



# Branching within branching: A model for host–parasite co-evolution

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## Abstract

We consider a discrete-time host–parasite model for a population of cells which are colonized by proliferating parasites. The cell population grows like an ordinary Galton–Watson process, but in reflection of real biological settings the multiplication mechanisms of cells and parasites are allowed to obey some dependence structure. More precisely, the number of offspring produced by a mother cell determines the reproduction law of a parasite living in this cell and also the way the parasite offspring is shared into the daughter cells. In this article, we provide a formal introduction of this branching-within-branching model and then focus on the property of parasite extinction. We establish equivalent conditions for almost sure extinction of parasites and find a strong relation of this event to the behavior of parasite multiplication along a randomly chosen cell line through the cell tree, which forms a branching process in random environment. We then focus on asymptotic results for relevant processes in the case when parasites survive. In particular, limit theorems for the processes of contaminated cells and of parasites are established by using martingale theory and the technique of size-biasing. The results for both processes are of Kesten–Stigum type by including equivalent integrability conditions for the martingale limits to be positive with positive probability. The case when these conditions fail is also studied. For the process of contaminated cells, we show that a proper Heyde–Seneta norming exists such that the limit is nondegenerate.

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## 1. Introduction and model description

The discrete-time *branching-within-branching process* (BwBP) studied in this paper describes the evolution of generations of a population of cells containing proliferating parasites. In an informal way, its reproduction mechanism may be described as follows:

- (1) At time  $n = 0$  there is just one cell containing one parasite.
- (2) Cells and their hosted parasites within one generation form independent reproduction units which behave independently and in the same manner.
- (3) Any cell splits into a random number  $N$ , say, of daughter cells in accordance with a probability distribution  $(p_k)_{k \geq 0}$ .
- (4) Then, given  $N$ , the hosted parasites, independently and in accordance with the same distribution, produce random numbers of offspring which are then shared into the daughter cells.
- (5) All cells and parasites obtained from a cell and its parasites in generation  $n$  belong to generation  $n + 1$ .

We are thus dealing with a hierarchical model of two subpopulations, viz. cells and parasites, with an entangled reproduction mechanism. The hierarchy stems from the fact that cells can survive without parasites but not vice versa.

Proceeding with a more formal introduction, let  $\mathbb{V}$  denote the infinite Ulam–Harris tree with root  $\emptyset$  and  $N_v$  the number of daughter cells of cell  $v \in \mathbb{V}$ . The  $(N_v)_{v \in \mathbb{V}}$  are independent and identically distributed (i.i.d.) copies of the  $\mathbb{N}_0$ -valued random variable  $N$  with distribution  $(p_k)_{k \geq 0}$  and finite mean  $\nu$ , viz.  $\mathbb{P}(N = k) = p_k$  for all  $k \in \mathbb{N}_0$  and

$$\nu = \mathbb{E}N < \infty.$$

The cell population thus forms a standard *Galton–Watson tree* (GWT)  $\mathbb{T} = \bigcup_{n \in \mathbb{N}_0} \mathbb{T}_n$  with  $\mathbb{T}_0 = \{\emptyset\}$  and

$$\mathbb{T}_n := \{v_1 \dots v_n \in \mathbb{V} \mid v_1 \dots v_{n-1} \in \mathbb{T}_{n-1} \text{ and } 1 \leq v_n \leq N_{v_1 \dots v_{n-1}}\}$$

(using the common tree notation  $v_1 \dots v_n$  for  $(v_1, \dots, v_n)$ ). Consequently, defining

$$\mathcal{T}_n := \#\mathbb{T}_n = \sum_{v \in \mathbb{T}_{n-1}} N_v \quad (1)$$

as the *number of cells in the  $n$ th generation* for  $n \in \mathbb{N}_0$ , the sequence  $(\mathcal{T}_n)_{n \geq 0}$  forms a standard *Galton–Watson process* (GWP) with reproduction law  $(p_k)_{k \geq 0}$  and reproduction mean  $\nu$ . For basic information on Galton–Watson processes see [12,34].

Let  $Z_v$  denote the number of parasites in cell  $v \in \mathbb{V}$  and  $\mathbb{T}_n^*$  the set of contaminated cells in generation  $n \in \mathbb{N}_0$  with cardinal number  $\mathcal{T}_n^*$ , so

$$\mathbb{T}_n^* := \{v \in \mathbb{T}_n : Z_v > 0\} \quad \text{and} \quad \mathcal{T}_n^* := \#\mathbb{T}_n^*. \quad (2)$$

We define the *number of parasites process* by

$$\mathcal{Z}_n := \sum_{v \in \mathbb{T}_n} Z_v, \quad n \in \mathbb{N}_0.$$

After these settings, the BwBP is defined as the pair

$$(\mathbb{T}_n, (Z_v)_{v \in \mathbb{T}_n})_{n \geq 0}$$

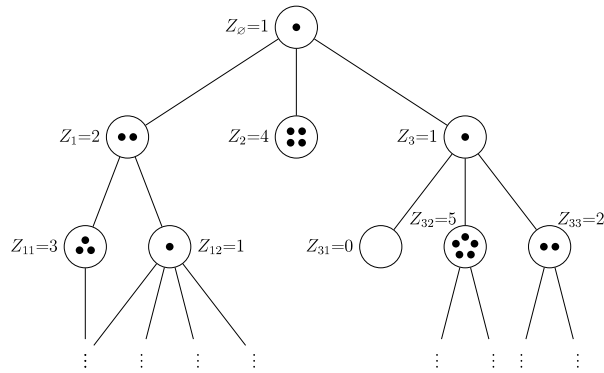


Fig. 1. A typical realization of the first three generations of a BwBP.

and now clearly seen as a description of the generations of any given population of cells and the number of parasites hosted by them.

As informally stated above, parasites at different cells are assumed to multiply independently of each other, whereas reproduction of parasites living in the same cell  $\mathbf{v}$  is conditionally i.i.d. given the number of daughter cells of  $\mathbf{v}$ . More precisely, let for each  $k \in \mathbb{N}$

$$X_{i,\mathbf{v}}^{(\bullet,k)} := \left( X_{i,\mathbf{v}}^{(1,k)}, \dots, X_{i,\mathbf{v}}^{(k,k)} \right), \quad i \in \mathbb{N}, \mathbf{v} \in \mathbb{V},$$

be i.i.d. copies of an  $\mathbb{N}_0^k$ -valued random vector  $X^{(\bullet,k)} := (X^{(1,k)}, \dots, X^{(k,k)})$ . The families  $(X_{i,\mathbf{v}}^{(\bullet,k)})_{i \in \mathbb{N}, \mathbf{v} \in \mathbb{V}}$ ,  $k \in \mathbb{N}$ , are assumed to be mutually independent and also independent of  $(N_{\mathbf{v}})_{\mathbf{v} \in \mathbb{V}}$ . They provide the numerical description of the reproduction and sharing of the parasites living in the cell tree. In detail, if the cell  $\mathbf{v} \in \mathbb{V}$  has  $k \in \mathbb{N}$  daughter cells  $\mathbf{v}1, \dots, \mathbf{v}k$ , then  $X_{i,\mathbf{v}}^{(j,k)}$ ,  $1 \leq j \leq k$ , gives the number of progeny of the  $i$ th parasite in cell  $\mathbf{v}$  which go in daughter cell  $\mathbf{v}j$ . The sum over all entries in  $X_{i,\mathbf{v}}^{(\bullet,k)}$  gives the total offspring number of this parasite. The number of parasites in the cells are thus recursively defined by  $Z_{\emptyset} := 1$  (see Fig. 1) and

$$Z_{\mathbf{v}j} := \sum_{k \geq j} \mathbb{1}_{\{N_{\mathbf{v}}=k\}} \sum_{i=1}^{Z_{\mathbf{v}}} X_{i,\mathbf{v}}^{(j,k)} = \sum_{i=1}^{Z_{\mathbf{v}}} X_{i,\mathbf{v}}^{(j,N_{\mathbf{v}})}, \quad j \in \mathbb{N}, \quad (3)$$

where, by convention,  $X_{i,\mathbf{v}}^{(j,k)} := 0$  if  $j > k$ . We further define

$$\mu_{j,k} := \mathbb{E} X^{(j,k)}$$

for  $j, k \in \mathbb{N}$  and

$$\gamma := \mathbb{E} \mathcal{Z}_1 = \sum_{k \geq 1} p_k \sum_{j=1}^k \mu_{j,k}$$

as the mean number of offspring per parasite, which is assumed to be positive and finite, i.e.

$$0 < \gamma < \infty. \quad (\text{A1})$$

This naturally implies  $\mu_{j,k} < \infty$  for all  $j \leq k$ , and  $\mathbb{P}(N = 0) < 1$ . To avoid trivial cases, we also assume that

$$p_1 = \mathbb{P}(N = 1) < 1 \quad \text{and} \quad \mathbb{P}(\mathcal{Z}_1 = 1) < 1. \quad (\text{A2})$$

If the first of these assumptions fails, the cell tree is just a cell line and  $(\mathcal{Z}_n)_{n \geq 0}$  a standard GWP with reproduction law  $\mathcal{L}(X^{(1,1)})$ , while failure of the second one entails the number of parasites in each generation to be the same, thus  $\mathcal{T}_n^* = \mathcal{T}_0^*$  a.s. for all  $n \in \mathbb{N}_0$ , or  $\mathcal{T}_n^* = \mathcal{Z}_0$  eventually. Finally, we always assume hereafter that

$$p_k \mathbb{P}(X^{(j,k)} \geq 2) > 0 \quad \text{for at least one } (j, k), \quad 1 \leq j \leq k \quad (\text{A3})$$

which rules out another simple case, namely, that every contaminated daughter cell contains only one parasite (as the root cell  $\emptyset$ ).

For each generation  $n = 0, 1, 2, \dots$ , let

$$\mathcal{T}_n := (\mathcal{T}_{n,0}, \mathcal{T}_{n,1}, \mathcal{T}_{n,2}, \dots)$$

denote the infinite vector of cell counts with a specific number of parasites, so  $\mathcal{T}_{n,0}$  gives the number of non-infected cells and  $\mathcal{T}_{n,k}$  for  $k \geq 1$  the number of cells with exactly  $k$  parasites in generation  $n$ . Then  $(\mathcal{T}_n)_{n \in \mathbb{N}_0}$  is a *multi-type branching process (MTBP)* with countably many types. The individuals are the cells and the type of each cell is given by the number of parasites it contains.

In situations where our BwBP has initially  $s_k$  cells of type  $k$  for  $k \in \mathbb{N}_0$  and thus a total number of cells  $\sum_{i \geq 0} s_i$ , we write  $\mathbb{P}_s$  for the underlying probability measure, where

$$\mathbf{s} = (s_0, s_1, \dots) \in \mathbf{N} := \{(x_i)_{i \geq 0} \in \mathbb{N}_0^\infty \mid x_i > 0 \text{ finitely often}\}. \quad (4)$$

Further, we write  $\mathbb{P}_z$ ,  $z \in \mathbb{N}_0$  if the process starts with one cell and  $z$  parasites, i.e.

$$\mathbb{P}_z(\mathcal{T}_0 = 1, Z_\emptyset = z) = 1.$$

The corresponding expectations are denoted as usual by  $\mathbb{E}_s$  and  $\mathbb{E}_z$ , respectively. Indices are dropped in the standard case, viz.  $\mathbb{P} = \mathbb{P}_1$  and  $\mathbb{E} = \mathbb{E}_1$ .

MTBP's with finite type-space are well-studied with results transferred from the classical theory of GWP's, see [12, Chapter V], [34, Chapter 4] or the monography by Mode [47]. If, on the other hand, the state space is infinite (countable or uncountable), a variety of behaviors may occur depending on the reproduction mechanism of types. For example, the branching random walk, an object of long standing interest [1,5,18–21,23,33,40], is obtained when type-space transitions are of independent additive kind. MTBP's are also studied in [9,24,36,46,48,52,53], and we refer to Kimmel and Axelrod [39, Chapter 7] for a series of examples with applications in biology.

Various examples of branching-within-branching models have already been studied in the literature, the first one presumably by Kimmel [38] who considered binary cell division in continuous time with symmetric sharing of parasites into the daughter cells. A discrete-time version of his model, and in fact a special case of ours, with possible asymmetric sharing of parasites was studied by Bansaye [13] and later extended in [14] by adding immigration of parasites and random environments. The latter means that parasites in a cell reproduce under the same but randomly chosen distribution. Subsequently, efforts have been made to generalize the underlying binary cell tree of the afore-mentioned models to arbitrary Galton–Watson trees in both, discrete and continuous time. The greatest progress in this direction has been achieved by Delmas and Marsalle in [26] and together with Bansaye and Tran in [16]. Both articles consider a random

cell splitting mechanism and asymmetric sharing but make ergodic hypotheses that rule out the possibility of parasite extinction which is the focus in the present article. Let us further mention work by Guyon [30] on another discrete-time model with asymmetric sharing and by Bansaye and Tran [17] on a bifurcating cell-division model in continuous time with parasite evolution following a Feller diffusion. There, the cell division rates depend on the quantities of parasites inside the cells and asymmetric sharing of parasites into the two daughter cells is assumed.

Besides the model in [13], our model also comprises the one of type-A cells studied in [7], where these cells produce daughter cells of either the same type A or of type B, and the sharing mechanism of parasites in a type-A cell may depend on the number of type-A and type-B daughter cells. As another special case, we mention the situation of multinomial repartition of parasites. Here all parasites multiply independently in accordance with the same offspring distribution so that the number of parasites process  $(\mathcal{Z}_n)_{n \geq 0}$  forms a standard GWP. After parasite reproduction, a cell divides into a random number  $N$  of descendants, and the offspring of each of its hosted parasites chooses independently the  $i$ th daughter cell with probability  $q_i(k) \in [0, 1]$  if  $N = k$ . Thus,

$$\sum_{j=1}^k X^{(j,k)} \stackrel{d}{=} X^{(1,1)} \quad (5)$$

for all  $k \in \mathbb{N}$ , and given  $\sum_{j=1}^k X^{(j,k)} = x$ , the vector  $(X^{(1,k)}, \dots, X^{(k,k)})$  has a multinomial distribution with parameters  $x$  and  $q_1(k), \dots, q_k(k) \in [0, 1]$ . Replacing (5) with

$$X^{(j,k)} \stackrel{d}{=} X^{(1,1)} \quad \text{for all } 1 \leq j \leq k < \infty,$$

we arrive at a case in which the number of offspring shared by a parasite into a daughter cell is always the same and thus independent of the number of such cells produced. This implies that along an infinite cell line the number of hosted parasites forms an ordinary GWP. As yet another specialization, one may consider the situation when

$$X^{(j,k)} = 0 \quad \text{a.s. for all } 2 \leq j \leq k < \infty,$$

while  $X^{(1,1)}, X^{(1,2)}, \dots$  are independent and positive-valued. Hence, starting with a single cell, parasites are only located in the leftmost cell  $1_n = 1 \dots 1$  ( $n$  times) in each generation  $n$  and  $(\mathcal{Z}_n)_{n \geq 0}$  forms a GWP in random environment (GWPRE), with the number of daughter cells of each  $1_n$  forming the (i.i.d.) random environment and hence determining the offspring distribution in each generation (see [11,54] for the definition of a GWPRE).

Regarding our model assumptions, let us note that it is not for pure mathematical generality when allowing cell division into more than two daughter cells. In the standard case, one of the two daughter cells after cell division may be viewed as the original mother cell which accumulates age-related damage throughout its replication phases and eventually loses the ability for cellular mitosis so that cell death occurs. This phenomenon, called cellular senescence, has been discovered recently even for several single-celled organisms (monads), see Stephens [55]. Genealogical aspects may be studied with the help of Galton–Watson trees when counting all cells stemming from a single cell during its lifetime and interpreting them as the succeeding generation. Since the infection level of the mother cell changes during its lifetime, different numbers of parasites in the daughter cells are to be expected, thus justifying the assumption of asymmetric sharing of parasites. As another reason for this assumption is the fundamental biological mechanism to generate cell diversity, see Jan and Jan [35] and Hawkins and Garriga [32]. For example, a stem

cell uses asymmetric sharing to give rise to a copy of itself and a second daughter cell which is coded to differentiate into cells with a particular functionality in the organism.

The purpose of this article is to establish equivalent conditions for almost sure extinction of parasites and to describe the limiting behavior of the BwBP in the case when parasites survive. We have organized this article as follows. In the next section, we describe an associated branching process in random environment that emerges from the definition of a random cell line. Sections 3 and 4 contain our main results on extinction and limit behavior in the case of survival, respectively. These are proved in Sections 5 and 8, while Section 6 collects some necessary results on branching processes in random environment with immigration and Section 7 provides the definition of yet another random cell line (spine) which are all colonized by at least one parasite. A glossary of the main symbols used throughout may be found at the end of the paper.

## 2. The associated branching process in random environment

The first step towards an analysis of the BwBP is to identify a certain *infinite random cell line* through the cell tree  $\mathbb{T}$  and to study its properties. This approach was first used by Bansaye in [13] who simply picked a random path in the infinite binary Ulam–Harris tree representing the cell population. Since the cell tree is here a general GWT and thus random, we must proceed in a different manner already introduced in [7]. In fact, we pick the random path  $(V_n)_{n \geq 0}$  in  $\mathbb{V}$  according to a certain size-biased distribution instead of uniformly.

To give details, let  $(C_n, T_n)_{n \geq 0}$  be a sequence of i.i.d. random vectors independent of  $(N_v)_{v \in \mathbb{V}}$  and  $(X_{i,v}^{(\bullet,k)})_{i,k \geq 1, v \in \mathbb{V}}$ . The law of  $T_n$  equals the size-biasing of the law of  $N$ , i.e.

$$\mathbb{P}(T_n = k) = \frac{k p_k}{v}$$

for each  $n \in \mathbb{N}_0$  and  $k \in \mathbb{N}$ , and

$$\mathbb{P}(C_n = l | T_n = k) = \frac{1}{k}$$

for  $1 \leq l \leq k$ , which means that  $C_n$  has a uniform distribution on  $\{1, \dots, k\}$  given  $T_n = k$ . Now,  $(V_n)_{n \geq 0}$  is recursively defined by  $V_0 = \emptyset$  and

$$V_n := V_{n-1} C_{n-1}$$

for  $n \geq 1$ . Then

$$\emptyset =: V_0 \rightarrow V_1 \rightarrow V_2 \rightarrow \dots \rightarrow V_n \rightarrow \dots$$

provides us with a random cell line in  $\mathbb{V}$  (not picked uniformly) as depicted in Fig. 2. The resulting path can be viewed as a so-called *spine* in a size-biased tree, each spine cell representing a “typical” cell of its generation in the ordinary cell tree. The concept of size-biasing in the branching context goes back to Lyons et al. in [45], who used it to give alternative proofs of classical limit theorems for GWP’s, and we refer to their work for a detailed construction of a spinal GWT.

Concentrating on the number of parasites along  $(V_n)_{n \geq 0}$ , we have  $Z_{V_0} = Z_{\emptyset}$  and, recursively,

$$Z_{V_{n+1}} = \sum_{k=1}^{\infty} \sum_{j=1}^k \mathbb{1}_{\{C_n=j, T_n=k\}} \sum_{i=1}^{Z_{V_n}} X_{i,V_n}^{(j,k)} = \sum_{i=1}^{Z_{V_n}} X_{i,V_n}^{(C_n, T_n)}$$

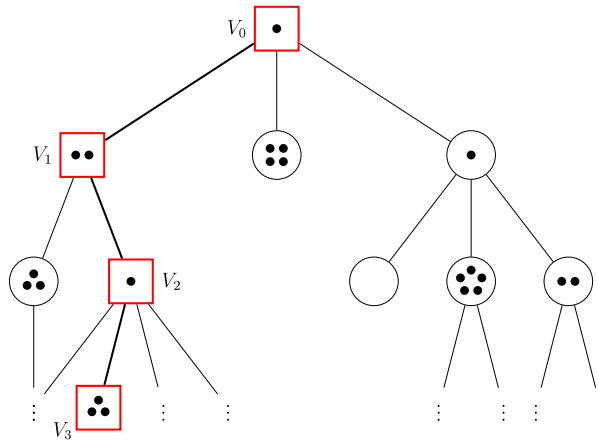


Fig. 2. Typical realization of a spine in the size-biased cell tree. A spinal cell is shown as a red square  $\square$ , all other cells as a circle  $\circ$ . (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

for  $n \geq 0$ . Hence, given  $(C_n, T_n)$ , all parasites in generation  $n$  produce offspring independently with the same distribution  $\mathcal{L}(X^{(C_n, T_n)})$ . Since the  $(C_n, T_n)$  are i.i.d. and independent of  $(X_{i,v}^{(\bullet, k)})_{i,k \geq 1, v \in \mathbb{V}}$ , the process of parasites along the spine  $(Z_{V_n})_{n \geq 0}$  forms a *branching process in i.i.d. random environment (BPRE)* as defined e.g. in [11, 54]. We summarize this observation in the following lemma (see also [7, Subsection 2.1]).

**Lemma 2.1.** *Let  $(Z'_n)_{n \geq 0}$  be a BPRE with  $Z_\emptyset$  ancestors and i.i.d. environmental sequence  $\Lambda := (\Lambda_n)_{n \geq 0}$  taking values in  $\{\mathcal{L}(X^{(j,k)}) | 1 \leq j \leq k < \infty\}$  and such that*

$$\mathbb{P}(\Lambda_0 = \mathcal{L}(X^{(j,k)})) = \frac{pk}{v}$$

*for all  $1 \leq j \leq k < \infty$ . Then  $(Z_{V_n})_{n \geq 0}$  and  $(Z'_n)_{n \geq 0}$  are equal in law.*

**Proof.** It suffices to point out that, by assumption,  $Z'_0 = Z_\emptyset$  a.s. and

$$\mathbb{P}(\Lambda_0 = \mathcal{L}(X^{(j,k)})) = \frac{pk}{v} = \frac{1}{k} \cdot \frac{kp_k}{v} = \mathbb{P}(C_0 = j, T_0 = k)$$

for all  $1 \leq j \leq k < \infty$ , i.e., both processes pick their reproduction law in each generation by the same random mechanism.  $\square$

The BPRE  $(Z'_n)_{n \geq 0}$  with environmental sequence  $\Lambda$  is called hereafter the *associated branching process in random environment (ABPRE)*. It is one of the major tools used in the study of the BwBP, and the following proposition provides a key relation between this process and its ABPRE.

