Branching Brownian Motion under Selection - Part 2

Sandra Kliem (Part 1) and **Kumarjit Saha (Part 2)**

Singapore - Genealogies of Interacting Particle Systems - 2017

Branching Brownian motion (BBM) underselection

- Berestycki, J., Berestycki, N. and Schweinsberg, J.
  "The genealogy of branching Brownian motion with absorption."
  Ann. Probab. **41** (2013) 527–618.

- Maillard, P.
  "Speed and fluctuations of N-particle branching Brownian motion with spatial selection."
  Probab. Theory and Relat. Fields **166** (2016) 1061–1173.

Two basic models of population under selection

For us, population under selection means *it can not grow too fast* (motivated from limited resources..).

- Start with N individuals on $\mathbb{R}^+$.
- Position of an individual on $\mathbb{R}^+$ measures his/her fitness.
- Due to mutation fitness of an individual evolves randomly around that of the parent.

BRW under selection

Start with N individuals on $\mathbb{R}^+$.

Time is **discrete** and at each step each individual produces $k \geq 2$ offspring.

The position (i.e., fitness) of an individual is given by position of its parent plus an i.i.d. displacement distribution μ.

(Selection step:) At each step, keep only the N rightmost (fittest) particles.

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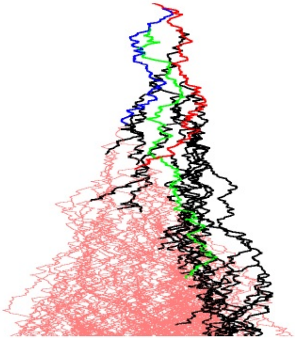
BBM under selection (N-BBM)



Picture by Éric Brunet

Figure: Different colors represent descendants of different parents except that the Pink shaded particles are *not selected* by nature

Start N independent branching Brownian motions starting from N locations on $\mathbb{R}^+$.

(Selection step:) At each transition, i.e., at each branching event keep the N rightmost Brownian particles only.

Brunet, Derrida conjecture

At any time $t \geq 0$, the position of the N fittest particles are given as

$$X_1(t) \leq \cdots \leq X_N(t).$$

The limit $\lim_{t\to\infty}(X_N(t)/t) = v_N$ exists a.s. with $v_N \leq v_{N+1}$.

The **question** is at what rate $v_N \uparrow v_\infty$?

Conjecture (BDMM06, BDMM07)

$$(v_\infty - v_N) \sim \frac{C}{(\log N)^2}.$$

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Under certain assumptions on displacement distribution μ, Bérard and Gouéré proved this (2010).

Brunet, Derrida conjecture

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- If two individuals are selected from the population at random in some generation, then the number of generations that we need to look back to find their most recent common ancestor is of the order of $(\log N)^3$.

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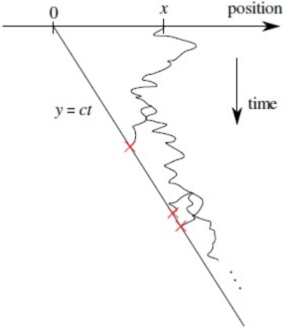
BBM with absorption



Take $f(t) = ct$ and start BBM from $x(> 0)$. Particles are killed as soon as they hit the linear barrier.

Equivalent to study BBM with drift $-c$ and particles are killed as soon as they hit 0.

From selection perspective, it can be viewed as **threshold is moving with a linear speed** and this does **not allow** the population to grow too much.

Theorem (Kesten (78))

For $c \geq \sqrt{2}$ this process dies a.s. and for $c < \sqrt{2}$ the process survives with positive probability.

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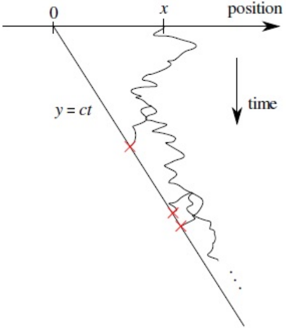

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BBM with absorption: (BBS13) setup

We want to study a sequence of BBM's $X_N : N \in \mathbb{N}$ indexed by N **near criticality**.

