

The Asymptotic Composition of Supercritical, Multi-Type Branching Populations

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Abstract

The life, past and future are described of a typical individual in an old, non-extinct branching population, where individuals may give birth as a point process and have types in an abstract type space. The type, age and birth-rank distributions of the typical individual are explicitly given, as well as the Markov renewal type process that describes her history. The convergence of expected and actual compositions towards stable, asymptotic compositions is proved.

1 Introduction

If a proper, branching population does not die out, then its size grows indefinitely (cf. Jagers 1992, e.g.), and by some sort of law of large numbers its composition will stabilize. One aspect of this, the *stable age distribution* of demography has been known for a long time. Indeed, its roots can be traced back more than two centuries, to Euler, 1760. In such a grand perspective, the complete picture of the asymptotic composition of one-type general, supercritical branching populations is certainly recent (Jagers and Nerman and vice versa, 1984). The multi-type case was then investigated and presented by Nerman at the 16th Conference on Stochastic Processes and their Applications (1984). His results were, however, never published. A first account, informal and incomplete, appears in Jagers (1991) and, somewhat more extensively, 1992). A quite pertinent recent paper, from a different, graph and computer algorithm oriented, tradition is Aldous (1991).

The purpose of the present exposition is to give the strict description, that is lacking up to now, of the asymptotic composition of general super-critical

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branching populations in abstract type spaces. It uses Markov renewal theory in Shurenkov's (1989) comprehensive formulation. The branching process framework and real time dynamics are from Jagers (1989).

2 The Population Space

Consider a typical individual of an old population. Call her *Ego* or, for short but less suggestively, 0; think of her as sampled at random from among all those born into the population, since its inception, long ago. She will have children, grandchildren *etc.*, whom we shall refer to in the classical Ulam-Harris manner, $x = (x_1, x_2, \dots, x_n)$ is the x_n th child of the ... of the x_1 th child of 0, the set of 0 and all her possible descendants being denoted by I ,

$$I := \bigcup_{n \geq 0} N^n, N^0 := \{0\}, N := \{1, 2, \dots\}.$$

But 0 also has a mother, to be called -1, a grandmother, -2, and so forth. We concatenate vectors by writing them together, so that $xy, x, y \in I$, has first x 's components, then y 's, and we make the convention $0x = x0 = x$. Then, all the possible progeny of -1, *except* 0 and her descendants, constitutes the set $(-1)I = \{(-1)x; x \in I\}$, and with $Z_- := \{0, -1, -2, \dots\}$, all the possible individuals of the whole population can be written

$$J := Z_- \times I.$$

A new-born individual is allotted (or chooses, depending upon your philosophy) a *life path* or life (career) from the *life space* (Ω, \mathcal{A}) . This should be thought of as abstract, with a countably generated σ -algebra, and rich enough to carry those functions that are of interest for the particular study. On Ω there is a sequence $0 \leq \tau(1) \leq \tau(2) \leq \dots \leq \infty$ of random variables giving the successive ages at child-bearing. If $\tau(j)(\omega) = \infty$, then the interpretation is that the life career ω involves fewer than j children.

At birth the new-born child inherits a *type* from a space (S, \mathcal{S}) , again with a countably generated σ -algebra. In other words, there are also measurable functions $\sigma(j) : \Omega \rightarrow S$, giving the type of the j 'th child. The *reproduction point process* ξ on $S \times R_+$ is defined by

$$\xi(A \times B) := \#\{i \in N; \sigma(i) \in A, \tau(i) \in B\}.$$

In order to define the basic probability space for the whole population, the *population space*, we need the life space for each possible individual but also something that ties the individuals in Z_- to their mothers, information about their *birth ranks*. These are natural numbers, and we make the interpretation that if $-j + 1$ has rank r then $-j$ is $-j$'s i 'th child for $i = 1, \dots, r - 1$ and it is the $i + 1$ 'th child for $i \geq r$. Finally, to anchor the population in real time,

we need information about Ego's age at sampling. Thus the population space is defined to be

$$\Omega := R_+ \times N^\infty \times \Omega^J$$

with the obvious product σ -algebra to be denoted by \mathcal{C} . This space can be restricted to a tree-type space of the kind advocated by Neveu (1986) and Charvin (1986). For the interpretation in terms of random trees (Aldous, 1991) that might indeed be an advantage.

Recall that a branching process started from a newborn 0-individual is suitably defined on $S \times \Omega^J$, the first coordinate being the ancestor's starting type. When referring to such a process, we shall write σ_x for the type of $x \in J$ and τ_x for her birth-time, defined recursively from $\tau_0 = 0$ and the successive ages at child bearing in the line leading to x , cf. Jagers, 1989, though notation is slightly different there.

