The tree length of an evolving coalescent
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Abstract

A well-established model for the genealogy of a large population in equilibrium is Kingman’s coalescent. For the population together with its genealogy evolving in time, this gives rise to a time-stationary tree-valued process. We study the sum of the branch lengths, briefly denoted as tree length, and prove that the (suitably compensated) sequence of tree length processes converges, as the population size tends to infinity, to a limit process with càdlàg paths, infinite infinitesimal variance, and a Gumbel distribution as its equilibrium.

1 Introduction

Kingman’s coalescent \([20, 21]\) is a widely used model for the single-locus genealogy in a population, see \([30]\) and references therein. It arises in a suitable rescaling of time under the assumptions of a neutral evolution and an exchangeable reproduction dynamics with short-tailed offspring distribution. An intuitive way to think of Kingman’s coalescent is to imagine a random tree with infinitely many leaves at time \(t\), where backwards in time any two lineages independently coalesce at rate 1. Taking \(N\) instead of infinitely many leaves gives Kingman’s \(N\)-coalescent. The latter figures as the genealogy of an \(N\)-sample taken from a large population, and also as the genealogy of the total population in a standard Moran model with population size \(N\).

Two functionals of coalescent trees are of particular interest: the distance from the root to the leaves, or depth, and the sum of branch lengths, or tree length. It is well known that the expected depth of Kingman’s \(N\)-coalescent equals \(2(1 - \frac{1}{N})\), whereas its expected tree length is \(\sim 2 \log N\) as \(N \to \infty\). More can be said: when compensated by \(2 \log N\), half the tree length of Kingman’s \(N\)-coalescent converges in law to a Gumbel distributed random variable (having the cumulative distribution function \(x \mapsto e^{-e^{-x}}\)). This result can be read off from \([28\text{ p. 153, first equation}]\); see also \([32, 29, 12\text{ and }30]\).

With individual offspring distributions that are not short-tailed, coalescents different from Kingman’s appear as the genealogies of large populations. In the so-called \(\Lambda\)-coalescents \([24]\), more than two lines can coalesce, giving rise to multiple mergers, and asymptotic tree length distributions arise that are different from Gumbel distributions. For special classes including those of Beta-coalescents, results on the asymptotic tree length were obtained in \([22, 12, 3\text{ and }8]\).

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With a population evolving in time, its genealogical relationships evolve as well. Their evolution is described by a *tree-valued process* [19] similarly as the change of allele frequencies is captured by measure-valued diffusions [7, 14]. Jumps of the tree depth correspond to the loss of one of the currently two oldest families from the population, and hence to the establishment of a new most recent common ancestor (MRCA) of the population. The resulting tree depth process in the case of Kingman’s coalescent was analyzed in [23] and [9].

In the present paper we focus on the (compensated) tree length in Kingman’s coalescent and describe its evolution in an infinite population. Our main result is that this process has càdlàg paths and infinite infinitesimal variance (Theorem 1). As already stated, the one-dimensional projections of this process are Gumbel distributed.

We construct the process of compensated tree length, denoted by $\mathcal{L}$, as a limit using tools from weak convergence of processes. In addition, we also provide a strong convergence result, i.e. a version of Theorem 1 in terms of convergence towards $\mathcal{L}$ in probability. For this, we use the lookdown process introduced in [11], which provides genealogies of Moran models of any population size on one and the same probability space. Our Proposition 3.2 shows that on this space, the compensated Kingman tree lengths lead to a càdlàg path-valued limit in probability. Hence, the process $\mathcal{L}$ can be defined directly in terms of a sequence Moran models – or in terms of the lookdown graph – and as such is a natural object to study. Some challenging questions remain, e.g. a) Is the limit robust in the sense that $\mathcal{L}$ describes also the limiting tree length process for (a large class of) Cannings models with short-tailed offspring distributions? b) Is there an intrinsic characterization of $\mathcal{L}$ in terms of a stochastic dynamics? In particular, is $\mathcal{L}$ a semimartingale?

The length of a coalescent is of relevance in empirical population genetics [30]. In the infinite sites model the number of mutations seen in a population of size $N$ at time $t$ is Poisson distributed with parameter proportional to tree length and to the mutation rate. The process of tree lengths has also attracted interest in the study of diversity in real populations [25, Fig. 2c]. There, sudden losses of diversity in a population are related to jumps of the tree length process. Such jumps occur at any resampling event and correspond to the length of an external branch breaking off the tree. The asymptotics of external branch lengths are investigated in detail in [6], see also Remark 2.2 and Section 4.2.

