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Workshop on Branching Processes and Their Applications

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Foreword

One of the charms of mathematics is the contrast between its generality and its applicability to concrete, even everyday, problems.

Branching processes are typical in this. Their niche of mathematics is the abstract pattern of reproduction, sets of individuals changing size and composition through their members reproducing; in other words, what Plato might have called the pure idea behind demography, population biology, cell kinetics, molecular replication, or nuclear fission, had he known these scientific fields. Even in the performance of algorithms for sorting and classification there is an inkling of the same pattern.

In special cases, general properties of the abstract ideal then interact with the physical or biological or whatever properties at hand. But the population, or branching, pattern is strong; it tends to dominate, and here lies the reason for the extreme usefulness of branching processes in diverse applications. Branching is a clean and beautiful mathematical pattern, with an intellectually challenging intrinsic structure, and it pervades the phenomena it underlies.

The problem that gave birth to branching processes, that of the astonishingly frequent extinction of noble families, illustrates the situation well. The starting point was a question, which today would seem more intriguing or amusing than serious: Where have all the well-known families gone? Where are all the Hohenstaufferns, Plantagenets, Tudors, Trastámaras, or Vasas? How come that they so often have died out, even though the populations they were part of increased? Degeneration?

But to Bienaymé and Galton, 150 years ago, this was a serious concern, and behind it lurks a question of general scientific interest: Can frequent extinction of separate family lines go hand in hand with a rapid increase of the whole population? Is this a general property of the branching pattern and not some oddity of human populations? If so, would it be part of an explanation of the extremely frequent extinction of species?

After a first disastrous mistake and 50 years of ensuing confusion, branching processes were able to prove that in natural conditions frequent extinction of separate family lines is completely compatible with exponential ("Malthusian") growth of the whole. This is, indeed, a mathematical property: a strongly supercritical branching process can still exhibit extinction probabilities say around 75%.

Extinction matters, like the time and path to extinction, remain important in branching processes and cutting-edge areas of application like conservation biology. But with time branching processes have developed into a full-fledged theory of population dynamics, encompassing the growth of populations as well as the stabilization of their composition, and their pedigrees looking backward. Mating can be dealt with, at least in simple processes, the effects of random environments clarified, and the first steps are being taken on models where there is a feedback from population size on individual behaviour. Today branching processes is a mature and important part of mathematics, and also of theoretical biology, theoretical chemistry, nuclear physics, computer algorithms, and demography.

Many aspects of the theory and its stance today were presented at the 2009 Badajoz workshop on branching processes, organized by the active branching process group of the University of Extremadura. This book contains most of the lectures given. It will be of great help to those wanting to acquaint themselves with contemporary branching process theory.

Gothenburg, Sweden
September 2009 *Peter Jagers*

Preface

The Workshop on Branching Processes and their Applications (WBPA) was held during 20–23 April 2009 in Badajoz, Spain. This conference gave continuity to such important previous meetings as the First World Conference on Branching Processes held in Varna, Bulgaria, in 1993, the IMA workshop on Classical and Modern Branching Processes held in Minnesota, USA, in 1994, and the more recent Symposium: Branching in Biology held in Gothenburg, Sweden, in 2005. The WBPA was promoted and organized by the Branching Processes Research Group belonging to the Department of Mathematics of the University of Extremadura, Spain. There were 35 invited participants from 15 countries from all over the world.

The papers presented at the workshop maintained a healthy balance between the theoretical and practical aspects of branching process theory, showing it to be an area of active and interesting research. They clearly indicated the importance of branching concepts in the development of theoretical approaches to solving problems in applied fields such as Epidemiology, Cell Kinetics, Genetics, and, of course Population Dynamics.

The Proceedings consists of 20 papers. All of them have been thoroughly reviewed. Parts covered by the workshop have been classified into the following areas:

1. Population Growth Models in Random and Varying Environments
2. Special Branching Processes
3. Limit Theorems and Statistics
4. Applications in Cell Kinetics and Genetics
5. Applications in Epidemiology
6. Two-Sex Branching Models

The first part deals with Population Growth Models in Random and Varying Environments. V. Vatutin considers critical branching processes in independent and identically distributed random environment. He shows the asymptotic behaviour of the survival probability and proves a conditional functional limit theorem under hypotheses which are milder than those used in classical papers. G. Alsmeyer revisits the extinction problem in branching processes in a stationary ergodic environment.

The use of random times in connection with the stationary environment leads him quite naturally to the use of Palm-duality theory in some of his arguments. C. Braumann compares the density-independent models of population growth; namely the Galton–Watson process, the simple birth and death process, and the Malthusian stochastic differential equation model, the first two being demographic stochasticity models, and the third an environmental stochasticity model. P. Mayster establishes the existence of stationary distributions for alternating branching processes, where two Markov branching processes act alternately in random time periods of observation and treatment.

In Part 2, Special Branching Processes, F. Klebaner considers models of population–size–dependent branching processes with the feature that they are supercritical when the population reaches a certain threshold, near critical around that value, and subcritical below it. G. Yanev reviews the existing results and presents new ones on certain subtrees of the Galton–Watson family tree. He considers rooted and complete subtrees, i.e., subtrees rooted at the ancestor and being family trees of a deterministic branching process. K. Mitov et al. study Bienaymé–Galton–Watson processes subordinated by a renewal process for which the interarrival periods have a finite mean or heavy tails. V. Topchii studies renewal measure densities associated with the problem of determining the expected number of particles at the origin of catalytic branching random walks.

Part 3 focuses on Limit Theorems and Statistics. I. Rahimov considers a branching stochastic process with non-stationary immigration given by an offspring distribution depending on an unknown parameter. He estimates this parameter and introduces a bootstrap process. The paper deals with how good the estimator must be in order for the bootstrap process to have the same asymptotic properties as the original process. M. Ispàny and G. Pap investigate critical and nearly critical Galton-Watson branching processes with immigration, obtaining related functional limit theorems by using a general convergence theorem for martingale differences. M. González and I. del Puerto propose a weighted conditional least squares estimator of the offspring mean matrix for a multitype controlled branching process and study its asymptotic properties in the supercritical case.

Part 4 comprises some applications of the branching processes theory in Cell Kinetics and Genetics. N. Yanev considers some new ideas for branching process theory that arise in cell proliferation modeling. He considers distributions of discrete and continuous labels and of ages and residual lifetimes, models of leukemia cell kinetics, age-dependent branching populations with randomly chosen paths of evolution as models of (in vitro) progenitor cell populations and the estimation of offspring distributions, multitype branching populations with a large number of ancestors, and asymptotic likelihood estimation of the basic mitotic parameters. M. Kimmel and M. Mathaes propose a modification of the discrete time branching process described by Griffith and Pakes to model the amplification, mutation, and selection forces of Alu elements. They derive a limit frequency spectrum of the Alu element distribution, which serves as the theoretical, neutral frequency with which real Alu insertion data can be compared through statistical goodness of fit tests. M. González et al. use a two-type bisexual branching process to model, in a two-sex monogamic population, the evolution of the number of carriers of the two alleles of a gene linked to the *Y* chromosome. They deal with inferential problems arising from this model, considering a frequentist and parametric approach. They consider the situation in which the only data available are the total number of females and the total number of males of each genotype in each generation. This leads them to use the expectation-maximization (EM) method in order to obtain maximum likelihood estimators.

Part 5 is about applications in Epidemiology. This is an applied area in which a number of new and exciting contributions were made at the Workshop. F. Ball and P. Neal are concerned with applications of branching processes to model the spread of an SIR (susceptible–infective–removed) epidemic among a closed, homogeneously mixing population consisting initially of certain numbers of infective and susceptible individuals. Each infective remains infectious for a period sampled independently from an arbitrary but specified distribution, during which he/she contacts susceptible individuals independently with some rate for each susceptible. C. Jacob et al. treat the problem of modeling the propagation of Bovine Spongiform Encephalopathy at the scale of a very large population (Great Britain) in order to predict its extinction time and to evaluate the efficiency of the main feed-ban regulation. They elaborate a multitype branching process in discrete time with age and population dependent individual transitions. The types are the health states at each age. M. González et al. use a Sevast'yanov age-dependent branching process to describe outbreaks of infectious diseases with an incubation period. They propose a method to obtain the optimal proportion of susceptible individuals that have to be vaccinated in order to eliminate the disease from the population. D. Heinzmann is interested in modeling the transmission dynamics of the macroparasite *Echinococcus granulosus.* He presents an approximation for the time to extinction in a sub-critical epidemic two-host interaction process for this macroparasite by using multitype branching processes.

Part 6, Two-Sex Branching Models, has contributions from S. Ma and Y. Xing who introduce and study a class of discrete time bisexual branching processes in which in each generation there is allowed the immigration of females and males, depending on the current numbers of females and males in the population, and from M. Molina who presents a summary of the literature associated with the classes of two-sex branching processes.

The organizers greatly appreciate the major response from the participants to submit contributions to the Proceedings. They would also like to thank all the people who actively participated in organizing the workshop, and those entities which provided financial and scientific support. The main funding came from the Spanish Ministry of Science and Innovation (Ministerio de Ciencia e Innovación), the University of Extremadura itself, and the Local Administration. The Spanish Society of Statistics and Operations Research (SEIO) supported the meeting scientifically.

Also, our very special thanks go to Peter Jagers for accepting the task of writing the foreword of this book. Finally, many thanks to Springer Publishers, particulary to Niels Peter Thomas and John Kimmel, for making it possible for this project to see the light.

Badajoz, Spain
September 2009

Miguel González
On behalf of the Editors

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Part I
Population Growth Models in Random and Varying Environments

1

A refinement of limit theorems for the critical branching processes in random environment

Vladimir Vatutin

Abstract For the critical branching processes in i.i.d. environment the asymptotic behavior of the survival probability is found and a conditional functional limit theorem is proved under the hypotheses which are milder than those used earlier.

Mathematics Subject Classification (2000): 60J80, 60F17, 60K37

Keywords: branching processes in random environment, associated random walk, Doney's condition, survival probability, conditional limit theorems.

1.1 Introduction and main results

In this paper we refine some results from [1] concerning the asymptotic behavior of the survival probability and the conditional functional limit theorem for the critical branching processes in i.i.d. random environment. To give a formal definition of the processes under consideration let $\varDelta$ be the space of probability measures on $\mathbb{N}_0 := \{0,1,2,\ldots\}$ and Q be a random variable taking values in $\varDelta$. An infinite sequence $\varPi = (Q_1, Q_2, \ldots)$ of i.i.d. copies of Q is said to form a *random environment*. A sequence of $\mathbb{N}_0$-valued random variables $Z_0, Z_1, \ldots$ is called a *branching process in the random environment* $\varPi$, if Z_0 is independent of $\varPi$ and, given $\varPi$, the process $Z = (Z_0, Z_1, \ldots)$ is a Markov chain with

$$\mathscr{L}\big(Z_n \mid Z_{n-1} = z_{n-1}, \varPi = (q_1, q_2, \ldots)\big) \;=\; \mathscr{L}\big(\xi_{n1} + \cdots + \xi_{nz_{n-1}}\big) \tag{1.1}$$

for every $n \geq 1$, $z_{n-1} \in \mathbb{N}_0$ and $q_1, q_2, \ldots \in \varDelta$, where $\xi_{n1}, \xi_{n2}, \ldots$ are i.i.d. random variables with distribution q_n. We can write this as

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$$Z_n := \sum_{i=1}^{Z_{n-1}} \xi_{ni} \tag{1.2}$$

where, given the environment, Z is an ordinary inhomogeneous Galton-Watson process. Thus, Z_n is the nth generation size of the population and Q_n is the distribution of the number of children of an individual at generation $n-1$.

We will denote the corresponding probability measure on the underlying probability space by $\mathbf{P}$. (If we refer to other probability spaces, then we use notation $\mathbb{P}$ and $\mathbb{E}$ for the respective probability measures and expectations.)

In the theorems below we assume $Z_0 = 1$ a.s. for convenience. For further details and background of the branching processes in random environment we refer the reader to [1–3, 12].

In what follows it is convenient to identify Q and $Q_n, n = 1, 2, \ldots$ with (random) generating functions

$$f(s) \ := \ \sum_{i=0}^{\infty} s^i \, Q(\{i\}) =: \mathbf{E}\left[s^{\xi} | Q\right], \qquad 0 \le s \le 1 \ ,$$

and

$$f_n(s) \ := \ \sum_{i=0}^{\infty} s^i \, Q_n(\{i\}) =: \mathbf{E}\left[s^{\xi_n} | Q_n\right], \qquad 0 \le s \le 1 \ ,$$

and to introduce the compositions

$$f_{k,n}(s) \ := \ f_{k+1}(f_{k+2}(\cdots f_n(s) \cdots)) \ , \ 0 \le k < n, \quad f_{n,n}(s) \ := s. \tag{1.3}$$

In the sequel we make no difference between the tuples $\varPi = (Q_1, Q_2, \ldots)$ and $\mathbf{f} = (f_1, f_2, \ldots)$. In particular, we rewrite the distributional identity (1.1) as

$$\mathbf{E}[s^{Z_n} \mid \mathbf{f}, Z_k] = \mathbf{E}[s^{Z_n} \mid \varPi, Z_k] = f_{k,n}(s)^{Z_k} \quad \mathbf{P}\text{–}a.s. \tag{1.4}$$

It follows from (1.4) that under the assumption $\mathbf{P}(Z_0 = 1) = 1$

$$\mathbf{P}(Z_n > 0 \mid \varPi) \ = \ 1 - f_{0,n}(0) \quad \mathbf{P}\text{–}a.s.$$

Later on for brevity we use the notation

$$\mathbf{P}_f(\cdot) := \mathbf{P}(\cdot \mid f, \, Z_0 = 1), \ \ \mathbf{E}_f[\cdot] := \mathbf{E}[\cdot \mid f, \, Z_0 = 1]$$

and

$$\mathbf{P}_{f_n}(\cdot) := \mathbf{P}(\cdot \mid f_n, \, Z_{n-1} = 1), \ \ \mathbf{E}_{f_n}[\cdot] := \mathbf{E}[\cdot \mid f_n, \, Z_{n-1} = 1]$$

for the probabilities and expectations related with functionals of the random variable ξ (respectively, ξ_n) given f (respectively, f_n) and

$$\mathbf{P}_{\mathbf{f}}(\cdot) := \mathbf{P}(\cdot \mid \mathbf{f}, \, Z_0 = 1), \ \ \mathbf{E}_{\mathbf{f}}[\cdot] := \mathbf{E}[\cdot \mid \mathbf{f}, \, Z_0 = 1]$$

for the probabilities and expectations related with functionals of the branching process Z given $\mathbf{f} = (f_1, f_2, \ldots)$.

It was demonstrated in [1] that the properties of Z are first of all determined by its associated random walk $S = (S_0, S_1, \ldots)$. This random walk has initial state $S_0 := 0$ and increments $X_n = S_n - S_{n-1}$, $n \geq 1$, defined as

$$X_n \; := \; \log \, f_n'(1),$$

which are i.i.d. copies of the logarithmic mean offspring number

$$X \; := \; \log \, f'(1) \, .$$

We assume that X is a.s. finite. In view of (1.1) the conditional expectation of Z_n given the environment $\mathbf{f}$ is calculated by the formula

$$\mu_n \; := \; \mathbf{E}[Z_n \mid Z_0, \mathbf{f}] = Z_0 \mathbf{E}_{\mathbf{f}}[Z_n] = Z_0 \, e^{S_n} \quad \mathbf{P}\text{–}a.s.$$

We assume that S is an oscillating random walk meaning that $\limsup_{n\to\infty} S_n = \infty$ a.s. and at the same time $\liminf_{n\to\infty} S_n = -\infty$ a.s., which implies $\limsup_{n\to\infty} \mu_n = \infty$ a.s. and $\liminf_{n\to\infty} \mu_n = 0$ a.s. Then we call Z a *critical* branching process. Here we do not require that the expectation of X exists.

We impose an assumption on the random walk S, which we call as *Doney's condition.*

Assumption A1. *There exists a number* $0 < \rho < 1$ *such that*

$$\mathbf{P}(S_n > 0) \; \to \; \rho \;\; \text{as} \;\; n \to \infty.$$

In fact, Doney [5] proved that Assumption A1 is equivalent to Spitzer's condition

$$\frac{1}{n} \sum_{m=1}^{n} \mathbf{P}(S_m > 0) \to \rho \;\; \text{as} \;\; n \to \infty.$$

Denote by $I(A)$ the indicator of the event A. In the sequel the random variables

$$a_f(x) := \mathbf{E}_f \left[\frac{\xi}{\mathbf{E}_f \xi} I \left(\frac{\xi}{\mathbf{E}_f \xi} > x \right) \right], \; x \in [0, \infty),$$

and

$$a_{f_n}(x) := \mathbf{E}_{f_n} \left[\frac{\xi_n}{\mathbf{E}_{f_n} \xi_n} I \left(\frac{\xi_n}{\mathbf{E}_{f_n} \xi_n} > x \right) \right], \; x \in [0, \infty),$$

$n = 1, 2, \ldots$ play an essential role and our next assumption requires a uniform integrability of $a_f(x)$ with respect to the probability measure $\mathbf{P}$.

Assumption A2. *There are an* $\varepsilon > 0$ *and a constant* $C \in (0, \infty)$ *such that*

$$\mathbf{P}\left(f : a_f(x) \leq \frac{C}{\log^{(\rho^{-1}-1)(1+\varepsilon)}(e + x)}, \; x \in (0, \infty) \right) = 1. \tag{1.5}$$

To formulate one more assumption we need additional notation.

Let $0=\gamma_0<\gamma_1<\gamma_2<\cdots$ and $0=\Gamma_0<\Gamma_1<\Gamma_2<\cdots$ be the descending and increasing strict ladder epochs of $\{S_n, n\geq 0\}$:

$$\begin{aligned}\gamma_{j+1} &:= \min(n>\gamma_j : S_n<S_{\gamma_j}), \qquad j\geq 0,\\ \Gamma_{j+1} &:= \min(n>\Gamma_j : S_n>S_{\Gamma_j}), \qquad j\geq 0.\end{aligned}$$

Introduce two renewal functions

$$\begin{aligned}V(x) &:= \sum_{j=0}^{\infty}\mathbf{P}\left(S_{\gamma_j}\geq -x\right), \quad x>0, \quad V(0)=1, V(x)=0, \quad x<0,\\ U(x) &:= \sum_{j=0}^{\infty}\mathbf{P}\left(S_{\Gamma_j}\leq x\right), \quad x>0, \quad U(0)=1, U(x)=0, \quad x<0. \qquad (1.6)\end{aligned}$$

Since S is an oscillating random walk under Doney's condition (see, e.g., Sect. XII.7 in [7]), it follows from Lemma 1 in [10] that $V(x)$ is a harmonic function, that is, for any $x\geq 0$

$$\mathbf{E}V(x+X)=V(x). \qquad (1.7)$$

Assumption A3. *There exists a nonnegative random variable Y with*

$$\mathbb{E}\left[YV\left(\log^{+}Y\right)U\left(\log^{+}Y\right)\right] < \infty$$

such that

$$\mathbf{P}\left(f:\mathbf{P}_f\left(\frac{\xi}{\mathbf{E}_f\xi}>x\right)\leq \mathbb{P}(Y>x), \, x\in(0,\infty)\right)=1. \qquad (1.8)$$

Some of our results are established under stronger conditions imposed on the characteristics of the branching process in random environment.

Assumption B1. *The distribution of X belongs without centering to the domain of attraction of some stable law with parameters $\alpha\in(0,2]$ and $|\beta|<1$.*

Observe, that under Assumption B1 Doney's condition holds with

$$\rho=\frac{1}{2}-\frac{1}{\pi\alpha}\arctan\left(-\beta\tan\frac{\pi\alpha}{2}\right)$$

(see, for instance, [4]).

Assumption B2. *Doney's condition holds and, in addition, if $\alpha\in[1,2]$ then there are $\varepsilon>0$ and a constant $C\in(0,\infty)$ such that*

$$\mathbf{P}\left(f:a_f(x)\leq \frac{C}{\log^{(\alpha-1)(1+\varepsilon)}(e+x)}, \, x\in(0,\infty)\right)=1 \qquad (1.9)$$

while if $\alpha\in(0,1)$ then there exists a random variable Y with $\mathbb{E}Y<\infty$ such that

$$\mathbf{P}\left(f:\mathbf{P}_f\left(\frac{\xi}{\mathbf{E}_f\xi}>x\right)\leq\mathbb{P}(Y>x),\, x\in(0,\infty)\right)=1. \tag{1.10}$$

It follows from Lemma 7 in [13] that under condition B1

$$V(x)U(x)=x^{\alpha}L(x) \tag{1.11}$$

for some function $L(x)$ slowly varying at infinity. Therefore, Assumption A3 may be rewritten in this case as

Assumption B3. *Assumption B1 is valid and there exists a nonnegative random variable Y with*

$$\mathbb{E}\left[Y\left(\log^{+}Y\right)^{\alpha}L\left(\log^{+}Y\right)\right]\;<\;\infty \tag{1.12}$$

such that

$$\mathbf{P}\left(f:\mathbf{P}_f\left(\frac{\xi}{\mathbf{E}_f\xi}>x\right)\leq\mathbb{P}(Y>x),\, x\in(0,\infty)\right)=1.$$

Observe that for $\alpha<1$ Assumption B2 is weaker than Assumption B3. Besides, condition (1.9) is less restrictive than Assumption A2 if $\alpha\rho<1$.

We formulate now the main results of the paper. The first theorem describes the asymptotic behavior of the survival probability at generation n.

Theorem 1.1. *Assume A1, A2 or A1, A3 or B1, B2. Then there exists a positive finite number θ such that*

$$\mathbf{P}(Z_n>0)\;\sim\;\theta\,\mathbf{P}(\min(S_1,\ldots,S_n)\geq 0)\sim\;\theta n^{-(1-\rho)}l(n)\quad as\ n\to\infty, \tag{1.13}$$

where $l(1),l(2),\ldots$ is a sequence slowly varying at infinity.

For integers $0\leq r\leq n$ consider the rescaled generation size process $W_{r,n}=(W_{r,n;t},\,0\leq t\leq 1)$ given by

$$W_{r,n;t}\;:=\;e^{-S_{r+[(n-r)t]}}Z_{r+[(n-r)t]},\quad 0\leq t\leq 1\;. \tag{1.14}$$

Our next theorem describes the structure of the rescaled process given the event $\{Z_n>0\}$.

Theorem 1.2. *Assume A1, A3 or A1, B3. Let $r_1,r_2,\ldots$ be a sequence of positive integers such that $r_n\to\infty$ and $r_n=o(n)$ as $n\to\infty$. Then*

$$\mathscr{L}\left(W_{r_n,n}\,\middle|\,Z_n>0\right)\;\Longrightarrow\;\mathscr{L}(W_t,0\leq t\leq 1)\quad as\ n\to\infty,$$

where the limiting process is a stochastic process with a.s. constant paths, i.e., $\mathbb{P}(W_t=W\ for\ all\ t\in[0,1])=1$ for some random variable W. Furthermore,

$$\mathbb{P}(0<W<\infty)\;=\;1\;.$$

Here, $\Longrightarrow$ denotes weak convergence w.r.t. the Skorokhod topology in the space $D[0,1]$ of càdlàg functions on the unit interval.

Theorems 1.1 and 1.2 complement, respectively, Theorems 1.1 and 1.3 in [1]. The mentioned theorems from [1] were proved (along with some other technical hypotheses) under Assumption A1 and $\mathbf{P}(f''(1) < \infty) = 1$. Our conditions A1-A3 and B1-B3 include a wide class of branching processes in random environment where $\mathbf{P}(f''(1) < \infty) = 0$.

The proofs of Theorems 1.1 and 1.2 combine approaches used in the mentioned article [1] and paper [6] containing some statements for branching processes in varying environment.

1.2 Branching in conditioned environment

Following [1] and [8] consider, along with $\mathbf{P}$ another probability measure $\mathbf{P}^+$. In order to define this measure let $\mathscr{F}_n$, $n \geq 0$ be the σ–field of events generated by the random variables $Q_1, \ldots, Q_n$ and $Z_0, \ldots, Z_n$. These σ–fields form a filtration $\mathscr{F}$. Let

$$L_n := \min(S_1, \ldots, S_n), \quad n \geq 1,$$

be the sequence of minima of the associated random walk.

Lemma 1.1. *[1] The random variables* $V(S_n)I(L_n \geq 0)$, $n = 0, 1, \ldots$, *form a martingale with respect to* $\mathscr{F}$ *under* $\mathbf{P}$.

Since $V(0) = 1$, we may introduce probability measures $\mathbf{P}_n^+$ on the σ-fields $\mathscr{F}_n$ by means of the densities

$$d\mathbf{P}_n^+ := V(S_n)I(L_n \geq 0)\, d\mathbf{P}\,.$$

Because of Lemma 1.1 the measures are consistent, i.e., $\mathbf{P}_{n+1}^+ | \mathscr{F}_n = \mathbf{P}_n^+$. Therefore (choosing a suitable underlying probability space), there exists a probability measure $\mathbf{P}^+$ on the σ-field $\mathscr{F}_\infty := \bigvee_n \mathscr{F}_n$ such that

$$\mathbf{P}^+ | \mathscr{F}_n = \mathbf{P}_n^+, \quad n \geq 0. \tag{1.15}$$

We note that (1.15) can be rewritten as

$$\mathbf{E}^+ Y_n = \mathbf{E}[Y_n V(S_n); L_n \geq 0] \tag{1.16}$$

for every $\mathscr{F}_n$–measurable nonnegative random variable Y_n.

It is easy to check that the change of measure from $\mathbf{P}$ to $\mathbf{P}^+$ keeps the sequence $Z_0, Z_1, \ldots$ as a branching process in a randomly fluctuating environment. However, the environment $Q_1, Q_2, \ldots$ is no longer built up from i.i.d. components. We call such new process as a *branching process in conditioned environment.*

Along with the initial branching process in conditioned environment we consider an auxiliary process $Z^* = \left\{Z_0^*, Z_1^*, \ldots\right\}$ which is constructed according to the rule $Z_0^* = 1$,

$$Z_n^* := \sum_{j=1}^{Z_{n-1}^*} \xi_{nj}(b_n),\ n \geq 1,$$

where, for a deterministic sequence $\{b_n, n \geq 1\}$ specified later

$$\xi_{nj}(b_n) := \min(\xi_{nj}, b_n \mathbf{E}_{f_n} \xi_{nj}).$$

Let

$$\xi_n(b_n) :\overset{d}{=} \xi_{nj}(b_n).$$

Evidently, for any $k \geq 1$

$$Var_{f_k} \xi_k(b_k) = Var_{f_k}\left[\xi_k I\left(\xi_k \leq b_k \mathbf{E}_{f_k} \xi_k\right)\right] \leq \left(\mathbf{E}_{f_k} \xi_k\right)^2 b_k^2$$

and

$$\begin{aligned}
\mathbf{E}_{f_k} \xi_k(b_k) &= \mathbf{E}_{f_k}\left[\xi_k I\left(\xi_k \leq b_k \mathbf{E}_{f_k} \xi_k\right)\right] \\
&= \mathbf{E}_{f_k} \xi_k - \mathbf{E}_{f_k}\left[\xi_k I\left(\xi_k > b_k \mathbf{E}_{f_k} \xi_k\right)\right] \\
&= \mathbf{E}_{f_k} \xi_k - \mathbf{E}_{f_k} \xi_k \times \mathbf{E}_{f_k}\left[\frac{\xi_k}{\mathbf{E}_{f_k} \xi_k} I\left(\frac{\xi_k}{\mathbf{E}_{f_k} \xi_k} > b_k\right)\right] \\
&= \left(1 - a_{f_k}(b_k)\right) \mathbf{E}_{f_k} \xi_k.
\end{aligned}$$

It is not difficult to understand that Z^* is, under fixed $\mathbf{f}$, an inhomogeneous branching process with finite variance of the offspring number of individuals. Hence

$$\mathbf{E}_{\mathbf{f}} Z_k^* = \prod_{i=1}^{k}\left(1 - a_{f_i}(b_i)\right) \mathbf{E}_{f_i} \xi_i = \prod_{i=1}^{k}\left(1 - a_{f_i}(b_i)\right) \mathbf{E}_{\mathbf{f}} Z_k,$$

and, for $n \geq 1$

$$Var_{\mathbf{f}} Z_n^* = Var_{f_n} \xi_n(b_n) \mathbf{E}_{\mathbf{f}} Z_{n-1}^* + \left(\mathbf{E}_{f_n} \xi_n(b_n)\right)^2 Var_{\mathbf{f}} Z_{n-1}^*$$

implying

$$\frac{Var_{\mathbf{f}} Z_n^*}{(\mathbf{E}_{\mathbf{f}} Z_n^*)^2} = \frac{Var_{f_n} \xi_n(b_n)}{\left(\mathbf{E}_{f_n} \xi_n(b_n)\right)^2 \mathbf{E}_{\mathbf{f}} Z_{n-1}^*} + \frac{Var_{\mathbf{f}} Z_{n-1}^*}{\left(\mathbf{E}_{\mathbf{f}} Z_{n-1}^*\right)^2}.$$

This leads us to the estimate

$$\begin{aligned}
\frac{Var_{\mathbf{f}} Z_n^*}{(\mathbf{E}_{\mathbf{f}} Z_n^*)^2} &\leq \sum_{k=1}^{\infty} \frac{Var_{f_k} \xi_k(b_k)}{\left(\mathbf{E}_{f_k} \xi_k(b_k)\right)^2 \mathbf{E}_{\mathbf{f}} Z_{k-1}^*} \\
&\leq \sum_{k=1}^{\infty} \frac{\left(\mathbf{E}_{f_k} \xi_k\right)^2 b_k^2}{\left(\mathbf{E}_{f_k} \xi_k \left(1 - a_{f_k}(b_k)\right)\right)^2 \prod_{i=1}^{k-1}\left(1 - a_{f_i}(b_i)\right) \mathbf{E}_{\mathbf{f}} Z_{k-1}} \\
&= \sum_{k=1}^{\infty} \frac{b_k^2}{\left(1 - a_{f_k}(b_k)\right)^2 \prod_{i=1}^{k-1}\left(1 - a_{f_i}(b_i)\right)} e^{-S_{k-1}} =: T_{\mathbf{f}}(b).
\end{aligned}$$

Below we denote by $C, C_1, C_2, \ldots$ some positive constants which may vary from formula to formula.

Before we pass to the prove of the next lemma we note that if Assumptions A2 and B2 are valid for some $\varepsilon = \varepsilon_0 > 0$ then they are valid for any $\varepsilon \in (0, \varepsilon_0]$. Thus, we may take $\varepsilon > 0$ as small as it is needed. With this in view let $\delta = \varepsilon/2$. It is not difficult to check that one can find $\varepsilon > 0$ such that, given Assumption A2

$$1 < (1+\varepsilon)(1-\delta) = 1 + \frac{\varepsilon}{2} - \frac{\varepsilon^2}{2} < \frac{1}{1-\rho},$$

and, given Assumption B2 and $\alpha \in [1,2]$,

$$1 < (1+\varepsilon)(1-\delta) < \frac{\alpha}{\alpha - 1}$$

with the agreement that the right-hand side of the last expression equals $+\infty$ for $\alpha = 1$.

Lemma 1.2. *Let one of the following conditions be valid:*

(i) Assumptions A1, A2 and $b_k := exp\{k^{(1-\delta)\rho}\} - e$ *for* $k = 1, 2, \ldots$;

(ii) Assumptions B1, B2 with $\alpha \in [1,2]$ *and* $b_k := \exp\{k^{(1-\delta)/\alpha}\} - e$ *for* $k = 1, 2, \ldots$;

(iii) Assumptions B1, B2 with $\alpha \in (0,1)$ *and* $b_k := \log(k+1)$ *for* $k = 1, 2, \ldots$.

Then

$$T_{\mathbf{f}}(b) < \infty \quad \mathbf{P}^+ - a.s.$$

Proof. **(i)** From the conditions of the lemma it follows that, as $k \to \infty$,

$$\left(1 - a_{f_k}(b_k)\right)^2 \prod_{i=1}^{k-1} \left(1 - a_{f_i}(b_i)\right) = \exp\left\{ -(1+o(1)) \sum_{i=1}^{k} a_{f_i}(b_i) \right\}.$$

Observing that under our choice of δ

$$\gamma := (\rho^{-1} - 1)(1+\varepsilon)(1-\delta)\rho = (1-\rho)(1+\varepsilon)(1-\delta) < 1$$

we see that

$$\begin{aligned} \sum_{i=1}^{k} a_{f_i}(b_i) &\le \sum_{i=1}^{k} \frac{C}{(\log b_i)^{(\rho^{-1}-1)(1+\varepsilon)}} = \sum_{i=1}^{k} \frac{C}{i^{\gamma}} \\ &\le C_1 k^{1-\gamma} = C_1 k^{\rho - (1-\rho)\varepsilon(1-\varepsilon)/2} < C_1 k^{\rho(1-\varepsilon_1)} \end{aligned} \tag{1.17}$$

for some $\varepsilon_1 > 0$. Thus, for all $k \ge 1$,

$$\left(1 - a_{f_k}(b_k)\right)^2 \prod_{i=1}^{k-1} \left(1 - a_{f_i}(b_i)\right) \ge C_2 e^{-C_3 k^{\rho(1-\varepsilon_1)}}.$$

Hence we conclude that

$$T_{\mathbf{f}}(b) \le C_2^{-1} \sum_{k=1}^{\infty} e^{C_3 k^{\rho(1-\varepsilon_1)}} e^{2k^{\rho(1-\delta)}} e^{-S_k}.$$

Finally, by formula (2.22) in [1] for any $\varepsilon_2 > 0$, as $k \longrightarrow \infty$,

$$e^{-S_k} = O\left(e^{-k^{\rho(1-\varepsilon_2)}}\right) \quad \mathbf{P}^+ - \text{a.s.} \tag{1.18}$$

From this estimate the desired statement follows with $0 < \varepsilon_2 < \min\{\varepsilon_1, \delta\}$.

(ii) Arguing as in point (i) with $\gamma := (\alpha - 1)(1+\varepsilon)(1-\delta) < 1$ it is not difficult to see that

$$T_{\mathbf{f}}(b) \le C_4^{-1} \sum_{k=1}^{\infty} e^{C_3 k^{\alpha^{-1}(1-\varepsilon_1)}} e^{2k^{\alpha^{-1}(1-\delta)}} e^{-S_k}.$$

To complete the proof of this point it remains to recall that by formula (2.23) in [1] for any $\varepsilon_2 > 0$

$$e^{-S_k} = O\left(e^{-k^{\alpha^{-1}(1-\varepsilon_2)}}\right) \quad \mathbf{P}^+ - \text{a.s.} \tag{1.19}$$

as $k \longrightarrow \infty$.

(iii) Under the conditions of this point for any $\varepsilon \in (0,1)$ there exists $x = x(\varepsilon)$ such that for all $k = 1, 2, \dots$

$$a_{f_k}(x) \le \int_x^{\infty} \mathbb{P}(Y > y)\, dy \le \varepsilon \quad \mathbf{P}^+ - \text{a.s.}$$

Thus, for any fixed $\varepsilon \in (0,1)$ and sufficiently small constant $C_3 = C_3(\varepsilon)$

$$\left(1 - a_{f_k}(b_k)\right)^2 \prod_{i=1}^{k-1} \left(1 - a_{f_i}(b_i)\right) \ge C_3 (1-\varepsilon)^k \ge C_3 e^{-C_4 \varepsilon k} \quad \mathbf{P}^+ - \text{a.s.}$$

for all $k \ge 1$, which, along with (1.19) used with $\alpha < 1$ justifies the desired statement.

The following lemma states that, with respect to $\mathbf{P}^+$ the population has a positive probability to survive forever.

Lemma 1.3. *Assume A1, A2 or B1, B2. Then*

$$\mathbf{P}_{\mathbf{f}}\left(Z_n > 0 \, \textit{for all } n\right) > 0 \qquad \mathbf{P}^+\text{–}\textit{a.s.}$$

In particular,

$$\mathbf{P}^+\left(Z_n > 0 \, \textit{for all } n\right) > 0 \, .$$

Proof. It is known that for any nonnegative random variable ς

$$\mathbb{P}(\varsigma > 0) \ge \left\{ \frac{Var \varsigma}{(\mathbb{E}\varsigma)^2} + 1 \right\}^{-1}.$$

This and Lemma 1.2 imply

$$\mathbf{P_f}(Z_n^* > 0) \geq \{T_{\mathbf{f}}(b)+1\}^{-1} > 0 \quad \mathbf{P}^+ - \text{a.s.} \tag{1.20}$$

To complete the proof of the first statement of the lemma it remains to observe that

$$\lim_{n\to\infty} \mathbf{P_f}(Z_n > 0) \geq \lim_{n\to\infty} \mathbf{P_f}(Z_n^* > 0) \quad \mathbf{P}^+ - \text{a.s.} \tag{1.21}$$

The second statement of the of the lemma follows easily from the first one.

Now we consider the branching processes satisfying either Assumption A3 or Assumption B3. To this aim for a nonnegative random variable Y with Laplace transform $F(u) := \mathbb{E}e^{-uY}$ and expectation $a := \mathbb{E}Y < \infty$ set

$$G(t) := \frac{F(e^{-t}) - 1 + at}{t} = \frac{\mathbb{E}\left[e^{-tY} - 1 + tY\right]}{t}, \quad t \geq 0.$$

Lemma 1.4. *If $V(x)$ and $U(x)$ are the renewal functions specified by (1.6) and*

$$\mathbb{E}\left[YV(\log^+ Y)U\left(\log^+ Y\right)\right] < \infty,$$

then for any $u > 0$

$$\int_0^\infty G(ue^{-x})V(x)dU(x) < \infty.$$

Proof. Setting $R(x) := \mathbb{P}(Y < y)$ we have

$$\begin{aligned}
&\int_0^\infty G(ue^{-x})V(x)dU(x) \\
&\quad = -\int_0^u G(t)V\left(\log\frac{u}{t}\right)dU\left(\log\frac{u}{t}\right) \\
&\quad = -\int_0^u \frac{\mathbb{E}\left[e^{-tY} - 1 + tY\right]}{t} V\left(\log\frac{u}{t}\right)dU\left(\log\frac{u}{t}\right) \\
&\quad = -\int_0^\infty ydR(y)\int_0^u \left[\frac{e^{-ty} - 1 + ty}{ty}\right] V\left(\log\frac{u}{t}\right)dU\left(\log\frac{u}{t}\right).
\end{aligned} \tag{1.22}$$

Let us show that there exists a constant $0 < C_1 < \infty$ such that for all $y \geq y_0$

$$\begin{aligned}
I(y) := -\int_0^u \left[\frac{e^{-ty} - 1 + ty}{ty}\right] V\left(\log\frac{u}{t}\right)dU\left(\log\frac{u}{t}\right) \\
\leq C_1 V(\log y)U(\log y).
\end{aligned} \tag{1.23}$$

Indeed, assuming that $u > y^{-1}$ and using the inequalities

$$0 \leq 1 - e^{-x} \leq x, \qquad 0 \leq e^{-x} - 1 + x \leq x^2, \quad x \geq 0, \tag{1.24}$$

we see that

$$\begin{aligned}I(y) &\le -\int_{y^{-1}}^{u} V\left(\log\frac{u}{t}\right) dU\left(\log\frac{u}{t}\right) - \int_0^{y^{-1}} tyV\left(\log\frac{u}{t}\right) dU\left(\log\frac{u}{t}\right)\\ &\le V(\log yu)U(\log yu) - \int_0^1 wV\left(\log\frac{yu}{w}\right) dU\left(\log\frac{yu}{w}\right).\end{aligned} \tag{1.25}$$

Since $U(x)$ and $V(x)$ are renewal functions, there exists a constant $C \in (0,\infty)$ such that

$$U(x+1) - U(x) \le C, \quad V(x+1) - V(x) \le C, \quad x \ge 0. \tag{1.26}$$

In particular,

$$U(\log yu) \le U(\log y) + C|\log u|$$

and, for all sufficiently large y

$$\begin{aligned}&-\int_0^1 wV\left(\log\frac{yu}{w}\right) dU\left(\log\frac{yu}{w}\right)\\ &= -\sum_{k=0}^{\infty}\int_{e^{-k-1}}^{e^{-k}} wV\left(\log\frac{yu}{w}\right) dU\left(\log\frac{yu}{w}\right)\\ &\le \sum_{k=0}^{\infty} e^{-k}V(\log yu + k + 1)\left[U(\log yu + k + 1) - U(\log yu + k)\right]\\ &\le C\sum_{k=0}^{\infty} e^{-k}V(\log yu + k + 1) \le C\sum_{k=0}^{\infty} e^{-k}\left[V(\log yu) + C(k+1)\right]\\ &\le C_1 V(\log yu) = o(V(\log yu)U(\log yu)),\ \text{as } y \to \infty.\end{aligned}$$

This in view of (1.25) and (1.26) gives

$$\limsup_{y\to\infty} \frac{I(y)}{V(\log y)U(\log y)} \le 1. \tag{1.27}$$

Combining (1.22)–(1.27) proves the lemma.

Lemma 1.5. *If Assumptions A1 and A3 are valid, then, as $n \to \infty$,*

$$e^{-S_n}Z_n \to W^+ \quad \mathbf{P}^+ - a.s., \tag{1.28}$$

where the random variable W^+ satisfies the property: for any $u > 0$

$$\mathbf{E_f} e^{-uW^+} \le e^{-u} + u\sum_{n=0}^{\infty} G\left(ue^{-S_n}\right) + u^2\sum_{n=0}^{\infty} e^{-S_n},$$

where the right-hand side is finite $\mathbf{P}^+$ - a.s.

Proof. Since $\left\{e^{-S_n}Z_n, n \ge 0\right\}$ is a nonnegative martingale $\mathbf{P}^+$−a.s., the limit in (1.28) exists. Moreover,

$$\mathbf{E_f} e^{-uW^+} = \lim_{n\to\infty} \mathbf{E_f}\left[\exp\left\{-ue^{-S_n}Z_n\right\}\right] = \lim_{n\to\infty} f_{0,n}\left(e^{-ue^{-S_n}}\right).$$

Setting

$$g_n(u) := \frac{f_n(e^{-u}) - 1 + e^{X_n}u}{u} = \frac{\mathbf{E}\left[e^{-u\xi_n} - 1 + u\xi_n\right]}{u}, \quad u \geq 0,$$

and using the second inequality in (1.24), we have for all $n \geq 1$

$$\begin{aligned}
&\left| f_{0,n}\left(e^{-ue^{-S_n}}\right) - f_{0,n-1}\left(e^{-ue^{-S_{n-1}}}\right)\right| \\
&\quad = \left| f_{0,n-1}\left(f_n\left(e^{-ue^{-S_n}}\right)\right) - f_{0,n-1}\left(e^{-ue^{-S_{n-1}}}\right)\right| \\
&\quad \leq e^{S_{n-1}}\left| f_n\left(e^{-ue^{-S_n}}\right) - e^{-ue^{-S_{n-1}}}\right| \\
&\quad \leq e^{S_{n-1}}\left(f_n\left(e^{-ue^{-S_n}}\right) - 1 + ue^{-S_{n-1}}\right) \\
&\qquad + e^{S_{n-1}}\left(e^{-ue^{-S_{n-1}}} - 1 + ue^{-S_{n-1}}\right) \\
&\quad \leq ue^{-X_n}\frac{f_n\left(e^{-ue^{-S_n}}\right) - 1 + e^{X_n}ue^{-S_n}}{ue^{-S_n}} + u^2e^{-S_{n-1}} \\
&\quad = ue^{-X_n}g_n\left(ue^{-S_n}\right) + u^2e^{-S_{n-1}}.
\end{aligned}$$

It is known (see Lemma 6 in [9] and formula (2.4) in [6]) that, given (1.8)

$$G(u) \geq e^{-X_n}g_n\left(ue^{-X_n}\right), \; u \geq 0, \quad \mathbf{P}-\text{a.s.}$$

and, therefore, this estimate is valid $\mathbf{P}^+$-a.s. as well. Hence we get for all $u \geq 0:$

$$\mathbf{E}_{\mathbf{f}}e^{-uW^+} = e^{-u} + \lim_{n\to\infty}\sum_{k=1}^{n}\left(f_{0,k}\left(e^{-ue^{-S_k}}\right) - f_{0,k-1}\left(e^{-ue^{-S_{k-1}}}\right)\right) \quad \mathbf{P}^+-\text{a.s.}$$

or

$$\mathbf{E}_{\mathbf{f}}e^{-uW^+} \leq e^{-u} + u\sum_{n=1}^{\infty}G\left(ue^{-S_n}\right) + u^2\sum_{n=0}^{\infty}e^{-S_n} \quad \mathbf{P}^+-\text{a.s.}$$

Let us show that the right-hand side of this inequality is finite $\mathbf{P}^+$-a.s. Since $U(x)$ and $V(x)$ are renewal functions, it is easy to check by (1.26) that

$$\mathbf{E}^+\sum_{n=0}^{\infty}e^{-S_n} = \sum_{n=0}^{\infty}\mathbf{E}e^{-S_n}V(S_n)I(L_n \geq 0) = \int_0^{\infty}e^{-x}V(x)dU(x) < \infty$$

and, by Assumption A3 and Lemma 1.4 that

$$\mathbf{E}^+\sum_{n=1}^{\infty}G\left(ue^{-S_n}\right) = \int_0^{\infty}G\left(ue^{-x}\right)V(x)dU(x) < \infty.$$

Hence

$$\sum_{n=0}^{\infty} e^{-S_n} + \sum_{n=1}^{\infty} G\left(ue^{-S_n}\right) < \infty \qquad \mathbf{P}^+ - \text{a.s.}$$

The lemma is proved.

Since $G(u) \to 0$ as $u \to 0+$, we have

$$\lim_{u\to 0+} \sum_{n=1}^{\infty} G\left(ue^{-S_n}\right) = 0 \quad \mathbf{P}^+ - \text{a.s.} \tag{1.29}$$

Therefore, for any $j = 0, 1, \ldots$ the random variable

$$\eta_j := \sup_{u>0} \left(1 - e^{-u} - u \sum_{n=1}^{\infty} G\left(ue^{-\left(S_{n+j}-S_j\right)}\right) - u^2 \sum_{n=0}^{\infty} e^{-\left(S_{n+j}-S_j\right)}\right)$$

is positive $\mathbf{P}^+-$a.s.

Let $0 =: \nu(0) < \nu(1) < \ldots$ be the times of *prospective minima* of S under $\mathbf{P}^+$, i.e.,

$$\nu(k) \ := \ \min\{m > \nu(k-1) \ : \ S_{m+i} \ge S_m \text{ for all } i \ge 0\}, \quad k \ge 1.$$

Corollary 1.1. *Under the conditions A1, A3 or A1, B3*

$$\mathbf{E_f} W^+ = 1 \quad \mathbf{P}^+ - a.s.$$

Besides, for any $k \ge 0$

$$\mathbf{P_f}\left(W^+ > 0 \,|\, Z_{\nu(k)} = 1\right) \ge \eta_{\nu(k)} > 0 \quad \mathbf{P}^+ - a.s. \tag{1.30}$$

and

$$\mathbf{P}^+\left(W^+ > 0 \,|\, Z_0 = 1\right) \ge \mathbf{E}^+ \eta_0 > 0. \tag{1.31}$$

Proof. By Fatou's lemma

$$\mathbf{E_f} W^+ = \mathbf{E_f}\left[\lim_{n\to\infty}\left(e^{-S_n} Z_n\right)\right] \le \lim_{n\to\infty} \mathbf{E_f}\left[e^{-S_n} Z_n\right] = 1 \quad \mathbf{P}^+ - \text{a.s.}$$

By Lemma 1.5 and relation (1.29) we conclude that

$$\begin{aligned}
\mathbf{E_f} W^+ &= \lim_{u\to 0+} \frac{1 - \mathbf{E_f} e^{-uW^+}}{u} \\
&\ge \lim_{u\to 0+} \left(\frac{1-e^{-u}}{u} - \sum_{n=1}^{\infty} G\left(ue^{-S_n}\right) - u \sum_{n=0}^{\infty} e^{-S_n}\right) = 1 \quad \mathbf{P}^+ - \text{a.s.}
\end{aligned}$$

Thus, $\mathbf{E_f} W^+ = 1 \quad \mathbf{P}^+-$a.s.

Further, for any $u > 0$

$$\mathbf{P_f}\left(W^+ > 0 \,|\, Z_0 = 1\right) \ge 1 - \mathbf{E_f} e^{-uW^+}.$$

This and Lemma 1.5 give

$$\mathbf{P_f}\left(W^+ > 0 \,|\, Z_0 = 1\right) \geq \eta_0 > 0 \quad \mathbf{P}^+ - \text{a.s.}$$

proving (1.30) for $k = 0$ and, therefore, (1.31).

To prove (1.30) for $k \geq 1$ it remains to observe that

$$\mathbf{E_f}\left[e^{-uW^+} \,|Z_{v(k)} = 1\right] \leq 1 - e^{-u} + u\sum_{n=1}^{\infty} G\left(ue^{-\left(S_{n+v(k)} - S_{v(k)}\right)}\right) + u^2 \sum_{n=0}^{\infty} e^{-\left(S_{n+v(k)} - S_{v(k)}\right)}$$

and by Lemma 2.6 in [1] the distribution of the right hand side of this inequality does not depend on k with respect to $\mathbf{P}^+$.

Theorem 1.3. *Under Assumptions A1, A3 or A1, B3*

$$\lim_{n\to\infty} \mathbf{P_f}\left(Z_n > 0\right) > 0 \quad \mathbf{P}^+ - a.s. \tag{1.32}$$

Besides, for $W^+ := \lim_{n\to\infty} e^{-S_n} Z_n$ *we have*

$$\left\{W^+ > 0\right\} = \left\{Z_n > 0 \, for\ all\ n\right\} \quad \mathbf{P}^+ - a.s. \tag{1.33}$$

Proof. Statement (1.32) follows from Corollary 1.1 with $k = 0$.

To demonstrate (1.33) observe first that, as shown in Proposition 3.1 in [1]

$$\sum_{n=1}^{\infty} \mathbf{P_f}\left(\xi_n \neq 1\right) \geq \sum_{j=1}^{\infty} \mathbf{P_f}\left(\xi_{v(j)+1} \neq 1\right) = \infty \quad \mathbf{P}^+ - \text{a.s.}$$

This, by Theorem 1 in [11] implies

$$\lim_{n\to\infty} \mathbf{P_f}\left(Z_n > 0\right) = \mathbf{P_f}\left(\lim_{n\to\infty} Z_n = \infty\right) \quad \mathbf{P}^+ - \text{a.s.} \tag{1.34}$$

To go further, note that by the properties of branching processes

$$\mathbf{P_f}\left(W^+ = 0 \,|Z_{v(k)} = j\right) = \left(\mathbf{P_f}\left(W^+ = 0 \,|Z_{v(k)} = 1\right)\right)^j$$

and, therefore,

$$\begin{aligned}\mathbf{P_f}\left(W^+ = 0\right) &= \mathbf{E_f}[\mathbf{P_f}\left(W^+ = 0 \mid Z_{v(k)}\right)] \\ &= \mathbf{E_f}\left[\left(\mathbf{P_f}\left(W^+ = 0 \,|Z_{v(k)} = 1\right)\right)^{Z_{v(k)}}\right] \leq \mathbf{E_f}\left[\left(\mathbf{1} - \eta_{v(k)}\right)^{Z_{v(k)}}\right].\end{aligned}$$

Since the sequence $v(k)$ and, as a result, the random variable $\eta_{v(k)}$ are specified by the environment only, we have for any $z \geq 1$

$$\mathbf{P_f}\left(W^+ = 0\right) \leq \mathbf{P_f}\left(Z_{v(k)} \leq z\right) + \left(1 - \eta_{v(k)}\right)^z \quad \mathbf{P}^+ - \text{a.s.} \tag{1.35}$$

By Lemma 2.6 in [1] the law of the second term in the right-hand side of (1.35) does not depend on k under $\mathbf{P}^+$. Taking the expectation with respect to the measure $\mathbf{P}^+$ and letting than $k \to \infty$ we see by (1.34) that

$$\mathbf{P}^+\left(W^+ = 0\right) \le \mathbf{P}^+\left(\lim_{n\to\infty} Z_n = 0\right) + \mathbf{E}^+\left[(1-\eta_0)^z\right].$$

Now letting $z \to \infty$ we conclude by Lemma 1.2 that

$$\mathbf{P}^+\left(W^+ = 0\right) - \mathbf{P}^+\left(\lim_{n\to\infty} Z_n = 0\right) \le \mathbf{P}^+\left(\eta_0 = \infty\right) = 0.$$

Combining this fact with the obvious estimate

$$\mathbf{P}^+\left(W^+ = 0\right) \ge \mathbf{P}^+\left(\lim_{n\to\infty} Z_n = 0\right),$$

we obtain statement (1.33).

1.3 Proof of Theorems 1.1 and 1.2

In this section for the reader convenience we first list some results from [1] that are essentially used in the subsequent proofs.

Lemma 1.6. *[1] Assume A1. For $k \in \mathbb{N}$ let Y_k be a bounded real-valued $\mathscr{F}_k$–measurable random variable. Then, as $n \to \infty$,*

$$\mathbf{E}[Y_k \mid L_n \ge 0] \ \to \ \mathbf{E}^+ Y_k \,.$$

More generally, let $Y_1, Y_2, \ldots$ be a uniformly bounded sequence of real-valued random variables adapted to the filtration $\mathscr{F}$, which converges $\mathbf{P}^+$–a.s. to some random variable Y_∞. Then, as $n \to \infty$,

$$\mathbf{E}[Y_n \mid L_n \ge 0] \ \to \ \mathbf{E}^+ Y_\infty \,.$$

Let

$$\tau_n := \min\left(i \le n : S_i = \min(S_0, \ldots, S_n)\right), \quad L_{k,n} := \min_{k \le j \le n} (S_n - S_k).$$

Lemma 1.7. *[1] Assume A1 and suppose that $V_1, V_2, \ldots$ is a uniformly bounded sequence of real-valued random variables, which for every $k \ge 0$ satisfy*

$$\mathbf{E}[V_n; Z_k > 0, L_{k,n} \ge 0 \mid \mathscr{F}_k] \ = \ \mathbf{P}(L_n \ge 0)\left(V_{k,\infty} + o(1)\right) \quad \mathbf{P}\text{–}a.s. \qquad (1.36)$$

Then

$$\mathbf{E}[V_n; Z_{\tau_n} > 0] \; = \; \mathbf{P}(L_n \geq 0) \left(\sum_{k=0}^{\infty} \mathbf{E}[V_{k,\infty}; \tau_k = k] + o(1) \right) , \tag{1.37}$$

where the right-hand side series is absolutely convergent.

Proof of Theorem 1.1 repeats almost literal the proof of Theorem 1.1 in [1]. We give here the needed arguments for completeness only.

For $z, n \in \mathbb{N}_0$ write

$$\psi(z,n) \; := \; \mathbf{P}(Z_n > 0, L_n \geq 0 \,|\, Z_0 = z) .$$

Note that $\psi(0,n) = 0$. Setting $Y_n := I(Z_n > 0)$ and $Y_\infty := I(Z_n > 0 \text{ for all } n \geq 0)$ in Lemma 1.6 we see that for any $z \geq 1$

$$\psi(z,n) \; \sim \; \mathbf{P}(L_n \geq 0)\, \mathbf{P}^+(Z_n > 0 \text{ for all } n \geq 0 \,|\, Z_0 = z) \;\; \text{as } n \to \infty. \tag{1.38}$$

In addition, for $k \leq n$ we have

$$\mathbf{P}\big(Z_n > 0, L_{k,n} \geq 0 \mid \mathscr{F}_k\big) \; = \; \psi(Z_k, n-k) \quad \mathbf{P}\text{–}a.s. \tag{1.39}$$

Relations (1.38) and (1.39) show that we may apply Lemma 1.7 to $V_n := I(Z_n > 0)$ and $V_{k,\infty} := \mathbf{P}^+(Z_n > 0 \text{ for all } n \geq 0 | Z_k)$ to obtain

$$\mathbf{P}(Z_n > 0) \; \sim \; \theta\, \mathbf{P}(L_n \geq 0) \;\; \text{as } n \to \infty,$$

where

$$\theta \; := \; \sum_{k=0}^{\infty} \mathbf{E}[\mathbf{P}^+(Z_n > 0 \text{ for all } n \geq 0 | Z_k) ; \tau_k = k] \; < \infty. \tag{1.40}$$

For θ being strictly positive observe that according to Lemma 1.3 and Theorem 1.3 $\mathbf{P}^+(Z_n > 0 \text{ for all } n \geq 0 | Z_0 = z) > 0$ for all $z \geq 1$.

Proof of Theorem 1.2 is reduced to the almost literal repetition of the arguments used in [1] to establish Theorem 1.3. It is necessary only to substitute everywhere our Theorem 1.3 for Proposition 3.1 of the mentioned paper. We omit the details referring the reader to paper [1].

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2

Branching processes in stationary random environment: The extinction problem revisited

Gerold Alsmeyer

Abstract A classical result by Athreya and Karlin states that a supercritical Galton-Watson process in stationary ergodic environment $\mathbf{f} = (f_0, f_1, \ldots)$ (these are the random generating functions of the successively picked offspring distributions) has a positive chance of survival $1 - q(\mathbf{f})$ for almost all realizations of $\mathbf{f}$ provided that $\mathbb{E}\log(1 - f_0(0)) > -\infty$. While in some cases like when $f_0, f_1, \ldots$ are i.i.d., this last condition together with supercriticality, viz. $\mathbb{E}\log f_0'(1) > 0$, is actually equivalent to $q(\mathbf{f}) < 1$ a.s., there are others where it is not. This is demonstrated by giving a rather simple counterexample which in turn draws on the main result of this paper. The latter is intended to shed further light on the relation between $\mathbb{E}\log(1 - f_0(0)) > -\infty$ and the almost sure noncertain extinction property, the most interesting outcome being that, if $\mathbb{E}\log f_0'(1)$ is also finite, then $q(\mathbf{f}) < 1$ a.s. holds iff $\mathbb{E}\log\left(\frac{1-f_0\circ\ldots\circ f_T(0)}{1-f_1\circ\ldots\circ f_T(0)}\right) > -\infty$ for some random time T. The use of random times in connection with the stationary environment $\mathbf{f}$ will lead us quite naturally to the use of Palm-duality theory in some of our arguments.

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2.1 Introduction

The *Galton–Watson process in random environment (GWPRE)* constitutes one of the various generalizations of the classical Galton–Watson branching process and is

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characterized by a random variation of the offspring distribution over generations. When originating from one ancestor, it is given by an integer-valued stochastic sequence $(Z_n)_{n\geq 0}$ on a probability space $(\Omega,\mathfrak{A},\mathbb{P})$, recursively defined as

$$Z_0 \;=\; 1 \quad\text{and}\quad Z_n \;=\; \sum_{k=1}^{Z_{n-1}} X_{n,k} \quad \text{for } n\geq 1,$$

where Z_n denotes the size of the n^{th} generation of the considered population and the following assumptions hold true:

(A1) $(X_{n,k})_{n,k\geq 1}$ forms a double array of integer-valued random variables that are conditionally independent and rowwise identically distributed given a random sequence $(f_n)_{n\geq 0}$ (the random environment);

(A2) each f_n is a random generating function, i.e., a random element in

$$\Gamma \overset{\text{def}}{=} \left\{ g:[0,1]\to[0,1] : g(s)=\sum_{n\geq 0} p_n s^n \text{ with } p_0,p_1,\ldots\geq 0 \text{ and } g(1)=1 \right\}.$$

(A3) $\mathbb{E}\left(s^{X_{n,k}}|f_0,f_1,\ldots\right)=f_n(s)$ for all $n\geq 0$ and $k\geq 1$.

In this note we will consider the case where

(A4) $(f_n)_{n\geq 0}$ forms a stationary ergodic sequence satisfying $\mathbb{P}(f_0(0)+f_0'(0)=1)<1$ and $\min(\mathbb{E}\log^+ f_0'(1),\mathbb{E}\log^- f_0'(1))<\infty$.

This model was first studied by Athreya and Karlin in two seminal papers [3], [4] shortly after the work by Smith and Wilkinson [17] who dealt with the special case of i.i.d. $f_0,f_1,\ldots$

It is well known that many of the properties of $(Z_n)_{n\geq 0}$ are intimately related to the behavior of the random walk $(S_n)_{n\geq 0}$ with $S_0\overset{\text{def}}{=}0$ and stationary ergodic increments

$$X_n \overset{\text{def}}{=} \log f_{n-1}'(1), \quad n\geq 1.$$

Indeed, we have

$$\mathbb{E}(s^{Z_n}|Z_0,\ldots,Z_{n-1},f_0,f_1,\ldots) \;=\; f_{0:n-1}(s) \overset{\text{def}}{=} f_0\circ\ldots\circ f_{n-1}(s)$$

for each $n\geq 1$ and $s\in[0,1]$, and therefore

$$\mu_n \overset{\text{def}}{=} \mathbb{E}(Z_n|Z_0,f_0,f_1,\ldots) \;=\; Z_0 e^{S_n} \quad \text{a.s.} \tag{2.1}$$

We can extend $(f_n)_{n\geq 0}$ to a doubly infinite stationary sequence $(f_n)_{n\in\mathbb{Z}}$ which in turn leads to a doubly infinite extension of $(X_n)_{n\geq 1}$ as well. Define S_n recursively by $S_{n-1}\overset{\text{def}}{=}S_n-X_n$ for $n=-1,-2,\ldots$ The sequence $(f_{0:n})_{n\geq 0}$, constitutes the backward system associated with the forward (iterated function) system $f_{n:0}\overset{\text{def}}{=}f_n\circ\ldots\circ f_0$, $n\geq 0$, of Lipschitz maps on the unit interval. Defining the usual Lipschitz constant

$$l(g) \overset{\text{def}}{=} \sup_{r,s\in[0,1],r\neq s} \frac{|g(s)-g(r)|}{|s-r|}$$

for $g \in \Gamma$, the fact that g and its derivative are nondecreasing and convex implies

$$l(g) = g'(1)$$

which may be infinite. Consequently,

$$l(f_{0:n}) = f'_{0:n}(1) = \prod_{k=0}^{n} f'_k(1) = \prod_{k=0}^{n} l(f_k) \in [0,\infty] \quad \text{a.s.}$$

and the product is not a.s. equal to zero because $\mathbb{P}(f_0(0)=1)<1$ by (A4) which in turn ensures $\mathbb{P}(f'_0(1)>0)>0$. With the help of this observation and Birkhoff's ergodic theorem we infer that $(f_{n:0})_{n\geq 0}$ possesses the (by ergodicity necessarily constant) Lyapunov exponent $\chi = \mathbb{E}\log f'_0(1) \in [-\infty,\infty]$, for

$$\chi = \lim_{n\to\infty} \frac{1}{n} \sum_{k=0}^{n-1} \log f'_k(1) = \lim_{n\to\infty} \frac{S_n}{n} = \mathbb{E}\log f'_0(1).$$

The cases where χ is positive, negative or zero mark quite different types of behavior for the associated GWPRE and lead to the following definition.

Definition 2.1. A GWPRE $(Z_n)_{n\geq 0}$ satisfying (A1–4) and associated random walk $(S_n)_{n\geq 0}$ is called

- *subcritical*, if $\mathbb{E}\log f'_0(1)<0$ and thus $\lim_{n\to\infty} S_n = -\infty$ a.s.
- *supercritical*, if $\mathbb{E}\log f'_0(1)>0$ and thus $\lim_{n\to\infty} S_n = \infty$ a.s.
- *critical*, if $\mathbb{E}\log f'_0(1)=0$.
- *strongly critical*, if $\mathbb{E}\log f'_0(1)=0$, $\liminf_{n\to\infty} S_n = -\infty$ and $\limsup_{n\to\infty} S_n = \infty$ a.s.

Let us note that strong criticality really constitutes a genuine subcase. In fact, Lalley [13, Prop. 6] has shown that $(S_n)_{n\geq 0}$ is L_1-bounded, i.e. $\sup_{n\geq 0}\mathbb{E}|S_n|<\infty$, iff $(\log f'_n(1))_{n\geq 0}$ is *null-homologous* which means that, for some measurable function $\xi : \mathbb{R}^{\mathbb{Z}} \to \mathbb{R}$,

$$\log f'_0(1) = \xi(\mathbf{f}_0) - \xi(\mathbf{f}_1) \quad \text{a.s.}$$

and thus

$$S_n = \xi(\mathbf{f}_0) - \xi(\mathbf{f}_n) \quad \text{a.s. for } n \geq 0,$$

where $\mathbf{f} = \mathbf{f}_0 \overset{\text{def}}{=} (\ldots, f_{-1}, f_0, f_1, \ldots)$ and $\mathbf{f}_n \overset{\text{def}}{=} (\ldots, f_{n-1}, f_n, f_{n+1}, \ldots)$ denotes the n-shift of this sequence for $n\in\mathbb{Z}$. Hence, if ξ is bounded we see that strong criticality fails albeit $\mathbb{E}\log f'_0(1)=0$. Conversely, if $(\log f'_n(1))_{n\geq 0}$ is not null-homologous, then $\mathbb{E}\log f'_0(1)=0$ does indeed imply strong criticality, see [2, Remark (b) after Thm. 3].

2.2 Classical results revisited

We continue with a short survey of some classical results concerning the asymptotic behavior of $(Z_n)_{n\geq 0}$. Church [5] and Lindvall [14] proved that Z_n always converges a.s. to a random variable Z_∞ taking values in $\mathbb{N}_0\cup\{\infty\}$, while Tanny [19] added to this that

$$\mathbb{P}(Z_\infty = 0 \text{ or } = \infty) = 1 \quad\text{iff}\quad \mathbb{P}(f_0'(0)=1) < 1.$$

In view of (A4) it is thus clear in the given setup that the considered population either explodes or dies out a.s. Turning to the extinction probability

$$q(\xi) \stackrel{\text{def}}{=} \mathbb{P}(Z_\infty = 0|\mathbf{f}=\xi)$$

for a given environment $\xi\in\Gamma^{\mathbb{Z}}$, let us first note that

$$\mathbb{P}(Z_\infty = 0|\mathbf{f}, Z_0 = k) \;=\; q(\mathbf{f})^k$$

for each $k\in\mathbb{N}_0$ whence it suffices to look at the case $Z_0=1$. Athreya and Karlin [3] proved that

$$q(\mathbf{f}) \;=\; f_0(q(\mathbf{f}_1)) \quad \text{a.s.}$$

and that $\{q(\mathbf{f})=1\}$ is a.s. shift-invariant, i.e. $\{q(\mathbf{f})=1\}=\{q(\mathbf{f}_1)=1\}$ a.s. Hence, by ergodicity,

$$\mathbb{P}(q(\mathbf{f})=1)\in\{0,1\}.$$

Putting

$$g_n(s) \stackrel{\text{def}}{=} \frac{1}{1-f_n(s)} - \frac{1}{f_n'(1)(1-s)}, \quad s\in[0,1),$$

and $\eta_{k,n} \stackrel{\text{def}}{=} g_k\circ f_{k+1:n-1}(0)$ for $0\leq k<n$, Geiger and Kersting [10] derived the useful formula

$$\mathbb{P}(Z_n>0|\mathbf{f}) \;=\; \left(e^{-S_n} + \sum_{k=0}^{n-1}\eta_{k,n}e^{-S_k}\right)^{-1} \tag{2.2}$$

for $n\geq 0$ which shows quite clearly the importance of $(S_n)_{n\geq 0}$ for the asymptotic behavior of the survival probability $\mathbb{P}(Z_n>0)$ as $n\to\infty$. The latter was then studied by them and later also in [11, 1] and [9] for critical and subcritical GWPRE in i.i.d. random environment; for earlier results of this type see Kozlov [12] and Dekking [7]. In the subcritical and strongly critical case, formula (2.2) also provides a quick proof of the following result first obtained by Athreya and Karlin [3, Cor. 1]:

Proposition 2.1. *Let $(Z_n)_{n\geq 0}$ be a GWPRE satisfying (A1–4). Then $q(\mathbf{f})=1$ a.s. if $(Z_n)_{n\geq 0}$ is subcritical or critical.*

Proof (in the subcritical and strongly critical case). If $(Z_n)_{n\geq 0}$ is subcritical or strongly critical then $\liminf_{n\to\infty} S_n = -\infty$ a.s. By using formula (2.2) and the monotonicity of $\mathbb{P}(Z_n>0|\mathbf{f})$, we hence infer

$$1-q(\mathbf{f}) \;=\; \lim_{n\to\infty}\mathbb{P}(Z_n>0|\mathbf{f}) \;\le\; \liminf_{n\to\infty} e^{S_n} \;=\; 0 \quad \text{a.s.},$$

that is $q(\mathbf{f})=1$ a.s.

In the subcritical case, there is yet another quick argument, for $\mathbb{E}\log f_0'(1)<1$ means nothing but the iterated function system $(f_{n:0})_{n\ge0}$ to be strictly mean contractive with unique stationary distribution δ_1, the Dirac measure at 1. Hence the associated backward system $(f_{0:n}(s))_{n\ge0}$ converges a.s. to 1 for any initial state s (see e.g. [8]), in particular $q(\mathbf{f})=\lim_{n\to\infty}f_{0:n}(0)=1$ a.s.

The proof is completed after Lemma 2.1. The next result, also obtained by Athreya and Karlin [3, Thm. 3], provides conditions ensuring $q(\mathbf{f})<1$ a.s.

Proposition 2.2. *Let $(Z_n)_{n\ge0}$ be a GWPRE satisfying (A1–4). Then $q(\mathbf{f})<1$ a.s. if $(Z_n)_{n\ge0}$ is supercritical and $\mathbb{E}\log(1-f_0(0))>-\infty$.*

The additionally occurring condition $\mathbb{E}\log(1-f_0(0))>-\infty$ in the supercritical case naturally raises the question of its necessity. Certain special cases for which the answer is positive are stated in the next result.

Proposition 2.3. *Let $(Z_n)_{n\ge0}$ be a GWPRE satisfying (A1–4) and $\mathbb{E}|\log f_0'(1)|<\infty$. Then*

$$\left\{\begin{matrix}\mathbb{E}\log(1-f_0(0))>-\infty\\ \mathbb{E}\log f_0'(1)>0\end{matrix}\right\} \quad\Longleftrightarrow\quad \mathbb{P}(q(\mathbf{f})<1)=1 \tag{2.3}$$

in any of the following two cases:

(C1) $f_0,f_1,\ldots$ are independent or m-dependent for some $m\in\mathbb{N}$.
(C2) $f_0,f_1,\ldots$ take values in a finite subset Γ_0 of Γ.

For the subcases where $f_0,f_1,\ldots$ are i.i.d. or a finite irreducible Markov chain, this result is due to Smith [16] and once again to Athreya and Karlin [3, Thm. 2], respectively. For a proof of the result in the stated form we refer to Section 5.

2.3 Main result and a counterexample

We proceed with a statement of our main result after some necessary notation. It provides necessary and sufficient conditions in the supercritical case for $q(\mathbf{f})<1$ a.s. as well as for $\mathbb{E}\log(1-f_0(0))>-\infty$. Then we give a counterexample which demonstrates that even in the case where the environment $\mathbf{f}$ constitutes a positive recurrent discrete Markov chain we cannot generally conclude $\mathbb{E}\log(1-f_0(0))>-\infty$ from $q(\mathbf{f})<1$ a.s. Thus equivalence (2.3) in Proposition 2.3 for finite irreducible Markov chains does not extend to general positive recurrent Markov chains with countable state space; for a positive result in the latter situation see again [3, Thm. 4].

Given a doubly infinite environment $\mathbf{f}$, denote by $\mathbb{T}=\mathbb{T}_{\mathbf{f}}$ the set of all a.s. finite random times T of the form

$$T \;=\; \inf\{n\ge m:\mathbf{f}_n\in C\}$$

for $m \in \mathbb{N}$ and some measurable subset C of Γ (the definition of a suitable σ-field on Γ is standard and will not be spelled out here, see e.g. [8] in the context of iterated random Lipschitz functions). We note that with T any $T+k$, $k \in \mathbb{Z}$, is also an element of $\mathbb{T}$, for $T = \inf\{n \geq m+k : \mathbf{f}_n \in \Theta^k C\}$ where Θ denotes the usual forward shift mapping $(\ldots, f_{-1}, f_0, f_1, \ldots) \mapsto (\ldots, f_0, f_1, f_2, \ldots)$. The following truncation has been introduced in [6]: For any function $v : \Gamma^{\mathbb{Z}} \to \mathbb{N}$ and given $\mathbf{f} = (f_n)_{n\in\mathbb{Z}}$ with $f_n(s) = \sum_k p_{n,k} s^k$, let $\mathbf{f}^v \overset{\text{def}}{=} (f_{n,v})_{n\in\mathbb{Z}}$ be the sequence of generating functions defined by

$$f_{n,v}(s) \overset{\text{def}}{=} \sum_{k=0}^{v(\mathbf{f}_n)-1} p_{n,k} s^k \;+\; s^{v(\mathbf{f}_n)} \sum_{k \geq v(\mathbf{f}_n)} p_{n,k}.$$

In the case of a constant truncation function $v \equiv c$ we simply write $f_{n,c}$ for $f_{n,v}$. It is easily verified that $\mathbf{f}^v$ is again stationary and ergodic if this holds true for $\mathbf{f}$.

Theorem 2.1. *Let $(Z_n)_{n\geq 0}$ be a GWPRE satisfying (A1–4). and consider the following assumptions:*

(B1) $\mathbb{E}\log(1 - f_0(0)) > -\infty$;

(B2) There exists $c \in \mathbb{N}$ such that $0 < \mathbb{E}\log f_{0,c}'(1) < \infty$;

(B3) $\mathbb{P}(q(\mathbf{f}) < 1) = 1, \quad \mathbb{E}\left|\log\left(\frac{1-q(\mathbf{f}_0)}{1-q(\mathbf{f}_1)}\right)\right| < \infty$ *and* $\mathbb{E}\log\left(\frac{1-q(\mathbf{f}_0)}{1-q(\mathbf{f}_1)}\right) = 0$;

(B4) There exists $T \in \mathbb{T}$ such that $\mathbb{E}\log\left(\frac{1-f_0\circ\ldots\circ f_T(0)}{1-f_1\circ\ldots\circ f_T(0)}\right) > -\infty$;

(B5) There exists $v : \Gamma^{\mathbb{Z}} \to \mathbb{N}$ such that $\left\{\begin{array}{c} 0 < \mathbb{E}\log f_{0,v}'(1) < \infty \\ \\ \lim_{n\to\infty} n^{-1}\log v(\mathbf{f}_n) = 0 \text{ a.s.} \\ \\ \mathbb{P}(q(\mathbf{f}^v) < 1) = \mathbb{P}(q(\mathbf{f}) < 1) = 1 \end{array}\right\}$;

(B6) $\lim_{n\to\infty} n^{-1}\log(1 - q(\mathbf{f}_n)) = 0$ *a.s.;*

(B7) $\lim_{n\to\infty} n^{-1}\log(1 - f_n(0)) = 0$ *a.s.*

(a) If $\mathbb{E}\log f_0'(1) > 0$*, then*

$$\begin{array}{ccl} (B1) & & (B4) \Rightarrow (B5) \Rightarrow (B6) \Rightarrow (B7) \\ \Updownarrow & & \Updownarrow \\ (B2) & \Rightarrow & (B3) \end{array}$$

(b) If $0 < \mathbb{E}\log f_0'(1) < \infty$*, then (B3–5) are equivalent.*

The proof of this result is rather long and postponed to Sect. 2.5. Let us point out that condition (B4) actually coincides with condition (B1) if $T \equiv 0$ and the term $f_1 \circ \ldots \circ f_T(0)$ is interpreted as 1 in this case. We will further see in Lemma 2.1 that, if $0 < \mathbb{E}\log f_0'(1) < \infty$, then $\mathbb{P}(q(\mathbf{f}) < 1) = 1$ alone already entails the other assertions in (B3). Consequently, in this situation we have equivalence of $\mathbb{P}(q(\mathbf{f}) < 1) = 1$ with condition (B4) for *some* random time T but not necessarily for $T \equiv 0$. This is exemplified by the subsequent already announced counterexample:

Example 2.1. Let $\Gamma_0 = \{g_0, g_1, \ldots\}$ be the countable subset of Γ, defined by

$$g_n(s) \overset{\text{def}}{=} 1 - e^{-n} + e^{-n}s^{m_n} \quad \text{for } n \geq 0,$$

where m_n is the smallest integer greater than e^{n+1}. Hence g_n is the generating function of the two-point distribution $Q_n \overset{\text{def}}{=} (1-e^{-n})\delta_0 + e^{-n}\delta_{m_n}$ and

$$e \;<\; g_n'(1) \;=\; m_n e^{-n} \;\leq\; e+1 \tag{2.4}$$

for each $n \geq 0$.

Suppose that $(f_n)_{n\geq 0}$ is a Markov chain on Γ_0 with transition matrix

$$\mathbf{P} \;=\; \begin{pmatrix} 0 & \alpha_1 & \alpha_2 & \alpha_3 & \alpha_4 & \ldots \\ 1 & 0 & 0 & 0 & 0 & \ldots \\ 0 & 1 & 0 & 0 & 0 & \ldots \\ 0 & 0 & 1 & 0 & 0 & \ldots \\ \vdots & & & \ddots & \ddots & 0 \end{pmatrix}$$

for suitable $\alpha_n > 0$ satisfying $\sum_n \alpha_n = 1$, $\kappa \overset{\text{def}}{=} \sum_n n\alpha_n < \infty$ and $\sum_n n^2\alpha_n = \infty$. Plainly, the (i,j)-component of $\mathbf{P}$ denotes the probability of $f_n = g_j$ given $f_{n-1} = g_i$ for any $n \geq 0$. As one can further readily check, $(f_n)_{n\geq 0}$ is positive recurrent with stationary distribution π, given by

$$\pi_n \overset{\text{def}}{=} \pi(g_n) \;=\; \frac{1}{\kappa+1}\sum_{k\geq n}\alpha_k, \quad n \geq 0.$$

and satisfying $\sum_n n\pi_n = \infty$, for $\sum_n n^2\alpha_n = \infty$. In the following, let $(f_n)_{n\geq 0}$ be in stationary regime under $\mathbb{P}$ (so $\mathbb{P} = \mathbb{P}_\pi$) and note that

$$\begin{aligned} &\mathbb{E}\log f_0'(1) \;=\; \sum_{n\geq 0}\pi_n \log g_n'(1) \;\in\; (1, \log(e+1)] \quad \text{[by (2.4)]} \\ \text{and} \quad &\mathbb{E}\log(1-f_0(0)) \;=\; \sum_{n\geq 0}\pi_n\log(1-g_n(0)) \;=\; -\sum_{n\geq 0} n\pi_n \;=\; -\infty. \end{aligned}$$

So we are in the supercritical case, but with condition (B1) being violated. On the other hand, condition (B4) will now be shown to hold true with $T \equiv 1$. Indeed, using

$$\lim_{n\to\infty} n^{-1}\log\left(e^n(1-e^{-n})^3\right) = 1 \quad \text{and} \quad \lim_{n\to\infty}(1-e^{-n+1})^{m_n} = \exp(-e^2),$$

we infer

$$\begin{aligned} 0 \;<\; &\mathbb{E}\left(\frac{1-f_0\circ f_1(0)}{1-f_1(0)}\right) \\ =\; &\pi_0\sum_{n\geq 1}\alpha_n\log\left(\frac{1-f_0\circ f_n(0)}{1-f_n(0)}\right) \;+\; \sum_{n\geq 1}\pi_n\log\left(\frac{1-f_n\circ f_{n-1}(0)}{1-f_{n-1}(0)}\right) \end{aligned}$$

$$
\begin{aligned}
&= \pi_0 \sum_{n\ge 1} \alpha_n \log\left(\frac{f_n(0)^{m_0}}{1-f_n(0)}\right) + \sum_{n\ge 1} \pi_n \log\left(\frac{e^{-n}(1-f_{n-1}(0)^{m_n})}{1-f_{n-1}(0)}\right)\\
&= \pi_0 \sum_{n\ge 1} \alpha_n \log(e^n(1-e^{-n})^3) + \sum_{n\ge 1} \pi_n \log\left(e^{-1}(1-(1-e^{-n+1})^{m_n})\right)\\
&\le C\Big(\pi_0 \sum_{n\ge 1} n\alpha_n + 1-\pi_0\Big) < \infty
\end{aligned}
$$

for a suitable constant $C \in (0,\infty)$. Having verified condition (B4), we infer from Theorem 2.1 that $q(\mathbf{f}) < 1$ a.s.

The flavor of this example is that the offspring distributions Q_n are picked in such a way that, as $n \to \infty$, individuals have no offspring with a chance $1-e^{-n}$ exponentially approaching 1, while with probability e^{-n} they produce an exponentially growing number of descendants. This is combined with a transition mechanism for picking the Q_n resulting in long runs of the form $Q_0 \to Q_1 \to \ldots \to Q_k$ where the population grows very rapidly on the event of survival, before it starts anew with a pick of Q_0. It is this transition mechanism that makes for an almost certain positive chance of survival. Indeed, if the f_n are i.i.d. with distribution π then $\mathbb{E}\log(1-f_0(0)) = -\infty$ and $0 < \mathbb{E}\log f_0'(1) < \infty$ clearly persist to hold while Proposition 2.3 now tells us that $q(\mathbf{f}) = 1$ a.s.

Let us finally note that Tanny [19, Ex. 2] has produced a counterexample of a similar kind but less explicit insofar as it requires to review a rather long and technical argument given in [18] in order to conclude $q(\mathbf{f}) < 1$ a.s.

2.4 Some useful facts from Palm-duality theory

Consider a doubly infinite sequence $\mathbf{X} = (X_n)_{n\in\mathbb{Z}}$ of random variables defined on a probability space $(\Omega,\mathfrak{A},\mathbb{P})$ and taking values in a Borel space $(\Lambda,\mathfrak{C})$. Put $\mathbf{X}_n \overset{\text{def}}{=} \Theta^n\mathbf{X} = (\ldots,X_{n-1},X_n,X_{n+1},\ldots)$ for $n \in \mathbb{Z}$. Let further $\mathbf{T} = (T_n)_{n\in\mathbb{Z}}$ be an increasing doubly infinite sequence of a.s. finite random epochs such that $\mathbf{T} = \tau(\mathbf{X})$ for a measurable function τ and $T_0 \le 0 < T_1$ holds true. The forward shift Θ is supposed to act on $(\mathbf{X},\mathbf{T})$ in the canonical manner, namely

$$\Theta \circ (\mathbf{X},\mathbf{T}) \overset{\text{def}}{=} (\Theta\mathbf{X}, \tau(\Theta\mathbf{X})).$$

Hence $(\mathbf{X},\mathbf{T})$ is stationary if this holds true for $\mathbf{X}$. The T_n divide $\mathbf{X}$ into the cycles (or segments)

$$Y_n \overset{\text{def}}{=} (X_{T_n},\ldots,X_{T_{n+1}-1}), \quad n \in \mathbb{Z}$$

which are generally not stationary under $\mathbb{P}$. The Palm-duality theory for stationary point processes tells us how the latter can be achieved (leading to so-called cycle stationarity) under an appropriate change of measure which, roughly speaking, means to condition the stationary $(\mathbf{X},\mathbf{T})$ to have a point at 0 (here points are the epochs T_n). For a detailed exposition of this topic we refer to the monographs by Thorisson

[20, Chap. 8] or Sigman [15]. Here we confine ourselves with a statement of some basic facts. Defining

$$\widehat{\mathbb{P}}(d\omega) \overset{\text{def}}{=} \frac{1}{c(T_1(\omega)-T_0(\omega))}\mathbb{P}(d\omega), \quad c \overset{\text{def}}{=} \mathbb{E}\left(\frac{1}{T_1-T_0}\right), \tag{2.5}$$

the main result may be stated as follows:

Proposition 2.4. *Given a stationary sequence* $(\mathbf{X},\mathbf{T})$ *on a probability space* $(\Omega,\mathfrak{A},\mathbb{P})$ *as introduced before, the following assertions hold true:*

(a) $(Y_n)_{n\in\mathbb{Z}}$ *is stationary under* $\widehat{\mathbb{P}}$.
(b) *Under* $\widehat{\mathbb{P}}$, $\Theta^{T_n}\circ(\mathbf{X},\mathbf{T}) \overset{d}{=} \Theta^{T_0}\circ(\mathbf{X},\mathbf{T})$ *for all* $n\in\mathbb{Z}$.
(c) $\widehat{\mathbb{E}}(T_n-T_{n-1}) = \frac{1}{c}$ *for all* $n\in\mathbb{Z}$.

A consequence of this result is the subsequent useful formula reminiscent of Dynkin's formula in the theory of Markov processes. We will use it in several places in the proof of Theorem 2.1.

Corollary 2.1. *Suppose that* $(\mathbf{X},\mathbf{T})$ *is stationary under* $\mathbb{P}$. *Let* $h:\Lambda^\infty\to\mathbb{R}$ *be any measurable function such that* $\mathbb{E}h^-(\mathbf{X})$ *or* $\mathbb{E}h^+(\mathbf{X})$ *is finite. Then*

$$\widehat{\mathbb{E}}\left(\sum_{k=T_0}^{T_1-1} h(\mathbf{X}_k)\right) \;=\; \mathbb{E}h(\mathbf{X})\,\widehat{\mathbb{E}}(T_1-T_0) \;=\; \frac{\mathbb{E}h(\mathbf{X})}{c}.$$

Proof. It suffices to consider the case of bounded h, for then the general assertion follows in the usual manner by monotone approximation of h^+ and h^- through nonnegative bounded functions. Observe that, by part (a) of the previous proposition, $\left(\sum_{k=T_{n-1}}^{T_n-1} h(\mathbf{X}_k)\right)_{n\in\mathbb{Z}}$ is stationary under $\widehat{\mathbb{P}}$. For bounded h, we now infer

$$\widehat{\mathbb{E}}\left(\sum_{k=T_0}^{T_1-1} h(\mathbf{X}_k)\right) \;=\; \frac{1}{n}\widehat{\mathbb{E}}\left(\sum_{k=T_0}^{T_n-1} h(\mathbf{X}_k)\right) \;=\; \frac{1}{n}\sum_{j=1}^{n}\widehat{\mathbb{E}}\left(\frac{T_j-T_{j-1}}{T_n-T_0}\sum_{k=T_0}^{T_n-1} h(\mathbf{X}_k)\right)$$

and each expectation in the last sum converges to $\mathbb{E}h(\mathbf{X})\widehat{\mathbb{E}}(T_1-T_0)$ as $n\to\infty$ by an appeal to Birkhoff's ergodic theorem (giving $(T_n-T_0)^{-1}\sum_{k=T_0}^{T_n-1} h(\mathbf{X}_k)\to\mathbb{E}h(\mathbf{X})$ $\mathbb{P}$-a.s. and thus $\widehat{\mathbb{P}}$-a.s.), the dominated convergence theorem and Proposition 2.4(b). This clearly yields the asserted result.

2.5 Proofs

Let us begin by recalling the following result by Athreya and Karlin [3, Thm. 1].

Lemma 2.1. *Let* $(Z_n)_{n\ge 0}$ *be a GWPRE satisfying (A1–4) and* $\mathbb{E}(\log f_0'(1))^+<\infty$. *Then* $\mathbb{P}(q(\mathbf{f})<1)=1$ *implies*

$$\mathbb{E}|\log f_0'(1)| < \infty \quad \textit{and} \quad \mathbb{E}\log f_0'(1) > 0$$

as well as

$$\mathbb{E}\left|\log\left(\frac{1-q(\mathbf{f}_0)}{1-q(\mathbf{f}_n)}\right)\right| < \infty \quad \textit{and} \quad \mathbb{E}\log\left(\frac{1-q(\mathbf{f}_0)}{1-q(\mathbf{f}_n)}\right) = 0 \tag{2.6}$$

for all $n \in \mathbb{N}$.

Proof (of Proposition 2.1 (Completion)). In view of the previous lemma we see that criticality (i.e., $\mathbb{E}\log f_0'(1) = 0$ and particularly $\mathbb{E}(\log f_0'(1))^+ < \infty$) always entails $q(\mathbf{f}) = 1$ a.s.

Proof (of Proposition 2.3). Suppose $\mathbb{E}|\log f_0'(1)| < \infty$. In view of Proposition 2.2 it remains to show that $q(\mathbf{f}) < 1$ a.s. implies $\mathbb{E}\log(1-f_0(0)) > -\infty$. That $\mathbb{E}\log f_0'(1) > 0$ holds true as well follows by an appeal to Proposition 2.1.

For all $n \geq 1$ and $\varepsilon \in (0,1)$, we infer with the help of Lemma 2.1 that

$$\begin{aligned}
\infty \;&>\; \mathbb{E}\left|\log\left(\frac{1-q(\mathbf{f}_0)}{1-q(\mathbf{f}_n)}\right)\right| \\
&=\; \mathbb{E}\left|\log\left(\frac{1-f_0\circ\ldots\circ f_{n-1}(q(\mathbf{f}_n))}{1-q(\mathbf{f}_n)}\right)\right| \\
&\geq\; \mathbb{E}\left|\log\left(\frac{1-f_0\circ\ldots\circ f_{n-1}(q(\mathbf{f}_n))}{1-q(\mathbf{f}_n)}\right)\right| \mathbb{1}_{[0,1-\varepsilon]}(q(\mathbf{f}_n)) \\
&\geq\; -\mathbb{E}\log(1-f_0\circ\ldots\circ f_{n-1}(q(\mathbf{f}_n)))\mathbb{1}_{[0,1-\varepsilon]}(q(\mathbf{f}_n)) \;+\; \log\varepsilon \\
&\geq\; -\mathbb{E}\log(1-f_0(0))\mathbb{1}_{[0,1-\varepsilon]}(q(\mathbf{f}_n)) \;+\; \log\varepsilon \\
&\geq\; -\mathbb{E}\Big(\log(1-f_0(0))\mathbb{P}(q(\mathbf{f}_n) \leq 1-\varepsilon|f_0)\Big) \;+\; \log\varepsilon.
\end{aligned} \tag{2.7}$$

Now we have

$$\mathbb{P}(q(\mathbf{f}_n) \leq 1-\varepsilon|f_0) \;=\; \mathbb{P}(q(\mathbf{f}) \leq 1-\varepsilon) \;>\; 0 \quad \text{a.s.}$$

for all $n > m$ and ε sufficiently small, if the f_n are m-dependent (notice that $q(\mathbf{f}_n)$ does actually only depend on $f_n, f_{n+1}, \ldots$), while in the case (C2)

$$\mathbb{P}(q(\mathbf{f}_n) \leq 1-\varepsilon|f_0) \;\geq\; \min_{g\in\Gamma_0}\mathbb{P}(q(\mathbf{f}_n) \leq 1-\varepsilon|f_0 = g) \;>\; 0 \quad \text{a.s.}$$

for ε sufficiently small. Consequently, by choosing n and ε in a suitable manner in (2.7), we infer $\mathbb{E}\log(1-f_0(0)) > -\infty$.

Proof (of Theorem 2.1). Put $h(\xi) \overset{\text{def}}{=} -\log\left(\frac{1-q(\xi)}{1-q(\Theta\xi)}\right)$ for any $\xi \in \Gamma^{\mathbb{Z}}$.

(a) Suppose $\mathbb{E}\log f_0'(1) > 0$.

"(B1)⇒(B2)" As, by convexity, $f_{0,c}'(1) \geq 1 - f_{0,c}(0) = 1 - f_0(0)$ for all $c \in \mathbb{N}$, we see that (B1) implies $\mathbb{E}\log f_{0,c}'(1) > -\infty$ for all $c \in \mathbb{N}$ and thereupon, by the monotone convergence theorem, that $\lim_{c\to\infty}\mathbb{E}\log f_{0,c}'(1) = \mathbb{E}\log f_0'(1) > 0$. This shows (B2).

