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# GALTON-WATSON PROCESSES IN VARYING ENVIRONMENT AND ACCESSIBILITY PERCOLATION

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ABSTRACT. This paper deals with branching processes in varying environment, namely, whose offspring distributions depend on the generations. We provide sufficient conditions for survival or extinction which rely only on the first and second moments of the offspring distributions. These results are then applied to branching processes in varying environment with selection where every particle has a real-valued label and labels can only increase along genealogical lineages; we obtain analogous conditions for survival or extinction. These last results can be interpreted in terms of accessibility percolation on Galton-Watson trees, which represents a relevant tool for modeling the evolution of biological populations.

**Keywords:** branching process, time inhomogeneous, varying environment, fitness, selection, accessibility percolation, generating function.

**AMS subject classification:** 60J80, 60J85.

## 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 distributions may vary according to the generations. The limit behavior of these processes was firstly studied in [1, 15, 25, 28], and later in [16, 18], among others. We refer the reader to [26] for a survey of earlier results about this topic and for biological motivations. See also [12] for a recent study on the survival properties of these processes and on its connection with percolation theory on trees.

A natural generalization of the branching process is the branching random walk (or *BRW*) where each particle is placed inside a space  $X$  or, equivalently, it is assigned a type (chosen in the space  $X$ ). BRWs are particularly relevant throughout the paper, since there is a natural identification of a BPVE with a BRW on the space  $\mathbb{N}$  (see Section 2 for details). The case when the space  $X$  is at most countable is well studied and understood in both continuous time and discrete time: we refer the reader, for details and results on BRWs to [4, 6, 9, 32] (continuous time), [11, 13, 14, 19, 23, 24, 29, 30] (discrete time); see also [7] for a survey on the topic. Examples of BRWs with countable space  $X$  (along with some variants) and their biological applications are presented in [27, Ch.7].

The case when either the space  $X$  is uncountable or there is a non-trivial interaction among the particles is less understood and there is not a well-established systematic theory available and, in general, different processes have to be studied with different tools (see for instance [3]). 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 [10], where the positions of the particles are interpreted as types (*reproductive prowess* to be exact) and it is assumed that a child is likely to be weaker (in some way) than its parent and children who are too weak will not reproduce; the authors obtain conditions for survival on a family line.

The purpose of this paper is twofold. On the one hand, we provide conditions for survival and extinction of a BPVE. These conditions are obtained with a different approach with respect to the ones found in the literature (see for instance [1, 12, 18]). In particular the strategy to prove survival is to study the associated BRW on  $\mathbb{N}$  and show that it is sufficient to control the growth of the ratio between the second moment and the square of the first moment of the reproduction laws. On the other hand, we apply these results to describe the behavior of a general class of branching processes

in varying environment with selection (or *BPWS*) which are, actually, BRWs in varying environment on an uncountable space. This class of processes is obtained by associating a (random) real value to each new individual, say a fitness, and by assuming that only those children who have a fitness greater than its parent may survive and reproduce. We shall see that the BPWS is related to the *accessibility percolation model* on regular trees introduced in [31], and recently studied on spherically symmetric trees in [17] (see Section 3). This BRWS is useful for modeling the evolution of species (for similar models see for instance [20, 21, 22]).

Here is the outline of the paper. In Section 2 we introduce the notion of BPVE and we describe the identification between a BPVE and a BRW on  $\mathbb{N}$ . By mean of this identification, we translate a characterization of survival for BRWs (Theorem 2.2) into a similar result for BPVEs (Proposition 2.3) which can be applied to obtain sufficient conditions for survival for BPVEs (Theorem 2.5 and Corollary 2.6). At the end of the Section we compare these conditions to other results found in the literature, while in Example 2.7 we describe some explicit families of offspring distributions to which Theorem 2.5 applies. A sufficient condition for extinction is given in Theorem 2.4. Unlike the time-homogeneous BP where, provided that the probability of having exactly one child is strictly smaller than one then extinction is equivalent to having an average number of children strictly smaller than one, in the time-inhomogeneous case slightly counterintuitive situations occur. Indeed, define by  $m_n$  the average number of children of a particle of the  $n$ th generation; on the one hand even when  $m_n < 1$  for all  $n \in \mathbb{N}$  there might be survival (see Example 2.8) and on the other hand given any sequence  $\{m_n\}_{n \in \mathbb{N}}$  it is possible to construct a corresponding BPVE which dies out (see Example 2.9).

Section 3 is devoted to the definition of a generic BPWS and its connection with the accessibility percolation model. A condition for the extinction of a BPWS is given in Proposition 3.2, while the main condition for survival is given in Theorem 3.3.

