LECTURE 1: Single-type Galton-Watson processes

8 июня 2011 г.
Model:
\( Z(n) \) - the number of individuals at time \( n \).
Initially \( Z(0) = 1 \), i.e. an individual with life-length equal to 1. Dying it produces \( \xi \) children where

\[
P(\xi = k) = p_k.
\]

They constitute the first generation: \( Z(1) = \xi_{Z(0)}^{(1)} = \xi \). The newborn particles have life-lengthes 1 and dying produce

\[
Z(2) := \xi_1^{(2)} + \ldots + \xi_{Z(1)}^{(2)}
\]

individuals in iid manner where \( \xi_i^{(2)} \overset{d}{=} \xi \) and so on. Thus,

\[
Z(n) = \xi_1^{(n)} + \ldots + \xi_{Z(n-1)}^{(n)},
\]

where \( \xi_i^{(n)} \overset{d}{=} \xi \) are iid.
One may consider $Z(0) = k \in \{1, 2, \ldots\}$ or even as a random variable. In view of the branching property

$$\{Z(n)|Z(0) = k_1 + k_2\} \overset{d}{=} \{Z(n)|Z(0) = k_1\} + \{Z(n)|Z(0) = k_2\}.$$
Classification

\[ m = E\xi = E[Z(1)|Z(0) = 1]. \]

The process is called subcritical if \( m < 1 \), critical, if \( m = 1 \) and supercritical, if \( m > 1 \).

Lemma

If \( m := E\xi < \infty \), then

\[ E[Z(n)|Z(0) = 1] = m^n. \]

If \( \sigma^2 := \text{Var}\xi < \infty \), then

\[ \text{Var}[Z(n)|Z(0) = 1] = \begin{cases} 
\sigma^2 \frac{m^{n-1}(m^n-1)}{m-1}, & \text{if } m \neq 1, \\
\sigma^2 n, & \text{if } m = 1.
\end{cases} \]
Generating functions

Let

$$f(s) = \mathbb{E}[s^{\xi}] = \sum_{k=0}^{\infty} P(\xi = k)s^k = \sum_{k=0}^{\infty} p_k s^k, 0 \leq s \leq 1$$

be the generating function of the random variable $\xi$ with nonnegative integer values.
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be the generating function of the random variable $\xi$ with nonnegative integer values.

We have

$$E\xi = f'(1), \quad E\xi(\xi - 1) = f''(1),$$

and

$$\text{Var}\xi = E\xi^2 - (E\xi)^2 = E\xi(\xi - 1) + E\xi - (E\xi)^2$$

$$= f''(1) + f'(1) - (f'(1))^2.$$
Generating functions
Let
\[ f(s) = E[s^\xi] = \sum_{k=0}^{\infty} P(\xi = k)s^k = \sum_{k=0}^{\infty} p_k s^k, \quad 0 \leq s \leq 1 \]
be the generating function of the random variable \( \xi \) with nonnegative integer values.
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and
\[ \text{Var}\xi = E\xi^2 - (E\xi)^2 = E\xi(\xi - 1) + E\xi - (E\xi)^2 \]
\[ = f''(1) + f'(1) - (f'(1))^2. \]

Iterations
\[ f_0(s) = s, \quad f_{n+1}(s) = f_n(f(s)). \]
Let

\[ F(n, s) = \sum_{k=0}^{\infty} P(Z(n) = k | Z(0) = 1) s^k. \]
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\[ F(n, s) = \sum_{k=0}^{\infty} P(Z(n) = k|Z(0) = 1) s^k. \]

Given \( Z(0) = 1 \) we have

\[ F(n, s) = E_s Z(n) = E \left[ E \left[ s^{Z(n)} | Z(n-1) \right] \right] \]
\[ = E \left[ E \left[ s^{\xi_1(n)} + \cdots + \xi_{Z(n-1)}(n) \right] | Z(n-1) \right] = E \left[ (E_s \xi)^{Z(n-1)} \right] \]
\[ = F(n-1, f(s)) = F(n-2, f_2(s)) = \ldots = F(0; f_n(s)) = f_n(s). \]
Calculation of iterations for the pure geometric reproduction law
\[ f(s) = \sum_{k=0}^{\infty} P(\xi = k) s^k = \sum_{k=0}^{\infty} q p^k s^k = \frac{q}{1 - ps}. \]
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Clearly, \( f'(1) = m = p/q \) and

\[ 1 - f(s) = \frac{p(1 - s)}{1 - ps} \]

and

\[ \frac{1}{1 - f(s)} - \frac{1}{m(1 - s)} = \frac{1 - ps}{p(1 - s)} - \frac{q}{p(1 - s)} = 1. \]
\[ f(s) = \sum_{k=0}^{\infty} P(\xi = k)s^k = \sum_{k=0}^{\infty} qp^k s^k = \frac{q}{1 - ps}. \]