"(B2)⇒(B1)" Using $f_{0,c}''(1) < \infty$ and the inequality $\frac{1-f_{0,c}(s)}{1-s} \ge f_{0,c}'(1) - \frac{1}{2}f_{0,c}''(1)(1-s)$ for $s \in [0,1)$, we infer

$$\mathbb{E}\log\left(\frac{1-f_{0,c}(s)}{1-s}\right) \;\ge\; \frac{1}{2}\mathbb{E}\log f_{0,c}'(1) \;>\; 0$$

by making $1-s$ sufficiently small. Picking such an s, (B1) now follows from

$$\begin{aligned}\mathbb{E}\log(1-f_0(0)) \;&=\; \mathbb{E}\log(1-f_{0,c}(0)) \;\ge\; \mathbb{E}\log(1-f_0(s))\\ &=\; \mathbb{E}\log\left(\frac{1-f_{0,c}(s)}{1-s}\right) \;+\; \log(1-s) \;\ge\; \log(1-s).\end{aligned}$$

"(B3)⇒(B4)" As $\mathbb{P}(q(\mathbf{f})<1)=1$, Birkhoff's ergodic theorem implies the existence of $\overline{q}\in(0,1)$ such that

$$\lim_{n\to\infty}\frac{1}{n}\sum_{k=0}^{n-1}\mathbb{1}_{[0,\overline{q}]}\big(q(\mathbf{f}_k)\big) \;=\; \mathbb{P}(q(\mathbf{f})\le\overline{q}) \;>\; 0 \quad \text{a.s.}$$

which in turn yields

$$\mathbb{P}\big(q(\mathbf{f}_n)\le\overline{q} \text{ infinitely often}\big) = 1.$$

Denote by $(T_n)_{n\in\mathbb{Z}}$ the sequence of successive random epochs with $q(\mathbf{f}_{T_n})\le\overline{q}$, where $T_0\le 0<T_1$ a.s. Defining $\widehat{\mathbb{P}}$ as in (2.5) for this sequence, Proposition 2.4 ensures that

$$\widehat{\mathbf{f}} \;=\; (\widehat{f}_n)_{n\in\mathbb{Z}}, \quad \widehat{f}_n \;\stackrel{\text{def}}{=}\; f_{T_n}\circ\ldots\circ f_{T_{n+1}-1},$$

is stationary and ergodic under $\widehat{\mathbb{P}}$. The latter holds true in particular for $(T_n - T_{n-1})_{n\in\mathbb{Z}}$ and $\widehat{\mathbb{E}}(T_1-T_0) = \left[\mathbb{E}\left(\frac{1}{T_1-T_0}\right)\right]^{-1} < \infty$ (see Proposition 2.4(c)). Now consider a stochastic sequence $(\widehat{Z}_n)_{n\in\mathbb{Z}}$ satisfying

$$\widehat{\mathbb{P}}((\widehat{Z}_n)_{n\ge0}\in\cdot|\widehat{\mathbf{f}}=\xi) = \mathbb{P}((\widehat{Z}_n)_{n\ge0}\in\cdot|\widehat{\mathbf{f}}=\xi) = \mathbb{P}((Z_n)_{n\ge0}\in\cdot|\mathbf{f}=\xi)$$

for all $\xi\in\Gamma^{\mathbb{Z}}$. It follows that $(\widehat{Z}_n)_{n\in\mathbb{Z}}$ forms a GWPRE under $\mathbb{P}$ as well as $\widehat{\mathbb{P}}$ with $\widehat{Z}_0=1$, (under $\widehat{\mathbb{P}}$ stationary ergodic) environment $(\widehat{f}_n)_{n\ge0}$ and

$$\widehat{\mathbb{P}}(\widehat{Z}_\infty=0|\widehat{\mathbf{f}}=\xi) = \mathbb{P}(\widehat{Z}_\infty=0|\widehat{\mathbf{f}}=\xi) = q(\xi).$$

By the choice of the T_n, we have

$$q(\widehat{\mathbf{f}}) \;=\; q(\mathbf{f}_{T_0}) \;\le\; \overline{q} \quad \mathbb{P}\text{-a.s.}$$

and therefore (since $\mathbb{P}$ and $\widehat{\mathbb{P}}$ are equivalent measures and $\widehat{f}_0(0)\le q(\widehat{\mathbf{f}})$)

$$\widehat{\mathbb{E}}\log(1-\widehat{f}_0(0)) \;\ge\; \log(1-\overline{q}) \;>\; -\infty. \tag{2.8}$$

Next use $\mathbb{E}(\log f_0'(1))^- < \infty$ (by assumption) and Corollary 2.1 to obtain

$$\begin{aligned}
\widehat{\mathbb{E}}(\log\widehat{f}_0'(1))^- \;&=\; \widehat{\mathbb{E}}\big(\log(f_{T_0}\circ\ldots\circ f_{T_1-1})'(1)\big)^- \\
&=\; \widehat{\mathbb{E}}\left(\sum_{k=T_0}^{T_1-1}\log f_k'(1)\right)^- \\
&=\; \widehat{\mathbb{E}}\left(\sum_{k=T_0}^{T_1-1}(\log f_k'(1))^-\right) \\
&=\; \mathbb{E}(\log f_0'(1))^-\,\widehat{\mathbb{E}}(T_1-T_0) \;<\; \infty
\end{aligned}$$

and then once again Corollary 2.1 to conclude

$$\widehat{\mathbb{E}}\log\widehat{f}_0'(1) \;=\; \mathbb{E}\log f_0'(1)\widehat{\mathbb{E}}(T_1-T_0) \;>\; 0.$$

Write next

$$\begin{aligned}
\widehat{\mathbb{E}}\log(1-\widehat{f}_0(0)) \;&=\; \widehat{\mathbb{E}}\left(\sum_{k=T_0}^{T_1-1}\log\left(\frac{1-f_k\circ\ldots\circ f_{T_1-1}(0)}{1-f_{k+1}\circ\ldots\circ f_{T_1-1}(0)}\right)\right) \\
&=\; \widehat{\mathbb{E}}\left(\sum_{k=T_0}^{T_1-1}g(\mathbf{f}_k)\right),
\end{aligned} \tag{2.9}$$

where, for any $\xi = (\xi_n)_{n\in\mathbb{Z}} \in \Gamma^{\mathbb{Z}}$,

$$g(\xi) \;\overset{\text{def}}{=}\; \log\left(\frac{1-\xi_0\circ\ldots\circ\xi_{\tau(\xi)-1}(0)}{1-\xi_1\circ\ldots\circ\xi_{\tau(\xi)-1}(0)}\right), \quad \tau(\xi) \;\overset{\text{def}}{=}\; \inf\{n\ge 1 : q(\Theta^n\xi)\le\overline{q}\}.$$

We show now that $\mathbb{E}g(\mathbf{f}) > -\infty$, which proves (B4) with $T = T_1 - 1 \in \mathbb{T}$. It follows with the help of the monotonicity of $\frac{1-f_0(s)}{1-s}$ that

$$\begin{aligned}
g^+(\mathbf{f}_n) \;&=\; \left(\log\left(\frac{1-f_n(f_{n+1}\circ\ldots\circ f_{T_1-1}(0))}{1-f_{n+1}\circ\ldots\circ f_{T_1-1}(0)}\right)\right)^+ \\
&\le\; \left(\log\left(\frac{1-f_n(q(\mathbf{f}_{n+1}))}{1-q(\mathbf{f}_{n+1})}\right)\right)^+ \\
&=\; \left(\log\left(\frac{1-q(\mathbf{f}_n)}{1-q(\mathbf{f}_{n+1})}\right)\right)^+ \;=\; h^-(\mathbf{f}_n)
\end{aligned}$$

for $T_0 \le n < T_1$. Since $\mathbb{E}|h(\mathbf{f})| < \infty$ by assumption (B3), we obtain by another appeal to Corollary 2.1

$$\widehat{\mathbb{E}}\left(\sum_{k=T_0}^{T_1-1} g^+(\mathbf{f}_k)\right) \;\le\; \widehat{\mathbb{E}}\left(\sum_{k=T_0}^{T_1-1} h^-(\mathbf{f}_k)\right) \;=\; \mathbb{E}h^-(\mathbf{f})\,\widehat{\mathbb{E}}(T_1-T_0) \;<\; \infty$$

which in combination with (2.8) and (2.9) gives $\widehat{\mathbb{E}}(\sum_{k=T_0}^{T_1-1} g^-(\mathbf{f}_k)) < \infty$ as well and thus

$$\mathbb{E}|g(\mathbf{f})| \;=\; \frac{1}{\widehat{\mathbb{E}}(T_1-T_0)}\,\widehat{\mathbb{E}}\left(\sum_{k=T_0}^{T_1-1} |g(\mathbf{f}_k)|\right) \;<\; \infty.$$

"(B4)⇒(B3)" Assuming (B4) with $T = \inf\{n \ge m : \mathbf{f}_n \in C\}$ for some measurable $C \subset \Gamma^{\mathbb{Z}}$ and $m \ge 0$, let T_n', $n \in \mathbb{Z}$, be the increasing sequence of successive random epochs where $\mathbf{f}_{T_n'} \in C$ and $T_0' \le 0 < T_1'$. Putting $T_n \stackrel{\text{def}}{=} T_{(m+1)n}$ for $n \in \mathbb{Z}$, we clearly have $T \le T_1 - 1$ and therefore

$$\begin{aligned} -\infty \;&<\; \mathbb{E}\log\left(\frac{1-f_0(f_1\circ\ldots\circ f_T(0))}{1-f_1\circ\ldots\circ f_T(0)}\right) \\ &\le\; \mathbb{E}\log\left(\frac{1-f_0(f_1\circ\ldots\circ f_{T_1-1}(0))}{1-f_1\circ\ldots\circ f_{T_1-1}(0)}\right). \end{aligned} \tag{2.10}$$

Now let $\widehat{\mathbb{P}}$ and $\widehat{\mathbf{f}}$ be defined as in the previous part but for the T_n just defined. Then Corollary 2.1 (applicable because of (2.10)) and (2.9) (with g adapted to the present T_n) implies

$$\widehat{\mathbb{E}}\log(1-\widehat{f}_0(0)) \;=\; \widehat{\mathbb{E}}(T_1-T_0)\,\mathbb{E}\log\left(\frac{1-f_0(f_1\circ\ldots\circ f_{T_1-1}(0))}{1-f_1\circ\ldots\circ f_{T_1-1}(0)}\right) \;>\; -\infty. \tag{2.11}$$

We further infer $\widehat{\mathbb{E}}\log\widehat{f}_0'(1) > 0$ as in the previous part which in combination with (2.11) gives

$$1 \;=\; \widehat{\mathbb{P}}(q(\widehat{\mathbf{f}}) < 1) \;=\; \mathbb{P}(q(\widehat{\mathbf{f}}) < 1) \;=\; \mathbb{P}(q(\mathbf{f}_{T_0}) < 1)$$

by an appeal to Proposition 2.2 and thus also $q(\mathbf{f}) < 1$ a.s.

Left with the proof of $\mathbb{E}|h(\mathbf{f})| < \infty$, we first note that $\mathbb{E}h^-(\mathbf{f}) < \infty$, for

$$\log\left(\frac{1-f_0(f_1\circ\ldots\circ f_T(0))}{1-f_1\circ\ldots\circ f_T(0)}\right) \;\le\; \log\left(\frac{1-f_0(q(\mathbf{f}_1))}{1-q(\mathbf{f}_1)}\right) \;=\; -h(\mathbf{f}) \quad \text{a.s.}$$

Then use $\sum_{k=0}^{n-1} h(\mathbf{f}_k) = -\log(1-q(\mathbf{f}_0)) + \log(1-q(\mathbf{f}_n))$ to infer

$$\limsup_{n\to\infty} \frac{1}{n}\sum_{k=0}^{n-1} h(\mathbf{f}_k) \;\le\; \lim_{n\to\infty} \frac{-\log(1-q(\mathbf{f}))}{n} \;=\; 0 \quad \text{a.s.}$$

which in combination with $n^{-1}\sum_{k=0}^{n-1} h^-(\mathbf{f}_k) = \mathbb{E}h^-(\mathbf{f}) < \infty$ a.s. by Birkhoff's ergodic theorem leads us to the conclusion

$$\mathbb{E}h^+(\mathbf{f}) \;=\; \lim_{n\to\infty}\frac{1}{n}\sum_{k=0}^{n-1}h^+(\mathbf{f}_k) \;\le\; \mathbb{E}h^-(\mathbf{f}) \;<\; \infty.$$

and thereupon to $\mathbb{E}h(\mathbf{f}) = \lim_{n\to\infty} n^{-1}\sum_{k=0}^{n-1} h(\mathbf{f}_k) = 0$.

"(B3)⇒(B5)" We first point out that for any truncation function v the inequality

$$f'_{0,v}(1) \;\ge\; \frac{1-q(\mathbf{f}_0)-q(\mathbf{f}_1)^{v(\mathbf{f})}}{1-q(\mathbf{f}_1)} \quad \text{a.s.}$$

holds true as was shown by Coffey and Tanny [6, Lemma 2]. Choose $\tilde{v}(\xi) \overset{\text{def}}{=} \inf\{n \ge 1 : q(\Theta\xi)^n \le (1-q(\xi))/2\}$ which is a.s. finite as $q(\mathbf{f}) < 1$ a.s. It follows that

$$\mathbb{E}\log f'_{0,\tilde{v}}(1) \;\ge\; \mathbb{E}\left(\frac{1-q(\mathbf{f}_0)}{2(1-q(\mathbf{f}_1))}\right) \;>\; -\infty.$$

Hence, by the monotone convergence theorem,

$$\mathbb{E}\log f'_{0,\tilde{v}+n}(1) \;=\; \mathbb{E}\log f'_0(1) \;>\; 0.$$

Nox fix N large enough such that, for $v \overset{\text{def}}{=} \tilde{v}+N$, we have $\mathbb{E}\log f'_{0,v}(1) > 0$. It is no loss of generality to assume $\mathbb{E}\log f'_{0,v}(1) < \infty$ as well, for otherwise we can choose m so large that

$$\mathbb{E}\log f'_{0,v}(1)\mathbb{1}_{\{\log f'_{0,v}(1)\le m\}} \;>\; 0$$

and replace $v(\mathbf{f})$ on the event $\{\log f'_{0,v}(1) > m\}$ by $v(\mathbf{f}) - w(\mathbf{f})$, where for $\xi \in \Gamma^{\mathbb{Z}}$ (recall $f_0(s) = \sum_k p_{0,k}s^k$)

$$w(\xi) \;\overset{\text{def}}{=}\; \inf\left\{n \ge 1 : \sum_{k=0}^{v(\xi)-n-1} kp_{0,k} + (v(\xi)-n)\sum_{k\ge v(\xi)-n} p_{0,k} \le m\right\}.$$

If $v(\mathbf{f}_n)$ satisfies the second condition of (B5) still to be verified, then this is obviously also true for the just defined modification. Turning to the verification of

$$\lim_{n\to\infty} n^{-1}\log v(\mathbf{f}_n) \;=\; 0, \quad \text{i.e.} \quad \lim_{n\to\infty} v(\mathbf{f}_n)^{1/n} \;=\; 1 \quad \text{a.s.}$$

note that it suffices to do so for $\tilde{v}$ instead of v. Since, by assumption and Birkhoff's ergodic theorem,

$$0 \;=\; \mathbb{E}h(\mathbf{f}) \;=\; -\lim_{n\to\infty}\sum_{k=0}^{n-1} h(\mathbf{f}_k) \;=\; \lim_{n\to\infty}\frac{1}{n}\log\left(\frac{1-q(\mathbf{f}_0)}{1-q(\mathbf{f}_n)}\right) \quad \text{a.s.} \tag{2.12}$$

we infer $n^{-1}\log(1-q(\mathbf{f}_n)) \to 0$ a.s. and thereby

$$\sum_{n\ge 0}\mathbb{1}_{[1-\exp(-\varepsilon n),1]}(q(\mathbf{f}_n)) \;<\; \infty \quad \text{a.s.} \tag{2.13}$$

for all $\varepsilon > 0$. Consequently,

$$\begin{aligned}\limsup_{n\to\infty} q(\mathbf{f}_n)^{\exp(2\varepsilon n)} &\le \lim_{n\to\infty}(1-e^{-\varepsilon})^{\exp(2\varepsilon n)} \quad \text{a.s.}\\ &= \lim_{n\to\infty}\exp\left(e^{2\varepsilon n}\log(1-e^{-\varepsilon n})\right) \;=\; \lim_{n\to\infty}\exp(-e^{\varepsilon n}) \;=\; 0\end{aligned}$$

which in turn implies

$$\lim_{n\to\infty} e^{-2\varepsilon n}\tilde{v}(\mathbf{f}_{n+1}) \;=\; 0 \quad \text{a.s.}$$

for all $\varepsilon > 0$ by going back to the definition of $\tilde{v}$ and using (2.13). Namely, for any sufficiently large n (depending on the fixed ε),

$$\begin{aligned}q(\mathbf{f}_{n+1})^{\exp(2\varepsilon n)} &\le (1-e^{-\varepsilon(n+1)})^{\exp(2\varepsilon n)} \;=\; \exp\left(e^{2\varepsilon n}\log(1-e^{-\varepsilon(n+1)})\right)\\ &\le 2\exp\left(-e^{\varepsilon(n-1)}\right) \;\le\; \frac{e^{-\varepsilon n}}{2} \;\le\; \frac{1-q(\mathbf{f}_n)}{2}.\end{aligned}$$

Since $\tilde{v} \ge 1$, we have thus particularly shown that

$$1 \;\le\; \limsup_{n\to\infty}\tilde{v}(\mathbf{f}_n)^{1/n} \;\le\; e^{2\varepsilon} \quad \text{a.s.}$$

for all $\varepsilon > 0$, and this clearly gives the desired assertion.

Since truncation always increases the chance of extinction, we have $q(\mathbf{f}^{v}) \ge q(\mathbf{f})$ a.s. and must therefore still verify $\mathbb{P}(q(\mathbf{f}^{v}) < 1) = 1$. Let $(Z_{n,v})_{n\ge 0}$ be a GWPRE with one ancestor and stationary environment $(f_{n,v})_{n\ge 0}$. Put $\mu_{n,v} \overset{\text{def}}{=} \mathbb{E}(Z_n|f_{0,v}, f_{1,v}, \ldots)$ (compare (2.1)) and notice that $W_{n,v} \overset{\text{def}}{=} Z_{n,v}/\mu_{n,v}$, $n \ge 0$, constitutes a mean one nonnegative martingale. Check that $f''_{n,v}(1) \le v(\mathbf{f}_n)^2$ a.s. for all $n \ge 0$ whence

$$\lim_{n\to\infty}\frac{1}{n}\log^{+} f''_{n,v}(1) \;\le\; \lim_{n\to\infty}\frac{2}{n}v(\mathbf{f}_n) \;=\; 0 \quad \text{a.s.}$$

But a combination of this fact with $0 < \mathbb{E}\log f'_{0,v}(1) < \infty$ and $\mathbb{E}\log f''_{0,v}(1) < \infty$ is now easily seen to imply the L_2-boundedness of W_n which in turn entails $\mathbb{P}(q(\mathbf{f}^{v}) < 1) = 1$ as claimed.

"(B5)⇒(B6)" As $\mathbb{P}(q(\mathbf{f}^{v}) < 1) = 1$ and $0 < \mathbb{E}\log f'_{0,v}(1) < \infty$, we infer from Lemma 2.1 that $\mathbb{E}\log\left(\frac{1-q(\mathbf{f}_0)}{1-q(\mathbf{f}_n)}\right) = 0$ for all $n \ge 1$. This yields the assertion by recalling (2.12) from above.

"(B6)⇒(B7)" This is immediate from $\log(1-q(\mathbf{f}_n)) \le \log(1-f_n(0)) \le 0$.

(b) Here it remains to show **"(B5)⇒(B3)"**. Since part (a) already gives $\mathbb{P}(q(\mathbf{f}) < 1) = 1$ and we now additionally assume $\mathbb{E}|\log f'_0(1)| < \infty$, the remaining assertions in (B3) are once again following from Lemma 2.1.

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3
Environmental versus demographic stochasticity in population growth

Carlos A. Braumann

Abstract Demographic stochasticity (sampling variation in births and deaths) and environmental stochasticity (effect of random environmental fluctuations on growth rate) in population growth are usually modeled using different approaches. Branching processes or birth and death processes (BDP) are used to model the effect of demographic stochasticity but do usually assume a constant environment. Stochastic differential equations (SDE) are used to model environmental stochasticity but usually ignore demographic stochasticity. We shall examine the similarities and the differences between these approaches in what concerns extinction and local behavior, using as a benchmark the particular case of the Malthusian (density-independent) models, namely the Galton–Watson process, the simple BDP and the Malthusian SDE model. For SDE density-dependent growth models, we then present a review of the results on extinction and existence of stationary densities. Such results are robust with respect to the form of density-dependence since we use general models (rather than specific models like the logistic). It would be worth studying the results for corresponding general density-dependent demographic stochasticity models.

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3.1 Introduction

Deterministic population growth models may take into account the effect of population size on the growth rate (density-dependence) but ignore the effect of chance

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events and the resulting random fluctuations in population size. Even for populations with positive average growth rate, there is always a risk of extinction that deterministic models do not show. There are two sources of randomness affecting population growth. One is the inevitable sampling variability in births and deaths, usually called demographic stochasticity. The other is due to the random fluctuations in the environmental conditions that affect the growth rate of the population, usually called environmental stochasticity.

Branching processes and birth and death processes (BDP) incorporate the effect of demographic stochasticity but usually assume birth/death rates that are not affected by environmental conditions. Stochastic differential equation (SDE) models are used to model the environmental stochasticity but usually ignore sampling variability in births and deaths.

The two sources of randomness affect the population growth differently, despite having some common effects. We will compare the effects of the two sources of randomness on extinction and local behavior for the benchmark case of density-independent or Malthusian growth. It is a benchmark because it would be the growth model under ideal conditions of unlimited resources. It is also a benchmark because we have detailed results for the two types of demographic stochasticity models and for the environmental stochasticity SDE model that allow us to compare them. In Sect. 3.2, we briefly present the well-known Malthusian models to be compared, namely the Galton–Watson process (GWP), the simple birth and death process (SBDP) and the Malthusian stochastic differential equation model (MSDE). We also compare the local behavior of the three models in terms of their infinitesimal means and standard deviations. In Sect. 3.3 we compare the extinction behavior of these models.

In wild populations, density-independence, however, is not very realistic since resources are limited and intraspecific competition for such resources becomes more intense for large populations, making it more difficult for individuals to survive and reproduce. So, we will look at density-dependent SDE models, which are generalizations of density-dependent ordinary differential equation models that incorporate a stochastic term describing the effect of environmental fluctuations on the growth rate. For such models, we will present results on extinction and existence of a stationary density (existence of a stationary distribution having a probability density function). The literature, starting with the pioneer work of Levins [15], considers specific density-dependent models, the logistic model being the most popular one. However, the exact form of density-dependence of a given population is not really known and so we prefer to use a general density-dependence model in which we do not specify any particular functional form for the density-dependence but only some biologically dictated properties of such dependence. In such a way, the model properties that we reach are robust with respect to the form of density-dependence. Despite this level of generality, we were able to obtain the same qualitative results that have been obtained for specific models and we briefly review these results in Sect. 3.4. We start with models with constant noise intensity and then generalize to density-dependent noise intensities.

Having presented the consequences of environmental stochasticity on density-dependent growth, we believe that a similar study on the effect of demographic stochasticity would be interesting if indeed we could obtain the qualitative behavior of quite general (rather than specific) density-dependent branching processes or density-dependent birth and death processes. Based on analogy, Sect. 3.5 speculates on the behavior of such models and presents the main conclusions.

3.2 Density-independent models and their local behavior

Let us denote by $X(t)$ the population size at time $t \geq 0$ and by $x_0 = X(0) > 0$ the initial population size.

In deterministic continuous-time ordinary differential equation models, let us call total growth rate to the growth rate of the entire population $\frac{\mathrm{d}X(t)}{\mathrm{d}t} = \lim_{\Delta t \downarrow 0} \frac{X(t+\Delta t)-X(t)}{\Delta t}$ and per capita growth rate, or simply growth rate, to $\frac{1}{X(t)}\frac{\mathrm{d}X(t)}{\mathrm{d}t}$.

In density-independent growth, the growth rate is independent of population size, which means that resources are abundant and we do not need to consider the intraspecific competition for such resources. So, the continuous-time deterministic density-independent model just states that the growth rate is a constant r, i.e., $\frac{1}{X(t)}\frac{\mathrm{d}X(t)}{\mathrm{d}t} = r$ or $\frac{\mathrm{d}X(t)}{\mathrm{d}t} = rX(t)$. This is the so-called Malthusian growth model, the solution being exponential growth: $X(t) = x_0 \exp(rt)$. The constant growth rate $r = \lambda - \mu$ is the difference between a constant birth rate λ and a constant death rate μ. As $t \to +\infty$, we get $X(t) \to 0$ if $r < 0$ and $X(t) \to +\infty$ if $r > 0$. For $r = 0$ the population size remains equal to its initial value.

Of course, such models allow non-integer values for $X(t)$ and can not hold exactly. This may be somewhat irrelevant for very large populations but it is certainly important for extinction studies. A more realistic model would consider that there are sampling variations in births and deaths. Then, in a continuous-time framework, the rates would be interpreted in a probabilistic sense, namely the probability that a given individual would give birth to a new individual in a time interval $[t, t+\Delta t]$ (with small $\Delta t > 0$) would be approximately $\lambda \Delta t$ and the probability that a given individual would die in such an interval would be approximately $\mu \Delta t$. We may then model $X(t)$ as a birth and death process.

As can be seen in any stochastic processes textbook, a general birth and death process is a particular type of continuous-time Markov chain having the non-negative integers as the state space and having an infinitesimal matrix of the form

$$\mathbf{Q} = \begin{pmatrix} -\lambda_0 & \lambda_0 & 0 & 0 & 0 & \ldots \\ \mu_1 & -(\lambda_1 - \mu_1) & \lambda_1 & 0 & 0 & \ldots \\ 0 & \mu_2 & -(\lambda_2 - \mu_2) & \lambda_2 & 0 & \ldots \\ 0 & 0 & \mu_3 & -(\lambda_3 - \mu_3) & \lambda_3 & \ldots \\ \ldots & \ldots & \ldots & \ldots & \ldots & \ldots \end{pmatrix},$$

where $\lambda_i \geq 0$ and $\mu_i \geq 0$ are, respectively, the total birth rate and the total death rate when population size is i ($i = 0, 1, 2, \ldots$), with $\mu_0 = 0$. Remember that the element q_{ij} ($i, j = 0, 1, 2, \ldots$) of matrix $\mathbf{Q}$ is the instantaneous rate of transition from population size i to population size j; for $i \neq j$, the probability of transition from i to j in a time interval $[t, t+\Delta t]$ (with $\Delta t > 0$ small) is approximately given by $q_{ij}\Delta t$. Some restrictions on the λ's and μ's need to be imposed for unicity and validity of the forward Kolmogorov equation (see, for instance [1]), but these are automatically satisfied in the density-independent case that we are going to consider.

In general, the per capita rates λ_i/i and μ_i/i may depend on population-size i (density-dependence). We will consider here the density-independent or Malthusian case, known as simple birth and death process (SBDP), in which these rates (interpreted in the probabilistic sense) are constants $\lambda > 0$ and $\mu > 0$. Then, $\lambda_i = \lambda \times i$ and $\mu_i = \mu \times i$. The growth rate is $r = \lambda - \mu$. One can see in any stochastic processes textbook (for example, in [13]) that, assuming the initial population size has a known x_0 value, the solution behaves on average like in the deterministic model: $\mathbf{E}[X(t)] = x_0 \exp(rt)$.

Since $X(t)$ assumes integer values, it can only stay or jump, so its derivative is either zero or infinite. So, the concept of total growth rate (or of per capita growth rate) makes no sense. But it makes sense to speak about the rate of growth of the expected value or of the variance, to which we call infinitesimal mean and infinitesimal variance. When the population size at time t is x, the infinitesimal mean will be given by

$$a(x) = \lim_{\Delta t \downarrow 0} \frac{\mathbf{E}[X(t+\Delta t) - x | X(t) = x]}{\Delta t}$$

and the infinitesimal variance by

$$b^2(x) = \lim_{\Delta t \downarrow 0} \frac{\mathbf{E}[(X(t+\Delta t) - x)^2 \, | X(t) = x]}{\Delta t}.$$

Since, for small $\Delta t > 0$, we have $\mathbf{P}(X(t+\Delta t) - x = 1 | X(t){=}x) = \lambda x \Delta t + o(\Delta t)$, $\mathbf{P}(X(t+\Delta t) - x = -1 | X(t){=}x) = \mu x \Delta t + o(\Delta t)$ and $\mathbf{P}(X(t+\Delta t) - x {=} 0 | X(t){=}x)$ $= 1 - (\lambda + \mu) x \Delta t + o(\Delta t)$, then $\mathbf{E}[X(t+\Delta t) - x | X(t) = x] = rx\Delta t + o(\Delta t)$ and $\mathbf{E}[(X(t+\Delta t) - x)^2 \, | X(t) = x] = (\lambda + \mu) x \Delta t + o(\Delta t)$. Therefore the infinitesimal mean of the SBDP is

$$a(x) = rx,$$

similar to the total growth rate in the deterministic model. The infinitesimal variance is $b^2(x) = (\lambda + \mu)x$, and so the infinitesimal standard deviation is

$$b(x) = \sqrt{\lambda + \mu}\sqrt{x}\,;$$

the proportionality to the square root of the sample size x is typical of sampling variation and should not come as a surprise.

Another way of taking into account sampling variations in births and deaths is to use classical branching processes models, a particular type of discrete-time Markov chains having the non-negative integers as the state space. Usually, although there are now available two-sex models (for a survey see [12]), one looks only at individuals of one sex, for instance females. An excellent quite comprehensive book on branching processes is [11].

For branching processes, the next generation $n+1$ consists of the offspring of the current generation n. Denote by ξ_{nj} the number of offspring of the individual number j of generation n. For the Malthusian type branching process, called Galton-Watson process (GWP), these random variables (r.v.) are assumed to be independent identically distributed (iid) for all n and j and do not depend on population size. Of course, $X_{n+1} = \sum_{j=1}^{X_n} \xi_{nj}$, where X_n represents the population size at generation n. Let $p_k = \mathbf{P}[\xi_{nj} = k]$ $(k = 0, 1, 2, \dots)$ with $\sum_{k=0}^{+\infty} p_k = 1$ be the offspring distribution and assume that it has positive and finite mean $m = \mathbf{E}[\xi_{nj}]$ and variance $\sigma^2 = \mathbf{VAR}[\xi_{nj}]$. Let us denote by $\phi(s) = \sum_{k=0}^{+\infty} p_k s^k$ the probability generating function (p.g.f.) of the offspring distribution. The average behavior is exponential growth like in the deterministic model: $\mathbf{E}[X_n] = x_0 m^n$.

To make the bridge to continuous-time models, let $\Delta t > 0$ be the time interval between consecutive generations, so that $X_n = X(n\Delta t)$ and make $\Delta t \to 0$. Then, for $t = n\Delta t$, $\mathbf{E}[X(t)] = \mathbf{E}[X_n] = x_0 m^n$; of course, for fixed t, as $\Delta t \to 0$, we must have $n = t/\Delta t \to +\infty$ and so, to keep the same average size at time t, m must decrease in such a way that m^n remains constant. Equating with the deterministic case $X(t) = x_0 \exp(rt)$ one gets $m^n = \exp(rt)$ and therefore $r = (n \ln m)/t = (n \ln m)/(n\Delta t) = \ln m/\Delta t$. So, denoting $r = \ln m/\Delta t$, which remains constant as $\Delta t \to 0$, we see that r plays for the average population size the same role as the Malthusian parameter r plays in the deterministic model.

With this approach we can define an analog to infinitesimal means and variances when the population size at generation n (time $t = n\Delta t$) is x:

$$a(x) = \lim_{\Delta t \downarrow 0} \frac{\mathbf{E}[X_{n+1} - x | X_n = x]}{\Delta t} = \lim_{\Delta t \downarrow 0} \frac{(m-1)x}{\Delta t} = rx$$

$$b^2(x) = \lim_{\Delta t \downarrow 0} \frac{\mathbf{E}[(X_{n+1} - x)^2 \,| X_n = x]}{\Delta t} = \lim_{\Delta t \downarrow 0} \frac{\sigma^2 x + (m-1)^2 x^2}{\Delta t} = \sigma^2 x.$$

So, we still get the same local behavior as the SBDP. In fact, the infinitesimal mean behaves similarly to the total growth rate in the deterministic model and the infinitesimal standard deviation is proportional to the square root of population size.

To take into account environmental stochasticity, the standard approach, since the pioneer work of [15], is to use SDE models. The reader interested in SDEs can consult, for instance, [2] or [16]. For the Malthusian (density-independent) case, the deterministic model would imply that, on a time interval $[t, t+\Delta t]$ (with small $\Delta t > 0$), the change in population size $\Delta X(t) = X(t+\Delta t) - X(t)$ should be approximately equal to $(r\Delta t)X(t)$, where $r\Delta t$ is the cumulative growth rate in that interval. In a randomly varying environment, we may assume that the growth rate has a constant average but fluctuates randomly about that average due to random fluctuations in the environmental conditions. If we assume that the random environmental perturbations about the average environmental conditions are in very large number and have approximately independent effects on the growth rate, then the central limit theorem suggests that the resulting accumulated perturbations on the growth rate in the time interval $[0,t]$ can be described by a stochastic process having approximately a Gaussian distribution with zero mean and variance proportional to t (variance should be proportional to the number of such perturbations, which is proportional to the length of the time interval); furthermore, the increments of such process in non-overlapping time intervals should be approximately independent. This suggests that we approximate such cumulative perturbations on growth rate by a Wiener process or Brownian motion process $\sigma W(t)$, where $W(t)$ is the standard Wiener process and $\sigma > 0$ is the proportionality constant that measures the strength of the effect of environmental fluctuations on growth; we may call it noise intensity and assume that is independent of population size. So, the cumulative growth rate on $[t,t+\Delta t]$ is now given by the average value $(r\Delta t)X(t)$ plus the accumulated perturbations $\sigma\Delta W(t)$ (with $\Delta W(t) = W(t+\Delta t) - W(t)$) it experiences on that interval. Going to the limit as $\Delta t \to 0$, we may write $\mathrm{d}X(t) = (r\mathrm{d}t + \sigma\mathrm{d}W(t))X(t)$ or $\mathrm{d}X(t) = rX(t)\mathrm{d}t + \sigma X(t)\mathrm{d}W(t)$. We call this SDE, which is written in its standard format, the Malthusian SDE (MSDE) model. It has also been used in the financial literature to describe the evolution of a stock price (Black–Scholes model) due to random changes in market conditions. Although $W(t)$ has no derivative almost surely (a.s.), we can define a generalized function derivative $\varepsilon(t) = \frac{\mathrm{d}W(t)}{\mathrm{d}t}$, which is a generalized stochastic process known as standard (continuous-time) white noise. If we do so, we can write the MSDE in the nonstandard but suggestive format $\frac{1}{X(t)}\frac{\mathrm{d}X(t)}{\mathrm{d}t} = r + \sigma\varepsilon(t)$. This can be read as the growth rate $\frac{1}{X(t)}\frac{\mathrm{d}X(t)}{\mathrm{d}t}$ having a constant average value r perturbed by a white noise $\sigma\varepsilon(t)$ induced by environmental fluctuations. Of course, the white noise, which is uncorrelated, is just an approximation to a real possibly slightly correlated noise; similarly, the Wiener process (the integral of white noise in the time interval $[0,t]$) is just an approximation to the real accumulated noise in $[0,t]$.

Of course, the solution $X(t)$ of the MSDE $\mathrm{d}X(t) = rX(t)\mathrm{d}t + \sigma X(t)\mathrm{d}W(t)$ with initial condition $X(0) = x_0 > 0$ is the solution to the integral equation $X(t) = x_0 + \int_0^t rX(s)ds + \int_0^t \sigma X(s)dW(s)$ and, since $W(s)$ is a stochastic process (which depends on chance, that is to say, on the environmental conditions that happen to occur), the solution is also a stochastic process. For a given trajectory (that is, for a given environmental scenario), the first integral is just an ordinary Riemann integral; however, the second integral cannot be defined as a Riemann-Stieltjes integral because $W(s)$ is a.s. of unbounded variation. In fact, choosing mean square (m.s.) limits for convenience, when we decompose the interval of integration into n subintervals (decompositions defined by $0 = t_{n,0} < t_{n,1} < t_{n,2} < \cdots < t_{n,n} = t$ with diameter converging to 0 as $n \to +\infty$), we see that the Riemann-Stieltjes sums $\sum_{j=1}^{n} \sigma X(\tau_{n,j}) \left(W(t_{n,j}) - W(t_{n,j-1})\right)$ converge to different limits according to the choice of the intermediate points $\tau_{n,j} \in [t_{n,j-1}, t_{n,j}]$. We have several stochastic integrals according to the choice we made of the intermediate points. The non-anticipative choice $\tau_{n,j} = t_{n,j-1}$ corresponds to the Itô integral, which has nice probabilistic properties but does not follow ordinary calculus rules. Another commonly used integral is the Stratonovich integral, which corresponds to taking as intermediate point the average between the initial and the end point of the subinterval $[t_{n,j-1}, t_{n,j}]$; this integral does not have such nice probabilistic properties but follows ordinary calculus rules. Since the two calculi lead to apparently different solutions, there has been a controversy on the literature on which calculus is more appropriate to describe population growth in a randomly varying environment. In [7] and [8] we have resolved the controversy in much more general contexts, but let us illustrate the resolution for the particular context of the MSDE. In this case, the resolution consists in showing that the "average" growth rate r does not have the same meaning under the two calculi. The literature on the controversy had assumed implicitly that, because they were using the same letter r for both models, the Itô Calculus model and the Stratonovich calculus model, it meant the same average and they did not even specify what average they were talking about; this could only lead to confusion because the growth rate is now fluctuating and therefore, when we write our results in terms of the average growth rate, we should clarify which average we are using. Indeed, for the present particular context of Malthusian growth models, when population size is x at time t, r means the arithmetic average growth rate $r_a = \frac{1}{x}\lim_{\Delta t \downarrow 0} \frac{\mathbf{E}[X(t+\Delta t)|X(t)=x]-x}{\Delta t}$ under Itô calculus and the geometric average growth rate $r_g = \frac{1}{x}\lim_{\Delta t \downarrow 0} \frac{\exp(\mathbf{E}[\ln X(t+\Delta t)|X(t)=x])-x}{\Delta t}$ under Stratonovich calculus and, taking into account the difference $\sigma^2/2$ between the two averages, the two calculi give exactly the same result.

The solution of the MSDE is, for both calculi, given by the geometric Brownian motion $X(t) = x_0 \exp(r_g t + \sigma W(t)) = x_0 \exp((r_a - \sigma^2/2)t + \sigma W(t))$. Therefore, $\ln X(t)$ has a Gaussian distribution with mean $\ln x_0 + r_g t$ and variance $\sigma^2 t$. The average behavior is similar to the deterministic model: $\mathbf{E}[X(t)] = x_0 \exp(r_a t)$.

From now on, we will use for convenience Stratonovich calculus and the MSDE model $(S)\mathrm{d}X(t) = r_g X(t)\mathrm{d}t + \sigma X(t)\mathrm{d}W(t)$ (the "(S)" stands for the use of Stratonovich calculus when solving the equation) with initial condition $X(0) = x_0$. Of course, since we use Stratonovich calculus, the parameter r is the geometric average growth rate and so, to avoid any risk of confusion, we write "r_g". The arithmetic average growth rate will be denoted by $r_a = r_g + \sigma^2/2$.

The solution of the MSDE is a homogeneous diffusion process. Since $X(t+\Delta t) = X(t)\exp(r_g \Delta t + \sigma(W(t+\Delta t) - W(t)))$, the infinitesimal mean (also called drift coefficient of the diffusion process), when the population size at time t is x, is given by

$$a(x) = \lim_{\Delta t \downarrow 0} \frac{\mathbf{E}[X(t+\Delta t) - x|X(t) = x]}{\Delta t} = \lim_{\Delta t \downarrow 0} \frac{(e^{(r_g+\sigma^2/2)\Delta t} - 1)x}{\Delta t} = r_a x,$$

which also has a behavior similar to the deterministic model. As for the infinitesimal variance (also called diffusion coefficient of the diffusion process), we obtain

$$b^2(x) = \lim_{\Delta t \downarrow 0} \frac{\mathbf{E}[(X(t+\Delta t) - x)^2 \,|X(t) = x]}{\Delta t} = \lim_{\Delta t \downarrow 0} \frac{(e^{(2r_a+\sigma^2)\Delta t} - 2e^{r_a \Delta t} + 1)x^2}{\Delta t} = \sigma^2 x^2.$$

Thus, for environmental stochasticity, the infinitesimal standard deviation is proportional to population size, not to the square root of population size, which is a fundamental difference with respect to demographic stochasticity. The reason is that favorable or unfavorable environmental variations affect in a similar manner the birth and death rates of all individuals. On the contrary, demographic stochasticity does not affect birth and death rates, only the sample realizations of such rates, which are independent among individuals.

3.3 Density-independent models and extinction

For the environmental stochasticity model the state space is the set of positive real numbers (like in the deterministic ordinary differential equation models) and we may consider two concepts of extinction. One is "mathematical" extinction, by which we mean the population size converging to 0 as $t \to +\infty$. From $X(t) = x_0 \exp(r_g t + \sigma W(t))$ and the fact that $W(t)/t \to 0$ as $t \to +\infty$, we have $X(t) \to 0$ a.s. if $r_g < 0$ and $X(t) \to +\infty$ a.s. if $r_g > 0$. Therefore, "mathematical" extinction occurs with probability one if $r_g < 0$ (with extinction time $+\infty$) and occurs with probability zero if $r_g > 0$. But, of course, these models cannot be accurate near extinction. For example, a constant population size of 0.4 individuals is not "mathematically" extinct. So, we can define "realistic" extinction as occurring when the solution of the SDE reaches an extinction threshold $a > 0$ (we assume $x_0 > a$ for otherwise we would start with an already extinct population) and the extinction time T is just the first passage time through a. For example, we can put $a = 1$ or $a = 2$ (for two-sex populations), or even a equal to an Allee effect threshold if such effects (not contemplated on the model) are present.

Since $X(t)$ is geometric Brownian motion, these results are known for a long time (one can see a review and extensions in [3]).The probability of "realistic" extinction is one if $r_g \leq 0$ and is $(a/x_0)^{2r_g/\sigma^2}$ (which is positive and smaller than one) if $r_g > 0$. If $r_g > 0$, the populations that do not become extinct, will grow to $+\infty$. One can also determine the distribution of the extinction time, which is an inverse Gaussian distribution (see, for example, [3]). Using an analogy with branching processes terminology, we may say that $r_g < 0$ corresponds to a subcritical population, $r_g = 0$ to a critical population and $r_g > 0$ to a supercritical population.

For the demographic stochasticity models the state space is the natural one, namely the set of non-negative integers and, therefore, we do not have any problems in precisely defining extinction. Extinction means population size equal to 0 and the extinction time T is the first passage time of $X(t)$ through 0.

For the GWP, it is well-known (see, for instance, [11]) that the probability of extinction occurring is q^{x_0}, where q is the first positive fix point of the p.g.f. $\phi(s)$ (i.e., the first positive solution of $\phi(s) = s$). In the critical ($m = 1$) and subcritical ($m < 1$) cases, we have $q = 1$ and, therefore, extinction occurs with probability one.

In the supercritical case ($m > 1$), we have $0 < q < 1$ and therefore extinction has a positive probability of occurring but that probability is smaller than one. Considering the limiting behavior as $\Delta t \to 0$, the critical, subcritical and supercritical cases correspond to $r = \ln m/\Delta t$ being $= 0$, < 0 and > 0, respectively. So, r plays here a role similar to the r_g in the MSDE model and the two models behave similarly with respect to extinction probabilities being one or smaller than one. In the supercritical case, however, the expressions for the extinction probability, although positive and smaller than one in both models and although decreasing with increasing initial population sizes, are quite different. For the MSDE, the extinction probability is a power function of x_0, while, for the GWP, the extinction probability is an exponential function of x_0. This is not surprising taking into account that the local behavior described by the infinitesimal standard deviation is quite different, particularly near zero population size (in the MSDE, it varies linearly with population size, while in the GWP it behaves more sharply, proportional to the square root of population size).

As for the SBDP, it is well known (see, for instance, [13]) that we have also a similar behavior concerning the extinction probability being one or smaller than one (but always positive). Again, in the subcritical ($r = \lambda - \mu < 0$) and critical ($r = 0$) cases, extinction occurs with probability one, while in the supercritical case ($r > 0$) extinction has a probability $(\mu/\lambda)^{x_0}$ of occurring, again an exponential function of the initial population size like in the GWP. The distribution of the extinction time can be easily obtained and its behavior is different from the MSDE model.

3.4 Density-dependent models for environmental stochasticity

Density-independence is not a realistic model, at least for wild populations. Let us first consider a deterministic model for a closed population (that is, a population with no migration). Under limited resources, as the population size becomes larger, the resources available for individual survival and reproduction become shorter and, therefore, the growth rate $\frac{1}{X(t)}\frac{\mathrm{d}X(t)}{\mathrm{d}t}$ should be a decreasing function of population size $g(X(t))$, contrary to the density-independent case in which we have a constant function of population size. There are many models that have been proposed in the literature. The most popular ones are $g(x) = r(1 - x/K)$ (the logistic or Pearl-Verhulst model) and $g(x) = r\ln(K/x)$ (the Gompertz model), but one may find many others in the literature. Notice that, in the two examples, K is the only zero of $g(x)$ and represents a stable equilibrium population, usually called carrying capacity of the environment. We will denote by $G(x) = g(x)x$ the total growth rate of the population.

When dealing with randomly varying environments, the literature also considers several alternative models (see, for instance, [7] for references) and there are two main ways in which the effect of environmental fluctuations has been introduced:

1. One assumes that the environmental fluctuations directly affect the growth rate $\frac{1}{X}\frac{\mathrm{d}X}{\mathrm{d}t}$ through an additive noise term. The rationale is similar to the one we have used above for the MSDE model. Using Stratonovich calculus for convenience, we obtain a model of the type $(S)\frac{1}{X(t)}\frac{\mathrm{d}X(t)}{\mathrm{d}t} = g(X(t)) + \sigma\varepsilon(t)$, where $g(x)$ is the geometric average growth rate when population size is x and $\sigma\varepsilon(t)$ is a noise term describing the fluctuations in the growth rate induced by the environmental variability, $\sigma > 0$ being a constant noise intensity.
2. The other assumes that the environmental fluctuations affect a parameter of the model. For example, in the logistic model, if r is affected by environmental fluctuations, we could replace it by $r + \sigma\varepsilon(t)$ to obtain the SDE model $\frac{1}{X(t)}\frac{\mathrm{d}X(t)}{\mathrm{d}t} = (r+\sigma\varepsilon(t))\left(1-\frac{X(t)}{K}\right)$, or $\mathrm{d}X(t) = rX(t)\left(1-\frac{X(t)}{K}\right)\mathrm{d}t + \sigma X(t)\left(1-\frac{X(t)}{K}\right)\mathrm{d}W(t)$. Notice that the noise term becomes zero when population size is $= K$ and one wonders why environmental fluctuations do not affect population growth any longer when the population reaches that precise size. So, this particular example is not a very realistic model. But there are other examples. In all cases, we get SDE models of the type $(S)\frac{1}{X(t)}\frac{\mathrm{d}X(t)}{\mathrm{d}t} = g(X(t)) + \sigma(X(t))\varepsilon(t)$, in which the noise intensity $\sigma(x)$ may depend on the population size x.

In the literature, always specific functions $g(x)$ have been considered. But, in reality, for each particular population, it is very difficult to know the exact form of the density-dependence function $g(x)$. So, we have obtained results for the case of a general function $g(x)$, satisfying only some assumptions mainly dictated by biological considerations. In so doing, we insure that the qualitative results we have obtained are model robust, that is, they are unaffected by the specific form of density-dependence.

We now review these results.

We will start with models with constant noise intensity σ (results in [4], also generalized for harvesting models in [5]). Afterwards, we generalize to density-dependent noise intensities $\sigma(x)$ (results in [6], which includes a generalization to harvesting models), but imposing some restrictions on $\sigma(x)$ in order to avoid non-realistic cases like the logistic example with noise in r mentioned above. This generalization responds to the issue that environmental fluctuations may have different effects on the growth rate for different population sizes, in which case the noise intensity (which measures the intensity of such effects) may depend on population size.

Let us start with the results for constant noise intensity σ, i.e. for the SDE model

$$(S)\mathrm{d}X(t) = g(X(t))X(t)\mathrm{d}t + \sigma X(t)\mathrm{d}W(t).$$

We will consider an absolutely arbitrary density-dependence function $g(\cdot) :]0, +\infty[\mapsto]-\infty, +\infty[$ satisfying only the following assumptions:

- g is continuously differentiable and strictly decreasing

- $g(0^+) := \lim_{x\to 0^+} g(x) \neq 0$ (technical assumption to avoid the undecided case $g(0^+) = 0$, which is extremely unlikely)
- $g(+\infty) < 0$ (the environment can not sustain an arbitrarily large population)
- $G(0^+) := \lim_{x\to 0^+} g(x)x = 0$ (because immigration is not allowed).

The continuous differentiability of g implies (see, for instance, [2]) the existence and unicity of the solution of the SDE up to a possible explosion time, the solution being a homogeneous diffusion process with diffusion coefficient (infinitesimal variance)

$$b^2(x) = \sigma^2 x^2$$

(the square of the coefficient of the stochastic part of the SDE) and drift coefficient (infinitesimal mean)

$$a(x) = g(x)x + \frac{1}{2}b(x)\frac{\mathrm{d}b(x)}{\mathrm{d}x} = (g(x)+\sigma^2/2)x$$

(coefficient of the deterministic part plus a correction term due to the use of Stratonovich calculus). Notice that the mean behavior is similar to the total growth rate in the deterministic model, but, like we have already seen in the density-independent case (MSDE model), using the arithmetic average growth rate $g(x) + \sigma^2/2$ instead of the geometric average growth rate $g(x)$. Notice also that the infinitesimal standard deviation $b(x) = \sigma x$ is also, like in the MSDE model, proportional to population size.

We now use the scale and speed measures (see, for instance, [14]) defined in the state space (in our case the interval with boundaries 0 and $+\infty$) by the scale and speed densities, respectively

$$s(x) = \exp\left(-\int_{x*}^{x} \frac{2a(\theta)}{b^2(\theta)}d\theta\right)$$

and

$$m(x) = \frac{1}{s(x)b^2(x)},$$

where $x*$ is an arbitrarily chosen point in the interior of the state space. We can also define the scale and speed functions

$$S(x) = \int_{x**}^{x} s(z)dz$$

and

$$M(x) = \int_{x**}^{x} m(z)dz,$$

where $x**$ is an arbitrarily chosen point in the interior of the state space. The scale and speed measures are defined for Borel sets B by $S(B) = \int_B s(z)dz$ and $M(B) = \int_B m(z)dz$. One can see, for instance in [14], that, given constant thresholds a and b in the interior of the state space such that $a < x_0 < b$ and denoting by T_c the first passage time through c, we have $u(x_0) := \mathbf{P}(T_b < T_a | X(0) = x_0) = \frac{S(x_0)-S(a)}{S(b)-S(a)}$, from which one deduces a criterion for non-attractiveness of a state space boundary.

In fact, the boundary 0 is non-attractive if there is a right neighborhood $R =]0, y[$ of zero such that, for any $0 < x_0 < n \in R$, $\mathbf{P}(T_{0^+} < T_n | X(0) = x_0) = 0$ (this means that, when $X(t)$ gets close to 0, it tends to move away from 0). Using the previous result, one sees that a necessary and sufficient condition for that to happen is $S(0^+) = -\infty$. In [14] one can see that a non-attractive boundary cannot be reached in finite nor in infinite time a.s. So, if the boundary 0 is non-attractive, "mathematical" extinction has a zero probability of occurring. We can similarly define non-attractiveness of the boundary $+\infty$ and show that a necessary and sufficient condition is that $S(+\infty) = +\infty$.

With the assumptions we made on the function $g(x)$, we have shown that the boundary $+\infty$ is always non-attractive, which means that an explosion of the solution can not occur and, therefore, the solution of the SDE exists and is unique for all $t \geq 0$. As for the boundary 0, it is non-attractive or attractive according to whether the geometric average growth rate at low population densities $g(0^+)$ is positive or negative.

When $g(0^+) > 0$, we therefore have both boundaries non-attractive. When that happens and simultaneously the speed measure is finite (that is, $M := \int_0^{+\infty} m(z)dz < +\infty$), then (see, for instance, [14]) the process is ergodic and there is a stationary density given by $p(x) = m(x)/M$ $(0 < x < +\infty)$, a kind of stochastic equilibrium. In fact, contrary to the deterministic model, for which the zero of g is a stable equilibrium, the random variations in environmental conditions move the population away from any possible equilibrium size. When there is a stationary density, although population size $X(t)$ is always changing and does not settle down to an equilibrium value, the probability distribution of $X(t)$ settles down to an equilibrium distribution as $t \to +\infty$ and that equilibrium distribution has a probability density function $p(x)$, which we call stationary density. Using the assumptions made on g, we were able to prove that, when $g(0^+) > 0$, we have $M < +\infty$.

So, we reach the following conclusion according to the sign of the geometric average growth rate at low population densities $g(0^+)$:

- When $g(0^+) < 0$, "mathematical" extinction (and therefore, also "realistic" extinction) occurs with probability one.
- When $g(0^+) > 0$, there is a zero probability of "mathematical" extinction and there is a stationary density for $X(t)$. Actually, for low noise intensities σ, the mode of this stationary density almost coincides with the deterministic equilibrium. As for "realistic" extinction, which means crossing of a low extinction threshold $a > 0$, since the process is ergodic, it will cross the threshold sooner or later. Therefore, "realistic" extinction occurs with probability one.

The important different qualitative conclusion for density-dependence of any kind (the result is model robust) in a randomly varying environment is that we always have "realistic" extinction with probability one, while in the density –

independent case we would have a probability of "realistic" extinction smaller than one when the geometric average growth rate was positive. With density-dependence and environmental stochasticty, the question is no longer whether extinction will or not occur (it will occur), but rather how long does it take to happen and, under some conditions, it may indeed take an extremely long time on average, while for others it may occur very quickly on average.

In [10] (see also [9]), we have obtained explicit (although cumbersome, involving multiple integrals) expressions for the mean and standard deviation of the extinction time and, for the particular case of the logistic and the Gompertz models, we have numerically calculated these moments for several combinations of parameter values and presented graphs of their variation as a function of x_0/a. The study of the behavior of such moments as a function of the parameters is quite illuminating and pretty much in accordance with the intuition. One striking fact is that the mean is not very representative of the extinction time behavior since the standard deviation is of the same order of magnitude as the mean.

Our conclusions were obtained assuming constant noise intensity σ, but the conclusions are exactly the same if we allow density-dependence noise intensities $\sigma(x)$ that are realistic (that is, do not become zero for particular values of population size, for otherwise a population of such particular sizes would be unaffected by environmental fluctuations) and satisfy some mild technical assumptions. Namely, we assume that $\sigma(\cdot) :]0,+\infty[\mapsto]0,+\infty[$ satisfies the following assumptions:

- It is twice continuously differentiable and strictly positive.
- The total noise intensity $V(0^+) := \lim_{x\to 0^+} \sigma(x)x = 0$ (since there is no immigration).
- $\int_{0^+}^{x*} \frac{1}{\sigma(x)x} = +\infty$ for some $x* > 0$.
- $\int_{y*}^{+\infty} \frac{1}{\sigma(x)x} = +\infty$ for some $y* > 0$.
- $|\sigma(x)/g(x)|$ is bounded in a right neighborhood of zero.
- $|\sigma(x)/g(x)|$ is bounded in a neighborhood of $+\infty$.

The last four assumptions are indeed quite mild since they are automatically satisfied by all bounded $\sigma(x)$ functions and by many unbounded functions.

3.5 Conclusions

We have compared the density-independent models for population growth, namely the Galton–Watson process (GWP), the simple birth and death process (SBDP) and the Maltusian stochastic differential equation (MSDE) model, the first two being demographic stochasticity models and the third being an environmental stochasticity model.

For the SDE models, just like in deterministic ordinary differential equation models, the concept of "mathematical" extinction (population size converging to 0 as $t \to +\infty$) seems to be not appropriate. In fact, the state space is the positive real line and so the population size may take values like 0.4 individuals, being really extinct but not "mathematically" extinct. Anyway, for the MSDE, "mathematical" extinction occurs with probability one if r_g (the geometric average growth rate) is negative and has a zero probability of occurrence if r_g is positive. The concept of "realistic" extinction (population size crossing a low extinction threshold size $a > 0$) was used instead. No such problem arises in the GWP and the SBDP, in which extinction means population actually reaching zero size.

Using branching processes terminology, we shall consider for the three models subcritical, supercritical and critical cases, corresponding to negative, positive or zero growth rate. In all three models we have extinction with probability one in the subcritical and critical cases and extinction with a positive probability smaller than one in the supercritical case. In the MSDE model the relevant criticality growth rate is the geometric average growth rate r_g. In the SBDP and GWP, the growth rates are not varying (since there are no environmental fluctuations) and are given by $r = \lambda - \mu$ in the SBDP and by $r = \ln m/\Delta t$ in the GWP, where m is the average number of offspring of an individual and Δt is the time interval between generations.

In the supercritical case, the extinction probability is in all cases positive and smaller than one but behaves differently as a function of the initial population size. It is an exponential function for the demographic stochasticity models and a power function for the environmental stochasticity model. This difference in behavior is not surprising considering the differences in local behavior of standard deviation.

Looking at the local behavior, the infinitesimal mean (rate of change of the mean population size) is in all three models similar to the deterministic total growth rate of the population, i.e., proportional to population size. In the demographic stochasticity models, the constant of proportionality is the growth rate. In the MSDE model, the constant of proportionality is an average rate, namely the arithmetic average growth rate (notice that this average is different from the geometric average, which was the relevant average for extinction behavior). The infinitesimal standard deviation (square root of the rate of change of the population size variance) has quite different behavior. It is proportional to the square root of population size in the demographic stochasticity models (which is typical of sampling variation). However, for the environmental stochasticity MSDE model, it is proportional to population size. This fundamental difference is due to the fact that favorable or unfavorable environmental variations affect in a similar manner the birth and death rates of all individuals.

Due to resource limitations, populations usually grow in a density-dependent fashion. We have considered a very general SDE model for the density-dependent growth of a population in a randomly varying environment, so that the results we have obtained previously and review here are unaffected by the specific form of density-dependence. In order to make results even more robust, we have considered not only the case of constant noise intensity but also the case of very general density-dependent noise intensities. The infinitesimal mean is similar to the total growth rate of the corresponding deterministic model and the infinitesimal standard deviation is proportional to population size in the constant noise intensity case.

When the geometric average growth rate at low population densities $g(0^+)$ is negative, "mathematical" and "realistic" extinction occur with probability one. When $g(0^+)$ is positive, "mathematical" extinction has zero probability of occurring, the process is ergodic and $X(t)$ has a stationary density (a kind of stochastic equilibrium); however, the ergodicity implies that "realistic" extinction occurs with probability one since the extinction threshold $a > 0$ will sooner or later be crossed.

In conclusion, environmental stochastic leads to inevitable extinction if any form of density-dependence is present, as it is likely to happen, at least in wild populations. The important issue now is how long does it take for the population to become extinct, which in some conditions can be extremely long on average. There are results on the distribution of the extinction time that are not shown in this paper.

It would be interesting to study the effect of density-dependence on demographic stochasticity models. But it would be important to obtain results, mainly on extinction, with a general (instead of a specific) form of density-dependence in order for the results to be robust. It is only reasonable to guess that, like in environmental stochasticity models, extinction would also be inevitable.

General density-dependent branching processes such that $X_{n+1} = \sum_{j=1}^{X_n} \xi_{nj}(X_n)$, in which the number of offspring is a function $\xi_{nj}(x)$ of the population size x (with offspring distributions $p_k(x) = \mathbf{P}[\xi_{nj}(x) = k]$) can be seen in [11] and references therein. However, in order to obtain interesting conclusions, we need some biologically reasonable assumptions on $p_k(x)$. Of course, one can immediately conclude that extinction is inevitable if one limits the number of offspring to zero and one for population sizes larger than a certain value L. The reason is that the state space $\{0,1,2,\dots,L\}$ would be finite and the only recurrent (and absorbing) class would be $\{0\}$. This is, however, a rather artificial (and unrealistic) way of introducing density-dependence and we need assumptions that are not so restrictive. Maybe one can do away with biologically realistic assumptions like the mean offspring size $m(x)$ being a decreasing function of x such that $m(+\infty) < 1$; probably the variance $\sigma(x)$ of the offspring distribution would need to be controlled (maybe boundedness would be sufficient).

For birth and death processes, the general formulation with total birth and death rates λ_i and μ_i that need not to be proportional to population size i is the standard one and automatically allows for density-dependence. However, as far as I know, there are no conclusions for sufficiently general density-dependence. Here, one may reasonably assume that the per capita birth rate λ_i/i would be a decreasing function of i (with $\lambda_0 = 0$) and the per capita death rate μ_i/i an increasing function of i, and that $r_i := (\lambda_i - \mu_i)/i$ satisfies $\lim_{i\to+\infty} r_i < 0$. Would that be sufficient to show that extinction is inevitable or further conditions would be required? That is certainly worth investigating.

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4
Stationary distributions of the alternating branching processes

Penka Mayster

Abstract We consider the model of alternating branching processes, where two Markov branching processes act alternately by the random time periods of observation and treatment. Stationary distributions can be obtained by feed-back control if the observation time δ is defined by the additive functional of total progeny of the supercritical Markov branching process $\xi(t)$, or by the explicit immigration of particles. We investigate the reproduction by n cycles and limit theorems to obtain the stationary distributions.

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Keywords: controlled branching process, state-dependent emigration, explicit immigration, feed-back control, random environment, stationary distributions.

4.1 Introduction

Controlled branching processes have a 30-years history. The model of controlled branching processes with deterministic control function has been introduced by Sevastyanov and Zubkov [18] in 1974 year, and then, with random control function, by Yanev [25] in 1976 year. The control function (deterministic or random) modifies the number of particles from the n-th generation accepted to continue the reproduction. The main tools of control have been: immigration or emigration of particles. Branching processes with emigration was investigated by Vinokurov [24], Kaverin [12]. Random migration has been studied by Yanev and Nick Yanev [26], Nagaev and Kharn [15]. Stationary distributions for the model of controlled branching processes with multiple control function have been investigated by del Puerto [5] and

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in collaboration with Yanev [6, 7]. Limit theorems and asymptotic behavior of controlled branching processes have been studied by González et al. in the chain of papers, see [8–10] and [11].

Branching processes with random environment started in 1969 with the article of Smith and Wilkinson [19] and then in 1971, this model has been developed by Athreya and Karlin [2, 3]. The remarkable contribution in the last time is done by Vatutin and Dyakonova [22], Afanasiev et al. [1]. They investigate the natural correspondence between the branching processes in random environment and the simple random walk with increments given by logarithm of the conditional expectation of reproduction, see also Vatutin and Wachtel [23].

In 2005 we introduced the model of autoregressive type control [13] by means of fractional thinning operator as “discrete multiplication”

$$\theta \otimes k = \mu(\tau|k) \quad \text{with} \quad \tau = -\log\theta, \quad \theta \in (0,1),$$

where $\mu(\tau|k)$ is a subcritical Markov branching process $\mu(t)$ starting with a random number of particles, $\mu(0) = k$, and stopped at the time τ, see for definition [20] and [21]. We interpret τ as a treatment time period. The Control process consists of testing every particle from the n-th generation according to a dying Markov branching process during an independent random time τ_n. This control approach keeps the local independence of evolution of particles and allows to introduce different kind of dependence between the reproduction and environment. The random environment is generated by the sequence of random variables (δ_n, τ_n), representing the observation and treatment times, respectively, and by the probability generating functions of the Markov branching processes stopped at the random times δ_n or τ_n. Considering over all the possibilities, there are two streams with opposite sense living together, but looking on the particular realization, they appear in the alternating way, when the random environment is created by independent identically distributed cycles. If the random environment is defined by the first order exponential autoregressive process, then this alternative character is disturbed: there appear the cycles with zero treatment time, see [14].

This communication describes the correspondence between the models of alternating branching processes, controlled branching processes and branching processes in random environment. First of all we define the branching mechanism of one cycle and reproduction by n cycles. We define the models of alternating branching process with explicit immigration and the model of feed-back control. Our main interests are the critical parameters of reproduction in random environment for different particular cases. We investigate the existence and properties of stationary distributions for the model of alternating branching process with explicit immigration and for the model of feed-back control.

4.2 Alternating branching process

We intend to control a Markov branching process (MBP) $\xi(t)$ defined by the composition semigroup of probability generating functions (p.g.f.) $f(t,s), t \geq 0$, by means of another MBP $\mu(t)$ defined by the composition semigroup of probability generating functions $g(t,s), t \geq 0$, see [13]. Let $u(s)$ and $v(s)$ be the infinitesimal generating functions to the composition semigroups $f(t,s)$ and $g(t,s)$, respectively. The first derivatives of $u(s)$ and $v(s)$ at the point $s = 1$ define the criticality of the MBP, see for the details on MBP [4], p. 106 and [17], p. 27. We suppose that $f(t,s)$ is supercritical, i.e. $u'(1) > 0$, and $g(t,s)$ is subcritical, i.e. $(v'(1) < 0)$. Traditionally q denotes the extinction probability, that is the smallest root in the closed interval [0,1] of the equation $u(s) = 0$ or $v(s) = 0$. The supercritical process $\xi(t)$ has the extinction probability $q(\xi) < 1$ and the subcritical process $\mu(t)$ has the extinction probability $q(\mu) = 1$. In order to describe the model of alternating branching process we consider the following sequences of independent identically distributed (i.i.d.) random variables (r.v.) representing observed processes and treatment processes:

$$\{\xi_n(.);\ \xi_{n,j}(.):\ n = 1,2,\ldots; j = 1,2,\ldots\},$$

$$\{\mu_n(.);\ \mu_{n,j}(.):\ n = 1,2,\ldots; j = 1,2,\ldots\},$$

being independent copies of $\xi(t)$ and $\mu(t)$, respectively. Let the immigration particles be represented by the following sequence:

$$\{\eta_n:\ n = 0,1,\ldots\},$$

of independent copies of a random variable η with probability generating function $h(s)$. Suppose the observation time periods $(\delta_1, \delta_2, \ldots)$ form a sequence of i.i.d. copies of a non-negative random variable δ and the treatment time periods $(\tau_1, \tau_2, \ldots)$ are independent copies of a random variable τ. First of all we define the model of alternating branching process without explicit immigration. Obviously, the initial conditions will play an important role. Suppose the reaction (X_n, Y_n), $n = 1,2,\ldots$, starts with one particle observed by the time δ_1. We have

$$X_0 = 0, \quad Y_0 = 1 \quad \text{and} \quad X_1 = \xi_1(\delta_1|1), \ldots,$$

$$X_n = \xi_n(\delta_n|Y_{n-1}) \quad \text{and} \quad Y_n = \mu_n(\tau_n|X_n), \ldots,$$

with $\xi_n(\delta_n|Y_{n-1})$ and $\mu_n(\tau_n|X_n)$ the supercritical and subcritical Markov branching processes $\xi_n(t)$ and $\mu_n(t)$, starting with the random number of particles $\xi_n(0) = Y_{n-1}$ and $\mu_n(0) = X_n$, and stopped at the times δ_n and τ_n, respectively. We shall compare it with the reaction $(X'_n, Y'_n), n = 1,2,\ldots$ starting with one particle treated by the time τ_1. We define

$$Y'_0 = 0, \quad X'_0 = 1 \quad \text{and} \quad Y'_1 = \mu_1(\tau_1|1), \ldots,$$

$$X'_n = \xi_n(\delta_n | Y'_n) \quad \text{and} \quad Y'_{n+1} = \mu_{n+1}(\tau_{n+1} | X'_n), \ldots.$$

The Markov chains (Y_n) and (X'_n) are conditioned on the random environment of cycles, respectively,

$$\sigma = \{ \text{ (observation, treatment) } = (\delta_i, \tau_i), i = 1, 2, \ldots\},$$

$$\sigma' = \{ \text{ (treatment, observation) } = (\tau_i, \delta_i), i = 1, 2, \ldots\}.$$

We shall denote it by $\{(Y_n, \sigma), n = 1, 2 \ldots\}$ and $\{(X'_n, \sigma'), n = 1, 2 \ldots\}$. They describe the reproduction by n successive cycles of (observation, treatment) or (treatment, observation) starting with one particles. The Markov chains (Y'_n) and (X_n) are conditioned on the delayed random environment of cycles:

$$d = \{ \text{ (observation, treatment) } = (\delta_i, \tau_{i+1}), i = 0, 1, \ldots, \quad \text{where} \quad \delta_0 = 0\},$$

$$d' = \{ \text{(treatment, observation) } = (\tau_i, \delta_{i+1}), i = 0, 1, \ldots, \quad \text{where} \quad \tau_0 = 0\}.$$

We shall denote it by $\{(X_n, d'), n = 0, 1, \ldots\}$ and $\{(Y'_n, d), n = 0, 1, \ldots\}$. We remark that for $n = 1, 2, \ldots$, the delayed cycles are equal in distribution to the "regular" one, since the r.v. $(\delta_i, \tau_{i+1}) \overset{D}{=} (\delta_i, \tau_i)$ and $(\tau_i, \delta_{i+1}) \overset{D}{=} (\tau_i, \delta_i)$, for $i = 1, 2, \ldots$, where "$\overset{D}{=}$" denotes the equality in distribution. The Markov chain $\{(Y'_n, d), n = 0, 1, \ldots\}$ represents the reproduction by $n - 1$ successive cycles of (observation, treatment) starting with $\mu_1(\tau_1)$. Respectively, $\{(X_n, d'), n = 0, 1, \ldots\}$ represents the reproduction by $n - 1$ successive cycles of (treatment, observation) starting with $\xi_1(\delta_1)$.

4.3 Alternating branching process with explicit immigration

We define the alternating branching process with explicit immigration by the sequence $(Z_n, W_n), n = 0, 1, 2, \ldots$ as follows:

$$Z_0 = 0 \quad \text{and} \quad W_0 = \eta_0,$$

$$Z_1 = \xi_1(\delta_1 | W_0) \quad \text{and} \quad W_1 = \mu_1(\tau_1 | Z_1) + \eta_1$$

$$Z_n = \xi_n(\delta_n | W_{n-1}) \quad \text{and} \quad W_n = \mu_n(\tau_n | Z_n) + \eta_n, \ldots.$$

We interpret the sequence $\{(W_n, \sigma), n = 1, 2, \ldots\}$ as a random control function describing state-dependent emigration and explicit immigration. The sequence given by $\{(Z_n, d'), \ n = 1, 2, \ldots\}$ describes the population before the control and the sequence $\{(W_n, \sigma), \ n = 1, 2, \ldots\}$ represents the controlled population accepted to splitting. In the particular case, when the observation time $\delta = 1$ we recognize the model of controlled Galton-Watson process with autoregressive control function, see [13].

Suppose $Z_n = k$, then the random control function

$$W_n = \mu_n(\tau_n|k) + \eta_n$$

is homogeneous by generation, depends on k and on the random environment. We have

$$W_n = W_n(k,\tau,\eta) \overset{D}{=} \sum_{j=1}^{k} \mu_{n,j}(\tau_n) + \eta_n,$$

where $\mu_{n,j}(.), j = 1,2,\ldots$ are independent copies of $\mu_n(.)$. The mean of random control function is linear by k, namely,

$$EW_n(k,\tau,\eta) = kE\mu(\tau) + E\eta.$$

Knowing the environment $\sigma = \{(\delta_i,\tau_i), i = 1,2,\ldots\}$, or the delayed environment $d = \{(\delta_i,\tau_{i+1}), i = 0,1,\ldots\}$ the reproduction by the n'th cycle of (observation, treatment)= $(\delta_n,\tau_n) \overset{D}{=} (\delta_n,\tau_{n+1}), n = 1,2,\ldots$ has random p.g.f.

$$\varphi_n(s,\sigma) = f(\delta_n, g(\tau_n,s)) \overset{D}{=} f(\delta_n, g(\tau_{n+1},s)) = \varphi_n(s,d), \text{ for } n = 1,2,\ldots,$$

$$\varphi_0(s,d) = f(0,g(\tau_1,s)) = g(\delta_1,s), \text{ since } \quad f(0,s) = s.$$

Indeed, one particle observed by the time δ_n and its offsprings tested by the time τ_n are transformed into ζ_n particles, such as

$$\zeta_n = \sum_{j=1}^{\xi_n(\delta_n)} \mu_{n,j}(\tau_n),$$

where $\mu_{n,j}(.), j = 1,2,\ldots$ are independent copies of $\mu_n(.)$. The random p.g.f.

$$\varphi_n(s,\sigma) = E(s^{\zeta_n} \mid \sigma), \quad n = 1,2,\ldots$$

are all independent and identically distributed. Knowing the environment $\sigma' = \{(\tau_i,\delta_i), i = 1,2\ldots\}$, or the delayed environment $d' = \{(\tau_i,\delta_{i+1}), i = 0,1,\ldots\}$, the reproduction by the n'th cycle of (treatment, observation)= $(\tau_n,\delta_n) \overset{D}{=} (\tau_n,\delta_{n+1}), n = 1,2,\ldots$ is given by

$$\zeta_n' = \sum_{j=1}^{\mu_n(\tau_n)} \xi_{n,j}(\delta_n),$$

and has random p.g.f.

$$\psi_n(s,\sigma') = g(\tau_n, f(\delta_n,s)) \overset{D}{=} g(\tau_n, f(\delta_{n+1},s)) = \psi_n(s,d'), \text{ for } n = 1,2,\ldots$$

and

$$\psi_0(s,d') = g(0,f(\delta_1,s)) = f(\delta_1,s), \text{ since } \quad g(0,s) = s.$$

Naturally, the delayed cycles are i.i.d. only for $n = 1, 2, \ldots$. The explicit immigration particles η_{n-1} arriving at the time $\sum_{i=1}^{n-1}(\delta_i + \tau_i)$ reproduce during the observation time period δ_n according to the MBP $\xi_n(.)$ and influence the population Z_n by $\xi_n(\delta_n|\eta_{n-1})$ particles having random p.g.f. $h(f(\delta_n, s))$.

Proposition 4.1. *If the random environments σ and d' consist of i.i.d. random cycles independent of the branching mechanisms $\xi(.)$ and $\mu(.)$, then the sequences (Z_n, d') and (W_n, σ) are Markov chains representing Galton-Watson processes with immigration in random environment. The sequence (Z_n, d') has random reproduction law $\psi_n(s, d')$ and immigration law $h(f(\delta_n, s))$. The sequence (W_n, σ) has random reproduction law $\varphi_n(s, \sigma)$ and immigration law h. The fundamental relations are*

$$E(s^{Z_{n+1}}|d') := F_{n+1}(s, d') = h(f(\delta_{n+1}, s))F_n(\psi_n(s, d'), d'), \quad F_0(s, d') = 1,$$

$$E(s^{W_{n+1}}|\sigma) := G_{n+1}(s, \sigma) = h(s)G_n(\varphi_{n+1}(s, \sigma), \sigma), \quad G_0(s, \sigma) = h(s).$$

$$F_{n+1}(s, d') = G_n(f(\delta_{n+1}, s), \sigma) \quad \textit{and} \quad G_n(s, \sigma) = h(s)F_n(g(\tau_n, s), d').$$

The independence of the evolution of the particles is manifested by the following equalities:

$$Z_{n+1} = \sum_{j=1}^{W_n} \xi_{n+1,j}(\delta_{n+1}) \quad \text{and} \quad W_n = \sum_{i=1}^{Z_n} \mu_{n,i}(\tau_n) + \eta_n.$$

The relation between the p.g.f. F_n and F_{n+1} describes the following equality:

$$Z_{n+1} = \sum_{i=1}^{Z_n} \sum_{j=1}^{\mu_{n,i}(\tau_n)} \xi_{n+1,j}(\delta_{n+1}) + \sum_{k=1}^{\eta_n} \xi_{n+1,k}(\delta_{n+1}).$$

4.4 Reproduction by *n* cycles

Denote by T the shift operator on the random environment, i.e. translation by one cycle, defined by $Td' = \{(\tau_i, \delta_{i+1}), i = 1, 2, \ldots\}$, $Td = \{(\delta_i, \tau_{i+1}), i = 1, 2 \ldots\}$, $T\sigma = \{(\delta_i, \tau_i), i = 2, 3, \ldots\}$ and $T\sigma' = \{(\tau_i, \delta_i), i = 2, 3 \ldots\}$. As the random environment consists of i.i.d. cycles, we have the following properties: The random environments σ, σ', d and d' are *stationary ergodic processes*, *exchangeable processes* and *uniformly mixing processes*, see [2, 3] for definition. Obviously, $Td' \overset{D}{=} \sigma'$ and $Td \overset{D}{=} \sigma$. The reproduction by the first n cycles is equal in distribution to the reproduction by n successive cycles, knowing the environments σ or σ'. Analytically, this property can be expressed by the composition of random p.g.f. to n cycles, defined by induction, as follows:

$$\varphi_1 \circ \varphi_2(s,\sigma) = f(\delta_1, g(\tau_1, f(\delta_2, g(\tau_2, s)))),$$

$$\varphi_1 \circ \varphi_2 \circ \varphi_3(s,\sigma) = f(\delta_1, g(\tau_1, f(\delta_2, g(\tau_2, f(\delta_3, g(\tau_3, s)))))),$$

and so on. Namely, let

$$\phi_n^{\rightarrow}(s,\sigma) := E(s^{Y_n}|\sigma) = \varphi_1 \circ \varphi_2 \circ \ldots \varphi_n(s,\sigma),\ n \geq 1;\ \phi_0^{\rightarrow}(s,\sigma) = s,$$

then for each $0 \leq s \leq 1$ the random probability generating function

$$\phi_n^{\rightarrow}(s,T\sigma) := \varphi_2 \circ \varphi_3 \circ \ldots \varphi_{n+1}(s,\sigma) \overset{D}{=} \phi_n^{\rightarrow}(s,\sigma).$$

In complete analogy, let

$$\psi_n^{\rightarrow}(s,\sigma') := E(s^{X'_n}|\sigma') = \psi_1 \circ \psi_2 \circ \ldots \psi_n(s,\sigma'),\ n \geq 1;\ \psi_0^{\rightarrow}(s,\sigma') = s,$$

then for each $0 \leq s \leq 1$ the random p.g.f.

$$\psi_n^{\rightarrow}(s,T\sigma') := \psi_2 \circ \psi_3 \circ \ldots \psi_{n+1}(s,\sigma') \overset{D}{=} \psi_n^{\rightarrow}(s,\sigma').$$

For the delayed random environments d and d' we can write in parallel

$$E(s^{X_n}|d') := f(\delta_1, \psi_{n-1}^{\rightarrow}(s,Td')) \overset{D}{=} f(\delta_1, \psi_{n-1}^{\rightarrow}(s,\sigma')),$$

$$E(s^{Y'_n}|d) := g(\tau_1, \phi_{n-1}^{\rightarrow}(s,Td)) \overset{D}{=} g(\tau_1, \phi_{n-1}^{\rightarrow}(s,\sigma)).$$

4.5 Criticality

Conditional mean of the reproduction by one cycle knowing the environment is given by the first derivative of the corresponding random p.g.f.: $\varphi'_n(1,\sigma)$ or $\psi'_n(1,\sigma')$, namely (see Proposition 3 in [13]),

$$E(\zeta_n|\sigma) = E(\zeta'_n|\sigma') = \exp\{u'(1)\delta_n + v'(1)\tau_n\}.$$

The main normalizing quantity is the conditional mean of the reproduction by n cycles

$$M_n = E(X'_n|\sigma') = E(Y_n|\sigma),$$

given by

$$M_n = \prod_{i=1}^{n} \varphi'_i(1,\sigma) = \prod_{i=1}^{n} \psi'_i(1,\sigma') = \exp\left\{\sum_{i=1}^{n} u'(1)\delta_i + v'(1)\tau_i\right\}.$$

The unconditional mean of the reproduction by one cycle (homogeneous by generation) is defined by the constant m as follows

$$m := E\varphi_n'(1,\sigma) = E\psi_n'(1,\sigma') = E\exp\{u'(1)\delta + v'(1)\tau\}.$$

Obviously, it is a Laplace transform of the mixture of random variables δ and τ. And it is well known, that it is not always finite. Then, let us consider the logarithm of the conditional mean, i.e. the sequence of i.i.d. random variables $\{u'(1)\delta_n + v'(1)\tau_n\}$.

Definition 4.1. Denote by

$$\gamma := E\log\varphi'(1,\sigma) = E\log\psi'(1,\sigma') = E\{u'(1)\delta + v'(1)\tau\}.$$

The reproductions by one cycle $\zeta = \zeta_n$ and $\zeta' = \zeta_n'$ will be labeled supercritical, critical or subcritical as $\gamma > 0$, $\gamma = 0$ or $\gamma < 0$, respectively.

This is the classical definition of criticality in random environment introduce by Athreya and Karlin, see [2, 3]. Now, we see that, if the observation and treatment times belong to the positive stable law, this definition of criticality is not convenient. And, we arrive to another criterium of criticality:

Definition 4.2. (Criticality by Afanasiev, Geiger, Kersting and Vatutin) The properties of the reproduction by n cycles are determined by its associated random walk $S = (S_0, S_1, \ldots)$, having initial state $S_0 = 0$ and increments $\{u'(1)\delta_n + v'(1)\tau_n\}$, i.e.

$$M_n = \exp\{S_n\}.$$

We assume that the r.v. $\{u'(1)\delta + v'(1)\tau\}$ is a.s. finite, but we do not assume that it has finite mean. According to the fluctuation theory of random walks, we distinguish three different types of BPRE, see [1, 23].

(a) Supercritical branching process with random environment corresponds to the random walk S with positive drift, which means that

$$\lim_{n\to\infty} S_n = \infty \quad a.s. \quad \text{and} \quad M_n \to \infty \quad a.s..$$

(b) Subcritical branching process with random environment corresponds to the random walk S with negative drift, having

$$\lim_{n\to\infty} S_n = -\infty \quad a.s. \quad \text{and implying} \quad M_n \to 0 \quad a.s..$$

(c) Critical branching process with random environment is characterized by the oscillating random walk, meaning that

$$\limsup_{n\to\infty} S_n = \infty \quad a.s. \quad \text{and} \quad \liminf_{n\to\infty} S_n = -\infty \quad a.s.$$

Example 4.1. If the observation and treatment times, being mutually independent, follow exponential distributions with parameters α and β respectively, then for $\alpha > u'(1)$,

$$m = \frac{\alpha\beta}{(\alpha - u'(1))(\beta - v'(1))}, \quad \text{and} \quad \gamma = \frac{u'(1)}{\alpha} + \frac{v'(1)}{\beta}.$$

The unconditional means of the BPRE (Y_n, σ) and (X'_n, σ') are given by:

$$E(Y_n) = E(X'_n) = m^n.$$

The Jensen's inequality provides $m \geq e^\gamma$ always.

Example 4.2. If the random environment σ is generated by the first order exponential autoregressive sequence EAR(1) then the random variables $\{u'(1)\delta_n + v'(1)\tau_n\}$ are identically distributed but dependent r.v. [14]. Denote by σ_n the length of the cycles

$$\sigma_n = \delta_n + \tau_n, n = 1, 2\ldots.$$

Suppose that the treatment times τ_n are i.i.d. non-negative random variables. We consider the model when the observation time of the n-th cycle is a deterministic part of the length of the previous $(n-1)$-th cycle, i.e.

$$\delta_n = \rho\sigma_{n-1}, 0 < \rho < 1, n = 1, 2\ldots$$

The lengths of the cycles $\sigma_n, n = 1, 2, \ldots$ constitute the sequence of identically distributed but dependent random variables with exponential distribution function $B(.)$ and intensity β. The observation times $\delta_n, n = 1, 2, \ldots$ form the sequence of identically distributed but dependent random variables with exponential distribution function $A(.)$ and intensity $\alpha = \frac{\beta}{\rho}$. The treatment times $\tau_n, n = 1, 2, \ldots$ form the innovation sequence for the EAR(1) of the i.i.d. random variables with degenerate exponential distribution $C(.)$ having the atom of mass ρ at 0 and density $B(dx) = \beta e^{-\beta x} dx$ with probability $(1-\rho)$. Denote by $\alpha_k(n)$ the following deterministic constants:

$$\alpha_k(n) = u'(1) \sum_{j=1}^{n-k} \rho^j + v'(1), \quad k = 1, 2\ldots, n-1,$$

$$\alpha_0(n) = u'(1) \sum_{j=1}^{n} \rho^j, \quad \alpha_n(n) = v'(1).$$

For the random environment σ generated by the EAR(1) we have:

$$S_n = \log M_n = \sigma_0 \alpha_0(n) + \sum_{k=1}^{n} \tau_k \alpha_k(n),$$

where σ_0 has p.d.f. B(.) and $\tau_k, k = 1, 2, \ldots$ have degenerate p.d.f. C(.). Suppose that $\beta - \alpha_0(n) > 0$ and $\beta - \alpha_k(n) > 0, k = 1, 2, \ldots$for any $\rho \in (0, 1)$, then

$$E(M_n) = \frac{\beta}{\beta - \alpha_0(n)} \prod_{k=1}^{n} \left\{ \rho + \frac{\beta(1-\rho)}{\beta - \alpha_k(n)} \right\}.$$

If $\gamma = 0$ and if $\beta > \max(u'(1), -v'(1))$ then the following limit exists

$$\lim_{n\to\infty} EM_n = \frac{\beta^2}{\beta^2 - (v'(1))^2}.$$

Example 4.3. Suppose, the length of the cycles is deterministic, say $\delta_n + \tau_n = 1$. Consider the particular case when $\delta_n, n = 1, 2, \dots$ are independent copies of the random variable δ having $Beta(\alpha, \beta)$ distribution with parameters (α, β). Then treatment time is given by $\tau_n = 1 - \delta_n$. Knowing the environments σ or σ' the reproductions by one cycle are defined by the random probability generating functions:

$$\varphi_n(s,\sigma) = f(\delta_n, g(1-\delta_n, s)) \quad \text{and} \quad \psi_n(s,\sigma') = g(1-\delta_n, f(\delta_n, s)).$$

The classical critical parameter in random environment is

$$\gamma = \frac{\alpha u'(1) + \beta v'(1)}{\alpha + \beta}.$$

4.6 Stationary distribution in random environment

Suppose the random environments σ, σ', d and d' are created by i.i.d. random variables of observation and treatment times. Consider the model of alternating branching processes with explicit immigration. Then, we announce the following results. The complete proofs will be done in a forthcoming paper.

Theorem 4.1. *The random p.g.f.* $G_n(s,\sigma)$ *and* $F_n(s,d')$ *can been expressed by the reproduction on i cycles* $(i = 1, 2, \dots n)$ *as follows:*

$$G_n(s,\sigma) = \prod_{i=0}^{n} h(\phi_i^{\rightarrow}(s,\sigma)),$$

$$F_n(s,d') = \prod_{i=0}^{n} h \circ f(\delta_{n-i}, \psi_i^{\rightarrow}(s,\sigma')).$$

Theorem 4.2. *If* $\gamma < 0$ *then for all* $0 < s < 1$ *we have*

$$\lim_{n\to\infty} \phi_n^{\rightarrow}(s,\sigma) = 1,$$

$$\lim_{n\to\infty} \psi_n^{\rightarrow}(s,\sigma') = 1.$$

In a general setting this convergence of random p.g.f. had been announced by Athreya and Karlin [3].

Theorem 4.3. *Suppose, there exists the logarithmic moment of the immigration particles:*

$$E \log \eta^+ < \infty.$$

If $\gamma < 0$ *then for all* $0 < s < 1$ *we have*

$$\lim_{n\to\infty} G_n(s,\sigma) = G(s,\sigma) \quad \textit{and} \quad G(s,\sigma) = G(f(\delta_1, g(\tau_1, s)), \sigma)h(s),$$

$$\lim_{n\to\infty} F_n(s,d') = F(s,d') \quad \textit{and} \quad F(s,d') = F(g(\tau_1, f(\delta_1, s)), d')h(f(\delta_1, s)).$$

Moreover, stationary distributions before control and after control are related by the following

$$G \circ f = F \quad \textit{and} \quad F \circ g = G.$$

4.7 Unconditional probability generating functions

Consider the averaging over one cycle and compare it with the averaging over entire environment. Suppose the observation times δ_n and treatment times τ_n, being mutually independent, have probability distribution functions $A(.)$ and $B(.)$, respectively. Then the unconditional probability generating functions to the reproduction by one cycle are defined by the following integrals:

$$\bar{\varphi}(s) := Ef(\delta, g(\tau, s)) \quad \text{and} \quad \bar{\psi}(s) := Eg(\tau, f(\delta, s)).$$

Let

$$\bar{f}(s) := Ef(\delta, s) = \int f(x,s)A(dx) \quad \text{and} \quad \bar{g}(s) := Eg(\tau, s) = \int g(y,s)B(dy).$$

The Jensen's inequality and convexity of the p.g.f. provide the inequalities

$$\bar{\varphi} \geq \bar{f} \circ \bar{g} \quad \text{and} \quad \bar{\psi} \geq \bar{g} \circ \bar{f}.$$

Suppose $Z_n = k$ then the unconditional probability generating function of the control function $W_n(k, \tau, \eta)$ is given by:

$$Es^{W_n(k,\tau,\eta)} = h(s) \int [g(y,s)]^k B(dy) \neq h(s)\bar{g}(s)^k.$$

The transition from one cycle to another has unconditional p.g.f.:

$$E(s^{Z_{n+1}} | Z_n = k) = \int h(f(x,s)) \int [g(y, f(x,s))]^k B(dy)A(dx).$$

We can create a Galton–Watson process $\bar{Z}_n$ with reproduction defined by averaging over one cycle: $\bar{\varphi}(s)$. Moreover, take the averaging over the n-th cycle and denote by

$$Z^*_{n+1} = \bigcup_{\delta_n,\tau_n} \sum_{j=1}^{Z^*_n} \zeta_{n,j}$$

the transition from one cycle to the next one. Its probability generating function holds the relation:

$$F^*_{n+1} = \int F^*_n(f(x,g(y,s))A(dx)B(dy).$$

Obviously, if we interpret the values of the observation and treatment times as a type of control, we recognize the analog of the multi-type random control function introduces by del Puerto and Yanev, see [6, 7]. The processes Z_n, $\bar{Z}_n$ and Z^*_n have the same parameter m as unconditional expectation of reproduction.

4.8 Feed-back control

Stationary distributions can be obtained also by feed-back control if the observation time δ depends on the observed branching process $\xi(t)$ without explicit immigration. It is well known that in a growing population the rate at which jumps occur increases with time. A remarkable time transformation show that the path of MBP is linked to the path of a compound Poisson process. Let $\xi(t), t \geq 0$, be a supercritical branching process having infinitesimal generating function $u(s) = a(U(s) - s)$, with $0 < a < \infty$, $U(0) = U'(0) = 0$, and $U'(1) < \infty$. Suppose that the observation time periods $\delta_n, n = 1,2,\dots$ depend on the observed branching mechanism $\xi(t)$. Namely, consider observation time δ defined by the additive functional of total progeny of the supercritical MBP process $\xi(t)$:

$$\int_0^\delta \xi(x)dx = y(\delta).$$

The inverse function of the additive functional is correctly defined:

$$y^{-1}(r) = \inf\{\delta : y(\delta) = r\}.$$

Then the value of the MBP $\xi(t)$ at the random time $\delta = y^{-1}(r)$ is represented by:

$$\xi(y^{-1}(r)) = C(r),$$

where $C(r)$ is a compound Poisson process with initial condition $C(0) = 1$. The probability generating function of $C(r)$ is given by:

$$Ee^{C(r)-C(0)} = e^{ar(\frac{U(s)}{s}-1)}.$$

The path of the compound Poisson process $C(r)$ has jumps whose distribution is supported in $(-1,0,1,2,\dots)$, stopped at the first instant that it hits zero. When $\xi(0) = 1$

the first jump of the MBP $\xi(t)$ occurs at the random time T_1 exponentially distributed with parameter a. Let the value of the MBP $\xi(t)$ at the first jump times is $x = \xi(T_1)$. Obviously, the value of the additive functional $y(T_1) = T_1$. Let T_2 be the time of the second jump of $\xi(t)$, then condition on the history $(\xi(t) : t \leq T_1)$ the random variable $T_2 - T_1$ is exponentially distributed with parameter ax as the minimum of x independent exponential random variables, each with parameter $a > 0$, and so on.

Consider the model of alternating branching process (X_n, Y_n) in random environment Σ defined as follows. Suppose the reaction starts with one particle observed by the random time δ_0 such that $\xi(\delta_0) = C(r)$. Then we continue the observation till $\xi(\delta_0 + \delta_1) = C(r+z) = (X_1, \Sigma)$. Following the results of Steutel and Van Harn (see [20, 21]) we can choose the treatment time τ_1 exponentially distributed with parameter β such that:

$$(Y_1, \Sigma) = C(r) = \theta^{\frac{1}{\beta}} \otimes C(r+z), \tau = -\log \theta^{\frac{1}{\beta}},$$

where the random variable θ is uniformly distributed on the interval $(0,1)$. Define the random environment

$$\Sigma = \{ \text{ (observation, treatment) } = (\delta_i, \tau_i), i = 1, 2, \ldots\},$$

by means of i.i.d. copies of δ_1 and τ_1. The alternating branching process (X_n, Y_n) with initial condition $Y_0 = C(r)$ is no longer transient because the observation time depends on the observed branching mechanism. This construction leads to the stationary distribution at the first cycle (δ_1, τ_1). Namely, knowing the environment Σ we have :

$$(X_n, \Sigma) = C(r+z) \quad \text{and} \quad (Y_n, \Sigma) = C(r), n = 1, 2, \ldots.$$

This way we realize a feed-back control at each observation time period. Relatively to the population created by the subcritical process $\mu(t)$, the influence of $C(r+z)$ on the successive cycles is equivalent to the stationary immigration.

