6.6 Growth of Populations with Sexual Reproduction

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In Section 5.9, we studied the effect of sexual reproduction on criticality and extinction risk of branching processes. Here, we consider the ultimately supercritical case ($m_\infty > 1$) and take a look at the question of how such populations grow in the event of survival. Since m_∞ describes the asymptotic growth rate per generation if the population becomes large, it is not unreasonable to believe that Z_n grows as m_∞^n in the event of survival. However, even for the simple Galton–Watson process, the famous Kesten–Stigum theorem has already shown that this is true only under an additional condition on the offspring distribution. Defining the normalized process

$$W_n = \frac{Z_n}{m_\infty^n}, \quad n \geq 0, \tag{6.100}$$

we have that

$$\begin{aligned} \mathbb{E}[W_{n+1}|W_n = im_\infty^{-n}] &= \mathbb{E}[W_{n+1}|Z_n = i] \\ &= m_\infty^{-(n+1)}\mathbb{E}[Z_{n+1}|Z_n = i] = im_i m_\infty^{-(n+1)} \leq im_\infty^{-n} \end{aligned} \tag{6.101}$$

for all i. Thus, $(W_n)_{n\geq 0}$ constitutes a non-negative supermartingale and, therefore, converges to a finite random variable W with expectation $\mathbb{E}[W|Z_0 = i] \leq \mathbb{E}[W_0|Z_0 = i] = i$ for all i. In other words, the long-run population growth rate is at most m_∞. This should not come as a surprise, because the average unit reproduction means are bounded by this value. However, when is m_∞^n also the correct normalization in the sense that the limiting variable W is positive in the event of survival?

The difficulty of this question is best understood when the approximation of Z_n by Wm_∞^n is considered as a two-step result. Writing Z_n as the product $\frac{Z_n}{Z_{n-1}} \cdot \frac{Z_{n-1}}{Z_{n-2}} \cdot \ldots \cdot \frac{Z_1}{Z_0}$, replace first each factor $\frac{Z_k}{Z_{k-1}}$ with its conditional expectation given Z_{k-1}, that is $m_{Z_{k-1}}$, and then the latter with its limit (and upper bound) m_∞ as Z_{k-1} tends to infinity. We thus arrive at the decomposition

$$W_n = V_n \cdot \prod_{k=0}^{n-1} \frac{m_{Z_k}}{m_\infty}, \tag{6.102}$$

where $V_0 = Z_0$ and

$$V_n = \frac{Z_n}{m_{Z_0} \cdot \ldots \cdot m_{Z_{n-1}}}, \quad n \geq 1. \tag{6.103}$$

Now, since

$$V_{n+1} = V_n \frac{Z_{n+1}}{Z_n m_{Z_n}}, \tag{6.104}$$

and the conditional expectation of $\frac{Z_{n+1}}{Z_n}$ given $Z_0, \ldots, Z_n$ equals m_{Z_n}, a similar computation as in Equation (6.101) shows that $(V_n)_{n\geq 0}$ constitutes a non-negative

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martingale, that is, $\mathbb{E}[V_{n+1}|V_n = v] = v$ for all n and v. Hence V_n converges to a random variable V, which is at least as large as W because $V_n \geq W_n$ for all n. Taking limits in Equation (6.102) now yields

$$W = V \cdot \prod_{k\geq 0} \frac{m_{Z_k}}{m_\infty} . \tag{6.105}$$

So Z_n indeed grows as m_∞^n in the event of survival, provided that both the martingale limit V and the infinite product $\prod_{k\geq 0} \frac{m_{Z_k}}{m_\infty}$ are positive in that event. The latter obviously holds true if m_j converges to m_∞ sufficiently quickly. However, without a restriction to special mating functions it seems difficult to translate these requirements into conditions on the offspring distribution $(p_{j,k})_{j,k\geq 0}$. González and Molina (1996, 1997) did some related work for general ζ, but circumvented the problem by directly imposing conditions on the *derived* quantities $d_j = m_j - m_\infty$, essential ones being that $d_j \leq g(j)$ for all j and a suitable concave function g that satisfies $\sum_{j\geq 1} j^{-1} g(j) < \infty$. By adding further conditions not reported here they could prove that Z_n grows as m_∞^n (W is positive) in an event of positive probability, but not necessarily the full event of survival.

At least for monogamous populations with mating function $\zeta(x, y) = \min(x, y)$, Bagley (1986) was able to provide a satisfactory answer, stated in Theorem 6.9 below, which is actually the perfect analog of the corresponding result for asexual populations described by simple Galton–Watson processes. Recall that p_j^F and p_k^M denote the probabilities that a couple has exactly j female and k male offspring, respectively, and hence $p_j^F = \sum_{k\geq 0} p_{j,k}$ and $p_k^M = \sum_{j\geq 0} p_{j,k}$.

