J Stat Phys (2013) 152:769–786
DOI 10.1007/s10955-013-0781-1

Identifiability of Age-Dependent Branching Processes from Extinction Probabilities and Number Distributions

Pak-Wing Fok · Tom Chou

Received: 19 November 2012 / Accepted: 6 June 2013 / Published online: 2 July 2013

Abstract Consider an age-dependent, single-species branching process defined by a progeny number distribution, and a lifetime distribution associated with each independent particle. In this paper, we focus on the associated *inverse* problem where one wishes to formally solve for the progeny number distribution or the lifetime distribution that defines the Bellman-Harris branching process. We derive results for the existence and uniqueness (the identifiability) of these two distributions given one of two types of information: the extinction time probability of the entire process (extinction time distribution), or the distribution of the total number of particles at one fixed time. We demonstrate that perfect knowledge of the distribution of extinction times allows us to formally determine either the progeny number distribution *or* the lifetime distribution. Furthermore, we show that these constructions are unique. We then consider "data" consisting of a perfectly known total number distribution given at one specific time. For a process with known progeny number distribution and exponentially distributed lifetimes, we show that the rate parameter is identifiable. For general lifetime distributions, we also show that the progeny distribution is globally unique. Our results are presented through four theorems, each describing the constructions in the four distinct cases.

Keywords Branching process · Bellman-Harris · Inverse problem

---

This work was supported by the National Science Foundation through grants DMS-1021818 and DMS-1032131, and the Army Research Office through grant 58386MA.

P.-W. Fok (✉)
Department of Mathematical Sciences, University of Delaware, Newark, DE 19716, USA
e-mail: pakwing@udel.edu

T. Chou
Departments of Biomathematics and Mathematics, UCLA, Los Angeles, CA 90095-1766, USA
e-mail: tomchou@ucla.edu

1 Introduction

Branching processes have proved useful in many applications, including modeling cell proliferation and differentiation, propagation of surnames, and analyzing radioactive chain reactions [1–4]. A mathematical model for the branching of a single species of identical particles is the Bellman-Harris process, defined by a particle lifetime distribution and a progeny number distribution. The lifetime distribution determines the statistics of the time a particle waits before branching, while the progeny number distribution determines the statistics of how many offspring particles each parent particle generates at each branching event. Schematics of the single-species branching process are shown in Fig. 1. Here, the process is initiated with a single parent particle that branches at a time between τ and $\tau + \mathrm{d}\tau$ with probability $G(\tau)\mathrm{d}\tau$. Each branching event results in the parent particle giving birth to $k \geq 2$ new particles with probability b_k, or dying with probability b_0. All particle lifetimes are independently and identically drawn from the probability distribution function $G(\tau)$.

Mathematically, the branching process is conveniently described via the probability generating function (pgf) $F(z,t)$ for the probability $f_n(t)$ of observing n total particles at time t:

$$F(z,t) = \sum_{n=0}^{\infty} f_n(t) z^n.$$

Note that normalization $\sum_{n=0}^{\infty} f_n(t) = 1$ yields $F(z=1,t) = 1$.

For completeness, we follow standard derivations of the age-dependent, continuous-time Bellman-Harris branching process by considering the process to be initially seeded by a single parent particle [1–4]. Defining $F(z,t|\tau)$ as the generating function of the process conditioned on the original parent particle having first branched between time τ and $\tau + \mathrm{d}\tau$, we find

$$F(z,t|\tau) = \begin{cases} z, & t < \tau, \\ B[F(z,t-\tau)], & t \geq \tau, \end{cases} \tag{1}$$

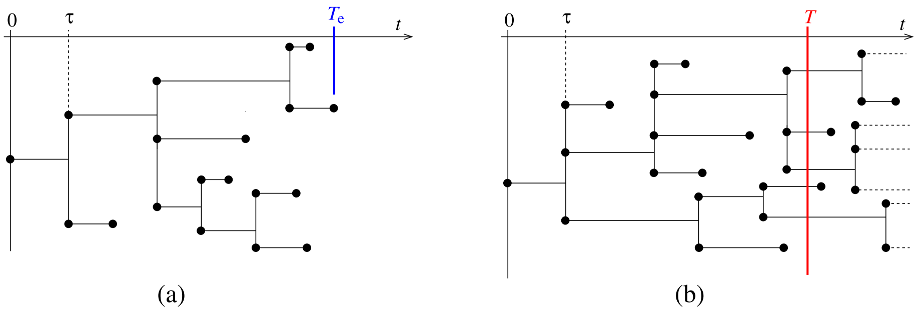

Fig. 1 (**a**) A realization of a Bellman-Harris branching process that went extinct at time T_e. If the process dies in finite time, can the distribution of extinction times be used to determine the progeny or lifetime distributions? (**b**) A realization of a Bellman-Harris branching process with a known number distribution of particles at time $t = T$. In the depicted realization there are five surviving particles at time T. Can the total number distribution at a fixed time be used to determine the progeny or lifetime distributions? In principle, both types of "data" can only be obtained from an infinite number of measurements (Color figure online)

where

$$B[z] = \sum_{k=0}^{\infty} b_k z^k, \tag{2}$$

is the generating function for the progeny number distribution $b_k \geq 0$. The coefficients of z^k in $B[z]$ correspond to the probability that k particles are born at each branching event. For processes with finite maximum offspring and branching probabilities $\{b_0, b_1, \ldots, b_N\}$, not all zero, our convention in Eq. (2) is to take $b_k = 0$ for $k > N$. Generating $k = 1$ particle at the time of branching is simply equivalent to renewing the particle's lifespan. This generally does not occur in cell proliferation or nuclear chain reactions (the main applications we have in mind) and so throughout this paper, we always assume that the particles either die, or generate $k > 1$ particles at each branching event. *Therefore we always take* $b_1 = 0$. Averaging Eq. (1) over the lifetime distribution $G(\tau)$, we find

$$F(z,t) \equiv \int_0^{\infty} F(z,t|\tau)G(\tau)\mathrm{d}\tau = z\int_t^{\infty} G(\tau)\mathrm{d}\tau + \int_0^t B\big[F(z,t-\tau)\big]G(\tau)\mathrm{d}\tau, \tag{3}$$

where $z \in [0,1]$ and $t \in [0,\infty)$. This branching process is defined by two parameter functions, $\mathbf{b}$, the vector of progeny number probabilities, and $G(\tau)$, the probability density function (pdf) of lifetimes for each particle before it branches. Given a set $\mathbf{b}$ and a lifetime distribution $G(\tau)$, Eq. (3), along with the initial condition $F(z,0) = z$, can be solved to find a $F(z,t)$, from which $f_n(t)$ can be recovered.

Equation (3), and its multispecies generalization have been well-studied by researchers across many disciplines [5–8], particularly in cell biology. In the forward problem one knows the set of progeny probabilities $\mathbf{b}$ and the lifetime distribution function $G(t)$, and wishes to calculate the total particle probability distribution $f_n(t)$ [3], the moments of the particle numbers (for example the mean $\sum_{n=0}^{\infty} n f_n(t)$), or the extinction probabilities of the process [9]. Often, exponentially-distributed lifetimes are assumed, turning Eq. (3) into a nonlinear ODE of the Riccati type. This nonlinear equation can be further reduced to a series of linear ODEs describing the evolution of the moments of the particle number.

Often however, the underlying details of the branching process are not precisely known *a priori*, but statistical properties of the branching process can be measured. Thus, inference and the inverse branching problem are also important topics. Maximum likelihood approaches have been used to estimate parameters defining simple branching processes [10–13]. Estimation of parameters in a more sophisticated branching model was done in [14] where the distribution of times to death and to reproduction may differ [15]. These studies attempt to estimate the parameters of a branching process from measurements of quantities such as the mean particle number [16]. Non-parametric approaches have also been explored. For example, in [17] the authors use a Bayesian approach to estimate offspring and lifetime distributions given the whole history of the process up to some fixed time.