**Proposition 2.2.** *For all  $n, k, z \in \mathbb{N}_0$ ,*

$$\mathbb{P}_z(Z'_n = k) = v^{-n} \mathbb{E}_z \mathcal{T}_{n,k} \quad \text{and} \quad \mathbb{P}_z(Z'_n > 0) = v^{-n} \mathbb{E}_z \mathcal{T}_n^*. \quad (6)$$

**Proof.** By definition of the involved random variables, we find that

$$\mathbb{P}_z(N_{V|0} = k_0, \dots, N_{V|n-1} = k_{n-1}) = \prod_{i=0}^{n-1} p_{k_i}$$

$$= v^n \mathbb{P}_z(V_n = \mathbf{v}, T_0 = k_0, \dots, T_{n-1} = k_{n-1})$$

and

$$\begin{aligned} \mathbb{P}_z(Z_{\mathbf{v}} = k | N_{\mathbf{v}|0} = k_0, \dots, N_{\mathbf{v}|n-1} = k_{n-1}) \\ = \mathbb{P}_z(Z_{\mathbf{v}} = k | V_n = \mathbf{v}, T_0 = k_0, \dots, T_{n-1} = k_{n-1}) \end{aligned}$$

for all  $n, k \in \mathbb{N}$ , vertices  $\mathbf{v} = \mathbf{v}_1 \dots \mathbf{v}_n$  and  $k_0 \geq \mathbf{v}_1, \dots, k_{n-1} \geq \mathbf{v}_n$ , where  $\mathbf{v}|0 := \emptyset$  and  $\mathbf{v}|j := \mathbf{v}_1 \dots \mathbf{v}_j$  for  $1 \leq j \leq n = |\mathbf{v}|$ . Hence it follows by summation over the  $k_i$  that

$$\mathbb{P}_z(Z_{\mathbf{v}} = k) = v^n \mathbb{P}_z(Z_{\mathbf{v}} = k, V_n = \mathbf{v})$$

for all  $\mathbf{v} \in \mathbb{V}$  with  $|\mathbf{v}| = n$ , which in turn leads to

$$\begin{aligned} v^n \mathbb{P}_z(Z_{V_n} = k) &= \sum_{|\mathbf{v}|=n} v^n \mathbb{P}_z(Z_{\mathbf{v}} = k, V_n = \mathbf{v}) \\ &= \sum_{|\mathbf{v}|=n} \mathbb{P}_z(Z_{\mathbf{v}} = k) = \sum_{|\mathbf{v}|=n} \mathbb{E}_z \mathbb{1}_{\{Z_{\mathbf{v}}=k\}} = \mathbb{E}_z \mathcal{T}_{n,k} \end{aligned}$$

and proves the first assertion in view of Lemma 2.1. The second equation then follows by summation over all  $k > 0$ .

We finish this section with a quick review of some relevant facts about the BPPE, relevant references being [2–4,10,11,15,25,29,54,56–58]. For  $n \in \mathbb{N}$  and  $s \in [0, 1]$ ,

$$\mathbb{E}(s^{Z'_n} | \Lambda) = g_{\Lambda_0} \circ \dots \circ g_{\Lambda_{n-1}}(s)$$

is the quenched generating function of  $Z'_n$  with i.i.d.  $g_{\Lambda_n}$  and  $g_{\lambda}$  defined by

$$g_{\lambda}(s) := \mathbb{E}(s^{Z'_1} | \Lambda_0 = \lambda) = \sum_{n \geq 0} \lambda_n s^n \quad (7)$$

for any distribution  $\lambda = (\lambda_n)_{n \geq 0}$  on  $\mathbb{N}_0$ . Moreover,

$$\mathbb{E} g'_{\Lambda_0}(1) = \mathbb{E} Z'_1 = \sum_{1 \leq j \leq k} \frac{p_k}{v} \mathbb{E} X^{(j,k)} = \frac{\mathbb{E} \mathcal{Z}_1}{v} = \frac{\gamma}{v} < \infty, \quad (8)$$

where  $\gamma = \mathbb{E} \mathcal{Z}_1$ . It is also well-known that  $(Z'_n)_{n \geq 0}$  survives with positive probability iff

$$\mathbb{E} \log g'_{\Lambda_0}(1) > 0 \quad \text{and} \quad \mathbb{E} \log^-(1 - g_{\Lambda_0}(0)) < \infty, \quad (9)$$

see e.g. [11,54], and recall that  $\gamma < \infty$  is assumed by (A1). Furthermore, by (A3), there exists  $1 \leq j \leq k < \infty$  such that  $p_k > 0$  and  $\mathbb{P}(X^{(j,k)} \neq 1) > 0$ , which ensures that  $\Lambda_0 \neq \delta_1$  with positive probability. The ABPRE is called *supercritical*, *critical* or *subcritical* if  $\mathbb{E} \log g'_{\Lambda_0}(1) > 0$ ,  $= 0$  or  $< 0$ , respectively. The subcritical case further divides into the three subregimes when  $\mathbb{E} g'_{\Lambda_0}(1) \log g'_{\Lambda_0}(1) < 0$ ,  $= 0$ , or  $> 0$ , respectively, called *strongly*, *intermediate* and *weakly subcritical case*. The quite different behavior of the process in each of the three subregimes is shown by the limit results derived in [29].

Focusing on the subcritical case hereafter, thus  $\mathbb{E} \log g'_{\Lambda_0}(1) < 0$ , we point out the following useful facts. If  $\mathbb{E} g'_{\Lambda_0}(1) \log g'_{\Lambda_0}(1) \leq 0$ , then the convexity of  $\theta \mapsto \mathbb{E} g'_{\Lambda_0}(1)^\theta$  implies that

$$\mathbb{E} g'_{\Lambda_0}(1) = \inf_{0 \leq \theta \leq 1} \mathbb{E} g'_{\Lambda_0}(1)^\theta.$$



Under the assumptions

$$\mathbb{P}(Z'_1 \leq C) = 1 \quad \text{and} \quad \mathbb{P}(0 < g'_{\Lambda_0}(1) < \varepsilon) = 0 \quad (\text{AsGe})$$

for suitable constants  $C > 0$  and  $\varepsilon > 0$ , Geiger et al. [29, Thms. 1.1–1.3] showed that

$$\mathbb{P}(Z'_n > 0) \simeq cn^{-\kappa} \left( \inf_{0 \leq \theta \leq 1} \mathbb{E} g'_{\Lambda_0}(1)^\theta \right)^n \quad \text{as } n \rightarrow \infty \quad (10)$$

for some  $c \in (0, \infty)$ , where

$$\kappa = \begin{cases} 0 & \text{if } \mathbb{E} g'_{\Lambda_0}(1) \log g'_{\Lambda_0}(1) < 0 \text{ (strongly subcritical case),} \\ \frac{1}{2} & \text{if } \mathbb{E} g'_{\Lambda_0}(1) \log g'_{\Lambda_0}(1) = 0 \text{ (intermediate subcritical case),} \\ \frac{3}{2} & \text{if } \mathbb{E} g'_{\Lambda_0}(1) \log g'_{\Lambda_0}(1) > 0 \text{ (weakly subcritical case).} \end{cases}$$

The condition (AsGe) can be strongly relaxed for the asymptotic relation of the survival probability in (10) to hold, see for example [29,59], but is enough for our purposes.

A combination of (6) and (10) provides us with the asymptotic relation

$$\mathbb{E} \mathcal{T}_n^* \simeq cn^{-\kappa} v^n \left( \inf_{0 \leq \theta \leq 1} \mathbb{E} g'_{\Lambda_0}(1)^\theta \right)^n \quad \text{as } n \rightarrow \infty, \quad (11)$$

in particular (with (AsGe) still in force)

$$\inf_{0 \leq \theta \leq 1} \mathbb{E} g'_{\Lambda_0}(1)^\theta \leq \frac{1}{v} \quad \text{if } \sup_{n \geq 1} \mathbb{E} \mathcal{T}_n^* < \infty. \quad (12)$$

### 3. The extinction problem

The trivial fact that non-contaminated cells are unable to produce infected daughter cells shows that the process

$$\mathcal{T}_n^* := (\mathcal{T}_{n,1}, \mathcal{T}_{n,2}, \dots)$$

also forms a MTBP with type space  $\{1, 2, 3, \dots\}$ . As a consequence, the following *extinction–explosion principle* is easily obtained for our model.

**Theorem 3.1** (*Extinction–Explosion Principle*). *The parasite population of a BwBP either dies out or explodes, i.e. for all  $\mathbf{s} \in \mathbb{N}$*

$$\mathbb{P}_{\mathbf{s}}(\mathcal{Z}_n \rightarrow 0) + \mathbb{P}_{\mathbf{s}}(\mathcal{Z}_n \rightarrow \infty) = 1.$$

We denote by

$$\text{Ext} := \{\mathcal{Z}_n \rightarrow 0\} \quad \text{and} \quad \text{Surv} := \text{Ext}^c = \{\mathcal{Z}_n \rightarrow \infty\}$$

the *event of extinction* and of *survival of parasites*, respectively, and put

$$\mathbb{P}_{\mathbf{s}}^* := \mathbb{P}_{\mathbf{s}}(\cdot | \text{Surv}) \quad \text{and} \quad \mathbb{E}_{\mathbf{s}}^* := \mathbb{E}_{\mathbf{s}}(\cdot | \text{Surv}),$$

for  $\mathbf{s} \in \mathbb{N}$ . Also, let  $\mathbb{P}_z^*$  and  $\mathbb{E}_z^*$  for  $z \in \mathbb{N}$  have the obvious meaning.

Turning to the process of contaminated cells, our second extinction result asserts that, ruling out a degenerate case, survival of parasites always goes along with the number of contaminated cells tending to infinity. In other words,  $\mathcal{T}_n^*$  tends to infinity as  $n \rightarrow \infty$  if this holds true for  $\mathcal{Z}_n$ . The degenerate case occurs if all parasites sitting in the same cell send their offspring to the same daughter cell which formally means that, for each  $k \geq 1$ ,

$$X^{(\bullet,k)} = (0, \dots, 0, X^{(j(k),k)}, 0, \dots, 0)$$

for some unique  $j(k) \in \{1, \dots, k\}$  or, equivalently,

$$\mathbb{P}_2(\mathcal{T}_1^* \geq 2) = 0.$$

Note that it is enough to consider a single root cell due to the branching property.

**Theorem 3.2.** *Let  $\mathbb{P}(\text{Surv}) > 0$ .*

- (a) *If  $\mathbb{P}_2(\mathcal{T}_1^* \geq 2) > 0$ , then  $\mathbb{P}_z^*(\mathcal{T}_n^* \rightarrow \infty) = 1$  and thus  $\text{Ext} = \{\sup_{n \geq 0} \mathcal{T}_n^* < \infty\}$   $\mathbb{P}_z$ -a.s. for all  $z \in \mathbb{N}$ .*  
 (b) *If  $\mathbb{P}_2(\mathcal{T}_1^* \geq 2) = 0$ , then  $\mathbb{P}_z^*(\mathcal{T}_n^* = 1 \text{ for all } n \geq 0) = 1$  for all  $z \in \mathbb{N}$ .*

Having provided extinction–explosion dichotomies the processes of contaminated cells and of parasites, we will now state the main result of this section which provides equivalent conditions for almost sure extinction of parasites. The proof will make use of the ABPRE introduced in Section 2.

**Theorem 3.3.** (a) *If  $\mathbb{P}_2(\mathcal{T}_1^* \geq 2) = 0$ , then  $\mathbb{P}(\text{Ext}) = 1$  if, and only if,*

$$\mathbb{E} \log \mathbb{E}(\mathcal{Z}_1 | N_\emptyset) \leq 0 \quad \text{or} \quad \mathbb{E} \log^- \mathbb{P}(\mathcal{Z}_1 > 0 | N_\emptyset) = \infty.$$

- (b) *If  $\mathbb{P}_2(\mathcal{T}_1^* \geq 2) > 0$ , then the following statements are equivalent:*

- (i)  $\mathbb{P}(\text{Ext}) = 1$ .  
 (ii)  $\mathbb{E} \mathcal{T}_n^* \leq 1$  for all  $n \in \mathbb{N}_0$ .  
 (iii)  $\sup_{n \in \mathbb{N}_0} \mathbb{E} \mathcal{T}_n^* < \infty$ .  
 (iv)  $\nu \leq 1$ , or

$$\nu > 1, \quad \mathbb{E} \log g'_{A_0}(1) < 0 \quad \text{and} \quad \inf_{0 \leq \theta \leq 1} \mathbb{E} g'_{A_0}(1)^\theta \leq \frac{1}{\nu}.$$

#### 4. Limit results

The results in this section focus on the problem of finding the proper normalizations of the processes  $(\mathcal{T}_n^*)_{n \geq 0}$  and  $(\mathcal{Z}_n)_{n \geq 0}$  so as to obtain a.s. limits which are positive with positive probability. This problem has been studied in many branching models, see e.g. [9,10,12,22,49,58], and our goal is to provide analogous results for the BwBP.

Two further standing assumptions will be added at this point. First, it is from now on always assumed that parasites survive with positive probability, thus

$$\mathbb{P}(\text{Surv}) > 0. \tag{A4}$$

Second, by assuming

$$\mathbb{P}_2(\mathcal{T}_1^* \geq 2) > 0, \tag{A5}$$

we make sure that not all parasites in a cell share their offspring into one and the same daughter cell. Otherwise, the BwBP would form a *branching process in i.i.d. random environment (BPRE)*

(see Lemma 2.1), for which the results to be derived here may be found in the literature, see e.g. [10,11,56–58]. Recall that (A5) ensures the *extinction–explosion dichotomy* for  $(\mathcal{T}_n^*)_{n \geq 0}$  and  $(\mathcal{Z}_n)_{n \geq 0}$ , i.e. these processes tend to infinity a.s. if parasites survive (Theorems 3.1 and 3.2). By Theorem 3.3, (A4) and (A5) together imply  $\nu > 1$  and  $\mathbb{P}^*(\mathcal{Z}_n \rightarrow \infty) = \mathbb{P}^*(\mathcal{T}_n^* \rightarrow \infty) = 1$ .

We first concentrate on the process of contaminated cells  $(\mathcal{T}_n^*)_{n \geq 0}$  before turning to the process of parasites  $(\mathcal{Z}_n)_{n \geq 0}$ . To prove the results for the latter, we use a spinal approach different from the one leading to the ABPRE and thus need more preparations and the construction of a size-biased parasitic branching within the branching cell tree (see Section 7). Let us stress once more that we only consider the case of a single ancestor cell hosting a single parasite, but that all subsequent results are easily generalized to arbitrary initial populations.

Let  $N$  denote an arbitrary random variable with distribution  $(p_k)_{k \geq 0}$  and  $(\mathcal{F}_n)_{n \geq 0}$  be the filtration, defined by  $\mathcal{F}_0 := \{\emptyset, \Omega\}$  and

$$\mathcal{F}_n := \sigma \left( Z_\nu, N_\nu, X_{i,\nu}^{(\bullet,k)} : |\nu| \leq n-1, i, k \geq 1 \right) \quad \text{for } n \geq 1$$

and  $\mathcal{F}_\infty := \sigma \left( \bigcup_{n \geq 0} \mathcal{F}_n \right)$ . It is obvious by definition that  $\mathcal{F}_n$  and  $X_{i,\nu}^{(\bullet,N_\nu)}$  are independent for all  $n \geq 0$ ,  $|\nu| \geq n$  and  $i \geq 1$ .

#### 4.1. Growth rate of $(\mathcal{T}_n^*)_{n \geq 0}$

Recall that  $(\mathcal{T}_n)_{n \geq 0}$  forms a standard GWP. The Kesten–Stigum theorem [12] ensures that in the supercritical regime  $\nu^n = \mathbb{E} \mathcal{T}_n$  is the right normalization of  $\mathcal{T}_n$  in the sense that  $\nu^{-n} \mathcal{T}_n$  converges a.s. to a positive limit on  $\text{Surv}$  iff  $\mathbb{E} N \log N < \infty$ . However, in order for this to be true also with  $\mathcal{T}_n^*$  instead of  $\mathcal{T}_n$  the parasite population evolving along a random cell line must have a positive chance to survive. In other words, the ABPRE must survive with positive probability.

**Theorem 4.1.**  *$(\nu^{-n} \mathcal{T}_n^*)_{n \geq 0}$  is a nonnegative supermartingale with respect to the filtration  $(\mathcal{F}_n)_{n \geq 0}$  and therefore almost surely convergent to an integrable random variable  $L$  as  $n \rightarrow \infty$ . Furthermore,*

- (a)  $L = 0$  a.s. iff one of the following conditions holds true:
- (i)  $\nu \leq 1$ .
  - (ii)  $\mathbb{E} N \log N = \infty$ .
  - (iii)  $\mathbb{E} \log g'_{A_0}(1) \leq 0$  or  $\mathbb{E} \log^-(1 - g_{A_0}(0)) = \infty$ .
- (b)  $\mathbb{P}(L = 0) < 1$  implies  $\{L = 0\} = \text{Ext}$  a.s.

The next two results address the question of growth rate in the case when  $L = 0$  a.s. Recalling  $\nu^n = \mathbb{E} \mathcal{T}_n^* / \mathbb{P}(Z'_n > 0)$  from (6), the previous theorem tells us that  $\mathcal{T}_n^*$  as  $n \rightarrow \infty$  should behave like its mean modulo an adjustment depending on the ABPRE. Since the environmental sequence of the ABPRE takes values in a countable set, [43, Theorem 1.1] states

$$\lim_{n \rightarrow \infty} \mathbb{P}(Z'_n > 0)^{1/n} = \inf_{0 \leq \theta \leq 1} \mathbb{E} g'_{A_0}(1)^\theta =: \rho \quad (13)$$

where

$$\rho = \begin{cases} 1, & \text{if } \mathbb{E} \log g'_{A_0}(1) \geq 0, \\ \nu^{-1} \gamma, & \text{if } \mathbb{E} \log g'_{A_0}(1) < 0 \text{ and } \mathbb{E} g'_{A_0}(1) \log g'_{A_0}(1) \leq 0, \\ 1 \wedge (\nu^{-1} \gamma), & \text{otherwise.} \end{cases}$$

Hence, we may expect that the number of contaminated cells grows approximately like  $(\nu \rho)^n$  and that a proper norming should not differ much from this sequence.

**Theorem 4.2.** Suppose  $\mathbb{P}(\text{Surv}) > 0$ , thus particularly  $\nu > 1$ . Then

$$\lim_{n \rightarrow \infty} \frac{1}{n} \log \mathcal{T}_n^* = \log \nu \rho \quad \mathbb{P}^* \text{-a.s.}$$

If the ABPRE survives with positive probability,  $(\mathcal{T}_n^*)_{n \geq 0}$  has nearly the same growth rate as the GWP  $(\mathcal{T}_n)_{n \geq 0}$  (see [Theorem 4.1](#)), whence the Heyde–Seneta norming of  $(\mathcal{T}_n)_{n \geq 0}$  gives the right normalization for the process of contaminated cells in this case as well.

**Theorem 4.3.** If  $\mathbb{E} \log g'_{A_0}(1) > 0$  and  $\mathbb{E} \log^-(1 - g_{A_0}(0)) < \infty$ , then there exists a sequence  $(c_n)_{n \geq 0}$  in  $(0, \infty)$  such that  $c_{n+1}/c_n \rightarrow \nu$  and  $c_n^{-1} \mathcal{T}_n^*$  converges a.s. to a finite random variable  $L^*$  satisfying  $\mathbb{P}(L^* > 0) = \mathbb{P}(\text{Surv})$ . Furthermore, the sequence  $(c_n)_{n \geq 0}$  is a proper Heyde–Seneta norming for  $(\mathcal{T}_n)_{n \geq 0}$  as well.

#### 4.2. Growth rate of $(\mathcal{Z}_n)_{n \geq 0}$

Recalling  $\mathbb{P}(\text{Surv}) > 0$ , it is readily seen that  $\mathbb{E} \mathcal{Z}_n = \gamma^n$  for all  $n \geq 0$  and that the normalized number of parasites process

$$W_n := \gamma^{-n} \mathcal{Z}_n, \quad n \geq 0,$$

forms a non-negative martingale with respect to  $(\mathcal{F}_n)_{n \geq 0}$ . It hence converges a.s. to an integrable random variable  $W$ . The following results show that  $(W_n)_{n \geq 0}$  has very similar properties as a normalized supercritical GWP. On the other hand, it turns out that in order for  $W$  to be positive on  $\text{Surv}$  an additional condition besides  $\mathbb{E} \mathcal{Z}_1 \log \mathcal{Z}_1 < \infty$  is needed, which guarantees that the partitioning of the parasite offspring into the daughter cells is sufficiently uniform.

Before stating the results, let us mention a related but weaker one by Biggins and Kyprianou [[24](#), Prop. 8.1] on normalized multi-type branching processes in a very general setting including our BwBP.

**Theorem 4.4.** The following statements are equivalent:

- (a)  $\mathbb{P}(W > 0) > 0$ .
- (b)  $\mathbb{E} W = 1$ .
- (c)  $(W_n)_{n \geq 0}$  is uniformly integrable.
- (d)  $\mathbb{E} (\sup_{n \geq 0} W_n) < \infty$ .

**Theorem 4.5.** The expectation of  $W$  is either 0 or 1, and

$$\mathbb{E} W = 1 \quad \text{iff} \quad \mathbb{E} \mathcal{Z}_1 \log \mathcal{Z}_1 < \infty \quad \text{and} \quad \mathbb{E} \left( \frac{g'_{A_0}(1)}{\gamma} \log \frac{g'_{A_0}(1)}{\gamma} \right) < 0$$

in which case  $\mathbb{P}(W > 0) = \mathbb{P}(\text{Surv})$ .

Our third theorem asserts that  $\mathcal{Z}_n$  still grows like its expected value  $\gamma^n$  on a logarithmic scale if  $\mathbb{E} \mathcal{Z}_1 \log \mathcal{Z}_1 = \infty$ . Thus, a proper normalization should not differ much from this sequence.

**Theorem 4.6.** If  $\mathbb{E} \left( \frac{g'_{A_0}(1)}{\gamma} \log \frac{g'_{A_0}(1)}{\gamma} \right) < 0$ , then  $W_n^{1/n} \rightarrow 1$  a.s. on  $\text{Surv}$  as  $n \rightarrow \infty$ .

The proofs of the stated result, especially [Theorem 4.5](#), will make use of the size-biasing technique, which since the work by Lyons et al. [45] has become a standard technique in the study of branching models, see e.g. [9,24,28,41,42,44,49,50] and also [60] for a similar construction in the context of multiplicative cascades. In Section 7, we will define a size-biased BwBP which is different from the ABPRE  $(Z'_n)_{n \geq 0}$  introduced in Section 2 and in fact strongly related to a *branching process in random environment with immigration (BPREI)*. The latter will therefore be discussed in the following section including the statement of limit results that will be useful for the analysis of the size-biased BwBP.

