_i)^{-1} < +\infty \text{ for some } n \in \mathbb{N};$
- 2. $\limsup_{n \to +\infty} \sqrt[n]{m_n^{(2)}/m_n^2} < C \liminf_{n \to +\infty} \sqrt[n]{\prod_{i=0}^{n-1} c_i};$
- 3. there exists a function $g: \mathbb{N} \to [1, +\infty)$ such that $m_n^{(2)}/m_n^2 \leq g(n)$ for every sufficiently large n and $\limsup_{n \to +\infty} g(n+1)/g(n) <$ $C \liminf_{n \to +\infty} \sqrt[n]{\prod_{i=0}^{n-1} c_i};$
- 4. $\lim_{n \to +\infty} c_n = +\infty$ and there exists $M, k \ge 1$ such that $m_n^{(2)}/m_n^2 \le kM^n$ for all sufficiently large $n \in \mathbb{N}$;

then the BPWS starting with one particle with fitness \bar{x} such that $\mu(\bar{x}, +\infty) > 0$ survives locally in every $I \subseteq [\bar{x}, +\infty)$ such that $\mu(I) > 0$.

As in Example 2.8, we are able to show some reproduction laws satisfying the conditions of Theorem 3.2.

Example 3.5. The following reproduction laws give rise to BPWSs which survive.

- 1. Geometric laws: $\rho_n \sim \mathcal{G}(1/(1+m_n))$ such that $\sum_{i=0}^{+\infty} 1/m_n < +\infty$.
- 2. Poisson laws: $\rho_n \sim \mathcal{P}(m_n)$ where $\sum_{i=0}^{+\infty} 1/m_i < +\infty$; 3. Binomial laws: $\rho_n \sim \mathcal{B}(k_n, r_n)$ such that $\sum_{i=0}^{+\infty} 1/k_i r_i < +\infty$;

in particular the geometric law corresponds to a continuous-time branching process with selection.

The role played by the sequence $\{c_i\}_{i\geq 0}$ is twofold: on the one hand it allows to treat cases where $\sum_{i=0}^{+\infty} 1/m_i = +\infty$ and, on the other hand, when $\sum_{i=0}^{+\infty} 1/m_i < +\infty$ it allows larger upper bounds for $(m_i^{(2)} - m_j)/m_j^2$. In the following example, we analyze two explicit cases.

Example 3.6. Let $\{W_n\}_{n \in \mathbb{N}}$ such that

$$m_n := \begin{cases} k+1 & n=2^k, \\ (n+1)^2 & \text{otherwise,} \end{cases}$$

and

$$c_n := \begin{cases} 1/(k+1) & n = 2^k, \\ 2 & \text{otherwise.} \end{cases}$$

Then $\sum_{n \in \mathbb{N}} 1/m_n = +\infty$ while $\sum_{n \in \mathbb{N}} c_n/m_n < +\infty$. Moreover, if $b \in (1, 2)$, it is easy to prove that $\prod_{i=0}^{n} c_i = 2^{n-\lfloor \log_2(n) \rfloor}/(\lfloor \log_2(n) \rfloor + 1)! \ge b^n$ eventually as $n \to +\infty$; whence, if $\limsup_{n \to +\infty} \sqrt[n]{m_n^{(2)}/m_n^2} < +\infty$ then Corollary 2.7(2) applies and there is survival for the BPWS.

Consider now a process where $m_n = b^n$ (for some b > 1). If $m_n^{(2)}/m_n^2 \le K\alpha^n c^{n(n-1)/2}$ for some K > 0, $c \in (1, b)$ and $\alpha \ge 1$ then Corollary 3.4(1) applies (with $c_i := (\alpha + 1)c^i$, C = 1 and n = 0) and there is survival for the BPWS.

4 Proofs

We begin by considering a fundamental result on BRWs. For a BRW, global survival can be characterized by using a generating function associated to the process: namely the function $G : [0, 1]^X \rightarrow [0, 1]^X$ where, for all $\mathbf{q} \in [0, 1]^X$, $G(\mathbf{q}) \in [0, 1]^X$ is the following weighted sum of (finite) products

$$G(\mathbf{q}|x) := \int_{S_X} \nu_x(\mathrm{d}f) \prod_{y \in X} \mathbf{q}(y)^{f(y)} = \sum_{f \in S_X} \nu_x(f) \prod_{y \in X} \mathbf{q}(y)^{f(y)},$$

 $G(\mathbf{q}|x)$ being the *x* coordinate of $G(\mathbf{q})$.

