Linear growth in the multi-type Galton-Watson process with density dependent reproduction*

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August 24, 1998

Abstract

The multitype Galton-Watson framework is used to model and analyse structured populations with density-dependent reproduction. Focussing on the near-critical case we find conditions which ensure that with positive probability the reproduction process neve r dies out. We prove that these conditions imply the linear growth of the population size and population structure stabilisation. These results are applied to a density-dependent version of the discrete-time Crump-Mode-Jagers branching process.

AMS 1980 Classification: Primary 60J80

Keywords: multi-type Galton-Watson process, density-dependent reproduction, structured population, Crump-Mode-Jagers process

*This work is part of the Bank of Sweden Tercentenary Foundation project "Dependence and Interaction in Stochastic Population Dynamics"

1 Introduction

The classical multi-type Galton-Watson (MGW) process is a multidimensional Markov chain $\bar{Z}_n = (Z_n(s), s \in S)$ satisfying the branching property:

$$\bar{Z}_{n+1} = \sum_{s \in S} \sum_{j=1}^{Z_n(s)} \bar{\nu}^{n,j}(s),$$

where $\bar{\nu}^{n,j}(s)$ are i.i.d. copies of a vector $\bar{\nu}(s) = (\nu(s,t), t \in S)$ with non-negative integer-valued components, $s \in S$. This process describes a system of particles with independent reproduction laws. Here a *finite set* S is the particle type space, $Z_n(s)$ is the number of type s particles at time n, and the random variable $\nu(s,t)$ is distributed as the number of the type t offsprings of a type s particle.

The multi-type feature makes the MGW framework flexible enough to address structured populations with overlapping generations and bounded reproduction. Indeed, one can think of the *individual* life as a chain of *particle* transformations with the particle type space S being the set of all possible life-stages of an individual. The particle type $s \in S$ may record individual characteristics like age, the number of individual's children born in the past, the physical size of the individual, e tc. If reproduction is bounded, then the set S of individual life-stages is finite.

The independent reproduction property has lead to an advanced theory of the MGW processes (cf. Athreya and Ney (1972)). At the same time this property is the major restriction for this model. Here we relax the independence condition and consider a *d ensity-dependent MGW process.* By density-dependent we mean a particle reproduction law influenced by the current population size $Z_n = \sum_{s \in S} Z_n(s)$ and independent from the current population structure $\bar{Z}_n/Z_n$.

To be more specific let $\nu(s,t,z)$ be a random variable distributed as the number of t-particles in the offspring of a s-particle from a population of the size z. The MGW branching process with density-dependent reproduction is a multidimensional Markov chain $\bar{Z}_n$ satisfying the branching property

$$\bar{Z}_{n+1} = \sum_{s \in S} \sum_{j=1}^{Z_n(s)} \bar{\nu}^{n,j}(s, Z_n), \tag{1}$$

where $\bar{\nu}^{n,j}(s,z)$ are i.i.d. copies of the vector $\bar{\nu}(s,z) = (\nu(s,t,z), t \in S)$.

We assume also that every particle has *no offspring with positive probability.* This assumption, in presence of the absorbing zero-state, turns all non-zero states of the chain $\bar{Z}_n$ transient. Therefore, there are only two possible fates for the population size process Z_n: either the process is eventually absorbed at zero or it grows to infinity

$$P[Z_n \to 0] + P[Z_n \to \infty] = 1 \text{ as } n \to \infty.$$

Introduce the $S \times S$ matrices

$$M(z) = \{E\nu(t, t', z)\}_{(t,t') \in S \times S};$$

$$\Gamma(s, z) = \{Cov[\nu(s, t, z), \nu(s, t', z)]\}_{(t,t') \in S \times S}, \ \ s \in S;$$

presenting the first and second moments of the particle reproduction law. Suppose that the particle reproduction law stabilises as the population grows larger so that the first and second moment matrices converge:

$$M(z) \to M, \ \ z \to \infty; \tag{2}$$

$$\Gamma(s, z) \to \Gamma(s), \quad s \in S, \ \ z \to \infty. \tag{3}$$

The classical theory of branching processes suggests that if the limit matrix M is positively regular with the Perron eigenvalue ρ, then the extinction probability $Q = 1$ when $\rho \leq 1$, and $Q < 1$ when $\rho > 1$. However, it is a known fact for th e single type Galton-Watson processes (cf. Klebaner (1984)) that density-dependence makes situation more delicate in the near-critical case (when $\rho = 1$). The limit behaviour of density-dependent branching processes is sensitive to the convergence rate in (2): if the convergence rate is above a certain threshold parameter the process can survive forever with positive probability so that $Q < 1$. Our Theorem 2.1 shows that in the multi-type case this threshold parameter is a linear combinat ion of the elements of the matrices $\Gamma(s)$. This theorem claims also that a surviving branching process grows linearly with its type structure aligning along the left Perron eigenvector of the matrix M.

Theorem 6.1 from Section 6 treats a more general situation when the matrix M may have a particular kind of decomposable structure. In Section 11 we apply Theorem 6.1 to a density-dependent version of the Crump-Mode-J agers (CMJ) process. The model is quite general: not only does it discerns between different age-stages but it also distinguishes between individuals with different numbers of daughters born in the past.

Situations when reproduction could also depend on the type structure of the population are beyond the scope of the paper. In particular, our results can not be applied to two-sex branching populations (cf. chapter 11 of the book by Asmussen and Hering (19 83)). Nevertheless, Theorem 2.1 indicates a way of relaxing the key assumptions made by Klebaner (1989b), (1991) for the state-dependent MGW processes to ensure the linear growth theorem.