3 The Life Kernel and its Stable Population Law

The probability structure of the process is determined by a *life kernel* P_s on (Ω, \mathcal{A}) , the probability measure according to which the choice of life-career of an s -type is performed. In Jagers (1989) it is shown how such a kernel determines a unique Markov branching probability measure over $(\Omega^J, \mathcal{A}^J)$, once Ego's type has been fixed. We denote this measure, as well, by P_s , $s \in S$ being this starting type. More generally, if Ego's type is chosen according to a probability measure π on (S, \mathcal{S}) , then P_π is the corresponding measure, $P_\pi = \int_S P_s \pi(ds)$. The expectations are E_s and E_π , respectively.

The crucial rôle for the development of a population is played by the reproduction kernel μ , defined as the expected number of births of children of various types and at various ages:

$$\mu(\tau, ds \times dt) := E_\tau[\{(ds \times dt)\}].$$

The population is supposed to be *Malthusian* and *supercritical*, this meaning that there is a number $\alpha > 0$, the Malthusian parameter, such that the kernel $\hat{\mu}(\alpha)$,

$$\hat{\mu}(\tau, ds; \alpha) := \int_0^\infty e^{-\alpha t} \mu(\tau, ds \times dt)$$

has Perron root one and is what Shurenkov (1989) calls *conservative*. (This corresponds to irreducibility and α -recurrence in the terminology of Niemi and Nummelin (1986).) By the abstract Perron-Frobenius theorem (Shurenkov, 1989, p. 43, or Nummelin, 1984, p. 70), there is then a σ -finite measure π on the type space (S, \mathcal{S}) , and strictly positive a.e. $[\pi]$ finite measurable function h on the same space, such that

$$\int_S \hat{\mu}(\tau, ds; \alpha) \pi(d\tau) = \pi(ds).$$

$$\int_S h(s) \hat{\mu}(\tau, ds; \alpha) = h(\tau).$$

Further we require strong or positive α -recurrence in the sense that $h \in L^1[\pi]$ and

$$0 < \beta = \int_{S \times S \times R_+} t e^{-\alpha t} h(s) \mu(\tau, ds \times dt) \pi(d\tau) < \infty.$$

(In population dynamics this entity might be interpreted as the stable age at childbearing, though some care has to be exercised about this in the multi-type case, as we shall see.) Then we can (and shall) norm to

$$\int_S h d\pi = 1.$$

Throughout we also make the homogeneity assumption that $\inf h > 0$. Then π is finite and can (and will) also be normed to a probability measure. These are the conditions (on μ alone) for the general Markov renewal theorem of Shurenkov (1989), p. 107. Finally, we assume that the reproduction kernel is non-lattice and satisfies the natural condition

$$\sup_s \mu(s, S \times [0, \epsilon]) < 1$$

for some $\epsilon > 0$. Note that we assume only non-latticeness, rather than spread-outness of the kernel. We shall summarize all these conditions by referring to the population as non-lattice *strictly Malthusian*. (Clearly there is a lattice analog of our results, relying upon the lattice Markov renewal theorem, cf. Shurenkov (1989), p. 122. There you will also find the concept of latticeness developed in a multitype context, with the meaning that there is a stepping time unit, independent of starting and ending position in the type space, but a phase which may depend on both: for some $d > 0$ and $c : S \rightarrow [0, d)$, and $L_{dc}(s) := \{(r, t) : \tau \in S, t \in R_+, t = c(\tau) - c(s) + nd, \text{ for some } n = 0, 1, \dots\}$

$$\pi(\{s; \mu(s, S \times R_+) > \mu(s, L_{dc}(s))\}) = 0).$$

In order, finally, to give a presentation of the stable population measure on (Ω, \mathcal{A}) we need notation for some random elements on this space: T_0 will denote Ego's age at sampling, S_0 her type, and R_0 her rank, i.e. ordinal number in her sibship. T_1 is Ego's mother's age, when she gave birth to Ego, S_1 her type, and R_1 her rank. And so on backwards. Similarly we let U_0, U_1, \dots denote the whole lives of Ego, Ego's mother, \dots , and Z^0 the population initiated by Ego. Z^1, Z^2, \dots can be used to denote Ego's mother's life and daughter process except Ego, grandmother's daughter process, except mother and her progeny etc. Thus, Z^j is the coordinate projection $\Omega \rightarrow \Omega^{-j}$. Similarly, T_0 is the projection of the population space onto its first coordinate R_+ and the sequence of ranks is the projection onto N^∞ , cf. the figure. Also recall that σ_i, τ_i are the type and

birth times in a branching process of the ancestor's i :th child (the latter equalling infinity, if no i :th child is ever born). In the following definition we shall interpret assertions ' $Z^j \in A_j$ ' also as assertions about a traditional branching process ($-j$ being its ancestor). Then we must supplement it by information about which of the ancestor's children, who has been withdrawn from the process in order to play the rôle of $-j + 1$. Indeed, the very careful reader should interpret $A_j, j = 1, 2, \dots$ on the right hand side beneath as the set

$$\{(\omega_{kx}; k \in Z_+, x \in I) \in \Omega^I; (\omega_{(k+1)(x \geq j-1)}x; k \in Z_+, x \in I) \in A_j\}.$$

Such subtleties are due to the convention we made about birth ranks in Section 2, where the concatenated vector kx was also defined.