In this paper, we shall consider only the *formal* inverse problem of finding the set $\mathbf{b}$ or the lifetime distribution $G(\tau)$ from exactly known statistics of the branching process. Rather than estimating parameters, we simply explore the mathematical uniqueness of the inverse problem defined by the nonlinear integral Eq. (3) and two types of perfect information. Whether $G(\tau)$ or $\mathbf{b}$ is identified depends on the application. For processes such as nuclear chain reactions, the progeny distribution $\mathbf{b}$ resulting from a neutron collision may be broadly distributed depending on the neutron energy, but the collision events may be exponentially distributed in time [18]. For biological organisms including cells, the life-cycle determines the distribution of reproductive events $G(\tau)$ that is typically non-exponential. However, in

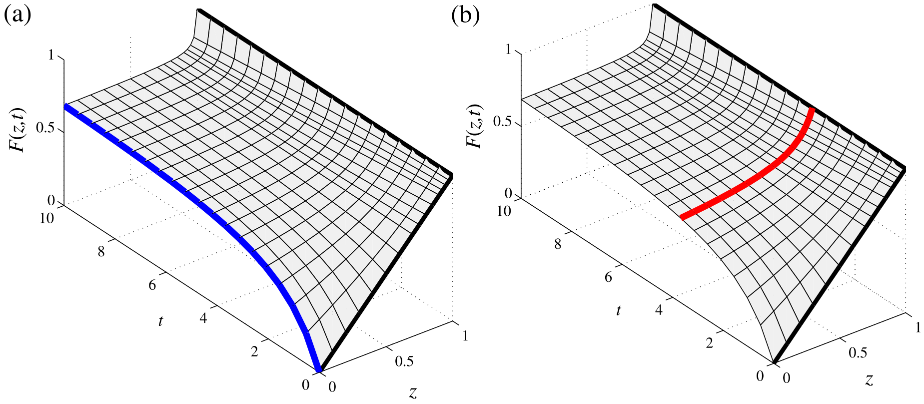

Fig. 2 Reconstruction of a branching process from two types of functional information. (**a**) The extinction time distribution, $F(0,t) \equiv f_0(t)$ (shown *in blue*). (**b**) The number distribution at a given time, $F(z,T)$ (shown *in red*). *Thick black lines* indicate common, known, information about the surface $F(z,t)$: $F(z,0) = z$ and $F(1,t) = 1$ (Color figure online)

cell proliferation the progeny number distribution b_k is nonzero only for $k = 0$ and $k = 2$, so that only two daughter cells are produced upon each division event (exceptions can arise in cancer cells that have been observed to produce up to five progeny ($b_5 > 0$) under confined conditions [19]). Therefore scenarios arise where one of $\mathbf{b}$ or $G(\tau)$ is known and the other must be determined from some statistical properties of the process.

One type of information that could be used to determine $\mathbf{b}$ or $G(\tau)$ is the cumulative distribution function of extinction times $F(0,t)$. Note that $\lim_{t\to\infty} F(0,t) < 1$ in general because the process may never extinguish. The extinction probability is positive only if $b_0 > 0$. Therefore the function $F(z,t)$ is known at $t = 0$, where $F(z,0) = z$; at $z = 1$, where $F(z = 1, t) = 1$ from normalization; and at $z = 0$. These known parts of the function $F(z,t)$ are indicated by the thick curves in Fig. 2(a). In particular, $F(0,0) = 0$.

Another possible type of information is the total particle number distribution of the branching processes at *one* fixed time T. This may in principle be derived from an infinite number of samples of the process. The resulting distribution of particle numbers at time T, $f_n(T)$, yields exactly the pgf $F(z,T) = \sum_{n=0}^{\infty} f_n(T) z^n$. In this case, $F(z,t)$ is known at $t = 0$, where $F(z,0) = z$; at $z = 1$, where $F(z = 1, t) = 1$ from normalization; and at time $0 < T < \infty$. These known parts of the function are indicated by the thick curves in Fig. 2(b).

The remainder of this paper essentially explores the conditions under which the rest of the function $F(z,t)$ can be reconstructed from these two types of information. Specifically, we wish to determine if the probabilities $\mathbf{b}$ and/or lifetime distribution $G(\tau)$ can be extracted from the thick curves in Figs. 2, and if so, whether or not they are unique.

Throughout this paper, we assume that the branching process is always seeded by a single particle at $t = 0$. We will refer to Eq. (3) and assume that:

(A1) $G(t)$ is a strictly positive continuous probability distribution function: $G(t) > 0$ if $t \geq 0$ and $\int_0^\infty G(t)\mathrm{d}t = 1$.

(A2) $B[z]$ is a bounded, infinitely differentiable function on $z \in [0, 1]$ through Eq. (2), with $b_0 > 0$, $b_1 = 0$ and $b_j \geq 0$ for $j \geq 2$.

Furthermore, we will freely use the fact that a probability distribution is uniquely defined by its Laplace transform [23] (i.e. $\mathcal{L}\{F_1(t)\} = \mathcal{L}\{F_2(t)\}$ if and only if $F_1(t) = F_2(t)$ for distributions $F_1(t)$ and $F_2(t)$) and we use both $\mathcal{L}$ and the tilde notation to denote Laplace transform:

$$\mathcal{L}\{H(t)\} = \tilde{H}(s) = \int_0^\infty e^{-st} H(t)\mathrm{d}t.$$

2 Reconstruction from Extinction time Distributions

In this section, we first consider Eq. (3) when the cumulative extinction probability $F(z=0,t)$ is perfectly measured (see Fig. 2(a)). We will use the following two lemmas throughout this paper. The first illustrates some general properties of the pgf $F(z,t)$. The second is used in several of the theorems to show convergence of certain integrals and is proved in [20].

Lemma 1 *Let $F(z,t)$ be a solution to Eq.* (3) *and let $G(t)$ be a continuous pdf. Then the pgf $F(z,t)$ satisfies* $0 \le F(z,t) \le 1$ *and is continuous on* $(z,t) \in [0,1) \times [0,\infty)$. *Furthermore, it has infinitely many z-derivatives on* $[0,1)$.

Proof A well-known property of pgfs like $F(z,t)$ is that they are continuous, infinitely differentiable and strictly monotonically increasing on $[0,1)$ for each $0 \le t < \infty$ (e.g. see Theorem 1 in [1])—and therefore bounded. Since all the integrands in (3) are bounded functions, $F(z,t)$ is also continuous for $t \in [0,\infty)$. Since $\sum_{i=0}^{\infty} f_i(t) = F(1,t) = 1$ and $F(0,t) \ge 0$, we have $0 \le F(z,t) \le 1$. □

Lemma 2 *Assume that $h(x)$ and all its derivatives exist on* $(0,\infty]$ *and vanish at $x=\infty$. Also for some $k > -1$, let $h(x) \sim x^k$ as $x \to 0^+$. Then as $\lambda \to \infty$,*

$$\int_0^\infty h(x) e^{\pm i\lambda x}\mathrm{d}x = O\big(\lambda^{-(k+1)}\big).$$

A proof this result can be found in [20].

2.1 Reconstruction of Lifetime Distribution $G(t)$ Given Progeny Number Distribution $\mathbf{b}$

If the progeny number distribution $\mathbf{b}$, and the corresponding generating function $B[z]$ is known, is there more than one lifetime distribution function $G(t)$ that yields the same extinction time statistics? To answer this question, we prove the following:

Theorem 1 (Reconstruction and uniqueness of lifetime probabilities from extinction probabilities) *For Eq.* (3), *assume that $B[z]$ is known and satisfies* (*A*2), *and there is an underlying probability distribution of lifetimes $G(t)$ that gives rise to $F(0,t)$, the cumulative extinction time distribution. Furthermore assume $F(0,t) = O(t)$ as $t \to 0^+$. Then $G(t)$ is given by*

$$G(t) = \int_\Gamma \frac{\widetilde{F}(0,s)e^{st}}{\widetilde{K}(s)} \frac{\mathrm{d}s}{2\pi i}, \qquad \widetilde{K}(s) = \mathcal{L}\big\{B\big[F(0,t)\big]\big\}, \tag{4}$$

where the contour Γ lies to the right of all the poles of the integrand. Furthermore, $G(t)$ is determined uniquely by (4): *if $F_1(0,t)$ and $F_2(0,t)$ are extinction time distributions and $G_1(t)$ and $G_2(t)$ are the associated lifetime distributions, then $F_1(0,t) = F_2(0,t) \Rightarrow G_1(t) = G_2(t)$.*

