Yaglom-type limit theorems for branching Brownian motion with absorption

by Jason Schweinsberg
University of California San Diego

(with Julien Berestycki, Nathanaël Berestycki, Pascal Maillard)

Outline

1. Definition of the process
2. Main results
3. Proof techniques
4. Application to populations undergoing selection

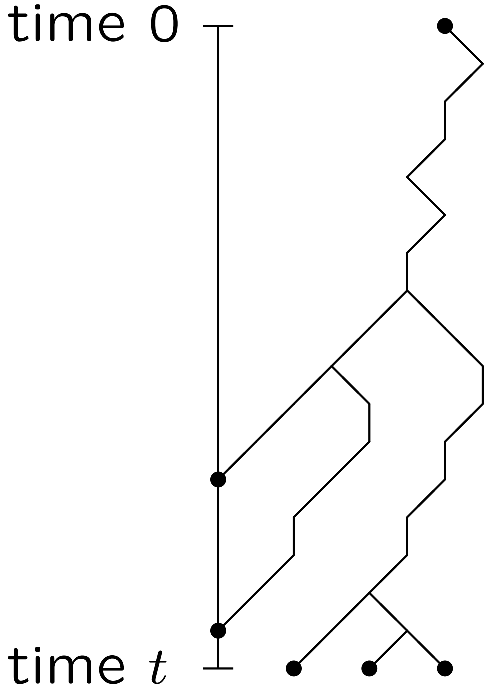
Branching Brownian motion with absorption

Begin with some configuration of particles in $(0, \infty)$.

Each particle independently moves according to standard one-dimensional Brownian motion with drift $-\mu$.

Each particle splits into two particles at rate $1/2$ (more general supercritical offspring distributions can also be handled).

Particles are killed if they reach the origin.



Condition for extinction

Theorem (Kesten, 1978): Branching Brownian motion with absorption dies out almost surely if $\mu \geq 1$. If $\mu < 1$, the process survives forever with positive probability.

Hereafter, we always assume $\mu = 1$ (critical drift).

Questions

- What is the probability that the process survives until a large time t?
- Conditional on survival until a large time t, what does the configuration of particles look like at time t? (Such results are known as Yaglom-type limit theorems.)

Long-run survival probability

Let $N(t)$ be the number of particles at time t.
Let $\zeta = \inf\{t : N(t) = 0\}$ be the extinction time.
Let $c = (3\pi^2/2)^{1/3}$.

Theorem (Kesten, 1978): There exists $K > 0$ such that for each $x > 0$, we have for sufficiently large t:

$$xe^{x - ct^{1/3} - K(\log t)^2} \leq P_x(\zeta > t) \leq (1 + x)e^{x - ct^{1/3} + K(\log t)^2}.$$

Theorem (BMS, 2017): There is a positive constant C such that for all $x > 0$, we have as $t \to \infty$,

$$P_x(\zeta > t) \sim Cxe^{x - ct^{1/3}}.$$

Remark:

- Derrida and Simon (2007) obtained result nonrigorously.
- The weaker bound $C_1 xe^{x - ct^{1/3}} \leq P_x(\zeta > t) \leq C_2 xe^{x - ct^{1/3}}$ was obtained by BBS (2014).

The process conditioned on survival

Let $N(t)$ be the number of particles at time t.
Let $R(t)$ be the position of the right-most particle at time t.

Theorem (Kesten, 1978): There are positive constants K_1 and K_2 such that for all $x > 0$,

$$\lim_{t \to \infty} P_x(N(t) > e^{K_1 t^{2/9} (\log t)^{2/3}} \,|\, \zeta > t) = 0$$

$$\lim_{t \to \infty} P_x(R(t) > K_2 t^{2/9} (\log t)^{2/3} \,|\, \zeta > t) = 0.$$

Theorem (BMS, 2017): If the process starts with one particle at $x > 0$, then conditional on survival until time t,

$$t^{-2/9} \log N(t) \Rightarrow V^{1/3}$$

$$t^{-2/9} R(t) \Rightarrow V^{1/3},$$

where V has an exponential distribution with mean $3c^2$.