## 5. Proofs of extinction results ([Theorems 3.1–3.3](#))

**Proof of Theorem 3.1.** Let  $\mathbf{s} \in \mathbb{N}$  with  $s_i > 0$  for at least one  $i \geq 1$ . We prove that  $\mathbf{s}$  is a transient state for the Markov chain  $(\mathcal{T}_n^*)_{n \geq 0}$ . Consider three cases: If  $\mathbb{P}(N = 0) > 1$ , then

$$\mathbb{P}(\mathcal{T}_n^* \neq \mathbf{s} \text{ for all } n \geq 1 | \mathcal{T}_0^* = \mathbf{s}) \geq \mathbb{P}(N = 0)^{\sum_i s_i} > 0.$$

Otherwise, if  $\mathbb{P}(N = 0) = 0$  but  $\mathbb{P}(\mathcal{Z}_1 = 0) > 0$ , then there exists a  $k \in \mathbb{N}$  such that  $p_k \mathbb{P}(\sum_{j=1}^k X^{(j,k)} = 0) > 0$  and thus

$$\mathbb{P}(\mathcal{T}_n^* \neq \mathbf{s} \text{ for all } n \geq 1 | \mathcal{T}_0^* = \mathbf{s}) \geq p_k^{\sum_i s_i} \mathbb{P}\left(\sum_{j=1}^k X^{(j,k)} = 0\right)^{\sum_i s_i} > 0.$$

Finally, consider the case when  $\mathbb{P}(N = 0) = 0$  and  $\mathbb{P}(\mathcal{Z}_1 = 0) = 0$ . Recalling [\(A2\)](#), we then have  $\mathbb{P}(\mathcal{Z}_1 > 1) > 0$  and thus  $p_k \mathbb{P}(\sum_{j=1}^k X^{(j,k)} > 1) > 0$  for some  $k \in \mathbb{N}$ . But this implies

$$\mathbb{P}(\mathcal{T}_n^* \neq \mathbf{s} \text{ for all } n \geq 1 | \mathcal{T}_0^* = \mathbf{s}) \geq p_k \mathbb{P}\left(\sum_{j=1}^k X^{(j,k)} > 1\right) > 0,$$

that is,  $\mathbf{s}$  is a transient state of the Markov chain  $(\mathcal{T}_n^*)_{n \geq 0}$ . Consequently, we infer that almost surely

$$\sum_{i \geq 1} \mathcal{T}_{n,i} \rightarrow 0, \quad \sum_{i \geq 1} \mathcal{T}_{n,i} \rightarrow \infty \quad \text{or, a fortiori,} \quad \mathcal{T}_{n,i} \rightarrow \infty \quad \text{for at least one } i \geq 1$$

as  $n \rightarrow \infty$ . In any case, the parasite population a.s. dies out or tends to infinity.  $\square$

**Proof of Theorem 3.2.** Fix any  $z \in \mathbb{N}$  and consider first the easier case (b). Note that  $\mathbb{P}_2(\mathcal{T}_1^* \geq 2) = 0$  implies  $\mathbb{P}_z(\mathcal{T}_n^* \leq 1 \forall n \geq 0) = 1$ . But since  $\text{Surv} = \{\mathcal{T}_n^* \geq 1 \text{ for all } n \geq 0\}$   $\mathbb{P}_z$ -a.s., (b) is proved.

For the proof of (a), we use the Markov chain  $(\mathcal{T}_n^*)_{n \geq 0}$  to show that  $(\mathcal{T}_n^*)_{n \geq 0}$  visits each  $t \geq 1$  only finitely often, that is

$$\mathbb{P}_z(1 \leq \mathcal{T}_n^* \leq t \text{ infinitely often}) = 0 \tag{14}$$

for all  $t \geq 1$ , hence  $\mathbb{P}_z(\lim_{n \rightarrow \infty} \mathcal{T}_n^* = 0 \text{ or } \infty) = 1$ . But since  $\text{Ext} = \{\mathcal{T}_n^* \rightarrow 0\}$   $\mathbb{P}_z$ -a.s., (a) follows.

Left with the proof of [\(14\)](#), we define (with  $\mathbf{N}$  given by [\(4\)](#))

$$A_k := \left\{ \mathbf{s} \in \mathbf{N} \mid \sum_{i \geq 1} s_i = k, s_1 \neq k \right\} \subseteq \mathbf{N}$$

for  $k \geq 1$  and observe that, for  $n \geq 0$ ,

$$\{\mathcal{T}_n^* = k\} = \{\mathcal{T}_n^* \in A_k\} \cup \{\mathcal{T}_n^* = (k, 0, 0, \dots)\} \quad \mathbb{P}_z\text{-a.s.}$$

Since  $(k, 0, 0, \dots) \in \mathbf{N}$  is a transient state by [Theorem 3.1](#), we obtain

$$\mathbb{P}_z(\mathcal{T}_n^* = k \text{ infinitely often}) = \mathbb{P}_z(\mathcal{T}_n^* \in A_k \text{ infinitely often}).$$

Therefore, it remains to prove that the Markov chain  $(\mathcal{T}_n^*)_{n \geq 0}$  visits the set  $A_k$  only finitely often with probability 1. For  $\mathbf{s} \in A_k$ , i.e.  $\sum_i s_i = k$  and  $s_j > 1$  for some  $j > 1$ , we infer with the help of the branching property

$$\begin{aligned} \mathbb{P}_{\mathbf{s}}(\mathcal{T}_n^* \notin A_k \text{ for all } n \geq 1) &\geq \mathbb{P}_{\mathbf{s}}(\mathcal{T}_1^* > k \text{ for all } n \geq 1) \\ &\geq \mathbb{P}_j(\mathcal{T}_1^* \geq 2) \mathbb{P}(\text{Surv})^2 \prod_{i: s_i > 0} (\mathbb{P}_i(\mathcal{T}_1^* \geq 1) \mathbb{P}(\text{Surv}))^{s_i} \\ &\geq \mathbb{P}_2(\mathcal{T}_1^* \geq 2) \mathbb{P}(\mathcal{T}_1^* \geq 1)^k \mathbb{P}(\text{Surv})^{k+2} \end{aligned}$$

and positivity of the last expression is guaranteed by our assumptions. Notice also that this expression is independent of the choice of  $\mathbf{s}$ . Next, let  $\tau_0 := 0$  and

$$\tau_{n+1} := \inf \{m > \tau_n \mid \mathcal{T}_m^* \in A_k\}$$

for  $n \geq 0$  be the successive return times of  $(\mathcal{T}_n^*)_{n \geq 0}$  to the set  $A_k$ , where as usual  $\inf \emptyset := \infty$  and  $\tau_{n+1} = \infty$  if  $\tau_n = \infty$ . Then the previous inequality and the strong Markov property of  $(\mathcal{T}_n^*)_{n \geq 0}$  imply the existence of a constant  $c < 1$  such that for all  $\mathbf{s} \in A_k$  and  $n \geq 0$

$$\mathbb{P}_z(\tau_{n+1} - \tau_n < \infty \mid \mathcal{T}_{\tau_n}^* = \mathbf{s}, \tau_n < \infty) = \mathbb{P}_{\mathbf{s}}(\tau_1 < \infty) \leq c < 1.$$

Therefore, we infer upon iteration that

$$\begin{aligned} \mathbb{P}_z(\tau_n < \infty) &= \sum_{\mathbf{s} \in A_k} \mathbb{P}_z(\mathcal{T}_{\tau_{n-1}}^* = \mathbf{s}, \tau_n - \tau_{n-1} < \infty, \tau_{n-1} < \infty) \\ &= \sum_{\mathbf{s} \in A_k} \mathbb{P}_z(\tau_n - \tau_{n-1} < \infty \mid \mathcal{T}_{\tau_{n-1}}^* = \mathbf{s}, \tau_{n-1} < \infty) \mathbb{P}_z(\mathcal{T}_{\tau_{n-1}}^* = \mathbf{s}, \tau_{n-1} < \infty) \\ &\leq c \mathbb{P}_z(\tau_{n-1} < \infty) \leq \dots \leq c^{n-1} \mathbb{P}_z(\tau_1 < \infty) \leq c^{n-1} \end{aligned}$$

for each  $n \geq 1$  and thereupon

$$\begin{aligned} \mathbb{P}_z(\mathcal{T}_n^* \in A_k \text{ infinitely often}) &= \mathbb{P}_z(\tau_n < \infty \text{ for all } n \geq 1) = \mathbb{P}_z\left(\bigcap_{n \geq 1} \{\tau_n < \infty\}\right) \\ &= \lim_{n \rightarrow \infty} \mathbb{P}_z(\tau_n < \infty) \leq \lim_{n \rightarrow \infty} c^{n-1} = 0 \end{aligned}$$

which completes the proof.  $\square$

**Proof of Theorem 3.3.** (a) If  $\mathbb{P}_2(\mathcal{T}_1^* \geq 2) = 0$ , then for all  $k \geq 1$  with  $p_k > 0$  there exists at most one  $1 \leq j \leq k$  such that  $\mathbb{P}(X^{(j,k)} > 0) > 0$ , see before [Theorem 3.2](#). As a consequence,  $(\mathcal{L}_n)_{n \geq 0}$  is a branching process in random environment, the latter given by the i.i.d. numbers of daughter cells produced by the unique cells which contain the parasites (their common law being the law of  $N_{\emptyset}$ ). Hence,  $(\mathcal{L}_n)_{n \geq 0}$  dies out almost surely if, and only if,  $\mathbb{E}(\log \mathbb{E}(\mathcal{L}_1 | N_{\emptyset})) \leq 0$  or  $\mathbb{E} \log^- \mathbb{P}(\mathcal{L}_1 > 0 | N_{\emptyset}) = \infty$  (see e.g. [\[54\]](#)).

(b) Suppose now  $\mathbb{P}_2(\mathcal{T}_1^* \geq 2) > 0$ .

“(i)  $\Rightarrow$  (ii)” (by contraposition) Fix  $m \in \mathbb{N}$  such that  $\mathbb{E}(\mathcal{T}_m^*) > 1$  and consider a supercritical GWP  $(S_n)_{n \geq 0}$  with  $S_0 = 1$  and offspring distribution

$$\mathbb{P}(S_1 = k) = \mathbb{P}(\mathcal{T}_m^* = k), \quad k \in \mathbb{N}_0.$$

Obviously,

$$\mathbb{P}(S_n > k) \leq \mathbb{P}(\mathcal{T}_{nm}^* > k)$$

for all  $k, n \in \mathbb{N}_0$ , hence

$$\lim_{n \rightarrow \infty} \mathbb{P}(\mathcal{T}_{nm}^* > 0) \geq \lim_{n \rightarrow \infty} \mathbb{P}(S_n > 0) > 0,$$

i.e. parasites survive with positive probability.

“(ii)  $\Rightarrow$  (iii)” is trivial.

“(iii)  $\Rightarrow$  (i)” Recall that  $\liminf_{n \rightarrow \infty} \mathcal{T}_n^* = \infty$  a.s. on **Surv** by [Theorem 3.2](#). On the other hand,  $\sup_{n \geq 0} \mathbb{E} \mathcal{T}_n^* < \infty$  implies

$$\infty > \liminf_{n \rightarrow \infty} \mathbb{E} \mathcal{T}_n^* \geq \mathbb{E} \left( \liminf_{n \rightarrow \infty} \mathcal{T}_n^* \right)$$

by Fatou’s lemma so that  $\mathbb{P}(\text{Surv}) = 0$ .

“(iv)  $\Rightarrow$  (i), (ii)” If  $\nu \leq 1$ , then  $\mathbb{E} \mathcal{T}_n^* \leq \mathbb{E} \mathcal{T}_n = \nu^n \leq 1$  for all  $n \in \mathbb{N}$ . So let us consider the situation when

$$\nu > 1, \quad \mathbb{E} \log g'_{A_0}(1) < 0 \quad \text{and} \quad \inf_{0 \leq \theta \leq 1} \mathbb{E} g'_{A_0}(1)^\theta \leq \frac{1}{\nu}$$

is valid. It is here where the ABPRE  $(Z'_n)_{n \geq 0}$  comes into play. By [\(6\)](#),

$$\mathbb{E} \mathcal{T}_n^* = \nu^n \mathbb{P}(Z'_n > 0)$$

for all  $n \in \mathbb{N}$ . We distinguish three cases:

Case A.  $\mathbb{E} g'_{A_0}(1) \log g'_{A_0}(1) \leq 0$ .

By [\(8\)](#) and what has been pointed out in the short review of BPRE’s at the end of the previous section, we then infer

$$\frac{\gamma}{\nu} = \mathbb{E} g'_{A_0}(1) = \inf_{0 \leq \theta \leq 1} \mathbb{E} g'_{A_0}(1)^\theta \leq \frac{1}{\nu}$$

and thus  $\gamma \leq 1$ , which in turn entails

$$\mathbb{E} \mathcal{T}_n^* \leq \mathbb{E} \mathcal{X}_n = \gamma^n \leq 1$$

for all  $n \in \mathbb{N}$  as claimed.

Case B.  $\mathbb{E} g'_{A_1}(1) \log g'_{A_1}(1) > 0$  and [\(AsGe\)](#).

Then, by [\(10\)](#),

$$\mathbb{P}(Z'_n > 0) \simeq cn^{-3/2} \left( \inf_{0 \leq \theta \leq 1} \mathbb{E} g'_{A_1}(1)^\theta \right)^n \quad \text{as } n \rightarrow \infty$$

holds true for a suitable constant  $c \in (0, \infty)$  whence, by Fatou’s lemma,

$$0 = \lim_{n \rightarrow \infty} \nu^n \mathbb{P}(Z'_n > 0) = \liminf_{n \rightarrow \infty} \mathbb{E} \mathcal{T}_n^* \geq \mathbb{E} \left( \liminf_{n \rightarrow \infty} \mathcal{T}_n^* \right).$$

Consequently,  $\mathbb{P}(\text{Surv}) = 0$  since  $\inf_{n \geq 0} \mathcal{T}_n^* \geq 1$  a.s. on **Surv**.

Case C.  $\mathbb{E} g'_{\Lambda_1}(1) \log g'_{\Lambda_1}(1) > 0$ .

Using contraposition, suppose  $\sup_{n \in \mathbb{N}} \mathbb{E} \mathcal{T}_n^* > 1$  and fix an arbitrary vector  $\alpha = (\alpha^{(j,k)})_{1 \leq j \leq k < \infty}$  of distributions on  $\mathbb{N}_0$  satisfying

$$\alpha_x^{(j,k)} \leq \mathbb{P}(X^{(j,k)} = x)$$

for  $x \geq 1$  and  $j, k$  as stated, hence

$$\alpha_0^{(j,k)} \geq \mathbb{P}(X^{(j,k)} = 0) \quad \text{and} \quad \sum_{x \geq n} \alpha_x^{(j,k)} \leq \mathbb{P}(X^{(j,k)} \geq n)$$

for each  $n \geq 0$ . Possibly after enlarging the underlying probability space, we can then construct a BwBP  $(N_v, Z_{\alpha,v}, X_{\alpha,i,v}^{(\bullet,k)})_{v \in \mathbb{V}, i, k \in \mathbb{N}}$  coupled with and of the same kind as the original BwBP such that

$$\mathbb{P}(X_{\alpha,i,v}^{(j,k)} = x) = \alpha_x^{(j,k)} \quad \text{and} \quad X_{\alpha,i,v}^{(j,k)} \leq X_{i,v}^{(j,k)} \quad \text{a.s.}$$

for all  $1 \leq j \leq k < \infty$ ,  $v \in \mathbb{V}$ ,  $i \geq 1$  and  $x \geq 1$ . Then  $Z_{\alpha,v} \leq Z_v$  a.s. for all  $v \in \mathbb{V}$  and since the choice of  $\alpha$  has no affect on the cell splitting process, we have  $v_\alpha = v > 1$  and thus for  $\theta \in [0, 1]$

$$\begin{aligned} \mathbb{E} g'_{\alpha, \Lambda_0}(1)^\theta &= \mathbb{E}(\mathbb{E}(Z'_{\alpha,1} | \Lambda_0)^\theta) = \sum_{1 \leq j \leq k < \infty} \frac{p_k}{v} \left( \mathbb{E} X_\alpha^{(j,k)} \right)^\theta \\ &\leq \sum_{1 \leq j \leq k < \infty} \frac{p_k}{v} \mu_{j,k}^\theta \leq \mathbb{E} g'_{\Lambda_0}(1)^\theta \end{aligned} \quad (15)$$

where  $v_\alpha$ ,  $Z'_{\alpha,n}$ ,  $X_\alpha^{(j,k)}$  and  $g_{\alpha, \Lambda_0}$  have the obvious meaning. Recalling  $\mu_{j,k} = \mathbb{E} X^{(j,k)}$ , a similar calculation as in (15) leads to

$$\mathbb{E} \log g'_{\alpha, \Lambda_0}(1) \leq \mathbb{E} \log g'_{\Lambda_0}(1) < 0. \quad (16)$$

We are now going to specify suitable  $\alpha$  to complete our argument.

For  $M \in \mathbb{N}$  let  $\alpha(M) = (\alpha^{(j,k)}(M))_{1 \leq j \leq k < \infty}$  be the vector defined by

$$\alpha_x^{(j,k)}(M) := \begin{cases} \mathbb{P}(X^{(j,k)} = x), & \text{if } 1 \leq x \leq M, \\ 0, & \text{if } x > M, \end{cases}$$

if  $\mu_{j,k} \geq 1/M$ , and  $\alpha_0^{(j,k)} = 1$  if  $\mu_{j,k} < 1/M$ . Then the BwBP with truncation  $\alpha(M)$  satisfies the condition (AsGe), and we can fix  $M \in \mathbb{N}$  such that  $\sup_{n \in \mathbb{N}} \mathbb{E} \mathcal{T}_{\alpha(M),n}^* > 1$ , because  $\mathcal{T}_{\alpha(M),n}^* \uparrow \mathcal{T}_n^*$  as  $M \rightarrow \infty$ . Then, by what has already been proved under Case B in combination with (15), (16) and  $v_{\alpha(M)} > 1$ , we infer

$$\inf_{0 \leq \theta \leq 1} \mathbb{E} g'_{\Lambda_0}(1)^\theta \geq \inf_{0 \leq \theta \leq 1} \mathbb{E} g'_{\alpha(M), \Lambda_0}(1)^\theta > \frac{1}{v} \quad (17)$$

which contradicts (iv).

“(ii)  $\Rightarrow$  (iv)” Suppose that  $\mathbb{E} \mathcal{T}_n^* \leq 1$  for all  $n \in \mathbb{N}_0$  and further  $v > 1$  which, by (6), entails  $\lim_{n \rightarrow \infty} \mathbb{P}(Z'_n > 0) = 0$ , thus  $\mathbb{E} \log g'_{\Lambda_0}(1) \leq 0$  or  $\mathbb{E} \log^-(1 - g_{\Lambda_0}(0)) = \infty$ . We must show that  $\mathbb{E} \log g'_{\Lambda_0}(1) < 0$  and  $\inf_{0 \leq \theta \leq 1} \mathbb{E} g'_{\Lambda_0}(1)^\theta \leq v^{-1}$ .

Assuming  $\mathbb{E} \log g'_{\Lambda_0}(1) < 0$ , the second condition follows from (12) if (AsGe) is valid. Dropping the latter condition, suppose that  $\inf_{0 \leq \theta \leq 1} \mathbb{E} g'_{\Lambda_0}(1)^\theta > v^{-1}$ . Then we can find a  $M \geq 1$



and construct a suitable “ $\alpha(M)$ -coupling” as described above such that (17) holds. But since (AsGe) is fulfilled for the truncated process, we arrive at the contradiction

$$\sup_{n \in \mathbb{N}} \mathbb{E} \mathcal{T}_n^* \geq \sup_{n \in \mathbb{N}} \mathbb{E} \mathcal{T}_{\alpha(M),n}^* > 1$$

by referring to (16) and by what has already been established for a BwBP with a subcritical ABPRE, i.e.  $\mathbb{E} \log g'_{\Lambda_0}(1) < 0$ . Thus  $\inf_{0 \leq \theta \leq 1} \mathbb{E} g'_{\Lambda_0}(1)^\theta \leq \nu^{-1}$  holds even if (AsGe) fails.

It remains to rule out that  $\mathbb{E} \log g'_{\Lambda_0}(1) \geq 0$ . Assuming the latter, we find with the help of Jensen’s inequality that

$$\inf_{0 \leq \theta \leq 1} \log \mathbb{E} g'_{\Lambda_0}(1)^\theta \geq \inf_{0 \leq \theta \leq 1} \theta \mathbb{E} \log g'_{\Lambda_0}(1) \geq 0$$

or, equivalently,

$$\inf_{0 \leq \theta \leq 1} \mathbb{E} g'_{\Lambda_0}(1)^\theta \geq 1 > \frac{1}{\nu}$$

(which implies  $\inf_{0 \leq \theta \leq 1} \mathbb{E} g'_{\Lambda_0}(1)^\theta = 1$ ). Use once more a suitable “ $\alpha$ -coupling” (not necessarily of the previous kind) and fix  $\alpha$  in such a way that

$$1 = \inf_{0 \leq \theta \leq 1} \mathbb{E} g'_{\Lambda_0}(1)^\theta > \inf_{0 \leq \theta \leq 1} \mathbb{E} g'_{\alpha, \Lambda_0}(1)^\theta > \frac{1}{\nu},$$

which implies subcriticality of the ABPRE  $(Z'_{\alpha,n})_{n \geq 0}$  by taking the logarithm and using Jensen’s inequality. As above, we thus arrive at the contradiction

$$\sup_{n \in \mathbb{N}} \mathbb{E} \mathcal{T}_n^* \geq \sup_{n \in \mathbb{N}} \mathbb{E} \mathcal{T}_{\alpha,n}^* > 1$$

by using the already established results for a BwBP with subcritical ABPRE. This completes the proof of (b).  $\square$

## 6. The branching process in random environment with immigration

The following can be seen as a stand-alone section and does therefore not refer to the notation previously introduced.

The Galton–Watson processes with immigration in fixed environment has been studied by many authors in the past, see [8] for the most important results and also references. In a multitype setting and random environment, Key [37] and Roitershtein [51] proved limit theorems in the subcritical case. Results for the single-type process in random environment for all three (subcritical, critical and supercritical) regimes have been obtained more recently by Bansaye [14]. On the other hand, a theorem of Kesten–Stigum type for the BPREDI, indispensable for our analysis of the BwBP, appears to be an open problem and is therefore presented below (Theorem 6.1).

Turning to a model description, denote by  $\mathcal{P}$  the set of probability laws on  $\mathbb{N}_0$  and by  $\mathcal{P}_1$  the subset of laws with finite mean. Let the environmental sequence  $\mathcal{U} = (\mathcal{U}_n)_{n \geq 0} = (\mathcal{U}_{n,1}, \mathcal{U}_{n,2})_{n \geq 0}$  consist of i.i.d. random variables taking values in the set  $\mathcal{P}_1 \times \mathcal{P}$  endowed with the  $\sigma$ -field induced by the total variation metric. Given  $\mathcal{U}$ , let  $\{X_{n,k} | (n, k) \in \mathbb{N}_0 \times \mathbb{N}\}$  and  $\{\xi_n | n \in \mathbb{N}_0\}$  be conditionally independent families of i.i.d.  $\mathbb{N}_0$ -valued random variables such that, for all  $n \geq 0$  and  $k \geq 1$ ,

$$\mathbb{P}(X_{n,k} \in \cdot | \mathcal{U}) = \mathcal{U}_{n,1} \quad \text{and} \quad \mathbb{P}(\xi_n \in \cdot | \mathcal{U}) = \mathcal{U}_{n,2} \quad \text{a.s.}$$

To ensure that immigration occurs with positive probability, we assume throughout this section that

$$\mathbb{P}(\xi_0 > 0) > 0. \quad (18)$$

The BPREI  $(Z_n)_{n \geq 0}$  with environmental sequence  $\mathcal{U}$  is then defined by  $Z_0 := 0$  and, recursively,

$$Z_{n+1} := \sum_{i=1}^{Z_n} X_{n,i} + \xi_n \quad (19)$$

for  $n \geq 0$ . The  $X_{k,n}$ ,  $k \geq 1$ , provide the numbers of offspring of the individuals at generation  $n$ , while  $\xi_n$  gives the number of immigrants at time  $n$ . It is clear by our assumptions that  $Z_n$  and  $\{X_{m,k}, \xi_m | m \geq n, k \geq 1\}$  are independent for all  $n \geq 0$  which in turn ensures the *Markov property* for  $(Z_n)_{n \geq 0}$ . Let

$$\mu_{\mathcal{U}_n} := \mathbb{E}(X_{1,n} | \mathcal{U}_n) = \mathbb{E}(X_{1,1} | \mathcal{U}_{n,1})$$

the mean of  $\mathcal{U}_{n,1}$ . As in the setting without immigration, we consider the *supercritical case*  $\mathbb{E} \log \mu_{\mathcal{U}_0} > 0$ , the *critical case*  $\mathbb{E} \log \mu_{\mathcal{U}_0} = 0$ , and the *subcritical case*  $\mathbb{E} \log \mu_{\mathcal{U}_0} < 0$ .

