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## ON THE EXTINCTION TIMES OF VARYING AND RANDOM ENVIRONMENT BRANCHING PROCESSES

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### Abstract

Bounds are derived for the probability of extinction by the  $n$ th generation for a branching process in a varying environment. From these bounds, necessary and sufficient conditions are established for such a process to become extinct with probability one. The extinction time of a random environment branching process in which the environmental random variables are independent but not necessarily identically distributed is stochastically bounded by the extinction times of two varying environment processes.

BRANCHING PROCESSES; VARYING ENVIRONMENT; RANDOM ENVIRONMENT; EXTINCTION TIME; PROBABILITY OF EXTINCTION; POISSON OFFSPRING

### 1. Introduction

In this paper we derive bounds on the extinction time distributions of two generalizations of the familiar Galton-Watson branching process — a non-homogeneous (varying environment) branching process and a branching process with random environment consisting of independent but non-identically distributed random variables. These bounds are used to obtain some results on the probability of extinction of such processes.

Suppose that the distribution for the offspring of an individual existing in the  $j$ th generation of the evolution of a population is represented by the probability generating function (p.g.f.)  $g_j(s)$ ,  $j \geq 0$ . If each individual produces offspring independently of the past and present history of the population, then the p.g.f. for the population size  $Z_n$  at the  $n$ th generation is

$$\pi_n(s) = [g_0(g_1(\cdots g_{n-1}(s)\cdots))]^{Z_0}, \quad 0 \leq s \leq 1,$$

given the initial size  $Z_0$  (which without loss of generality we assume equals one). A discrete time branching process of this nature has been referred to as a non-homogeneous Galton-Watson process, or a branching process with varying environment. Jagers (1974) showed that many of the limiting characteristics of the Galton-Watson process are retained by the varying environment process. In Section 2, we obtain bounds for  $P(T \leq n) = \pi_n(0)$  that depend on  $\{g'_j(1), g''_j(1), g''_j(0), 0 \leq j \leq n-1\}$ , where  $T$  is the extinction time of the varying environment process. As a direct consequence of these bounds, we show in Theorem 2 that under cer-

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tain conditions the probability of extinction  $q = 1$  if and only if  $\sum_{j=0}^{\infty} (\prod_{i=0}^j g'_i(1))^{-1} = \infty$ .

A branching process with random environment is characterized by an environmental stochastic process  $\{\zeta_j, j \geq 0\}$  whose realization determines a sequence of generational offspring p.g.f.'s  $\{g_j(\zeta_j; s), j \geq 0\}$ . That is, given  $\bar{\zeta} = \{\zeta_0, \zeta_1, \dots\}$ , the process develops as a varying environment process, with p.g.f.

$$\pi_n(\bar{\zeta}; s) = [g_0(\zeta_0; \dots; g_{n-1}(\zeta_{n-1}; s) \dots)]^{Z_0}$$

for  $Z_n$ . Unconditionally, the p.g.f. for  $Z_n$  is  $\pi_n(s) = E\pi_n(\bar{\zeta}; s)$ , so that  $P(T \leq n) = \pi_n(0)$ . Athreya and Karlin (1971) derived several properties of such a process under general settings for the environmental process. In Section 3, we obtain bounds for the extinction time distribution of some branching processes with independent non-identically distributed environmental random variables. These bounds correspond to bounding stochastically the extinction time of such a process by the extinction times of two varying environment processes. An example is given for the Poisson offspring distribution.