First moment calculations

Consider a single Brownian particle started at x, with drift -1 and absorption at 0. The "density" of the position of the particle at time t is

$$p_t(x,y) = \frac{1}{\sqrt{2\pi t}}\Big(e^{-(x-y)^2/2t} - e^{-(x+y)^2/2t}\Big) \cdot e^{x-y-t/2}.$$

For BBM with absorption, let $X_1(t) \geq X_2(t) \geq \cdots \geq X_{N(t)}(t)$ be the positions of particles at time t. Let

$$q_t(x,y) = e^{t/2} p_t(x,y).$$

Many-to-One Lemma: If $f : (0,\infty) \to \mathbb{R}$, then

$$E_x\Bigg[\sum_{i=1}^{N(t)} f(X_i(t))\Bigg] = \int_0^\infty f(y) q_t(x,y)\, dy.$$

Take $f = \mathbf{1}_A$ to get expected number of particles in a set A.

Second moment calculations

Theorem (Ikeda, Nagasawa, Watanabe, 1969): If $f : (0, \infty) \to \mathbb{R}$, then

$$E_x\left[\left(\sum_{i=1}^{N(t)} f(X_i(t))\right)^2\right] = \int_0^\infty f(y)^2 q_t(x,y)\, dy +$$

$$2 \int_0^t \int_0^\infty \int_0^\infty \int_0^\infty f(y_1) f(y_2) q_s(x,z) q_{t-s}(z,y_1) q_{t-s}(z,y_2)\, dy_1\, dy_2\, dz\, ds.$$

Moments are dominated by rare events in which one particle drifts unusually far to the right and has many surviving offspring.

Truncation: kill particles that get too far to the right.

Moments can be calculated the same way, after adjusting $q_t(x,y)$.

Branching Brownian motion in a strip

Consider Brownian motion killed at 0 and L. If there is initially one particle at x, the "density" of the position at time t is:

$$p_t^L(x,y) = \frac{2}{L} \sum_{n=1}^{\infty} e^{-\pi^2 n^2 t/2L^2} \sin\left(\frac{n\pi x}{L}\right) \sin\left(\frac{n\pi y}{L}\right).$$

Add branching at rate 1/2 and drift of -1, "density" becomes:

$$q_t^L(x,y) = p_t^L(x,y) \cdot e^{(x-y)-t/2} \cdot e^{t/2},$$

meaning that if $A \subset (0,L)$, the expected number of particles in A at time t is $\int_A q_t^L(x,y)\,dy$. For $t \gg L^2$,

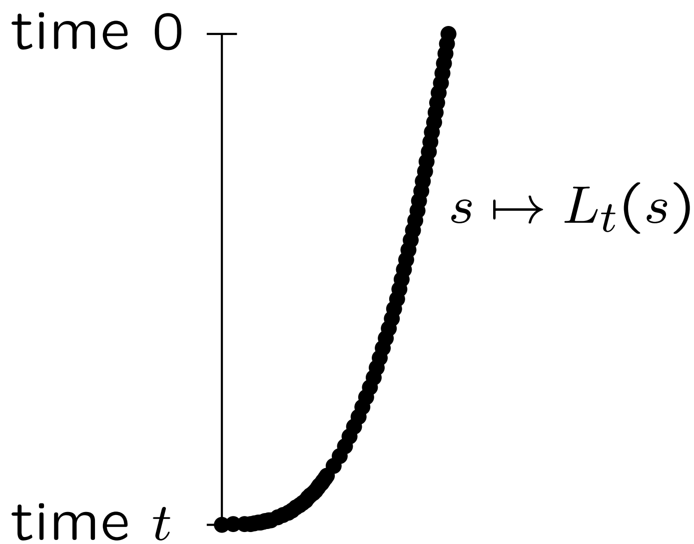
$$q_t^L(x,y) \approx \frac{2}{L} e^{-\pi^2 t/2L^2} \cdot e^x \sin\left(\frac{\pi x}{L}\right) \cdot e^{-y} \sin\left(\frac{\pi y}{L}\right).$$