## 2. BRANCHING PROCESSES IN VARYING ENVIRONMENT

**2.1. Basic definitions.** 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  $\mathbb{P}(W_n = i) := \rho_n(i)$ . Thus,  $W_n$  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

$$Z_{n+1} := \sum_{j=1}^{Z_n} W_{n,j}, \quad n \geq 0$$

where  $Z_n$  is the number of particles in the  $(n+1)$ 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  $W_n$ . As usual, we say that the BPVE becomes extinct almost surely if  $p_e := \mathbb{P}(\bigcup_{n \geq 1} \{Z_n = 0\}) = 1$  (“almost surely” will be often tacitly understood); otherwise, we say that it survives with positive probability (“with positive probability” will be often tacitly understood). If we define  $H_0(z) := z$  for all  $z \in [0, 1]$  and, recursively,  $H_{n+1} := H_n \circ \Phi_{n+1}$ , 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  $n \rightarrow \infty$ . The probability of extinction is monotone with respect to  $\{\Phi_n\}_{n \in \mathbb{N}}$ , meaning that, if  $\Phi_n \geq \bar{\Phi}_n$  (where  $\{\bar{\Phi}_n\}_{n \in \mathbb{N}}$  defines another BPVE), then by induction  $H_n \geq \bar{H}_n$  thus  $p_e \geq \bar{p}_e$  (see Theorem 2.4 for an application of this inequality).

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 branching random walk. Indeed 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*). More precisely, given a BPVE, we associate a BRW by considering the time variable  $n$  as a spatial variable.

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  $\mu = \{\nu_x\}_{x \in X}$  of probability measures on the (countable) measurable space  $(S_X, 2^{S_X})$  where  $S_X := \{f : X \rightarrow \mathbb{N} : \sum_y f(y) < \infty\}$ . 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  $\nu_x$  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  $\mathbb{P}^{\delta_x}$  be the law of this process.

**Definition 2.1.** *The BRW survives (globally) with positive probability starting from  $x$  if  $\bar{\mathbf{q}}(x) := 1 - \mathbb{P}^{\delta_x} \left( \sum_{w \in X} \eta_n(w) > 0, \forall n \in \mathbb{N} \right) < 1$ .*

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 [5, 35] for details.

Global survival can be characterized by using a generating function associated to the BRW: 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

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

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

Note that  $[0, 1]^X$  is a partially ordered set where  $\mathbf{q} \geq \mathbf{z}$  if and only if  $\mathbf{q}(x) \geq \mathbf{z}(x)$  for all  $x \in X$ ; clearly  $\mathbf{q} > \mathbf{z}$  stands for “ $\mathbf{q} \geq \mathbf{z}$  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  $\{\nu_x\}_{x \in X}$  is uniquely determined by this generating function.

It is easy to show (see for instance [5, Corollary 2.2]) 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  $G(\bar{\mathbf{q}}) = \bar{\mathbf{q}}$ . The following theorem characterizes global survival; it appears, in different flavors, in [35, Theorem 4.1] or [8, Theorem 3.1] and it is based on [5, Proposition 2.1].

**Theorem 2.2.** *Consider a BRW and a fixed  $x \in X$ . The following assertions 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  $G(\mathbf{q}) \leq \mathbf{q}$  (i.e.  $G(\mathbf{q}|y) \leq \mathbf{q}(y)$ , 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  $\mathbf{q}$  satisfies either (2) or (3), then  $\mathbf{q} \geq \bar{\mathbf{q}}$ .

Given a BPVE with a sequence  $\{\Phi_n\}_{n \in \mathbb{N}}$  of generating functions we can construct the associated BRW on  $\mathbb{N}$  as follows: each particle at  $n \in \mathbb{N}$  has a random number of children according to the  $n$ th generation law of the BPVE and they are all placed at  $n + 1$ . This is a reducible BRW whose generating function  $G : [0, 1]^{\mathbb{N}} \rightarrow [0, 1]^{\mathbb{N}}$  satisfies

$$G(\mathbf{q}|n) := \Phi_n(\mathbf{q}(n + 1)), \quad \forall \mathbf{q} \in [0, 1]^{\mathbb{N}} \tag{2.1}$$

(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  $X \times \mathbb{N}$ ). Applying Theorem 2.2 to the BRW associated to the BPVE we have the following characterization of survival for the BPVE.

**Proposition 2.3.** *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  $n \geq n_0$ .*

*Proof.* According to Theorem 2.2 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  $i = 0, 1, \dots, n_0 - 1$  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.  $\square$

**2.2. Main results.** We consider a BPVE and its sequence  $\{\Phi_n\}_{n \in \mathbb{N}}$  of generating functions. We denote by  $m_n$  the first moment  $\mathbb{E}[W_n] = \Phi'_n(1)$  of the reproduction law of the  $n$ th generation. The first results is a sufficient condition for extinction (compare with Example 2.8).