We begin by considering the varying environment process with fractional linear offspring generating functions, which are p.g.f.'s of the form

$$f(s) = 1 - \frac{b}{1-c} + \frac{bs}{(1-cs)}, \quad 0 \leq s \leq 1,$$

where  $0 \leq b \leq 1$ ,  $0 \leq c < 1$ , and  $b + c \leq 1$ . When the offspring p.g.f. for the  $j$ th generation in a branching process with varying environment is  $f_j(s)$ ,  $j \geq 0$ , then  $\pi_n(s) = f_0(\dots f_{n-1}(s) \dots)$  also has the fractional linear form. By composing  $h_j(s) = f'_j(1)s/[1 + \frac{1}{2}f''_j(1)s/f'_j(1)]$  and noting that  $\pi_n(s) = 1 - h_0(\dots h_{n-1}(1-s) \dots)$ , it is easily verified that

$$(1.1) \quad \pi_n(s) = 1 - \left[ \left( (1-s) \prod_{j=0}^{n-1} f'_j(1) \right)^{-1} + \frac{1}{2} \sum_{j=0}^{n-1} \left( f''_j(1)/f'_j(1) \prod_{i=0}^j f'_i(1) \right) \right]^{-1}.$$

Hence,

$$(1.2) \quad P(T \leq n) = 1 - \left[ \left( \prod_{j=0}^{n-1} f'_j(1) \right)^{-1} + \frac{1}{2} \sum_{j=0}^{n-1} \left( f''_j(1)/f'_j(1) \prod_{i=0}^j f'_i(1) \right) \right]^{-1}.$$

Results (1.1) and (1.2) are exploited in Sections 2 and 3 in deriving the main results of the paper.

### 2. Bounds for varying environment processes

We consider now a varying environment process in which the offspring p.g.f.'s are allowed to have a very arbitrary form. A Taylor expansion is used in Lemma 1 to obtain a lower bound for  $\pi_n(s)$ , and hence for  $P(T \leq n)$ . For convenience, set  $P_n = \prod_{j=0}^{n-1} g'_j(1)$ .

**Lemma 1.** For any sequence of p.g.f.'s  $\{g_j(s), j \geq 0\}$  satisfying  $g'_j(1) < \infty$ ,  $j \geq 0$ ,

$$(2.1) \quad \pi_n(s) \geq 1 - \left[ (P_n(1-s))^{-1} + \frac{1}{2} \sum_{j=0}^{n-1} (g''_j(0)/g'_j(1)P_{j+1}) \right]^{-1},$$

$0 \leq s \leq 1$  and  $n \geq 1$ .

*Proof.* Let  $\pi_{i,n}(s) = g_i(g_{i+1}(\dots g_{n-1}(s)\dots))$ ,  $i = 0, \dots, n-1$ , and let  $\pi_{n,n}(s) = s$ . Then,

$$\pi_n(s) = \pi_{0,n}(s) = g_0(\pi_{1,n}(s)).$$

By Taylor's Theorem,

$$\begin{aligned} 1 - \pi_n(s) &= \pi_n(1) - \pi_n(s) = g_0(1) - g_0(\pi_{1,n}(s)) \\ &= (1 - \pi_{1,n}(s))g'_0(1) - \frac{(1 - \pi_{1,n}(s))^2}{2} g''_0(\eta_0), \end{aligned}$$

where  $\pi_{1,n}(s) < \eta_0(s) < 1$ . Thus,

$$(2.2) \quad \begin{aligned} [1 - \pi_n(s)]^{-1} &= \left\{ [1 - \pi_{1,n}(s)]g'_0(1) \left[ 1 - \frac{(1 - \pi_{1,n}(s))g''_0(\eta_0)}{2g'_0(1)} \right] \right\}^{-1} \\ &= \frac{1}{[1 - \pi_{1,n}(s)]g'_0(1)} + \frac{[1 - \pi_{1,n}(s)]g''_0(\eta_0)}{2[1 - \pi_n(s)]g'_0(1)}. \end{aligned}$$

Now

$$1 - \pi_n(s) = g_0(1) - g_0(\pi_{1,n}(s)) \leq (1 - \pi_{1,n}(s))g'_0(1),$$

or

$$\frac{1 - \pi_{1,n}(s)}{1 - \pi_n(s)} \geq \frac{1}{g'_0(1)}.$$

Thus, from (2.2),

$$\frac{1}{1 - \pi_n(s)} \geq \frac{1}{[1 - \pi_{1,n}(s)]g'_0(1)} + \frac{g''_0(\eta_0)}{2g'_0(1)^2}.$$

