

EXTINCTION PROBABILITIES OF BRANCHING PROCESSES IN RANDOM ENVIRONMENTS

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Abstract

In the supercritical branching process with independent and identically distributed environments, it is shown that under certain regularity conditions there exists a parameter $\theta_0 > 0$ such that the probability of extinction starting with k individuals, q_k , is asymptotically of order not less than $k^{-\theta_0}$ and of smaller order than $k^{-\theta}$ for any $\theta < \theta_0$. An application to the optimal choice of strategy for minimizing the probability of extinction is mentioned.

1. Introduction and Statement of Results. We consider a branching process $\{Z_n; n = 0, 1, 2, \dots\}$, where Z_n denotes the population size at time n . Reproduction is affected by a sequence of environment variables $\bar{\zeta} = \{\zeta_0, \zeta_1, \zeta_2, \dots\}$ in the following way: for each n , conditional on $\bar{\zeta}$ and Z_0, Z_1, \dots, Z_n , the family sizes of the Z_n individuals at time n are independent random variables each with a distribution which is determined by ζ_n , and whose probability generating function (p.g.f.) we shall denote by ϕ_{ζ_n} . Then Z_{n+1} is just the sum of these family sizes.

Particular models for the environment variables are a sequence of independent identically distributed (i.i.d.) random variables (Smith and Wilkinson [4]) and, more generally, a stationary ergodic sequence (Athreya and Karlin [1]). In this paper, we consider only the Smith-Wilkinson model, although subsequent work has generalized the results to certain types of Athreya-Karlin model.

Let $q(\bar{\zeta})$ be the probability, conditional on $\bar{\zeta}$, that the population becomes extinct starting with a single ancestor:

$$q(\bar{\zeta}) = P(Z_n \rightarrow 0 \text{ as } n \rightarrow \infty \mid \bar{\zeta}, Z_0 = 1).$$

Then, because, conditional on the environment sequence, lines of descent are independent, the unconditional probability of extinction starting with k ancestors is

$$q_k = E[q(\bar{\zeta})^k]$$

where the expectation is taken over the environment.

We shall only be interested in the *supercritical* case where $P(q(\bar{\xi}) < 1) > 0$, or equivalently $q_k < 1$ for all $k \geq 1$; well-known sufficient conditions for supercriticality are

$$(i) \quad 0 < E[\log \phi'_\zeta(1)] < \infty$$

$$\text{and (ii) } E[-\log(1 - \phi_\zeta(0))] < \infty$$

and we shall adopt these conditions. Note that since the ζ_n are i.i.d. we may drop the suffix n in the above expressions.

Write $\xi = \log \phi'_\zeta(1)$, the log mean family size for environment ζ , and let $F(\theta) = E(e^{-\theta\xi})$, the Laplace transform of the distribution of ξ . By condition (i) above we have $F'(0) < 0$, and since F is convex there may exist $\theta_0 > 0$ such that $F(\theta_0) = 1$ and $F'(\theta_0) < \infty$; if θ_0 exists, it is unique. Under this condition, we have the following result.

Theorem. *Let $\theta_0 > 0$ exist such that $F(\theta_0) = 1$ and $F'(\theta_0) < \infty$ where F is as defined above. Then*

$$(a) \quad \liminf_{k \rightarrow \infty} k^\theta q_k > 0;$$

$$(b) \quad \text{if in addition } E[(1 - \phi_\zeta(0))^{-\theta_0}] < \infty, \text{ then}$$

$$q_k = o(k^{-\theta}) \text{ as } k \rightarrow \infty \text{ for all } \theta < \theta_0.$$

This gives a fairly precise idea of the asymptotic behaviour of q_k as $k \rightarrow \infty$. Note that in the Galton-Watson (constant environment) case, $\{q_k\}$ is a geometric sequence, which is possible since θ_0 does not exist, as $F(\theta) = e^{-\theta\xi}$ for some constant ξ . However, if the environment may be either favourable ($\xi > 0$) or unfavourable ($\xi < 0$) then the existence of θ_0 is not unreasonable as a regularity condition.

In Section 2 we shall prove the above theorem and in Section 3 we shall describe an application to an optimal strategy for survival.

2. Proof of the Theorem. Intuitively, if the population size is large then, by the law of large numbers, its fluctuations are almost entirely determined by the environment variables, and, more specifically, $\{\log Z_n\}$ behaves rather like a

random walk with increments $\log \phi'_{\zeta_n}(1) = \xi_n$. Therefore, the probability of extinction should behave like the probability that a random walk with positive drift ever reaches a low level, and this is the key to our proof.