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\[ \frac{1}{1 - f(s)} - \frac{1}{m(1 - s)} = \frac{1 - ps}{p(1 - s)} - \frac{q}{p(1 - s)} = 1. \]

Thus,

\[ \frac{1}{1 - f_n(s)} - \frac{1}{m(1 - f_{n-1}(s))} = \frac{1}{1 - f(f_{n-1}(s))} - \frac{1}{m(1 - f_{n-1}(s))} = 1. \]
Thus,
\[
\frac{1}{1 - f_n(s)} = 1 + \frac{1}{m(1 - f_{n-1}(s))} = 1 + \frac{1}{m} + \frac{1}{m^2(1 - f_{n-2}(s))} = \ldots.
\]

Hence
\[
\frac{1}{1 - f_n(s)} = 1 + \frac{1}{m} + \frac{1}{m^2} + \ldots + \frac{1}{m^{n-1}} + \frac{1}{m^n(1-s)}
\]
\[
= \begin{cases} 
\frac{m^n-1}{m^n(m-1)} + \frac{1}{m^n(1-s)} & \text{if } m \neq 1 \\
 n + \frac{1}{1-s} & \text{if } m = 1.
\end{cases}
\]
Therefore, if \( m \neq 1 \) then

\[
1 - f_n(s) = \frac{m^n(m - 1)(1 - s)}{m(m^n - 1)(1 - s) + m - 1}.
\]

(1)

and if \( m = 1 \) then

\[
1 - f_n(s) = \frac{1}{n + (1 - s)^{-1}}.
\]
Remark If $f(s)$ is a fractional-linear probability generating function and $h(s)$ is such that

$$g(s) := h^{-1}(f(h(s)))$$

is a probability generating function then

$$g_n(s) = h^{-1}(f_n(h(s))).$$
Remark If $f(s)$ is a fractional-linear probability generating function and $h(s)$ is such that

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Example If

$$f(s) = \frac{s}{A - (A - 1)s}, \quad A > 1, \quad \text{and} \quad h(s) = s^k, \quad k - \text{positive integer}$$

then

$$g(s) = h^{-1}(f_n(h(s))) = \frac{s}{(A - (A - 1)s^k)^{1/k}},$$

and

$$g_n(s) = \frac{s}{(A^n - (A^n - 1)s^k)^{1/k}}, \quad n = 1, 2, \ldots.$$
Exercises. 1) For the processes with pgf

\[ f(s) = \frac{1}{2 - s} \]

and

\[ f(s) = \frac{2}{3 - s}, \quad f(s) = \frac{1}{4 - 3s} \]

calculate

\[ P(Z(10) > 0), \quad P(Z(10) > 0, Z(15) = 0), \quad P(Z(15) \geq 3). \]

2) Let

\[ f(s) = 1 - p (1 - s)^\beta, \quad 0 < p < 1, \quad 0 < \beta < 1. \]

Show that this is a probability generating function and find \( f_n(s) \).
Elementary properties of PGF

Let

\[ f(s) = \mathbb{E}s^\xi = \sum_{k=0}^{\infty} P(\xi = k) s^k = \sum_{k=0}^{\infty} p_k s^k \]

be a PGF with \( p_0 + p_1 < 1 \). Then

PICTURES
Extinction

Since

\[ f_n(s) = \mathbb{E}_s Z^{(n)} = \sum_{k=0}^{\infty} P(Z(n) = k) s^k, \]

we have \( P(Z(n) = 0) = f_n(0) \).
Extinction

Since

\[ f_n(s) = E s^{Z(n)} = \sum_{k=0}^{\infty} P(Z(n) = k) s^k, \]

we have \( P(Z(n) = 0) = f_n(0). \) Hence

\[ f_n(0) = P(Z(n) = 0) \leq P(Z(n + 1) = 0) = f_{n+1}(0). \]

Thus,

\[ P(n) = P(Z(n) = 0) = f_n(0), \quad n = 1, 2 \ldots \]

is a monotone increasing sequence having the limit

\[ \lim_{n \to \infty} P(n) = P. \]
Extinction
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\[ \lim_{n \to \infty} P(n) = P. \]

\( P \) is the probability of extinction of the process which is the minimal nonnegative root of the equation \( s = f(s) \).
Asymptotic behavior of the survival probability for subcritical processes

\[ Q(n) : = P(Z(n) > 0 | Z(0) = 1) = \sum_{k=1}^{\infty} P(Z(n) = k) \leq \sum_{k=1}^{\infty} kP(Z(n) = k) = EZ(n) = m^n. \]

Is this estimate sharp?
Asymptotic behavior of the survival probability for subcritical processes

\[ Q(n) : = \mathbb{P}(Z(n) > 0|Z(0) = 1) = \sum_{k=1}^{\infty} \mathbb{P}(Z(n) = k) \]

\[ \leq \sum_{k=1}^{\infty} k \mathbb{P}(Z(n) = k) = \mathbb{E}Z(n) = m^n. \]

Is this estimate sharp?