Proof We first show that Eq. (4) is true for any cumulative extinction time distribution $F(0,t)$. Upon taking the Laplace transform of the Bellman-Harris equation (3) at $z=0$, we find

$$\widetilde{F}(0,s)=\widetilde{K}(s)\widetilde{G}(s), \tag{5}$$

and $\widetilde{K}(s)$ is the Laplace transform of the function

$$K(t)\equiv B\big[F(0,t)\big]. \tag{6}$$

Since F and G are bounded functions by Lemma 1(i) and assumption (A1), all three Laplace-transformed functions in (5) exist providing $\mathrm{Re}(s)>0$. Upon inverse Laplace transforming $\widetilde{G}(s)$, we find

$$G(t)=\int_{\gamma-i\infty}^{\gamma+i\infty}\frac{\widetilde{F}(0,s)e^{st}}{\widetilde{K}(s)}\frac{\mathrm{d}s}{2\pi i}, \tag{7}$$

where $\gamma>0$. To show that the integral (7) converges for all $t\geq 0$, let $s=\gamma+i\mu$, $\mu\in\mathbb{R}$. Lemma 2 implies that as $\mu\to\pm\infty$,

$$\widetilde{F}(0,\gamma+i\mu)=\int_0^\infty e^{-i\mu t}g_0(t)\mathrm{d}t=O\big(\mu^{-2}\big), \tag{8}$$

$$\widetilde{K}(\gamma+i\mu)=\int_0^\infty e^{-i\mu t}g_1(t)\mathrm{d}t=O\big(\mu^{-1}\big), \tag{9}$$

where $g_0(t)=e^{-\gamma t}F(0,t)=O(t)$ and $g_1(t)=e^{-\gamma t}\sum_{m=0,\neq 1}^{\infty}b_mF^m(0,t)=O(1)$ as $t\to 0^+$. Note that $F^m(z,t)\equiv[F(z,t)]^m$. Since

$$G(t)=\frac{e^{\gamma t}}{2\pi}\int_{-\infty}^{\infty}e^{i\mu t}\frac{\widetilde{F}(0,\gamma+i\mu)}{\widetilde{K}(\gamma+i\mu)}\mathrm{d}\mu, \tag{10}$$

we see that $G(t)$ is proportional to the inverse Fourier transform of $\widetilde{F}(0,\gamma+i\mu)/\widetilde{K}(\gamma+i\mu)$. This ratio is square integrable at $\mu=\pm\infty$ by (8) and (9). Furthermore $\widetilde{F}(0,\gamma+i\mu)/\widetilde{K}(\gamma+i\mu)$ is non-singular for finite μ since the contour in (7) lies to the right of all singularities in the integrand. Therefore (7) and (10) must exist for all t [22]. In particular $G(t)\equiv 0$ when $t<0$.

What remains is for us to show that this $G(t)$ is unique. Assume there are two lifetime distributions $G_1(t)$ and $G_2(t)$ that give rise to extinction probabilities $F_1(0,t)$ and $F_2(0,t)$. If $F_1=F_2$, we can subtract the corresponding integral equations (Eq. (3)) evaluated at $z=0$ to find

$$0=\int_0^t B\big[F(0,t-\tau)\big]\big(G_1(\tau)-G_2(\tau)\big)\mathrm{d}\tau.$$

This equation can be written in terms of the Laplace transforms of $K(t)\equiv B[F(0,t)]$ and $G_1(t)-G_2(t)$:

$$\tilde{K}(s)\big(\tilde{G}_1(s)-\tilde{G}_2(s)\big)=0.$$

Since $b_0>0$ by (A2), then $F(0,t)>0$ and $B[F(0,t)]>0$. Therefore, $\tilde{K}(s)>0$, implying $\tilde{G}_1(s)=\tilde{G}_2(s)$ and $G_1(t)=G_2(t)$ (two distributions are identical if and only if their Laplace transforms are identical [23]). As long as extinction occurs with nonzero probability, and one lifetime distribution $G(t)$ leads to a specific extinction time distribution $F(0,t)$, then no other different lifetime distribution can lead to the same extinction time distribution. □

In Theorem 1, we assumed that there exists an underlying Bellman-Harris process with associated branching probabilities $\{b_j\}$ and lifetime distribution function $G(t)$ that generated the cumulative extinction time distribution $F(0,t)$; the main result of the theorem was that $G(t)$ can be found from $F(0,t)$ and $\{b_j\}$ through (4). However, if we are simply given $F(0,t)$ without any conditions on the existence of G, we also need to show that (4) is indeed a pdf, i.e. $G(t) \geq 0$ for all $t > 0$ and $\int_0^\infty G(t)\mathrm{d}t = 1$. Conditions for $G(t)$ to be a pdf in terms of its Laplace transform can be found in [23], namely:

- $\widetilde{F}(0,s)/\tilde{K}(s)$ has infinitely many derivatives in s and $(-1)^n \frac{\mathrm{d}^n}{\mathrm{d}s^n} \frac{\widetilde{F}(0,s)}{\tilde{K}(s)} \geq 0$ when $s > 0$ for every integer n.
- $\lim_{s\to 0} \frac{\widetilde{F}(0,s)}{\tilde{K}(s)} = 1$.

If the conditions of Theorem 1 *and* these two conditions above are satisfied, then the extinction time data $F(0,t)$ corresponds to a Bellman-Harris branching process and the corresponding pdf of lifetimes $G(t)$ can be found through (4).

2.2 Reconstruction of Progeny Number Distribution b Given $G(t)$

Now, consider the complementary problem where the lifetime distribution $G(t)$ is known. Can one find a unique progeny number distribution **b** for each cumulative extinction probability distribution? We prove

Theorem 2 (Reconstruction and uniqueness of progeny number probabilities from extinction probabilities) *Consider Eq.* (3) *with an unknown underlying progeny number distribution* b_j, $j = 0, 1, 2, \ldots$. *With a known lifetime distribution* $G(t)$ *satisfying* $(A1)$, *assume the process generates a cumulative extinction time distribution* $F(0,t)$ *which is strictly increasing in* t. *Furthermore, assume* $F(0,t) = O(t)$ *as* $t \to 0^+$. *Then the* b_j *are* (*i*) *uniquely determined by* $F(0,t)$ *and* (*ii*) *formally given in terms of the cumulative extinction time distribution by*

$$b_0 = K(0), \tag{11}$$

$$b_j = \lim_{t\to 0} \frac{K(t) - \sum_{k=0}^{j-1} b_k F^k(0,t)}{F^j(0,t)}, \quad j > 0, \tag{12}$$

where

$$K(t) = \int_\Gamma \frac{\widetilde{F}(0,s)e^{st}}{\widetilde{G}(s)} \frac{\mathrm{d}s}{2\pi i},$$

and Γ *lies to the right of all singularities of the integrand.*

Proof We first prove uniqueness. Consider two branching processes with the same lifetime distribution $G(t)$, but with different sets of progeny number probabilities **b** and $\mathbf{b}^*$ corresponding to the coefficients of $B[z]$ and $B^*[z]$ respectively. If these two branching processes generate the same extinction time distribution $F(0,t)$, the difference between the corresponding Eqs. (3) becomes

$$\int_0^t \big(B\big[F(0,t-\tau)\big] - B^*\big[F(0,t-\tau)\big]\big)G(\tau)\mathrm{d}\tau = 0.$$

Introducing $K(t)=B[F(0,t)]$, $K^*(t)=B^*[F(0,t)]$, and $\widetilde{K}(s)$, $\widetilde{K^*}(s)$ as the corresponding Laplace transforms—valid for $\mathrm{Re}(s)>0$—we find

$$\big(\widetilde{K}(s)-\widetilde{K^*}(s)\big)\widetilde{G}(s)=0, \tag{13}$$

where $\widetilde{G}(s)$ is also defined for $\mathrm{Re}(s)>0$. Since $\widetilde{G}(s)\not\equiv 0$ when $\mathrm{Re}(s)>0$, condition (13) is satisfied only if $\widetilde{K}(s)=\widetilde{K^*}(s)$, which means $B[F(0,t)]=B^*[F(0,t)]$. After expanding $B[F]=b_0+\sum_{j=2}^{\infty}b_jF^j$ and $B^*[F]=b_0^*+\sum_{j=2}^{\infty}b_j^*F^j$ we find

$$\big(b_0-b_0^*\big)+\sum_{j=2}^{\infty}\big(b_j-b_j^*\big)F^j(0,t)=0,$$

which must hold for $0\le F(0,t)\le F_{\max}$ where $F_{\max}=\lim_{t\to\infty}F(0,t)$. Since $\{1, F^2, F^3,\ldots\}$ are linearly independent on $F\in[0, F_{\max}]$, $b_j=b_j^*$ for $j=0,1,2,\ldots$, *i.e.* $\mathbf{b}=\mathbf{b}^*$.