2 Linear growth theorem in the irreducible case

In the next theorem the matrix M from the condition (2) is supposed to be positively regular with the Perron eigenvectors

$$\bar{v} = (v(s),\ s \in S),\ \bar{u} = (u(s),\ s \in S)),\ v(s) > 0,\ u(s) > 0,\ s \in S$$

satisfying

$$\bar{v}M = \rho\bar{v};\ M\bar{u} = \rho\bar{u},\ \sum_{s\in S} v(s) = \sum_{s\in S} v(s)u(s) = 1. \tag{4}$$

Moreover, we assume the linear rate of convergence in (2):

$$z(M(z) - M) \to D,\ z \to \infty. \tag{5}$$

Theorem 2.1 *Consider a MGW process with bounded reproduction under the reproduction stabilisation conditions (5) and (3). If the matrix M is positively regular with the Perron eigenvalue $\rho = 1$ and*

$$0 < \gamma < 2d,\ \text{where } d = \bar{v}D\bar{u},\ \gamma = \sum_{s\in S} v(s)\bar{u}\Gamma(s)\bar{u}; \tag{6}$$

then the extinction probability $Q = \lim_n P[Z_n = 0]$ is strictly less than one, and $\bar{Z}_n/n$ converges in distribution to $\eta\bar{v}$,

$$P[\eta \le x] = Q + (1-Q)\frac{a^b}{\Gamma(b)}\int_0^x t^{b-1}e^{-at}dt, \tag{7}$$

where $a = 2/\gamma,\ b = 2d/\gamma$.

Remark. In the single type case this asymptotic pattern is similar to that of the critical GW process with Poisson immigration stopped at zero (cf. Zubkov (1972), Vatutin (1977), Ivanoff and Seneta (1985)). A close connection between the state-depe ndent GW process and the GW process with the stopped immigration was noticed by Höpfner (1985). The idea is to view a near-critical GW process as a critical GW process with a state-dependent immigration. The inequality $d > \gamma/2$ insures that the " immigration" is intensive enough to overcome the critical branching extinction effect.

3 Population structure stabilisation

It is shown here that due to the Perron-Frobenius theorem the vector $\bar{Z}_n$ for large populations could be approximated by the non-random vector $\bar{v}$ times the weighted population size $X_n = \bar{Z}_n\bar{u}$. Let $\mathcal{F}_n = \sigma(\bar{Z}_0, \ldots, \bar{Z}_n)$ be the σ-algebra of the population past up to the time n.

Lemma 3.1 *Let the conditions of Theorem 2.1 hold. For arbitrary $\epsilon > 0$ there exist such numbers $i(\epsilon)$ that for $i \geq i(\epsilon)$*

$$P[\|\bar{Z}_{n+i} - \bar{v}X_{n+i}\| > \epsilon X_{n+i}|\mathcal{F}_n] \to 0, \ X_n \to \infty.$$

Proof. The branching property (1) implies

$$E[\bar{Z}_{n+1}|\bar{Z}_n] = \bar{Z}_n M(Z_n)$$

so that the decomposition

$$\bar{Z}_{n+1} = \bar{Z}_n M(Z_n) + \bar{\xi}_n, \tag{8}$$

takes place with

$$\bar{\xi}_n = (\xi_n(t), t \in S), \ \xi_n(t) = \sum_{s \in S} \sum_{j=1}^{Z_n(s)} \nu_0^j(s, t, Z_n),$$

where $\nu_0^j(s, t, z)$ are i.i.d. copies of $[\nu(s, t, z) - E\nu(s, t, z)]$. Transform (8) into

$$\bar{Z}_{n+1} = \bar{Z}_n M + \bar{Z}_n[M(Z_n) - M] + \bar{\xi}_n$$

and then iterate i times:

$$\bar{Z}_{n+i} = \bar{Z}_n M^i + \sum_{j=0}^{i-1} (\bar{Z}_{n+j}[M(Z_{n+j}) - M] + \bar{\xi}_{n+j}]) M^{i-j-1}.$$

Using the Perron-Frobenius theorem:

$$M^i \to W,\ i \to \infty;\ W = \{u(s)v(t)\}_{(s,t)\in S\times S}. \tag{9}$$

we deduce that for large i

$$\limsup_{X_n\to\infty} P[\|\bar{Z}_{n+i} - \bar{v}X_n\| > \epsilon X_n|\mathcal{F}_n]$$

$$\leq \limsup_{X_n\to\infty} P[\|\sum_{j=0}^{i-1}(\bar{Z}_{n+j}[M(Z_{n+j}) - M] + \bar{\xi}_{n+j})M^{i-j-1}\| > \epsilon X_n|\mathcal{F}_n].$$

Due to (5) the vectors $\bar{Z}_n[M(Z_n) - M]$ are uniformly bounded. Furthermore, Chebyshev's inequality gives

$$P[\|\bar{\xi}_{n+i}\| > \epsilon X_n|\mathcal{F}_n] \leq \frac{C'}{\epsilon^2 X_n^2} E[Z_{n+i}|\mathcal{F}_n] \leq \frac{C''}{\epsilon^2 X_n}.$$

Therefore we can claim that for large i

$$P[\|\bar{Z}_{n+i} - \bar{v}X_n\| > 2\epsilon X_n|\mathcal{F}_n] \to 0,\ X_n \to \infty$$

and consequently

$$P[|X_{n+i} - X_n| > 2\epsilon X_n|\mathcal{F}_n] \to 0,\ X_n \to \infty.$$

The asserted convergence follows from the last two convergences.

4 A supermartingale inequality

Lemma 4.1 *Under the conditions of Theorem 2.1 there exist such natural* $k = k_\epsilon$ *and* T_ϵ *that for all* $\epsilon > 0$

$$|\frac{1}{k}E[X_{n+k} - X_n|\mathcal{F}_n] - d| \leq \epsilon,\ \textit{if } X_n > T_\epsilon;$$

$$\frac{1}{kX_n}|E[(X_{n+k} - X_n)^2|\mathcal{F}_n] - \gamma| \leq \epsilon,\ \textit{if } X_n > T_\epsilon;$$

$$\frac{1}{kX_n}E[|X_{n+k} - X_n|^j|\mathcal{F}_n] \leq C,\ \textit{if } X_n > T_\epsilon;\ j \geq 3.$$

