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Size-biased Galton-Watson processes in the linear fractional case

(based on a forthcoming paper with F.C. Klebaner and U. Rösler)

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1 The Galton-Watson process

The Galton-Watson process (GWP) is one of the basic population models in population genetics. This is a Markov chain describing

- consecutive generation sizes of a population of mortal particles
- particles have iid offspring numbers.

The GWP is a relevant model for a population experiencing no limitations in resource supply. Various transformations of the GWP also can be used in population genetics. For example

- GWP conditioned on non-extinction - describes the initial fate a mutant allele getting fixed in a large population,
- time-reversed GWP - gives a backward view on random demographic fluctuations.

Let p_i be the probability that a particle produces i children with the average offspring number $m = \sum_{i\geq 1} ip_i$. The probability generating function

$$f(s) = \sum_{i\geq 0} p_i s^i, \ \ f'(1) = m.$$

Then the n-step transitional probabilities of the GWP satisfy

$$\begin{aligned} \sum_{j\geq 0} P_n(1,j)s^j &= f_n(s) = \underbrace{f(\ldots(f}_{n \text{ times}}(s))\ldots) \\ \sum_{j\geq 0} P_n(i,j)s^j &= f_n^i(s), \ \ i = 0,1,2,\ldots \end{aligned}$$

and after taking derivatives over s

$$\sum_{j=1}^{\infty} P_n(i,j)js^j = isf_n'(s)f_n^{i-1}(s), \ \ i = 1,2,\ldots \tag{1}$$

Solutions of the equation $x = f(x)$

- $x = 1$ is always a solution
- if $m < 1$, then there is a second root $r > 1$
- if $m > 1$, then there is a second root $0 \le r < 1$
- if $m = 1$, put $r = 1$
- $q = f(q)$, where $q = \min(r, 1)$ is the extinction probability
- $r_1 = f(r_1)$, where $r_1 = r/q = \max(r, 1)$
- if $x = f(x)$, then for $\phi(s) = f(xs)/x$ we have

$$\phi_n(s) = f_n(xs)/x, \ \phi_n'(s) = f_n'(xs)$$

2 Linear fractional reproduction

Consider a modified geometric distribution $\mathsf{LF}(q_0, u)$, $0 < u < 1$

$$\begin{aligned} p_0 &= 1 - q_0 \\ p_i &= q_0 u^{i-1}(1-u),\ i = 1, 2, \ldots \end{aligned}$$

so that $m = \frac{q_0}{1-u}$, $r = \frac{p_0}{u}$.

$$\boxed{\mathsf{LF}(u,u) = \mathsf{Geom}(1-u)}$$

Linear-fractional pgf

$$f(s) = 1 - \frac{q_0(1-s)}{1-us} \quad \text{and} \quad f_n(s) = 1 - \frac{q_n(1-s)}{1-u_n s}$$

where

$$q_n = \frac{m^n(1-r)}{m^n - r},\ u_n = \frac{m^n - 1}{m^n - r}, \quad \text{if } m \neq 1.$$

The double generating function

$$\sum_{i\geq 0}\sum_{j\geq 0} t^i P_n(i,j)s^j = \sum_{i\geq 0} t^i f_n^i(s) = \frac{1}{1-tf_n(s)}$$
$$= \frac{1-u_n s}{1-t(1-q_n)-[u_n+t(q_n-u_n)]s}$$

has a linear fractional pgf representation

$$\sum_{i\geq 0}\sum_{j\geq 0} t^i(1-t)P_n(i,j)s^j = 1-\frac{tq_n(1-s)}{1-t(1-q_n)-[u_n+t(q_n-u_n)]s}$$
$$= 1-\frac{b(1-s)}{1-cs}$$

with $b=\frac{q_n t}{1-(1-q_n)t}$, $c = 1-\frac{(1-u_n)(1-t)}{1-(1-q_n)t}$.

Thus

$$\begin{aligned}
\sum_{i=0}^{\infty} t^i P_n(i,j) &= \frac{b(1-c)c^{j-1}}{1-t} \\
&= \frac{q_n v_n t}{(1-(1-q_n)t)^2}\left(1-\frac{(1-u_n)(1-t)}{1-(1-q_n)t}\right)^{j-1}
\end{aligned}$$

resulting in a key relation in the linear fractional case

$$\sum_{i=1}^{\infty} t^i P_n(i,j) = tr^{1-j} f_n'(rt) f_n^{j-1}(rt),\ \ j \geq 1. \tag{2}$$