Note that $[0, 1]^X$ is a partially ordered set where $\mathbf{q} \ge \mathbf{z}$ if and only if $\mathbf{q}(x) \ge \mathbf{z}(x)$ for all $x \in X$; clearly $\mathbf{q} > \mathbf{z}$ stands for " $\mathbf{q} \ge \mathbf{z}$ and $\mathbf{q}(x) > \mathbf{z}(x)$ for some $x \in X$ ". The function *G* is nondecreasing and continuous with respect to the product topology on $[0, 1]^X$ and the family $\{v_x\}_{x \in X}$ is uniquely determined by this generating function.

It is easy to show (see for instance Bertacchi and Zucca (2009a, Corollary 2.2) or the proof of Theorem 4.1) that $\bar{\mathbf{q}}$ is the smallest solution of $G(\mathbf{q}) \leq \mathbf{q}$ in $[0, 1]^X$, in particular it is the smallest fixed point of G in $[0, 1]^X$, that is $G(\bar{\mathbf{q}}) = \bar{\mathbf{q}}$.

Define the first moments $m_{xy} := \sum_{f \in S_X} f(y)v_x(f)$; denote by $m_{xy}^{(0)} := \delta_{xy}$ and $m_{xy}^{(n+1)} := \sum_{w \in X} m_{xw}^{(n)} m_{wy}$ for all $n \in \mathbb{N}$ (clearly, by using $+\infty \cdot 0 := 0$ and $+\infty \cdot x := +\infty$ for all x > 0, we have $m_{xy}^{(n)} \in [0, +\infty]$ for all $n \in \mathbb{N}$, $x, y \in X$). Given $\mathbf{v} \in [0, +\infty]^X$ we define $Mv \in [0, +\infty]^X$ by $Mv(x) := \sum_{w \in X} m_{xw}v(w)$; clearly $M^n v(x) = \sum_{w \in X} m_{xw}^{(n)}v(w)$. The following theorem characterizes global survival; it appears, in different flavors, in Zucca (2011, Theorem 4.1) or Bertacchi and Zucca (2014, Theorem 3.1) and it is based on Bertacchi and Zucca (2009a, Proposition 2.1). Unlike those results, here we remove the requirement that $\sum_{y \in X} m_{xy}$ is uniformly bounded; hence we write the proof which is slightly different from the ones in the above cited papers. We point out that it is essential to remove the above uniform bound on $\sum_{y \in X} m_{xy}$ in order to avoid a similar bound $\sup_{n \in \mathbb{N}} m_n < +\infty$ which, according to Proposition 3.1, would imply extinction for a BPWS. Henceforth, by $\mathbf{0}, \mathbf{1} \in [0, 1]^X$ we mean the constant functions $\mathbf{0}(x) := 0, \mathbf{1}(x) := 1$ for all $x \in X$; note that $G(\mathbf{1}) = \mathbf{1}$.

Theorem 4.1. Consider a BRW and a fixed $x \in X$. The following statements are equivalent:

- 1. $\bar{\mathbf{q}}(x) < 1$ (*i.e. there is global survival starting from x*);
- 2. there exists $\mathbf{q} \in [0,1]^X$ such that $\mathbf{q}(x) < 1$ and $G(\mathbf{q}) \le \mathbf{q}$ (i.e. $G(\mathbf{q}|y) \le \mathbf{q}(y)$, for all $y \in X$);
- 3. there exists $\mathbf{q} \in [0, 1]^X$ such that $\mathbf{q}(x) < 1$ and $G(\mathbf{q}) = \mathbf{q}$ (i.e. $G(\mathbf{q}|y) = \mathbf{q}(y)$, for all $y \in X$).

If **q** satisfies either (2) or (3), then $\mathbf{q} \ge \bar{\mathbf{q}}$. Moreover, global survival starting from x implies that $\liminf_{n \to +\infty} \sum_{y \in X} m_{xy}^{(n)} > 0$.

Proof. Consider the sequence $\{\mathbf{q}_n\}_{n \in \mathbb{N}}$ defined as

$$\begin{cases} \mathbf{q}_0 := \mathbf{0}, \\ \mathbf{q}_{n+1} := G(\mathbf{q}_n), \quad \forall n \in \mathbb{N}, \end{cases}$$

clearly $\mathbf{q}_n(x)$ is the probability that the process, which starts with one particle at x at time 0, has no particles at time n. Moreover \mathbf{q}_n converges pointwise to $\bar{\mathbf{q}}$ (that is, with respect to the product topology). By the continuity of G we have $\bar{\mathbf{q}} = G(\bar{\mathbf{q}})$.