Our paper is organized as follows. After specifying the model we present our results on weak (Section 2) and strong (Section 3) convergence of tree lengths and tree length processes. In Section 4 we provide some auxiliary results on Kingman’s coalescent for fixed times and on Moran models. Section 5 completes the proof of Theorem 1 and Section 6 contains the proofs of the strong convergence results, Propositions 3.1 and 3.2.

## 2 Convergence of tree length distributions

Consider a *Moran model* with constant population size $N$, started at time $-\infty$. Each (unordered) pair of individuals resamples at rate 1; in any such resampling event, one of the two individuals reproduces and the other one dies. See Figure 1(A) for an illustration.

At any time $t \in \mathbb{R}$, the common ancestry of all individuals in the population is described by a random genealogical tree, which is Kingman’s N-coalescent [20]. With time $t$ varying, we obtain a tree-valued process denoted by $\mathcal{T}^N = (\mathcal{T}^N_t)_{t \in \mathbb{R}}$, whose random path we can read off from the graphical representation, see Figure 1(B) and (C).

Let $\ell$ be the map that sends a (finite) tree to its length, i.e. to the sum of the lengths of all branches. Back from a fixed time $t$, each (unordered) pair of ancestral lines coalesces at rate 1, therefore the length of the time interval during which the genealogical tree $\mathcal{T}^N_t$ has $k$ lines is exponentially distributed with the number of pairs, $\binom{k}{2}$, as parameter. Consequently, the

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1 We use roman upper case letters $K, N, \ldots$ for real (non-random) numbers in order to distinguish them from random variables denoted by $K, N, \ldots$.
expectation and the variance of the tree length are

\[ \mathbb{E}[\tilde{\ell}(\mathcal{T}_t^N)] = \sum_{i=2}^{N} \frac{1}{(i-1)}, \quad \mathbb{V}[\tilde{\ell}(\mathcal{T}_t^N)] = \sum_{i=2}^{N} \frac{1}{i^2} \]

We are going to study the compensated tree length process

\[ \mathcal{L}_t := (\tilde{\ell}(\mathcal{T}_t^N) - 2\log N)_{t \in \mathbb{R}} \tag{2.1} \]

in the limit \( N \to \infty \).

One realization of the process \( \mathcal{L}_{100} \) can be seen in Figure 2. Here, several large jumps of the tree length can be observed. Particularly large jumps in the tree length arise when the MRCA of the total population changes.

### 2.1 Tree lengths at fixed times

We recall a basic fact about the asymptotics of the law of \( \mathcal{L}_t^N \) as \( N \to \infty \).

**Proposition 2.1** (Tree lengths for fixed times). For \( t \in \mathbb{R} \), the law of \( \frac{1}{2} \mathcal{L}_t^N \) converges as \( N \to \infty \) weakly to the standard Gumbel distribution with cumulative distribution function \( x \mapsto e^{-e^{-x}} \).

**Proof.** We briefly repeat the argument from [32, p. 255]. Let \( X_2, X_3, \ldots \) be independent random variables such that \( X_j \) has an exponential distribution with rate \( \frac{1}{2} \). In addition, let \( Y_1, Y_2, \ldots \) be independent such that \( Y_j \) has an exponential distribution with rate \( j \) and \( Z_1, Z_2, \ldots \) be independent exponential, each with parameter 1. Then

\[ \frac{1}{2} \tilde{\ell}(\mathcal{T}_t^N) \overset{d}{=} \frac{1}{2} \sum_{j=2}^{N} j X_j \overset{d}{=} \sum_{j=1}^{N-1} Y_j \overset{d}{=} \max_{1 \leq j \leq N-1} Z_j, \]

which when shifted by \( \log N \) has the asserted limit in distribution as \( N \to \infty \). \( \square \)
2.2 The evolution of tree lengths

Next, we come to our main result on the limit of the compensated tree length processes \( \mathcal{L}^N \). We denote by \( \mathbb{D} \) the space of real-valued càdlàg functions on the time axis \((-\infty, \infty)\), equipped with the Skorokhod topology.

