

## Branching processes evolving in asynchronous environments

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### Abstract

A pure decomposable two-type branching process in an asynchronous random environment is considered under the quenched approach. We suppose that particles of this process produce offspring of their own type only and that the restriction of the evolution of the population to any of the two types leads to a single-type branching process evolving in random environment generated by a sequence of independent probability laws. Assuming that both processes are (individually) critical and that the logarithms of the mean number of offspring of different types are negatively correlated in each generation, we prove a Yaglom-type conditional limit theorem for the number of individuals in the process at a distant moment given survival of both types up to this moment. It is shown that the population sizes of both types are subject to very big oscillations which may be treated as bottlenecks and periods of growth in a model of predator-pray coexistence.

Keywords: bottlenecks, branching processes, conditional limit theorems

### 1. Model

Let  $\mathcal{M}$  be the space of probability measures on  $\mathbb{N}_0 := \{0, 1, 2, \dots\}$  and let  $\mathbf{Q} := (Q_1, Q_2)$  be a vector whose components take values in  $\mathcal{M}$ . An infinite sequence  $\mathcal{Q} = (\mathbf{Q}(1), \mathbf{Q}(2), \dots)$  of independent identically distributed (i.i.d.) copies of  $\mathbf{Q}$  is said to form a *random environment*. A sequence of  $\mathbb{N}_0 \times \mathbb{N}_0$ -valued random vectors  $\mathbf{Z}(0), \mathbf{Z}(1), \dots$  is called a two-type *pure decomposable branching process in the random environment*  $\mathcal{Q}$ , if  $\mathbf{Z}(0) = (Z_1(0), Z_2(0))$  is independent of  $\mathcal{Q}$  and, given  $\mathcal{Q}$ , the process  $\mathcal{Z} = (\mathbf{Z}(0), \mathbf{Z}(1), \dots)$  with components  $\mathbf{Z}(k) = (Z_1(k), Z_2(k))$ ,  $k = 0, 1, \dots$  is a Markov chain such that for every  $n \geq 1$ ,  $(z_1(n-1), z_2(n-1)) \in \mathbb{N}_0 \times \mathbb{N}_0$  and  $\mathbf{q}(n) = (q_1(n), q_2(n)) \in \mathcal{M} \times \mathcal{M}$

$$\begin{aligned} \mathcal{L}(\mathbf{Z}(n) \mid \mathbf{Z}(n-1) = (z_1(n-1), z_2(n-1)), \mathcal{Q} = (\mathbf{q}(1), \mathbf{q}(2), \dots)) \\ = \mathcal{L}(\xi_{1,1}(n) + \dots + \xi_{1,z_1(n-1)}(n), \xi_{2,1}(n) + \dots + \xi_{2,z_1(n-1)}(n)) \end{aligned}$$

where  $\xi_{i,1}(n), \xi_{i,2}(n), \dots$  are i.i.d. random variables with distribution  $q_i(n)$ . Thus,

$$Z_i(n) := \sum_{j=1}^{Z_i(n-1)} \xi_{i,j}(n), \quad i = 1, 2,$$

where, given the environment,  $\mathbf{Z}(k)$ ,  $k = 0, 1, \dots$  is an ordinary inhomogeneous decomposable two-type Galton-Watson process and  $\mathbf{q}(n)$  is the vector specifying the distribution of the offspring sizes of individuals of the respective types at generation  $n - 1$ . Observe that particles in this process produce offspring of their own type only. We denote by  $\mathbf{P}$  the corresponding probability measure on the underlying probability space and let  $\mathbf{P}_{\mathcal{Q}}(\cdot) := \mathbf{P}(\cdot \mid \mathcal{Q})$  and  $\mathbf{E}_{\mathcal{Q}}[\cdot] := \mathbf{E}[\cdot \mid \mathcal{Q}]$  be

the probability and expectation given the environment  $\mathcal{Q}$ . The model described is a two-type version of the branching processes in random environment introduced by Smith and Wilkinson (1969).