Definition 1 The stable population measure \mathbf{P} on (Ω, \mathcal{A}) is determined by

$$\begin{aligned} \mathbf{P}(Z^0 \in A_0, T_0 \in dt_0, S_0 \in ds_0, R_0 = i_0; Z^1 \in A_1, T_1 \in dt_1, S_1 \in ds_1, R_1 = i_1; \\ \dots; Z^n \in A_n, T_n \in dt_n, S_n \in ds_n, R_n = i_n) = \\ E_\pi[e^{-\alpha t_{i_n}}; \sigma_{i_n} \in ds_n] E_{s_n}[e^{-\alpha t_n}; A_n \cap \{\sigma_{i_{n-1}} \in ds_{n-1}, \tau_{i_{n-1}} \in dt_n\}] \dots \\ \dots E_{s_1}[e^{-\alpha t_1}; A_1 \cap \{\sigma_{i_0} \in ds_0, \tau_{i_0} \in dt_1\}] P_{s_0}(A_0) \alpha e^{-\alpha t_0} dt_0 \end{aligned}$$

for all $n \in \mathbb{N}, A_j \in \mathcal{A}^j, t_j \in \mathbb{R}_+, s_j \in \mathbb{S}, i_j \in \mathbb{N}, j = 0, 1, \dots, n$.

By the eigenmeasure and eigenfunction properties of π and h it can be checked that changes in n yield a projective system defining \mathbf{P} , and in the next section we shall see how the stable population appears as a limit of growing branching processes. Here we shall try to understand its substance, by formulating some consequences of the definition. In them we write $\hat{\mu}(\tau, ds)$ as an abbreviation for $\hat{\mu}(\tau, ds; \alpha) = \int_0^\infty e^{-\alpha t} \mu(\tau, ds \times dt)$. Powers $\hat{\mu}^n$ are iterated kernels and $\mu_\alpha(\tau, ds \times dt) := e^{-\alpha t} \mu(\tau, ds \times dt)$.

Proposition 1 The sequence of types backwards from Ego, $\{S_n\}_0^\infty$, is a Markov chain with transition probabilities

$$\mathbf{P}(S_{n+1} \in ds | S_n = r) = \pi(ds) \frac{\hat{\mu}(s, dr)}{\pi(dr)}.$$

The distribution of S_0 is π , whereas $S_n \sim \hat{\mu}^n(s, S) \pi(ds) \rightarrow h(s) \pi(ds)$, as $n \rightarrow \infty$, the latter limit also being the stationary distribution of the chain.

Proof Integrating and summing in the theorem yields

$$\begin{aligned} \mathbf{P}(S_0 \in ds_0, \dots, S_n \in ds_n) = \\ = E_\pi \left[\sum_{i_n} e^{-\alpha \tau(i_n)}; \sigma(i_n) \in ds_n \right] E_{s_n} \left[\sum_{i_{n-1}} e^{-\alpha \tau(i_{n-1})}; \sigma(i_{n-1}) \in ds_{n-1} \right] \dots \end{aligned}$$