Before stating the main results of this section, we recall the standard fact that

$$\limsup_{n \rightarrow \infty} \frac{X_n}{n} = \begin{cases} 0, & \text{if } \mathbb{E} X_0 < \infty, \\ \infty, & \text{if } \mathbb{E} X_0 = \infty \end{cases} \quad (20)$$

for any sequence  $(X_n)_{n \geq 0}$  of i.i.d. and non-negative random variables.

The following martingale limit theorem of Kesten–Stigum type for the supercritical BPREI will be of great use for our later analysis of the BwBP. The proof follows arguments of Asmussen and Hering in [8] for the branching process with immigration.

**Theorem 6.1.** *Let  $\mathbb{E} \log \mu_{\mathcal{U}_0} > 0$  and recall that  $\mu_{\mathcal{U}_0} < \infty$  a.s.*

(a) *If  $\mathbb{E} \log^+ \xi_0 < \infty$ , then there exists a finite random variable  $Z_\infty$  such that*

$$\lim_{n \rightarrow \infty} \frac{Z_n}{\prod_{i=0}^{n-1} \mu_{\mathcal{U}_i}} = Z_\infty \quad \text{a.s.}$$

*and the following assertions are equivalent:*

- (i)  $\mathbb{P}(Z_\infty > 0) = 1$ .
  - (ii)  $\mathbb{P}(Z_\infty > 0) > 0$ .
  - (iii)  $\mathbb{E}((X_{1,0} \log^+ X_{1,0}) / \mu_{\mathcal{U}_0}) < \infty$ .
- (b) *If  $\mathbb{E} \log^+ \xi_0 = \infty$ , then  $\limsup_{n \rightarrow \infty} c^{-n} Z_n = \infty$  a.s. for every  $c \in (0, \infty)$ .*

**Proof.** (a) Defining the filtration

$$\mathcal{F}_n := \sigma(Z_0, Z_1, \dots, Z_n, (\xi_k)_{k \geq 0}, \mathcal{U}), \quad n \in \mathbb{N}_0,$$

thus  $\mathcal{F}_0 = \sigma((\xi_k)_{k \geq 0}, \mathcal{U})$ , the sequence  $((\prod_{i=0}^{n-1} \mu_{\mathcal{U}_i})^{-1} Z_n)_{n \geq 0}$  is adapted and a.s. a  $L^1$ -bounded, nonnegative and thus a.s. convergent submartingale with respect to the conditional measure  $\mathbb{P}(\cdot | \mathcal{F}_0)$  as the subsequent arguments show. We have

$$\mathbb{E}(Z_{n+1} | \mathcal{F}_n) = \sum_{k=1}^{Z_n} \mathbb{E}(X_{n,k} | \mathcal{F}_n) + \xi_n \geq \sum_{k=1}^{Z_n} \mathbb{E}(X_{n,k} | \mathcal{U}) = Z_n \mu_{\mathcal{U}_n} \quad \text{a.s.}$$

and thereby

$$\begin{aligned}\mathbb{E}(Z_{n+1}|\mathcal{F}_0) &= \mathbb{E}(\mathbb{E}(Z_{n+1}|\mathcal{F}_n)|\mathcal{F}_0) = \mathbb{E}\left(\sum_{k=1}^{Z_n} \mathbb{E}(X_{n,k}|\mathcal{F}_n) + \xi_n \middle| \mathcal{F}_0\right) \\ &= \mathbb{E}(Z_n|\mathcal{F}_0)\mu_{\mathcal{U}_n} + \xi_n \quad \text{a.s.}\end{aligned}$$

for  $n \geq 0$ . It then follows by iteration that, for all  $n \geq 0$ ,

$$\begin{aligned}\mathbb{E}\left(\frac{Z_{n+1}}{\prod_{i=0}^n \mu_{\mathcal{U}_i}} \middle| \mathcal{F}_0\right) &= \mathbb{E}\left(\frac{Z_n}{\prod_{i=0}^{n-1} \mu_{\mathcal{U}_i}} \middle| \mathcal{F}_0\right) + \frac{\xi_n}{\prod_{i=0}^n \mu_{\mathcal{U}_i}} \\ &= \sum_{k=0}^n \frac{\xi_k}{\prod_{i=0}^k \mu_{\mathcal{U}_i}} \leq \sum_{k \geq 0} \frac{\xi_k}{\prod_{i=0}^k \mu_{\mathcal{U}_i}}\end{aligned}\tag{21}$$

$$\begin{aligned}&\leq \sum_{k \geq 0} \exp\left(\log^+ \xi_k - \sum_{i=0}^k \log \mu_{\mathcal{U}_i}\right) \\ &= \sum_{k \geq 0} \left(\exp\left[\frac{1}{k+1} \left(\log^+ \xi_k - \sum_{i=0}^k \log \mu_{\mathcal{U}_i}\right)\right]\right)^{k+1} \quad \text{a.s.}\end{aligned}\tag{22}$$

Since  $(\xi_n)_{n \geq 0}$  and  $(\mu_{\mathcal{U}_n})_{n \geq 0}$  are i.i.d. sequences and  $\mathbb{E} \log^+ \xi_0 < \infty$ , (20) and the strong law of large numbers provide us with

$$\limsup_{k \rightarrow \infty} \frac{1}{k+1} \left(\log^+ \xi_k - \sum_{i=0}^k \log \mu_{\mathcal{U}_i}\right) = -\mathbb{E} \log \mu_{\mathcal{U}_0} < 0 \quad \text{a.s.}$$

and thus the almost sure finiteness of the sums in (21) and (22). As a consequence,  $((\prod_{i=0}^{n-1} \mu_{\mathcal{U}_i})^{-1} Z_n)_{n \geq 0}$  is indeed a  $L^1$ -bounded and thus a.s. convergent submartingale under  $\mathbb{P}(\cdot|\mathcal{F}_0)$  which leaves us with a proof of the equivalence of (i)–(iii).

Denote by  $(\bar{Z}_n)_{n \geq 0}$  a BPPE starting with one ancestor, environmental sequence  $\mathcal{U}$  and no immigration. By [58, Theorem 2],  $(\bar{Z}_n/\mathbb{E}(\bar{Z}_n|\mathcal{U}))_{n \geq 0}$  converges a.s. to a limit  $\bar{W}$  as  $n \rightarrow \infty$ , which is nondegenerate, i.e.  $q(\mathcal{U}) := \mathbb{P}(\bar{W} = 0|\mathcal{U}) < 1$  with positive probability, iff (iii) holds true, i.e.  $\mathbb{E}((X_{1,0} \log^+ X_{1,0})/\mu_{\mathcal{U}_0}) < \infty$ . So it remains to verify the implications

$$\mathbb{P}(Z_\infty > 0) > 0 \Rightarrow \mathbb{P}(q(\mathcal{U}) < 1) > 0 \Rightarrow \mathbb{P}(Z_\infty > 0) = 1.\tag{23}$$

We show the first one by contraposition and assume that  $q(\mathcal{U}) = 1$  a.s. Note that

$$Z_n = \sum_{k=0}^n \sum_{i=1}^{\xi_k} Z_{k,n-k}(i),\tag{24}$$

where  $Z_{k,n-k}(i)$  denotes the number of individuals in the  $(n-k)^{th}$  generation of a BPPE started with the  $i$ th immigrant at time  $k$  and with reproduction laws given by  $\mathcal{U}_{k,1}, \mathcal{U}_{k+1,1} \dots$  (see [37] and recall  $Z_0 = 0$ ). Moreover, the  $(Z_{k,n}(i))_{n \geq 0}$  for  $k \geq 0$  and  $i \geq 1$  are conditionally independent given  $\mathcal{U}$  and

$$\mathbb{P}((Z_{k,n}(i))_{n \geq 0} \in \cdot | (\mathcal{U}_k)_{k \geq n} = \mathbf{u}) = \mathbb{P}((\bar{Z}_n)_{n \geq 0} \in \cdot | \mathcal{U} = \mathbf{u})\tag{25}$$

for  $\mathbb{P}(\mathcal{U} \in \cdot)$ -almost all  $\mathbf{u} \in \mathcal{P}_1 \times \mathcal{P}$ . As  $(\mathcal{U}_n)_{n \geq k} \stackrel{d}{=} \mathcal{U}$  and thus  $q((\mathcal{U}_n)_{n \geq k}) = q(\mathcal{U}) = 1$  a.s., it follows that

$$\frac{Z_{k,n-k}(i)}{\prod_{j=0}^{n-1} \mu_{\mathcal{U}_j}} = \frac{1}{\prod_{j=0}^{k-1} \mu_{\mathcal{U}_j}} \frac{Z_{k,n-k}(i)}{\prod_{j=k}^{n-1} \mu_{\mathcal{U}_j}} \rightarrow 0 \quad \text{a.s.}$$

as  $n \rightarrow \infty$  for all  $i \geq 1$  and  $k \geq 0$ . By using these facts in (24), we now infer for each  $m \in \mathbb{N}$  that

$$\frac{Z_n}{\prod_{j=0}^{n-1} \mu_{\mathcal{U}_j}} = \underbrace{\sum_{k=0}^m \sum_{i=1}^{\xi_k} \frac{Z_{k,n-k}(i)}{\prod_{j=0}^{n-1} \mu_{\mathcal{U}_j}}}_{\rightarrow 0 \text{ a.s.}} + \frac{1}{\prod_{j=0}^{m-1} \mu_{\mathcal{U}_j}} \underbrace{\sum_{k=m+1}^n \sum_{i=1}^{\xi_k} \frac{Z_{k,n-k}(i)}{\prod_{j=m}^{n-1} \mu_{\mathcal{U}_j}}}_{=: Y_{m,n-m}} \xrightarrow{d} \frac{Z'_\infty}{\prod_{j=0}^{m-1} \mu_{\mathcal{U}_j}}$$

as  $n \rightarrow \infty$ , where  $Z'_\infty$  is a copy of  $Z_\infty$  and independent of  $(\mu_{\mathcal{U}_0}, \dots, \mu_{\mathcal{U}_{m-1}})$ . To see this, one should observe that

$$\mathbb{P}(Y_{m,n} \in \cdot | \mathcal{U}) = \mathbb{P}(Z_{n-m} \in \cdot | (\mathcal{U}_k)_{k \geq m})$$

and the independence of  $Y_{m,n}$  and  $(\mathcal{U}_0, \dots, \mathcal{U}_{m-1})$  for any  $m = 1, \dots, n$ . The distributional equation just derived, viz.

$$Z_\infty \stackrel{d}{=} \frac{Z'_\infty}{\prod_{j=0}^{m-1} \mu_{\mathcal{U}_j}}$$

for all  $m \in \mathbb{N}$ , in combination with  $Z_\infty < \infty$  a.s. and

$$\prod_{j=0}^{m-1} \mu_{\mathcal{U}_j} = \exp\left(\sum_{j=0}^{m-1} \log \mu_{\mathcal{U}_j}\right) \rightarrow \infty \quad \text{a.s.}$$

by the strong law of large numbers obviously entails  $Z_\infty = 0$  a.s.

For the second implication in (23) suppose now  $\mathbb{P}(q(\mathcal{U}) < 1) > 0$ , which particularly implies  $\bar{Z}_n \rightarrow \infty$  with positive probability, see [56]. But this in combination with (18), (24) and (25) easily implies  $Z_n \rightarrow \infty$  a.s. Fix  $\varepsilon > 0$  and choose  $\eta > 0$  such that

$$\mathbb{P}(q(\mathcal{U}) < 1 - \eta) \geq 1 - \varepsilon.$$

For any  $k \in \mathbb{N}$ , we then find that

$$\begin{aligned} \mathbb{P}(Z_\infty = 0 | Z_k, \mathcal{U}) &= \mathbb{P}\left(\lim_{n \rightarrow \infty} \frac{Z_n}{\prod_{i=0}^{n-1} \mu_{\mathcal{U}_i}} = 0 \middle| Z_k, \mathcal{U}\right) \\ &\leq \mathbb{P}\left(\lim_{n \rightarrow \infty} \sum_{j=1}^{Z_k} \frac{\bar{Z}_{n-k}(j)}{\prod_{i=k}^{n-1} \mu_{\mathcal{U}_i}} = 0 \middle| Z_k, \mathcal{U}\right) \\ &= \mathbb{P}(\bar{W} = 0 | (\mathcal{U}_i)_{i \geq k})^{Z_k} \quad \text{a.s.} \end{aligned}$$

where  $\bar{Z}_n(j)$  describes the offspring in generation  $n$  stemming from the  $j$ th individual in generation  $k$  and thus behaves like the BPPE  $\bar{Z}_n$  (modulo a  $k$ -shift of the environment). Since the population of the BPPE explodes almost surely and  $\mathcal{U}$  consists of i.i.d. random variables, we finally conclude

$$\mathbb{P}(Z_\infty = 0) \leq \mathbb{E} q((\mathcal{U}_i)_{i \geq k})^{Z_k} \leq \mathbb{E}(1 - \eta)^{Z_k} + \varepsilon \xrightarrow{k \rightarrow \infty} \varepsilon$$

which proves (a) because  $\varepsilon > 0$  was arbitrarily chosen.

(b) Let  $c > 0$  and notice that  $Z_{n+1} \geq \xi_n$  a.s. for all  $n \geq 0$  by (19). Now use (20) in combination with  $\mathbb{E} \log^+ \xi_0 = \infty$  to conclude

$$\limsup_{n \rightarrow \infty} \frac{Z_n}{c^n} \geq \limsup_{n \rightarrow \infty} \frac{\xi_n}{c^n} = \limsup_{n \rightarrow \infty} \left( \frac{1}{c} \exp \left( \frac{\log \xi_n}{n} \right) \right)^n = \infty \quad \text{a.s.}$$

as claimed.  $\square$

As a consequence of the proof of the above theorem, we note the following corollary.

**Corollary 6.2.** *In all three regimes, it is true that*

$$\limsup_{n \rightarrow \infty} \frac{1}{c^n} \mathbb{E}(Z_n | \mathcal{F}_0) = 0 \quad \text{a.s.}$$

for each  $c > 1$  such that  $\mathbb{E} \log \mu_{\mathcal{U}_0} < \log c$ , where  $\mathcal{F}_0 = \sigma((\xi_n)_{n \geq 0}, \mathcal{U})$ .

**Proof.** Let  $c > 1$ . By (21), we have

$$\frac{1}{c^{n+1}} \mathbb{E}(Z_{n+1} | \mathcal{F}_0) \leq \left( \prod_{k=0}^n \frac{\mu_{\mathcal{U}_k}}{c} \right) \sum_{k \geq 0} \frac{\xi_k}{\prod_{i=0}^k \mu_{\mathcal{U}_i}} \quad \text{a.s.}$$

If  $\mathbb{E} \log \mu_{\mathcal{U}_0} > 0$ , the proof of Theorem 6.1 has already shown that the sum on the right side is almost surely finite. Since the  $\mu_{\mathcal{U}_n}$ ,  $n \in \mathbb{N}_0$ , are i.i.d., we further get

$$\limsup_{n \rightarrow \infty} \prod_{k=0}^n \frac{\mu_{\mathcal{U}_k}}{c} = \limsup_{n \rightarrow \infty} \exp \left( \sum_{k=0}^n \log \frac{\mu_{\mathcal{U}_k}}{c} \right) = 0$$

by the law of large numbers, hence

$$\limsup_{n \rightarrow \infty} \frac{1}{c^{n+1}} \mathbb{E}(Z_{n+1} | \mathcal{F}_0) = 0 \quad \text{a.s.}$$

If  $\mathbb{E} \log \mu_{\mathcal{U}_0} \leq 0$ , then the assertion follows by a simple stochastic comparison argument (replace  $\mathcal{U}$  by  $\mathcal{U}' = (\mathcal{U}'_n)_{n \geq 0}$  satisfying  $\mathbb{E} \log \mu_{\mathcal{U}'_0} \in (0, \log c)$  and use that the assertion is true in the supercritical case). We omit further details.  $\square$

## 7. Size-biased branching within branching

Unlike the size-biased construction to define the ABPRE, which was purely based on the cell tree, the following size-biased version  $\widehat{\mathbf{BT}}$  of the whole BwBP will be obtained by picking a

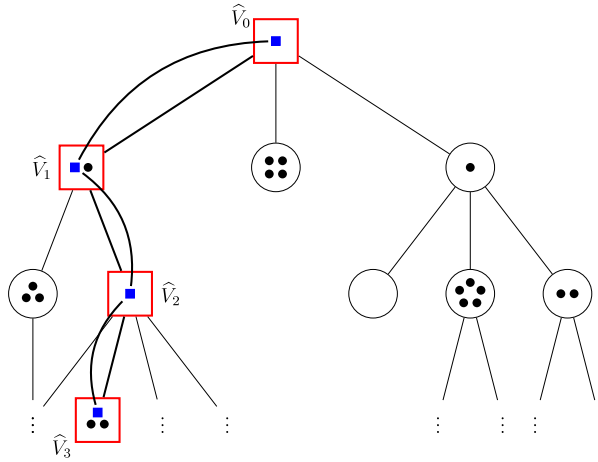


Fig. 3. A typical realization of a size-biased BwBP. Spinal parasites are shown as ■ and cells hosting these parasites as □. All other parasites and cells are shown as • and ○, respectively. Bended edges are used to indicate the line of cells containing the spinal parasites.

spine (random line) of parasites. Yet, since the spinal parasites are hosted by unique cells, this will again determine a random cell line as well (see Fig. 3), but its properties are different from those of the cell line related to the ABPRE.

### Construction of the size-biased process

Let

$$\left( \hat{X}_n^{(\bullet, \hat{T}_n)}, \hat{T}_n, \hat{C}_n \right), \quad n \geq 0,$$

be i.i.d. copies of the random vector  $\left( \hat{X}^{(\bullet, \hat{T})}, \hat{T}, \hat{C} \right)$  independent of  $(X_{i,v}^{(\bullet, k)})_{i,k \geq 1, v \in \mathbb{V}}$  and  $(N_v)_{v \in \mathbb{V}}$ , where  $\hat{T}, \hat{C}$  take values in  $\mathbb{N}$  and  $\hat{X}^{(\bullet, \hat{T})} := (X^{(1, \hat{T})}, \dots, X^{(\hat{T}, \hat{T})})$  is a vector of random length  $\hat{T}$ . These random variables have the following distributions: For  $k \in \mathbb{N}$ ,  $x = (x_1, \dots, x_k) \in \mathbb{N}_0^k$  and  $1 \leq m \leq \sum_{j=1}^k x_j$ , we have

$$\mathbb{P}(\hat{T} = k) = \frac{p_k \sum_{j=1}^k \mu_{j,k}}{\gamma}, \quad (26)$$

$$\mathbb{P}(\hat{X}^{(\bullet, \hat{T})} = x | \hat{T} = k) = \frac{\sum_{j=1}^k x_j}{\sum_{j=1}^k \mu_{j,k}} \mathbb{P}(X^{(\bullet, k)} = x), \quad (27)$$

and

$$\mathbb{P}(\hat{C} = m | \hat{X}^{(\bullet, \hat{T})} = x, \hat{T} = k) = \frac{1}{\sum_{j=1}^k x_j}, \quad (28)$$

i.e.,  $\widehat{C}$  is uniformly distributed on  $\{1, \dots, \sum_{j=1}^k x_j\}$  given  $\widehat{X}^{(\bullet, \widehat{T})} = x$  and  $\widehat{T} = k$ . In particular,

$$\mathbb{P}(\widehat{X}^{(\bullet, \widehat{T})} = x, \widehat{T} = k, \widehat{C} = m) = \frac{pk}{\gamma} \mathbb{P}(X^{(\bullet, k)} = x). \quad (29)$$

These random variables determine a random path (spine) through the parasites as depicted in Fig. 3 by the following 3-step procedure:

*Step 1* The root cell  $\widehat{V}_0 = \emptyset$  splits into  $\widehat{T}_0$  daughter cells.

*Step 2* If  $\widehat{T}_0 = k$ ,  $\widehat{X}_0^{(\bullet, k)} = (x_1, \dots, x_k)$  and  $x = \sum_{j=1}^k x_j$ , then the parasite in  $\emptyset$  has  $x$  descendants of which  $x_j$  go into daughter cell  $j$  for  $j = 1, \dots, k$ .

*Step 3* The *spinal parasite* of the first generation is picked by  $\widehat{C}_0$  uniformly at random from the  $x$  offspring parasites and the cell hosting it is the spinal cell  $\widehat{V}_1$  of the first generation.

The procedure is then successively applied to the spinal cell and its spinal parasite of generation  $n = 1, 2, \dots$ . So, being at generation  $n$ , the spinal cell  $\widehat{V}_n$  splits into  $\widehat{T}_n$  daughter cells,  $\widehat{X}_n^{(\bullet, \widehat{T}_n)}$  provides the offspring numbers of the associated spinal parasite and  $\widehat{C}_n$  the spinal parasite in generation  $n + 1$ . All remaining parasites in  $\widehat{V}_n$  multiply independently with the law of  $X^{(\bullet, \widehat{T}_1)}$ . We thus obtain a random cell line  $(\widehat{V}_n)_{n \geq 0}$  with  $\widehat{V}_0 := \emptyset$  and

$$\widehat{V}_{n+1} := \widehat{V}_n \widehat{U}_n$$

for  $n \geq 0$ , where  $\widehat{U}_n$  denotes the *daughter cell containing the spinal parasite of the next generation*. Since the  $(\widehat{X}_n^{(\bullet, \widehat{T}_n)}, \widehat{T}_n, \widehat{C}_n)$ ,  $n \geq 0$ , are i.i.d., so are the  $\widehat{U}_n$ ,  $n \geq 0$ , and we get from (26)–(29)

$$\mathbb{P}(\widehat{T}_0 = k, \widehat{U}_0 = j) = \frac{pk\mu_{j,k}}{\gamma} \quad \text{for } 1 \leq j \leq k < \infty. \quad (30)$$

All parasites and cells not in the spine reproduce with the usual law. Thus,  $\widehat{Z}_{\emptyset} = 1$ , and the children of each cell and their parasites in the *size-biased BwBP*

$$(\widehat{\mathbb{T}}_n, (\widehat{V}_n, \widehat{C}_n), (\widehat{Z}_v)_{v \in \widehat{\mathbb{T}}_n})_{n \geq 0}$$

are given by

$$\widehat{N}_v = \begin{cases} \widehat{T}_n, & \text{if } v = \widehat{V}_n, \\ N_v, & \text{if } v \neq \widehat{V}_n, \end{cases}$$

and

$$\widehat{Z}_{vj} := \begin{cases} \sum_{i=1}^{\widehat{Z}_v-1} X_{i,v}^{(j, \widehat{T}_n)} + \widehat{X}_n^{(j, \widehat{T}_n)}, & \text{if } v = \widehat{V}_n, \\ \sum_{i=1}^{\widehat{Z}_v} X_{i,v}^{(j, N_v)}, & \text{if } v \neq \widehat{V}_n \end{cases}$$

for  $v \in \mathbb{V}$  with  $|v| = n$  and  $j \in \mathbb{N}$ . Finally, let  $\widehat{\mathbb{T}}$  and  $\widehat{\mathcal{Z}}_n$  have the obvious meaning.