Now (1) \Longrightarrow (2) \Longrightarrow (2) are trivial. Assume (2); by induction on *n* we have that $\mathbf{q}_n \leq \mathbf{q}$; indeed $\mathbf{0} \leq \mathbf{q}$ and, since *G* is nondecreasing, $\mathbf{q}_{n+1} = G(\mathbf{q}_n) \leq G(\mathbf{q}) \leq \mathbf{q}$. By taking the limit as $n \to +\infty$ we have $\bar{\mathbf{q}} \leq \mathbf{q}$. This implies $\bar{\mathbf{q}}(x) \leq \mathbf{q}(x) < 1$; thus (1) is proven.

We are left to prove that, say, (1) implies $\liminf_{n \to +\infty} \sum_{y \in X} m_{xy}^{(n)} > 0$. To this aim consider a realization $\{\eta_n\}_{n \in \mathbb{N}}$ of the BRW and denote by \mathbb{E}^x the expectation with respect to \mathbb{P}^{δ_x} . If $\mathbb{P}^{\delta_x}(S) > 0$ where $S := \{\sum_{y \in X} \eta_n(y) > 0, \forall n \in \mathbb{N}\}$ then, since $\sum_{y \in X} \eta_n(y) \ge 1$ on *S*, we have

$$\sum_{y \in X} m_{xy}^{(n)} = \mathbb{E}^x \left[\sum_{y \in X} \eta_n(y) \right] \ge \mathbb{E}^x \left[\sum_{y \in X} \eta_n(y) | S \right] \mathbb{P}^{\delta_x}(S) \ge \mathbb{P}^{\delta_x}(S) > 0.$$

This implies that $\inf_{n \in \mathbb{N}} \sum_{y \in X} m_{xy}^{(n)} > 0$ which is also equivalent to $\liminf_{n \to +\infty} \sum_{y \in X} m_{xy}^{(n)} > 0$ (since $\sum_{y \in X} m_{xy}^{(n)} = 0$ for some *n* implies the same equality for all subsequent values of *n*).

Applying Theorem 4.1 to the BRW associated to the BPVE we can prove the Propositions 2.4 and 2.5.

Proof of Proposition 2.4. It can be easily derived from Theorem 4.1. This could also be seen as a consequence of Jagers (1974, Corollary 3). \Box

Proof of Proposition 2.5. According to Theorem 4.1 the associated BRW survives globally if and only if there exists $\mathbf{q} \in [0, 1]^{\mathbb{N}}$ such that $G(\mathbf{q}) \leq \mathbf{q}$ and $\mathbf{q}(n) < 1$ for some $n \in \mathbb{N}$ (that is, $\mathbf{q} < \mathbf{1}$). By equation (2.1) the condition is equivalent to $\Phi_n(\mathbf{q}(n+1)) \leq \mathbf{q}(n)$ for all $n \geq n_0$ and $\mathbf{q}(n_0) < 1$ for some n_0 ; indeed we can always define $\mathbf{q}(i) = 1$ for all $i = 0, 1, ..., n_0 - 1$ and we have $\Phi_n(\mathbf{q}(n+1)) \leq \mathbf{q}(n)$ for all $n \in \mathbb{N}$. This implies survival starting from the n_0 th generation.

However, since $\Phi_n(0) < 1$ for all $n \in \mathbb{N}$, there is a positive probability for the BPVE to survive up to the n_0 th generation (for every fixed $n_0 \in \mathbb{N}$). Thus, there is survival starting from the 0th generation if and only if there is survival starting from the n_0 th generation. \Box

Proof of Theorem 2.6. The idea is to construct a solution **q** as in Proposition 2.5. To this aim, we make use of an upper bound due to Agresti (1974): $\Phi_n(x) \le f_n(x)$ for all $x \in [0, 1]$ where $f_n(x) := 1 - b_n/(1 - c_n) + b_n x/(1 - c_n x)$ with $b_n := m_n^3/(m_n^{(2)})^2$ and $c_n := (m_n^{(2)} - m_n)/m_n^{(2)}$. In particular, by defining $1/0 := +\infty$ and $1/+\infty := 0$, we have

$$f_n(x) = 1 - \frac{1}{\xi_n(1/(1-x))}$$

for all $x \in [0, 1]$ where

$$\xi_n(s) := \begin{cases} s/m_n + (m_n^{(2)} - m_n)/m_n^2 & s \in \mathbb{R}, \\ +\infty & s = +\infty. \end{cases}$$

