Branching Processes with Dependence but Homogeneous Growth*

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Abstract

A (general) branching process, where individuals need not reproduce independently, satisfies a homogeneous growth condition if, vaguely, one would not expect the progeny from any one individual to make out more than its proper fraction of the whole population at any time in the future. This notion is made precise, and it is shown how it entails classical Malthusian growth in supercritical cases, in particular for population size dependent Bienaymé-Galton-Watson and Markov branching processes, and for non-decreasing age-dependent processes with continuous life span distributions.

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1 Introduction

It is easy to envisage general branching processes with possible interaction between individuals, instead of the classical independence. If the interaction stabilizes during supercritical growth, so that in the limit individuals reproduce independently, like members of a classical, general multitype and supercritical branching population, then a coupling device can be used to establish Malthusian, i.e. exponential, growth.

Indeed, assume that individual reproductions in the limiting infinite population tend not to exceed those of finite populations. Then the coupling can be

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constructed through imaginary abortions so that the resulting, thinned reproduction process equals what would have been the case, had the population been infinite (Jagers, 1997). The population of non-aborted individuals, from any time onwards, must asymptotically grow exponentially (or die out), and if no abortions occur after a finite (but random) time the same must be ultimately true of the original, not thinned population.

A particularly lucid case is that of population size dependence in single-type populations. If $m(n)$ denotes the expected offspring per individual in an n-size generation and $m = m(\infty)$ the same in an imaginary infinite population, then in many cases the coupling will be successful — and Malthusianness thus established — if

$$\sum\{m(n) - m\} < \infty.$$

However, as pointed out (*ibid.*) exponential growth can occur even in cases where this coupling fails. In particular Klebaner (1984, 1985, and 1989) managed to show that,

$$\sum\{m(n) - m\}/n < \infty$$

essentially suffices for Bienaymé-Galton-Watson processes to exhibit Malthusian growth $\sim m^n$.

For a binary splitting cell model Gyllenberg and Webb (1990) arrived at the same type of main condition in a determinisrtic context.

The purpose of the present paper is to establish Klebaner type criteria for simple and certain age-dependent branching processes, thus replacing the — in that regard — rather preliminary attempts made in (Jagers, 1997).

Basic in this is the concept of symmetric or homogeneous growth (*ibid.*) crucially linked to the factor $1/n$ in Klebaner's formula:

Consider a general (possibly multitype) branching population. Its probability space can be constructed explicitly in the traditional Ulam-Harris or Neveu tree manner, only the probability measure is not required to have the (conditional) independence properties of classical branching. But it must be required that only finitely many individuals are born in finite time intervals, so that individuals can be numbered as they are born into the population, arbitrarily for individuals born together but always so that a mother precedes her daughter, $X_1, X_2, X_3, \ldots$.

The population size at time t, z_t^χ, can be generally defined by some characteristic χ (cf. Jagers 1989), though a certain care has to be excerted in allowing the population as a whole to affect the measure used. We shall only consider simple size processes like those alive, $\{z_t\}$, or $\{y_t\}$, the total population of all those born. In the specific cases we shall go deeper into, life spans of different individuals will be presumed independent of one another and of everything else. In a model where dependence is on population-size the latter may thus influence reproductions but not life spans.

Denote the birthtime of an individual x by τ_x and x's daughter process, the number of individuals stemming from x and alive at t by $z_t(x)$. Further write

$y_t(x)$ for all those stemming from x born by t, alive or not. For simplicity, write τ_i instead of τ_{X_i}, even though that is ambigious with individuals labelled in the Ulam-Harris manner. Let $\mathcal{G}_x$ be the σ-algebra containing all information about matters that occurred up to τ_x, i.e. $\mathcal{G}_{\tau_x}$, and abbreviate $\mathcal{G}_{X_i}$ further into $\mathcal{G}_i$. Interprete $0/0$ and $1/z_\infty$ as zero, and keep in mind that the latter convention means that sums over elements divided by z_{τ_x} will only be taken over those where $\tau_x < \infty$, finitely many in case of extinction. To avoid uninteresting complications we assume that a daughter cannot be born simultaneously with her mother.

Definition 1 *A branching process with possible dependence between individuals is said to* grow homogeneously *if there is a constant K such that*

$$\mathbb{E}[\frac{z_{t-\tau_x}(x)}{z_t}|\mathcal{G}_x] \leq \frac{K}{z_{\tau_x}}.$$

for all individuals x and $t \geq \tau_x$.

This means that the expected fraction of the future population, stemming from anyone of the z_t alive at any time t is of the same order of magnitude.

The obvious example of such a process is a Bienaymé-Galton-Watson process with population-size dependence. Since the reproductions of all individuals in the same, say k:th, generation are affected by the same population size, and are otherwise independent, symmetry implies that

$$\mathbb{E}[\frac{z_{n-k}(x)}{z_n}|\mathcal{G}_x] = \frac{1}{z_k},$$

for any x with $\tau_x = k$. More about that in the next section.

Now we shall give the general result about Malthusianness for homogeneously growing populations, whose reproductions approach those of an independent-individual Malthusian population from above.