Theorem 4.4. *In the feed-back control model the stationary distribution is of the form*

$$C(.) = S_\varepsilon(T(.)),$$

where $S_\varepsilon(.)$ is a $g(t,s)$-stable with exponent ε integer-valued process and $T(.)$ is a gamma Lévy process with shape parameter $\frac{1}{z}$, the so called gamma-subordinator. The constants $\{\varepsilon, r, z, -v'(1)\}$ are related by:

$$\varepsilon = \beta \frac{z}{r} \leq -v'(1).$$

The complete proof will be done in the forthcoming paper. For the convenience we quote here the relevant definitions. The real valued random variable Z is said to be self-decomposable if for every $\theta \in (0,1)$ there is a random variable η such that $Z = \theta Z + \eta$, where Z and η are independent random variables. The non-degenerate self-decomposable distributions are known to be absolutely continuous. It is clear that a non-degenerate discrete distribution cannot be self-decomposable, but it can be $g(t,s)$-self-decomposable.

Definition 4.3. Let $g(t,s)$ be the p.g.f. of a subcritical MBP $\mu(t)$. An integer valued random variable Z is said to be $g(t,s)$-self-decomposable if for every $\theta \in (0,1)$ there is a random variable η such that $Z = \theta \otimes Z + \eta$, where Z and η are independent random variables and $\otimes$ is the fractional thinning operator representing the " discrete multiplication".

Definition 4.4. Let $g(t,s)$ be the p.g.f. of a subcritical MBP $\mu(t)$. An integer valued random variable Z is said to be $g(t,s)$-stable with exponent $\varepsilon > 0$ if independent random variables $z_1, z_2, \ldots$ exist being all independent copies of Z such that for all $n \in N$,

$$Z = \theta \otimes (z_1 + z_2 + \ldots + z_n) \quad \text{with} \quad \theta = n^{-\frac{1}{\varepsilon}}.$$

If Z is $g(t,s)$-self-decomposable then Z and η are infinitely divisible random variables. Moreover, if Z is $g(t,s)$-stable then Z is $g(t,s)$-self-decomposable. The stationary solution of equation

$$\theta \otimes C(r+z) = C(r)$$

has been studied by Van Harn, Steutel [21], and Pakes [16]. They investigated the properties of the limiting distribution in the MBP with immigration to be self-decomposable and infinitely divisible.

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Part II
Special Branching Processes

5

Approximations in population-dependent branching processes

Fima C. Klebaner

Abstract We consider models of population size dependent branching processes with the feature that they are supercritical until population reaches some threshold K, near critical around that value, and subcritical above it. Although such population die out with probability one, their time to extinction is large. We show that this time is exponential in K. Approximations to the populations size in various domains are given, and a problem of small initial population size is discussed. From a technical point of view, analysis of such processes involves techniques of density dependent models as small random perturbations of dynamical systems, and size-dependent bounds.

Mathematics Subject Classifications (2000): 60J80, 60F10

Keywords: population models, extinction, size-dependence, density-dependence, large deviations, exit times, time to extinction, random perturbations.

5.1 Introduction and a motivating example

We consider here some classes of branching processes with reproduction depending on the population size z. Typically such processes were termed population-size-dependent, e.g. [5], to differentiate them from models where reproduction depends on the size through population density z/K, where K is some large number (carrying capacity or threshold). At first glance it seems such difference is not important, since K is a fixed quantity. However, it turns out that when it is taken as a parameter, analysis simplifies when K is large, where certain deterministic dynamical systems emerge as first order approximations to the population process. In order to invoke

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such approximation the initial population size should also be large, as it must be proportional to K. This assumption is not satisfied in some biological models considered here. The reason we use population-dependent in the title is because our analysis shows that the same process can be approximated as a density-dependent process in some domain, and as a population-size-dependent process in another domain. We present here analysis for such models and pose unsolved yet questions about their approximations.

We describe the organization of the paper next. After the definition of the processes under consideration, we give the basic decomposition of the process into a predictable component, and uncorrelated martingale difference component. Together with the original process we also consider the re-scaled version, which we call the population density process, and obtain a similar decomposition for those. This is done in Sect. 5.2. It follows from this representation that on the scale of densities the process behaves as a randomly perturbed dynamical system with a small noise. To appreciate the effect small noise has on the dynamics, we describe briefly the behaviour of the dynamical system without noise. Without noise the system is attracted to one of its stable fixed points, and never dies out provided it starts with a positive initial population. But due to noise it will die out for sure. However, the event of extinction is a particular event of exit from a domain of attraction of a stable fixed point, and as such is explained by uncharacteristically large values occurring in the small noise. Therefore, if the carrying capacity is large, extinction can be analyzed by the Large Deviations techniques and is done in Sect. 5.3. In Sect. 5.4 we look at the typical size of the population conditioned on its survival, ie prior to extinction. Section 5.5 considers the case of small initial populations. The approximations developed previously are not informative for this case and new results are given. These include a bound on the probability becoming extinct before reaching high level as well as time to reach high level. Finally, in Sect. 5.6 we give a qualitative description of the process before its ultimate extinction.

Some of the theory is rather technical. So for the sake of ease of exposition we choose to present and follow an example. This motivating example is a binary splitting in discrete time ($n = 0, 1, 2, \ldots$) with the splitting probability

$$p = \frac{K}{K+z},$$

where z is the size of the population. At each time n, a particle either splits into two with probability p or dies. This generic random variable is denoted by ξ. Clearly, the splitting probability is a function of population size, $p = p(z)$, and denote the mean of offspring distribution by

$$m(z) = E\xi = 2p(z).$$

This process arises naturally in a model for polymerase chain reaction, see [11, 12], and [3], as well as other models. In this model, whenever $z < K$ then $p > 0.5$ and reproduction is supercritical, whenever $z = K$ then $p = 0.5$ and reproduction is critical, and whenever $z > K$ then $p < 0.5$ and reproduction is subcritical. Let Z_n

denote the population size at time n. Then

$$Z_{n+1} = \sum_{i=1}^{Z_n} \xi_i = 2\sum_{i=1}^{Z_n} \xi_i/2,$$

where $\xi_i/2$ are i.i.d zero-one random variables. Hence conditionally on Z_n, Z_{n+1} is twice the Binomial distribution with parameters Z_n and $p(Z_n)$,

$$Z_{n+1} \sim 2Bin(Z_n, p(Z_n)).$$

For this example, as well as in more general models of population-size-dependent processes, Z_n is a Markov Chain on nonnegative integers with 0 the only absorbing state. Since $E\xi(z) = m(z) > 1$ only for finitely many z, extinction is certain, eg. [5], Corollary to Theorem 1.1, p. 34. But for large K's the time to extinction is large. The suggested approximations explains why it is so, and also describe what happens to the process before extinction. It is important to note that we are interested in the population size process Z_n but at various stages of population development it is convenient to look at and develop approximations for the density process $X_n = Z_n/K$.

5.2 A Representation of the process and its re-scaled version

Here we give an insightful representation of the processes we consider. We have, obviously,

$$Z_{n+1} = E(Z_{n+1}|Z_n) + (Z_{n+1} - E(Z_{n+1}|Z_n)). \tag{5.1}$$

The term

$$E(Z_{n+1}|Z_n) = Z_n E(\xi) = Z_n m(Z_n)$$

represent dynamics and the term

$$Z_{n+1} - E(Z_{n+1}|Z_n) = \sum_{i=1}^{Z_n} \xi_i - E(\xi_i)$$

is a martingale difference and represents the noise. Hence

$$Z_{n+1} = Z_n m(Z_n) + (Z_{n+1} - E(Z_{n+1}|Z_n)). \tag{5.2}$$

Introduce the re-scaled process, or the density process

$$X_n = \frac{Z_n}{K} \tag{5.3}$$

and note that the splitting probability is in fact a function of the density z/K

$$p = \frac{K}{K+z} = \frac{1}{1+x}, \tag{5.4}$$

with $x = z/K$. In view of representation 5.2 the density process has a representation

$$X_{n+1} = X_n m(X_n) + \frac{1}{K}\sum_{i=1}^{KX_n}(\xi_i - m(X_n)). \tag{5.5}$$

5.2.1 Re-scaled process: Dynamics plus small noise

Let $f(x) = xm(x)$. Then

$$X_{n+1} = f(X_n) + \frac{1}{\sqrt{K}}\eta_{n+1}, \text{where } \eta_{n+1} = \frac{1}{\sqrt{K}}\sum_{i=1}^{KX_n}(\xi_i - m(X_n)). \tag{5.6}$$

$$E(\eta_{n+1}) = 0,\ \ Var(\eta_{n+1}) = O(1),$$

and under mild conditions η_n converges to Normal as $K \to \infty$. In fact as a process $\{\eta_n\}$ converge to a Gaussian process with a computable covariance function, [6].

5.2.2 Dynamics without noise in binary splitting

In binary splitting

$$f(x) = xm(x) = \frac{2x}{1+x},\ \ x \geq 0.$$

When noise is zero, the dynamics is

$$x_{n+1} = f(x_n).$$

For any $x_0 \geq 0$, there exists a limit

$$\lim_{n\to\infty} x_n \in \{0,1\} - \text{the set of fixed points of } f.$$

If $x_0 = 0$ then $x_n \equiv 0$, but for any $x_0 > 0$, $\lim_{n\to\infty} x_n = 1$.

Proof. The function $f : R^+ \to [0,2)$. $f(x) < 1$ for $x < 1$ and $f(x) > 1$ for $x > 1$. For any $0 < x_0 < 1$, $x_1 = f(x_0) > x_0$ and $x_1 < 1$. Hence the sequence of iterates is monotone increasing and converges. The limit must be a fixed point, so it is 1. For any $x_0 > 1$, $x_1 = f(x_0) < x_0$, because $f(x) < x$ in this region. Also $x_1 > 1$. Hence the sequence of iterates is monotone decreasing and converges. The limit must be a fixed point, and since they are all greater than 1, it must be 1. The point 1 is globally attracting (even though $f'(1) = 1$) and 0 is repelling ($f'(0) = 2$). Hence for any initial point but 0, $\lim_{n\to\infty} x_n = 1$. $\square$

5.3 Time to extinction

Extinction time of Z_n and $X_n^K = Z_n/K$ is clearly the same. Provided $X_0^K \to x_0 > 0$, for large K, the starting point is in the domain of attraction of the stable fixed point 1. According to dynamics the process gets pushed towards 1, but due to noise it will exit the neighbourhood of 1. The exit when it occurs is due to uncharacteristically large value of the noise, or as it is known a large deviation. In fact, it is much more likely that a sequence of uncharacteristically large values of noise, all lined up in the same direction will occur rather than a one huge value that will take the process outside the domain of attraction. Large deviations will take the process out of this domain. Time for it to happen is exponential in K. This is by the extension of the Freidlin-Wentzell theory, eg. [4], in branching context [7]. In our example, these large deviations events occur when many particles die out simultaneously without leaving offspring.

More precisely about a Domain of attraction and exit from it. A fixed point x^* is attracting (stable) if there is an interval I around it so that for all $x \in I$ $f^{(n)}(x) \to x^*$. The domain of attraction of x^* is a largest such set.

Theorem 5.1 [7]. *Let* $T^K = \inf\{n : X_n^K \notin B_{x^*}, X_0^K = x_0 \in B_{x^*}\}$ *be the first exit time from the domain of attraction of* x^*. *Then there is a constant c, which does not depend on the initial point* x_0, *and K, such that for any* $\delta > 0$

$$P(e^{K(c-\delta)} < T^K < e^{K(c+\delta)}) \to 1, \text{ as } K \to \infty.$$

So roughly,

$$T^K \approx e^{cK}.$$

All we can say about time to extinction in general is that it is larger than the time to exit the domain of attraction.

5.4 The size of the population after a long time provided it has survived

In this section we look at approximations when the time n goes to infinity for a fixed parameter K. It turns out that the limiting behaviour is possible to describe for large K.

Define

$$\rho^K(A) = \lim_{n\to\infty} P(X_n^K \in A | X_n^K > 0).$$

This is so-called the quasi-stationary distribution of X_n^K.

Using a Theorem of Harris 1989, [1] (an analogue of the Perron-Frobenius theorem) the limit exists and satisfies

$$\rho^K(A) = R^{(K)} \int P^{(K)}(x,A)\rho^K(dx),$$

for some number $R^{(K)} > 1$. Here $P^{(K)}(x,A)$ denotes the transition probability kernel

$$P^{(K)}(x,A) = P(X_1^K \in A | X_0^K = x).$$

It is easy to see that any weak limit

$$\lim_{K\to\infty} \rho^K(A) = \rho(A)$$

is invariant measure for f, ie

$$\rho(A) = \rho(f^{-1}(A)).$$

Moreover, in our example ρ is invariant for f if and only if

$$\rho(0) + \rho(1) = 1.$$

Finally, the measures ρ^K converge weakly to the measure $\rho(\{1\}) = 1$ concentrated on the stable fixed point.

These results were proven in [9], and a particular case of a more general set up when the function f can have many fixed points, none of them attracting, but will have an attracting cycle. Results showing convergence to the measure on the attracting cycle are given in [8, 2, 10]. (Chaotic case was solved in [4] under the Axiom A assumption on f. In [10] a condition similar to Axiom A for discrete dynamical systems was given.)

Applied to our process these result say that if after a long time our process has survived then the population size will be in the vicinity of K, ie. if given a large n, $Z_n > 0$, then $Z_n \approx K$.

5.5 Case of small initial population

In this section we address the question as to what happens when the process starts with one particle $Z_0 = 1$. If the initial population size is $Z_0 = 1$ (or for that matter any fixed number not depending on K) then $X_0^K = 1/K \to 0$ and according to above approximation Theorem 5.1 the processes

$$X^K \to 0.$$

But in this case the limiting (in K) process does not give a useful approximation to the actual process. As we need behaviour as $n \to \infty$ for a large but fixed K. What happens here is that the initial point is small and goes to 0 as $K \to \infty$, but for a fixed K it is positive and dynamics takes it to 1. What is a correct approximation to trajectories in this case? To answer this question note that because of absorbtion at zero, we can have extinction before we reach a level comparable to K, say aK, for some $a \in (0,1)$.

5.5.1 Probability of becoming large and time for it to happen

Here we give a result on the probability of extinction before reaching level aK.

Theorem 5.2. *The probability of becoming extinct before reaching level dK does not exceed d^{Z_0}.*

Proof. As long as $z < Kd$ the probability of splitting is greater than the $K/(K+aK) = 1/(1+a)$. It is clear therefore that the required probability is smaller than the corresponding probability in the GW binary splitting $\hat{Z}$ with probability of no offspring $a/(1+a)$. It is clearly smaller than extinction $P(\hat{Z}_n \to 0) = \hat{q}$.

$$\frac{a}{1+a} + \frac{1}{1+a}\hat{q}^2 = \hat{q},$$

which is a. □

Next, we look at how long it takes to reach level aK.

Theorem 5.3. *The time to reach level aK, τ_{aK} satisfies asymptotic as $K \to \infty$*

$$\tau_{aK} = O\Big(\frac{\log K}{\log 2/(1+a)}\Big).$$

Proof. The process grows faster than the GW binary splitting with the smallest splitting probability in the range $[1, aK]$, which is $1/(1+a)$. Hence the time it takes for it to reach level aK is shorter that in the corresponding GW binary splitting with the mean $\hat{m} = 2/(1+a)$. Clearly, $Z_{\tau_{aK}} \approx aK$. Replacing the variable on the left by is mean we have an approximation $\hat{m}^{\tau_{aK}} \approx aK$, hence the result. □

Remark 5.1. The probability of extinction before reaching a certain level in the Galton-Watson process does not seem to be known. Note that such probability is well known for diffusion models, and is obtained by martingale arguments (optional stopping of some martingales) in terms of the scale function. It is remarkable that for Galton-Watson process there is no mention of it in the literature. Use of the same techniques as for diffusions produces only a bound.

5.6 Behaviour before extinction

Here we give qualitative description of our process before it becomes extinct, having started with a number of particles below level aK, in particular a single particle.

The probability of early extinction before reaching aK is less than a. If the process does not extinct it will reach level aK after time τ^1 of order $\log K$. After that time the process will stay above aK for time T^1, which is exponential in K, of order e^{cK}, for some constant c. After that time the process will drop below the level aK. Denote by d_i, τ^i for the i-th time the process below aK the value and the time spent below respectively, and by u_i, T_i the value it takes and time it spends above that level. By Markov property, conditional on d_i's and u_i's the random variables τ^i's and T_i's are independent. τ^i's are intervals of order $\log K$, but during one of such time absorbtion may occur, whereas intervals T_i's are of exponential in K length with extinction possible with extremely low probability. Approximately, the process of survival has the structure of independent trials where the probability of survival is rather large (1 minus the extinction probability), but varies somewhat each time since every time the population falls below aK it is different. Overall, since a sum of quantities of order exponential in K is again exponential in K, we conclude that the survival time is exponential in K.

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6

Extension of the problem of extinction on Galton–Watson family trees

George P. Yanev

Abstract We review the existing and present new results on certain subtrees of the Galton-Watson family tree. For a positive integer N, define an N-ary subtree to be the tree of a deterministic N-splitting, rooted at the ancestor. Dekking (Amev. Math. Monthly 98:728–731, 1991) raised and answered the question how to compute the probability for a branching process to possess the binary splitting property, i.e., $N = 2$. Pakes and Dekking (J. Theor. Probab. 4:353–369, 1991) studied the general situation when $N \geq 2$. Surprisingly, the case $N \geq 2$ is studied so late, whereas the question for extinction of a branching process, i.e., non-existence of an infinite unary subtree ($N = 1$) has been studied extensively over the past 120–150 years.

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6.1 Introduction

Let $\{Z_n\}$ be a Bienaymé–Galton–Watson process with offspring probability generating function (pgf) $f(s) = \sum_{k=0}^{\infty} p_k s^k$. Suppose $Z_0 = 1$ and as usual assume $p_k < 1$ for all k, and also that $p_k > 0$ for some $k > N$ where N is an integer. Galton [3] formulated his famous problem of "the decay of the families of men", which is to determine the probability that the process $\{Z_n\}$ becomes extinct, i.e., $Z_n = 0$ for some $n \geq 1$. Let us consider the family tree of $\{Z_n\}$ (see [4], pp. 122–125 for a formal description). Note that the family tree is finite if and only if the process becomes extinct. As it was pointed out by Dekking in [2], the problem of non-extinction can be formulated as "with what probability does the family tree contain the (infinite)

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unary tree as a subtree, rooted at the root of the family tree?" Then he asked the question, "with what probability does the family tree of a branching process contain the (infinite) binary tree as a subtree, rooted at the root of the family tree (binary splitting property)?" Here the binary tree is the family tree associated to the branching process with offspring distribution given by $p_2 = 1$. It is surprising that this extension of the classical question for extinction of a branching process is studied so late, whereas the latter has been studied extensively over the past 120–150 years.

In this paper we study characteristics of certain subtrees of the family tree of $\{Z_n\}$. We call two subtrees disjoint if they do not have a common node different from the root of the entire tree. In addition, we consider only rooted and complete subtrees, i.e., subtrees rooted at the ancestor and being family trees of the deterministic branching process with pgf $f(s) = s^N$. Let the random variable V_N be the number of complete infinite and disjoint N-ary subtrees of a branching tree, rooted at the ancestor. The event $\{V_1 > 0\}$ implies that there is at least one infinite unary subtree and thus the process would never die. The event $\{V_2 > 0\}$ can be interpreted as the set of process' trajectories where the family tree grows faster than binary splitting. Dekking [2] computes the probability for a branching process to possess the "binary splitting property", i.e., $P(V_2 > 0)$. Pakes and Dekking [8] study the general situation when $N \geq 2$. Mutafchiev [7] proves limit results for the survival probability of an N-ary subtree. In [11], Yanev and Mutafchiev study the distribution of V_N.

In Sects. 6.2 and 6.3 we review some existing results. In Sect. 6.5 we prove a limit theorem for the ratio of the conditional expectations of Z_n, provided that an infinite N-ary and an unary subtree exist. Sections 6.6, 6.7 and 6.8 cover the particular cases of geometric, Poisson, and "one-or-many" offspring distributions. There we discuss corollaries of the general results as well as some numerical illustrations. Finally, in the concluding remarks, we point out some links between the problem of existence of an infinite complete N-ary subtree and other research results.

6.2 Critical phenomenon

Define $T_2 - 1$ to be the maximum height of a complete binary subtree rooted at the ancestor. Note that $T_2 = 0$ if $Z_1 < 2$. Also, $T_1 - 1$ is the maximum height of a unary subtree rooted at the ancestor and thus T_1 is the extinction time of $\{Z_n\}$. We start this section with a theorem about the probability $\gamma_2 = P(T_2 < \infty)$ that there is no infinite complete binary subtree, i.e., the growth is slower than binary splitting. Notice that $\gamma_1 = P(T_1 < \infty)$ is the probability that there is no infinite unary subtree, i.e., the extinction probability of the process.

The following result is fundamental. We present the original Dekking's proof.

Theorem 6.1 [2]. *The probability γ_2 is the smallest root in $[0,1]$ of the fixed point equation*

$$x = g_2(x), \tag{6.1}$$

where

$$g_2(x) = f(x) + (1-x)f'(x).$$

Proof. For $n = 1, 2, \dots$ let $\gamma_2(n)$ be the probability that the family tree associated to $\{Z_n\}$ does not contain a complete binary subtree of height n rooted at the ancestor. If the family tree has k nodes at level 1 (i.e., $Z_1 = k$), then it does not contain a complete binary subtree of height $n+1$ iff $k = 0$ or 1, or either all or all but one of the k subtrees rooted at these nodes do not contain a complete binary subtree of height n. Therefore one has

$$\begin{aligned}\gamma_2(n+1) &= p_0 + p_1 + \sum_{k=2}^{\infty}[\gamma_2^k(n) + k\gamma_2^{k-1}(n)(1-\gamma_2(n))]p_k \\ &= p_0 + p_1 + f(\gamma_2(n)) - p_0 - p_1\gamma_2(n) + (1-\gamma_2(n))(f'(\gamma_2(n) - p_1),\end{aligned}$$

and hence

$$\begin{aligned}\gamma_2(n+1) &= f(\gamma_2(n)) + (1-\gamma_2(n))f'(\gamma_2(n)) \\ &= g_2(\gamma_2(n)).\end{aligned} \tag{6.2}$$

Therefore, $\gamma_2 = \lim_{n\to\infty}\gamma_2(n)$ satisfies (6.1). Furthermore, if we put $\gamma_0 = 0$, then (6.2) is also true for $n = 0$. Since $g_2'(x) = (1-x)f''(x)$ is nonnegative, $g_2(x)$ is increasing and it follows that $\gamma_2 = \lim_{n\to\infty} g_2^n(0)$ is the smallest root in $[0,1]$ of (6.1). □

Note that a similar recurrent argument can be applied to derive the equation $x = f(x)$ for the probability of extinction γ_1 (see Kemeny and Snell [6], pp. 80–81).

It turns out that no simple expression involving the moments of the offspring distribution can be found that will yield whether $\gamma_2 = 1$ or not. In fact, Dekking [2] shows (see Theorem 6.2) by a counterexample that γ_2 cannot be a continuous function of the moments of the offspring distribution, nor of any other parameter of the process which depends continuously on p_k, $k = 0, 1, 2, \dots$.

In [8], Theorem 6.1 is generalized to the case of the presence of a complete N-ary subtree ($N \geq 2$) rooted at the ancestor, i.e., the family tree of the deterministic branching process with pgf $f(s) = s^N$. The following theorem for the probability γ_N that there is no such N-ary subtree with infinite height holds.

Theorem 6.2 [8]. *The probability* γ_N *is the smallest root in* $[0,1]$ *of the fixed point equation*

$$x = g_N(x), \tag{6.3}$$

where

$$g_N(x) = \sum_{i=0}^{N-1} \frac{(1-x)^i}{i!} f^{(i)}(x).$$

In examples when the offspring distribution can be parameterized by its mean m, Pakes and Dekking [8] observe the following unusual critical phenomenon. There is an (critical) offspring mean value $m_N^c > 1$ for $N \geq 2$ such that

$$\begin{cases} \gamma_N = 1, \; m < m_N^c; \\ \gamma_N < 1, \; m \geq m_N^c. \end{cases}$$

This is qualitatively different to the behavior of the extinction (or not having an infinite unary subtree) probability γ_1, when the critical offspring mean is $m_1^c = 1$ and

$$\begin{cases} \gamma_1 = 1, \; m \leq 1; \\ \gamma_1 < 1, \; m > 1. \end{cases}$$

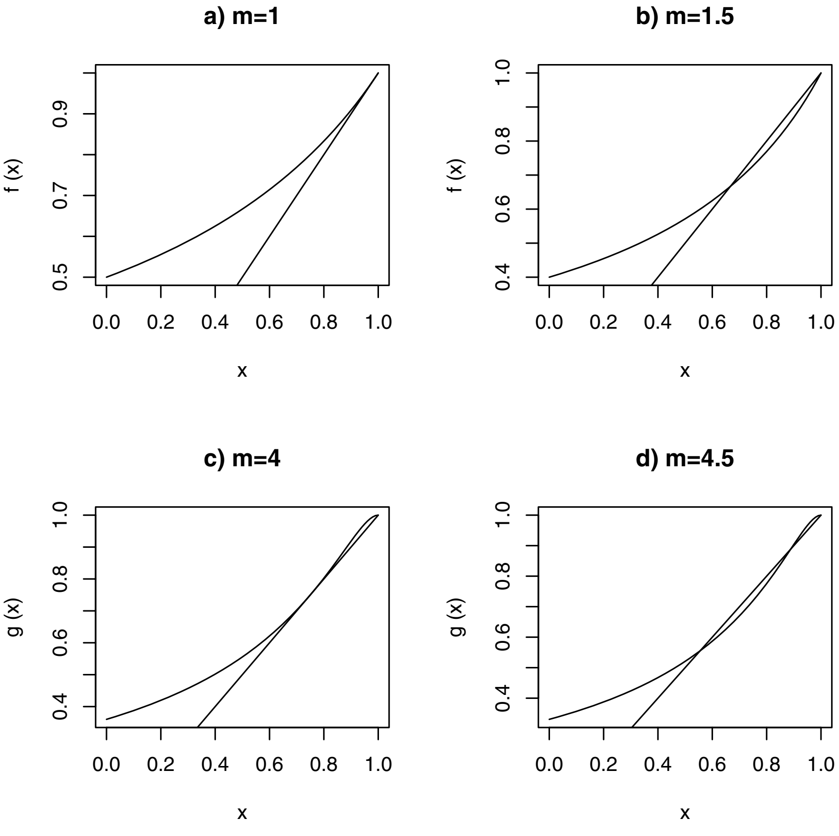

Fig. 6.1 Geometric offspring.

This difference occurs because $g_N(x)$ is increasing but not convex; $g'_N(1) = 0$. Thus the critical case occurs when $g_N(x)$ first touches the diagonal of the unit square somewhere other than unity. Figure 6.1 illustrates the situation for geometric offspring: (a) $m = 1$ - critical case for unary subtree; (b) $m = 1.5$ - supercritical case for unary subtree; (c) $m = 4$ - critical case for binary subtree; (d) $m = 4.5$ - supercritical case for binary subtree.

Next theorem gives a sufficient and a necessary condition for $\gamma_N < 1$.

Theorem 6.3 [8]. *(i) If $\gamma_N < 1$, then for some $s \in (0,1)$*

$$(1-s)^{N-1} f^{(N)}(s) \geq (N-1)!.$$

(ii) If

$$2N \sum_{k \geq N} \frac{p_k}{k+1} \leq \left(\sum_{k \geq N} p_k \right)^2 ,$$

then $\gamma_N < 1$.

We will finish this section with a remark from [8]. “Inspection of (6.3) should make it clear that there is virtually no hope of finding explicit expressions for the distribution of T_N for $N \geq 2$. It is even more unaccessible than the extinction time (T_1) distribution.”

6.3 Distribution of the number of complete and disjoint subtrees, rooted at the ancestor

Recall that the random variable V_N for $N = 1,2,\ldots$ is the number of disjoint complete N-ary subtrees with infinite height, rooted at the ancestor of $\{Z_n\}$. As the following result shows, the probability mass function of V_N can be obtained using the Taylor expansion of the pgf $f(s)$ about the point γ_N evaluated at $s = 1$.

Theorem 6.4 [11]. *For $j = 0,1,2,\ldots$ and $N \geq 1$*

$$P(V_N = j) = \sum_{k=jN}^{jN+N+1} \frac{(1-\gamma_N)^k}{k!} f^{(k)}(\gamma_N).$$

It is worth mentioning that $P(V_N = j)$ is the $(j+1)$st segment of length N in the Taylor expansion of $f(1)$ about γ_N. Indeed, set (for simplicity) $N = 2$ and consider the Taylor expansion of $f(1)$ about the point γ_2. Then

$$\begin{aligned}
P(V_2 = 0) &= f(\gamma_2) + (1-\gamma_2) f'(\gamma_2) \\
P(V_2 = 1) &= \frac{(1-\gamma_2)^2}{2!} f''(\gamma_2) + \frac{(1-\gamma_2)^3}{3!} f'''(\gamma_2) \\
&\cdots \\
P(V_2 = j) &= \frac{(1-\gamma_2)^{2j}}{(2j)!} f^{(2j)}(\gamma_2) + \frac{(1-\gamma_2)^{2j+1}}{(2j+1)!} f^{(2j+1)}(\gamma_2)
\end{aligned}$$

Denote by $V_N(n)$ the number of complete, disjoint, and rooted subtrees of maximum height n, ($n = 0,1,2,\ldots$), i.e., for which $T_N = n$. Mutafchiev [7] studies the survival probability $P(V_N(n) > 0 | V_N = 0)$. Observing that $P(V_N(n) > 0) = P(T_N > n)$ and $P(V_N(n) = 0) = P(T_N < \infty)$, we can state his results as follows. Denote $a_N = g_N'(\gamma_N)$

and $2b_N = g_N''(\gamma_N)$. One can see that

$$a_N = \frac{(1-\gamma_N)^{N-1}}{(N-1)!} f^{(N)}(\gamma_N) \tag{6.4}$$

and if $a_N = 1$, then

$$2b_N = \frac{f^{(N+1)}(\gamma_N)}{f^{(N)}(\gamma_N)} - \frac{N-1}{1-\gamma_N}. \tag{6.5}$$

Theorem 6.5 [7]. *Assume* $\gamma_N \in (0,1)$ *for* $N \geq 2$. *Then* $a_N \leq 1$.

(i) If $a_N < 1$ *(supercritical case), then as* $n \to \infty$

$$P(T_N > n \mid T_N < \infty) = c_N a_N^n + O(a_N^{2n}), \tag{6.6}$$

where $c_N > 0$ *is certain constant.*

(ii) If $a_N = 1$ *(critical case) and* $b_N < \infty$, *then* $b_N > 0$ *and as* $n \to \infty$

$$P(T_N > n \mid T_N < \infty) \sim \frac{1}{\gamma_N b_N n}. \tag{6.7}$$

Remark 6.1. (i) Note that if $a_N = 1$ and $f^{(N+1)}(1-) < \infty$, then $b_N < \infty$, see (6.5). (ii) (6.6) extends to $N \geq 2$ the classical results (e.g., [4], Theorem 8.4) for $P(Z_n > 0) = P(T_1 > n)$ when $m > 1$. (iii) For $P(Z_n > 0) = P(T_1 > n)$, when $m = 1$, we have $\gamma_1 = 1$ and hence (6.7) for $N = 1$ is consistent with the Kolmogorov's result $P(Z_n > 0) \sim 1/(b_1 n)$ as $n \to \infty$.

The subcritical case $\gamma_N = 1$ ($N \geq 2$) is treated in the following theorem.

Theorem 6.6 [8]. *Assume* $\gamma_N = 1$ *for* $N \geq 2$ *and that* $f^{(N)}(1-) < \infty$. *Then*

$$P(T_N > n) \sim \exp\{-k_N N^n\} \qquad (n \to \infty),$$

where $k_N > 0$ *is certain constant.*

In Sects. 6.6, 6.7 and 6.8 we will come back to Theorem 6.5 discussing its corollaries for particular offspring distributions.

6.4 Ratio of expected values of Z_ns provided infinite subtrees exist

In this section we prove a limit theorem for the ratio of the expected values of the nth generation's size, Z_n, as $n \to \infty$, conditioned on the existence of an N-ary and a unary subtree. Recall that $a_N = g_N'(\gamma_N)$ and $m = f'(1)$ is the offspring mean.

Theorem 6.7. *Assume $\gamma_N < 1$ for $N \geq 1$. If $E(Z_1 \log(1+Z_1)) < \infty$, then*

$$\lim_{n\to\infty} \frac{E(Z_n \mid T_N > n)}{E(Z_n \mid T_1 > n)} = \alpha_N \, \frac{1-\gamma_1}{1-\gamma_N} \tag{6.8}$$

where

$$\alpha_N = \frac{1}{m-a_N}\left[m - \sum_{j=0}^{N-1} \frac{1}{j!}(1-\gamma_N)^j f^{(j+1)}(\gamma_N)\right] \in (0,1]. \tag{6.9}$$

Proof. Under the assumption $E(Z_1 \log(1+Z_1)) < \infty$, there exists a random variable W such that $Z_n/m^n \to W$ in L_1 and $EW = 1$ (e.g., [5], Theorem 2.7.3). Thus,

$$\alpha_N := \lim_{n\to\infty} E\left(\frac{Z_n}{m_n}; T_N > n\right) = E(W; T_N = \infty)$$

and, since $\gamma_N < 1$, we have

$$\begin{aligned}\lim_{n\to\infty} \frac{E(Z_n \mid T_N > n)}{E(Z_n \mid T_1 > n)} &= \lim_{n\to\infty} \frac{E(Z_n\,;\,T_N > n)P(T_1 > n)}{E(Z_n\,;\,T_1 > n)P(T_N > n)} \\ &= \lim_{n\to\infty} \frac{E(Z_n\,;\,T_N > n)P(T_1 > n)}{m^n P(T_N > n)} \\ &= \alpha_N \frac{1-\gamma_1}{1-\gamma_N},\end{aligned}$$

which is (6.8). Next, we shall derive formula (6.9) for α_N. Denote

$$\psi_n(s) = E\left(s^{Z_n}; T_N > n\right) \qquad \text{and} \qquad \phi_n(s) = E\left(s^{Z_n}; T_N \leq n\right).$$

From [8], Theorem 6.1, we have

$$\psi_{n+1}(s) = f_{n+1}(s) - \sum_{j=0}^{N-1} \frac{1}{j!}\psi_n^j(s) f^{(j)}(\varphi_n(s)).$$

Differentiating with respect to s, we obtain

$$\psi'_{n+1}(s) = f'_{n+1}(s) - \sum_{j=1}^{N-1} \frac{1}{(j-1)!}\psi_n^{j-1}(s)\psi'_n(s) f^{(j)}(\varphi_n(s)) - \sum_{j=0}^{N-1} \frac{1}{j!}\psi_n^j(s) f^{(j+1)}(\varphi_n(s))\varphi'_n(s)$$

Setting $s = 1$, gives us

$$\begin{aligned}E\left(Z_{n+1}; T_N > n+1\right) = EZ_{n+1} - E(Z_n; T_N > n) &\sum_{j=1}^{N-1} \frac{1}{(j-1)!}(1-\gamma_{N(n)})^{j-1} f^{(j)}(\gamma_{N(n)}) \\ -[EZ_n - E(Z_n; T_N > n)] &\sum_{j=0}^{N-1} \frac{1}{j!}(1-\gamma_{N(n)})^j f^{(j+1)}(\gamma_{N(n)})\end{aligned}$$

Therefore,

$$E\left(Z_{n+1};T_N>n+1\right)-E(Z_n;T_N>n)\frac{1}{(N-1)!}(1-\gamma_{N(n)})^{N-1}f^{(N)}(\gamma_{N(n)})$$
$$=m^{n+1}-m^n\sum_{j=0}^{N-1}\frac{1}{j!}(1-\gamma_{N(n)})^j f^{(j+1)}(\gamma_{N(n)})$$

Referring to (6.4), we have

$$E\left(Z_{n+1};T_N>n+1\right)-a_{N(n)}E(Z_n;T_N>n)=m^{n+1}-m^n\sum_{j=0}^{N-1}\frac{1}{j!}(1-\gamma_{N(n)})^j f^{(j+1)}(\gamma_{N(n)})$$

Dividing both sides by m^n, we find

$$\frac{m^{n+1}}{m^n}E\left(\frac{Z_{n+1}}{m^{n+1}};T_N>n+1\right)-a_{N(n)}E\left(\frac{Z_n}{m^n};T_N>n\right)=m-\sum_{j=0}^{N-1}\frac{1}{j!}(1-\gamma_{N(n)})^j f^{(j+1)}(\gamma_{N(n)})$$

Passing to the limit as $n\to\infty$, we obtain

$$\alpha_N(m-a_N)=m-\sum_{j=0}^{N-1}\frac{1}{j!}(1-\gamma_N)^j f^{(j+1)}(\gamma_N) \tag{6.10}$$

Note that since $\gamma_1<\gamma_N<1$, we have $m>1$ and on the other hand by Theorem 6.5, $a_N\le 1$. Hence $m-a_N>0$. Dividing (6.10) by $m-a_N$, we arrive at (6.9). □

In the next three sections, we will prove corollaries of Theorem 6.7 for three particular cases of offspring distributions.

6.5 Geometric offspring distribution

In this section we present results for the case when the offspring distribution is geometric, i.e., $p_k=(1-p)p^k$, $k\ge 0$ and $p\in(0,1)$. Then for $|s|<1$ and $N\ge 2$

$$f(s)=\frac{1-p}{1-ps}\qquad\text{and}\qquad g_N(s)=1-\left[\frac{p(1-p)}{1-ps}\right]^N.$$

The number of N-ary subtrees V_N is geometric too (see [11]) given by

$$P(V_N=j)=\gamma_N(1-\gamma_N)^j,\qquad j\ge 0,$$

where γ_N is the smallest solution in $[0,1]$ of

$$(1-x+m^{-1})^N=(1-x)^{N-1}. \tag{6.11}$$

It is clear from (6.11) that in the geometric case $\gamma_N\to 0$ as $m\to\infty$ and, as it is pointed out in [8],

$$\gamma_N = \frac{N}{m} + O(m^{-2}), \qquad m \to \infty.$$

The critical value m_N^c for the offspring mean m is (see [8])

$$m_N^c = (N-1)\left(1-\frac{1}{N}\right)^{-N} \tag{6.12}$$

and the corresponding probability of not having a N-ary subtree

$$\gamma_N^c = 1-\left(1-\frac{1}{N}\right)^{N}. \tag{6.13}$$

Note that if $m = m_N^c$, then as $N \to \infty$

$$\gamma_N^c \to 1-\frac{1}{e} \approx 0.6321 \qquad \text{and} \qquad EV_N^c = \frac{1-\gamma_N^c}{\gamma_N^c} \to \frac{1}{e-1} \approx 0.5820.$$

In Table 6.1 we list some values of m_N^c, γ_N^c, and EV_N^c.

N	2	3	4	6	10	20	100
m_N^c	4	6.750	9.481	14.930	25.812	53.001	270.468
γ_N^c	0.750	0.704	0.684	0.665	0.651	0.641	0.634
EV_N^c	0.333	0.421	0.463	0.504	0.535	0.559	0.577

Table 6.1 Values of m_N^c, γ_N^c, and EV_N^c for geometric offspring.

Next corollary of Theorem 6.5(ii) (critical case) is straightforward.

Corollary 6.1. *Assume geometric offspring. If* $m = m_N^c$*, where* m_N^c *is given by (6.12), then as* $n \to \infty$

$$P(T_N^c > n \mid T_N^c < \infty) \sim \frac{2\left(1-N^{-1}\right)^{N-1}}{1-(1-N^{-1})^N}\,\frac{1}{n}.$$

Next result is a corollary of Theorem 6.7 for geometric offspring.

Corollary 6.2. *Assume geometric offspring with* $m \geq m_N^c$*. Then for any* $N = 2,3,\ldots$

$$\lim_{n\to\infty} \frac{E(Z_n|T_N > n)}{E(Z_n|T_1 > n)} = \frac{m-1}{m-a_N}\,(1+a_N). \tag{6.14}$$

Remark 6.2. It is interesting to note that if $a_N = 1$ (critical case) than the limit (6.14) equals the constant 2 for any N. This is rather unexpected.

Proof. We shall calculate $\alpha(1-\gamma_N)/(1-\gamma_N)$, which is the limit in Theorem 6.7. First, using (6.11) and $p = m/(m+1)$, we obtain

$$
\begin{aligned}
a_N &= g_N'(\gamma_N) \\
&= \frac{(1-\gamma_N)^{N-1}}{(N-1)!}\frac{N!p^N(1-p)}{(1-p\gamma_N)^{N+1}} \\
&= \frac{N}{m(1-\gamma_N)+1}.
\end{aligned} \tag{6.15}
$$

Also, since for $j = 1, 2, \dots$

$$
f^{(j)}(s) = \frac{j!p^j(1-p)}{(1-ps)^{j+1}},
$$

we have

$$
\begin{aligned}
\sum_{j=0}^{N-1}\frac{1}{j!}(1-\gamma_N)^j f^{(j+1)}(\gamma_N) &= \sum_{j=0}^{N-1}\frac{1}{j!}(1-\gamma_N)^j\frac{(j+1)!(1-p)p^{j+1}}{(1-p\gamma_N)^{j+2}} \\
&= \frac{p(1-p)}{(1-p\gamma_N)^2}\sum_{j=0}^{N-1}(j+1)\left[\frac{p(1-\gamma_N)}{1-p\gamma_N}\right]^j \\
&= \frac{m}{(1+m-m\gamma_N)^2}\sum_{j=0}^{N-1}(j+1)\left[\frac{m(1-\gamma_N)}{m+1-m\gamma_N}\right]^j \\
&= \frac{m}{(1+m(1-\gamma_N))^2}\left[1+\sum_{j=1}^{N-1}(j+1)\left[\frac{m(1-\gamma_N)}{1+m(1-\gamma_N)}\right]^j\right].
\end{aligned}
$$

Denote $S_N(x) = \sum_{j=1}^{N-1}(j+1)x^j$ for some $x > 0$. One can see that

$$
\begin{aligned}
S_N(x) - xS_N(x) &= 2x + \sum_{i=2}^{N-1} x^i - Nx^N \\
&= 2x + x^2\frac{1-x^{N-2}}{1-x} - Nx^N
\end{aligned}
$$

and thus,

$$
\begin{aligned}
1 + S_N(x) &= 1 + \frac{2x}{1-x} + x^2\frac{1-x^{N-2}}{(1-x)^2} - \frac{Nx^N}{1-x} \\
&= \frac{Nx^{N+1} - (N+1)x^N + 1}{(1-x)^2}.
\end{aligned}
$$

Set $x = m(1-\gamma_N)/[1+m(1-\gamma_N)]$ and thus $1-x = [1+m(1-\gamma_N)]^{-1}$. Now, after some algebra and using (6.11) and (6.15), we obtain

$$
\begin{aligned}
\alpha_N(m-a_N) &= m - \sum_{j=0}^{N-1} \frac{1}{j!}(1-\gamma_N)^j f^{(j+1)}(\gamma_N) \qquad (6.16)\\
&= m[1-(Nx^{N+1}-(N+1)x^N+1)]\\
&= m\left[\frac{m(1-\gamma_N)}{1+m(1-\gamma_N)}\right]^N \left[N+1-N\frac{m(1-\gamma_N)}{1+m(1-\gamma_N)}\right]\\
&= \frac{m^{N+1}(1-\gamma_N)^N}{[1+m(1-\gamma_N)]^N}\frac{N+1+m(1-\gamma_N)}{1+m(1-\gamma_N)}\\
&= m(1-\gamma_N)\frac{N+1+m(1-\gamma_N)}{1+m(1-\gamma_N)}.
\end{aligned}
$$

Therefore, using (6.15), (6.16), and $\gamma_1 = 1/m$, we have for the limit in Theorem 6.7

$$
\begin{aligned}
\alpha_N\frac{1-\gamma_1}{1-\gamma_N} &= \frac{m(1-\gamma_1)}{m-a_N}\left[1+\frac{N}{1+m(1-\gamma_N)}\right]\\
&= \frac{m-1}{m-a_N}\,(1+a_N),
\end{aligned}
$$

which completes the proof of the corollary. □

6.6 Poisson offspring distribution

Consider Poisson offspring distribution with pgf $f(s) = e^{m(s-1)}$, $m > 0$. Whence

$$
g_N(s) = e^{-m(1-s)}\sum_{j=0}^{N-1}\frac{1}{j!}[m(1-s)]^j. \qquad (6.17)
$$

The distribution of V_N (see [11]) can be presented for $j = 0,1,\dots$ as

$$
P(V_N = j) = P(jN \le Y_N \le jN+N-1),
$$

where Y_N is a Poisson random variable with mean $m(1-\gamma_N)$. That is, $P(V_N = j)$ is the $(j+1)$st segment of length N in the distribution of Y_N. Some values of EV_N^c are given in Table 6.2. In the Poisson case, one also has $\gamma_N \to 0$ as $m \to \infty$. Now, (6.3) and (6.17) lead to

$$
\gamma_N \sim \frac{m^{N-1}e^{-m}}{(N-1)!}, \qquad m \to \infty.
$$

Denote $y = m_N^c(1-\gamma_N^c)$. It is shown in [8] that m_N^c and γ_N^c satisfy the equations

$$
\frac{y^N}{(N-1)!} + \sum_{j=0}^{N-1}\frac{y^j}{j!} = e^y \qquad (6.18)
$$

and

$$m_N^c y^{N-1} = (N-1)!e^y. \tag{6.19}$$

Since (6.18) has a unique positive solution, one can find m_N^c and γ_N^c from (6.18) and then (6.19). Some values are given in Table 6.2 below. It is proved in [8] that as $N \to \infty$

$$m_N^c = N + \sqrt{N \log N}(1+o(1)) \qquad \text{and} \qquad \gamma_N^c = \sqrt{\pi/(2N)}(1+o(1)).$$

N	2	3	4	6	10	20	40
m_N^c	3.351	5.150	6.800	9.876	15.582	28.775	53.434
γ_N^c	0.465	0.343	0.282	0.218	0.160	0.107	0.072
EV_N^c	0.654	0.793	0.844	0.876	0.886	0.899	0.929

Table 6.2 Values of m_N^c, γ_N^c, and EV_N^c for Poisson offspring.

Here we state a straightforward corollary of Theorem 6.5(ii) (critical case).

Corollary 6.3. *Assume Poisson offspring. If* $m = m_N^c$, *then as* $n \to \infty$

$$P(T_N^c > n \mid T_N^c < \infty) \sim \frac{2(1-\gamma_N^c)}{m_N^c(1-\gamma_N^c) - N + 1}\,\frac{1}{n}.$$

Next result is a corollary of Theorem 6.7 for Poisson offspring.

Corollary 6.4. *Assume Poisson offspring with* $m \geq m_N^c$. *Then for any* $N = 2, 3, \ldots$

$$\lim_{n\to\infty} \frac{E(Z_n \mid T_N > n)}{E(Z_n \mid T_1 > n)} = \frac{m(1-\gamma_1)}{m - a_N}. \tag{6.20}$$

Remark 6.3. (i) The limit in (6.20) can be expressed in the form

$$(1-\gamma_1)\left\{1 - \frac{[m(1-\gamma_N)]^{N-1}}{(N-1)!}e^{-m(1-\gamma_N)}\right\}^{-1}.$$

(ii) Let $m_N = m_N^c$. Then $a_N^c = 1$ and since the probability of extinction γ_1^c satisfies $\gamma_1^c = \exp\{-m_N^c(1-\gamma_1^c)\}$, one can see that for the limit in (6.20) it is true that

$$\frac{m_N^c(1-\gamma_1^c)}{m_N^c - 1} > 1 \quad \text{and} \quad \frac{m_N^c(1-\gamma_1^c)}{m_N^c - 1} \downarrow 1 \quad \text{as} \quad N \to \infty.$$

Proof. We have $f(s) = \exp\{-m(1-s)\}$ and thus for $j = 1, 2, \ldots$

$$f^{(j+1)}(s) = m^{j+1}e^{-m(1-s)} = mf^{(j)}(s)$$

Therefore, referring to (6.9) and (6.17),

$$\begin{aligned}
\alpha_N &= \frac{1}{m-a_N}\left[m - \sum_{j=0}^{N-1}\frac{1}{j!}(1-\gamma_N)^j f^{(j+1)}(\gamma_N)\right] \\
&= \frac{m}{m-a_N}\left[1 - m^{-1}\sum_{j=0}^{N-1}\frac{1}{j!}(1-\gamma_N)^j mf^{(j)}(\gamma_N)\right] \\
&= \frac{m}{m-a_N}\left[1 - e^{-m(1-\gamma_N)}\sum_{j=0}^{N-1}\frac{1}{j!}[m(1-\gamma_N)]^j\right] \\
&= \frac{m(1-\gamma_N)}{m-a_N}.
\end{aligned}$$

Hence,

$$\alpha_N\frac{1-\gamma_1}{1-\gamma_N} = \frac{m(1-\gamma_1)}{m-a_N}$$

and the limit in (6.20) follows from Theorem 6.7. □

6.7 One-or-many offspring distribution

In this section we consider a two-parameter family of offspring distributions $\{p_k\}$ defined for $p \in (0,1)$ and some integer $r > N > 1$ by $p_1 = 1-p$, $p_k = 0$ for $2 \le k \le r-1$, and $p_r = p$. Clearly $m = 1-p+rp$ and $f(s) = (1-p)s + ps^r$. Hence

$$g_N(s) = 1 - p\sum_{j=N}^{r}\binom{r}{j}(1-s)^j s^{r-j}.$$

Consequently, Theorem 6.2 shows that γ_N is the smallest solution in $[0,1]$ of

$$s = p\sum_{j=N}^{r}\binom{r}{j}s^j(1-s)^{r-j}.$$

Let $B_r(\gamma_N)$ denote a binomial $(r, 1-\gamma_N)$ random variable. It is shown in [11] that $P(V_N = 0) = 1-p+pP(B_r(\gamma_N) \le N-1)$ and for $j = 1,2,\ldots$

$$P(V_N = j) = \begin{cases} pP(jN \le B_r(\gamma_N) \le jN+U) & \text{if } jN \le r, \\ 0 & \text{if } jN > r, \end{cases}$$

where $U = \min\{N-1, r-jN\}$. That is, $P(V_N = j)$ is the $(j+1)$st segment of length U in the distribution of $B_r(\gamma_N)$. It is shown in [8] that γ_N^c is the unique solution of

$$\sum_{j=N}^{r}\binom{r}{j}\left(\frac{1-x}{x}\right)^{j-N}=r\binom{r-1}{N-1}$$

and also for the critical value p_N^c

$$(p_N^c)^{-1}=r\binom{r-1}{N-1}(1-\gamma_N^c)^{N-1}(\gamma_N^c)^{r-N}. \tag{6.21}$$

In particular, if $r=N+1$ then

$$m_N^c=1+(N-1)\left(1-\frac{1}{N^2}\right)^{-N}, \quad \gamma_N^c=N^{-2}, \quad \text{and} \quad EV_N^c=1-N^{-2}. \tag{6.22}$$

We list some values of m_N^c, γ_N^c, and EV_N^c in Table 6.3.

N	2	3	4	6	10	20	40
m_N^c	2.778	3.848	4.884	6.921	10.952	20.975	40.988
γ_N^c	0.250	0.111	0.063	0.028	0.010	0.003	0.001
EV_N^c	0.750	0.889	0.938	0.972	0.990	0.998	0.999

Table 6.3 Values of m_N^c, γ_N^c, and EV_N^c for one-or-$(N+1)$ offspring.

The following straightforward corollary of Theorem 6.5(ii) holds.

Corollary 6.5. *Assume one-or-$(N+1)$ offspring distribution. If $m=m_N^c$, then*

$$P(T_N^c>n \mid T_N^c<\infty)\sim 2\left(N-\frac{1}{N}\right)\frac{1}{n} \qquad (n\to\infty).$$

Next result is a corollary of Theorem 6.7 for one-or-$(N+1)$ offspring.

Corollary 6.6. *Assume one-or-$(N+1)$ offspring distribution. If $m=m_N^c$, then*

$$\lim_{n\to\infty}\frac{E(Z_n \mid T_N^c>n)}{E(Z_n \mid T_1^c>n)}=\frac{N}{N-1}\left(1-\frac{2^N-1}{N^{2N}}\right).$$

Proof. We have for $j\geq 1$

$$f'(s)=1-p+p(N+1)s^N \quad \text{and} \quad f^{(j+1)}(s)=p(N+1)N\dots(N+1-j)s^{N-j} \tag{6.23}$$

It follows from (6.9) and (6.21)–(6.23), after some algebra, that

$$\begin{aligned}\alpha_N &= \frac{1}{m_N^c - 1}\left[m_N^c - f'(\gamma_N^c) - \sum_{j=1}^{N-1}\frac{1}{j!}(1-\gamma_N^c)f^{(j+1)}(\gamma_N^c)\right]\\ &= \frac{(1-N^{-2})^N}{(N-1)}\left[\frac{N-N^{-1}}{(1-N^{-2})^N} - \frac{1-N^{-1}}{(1-N^{-2})^N N^{2N}}\sum_{j=0}^{N-1}\frac{(N+1)\dots(N+1-j)}{j!}\right]\\ &= \left(1+N^{-1}\right) - \frac{1}{N^{2N+1}}\sum_{j=0}^{N-1}\frac{(N+1)N\dots(N+1-j)}{j!}\\ &= \left(1+N^{-1}\right) - \frac{(N+1)\left(2^N-1\right)}{N^{2N+1}}\end{aligned}$$

and the corollary follows from Theorem 6.7. □

6.8 Concluding remarks

Pakes and Dekking [8] point out that constructions of complete N-ary subtrees of a Galton-Watson family tree, have appeared in the study of Mendelbrot's percolation process by Chayes et al. [1] and in Pemantle's work [9] on reinforced random walks. In particular, Pemantle's results imply that: if there exists $s_0 \in (0,1)$, such that $g_N(s_0) \le s_0$, then $\gamma_N \le s_0 < 1$. In [7], Mutafchiev discusses an interesting connection between the subject matter N-ary trees and the existence of a giant k-core in a random graph. Consider an Erdös-Rényi random graph $G(n,p)$ with n vertices in which the possible arcs are present independently, each with probability p. Pittel et al. [10] construct a Galton–Watson family tree rooted at a vertex of the graph $G(n,\lambda/n)$, $(\lambda > 0)$, assuming Poisson offspring distribution with mean λ. They show that a giant k-core appears suddenly when the number of arcs reaches $c_k n/2$, where the constant c_k can be explicitly computed. It is remarkable that the values of c_k coincide with those of m_{k-1}^c for $k = 3,4,5$ in case of Poisson offspring distribution (see Table 6.2 and [10], p. 114). This needs further investigation.

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7

Limit theorems for critical randomly indexed branching processes

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Abstract We investigate a BGW process subordinated by a renewal process for which the interarrival periods have a finite mean or heavy tails. The branching process is critical with finite or infinite offspring variance and started with a random number of ancestors with infinite mean. The asymptotic behavior of the probability for non-extinction is investigated and limiting distributions are obtained.

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7.1 Introduction

A randomly indexed branching process was introduced by Epps [5] for modeling of daily stock prices as an alternative of the geometric Brownian motion. He considered a Bienaymé–Galton–Watson (BGW) branching process indexed by a Poisson process, assuming four particular discrete offspring distributions. Under these conditions, Epps obtained the asymptotic behavior of the moments, submitted certain estimates of the parameters of the process, and made the calibration of the model using real data from the New York Stock Exchange (NYSE). Assuming this stock

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price process, two formulas for pricing of European Call Option and Up-and-Out Barrier Option were derived in [8] and [10], respectively.

Dion and Epps [4] noted that the process is a particular case of branching processes in random environments. Therefore, one can derive their general properties from the results for branching processes in random environments. On the other hand, the particular assumptions provide some important characteristics which are not exhibited in the general framework.

In the present paper we continue the investigation of the randomly indexed branching processes initiated in [7] and [9]. Let us briefly recall the definition.

Assume that on the probability space $(\Omega,\mathscr{A},\mathbf{P})$ are given:

(i) The set $X=\{X_i(n), n=1,2,\ldots; i=1,2,\ldots\}$ of i.i.d. nonnegative integer valued random variables (r.v.) with the probability generating function (p.g.f.) $f(s)=\mathbf{E}\left[s^{X_i(n)}\right]=\sum_{k=0}^{\infty}p_k s^k,\ s\in[0,1]$.

(ii) An independent of X set $J=\{J_1,J_2,\ldots\}$ of positive i.i.d. r.v. with the cumulative distribution function (c.d.f.) $F(x)=\mathbf{P}(J_n\le x)$.

The classical BGW branching process starting by I ancestors can be defined as follows

$$Z_0=I,\ Z_{n+1}=\sum_{i=1}^{Z_n}X_i(n+1),\ n=0,1,2,\ldots \tag{7.1}$$

It is well known that the p.g.f. $f_n(s)=\mathbf{E}[s^{Z_n}|Z_0=1]$, $|s|\le 1$, is the n-fold iteration of $f(s)$; that is $f_n(s)=f(f_{n-1}(s))$, $f_1(s)=f(s)$, $f_0(s)=s$ (see e.g. [1]). The initial number of particles is assumed to be a r.v. I independent of the set X. Denote by $g(s)=\mathbf{E}\left[s^I\right]$. Then from the independence of the evolution it follows that

$$\mathbf{E}\left[s^{Z_n}|Z_0=I\right]=g(f_n(s)),\ n=0,1,2,\ldots,\ s\in[0,1]. \tag{7.2}$$

Define also the ordinary renewal process

$$S_0=0,\quad S_n=\sum_{j=1}^{n}J_j,\ n=0,1,\ldots, \tag{7.3}$$

and the corresponding counting process

$$N(t)=\max\{n\ge 0: S_n\le t\},\quad t\ge 0. \tag{7.4}$$

Denote the renewal function of $N(t)$ by $H(t)=\mathbf{E}[N(t)]=\sum_{n=0}^{\infty}F^{*n}(t),\ \ t\ge 0$, and $P_k(t)=\mathbf{P}(N(t)=k),\quad k=0,1,2,\ldots$. Here and later $F^{*n}(t)$ denotes the $n-$fold convolution of the distribution function $F(t)$; that is $F^{*1}(t)=F(t),\ \ F^{*n}(t)=\int_0^t F^{*(n-1)}(t-u)dF(u),\ F^{*0}(t)=1$.

Definition 7.1. The continuous time process $\{Y(t),\ t\ge 0\}$ defined by

$$Y(t)=Z_{N(t)},\ t\ge 0,$$

is called a randomly indexed BGW branching process.

Applying the total probability law we obtain by the independence of the processes $Z(n)$ and $N(t)$ that

$$\Phi(t;s) = \mathbf{E}\left[s^{Y(t)}\right] = \sum_{n=0}^{\infty} P_n(t) g(f_n(s)).$$

In the investigation of the limiting behavior of the process we need also the following equation for the conditional distribution of $Y(t)$

$$\begin{aligned} &\mathbf{P}(Y(t) \leq x \,|\, Y(t) > 0) \\ &= \int_0^{\infty} \mathbf{P}\left(Z_{[y]} \leq x \,|\, Z_{[y]} > 0\right) d\mathbf{P}\left(N(t) \leq y \,|\, Z_{N(t)} > 0\right). \end{aligned} \tag{7.5}$$

Relating to this equation, the following interesting problem arises:

If we know the limiting behavior of the processes $N(t)$ and Z_n, what can be said about the limiting distribution of

$$\mathbf{P}\left(N(t) \leq x \,|\, Z_{N(t)} > 0\right)$$

as $t \longrightarrow \infty$?

The solution of this problem in more general settings is given in Sect. 7.2. Section 7.3 presents the results for renewal processes needed later. In Sect. 7.4 it is proved a limit theorem for BGW branching process starting with random number of ancestors. In Sect. 7.5, using the results from the previous sections, it is established the limiting behavior of a randomly indexed branching process in critical case.

7.2 A conditional limit theorem for random time change

Assume that on the common probability space $(\Omega, \mathscr{A}, \mathbf{P})$ are given two independent processes:

(i) The integer valued process $N(t)$ and the real valued function $K(t)$ such that as $t \longrightarrow \infty$

$$N(t) \uparrow \infty, \quad K(t) \uparrow \infty, \quad \text{and} \quad \frac{N(t)}{K(t)} \xrightarrow{d} \xi, \tag{7.6}$$

where the random variable ξ is almost surely positive. Here and later $\xrightarrow{d}$ denotes convergence in distribution.

(ii) The process $Z_n,\ n = 0, 1, 2, \ldots$ is a discrete time stochastic process having 0 as its absorbing state (e.g. branching process) and such that

$$\left.\begin{array}{l} Q(n) := \mathbf{P}(Z_n > 0) \downarrow 0, \ \ n \longrightarrow \infty, \\ Q(0) = 1, \ \ \text{i.e.} \ \ Z_0 > 0 \ \ \text{a.s.}, \\ Q(n) \sim n^{-\theta} L(n) \ \ n \longrightarrow \infty, \end{array}\right\} \tag{7.7}$$

where $0 < \theta < 1$ and $L(x)$ is a function slowly varying at infinity. Define for $x \in [0,\infty)$, $Q(x) = Q([x])$.

Theorem 7.1. *Assume the conditions (7.6), (7.7), and* $\mathbf{E}\left[\xi^{-\theta}\right] < \infty$. *Then as* $t \to \infty$,

$$G_t(x) = \mathbf{P}\left(\frac{N(t)}{K(t)} \leq x \,|\, Z_{N(t)} > 0\right) \to G(x) \tag{7.8}$$

for every x *which is a point of continuity of* $G(.)$, *where*

$$G(x) = \frac{\mathbf{E}\left[\xi^{-\theta}\mathbf{I}_{\{\xi \leq x\}}\right]}{\mathbf{E}\left[\xi^{-\theta}\right]}.$$

Proof. The following representation holds

$$G_t(x) = R(t)^{-1} \sum_{n \leq xK(t)} \mathbf{P}(N(t) = n)\, Q(n), \tag{7.9}$$

where

$$R(t) = \mathbf{P}\left(Z_{N(t)} > 0\right) = \sum_{n=0}^{\infty} \mathbf{P}(N(t) = n)\, Q(n) = \mathbf{E}\left[Q(N(t))\right].$$

Indeed,

$$\begin{aligned} G_t(x) &= \mathbf{P}\left(\frac{N(t)}{K(t)} \leq x \,|\, Z_{N(t)} > 0\right) = R(t)^{-1}\mathbf{P}\left(N(t) \leq xK(t),\, Z_{N(t)} > 0\right) \\ &= R(t)^{-1} \sum_{n=0}^{\infty} \mathbf{P}\left(N(t) = n,\, N(t) \leq xK(t),\, Z_{N(t)} > 0\right) \\ &= R(t)^{-1} \sum_{n \leq xK(t)} \mathbf{P}(Z_n > 0)\, \mathbf{P}(N(t) = n) = R(t)^{-1}\mathbf{E}\left[Q(N(t))\mathbf{I}_{\{N(t) \leq xK(t)\}}\right]. \end{aligned}$$

First, we shall prove that as $t \to \infty$,

$$R(t) = \sum_{n=0}^{\infty} \mathbf{P}(N(t) = n)\, Q(n) = \mathbf{E}\left[Q(N(t))\right] \sim \mathbf{E}\left[\xi^{-\theta}\right] Q(K(t)). \tag{7.10}$$

Since $Q(0) = 1$, and $Q(n) \downarrow 0$, we can write for every $n \geq 0$ that

$$Q(n) = \sum_{k=n}^{\infty} (Q(k) - Q(k+1)),$$

where $p(k) = Q(k) - Q(k+1) \geq 0,\ k = 0,1,2,\ldots$ and $\sum_{k=0}^{\infty} p(k) = 1$, that is $p(k)$ is a probability distribution on $0,1,2,\ldots$ and the corresponding to it c.d.f. is $1 - Q(x)$. Using this we obtain

$$R(t)=\sum_{n=0}^{\infty}\mathbf{P}\left(N(t)=n\right)Q(n)=\sum_{n=0}^{\infty}\sum_{k=n}^{\infty}\mathbf{P}\left(N(t)=n\right)\left(Q(k)-Q(k+1)\right).$$

Changing the order of summation one gets

$$\begin{aligned}R(t)&=\sum_{k=0}^{\infty}\sum_{n=0}^{k}\mathbf{P}\left(N(t)=n\right)\left(Q(k)-Q(k+1)\right)\\&=\sum_{k=0}^{\infty}\left(Q(k)-Q(k+1)\right)\sum_{n=0}^{k}\mathbf{P}\left(N(t)=n\right)=\sum_{k=0}^{\infty}p(k)\mathbf{P}\left(N(t)\le k\right).\end{aligned}$$

Therefore, we can write $R(t)=\int_0^{\infty}\mathbf{P}\left(N(t)\le x\right)d(1-Q(x))$, and

$$\begin{aligned}\frac{R(t)}{Q(K(t))}&=-\int_0^{\infty}\mathbf{P}\left(N(t)\le x\right)d\frac{Q(x)}{Q(K(t))}\\&=-\int_0^{\infty}\mathbf{P}\left(\frac{N(t)}{K(t)}\le\frac{x}{K(t)}\right)d\frac{Q(x)}{Q(K(t))}=-\int_0^{\infty}\mathbf{P}\left(\frac{N(t)}{K(t)}\le y\right)d\frac{Q(yK(t))}{Q(K(t))}.\end{aligned}$$

In the last step we substitute $x=yK(t)$. Since (7.6) and the fact that $Q(x)$ varies regularly it follows that as $t\to\infty$,

$$-\int_0^{\infty}\mathbf{P}\left(\frac{N(t)}{K(t)}\le y\right)d\frac{Q(yK(t))}{Q(K(t))}\to-\int_0^{\infty}\mathbf{P}\left(\xi\le y\right)d(y^{-\theta}).$$

Substituting in the last integral $y^{-\theta}=z\Leftrightarrow y=z^{-1/\theta}$ we prove (7.10).

Let us consider now

$$\frac{\mathbf{P}\left(N(t)>xK(t),Z_{N(t)}>0\right)}{Q(K(t))}=\mathbf{E}\left[\frac{Q(N(t))}{Q(K(t))}\mathbf{I}_{\{N(t)>xK(t)\}}\right].$$

Since $Q(.)$ is non increasing then almost surely,

$$\frac{Q(N(t))}{Q(K(t))}\mathbf{I}_{\{N(t)>xK(t)\}}\le\frac{Q(x(K(t))}{Q(K(t))}\mathbf{I}_{\{N(t)>xK(t)\}}. \tag{7.11}$$

Since (7.6) and the regular variation of $Q(.)$, the following relations hold as $t\to\infty$,

$$\begin{aligned}&\frac{Q(N(t))}{Q(K(t))}\mathbf{I}_{\{N(t)>xK(t)\}}\xrightarrow{d}\xi^{-\theta}\mathbf{I}_{\{\xi>x\}},\quad\frac{Q(x(K(t))}{Q(K(t))}\mathbf{I}_{\{N(t)>xK(t)\}}\xrightarrow{d}x^{-\theta}\mathbf{I}_{\{\xi>x\}},\\&\mathbf{E}\left[\frac{Q(xK(t))}{Q(K(t))}\mathbf{I}_{\{N(t)>xK(t)\}}\right]=\frac{Q(xK(t))}{Q(K(t))}\mathbf{P}\left(\frac{N(t)}{K(t)}>x\right)\to x^{-\theta}\mathbf{P}\left(\xi>x\right).\end{aligned}$$

These relations, the inequality (7.11), and the Lebesgue's theorem for dominated convergence yield

$$\frac{\mathbf{P}\left(N(t)>xK(t),Z_{N(t)}>0\right)}{Q(K(t))}$$
$$=\mathbf{E}\left[\frac{Q(N(t))}{Q(K(t))}\mathbf{I}_{\{N(t)>xK(t)\}}\right]\to\mathbf{E}\left[\xi^{-\theta}\mathbf{I}_{\{\xi>x\}}\right],$$

as $t\to\infty$. Therefore,

$$\frac{\mathbf{P}\left(N(t)\le xK(t),Z_{N(t)}>0\right)}{Q(K(t))}\to\mathbf{E}\left[\xi^{-\theta}\mathbf{I}_{\{\xi\le x\}}\right], \tag{7.12}$$

as $t\to\infty$. Now, from (7.12), (7.10), and (7.9) we get (7.8). The theorem is proved. □

7.3 Renewal processes

In this section we apply Theorem 7.1 to the ordinary renewal process defined by (7.3) and (7.4).

Denote the distribution function of the interarrival times J_k by $F(x),\ F(0+)=0$ and assume one of the following conditions:

The mean of interarrival times J_k is finite,

$$\mu=\mathbf{E}[J_n]=\int_0^\infty(1-F(y))dy\in(0,\infty). \tag{7.13}$$

The interarrival times J_k have an infinite mean, and

$$1-F(t)\sim\frac{t^{-\beta}\mathscr{L}(t)}{\Gamma(1-\beta)},\quad t\to\infty,\quad \beta\in(0,1), \tag{7.14}$$

where $\mathscr{L}(.)$ is a function slowly varying at infinity.

If condition (7.13) holds, then by the SLLN it follows that (see e.g. [6])

$$\frac{S_n}{\mu n}\overset{a.s.}{\to}1,\ n\to\infty,\ \text{ and }\ \frac{N(t)}{t/\mu}\overset{a.s.}{\to}1,\ t\to\infty,$$

where $\overset{a.s.}{\to}$ denotes the convergence almost surely.

Suppose that condition (7.14) is satisfied. Then the function

$$\tilde r(t)=\frac{1}{\Gamma(1-\beta)(1-F(t))}\sim\frac{t^{\beta}}{\mathscr{L}(t)},\ \text{as } t\to 0, \tag{7.15}$$

and its asymptotic inverse $r(t)>0,\ t\ge 0$, defined by (see e.g. Theorem 1.5.12 in [2])

$$r(\tilde r(t))\sim\tilde r(r(t))\sim t\quad\text{as } t\to\infty,$$

provide the appropriate normalization for the renewal sequence and the counting process,

$$\frac{S_n}{r(n)} \xrightarrow{d} D_\beta, \quad \text{as } n \longrightarrow \infty$$
$$\frac{N(t)}{\tilde{r}(t)} \xrightarrow{d} W_\beta, \quad \text{as } t \longrightarrow \infty.$$

The random variable D_β has an one-sided β-stable distribution. That is $D_\beta > 0$ a.s. and

$$\mathbf{E}\left[e^{-\lambda D_\beta}\right] = e^{-\lambda^\beta}, \ \lambda > 0.$$

(See also Sect. 13.6 in [6]). The random variable W_β is also almost surely positive and its distribution is defined by

$$W_\beta \stackrel{d}{=} (D_\beta)^{-\beta}.$$

The r.v. W_β has Laplace transform

$$\mathbf{E}\left[e^{-\lambda W_\beta}\right] = \sum_{n=0}^{\infty} \frac{(-\lambda^\beta)^n}{\Gamma(1+n\beta)}.$$

The distribution of this type is known as the Mittag-Lefler distribution.

It is known that (see e.g. [6], Sect. XIII.6, Theorem 1)

$$\mathbf{P}\left(D_\beta > x\right) \sim x^{-\beta}, \quad \text{as} \quad x \longrightarrow \infty. \tag{7.16}$$

Further, if $\theta > 0$ then

$$\mathbf{P}\left((W_\beta)^{-\theta} > x\right) = \mathbf{P}\left(((D_\beta)^{-\beta})^{-\theta} > x\right) = \mathbf{P}\left(D_\beta > x^{\frac{1}{\beta\theta}}\right).$$

This chain of equalities and the relation (7.16) show that

$$\mathbf{P}\left((W_\beta)^{-\theta} > x\right) \sim x^{-\frac{1}{\theta}}, \quad \text{as } x \longrightarrow \infty.$$

Therefore, if $\theta \in (0,1)$ we have $\mathbf{E}\left[(W_\beta)^{-\theta}\right] < \infty$.

Assuming that the process Z_n is the same as in the previous section, we are ready to formulate the following consequence from Theorem 7.1.

Theorem 7.2. *Suppose that on the same probability space we have a renewal counting process $N(t)$ and a process Z_n satisfying the conditions (7.7) from Sect. 7.2.*

If for $N(t)$ condition (7.13) is satisfied then

$$\lim_{t\to\infty} \mathbf{P}\left(\frac{N(t)}{t/\mu} \le x \,|\, Z_{N(t)} > 0\right) = \mathbf{I}_{\{1\le x\}}. \tag{7.17}$$

If for $N(t)$ *condition (7.14) is satisfied and* $\theta \in (0,1)$ *then*

$$\lim_{t\to\infty} \mathbf{P}\left(\frac{N(t)}{\tilde{r}(t)} \le x \,|\, Z_{N(t)} > 0\right) = \frac{\mathbf{E}\left[(W_\beta)^{-\theta}\mathbf{I}_{\{W_\beta \le x\}}\right]}{\mathbf{E}\left[(W_\beta)^{-\theta}\right]}. \tag{7.18}$$

In this case

$$\mathbf{E}\left[(W_\beta)^{-\theta}\right] = \frac{\Gamma(1-\theta)}{\Gamma(1-\theta\beta)}. \tag{7.19}$$

Proof. The limits (7.17) and (7.18) follow immediately from Theorem 7.1. We have to prove only (7.19). Since $N(t)$ is a renewal counting process it follows from the Eq. (7.11) that

$$R(t) = \sum_{k=0}^{\infty} p(k)\mathbf{P}(S_k > t).$$

Let us denote by $\Phi(t) = 1 - R(t), t \ge 0$. Then

$$\Phi(t) = \sum_{k=0}^{\infty} p(k)\mathbf{P}(S_k \le t)$$

is a proper distribution function on $[0,\infty)$. Taking the Laplace-Stieltjes transform from both sides of the last equation we obtain for $\lambda > 0$

$$\hat{\Phi}(\lambda) = \sum_{k=0}^{\infty} p(k)\hat{F}^k(\lambda),$$

where $\hat{\Phi}(\lambda) = \int_0^\infty e^{-\lambda t} d\Phi(t)$, and $\hat{F}(\lambda) = \int_0^\infty e^{-\lambda t} dF(t)$. Then

$$\begin{aligned} 1 - \hat{\Phi}(\lambda) &= \sum_{k=1}^{\infty} p(k)(1 - \hat{F}^k(\lambda)) \\ &= (1 - \hat{F}(\lambda)) \sum_{k=1}^{\infty} p(k)(1 + \hat{F}(\lambda) + \ldots + \hat{F}^{k-1}\lambda)). \end{aligned}$$

Changing the order of summation in the last equation we get

$$1 - \hat{\Phi}(\lambda) = (1 - \hat{F}(\lambda)) \sum_{k=0}^{\infty} Q(k+1)\hat{F}^k(\lambda), \;\; \lambda > 0. \tag{7.20}$$

Since $F(.)$ is a proper distribution function then $\hat{F}(\lambda) \uparrow 1$ as $\lambda \downarrow 0$. From this fact and the asymptotic behavior of $Q(k)$ (see Sect. 7.2, (ii)) one gets from Theorem 5, Sect. XIII.5, [6], that

$$\sum_{k=0}^{\infty} Q(k+1)\hat{F}^k(\lambda) \sim \Gamma(1-\theta)\frac{1}{(1-\hat{F}(\lambda))^{1-\theta}} L\left(\frac{1}{1-\hat{F}(\lambda)}\right), \;\; \lambda \downarrow 0.$$

From this relation and (7.20) it follows that

$$1-\hat{\Phi}(\lambda) \sim \Gamma(1-\theta)(1-\hat{F}(\lambda))^{\theta} L\left(\frac{1}{1-\hat{F}(\lambda)}\right), \ \lambda \downarrow 0. \tag{7.21}$$

Now we will use (7.14) which is equivalent to the following relation (see e.g. [6], Sect. XIII.5, or [2], Corollary 8.1.7)

$$1-\hat{F}(\lambda) \sim \lambda^{\beta} \mathscr{L}(1/\lambda), \ \lambda \downarrow 0. \tag{7.22}$$

From (7.21) and (7.22) we get

$$\begin{aligned} 1-\hat{\Phi}(\lambda) &\sim \Gamma(1-\theta)(\lambda^{\beta}\mathscr{L}(1/\lambda))^{\theta} L\left(\frac{1}{\lambda^{\beta}\mathscr{L}(1/\lambda)}\right) \\ &\sim \Gamma(1-\theta)\lambda^{\beta\theta}(\mathscr{L}(1/\lambda))^{\theta} L\left(\frac{1}{\lambda^{\beta}\mathscr{L}(1/\lambda)}\right), \ \lambda \downarrow 0. \end{aligned}$$

The last relation is equivalent to (see e.g. [6], Sect. XIII.5, or [2], Corollary 8.1.7)

$$R(t) = 1-\Phi(t) \sim \frac{\Gamma(1-\theta)}{\Gamma(1-\theta\beta)} t^{-\theta\beta} \mathscr{L}^{\theta}(t) L\left(\frac{t^{\beta}}{\mathscr{L}(t)}\right), \ t \to \infty. \tag{7.23}$$

On the other hand, from (7.15) and the asymptotic of $Q(.)$ it follows that

$$Q(\tilde{r}(t)) \sim \left(\frac{t^{\beta}}{\mathscr{L}(t)}\right)^{-\theta} L\left(\frac{t^{\beta}}{\mathscr{L}(t)}\right), \ t \to \infty.$$

Now from the last relation and (7.23) we get

$$\frac{R(t)}{Q(\tilde{r}(t))} \to \frac{\Gamma(1-\theta)}{\Gamma(1-\theta\beta)}, \ t \to \infty,$$

which together with (7.10) completes the proof of (7.19). □

7.4 BGW branching processes starting with random number of particles

In this section we obtain a limit theorem for the BGW processes defined by (7.1), (7.2) under the following “branching” conditions:

(B1) The process $Z(n)$ is critical with finite variance, i.e.

$$\begin{aligned} &\mathbf{E}\,[X_i(n)] = f'(1) = 1, \\ &\mathbf{E}\,[X_i(n)(X_i(n)-1)] = f''(1) = b \in (0,\infty). \end{aligned}$$

(B2) The initial number of particles I is a positive random variable independent of the set X, with infinite mean and

$$g(s) = \mathbf{E}\left[s^I\right] = 1-(1-s)^{\theta} l\left(\frac{1}{1-s}\right),$$

where $\theta \in (0,1)$ and $l(.)$ is a slowly varying at infinity function.

The following theorem is valid for BGW branching processes starting with random number of ancestors.

Theorem 7.3. *Assume that the conditions (B1) and (B2) hold. Then*

$$\mathbf{P}(Z_n > 0) = 1-g(f_n(0)) \sim (bn)^{-\theta} l(n), \;\; n \to \infty, \tag{7.24}$$

$$\lim_{n\to\infty} \mathbf{P}(Z_n(1-f_n(0))\,|\,Z_n > 0) = \mathscr{E}_\theta, \tag{7.25}$$

where $\mathscr{E}_\theta$ is a random variable with Laplace-Stieltjes transform $\mathbf{E}\left[e^{-\lambda\mathscr{E}_\theta}\right] = 1-\lambda^\theta(1+\lambda)^{-\theta}$.

Proof. The proof of (7.24) follows from the representation

$$\mathbf{P}(Z_n > 0\,|\,Z_0 = I) = 1-g(f_n(0)) = (1-f_n(0))^\theta l\left(\frac{1}{1-f_n(0)}\right),$$

and the well known Kolmogorov's result $1-f_n(0) \sim \frac{1}{bn}$, $n \to \infty$.

For the proof of (7.25) we can use the conditional p.g.f. of the process Z_n,

$$\mathbf{E}\left[s^{Z_n}\,|\,Z_n > 0\right] = 1-\frac{1-g(f_n(s))}{1-g(f_n(0))}, \; s \in [0,1], n = 1,2,\ldots.$$

Let $\lambda > 0$ be fixed. Then

$$\mathbf{E}\left[e^{-\lambda Z_n(1-f_n(0))}\,|\,Z(n) > 0\right] = 1-\frac{1-g(f_n(e^{-\lambda(1-f_n(0))}))}{1-g(f_n(0))}.$$

Further, we have

$$\begin{aligned}&\frac{1-g(f_n(e^{-\lambda(1-f_n(0))}))}{1-g(f_n(0))}\\ &= \left(\frac{1-f_n(e^{-\lambda(1-f_n(0))})}{1-f_n(0)}\right)^\theta \frac{l\left((1-f_n(e^{-\lambda(1-f_n(0))}))^{-1}\right)}{l((1-f_n(0)^{-1}))}\end{aligned}$$

This representation, the well known Yaglom's limit theorem for critical BGW, and the uniform convergence of slowly varying functions give

$$\lim_{n\to\infty} \frac{1-g(f_n(e^{-\lambda(1-f_n(0))}))}{1-g(f_n(0))} = \frac{\lambda^\theta}{(1+\lambda)^\theta}, \ \ \lambda > 0.$$

This completes the proof of (ii). □

7.5 Limit theorems for the process $Y(t)$

Using the results from Sects. 7.3 and 7.4 we will find the limiting behavior of the process $Y(t)$.

Theorem 7.4. *Suppose the conditions (B1), (B2), and (7.13) hold. Then as* $t \to \infty$,

$$\mathbf{P}(Y(t) > 0) \sim \left(\frac{bt}{\mu}\right)^{-\theta} l(t), \tag{7.26}$$

and

$$\lim_{t\to\infty} \mathbf{P}\left(\frac{Y(t)}{t/\mu} \le x \,|\, Y(t) > 0\right) = \mathbf{P}\left(\mathscr{E}_\theta \le \frac{x}{b}\right), \quad x > 0. \tag{7.27}$$

Proof. We have that $R(t) = \mathbf{P}(Y(t) > 0) = \mathbf{P}\left(Z_{N(t)} > 0\right)$. Under the conditions of the theorem one has

$$Q(n) = 1 - g(f_n(0)) \sim (bn)^{-\theta} l(n), n \to \infty, \qquad \text{(see (7.24))},$$

and

$$K(t) = \frac{t}{\mu},\ t \to \infty, \text{ and } \ \xi = 1, \qquad \text{(see (7.17))}.$$

These relations and (7.10) complete the proof of (7.26). From the Eq. (7.5) one gets

$$\begin{aligned}
&\mathbf{P}\left(\frac{Y(t)}{t/\mu} \le x \,|\, Y(t) > 0\right) = \mathbf{P}(Y(t) \le xt/\mu \,|\, Y(t) > 0) \\
&= \int_0^\infty \mathbf{P}\left(Z_{[y]} \le \frac{xt}{\mu} \,|\, Z_{[y]} > 0\right) d\mathbf{P}\left(N(t) \le y \,|\, Z_{N(t)} > 0\right)
\end{aligned}$$

[Substituting $y = (ut)/\mu$]

$$\begin{aligned}
&= \int_0^\infty \mathbf{P}\left(Z_{[ut/\mu]} \le xt/\mu \,|\, Z_{[ut/\mu]} > 0\right) d\mathbf{P}\left(N(t) \le ut/\mu \,|\, Z_{N(t)} > 0\right) \\
&= \int_0^\infty \mathbf{P}\left(\frac{Z_{[ut/\mu]}}{b[ut/\mu]} \le \frac{xt/\mu}{b[ut/\mu]} \,|\, Z_{[ut/\mu]} > 0\right) d\mathbf{P}\left(\frac{N(t)}{t/\mu} \le u \,|\, Z_{N(t)} > 0\right)
\end{aligned}$$

[Letting $t \to \infty$ and having in mind the limits (7.25) and (7.17) we obtain]

$$\to \int_0^\infty \mathbf{P}\left(\mathscr{E}_\theta \le \frac{x}{by}\right) d_y\mathbf{P}(1 \le y) = \mathbf{P}\left(\mathscr{E}_\theta \le \frac{x}{b}\right).$$

This completes the proof of (7.27) and the theorem. □

Theorem 7.5. *Suppose the conditions (B1), (B2) and (7.14) hold. Then as $t \to \infty$,*

$$\mathbf{P}(Y(t) > 0) \sim \frac{\Gamma(1-\theta)}{\Gamma(1-\theta\beta)} b^{-\theta} t^{-\beta\theta} L^*(t), \tag{7.28}$$

where $L^*(t) = (\mathscr{L}(t))^\theta l\left(\frac{t^\beta}{\mathscr{L}(t)}\right)$ is a s.v.f. and

$$\begin{aligned}&\lim_{t\to\infty} \mathbf{P}\left(\frac{Y(t)}{\tilde{r}(t)} \le x \,|\, Y(t) > 0\right)\\ &= \frac{\Gamma(1-\theta\beta)}{\Gamma(1-\theta)} \int_0^\infty \mathbf{P}\left(\mathscr{E}_\theta \le \frac{x}{by}\right) y^{-\theta} d\mathbf{P}\left(W_\beta \le y\right), \ x > 0,\end{aligned} \tag{7.29}$$

where $\tilde{r}(t)$ is defined by (7.15).

Proof. Since $R(t) = \mathbf{P}(Y(t) > 0) = \mathbf{P}\left(Z_{N(t)} > 0\right)$ we have to use Eq. (7.10), i.e.

$$R(t) \sim \mathbf{E}\left[\xi^{-\theta}\right] Q(K(t)), \qquad t \to \infty.$$

Furthermore, under the conditions of the theorem one has

$$Q(n) = 1 - g(f_n(0)) \sim (bn)^{-\theta} l(n), \quad n \to \infty, \qquad \text{(see (7.24))},$$

and

$$K(t) = \tilde{r}(t) \sim \frac{t^\beta}{\mathscr{L}(t)}, \quad t \to \infty, \qquad \text{(see (7.15))}$$

$$\xi = W_\beta, \quad \text{with } \mathbf{E}\left[W_\beta^{-\theta}\right] = \frac{\Gamma(1-\theta)}{\Gamma(1-\theta\beta)} \qquad \text{(see (7.18), (7.19))}.$$

Substituting $Q(.)$, $K(.)$, and $E\left[W_\beta^{-\theta}\right]$ in the asymptotic formula for $R(t)$ one gets

$$\begin{aligned}R(t) &\sim \frac{\Gamma(1-\theta)}{\Gamma(1-\beta\theta)} b^{-\theta} (K(t))^{-\theta} l(K(t))\\ &\sim \frac{\Gamma(1-\theta)}{\Gamma(1-\beta\theta)} b^{-\theta} t^{-\theta\beta} (\mathscr{L}(t))^\theta l\left(\frac{t^\beta}{\mathscr{L}(t)}\right), \ t \to \infty,\end{aligned}$$

which completes the proof of (7.28).

From Eq. (7.5) we have that

$$\begin{aligned} D_t(x) &:= \mathbf{P}\left(\frac{Y(t)}{\tilde{r}(t)} \le x | Y(t) > 0\right) = \mathbf{P}\left(Y(t) \le x\tilde{r}(t) | Y(t) > 0\right) \\ &= \int_0^\infty \mathbf{P}\left(Z_{[y]} \le x\tilde{r}(t) | Z_{[y]} > 0\right) d\mathbf{P}\left(N(t) \le y | Z_{N(t)} > 0\right). \end{aligned}$$

The substitution $y = u\tilde{r}(t)$ in the last integral gives

$$\begin{aligned} D_t(x) &= \int_0^\infty \mathbf{P}\left(Z_{[u\tilde{r}(t)]} \le x\tilde{r}(t) \,|\, Z_{[u\tilde{r}(t)]} > 0\right) d\mathbf{P}\left(N(t) \le u\tilde{r}(t) \,|\, Z_{N(t)} > 0\right) \\ &= \int_0^\infty \mathbf{P}\left(\frac{Z_{[u\tilde{r}(t)]}}{b[u\tilde{r}(t)]} \le \frac{x\tilde{r}(t)}{b[u\tilde{r}(t)]} \,|\, Z_{[u\tilde{r}(t)]} > 0\right) d\mathbf{P}\left(\frac{N(t)}{\tilde{r}(t)} \le u \,|\, Z_{N(t)} > 0\right). \end{aligned}$$

Therefore, the relations (7.25) and (7.18) allow us to pass to the limit in the last integral, which leads to

$$\lim_{t\to\infty} D_t(x) = \int_0^\infty \mathbf{P}\left(\mathscr{E}_\theta \le \frac{x}{by}\right) d_y \frac{\mathbf{E}\left[W_\beta^{-\theta} \mathbf{I}_{\{W_\beta \le y\}}\right]}{\mathbf{E}\left[W_\beta^{-\theta}\right]}.$$

Finally, using (7.19) and the equality

$$d_y \mathbf{E}\left[W_\beta^{-\theta} \mathbf{I}_{\{W_\beta \le y\}}\right] = d_y \int_0^y z^{-\theta} d\mathbf{P}\left(W_\beta \le z\right) = y^{-\theta} d\mathbf{P}\left(W_\beta \le y\right),$$

we complete the proof of (7.29). □

7.6 Concluding remarks

Although the randomly indexed branching processes appeared as models in Financial Mathematics, it seems that they could be applied also in the Cell Biology, especially for analysis of clonal data, PCR processes or cell proliferation models considered by Crump and Mode [3]. Since the cell proliferation processes usually begin from a large random population of cells then the initial condition (B2) seems quite natural in this case, as well as the slowly extinction of the considered population obtained in (7.26) of Theorem 7.4 and (7.28) of Theorem 7.5. Note that the limiting random variable in Theorem 7.5 can be presented as a product of two independent random variables with known c.d.f. In fact, the limiting distribution (7.29) is quite new in the theory of branching processes. Finally we recall that some generalizations and new problems concerning randomly indexed branching processes are proposed in [9].

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8

Renewal measure density for distributions with regularly varying tails of order $\alpha \in (0, 1/2]$

Valentin Topchii

Abstract Increments of the renewal function related to the distributions with infinite means and regularly varying tails of orders $\alpha \in (0, 1]$ were described by Erickson in 1979 (Trans. Amer. Math. Soc. 151: 263–291, 1970). However, explicit asymptotics for the increments are known for $\alpha \in (1/2, 1]$ only. For smaller α one can get, generally speaking, only the lower limit of the increments. There are many examples showing that this statement cannot be improved in general.

We refine Erikson's results by describing sufficient conditions for regularity of the renewal measure density of the distributions with regularly varying tails with $\alpha \in (0, 1/2]$. We also discuss the reasons of non-regular behavior of the renewal function increments in the general situation.

Mathematics Subject Classification (2000): 60K05, 60E07, 60J80

Keywords: regularly varying tails of order $\alpha \in (0, 1/2]$, renewal measure density, branching random walks, attraction to a stable law.

8.1 Introduction

One of the important characteristics of the continuous time symmetric catalytic random walks on the multi-dimensional integer lattice with only source at the origin is the average number of particles at the origin [2]. Vatutin and Topchii [3] reduced the study of such branching random walks to the investigation of the multi-dimensional branching Bellman-Harris processes. The expected number of particles at the origin is a solution to the well-known renewal equation. In some dimensions, the expectation is infinite. Studying the random walks in $\mathbf{R}^3$ requires explicit asymptotics for the renewal densities whose distribution belongs to the domain of attraction of stable

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laws with parameter $\alpha = 1/2$. In general, no explicit asymptotics is know for such a case and they can be found only under additional restrictions. We slightly extend this problem and describe some conditions for the case $\alpha \in (0, 1/2]$ under which one can find an explicit form of the renewal density function and analyze the role of the introduced conditions for the n-fold convolution of the initial distribution.

Let $F_\alpha(t)$ be a distribution function with regularly varying tail of order $\alpha \in (0,1)$ with $F_\alpha(0) = 0$, and let $L(t)$ be a function slowly varying as $t \to \infty$ [4, Chap. VIII Sect. 8] such that

$$1 - F_\alpha(t) \underset{t\to\infty}{\sim} t^{-\alpha} L(t). \tag{8.1}$$

Here and below, the symbol $\underset{t\to\infty}{\sim}$ denotes convergence of the ratio of the left- and right-hand sides to 1.

We study the density of the renewal function $U(t) \overset{\text{def}}{=} \sum\limits_{n=0}^{\infty} F_\alpha^{*n}(t)$ for $t > 0$, where the upper index $*n$ denotes the usual n-fold convolutions of distributions (or densities).

Theorem 8.1 below is a restatement of the respective results from [1].

Theorem 8.1. *If condition (8.1) hold, then for every fixed $h > 0$*

$$U(t+h) - U(t) \underset{t\to\infty}{\sim} \frac{hC_\alpha}{\int_0^t (1 - F_\alpha(u))du}, \quad \textit{for} \;\; 1/2 < \alpha \le 1, \tag{8.2}$$

where $C_\alpha = \Gamma^{-1}(\alpha)\Gamma^{-1}(2-\alpha)$ or $C_\alpha(1-\alpha) = \frac{\sin \pi\alpha}{\pi}$ for $\alpha \neq 1$, and $\Gamma(\alpha)$ is the Euler gamma function, and

$$\liminf_{t\to\infty} t^{1-\alpha} L(t)(U(t+h) - U(t)) = h\frac{\sin \pi\alpha}{\pi}, \quad \textit{for} \;\; 0 < \alpha \le 1/2, \tag{8.3}$$

Equation (8.2) gives the asymptotic of the renewal density function for $1/2 < \alpha \le 1$, if it exists. There are many examples of the distributions F_α with $0 < \alpha \le 1/2$ showing that the respective densities and increments of $F_\alpha^{*n}(t)$ can be infinitely large with respect to $t^{\alpha-1}/L(t)$, i.e. estimate (8.3) cannot be refined to the form (8.2). Thus, it is impossible to have an analog of (8.2) for $0 < \alpha \le 1/2$ without additional conditions on the increments of $F_\alpha(t)$. The point is that condition (8.1) implies

$$F_\alpha(t+h) - F_\alpha(t) \underset{t\to\infty}{=} o(t^{-\alpha} L(t)), \tag{8.4}$$

but the increment of the renewal function should be of order $t^{\alpha-1}L^{-1}(t)$. This term can be infinitely small with respect to the increment from (8.4). The fact of possible dominating influence of starting summands of the renewal function is a basis for counter-examples and irregular behavior of increments of the renewal function or its density for $0 < \alpha \le 1/2$.

