

AGE AND RESIDUAL LIFETIME DISTRIBUTIONS FOR BRANCHING PROCESSES

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Abstract. We introduce and investigate age and residual lifetime distributions associated with branching stochastic processes and motivated by biological applications. The required distributions and their limiting forms are derived in a general class of age-dependent branching processes with non-homogeneous Poisson immigration.

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1. Introduction.

The age (spent time or backward time) and the residual time (excess time or forward time) distributions play an important role in the renewal theory (Feller, 1971; Taylor and Karlin, 1998). For recent relevant results in this theory and extensions to regenerative and branching processes see Mitov and Yanev (2001a, 2001b, 2002, 2005) and Yanev and al. (2004). In his famous book, Harris (1963, Chapter 6) introduced the so-called limiting age distribution $A(x)$ (see (24.2) and (24.2a)) and obtained an explicit expression for this distribution in conjunction with the Bellman-Harris process. Athreya and Kaplan (1976) investigated the so-called empirical distribution $A(t, x) = Z(t, x)/Z(t)$, where $Z(t, x)$ is the number of individuals living at time t with age $\leq x$ and $Z(t) = Z(t, \infty)$ is the Bellman-Harris branching process. Note that this distribution is well defined only if $Z(t)$ does not become extinct as $t \rightarrow \infty$. In the supercritical case Athreya and Kaplan proved a.s. convergence of $A(t, x)$ to $A(x)$ under the well-known $x \log x$ condition. Taylor (1982) introduced the empirical residual and current total life distributions and proved a.s. convergence to deterministic laws (see Lemma 4.1, (4.5)) on the set of explosion. He also gave an interesting motivation for the residual and current total life within the framework of branching processes. An alternative approach that does not resort to methods of the theory of branching processes was developed by Bartlett (1969, 1970). Yakovlev and Yanev (1989) discussed age distributions in the context of cell proliferation kinetics. Asymptotic properties of age distributions associated with age-dependent branching processes allowing for cell death were studied by Nooney (1968) and Jagers (1975).

The theory of branching processes has proven itself as a powerful tool for many applied problems. It plays an especially important role in cell kinetics studies. A motivating example given in Section 2 illustrates the conceptual and technical importance of the notion of residual lifetime in such studies. This motivation calls for consideration of branching processes with non-homogeneous (in time) immigration. The present paper is concerned with the most general class of Sevastyanov's processes with and without non-homogeneous Poisson immigration and covers all (subcritical, critical, supercritical) cases. We provide closed-form formulas for the limiting age and residual time distributions that may be useful in cell kinetics studies.

The paper is organized as follows. The definitions of the so-called *average age* and *average residual lifetime* distributions are introduced in Section 3. Note that these distributions are well defined everywhere and not only on the non-extinction set as their empirical counterparts. In Section 4, a general class of age-dependent branching processes, known as the Sevastyanov processes, is investigated and the limiting average age and residual lifetime distributions are obtained. The Bellman-Harris and Markov branching processes are discussed as particular cases. In terms of the average age and residual lifetime distributions, the above-mentioned results by Harris (1963) and Taylor (1982) follow from the theory of Section 4 (formulas (4.13a) and (4.14b)) as special cases. It is worth pointing out that these formulas are now proved not only in the supercritical case but also in the subcritical and critical cases. In Section 5, the processes introduced earlier in Section 4 are generalized to include a non-homogeneous Poisson immigration component. The Poisson immigration is also generalized to allow for a random number of immigrants at each of the arrival times governed by the underlying non-homogeneous Poisson process. The probability generating functions of the processes with

immigration are shown to be related to the Poisson rate via simple analytical formulas presented in Theorem 1 of Section 5. To the best of our knowledge, such a construction has never been considered in the theory of branching processes. The limiting age and residual lifetime distributions are derived in the case where the Poisson rate $r(t)$ tends to a constant r as $t \rightarrow \infty$. Finally the Markov branching process with homogeneous Poisson immigration is investigated in greater details in Section 6.

2. A Motivating Example Pertaining to Cell Biology

The cell cycle can be broken down into four stages (phases) denoted by G_1 , S , G_2 and M (see Yakovlev and Yanev, 1989, for more explanations). The M -phase is the final stage of the mitotic cycle (MC). Upon completing this stage a cell typically divides into two daughter cells of the same type. Under some experimental conditions, there may be other possible outcomes of the cell cycle such as cell death or the formation of a single giant (polyploid) cell (Yakovlev and Zorin, 1988). It is the S -phase where DNA synthesis normally occurs. The cells in the S -phase are distinguishable by labeling with certain exogenous markers such as BrdU. These cells can then be counted in the dissociated tissue by using flow cytometry. While BrdU represents a relatively stable marker for labeling the S -phase, Ki-67 is a nuclear protein expressed in all periods of the cell cycle except the resting phase (Kee et al., 2002). Using Ki-67 it is possible to label all proliferating cells at different times after a pulse BrdU label administered at time $t = 0$. Analyzing the kinetics of cells that have been pulse-labeled with BrdU and Ki-67 on a fluorescence activated cell sorter is a routine experimental technique available to biologists.