Thus, denote the reproductions of any individual x by ξ_x. In the general case this is a point process telling at which ages x begets children of what types from a general type space S. For single-type, age-dependent or Galton-Watson processes it reduces to a random variable, telling us how many children x splits into at death. Similarly, let η_x be the reproduction process of a general Malthusian branching population with the finite reproduction kernel μ (defining the Malthusian parameter α, stable type distribution π, and fitness h). Interpret 'Malthusian branching population' to mean that the classical supercritical convergence theorem should hold (Jagers 1989). Assume that for any measurable set A of types and age interval B, $\xi_x(A \times B) \geq \eta_x(A \times B)$ in distribution given $\mathcal{G}_x$.

Then, by Strassen's theorem (Lindvall, 1992) the two processes can be coupled through imaginary abortions: η_x, can be thought of as arising from ξ_x through deletion of some children. Again abusing notation somewhat, we let

ξ_x, η_x stand for a coupled version, and write δ_x to indicate abortion or not of x, so that $\delta_x = 1$ if and only if x is an atom of ξ_{mx} but not of η_{mx}, mx denoting x's mother in the Ulam-Harris tree.

We now think of $\mathcal{G}_x$ as referring to the process as defined on this new space. Note that in a splitting process $\xi_{mx} \in \mathcal{G}_x$ but generally this need not be the case. But except for this general section we shall only deal with splitting populations in ths paper, i.e. populations where child-bearing can only occur once in a mother's life, at her death. Therefore we refrain from further discussion of the measurability aspects of the problem. However, we shall assume that the coupling has been so constructed that the future of the actual process from any τ_x onwards is independent of η_{mx}, given $\mathcal{G}_x$ and ξ_{mx}.

Theorem 2 *Let $\{z_t\}$ be a general branching process with symmetric growth. Assume that there is a general supercritical Malthusian branching population with minorizing reproductions as above. Assume that $w_t := e^{-\alpha t} z_t$ is tight. Then,*

$$\sum_i \mathbb{E}[\delta_i / z_{\tau_i}] < \infty$$

implies that w_t tends in probability to some finite $w \geq 0$, not identically zero on the set of non-extinction.

Proof. The proof, is from (Jagers, 1997), where there is also more about the coupling and general construction. It is reproduced here for completeness, and since there are slight differences in setup:

Write twiddles over processes that count only imaginary individuals, i.e. individuals born according to the η reproduction processes. Thus, $\tilde{z}_{t-\tau_x}(x)$ stands for the imaginary process starting from the individual x in the actual population at time τ_x. Similarly, $\tilde{w}_{t-\tau_x}(x) := e^{-\alpha(t-\tau_x)} \tilde{z}_{t-\tau_x}(x)$ *etc.*

For any u, z_t^u records at time $t+u$ the number of all living individuals born up to u but only living individuals not stemming from an aborted individual after u. If $\delta_{xu} = 0$ precisely if x stems from an x' with $\tau_{x'} > u$ and $\delta_{x'} = 1$, and $\delta_{xu} = 1$ otherwise, and $\chi_x(a)$ indicates whether x is alive or not at age a, thus

$$z_t^u = \sum_{\tau_x \leq t+u} \delta_{xu} \chi_x(t + u - \tau_x).$$

In analogy with other notation $w_t^u := e^{-\alpha(t+u)} z_t^u$.

Clearly,

$$0 \leq z_{t+u} - z_t^u \leq \sum_{\tau_x > u} \delta_x z_{t+u-\tau_x}(x)$$

and

$$|w_{t+u} - w_t^u| \leq w_{t+u} \sum_{\tau_x > u} \delta_x \frac{z_{t+u-\tau_x}(x)}{z_{t+u}}.$$

Thus for any $\epsilon', v > 0$ the homogeneous growth condition yields

$$\mathbb{P}(|w_{t+u} - w_t^u| > \epsilon', w_{t+u} \leq v) \leq (v/\epsilon')K\mathbb{E}[\sum_{\tau_x > u} \delta_x / z_{\tau_x}]$$

for all t and starting types $s \in S$. But

$$|w_{t+u} - w_{t'+u}| \leq |w_{t+u} - w_t^u| + |w_t^u - w_{t'}^u| + |w_{t'+u} - w_{t'}^u|.$$

Since, with $I_u := \{x; \tau_{mx} \leq t < \tau_x < \infty\}$,

$$w_t^u = \sum_{x \in I_u} e^{-\alpha \tau_x} \tilde{w}_{t+u-\tau_x}(x) \to \sum_{x \in I_u} e^{-\alpha \tau_x} \tilde{w}(x),$$

as $t \to \infty$, the twiddled daughter processes being independent individual supercritical branching process with Malthusian parameter α, it follows that

$$\lim_{t,t' \to \infty} \mathbb{P}(|w_t^u - w_{t'}^u| > \epsilon') = 0.$$

Hence,

$$\limsup_{t,t' \to \infty} \mathbb{P}(|w_{t+u} \wedge v - w_{t'+u} \wedge v| > \epsilon') \leq 2(v/\epsilon')K\mathbb{E}[\sum_{\tau_x > u} \delta_x / z_{\tau_x}].$$

Since u can be chosen so as to render the right hand side arbitrarily small, the convergence in probability follows by completeness and tightness.