We now show how to determine the unique progeny number distribution $\mathbf{b}$ from a known extinction time distribution $F(0,t)$. From Eq. (3),

$$F(0,t)=\int_0^t K(t-\tau)G(\tau)\mathrm{d}\tau, \tag{14}$$

where $K(t)\equiv B[F(0,t)]$. By taking Laplace transforms of (14), we find $\widetilde{F}(0,s)=\widetilde{K}(s)\widetilde{G}(s)$ when $\mathrm{Re}(s)>0$, leading to

$$K(t)=\int_{\gamma-i\infty}^{\gamma+i\infty}\frac{\tilde{F}(0,s)e^{st}}{\tilde{G}(s)}\frac{\mathrm{d}s}{2\pi i},\quad \gamma>0. \tag{15}$$

Using Lemma 2, we find

$$\widetilde{F}(0,\gamma+i\mu)=\int_0^{\infty}e^{-i\mu t}\big\{e^{-\gamma t}F(0,t)\big\}\mathrm{d}t=O\big(\mu^{-2}\big), \tag{16}$$

$$\widetilde{G}(\gamma+i\mu)=\int_0^{\infty}e^{-i\mu t}\big\{e^{-\gamma t}G(t)\big\}\mathrm{d}t=O\big(\mu^{-1}\big), \tag{17}$$

as $\mu\to\pm\infty$ since $e^{-\gamma t}F(0,t)=O(t)$ and $\lim_{t\to 0^+}e^{-\gamma t}G(t)>0$. Furthermore, since

$$K(t)=e^{\gamma t}\int_{-\infty}^{\infty}\frac{\widetilde{F}(0,\gamma+i\mu)}{\widetilde{G}(\gamma+i\mu)}e^{i\mu t}\frac{\mathrm{d}\mu}{2\pi},$$

$K(t)$ is proportional to an inverse Fourier transform. At $\mu=\pm\infty$, $\widetilde{F}(0,\gamma+i\mu)/\widetilde{G}(\gamma+i\mu)$ is square integrable by (16) and (17). It is also non-singular for finite μ since the contour in (15) lies to the right of all singularities in the integrand. Therefore $\widetilde{F}(0,\gamma+i\mu)/\widetilde{G}(\gamma+i\mu)$ is square integrable on $\mu\in[-\infty,+\infty]$ and the integral (15) must converge for all t [22]. In particular, $K(t)\equiv 0$ for $t<0$.

The probabilities b_j can be extracted from $F(0,t)$ through

$$K(t)=b_0+b_2F^2(0,t)+b_3F^3(0,t)+\cdots. \tag{18}$$

Since $F(0,0)=0$, the single-particle decay probability $b_0=K(0)$. Likewise, b_j for $j>0$ are reconstructed recursively from (18) by the relations

$$b_j=\lim_{t\to 0}\frac{K(t)-\sum_{k=0}^{j-1}b_kF^k(0,t)}{F^j(0,t)}. \qquad \square$$

We have shown in this theorem that a completely known extinction time distribution function $F(0,t)$ allows one to uniquely find constants $\{b_i\}$ providing the lifetime distribution $G(t)$ is given. If it is known *a priori* that there are probabilities $\{b_i\}$ that generated $F(0,t)$ in a Bellman-Harris process, they can be reconstructed through formulas (11) and (12). However, if $F(0,t)$ is an arbitrary function, application of (11) and (12) will not guarantee that the resulting $\{b_i\}$ are probabilities (e.g. some of the b_i could be negative, or they may not sum to 1). Therefore $b_i \geq 0$, $\sum_i b_i = 1$ with b_i defined through (11) and (12) are necessary conditions for $F(0,t)$ to correspond to the cumulative extinction probability for a Bellman-Harris branching process. In principle, these conditions define the class of cumulative distribution functions $F(0,t)$ that can arise from Bellman-Harris processes.

3 Reconstruction from a Single Number Distribution

In this section, we consider the reconstruction of either the lifetime distribution $G(t)$ or the progeny number distribution $\mathbf{b}$ from a known total number probability distribution at a single fixed time $0 < T < \infty$. Since $f_n(T)$ are known for all n, the generating function $F(z,T)$ is also precisely known for all $0 \leq z \leq 1$, as shown in Fig. 2(b). Our results focus on uniqueness of the reconstruction.

3.1 Uniqueness of Lifetime Distribution $G(t)$ Given $\mathbf{b}$

We first prove some lemmas to illustrate properties of the solution to (3).

Lemma 3 *Consider the integral equation*

$$y(t) = \int_0^t y(t-\tau)H(\tau)\mathrm{d}\tau + cP(t), \tag{19}$$

where $H(t)$ and $P(t)$ are strictly positive and continuous for $t \geq 0$. Then $y(t) \gtrless 0$ for $t \geq 0$ if $c \gtrless 0$.

Proof Because of the continuity of H and P, it can be shown [24] that $y(t)$ is continuous for $t > 0$. Let $c > 0$. Then $y(0) > 0$. Suppose that $y(t)$ is not positive for all t. Since y is continuous, there is a point $t^* > 0$ such that $y(t^*) = 0$ and $y(t) > 0$ for $t < t^*$. Then Eq. (19) implies

$$\int_0^{t^*} y\big(t^* - \tau\big)H(\tau)\mathrm{d}\tau = -cP\big(t^*\big) < 0.$$

But since $H(t) > 0$, the integral is positive and we have a contradiction. Therefore $y(t) > 0$ for all t. The proof for $c < 0$ is similar. □

Definition 1 A *trajectory* $F(z,t)$ is a solution of (3) for a particular value of z.

Definition 2 A *fixed point* of (3) is a value of z^* that satisfies $B[z^*] - z^* = 0$.

We will show below in Lemma 4 that a fixed point is a constant-in-time trajectory of Eq. (3).

Definition 3 A fixed point z^* is *stable* if for any fixed $z \in (0,1)$, the trajectory $F(z,t) \to z^*$ as $t \to \infty$.

The next lemma suggests that solutions to (3) can be understood in terms of the stability of individual trajectories, analogous to the theory of autonomous differential equations.

Lemma 4 *Consider the integral equation* (3) *and let* $G(t)$ *satisfy the conditions in* ($A1$). *Then*:

(i) *When* $B'[1] > 1$, (3) *has two distinct fixed points at* $z = z^* < 1$ *and* $z = 1$, *and* $F(z,t) = z^*, 1$ *are two constant-in-time trajectories of Eq.* (3). *If* $0 \le z < 1$, *then* z^* *is stable with* $F(z,t)$ *strictly monotonically increasing* (*decreasing*) *if* $z < z^*$ ($z > z^*$). *This case is commonly known as the supercritical case.*
(ii) *When* $B'[1] = 1$ *or* $B'[1] < 1$, $z^* = 1$ *is the only stable fixed point of* (3). *If* $0 \le z < 1$, $F(z,t)$ *is strictly monotonically increasing. These are also known as the critical* ($B'[1] = 1$) *and subcritical* ($B'[1] < 1$) *cases.*

Proof Since $B''[z] > 0$ for all $z \in [0,1]$, $B[z] - z$ can have either 0, 1 or 2 distinct roots. But $z = 1$ is clearly a root because $\sum_{m=0}^{\infty} b_m = 1$. Therefore $B[z] - z$ either has 1 or 2 roots. If $b_0 = 0$ then the second root is $z^* = 0$. Now consider $b_0 > 0$. If $B'[1] > 1$, it is clear that $B[z] - z < 0$ for $z = 1^-$. Since $B[0] > 0$, there must be a second root in $(0,1)$ by the Intermediate Value Theorem. We call this root z^*. If $B'[1] = 1$ or < 1, then $z = 1$ is the only root.

