The genealogy of an exactly solvable Ornstein–Uhlenbeck type branching process with selection

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Abstract

We study the genealogy of an exactly solvable population model with N particles on the real line, which evolves according to a discrete-time branching process with selection. At each time step, every particle gives birth to children around a times its current position, where $a > 0$ is a parameter of the model. Then, the N rightmost newborn children are selected to form the next generation. We show that the genealogy of the process converges toward a Beta coalescent as $N \to \infty$. The process we consider can be seen as a toy model version of a continuous-time branching process with selection, in which particles move according to independent Ornstein–Uhlenbeck processes. The parameter a is akin to the pulling strength of the Ornstein–Uhlenbeck process.

1 Introduction

A *branching–selection particle system* is a Markov process of particles on the real line that evolves through the repeated application of the two following steps:

Branching step: each particle currently alive in the process independently gives birth to children according to a point process whose law might depend on the position of the particle.

Selection step: some of the newborn children are selected to form the next generation and reproduce at the next *branching step*, while the other particles are "discarded" from the process.

From a biological perspective, such models can be thought of as toy models for the competition between individuals in a population evolving in an environment with limited resources: *natural selection*. In this sense, the positions of particles (also seen as individuals) may be interpreted as their *fitness*: individuals with large fitness have more propensity to reproduce and transfer their genetic advantage to their offspring.

The prototypical example of such systems is the so-called N-branching random walk, which was introduced by Brunet and Derrida in [10]. It consists of a discrete-time random process where particles reproduce independently of each other, making children around their current position. Then, only the N rightmost children are selected to survive and reproduce in the next branching step. Based on numerical simulations and the analysis of solvable models (see [10,11]), it has been predicted that many branching random walks with similar selection procedures satisfy universal properties. For example, it is expected that the cloud of particles travels at a deterministic speed v_N that should satisfy

$$v_N - v_\infty = \frac{-\chi}{(\log N + 3\log\log N + o(\log\log N))^2}, \tag{1.1}$$

where χ is an explicit constant depending on the reproduction law. Moreover, the genealogical tree of the process, seen as a discrete-time coalescent, is expected to converge towards the so-called

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Bolthausen–Sznitman coalescent [9]. We refer to [8] for further details about coalescent processes and an overview of the subject.

Some of the above conjectures have been partially verified. Bérard and Gouéré [5] proved that the speed of the cloud of particles satisfies $v_N - v_\infty \sim \frac{-\chi}{(\log N)^2}$ as $N \to \infty$ for many branching random walks, in accordance with (1.1). This result has been extended to branching random walks with different integrability conditions in [6,15,21] and to other related models in [12,20,22]. Other results, such as the hydrodynamic limit of the shape of the front of a branching random walk with selection were obtained. It was proved in [16,17] that the empirical measure of a continuous-time N-branching random walk converges toward the solution of an integro-differential equation with a free boundary condition.

Questions concerning the genealogy of branching random walks with selection appear to be more difficult to study and have been so far verified only for specific models: the branching Brownian motion with absorption and some exactly solvable branching-selection particle systems. It has been proved in [7] that the genealogy of particles in a branching Brownian motion with quasi-critical absorption (starting from a proper initial distribution) converges toward the Bolthausen–Sznitman coalescent. To the best of our knowledge, this is the only natural example of branching-selection particle system for which the conjecture from [10] on the genealogy has been proved. A key property allowing the mathematical treatment of the model is the branching property: in a branching Brownian motion with absorption, particles behave independently after splitting. This is not the case for N-branching random walks as the progeny of particles ahead in the front determines the selection of the leftmost particles.

Other examples for which above conjecture has been verified consist in models where the system becomes exactly solvable [11, 13, 14]. This is in particular the case for the so-called *exponential model* [11]: it consists in a discrete-time N-branching random walk where particles reproduce according to independent Poisson point processes with intensity $\mathrm{e}^{-x}\mathrm{d}x$. Observe that in this model each individual branches into infinitely many offspring, which is not a "natural" assumption for a biological model. As observed in [11], a useful property of the exponential model is that the relative positions of particles at any given generation form a family of i.i.d. point processes with an explicit distribution. Moreover, the law of the genealogical relation between two consecutive generations depends only on the relative positions of the parents in the older generation. Relying on this property, the authors in [11] obtained the asymptotic behavior of the average coalescent time of k individuals, which turns out to be consistent with the convergence of the genealogical trees toward a Bolthausen–Sznitman coalescent. In [14], we studied a generalized version of the exponential model, where particles are randomly sampled to constitute the next generation. In the model we consider, individuals reproduce as in the exponential model but instead of keeping the rightmost offspring, we sample (without replacement) N children, choosing an individual at position x with probability proportional to $\mathrm{e}^{\beta x}$, where $\beta > 1$ is a constant tuning the intensity of the selection. One may recover the exponential model by taking $\beta \to \infty$. We show that for all values of $\beta > 1$, including the exponential model ($\beta = \infty$), the limiting coalescent is the Bolthausen–Sznitman, which strengthens the conjectures from [11].

The above behavior contrasts with classical results about the convergence of the genealogical trees in "neutral" population models, such as Wright–Fisher and Moran models [18, 29]. In these models, the particles in a generation "choose" their parent at random from the previous generation, regardless of their fitness. It is well known that the genealogy of individuals in such cases is governed by the so-called Kingman coalescent [19]. Hence, a natural question is to find branching–selection particle systems that interpolate between the neutral selection case (Kingman) and the N-branching random walk (Bolthausen–Sznitman).