Similarly, by recurrence on the term  $[1 - \pi_{i,n}(s)]^{-1}$ , we get

$$\frac{1}{1 - \pi_n(s)} \geq \frac{1}{(1-s)g'_0(1) \dots g'_{n-1}(1)} + \frac{1}{2} \sum_{j=0}^{n-1} \frac{g''_j(\eta_j)}{g'_j(1)^2 g'_{j-1}(1) \dots g'_0(1)},$$

where

$$\pi_{j+1,n}(s) < \eta_j < 1,$$

or

$$\pi_n(s) \geq 1 - \left[ \frac{1}{(1-s)P_n} + \frac{1}{2} \sum_{j=0}^{n-1} \frac{g''_j(0)}{g'_j(1)P_{j+1}} \right]^{-1}.$$

since  $g''_j(\eta_j) \geq g''_j(0)$ .

An upper bound of  $1 - [(P_n(1-s))^{-1} + \frac{1}{2} \sum_{j=0}^{n-1} (g''_j(1)/g'_j(0)P_{j+1})]^{-1}$  is obtained for  $\pi_n(s)$  using a similar argument. We shall not use it, though, due to its uselessness for  $n \geq j$  if  $g'_j(0) = 0$ . Using (1.1), it is easy to exploit a result on f.l.g.f. bounds for a p.g.f. to obtain another upper bound for  $\pi_n(s)$ .

*Lemma 2.* For any sequence of p.g.f.'s  $\{g_j(s), j \geq 0\}$  satisfying  $g''_j(1) < \infty, j \geq 0$ .

$$(2.3) \quad \pi_n(s) \leq 1 - \left[ (P_n(1-s))^{-1} + \sum_{j=0}^{n-1} (g''_j(1)/g'_j(1)P_{j+1}) \right]^{-1}, \quad 0 \leq s \leq 1 \text{ and } n \geq 1.$$

*Proof.* Agresti (1974) showed that any p.g.f.  $g_j(s)$  with  $g''_j(1) < \infty$  is bounded above for  $0 \leq s \leq 1$  by the f.l.g.f.  $f_j(s)$  with  $f'_j(1) = g'_j(1)$  and  $f''_j(1) = 2g''_j(1)$ . Now  $g_j(s) \leq f_j(s), 0 \leq s \leq 1$  and  $j \geq 0$ , and the fact that these are monotone increasing functions implies that

$$\pi_n(s) = g_0(\dots g_{n-1}(s) \dots) \leq f_0(\dots f_{n-1}(s) \dots), \quad 0 \leq s \leq 1 \text{ and } n \geq 1,$$

and by (1.1),

$$f_0(\dots f_{n-1}(s) \dots) = 1 - \left[ (P_n(1-s))^{-1} + \sum_{j=0}^{n-1} (g''_j(1)/g'_j(1)P_{j+1}) \right]^{-1}.$$

If  $g'_j(1) \leq 1$  all  $j \geq 0$ , then the lower bounding f.l.g.f.'s derived by Agresti (1974) can be used in the same way to obtain a lower bound for  $\pi_n(s)$  which is better than (2.1). Letting  $s = 0$  in the inequalities on compositions of p.g.f.'s in Lemmas 1 and 2, we have relatively simple bounds for the probability of extinction by the  $n$ th generation for a branching process with varying environment.