□

Now define the (conditional) abortion probability

$$\epsilon_x := \mathbb{E}[\delta_x | \mathcal{G}_{x-}],$$

where $\mathcal{G}_{x-}$ is $\mathcal{G}_{\tau_x -}$, the σ-algebra of events strictly preceding τ_x. We write ϵ_i for ϵ_{X_i} and $\mathcal{G}_{i-}$ for $\mathcal{G}_{X_i -}$. If ϵ_x turns out to be a function of some population size immediately before τ_x, $z_{\tau_x -}$, the process is said to be *population-size dependent.*

Corollary 3 *The summation convergence condition of Theorem 2 can be replaced by*

$$\sum \mathbb{E}[\epsilon_i / z_{\tau_i}] < \infty.$$

Proof. Write m_i for X_i's mother and r_i for her rank among her sisters, and let $r_i \notin \eta_{m_i}$ mean that the individual would not have been born, had the population been infinite (and hence since she is born into the actual one that she is aborted). With superscripts denoting conditional expectation then,

$$\mathbb{E}^{\mathcal{G}_{i-}}[\delta_i / z_{\tau_i}] = \mathbb{P}^{\mathcal{G}_{i-}}(\delta_i = 1)\mathbb{E}^{\mathcal{G}_{i-}}[1/z_{\tau_i} | \delta_i = 1] =$$

$$= \epsilon_i \mathbb{E}^{\mathcal{G}_{i-}}[1/z_{\tau_i}|\tau_i < \infty, r_i \notin \eta_{m_i}],$$

Since z_{τ_i} is independent of η_{m_i}, given $\mathcal{G}_{i-}$ and $\tau_i < \infty$, and $1/z_{\tau_i} = 0$ if $\tau_i = \infty$, indeed

$$\mathbb{E}^{\mathcal{G}_{i-}}[\delta_i/z_{\tau_i}] = \epsilon_i \mathbb{E}^{\mathcal{G}_{i-}}[1/z_{\tau_i}|\tau_i < \infty] = \epsilon_i \mathbb{E}^{\mathcal{G}_{i-}}[1/z_{\tau_i}]/\mathbb{P}^{\mathcal{G}_{i-}}(\tau_i < \infty) =$$

$$= \epsilon_i \mathbb{E}^{\mathcal{G}_{i-}}[1/z_{\tau_i}],$$

as for any t, $\{\tau_i < \infty\} \cap \{\tau_i \leq t\} \in \mathcal{G}_t$, so that τ_i is measurable with respect to $\mathcal{G}_{i-}$, and thus $\mathbb{P}^{\mathcal{G}_{i-}}(\tau_i < \infty) = 1$ on the set $\tau_i < \infty$. But only such sets matter in the expectations summed.

□

Corollary 4 *Consider a single-type splitting population with continuously distributed life spans. Write* $T_1 < T_2 < \ldots$ *for the successive splitting times,* $m_x := \mathbb{E}[\xi_x|\mathcal{G}_{x-}]$, ξ_x *now simply denoting* x*'s number of children, and* $m := \mathbb{E}[\eta_x|\mathcal{G}_{x-}] = \mathbb{E}[\eta_x]$. *Then,*

$$\sum \mathbb{E}[\epsilon_i/z_{\tau_i}] = \sum \mathbb{E}[(m_i - m)/z_{T_i}],$$

m_i *being short for* m *indexed by the individual splitting at* T_i.

In particular, if the process is population size dependent, then $m_i = m(z_{T_i})$.

The proof of this is straightforward (and the corollary can easily be generalized to cases where many mothers may give birth simultaneously, like the discrete time situation below).

□

2 The Bienaymé-Galton-Watson case

A population-size (or state-) dependent (Bienaymé-)Galton-Watson process is a discrete time branching process $\{z_n\}$, where given the history $\mathcal{A}_n$ during the first n generations, z_{n+1} is the sum of z_n i.i.d. non-negative integer valued random variables, whose distribution $\{p_k(z_n)\}$ is determined by the present population size, z_n. The minorization condition can be expressed as

$$\sum_{k \geq j} p_k(n) \geq \sum_{k \geq j} p_k$$

for all j and n, $p_k = p_k(\infty)$ being thought of as the reproduction law 'if the population were infinite'. The latter is supposed to define a supercritical Malthusian Galton-Watson process,

$$m = m(\infty) = \sum_k k p_k > 1, \sum_k k(\log k) p_k < \infty.$$

Similarly, we use the obvious notation $f^{(n)}, m(n)$, and $q(n)$ for generating function, mean, and extinction probability as determined by $\{p_k(n)\}$, and also $\gamma(n) := f^{(n)'}(q(n))$. We write m, q, γ when $n = \infty$.