It is intuitive to take $\mu_N \uparrow \sqrt{2}$ where μ_N denotes the drift of BBM X_N. Take

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

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Further predictions in [BDMM06] and [BDM07]

For BBM under selection the authors of [BDMM06] and [BDMM07] provided further heuristic predictions of the evolving particle system

- Meta-stable state:
  - cloud of particles moves at speed $v_N^{\text{det}} = \sqrt{1 - \pi^2/(\log N)^2}$
  - diameter of the cloud remains of the order of $\log N$.
- Empirical measure seen from the leftmost particle is approximately proportional to $\sin(\pi x/\log N)e^{-x}\mathbf{1}_{(0,\log N)}(x)$
- This state is perturbed by particles moving **far to the right**. A particle moving up to the point $\log N + x$ causes, a shift by $\Delta = \log(1 + Ce^x/\log^3 N)$. Hence a particle reaching $\log N + 3\log\log N$ after a relaxation time $\log^2 N$ gives rise to $O(N)$ descendants and causes a detectable shift.

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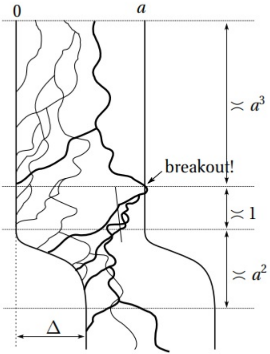

Figure: Figure 1 of [M13]

So, particles reaching distance L_N is *special* as they are causing **shift**.

Question: Can we chose μ_N so that for a BBM with **drift** $-\mu_N$ with **absorbing barrier** at 0 and L_N, the number of particles **do not** fluctuate much?

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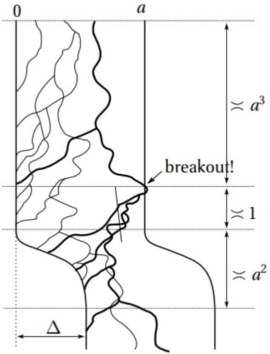

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BBM with absorption: [BBS13] set up

For a branching Brownian motion with drift $-\mu$ starting from a single particle at $x \in (0, L)$, and particles *killed* upon reaching 0 or L, the expected number of particles in a set $B \subset [0, L]$ at a sufficiently large time t is approximately given by $\int_B p_t(x,y)dy$, where

$$p_t(x,y) = \frac{2}{L} e^{(1-\mu^2/2-\pi^2/(2L^2))t} . e^{\mu x} \sin(\frac{\pi x}{L}) e^{-\mu y} \sin(\frac{\pi y}{L}).$$

This explains the choice of $\mu_N := \sqrt{2 - \frac{2\pi^2 \log N}{(\log N + 3 \log \log N)}}$.

This illustrates the connection with population under selection model.

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Notation

We start N-th process with multiple particles, rather than just one, satisfying two technical assumptions.

For N-th BBM (or collection of BBM's) with absorbtion

$M_N(t)$ = population size at time t

$X_{1,N}(t) \leq X_{2,N}(t) \leq \cdots \leq X_{M_N,N}(t)$ position of particles

Let

$$Z_N(t) = \sum_{i=1}^{M_N(t)} e^{\mu X_{i,N}(t)} \sin\left(\frac{\pi X_{i,N}(t)}{L}\right) \mathbf{1}_{X_{i,N}(t) \leq L} \text{ and}$$

$$Y_N(t) = \sum_{i=1}^{M_N(t)} e^{\mu X_{i,N}(t)}.$$

Initial conditions

Couple of technical conditions (which ensures that the system starts from *'stable'* configuration and stays of the order of N)

- $\frac{Z_N(0)}{N(\log^2 N)}$ converges in distribution to ν where ν is a probability distribution over $[0, \infty)$ as $N \to \infty$ and
- $\left(\sum_{i=1}^{M_N(0)} e^{\mu X_{i,N}(0)}\right)/(N(\log^3 N))$ converges to 0 in probability as $N \to \infty$.

Convergence to CSBP

Theorem (Berestycki, Berestycki, Schweinsberg)

As $N \to \infty$, *the finite-dimensional distributions of the process* $\{M_N((\log^3 N)t)/(2\pi N) : t > 0\}$ *converge to the finite-dimensional distributions of the continuous-state branching process (CSBP) with branching mechanism* $\psi(u) = au + 2\pi u \log u$ *started with distribution* ν *at time zero, where* a *and* ν *comes from the initial conditions.*

Convergence to CSBP

This result proves that the size of the population remains of order N at $\log^3 N$ time scaling.