Define $S_{n,l} := \sum_{j=n}^{l} \frac{m_j^{(2)} - m_j}{m_j} (\prod_{i=n}^{j} m_i)^{-1}$ and $\beta_{n,l} := S_{n,l} + (\prod_{i=n}^{l} m_i)^{-1}$ (for all $0 \le n \le l$). Note that $S_{n,l}$ is nondecreasing with respect to l: indeed, W_j is an integer-valued random variable, whence $m_j^{(2)} \ge m_j$. Now we prove that also $l \mapsto \beta_{n,l}$ is nondecreasing. Indeed it is trivial to show that $\beta_{n,l+1} - \beta_{n,l} = (m_{l+1}^{(2)}/m_{l+1}^2 - 1)(\prod_{i=n}^{l} m_i)^{-1} \ge 0$. Observe that, for every $n \in \mathbb{N}$, $\inf_{j\ge n} \prod_{i=n}^{j} m_i > 0$ if and only if $\inf_{j\in\mathbb{N}} \prod_{i=0}^{j} m_i > 0$; moreover, $\prod_{i=0}^{j} m_i$ and $\prod_{i=n}^{j} m_i$ have the same behaviour as $j \to +\infty$.

(1) \implies (2). Indeed if $S_{n,n+k}$ converges as $k \to +\infty$ and $\beta_{n,n+k} - S_{n,n+k}$ is bounded from above with respect to k, then $\beta_{n,n+k}$ is bounded from above with respect to k, thus the convergence follows from the monotonicity.

(2) \implies (1). Clearly $S_{n,n+k} \leq \beta_{n,n+k}$; if $\beta_{n,n+k}$ converges as $k \to +\infty$, since $S_{n,n+k}$ is non decreasing then it converges, thus $\beta_{n,n+k} - S_{n,n+k}$ is bounded from above with respect to k.

(2) \implies survival. Denote $\lim_{k\to+\infty} \beta_{n,n+k}$ by b_n . Now we prove that: (a) $\mathbf{q}(n) := 1 - 1/b_n \in [0, 1]$ for all $n \in \mathbb{N}$, (b) $\mathbf{q}(n) < 1$ for some *n* and (c) \mathbf{q} is a solution of $\Phi_n(\mathbf{q}(n+1)) \leq \mathbf{q}(n)$. Thus Proposition 2.5 applies.

Clearly $b_n \ge \beta_{n,n} = 1/m_n + (m_n^{(2)} - m_n)/m_n^2 = m_n^{(2)}/m_n^2 \ge 1$, whence $\mathbf{q}(n) \in [0, 1]$ and (a) is proved. Moreover (2) implies $1 - 1/b_n < 1$, that is, (b). To prove (c) it suffices to show that $\mathbf{q}(n) = f_n(\mathbf{q}(n+1)) \ge \Phi_n(\mathbf{q}(n+1))$. To this aim we show that $\xi_n(b_{n+1}) = b_n$. Indeed, by using the continuity of ξ_n ,

$$\xi_{n}(b_{n+1}) = \lim_{k \to +\infty} (\beta_{n+1,n+k+1}/m_{n} + (m_{n}^{(2)} - m_{n})/m_{n}^{2})$$

$$= \lim_{k \to +\infty} \left[\left(\prod_{i=n}^{n+k+1} m_{i} \right)^{-1} + \sum_{j=n+1}^{n+k+1} \frac{m_{j}^{(2)} - m_{j}}{m_{j}} \left(\prod_{i=n}^{j} m_{i} \right)^{-1} + \frac{m_{n}^{(2)} - m_{n}}{m_{n}^{2}} \right]$$

$$= \lim_{k \to +\infty} \beta_{n,n+k+1} = b_{n}.$$

Proof of Corollary 2.7. It is enough to prove that $(4) \Longrightarrow (3) \Longrightarrow (2) \Longrightarrow (1) \Longrightarrow$ survival. (1) \Longrightarrow survival. Since $m_j^{(2)}/m_j \ge 1$ then $\sum_{j=n}^{+\infty} \frac{m_j^{(2)}}{m_j} (\prod_{i=n}^j m_i)^{-1} < +\infty$ implies both $\lim_{n \to +\infty} \prod_{i=0}^n m_i = +\infty$ and $\sum_{j=n}^{+\infty} \frac{(m_j^{(2)} - m_j)}{m_j} (\prod_{i=n}^j m_i)^{-1} < +\infty$ whence condition (1) of Theorem 2.6 holds and the survival follows.