In this paper we study a solvable branching–selection particle system, whose limiting genealogy interpolates between the Kingman and the Bolthausen–Sznitman coalescents. We consider another variant of the exponential model, in which particles are subjected to a pulling force attracting them to 0. Let $N \in \mathbb{N}$ denote the size of the population and $a > 0$ be a parameter governing the intensity of the attractive force. The process is defined as follows: it starts with N particles scattered on the real line. At each discrete time n, every particle gives birth to children whose positions are determined by independent Poisson point processes centered around a times their current position. In other words, the offspring of an individual located at $x \in \mathbb{R}$ are positioned according to a Poisson point process with intensity $\mathrm{e}^{ax-y}\mathrm{d}y$. We then select the N rightmost newborn individuals to form the next generation of the process. We call this process the (N, a)-*exponential model*.

When $a < 1$, the pulling force can be interpreted as modeling *regression to the mean*, which is a natural biological phenomenon. Broadly speaking, the regression to the mean is the observation that individuals with an exceptionally large fitness typically have descendants with a better than average fitness, but not as large as their parent. A famous example of regression to the mean was reported by Pearson and Lee [23], who observed that when a father is taller than average, his son is also likely to be taller than average, but not as tall as his father.

For what follows in the paper, we denote by $X_n^N(1) > X_n^N(2) > \cdots > X_n^N(N)$ the positions of particles alive at generation $n \in \mathbb{N}$, ranked in decreasing order[1]. For $1 \le i, j \le n$, we write $A_n^N(i) = j$ if the particle at position $X_{n-1}^N(j)$ has given birth to the particle at position $X_n^N(i)$. We study in this paper the (N, a)-exponential model as $N \to \infty$ for a fixed. Therefore, we shall only display the dependence on N, omitting the dependence on a. Next, we introduce very quickly the coalescent processes and the associated notion of convergence we will be using in this article. We refer to the book of Berestycki [8] for a detailed account. In particular, we refer to Examples 1–3 (p66) for the precise definitions of the Kingman, Bolthausen–Sznitman and Beta coalescents. In Section 1.1 of the referred book, the topology we use in for our results is introduced.

We encode the genealogical tree of the (N, a)-exponential model via the *ancestral partition process*, which is a process in the space of partitions of $\mathbb{N}$. We fix a time horizon $T \in \mathbb{N}$, and for $1 \le k \le T$, we denote by $\Pi_k^{(N,T)}$ the partition such that i and j belong to the same block if and only if the particles at positions $X_T(i)$ and $X_T(j)$ share a common ancestor at time $T - k$. It is a consequence of Lemma 2.1 that for any $n \in \mathbb{N}$, the law of $(\Pi_k^{(N,T)}, k \le n)$ does not depend on $T > n$. Thus, we denote by $(\Pi_k^N, k \ge 0)$ the partition process having the same finite-dimensional distributions as $\Pi^{(N,T)}$, for T large enough.

As we shall see in Theorem 1.1, the $N \to \infty$ scaling limit of this partition process is a Λ-*coalescent*. This process was introduced by Pitman [24] and Sagitov [26] and it is constructed as follows. With Λ a finite measure on $[0, 1]$, the Λ-coalescent is a continuous-time Markov process Π taking values in the set of partitions of $\mathbb{N}$ which satisfies the property that we now describe. For all $N \in \mathbb{N}$, its restriction to $\{1, \dots, N\}$ is Markov chain such that if at time $t \ge 0$ there are b blocks in total, then any k blocks merge into a single one at rate

$$\lambda_{b,k} = \int x^{k-2}(1-x)^{b-k}\Lambda(\mathrm{d}x).$$

An important class of Λ coalescent processes is the Beta$(2 - \alpha, \alpha)$ coalescent, which forms a one parameter family parametrized by $\alpha \in [0, 2]$. They are defined by the measure

$$\Lambda(\mathrm{d}x) = \frac{1}{\Gamma(\alpha)\Gamma(2-\alpha)} x^{1-\alpha}(1-x)^{\alpha-1}\mathrm{d}x.$$

Such a family appears in the context of Galton–Watson trees [27] interpolating between the Kingman and the Bolthausen–Sznitman coalescent. Precisely, for $\alpha = 2$ ($\Lambda(\mathrm{d}x) = \delta_0$) the process is the Kingman coalescent, in which every pair of block merges at rate one. When $\alpha = 1$ (Λ is the uniform measure in $[0, 1]$), it corresponds to the Bolthausen–Sznitman coalescent.

Let $(a_N) \in \mathbb{R}_+^{\mathbb{N}}$ such that $\lim_{N\to\infty} a_N = \infty$ and $(\Pi_t^N, t \ge 0)_{N\in\mathbb{N}}$ be a family of discrete time partition processes. We say that $(\Pi_{\lfloor a_N t\rfloor}^N, t \ge 0)$ converges in law toward a Λ-coalescent if for every $k \in \mathbb{N}$, the restrictions to $\{1, \dots k\}$ of the finite-dimensional distributions of $(\Pi_{\lfloor a_N t\rfloor}^N, t \ge 0)$ converge toward those of $(\Pi_t, t \ge 0)$. The main result of this paper is the following theorem about the convergence in law of the ancestral partition process associated with the (N, a)-exponential model.

Theorem 1.1. *As $N \to \infty$, we have:*

a) If $0 < a < 1/2$, then $(\Pi_{\lfloor tN\rfloor}^N, t \ge 0)$ converges in law to the Kingman coalescent.

b) If $a = 1/2$, then $(\Pi_{\lfloor tN/\log N\rfloor}^N, t \ge 0)$ converges in law to the Kingman coalescent.