The aim of the present article is to find some conditions on the density of $F_\alpha(t)$ providing an analog of estimate (8.2) in the case $0 < \alpha \le 1/2$. It is a folklore that a sufficient condition for (8.2) to hold is the monotonicity of the density for $t \ge t_0$. However, no published proofs are known to the author.

8.2 Effects of attraction to a stable law

By Theorem 2.6.1 in [5], the distribution of $F_\alpha(t)$ from (8.1) with support on $\mathbf{R}_+ \overset{\text{def}}{=} [0,\infty)$ belongs to the domain of attraction of a stable law of order α whose distribution function we denote by $G_\alpha(t)$. According to Theorem 2.2.2 in [5] with $\beta = 1$ corresponding to distributions on $\mathbf{R}_+$ and Remark 2 in [5, p. 54] the logarithm of characteristic function for $G_\alpha(t)$ has the form,

$$-c_\alpha|\theta|^\alpha\left(1 - i\frac{|\theta|}{\theta}\tan\frac{\pi\alpha}{2}\right) = -\Gamma(1-\alpha)|\theta|^\alpha\exp\left\{-\frac{i\pi\alpha|\theta|}{2\theta}\right\}$$
$$\overset{\text{def}}{=} c_{1,\alpha}|\theta|^\alpha\exp\left\{-\frac{i\pi\alpha|\theta|}{2\theta}\right\},$$

where $c_\alpha = \Gamma(1-\alpha)\cos(\alpha\pi/2)$.

Theorem 2.1.1 in [5] states that there is a sequence $B_n = n^{1/\alpha}h(n)$, where $h(n)$ is an explicitly defined slowly varying function as $n \to \infty$, such that

$$F_\alpha^{*n}(B_n x) \underset{n\to\infty}{\to} G_\alpha(x).$$

In general, we should check existence of sequences A_n and B_n such that the normed sums $\left(\sum_{j=1}^n \xi_\alpha^{(j)} - A_n\right)B_n^{-1}$ converge in distribution to a stable law of order $\alpha < 1$, where $\xi_\alpha^{(j)}$ are independent identically distributed random variables with distribution function $F_\alpha(t)$ [4, Chap. XVII, Sect. 5, the remark following Theorem 3]. In this case one may take $A_n = 0$, and the theorem gives the asymptotic form of B_n shown in Eq. (5.23) in [4, Chap. XVII, Sect. 5] or in [5, p. 94, Eq. (2.6.4)]. In our notation,

$$n(1 - F_\alpha(B_n x)) \underset{n\to\infty}{\to} cx^{-\alpha}, \tag{8.5}$$

where $c > 0$ is arbitrary and fixed. We set $c = 1$.

Rewrite the Eq. (8.5) for $t \in \mathbf{R}_+$ as follows,

$$t(1 - F_\alpha(B_t x)) = t(B_t x)^{-\alpha}L(B_t x) \underset{t\to\infty}{\to} x^{-\alpha},$$

or

$$B_t \underset{t\to\infty}{\sim} t^{1/\alpha}h(t),$$

where $h(t) \underset{t\to\infty}{\sim} L^{1/\alpha}(B_t)$ and in Karamata's representation [4, Chap. VIII, Sect. 8, formula (9.9)] the multiplier in front of the exponential can be taken constant. In this case $h'(t) \underset{t\to\infty}{=} o(h(t)/t)$. Here and below we assume that the slowly varying function $L(\cdot)$ satisfies the mentioned regularity condition, and $B_n = n^{1/\alpha}h(n)$.

If $F_\alpha^{*N}(t)$ has a bounded density for some $N > 0$, i.e.,

$$\max_x f_\alpha^{*N}(x) < \infty, \tag{8.6}$$

it follows that $F_\alpha^{*n}(t)$ has a bounded density for every $n \geq N$. Note that the convolution $F_\alpha^{*n}(t)$ may have no density for some $n < N$.

By Theorem 4.3.1 in [5], in this case

$$\max_x |B_n f_\alpha^{*n}(B_n x) - g_\alpha(x)| \overset{\text{def}}{=} \Delta_n \underset{n\to\infty}{\to} 0, \tag{8.7}$$

or

$$\max_x |f_\alpha^{*n}(x) - B_n^{-1} g_\alpha(x B_n^{-1})| = \Delta_n B_n^{-1}. \tag{8.8}$$

This fact allows us to describe the asymptotic of a sum related with the density of the renewal function. The case $\alpha \in (1/2, 1]$ has been treated in Theorem 8.1. Therefore, we will study the mentioned asymptotic for $\alpha \in (0, 1/2]$.

Fix a monotone step function $n_1(t) \in \mathbf{N}$ satisfying $tB_{n_1(t)} \underset{t\to\infty}{\sim} 1$. For all $N_0 \in \mathbf{N}$ define $n_0(t) = n_0(t, N_0) \overset{\text{def}}{=} n_1(N_0^{-1/\alpha} t)$. Then $t \underset{t\to\infty}{\sim} L^{1/\alpha}(t) n_1^{1/\alpha}(t)$, $n_1(t) \underset{t\to\infty}{\sim} t^\alpha / L(t)$ and $n_0(t) \overset{\text{def}}{=} n_1(N_0^{-1/\alpha} t) \underset{t\to\infty}{\sim} N_0^{-1} n_1(t)$.

Theorem 8.2. *Let $F_\alpha(t)$ be the distribution function satisfying condition (8.1) with $\alpha \in (0, 1/2]$, and let the density of $F_\alpha^{*N}(t)$ exist and bounded for some $N > 0$, i.e. condition (8.6) holds true. Then uniformly in integer fixed N_0 such that $n_0(t) > N$, the density of the renewal function tail with increasing cut off level has the asymptotic,*

$$\sum_{j=n_0(t)}^{\infty} f_\alpha^{*j}(t) \underset{t\to\infty}{=} \frac{t^{\alpha-1} \sin \pi\alpha}{\pi L(t)} \left(1 + N_0^{1/\alpha - 1} o(1) + N_0^{-2} O(1)\right).$$

Proof. The integral of the density $g_\alpha(t)$ of $G_\alpha(t)$ on $\mathbf{R}_+$ equals 1, therefore for each $\delta > 0$ there exist $\varepsilon > 0$ and $\varepsilon < N_\varepsilon < \infty$ such that

$$1 > \int_\varepsilon^{N_\varepsilon} g_\alpha(x) dx > 1 - \delta.$$

Let $x_j(t) \overset{\text{def}}{=} (tB_j^{-1})^\alpha h^\alpha(j)/L(t)$, $j \geq n_0(t)$, then $x_{n_0(t)}(t) \underset{t\to\infty}{\sim} N_0$,

$$\begin{aligned} -\Delta x_j(t) &\overset{\text{def}}{=} x_j(t) - x_{j+1}(t) = \frac{t^\alpha (B_{j+1}^\alpha h^\alpha(j) - B_j^\alpha h^\alpha(j+1))}{L(t) B_{j+1}^\alpha B_j^\alpha} \\ &\underset{j\to\infty}{=} \frac{t^\alpha h^{2\alpha}(j)(1+o(1))}{L(t)(B_j^\alpha)^2} = \frac{L(t) x_j^2(t)(1+o(1))}{t^\alpha} \frac{tL^{1/\alpha}(t)}{h(j) x_j^{1/\alpha}(t) B_j}. \end{aligned}$$

Using (8.8), one gets,

$$\sum_{j=n_0(t)}^{\infty} f_\alpha^{*j}(t) = \sum_{j=n_0(t)}^{\infty} \frac{\Delta_j}{B_j} - \sum_{j=n_0(t)}^{\infty} \frac{t^{\alpha-1} h(j) x_j^{1/\alpha}(t)(1+o(1))}{\alpha L(t) L^{1/\alpha}(t) x_j^2(t)} g_\alpha(x_j^{1/\alpha}) \Delta x_j(t). \tag{8.9}$$

If tB_j^{-1} is bounded away from 0 and infinity, the $h^{\alpha}(j)/L(t) \underset{t\to\infty}{\longrightarrow} 1$. This fact implies boundedness of $x_j(t)$ away from 0 and infinity. If $tB_j^{-1} \to 0$, which is true as $j/n_1(t) \to \infty$, then $x_j(t) \to 0$. For each fixed N_0, the condition $n_0(t) \underset{t\to\infty}{\longrightarrow} \infty$ and convergence $\sup_{j\geq n_0(t)} \Delta x_j(t) \underset{t\to\infty}{\sim} \Delta x_{n_0(t)}(t) \underset{t\to\infty}{\sim} N_0^2 L(t) t^{-\alpha} \underset{t\to\infty}{\longrightarrow} 0$ holds. Clearly,

$$-\sum_{j=n_0(t)}^{\infty} \frac{h(j)x_j^{1/\alpha}(t)(1+o(1))}{L^{1/\alpha}(t)x_j^2(t)} g_\alpha(x_j^{1/\alpha})\Delta x_j(t) \underset{t\to\infty}{\longrightarrow} \int_0^{N_0} u^{1/\alpha-2} g_\alpha(u^{1/\alpha})du,$$

and due to Theorem 1 in [4, Chap. XVII, Sect. 9]

$$\begin{aligned}\sum_{j=n_0(t)}^{\infty} \frac{1}{B_j} \underset{n_0(t)\to\infty}{\sim} \sum_{j=n_0(t)}^{\infty} \frac{1}{j^{1/\alpha}h(j)} &\underset{n_0(t)\to\infty}{\sim} \frac{\alpha n_0^{-1/\alpha+1}(t)}{(1-\alpha)h(n_0(t))} \\ &\underset{t\to\infty}{\sim} \frac{\alpha}{1-\alpha} N_0^{1/\alpha-1} t^{\alpha-1}/L(t).\end{aligned}$$

For each fixed N_0 such that $N_0 L^{-1}(t)t^{\alpha} > N$ by (8.7) and representations above, Eq. (8.9) is rewritten as an estimate uniform in N_0,

$$\sum_{j=n_0(t)}^{\infty} f_\alpha^{*j}(t) \underset{t\to\infty}{=} \frac{\alpha t^{\alpha-1}}{L(t)} \left(\int_0^{N_0^{1/\alpha}} g_\alpha(u)u^{-\alpha}du + N_0^{1/\alpha-1}o(1) \right). \tag{8.10}$$

By Theorem 2.4.1 in [5]

$$g_\alpha(t) \underset{t\to\infty}{\sim} \pi^{-1}\sin(\pi\alpha)\alpha\Gamma(\alpha)t^{-1-\alpha}.$$

Hence,

$$\int_{N_0}^{1/\alpha} g_\alpha(u)u^{-\alpha}du \underset{N_0\to\infty}{=} O\left(N_0^{-2}\right)$$

and (8.10) takes the form,

$$\sum_{j=n_0(t)}^{\infty} f_\alpha^{*j}(t) \underset{t\to\infty}{=} \frac{t^{\alpha-1}}{\alpha L(t)} \left(\int_0^{\infty} g_\alpha(u)u^{-\alpha}du + N_0^{1/\alpha-1}o(1) + N_0^{-2}O(1) \right). \tag{8.11}$$

Now we calculate $I_\alpha \overset{\text{def}}{=} \alpha\int_0^\infty g_\alpha(u)u^{-\alpha}du$. To this aim we observe that by Theorem 2.3.1 and relation (2.3.1) in [5], $g_\alpha(x) = x^{-1}\Phi_1\left(x^{-\alpha}c_{1,\alpha}\right)$. The explicit expression for $\Phi_1(x)$ (in our case with $\beta = 1$) is given by the integral,

$$I_\alpha = \frac{1}{c_{1,\alpha}} \int_0^\infty \Phi_1(u)du = \frac{1}{\pi\Gamma(1-\alpha)} \int_0^\infty \int_0^\infty e^{-t-t^{\alpha}u\cos\pi\alpha} \sin(t^{\alpha}u\sin\pi\alpha)dtdu.$$

For $\alpha \neq 1/2$, the double integral converges and one can change the order of integrals. By formula 472 1, p. 555 in [6]

$$\int_0^\infty e^{-t^\alpha u \cos \pi\alpha} \sin(t^\alpha u \sin \pi\alpha) du = t^{-\alpha} \sin \pi\alpha.$$

Hence,

$$I_\alpha = \frac{\sin \pi\alpha}{\pi\Gamma(1-\alpha)} \int_0^\infty e^{-t} t^{-\alpha} dt = \frac{\sin \pi\alpha}{\pi}.$$

Along with (8.11) it proves Theorem 8.2 for $\alpha \neq 1/2$.

If $\alpha = 1/2$,

$$I_\alpha = \frac{1}{\pi\Gamma(1/2)} \int_0^\infty \int_0^\infty e^{-t} \sin(\sqrt{t}u) dt du$$

and straightforward calculations are feasible. By changing variables $\sqrt{t} = u$ and formula 3.952 1 in [7] one gets,

$$\int_0^\infty e^{-t} \sin(\sqrt{t}u) dt = \frac{u\sqrt{\pi}}{2} e^{-u^2/4}.$$

Thus

$$I_\alpha = \frac{1}{\pi} \int_0^\infty \frac{u}{2} e^{-u^2/4} du = \pi^{-1},$$

which finishes the proof of Theorem 8.2. □

8.3 Asymptotics of renewal function density

In order to get a really useful renewal theorem for density $u(t) \overset{\text{def}}{=} \sum_{j=1}^{\infty} f_\alpha^{*j}(t)$, we suppose that for

$$n_0(t) \underset{t\to\infty}{\sim} N_0^{-1} L^{-1}(t) t^\alpha \tag{8.12}$$

the condition

$$\underline{u}(t) \overset{\text{def}}{=} \sum_{j=1}^{n_0(t)-1} f_\alpha^{*j}(t) \underset{t\to\infty}{=} o\left(\frac{t^{\alpha-1}}{L(t)}\right) \tag{8.13}$$

is valid as $N_0 \to \infty$.

Note that in contrast with Theorem 8.2 we require the existence of the density $f_\alpha(t)$.

Evidently, a necessary condition for (8.13) is

$$f_\alpha(t) = o\left(\frac{t^{\alpha-1}}{L(t)}\right). \tag{8.14}$$

We suggest a sufficient condition for (8.13) to hold which generalizes the (folklore) claim that for (8.13) to be valid the density must be monotone for the arguments large enough.

Introduce two auxiliary differentiable decreasing functions,

$$f_{0,\alpha}(t) \overset{\text{def}}{=} \min(1, t^{-\alpha}) L_1(t) \text{ and } f_{1,\alpha}(t) \overset{\text{def}}{=} \min(1, t^{-1-\alpha}) L_1(t),$$

where $L_1(t) \underset{t\to\infty}{\sim} L(t)$ and $L_1'(t) \underset{t\to\infty}{=} o(L(t)/t)$. The last always exists and corresponds to the choice $a(x) \equiv const$ in Karamata's representation for slowly varying functions [4, Chap. VIII Sect. 9, formula (9.9)].

Below we assume that there exist $t_0 > 0$ and a constant $c \in \mathbf{R}_+$ such that the estimate

$$f_\alpha(t) \le c f_{1,\alpha}(t) \tag{8.15}$$

is true for fixed $\alpha \in (0, 1/2]$ and for all $t > t_0$. The case $\alpha \in (1/2, 1)$ is omitted because condition (8.15) is not needed for this case and the proofs have to be changed in a natural way.

Fix t_0 and $T_0 > 4t_0$ large enough. We evaluate the derivatives of the functions $g(t) = t^{-1-k\alpha} L_1^k(t) = f_{0,\alpha}^k(t) t^{-1} = f_{0,\alpha}^{k-1}(t) f_{1,\alpha}(t)$, for $k \in N$ and $t > T_0$ large enough. Let $c_0(2) = c_0(2, T_0) > 2^\alpha$ and $c_1(2) = c_1(2, T_0) > 2^{1+\alpha}$ be defined by the relations

$$c_0(2) \overset{\text{def}}{=} \sup_{T_0 < t} \frac{f_{0,\alpha}(t/2)}{f_{0,\alpha}(t)}, \quad c_1(2) \overset{\text{def}}{=} \sup_{T_0 < t, t/2 \le u \le t} \frac{f'_{0,\alpha}(u)}{f'_{0,\alpha}(t)}.$$

Note that both functions are non-increasing in T_0 and

$$\lim_{T_0\to\infty} c_0(2) = 2^\alpha \text{ and } \lim_{T_0\to\infty} c_1(2) = 2^{1+\alpha}.$$

In view of (8.15) there exists a constant $c(1) > 0$ such that for every $t > T_0$ and $j \in N$

$$\int_0^{t/2} f_\alpha(t-u) f_\alpha^{*j}(u)du \le c f_{1,\alpha}(t) + cc(1) j f_{0,\alpha}(t) f_{1,\alpha}(t). \tag{8.16}$$

Indeed,

$$\begin{aligned}
&\int_0^{t/2} f_\alpha(t-u) f_\alpha^{*j}(u)du \\
&\qquad \le c f_{1,\alpha}(t) \int_0^{t/2} f_\alpha^{*j}(u)du + c \int_0^{t/2} f_\alpha^{*j}(u)(f_{1,\alpha}(t-u) - f_{1,\alpha}(t))du \\
&\qquad \le c f_{1,\alpha}(t) - c \int_0^{t/2} f_\alpha^{*j}(u) \int_0^u f'_{1,\alpha}(t-v)dvdu \\
&\qquad \le c f_{1,\alpha}(t) - cc_1(2) f'_{1,\alpha}(t) \int_0^{t/2} u f_\alpha^{*j}(u)du.
\end{aligned}$$

In view of the definition of $f_{1,\alpha}(t)$, the well-known properties of regularly varying functions [4, Chap. VIII Sect. 9] and their integrals and evident inequality $E(\eta_1 + \eta_2)I(\eta_1 + \eta_2 < z) \le E\eta_1 I(\eta_1 < z) + E\eta_2 I(\eta_2 < z)$ for non-negative random variables this proves Eq. (8.16).

It follows from the mean value theorem for differentiable functions that

$$\int_{t/2}^{t} f_\alpha(t-u)(g(u)-g(t))du \le \sup_{t/2\le v\le t} |g'(v)| \int_{t/2}^{t} f_\alpha(t-u)(t-u)du.$$

Modifying the proof of (8.16) in a natural way we can show that there exists a constant $c(2) = c(2,T_0) > 0$ such that for every $t > 2T_0$ and $k \ge 0$

$$\int_{t/2}^{t} f_\alpha(t-u) f_{0,\alpha}^{k}(u) f_{1,\alpha}(u)du \\ \le f_{0,\alpha}^{k}(t) f_{1,\alpha}(t) + c(2)(k+1)c_0^k(2) f_{0,\alpha}^{k+1}(t) f_{1,\alpha}(t). \quad (8.17)$$

Indeed,

$$\begin{aligned}
&\int_{t/2}^{t} f_\alpha(t-u) f_{0,\alpha}^{k}(u) f_{1,\alpha}(u)du \\
&\quad \le f_{0,\alpha}^{k}(t) f_{1,\alpha}(t) + \int_{t/2}^{t} f_\alpha(t-u)\left(f_{0,\alpha}^{k}(u) f_{1,\alpha}(u) - f_{0,\alpha}^{k}(t) f_{1,\alpha}(t)\right)du \\
&\quad \le f_{0,\alpha}^{k}(t) f_{1,\alpha}(t) + \sup_{t/2\le v\le t} \left|\left(v^{-(k+1)\alpha-1} L_1^{k+1}(v)\right)'\right| \int_{t/2}^{t} f_\alpha(t-u)(t-u)du \\
&\quad \le f_{0,\alpha}^{k}(t) f_{1,\alpha}(t) + c \sup_{t/2\le v\le t} \left|\left(v^{-(k+1)\alpha-1} L_1^{k+1}(v)\right)'\right| \int_{0}^{t/2} f_{1,\alpha}(u)udu.
\end{aligned}$$

By (8.16) and (8.17) we conclude that

$$f_\alpha^{*2}(t) = \int_0^t f_\alpha(t-u) f_\alpha(u)du \le 2c f_{1,\alpha}(t) + c(c(1)+c(2)) f_{0,\alpha}(t) f_{1,\alpha}(t). \quad (8.18)$$

Note that condition (8.12) may be written as

$$n_0(t) \underset{t\to\infty}{\sim} N_0^{-1} f_{0,\alpha}^{-1}(t).$$

Therefore, for t and N_0 large enough and every $j < n_0(t)$ we have

$$\sup_{j\le n_0(t)} j f_{0,\alpha}(t) \underset{n_0(t),N_0\to\infty}{\longrightarrow} 0. \quad (8.19)$$

Now we demonstrate by induction that for every $j < n_0(t)$

$$f_\alpha^{*j}(t) \le jc f_{1,\alpha}(t) + j^2 c(c(1)+c(2)) f_{0,\alpha}(t) f_{1,\alpha}(t). \quad (8.20)$$

We use (8.18) and (8.19) as the starting step of induction.
Assume that (8.20) is true for $j \le n < n_0(t) - 1$ and prove it for $j = n+1$.
By induction hypothesis and (8.17)

$$\int_{t/2}^{t} f_\alpha(t-u) f_\alpha^{*n}(u)du \le nc \int_{t/2}^{t} f_\alpha(t-u) f_{1,\alpha}(u)du$$
$$+ n^2 c(c(1)+c(2)) \int_{t/2}^{t} f_\alpha(t-u) f_{0,\alpha}(u) f_{1,\alpha}(u)du$$
$$\le ncf_{1,\alpha}(t) + ncc(2) f_{0,\alpha}(t) f_{1,\alpha}(t) + n^2 c(c(1)+c(2)) f_{0,\alpha}(t) f_{1,\alpha}(t)$$
$$+ 2n^2 c(c(1)+c(2)) c(2) c_0(2) f_{0,\alpha}^2(t) f_{1,\alpha}(t)$$

In view of (8.19) for $n < n_0(t)$ and T_0 and N_0 large enough, the quantity $2n(c(1)+c(2))c_0(2)f_{0,\alpha}(t)$ is negligibly small. Fix the low bounds of the parameters T_0 and N_0 such that the mentioned quantity is less than 1. Then the last inequality for the integral and (8.16) give,

$$f_\alpha^{*(n+1)}(t) \le (n+1)cf_{1,\alpha}(t) + (2n+n^2)c(c(1)+c(2)) f_{0,\alpha}(t) f_{1,\alpha}(t),$$

which justifies the induction transition $n \to n+1$.

Using (8.20) we demonstrate (8.13). By the inequality

$$\underline{u}(t) \le cf_{1,\alpha}(t) \sum_{j=1}^{n_0(t)-1} j + c(c(1)+c(2)) f_{0,\alpha}(t) f_{1,\alpha}(t) \sum_{j=1}^{n_0(t)-1} j^2$$

and (8.12) one can show that there is a constant $\tilde{c}$, and values T_0 and N_0 large enough such that the inequality

$$\underline{u}(t) \le cf_{1,\alpha}(t) n_0^2(t) + c(c(1)+c(2)) f_{0,\alpha}(t) f_{1,\alpha}(t) n_0^3(t) \le \tilde{c} \frac{t^{\alpha-1}}{N_0^2 L(t)}$$

holds for $t > T_0$.

Taking into account that N_0 can be selected arbitrary and recalling Theorem 8.2, we see that the following statement is valid:

Theorem 8.3. *Let $F_\alpha(t)$ be an absolute continuous distribution function satisfying condition (8.1) with $\alpha \in (0,1/2]$, and let its density $f_\alpha(t)$ satisfy conditions (8.6) and (8.15). Then the density of the renewal function has the asymptotic representation*

$$u(t) \underset{t\to\infty}{\sim} \frac{t^{\alpha-1} \sin \pi\alpha}{\pi L(t)}.$$

Remark 8.1. Evidently, Theorem 8.3 remains valid if condition (8.15) is replaced by conditions (8.14) and

$$f_\alpha^{*m}(t) \le cf_{1,\alpha}(t)$$

for some $m > 1$.

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Part III
Limit Theorems and Statistics

9

Approximation of a sum of martingale differences generated by a bootstrap branching process

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Abstract Let $\{Z(k), k \geq 0\}$ be a branching stochastic process with non-stationary immigration given by offspring distribution $\{p_j(\theta), j \geq 0\}$ depending on unknown parameter $\theta \in \Theta$. We estimate θ by an estimator $\hat{\theta}_n$ based on sample $\mathscr{X}_n = \{Z(i), i = 1, \ldots, n\}$. Given $\mathscr{X}_n$, we generate bootstrap branching process $\{Z^{\mathscr{X}_n}(k), k \geq 0\}$ for each $n = 1, 2, \ldots$ with offspring distribution $\{p_j(\hat{\theta}_n), j \geq 0\}$. In the paper we address the following question: How good must be estimator $\hat{\theta}_n$, the bootstrap process to have the same asymptotic properties as the original process? We obtain conditions for the estimator which are sufficient and necessary for this in critical case. To derive these conditions we investigate a weighted sum of martingale differences generated by an array of branching processes. We provide a general functional limit theorem for this sum, which includes critical or nearly critical processes with increasing or stationary immigration and with large or fixed number of initial ancestors. It also includes processes without immigration with increasing random number of initial individuals. Possible applications in estimation theory of branching processes are also be provided.

Mathematics Subject Classification (2000): 60J80

Keywords: bootstrap branching processes, conditioned process random measure, asymptotic behavior, functional limit theorem.

9.1 Introduction

We consider a discrete time branching stochastic process $\{Z(k), k \geq 0\}, Z(0) = 0$. It can be defined by two families of independent, nonnegative integer valued random

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variables $\{X_{ki}, k, i \geq 1\}$ and $\{\xi_k, k \geq 1\}$ recursively as

$$Z(k) = \sum_{i=1}^{Z(k-1)} X_{ki} + \xi_k, \quad k \geq 1. \tag{9.1}$$

Assume that X_{ki} have a common distribution for all k and i, families $\{X_{ki}\}$ and $\{\xi_k\}$ are independent. Variables X_{ki} will be interpreted as the number of offspring of the ith individual in the $(k-1)$th generation and ξ_k is the number of immigrating individuals to the kth generation. Then $Z(k)$ can be considered as the size of kth generation of the population.

In this interpretation $a = EX_{ki}$ is the mean number of offspring of a single individual. Process $Z(k)$ is called *subcritical, critical* or *supercritical* depending on $a < 1, a = 1$ or $a > 1$ respectively. The independence assumption of families $\{X_{ki}\}$ and $\{\xi_k\}$ means that reproduction and immigration processes are independent. However, in contrast of classical models, we do not assume that $\xi_k, k \geq 1$, are identically distributed, i.e. immigration rate may depend on the time of immigration.

The process with time-dependent immigration is given by the offspring distribution of $\{X_{ki}, k, i \geq 1\}$, and by the family of distributions of the number of immigrating individuals $\{\xi_k, k \geq 1\}$. We assume that the offspring distribution has the probability mass function

$$p_j(\theta) = P\{X_{ki} = j\}, \ j = 0, 1, \ldots \tag{9.2}$$

depending on unknown parameter θ, where $\theta \in \Theta \subseteq \mathbb{R}$. We also assume that ξ_k for any $k \geq 1$ follows a known distribution with the probability mass function

$$q_j(k) = P\{\xi_k = j\}, \ j = 0, 1, \ldots \tag{9.3}$$

We estimate θ by an estimator $\hat{\theta}_n$ based on sample $\mathscr{X}_n = \{Z(i), i = 1, \ldots, n\}$ and generate bootstrap branching process $\{Z^{\mathscr{X}_n}(k), k \geq 0\}$ for each $n = 1, 2, \ldots$ as following. Given $\mathscr{X}_n$, let $\{X_{ki}^{\mathscr{X}_n}, k, i \geq 1\}$ be a family of i.i.d. random variables with the probability mass function $\{p_j(\hat{\theta}_n), j = 0, 1, \ldots\}$. Now we obtain the process $\{Z^{\mathscr{X}_n}(k), k \geq 0\}$ recursively from

$$Z^{\mathscr{X}_n}(k) = \sum_{i=1}^{Z^{\mathscr{X}_n}(k-1)} X_{ki}^{\mathscr{X}_n} + \xi_k, \quad n, k \geq 1, \tag{9.4}$$

with $Z^{\mathscr{X}_n}(0) = 0$, where $\xi_k, k \geq 1$, are independent random variables with the probability mass functions $\{q_j(k), j = 0, 1, \ldots\}$.

Related to the process $\{Z^{\mathscr{X}_n}(k), k \geq 0\}$ the following question is of interest. How good must be the estimator $\hat{\theta}_n$, the bootstrap branching process $\{Z^{\mathscr{X}_n}(k), k \geq 0\}$ to have the same asymptotic properties as the process $\{Z(k), k \geq 0\}$? For example, if we denote $\mathscr{Z}_n(t) = Z([nt])/E(Z(n))$ and $\{\mathscr{Z}_n(t), t \in \mathbb{R}_+\}$ converges weakly as $n \to \infty$ to some process $\{\mathscr{Z}(t), t \in \mathbb{R}_+\}$, in Skorokhod space $D(\mathbb{R}_+, \mathbb{R}_+)$, will the same be true for $\mathscr{Z}_n^{\mathscr{X}_n}(t) = Z^{\mathscr{X}_n}([nt])/E[Z^{\mathscr{X}_n}(n)|\mathscr{X}_n]$? Similar question for the process of fluctuations of $\{Z^{\mathscr{X}_n}(k),\ k \geq 0\}$ can also be considered.

To answer these questions without concretization of the process in the sense of criticality is difficult, because the asymptotic properties of the process strictly depend on whether the process subcritical, critical or supercritical. In this paper we address the above question in the critical case.

It is clear that the problem, which we are going to consider, closely related to the question on validity of the bootstrap procedure. In particular, if the process preserves its asymptotical properties after "bootstrapping", it can be used to generate multiple bootstrap samples. These new samples can further be used in statistical inference about the process. This is very important in branching process models, since in statistics of branching processes, usually, a generation number plays the role of the sample size and, therefore, it is difficult to obtain samples of a large size. On the other hand, sometimes, in applications (for example in epidemic processes) one needs to make a decision on criticality of the processes when it is still at the early stages.

In Sect. 9.2 we provide main results giving conditions for the bootstrap process to preserve asymptotic properties of the original process. Section 9.3 contains functional limit Theorem 9.5 for a sum of martingale differences generated by array of branching processes. Since the conditioned bootstrap process is the array branching process, to prove main theorems one needs just to check conditions of corresponding consequences of Theorem 9.5. Naturally, the proof of Theorem 9.5 is based on a functional martingale central limit theorem. Detailed proofs of announced here results will be published elsewhere.

9.2 Main theorems

It follows from (9.2) that $a =: E_\theta X_{ki} = f_a(\theta)$ and $b = Var_\theta X_{ki} = f_b(\theta)$ for some functions f_a and f_b, when they do exist. Let the following assumptions be satisfied.
A1. *Function f_a is a one-to-one mapping of Θ to $[0,\infty)$ and is continuous with continuous inverse (which means that it is a homeomorphism between its domain and range).*
A2. *Function f_b is continuous on its domain.*

We note that A1 and A2 are satisfied, for example, for distributions of the power series family [1]. Given a sample $\mathscr{X}_n$, we now estimate the offspring mean a by an estimator $\hat{a}_n$ and derive the estimate of parameter θ as $\hat{\theta}_n = f_a^{-1}(\hat{a}_n)$. Let $\{Z^{\mathscr{X}_n}(k), k \geq 0\}$ be the bootstrap branching process defined by (1.4). This construction reduces the stated above problem to finding out conditions for estimator $\hat{a}_n$, which are sufficient to preserve asymptotic properties of the process. Since the weak convergence of the conditioned process $\{\mathscr{Z}_n^{\mathscr{X}_n}(t), t \in \mathbb{R}_+\}$ given $\mathscr{X}_n$ is equivalent to convergence of conditional probability measures generated by $\mathscr{Z}_n^{\mathscr{X}_n}$, now we provide necessary definitions of convergence of random probability measures defined on Skorokhod space.

Let $(\Omega, \mathscr{A}, \mathbb{P})$ be a probability space and $(D, \mathscr{B}(D))$ be a measurable Skorokhod space, where $\mathscr{B}(D)$ is the Borel field on D. A function $\mu : \Omega \times \mathscr{B} \mapsto [0,1]$ is called a random probability measure on D, if

(a) for each $B \in \mathscr{B}(D), \mu(\cdot,\, B)$ is a random variable on $(\Omega, \mathscr{A})$;

(b) for each $\omega \in \Omega, \mu(\omega,\, \cdot)$ is a probability measure on $(D, \mathscr{B}(D))$.

Definition 9.1. *Let μ_n for each n be a random probability measure on $(D, \mathscr{B}(D))$.*
(a) We say that μ_n converges weakly to μ on the set $A \in \mathscr{A}$, if for each $\omega \in A$ as $n \to \infty$

$$\int_D g(x)\mu_n(\omega, dx) \to \int_D g(x)\mu(\omega, dx)$$

for any bounded and continuous in Skorokhod metric function $g = g(x)$. If $P\{A\} = 1$, we say that μ_n converges weakly to μ almost surely.
(b) We say that μ_n converges weakly to μ in probability (in distribution), if as $n \to \infty$

$$\int_D g(x)\mu_n(\omega, dx) \overset{P(d)}{\to} \int_D g(x)\mu(\omega, dx).$$

Here and throughout the paper "$\overset{D}{\to}$", "$\overset{d}{\to}$" and "$\overset{P}{\to}$" will denote convergence of random functions in Skorokhod topology and convergence of random variables in distribution and in probability, respectively. Also $X \overset{d}{=} Y$ denotes equality of distributions. In [7], the authors discussed the weak convergence of distributions of random probability measures. We note that in the case of conditional distributions Definition 9.1 coincides with their definition of weak convergence in probability. For different modes of convergence of conditional probability distributions see also [6].

Let $X(t), X_n(t), n \geq 1$, be conditioned processes with paths on Skorokhod space $D(\mathbb{R}_+, \mathbb{R})$ and $\mu, \mu_n, n \geq 1$, be corresponding random probability measures. Convergence of conditioned processes can now be defined as following.

Definition 9.2. *We say that the sequence of conditioned processes $\{X_n, n \geq 1\}$ as $n \to \infty$ converges weakly in Skorokhod space $D(\mathbb{R}_+, \mathbb{R})$ to X on the set A, in probability or in distribution, if the sequence of corresponding random probability measures $\{\mu_n, n \geq 1\}$ converges weakly to μ on the set A, in probability or in distribution, respectively.*

If a sequence $(f(k))_{k=1}^{\infty}$ is regularly varying with exponent d, we will write $(f(k))_{k=1}^{\infty} \in R_d$. We assume that $a = EX_{ij}$ and $b = VarX_{ij}$ are finite. We also assume that $\alpha(k) =: E\xi_k < \infty$, $\beta(k) =: Var\xi_k < \infty$ for each $k \geq 1$ and $(\alpha(k))_{k=1}^{\infty} \in R_\alpha, (\beta(k))_{k=1}^{\infty} \in R_\beta$ with $\alpha, \beta \geq 0$. Then $A(a,n) = EZ(n)$ and $B^2(a,n) = VarZ(n)$ are finite for each $n \geq 1$, and by a standard technique we find that

$$A(a,n) = \sum_{i=1}^{n} \alpha(i) a^{n-i}, \quad B^2(a,n) = \Delta^2(a,n) + \sigma^2(a,n), \tag{9.5}$$

where

$$\Delta^2(a,n) = \sum_{i=1}^{n} \alpha(i) Var(X(n-i)), \quad \sigma^2(a,n) = \sum_{i=1}^{n} \beta(i) a^{2(n-i)},$$

$$Var(X(i)) = \begin{cases} \frac{b}{1-a} a^{i-1}(1-a^i), & a \neq 1, \\ \\ bi, & a = 1. \end{cases}$$

Here $\{X(i), i \geq 0\}$ is corresponding branching process without immigration with offspring distribution (9.2) and $X(0) = 1$.

In particular, we denote $A(n) = A(1,n)$, $B^2(n) = B^2(1,n)$, $\Delta^2(n) = \Delta^2(1,n)$, $\sigma^2(n) = \sigma^2(1,n)$ and put

$$\mathscr{Z}_n^{\mathscr{X}_n}(t) = \frac{Z^{\mathscr{X}_n}([nt])}{A(\hat{a}_n, n)},\ \mathscr{Y}_n^{\mathscr{X}_n}(t) = \frac{Z^{\mathscr{X}_n}([nt]) - A(\hat{a}_n, [nt])}{B(\hat{a}_n, n)}.$$

Now we provide first result for the bootstrap process. We denote
$A = \{\omega \in \Omega : n(\hat{a}_n - 1) \to 0, n \to \infty\}$, $\mu_\alpha(t) = t^{1+\alpha}, t \in \mathbb{R}_+$.

Theorem 9.1. *Let A1 and A2 be satisfied and* $\alpha(n) \to \infty$, $\beta(n) = o(n\alpha^2(n))$ *as* $n \to \infty$.
(a) Conditioned process $\{\mathscr{Z}_n^{\mathscr{X}_n} | \mathscr{X}_n\}$ *as* $n \to \infty$ *converges weakly in Skorokhod space* $D(\mathbb{R}_+, \mathbb{R}_+)$ *to* μ_α *on the set A.*
(b) If $n(\hat{a}_n - 1) \xrightarrow{P} 0$, *then* $\{\mathscr{Z}_n^{\mathscr{X}_n} | \mathscr{X}_n\}$ *as* $n \to \infty$ *converges weakly in Skorokhod space* $D(\mathbb{R}_+, \mathbb{R}_+)$ *to* μ_α *in probability.*

The next result is related to the fluctuations of the bootstrap process. Let $\bar{\xi}_k = \xi_k - \alpha(k)$, $\chi(A)$ denotes the indicator of event A and

$$\delta_n(\varepsilon) = \frac{1}{B^2(n)} \sum_{k=1}^{n} E[(\bar{\xi}_k)^2 \chi(|\bar{\xi}_k| > \varepsilon B(n))].$$

We also denote $\psi(t) = \gamma_1 t^{2+\alpha} + \gamma_2 t^{1+\beta}$, where

$$\gamma_1 = \lim_{n\to\infty} \frac{\Delta^2(n)}{B^2(n)},\ \gamma_2 = \lim_{n\to\infty} \frac{\sigma^2(n)}{B^2(n)},\ \gamma_1 + \gamma_2 = 1.$$

We need two more conditions to be satisfied.
A3. Moment $E_\theta[(X_{ki})^{2+l}]$ is a continuous function of θ for some $l > 0$.
A4. $\delta_n(\varepsilon) \to 0$ as $n \to \infty$ for each $\varepsilon > 0$.

Theorem 9.2. *Let A1-A4 be satisfied and* $\alpha(n) \to \infty$ *as* $n \to \infty$.
(a) Conditioned process $\{\mathscr{Y}_n^{\mathscr{X}_n} | \mathscr{X}_n\}$ *converges weakly in Skorokhod space* $D(\mathbb{R}_+, \mathbb{R})$ *to* $\mathscr{Y}$ *on the set A, where* $\mathscr{Y}(t) = W(\psi(t))$ *and* $W(t)$ *is the standard Wiener process.*
(b) If $n(\hat{a}_n - 1) \xrightarrow{P} 0$, *then* $\{\mathscr{Y}_n^{\mathscr{X}_n} | \mathscr{X}_n\}$ *converges weakly in Skorokhod space* $D(\mathbb{R}_+, \mathbb{R})$ *to* $\mathscr{Y}$ *in probability.*
Remarks. (a) It follows from Theorem 9.1(a) and Theorem 2.1 in [5] that the conditioned bootstrap process $\{Z^{\mathscr{X}_n}(k) | \mathscr{X}_n, k \geq 0\}$ generated by estimator $\hat{a}_n$ such that $n(\hat{a}_n - 1) \to 0$ a.s., under some conditions, a.s. has the same asymptotic behavior as the original process.

(b) Comparing Theorem 9.2(a) with Theorems 1, 2 and 3 in [4], one can see that the same is true for fluctuations of the bootstrap process.

Now we provide an example of the estimator that satisfies conditions of parts (b) of the above theorems. Let $\hat{a}_n$ be the weighted conditional least squares estimator (WCLSE), derived in [5] from a “standardized” stochastic regression equation. If the sample $\mathscr{X}_n$ is available and the immigration mean is known, it is defined as

$$\hat{a}_n = \frac{\sum_{k=1}^{n}(Z(k)-\alpha(k))}{\sum_{k=1}^{n}Z(k-1)}. \tag{9.6}$$

To provide the asymptotic distribution of $\hat{a}_n$, we assume that there exists $c \in [0,\infty]$ such that

$$\lim_{n\to\infty}\frac{\beta(n)}{n\alpha(n)} = c. \tag{9.7}$$

As it was proved in [5] (Theorem 3.1), if $a = 1$, $b \in (0,\infty)$, $\alpha(n) \to \infty$, $\beta(n) = o(n\alpha^2(n))$, condition (9.7) is satisfied and $\delta_n(\varepsilon) \to 0$ as $n \to \infty$ for each $\varepsilon > 0$, then as $n \to \infty$

$$\frac{nA(n)}{B(n)}(\hat{a}_n - a) \xrightarrow{d} (2+\alpha)\mathscr{N}(0,1). \tag{9.8}$$

Furthermore, under the above conditions, $A(n)/B(n) \to \infty$ as $n \to \infty$ and when $c = 0$ the condition $\delta_n(\varepsilon) \to 0$ is satisfied automatically. More detailed discussion and examples can be seen in [5].

From (9.8) we immediately obtain that $n(\hat{a}_n - 1) \xrightarrow{P} 0$ as $n \to \infty$. Thus the following result holds.

Corollary 9.1. *Let $\hat{a}_n$ be the WCLSE defined in (9.6), $\alpha(n) \to \infty$, $\beta(n) = o(n\alpha^2(n))$ and $\delta_n(\varepsilon) \to 0$ as $n \to \infty$.*
(a) If A1 and A2 are satisfied, then $\{\mathscr{Z}_n^{\mathscr{X}_n}|\mathscr{X}_n\}$ as $n \to \infty$ converges weakly in Skorokhod space $D(\mathbb{R}_+,\mathbb{R}_+)$ to μ_α in probability.
(b) If A1-A3 are satisfied, then $\{\mathscr{Y}_n^{\mathscr{X}_n}|\mathscr{X}_n\}$ converges weakly in Skorokhod space $D(\mathbb{R}_+,\mathbb{R})$ to $\mathscr{Y}$ in probability, where $\mathscr{Y}(t) = W(\psi(t))$.
The next theorem is related to the case

$$n(\hat{a}_n - 1) \xrightarrow{d} W_0 \tag{9.9}$$

as $n \to \infty$, where W_0 is a random variable. We denote

$$\mu_\alpha(d,t) = \int_0^t u^\alpha e^{d(t-u)}du,\ \pi_\alpha(d,t) = \frac{\mu_\alpha(d,t)}{\mu_\alpha(d,1)}.$$

Theorem 9.3. *If A1, A2 and (9.9) are satisfied and $\alpha(n) \to \infty$, $\beta(n) = o(n\alpha^2(n))$ as $n \to \infty$, then $\{\mathscr{Z}_n^{\mathscr{X}_n}|\mathscr{X}_n\}$ as $n \to \infty$ converges weakly in Skorokhod space $D(\mathbb{R}_+,\mathbb{R}_+)$ to $\pi_\alpha(W_0,\cdot)$ in distribution.*

Let $(a_n)_{n=1}^{\infty}$ be a sequence of positive numbers, such that $n(a_n - 1) \to d \in \mathbb{R}$ as $n \to \infty$. We assume that there exist limits

$$\lim_{n\to\infty}\frac{\Delta^2(a_n,n)}{B^2(a_n,n)}=\gamma_1(d),\ \lim_{n\to\infty}\frac{\sigma^2(a_n,n)}{B^2(a_n,n)}=\gamma_2(d). \tag{9.10}$$

Naturally $\gamma_1(d)+\gamma_2(d)=1$ for each d.

To provide the next theorem, we need some additional notation. We denote

$$\nu_\alpha(d,t)=\int_0^t u^\alpha e^{d(t-u)}(1-e^{d(t-u)})du,\ \nabla_\beta(d,t)=\int_0^t u^\beta e^{2d(t-u)}du, \tag{9.11}$$

$$\psi(d,t)=\frac{\gamma_1(d)d}{\nu_\alpha(d,1)}\int_0^t \mu_\alpha(d,u)e^{2d(t-u)}du+\frac{\gamma_2(d)}{\nabla_\beta(d,1)}\int_0^t u^\beta e^{2d(t-u)}du. \tag{9.12}$$

It is clear that limits (9.10) do exist, if ratio $\sigma^2(a_n,n)/\Delta^2(a_n,n)$ as $n\to\infty$ has a (finite or infinite) limit. It is also not difficult to show that

$$\lim_{n\to\infty}\frac{\sigma^2(a_n,n)}{\Delta^2(a_n,n)}=\frac{bc}{d}\nu(d,1)\nabla_\beta(d,1) \tag{9.13}$$

under our conditions, where c is defined in (9.7).

Theorem 9.4. *If A1–A4 and (9.9) are satisfied and $\alpha(n)\to\infty$ as $n\to\infty$, then the process $\{\mathscr{Y}_n^{\mathscr{X}_n}|\mathscr{X}_n\}$ as $n\to\infty$ converges weakly in Skorokhod space $D(\mathbb{R}_+,\mathbb{R})$ to $\mathscr{Y}(W_0,\cdot)$ in distribution, where $\mathscr{Y}(W_0,t)=W(\psi(W_0,t))$.*

Remarks. (a) Theorems 9.3 and 9.4 show that, when the estimator $\hat{a}_n$ is such that (9.9) holds with $P(W_0=0)<1$, then the asymptotic behavior of the bootstrap process is different from the behavior of the original process. In other words, condition $n(\hat{a}_n-1)\to 0$ as $n\to\infty$ a.s. or in probability is necessary for the conditioned bootstrap process to have the same asymptotic behavior as the initial process in the sense of convergence a.s. or in probability, respectively.

(b) It follows from Theorem 3.2 in [5] that convergence (9.9) holds, for example, when ratio $n\alpha^2(n)/\beta(n)$ has a finite limit. In this case W_0 can be expressed in terms of certain functionals of the Wiener process.

9.3 Array of processes

In this section we provide a functional limit theorem for an array of branching processes, which will be used in the proof of our theorems. Let $\{X_{ki}^{(n)},k,i\geq 1\}$ and $\{\xi_k^{(n)},k\geq 0\}$ be two families of independent, nonnegative and integer valued random variables for each $n\in\mathbb{N}$. We consider a weighted sum of martingale-differences generated by sequence of branching processes $(Z^{(n)}(k),k\geq 0)_{n\geq 1}$ defined recursively as

$$Z^{(n)}(k)=\sum_{i=1}^{Z^{(n)}(k-1)}X_{ki}^{(n)}+\xi_k^{(n)},\quad k,n\geq 1, \tag{9.14}$$

with $Z^{(n)}(0) = \xi_0^{(n)}, n \geq 1$. As before, we assume that $X_{ki}^{(n)}$ have a common distribution for all k and i, and families $\{X_{ki}^{(n)}\}$ and $\{\xi_k^{(n)}\}$ are independent. Variables $X_{ki}^{(n)}$ will be interpreted as the number of offspring of the ith individual in the $(k-1)$th generation and $\xi_k^{(n)}$ is the number of immigrating individuals in the kth generation. Then $Z^{(n)}(k)$ can be considered as the size of population of kth generation in nth process. Unlike the initial model, here we assume that the initial number of individuals is a random variable $\xi_0^{(n)}$, which can also be large.

Let $a_n = EX_{ki}^{(n)}$ be the mean number of offspring of a single individual in the nth process. The process with non-stationary immigration is a natural generalization of the classical model. It turned out that the long run behavior of the process is largely influenced by the non-homogeneity of the immigration process in time. As a result certain new problems, regarding the asymptotic behavior of the process when the immigration rate increases, decreases or remains bounded, emerged in the literature. Therefore, in solving these problems one needs certain regularity assumptions for parameters of the immigration process. The family of branching processes (9.14) is said to be *nearly critical* if $a_n \to 1$ as $n \to 1$.

For each $n \geq 1$, we denote by $\Im^{(n)}(k)$ the σ-algebra containing the history of the nth process up to kth generation, i.e. it is generated by $\{Z^{(n)}(0), Z^{(n)}(1), \ldots, Z^{(n)}(k)\}$. Let $M^{(n)}(k) = Z^{(n)}(k) - E[Z^{(n)}(k)|\Im^{(n)}(k-1)]$, n, $k \geq 1$ be the array of the martingale differences generated by (1.1) and $M^{(n)}(0) = Z^{(n)}(0) - EZ^{(n)}(0)$. First we investigate asymptotic behavior of the sum

$$S_n(k) = \sum_{i=0}^{k} c_n^{\rho i} M^{(n)}(i), n, k \geq 1, \tag{9.15}$$

where $(c_n, n \geq 1)$ is a sequence of positive numbers and $\rho \in \mathbb{R}$.

It turns out that various variables and processes, related to the process (9.14) can be expressed in terms of the sum (9.15). Let us consider the following trivial identity

$$a_n^{-k} Z^{(n)}(k) = \sum_{i=1}^{k} (a_n^{-i} Z^{(n)}(i) - a_n^{1-i} Z^{(n)}(i-1)) + Z^{(n)}(0).$$

Since $M^{(n)}(i) = Z^{(n)}(i) - a_n Z^{(n)}(i-1) - E\xi_i^{(n)}$ and $EZ^{(n)}(k) = a_n^k E\xi_0^{(n)} + a_n^{k-1} E\xi_1^{(n)}$ $+ \ldots + E\xi_k^{(n)}$, we easily obtain the following representation for the process:

$$Z^{(n)}(k) = a_n^k S_n(k) + EZ^{(n)}(k), \tag{9.16}$$

where $S_n(k)$ is defined by (9.15) with $\rho = -1$ and $c_n = a_n$. Equality (9.16) allows to express in terms of $S_n(k)$ "broken line" processes obtained from $Z^{(n)}(k)$ by a scaling and fluctuation processes of $Z^{(n)}(k)$ from its mean. In estimation problems of the offspring mean pivots, related to an estimator, sometimes, will have a form of certain functionals of sum (9.15).

Here we provide an approximation theorem for normalized process $S_n([nt])$, $t \in \mathbb{R}_+$ as $n \to \infty$ when the initial array of processes (9.14) contains critical or nearly critical branching processes. As applications of the obtained theorem, derive an approximation for the process $Z^{(n)}([nt])$, normalized by its mean, and by obtaining a time-changed Wiener process approximation for the fluctuations of the process around its mean. These approximations contain both cases of large and finite number of initial individuals in the process. The results obtained for the array of processes naturally include the functional limit theorems for a single critical process [4] and some of theorems for the process without immigration with random or deterministic large number of initial individuals [2, 3].

We assume that $a_n = EX_{ij}^{(n)}$ and $b_n = VarX_{ij}^{(n)}$ are finite for each $n \geq 1$ and $\alpha(n,i) = E\xi_i^{(n)} < \infty$, $\beta(n,i) = Var\xi_i^{(n)} < \infty$ for all $n \geq 1$ and $i \geq 0$. Furthermore, we assume that the following condition is satisfied.
C1. There are sequences $(\alpha(i))_{i=1}^{\infty} \in R_\alpha$ and $(\beta(i))_{i=1}^{\infty} \in R_\beta$ with $\alpha, \beta \geq 0$, such that, as $n \longrightarrow \infty$ for each $s \in \mathbb{R}_+$,

$$\max_{1 \leq k \leq ns} |\alpha(n,k) - \alpha(k)| = o(\alpha(n)), \max_{1 \leq k \leq ns} |\beta(n,k) - \beta(k)| = o(\beta(n)). \tag{9.17}$$

In the above assumptions $A_n(a_n,i) = EZ^{(n)}(i)$ and $B_n^2(a_n,i) = VarZ^{(n)}(i)$ are finite for each $n \geq 1$, $0 \leq i \leq n$, and one can find that $A_n(a_n,k) = \sum_{i=0}^{k} \alpha(n,i) a_n^{k-i}$ and $B_n^2(a_n,k) = \sum_{i=1}^{4} C_i^2(a_n,n,k)$ with $A_n(a_n,0) = \alpha(n,0), B_n^2(a_n,0) = \beta(n,0)$, where

$$C_1^2(a_n,n,k) = \sum_{i=1}^{k} \alpha(n,i) Var(X^{(n)}(k-i)), \quad C_2^2(a_n,n,k) = \sum_{i=1}^{k} \beta(n,i) a_n^{2(k-i)},$$

$$C_3^2(a_n,n,k) = \alpha(n,0) Var(X^{(n)}(k)), \; C_4^2(a_n,n,k) = \beta(n,0) a_n^k,$$

$$Var(X^{(n)}(i)) = \begin{cases} \frac{b_n}{1-a_n} a_n^{i-1}(1-a_n^i), & a_n \neq 1, \\ b_n i, & a_n = 1. \end{cases}$$

Here $X^{(n)}(i)$ is corresponding branching process without immigration and, as usual, is defined by relation

$$X^{(n)}(k) = \sum_{i=1}^{X^{(n)}(k-1)} X_{ki}^{(n)}, \quad X^{(n)}(0) = 1, \quad k,n \geq 1.$$

We also note that the following representation holds for each $n,k \geq 1$

$$Z^{(n)}(k) = \sum_{i=0}^{k} \sum_{j=1}^{\xi_i^{(n)}} X_{ij}^{(n)}(k-i) = \sum_{j=1}^{\xi_0^{(n)}} X_{0j}^{(n)}(k) + \bar{Z}^{(n)}(k), \tag{9.18}$$

where $\{X_{ij}^{(n)}(k)\}_{k \geq 0}$ is the corresponding branching process without immigration, generated by j-th immigrant in i-th generation, $\bar{Z}^{(n)}(k)$ is a process with the same immigration and offspring distributions as $Z^{(n)}(k)$ with $\bar{Z}^{(n)}(0) = 0$. We denote

$\bar{A}_n(a_n,k) = E\bar{Z}^{(n)}(k)$ and $\bar{B}_n^2(a_n,k) = Var\bar{Z}^{(n)}(k)$. Then we obtain from (9.18) that $A_n(a_n,k) = a_n^k\alpha(n,0) + \bar{A}_n(a_n,k)$ and $\bar{B}_n^2(a_n,k) = C_1^2(a_n,n,k) + C_2^2(a_n,n,k)$. In particular, when $k = n$ we use also notation $A(a_n,n) = A_n(a_n,n)$, $B^2(a_n,n) = B_n^2(a_n,n)$, $\bar{A}(a_n,n) = \bar{A}_n(a_n,n)$, $\bar{B}^2(a_n,n) = \bar{B}_n^2(a_n,n)$ and $C_i^2(a_n,n) = C_i^2(a_n,n,n), i = 1,\ldots,4$.

We denote "centered" offspring and immigration variables as $\bar{X}_{ki}^{(n)} = X_{ki}^{(n)} - a_n$, $\bar{\xi}_k^{(n)} = \xi_k^{(n)} - \alpha(n,k)$ and put $\Theta_i(a_n,n) = C_i^2(a_n,n)/B^2(a_n,n), i = 1,\ldots,4$. Let $\delta_n^{(1)}(\varepsilon) = \max\{\Theta_1(a_n,n),\Theta_3(a_n,n)\}E[(\bar{X}_{ki}^{(n)})^2\chi(|\bar{X}_{ki}^{(n)}| > \varepsilon B(a_n,n))]$ and

$$\delta_n^{(2)}(\varepsilon) = \frac{1}{B^2(a_n,n)}\sum_{k=1}^{n} E[(\bar{\xi}_k^{(n)})^2\chi(|\bar{\xi}_k^{(n)}| > \varepsilon B(a_n,n))],$$

where $\chi(A)$, as before, stands for the indicator of event A. Further, we assume that there exist limits

$$\Theta_i = \lim_{n\to\infty}\Theta_i(a_n,n),\ i = 1,\ldots,4. \tag{9.19}$$

It is clear that $0 \le \Theta_i \le 1$ and $\Theta_1 + \ldots + \Theta_4 = 1$. We approximate normalized process

$$W_n(t) = \frac{S_n([nt])}{B(a_n,n)}\ ,t \in \mathbb{R}_+,$$

weakly in Skorokhod topology. In addition to C1, we need the following conditions to be satisfied.

C2. $a_n = 1 + n^{-1}a + o(n^{-1})$ and $c_n = 1 + n^{-1}c + o(n^{-1})$ as $n \to \infty$ for some $a, c \in \mathbb{R}$.

C3. $b_n \to b \in \mathbb{R}_+$, $\delta_n^{(i)}(\varepsilon) \to 0$ as $n \to \infty$ for each $\varepsilon > 0$ and $i = 1,2$.

C4. $\Theta_4 = 0$ and $B(a_n,n)/n \to \infty$ as $n \to \infty$.

The following functions appear in the approximating processes:

$$\varphi_1(t) = \frac{a}{\nu_\alpha(a,1)}\int_0^t e^{2\rho cu}\mu_\alpha(a,u)du,\ \varphi_2(t) = \frac{1}{\nabla_\beta(a,1)}\int_0^t u^\beta e^{2\rho cu}du,$$

$$\varphi_3(t) = \frac{a}{e^a(e^a-1)}\int_0^t e^{(a+2\rho c)u}du,\ \varphi(t) = \Theta_1\varphi_1(t) + \Theta_2\varphi_2(t) + \Theta_3\varphi_3(t).$$

In particular, it is useful to note that $\mu_\alpha(a,t) = t^{\alpha+1}/(\alpha+1)$ when $a = 0$, and $\lim_{a\to 0}\nu_\alpha(a,t)/a = t^{\alpha+2}/(\alpha+1)(\alpha+2)$.

Theorem 9.5. *If conditions C1–C4 are satisfied, then* $W_n \xrightarrow{D} Y$ *as* $n \to \infty$ *weakly in Skorokhod space* $D(\mathbb{R}_+,\mathbb{R})$*, where* $Y(t) = W(\varphi(t))$*,* $t \in \mathbb{R}_+$*,* $W(t)$ *is a standard Brownian motion.*

Remarks. (a) The first part of condition C1, related to the immigration mean is satisfied when $\alpha(n) \to \infty$, if just $lim_{n\to\infty}\max_{1\le k\le ns}|\alpha(n,k) - \alpha(k)| < \infty$. In general, C1 is satisfied, for example, if there are $\varepsilon_i(n) \to 0$ as $n \to \infty$, $i = 1,2$, such that $\alpha(n,k) = \alpha(k)(1+\varepsilon_1(n))$ and $\beta(n,k) = \beta(k)(1+\varepsilon_2(n))$.

(b) Note that the Lindeberg-type condition for the family $\{X_{ki}^{(n)}, k,i \ge 1\}$ is trivially satisfied, if $\Theta_{13} = \max\{\Theta_1,\Theta_3\} = 0$. If $\Theta_{13} \ne 0$ and $E(X_{ki}^{(n)})^{2+l} < \infty$ for all $n \in \mathbb{N}$

and some $l \in \mathbb{R}_+$, then

$$\frac{\delta_n^{(1)}(\varepsilon)}{\Theta_{13}} \le \frac{1}{\varepsilon^l B^l(a_n,n)} E|X_{ki}^{(n)} - a_n|^{2+l}.$$

Since $B^2(a_n,n) \ge C_1^2(a_n,n) \sim Kn^2\alpha(n)$ as $n \to \infty$, where K is a positive constant, the Lindeberg-type condition is satisfied, for example, if $E|X_{ki}^{(n)} - a_n|^3 = o(n\sqrt{\alpha(n)})$ and $\alpha(n) \to \infty$ as $n \to \infty$.
(c) What concerns the Lindeberg-type condition for the immigration variables, it is automatically satisfied when $\Theta_{13} \neq 0$, since in this case $C_2^2(n) = o(B^2(n))$ as $n \to \infty$. If $\Theta_{13} = \Theta_4 = 0$, then it is equivalent to the Lindeberg condition for the array $\{\xi_k^{(n)}, k,n \ge 1\}$.
Now we provide some consequences of Theorem 9.5 which will be used in the proof of main theorems. We consider the following processes.

$$Z_n(t) = \frac{Z^{(n)}([nt])}{A(a_n,n)},\ Y_n(t) = \frac{Z^{(n)}([nt]) - EZ^{(n)}([nt])}{B(a_n,n)}.$$

If we denote $A_n(t) = EZ_n(t)$, we easily obtain from (9.16) the following representation.

$$Z_n(t) = W_n(t)\frac{a_n^{[nt]}B(a_n,n)}{A(a_n,n)} + A_n(t). \tag{9.20}$$

We assume that there exist finite limits

$$\lambda_0(t) = \lim_{n\to\infty} A_n(t),\ \ \lambda_1 = \lim_{n\to\infty} \frac{B(a_n,n)}{A(a_n,n)}. \tag{9.21}$$

The following result is a direct consequence of Theorem 3.1.

Theorem 9.6. *If conditions C1–C4 are satisfied, then $Z_n \xrightarrow{D} \mathscr{Z}$ as $n \to \infty$ weakly in Skorokhod space $D(\mathbb{R}_+,\mathbb{R})$, where $\mathscr{Z}(t) = \lambda_0(t) + \lambda_1 W(\omega(t))$, $t \in \mathbb{R}_+$, $W(t)$ is a standard Brownian motion and*

$$\omega(t) = \frac{\Theta_1 a}{\nu_\alpha(a,1)}\int_0^t \mu_\alpha(a,u)e^{2a(t-u)}du + \frac{\Theta_2}{\nabla_\beta(a,1)}\int_0^t u^\beta e^{2a(t-u)}du + \Theta_3 e^{2at}\frac{1-e^{-at}}{1-e^{-a}}.$$

Remark. One can obtain that limits in (9.21) are computed as

$$\lambda_0(t) = \lim_{n\to\infty} \lambda_0(n,t)/\lambda_0(n,1) \ \text{ and } \ \lambda_1 = \lim_{n\to\infty} \lambda_1(n,1)/\lambda_0(n,1),$$

where

$$\lambda_0(n,t) = \alpha(n,0)e^{at} + n\alpha(n)\mu_\alpha(a,t),$$

$$\lambda_1^2(n,t) = n^2\alpha(n)\mu_\alpha(a,t) + n\beta(n)\nabla_\beta(a,t) + \frac{n\alpha(n,0)b}{a}e^{at}(e^{at}-1).$$

Let $\Theta_1 = 1$ and $\alpha(n) \to \infty$ as $n \to \infty$. In this case the approximating process is deterministic and the following result holds.

Corollary 9.2. *If C1-C4 are satisfied, $\Theta_1 = 1$ and $\alpha(n) \to \infty$ as $n \to \infty$, then $Z_n \xrightarrow{D} \mathscr{X}$ as $n \to \infty$, where $\mathscr{X}(t) = \lambda_0(t) = \mu_\alpha(a,t)/\mu_\alpha(a,1)$.*

Next result is related to the case of large immigration variance.

Corollary 9.3. *If C1-C4 are satisfied, $\Theta_2 = 1$, then $Z_n \xrightarrow{D} \mathscr{X}$ as $n \to \infty$, where $\mathscr{X}(t) = \lambda_0(t) + \lambda_1 W(\omega(t))$ with*

$$\lambda_1 = \lim_{n\to\infty} (n\beta(n)\nabla_\beta(a,1))^{1/2}/\lambda_0(n,1) \text{ and } \omega(t) = \int_0^t u^\beta e^{2a(t-u)} du/\nabla_\beta(a,1).$$

Now we consider process $Y_n(t)$. We obtain from (9.16) that $Y_n(t) = a_n^{[nt]} W_n(t)$ with $c_n = a_n$ and $\rho = -1$ and the following result follows immediately from Theorem 9.5.

Theorem 9.7. *If conditions C1-C4 are satisfied, then $Y_n \xrightarrow{D} \mathscr{Y}$ as $n \to \infty$ weakly in Skorokhod space $D(\mathbb{R}_+,\mathbb{R})$, where $\mathscr{Y}(t) = W(\omega(t)), t \in \mathbb{R}_+$.*

Remark. When processes $\{Z^{(n)}(k), k \geq 0\}, n \geq 1$, are critical with the same offspring and immigration distributions conditions C1 and C2 are satisfied with $a = 0$. If, in addition, $Z^{(n)}(0) = 0$ and $\alpha(n) \to \infty$ as $n \to \infty$, then condition C4 is also satisfied with $\Theta_3 = 0$, and from Theorem 9.7 we obtain assertions of Theorems 1, 2 and 3 in [4] in cases $\Theta_1 = 1$, $\Theta_2 = 1$ and $0 < \Theta_i < 1$, $i = 1,2$, respectively.

Let now $\Theta_3 = 1$ in Theorem 9.7. In this case $EZ^{(n)}([nt]) \sim \alpha(n,0)e^{at}$ and $B^2(n) \sim n\alpha(n,0)be^a(e^a - 1)/a$ as $n \to \infty$. If we denote

$$Y_n^{(1)}(t) = (Z^{(n)}([nt]) - \alpha(n,0)e^{at})/(n\alpha(n,0))^{1/2},$$

the following result holds.

Corollary 9.4. *If conditions C1-C4 are satisfied and $\Theta_3 = 1$, then $Y_n^{(1)} \xrightarrow{D} \mathscr{Y}^{(1)}$ as $n \to \infty$ weakly in Skorokhod space $D(\mathbb{R}_+,\mathbb{R})$, where $\mathscr{Y}^{(1)}(t) = W(\psi(t)), t \in \mathbb{R}_+$ with*

$$\psi(t) = e^{2at}\frac{1 - e^{-at}}{1 - e^{-a}}.$$

Remark. If $\xi_0^{(n)}, n \geq 1$ are degenerate, $\xi_k^{(n)} \equiv 0$, $n, k \geq 1$ and processes $\{X^{(n)}(k), k \geq 0\}, n \geq 1$, are critical with the same offspring distribution, we obtain from Corollary 9.4 the assertion of Theorem 1 in [3].

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10
Critical branching processes with immigration

Márton Ispány and Gyula Pap

Abstract In this paper we give a survey on some results concerning critical and nearly critical Galton–Watson branching processes with immigration. As a byproduct of a general limit theorem for weak convergence of step processes of martingale differences towards a diffusion process, functional limit theorems can be proved for different models. The limit process is either a squared Bessel process or an Ornstein–Uhlenbeck type process. The asymptotic behavior of conditional least squares estimator of the offspring mean will also be described. The results are applied in the theory of integer-valued autoregression as well.

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10.1 Introduction

The theory of branching processes allowing immigrants joining to the population in each generation has been studied for a long time, see, e.g., Sevastyanov [26] and Harris [8]. The limit distribution of a branching process with immigration has been described by Heathcote [9] and Foster [4] in the most elementary cases. They proved that if the offspring mean is greater than or equal to 1, i.e., the model is supercritical or critical, then the process tends to infinity, while if the offspring mean is less than 1, i.e., the model is subcritical, and the immigration mean is finite then

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the process converges weakly to the (unique) stationary distribution. A necessary and sufficient condition for convergence in distribution to a proper random variable has been proved by Foster and Williamson [5], see Athreya and Ney [2, Theorem VI.7.2]. Moreover, in the supercritical case Seneta [24] proved that under appropriate normalization the process converges almost surely to a random variable. Finally, in the critical case Foster [4] and Seneta [25] showed that the process normalized by the number of generation converges in distribution to a gamma distribution.

In this paper critical and nearly critical Galton–Watson branching processes with immigration are investigated and related functional limit theorems are presented. That is, we prove not only the weak convergence of the one dimensional distributions but the weak convergence of finite dimensional distributions and tightness. Our technique is the martingale method and the proofs are based on a general convergence theorem for martingale differences, see Theorem 10.1. The first such theorem in the critical case has been proved by Wei and Winnicki [29, 30], see Theorem 10.2.

The paper is organized as follows. In Sect. 10.2 a two-way connection is presented between the branching processes with immigration and conditionally heteroscedastic autoregressive processes. Section 10.3 is devoted to the main functional limit theorem with application to the Wei–Winnicki's theorem. In Sect. 10.4 nearly critical branching processes with immigration are considered. Finally, in the last section, as an application, the asymptotic behaviour of the conditional least squares estimator of the offspring mean is investigated under various assumptions.

10.2 Branching and autoregressive processes

Let $\{\xi_{k,j}, \varepsilon_k : k, j \in \mathbb{N}\}$ be independent, non-negative, integer-valued random variables such that $\{\xi_{k,j} : k, j \in \mathbb{N}\}$ and $\{\varepsilon_k : k \in \mathbb{N}\}$ are identically distributed. Define recursively

$$X_k = \sum_{j=1}^{X_{k-1}} \xi_{k,j} + \varepsilon_k \quad \text{for } k \in \mathbb{N}, \qquad X_0 = 0. \tag{10.1}$$

The sequence $(X_k)_{k\in\mathbb{Z}_+}$ is called a *branching process with immigration*. We can interpret X_k as the size of the k^{th} generation of a population, where $\xi_{k,j}$ is the number of offsprings of the j^{th} individual in the $(k-1)^{\text{st}}$ generation and ε_k is the number of immigrants contributing to the k^{th} generation. Assume that

$$m := \mathsf{E}\xi_{1,1} < \infty, \quad \lambda := \mathsf{E}\varepsilon_1 < \infty, \quad \sigma^2 := \mathsf{Var}\xi_{1,1} < \infty, \quad b^2 := \mathsf{Var}\varepsilon_1 < \infty.$$

The cases $m < 1$, $m = 1$ and $m > 1$ are referred to respectively as *subcritical*, *critical* and *supercritical*. Such processes have a number of applications in biology, finance, economics, queueing theory etc., see e.g. Haccou et al. [7].

In particular, if the offspring distribution is a Bernoulli distribution then the branching process with immigration is called *first order integer-valued autoregres-*

sive (INAR(1)) *time series*. It has been introduced by Al–Osh and Alzaid [1]. An INAR(1) process may also be written in the form

$$X_k = m \circ X_{k-1} + \varepsilon_k \quad \text{for } k \in \mathbb{N}, \qquad X_0 = 0, \tag{10.2}$$

where we use the *thinning* or *Steutel and van Harn operator* $m\circ$ which is defined for $m \in [0,1]$ and for a non-negative integer-valued random variable X by

$$m \circ X := \begin{cases} \sum\limits_{j=1}^{X} \xi_j, & X > 0, \\ 0, & X = 0, \end{cases}$$

where the counting sequence $(\xi_j)_{j\in\mathbb{N}}$ consists of independent and identically distributed Bernoulli random variables with mean m, independent of X (see Steutel and van Harn [28]), and the counting sequences involved in $m \circ X_{k-1}$, $k \in \mathbb{N}$, are mutually independent and independent of $(\varepsilon_n)_{n\in\mathbb{N}}$. Formula (10.2) shows the analogy with the common AR(1) process, i.e., m plays the role of an autoregressive parameter and $\{\varepsilon_k : k \in \mathbb{N}\}$ is an innovation or driving process. Motivation in order to include discrete data models comes from the need to account for the discrete nature of certain data sets, often counts of events, objects or individuals. Branching process with immigration is a promising model to describe such phenomenas. Examples of applications can be found in review papers by McKenzie [20], Jung and Tremayne [19], and Weiß [32].

For $k \in \mathbb{Z}_+$, let $\mathscr{F}_k$ denote the σ-algebra generated by $X_0, X_1, \dots, X_k$. Then, by (10.1), we have the conditional expectation

$$\mathsf{E}(X_k \mid \mathscr{F}_{k-1}) = mX_{k-1} + \lambda, \qquad k \in \mathbb{N}.$$

Clearly,

$$M_k := X_k - \mathsf{E}(X_k \mid \mathscr{F}_{k-1}) = X_k - mX_{k-1} - \lambda, \quad k \in \mathbb{N}, \tag{10.3}$$

defines a martingale difference sequence $(M_k)_{k\in\mathbb{N}}$ with respect to the filtration $(\mathscr{F}_k)_{k\in\mathbb{Z}_+}$, thus we have the recursion

$$X_k = \lambda + mX_{k-1} + M_k \quad \text{for } k \in \mathbb{N}, \qquad X_0 = 0. \tag{10.4}$$

Hence a branching process with immigration can be rewritten as an autoregressive process with drift, where the driving process $(M_k)_{k\in\mathbb{N}}$ is a sequence of martingale differences. The main difference from the common autoregressive process is in the nature of conditional variance. An AR(1) process is homoscedastic, i.e., $\mathsf{E}(M_k^2 \mid \mathscr{F}_{k-1})$ is constant for all $k \in \mathbb{N}$. Contrarily, the autoregressive representation of branching processes with immigration has heteroscedastic conditional structure. Namely, for the conditional variance we have $\mathsf{E}(M_k^2 \mid \mathscr{F}_{k-1}) = \sigma^2 X_{k-1} + b^2$ since, by (10.3) and (10.1),

$$M_k = X_k - mX_{k-1} - \lambda = \sum_{j=1}^{X_{k-1}} (\xi_{k,j} - m) + (\varepsilon_k - \lambda).$$

Summarizing, there is a natural two-way connection between the branching processes with immigration and autoregressive processes. On one hand, branching process with immigration is a useful alternative to model integer-valued time series. On the other hand, a branching process with immigration is an autoregressive process with conditionally heteroscedastic innovation. Thus, to prove functional limit theorem for branching processes with immigration we may apply limit theorems developed for heteroscedastic autoregressive processes and more general stochastic processes.

10.3 Functional limit theorems

The functional limit theorems of this section are based on a general limit theorem for martingale differences. For each $n \in \mathbb{N}$, let $(U_k^n)_{k\in\mathbb{N}}$ be a sequence of $\mathbb{R}^d$-valued *square-integrable martingale differences* with respect to a filtration $(\mathscr{F}_k^n)_{k\in\mathbb{Z}_+}$, i.e., (i) U_k^n is $\mathscr{F}_k^n$-measurable for all $k,n \in \mathbb{N}$, and (ii) $\mathsf{E}\|U_k^n\|^2 < \infty$, $\mathsf{E}\big(U_k^n \mid \mathscr{F}_{k-1}^n\big) = 0$ for all $k,n \in \mathbb{N}$. Introduce the random step functions

$$\mathscr{U}_t^n := \sum_{k=1}^{\lfloor nt \rfloor} U_k^n, \qquad t \in \mathbb{R}_+, \quad n \in \mathbb{N}.$$

Moreover, let $(\mathscr{U}_t)_{t\in\mathbb{R}_+}$ be a (not necessarily time-homogeneous) d-dimensional *diffusion process* with zero drift, i.e.,

$$\mathrm{d}\mathscr{U}_t = \gamma(t,\mathscr{U}_t)\,\mathrm{d}\mathscr{W}_t, \qquad t \in \mathbb{R}_+,$$

where $\gamma : \mathbb{R}_+ \times \mathbb{R}^d \to \mathbb{R}^{d\times r}$ is a continuous function and $(\mathscr{W}_t)_{t\in\mathbb{R}_+}$ is an r-dimensional standard Wiener process. Assume that the SDE has a unique weak solution with $\mathscr{U}_0 = x_0$ for all $x_0 \in \mathbb{R}^d$. Let $(\mathscr{U}_t)_{t\in\mathbb{R}_+}$ be a solution with $\mathscr{U}_0 = 0$.

Our martingale limit theorem is derived from a general semimartingale limit theorem due to Jacod and Shiryayev [18, Theorem IX.3.39], but the assumptions of the following theorem are much easier to verify.

Theorem 10.1. *Suppose that for each* $T > 0$,

(i) $$\sup_{t\in[0,T]} \left\| \sum_{k=1}^{\lfloor nt \rfloor} \mathsf{E}\big(U_k^n (U_k^n)^\top \mid \mathscr{F}_{k-1}^n\big) - \int_0^t \gamma(s,\mathscr{U}_s^n)\gamma(s,\mathscr{U}_s^n)^\top \mathrm{d}s \right\| \xrightarrow{\mathsf{P}} 0,$$

(ii) $$\sum_{k=1}^{\lfloor nT \rfloor} \mathsf{E}\big(\|U_k^n\|^2 \mathbb{1}_{\{\|U_k^n\|>\theta\}} \mid \mathscr{F}_{k-1}^n\big) \xrightarrow{\mathsf{P}} 0 \quad \textit{for all} \quad \theta > 0.$$

Then

$$\mathscr{U}^n \xrightarrow{\mathscr{D}} \mathscr{U} \quad \textit{as} \quad n \to \infty,$$

that is, weakly in the Skorokhod space $D(\mathbb{R}_+, \mathbb{R}^d)$.

We note that in assumption (i) uniform convergence on compacts in probability is involved and assumption (ii) is the conditional Lindeberg condition. The proof of this theorem can be found in Ispány and Pap [12, 13]. In the sequel, we check only assumption (i) in the proof of limit theorems. Assumption (ii) can be verified in the same manner, see the cited reference in each case.

The celebrated Wei–Winnicki's theorem, see [29] and [30], describes the asymptotic behaviour of a critical branching process with immigration. Introduce the random step functions

$$\mathscr{X}_t^n := X_{\lfloor nt \rfloor} \qquad \text{for } t \in \mathbb{R}_+,\ n \in \mathbb{N}.$$

Theorem 10.2. *For a critical branching process with immigration we have*

$$n^{-1}\mathscr{X}^n \xrightarrow{\mathscr{D}} \mathscr{X} \qquad \text{as } n \to \infty, \tag{10.5}$$

where $(\mathscr{X}_t)_{t \in \mathbb{R}_+}$ *is the solution of the stochastic differential equation*

$$\mathrm{d}\mathscr{X}_t = \lambda\,\mathrm{d}t + \sigma\sqrt{(\mathscr{X}_t)_+}\,\mathrm{d}\mathscr{W}_t, \quad t \in \mathbb{R}_+, \qquad \mathscr{X}_0 = 0, \tag{10.6}$$

where $x_+ := \max\{x, 0\}$, *and* $(\mathscr{W}_t)_{t \in \mathbb{R}_+}$ *is a standard Wiener process.*

It is well known that the SDE (10.6) has a unique global strong solution such that $X_t \geq 0$ almost surely for all $t \in \mathbb{R}_+$. Thus, one may replace $(\mathscr{X}_t)_+$ by $\mathscr{X}_t$ under the square root. (See, e.g., Ikeda and Watanabe [10, Example IV.8.2].) The process $(\mathscr{X}_t)_{t \in \mathbb{R}_+}$ is a continuous branching process called square-root process, squared Bessel process, or Cox–Ingersoll–Ross model.

Proof. We apply the martingale limit theorem, Theorem 10.1, with the choice $\gamma(x,t) := \sigma\sqrt{(x + \lambda t)_+}$, and prove that $\mathscr{M}^n \xrightarrow{\mathscr{D}} \mathscr{M}$ as $n \to \infty$, where $\mathscr{M}_t^n := \frac{1}{n}\sum_{k=1}^{\lfloor nt \rfloor} M_k$ and $\mathrm{d}\mathscr{M}_t = \sigma\sqrt{(\mathscr{M}_t + \lambda t)_+}\,\mathrm{d}\mathscr{W}_t$, $t \in \mathbb{R}_+$, $\mathscr{M}_0 = 0$. Indeed, by (10.4), $X_k = X_{k-1} + \lambda + M_k$ implies $X_k = \sum_{j=1}^{k}(M_j + \lambda)$. Hence the following heuristics proves condition (i). The conditional covariances admit the asymptotics

$$\begin{aligned} \frac{1}{n^2}\sum_{k=1}^{\lfloor nt \rfloor} \mathsf{E}(M_k^2 \mid \mathscr{F}_{k-1}) &= \frac{1}{n^2}\sum_{k=1}^{\lfloor nt \rfloor}(\sigma^2 X_{k-1} + b^2) \approx \frac{\sigma^2}{n^2}\sum_{k=1}^{\lfloor nt \rfloor}\sum_{j=1}^{k-1}(M_j + \lambda) \\ &= \frac{\sigma^2}{n}\sum_{k=1}^{\lfloor nt \rfloor}\left(\mathscr{M}_{k/n}^n + \lambda\frac{k-1}{n}\right) \approx \sigma^2\int_0^t (\mathscr{M}_s^n + \lambda s)\,\mathrm{d}s. \end{aligned}$$

The conditional Lindeberg condition (ii) can be verified as in Ispány [11] or Ispány et al. [16]. Finally, the continuous mapping theorem proves (10.5) since

$$\frac{1}{n}X_{\lfloor nt \rfloor} = \frac{1}{n}\sum_{j=1}^{\lfloor nt \rfloor}(M_j + \lambda) \xrightarrow{\mathscr{D}} \mathscr{M}_t + \lambda t = \mathscr{X}_t \qquad \text{as} \quad n \to \infty. \qquad \square$$

10.4 Nearly critical branching processes with immigration

In this section we study branching processes with immigration which are close to the criticality. To be precise we consider a sequence of branching processes with immigration $(X_k^n)_{k\in\mathbb{Z}_+}$, $n\in\mathbb{N}$, given by the recursion

$$X_k^n = \sum_{j=1}^{X_{k-1}^n} \xi_{k,j}^n + \varepsilon_k^n \quad \text{for } k,n\in\mathbb{N}, \qquad X_0^n = 0, \tag{10.7}$$

where $\{\xi_{k,j}^n, \varepsilon_k^n : k, j, n\in\mathbb{N}\}$ are independent, nonnegative, integer-valued random variables such that $\{\xi_{k,j}^n : k, j\in\mathbb{N}\}$ and $\{\varepsilon_k^n : k\in\mathbb{N}\}$ for each $n\in\mathbb{N}$ are identically distributed. Assume furthermore that, for all $n\in\mathbb{N}$,

$$m_n := \mathsf{E}\xi_{1,1}^n < \infty, \quad \lambda_n := \mathsf{E}\varepsilon_1^n < \infty, \quad \sigma_n^2 := \mathsf{Var}\xi_{1,1}^n < \infty, \quad b_n^2 := \mathsf{Var}\varepsilon_1^n < \infty.$$

Definition 10.1. A sequence of branching processes with immigration is called *nearly critical* with rate $\alpha\in\mathbb{R}$ if $m_n = 1+\alpha n^{-1}+o(n^{-1})$ as $n\to\infty$.

This kind of the parametrization of the offspring mean has been considered by Sriram [27] for the first time. The notion of nearly criticality or nearly unstability has been suggested by Chan and Wei [3] in case of AR(1) models. The main motivation comes from the econometrics, where the so-called "unit-root problem" plays an important role.

The following theorem, see Ispány [11, Theorem 2.1] is a generalization of the Wei–Winnicki's theorem and Sriram's theorem, see [27, Theorem 3.1]. In the limit theorem we apply a kind of "self-normalization", namely we divide by the offspring variance. Such kind of normalization is investigated recently by Rahimov [21], where the offspring variance is modelled by a slowly varying function. Introduce the random step functions

$$\mathscr{X}_t^n := X_{\lfloor nt\rfloor}^n, \qquad \mathscr{M}_t^n := \sum_{k=1}^{\lfloor nt\rfloor} M_k^n \qquad \text{for } t\in\mathbb{R}_+,\ n\in\mathbb{N}.$$

Theorem 10.3. *Suppose that* $\sigma_n^2>0$ *for all* $n\in\mathbb{N}$, *and*

(i) $\mathsf{E}\left(|\xi_{1,1}^n-m_n|^2\mathbb{1}_{\{|\xi_{1,1}^n-m_n|>\theta n\sigma_n^2\}}\right) = o(\sigma_n^2)$ *as* $n\to\infty$ *for all* $\theta>0$,
(ii) $\lambda_n = \lambda\sigma_n^2+o(\sigma_n^2)$ *as* $n\to\infty$ *for some* $\lambda\ge 0$,
(iii) $b_n^2 = o(n\sigma_n^4)$ *as* $n\to\infty$.

Then

$$\left(n\sigma_n^2\right)^{-1}\mathsf{E}\mathscr{X}_t^n \to \lambda\int_0^t \mathrm{e}^{\alpha s}\,\mathrm{d}s \qquad \text{as } n\to\infty \tag{10.8}$$

for all $t\in\mathbb{R}_+$, *and*

$$\left(n\sigma_n^2\right)^{-1}\mathscr{X}^n \xrightarrow{\mathscr{D}} \mathscr{X} \qquad \text{as } n\to\infty,$$

that is, weakly in the Skorokhod space $D(\mathbb{R}_+, \mathbb{R})$, *where* $\big(\mathscr{X}_t\big)_{t\in\mathbb{R}_+}$ *is the unique solution of the stochastic differential equation (SDE)*

$$\mathrm{d}\mathscr{X}_t = (\lambda + \alpha\mathscr{X}_t)\,\mathrm{d}t + \sqrt{(\mathscr{X}_t)_+}\,\mathrm{d}\mathscr{W}_t, \quad t \in \mathbb{R}_+, \qquad \mathscr{X}_0 = 0, \tag{10.9}$$

where $(\mathscr{W}_t)_{t\in\mathbb{R}_+}$ *is a standard Wiener process.*

If the offspring variance tends to 0, e.g., in case of Bernoulli offspring distribution, then the above theorem gives a trivial deterministic limit process. However, in this case going one step further a fluctuation theorem holds with Ornstein–Uhlenbeck type limit process, see Ispány et al. [16, Theorem 2.2].

Theorem 10.4. *Suppose that*

(i) $\sigma_n^2 = \beta n^{-1} + o(n^{-1})$ *as* $n \to \infty$ *with some* $\beta \geq 0$,
(ii) $n\mathsf{E}\left(|\xi_{1,1}^n - m_n|^2 \mathbb{1}_{\{|\xi_{1,1}^n - m_n| > \theta\sqrt{n}\}}\right) \to 0$ *as* $n \to \infty$ *for all* $\theta > 0$,
(iii) $\lambda_n \to \lambda$ *and* $b_n^2 \to b^2$ *as* $n \to \infty$ *with some* $\lambda \geq 0$ *and* $b^2 \geq 0$,
(iv) $\mathsf{E}\left(|\varepsilon_1^n - \lambda_n|^2 \mathbb{1}_{\{|\varepsilon_1^n - \lambda_n| > \theta\sqrt{n}\}}\right) \to 0$ *as* $n \to \infty$ *for all* $\theta > 0$.

Then

$$n^{-1/2}\left(\mathscr{X}^n - \mathsf{E}\mathscr{X}^n, \mathscr{M}^n\right) \xrightarrow{\mathscr{D}} \left(\widetilde{\mathscr{X}}, \widetilde{\mathscr{M}}\right) \qquad \text{as } n \to \infty,$$

that is, weakly in the Skorokhod space $D(\mathbb{R}_+, \mathbb{R}^2)$, *where* $\left(\widetilde{\mathscr{M}}_t\right)_{t\in\mathbb{R}_+}$ *is a time-changed Wiener process, namely,* $\widetilde{\mathscr{M}}_t = \mathscr{W}(T_t)$, $t \in \mathbb{R}_+$ *with*

$$T_t := \int_0^t \rho(s)\,\mathrm{d}s, \qquad \rho(t) := b^2 + \beta\lambda \int_0^t \mathrm{e}^{\alpha s}\,\mathrm{d}s, \qquad t \in \mathbb{R}_+,$$

$(\mathscr{W}(t))_{t\in\mathbb{R}_+}$ *is a standard Wiener process, and*

$$\widetilde{\mathscr{X}}_t := \int_0^t \mathrm{e}^{\alpha(t-s)}\,\mathrm{d}\widetilde{\mathscr{M}}_s, \qquad t \in \mathbb{R}_+,$$

is an Ornstein–Uhlenbeck type process driven by $(\widetilde{\mathscr{M}}_t)_{t\in\mathbb{R}_+}$.

A more general approximation theorem has been proved in Ispány et al. [17] for Ornstein–Uhlenbeck processes using sequence of branching processes with immigration.

Finally, we may investigate the nearly critical behaviour in the framework of one model only allowing inhomogeneous parameters, i.e., considering branching processes with immigration in varying environment. The next theorem, see Györfi et al. [6, Theorem 2], shows that if the convergence to criticality is slow, then the limit is a Poisson distribution and we do not need any normalization. The inhomogeneous INAR(1) process $(X_n)_{n\in\mathbb{Z}_+}$ is defined by

$$X_k = m_k \circ X_{k-1} + \varepsilon_k \quad \text{for } k \in \mathbb{N}, \qquad X_0 = 0,$$

where $\{\varepsilon_k : k \in \mathbb{N}\}$ are non-negative integer-valued random variables with $\lambda_k := \mathsf{E}\varepsilon_k < \infty$ and $b_k^2 := \mathsf{Var}\varepsilon_k < \infty$.

Theorem 10.5. *Assume that*

(i) $m_n < 1$ *for all* $n \in \mathbb{N}$, $\lim_{n\to\infty} m_n = 1$, $\sum_{n=1}^{\infty}(1-m_n) = \infty$,

(ii) $\lim_{n\to\infty} \frac{\lambda_n}{1-m_n} = \lambda \in [0,\infty)$, $\lim_{n\to\infty} \frac{b_n^2}{1-m_n} = 0.$

Then

$$X_n \xrightarrow{\mathscr{D}} \mathrm{Po}(\lambda) \quad as \quad n \to \infty.$$

The proof of this theorem is based on Poisson approximation.

10.5 Conditional least squares estimators

Let us consider the branching process (10.1). The conditional least squares estimator (CLSE) $\widehat{m}_n$ of m based on the observations $X_1,\dots,X_n$ assuming that λ is known can be obtained minimizing the sum of squares

$$\sum_{k=1}^{n}(X_k - mX_{k-1} - \lambda)^2$$

with respect to m, and it has the form

$$\widehat{m}_n = \frac{\sum_{k=1}^{n}(X_k-\lambda)X_{k-1}}{\sum_{k=1}^{n}X_{k-1}^2},$$

hence

$$\widehat{m}_n - m = \frac{\sum_{k=1}^{n}M_kX_{k-1}}{\sum_{k=1}^{n}X_{k-1}^2}.$$

Theorem 10.6. *For a subcritical branching process with immigration under the assumptions* $\mathsf{E}\xi_{1,1}^3 < \infty$, $\mathsf{E}\varepsilon_1^3 < \infty$ *we have*

$$n^{1/2}(\widehat{m}_n - m) \xrightarrow{\mathscr{D}} \mathscr{N}(0,\sigma_{\mathrm{sub}}^2)$$

with

$$\sigma_{\mathrm{sub}}^2 := \frac{\sigma^2\sum_{j=0}^{\infty} j^3 p_j + b^2\sum_{j=0}^{\infty} j^2 p_j}{\left(\sum_{j=0}^{\infty} j^2 p_j\right)^2},$$

where $(p_j)_{j\in\mathbb{Z}_+}$ *denotes the unique stationary distribution of the Markov chain* $(X_k)_{k\in\mathbb{Z}_+}$.

Proof. First observe $\sum_{k=1}^{n} X_{k-1}^2 \to \sum_{j=0}^{\infty} j^2 p_j$ a.s. by the Ergodic Theorem. Then by the Martingale Central Limit Theorem we obtain $n^{-1/2}\sum_{k=1}^{\lfloor nt\rfloor} M_k X_{k-1} \xrightarrow{\mathscr{D}} c\mathscr{W}_t$, where $(\mathscr{W}_t)_{t\in\mathbb{R}_+}$ is a standard Wiener process and $c^2 := \sigma^2\sum_{j=0}^{\infty} j^3 p_j + b^2\sum_{j=0}^{\infty} j^2 p_j$. Indeed, the conditional covariances admit the asymptotics

$$\frac{1}{n}\sum_{k=1}^{\lfloor nt\rfloor} \mathsf{E}(M_k^2 X_{k-1}^2 \mid \mathscr{F}_{k-1}) = \frac{1}{n}\sum_{k=1}^{\lfloor nt\rfloor} (\sigma^2 X_{k-1} + b^2) X_{k-1}^2 \approx c^2 t$$

again by the Ergodic Theorem. □

The asymptotic behaviour of the CLSE of the offspring mean is unknown if the offspring or immigration distribution have infinite third moment. Simulations suggest that the limit distribution is not normal, we suspect it is a stable distribution.

Wei and Winnicki [29, 31] described the asymptotic behavior of the CLSE in the critical case $m = 1$ with $\sigma^2 > 0$.

