Bernoulli **1(1/2)**, 1995, 171–189

Limits of spatial branching populations

ANTON WAKOLBINGER

Fachbereich Mathematik, Johann Wolfgang Goethe-Universität, D-60054 Frankfurt am Main, Germany

In critical branching and migrating populations, mobility of the individuals counteracts, and the clumping effect caused by the branching favours local extinction of the population in the large time limit. For example, d-dimensional critical binary branching Brownian motion ($d > 1$) with a spatially inhomogeneous branching rate $V(x)$, when started off with a homogeneous Poisson population, persists if $V(x) \sim \|x\|^{d-2}(\log\|x\|)^{-(1+\epsilon)}$, and suffers local extinction if $V(x) \sim \|x\|^{d-2}(\log\|x\|)^{-1}$ as $\|x\| \to \infty$; this can be derived from a probabilistic persistence criterion (Theorem 2). Besides presenting this result, the paper reviews conditions on the parameters of various other models which are necessary and sufficient for persistence, and discusses related results for superprocesses. Common to the proofs is the method of analysing the backward tree of an individual encountered in an old population, originally due to Kallenberg (1977) and Liemant (1981) in discrete time settings.

Keywords: backward trees; branching populations; large time limits; local extinction; persistence; spatially inhomogeneous critical branching; superprocess limits

1. Introduction

This paper focuses on two kinds of limits of spatial branching populations, namely 'large time limits' and 'superprocess limits', and some of their interplay.

As to the former, it is well known that 'there are no freely reproducing populations of stable sizes' (Jagers 1991). Nevertheless, for a large class of models, 'stabilization' of (initially finite) *supercritical* branching populations has been proved in the sense that the distribution of the pedigree of an individual sampled among all those alive in the population at time t converges as $t \to \infty$ (Jagers and Nerman 1984; Nerman and Jagers 1984). Taib (1992) gives a good account of this and also treats applications to population genetics.

The situation is somewhat different in models of infinite spatially (or 'geographically') distributed populations, whose individuals perform migration and branching: here, *convergence to a non-trivial equilibrium* may occur in situations of *purely critical* branching, provided that the *mobility* of the individuals is strong enough to counteract the *clumping effect* caused by the critical branching. We will illustrate this in the present paper with a series of examples. These were primarily motivated not from the point of view of biological applications (though a point of contact might be the work of Sawyer (e.g. Sawyer 1976; cf. also the discussion in Jagers 1991), but rather from the theoretical interest in investigating by probabilistic methods the borderline between persistence and local extinction of infinite critical branching populations, and sometimes also in obtaining nice analytic corollaries, like that of Theorem 5 below.

All the examples presented in Section 2 are very simple ones within the general class of (Crump–Mode–Jagers) branching processes, since the individuals are allowed to generate their offspring only

1350-4864

at the end of their lifetimes (and develop independently in all other respects). Nevertheless, the question for which model parameters these critical branching populations are *persistent*, in the sense that they converge towards a locally non-extinct equilibrium, is not so simple, and will be attacked by the method of 'backward trees' described in Section 2.2 below. There is a close connection between these backward trees and the 'stable pedigrees' mentioned above: the backward tree *rooted at site* x arises as the pedigree of an individual sampled from all those in the old population which are situated *at site* x, given there is at least one.

In all the models described in Section 2, the expected number of individuals in a bounded region (though not always its second moment) remains finite; in addition, all the branching equilibria which occur are 'of Poisson type' in the sense that they consist of a Poisson system of *clans* or *families* of mutually related individuals (cf. Liemant *et al.* 1988, Section 2.7). The 'backward tree method' also turns out to be helpful in answering the question whether these equilibrium clans behave in a recurrent way in the sense that they come back to populate a bounded region again and again (see Theorem 7).

When speaking of 'convergence into equilibrium' we will, for simplicity, have in mind a Poisson initial population whose intensity measure is invariant for the migration process (cf. the remark at the end of Section 2.2). Conditions on non-Poisson initial populations which also guarantee the same convergence are established in Liemant *et al.* (1988), Cox (1994), and Gorostiza and Wakolbinger (1992; 1994).

All the models we consider in Sections 2.3–2.6 have (apart from a possible *type dependence*) spatially homogeneous branching mechanisms. If one, instead, considers models with strong spatial inhomogeneities in the branching mechanism, then also questions like that of spatial tail triviality of the equilibrium populations, and of recurrence/transience of ancestral lines in equilibrium, gain a new interest (Matthes *et al.* 1992; 1992–3).

There is one particular *scaling limit* of branching populations, namely that of *measure-valued branching processes* or *superprocesses*, in which the individual branching rate has been speeded up to infinity (whereas the individual mass has been scaled down to zero). Therefore one can observe certain features, which in branching populations arise only in the large time limit, in superprocesses – as it were, under the microscope – already after a finite time; one instance of this, as well as some other links between superprocesses and branching populations, will be mentioned in Section 3. The term 'superprocess', which has now more or less become a synonym for measure-valued branching processes, was originally coined by Dynkin (1989) for a more general class of infinite-dimensional processes 'projecting down' in a suitable way. In the case of measure-valued branching processes or Dawson–Watanabe superprocesses, the branching dynamics is 'superimposed' over the motion dynamics, and the superprocess projects down to the semigroup of the motion process by taking expectations.

2. Large time limits of critical branching populations

In this part we will give, for various models of spatial critical branching populations, conditions on the model parameters which are necessary and sufficient for persistence. All these examples display a qualitative feature which could be formulated as follows: 'The more branching, the higher the tendency towards extinction; the more mobility, the higher the tendency towards stabilization or persistence'.

2.1. BRANCHING RANDOM WALKS

Recall that in a *branching random walk* on $\mathbb{Z}^d$, an individual performs a motion step according to a random walk and, at the site at which it arrives, is replaced by a random number of offspring, the law of this random number remaining constant over space and time, and the offspring individuals continuing independently in the same manner. The branching law is called *critical* if the mean number of offspring is 1; let us speak of an *ordinary* branching random walk if the motion is a simple (symmetric) random walk and the branching law is critical and binary.

Why does a branching random walk (with a uniform initial population) in two dimensions go to extinction, while in three dimensions it persists? A rough heuristic argument rendering at least the 'critical dimension' would be the following: after n generations, approximately every nth ancestor has given rise to an offspring of size about n, whereas the other families have died out. So, loosely speaking, in order to guarantee persistence, in the long run each of these surviving clusters of size n has the responsibility of spreading over a cube of side (at least) $n^{1/d}$. Since the mean square displacement of a symmetric random walker in n time steps is $n^{1/2}$, dimension $d = 2$ will play the role of a boundary case. The following more general result (Kallenberg 1977; Matthes *et al.* 1978, Theorem 12.6.4) implies local extinction also in dimension $d = 2$:

Proposition 1 A branching random walk with critical branching law having finite second moment is persistent if and only if the symmetrized motion is transient.

A word concerning the terminology. We call a branching population *persistent* (with respect to a locally finite invariant measure ρ for the particle motion) if the system, starting off with a Poisson distribution with intensity ρ, converges in the large time limit to an equilibrium distribution with intensity ρ. This, by the way, is equivalent to the existence of some equilibrium distribution with intensity ρ. If there is, up to a constant factor, just one locally finite invariant measure ρ for the particle motion, then the following dichotomy holds: either the system is persistent, or it is *unstable*, i.e. suffers local extinction when starting off with some initial distribution whose intensity is majorized by ρ (see Liemant *et al.*, 1988, Sections 2.3 and 2.6).