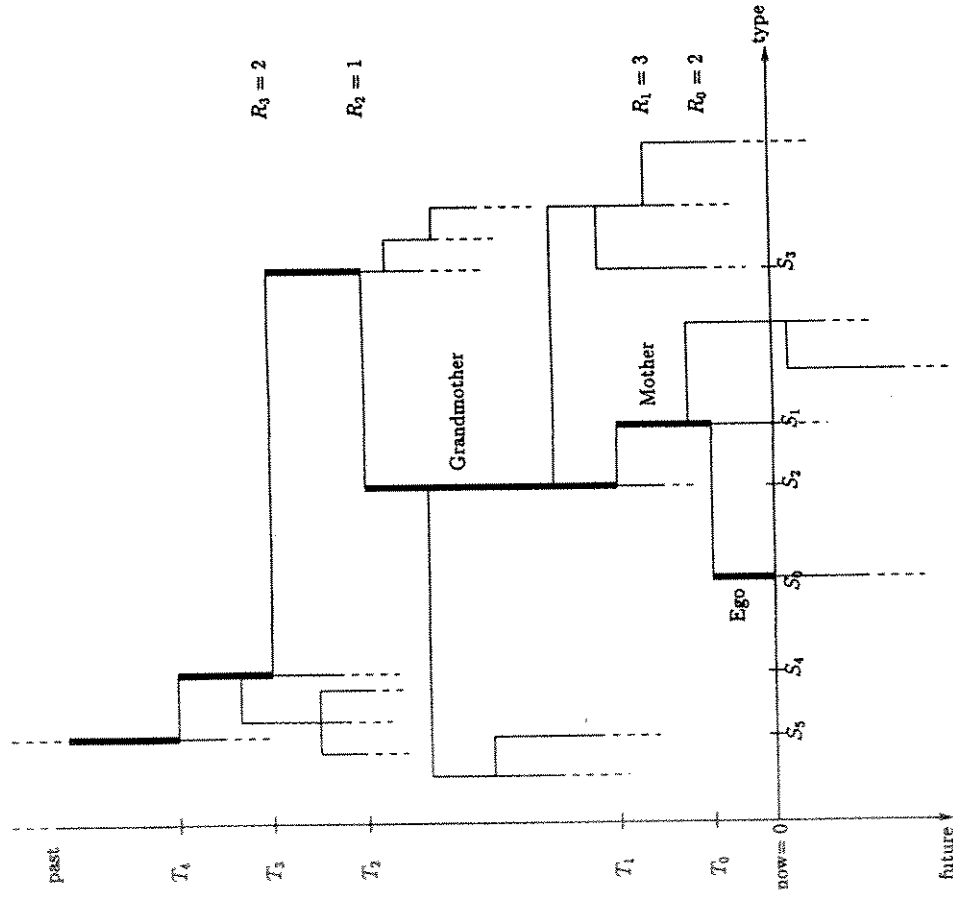


Figure. The doubly infinite population space.

$$\begin{aligned} & \dots E_{s_1} \left[\sum_{i_0} e^{-\alpha \tau(i_1)} ; \sigma(i_0) \in ds_0 \right] = \\ & = E_{\pi} [\xi(ds_n; \alpha)] E_{s_n} [\xi(ds_{n-1}; \alpha)] \dots E_1 [\xi(ds_0; \alpha)] \end{aligned}$$

$$\pi(ds_n) \mu(s_n, ds_{n-1}) \dots \mu(s_1, ds_0),$$

where

$$\xi(A; \alpha) := \int_0^{\infty} e^{-\alpha t} \xi(A \times dt),$$

we have used the eigenmeasure property $\int \hat{\mu}(s, ds_n) \pi(ds) = \pi(ds_n)$, and written $\sigma(i)$, $\tau(i)$ instead of σ_i , τ_i , since the P_s reduce to measures over the life space here. The asserted form of transition and marginal probabilities follow from this joint distribution of types. The convergence $\hat{\mu}^n(s, S) \rightarrow h(s)$ follows directly from the lattice Markov renewal theorem (Shurenkov, 1989, p. 122). Of course, it can also be brought back to a limit theorem for Markov chains by the trick of norming $\hat{\mu}$ to a kernel with mass one, $h(r)\hat{\mu}(s, dr)/h(s)$. The stationarity can be checked directly. \square

Without spelling this out as another proposition, let us state that the sequence $\{(R_n, S_n)\}$ of ranks and types also constitutes a Markov chain. Indeed, given the sequence of types, the ranks even become conditionally independent. The rank marginals are given by $\mathbf{P}(R_0 = i) = E_{\pi}[e^{-\alpha \tau(i)}]$, and

$$\mathbf{P}(R_n = i) = \int_S \hat{\mu}^n(s, S) E_{\pi}[e^{-\alpha \tau(i)}; \sigma(i) \in ds] \rightarrow \int_S h(s) E_{\pi}[e^{-\alpha \tau(i)}; \sigma(i) \in ds],$$

as $n \rightarrow \infty$. Though the distribution of, at least, R_0 is important for birth rank studies, the joint behaviour of types and times between births seems of greater import both mathematically, and in tracing populations backwards, e.g. in evolutionary genetics.

Proposition 2 *The sequence of types and interbirth times backwards from Ego, $\{S_n, T_n\}_0^{\infty}$ define a Markov renewal process. They have the transition kernel*

$$\mathbf{P}(S_{n+1} \in ds, T_{n+1} \in dt | S_n = r) = \pi(ds) \frac{\mu_{\alpha}(s, dr \times dt)}{\pi(dr)}.$$

The distribution of S_0 is π , T_0 is exponentially distributed with the Malthusian parameter, and independent of the rest.

$$(S_n, T_n) \sim \int_S \hat{\mu}^{n-1}(\tau, S) \mu_{\alpha}(s, dr \times dt) \pi(ds) \rightarrow \int_S h(r) \mu_{\alpha}(s, dr \times dt) \pi(ds),$$

as $n \rightarrow \infty$.