**Theorem 2.4.** *If  $\limsup_{n \rightarrow \infty} m_n < 1$ , then the BPVE dies out.*

*Proof.* Let  $\delta \in (0, 1)$  and  $n_0 \in \mathbb{N}$  such that  $m_n \leq \delta$  for all  $n \geq n_0$ . Then, by convexity, since  $\Phi'_n(1) = m_n$ , we have

$$\Phi_n(z) \geq 1 - m_n + m_n z \geq 1 - \delta + \delta z, \quad \forall z \in [0, 1], n \geq n_0.$$

By using the previous inequality,

$$H_{i+n_0}(0) \geq H_{n_0} \circ \Phi_{n_0+1} \circ \dots \circ \Phi_{n_0+i}(0) \geq H_{n_0}(1 - \delta^i) \uparrow 1$$

as  $i \rightarrow \infty$ . Thus  $p_e = 1$ .  $\square$

We denote now 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  $m_n^{(2)} = \Phi_n''(1) + m_n$ . In view of Theorem 2.5 and Corollary 2.6 we define

$$a_c := \begin{cases} (c + \sqrt{c^2 - 2c + 2})/2 & 1 \leq c < +\infty \\ +\infty & c = +\infty \end{cases} \quad (2.2)$$

which is a strictly increasing and continuous function from  $[1, +\infty]$  onto itself. Theorem 2.5 and Corollary 2.6 provide sufficient conditions for survival (compare with Example 2.9).

**Theorem 2.5.** *Consider a BPVE such that  $\bar{c} := \liminf_{n \rightarrow \infty} m_n > 1$ . Suppose that  $m_n^{(2)}/m_n^2 \leq g(n)$  for every sufficiently large  $n$ , where  $\limsup_{n \rightarrow \infty} g(n+1)/g(n) < a_{\bar{c}}$  ( $a_{\bar{c}} > 1$  defined by equation (2.2)). Then the BPVE survives.*

*Proof.* Since  $c \mapsto a_c$  is strictly increasing and continuous from  $(1, +\infty)$  onto itself, let us fix  $c$  such that  $1 < c < \bar{c}$  and  $\limsup_{n \rightarrow \infty} g(n+1)/g(n) < a_c$ . Clearly  $m_n \geq c$  for every sufficiently large  $n$ .

Let  $a \in ((c - \sqrt{c^2 - 2c + 2})/2, a_c)$  such that  $a \geq \limsup_{n \rightarrow \infty} g(n+1)/g(n)$ . Note that we can suppose, without loss of generality, that  $\lim_{n \rightarrow \infty} g(n+1)/g(n) = a$ . Indeed, define  $\bar{g}(n) := a^n \max\{g(i)/a^i : i = 0, \dots, n\}$ . Clearly, since  $\bar{g}(n) \geq g(n)$ , we have  $m_n^{(2)}/m_n^2 \leq \bar{g}(n)$ ; moreover

$$\bar{g}(n+1) = a^{n+1} \max(g(n+1)/a^{n+1}, \bar{g}(n)/a^n) = \max(g(n+1), a\bar{g}(n)). \quad (2.3)$$

If  $\bar{g}(n+1) = g(n+1)$  then equation (2.3) implies  $\bar{g}(n+1) \geq a\bar{g}(n)$  and  $a \leq \bar{g}(n+1)/\bar{g}(n) = g(n+1)/\bar{g}(n) \leq g(n+1)/g(n)$ ; if  $\bar{g}(n+1) = a\bar{g}(n)$  then  $\bar{g}(n+1)/\bar{g}(n) = a$ . Whence  $\bar{g}(n+1)/\bar{g}(n) \in [a, \max(a, g(n+1)/g(n))]$ , thus  $\limsup_{n \rightarrow \infty} g(n+1)/g(n) \leq a$  implies  $\lim_{n \rightarrow \infty} \bar{g}(n+1)/\bar{g}(n) = a$ .