Let us revert to the two-dimensional random walk and drastically reduce the branching, by allowing critical branching only at one 'catalyst site', say the origin, and let us see what the simple heuristics from above tells now: a simple random walk path's nth visit at the origin occurs at random times R_n such that R_n/n^2 converges in distribution towards a non-trivial limit. Thus, roughly speaking, in n time steps, a path gets about $n^{1/2}$ opportunities to branch. This would produce clusters of size $n^{1/2}$, which may well spread out for a distance of at least $n^{1/4}$, thus yielding persistence. Of course, an argument like this is somewhat sloppy, but indeed the following proposition holds.

Proposition 2 (Wakolbinger 1991) A simple random walk on $\mathbb{Z}^2$ with a critical binary branching at the origin is persistent.

This is an easy consequence of a second-order persistence due to Liemant (see Liemant *et al.* 1988, Theorem 2.5.4), which is related to the analytic persistence criterion (P) described below.

2.2. BRANCHING BROWNIAN MOTION WITH AN INHOMOGENEOUS BRANCHING RATE

Now consider a critical binary branching Brownian motion in $\mathbb{R}^2$ with a (possibly spatially inhomogeneous) branching rate $V(x)$; by this we mean that every individual migrates, independently of the others, according to a Brownian motion, dies at a rate $V(x)$ depending on its actual position x, and gives rise to 0 or 2 offspring, each with probability $\frac{1}{2}$, at its death position. Proposition 1 suggests that a branching population of this kind should be persistent if V is bounded and has a bounded support. As the following proposition says, there also is persistence if the branching rate $V(x)$ has a suitable decay (say $O((\log(\|x\|)^{-1-\epsilon})$ as $\|x\| \to \infty$:

Proposition 3 For $d \geq 2$, critical binary branching Brownian motion in $\mathbb{R}^d$ is persistent provided its branching rate obeys

$$\int_B V(x)\,\mathrm{d}x < \infty \tag{2.1}$$

and

$$\int_{\mathbb{R}^d \setminus B} \frac{V(x)}{\|x\|^{2(d-1)}}\,\mathrm{d}x < \infty, \tag{2.2}$$

where B denotes the unit ball in $\mathbb{R}^d$.

Proof

There are at least two ways of proving this: one is basically *analytic*, exploiting the fact that the Laplace transform of the limiting population (modelled by a random counting measure N_∞ on $\mathbb{R}^d$) has the form

$$\mathrm{E}\mathrm{e}^{-\langle N_\infty, f\rangle} = \exp\left[-\langle \lambda^d, 1-\mathrm{e}^{-f}\rangle + \int_0^\infty \langle \lambda^d, V(.)\tfrac{1}{2}\{1-u_f(.,t)\}^2\rangle\,\mathrm{d}t\right],$$

where u_f solves the nonlinear partial differential equation

$$\frac{\partial}{\partial t}u_f(x,t) = Au_f(.,t)(x) - V(x)\tfrac{1}{2}\{1-u_f(.,t)\}^2, \qquad u(x,0) = \mathrm{e}^{-f(x)},$$

$A = \frac{1}{2}\Delta$ is the generator of the particle motion, the function f is non-negative and continuous with compact support, λ^d is Lebesgue measure on $\mathbb{R}^d$, and the symbol $\langle N_\infty, f\rangle$ denotes the integral $\int_{\mathbb{R}^d} f(x)\,N_\infty(\mathrm{d}x)$.

The 'persistence requirement' that the random population N_∞ has intensity λ^d, i.e. $\mathrm{E}\langle N_\infty, f\rangle = \langle \lambda^d, f\rangle$, is guaranteed by the criterion

$$\int_0^\infty \int_{\mathbb{R}^d} V(x)(\pi_t g)(x)^2 \lambda^d(\mathrm{d}x)\,\mathrm{d}t < \infty, \tag{P}$$

where π_t denotes the transition semigroup of Brownian motion, and g is non-negative and continuous with compact support. For more details, we refer to Gorostiza and Wakolbinger (1994), where the corresponding version of criterion (P) is derived for a much larger class of particle motions and branching mechanisms, and also a proof of Proposition 3 is included for the case $d = 2$. In fact, it was Ted Cox who realized (first for the case $d = 2$) in joint discussions in autumn 1992 that criterion (P) for critical binary branching Brownian motion boils down to the assertion of Proposition 3.

Another more probabilistic way of proving Proposition 3 relies on the so called 'backward tree' method originally developed by Kallenberg (1977) and Liemant (1981) for discrete-time models and adapted to continuous-time settings in Gorostiza and Wakolbinger (1991), Gorostiza *et al.* (1992) and Chauvin *et al.* (1991). The basic intuitive idea is the following: persistence holds if and only if the random population of relatives of an individual encountered at a certain site z in a population of age t remains a.s. locally finite as $t \to \infty$. (In other, still more descriptive, words: instability in a critical branching population goes along with the phenomenon that an individual alive at a late time is surrounded by a host of relatives.) The random population of relatives of an individual, δ_z, encountered in the limit population at site z arises as follows:

1. First construct the random ancestral path $W = (W_t)$, which in our setting follows the same dynamics as the forward particle motion, namely Brownian motion starting at z, due to the fact that the invariant measure λ^d is *reversible*. Note that the event $\{W_t = x\}$ has the interpretation that the ancestral path passed through site x 'at time t before present time'.
2. Next, generate the time points $t_0 < t_1 < \ldots$ at which the ancestors died, or equivalently, at which a branching happened along the ancestral line. This is a Poisson point process on $[0, \infty)$ with intensity $V(W_t)\,\mathrm{d}t$.
3. Finally, superpose all the independent side trees, one originating at each site W_{t_n} and developing over a time horizon t_n, thus giving rise to the population of nth-degree cousins of the individual δ_z.

Note that, conditioned on the ancestral path W, due to criticality of the branching, the expected number of relatives of the individual δ_z in a ball K is

$$\int_0^\infty \pi_t(W_t, K)\, V(W_t)\, \mathrm{d}t. \tag{2.3}$$

Now the a.s. finiteness of (2.3) certainly is *sufficient* for the a.s. local finiteness of the cluster of relatives, and thus for persistence. But (2.1) and (2.2) actually even render the finiteness of the *expectation* of (2.3), as the following computation shows:

$$\begin{aligned} \mathrm{E}\left[\int_0^\infty \pi_t(W_t, K)\, V(W_t)\, \mathrm{d}t\right] &= \int_{\mathbb{R}^d}\int_{\mathbb{R}^d} V(x) 1_K(y) \int_0^\infty \frac{1}{(2\pi t)^d} \exp\left(-\frac{\|x\|^2}{2t}\right) \\ &\quad \times \exp\left(-\frac{\|y-x\|^2}{2t}\right) \mathrm{d}t\, \mathrm{d}y\, \mathrm{d}x \\ &= \int_B V(x)\ldots + \int_{\mathbb{R}^d \setminus B} V(x)\ldots \end{aligned}$$

where 1_K denotes the indicator function of the set K. The first summand is finite due to (2.1), and the second is majorized by

$$\int_{\mathbb{R}^d \setminus B} \frac{V(x)}{\|x\|^{2(d-1)}} \int_0^\infty \frac{1}{(2\pi t)^d} \|x\|^{2(d-1)} \exp\left(-\frac{\|x\|^2}{2t}\right) \mathrm{d}t \, \mathrm{d}x \, \lambda^d(K).$$

This, however, is finite due to (2.2), since the time integral is finite and independent of x, and that completes the proof of Proposition 3. □

The following result (which is based on Theorem 2 below) is due to Ted Cox:

Theorem 1 In dimension 2, for a radially symmetric branching rate $V(x) = v(\|x\|)$ which is finite and non-increasing in $\|x\|$, condition (2.2) is not only sufficient but also necessary for persistence of critical binary branching Brownian motion.