Proof. We estimate the moments of $(X_{n+k} - X_n)$ using the equation

$$X_{n+1} = X_n + g(\bar{Z}_n) + \xi_n,$$

where

$$g(\bar{Z}_n) = \bar{Z}_n[M(Z_n) - M]\bar{u}, \ \xi_n = \bar{\xi}_n\bar{u}.$$

This equation comes from (8) after multiplying both sides by $\bar{u}$. After iterating it k times we find

$$X_{n+k} - X_n = \sum_{i=n}^{n+k-1} (g(\bar{Z}_i) + \xi_i). \tag{10}$$

Note that under (5) the values $g(\bar{Z}_n)$ are uniformly bounded and according to the definition of $\bar{\xi}_n$ and ξ_n

$$E[\xi_n|\mathcal{F}_n] = 0; \ E[\xi_n^2|\mathcal{F}_n] = \sum_{s\in S} Z_n(s)\bar{u}\Gamma(s, Z_n)\bar{u}.$$

To prove the first asserted estimate turn to (10) and get

$$E[X_{n+k} - X_n|\mathcal{F}_n] = \sum_{i=0}^{k-1} E[g(Z_{n+i})|\mathcal{F}_n].$$

Thus the point is to observe that due to (5) and Lemma 3.1

$$|E[g(Z_{n+i})|\mathcal{F}_n] - d| \le \epsilon, \ i > k'_\epsilon, \ X_n > T'_\epsilon.$$

Similarly it is proved that the second asserted estimate follows from (3) and Lemma 3.1. Finally, the third estimate follows from

$$E[|\xi_n|^j|\mathcal{F}_n] < C_j Z_n, \ j \ge 3$$

which holds because the reproduction is bounded.

Lemma 4.2 *Put $f(x) = 1/\log(x+3)$. Under the conditions of Theorem 2.1 there exist such natural k and T that*

$$E[f(X_{n+k})|\mathcal{F}_n] \le f(X_n), \ \textit{if } X_n > T.$$

Proof. As it was shown by Kersting (1986) there is such a positive constant C that for all $x \geq 3$ and $h \geq 3 - x$

$$f(x+h) \leq f(x) + f'(x)h + \frac{1}{2}f''(x)h^2 + C|f'''(x)||h|^3 + I\{h \leq -\frac{x}{2}\}.$$

Therefore for large values of X_n

$$f(X_n) - f(X_{n+k}) \geq \frac{X_{n+k} - X_n}{X_n \ln^2 X_n} - \frac{1+\epsilon}{2X_n^2 \ln^2 X_n}(X_{n+k} - X_n)^2$$

$$-\frac{C}{X_n^3 \ln^2 X_n}|X_{n+k} - X_n|^3 - I\{X_{n+k} - X_n \leq -\frac{X_n}{2}\}.$$

Apply the Chebyshev inequality

$$P[X_{n+k} - X_n \leq -\frac{X_n}{2}|\mathcal{F}_n] \leq 8X_n^{-3}E|X_{n+k} - X_n|^3$$

to see that

$$\frac{X_n \ln^2 X_n}{k}E[f(X_n) - f(X_{n+k})|\mathcal{F}_n] \geq \frac{1}{k}E[X_{n+k} - X_n|\mathcal{F}_n]$$

$$-\frac{1+\epsilon}{2kX_n}E[(X_{n+k} - X_n)^2|\mathcal{F}_n] - \frac{C'}{X_n^3}E[|X_{n+k} - X_n|^3|\mathcal{F}_n].$$

Now in view of Lemma 4.1 it becomes clear how the threshold parameter for d comes out. If $d > \gamma/2$ then we can pick up such a small $\epsilon > 0$ that the RHS of the last inequality is positive for $k = k_\epsilon$ and $X_n > T_\epsilon$.

5 Proof of Theorem 2.1

Our proof of the strict inequality $Q < 1$ is based on the ideas of Kersting (1986). It hinges on the supermartingale inequality from Lemma 4.2.

Let the conditions of Theorem 2.1 hold and suppose that our branching process degenerates with probability $Q = 1$. This entails that the convergence

$$E[f(X_{n+i} \vee T)] \to f(T), \; n \to \infty \tag{11}$$

holds for any fixed natural i, T. Here $x \vee y$ stands for $\max(x, y)$.

To arrive at a contradiction observe first that since the function $f(x)$ is monotone we have

$$E[f(X_{n+k} \vee T) - f(X_n \vee T)]I\{X_n \leq T\} \leq 0.$$

On the other hand, due to Lemma 4.2 for all n

$$E[f(X_{n+k} \vee T); X_n > T] \leq E[f(X_{n+k}; X_n > T]$$

$$\leq E[f(X_n; X_n > T] = E[f(X_n \vee T); X_n > T].$$

Thus for all natural n

$$Ef(X_{n+k} \vee T) \leq Ef(X_n \vee T),$$

and for all natural l, n

$$Ef(X_{n+kl} \vee T) \leq Ef(X_n \vee T).$$

After letting $l \to \infty$ under the assumption (11) we get $Ef(X_n \vee T) \geq f(T)$, and therefore $P[X_n \leq T] = 1$ for all n. Since the last is obviously false for any finite T, we conclude that $Q < 1$.

We prove the weak convergence of $\bar{Z}_n/n$ by the method of moments used in Klebaner (1989a), (1989b), (1991). Note that the bounded reproduction case under consideration perfectly suits the method of moments.