 $(2) \Longrightarrow (1)$. It follow easily from Cauchy's Root Test.

(3) \Longrightarrow (2). We observe that since $g : \mathbb{N} \to [1, +\infty)$ then $\limsup_{n \to +\infty} g(n+1)/g(n) \ge 1$. For every $\varepsilon > 0$ define

$$K_{\varepsilon} := \sup_{n} \left(\prod_{i=0}^{n-1} g(i+1)/g(i) \right) / \left(\limsup_{i \to +\infty} g(i+1)/g(i) + \varepsilon \right)^{n} < +\infty;$$

then

$$m_n^{(2)}/m_n^2 \le g(n) = g(0) \prod_{i=0}^{n-1} g(i+1)/g(i) \le g(0) K_{\varepsilon} \left(\limsup_{i \to +\infty} g(i+1)/g(i) + \varepsilon\right)^n$$

which implies $\limsup_{n \to +\infty} \sqrt[n]{m_n^{(2)}/m_n^2} \le \limsup_{n \to +\infty} g(n+1)/g(n) + \varepsilon$. This can be done for every $\varepsilon > 0$, hence

$$\limsup_{n \to +\infty} \sqrt[n]{m_n^{(2)}/m_n^2} \le \limsup_{n \to +\infty} g(n+1)/g(n) < \liminf_{n \to +\infty} \sqrt[n]{\prod_{i=0}^{n-1} m_i}.$$

(4) \implies (3). It is enough to choose $g(n) := kM^n$.

Proof of Proposition 3.1. We start by supposing that the initial fitness *x* is chosen according to μ . We use the identification of the BPWS with the associated accessibility percolation model on its infinite Galton–Watson tree: indeed, if the tree is finite, i.e. there is extinction before selection, there is extinction also for the BPWS. Suppose that the Galton–Watson tree τ is infinite; then, almost surely, the number of leaves at distance *n* from the root, say $s_n(\tau)$, has an asymptotic value $s_n(\tau) \sim W \prod_{i=0}^{n-1} m_i$ as $n \to +\infty$ for a suitable random variable W (it is enough to use a martingale argument as in Harris (1963, Chapter I, Section 8.1)). Note that there is a unique path of length *n* from the root to each leaf. The probability that a fixed path of length *n* is admissible is 1/(n + 1)! since there are (n + 1)! possible orderings for the n + 1 labels and all orderings have the same probability. Denote by A_n the event "there exists an admissible path of length *n* from the root" and by \mathbb{P}_{τ} the probability conditioned on the realization τ of the Galton–Watson tree. Thus for every τ , $\mathbb{P}_{\tau}(A_n) \leq s_n(\tau)/(n + 1)!$. On the other hand, for almost every τ , $s_n(\tau)/(n + 1)! \sim (W \prod_{i=0}^{n-1} m_i)/(n + 1)!$ as $n \to +\infty$; thus $\liminf_{n \to +\infty} s_n(\tau)/(n + 1)! = 0$. Hence,

$$\lim_{n \to +\infty} \mathbb{P}_{\tau}(A_n) = \liminf_{n \to +\infty} \mathbb{P}_{\tau}(A_n) \le \liminf_{n \to +\infty} s_n(\tau)/(n+1)! = 0.$$

This yields the result when $n_0 = 0$.

ľ

Suppose $n_0 > 0$ and consider a new BPWS with generating functions $\{\hat{\Phi}_n\}_{n \in \mathbb{N}}$ (before selection) where $\hat{\Phi}_n(z) := z$ if $n < n_0$ and $\hat{\Phi}_n(z) := \Phi_{n-n_0}(z)$ if $n \ge n_0$ (for all $z \in [0, 1]$). This means that every individual from generation 0 to $n_0 - 1$ has exactly one child. This new BPWS survives with positive probability if and only if the original one does; indeed, it is enough to note that there is always a positive probability that the unique path from generation 0 to generation n_0 is admissible. The result follows by the first part of the proof by noting that $\prod_{i=0}^{n+n_0-1} \hat{m}_i = \prod_{i=0}^{n-1} m_i$.