*Theorem 1.* For a varying environment branching process with offspring p.g.f.'s  $\{g_j(s), j \geq 0\}$  satisfying  $g''_j(1) < \infty, j \geq 0$ ,

$$(2.4) \quad 1 - \left[ P_n^{-1} + \frac{1}{2} \sum_{j=0}^{n-1} (g''_j(0)/g'_j(1)P_{j+1}) \right]^{-1} \leq P(T \leq n) \leq 1 - \left[ P_n^{-1} + \sum_{j=0}^{n-1} (g''_j(1)/g'_j(1)P_{j+1}) \right]^{-1}.$$

Noting that (i)  $q = \lim_{n \rightarrow \infty} P(T \leq n)$  is the limit of an increasing sequence, so that

$$\inf_{n \geq 0} \left[ P_n^{-1} + \frac{1}{2} \sum_{j=0}^{n-1} (g''_j(0)/g'_j(1)P_{j+1}) \right]^{-1} = 0.$$

implies that  $q = 1$ , and that (ii) the upper bound for  $P(T \leq n)$  is a composition of f.l.g.f.'s evaluated at zero, so that  $q = 1$  implies that

$$\lim_{n \rightarrow \infty} \left[ P_n^{-1} + \sum_{j=0}^{n-1} (g''_j(1)/g'_j(1)P_{j+1}) \right]^{-1} = \infty,$$

we see next that Theorem 1 suggests necessary and sufficient conditions that  $q = 1$ , under certain assumptions.

*Theorem 2.* For a varying environment branching process with offspring p.g.f.'s  $\{g_j(s), j \geq 0\}$  satisfying  $\sup_{j \geq 0} (g_j''(0)/g_j'(1)) < \infty$  and  $\inf_{j \geq n_0} (g_j''(0)/g_j'(1)) > 0$  for some finite  $n_0 \geq 0$ ,

$$(2.5) \quad q = 1 \text{ if and only if } \sum_{j=0}^{\infty} P_{j+1}^{-1} = \infty.$$

As an example, if for some  $k \geq 0$ ,  $g'_{n+k}(1) \leq 1 + 1/(n + 1)$  for  $n \geq 0$ , (so that  $P_n \lesssim cn$  for some  $c > 0$ ), then  $q = 1$  under the other conditions on the offspring p.g.f.'s in Theorem 2. Such a model might be appropriate for a mutant gene which has a selective advantage which is gradually lost. This situation was treated by Pollak (1966) for the Poisson offspring case. Also if  $\sum_{j=0}^{\infty} (1 - g_j'(0)) = \infty$ , then  $q < 1$  implies that  $\lim_{n \rightarrow \infty} P_n = \infty$  (see Jagers (1974)), so that by Theorem 1,

$$1 - \left[ \frac{1}{2} \sum_{j=0}^{\infty} (g_j''(0)/g_j'(1)P_{j+1}) \right]^{-1} \leq q \leq 1 - \left[ \sum_{j=0}^{\infty} (g_j''(1)/g_j'(1)P_{j+1}) \right]^{-1}.$$

### 3. Some bounds for a random environment process

Suppose now that  $\{\zeta_j, j \geq 0\}$  is a sequence of independent non-identically distributed random variables that determines the succession of offspring p.g.f.'s  $\{g_j(\zeta_j; s), j \geq 0\}$  in a branching process with random environment. We shall assume, unless otherwise stated, that  $Z_0 = 1$  and that all expectations used in the results stated below exist and are finite.

For fixed  $\zeta_j, g_j(\zeta_j; s)$  is a convex function of  $s$  for  $j \geq 0$  and  $0 \leq s \leq 1$ , so by Jensen's inequality,

$$\begin{aligned} \pi_n(s) &= E\pi_n(\bar{\zeta}; s) = E[g_0(\zeta_0; g_1(\zeta_1; \dots; g_{n-1}(\zeta_{n-1}; s) \dots))] \\ &\geq Eg_0(\zeta_0; Eg_1(\zeta_1; \dots; g_{n-1}(\zeta_{n-1}; s) \dots)) \\ &\geq \dots \geq Eg_0(\zeta_0; Eg_1(\zeta_1; \dots; Eg_{n-1}(\zeta_{n-1}; s) \dots)). \end{aligned}$$