In the present case ξ_x is just a random variable, x's number of children, and η_x the number retained. Hence, if x belongs to the n:th generation, $\xi_x|\mathcal{A}_n \sim \{p_k(z_n)\}$ and $\eta_x|\mathcal{A}_n \sim \{p_k\}$. Since

$$\delta_{xj} = 1_{\{\xi_x \geq j\}} - 1_{\{\eta_x \geq j\}},$$

$$\epsilon_{xj} = \sum_{k \geq j} p_k(z_n) - \sum_{k \geq j} p_k,$$

and

$$\sum_j \epsilon_{xj} = m(z_n) - m.$$

Theorem 5 *A population-size-dependent Galton-Watson process is symmetrically dependent. Make the minorization assumption above, assume that* $m(n) \searrow m > 1$ *and*

$$\sum_n \{m(n) - m\}/n < \infty.$$

Then $\{w_n := z_n/m^n\}$ *is tight. If further* $\gamma m < 1$ *and* $\sum k \log k p_k < \infty$*, then* w_n *has a non-trivial limit in probability.*

The condition $\gamma m < 1$ enters the proof in quite an intriguing way, in order to bound $\mathbb{E}[1/z_n; z_n > 0]$. Recall that it is always true that $\gamma < 1$ but certainly not that $\gamma < 1/m$. Indeed, for supercritical binary splitting $q = (1-p)/p$ and $\gamma m = 4p(1-p) < 1$, whereas for geometrically distributed offspring it can be checked that $\gamma m \equiv 1$, (*cf.* Athreya and Ney, 1972, p. 6-7).

Lemma 6 *Let* $\{z_n\}$ *be a Galton-Watson process with the generating function* f*, extinction probability* $q, f'(1) = m > 1, f''(1) < \infty$ *and* $\gamma := f'(q) < 1/m$. *Then, as* $n \to \infty$,

$$\mathbb{E}[1/z_n; z_n \geq 1] \sim m^{-n} \int_0^\infty \mathbb{E}[e^{-tw}; w > 0] dt,$$

where $w := \lim z_n/m^n$ *and the integral converges.*

This is due to Badalbaev and Muhitdinov (1990, p. 16-21). Their topic is actually the variance of y_n/y_{n-1}, $y_n := \sum_0^n z_k$, which behaves as $\sigma^2\mathbb{E}[1/z_n; z_n \geq 1], \sigma^2 = f''(1) - m^2 + m$. For our purposes the variance condition can be replaced by $\sum k \log k p_k < \infty$.

Proof of the theorem. With y_k still denoting the total population, $\tau_i = k \Leftrightarrow y_{k-1} < i \leq y_k$. Thus, if $\mathcal{Z}_k$ denotes the realized k:th generation, $\{x \in N^k; \tau_x < \infty\}$ in Ulam-Harris notation, then

$$\sum \epsilon_i/z_{\tau_i} = \sum_k \sum_{i=y_{k-1}+1}^{y_k} \epsilon_i/z_k =$$

$$\sum_k \sum_{x \in \mathcal{Z}_{k-1}} \sum_j \epsilon_{xj}/z_k = \sum_k \sum_{x \in \mathcal{Z}_{k-1}} \{m(z_{k-1}) - m\}/z_k =$$

$$= \sum_k z_{k-1}\{m(z_{k-1}) - m\}/z_k.$$

Writing $g(n) := m(n) - m$, we can conclude that

$$\sum \mathbb{E}[\epsilon_i/z_{\tau_i}] = \sum \mathbb{E}[z_{k-1}g(z_{k-1})/z_k].$$

But given $\mathcal{A}_{k-1}, z_k$ is larger than or equal to a variable U which is binomial $z_{k-1}, 1 - p_0(z_{k-1})$. Since if Z is $\text{Bin}(n,p)$,

$$\mathbb{E}[\frac{1}{Z+1}] = \frac{1-(1-p)^{n+1}}{(n+1)p},$$

$$\mathbb{E}[1/z_k; z_k \geq 1 | \mathcal{A}_{k-1}] \leq \mathbb{E}[1/U; U \geq 1] \leq$$

$$\leq \mathbb{E}[2/(U+1)] \leq 2/(z_{k-1}\{1 - p_0(z_{k-1})\}) \leq 2/(z_{k-1}(1-p_0)).$$

Further, by the assumptions on g, or rather $m(n) - m$, there exists a $G \geq g$, which does not increase, the function $xG(x)$ is nondecreasing and concave on $\mathbb{R}_+$, and $\sum G(n)/n < \infty$ (Klebaner, 1989). In terms of such a G thus

$$\sum \mathbb{E}[\epsilon_i/z_{\tau_i}] \leq \sum C\mathbb{E}[G(z_{k-1}); z_{k-1} \geq 1]$$

for some constant C. Now, $z_k \overset{d}{\geq} z_k^\infty$, where the latter is Galton-Watson with reproduction distribution $\{p_k\}$, 'as if the population were infinite all the time'. By G's all properties, the negative correlation between increasing and decreasing functions and finally Lemma 6:

$$\mathbb{E}[G(z_k); z_k \geq 1] \leq \mathbb{E}[G(z_k^\infty); z_k^\infty \geq 1] =$$