Let η be a random variable with the distribution function (7). Due to Lemma 3.1 it suffices to show that

$$P[X_n \leq nx] \to P[\eta \leq x],\ n \to \infty.$$

Since the set of moments

$$E\eta^i = Q \prod_{j=1}^{i-1} (d + \gamma \frac{j}{2}),\ i \geq 0$$

uniquely determines the distribution of η, the weak convergence under the question is equivalent to

$$E[X_n/n]^i \to E\eta^i,\ n \to \infty,\ i = 0, 1, \ldots. \quad (12)$$

This is proved by induction over i. The case $i=0$ easily comes from the equality $EX_n^0 = P[X_n = 0]$. Assume that

$$E[X_n/n]^j \to E\eta^j, \; n \to \infty, \; j \in [0, i-1].$$

Take an arbitrary $\epsilon > 0$ and $k = k_\epsilon$ introduced in Lemma 4.1. Present the binomial expansion for

$$X_{l+k(n+1)}^i = [X_{l+kn} + (X_{l+k(n+1)} - X_{l+kn})]^i$$

in the form

$$E[X_{l+k(n+1)}^i | \mathcal{F}_{l+kn}] = X_{l+kn}^i + iX_{l+kn}^{i-1} E[X_{l+k(n+1)} - X_{l+kn} | \mathcal{F}_{l+kn}]$$

$$+ \frac{i(i-1)}{2} X_{l+kn}^{i-2} E[(X_{l+k(n+1)} - X_{l+kn})^2 | \mathcal{F}_{l+kn}] + B_{n,i}.$$

According to Lemma 4.1

$$E[X_{l+k(n+1)}^i | \mathcal{F}_{l+kn}] = X_{l+kn}^i + k[di + \gamma \frac{i(i-1)}{2}] X_{l+kn}^{i-1} + B'_{n,i},$$

where

$$|B'_{n,i}| \le C' \epsilon k X_{l+kn}^{i-1} I_{\{X_{l+kn} > T_\epsilon\}} + C'' k [T_\epsilon]^{i-1} I_{\{X_{l+kn} \le T_\epsilon\}}.$$

Therefore

$$EX_{l+k(n+1)}^i = EX_{l+kn}^i + k[di + \gamma \frac{i(i-1)}{2}] EX_{l+kn}^{i-1} + O[\epsilon (kn)^{i-1})], \; n \to \infty.$$

After iterating over n we obtain

$$EX_{l+k(n+1)}^i = k[di + \gamma \frac{i(i-1)}{2}] \sum_{j=0}^{n-1} EX_{l+kj}^{i-1} + O[\epsilon (kn)^i].$$

Divide both sides by $(l+kn)^i$ and use the induction assumption. This results in

$$E\left[\frac{X_{l+kn}}{l+kn}\right]^i = [d + \gamma \frac{i-1}{2}] E\eta^{i-1} + O(\epsilon), \; n \to \infty, \; l \in [0, k-1].$$

In other words, for any $l \in [0, k-1]$ there exists such n_l that

$$|E\left[\frac{X_{l+kn}}{l+kn}\right]^i - E\eta^i| \le C\epsilon, \; n > n_l.$$

It follows that

$$|E[X_n/n]^i - E\eta^i| \le C\epsilon, \; n > k(\max_l n_l + 1).$$

which means (12).

6 Linear growth in presence of absorbing types

The positive regularity condition of Theorem 2.1 becomes a restriction for biological populations with old individuals having zero fertility. Responding to this we consider a decomposable case when the type set S could be splitted in two parts $S = S_0 + S_1$ such that S_1 types particles have no progeny of types S_0. The S_0 types particles form an irreducible subprocess and in the particular case when the class S_1 is empty we arrive at the previous section setting.

Denote by M_{ij} the $S_i \times S_j$ sub-matrix of M so that the following diagram holds

$$M = \left[\begin{array}{cc} M_{00} & M_{01} \\ 0 & M_{11} \end{array} \right] \tag{13}$$

In this section we assume that:

(A) the matrix M_{00} is positively regular with the Perron eigenvalue $\rho_0 = 1$;

(B) $[M_{11}]^{k_1} = 0$ for some natural number k_1.

ditions (B) and (C) ensure that a process started by a S_1-particle dies out in k_1 years. Thus the class S_1 corresponds to the set of the life-stages with zero fertility.

Let $\bar{v}_0$ and $\bar{u}_0$ be positive eigenvectors of M_{00} corresponding to the Perron eigenvalue. Introduce such S-vectors $\bar{v}$ and $\bar{u}$ that

a) their S_0-subvectors coincide with $\bar{v}_0$ and $\bar{u}_0$ respectively,

b) the S_1-components of the vector $\bar{u}$ are all zero,

c) the S_1-subvector of the vector $\bar{v}$ equals $\bar{v}_0 M_{01} \sum_{i \geq 0} [M_{11}]^i$.

It is not difficult to check that $\bar{v}M = \bar{v}$; $M\bar{u} = \bar{u}$ and therefore we can choose such $\bar{v}$ and $\bar{u}$ that (4) holds with $\rho = 1$. This allows us to extend the Perron-Frobenius theorem (9) and thereby Theorem 2.1.

Theorem 6.1 *Consider a MGW process with bounded reproduction under the reproduction stabilisation conditions (5) and (3). Let the type of the initial particle belong to* S_0. *If* M *satisfies (A), (B), and (6) is valid, then the extinction probability* $Q = \lim_n P[Z_n = 0]$ *is strictly less than one, and* $\bar{Z}_n/n$ *converges in distribution to* $\eta\bar{v}$. *The limit distribution is (7) with* $a = 2/\gamma$, $b = 2d/\gamma$.

7 Application to age-structured branching processes

The major motivation for Theorem 6.1 was the possibility to apply it to discrete-time reproduction models with overlapping generations where individuals can have random life-lengths. The idea is to focus on yearly [1] performances of individuals and think of individual's life as a chain of particle transformations. The single type setting on the individual level translates into a certain multitype setting on the particle level. In this sect ion we treat a relatively simple age-dependent branching process and discuss the conditions of Theorem 6.1 in the light of this model. The purpose of this discussion is to simplify understanding of the next two sections devoted to a density-depen dent version of the CMJ process. All formulae given here without proof follow from their more general counterparts obtained later on.

Consider a one-sex population of individuals that live random number of years and are able to give multiple births through their lives. Assume that the random number of daughters produced by any individual in the population at time n can depend only on the current population size and the individual age. This branching process has a well-established counterpart in the Population Dynamics literature (cf. Tuljapurkar and Caswell (1997)).

Such a population can be described by a MGW-particle system with the particle type set $S = \{0, 1, \ldots, J\}$ listing all possible age-stages for an individual. Particles of the type $s \in S$ giving birth to ν particles of type 0 and one particle of t ype $(s + 1)$ correspond to individuals of age s giving birth to ν daughters and surviving another year.