Let $X(t)$ be an age-dependent branching process representing the number of doubly labeled cells at time $t > 0$, and let $I(0)$ be the number of cells in the S -phase (labeled with BrdU) at time $t = 0$. Suppose that, upon the completion of its MC, every cell divides with probability β or exits the cycle with probability $1 - \beta$. This gives the offspring probability generating function (p.g.f.) of the form: $h(s) = 1 - \beta + \beta s^2$, $|s| \leq 1$. We also assume that the lengths of the MC phases are independent random variables (r.v.'s). Let $F_S(x)$ and $F_{G_2+M}(x)$ stand for the cumulative distribution functions (c.d.f.'s) of the lengths of the S and $G_2 + M$ phases, respectively. The distribution of the whole MC duration is denoted by $G(x)$.

Let $Z(t)$ be a Bellman-Harris branching process (without immigration) representing the number of cells produced by a single cell with the above-described (G, h) -evolution and denote its p.g.f. by $\psi(t; s) = \mathbb{E}\{s^{Z(t)} | Z(0) = 1\}$. The p.g.f. $\varphi(t; s) = E\{s^{X(t)} | X(0) = 1\}$ satisfies the integral equation

$$\varphi(t; s) = \int_0^t h[\psi(t-u; s)] dW_0(u) + s[1 - W_0(t)], \quad \varphi(0, s) = s \quad |s| \leq 1$$

$$\psi(t; s) = \int_0^t h[\psi(t-u; s)] dG(u) + s[1 - G(t)], \quad \psi(0, s) = s \quad |s| \leq 1$$

where $W_0(x) = (R_S * F_{G_2+M})(x)$, and $R_S(0, x)$ is the stationary c.d.f. of the residual time in the S -phase given the start of the labeling experiment at time $t = 0$ and the symbol $*$ stands for the convolution. The c.d.f. $R_S(0, x)$ is essentially a limiting distribution requiring an indefinitely long prehistory of the cell population. Therefore, the c.d.f. $R_S(0, x)$ is expected

to depend on all characteristics of the process before $t = 0$, including the influx of cells from another compartment. To allow for biological variability, we treat the initial number of cells $I(0)$ in the S -phase as a r.v. with p.g.f. $g(s)$. Then the p.g.f. of the number of doubly labeled cells at time t is given by $g(\varphi(t; s))$.

The usefulness of the above-described model depends critically on our ability to specify the residual time distribution $R_S(0, x)$ on mechanistic grounds. This can be accomplished through modeling the prehistory of cell proliferation kinetics before the time of labeling and then taking the corresponding limiting distribution as a pertinent form of $R_S(0, x)$ in practical applications. The present paper is concerned with theoretical aspects of this approach.

3. Age and Residual Lifetime Distributions

Let $Z(t)$ be a continuous-time branching process representing the total number of individuals (cells) at time t , and let $Z(t, x)$ be the number of individuals (cells) at time t of age $\leq x$. Let $\bar{Z}_t(y)$ represent the number of individuals at time t whose residual lifetime is greater than y , $y \geq 0$. Note that $Z(t) = Z(t, x)$ if $x \geq t$. Denote their p.g.f.'s by $F(t; s) = \mathbb{E}\{s^{Z(t)}\}$ and $F(t, x; s) = \mathbb{E}\{s^{Z(t, x)}\}$, $t, x \geq 0$, with the corresponding expectations denoted by $M(t) = EZ(t) = \frac{\partial F(t; s)}{\partial s}|_{s=1}$ and $M(t, x) = EZ(t, x) = \frac{\partial F(t, x; s)}{\partial s}|_{s=1}$, respectively.

Definition 1. For the process $Z(t)$, the average age distribution at time $t \geq 0$ is given by

$$A_t(x) = M(t, x)/M(t), \quad x \geq 0. \quad (3.1)$$

The limiting average age distribution is defined as

$$A(x) = \lim_{t \rightarrow \infty} A_t(x). \quad (3.2)$$

Definition 2. For the process $Z(t)$ the average residual lifetime distribution at time $t \geq 0$ is given by

$$R_t(y) = 1 - \bar{R}_t(y) = 1 - \mathbb{E}\bar{Z}_t(y)/M(t), \quad y \geq 0. \quad (3.3)$$

Then the limiting average residual lifetime distribution is defined as

$$R(y) = \lim_{t \rightarrow \infty} R_t(y). \quad (3.4)$$

Note that $\mathbb{E}\bar{Z}_t(y) = M(t+y) - M(t+y, y)$. Therefore, one can write

$$\bar{R}_t(y) = \frac{M(t+y) - M(t+y, y)}{M(t)} = \frac{M(t+y)}{M(t)} \left[1 - \frac{M(t+y, y)}{M(t+y)} \right], \quad (3.5)$$

which offers some advantages over (3.3).