Proof The proof follows the pattern of the preceding one, and is left out. \square

Among other things, this shows that the expected age of the mother at the birth of a random child is

$$\mathbf{E}[T_1] = \int_{S \times R_+} t e^{-\alpha t} \mu(\pi, ds \times dt),$$

whereas the expectation of the asymptotic distribution of T_n , $n \rightarrow \infty$ is

$$\beta = \int_{S \times R_+} t e^{-\alpha t} h(s) \mu(\pi, ds \times dt).$$

Here, of course, $\mu(\pi, ds \times dt) = \int_S \mu(\tau, ds \times dt) \pi(dr)$

In analogy with Proposition 2, the sequence $\{R_n, S_n, T_n\}$ constitutes a Markov renewal process, with a transition kernel that is easily determined from Definition 1. Actually, more generally:

Proposition 3 *The sequence of ranks, types, and lives backwards from Ego has the Markov property*

$$\begin{aligned} \mathbf{P}(R_{n+1} = j, S_{n+1} \in ds, U_{n+1} \in A | R_n = i, S_n = r, U_n, R_{n-1}, S_{n-1}, \dots) = \\ = E_{\pi}[e^{-\alpha \tau(j)}; \sigma(j) \in ds] \frac{E_s[e^{-\alpha \tau(i)}; A \cap \{\sigma(i) \in dr\}]}{E_{\pi}[e^{-\alpha \tau(i)}; \sigma(i) \in dr]}. \end{aligned}$$

The distribution of (R_0, S_0, U_0) is $E_{\pi}[e^{-\alpha \tau(i)}; \sigma(i) \in ds] P_s(A)$, $i \in N$, $s \in S$, $A \in \mathcal{A}$, whereas in the notation

$$\mu_A(s, B) := E_s[\xi(B; \alpha); A],$$

$$\mathbf{P}(R_n = i, S_n \in ds, U_n \in A) =$$

$$\begin{aligned} = E_{\pi}[e^{-\alpha \tau(i)}; \sigma(i) \in ds] \int_S \hat{\mu}^{n-2}(\tau, S) \mu_A(s, dr) \rightarrow \\ \rightarrow E_{\pi}[e^{-\alpha \tau(i)}; \sigma(i) \in ds] \int_S h(r) \mu_A(s, dr), \end{aligned}$$

as $n \rightarrow \infty$.

Proof The proof is again (rather complicated but) not hard by insertion. \square

The stable population measure \mathbf{P} describes a typical individual, her background and future when *sampling from among all those born, dead or alive*. Though this is artificial from, say, a biological viewpoint, it is not only mathematically convenient but also conceptually the fundamental situation. Being alive or not is a property of your age and your life career. Therefore the stable measure when *sampling in the live population* is obtained by conditioning in \mathbf{P} on Ego being alive, and correspondingly for sampling from other subsets of individuals.

To express this more formally, assume a *life span*, $\lambda : \Omega \rightarrow [0, \infty]$, defined and let L_0 denote Ego's life span. Then, $L_0 > T_0$ means that Ego is alive.

Proposition 4 *The probability law describing a typical individual, sampled from among those alive is $\mathbf{P}(\cdot | L_0 > T_0)$.*

Corollary 1 *The probability that a typical, live individual is of rank i , has type in ds and a life career in a set $A \in \mathcal{A}$ is*

$$E_{\pi}[e^{-\alpha r(t)}, \sigma(t) \in ds] \int_0^{\infty} P_{\pi}(A, \lambda > t) \alpha e^{-\alpha t} dt / \int_0^{\infty} P_{\pi}(\lambda > t) \alpha e^{-\alpha t} dt.$$

The probability of having just the property A is

$$\frac{\int_0^{\infty} P_{\pi}(A, \lambda > t) e^{-\alpha t} dt}{\int_0^{\infty} P_{\pi}(\lambda > t) e^{-\alpha t} dt}.$$

In the next section we shall see that this is, indeed, the limit of the probability measure describing the properties of an individual sampled from among all those alive.

4 Convergence towards Stable Population Composition

Let J_n denote the class of individuals stemming from $-n$, i.e. $\{-n, \dots, -1, 0\} \times I$. Recall that by convention $0 \in I, 0x = x$, and $-j0 = (-j, 0) = -j$. Therefore $-jI = \{-j\} \times I$ denotes $-j$ and all her possible descendants except $-j + 1$ and her progeny. Observe that if $-n$ is mapped to 0, all her progeny being mapped onto I so as to preserve all family relations, then $(\Omega^n, \mathcal{A}^n)$ is mapped to $(\Omega^I, \mathcal{A}^I)$, and the two spaces can be thus identified. Fix $n, t = (i_{n-1} \dots i_0) \in N^n, A \in \mathcal{A}^n$ and $a \in R_+$, and consider the subset $E \in \mathcal{C}$,

$$E := [0, a] \times (i_0 \dots i_{n-1}) \times N^{\infty} \times A \times \Omega^{n \setminus I_n}.$$

Define Π_x as the projection mapping $(s, \{\omega_y; y \in I\})$ to $(\sigma_x, \{\omega_{xy}; y \in I\})$, the daughter process of $x \in I$, cf. Jagers, 1989. In an obvious sense $y \in I$ has the property E at time t if and only if

- $y = x_1$ for some $x_1 \in I$,
- $0 \leq t - \tau_{x_1} \leq a$, and
- $\Pi_x \in S \times A$.