Let an individual of age $s \in S$ survive another year with the probability

$$q_0(s, z) = P[\nu(s, s + 1, z) = 1],$$

and produce k daughters with the probability

$$p_k(s, z) = P[\nu(s, 0, z) = k]$$

independently of the survival event. Since J stands for the maximal life-length, we take $q_0(s, z) > 0$ for all s except for $q_0(J, z) = 0$.

[1] we write "a year" in stead of "a unit of time"

Using the moment functions

$$m(s,z) = \sum_k k p_k(s,z); \ \ h(s,z) = \sum_k k^2 p_k(s,z).$$

we can write the reproduction stabilisation conditions (2) and (3) as:

$$m(s,z) \to m(s), \ \ q_0(s,z) \to q_0(s);$$

$$h(s,z) \to h(s), \ \ z \to \infty, \ \ s \in S.$$

The corresponding limit matrix M is a Leslie matrix

$$M = \begin{bmatrix} m(0) & q_0(0) & 0 & \dots & 0 & 0 \\ m(1) & 0 & q_0(1) & \dots & 0 & 0 \\ \dots & \dots & \dots & \dots & \dots & \dots \\ m(J-1) & 0 & 0 & \dots & 0 & q_0(J-1) \\ m(J) & 0 & 0 & \dots & 0 & 0 \end{bmatrix}$$

and the condition (5) is equivalent to

$$z[m(s,z) - m(s)] \to d(s), \ \ z \to \infty, \ \ s = 0, \dots J;$$

$$z[q_0(s,z) - q_0(s)] \to d'(s), \ \ z \to \infty, \ \ s = 0, \dots J-1.$$

The corresponding matrix D has the elements $d(s)$ at places $(0,s)$, $s = 0, \dots J$, the elements $d'(s)$ at places $(s, s+1)$, $s = 0, \dots J-1$, and zero elements elsewhere.

Observe that if old individuals can not have children:

$$m(J_0) > 0, \ \ m(J_0+1) = \dots = m(J) = 0$$

the matrix M has the decomposable structure (13) satisfying the condition (B) of Theorem 6.1. To ensure the condition (A) of Theorem 6.1 we should consider only *non-cyclical* individual reproduction laws. In other words, we exclude cyclical type-transformations when, for example, at even years only individuals of age 0, 2, 4, ... are present. In particular, the reproduction law is non-cyclical if $m(j) > 0$ for all $j \in [0, J_0]$.

As to the condition $\rho = 1$ in Theorem 6.1 it is equivalent to the requirement that the limit (as the population size tends to infinity) of the average offspring size per individual equals one. To express this limit, say μ, in terms of $q_0(s,z)$ and $m(s,z)$ note first that the average offspring size in a population of size z is

$$\mu(z) = \sum_{s=0}^{J} q_0(0,z)\dots q_0(s-1,z)m(s,z).$$

Thus $\mu = \sum_{s=0}^{J} q(s)m(s)$, where $q(s) = q_0(0)\dots q_0(s-1)$, $j = 1,\dots J$ and $q(0) = 0$.

It turns out that the vectors $\bar{q} = (q(s), s \in S)$, $\bar{w} = (w(s), s \in S)$ where

$$w(s) = \frac{1}{q(s)} \sum_{i \geq s} q(i)m(i)$$

satisfy

$$\bar{q}M = \bar{q} + (\mu - 1)\bar{e}_0,\ \ \bar{e}_0 = (1,0,\dots,0);$$

$$M\bar{w} = \bar{w} + (\mu - 1)\bar{m},\ \ \bar{m} = (m(s), s \in S).$$

When $\mu = 1$ it follows that $\bar{q}$ and $\bar{w}$ are a left and a right Perron eigenvectors of the matrix M. Therefore, in this case we can use the parameters $\lambda = \sum_{s \in S} q(s)$ (the limit average life-length) and

$$\beta = \bar{q}\bar{w} = \sum_{s \in S} sq(s)m(s)$$

(the limit average age at childbearing) to calculate the normalised Perron eigenvectors $\bar{v} = \bar{q}/\lambda$ and $\bar{u} = \frac{\lambda}{\beta}\bar{w}$.

Now we can turn to the key condition (6). For the given D, $\bar{v}$ and $\bar{u}$ we get $d\beta = c$, where the parameter

$$c = \sum_{s=0}^{J} q(s)d(s) + \sum_{s=0}^{J-1} \frac{d'(s)}{q_0(s)} \sum_{i>s} q(i)m(i)$$

happens to be the limit for $z[\mu(z) - 1]$ as $z \to \infty$. It can be shown also that $\gamma = \frac{\lambda\sigma^2}{\beta^2}$, where

$$\sigma^2 = \sum_{s \in S} q(s)[h(s) + 2m(s-1)w(s)] - 1$$

is the limit for the offspring size variance. Thus (6) is equivalent to $0 < \sigma^2 < \frac{2c\beta}{\lambda}$.

8 The MGW representation of the discrete time CMJ process

The CMJ process develops the basic Galton-Watson model by allowing for the general reproduction law on the individual level. An introduction to the theory and applications of the CMJ processes could be found in Jagers (1975), where the CMJ processes are named "general branching processes". In the discrete time setting the life law for a CMJ-individual is described by a point process

$$\xi(dt) = \sum_{i=1}^{l} \nu_i \delta_i(dt),$$

where l stands for the life-length and ν_i gives the number of daughters born at the age i. These random variables may depend on each other but for different individuals the reproduction point processes are i.i.d.

Given the distribution of the bounded point process ξ we can introduce a MGW particle process fully describing the corresponding discrete time CMJ process with bounded reproduction. A particle is meant to follow the fate of an individual during a cert ain year. In the next section using the MGW representation of the CMJ process we introduce a density-dependent version of the CMJ process and apply Theorem 6.1.