Notice that

$$\frac{f'(s)}{m} = \left(\frac{1-u}{1-us}\right)^2$$

3 Harris-Sevastyanov transformation

Define the HS-transformation of the GWP as a new Markov chain by

$$\hat{P}(i,j) = P(i,j)r^{j-i}, \ i \geq 0, \ j \geq 0$$

Then

$$\begin{aligned}
\hat{P}_2(i,j) &= \sum_{k\geq 0} P(i,k)r^{k-i}P(k,j)r^{j-k} = P_2(i,j)r^{j-i} \\
\hat{P}_n(i,j) &= P_n(i,j)r^{j-i}
\end{aligned}$$

and

$$\begin{aligned}
\sum_{j=0}^{\infty} \hat{P}_n(i,j)s^j &= \sum_{j=0}^{\infty} P_n(i,j)s^j r^{j-i} \\
&= (f_n(rs)/r)^i = \hat{f}_n^i(s)
\end{aligned}$$

The new chain is a GWP with a **dual reproduction law**

$$\hat{f}(s) = f(rs)/r, \ \hat{p}_i = p_i r^{i-1}.$$

If the original GWP $\{Z_n\}_{n\geq 0}$ is supercritical $m > 1$, then the HS-transformation is a subcritical GWP. It is the original process conditioned on extinction:

$$\begin{aligned} P(Z_n = j | Z_0 = i, Z_\infty = 0) &= \frac{P(Z_n = j, Z_\infty = 0 | Z_0 = i)}{P(Z_\infty = 0 | Z_0 = i)} \\ &= q^{-i} P(Z_\infty = 0 | Z_n = j) P_n(i,j) \\ &= q^{j-i} P_n(i,j) \\ &= \hat{P}_n(i,j) \end{aligned}$$

Observe that

- $\hat{m} = f'(r),\ \hat{r} = 1/r,\ \hat{q} = 1/r_1,\ \hat{r}_1 = 1/q$
- if $x = f(x)$, then $1/x = \hat{f}(1/x)$
- $\hat{\hat{f}}(s) = \hat{f}(\hat{r}s)/\hat{r} = f(r\hat{r}s)/(r\hat{r}) = f(s)$

> The HS-transformation of a subcritical GWP
> is the supercritical GWP whose HS-transformation
> brings back the original subcritical GWP.

In the LF(q_0, u) case the dual reproduction law is LF$(\hat{q}_0, \hat{u})$

$$\hat{f}(s) = 1 - \frac{\hat{q}_0(1-s)}{1-\hat{u}s}$$

with the dual parameters $\hat{q}_0 = 1 - u$, $\hat{u} = 1 - q_0$, and $\hat{m} = \frac{1}{m}$.

4 Transformations excluding zero state

The GWP is a transient Markov chain with an absorbing state 0. After taking away the absorbing state, consider positive eigen-functions

$$\sum_{j \geq 1} P(i,j)h(j) = \lambda h(i), \; i \geq 1$$

and introduce new Markov chains on the state space $\{1, 2, 3, \ldots\}$ with one-step transition probabilities

$$Q(i,j) \quad = \quad \frac{P(i,j)h(j)}{\lambda h(i)}, \; \sum_{j \geq 1} Q(i,j) = 1.$$

The weighted probabilities make more frequent the transitions with larger values of the ratio $h(j)/h(i)$.

The n-step transitional probabilities

$$Q_2(i,j) = \sum_{k\geq 0} \frac{P(i,k)h(k)}{\lambda h(i)} \cdot \frac{P(k,j)h(j)}{\lambda h(k)} = \frac{P_2(i,j)h(j)}{\lambda^2 h(i)}$$

$$Q_n(i,j) = \frac{P_n(i,j)h(j)}{\lambda^n h(i)}$$

If $x = f(x)$ and $h(i) = ix^i$, then due to (1)

$$\sum_{j=1}^{\infty} P(i,j)h(j) = \lambda h(i) \text{ with } \lambda = f'(x)$$

- case $x = 1$: Lyons, Pemantle, Peres (1995)
- case $x = q$: Lamperti-Ney (1968)

Similarly, a positive eigen-measure neglecting the zero state

$$\sum_{i\geq 1} \mu(i)P(i,j) = \lambda\mu(j), \ j \geq 1$$

leads to time-reversed transition probabilities

$$R_n(i,j) = \frac{\mu(j)P_n(j,i)}{\lambda^n \mu(i)}.$$

If $x = f(x)$ and $\mu(i) = x^{-i}$, then in the LF-case due to (2)

$$\sum_{i=1}^{\infty} \mu(i)P(i,j) = \lambda\mu(j) \text{ with } \lambda = f'(r/x).$$

Important particular case $x = r_1$.