Convergence does not hold for $M_N(0)$, as the assumptions about initial configurations do not tell anything about initial population size.

Because of fluctuations, one can not have process convergence w.r.t. the usual Skorohod topology. It might be of interest to see whether it is possible to achieve process convergence w.r.t. some other topology (e.g., Skorohod M_1 topology).

Convergence to Bolthausen-Sznitman coalescent

Choose n particles uniformly at random from the $M_N((\log^3 N)t)$ particles at time $(\log^3 N)t$.

Fix $t > 0$ and choose n individuals at random from the population. For $0 \leq s \leq 2\pi t$, let $\Pi_N(s)$ to be the **partition** of $\{1, \cdots, n\}$ such that i and j are in the same block of $\Pi_N(s)$ if both the particles have the **same ancestor** at time $(t - s/(2\pi))(\log^3 N)$.

Theorem

As $N \to \infty$, the finite-dimensional distributions of of the process $(\Pi_N(s), 0 \leq s \leq 2\pi t)$ converge to Bolthausen-Sznitman n coalescent running for time $2\pi t$.

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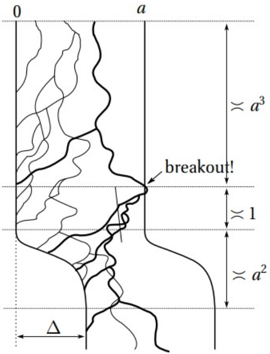
Contribution of the special points



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Divide the population into two parts

- those that have stayed inside the interval $(0, L_N)$ throughout,
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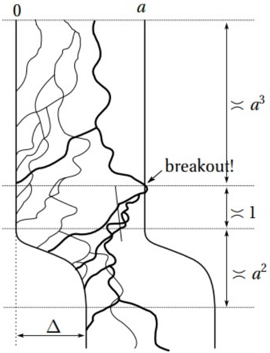

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Contribution of the special points

The contribution of a special point is of the order of WN, where W is a random variable with tail $\mathbb{P}(W > x) \sim 1/x$ as $x \to \infty$.

For a BBM with drift $\sqrt{2}$ starting with a single particle at 0 we kill particles as soon as they reach y. Then Z_y denote the number of particles that reach y, which is **finite** a.s.

Proposition (Neveu 1988)

There exists a random variable W such that a.s.

$$\lim_{y \to \infty} y e^{\sqrt{2} y} Z_y = W.$$

This together with good estimate on the number of times particles hitting L_N proves Theorem 2.

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How to obtain genealogy for a CSBP

Definition

CSBP is a Markov process with RCLL paths with values in $[0, \infty]$ whose transition kernels $(P_t)_{t \geq 0}$ satisfy the branching property

$$P_t(x, \cdot) * P_t(y, \cdot) = P_t(x + y, \cdot) \text{ for all } t, x, y \geq 0. \quad (1)$$

In words, if Z^x and Z^y are two independent copies of CSBP Z started respectively at x and y, then $Z^x + Z^y$ has the same law of Z started at $x + y$.

For every $\lambda > 0$ and $a \in [0, \infty)$, let

$$\mathbb{E}(e^{-\lambda X_t} | X_0 = a) = e^{(-a u_t(\lambda))}.$$

How to obtain genealogy for a CSBP

Let $Z(t,a)$ denote that the CSBP $(Z_t : t \geq 0)$ starts from $Z_0 = a \in \mathbb{R}$.

On some probability space, the CSBP's, $Z(\cdot, a)$ and $Z(\cdot, a+b)$, are defined such that $Z(\cdot, a+b) - Z(\cdot, a)$ is **independent** of $Z(\cdot, a)$ and has the same law as $Z(\cdot, b)$.

By Kolmogorov's theorem, we can construct a process $(Z(t,a) : t \geq 0 \text{ and } a \geq 0)$ such that

- $Z(\cdot, 0) = 0$,
- for every $a, b \geq 0$, $Z(\cdot, a+b) - Z(\cdot, a)$ has law $Z(\cdot, b)$ and
- for every $a, b \geq 0$, $Z(\cdot, a+b) - Z(\cdot, a)$ is independent of the family of the processes $\{Z(\cdot, c) : 0 \leq c \leq a\}$.