Now, note that $\tau_{x_1} = \tau_x + \tau_1 \circ \Pi_x$, so that defining a *random characteristic* on $(S \times \Omega^I, S \times \mathcal{A}^I)$ (cf. Jagers, 1989)

$$\chi^E(t) := 1_A 1_{[0, a]}(t - \tau_1),$$

(A thus viewed as a subset of Ω^I), the number of individuals having the property E at time t in a branching population started at time 0 from a newborn ancestor will be

$$z_t^{\chi^E} := \sum_{x \in I} \chi^E(t) \circ \Pi_x = \sum_{x \in I} 1_{\{\Pi_x \in S \times A\}} 1_{\{0 \leq t - \tau_{x_1} \leq a\}}.$$

But adapting the convergence theorem for means of supercritical general branching populations (cf. op. cit.) to the Markov renewal theorems of Shurenkov (1989, pp. 107, 127, 134) we have:

Theorem 1 *Consider a non-lattice, strictly Malthusian, supercritical branching population, counted with a bounded characteristic χ such that the function $e^{-\alpha t} E_s[\chi(t)]$ is directly Riemann integrable (π). Then, for π -almost all s ,*

$$\lim_{t \rightarrow \infty} e^{-\alpha t} E_s[z_t^{\chi}] = h(s) \int_{S \times R} e^{-\alpha t} E_r[\chi(t)] \pi(dr) dt / \beta := h(s) E_{\pi}[\tilde{\chi}(\alpha)] / \alpha \beta,$$

in the obvious notation for Laplace transform.

If the population is as above and some convolution power of the reproduction kernel is, further, non-singular (cf. beneath), then for π -almost all $s \in S$

$$\lim_{t \rightarrow \infty} e^{-\alpha t} E_s[z_t^{\chi}] = h(s) E_{\pi}[\tilde{\chi}(\alpha)] / \alpha \beta,$$

uniformly in all χ with $E_s[\chi(t)] \leq 1$ (without any Riemann integrability requirement).

The notion of direct Riemann integrability used is that of Shurenkov (1989) pp. 80 ff.: A measurable function $g : S \times R_+ \rightarrow R$ is directly Riemann integrable (π) if for any $\epsilon > 0$ we can find $\delta > 0$ and functions g^- and g^+ both in $L^1[\pi \times d\delta]$ such that for π -almost all $s, g^-(s, \cdot) \leq g(s, \cdot) \leq g^+(s, \cdot), g^{\pm}(s, t) = g^{\pm}(s, n\delta)$ for $n\delta \leq t < (n+1)\delta$, and the $L^1[\pi \times d\delta]$ -distance between g^+ and g^- is less than ϵ . Convolution means convolution in time combined with transition in type. Non-singularity is Shurenkov's term (1989, p. 127) for spread-outness: For fixed $r \in S$ and a Borel set B , the reproduction kernel $\mu(r, \cdot \times B)$ is absolutely continuous with respect to $\tilde{\mu}(r, \cdot)$. It is possible to choose a regular version of the Radon-Nikodym derivative, $F(r, s, dt)$, which is a measure on R_+ in its

last coordinate. Non-singularity means that for almost all τ, s with respect to $\pi(dt)\mu(\tau, ds)$ this measure is non-singular with respect to Lebesgue measure.

Thanks to this strong Markov renewal theory, the proof is rather straightforward, cf. Jagers (1992), by use of the regularity condition $\sup \mu(s, S \times [0, \epsilon]) < 1$ for some $\epsilon > 0$, in order to guarantee boundedness of $e^{-\alpha t} E_s[y_t]$, where

$$y_t = \#\{x \in I; \tau_x \leq t\} = \sum_{x \in I} 1_{R_+}(t - \tau_x) = z_t^{1^{R_+}}$$

is the total population at time t of a branching process started at time 0. Of course, there is also a lattice variant of this result, cf. Shurenkov (1989, p. 122 and 134).

For sets E as above, we call

$$P_{s,t}^\epsilon(E) := E_s[z_t^X] / E_s[y_t],$$

the composition in expectation of a branching population at time t , started at time 0 from an ancestor of type $s \in S$. By summation over various $\tau \in N^n$ and replacing the interval $[0, a]$ by Borel sets B , this can obviously be extended to a probability measure over the measurable subsets of $R_+ \times N^\infty \times \Omega^J$ which depend only upon $n \in N$ steps backwards, i.e. belong to the σ -algebra generated by sets of the form $E = B \times M \times N^\infty \times A \times \Omega^J \setminus J_n$, $B \in \mathcal{B}(R_+)$, $M \subset N^n$, $A \in \mathcal{A}^{J_n}$ for fixed, but arbitrary $n \in N$. We denote the latter by \mathcal{C}_n and write $\mathcal{C}_n(B)$ for the sub- σ -algebra, where the first coordinate is fixed to be B .