- The expected number of future descendants of a particle at x is proportional to $e^x \sin(\pi x/L)$.
- For $t \gg L^2$, particles settle into a fairly stable configuration, number of particles near y is proportional to $e^{-y} \sin(\pi y/L)$.

A curved right boundary

Fix $t > 0$. Let $L_t(s) = c(t-s)^{1/3}$, where $c = (3\pi^2/2)^{1/3}$.
Consider BBM with particles killed at 0 and $L_t(s)$.
This right boundary was previously used by Kesten (1978).

Roughly, a particle that gets within a constant of $L_t(s)$ at time s has a good chance to have a descendant alive at time t.



Use methods of Novikov (1981) and Roberts (2012) to approximate the density and then compute moments.

Density formula resembles that for BBM in a strip.

Beyond truncated moment calculations

When particles are killed at 0 and at $L_t(s)$:

- Second moment is too large to conclude that the number of particles in the system stays close to its expectation.
- The probability that a particle is killed at $L_t(s)$ does not tend to zero, though the expected number of such particles is bounded by a constant.

Idea: kill particles instead at $L_t(s) + A$:

- Let $A \to -\infty$, and then the number of particles stays close to its expectation.
- Let $A \to \infty$, and then the probability that a particle hits the right boundary tends to zero.

Because we can't do both, proceed as follows:

- Stop particles when they reach $L_t(s) - A$, for large A.
- After a particle hits $L_t(s) - A$, follow the descendants of this particle until they reach $L_t(s) - A - y$ for large y. Then re-incorporate them into the process.

The particles that hit $L_t(s) - A$

Consider branching Brownian motion with drift -1 started with one particle at L.

Let $M(y)$ be the number of particles that reach $L-y$, if particles are killed upon reaching $L - y$.

Conditional on $M(x)$, the distribution of $M(x+y)$ is the distribution of $M(x)$ independent random variables with the same distribution as $M(y)$. Therefore, $(M(y), y \geq 0)$ is a continuous-time branching process.

Theorem (Neveu, 1987): There exists a random variable W such that almost surely

$$\lim_{y \to \infty} y e^{-y} M(y) = W.$$

Proposition (Maillard, 2012): $P(W > x) \sim x^{-1}$ as $x \to \infty$.

Putting the pieces together

Consider BBM with drift at rate -1, branching at rate 1/2, and absorption at 0.

Let $N(s)$ be the number of particles at time s.

Let $X_1(s) \geq X_2(s) \geq \cdots \geq X_{N(s)}(s)$ be the positions of the particles at time s.

Let $t > 0$. For $0 \leq s \leq t$, let

$$Z_t(s) = \sum_{i=1}^{N(s)} L_t(s) e^{X_i(s) - L_t(s)} \sin\left(\frac{\pi X_i(s)}{L_t(s)}\right) \mathbb{1}_{\{0 < X_i(s) < L_t(s)\}}.$$

The processes $(Z_t(s), 0 \leq s \leq t)$ converge as $t \to \infty$:

- The limit process has jumps of size greater than x at a rate proportional to x^{-1}.
- The jump rate at time s is also proportional to $Z_t(s)$.

Limit is a continuous-state branching process.

Continuous-state branching processes (Lamperti, 1967)

A continuous-state branching process (CSBP) is a $[0, \infty)$-valued Markov process $(X(t), t \geq 0)$ whose transition functions satisfy

$$p_t(a + b, \cdot) = p_t(a, \cdot) * p_t(b, \cdot).$$

CSBPs arise as scaling limits of Galton-Watson processes.