This proves that the probability of extinction is 1 for almost every starting fitness x with respect to μ ; since this probability is nondecreasing with respect to the starting fitness x we have that it is 1, for all $x \in \mathbb{R}$.

Proof of Theorem 3.2. Note that it is enough to prove local survival in $[\bar{x}, y)$ where $\mu(\bar{x}, y) > 0$. Indeed, if $\mu([y, +\infty) \cap I) > 0$ then, according to the Borel-Cantelli lemma local survival in $[\bar{x}, y)$ implies that an infinite number of particles have fitness in $[y, +\infty) \cap I$. Furthermore, *C* can always be chosen as equal to 1, by using a new sequence $c'_i := Cc_i$ instead of c_i ; thus, we assume, without loss of generality, C = 1. Finally, observe that if the condition (3.1) holds for some $n = n_1$ then it holds for every $n \ge n_1$.

Fix $\delta \in (0, \mu(\bar{x}, +\infty))$ and, using the continuity of μ , pick y such that $\mu(\bar{x}, y) = \delta$. Let $n_0 \in \mathbb{N}$ be such that $\sum_{n \ge n_0} c_n/m_n < \delta/2$; n_0 can always be chosen larger than n_1 . Let $p_n := \delta/(2n_0)$ for all $n < n_0$ and $p_n := c_n/m_n$ for all $n \ge n_0$. We construct recursively a strictly increasing sequence $\{x_n\}_{n \in \mathbb{N}}$ satisfying

$$\begin{cases} x_0 = \bar{x}, \\ \mu(x_n, x_{n+1}) = p_n \end{cases}$$

Clearly $\sum_{n>n_0} p_n < \delta/2$ and $\lim_{n\to+\infty} x_n < y$. Indeed

$$\mu(\bar{x}, \lim_{n \to +\infty} x_n) = \sum_{n \in \mathbb{N}} \mu(x_n, x_{n+1}) = \sum_{n < n_0} p_n + \sum_{n \ge n_0} p_n < \delta = \mu(\bar{x}, y).$$

Thus, if we can prove local survival of the BPWS in $[\bar{x}, \lim_{n \to +\infty} x_n)$ we have local survival in $[\bar{x}, y)$.

We proceed by constructing a BPVE which is stochastically dominated by the BPWS as follows: at each generation $n \ge 1$ we obtain a BPVE by removing all the particles of the BPWS with fitness outside the interval $[x_{n-1}, x_n)$ (along with their progenies). More precisely the BPVE starts with one particle with fitness \bar{x} which breeds according to the law of W_0 and kills all the particles with fitness outside the interval $[x_0, x_1)$; this is equivalent to removing each child independently with probability $1 - p_0$. Given the *n*th generation, we construct the next one by keeping all children of the particles of the *n*th generation whose fitness belongs to the interval $[x_n, x_{n+1})$; again, this is like removing each newborn independently with probability $1 - p_n$. This is a BPVE which is dominated by the original BPWS since if a particle has fitness $x \in [x_{n-1}, x_n)$, in the BPWS we keep every child with fitness in the interval $[x, +\infty)$ while in the BPVE we keep only those children whose fitness belongs to $[x_n, x_{n+1}) \subset [x, y] \subset [x, +\infty)$. Hence, the survival of the BPVE implies the local survival of the BPWS in $[\bar{x}, y)$.

Denote by \widetilde{m}_n and $\widetilde{m}_n^{(2)}$ the first and second moments respectively of this BPVE. They are related to the moments of the original process: $\widetilde{m}_n = p_n m_n$ and $\widetilde{m}_n^{(2)} - \widetilde{m}_n = p_n^2 (m_n^{(2)} - m_n)$. Note that $\widetilde{m}_n = c_n$ and $(\widetilde{m}_n^{(2)} - \widetilde{m}_n) / \widetilde{m}_n (\prod_{i=n_0}^n \widetilde{m}_i)^{-1} = (m_n^{(2)} - m_n) / m_n^2 (\prod_{i=n_0}^{n-1} c_i)^{-1}$ for all $n \ge n_0$. Theorem 2.6 yields the conclusion.