## 2. Basic conditions

Let

$$X_i(k) := \log \mathbf{E}_{\mathcal{Q}} [\xi_{i,1}(k)], \quad k = 1, 2, \dots$$

be the logarithms of the conditional expectations of the offspring size of particles of types  $i = 1, 2$  given the environment. We assume that the following condition is valid:

**Condition A1.** For any  $k = 1, 2, \dots$

$$X_2(k) = -X_1(k) \quad \mathbf{P}\text{-a.s.}$$

Thus, the processes  $Z_i(n), i = 1, 2$  are dependent through the environment only and, according to Condition A1, evolve asynchronously: a favorable environment for the population generated by the type 1 particles at moment  $n$  (meaning  $X_1(n) > 0$ ) is unfavorable for the the population generated by the type 2 particles at moment  $n$  (meaning  $X_2(n) < 0$ ) and vice versa.

Condition A1 has an intuitive justification within the following predator-pray model in a random environment with nonoverlapping generations where the numbers of predators and prays in generation  $n \geq 1$  are equal to  $Z_1(n)$  and  $Z_2(n)$ , respectively. In this predator-pray system the offspring number of a particle of our branching process in random environment is treated as the number of her children attaining the reproduction age. Now Condition A1 may be viewed as follows. If the environment is favorable for the reproduction of the predators of the  $n$ th generation (i.e.,  $X_1(n) > 0$ ) then the average number of children per predator which have a chance to survive up to the reproduction age in generation  $n$  is greater than 1. This leads to a heavy pressure of predators on the pray population of the  $n$ th generation expressed within the framework of our model as the assumption that the average number of children per pray attaining the reproduction age is less than 1 (i.e.,  $X_2(n) < 0$ ).

If, however, the environment is not favorable for the predators of the  $n$ th generation ( $X_1(n) < 0$ ) then the average number of children per predator which have a chance to survive up to the reproduction age in generation  $n$  is less than 1 and, in view of a weak predator pressure on the pray population, the average number of children per pray attaining the reproduction age in generation  $n$  exceeds 1 (i.e.,  $X_2(n) > 0$ ).

Introduce a random walk

$$S(0) := 0, \quad S(n) := \sum_{k=1}^n X_1(k).$$

In the sequel we use the notation  $X = X_1(1)$ . Note that by Condition A1

$$\mathbf{E} [Z_1(n)|\mathcal{Q}] = e^{S(n)}, \quad \mathbf{E} [Z_2(n)|\mathcal{Q}] = e^{-S(n)}. \tag{1}$$

**Condition A2.** The distribution of  $X$  is nonlattice and there are numbers  $c_n \rightarrow \infty$  such that the sequence  $S(n)/c_n$  converges in distribution to an  $\alpha$ -stable random variable  $Y$  with  $\alpha \in (0, 1) \cup (1, 2]$  and positivity parameter  $\rho := \mathbf{P} (Y > 0) \in (0, 1)$  such that either  $\alpha\rho < 1$  or  $\mathbf{E}X^2 < \infty$ .

Condition A2 means, in particular, that  $\{S(n), n \geq 0\}$  is an oscillating random walk and, therefore,  $Z_i(n), i = 1, 2$  are critical processes according to the classification given by Afanasyev et al. (2005).

Introduce the random variables

$$L_n := \min(S(1), \dots, S(n)), \quad \tau(n) := \min\{0 \leq k \leq n : S(k) = \min(0, L_n)\},$$

and

$$M_n := \max(S(1), \dots, S(n)), \quad \mu(n) := \max\{1 \leq k \leq n : S(k) = M_n\}.$$

It is known (see, for instance, Spitzer (1964), Section 20) that under Condition A2 for any  $t \in (0, 1]$ , as  $n \rightarrow \infty$

$$\frac{\tau(nt)}{n} \xrightarrow{d} \tau_t, \quad \frac{\mu(nt)}{n} \xrightarrow{d} \mu_t,$$

where  $t^{-1}\tau_t$  and  $t^{-1}\mu_t$  are random variables subject to the generalized arcsine distributions on  $[0, 1]$  with densities

$$\frac{1}{\Gamma(\rho)\Gamma(1-\rho)} \frac{1}{x^\rho(1-x)^{1-\rho}} \quad \text{and} \quad \frac{1}{\Gamma(\rho)\Gamma(1-\rho)} \frac{1}{x^{1-\rho}(1-x)^\rho}.$$

Denote by  $I\{A\}$  the indicator of the event  $A$ .