However, rather than work with $\{\log Z_n\}$ it is easier to consider the *dual process* $\{X_n\}$ defined by Smith and Wilkinson [4]:

$$X_{n+1} = \phi_{\zeta_n}(X_n)$$

with $X_0 = 0$. This is a Markov process with state space $[0,1]$ and with a proper limiting/equilibrium distribution in the supercritical case. Moreover, if X is a random variable with this distribution then we may write

$$q_k = EX^k$$

since in fact X has the same distribution as $q(\bar{\zeta})$. Thus, the behaviour of q_k as $k \rightarrow \infty$ may be investigated via the behaviour of the distribution of X close to 1.

We make the transformations

$$Y_n = -\log(1 - X_n)$$

$$\text{and } Y = -\log(1 - X).$$

Clearly $\{Y_n\}$ is also a Markov process and Y possesses its limiting/equilibrium distribution. We are interested in the tail behaviour of this distribution at $+\infty$.

$$\begin{aligned} Y_{n+1} &= -\log(1 - \phi_{\zeta_n}(X_n)) \\ &= -\log(1 - X_n) + \left(-\log\left(\frac{1 - \phi_{\zeta_n}(X_n)}{1 - X_n}\right) \right) \\ &\geq Y_n + (-\log \phi'_{\zeta_n}(1)) \quad \text{since } \phi_{\zeta_n} \text{ is a p.g.f.} \\ &= Y_n + (-\xi_n). \end{aligned}$$

Also $Y_{n+1} \geq 0$. Hence

$$Y_{n+1} \geq \max(0, Y_n + (-\xi_n)).$$

Define $W_0 = 0$ and

$$W_{n+1} = \max(0, W_n + (-\xi_n)) \quad \text{for } n = 0, 1, 2, \dots$$

Then $\{W_n\}$ is a random walk with left reflecting barrier at 0 and jumps $\{-\xi_n\}$. It

is easy to show by induction on n that $Y_n \geq W_n$ for all n , and thence that

$$P(Y \geq y) \geq P(W \geq y)$$

for all $y \geq 0$, where W is a random variable with the limiting/equilibrium distribution of $\{W_n\}$.

The following duality argument is familiar:

$$\begin{aligned} W_n &= \max(0, -\xi_{n-1}, -\xi_{n-1} - \xi_{n-2}, \dots, -\xi_{n-1} - \dots - \xi_0) \\ &= -\min(0, \xi_0, \xi_0 + \xi_1, \dots, \xi_0 + \dots + \xi_{n-1}) \text{ in distribution} \end{aligned}$$

so that $-W$ has the same distribution as the all-time minimum M of an unrestricted random walk with jumps $\{\xi_n\}$. But by the assumption of the existence of θ_0 and the result of Feller [2], Ch. XII, we know

$$P(M \leq -t) \sim ce^{-\theta_0 t}$$

as $t \rightarrow \infty$, for some constant $c > 0$. Hence

$$P(Y \geq y) \geq P(W \geq y) \geq c'e^{-\theta_0 y}$$

for all $y \geq 0$ for some constant $c' > 0$. In terms of X , this becomes

$$P(X \geq x) \geq c'(1-x)^{\theta_0}$$

for $0 \leq x < 1$. Hence, denoting the distribution function of X by H ,

$$\begin{aligned} q_k &= EX^k = \int_0^1 x^k dH(x) \\ &= k \int_0^1 x^{k-1} (1-H(x)) dx \\ &\geq c'k \int_0^1 x^{k-1} (1-x)^{\theta_0} dx \\ &= c'kB(k, \theta_0 + 1) \end{aligned}$$

where B is the Beta function. Finally, since

$$B(k, \theta_0 + 1) \sim \frac{\Gamma(\theta_0 + 1)}{k^{\theta_0 + 1}}$$

as $k \rightarrow \infty$, we deduce that $q_k \geq c''k^{-\theta_0}$ for all k , some $c'' > 0$, and part (a) of the theorem is proved.

To prove part (b) of the theorem, fix $x_0 \in [0, 1[$ and let $y_0 = -\log(1-x_0)$.

Also let

$$\hat{\xi}_n = \log \left(\frac{1 - \phi_{\zeta_n}(x_0)}{1 - x_0} \right)$$

and define $U_0 = y_0$ and

$$U_{n+1} = \max(y_0, U_n + (-\hat{\xi}_n))$$

so that $\{U_n\}$ is a random walk with left reflecting barrier at y_0 and jumps $\{-\hat{\xi}_n\}$.