It is important to point out that not only the spinal parasites but also those sharing a cell with them have a different offspring distribution as parasites sitting in regular cells. This is caused by the fact that a spinal cell always produces at least one daughter cell whereas regular ones may die. The next lemma provides us with the reproduction distribution of a spinal cell and the parasites it contains.

**Lemma 7.1.** *The conditional distribution of  $(\widehat{T}_n, \widehat{U}_n, (\widehat{Z}_{\widehat{v}_{nj}})_{1 \leq j \leq \widehat{T}_n})$  given  $\widehat{Z}_{\widehat{v}_{n-1}} = z$ , the number of parasites in  $\widehat{v}_{n-1}$ , equals the distribution of  $(\widehat{T}_0, \widehat{U}_0, (\widehat{Z}_j)_{1 \leq j \leq \widehat{T}_0})$  under  $\mathbb{P}_z$  for all  $n, z \in \mathbb{N}$ , and*

$$\mathbb{P}_z(\widehat{T}_0 = k, \widehat{U}_0 = l, \widehat{Z}_j = z_j \text{ for } j = 1, \dots, k) = \frac{p_k z_l}{z\gamma} \mathbb{P}_z(Z_j = z_j \text{ for } j = 1, \dots, k)$$

for all  $k \in \mathbb{N}$ ,  $1 \leq l \leq k$ , and  $(z_j)_{1 \leq j \leq k} \in \mathbb{N}_0^k$ .

**Proof.** Let  $k \in \mathbb{N}$ ,  $l \in \{1, \dots, k\}$ ,  $(z_j)_{1 \leq j \leq k} \in \mathbb{N}_0^k$  and  $z \in \mathbb{N}$ . Using the independence of  $\widehat{X}^{(\bullet, \widehat{T}_0)}$  and  $(X_{i,v}^{(\bullet, k)})_{i,k \geq 1, v \in \mathbb{V}}$ , we then obtain

$$\begin{aligned} & \mathbb{P}_z(\widehat{T}_0 = k, \widehat{U}_0 = l, (\widehat{Z}_j)_{1 \leq j \leq k} = (z_j)_{1 \leq j \leq k}) \\ &= \mathbb{P}_z\left(\widehat{T}_0 = k, \widehat{U}_0 = l, \sum_{i=1}^{z-1} X_{i,\emptyset}^{(j,k)} + \widehat{X}_0^{(j,k)} = z_j \text{ for } j = 1, \dots, k\right) \\ &= \sum_{x_j \leq z_j} \mathbb{P}(\widehat{X}_0^{(\bullet, k)} = (x_1, \dots, x_k), \widehat{T}_0 = k, \widehat{U}_0 = l) \\ &\quad \times \mathbb{P}\left(\sum_{i=1}^{z-1} X_{i,\emptyset}^{(j,k)} = z_j - x_j \text{ for } j = 1, \dots, k\right) \\ &= \frac{p_k}{\gamma} \sum_{x_j \leq z_j} x_l \mathbb{P}\left(X^{(\bullet, k)} = (x_1, \dots, x_k)\right) \mathbb{P}\left(\sum_{i=1}^{z-1} X_{i,\emptyset}^{(j,k)} = z_j - x_j \text{ for } j = 1, \dots, k\right) \\ &= \frac{p_k}{\gamma} \sum_{x_j \leq z_j} x_l \mathbb{P}\left(\sum_{i=1}^z X_{i,\emptyset}^{(j,k)} = z_j, X_{z,\emptyset}^{(j,k)} = x_j \text{ for } j = 1, \dots, k\right) \\ &= \frac{p_k}{\gamma} \mathbb{E}\left(X_{z,\emptyset}^{(l,k)} \middle| \sum_{i=1}^z X_{i,\emptyset}^{(j,k)} = z_j \text{ for } j = 1, \dots, k\right) \mathbb{P}_z(Z_j = z_j \text{ for } j = 1, \dots, k) \\ &= \frac{p_k}{\gamma} \mathbb{E}\left(X_{z,\emptyset}^{(l,k)} \middle| \sum_{i=1}^z X_{i,\emptyset}^{(l,k)} = z_l\right) \mathbb{P}_z(Z_j = z_j \text{ for } j = 1, \dots, k), \end{aligned}$$

where (29) was used for the third equality. Since a random walk  $(S_n)_{n \geq 0}$  with  $S_0 = 0$  and i.i.d. increments  $X_1, X_2, \dots$  satisfies  $\mathbb{E}(X_1 | S_n) = S_n/n$  a.s., we conclude the desired result.  $\square$

### Dichotomy of the size-biased process

The next (common) step is to establish equivalent conditions on the size-biased BwBP for the martingale limit  $W = \lim_{n \rightarrow \infty} \gamma^{-n} \mathcal{Z}_n$  to be finite which can be done by drawing on a measure-theoretic result to be found in [27]. For formal convenience, the dagger symbol  $\dagger$  is used hereafter to indicate that a node  $v \in \mathbb{V}$  is absent in the cell tree and thus called a dead cell.



Put  $\mathcal{N} := \mathbb{N}_0 \cup \{\dagger\}$  and define

$$Z_v := Z_v \mathbb{1}_{\{v \in \mathbb{T}\}} + \dagger \mathbb{1}_{\{v \notin \mathbb{T}\}} \quad \text{and} \quad \widehat{Z}_v := \widehat{Z}_v \mathbb{1}_{\{v \in \widehat{\mathbb{T}}\}} + \dagger \mathbb{1}_{\{v \notin \widehat{\mathbb{T}}\}}.$$

Then  $Z_v = 0$  means that  $v$  is a living cell with no parasites, whereas  $Z_v = \dagger$  indicates that  $v$  is not present in  $\mathbb{T}$  and thus a dead cell. We put

$$\mathbf{BT} := (Z_v)_{v \in \mathbb{V}} \quad \text{and} \quad \widehat{\mathbf{BT}} := (\widehat{Z}_v)_{v \in \mathbb{V}}$$

and call these objects the *branching within branching tree (BwBT)* and the *size-biased BwBT*, respectively. It is important to note that previously introduced random variables of the BwBP and its size-biased counterpart, in particular  $\mathcal{I}_n$ , can be defined as measurable functions of  $\mathbf{BT}$  or  $\widehat{\mathbf{BT}}$ .

Let  $\mathbb{S} := \mathcal{N}^{\mathbb{V}}$  be the set of BwBT's which assigns a nonnegative integer or  $\dagger$  to each node of  $\mathbb{V}$ . Put  $\mathbb{V}_{\leq n} := \{v : |v| \leq n\}$  and  $\mathbb{V}_n := \{v \in \mathbb{V} : |v| = n\}$  for  $n \in \mathbb{N}_0$ . Let  $\mathcal{S}$  be the standard  $\sigma$ -field on  $\mathbb{S}$  generated by the projections on the components, and let  $\mathcal{S}_n \subseteq \mathcal{S}$  denote the sub- $\sigma$ -field which is induced by the projections on components in  $\mathbb{V}_{\leq n}$ . Clearly,  $(\mathcal{S}_n)_{n \geq 0}$  is a filtration in  $\mathcal{S}$ , and  $\mathbf{BT}$  and  $\widehat{\mathbf{BT}}$  are both  $(\mathbb{S}, \mathcal{S})$ -measurable. For  $n \in \mathbb{N}_0$ , we denote by  $\mathbf{BT}_n$  and  $\widehat{\mathbf{BT}}_n$  the BwBT and size-biased BwBT up to level  $n$ , respectively, i.e.  $\mathbf{BT}_n := (Z_v)_{v \in \mathbb{V}_{\leq n}}$  and  $\widehat{\mathbf{BT}}_n := (\widehat{Z}_v)_{v \in \mathbb{V}_{\leq n}}$ . Further, let  $z_n : \mathbb{S} \rightarrow \mathbb{N}_0$  denote the number of parasites in the  $n$ th generation of a host–parasite tree, thence  $\mathcal{I}_n = z_n(\mathbf{BT})$  and  $\widehat{\mathcal{I}}_n = z_n(\widehat{\mathbf{BT}})$ , and put

$$w_n : \mathbb{S} \rightarrow [0, \infty), \quad w_n(\tau) := \frac{1}{\gamma^n} z_n(\tau) \quad (31)$$

for  $n \in \mathbb{N}_0$ . We further set  $w := \limsup_{n \rightarrow \infty} w_n$ . Thus  $w_n$  is  $\mathcal{S}_n$ -measurable by definition, and we have the representations

$$W_n = w_n \circ \mathbf{BT} \quad \text{and} \quad \widehat{W}_n = w_n \circ \widehat{\mathbf{BT}}.$$

As a consequence of the following lemma, the uniform integrability of  $(W_n)_{n \geq 0}$  is directly linked to the almost sure finiteness of  $\widehat{W}$ .

**Lemma 7.2.** (a) For all  $n \in \mathbb{N}_0$ ,  $\mathbf{z} = (z_v)_{v \in \mathbb{V}_{\leq n}} \in \mathcal{N}^{\mathbb{V}_{\leq n}}$  and  $\mathbf{u} \in \mathbb{V}_n$

$$\mathbb{P}(\widehat{\mathbf{BT}}_n = \mathbf{z}, \widehat{V}_n = \mathbf{u}) = \frac{z_{\mathbf{u}}}{\gamma^n} \mathbb{P}(\mathbf{BT}_n = \mathbf{z}).$$

(b) Let  $n \in \mathbb{N}_0$  and  $h : (\mathbb{S}, \mathcal{S}_n) \rightarrow (\mathbb{R}, \mathcal{B})$  be a measurable and non-negative (or bounded) function. Then,

$$\mathbb{E}(h(\widehat{\mathbf{BT}})) = \mathbb{E}(W_n h(\mathbf{BT})),$$

in particular, for  $A \in \mathcal{S}_n$ ,

$$\widehat{Q}(A) = \mathbb{E}(W_n \mathbb{1}_{\{\mathbf{BT} \in A\}}) = \int_A w_n(\tau) Q(d\tau), \quad (32)$$

where  $Q(\cdot) := \mathbb{P}(\mathbf{BT} \in \cdot)$  and  $\widehat{Q}(\cdot) := \mathbb{P}(\widehat{\mathbf{BT}} \in \cdot)$ .

(c) The following dichotomy holds true:

- (i)  $\mathbb{P}(\widehat{W} < \infty) = 1 \Leftrightarrow \mathbb{E}W = 1$ ,
- (ii)  $\mathbb{P}(\widehat{W} = \infty) = 1 \Leftrightarrow \mathbb{P}(W = 0) = 1$ .

**Proof.** All assertions are proved in a standard manner by following similar arguments as those given by Lyons et al. [45] for the simple Galton–Watson process. As for part (c), we note that it follows from (b) in combination with [27, Theorem 5.3.3]. Further details are omitted.  $\square$

**Remark 7.3.** Since  $\log^+(w_1(\cdot))$  is  $\mathcal{S}_1$ - $\mathcal{B}$ -measurable and nonnegative, the above theorem provides us with  $\mathbb{E} \log^+ \widehat{W}_1 = \mathbb{E} W_1 \log^+ W_1$ , which in turn yields

$$\mathbb{E} \mathcal{Z}_1 \log \mathcal{Z}_1 < \infty \quad \text{iff} \quad \mathbb{E} \log \widehat{\mathcal{Z}}_1 < \infty.$$

### The process of parasites along the spine

We take a closer look at the process  $(\widehat{Z}_{\widehat{V}_n})_{n \geq 0}$  of parasites along the spine and its recursive formula

$$\widehat{Z}_{\widehat{V}_{n+1}} = \sum_{i=1}^{\widehat{Z}_{\widehat{V}_{n+1}}-1} X_{i, \widehat{V}_n}(\widehat{U}_n, \widehat{T}_n) + \widehat{X}_n(\widehat{U}_n, \widehat{T}_n), \quad n \in \mathbb{N}_0. \quad (33)$$

Observe that all but the spinal parasite in a spinal cell multiply with the same distribution, whereas the *spinal parasite* produces offspring according to a different law. We can figure the spinal parasite to be outside the cell and its progeny as immigrants of the spinal cell of the next generation. Then all remaining parasites in the spinal cell reproduce with the same distribution and we thus see that  $(\widehat{Z}_{\widehat{V}_n})_{n \geq 0}$  behaves like a BPREL.

**Theorem 7.4.** Let  $(\widehat{Z}'_n)_{n \geq 0}$  be a BPREL in i.i.d. random environment  $\Delta = (\Delta_n)_{n \geq 0}$  taking values in  $\{\mathcal{L}((X^{(j,k)}, \widehat{X}^{(j,k)} - 1) | (\widehat{U}, \widehat{T}) = (j, k)) : 1 \leq j \leq k < \infty\}$  and such that

$$\mathbb{P}(\Delta_0 = \mathcal{L}((X^{(j,k)}, \widehat{X}^{(j,k)} - 1) | (\widehat{U}, \widehat{T}) = (j, k))) = \frac{p_k \mu_{j,k}}{\gamma}$$

for all  $1 \leq j \leq k < \infty$  and  $\widehat{Z}'_0 \stackrel{d}{=} \widehat{Z}_{\widehat{V}_0}$ . Then the law of  $(\widehat{Z}'_n - 1)_{n \geq 0}$  equals the law of the BPREL.

**Proof.** It suffices to verify that, for each  $n \geq 0$ , the conditional laws of  $\widehat{Z}'_{n+1}$  given  $\widehat{Z}'_{n+1}$ ,  $\Delta_n$  and  $\widehat{Z}_{\widehat{V}_{n+1}}$  given  $\widehat{Z}_{\widehat{V}_n}$ ,  $\Delta_n$  coincide, for both sequences are Markovian. It follows from the definition of  $(\widehat{Z}'_n)_{n \geq 0}$  and its recursive structure (see (19)) that

$$\begin{aligned} \mathbb{E} \left( s^{\widehat{Z}'_{n+1}} \middle| \widehat{Z}'_n = z, \Delta_n = \mathcal{L}((X^{(j,k)}, \widehat{X}^{(j,k)} - 1) | (\widehat{U}, \widehat{T}) = (j, k)) \right) \\ = \mathbb{E} \left( s^{X^{(j,k)}} \right)^z \mathbb{E} \left( s^{\widehat{X}^{(j,k)} - 1} \middle| (\widehat{U}, \widehat{T}) = (j, k) \right) \end{aligned}$$

for all  $n, z \in \mathbb{N}_0$  and  $1 \leq j \leq k < \infty$ . Further, (33) and the i.i.d. assumption of the involved random variables imply

$$\begin{aligned} \mathbb{E} \left( s^{\widehat{Z}_{\widehat{V}_{n+1}} - 1} \middle| \widehat{Z}_{\widehat{V}_n} - 1 = z, (\widehat{U}_n, \widehat{T}_n) = (j, k) \right) \\ = \mathbb{E} \left( s^{\sum_{i=1}^z X_{i, \emptyset}^{(j,k)} + \widehat{X}_n^{(j,k)} - 1} \middle| (\widehat{U}_n, \widehat{T}_n) = (j, k) \right) \\ = \mathbb{E} \left( s^{X^{(j,k)}} \right)^z \mathbb{E} \left( s^{\widehat{X}^{(j,k)} - 1} \middle| (\widehat{U}, \widehat{T}) = (j, k) \right) \end{aligned}$$

for all  $1 \leq j \leq k < \infty$ , hence

$$\mathbb{E} \left( s^{\widehat{Z}_{\widehat{V}_{n+1}}-1} \middle| \widehat{Z}_{\widehat{V}_n} - 1 = z \right) = \mathbb{E} \left( s^{\widehat{Z}'_{n+1}} \middle| \widehat{Z}'_n = z \right)$$

for all  $n \in \mathbb{N}_0$  and  $z \in \mathbb{N}_0$ .  $\square$

We call the BPREI  $(\widehat{Z}'_n)_{n \geq 0}$  in i.i.d. random environment  $\Delta$  the *associated branching process in random environment with immigration (ABPREI)* and denote by

$$\widehat{g}_{\Delta_n}(s) = \sum_{j \leq k} \mathbb{E} \left( s^{X^{(j,k)}} \right) \mathbb{1}_{\{\Delta_n = \mathcal{L}((X^{(j,k)}, \widehat{X}^{(j,k)} - 1) | (\widehat{U}, \widehat{T}) = (j, k))\}}$$

the generating function of the first marginal distribution given by  $\Delta_n$ . The process is called *supercritical*, *critical* or *subcritical* if  $\mathbb{E} \log \widehat{g}'_{\Delta_0}(1) > 0$ ,  $= 0$  or  $< 0$ , respectively.

**Remark 7.5.** There is a strong connection between the behaviors of the ABPRE and the ABPREI. Namely, if  $\mu_{j,k} \neq 1$  and  $p_k > 0$  for at least one pair  $(j, k)$ ,  $1 \leq j \leq k$ , then (see at the end of Section 2 for the definitions of different subcritical subregimes of the ABPRE)

$$\text{ABPREI} \begin{cases} \text{subcritical,} \\ \text{critical,} \\ \text{supercritical,} \end{cases} \quad \text{iff} \quad \text{ABPRE} \begin{cases} \text{strongly subcritical,} \\ \text{intermediate subcritical,} \\ \text{weakly subcritical or non-subcritical.} \end{cases}$$

This can be easily assessed by a look at the equation

$$\mathbb{E} \log \widehat{g}'_{\Delta_0}(1) = \sum_{1 \leq j \leq k < \infty} \frac{p_k \mu_{j,k}}{\gamma} \log \mu_{j,k} = \frac{\nu}{\gamma} \mathbb{E} g'_{\Lambda_0}(1) \log g'_{\Lambda_0}(1), \quad (34)$$

where the random generating function  $g_{\Lambda_0}(s)$  has been defined in (7). Since the function  $x \mapsto x \log x$  is strictly convex and  $g'_{\Lambda_0}(1) \neq 1$  with positive probability, Jensen's inequality provides us with

$$\mathbb{E} g'_{\Lambda_0}(1) \log g'_{\Lambda_0}(1) > \mathbb{E} g'_{\Lambda_0}(1) \log \mathbb{E} g'_{\Lambda_0}(1) > \mathbb{E} g'_{\Lambda_0}(1) \mathbb{E} \log g'_{\Lambda_0}(1),$$

which combined with (34) shows the assertion.

## 8. Proofs of limit results (Theorems 4.1–4.6)

**Proof of Theorem 4.1.** Recalling the definition of  $(\mathcal{F}_n)_{n \geq 0}$  from Section 4 and noting the independence of  $N_v$  and  $\mathcal{F}_n$  for each  $v \in \mathbb{T}_n$ , the supermartingale property and thus a.s. convergence to an integrable random variable  $L$  of  $(v^{-n} \mathcal{F}_n^*)_{n \geq 0}$  follow from

$$\begin{aligned} \mathbb{E}(\mathcal{F}_{n+1}^* | \mathcal{F}_n) &= \sum_{v \in \mathbb{T}_n^*} \mathbb{E} \left( \sum_{j=1}^{N_v} \mathbb{1}_{\{Z_{vj} > 0\}} \middle| \mathcal{F}_n \right) \leq \sum_{v \in \mathbb{T}_n^*} \mathbb{E}(N_v | \mathcal{F}_n) \\ &= \sum_{v \in \mathbb{T}_n^*} \mathbb{E}(N_v) = \nu \mathcal{F}_n^* \quad \text{a.s.} \end{aligned}$$

for each  $n \geq 0$ .

If  $\nu > 1$  and  $\mathbb{E} N \log N < \infty$ , then  $(v^{-n} \mathcal{F}_n^*)_{n \geq 0}$  is even uniformly integrable because the obvious majorant  $(v^{-n} \mathcal{F}_n)_{n \geq 0}$  forms a normalized supercritical GWP satisfying the  $(Z \log Z)$ -condition of the Kesten–Stigum theorem (see [12, Section I.10]). Consequently,

$$\mathbb{E} L = \lim_{n \rightarrow \infty} \mathbb{E} \left( \frac{\mathcal{F}_n^*}{\nu^n} \right) = \lim_{n \rightarrow \infty} \mathbb{P}(Z'_n > 0), \quad (35)$$

where the second equality follows from (6). The theory of BPRE (see e.g. [11] or [6, Prop. 2.3]) now implies in this case that  $L = 0$  a.s. if and only if condition (iii) holds true. If, on the other hand,  $\nu \leq 1$ , then  $\mathcal{T}_n^* \leq \mathcal{T}_n = 0$  eventually, and if  $\mathbb{E}N \log N = \infty$ , then the Kesten–Stigum theorem implies

$$L = \lim_{n \rightarrow \infty} \frac{\mathcal{T}_n^*}{\nu^n} \leq \lim_{n \rightarrow \infty} \frac{\mathcal{T}_n}{\nu^n} = 0 \quad \text{a.s.}$$

In both cases we obtain  $L = 0$  a.s., which completes the proof of (a).