Let

$$\gamma_0 := 0, \quad \gamma_{j+1} := \min\{n > \gamma_j : S(n) < S(\gamma_j)\}$$

and

$$\Gamma_0 := 0, \quad \Gamma_{j+1} := \min\{n > \Gamma_j : S(n) > S(\Gamma_j)\}, \quad j \geq 0,$$

be the strict descending and ascending ladder epochs of  $\{S(n), n \geq 0\}$ . Given  $S(0) = 0$ , we specify the renewal functions  $U : \mathbb{R} \rightarrow \mathbb{R}_+$  and  $V : \mathbb{R} \rightarrow \mathbb{R}_+$  by the equalities

$$U(x) := I\{0 < x\} + \sum_{j=1}^{\infty} \mathbf{P}(S(\Gamma_j) < x), \quad x \in \mathbb{R}_+ := [0, \infty), \quad U(x) = 0, \quad x < 0,$$

$$V(x) := \sum_{j=0}^{\infty} \mathbf{P}(S(\gamma_j) \geq -x), \quad x \in \mathbb{R}_+, \quad V(x) = 0, \quad x < 0,$$

(see Vatutin and Dyakonova (2004) where some properties of the functions are discussed in more detail). Let, further,

$$\Theta_i(r) := \frac{\mathbf{E}_{\mathcal{Q}} \left[ \xi_{i,1}^2(1) I\{\xi_{i,1}(1) \geq r\} \right]}{(\mathbf{E}_{\mathcal{Q}} [\xi_{i,1}(1)])^2}, \quad r \in \mathbb{N}_0, \quad i = 1, 2.$$

**Condition A3.** For an  $\varepsilon_0 > 0$ , an  $r \in \mathbb{N}_0$  and  $i = 1, 2$

$$\mathbf{E} \left[ (\log^+ \Theta_i(r))^{\max(1/\rho, 1/(1-\rho)) + \varepsilon_0} \right] < \infty$$

and

$$\mathbf{E} \left[ (U(-X) + V(X)) (\log^+ \Theta_i(r))^{1+\varepsilon_0} \right] < \infty.$$

### 3. Results

Denote by  $\mathbf{L} = \{\mathcal{L}\}$  the set of all (may be, improper) probability laws  $\mathcal{L}(\cdot) = \mathcal{L}_\xi(\cdot)$  of random  $b$ -dimensional vectors  $(\xi_1, \dots, \xi_b)$  with nonnegative components and let  $\mathbf{L}^+ \subset \mathbf{L}$  be the set of all probability laws in  $\mathbf{L}$  corresponding to the random vectors  $(\xi_1, \dots, \xi_b)$  with  $\mathbf{P}(\xi_i > 0, i = 1, \dots, b) = 1$ . Let  $\mathbf{x}, \mathbf{y} \in [0, \infty)^b$  and let  $\Phi = \{\Phi\}$  and  $\Phi^+ \subset \Phi$  be the spaces of Laplace transforms  $\Phi(\mathbf{x}) = \int e^{-(\mathbf{x}, \mathbf{y})} \mathcal{L}(d\mathbf{y})$  of the laws from  $\mathbf{L}$  and  $\mathbf{L}^+$  endowed with the metric  $d_\Lambda, \Lambda > 1$ :

$$d_\Lambda(\Phi^*, \Phi^{**}) := \sup_{\mathbf{x} \in [1, \Lambda]^b} |\Phi^*(\mathbf{x}) - \Phi^{**}(\mathbf{x})|. \tag{2}$$

Let  $\Phi_N(\mathbf{x}) = \int e^{-(\mathbf{x}, \mathbf{y})} \mathcal{L}_N(d\mathbf{y}), N = 1, 2, \dots$  be a sequence of elements of  $\Phi$ . Clearly, the convergence  $\Phi_N \rightarrow \Phi, N \rightarrow \infty$ , in metric  $d_\Lambda$  is equivalent to the weak convergence of distributions  $\mathcal{L}_N \xrightarrow{w} \mathcal{L}$  corresponding to the Laplace transforms  $\Phi_N$  and  $\Phi$ . Besides, all the metrics in the set  $\{d_\Lambda, \Lambda > 1\}$  are equivalent.