$$= \mathbb{E}[z_k^\infty G(z_k^\infty)1/z_k^\infty; z_k^\infty \geq 1] \leq \mathbb{E}[z_k^\infty G(z_k^\infty)]\mathbb{E}[1/z_k^\infty; z_k^\infty \geq 1] \leq$$

$$\leq \mathbb{E}[z_k^\infty]G(\mathbb{E}[z_k^\infty])\mathbb{E}[1/z_k^\infty; z_k^\infty \geq 1] \sim$$

$$\sim cm^k G(m^k)m^{-k},$$

where c is the integral from Lemma 6. It follows that $\sum \mathbb{E}[\epsilon_i/z_{\tau_i}]$ converges, if so does $\sum G(m^i)$. But comparison with integrals and a change of variable shows that to be the case, since $\sum G(n)/n < \infty$.

It remains to check the asserted tightness of $\{w_n\} = \{z_n/m^n\}$. We shall show that $\{\mathbb{E}[w_n]\}$ is bounded.

$$\mathbb{E}[w_n|\mathcal{A}_{n-1}] = w_{n-1} + z_{n-1}g(z_{n-1})/m^n \leq w_{n-1} + z_{n-1}G(z_{n-1})/m^n$$

for any n. Hence,

$$\mathbb{E}[w_n] \leq \mathbb{E}[w_{n-1}] + \mathbb{E}[z_{n-1}G(z_{n-1})]/m^n \leq$$
$$\leq \mathbb{E}[w_{n-1}] + \mathbb{E}[z_{n-1}]G(\mathbb{E}[z_{n-1}])/m^n \leq$$
$$\leq \mathbb{E}[w_{n-1}]\{1 + G(m^{n-1})/m\},$$

where we used in turn the concavity of $xG(x)$, that $\mathbb{E}[z_{n-1}] \geq m^{n-1}$, and that G does not increase. It follows that

$$\mathbb{E}[w_n] \leq \prod_{k=1}^{\infty}\{1 + G(m^k)\} < \infty,$$

as $\sum G(k)/k < \infty \Leftrightarrow \sum G(m^k) < \infty$.

□

3 Markov branching

In continuous time the natural formulation of Markovian population size dependent branching is to make the death intensity population size dependent — call it $\mu(n)$ — and the same for the reproduction distribution, $p_k(n)$, as in the Galton Watson case.

Since individuals do not age, there is complete symmetry between all those present in a population at the birth of any new member, and like in the Galton Watson case

$$\mathbb{E}[\frac{z_{t-\tau_x}(x)}{z_t}|\mathcal{G}_x] = \frac{1}{z_{\tau_x}}$$

for all $t \geq \tau_x$. In other words,

Lemma 7 *Population size dependent Markov branching processes grow homogeneously.*

□

Now write $\mu := \mu(\infty), m(n) := \sum kp_k(n), m := m(\infty)$ and introduce the corresponding Malthusian parameters $\alpha(n) := \mu(n)\{m(n) - 1\}, n = 1, 2 \ldots \infty, \alpha := \alpha(\infty)$.

Lemma 8 *Assume that* $\mu(n) \to \mu > 0, m(n) \geq m$,

$$\sum \{m(n) - m\}/n < \infty,$$

and that for all n *and* k

$$\mu(n) \sum_{i \geq k} p_i(n) \geq \mu \sum_{i \geq k} p_i.$$

Then $\{e^{-\alpha t} z_t, t \geq 0, \}$ *is tight.*

Proof. With

$$A_t := \int_0^t \alpha(z_u) du$$

the random variables

$$W_t := e^{-A_t} z_t, t \geq 0,$$

constitute a nonnegative martingale with respect to its natural filtration. Hence, $W_\infty := \lim_{t \to \infty} W_t$ exists almost surely and

$$\mathbb{E}[W_\infty] \leq \lim_{t \to \infty} \mathbb{E}[W_t] = 1.$$

But

$$e^{-\alpha t} z_t = W_t e^{A_t - \alpha t} = W_t e^{\int_0^t \{\alpha(z_u) - \alpha\} du}.$$

The last assumption of the lemma serves to ensure that the population grows at least as fast as it would have done in an environment of an infinite population, $z_u \overset{d}{\geq} z_u^\infty$, if z_u^∞ denotes the size of the latter population, i.e. a Markov branching process defined by parameters μ and p_k and no population size dependence. Since the latter grows as $e^{\alpha u}$, if it does not die out (and only this case needs checking), it is enough that

$$\int_0^\infty \{\alpha(ce^{\alpha u}) - \alpha\} du$$

converges or equivalently

$$\int_0^\infty \{m(ce^{\alpha u}) - m\} du < \infty.$$

But that follows from the the first assumption, after a substitution of variable.

□

Theorem 9 *Let* $\{z_t\}$ *be a continuous time, single type, population size dependent Markov branching process, satisfying the* $x \log x$*-condition* $\sum k(\log k) p_k < \infty$ *as well as the conditions of the preceding lemma. Then the process exhibits Malthusian growth,* $z_t \sim e^{\alpha t}$ *on the set of non-extinction, as* $t \to \infty$.