Let $(Y(s), s \geq 0)$ be a Lévy process with no negative jumps with $Y(0) > 0$, stopped when it hits zero. Let

$$S(t) = \inf \left\{ u : \int_0^u Y(s)^{-1} \, ds > t \right\}.$$

The process $(X(t), t \geq 0)$ defined by $X(t) = Y(S(t))$ is a CSBP. Every CSBP can be obtained this way.

If $Y(0) = a$, then $E[e^{-qY(t)}] = e^{aq + t\Psi(q)}$, where

$$\Psi(q) = \alpha q + \beta q^2 + \int_0^\infty (e^{-qx} - 1 + qx 1_{\{x \leq 1\}}) \, \nu(dx).$$

The function Ψ is the branching mechanism of the CSBP.

Convergence to the CSBP

Neveu (1992) considered the CSBP with branching mechanism

$$\Psi(q) = aq + bq \log q = cq + \int_0^\infty (e^{-qx} - 1 + qx\mathbf{1}_{\{x \leq 1\}})\, bx^{-2}\, dx.$$

Rate of jumps of size at least x is proportional to x^{-1}.

Theorem (BMS, 2017): If $Z_t(0) \Rightarrow Z$ and $L_t(0) - R(0) \to_p \infty$ as $t \to \infty$, then the finite-dimensional distributions of

$$(Z_t((1 - e^{-u})t), u \geq 0)$$

converge as $t \to \infty$ to the finite-dimensional distributions of $(X(u), u \geq 0)$, which is a CSBP with $X(0) =_d Z$ and branching mechanism $\Psi(q) = aq + \frac{2}{3} q \log q$.

Note: The value of the constant $a \in \mathbb{R}$ is unknown.

Asymptotics for the CSBP

Let $(X(u), u \geq 0)$ be a CSBP with $X(0) = x > 0$ and branching mechanism $\Psi(q) = aq + \frac{2}{3} q \log q$.

Results of Gray (1974) give

$$P_x(0 < X(u) < \infty \text{ for all } u \geq 0) = 1.$$

Letting $\alpha = e^{-3a/2}$,

$$P_x\Big(\lim_{u \to \infty} X(u) = \infty\Big) = 1 - e^{-\alpha x}, \qquad P_x\Big(\lim_{u \to \infty} X(u) = 0\Big) = e^{-\alpha x}.$$

Interpretation (Bertoin, Fontbona, Martinez, 2008): The CSBP at time zero may include "prolific individuals", whose number of descendants at time u tends to infinity as $u \to \infty$. The number of prolific individuals has a Poisson distribution with mean αx.

Survival of BBM until time t corresponds to $\lim_{u \to \infty} X(u) = \infty$.

Survival probability for BBM

Theorem (BMS, 2017): Assume the initial configuration of particles is deterministic, but may depend on t. Recall that ζ denotes the extinction time.

- If $Z_t(0) \to z$ and $L_t(0) - R(0) \to \infty$ as $t \to \infty$, then

$$\lim_{t \to \infty} P(\zeta > t) = 1 - e^{-\alpha z}.$$

- If $Z_t(0) \to 0$ and $L_t(0) - R(0) \to \infty$, then

$$P(\zeta > t) \sim \alpha Z_t(0).$$

- If at time zero there is only a single particle at x, then

$$P_x(\zeta > t) \sim \alpha \pi x e^{x - L_t(0)}.$$

- If at time zero there is a single particle at $L_t(0) + x$, then

$$\lim_{t \to \infty} P_{L_t(0)+x}(\zeta > t) = \phi(x),$$

  where $\lim_{x \to \infty} \phi(x) = 1$ and $\lim_{x \to -\infty} \phi(x) = 0$.