Theorem 6.9 *Let $(Z_n)_{n\geq 0}$ be an ultimately supercritical Galton–Watson process with a monogamous mating function ζ and an offspring distribution $(p_{j,k})_{j,k\geq 0}$ that satisfies Assumption 5.2 (Section 5.9), then $\sum_{k\geq 1} p_k^F k \ln k < \infty$ implies that W is positive in the event of survival, that is, $\mathbb{P}(W > 0|Z_0 = i) = 1 - Q_i$ for all i, while $\sum_{k\geq 1} p_k^F k \ln k = \infty$ implies $W = 0$.*

As one can verify easily, $\sum_{k\geq 1} p_k^F k \ln k < \infty$ and $\sum_{k\geq 1} p_k^M k \ln k < \infty$ are equivalent conditions under Assumption 5.2 because $0 < \theta < 1$.

Sketch of Proof. We content ourselves with the following very intuitive heuristic argument under the additional assumption $m^F \neq m^M$ or, equivalently, $\theta \neq \frac{1}{2}$. To be specific, suppose $m^F < m^M$. If the population survives and hence grows to infinity, eventually the total number of female offspring produced by a generation is always smaller than the respective number of male offspring. In fact, the Law of Large Numbers even shows that

$$\frac{1}{Z_n}(M_{n+1} - F_{n+1}) = \frac{1}{Z_n} \sum_{k=1}^{Z_n} (Y_{n+1,k} - X_{n+1,k}) \tag{6.106}$$

tends to $m^M - m^F > 0$, if $Z_n \to \infty$. Consequently, for large n the number of couples that form the $(n + 1)$th generation just equals the number of female offspring of the previous one, whence $(Z_n)_{n\geq 0}$ ultimately behaves as the simple branching process obtained by considering only the females. The assertions of the theorem now follow by invoking the

Kesten–Stigum theorem. It is quite clear that the heuristic just given remains true if the offspring distribution satisfies Assumption 5.3 (Section 5.9). Since $m_\infty = \min(m^F, m^G)$, Theorem 6.9 shows that, even if $m^F = m^M$, a surviving monogamous population grows at the same order of magnitude as one of its associated asexual counterparts in which females and males, respectively, reproduce without mating. Of course, the probability of survival is always smaller in the case with sexual reproduction. The same heuristic becomes exact for (unilateral) promiscuous populations because, in the case of survival, the number of couples precisely equals the number of females in each generation. The male subpopulation enters into the analysis only by causing an increased chance of extinction.

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6.7 Immigration in Subcritical Populations

In Section 2.10 we calculated the expected size of populations with recurrent immigration. Here we continue to study the properties of such populations and concentrate on the situation in which the local branching process is subcritical. From Section 2.10 we know that in that case the average number of individuals stabilizes. Here we show that, moreover, the distribution of the population size is stationary.

Let $f(s)$ be the local reproduction generating function and denote the probability generating function of the number of invaders per period by $g(s)$. We denote the probability generating function of the number of individuals in generation n in the resultant branching process with immigration by $F(n, s) = \mathbb{E}[\, s^{Z_n}\,]$. Applying the conditional expectation argument (see the Appendix), we obtain

$$\begin{aligned} F(n, s) &= \mathbb{E}[\, s^{\xi_1+\xi_2+\cdots+\xi_{Z_{n-1}}+Y_n}\,] \\ &= \mathbb{E}[\,\mathbb{E}[\, s^{\xi_1+\xi_2+\cdots+\xi_{Z_{n-1}}+Y_n} \,|Z_{n-1}\,]] \\ &= \mathbb{E}[\,\mathbb{E}[\, s^{\xi_1} s^{\xi_2} \cdots s^{\xi_{Z_{n-1}}} s^{Y_n} \,|Z_{n-1}\,]]\,, \end{aligned} \tag{6.107}$$

where, as before, ξ_i is the number of children of the ith individual in generation $(n-1)$, and Y_n is the number of immigrants in the nth generation. Since Y_n is independent of Z_{n-1}

$$\begin{aligned} F(n, s) &= \mathbb{E}[\,\mathbb{E}[\, s^{\xi_1} s^{\xi_2} \cdots s^{\xi_{Z_{n-1}}} \mid Z_{n-1}\,]]\mathbb{E}[s^{Y_n}] = \mathbb{E}[f(s)^{Z_{n-1}}]g(s) \\ &= F(n-1, f(s))g(s) = F(n-2, f_2(s))g(f(s))g(s) = \cdots \\ &= F(0, f_n(s))g(f_{n-1}(s))g(f_{n-2}(s)) \cdots g(s)\,. \end{aligned} \tag{6.108}$$

Thus, if the population is initiated at $n = 0$ by a random number of invaders distributed according to the probability generating function $F(0, s) = g(s)$,

$$F(n, s) = \prod_{k=0}^{n} g(f_k(s))\,, \tag{6.109}$$

and if there were a non-random number z_0 of individuals at $n = 0$,

$$F(n, s) = (f_n(s))^{z_0} \prod_{k=0}^{n-1} g(f_k(s))\,. \tag{6.110}$$

References

References in the book in which this section is published are integrated in a single list, which appears on pp. 295–305. For the purpose of this reprint, references cited in the section have been assembled below.

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