BRANCHING PROCESSES AND THEIR APPLICATIONS: LECTURE 4: Expected time to extinction for for subcritical processes; stationarity of subcritical populations; supercritical processes which die out sooner or later

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1 The time to extinction of subcritical processes

We start by the following statement.

Theorem 1 *If* $A < 1$ *and* $E\xi \log^+ \xi < \infty$ *then*

$$\mathbf{E}_N[\tau] = \mathbf{E}_N[\tau \mid Z(0) = N] \sim \frac{\ln N}{|\ln A|}, \ N \to \infty. \tag{1}$$

Proof. We know that

$$KA^n \le \mathbf{P}_1(Z(n) > 0) = \mathbf{P}_1(\tau > n) \le A^n \tag{2}$$

with

$$K^{-1} = \lim_{n\to\infty} E\left[Z(n)|Z(n) > 0\right],$$

and

$$\mathbf{P}_N(\tau > n) \le NA^n. \tag{3}$$

Set

$$\phi(N) = \frac{\ln N}{|\ln A|}, \quad \psi(N) = \frac{\ln\ln N - \ln K}{|\ln A|} \ge 0 \ .$$

Observe that $NA^{\phi(N)} = NA^{-(\ln N)/\ln A} = 1$ and

$$\exp\left\{-KNA^{\phi(N)-\psi(N)}\right\} = \exp\left\{-KA^{-\psi(N)}\right\} = \exp\left\{-\ln N\right\} = 1/N.$$

Further,

$$\mathbf{E}_N[\tau] = \sum_{n=0}^{\infty} \mathbf{P}_N(\tau > n)$$

and, therefore, in view of (3)

$$\begin{aligned}\mathbf{E}_N[\tau] &\le \sum_{0\le n<\phi(N)} \mathbf{P}_N(\tau > n) + N \sum_{n\ge\phi(N)}^{\infty} A^n \\ &\le \phi(N) + 1 + \frac{NA^{\phi(N)}}{1-A} = \frac{\ln N}{|\ln A|} + \frac{2-A}{1-A}.\end{aligned}$$

On the other hand,

$$\begin{aligned}\mathbf{E}_N[\tau] &\ge \sum_{0\le n<\phi(N)-\psi(N)} \mathbf{P}_N(\tau > n) \\ &\ge (\phi(N) - \psi(N) - 1)\,\mathbf{P}_N(\tau \ge \phi(N) - \psi(N)) \\ &= (\phi(N) - \psi(N) - 1)\,(1 - \mathbf{P}_N(\tau < \phi(N) - \psi(N)).\end{aligned}$$

By (2) for any $n \ge 0$

$$\begin{aligned}\mathbf{P}_N(\tau \le n) &= \mathbf{P}_1^N(\tau \le n) = (1 - \mathbf{P}_1(\tau > n))^N \\ &\le e^{-N\mathbf{P}_1(\tau>n)} \le e^{-KNA^n}\end{aligned}$$

where we have used the inequality $1 - x \le e^{-x},\ x > 0$. Therefore,

$$\mathbf{P}_N(\tau \le \phi(N) - \psi(N)) \le e^{-KNA^{\phi(N)-\psi(N)}} = \frac{1}{N}.$$

As a result we get

$$\frac{\ln N}{|\ln A|}\left(1 - \frac{\ln\ln N - \ln K + |\ln A|}{\ln N}\right)\left(1 - \frac{1}{N}\right) \le \mathbf{E}_N[\tau] \le \frac{\ln N}{|\ln A|} + \frac{2-A}{1-A}.$$

From here the statement of the theorem follows easily.

Example

We consider again the example

Caswell,H., Fujiwara, M., and Brault S., *Declining survivial probability threatens the North Atlanitic right whale*, Proc. Nath. Acad . USA , 96 (1999), 3308-3313.

They study the following model.