Proof
Sufficiency of (2.2) has been stated in Proposition 3. Conversely, assume that a system of Brownian particles performing a critical binary branching at rate $V(x)$ is persistent. Let (W_t) be a random Brownian path starting at the origin. By Theorem 2, by the fact that $\|W_t\| \le t$ for all large t a.s., and since $v(t)$ is non-increasing, we obtain

$$\int_1^\infty \pi_t(W_t, B)\, v(t) \, \mathrm{d}t < \infty \qquad \text{a.s.}$$

By the same reasoning as in part 4 of the proof of Proposition 4.4 of Gorostiza and Wakolbinger (1991) this implies the finiteness of $\int_1^\infty \pi_t(0, B)\, v(t)\, \mathrm{d}t$, and therefore also the finiteness of $\int_1^\infty t^{-1} v(t)\, \mathrm{d}t$. □

Theorem 2 For a locally bounded branching rate V, almost sure finiteness of (2.3) is not only sufficient, but also necessary for persistence of critical binary branching Brownian motion on $\mathbb{R}^d$.

Proof
For the sufficiency part, see the remark after (2.3). Let us now turn to the necessity part, assuming that critical binary branching Brownian motion on $\mathbb{R}^d$ with branching rate $V = V(x)$ is persistent. Let ν be a probability measure having a continuous density $n(x)$ which is constant on B and outside B equals const. $|x|^{-\delta}$ for some $\delta > 0$.

For all $z \in \mathbb{R}^d$ and $t \ge 0$, let $X_{t,\nu}^z$ denote the random offspring of a single ancestor in z, which has developed over a time horizon t according to critical binary branching Brownian motion with branching rate V, and whose final positions have been 'shifted independently' according to the distribution ν. Let $h(t, z)$ denote the probability that $X_{t,\nu}^z$ populates the ball K.

It follows from the assumed persistence of λ^d that, for almost all W,

$$\sum_{m=1}^\infty h(t_m, W_{t_m}) < \infty \qquad \text{a.s.},$$

where $\boldsymbol{t} = (t_1, t_2, \ldots), t_1 \le t_2 \le \ldots$ is the random point configuration of a Poisson process on $\mathbb{R}_+$ with intensity measure $V(W_t)\, \mathrm{d}t$. (See Gorostiza and Wakolbinger 1991, Section 5; the arguments – given in detail there for constant V – essentially remain unchanged.)

Let $g\colon [0,\infty[\to [1,\infty[$ be continuous and such that for all $t>0$

$$g(t) \geq \sup\{V(x) \,|\, |x| \leq t\}.$$

For all $n \in N$, let u_n be such that $\int_0^{u_n} g(t)\,\mathrm{d}t = n$; note that (u_n) increases strictly towards infinity. For all n, put $\tau_n := \max\{t_m \,|\, m \geq 0, t_m \leq n\}$ (where we set $t_0 := 0$). Then (cf. Gorostiza and Wakolbinger 1991, Lemma 5.5) we have that, for almost all paths W and almost all Poisson configurations $\boldsymbol{t} = (t_1, t_2, \ldots)$, $t_1 \leq t_2 \leq \ldots$, there exists a constant $c = c(W, \boldsymbol{t})$ such that for all large enough n one has

$$ch(\tau_n, W_{\tau_n}) \geq \pi_{\tau_n}(W_{\tau_n}, K).$$

Let $\boldsymbol{s} = \boldsymbol{s}(\boldsymbol{t}) = (s_1, s_2, \ldots)$, $s_1 < s_2 < \ldots$, denote the point configuration obtained from $\boldsymbol{t}$ by deleting all those t_m for which there exists an n such that $u_{n-1} \leq t_{m-1} \leq t_m \leq u_n$ or $u_{n-1} \leq t_m \leq t_{m+1} \leq u_n$. Obviously, $\boldsymbol{s}$ is a subsequence of (τ_n), and thus there holds for large enough k:

$$ch(s_k, W_{s_k}) \geq \pi_{s_k}(W_{s_k}, K).$$

On the other hand, $\boldsymbol{s}$ is a subsequence of $\boldsymbol{t}$, and therefore $\sum_{k=1}^{\infty} h(s_k, W_{s_k}) < \infty$. Consequently,

$$\sum_{k=1}^{\infty} \pi_{s_k}(W_{s_k}, K) < \infty \qquad \text{a.s.}$$

Put $Z_n := \pi_{s_k}(W_{s_k}, K)$ if there is an s_k between u_{n-1} and u_n, and $Z_n := 0$ otherwise. Writing $a_n := \int_{u_{n-1}}^{u_n} V(W_t)\,\mathrm{d}t$, we obtain that $\mathrm{E}Z_n = \mathrm{e}^{-a_n} \int_{u_{n-1}}^{u_n} \pi_t(W_t, K)\, V(W_t)\,\mathrm{d}t$. Since the sequence of random variables Z_n is independent, uniformly bounded and a.s. has a finite sum, the strong law of large numbers yields $\sum_{n=1}^{\infty} \mathrm{E}Z_n < \infty$. For large enough t, $|W_t| \leq t$ holds, and therefore $V(W_t) \leq g(t)$, implying $a_n \leq 1$ for n large enough. This ensures that $\sum_{n=1}^{\infty} \int_{u_{n-1}}^{u_n} \pi_t(W_t, K)\, V(W_t)\,\mathrm{d}t < \infty$. ☐

Obviously, condition (2.2) is violated for constant $V > 0$ if $d = 2$, revealing once again the well-known instability of two-dimensional binary critical Brownian motion. It should be noted at this point that Bramson *et al.* (1993) proved by analytic methods that two-dimensional critical binary branching Brownian motion not only is unstable in the sense that it has no equilibrium distribution with Lebesgue intensity, but also has no non-trivial equilibrium distribution at all.

It would be nice to have an appropriate version of Theorem 1 also in the non-radially symmetric case and in higher dimensions; at present I can only prove that for $d \geq 3$ local extinction holds if the branching rate $V(x)$ has a suitable growth as $\|x\| \to \infty$:

Proposition 4 Let $d \geq 2$, and assume that

$$V(x) \geq c\|x\|^{d-2}(\log\|x\|)^{-1} \qquad \text{for suitably large } x \tag{2.4}$$

and that for $d = 2$ in addition V is locally bounded away from zero. Then critical binary branching Brownian motion with branching rate V suffers local extinction.

Proof

For $d = 2$, first apply Theorem 1 to

$$v(\|x\|) := \begin{cases} \epsilon & \text{if } \|x\| \le r_0 \\ c_1(\log\|x\|)^{-1} & \text{if } \|x\| > r_0 \end{cases}$$

(for appropriate constants ϵ, r_0, c_1 such that $V(x) \geq v(\|x\|)$ and $v(r)$ is non-increasing in r) to conclude that the branching rate $v(\|x\|)$ leads to local extinction. Now apply the backward tree persistence criterion as a 'comparison criterion' to infer that, a fortiori, $V(x)$ leads to local extinction.