Asymptotics of survival time

Theorem (BMS, 2017): Assume the initial configuration is deterministic and satisfies $Z_t(0) \to 0$ and $L_t(0) - R(0) \to \infty$ as $t \to \infty$. Conditional on $\zeta > t$,

$$t^{-2/3}(\zeta - t) \Rightarrow V,$$

where V has an exponential distribution with mean $3/c$.

Proof: By the previous result,

$$P(\zeta > t + yt^{2/3} \,|\, \zeta > t) = \frac{P(\zeta > t + yt^{2/3})}{P(\zeta > t)} \sim \frac{\alpha Z_{t+yt^{2/3}}(0)}{\alpha Z_t(0)} \sim e^{-cy/3}.$$

A Yaglom-type result

For BBM at time t that will go extinct at time $t+s$:

- $Z_{t+s}(t)$ will not be close to 0 or ∞.
- "density" of particles near y is proportional to $e^{-y} \sin\left(\frac{\pi y}{L_{t+s}(t)}\right)$.
- right-most particle is near $L_{t+s}(t) = cs^{1/3}$.
- $N(t)$ is of the order $s^{-1} e^{L_{t+s}(t)}$, so $\log N(t) \approx cs^{1/3}$.

Conditional on $\zeta > t$, the process will survive an additional $t^{2/3}V$ time units. Then $R(t) \approx \log N(t) \approx c(t^{2/3}V)^{1/3} = ct^{2/9}V^{1/3}$.

Theorem (BMS, 2017): Assume the initial configuration is deterministic and satisfies $Z_t(0) \to 0$ and $L_t(0) - R(0) \to \infty$ as $t \to \infty$. Conditional on $\zeta > t$,

$$t^{-2/9} \log N(t) \Rightarrow cV^{1/3},$$

$$t^{-2/9} R(t) \Rightarrow cV^{1/3}.$$

The conditioned BBM before time t

Theorem (BMS, 2017): Assume the initial configuration is deterministic and satisfies $Z_t(0) \to 0$ and $L_t(0) - R(0) \to \infty$ as $t \to \infty$. Conditional on $\zeta > t$, the finite-dimensional distributions of the processes

$$(Z_t((1 - e^{-u})t), u \geq 0)$$

converge as $t \to \infty$ to the finite-dimensional distributions of a CSBP with branching mechanism $\Psi(q) = aq + \frac{2}{3} q \log q$ started at 0 and conditioned to go to infinity.

Remark: The law of the CSBP started at $x > 0$ and conditioned to go to infinity has a limit as $x \to 0$. The limit can be interpreted as the process that keeps track of the number of descendants of a single prolific individual.

Population models with selection

Can use BBM with absorption to model populations subject to natural selection, as proposed by Brunet, Derrida, Mueller, and Munier (2006).

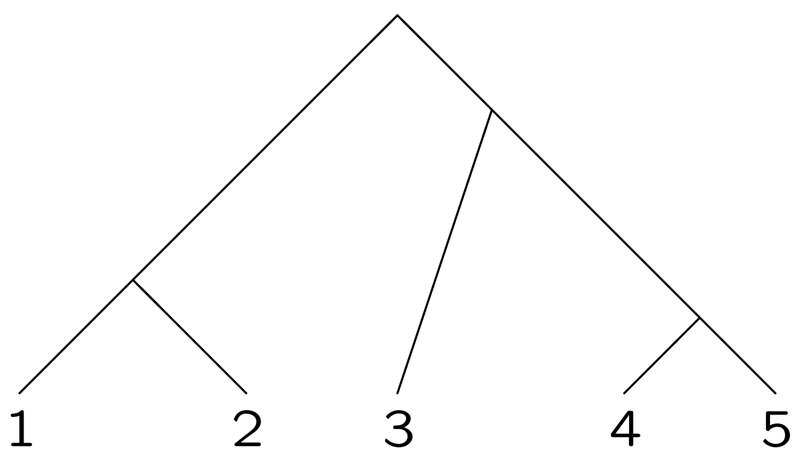
particles	$\rightarrow$	individuals in the population
positions of particles	$\rightarrow$	fitness of individuals
branching events	$\rightarrow$	births
absorption at 0	$\rightarrow$	deaths of unfit individuals
movement of particles	$\rightarrow$	changes in fitness over generations