Theorem 10.7. *For a critical branching process with immigration under the assumption* $\sigma^2 > 0$ *we have*

$$n\,(\widehat{m}_n - 1) \xrightarrow{\mathscr{D}} \frac{\int_0^1 \mathscr{X}_t \,\mathrm{d}(\mathscr{X}_t - \lambda t)}{\int_0^1 \mathscr{X}_t^2 \,\mathrm{d}t},$$

where the process $(\mathscr{X}_t)_{t\in\mathbb{R}_+}$ *is given in Theorem 10.2.*

Proof. This can be proved using the general martingale limit theorem, Theorem 10.1. For each $n \in \mathbb{N}$, consider the martingale differences

$$U_k^n := \begin{bmatrix} n^{-1} M_k \\ n^{-2} M_k X_{k-1} \end{bmatrix} = M_k \begin{bmatrix} n^{-1} \\ n^{-2} X_{k-1} \end{bmatrix}, \qquad k \in \mathbb{N},$$

with respect to the filtration $\mathscr{F}_k^n := \sigma(M_1, \ldots, M_k)$. The conditional covariances admit the asymptotics

$$\begin{aligned}\sum_{k=1}^{\lfloor nt\rfloor} \mathsf{E}[U_k^n (U_k^n)^\top \mid \mathscr{F}_{k-1}^n] &= \sum_{k=1}^{\lfloor nt\rfloor} \mathsf{E}(M_k^2 \mid \mathscr{F}_{k-1}) \begin{bmatrix} n^{-1} \\ n^{-2} X_{k-1} \end{bmatrix} \begin{bmatrix} n^{-1} \\ n^{-2} X_{k-1} \end{bmatrix}^\top \\ &= \sum_{k=1}^{\lfloor nt\rfloor} (\sigma^2 X_{k-1} + b^2) \begin{bmatrix} n^{-2} & n^{-3} X_{k-1} \\ n^{-3} X_{k-1} & n^{-4} X_{k-1}^2 \end{bmatrix} \approx \int_0^t \gamma(s, \mathscr{U}_s^n)\gamma(s, \mathscr{U}_s^n)^\top \mathrm{d}s\end{aligned}$$

with $\gamma : \mathbb{R}_+ \times \mathbb{R}^2 \to \mathbb{R}^{2\times 1}$, $\gamma\left(s, \begin{bmatrix} x \\ y \end{bmatrix}\right) = \sigma \begin{bmatrix} (x+\lambda s)_+^{1/2} \\ (x+\lambda s)_+^{3/2} \end{bmatrix}$, since (10.4) yields $X_k = \sum_{j=1}^{k} (M_j + \lambda) = \sum_{j=1}^{k} M_j + k\lambda$.

By Theorem 1 we obtain $\left(n^{-1}\sum_{k=1}^{\lfloor nt\rfloor} M_k,\, n^{-2}\sum_{k=1}^{\lfloor nt\rfloor} M_k X_{k-1}\right) \xrightarrow{\mathscr{D}} (\mathscr{M}_t, \mathscr{Y}_t)$, where

$$\begin{bmatrix} \mathrm{d}\mathscr{M}_t \\ \mathrm{d}\mathscr{Y}_t \end{bmatrix} = \gamma\left(t, \begin{bmatrix} \mathscr{M}_t \\ \mathscr{Y}_t \end{bmatrix}\right) \mathrm{d}\mathscr{W}_t = \sigma \begin{bmatrix} (\mathscr{M}_t + \lambda t)_+^{1/2} \\ (\mathscr{M}_t + \lambda t)_+^{3/2} \end{bmatrix} \mathrm{d}\mathscr{W}_t, \quad t \in \mathbb{R}_+,$$

$\mathscr{M}_0 = \mathscr{Y}_0 = 0$. Hence

$$\begin{aligned} \mathrm{d}\mathscr{M}_t &= \sigma(\mathscr{M}_t + \lambda t)_+^{1/2} \,\mathrm{d}\mathscr{W}_t, \\ \mathscr{Y}_t &= \sigma \int_0^t (\mathscr{M}_s + \lambda s)_+^{3/2} \,\mathrm{d}\mathscr{W}_s = \int_0^t (\mathscr{M}_s + \lambda s)_+ \,\mathrm{d}\mathscr{M}_s. \end{aligned}$$

We also obtain $n^{-1}X_{\lfloor nt \rfloor} = n^{-1}\sum_{j=1}^{\lfloor nt \rfloor}(M_j + \lambda) \xrightarrow{\mathscr{D}} \mathscr{M}_t + \lambda t = \mathscr{X}_t$ (compare with Theorem 10.2). Consequently $\mathscr{Y}_t = \int_0^t \mathscr{X}_s \,\mathrm{d}\mathscr{M}_s$ and

$$\left(n^{-3}\sum_{k=1}^{\lfloor nt \rfloor} X_{k-1}^2, \, n^{-2}\sum_{k=1}^{\lfloor nt \rfloor} M_k X_{k-1}\right) \xrightarrow{\mathscr{D}} \left(\int_0^t \mathscr{X}_s^2 \,\mathrm{d}t, \int_0^t \mathscr{X}_s \,\mathrm{d}\mathscr{M}_s\right),$$

hence

$$n\left(\widehat{m}_n - 1\right) = \frac{n^{-2}\sum_{k=1}^n X_{k-1}M_k}{n^{-3}\sum_{k=1}^n X_{k-1}^2} \xrightarrow{\mathscr{D}} \frac{\int_0^1 \mathscr{X}_t \,\mathrm{d}\mathscr{M}_t}{\int_0^1 \mathscr{X}_t^2 \,\mathrm{d}t}$$

as $n \to \infty$. □

The critical case $m = 1$ with $\sigma^2 = 0$ has been described by Ispány et al. [14].

Theorem 10.8. *For a critical branching process with immigration under the assumptions* $\sigma^2 = 0$ *and* $\lambda > 0$ *we have*

$$n^{3/2}\left(\widehat{m}_n - 1\right) \xrightarrow{\mathscr{D}} \mathscr{N}(0, \sigma_{\mathrm{crit}}^2) \qquad \textit{with} \qquad \sigma_{\mathrm{crit}}^2 := \frac{3b^2}{\lambda^2}.$$

Proof. This can be proved again using Theorem 10.1. For each $n \in \mathbb{N}$, consider now the martingale differences

$$U_k^n := \begin{bmatrix} n^{-1/2}M_k \\ n^{-3/2}M_k X_{k-1} \end{bmatrix} = M_k \begin{bmatrix} n^{-1/2} \\ n^{-3/2}X_{k-1} \end{bmatrix}, \qquad k \in \mathbb{N},$$

with respect to the filtration $\mathscr{F}_k^n := \sigma(M_1, \dots, M_k)$. The conditional covariances admit the asymptotics

$$\begin{aligned} \sum_{k=1}^{\lfloor nt \rfloor} \mathsf{E}[U_k^n (U_k^n)^\top \mid \mathscr{F}_{k-1}^n] &= \sum_{k=1}^{\lfloor nt \rfloor} \mathsf{E}(M_k^2 \mid \mathscr{F}_{k-1}) \begin{bmatrix} n^{-1/2} \\ n^{-3/2}X_{k-1} \end{bmatrix} \begin{bmatrix} n^{-1/2} \\ n^{-3/2}X_{k-1} \end{bmatrix}^\top \\ &= \sum_{k=1}^{\lfloor nt \rfloor} b^2 \begin{bmatrix} n^{-1} & n^{-2}X_{k-1} \\ n^{-2}X_{k-1} & n^{-3}X_{k-1}^2 \end{bmatrix} \approx \int_0^t \gamma(s, \mathscr{U}_s^n)\gamma(s, \mathscr{U}_s^n)^\top \mathrm{d}s \end{aligned}$$

with $\gamma : \mathbb{R}_+ \times \mathbb{R}^2 \to \mathbb{R}^{2\times 1}$, $\gamma\left(s, \begin{bmatrix} x \\ y \end{bmatrix}\right) = b \begin{bmatrix} 1 \\ \lambda s \end{bmatrix}$, since now $X_k = X_{k-1} + \varepsilon_k = \sum_{j=1}^{k} \varepsilon_j$ yields $n^{-1} X_{\lfloor nt \rfloor} = n^{-1} \sum_{j=1}^{\lfloor nt \rfloor} \varepsilon_j \xrightarrow{\mathcal{D}} \lambda t =: \mathscr{X}_t$. By Theorem 10.1 we obtain $\left(n^{-1/2} \sum_{k=1}^{\lfloor nt \rfloor} M_k, n^{-3/2} \sum_{k=1}^{\lfloor nt \rfloor} M_k X_{k-1}\right) \xrightarrow{\mathcal{D}} (\mathscr{M}_t, \mathscr{Y}_t)$, where

$$\begin{bmatrix} \mathrm{d}\mathscr{M}_t \\ \mathrm{d}\mathscr{Y}_t \end{bmatrix} = \gamma\left(t, \begin{bmatrix} \mathscr{M}_t \\ \mathscr{Y}_t \end{bmatrix}\right) \mathrm{d}\mathscr{W}_t = b \begin{bmatrix} 1 \\ \lambda t \end{bmatrix} \mathrm{d}\mathscr{W}_t, \quad t \in \mathbb{R}_+,$$

$\mathscr{M}_0 = \mathscr{Y}_0 = 0$. Thus $\mathscr{M}_t = b\mathscr{W}_t$ and $\mathscr{Y}_t = b\lambda \int_0^t s \,\mathrm{d}\mathscr{W}_s = \int_0^t \mathscr{X}_s \,\mathrm{d}\mathscr{M}_s$, and $\left(n^{-3} \sum_{k=1}^{\lfloor nt \rfloor} X_{k-1}^2, n^{-3/2} \sum_{k=1}^{\lfloor nt \rfloor} M_k X_{k-1}\right) \xrightarrow{\mathcal{D}} \left(\int_0^t \mathscr{X}_s^2 \,\mathrm{d}s, \int_0^t \mathscr{X}_s \,\mathrm{d}\mathscr{M}_s\right)$, hence

$$n^{3/2}\left(\widehat{m}_n - 1\right) = \frac{n^{-3/2} \sum_{k=1}^{n} X_{k-1} M_k}{n^{-3} \sum_{k=1}^{n} X_{k-1}^2} \xrightarrow{\mathcal{D}} \frac{\int_0^1 \mathscr{X}_t \,\mathrm{d}\mathscr{M}_t}{\int_0^1 \mathscr{X}_t^2 \,\mathrm{d}t} \stackrel{\mathcal{D}}{=} \mathscr{N}(0, \sigma_{\mathrm{crit}}^2),$$

since $\int_0^1 \mathscr{X}_t^2 \,\mathrm{d}t = \frac{1}{3}\lambda^2$ and $\int_0^1 \mathscr{X}_t \,\mathrm{d}\mathscr{M}_t \stackrel{\mathcal{D}}{=} \mathscr{N}\left(0, \frac{1}{3}\lambda^2 b^2\right)$. $\square$

The case of unknown immigration mean has been described by Ispány et al. [15]. Rahimov [22] has proved that in the non-degenerate case $\sigma^2 > 0$ if the immigration is time-dependent with regularly varying mean and variance then the limit is normal or certain functional of a time-changed Wiener process. The aymptotics of weighted CLSE has been studied in [23] using the same framework.

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Weighted conditional least squares estimation in controlled multitype branching processes

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Abstract The multitype controlled branching process provides a useful way to model generation sizes in population dynamics studies, where several types of individuals coexist and a control on the growth of population size is necessary at each generation. From a probabilistic viewpoint this model has been studied in González et al. (Bernoulli 11(3):559–570, 2005; J. Appl. Probab. 42:1015–1030, 2005; Pliska Stud. Math. Bulgar. 17: 85–96, 2005; J. Appl. Probab. 43: 159–174, 2006; Pliska Stud. Math. Bulgar. 18: 103–110, 2007; Stoch. Models 24: 401–424, 2008). In this paper we are interested in developing its inferential theory, not considered until now. We propose a weighted conditional least squares estimator of the offspring mean matrix. For the supercritical case, we establish the strong consistency of the proposed estimator.

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Keywords: multitype branching processes, random control function, weighted conditional least squares estimator, strong consistency.

11.1 Introduction

The multitype Galton–Watson process is a well-known branching model which has received considerable attention in the scientific literature (e.g. see [14]). From this model, the possibility of achieving in each generation a control in the number of particles/individuals of each type that participates in the reproduction process is considered in [16] where the control was introduced in a deterministic way. Later

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on, as a generalization of the one-dimensional model with random control and reproduction dependent on the population size considered by [13], a multitype model that puts together random control mechanism and size dependent reproduction is introduced in [1]. In this model, called controlled multitype branching process with random control and population-size-dependent reproduction, the reproduction phase in a generation is conditioned by the size of the previous generation, the number of progenitors of each type is controlled by means of a random mechanism and possible dependence among individuals of the same generation at reproduction time is allowed. The asymptotic behaviour of this process has been investigated in [1–6]. The study of inference problems arising from this model has not been considered yet. The purpose of this article is to consider the estimation problem of the offspring mean matrix. As a first approach, we will focus our attention on controlled multitype branching process with random control, non-population-size-dependent reproduction and independence at the reproduction phase between individuals of the same generation. In Sect. 11.2 we will introduce the model and some notation and basic results will be provided. Moreover, analogously to the classification of the multitype Galton–Watson process, we will introduce a threshold parameter to establish a classification for the CMBP. In Sect. 11.3, making use of the weighted conditional least squares procedure we will propose an estimator for the offspring mean matrix and we will investigate its asymptotic behaviour in the supercritical case.

11.2 Probability model

A controlled multitype branching process with random control (CMBP), $\{Z(n)\}_{n\geq 0}$, is a m-dimensional random vector sequence defined as follows:

$$Z(0) = z \in \mathbb{N}_0^m;\;\; Z(n+1) = \sum_{i=1}^{m} \sum_{j=1}^{\phi_i^n(Z(n))} X^{i,n,j},\;\; n = 0,1,\ldots \tag{11.1}$$

where $\{X^{i,n,j} = (X_1^{i,n,j},\ldots,X_m^{i,n,j}) : i = 1,\ldots,m,\; n = 0,1,\ldots,\; j = 1,2,\ldots\}$ and $\{\phi^n(z) = (\phi_1^n(z),\ldots,\phi_m^n(z)) : n = 0,1,\ldots; z \in \mathbb{N}_0^m\}$ are two independent sequences of m-dimensional, non-negative, integer valued random vectors defined on the same probability space such that:

(i) The stochastic processes $\{X^{i,n,j} :\; i = 1,\ldots,m,\; j = 1,2,\ldots\}$, $n = 0,1,\ldots$, are independent and identically distributed. Moreover, for each $i \in \{1,2,\ldots,m\}$, the random vectors $\{X^{i,n,j} :\;\; j = 1,2,\ldots,\; n = 0,1,\ldots\}$ are independent and identically distributed.

(ii) For each $z \in \mathbb{N}_0^m$, the random vectors $\{\phi^n(z)\}_{n\geq 0}$ are independent and identically distributed and if $n,\widetilde{n} \in \mathbb{N}_0$ are such that $n \neq \widetilde{n}$, then the random vectors $\phi^n(z)$ y $\phi^{\widetilde{n}}(\widetilde{z})$ are independent, for every $z,\widetilde{z} \in \mathbb{N}_0^m$. Moreover we will assume that for each $n \in \mathbb{N}_0$ and $z \in \mathbb{N}_0^m$ the variables $\{\phi_1^n(z), \dots, \phi_m^n(z)\}$ are independent.

As usually the empty sum is considered as zero. Intuitively, m represents the number of different types of individuals in the population. Each random vector $X^{i,n,j}$ governs the reproduction phase and, intuitively, represents the vector of descendants of the jth i-type individual in the nth generation. Each random vector $\phi^n(z)$ describes the control made on the population and, intuitively, represents the number of individuals of the different types allowed to be parents in the nth generation, provided that the population size in this generation is given by the vector z. Consequently the vector $Z(n+1)$ represents the total number of individuals of the different types in the $(n+1)$st generation. This CMBP is a particular model of the one introduced in [1]. It is easy to check that a CMBP is a homogeneous multitype Markov chain. From the relationship between the control and the offspring vectors, it is not difficult to prove that the null state is absorbing if and only if

$$P(\phi^0(\mathbf{0}) = \mathbf{0}) = 1,$$

where $\mathbf{0}$ denotes the null-vector. Also every non-null vector $z \in \mathbb{N}_0^m$ is transient if

$$P\left(\bigcap_{i=1}^{m} \left(\{\phi_i^0(z) = 0\} \cup \{\phi_i^0(z) > 0, X^{i,0,j} = \mathbf{0},\ j = 1, \dots, \phi_i^0(z)\}\right)\right) > 0.$$

If these conditions are satisfied, then

$$P(Z(n) \to \mathbf{0}) + P(\|Z(n)\| \to \infty) = 1$$

holds, where $\|\cdot\|$ is an arbitrary norm in $\mathbb{R}^m$.

Let us introduce the following notation for the main moments associated to the random variables that define the model:

$$m_{ij} = E[X_j^{i,0,1}], \quad i,j = 1, \dots, m,$$

$$\sigma_{ij}^2 = Var[X_j^{i,0,1}],\ \sigma_{i,jk} = Cov(X_j^{i,0,1}, X_k^{i,0,1}), \quad i,j,k = 1, \dots, m;\ j \neq k,$$

and

$$\varepsilon_i(z) = E[\phi_i^0(z)],\ v_i^2(z) = Var[\phi_i^0(z)], \quad i = 1, \dots, m.$$

We assume all the latter moments finite. Let M be the offspring mean matrix and Σ_i denote the variance-covariance of the vector $X^{i,0,1} = (X_1^{i,0,1}, \dots, X_m^{i,0,1})$, $i = 1, \dots, m$.

In order to obtain a classification of this model similar to the classical multitype branching process, from now on we assume that, for $i = 1, \dots, m$, there exist $\lambda_i \geq 0$ such that:

$$\varepsilon_i(z) = \lambda_i z_i + h_i(z),\ h_i(z) = o(\|z\|), \text{ as } \|z\| \to \infty. \tag{11.2}$$

Remark 11.1. (a) Condition (11.2) means that the average number of progenitors of a type is proportional to the number of individuals of this type plus/minus certain quantity of progenitors which is negligible with respect to the total amount of population. Notice that under (11.2) immigration/emigration of progenitors of each type is allowed. Immigration is possible even if there are not individuals of a type. This could not happen if $h_i(z) = z_i o(1)$. However, in this case we could determine λ_i explicitly as $\lambda_i = \lim_{\|z\| \to \infty; z_i \neq 0} z_i^{-1} \varepsilon_i(z)$.

(b) For $m = 1$, condition (11.2) was also considered in the study of the behaviour of single-type controlled branching processes (see [7–10]).

We further assume that $\widetilde{M} = (\lambda_i m_{ij})_{1 \leq i,j \leq m}$ is irreducible in the sense of [15]. Notice that $\widetilde{M}$ is irreducible iff λ_i is non null for each i and the offspring mean matrix M is irreducible. In this case, there exists ρ, the Perron-Frobenius eigenvalue of $\widetilde{M}$, which will play an important role in the study of extinction problem. Under these conditions, we say that a CMBP is subcritical if $\rho < 1$, near-critical if $\rho = 1$, and supercritical if $\rho > 1$ (as was given in [3]). Criteria for deciding whether or not the model grows indefinitely with positive probability, and in consequence the extinction does not happen almost surely, are given in [1] and [3].

11.3 Weighted conditional least squares estimator of the offspring mean matrix

For notational simplicity, we consider the case $m = 2$, the two-type controlled branching process with random control function.

Before we develop a method of estimation for the offspring mean matrix, we have to determine what is observable. It is worthwhile to note here that if $\phi_i^n(z) = z_i + Y_i^n$, $i = 1,2$, where $\{Y^n = (Y_1^n, Y_2^n) : n = 0,1,\ldots\}$ are independent and identically non-negative integer valued random vectors and independent of $\{X^{i,n,j} : i = 1,\ldots,m;\ n = 0,1,\ldots;\ j = 1,2,\ldots\}$, then $\{Z(n)\}_{n \geq 0}$ is a multitype branching process with immigration (MBPI). Shete (see [17], Sect. 4.2 for details) established that for a MBPI there are not consistent estimators of the offspring mean matrix if only we observe the generation sizes of each type. Thus in order to obtain consistent estimators for the offspring matrix for a CMBP we have to assume a little more information about the process than just the generation sizes are observed.

To this end, we define, for $i,j = 1,2$, $n = 0,1,\ldots$,

$$Z_j^{n+1,i} = \sum_{k=1}^{\phi_i^n(Z(n))} X_j^{i,n,k},$$

which intuitively represents the number j-type individuals in the nth generation whose parent are of type i. We assume we observe $\widetilde{Z}_j = (Z_1^{j,1}, Z_2^{j,1}, Z_1^{j,2}, Z_2^{j,2})$, $j = 1,2,\ldots,n$. Note then that $Z_i(n) = Z_i^{n,1} + Z_i^{n,2}$, $i = 1,2$, $n = 0,1,\ldots$. Let define $\mathscr{F}_n = \sigma(Z(0),\ldots,Z(n))$, $n = 0,1,\ldots$. From the model we have that, for $i,j = 1,2$,

$$E[Z_j^{n,i} \mid \mathscr{F}_{n-1}] = \varepsilon_i(Z(n-1))m_{ij} \quad a.s.$$

We can use this to represent $Z_j^{n,i}$ as

$$Z_j^{n,i} = \varepsilon_i(Z(n-1))m_{ij} + \tilde{\delta}_j^{n,i},\ n = 1,2,\ldots, \tag{11.3}$$

where the error term $\tilde{\delta}_j^{n,i}$ has $E[\tilde{\delta}_j^{n,i} \mid \mathscr{F}_{n-1}] = 0$ almost surely.

Let $\tilde{\delta}_n = (\tilde{\delta}_1^{n,1}, \tilde{\delta}_2^{n,1}, \tilde{\delta}_1^{n,2}, \tilde{\delta}_2^{n,2})$, $n = 1,2,\ldots$. Taking into account the independence properties between the control and offspring vectors, the conditional variance-covariance matrix of $\tilde{\delta}_n$ is given by

$$Var[\tilde{\delta}_n \mid \mathscr{F}_{n-1}] = \begin{pmatrix} \tilde{d}_{11} & \tilde{d}_{1,12} & 0 & 0 \\ \tilde{d}_{1,12} & \tilde{d}_{12} & 0 & 0 \\ 0 & 0 & \tilde{d}_{21} & \tilde{d}_{2,12} \\ 0 & 0 & \tilde{d}_{2,12} & \tilde{d}_{22} \end{pmatrix},$$

where

$$\tilde{d}_{ij} = Var[\tilde{\delta}_j^{n,i}] = \sigma_{ij}^2 \varepsilon_i(Z(n-1)) + m_{ij}^2 \nu_i^2(Z(n-1)),\ i,j = 1,2$$

and

$$\tilde{d}_{i,12} = Cov(\tilde{\delta}_1^{n,i}, \tilde{\delta}_2^{n,i}) = \sigma_{i,12} E[(\phi_i^n(Z(n-1)))^2] + m_{i1}m_{i2}\nu_i^2(Z(n-1)),\ i = 1,2.$$

Note that $Var[\tilde{\delta}_n \mid \mathscr{F}_{n-1}]$ can be unbounded if $\|Z(n)\| \to \infty$ almost surely as $n \to \infty$. To overcome this, we construct the weighted conditional least squares estimator by normalizing (11.3) by $(\varepsilon_i(Z(n-1))+1)^{1/2}$, i.e. we consider, for $n = 1,2,\ldots$,

$$\frac{Z_j^{n,i}}{(\varepsilon_i(Z(n-1))+1)^{1/2}} = \frac{\varepsilon_i(Z(n-1))m_{ij}}{(\varepsilon_i(Z(n-1))+1)^{1/2}} + \delta_j^{n,i}, \tag{11.4}$$

where $\delta_j^{n,i} = (\varepsilon_i(Z(n-1))+1)^{-1/2}\tilde{\delta}_j^{n,i}$. Let $\delta_n = (\delta_1^{n,1}, \delta_2^{n,1}, \delta_1^{n,2}, \delta_2^{n,2})$, $n = 1,2,\ldots$. Then we have almost surely that $E[\delta_n \mid \mathscr{F}_{n-1}] = 0$ and

$$Var[\delta_n \mid \mathscr{F}_{n-1}] = \begin{pmatrix} d_{11} & d_{1,12} & 0 & 0 \\ d_{1,12} & d_{12} & 0 & 0 \\ 0 & 0 & d_{21} & d_{2,12} \\ 0 & 0 & d_{2,12} & d_{22} \end{pmatrix},$$

where, for $j = 1,2$,

$$\begin{aligned} d_{ij} &= (\varepsilon_i(Z(n-1))+1)^{-1}\tilde{d}_{ij} \\ &= (\varepsilon_i(Z(n-1))+1)^{-1}(\sigma_{ij}^2\varepsilon_i(Z(n-1)) + m_{ij}^2\nu_i^2(Z(n-1))), \end{aligned}$$

and, for $i = 1,2$,

$$\begin{aligned} d_{i,12} &= (\varepsilon_i(Z(n-1))+1)^{-1}\tilde{d}_{i,12} \\ &= (\varepsilon_i(Z(n-1))+1)^{-1}(\sigma_{i,12}E[(\phi_i^n(Z(n-1)))^2]+m_{i1}m_{i2}\nu_i^2(Z(n-1))). \end{aligned}$$

In this paper we will impose certain conditions on $\varepsilon_i(z)$ and $\nu_i^2(z)$ so that the elements of the matrix $Var[\delta_n \mid \mathscr{F}_{n-1}]$ stay bounded as $\|Z(n)\| \to \infty$. These considerations lead us to the following conditional weighted least squares estimators of m_{ij}, $i,j=1,2$:

$$\widehat{m}_{ij} = \left(\sum_{k=1}^{n} \frac{Z_j^{k,i}\varepsilon_i(Z(k-1))}{\varepsilon_i(Z(k-1))+1}\right)\left(\sum_{k=1}^{n} \frac{\varepsilon_i^2(Z(k-1))}{\varepsilon_i(Z(k-1))+1}\right)^{-1}. \tag{11.5}$$

From these, the conditional weighted least squares estimator of the offspring mean matrix is given by

$$\widehat{M} = \begin{pmatrix} \widehat{m}_{11} & \widehat{m}_{12} \\ \widehat{m}_{21} & \widehat{m}_{22} \end{pmatrix},$$

where $\widehat{m}_{ij}$ are defined in (11.5).

Remark 11.2. (a) The validity of the estimators $\widehat{m}_{i,j}$, $i,j=1,2$, defined in (11.5) does not requiere condition (11.2).

(b) Note that the maximal eigenvalue ρ of $\widetilde{M}$ is given by

$$\rho = 2^{-1}(\lambda_1 m_{11} + \lambda_2 m_{22} + ((\lambda_1 m_{11} - \lambda_2 m_{22})^2 + 4\lambda_1\lambda_2 m_{12}m_{21})^{1/2}). \tag{11.6}$$

Therefore, we propose as estimator of ρ the one obtained from replacing in (11.6) m_{ij} by $\widehat{m}_{ij}$, given λ_i, $i=1,2$, known.

(c) For the single-type controlled branching process, this estimator was proposed in [19].

Next, we state the strong consistency of the estimator of the offspring mean matrix in the supercritical case, i.e. $\rho > 1$. To this end, note that under some conditions the following results hold for the supercritical CMBP:

(A1) $P(\|Z(n)\| \to \infty) > 0$

(A2) $\lim_{n\to\infty} \rho^{-n} Z(n) = W$ a.s. on $\{\|Z(n)\| \to \infty\}$ with W_i, the ith coordinate of W, non degenerate in 0, $i=1,2$.

Remark 11.3. Conditions that guarantee (A1)–(A2) can be found in the papers [1–3] and [6]. Moreover, using the similar reasoning as given in [11] one can derive that $\{W_i > 0\} = \{\|Z(n)\| \to \infty\}$ almost surely for each i.

Firstly to state the strong consistency of the offspring mean matrix, we establish the following preliminary result:

Lemma 11.1. *Let $\{Z(n)\}_{n\geq 0}$ be a CMBP defined by (11.1) satisfying (11.2). Define, for i=1,2, $\{U_{n,i}\}_{n\geq 1}$ as*

$$U_{n,i} = \sum_{k=1}^{n} \varepsilon_i^2(Z(k-1))(\varepsilon_i(Z(k-1))+1)^{-1}.$$

Then, for $i=1,2$, $U_{n,i}\to\infty$ almost surely on $\{\|Z(n)\|\to\infty\}$ as $n\to\infty$.

Proof. It follows that, on $\{\|Z(n)\|\to\infty\}$, for $i=1,2$,

$$\frac{\varepsilon_i(Z(n))}{\rho^n}\to\lambda_i W e_i \qquad a.s. \text{ as } n\to\infty, \tag{11.7}$$

being W introduced in (A2) and e_i a two dimensional vector with its ith coordinate equal to one and the other equal to zero, $i=1,2$. Indeed, using (11.2)

$$\frac{\varepsilon_i(Z(n))}{\rho^n}=\frac{\lambda_i Z_i(n)}{\rho^n}+\frac{h_i(Z(n))}{\|Z(n)\|}\frac{\|Z(n)\|}{\rho^n}$$

and from (A1)–(A2), we have (11.7). Moreover, from (11.7) and using Cesàro's lemma we obtain that, on $\{\|Z(n)\|\to\infty\}$,

$$\frac{1}{\rho^n}\sum_{k=1}^{n}\frac{\varepsilon_i^2(Z(k-1))}{\varepsilon_i(Z(k-1))+1}\to\frac{\lambda_i W e_i}{(\rho-1)} \qquad a.s. \text{ as } n\to\infty. \tag{11.8}$$

Thus, using (11.8) and since $\rho>1$, we deduce, for $i=1,2$, that on $\{\|Z(n)\|\to\infty\}$, $U_{n,i}\to\infty$ almost surely as $n\to\infty$. $\square$

Theorem 11.1. *Let $\{Z(n)\}_{n\geq 0}$ be a CMBP defined by (11.1) satisfying (11.2) and*

$$v_i^2(z)=O(\varepsilon_i(z)), \quad \text{as } \|z\|\to\infty. \tag{11.9}$$

Then, for $i,j=1,2$, $\widehat{m}_{ij}$ defined in (11.5) is strongly consistent for m_{ij} on $\{\|Z(n)\|\to\infty\}$, as $n\to\infty$.

Proof. It is easy to check that, for $i,j=1,2$,

$$\widehat{m}_{ij}-m_{ij}=\left(\sum_{k=1}^{n}\frac{(Z_j^{k,i}-m_{ij}\varepsilon_i(Z(k-1)))\varepsilon_i(Z(k-1))}{\varepsilon_i(Z(k-1))+1}\right)U_{n,i}^{-1},$$

being $U_{n,i}$ defined in Lemma 11.1. We will prove that on $\{\|Z(n)\|\to\infty\}$, for $i,j=1,2$, the estimator $\widehat{m}_{ij}$ is strongly consistent for m_{ij} making use of Theorem 2.18 of [12]. Note that, for $i=1,2$,

$$\sum_{k=1}^{n}\frac{(Z_j^{k,i}-m_{ij}\varepsilon_i(Z(k-1)))\varepsilon_i(Z(k-1))}{\varepsilon_i(Z(k-1))+1} \qquad \text{is a martingale.}$$

Recalling that $\mathscr{F}_n=\sigma(Z(0),\ldots,Z(n))$, if we show that, as $n\to\infty$, almost surely on $\{\|Z(n)\|\to\infty\}$

$$\sum_{k=1}^{\infty}\frac{E\left[((Z_j^{k,i}-m_{ij}\varepsilon_i(Z(k-1)))\varepsilon_i(Z(k-1)))^2(\varepsilon_i(Z(k-1))+1)^{-2}\,|\mathscr{F}_{k-1}\right]}{U_{k,i}^2}<\infty,$$

then, since by Lemma 11.1, for $i = 1, 2$, on $\{\|Z(n)\| \to \infty\}$, $U_{n,i} \to \infty$, as $n \to \infty$, we have that on $\{\|Z(n)\| \to \infty\}$

$$\frac{\sum_{k=1}^{n} (Z_j^{k,i} - m_{ij}\varepsilon_i(Z(k-1)))\varepsilon_i(Z(k-1))(\varepsilon_i(Z(k-1))+1)^{-1}}{U_{k,i}} \to 0 \text{ a.s. as } n \to \infty,$$

that is, the strong consistency of the estimator $\widehat{m}_{ij}$.

Now, taking into account (11.9), for some positive constant K,

$$\begin{aligned} &E\left[((Z_j^{k,i} - m_{ij}\varepsilon_i(Z(k-1)))\varepsilon_i(Z(k-1)))^2(\varepsilon_i(Z(k-1))+1)^{-2} | \mathscr{F}_{k-1}\right] \\ &= \frac{(\sigma_{ij}^2\varepsilon_i(Z(k-1)) + m_{ij}^2 v_i^2(Z(k-1)))\varepsilon_i^2(Z(k-1))}{(\varepsilon_i(Z(k-1))+1)^2} \\ &\le K\frac{\varepsilon_i^2(Z(k-1))}{\varepsilon_i(Z(k-1))+1}. \end{aligned}$$

Therefore,

$$\begin{aligned} &\sum_{k=1}^{\infty} \frac{E\left[((Z_j^{k,i} - m_{ij}\varepsilon_i(Z(k-1)))\varepsilon_i(Z(k-1)))^2(\varepsilon_i(Z(k-1))+1)^{-2} | \mathscr{F}_{k-1}\right]}{U_{k,i}^2} \\ &\le K\sum_{k=1}^{\infty} \frac{\varepsilon_i^2(Z(k-1))(\varepsilon_i(Z(k-1))+1)^{-1}}{U_{k,i}^2} \\ &= K\sum_{k=1}^{\infty} \frac{(U_{k,i} - U_{k-1,i})}{U_{k,i}^2} < \infty. \quad \square \end{aligned}$$

Remark 11.4. (a) Notice that if we assume in condition (11.2) that $h_i(z) = z_i o(1)$, as $\|z\| \to \infty$, then (11.9) is verified if $v_i^2(z) = O(z_i)$, as $\|z\| \to \infty$. This is the condition required to check the strong consistency of the estimator of the offspring mean for the single-type controlled branching process (see [19]).

(b) Note that in the construction of our estimator of the offspring matrix we implicitly assume that $\varepsilon_i(z)$, $z \in \mathbb{N}_0^m$, $i = 1, 2$, are known. It is possible that this assumption is not valid, for instance, in the special case of MBPI, defined at the beginning of Sect. 11.3, with unknown $E[Y^n]$, i.e. immigration mean vector. In the case of unknown $\varepsilon_i(z)$, we can replace $\varepsilon_i(Z(k-1))$ in (11.5) by $\phi_i(Z(k-1))$ and define a modified estimator of the offspring mean vector by

$$\widehat{\widehat{m}}_{ij} = \left(\sum_{k=1}^{n} \frac{Z_j^{k,i}\phi_i(Z(k-1))}{\phi_i(Z(k-1))+1}\right)\left(\sum_{k=1}^{n} \frac{\phi_i^2(Z(k-1))}{\phi_i(Z(k-1))+1}\right)^{-1}.$$

With minor modifications in the proof of Theorem 11.1, it is possible to show the strong consistency of $\widehat{\widehat{m}}_{ij}$ in the supercritical case. Finally, note that our results extend those of [18] for the estimation of the offspring mean matrix in the case of known $E[Y^n]$.

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Part IV
Applications in Cell Kinetics and Genetics

12
Branching processes in cell proliferation kinetics

Nikolay M. Yanev

Abstract This is a memorial survey paper on some joint works with Andrei Yu. Yakovlev† in the field of branching processes and their applications in cell proliferation kinetics. The following topics are considered: distributions of discrete and continuous labels, age and residual lifetime distributions, models of leukemia cell kinetics, age-dependent branching populations with randomly chosen paths of evolution as models of progenitor cell populations (in vitro) and estimating of offspring distributions, multitype branching populations with a large number of ancestors and asymptotic likelihood estimation of the basic mitotic parameters. A part of the presented results is not published yet. The paper is focused on some new ideas for branching processes theory arising in cell proliferation modeling.

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Keywords: branching processes, cell proliferation, discrete and continuous labels, label distributions, immigration, age and residual lifetime distributions, age-dependent processes, large number of ancestors, multitype branching processes, limiting distributions, asymptotic normality, statistical inference.

† http://www.urmc.rochester.edu/smd/biostat/Andrei_Yakovlev.pdf
http://www.biology-direct.com/content/3/1/10

12.1 Introduction

The theory of branching processes has a long history of biological applications. It is worth to point out that the first asymptotic result for branching processes was obtained by Kolmogorov [12] considering some biological problems. Recall that

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the terminology "branching processes" was first introduced by Kolmogorov and his coauthors [14, 15] proposing multitype branching processes, which received much attention in biological applications. For a further development of the theory of branching processes and their applications in Biology we refer the reader to several books [1, 4–6, 10, 11, 17, 19, 22].

The main purpose of this work is to present some new ideas and results (in the theory of branching processes) obtained in modeling of cell proliferation kinetics (and based on [21–28]). The paper is organized as follows. The distribution of the discrete marks (labels) is given in *Section* 12.2 (see [22, 35]) using a model with infinite many types of Bellman-Harris branching processes. Generalizations in the case of continuous labels are presented in Sect. 12.3 (see [23] and [25]). This work is concerned with an age-dependent branching process with cells bearing a label, the latter being treated as a continuous parameter. The proposed stochastic model is motivated by applications in cell biology. It is assumed that the mitotic division results in a random distribution of the label among daughter cells in accordance with some bivariate probability distribution. In the event of cell death the label borne by that cell disappears. The main focus is on the label distribution as a function of the time elapsed from the moment of label administration. Explicit expressions for this distribution are derived in some particular cases which are of practical interest in the analysis of cell cycle. The Markov branching process with the same evolution of a continuously distributed label is considered as well. Note that processes with continuous labels are first considered by Kolmogorov [13].

New models of renewing cell populations (in vivo) using age-dependent branching processes with non-homogeneous Poisson immigration are proposed in Sect. 12.4, where is considered an interesting and important problem arising from cell proliferation kinetics: definition and limiting behavior of age and residual lifetime distributions for branching processes (see [24] and [26]). Leukemia cell kinetics with a stem cell immigration component is studied in Sect. 12.5 (see [33]). Multitype age-dependent branching processes with randomly chosen paths of evolution are proposed in Sect. 12.6 as models of progenitor cell populations (in vitro) with estimating of the offspring distributions using real data as well as bootstrap methods (see also [30]).

The relative frequencies of distinct types of cells in multitype branching processes with a large number of ancestors are investigated in Sect. 12.7 (see [27] and [28]). The reported limiting results are of advantage in cell kinetics studies where the relative frequencies but not the absolute cell counts are accessible to measurement. In [27] some relevant statistical applications are discussed in the context of asymptotic maximum likelihood inference for multitype branching processes. In [28] the asymptotic behavior of multitype Markov branching processes with discrete or continuous time is investigated in the positive regular and nonsingular case when both the initial number of ancestors and the time tend to infinity. Some limiting distributions are obtained as well as multivariate asymptotic normality is proved. The results from [27] and [28] have specific applications in cell proliferation kinetics.

Finally it is worth to point out that the new problems in the theory of branching processes appeared as a result of cell proliferation modeling and the paper is focused on some of these new ideas.

12.2 Distributions of discrete marks over a proliferating cell populations

Among many applied problems for which methods of branching stochastic processes hold much promise is the analysis of labeling experiments. These experimental techniques are intended for making quantitative inference of the mitotic cycle parameters in renewing cell populations from observed dynamics of cells after a fraction of the cell population is labeled with specially designed molecular markers. DNA precursors labeled either with radioactive isotopes (e.g., ^{3}H-thymidine) or with fluorescent antibodies are typically used for this purpose. Such labeling of the cells occurs during their progression through the S-phase of the mitotic cycle. When using ^{3}H-thymidine and autoradiographic technique, one can obtain data on grain counts, the latter being interpreted as discrete marks attached to each labeled cell. The distribution of such marks as a function of the time elapsed from the administration of a pulse label yields the needed information on the structure of the mitotic cycle to be extracted by methods of mathematical modeling. Assuming that the initial distribution of marks is Poisson, and treating the evolution of labeled cells as a Bellman-Harris age-dependent branching process with infinitely many cell types, Yanev and Yakovlev [35] derived an analytical form of this distribution. On the other hand, analyzing the kinetics of cells that have been pulse-labeled with BrdU on a fluorescence-activated cell sorter has become a method of choice in this field of research. This technique calls for modeling the distribution of BrdU intensity and its variations with time. However, little attention has been given to this problem within the framework of stochastic branching processes.

The problem for the distribution of the discrete labels was solved completely in [35] for the case of impulsive labels at $t = 0$ and initial Poisson distribution $Po(\theta)$ of the labels among cells. It is proved that the states of the system can be described by a Bellman-Harris branching process with infinitely many types of particles $\tilde{Z} = (Z_0(t), Z_1(t), \ldots, Z_j(t), \ldots)$, where $Z_j(t)$ is the number of cells with label j at time t. For the distribution $\Pi_j(t) = \mathbf{E}[Z_j(t)] / \mathbf{E}[\sum_{k=0}^{\infty} Z_k(t)]$, $j = 0, 1, 2, ...; t \geq 0$, it is obtained (in case of synchronized population) that

$$\Pi_j(t) = \frac{\theta^j}{j!} \sum_{k=0}^{\infty} (p2^{1-j})^k e^{-\theta/2^k} (\overline{G} * G^{*k})(t) / \sum_{k=0}^{\infty} (2p)^k (\overline{G} * G^{*k})(t),$$

where $G(t)$ is the cumulative distribution function (c.d.f.) of the mitotic cycle, G^{*k} denotes the k-fold convolution of G, $\overline{G} = 1 - G$ and p is the probability for successful division. The generalization of these results and further applications are continued in [36]. Henceforth the introduced notation will be used throughout the paper.

A comprehensive presentation of biological applications of branching processes by that time can be found in the book of Yakovlev and Yanev [22].

12.3 Distributions of continuous labels in branching populations of cells

The case of a randomly distributed continuous label is more complicated than its discrete counterpart and involves modeling of a branching process with states characterized by a real-valued parameter (see [23, 25]). Recall that Kolmogorov [13] was the first to consider a branching process (particle splitting) of this type with the continuous parameter being the particle size.

Suppose that every cell has a life time τ with distribution function $G(x) = \mathbf{P}(\tau \leq x)$ and at the end of its life it either divides into two cells with probability p $(0 < p \leq 1)$ or it dies with probability $1-p$. If a cell divides, its label L is distributed randomly between daughter cells so that their labels L_1 and L_2 satisfy the condition $L_1 + L_2 \leq L$. Introduce the conditional distribution

$$\mathbf{P}(L_1 \leq y_1, L_2 \leq y_2 | L = y) = K(y_1/y, y_2/y), \ \ 0 \leq y_1 \leq y, \ 0 \leq y_2 \leq y,$$

where the bivariate distribution function $K(x_1,x_2)$ is symmetric, that is $K(x_1,x_2) = K(x_2,x_1)$, $0 \leq K(x_1,x_2) \leq 1$ for $0 \leq x_1 \leq 1, 0 \leq x_2 \leq 1$. Let $K(x) = K(x,1) = K(1,x)$ be the one-dimensional distribution that defines both marginal distributions of $K(x_1,x_2)$. In the event of cell death the label borne by that cell disappears.

We assume for simplicity that the process begins with one cell of age zero at time $t = 0$ and the initial cell bears a certain amount L_0 of label. The results can readily be generalized to include an arbitrary initial distribution of the random variable L_0 and then the resultant formulas can be compounded with respect to this distribution. The initial distribution can be estimated non-parametrically from the data on label intensity available at time $t = 0$.

Let $Z(t,x)$ be the number of cells at time $t > 0$ with the label intensity of $x \leq L_0$. It is clear that $Z(t,x) = 0$ if $x > L_0$. Introduce the notation: $P_n(t,x|L_0) = \mathbf{P}(Z(t,x) = n)$. Then $P_n(t,x|L_0) = P_n(t,x/L_0|1), x \leq L_0$, and in what follows, we will use the notation $P_n(t,x) = P_n(t,x|1)$, $0 \leq x \leq 1$. Note that $P_n(t,x) = 0$ for $n > 1/x$.

Introducing the p.g.f. $\Psi(t,x,s) = \mathbf{E}\left[s^{Z(t,x)}\right]$ one can obtain the equation

$$\begin{aligned}\Psi(t,x,s) &= (1-p)G(t) + s[1-G(t) \\ &+ p\int_0^t \left\{\int_x^1 \int_x^1 \Psi(t-y,x/u_1,s)\Psi(t-y,x/u_2,s)K(du_1,du_2)\right\} dG(y)],\end{aligned}$$

which has a unique solution in the class of the p.g.f.

Introduce the notations

$$
\begin{aligned}
A(t,x) &= \mathbf{E}\,[Z(t,x)] = \frac{\partial}{\partial s}\Psi(t,x,s)|_{s=1},\\
B(t,x) &= \mathbf{E}\,[Z(t,x)(Z(t,x)-1)] = \frac{\partial^2}{\partial s^2}\Psi(t,x,s)|_{s=1}.
\end{aligned}
$$

Then one can obtain the following equations:

$$
\begin{aligned}
A(t,x) &= 2p\int_0^t\left\{\int_x^1 A(t-y,x/u)dK(u)\right\}dG(y)+1-G(t),\\
B(t,x) &= 2p\int_0^t\left\{\int_x^1 B(t-y,x/u)dK(u)\right\}dG(y)\\
&\quad +2p\int_0^t\left\{\int_x^1\int_x^1 A(t-y,x/u_1)A(t-y,x/u_2)K(du_1,du_2)\right\}dG(y).
\end{aligned}
$$

Setting $x=0$ one has

$$
\begin{aligned}
\Psi(t,0,s) &= (1-p)G(t)+s[1-G(t)+p\int_0^t \Psi^2(t-y,0,s)dG(y)],\\
A(t,0) &= 2p\int_0^t A(t-y,0)dG(y)+1-G(t),\\
B(t,0) &= 2p\int_0^t B(t-y,0)dG(y)+2p\int_0^t A^2(t-y,0)dG(y),
\end{aligned}
$$

describing an age-dependent binary branching process considered by Bellman and Harris.

Definition 12.1. The label distribution $D_t(x)$ is defined as follows:

$$
\overline{D}_t(x) = 1-D_t(x) = A(t,x)/A(t,0).
$$

A closed form solution can be obtained in the special case where one of the daughter cells receives a fixed fraction c $(0<c<1)$ of the mother label while the complement $1-c$ goes to the second daughter cell. By a symmetry argument we have the condition: $0<c\le 1/2$.

Theorem 12.1. *If $K_c(u)=0$ for $u<c$ and $K_c(u)=1$ for $u\ge c$, then the following label distribution holds:*

(i) For $x<c\le 1/2$,

$$
\overline{D}_t(x) = \left\{\sum_{k=0}^{N}(2p)^k(\overline{G}*G^{*k})(t)\right\}/\sum_{k=0}^{\infty}(2p)^k(\overline{G}*G^{*k})(t),
$$

where $N=N(x,c)=\langle \ln(x/c)/\ln c\rangle$ and $\langle z\rangle$ denotes the smallest integer greater or equal to z;

(ii) If $x\ge c$, then

$$\overline{D}_t(x) = \overline{G}(t) / \sum_{k=0}^{\infty} (2p)^k (\overline{G} * G^{*k})(t)$$

for every $c \in (0, 1/2]$.

Corollary 12.1. *The distribution given by Theorem 12.1 assumes a particularly simple form in the biologically plausible case of* $c = 1/2$. *In this case,* $N = N(x, 1/2) = \langle -(\ln 2x)/\ln 2 \rangle$ *for* $x < 1/2$.

Let $G(x) = 1 - e^{-\lambda x}, \lambda > 0$, which means that the considered process is a Markovian one.

Theorem 12.2. *In the Markov case* $\overline{D}_t(x) = \sum_{n=0}^{\infty} \Pi_n(2p\lambda t) R^{*n}(-\log x)$, *where* $R(y) = 1 - K(e^{-y})$ *and* $\Pi_n(z) = z^n e^{-z}/n!$ *is the Poisson distribution.*

Corollary 12.2. *Assuming in addition that* $K(u) = u$ *for* $0 \le u \le 1$, *then* $\overline{D}_t(x) = \sum_{n=0}^{\infty} \Pi_n(2p\lambda t) \Gamma_n(-\log x)$, *where* $\Gamma_n(y) = \frac{1}{(n-1)!} \int_0^y z^{n-1} e^{-z} dz$.

Theorem 12.3. *Let* $\alpha = \int_0^1 \log(1/x) dK(x) < \infty$, $\beta = \int_0^1 \log^2(1/x) dK(x) < \infty$ *and* $\Delta_t(z) = \exp\{-2p\lambda \alpha t - z(2p\lambda t\beta)^{1/2}\}$. *Then in the Markov case*

$$\lim_{t \to \infty} \overline{D}_t(\Delta_t(z)) = 1/(2\pi)^{1/2} \int_{-\infty}^{z} e^{-u^2/2} du$$

for every $z \in (-\infty, \infty)$.

The label distribution can be generalized in many different ways by replacing $A(t,x)$ and $A(t,0)$ with other pertinent models of cell proliferation kinetics. In particular, age dependent branching processes with immigration are gaining in importance in conjunction with recent advancements in experimental approaches to cell proliferation kinetics in analysis of renewing cell populations (see [24]). These advancements have made it possible to distinguish many cell types by antibody labeling so that cells of different types can be counted in the dissociated tissue by using flow cytometry. Finally it is interesting to point out that the asymptotic results in Theorem 12.3 remain open problems in the non-Markov cases.

12.4 Age and residual lifetime distributions for branching processes

Let $Z(t)$ be a continuous-time branching process and let $Z(t,x)$ be the number of individuals (cells) at time t of age $\le x$. Let $\overline{Z}_t(y)$ represent the number of individuals at time t whose residual lifetime is greater than y, $y \ge 0$. Note that $Z(t) = Z(t,x)$ if

$x \geq t$. Denote their p.g.f.'s by $F(t;s) = \mathbf{E}\left[s^{Z(t)}\right]$ and $F(t,x;s) = \mathbf{E}\left[s^{Z(t,x)}\right]$, $t,x \geq 0$, with the corresponding expectations denoted by $M(t) = \mathbf{E}\left[Z(t)\right] = \frac{\partial F(t;s)}{\partial s}|_{s=1}$ and $M(t,x) = \mathbf{E}\left[Z(t,x)\right] = \frac{\partial F(t,x;s)}{\partial s}|_{s=1}$, respectively.

Definition 12.2. For the process $Z(t)$, the average age distribution at time $t \geq 0$ is given by $A_t(x) = M(t,x)/M(t)$, $x \geq 0$. The limiting average age distribution is defined as $A(x) = \lim_{t\to\infty} A_t(x)$.

Definition 12.3. For the process $Z(t)$ the average residual lifetime distribution at time $t \geq 0$ is given by $R_t(y) = 1 - \overline{R}_t(y) = 1 - \mathbf{E}\left[\overline{Z}_t(y)\right]/M(t)$, $y \geq 0$. Then the limiting average residual lifetime distribution is defined as $R(y) = \lim_{t\to\infty} R_t(y)$.

Note that $E\left[\overline{Z}_t(y)\right] = M(t+y) - M(t+y,y)$. Therefore, one can write

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

which offers some advantages.

Remark 12.1. Since every renewal process is a particular case of the age-dependent branching process in which every individual produces exactly one offspring, the introduced notions 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.

Let us first consider a class of age-dependent branching processes with a randomly chosen paths of evolution (without immigration) defined as follows (see also Sect. 12.7).

Evolution. Every cell with probability p has a random lifetime ξ with c.d.f. $G(x) = \mathbf{P}(\xi \leq x)$, $x \geq 0$, or with probability $1-p$ it differentiates into another cell type. In other words, the lifetime ξ is identical to the mitotic cycle (MC) duration. At the end of its life, every cell gives rise to ν offspring (of the same cell type) with discrete distribution $p_k(u) = \mathbf{P}(\nu = k|\xi = u)$, $\sum_{k=0}^{\infty} p_k(u) = 1$, $u \geq 0$. It takes a random time η with c.d.f. $L(x) = \mathbf{P}(\eta \leq x)$, $x \geq 0$, for the event of differentiation to actually occur. If $p = 1$, the stochastic process thus defined reduces to the Sevastyanov branching process [19]. The mixture-type branching (allowing non-identical distributions of the time to division and the time to differentiation) was introduced by Jagers [10]. Denote the offspring p.g.f. by $h(u;s) = \mathbf{E}\left[s^{\nu}|\xi = u\right] = \sum_{k=0}^{\infty} p_k(u)s^k$, $|s| \leq 1, u \geq 0$. 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.

Let $F(t;s) = \mathbf{E}\left[s^{Z(t)}\right]$ 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. $F(t,x;s) = \mathbf{E}\left[s^{Z(t,x)}\right]$, $t,x \geq 0$. The p.g.f.'s $F(t;s)$ and $F(t,x;s)$ satisfy the following integral equations

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

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

with $F(0;s) = F(0,0;s) = s$, 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). It is not difficult to obtain equations for the corresponding expectations by taking partial derivatives with respect to s at the point $s = 1$.

Let α be the Malthus parameter of the equation $p\int_0^\infty e^{-\alpha u}m(u)dG(u) = 1$ and assume the conditions

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

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

Theorem 12.4. *Under the conditions the following limiting age and residual lifetime distributions hold*

$$\text{(i) } A(x) = \frac{p\int_0^x e^{-\alpha u}[1-G(u)]du + (1-p)\int_0^x e^{-\alpha u}[1-L(u)]du}{p\int_0^\infty e^{-\alpha u}[1-G(u)]du + (1-p)\int_0^\infty e^{-\alpha u}[1-L(u)]du},$$
$$\text{(ii) } R(y) = 1 - e^{\alpha y}\frac{p\int_y^\infty e^{-\alpha u}[1-G(u)]du + (1-p)\int_y^\infty e^{-\alpha u}[1-L(u)]du}{p\int_0^\infty e^{-\alpha u}[1-G(u)]du + (1-p)\int_0^\infty e^{-\alpha u}[1-L(u)]du}.$$

Note that in the critical case $\alpha = 0$

$$A(x) = R(x) = \frac{p\int_0^x[1-G(u)]du + (1-p)\int_0^x[1-L(u)]du}{p\int_0^\infty[1-G(u)]du + (1-p)\int_0^\infty[1-L(u)]du}.$$

Remark 12.2. Let us now set $p = 1$. If we assume in addition that $h(s) \equiv h(u;s)$, $m = h'(1)$, then $Z(t)$ will be the classical Bellman–Harris branching process generated by the (G,h)-evolution of cells. Hence one obtains the limiting age distribution $A(x) = \frac{\int_0^x e^{-\alpha u}(1-G(u))du}{\int_0^\infty e^{-\alpha u}(1-G(u))du}$, which can be found in Harris [6] but only for $\alpha > 0$. Note that $R(y) = 1 - e^{\alpha y}(1-A(y))$.

Remark 12.3. Consider now the Markov case $G(t) = 1 - e^{-\lambda t}$, $t \geq 0$, with $h(u;s) \equiv h(s)$. Assuming additionally that $p = 1$, one obtains the age distribution $A_t(x) = 1 - e^{-m\lambda x}$. Note that the age distribution for the Markov branching process is stationary, but it depends of the critical parameter m. It is not difficult to see also that $R_t(y) = 1 - e^{-\lambda y}$, i.e. the residual lifetime distribution in the Markov case is also stationary and identical to the lifetime distribution.

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

Immigration. Let $0 = S_0 < S_1 < S_2 < S_3 < \ldots$ 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 $S_k = \sum_{i=1}^k T_i$, $k = 1,2,\ldots$. 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. $g(s) = \mathbf{E}\left[s^{I_k}\right] = \sum_{i=0}^{\infty} q_i s^i$.

This process can be represented as $Y(t) = \sum_{k=1}^{\xi(t)} Z_{(k)}(t - S_k)$ if $\xi(t) > 0$ and $Y(t) = 0$ if $\xi(t) = 0$, 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. $F^*(t;s) = g(F(t;s))$. The p.g.f. of the process $Y(t)$ is denoted by $\Psi(t;s)$.

Let $Y(t,x)$ be the number of cells of age $\leq x$ at time t in this branching model with immigration. Introduce the p.g.f. $\Psi(t,x;s) = E\left[s^{Y(t,x)} | Y(0,0) = 0\right]$. Note that if $x \geq t$ then $Y(t) = Y(t,x)$. Let $\overline{Y}_t(y)$ be the number of cells at time t whose residual lifetime is greater than y.

Theorem 12.5. *The p.g.f.'s of the processes $Y(t)$ and $Y(t,x)$ are given by*

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

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

where $F^*(t;s) = g(F(t;s))$, $F^*(t,x;s) = g(F(t,x;s))$.

Further on we will use Definitions 12.2 and 12.3, where the process Z is replaced by the process Y.

Theorem 12.6. *Assume conditions of Theorem 12.4 and let $\lim_{t\to\infty} r(t) = r > 0$. Then the limiting age distribution $A(x)$ is given by Theorem 12.4 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 $\alpha > 0$.*

Remark 12.4. 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.

Let us consider the Markov case with $p = 1$ and $r(t) \equiv r$. Sevastyanov (see [19]) was the first to study this Markov branching process with homogeneous Poisson immigration (MBPwHPI) .

Theorem 12.7. *In the MBPwHPI there exists a stationary age distribution $A_t(x) = N(t,x)/N(t) = 1 - e^{-m\lambda x}$, $x \geq 0$, and the limiting residual lifetime distribution is given as follows $R(y) = 1 - e^{-m\lambda y}$, $m < 1$ and $R(y) = 1 - e^{-\lambda y}$, $m \geq 1$.*

Remark 12.5. 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 in the subcritical case it is exponential with parameter $m\lambda$.

12.5 Branching processes with immigration as models of leukemia cell kinetics

The purpose of the considered work [33] is to introduce and investigate a class of two-type decomposable Markov branching processes with immigration which has the most direct bearing on mathematical modeling of leukemia cell kinetics. It is well known that no general theory is available for the multi-type decomposable branching processes so that every particular case is of mathematical interest. Let us first consider the biological motivation for the problem under study.

Malignant stem cells have now been described for cancers of the blood, breastand brain. In each case, the unifying feature of such cancers is a unique subpopulation of stem cells that are responsible for tumor genesis and perpetuation. Such cells are poorly defined and found at relatively low frequency, thus making their identification difficult. There is currently no experimental method by which drug effects on cancer stem cells can easily be measured. That is why mathematical modeling can greatly augment our understanding of cancer stem cell growth kinetics and provide a direct means by which drugs may be screened for cancer stem cell specific effects.

The initiation and perpetuation of leukemia derives from the *leukemic stem cell* (LSC) population while the propagation of leukemic disease depends critically on the immediate downstream progeny of LSC, the *leukemic progenitor* (LP) population. In what follows, the LP cells will be referred to as Type T_1 cells. The latter cell type can be easily screened using common in vitro colony assays. The same is true for the population of *blast cells* (BC) (referred to as Type T_2 cells).

From a modeling standpoint, we intend to explore the possibility of modeling the system under study as a two-type branching stochastic process. The most serious complication here is that the processes of leukemic cell development involve the transition of LSCs to the LP cell compartment. This influx of the LP cells is unobservable and one has to reconstruct it in order to describe the dynamics of progenitor and blast cells.

We first consider the process of immigration of cells into the LP compartment. Suppose that the time intervals between successive arrivals form a renewal stochastic process $\mu(t) = \{\#\ \textit{arrivals by time}\}$. These arrivals do not include those resulting from mitotic divisions of the LP cells. Given below is a sound reason for treating $\mu(t)$ as a Poisson process. Experimental studies of the central nervous system (CNS) development support the hypothesis of asymmetric division of multipotent stem cells that generate diverse cell types in the CNS, indicating a crucial role of the membrane-associated protein NUMB in this process. The asymmetric division is a mechanism by which stem cells prevent their extinction and it seems highly plausible that LSC divide asymmetrically as well. If we hypothesize in addition that the dynamics of LSC's follows the Smith and Martin model, then the immigration process of LP's is Poisson with intensity r. Indeed, the asymmetric mitosis of stem cells ensures ordinariness of the immigration process while the Smith and Martin model postulates a Markovian transition of resting stem cells to the state of active proliferation (see [20]).

Upon arrival, every LP cell enters the MC. The outcomes of the MC include symmetric or asymmetric mitotic division, differentiation into a blast cell, and cell death. The evolution of cells under a general two-compartment model can be described as follows.

General Model. Every cell of type T_1 has a life-time τ_1 with a d.f. $G_1(x) = \mathbf{P}(\tau_1 \leq x)$ and at the end of its life-time it gives rise to a random number of offspring with probability generating function (p.g.f.) $h_1(s_1,s_2) = p_0 + p_1 s_1^2 + p_2 s_2^2 + p_3 s_1 s_2$, $h_1(1,1) = 1$.

In other words, every cell of type T_1 produces either two cells of type T_1 with probability $p_1 > 0$, or two cells of type T_2 with probability $p_2 > 0$, or one cell of type T_1 and one cell of type T_2 with probability $p_3 > 0$, or it dies (or exits the population under study) with probability $p_0 = 1 - p_1 - p_2 - p_3 \geq 0$. The usual independence assumptions are also adopted.

The following important particular cases are worth considering:

Model 1 – *symmetric mitosis* $(p_3 = 0)$: $h_1(s_1,s_2) = p_0 + p_1 s_1^2 + p_2 s_2^2$.

Model 2 – *symmetric and asymmetric mitoses* $(p_2 = 0)$: $h_1(s_1,s_2) = p_0 + p_1 s_1^2 + p_3 s_1 s_2$.

We hypothesize in addition that every cell type T_2 has a life-time τ_2 with d.f. $G_2(x) = \mathbf{P}(\tau_2 \leq x)$ giving rise to a random number of offspring with with p.g.f. $h_2(s_2) = 1 - q + q s_2^2$, $h_2(1) = 1$. In other words, every cell of type T_2 produces two daughter cells of the same type with probability $q > 0$ and it dies with probability $1 - q$.

Independently of the processes of cell proliferation and differentiation, there is a process of immigration of type T_1 cells. The moments of immigration events form a homogeneous Poisson process with cumulative rate $R(t) = rt$, $r > 0$, so that exactly one cell of type T_1 enters the population at every given moment of immigration.

Let $Y_k(t)$ be the number of cells of type T_k, $k = 1,2$, at time $t \geq 0$. It is obtained a joint *p.g.f.*

$$\Psi(t;s_1,s_2) = E[s_1^{Y_1(t)} s_2^{Y_2(t)}] = \exp\{-r \int_0^t [1 - F_1(u;s_{1,}s_2)]du\}, \ \ \Psi(0;s_1,s_2) \equiv 1,$$

where

$$F_1(t;s_{1,}s_2)$$
$$= \int_0^t h_1(F_1(t-u;s_{1,}s_2),F_2(t-u;s_2))dG_1(u)+s_1(1-G_1(t)), \quad F_1(0;s_{1,}s_2)=s_1$$
$$F_2(t;s_2)=\int_0^t h_2(F_2(t-u;s_2))dG_2(u)+s_2(1-G_1(t)), \quad F_2(0;s_2)=s_2.$$

Consider now the Markov case, when $G_1(x)=1-e^{-\lambda x}$ and $G_2(x)=1-e^{-\mu x}$, introducing the infinitesimal g.f. $f_1(s_1,s_2)=\lambda(h_1(s_1,s_2)-s_1)$, $f_2(s_2)=\mu(h_2(s_2)-s_2)$ and the corresponding infinitesimal parameters $a=\lambda(2p_1-1)$, $b=\lambda p_1$, $c=\lambda p_2$, $\rho=\lambda p_3$, $\alpha=\mu(2q-1)$, $\beta=\mu q$.

Defining the functions $R_1(t;s_{1,}s_2)=1-F_1\ (t;s_{1,}s_2)$ and $R_2(t;s_2)=1-F_2\ (t;s_2)$ one can obtain the following Riccati equations:

(i) For *Model 1*

$$\frac{\partial}{\partial t}R_1(t;s_{1,}s_2)=aR_1(t;s_{1,}s_2)-bR_1^2(t;s_{1,}s_2)+2cR_2(t;s_2)-cR_2^2(t;s_2).$$

(ii) For *Model 2*

$$\frac{\partial}{\partial t}R_1(t;s_{1,}s_2)$$
$$=(a+\rho)R_1(t;s_{1,}s_2)-bR_1^2(t;s_{1,}s_2)-\rho R_1(t;s_{1,}s_2)R_2(t;s_2)+\rho R_2(t;s_2).$$

In both cases

$$R_2(t;s_2)=(1-s_2)/\{1+\beta t(1-s_2)\}, \text{ for } \alpha=0,$$
$$R_2(t;s_2)=e^{\alpha t}(1-s_2)/\{1+\beta(e^{\alpha t}-1)(1-s_2)/\alpha\}, \text{ for } \alpha\neq 0.$$

Note that the above-considered two-type branching processes are decomposable. Since no general theory is available for decomposable processes then every particular case is of interest. Further on, our focus is on the *General Model*. Asymptotic results for *Model 1* ($\rho=0$) and *Model 2* ($c=0$) easily follow as special cases.

Let us introduce the moments (under the condition $Y_1(0)=Y_2(0)=0$): $M_1(t)=\mathbf{E}[Y_1(t)]$, $\Sigma_1(t)=Var[Y_1(t)]$, $M_2(t)=\mathbf{E}[Y_2(t)]$, $\Sigma_2(t)=Var[Y_2(t)]$, $C_{1,2}(t)=Cov[Y_1(t)Y_2(t)]$.

The asymptotic (as $t\to\infty$) behavior of the above quantities depends on relations between the critical parameters $a+\rho$ (type T_1) and α (type T_2). We will distinguish between the *subcritical case*, where both parameters are negative, the *critical case*, where at least one of the two parameters is equal to zero while the other is non-positive, and the *supercritical case*, where at least one of the parameters is positive. The obtained results demonstrate that the mean values $M_1(t)$ and $M_2(t)$, the variances $\Sigma_1(t)$ and $\Sigma_2(t)$, as well as the covariance $C_{1,2}(t)$, all converge to some constants in the *subcritical case,* they show an exponential growth in the *supercritical case* and a polynomial growth (with degrees from 1 to 4) in the *critical case*.

The following limit theorem holds in the biologically most interesting *subcritical* case.

Theorem 12.8. *In the subcritical case* $(a+\rho<0, \alpha<0)$ *there exists a stationary distribution*

$$\mathbf{P}\left(Y_1^*=n_1, Y_2^*=n_2\right)=\lim_{t \longrightarrow \infty} \mathbf{P}\left(Y_1(t)=n_1, Y_2(t)=n_2\right), \quad n_1, n_2=0,1,2, \ldots$$

with joint p.g.f.

$$\Psi^*\left(s_1, s_2\right)=E\left[s_1^{Y_1^*}, s_2^{Y_2^*}\right]=\exp \left\{-r \int_0^{\infty}\left(1-F_1\left(x ; s_1, s_2\right)\right) d x\right\}, \quad \Psi^*(1,1)=1.$$

The stationary marginal distribution for the cells of type T_1 *is negative-binomial with p.g.f.*

$$\Psi^*\left(s_1, 1\right)=E\left[s_1^{Y_1^*}\right]=\left((1-p) /\left(1-p s_1\right)\right)^{r / b}, \quad p=b /(b-(a+\rho)).$$

Remark 12.6. The limiting distributions in the critical and supercritical cases remain to be open problems.

The results of this paper demonstrate that the problem of stochastic modeling of such complex cell systems as the heterogeneous population of leukemic cells is mathematically approachable. From a biological standpoint, the most important conclusion is that it is possible to make inferences on the dynamics of the population of stem cells by the indirect route, i.e., by estimating the rate of transition between the populations of stem cells and more differentiated progenitor cells. From a mathematical standpoint, the decomposable branching process under consideration is tractable in terms of its moments and relevant asymptotic results have been obtained. Since experimental techniques are now available to count the numbers of cells of various types as functions of time, it is a technical problem to develop associated methods of statistical inference along the lines of the earlier work in the field. Extending the results reported in this paper to the case of non-homogeneous Poisson immigration represents a challenging problem for future research. Such an extension is necessary to model the effects of anti-tumor drugs on the population of leukemic cells.

12.6 Age-dependent branching populations with randomly chosen paths of evolution

Consider a multitype population with the following cell evolution (see Appendix in [30]). Every newborn cell of type T_k $(k=1,2,\ldots,d)$ with probability $r_{k,i}$ $\left(\sum_{i=1}^d r_{k,i}=1\right)$ has a life-time c.d.f. $F_{k,i}(t)$ and at the end of its life produces progeny in accordance with p.g.f. $h_{k,i}(\mathbf{s})$, $\mathbf{s}=(s_1,s_2,\ldots,s_d)$.

Let $\mathbf{Z}(t)=(Z_1(t),Z_2(t),\ldots,Z_d(t))$, where $Z_k(t)$ denotes the number of cells of type T_k at time t. Introduce p.g.f.s $\Phi_k(t;\mathbf{s})=\mathbf{E}\left[\mathbf{s}^{\mathbf{Z}(t)} | \mathbf{Z}(0)=\mathbf{e}_k\right]$ and $\boldsymbol{\Phi}(t;\mathbf{s})=$

$(\Phi_1(t;\mathbf{s}),\Phi_2(t;\mathbf{s}),...,\Phi_d(t;\mathbf{s}))$, where $\mathbf{e}_k = (0,...,0,1,0,...0)$ with 1 at the k-th place. Then the following system of integral equations holds:

$$\Phi_k(t;\mathbf{s}) = \sum_{i=1}^{d} r_{k,i} \int_0^t h_{k,i}(\boldsymbol{\Phi}(t-u;\mathbf{s}))dF_{k,i}(u) + s_k \sum_{j=1}^{d} r_{k,j}\overline{F}_{k,j}(t), \quad k = 1,2,...,d,$$

which is equivalent to the system of equations:

$$\Phi_k(t;\mathbf{s}) = \int_0^t h_k(u;\boldsymbol{\Phi}(t-u;\mathbf{s}))dG_k(u) + s_k\overline{G}_k(t), \quad k = 1,2,...,d,$$

where $\overline{F}_{k,j}(t) = 1 - F_{k,j}(t)$, $G_k(t) = \sum_{i=1}^{d} r_{k,i}F_{k,i}(t)$, $\overline{G}_k(t) = 1 - G_k(t)$ and $h_k(u;\mathbf{s}) = \sum_{i=1}^{d} \alpha_{k,i}(u)h_{k,i}(\mathbf{s})$ with $\alpha_{k,i}(u) = r_{k,i}/\sum_{j=1}^{d} r_{k,j}(dF_{k,j}(u)/dF_{k,i}(u))$, $\sum_{i=1}^{d} \alpha_{k,i}(u) = 1$. We use the notation $dF_{k,j}(u)/dF_{k,i}(u)$ for the corresponding Radon–Nikodym derivatives. The above model represents a special case of the d-type Sevastyanov branching process.

In [30], two new models of an age-dependent branching process with two types of cells are proposed to describe the kinetics of progenitor cell populations cultured *in vitro*. Another approach is given in Hyrien et al. [7, 8], Yakovlev [29] and Zorin et al. [37]. Our models considered in [30] with two cell types can be derived by the general case setting $d = 2$, $r_{1,1} = p$, $r_{1,2} = 1 - p$, $F_{1,1}(t) = F_1(t)$, $F_{1,2}(t) = F_3(t)$, $h_{1,2}(s_1,s_2) \equiv 1$, $r_{2,1} = 0$, $r_{2,2} = 1$, $F_{2,2}(t) = F_2(t)$, $h_{2,2}(s_1,s_2) \equiv 1$. The most biologically relevant example of the p.g.f. $h_{1,1}(s_1,s_2)$ is given by $h_{1,1}(s_1,s_2) = p_0 + p_1s_1^2 + p_2s_2$, $h(1,1) = p_0 + p_1 + p_2 = 1$.This form of $h_{1,1}(s_1,s_2)$ implies that every cell of type T_1 either dies with probability p_0, or divides into two new T_1 cells with probability p_1, or differentiates into a new cell type T_2 with probability p_2, all the transformations occurring upon completion of its mitotic cycle.

The main focus is on the estimation of the offspring distribution from data on individual cell evolutions. Such data are typically provided by time-lapse video-recording of cultured cells. Some parameters of the life-cycle of progenitor cells, such as the mean (median) and variance of the mitotic cycle time, can be estimated nonparametrically without resorting to any mathematical model of cell population kinetics. For other parameters, such as the offspring distribution, a model-based inference is needed. Age-dependent branching processes have proven to be useful models for this purpose. Within the framework of branching processes, the loss of cells to follow-up can be modeled as a process of emigration that precludes other cell transformations from occurring. This motivates the development of branching models with emigration and associated estimation techniques. The considered work [30] develops the needed methodology and put it to practical use.

The basic idea behind our approach is to consider a hidden discrete process that would have been observed in the absence of emigration. The net reproduction probabilities of such a process represent the parameters of interest and we develop a procedure that makes it possible to estimate them from experimental observations.

This approach allows us to employ the theory of statistical inference for branching processes with a large number of ancestors (see Yanev [31, 32] and Dion and Yanev [2]).

The proposed new models of a two-type age-dependent branching process with emigration are motivated by a specific biological application. In this application, the first type of cells represents immediate precursors of oligodendrocytes while the second type represents terminally differentiated oligodendrocytes. The proposed methodology can be readily extended to branching processes with any finite number of cell types.

12.7 Multitype branching populations with a large number of ancestors

Usually branching processes with discrete or continuous time are investigated separately but in this section we will treat them together. We will consider first a multitype Markov branching process

$$\mathbf{Z}(t;N) = (Z_1(t;N), Z_2(t;N), ..., Z_d(t;N)),$$

where $Z_k(t;N)$ denotes the number of cells of type k ($k = 1,2,...,d$) at time $t \in \mathbf{T}$ with $\mathbf{Z}(0) = (N,0,...,0)$. The time may be discrete $\mathbf{T} = \mathbf{N}_0 = \{0,1,2,...\}$ or continuous $\mathbf{T} = \mathbf{R}^+ = [0,\infty)$, but the process is assumed to be positive regular and nonsingular. Let R and r denote Perron-Frobenius eigenvalues respectively for a discrete or continuous time and with a left eigenvector $\mathbf{v} = (v_1,...,v_d)$.

The relative frequencies (fractions, proportions) of types can be defined on the non-extinction set as follows:

$$\Delta_i(t;N) = Z_i(t;N) / \sum_{j=1}^{d} Z_j(t;N), \quad i = 1,2,...,d.$$

The investigation of the relative frequencies is very important for the applications (especially in the cell biology) because there are a lot of situations when it is not possible to observe the numbers of cells but only their relative proportions. In what follows, we will also need the following deterministic proportions $p_i(t) = A_{1i}(t)/M(t)$, where $M(t) = \sum_{j=1}^{d} A_{1j}(t)$ and $A_{1j}(t) = \mathbf{E}[Z_j(t;1)]$, $i,j = 1,2,...,d$; $t \in \mathbf{T}$.

Theorem 12.9. *([28]) Let* $p_k = v_k/V$, $k = 1,...,d$, $V = \sum_{k=1}^{d} v_k$, *and* $N,t \to \infty$.

(i) If $\{R < 1, NR^t \to \infty$ *or* $r < 0, N\mathbf{e}^{rt} \to \infty\} \vee \{R = 1$ *or* $r = 0$ *and* $N/t \to \infty\}$ *then* $\Delta_k(t;N) \to p_k$ *in probability,* $k = 1,2,...,d;$

(ii) If $\{R > 1$ *or* $r > 0\}$ *then* $\Delta_k(t;N) \to p_k$ *a.s.,* $k = 1,2,...,d.$

Consider now $\mathbf{X}(t;N) = (X_1(t;N),...,X_d(t;N))$, $t \in \mathbf{T}$, where for some normalizing functions $D_k(t)$

$$X_k(t;N) = (Z_k(t;N) - A_{1k}(t;N))/(D_k(t)\sqrt{N})$$

with $A_{1k}(t;N) = \mathbf{E}\,[Z_k(t;N)]$, $k = 1,...,d$.

Theorem 12.10. *([28]) Assume finite second moments and $N, t \to \infty$.*

(i) If $\{R < 1, NR^t \to \infty$, or $r < 0, N\mathbf{e}^{rt} \to \infty\}$ and $D_k(t) \equiv D(t) \sim \{\sqrt{R^t}$ or $\sqrt{\mathbf{e}^{rt}}\}$ for $k = 1,...,d$, then

$$\mathbf{X}(t;N) \xrightarrow{d} \boldsymbol{\xi} = (\xi_1,...,\xi_d), \tag{12.1}$$

and $\boldsymbol{\xi} = (\xi_1,...,\xi_d)$ has a multivariate normal distribution with $\mathbf{E}\,[\xi_i] = 0$ and a covariance matrix $C = \left\|C_{jk}\right\|$, where $C_{jk} = \lim B^{(1)}_{jk}(t)/R^t$, $t \in \mathbf{N}_0$ or $C_{jk} = \lim B^{(1)}_{jk}(t)/\mathbf{e}^{rt}$, $t \in \mathbf{R}^+$.

(ii) If $\{R = 1$ or $r = 0$ with $N/t \to \infty\}$ and $D_k(t) \sim \{v_k\sqrt{u_1Bt}$ or $v_k\sqrt{u_1bt}\}$, $k = 1,...,d$, then

$$\mathbf{X}(t;N) \xrightarrow{d} \boldsymbol{\eta} = (\eta_1,...,\eta_d), \tag{12.2}$$

where $\eta_1 = ... = \eta_d$ a.s. and η_1 has $N(0,1)$ distribution.

(iii) If $R > 1$ or $r > 0$ and $D_k(t) \sim \{v_kR^t$ or $v_k\mathbf{e}^{rt}\}$, $k = 1,...,d$, then

$$\mathbf{X}(t;N) \xrightarrow{d} \boldsymbol{\zeta} = (\zeta_1,...,\zeta_d), \tag{12.3}$$

where $\zeta_1 = ... = \zeta_d$ a.s., ζ_1 has $N(0,\tau^2)$ distribution and $\tau^2 = \mathbf{E}\left[W^2 \mid \mathbf{Z}(0) = \boldsymbol{\delta}_1\right]$ is defined in [1].

Theorem 12.11. *([28]) Assume $N, t \to \infty$ and Condition (i) of Theorem 12.10. Then*

(i) For every $k = 1,2,...,d$

$$\Phi_k(t;N) = u_1V\sqrt{ND(t)}[\Delta_k(t;N) - p_k(t)] \xrightarrow{d} Y_k,$$

where Y_k is a normally distributed r.v. with $\mathbf{E}\,[Y_k] = 0$ and

$$Var\,[Y_k] = C_{kk} - 2p_k\sum_{j=1}^{d} C_{kj} + p_k^2\sum_{i,j=1}^{d} C_{ij}.$$

(ii) For every $k = 2,3,...,d-1$ and every subset $(n_1, n_2, ..., n_k)$ with nonrecurring elements from the set $\{1,2,...,d\}$ the following joint distributions hold

$$(\Phi_{n_1}(t;N),...,\Phi_{n_k}(t;N)) \xrightarrow{d} (Y_{n_1},...,Y_{n_k}),$$

where the random variables $(Y_{n_1},...,Y_{n_k})$ have a multivariate normal distribution with

$$Cov[Y_i,Y_j] = C_{ij} - p_i\sum_{k=1}^{d} C_{kj} - p_j\sum_{l=1}^{d} C_{li} + p_ip_j\sum_{k,l=1}^{d} C_{kl}.$$

Remark 12.7. Surprisingly in the critical and supercritical cases there are not analogs of Theorem 12.11.

Introduce the following notions:

$$\begin{aligned}
&\sigma_i^2(t) = Var[Z_i(t,1)],\ i = 1,2,...,d,\\
&\mathbf{R}^{(d)}(t) = ||r_{ij}(t)||,\ \ r_{ij}(t) = Cor[Z_i(t,1),Z_j(t,1)],\ i,j = 1,2,...,d,\\
&\mathbf{C}^{(d)}(t) = ||c_{ij}(t)||,\ c_{ii}(t) = \sigma_i(t)(1-p_i(t)),\ c_{ij}(t) = -\sigma_i(t)p_j(t)
\end{aligned}$$

for $i \neq j;\ i,j = 1,2,...,d$.

As a contrast of the previous obtained results the following theorem is valid for any kind of branching processes with discrete or continuous time (Markov or non Markov, reducible or irreducible) assuming only the usual independence of the individual evolutions. Let, for $i = 1,2,...,d$,

$$V_i(t;N) = (Z_i(t;N) - A_{1i}(t;N))/(\sigma_i(t)\sqrt{N}) \text{ and } W_i(t;N) = M(t)\sqrt{N}(\Delta_i(t;N) - p_i(t)).$$

Theorem 12.12. *([27]) Let t be fixed and $N \to \infty$. Then the following statements are valid:*

(i) $\quad (V_1(t;N),...,V_d(t;N)) \xrightarrow{d} (X_1(t),...,X_d(t)),$
where the random vector $\mathbf{X}^{(d)}(t) = (X_1(t),...,X_d(t))$ has a joint normal distribution with $\mathbf{E}[X_i(t)] = 0$, $Var[X_i(t)] = 1$, and $Cor[X_i(t),X_j(t)] = r_{ij}(t)$.

(ii) $\quad W_i(t;N) \xrightarrow{d} Y_i(t),$
where the r.v. $Y_i(t)$ is normally distributed with $\mathbf{E}[Y_i(t)] = 0$ and $Var[Y_i(t)] = \sum_{j,k=1}^{d} r_{jk}(t)c_{ji}(t)c_{ki}(t)$, $i = 1,2,...,d$;

(iii) For every $k = 2,3,...,d-1$,

$$(W_1(t;N),...,W_k(t;N)) \xrightarrow{d} (Y_1(t),...,Y_k(t)),$$

and $\mathbf{Y}^{(k)}(t) = (Y_1(t),...,Y_k(t))$ has a multivariate normal distribution with a covariance matrix which can be calculated as follows:

$$\mathbf{D}^{(k)}(t) = ||Cov[Y_i(t),Y_j(t)]|| = [\mathbf{C}_{d\times k}(t)]^T \mathbf{R}^{(d)}(t)\mathbf{C}_{d\times k}(t),$$

where $[\mathbf{C}_{d\times k}(t)]^T = ||c_{ji}(t)||$, $j = 1,2,...,k$; $i = 1,2,...,d$, is the corresponding transposed matrix of $[k \times d]$ dimensions.

In particular, the following observation process is directly relevant to quantitative studies of proliferation, differentiation, and death of cells. Suppose that the process under study begins with $N = \sum_{k=1}^{n} N_k$ cells of type T_1 and the values of N_k are all large, i.e., $N_0 = \min\{N_1, N_2, ..., N_n\} \to \infty$. The descendants of the first N_1 ancestors are examined only once at time t_1 to determine the observations of $Z_i(t_1;N_1)$ or $\Delta_i(t_1;N_1), i = 1,2,...,d$, whereupon the observation process is discontinued (i.e. the cells under examination are destroyed). At the next moment $t_2 \geq t_1$, the process

$Z_i(t_2;N_2)$ or the fractions $\Delta_i(t_2;N_2), i = 1,2,...,d$, related to the descendants of the second N_2 ancestors are observed, and so on. This procedure results in n independent observations of the form:

$$\boldsymbol{\zeta}_k = \mathbf{Z}(t_k;N_k) = (Z_1(t_k;N_k),...,Z_d(t_k;N_k)), \quad k = 1,2,...,n;\ t_1 \le t_2 \le ... \le t_n,$$

or

$$\boldsymbol{\zeta}_k = \Delta(t_k;N_k) = (\Delta_1(t_k;N_k),...,\Delta_d(t_k;N_k)), \quad k = 1,2,...,n;\ t_1 \le t_2 \le ... \le t_n,$$

where each vector $\boldsymbol{\zeta}_k$ is asymptotically normal in accordance with Theorems 12.10, 12.11 and 12.12.

Denoting the corresponding contribution to the asymptotic log-likelihood function by $L_k(\boldsymbol{\zeta}_k;\, t_k, N_k)$, the overall log-likelihood is given by

$$\Lambda_n(\boldsymbol{\zeta}_1, \boldsymbol{\zeta}_2, ..., \boldsymbol{\zeta}_n) = \sum_{k=1}^{n} L_k(\boldsymbol{\zeta}_k; t_k, N_k).$$

The log-likelihood depends on the offspring parameters only, which are of primary interest in applications and especially in cell kinetics studies. Finally the parameters can be estimated from the data on the process or the relative frequencies by maximizing the log-likelihood. In this way, the asymptotic results give a new direction toward statistical inference and applications of branching processes in cell proliferation kinetics (see [27]).

Feller [3] considered first branching process with a large number of ancestors. For a classical Bienaymé–Galton–Watson (BGW) process he showed a diffusion approximation in the near-critical case. Lamperti [16] derived also some interesting limiting distributions for BGW process. These results were summarized and discussed by Jagers [10]. Statistical inference for BGW processes with an increasing number of ancestors as well as limiting distributions when N and t tend to infinity were developed by Yanev [31] and Dion and Yanev [2] (see also a review chapter by Yanev [32]).

Jagers [9] was probably the first to consider relative frequencies (proportions, fractions) of cells within the framework of multitype branching processes. He studied asymptotic (as $t \to \infty$) properties of a reducible age-dependent branching process with two types of cells and proved convergence of their relative frequencies to non-random limits in mean square and almost surely on the non-extinction set. The usefulness of such frequencies in cell cycle analysis was further demonstrated by Mode [18] considering a four-type irreducible age-dependent branching process. Mode built his cell cycle analysis on a model of multitype positively regular age-dependent branching process. In the supercritical case, he proved that $\lim \Delta_k(t) = \delta_k \ \ a.s.$ as $t \to \infty$, providing the population does not become extinct. In his monograph, Mode [17] also considered the utility of fractions and reported a similar result for the BGW process.

12.8 Concluding remarks

The presented results were planed as a part of a joint book with Andrei Yakovlev on branching processes as models in cell proliferation kinetics. Unfortunately the book will appear never. This paper is a tribute to the stimulating ideas of Andrei Yakovlev and the friendship that we shared in our collaboration.

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13

Griffiths–Pakes branching process as a model for evolution of Alu elements

Marek Kimmel and Matthias Mathaes

Abstract Alu elements occupy about eleven percent of the human genome and are still growing in copy numbers. Since Alu elements substantially impact the shape of our genome, there is a need for modeling the amplification, mutation and selection forces of these elements. Our proposed theoretical neutral model follows a discrete-time branching process described by Griffith and Pakes. From this model, we derive a limit frequency spectrum of the Alu element distribution, which serves as the theoretical, neutral frequency to which real Alu insertion data can be compared through statistical goodness of fit tests. Departures from the neutral frequency spectrum may indicate selection. A comparison of the Alu sequence data, obtained by courtesy of Dr. Jerzy Jurka, with our model shows that the distributions of Alu sequences in the AluY family systematically deviate from the expected distribution derived from the branching process. This observation suggests that Alu sequences do not evolve neutrally and might be under selection.

Mathematics Subject Classification (2000): 92D10, 92D15, 92D20, 60J80, 60J85.

Keywords: Bienayme–Galton–Watson branching process, infinite-allele model, Alu elements, evolution, human genome, Pakes–Griffiths process.

13.1 Introduction

We present a biological application of a special case of the Griffiths–Pakes discrete-time branching process with infinite-allele mutations. The process seems to be

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almost ideally suitable for modeling the evolution of the so-called Alu elements, which are movable sequences of DNA, very abundant in the human genome. For the biologically important special case of the linear-fractional offspring distribution we derive the semi-explicit expressions for the expected frequency spectra of classes of alleles existing in a given number of copies (an analogue of the Ewens sampling formula). We compare the outcome with Alu-element statistics data.

13.2 Alu repeat sequences

13.2.1 Background on Alus

Alu elements belong to the group of transposable or mobile elements, which occupy nearly 45% of the human genome [2]. Within this group of transposable and also highly repetitive elements, LINEs (Long INterspersed Elements) and SINEs (Short INterspersed Elements) form the two largest groups. They occupy 21 and 13% of the human genome respectively [5]. Whereas the LINEs are dominated by L1 elements, the largest and hence most studied group of the SINEs are comprised of the Alu elements. While many transposable elements are present in all eukaryotic genomes, Alu elements appear only in mammals. A typical full-length Alu sequence is approximately 300 bp long. Alu sequences amplify by retrotransposition, also known as “the copy and paste” mechanism. At present it is estimated that more than one million copies of Alu elements occupy about eleven percent of the human genome, and the number of elements seems to be growing [2].

Based on diagnostic mutations, Alu elements are divided into subfamilies. The three major families of Alu sequences are J, S and Y. The letters are chosen in alphabetical order to convey the different ages of each family. Alu sequences in the J family are the oldest, while Alu sequences in the Y family are the youngest. The most interesting family in the current research of Alu elements is the Y family, which contains the youngest and most active Alu elements [6]. Due to their recent integration, 25% of their loci are still polymorphic [2]. An Alu locus is defined to be polymorphic if some individuals have an Alu element at that particular location while others do not. These polymorphic loci can be used as genetic markers for disease association studies.

13.2.2 Alu sequence data used in this study

Dr. Jerzy Jurka of the Genetic Information Research Institute (GIRI) kindly provided Alu sequence data for our analysis. All Alu subfamilies were extracted from the March 2006 assembly of the USCS Human Genome database. Only recognizable full-length Alu sequences were retained for analysis. Overall, Alu sequences for nine different Alu subfamilies were extracted from the USCS reference genome: AluYa1, AluYa4, AluYa5, AluYa8, AluYb8, AluYc1, AluYd2, AluYe2, and AluYe5.

Following preparatory steps described elsewhere [4], we obtained the counts of Alu sequences that were unique, had two identical copies, three identical copies, or n identical copies in the sample. To obtain these counts for each Alu subfamily, a program was written in R-language. The counts, as presented in Table 13.1, or corresponding percentages constitute our final data, which were tested against the theoretical distribution based on the branching process model.

Number of copies	1	2	3	4	5	6	7	8	9	10	11	12	13	14	16	18
Ya1	3761	25	2	4	1	1										
Ya4	426	6	2	2	1									1		
Ya5	1722	75	15	16	11	10	5	4	2	5	1	1	2	1		2
Ya8	28	3							1							
Yb8	1489	71	11	15	8	9	4	4	1		1		1	1	1	
Yc1	3162	42	9	4	1	1	1		1							
Yd2	401	1														
Ye2	1130	3	1													
Ye5	853	10	7	2	1											
All	12970	237	47	43	23	21	10	8	5	5	2	1	3	3	1	2

Table 13.1 Frequencies of alleles (mutant types) with j copies (class j alleles). Classes with $j > 20$ have been omitted.

13.3 Discrete branching process of Griffiths and Pakes with infinite allele mutations

Branching processes have been widely used in modeling cell population dynamics. An insertion of an Alu sequence into a new genomic location can be considered a proliferation process not dissimilar from cell division. Therefore proliferation and mutation of Alu sequences can be described in a mathematical way using a branching process. The branching process has to account for the fact that Alu sequences are still growing in numbers in the human genome. Therefore we focus on the supercritical branching processes, in which the expected number of offspring is greater than one ($m > 1$). One interesting model prediction, which can be compared to data is how many different Alu sequences occur in each Alu subfamily or more specifically how many Alu alleles with frequency j exist in each subfamily. Based on a discrete-time branching process with infinite allele mutations, Griffiths and Pakes (see [3]) derived a limit result for the expected proportion of alleles having frequencies in j.

Griffiths and Pakes process [3] is a modification of the standard Bienayme-Galton-Watson branching process to allow individuals infinitely many possible identifiable types. In our application, the types are alleles (variants) of the Alu sequence identified by specific point mutations. From time $t = 0$, a non-mutant clone of particles is evolving in time according to a single-type branching process (Fig. 13.1).

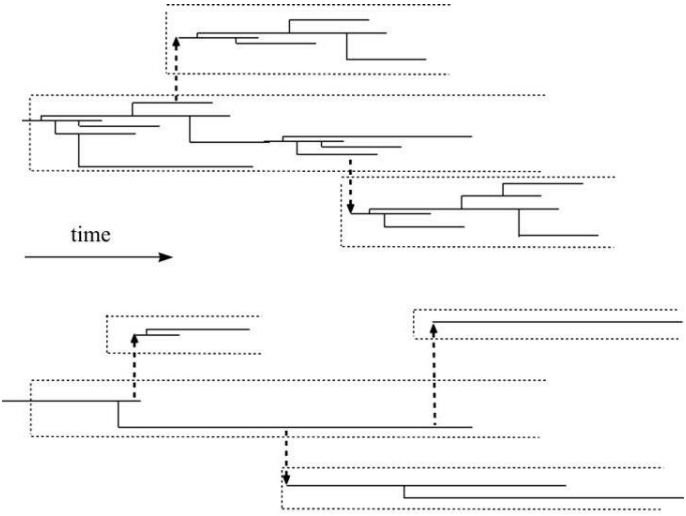

Fig. 13.1 Griffiths–Pakes branching process with infinite-allele mutations. A non-mutant clone of particles is evolving in time according to a single-type branching process (in our case, time discrete). With probability μ per time step, a particle mutates and initiates a clone of new previously nonexistent type, which evolves according to the same rules as the original non-mutant clone. As a result, a set of clones of different types emerges, spawning further clones, some of which may die out. *Upper panel*: low μ; *lower panel*: high μ.

With probability μ per time step, a particle mutates and initiates a clone of new previously nonexistent type, which evolves according to the same rules as the original non-mutant clone. As a result, a set of clones of different types emerges, spawning further clones, some of which may die out. We are interested in deriving, using Griffith-Pakes theory (see [3]), expected frequencies of allele classes such that allele is in class k if it exists in k copies, for a specific version of the process, which is biologically justifiable.