For $d \geq 3$, we have, for almost all W and suitably large t, by the law of iterated logarithms: $\|W_t\| \geq \sqrt{t}/\log t$. This implies by means of (2.4) the existence of a non-negative, locally bounded function $f(t)$ such that

$$\text{for almost all paths } W \text{ and sufficiently large } t,\ V(W_t) \geq f(t) \tag{2.5}$$

and

$$\int_1^\infty t^{-d/2} f(t)\, \mathrm{d}t = \infty. \tag{2.6}$$

Proceeding as in part 4 of the proof of Proposition 4.4 in Gorostiza and Wakolbinger (1991), one infers from (2.6) that

$$\int_1^\infty \pi_t(W_t, B) f(t)\, \mathrm{d}t = \infty \text{ with positive probability,}$$

and thus by (2.5) also

$$\int_1^\infty \pi_t(W_t, B)\, V(W_t)\, \mathrm{d}t = \infty \text{ with positive probability.}$$

This, however, violates the necessary condition for persistence in Theorem 2. □

Remark

Theorem 2 can also be used to obtain a simple proof of the fact that one-dimensional branching Brownian motion with a branching rate bounded away from zero on some interval is unstable. In fact, even if the branching rate of the individuals is governed by their local time spent at the origin of $\mathbb{R}$ (which then can be viewed as a 'one-point branching catalyst'), a suitable modification of Theorem 2 easily shows that the branching population, starting off with a homogeneous Poisson configuration, suffers local extinction. For the corresponding superprocess limit of the latter system, this local extinction result was obtained by Dawson and Fleischmann (1994).

2.3. AN INTERPLAY OF MOTION, OFFSPRING DISTRIBUTION, DIMENSION AND LIFETIME DISTRIBUTION

Let us revert to spatially homogeneous models in $\mathbb{R}^d$, and first review the main result of Gorostiza and Wakolbinger (1991). As motion processes, we consider *spherically symmetric* α*-stable motion* of particles ($0 < \alpha \leq 2$), having as generator the fractional power $\Delta_\alpha := -(-\Delta)^{\alpha/2}$ of the Laplacian, and thus rendering Brownian motion in the case $\alpha = 2$. Note that for $\alpha < 2$ this motion process is a pure jump process with independent increments, the increment distribution density having a decay of order $\| x \|^{-d-\alpha}$. Let p_n be the probability of n offspring at the mother's death; the critical offspring law (p_n) we consider has generating function $\varphi(\zeta) = \Sigma p_n \zeta^n = \zeta + \frac{1}{2}(1-\zeta)^{1+\beta}$ (where $0 < \beta \leq 1$), rendering critical binary branching for $\beta = 1$. For $\beta < 1$, the probability weights p_n of this offspring law have a decay of order $n^{-2-\beta}$. We will refer to α and β as *mobility* and *clustering* parameters, respectively. For the moment, we consider a constant branching rate V, i.e. exponentially (with parameter V) distributed particle lifetimes.

Theorem 3 (Gorostiza and Wakolbinger 1991) The (above-described) critical branching particle system in $\mathbb{R}^d$ with mobility parameter α and clustering parameter β is persistent if and only if $d > \alpha/\beta$.

This is proved in the quoted paper by means of the backward technique; here, we will once again repeat the rough (but intuitive) argument (already encountered in Section 2.1) which balances 'clusters versus holes': after time t, a surviving cluster is typically of size $t^{1/\beta}$, and thus, to guarantee persistence, 'must fill a hole' of diameter $t^{1/d\beta}$. But in time t, particles travel typically a distance $t^{1/\alpha}$, revealing that $\alpha = d\beta$ is the 'border case'.

Next let us consider another case in which particle motion and offspring distribution are as in Theorem 3. As there, particles are supposed to give rise to their offspring at the end of their lifetime; the latter, however, is now assumed to have a long-tailed distribution. To be specific, we assume that each particle's lifetime has a stable distribution with parameter $\gamma \in (0, 1)$. Initially, the system is started off with a population of individuals with i.i.d. ages, the positions forming a Poisson process with Lebesgue intensity, and the initial ages and positions being independent.

Theorem 4 (Stöckl and Wakolbinger 1993) In the model with mobility parameter α, clustering parameter β and lifetime parameter γ (as described above), the particles' positions converge, as $t \to \infty$, to a Poisson process with Lebesgue intensity, provided that $d > \alpha\gamma/\beta$.

Intuitively, this 'asymptotic Poisson property' means that, as $t \to \infty$, an individual encountered at time t has, asymptotically with probability 1, no relative in its surroundings. (Actually we derived Theorem 4 by first proving this latter statement.) Of course the 'tendency to long individual life' favours this: an individual sampled at a late time then has a high probability of being very old, and so its brothers and sisters (and even more its cousins) have had a good chance of moving far out.

It is an open question whether the converse of Theorem 4 is true, i.e. whether the system suffers local extinction if $d \leq \alpha\gamma/\beta$.

2.4. A MULTITYPE MODEL

The model discussed in this subsection is of the same type as that described at the beginning of the previous subsection, except that we now have not one, but k different types of particle, and a particle at its death may branch into an offspring of a different type. To be precise, the model is as follows:

The particles are of types $i = 1, \ldots, k$, and $(m_{ij})_{1 \leq i, j \leq k}$ is an irreducible stochastic matrix. A particle of type i moves in $\mathbb{R}^d$ according to a spherically symmetric stable process with index $\alpha_i \in (0,2]$ during a random amount of time exponentially distributed with parameter V_i. At the end of this time a type j is chosen with probability $m_{ij}, j = 1,\dots,k$, and then the particle is replaced at its own site by n particles of type j with probability $p_n^{ij}, n = 0,1,2,\dots$, such that the generating function $\varphi_{ij}(\zeta) = \sum_{n=0}^{\infty} p_n^{ij}\zeta^n, \zeta \in [0,1]$, is of the form

$$\varphi_{ij}(\zeta) = \zeta + \frac{c_{ij}}{m_{ij}}(1-\zeta)^{1+\beta_{ij}},$$

where $\beta_{ij} \in (0,1]$ and $c_{ij} \in [0, m_{ij}/(1+\beta_{ij})]$ (this condition is enforced by $\varphi'_{ij}(0) = p_1^{ij} \in [0,1]$). Note that the case $c_{ij} > 0$ corresponds to a 'non-trivial' critical branching law, whereas the case $c_{ij} = 0$ represents a selection of type j without branching.

Let the initial population on $\mathbb{R}^d \times \{1,\dots,k\}$ be Poisson distributed with intensity $\lambda^d \times \rho$, where λ^d is Lebesgue measure on $\mathbb{R}^d$ and ρ is an arbitrary distribution on the type space $\{1,\dots,k\}$.

Theorem 5 (Gorostiza and Wakolbinger 1993) The system just described converges towards an equilibrium distribution with intensity measure $\lambda^d \times \gamma_{\text{inv}}$ (where γ_{inv} denotes the invariant distribution for the stochastic matrix (m_{ij})) if $d > \min\alpha_i/\min\{\beta_{ij} \mid c_{ij} > 0\}$, and suffers local extinction otherwise.

Theorem 5 thus says that the most mobile type (smallest α_i) and the most clumping branching mechanism (smallest β_{ij}) account for survival or extinction. A reason for this is that all the types $i = 1,\dots,k$ are interconnected in a recurrent way due to the assumed irreducibility of the matrix (m_{ij}).

In the case $c_{ij} = 0$ for $i \neq j$ (corresponding to 'mutation and monotype branching'), and $\rho = \gamma_{\text{inv}}$, Theorem 5 was proved by Gorostiza *et al.* (1992). The more general case of 'branching into different types' then required another non-trivial extension of the backward tree method.