**Theorem**

*If* \( m < 1 \) *then*

\[ \mathbb{P}(Z(n) > 0) = Q(n) \sim K m^n (1 + o(1)), \; K > 0, \]

*if and only if*

\[ \mathbb{E} \xi \log^+ \xi = \mathbb{E}Z(1) \log^+ Z(1) \]

\[ = \sum_{k=1}^{\infty} p_k k \log k < \infty. \]
NOTE THAT

\[
\frac{\mathbb{P}(Z(n + 1) > 0)}{m^{n+1}} = \frac{1 - f_{n+1}(0)}{m^{n+1}} = \frac{1 - f(f_n(0))}{m^{n+1}} \leq \frac{m(1 - f_n(0))}{m^{n+1}} = \frac{\mathbb{P}(Z(n) > 0)}{m^n}.
\]
NOTE THAT

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\]

This, in view of the theorem gives

\[
\lim_{n \to \infty} \frac{\mathbb{P}(Z(n) > 0)}{m^n} = K > 0
\]

and

\[
\frac{\mathbb{P}(Z(n) > 0)}{m^n} \geq K
\]

for ALL \(n\).
NOTE THAT

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\]

This, in view of the theorem gives

\[
\lim_{n \to \infty} \frac{P(Z(n) > 0)}{m^n} = K > 0
\]

and

\[
\frac{P(Z(n) > 0)}{m^n} \geq K
\]

for ALL \( n \).

Besides,

\[
\frac{m^n}{Q(n)} = \frac{E Z(n)}{P(Z(n) > 0)} = E [Z(n) | Z(n) > 0] \approx K^{-1}, \: n \to \infty.
\]
Practical estimates for the survival probability

**Lemma**

If $\xi \geq 0$ with probability 1 and is not identical to zero then

$$P(\xi > 0) \geq \frac{(E\xi)^2}{E\xi^2}.$$  

**Proof.** EXERCISE
We have

\[ P(Z(n) > 0) \geq \frac{(EZ(n))^2}{EZ^2(n)} = \frac{(EZ(n))^2}{\text{Var} Z(n) + (EZ(n))^2} \]

\[ = \frac{m^{n+1}(1 - m)}{\sigma^2 (1 - m^n) + m^{n+1}(1 - m)}. \]
We have

\[ P(Z(n) > 0) \geq \frac{(EZ(n))^2}{EZ^2(n)} = \frac{(EZ(n))^2}{\text{Var} Z(n) + (EZ(n))^2} = \frac{m^{n+1}(1 - m)}{\sigma^2(1 - m^n) + m^{n+1}(1 - m)}. \]

Therefore, for any fixed $n$

\[ \frac{P(Z(n) > 0)}{m^n} \geq \lim_{l \to \infty} \frac{P(Z(l + n) > 0)}{m^{l+n}} = K \]

\[ \geq \lim_{l \to \infty} \frac{m(1 - m)}{\sigma^2(1 - m^l) + m^{l+1}(1 - m)} = \frac{m(1 - m)}{\sigma^2}. \]
Set

\[ P_N(Z(n) > 0) = P(Z(n) > 0|Z(0) = N), \quad E_N[Z(n)] = E[Z(n)|Z(0) = N]. \]

By Markov inequality

\[ P_N(Z(n) > 0) = P(Z(n) \geq 1|Z(0) = N) \leq E_N[Z(n)] = Nm^n, \]

where \( N \) is the number of founders of the population.
Theorem

Consider a subcritical Galton-Watson process, initiated by $Z(0) = N$ individuals. Then

$$NP_1(Z(n) > 0) \left(1 - P_1(Z(n) > 0)\right)^N \leq P_N(Z(n) > 0) \leq NP_1(Z(n) > 0).$$

If the reproduction variance $\sigma^2 < \infty$, then

$$Nm^n \times \left(\frac{1-m}{\sigma^2}\right) (1 - m^n)^{N-1} \leq P_N(Z(n) > 0) \leq Nm^n.$$
Survival probability for the North Atlantic right whales
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.
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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 $\mu$ 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

$$m = p(1 - \mu) + 2p\mu = p(1 + \mu).$$
The following estimates for $p$, $\mu$, and, as a result, for $m$ are known:

<table>
<thead>
<tr>
<th></th>
<th>$\mu = 0.051$</th>
<th>$\mu = 0.038$</th>
</tr>
</thead>
<tbody>
<tr>
<td>$p = 0.94$</td>
<td>$m = 0.988$</td>
<td>$m = 0.976$</td>
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</tbody>
</table>

Applying our results to the data and knowing that there are now around 150 female members of the North Atlantic right whales we get

<table>
<thead>
<tr>
<th>Survival</th>
<th>$m$</th>
<th>0.988</th>
<th>0.976</th>
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</thead>
<tbody>
<tr>
<td>$n \approx 357$</td>
<td>$n \approx 177$</td>
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<table>
<thead>
<tr>
<th>Extinction</th>
<th>$m$</th>
<th>0.988</th>
<th>0.976</th>
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</thead>
<tbody>
<tr>
<td>$n \approx 796$</td>
<td>$n \approx 395$.</td>
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</table>
Conditional limit theorem for subcritical case

**Theorem**

If \( m < 1 \) then

\[
\lim_{n \to \infty} \mathbb{E}[s^{Z(n)}|Z(n) > 0] = F^*(s) = \sum_{k=1}^{\infty} r_k s^k,
\]

where \( r_1 + r_2 + \cdots = 1 \).
Multidimensional limit theorems for subcritical case

Theorem

If \( m < 1 \) and

\[
N_r = n_1 + n_2 + \cdots + n_r, \quad r = 1, 2, \ldots
\]

are such that \( n_1 \to \infty, n_{r+1} - n_r \to \infty \), then

\[
\mathcal{L}(Z(N_1), \ldots, Z(N_{k+1}) | Z(N_{k+1}) > 0) \to \mathcal{L}(Z^*_1, \ldots, Z^*_{k+1}),
\]

where \( Z^*_1, \ldots, Z^*_k \) are iid with \( \mathbb{E} S^{Z^*_i} = F^*(s) \) and are independent of \( Z^*_{k+1} \).
The time to extinction of subcritical processes

**Theorem**

If $m < 1$ and $E\xi \log^+ \xi < \infty$ then

$$E_N[\tau] = E_N[\tau \mid Z(0) = N] \sim \frac{\ln N}{|\ln m|}, \quad N \to \infty.$$
The time to extinction of subcritical processes

**Theorem**

*If \( m < 1 \) and \( \mathbb{E} \xi \log^+ \xi < \infty \) then*

\[
\mathbb{E}_N[\tau] = \mathbb{E}_N[\tau | Z(0) = N] \sim \frac{\ln N}{|\ln m|}, \ N \to \infty.
\]

**Proof.** We know that

\[
K m^n \leq \mathbb{P}_1(Z(n) > 0) = \mathbb{P}_1(\tau > n) \leq m^n
\]

with

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

and

\[
\mathbb{P}_N(\tau > n) \leq N m^n.
\]
Set

\[ \phi(N) = \frac{\ln N}{|\ln m|}, \quad \psi(N) = \frac{\ln \ln N - \ln K}{|\ln m|} \geq 0. \]

Observe that

\[ N m^{\phi(N)} = N m^{-\frac{\ln N}{\ln m}} = 1 \]

and

\[ \exp \left\{ -K N m^{\phi(N) - \psi(N)} \right\} = \exp \left\{ -K m^{-\psi(N)} \right\} = \exp \{ -\ln N \} = 1/N. \]
For

\[ E_N[\tau] = \sum_{n=0}^{\infty} P_N(\tau > n) \]

we have

\[ E_N[\tau] \leq \sum_{0 \leq n < \phi(N)} P_N(\tau > n) + N \sum_{n \geq \phi(N)} m^n \]

\[ \leq \phi(N) + 1 + \frac{Nm^{\phi(N)}}{1 - m} = \frac{\ln N}{|\ln m|} + \frac{2 - m}{1 - m}. \]
For 

\[ E_N[\tau] = \sum_{n=0}^{\infty} P_N(\tau > n) \]

we have

\[
E_N[\tau] \leq \sum_{0 \leq n < \phi(N)} P_N(\tau > n) + N \sum_{n \geq \phi(N)} m^n \\
\leq \phi(N) + 1 + \frac{Nm^{\phi(N)}}{1-m} = \frac{\ln N}{|\ln m|} + \frac{2-m}{1-m}.
\]

On the other hand,

\[
E_N[\tau] \geq \sum_{0 \leq n < \phi(N) - \psi(N)} P_N(\tau > n) \\
\geq (\phi(N) - \psi(N) - 1) P_N(\tau \geq \phi(N) - \psi(N)) \\
= (\phi(N) - \psi(N) - 1) (1 - P_N(\tau < \phi(N) - \psi(N))).
\]
For any $n \geq 0$

\[
P_N(\tau \leq n) = P_1^N(\tau \leq n) = (1 - P_1(\tau > n))^N \\
\leq e^{-NP_1(\tau > n)} \leq e^{-KNm^n}
\]