The number of individuals at $t = 0$ is defined as $Z_0 = 1$. Let G_n be the collection of individuals in generation n and let Z_n denote their number. Each generation size depends on the previous generation size through the branching property

$$Z_{n+1} = \sum_{j=1}^{Z_n} \xi_{j,n},$$

where $\xi_{j,n}$ are independent identically distributed (iid) integer-valued random variables, which represent the number of offspring born to the jth member of G_n. The distribution of $\xi_{j,n}$ is characterized by its probability generating function (pgf)

$$f(s) = \sum_{k=0}^{\infty} p_k s^k,$$

where $p_k = P[\xi_{j,n} = k]$, and it is assumed that $p_0 + p_1 < 1$, i.e., the branching process is nontrivial. We have $m = f'(1)$.

If an individual produces j offspring then the number of progeny having the parental allele is distributed binomially with parameters j and $1-\mu$, hence its pgf is equal to $(\mu + (1-\mu)s)^j$. This implies that any new allele is followed by a branching process of its like-type descendants with offspring pgf $H(s) = f(\mu + (1-\mu)s)$. This process is supercritical if its expected progeny count $M = m(1-\mu)$ is greater than 1. Within this framework let us define $\alpha_n(j)$ as the number of alleles in G_n having j representatives in G_n. Let $K_n = \sum_{j\geq 1} \alpha_n(j)$ be the number of alleles in G_n and then Z_n can be expressed as $Z_n = \sum_{j\geq 1} j\alpha_n(j)$.

The number of alleles $\alpha_n(j)$ can be counted in the following way. Define indicator $I_{1,0,n}(j) = 1$ if the ancestor allele has j representatives in G_n. Define indicator $I_{k,r,n-r}(j) = 1$ if the kth member of G_r has a new allele and has j like-type descendants in G_n. With these indicator definitions

$$\alpha_n(j) = I_{1,0,n}(j) + \sum_{r=1}^{n-1} \sum_{k=1}^{Z_r} I_{k,r,n-r}(j).$$

The indicators are independent within generations, but dependent across generations. Taking expectations and letting $n \to \infty$ leads to the unnormalized frequency spectrum ϕ_j:

$$\phi_j = \lim_{n\to\infty} m^{-n} E\alpha_n(j) = \mu \sum_{r=1}^{\infty} m^{-r} q_{1j}^{(r)},$$

with the symbol $q_{1j}^{(r)} = (j!)^{-1} d^j H^{(r)}(s)/ds^j|_{s=0}$, where $H^{(r)}(s)$ is the rth iterate of pgf $H(s)$, is the probability that there are j individuals at time r in a nonmutant clone started at time 0 by a single individual. The frequency spectrum sequence $(\phi_j)_{j\geq 1}$ can be normalized by $A = \sum_{j=1}^{\infty} \phi_j$:

$$\Psi_j = A^{-1}\phi_j = \frac{\mu \sum_{r=1}^{\infty} m^{-r} q_{1j}^{(r)}}{\mu \sum_{n=1}^{\infty} m^{-n}(1 - q_{10}^{(n)})}.$$

The Ψ_j is the long-term expected proportion of alleles with frequency j, which is the formula that we will use to compute the theoretical distribution of Alu allele classes for given offspring pgfs.

13.3.1 Linear fractional offspring distribution

The process of creation of new Alu repeats by retrotransposition can be naturally described by the age dependent Markov branching process $\{Z_t\}$ (i.e., process with exponentially distributed individuals' lifelengths) with quadratic offspring distribution. If such process is sampled at constant time intervals, the resulting discrete-time process $\{Z_{k\Delta t}\}$ is a Galton–Watson branching process with linear fractional pgf [1]. A unique property of the linear fractional case is that the iterations of the pgf can be computed explicitly and also are of linear fractional form. Let us start with the generating function of the linear fractional case:

$$f(s) = 1 - \frac{b}{1-p} + \frac{bs}{1-ps}.$$

The probability distribution corresponding to this generating function is:

$$\begin{aligned} p_0 &= 1 - \sum_{i=1}^{\infty} p_i = \frac{1-b-p}{1-p}, \\ p_k &= bp^{k-1},\ k = 1,2,\ldots \end{aligned}$$

The parameters b and p are subject to certain restrictions,

$$\begin{aligned} p,\, b &> 0, \\ b + p &\le 1. \end{aligned}$$

To ensure that this process is supercritical, i.e., $m > 1$, additional constraints on b and p are needed. The mean of $f(s)$ is $m = (df/ds)_{|s\uparrow 1} = \frac{b}{(1-p)^2}$, so supercriticality yields an additional restriction on parameters b and p, $b > (1-p)^2$, or equivalently

$$p > 1 - \sqrt{b}.$$

To compute $q_{1j}^{(n)}$, the nth iterate of $f(s)$ is derived, which we define as $f_n(s)$. For every supercritical pgf $f(s)$, the equation $f(s) = s$ has two roots, $s = 1$ and $s_0 = (1-b-p)/[p(1-p)] \in [0,1)$.

We have

$$f_n(s) = 1 - m^n \left(\frac{1-s_0}{m^n - s_0} \right) + \frac{m^n (\frac{1-s_0}{m^n - s_0})^2 s}{1 - (\frac{m^n - 1}{m^n - s_0}) s}.$$

Allowing for mutation in this linear fractional case leads to following pgf:

$$\begin{aligned} H(s) &= f(\mu + (1-\mu)s) \\ &= 1 - \frac{b}{1-p} + \frac{b(\mu + (1-\mu)s)}{1 - p(\mu + (1-\mu)s)}. \end{aligned}$$

To use to above results, we rearrange the parameters in $H(s)$ so that it is represented in the linear fractional form,

$$H(s) = 1 - \frac{b^*}{1-p^*} + \frac{b^* s}{1-p^* s}.$$

We find that $b^* = \frac{b(1-\mu)}{(1-p\mu)^2}$ and $p^* = \frac{p(1-\mu)}{1-p\mu}$.
The constraints for the new parameters b^* and p^*,

$$\begin{aligned} p^*,\, b^* &> 0, \\ p^* + b^* &\leq 1, \\ p^* &> 1 - \sqrt{b^*}, \end{aligned}$$

lead to modified constraints on p, b, and μ:

$$\begin{aligned} \mu &\neq \frac{1}{p}, \\ p,\, b &> 0, \\ \frac{(1-p)^2}{1-\mu} < \; b \; &\leq \frac{1-p(1+(1-p)\mu)}{1-\mu}, \\ 1-\sqrt{b(1-\mu)} < \; p \; &\leq \frac{1+\mu-\sqrt{(1-\mu)^2+4b\mu(1-\mu)}}{2\mu}. \end{aligned}$$

The lower bounds on b and p result from the condition $m = \frac{b^*}{(1-p^*)^2} > 1$, whereas the upper bounds come from the restriction $b^* + p^* \leq 1$.

We now compute the $q_{1j}^{(n)}$, to obtain the distribution of the long-term expected proportion of alleles having frequencies in j, referred to as Ψ_j's. As before, the $q_{1j}^{(n)}$'s are derived from the offspring pgf $H_n(s)$ by equating the coefficients of s.

$$\begin{aligned} H_n(s) &= 1 - \frac{m^n(1-s_0)}{m^n - s_0} + \frac{m^n\left(\frac{1-s_0}{m^n-s_0}\right)^2 s}{1-\left(\frac{m^n-1}{m^n-s_0}\right)s} \\ &= 1 - m^n x_n + m^n \frac{x_n^2 s}{1-z_n s} \end{aligned}$$

where $x_n = \frac{(1-s_0)}{m^n-s_0}$ and $z_n = \frac{m^n-1}{m^n-s_0}$.

To compute the $q_{1j}^{(n)}$ we solve

$$\begin{aligned} H_n(s) &= \sum_{j=0}^{\infty} q_{1j}^{(n)} s^j \\ 1 - m^n x_n + \frac{m^n x_n^2 s}{1 - z_n s} &= \sum_{j=0}^{\infty} q_{1j}^{(n)} s^j \\ 1 - m^n x_n + \frac{m^n x_n^2}{z_n} \sum_{j=1}^{\infty} (z_n s)^j &= q_{10}^{(n)} s^0 + \sum_{j=1}^{\infty} q_{1j}^{(n)} s^j \qquad (13.1) \end{aligned}$$

From Eq. (13.1) we see that $q_{10}^{(n)} = 1 - m^n x_n$ and $q_{1j}^{(n)} = m^n x_n^2 z_n^{j-1}$ for $j \geq 1$. In the terms of m and s_0,

$$q_{10}^{(n)} = 1 - \frac{m^n(1 - s_0)}{m^n - s_0} = \frac{s_0(m^n - 1)}{m^n - s_0} \text{ and } q_{1j}^{(n)} = m^n \left(\frac{1 - s_0}{m^n - s_0} \right)^2 \left(\frac{m^n - 1}{m^n - s_0} \right)^{j-1}.$$

Applying these expressions to the expression for Ψ_j gives us:

$$\begin{aligned} \Psi_j &= A^{-1} \phi_j \\ &= \frac{\sum_{r=1}^{\infty} m^{-r} q_{1j}^{(r)}}{\sum_{n=1}^{\infty} m^{-n}(1 - q_{10}^{(n)})} \\ &= \frac{\sum_{r=1}^{\infty} (\frac{1-s_0}{m^r - s_0})^2 (\frac{m^r - 1}{m^r - s_0})^{j-1}}{\sum_{n=1}^{\infty} \frac{(1-s_0)}{m^n - s_0}} \\ &= \frac{\sum_{r=1}^{\infty} (1 - s_0) \frac{(m^r-1)^{j-1}}{(m^r - s_0)^{j+1}}}{\sum_{n=1}^{\infty} \frac{1}{m^n - s_0}} \end{aligned}$$

The infinite sums in the numerator and denominator are numerically computed. A program was written in R-language to compute the $q_{1j}^{(n)}$ and Ψ_j. Since Alu sequence data in Table 13.1 suggest a high value for Ψ_1, we verify that the theoretical Ψ_1 attains such values for any choices of parameters b**,** p, and μ. For fixed $\mu = 10^{-6}$, we established a grid of b and p from 0 to 1 in steps of 0.01. Figure 13.2 shows that Ψ_1 can assume any value between 0 and 1, and that high values of Ψ_1 occur for a combination of low values of b and high values of p.

13.4 Fitting results

To fit the branching process model to the Alu sequence data, we use the maximum likelihood method. The highest value of the likelihood determines the estimates for our parameters. Since the log-likelihood of does not exist in a closed form, we evaluate it numerically. Our estimates of b and p are accurate to the fifth digit. For

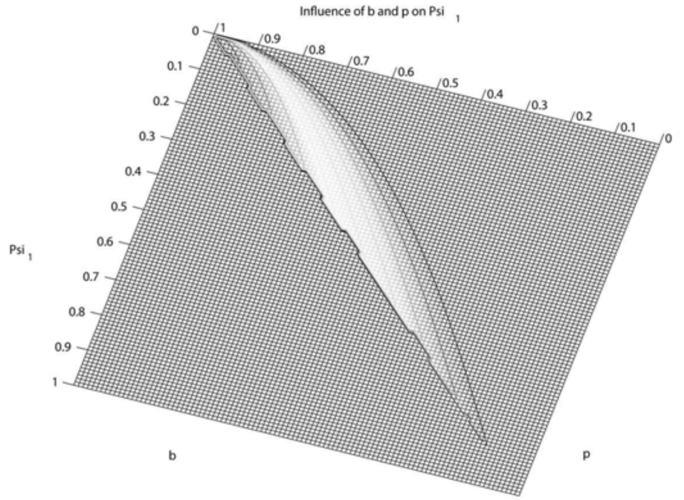

Fig. 13.2 Contour plot illustrating the influence of parameters *b* and *p* on Ψ_1, based on Griffiths–Pakes process with linear-fractional distribution. As evident from the plot, the highest valuest of Ψ_1 are located at the upper left end of the unit square, i.e., at large *b* and small *p* vaues. Range of Ψ_1-values, from 0 to 1.

these runs we fixed $\mu = 10^{-6}$. Sensitivity of the outcome to variation in parameter μ is very slight as along as this parameter is small (such as $10^{-5} - 10^{-9}$ per division).

Figures 13.3 and 13.4 depict the maximum-likelihood fits of the model to the data from AluYa1 and AluYa5 subfamilies, respectively. They are presented in the semi-logarithmic scale, to amplify the tail probabilities.

The graphical comparison that the data fit relatively well for allele classes 1 and 3–7. Notably, the allele class 2 shows the worst fit among the first seven allele classes. These seven classes account for at least 0.99 cumulative class frequency observed in the data.

13.5 Discussion

The current study seems to constitute the first application of the Griffiths–Pakes process to biological data. The outcome is interesting in the sense that a generally plausible fit is obtained to the Alu element frequency distribution. It is not quite clear, why the fit fails worst at the frequency class 2. This may have something to do with initial steps of data preparation. Indeed, if a region containing a relatively frequent variant were removed so that sequences could be aligned, some unique variants might migrate to class 2.

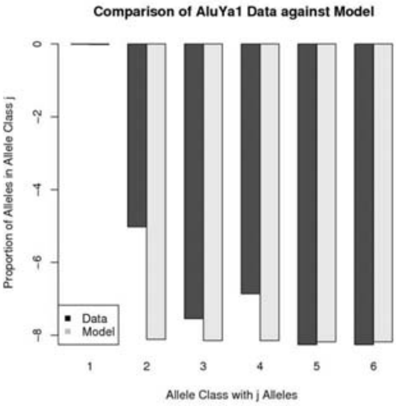

Fig. 13.3 AluYa1 data-based class frequencies against the theoretical $\{\Psi_k\}$ in log scale. Fitted by Griffiths–Pakes process with linear-fractional distribution, with $b = 0.016$, $p = 0.983$.

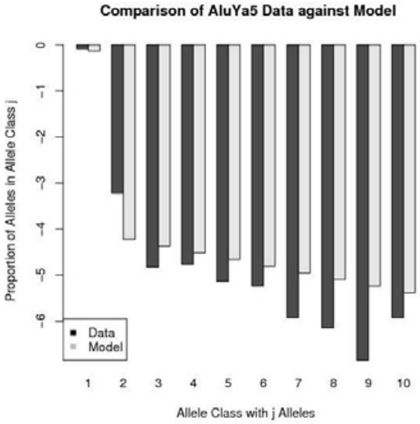

Fig. 13.4 AluYa5 data-based class frequencies against the theoretical $\{\Psi_k\}$ in log scale. Fitted by Griffiths–Pakes process with linear-fractional distribution, with $b = 0.139$, $p = 0.861$.

A more detailed discussion is contained in the companion paper [4], but we should notice that the current model does not involve genetic drift. Indeed, the genomes evolve within individuals and properly, the branching process should have been embedded in a population genetic model of Wright-Fisher or Moran type. However, this would lead to enormous complications.

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Parametric inference for Y-linked gene branching models: Expectation-maximization method

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Abstract Inferential problems for Y-linked bisexual branching processes are studied. A parametric frequentist framework is considered, with the reproduction laws belonging to the power series family of distributions. This kind of model is appropriate for the analysis of the generation-by-generation evolution of the number of carriers of two alleles of a Y-linked gene in a two-sex monogamic population, assuming that females prefer males carrying one of the alleles. It is assumed that the only available data are the total number of females and the total number of males of each genotype in each generation. The estimation problem is tackled as an incomplete data problem. Maximum likelihood estimators for the main parameters of the model are derived using expectation-maximization method. Predictive distributions for as yet unobserved generations are derived, and the accuracy of the algorithm is illustrated by way of a simulated example.

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14.1 Introduction

The XX/XY sex-determination system is one of the most familiar, and is found in the populations of most mammals, including humans. In these populations, females

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have XX chromosomes, while males have two distinct chromosomes, XY. Therefore, the Y chromosome is exclusive of males. Recent research has shown the importance of some Y-linked genes or markers, such as long-arm Y-chromosomal microdeletions, certain DNA polymorphisms, transmission of surnames, or the spread of melanistic pigmentation (see, e.g., [1, 2, 10], and [13]).

Determining the evolution of these kinds of Y-linked characters in a population plays an important role in solving certain questions with a practical importance. In this sense, bisexual branching processes have recently been introduced in [5] and [7] to model the evolution in the number of carriers of Y-linked characters of populations. Both these models consider perfect fidelity mating and a Y-linked gene with a pair of alleles. These alleles could represent the presence or absence of a character in an individual. We here consider the model presented in [5], which assumes that the alleles are expressed in the male phenotype, and that females have a preference for males carrying one of the alleles of the gene. Melanistic pigmentation in the Eastern Mosquitofish and certain surnames in humans are two notable examples of this kind of Y-linked character.

Using this Y-linked bisexual branching process, one deduces that the behaviour (extinction/survival) of this kind of Y-linked gene depends on certain parameters of the model (see [5] and [6]). In most real situations, these parameters are unknown and they have to be estimated. In the present work, we deal with the problem of making inferences about these parameters. We take a frequentist and parametric approach, with the reproduction laws belonging to the power series family of distributions. In relation to this, a major problem is what information one can expect to obtain from the sample. In this sense, we consider a realistic situation in which the only data available are the total number of females and the total number of males of each genotype in each generation. This is a relatively small amount of sample information, and we view the estimation problem using such a sample as analogous to an incomplete data problem. This leads us to use the expectation-maximization (EM) method (see [4]) in order to obtain maximum likelihood estimators (MLEs).

The communication is organized in four sections. In Sect. 14.2, we provide the definition of the Y-linked bisexual branching process. Then, in Sect. 14.3, we set out the inference problem, and provide MLEs of the main parameters of the model using the EM method. We also derive predictive distributions for as yet unobserved generations. Finally, a simulation study is described in Sect. 14.4.

14.2 The probability model

The probability model we are concerned with is the Y-linked bisexual branching process introduced in [5]. This model is a discrete-time stochastic process which determines generation-by-generation the evolution of the number of carries of the two alleles, R and r, of a Y-linked gene. These alleles are expressed in the phenotype of males. Hence, the males are designated by R-type or r-type according to allele they carry. Thus, for each $n \geq 1$, F_n, MR_n, and Mr_n denote the total number of females, and R-type and r-type males at generation n, respectively. Since females and males form mating units to produce offspring, a couple (female–male) is classified as R-type or r-type according to the genotype of the male. The total numbers of R-type and r-type mating units at generation n are denoted by ZR_n and Zr_n, respectively. The number of mating units of each type in the initial generation ($n = 0$) is fixed, and from this vector (ZR_0, Zr_0) the population size is determined in each generation according to two phases: reproduction and mating.

According to the inheritance rules, in the reproduction phase, R-type mating units can generate females and R-type males, while r-type mating units can produce females and r-type males. Moreover, each couple is assumed to randomly produce offspring independently of the other couples. The probability distribution of these variables will be the same for all the couples with a given genotype, irrespective of the generation they belong to, and will be called the reproduction law of that genotype. Formally therefore, we consider two independent sequences

$$\{(FR_{n,l}, MR_{n,l}) : l = 1,2,\dots; n = 0,1,\dots\}$$

and

$$\{(Fr_{n,l}, Mr_{n,l}) : l = 1,2,\dots; n = 0,1,\dots\}$$

of independent, identically distributed, non-negative, and integer-valued bivariate random vectors, where $(FR_{n,l}, MR_{n,l})$ (resp. $(Fr_{n,l}, Mr_{n,l})$) represents the number of females and males generated by the lth R-type (resp. r-type) mating unit in generation n.

In general, $(FR_{0,1}, MR_{0,1})$ and $(Fr_{0,1}, Mr_{0,1})$ may have different distributions, meaning that R-type and r-type couples may have differences in their reproductive abilities. With respect to the distribution of these vectors, we assume the binomial reproduction scheme introduced in [3]. That is, the total number of descendants generated by an R-type (resp. r-type) couple is specified by a given probability distribution, $\{p_k^R\}_{k\geq 0}$ (resp. $\{p_l^r\}_{l\geq 0}$), where $p_k^R = P(FR_{0,1} + MR_{0,1} = k)$, with $k \geq 0$ (resp. $p_l^r = P(Fr_{0,1} + Mr_{0,1} = l)$, with $l \geq 0$), called the reproduction law of the R-type (resp. r-type) mating units. We denote by m_R (resp. m_r) the average number of offspring (i.e., "the reproduction mean") generated by an R-type (resp. r-type) couple.

Furthermore, an offspring will be female with probability α, $0 < \alpha < 1$, and male with probability $1 - \alpha$. These sex designations are made independently among the offspring of any couple, and it is assumed that the genotype has no influence on the sex determination, so that α is the same for both genotypes. Then, given that an R-type (resp. r-type) mating unit produces k (resp. l) offspring, i.e., $FR_{0,1} + MR_{0,1} = k$ (resp. $Fr_{0,1} + Mr_{0,1} = l$), the number of females among these, $FR_{0,1}$ (resp. $Fr_{0,1}$), follows a binomial distribution of size k (resp. l) and probability α. Thus the average number of females and males per R-type (resp. r-type) couple will be αm_R and $(1-\alpha)m_R$ (resp. αm_r and $(1-\alpha)m_r$), respectively.

As was noted in the Introduction, we consider a parametric framework. We then assume that the reproduction laws belong to the power series family of distributions, i.e.,

$$p_k^R = a_{R,k}\theta_R^k(A_R(\theta_R))^{-1} \quad \text{and} \quad p_l^r = a_{r,l}\theta_r^l(A_r(\theta_r))^{-1}, \text{ for all } k,l \geq 0, \tag{14.1}$$

where $\{a_{R,k}\}_{k\geq 0}$ and $\{a_{r,l}\}_{l\geq 0}$ are known non-negative sequences of real values, $A_R(\theta_R) = \sum_{k=0}^{\infty} a_{R,k}\theta_R^k$ and $A_r(\theta_r) = \sum_{l=0}^{\infty} a_{r,l}\theta_r^l$, with $a_{R,k}\theta_R^k \geq 0$ and $a_{r,l}\theta_r^l \geq 0$, for all $k,l \geq 0$, and $\theta_R \in \mathbb{R}$ and $\theta_r \in \mathbb{R}$, such that $0 < A_R(\theta_R) < \infty$ and $0 < A_r(\theta_r) < \infty$. For these distributions, it is not hard to deduce that

$$m_R = m_R(\theta_R) = \theta_R \frac{d}{d\theta_R}\log A_R(\theta_R) \quad \text{and} \quad m_r = m_r(\theta_r) = \theta_r \frac{d}{d\theta_r}\log A_r(\theta_r). \tag{14.2}$$

The power series is an exponential family that includes most of the usual distributions used in practice (e.g., Poisson, geometric, binomial, negative binomial,...).

For a fixed generation n with known total numbers of R-type and r-type mating units, and taking into account the basis of the genetic rules described above, the female offspring of all the couples in generation n yield the total number of females in generation $n+1$, i.e.,

$$F_{n+1} = \sum_{i=1}^{ZR_n} FR_{n,i} + \sum_{j=1}^{Zr_n} Fr_{n,j}. \tag{14.3}$$

Similarly, the male offspring of all the R-type (resp. r-type) couples in generation n yield the total number of R-type (resp. r-type) males in generation $n+1$, i.e.,

$$MR_{n+1} = \sum_{i=1}^{ZR_n} MR_{n,i} \quad \text{and} \quad Mr_{n+1} = \sum_{j=1}^{Zr_n} Mr_{n,j}. \tag{14.4}$$

Now we deal with the mating phase. Since the generations do not overlap, from F_{n+1}, MR_{n+1}, and Mr_{n+1}, the number of couples of each genotype in generation $n+1$ is obtained in the following way. We assume perfect fidelity and preference in mating, i.e., each individual mates with only one individual of the opposite sex provided that some of them are still available, and females prefer R-type males as mates. Therefore, since R-type males are chosen first as mates, the number of R-type mating units is

$$ZR_{n+1} = \min\{F_{n+1}, MR_{n+1}\}. \tag{14.5}$$

The number of females which do not mate with R-type males is

$$\max\{0, F_{n+1} - MR_{n+1}\}.$$

These females (if any) mate with r-type males and the assumption of perfect fidelity implies that the number of r-type mating units is

$$Zr_{n+1} = \min\{\max\{0, F_{n+1} - MR_{n+1}\}, Mr_{n+1}\}. \tag{14.6}$$

Notice that the number of couples of each genotype in the $(n+1)$st generation depends only on the present number of mating units, and not on the number of ancestors that belonged to past generations. Therefore, knowing the present number of mating units of each type and the parameters of the model, i.e., the probability that a descendant is female, α, and the reproduction laws of both types defined by θ_R and θ_r, one obtains by recursion the number of females, males, and mating units of each type in the following generations by Eqs. (14.3), (14.4), (14.5) and (14.6).

In [5] and [6], the extinction problem for a Y-linked gene was considered using this model, providing conditions for the almost sure extinction of the whole population, and also for each genotype to have a positive probability of survival/fixation. These conditions depend on the magnitudes of α and the means of the reproduction laws of the two types, m_R and m_r. In [6], it was shown that these parameters determine the asymptotic behaviour of the genotypes.

In practice, the parameters α, θ_R, θ_r, m_R, and m_r are usually unknown. In order to apply this model to real situations, it is therefore necessary to develop the theory of its estimation.

14.3 The estimation problem: The expectation-maximization method

Restricting ourselves to a frequentist approach in the parametric context described in the previous section, we next attempt to find MLEs of the parameters $(\alpha,\theta_R,\theta_r)$ and the reproduction means (m_R,m_r). We shall also make inferences of the future population sizes of females and of the two types of males, i.e., of the vector $(F_{N+s},MR_{N+s},Mr_{N+s})$, for any $s>0$. To this end, we first assume that the entire family tree up to generation N, denoted by $\mathscr{Z}\mathscr{F}\mathscr{M}_N$, is observed, i.e., the vectors

$$\{(FR_{n,l},MR_{n,l}),(Fr_{n,k},Mr_{n,k}) : l=1,\dots,ZR_n; k=1,\dots,Zr_n; n=0,\dots,N-1\}$$

are known. Given that mating units reproduce independently, that reproduction laws belong to the power series family given by (14.1), and the binomial scheme, it is straightforward to obtain that the likelihood function of $(\alpha,\theta_R,\theta_r)$ based on $\mathscr{Z}\mathscr{F}\mathscr{M}_N$ is given by

$$L((\alpha,\theta_R,\theta_r)|\mathscr{Z}\mathscr{F}\mathscr{M}_N) \propto$$

$$\prod_{n=0}^{N-1} \alpha^{F_{n+1}}(1-\alpha)^{MR_{n+1}+Mr_{n+1}}\theta_R^{FR_{n+1}+MR_{n+1}}(A_R(\theta_R))^{-ZR_n}\theta_r^{Fr_{n+1}+Mr_{n+1}}(A_r(\theta_r))^{-Zr_n}, \tag{14.7}$$

with FR_n (resp. Fr_n) the number of females in generation n generated by all ZR_{n-1} (resp. Zr_{n-1}) R-couples (resp. r-couples), i.e.,

$$FR_n = \sum_{i=1}^{ZR_{n-1}} FR_{n,i} \text{ (resp. } Fr_n = \sum_{j=1}^{Zr_{n-1}} Fr_{n,j}).$$

From (14.2) and (14.7), it is easy to prove by applying a standard procedure (see [8]) that MLEs of (α, m_R, m_r) based on $\mathscr{Z}\mathscr{F}\mathscr{M}_N$ are given by

$$\widehat{\alpha} = \frac{\sum_{n=1}^{N} F_n}{\sum_{n=1}^{N} (F_n + MR_n + Mr_n)}, \; \widehat{m}_R = \frac{\sum_{n=1}^{N} (FR_n + MR_n)}{\sum_{n=0}^{N-1} ZR_n}, \text{ and } \widehat{m}_r = \frac{\sum_{n=1}^{N} (Fr_n + Mr_n)}{\sum_{n=0}^{N-1} Zr_n}.$$

We assume that $m_R(\theta_R)$ and $m_r(\theta_r)$ are one-to-one functions. Then, one deduces that MLEs of θ_R and θ_r, denoted by $\widehat{\theta}_R$ and $\widehat{\theta}_r$, respectively, are the unique solutions of the equations

$$\sum_{n=1}^{N} (FR_n + MR_n) = m_R(\widehat{\theta}_R) \sum_{n=0}^{N-1} ZR_n \quad \text{and} \quad \sum_{n=1}^{N} (Fr_n + Mr_n) = m_r(\widehat{\theta}_r) \sum_{n=0}^{N-1} Zr_n,$$

respectively.

Note that the above estimators depend only on the total number of mating units of each type and the females and individuals generated by them, that is, on the variables ZR_n, Zr_n, F_{n+1}, $TR_{n+1} = FR_{n+1} + MR_{n+1}$ and $Tr_{n+1} = Fr_{n+1} + Mr_{n+1}$, for $n = 0, \ldots, N-1$. Using a standard procedure (see [9] for details), one obtains that $(\widehat{\alpha}, \widehat{\theta}_R, \widehat{\theta}_r, \widehat{m}_R, \widehat{m}_r)$ are also the MLEs of $(\alpha, \theta_R, \theta_r, m_R, m_r)$ based on the sample

$$\{(ZR_n, Zr_n), (F_{n+1}, TR_{n+1}, Tr_{n+1}), n = 0, \ldots, N-1\}.$$

However, in most real situations, it is impossible to observe the random variables TR_{n+1} and Tr_{n+1} because the females are indistinguishable. Only the two types of males can be differentiated. This leads us to the interesting problem of how to estimate the parameters of the model only assuming as available data the total number of females and the total number of males of each type in each generation up to the Nth generation, i.e., the vectors

$$\{(F_{n+1}, MR_{n+1}, Mr_{n+1}), n = 0, \ldots, N-1\}.$$

Moreover, we assume that the vector (ZR_0, Zr_0) is known, i.e., the total number of mating units of each type at the initial generation. Since Eqs. (14.5) and (14.6) give the number of mating units of each type deterministically, the above set of vectors contains the same information as

$$\{(ZR_n, Zr_n), (F_{n+1}, MR_{n+1}, Mr_{n+1}), n = 0, \ldots, N-1\}.$$

To simplify the notation, we shall refer to this set as $\mathscr{F}\mathscr{M}_N$.

The question posed above can then be studied as a problem of estimation with incomplete data. In this sense, the expectation-maximization (EM) method (see [4] and [11]) is appropriate to deal with the problem, allowing one to obtain MLEs.

To apply the EM method, we write

$$\mathscr{F}Rr_N = \{(FR_{n+1}, Fr_{n+1}), n = 0, \ldots, N-1\}.$$

This set of unobserved vectors is taken to be a latent vector, and is required to make inferences completing the information given by $\mathscr{F}\mathscr{M}_N$.

First we shall describe the distribution of the latent vector $\mathscr{F}Rr_N$ given the sample $\mathscr{F}\mathscr{M}_N$ and the parameters of the model $(\alpha, \theta_R, \theta_r)$, denoted by

$$\mathscr{F}Rr_N|(\mathscr{F}\mathscr{M}_N, \alpha, \theta_R, \theta_r).$$

14.3.1 Determining the distribution of $\mathscr{F}Rr_N|(\mathscr{F}\mathscr{M}_N, \alpha, \theta_R, \theta_r)$

To determine the distribution of the unobserved vector $\mathscr{F}Rr_N$ given the sample $\mathscr{F}\mathscr{M}_N$ and the parameters of the model $(\alpha, \theta_R, \theta_r)$, we shall first prove that this distribution satisfies

$$f(\mathscr{F}Rr_N|(\mathscr{F}\mathscr{M}_N, \alpha, \theta_R, \theta_r)) = \prod_{n=0}^{N-1} f((FR_{n+1}, Fr_{n+1})|(ZFM_n, \alpha, \theta_R, \theta_r)), \quad (14.8)$$

where, for $n = 0, \ldots, N-1$, ZFM_n is the vector $(ZR_n, Zr_n, F_{n+1}, MR_{n+1}, Mr_{n+1})$. Computationally, this means that to generate the vector $\mathscr{F}Rr_N$ we must proceed generation-by-generation. Specifically, once we know the total number of mating units in generation n, (ZR_n, Zr_n), and the total number of females and of males of each type in the $(n+1)$st generation, $(F_{n+1}, MR_{n+1}, Mr_{n+1})$, it is enough to sample the vectors (FR_{n+1}, Fr_{n+1}). In proving (14.8), we shall write $P(\cdot|\cdot)$ to denote the conditional probability with parameters $(\alpha, \theta_R, \theta_r)$. Let fRr_N and fm_N be vectors of non-negative integers with

$$fRr_N = (fR_{n+1}, fr_{n+1}, n = 0, \ldots, N-1)$$

and

$$fm_N = (zR_n, zr_n, f_{n+1}, mR_{n+1}, mr_{n+1}, n = 0, \ldots, N-1),$$

where $zR_{n+1} = \min\{f_{n+1}, mR_{n+1}\}$ and $zr_{n+1} = \min\{\max\{0, f_{n+1} - mR_{n+1}\}, mr_{n+1}\}$, for $n = 0, \ldots, N-1$. Since mating units reproduce independently, one has that

$$\begin{aligned}
&P(\mathscr{F}Rr_N = fRr_N|\mathscr{F}\mathscr{M}_N = fm_N) \\
&= \prod_{n=0}^{N-1} \frac{P((ZR_n, Zr_n) = (zR_n, zr_n), A_{mR_{n+1}}, A_{mr_{n+1}}, A_{f_{n+1}}, A_{fR_{n+1}}, A_{fr_{n+1}})}{P((ZR_n, Zr_n) = (zR_n, zr_n), A_{mR_{n+1}}, A_{mr_{n+1}}, A_{f_{n+1}})} \\
&= \prod_{n=0}^{N-1} P(A_{fR_{n+1}}, A_{fr_{n+1}}|(ZR_n, Zr_n) = (zR_n, zr_n), A_{mR_{n+1}}, A_{mr_{n+1}}, A_{f_{n+1}}),
\end{aligned}$$

where, for each $n = 0, \ldots, N-1$, we have defined the sets

$$A_{mR_{n+1}} = \{MR_{n+1} = mR_{n+1}\} = \{\sum_{i=1}^{ZR_n} MR_{n,i} = mR_{n+1}\},$$

$$\begin{aligned}
A_{mr_{n+1}} &= \{Mr_{n+1} = mr_{n+1}\} = \{\sum_{j=1}^{Zr_n} Mr_{n,j} = mr_{n+1}\},\\
A_{f_{n+1}} &= \{F_{n+1} = f_{n+1}\} = \{\sum_{i=1}^{ZR_n} FR_{n,i} + \sum_{j=1}^{Zr_n} Fr_{n,j} = f_{n+1}\},\\
A_{fR_{n+1}} &= \{FR_{n+1} = fR_{n+1}\} = \{\sum_{i=1}^{ZR_n} FR_{n,i} = fR_{n+1}\},\\
A_{fr_{n+1}} &= \{Fr_{n+1} = fr_{n+1}\} = \{\sum_{j=1}^{Zr_n} Fr_{n,j} = fr_{n+1}\}.
\end{aligned}$$

Specifically, knowing that $ZR_n = zR_n$ and $Zr_n = zr_n$, the set $A_{mR_{n+1}}$ (resp. $A_{fR_{n+1}}$) means that mR_{n+1} (resp. fR_{n+1}) R-type males (resp. females) have been generated by all zR_n R-type mating units. Analogous descriptions can be given for the sets $A_{mr_{n+1}}$ and $A_{fr_{n+1}}$. Finally, the set $A_{f_{n+1}}$ means that all $zR_n + zr_n$ mating units have generated f_{n+1} females.

Having shown that the distribution of $\mathscr{F}Rr_N$ given $\mathscr{F}\mathscr{M}_N$ when the underlying parameters are $(\alpha, \theta_R, \theta_r)$ can be simulated generation-by-generation, we now determine, for a fixed generation n, the distribution of the (FR_{n+1}, Fr_{n+1}) given ZFM_n, i.e.,

$$f((FR_{n+1}, Fr_{n+1})|(ZFM_n, \alpha, \theta_R, \theta_r)).$$

Applying the multiplication rule, one straightforwardly obtains that

$$P(A_{fR_{n+1}}, A_{fr_{n+1}}|(ZR_n, Zr_n) = (zR_n, zr_n), A_{mR_{n+1}}, A_{mr_{n+1}}, A_{f_{n+1}})$$

is proportional to the product of the probabilities

$$P(A_{mR_{n+1}}, A_{mr_{n+1}}, A_{fR_{n+1}}, A_{fr_{n+1}}|(ZR_n, Zr_n) = (zR_n, zr_n)) \tag{14.9}$$

and

$$P(A_{f_{n+1}}|(ZR_n, Zr_n) = (zR_n, zr_n), A_{mR_{n+1}}, A_{mr_{n+1}}, A_{fR_{n+1}}, A_{fr_{n+1}}). \tag{14.10}$$

Given that mating units reproduce independently, (14.9) is equal to

$$P(A_{mR_{n+1}}, A_{fR_{n+1}}|ZR_n = zR_n)P(A_{mr_{n+1}}, A_{fr_{n+1}}|Zr_n = zr_n).$$

Since the total number of descendants produced by all R-type couples at generation n is given by $FR_{n+1} + MR_{n+1}$, and the reproduction scheme considered is binomial, then the probability that mR_{n+1} R-type males and fR_{n+1} females are produced by all R-type mating units, given by $P(A_{mR_{n+1}}, A_{fR_{n+1}}|ZR_n = zR_n)$, is the product of the probabilities

$$P(FR_{n+1} + MR_{n+1} = fR_{n+1} + mR_{n+1}|ZR_n = zR_n) \tag{14.11}$$

and

$$P(A_{fR_{n+1}}|ZR_n = zR_n, FR_{n+1} + MR_{n+1} = fR_{n+1} + mR_{n+1}). \tag{14.12}$$

Considering that the reproduction law, that is the distribution of the random variable $FR_{n,i} + MR_{n,i}$, belongs to the power series family of parameter θ_R and that the conditional distribution of $FR_{n+1} + MR_{n+1}$ is a convolution of ZR_n copies of the reproduction law, one obtains that the probability given in (14.11) is proportional to

$$(A_R(\theta_R))^{-zR_n} \theta_R^{fR_{n+1}+mR_{n+1}},$$

and therefore, this distribution belongs also to the power series family. Special cases in which one can easily obtain this distribution are the Poisson and the geometric distributions, because the sum of independent random variables with these distributions follows a Poisson or a negative binomial distribution, respectively. Furthermore, taking into account the binomial reproduction scheme, the probability given in (14.12) is obtained from a binomial distribution with size $fR_{n+1} + mR_{n+1}$ and probability α. One can obtain $P(A_{mr_{n+1}}, A_{fr_{n+1}}|Zr_n = zr_n)$ analogously.

Finally, the probability given in (14.10) is obviously unity if $f_{n+1} = fR_{n+1} + fr_{n+1}$, and zero otherwise.

In sum, computationally, to determine the probability distribution of $\mathscr{F}Rr_N$ given $(\mathscr{F}\mathscr{M}_N, \alpha, \theta_R, \theta_r)$ it is sufficient to determine it generation-by-generation. Fixed $n = 0, \ldots, N-1$ and given $(ZR_n, Zr_n, F_{n+1}, MR_{n+1}, Mr_{n+1})$, we have shown that this can be done by determining the convolution of ZR_n and Zr_n distributions belonging to the power series family defined by θ_R and θ_r, respectively, and independent binomial distributions with size the total number of descendants generated by all mating units of each type and probability α, subject to the constraint $F_n = FR_n + Fr_n$.

14.3.2 The expectation-maximization method

Now that we know the distribution of $\mathscr{F}Rr_N|(\mathscr{F}\mathscr{M}_N, \alpha, \theta_R, \theta_r)$, we shall describe the EM method. This is an iterative method that runs as follows. For $i \geq 0$, let $(\alpha^{(i)}, \theta_R^{(i)}, \theta_r^{(i)})$ be the estimated parameters in the i-th iteration of the algorithm. The $(i+1)$st iteration starts with the expectation step (E), where the expected value of the log-likelihood with respect to the available data $(\mathscr{F}\mathscr{M}_N, \alpha^{(i)}, \theta_R^{(i)}, \theta_r^{(i)})$ is calculated, i.e.,

$$E_{\mathscr{F}Rr_N|(\mathscr{F}\mathscr{M}_N, \alpha^{(i)}, \theta_R^{(i)}, \theta_r^{(i)})}\left[\log(L((\alpha, \theta_R, \theta_r)|(\mathscr{F}\mathscr{M}_N, \mathscr{F}Rr_N)))\right].$$

The maximization step (M) consists of finding the values $(\alpha^{(i+1)}, \theta_R^{(i+1)}, \theta_r^{(i+1)})$ of the parameters which maximize this expectation. Writing

$$E_i^*[\cdot] = E_{\mathscr{F}Rr_N|(\mathscr{F}\mathscr{M}_N, \alpha^{(i)}, \theta_R^{(i)}, \theta_r^{(i)})}[\cdot],$$

taking into account (14.2) and (14.7), and applying a standard procedure, one obtains that

$$\alpha^{(i+1)} = \frac{\sum_{n=1}^{N} F_n}{\sum_{n=1}^{N}(F_n + MR_n + Mr_n)},$$

$$m_R^{(i+1)} = \frac{\sum_{n=1}^{N}(E_i^*[FR_n] + MR_n)}{\sum_{n=0}^{N-1} ZR_n}, \quad \text{and} \quad m_r^{(i+1)} = \frac{\sum_{n=1}^{N}(E_i^*[Fr_n] + Mr_n)}{\sum_{n=0}^{N-1} Zr_n}.$$

Note that the sequence $\{\alpha^{(i)}\}_{i\geq 1}$ is constant and is equal to $\widehat{\alpha}$, the MLE of α. This is because $\widehat{\alpha}$ only depends on $\mathscr{F}\mathscr{M}_N$. Moreover, $m_R^{(i+1)}$ and $m_r^{(i+1)}$ depend on the expectations given by $\sum_{n=1}^{N} E_i^*[FR_n]$ and $\sum_{n=1}^{N} E_i^*[Fr_n]$, respectively, since $\sum_{n=1}^{N} FR_n$ and $\sum_{n=1}^{N} Fr_n$ are not observed. Finally, since $m_R(\theta_R)$ and $m_r(\theta_r)$ are one-to-one, then $\theta_R^{(i+1)}$ and $\theta_r^{(i+1)}$ are the unique solutions of the equations

$$\sum_{n=1}^{N}(FR_n + MR_n) = m_R(\theta_R^{(i+1)})\sum_{n=0}^{N-1} ZR_n \text{ and } \sum_{n=1}^{N}(Fr_n + Mr_n) = m_r(\theta_r^{(i+1)})\sum_{n=0}^{N-1} Zr_n,$$

respectively, where $m_R(\theta_R^{(i+1)}) = m_R^{(i+1)}$ and $m_r(\theta_r^{(i+1)}) = m_r^{(i+1)}$.

Therefore, given the known sample $\mathscr{F}\mathscr{M}_N$, the EM algorithm is as follows:

```
Fixed $(\alpha^{(0)}, \theta_R^{(0)}, \theta_r^{(0)})$ for some positive values
Do $i = 1$
E Step:
  Determine $\mathscr{F}Rr_N|(\mathscr{F}\mathscr{M}_N, \alpha^{(i)}, \theta_R^{(i)}, \theta_r^{(i)})$
  Calculate $\sum_{n=1}^{N} E_i^*[FR_n]$ and $\sum_{n=1}^{N} E_i^*[Fr_n]$
M Step:
  Calculate
  $(\alpha^{(i+1)}, \theta_R^{(i+1)}, \theta_r^{(i+1)}) = \arg\max_{(\alpha,\theta_R,\theta_r)} E_i^*\left[\log(L((\alpha, \theta_R, \theta_r)|(\mathscr{F}\mathscr{M}_N, \mathscr{F}Rr_N)))\right]$
Do $i = i + 1$
```

One hence obtains a sequence $\{(\alpha^{(i)}, \theta_R^{(i)}, \theta_r^{(i)}, m_R^{(i)}, m_r^{(i)})\}_{i>0}$ which converges to $(\widehat{\alpha}^{EM}, \widehat{\theta}_R^{EM}, \widehat{\theta}_r^{EM}, \widehat{m}_R^{EM}, \widehat{m}_r^{EM})$, i.e., MLEs of $(\alpha, \theta_R, \theta_r, m_R, m_r)$ based on the sample $\mathscr{F}\mathscr{M}_N$. A discussion of the convergence of the EM method can be found in [11]. Note that, as was pointed out above, $\widehat{\alpha}^{EM} = \widehat{\alpha}$. We can obtain a sample of the distribution of $(F_{N+s}, MR_{N+s}, Mr_{N+s})$ knowing $\mathscr{F}\mathscr{M}_N$ for any $s > 0$ by simulating, through the Monte-Carlo method, s generations of a Y-linked bisexual branching process starting with (ZR_N, Zr_N) and considering $(\widehat{\alpha}^{EM}, \widehat{\theta}_R^{EM}, \widehat{\theta}_r^{EM})$ as the parameters of the model.

14.4 Simulation study

In this section, we describe the application of the above algorithm to simulated data. To this end, we considered a Y-linked bisexual branching process where the

R-type reproduction law follows a Poisson distribution and the r-type reproduction law follows a geometric distribution, with unknown parameters, $\lambda_R > 0$ and $0 < p_r < 1$, respectively, i.e.,

$$p_k^R = e^{-\lambda_R} \frac{\lambda_R^k}{k!} \quad \text{and} \quad p_l^r = p_r(1-p_r)^l, \text{ for all } k,l \geq 0.$$

For these reproduction laws, taking into account expressions (14.1) and (14.2), one has that $\theta_R = \lambda_R = m_R$, $A_R(\theta_R) = e^{\lambda_R}$, $\theta_r = 1 - p_r$, $m_r = (1-\theta_r)^{-1}\theta_r$, and $A_r(\theta_r) = p_r^{-1}$. Therefore, $m_R(\theta_R)$ and $m_r(\theta_r)$ are strictly increasing functions.

To determine the distribution of the latent vector $\mathscr{F}Rr_N$, one notes that, since the R-type reproduction law follows a Poisson distribution, then the probability given by (14.11) is obtained from a Poisson distribution with parameters $zR_n\lambda_R$. For the r-type case, this probability is derived from a negative binomial distribution with size zr_n and probability p_r since the r-type reproduction law is a geometric distribution.

By way of illustration, we considered a Y-linked bisexual branching process with $\alpha = 0.4$, $m_R = 1.7$, and $p_r = 5/18$, simulating 20 generations starting with $(ZR_0, Zr_0) = (3, 10)$. Table 14.1 lists the total numbers of females and of males of each type for each generation.

Table 14.1 Simulated data.

n	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
F_n	30	33	39	44	46	56	57	47	39	47	48	50	39	48	52	67	69	79	56	50
MR_n	5	5	4	4	3	6	6	3	2	2	3	6	9	10	11	7	3	2	1	1
Mr_n	25	31	37	42	59	62	86	83	44	51	67	78	73	57	75	88	86	114	93	86

Note that it would be difficult to determine at a glance anything about the future behaviour of a Y-linked character on the basis of these observations. To apply the EM method, we took as starting values $(\alpha^{(0)}, m_R^{(0)}, p_r^{(0)}) = (0.5, 1, 0.5)$, where $m_R^{(i)} = \theta_R^{(i)}$ and $p_r^{(i)} = 1 - \theta_r^{(i)}$, for all $i \geq 0$, and then applied the algorithm given in the previous section. The resulting sequence $\{(\alpha^{(i)}, m_R^{(i)}, p_r^{(i)})\}_{i \geq 0}$ converged from iteration 50 onwards – the difference between consecutive elements of the sequence was less than 10^{-7}– (see Fig. 14.1). A discrete sensitivity analysis applied to study the influence of the initial values $(\alpha^{(0)}, m_R^{(0)}, p_r^{(0)})$ on the convergence of the method showed the procedure to be stable with respect to the initial values. There were no changes in the limit.

Figure 14.2 shows the expectation–maximization MLEs by generation up to generation 20 for α, m_R, and p_r. The estimates converge to the true values of the parameters. Indeed, under weak general conditions, the EM method leads to consistent estimates (see [4] or [11]), as is the case of the usual MLEs. Figure 14.3 shows a Monte-Carlo approximation to the sampling distribution of $\widehat{\alpha}^{EM}$, $\widehat{m}_R^{EM}$, and $\widehat{p}_r^{EM}$ in generation 20, when neither genotype has become extinct, with $\widehat{p}_r^{EM}$ denoting

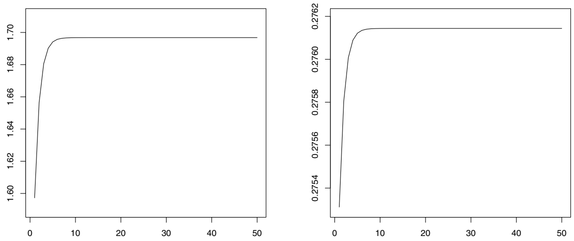

Fig. 14.1 Evolution of $m_R^{(i)}$ (left) and $p_r^{(i)}$ (right), for $i = 1, \ldots, 50$, in generation 20.

the expectation–maximization MLE of p_r. Figure 14.4 illustrates the bootstrap approximation to these sampling distributions. One can see how the bootstrap method works quite well.

An interesting question is to predict on the basis of the observed data whether or not the process will survive over time. From the Monte-Carlo approximation to the sampling distribution of $\widehat{\alpha}^{EM}$, $\widehat{m}_R^{EM}$ and $\widehat{p}_r^{EM}$, we calculated the proportion of samples in generation 20 which satisfy $\widehat{\alpha}^{EM} < 0.5$ and $(1-\widehat{\alpha}^{EM})\widehat{m}_R^{EM} < \widehat{\alpha}^{EM}\widehat{m}_r^{EM}$, finding the value 0.861. Since the condition $\alpha < 0.5$ and $(1-\alpha)m_R < \alpha m_r$ ensures that there exists a positive probability for both genotypes to grow without limit over time (see [6]), the high value of the calculated proportion is indicative that this condition might be satisfied. In fact, the true values of the parameters indeed satisfy this condition, and therefore there exists a positive probability that both genotypes grow over the generations.

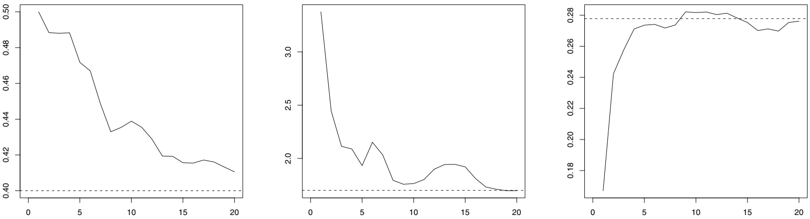

Fig. 14.2 Evolution of $\widehat{\alpha}^{EM}$ (*left*), $\widehat{m}_R^{EM}$ (*middle*), and $\widehat{p}_r^{EM}$ (*right*) over the generations, together with the true value of each parameter (*dashed line*).

Finally, Fig. 14.5 illustrates the predictive distribution of the total numbers of females and of each type of male in the 21st generation. The predicted behaviour in this generation is in keeping with the fact that there is a positive probability (which may be small) that both genotypes grow without limit over time.

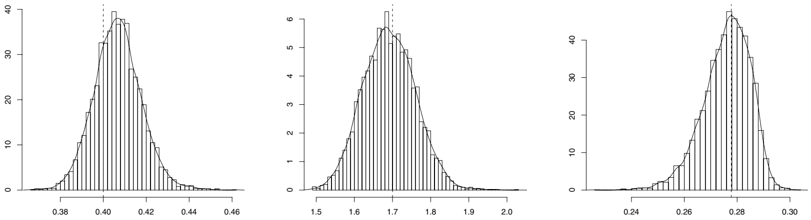

Fig. 14.3 Monte-Carlo approximation to the sampling distribution of $\widehat{\alpha}^{EM}$ (*left*), $\widehat{m}_R^{EM}$ (*middle*), and $\widehat{p}_r^{EM}$ (*right*), in generation 20, together with the true value of each parameter (*dashed line*).

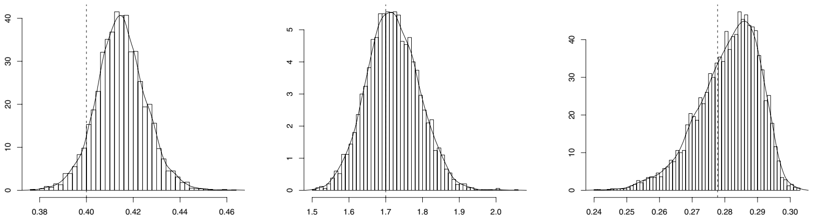

Fig. 14.4 Bootstrap approximation to the sampling distribution of $\widehat{\alpha}^{EM}$ (*left*), $\widehat{m}_R^{EM}$ (*middle*), and $\widehat{p}_r^{EM}$ (*right*), in generation 20, together with the true value of each parameter (*dashed line*).

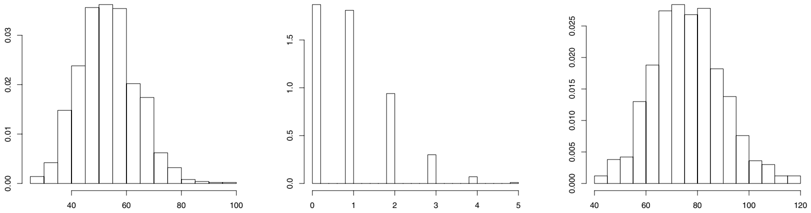

Fig. 14.5 Histogram of the estimated predictive distribution of F_{21} (*left*), MR_{21} (*middle*), and Mr_{21} (*right*), when $\mathscr{F}\mathscr{M}_{20}$ is observed.

Remark 14.1. To carry out the simulation study, we used the statistical computing and graphics language and environment **R** ("GNU S") (see [12]).

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Part V
Applications in Epidemiology

15

Applications of branching processes to the final size of SIR epidemics

Frank Ball and Peter Neal

Abstract This paper considers applications of branching processes to a model for the spread of an SIR (susceptible → infective → removed) epidemic among a closed, homogeneously mixing population, consisting initially of m infective and n susceptible individuals. Each infective remains infectious for a period sampled independently from an arbitrary but specified distribution, during which he/she contacts susceptible individuals independently with rate $n^{-1}\lambda$ for each susceptible. The well-known approximation of the early stages of this epidemic model by a branching process is outlined. The main thrust of the paper is to use branching processes to obtain, when the infectious period is constant, new and probabilistically direct proofs of central limit theorems for the size of an epidemic which becomes established. Two asymptotic situations are considered: (i) many initial infectives, where m and n both become large, for which establishment is asymptotically certain; and (ii) few initial infectives, where m is held fixed and only n becomes large, for which asymptotically establishment is not certain and may not be possible. The model with constant infectious periods is closely related to the Erdös-Rényi random graph and our methodology provides an alternative proof of the central limit theorem for the size of the giant component in that graph.

Mathematics Subject Classification (2000): 92D30, 60J80, 60F05, 05C80

Keywords: SIR epidemics, final outcome of epidemic, susceptibility set, coupling, total progeny of branching process, central limit theorems, random graphs.

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15.1 Introduction

This paper is concerned with applications of branching processes to the following model for the spread of an SIR (susceptible → infective → removed) epidemic among a closed, homogeneously mixing population. Suppose that initially the population comprises m infectives (that have just become infected) and n susceptibles. The infectious periods of infectives are distributed according to a random variable I, having an arbitrary but specified distribution. Throughout its infectious period a given infective makes infectious contact with any given individual at the points of a homogeneous Poisson process with rate $n^{-1}\lambda$. If a contacted individual is susceptible then he/she becomes infected and is immediately able to infect other individuals. If a contacted individual is no longer susceptible then nothing happens. An individual is removed (and plays no further role in the epidemic) when his/her infectious period ends. All infectious periods and Poisson processes describing contacts between individuals are mutually independent. The epidemic ceases as soon as there is no infective present in the population.

By linearly changing the time scale we may assume without loss of generality that $\mathrm{E}[I] = 1$. Denote the epidemic by $E_{n,m}$. Important special cases are (a) when I follows the exponential distribution with mean 1 and (b) when $I \equiv 1$ (i.e. $\mathrm{P}(I = 1) = 1$). In (a), the model becomes a continuous-time Markov chain, the so-called general stochastic epidemic (see e.g. Bailey [4], Chap. 6) – this is by far the most studied epidemic model. In (b), the final size of the epidemic (i.e. the number of susceptibles that are ultimately infected) has the same distribution as that of the Reed–Frost epidemic – a discrete time Markov chain model in which infectious individuals infect susceptibles independently, each with probability $p = 1 - \mathrm{e}^{-\lambda}$ (see e.g. Bailey [4], Chap. 14).

Suppose that the initial number of infectives m is small and the initial number of susceptibles n is large. Then in the early stages of the epidemic it is very likely that each infectious contact is with a susceptible. (Note that an equivalent description of the infection process is that an infective makes contacts according to a Poisson process with rate λ and each contact is sampled uniformly and independently from the n initial susceptibles.) It follows that at the start of an epidemic, the process of infectives may be approximated by a branching process. This approximation has a long history going back to Bartlett [16] and Kendall [25], and it leads to a threshold theorem for the epidemic (see Whittle [37] and Williams [38] in the context of the general stochastic epidemic). The approximation is made exact in Metz [27], Ball [5] and Ball and Donnelly [6] by considering a sequence of epidemics, indexed by n, and proving convergence to the branching process as $n \longrightarrow \infty$.

Let R be the number of contacts made by a typical infective in $E_{n,m}$, so

$$\mathrm{P}(R = k) = (-\lambda)^k \phi_I^{(k)}(\lambda)/k! \quad (k = 0, 1, \ldots),$$

where $\phi_I(\theta) = E[\mathrm{e}^{-\theta I}]$ $(\theta \geq 0)$ is the moment-generating function of R and $\phi_I^{(k)}$ denotes the kth derivative of ϕ_I. Let $R_0 = \mathrm{E}[R] = \lambda$ and let Z denote the total progeny of the above branching process. (Throughout this paper total progeny excludes the initial ancestors.) Then, see e.g. Jagers [24], Theorem 2.11.2,

$$\mathrm{P}(Z=k)=\frac{m}{m+k}\mathrm{P}(R_1+R_2+\cdots+R_{m+k}=k) \quad (k=0,1,\ldots), \tag{15.1}$$

where $R_1, R_2, \ldots$, are independent and identically distributed (i.i.d.) copies of R. Note that $\mathrm{P}(Z<\infty)<1$ if and only if $R_0>1$, so R_0 is a threshold parameter for the epidemic model, in the sense that if n is large and m small, the epidemic can become established with non-zero probability only if $R_0>1$. The parameter R_0 is called the basic reproduction number, see e.g. Heesterbeek and Dietz [23].

The above branching process approximation yields information concerning epidemics that die out quickly (corresponding to extinction of the branching process) but it says little concerning major epidemics, i.e. ones that become established. Consider first the case when there are many initial infectives, specifically the sequence of epidemics E_{n,m_n} $(n=1,2,\ldots)$, where $n^{-1}m_n\to\mu>0$ as $n\to\infty$. Let Z_n denote the final size of E_{n,m_n} and $Z'_n=Z_n+m_n$. Then, see e.g. Andersson and Britton [2], Theorem 4.1,

$$n^{-1}Z'_n\xrightarrow{D}\tau \quad \text{as} \quad n\to\infty, \tag{15.2}$$

where τ is the unique positive solution of

$$1+\mu-\tau=\mathrm{e}^{-\lambda\tau}, \tag{15.3}$$

and

$$n^{-\frac{1}{2}}(Z'_n-n\tau)\xrightarrow{D}N(0,\sigma^2) \quad \text{as} \quad n\to\infty, \tag{15.4}$$

where

$$\sigma^2=\frac{\rho(1-\rho)+\lambda^2\tau\rho^2\,\mathrm{var}(I)}{(1-\lambda\rho)^2} \quad \text{with} \quad \rho=1+\mu-\tau, \tag{15.5}$$

$\xrightarrow{D}$ denotes convergence in distribution and $N(0,\sigma^2)$ denotes the normal distribution with mean zero and variance σ^2.

Suppose instead that there are few initial infectives, i.e. $m_n=m$ for all n, so the initial number of infectives is held fixed as $n\to\infty$. Then $Z_n\xrightarrow{D}Z$ as $n\to\infty$ (Ball [5]). If $R_0\le 1$ then $\mathrm{P}(Z<\infty)=1$, so only minor epidemics occur in the limit as $n\to\infty$. If $R_0>1$ then $\mathrm{P}(Z<\infty)=\pi^m$, where π is the extinction probability of the branching process assuming one initial ancestor. Thus, for large n, the probability that the epidemic becomes established is approximately $1-\pi^m$. Further, see e.g. Andersson and Britton [2], Theorem 4.2, *conditional upon the epidemic becoming established*,

$$n^{-1}Z_n\xrightarrow{D}\tau \quad \text{as} \quad n\to\infty, \tag{15.6}$$

where now τ is the non-zero solution of

$$1-\tau=\mathrm{e}^{-\lambda\tau}, \tag{15.7}$$

and

$$n^{-\frac{1}{2}}(Z_n - n\tau) \xrightarrow{D} N(0,\sigma^2) \quad \text{as} \quad n \to \infty, \tag{15.8}$$

where σ^2 is given by (15.5) with $\mu = 0$.

There are several, markedly different proofs of the above central limit theorems. It was first proved for the general stochastic epidemic with many initial infectives by Nagaev and Startsev [28], by exploiting an embedded random walk, and subsequently by Watson [35], using a random time scale transformation, and by Watson [36], using a martingale argument. Other proofs for this case include those based on rigorous diffusion approximations to continuous-time Markov jump processes (e.g. Barbour [12] and Ethier and Kurtz [21], Chap. 11). Watson [36] considered also the case of few initial infectives. The first proof of (15.4) and (15.8) for the Reed–Frost epidemic was by von Bahr and Martin-Löf [3], via a rather technical analysis using a family of martingales based on harmonic functions for the discrete-time Markov chain which describes that model. These authors also considered a randomised version of the Reed–Frost model, which extends their proof to the general stochastic epidemic and indeed to the model $E_{n,m}$. Martin-Löf [26] proved (15.4) and (15.8) for an even more general Reed–Frost model, by exploiting an embedded random walk that is similar to that used by Dwass [19] for studying the total progeny of a Galton–Watson process. Another proof of (15.4) and (15.8) for $E_{n,m}$ is via the elegant embedding construction of Scalia-Tomba [33, 34]. This latter method is widely applicable, e.g. to multitype epidemics among a population of households (Ball and Lyne [7]) and to epidemics on random networks incorporating casual contacts (Ball and Neal [9, 10]).

The main aim of the present paper is to use ideas developed recently in Ball and Neal [10] to give new, probabilistically direct proofs of the above central limit theorems in the case when $I \equiv 1$, i.e. for the Reed–Frost epidemic. The case when the infectious period I follows any specified distribution with finite variance will be considered in a separate paper (Ball and Neal [11]), within the framework of the collective Reed–Frost model (Picard and Lèfevre [31]) that is equivalent to the general Reed–Frost model of Martin-Löf [26].

As discussed for example by Barbour and Mollison [13], the Reed–Frost model is closely related to the Erdös-Rényi random graph (see e.g. Durrett [18], Chap. 2), in which there are n vertices and between any distinct pair of vertices an edge is present independenty with probability p. Suppose that $p = \lambda/n$. Then, as $n \to \infty$, if $\lambda < 1$, all connected components of the graph are small, whilst if $\lambda > 1$, there is precisely one large connected component, called the giant component, with all other connected components being small. The size of the giant component has the same distribution as the size of a major epidemic in the Reed–Frost model with few initial infectives. Thus our methods give an alternative proof of the central limit theorem for the size of the giant component (cf. Pittel [32] and Barrez et al. [15]).

The remainder of the paper is organised as follows. Approximation of the early stages of an epidemic by a branching process is considered briefly in Sect. 15.2, where results required for analysing the final outcome of a major epidemic when there are few initial infectives are developed. Central limit theorems for the final size of a major epidemic for the Reed–Frost model are proved in Sect. 15.3.

15.2 Early stages of epidemic

We use the construction of Ball and Donnelly [6] to define a sequence of epidemics $E_{n,m}$ $(n = 1,2,\ldots)$, where m is held fixed, on a common probability space. Let $(\Omega_1, \mathscr{F}_1, \mathrm{P}_1)$ be a probability space on which is defined a realisation of a general (Crump–Mode–Jagers) branching process, $\mathscr{B}$ say, having m initial ancestors, in which a typical individual lives until age distributed according to I during which he/she has one offspring at each of the points of a homogeneous Poisson process with rate λ. Let $(\Omega_2, \mathscr{F}_2, \mathrm{P}_2)$ be a probability space on which is defined, for each $n = 1,2,\ldots$, i.i.d. random variables $\xi_1^n, \xi_2^n, \ldots$, that are uniformly distributed on the integers $1,2,\ldots,n$.

For $n = 1,2,\ldots$, a realisation of the epidemic $E_{n,m}$ can be defined on the product space $(\Omega, \mathscr{F}, \mathrm{P}) = (\Omega_1 \times \Omega_2, \mathscr{F}_1 \times \mathscr{F}_2, \mathrm{P}_1 \times \mathrm{P}_2)$ as follows. Label the initial susceptibles $1,2,\ldots,n$. Births in $\mathscr{B}$ correspond to infectious contacts in $E_{n,m}$. For the kth birth in $\mathscr{B}$, the individual contacted in $E_{n,m}$ is ξ_k^n. If the contacted individual is susceptible then he/she becomes infected in $E_{n,m}$ and makes infectious contacts according to the corresponding individual in $\mathscr{B}$. If the contacted individual is not susceptible then that contact, together with any descendants of the corresponding individual in $\mathscr{B}$, is ignored in $E_{n,m}$.

Let Z denote the total progeny of $\mathscr{B}$ and, for $n = 1,2,\ldots$, let Z_n denote the final size of $E_{n,m}$. Let $M_n = \min\{k \geq 2\colon \xi_k^n \in \{\xi_1^n, \xi_2^n, \ldots, \xi_{k-1}^n\}\}$. The key observation is that $\mathscr{B}$ and $E_{n,m}$ coincide up until, but not including, the M_nth birth in $\mathscr{B}$. Thus, for $k = 0,1,\ldots$,

$$\begin{aligned}\mathrm{P}(Z_n = k) &= \mathrm{P}(Z_n = k, M_n > k) + \mathrm{P}(Z_n = k, M_n \leq k)\\ &= \mathrm{P}(Z = k, M_n > k) + \mathrm{P}(Z_n = k, M_n \leq k),\end{aligned}$$

whence

$$|\mathrm{P}(Z_n = k) - \mathrm{P}(Z = k)| \leq \mathrm{P}(M_n \leq k).$$

Now, for $k = 2,3,\ldots$,

$$\mathrm{P}(M_n \leq k) = 1 - \prod_{i=1}^{k-1}\left(1 - \frac{i}{n}\right) \leq \frac{k(k-1)}{2n}. \tag{15.9}$$

Thus, $\lim_{n\to\infty} \mathrm{P}(Z_n = k) = \mathrm{P}(Z = k)$ $(k = 0,1,\ldots)$, i.e. $Z_n \xrightarrow{D} Z$ as $n \to \infty$. The distribution of Z is defective (i.e. has a mass at ∞) if $\mathscr{B}$ is supercritical.

Note that (15.9) implies that $\lim_{n\to\infty} \mathrm{P}(M_n \leq n^\delta) = 0$ for any $\delta \in (0, \frac{1}{2})$. Thus, for such δ and large n, the total variation distance between $E_{n,m}$ and $\mathscr{B}$ remains small until n^δ individuals have been infected in $E_{n,m}$. (Using a different approach, Barbour and Utev [14] show for the Reed–Frost epidemic that this holds for any $\delta < \frac{2}{3}$.) Further, $n^{-\frac{1}{2}} M_n \xrightarrow{D} M$ as $n \to \infty$, where M has probability density function $f(x) = x\mathrm{e}^{-\frac{1}{2}x^2}$ $(x > 0)$ (see e.g. Aldous [1], p. 96), so (Ball and Donnelly [6], Theorem 2.1) the Skorokhod representation theorem can be invoked to define ξ_i^n $(n, i = 1,2,\ldots)$

such that $M_n \overset{a.s.}{\to} M$ as $n \to \infty$, where $\overset{a.s.}{\to}$ denotes almost sure convergence. Hence, $E_{n,m}$ $(n = 1,2,\dots)$ and $\mathscr{B}$ can be coupled so that almost surely, for any $\delta < \frac{1}{2}$, $E_{n,m}$ and $\mathscr{B}$ coincide up until n^δ individuals have been infected in $E_{n,m}$ for all sufficiently large n, whence $Z_n \overset{a.s.}{\to} Z$ as $n \to \infty$.

The above convergence of Z_n to Z can be used to give a threshold theorem for the epidemic $E_{n,m}$ (Williams [38], Ball [5] and Ball and Donnelly [6]). Specifically, a *major epidemic* is said to occur if in the limit as $n \to \infty$ the epidemic infects infinitely many individuals. Standard branching process theory then yields (i) that a major epidemic occurs with non-zero probability if and only if $R_0 > 1$; and (ii) the probability that a major epidemic occurs.

For $\varepsilon \in (0,1)$, let $\mathscr{B}_\varepsilon$ denote the branching process obtained from $\mathscr{B}$ by aborting births independently with probability ε and let Z_ε denote the total progeny of $\mathscr{B}_\varepsilon$. Note that if $E_{n,m}$ infects $\leq n\varepsilon$ individuals then the above construction can be extended so that almost surely $E_{n,m}$ is bounded between $\mathscr{B}_\varepsilon$ and $\mathscr{B}$, whence

$$\mathrm{P}(Z_\varepsilon \geq n\varepsilon) \leq \mathrm{P}(Z_n \geq n\varepsilon) \leq \mathrm{P}(Z \geq n\varepsilon). \tag{15.10}$$

This is the key idea underlying Whittle's [37] stochastic epidemic threshold theorem. Let $g(n)$ be any non-decreasing sequence of positive numbers satisfying $\lim_{n\to\infty} n^{-1}g(n) = 0$. Then the right-hand inequality in (15.10) implies that

$$\limsup_{n\to\infty} \mathrm{P}(Z_n \geq g(n)) \leq \lim_{n\to\infty} \mathrm{P}(Z \geq g(n)) = \mathrm{P}(Z = \infty) \tag{15.11}$$

and, for any $\varepsilon \in (0,1)$, since $g(n) < n\varepsilon$ for all sufficiently large n, the left-hand inequality in (15.10) implies that

$$\liminf_{n\to\infty} \mathrm{P}(Z_n \geq g(n)) \geq \lim_{n\to\infty} \mathrm{P}(Z_\varepsilon \geq g(n)) = \mathrm{P}(Z_\varepsilon = \infty). \tag{15.12}$$

Letting $\varepsilon \downarrow 0$ in (15.12) and using (15.11) yields

$$\lim_{n\to\infty} \mathrm{P}(Z_n \geq g(n)) = \mathrm{P}(Z = \infty). \tag{15.13}$$

The above definition of a major epidemic is not very practical. Instead we say that a realisation of $E_{n,m}$ is a major epidemic if it infects at least $\log n$ susceptibles. Let $G_n = \{Z_n \geq \log n\}$. Then (15.13) implies that $\lim_{n\to\infty} \mathrm{P}(G_n) = \mathrm{P}(Z = \infty)$, so this definition of a global epidemic is asymptotically equivalent to the previous one. Equation (15.13) also implies that for, any $\delta \in (0,1)$, $\lim_{n\to\infty} \mathrm{P}(Z_n \geq n^\delta \mid G_n) = 1$. Thus, asymptotically, a major epidemic infects at least n^δ individuals, for any $\delta < 1$.

15.3 Final outcome of Reed–Frost epidemic

15.3.1 Preliminaries

15.3.1.1 Susceptibility sets

Consider the epidemic $E_{n,m}$. Label the m initial infectives $-(m-1),-(m-2),\ldots,0$, and the n susceptibles $1,2,\ldots,n$. Let $\mathscr{N}=\{-(m-1),-(m-2),\ldots,n\}$, $\mathscr{I}_0=\{-(m-1),-(m-2),\ldots,0\}$ and $\mathscr{X}_0=\{1,2,\ldots,n\}$ denote respectively the entire population, the set of initial infectives and the set of initial susceptibles. Let $\mathscr{G}$ denote the random directed graph on $\mathscr{N}$, in which for any distinct $i,j\in\mathscr{N}$ there is a directed edge from i to j if and only if i, if infected, makes infectious contact with j. Thus $\mathscr{G}$ is constructed as follows. For $i\in\mathscr{N}$, let I_i denote individual i's infectious period if they were to become infected. Then, given $I_i=t$, the edge from i to j is present with probability $1-e^{-\frac{\lambda t}{n}}$, independently for $j\in\mathscr{N}\setminus\{i\}$.

For distinct $i,j\in\mathscr{N}$, write $i\rightsquigarrow j$ if and only if there is a chain of directed edges from i to j. Then the set of initial susceptibles who are ultimately infected by the epidemic is given by $\{i\in\mathscr{X}_0\colon j\rightsquigarrow i \text{ for some } j\in\mathscr{I}_0\}$. Note that this set does not depend on the times of the potential infections; see Pellis et al. [30] for a recent discussion. For $i\in\mathscr{X}_0$, define the *susceptibility set* of individual i by $\mathscr{S}_i=\{j\in\mathscr{N}\setminus\{i\}\colon j\rightsquigarrow i\}$ (see e.g. Ball and Lyne [7] and Ball and Neal [8]). Thus i becomes infected by the epidemic if and only if $\mathscr{S}_i\cap\mathscr{I}_0\neq\emptyset$.

15.3.1.2 Mean and variance of final size

For $i\in\mathscr{X}_0$, let $S_i=|\mathscr{S}_i|$ denote the cardinality of $\mathscr{S}_i$ and $\chi_i=1_{\{\mathscr{S}_i\cap\mathscr{I}_0\neq\emptyset\}}$, the indicator function of the event $\{\mathscr{S}_i\cap\mathscr{I}_0\neq\emptyset\}$ (i.e. of the event that i is infected by the epidemic). Then the final size Z_n of the epidemic is given by

$$Z_n=\sum_{i=1}^{n}\chi_i. \tag{15.14}$$

Note that, by symmetry, the random variables $\chi_1,\chi_2,\ldots,\chi_n$ are exchangeable and, for $i=1,2,\ldots,n$,

$$\mathrm{P}(\chi_i=1\mid S_i=l)=1-\theta_0^{n,m}(l)\quad(l=0,1,\ldots,n+m-1),$$

where $\theta_0^{n,m}(0)=1$, $\theta_0^{n,m}(l)=0$ if $l\geq n$ and

$$\theta_0^{n,m}(l)=\frac{\binom{n-1}{l}}{\binom{n+m-1}{l}}=\prod_{i=1}^{l}\left(\frac{n-i}{n+m-i}\right)\quad(l=1,2,\ldots,n-1).$$

By (15.14) and exchangeability, it follows that

$$\mathrm{E}[Z_n] = n\mathrm{E}[\chi_1] = n(1 - \mathrm{E}[\theta_0^{n,m}(S_1)]). \tag{15.15}$$

Further, using (15.14) and exchangeability,

$$\begin{aligned} \mathrm{var}(Z_n) &= n\,\mathrm{var}(\chi_1) + n(n-1)\mathrm{cov}(\chi_1, \chi_2) \\ &= n\mathrm{E}[\chi_1](1 - E[\chi_1]) + n(n-1)\mathrm{cov}(1-\chi_1, 1-\chi_2). \end{aligned} \tag{15.16}$$

Now,

$$\begin{aligned} \mathrm{cov}(1-\chi_1, 1-\chi_2) &= \mathrm{P}(\chi_1 = 0, \chi_2 = 0) - \mathrm{P}(\chi_1 = 0)\mathrm{P}(\chi_2 = 0) \\ &= \mathrm{E}[\mathrm{P}(\chi_1 = 0 \mid \mathscr{S}_1)\{\mathrm{P}(\chi_2 = 0 \mid \chi_1 = 0, \mathscr{S}_1) - \mathrm{P}(\chi_2 = 0)\}] \end{aligned} \tag{15.17}$$

and

$$\begin{aligned} \mathrm{P}(\chi_2 = 0 \mid \chi_1 = 0, \mathscr{S}_1) &= \mathrm{P}(\chi_2 = 0 \mid \chi_1 = 0, \mathscr{S}_1, 2 \in \mathscr{S}_1)\mathrm{P}(2 \in \mathscr{S}_1 \mid \chi_1 = 0, \mathscr{S}_1) \\ &+ \mathrm{P}(\chi_2 = 0 \mid \chi_1 = 0, \mathscr{S}_1, 2 \notin \mathscr{S}_1)\mathrm{P}(2 \notin \mathscr{S}_1 \mid \chi_1 = 0, \mathscr{S}_1). \end{aligned} \tag{15.18}$$

By symmetry,

$$\mathrm{P}(2 \in \mathscr{S}_1 \mid \chi_1 = 0, \mathscr{S}_1) = \frac{S_1}{n-1} \tag{15.19}$$

and, if $2 \in \mathscr{S}_1$ then $\mathscr{S}_2 \subseteq \mathscr{S}_1$, so

$$\mathrm{P}(\chi_2 = 0 \mid \chi_1 = 0, \mathscr{S}_1, 2 \in \mathscr{S}_1) = 1. \tag{15.20}$$

Let $\mathscr{S}_{2\setminus 1} = \mathscr{S}_2 \setminus (\mathscr{S}_1 \cup \{1\})$ and $S_{2\setminus 1} = |\mathscr{S}_{2\setminus 1}|$. If $\chi_1 = 0$ and $2 \notin \mathscr{S}_1$, then $S_1 \le n-2$. Therefore, by symmetry, for $k = 0, 1, \ldots, n-2$ and $l = 0, 1, \ldots, n+m-k-2$,

$$\mathrm{P}(\chi_2 = 0 \mid \chi_1 = 0,\, S_1 = k,\, S_{2\setminus 1} = l,\, 2 \notin \mathscr{S}_1) = \theta_{k+1}^{n,m}(l),$$

where, for $k = 0, 1, \ldots, n-1$, $\theta_k^{n,m}(0) = 1$, $\theta_k^{n,m}(l) = 0$ if $l \ge n-k$ and

$$\begin{aligned} \theta_k^{n,m}(l) &= \frac{\binom{n-k-1}{l}}{\binom{n+m-k-1}{l}} \\ &= \prod_{i=1}^{l} \left(\frac{n-k-i}{n+m-k-i} \right) \quad (l = 1, 2, \ldots, n-k-1). \end{aligned}$$

Thus,

$$\mathrm{P}(\chi_2 = 0 \mid \chi_1 = 0, \mathscr{S}_1) = \frac{S_1}{n-1} + \left(1 - \frac{S_1}{n-1}\right)\mathrm{E}[\theta_{S_1+1}^{n,m}(S_{2\setminus 1}) \mid S_1]. \tag{15.21}$$

Substituting (15.18) to (15.21) into (15.17) yields

$$\begin{aligned}\operatorname{cov}(1-\chi_1,1-\chi_2) &= \frac{1}{n-1}\mathrm{E}[\theta_0^{n,m}(S_1)S_1(1-\mathrm{E}[\theta_0^{m,n}(S_2)])] \\ &\quad+\mathrm{E}[\theta_0^{n,m}(S_1)\{\mathrm{E}[\theta_{S_1+1}^{n,m}(S_{2\setminus 1}) \mid S_1]-\mathrm{E}[\theta_0^{n,m}(S_2)]\}] \\ &\quad-\frac{1}{n-1}\mathrm{E}[\theta_0^{n,m}(S_1)S_1\{\mathrm{E}[\theta_{S_1+1}^{n,m}(S_{2\setminus 1}) \mid S_1]-\mathrm{E}[\theta_0^{n,m}(S_2)]\}] \\ &= \frac{1}{n-1}(A_n+B_n-C_n), \quad \text{say.} \end{aligned} \tag{15.22}$$

We now restrict attention to the case when the infectious period $I \equiv 1$. Note that in this case $\mathscr{G}$ is the random directed graph in which for any ordered pair (i,j) of distinct vertices there is a directed edge from i to j with probability $1-\mathrm{e}^{-\frac{\lambda}{n}}$, independently for different ordered pairs (This is not the case if I is not constant since the presence/absence of edges from a given individual, i say, are correlated through i's infectious period.) It follows that S_1 has the same distribution as the final size of an epidemic with 1 initial infective and $m+n-1$ initial susceptibles and hence can be approximated by the total progeny of a Galton–Watson process with 1 initial ancestor and a Poisson offspring distribution, cf. Sect. 15.2.

We consider a sequence of epidemics E_{n,m_n}, indexed by the initial number of susceptibles n and study two asymptotic regimes; namely (i) *many initial infectives*, in which $\mu_n = n^{-1}m_n \to \mu > 0$ as $n \to \infty$ and (ii) *few initial infectives*, in which $m_n = m$ $(n=1,2,\ldots)$, where m is fixed. Note that under (i), the offspring distribution of the above-mentioned approximating Galton–Watson process for S_1 has mean $\lambda(1+\mu)$, whereas under (ii) it has mean λ. We now use superfixes to show explicitly the dependence of quantities such as $\mathscr{S}_1$, $S_{2\setminus 1}$ and χ_1 on n, i.e. we write $\mathscr{S}_1^n$, $S_{2\setminus 1}^n$ and χ_1^n etc.

Before proceeding, it is useful to give some results concerning the quantities $\theta_k^{n,m}(l)$, whose proofs are elementary and hence omitted. For $k=0,1,\ldots,n$, let

$$\theta_k^{n,m} = \frac{n-k}{n+m-k},$$

and, for $k=0,1,\ldots,n-1$ and $l=0,1,\ldots,n-k-1$, let

$$R_{k,1}^{n,m}(l) = \frac{m}{n-k}\sum_{i=1}^{l}\frac{i}{n+m-k-i}$$

and

$$R_{k,2}^{n,m}(l) = \left(\frac{m}{n-k}\right)^2 \sum_{\substack{i=1 \\ i\neq j}}^{l}\sum_{j=1}^{l}\frac{ij}{(n+m-k-i)(n+m-k-j)},$$

where a sum is zero if vacuous. Then, for $k=0,1,\ldots,n-1$ and $l=0,1,\ldots,n-k-1$,

$$(\theta_k^{n,m})^l(1-R_{k,1}^{n,m}(l)) \le \theta_k^{n,m}(l) \le (\theta_k^{n,m})^l \tag{15.23}$$

and

$$(\theta_k^{n,m})^l(1-R_{k,1}^{n,m}(l)) \leq \theta_k^{n,m}(l) \leq (\theta_k^{n,m})^l(1-R_{k,1}^{n,m}(l)+R_{k,2}^{n,m}(l)). \tag{15.24}$$

15.3.2 Many initial infectives

15.3.2.1 Limiting mean final size

Let $\mathscr{B}(\lambda)$ denote a Galton–Watson process with one initial ancestor whose offspring distribution is Poisson with mean λ. For $n = 1,2,\ldots$, we construct coupled realisations of the susceptibility set $\mathscr{S}_1^n$ and its approximating branching process, $\mathscr{B}_1^n$ say, as follows. Let $(\Omega,\mathscr{F},\mathrm{P})$ be a probability space on which, for each n, is defined a realisation $\mathscr{B}_1^n$ of $\mathscr{B}(\lambda(1+\mu_n))$ and a sequence of i.i.d. random variables $\eta_1^n,\eta_2^n,\ldots$ that are uniformly distributed on $\mathscr{N}^n = \{-(m_n-1),-(m_n-2),\ldots,n\}$. The susceptibility set $\mathscr{S}_1^n$ is constructed in the obvious fashion. Set $\eta_0^n = 1$ and label the individuals in $\mathscr{B}_1^n$ (excluding the initial ancestor) $1,2,\ldots$, in the order in which they are born, splitting ties so that siblings have consecutive labels. Then $\mathscr{S}_1^n$ follows $\mathscr{B}_1^n$ except that whenever $\eta_i^n \in \{\eta_0^n,\eta_1^n,\ldots,\eta_{i-1}^n\}$ individual i in $\mathscr{B}_1^n$, together with all of its descendants in $\mathscr{B}_1^n$, are ignored in $\mathscr{S}_1^n$. For $n = 1,2,\ldots$, let $M_n = \min\{i \geq 1\colon\ \eta_i^n \in \{\eta_0^n,\eta_1^n,\ldots,\eta_{i-1}^n\}\}$. Thus, as in Sect. 15.2, $\mathscr{S}_1^n$ and $\mathscr{B}_1^n$ coincide up until but not including the M_nth birth in $\mathscr{B}_1^n$.

Note that $\theta_0^{n,m_n} \to \theta = (1+\mu)^{-1} < 1$ as $n \to \infty$, so there exists $\varepsilon < 1$ such that $\theta_0^{n,m_n} < \varepsilon$ for all sufficiently large n. Hence, if $g(n)$ is any increasing strictly positive function that tends to infinity as $n \to \infty$ then, using (15.23),

$$\lim_{n\to\infty} \mathrm{E}[\theta_0^{n,m_n}(S_1^n)1_{\{S_1^n>g(n)\}}] \leq \lim_{n\to\infty} \varepsilon^{g(n)} = 0,$$

whence, from (15.15),

$$\lim_{n\to\infty} n^{-1}\mathrm{E}[Z_n] = 1 - \lim_{n\to\infty} \mathrm{E}\left[\theta_0^{n,m_n}(S_1^n)1_{\{S_1^n\leq g(n)\}}\right]. \tag{15.25}$$

Let $W(\lambda)$ be the total progeny of $\mathscr{B}(\lambda)$ and $h(\lambda,s) = \mathrm{E}[s^{W(\lambda)}]$ $(\lambda > 0,\ 0 \leq s \leq 1)$. For $n = 1,2,\ldots$, let W_1^n be the total progeny of $\mathscr{B}_1^n$, and let W_1 be distributed as $W(\lambda(1+\mu))$. Then, arguing as in Sect. 15.2, for $k = 0,1,\ldots$,

$$\begin{aligned}\lim_{n\to\infty} \mathrm{P}(S_1^n = k) &= \lim_{n\to\infty} \mathrm{P}(W_1^n = k)\\ &= \mathrm{P}(W_1 = k),\end{aligned} \tag{15.26}$$

where the last equality follows using (15.1), since $\mu_n \to \mu$ as $n \to \infty$.
Take $g(n) = \log n$. Now, (15.23) implies that $\theta_0^{n,m_n}(l) \to \theta^l$ as $n \to \infty$, uniformly for $l = 0,1,\ldots,g(n)$, whence (15.25) and (15.26) imply

$$\lim_{n\to\infty} n^{-1}\mathrm{E}[Z_n] = 1 - h(\lambda(1+\mu),\theta). \tag{15.27}$$

For $\lambda > 0$, let $f(\lambda,s) = \exp(-\lambda(1-s))$ $(0 \le s \le 1)$ be the probability generating function of the Poisson distribution with mean λ. Then by a standard result for Galton–Watson processes (cf. Jagers [24], Sect. 2.11), $h(\lambda,s)$ is the unique solution in $[0,1]$ of

$$h(\lambda,s) = f(\lambda, sh(\lambda,s)). \tag{15.28}$$

Let $\tau = \lim_{n\to\infty} n^{-1}(m_n + \mathrm{E}[Z_n])$. Then (15.27) implies that $\tau = \mu + 1 - h(\lambda(1+\mu),\theta)$. Using (15.28) and recalling that $\theta = (1+\mu)^{-1}$ then yields that τ is the unique positive solution of $1+\mu-\tau = \mathrm{e}^{-\lambda\tau}$, agreeing with (15.3).

15.3.2.2 Limiting variance final size

First note, using (15.16) and (15.27), that

$$\begin{aligned}\lim_{n\to\infty} \mathrm{var}(\chi_1^n) &= h(\lambda(1+\mu),\theta)[1-h(\lambda(1+\mu),\theta)] \\ &= \rho(1-\rho),\end{aligned} \tag{15.29}$$

where $\rho = h(\lambda(1+\mu),\theta) = 1+\mu-\tau$.

To determine $\lim_{n\to\infty}(n-1)\mathrm{cov}(1-\chi_1^n, 1-\chi_2^n)$, we consider separately the three terms on the right hand side of (15.22).

First note that

$$\begin{aligned}\lim_{n\to\infty} A_n &= \lim_{n\to\infty} \mathrm{E}[\theta_0^{n,m_n}(S_1^n)S_1^n](1-h(\lambda(1+\mu),\theta)) \\ &= \mathrm{E}[\theta^{W_1}W_1](1-h(\lambda(1+\mu),\theta)) \\ &= \theta h_s(\lambda(1+\mu),\theta)(1-h(\lambda(1+\mu),\theta)),\end{aligned} \tag{15.30}$$

where $h_s(\lambda,s)$ denotes $\frac{\partial h}{\partial s}(\lambda,s)$. (Note that $\sup_{k\ge 0} k\varepsilon^k < \infty$, so the random variables $\theta_0^{n,m_n}(S_1^n)S_1^n$ $(n = 1,2,\ldots)$ are uniformly bounded, and with $[x]$ denoting the greatest integer $\le x$, $\lim_{n\to\infty}\mathrm{E}[\theta_0^{n,m_n}(S_1^n)S_1^n 1_{\{S_1^n > \log n)\}}] \le \lim_{n\to\infty}\sum_{i=[\log n]}^{\infty} i\varepsilon^i = 0$.)

For the other two terms, it is convenient to let $\mathscr{S}_{2\backslash 1}^n(k) = \mathscr{S}_{2\backslash 1}^n \mid S_1^n = k, \chi_1^n = 0$ $(k = 0,1,\ldots)$ and, for fixed k, construct coupled realisations of $\mathscr{S}_2^n$, $\mathscr{S}_{2\backslash 1}^n(k)$ and their approximating branching processes as follows. Let $(\Omega, \mathscr{F}, \mathrm{P})$ be a probability space on which, for each n, is defined a realisation $\mathscr{B}_2^n$ of $\mathscr{B}(\lambda(1+\mu_n))$ and a sequence of i.i.d. random variables $\eta_1^n, \eta_2^n, \ldots$ that are uniformly distributed on $\mathscr{N}^n$. The susceptibility set $\mathscr{S}_2^n$ is constructed like $\mathscr{S}_1^n$ in Section 15.3.2.1, except now $\eta_0^n = k+2$. The set $\mathscr{S}_{2\backslash 1}^n(k)$ is constructed in the same fashion, except individual i (and all of its descendants) in $\mathscr{B}_2^n$ is also deleted if $\eta_i^n \in A_k = \{1,2,\ldots,k+1\}$. Finally, for $n = 1,2,\ldots$, let $\mathscr{B}_2^n(k)$ be the Galton–Watson process obtained from $\mathscr{B}_2^n$ by deleting individual i (and all of its descendants) if $\eta_i^n \in A_k$.

For $n = 1,2,\ldots$, let $M_n = \min\{i \ge 1\colon \eta_i^n \in \{\eta_0^n, \eta_1^n, \ldots, \eta_{i-1}^n\}\}$ and $M_n^A(k) = \min\{i \ge 1\colon \eta_i^n \in A_k\}$. Let W_2^n and $W_2^n(k)$ denote the total progenies of $\mathscr{B}_2^n$ and $\mathscr{B}_2^n(k)$, respectively. Observe that, for $l = 0,1,\ldots$, if $M_n \wedge M_n^A(k) > l$ and $W_2^n = l$, then $S_2^n = S_{2\backslash 1}^n(k) = W_2^n = W_2^n(k)$. (Here, $x \wedge y = \min\{x,y\}$ and $S_{2\backslash 1}^n(k) = |\mathscr{S}_{2\backslash 1}^n(k)|$.)

Thus, considering C_n in (15.22), note that for any $k \le \log n$,

$$\begin{aligned}
&\lim_{n\to\infty} |E[\theta^{n,m_n}_{S_1+1}(S^n_{2\backslash 1})|S^n_1 = k] - \mathrm{E}[\theta^{n,m_n}_0(S^n_2)]| \\
&= \lim_{n\to\infty} |E[\theta^{n,m_n}_{S_1+1}(S^n_{2\backslash 1}(k))1_{\{S^n_{2\backslash 1}\le \log n\}}] - \mathrm{E}[\theta^{n,m_n}_0(S^n_2)1_{\{S^n_2 \le \log n\}}]| \\
&\le \lim_{n\to\infty} [\mathrm{P}(M_n \le \log n) + \mathrm{P}(M^A_n(k) \le \log n)] \\
&\le \frac{\log n(2\log n + 1)}{m_n + n} \to 0 \quad \text{as} \quad n \to \infty,
\end{aligned}$$

whence $C_n \to 0$ as $n \to \infty$.