We show by induction on n that $Y_n \leq U_n$ for all n . Obviously $Y_0 = 0 \leq y_0 = U_0$. If $Y_n \leq U_n$ then either $Y_n \leq y_0$ in which case

$$\begin{aligned} Y_{n+1} &= -\log(1 - \phi_{\zeta_n}(X_n)) \\ &\leq -\log(1 - \phi_{\zeta_n}(x_0)) \quad \text{since } X_n \leq x_0 \\ &= y_0 + \left(-\log \left(\frac{1 - \phi_{\zeta_n}(x_0)}{1 - x_0} \right) \right) \\ &\leq U_n + (-\hat{\xi}_n) \\ &\leq U_{n+1} \end{aligned}$$

or, alternatively, $y_0 \leq Y_n \leq U_n$ in which case

$$\begin{aligned} Y_{n+1} &= Y_n + \left(-\log \left(\frac{1 - \phi_{\zeta_n}(X_n)}{1 - X_n} \right) \right) \\ &\leq Y_n + \left(-\log \left(\frac{1 - \phi_{\zeta_n}(x_0)}{1 - x_0} \right) \right) \quad \text{since } \phi_{\zeta_n} \text{ is a p.g.f.} \\ &\leq U_n + (-\hat{\xi}_n) \\ &\leq U_{n+1}. \end{aligned}$$

It follows using similar arguments to those used in the proof of part (a), but with the inequalities reversed, that if $\theta > 0$ can be found such that $\{U_n\}$ has an equilibrium distribution whose tail is of order $e^{-\theta y}$ as $y \rightarrow \infty$, then $q_k = O(k^{-\theta})$ as $k \rightarrow \infty$ for any such θ . We show that for all choices of x_0 sufficiently close to 1, such $\theta = \theta(x_0)$ can indeed be found, and moreover that $\theta(x_0) \uparrow \theta_0$ as $x_0 \uparrow 1$, which is sufficient to establish part (b) of the theorem.

Let

$$F_x(\theta) = E\left(e^{-\theta\xi}\right) = E\left(\frac{1-\phi_\zeta(x)}{1-x}\right)^{-\theta}$$

where, for ease of notation, we replace x_0 by x and suppress the suffix n . By the properties of p.g.f.'s,

$$\phi'_\zeta(1)^{-\theta} \leq \left(\frac{1-\phi_\zeta(x)}{1-x}\right)^{-\theta} \leq (1-\phi_\zeta(0))^{-\theta}$$

and so, using the extra condition of the statement of part (b) of the theorem, we know that $F_x(\theta)$ is finite for $0 \leq \theta \leq \theta_0$. Also, using dominated convergence, $F_x(\theta) \rightarrow E(\phi'_\zeta(1))^{-\theta} = F(\theta)$ as $x \rightarrow 1$ for each $\theta \in [0, \theta_0]$. Hence, since $F(\theta) < 0$ for $0 < \theta < \theta_0$, it follows that for all x sufficiently close to 1, $F_x(\theta) < 0$ for some θ and therefore, since F_x is convex, $F'_x(0) < 0$; moreover, $F_x(\theta_0) \geq 1$ and so there exists $\theta = \theta(x) > 0$ such that $F_x(\theta) = 1$ and obviously $F'_x(\theta) < \infty$. The fact that $\theta(x) \rightarrow \theta_0$ as $x \rightarrow 1$ also follows easily from the fact that $F_x(\theta) \rightarrow F(\theta)$ as $x \rightarrow 1$. This completes the proof of the theorem.

3. Application to an optimal strategy for survival. In Grey [3] a model was described in which laying birds may choose randomized strategies for clutch size and thereby effectively choose between different family size distributions, in an attempt to minimize the probability of extinction of the species. It was stated loosely that maximizing the parameter θ_0 which appears in this paper should be optimal for large populations, and an intuitive justification was given. A numerical example showed that this criterion may lead to a genuinely randomized strategy, which may be interpreted as hedging one's bets against unknown future environments.

The results of this paper provide a sound theoretical justification for the criterion suggested above, insofar as they prove that between any two strategies with different values of θ_0 , the one with the larger value will indeed yield a smaller probability of extinction provided that the initial population size is sufficiently large.

References

- [1] Athreya, K.B. and Karlin, S. (1971). On branching processes in random environments I & II. *Ann. Math. Stat.* **42**, 1499-1520 & 1843-1858.

- [2] Feller, W. (1971). *An Introduction to Probability Theory and its Applications* Vol. II, Second Edition. Wiley, New York.
- [3] Grey, D.R. (1980). Minimisation of extinction probabilities in reproducing populations. *Theoretical Population Biology* **18** , 430-443.
- [4] Smith, W.L. and Wilkinson, W.E. (1969). On branching processes in random environments. *Ann. Math. Stat.* **40** , 814-827.