Define  $\xi_n := (m_n^{(2)} - m_n)/m_n^2$  and let  $n_0$  be such that  $c/m_n \leq 1$ ,  $\xi_n \leq g(n)$  whenever  $n \geq n_0$ . The original BPVE stochastically dominates the BPVE obtained by keeping each child of a particle of generation  $n$  independently with probability  $p_n$  where

$$p_n := \begin{cases} c/m_n & n \geq n_0 \\ 1 & n < n_0. \end{cases}$$

The generating function of the random number of children of a particle in the  $n$ th generation of this new BPVE is  $G_n(z) = \Phi_n(zp_n + 1 - p_n)$ , which is,  $G_n(z) = \sum_{i \in \mathbb{N}} \mathbb{P}(W_n = i)(zp_n + 1 - p_n)^i$ . According to Proposition 2.3, to prove the survival of the BPVE it is enough to prove the existence of  $\mathbf{q} \in [0, 1]^{\mathbb{N}}$ ,  $\mathbf{q} < \mathbf{1}$ , such that  $G_n(\mathbf{q}(n+1)) \leq \mathbf{q}(n)$  for every sufficiently large  $n$ .

To this aim, we compute the Taylor expansion of  $G_n$  at 1 and we obtain the following upper bound (where  $\theta_n \in (0, x)$ )

$$\begin{aligned} G_n(1-x) &= 1 - G'_n(1)x + \frac{G''_n(\theta_n)}{2}x^2 \leq 1 - G'_n(1)x + \frac{G''_n(1)}{2}x^2 \\ &= 1 - p_n m_n x + \frac{p_n^2}{2}(m_n^{(2)} - m_n)x^2 = 1 - cx + \frac{c^2}{2}\xi_n x^2 \end{aligned}$$

and the last equality holds for all  $n \geq n_0$ . Clearly, the chain of inequalities  $G_n(\mathbf{q}(n+1)) \leq \mathbf{q}(n)$  (for all  $n \geq n_0$ ) is implied by the following one (just take  $x = 1 - \mathbf{q}(n+1)$ )

$$1 - \mathbf{q}(n) - c(1 - \mathbf{q}(n+1)) + \frac{c^2}{2}\xi_n(1 - \mathbf{q}(n+1))^2 \leq 0, \quad \forall n \geq n_0.$$

The above chain of inequalities is satisfied by taking  $1 - \mathbf{q}(n) := (c-1)/(c^2g(n))$ ; note that  $(c-1)/(c^2g(n)) \in (0, 1/4]$  since  $c > 1$  and  $g(n) \geq 1$ . Indeed,

$$\begin{aligned} \frac{c-1}{c^2g(n)} - \frac{c-1}{cg(n+1)} + \frac{c^2}{2}\xi_n \left( \frac{c-1}{c^2g(n+1)} \right)^2 &= \frac{c-1}{c^2g(n)} \left[ 1 - c \frac{g(n)}{g(n+1)} + \frac{c^2}{2}\xi_n \frac{(c-1)g(n)}{c^2g(n+1)^2} \right] \\ &\leq \frac{c-1}{c^2g(n)} \left[ 1 - c \frac{g(n)}{g(n+1)} + \frac{c-1}{2} \left( \frac{g(n)}{g(n+1)} \right)^2 \right] < 0 \end{aligned} \quad (2.4)$$

where the last inequality holds for all sufficiently large  $n$ , since  $1 - cg(n)/g(n+1) + (c-1)(g(n)/g(n+1))^2/2 \rightarrow 1 - c/a + (c-1)/(2a^2) < 0$  as  $n \rightarrow \infty$  (recall our choice of  $a$ ).  $\square$

**Corollary 2.6.** *Consider a BPVE such that  $m_n \rightarrow +\infty$  and there exists  $M, k \geq 1$  such that  $m_n^{(2)}/m_n^2 \leq kM^n$  for all sufficiently large  $n \in \mathbb{N}$ . Then the BPVE survives.*

*Proof.* The condition in this corollary is the particular case of the condition in Theorem 2.5 where  $\bar{c} = +\infty$ . More precisely, if  $m_n \rightarrow +\infty$ , that is,  $\bar{c} = +\infty$ , then  $a_{\bar{c}} = +\infty$  and the requirement  $\limsup_{n \rightarrow \infty} g(n+1)/g(n) < +\infty$  becomes simply  $g(n+1)/g(n) \leq M$  for all  $n \in \mathbb{N}$  and some  $M > 0$ . This is equivalent to  $m_n^{(2)}/m_n^2 \leq g(0)M^n$ .  $\square$

Note that the existence of the  $k$ th moment  $m_n^{(k)} = \mathbb{E}[W_n^k]$  (where  $k \geq 2$ ) satisfying  $m_n^{(k)}/m_n^k \leq g(n)$  implies the same inequality for the second moment with  $g(n)^{2/k}$ .