First, we label all possible life-stages for an individual with the reproduction point process ξ. Let 0 label the new born individuals and the vector $s^n = (0, s_1, \ldots, s_n)$ stand for the individuals of age n with s_n daughters born presently, s_{n-1} daughters born a year ago, and so on. We see that the set S of all individual life-stages is the set of vertices in a finite tree. This tree not only gives us the type set S for the MGW process but also shows what kind of particle transformati ons can happen in the MGW process behind the CMJ process. (Figures 1 and 2 give an example of the type tree S and the corresponding CMJ reproduction picture.)

If s^{n+1} belongs to S then a particle of the type s^n may transform into s_{n+1} 0-particles plus at most one s^{n+1}-particle. This reflects the fact that an individual with the past record s^n in the coming year with positive probability p roduces s_{n+1} daughters and either dies or stays in the population. In the language of the MGW model, for any pair $(s^n, s^{n+1}) \in S \times S$ the joint distribution of $\nu(s^n, 0)$ and $\nu(s^n, s^{n+1})$ coincides with the conditional joint

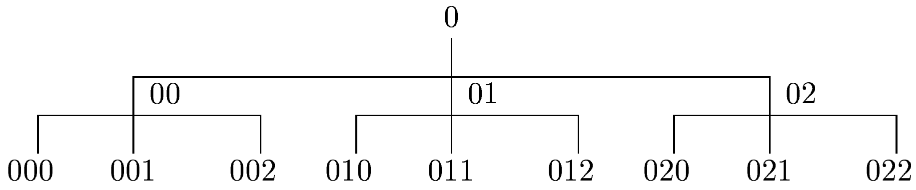

Figure 1: The type set S

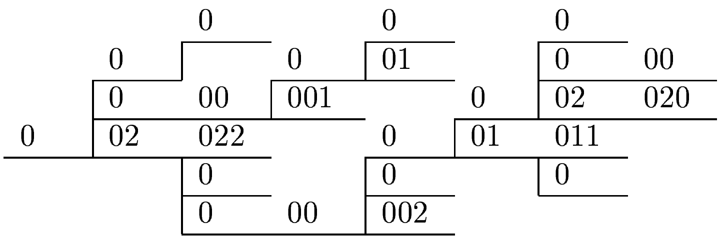

Figure 2: CMJ reproduction

distribu tion of ν_{n+1} and $I_{\{\nu_{n+1}=s_{n+1}\}}I_{\{l>n+1\}}$ given that $\nu_1 = s_1, \ldots, \nu_n = s_n, l > n$. For all other pairs (s,t) we have $P[\nu(s,t) = 0] = 1$.

Sometimes instead of s^n and s^{n+1} we write s and sk if $s_{n+1} = k$. We may even write st instead of s^{n+i} assuming that $s = s^n$ and $t = (s_{n+1}, \ldots, s_{n+i})$.

9 The matrix of the first moments for the CMJ reproduction

Denote $r_k(s) = E\nu(s, sk)$ and $m(s) = E\nu(s, 0)$. These are the following characteristics of the point process ξ:

$$r_k(s^n) = P[\nu_{n+1} = k; l > n+1 | \nu_1 = s_1, \ldots, \nu_n = s_n, l > n],$$

$$m(s^n) = E[\nu_{n+1} | \nu_1 = s_1, \ldots, \nu_n = s_n, l > n].$$

The first moment matrix $M = \{E\nu(s,t)\}_{(s,t)\in S\times S}$ belongs to a class of matrices somewhat wider than the Leslie class and looks like

$$M = \begin{bmatrix} m(0) & r_0(0) \ldots r_{k_0}(0) & 0 \ldots 0 & 0 \quad \ldots \quad 0 & 0 \ldots 0 \\ \ldots & \ldots & \ldots & \ldots & \ldots \\ m(s) & 0 \quad \ldots \quad 0 & 0 \ldots 0 & r_0(s) \ldots r_{k_s}(s) & 0 \ldots 0 \\ \ldots & \ldots & \ldots & \ldots & \ldots \end{bmatrix}$$

To be precise, the row s of M has $m(s)$ for the component 0, while its component sk is equal to $r_k(s)$, $k \geq 0$ and all other components in the row s are zeros.

Let $\mu = E[\nu_1 + \ldots + \nu_l]$ stand for the average offspring size. In the critical case when $\mu = 1$ the Perron eigenvector of M equals one. Moreover, in the critical case we can explicitly calculate both the left and the right Perron eigenvectors of t he matrix M. Note that we deal here with the situation described in Section 6 when the Perron-Frobenius result holds for a certain class of decomposable matrices.

Observe that the vector $\bar{q}$ with the components

$$q(0) = 1,\ q(s^n) = P[\nu_1 = s_1, \ldots, \nu_n = s_n, l > n],\ s^n \in S,\ n \geq 1$$

satisfies

$$(\bar{q}M)(0) = \sum_{s^n \in S} E[\nu_{n+1}; \nu_1 = s_1, \ldots, \nu_n = s_n, l > n]$$

$$= \sum_n E[\nu_n; l \geq n] = E[\nu_1 + \ldots + \nu_l] = \mu,$$

and

$$(\bar{q}M)(sk) = q(s) r_k(s) = q(sk).$$

Therefore, $\bar{q}M = \bar{q}$ if $\mu = 1$. Furthermore,

$$\bar{q}\bar{1} = \sum_{s^n \in S} P[\nu_1 = s_1, \ldots, \nu_n = s_n, l > n] = \sum_{n \geq 1} P[l > n] = \lambda,$$

where $\lambda = El$ is the average individual life length.