Remark 1. Note that (3.1) and (3.2) can be interpreted as distributions of the age and of the residual lifetime for a randomly chosen individual at the moment t . Indeed, if $Z(t) = n$ then $Z(t, x)$ will have a binomial distribution with parameters n and $p = A_t(x)$, because of the usual independence assumptions of the individual evolutions in branching processes. Therefore

$$\mathbb{E}Z(t, x) = \sum_{n=0}^{\infty} P\{Z(t) = n\} \mathbb{E}\{Z(t, x) | Z(t) = n\} = \sum_{n=0}^{\infty} P\{Z(t) = n\} n A_t(x) = A_t(x) \mathbb{E}Z(t),$$

which gives (3.1). The same applies equally to $\bar{Z}_t(y)$ and the distribution $R_t(y)$ given by (3.3). See also Boucher et al. (1999) for the discussion of this issue.

Remark 2. Since every renewal process is a particular case of the age-dependent branching process, in which every individual produces exactly one offspring, the notions introduced in (3.1) – (3.4) can be considered as a generalization of the age and residual lifetime distributions encountered in the renewal theory. However, these characteristics are more difficult to handle in the context of branching processes.

4. Age-dependent Branching Processes

Let us first consider a class of age-dependent branching processes without immigration defined by the following evolution of individual cells.

Evolution. Every cell with probability p has a random lifetime ξ with c.d.f. $G(x) = \Pr(\xi \leq x)$, $x \geq 0$, or with probability $1 - p$ it differentiates into another cell type. In other words, the lifetime ξ is identical to the MC duration. At the end of its life, every cell gives rise to ν offsprings (of the same cell type) with discrete distribution $p_k(u) = P(\nu = k | \xi = u)$, $\sum_{k=0}^{\infty} p_k(u) = 1$, $u \geq 0$. It takes a random time η with c.d.f. $L(x) = \Pr(\eta \leq x)$, $x \geq 0$, for the event of differentiation to actually occur. If $p = 1$, the stochastic process thus defined reduces to the Sevastyanov branching process (Sevastyanov, 1971). The mixture-type branching that allows for non-identical distributions of the time to division and the time to differentiation (or death) was introduced by Jagers (1975). Hyrien et al. (2005) resorted to this idea when analyzing the development of oligodendrocytes in cell culture. Denote the offspring p.g.f. by $h(s; u) = \mathbb{E}\{s^\nu | \xi = u\} = \sum_{k=0}^{\infty} p_k(u) s^k$, $|s| \leq 1$, $u \geq 0$. The most representative example is given by $h(u, s) = 1 - \beta(u) + \beta(u)s^2$, implying that the cell divides with probability $\beta(u)$ or dies with probability $1 - \beta(u)$. In what follows, our focus will be on the general case.

Using the notation introduced in Section 3, let $F(t; s) = \mathbb{E}\{s^{Z(t)}\}$ be the p.g.f. of the number of cells $Z(t)$ at time t produced by one cell of zero age and let $Z(t, x)$ be the number of cells of age $\leq x$ that are present at time t . The latter process has p.g.f. $F(t, x; s) = \mathbb{E}\{s^{Z(t, x)}\}$, $t, x \geq 0$. The p.g.f.'s $F(t; s)$ and $F(t, x; s)$ satisfy the following integral equations

$$F(t; s) = p \int_0^t h(u; F(t-u; s)) dG(u) + s\{p[1 - G(t)] + (1-p)[1 - L(t)]\} + (1-p)L(t), \quad (4.1)$$

$$F(t, x; s) = p \int_0^t h(u; F(t-u, x; s)) dG(u) + [s\delta(x-t) + 1 - \delta(x-t)]\{p[1 - G(t)] + (1-p)[1 - L(t)]\} + (1-p)L(t), \quad (4.2)$$

with initial conditions $F(0; s) = F(0, 0; s) = s$, where $\delta(z) = 1$ for $z \geq 0$ and $\delta(z) = 0$ for $z < 0$. These equations are obtained by conditioning on the evolution of the first cell and applying the law of total probability (LTP). From (4.1) and (4.2) it is not difficult to obtain equations for the corresponding expectations by taking partial derivatives with respect to s at the point $s = 1$: $M(t) = \mathbb{E}\{Z(t)\} = \partial F(t; s) / \partial s$, $M(t, x) = \mathbb{E}\{Z(t, x)\} = \partial F(t, x; s) / \partial s$, $m(u) = \partial h(u; s) / \partial s$. Then one has

$$M(t) = p \int_0^t M(t-u)m(u)dG(u) + p[1 - G(t)] + (1-p)(1 - L(t)), \quad (4.3)$$

$$M(t, x) = p \int_0^t M(t-u, x) m(u) dG(u) + \delta(x-t) \{p[1-G(t)] + (1-p)(1-L(t))\}, \quad (4.4)$$

with initial conditions $M(0) = 1 = M(0, 0)$.