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

\[
P_N(\tau \leq \phi(N) - \psi(N)) \leq e^{-KNm^\phi(N) - \psi(N)} = \frac{1}{N}.
\]
For any \( n \geq 0 \)

\[
\mathbf{P}_N(\tau \leq n) = \mathbf{P}_1^N(\tau \leq n) = (1 - \mathbf{P}_1(\tau > n))^N \\
\leq e^{-N\mathbf{P}_1(\tau > n)} \leq e^{-KNm^n}
\]

where we have used the inequality \( 1 - x \leq e^{-x} \), \( x > 0 \). Therefore,

\[
\mathbf{P}_N(\tau \leq \phi(N) - \psi(N)) \leq e^{-KNm^{\phi(N)-\psi(N)}} = \frac{1}{N}.
\]

As a result we get

\[
\frac{\ln N}{|\ln m|} \left( 1 - \frac{\ln \ln N - \ln K + |\ln m|}{\ln N} \right) \left( 1 - \frac{1}{N} \right) \leq \mathbf{E}_N[\tau] \\
\leq \frac{\ln N}{|\ln m|} + \frac{2 - m}{1 - m}.
\]
Example with North Atlantic right whales
The reproduction generating function of the process is

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

with mean

\[ m = p(1 - \mu) + 2p\mu = p(1 + \mu). \]

For the North Atlantic right whales we get the following estimates for the expected time to extinction in the subcritical situation:

<table>
<thead>
<tr>
<th>( m )</th>
<th>0.988</th>
<th>0.976</th>
</tr>
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<tbody>
<tr>
<td>( \mathbb{E}[\tau</td>
<td>Z(0) = 150] \approx )</td>
<td>415</td>
</tr>
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</table>
Supercritical processes
Consider now the situation $m = E\xi > 1$. 
The survival probability of a slightly advantageous mutant gene in a large stationary population
Assume that in a homogeneous well established large population, that is in the population where the average offspring size equals 1, a mutant individual appears with advantageous reproduction, i.e., that one whose the average offspring size equals \( m > 1 \).
The survival probability of a slightly advantageous mutant gene in a large stationary population

Assume that in a homogeneous well established large population, that is in the population where the average offspring size equals 1, a mutant individual appears with advantageous reproduction, i.e., that one whose the average offspring size equals \( m > 1 \).

Let \( f(s) = \mathbb{E}s^\xi \) be the offspring generating function of the mutant gene and let \( Q = 1 - P \) be the survival probability of the corresponding Galton-Watson process. Thus, for some \( \theta \in [s, 1] \)

\[
Q = 1 - f(1 - Q) \\
= f'(1)Q - \frac{f''(\theta)}{2!}Q^2 \geq f'(1)Q - \frac{f''(1)}{2!}Q^2.
\]
The survival probability of a slightly advantageous mutant gene in a large stationary population

Assume that in a homogeneous well established large population, that is in the population where the average offspring size equals 1, a mutant individual appears with advantageous reproduction, i.e., that one whose the average offspring size equals \( m > 1 \).

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\[
Q = 1 - f(1 - Q) \\
= f'(1)Q - \frac{f'''(\theta)}{2!}Q^2 \geq f'(1)Q - \frac{f'''(1)}{2!}Q^2.
\]

Since \( \mathbb{E}[\xi(\xi - 1)] = f'''(1) \) we get

\[
Q \geq mQ - \mathbb{E}[\xi(\xi - 1)]Q^2/2. 
\]
The survival probability of a slightly advantageous mutant gene in a large stationary population

Assume that in a homogeneous well established large population, that is in the population where the average offspring size equals 1, a mutant individual appears with advantageous reproduction, i.e., that one whose the average offspring size equals $m > 1$.

Let $f(s) = E s^\xi$ be the offspring generating function of the mutant gene and let $Q = 1 - P$ be the survival probability of the corresponding Galton-Watson process. Thus, for some $\theta \in [s, 1]$

$$Q = 1 - f(1 - Q)$$

$$= f'(1)Q - \frac{f'''(\theta)}{2!}Q^2 \geq f'(1)Q - \frac{f'''(1)}{2!}Q^2.$$

Since $E[\xi(\xi - 1)] = f'''(1)$ we get

$$Q \geq mQ - E[\xi(\xi - 1)]Q^2 / 2.$$

Hence

$$Q \geq \frac{2(m - 1)}{E[\xi(\xi - 1)]}.$$
Thus, for any Galton-Watson process with reproduction mean $m = 1 + \varepsilon > 1$ and variance $\sigma^2$

$$Q \geq \frac{2\varepsilon}{\sigma^2 + m\varepsilon}.$$ 

**Exercise.** Show that for the case of binary splitting, $f(s) = q + ps^2$, $q + p = 1$ with $E[\xi] = m = 2p > 1$ this estimate is sharp.
Thus, for any Galton-Watson process with reproduction mean \( m = 1 + \varepsilon > 1 \) and variance \( \sigma^2 \)

\[
Q \geq \frac{2\varepsilon}{\sigma^2 + m\varepsilon}.
\]