Next, put

$$w(s^n) = E[\nu_{n+1} + \ldots + \nu_l | \nu_1 = s_1, \ldots, \nu_n = s_n, l > n]$$

and in particular $w(0) = \mu$. Since

$$w(s^n) = \frac{1}{q(s^n)} \sum_{i > n} E[\nu_{n+i}; \nu_1 = s_1, \ldots, \nu_n = s_n, l > n + i]$$

$$= \frac{1}{q(s^n)} \sum_{i > n} \sum_{s_{n+1}, \ldots, s_{n+i}} E[\nu_{n+i}; \nu_1 = s_1, \ldots, \nu_{n+i} = s_{n+i}, l > n + i]$$

we conclude that in terms of the functions $q(s)$ and $m(s)$ the formula for $w(s)$ will be

$$w(s) = \frac{1}{q(s)} \sum_{t:st\in S} q(st)m(st).$$

The vector $\bar{w} = (w(s), s \in S)$ satisfies the relation

$$(M\bar{w})(s) = m(s)w(0) + \sum_k r_k(s)w(sk)$$

$$= m(s)\mu + \sum_k \frac{r_k(s)}{q(sk)} \sum_{t:skt\in S} q(skt)m(skt)$$

$$= m(s)\mu + \frac{1}{q(s)}[\sum_{t:st\in S} q(st)m(st) - q(s)m(s)] = m(s)(\mu - 1) + w(s).$$

Thus

$$M\bar{w} = (\mu - 1)\bar{m} + \bar{w},\ \ \bar{m} = (m(s), s \in S),$$

and $M\bar{w} = \bar{w}$ if $\mu = 1$.

The scalar product $\beta = \bar{q}\bar{w}$ can be computed in two ways:

$$\bar{q}\bar{w} = \sum_{s^n\in S} E[\nu_{n+1} + \ldots + \nu_l; \nu_1 = s_1, \ldots, \nu_n = s_n, l > n]$$

$$= \sum_{n\geq 0} E[\sum_{i\geq n+1} \nu_i] = E[\sum_{i\geq 1} i\nu_i]$$

and

$$\bar{q}\bar{w} = \sum_{(s,st)\in S\times S} q(st)m(st)$$

$$= \sum_{(s^i,s^n)\in S\times S, 0\leq i<n} q(s^n)m(s^n) = \sum_{s^n\in S} nq(s^n)m(s^n).$$

The first result demonstrates that β is the so called average age at childbearing. The equalities $\bar{q}\bar{w} = \beta$ and $\bar{q}\bar{1} = \lambda$ show that the vectors $\bar{v} = \frac{1}{\lambda}\bar{q}$ and $\bar{u} = \frac{\beta}{\lambda}\bar{w}$ provide with the pair $(\bar{v}, \bar{u})$ ensuring (4) with $\rho = 1$.

10 The second moments for the CMJ reproduction

Turning to the second moment characteristics put

$$h(s^n) = E\nu^2(s^n, 0) = E[\nu_{n+1}^2 | \nu_1 = s_1, \ldots, \nu_n = s_n, l > n];$$

$$\sigma^2 = \sum_{s^n \in S} q(s^n)[h(s^n) + 2s_n w(s^n)] - 1.$$

Observe that

$$E(\nu_1 + \ldots + \nu_l)^2 = \sum_{n \geq 1} E[\nu_n^2 + 2\nu_n(\nu_{n+1} + \ldots \nu_l)]$$

$$= \sum_{s^n \in S} [h(s^n)q(s^n) + 2s_n q(s^n)w(s^n)] = \sigma^2 + 1.$$

This implies that in the critical case σ^2 is the individual offspring variance.

Introduce the second moment matrices $\Gamma(s),\ s \in S$ with the elements

$$\Gamma_s(t, t') = \mathrm{Cov}[\nu(s,t), \nu(s,t')],\ t \in S,\ t' \in S.$$

It is easy to see that for the MGW representation of the CMJ process

$$\Gamma_s(0,0) = h(s) - m^2(s); \quad \Gamma_s(0, sk) = \Gamma_s(sk, 0) = (k - m(s))r_k(s);$$

$$\Gamma_s(sk, sk) = r_k(s)(1 - r_k(s)); \quad \Gamma_s(sk, sj) = -r_k(s)r_j(s);$$

and all other elements of $\Gamma(s)$ equal to zero.

We finish this section by proving that

$$\sum_{s \in S} q(s)\bar{w}\Gamma(s)\bar{w} = \sigma^2, \text{ if } \mu = 1. \tag{14}$$

(Recall that all the sums appearing here have a finite number of summands due to the bounded reproduction condition.) Since

$$\begin{aligned} \bar{w}\Gamma(s)\bar{w} &= w^2(0)(h(s) - m^2(s)) + 2\sum_k w(0)w(sk)(k - m(s))r_k(s) \\ &+ \sum_k w^2(sk)r_k(s)(1 - r_k(s)) - 2\sum_{k<j} w(sk)w(sj)r_k(s)r_j(s) \end{aligned}$$

and $w(0) = 1$ we have

$$\begin{aligned}\bar{w}\Gamma(s)\bar{w} &= h(s) - m^2(s) + 2\sum_k w(sk)kr_k(s) - 2m(s)\sum_k w(sk)r_k(s) \\ &\quad + \sum_k w^2(sk)r_k(s) - \left[\sum_k w(sk)r_k(s)\right]^2 \\ &= h(s) + 2\sum_k w(sk)kr_k(s) + \sum_k w^2(sk)r_k(s) - w^2(s).\end{aligned}$$

The last equality is due to

$$m^2(s) + 2m(s)\sum_k w(sk)r_k(s) + \left[\sum_k w(sk)r_k(s)\right]^2$$

$$= \left[m(s) + \sum_k w(sk)r_k(s)\right]^2 = w^2(s).$$

It follows

$$\begin{aligned}\sum_{s\in S} q(s)\bar{w}\Gamma(s)\bar{w} &= \sum_{s\in S} q(s)h(s) + 2\sum_{s\in S}\sum_k kq(sk)w(sk) \\ &\quad + \sum_{sk\in S} q(sk)w^2(sk) - \sum_{s\in S} q(s)w^2(s)\end{aligned}$$

and to arrive at (14) it remains to see that

$$\sum_{s\in S} q(s)h(s) + 2\sum_{s\in S}\sum_k kq(sk)w(sk) = \sum_{s^n\in S} q(s^n)[h(s^n) + 2s_n w(s^n)] = \sigma^2 + 1,$$

and

$$\sum_{sk\in S} q(sk)w^2(sk) - \sum_{s\in S} q(s)w^2(s) = -q(0)w^2(0) = -1.$$

11 Linear growth theorem for the density-dependent CMJ process

Jagers (1997) introduces a general density-dependent branching process via a sequence of point processes: the point process indexed by z gives the life-law to individuals born into the population of size z. With the discrete-time setting under the ass umption of bounded reproduction we are in a position to give a more flexible definition of the density-dependent CMJ process which takes into account the fact that at various ages the same individual belongs to populations of different sizes.