Let us now consider equations (4.3) and (4.4) more closely. Let α be a real root of the characteristic equation

$$p \int_0^\infty e^{-\alpha u} m(u) dG(u) = 1. \quad (4.5)$$

Remark 3. If $M = p \int_0^\infty m(u) dG(u) > 1$ there exists a unique α which is known to be positive (supercritical case). If $M = 1$ then $\alpha = 0$ (critical case). If $M < 1$ then it is possible that the equation (4.5) has no solution, but if it exists it has to be negative (subcritical case).

From this point on, it will be assumed that (4.5) has a unique solution α . This critical parameter (known also as the Malthusian parameter) determines the asymptotic behavior of the process $Z(t)$. Introducing the notation:

$$M_\alpha(t) = M(t)e^{-\alpha t}, \quad M_\alpha(t, x) = M(t, x)e^{-\alpha t},$$

$$G_{\alpha,p}(t) = p \int_0^t e^{-\alpha u} m(u) dG(u),$$

$$W_{\alpha,p}(t) = e^{-\alpha t} \{p[1-G(t)] + (1-p)[1-L(t)]\} \text{ and}$$

$$W_{\alpha,p,x}(t) = e^{-\alpha t} \delta(x-t) \{p[1-G(t)] + (1-p)[1-L(t)]\},$$

it is not difficult to see that (4.3) and (4.4) are equivalent to the following renewal-type equations

$$M_\alpha(t) = \int_0^t M_\alpha(t-u) dG_{\alpha,p}(u) + W_{\alpha,p}(t), \quad (4.6)$$

$$M_\alpha(t, x) = \int_0^t M_\alpha(t-u, x) dG_{\alpha,p}(u) + W_{\alpha,p,x}(t). \quad (4.7)$$

Equations (4.6) and (4.7) have unique solutions which are bounded on every finite interval. The solutions are given by

$$M_\alpha(t) = \int_0^t W_{\alpha,p}(t-u) dH_{\alpha,p}(u) = \sum_{k=0}^{\infty} (W_{\alpha,p} * G_{\alpha,p}^{*k})(t), \quad (4.8)$$

$$M_\alpha(t, x) = \int_0^t W_{\alpha,p,x}(t-u) dH_{\alpha,p}(u) = \sum_{k=0}^{\infty} (W_{\alpha,p,x} * G_{\alpha,p}^{*k})(t), \quad (4.9)$$

where $H_{\alpha,p}(t) = \sum_{k=0}^{\infty} G_{\alpha,p}^{*k}(t)$ is the renewal function and $G_{\alpha,p}^{*k}(t)$ is the k -th convolution of $G_{\alpha,p}(t)$. The distributions (4.1) and (4.5) are now readily obtained from (4.8) and (4.9).

Further on we assume the following conditions

$$\int_0^\infty u e^{-\alpha u} m(u) dG(u) < \infty, \quad \int_0^\infty e^{-\alpha u} [1-G(u)] du < \infty, \quad \int_0^\infty e^{-\alpha u} [1-L(u)] du < \infty. \quad (4.10)$$

Note that in the supercritical case $\alpha > 0$, the last two conditions are automatically met.

Proposition 1. *Under conditions (4.10), the limiting age and residual lifetime distributions are given by*

$$A(x) = \frac{p \int_0^x e^{-\alpha u} [1 - G(u)] du + (1-p) \int_0^x e^{-\alpha u} [1 - L(u)] du}{p \int_0^\infty e^{-\alpha u} [1 - G(u)] du + (1-p) \int_0^\infty e^{-\alpha u} [1 - L(u)] du}, \quad (4.11)$$

$$R(y) = 1 - e^{\alpha y} \frac{p \int_y^\infty e^{-\alpha u} [1 - G(u)] du + (1-p) \int_y^\infty e^{-\alpha u} [1 - L(u)] du}{p \int_0^\infty e^{-\alpha u} [1 - G(u)] du + (1-p) \int_0^\infty e^{-\alpha u} [1 - L(u)] du}. \quad (4.12)$$

Proof. Proceeding from (4.6) – (4.7) and applying the Key Renewal Theorem (see, e.g., Feller, 1971), one can arrive at the following asymptotic results as $t \rightarrow \infty$:

$$M(t) \sim K e^{\alpha t}, \quad (4.13)$$

$$M(t, x) \sim K(x) e^{\alpha t}, \quad (4.14)$$

where $K = K(\infty) < \infty$ and

$$K(x) = \{p \int_0^x e^{-\alpha u} [1 - G(u)] du + (1-p) \int_0^x e^{-\alpha u} [1 - L(u)] du\} / p \int_0^\infty u e^{-\alpha u} m(u) dG(u). \quad (4.15)$$

Now from (3.1) and (3.2), using (4.10) and applying (4.13) – (4.15), one can obtain the limiting age distribution (4.11). On the other hand, from (4.13) – (4.15) it follows that

$$\lim_{t \rightarrow \infty} M(t+y)/M(t) = e^{\alpha y}, \quad \lim_{t \rightarrow \infty} M(t+y, y)/M(t+y) = A(y).$$

Therefore, from (3.4) and (3.5) one obtains the limiting residual lifetime distribution (4.12).