Let  $\mathbf{P}$  be a measure specified on the Borel  $\sigma$ -algebra of the metric space  $\Phi$  and  $\Phi_N(\mathbf{x}), N = 1, 2, \dots$  be a sequence of i.i.d. elements of  $\Phi$  selected in accordance with  $\mathbf{P}$ . We say that the sequence of (random) measures  $\mathcal{L}_N(d\mathbf{y})$  converges weakly, as  $N \rightarrow \infty$  to a random measure  $\mathcal{L}(d\mathbf{y})$  with Laplace transform  $\Phi(\mathbf{x})$  and write

$$\mathcal{L}_N(\cdot) \Rightarrow \mathcal{L}(\cdot)$$

if for any nonrandom bounded function  $J: \mathbb{R}^b \rightarrow \mathbb{R}$  and any nonrandom bounded continuous function  $g: \mathbb{R} \rightarrow \mathbb{R}$

$$\lim_{N \rightarrow \infty} \mathbf{E} \left[ g \left( \int J(\mathbf{y}) \mathcal{L}_N(d\mathbf{y}) \right) \right] = \mathbf{E} \left[ g \left( \int J(\mathbf{y}) \mathcal{L}(d\mathbf{y}) \right) \right]$$

or, in terms of the respective Laplace transforms that

$$\lim_{N \rightarrow \infty} \mathbf{E} [g(\Phi_N(\mathbf{x}))] = \mathbf{E} [g(\Phi(\mathbf{x}))].$$

In what follows  $\mathbf{P}$  is the measure specifying the random environment  $\mathcal{Q}$  for our decomposable two-type branching process.

Denote

$$\zeta_1(n) := e^{-S(\tau(n))} \mathbf{P}_\mathcal{Q}(Z_1(n) > 0), \quad \zeta_2(n) := e^{S(\mu(n))} \mathbf{P}_\mathcal{Q}(Z_2(n) > 0),$$

and let, for  $x \in \mathbb{R}_+$  and  $0 \leq k \leq n$

$$\Phi_{k,n}^{(i)}(x) := \mathbf{E}_\mathcal{Q} \left[ \exp \left\{ -x \frac{Z_i(k)}{\mathbf{E}_\mathcal{Q}[Z_i(k) | Z_i(k) > 0]} \right\} \mid Z_i(n) > 0 \right], \quad i = 1, 2. \tag{3}$$

**Theorem 1** Under Conditions A1-A3 as  $n \rightarrow \infty$

$$(\zeta_1(n), \zeta_2(n)) \xrightarrow{d} (\zeta_1, \zeta_2), \tag{4}$$

where the random variables  $\zeta_i$  are i.i.d. and take values in  $(0, 1]$  with probability 1. In addition, for any  $t \in (0, 1]$ , as  $n \rightarrow \infty$

$$\begin{aligned} (\Phi_{nt,n}^{(1)}(x_1), \Phi_{nt,n}^{(2)}(x_2)) &\Rightarrow (\Phi_1(x_1), \Phi_2(x_2)) I \{\max\{\tau_1, \mu_1\} < t\} \\ &\quad + (\Phi_1(x_1), -\Phi'_2(x_2)) I \{\tau_1 < t < \mu_1\} \\ &\quad + (-\Phi'_1(x_1), \Phi_2(x_2)) I \{\mu_1 < t < \tau_1\} \\ &\quad - (\Phi'_1(x_1), \Phi'_2(x_2)) I \{\min\{\tau_1, \mu_1\} > t\}, \end{aligned} \tag{5}$$

where  $\Phi_i(x_i), i = 1, 2$  are the (random) Laplace transforms of proper random variables. Moreover,  $\Phi_i(x_i), i = 1, 2$  are independent of each other and of  $\mu_1, \tau_1$  and  $\tau_1$ .