Theorem 5 has a purely analytic corollary, which deals with the asymptotic behaviour of the following system of nonlinear partial differential equations for $u_i(x,t), i = 1,\dots,k, x \in \mathbb{R}^d$, $t \geq 0$:

$$\begin{aligned} \frac{\partial}{\partial t}u_i &= \Delta_{\alpha_i} u_i + V_i \sum_{j=1}^{k}(m_{ij} - \delta_{ij})u_i - V_i \sum_{j=1}^{k} c_{ij} u_j^{1+\beta_{ij}} \\ u_i(x,0) &= f_i(x) \end{aligned} \tag{2.7}$$

where the parameters $\alpha_i, \beta_{ij}, c_{ij}$ are as above, Δ_{α_i} is the $\alpha_i/2$ power of the Laplacian, (m_{ij}) is an irreducible matrix with non-negative entries and maximum eigenvalue 1, and the initial conditions $f_i : \mathbb{R}^d \to \mathbb{R}_+$ are continuous with compact support. Note that (2.7) has a unique global solution (see, for example, Pazy 1983) which is non-negative for all t. In fact, if (m_{ij}) is a stochastic matrix and all the f_i are bounded by 1, then the solution u_i of (2.7) has the probabilistic representation

$$u_i(x,t) = 1 - \mathrm{E}[\exp\{-\langle N_t, \log(1-f)\rangle\} \mid N_0 = \delta_{(x,i)}], \qquad i = 1,\dots,k,$$

where N_t is the (multitype) branching population on $\mathbb{R}^d \times \{1,\dots,k\}$ and $f(y,j) := f_j(y)$. This probabilistic representation is the key to the following corollary:

Corollary 6 (Gorostiza and Wakolbinger 1993) Let (u_i) be the solution of (2.7). If at least one f_i is not identically zero, then for each $i = 1, \ldots, k$,

$$\lim_{t\to\infty} \| u_i(.,t) \|_{L^1} \begin{cases} > 0 & \text{if } d > d_c \\ = 0 & \text{if } d \le d_c, \end{cases}$$

where $d_c := \min \alpha_i / \min \{\beta_{ij} \mid c_{ij} > 0\}$.

2.5. TWO-LEVEL BRANCHING BROWNIAN MOTION

Consider the following system, which belongs to a class of models introduced and investigated by Dawson and Hochberg (1991) and Wu (1994):

Initially there is a homogeneous Poisson system of particles in $\mathbb{R}^d$, which is now, in addition, interpreted as a system of 'singleton clans'. The particles undergo independent Brownian motions; each individual carries an 'exponential clock' with parameter V_1, and each clan carries an exponential clock with parameter V_2, all the clocks being independent. When an 'individual clock' rings, this individual either branches into two (which then belong to the same clan as their predecessor) or vanishes, each with probability $\frac{1}{2}$. When a 'clan clock' rings, this clan either is 'doubled' or vanishes as a whole, each with probability $\frac{1}{2}$.

From a result of Wu (1994) on the corresponding superprocess limit (cf. Section 3) there is strong evidence that the following holds true:

The above-described 'two-level branching population' converges, as $t \to \infty$, to a non-trivial limit if $d \ge 5$, and suffers local extinction if $d \le 4$. (C)

A modification of this two-level particle model is the following. First put $V_2 := 0$, i.e. let the system develop according to branching Brownian motion, keeping track, however, of the clans which arise out of the original singletons. In dimension $d \ge 3$, this system converges to a non-trivial equilibrium (cf. Section 2.3). The equilibrium system can also be partitioned by collecting all those individuals into one clan whose ancestral paths eventually coalesce. Now start the system afresh from this equilibrium, this time not only with the individual, but also with the clan branching mechanism switched on. The two-level superprocess corresponding to this particle system is considered in Gorostiza *et al.* (1993), where persistence is proved for dimensions $d \ge 5$, thus complementing the local extinction result of Wu (1994).

Conceptually replacing individuals by clans, we now have (just 'one level higher') exactly the situation described in Section 2.2: initially there is a Poisson system of clans. The 'clan migration' (caused by the individual branching Brownian motion) would leave this system in equilibrium, but now there is the additional 'clan splitting'. As it turns out (Theorem 7), this clan migration is recurrent for $d \le 4$, and transient for $d \ge 5$ (if one uses on the space of clans a metric defined in Matthes *et al.* 1978, Proposition 3.3.2.) If a result such as Proposition 1 were now to hold in suitably greater generality, then this would give both a proof and a new explanation of (C). (Notably, there is a recent result of Etheridge 1993, proved by analytic methods, which states that under certain additional assumptions a superprocess over a recurrent migration suffers local extinction. This result can easily be translated from superprocesses to particle systems, cf. Section 3, but at the moment it is not clear to me whether its additional assumptions are met by the clan migration process.)

The above-mentioned result on clan migration is the following.

Theorem 7 (Stöckl and Wakolbinger 1992) In a time-stationary critical binary branching Brownian population in $\mathbb{R}^d$ in dimensions 3 and 4 with probability 1 each clan populates a fixed ball $B \subseteq \mathbb{R}^d$ at arbitrarily late and early times, whereas for $d \geq 5$ with probability 1 each clan populates B only over some bounded horizon of time. (In this sense, the time-stationary clan migration process of branching Brownian particles in $\mathbb{R}^d$ is *recurrent* if $d = 3$ or 4 and *transient* if $d \geq 5$.)

The proof of Theorem 7, which again employs the backward tree representation described in subsection 2.2, also reveals the following corollary:

Corollary 8 (Stöckl and Wakolbinger 1992) Critical binary branching Brownian motion in $\mathbb{R}^d$ starting from one individual and conditioned to survive comes back to populate a ball $B \subseteq \mathbb{R}^d$ at arbitrarily late times if and only if $d \leq 4$.

3. Some links to superprocesses

A – by now very prominent – scaling limit of branching populations has its origins in Feller's diffusion limit of Galton–Watson processes: a large number, n, of particles (each of mass $1/n$) start to perform i.i.d. critical Galton–Watson processes with branching rate Vn and finite offspring variance σ^2. Then the process counting the total mass at time t converges as $n \to \infty$ to a diffusion process X_t with diffusion coefficient $V\sigma^2 x$ and drift zero; a non-zero drift occurs in this limit if the difference between the mean number of offspring and unity (i.e. the *defect of criticality*) is of order $1/n$. By allowing the particles not only to *branch*, but also to *migrate* in a certain space S of positions, and counting the total mass of all particles situated at time t in the measurable subsets $B \subseteq S$, one obtains in the limit $n \to \infty$ a 'measure-valued diffusion' process $X_t(B)$.

Pioneering work on measure-valued branching processes is due to Jiřina (1964), Watanabe (1968) and Dawson (1977), and during the last two decades – particularly, however, in the last few years – a wealth of both models and results have emerged around what is now known as 'Dawson–Watanabe processes' or 'superprocesses'. The latter terminology follows a suggestion by Dynkin and refers to the branching mechanism being built 'above' the migration process, or viewing the migration process as a 'projection' of the superprocess (cf. Dynkin 1989).