That is, the p.g.f. for  $Z_n$  in a branching process with independent non-identically distributed environment is bounded below by the composition of the  $n$  corresponding expected offspring p.g.f.'s. Thus,

$$(3.1) \quad P(T \leq n) \geq Eg_0(\zeta_0; \dots; Eg_{n-1}(\zeta_{n-1}; 0) \dots),$$

so that extinction of the random environment process occurs stochastically faster than extinction of the varying environment process with offspring p.g.f.'s  $\{Eg_j(\zeta_j; s), j \geq 0\}$ . Also, applying Theorem 1 to (3.1),

$$(3.2) \quad P(T \leq n) \geq 1 - \left[ \left( \prod_{j=0}^{n-1} m_j \right)^{-1} + \frac{1}{2} \sum_{j=0}^{n-1} \left( Eg'_j(\zeta_j; 0) / m_j \prod_{i=0}^j m_i \right) \right]^{-1},$$

where  $m_i = Eg'_i(\zeta_i; 1)$ . If  $Z_0 = k > 1$ , the p.g.f. for  $Z_n$  is

$$E[g_0(\zeta_0; \dots g_{n-1}(\zeta_{n-1}; s) \dots)]^k \geq [Eg_0(\zeta_0; \dots g_{n-1}(\zeta_{n-1}; s) \dots)]^k = [\pi_n(s)]^k$$

by Jensen's inequality, and (3.2) can be applied again.

Let  $P_n = \prod_{j=0}^{n-1} g'_j(\zeta_j; 1)$  now. Conditional upon  $\bar{\zeta} = \{\zeta_0, \zeta_1, \dots\}$ ,

$$\pi_n(\bar{\zeta}; s) \leq 1 - \left[ (P_n(1-s))^{-1} + \sum_{j=0}^{n-1} (g''_j(\zeta_j; 1) / g'_j(\zeta_j; 1) P_{j+1}) \right]^{-1}, \quad n \geq 1,$$

by Lemma 2. Thus, again using Jensen's inequality, the unconditional p.g.f. for  $Z_n$  is

$$(3.3) \quad \begin{aligned} \pi_n(s) &= E\pi_n(\bar{\zeta}; s) \leq 1 - \left\{ E \left[ (P_n(1-s))^{-1} + \sum_{j=0}^{n-1} (g''_j(\zeta_j; 1) / g'_j(\zeta_j; 1) P_{j+1}) \right] \right\}^{-1} \\ &= 1 - \left[ \left( \prod_{j=0}^{n-1} \mu_j(1-s) \right)^{-1} + \sum_{j=0}^{n-1} \left( E(g''_j(\zeta_j; 1) / g'_j(\zeta_j; 1)^2) / \prod_{i=0}^{j-1} \mu_i \right) \right]^{-1}, \end{aligned}$$

where  $\mu_i = (Eg'_i(\zeta_i; 1))^{-1}$ . Letting  $s = 0$ ,

$$(3.4) \quad P(T \leq n) \leq 1 - \left[ \left( \prod_{j=0}^{n-1} \mu_j \right)^{-1} + \sum_{j=0}^{n-1} \left( E(g''_j(\zeta_j; 1) / g'_j(\zeta_j; 1)^2) / \prod_{i=0}^{j-1} \mu_i \right) \right]^{-1}.$$

Now, comparing (3.4) to (1.2), we see that this random environment process becomes extinct stochastically slower than the varying environment process composed of f.l.g.f.'s with  $j$ th offspring mean  $\mu_j$  and  $j$ th second derivative at one equal to  $2\mu_j^2 E(g''_j(\zeta_j; 1) / g'_j(\zeta_j; 1)^2)$ .

In the i.i.d. case, (3.4) implies that the random environment process becomes extinct stochastically slower than the Galton-Watson process with a f.l.g.f. and offspring mean  $\mu = (Eg'_0(\zeta_0; 1))^{-1}$ , and (3.1) implies that the process becomes extinct stochastically faster than the Galton-Watson process with p.g.f.  $\pi_1(s) = Eg_0(\zeta_0; s)$ . Thus, simple bounds can be given for the percentiles and mean of the time to extinction using inequalities for the Galton-Watson process given by Agresti (1974).