[1] Note that we assume here that two different particles are always in different positions. By definition of the process, this is necessarily the case for $n \ge 1$, and it will become clear after Lemma 2.1 that the starting position plays no role in the law of the process after time 1.

c) If $1/2 < a < 1$, then $(\Pi^N_{\lfloor tN^{(1-a)/a}\rfloor}, t \geq 0)$ converges in law to the Beta$(2 - a^{-1}, a^{-1})$-coalescent.

d) If $a = 1$, then $(\Pi^N_{\lfloor t \log N\rfloor}, t \geq 0)$ converges in law to the Bolthausen–Sznitman coalescent.

e) If $a > 1$, then Π^N converges in law toward a discrete-time coalescent.

To the best of our knowledge, the (N, a)-exponential model is the first mathematical model of natural selection with limiting genealogical tree other than Kingman or Bolthausen-Sznitman. However, the fact that there are no overlapping generations and that every individual gives birth to a very large number of children is not satisfying as a true biological model. We point out in Section 3 a link between this exponential model and a more natural branching-selection particle system, in which particles move according to i.i.d. Ornstein-Uhlenbeck processes and branch at rate 1.

In view of the above result, $a = 1$ and $a = 1/2$ mark phase transitions in the behavior of the genealogy of the process. We also show that a similar transition happens in the dynamical evolution of particles at $a = 1$. Indeed, as long as $a < 1$, the cloud of particles remains within finite distance from 0. Whereas for $a = 1$, we proved in [14] that it drifts toward ∞ at positive speed. Finally, one can easily show that when $a > 1$ the cloud moves away from 0 at an exponential rate. For $a < 1$, we have the following more precise estimates:

Proposition 1.2. *Let $a \in (0, 1)$ and assume that $\sup_{N\in\mathbb{N}} \mathbf{E}\left(\left|\log \sum_{j=1}^N e^{aX_n^N(j)}\right|\right) < \infty$, then*

$$\lim_{N\to\infty} \lim_{n\to\infty} \mathbf{E}(X_n^N(1)) - \log N = \gamma - \frac{\log(1-a)}{1-a} \quad \text{and} \quad \lim_{N\to\infty} \lim_{n\to\infty} \mathbf{E}(X_n^N(N)) = -\frac{\log(1-a)}{1-a},$$

where γ is the Euler–Mascheroni constant.

Proposition 1.2 shows that the cloud of particles in the (N, a)-exponential model is roughly of size $\log N$, which is typical in many branching selection particle systems. The proofs of both Proposition 1.2 and Theorem 1.1 rely on the observation that the distribution of the children at time $n + 1$ is a Poisson point process with exponential intensity around the position of a unique fictitious particle. This construction was introduced in [11] and further developed in [14].

Outline of the paper: In the next section, we prove the two main results of the paper, namely, Theorem 1.1 and Proposition 1.2. In Section 3, we define the *branching Ornstein–Uhlenbeck processes with selection* and discuss its relationship with the (N, a)-exponential model.

2 Proofs of main results

We start with a mathematical construction of the (N, a)-exponential model. Let $(\mathcal{P}_{n,j}, (n, j) \in \mathbb{N}^2)$ be an infinite array of i.i.d. copies of a Poisson point processes with intensity measure $e^{-x}dx$ and recall that $X_0^N(1) > X_0^N(2) > \cdots > X_0^N(N)$ denote the ranked positions of the particles at time 0, which we shall assume distinct for the sake of simplicity. We construct the process in such a way that the children of the ith rightmost individual at time n, which is at position $X_n^N(i)$, are positioned according to the point process $\mathcal{P}_{n+1,i}$, shifted by $aX_n(i)$. Then, we select the N rightmost children to form the $(n + 1)$th generation. In other words, for each $n \in \mathbb{N}$ and $i \leq N$, we have that

i) $X_{n+1}^N(i)$ is the ith largest atom of the point process $\sum_{j=1}^N \sum_{p\in\mathcal{P}_{n+1,j}} \delta_{aX_n^N(j)+p}$,

ii) $A_{n+1}^N(i)$ is the (a.s. unique) integer $j \leq N$ such that $X_{n+1}^N(i) - aX_n^N(j) \in \mathcal{P}_{n+1,j}$.

By standard properties of Poisson point processes, the (N, a)-exponential model is well defined for all $n \in \mathbb{N}$ and the law of $(X_{n+1}^N(k), k \leq N)$ is the same as the law of the N largest points in a Poisson point process centered at

$$X_n^N(\mathrm{eq}) := \log\left(\sum_{j=1}^N e^{aX_n^N(j)}\right). \tag{2.1}$$

Therefore, one may think of $X_n^N(\mathrm{eq})$ as the "equivalent" position of the front, that is, a fictitious particle that generates the entire front in generation $n+1$ as a Poisson point process around its position. In the next lemma we prove the above claim and characterize the (conditional) law of $A_n^N(\cdot)$.

Lemma 2.1. *The point processes* $\left(\sum_{j=1}^N \delta_{X_{n+1}^N(j)-X_n^N(\mathrm{eq})}, n \in \mathbb{N}\right)$ *are i.i.d. with common distribution given by the N rightmost points in a Poisson point process with intensity measure* $\mathrm{e}^{-x}\mathrm{d}x$. *Moreover, let* $\mathcal{H} := \sigma\left(X_n^N(j), j \le N, n \in \mathbb{N}\right)$ *and* $k_1, \ldots, k_N \in \mathbb{Z}_+^N$ *such that* $k_1 + \ldots + k_N = N$, *then*

$$\mathbf{P}\left(A_{n+1}^N(j) = k_j;\, 1 \le j \le N \middle| \mathcal{H}\right) = \prod_{j=1}^N \theta_n(k_j), \quad \text{where } \theta_n(k) := \frac{\mathrm{e}^{aX_n^N(k)}}{\sum_{i=1}^N \mathrm{e}^{aX_n^N(i)}}. \tag{2.2}$$

Proof. This result is obtained with a reasoning similar to [14, Proposition 1.3 and Lemma 1.6]. Therefore we only outline the main parts of the proof and omit some technical details.