Proof. It remains to check the convergence condition of Corollary 4. In terms of $g(n) := m(n) - m$ and Klebaner's $G \geq g$ of the preceding section:

$$\sum \mathbb{E}[g(z_{T_i})/z_{T_i}] \leq \sum \mathbb{E}[z_{T_i} G(z_{T_i})/z_{T_i}^2] \leq \sum \mathbb{E}[z_{T_i} G(z_{T_i})]\mathbb{E}[1/z_{T_i}^2; z_{T_i} \geq 1],$$

since $zG(z)$ increases whereas $1/z^2$ decreases. In the next step use that $zG(z)$ is concave and that $\mathbb{E}[z_{T_i}] \leq ci$ for any $c > m(1) - 1$ in order to conclude that

$$\mathbb{E}[z_{T_i} G(z_{T_i})] \leq ciG(ci).$$

But by a large deviations argument it is easy to check that for an $\epsilon < m - 1$ — the superscript ∞ denoting a process in the environment of infinitely many individuals, $z_t^\infty \overset{d}{\leq} z_t$ —

$$\mathbb{E}[1/z_{T_i}^2; z_{T_i} \geq 1] \leq \mathbb{E}[1/(z_{T_i}^\infty)^2; z_{T_i}^\infty \geq 1] \leq$$

$$\leq \mathbb{E}[1/(z_{T_i}^\infty)^2; z_{T_i}^\infty \geq \epsilon i] + \mathbb{P}(z_{T_i}^\infty \leq \epsilon i) \leq C/i^2.$$

The claimed convergence follows.

□

4 Binary splitting with quiescence and ageing

Consider (population-size dependent) binary splitting processes, where cells either have i.i.d. cycle times (i.e. life spans) with a continuous distribution function L, ending with a mitotic division, or else they are quiescent, i.e. remain and do not divide. Assume that cycling cells age in the sense that if T is a typical cycle time, then

$$\mathbb{P}(T > t + u | T > u) = \frac{1 - L(t+u)}{1 - L(u)} \leq 1 - L(t) = \mathbb{P}(T > t).$$

Loosely speaking, death intensity increases with age. Population size dependence enters through the probability $p(z_t)$ with which a newborn cell embarks upon the cell cycle, otherwise turning quiescent. The population (tumour) size at t is denoted by z_t. Again we consider the supercritical case: $p(n) \searrow p > 1/2$, and refer to this process as population-size-dependent supercritical splitting with ageing. It is an age-dependent version of the Bell-Anderson cell-size dependent tumour model considered by Gyllenberg and Webb (1990).

Lemma 10 *The population-size-dependent supercritical splitting process with ageing displays homogeneous growth.*

Proof. At each split one mother cell disappears and two new cells are added. Therefore, starting from one ancestor, $z_{\tau_n} = [n/2] + 1, n = 1, 2, 3, \dots$ as long as $\tau_n < \infty$. By the ageing assumption the expected contribution from a newborn cell to the population later will not exceed that of an older cell. If $\mathcal{L}_k$ denotes the set of cells cycling at τ_k, then by symmetry it is even true that

$$\mathbb{E}[z_{\tau_n-\tau_k}(X_k); \tau_n \le t < \tau_{n+1} | \mathcal{G}_k] \le \mathbb{E}[z_{\tau_n-\tau_k}(x); \tau_n \le t < \tau_{n+1} | \mathcal{G}_k]$$

for any $x \in \mathcal{L}_k$. Hence,

$$\begin{aligned}
&\mathbb{E}[\frac{z_{t-\tau_k}(X_k)}{z_t}|\mathcal{G}_k] = \\
&= \sum_{n\ge k} \mathbb{E}[\frac{z_{t-\tau_k}(X_k)}{z_t}; \tau_n \le t < \tau_{n+1}|\mathcal{G}_k] = \\
&= \sum_{n\ge k} \mathbb{E}[\frac{z_{\tau_n-\tau_k}(X_k)}{z_{\tau_n}}; \tau_n \le t < \tau_{n+1}|\mathcal{G}_k] = \\
&= \sum_{n\ge k} \frac{1}{[n/2]+1} \mathbb{E}[z_{\tau_n-\tau_k}(X_k); \tau_n \le t < \tau_{n+1}|\mathcal{G}_k] \le \\
&\le \sum_{n\ge k} \frac{1}{[n/2]+1} \mathbb{E}[\frac{1}{z_{\tau_k}} \sum_{x\in\mathcal{L}_k} z_{\tau_n-\tau_k}(x); \tau_n \le t < \tau_{n+1}|\mathcal{G}_k] \le \\
&\le \sum_{n\ge k} \frac{1}{[n/2]+1} \mathbb{E}[\frac{z_{\tau_n}}{z_{\tau_k}}; \tau_n \le t < \tau_{n+1}|\mathcal{G}_k] = \\
&= \frac{1}{z_{\tau_k}} \sum_{n\ge k} \mathbb{P}(\tau_n \le t < \tau_{n+1}|\mathcal{G}_k) \le 1/z_{\tau_k}.
\end{aligned}$$

□

Define α as the Malthusian parameter of the limiting, infinite population,

$$2p \int_0^\infty e^{-\alpha t} L(dt) = 1.$$

If $\{z_t^\infty\}$ denotes an independent individual, binary splitting branching process, whose probability law is defined by p and L, then clearly $e^{-\alpha t} z_t^\infty$ has a non-trivial limit, as $t \to \infty$. Write y_t for the total population at t, i.e. all those born up to t and let the superscript c indicate that we only count cycling cells in z_t^c or y_t^c.