We now treat the two subcases $B'[1] > 1$ and $B'[1] = 1$, <1 separately.

(i) Upon taking time derivatives of (3), we have

$$\frac{\partial F(z,t)}{\partial t} = \big(B[z] - z\big)G(t) + \int_0^t \frac{\partial F}{\partial t}(z, t-\tau) B'\big[F(z,t-\tau)\big] G(\tau)\,\mathrm{d}\tau, \tag{20}$$

where $\frac{\partial F}{\partial t}$ is treated as the unknown and F is the solution to (3). We look for a trajectory $F(z,t)$ that is constant in t for a fixed z. Then (20) implies $B[z] - z = 0$ so the only constant solutions are $F(z^*,t) = z^*$ and $F(1,t) = 1$. The kernel of (20) $B'[F(z,t-\tau)]G(\tau)$ is continuous and strictly positive since G is continuous and positive by assumption and F is continuous by Lemma 1(i). Therefore, by Lemma 3, we have $\frac{\partial F}{\partial t} \gtrless 0$ if $B[z] - z \gtrless 0$. Hence $F(z,t)$ is monotonically increasing in t if $z < z^*$ and monotonically decreasing if $1 > z > z^*$. Given $G(t)$ and $B[z]$, uniqueness of F in (3) for $t > 0$ [1] means that solutions cannot cross: increasing (decreasing) solutions are bounded from above (below) by z^* and so these solutions must asymptote to a constant, F_0 say. In (3), as $t \to \infty$, $z \int_t^{\infty} G(\tau)\,\mathrm{d}\tau \to 0$ and $\int_0^t B[F(t-\tau)]G(\tau)\,\mathrm{d}\tau \to B[F_0] \int_0^{\infty} G(\tau)\,\mathrm{d}\tau$. Therefore F_0 satisfies $B[F_0] - F_0 = 0$ or $F_0 = z^*, 1$. Therefore $F(z,t) \to z^*$ if $0 \le z < 1$ and $F(z,t) = 1$ if $z = 1$.
(ii) If $z = 1$, then $B[z] - z = 0$ and $F(1,t) = 1$ is the only constant solution to (20). If $z < 1$, $B[z] - z > 0$. Using Lemma 3 on (20), we find that $\frac{\partial F(z,t)}{\partial t} > 0$. Using a similar argument to (i), we conclude that $F(z,t) = 1$ is globally attracting. ☐

We now restrict ourselves to exponential lifetime distributions to show global uniqueness in the rate parameter. Then we consider a small perturbation of an arbitrary lifetime distribution in Lemma 5 and derive an integral equation that determines its relationship to the corresponding perturbation in the number distribution. The properties of the integral equation remain open to further study.

Theorem 3 (Global uniqueness of exponential lifetime probabilities from number distribution) *Consider two branching processes with progeny number distribution* $B[z]$ *satisfying* (*A*2) *and exponential lifetime distributions* $G_1(t) = \lambda_1 e^{-\lambda_1 t}$ *and* $G_2(t) = \lambda_2 e^{-\lambda_2 t}$. *Suppose these branching processes give rise to z-transformed number distributions* $F_1(z, T)$ *and* $F_2(z, T)$ *respectively through Eq.* (3) *where* $T > 0$ *is a fixed measuring time. Then* $F_1(z, T) \neq F_2(z, T)$ *for* $0 \le z \le 1$ *if and only if* $\lambda_1 \neq \lambda_2$.

Proof When the lifetime distributions are exponentially distributed with $G(t) = \lambda e^{-\lambda t}$, it is simple to show [1] that (3) reduces to the nonlinear ordinary differential equation

$$\frac{\partial F}{\partial t} = -\lambda\big(F(z,t) - B\big[F(z,t)\big]\big), \tag{21}$$

with initial condition $F(z, 0) = z$. Dividing by λ, and setting $t' = \lambda t$ and $F(z,t) = \Phi(z, t') = \Phi(z, \lambda t)$ we find that

$$\frac{\partial \Phi\big(z,t'\big)}{\partial t'} = -\big(\Phi - B[\Phi]\big), \tag{22}$$

with initial condition $\Phi(z, t' = 0) = z$. For a given $0 \le z \le 1$, the solution of (22) is unique so we have

$$F_1(z,t) = \Phi(z, \lambda_1 t), \tag{23}$$

$$F_2(z,t) = \Phi(z, \lambda_2 t). \tag{24}$$

It is clear from (23) and (24) that $\lambda_1 = \lambda_2 \Rightarrow F_1(z,T) = F_2(z,T)$. Now assume that $\lambda_1 \neq \lambda_2$. Although (22) is a nonlinear differential equation, it is just a special case of (3) so Lemma 4 still applies.

1. In the supercritical case, $\Phi(z, t')$ in Eq. (22) is strictly monotonically increasing (decreasing) if $z < z^*$ ($z > z^*$) where z^* satisfies $B[z^*] - z^* = 0$. Therefore for $0 \le z < z^*$, when $\lambda_1 \gtrless \lambda_2$ $F_1(z,T) \gtrless F_2(z,T)$ since $\Phi(z, \lambda_1 T) \gtrless \Phi(z, \lambda_2 T)$. For $z^* < z < 1$, $F_1(z,T) \lessgtr F_2(z,T)$ when $\lambda_1 \gtrless \lambda_2$. Therefore $\lambda_1 \neq \lambda_2 \Rightarrow F_1(z,T) \neq F_2(z,T)$.
2. In the critical and subcritical cases, $\Phi(z, t')$ is strictly monotonically increasing if $0 \le z < 1$. Therefore $F_1(z,T) \gtrless F_2(z,T)$ if $\lambda_1 \gtrless \lambda_2$ and $\lambda_1 \neq \lambda_2 \Rightarrow F_1(z,T) \gtrless F_2(z,T)$.

□

If we do not restrict the class of $G(t)$ to be exponential, the problem of global uniqueness becomes much harder. Note that we are only interested in uniqueness/non-uniqueness of $G(t)$ for $0 \le t \le T$. In fact, by writing Eq. (3) with $t = T$ as

$$F(z,T) = z + \int_0^T \big(B\big[F(z, T-\tau)\big] - z\big) G(\tau) \mathrm{d}\tau,$$

it is easy to see that two functions $G(\tau)$ that are identical for $\tau \le T$, but not for $\tau > T$, would yield the same number distribution $f_n(T)$.

In the next lemma we explore the issue of local uniqueness. Suppose that for a given $B[z]$, the lifetime distribution G gives rise to a number distribution $F(z,t)$. How do small changes in the lifetime distribution, $\delta G(t)$ relate to small changes in the number distribution at a fixed time T, $\delta F(z,T)$? The changes are assumed to be square integrable functions so that $\delta G \in L^2[0,T]$ and $\delta F \in L^2[0,1]$ where $L^2[a,b]$ denotes the space of all square integrable functions on $[a,b]$.