First, using the superposition property of Poisson point processes, we obtain that

$$\sum_{j=1}^N \sum_{p \in \mathcal{P}_{n+1,j}} \delta_{aX_n^N(j)+p} \overset{(d)}{=} \sum_{p \in \mathcal{P}} \delta_{X_n^N(\mathrm{eq})+p},$$

where $\mathcal{P}$ is an independent Poisson point process with intensity measure $\mathrm{e}^{-x}\mathrm{d}x$.

Next, we note that for all $i, j, n \in \mathbb{N}$

$$\begin{aligned}\mathbf{P}\left(A_{n+1}^N(j) = i \middle| \mathcal{H}\right) &= \mathbf{P}\left(X_{n+1}^N(j) - aX_n^N(i) \in \mathcal{P}_{n+1,i} \middle| \mathcal{H}\right)\\ &= \frac{\mathrm{e}^{-(X_{n+1}^N(j)-aX_n^N(i))}}{\sum_{k=1}^N \mathrm{e}^{-(X_{n+1}^N(j)-aX_n^N(k))}} = \frac{\mathrm{e}^{aX_n^N(i)}}{\sum_{k=1}^N \mathrm{e}^{aX_n^N(k)}}.\end{aligned}$$

Moreover, the $A_{n+1}^N(j)$'s are (conditionally) independent, which concludes the proof. □

By Lemma 2.1, the following recursion equation

$$X_{n+1}^N(\mathrm{eq}) - aX_n^N(\mathrm{eq}) = \log\left(\sum_{j=1}^N \mathrm{e}^{a(X_{n+1}^N(j)-X_n^N(\mathrm{eq}))}\right) \overset{(d)}{=} \log\left(\sum_{j=1}^N \mathrm{e}^{ap(j)}\right) \tag{2.3}$$

holds in distribution, where $\left(p(j), j \in \mathbb{N}\right)$ are the ranked atoms of a Poisson point process with intensity measure $\mathrm{e}^{-x}\mathrm{d}x$. This allows us to construct a bi-infinite (stationary) version of $(X_n^N, A_n^N, n \ge 0)$, that we now introduce. Let $(\xi_j, j \in \mathbb{N})$ denote an i.i.d. sequence of random variables with the same law as $\xi := X_1(\mathrm{eq}) - aX_0(\mathrm{eq})$, then

$$X_n^N(\mathrm{eq}) \overset{(d)}{=} \sum_{j=0}^{n-1} a^j \xi_{n-j} + a^n X_0(\mathrm{eq}). \tag{2.4}$$

Since $\mathbf{E}(\xi_1) < \infty$, one can easily check that $X_n^N(\mathrm{eq})$ converges in distribution to $Y_\infty := \sum_{n\ge 0} a^n \xi_n$ as $n \to \infty$, which satisfies the distributional equation $Y_\infty \overset{(d)}{=} aY_\infty + \xi$.

Hence, we can construct a probability space with i.i.d. Poisson point processes $(\mathcal{P}_n, n \in \mathbb{Z})$ with intensity $\mathrm{e}^{-x}\mathrm{d}x$, and a process $(Y_n, n \in \mathbb{Z})$, such that Y_n has same law as Y_∞ for all $n \in \mathbb{Z}$ and

$$Y_{n+1} = aY_n + \log\left(\sum_{j=1}^N \mathrm{e}^{ap_{n+1}(j)}\right) \quad \text{a.s.} \quad \forall n \in \mathbb{Z},$$

where $(p_n(j), j \in \mathbb{N})$ are the atoms of $\mathcal{P}_n$ ranked in decreasing order. We then set for $n \in \mathbb{Z}$ and $j \le N$,

$$\overline{X}_n^N(j) = aY_{n-1} + p_n(j),$$

and conditionally on $(\overline{X}_n^N, n \in \mathbb{Z})$ we construct $((\overline{A}_n^N(j), j \leq N), n \in \mathbb{N})$ as independent random vectors whose (conditional on $\overline{X}_n^N$) probability satisfy (2.2).

The process $(\overline{X}_n^N, \overline{A}_n^N, n \in \mathbb{Z})$ is a stationary version of the (N, a)-exponential model. It is straightforward to check that it satisfies the same transition probabilities as the original process. Thanks to this construction, we can define without ambiguity the genealogy of the (N, a)-exponential model for all $n \in \mathbb{Z}$. We rely on this construction to prove Theorem 1.1.