It is easily seen that inequalities (3.2) and (3.4) imply an analogue of Theorem 2 for the probability of extinction  $q$  of a random environment process, for any  $Z_0 \geq 1$ : If  $\inf_{j \geq n_0} (Eg''_j(\zeta_j; 1) / Eg'_j(\zeta_j; 1)) > 0$  for some finite  $n_0 \geq 0$ , then

$$(3.5) \quad \sum_{j=0}^{\infty} \left( \prod_{i=0}^j m_i \right)^{-1} = \infty \text{ implies that } q = 1;$$

if  $\sup_{j \geq 0} E(g''_j(\zeta_j; 1) / g'_j(\zeta_j; 1)^2) < \infty$ , then

$$(3.6) \quad q = 1 \text{ implies that } \sum_{j=0}^{\infty} \left( \prod_{i=0}^j \mu_i \right)^{-1} = \infty.$$

**4. An application to Poisson branching processes**

The Poisson p.g.f.  $e^{\lambda(s-1)}$  has been widely used in branching process models for biological populations. However, some researchers (e.g., Kojima and Kelleher (1962)) have noted that offspring counts often display more variability than allowed for in a Poisson model, and have proposed using a negative binomial p.g.f. as an alternative. This is the model derived from the assumption that each individual produces offspring according to a Poisson distribution, but the mean  $\lambda$  varies among individuals according to the gamma density  $[\Gamma(\beta)]^{-1} \alpha^\beta \lambda^{\beta-1} e^{-\alpha\lambda}$ . Although the Galton-Watson process has been used most commonly in these models, the varying and random environment models would be more appropriate in many situations.

Consider the branching process with random environment in which the offspring distributions are Poisson with means  $\{\lambda_i, i \geq 0\}$  determined by a sequence of independent non-identically distributed gamma variables with parameters  $\{\alpha_i, \beta_i, i \geq 0\}$ . If  $Z_0 = 1$ , this random environment process becomes extinct stochastically slower than a varying environment process composed of f.l.g.f.'s with means  $\{\mu_i = (E\lambda_i^{-1})^{-1} = (\beta_i - 1)/\alpha_i, i \geq 0\}$ , by (3.4). Also, by (3.1) this process becomes extinct stochastically faster than the varying environment process with negative binomial p.g.f.'s  $[1 + (1-s)/\alpha_i]^{-\beta_i} = Ee^{\lambda_i(s-1)}$  and means  $\beta_i/\alpha_i = E\lambda_i, i \geq 0$ .

Now if for all  $i \geq 0$ ,  $\Theta_i$  is a convex set in which  $\zeta_i$  falls with probability one,  $g_i(\theta; s)$  is a convex function of  $\theta$  in  $\Theta_i$ , and  $E\zeta_i$  exists, then by Jensen's inequality,

$$Eg_0(\zeta_0; Eg_1(\zeta_1; \dots Eg_{n-1}(\zeta_{n-1}; s) \dots)) \geq g_0(E\zeta_0; g_1(E\zeta_1; \dots; g_{n-1}(E\zeta_{n-1}; s) \dots)),$$

$0 \leq s \leq 1$ . In particular, letting  $g_i(\lambda_i; s) = e^{\lambda_i(s-1)}$ , the varying environment process with negative binomial p.g.f.'s  $\{[1 + (1-s)/\alpha_i]^{-\beta_i} = Ee^{\lambda_i(s-1)}, i \geq 0\}$  itself becomes extinct stochastically faster than the varying environment process with Poisson p.g.f.'s  $\{e^{(E\lambda_i)(s-1)} = e^{(\beta_i/\alpha_i)(s-1)}, i \geq 0\}$ . As a special case, we see then that the Poisson offspring i.i.d. gamma environment process becomes extinct stochastically faster than the negative binomial offspring Galton-Watson process, which itself becomes extinct stochastically faster than the familiar Poisson offspring Galton-Watson process. For each process,  $E(Z_n | Z_0) = Z_0(\beta/\alpha)^n$ .

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