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Definition

Subordinator is a non-decreasing Lévy process taking values in $\mathbb{R}$.

The process $Z(t, \cdot)$ is a 'subordinator'.

Genealogy for a CSBP

Proposition (Bertoin and Le Gall (2000))

On some probability space, there exists a process

$$(S^{(s,t)}(a), 0 \leq s \leq t \text{ and } a \geq 0) \text{ such that:}$$

(i) For every $0 \leq s \leq t$, $(S^{(s,t)} = S^{(s,t)}(a), a \geq 0)$ is a subordinator with Laplace exponent $u_{t-s}(\cdot)$.

(ii) For every integer $p \geq 2$ and $0 \leq t_1 \leq \cdots \leq t_p$, the subordinators $S^{(t_1,t_2)}, \cdots, S^{(t_{p-1},t_p)}$ are independent and

$$S^{(t_1,t_p)}(a) = S^{(t_{p-1},t_p)} \circ \cdots \circ S^{(t_1,t_2)}(a) \text{ for all } a \geq 0 \text{ a.s.}$$

Finally, the processes $(S^{(0,t)}(a), t \geq 0 \text{ and } a \geq 0)$ and $(Z(t,a) : t \geq 0 \text{ and } a \geq 0)$ have the same finite-dimensional marginals.

Definition (Bertoin and Le Gall (2000))

For every $b, c \geq 0$ and $0 \leq s < t$, we say that the individual c in the population at time t has **ancestor** (or is a descendant of) the individual b in the population at time s if b is a jump time of $S^{(s,t)}$ and

$$S^{(s,t)}(b) < c < S^{(s,t)}(b).$$

Under the assumption that $S^{(s,t)}$ has zero drift, the individuals in the population at time t having no ancestor at time s are of Lebesgue measure **zero a.s.**

Genealogy for a CSBP

Suppose $0 \leq r < s < t$. The individual d in the population at time t has ancestor c at time s, and c has ancestor b at time r. Then,

$$S^{(s,t)}(c-) < d < S^{(s,t)}(c) \text{ and } S^{(s,t)}(b-) < c < S^{(s,t)}(b).$$

Since $S^{(r,t)} = S^{(s,t)} \circ S^{(r,s)}$, by monotonicity we have

$$S^{(r,t)}(b-) < d < S^{(r,t)}(b),$$

i.e., the individual d at time t has ancestor b at time r.

Flow of bridges for a CSBP

Fix an integer $p \geq 1$ and choose finitely many ordered time points $0 \leq t_0 < t_1 < \cdots < t_p \leq t$. For $0 \leq k \leq p$, take

$a_k = Z(t_k, a) = S^{(0,t_k)}(a)$.

For $0 \leq k \leq p-1$, define

$$B_k(s) = \left(S^{(t_k,t_{k+1})}(sa_k)\right)/\left(S^{(t_k,t_{k+1})}(a_k)\right) \text{ for } s \in [0,1].$$

Clearly, $B_k(0) = 0$ and $B_k(1) = 1$ and B_k has *non-decreasing RCLL paths.*

Motivation: Here population size varies and we have to *normalize* appropriately.

Flow of bridges for a CSBP

Definition

$B = (B_{s,t}(x), 0 \leq s \leq t, 0 \leq x \leq 1)$ is a flow of bridges, which is a collection $(B_{s,t}, 0 \leq s \leq t)$ of bridges such that:

- For every $s < t < u$, we have $B_{s,u} = B_{t,u} \circ B_{s,t}$.
- The law of $B_{s,t}$ only depends on $t - s$.
- If $s_1 < s_2 < \cdots < s_n$, then the bridges $B_{s_1,s_2}, \ldots, B_{s_{n-1},s_n}$ are independent.
- $B_{0,0} = \mathrm{Id}$ and $B_{0,t} \to \mathrm{Id}$ as $t \to 0$ in probability, in the sense of Skorohod topology.