We first observe that in the bi-infinite version $(\overline{X}^N, \overline{A}^N)$ of the (N, a)-exponential model, the family $(\overline{A}_n^N, n \in \mathbb{Z})$ is i.i.d. We can then use the $\overline{A}^N$'s to reconstruct the ancestral partition process of the process as follows: for every $n \in \mathbb{N}$, we say that i and j belong to the same block of Π_n^N if

$$\overline{A}_{-n}^N(\overline{A}_{-(n-1)}^N(\dots \overline{A}_{-1}^N(i))) = \overline{A}_{-n}^N(\overline{A}_{-(n-1)}^N(\dots \overline{A}_{-1}^N(j))).$$

This allows us to express the law of Π^N in terms of population dynamics with independent generations. Precisely, let

$$\theta_n^N(j) = \frac{\mathrm{e}^{a\overline{X}_n^N(j)}}{\sum_{k=1}^N \mathrm{e}^{a\overline{X}_n^N(k)}} = \frac{\mathrm{e}^{a(\overline{X}_n^N(j)-aY_{n-1})}}{\sum_{k=1}^N \mathrm{e}^{a(\overline{X}_n^N(k)-aY_{n-1})}} = \frac{\mathrm{e}^{ap_{n-1}(j)}}{\sum_{k=1}^N \mathrm{e}^{ap_{n-1}(k)}}.$$

Then conditionally on $(\theta_n^N(j), n \in \mathbb{Z}, j \leq N)$, each individual at generation $-n \leq 0$ chooses its parent at generation $-n-1$ independently at random, selecting the parent j with probability $\theta_{-n-1}^N(j)$. This process is often called a Cannings model, defined by a multinomial distribution with N independent trials and probabilities outcomes $(\theta_{-n}^N(j), j \leq N)$ (see [8, Section 2.2.3] for a definition of such processes).

Thanks to this observation, we now prove Theorem 1.1.

Proof of Theorem 1.1. Thinking of Π^N as the ancestral partition process of a Cannings model, Lemma 2.1 together with [14, Proposition 4.2] yields

$$\{\theta_1^N(i), i \leq N\} := \left\{ \frac{\mathrm{e}^{a\overline{X}_{-1}^N(i)}}{\sum_{k=1}^N \mathrm{e}^{a\overline{X}_{-1}^N(k)}}, i \leq N \right\} \overset{(d)}{=} \left\{ \frac{\mathrm{e}^{aE_i}}{\sum_{k=1}^N \mathrm{e}^{aE_k}}, i \leq N \right\},$$

where $(E_j, j \in \mathbb{N})$ i.i.d. exponential random variables with mean 1. Moreover, for any $y \geq 1$, we have $\mathbf{P}(\mathrm{e}^{aE_j} \geq y) = y^{-1/a}$. Therefore, applying [13, Theorem 1.2], we conclude the proof of Theorem 1.1. □

We now focus on the dynamical behavior of the cloud of particles in the (N, a)-exponential model and prove Proposition 1.2. In this case, we are interested in the behavior of the process as time goes to infinity. We shall therefore consider the original particles system X^N, instead of its bi-infinite version $\overline{X}^N$.

Proof of Proposition 1.2. Using Lemma 2.1, we observe that

$$X_{n+1}^N(1) - X_n^N(\mathrm{eq}) \overset{(d)}{=} p(1) \quad \text{and} \quad X_{n+1}^N(N) - X_n^N(\mathrm{eq}) \overset{(d)}{=} p(N), \tag{2.5}$$

where $p(1) > p(2) > \dots$ are the ranked atoms in a Poisson point process with intensity $\mathrm{e}^{-x}\mathrm{d}x$. At the same time, the elements in the sequence $(\mathrm{e}^{-p(j)}, j \geq 1)$ are distributed according to the (ranked) atoms in a homogeneous Poisson point process in $[0, \infty)$ and hence $\mathrm{e}^{-p(j)}$ is Gamma(j,1) distributed. In particular, the above yields

$$\mathbf{E}\left(p(j)\right) = \mathbf{E}\left(-\log(\mathrm{e}^{-p(j)})\right) = \frac{1}{\Gamma(j)} \int_0^\infty (-\log t) t^{j-1} \mathrm{e}^{-t} dt = \frac{\Gamma'(j)}{\Gamma(j)} =: \psi(j),$$

where $\psi(N) := \Gamma'(N)/\Gamma(N)$ is the digamma function, which satisfies $\psi(N) = \log N + \mathcal{O}(N^{-1})$ as $N \to \infty$. Using the above with $j = 1$ and $j = N$ in (2.5), we get

$$\mathbf{E}(X_{n+1}^N(1)) = \mathbf{E}(X_n^N(\mathrm{eq})) + \gamma \quad \text{and} \quad \mathbf{E}(X_{n+1}^N(N)) = \mathbf{E}(X_n^N(\mathrm{eq})) - \log(N) + \mathcal{O}(N^{-1}). \tag{2.6}$$

It is therefore enough to compute the asymptotic behavior of $\mathbf{E}(X_n^N(\mathrm{eq}))$ as $n \to \infty$ then $N \to \infty$ to conclude the proof.

For what follows in the proof, we shall assume that $a < 1$ and $\mathbf{E}(X_0^N(\mathrm{eq})) < \infty$. Thus, taking the expected value in (2.4), one gets

$$\mathbf{E}(X_n^N(\mathrm{eq})) = a^n\, \mathbf{E}(X_0^N(\mathrm{eq})) + \frac{1-a^n}{1-a}\, \mathbf{E}(\xi_1), \quad \text{yielding} \lim_{n\to\infty} \mathbf{E}(X_n^N(\mathrm{eq})) = \frac{1}{1-a}\, \mathbf{E}(\xi_1). \tag{2.7}$$

It remains therefore to compute $\mathbf{E}(\xi_1)$. For this purpose, we will first compute the Laplace transform $L(\lambda)$ of ξ_1, then recover its mean via $\mathbf{E}(\xi_1) = -(\log L)'(0)$.