Lemma 11 *The process* $\{e^{-\alpha t} z_t\}$ *is tight, provided* $\mathbb{E}[T] < \infty$ *and* $n\{p(n) - p\} \to 0$, *as* $n \to \infty$.

Proof. Note that for any fixed t_0, $e^{-\alpha t}z_t \leq y_{t_0} < \infty$ for $0 \leq t \leq t_0$. Therefore it is enough to check that $\limsup e^{-\alpha t}z_t$ is a finite random variable, and indeed since each quiescent cell had a cycling mother that $\limsup e^{-\alpha t}y_t^c$ is finite.

Define α_n by

$$2p(n)\int_0^\infty e^{-\alpha_n t}L(dt) = 1.$$

Then $\alpha_n \searrow \alpha$. It is easy to check that indeed

$$0 \leq \alpha_n - \alpha \leq a\{p(n) - p\}$$

for some $a > 0$. For any individual x, let bx denote its mother, b^2x grandmother etc., gx its generation and T_x its life span (cell cycle duration). Define $r_x := \alpha_{z_{\tau_x}}$ and write

$$r_n = r_{X_n} = \alpha_{z_{\tau_n}} = \alpha_{[(n+2)/2]}$$

as before. Further, for any x, besides the ancestor, define

$$A_x := \sum_{k=1}^{gx} r_{b^k x}T_{b^k x} \text{ and } A_n := A_{X_n}$$

Adapted to varying Malthusian parameters, and considering only cycling cells, Nerman's (1981) martingale then takes the form

$$R_n := 1 + \sum_{k=1}^{n} e^{-A_k}(\xi_k e^{-r_k T_k} - 1),$$

where again somewhat cavalierly T_k stands for T_{X_k} and ξ_k gives the number of cycling children of X_k. Since it is non-negative, it has an almost sure limit, R_∞. Following the approach from the paper quoted, $N(t, u)$, the number of births between t and $t + u$ from mothers themselves born before t, satisfies

$$N(t,u) \geq \sum_{k=1}^{y_t^c}\{\xi_k 1_{[0,u]}(T_k) - 1\} \geq \sum_{k=1}^{y_t^c}\{\eta_k 1_{[0,u]}(T_k) - 1\},$$

the η in place of ξ indicating that some individuals may have been removed so that the limiting branching process is obtained. But the martingale $M_t := R_{y_t^c}$ and the function $r(t) := r_n$ on $\tau_n \leq t < \tau_{n+1}$ in their turn satisfy

$$M_t \geq e^{-r(t)(t+u)}N(t,u) \geq e^{-\alpha(t+u)}N(t,u)e^{-\alpha(t+u)g(z_t)}$$

in terms of $g(n) := p(n) - p$.

To investigate $(t + u)g(z_t)$, as $t \to \infty$ note that $z_{\tau_n} = [n/2] + 1$, whereas $\mathbb{E}[\tau_n] \leq n\mathbb{E}[T]$ on the set of growth (by induction e.g.). Hence $\mathbb{E}[\tau_n g(z_{\tau_n})] \to 0$ and the same must be true a.s. for $(t + u)g(z_t)$, as $t \to \infty$. By martingale convergence further $M_t \to R_\infty$ (on the set where $y_t \to \infty$), and by the law of large numbers

$$\sum_{k=1}^{y_t^c} \{\eta_k 1_{[0,u]}(T_k) - 1\}/y_t \to 2pL(u) - 1 > 0$$

for a suitable u. It follows that

$$\limsup e^{-\alpha t} y_t^c \leq$$

$$\leq \limsup e^{-\alpha t} y_t^c \frac{N(t,u)}{\sum_{k=1}^{y_t^c} \{\eta_k 1_{[0,u]}(T_k) - 1\}} \leq$$

$$\leq C \limsup e^{-\alpha t} N(t,u) \leq C' \limsup M_t = C' R_\infty < \infty.$$

Here C and C' are positive constants.

□

The main result is rather direct from these lemmas and the basic Theorem 2:

Theorem 12 *Let $\{z_t\}$ be a binary splitting population-size-dependent process with ageing and a continuous life length distribution L with a finite mean, as defined. Assume that the probability of a newborn cell in an n-size population entering the cell cycle satisfies $p(n) \searrow p > 1/2$ and $\sum \{p(n) - p\}/n < \infty$. Let α be the root of*

$$2p \int_0^\infty e^{-\alpha t} L(dt) = 1.$$

Then, $e^{-\alpha t} z_t$ converges to a non-zero limit in probability on the set where the population does not die out.