Thus, there is no smaller bound valid for all Galton-Watson processes, and it is natural to suspect that for little \( \varepsilon \) indeed

\[
Q \approx \frac{2\varepsilon}{\sigma^2 + m\varepsilon} \approx \frac{2(m - 1)}{\sigma^2}.
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Thus, there is no smaller bound valid for all Galton-Watson processes, and it is natural to suspect that for little $\varepsilon$ indeed

$$Q \approx \frac{2\varepsilon}{\sigma^2 + m\varepsilon} \approx \frac{2(m - 1)}{\sigma^2}.$$ 

Thus, the survival probability is proportional to the ratio between the selective advantage of the mutant gene and variance of the offspring size.
Theorem

Assume that the reproduction generating functions

\[ f^{(\varepsilon)}(s) = \mathbb{E}[s^{\xi^{(\varepsilon)}}], \quad \varepsilon \geq 0, \]

are such that \( \mathbb{E}[\xi^{(\varepsilon)}] = 1 + \varepsilon \) and for some \( \varepsilon_0 > 0 \)

\[ \sup_{0 \leq \varepsilon \leq \varepsilon_0} \mathbb{E}[(\xi^{(\varepsilon)})^3] = c_3 < \infty, \quad \inf_{0 \leq \varepsilon \leq \varepsilon_0} \mathbb{E}[\xi^{(\varepsilon)}(\xi^{(\varepsilon)} - 1)] = c_2 > 0, \]

\[ \inf_{0 \leq \varepsilon \leq \varepsilon_0} f^{(\varepsilon)}(0) = c_0 > 0. \]

Then

\[ Q = \frac{2\varepsilon}{\mathbb{E}[\xi^{(\varepsilon)}(\xi^{(\varepsilon)} - 1)]]} + o(\varepsilon) \quad \text{as} \quad \varepsilon \to 0. \]

If further

\[ \sigma_\varepsilon^2 = \text{Var}[\xi^{(\varepsilon)}] \to \sigma_0^2 > 0, \]

as \( \varepsilon \to 0 \), then

\[ Q = \frac{2\varepsilon}{\sigma_0^2} + o(\varepsilon). \]
Accumulated population size of supercritical populations which are known to die out
It is known that supercritical populations, which are known to die out sooner or later, behave as subcritical populations. We study only the accumulated populations size

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

up to generation \( n \). If \( Z(0) = 1 \), then

\[
\mathbb{E}[T(n)] = \mathbb{E}[Z(0) + Z(1) + \cdots + Z(n-1)] = \mathbb{E}[Z(0)] + \mathbb{E}[Z(1)] + \cdots + \mathbb{E}[Z(n-1)] = 1 + m + \cdots + m^n.
\]
If $m < 1$ 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

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

On the other hand, if $m \geq 1$ then $\mathbf{E} [T(n)] \to \infty$, 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 $\tau$, we get the following statement.
Theorem

If $m > 1$ then

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

where $P = P(\tau < \infty)$ is the extinction probability of the process (check that $f'(P) < 1$).
Proof. We write

$$E \left[ T \mid \tau < \infty \right] = \frac{E \left[ T ; \tau < \infty \right]}{P(\tau < \infty)}.$$
Proof. We write

\[ E[T \mid \tau < \infty] = \frac{E[T ; \tau < \infty]}{P(\tau < \infty)}. \]

Further,

\[ E[T ; \tau < \infty] = \sum_{n=0}^{\infty} E[Z(n) ; n < \tau < \infty]. \]
**Proof.** We write

\[
E[T \mid \tau < \infty] = \frac{E[T ; \tau < \infty]}{P(\tau < \infty)}.
\]

Further,

\[
E[T ; \tau < \infty] = \sum_{n=0}^{\infty} E[Z(n) ; n < \tau < \infty].
\]

Now observe that

\[
E[Z(n) ; n < \tau < \infty] = \sum_{k=1}^{\infty} kP(Z(n) = k ; n < \tau < \infty)
\]

\[
= \sum_{k=1}^{\infty} kP(Z(n) = k)P^k,
\]

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

\[
\mathbb{E} \left[ Z(n); n < \tau < \infty \right] = P \sum_{k=1}^{\infty} kP(Z(n) = k)P^{k-1}
\]

\[
= Pf'_{n}(P) = P \left( f'(P) \right)^{n}.
\]