(b) Defining  $\tau_n = \inf\{m \in \mathbb{N} : \mathcal{T}_m^* \geq n\}$ , we find that, for any  $n \in \mathbb{N}$ ,

$$\begin{aligned} \mathbb{P}(L = 0) &\leq \mathbb{P}(L = 0 | \tau_n < \infty) + \mathbb{P}(\tau_n = \infty) \\ &= \mathbb{P}\left(\lim_{m \rightarrow \infty} \frac{1}{\nu^{\tau_n}} \sum_{\mathbf{v} \in \mathbb{T}_{\tau_n}^*} \nu^{-(m-\tau_n)} \mathcal{T}_m^*(\mathbf{v}) = 0 \mid \tau_n < \infty\right) + \mathbb{P}(\tau_n = \infty) \\ &\leq \mathbb{P}\left(\bigcap_{\mathbf{v} \in \mathbb{T}_{\tau_n}^*} \{\nu^{-m} \mathcal{T}_m^*(\mathbf{v}) \rightarrow 0\} \mid \tau_n < \infty\right) + \mathbb{P}(\tau_n = \infty) \\ &\leq \mathbb{P}(\nu^{-m} \mathcal{T}_m^* \rightarrow 0)^n + \mathbb{P}(\tau_n = \infty) \\ &= \mathbb{P}(L = 0)^n + \mathbb{P}(\tau_n = \infty), \end{aligned}$$

where  $\mathcal{T}_m^*(\mathbf{v})$  denotes the number of contaminated cells in the  $m$ th generation of the subtree rooted in cell  $\mathbf{v} \in \mathbb{T}_{\tau_n}^*$ . Since  $\mathbb{P}(L = 0) < 1$  and  $\text{Ext} = \{\sup_{n \geq 1} \mathcal{T}_n^* < \infty\}$  a.s. by Theorem 3.2(a), we arrive at the conclusion

$$\mathbb{P}(L = 0) \leq \lim_{n \rightarrow \infty} \mathbb{P}(\tau_n = \infty) = \mathbb{P}\left(\sup_{n \geq 1} \mathcal{T}_n^* < \infty\right) = \mathbb{P}(\text{Ext}),$$

which in combination with  $\text{Ext} \subseteq \{L = 0\}$  a.s. proves the assertion.  $\square$

**Proof of Theorem 4.2.** For each  $\varepsilon > 0$ , use Markov's inequality it obtain

$$\sum_{n=0}^{\infty} \mathbb{P}\left(\left(\frac{\mathcal{T}_n^*}{\mathbb{E}\mathcal{T}_n^*}\right)^{1/n} \geq 1 + \varepsilon\right) \leq \sum_{n=0}^{\infty} \frac{1}{(1 + \varepsilon)^n} < \infty,$$

whence by the Borel–Cantelli lemma

$$\limsup_{n \rightarrow \infty} \left(\frac{\mathcal{T}_n^*}{\mathbb{E}\mathcal{T}_n^*}\right)^{1/n} \leq 1 \quad \text{a.s.}$$

But from (6), (13) and with Jensen's inequality, we infer

$$(\mathbb{E}\mathcal{T}_n^*)^{1/n} = \nu \mathbb{P}(Z'_n > 0)^{1/n} \rightarrow \nu\rho,$$

as  $n \rightarrow \infty$  and thus

$$\limsup_{n \rightarrow \infty} \frac{1}{n} \log \mathcal{T}_n^* \leq \log \nu\rho \quad \text{a.s.}$$

Left with the proof of  $\liminf_{n \rightarrow \infty} n^{-1} \log \mathcal{T}_n^* \geq \log \nu\rho$  a.s., we have  $\mathcal{T}_n^* \rightarrow \infty$  a.s. on  $\text{Surv}$  by another appeal to Theorem 3.2(a). Therefore, by Fatou's lemma,

$$\infty = \mathbb{E} \liminf_{n \rightarrow \infty} \mathcal{T}_n^* \leq \liminf_{n \rightarrow \infty} \mathbb{E}\mathcal{T}_n^*. \quad (36)$$

We proceed with the following construction of a sequence  $(\mathbb{T}_{m,n}^*)_{n \geq 0}$  of sets of contaminated cells for each  $m \in \mathbb{N}$ .

*Step 1* Put  $\mathbb{T}_{m,0}^* := \{\emptyset\}$  and suppose the root cell to host a single parasite.

*Step 2* Let  $\mathbb{T}_{m,1}^* := \mathbb{T}_m^*$  be the set of contaminated cells in generation  $m$ . From any of these cells, pick an arbitrary parasite and let  $\mathbb{T}_{m,2}^*$  be the set of contaminated cells in generation  $2m$  containing at least one of their descendants.

*Step 3* Recursively define  $\mathbb{T}_{m,n+1}^*$  as in Step 2 with the help of  $\mathbb{T}_{m,n}^*$  for each  $n = 2, 3, \dots$

Then we obviously have

$$\mathcal{T}_{mn}^* \geq S_{m,n} := \#\mathbb{T}_{m,n}^* \quad \mathbb{P}\text{-a.s.}$$

for all  $n \in \mathbb{N}_0$ , and  $(S_{m,n})_{n \geq 0}$  forms a simple GWP with offspring law  $\mathbb{P}(\mathcal{T}_m^* \in \cdot)$ . It is supercritical for sufficiently large  $m$  by (36). Let  $\text{Surv}_m$  denote the set of survival of  $(S_{m,n})_{n \geq 0}$ . Obviously,  $\text{Surv}_m \subseteq \text{Surv}$  for all  $m \in \mathbb{N}$ . Fix  $m_0$  such that  $\mathbb{P}(\text{Surv}_{m_0}) > 0$  and note that  $\text{Surv}_{m_0} \subseteq \text{Surv}_{2m_0} \subseteq \dots \subseteq \text{Surv}$  a.s. because a GWP considered only at the points in time  $l\mathbb{N}_0$  for any fixed  $l \in \mathbb{N}$  is also a GWP and survives if the original one does. Using these inclusions and the branching property of a GWP, we find

$$\mathbb{P}(\text{Surv}_{km_0}) = \sum_{j \geq 1} \mathbb{P}(\mathcal{T}_{km_0}^* = j)(1 - \mathbb{P}(\text{Surv}_{km_0}^c)^j) \geq (1 - \mathbb{P}(\text{Surv}_{m_0}^c)^s) \mathbb{P}(\mathcal{T}_{km_0}^* \geq s)$$

for all  $s, k \in \mathbb{N}$ . Hence,

$$\mathbb{P}(\text{Surv}) \geq \mathbb{P}\left(\bigcup_{k \geq 0} \text{Surv}_{km_0}\right) = \lim_{k \rightarrow \infty} \mathbb{P}(\text{Surv}_{km_0}) \geq (1 - \mathbb{P}(\text{Surv}_{m_0}^c)^s) \mathbb{P}(\text{Surv})$$

for all  $s \in \mathbb{N}$ , and since  $\mathbb{P}(\text{Surv}_{m_0}) > 0$  is assumed, we arrive at

$$\bigcup_{k \geq 0} \text{Surv}_{km_0} = \text{Surv} \quad \text{a.s.} \quad (37)$$

by letting  $s$  tend to infinity in the above inequality.

Fixing now any  $m \in m_0\mathbb{N}$  and then  $k_n \in \mathbb{N}$ ,  $l_n \in \{0, \dots, m-1\}$  such that  $n = k_n m + l_n$ , it follows on  $\text{Surv}_m$  that

$$\mathcal{T}_n^* \geq \sum_{\mathbf{v} \in \mathbb{T}_{m,n}^*} \mathcal{T}_{l_n, \mathbf{v}}^* \quad \text{a.s.,}$$

for all  $n \in \mathbb{N}$ , where  $\mathcal{T}_{l_n, \mathbf{v}}^*$  denotes the number of contaminated cells in generation  $n$  stemming from  $\mathbf{v} \in \mathbb{T}_{m,n}^*$ . Using Jensen's inequality, this yields on  $\text{Surv}_m$

$$\log \mathcal{T}_n^* = \log^+ \mathcal{T}_n^* \geq \frac{1}{S_{m,k_n}} \sum_{\mathbf{v} \in \mathbb{T}_{m,n}^*} \log^+ \mathcal{T}_{l_n, \mathbf{v}}^* + \log^+ S_{m,k_n} \geq \log^+ S_{m,k_n} \quad \text{a.s.,}$$

and the classical theory of GWP's (for example the Heyde–Seneta theorem [8, Theorem 5.1 in Chapter II]) provides us with

$$\liminf_{n \rightarrow \infty} \frac{1}{n} \log \mathcal{T}_n^* \geq \liminf_{n \rightarrow \infty} \frac{1}{n} \log^+ S_{m,k_n} = \frac{1}{m} \log \mathbb{E} \mathcal{T}_m^* = \log v + \frac{1}{m} \log \mathbb{P}(Z'_m > 0) \quad \text{a.s.}$$

on  $\text{Surv}_m$ , where (6) has been used for the last equality. As  $m = km_0$  for some  $k \in \mathbb{N}$ , we finally obtain by using (13) and recalling (37) that

$$\liminf_{n \rightarrow \infty} \frac{1}{n} \log \mathcal{T}_n^* \geq \log v + \lim_{k \rightarrow \infty} \frac{1}{km_0} \log \mathbb{P}(Z'_{km_0} > 0) = \log v \rho \quad \text{a.s.}$$

on  $\text{Surv}$ . This proves the theorem.  $\square$

**Proof of Theorem 4.3.** W.l.o.g. we may assume that  $\mathbb{E}N \log N = \infty$ , for otherwise  $(v^n)_{n \geq 0}$  provides a suitable norming sequence by Theorem 4.1. For each  $a > 0$  such that  $\mathbb{E}N \mathbb{1}_{\{N \leq a\}} > 1$ , we define

$$c_0(a) := a \quad \text{and} \quad c_n(a) := c_{n-1}(a) \mathbb{E} \left( N \mathbb{1}_{\{N \leq c_{n-1}(a)\}} \right) \quad \text{for } n \geq 1, \quad (38)$$

which is obviously uniquely determined by  $a$ . Let  $(c_n)_{n \geq 0}$  be a particular choice which is kept fixed hereafter. Recall that  $(\mathcal{T}_n)_{n \geq 0}$  is a supercritical GWP with reproduction law  $\mathcal{L}(N)$  and mean  $v$ . The classical theory of GWP's (see e.g. [8, Chapter II]) tells us that any  $(c_n(a))_{n \geq 0}$  provides a suitable Heyde–Seneta norming for  $(\mathcal{T}_n)_{n \geq 0}$  with

$$\lim_{n \rightarrow \infty} \frac{c_{n+1}(a)}{c_n(a)} = v \quad \text{and} \quad \lim_{a \rightarrow \infty} \frac{1}{a} \sum_{n \geq 0} c_n(a) \mathbb{P}(N > c_n(a)) = 0. \quad (39)$$

Moreover, all  $(c_n(a))_{n \geq 0}$  are asymptotically equivalent in the sense that there exist constants  $\eta(a) \in (0, \infty)$  such that  $c_n(a)/c_n \rightarrow \eta(a)$  as  $n \rightarrow \infty$ .

For  $n \in \mathbb{N}_0$  and  $v \in \mathbb{V}$  with  $|v| = n$ , put

$$N_v(a) := N_v \mathbb{1}_{\{N_v \leq c_n(a)\}}, \quad (40)$$

and let  $\mathbb{T}_n^*(a)$ ,  $\mathcal{T}_n^*(a)$  and  $\mathcal{T}_n(a)$  be the obvious variables in a BwBP with underlying cell process given by  $(N_v(a))_{v \in \mathbb{V}}$ . Classical theory asserts that the process  $(c_n^{-1}(a) \mathcal{T}_n(a))_{n \geq 0}$  is a  $L^2$ -bounded martingale (see e.g. [12, Theorem 2 on p. 9]). As in the proof of Theorem 4.1, we derive for  $n \in \mathbb{N}_0$

$$\begin{aligned} \mathbb{E}(\mathcal{T}_{n+1}^*(a) | \mathcal{T}_n) &= \sum_{v \in \mathbb{T}_n^*(a)} \mathbb{E} \left( \sum_{j=1}^{N_v(a)} \mathbb{1}_{\{Z_{vj} > 0\}} \mid \mathcal{T}_n \right) \leq (\mathbb{E}N \mathbb{1}_{\{N \leq c_n(a)\}}) \mathcal{T}_n^*(a) \\ &= \frac{c_{n+1}(a)}{c_n(a)} \mathcal{T}_n^*(a) \end{aligned}$$

a.s. Hence,  $(c_n^{-1}(a) \mathcal{T}_n^*(a))_{n \geq 0}$  forms a positive supermartingale with  $\mathbb{E} \mathcal{T}_n^*(a) \leq c_n(a)/a$ , and since the obvious majorant  $(c_n^{-1}(a) \mathcal{T}_n(a))_{n \geq 0}$  is  $L^2$ -bounded, there is an almost surely finite random variable  $L^*(a)$  such that

$$\frac{\mathcal{T}_n^*(a)}{c_n(a)} \rightarrow L^*(a) \quad \text{a.s. and in } L^1 \quad (41)$$

as  $n \rightarrow \infty$ . The rest of the proof splits into several parts.

(1) CONVERGENCE OF  $\mathcal{T}_n^*/c_n$ 

With calculations as in the proof of [22, Prop. 1], we obtain

$$\begin{aligned}
 & \mathbb{P}(\mathcal{T}_n^*(a) \neq \mathcal{T}_n^* \text{ for some } n \in \mathbb{N}_0) \\
 &= \sum_{n \geq 1} \mathbb{P}(\mathcal{T}_1^*(a) = \mathcal{T}_1^*, \dots, \mathcal{T}_{n-1}^*(a) = \mathcal{T}_{n-1}^*, \mathcal{T}_n^*(a) \neq \mathcal{T}_n^*) \\
 &\leq \sum_{n \geq 1} \sum_{k \geq 0} \mathbb{P}(\mathcal{T}_{n-1}^*(a) = \mathcal{T}_{n-1}^* = k, \mathcal{T}_n^*(a) \neq \mathcal{T}_n^*) \\
 &\leq \sum_{n \geq 1} \mathbb{P}(N > c_{n-1}(a)) \sum_{k \geq 0} k \mathbb{P}(\mathcal{T}_{n-1}^*(a) = k) \\
 &\leq \sum_{n \geq 1} \mathbb{P}(N > c_{n-1}(a)) \mathbb{E} \mathcal{T}_{n-1}^*(a) \\
 &\leq \frac{1}{a} \sum_{n \geq 1} c_{n-1}(a) \mathbb{P}(N > c_{n-1}(a)) \rightarrow 0 \quad \text{as } a \rightarrow \infty,
 \end{aligned}$$

where the convergence follows from (39). Hence, by (41), we infer for almost every  $\omega \in \Omega$  the existence of an  $a_0$  such that for all  $a \geq a_0$

$$\frac{\mathcal{T}_n^*(\omega)}{c_n} = \frac{c_n(a)}{c_n} \frac{\mathcal{T}_n^*(a)(\omega)}{c_n(a)} \rightarrow \eta(a) L^*(a)(\omega) \quad (42)$$

where  $\eta(a) \in (0, \infty)$  should be recalled. Hence,  $c_n^{-1} \mathcal{T}_n^*$  converges a.s. to a random variable  $L^*$ .

(2)  $\mathbb{P}(L^* > 0) > 0$ 

In view of (42), it suffices to verify  $\mathbb{P}(L^*(a) > 0) > 0$  for some  $a > 0$ . Let  $\Lambda(a) = (\Lambda_n(a))_{n \geq 0}$  be a sequence of independent random variables taking values in the set of probability measures on  $\mathbb{N}_0$  such that

$$\mathbb{P}(\Lambda_n(a) = \mathcal{L}(X^{(j,k)})) = \frac{p_k}{\mathbb{E}(N \mathbb{1}_{\{N \leq c_n(a)\}})} = \frac{c_n(a)}{c_{n+1}(a)} p_k \quad (43)$$

for all  $n \in \mathbb{N}_0$  and  $1 \leq j \leq k \leq c_n(a)$ . Let further  $(Z'_n(a))_{n \geq 0}$  be a branching process in random environment  $\Lambda(a)$ , and let  $g_{\Lambda_n(a)}$  denote the random generating function of the individuals in the  $n$ th generation. Recall that  $(Z'_n)_{n \geq 0}$  is the ABPRE with environmental sequence  $\Lambda$ . Clearly,

$$\mathbb{P}(Z'_n(a) > 0 | \Lambda(a) = \lambda) = \mathbb{P}(Z'_n > 0 | \Lambda = \lambda)$$

as well as

$$\mathbb{P}(\Lambda_0(a) = \lambda_0, \dots, \Lambda_n(a) = \lambda_n) = \frac{1}{c_n(a)} \prod_{k=0}^n p_{\lambda_k}$$

for any sequence of probability measures  $\lambda = (\lambda_i)_{i \geq 0}$  with  $\lambda_i = \mathcal{L}(X^{(j_i, k_i)})$  and  $j_i \leq k_i \leq c_i(a)$  for each  $i \in \mathbb{N}_0$ . Hence, by a straightforward adjustment of the calculations in the proof of Proposition 2.2, we obtain

$$\mathbb{P}(Z'_n(a) > 0) = c_n^{-1}(a) \mathbb{E} \mathcal{T}_n^*(a) \quad (44)$$

for any  $n \in \mathbb{N}_0$ , and since  $c_n^{-1}(a) \mathcal{T}_n^*(a) \rightarrow L^*(a)$  in  $L^1$ , we obtain

$$\mathbb{E} L^*(a) = \lim_{n \rightarrow \infty} \mathbb{P}(Z'_n(a) > 0).$$

For  $\lambda = \mathcal{L}(X^{(j,k)})$  and  $m > 0$  let

$$g_{\lambda,m}(s) = \sum_{k=0}^{m-1} s^k \mathbb{P}(X^{(j,k)} = k) + s^m \mathbb{P}(X^{(j,k)} \geq m)$$

be the generating function of the truncated random variable  $X^{(j,k)} \wedge m$ . As truncation reduces the reproduction, obviously

$$\mathbb{E}L^*(a) = \lim_{n \rightarrow \infty} \mathbb{P}(Z'_n(a) > 0) \geq \lim_{n \rightarrow \infty} \mathbb{P}(Z'_{n,m}(a) > 0),$$

where  $(Z'_{n,m}(a))_{n \geq 0}$  is the branching process with environmental sequence  $\Lambda(a)$  and truncated reproduction laws. The truncation further ensures

$$\sup_{n \geq 0} g''_{\Lambda_n(a),m}(1) / g'_{\Lambda_n(a),m}(1) < \infty \quad \text{a.s.}$$

whence, by Theorem 1 in [4],

$$\lim_{n \rightarrow \infty} \mathbb{P}(Z'_{n,m}(a) > 0) > 0 \quad \text{if} \quad \sum_{n=0}^{\infty} \left( \prod_{i=0}^{n+1} g'_{\Lambda_i(a),m}(1) \right)^{-1} < \infty \quad \text{a.s.} \quad (45)$$

Due to the given assumptions, Theorem 2.1 in [6] provides us with the existence of a constant  $m > 0$  such that

$$0 < \mathbb{E} \log g'_{\Lambda_0,m}(1) < \infty.$$

A look at (43) shows that

$$\mathbb{P}(\Lambda_n(a) = \mathcal{L}(X^{(j,k)})) = \frac{c_n(a)}{c_{n+1}(a)} p_k \xrightarrow{n \rightarrow \infty} \frac{p_k}{v} = \mathbb{P}(\Lambda_0 = \mathcal{L}(X^{(j,k)}))$$

so that, by making use of (39),

$$\begin{aligned} \lim_{n \rightarrow \infty} \mathbb{E} \log g'_{\Lambda_n(a),m}(1) &= \lim_{n \rightarrow \infty} \sum_{1 \leq j \leq k \leq c_n(a)} \frac{c_n(a)}{c_{n+1}(a)} p_k \log \mathbb{E}(X^{(j,k)} \wedge m) \\ &= \sum_{1 \leq j \leq k < \infty} \frac{p_k}{v} \log \mathbb{E}(X^{(j,k)} \wedge m) = \mathbb{E} \log g'_{\Lambda_0,m}(1). \end{aligned}$$

Moreover, for any  $x > 0$ ,

$$\begin{aligned} \mathbb{P}(\log^{\pm} g'_{\Lambda_n(a),m}(1) > x) &= \sum_{\substack{1 \leq j \leq k \leq c_n(a), \\ \log^{\pm} \mu_{j,k} > x}} \frac{c_n(a)}{c_{n+1}(a)} p_k \leq \frac{av}{c_1(a)} \sum_{\substack{1 \leq j \leq k < \infty, \\ \log^{\pm} \mu_{j,k} > x}} \frac{p_k}{v} \\ &= \frac{av}{c_1(a)} \mathbb{P}(\log^{\pm} g'_{\Lambda_0,m}(1) > x) \end{aligned}$$

and therefore an extension of the law of large numbers (see [31, Theorem 2.19]) ensures the existence of an a.s. finite random variable  $M$  such that

$$\frac{1}{n} \sum_{k=0}^{n-1} \log g'_{\Lambda_k(a),m}(1) \geq \frac{1}{2} \mathbb{E} \log g'_{\Lambda_0,m}(1) > 0 \quad \text{for all } n \geq M.$$



But from this, we finally deduce

$$\begin{aligned} \sum_{n \geq 0} \prod_{i=0}^{n+1} \frac{1}{g'_{\Lambda_i(a),m}(1)} &= \sum_{n=0}^{M-1} \prod_{i=0}^{n+1} \frac{1}{g'_{\Lambda_i(a),m}(1)} + \sum_{n \geq M} \exp \left( - \sum_{i=0}^{n+1} \log g'_{\Lambda_i(a),m}(1) \right) \\ &\leq \sum_{n=0}^{M-1} \prod_{i=0}^{n+1} \frac{1}{g'_{\Lambda_i(a),m}(1)} + \sum_{n \geq M} \left[ \exp \left( - \frac{1}{2} \mathbb{E} \log g'_{\Lambda_0,m}(1) \right) \right]^{n+1} \\ &< \infty \quad \text{a.s.} \end{aligned}$$

and thereupon  $\mathbb{E}L^*(a) > 0$  by an appeal to (45).

$L^*$  VANISHES ONLY ON  $\text{Ext}$

We adapt the proof of Theorem 4.1(b) and set  $\tau_n := \inf\{m \in \mathbb{N}_0 \mid \mathcal{J}_m^* \geq n\}$  for each  $n \in \mathbb{N}$ . Then

$$\begin{aligned} \mathbb{P}(L^* = 0) &\leq \mathbb{P}(L^* = 0 \mid \tau_n < \infty) + \mathbb{P}(\tau_n = \infty) \\ &= \mathbb{P} \left( \lim_{m \rightarrow \infty} \frac{c_m}{c_{m+\tau_n}} \sum_{v \in \mathbb{T}_{\tau_n}^*} c_m^{-1} \mathcal{J}_m^*(v) = 0 \mid \tau_n < \infty \right) + \mathbb{P}(\tau_n = \infty) \\ &\leq \mathbb{P}(\mathcal{J}_m^*/c_m \rightarrow 0)^n + \mathbb{P}(\tau_n = \infty) \\ &= \mathbb{P}(L^* = 0)^n + \mathbb{P}(\tau_n = \infty), \end{aligned}$$

where (39) entered in the penultimate inequality. As  $\mathbb{P}(L^* = 0) < 1$ , the proof is completed by letting  $n$  tend to infinity and an appeal to Theorem 3.3.  $\square$

**Proof of Theorem 4.4.** The implications “(iv)  $\Rightarrow$  (iii)  $\Rightarrow$  (ii)  $\Rightarrow$  (i)” follow directly from standard martingale theory so that it remains to argue that  $\mathbb{P}(W > 0) > 0$  implies  $\mathbb{E}(\sup_{n \geq 0} W_n) < \infty$ . Modulo minor modifications the subsequent proof follows the arguments of [20, Lemma 2] and [8, Lemma 2.6 in Chapter II], and we estimate the tail probabilities of  $\sup_{n \geq 0} W_n$ .