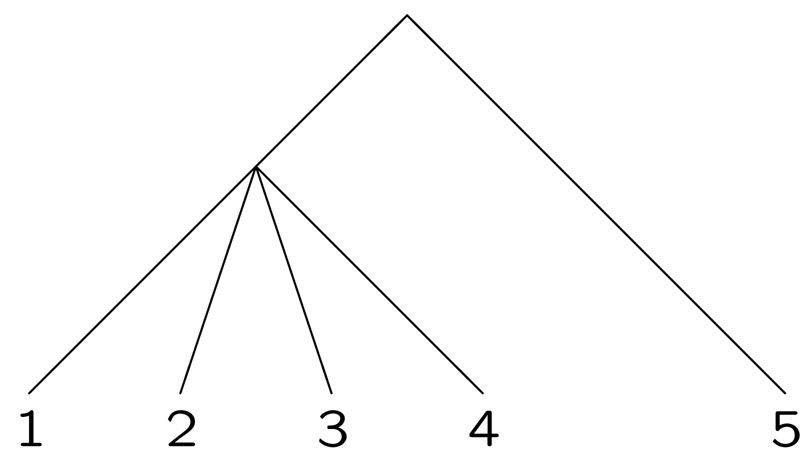
Coalescent Processes

Sample n individuals at random from a population. Follow their ancestral lines backwards in time. The lineages coalesce, until they are all traced back to a common ancestor.

Represent by a stochastic process $(\Pi(t), t \geq 0)$ taking its values in the set of partitions of $\{1, \ldots, n\}$.

Kingman's Coalescent (Kingman, 1982): Only two lineages merge at a time. Each pair of lineages merges at rate one.





Coalescents with multiple mergers (Pitman, 1999; Sagitov, 1999): Many lineages can merge at a time.

Bolthausen-Sznitman coalescent

When there are b lineages, each k-tuple ($2 \leq k \leq b$) of lineages merges at rate

$$\lambda_{b,k} = \int_0^1 p^{k-2}(1-p)^{b-k}\,dp.$$

Consider a Poisson point process on $[0,\infty) \times (0,1]$ with intensity

$$dt \times p^{-2}\,dp.$$

Begin with n lineages at time 0. If (t,p) is a point of this Poisson process, then at time t, there is a merger event in which each lineage independently participates with probability p.

Rate of mergers impacting more than a fraction $x/(1+x)$ of lineages is

$$\int_{x/(1+x)}^1 p^{-2}\,dp = x^{-1}.$$

Bolthausen-Sznitman coalescent describes the genealogy when, if the population has size K, new "families" of size at least Kx appear at a rate proportional to x^{-1}. This applies to Neveu's CSBP (Bertoin and Le Gall, 2000).

The genealogy of BBM

Consider branching Brownian motion with absorption at zero, branching at rate 1 and drift $-\mu$, where

$$\mu = \sqrt{2 - \frac{2\pi^2}{(\log N + 3 \log \log N)^2}}\,.$$

We make certain assumptions on the initial conditions so that the number of particles is of order N for a long time.

Theorem (BBS, 2013): Fix $t > 0$, and pick n particles at random at time $t(\log N)^3$. Let $\Pi_N(s)$ be the partition of $\{1, \dots, n\}$ such that $i \sim j$ if and only if the ith and jth sampled particles have the same ancestor at time $(t - s/2\pi)(\log N)^3$. The finite-dimensional distributions of $(\Pi_N(s), 0 \leq s \leq 2\pi t)$ converge to those of the Bolthausen-Sznitman coalescent.

Brunet, Derrida, Mueller, and Munier (2007) obtained result by nonrigorous methods.