Lemma 5 *For Eq.* (3), *let* $G(t)$ *and* $\{b_k\}$ *be given and let* $F(z,t)$ *be the corresponding solution, which is known for* $0 \le z \le 1$ *and* $t > 0$. *Let* $T > 0$ *be a fixed measurement time and consider an infinitesimal perturbation* $\delta G(t) \in L^2[0,T]$ *of the lifetime distribution* $G(t)$ *leading to a corresponding perturbation* $\delta F(z,T) \in L^2[0,1]$. *Let* $\int_0^\infty \int_0^\infty G^2(t-\tau)\mathrm{d}t\mathrm{d}\tau < \infty$, *with* $G(t) = 0$ *when* $t < 0$. *Then* δG *and* δF *are related through the first-kind Fredholm equation*

$$\int_0^T M(z,\tau)\delta G(\tau)\mathrm{d}\tau = \delta F(z,T), \quad 0 \le z \le 1, \tag{25}$$

where:

$$M(z,\tau) = B\big[F(z,T-\tau)\big] - z + \int_\tau^T \mathrm{d}\tau' \Gamma\big(T,\tau',z\big)\big(B\big[F\big(z,\tau'-\tau\big)\big] - z\big), \tag{26}$$

$$\begin{aligned}\Gamma(t,\tau,z) = {} & K(t,\tau,z) + \int_\tau^t \mathrm{d}t' K\big(t,t',z\big)K\big(t',\tau,z\big) \\ & + \int_\tau^t \mathrm{d}t' \int_\tau^{t'} \mathrm{d}t'' K\big(t,t',z\big)K\big(t',t'',z\big)K\big(t'',\tau,z\big) + \cdots,\end{aligned} \tag{27}$$

and

$$K(t,\tau,z) = \frac{\mathrm{d}B[F(z,\tau)]}{\mathrm{d}F} G(t-\tau). \tag{28}$$

Proof Let the functions $F(z,t)$ and $G(t)$ satisfy Eq. (3). Suppose G is perturbed by $\delta G(t)$, resulting in a small perturbation $\delta F(z,t)$. Then $G(t) + \delta G(t)$ and $F(z,t) + \delta F(z,t)$ satisfy Eq. (3):

$$F + \delta F = z \int_t^\infty (G + \delta G)\mathrm{d}\tau + \int_0^t B[F + \delta F](G + \delta G)\mathrm{d}\tau. \tag{29}$$

Upon taking the difference between (29) and (3), assuming $\delta G, \delta F \ll 1$ and neglecting second and higher order terms, we find that the perturbations δG and δF are linearly related through

$$\delta F(z,t) - \int_0^t K(t,\tau,z)\delta F(z,\tau)\mathrm{d}\tau = \delta S(z,t), \tag{30}$$

where $K(t,\tau,z)$ is defined in (28) and

$$\delta S(z,t) = \int_0^t \mathrm{d}\tau \big(B\big[F(z,t-\tau)\big] - z\big)\delta G(\tau). \tag{31}$$

Our goal is to find an integral equation for δG from (30) and (31) by eliminating δS. Equation (30) is a linear Volterra equation of the second kind. From Lemma 1, $F(z,t)$ is bounded on $0 \le z \le 1$ and $0 \le t < \infty$ and $B'[z]$ is increasing in z. Therefore

$$\begin{aligned}\int_0^\infty \int_0^\infty \big|K^2(t,\tau,z)\big|\mathrm{d}t\mathrm{d}\tau &= \int_0^\infty \int_0^\infty \left|\frac{\mathrm{d}B[F(z,\tau)]}{\mathrm{d}F} G(t-\tau)\right|^2 \mathrm{d}t\mathrm{d}\tau, \\ &< B'[1]^2 \int_0^\infty \int_0^\infty \big|G(t-\tau)\big|^2 \mathrm{d}t\mathrm{d}\tau, \\ &< \infty,\end{aligned}$$

and

$$\begin{aligned}
\big|\delta S(z,t)\big| &\le \int_0^T \big|B\big[F(z,t-\tau)\big]-z\big|\big|\delta G(\tau)\big|\mathrm{d}\tau,\\
&\le \left\{\int_0^T \big|B\big[F(z,t-\tau)\big]-z\big|^2\mathrm{d}\tau\right\}^{1/2}\left\{\int_0^T \big|\delta G(\tau)\big|^2\mathrm{d}\tau\right\}^{1/2},\\
&\le \left\{\int_0^T \big|B\big[F(z,t-\tau)\big]\big|^2+|z|^2\mathrm{d}\tau\right\}^{1/2}\left\{\int_0^T \big|\delta G(\tau)\big|^2\mathrm{d}\tau\right\}^{1/2},\\
&\le (2T)^{1/2}\left\{\int_0^T \big|\delta G(\tau)\big|^2\mathrm{d}\tau\right\}^{1/2},\\
&< \infty
\end{aligned}$$

since δG is square integrable on $[0,T]$. Therefore $\int_0^T |\delta S(z,t)|^2\mathrm{d}t<\infty$. Since K and δS are square integrable in (30), it can be solved in terms of a resolvent kernel Γ:

$$\delta F(z,t)=\delta S(z,t)+\int_0^t \Gamma(t,\tau,z)\delta S(z,\tau)\mathrm{d}\tau,\quad 0\le z\le 1, \tag{32}$$

where Γ is defined through a Liouville-Neumann series in (27). Evaluating (32) at $t=T$, we have for $0\le z\le 1$,

$$\delta S(z,T)+\int_0^T \Gamma(T,\tau,z)\delta S(z,\tau)\mathrm{d}\tau=\delta F(z,T). \tag{33}$$

Substituting Eq. (31) into (33), we have

$$\begin{aligned}
&\int_0^T \big(B\big[F(z,T-\tau)\big]-z\big)\delta G(\tau)\mathrm{d}\tau\\
&\quad+\int_0^T \mathrm{d}\tau\,\Gamma(T,\tau,z)\int_0^\tau \big(B\big[F\big(z,\tau-\tau'\big)\big]-z\big)\delta G\big(\tau'\big)\mathrm{d}\tau'=\delta F(z,T),
\end{aligned}$$

which can be rewritten as

$$\mathcal{M}\delta G\equiv\int_0^T M(z,\tau)\delta G(\tau)\mathrm{d}\tau=\delta F(z,T), \tag{34}$$

where $M(z,\tau)$ is given by (26). □

Now suppose that the two lifetime distributions G and $G+\delta G$ generate exactly the same number distribution so that $\delta F(z,T)=0$ in (34). Then local uniqueness of $G(t)$ from $F(z,T)$ would imply that $\delta G(t)=0$ for $0\le t\le T$. Likewise, local non-uniqueness would imply that there is a non-zero (non-trivial) δG that satisfies $\mathcal{M}\delta G=0$.

Currently it is still an open question if $\delta F(z,T)=0$ for $0\le z\le 1\Rightarrow\delta G(t)=0$ for $0\le t\le T$. Further work must be done to characterize the null space of the operator $\mathcal{M}$, or equivalently the closure of the range of the adjoint $\mathcal{M}^*$ where $\mathcal{M}^*\delta H(z)\equiv\int_0^1 \mathrm{d}z M(z,\tau)\delta H(z)$.

3.2 Reconstruction of Progeny Distribution **b** Given Lifetime Distribution $G(t)$

Lemma 6 *Let* $G(t) > 0$ *and* $P(t) > 0$ *for* $t \geq 0$. *For the two integral equations*

$$y_1(t) = c_1 \int_0^t y_1(t-\tau)G(\tau)\mathrm{d}\tau + P(t),$$

$$y_2(t) = c_2 \int_0^t y_2(t-\tau)G(\tau)\mathrm{d}\tau + P(t),$$

assume that $c_1, c_2 > 0$. *Then* $y_1(t) \gtrless y_2(t)$ *for all* $t \geq 0$ *if* $c_1 \gtrless c_2$.

Proof Let $c_2 > c_1 > 0$. Then for $t \geq 0$ y_1 and y_2 are strictly positive by Lemma 3 and we have

$$\begin{aligned} y_1(t) - y_2(t) &= \int_0^t \big[c_1 y_1(t-\tau) - c_2 y_2(t-\tau)\big]G(\tau)\mathrm{d}\tau, \\ &< c_2 \int_0^t \big[y_1(t-\tau) - y_2(t-\tau)\big]G(\tau)\mathrm{d}\tau, \end{aligned}$$

so that

$$y_1(t) - y_2(t) = c_2 \int_0^t \big[y_1(t-\tau) - y_2(t-\tau)\big]G(\tau)\mathrm{d}\tau + C(t),$$

where $C(t) < 0$ for all $t \geq 0$. Since $y_1(t)$ and $y_2(t)$ are continuous for $t \geq 0$ [24], $C(t) \equiv y_1(t) - y_2(t) - c_2 \int_0^t [y_1(t-\tau) - y_2(t-\tau)]G(\tau)\mathrm{d}\tau$ is also continuous for $t > 0$. By Lemma 3, $y_1(t) - y_2(t) < 0$. The proof for $0 < c_2 < c_1$ is similar. □

Lemma 7 *Consider the two integral equations*

$$y_1(t) = \int_0^t y_1(t-\tau)G(\tau)\mathrm{d}\tau + c_1 P(t) + Q(t),$$

$$y_2(t) = \int_0^t y_2(t-\tau)G(\tau)\mathrm{d}\tau + c_2 P(t) + Q(t),$$

and assume $Q(t)$ *is continuous*, $G(t) > 0$ *and* $P(t) > 0$ *for* $t \geq 0$. *Then* $y_1(t) \gtrless y_2(t)$ *for all* $t \geq 0$ *if* $c_1 \gtrless c_2$.