Acknowledgments

The authors acknowledge financial support from INDAM-GNAMPA (Istituto Nazionale di Alta Matematica). The second author also thanks FAPESP (2015/03868-7, 2016/11648-0, 2017/10555-0) and CNPq (304676/2016-0) for financial support. Part of this work was carried out during a stay of the second author at Laboratoire de Probabilités et Modèles Aléatoires, Université Paris-Diderot, and a visit at Università di Milano-Bicocca. He is grateful for their hospitality and support. Finally, the authors are grateful to the anonymous referees for their useful suggestions.

References

- Agresti, A. (1974). Bounds on the extinction time distribution of a branching process. Advances in Applied Probability 6, 322–335. MR0423562 https://doi.org/10.2307/1426296
- Agresti, A. (1975). On the extinction times of varying and random environment branching processes. *Journal of Applied Probability* 12, 39–46. MR0365733 https://doi.org/10.2307/3212405
- Berestycki, J., Brunet, É. and Shi, Z. (2016). The number of accessible paths in the hypercube. *Bernoulli* 22, 653–680. MR3449796 https://doi.org/10.3150/14-BEJ641
- Bertacchi, D., Posta, G. and Zucca, F. (2007). Ecological equilibrium for restrained branching random walks. *The Annals of Applied Probability* 17, 1117–1137. MR2344301 https://doi.org/10.1214/105051607000000203
- Bertacchi, D. and Zucca, F. (2008). Critical behaviours and critical values of branching random walks on multigraphs. *Journal of Applied Probability* 45, 481–497. MR2426846 https://doi.org/10.1239/jap/1214950362
- Bertacchi, D. and Zucca, F. (2009a). Characterization of the critical values of branching random walks on weighted graphs through infinite-type branching processes. *Journal of Statistical Physics* 134, 53–65. MR2489494 https://doi.org/10.1007/s10955-008-9653-5
- Bertacchi, D. and Zucca, F. (2009b). Approximating critical parameters of branching random walks. *Journal of Applied Probability* 46, 463–478. MR2535826 https://doi.org/10.1239/jap/1245676100