A major impetus in the development of measure-valued branching processes came with the work of Dawson and Perkins (1991) on *historical processes*: there they studied not only the continuum limit of populations of branching individuals, but also that of the population of their ancestral paths. One of the advantages of this historical picture is that it leads to a much better probabilistic understanding of certain features of the measure-valued branching process X_t. As an example I would like to mention the method applied by Dawson (1992, Theorem 7.3.1) to obtain the lower estimate α/β for the 'carrying Hausdorff–Besicovitch dimension' of an (α, d, β) superprocess X_t (which is a scaling limit of the branching population described before Theorem 3): this relies on proving that the random cluster of relatives of an individual encountered at site $y \in \mathbb{R}^d$ at time t

(which, in mathematical terms, follows the Palm distribution of the canonical measure of X_t, and again is represented in terms of a backward tree) a.s. integrates the function $x \to \|x - y\|^{-(\alpha/\beta)+\epsilon}$ locally around y for all $\epsilon > 0$, which then gives the appropriate lower bound on the local clumping of X_t. In fact, α/β *equals* the carrying dimension of X_t (cf. Dawson 1992, Theorem 7.3.4). On the other hand, when started off with d-dimensional Lebesgue measure, X_t suffers local extinction if and only if $d \leq \alpha/\beta$ (Gorostiza *et al.* 1990); this follows from Theorem 3 and the fact that branching particle systems can be restored from their corresponding superprocess limits through 'Poissonization'. For $d > \alpha/\beta$, Dawson and Perkins (1991, Theorems 6.6 and 6.7) prove (again by the backward tree representation) that the (equilibrium) clans of X_∞ are 'α/β-self-similar'. In the case, $\alpha = 2$, $\beta = 1$, Wu (1994) exploits this self-similarity in his (mainly analytic) proof of local extinction of two-level super-Brownian motion (this is a superprocess built over super-Brownian motion, and it arises as a scaling limit of the two-level branching population described at the beginning of Section 2.6) for $d \leq 4$.

The above-mentioned equivalence of local extinction for branching populations and their superprocess limits might raise the question whether one should not focus from the beginning *only* on the study of superprocesses, if, say, one is interested in analytic results such as Corollary 6. But the point is here that it seems (though further research is required) that particle systems with *non-local branching* (such as that of Section 2.4, where the particles may change type at the instant of branching) in general do not have a superprocess limit, at least not in the 'classical sense' – some evidence for this is given in Gorostiza and Wakolbinger (1994).

Certainly, however, the subject of superprocesses *per se* is a fascinating and topical one. As particular instances, I want to mention Le Gall's (1991; 1993) approach to superprocesses in terms of Brownian excursions, and recent work by Evans and Perkins (1994) on superprocesses with interactions. Aldous's (1991, 1993) work on continuum random trees (which may be considered as fundamental also for superprocesses), is highly original and important in its own right. Dynkin (1993) gives a comprehensive treatment of links between superprocesses and partial differential equations, and an excellent account of much of the recent development in measure-valued branching processes and also in neighbouring topics is provided by Dawson (1993).

Bibliography

Aldous, D. (1991) The continuum random tree, II: an overview. In M.T. Barlow and N.H. Bingham (eds), *Stochastic Analysis*. Cambridge: Cambridge University Press.

Aldous, D. (1993) The continuum random tree III. *Ann. Probab.*, **21**, 248–289.

Bramson, M., Cox, J.T. and Greven, A. (1993) Ergodicity of critical spatial branching processes in low dimensions. *Ann. Probab.*, **21**, 1946–1957.

Chauvin, B., Rouault, A. and Wakolbinger, A. (1991) Growing conditioned trees. *Stochastic Process. Appl.*, **39**, 117–130.

Cox, J.T. (1994) On the ergodic theory of critical branching Markov chains. *Stochastic Process. Appl.*, **50**, 1–20.

Dawson, D.A. (1977) The critical measure diffusion. *Z. Wahrscheinlichkeitstheorie Verw. Geb.*, **40**, 125–145.

Dawson, D.A. (1992) Infinitely divisible random measures and superprocesses. In *Stochastic Analysis and Related Topics (Silivri, 1990)*, Progr. Probab. 31. pp 1–129. Boston: Birkhäuser.

Dawson, D.A. (1993) Measure-valued Markov processes. In *Ecole d'été de Saint Flour 1991*, Lecture Notes in Math. 1541, pp. 1–260. Berlin: Springer-Verlag.

Dawson, D.A. and Fleischmann, K. (1994) A super-Brownian motion with a single point catalyst. *Stochastic Process. Appl.*, **49**, 3–40.

Dawson, D.A. and Hochberg, K. (1991) A multilevel branching model. *Adv. Appl. Probab.*, **23**, 701–715.

Dawson, D.A. and Perkins, E.A. (1991) Historical processes, *Mem. Amer. Math. Soc.*, 93 (454).

Dynkin, E.B. (1989) Three classes of infinite dimensional diffusions. *J. Funct. Anal.*, **86**, 75–110.

Dynkin, E.B. (1993) Superprocesses and partial differential equations. *Ann. Probab.*, **21**, 1185–1262.

Etheridge, A. (1993) Asymptotic behavior of measure-valued critical branching processes. *Proc. Amer. Math. Soc.*, **118**, 1251–1261.

Evans, S.N. and Perkins, E.A. (1994) Measure-valued branching diffusions with singular interactions. *Can. J. Math.*, **46**, 120–168.

Gorostiza, L.G. and Wakolbinger, A. (1991) Persistence criteria for a class of critical branching particle systems in continuous time. *Ann. Probab.*, **19**, 266–288.

Gorostiza, L.G. and Wakolbinger, A. (1992) Convergence to equilibrium of critical branching particle systems and superprocesses, and related nonlinear partial differential equations. *Acta Appl. Math.*, **27**, 269–291.

Gorostiza, L.G. and Wakolbinger, A. (1993) Asymptotic behavior of a reaction–diffusion system. A probabilistic approach. *Random Comput. Dynamics*, **1**, 445–463.

Gorostiza, L.G. and Wakolbinger, A. (1994) Long time behavior of critical branching particle systems and applications. In D. Dawson (ed.) *Measure-Valued Processes, Stochastic Partial Differential Equations and Interacting Systems*, CRM Proc. Lecture Notes and Monographs 5, pp. 119–137. Providence, RI: American Mathematical Society.

Gorostiza, L.G., Roelly-Coppoletta, S. and Wakolbinger, A. (1990) Sur la persistance du processus de Dawson-Watanabe stable; l'interversion de la limite en temps et de la renormalisation. In *Sém. Probab. XXIV*, Lecture Notes in Math. 1426, pp. 275–281. Berlin: Springer-Verlag.

Gorostiza, L.G., Roelly, S. and Wakolbinger, A. (1992) Persistence of critical multitype particle and measure branching processes. *Probab. Theory Related Fields*, **92**, 313–335.

Gorostiza, L.G., Hochberg, K. and Wakolbinger, A. (1993) Persistence of a critical super-2 process. To appear in *J. Appl. Probab.*

Jagers, P. (1991) The growth and stabilization of populations (with discussions by J.E. Cohen, P. Donnelly and S. Sawyer). *Statist. Sci.*, **6**, 269–283.

Jagers, P. and Nerman, O. (1984) The growth and composition of branching populations. *Adv. Appl. Probab.*, **16**, 221–259.

Jiřina, M. (1964) Branching processes with measure-valued states. In *Trans. Third Prague Conf. on Inform. Theory, Statist. Decision Functions, Random Processes*. Prague, Czech. Academy of Sciences, pp. 333–357.

Kallenberg, O. (1977) Stability of critical cluster fields. *Math. Nachr.*, **77**, 7–43.

Le Gall, J.F. (1991) Brownian excursions, trees and measure-valued branching processes. *Ann. Probab.*, **19**, 1399–1439.

Le Gall, J.F. (1993) A class of path-valued Markov processes and its application to superprocesses. *Probab. Theory Related Fields*, **95**, 25–49.

Liemant, A. (1981) Kritische Verzweigungsprozesse mit allgemeinem Phasenraum, IV. *Math. Nachr.*, **102**, 235–254.

Liemant, A., Matthes, K. and Wakolbinger, A. (1988) *Equilibrium Distributions of Branching Processes*. Berlin: Akademie-Verlag; and Dordrecht: Kluwer Academic Publishers.

Matthes, K., Kerstan, J. and Mecke, J. (1978) *Infinitely Divisible Point Processes*. Chichester: Wiley.