Proof The proof follows immediately if we consider the integral equation for $y_1 - y_2$ and apply Lemma 3. □

We now prove that perfect measurement of the number distribution at a fixed time $T > 0$ uniquely determines the branching probabilities. Our proof relies on a local analysis of the trajectories of (3) near the fixed points $z = z^*$. Recall that such points satisfy $B[z] - z = 0$. In the critical and subcritical cases, $z^* = 1$ is attracting and in the supercritical case $0 \leq z^* < 1$ is attracting. Although our method is local in z, it is *global* in t. The idea is to linearize Eq. (3) about the fixed points and show that when $B_1[\cdot] \not\equiv B_2[\cdot]$, if z is close to z^* then $F_1(z,t) \neq F_2(z,t)$ for $t > 0$. Moreover, we show that if $B_1[z] \equiv B_2[z]$, $F_1(z,t) = F_2(z,t)$ for $t \geq 0$ and $z \in [0, 1]$.

Theorem 4 (Global uniqueness of progeny number probabilities from a number distribution) *Consider two branching processes with the same continuous lifetime distribution $G(t)$ satisfying the conditions in* (A1). *Suppose their progeny number distributions*, *defined by their generating functions $B_1[z]$ and $B_2[z]$*, *give rise to the pgfs of two number distributions $F_1(z,T)$ and $F_2(z,T)$ at time $t=T$. Then $F_1(z,T)=F_2(z,T)$ for all z if and only if $B_1[z]\equiv B_2[z]$.*

Proof We show that:

(i) When $B_1[z]\equiv B_2[z]$, $F_1(z,T)=F_2(z,T)$ for all $T\geq 0$ and $0\leq z\leq 1$.
(ii) When $B_1[z]\not\equiv B_2[z]$, there cannot exist a $T>0$ such that $F_1(z,T)=F_2(z,T)$ for all $0\leq z\leq 1$.

Item (i) is quickly proved as follows: first suppose that $B_1[z]\equiv B_2[z]$. Since the solution to Eq. (3) is unique for a given branching function [21], we must have $F_1(z,t)=F_2(z,t)$ on $[0,1]\times[0,\infty)$ and clearly $F_1(z,T)=F_2(z,T)$.

The remainder of the proof is to show (ii). Let z_1^* be any stable fixed point of $B_1[z]$ and z_2^* be any stable fixed point of $B_2[z]$. If $z_1^*\neq z_2^*$, then without loss of generality, let $z_1^*<z_2^*$ and fix a point z satisfying $z_1^*<z<z_2^*$. Then by Lemma 4, $F_1(z,t)\to z_1^*$ is a strictly decreasing trajectory in t while $F_2(z,t)\to z_2^*$ is a strictly increasing trajectory. Therefore $F_1(z_1^*,t)\neq F_2(z_2^*,t)$ for $t>0$ so there cannot exist a $T>0$ such that $F_1(z,T)=F_2(z,T)$ for all $0\leq z\leq 1$.

Now suppose that $z_1^*=z_2^*=z^*$. This would be the case, for example, when both branching process are subcritical and $z_1^*=z_2^*=1$. For $|\delta z|\ll 1$, the Bellman-Harris integral equation is still satisfied at $z=z^*+\delta z$:

$$F_j\big(z^*+\delta z,t\big)=\big(z^*+\delta z\big)\int_t^\infty G(\tau)\mathrm{d}\tau+\int_0^t B_j\big[F_j\big(z^*+\delta z,t-\tau\big)\big]G(\tau)\mathrm{d}\tau, \tag{35}$$

for $j=1,2$. Expanding F_1, B_1 and F_2, B_2 in a Taylor series about z^*, we find

$$F_1\big(z^*+\delta z,t\big)=\sum_{n=0}^{\infty}\frac{F_1^{(n)}(z^*,t)}{n!}\delta z^n, \tag{36}$$

$$B_1\big[z^*+\delta z\big]=\sum_{n=0}^{\infty}\frac{B_1^{(n)}[z^*]}{n!}\delta z^n, \tag{37}$$

$$F_2\big(z^*+\delta z,t\big)=\sum_{n=0}^{\infty}\frac{F_2^{(n)}(z^*,t)}{n!}\delta z^n, \tag{38}$$

$$B_2\big[z^*+\delta z\big]=\sum_{n=0}^{\infty}\frac{B_2^{(n)}[z^*]}{n!}\delta z^n, \tag{39}$$

where $F'(z,t)=\partial_z F(z,t)$ and $F^{(m)}(z,t)=\partial_z^m F(z,t)$. Our strategy is to substitute (36)–(39) into (35), and equate powers of δz^n to find *linear* integral equations for $F_j^{(n)}(z^*,t)$.

If $B_1[z]\not\equiv B_2[z]$, some terms of their Taylor series must differ. Suppose $B_1^{(n)}[z^*]=B_2^{(n)}[z^*]$ for $n=0,1,\ldots,m-1$ but $B_1^{(m)}[z^*]\neq B_2^{(m)}[z^*]$. We complete the proof by showing that $F_1^{(m)}(z^*,t)\neq F_2^{(m)}(z^*,t)$ for $t>0$.

- *Case* $m = 1$

  We have $B_1[z^*] = B_2[z^*]$ and $B_1'[z^*] \neq B_2'[z^*]$. Then at $O(\delta z^0)$, $F_1^{(0)}(z^*, t) = F_2^{(0)}(z^*, t) = z^*$ are solutions to Eq. (3). However, at $O(\delta z)$, F_1' and F_2' satisfy

$$F_1'\big(z^*, t\big) = \int_t^\infty G(\tau)\mathrm{d}\tau + B_1'\big[z^*\big]\int_0^t F_1'\big(z^*, t-\tau\big)G(\tau)\mathrm{d}\tau, \tag{40}$$

$$F_2'\big(z^*, t\big) = \int_t^\infty G(\tau)\mathrm{d}\tau + B_2'\big[z^*\big]\int_0^t F_2'\big(z^*, t-\tau\big)G(\tau)\mathrm{d}\tau. \tag{41}$$

  By Lemma 6, $F_1'(z^*, t) \neq F_2'(z^*, t)$ for $t > 0$ so $F_1(z, t) \neq F_2(z, t)$ for $t > 0$ when $z = z^* + \delta z$.

- *Case* $m = 2$

  For this case, $B_1[z^*] = B_2[z^*]$, $B_1'[z^*] = B_2'[z^*]$, $F_1^{(0)}(z^*, t) = F_2^{(0)}(z^*, t)$ and (40) and (41) imply $F_1'(z^*, t) = F_2'(z^*, t) \equiv F'(z^*, t)$: we have to go to higher order in δz to show $F_1(z, t) \neq F_2(z, t)$.

  Suppose that $B_1'[z^*] = B_2'[z^*] = B'[z^*]$ but that $B_1''[z^*] \neq B_2''[z^*]$. Then at $O(\delta z^2)$, F_1'' and F_2'' satisfy

$$F_1''\big(z^*, t\big) = B'\big[z^*\big]\int_0^t F_1''\big(z^*, t-\tau\big)G(\tau)\mathrm{d}\tau + B_1''\big[z^*\big]P(t),$$

$$F_2''\big(z^*, t\big) = B'\big[z^*\big]\int_0^t F_2''\big(z^*, t-\tau\big)G(\tau)\mathrm{d}\tau + B_2''\big[z^*\big]P(t),$$

  where $P(t) \equiv \int_0^t (F'(z^*, t-\tau))^2 G(\tau)\mathrm{d}\tau$ is continuous. It is clear that the second derivative of B is now responsible for distinguishing the two solutions $F_1(z^* + \delta z, t)$ and $F_2(z^* + \delta z, t)$. Since $B'[z^*] > 0$, upon using Lemma 7, $F_1''(z^*, t) \neq F_2''(z^*, t)$ for $t > 0$ and therefore $F_1(z, t) \neq F_2(z, t)$ for $t > 0$.