One may wonder what kind of functions  $g$  are admissible: as an example we can take  $g(n) \sim ka^n n^b \exp(n^{1-\varepsilon})$  where  $k \geq 1$ ,  $b \geq 0$ ,  $\varepsilon \in (0, 1]$  and  $a < a_{\bar{c}} \in (1, +\infty]$ . Moreover, as shown in the proof of Theorem 2.5, the ‘‘typical’’ case is  $\lim_{n \rightarrow \infty} g(n+1)/g(n) = a$  (which can be assumed without loss of generality): in view of Theorem 3.3, the case  $a = 1$  is particularly interesting.

In the following example we consider some relevant laws for  $W_n$  which satisfy the sufficient conditions of Theorem 2.5.

**Example 2.7.** *Consider  $\Phi_n(z) := 1/(1 + m_n(1 - z))$  which comes from the following geometric reproduction law  $\rho_n(i) = m_n^i/(1 + m_n)^{i+1}$ . This family of laws is particularly relevant since they represent the total number of children of a particle in a continuous-time branching process with breeding rate  $m_n$  and death rate 1. If  $\liminf_n m_n > 1$  then the BPVE survives. Indeed the average*

number of children is  $\frac{d}{dz}\Phi_n(z)|_{z=1} = m_n$  and  $m_n^{(2)} - m_n = \frac{d^2}{dz^2}\Phi_n(z)|_{z=1} = 2m_n^2$  which implies  $m_n^{(2)}/m_n^2 = 2 + 1/m_n \leq 3 =: g(n)$  for all sufficiently large  $n$ . The result follows from Theorem 2.5.

Besides geometric laws, other examples are: Poisson laws  $W_n \sim \mathcal{P}(m_n)$  where  $\liminf_n m_n > 1$  and binomial laws  $W_n \sim \mathcal{B}(k_n, r_n)$  where  $\liminf_n k_n r_n > 1$  (take  $g(n) := 2$  in both cases).

The following two examples show that a BPVE can survive even if  $m_n < 1$  for all  $n$ , while it can die out even if  $\inf_{n \in \mathbb{N}} m_n > 1$ .

**Example 2.8.** Let us consider a sequence  $\{a_n\}_{n \in \mathbb{N}}$  such that  $a_n \in (0, 1)$  for all  $n$  and  $\sum_{n \in \mathbb{N}} a_n < +\infty$ . Define  $W_n$  as a Bernoulli variable with parameter  $1 - a_n$ . Clearly  $m_n = 1 - a_n < 1$  for all  $n$ , nevertheless the corresponding BPVE survives with positive probability.

Indeed, consider the following relation which holds for every sequence of events  $\{A_i\}_i$ :

$$\mathbb{P}\left(\bigcap_{i=0}^{\infty} A_i\right) > 0 \iff \begin{cases} \mathbb{P}(A_i^c | \bigcap_{j=0}^{i-1} A_j) < 1, & \forall i \geq 0 \\ \sum_{i=0}^{\infty} \mathbb{P}(A_i^c | \bigcap_{j=0}^{i-1} A_j) < +\infty \end{cases} \quad (2.5)$$

where  $\mathbb{P}(A_1^c | \bigcap_{j=0}^{-1} A_j) := \mathbb{P}(A_0^c)$ . Denote by  $A_n$  the event “the BPVE survives up to time  $n$ ”. Hence  $\mathbb{P}(A_n^c | \bigcap_{j=1}^{n-1} A_j) = a_n$ ,  $\bigcap_{i=1}^{\infty} A_i$  is the event of survival and the result follows from equation (2.5).

**Example 2.9.** Consider a nonnegative sequence  $\{m_n\}_n$  (note that even  $m_n \rightarrow \infty$  will do). 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  $\{k_n\}_n$  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  $\{k_n\}_n$  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 such a way that  $(1 - m_n/k_n)^{\prod_{i=0}^{n-1} k_i} \geq a_n$ . Fix  $k_0 \in \mathbb{N}$  such that  $1 - m_0/k_0 \geq a_0$ . Suppose we already defined  $k_i$  for all  $i \leq n-1$ ; since  $(1 - m_n/x)^{\prod_{i=0}^{n-1} k_i} \rightarrow 1$  as  $x \rightarrow \infty$ , there exists  $k_n \in \mathbb{N}$  such that  $(1 - m_n/k_n)^{\prod_{i=0}^{n-1} k_i} \geq a_n$ .

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  $\mathbb{P}(A_n^c | \bigcap_{j=1}^{n-1} A_j) \geq (1 - m_n/k_n)^{\prod_{i=0}^{n-1} k_i} \geq a_n$ . The result follows again from equation (2.5).

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

We compare our results with other sufficient conditions found in the literature (see for instance [1, 12, 18]). As we see here, there is an overlap between these conditions and Theorem 2.5 (or Theorem 2.4) but there are BPVEs which satisfy only our conditions and other processes which satisfy only some of the conditions in [1, 12, 18].