- Bertacchi, D. and Zucca, F. (2012). Recent results on branching random walks. In *Statistical Mechanics and Random Walks: Principles, Processes and Applications*, 289–340. New York: Nova Science Publishers.
- Bertacchi, D. and Zucca, F. (2014). Strong local survival of branching random walks is not monotone. Advances in Applied Probability 46, 400–421. MR3215539 https://doi.org/10.1239/aap/1401369700
- Bertacchi, D. and Zucca, F. (2015). Branching random walks and multi-type contact-processes on the percolation cluster of \mathbb{Z}^d . *The Annals of Applied Probability* **25**, 1993–2012. MR3348999 https://doi.org/10.1214/14-AAP1040
- Biggins, J. D., Lubachevsky, B. D., Shwartz, A. and Weiss, A. (1991). A branching random walk with a barrier. *The Annals of Applied Probability* 1, 573–581. MR1129775
- Braunsteins, P., Decrouez, G. and Hautphenne, S. (2019). A pathwise iterative approach to the extinction of branching processes with countably many types. *Stochastic Processes and Their Applications* **129**, 713–739. MR3913265 https://doi.org/10.1016/j.spa.2018.03.013
- Broman, E. and Meester, R. (2008). Survival of inhomogeneous Galton–Watson processes. Advances in Applied Probability 40, 798–814. MR2454033 https://doi.org/10.1239/aap/1222868186
- Bulinskaya, E. V. (2015a). Strong and weak convergence of population size in a supercritical catalytic branching process. *Doklady Mathematics* 92, 714–718. MR3496751 https://doi.org/10.1134/s1064562415060228
- Bulinskaya, E. V. (2015b). Complete classification of catalytic branching processes. Theory of Probability and Its Applications 59, 545–566. MR3431695 https://doi.org/10.1137/S0040585X97T987314
- Church, J. D. (1971). On infinite composition products of probability generating functions. Zeitschrift für Wahrscheinlichkeitstheorie und Verwandte Gebiete 19, 243–256. MR0300318 https://doi.org/10.1007/ BF00534112
- Cohn, H. and Jagers, P. (1994). General branching processes in varying environment. *The Annals of Applied Probability* **4**, 184–193. MR1258179
- Coletti, C. F., Gava, R. J. and Rodriguez, P. M. (2018). On the existence of accessibility in a tree-indexed percolation model. *Physica A* 492, 382–388. MR3735120 https://doi.org/10.1016/j.physa.2017.10.019
- Cox, J. T. and Schinazi, R. B. (2014). A stochastic model for the evolution of the influenza virus. *Markov Processes and Related Fields* 20, 155–166. MR3185560
- D'Souza, J. C. and Biggins, J. D. (1992). The supercritical Galton–Watson process in varying environments. Stochastic Processes and Their Applications 42, 39–47. MR1172506 https://doi.org/10.1016/0304-4149(92) 90025-L
- Gantert, N., Müller, S., Popov, Yu, S. and Vachkovskaia, M. (2010). Survival of branching random walks in random environment. *Journal of Theoretical Probability* 23, 1002–1014. MR2735734 https://doi.org/10.1007/ s10959-009-0227-5
- Guiol, H., Machado, F. P. and Schinazi, R. (2011). A stochastic model of evolution. *Markov Processes and Related Fields* 17, 253–258. MR2856242
- Guiol, H., Machado, F. P. and Schinazi, R. (2013). On a link between a species survival time in an evolution model and the Bessel distributions. *REBRAPE Revista Brasileira de Probabilidade E Estatística* 27, 201–209. MR3028804 https://doi.org/10.1214/11-BJPS167
- Harris, T. E. (1963). The Theory of Branching Processes. Berlin: Springer. MR0163361
- Hautphenne, S. (2012). Extinction probabilities of supercritical decomposable branching processes. *Journal of Applied Probability* 49, 639–651. MR3012089 https://doi.org/10.1239/jap/1346955323
- Hautphenne, S., Latouche, G. and Nguyen, G. (2013). Extinction probabilities of branching processes with countably infinitely many types. *Advances in Applied Probability* 45, 1068–1082. MR3161297 https://doi.org/10. 1239/aap/1386857858
- Jagers, P. (1974). Galton–Watson processes in varying environments. *Journal of Applied Probability* 11, 174–178. MR0368197 https://doi.org/10.2307/3212594
- Jagers, P. (1975). Branching Processes with Biological Applications. New York: Wiley. MR0488341
- Kimmel, M. and Axelrod, D. E. (2002). Branching Processes in Biology. New York: Springer. MR1903571 https://doi.org/10.1007/b97371
- Liggett, T. M. and Schinazi, R. B. (2009). A stochastic model for phylogenetic trees. *Journal of Applied Probability* 46, 601–607. MR2535836 https://doi.org/10.1239/jap/1245676110
- Lindvall, T. (1974). Almost sure convergence of branching processes in varying and random environment. Annals of Probability 2, 344–346. MR0378130 https://doi.org/10.1214/aop/1176996717
- Machado, F. P., Menshikov, M. V., Popov and Yu, S. (2001). Recurrence and transience of multitype branching random walks. *Stochastic Processes and Their Applications* 91, 21–37. MR1807360 https://doi.org/10.1016/ S0304-4149(00)00055-7
- Machado, F. P., Popov and Yu, S. (2003). Branching random walk in random environment on trees. Stochastic Processes and Their Applications 106, 95–106. MR1983045
- Nowak, S. and Krug, J. (2013). Accessibility percolation on *n*-trees. *Europhysics Letters* 101, 66004.

Pemantle, R. and Stacey, A. M. (2001). The branching random walk and contact process on Galton–Watson and nonhomogeneous trees. *Annals of Probability* 29, 1563–1590. MR1880232 https://doi.org/10.1214/aop/ 1015345762

Roberts, M. I. and Zhao, L. Z. (2013). Increasing paths in regular trees. *Electronic Communications in Probability* 18, 87. MR3141796 https://doi.org/10.1214/ECP.v18-2784

Schmiegelt, B. and Krug, J. (2014). Evolutionary accessibility of modular fitness landscapes. *Journal of Statistical Physics* **154**, 334–355. MR3162544 https://doi.org/10.1007/s10955-013-0868-8

Zucca, F. (2011). Survival, extinction and approximation of discrete-time branching random walks. *Journal of Statistical Physics* **142**, 726–753. MR2773785 https://doi.org/10.1007/s10955-011-0134-x

D. Bertacchi Università di Milano–Bicocca via Cozzi 53 20125 Milano Italy E-mail: daniela.bertacchi@unimib.it P. M. Rodriguez Universidade de São Paulo Av. Trabalhador São-carlense 400, Centro 13560-590 São Carlos, SP Brazil E-mail: pablor@icmc.usp.br

F. Zucca Dipartimento di Matematica Politecnico di Milano Piazza Leonardo da Vinci 32 20133 Milano Italy E-mail: fabio.zucca@polimi.it