Corollary 2 Under the assumptions of Theorem 1, consider a $B \in \mathcal{B}(R_+)$, $n \in N$, and any $E \in \mathcal{C}_n(B)$ such that $R_j = i_j, j = 0, \dots, n-1$. Write $\tau = (i_{n-1}, \dots, i_0)$ and assume that $e^{-\alpha t} P_s(t - \tau, E)$ is directly Riemann integrable. Then, the composition in expectation of a non-lattice, strictly Malthusian, and supercritical branching population at time t , started at time 0 from an ancestor of π -almost any type $s \in S$, satisfies

$$P_{s,t}^\epsilon(E) = E_s[z_t^X] / E_s[y_t] \rightarrow \int_B \alpha e^{-\alpha t} dt E_\pi[e^{-\alpha \tau}, A] = \mathbf{P}(E),$$

as $t \rightarrow \infty$.

Proof This is only checking the direct Riemann integrability. Note that τ is fixed, and of course matters in the coordinate projection singling out A from E , cf. the discussion preceding Definition 1. \square

Corollary 3 If reproduction (i.e. some convolution power of the reproduction kernel) is non-singular, besides the conditions of Theorem 1, then for π -almost all s $P_{s,t}^\epsilon \rightarrow \mathbf{P}$ in total variation, as $t \rightarrow \infty$.

Proof By Theorem 1, the convergence is uniform over sets $E \in \mathcal{C}_n$ for n fixed, at least if they are of the form $E = B \times M \times N^\infty \times A \times \Omega^J \setminus J_n$, $B \in \mathcal{B}(R_+)$, $M \subset N^n$, $A \in \mathcal{A}^{J_n}$. But these sets, $n \in N$ constitute an algebra that generates $\mathcal{C} = \bigvee_n \mathcal{C}_n$. The rest follows by approximation. \square

Leaving composition in expectation, we turn to the actual composition,

$$P_{\sigma_0,t}(E) := z_t^X / y_t.$$

As for classical cases, convergence here requires the famed $x \log x$ -condition. It has the following general form: Write

$$\tilde{\xi} := \int_{S \times R_+} e^{-\alpha t} h(s) \xi(ds \times dt).$$

Then the condition is

$$E_\pi[\tilde{\xi} \log^+ \tilde{\xi}] < \infty.$$

From Jagers (1989) we have:

Theorem 2 Add the $x \log x$ -condition and finiteness of $\xi(S \times R_+)$ to the assumptions of Theorem 1. Further assume that, for fixed t , y_t is uniformly integrable over its starting type $\sigma_0 = s \in S$. Then, as $t \rightarrow \infty$,

$$e^{-\alpha t} z_t^X \rightarrow w E_\pi[X(\alpha)] / \alpha \beta$$

in $L^1[\mathcal{P}_s]$, for π -almost all $s \in S$. Here w is a non-negative random variable with $E_s[w] = h(s)$.

Note that we have w with $E_s[w] = h(s)$, rather than expectation one as asserted in *op. cit.* It is the unnormalized random variable w that is the limit of the intrinsic martingale

$$w_L = \sum_{z \in L} e^{-\alpha \tau_z} h(\sigma_z)$$

(a.s. if only sequences of lines L are considered, in L^1 otherwise, cf. *op. cit.*).

From its definition (and Theorem 2) it is clear that $w > 0 \Rightarrow y_t \rightarrow \infty$. The converse of this is needed to show that for bounded characteristics X

$$z_t^X / y_t \rightarrow E_\pi[X(\alpha)]$$

if only $y_t \rightarrow \infty$.

Lemma 1 For a strictly Malthusian process, assume that $\inf_{s \in S} P_s(w > 0) > 0$. Then, $w > 0 \Leftrightarrow y_t \rightarrow \infty$ a. s. $P_s, s \in S$.

Proof Enumerate individuals in the order they are born into the population: $X_0 = 0 \in I$, $0 = \tau X_0 \leq \tau X_1 \leq \dots$ by some rule that guarantees that mothers precede their daughters (if individuals happen to appear simultaneously). Then

$$y_t = \sup\{n; \tau X_n \leq t\}.$$

If $y_t \rightarrow \infty$, then the sequence $\{X_n\}$ is already well defined. Otherwise, just continue somehow, respecting the rule that mothers must precede daughters. The assumption of strict Malthusianity prevents explosion in finite time. Hence $\tau X_n \rightarrow \infty$ whether $y_t \rightarrow \infty$ or not.