In [1, Theorem 2] the author gives a characterization of survival under the conditions  $\sup_{j \in \mathbb{N}} \rho_j(2)/(m_j^{(2)} - m_j) < +\infty$  and  $\inf_{j \in \mathbb{N}} \rho_j(2)/m_j > 0$  which are more restrictive than the ones we postulate in Theorem 2.5. Similarly in [12, Proposition 1.1] a powerful sufficient condition for survival is given under the (restrictive) conditions  $\sup_{j \in \mathbb{N}} m_j^{(2)} < +\infty$  and  $\inf_{j \in \mathbb{N}} m_j > 0$  (which, together, imply our condition in Theorem 2.5).

Another sufficient condition for survival of a BPVE, given by [18, Theorem 1], is the existence of a random variable  $X$  with finite expected value such that

$$\mathbb{P}(W_n/m_n > x) \leq \mathbb{P}(X > x), \quad \forall x \geq 0, n \in \mathbb{N}. \quad (2.6)$$

Theorem 2.5 and [18, Theorem 1] are not in general comparable.

More precisely, condition (2.6) does not imply the finiteness of the second moment  $m_n^{(2)} = \mathbb{E}[W_n^2]$ ; on the other hand, there are examples of sequences  $\{W_n\}_{n \in \mathbb{N}}$ , satisfying the conditions of Theorem 2.5, such that condition (2.6) does not hold for any  $X$  with finite first moment. Indeed, define  $W_n = n^2 B_n$  where  $B_n$  is a Bernoulli random variable with parameter  $1/n^2$ : clearly,  $m_n^{(2)}/m_n^2 = \mathbb{E}[W_n^2]/\mathbb{E}[W_n]^2 = n^2 =: g(n)$  and  $g(n+1)/g(n) \rightarrow 1$  as  $n \rightarrow \infty$ , while  $\mathbb{P}(X > x) \geq \sup_{n \in \mathbb{N}} \mathbb{P}(W_n > x) = 1/n^2$  for  $x \in [(n-1)^2, n^2)$  which implies  $\mathbb{E}[X] = \int_0^\infty \mathbb{P}(X > x) dx = +\infty$ .

A partial equivalence between these conditions can be obtained under the assumptions  $g(n) = M \in \mathbb{R}$  for every  $n \in \mathbb{N}$ . More precisely, assume that  $m_n^{(k)}/m_n^k \leq M$  (for some  $k > 1$ ) then, it is easy to prove condition (2.6) for the random variable  $X$  with the following tails

$$\mathbb{P}(X > x) := \begin{cases} 1 & \text{if } x \leq \sqrt[k]{M} \\ \frac{M}{x^k} & \text{if } x > \sqrt[k]{M}. \end{cases}$$

On the other hand, if condition (2.6) is satisfied for some  $X$  and  $\mathbb{E}[X^k] \leq M$  then

$$\frac{m_n^{(k)}}{m_n^k} = \mathbb{E}[(W_n/m_n)^k] = \int_0^\infty \mathbb{P}(W_n/m_n > \sqrt[k]{x}) dx \leq \int_0^\infty \mathbb{P}(X > \sqrt[k]{x}) dx = \mathbb{E}[X^k] \leq M.$$

### 3. BRANCHING PROCESSES WITH SELECTION AND ACCESSIBILITY PERCOLATION

**3.1. Basic definitions.** 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  $\mu$  on  $\mathbb{R}$  (that is,  $x \mapsto \mu(-\infty, x)$  is a continuous map).

By using this label we can define a selection mechanism as follows: all children of a particle living at  $x \in \mathbb{R}$  survive if and only if they are placed in 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 after selection of number of children of a particle at  $x$  of generation  $n$  is  $G_{n,x}(z) := \Phi_n(z\mu(x, +\infty) + 1 - \mu(x, +\infty))$ . The expected number of children, before selection, of a particle in generation  $n$  is  $m_n = \mathbb{E}[W_n] = \Phi'(1) = \sum_{i \in \mathbb{N}} i \rho_n(i)$ ; after selection, given the position  $x$  of the parent, is clearly  $G'_{n,x}(1) = \Phi'_n(1)\mu(x, +\infty) = m_n \mu(x, +\infty)$ . We call this process *Branching Process in varying environment with selection* or *BPWS*. Note that a BPVE is a particular case of time-inhomogeneous BRW on an uncountable space.

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  $X_v \sim \mu$ . Clearly the BPWS erases all the subtrees branching from a vertex  $v'$  such that  $X_{v'} < X_v$ , where  $v$  is the parent of  $v'$ .