Note that in the critical case $\alpha = 0$ the distribution (4.12) assumes the form

$$R(y) = \frac{p \int_0^x [1 - G(u)] du + (1-p) \int_0^x [1 - L(u)] du}{p \int_0^\infty [1 - G(u)] du + (1-p) \int_0^\infty [1 - L(u)] du}, \quad (4.16)$$

which is the same as (4.11) with $\alpha = 0$.

Example 1. Let us now set $p = 1$. If we assume in addition that $h(s) \equiv h(u; s)$, $m = h'(1)$, the process $Z(t)$ will be the classical *Bellman-Harris branching process* generated by the (G, h) -evolution of cells. Then from (4.11) one obtains the limiting age distribution

$$A(x) = \frac{\int_0^x e^{-\alpha u} (1 - G(u)) du}{\int_0^\infty e^{-\alpha u} (1 - G(u)) du}, \quad (4.11a)$$

which can be found in Harris (1963). On the other hand, using (4.5) with $p = 1$ it is not difficult to present (4.11a) in the case $\alpha \neq 0$ by the following equivalent form (see Taylor (1982), formula (1.7)):

$$A(x) = \frac{m\alpha}{(m-1)} \int_0^x e^{-\alpha u} (1 - G(u)) du, \quad (4.11b)$$

From (4.12) one readily obtains the limiting residual lifetime distribution

$$R(y) = 1 - \frac{e^{\alpha y} \int_y^\infty e^{-\alpha u} (1 - G(u)) du}{\int_0^\infty e^{-\alpha u} (1 - G(u)) du}. \quad (4.12a)$$

Using (4.11b) and (4.12a) it is not difficult to derive the equivalent form

$$R(y) = 1 - e^{\alpha y}(1 - A(y)), \quad (4.12b)$$

which was obtained by Taylor (1982, (4.5)) in the supercritical case.

In the critical case $\alpha = 0$, the distributions (4.11a) and (4.12a) become identical:

$$A(y) = R(y) = \frac{\int_0^y (1 - G(u)) du}{\int_0^\infty (1 - G(u)) du}. \quad (4.16a)$$

Example 2. Consider now the Markov case

$$G(t) = 1 - e^{-\lambda t}, \quad t \geq 0, \quad (4.17)$$

with $h(u, s) \equiv h(s)$. From (4.5) it follows that $\alpha = \lambda(mp - 1)$, where $m = h'(1)$. Now by (4.6) and (4.7) one obtains

$$M(t) = \sum_{n=0}^{\infty} (mp)^n (f * \Gamma_{n,\lambda})(t), \quad (4.18)$$

$$M(t, x) = \sum_{n=0}^{\infty} (mp)^n (f_x * \Gamma_{n,\lambda})(t), \quad (4.19)$$

where

$$f(t) = pe^{-\lambda t} + (1 - p)(1 - L(t)), \quad f_x(t) = \delta(x - t)\{pe^{-\lambda t} + (1 - p)(1 - L(t))\},$$

and

$$\Gamma_{n,\lambda}(t) = (\lambda^n / (n - 1)!) \int_0^t u^{n-1} e^{-\lambda u} du.$$

Assuming additionally that $p = 1$, one arrives at the classical *Markov branching process* with

$$f(t) = e^{-\lambda t}, \quad f_x(t) = \delta(x - t)e^{-\lambda t}.$$

Hence from (4.18) and (4.19) one has

$$M(t) = e^{\lambda(m-1)t} \quad \text{if } m \neq 1, \quad M(t) \equiv 1 \quad \text{if } m = 1, \quad (4.20)$$

$$M(t, x) = e^{\lambda(m-1)t}(1 - e^{-m\lambda x}) \quad \text{if } m \neq 1, \quad M(t, x) = 1 - e^{-\lambda x} \quad \text{if } m = 1. \quad (4.21)$$

Therefore, from (4.20) and (4.21) it follows $M(t, x) = 1 - e^{-\lambda x}$

$$M(t, x) = M(t)(1 - e^{-m\lambda x}), \quad (4.22)$$

and from (4.1) one obtains the age distribution

$$A_t(x) = 1 - e^{-m\lambda x}. \quad (4.23)$$

Note that the age distribution for the Markov branching process is stationary, but it depends of the critical parameter m . Using (3.5), (3.3), and (4.20)–(4.23), it is not difficult to see that

$$R_t(y) = 1 - e^{-\lambda y}, \quad (4.24)$$

that is the residual lifetime distribution in the Markov case is also stationary and identical to the lifetime distribution (4.17).