But for any $n \in \mathbb{N}$

$$w \circ S X_n > 0 \Rightarrow w > 0 \text{ or } y_t \not\rightarrow \infty.$$

(As the reader has noted we are far from finical about spelling out a.s.-qualifications.) If \mathcal{A}_n denotes the σ -algebra generated by the ancestor's type σ_0 and the lives $\omega X_0, \omega X_1, \dots, \omega X_n$, then Lévy's theorem yields that

$$0 < \inf_r P_r(w > 0) \leq P_{\sigma X_n}(w \circ S X_n > 0) =$$

$= P_s(w \circ S X_n > 0 \mid \mathcal{A}_{n-1}) \leq P_s(w > 0 \text{ or } y_t \not\rightarrow \infty \mid \mathcal{A}_{n-1}) \rightarrow 1_{\{w > 0 \text{ or } y_t \not\rightarrow \infty\}}$, as $n \rightarrow \infty$. Hence, a.s. $y_t \rightarrow \infty \Rightarrow w > 0$, the converse implication being already noted. □

Note that under the conditions of Theorem 2, $E_s[w] = h(s) > 0$. Hence, for all $s \in S$, $P_s(w > 0) > 0$ and suitable compactness assumptions yield the same for the infimum.

Corollary 4 *Let the assumptions of Theorem 2 hold and add that $\inf_s P_s(w > 0) > 0$. Then, for any E as in Corollary 2, the actual composition converges to the stable composition on the set of non-extinction:*

$$P_{s,t}(E) \rightarrow \mathbf{P}(E)$$

in P_s -probability on $\{y_t \rightarrow \infty\}$ for π -almost any $s \in S$, as $t \rightarrow \infty$.

By invoking Aldous's paper (1991) we could have made the argument marginally simpler, proving Corollary 2 just in the setting where E depends only upon Ego's and her progeny's lives. That yields the convergence of his fringe tree, which is Ego's daughter process in our terminology. Realizations of our stable population process $(\Omega, \mathcal{A}, \mathbf{P})$ are "sin-trees" in Aldous's parlance: they have a single infinite path. Thus the convergence of the extended fringe follows from Aldous's Proposition 11. Unfortunately, his main theorem on extremality of invariant laws, and the ensuing convergence in probability of the fringe distribution, is of

little avail here, since we have this type of convergence from the beginning and it is not easier to prove convergence in distribution.

Finally, note that in order to obtain average χ -values among those alive we should just consider ratios z_t^χ/z_t rather than z_t^χ/y_t , $z_t = z_t^{(e,\lambda)}$ denoting the number of individuals alive at time t . (This interpretation presumes that χ counts only living individuals, i. e. that it vanishes outside the interval $[0, \lambda)$.)

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UN LIEN ENTRE RÉSEAUX DE NEURONES ET SYSTÈMES DE PARTICULES: UN MODELE DE RÉTINOTOPIE

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Résumé

Nous étudions un modèle stochastique de rétinitopie introduit par M. Cottrell et J.C. Fort. Nous faisons une nouvelle démonstration qui généralise leurs résultats sur la convergence de ce processus, grâce à des techniques de systèmes de particules. Celles-ci fournissent également une méthode de simulation de la loi limite.

1. Introduction

L'algorithme de Kohonen (écrit en 1982, voir [10],[11]) modèle un processus d'auto-organisation des liens neuronaux, la rétinitopie. Il s'agit de l'établissement d'une bijection bicontinue entre des cellules de la rétine (représentée par $\{0, \dots, n + 1\}^2$) et du cortex (représenté par $[0, 1]^2$). Chaque cellule rétinienne est reliée à plusieurs cellules corticales, les liens sont renforcés proportionnellement au produit de l'intensité des stimuli reçus par la rétine, et de l'excitation des cellules corticales (principe de Hebb). Les cellules corticales images de cellules réiniennes voisines deviennent elles-mêmes voisines dans $[0, 1]^2$ (auto-organisation).

Toutefois, une étude rigoureuse de ce modèle historique est délicate en dimension supérieure à 1 (voir [1],[4],[9]). Nous nous intéressons donc ici à un algorithme modifié proposé en 1986 par M. Cottrell et J.C. Fort ([3]), qui est à bords fixés, et qui localise l'interaction (le prix en est malheureusement une perte du réalisme biologique). Dans [3], ce modèle est complètement analysé en dimension 1, et certains résultats étendus en dimension 2.

Nous souhaitons illustrer par cet article l'intérêt de l'utilisation des techniques de systèmes de particules (ici la *duaité*) pour l'analyse de réseaux à interaction locale: dans la section 2, nous décrivons le modèle de Cottrell et Fort, puis nous l'interprétons comme un système de particules, le processus de lissage. Celui-ci est dual d'un processus de marches aléatoires couplées. Cette dualité fournit une nouvelle démonstration de la convergence du processus initial, via le calcul des moments de la variable limite, et permet une simulation plus rapide de cette dernière (section 3).

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