Matthes, K., Siegmund-Schultze, R. and Wakolbinger, A. (1992) A spatial zero–one law for equilibria of branching particle systems. *J. Theoret. Probab.*, **6**, 699–711.

Matthes, K., Siegmund-Schultze, R. and Wakolbinger, A. (1992–3) Equilibrium distributions of age dependent Galton–Watson processes I, *Math. Nachr.* **156**, 233–267; II, *Math. Nachr.* **169**, 313–324.

Nerman, O. and Jagers, P. (1984) The stable doubly infinite pedigree process of supercritical branching processes. *Z. Wahrscheinlichkeitstheorie Verw. Geb.*, **65**, 445–460.

Pazy, A. (1983) *Semigroups of Linear Operators and Applications to Partial Differential Equations*. New York: Springer-Verlag.

Sawyer, S. (1976) Branching diffusion processes in population genetics. *Adv. Appl. Probab.*, **8**, 659–689.

Stöckl, A. and Wakolbinger, A. (1992) On clan recurrence and transience in time stationary branching Brownian particle systems. In D. Dawson (ed.) *Measure-Valued Processes, Stochastic Partial Differential Equations and Interacting Systems*, CRM Lecture Notes and Monographs 5, pp. 213–219. Providence, RI: American Mathematical Society.

Stöckl, A. and Wakolbinger, A. (1993) Critical branching populations with infinite mean individual lifetime may have Poisson limits. Preprint.

Taib, Z. (1992) *Branching Processes and Neutral Evolution*, Lecture Notes in Biomath. 93. Berlin: Springer-Verlag.

Wakolbinger, A. (1991) On the structure of entrance laws in discrete spatial critical branching processes. *Math. Nachr.*, **151**, 51–57.

Watanabe, S. (1968) A limit theorem of branching processes and continuous state branching. *J. Math. Kyoto Univ.* **8**, 141–167.

Wu, Y. (1994) Asymptotic behavior of two level measure branching processes. *Ann. Probab.*, **22**, 854–874.

Discussion

PETER JAGERS

School of Mathematical and Computing Sciences, Chalmers University of Technology and Gothenburg University, S-412 96 Göteborg, Sweden

Professor Wakolbinger's starting point is the insight that no freely reproducing finite population can persist for ever. They either die out or they grow beyond all limits. And, in our biological – and everyday physical – world of finite resources the latter alternative leads to a collapse that brings it to nought. How can we then explain the stabilities that we seem to observe around us? (As an intriguing aside, one might speculate whether the not-so-everyday worlds of quantum and relativistic physics offer a way out, for the populations of very small splitting particles or of huge separating galaxies.)

It might appear that the most obvious solution would be to ascribe stability to dependencies, environmental inhomogeneities and feedback, outside the realm of population dynamics proper. Maybe individuals reproduce more whenever their population is threatened? Maybe the environment can recover after a period of not so heavy exploitation? However, to accomplish stability such feedback etc. would have to be complicated, indeed: the very slightest Markovian tendency establishes the dichotomy of extinction or explosion.

This is well described by the following straightforward but quite general fact. Consider a sequence of random variables $X_1, X_2, \ldots$ defined on some probability space and taking values in $\mathbb{R}_+$. Assume 0 absorbing in the sense that $X_n = 0 \Rightarrow X_{n+1} = 0$ and suppose that there is always a risk of extinction in the following way. For any x there is a $\delta > 0$ such that

$$P(\exists n; X_n = 0 \mid X_1, \ldots, X_k) \geq \delta,$$

if only $X_k \leq x$. Then, with probability 1, either

- there is an n such that all $X_k = 0$ for $k \geq n$ or
- $X_k \to \infty$ as $k \to \infty$.

Thus, there seems to be no easy way out, and we are brought back to the possibility of trying to grasp stabilities through the fundamentally unstable branching populations of free population growth. A classical approach, underlying much of my own work in the area, is to accept the dichotomy between extinction and explosion, and then conclude, as it were, from the observed non-extinction yet that we are observing essentially supercritical populations, long since on their route of exponential growth. Hence, they should be well described by the theory of stable composition of old supercritical branching populations. Their age distribution should be the classical stable age distribution, dating back to Euler, and the composition in other respects, the family structure in particular, obtained from the stable, doubly infinite pedigree measures (Jagers 1993).

This is a mathematically rich and quite general theory, and I believe that it sheds light on the composition of actual physical and biological populations. But here the time-scale is important. For quickly reproducing unrestrained populations, the theory of supercritical branching processes is much more relevant than for a slowly evolving population, in an environment that can hardly be thought of as stable and sustaining an exponential growth for, say, millions of years, as is the case with the evolution of species. Thus, one might turn to critical populations conditioned not to die out, or since these constitute a very special class, to 'near-critical' processes. Interesting work in that direction, which is relevant to problems of genealogy – When did our last common ancestor, the famed 'mitochondrial Eve', live? – is due to Zubkov (1975), Durrett (1977) and others, most recently to O'Connell (1993). There is much work about critical branching processes by the Moscow school, besides Zubkov, that deserves to be better known: Sagitov, Topcii and Vatutin, to mention some authors.

In a famous lecture at Oberwolfach, a quarter century ago, Kolmogorov pointed at the instability of branching processes as their main drawback as models for population dynamics. He made two suggestions: to replace branching by diffusions for big populations, or to study branching processes with immigration. However, the usual branching-with-immigration models are far from satisfactory, immigration just appearing as another *deus ex machina* at mathematically tractable renewal points, in order to salvage stability, or possibly to give us some more theorems to prove.

How much more interesting, then, is the statistical physical tradition of considering a specified subset of an infinite (macrocanonical) space, which can sustain a persistent population, and send immigrants into the (microcanonical) population in the subset? In that way we are led to at least three important questions:

1. What kind of (infinite) populations can persist in what kind of (infinite) spaces?
2. What kind of immigration patterns into specified bounded subsets would they result in?
3. What kind of stable populations would arise on the micro level of such sets?

This is the general framework in which I would like to view Wakolbinger's paper. It may well be that there are other motivations for work on spatial branching – in my first paragraph I speculated about relations to quantum relativistic physics. And my first question to Professor Wakolbinger is certainly: This is a thriving mathematical area. To some this may be sufficient reason to pursue it. To others, like me, it is important to see it in a wider context. What are your views?

Turning back to my perspective of finite, non-spatial branching, it is certainly easy (but not unimportant!) to pose questions of vague generality, like my triple above. It is much harder to give answers that are both general and precise. As Professor Wakolbinger – somewhat apologetically – points out, he has chosen preciseness before generality. In cases where you cannot have both, I agree this is good mathematical tradition. However, the important question of generalization then remains.

In the present case, the persistence question is given a precise answer in terms of critical binary splitting Brownian motion, and a beautiful condition on its branching rate in Proposition 3.

Binary splitting is, of course, a very special form of reproduction. Brownian motion is also a special type of motion, albeit archetypical in several ways. To what extent are they just symbols of more general natural reproductions and motions? Note that they appear essentially only in conditions and not in the conclusions of the proposition. Are all 'physically or biologically natural' processes in some sense covered by Proposition 3? What is the most general form in which you believe some form of it to be true?

The closest Professor Wakolbinger comes to my third question, that of characterizing the stable micropopulations is his fifth theorem (with Luis Gorostiza). Here a somewhat different, but again rather special framework is considered. Particles move in spherically symmetric stable processes (including the case of Brownian motion). They have exponentially distributed lifespans, so the possibility of state dependence has disappeared. On the other hand, the assumed critical binomial offspring distribution is more general than the binary. The process is also multitype, but again in a somewhat specialized sense. For such systems the theorem yields an equilibrium distribution over types and states. Again, the natural questions are: Do the particular forms of lifespans and reproduction play a role in the theorem? What is the role of the motion law?