Remark 4. Setting $G(t) = 1 - e^{-\lambda t}$, $t \geq 0$, in formulas (4.11a) and (4.12a), it is also possible to obtain the corresponding stationary distributions (4.23) and (4.24) in the Markov case.

5. Age-dependent Branching Processes with a Generalized Non-homogeneous Poisson Immigration

Let $Y(t)$ be an age-dependent process with the evolution as defined in Section 4 and the following immigration component.

Immigration. Let $0 = S_0 < S_1 < S_2 < S_3 < \dots$ be a sequence of time points in a non-homogeneous Poisson process $\xi(t)$ with rate $r(t)$. The notation $\Lambda(t)$ is used for the cumulative rate $\Lambda(t) = \int_0^t r(u)du$. We also use the notation: $T_i = S_i - S_{i-1}$ then $S_k = \sum_{i=1}^k T_i$, $k = 1, 2, \dots$. Associated with every point S_k is an independent immigration component I_k , where $\{I_k\}$ are i.i.d. r.v.'s with p.g.f. $g(s) = Es^{I_k} = \sum_{i=0}^{\infty} q_i s^i$.

The p.g.f. of the process $Y(t)$ is denoted by $\Psi(t; s)$. This process can be represented as

$$Y(t) = \sum_{k=1}^{\xi(t)} Z_{(k)}(t - S_k) \quad \text{if } \xi(t) > 0, \quad Y(t) = 0 \quad \text{if } \xi(t) = 0, \quad (5.1)$$

where $Z_{(k)}(t)$ are *i.i.d.* branching processes with the same evolution as $Z(t)$ but originated from a random number of ancestors I_k . Each of the processes $Z_{(k)}(t)$ has p.g.f. $F^*(t; s) = g(F(t; s))$ with $F(t; s)$ satisfying the non-linear integral equation (4.1). Let $Y(t, x)$ be the number of cells of age $\leq x$ at time t in the general branching model with immigration defined by (5.1). Introduce the p.g.f. $\Psi(t, x; s) = E\{s^{Y(t, x)} | Y(0, 0) = 0\}$. Note that if $x \geq t$ then $Y(t) = Y(t, x)$. Let $\bar{Y}_t(y)$ be the number of cells at time t whose residual lifetime is greater than y .

Theorem 1. *The p.g.f.'s of the processes $Y(t)$ and $Y(t, x)$ are given by*

$$\Psi(t; s) = \exp\left\{-\int_0^t r(t-u)[1 - F^*(u; s)]du\right\}, \quad \Psi(0; s) = 1, \quad (5.2)$$

$$\Psi(t, x; s) = \exp\left\{-\int_0^t r(t-u)[1 - F^*(u, x; s)]du\right\}, \quad \Psi(0, 0; s) = 1, \quad (5.3)$$

where $F^*(t; s) = g(F(t; s))$, $F^*(t, x; s) = g(F(t, x; s))$, while the p.g.f.'s $F(t; s)$ and $F(t, x; s)$ satisfy equations (4.1) and (4.2).

Proof. By (5.1) one has

$$\Psi(t; s) = Es^{Y(t)} = E\left\{s^{\sum_{i=1}^{\xi(t)} Z_{(i)}(t-S_i)}\right\} = \sum_{n=0}^{\infty} P(\xi(t) = n) E\left\{s^{\sum_{i=1}^{\xi(t)} Z_{(i)}(t-S_i)} | \xi(t) = n\right\}.$$

Let us first compute the following expectation

$$\begin{aligned} \Delta_n(t; s) &= E\left\{s^{\sum_{i=1}^{\xi(t)} Z_{(i)}(t-S_i)} | \xi(t) = n\right\} \\ &= \int_0^t \int_{u_1}^t \dots \int_{u_{n-1}}^t E\left\{s^{\sum_{i=1}^n Z_{(i)}(t-u_i)}\right\} dP_{S_1, S_2, \dots, S_n}(u_1, u_2, \dots, u_n) \end{aligned}$$

$$= \int_0^t \int_{u_1}^t \dots \int_{u_{n-1}}^t \prod_{i=1}^n F^*(t - u_i; s) dP_{S_1, S_2, \dots, S_n}(u_1, u_2, \dots, u_n),$$

where $P_{S_1, S_2, \dots, S_n}(u_1, u_2, \dots, u_n) = \mathbf{P}(S_1 \leq u_1, S_2 \leq u_2, \dots, S_n \leq u_n)$.