Take a sequence of uniformly bounded point processes

$$\xi(dt, z) = \sum_{i=1}^{l(z)} \nu_i(z)\delta_i(dt), \; z = 1, 2, \dots$$

In view of Section 8 and the introduction we can speak about a density-dependent MGW process $\bar{Z}_n = (Z_n(s), s \in S)$ corresponding to the sequence $\xi(dt, z)$. The resulting population size process $Z_n = \sum_{s \in S} Z_n(s)$ is called here a *phdensity-dependent CMJ process.*

The following theorem is Theorem 6.1 applied to the density-dependent CMJ processes. We use the notation of Sections 8, 9, and 10 just adding an extra parameter z when necessary.

For the density-dependent MGW process governed by the sequence of point processes $\xi(dt, z)$ we can write the reproduction stabilisation conditions (2) and (3) as:

$$m(s, z) \to m(s), \; r_k(s, z) \to r_k(s), \; z \to \infty, \; s \in S, \; k \geq 0;$$

plus

$$h(s, z) \to h(s), \; z \to \infty, \; s \in S. \tag{15}$$

Given the three limit functions $m(s)$, $r_k(s)$, and $h(s)$ we can introduce a number of functions and parameters whose clear interpretations are presented in Sections 9 and 10:

$$q(s^n) = \prod_{i=1}^{n} r_{s_i}(s^{i-1}), \; w(s) = \frac{1}{q(s)} \sum_t q(st)m(st),$$

$$\mu = \sum_{s \in S} m(s)q(s), \; \lambda = \sum_{s \in S} q(s), \; \beta = \sum_{s^n \in S} nq(s^n)m(s^n),$$

$$\sigma^2 = \sum_{s^n \in S} q(s^n)[h(s^n) + 2s_n w(s^n)] - 1.$$

It follows from Section 9 that if $\mu = 1$ the limit matrix M consisting of elements $m(s)$ and $r_k(s)$ has the Perron eigenvalue 1 and the normalised Perron eigenvectors $\bar{v} = \frac{1}{\lambda}\bar{q}$, $\bar{u} = \frac{\beta}{\lambda}\bar{w}$.

Further, the condition (5) of Theorem 6.1 transforms into

$$z[m(s,z) - m(s)] \to d(s),\ z \to \infty,\ s \in S; \tag{16}$$

and

$$z[r_k(s,z) - r_k(s)] \to d_k(s),\ z \to \infty,\ sk \in S. \tag{17}$$

The corresponding matrix D has the elements $d(s)$ at places $(0,s)$, $s \in S$, the elements $d_k(s)$ at places (s,sk), $sk \in S$, and zero elements elsewhere. Thus the parameter $d = \bar{v}D\bar{u}$ is equal to $\frac{c}{\beta}$, where

$$c = \bar{q}D\bar{w} = \sum_{s\in S} q(s)[d(s) + \sum_k d_k(s)w(sk)].$$

Next we show that the parameter c has a clear interpretation in the CMJ-population terms as the convergence rate for the average offspring size:

$$z[\mu(z) - \mu] \to c,\ z \to \infty.$$

Observe that the LHS equal

$$z[\sum_{s\in S} q(s,z)m(s,z) - \sum_{s\in S} q(s)m(s)]$$

$$= z\sum_{s\in S}[q(s,z) - q(s)]m(s,z) + z\sum_{s\in S} q(s)[m(s,z) - m(s)].$$

We should verify that

$$z\sum_{s\in S}[q(s,z) - q(s)]m(s) \to \sum_{s\in S} q(s)\sum_k d_k(s)w(sk),\ z \to \infty.$$

The LHS equals

$$\sum_{s^n\in S} z\left[\prod_{i=1}^{n} r_{s_i}(s^{i-1},z) - \prod_{i=1}^{n} r_{s_i}(s^{i-1})\right] m(s^n)$$

which converges as $z \to \infty$ to

$$\sum_{s^n\in S}\sum_{j=1}^{n}\prod_{i=1}^{j-1} r_{s_i}(s^{i-1})d_{s_j}(s^{j-1})\prod_{i=j}^{n} r_{s_i}(s^{i-1})m(s^n)$$

$$= \sum_{s^n\in S}\sum_{j=1}^{n} q(s^{j-1})d_{s_j}(s^{j-1})\frac{q(s^n)}{q(s^j)}m(s^n)$$

$$= \sum_{s\in S} q(s) \sum_{kt:skt\in S} d_k(s) \frac{q(skt)}{q(sk)} m(skt) = \sum_{s\in S} q(s) \sum_k d_k(s) w(sk).$$

Now we can turn to the key condition (6). Since $d = \frac{c}{\beta}$ *and, due to (14),* $\gamma = \frac{\sigma^2\lambda}{\beta^2}$*, the inequality (6) is equivalent to* $0 < \sigma^2 < \frac{2c\beta}{\lambda}$.

Theorem 11.1 *Consider a density-dependent CMJ process with bounded non-cyclical reproduction satisfying stabilisation conditions (16), (17) and (15). If* $\mu = 1$ *and* $0 < \sigma^2 < \frac{2c\beta}{\lambda}$*, then with the positive probability* $(1 - Q)$ *the branching process never dies out and* $\frac{1}{n} Z_n$ *has the limit distribution (7) with* $a = \frac{2\beta^2}{\sigma^2\lambda}$, $b = \frac{2c\beta}{\sigma^2\lambda}$.

Acknowledgements. *The author wishes to thank Peter Jagers, Olle Nerman and Fima Klebaner for helpful discussions and comments.*

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