- *Case* $m > 2$

  Suppose that $B_1^{(n)}[z^*] = B_2^{(n)}[z^*] = B^{(n)}[z^*]$ for $n = 0, 1, \ldots, m-1$, $B_1^{(m)}[z^*] \neq B_2^{(m)}[z^*]$ and $F_1^{(n)}(z^*, t) = F_2^{(n)}(z^*, t) = F^{(i)}(z^*, t)$ for $n = 0, 1, \ldots, m-1$. To order $O(\delta z^m)$ we have

$$\begin{aligned} F_1^{(m)}\big(z^*, t\big) = B'\big[z^*\big]&\int_0^t F_1^{(m)}\big(z^*, t-\tau\big)G(\tau)\mathrm{d}\tau \\ &+ B_1^{(m)}\big[z^*\big]P_m(t) + Q_m(t), \end{aligned} \tag{42}$$

$$\begin{aligned} F_2^{(m)}\big(z^*, t\big) = B'\big[z^*\big]&\int_0^t F_2^{(m)}\big(z^*, t-\tau\big)G(\tau)\mathrm{d}\tau \\ &+ B_2^{(m)}\big[z^*\big]P_m(t) + Q_m(t), \end{aligned} \tag{43}$$

  where

$$P_m(t) = \int_0^t \left[\frac{\partial F}{\partial z}\big(z^*, t-\tau\big)\right]^m G(\tau)\mathrm{d}\tau,$$

$$Q_m(t) = \int_0^t G(\tau)R_m\big[F', \ldots, F^{(m-1)}; B'', \ldots, B^{(m-1)}\big]\mathrm{d}\tau,$$

and $R_m[F'(z^*, t-\tau), \ldots, F^{(m-1)}(z^*, t-\tau); B''[z^*], \ldots, B^{(m-1)}[z^*]]$ is an algebraic function whose exact form is not important. Applying Lemma 7 on Eqs. (42) and (43), we conclude that $F_1^{(m)}(z^*, t) \neq F_2^{(m)}(z^*, t)$ for $t > 0$. □

4 Conclusions

We have investigated the reconstructibility of lifetime distributions and progeny number distributions of a single-species Bellman-Harris process. We assumed perfectly known data of two types: an extinction time distribution (equivalent to the survival probability of the processes), and the total number distribution at a single fixed time T. We find that for a given extinction time distribution, both the lifetime distribution function $G(\tau)$ and progeny number distribution $\mathbf{b}$ can be found provided the other is given. Moreover, these distributions are unique and injective with respect to the cumulative extinction probability $F(0, t)$.

For perfect number distributions, known at a single fixed time T, we showed global identifiability of the lifetime distribution by restricting the class of distributions to be exponential. For the case of arbitrary lifetimes, we explored local identifiability by linearizing (3) and found a relation between small changes in $G(t)$ and small changes in $F(z, T)$. Therefore, for a known $B[z]$, local identifiability of G remains an open problem. On the other hand, for a known $G(t)$, we established global identifiability of the progeny number distribution $B[z]$.

Again, we emphasize that Theorems 1 and 2 give reconstructions for $G(t)$ and $\{b_j\}$ only if the exact data were derived from an underlying Bellman-Harris process. Formulas (4) and (11)–(12) assume that the underlying process that generated $F(0, t)$ is a Bellman-Harris process. For an arbitrary set of exact data $F(0, t)$, however, there is no guarantee that $G(t)$ is a pdf or $\{b_j\}$ are a set of probabilities. For example, if $F(0, t)$ is generated by a process where particles branch after living for a random amount of time *and* are removed at a time-dependent rate, applying formulas (4) and (11)–(12) could generate $G(t)$ that do not integrate to unity or $\{b_j\}$ that do not sum to unity. In fact, whether or not "sensible" $G(t)$ or $\{b_j\}$ can be obtained would provide arguments for model selection. We leave as future work the task of characterizing in more detail those functions $F(0, t)$ that are the cumulative extinction probabilities of some underlying Bellman-Harris branching process.

Our results define which parameter functions of the Bellman-Harris process can be uniquely determined. These findings may guide numerical and statistical approaches to inference of branching processes, even though perfect data is not available. Possible extensions of our analyses include the utilization of perfectly measured pgfs at multiple discrete times $F(z, T_1), F(z, T_2), \ldots$, to better reconstruct the parameterizing functions in the branching model.

References

1. Kimmel, M., Axelrod, D.E.: Branching Processes in Biology. Springer, New York (2002)
2. Athreya, K.B., Ney, P.E.: Branching Processes. Springer, New York (1972)
3. Allen, L.J.S.: An Introduction to Stochastic Processes with Applications to Biology. Pearson Education Inc, Upper Saddle (2003)
4. Harris, T.E.: Branching processes. Ann. Math. Stat. **19**, 474–494 (1948)
5. Sorarrain, O.M., Boggio, R., Cordo, C.: An actual Bellman-Harris epidemic process. The infection of septoria in barley or wheat. J. Theor. Biol. **80**, 425–433 (1979)
6. Zilman, A., Ganusov, V.V., Perelson, A.S.: Stochastic models of lymphocyte proliferation and death. PLoS ONE, **5**, 9 (2010)

7. Antal, T., Krapivsky, P.L.: Exact solution of a two-type branching process: clone size distribution in cell division kinetics. J. Stat. Mech. Theory Exp. **2010**, P07028 (2010)
8. Klein, A.M., Doupe, D.P., Jones, P.H., Simons, B.D.: Kinetics of cell division in epidermal maintenance. Phys. Rev. E **76**, 021910 (2007)
9. Jacobson, M.E.: Computation of extinction probabilities for the Bellman-Harris branching process. Math. Biosci. **77**, 173–177 (1985)
10. Hyrien, O., Mayer-Pröschel, M., Noble, M., Yakovlev, A.: A stochastic model to analyze clonal data on multi-type cell populations. Biometrics **61**, 199–207 (2005)
11. Hyrien, O.: Pseudo-likelihood estimation for discretely observed multitype Bellman-Harris branching processes. J. Stat. Plan. Inference **137**, 1375–1388 (2007)
12. Bhat, B.R., Adke, S.R.: Maximum likelihood estimation for branching processes with immigration. Adv. Appl. Probab. **13**, 498–509 (1981)
13. Kale, M.M., Deshmukh, S.R.: Maximum likelihood estimation in branching processes with continuous state space. Stat. Probab. Lett. **18**, 245–251 (1993)
14. O'N Waugh, W.A.: Age-dependent birth and death process. Biometrika **42**, 291–306 (1955)
15. Nedelman, J., Downs, H., Pharr, P.: Inference for an age-dependent, multitype branching-process model of mast cells. J. Math. Biol. **25**, 203–226 (1987)
16. Dion, J.P.: Estimation of the variance of a branching process. Ann. Stat. **3**, 1183–1187 (1975)
17. Johnson, R.A., Susarla, V., van Ryzin, J.: Bayesian non-parametric estimation for age-dependent branching processes. Stoch. Process. Appl. **9**, 307–318 (1979)
18. Pazsit, I., Pal, L.: Neutron Fluctuations: A Treatise on the Physics on Branching Processes. Elsevier, Amsterdam (2008)
19. Tse, H.T.K., Weaver, W.M., Di Carlo, D.: Increased asymmetric and multi-daughter cell division in mechanically confined microenvironments. PLoS ONE **7**, e38986 (2012)
20. Erdelyi, A.: Asymptotic Expansions. Dover, New York (1956)
21. Kiffe, T., Stecher, M.: Existence and uniqueness of solutions to abstract Volterra integral equations. Proc. Am. Math. Soc. **68**, 169–175 (1978)
22. Ablowitz, M.J., Fokas, A.S.: Complex Variables. Cambridge University Press, Cambridge (1997)
23. Feller, W.: An Introduction to Probability Theory and Its Applications, vol. 2. Wiley, New York (1957)
24. Kress, R.: Linear Integral Equations. Springer, Berlin (1989)