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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

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

Then the  $n$ -step transitional probabilities of the GWP satisfy

$$\sum_{j \geq 0} P_n(1, j) s^j = f_n(s) = \underbrace{f(\dots(f(s))\dots)}_{n \text{ times}}$$

$$\sum_{j \geq 0} P_n(i, j) s^j = f_n^i(s), \quad i = 0, 1, 2, \dots$$

and after taking derivatives over  $s$

$$\sum_{j=1}^{\infty} P_n(i, j) j s^j = i s f_n'(s) f_n^{i-1}(s), \quad i = 1, 2, \dots \quad (1)$$

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  $0 \leq r < 1$
- 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

$$\phi_n(s) = f_n(xs)/x, \quad \phi'_n(s) = f'_n(xs)$$

## 2 Linear fractional reproduction

Consider a modified geometric distribution  $LF(q_0, u)$ ,  $0 < u < 1$

$$p_0 = 1 - q_0$$

$$p_i = q_0 u^{i-1} (1 - u), \quad i = 1, 2, \dots$$

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

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

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

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

The double generating function

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

has a linear fractional pgf representation

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

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

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

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

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

Then

$$\hat{P}_2(i, j) = \sum_{k \geq 0} P(i, k)r^{k-i}P(k, j)r^{j-k} = P_2(i, j)r^{j-i}$$

$$\hat{P}_n(i, j) = P_n(i, j)r^{j-i}$$

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

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

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

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

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

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

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

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

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

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

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

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

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

GW $\hat{I}$  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: GW $\hat{I} = \text{GW}_{I+1}$  has transitions

$$H_n(i, j) = \tilde{H}_n(i - 1, j - 1), \quad i \geq 1, \quad j \geq 1$$

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

Notice that

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

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

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

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

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

- $h(i) = i x^i \Rightarrow \widehat{\text{GWP}}$  with the reproduction pgf  $\frac{f(xs)}{x}$
- $\mu(i) = x^{-i}$  and LF  $\Rightarrow \widehat{\text{GWP}}$  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:

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

It is a Markov chain with transition probabilities

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

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

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

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

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

**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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