Turning to $\lim_{n\to\infty} B_n$, let $M^{(2)}_n(k) = \min\{i > M_n \wedge M^A_n(k)\colon\ \eta^n_i \in \{\eta^n_0, \eta^n_1, \ldots, \eta^n_{i-1}\} \cup A_k\}$. Fix k and observe that, for $l = 0, 1, \ldots$, if $M_n > k + l + 2$ then $S^n_2 = l \Leftrightarrow W^n_2 = l$ and $S^n_{2\backslash 1}(k) = l \Leftrightarrow W^n_2(k) = l$; and also, if $M_n \le k + l + 2$ and $M^{(2)}_n(k) > k + l + 2$ (so $M^A_n(k) > k + l + 2$) then again $S^n_2 = l \Leftrightarrow W^n_2 = l$ and $S^n_{2\backslash 1}(k) = l \Leftrightarrow W^n_2(k) = l$. It follows that

$$|\mathrm{P}(S^n_{2\backslash 1}(k) = l) - \mathrm{P}(S^n_2 = l) - (\mathrm{P}(W^n_2(k) = l) - \mathrm{P}(W^n_2 = l))| \le 2\mathrm{P}(M^{(2)}_n(k) \le k + l + 2). \tag{15.31}$$

Let

$$D_n(k) = (n-1)(E[\theta^{n,m_n}_{k+1}(S^n_{2\backslash 1}(k))] - \mathrm{E}[\theta^{n,m_n}_0(S^n_2)]),$$

$$E_n(k) = (n-1)(\mathrm{E}[\theta^{n,m_n}_{k+1}(W^n_2(k))] - \mathrm{E}[\theta^{n,m_n}_0(W^n_2)])$$

and

$$F_n(k) = (n-1)(\mathrm{E}[(\theta^{n,m_n}_{k+1})^{W^n_2(k)}] - \mathrm{E}[(\theta^{n,m_n}_0)^{W^n_2}]).$$

Let $g(n) = (\log n)^2$ and note that $\lim_{n\to\infty} n\varepsilon^{g(n)} = 0$. Also,

$$\mathrm{P}(M^{(2)}_n(k) \le k + l + 2) \le \binom{k+l+2}{2}\left(\frac{k+l+2+k+1}{n+m_n}\right)^2,$$

so $\lim_{n\to\infty}(n-1)\mathrm{P}(M^{(2)}_n(k) \le k + l + 2) = 0$, uniformly for $k, l \le g(n)$. It then follows, using (15.31), that $\lim_{n\to\infty} |D_n(k) - E_n(k)| = 0$, uniformly for $k \le g(n)$. Further, (15.24) implies that

$$\lim_{n\to\infty} |(n-1)[\theta^{n,m_n}_k(l) - \theta^{n,m_n}_0(l) - ((\theta^{n,m_n}_k)^l - (\theta^{n,m_n}_0)^l)]| = 0,$$

uniformly for $k, l \le g(n)$, whence $\lim_{n\to\infty} |E_n(k) - F_n(k)| = 0$, uniformly for $k \le g(n)$.

The offspring distributions of $\mathscr{B}^n_2$ and $\mathscr{B}^n_2(k)$ are Poisson, with means $\lambda(1+\mu_n)$ and $\lambda_n(k) = \lambda(1+\mu_n)(1-(1+k)/(n+m_n))$, respectively. Thus,

$$D_n(k) = (n-1)(h(\lambda_n(k), \theta^{n,m_n}_{k+1}) - h(\lambda(1+\mu_n), \theta^{n,m_n}_0)) + r_n(k),$$

where $\lim_{n\to\infty} r_n(k) = 0$, uniformly for $k \le g(n)$. Note that $\lim_{n\to\infty} n(\lambda_n(k) - \lambda(1+\mu_n)) = -\lambda(1+k)$ and $\lim_{n\to\infty} n(\theta_{k+1}^{n,m_n} - \theta_0^{n,m_n}) = -\frac{\mu(k+1)}{(1+\mu)^2}$ both uniformly for $k \le g(n)$.

Let $h_\lambda(\lambda,s) = \frac{\partial h}{\partial \lambda}(\lambda,s)$ ($\lambda > 0$, $0 \le s \le 1$) and define $h_s(\lambda,s)$ similarly. Application of (bivariate) Taylor's theorem to $h(\lambda,s)$ yields, after some analysis, that

$$\lim_{n\to\infty} D_n(k) = -\lambda(1+k)h_\lambda(\lambda(1+\mu),\theta) - \frac{\mu(1+k)}{(1+\mu)^2}h_s(\lambda(1+\mu),\theta),$$

uniformly for $k \le g(n)$. Finally, it then follows using similar arguments to the derivation of (15.27) that

$$\begin{aligned}\lim_{n\to\infty} B_n &= \lim_{n\to\infty} \mathrm{E}[\theta_0^{n,m_n}(S_1^n)D_n(S_1^n)]\\ &= \lim_{n\to\infty} \mathrm{E}[\theta_0^{n,m_n}(S_1^n)D_n(S_1^n)1_{\{S_1^n \le g(n)\}}]\\ &= -\mathrm{E}[\theta^W(1+W)]g(\lambda,\mu,\theta)\\ &= -[h(\lambda(1+\mu),\theta) + \theta h_s(\lambda(1+\mu),\theta)]g(\lambda,\mu,\theta), \qquad (15.32)\end{aligned}$$

where

$$g(\lambda,\mu,\theta) = \lambda h_\lambda(\lambda(1+\mu),\theta) + \frac{\mu}{(1+\mu)^2}h_s(\lambda(1+\mu),\theta).$$

Differentiating (15.28) yields

$$h_\lambda(\lambda,s) = -\frac{(1-sh(\lambda,s))h(\lambda,s)}{1-\lambda sh(\lambda,s)} \quad \text{and} \quad h_s(\lambda,s) = \frac{\lambda h(\lambda,s)^2}{1-\lambda sh(\lambda,s)}.$$

Recall that $\theta = (1+\mu)^{-1}$ and $\rho = h(\lambda(1+\mu),\theta)$. Equations (15.30) and (15.32) yield that $\lim_{n\to\infty} A_n = \lambda\rho^2(1-\rho)/(1-\lambda\rho)$ and $\lim_{n\to\infty} B_n = \lambda\rho^2(1-\rho)/(1-\lambda\rho)^2$, whence using (15.16), (15.22) and (15.29), and recalling that $\lim_{n\to\infty} C_n = 0$,

$$\lim_{n\to\infty} n^{-1}\,\mathrm{var}(Z_n) = \frac{\rho(1-\rho)}{(1-\lambda\rho)^2}, \qquad (15.33)$$

agreeing with (15.5) (recall that $\mathrm{var}(I) = 0$). The law of large numbers (15.2) follows immediately from (15.27) and (15.33) using Chebyshev's inequality.

15.3.3 Few initial infectives

Recall that m is now held fixed as $n \to \infty$, that G_n is the event that $E_{n,m}$ infects at least $\log n$ individuals and, from the end of Sect. 15.2, that $\lim_{n\to\infty} \mathrm{P}(Z_n \ge n^{\delta_1} \mid G_n) = 1$, for all $\delta_1 < 1$. Thus, we can study major outbreaks by considering the epidemic $E_{n',m'}$, where $m' = [n^{\delta_1}]$ and $n' = n + m - [n^{\delta_1}]$ (Note that m' and n' are implicitly indexed by n.) Elementary analysis shows that, for any $\delta_1, \delta_2 > 0$ and any

$k \le (\log n)^2$,

$$\lim_{n\to\infty} \theta_k^{n',m'}([n^{\delta_2}]) = \begin{cases} 0 \text{ if } \delta_1+\delta_2 > 1, \\ 1 \text{ if } \delta_1+\delta_2 < 1. \end{cases}$$

Further, by the paragraph after Eq. (15.9) in Sect. 15.2, the susceptibility set $\mathscr{S}_1^n$ can be coupled with its approximating branching process $\mathscr{B}_1^n$, so that, given any $\delta_2 < \frac{1}{2}$, for all sufficiently large n they coincide up until n^{δ_2} individuals have been added to the susceptibility set. A similar comment holds for $\mathscr{S}_{2\setminus 1}^n(k)$ and its approximating branching process. Thus, if we choose $\delta_1, \delta_2 \in (0,1)$ so that $\delta_1+\delta_2 > 1$ and $\delta_2 < \frac{1}{2}$, it follows that $\lim_{n\to\infty} \mathrm{P}(\chi_1^n = 0) = \pi(\lambda)$, where $\pi(\lambda)$ denotes the extinction probability of $\mathscr{B}(\lambda)$, and $\lim_{n\to\infty} \left[\mathrm{P}(\chi_2^n = 0 \mid S_1^n = k) - \pi\left(\lambda\left(1-\frac{k+1}{n}\right)\right)\right] = 0$.

Suppose that $\lambda > 1$ and that a major epidemic occurs. Then it follows immediately using (15.15) that

$$\lim_{n\to\infty} n^{-1}\mathrm{E}[Z_n] = 1-\pi(\lambda) \tag{15.34}$$

and

$$\lim_{n\to\infty} \mathrm{var}(\chi_1^n) = \pi(\lambda)(1-\pi(\lambda)). \tag{15.35}$$

Also, using (15.22) and a similar asymptotic analysis to before,

$$\begin{aligned} \lim_{n\to\infty}(n-1)\mathrm{cov}(1-\chi_1^n, 1-\chi_2^n) &= \mathrm{E}[W_1 1_{\{W_1<\infty\}}](1-\pi(\lambda)) \\ &+ \lim_{n\to\infty}(n-1)\mathrm{E}\left[1_{\{W_1<\infty\}}\left\{\pi\left(\lambda\left(1-\frac{W_1+1}{n}\right)\right)-\pi(\lambda)\right\}\right]. \end{aligned}$$

where W_1 is now the total progeny of $\mathscr{B}(\lambda)$.

Let $\tilde{W}_1$ be distributed according to W_1 conditional upon $\mathscr{B}(\lambda)$ going extinct. Then

$$\lim_{n\to\infty}(n-1)\mathrm{cov}(1-\chi_1^n, 1-\chi_2^n) = E[\tilde{W}_1]\pi(\lambda)(1-\pi(\lambda)) - \lambda(E[\tilde{W}_1]+1)\pi(\lambda)\pi'(\lambda), \tag{15.36}$$

where π' denotes the derivative of π with respect to λ.

By standard branching process theory (e.g. Haccou et al. [22], Sect. 5.3), for $\lambda > 1$, $\pi(\lambda)$ is the unique solution in $(0,1)$ of

$$f(\lambda, \pi(\lambda)) = \pi(\lambda). \tag{15.37}$$

Let $\tau = \lim_{n\to\infty} n^{-1}\mathrm{E}[Z_n]$, so (15.34) yields $\tau = 1-\pi(\lambda)$. Recall that $f(\lambda, s) = \exp(-\lambda(1-s))$. Then (15.37) implies that τ is the non-zero solution of $1-\tau = \mathrm{e}^{-\lambda\tau}$, agreeing with (15.7), and (15.35) yields $\lim_{n\to\infty} \mathrm{var}(\chi_1^n) = \rho(1-\rho)$, where $\rho = \pi(\lambda) = 1-\tau$.

Let $p_k(\lambda) = \lambda^k \mathrm{e}^{-\lambda}/k!$ $(k = 0,1,\ldots)$. Then Daly [17] implies that $\tilde{W}_1$ is distributed as the total progeny of a Galton–Watson process with offspring distribution given by $\mathrm{P}(\tilde{Y} = k) = (\pi(\lambda))^{k-1} p_k(\lambda)$ $(k = 0,1,\ldots)$, whence $\mathrm{E}[\tilde{Y}] = f_s(\lambda, \pi(\lambda)) = \lambda f(\lambda, \pi(\lambda)) = \lambda\pi(\lambda) = \lambda\rho$, so $\mathrm{E}[\tilde{W}_1+1] = \sum_{k=0}^{\infty}(\mathrm{E}[\tilde{Y}])^k = (1-\lambda\rho)^{-1}$. Also, differentiating (15.37) yields

$$\pi'(\lambda) = -\frac{\pi(\lambda)(1-\pi(\lambda))}{1-\lambda\pi(\lambda)},$$

whence substitution into (15.36) and using (15.16) gives

$$\begin{aligned}\lim_{n\to\infty} n^{-1}\operatorname{var}(Z_n) &= \rho(1-\rho) + \frac{\lambda\rho^2(1-\rho)}{1-\lambda\rho} + \frac{\lambda\rho^2(1-\rho)}{(1-\lambda\rho)^2} \\ &= \frac{\rho(1-\rho)}{(1-\lambda\rho)^2},\end{aligned}$$

agreeing with (15.8). The law of large numbers (15.6) follows immediately.

15.3.4 Central limit theorem

The central limit theorems (15.4) and (15.8) follow from the preceding results by using the central limit theorem of Peligrad and Utev [29] for an associated sequence of random variables. The random variables $X_1, X_2, \ldots, X_n$ are called *associated* if $\operatorname{cov}(f(X_1,X_2,\ldots,X_n), g(X_1,X_2,\ldots,X_n)) \geq 0$ for any coordinatewise nondecreasing functions $f(x_1,x_2,\ldots,x_n)$ and $g(x_1,x_2,\ldots,x_n)$ for which the covariance is defined (Esary *et al.* [20]).

Consider the random directed graph $\mathscr{G}$ described in Sect. 15.3.1.1. Let $\mathscr{E} = \{(i,j) \in \mathscr{N}^2 : i \neq j\}$ be the set of possible edges and, for $e \in \mathscr{E}$, let ψ_e be the indicator random variable that takes the value one if the directed edge e is present in $\mathscr{G}$ and zero otherwise. For the Reed–Frost epidemic, the random variables $(\psi_e : e \in \mathscr{E})$ are independent, and hence associated. For $i = 1,2,\ldots,n$, χ_i is a nondecreasing function of $(\psi_e : e \in \mathscr{E})$, hence, by property (P_4) of Esary et al. [20], the random variables $\chi_1, \chi_2, \ldots, \chi_n$ are associated.

For $n = 1,2,\ldots$, let $\kappa(n) = [n^{\frac{1}{2}}]$, $\iota(n) = [n/\kappa(n)]$, $Y_i^n = \sum_{j=(i-1)\kappa(n)+1}^{i\kappa(n)} \chi_j^n$ $(i = 1,2,\ldots,\iota(n))$ and $R^n = \sum_{j=\iota(n)\kappa(n)+1}^{n} \chi_j^n$. The results of Sects. 15.3.2 and 15.3.3 imply that, under the two asymptotic regimes considered, $c = \sup_{n\geq 1} \operatorname{var}(\chi_1^n)$ and $d = \sup_{n\geq 1} n \operatorname{cov}(\chi_1^n, \chi_2^n)$ are both finite. It follows that $n^{-1}\operatorname{var}(R^n) \to 0$ as $n \to \infty$, hence $n^{-\frac{1}{2}}(R^n - (n-\kappa(n)\iota(n))\mathrm{E}[\chi_1^n]) \xrightarrow{D} 0$ as $n \to \infty$ and, by Slutsky's theorem, $n^{-\frac{1}{2}}\sum_{i=1}^n(\chi_i^n - n\mathrm{E}[X_1^n])$ and $n^{-\frac{1}{2}}\sum_{i=1}^{\iota(n)}(Y_i^n - \kappa(n)\mathrm{E}[\chi_1^n])$ have the same limiting distribution as $n \to \infty$. Also, $\operatorname{cov}(Y_1^n, Y_2^n) = \kappa(n)^2 \operatorname{cov}(\chi_1^n, \chi_2^n) \leq d\kappa(n)^2/n$ $(n = 1,2,\ldots)$. Thus $n^{-1}\sum_{i=2}^{\iota(n)} \operatorname{cov}(Y_1^n, Y_i^n) \leq d\iota(n)\kappa(n)^2/n^2 \to 0$ as $n \to \infty$. For $n = 1,2,\ldots$, $Y_1^n, Y_2^n, \ldots, Y_{\iota(n)}^n$ are each nondecreasing functions of $(\chi_1^n, \chi_2^n, \ldots, \chi_n^n)$, so $Y_1^n, Y_2^n, \ldots, Y_{\iota(n)}^n$ are associated. Hence, using Theorem 2.3 of Peligrad and Utev [29], which may be extended to a triangular array of random variables (Sergey Utev, personal communication), $n^{-\frac{1}{2}}\sum_{i=1}^{\iota(n)}(Y_i^n - \kappa(n)\mathrm{E}[\chi_1^n])$ converges in distribution to a zero-mean normal distribution as $n \to \infty$, and therefore so does $n^{-\frac{1}{2}}\sum_{i=1}^n(\chi_i^n - \mathrm{E}[\chi_i^n])$. The central limit theorems (15.4) and (15.8) follow immediately.

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16

A branching process approach for the propagation of the Bovine Spongiform Encephalopathy in Great-Britain

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Abstract The goal of this work is the modelling of the propagation of BSE (Bovine Spongiform Encephalopathy) at the scale of a very large population (Great-Britain) in order to predict its extinction time and to evaluate the efficiency of the main feed-ban regulation. To this end, we first elaborated a multitype branching process in discrete time with age and population dependent individual transitions. The types are the health states at each age. Then, assuming that the disease is rare at the initial time, and assuming that the probability for an animal to be exposed to a given infective is inversely proportional to the total population size, we derived from this model, as the initial size of the population increases to ∞, a limit process on the incidence of clinical cases. This limit process may be either considered as a single-type d-Markovian process with a Poissonian transition distribution, or a multitype Bienaymé–Galton–Watson process having d types corresponding to the memory of the process. We studied the behavior of the limit process and estimated its unknown parameters using a Bayesian approach.

Mathematics Subject Classification (2000): 60J80, 60J85, 92D30; 62F15, 92D25

Keywords: branching process, epidemiology, extinction time, Bayesian estimation, Bovine spongiform encephalopathy.

16.1 Introduction

BSE (Bovine Spongiform Encephalopathy), also known as “mad cow disease”, was initially recognized in Great-Britain in 1986. This disease was due to a change in the early 1980s of the rendering process by which livestock carcasses are converted

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to protein supplements for livestock feed. It is a fatal neurodegenerative transmissible disease in cattle due to self-replicating proteins, the prions. It causes a spongy degeneration in the brain and spinal cord leading to death. The main routes of transmission are horizontal via the protein supplements (MBM (Meat and Bone Meal), milk replacers) and maternal from a cow to its calf [5]. It may be transmitted to human by the food route. The human disease, called nvCJD, was first detected in the mid 1990s and caused 164 deaths in Great Britain until now. The main measures for controlling BSE were first of all the ban of feeding ruminants with ruminant-derived proteins in July 1988, and then the extension in 1996 of this ban to mammalian-derived proteins and to all farmed livestock [4].

The main questions adressed here consist in the quantification of the infection according to the different sources (feed, maternal, excretion), in the estimation of the efficiency of the main feed ban law (July 1988), and in the prediction of the propagation of the disease, in particular the extinction time distribution.

To this end, we first built a multitype branching process in discrete time with age and population dependent individual transitions. The types were the ages crossed with the health states. Then, assuming a rare disease at the initial time and the probability for an animal to be exposed to a given infective inversely proportional to the population size, we recursively derived from this model, as the initial size of the population increases to ∞, a limit model on the incidence of clinical cases. We showed that this limit model may be written either as a singletype Markovian model of order $a_M - 1$ with a Poissonian transition distribution, where a_M is the largest survival age of an healthy animal, or as a multitype branching process with $a_M - 1$ types corresponding to the memory of the process, where the offsprings distributions are Poisson distributions. Moreover this branching process is a BGW (Bienaymé-Galton-Watson) process on periods without any control regulation. The limit model has the advantage to depend only on the incidence of clinical cases at successive times, which corresponds to the observations. Using either one model (multitype branching process) or the other one ($a_M - 1$-Markovian model with a Poissonian transition), we studied the behavior of the process and estimated its unknown parameters using a Bayesian approach (efficiency of the Meat and Bone Meal (MBM) ban in 1988, infection parameters, incubation period distribution parameters, initial cases numbers in 1982, 1984, 1985 and 1986). Details of the proofs may be found in [7].

16.2 Initial branching model

The propagation of a disease with a long incubation time with respect to the population dynamics (offspring and death) being due to interaction of the disease dynamics and the population dynamics, we first built a branching process based on the population dynamics, the disease propagating on each random tree, according to the different steps of the disease evolution within each animal. These steps are described in Fig. 16.1.

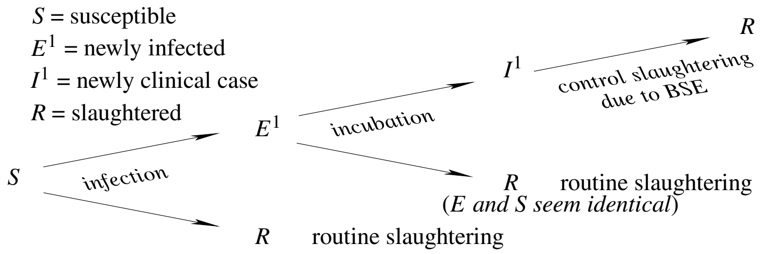

Fig. 16.1 The different steps of the disease.

The incubation period is random and may last several years while the clinical state lasts at most a few months.

We chose a discrete time approach with a time unit of 1 year for consistence with the observations on one hand, and for removing both seasonal effects and unknown effects linked to continuous time approach such as the duration of the clinical state, on the other hand.

Let $I^1_{a,n}$ and $I_{a,n}$ be the respective number of new clinical cases and the total number of clinical cases, aged a at time n, According to the chosen unit time, $I_{a,n} = I^1_{a,n}$. Let $E^1_{a,n}$ and $E_{a,n}$ be the respective number of newly infected animals and the total number of infected animals in incubation, aged a at time n, and let $N_{a,n}$ be the total number of animals aged a at time n. Moreover let, for $(X_0,X_1) \in \{(S,E^1),(E^1,I^1),(S,R),(E^1,R),(I^1,R)\}$, $\delta^{X_0,X_1}_{a_0,l_0,l_1,i}$ be the Bernoulli variable equal to 1 if animal i aged a_0 and in state X_0 at time l_0, undergoes transition $X_0 \to X_1$ at time l_1, let $\delta^{E^1}_{1,l_1,i'}$ and $\delta^{R}_{1,l_1,i'}$ be similar Bernoulli variables for the newborn animals, and $\delta^{(S,a_0-1)}_{l_0-1,i}$ be the Bernoulli variable equal to 1 if animal i is S and is aged a_0-1 at time l_0-1, and let $Y_{n,i}$ the number of newborn animals with parent i. Then in a natural way denoting E the incubation state,

$$I_{a,n} = I^1_{a,n} = \sum_{l<n} \sum_{i=1}^{E^1_{a-(n-l),l}} \delta^{E^1,I^1}_{a-(n-l),l,n,i} \text{ (clinical cases)} \tag{16.1}$$

$$E^1_{a,n} = \sum_{i=1}^{N_{n-1}} [1_{\{a\geq 2\}} \delta^{(S,a-1)}_{n-1,i} \delta^{S,E^1}_{a-1,n-1,n,i} + 1_{\{a=1\}} \sum_{j=1}^{Y_{n,i}} \delta^{E^1}_{1,n,i,j}] \text{ (new infected)} \tag{16.2}$$

$$E_{a,n} = \sum_{l<n} \sum_{i=1}^{E^1_{a-(n-l),l}} \delta^{E^1,E}_{a-(n-l),l,n,i} + E^1_{a,n} \text{ (total number of infected)}$$

$$N_n = \sum_{a=1}^{a_M} N_{a,n},\ N_{a,n} = (I_{a,n} + E_{a,n} + S_{a,n}) \text{ (total population size).}$$

The process defined by these relationships is a multitype branching process with age and population dependent individual transitions since the incubation time distribution cannot be assumed geometric and the probability to be infected depends on the number of infectives. The types are the ages, $1 \leq a \leq a_M$, crossed with the health states S, E, I. In order to completely define the process, we must determine the distribution of the set of the Bernoulli variables involved in this model. To this end, we assumed the following hypotheses:

1. A_1: the S and E animals have the same time-homogeneous survival law $\{\mathscr{S}_a\}_a$;
2. A_2: the survival law has the exponential form $\mathscr{S}_a = \mathscr{S}_{a-1}\exp(-\lambda)$, for $a \geq 2$ (this assumption is used only for simplifying the expression of infection parameters);
3. A_3: $|E^I| < 1$ year, $|E| \geq 1$ year, where $|E^I|$ is the duration of the infectious stage of the incubation period and $|E|$ is the duration of the whole incubation period. Therefore, according to observations, a newborn animal cannot become a clinical case during its first time unit of life.
4. A_4: there is no overcontamination during the incubation period or the clinical state;
5. A_5: the intrinsic incubation period distribution is assumed independent of the infection age and time;
6. A_6: the birth dates are at the beginning of each time unit (this assumption allows to consider the first age class in the same way as the other ones especially for the incubation distribution);
7. A_7: the number of newborn animals $Y_{l,i}$ at each calving per animal at time l, is independent of l, i, and of the health state of i (but the health state of each newborn animal and his survival during the first time step may depend on the health state of i);
8. A_{8a}: the contamination of a S animal at time l is due either to the ingestion of excreted prions from clinical cases at this time, or to the ingestion of prions in the MBM or milk replacers resulting from slaughtered animals which were in the infectious stage E^I at the previous time $l-1$;
   A_{8b}: the probability for a given susceptible animal to be infected at l by a given set of prions is inversely proportional to the total population size N_l (note: this probability is proportional to the exposure probability of S to this set of prions, and in classical infectious diseases with direct transmission, this probability is the probability of efficient contacts during the time unit of a given S with a given I);
   A_{8c}: the probability of infection via dead animals (and similarly via alive animals) follows a Reed-Frost's type model.
   Consequently the infection probability via the slaughtered animals has the form:

$$
\begin{aligned}
& P(S \text{ is not infected at } n \text{ by } \gamma^R E^{I,R}_{n-1,n}) \\
\overset{A_{8a},A_{8c}}{=} \; & P(S \text{ is not infected at } n \text{ by a set of prions})^{\gamma^R E^{I,R}_{n-1,n}} \\
\overset{A_{8b}}{=} \; & (1-\frac{\mu^R}{N_n})^{\gamma^R E^{I,R}_{n-1,n}} \\
\simeq \; & 1-\frac{\mu^R \gamma^R E^{I,R}_{n-1,n}}{N_n} + O\left(\left(\frac{E^I_{n-1}}{N_n}\right)^2\right),
\end{aligned}
$$

where γ^R is the mean number of prions aggregates produced in MBM by a dead infectious animal and $E^{I,R}_{n-1,n}$ is the number of infectives in E^I at time $n-1$ who are slaughtered at time n and entered in the MBM production. And similarly for the infection probability via the alive cattle.

9. A_9: the disease is very rare at the initial time: $\lim_{N_0 \to \infty} E_0^2 N_0^{-1} \overset{a.s.}{=} 0$.

Then the distributions of the Bernoulli variables were deduced from these assumptions [7].

16.3 Limit process as $N_0 \to \infty$

We study here the number of clinical cases at time n, $I_n = \sum_{a \le a_M} I_{a,n}$, as $N_0 \to \infty$, where a_M is the largest survival age, and we also denote $\{I_n\}$ the limit process. We denote $\mathscr{I}_k$ the σ-algebra generated by $\{I_l\}_{l \le k}$ and $\mathscr{I}_k^*$ the σ-algebra generated by $\{I_l\}_{l \le k}, \{N_{a,l}\}_{a,l<k}, \{N_{Y,l}\}_{l<k}$, where $N_{Y,l} = \sum_{i=1}^{N_{l-1}} Y_{l,i}$ is the total number of newborn animals (at the birth time).

Proposition 16.1. *The limit process, as $N_0 \to \infty$, is a singletype Markovian process of order $a_M - 1$ with a Poissonian transition law:*

$$\mathscr{L}\left(I_n | \mathscr{I}_{n-1}\right) = Poisson\left(\sum_{h=1}^{a_M-1} \Psi_{h|n-h} I_{n-h}\right), \tag{16.3}$$

$$\Psi_{h|n-h} := \sum_{a=1+h}^{a_M} (\theta^{a-h,R^c} + \theta^{a-h,R}\phi_{n-h} + 1_{\{a-h=1\}} p_{mat.}) P(a) P_{inc.}(h), \tag{16.4}$$

where θ^{a-h,R^c} and $\theta^{a-h,R}(\exp\lambda - 1)^{-1}\phi_{n-h}$ represent the mean numbers of new infected animals aged $a-h$ per infective at time $n-h$ respectively via excretion of alive animals and via slaughtered animals, $\phi_{n-h} \in [0,1]$ represents the efficiency at time $n-h$ of the MBM ban of 1988, $p_{mat.}$ is the probability for a newborn animal to be infected by his mother, $P(a)$ is the probability at each time for an animal to have age a, and $P_{inc.}(h)$ is the probability for an infected animal to have an intrinsic incubation time equal to h, which is defined by the censored process that is, at each time, not allowed to die. So $\Psi_{h|n-h}$ represents the mean number of new clinical cases produced with a delay h by a clinical case at time $n-h$.

Proof. We have $I_{a,n} = \sum_{h=1}^{a-1} I_{a,n-h,n}$, where according to (16.1) and (16.2),

$$\begin{aligned} I_{a,n-h,n} := {} & 1_{\{a-h\ge 2\}} \sum_{i=1}^{N_{n-h-1}} \delta^{(S,a-1-h)}_{n-h-1,i} \delta^{S,E^1}_{a-1-h,n-h-1,n-h,i} \delta^{E^1,I^1}_{a-h,n-h,n,i} \\ & + 1_{\{a-h=1\}} \sum_{i'=1}^{N_{Y,n-h}} \delta^{E^1}_{1,n-h,i'} \delta^{E^1,I^1}_{1,n-h,n,i'}. \end{aligned}$$

We first show that $\lim_{N_0\to\infty} E(I_{a,n-h,n}|\mathscr{I}_{n-1})$ is a finite quantity depending only on the past clinical cases until $n-h$. Then we show using this result that the limit transition law of $I_{a,n-h,n}$ given $\mathscr{I}_{n-1}$, as $N_0 \to \infty$, is Poissonian and that the $\{I_{a,n-h,n}\}_{a,h}$ given $\mathscr{I}_{n-1}$ are independent, as $N_0 \to \infty$.

1. We use $E(I_{a,n-h,n}|\mathscr{I}_{n-1}) = E(E(I_{a,n-h,n}|\mathscr{I}^*_{n-1})|\mathscr{I}_{n-1})$, where according to A_4,

$$
\begin{aligned}
&E(I_{a,n-h,n}|\mathscr{I}^*_{n-1})\\
&= 1_{\{a-h\geq 2\}} N_{n-h-1} E(\delta^{(S,a-1-h)}_{n-h-1,i}\, \delta^{S,E^1}_{a-1-h,n-h-1,n-h,i} \delta^{E^1,I^1}_{a-h,n-h,n,i}|\mathscr{I}^*_{n-h})\\
&+ 1_{\{a-h=1\}} N_{Y,n-h} E(\delta^{E^1}_{1,n-h,i'} \delta^{E^1,I^1}_{1,n-h,n,i'}|\mathscr{I}^*_{n-h})\\
&= 1_{\{a-h\geq 2\}} N_{n-h-1} P(\delta^{(S,a-1-h)}_{n-h-1,i} = 1, \delta^{S,E^1}_{a-1-h,n-h-1,n-h,i} = 1,\\
&\quad \delta^{E^1,I^1}_{a-h,n-h,n,i} = 1|\mathscr{I}^*_{n-h}) + 1_{\{a-h=1\}} N_{Y,n-h} P(\delta^{E^1}_{1,n-h,i'} = 1, \delta^{E^1,I^1}_{1,n-h,n,i'} = 1|\mathscr{I}^*_{n-h}).
\end{aligned}
$$

Then using Bayes' formula, we get

$$
\begin{aligned}
&E(I_{a,n-h,n}|\mathscr{I}^*_{n-1}) \qquad (16.5)\\
&= 1_{\{a-h\geq 2\}} N_{n-h-1} P(\delta^{(S,a-1-h)}_{n-h-1,i} = 1|\mathscr{I}^*_{n-h})\\
&\times P(\delta^{S,E^1}_{a-1-h,l-1,n-h,i} = 1|\mathscr{I}^*_{n-h}, \delta^{(S,a-1-h)}_{n-h-1,i} = 1)\\
&\times P(\delta^{E^1,I^1}_{a-h,n-h,n,i} = 1|\mathscr{I}^*_{n-h}, \delta^{(S,a-1-h)}_{n-h-1,i}\, \delta^{S,E^1}_{a-1-h,n-h-1,n-h,i} = 1)\\
&+ 1_{\{a-h=1\}} N_{Y,n-h} P(\delta^{E^1}_{1,n-h,i'} = 1|\mathscr{I}^*_{n-h}) P(\delta^{E^1,I^1}_{1,n-h,n,i'} = 1|\mathscr{I}^*_{n-h}, \delta^{E^1}_{1,n-h,i'} = 1).
\end{aligned}
$$

So we need to calculate each conditional probability of this formula using $\{A_i\}$. Let $\tilde{\delta}^{E^1}_{a-h,n-h,i} := 1_{\{a-h\geq 2\}} \delta^{(S,a-h-1)}_{n-h-1,i}\, \delta^{S,E^1}_{a-h-1,n-h-1,n-h,i} + 1_{\{a-h=1\}} \delta^{E^1}_{a-h,n-h,i}$.

a. Let us assume A_1, A_4 and A_5. Then

$$
P(\delta^{E^1,I^1}_{a-h,n-h,n,i} = 1|\tilde{\delta}^{E^1}_{a-h,n-h,i} = 1, \mathscr{I}^*_{n-h}) = \frac{\widehat{\mathscr{S}}_{a,n|n-h}}{\widehat{\mathscr{S}}_{a-h,n-h|n-h}} P_{inc.}(h) \quad (16.6)
$$

where $\widehat{\mathscr{S}}_{a',n'|n'-h} = P(A^R_{n'-(a'-1),n'} > a'|\mathscr{N}_{n'-h})$ is the survival probability at age a' and time n' for an animal born at time $n'-(a'-1)$, given the set $\mathscr{N}_{n'-h}$ of sizes of the populations until time $n'-h$, and $P_{inc.}(h)$ is the distribution of the intrinsic incubation time (for the censored process that is not allowed to die, defined by $P^c_E(\delta^{E,I^1}_{a',l,l+1,i} = 1) = P_E(\delta^{E,I^1}_{a',l,l+1,i} = 1|\{\delta^{E,I^1}_{a',l,l+1,i} = 1\} \cup \{\delta^{E,E}_{a',l,l+1,i} = 1\})$.

b. Under A_2 and A_8, the infection probabilities have the following forms:

$$\begin{aligned} &P(\delta^{E^1}_{1,n-h,i'} = 1 | \mathscr{I}^*_{n-h}, A^R_{n-h,n-h}(i') > 1) \\ &= [\overline{q} + \widehat{\theta}^{1,R^c} + \widehat{\theta}^{1,R}\phi_{n-h}]\frac{I_{n-h}}{N_{n-h}} + O\left(\left(\frac{E^I_{n-h-1}}{N_{n-h}}\right)^2\right) \end{aligned} \tag{16.7}$$

$$\begin{aligned} &P(\delta^{S,E^1}_{a-h-1,n-h-1,n-h,i} = 1 | \mathscr{I}^*_{n-h}, \delta^S_{a-h-1,n-h-1} = 1, A^R_{n-(a-1),n-h}(i) > a-h) \\ &= [\widehat{\theta}^{a-h,R^c} + \widehat{\theta}^{a-h,R}\phi_{n-h}]\frac{I_{n-h}}{N_{n-h}} + O\left(\left(\frac{E^I_{n-h-1}}{N_{n-h}}\right)^2\right), \end{aligned} \tag{16.8}$$

where $\widehat{\theta}^{a-h,R^c}$ and $\widehat{\theta}^{a-h,R}(\exp\lambda - 1)^{-1}\phi_{n-h}$ represent the mean numbers of new infected animals aged $a-h$ per infective at time $n-h$ respectively via excretion of alive animals and via slaughtered animals given $\mathscr{I}^*_{n-h}$.

c. Under A_1, A_3, A_7 and A_9, the disease is rare at any time: $\lim_{N_0\to\infty} E^2_{l-1}N_l^{-1} \overset{a.s.}{=} 0$, for all $l \geq 0$.

d. Under A_7 and A_9, then the population remains stable at any time, that is, for all $l \geq 1$,

$$\lim_{N_0\to\infty} N_l N_{l-1}^{-1} \overset{a.s.}{=} 1, P_l(a) = m, \mathscr{S}_a =: P(a), \tag{16.9}$$

where $P_l(a)$ is the probability at time l for an healthy animal to have the age $a \geq 1$, and $m = [\sum_{a'\geq 1}\mathscr{S}_{a'}]^{-1} = \lim_{N_0\to\infty} N_{Y,l}N_{l-1}^{-1} =: E(Y_{l,i})$ is the mean number of calves at time l per cow at the birth time, and $m\mathscr{S}_1 = P(1)$ is the mean number of calves at each time per cow, that are still alive at the end of their first year.

e. Let us assume A_1, A_7 and A_9. Then

$$\lim_{N_0\to\infty} E(\delta^{(S,a-h-1)}_{n-h-1,i} | \mathscr{I}^*_{n-h}) \overset{a.s.}{=} P(a-h-1). \tag{16.10}$$

Then, according to (16.5), using (16.6), (16.7), (16.8), (16.10) and (16.9), we get

$$\begin{aligned} &E(I_{a,n-h,n} | \mathscr{I}^*_{n-h}) \\ &= 1_{\{a-h\geq 2\}}\frac{N_{n-h-1}}{N_{n-h}}\widehat{P}_{n-h-1}(a-1-h)\frac{S_{n-h-1}}{N_{n-h-1}}\frac{\widehat{\mathscr{S}}_{a,n|n-h}}{\widehat{\mathscr{S}}_{a-1-h,n-h-1|n-h-1}} \\ &\times (\widehat{\theta}^{a-h,R^c} + \widehat{\theta}^{a-h,R}\phi_{n-h})P_{inc.}(h)I_{n-h} \\ &+ 1_{\{a-h=1\}}\frac{N_{Y,n-h}}{N_{n-h}}\widehat{\mathscr{S}}_{1,n-h|n-h}(\overline{q} + \widehat{\theta}^{1,R^c} + \widehat{\theta}^{1,R}\phi_{n-h}) \\ &\times \frac{\widehat{\mathscr{S}}_{a,n|n-h}}{\widehat{\mathscr{S}}_{a-h,n-h|n-h}}P_{inc.}(h)I_l + O\left(\left(\frac{E^I_{n-h-1}}{N_{n-h}}\right)^2\right)N_{n-h-1}. \end{aligned}$$

which leads to

$$\begin{aligned}
&\lim_{\{N_0 \to \infty\}} E(I_{a,n-h,n} | \mathscr{I}^*_{n-h}) \\
&\overset{a.s.}{=} (\theta^{a-h,R^c} + \theta^{a-h,R}\phi_{n-h} + 1_{\{a-h=1\}}\overline{q})P(a)P_{inc.}(h)I_{n-h} \qquad (16.11) \\
&=: \lambda_a(I_{n-h}) \qquad (16.12)
\end{aligned}$$

implying (16.4).

f. Let us consider the distribution of $I_{a,n-h,n}$ given $\mathscr{I}_{n-1}$. We show that this distribution is a Poisson one. According to its definition (see previous item), $I_{a,n-h,n}$ is the sum of 2 independent Binomial variables given $\mathscr{I}^*_{n-h}$:

$$\begin{aligned}
&\mathscr{L}(I_{a,n-h,n} | \mathscr{I}^*_{n-h}) \\
&= 1_{\{a-h \geq 2\}} \mathscr{B}(N_{n-h-1}, E(\delta^{(S,a-1-h)}_{n-h-1,i}\, \delta^{S,E^1}_{a-1-h,n-h-1,n-h,i}\, \delta^{E^1,I^1}_{a-h,n-h,n,i} | \mathscr{I}^*_{n-h})) \\
&\oplus\ 1_{\{a-h=1\}} \mathscr{B}(N_{1,n-h}, E(\delta^{E^1}_{1,n-h,i'}\, \delta^{E^1,I^1}_{1,n-h,n,i'} | \mathscr{I}^*_{n-h})), \qquad (16.13)
\end{aligned}$$

where $\mathscr{B}(N,p)$ represents the Binomial variable $\sum_{i=1}^{N} \delta_i$, $E(\delta_i) = p(N)$. Using (16.11) and (16.12), and since $P(I_{a,n-h,n} = i_{a-h,n-h} | \mathscr{I}^*_{n-h}) \leq 1$, then according to Lebesgue's dominated convergence theorem, we get

$$\begin{aligned}
&\lim_{N_0 \to \infty} E(P(I_{a,n-h,n} = i_{a-h,n-h} | \mathscr{I}^*_{n-h}) | \mathscr{I}_{n-h}) \\
&\overset{a.s.}{=} E(\lim_{N_0 \to \infty} P(I_{a,n-h,n} = i_{a-h,n-h} | \mathscr{I}^*_{n-h}) | \mathscr{I}_{n-h}) = \lambda_a(I_{n-h}). \qquad (16.14)
\end{aligned}$$

Therefore according to (16.12), (16.13) and (16.14), $I_{a,n-h,n}$ given $\mathscr{I}_{n-1}$ is asymptotically Poisson distributed as $N_0 \to \infty$:

$$\begin{aligned}
&\lim_{N_0 \to \infty} \mathscr{L}(I_{a,n-h,n} | \mathscr{I}_{n-h}) = Poisson(\lambda_a(I_{n-h})), \\
&\lambda_a(I_{n-h}) = \lim_{N_0 \to \infty} E(I_{a,n-h,n} | \mathscr{I}^*_{n-h}).
\end{aligned}$$

g. Next, for a given k, we show that the $\{I_{a,n-h,n}\}_{a,h}$ are independent given $\mathscr{I}_{n-1}$. This property is due to A_4 (no overinfection during the incubation) on one hand and to the property of rare disease which means that the number of S animals at time $n - h' < n$ is independent, as $N_0 \to \infty$, of the number of infected animals at the previous times $n - h < n - h'$, on the other hand.

h. Finally let us consider $\lim_{N_0 \to \infty} \mathscr{L}(I_{a,n} | \mathscr{I}_{n-1})$, $a \geq 2$. Let $I_{a,n} = \sum_{h \leq a-1} I_{a,n-h,n}$, where the $\{I_{a,n-h,n}\}_{a,h}$ are asymptotically, as $N_0 \to \infty$, independent given $\mathscr{I}_{n-1}$, and moreover according to A_4, $\mathscr{L}(I_{a,n-h,n} | \mathscr{I}_{n-1}) = Poisson(\lambda_a(I_{n-h}))$. Therefore

$$\lim_{N_0 \to \infty} \mathscr{L}(I_{a,n} | \mathscr{I}_{n-1}) = \oplus_{h=1}^{a-1} Poisson(\lambda_a(I_{n-h})) =: Poisson(\lambda_a(\mathscr{I}_n)),$$

where $\lambda_a(\mathscr{I}_n) := \sum_{h=1}^{a-1} \lambda_a(I_{n-h})$.

Corollary 16.1. *The limit process has the same distribution as:*

$$I_n = \sum_{h=1}^{a-1} \sum_{i=1}^{I_{n-h}} Y^{E,I}_{n-h,n,i}, \tag{16.15}$$

where $\mathscr{L}(Y^{E,I}_{n-h,n,i} | \mathscr{I}_{n-1}) = Poisson(\Psi_{h|n-h})$, $\Psi_{h|n-h} = E(Y^{E,I}_{n-h,n,i} | \mathscr{I}_{n-1})$, *and given* $\mathscr{I}_{n-1}$, *the* $\{Y^{E,I}_{n-h,n,i}\}_{i,h}$ *are independent.*

This result is just a direct consequence of the linearity of (16.3) in I_{n-h}.

Notice that (16.15) may be considered as a singletype discrete time Crump-Mode-Jagers process with bounded support of offspring production period, when $\Psi_{h|n-h} = \Psi_h$ (homogeneous setting).

In the same way as a unidimensional Markovian chain of order d may be represented by a d-multidimensional Markovian chain of order 1, we may also represent the limit process $I_n = \sum_{h=1}^{a_M-1} \sum_{i=1}^{I_{n-h}} Y^{E,I}_{n-h,n,i}$ according to a multitype Markovian branching process. Let $d := a_M - 1$ and, for $n \geq 0$, $\mathbf{I}_n =: (I_{n,1}, I_{n,2}, ..., I_{n,d}) := (I_n, I_{n-1}, ..., I_{n-(d-1)})$.

Proposition 16.2. *Process* $\{\mathbf{I}_n\}$ *is a multitype Markovian branching process defined by:*

$$I_{n,k} = \sum_{h=1}^{d} \sum_{i=1}^{I_{n-1,h}} Y^{(h,k)}_{n,i}, \ 1 \leq k \leq d,$$

where $Y^{(h,k)}_{n,i}$ *is the number of offspring of type k generated at time n by an animal of type h, and for* $k = 1$, $I_{n,1} = I_n$ *with* $Y^{(h,1)}_{n,i} = Y^{E,I}_{n-h,n,i}$, *and for* $k > 1$, $I_{n,k} = I_{n-(k-1)}$ *with* $Y^{(h,k)}_{n,i} = 1$, *for* $h = k-1$, *and* $Y^{(h,k)}_{n,i} = 0$, *for* $h \neq k-1$.

Moreover in the particular homogeneous case $\Psi_{n-h,n} = \Psi_h$ *(same infection at each time), then* $\{\mathbf{I}_n\}$ *is a multitype Bienaymé–Galton–Watson process.*

Proposition 16.3. *Let* $\mathbf{f}(\mathbf{s}) := (f^{(1)}(\mathbf{s}), ..., f^{(d)}(\mathbf{s}))$ *be the offspring generating function, where* $\mathbf{s} := (s_1, ..., s_{h+1}, ..., s_d)$, $f^{(h)}(\mathbf{s}) := E(s_1^{Y^{(h,1)}_{n,1}} ... s_d^{Y^{(h,d)}_{n,1}})$. *Then*

$$f^{(h)}(\mathbf{s}) = s_{h+1} \exp(-\Psi_h(1 - s_1)),$$

where $s_{d+1} = 1$, *and the generating function of* $\mathbf{I}_n$ *is*

$$F_n(\mathbf{s}) := E(s_1^{I_{n,1}} ... s_d^{I_{n,d}} | \mathbf{I}_0) = F_{n-1}(\mathbf{f}(\mathbf{s})) = F_{n-2}(\mathbf{f}(\mathbf{f}(\mathbf{s}))) = ... = F_0(\mathbf{f}_n(\mathbf{s})).$$

16.4 Behavior of the BGW limit process

We assume here the homogenous setting $\Psi_{h|n-h} = \Psi_h$, for all h, n.

Let $\mathbf{M}$ be the $d \times d$ matrix defined by $E(\mathbf{I}_n | \mathscr{I}_{n-1}) = \mathbf{I}_{n-1}\mathbf{M}$. Then

$$\mathbf{M} = \begin{pmatrix} \Psi_1 & 1\,0\,...\,0 \\ \Psi_2 & 0\,1\,...\,0 \\ ... & ... \\ \Psi_{d-1} & 0\,0\,...\,1 \\ \Psi_d & 0\,0\,...\,0 \end{pmatrix}$$

Except (16.16) and propositions (16.9) and (16.10) that are based on the Poissonian character of the transition law of the process $\{I_n\}$, the following results are based on classical results in multitype branching processes [2].

Proposition 16.4. *Let* ρ *be the first eigenvalue of* $\mathbf{M}$. *Then* $\rho \in \mathbb{R}_+$ *and satisfies* $\sum_{h=1}^{d} \Psi_h \rho^{-h} = 1$. *Moreover* $\rho \leq 1$ *is equivalent to* $R_0^{stoch} \leq 1$, *where* $R_0^{stoch} = \sum_h \Psi_h$.

Notice that according to the definition of $\{\Psi_h\}$, R_0^{stoch} corresponds to the usual basic reproductive number used in epidemiology (mean number of secondary cases produced by one case, see for example [1]). This comes from the fact that the limit model is not state-dependent.

Proposition 16.5. *Let* $\mathbf{u}$ *and* $\mathbf{v}$ *be the corresponding right and left eigenvectors associated to* ρ, *that is* $\mathbf{vM} = \rho\mathbf{v}$, $\mathbf{Mu}^T = \rho\mathbf{u}^T$, *with* $\mathbf{u}.\mathbf{v} = 1$, $\mathbf{u}.\mathbf{1} = 1$. *Then*

$$u_h = [\rho^{h-1}\sum_{l=h}^{d}\rho^{-l}\Psi_l]u_1,\ h = 1,...,d,\ u_1 = [\sum_{h=1}^{d}\rho^{h-1}\sum_{l=h}^{d}\rho^{-l}\Psi_l]^{-1}$$

$$v_h = \rho^{-(h-1)}v_1,\ v_1 = [\sum_{h=1}^{d}\rho^{h-1}\sum_{l=h}^{d}\rho^{-l}\Psi_l][\sum_{h=1}^{d}\sum_{l=h}^{d}\rho^{-l}\Psi_l]^{-1}.$$

From now on let us assume $\Psi_1 > 0,...,\Psi_d > 0$.

Proposition 16.6. *1. The process* $\{\mathbf{I}_n\}$ *is positive regular and nonsingular;*
2. $E(\|\mathbf{I}_1\| \ln(\|\mathbf{I}_1\|)) < \infty$, *where* $\|\mathbf{I}_1\| = \max\{I_1, I_0, ..., I_{-(d-2)}\}$;
3. $P(\lim_{n\to\infty} I_n = 0 \cup \lim_{n\to\infty} I_n = \infty) = 1$;
4. *In the supercritical case* $\rho > 1$, ($\Longleftrightarrow R_0^{stoch} > 1$), *then there exists a proper nonnegative random variable* W *such that* $\lim_{n\to\infty} \frac{I_n}{\rho^n} \overset{a.s.}{=} W$ *with* $q_h := P_h(\lim_{n\to\infty} I_n = 0) = P_h(W = 0)$ *(extinction probability starting from an animal of the h-type).*
5. *In the subcritrical and critical cases* $\rho \leq 1$, *then* $P(\lim_{n\to\infty} I_n = 0) = 1$ *(a.s. extinction).*

16.4.1 Extinction probability

Let $\mathbf{I}_0 = (i_0, i_{-1}, ..., i_{-(d-1)})$ be the initial state of the multitype BGW process. Notice that if $\mathbf{I}_0$ corresponds to the appearance of the first clinical case, then $i_0 = 1$ and $i_l = 0$, $l < 0$.

Proposition 16.7. *The extinction probability of* $\{I_n\}$ *is* $q := P(\lim_{n\to\infty} \mathbf{I}_n = 0|\mathbf{I}_0) = q_1^{i_0} \ldots q_d^{i_{-(d-1)}}$, *where*

$$q_h = \exp(-\sum_{l=h}^{d} \Psi_l (1-q_1)), \;\; h = 1, \ldots, d. \tag{16.16}$$

As a consequence, $R_0^{stoch} \leq 1 \Longrightarrow q_1 = 1 \Longrightarrow q_2 = 1 \Longrightarrow \ldots, q_d = 1$.

16.4.2 Extinction time distribution

Let T_{ext} be the extinction time of the process. Then $\{T_{ext.} \leq n\} := \{\mathbf{I}_n = 0\}$.

Proposition 16.8. *When* $R_0^{stoch} < 1$, *then* $\lim_{n\to\infty} \rho^{-n} P(T_{ext.} > n|\mathbf{I}_0) = Q(0)\mathbf{I}_0.\mathbf{u} > 0$, *where*
$Q(\mathbf{0}) := \lim_{n\to\infty} \rho^{-n} \mathbf{v}.(\mathbf{1} - \mathbf{f}_n(\mathbf{s}))$.

Proposition 16.9. *The extinction time distribution is given by:*

$$P(T_{ext.} \leq n|\mathbf{I}_0) = E\Big(\exp(-\sum_{l=0}^{d-1} I_{n-d-l} \sum_{h=l+1}^{d} \Psi_h)|\mathbf{I}_0\Big), \textit{ for } n \geq d.$$

Notice that $\sum_{l=0}^{d-1} I_{n-d-l} \sum_{h=l+1}^{d} \Psi_h$ is the mean number of secondary cases produced on the period $n-d, \ldots, n$ corresponding to the memory of $\mathbf{I}_n$, by the existing cases before time $n-d$.

16.4.3 Size of the epidemic

Proposition 16.10. *The distribution of the epidemic size is given by:*

$$\begin{aligned} &P(\sum_{h\geq 1}^{T_{ext.}} I_h = n|\mathbf{I}_0) \\ &= \sum_{l\geq 0} \sum_{\{i_j\}:\sum_{j=1}^{l} i_j = n} \exp\Big(-\sum_{h=1}^{d} \Psi_h \sum_{j=1}^{l+d} i_{j-h}\Big) \frac{(\sum_{h=1}^{d} \Psi_h i_{l-h})^{i_l}}{i_l!} \ldots \frac{(\sum_{h=1}^{d} \Psi_h i_{1-h})^{i_1}}{i_1!}. \end{aligned}$$

16.5 Estimation

We used a bayesian approach which has the double advantage to lead to the construction of exact credibility intervals from the posterior marginal distributions of the parameters on one hand, and to take into account the support of each parameter in its prior distribution.

For each parameter, the chosen prior distribution $P(\theta_j)$ expresses the lack of information (uncertainty) about this parameter. Assuming that the parameters are a priori independent, then the posterior distribution satisfies

$$P(\theta|I_1 = i_1,...,I_n = i_n) \propto \Pi_j P(\theta_j)P(I_1 = i_1,...,I_n = i_n|\theta),$$

where $P(I_1 = i_1,...,I_n = i_n|\theta)$ is the likelihood of $(I_1,...,I_n)$. .

16.5.1 Observations

The data set (Table 16.1) consisted of the number of cases of BSE per year reported in Great Britain until 2007 by the World Organisation for Animal Health [11], where the observations until 1987 have been detailed attributing 9 cases in 1986, 1 case in 1985 and 0 case before 1985. Recall that the disease was notifiable from 1988 [4] and that different types of active surveillance began since 1999, in particular the most efficient one required by the European Union starts in 2001 (see Department for Environment Food and Rural Affairs [3]). So the accuracy of the observations increases with time; in particular, the first observations concern only the clinical status while the current observations from 2001 concern not only the clinical status but also the last stage of the incubation period. However we did not take into account these changes of accuracy of the data.

n	1981	1982	1983	1984	1985	1986	1987	**1988**	1989	1990	1991	1992	1993	1994	1995	**1996**	1997	1998	1999	2000	2001	2002	2003	2004	2005	2006	2007
I_n	0	0	0	0	1	9	432	2469	7137	14181	25032	36682	34370	23945	14302	8016	4312	3179	2274	1355	1113	1044	549	309	203	104	53

Table 16.1 Number of cases per year until 2007 in Great-Britain. The epidemic peaks in 1992 and then decreases.

The observed survival probabilities until $a_M = 10$ were drawn from [10]. We also extrapolated these data until $a_M = 19$ in order to evaluate the influence of a_M on the estimation of θ and of derived quantities.

16.5.2 Model and parameters

In this section, $\{I_n\}$ was assumed to follow the limit model described in Sect. 16.3. We assumed in a parcimony purpose that $\theta^{a,R^c} = \theta^{R^c}$, for all a, $\theta^{a,R} = \theta^{1,R}$, for $a = 1$, $\theta^{a,R} = \theta^{2,R}$, for $a \geq 2$. Because of an identifiability problem concerning

$(\theta^{R^c}, p_{mat.})$, we set $p_{mat.} = 0.1$ which is the largest potential value based on observations. We assumed that $\phi_l = 1$ until 1988, $\phi_l = \phi$, for $l \in [1989, 1996]$, where $\phi \in [0,1]$, and $\phi_l = 0$, for $l \geq 1997$. Parameter ϕ represents the efficiency of the feed ban of 1988.

The transition law of the process was for $n \geq 1986$, $\mathscr{L}(I_n|\mathscr{I}_{n-1}) = Poisson(\lambda(\mathscr{I}_n))$, where $\lambda(\mathscr{I}_n) = \sum_a \sum_{h=1}^{a-1} \lambda_a(I_{n-h})$, $\lambda_a(I_{n-h})$ being given by (16.12).

We chose for the intrinsic incubation time distribution in continuous time a Weibull distribution of parameters c and d with density $dP(T_{inc} = x)/dx = cdx^{d-1}e^{-cx^d}$ in continuous time since the Weibull density covers a very large set of unimodal probability densities.

Therefore the distribution in discrete time was defined by $P_{inc}(j) = P(T_{inc} \geq j - 1) - P(T_{inc} \geq j) = e^{-c(j-1)^d} - e^{-cj^d}$, where $c = (d-1)[db^d]^{-1}$, $b = \arg\max_x dP(T_{inc} = x)/dx$ (mode of the probability density), and d is a shape parameter (for a convex density in a neighborhood of 0, d should be larger than 2).

Since the disease was unknown until 1986, the unknown parameter that we estimated was

$$\theta = ((i_{1982}, ..., i_{1986}), (b,d), \phi, (\theta^{1R}, \theta^{2R}, \theta^{R^c})).$$

16.5.3 Prior distributions

Due to the lack of knowledge of the parameters values, we assumed that all prior distributions were uniform distributions:

- $I_h \sim Uniform(0, 1000)$, for $h = 1982, ..., 1986$;
- $b \sim Uniform(3, 10)$, $d \sim Uniform(1, 5)$;
- $\phi \sim Uniform(0, 1)$;
- $\theta^{1R} \sim Uniform(0, 100000)$ (calves), $\theta^{2R} \sim Uniform(0, 100000)$ (cows);
- $\theta^{R^c} \sim Uniform(0, 100)$.

16.5.4 Algorithm and software

All calculations were performed with the software OpenBUGS [8]. BUGS means Bayesian inference Using Gibbs Sampling. This software mainly developed at the MRC Biostatistics Unit, Cambridge, UK, automatically implements MCMC algorithms for a very wide variety of models. Convergence of the algorithm was assessed by the Gelman and Rubin procedure [6].

16.5.5 Main results

We present here only the main results.

16.5.5.1 Parameters estimation

Recall that $\theta = ((i_{1982},...,i_{1986}),(b,d),\phi,(\theta^{1R},\theta^{2R},\theta^{R^c}))$. The empirical marginal posterior distributions for each parameter were computed from $N = 26,000$ simulations of θ according to the Markov Chain leading to the posterior distribution. The MAP $\widehat{\theta}_n$ (Maximum a posteriori Bayesian estimation, [9]), where the number of observations was $n = 22$. was

$$\widehat{\theta}_n = ((0,0,0,181,545),(7.46,3.84),0,(838,1200,2.43), \text{ for } a_M = 10$$
$$\widehat{\theta}_n = ((0,0,0,236,540),(5.953,4.14),0,(233,616,1.056), \text{ for } a_M = 19.$$

Parameter	Mean	s.d.	MC_error	$Q_{0.025}$	Median	$Q_{0.975}$
I_{1982}	0.6955	0.6921	0.004654	0.01762	0.4899	2.543
I_{1983}	0.9755	0.967	0.006083	0.02544	0.6809	3.589
I_{1984}	2.541	2.519	0.01526	0.06208	1.778	9.255
I_{1985}	177.4	13.42	0.09923	149.5	178.0	202.3
I_{1986}	545.1	35.19	0.2557	478.2	544.6	616.8
b	7.46	0.1347	0.003829	7.204	7.457	7.737
d	3.84	0.03425	4.527E-4	3.772	3.841	3.907
ϕ	7.75E-5	6.079E-5	5.99E-7	2.76E-6	6.381E-5	2.251E-4
θ^{1R}	842.8	34.29	0.5332	775.7	842.6	910.9
θ^{2R}	1202.0	134.2	3.836	949.6	1198.0	1479.0
θ^{R^c}	2.464	0.1266	0.003252	2.231	2.458	2.728

Table 16.2 Empirical statistics computed from the empirical marginal posterior distributions corresponding to each parameter using $a_M = 10$; s.d. stands for empirical standard deviation, MC_error for Monte Carlo standard error for the mean that is $s.d./\sqrt{N}$, Q_α is defined by $\widehat{P}(\theta_j \le Q_\alpha | i_{1981}, i_{1987}, ..., i_{2007}) = \alpha$ (quantile).

According to Table 16.3, the mode of the incubation distribution is correlated with the infection parameters. So these estimations must be interpreted with caution.

16.5.5.2 Prediction of the epidemic

The observed epidemic until 2007 is represented in Fig. 16.2 with a credibility band of probability 0.95 simulated from 1982 until 2040. This credibility band was calculated as follows: for each θ_l, $l = 1,...,N$, we simulated a trajectory $\{i_{1987,l},...,i_{2040,l}\}$ according to the branching process with parameter θ_l and the first data $i_{1982},...,i_{1986}$

	I_{1982}	I_{1983}	I_{1984}	I_{1985}	I_{1986}	b	d	ϕ	θ^{1R}	θ^{2R}	θ^{R^c}
I_{1982}	1.00	−0.02	0.00	−0.20	0.17	0.06	0.06	0.02	−0.02	0.04	0.05
I_{1983}	−0.02	1.00	−0.02	−0.27	0.20	0.05	0.06	0.02	−0.01	0.03	0.04
I_{1984}	0.00	−0.02	1.00	−0.49	0.26	0.05	0.07	0.02	−0.01	0.03	0.04
I_{1985}	−0.20	−0.27	−0.49	1.00	−0.54	−0.17	0.17	0.00	−0.21	−0.05	−0.15
I_{1986}	0.17	0.20	0.26	−0.54	1.00	0.16	0.53	0.08	−0.10	0.10	0.15
b	0.06	0.05	0.05	−0.17	0.16	1.00	0.31	0.25	−0.35	0.96	0.89
d	0.06	0.06	0.07	0.17	0.53	0.31	1.00	0.22	−0.76	0.46	0.27
ϕ	0.02	0.02	0.02	0.00	0.08	0.25	0.22	1.00	−0.29	0.29	−0.17
θ^{1R}	−0.02	−0.01	−0.01	−0.21	−0.10	−0.35	−0.76	−0.29	1.00	−0.58	−0.31
θ^{2R}	0.04	0.03	0.03	−0.05	0.10	0.96	0.46	0.29	−0.58	1.00	0.86
θ^{R^c}	0.05	0.04	0.04	−0.15	0.15	0.89	0.27	−0.17	−0.31	0.86	1.00

Table 16.3 Empirical correlations between the parameters for $a_M = 10$.

of this trajectory were given by the corresponding elements of θ_l. Therefore we got N trajectories $\{i_{1982,l},\ldots,i_{2040,l}\}_{l=1,\ldots,N}$ defining, at each time k, an empirical distribution of $I_k(\theta)$ from which we determined the quantiles $Q^{I_k(\theta)}_{0.025}$ and $Q^{I_k(\theta)}_{0.975}$. So the credibility band of $\{I_k(\theta)\}$ with probability 0.95 is defined as $\cup_k(Q^{I_k(\theta)}_{0.025},Q^{I_k(\theta)}_{0.975}]$, and by construction $P\left(I_k(\theta)\in(Q^{I_k(\theta)}_{0.025},Q^{I_k(\theta)}_{0.975}]\right)=0.95$. Notice that $(Q^{I_k(\theta)}_{0.025},Q^{I_k(\theta)}_{0.975}]$ depends by construction of the set of simulations $\{i_{k,i}\}_i$. But since these values are simulated independently given the past by using the process variability (Poisson transitions), then the variability of the process should also be represented in $(Q^{I_k(\theta)}_{0.025},Q^{I_k(\theta)}_{0.975}]$ for N large enough. So finally the credibility band should be (quasi)-independent of the given simulated set $\{i_{k,i}\}_{i,k}$, which was shown by different simulations.

Moreover, for each simulated trajectory starting in 1982, we determined the extinction time as the first year without any BSE case followed by $d-1$ years without any BSE case, and we determined using this set of simulated trajectories the empirical extinction time distribution and its quantiles $Q^{T_{ext.}}_{0.025}$ and $Q^{T_{ext.}}_{0.975}$ (Fig. 16.2). We see that this distribution is quite narrow with the most probable value at around 2021 (median at 2022).

16.6 Conclusion

Starting from a general detailed and complex branching process describing the propagation of the disease on branching trees relative to the population dynamics, and assuming reasonable epidemiological assumptions, we got, as $N_0 \to \infty$ a simple branching process on the clinical cases allowing easily the study of the behavior of the process and estimations from the observed incidences of cases. We also derived in the same way as for $\{I_n\}$ the incidences of infected animals $\{E^1_n\}$ [7]. The

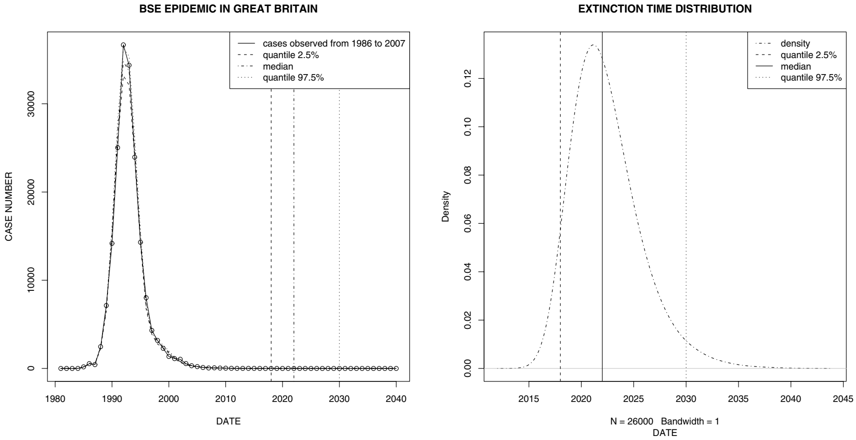

Fig. 16.2 On the *left*, the observed epidemic with a credibility band of probability 0.95; on the *right* the empirical distribution of the extinction time with a credibility interval of probability 0.95.

Bayesian estimation showed the great efficiency of the feed ban of 1988 and allowed us to calculate the extinction time distribution.

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17
Time to extinction of infectious diseases through age-dependent branching models

Miguel González, Rodrigo Martínez and Maroussia Slavtchova-Bojkova

Abstract This paper is concerned with a Sevast'yanov age-dependent branching process, describing outbreaks of an infectious disease with incubation period. The main goal was to define the optimal proportion of susceptible individuals that has to be vaccinated in order to eliminate the disease. To this end we study the properties of the time to extinction of an infection according to the proportion of immune individuals in the population. The results lead us to suggest a vaccination policy based on the mean of the infection survival time. Finally, we provide a simulation-based method to determine the optimal vaccination level, and as an illustration analyze the data of outbreaks of avian influenza spreading in Vietnam at the end of 2006.

Mathematics Subject Classification (2000): 60J80, 92D30

Keywords: Sevast'yanov age-dependent branching process, SIR model, time to extinction, vaccination policies, Monte Carlo method, avian influenza.

17.1 Introduction

When an infectious disease is strongly detrimental to the population in which it is spreading, control measures are needed to protect susceptible individuals. Vaccination programs represent one of the most effective forms of control. However,

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immunizing the whole population is not an option in most cases (either because it is logistically impossible or because it is too costly), so that only a proportion of susceptible individuals can be vaccinated. In this case therefore, infections can still occur, and their spread will depend on the level of immunization. How to determine the necessary proportion is an important public health problem in its own right, and depends on multiple factors. One of these factors that is particularly significant for public health authorities to assess vaccination efficiency is the time that elapses for the infectious disease to become extinct after vaccination, known as the disease's time to extinction.

The aim of the present work is to provide an approach to this problem by using branching processes to model the spread of epidemics in order to estimate their time to extinction. These processes have been widely applied to modeling the spread of epidemics (see for example the monographs [1, 4, 15], or [17]).

We centre our attention on the SIR (Susceptible-Infective-Removed) model. Measles, mumps, and avian influenza are examples of infectious diseases whose spread obeys this scheme. Since the branching process approach is appropriate for a homogeneously mixing population, when the number of infected individuals is small in relation to the total population size (see [11]), we shall assume this scenario, which clearly would correspond to the early stages of an epidemic.

The study of the spread of infectious disease following the SIR model and depending on a vaccination/immunized level has been considered in [5], using branching processes in discrete time. However, these generation-by-generation models are inappropriate for evaluating the time to extinction in real time. We hence propose here a more accurate approach to the problem, modeling the number of infectious individuals in the population according to the vaccination level by means of Sevast'yanov age-dependent branching processes (see [19]). This model is a particular case of the general branching process (see [12]), also called the Crump-Mode-Jagers (CMJ) branching process, and is the model best suited to the behaviour of infectious diseases that follow the SIR scheme (see [2]). The Sevast'yanov branching process (SBP) is especially well suited to modeling the evolution of diseases with an incubation period (and a negligible contact period in comparison with this) for which the disease's virulence may be a function of that period. Therefore, our target is to use SBPs to determine the optimal proportion of susceptible individuals which could be immunized by vaccination to guarantee the extinction of the disease within a given time. An advance of this work has been published in [8].

The paper is divided into 6 sections. In Sect. 17.2 we model the spread of the disease by means of SBPs that depend on the proportion of immune individuals in the population. In Sect. 17.3, we first model the time to extinction of an infectious disease according to the proportion of immune individuals in the population, and then study the main monotonicity and continuity properties of the time to extinction. In Sect. 17.4, we propose a policy for defining the optimal vaccination/immunized level based on the mean of the time to extinction of the disease. We then describe a simulation-based method to calculate the optimal proportion of susceptible individuals to be vaccinated, and end the section by analyzing the data of the spread of avian influenza in Vietnam at the end of 2006. In Sect. 17.5, we present our concluding remarks. Finally, the proofs are consigned to the end of the paper in Sect. 17.6.

17.2 Model of epidemic spread

We assume that the population consists of three types of individuals: infected, healthy but susceptible of infection (susceptible individuals), and healthy and immune to this disease (immune individuals). The disease spreads whenever an infected individual comes into contact with a susceptible one. The survival time of the disease in an infected individual will be treated as the "age" of this individual in the branching model. Essential assumption for the epidemic we are modeling is that the survival time of the disease consists of two periods: an incubation or latency period and a comparatively very short (negligible) contact period. During the incubation period, the infected individual as yet neither shows any symptoms of the disease nor passes the disease to any susceptible individual. Moreover, when the infectious disease is observed in an individual, this individual is either isolated (in the case of human populations, for instance) or culled (for instance, in the case of very contagious animal diseases such as classical swine fever, foot-and-mouth disease, or avian influenza), so that the individual ceases to be infective. For that reason, we consider that the "offspring", meaning in an epidemic setting the number of contacts, are produced in a very short period of time (called the contact period) and that this happens only once after the incubation period. One final but very essential aspect is that a disease may have different levels of severity during its survival period. Thus, it would be a mistake to model a survival time of a disease and the number of contacts as mutually independent. All the above considerations lead us to conclude that an SBP is appropriate to fit the evolution of an infectious disease with these characteristics.

In particular, to model the spread of an epidemic, we denote by $p_k(u)$ the probability that an infected individual with survival time (incubation plus contact periods) $u > 0$ contacts k healthy individuals, $k \geq 0$, and by α ($0 \leq \alpha \leq 1$) the proportion of immune individuals in the population. We assume that the population size is fixed and large enough for α and the family of contact distribution laws, $\{p_k(u)\}_{k\geq 0}$, $u > 0$, to be considered stable over time. Then, it is straightforward to verify that the probability that an infected individual with survival time $u > 0$ transmits the disease to k susceptible individuals is given by

$$p_{\alpha,k}(u) = \sum_{j=k}^{\infty} \binom{j}{k} \alpha^{j-k}(1-\alpha)^k p_j(u), \tag{17.1}$$

i.e., the infected individual with survival time u has been in contact with $j(\geq k)$ healthy individuals, and among them there were k susceptible individuals. We call the family $\{p_{\alpha,k}(u)\}_{k\geq 0}$, $u > 0$, the infection distribution laws when the proportion of immune individuals in the population is α. Note that, if no individual is immune, $\alpha = 0$, then every individual will be infected whenever it contacts an infected one, i.e., $p_{0,k}(u) = p_k(u)$, for all $k \geq 0$, $u > 0$. Also, if all individuals are immune, $\alpha = 1$, then the infection does not spread, i.e., $p_{1,k}(u) = 0$, for all $k \geq 0$, $u > 0$. With this spreading scheme over time, infected individuals pass the disease on at the end of their survival time to other susceptible individuals, and so on. We model the number of infected individuals when the proportion of immune individuals in the population is α by an SBP such that its offspring law is determined by the family of infection distribution laws $\{p_{\alpha,k}(u)\}_{k\geq 0}$, $u>0$, and the distribution function (d.f.) of the survival time of an infected individual is given by an arbitrary d.f. $G(\cdot)$ on the non-negative real numbers. Recall that by survival time we mean the period (measured in real time) consisting of the incubation period plus the comparatively very short (negligible) contact period, and note that we assume the family of contact distribution laws to depend on the survival time of each infected individual.

17.3 The epidemic's time to extinction

The objective of this section is to investigate the distribution of the time to extinction of an SBP according to the vaccination level α and for the family of contact distribution laws $\{p_k(u)\}_{k\geq 0}$, $u>0$. To this end, for each α, $0\leq\alpha\leq 1$, we denote by T_α the time to extinction of an SBP initiated at time 0 with a single infected individual, with family of infection distribution laws $\{p_{\alpha,k}(u)\}_{k\geq 0}$, $u>0$, and with d.f. of the survival time $G(\cdot)$. Intuitively, T_α is the maximum time that the infection survives in the population when the proportion of immune individuals is α. Henceforth, we denote by $v_\alpha(\cdot)$ the d.f. of the extinction time T_α, i.e., $v_\alpha(t)=P(T_\alpha\leq t)$ for all $t\in\mathbb{R}$. For each $u>0$ we also denote by $f_\alpha(u,\cdot)$ the probability generating function (p.g.f.) of $\{p_{\alpha,k}(u)\}_{k\geq 0}$. Moreover, we suppose that $G(0^+)=0$, i.e., there is null probability of instantaneous *death* and consequently $v_\alpha(0)=0$. Then, from [19], we deduce that $v_\alpha(\cdot)$ is the unique bounded function such that

$$v_\alpha(t)=\begin{cases}0, & t<0\\ \int_0^t f_\alpha(u,v_\alpha(t-u))dG(u), & t\geq 0.\end{cases} \tag{17.2}$$

This expression will play an important role in our study, together with the following relationship between α and the family of contact distribution laws. Let $m(u)$ be the mean of contacts of an infected individual with survival time u, and $m_\alpha(u)$ be the mean number of susceptible individuals which are infected by a contagious individual with survival time u given a proportion α of immune individuals in the population. Also let $m=\int_0^\infty m(u)dG(u)<\infty$ and $m_\alpha=\int_0^\infty m_\alpha(u)dG(u)<\infty$, $0\leq\alpha\leq 1$. Intuitively, m is the average number of individuals contacted by a contagious individual during its survival time, and m_α is the average number of infected individuals when the vaccination level is α. Then, from (17.1) one straightforwardly obtains that

$$m_\alpha=(1-\alpha)m. \tag{17.3}$$

Also, it is easy to prove that

$$f_\alpha(u,s)=f(u,\alpha+(1-\alpha)s),\ 0\leq s\leq 1,\ u>0, \tag{17.4}$$

with $f(u,\cdot)$ being the p.g.f. of the contact distribution law $\{p_k(u)\}_{k\geq 0}$, $u>0$.

Let $q_\alpha = P(T_\alpha < \infty)$ be the extinction probability of an SBP with family of reproduction laws $\{p_{\alpha,k}(u)\}_{k\geq 0}$, $u > 0$. It is well known that $q_\alpha = 1$ iff $m_\alpha \leq 1$ (see [19]). Notice that m_α is the critical threshold parameter of our model, so that, for an α for which $m_\alpha > 1$, $v_\alpha(\cdot)$ is the d.f. of a non-proper random variable because $P(T_\alpha < \infty) < 1$.

Henceforth, we consider α such that the extinction time T_α is a proper random variable, i.e., $m_\alpha \leq 1$, which implies that the infectious disease becomes extinct almost surely. We are interested in how fast the process becomes extinct depending on α. From (17.3), $m_\alpha \leq 1$ is equivalent to $\max\{0, 1-m^{-1}\} \leq \alpha \leq 1$, which depends on the mean of contacts of an infected individual. In order to simplify the notation, we shall denote by $\alpha_{inf} = \max\{0, 1-m^{-1}\}$ the smallest proportion of immune individuals, so that the infectious disease becomes extinct almost surely Notice that the corresponding mean $m_{\alpha_{inf}} = \min\{1, m\}$ is the greatest mean number of susceptible individuals catching the disease from an infected individual, so that it is guaranteed that the disease becomes extinct almost surely Moreover, $m_1 = 0$, i.e., the infectious disease does not spread to any susceptible individual and therefore the extinction time is given by the survival time of the initial infected individual, i.e., $v_1(t) = G(t)$ for all $t \geq 0$. It stands to reason that if there are non-immune individuals in the population, then it is probable that the infectious disease takes more time to become extinct. In the following result, we show that this is so by investigating the behaviour of $v_\alpha(\cdot)$ depending on the parameter α and when the family of contact distribution laws is fixed.

Theorem 17.1. *If* $0 \leq \alpha_1 < \alpha_2 \leq 1$, *then* $v_{\alpha_1}(t) \leq v_{\alpha_2}(t)$ *for all* $t \geq 0$.

Intuitively, it is clear that the greater the proportion of immune individuals, the more probable that the infectious disease will disappears faster. Consequently, for any α with $\alpha_{inf} \leq \alpha \leq 1$, the d.f. $v_\alpha(\cdot)$ has the upper bound $v_1(\cdot) = G(\cdot)$ and the lower bound $v_{\alpha_{inf}}(\cdot)$. Furthermore, they all have the lower bound $v_0(\cdot)$, which is not necessarily a proper d.f.

Moreover, we obtain that minor changes in the proportion of the immune individuals generate minor changes in the extinction time.

Theorem 17.2. *Let* α *be such that* $m_\alpha < m_{\alpha_{inf}}$. *Then for each* $\varepsilon > 0$ *there exists* $\eta = \eta(\varepsilon, \alpha) > 0$ *such that for all* α^*, *with* $m_{\alpha^*} \leq 1$ *and* $|\alpha - \alpha^*| \leq \eta$,

$$\sup_{0\leq t<\infty} |v_\alpha(t) - v_{\alpha^*}(t)| \leq \varepsilon.$$

In particular, we have proved the continuity of the d.f. $v_\alpha(\cdot)$ depending on α, for $\alpha_{inf} < \alpha \leq 1$. Notice that α_{inf} has been excluded as corresponding to $m_\alpha = \min\{1, m\}$. This is not necessary if $m < 1$. Moreover, the continuity is uniform over time.

Furthermore, some parameters of T_α inherit these properties of $v_\alpha(\cdot)$. In what follows we establish the monotonicity and continuity properties of the mean of the distribution of the infection extinction time, depending on α. Denote by μ_α the mean time to extinction of the infectious disease when the proportion of immune individuals is α. Since T_α is a non-negative random variable, then

$$\mu_\alpha = E[T_\alpha] = \int_0^\infty (1 - v_\alpha(t))dt. \tag{17.5}$$

Theorem 17.3.

1. *If* $\alpha_{inf} \leq \alpha_1 < \alpha_2 \leq 1$*, then* $\mu_{\alpha_2} \leq \mu_{\alpha_1}$.
2. *If* $\overline{\alpha}$ *is such that* $0 < m_{\overline{\alpha}} < m_{\alpha_{inf}}$ *and* $\sup\{\mu_\alpha : \overline{\alpha} < \alpha \leq 1\} < \infty$*, then* $\mu_{\overline{\alpha}}$ *is finite and* $\mu_{\overline{\alpha}} = \lim_{\widetilde{\alpha} \to \overline{\alpha}^+} \mu_{\widetilde{\alpha}}$*. Moreover, for all* α *with* $\overline{\alpha} < \alpha \leq 1$*, it follows that* $\lim_{\widetilde{\alpha} \to \alpha} \mu_{\widetilde{\alpha}} = \mu_\alpha$.

Remark 17.1. If the process starts with z infected individuals, then its time to extinction when the proportion of immune individuals in the population is α will be $T_{\alpha,z} = \max\{T_\alpha^{(1)}, \ldots, T_\alpha^{(z)}\}$, where $T_\alpha^{(i)}$ are i.i.d. random variables with the same distribution as T_α. Then, denoting by $v_{\alpha,z}(\cdot)$ the distribution function of $T_{\alpha,z}$, one has that $v_{\alpha,z}(t) = (v_\alpha(t))^z$, $t \in \mathbb{R}$. From this expression and considering the properties of the power functions, it is easy to establish for $v_{\alpha,z}(\cdot)$ the same properties of monotonicity and continuity as those of $v_\alpha(\cdot)$. Moreover, these properties can be extended to the mean value of $T_{\alpha,z}$, that we shall denote by $\mu_{\alpha,z}$.

17.4 Determining vaccination policies

In this section we propose a method of determining the optimal proportion of susceptible individuals to be immunized. To guarantee the extinction of the disease almost surely, the proportion of immune individuals in the population after vaccination, α, should be at least equal to α_{inf}. But we shall propose a possible way to define the optimal proportion of individuals to be vaccinated (immunized) to guarantee not only that the infection terminates after the vaccination period, but also that this happens within a given period of time. The procedure is based on the mean of the time to extinction.

Let us recall that we model the spread of the disease by an SBP as follows. Without loss of generality, we suppose that, before vaccination, every healthy individual which comes into contact with an infected individual is non-immune, i.e., the contact always produces infection. At some arbitrary time t_0 after the infection entered the population, the process of vaccination of susceptible individuals starts. We suppose that this vaccination process finishes at time t_1. Therefore $t_1 - t_0$ is the period of time that is taken for immunization, termed the vaccination period. We suppose that this vaccination period is fixed a priori by public authorities and that it does not depend on the proportion to be vaccinated. We also suppose that every vaccinated individual is immune to the infectious disease at least after time t_1. Actually therefore, we are considering the vaccination period to include not only the vaccination process but also the time that each vaccinated individual takes to develop the immunological response, and that the efficacy of vaccination is complete. Given the binomial scheme, this latter assumption does not lack generality.

17.4.1 Vaccination based on the mean value of the time to extinction

For fixed $\tau > 0$, we are interested in investigating vaccination policies which guarantee that the average time to extinction of an infection after the vaccination period, t_1, is less than or equal to $t_1 + \tau$. We determine these vaccination policies by applying the results of the previous section as follows. Let us suppose that a proportion α of susceptible individuals have been vaccinated. If at the end of the vaccination period there is a single infected individual in the population, then this infected individual might have already lived some time before time t_1. Therefore the probability that the disease becomes extinct no later than time $t_1 + \tau$ is greater than or equal to $v_\alpha(\tau)$.

However, the number of infected individuals at time t_1 is a random variable depending on α and on the number of infected individuals at the time t_0. We shall approximate it by its expected value. In general this is hard to calculate, but it is bounded above by the expected number of infected individuals at time t_1 in the case that no vaccination policy was applied. Indeed, if $Z(t_1)$ denotes the number of infected individuals at time t_1 assuming that there has been no vaccination and the individuals have already lived some time before t_1, then the probability that the disease becomes extinct no later than time $t_1 + \tau$ is greater than or equal to $F(t_1, v_\alpha(\tau))$, where $F(t_1, \cdot)$ denotes the p.g.f. of $Z(t_1)$. By Jensen's inequality, $F(t_1, v_\alpha(\tau)) \leq (v_\alpha(\tau))^{E[Z(t_1)]}$. Therefore, if z is the greatest integer less than or equal to the expected value $E[Z(t_1)]$, then the probability that the disease becomes extinct no later than time $t_1 + \tau$ can be bounded by $v_{\alpha,z}(\tau) = (v_\alpha(\tau))^z$. The expected value of $Z(t_1)$ can be determined by means of a renewal integral equation (see [19]).

Then, any vaccination level α such that $\mu_{\alpha,z} \leq \tau$ would be acceptable. The optimal vaccination policy is that which corresponds to the smallest α, i.e.,

$$\alpha_{opt}(\tau, z) = \inf\{\alpha : \alpha_{inf} \leq \alpha \leq 1, \mu_{\alpha,z} \leq \tau\}.$$

By simplicity, when the meaning is clear, let us write α_{opt} instead of $\alpha_{opt}(\tau, z)$. Taking into account the results of the previous section, one has that $\mu_{\alpha_{opt},z} \leq \tau$ if $\alpha_{opt} > \alpha_{inf}$. Therefore, by vaccinating a proportion α_{opt} of susceptible individuals, the infectious disease becomes extinct on average no later than time τ after the vaccination period. Moreover, although τ has been chosen arbitrarily, to find a solution of the problem, it must be satisfied the natural condition $\tau \geq \mu_{1,z}$.

The vaccination policy α_{opt} depends on the d.f. of time to extinction. Therefore, to calculate α_{opt}, it is necessary to know $v_\alpha(\cdot)$ for α such that $\alpha_{inf} \leq \alpha \leq 1$. Although $v_\alpha(\cdot)$ satisfies the integral equation defined by (17.2), in general it is not possible to obtain this function in a closed form. Recently, some numerical and simulation methods have been described for the approximation of the solution of integral equations (see for example [3] or [14]). We determine α_{opt} by approximating $v_\alpha(\cdot)$ using a simulation-based method when $\{p_k(u)\}_{k\geq 0}$, $u > 0$, and $G(\cdot)$ are considered known. For each fixed α we apply the Monte Carlo method to approximate the d.f. of the time to extinction, $v_\alpha(\cdot)$. We approximated α_{opt} by simulating various sufficiently close α's. To simulate the spread of the disease when the proportion of immune individuals is α, it is enough to know $G(\cdot)$ and $\{p_k(u)\}_{k\geq 0}$, $u > 0$. Usually, the survival time distribution and the family of contact distribution laws are estimated from the information that becomes available as the epidemic proceeds (see, for example [9] and [13]).

17.4.2 Analyzing the control measures for avian influenza in Vietnam

It is well-known that the highly pathogenic H5N1 avian influenza virus requires an incubation period after which it appears to be extremely virulent for a variety of domestic and wild bird species (see for example [10]). The usual routes of bird-to-bird transmission are airborne transmission if birds are in close proximity, or direct contact with contaminated respiratory secretions. Also, since the contact period is considered to be very short (negligible) in comparison with the incubation period, an SBP is appropriate to model the spread of the H5N1 virus in birds.

According to the official reports of the World Organization for Animal Health (see the Web site http://www.oie.int), Vietnam has been the country with the greatest number of outbreaks of avian influenza in domestic birds since the end of 2003. On the 7th December 2006, an outbreak started to spread widely in the southern part of the country, and became extinct on 14th January 2007 (see [16]). The left plot of Fig. 17.1 shows the numbers of infected domestic birds detected each day during this period. The non-null values are also given in Table 17.1. From 20th December the number of cases decreased, probably because some control measures were taken (see [16]). We guess that these strategies must have started before 19th December.

Table 17.1 Non-null values of infected domestic birds detected between 7th December 2006 and 14th January 2007.

Date	Cases	Date	Cases	Date	Cases	Date	Cases	Date	Cases
7 Dec	80	22 Dec	382	27 Dec	140	1 Jan	8	7 Jan	330
13 Dec	188	23 Dec	127	28 Dec	189	3 Jan	160	8 Jan	42
14 Dec	225	24 Dec	12	29 Dec	60	4 Jan	378	9 Jan	10
19 Dec	6,073	25 Dec	262	30 Dec	18	5 Jan	240	12 Jan	880
20 Dec	40	26 Dec	1,908	31 Dec	130	6 Jan	300	14 Jan	1,621

Next, we analyze the spread of the H5N1 avian influenza virus in Vietnam from 19th December until 14th January by comparing it with the simulated times to extinction of the SBP for different vaccination levels. First, in order to apply the above simulation-based method, we consider that $G(\cdot)$ is the d.f. of a gamma distribution, and, for each $u > 0$, $\{p_k(u)\}_{k\geq 0}$ follows a Poisson distribution with parameter λu, with $\lambda > 0$. These types of distribution have been found to be appropriate for the survival time (including incubation and contact periods) and the number of contacts, respectively (see for example [4, 6, 7] or [15]). Intuitively, λ represents the power of the virus. The average number of infected individuals is considered to be proportional to time, i.e., the longer the survival period (in our case almost equal to the incubation period because the contact period is negligible), the more infected individuals there will be. Taking into account that the incubation period of the H5N1 avian influenza virus is estimated at between 3 and 7 days (see [10])—this can be observed in our data at the beginning of the outbreak— we consider a gamma distribution with mean 5 and shape parameter 16 to guarantee that the survival period in 90% of the individuals is between 3 and 7 days. Therefore, we deduce that $m = 5\lambda$. Since the number of infected individuals at the first outbreak (on 7th December) was 80, and after the incubation period (on 13th and 14th December) the total number of infected individuals was 413, we can estimate the rate m, using Lotka's estimator, as $\widehat{m} = 413/80$ (see [9]). We did not take more outbreaks into account in our consideration because, as was observed above, some control measures must have been applied before 19th December. Thus, in order to apply our method, we consider this date to be the end of the vaccination period. We estimate the number of individuals incubating the virus at this date at $z = 413\widehat{m} \simeq 2,132$. Finally, for each vaccination level, α, $0 \leq \alpha \leq 1$, we deduce from (17.4) that $\{p_{k,\alpha}(u)\}_{k\geq 0}$ also follows a Poisson distribution with parameter $u(1-\alpha)\lambda$, $u > 0$.

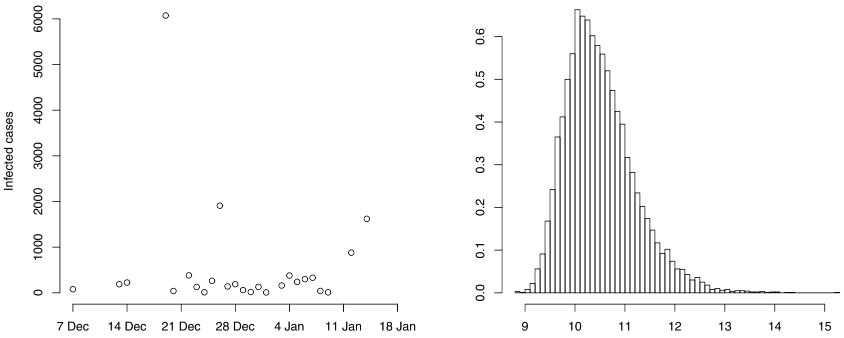

Fig. 17.1 *Left*: Numbers of infected domestic birds detected between 7th December 2006 and 14th January 2007. *Right*: Histogram of simulated times to extinction for $\alpha = 1$.

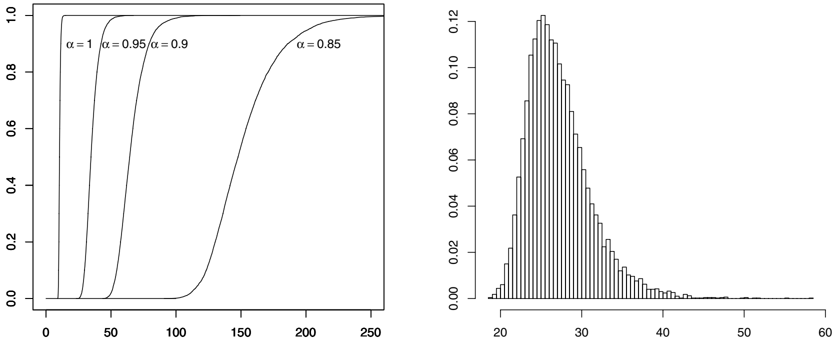

Fig. 17.2 *Left*: Empirical d.f. of the time to extinction for $\alpha = 0.85, 0.90, 0.95$ and 1. *Right*: Histogram of simulated extinction times for $\alpha = 0.97$.

The right-hand plot of Fig. 17.1 shows the histogram of 10,000 simulated times to extinction for $\alpha = 1$, i.e., when all susceptible individuals are immunized. Assuming that our model fits well, we deduce from the fact that the virus took close to 30 days to become extinct after the vaccination time, while the maximum of the simulated extinction times is less than 30, that the control measures followed in Vietnam did not cover all the susceptible individuals. Consequently, the control measures in Vietnam correspond to a vaccination level $\alpha < 1$ in our setting. Let us now determine α_{opt} which corresponds to these control measures. From Theorem 17.1 we deduce that the smaller is α, the longer the time to extinction. This behaviour is shown in the left-hand panel of Fig. 17.2 where the empirical d.f. of the time to extinction is plotted for $\alpha = 1, 0.95, 0.90$, and 0.85. Since the virus took close to 30 days to become extinct, we deduce that the vaccination level must have been close to 1. Taking into account the vaccination policy based on the mean value of the time to extinction, we obtain by applying the simulation-based method that $\alpha_{opt}(\tau = 30, z = 2132) = 0.97$. The right-hand panel of Fig. 17.2 shows the histogram of 10,000 simulated times to extinction for $\alpha = 0.97$. In conclusion, the control strategies followed in Vietnam correspond, in our setting, to a vaccination level close to 1 ($\alpha_{opt} = 0.97$). Of course one must observe that such a high proportion is connected with the great risk of death not only in the birds but also in the human population in the case of bird-to-human transmission.

Remark 17.2. For the computer simulation, we used the language and environment for statistical computing and graphics **R** (“GNU S”) (see [18]).

17.5 Concluding remarks

We have presented a method for defining an optimal vaccination level of a population in which a strongly detrimental disease has started to spread following a SIR scheme. We tackled this problem using a continuous-time branching model, namely the Sevast'yanov age-dependent branching process, taking the age and reproduction of an individual not to be independent. In epidemiological terms, this lack of independence takes into account that the number of contacts of an infected individual will depend on the survival time of an infection.