A female right whale may produce 0, 1, or 2 females the following year. It is assumed that the death of a parent results in the death of a calf in the first year. Thus, a female at time n produces no offspring if she dies before $n + 1$, one offspring (herself) if she survives without reproducing female offspring and two offspring (herself and her calf) if she survives and gives birth to a female calf. Generation length is then one year. Let p be the survival probability and

μ be the probability of begetting a female calf. The reproduction generating function of the process becomes

$$f(s) = 1 - p + p(1-\mu)s + p\mu s^2$$

with mean $A = p(1-\mu)+2p\mu = p(1+\mu)$. Caswell *et al.* (1999) give the following estimates for p, μ, and, as a result, for A:

	$\mu = 0.051$	$\mu = 0.038$
$p = 0.94$	$A = 0.988$	$A = 0.976$

For the North Atlantic right whales we get by means of (1) the following estimates:

A	0.988	0.976
$E[\tau \vert Z(0) = 150] \approx$	415	206

for the expected time to extinction in the subcritical situation (the last line of the table). These figures agree with the results given in Caswell *et al.* (1999), showing through direct calculations that $E[\tau|Z(0) = 150] \approx 191$ if $p = 0.94$ and $\mu = 0.038$ and, therefore, $A = 0.976$. Our method is however robust in the sense that it is built upon (1), so the result does not depend on the particular form of the reproduction distribution.

2 Limit theorem for the distribution of the population size

Now we show that in the subcritical case the population size will stabilize given that the population has not died out.

Theorem 2 *If $A < 1$ then*

$$\lim_{n\to\infty} \mathbf{P}(Z(n) = k|Z(n) > 0) = P_k^*, \quad \sum_{k=1}^{\infty} P_k^* = 1,$$

and

$$f^*(s) = \sum_{k=1}^{\infty} P_k^* s^k$$

satisfies

$$1 - f^*(f(s)) = A(1 - f^*(s)).$$

Proof. We have

$$\mathbf{E}\left[s^{Z(n)}|Z(n) > 0\right] = 1 - \frac{1 - f_n(s)}{1 - f_n(0)}.$$

Clearly,

$$\frac{1-f(s)}{1-s}\uparrow A$$

as $s\uparrow 1$. Hence

$$\frac{1-f_{n+1}(s)}{1-f_n(s)}=\frac{1-f(f_n(s))}{1-f_n(s)}\geq\frac{1-f(f_n(0))}{1-f_n(0)}$$

or

$$\frac{1-f_n(s)}{1-f_n(0)}\leq\frac{1-f_{n+1}(s)}{1-f_{n+1}(0)}.$$

Hence,

$$\lim_{n\to\infty}\frac{1-f_n(s)}{1-f_n(0)}=1-f^*(s)$$

exists. Besides,

$$\begin{aligned}1-f^*(s) &= \lim_{n\to\infty}\frac{1-f_{n+1}(s)}{1-f_{n+1}(0)}=\lim_{n\to\infty}\frac{1-f(f_n(s))}{1-f_n(0)}\frac{1-f_n(0)}{1-f(f_n(0))}\\ &= \lim_{n\to\infty}\frac{1-f(f_n(s))}{1-f_n(0)}\times\lim_{n\to\infty}\frac{1-f_n(0)}{1-f(f_n(0))}=\frac{1-f^*(s)}{A}\end{aligned}$$

implying

$$1-f^*(f(s))=A(1-f^*(s))$$

and as $s\uparrow 1$

$$1-f^*(f(1))=A\left(1-f^*(1)\right).$$

Hence $f^*(1)=1$.

Theorem 3 $f^{*'}(1)<\infty$ *if and only if* $\mathbf{E}\xi\log^+\xi<\infty$.

Proof. Clearly,

$$\begin{aligned}1-f^*(f_n(s)) &= 1-f^*(f(f_{n-1}(s)))=A(1-f^*(f_{n-1}(s)))\\ &= \ldots=A^n(1-f^*(s)).\end{aligned}$$

Thus, on account of $f^*(0)=0$

$$\lim_{n\to\infty}\frac{1-f^*(f_n(0))}{1-f_n(0)}=\lim_{n\to\infty}\frac{A^n}{Q(n)}<\infty$$

if and only if $\mathbf{E}\xi\log^+\xi<\infty$.