Proof. With $\epsilon_i = g(z_{\tau_i}) = p(z_{\tau_i}) - p$, we must only check that

$$\sum_i \mathbb{E}[\epsilon_i / z_{\tau_i}] < \infty.$$

But this is clear since, as we have seen repeatedly, $z_{\tau_i} = [i/2] + 1$ on $\{\tau_i < \infty\}$.

□

5 Bellman-Harris type processes

The crucial step in Lemma 10 was the monotonicity: when a process is delayed splittings occur later and therefore the process tends to be smaller, provided the probability of dying without children is nil. This makes it plausible that results from the preceding section can be extended to general population-size dependent splitting processes with a probability $p_k(n)$ of begetting k children if you die when population size is n, at least provided life-spans are i.i.d., ageing is there, and $p_0(n) = 0$ for all n.

We refer to such processes as population-size dependent Bellman-Harris processes, and keep the notation from the preceding section wherever suitable. Without mentioning we also assume that reproduction decreases in distribuition with increasing population sizes (as in the Galton-Watson case) and that in the limit $p_k := p_k(\infty)$, together with the continuous life span distribution L, defines a supercritical process with the Malthusian parameter α.

Lemma 13 *Population-size dependent Bellman-Harris processes as above with ageing and* $p_0(n) = 0$*, for all* n*, exhibit homogeneous growth.*

Proof. Let $\mathcal{Z}_x$ denote the set of individuals alive at τ_x, besides x herself. (We regard her mother but not possible sisters as dead.) Define a new branching population starting at τ_x by replacing the remaining life spans by i.i.d. L life spans $\tilde{\lambda}_{x'}, x' \in \mathcal{Z}_x$ but making no other changes. By the ageing assumption the new initiating life spans are longer in distribution than the original ones, and we can construct them on a sutiably enlarged probability space so that indeed $\tilde{\lambda}_{x'} \geq \lambda_{x'} - \tau_x + \tau_{x'}$.

Let $\tilde{z}_t$ denote the resulting process, and write $\tilde{T}_1 < \tilde{T}_2 < \ldots$ for its successive splitting times after start at τ_x. $T_1, T_2, \ldots$ are the corresponding times in the original process. By construction $T_i \leq \tilde{T}_i$. Clearly the probability distribution for the number of children born in the original population at T_1 is the same as that ruling the number in the new population at $\tilde{T}_1$, namely $\{p_k(z_{\tau_x})\}$. By induction, this equality of reproduction distributions holds also later and we can make the construction so that $z_{T_i} = \tilde{z}_{\tilde{T}_i}$ for all i.

But since the processes z_t and $\tilde{z}_t$ both increase, the postponed version must be smaller. We conclude that

$$\mathbb{E}[z_{t-\tau_x}(x)/z_t|\mathcal{G}_x] \leq \mathbb{E}[z_{t-\tau_x}(x)/\tilde{z}_t|\mathcal{G}_x].$$

But since $\tilde{z}_t \leq z_t$, the number of children being added to x's daughter process according to $\{p_k(z_{t-})\}$ is smaller in distribution than if $\{p_k(\tilde{z}_{t-})\}$ governs possible reproduction at t. We conclude that

$$\mathbb{E}[z_{t-\tau_x}(x)/\tilde{z}_t|\mathcal{G}_x] \leq \mathbb{E}[\tilde{z}_{t-\tau_x}(x)/\tilde{z}_t|\mathcal{G}_x] = 1/z_{\tau_x}.$$

$\square$

Lemma 14 *Consider a population-size dependent Bellman-Harris process with continuous life spans,* $m(n) \searrow m > 1$*, and* $\sum\{m(n) - m\}/n < \infty$*. Then, in terms of the splitting times* $T_1 < T_2 \ldots$*,* $\sum_n \mathbb{E}[(m(z_{T_n}) - m)/z_{T_n}] < \infty$*.*

Proof. As in the Markov case.

□

Finally tightness follows like in Lemma 11.

Theorem 15 *Consider a Bellman-Harris process with population-size dependence and i.i.d. continuously distributed life spans with ageing and finite expectation. Denote the life span distribution by L. Assume that reproduction distributions, $\{p_k(n), k = 1, 2, \ldots\}$ if population size is n, distributionally majorize a reproduction $\{p_k, k = 1, 2, \ldots\}$ with mean $m > 1$ and $\sum_k p_k k \log k < \infty$, that $m(n) \searrow m$, and that*

$$\sum_n \{m(n) - m\}/n < \infty.$$

Then, as $t \to \infty$, $e^{-\alpha t} z_t$ has a non-trivial limit in probability for α the Malthusian parameter of the imaginary process in an infinite population environment, $m \int_0^\infty e^{-\alpha t} L(dt) = 1$.

□

Do not overlook that we have, alas, had to require that $p_0(n) = 0$ for all n. It remains open to extend the symmetry argument from Lemma 10 to more general population processes

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