By [14, Proposition 4.2], we remark that

$$\mathrm{e}^{\xi_1} = \sum_{j=1}^N \mathrm{e}^{ap(j)} \overset{(d)}{=} \mathrm{e}^{aZ_n} \sum_{j=1}^N \mathrm{e}^{aE_j},$$

where $(E_j, j \geq 1)$ are i.i.d. exponential random variables with parameter 1 and Z_N is an independent random variable whose distribution has density $(N!)^{-1}\mathrm{e}^{-(N+1)x-\mathrm{e}^{-x}}$ with respect to the Lebesgue measure. Therefore, we have

$$L(\lambda) := \mathbf{E}\left(\mathrm{e}^{-\lambda\xi_1}\right) = \mathbf{E}\left(\left(\sum_{j=1}^N \mathrm{e}^{aE_j}\right)^{-\lambda}\right) \mathbf{E}\left(\mathrm{e}^{-\lambda a Z_N}\right).$$

By direct computations, we obtain $\mathbf{E}\left(\mathrm{e}^{-\lambda a Z_N}\right) = \Gamma(N+1+a\lambda)/\Gamma(N+1)$ and

$$\mathbf{E}\left(\left(\sum_{j=1}^N \mathrm{e}^{aE_j}\right)^{-\lambda}\right) = \frac{1}{\Gamma(\lambda)} \int_0^\infty t^{\lambda-1}\, \mathbf{E}\left(\mathrm{e}^{-t\sum_{j=1}^N \mathrm{e}^{aE_j}}\right) \mathrm{d}t = \frac{1}{\Gamma(\lambda)} \int_0^\infty t^{\lambda-1} I(t)^N \mathrm{d}t, \tag{2.8}$$

where $I(t)$ is the function defined by

$$I(t) := \mathbf{E}\left(\mathrm{e}^{-t\mathrm{e}^{aE_1}}\right) = \int_0^\infty \mathrm{e}^{-x}\mathrm{e}^{-t\mathrm{e}^{ax}} \mathrm{d}x = \frac{t^{1/a}}{a} \int_t^\infty u^{-(1+1/a)}\mathrm{e}^{-u}\mathrm{d}u.$$

Making the change of variable $t = x/N$ in the right-hand side of (2.8) one obtains

$$\mathbf{E}\left(\left(\sum_{j=1}^N \mathrm{e}^{aE_j}\right)^{-\lambda}\right) = \frac{1}{N^\lambda} \int_0^\infty I(x/N)^N \frac{x^{\lambda-1}\mathrm{d}x}{\Gamma(\lambda)} =: \frac{J_N(\lambda)}{N^\lambda},$$

where $J_N(\lambda)$ is a $\mathcal{C}^\infty$ function such that $J_N(0) = 1$. Collecting all pieces, we obtain that $L(\lambda) = J_N(\lambda)\frac{\Gamma(N+a\lambda+1)}{N^\lambda\Gamma(N+1)}$, which yields

$$\mathbf{E}\left(\xi_1\right) = -\left(\log L\right)'(0) = \log N - a\psi(N+1) - J_N'(0), \tag{2.9}$$

where we recall that ψ is the digamma function and $(\log J_N)'(0) = \frac{J_N'(0)}{J_N(0)} = J_N'(0)$.

To compute $J_N'(0)$, we will take the $\lambda \to 0$ limit of

$$\frac{J_N(\lambda)-1}{\lambda} = \frac{1}{\lambda\Gamma(\lambda)} \int_0^\infty x^{\lambda-1}(I(x/N)^N - \mathrm{e}^{-x})\mathrm{d}x = \frac{1}{\Gamma(\lambda+1)} \int_0^\infty x^{\lambda-1}(I(x/N)^N - \mathrm{e}^{-x})\mathrm{d}x. \tag{2.10}$$

By definition, $e^t I(t) \in [0,1]$ for all $t \in \mathbb{R}_+$ which implies that

$$\mathrm{e}^x \left|x^{\lambda-1}(I(x/N)^N - \mathrm{e}^{-x})\right| \leq x^{\lambda-1} \left|\left(\mathrm{e}^{x/N} I(x/N)\right)^N - 1\right| \leq 1, \tag{2.11}$$

for all $x \geq 1$ and $\lambda \in (0,1)$. On the other hand, we observe that for all $t \in (0,1]$, we have

$$\begin{aligned}
I(t) &= \frac{t^{1/a}}{a}\left(\int_t^\infty u^{-(1+1/a)}(1-u)\mathrm{d}u + \int_t^\infty u^{-(1+1/a)}(\mathrm{e}^{-u}-1+u)\mathrm{d}u\right)\\
&= \frac{t^{1/a}}{a}\left(at^{-1/a} + \frac{t^{1-1/a}}{1-1/a} + \int_t^\infty u^{-(1+1/a)}(\mathrm{e}^{-u}-1+u)\mathrm{d}u\right)\\
&= 1 - \frac{t}{1-a} + \mathcal{O}(t^b) \quad \text{as } t \to 0,
\end{aligned}$$

for some $b > 1$. Indeed, we have $t^{1/a}\int_1^\infty u^{-(1+1/a)}(\mathrm{e}^{-u}-1+u)\mathrm{d}u = \mathcal{O}(t^{1/a})$ as $t \to 0$, and relying on the fact that $(\mathrm{e}^{-u}-1+u) = \mathcal{O}(u^2)$ for all $u \leq 1$ one gets

$$t^{1/a}\int_t^1 u^{-(1+1/a)}(\mathrm{e}^{-u}-1+u)\mathrm{d}u = \begin{cases} \mathcal{O}(t^{1/a}) & \text{if } a > 1/2;\\ \mathcal{O}(t^{1/a})\log t & \text{if } a = 1/2;\\ \mathcal{O}(t^2) & \text{if } a < 1/2. \end{cases}$$