**Remark 1.** The facts that  $\zeta_1(n) \xrightarrow{d} \zeta_1$  and

$$\Phi_{nt,n}^{(1)}(x_1) \Rightarrow \Phi_1(x_1)I\{\tau_1 < t\} - \Phi_1'(x_1)I\{t < \tau_1\}$$

have been established by Vatutin and Dyakonova (2004). An interesting feature of the decomposable process under consideration is that the limiting vectors in (4) and (5) are independent while the prelimiting ones are, of course, dependent.

**Remark 2.** One may prove that if the reproduction generating functions of particles of both types are fractional-linear with probability 1 then

$$\Phi_i(x) = \frac{1}{1+x}, \quad \Phi_i'(x) = \frac{1}{(1+x)^2}, \quad i = 1, 2.$$

For  $s \in [0, 1]$  let

$$\varphi_{k,n}^{(1)}(s) := \mathbf{E}_{\mathcal{Q}} \left[ s^{Z_1(k)} \mid Z_1(n) > 0 \right].$$

Now we formulate a statement describing the offspring size distribution of both types at random moments  $\tau(nt), 0 < t \leq 1$ , given  $\{Z_1(n) > 0, Z_2(n) > 0\}$ .

**Theorem 2** Under Conditions A1-A3 for  $t \in (0, 1]$  as  $n \rightarrow \infty$

$$\begin{aligned} \left( \varphi_{\tau(nt),n}^{(1)}(s), \Phi_{\tau(nt),n}^{(2)}(x) \right) &\Rightarrow (\varphi_1(s), \Phi_2(x)) I\{\mu_1 < \tau_t = \tau_1\} \\ &\quad + (\varphi_1(s), -\Phi_2'(x)) I\{\mu_1 > \tau_t = \tau_1\} \\ &\quad + (\varphi^*(s), \Phi_2(x)) I\{\mu_1 < \tau_t < \tau_1\} \\ &\quad + (\varphi^*(s), -\Phi_2'(x)) I\{\tau_t < \min\{\tau_1, \mu_1\}\}, \end{aligned} \quad (6)$$

where  $\varphi_1(s), \varphi^*(s)$  are the (random) generating functions of proper distributions with supports in the set  $\{1, 2, \dots\}$  and  $\Phi_2(x)$  has the same distribution as in Theorem 1. In addition,  $\varphi_1(s), \varphi^*(s)$  and  $\Phi_2(x)$  are mutually independent and are independent of  $\mu_1, \tau_t, \tau_1$ .

**Remark 3.** The fact that

$$\varphi_{\tau(nt),n}^{(1)}(s) \Rightarrow \varphi_1(s)I\{\tau_t = \tau_1\} + \varphi^*(s)I\{\tau_t < \tau_1\}$$

has been established by Vatutin and Dyakonova (2006).

**Remark 4.** In view of (4) and (1) the second statement of Theorem 1 means, roughly speaking, that, given both types survive up to moment  $n$ , the number of type 1 individuals at moment  $nt$  is proportional to  $\exp\{S(nt) - S(\tau(nt))\}$  while the number of type 2 individuals is proportional to  $\exp\{S(\mu(nt)) - S(nt)\}$ . Note that the population sizes of both types are of order  $\exp\{O(\sqrt{n})\}$  if  $\mathbf{E}X_1(1) < \infty$ . On the other hand, Theorem 2 shows, under the same survival assumption for both types up to moment  $n \rightarrow \infty$ , that the number of type 1 individuals at moment  $\tau(nt)$  was small (the limiting distribution of  $Z_1(\tau(nt))$  is discrete) while the mean size of the type 2 population was very big (proportional to  $\exp\{S(\mu(\tau(nt))) - S(\tau(nt))\}$ ). Of course, a similar picture (with interchanging types 1 and 2) takes place at moments  $\mu(nt)$ . In fact, one can show that such phenomena take place at moments  $\tau(nt) \pm m, \mu(nt) \pm m$  for any fixed  $m = 1, 2, \dots$  (see Vatutin and Liu (2012) for more detail).

Coming back to the predator-pray model in random environment described earlier we see that the phenomena may be treated, for instance, as bottlenecks for the pray population when the predator population is large, periods of rapid growth of the pray population when the predator population is small and periods of a relatively "peaceful" coexistence of the populations when the amount of individuals in each population is large.

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