Let  $\mathbb{P}(W > 0) > 0$ . Assuming the existence of constants  $a, b > 0$  such that

$$\mathbb{P}(W > at) \geq b \mathbb{P} \left( \sup_{n \geq 0} W_n > t \right) \quad (46)$$

for all  $t \in [1, \infty)$ , it follows by a standard computation that

$$\mathbb{E} \sup_{n \geq 0} W_n \leq 1 + \frac{\mathbb{E}W}{ab} < \infty$$

which proves the implication “(i)  $\Rightarrow$  (iv)”. So we must only verify (46) to complete the proof of the theorem.

**Proof of (46).** Clearly,  $\mathbb{P}(W > 0) > 0$  implies  $\mathbb{E}W > 0$ , and for each  $c \in (0, \mathbb{E}W)$  we can find some  $w \geq c$  such that  $\mathbb{E}(W \wedge w) \geq c$ . Fix  $t \in [1, \infty)$  and define

$$E_n := \left\{ W_n > t, \sup_{0 \leq k < n} W_k \leq t \right\}$$

for  $n \in \mathbb{N}_0$ . Then, for any  $a > 0$ ,

$$\mathbb{P}(W > at) \geq \mathbb{P} \left( W > at, \sup_{n \geq 0} W_n > t \right) = \sum_{n \geq 0} \mathbb{P}(W > at \mid E_n) \mathbb{P}(E_n). \quad (47)$$

For  $\mathbf{v} \in \mathbb{V}$  and  $n \in \mathbb{N}_0$  let  $\mathcal{Z}_n^{(\mathbf{v})}$  denote the number of parasites in the  $n$ th generation of the subtree with root cell  $\mathbf{v}$ , the latter containing  $Z_{\mathbf{v}}$  parasites. Since  $(W_n)_{n \geq 0}$  is a martingale (under any  $\mathbb{P}_z$ ), we obtain the almost sure convergence of  $\gamma^{-n} \mathcal{Z}_n^{(\mathbf{v})}$  conditioned under  $Z_{\mathbf{v}}$  and denote its limit by  $W^{(\mathbf{v})}$ . For all  $n \in \mathbb{N}_0$ , we then have the representation

$$W = \frac{1}{\gamma^n} \lim_{k \rightarrow \infty} \sum_{\mathbf{v} \in \mathbb{T}_n^*} \frac{\mathcal{Z}_k^{(\mathbf{v})}}{\gamma^k} = \frac{1}{\gamma^n} \sum_{\mathbf{v} \in \mathbb{T}_n^*} W^{(\mathbf{v})} \quad \text{a.s.}$$

Consequently,

$$\begin{aligned} \mathbb{P}(W > at | E_n) &= \mathbb{P}\left(\frac{1}{\gamma^n} \sum_{\mathbf{v} \in \mathbb{T}_n^*} W^{(\mathbf{v})} > at \mid E_n\right) = \mathbb{P}\left(\frac{1}{\gamma^n W_n} \sum_{\mathbf{v} \in \mathbb{T}_n^*} W^{(\mathbf{v})} > \frac{at}{W_n} \mid E_n\right) \\ &\geq \mathbb{P}\left(\frac{1}{\mathcal{Z}_n} \sum_{\mathbf{v} \in \mathbb{T}_n^*} W^{(\mathbf{v})} > a \mid E_n\right) \geq \mathbb{P}\left(\frac{1}{\mathcal{Z}_n} \sum_{\mathbf{v} \in \mathbb{T}_n^*} (W^{(\mathbf{v})} \wedge Z_{\mathbf{v}} w) > a \mid E_n\right) \\ &= \mathbb{P}(E_n)^{-1} \int_{E_n} \mathbb{P}\left(\frac{1}{\mathcal{Z}_n} \sum_{\mathbf{v} \in \mathbb{T}_n^*} (W^{(\mathbf{v})} \wedge Z_{\mathbf{v}} w) > a \mid \mathcal{F}_n\right) d\mathbb{P}. \end{aligned} \quad (48)$$

For  $Z_{\emptyset} = z \in \mathbb{N}_0$  let  $\mathcal{Z}_{k,j}$  denote the number of parasites in generation  $k \in \mathbb{N}_0$  stemming from the ancestor parasite  $j \in \{1, \dots, z\}$ . If any of these ancestors has at most  $w\gamma^k$  in generation  $k$ , then the total number of offspring is at most  $zw\gamma^k$ , i.e.

$$\sum_{j=1}^z (\mathcal{Z}_{k,j} \wedge w\gamma^k) \leq \left(\sum_{j=1}^z \mathcal{Z}_{k,j}\right) \wedge zw\gamma^k \quad \mathbb{P}_z\text{-a.s.}$$

As a consequence,

$$\begin{aligned} \mathbb{E}_z(W \wedge zw) &= \mathbb{E}_z\left(\lim_{k \rightarrow \infty} \left(\frac{1}{\gamma^k} \sum_{j=1}^z \mathcal{Z}_{k,j}\right) \wedge zw\right) \geq \mathbb{E}_z\left(\sum_{j=1}^z \left(\lim_{k \rightarrow \infty} \frac{1}{\gamma^k} \mathcal{Z}_{k,j} \wedge w\right)\right) \\ &= z\mathbb{E}(W \wedge w) \geq zc \end{aligned}$$

for all  $z \in \mathbb{N}_0$ , which in turn implies

$$\begin{aligned} \mathbb{E}\left(\frac{1}{\mathcal{Z}_n} \sum_{\mathbf{v} \in \mathbb{T}_n^*} (W^{(\mathbf{v})} \wedge Z_{\mathbf{v}} w) \mid \mathcal{F}_n\right) &= \frac{1}{\mathcal{Z}_n} \sum_{\mathbf{v} \in \mathbb{T}_n^*} \sum_{z=1}^{\infty} \mathbb{E}_z(W \wedge zw) \mathbb{1}_{\{Z_{\mathbf{v}}=z\}} \\ &\geq \frac{1}{\mathcal{Z}_n} \sum_{\mathbf{v} \in \mathbb{T}_n^*} Z_{\mathbf{v}} c = c \quad \text{a.s.} \end{aligned}$$

for all  $n \in \mathbb{N}_0$ . Let us put  $W_n(w) := \frac{1}{\mathcal{Z}_n} \sum_{\mathbf{v} \in \mathbb{T}_n^*} (W^{(\mathbf{v})} \wedge Z_{\mathbf{v}} w)$  and note that  $W_n(w) \leq w$  a.s. for all  $n \in \mathbb{N}_0$ . Then it follows for all  $a \in (0, c)$  that

$$\begin{aligned} c &\leq \mathbb{E}(W_n(w) | \mathcal{F}_n) = \int_0^w \mathbb{P}(W_n(w) > x | \mathcal{F}_n) dx \\ &\leq a + \int_a^w \mathbb{P}(W_n(w) > x | \mathcal{F}_n) dx \leq a + (w - a) \mathbb{P}(W_n(w) > a | \mathcal{F}_n) \end{aligned}$$

and thus

$$\mathbb{P}(W_n(w) > a | \mathcal{F}_n) \geq \frac{c-a}{w-a} \quad \text{a.s.}$$

Plugging this inequality into (48) with  $a := c/2$  and setting  $b := c/(2w - c)$ , we obtain

$$\mathbb{P}(W > at | E_n) \geq b$$

for all  $n \in \mathbb{N}_0$  and  $t \in [1, \infty)$ , and in combination with (47) this finally yields

$$\mathbb{P}(W > at) \geq \sum_{n \geq 0} \mathbb{P}(W > at | E_n) \mathbb{P}(E_n) \geq b \sum_{n \geq 0} \mathbb{P}(E_n) = b \mathbb{P}\left(\sup_{n \geq 0} W_n > t\right)$$

for all  $t \in [1, \infty)$ , that is (46).  $\square$

**Proof of Theorem 4.5.** First note that  $\mathbb{E}W \in \{0, 1\}$  is already verified by Theorem 4.4. The remaining proof is quite long and therefore split into several parts which are proved independently.

**Assertion 1.**  $\mathbb{P}(W > 0) > 0 \Rightarrow \mathbb{P}(W > 0) = \mathbb{P}(\text{Surv})$ .

**Proof of Assertion 1.** Let  $\tau_n = \inf\{m \in \mathbb{N} | \mathcal{F}_m^* \geq n\}$ . A similar argument as in the proof of Theorem 4.1(b) yields

$$\mathbb{P}(W = 0) \leq \mathbb{P}(W = 0)^n + \mathbb{P}(\tau_n = \infty)$$

for all  $n \in \mathbb{N}$ . Since  $\mathbb{P}(W = 0) < 1$  and by Theorem 3.2, this further implies

$$\mathbb{P}(W = 0) \leq \lim_{n \rightarrow \infty} \mathbb{P}(\tau_n = \infty) = \mathbb{P}\left(\sup_{m \geq 0} \mathcal{F}_m^* < \infty\right) = \mathbb{P}(\text{Ext})$$

and then the assertion, for  $\text{Ext} \subseteq \{W = 0\}$ .  $\square$

**Assertion 2.**  $\mathbb{E}\mathcal{Z}_1 \log \mathcal{Z}_1 < \infty$  and  $\mathbb{E}\left(\frac{g'_{A_0}(1)}{\gamma} \log \frac{g'_{A_0}(1)}{\gamma}\right) < 0 \Rightarrow \mathbb{E}W = 1$ .

**Proof of Assertion 2.** To prove the stated result, we use the size-biased tree introduced in Section 7 and show that  $\widehat{W} := \limsup_{n \rightarrow \infty} \widehat{W}_n$  is almost surely finite. Then  $\mathbb{E}W = 1$  follows by the dichotomy in Lemma 7.2(c).

Recalling the notation of the size-biased process, we have the recursive representation

$$\widehat{\mathcal{Z}}_{n+1} = \sum_{v \in \widehat{\mathbb{T}}_n} \sum_{j \geq 1} \widehat{Z}_{vj} = \sum_{j=1}^{\widehat{T}_n} \widehat{Z}_{\widehat{V}_n j} + \sum_{v \in \widehat{\mathbb{T}}_n \setminus \{\widehat{V}_n\}} \sum_{j=1}^{N_v} \sum_{i=1}^{\widehat{Z}_v} X_{i,v}^{(j, N_v)}, \quad n \geq 0.$$

Define the  $\sigma$ -field

$$\mathcal{G} := \sigma\left((\widehat{T}_n)_{n \geq 0}, (\widehat{X}_n^{(\bullet, k)})_{n \geq 0, k \geq 1}, (\widehat{V}_n)_{n \geq 0}\right). \quad (49)$$

Using the above recursive formula of  $\widehat{\mathcal{Z}}_{n+1}$ , we obtain

$$\begin{aligned}\mathbb{E}(\widehat{\mathcal{Z}}_{n+1} \mid \mathcal{G}) &= \mathbb{E}\left(\sum_{j=1}^{\widehat{T}_n} \widehat{Z}_{\widehat{v}_n j} \mid \mathcal{G}\right) + \mathbb{E}\left(\sum_{v \in \widehat{\mathbb{T}}_n \setminus \{\widehat{v}_n\}} \sum_{j=1}^{N_v} \sum_{i=1}^{\widehat{Z}_v} X_{i,v}^{(j, N_v)} \mid \mathcal{G}\right) \\ &= \mathbb{E}\left(\sum_{j=1}^{\widehat{T}_n} \widehat{Z}_{\widehat{v}_n j} \mid \mathcal{G}\right) + \mathbb{E}\left(\underbrace{\sum_{v \in \widehat{\mathbb{T}}_n \setminus \{\widehat{v}_n\}} \sum_{i=1}^{\widehat{Z}_v} \mathbb{E}\left(\sum_{j=1}^{N_v} X_{i,v}^{(j, N_v)}\right)}_{=\gamma} \mid \mathcal{G}\right) \\ &\leq \mathbb{E}\left(\sum_{j=1}^{\widehat{T}_n} \widehat{Z}_{\widehat{v}_n j} \mid \mathcal{G}\right) + \gamma \mathbb{E}(\widehat{\mathcal{Z}}_n \mid \mathcal{G}) \\ &\leq \dots \leq \sum_{k=0}^n \gamma^{n-k} \mathbb{E}\left(\sum_{j=1}^{\widehat{T}_k} \widehat{Z}_{\widehat{v}_k j} \mid \mathcal{G}\right) \quad \text{a.s.}\end{aligned}$$

for all  $n \geq 0$ . Using the definition of the size-biased variables and the fact that, for fixed  $(j, k)$ , the  $X_{i,v}^{(j,k)}$ ,  $i \in \mathbb{N}$ ,  $v \in \mathbb{V}$ , are i.i.d., we further obtain

$$\begin{aligned}\mathbb{E}(\widehat{\mathcal{Z}}_{n+1} \mid \mathcal{G}) &\leq \sum_{k=0}^n \gamma^{n-k} \sum_{j=1}^{\widehat{T}_k} \left( \widehat{X}_k^{(j, \widehat{T}_k)} + \mathbb{E}\left(\sum_{i=1}^{\widehat{Z}_{\widehat{v}_k} - 1} X_{i, \widehat{v}_k}^{(j, \widehat{T}_k)} \mid \mathcal{G}\right) \right) \\ &= \sum_{k=0}^n \gamma^{n-k} \sum_{j=1}^{\widehat{T}_k} \left( \widehat{X}_k^{(j, \widehat{T}_k)} + \underbrace{\mathbb{E}(\widehat{Z}_{\widehat{v}_k} - 1 \mid \mathcal{G}) \mathbb{E}(X^{(j, \widehat{T}_k)} \mid \widehat{T}_k)}_{=\mu_{j, \widehat{T}_k}} \right) \quad \text{a.s.}\end{aligned} \quad (50)$$

Thus, letting  $n$  tend to infinity on the right hand side, leads to

$$\mathbb{E}(\widehat{W}_{n+1} \mid \mathcal{G}) \leq \underbrace{\sum_{k \geq 0} \frac{1}{\gamma^k} \sum_{j=1}^{\widehat{T}_k} \widehat{X}_k^{(j, \widehat{T}_k)}}_{=: J_1} + \underbrace{\sum_{k \geq 0} \frac{1}{\gamma^k} \mathbb{E}(\widehat{Z}_{\widehat{v}_k} - 1 \mid \mathcal{G}) \sum_{j=1}^{\widehat{T}_k} \mu_{j, \widehat{T}_k}}_{=: J_2} \quad (51)$$

a.s. for all  $n \in \mathbb{N}_0$ . Next is to show that both sums  $J_1$  and  $J_2$  are almost surely finite. Recall that  $\gamma > 1$  as a consequence of  $\mathbb{P}(\text{Ext}) < 1$  and [Theorem 3.3](#).

**FINITENESS OF  $J_1$ :** By definition, the  $\sum_{j=1}^{\widehat{T}_k} \widehat{X}_k^{(j, \widehat{T}_k)}$ ,  $k \geq 0$ , are i.i.d. with the same law as  $\widehat{\mathcal{Z}}_1$ . Moreover,  $\mathbb{E} \mathcal{Z}_1 \log \mathcal{Z}_1 < \infty$  is equivalent to  $\mathbb{E} \log \widehat{\mathcal{Z}}_1 < \infty$  (see [Remark 7.3](#)) so that, by (20),

$$\lim_{k \rightarrow \infty} \frac{1}{k} \log \left( \sum_{j=1}^{\widehat{T}_k} \widehat{X}_k^{(j, \widehat{T}_k)} \right) = 0 \quad \text{a.s.}$$

which in turn entails that with probability one

$$\sum_{j=1}^{\widehat{T}_k} \widehat{X}_k^{(j, \widehat{T}_k)} \leq \left(\frac{\gamma}{2}\right)^k \quad \text{eventually,}$$

in particular  $J_1 < \infty$  a.s.

FINITENESS OF  $J_2$ : By [Theorem 7.4](#),  $(\widehat{Z}_{\widehat{V}_n} - 1)_{n \geq 0}$  is a BPREI in i.i.d. random environment  $(\widehat{U}_n, \widehat{T}_n)_{n \geq 0}$  with immigration sequence  $(\widehat{X}_n^{(\widehat{U}_n, \widehat{T}_n)} - 1)_{n \geq 0}$ . Consequently,  $\mu_{\widehat{U}_i, \widehat{T}_i}$ ,  $i \in \mathbb{N}_0$ , is the (random) reproduction mean of parasites in cell  $\widehat{V}_i$ , and thus of the first marginal distribution of individuals in the  $i$ th generation of the ABPREI. As previously pointed out,  $\mathbb{E} \mathcal{Z}_1 \log \mathcal{Z}_1 < \infty$  implies  $\mathbb{E} \log \mathcal{Z}_1 < \infty$ , and thus the immigration components satisfy

$$\mathbb{E} \log^+ \left( \widehat{X}_0^{(\widehat{U}_0, \widehat{T}_0)} - 1 \right) \leq \mathbb{E} \log \widehat{\mathcal{Z}}_1 < \infty.$$

By the assumptions in the theorem and  $\mathbb{E} g'_{A_0}(1) = \gamma/\nu$  (see [\(8\)](#)), we get

$$\mathbb{E} \left( g'_{A_0}(1) \log \frac{g'_{A_0}(1)}{\gamma} \right) = \mathbb{E} g'_{A_0}(1) \log g'_{A_0}(1) - \frac{\gamma}{\nu} \log \gamma < 0,$$

whence, by an appeal to [\(34\)](#),

$$\mathbb{E} \log \mu_{\widehat{U}_0, \widehat{T}_0} = \frac{\nu}{\gamma} \mathbb{E} g'_{A_0}(1) \log g'_{A_0}(1) < \log \gamma. \quad (52)$$

Consequently,  $\mathbb{E} \log \mu_{\widehat{U}_0, \widehat{T}_0} = \log c$  for some  $c \in (1, \gamma)$  and [Corollary 6.2](#), applied to  $(\widehat{Z}_{\widehat{V}_n} - 1)_{n \geq 0}$ , provides us with

$$\widehat{Z}_\infty := \sup_{n \geq 0} \frac{1}{c^n} \mathbb{E} \left( \widehat{Z}_{\widehat{V}_n} - 1 | \mathcal{G} \right) < \infty \quad \text{a.s.}$$

We are thus led to a new upper bound for  $J_2$ , namely

$$J_2 \leq \widehat{Z}_\infty \sum_{k \geq 0} \left( \frac{c}{\gamma} \right)^k \sum_{j=1}^{\widehat{T}_k} \mu_{j, \widehat{T}_k} \leq \widehat{Z}_\infty \sum_{k \geq 0} \left( \exp \left[ \log \frac{c}{\gamma} + \frac{1}{k} \log^+ \left( \sum_{j=1}^{\widehat{T}_k} \mu_{j, \widehat{T}_k} \right) \right] \right)^k \quad \text{a.s.} \quad (53)$$

Using Jensen's inequality and [\(26\)](#), we obtain

$$\begin{aligned} \mathbb{E} \log^+ \left( \sum_{j=1}^{\widehat{T}_0} \mu_{j, \widehat{T}_0} \right) &= \sum_{k \geq 1} \mathbb{P}(\widehat{T}_0 = k) \log^+ \mathbb{E} \left( \sum_{j=1}^k X^{(j, k)} \right) \\ &= \sum_{k \geq 1} \frac{pk}{\gamma} \mathbb{E} \left( \sum_{j=1}^k X^{(j, k)} \right) \log^+ \mathbb{E} \left( \sum_{j=1}^k X^{(j, k)} \right) \\ &\leq \frac{1}{\gamma} \sum_{k \geq 1} pk \mathbb{E} \left( \sum_{j=1}^k X^{(j, k)} \log^+ \sum_{j=1}^k X^{(j, k)} \right) = \frac{1}{\gamma} \mathbb{E} \mathcal{Z}_1 \log \mathcal{Z}_1 < \infty, \end{aligned}$$

and since the  $\sum_{j=1}^{\widehat{T}_k} \mu_{j, \widehat{T}_k}$ ,  $k \geq 0$ , are i.i.d., [\(20\)](#) yields

$$\limsup_{n \rightarrow \infty} \frac{1}{k} \log^+ \left( \sum_{j=1}^{\widehat{T}_0} \mu_{j, \widehat{T}_0} \right) = 0 \quad \text{a.s.}$$

Hence,  $J_2 < \infty$  a.s. follows when using this fact in [\(53\)](#).

Having verified that  $J_1$  and  $J_2$  are a.s. finite, inequality (51) gives

$$\sup_{n \geq 0} \mathbb{E}(\widehat{W}_n | \mathcal{G}) < \infty \quad \text{a.s.}$$

while Fatou's lemma ensures almost sure finiteness of  $\liminf_{n \rightarrow \infty} \widehat{W}_n$ , i.e.

$$\mathbb{P}(\liminf_{n \rightarrow \infty} \widehat{W}_n < \infty) = \widehat{Q}(\liminf_{n \rightarrow \infty} w_n < \infty) = 1,$$

where  $\widehat{Q} = \mathbb{P}(\widehat{\mathbf{BT}} \in \cdot)$  and  $\widehat{W}_n = w_n \circ \widehat{\mathbf{BT}}$ . It remains to show that  $(w_n)_{n \geq 0}$  converges  $\widehat{Q}$ -a.s., because then  $\widehat{W} = \liminf_{n \rightarrow \infty} \widehat{W}_n$  and  $\widehat{W}$  is almost surely finite, which completes the proof of the theorem.

We show that  $(1/w_n)_{n \geq 0}$  is a  $\widehat{Q}$ -supermartingale with respect to the filtration  $(\mathcal{S}_n)_{n \geq 0}$  defined in Section 7 to which is adapted by definition. For each  $n \geq 0$ , we have

$$\widehat{Q}(w_n = 0) = \int_{\{w_n=0\}} w_n d\widehat{Q} = 0$$

by Lemma 7.2(b). Let  $\mathbb{E}_P$  denote expectation with respect to a probability measure  $P$ . By using Lemma 7.2 and Remark 7.3, we infer for any  $A \in \mathcal{S}_n \subseteq \mathcal{S}_{n+1}$

$$\begin{aligned} \int_A \mathbb{E}_{\widehat{Q}} \left( \frac{1}{w_{n+1}} | \mathcal{S}_n \right) d\widehat{Q} &= \int_A \frac{1}{w_{n+1}} d\widehat{Q} = \mathbb{E}_{\widehat{Q}} \left( \frac{1}{w_{n+1}} \mathbb{1}_{\{A \cap \{w_{n+1} > 0\}\}} \right) \\ &= \mathbb{E}_Q \left( \frac{1}{w_{n+1}} w_{n+1} \mathbb{1}_{\{A \cap \{w_{n+1} > 0\}\}} \right) = Q(A \cap \{w_{n+1} > 0\}) \\ &\leq Q(A \cap \{w_n > 0\}) = \int_A \frac{1}{w_n} d\widehat{Q}, \end{aligned}$$

where the last equality follows by making the previous calculations backwards. We have thus verified that  $(1/w_n)_{n \geq 0}$  is indeed a  $\widehat{Q}$ -supermartingale with  $\mathbb{E}_{\widehat{Q}}(1/w_n) \leq \mathbb{E}_{\widehat{Q}}(1/w_0) = 1$ . It hence converges  $\widehat{Q}$ -a.s. by the martingale convergence theorem which completes the proof of the assertion.  $\square$

**Assertion 3.**  $\mathbb{E} \mathcal{Z}_1 \log \mathcal{Z}_1 = \infty$  or  $\mathbb{E} \left( \frac{g'_{\Lambda_0}(1)}{\gamma} \log \frac{g'_{\Lambda_0}(1)}{\gamma} \right) \geq 0 \Rightarrow \mathbb{P}(W = 0) = 1$

**Proof of Assertion 3.** First note, that our basic assumptions (A5) and (A4) imply

$$\mathbb{P}(g'_{\Lambda_0}(1) \in \{\gamma, 0\}) < 1, \tag{54}$$

for otherwise  $\mu_{j,k} \in \{0, \gamma\}$  for all  $1 \leq j \leq k < \infty$  with  $p_k > 0$  and so

$$\gamma = \sum_{k \geq 0} p_k \sum_{j=1}^k \mu_{j,k} = \underbrace{\gamma \sum_{k \geq 0} p_k \# \{1 \leq j \leq k : \mathbb{P}(X^{(j,k)} > 0) > 0\}}_{=:c=1}.$$

Since  $c$  denotes the mean number of cells that are able to host parasites, we infer  $\mathbb{E}_z(\mathcal{T}_1^*) \leq c = 1$  for all  $z \in \mathbb{N}$ . Hence,

$$\mathbb{E}_{\mathcal{T}_{n+1}^*} = \mathbb{E} \left( \sum_{v \in \mathbb{T}_n^*} \sum_{z=1}^{\infty} \mathbb{E}_z(\mathcal{T}_1^*) \mathbb{1}_{\{Z_v=z\}} \right) \leq \mathbb{E}_{\mathcal{T}_n^*} \leq \dots \leq 1.$$

But this contradicts Theorem 3.3 and so (54) must hold.