This gives the desired statement.
In particular, in the supercritical geometric case \( P = q/p = m^{-1} < 1 \) and
\[
f'(P) = \frac{qp}{(1-pP)^2} = \frac{1}{m}.
\]
Hence,
\[
\mathbb{E}[T | \tau < \infty] = \frac{1}{1 - m^{-1}} = \frac{m}{m - 1} = 1 + \frac{1}{m - 1}.
\]
Note that this expectation is monotone decreasing to 1 when \( m \) increases.
Conditional limit theorem for critical processes

**Theorem**

If

\[ m = f'(1) = 1, \quad f''(1) = 2B \in (0, \infty). \]

then

\[ Q(n) = P(Z(n) > 0) \sim \frac{1}{Bn}, \quad n \to \infty, \]

and

\[ \lim_{n \to \infty} E \left[ \exp \left\{ -\lambda \frac{Z(n)}{Bn} \right\} \mid Z(n) > 0 \right] = \frac{1}{1 + \lambda}. \]
Proof. First is well known (EXERCISE). For the second:

\[ \mathbb{E} \left[ \exp \left\{ -\lambda \frac{Z(n)}{Bn} \right\} \middle| Z(n) > 0 \right] = 1 - \frac{1 - f_n \left( \exp \left\{ -\frac{\lambda}{Bn} \right\} \right)}{Q(n)}. \]
Proof. First is well known (EXERCISE). For the second:

\[
E \left[ \exp \left\{ -\lambda \frac{Z(n)}{B_n} \right\} \middle| Z(n) > 0 \right] = 1 - \frac{1 - f_n \left( \exp \left\{ -\frac{\lambda}{B_n} \right\} \right)}{Q(n)}.
\]

Now let \( l = l(n) \) be such that

\[
f_l(0) \leq \exp \left\{ -\frac{\lambda}{B_n} \right\} \leq f_{l+1}(0)
\]

or

\[
1 - f_l(0) \geq 1 - \exp \left\{ -\frac{\lambda}{B_n} \right\} \geq 1 - f_{l+1}(0)
\]
Proof. First is well known. For the second:

$$
\mathbb{E} \left[ \exp \left\{ -\lambda \frac{Z(n)}{Bn} \right\} \mid Z(n) > 0 \right] = 1 - \frac{1 - f_n \left( \exp \left\{ -\frac{\lambda}{Bn} \right\} \right)}{Q(n)}.
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$$

or

$$
1 - f_l(0) \geq 1 - \exp \left\{ -\frac{\lambda}{Bn} \right\} \geq 1 - f_{l+1}(0)
$$

or

$$
Q(l) \geq \frac{\lambda}{Bn} (1 + \varepsilon^*(n)) \geq Q(l + 1).
$$

where $\varepsilon^*(n) \to 0$, $n \to \infty$. 
Proof. First is well known. For the second:

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E \left[ \exp \left\{ -\lambda \frac{Z(n)}{Bn} \right\} \mid Z(n) > 0 \right] = 1 - \frac{1 - f_n \left( \exp \left\{ -\frac{\lambda}{Bn} \right\} \right)}{Q(n)}.
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\]

or

\[
Q(l) \geq \frac{\lambda}{Bn} \left( 1 + \varepsilon^*(n) \right) \geq Q(l + 1).
\]

where \( \varepsilon^*(n) \to 0, \ n \to \infty \). Hence,

\[
\frac{1}{Bl} \sim Q(l) \sim \frac{\lambda}{Bn} = \frac{1}{B \left( n/\lambda \right)}.
\]
Consequently, \( l \sim \lfloor n/\lambda \rfloor \).
Consequently, $l \sim \lfloor n/\lambda \rfloor$. Thus, in view of

$$1 - f_n(f_{l+1}(0)) \leq 1 - f_n \left( \exp \left\{ -\frac{\lambda}{Bn} \right\} \right) \leq 1 - f_n(f_l(0))$$

we have

$$1 - f_n \left( \exp \left\{ -\frac{\lambda}{Bn} \right\} \right) \sim 1 - f_{n+l}(0) \sim \frac{1}{B(n+l)}$$

$$\sim \frac{1}{Bn(1 + \lambda^{-1})} = \frac{\lambda}{Bn(1 + \lambda)}.$$
Consequently, \( l \sim [n/\lambda] \). Thus, in view of

\[
1 - f_n(f_{l+1}(0)) \leq 1 - f_n\left(\exp\left\{-\frac{\lambda}{Bn}\right\}\right) \leq 1 - f_n(f_l(0))
\]

we have

\[
1 - f_n\left(\exp\left\{-\frac{\lambda}{Bn}\right\}\right) \sim 1 - f_{n+l}(0) \sim \frac{1}{B(n+l)}
\]

\[
\sim \frac{1}{Bn(1 + \lambda^{-1})} = \frac{\lambda}{Bn(1 + \lambda)}.
\]