We are aware of the fact that the Sevast'yanov branching model we have proposed here is a particular case of the general branching process. In particular, SBPs follow from general branching processes if reproduction is assumed to occur once at the end of the individual's life and the offspring depend on the age of the individual. They are therefore appropriate for modeling infectious diseases with an incubation period and negligibly short contact period. Using this SBP model, we were able to define an optimal vaccination level using the mean value of the time to extinction of the epidemic after vaccination took place.

We used a real set of data from the outbreaks of avian influenza virus that spread in South Vietnam at the end of 2006 to illustrate the application of the technique. Our analysis, assuming SBP fits the situation well, showed that the model would indeed be useful for controlling the spread of avian influenza virus.

Mathematically, we established monotonicity and continuity properties for the time to extinction of SBPs.

Generalization of the results in the framework of general branching processes seems to be an important direction for further investigations.

17.6 Proofs

In this section we provide the proofs of the foregoing results. For each α such that $0 \leq \alpha \leq 1$, we introduce the functional operator $H_\alpha(\cdot)$, defined on a set of functions $h(\cdot)$ from non-negative real numbers, $\mathbb{R}_+$, to the interval [0,1], as follows:

$$H_\alpha(h)(t) = \int_0^t f_\alpha(s, h(t-s))dG(s),\ t \geq 0.$$

Also, for all $n \geq 1$, we denote by $H_\alpha^n(\cdot)$ the n-th composition of the operator $H_\alpha(\cdot)$. With this notation, (17.2) can be rewritten as the fixed-point equation $v_\alpha(t) = H_\alpha(v_\alpha)(t), t \geq 0$. Moreover, $v_\alpha(\cdot)$ has the following property:

Proposition 17.1. *For any fixed* α, $0 \leq \alpha \leq 1$, *and for any function* $h(\cdot)$ *from* $\mathbb{R}_+$ *to the interval* $[0,1]$, *one has that*

$$v_\alpha(t) = \lim_{n\to\infty} H_\alpha^n(h)(t), \quad t \geq 0.$$

Proof. Let α, $0 \le \alpha \le 1$, and $h\colon \mathbb{R}_+ \to [0,1]$. To prove the result it will be sufficient to establish the following statements:

S1. For each $t \ge 0$,
$$\widetilde{G}(t) \le H_\alpha(h)(t) \le G(t)$$
with $\widetilde{G}(t) = \int_0^t f_\alpha(s,0)dG(s)$.

S2. $H_\alpha(\cdot)$ is a non-decreasing functional operator, i.e., if $h_i\colon \mathbb{R}_+ \to [0,1]$, $i = 1,2$, are functions such that $h_1(t) \le h_2(t)$ for all $t \ge 0$, then
$$H_\alpha(h_1)(t) \le H_\alpha(h_2)(t), \quad \text{for all } t \ge 0.$$

S3. For each $t \ge 0$, there exist
$$u_1(t) = \lim_{n\to\infty} H_\alpha^n(\widetilde{G})(t) \quad \text{and} \quad u_2(t) = \lim_{n\to\infty} H_\alpha^n(G)(t).$$

S4. $u_1(\cdot)$ and $u_2(\cdot)$ are solutions of the fixed-point equation $h(\cdot) = H_\alpha(h)(\cdot)$, and then $v_\alpha(\cdot) = u_1(\cdot) = u_2(\cdot)$.

Indeed, from these four statements one can establish that, for $t \ge 0$,
$$\begin{aligned} v_\alpha(t) &= u_1(t) = \lim_{n\to\infty} H_\alpha^n(\widetilde{G})(t) \le \lim_{n\to\infty} H_\alpha^{n+1}(h)(t) \\ &\le \lim_{n\to\infty} H_\alpha^n(G)(t) = u_2(t) = v_\alpha(t). \end{aligned}$$

Let us now prove *S1–S4*.

S1. This statement is clear from considering that, for each $s \ge 0$ and $0 \le t \le 1$,
$$f_\alpha(s,0) \le f_\alpha(s,t) \le f_\alpha(s,1) = 1.$$

S2. This statement is clear from the fact that, for every $s \ge 0$, $f_\alpha(s,\cdot)$ is an increasing function.

S3. By *S1–S2*, for each $t \ge 0$
$$\widetilde{G}(t) \le H_\alpha(\widetilde{G})(t) \le H_\alpha(G)(t) \le G(t).$$

Hence, by iteration, for $n \ge 1$ and each $t \ge 0$
$$H_\alpha^n(\widetilde{G})(t) \le H_\alpha^{n+1}(\widetilde{G})(t) \le H_\alpha^{n+1}(G)(t) \le H_\alpha^n(G)(t).$$

Therefore, $\{H_\alpha^n(\widetilde{G})(t)\}_{n\ge1}$ is a non-decreasing sequence bounded above by 1, and hence there exists $u_1(t) = \lim_{n\to\infty} H_\alpha^n(\widetilde{G})(t)$, $t \ge 0$. Moreover, $\{H_\alpha^n(G)(t)\}_{n\ge1}$ is a non-increasing sequence bounded below by 0, and hence there exists $u_2(t) = \lim_{n\to\infty} H_\alpha^n(G)(t)$, $t \ge 0$.

S4. Let us prove this statement for $u_1(\cdot)$. Then the proof for $u_2(\cdot)$ will be similar.

Let $t \ge 0$. Then, using *S3*, the fact that $f_\alpha(s,\cdot)$ is increasing and continuous for each $s \ge 0$, and the dominated convergence theorem, one can establish that

$$\begin{aligned}
u_1(t) &= \lim_{n\to\infty} H_\alpha^{n+1}(\widetilde{G})(t) \\
&= \lim_{n\to\infty} \int_0^t f_\alpha(s, H_\alpha^n(\widetilde{G})(t-s))dG(s) \\
&= \int_0^t \lim_{n\to\infty} f_\alpha(s, H_\alpha^n(\widetilde{G})(t-s))dG(s) \\
&= \int_0^t f_\alpha(s, \lim_{n\to\infty} H_\alpha^n(\widetilde{G})(t-s))dG(s) \\
&= \int_0^t f_\alpha(s, u_1(t-s))dG(s) \\
&= H_\alpha(u_1)(t).
\end{aligned}$$

Since $u_1(\cdot)$ is a bounded function verifying the fixed-point equation $h(\cdot) = H_\alpha(h)(\cdot)$ and $v_\alpha(\cdot)$ is the unique bounded function verifying this equation, then $u_1(t) = v_\alpha(t)$ for all $t \geq 0$. This concludes the proof. □

Proof of Theorem 17.1

Let α_1, α_2 be such that $0 \leq \alpha_1 < \alpha_2 \leq 1$. Then, as $v_{\alpha_1}(\cdot)$ is a distribution function,

$$\alpha_1 + (1-\alpha_1)v_{\alpha_1}(t-s) \leq \alpha_2 + (1-\alpha_2)v_{\alpha_1}(t-s)$$

for all $0 \leq s \leq t$. Therefore

$$\begin{aligned}
f_{\alpha_1}(s, v_{\alpha_1}(t-s)) &= f(s, \alpha_1 + (1-\alpha_1)v_{\alpha_1}(t-s)) \\
&\leq f(s, \alpha_2 + (1-\alpha_2)v_{\alpha_1}(t-s)) = f_{\alpha_2}(s, v_{\alpha_1}(t-s)),
\end{aligned}$$

and then $v_{\alpha_1}(t) = H_{\alpha_1}(v_{\alpha_1})(t) \leq H_{\alpha_2}(v_{\alpha_1})(t)$, for all $t \geq 0$.

Since the functional operators $H_\alpha(\cdot)$ are non-decreasing (see *S2* in the proof of Proposition 17.1), it is clear that $v_{\alpha_1}(t) \leq H_{\alpha_2}^n(v_{\alpha_1}(t))$, for all $t \geq 0$ and $n \geq 1$. Then, applying Proposition 17.1, for all $t \geq 0$,

$$v_{\alpha_1}(t) \leq \lim_{n\to\infty} H_{\alpha_2}^n(v_{\alpha_1}(t)) = v_{\alpha_2}(t),$$

concluding the proof. □

Proof of Theorem 17.2

Let $\varepsilon > 0$ and let α be such that $m_\alpha < m_{\alpha_{inf}} = \min\{1, m\}$. Also let $\eta = \eta(\varepsilon, \alpha) = \varepsilon(1-m_\alpha)m^{-1}$. Given α^* such that $m_{\alpha^*} \leq 1$ and $|\alpha - \alpha^*| \leq \eta$, since for all t, $0 \leq t \leq 1$, $|\alpha + (1-\alpha)t - (\alpha^* + (1-\alpha^*)t)| \leq |\alpha - \alpha^*|$, from the mean value theorem and (17.4), it follows that for every $s > 0$ and $0 \leq t \leq 1$,

$$|f_\alpha(s,t) - f_{\alpha^*}(s,t)| \leq m(s)|\alpha - \alpha^*| \leq m(s)\eta. \tag{17.6}$$

Taking this into account, we next show by induction on n, for each $n \geq 1$, that

$$|H_{\alpha}^{n}(G)(t) - H_{\alpha^*}^{n}(G)(t)| \leq \varepsilon(1 - m_{\alpha}^{n}),\ t \geq 0. \tag{17.7}$$

For a given $t \geq 0$, for $n = 1$ we deduce from (17.6), that

$$\begin{aligned} |H_{\alpha}(G)(t) - H_{\alpha^*}(G)(t)| &\leq \int_0^t |f_{\alpha}(s, G(t-s)) - f_{\alpha^*}(s, G(t-s))| dG(s) \\ &\leq \varepsilon(1 - m_{\alpha}) m^{-1} \int_0^{\infty} m(s) dG(s) \varepsilon(1 - m_{\alpha}). \end{aligned}$$

By the hypothesis of induction, (17.7) holds for n. Then for $n+1$ we have that

$$\begin{aligned} |H_{\alpha}^{n+1}(G)(t) - H_{\alpha^*}^{n+1}(G)(t)| \leq{} & |H_{\alpha}(H_{\alpha}^{n}(G))(t) - H_{\alpha}(H_{\alpha^*}^{n}(G))(t)| \\ & + |H_{\alpha}(H_{\alpha^*}^{n}(G))(t) - H_{\alpha^*}(H_{\alpha^*}^{n}(G))(t)|. \end{aligned}$$

Moreover, using the mean value theorem again,

$$\begin{aligned} & |H_{\alpha}(H_{\alpha}^{n}(G))(t) - H_{\alpha}(H_{\alpha^*}^{n}(G))(t)| \leq \\ & \leq \int_0^t |f_{\alpha}(s, H_{\alpha}^{n}(G)(t-s)) - f_{\alpha}(s, H_{\alpha^*}^{n}(G)(t-s))| dG(s) \\ & \leq \int_0^t m_{\alpha}(s) |H_{\alpha}^{n}(G)(t-s) - H_{\alpha^*}^{n}(G)(t-s)| dG(s) \\ & \leq m_{\alpha} \sup_{0 \leq s < \infty} |H_{\alpha}^{n}(G)(s) - H_{\alpha^*}^{n}(G)(s)| \\ & \leq \varepsilon(1 - m_{\alpha}^{n}) m_{\alpha}, \end{aligned}$$

and, from (17.6),

$$\begin{aligned} & |H_{\alpha}(H_{\alpha^*}^{n}(G))(t) - H_{\alpha^*}(H_{\alpha^*}^{n}(G))(t)| \leq \\ & \leq \int_0^t |f_{\alpha}(s, H_{\alpha^*}^{n}(G)(t-s)) - f_{\alpha^*}(s, H_{\alpha^*}^{n}(G)(t-s))| dG(s) \\ & \leq \varepsilon(1 - m_{\alpha}). \end{aligned}$$

Therefore, we conclude that

$$|H_{\alpha}^{n+1}(G)(t) - H_{\alpha^*}^{n+1}(G)(t)| \leq \varepsilon(1 - m_{\alpha}^{n}) m_{\alpha} + \varepsilon(1 - m_{\alpha}) = \varepsilon(1 - m_{\alpha}^{n+1}).$$

Finally, using Proposition 17.1 and the fact that $m_{\alpha} < 1$, from (17.7), we obtain that

$$\sup_{0 \leq t < \infty} |v_{\alpha}(t) - v_{\alpha^*}(t)| \leq \varepsilon,$$

and then the proof is complete. □

Proof of Theorem 17.3

1. Let α_1, α_2 be such that $\alpha_{inf} \leq \alpha_1 < \alpha_2 \leq 1$. From Theorem 17.1, we have that $v_{\alpha_1}(t) \leq v_{\alpha_2}(t)$, $t \geq 0$, and taking into account (17.5), it follows that $\mu_{\alpha_2} \leq \mu_{\alpha_1}$.

2. Let $\overline{\alpha}$ be such that $0 < m_{\overline{\alpha}} < m_{\alpha_{inf}}$ and $M = \sup\{\mu_\alpha : \overline{\alpha} < \alpha \leq 1\} < \infty$. First we show that $\mu_{\overline{\alpha}}$ is finite. For a given $\varepsilon > 0$ and $N > 0$, applying Theorem 17.2, there exists $\eta = \eta(\overline{\alpha}, \varepsilon, N)$ such that for all $\alpha > \overline{\alpha}$, with $\alpha - \overline{\alpha} \leq \eta$, it follows that

$$v_\alpha(t) - v_{\overline{\alpha}}(t) \leq N^{-1}\varepsilon,\ t \geq 0.$$

Therefore,

$$\int_0^N (1 - v_{\overline{\alpha}}(t))dt \leq \int_0^N (N^{-1}\varepsilon + 1 - v_\alpha(t))dt \leq \varepsilon + M,$$

and we deduce that $\mu_{\overline{\alpha}}$ is finite. Hence, there exists $n_0 = n_0(\varepsilon, \overline{\alpha}) > 0$ such that

$$\int_{n_0}^{\infty} (1 - v_{\overline{\alpha}}(t))dt \leq 2^{-1}\varepsilon. \tag{17.8}$$

Let α be such that $\alpha \geq \overline{\alpha}$. Then, by applying Theorem 17.2, we guarantee that there exists $\eta = \eta(\alpha, \varepsilon, n_0) > 0$ such that, if $|\widetilde{\alpha} - \alpha| \leq \eta$, then $|v_\alpha(t) - v_{\widetilde{\alpha}}(t)| \leq (2n_0)^{-1}\varepsilon$ for all $t \geq 0$, and therefore

$$\int_0^{n_0} |v_\alpha(t) - v_{\widetilde{\alpha}}(t)|dt \leq 2^{-1}\varepsilon.$$

Moreover, since (17.8) holds, from Theorem 17.1 we have, for $\widetilde{\alpha} \geq \overline{\alpha}$, that

$$\int_{n_0}^{\infty} |v_{\widetilde{\alpha}}(t) - v_\alpha(t)|dt \leq 2^{-1}\varepsilon,$$

and the proof is complete. □

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18

Time to extinction in a two-host interaction model for the macroparasite *Echinococcus granulosus*

Dominik Heinzmann

Abstract An approximation is derived for the time to extinction in a sub-critical epidemic two-host interaction process for the macroparasite *Echinococcus granulosus*. The argument is based on coupling the epidemic model with a two-type branching process, and then to approximate the time to extinction for the branching process. It is shown that the approximate time is proportional to the logarithm of a weighted sum of the initially infectives in the host populations plus a Gumbel random variable. The accuracy of the approximation is illustrated.

Mathematics Subject Classification (2000): 60J80; 92D30

Keywords: multitype branching process, coupling, extinction time, *Echinococcus*.

18.1 Introduction

This paper is concerned with approximate the time to extinction in a sub-critical stochastic two-host interaction process for the macroparasite *Echinococcus granulosus*. Macroparasites, as opposite to microparasites as viruses and bacteria, do in general not multiply within the definitive hosts, but produce transmission stages such as eggs and larvae which pass into the external environment, resulting in rather complex transmission cycles. The life cycle of *Echinococcus granulosus* is between dogs and sheep as primary definitive and intermediate hosts. The dog harbors the adult parasite in the small intestine. It releases eggs that are passed in the feces. The sheep ingests the eggs on pasture, which then develop into cysts. The development of such space occupying cystic lesions is known as cystic echinocococcosis which is a zoonotic parasitic diseases. Humans are ecologically aberrant intermediate hosts who also develops such space occupying cystic lesions. The definitive host

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acquires the infection by ingesting organs containing infective material. The parasite is endemic in many parts of the world (see [7] and [14]) and continues to exert an unacceptable burden on human health, livestock production and wildlife ecology (see [6]).

Whittle (see [17]) has shown that initial and final stages of epidemic processes can often be approximated by suitable branching processes. More recently, Ball [1], Ball and Donnelly [2], Barbour and Utev [4], and Barbour [3] have used different construction arguments to quantify the accuracy of such approximations. We will use the argument in [1] and [2] to couple our sub-critical epidemic process, which models the transmission dynamics of *Echinococcus granulosus*, to a suitable branching process. We then derive an approximation for the time to extinction of the process. The basic idea is to construct the epidemic and branching processes on a same probability space and then to show that they coincide with high probability. Finally, the distributional approximation of the time to extinction for multi-type branching processes derived in [11] can be applied to obtain an approximate time to extinction for the epidemic process. It is shown that the approximate time is proportional to the logarithm of a weighted sum of the initially infectives in the host populations plus a Gumbel random variable. Numerical illustrations indicate that the approximation performs well.

18.2 Prevalence-based interaction model

Based on the natural life-cycle of *Echinococcus granulosus* [6], we introduce an interaction model for the transmission of infection between dogs and sheep, the primary definitive and intermediate hosts. Suppose that transmission takes place in a homogeneous, homogeneously mixing closed community with constant population sizes of $n^{(1)}$ dogs and $n^{(2)}$ sheep. Let $\boldsymbol{E} = (D,S) = \{(D(t),S(t))\}_{t\geq 0}$ be the numbers of infective dogs and sheep at time t. The epidemic can be described as follows. Infective dogs infect susceptible sheep by indirect transmission based on free-living stages in their excreta. The contacts of individual sheep with the excreta of dogs is assumed to occur according to independent Poisson processes with rate θ. The rate θ depends on the density of infective dogs and the grazing activity of sheep, so that infection of a susceptible sheep occurs at rate $\theta D/n^{(1)}$. Infections are assumed to be permanent (see [8] and [16]). Sheep live for an exponentially distributed time with rate λ_2 before they die (or are slaughtered) and are fed directly to a dog. An infection is established if the dog is susceptible and the dead sheep is infectious. The infectious period in dogs is exponentially distributed with rate λ_1 and the loss of infection happens either through loss of parasites or through death. It is further assumed that there is no acquired immunity (see [8] and [13]) and that all subjects at death are replaced by susceptibles (newborn) of the same type.

The process $\boldsymbol{E}$ takes values in $\{0,1,\ldots,n^{(1)}\} \times \{0,1,\ldots,n^{(2)}\}$ and is characterized by the set of Markov transitions given in Table 18.1.

Table 18.1 Transitions of the interaction model.

Transition	Rate
$D \to D-1,\ S \to S$	$\lambda_1 D$
$D \to D,\quad S \to S+1$	$\theta(n^{(2)}-S)(D/n^{(1)})$
$D \to D,\quad S \to S-1$	$\lambda_2 S(D/n^{(1)})$
$D \to D+1,\ S \to S-1$	$\lambda_2 S(1-(D/n^{(1)}))$.

18.3 Approximating branching processes

Let $\boldsymbol{Z} = (Z_1, Z_2) = \{(Z_1(t), Z_2(t))\}_{t \geq 0}$ be a multitype Markov branching process, where Z_1 and Z_2 denote the number of animals of type 1 and 2 respectively, with corresponding transitions given in Table 18.2. This process represents a birth and death process, with events (i) an animal of type 2 lives for an exponential time of rate λ_2 and produces at its death one offspring of type 1, (ii) an animal of type 1 lives for an exponential time with rate $\lambda_1 + \theta\rho$ and produces at its death either no offspring with probability $\lambda_1/(\lambda_1 + \theta\rho)$ or one type 1 and one type 2 offspring with probability $\theta\rho/(\lambda_1 + \theta\rho)$, where $\rho = n^{(2)}/n^{(1)}$, the population rate.

Table 18.2 Transitions of the approximating branching process.

Transition	Rate
$Z_1 \to Z_1 - 1,\ Z_2 \to Z_2$	$\lambda_1 Z_1$
$Z_1 \to Z_1,\quad Z_2 \to Z_2 + 1$	$\theta\rho Z_1$
$Z_1 \to Z_1 + 1,\ Z_2 \to Z_2 - 1$	$\lambda_2 Z_2$.

Let $z_1 := Z_1/n^{(1)}$ and $z_2 := Z_2/n^{(2)}$. Then the corresponding mean field dynamics are given by

$$\begin{aligned} \frac{dz_1}{dt} &= -\lambda_1 z_1 + \rho\lambda_2 z_2\,, \\ \frac{dz_2}{dt} &= \theta z_1 - \lambda_2 z_2\,. \end{aligned} \tag{18.1}$$

Applying the results given in [5] and [10], it is straightforward to verify that the type-reproduction number R_1, a threshold for the extinction of the process, is given by the following result.

Theorem 18.1. *The quantity*

$$R_1 := \frac{\theta\rho}{\lambda_1}$$

is a threshold for the deterministic model (18.1) such that as $t \to \infty$, $R_1 < 1$ implies that $(z_1, z_2) \to (0,0)$ and $R_1 > 1$ implies that $(z_1, z_2) \to (\bar{z}_1, \bar{z}_2)$, where

$$\bar{z}_1 = \frac{\lambda_2(\rho\theta - \lambda_1)}{\theta(\rho\lambda_2 + \lambda_1)} \quad \textit{and} \quad \bar{z}_2 = \frac{\rho\theta - \lambda_1}{\rho(\theta + \lambda_2)}.$$

We will see that the epidemic process $\boldsymbol{E}$ described in Table 18.1 and the branching process $\boldsymbol{Z}$ described in Table 18.2 can be constructed on a same probability space so that there is a direct correspondence between the number of infective dogs D and the number of type 1 individuals Z_1, respectively between the number of infective sheep S and the number of type 2 animals Z_2. It is shown that the construction implies that $D \leq Z_1$ and $S \leq Z_2$ almost surely. Hence $R_1 < 1$ for the branching process implies extinction behavior in $\boldsymbol{E}$.

Under some assumptions that we will discuss below, the construction of the processes on a same probability space indicates that $\boldsymbol{Z}$ and $\boldsymbol{E}$ coincide with high probability. Then, the biological interpretation of R_1 is as follows. The mean duration of an infection in dogs is $1/\lambda_1$. Given an infectious dog, it infects sheep at rate $\theta\rho$. Thus the expected number of sheep infected by a single infectious dog is R_1. Since an infected sheep is connected with exactly one dog, R_1 is the mean number of infections in the dog population caused (indirectly) by a single infectious dog.

18.4 Coupling

Let $\boldsymbol{I} = (I_1, I_2)$ be the initial numbers of infective dogs and sheep respectively, and denote with $\boldsymbol{M} = (M_1, M_2)$ the initial numbers of susceptible dogs and sheep respectively so that $M_i = n^{(i)} - I_i$ $(i = 1, 2)$. Let the epidemic process described in Table 18.1 be given by $\boldsymbol{E}_{\boldsymbol{I}}^{\boldsymbol{M}}$ and denote with $\boldsymbol{Z}_{\boldsymbol{I}}$ the branching process described in Table 18.2. Note that both processes are Markov. Assume that $R_1 < 1$, so that $\boldsymbol{Z}_{\boldsymbol{I}}$ and thus $\boldsymbol{E}_{\boldsymbol{I}}^{\boldsymbol{M}}$ are sub-critical as seen before.

We use the construction argument in [1] and [2] to couple $\boldsymbol{E}_{\boldsymbol{I}}^{\boldsymbol{M}}$ and $\boldsymbol{Z}_{\boldsymbol{I}}$. They described the construction of a single-host epidemic model from a limiting branching process. They showed that if the branching process is sub-critical, the epidemic and branching processes coincide for $N \to \infty$, where N is the number of susceptible hosts. For that, we need to adapt to our model the independent and identically distributed life histories of the individuals, given as (L, ξ) in [2], where L is the time elapsing between an individual's infection and its death, and ξ is a Poisson process of times at which contacts are made. We specify the life histories for dogs as (L_1, ξ_1), where L_1 is exponentially distributed with rate λ_1 and ξ_1 is a point process of rate $\theta\rho$ at which sheep make infective contacts with its excreta, and the life histories for sheep with (L_2, ξ_2), where L_2 is exponentially distributed with rate λ_2 and $\xi_2[0, L_2) = 0$ and $\xi_2\{L_2\} = 1$, since an infected sheep is connected with exactly one dog and the infection is transmitted at death of the sheep. The construction of the process is now similar to the construction in the proof of Theorem 2.1 in [2], except that in our case, individuals contacted during an infection event are chosen independently and uniformly from the M_i $(i = 1,2)$ initial susceptibles in the corresponding host population. It follows that $D \leq Z_1$ and $S \leq Z_2$ almost surely.

Let B_1 and B_2 be the random variables for the total number of new births of type 1 and 2 individuals respectively into the branching process $\boldsymbol{Z_I}$.

Lemma 18.1. *We have*

$$\begin{aligned}\mathbb{E}(B_1|\boldsymbol{I} = (I_1,I_2)) &= 2a(I_1+I_2)+I_2\,,\\ \mathbb{E}(B_2|\boldsymbol{I} = (I_1,I_2)) &= a(I_1+I_2)\,,\end{aligned}$$

where $a = \theta\rho/(\lambda_1 - \theta\rho)$.

Proof. Define $m_i := \mathbb{E}(B_i|\boldsymbol{I} = (1,0))$ and $k_i := \mathbb{E}(B_i|\boldsymbol{I} = (0,1))$ for $i = 1,2$, where $\boldsymbol{I} = (1,0)$ highlights that the branching process is started with a single type 1 individual and $\boldsymbol{I} = (0,1)$ analogously. Define $a := \theta\rho/(\lambda_1 - \theta\rho)$. Starting with a type 1 individual, we can have a splitting into a type 1 and type 2 individual with probability $p := \theta\rho/(\lambda_1+\theta\rho)$, or no offspring with probability $1-p$. When starting with a type 2 individual, there will be exactly one offspring of type 1, thus $m_1 = p(1+m_1+k_1)$ and $m_2 = p(1+m_2+k_2)$. We have $k_1 = 1+m_1$ and $k_2 = m_2$. Since $R_1 < 1$, then m_i and k_i, for $i = 1,2$, are finite. Then, using $k_1 = 1+m_1$ in the expression for m_1 implies that $m_1 = 2a$ and thus $k_1 = 2a+1$. Analogously, we obtain $m_2 = k_2 = a$. Hence the lemma follows immediately. □

Lemma 18.2. *It holds that*

$$\begin{aligned}\mathbb{E}(B_1^2|\boldsymbol{I} = (I_1,I_2)) &= 4a^2I_1^2+(1+4a+4a^2)I_2^2+4a(1+3a+2a^2)(I_1+I_2)\\ &\quad +4a(1+2a)I_1I_2\,,\\ \mathbb{E}(B_2^2|\boldsymbol{I} = (I_1,I_2)) &= a^2(I_1+I_2)^2+a(1+3a+2a^2)(I_1+I_2)\,,\end{aligned}$$

where $a = \theta\rho/(\lambda_1 - \theta\rho)$.

Proof. Define $g_i = \mathbb{E}(B_i^2|\boldsymbol{I} = (1,0))$ and $h_i = \mathbb{E}(B_i^2|\boldsymbol{I} = (0,1))$ for $i = 1,2$. Let a, p, m_i and k_i be given as in the proof of Lemma 18.1. Conditioning on the first event as before, we have $g_1 = p(1+2m_1+2k_1+2m_1k_1+g_1+h_1)$ and $h_1 = 1+2m_1+g_1$. Thus using the previous results, $g_1 = p(4+16a+8a^2+2g_1)$ and $h_1 = 1+4a+g_1$. Since $p/(1-2p) = a$, it follows that $g_1 = 4a(1+4a+2a^2)$ and $h_1 = 1+8a(1+2a+a^2)$. Similarly, we have $g_2 = p(1+4a+2a^2+2g_2)$ and $h_2 = g_2$, which results in $g_2 = h_2 = a(1+4a+2a^2)$. These imply that $\mathrm{Var}(B_1|\boldsymbol{I} = (1,0)) = \mathrm{Var}(B_1|\boldsymbol{I} = (0,1)) = g_1 - 4a^2 = 4a(1+3a+2a^2)$ and $\mathrm{Var}(B_2|\boldsymbol{I} = (1,0)) = \mathrm{Var}(B_2|\boldsymbol{I} = (0,1)) = g_2 - a^2 = a(1+3a+2a^2)$. Since individuals reproduce independently of each other, $\mathrm{Var}(B_1|\boldsymbol{I} = (I_1,I_2)) = 4a(1+3a+2a^2)(I_1+I_2)$ and $\mathrm{Var}(B_2|\boldsymbol{I} = (I_1,I_2)) = a(1+3a+2a^2)(I_1+I_2)$, which implies the lemma. □

Based on the construction of the processes described above, Theorem 4.1 and Eq. (4.3) in [2] yields that the probability, given B_1 and B_2, that $\boldsymbol{Z_I}$ and $\boldsymbol{E_I^M}$ do not coincide is

$$\begin{aligned} p_{\boldsymbol{I},\boldsymbol{M}}^{(B_1,B_2)} &= 1-\prod_{k=1}^{B_1}\left[1-\frac{k-1}{M_1}\right]\prod_{l=1}^{B_2}\left[1-\frac{l-1}{M_2}\right] \\ &\le 1-\exp\left(-\frac{B_1(B_1-1)}{2M_1}-\frac{B_2(B_2-1)}{2M_2}\right) \\ &\le \left(\frac{B_1(B_1-1)}{2M_1}+\frac{B_2(B_2-1)}{2M_2}\right), \end{aligned}$$

since $x > 1-\exp(-x)$ for $x > 0$. Thus the corresponding unconditional probability $p_{\boldsymbol{I},\boldsymbol{M}}$ satisfies

$$p_{\boldsymbol{I},\boldsymbol{M}} \le \mathbb{E}\left(\frac{B_1(B_1-1)}{2M_1}+\frac{B_2(B_2-1)}{2M_2}\right),$$

so that Lemmas 1 and 2 imply that

$$p_{\boldsymbol{I},\boldsymbol{M}} = O(\max\{I_1,I_2\}^2/\min\{M_1,M_2\}),$$

leading to the following result.

Theorem 18.2. *If* $\max\{I_1,I_2\}^2/\min\{M_1,M_2\} \to 0$ *as* $\min\{M_1,M_2\} \to \infty$, *it follows that*

$$\lim_{\min\{M_1,M_2\}\to\infty} \mathbb{P}(\boldsymbol{E}_{\boldsymbol{I}}^{\boldsymbol{M}} = \boldsymbol{Z}_{\boldsymbol{I}} \textit{ for all } t \ge 0) = 1.$$

18.5 Time to extinction

Let $R_1 < 1$ and assume that $\max\{I_1,I_2\}^2$ is much smaller than $\min\{M_1,M_2\}$, with $\min\{M_1,M_2\} \to \infty$. Then Theorem 18.2 indicates that the epidemic process $\boldsymbol{E}_{\boldsymbol{I}}^{\boldsymbol{M}}$ and its approximating branching process $\boldsymbol{Z}_{\boldsymbol{I}}$, given that they start with $\boldsymbol{I} = (I_1,I_2)$ infectious and $\boldsymbol{M} = (M_1,M_2)$ susceptibles animals, coincide with high probability. Thus we can now use the distributional approximation of the time to extinction of a multitype Markov branching process derived in [11].

We proceed analogous to the application in [11]. Let $T_{\boldsymbol{I}}$ be the extinction time of the branching process $\boldsymbol{Z}_{\boldsymbol{I}}$, and define the survival probability of the process until time t, with $t > 0$, when starting with a single type i ($i = 1,2$) individual as $q_i(t) = 1-\mathbb{P}(T_{\boldsymbol{I}} \le t | \boldsymbol{I} = (\delta_{i1},\delta_{i2}))$, where δ_{ij} is the Kronecker Delta. Then Eq. (2.2) in [11] yields

$$\frac{d\boldsymbol{q}(t)}{dt} = \begin{pmatrix} -\lambda_1 & \rho\theta \\ \lambda_2 & -\lambda_2 \end{pmatrix}\boldsymbol{q}(t) - \begin{pmatrix} \rho\theta q_1(t)q_2(t) \\ 0 \end{pmatrix} =: \boldsymbol{B}\boldsymbol{q}(t) - \boldsymbol{v}(t),$$

where $\boldsymbol{v}(t) = (v_1(t),v_2(t))^T$ and $\boldsymbol{q}(t) = (q_1(t),q_2(t))$. Since the number of offspring of each type in the branching process is ≤ 2, Corollary 2.1 in [11] can be applied with $\alpha = 1$, stating that $0 \le v_i(t) \le a_i\|\boldsymbol{q}(t)\|^2$ for $i = 1,2$, were a_i is a constant.

Hence the behavior of the solution $\boldsymbol{q}(t)$ can be approximated by that of $\tilde{\boldsymbol{q}}(t)$ given by $d\tilde{\boldsymbol{q}}(t)/dt = \boldsymbol{B}\tilde{\boldsymbol{q}}(t)$.

Since $\boldsymbol{B}$ has only non-negative elements off the diagonal and is irreducible, Theorem 2.1 in [11] implies that $\boldsymbol{B}$ has a unique real largest eigenvalue $-r$, with corresponding positive left $\boldsymbol{f}_1^T$ and right $\boldsymbol{b}_1$ eigenvectors, which are given by $-r = (-(\lambda_1+\lambda_2)+\sqrt{D})/2$ and

$$\boldsymbol{f}_1^T = \frac{1}{N_1}\left(\frac{\lambda_2-\lambda_1+\sqrt{D}}{2\rho\theta},1\right), \ \boldsymbol{b}_1^T = \frac{1}{N_2}\left(\frac{\lambda_2-\lambda_1+\sqrt{D}}{2\lambda_2},1\right),$$

with $D = (\lambda_1+\lambda_2)^2 - 4\lambda_2(\lambda_1-\rho\theta)$, N_1 and N_2 are appropriate constants such that $|\boldsymbol{f}_1| = 1$ and $\boldsymbol{f}_1^T\boldsymbol{b}_1 = 1$. Theorem 4.2 in [11] implies that the approximate time to extinction for the branching process $\boldsymbol{Z_I}$ is given by $\tilde{T}_{\boldsymbol{I}} = \log C_{\boldsymbol{I}}/r + V/r$, where $C_{\boldsymbol{I}} = c_1I_1 + c_2I_2$ with $c_1, c_2 > 0$ constants and V is a Gumbel random variable. The theorem also states that the bound on the error in total variation distance is inversely proportional to $C_{\boldsymbol{I}}$. The c_i's can be computed as described in Sect. 5 of [11] by using the above eigen elements of $\boldsymbol{B}$. The coupling argument in Sect. 18.4 implies that $\tilde{T}_{\boldsymbol{I}}$ is also an approximation for the time to extinction of the initial epidemic process $\boldsymbol{E_I^M}$.

18.6 Numerical illustration

To verify our approach, the distribution of the true extinction time of $\boldsymbol{E_I^M}$ can be compared with that of $\tilde{T}_{\boldsymbol{I}}$. This true distribution is theoretically not amenable, and thus needs to be computed by simulation. The Markov chain in Table 18.1 can easily be simulated by the classical Gillespie algorithm (see [9]).

The parameters of the epidemic process are chosen such that they reasonably reflect a “typical” situation in Central Asia. The population ratio ρ is approximated by 10 based on an estimate of 10.368 from (unpublished) field data in Kazakhstan, where during a purgation study in dogs, the owners have been asked how many sheep and dogs they own. It is assumed that there are $n^{(1)} = 500$ dogs, and thus $n^{(2)} = n^{(1)}\rho = 5{,}000$ sheep. The death rate λ_2 is set to 0.5 based on an estimate of 0.491 $(95\% CI : 0.473, 0.501)$ in a sheep sample from Kazakhstan (see [15]). R.C.A. Thompson and A.J. Lymbery (see [12]) suggested a loss of infection rate of about $1-1.2$ infections per dog per year, and thus we choose $\lambda_1 \in \{1, 1.2\}$. There is no appropriate estimate available for the contact rate θ, and thus we select $\theta \in \{0.01, 0.05\}$ such that $R_1 < 1$.

Figure 18.1 displays the distribution of the approximate time to extinction $\tilde{T}_{\boldsymbol{I}}$ and the simulated distribution of the true time to extinction for the different parameter settings of $\boldsymbol{E_I^M}$. The resulting values for c_1, c_2 and r are represented in Table 18.3.

The approximate time to extinction is well in line with the simulated distribution of the true time for all settings. Longer mean times to extinction are observed for decreasing values of λ_1 (see in Fig. 18.1, (x1)–(x2) for x=a,b,c), and for increasing

Table 18.3 Computed values of r, c_1 and c_2 for different parameter settings. Note that $\rho = 10$ and $\lambda_2 = 0.5$.

λ_1	θ	r	c_1	c_2
1	0.01	0.408	0.252	1.491
1.2	0.01	0.427	0.186	1.437
1.2	0.05	0.236	0.420	0.809

values of θ (see in Fig. 18.1, (x2)–(x3) for x = a,b,c). These observations can be explained as follows. Recall the construction argument of the branching process in Section 18.4, where the life histories of infections in dogs are specified as (L_1, ξ_1), with L_1 exponentially distributed with mean $1/\lambda_1$ and with ξ_1 a Poisson process of rate $\theta\rho$ at the points of which sheep make infective contacts with its excreta, and the life histories for sheep with (L_2, ξ_2), where L_2 is exponentially distributed with rate λ_2 and $\xi_2[0, L_2) = 0$ and $\xi_2\{L_2\} = 1$, since an infected sheep is connected with exactly one dog and the infection is transmitted at death of the sheep. Let $\mathscr{P}_1$ be a Poisson process with rate λ_1. Let $T_1, T_2, \ldots$ be the arrival times of the Poisson process. Introduce two marked point processes based on $\mathscr{P}_1$. In the first, mark all occurrence times of $\mathscr{P}_1$ with probability 1. In the second, mark the occurrence times with probability $\lambda_1'/\lambda_1 < 1$, where $\lambda_1' < \lambda_1$. Define L_1 as the first marked occurrence time. Hence $L_1 = T_1$ for the first marked process and $L_1 = T_j$ with probability $(1 - \lambda_1'/\lambda_1)^{j-1}(\lambda_1'/\lambda_1)$, $j \geq 1$, for the second. Note that for the second process, L_1 has the exponential distribution with mean $1/\lambda_1'$, and so corresponds to the lifetime of an infection of a dog, when the recovery rate λ_1' is smaller than λ_1. Hence each infection duration can be constructed to be longer almost surely in dogs for the latter process, so that dogs in the second process will infect more sheep if the same constant process ξ_2 is used in both cases. Since infection is transmitted back to the dog population with probability 1, the second process implies an increased time to extinction almost surely, and hence also in mean. A similar argument can be used to show that increasing θ implies increasing the mean time to extinction. Finally, increasing values of the initial conditions I_1 and I_2 imply longer mean times to extinction since $\tilde{T}_{\boldsymbol{I}}$ grows like $\log C_{\boldsymbol{I}} = \log(c_1 I_1 + c_2 I_2)$, with $c_1, c_2 > 0$ fixed. Despite the shift of the mean, it is clear from the definition of $\tilde{T}_{\boldsymbol{I}}$ that the shape remains the same for different values of the initial conditions (see in Fig. 18.1, (ai)–(ci) for $i = 1, 2, 3$).

Remark 18.1. Since the final stages of epidemic processes can often be approximated by suitable branching processes (see [17]), the approach in this paper can be extended to other (sub-critical) epidemic multi-host interaction processes.

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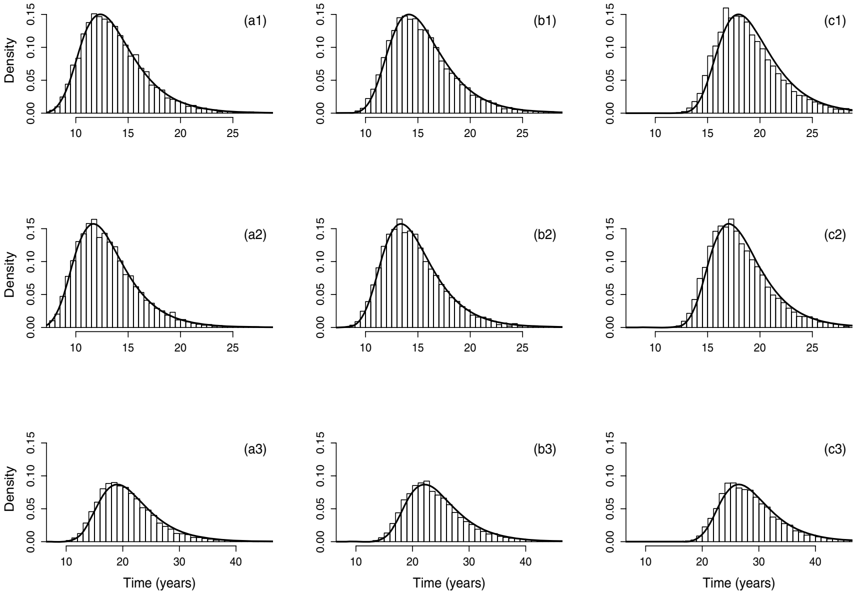

Fig. 18.1 Density distribution of $\tilde{T}_I$ (*solid line*) versus the simulated distribution of the true extinction time (histogram of 10,000 simulations) for the epidemic process $\boldsymbol{E}_I^M$, with $n^{(1)} = 500$, $n^{(2)} = 5{,}000$, $\rho = 10$ and $\lambda_2 = 0.5$. The parameter pair (λ_1, θ) is $(1, 0.01)$ for (a1)–(c1), $(1.2, 0.01)$ for (a2)–(c2) and $(1.2, 0.05)$ for (a3)–(c3). The initial conditions (I_1, I_2) are $(20, 100)$ for (a1)–(a3), $(100, 200)$ for (b1)–(b3), and $(100, 1000)$ for (c1)–(c3).

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Part VI
Two-Sex Branching Models

19

Bisexual branching processes with immigration depending on the number of females and males

Shixia Ma and Yongsheng Xing

Abstract In this work, we introduce a class of discrete time bisexual branching processes where, in each generation, it is allowed the immigration of females and males. The immigration depends on the numbers of females and males in the population. For such a class of processes, some results about its probabilistic evolution are established. First, the existence of the asymptotic growth rate is proved. Then, assuming the supercritical case, namely, when the asymptotic growth rate is greater than one, several limiting results are derived.

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19.1 Introduction

Nowadays, the branching process theory is an active research area with theoretical interest and practical applications in fields such as biology; demography; ecology; epidemiology; genetics; medicine; population dynamics; physics and so on. With the aim to describe the evolution of populations where females and males coexist and form couples (one female and one male) several classes of bisexual branching processes have been studied, see e.g. [1, 2, 4, 6–8, 10, 12, 13, 16, 18–21, 23, 22] and [25]. In particular with the purpose to consider the possible immigration of females and males from outside populations, it was introduced in [8] a bisexual process where the immigration of females and males is governed through a sequence of

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independent and identically distributed random vectors. Several theoretical results about such a class of bisexual models with immigration were developed in [9, 11] and [17]. In this work, we shall introduce a more general class of bisexual processes where, in each generation, the immigration of females and males depends on the numbers of females and males in the population. The paper is organized as follows: In Sect. 19.2, the bisexual process with immigration of females and males is formally described and its intuitive interpretation is provided. In Sect. 19.3, the mean growth rates per couple for the new model are introduced. Then, the existence of the asymptotic growth rate is proved in Theorem 19.1. Sect. 19.4 deals with the supercritical case, namely, when the asymptotic growth rate is greater than one. For such a situation, several limiting results are derived in Theorems 19.2, 19.3 and 19.4.

19.2 The bisexual process with immigration

On a sufficiently probability space $(\Omega, \mathscr{F}, P)$, let us define the following bisexual branching process with immigration of females and males initiated with $Z_0 = N_0$ couples:

$$(F_{n+1}, M_{n+1}) = \sum_{i=1}^{Z_n} (f_{n,i}, m_{n,i}) + \left(F^I_{n+1}(f_{n\star}), M^I_{n+1}(m_{n\star})\right),$$

$$Z_{n+1} = L(F_{n+1}, M_{n+1}),\ n \in \mathrm{Z}^+ \tag{19.1}$$

where the empty sum is considered to be $(0,0)$ and Z^+ denotes the set of nonnegative integers. The random vector $(f_{n,i}, m_{n,i})$ represents the numbers of females and males descending from the ith couple of the nth generation, $\{(f_{n,i}, m_{n,i}),\ i \geq 1;\ n \geq 0\}$ is a sequence of independent and identically distributed random vectors, its common probability law will be referred as the offspring probability distribution. On the other hand, $(F^I_{n+1}(f_{n\star}), M^I_{n+1}(m_{n\star}))$, with $f_{n\star} = \sum_{i=1}^{Z_n} f_{n,i}$ and $m_{n\star} = \sum_{i=1}^{Z_n} m_{n,i}$, represents the numbers of immigrant females and males in the $(n+1)$th generation. Given $j, l \in \mathrm{Z}^+$, it is assumed that $\{(F^I_{n+1}(j), M^I_{n+1}(l))\}_{n=0}^{\infty}$ is a sequence of independent and identically distributed random vectors. We shall denote by (μ_f, μ_m) and $(\mu_f^{j,l}, \mu_m^{j,l})$, $j, l \in \mathrm{Z}^+$, respectively, the offspring mean vector and the immigration mean vectors assumed to be positive and finite. Finally, $L : \mathrm{R}^+ \times \mathrm{R}^+ \to \mathrm{R}^+$ is the mating function, assumed to be nondecreasing in each argument, integer-valued on the integers, and such that $L(x,0) = L(0,y) = 0$, $x, y \in \mathrm{R}^+$, with R^+ denoting the set of nonnegative real numbers. Also, throughout this paper, we shall consider that L is a superadditive function, namely:

$$L(x_1 + x_2, y_1 + y_2) \geq L(x_1, y_1) + L(x_2, y_2),\ x_i, y_i \in \mathrm{R}^+,\ i = 1, 2.$$

Note that in this class of models the immigration of females and males depends on the numbers of females and males in the population. Intuitively, (F_{n+1}, M_{n+1}) represents the numbers of females and males in the $(n+1)$th generation which form Z_{n+1} couples according to the mating function L. It can be verified that $\{Z_n\}_{n=0}^{\infty}$ and $\{(F_n, M_n)\}_{n=1}^{\infty}$ are Markov chains with stationary transition probabilities.

It is pointing out that in addition its theoretical interest, the class of processes introduced in (19.1) has also practical implications, especially in population dynamics. It includes as particular cases the bisexual processes introduced in [6] and [8]. In order to derive some theoretical results about its limiting behaviour we introduce the following working assumption:

(A): The sequences $\{F_1^I(j)\}_{j=0}^{\infty}$ and $\{M_1^I(l)\}_{l=0}^{\infty}$ are such that, for $j, l \in \mathrm{Z}^+$, $E\left[g(F_1^I(j+1))\right] \leq E[g(F_1^I(j))]$ and $E\left[g(M_1^I(l+1))\right] \leq E[g(M_1^I(l))]$, where g is a nondecreasing function.

Remark 19.1. From *(A) it is derived (see for details [14]) the existence of random variables $F^I(j)$ and $F^I(j+1)$ defined on the same probability space and having the same respective probability distributions than $F_1^I(j)$ and $F_1^I(j+1)$ and the existence of a nonnegative integer-valued random variable $F^I(j, j+1)$ such that $F^I(j) = F^I(j+1) + F^I(j, j+1)$, $j \in \mathrm{Z}^+$. Similarly, it is deduced the existence of random variables $M^I(l))$ and $M^I(l+1))$ defined on the same probability space and having the same respective probability distributions that $M_1^I(l)$ and $M_1^I(l+1))$ and the existence of a nonnegative integer-valued random variable $M^I(l, l+1)$ such that $M^I(l) = M^I(l+1) + M^I(l, l+1)$, $l \in \mathrm{Z}^+$. Also, it is deduced that*

(i) $\{F^I(j)\}_{j=0}^{\infty}$ *(respectively* $\{M^I(l)\}_{l=0}^{\infty}$*) is a monotone nonincreasing sequence which converges almost surely to a nonnegative, integer-valued random variable* F^I *(respectively* M^I*).*

(ii) $\{E[g(F^I(j))]\}_{j=0}^{\infty}$ *(respectively* $\{E[g(M^I(l))]\}_{l=0}^{\infty}$*) is a monotone nonincreasing sequence which converges to* $E[g(F^I)]$ *(respectively* $E[g(M^I)]$*), for every nondecreasing function g.*

19.3 The asymptotic growth rate

The concept of mean growth rate per couple, defined in [5] for the Daley's bisexual Galton–Watson process introduced in [6] may be extended for the class of processes given in (19.1).

Definition 19.1. For every positive integer k, we define the mean growth rate per couple as:

$$R_k := \frac{1}{k} E[Z_{n+1} \mid Z_n = k] = \frac{1}{k} E\left[L\left(\sum_{i=1}^{k} f_{n,i} + F_{n+1}^I(f_{n\star}),\ \sum_{i=1}^{k} m_{n,i} + M_{n+1}^I(f_{n\star}) \right) \right].$$

Next we establish conditions which guarantee the existence of the asymptotic growth rate, namely $R := \lim_{k\to\infty} R_k$.

Theorem 19.1. *Assume (A) and mating function L such that* $L(x,y) \le x+y,\ x,y \in \mathrm{R}^+$. *Then,*

$$R = \lim_{k\to\infty} \frac{1}{k} L(k\mu_f, k\mu_m)$$

where recall that $\mu_f = E[f_{0,1}]$ *and* $\mu_m = E[m_{0,1}]$ *both assumed to be positive and finite values.*

Proof. Let $\{(F_n^{j,l}, M_n^{j,l})\}_{n=1}^{\infty}$ (with $j,l \in \mathrm{Z}^+$ fixed) and $\{(F_n', M_n')\}_{n=1}^{\infty}$ be the bisexual processes with immigration of females and males defined, for $n \in \mathrm{Z}^+$, as follows:

$$(F_{n+1}^{j,l}, M_{n+1}^{j,l}) = \sum_{i=1}^{Z_n^{j,l}} (f_{n,i}, m_{n,i}) + \left(F_{n+1}^I(j), M_{n+1}^I(l)\right),\ Z_{n+1}^{j,l} = L(F_{n+1}^{j,l}, M_{n+1}^{j,l}) \quad (19.2)$$

$$(F_{n+1}', M_{n+1}') = \sum_{i=1}^{Z_n'} (f_{n,i}, m_{n,i}) + (F_{n+1}^I, M_{n+1}^I),\ \ Z_{n+1}' = L(F_{n+1}', M_{n+1}') \qquad (19.3)$$

where $Z_0^{j,l} = Z_0' = N_0$.

Notice that (19.2) and (19.3) are bisexual processes with the same offspring probability distribution and the same mating function than the considered in the process introduced in (19.1), but now the immigration of females and males is governed, respectively, by the sequences $\{(F_n^I(j), M_n^I(l))\}_{n=1}^{\infty}$ and $\{(F_n^I, M_n^I)\}_{n=1}^{\infty}$, being (F_n^I, M_n^I) random vectors independent and with the same probability distribution that (F^I, M^I), see Remark 19.1.

For each positive integer k, let us consider the mean growth rates:

$$R_k^{j,l} := \frac{1}{k} E\left[Z_{n+1}^{j,l} \mid Z_n^{j,l} = k\right] = \frac{1}{k} E\left[L\left(\sum_{i=1}^{k} f_{n,i} + F_{n+1}^{j,l}(j),\ \sum_{i=1}^{k} m_{n,i} + M_{n+1}^{j,l}(l)\right)\right]$$

and

$$R_k' := \frac{1}{k} E\left[Z_{n+1}' \mid Z_n' = k\right] = \frac{1}{k} E\left[L\left(\sum_{i=1}^{k} f_{n,i} + F_{n+1}^I,\ \sum_{i=1}^{k} m_{n,i} + M_{n+1}^I\right)\right].$$

By using the fact that the mean vectors (μ_f, μ_m) and $(\mu_f^{j,l}, \mu_m^{j,l})$ are positive and finite and taking into account Propositions 2.1 and 2.2 in [11], one deduces the existence of the asymptotic growth rates:

$$R^{j,l} := \lim_{k\to\infty} R_k^{j,l} \quad \text{and} \quad R' := \lim_{k\to\infty} R_k'.$$

Moreover

$$R^{j,l} = R' = \lim_{k\to\infty} \frac{1}{k} L(k\mu_f, k\mu_m) \tag{19.4}$$

Now, by Remark 19.1, one has for $k \geq 1$,

$$E\left[L\left(\sum_{i=1}^{k} f_{n,i} + F_{n+1}^{I}(f_{n\star}),\ \sum_{i=1}^{k} m_{n,i} + M_{n+1}^{I}(m_{n\star})\right)\right]$$
$$\geq E\left[L\left(\sum_{i=1}^{k} f_{n,i} + F_{n+1}^{I},\ \sum_{i=1}^{k} m_{n,i} + M_{n+1}^{I}\right)\right].$$

Hence

$$\liminf_{k\to\infty} \frac{1}{k} E\left[L\left(\sum_{i=1}^{k} f_{n,i} + F_{n+1}^{I}(f_{n\star}),\ \sum_{i=1}^{k} m_{n,i} + M_{n+1}^{I}(m_{n\star})\right)\right] \geq R'. \tag{19.5}$$

On the other hand, for $j,l \in \mathrm{Z}^{+}$ fixed again by Remark 19.1, one deduces that

$$\limsup_{k\to\infty} \frac{1}{k} E\left[L\left(\sum_{i=1}^{k} f_{n,i} + F_{n+1}^{I}(f_{n\star}),\ \sum_{i=1}^{k} m_{n,i} + M_{n+1}^{I}(m_{n\star})\right)\right]$$

$$\leq \lim_{k\to\infty} \frac{1}{k} E\left[L\left(\sum_{i=1}^{k} f_{n,i} + F_{n+1}^{I}(j),\ \sum_{i=1}^{k} m_{n,i} + M_{n+1}^{I}(l)\right)\right] = R^{j,l}. \tag{19.6}$$

Finally, by (19.4), (19.5) and (19.6), one derives the existence of $R = \lim_{k\to\infty} R_k$ and the fact that $R = \lim_{k\to\infty} \frac{1}{k} L(k\mu_f, k\mu_m)$. □

Definition 19.2. The bisexual process presented in (19.1) is said to be subcritical, critical, or supercritical if $R < 1$, $R = 1$, or $R > 1$, respectively.

19.4 Limit behavior for the supercritical case

In this Section, we shall focuss the interest in a supercritical bisexual process (19.1) verifying condition (A). We shall investigate the limiting behaviour of the sequences:

$$\{R^{-n}Z_n\}_{n=0}^{\infty},\ \{{Z_n}^{-1}F_{n+1}\}_{n=0}^{\infty},\ \{{Z_n}^{-1}M_{n+1}\}_{n=0}^{\infty},\ \{R^{-n}F_n\}_{n=1}^{\infty} \text{ and } \{R^{-n}M_n\}_{n=1}^{\infty}.$$

Let us consider the sequence $\{\mathscr{E}_k\}_{k=1}^{\infty}$ where $\mathscr{E}_k = R - R_k$. By Theorem 19.1, it is clear that $\lim_{k\to\infty} \mathscr{E}_k = 0$.

Theorem 19.2. *Assume that, for some constants $H, \alpha > 0$, $|\mathscr{E}_k| < Hk^{-\alpha}$, $k \geq 1$. Then $\{W_n\}_{n=0}^{\infty}$, with $W_n = R^{-n}Z_n$, converges almost surely to a nonnegative and finite random variable W as $n \to \infty$.*

Proof. Let $\mathscr{F}_n = \sigma(Z_0, \ldots, Z_n)$ be the σ-algebra generated by the variables $Z_0, \ldots, Z_n$.

One has that

$$E[Z_{n+1} \mid \mathscr{F}_n] = Z_n R_{Z_n} = Z_n R - Z_n \mathscr{E}_{Z_n} \quad a.s.$$

Hence, it is derived that

$$|E[Z_{n+1} \mid \mathscr{F}_n] - Z_n R| = |Z_n \mathscr{E}_{Z_n}| < H{Z_n}^{1-\alpha} \quad a.s.$$

Therefore,

$$|E[W_{n+1} \mid \mathscr{F}_n] - W_n| < HW_n^{1-\alpha} R^{-n\alpha-1} \quad a.s. \tag{19.7}$$

Taking expectations and using the fact that $\phi(x) = x^{1-\alpha}$, $x \in \mathrm{R}^+$ is a concave function, one deduces that

$$|E[W_{n+1}] - E[W_n]| < HE[W_n^{1-\alpha}]R^{-n\alpha-1} \leq H(E[W_n])^{1-\alpha}R^{-n\alpha-1}. \tag{19.8}$$

Finally, from (19.7) and (19.8), using a similar reasoning to that one considered in Theorem 1.7 of [15] the proof is complete. □

Theorem 19.3. *On $[Z_n \to \infty]$, the sequences $\{{Z_n}^{-1}F_{n+1}\}_{n=0}^{\infty}$ and $\{{Z_n}^{-1}M_{n+1}\}_{n=0}^{\infty}$ converge almost surely to μ_f and μ_m, respectively, as $n \to \infty$.*

Proof. From condition (A) and taking into account Remark 19.1 and Theorem 4.1 (i) in [11], one deduces on $[Z_n \to \infty]$ that

$$\liminf_{n\to\infty} Z_n^{-1}\left(\sum_{i=1}^{Z_n} f_{n,i} + F_{n+1}^I(f_{n\star})\right) \geq \lim_{n\to\infty} Z_n^{-1}\left(\sum_{i=1}^{Z_n} f_{n,i} + F_{n+1}^I\right) = \mu_f \quad a.s. \tag{19.9}$$

where $\{F_n^I\}_{n=1}^{\infty}$ is a sequence of independent and identically distributed random variables, being their common probability distribution the corresponding to F^I.

From a similar reasoning one has, on $[Z_n \to \infty]$, and $j, l \in \mathrm{Z}^+$ fixed, that

$$\limsup_{n\to\infty} Z_n^{-1}\left(\sum_{i=1}^{Z_n} f_{n,i} + F_{n+1}^I(f_{n\star})\right) \leq \lim_{n\to\infty} Z_n^{-1}\left(\sum_{i=1}^{Z_n} f_{n,i} + F_{n+1}^I(j)\right) = \mu_f \quad a.s. \tag{19.10}$$

By (19.9) and (19.10) one obtains, on $[Z_n \to \infty]$, that

$$\lim_{n\to\infty} Z_n^{-1}\left(\sum_{i=1}^{Z_n} f_{n,i} + F_{n+1}^I(f_{n\star})\right) = \lim_{n\to\infty} {Z_n}^{-1}F_{n+1} = \mu_f \quad a.s.$$

Analogously it is derived, on the set $[Z_n \to \infty]$, that $\{{Z_n}^{-1}M_{n+1}\}_{n=0}^{\infty}$ converges almost surely to μ_m as $n \to \infty$. □

Next we establish an analogous result for the class of processes introduced in (19.1) to the classical Kesten-Stigum result, see e.g. [3].

Theorem 19.4. *Assume that* $\mathscr{E}_k \geq 0,\ k \geq 1.$

(i) If $\{R^{-n}F_n\}_{n=1}^{\infty}$ *converges almost surely to* F *as* $n \to \infty$ *where* $P(0 \leq F < \infty) = 1$ *then,* $E[f_{0,1} \log^+ f_{0,1}] < \infty$ *is a necessary condition in order that* F *be a nondegenerate at 0 random variable.*

(ii) If $\{R^{-n}M_n\}_{n=1}^{\infty}$ *converges almost surely to* M *as* $n \to \infty$ *where* $P(0 \leq M < \infty) = 1$ *then,* $E[m_{0,1} \log^+ m_{0,1}] < \infty$ *is a necessary condition in order that* M *be a nondegenerate at 0 random variable.*

Proof. First, note that

$$E[W_{n+1} \mid \mathscr{F}_n] = R^{-(n+1)}(R - \mathscr{E}_{Z_n} Z_n) = W_n - R^{-(n+1)} \mathscr{E}_{Z_n} Z_n \quad a.s.$$

Then, taking expectation and using the fact that $\mathscr{E}_k \geq 0,\ k \geq 1$, one deduces that

$$E[W_{n+1}] = E[W_n] - R^{-(n+1)} E\left[\mathscr{E}_{Z_n} Z_n\right] \leq E[W_n] \leq \cdots \leq E[Z_0] = N_0. \qquad (19.11)$$

Now, by condition (A) and Remark (2.1)(i), it is deduced (see e.g. [14]) that the sequences $\{(F^I(j)\}_{j=0}^{\infty}$ and $\{M^I(l))\}_{l=0}^{\infty}$ are such that, for each $j, l \in \mathrm{Z}^+$,

$$F^I \leq_{st} F^I(j) \leq_{st} F^I(0) \quad \text{and} \quad M^I \leq_{st} M^I(l) \leq_{st} F^I(0) \qquad (19.12)$$

where $\leq_{st}$ denotes the stochastic order[1].

Let $\{\widetilde{Z}_n\}_{n=0}^{\infty}$ and $\{\widehat{Z}_n\}_{n=0}^{\infty}$ be the sequences defined, for $n \in \mathrm{Z}^+$, in the form:

$$\widetilde{Z}_{n+1} = L(\widetilde{F}_{n+1}, \widetilde{M}_{n+1}), \quad (\widetilde{F}_{n+1}, \widetilde{M}_{n+1}) = \sum_{i=1}^{Z_n} (\widetilde{f}_{n,i}, \widetilde{m}_{n,i}) + (F^I, M^I),$$

$$\widehat{Z}_{n+1} = L(\widehat{F}_{n+1}, \widehat{M}_{n+1}), \quad (\widehat{F}_{n+1}, \widehat{M}_{n+1}) = \sum_{i=1}^{Z_n} (\widehat{f}_{n,i}, \widehat{m}_{n,i}) + (F^I(0), M^I(0))$$

where $\widetilde{Z}_0 = \widehat{Z}_0 = Z_0 = N_0$, $(\widetilde{f}_{n,i}, \widetilde{m}_{n,i})$ and $(\widehat{f}_{n,i}, \widehat{m}_{n,i})$ being random vectors with the same distribution that $(f_{n,i}, m_{n,i})$. Hence $E[\widetilde{f}_{0,1}] = E[\widehat{f}_{0,1}] = E[f_{0,1}] = \mu_f$ and $E[\widetilde{m}_{0,1}] = E[\widehat{m}_{0,1}] = E[m_{0,1}] = \mu_m$. Finally, L and $\{Z_n\}_{n=0}^{\infty}$ are the mating function and the sequence of couples, respectively, given in (19.1).

From (19.12), by stochastic order properties (see e.g. [24]) one deduces that

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[1] Given the random variables X and Y we say that X is stochastically smaller than Y and we write $X \leq_{st} Y$ if $P(X \leq t) \geq P(Y \leq t),\ t \in \mathrm{R}$

$$\widetilde{F}_{n+1} \leq_{st} F_{n+1} \leq_{st} \widehat{F}_{n+1},\ n \in \mathrm{Z}^+. \tag{19.13}$$

Now, taking into account the proof in Theorem 19.1, it is derived the existence of the asymptotic growth rates:

$$\widetilde{R} := \lim_{k\to\infty} k^{-1} E[\widetilde{Z}_{n+1} \mid \widetilde{Z}_n] \text{ and } \widehat{R} := \lim_{k\to\infty} k^{-1} E[\widehat{Z}_{n+1} \mid \widehat{Z}_n].$$

Moreover $\widetilde{R} = \widehat{R} = R$.

Hence, by (19.13), one has that

$$\widetilde{R}^{-(n+1)}\widetilde{F}_{n+1} \leq_{st} R^{-(n+1)}F_{n+1} \leq_{st} \widehat{R}^{-(n+1)}\widehat{F}_{n+1},\ n \in \mathrm{Z}^+.$$

By Theorem 19.3, one derives that, on $[Z_n \to \infty]$, the sequences $\{\widetilde{Z}_n^{-1}\widetilde{F}_{n+1}\}_{n=0}^{\infty}$ and $\{\widehat{Z}_n^{-1}\widehat{F}_{n+1}\}_{n=0}^{\infty}$ converge almost surely to μ_f as $n \to \infty$.

Taking into account (19.11) and Theorem 2.1 in [17], result in Theorem 19.4(i) holds. In a similar way it is proved result in Theorem 19.4(ii). □

Corollary 19.1. *Assume* $P(Z_n \to \infty) = 1$. *Then, under requirements in Theorem 19.4,* $E[f_{0,1} \log^+ f_{0,1}] < \infty$ *and* $E[m_{0,1} \log^+ m_{0,1}] < \infty$ *are necessary conditions in order that* $P(0 < W < \infty) = 1$, *where recall that* W *is the almost sure limit of* $\{W_n\}_{n=0}^{\infty}$ *as* $n \to \infty$.

Proof. By the definition of $\{\widetilde{Z}_n\}_{n=0}^{\infty}$ and $\{\widehat{Z}_n\}_{n=0}^{\infty}$ given in Theorem 19.4, it is verified that

$$\widetilde{Z}_n \leq_{st} Z_n \leq_{st} \widehat{Z}_n, \quad n \in \mathrm{Z}^+.$$

Thus, using that $\widetilde{R} = \widehat{R} = R$,

$$\widetilde{W}_n \leq_{st} W_n \leq_{st} \widehat{W}_n, \quad n \in \mathrm{Z}^+$$

where $\widetilde{W}_n = \widetilde{R}^{-n}\widetilde{Z}_n$, $W_n = R^{-n}Z_n$ and $\widehat{W}_n = \widehat{R}^{-n}\widehat{Z}_n$.

Then, by considering Theorem 19.4, we conclude the proof. □

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20
Two-sex branching process literature

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Abstract With the purpose to model the probabilistic evolution of populations where females and males coexist and form couples, in 1968, D. J. Daley introduced the called bisexual Galton–Watson branching process. From Daley's process general setting, new classes of discrete time two-sex branching processes have been investigated. They include processes with immigration, in varying environments, in random environments, depending on the number of couples in the population, and controlled processes. Also, some classes of continuous time two-sex branching processes have been studied. This work is intended to be a summary of the literature associated with such classes of two-sex branching processes.

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20.1 Introduction

D. J. Daley in his paper entitled *Extinction conditions for certain bisexual Galton–Watson branching processes* (see [8]) introduced the first two-sex branching process, the called *bisexual Galton–Watson branching process*.

Since Daley's work, the interest on two-sex (bisexual) branching processes increased and more than 30 authors from different countries have contributed 56 papers in several journals until the year 2008. Nowadays, the two-sex branching process theory is an active research area of both theoretical interest and applicability to such fields as biology, demography, ecology, genetics, medicine, population dynamics, and physics.

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In this work, a survey of the research papers associated with two-sex branching processes is provided. In addition to this introductory Section, five additional Sections are included. In Sect. 20.2, we concentrate our attention on the Daley's bisexual process and its literature associated. In Sects. 20.3 and 20.4, we provide a brief summary about the new classes of discrete time and continuous time two-sex branching processes investigated, respectively. Section 20.5 is devoted to considering the main fields of applications where two-sex branching processes have been used as mathematical models. Finally, in Sect. 20.6, some suggestions for further research are pointed out.

20.2 The Daley's two-sex branching process

In Daley's two-sex process, the population consists in two disjoint classes, the females and the males. The reproduction is accomplished only through couples (also called mating units). A couple is formed by one female and one male of the same generation who come together for the main purpose of procreation. Each couple produces offspring, independently of the others couples, according to a given offspring probability distribution $\{p_k\}_{k\geq 0}$, p_k being the probability that a couple produces k new individuals. It is assumed that an individual is female with probability $\alpha \in (0,1)$ and male with probability $1-\alpha$. An alternative approach is to consider an offspring probability distribution $\{p_{i,j}\}_{i,j\geq 0}$ where $p_{i,j}$ denotes the probability that a couple produces i females and j males.

Let Z^+ be the set of nonnegative integers. Formally, the bisexual Galton–Watson process $\{(F_n,M_n)\}_{n\geq 1}$ is defined as follows:

$$(F_{n+1},M_{n+1}) = \sum_{i=1}^{Z_n}(f_{n,i},m_{n,i}), \quad Z_{n+1} = L(F_{n+1},M_{n+1}), \ \ n \in \mathrm{Z}^+$$

where:

1. The empty sum is considered to be $(0,0)$.
2. (F_{n+1},M_{n+1}) represents the number of females and males in the $(n+1)$th generation. These females and males form $Z_{n+1} = L(F_{n+1},M_{n+1})$ couples which reproduce independently and with the same offspring probability distribution. Initially there are a positive number N_0 of couples in the population, i.e. $Z_0 = N_0$.
3. $(f_{n,i},m_{n,i})$ represents the number of females and males descending from the ith couple of the nth generation. It is assumed that $\{(f_{n,i},m_{n,i}),\ n \in \mathrm{Z}^+,\ i = 1,\ldots,Z_n\}$ are independent and identically distributed nonnegative random vectors.
4. L is a function defined on $\mathrm{R}^+ \times \mathrm{R}^+$ and taking values in R^+, with R^+ denoting the set of nonnegative real numbers. It is called the mating function and is assumed to be nondecreasing in each argument, integer-valued on the integers and such that $L(x,0) = L(0,y) = 0,\ x,y \in \mathrm{R}^+$.

It is easy to verify that $\{Z_n\}_{n\geq 0}$ is a Markov chain with the nonnegative integers as the state space, 0 being an absorbing state and each positive integer k being a transient state.

If, for some n, $Z_n = 0$ then the two-sex population extinction will occur. Let $q_j = P(\lim_{n\uparrow\infty} Z_n = 0 \mid Z_0 = j)$ be the extinction probability when initially there are $j \geq 1$ couples in the population.

In Daley's initial work the extinction problem was investigated for the following two intuitive mating functions:

(A) $L(x,y) = x\min\{1,y\}$.

It was called the *completely promiscuous mating* and assumes that a single male will emerge in each generation and then will mate with every female of that generation. All other males of this generation are excluded from the mating process. By using some techniques based in analytic iteration of functions it was proved that:

$$q_j = 1,\ j \geq 1 \quad \text{if and only if} \quad \alpha m \leq 1$$

where $m = \sum_{k=0}^{\infty} k p_k$.

(B) $L(x,y) = \min\{x, dy\}$, d being a positive integer.

It was called the *polygamous mating with perfect fidelity*. The females practice perfect fidelity, they are allowed to have at most one mate, and the males (or at least some males) practice polygamy, a male may have up to d wives if enough females are available. The particular case $d = 1$ corresponds to the perfect fidelity mating function. D.J. Daley proved that:

$$q_j = 1,\ j \geq 1 \quad \text{if and only if} \quad \min\{\alpha m\ ,\ d(1-\alpha)m\} \leq 1.$$

By considering a different probabilistic approach, similar conclusions were obtained in [37].

The first attempt to use mating functions other than Daley's two mating functions was made by Hull [31]. He considered superadditive mating functions, namely functions L such that

$$L(x_1 + x_2, y_1 + y_2) \geq L(x_1, y_1) + L(x_2, y_2),\ x_i, y_i \in \mathrm{R}^+,\ i = 1,2.$$

Superadditivity expresses the intuitive notion that $x_1 + x_2$ females and $y_1 + y_2$ males coexisting together will form a number of couples that is at least at great as the total number of couples formed by x_1 females and y_1 males, and x_2 females and y_2 males, living separately.

By comparison with an stochastic process where only offspring produced by the same couple are able to mate, D. M. Hull proved that $E[Z_1 \mid Z_0 = 1] \leq 1$ was a necessary condition for $q_j = 1,\ j \geq 1$. By using a counterexample, he showed that it was not a sufficient condition.

An alternative proof of Hull's necessary condition for certain extinction it was provided by González and Molina [15]. They established that:

$$f_n(s) \leq f_{n-1}(f_1(s)),\ s \in [0,1],\ n = 1,2,\ldots$$

where $f_n(s) = E[s^{Z_n}]$. As consequence, they derived that $E[Z_n] \geq (E[Z_1])^n,\ n \geq 1$ and the Hull's necessary condition.

In order to obtain sufficient conditions for the population extinction, F.T. Bruss (see [6]) introduced the concept of *mean growth rate per couple* defined for each positive integer j in the form:

$$r_j = j^{-1}E[Z_1 \mid Z_0 = j],\ j \geq 1.$$

He proved that $r_j \leq 1$ for all sufficiently large j is a sufficient condition for the almost sure extinction of the two-sex population. Also, making use of an auxiliary multitype branching process and taking into account some results of the multitype branching process theory, conditions which are both necessary and sufficient for extinction were provided in [32].

The paper by Daley et al. (see [9]) contributed important results to the bisexual Galton–Watson process theory. They derived several monotonicity properties, proved that $\{r_j\}_{j\geq 1}$ has a limit r, the called *asymptotic growth rate*, and deduced that $r = \sup_{j\geq 1} r_j$. Moreover, for a bisexual Galton–Watson process with superadditive mating function, they proved that

$$q_j = 1,\ j \geq 1 \quad \text{if and only if} \quad r \leq 1$$

and determined upper and lower bounds for the extinction probability.

Note that, in [9] it was established conditions which guarantee the extinction for all possible positive values of Z_0. But, if these conditions do not hold, the question is: How large a value of Z_0 will move the process away from certain extinction?

A first attempt to answer this question was provided by Hull [33]. He considered *population bounded superadditive functions*, namely superadditive functions verifying that $L(1,1) = 1$ and $L(x,y) \leq \min\{xy, x+y\}$. For a bisexual Galton–Watson process governed by a population bounded mating function and such that $r > 1$ he proved that:

$$q_j < 1 \quad \text{if and only if} \quad P(Z_1 > j \mid Z_0 = j) > 0.$$

Alsmeyer and Rösler [1] investigated the sequence of ratios $\{q_j/q^j\}_{j\geq 1}$ where the numerator is the extinction probability of the process governed by the completely promiscuous mating function and the denominator represents the extinction probability of the process governed by the mating function $L(x,y) = x$ when $Z_0 = j$. They obtained upper and lower bounds for such a sequence and established a linkage to the standard Galton–Watson branching theory by comparing the completly promiscuous process to a standard process based on female lines of descent where extinction can also occur because there are no males in the generation. Also, they determined an equation, which when solved provides the extinction probability for a completely promiscuous process.

In a second paper (see [2]) they continued their research about the sequence $\{q_j/q^j\}_{j\geq 1}$, identifying these ratios as a certain functional of a classical subcritical

Galton–Watson branching process. Then, by using such functionals, a distinction was made between the convergence of these ratios and a second case where these ratios do not converge, but rather oscillate very slowly.

Also, sequences of lower and upper bounds for the extinction probabilities were derived in [35].

The first paper about convergence results concerning the bisexual Galton–Watson process was published by Bagley [5]. Assuming $Z_0 = 1$ and $L(x,y) = \min\{x,y\}$, he proved that if $\tau = \min\{\alpha m, (1-\alpha)m\} > 1$ then there exists a nonnegative and finite random variable W such that $\{\tau^{-n}M_n\}_{n\geq 1}$ and $\{\tau^{-n}F_n\}_{n\geq 1}$ converge almost surely to W and $\alpha(1-\alpha)^{-1}W$, respectively, as $n \to \infty$. Also, he established that:

$$E[M_1 \log^+ M_1] = \infty \text{ (or } E[F_1 \log^+ F_1] = \infty\text{) implies that } P(W = 0) = 1$$

and

$$E[M_1 \log^+ M_1] < \infty \text{ (or } E[F_1 \log^+ F_1] < \infty\text{) implies that } P(W > 0) = 1 - q_1.$$

Thanks to the probabilistic techniques considered by F. Klebaner (see [38] and [39]) in his research on population-size dependent asexual branching processes, Bagley's results were extended to superadditive mating functions in the papers by M. González and M. Molina (see [16–20]) where several limiting results about the almost sure, L^1 and L^2 convergence of the sequences $\{r^{-n}Z_n\}_{n\geq 0}$, $\{r^{-n}F_n\}_{n\geq 1}$ and $\{r^{-n}M_n\}_{n\geq 1}$ were provided. Also, the limiting behaviour of $\{\sum_{i=0}^{n} Z_i\}_{n\geq 0}$ suitably normalized was investigated.

Statistical inference about the Daley's bisexual process has been developed. In fact, a substancial number of estimators having good properties have been proposed for the estimation of the offspring probability distribution, the offspring mean vector, the offspring covariance matrix, and the asymptotic growth rate.

Assuming superadditive mating function such that $L(x,y) \leq x$, maximun likelihood estimators for the offspring mean vector and the asymptotic growth rate were determined in [29].

Unbiased, consistent, and asymptotically normal ratio estimators for the offspring mean vector were provided in [28].

Several classes of estimators, under non-parametric or parametric context and from a classical or a Bayesian point of view, for the above mentioned parameters were determined, and their asymptotic properties studied in [23] and [42].

Finally, some multitype versions of the bisexual Galton–Watson branching process were considered in [34] and [37].

For more information about the literature on the bisexual Galton–Watson branching process we refer the reader to the references [30] and [36].

20.3 Discrete time two-sex branching processes

In order to describe the probabilistic evolution of more complicated populations that Daley's two-sex population, several classes of discrete time two-sex branching processes have been introduced and some theoretical contributions about them derived. Next we provide, from a historical outlook, some brief information about such classes of processes. To simplify, the discrete time two-sex processes investigated until now (from Daley's process setting) could be grouped in the general classes:

1. Processes with immigration.
2. Processes in varying or in random environments.
3. Processes depending on the number of couples in the population.
4. Processes with control on the number of progenitor couples.
5. Others classes of two-sex processes

The main topics investigated have been: Probabilistic properties, extinction problem, asymptotic behaviour, statistical inference, and applications.

20.3.1 Processes with immigration

(A) *Processes with immigration of females and males.*

The novelty with respect the Daley's model is that it is allowed, in each generation, the incorporation of females and males from others populations:

$$(F_{n+1}, M_{n+1}) = \sum_{i=1}^{Z_n} (f_{n,i}, m_{n,i}) \ + \ (F^I_{n+1}, M^I_{n+1}), \ Z_{n+1} = L(F_{n+1}, M_{n+1}), \ n \in \mathrm{Z}^+$$

where $Z_0 = N_0 \geq 1$. The random vector (F^I_{n+1}, M^I_{n+1}) represents the number of immigrant females and males in the $(n+1)$th generation, $\{(F^I_n, M^I_n)\}_{n\geq 1}$ is a sequence of independent and identically distributed nonnegative random vectors. It is assumed that $\{(F^I_n, M^I_n)\}_{n\geq 1}$ and $\{(f_{n,i}, m_{n,i}),\ n \in \mathrm{Z}^+,\ i = 1, \ldots, Z_n\}$ are independent sequences. Some probabilistic properties, limiting results, and inferential questions for this class of processes were established in [21, 22] and [25].

(B) *Processes with immigration of couples.*

In this class of processes it is allowed, in each generation, the immigration of couples from outside populations:

$$(F_{n+1}, M_{n+1}) = \sum_{i=1}^{Z_n} (f_{n,i}, m_{n,i}), \ Z_{n+1} = L(F_{n+1}, M_{n+1}) + I_{n+1}, \ n \in \mathrm{Z}^+$$

where $Z_0 = N_0 \geq 1$. The variable I_{n+1} represents the number of immigrant couples in the $(n+1)$th generation, $\{I_n\}_{n\geq 1}$ is a sequence of independent and identically distributed nonnegative random variables. It is assumed that $\{I_n\}_{n\geq 1}$ and $\{(f_{n,i}, m_{n,i}),\ n \in \mathrm{Z}^+,\ i = 1, \ldots, Z_n\}$ are independent. Some probabilistic properties and results about its limiting evolution were derived in [21, 24] and [41].

20.3.2 Processes in varying or in random environments

(A) *Processes in varying environments.*
It is allowed a different offspring probability distribution in each generation:

$$(F_{n+1}, M_{n+1}) = \sum_{i=1}^{Z_n} (f_{n,i}, m_{n,i}),\ Z_{n+1} = L(F_{n+1}, M_{n+1}),\ n \in \mathrm{Z}^+.$$

where $Z_0 = N_0 \geq 1$. For each n, $\{(f_{n,i}, m_{n,i})\}_{i\geq 1}$ is a sequence of independent and identically distributed nonnegative random vectors with common probability distribution $p_{k,l}^{(n)} = P(f_{n,1} = k, m_{n,1} = l),\ k,l \in \mathrm{Z}^+$. In this class of processes, the sequences $\{(F_n, M_n)\}_{n\geq 1}$ and $\{Z_n\}_{n\geq 0}$ are nonhomogeneous Markov chains. Some probabilistic properties, necessary and sufficient conditions for the almost sure extinction, and limiting results were investigated in [44–47] and [50].

(B) *Processes in random environments.*
The offspring probability distribution is governed according to a random environment process $\{\xi_n\}_{n\geq 0}$:

$$(F_{n+1}, M_{n+1}) = \sum_{i=1}^{Z_n} (f_{n,i}(\xi_n), m_{n,i}(\xi_n)),\ Z_{n+1} = L(F_{n+1}, M_{n+1}),\ n \in \mathrm{Z}^+$$

This class of processes was introduced by Ma [40] where several probabilistic properties and some results concerning its extinction probability where provided. Recently, Fernández et al. [11] have introduced a two-sex process where the offspring probability distribution depends on some fertility parameters which evolve randomly in time. They have proved that the total population increases, in some stochastic sense, as the positive dependence between the fertility indexes increases.

20.3.3 Processes depending on the number of couples in the population

(A) *Processes with mating function depending on the number of couples.*

$$(F_{n+1}, M_{n+1}) = \sum_{i=1}^{Z_n} (f_{n,i}, m_{n,i}),\ Z_{n+1} = L_{Z_n}(F_{n+1}, M_{n+1}), \quad n \in \mathrm{Z}^+$$

where $Z_0 = N_0 \geq 1$ and $\{L_k\}_{k\geq 0}$ is a sequence of mating functions. If, for some n, $Z_n = k$ then L_k is the function that determine the number of couples formed in the $(n+1)$th generation. Some contributions about stochastic monotony properties, accumulated progeny, extinction probability, and limiting behaviour for such a class of processes have been established in [43, 48, 49, 51] and [52]. Also, statistical inference for its main parameters has been considered from a classical point of view in [27] and from a Bayesian perspective in [57].

(B) *Processes with offspring depending on the number of couples.*

$$(F_{n+1}, M_{n+1}) = \sum_{i=1}^{Z_n} (f_{n,i}(Z_n), m_{n,i}(Z_n)),\ Z_{n+1} = L(F_{n+1}, M_{n+1}),\ n \in \mathrm{Z}^+$$

where $Z_0 = N_0 \geq 1$. This class of processes was introduced by Xing and Wang [60]. Assuming that for every bounded, componentwise-increasing function g, the sequence $\{E[g(f_{0,1}(k), m_{0,1}(k))]\}_{k\geq 0}$ is nonincreasing, they established a criterion to identify when the process admits ultimate extinction with probability one.

(C) *Processes with offspring and mating depending on the number of couples.*

$$(F_{n+1}, M_{n+1}) = \sum_{i=1}^{Z_n} (f_{n,i}(Z_n), m_{n,i}(Z_n)),\ Z_{n+1} = L_{Z_n}(F_{n+1}, M_{n+1}),\ n \in \mathrm{Z}^+$$

where $Z_0 = N_0 \geq 1$. This class of process has been investigated by Molina et al. [56] where several probabilistic properties and results about its extinction probability and limiting evolution have been determined. Recently, Xing and Wang [61], assuming again that for every bounded, componentwise-increasing function g, the sequence $\{E[g(f_{0,1}(k), m_{0,1}(k))]\}_{k\geq 0}$ is nonincreasing, have obtained a criterion to identify whether the process is extinct with probability one.

(D) *Processes with immigration depending on the number of couples.*

$$(F_{n+1}, M_{n+1}) = \sum_{i=1}^{Z_n} (f_{n,i}(Z_n), m_{n,i}(Z_n)) + (f^I_{n+1}(Z_n), m^I_{n+1}(Z_n)),$$

$$Z_0 = N_0 \geq 1,\ Z_{n+1} = L_{Z_n}(F_{n+1}, M_{n+1}) + I_{n+1}(Z_n), \quad n \in \mathrm{Z}^+.$$

This general class of two-sex models has been investigated in [53] and [54] where several probabilistic properties have been established.

20.3.4 Processes with control on the number of progenitor couples

The following class of two-sex processes with a deterministic control on the number of progenitor couples has been introduced in [55]:

$$(F_{n+1}, M_{n+1}) = \sum_{i=1}^{Z_n^*} (f_{n,i}, m_{n,i}),\ Z_{n+1} = L_{Z_n^*}(F_{n+1}, M_{n+1}),\ Z_{n+1}^* = \phi(Z_{n+1}),\ n \in \mathrm{Z}^+$$

where $Z_0^* = N_0^* \geq 1$, $\{L_k\}_{k\geq 0}$ is a sequence of mating functions and $\phi : \mathrm{R}^+ \to \mathrm{R}^+$ is a deterministic function integer-valued on the integers and such that $\phi(0) = 0$. The variable Z_{n+1} represents the number of couples originated according to the mating function $L_{Z_n^*}$ where $Z_n^* = \phi(Z_n)$ denotes the number of couples that, after the control governed by ϕ, really participated in the reproduction phase. The role of ϕ is to control, in each generation, the number couples that will intervene in the reproduction. Note that, if $\phi(Z_n) > Z_n$ then $\phi(Z_n) - Z_n$ couples will be introduced in the population, if $\phi(Z_n) < Z_n$ then $Z_n - \phi(Z_n)$ couples will be removed of the population, and if $\phi(Z_n) = Z_n$ then no control will be considered.

20.3.5 Others classes of two-sex processes

It is worth noticing that in [10] two new classes of two-sex branching processes were introduced and some contributions about their limiting behaviours investigated. First, the author considered a class of two-sex models which, in each generation, the conditional distribution corresponding to the number of couples produced by a daughter descending from certain couple depends on the number of couples in the previous generation as well as the average number of offspring per couple. Then, this class was generalized to a second class of two-sex models which considers that, in each generation, the conditional distribution of the total number of couples formed by the daughters descending from certain couple depends on the number of couples as well as the numbers of females and males per couple and the average number of offspring per couple in all the previous generations.

20.4 Continuous time two-sex branching processes

A continuous time two-sex branching process theory has not been sufficiently developed until now. The first model was introduced by Asmussen [3]. He considered a process $\{(F_t, M_t)\}_{t\geq 0}$, where F_t and M_t represent, respectively, the number of females and males present at time t in the population. He assumed that births take place at rates which at time t are $fL(F_t, M_t)$ and $mL(F_t, M_t)$ for females and males respectively, where f and m are the female and male birth rates and L is the mating function. Considering a mating function of the form $L(F,M) = (F+M)\varphi(M(F+M)^{-1})$ where φ is a sufficiently smooth function, and assuming that each couple only produces one female or one male, S. Asmussen established some limiting results for such a continuous time two-sex process. For more information about this process we refer the reader to chapter XI in [4].

In an attempt to widen knowledge of this subject, Molina and Yanev (see [58]) formulated the following general continuous time two-sex process, denoted by $\{(F(t),M(t))\}_{t>0}$:

$$F(t) = \sum_{j=0}^{\nu(t)} \sum_{k=1}^{Z_j} 1_{\{S_{\nu(t)} < S_j + \eta_{j,k} \le t\}} \sum_{i=1}^{f_{j,k}} 1_{\{S_j + \eta_{j,k} + \tau^f_{j,k,i} \ge t\}}$$

$$M(t) = \sum_{j=0}^{\nu(t)} \sum_{k=1}^{Z_j} 1_{\{S_{\nu(t)} < S_j + \eta_{j,k} \le t\}} \sum_{i=1}^{m_{j,k}} 1_{\{S_j + \eta_{j,k} + \tau^m_{j,k,i} \ge t\}}$$

where:

1. The process starts with $Z(0) = N_0 \ge 1$ couples.
2. $\{S_n\}_{n\ge 0}$ is an increasing random sequence. S_n is interpreted as the moment of the forming of the nth generation of couples ($S_0 = 0$).
3. $Z_n = L(F_n, M_n)$ is the number of couples in the nth generation, L being the mating function, and $F_n = F(S_n)$ (respectively $M_n = M(S_n)$) denoting the number of females (respectively males) at the moment of the nth generation.
4. $\eta_{n,k}$ is the life-period of the kth couple which is formed in the nth generation.
5. $f_{n,k}$ and $m_{n,k}$ represent the number of females and males, respectively, born at zero age in the end of the life period of the kth couple.
6. The random variables $\tau_f(n,k;i)$ and $\tau_m(n,k;i)$ represent, respectively, the life-period of the ith female and male born by the kth couple of the nth generation.
7. $\nu(t) = \max\{n \in \mathrm{Z}^+ :\ S_n \le t\}$, $t > 0$.
8. The evolutions corresponding to the couples and the individuals are independent.

In such a paper, several especial situations of this general continuous time two-sex model were described. In particular, it contains Asmussen's and Daley's two-sex procesess.

20.5 Applications

To describe the probabilistic evolution of several populations, some classes of two-sex branching processes have been used as appropriate mathematical models. The main fields where such applications have been considered are:

1. Epidemiology.
2. Genetics.
3. Population dynamics.

20.5.1 Application in the field of the Epidemiology

It is well-known that macroparasites are characterised by the fact that part of their life-cycles is outside the host, so that the host's parasite burdens increase only through re-infection. Therefore, unlike the models for microparasite infections, the models for macroparasite infections must include both the actual parasite loads of the host and the re-infection process.

Several stochastic epidemic models have been developed for macroparasite infections. In particular, in [7] a modified two-sex Galton–Watson process has been applied as appropriate epidemic model and some questions about its extinction probability have been investigated. The authors consider a bisexual parasite, with 50:50 sex ratio, that lives in discrete non-overlapping generations. Such parasites are distributed among n hosts. In each generation, each female parasite mates and produces eggs, provided there is at least one male in the same host. The eggs pass out of the host and mature to join a pool of infectious larvae outside the host. After that, some of these larvae die, but some infect a host and form the next generation of adult parasites. They assume that the number of offspring of each female parasite which survive to contribute to the next generation of adults has a Poisson probability distribution, independently of the number of males in the same host, provided only that there is at least one. Offspring from distinct females are produced independently, and each offspring is, again independently, equally likely to be male or female.

20.5.2 Applications in the field of the Genetics

In the XY sex-determination system, the females have two chromosomes belonging to the same kind (XX) while the males have two distinct sex chromosomes (XY). Certain genetics characteristics are due to genes linked to the Y chromosome and, consequently, they are only associated to the males.

In [12] with the aim to model the evolution of Y-linked genes from generation to generation a multitype two-sex model has been proposed, the called Y-linked bisexual branching process. Such a model considers the necessity of sexual interaction between a female and a male and assumes a mating mechanism where an individual may mate with no more than one individual of the opposite sex. Several results about the extinction problem for the total population and for each genotype were derived.

In a second paper, González et al. [13], this research has been continued and the rate of growth of a genotype provided its extinction has not happened has been investigated. Also, in [14] assuming two-sex monogamic populations, a multitype two-sex process has been introduced. The aim is to analyze the evolution of the number of carriers of each allele of a Y-linked gene which does not have influence on the mating process. Results concerning the extinction problem for both the whole population and each genotype have been obtained.

20.5.3 *Applications in population dynamics*

Let us consider phenomena concerning to populate or re-populate environments with animal species, possibly in danger of extinction or previously disappeared, which we know that they reproduce through the formation of couples female–male. In these situations, frequently several attempts are needed until to get the wanted success. It is assumed that if an attempt fails then we introduce new couples in the habitat with the purpose that reproduction process begins again. An interesting question is to investigate the probabilistic evolution of some random variables with an environmental interest. For example, considering certain attempt of re-population, the variable *Number of generations before extinction of the population occurs*, or taking into account the number of necessary life-periods until obtaining the wanted re-population, the variable *Number of generations until the implementation of the animal species in the habitat.*

Such questions were considered in [26] by using as mathematical model the bisexual Galton–Watson branching process.

More recently, it has been considered in [59] such problems under the perspective that the mating process could be affected by the number of couples in the population. Hence they have used as stochastic model the two-sex branching process with mating depending on the number of couples in the population (see Sect. 20.3.3(A)).

20.6 Some suggestions for research

1. Much of the research associated with two-sex branching processes has been concentrated on extinction probabilities. Significant progress has been made on this topic. However, research on the time of extinction has not been thoroughtly considered. This topic needs to be addressed with greater intensity.
2. It is necessary to complete both the probabilistic and the inferential theory concerning the new classes of discrete time two-sex branching processes introduced. For example, an important question is to investigate properties about the limiting random variables.
3. It can be stated that significant efforts have been made regarding discrete time two-sex branching processes. Now, similar efforts should be made to develop a continuous time two-sex branching process theory.
4. Other interesting question is to explore new fields where the two-sex branching processes introduced can be applied as appropriate mathematical models.

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