Bolthausen-Sznitman coalescent for the CSBP Z

Theorem (Bertoin, Le Gall (2003))

Fix $a, t > 0$. Let $V_1, V_2, \cdots$ be a sequence of random variables such that conditionally on $\mathcal{F}_t$, V_i's are independently and uniformly distributed over $[0, Z(t,a)]$. For any $0 \le s \le t$ the equivalence relation $\tilde{\Pi}_s$ on $\mathbb{N}$ is given by declaring m and n belong to the same class of $\tilde{\Pi}_s$ if V_m and V_n has the same ancestor at time $t - s$. Then

$$(\tilde{\Pi}_s : 0 \le s \le t) \text{ and } (\Pi_s : 0 \le s \le t) \text{ has the same f.d.d.'s.},$$

where $(\Pi_s : 0 \le s \le t)$ is the Bolthausen-Sznitman coalescent running for time t.

Convergence of flow of bridges

Let $D([0,1],\mathbb{R}_+)$ be the metric space of RCLL non-decreasing paths defined over $[0,1]$ such that $f(0)=0$ and $f(1)=1$ with the usual Skorohod metric.

Proposition

Consider a sequence of bridges $\{B_n : n \in \mathbb{N}\}$. The following are equivalent.

(i) The exchangeable partition $\Pi(B_n) \Rightarrow \Pi(B_\infty)$.

(ii) $B_n \Rightarrow B_\infty$ in $D([0,1],\mathbb{R}_+)$ endowed with the Skorohod topology.

So, we have to come up with a flow of bridges $(B^N_{s_1,s_2} : 0 \leq s_1 \leq s_2 \leq t)$ for N-th family of BBM with absorption.

Convergence of flow of bridges

Let $D([0,1],\mathbb{R}_+)$ be the metric space of RCLL non-decreasing paths defined over $[0,1]$ such that $f(0)=0$ and $f(1)=1$ with the usual Skorohod metric.

Proposition

Consider a sequence of bridges $\{B_n : n \in \mathbb{N}\}$. The following are equivalent.

(i) The exchangeable partition $\Pi(B_n) \Rightarrow \Pi(B_\infty)$.

(ii) $B_n \Rightarrow B_\infty$ in $D([0,1],\mathbb{R}_+)$ endowed with the Skorohod topology.

So, we have to come up with a flow of bridges $(B^N_{s_1,s_2} : 0 \leq s_1 \leq s_2 \leq t)$ for N-th family of BBM with absorption.

Convergence of flow of bridges

A natural choice for flow of bridges are as follows:

- Select an ordering of the individuals which **respects ancestry**.
- For $0 \le j \le k$ and $1 \le i \le M_N(t_j \log^3 N)$ we take

$$w(i,j) = \frac{1}{M_N(t_j \log^3 N)}.$$

- Let

$$A_i(j,k) = \{l : x_{l,k} \text{ (at time } (t_k \log^3 N)) \text{ is a descendant of } x_{i,j} \text{ at time } (t_j \log^3 N)\}$$

represents the set of descendants of $x_{i,j}$ (i-th individual w.r.t. ordering at time $(t_j \log^3 N)$).

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$$L_j(y) = \max\{l \in \mathbb{N} : \sum_{i=1}^{l} w_{(i,j)} \le y\},$$

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Convergence of the flow of bridges

Finally construct the bridges as follows: for $0 \leq y \leq 1$ and $0 \leq j < k \leq K$, let

$$B^N_{t_j,t_k}(y) = \sum_{i=1}^{L_j(y)} \sum_{m \in A_i(j,k)} w(m,k).$$

But this choice does not work.

For $0 \leq j \leq k$ and $1 \leq i \leq M_N(t_j \log^3 N)$ we take

$$w(i,j) = \begin{cases} \frac{1}{Z_N(t_j \log^3 N)} e^{\mu x_{i,j}} \sin(\pi x_{i,j}/L) \mathbf{1}_{x_{i,j} \leq L} & \text{if } 0 \leq j \leq k-1 \\ \frac{1}{M_N(t_k \log^3 N)} & \text{if } j = k. \end{cases} \tag{2}$$

i.e., the particles are weighted according to their contribution to $Z_N(t_j \log^3 N)$.

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The brides $B^N_{s_1,s_2}$ do not have exchangeable increments.