Hence

\[
\frac{1 - f_n\left(\exp\left\{-\frac{\lambda}{Bn}\right\}\right)}{Q(n)} \sim \frac{Bn\lambda}{Bn(1 + \lambda)} = \frac{\lambda}{1 + \lambda}
\]
Consequently, \( l \sim \lfloor n/\lambda \rfloor \). Thus, in view of

\[
1 - f_n(f_{l+1}(0)) \leq 1 - f_n \left( \exp \left\{ -\frac{\lambda}{Bn} \right\} \right) \leq 1 - f_n(f_l(0))
\]

we have

\[
1 - f_n \left( \exp \left\{ -\frac{\lambda}{Bn} \right\} \right) \sim 1 - f_{n+l}(0) \sim \frac{1}{B(n+l)}
\]

\[
\sim \frac{1}{Bn(1 + \lambda^{-1})} = \frac{\lambda}{Bn(1 + \lambda)}.
\]

Hence

\[
\frac{1 - f_n \left( \exp \left\{ -\frac{\lambda}{Bn} \right\} \right)}{Q(n)} \sim \frac{Bn\lambda}{Bn(1 + \lambda)} = \frac{\lambda}{1 + \lambda}
\]

and, therefore,

\[
\lim_{n \to \infty} \mathbb{E} \left[ \exp \left\{ -\lambda \frac{Z(n)}{Bn} \right\} \mid Z(n) > 0 \right] = 1 - \lim_{n \to \infty} \frac{1 - f_n \left( \exp \left\{ -\frac{\lambda}{Bn} \right\} \right)}{Q(n)}
\]

\[
= 1 - \frac{\lambda}{1 + \lambda} = \frac{1}{1 + \lambda}
\]

proving the theorem.
Exercise. Let $Z(k, n), \ 0 \leq k < n$ be the number of particles at moment $k$ which have nonempty offspring at moment $n$. Show that if
\[ m = f'(1) = 1, \ f''(1) = 2B \in (0, \infty), \]
then
\[ \lim_{n \to \infty} \mathbb{E} \left[ s^{Z(nt, n)} | Z(n) > 0 \right] = \frac{s(1-t)}{1-st}, \]
and, therefore, for any $k = 1, 2, \ldots$
\[ \lim_{n \to \infty} \mathbb{P} (Z(nt, n) = k | Z(n) > 0) = (1-t)t^{k-1}. \]
Exercise 2. Show that if

\[ m = f'(1) = 1, \quad f''(1) = 2B \in (0, \infty), \]

then for any \( t \in (0, 1) \)

\[ \left\{ \frac{2Z(nt)}{Bn} | Z(n) > 0 \right\} \quad \overset{d}{\rightarrow} \quad \eta + \zeta \]

where \( \eta, \zeta \) are independent exponentially distributed random variables with parameters

\[ \frac{1}{t} \quad \text{and} \quad \frac{1}{(1 - t) t}. \]
The Galton-Watson process with immigration:
Specified by

\[ f(s) = \mathbb{E} s^\xi, \quad g(s) = \mathbb{E} s^\eta = \sum_{k=1}^{\infty} P(\eta = k) s^k, \]

and

\[ Y(n + 1) = \xi_1^{(n)} + \ldots + \xi_{Y(n)}^{(n)} + \eta^{(n)}, \quad \eta^{(n)} \overset{d}{=} \eta, \text{ and iid.} \]
The Galton-Watson process with immigration:
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and

\[ Y(n+1) = \xi_1^{(n)} + \ldots + \xi_{Y(n)}^{(n)} + \eta^{(n)}, \quad \eta^{(n)} \overset{d}{=} \eta, \text{ and iid}. \]

We have

\[
\Phi(n+1, s) = \mathbb{E} \left[ s^{Y(n+1)} | Y(0) = 0 \right] \\
= \mathbb{E} \left[ s^{\xi_1^{(n)} + \ldots + \xi_{Y(n)}^{(n)} + \eta^{(n)}} | Y(0) = 0 \right] \\
= g(s)\Phi(n, f(s)) = \ldots = \prod_{k=0}^{n+1} g(f_k(s)).
\]
Exercise 3
Show that if
\[ g'(1) = b < \infty \]
and
\[ f'(1) = 1, \quad B = f''(1)/2 \in (0, \infty) \]
then for \( \theta = b/B \)

\[ \lim_{n \to \infty} P \left( \frac{Y(n)}{Bn} \leq x \right) = \frac{1}{\Gamma(\theta)} \int_0^x y^{\theta-1} e^{-y} dy. \]