As a result, we obtain $|I(x/N)^N - \mathrm{e}^{-x}| \leq \frac{a}{a-1}x + C\left(\frac{x^b}{N^{b-1}} + x^2\right)$ for all $x \leq 1$, where $C > 0$ is a constant not depending on N. Thus, one can find a (possibly larger) constant $\widetilde{C} > 0$ such that

$$\left|x^{\lambda-1}(I(x/N)^N - \mathrm{e}^{-x})\right| \leq \widetilde{C}, \qquad \text{for all } x < 1. \tag{2.12}$$

Thanks to (2.11) and (2.12), we can apply dominated convergence in (2.10), to obtain

$$J_N'(0) = \lim_{\lambda\to 0}\frac{J_N(\lambda)-1}{\lambda} = \int_0^\infty x^{-1}(I(x/N)^N - \mathrm{e}^{-x})\mathrm{d}x.$$

Now, we plug the above in (2.9) and use the fact that $\lim_{N\to\infty}\psi(N+1) - \log N = 0$ to get

$$\mathbf{E}(\xi_1) = (1-a)\log N + \int_0^\infty x^{-1}(\mathrm{e}^{-x} - I(x/N)^N)\mathrm{d}x + o(1) \quad \text{as } N \to \infty. \tag{2.13}$$

Finally, we notice that $I(x/N)^N$ tends to $\mathrm{e}^{-\frac{x}{1-a}}$ as $N \to \infty$. Therefore, we can rely again on (2.11) and (2.12), to apply dominated convergence thereby obtaining

$$\begin{aligned}
\lim_{N\to\infty}\int_0^\infty x^{-1}(\mathrm{e}^{-x} - I(x/N)^N)\mathrm{d}x &= \int_0^\infty x^{-1}(\mathrm{e}^{-x} - \mathrm{e}^{-\frac{x}{1-a}})\mathrm{d}x\\
&= \int_0^\infty\int_1^{\frac{1}{1-a}} \mathrm{e}^{-ux}\mathrm{d}u\mathrm{d}x = \int_1^{\frac{1}{1-a}}\frac{\mathrm{d}u}{u} = -\log(1-a),
\end{aligned}$$

which, in view of (2.6), (2.7) and (2.13), concludes the proof. □

3 Branching Ornstein–Uhlenbeck process with selection

In this section, we draw a parallel between branching Ornstein–Uhlenbeck processes with selection and the (N,a)-exponential model. We then rely on Theorem 1.1 to conjecture the asymptotic behavior of the genealogy of the branching Ornstein–Uhlenbeck process with selection [1]. We first recall that an Ornstein–Uhlenbeck process is a continuous-time diffusion that solves the stochastic differential equation:

$$\mathrm{d}X_t = -\mu X_t\mathrm{d}t + \sigma\mathrm{d}W_t, \tag{3.1}$$

where $\mu \geq 0$ is the *pulling strength* of the process, $\sigma > 0$ is the diffusion coefficient and W is a standard Brownian motion. Recall that an Ornstein–Uhlenbeck process X with pulling strength μ and starting position x can be constructed with a Wiener process W through the following transformation:

$$X_t = \mathrm{e}^{-\mu t}\left(x + W_{\frac{\mathrm{e}^{2\mu t}-1}{2\mu}}\right), \quad t \geq 0. \tag{3.2}$$

The branching Ornstein–Uhlenbeck process with parameters β, μ, σ is a continuous-time branching process, in which particles move independently according to Ornstein–Uhlenbeck processes with pulling strength μ and diffusion σ, and branch at rate β. More precisely, it starts at time 0 with a unique particle at 0, which evolves according to (3.1). After an independent exponential random time of parameter β, it splits into two children, which then start evolving independently in the same way. Up to a space-time linear transform, we may assume without loss of generality that $\beta = \sigma = 1$. To the best of our knowledge, there are not many rigorous results about this branching process. Adamczak and Miłoś [1, 2] study the behavior of particles in the bulk and show that a CLT type result holds when the pulling strength is strong, whereas a different asymptotic holds in the weak pulling strength case. Nevertheless, the behavior of extreme particles and their genealogy is still an open question. We also mention the work of Shi [28], where he introduces branching Ornstein–Uhlenbeck type processes with potentially infinite branching rate.

In evolutionary biology, Ornstein–Uhlenbeck processes may be used to model genetic drift [25]. Thus, branching Ornstein–Uhlenbeck processes are natural candidates to model the evolution of fitnesses in a population. In order to introduce natural selection, we modify the above model in the following way. Let $N \in \mathbb{N}$ denote the total size of the population. If at a given time a new particle is born which would bring the total population size to $N + 1$, then the leftmost particle is immediately killed. We call this process the (N, μ)-*branching Ornstein–Uhlenbeck process*, or (N, μ)-BOU for short.

We believe there exists a close connection between the $(N, \gamma(\log N)^{-2})$-BOU and the (N, a)-exponential model. In both processes, particles are subjected to a pulling strength that depends linearly on their position. Such a connection extends the one described in [11, Section IV] when there is no attractive force ($a = 1$), which corresponds to the N-branching Brownian motion case ($\gamma = 0$). We now explain this connection in more detail. For what follows we set $\mu_N = \gamma(\log N)^{-2}$ for a fixed $\gamma > 0$.