Proposition (Berestycki, Berestycki and Schweinsberg (2013))

Suppose $b, b_1, b_2, \cdots$ are functions from $[0,1]$ to $[0,1]$ that are non-decreasing and right continuous and have left limits at every point other than 0. Suppose $\lim_{n\to\infty} \rho(b_N, b) = 0$, where ρ denotes the Skorohod metric. Suppose $(x_n)_{n=1}^{\infty}$ and $(y_n)_{n=1}^{\infty}$ are sequences in $[0,1]$ such that $x_n \to x$ and $y_n \to y$ as $n \to \infty$. Suppose x and y are **not in the closure** of the range of b. Then for sufficiently large n we have $b_n^{-1}(x_n) = b_n^{-1}(y_n)$ if and only if $b^{-1}(x) = b^{-1}(y)$. Furthermore,

$$\lim_{n\to\infty} b_n^{-1}(x_n) = b^{-1}(x).$$

The proof uses the following interpretation of convergence with respect to Skorohod metric.

Let $\Lambda : [0,1] \mapsto [0,1]$ denote the class of strictly increasing continuous onto functions.

For a collection of RCLL paths $f, f_1, f_2, \ldots$, we have $\lim_{n\to\infty} \rho(f_n, f) = 0$ if and only if there exists a sequence of functions $(\lambda_n)_{n=1}^{\infty}$ in Λ such that

$$\lim_{n\to\infty} \sup\{|f_n(\lambda_n(t)) - f(t)| : 0 \le t \le 1\}$$
$$= \lim_{n\to\infty} \sup\{|\lambda_n(t) - \lambda(t)| : 0 \le t \le 1\} = 0.$$

Maillard's result on N-BBM

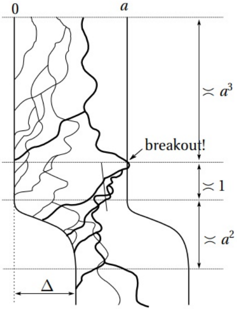

Figure: Figure 2 of [M13]

Question: Can we work with BBM with **random** absorbing barrier where the absorbing process is taking jumps at *'breakout'* events?

Maillard's result on N-BBm

Theorem (Maillard)

Suppose at time 0, there are N particles distributed independently in $(0, L_N)$ according to density proportional to $\sin(\pi x/L_N)e^{-x}$. Then, for every $\alpha \in (0,1)$,

$$(X_{\lfloor \alpha N \rfloor, N}(t \log^3 N) - v_N t \log^3 N)_{t \geq 0} \Rightarrow_{fdd} (Y_t)_{t \geq 0}.$$

Here, $(Y_t)_{t\geq 0}$ is a Lévy process with certain drift and Lévy measure (the image of $\pi^2 x^{-2} \mathbf{1}_{x>0} dx$ by the map $x \mapsto \log(1+x)$).

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The proof idea is to couple both the processes, N-BBM and B-BBM (BBM with **random** absorbing barrier).

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The proof idea is to couple both the processes, N-BBM and B-BBM (BBM with **random** absorbing barrier).

But the dependencies between the particles are too difficult to handle.

Kill a particle

- whenever it hits 0 or
- whenever it has N particles to its right (particles in the figure).

$\Rightarrow$ **More** particles are being killed than in N-BBM.

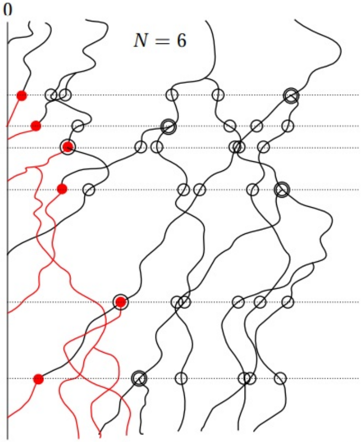

Figure: Figure 2 of [M13]

$B^{\#}$-BBM

Kill a particle

- whenever it hits 0 *and at the same time*
- it has N particles to its right (particles in the figure).

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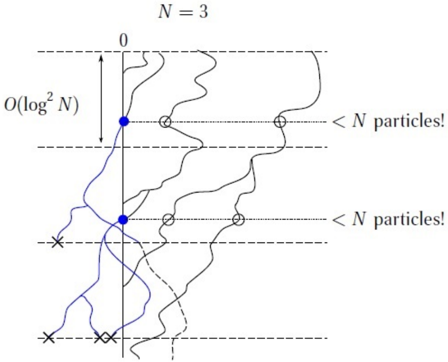

Figure: Figure 2 of [M13]

Thank you