This process can be seen as a particular case of a more general family of processes, namely the *accessibility percolation model*, introduced in [31] and inspired by evolutionary biology questions. In this model one considers a graph  $G = (\mathcal{V}, \mathcal{E})$ , and associates to each vertex  $v \in \mathcal{V}$  a random variable  $X_v$  belonging to a sequence of independent identically distributed, continuous random variables. The main question of interest is the existence of a self-avoiding path of vertices  $\{v_i\}_{i \in \mathbb{N}}$  crossing the entire graph, 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 [2, 31, 33, 34].

In order to study the behavior of a BPWS, we denote by  $\mathcal{A}_n$  the random set of positions of the particles of generation  $n$ ; hence, the size of the population is  $N_n := \#\mathcal{A}_n$  ( $\#$  represents the cardinality of a set) almost surely.



- Definition 3.1.** (1) We define the probability of local extinction in  $I \subseteq \mathbb{R}$  starting from  $x$  by  $\mathbb{P}(\liminf_n \{\mathcal{A}_n \cap I = \emptyset\} | \mathcal{A}_0 = \{x\})$ . We say that there is local survival when this probability is strictly smaller than 1.
- (2) We say that there is global extinction starting from  $x$  if and only if there is local extinction in  $\mathbb{R}$  starting from  $x$ . There is global survival starting from  $x$  if and only if  $\mathbb{P}(\mathcal{A}_n \neq \emptyset, \forall n \in \mathbb{N} | \mathcal{A}_0 = \{x\}) \equiv \mathbb{P}(N_n > 0, \forall n \in \mathbb{N} | \mathcal{A}_0 = \{x\}) > 0$ .

Clearly, given a BPWS global survival is equivalent to accessibility percolation on its (infinite) Galton-Watson tree. It is clear from the definition that local survival implies global survival. We note that the progeny of a particle living at  $x$  is located in  $[x, +\infty)$ ; moreover, if we are interested in *local survival*, that is, the survival of the progeny in an interval  $(a, b)$ , we can disregard (or “kill”) all particles placed in  $[b, +\infty)$ . 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 position of the leftmost particle which we denote by  $l_n := \min \mathcal{A}_n$  (where  $\min(\emptyset) := +\infty$ ). By the nature of the selection process and the fact that  $\mu$  is non-atomic,  $\{l_n\}_{n \in \mathbb{N}}$  is a strictly increasing random sequence almost surely. We denote the almost sure limit by  $l = \lim_{n \rightarrow \infty} l_n \in \mathbb{R} \cup \{+\infty\}$ . 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  $\mathbb{P}(\mu((\lim_n l_n, +\infty) \cap \text{co}(I)) > 0) > 0$  (where  $\text{co}(I)$  is the *essential* convex hull of  $I$ , that is the smallest interval  $J$  such that  $\mu(I \setminus J) = 0$ ). Indeed no contribution to  $\text{co}(I)$  can come from its right since particles cannot be placed on the left of their parent and, by definition of  $l_n$ , there are no particles of generation  $n$  in  $(-\infty, l_n)$ . Once there is survival in  $\text{co}(I)$  then it is easy to show, by using a Borel-Cantelli argument, that there is survival in  $I$ .

**3.2. Results.** Throughout this section we consider a BPWS with label measure  $\mu$ ; 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 function 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 [17].

**Proposition 3.2.** *Given a BPWS, if there exists  $n_0 \geq 0$  such that*

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

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

*Proof.* We start by supposing that the initial point  $x$  is chosen according to  $\mu$ . 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 is infinite; then, almost surely, the number of leaves at distance  $n$  from the root, say  $s_n$ , has an asymptotic value  $s_n \sim \prod_{i=0}^{n-1} m_i$  as  $n \rightarrow \infty$  (use a martingale argument). 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. Thus for any given infinite Galton-Watson tree, the probability of the existence of an admissible path of length  $n$  from the root is bounded from above by  $s_n/(n+1)!$ . But for almost all infinite trees, this conditional probability is asymptotically  $(\prod_{i=0}^{n-1} m_i)/(n+1)! \rightarrow 0$  as  $n \rightarrow \infty$ . This yields the result when  $n_0 = 0$ .

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  $n \geq n_0$  (for all  $z \in [0, 1]$ ). This means that every particle 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 point  $x$  with respect to  $\mu$ ; since this probability is nondecreasing with respect to the starting point  $x$  we have that it is 1 for all  $x \in \mathbb{R}$ .  $\square$

The interpretation of the previous result in terms of accessibility percolation is the following: given the conditions of Proposition 3.2 then for almost every Galton-Watson tree there is no accessibility percolation starting from any label  $x$ . The following theorem gives a sufficient condition for survival of a BPWS.