We first study the behavior of a (N, μ_N)-BOU on a time scale of order $\log N$. It corresponds to the typical time in which a particle would have N descendants in the process without selection. In view of (3.2), X_t does not feel the effects of the attractive force on this time scale. That is, its evolution resembles the one of a Brownian motion. Using an argument similar to [5, Proposition 1], we deduce that the size of the cloud of particles in the (N, μ_N)-BOU should typically be of order $\log N$. As a result, the coupling technique developed in [20, Section 4] should allow us to compare the (N, μ_N)-BOU with an Ornstein–Uhlenbeck process in which particles going below a certain barrier are killed. The barrier is chosen such that the number of particles lying above it is typically of order N.

We now study the process on the time scale $(\log N)^2$. On this time scale, particles feel effects of the attractive force. By (3.2), their final position is multiplied by a factor, when compared to the underlying branching Brownian motion. Hence, the branching Ornstein–Uhlenbeck with a killing barrier should behave as a branching Brownian motion with the same killing barrier, with final positions multiplied by a fixed constant.

Next, we recall that the *extremal process* of a branching Brownian motion (the point process describing the position of the particles close to the maximal displacement) converges toward a decorated Poisson point process [3, 4]. It is well known that this limiting point process can be decomposed according to the genealogy of the particles: each decoration corresponds to a family of closely related particles that has followed the same trajectory. This trajectory asymptotically behaves like a Brownian excursion. Now, if we consider the process killed by a barrier at depth of order $\log N$, only a proportion of such particles will survive at time $(\log N)^2$. Asymptotically, those correspond to Brownian excursions that stay below a certain barrier.

Summing up, we expect that at time $(\log N)^2$ each particle in a (N, μ_N)-BOU gives birth to descendants, whose positions are given by independent decorated Poisson point processes, centered around c_γ times their starting position. Here, $c_\gamma \in (0, 1]$ is a constant depending on γ. Therefore, $(\log N)^2$ units of time in the (N, μ_N)-BOU would correspond to one time step of the (N, c_γ)-exponential model. This was already the case in [11], where $(\log N)$ units of time of the $(N, 1)$-exponential model were in correspondence with $(\log N)^3$ units of times for the N-branching random walk. This leads to the following conjecture.

Conjecture 3.1. *For all $\gamma > 0$, there exists $d_\gamma \in [0, 1]$ such that $\left(\Pi^N_{\lfloor N^{d_\gamma} \ell(N) t \rfloor}, t \geq 0\right)$ converges* *in law toward a Beta$(1-d_\gamma, 1+d_\gamma)$-coalescent as $N \to \infty$, where ℓ is a slowly varying function.*

Roughly speaking, the above conjecture states that a branching Ornstein–Uhlenbeck process with pulling strength $\gamma(\log N)^{-2}$ and selection of the N rightmost individuals can be associated with the $(N, (d_\gamma + 1)^{-1})$-exponential model.

We ran a few simulations that reinforce the above heuristics. We considered discrete-time/space branching–selection particles systems which mimic branching Ornstein–Uhlenbeck processes with selection. The results are displayed in Figure 1. We observe that when the pulling strength has the order $(\log N)^{-2}$, then the average coalescent time of two individuals chosen uniformly at random seems to grow polynomially with N. Heuristics suggest that the function ℓ in the above conjecture should be $\ell(N) = c(\log N)^2$, but the (arguably limited) simulations are more consistent with a constant function $\ell \equiv c$.

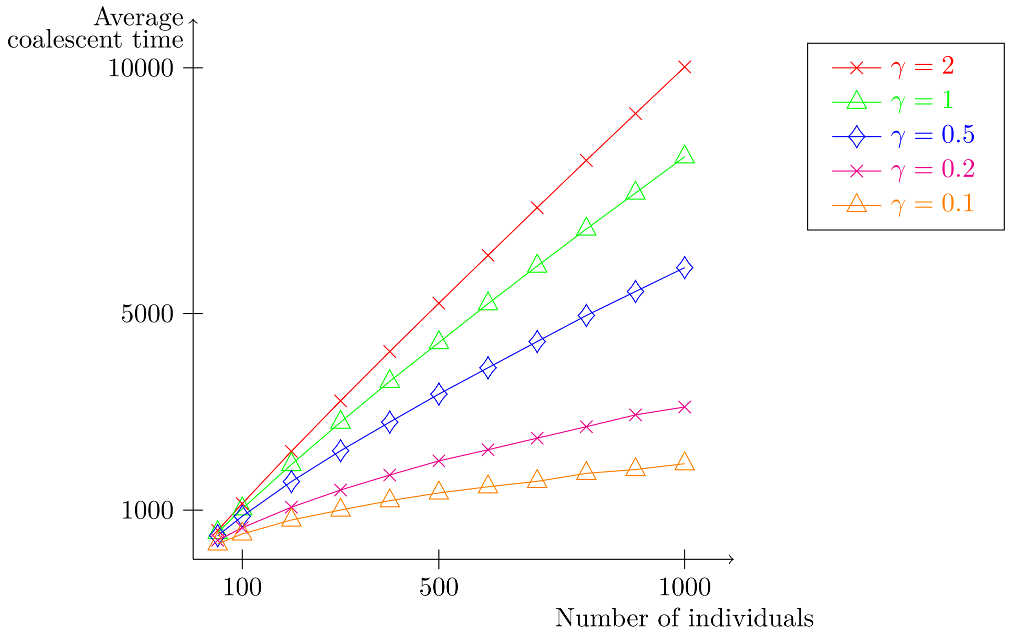

Figure 1: Average age of the most recent common ancestor of two individuals sampled at random.

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