5 Size-biased GWP

A GWP with immigration (GWI) is a Markov chain with transition probabilities

$$\tilde{H}(i,j) = \sum_{k=0}^{j} P(i,j-k)\tilde{p}_k, \;\; i \geq 0, \;\; j \geq 0,$$

where $\{\tilde{p}_k\}_{k=0}^{\infty}$ is the distribution of the number of immigrants. If $g(s) = \sum_{k=0}^{\infty} \tilde{p}_k s^k$, then the generating functions of the GWI are

$$\sum_{j=0}^{\infty} \tilde{H}(i,j)s^j = g(s)f^i(s)$$

$$\sum_{j=0}^{\infty} \tilde{H}_n(i,j)s^j = g(s)g(f(s))\dots g(f_{n-1}(s))f_n^i(s)$$

GWI is the number of mortals in a GWP with an immortal particle

- the immortal particle reproduces itself and a number of mortal particles with pgf $g(s)$
- mortal particles reproduce according pgf $f(s)$

GWP with an immortal particle: GWÎ $=$ GWI$+1$ has transitions

$$H_n(i,j) = \tilde{H}_n(i-1, j-1),\ i \geq 1,\ j \geq 1$$
$$\sum_{j=1}^{\infty} H_n(i,j)s^j = sg(s)g(f(s))\dots g(f_{n-1}(s))f_n^{i-1}(s)$$

Notice that

$$f_n'(s) = f'(s)f'(f(s))\dots f'(f_{n-1}(s))$$

Size-biased GWP: $\widehat{\mathrm{GW}}$P = GW$\hat{\mathrm{I}}$ with $g(s) = \frac{f'(s)}{m}$

$$\sum_{j=0}^{\infty} H_n(i,j)s^j = sm^{-n}f_n'(s)f_n^{i-1}(s)$$

In the $\widehat{\mathrm{GW}}$P with a LF(q_0, u) reproduction the number of immigrants is the sum of two independent Geom$(1-u)$ r.v.

If $x = f(x)$, then due to (1) and (2)

- $h(i) = ix^i \Rightarrow \widehat{\mathrm{GW}}$P with the reproduction pgf $\frac{f(xs)}{x}$
- $\mu(i) = x^{-i}$ and LF $\Rightarrow \widehat{\mathrm{GW}}$P with reproduction $\frac{x}{r} f\left(\frac{rs}{x}\right)$

Case $h(i) = ix^i$ with $x = 1$

- reproduction pgf $\frac{f(xs)}{x} = f(s)$
- a GWP with an immortal lineage of size-biased offspring numbers

Case $h(i) = ix^i$ with $x = q$

- reproduction pgf $\frac{f(xs)}{x} = \begin{cases} f(s) & \text{if } m \leq 1 \\ \hat{f}(s) & \text{if } m > 1 \end{cases}$
- a GWP conditioned on not being extinct in the distant future but being extinct in the even more distant future

LF-case $\mu(i) = x^{-i}$ with $x = r_1$

$$\frac{x}{r} f\left(\frac{rs}{x}\right) = \begin{cases} f(s) & \text{if } m \leq 1 \\ \hat{f}(s) & \text{if } m > 1 \end{cases}$$

6 Esty's time-reversal

Let $\{Z_n\}_{n\geq 0}$ be a GWP with a reproduction law $\{p_i\}_{i\geq 0}$ such that $p_1 > 0$. Esty [2] introduced a reverse GW process $\{Y_n\}_{n\geq 0}$ in terms of the finite-dimensional distributions:

$$\begin{aligned}
&\mathrm{P}(Y_{n_1} = i_1, \ldots, Y_{n_k} = i_k | Y_0 = i_0) \\
&\quad = \lim_{N\to\infty} \mathrm{P}(Z_{N-n_1} = i_1, \ldots, Z_{N-n_k} = i_k | Z_N = i_0).
\end{aligned}$$

It is a Markov chain with transition probabilities

$$R(i,j) = \frac{\mu(j)}{\mu(i)\lambda} \cdot P(j,i), \ i \geq 1, \ j \geq 1,$$

where $\lambda = f'(q)$ and

$$\mu(i) \quad = \quad \lim_{n\to\infty} \frac{P_n(1,i)}{P_n(1,1)}.$$

In the linear-fractional case $\{P_n(1,i)\}_{i\geq 0}$ is the LF(q_n, u_n) distribution and therefore

$$\begin{aligned}\mu(i) &= \lim_{n\to\infty} \frac{P_n(1,i)}{P_n(1,1)} \\ &= \lim_{n\to\infty} \frac{q_n u_n^{i-1}(1-u_n)}{q_n(1-u_n)} = r_1^{1-i}.\end{aligned}$$

Theorem 1 *Consider a linear-fractional GWP with the mean offspring number m. Its Esty time-reversal process as well as its Lamperti-Ney transformation are distributed as a size-biased GWP with*

- *the original reproduction law if $m \leq 1$*
- *or the dual reproduction law if $m > 1$.*

7 References

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