Now we use the fact that $\mu(t) = \Lambda(\xi(t))$ is a homogeneous Poisson process with rate $\lambda = 1$ and the r.v. $\Lambda(S_k) = \Gamma_k$ has $\Gamma(k, 1)$ distribution, $k = 1, 2, \dots$. Let $\Lambda^{-1}(\cdot)$ be the inverse function of the rate $\Lambda(t)$. Then

$$\begin{aligned} P_{S_1, \dots, S_n}(u_1, u_2, \dots, u_n) &= \Pr \{ \Lambda^{-1}(\Gamma_1) \leq u_1, \dots, \Lambda^{-1}(\Gamma_n) \leq u_n \} \\ &= P_{\Gamma_1, \dots, \Gamma_n}(\Lambda(u_1), \Lambda(u_2), \dots, \Lambda(u_n)). \end{aligned}$$

By employing the Order Statistic Property one has

$$\begin{aligned} \Delta_n(t; s) &= \frac{n!}{\Lambda^n(t)} \int_0^t \int_{u_1}^t \dots \int_{u_{n-1}}^t \prod_{i=1}^n F^*(t - u_i; s) d\Lambda(u_n) \dots d\Lambda(u_2) d\Lambda(u_1) \\ &= (n!/\Lambda^n(t)) \int_0^t \int_{u_1}^t \dots \int_{u_{n-1}}^t \prod_{i=1}^n r(u_i) F^*(t - u_i; s) du_n \dots du_2 du_1 \\ &= (1/\Lambda^n(t)) \int_0^t \int_0^t \dots \int_0^t \prod_{i=1}^n r(u_i) F^*(t - u_i; s) du_1 du_2 \dots du_n \end{aligned}$$

by virtue of the fact that $f(u_1, \dots, u_n) = \prod_{i=1}^n r(u_i) F^*(t - u_i; s)$ is a symmetric function. Therefore one obtains

$$\Delta_n(t; s) = \frac{1}{\Lambda^n(t)} \prod_{i=1}^n \int_0^t r(u_i) F^*(t - u_i; s) du_i = \frac{1}{\Lambda^n(t)} \left\{ \int_0^t r(u) F^*(t - u; s) du \right\}^n.$$

Hence

$$\begin{aligned} \Psi(t; s) &= \sum_{n=0}^{\infty} P(\xi(t) = n) \Delta_n(t; s) \\ &= e^{-\Lambda(t)} \sum_{n=0}^{\infty} (\Lambda^n(t)/n!) (1/\Lambda^n(t)) \left\{ \int_0^t r(u) F^*(t - u; s) du \right\}^n \\ &= \exp \left\{ -\Lambda(t) + \int_0^t r(u) F^*(t - u; s) du \right\} \\ &= \exp \left\{ -\int_0^t r(u) [1 - F^*(t - u; s)] du \right\} \\ &= \exp \left\{ -\int_0^t r(t - u) [1 - F^*(u; s)] du \right\} \end{aligned}$$

which proves (5.2). The proof of (5.3) is similar.

Proposition 2. *Assume conditions (4.10) and let*

$$\lim_{t \rightarrow \infty} r(t) = r > 0. \quad (5.4)$$

Then the limiting age distribution $A(x)$ is given by (4.11) and for the limiting residual lifetime one has: $R(y) = A(y)$ for $\alpha \leq 0$ and $R(y) = 1 - e^{\alpha y}(1 - A(y))$ for $\alpha > 0$.

Proof. From (4.1) – (4.2) and (5.2) – (5.3) it is not difficult to derive all moments. Let us introduce the process mean $N(t) = EY(t) = \frac{\partial}{\partial s} \Psi(t; s)|_{s=1}$ and the immigration mean $\gamma = EI_k = g'(1)$. Then by (5.2) one has

$$N(t) = \gamma \int_0^t r(t - u) M(u) du, \quad N(0) = 0, \quad (5.5)$$

where $M(t)$ is well defined by equation (4.3). Let $N(t, x) = E\{Y(t, x)\} = \frac{\partial \Psi(t, x; s)}{\partial s}|_{s=1}$. Then from (5.3) one has

$$N(t, x) = \gamma \int_0^t r(t - u) M(u, x) du, \quad N(0, x) = 0, \quad (5.6)$$

where $M(t, x)$ is defined by (4.4).

Using (5.4) – (5.6) and (4.13) – (4.15) under conditions (4.10) one can prove the following asymptotic results as $t \rightarrow \infty$:

- (i) If $\alpha > 0$ then $N(t) \sim \gamma r K e^{\alpha t} / \alpha$; $N(t, x) \sim \gamma r K(x) e^{\alpha t} / \alpha$;
- (ii) If $\alpha = 0$ then $N(t) \sim \gamma r K t$; $N(t, x) \sim \gamma r K(x) t$;
- (iii) If $\alpha < 0$ then $N(t) \rightarrow -\gamma r K / \alpha$; $N(t, x) \rightarrow -\gamma r K(x) / \alpha$.