This concludes my comments and questions. As should be clear, I have found this to be a thought-provoking paper full of beautiful mathematical results, which I believe are of great potential relevance for our understanding of the fundamentals of population dynamics in its widest sense.

References

Durrett, R. (1978) The genealogy of critical branching processes. *Stochastic Process Appl.*, **8**, 101–116.

Jagers, P. (1992) Stabilities and instabilities in population dynamics. *J. Appl. Probab.*, **29**, 770–780.

O'Connell, N. (1994) The genealogy of branching processes and the age of our most recent common ancestor. *J. Appl. Probab.* (to appear).

Zubkov, A.M. (1975) Limiting distributions of the distance to the closest common ancestor. *Theory Probab. Appl.*, **20**, 602–612.

Author's reply

Let me first focus on Professor Jagers' Question 1. It is a classical result due to Kallenberg (1977) that for a random walk with a spatially homogeneous critical branching, transience of the motion is necessary for persistence of the infinite population. One might conjecture (I am not aware of a proof) that this also holds for Markovian migrations in general. Conversely, transience of the motion does not yet imply persistence of a (finite-variance, critical and spatially homogeneous) branching population with invariant intensity, as the simple example of one-dimensional critical branching Brownian motion with constant drift shows: in that case the clumping travels with the drift and finally leads to local extinction. Possibly this implication does hold if the migration process is reversible.

If the branching rate is space-dependent, things look different: a suitable decay of the branching rate $V(x)$ as $\|x\|$ increases leads to persistence of branching Brownian motion in $\mathbb{R}^2$, and a suitable increase of the branching rate $V(x)$ as $\|x\|$ increases enforces its local extinction in $\mathbb{R}^3$. In this context, Professor Jagers raises the question of possible generalizations of Proposition 3. Indeed, in Gorostiza and Wakolbinger (1993), the persistence criterion (P) is proved for all critical branching mechanisms with uniformly bounded second moments and arbitrary Markovian migration processes. (By the way, the same generalization can be made for Theorem 2.) Therefore the conclusion of Proposition 3 remains true for all such branching mechanisms and all Markovian migration processes whose transition probabilities π_t satisfy, for all bounded subsets K of $\mathbb{R}^d$,

$$\int_0^\infty \pi_t(x, K)^2 \,\mathrm{d}t = O(\|x\|^{-2(d-1)}) \qquad \text{as } \|x\| \to \infty.$$

In this sense, binary splitting and Brownian motion are indeed just symbols for a larger class of dynamics.

If the offspring does not have finite second moments, then more mobility than just transience of the migration seems to be necessary to keep the system persistent, and in the case of a system with finitely many types, the most mobile type and the most clumping type are responsible for the long-time behaviour. This can be seen in the examples in Sections 2.3 and 2.4. Indeed, as Professor Jagers points out, the offspring distribution in Theorem 5 is only multitype in a somewhat specialized sense: the individuals randomly mutate, and at the instant of mutation perform monotype branching in the mutant type. Current work with J.A. López Mimbela, however, proves that the assertion of Theorem 5 extends to genuine multitype offspring laws in which the total number of offspring of a type i individual is in the normal domain of attraction of a stable law with exponent β_i. Extensions to more general migrations, and to the interesting case of infinitely many types, are still open.

In his Question 2 concerning the immigration patterns of persistent populations into a specified bounded subset, Professor Jagers addresses the space-time picture of equilibrium branching populations. A satisfactory answer to this interesting question seems quite difficult. At least one specific feature, however, is touched upon in the paper. Consider, in an equilibrium binary branching Brownian motion in $\mathbb{R}^d$, the individuals presently in a compact set B with positive volume. By time stationarity there must occur infinitely many future B-immigrants (where we call an individual in B a B-immigrant if its ancestral path has not visited B before.) Does every present individual in B have relatives among these immigrants almost surely? Theorem 7 tells that this is the case if and only if $d \leq 4$. In the case of stationary inhomogeneous branching mechanisms, there are also examples of equilibrium populations with infinitely many future immigrants into a bounded set B, each of which is a relative of all individuals presently in B, simply because the whole population consists of one infinite clan sustaining itself in equilibrium (see Liemant *et al.* 1988, Example 2.8.4; Matthes *et al.* 1994).

In connection with Professor Jagers' Question 3 one could ask about the spatial pattern on the micro level, i.e. certain features of the equilibrium population restricted to a bounded set B, but also about the genealogical relationships of individuals sampled in B, e.g. for the probability that two such individuals have a common ancestor. For all these questions, the analysis of backward trees seems very appropriate, as it is also for the study of the 'macro pattern' of equilibrium clusters such as the number of individuals in large balls.

It is these large-scale patterns of equilibrium clusters which display close analogies to the small-scale patterns of the superprocess clusters (as I pointed out in Section 3). Much is known here in the case of homogeneous branching, and less in the inhomogeneous case. Recent work by Fleischmann and Le Gall (1994) is an example of exploiting the superprocess genealogy for investigating superprocess 'micro patterns' in the case of branching only at a single point in $\mathbb{R}^d$.

Professor Jagers also discusses, as a possible model for certain phenomena, critical branching populations starting from one ancestor and conditioned to non-extinction. These indeed come close to the equilibrium clusters mentioned above. In fact, the equilibrium populations considered in the paper always consist of the few (but still infinitely many) clans which managed to survive in the long run. For this reason, Theorem 7 gives as a corollary that a binary branching Brownian population in $\mathbb{R}^d$ starting off from one ancestor and conditioned to non-extinction visits a ball only over a finite time horizon if and only if $d \geq 5$, answering a conjecture raised by S. Evans in 1992.

It would certainly be of interest to explore the geometry of equilibrium clusters in the case of an inhomogeneous branching such as that in Section 2.2, to pursue the study of superprocesses with spatially inhomogeneous branching, and to see which parallels or dissimilarities turn up to the corresponding Fleming–Viot processes with selection (cf. Ethier and Kurtz 1993; Dawson 1993).

Finally, let me turn to Professor Jagers's basic question about the context in which one should see the subject of spatial branching systems. To begin with, I am sceptical that the rather idealized assumptions (such as independence of branching) will permit direct applications in physics. On the other hand, a proper context is certainly that of population genetics. Indeed, there are certain general ideas about spatial branching populations which are well reflected in contemporary population genetics. One of them is that migration counteracts local extinction in critical branching systems, just as migration counteracts 'local fixation' in genetics. Another, more methodological connection, is that for the study of certain features of the system it is more convenient to 'look into the past' (i.e. to study the genealogy) than to 'look into the future' (i.e. to study the forward evolution of the system) (cf. Ewens 1990).

Additional references

Ethier, S.N. and Kurtz, Th. (1993) Fleming–Viot processes in population genetics. *SIAM J. Control Optim.*, **31**, 345–386.

Ewens, W.J. (1990) Population genetics theory – the past and the future. In S. Lessard (ed.), *Mathematical and Statistical Developments of Evolutionary Theory*, pp. 177–227. Dordrecht: Kluwer Academic Publishers.

Fleischmann, K. and LeGall, J.F. (1994) A new approach to the single point catalytic super-Brownian motion. Preprint No. 81. Berlin: IAAS.

Matthes, K., Siegmund-Schultze, R. and Wakolbinger, A. (1994) Recurrence of ancestral lines and offspring trees in time stationary branching populations, Preprint No. 83. Berlin: IAAS.

Received December 1993 and revised April 1994