**Theorem 3.3.** *Suppose that  $\sum_{n \in \mathbb{N}} 1/m_n < +\infty$  and  $m_n^{(2)}/m_n^2 \leq kM^n$  for every sufficiently large  $n$ , for some  $k, M \geq 1$ . The BPWS starting with one particle at  $\bar{x}$  such that  $\mu(\bar{x}, \infty) > 0$  survives locally in  $I \subseteq [\bar{x}, \infty)$  such that  $\mu(I) > 0$ .*

*Proof.* Define  $g(n) := kM^n$  for all  $n \in \mathbb{N}$ . Clearly  $g(n+1)/g(n) = M$ , for all  $n \in \mathbb{N}$ . Let  $c > 1$  be such that  $a_c > M$ .

Note that it is enough to prove local survival in  $[\bar{x}, y)$  where  $\mu(\bar{x}, y) > 0$  (that is,  $\mathbb{P}(l \leq y) > 0$ ). Indeed, if  $\mu([y, +\infty) \cap I) > 0$  then, according to Borel-Cantelli lemma local survival in  $[\bar{x}, y)$  implies that an infinite number of particles will be placed in  $[y, +\infty) \cap I$ .

Fix  $\delta \in (0, \mu(\bar{x}, \infty))$  and, using the continuity of  $\mu$ , pick  $y$  such that  $\mu(\bar{x}, y) = \delta$ . Let  $n_0 \in \mathbb{N}$  be such that  $\sum_{n \geq n_0} 1/m_n < \delta/(2c)$ . Define  $\varepsilon := \delta/(2n_0)$ , and let  $p_n := \varepsilon$  for all  $n < n_0$  and  $p_n := c/m_n$  for all  $n \geq n_0$ . We can 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  $\sum_{n \geq n_0} c/m_n < \delta/2$  and  $\lim_{n \rightarrow \infty} x_n < y$ . Indeed

$$\begin{aligned} \mu(\bar{x}, \lim_{n \rightarrow \infty} x_n) &= \sum_{n \in \mathbb{N}} \mu(x_n, x_{n+1}) = \sum_{n \in \mathbb{N}} p_n \\ &= \sum_{n < n_0} p_n + \sum_{n \geq n_0} p_n < \delta/2 + \delta/2 = \delta = \mu(\bar{x}, y). \end{aligned}$$

thus, if we can prove local survival of the BPWS in  $[\bar{x}, \lim_{n \rightarrow \infty} x_n)$  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  $n \geq 1$  we obtain a BPVE by removing all the particles of the BPWS outside the interval  $[x_{n-1}, x_n)$  (along with their progenies). More precisely the BPVE starts with one particle at  $\bar{x}$  which breeds according to the law of  $W_n$  and kills all the particles 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 which are placed in 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 is located at  $x \in [x_{n-1}, x_n)$ , in the BPWS we keep every child in the interval  $[x, \infty)$  while in the BPVE we keep only those children which are placed in  $[x_n, x_{n+1}) \subset [x, y) \subset [x, \infty)$ . Hence, the survival of the BPVE implies the local survival of the BPWS in  $[\bar{x}, y)$ .

The first and second moments of this BPVE are, respectively,  $\tilde{m}_n = p_n m_n$  and  $\tilde{m}_n^{(2)} = p_n^2 m_n^{(2)}$ . Note that  $\tilde{m}_n = c > 1$  for all  $n \geq n_0$ ,  $\tilde{m}_n^{(2)}/\tilde{m}_n^2 \leq g(n)$  for all sufficiently large  $n$  and  $g(n+1)/g(n) = M < a_c$  for all  $n \in \mathbb{N}$ . Thus Theorem 2.5 applies.  $\square$

The interpretation of Theorem 3.3 in terms of accessibility percolation is the following: the probability of choosing a Galton-Watson tree where there is no accessibility percolation is strictly smaller than one.

As in Example 2.7, explicit examples of laws of  $W_n$  satisfying the conditions of the previous theorem are:

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

**Remark 3.4.** *Consider a BPWS such that  $m_n \sim n^\alpha$ . For  $\alpha < 1$ , Proposition 3.2 holds and there is extinction; for  $\alpha > 1$  (if the condition on the second moment in Theorem 3.3 is satisfied) then by Theorem 3.3 there is survival. Thus, there is phase transition at the critical exponent  $\alpha = 1$ .*

*More generally, one can show that (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 the condition on the second moment in Theorem 3.3 is satisfied) then there is survival.*

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