For the Geometric distribution with

$$f(s)=\frac{q}{1-ps}=\frac{q}{q+p-ps}=\frac{q}{q+p(1-s)}=\frac{1}{1+A(1-s)}$$

and $A=p/q$ we have

$$1 - f_n(s) = \frac{A^n(A-1)(1-s)}{A(A^n-1)(1-s)+A-1}$$

and

$$\mathbf{P}\left(Z(n)>0\right) = 1 - f_n(0) = \frac{A^n(A-1)}{A^{n+1}-1}$$

giving

$$\begin{aligned}\lim_{n\to\infty}\mathbf{E}\left[s^{Z(n)}|Z(n)>0\right] &= \lim_{n\to\infty}\left[1-\frac{1-f_n(s)}{1-f_n(0)}\right] \\ &= 1-\frac{1-s}{1-As} = \frac{s(1-A)}{1-As} = \frac{s(q-p)}{q-ps} = f^*(s).\end{aligned}$$

3 Accumulated population size of supercritical populations which are know to die out

Now we show that supercritical populations, which are known to die out later, behave as subcritical populations. Contrarily to what one might guess, they do not first grow exponentially and later drop drastically. In fact, their size stabilizes. First we study the accumulated populations size $T(n)$ up to generation n which is defined as

$$T(n) = Z(0) + Z(1) + \cdots + Z(n-1).$$

If $Z(0) = 1$, then

$$\begin{aligned}\mathbf{E}\left[T(n)\right] &= \mathbf{E}\left[Z(0)+Z(1)+\cdots+Z(n-1)\right] \\ &= \mathbf{E}\left[Z(0)\right]+\mathbf{E}\left[Z(1)\right]+\cdots+\mathbf{E}\left[Z(n-1)\right] \\ &= 1+A+\cdots+A^n.\end{aligned}$$

If $A<1$ then the process dies out rapidly, the total number of individuals ever born

$$T(\infty) = Z(0)+Z(1)+\cdots+Z(n)+\cdots$$

is finite and

$$\mathbf{E}\left[T(\infty)\right] = \sum_{k=0}^{\infty} A^k = \frac{1}{1-A}.$$

On the other hand, if $A \geq 1$ then $\mathbf{E}\left[T(n)\right] \to \infty$, as $n \to \infty$. However, if we condition on the event that a supercritical process dies sooner or later and denote the extinction moment by τ, we get

Theorem. If $A>1$ then

$$\mathbf{E}\left[T\,|\tau<\infty\right] = \frac{1}{1-f'(P)}, \tag{4}$$

where $P = \mathbf{P}(\tau < \infty)$ is the extinction probability of the process (observe that $f^{'}(P) < 1)$.

Proof. To establish (4) we write

$$\mathbf{E}\left[T \mid \tau < \infty\right] = \frac{\mathbf{E}\left[T\, ; \tau < \infty\right]}{\mathbf{P}(\tau < \infty)}. \tag{5}$$

Further,

$$\mathbf{E}\left[T\, ; \tau < \infty\right] = \sum_{n=0}^{\infty} \mathbf{E}\left[Z(n)\, ; n < \tau < \infty\right]. \tag{6}$$

Now observe that

$$\mathbf{E}\left[Z(n)\, ; n < \tau < \infty\right] = \sum_{k=1}^{\infty} k\mathbf{P}(Z(n) = k; n < \tau < \infty) = \sum_{k=1}^{\infty} k\mathbf{P}(Z(n) = k)P^{k},$$

since each of the populations stemming from the $Z(n) = k$ individuals at time n should die out. Thus, we get

$$\mathbf{E}\left[Z(n)\, ; n < \tau < \infty\right] = P\sum_{k=1}^{\infty} k\mathbf{P}(Z(n) = k)P^{k-1} = Pf_n^{\prime}(P) = P\left(f^{'}(P)\right)^{n}.$$

Substituting this sequentially in (6) and (5) gives (4). In particular, in the supercritical geometric case $P = q/p = A^{-1} < 1$ and

$$f^{'}(P) = \frac{qp}{(1 - pP)^2} = \frac{1}{A}.$$

Hence,

$$\mathbf{E}\left[T \mid \tau < \infty\right] = \frac{1}{1 - A^{-1}} = \frac{A}{A - 1} = 1 + \frac{1}{A - 1}.$$

Note that this expectation is monotone *decreasing* to 1 when A increases.

And we get an (at the first sight) unexpected result: if a *supercritical* process dies out rather rapidly (and, therefore, the total amount of ever born individuals in the population is small) it may be an indicator to the fact that the expected value of the offspring number in this process is large. However, after some thoughts one can see that since the process is supercritical it either dies out almost of the beginning of the evolution (and therefore, the accumulated size indeed, is small) or if this is not the case it hardly be able to extinct since the size of the population becomes large after several (surviving) generations.