From the above properties one obtains the limiting age distribution

$$\lim_{t \rightarrow \infty} \{N(t, x) / N(t)\} = K(x) / K = A(x), \quad (5.7)$$

which is identical to (4.11). On the other hand, it follows from these properties that

$$\lim_{t \rightarrow \infty} \{N(t + y, y) / N(t + y)\} = K(y) / K = A(y). \quad (5.8)$$

Similarly one has:

- (i) If $\alpha > 0$ then $\lim_{t \rightarrow \infty} \{N(t + y) / N(t)\} = e^{\alpha t}$;
- (ii) If $\alpha \leq 0$ then $\lim_{t \rightarrow \infty} \{N(t + y) / N(t)\} = 1$.

Now it is not difficult to obtain the limiting residual lifetime distribution:

- (i) If $\alpha \leq 0$ then $R(y) = 1 - \lim_{t \rightarrow \infty} [N(t + y) / N(t)] \{1 - N(t + y, y) / N(t + y)\} = A(y)$;
- (ii) If $\alpha > 0$ then $R(y) = 1 - e^{\alpha y} (1 - A(y))$,

the latter being equivalent to (4.12b).

Remark 5. Under condition (5.4), the limiting age distributions in the general age-dependent branching processes with and without immigration are identical. The same statement is valid for the limiting residual lifetime distributions.

6. Markov Branching Processes with Homogeneous Poisson Immigration.

Let us consider the Markov case with $p = 1$, $r(t) \equiv r$, and the lifetime *c.d.f.* given by (4.17). Sevastyanov (1957) was the first to study this Markov branching process with homogeneous Poisson immigration (MBPwHPI).

Proposition 3. *In the MBPwHPI, the limiting age and residual lifetime distributions are given by*

$$A_t(x) = N(t, x) / N(t) = 1 - e^{-m\lambda x}, \quad x \geq 0, \quad (6.1)$$

$$R(y) = 1 - e^{-m\lambda y}, \quad m < 1; \quad R(y) = 1 - e^{-\lambda y}, \quad m \geq 1. \quad (6.2)$$

Proof. Using (4.20) – (4.22) one deduces from (5.4) and (5.5) that

$$N(t) = \frac{\gamma r (e^{\lambda(m-1)t} - 1)}{\lambda(m-1)}, \quad \text{if } m \neq 1; \quad N(t) = \gamma r t, \quad \text{if } m = 1; \quad (6.3)$$

$$N(t, x) = \frac{\gamma r (e^{\lambda(m-1)t} - 1)(1 - e^{-m\lambda x})}{\lambda(m-1)} \quad \text{if } m \neq 1, \quad N(t, x) = \gamma r t (1 - e^{-\lambda x}) \quad \text{if } m = 1. \quad (6.4)$$

The relations (6.3) and (6.4) lead to the following age distribution at time $t \geq 0$:

$$A_t(x) = N(t, x)/N(t) = 1 - e^{-m\lambda x}, \quad x \geq 0,$$

which is the same as (4.23). In other words, the MBPwHPI has the stationary age distribution given by (6.1), which is the same as that in the case without immigration. Since the tail function of the residual lifetime distribution can be represented as

$$\bar{R}_t(y) = [M(t+y)/M(t)]\{1 - M(t+y, y)/M(t+y)\},$$

it follows from (5.1) and (5.2) that

$$\bar{R}_t(y) = e^{-m\lambda y} \{1 - e^{-\lambda(1-m)(t+y)}\} / \{1 - e^{-\lambda(1-m)t}\}, \quad m < 1;$$

$$\bar{R}_t(y) = e^{-\lambda y} (1 + \frac{y}{t}), \quad m = 1;$$

$$\bar{R}_t(y) = e^{-m\lambda y} \{e^{\lambda(m-1)y} - e^{-\lambda(m-1)t}\} / \{1 - e^{-\lambda(m-1)t}\}, \quad m > 1.$$

Now it is not difficult to obtain the limiting residual lifetime distribution (6.2)

$$R(y) = 1 - \lim_{t \rightarrow \infty} \bar{R}_t(y) = 1 - e^{-m\lambda y}, \quad m < 1; \quad R(y) = 1 - \lim_{t \rightarrow \infty} \bar{R}_t(y) = 1 - e^{-\lambda y}, \quad m \geq 1.$$

Remark 6. The residual lifetime distributions associated with the Markov branching process with homogeneous Poisson immigration depend on the critical parameter m . It is interesting to note that in the critical and supercritical cases the limiting residual lifetime distribution is the same as the lifetime distribution (just as it comes about when considering the Markov process without immigration), while it is exponential with parameter $m\lambda$ in the subcritical case.

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