Using again the size-biased tree defined in Section 7, we show that  $\mathbb{P}(\widehat{W} = \infty) = 1$  for  $\widehat{W} := \limsup_{n \rightarrow \infty} \widehat{W}_n$ . Then Lemma 7.2(c) gives  $\mathbb{P}(W = 0) = 1$ .

First, note that

$$\widehat{W}_n = \frac{1}{\gamma^n} \sum_{v \in \widehat{\mathbb{T}}_n} \widehat{Z}_v \geq \frac{1}{\gamma^n} \sum_{j=1}^{\widehat{T}_{n-1}} \widehat{Z}_{\widehat{V}_{n-1}u} \geq \frac{1}{\gamma^n} \sum_{j=1}^{\widehat{T}_{n-1}} \widehat{X}_{n-1}^{(j, \widehat{T}_{n-1})} \quad \text{a.s.}$$

for  $n \in \mathbb{N}$ . Since  $\mathbb{E} \mathcal{Z}_1 \log \mathcal{Z}_1 = \infty$  gives  $\mathbb{E} \log \widehat{\mathcal{Z}}_1 = \infty$  by Remark 7.3, and the random sums  $\sum_{j=1}^{\widehat{T}_{n-1}} \widehat{X}_{n-1}^{(j, \widehat{T}_{n-1})}$ ,  $n \in \mathbb{N}$ , are independent and identically distributed as  $\widehat{\mathcal{Z}}_1$ , we infer

$$\begin{aligned} \limsup_{n \rightarrow \infty} \widehat{W}_n &\geq \limsup_{n \rightarrow \infty} \frac{1}{\gamma^n} \sum_{j=1}^{\widehat{T}_{n-1}} \widehat{X}_{n-1}^{(j, \widehat{T}_{n-1})} \\ &= \limsup_{n \rightarrow \infty} \exp \left( \frac{1}{n} \log \sum_{j=1}^{\widehat{T}_{n-1}} \widehat{X}_{n-1}^{(j, \widehat{T}_{n-1})} - \log \gamma \right)^n = \infty \quad \text{a.s.} \end{aligned}$$

by another appeal to (20). This proves the assertion in the case when  $\mathbb{E} \mathcal{Z}_1 \log \mathcal{Z}_1 = \infty$ .

Suppose now  $\mathbb{E} \mathcal{Z}_1 \log \mathcal{Z}_1 < \infty$ . Once again, by the definition of  $\widehat{W}_n$ , we get

$$\widehat{W}_n = \frac{1}{\gamma^n} \sum_{v \in \widehat{\mathbb{T}}_n} \widehat{Z}_v \geq \frac{1}{\gamma^n} \widehat{Z}_{\widehat{V}_n} \geq \frac{1}{\gamma^n} (\widehat{Z}_{\widehat{V}_n} - 1) \quad \text{a.s.} \quad (55)$$

for  $n \in \mathbb{N}_0$ . As stated earlier,  $(\widehat{Z}_{\widehat{V}_n} - 1)_{n \geq 0}$  forms a BPRED in i.i.d. random environment  $(\widehat{U}_n, \widehat{T}_n)_{n \geq 0}$  and with immigration sequence  $(\widehat{X}_n^{(\widehat{U}_n, \widehat{T}_n)} - 1)_{n \geq 0}$ . The assumption  $\mathbb{P}(g'_{A_0}(1) \in \{\gamma, 0\}) < 1$  implies  $\mu_{j,k} \neq \gamma$  for some  $(j, k)$ ,  $j \leq k$ , with  $p_k > 0$  and  $\mathbb{P}(X^{(j,k)} > 0) > 0$ , thus

$$\mathbb{P}(\mu_{\widehat{U}_0, \widehat{T}_0} \neq \gamma) > 0. \quad (56)$$

Moreover,  $\mathbb{E} \mathcal{Z}_1 \log \mathcal{Z}_1 < \infty$  implies

$$\mathbb{E} \log^+ \left( \widehat{X}_0^{(\widehat{U}_0, \widehat{T}_0)} - 1 \right) < \infty$$

as pointed out before. By adapting the argument in (52), we find

$$\mathbb{E} \log \mu_{\widehat{U}_0, \widehat{T}_0} = \frac{\nu}{\gamma} \mathbb{E} g'_{A_0}(1) \log g'_{A_0}(1) \geq \log \gamma > 0. \quad (57)$$

Hence, by Theorem 6.1(a), there exists an almost surely finite random variable  $Z_\infty$  such that

$$\lim_{n \rightarrow \infty} \frac{\widehat{Z}_{\widehat{V}_n} - 1}{\prod_{i=0}^{n-1} \mu_{\widehat{U}_i, \widehat{T}_i}} = Z_\infty \quad \text{a.s.} \quad (58)$$

Theorem 6.1(a) further ensures that  $Z_\infty$  is a.s. positive, because

$$\begin{aligned} \mathbb{E} \left( \frac{X^{(\widehat{U}_0, \widehat{T}_0)}}{\mu_{\widehat{U}_0, \widehat{T}_0}} \log^+ X^{(\widehat{U}_0, \widehat{T}_0)} \right) &= \sum_{1 \leq j \leq k < \infty} \mathbb{P}(\widehat{U}_0 = j, \widehat{T}_0 = k) \mathbb{E} \left( \frac{X^{(j,k)}}{\mu_{j,k}} \log^+ X^{(j,k)} \right) \\ &= \frac{1}{\gamma} \sum_{1 \leq j \leq k < \infty} p_k \mathbb{E} \left( X^{(j,k)} \log^+ X^{(j,k)} \right) \end{aligned}$$

$$\begin{aligned}
&\leq \frac{1}{\gamma} \sum_{1 \leq j \leq k < \infty} p_k \mathbb{E} \left( X^{(j,k)} \log^+ \sum_{j=1}^k X^{(j,k)} \right) \\
&= \frac{1}{\gamma} \mathbb{E} \mathcal{Z}_1 \log^+ \mathcal{Z}_1 < \infty,
\end{aligned}$$

where (29) has been utilized for the second equation. From (55), (56), (57), (58) and the fact that the  $\mu_{\widehat{U}_i, \widehat{T}_i}$ ,  $i \in \mathbb{N}_0$ , are i.i.d., we finally obtain

$$\begin{aligned}
\widehat{W} &= \limsup_{n \rightarrow \infty} \widehat{W}_n \geq Z_\infty \limsup_{n \rightarrow \infty} \frac{\prod_{i=0}^{n-1} \mu_{\widehat{U}_i, \widehat{T}_i}}{\gamma^n} \\
&= Z_\infty \exp \left( \limsup_{n \rightarrow \infty} \sum_{i=0}^{n-1} \log \left( \frac{\mu_{\widehat{U}_i, \widehat{T}_i}}{\gamma} \right) \right) = \infty \quad \text{a.s.}
\end{aligned}$$

by the law of large numbers or, equivalently (Lemma 7.2(c)),  $W = 0$  a.s.  $\square$

This completes the proof of Theorem 4.5.  $\square$

**Proof of Theorem 4.6.** Since  $W_n$  converges a.s. to a finite random variable, it follows immediately that  $\limsup_{n \rightarrow \infty} W_n^{1/n} \leq 1$  a.s.

To derive the lower bound, we distinguish two cases and use the truncation argument given in [22]. Recall from (54) in the previous proof that (A5) and (A4) imply  $P(g'_{\Lambda_0}(1) \in \{\gamma, 0\}) < 1$ .

Case I: Let  $N$  be bounded, i.e.  $N \leq c$  a.s. for some  $c \in (0, \infty)$ . For  $a > 0$  and  $1 \leq j \leq k \leq c$ , we define

$$X^{(j,k)}(a) := X^{(j,k)} \mathbb{1}_{\{X^{(j,k)} \leq a\}}$$

and let  $(\mathcal{Z}_n(a))_{n \geq 0}$  denote the associated process of parasites and  $(\mathcal{T}_n^*(a))_{n \geq 0}$  the process of contaminated cells having the truncated reproductions laws. Put further  $\gamma(a) := \mathbb{E} \mathcal{Z}_1^*(a)$  and let  $g_{\Lambda_0, a}(s)$  and  $W_n(a)$  have the obvious meaning. Since  $\mathcal{T}_n^*(a) \uparrow \mathcal{T}_n^*$  as  $a \rightarrow \infty$  for each  $n \in \mathbb{N}$ , we see that  $\mathbb{P}_2(\mathcal{T}_1^*(a) \geq 2) > 0$  as well as  $\sup_{n \geq 0} \mathbb{E} \mathcal{T}_n^*(a) > 1$  for sufficiently large  $a > 0$ , which entails  $\mathbb{P}(\mathcal{Z}_n(a) \rightarrow 0) < 1$  for such  $a$  by Theorem 3.3. Moreover,

$$\begin{aligned}
\mathbb{E} g'_{\Lambda_0, a}(1) \log \frac{g'_{\Lambda_0, a}(1)}{\gamma(a)} &= \mathbb{E} g'_{\Lambda_0, a}(1) \log g'_{\Lambda_0, a}(1) - \mathbb{E} g'_{\Lambda_0, a}(1) \log \gamma(a) \\
&\leq \mathbb{E} g'_{\Lambda_0}(1) \log g'_{\Lambda_0}(1) - \mathbb{E} g'_{\Lambda_0, a}(1) \log \gamma(a) \\
&\searrow \mathbb{E} g'_{\Lambda_0}(1) \log g'_{\Lambda_0}(1) - \mathbb{E} g'_{\Lambda_0}(1) \log \gamma \quad \text{as } a \rightarrow \infty \\
&= \mathbb{E} g'_{\Lambda_0}(1) \log \frac{g'_{\Lambda_0}(1)}{\gamma} < 0,
\end{aligned}$$

for  $\gamma(a)$  increases in  $a$ . Therefore we can find  $a_0 > 0$  such that

$$\mathbb{E} g'_{\Lambda_0, a}(1) \log \frac{g'_{\Lambda_0, a}(1)}{\gamma(a)} < 0$$

for all  $a \geq a_0$ . Since  $\mathbb{E} \mathcal{Z}_1^*(a) \log \mathcal{Z}_1^*(a) \leq ac \log ac$ , Theorem 4.5 implies the existence of a finite random variable  $W(a)$  such that  $W_n(a) \rightarrow W(a)$  in  $L^1$  as  $n \rightarrow \infty$ . In particular,  $\mathbb{P}(W(a) > 0) > 0$ .



Now fix any  $\varepsilon > 0$  and  $a \geq a_0$  such that  $\gamma(a) \geq (1 - \varepsilon)\gamma$ . Then

$$\mathbb{E}\mathcal{Z}_n(a) = \gamma(a)^n \geq (1 - \varepsilon)^n \gamma^n$$

for all  $n \geq 0$ . Let  $(\mathcal{Z}_{n,k}(a))_{n \geq 0}$  be the number of parasites process, when parasites produce offspring according to the original reproduction laws up to generation  $k$  and with the truncated laws from generation  $k + 1$  onwards. By the previously established lower bound of the means, this yields

$$\mathbb{E}\mathcal{Z}_{n,k}(a) = \gamma^k \mathbb{E}\mathcal{Z}_{n-k}(a) \geq (1 - \varepsilon)^n \gamma^n$$

for all  $k, n \geq 0$  with  $k \leq n$ . Moreover, we find that

$$\frac{\mathcal{Z}_n}{(1 - \varepsilon)^n \gamma^n} \geq \frac{\mathcal{Z}_{n,k}(a)}{(1 - \varepsilon)^n \gamma^n} \geq \frac{\mathcal{Z}_{n,k}(a)}{\mathbb{E}\mathcal{Z}_{n,k}(a)} \geq \frac{1}{\gamma^k} \sum_{v \in \mathbb{T}_k^*} \frac{\mathcal{Z}_{n-k}^{(v)}(a)}{\mathbb{E}\mathcal{Z}_{n-k}(a)} \quad \text{a.s.,}$$

where  $\mathcal{Z}_{n-k}^{(v)}(a)$ ,  $v \in \mathbb{T}_k^*$ , are i.i.d. random variables with the same law as  $\mathcal{Z}_{n-k}(a)$  when starting with a single parasite. Because of our choice of  $a$ , taking the limit in the above inequality yields

$$\liminf_{n \rightarrow \infty} \frac{\mathcal{Z}_n}{(1 - \varepsilon)^n \gamma^n} \geq \liminf_{n \rightarrow \infty} \frac{1}{\gamma^k} \sum_{v \in \mathbb{T}_k^*} \frac{\mathcal{Z}_{n-k}^{(v)}(a)}{\mathbb{E}\mathcal{Z}_{n-k}(a)} = \frac{1}{\gamma^k} \sum_{v \in \mathbb{T}_k^*} W^{(v)}(a),$$

where  $W^{(v)}(a)$ ,  $v \in \mathbb{T}_k^*$ , are independent and distributed as  $W(a)$ . Recalling that  $\mathcal{F}_k$  is the  $\sigma$ -algebra of the  $k$ -past, we get from this inequality

$$\begin{aligned} \mathbb{P}\left(\liminf_{n \rightarrow \infty} \frac{\mathcal{Z}_n}{(1 - \varepsilon)^n \gamma^n} > 0 \mid \mathcal{F}_k\right) &\geq \mathbb{P}\left(\frac{1}{\gamma^k} \sum_{v \in \mathbb{T}_k^*} W^{(v)}(a) > 0 \mid \mathcal{F}_k\right) \\ &= 1 - \mathbb{P}(W(a) = 0)^{\mathcal{F}_k^*} \quad \text{a.s.} \end{aligned}$$

Now use  $\mathbb{P}(W(a) > 0) > 0$  to obtain upon letting  $k$  tend to infinity

$$\text{Surv} = \{\mathcal{F}_n^* \rightarrow \infty\} \subseteq \left\{ \liminf_{n \rightarrow \infty} \frac{\mathcal{Z}_n}{(1 - \varepsilon)^n \gamma^n} > 0 \right\} \quad \text{a.s.,}$$

and then finally

$$\liminf_{n \rightarrow \infty} W_n^{1/n} \geq 1 - \varepsilon \quad \text{a.s.}$$

on the survival set  $\text{Surv}$ . This proves the theorem in the first case.

*Case II:* Let  $N$  be unbounded. We use truncation to reduce to bounded  $N$  and make use of the results just shown for that case. For  $b > 0$ , put

$$N(b) := N \mathbf{1}_{\{N \leq b\}}.$$

Let  $(\mathcal{Z}_n(b))_{n \geq 0}$  be the associated number of parasites process and  $(\mathcal{T}_n^*(b))_{n \geq 0}$  the process of contaminated cells having the truncated reproductions law for the cells. Further, let  $\gamma(b) = \mathbb{E}\mathcal{Z}_1(b)$ ,  $v(b) = \mathbb{E}\mathcal{T}_1(b)$  and  $g_{\Lambda_0, b}$  be the generating function of the ABPRE of the truncated BwBP. For the truncated process, we have

$$\mathbb{E}g'_{\Lambda_0, b}(1) \log g'_{\Lambda_0, b}(1) = \sum_{1 \leq j \leq k \leq b} \frac{p_k}{v(b)} \mu_{j,k} \log \mu_{j,k} \xrightarrow{b \rightarrow \infty} \mathbb{E}g'_{\Lambda_0}(1) \log g'_{\Lambda_0}(1)$$

as well as

$$\mathbb{E}g'_{A_0,b}(1) \log \gamma(b) = \frac{v}{v(b)} \frac{\gamma(b)}{v} \log \gamma(b) \xrightarrow{b \rightarrow \infty} \frac{\gamma}{v} \log \gamma = \mathbb{E}g'_{A_0}(1) \log \gamma \in (0, \infty).$$

Putting these two equations together and using  $\gamma(b) \uparrow \gamma$  as  $b \rightarrow \infty$ , we obtain

$$\begin{aligned} \mathbb{E}g'_{A_0,b}(1) \log \frac{g'_{A_0,b}(1)}{\gamma(b)} &= \mathbb{E}g'_{A_0,b}(1) \log g'_{A_0,b}(1) - \mathbb{E}g'_{A_0,b}(1) \log \gamma(b) \\ &\xrightarrow{b \rightarrow \infty} \mathbb{E}g'_{A_0}(1) \log g'_{A_0}(1) - \mathbb{E}g'_{A_0}(1) \log \gamma \\ &= \mathbb{E}g'_{A_0}(1) \log \frac{g'_{A_0}(1)}{\gamma} < 0. \end{aligned}$$

Hence, for each  $\varepsilon > 0$ , we can fix as in Case I some  $b > 0$  such that

$$\gamma(b) \geq (1 - \varepsilon)\gamma, \quad \mathbb{P}_2(\mathcal{T}_1^*(b) \geq 2) > 0, \quad \mathbb{P}(\mathcal{Z}_n(b) \rightarrow 0) < 1$$

and  $\mathbb{E}g'_{A_0,b}(1) \log \frac{g'_{A_0,b}(1)}{\gamma(b)} < 0$ . In other words, all conditions of *Case I* are fulfilled, and so

$$\liminf_{n \rightarrow \infty} W_n^{1/n} \geq (1 - \varepsilon) \liminf_{n \rightarrow \infty} \left( \frac{\mathcal{Z}_n(b)}{\gamma(b)^n} \right)^{1/n} \geq 1 - \varepsilon \quad \text{a.s.}$$

This completes the proof.  $\square$

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## Glossary

$(p_k)_{k \geq 0}$ : offspring distribution of the cell population

$\mathbb{T}$ : Cell tree in Ulam–Harris labeling

$\mathbb{T}_n$ : Subpopulation at time (generation)  $n$  [ $= \{v \in \mathbb{T} : |v| = n\}$ ]

$N_v$ : Number of daughter cells of cell  $v \in \mathbb{T}$

$\mathcal{T}_n$ : Cell population size at time  $n$  [ $= \#\mathbb{T}_n = \sum_{|v|=n} N_v$ ]

$\mathcal{T}_{n,k}$ : Number of cells at time  $n$  containing  $k$  parasites

$\mathcal{T}_n$ : The infinite vector  $(\mathcal{T}_{n,0}, \mathcal{T}_{n,1}, \dots)$

$\mathcal{T}_n^*$ : The infinite vector  $(\mathcal{T}_{n,1}, \mathcal{T}_{n,2}, \dots)$

$Z_v$ : Number of parasites in cell  $v$

$BT$ : Branching within branching tree [ $= (Z_v)_{v \in \mathbb{V}}$ ]

$\mathcal{Z}_n$ : Number of parasites at time  $n$  [ $= \sum_{v \in \mathbb{T}_n} Z_v$ ]

$\mathbb{T}_n^*$ : Population of contaminated cells at time  $n$  [ $\{v \in \mathbb{T}_n : Z_v > 0\}$ ]

$\mathcal{T}_n^*$ : Number of contaminated cells at time  $n$  [ $= \#\mathbb{T}_n^*$ ]

$X_{i,v}^{(\bullet,k)}$ : Given that the cell  $v$  has  $k$  daughter cells  $v_1, \dots, v_k$ , the  $j$ th component  $X_{i,v}^{(j,k)}$  of this  $\mathbb{N}_0^k$ -valued random vector gives the number of offspring of the  $i$ th parasite in  $v$  which is shared into daughter cell  $v_j$

$X^{(\bullet,k)}$ : Generic copy of the  $X_{i,v}^{(\bullet,k)}$ ,  $i \in \mathbb{N}$ ,  $v \in \mathbb{V}$  with components  $X^{(j,k)}$

$\mu_{j,k} = \mathbb{E}X^{(j,k)}$

$\gamma$ : Mean number of offspring per parasite [ $= \mathbb{E}\mathcal{Z}_1 = \sum_{k \geq 1} p_k \sum_{j=1}^k \mu_{j,k}$ ]

$v$ : Mean number of daughter cells per cell [ $= \mathbb{E}N = \sum_{k \geq 1} p_k$ ]

$(V_n)_{n \geq 0}$ : Infinite random cell line in  $\mathbb{V}$  starting at  $V_0 = \emptyset$

- $(Z'_n)_{n \geq 0}$ : Associated branching process in i.i.d. random environment (ABPRE)  $\Lambda = (\Lambda_n)_{n \geq 0}$  and a copy of  $(Z_{V_n})_{n \geq 0}$
- $(\widehat{V}_n)_{n \geq 0}$ : Infinite parasitic random cell line in  $\mathbb{V}$  starting at  $\widehat{V}_0 = \emptyset$ , where  $\widehat{V}_n$  denotes the cell containing the spinal parasite picked at time  $n$
- $\widehat{N}_v$ : Number of daughter cells of cell  $v$  in the size-biased tree  $\widehat{\mathbb{T}}$
- $\widehat{Z}_v$ : Number of parasites in cell  $v$  in the size-biased tree  $\widehat{T}$
- $\widehat{T}_n$ : Number of daughter cells of the spinal cell  $\widehat{V}_n$
- $\widehat{BT}$ : Size-biased branching withing branching tree  $[= (\widehat{Z}_v)_{v \in \mathbb{V}}]$
- $\widehat{\mathcal{Z}}_n$ : Number of parasites at time  $n$  under size-biasing  $[= \sum_{v \in \widehat{\mathbb{T}}_n} \widehat{Z}_v]$
- $\widehat{W}_n$ : Normalized number of parasites at time  $n$   $[= \gamma^{-n} \widehat{\mathcal{Z}}_n = w_n \circ \widehat{BT}]$
- $(\widehat{Z}'_n)_{n \geq 0}$ : Associated branching process in i.i.d. random environment  $\Delta = (\Delta_n)_{n \geq 0}$  with immigration (ABPREI) and a copy of  $(\widehat{Z}_{\widehat{V}_n} - 1)_{n \geq 0}$