**Theorem 1.** There is a process \( \mathcal{L} = (\mathcal{L}_t)_{t \in \mathbb{R}} \) with sample paths in \( \mathbb{D} \) such that
\[
\mathcal{L}^N \Rightarrow \mathcal{L} \quad \text{as} \quad N \to \infty.
\]
The distribution of \( \frac{1}{2} \mathcal{L}_t \) is Gumbel for all \( t \in \mathbb{R} \). The process \( \mathcal{L} \) has infinite infinitesimal variance, with
\[
\frac{1}{t|\log t|} \mathbb{E}[(\mathcal{L}_t - \mathcal{L}_0)^2] \xrightarrow{t \to 0} 4.
\]

**Remark 2.2** (Connection to external branch lengths). An important characteristics of the tree length process is its jump size statistics. For this, let \( F \) be a randomly chosen jump time for the equilibrium process \( \mathcal{L}^N \). By the independence properties of the Poisson processes which generate \( \mathcal{S}_N \), we have \( \mathcal{S}_F^N \overset{d}{=} \mathcal{S}_0^N \) and consequently \( \mathcal{L}_F^N \overset{d}{=} \mathcal{L}_0^N \). Moreover, the jump removes a randomly chosen external branch from \( \mathcal{S}_F^N \). Since the N-coalescent, restricted to \( N - 1 \) randomly chosen individuals, is in distribution identical to the \((N - 1)\)-coalescent, it follows that \( \mathcal{S}_F^N \overset{d}{=} \mathcal{S}_0^{N-1} \) and consequently \( \mathcal{L}_F^N \overset{d}{=} \mathcal{L}_0^{N-1} + 2 \log \left(1 - \frac{1}{N}\right)\). Moreover, the jump size, given by \( \mathcal{L}_F^N - \mathcal{L}_F^N \), is in distribution identical to a randomly chosen external branch of a N-coalescent in equilibrium. Properties of the external branch length distribution are recalled in Section 4.2 and were studied in more detail in [6]. For our setup, these results imply
\[
N(\mathcal{L}_F^N - \mathcal{L}_F^N) \xrightarrow{N \to \infty} J
\]
for some random variable \( J \), taking values in the positive reals with expectation 2 and density \( x \mapsto 8/(2 + x)^3 \). This power law with exponent 3 was already guessed in [25] based on simulations.
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Figure 3: Schematic picture of tree change between two times 0 and t for a population of size N. Tree topology is ignored in the figure and only the number of ancestral lines is given. The population at time t has \( S_t^N \) ancestors at time 0. The genealogical tree at time t overlaps with the tree at time 0. The subset of the time-\( t \) tree which does not belong to the time-0 tree is \( \tilde{A}_{0,t}^N \). Reversely, the subset of the time-0 tree which is lost between time 0 and \( t \) is \( \tilde{B}_{0,t}^N \). The net difference in tree length is \( L_t^N - L_0^N \approx \tilde{A}_{0,t}^N - \tilde{B}_{0,t}^N \).

The random variable \( J \) has unbounded variance. For the asymptotics of this variance, [18] already showed (see also Proposition 4.2) that\(^2\)

\[
V[N(L_t^N - L_0^N)] \approx 8 \log N.
\]

Remark 2.3 (Heuristics on jump sizes). The fact that the approximate size of a randomly chosen jump is of the order \( 2/N \) can also be seen from the dynamics of \( L^N \). In one time unit, tree length is gained by growth of the tree at constant speed \( N \). Moreover, the process \( T^N \) makes approximately \( (N^2) \) jumps. Since \( L^N \) is in equilibrium, the tree growth and the jumps have to compensate each other. Therefore the expected size of a single jump must be \( 2/N - 1 \); compare also with Proposition 4.2.

In the light of (2.3), the fact that the limit process \( L \) has infinite infinitesimal variance would not be surprising if there were no dependencies between jump sizes: In a short time \( t \), the process \( L^N \) makes approximately \( (N^2) t \) downward jumps as \( N \to \infty \). If jumps would be independent, we would get from (2.3) that the variance of \( L_t^N - L_0^N \) is approximately \( 4t \log N \).

Remark 2.4 (Idea of the proof of Theorem 1). The crucial step in the proof, whose details are given in Section 5, is to establish tightness of the family \( L^N \). This uses auxiliary calculations on the evolution of Moran models (Section 4.6): it suffices to show that 'large' jumps in the tree length do not happen too often. To be more specific, we must show that during times \( (t-h,t) \) and \( (t,t+h) \) some moment of the smaller jump, \( L_t^N - L_{t-h}^N \) or \( L_t^N - L_{t+h}^N \), is bounded by \( Ch^f \) for some constant \( C \) and \( h > 1 \). Heuristically, such a statement is true since it can be shown that the times at which one of the \( f \) oldest families of the coalescent tree dies out build a Poisson process with rate \( \left( \frac{f}{2} \right) \), \( f = 2,3,\ldots \) (see Lemma 4.12). Dying out of one of the \( f \) oldest families implies larger jumps for smaller \( f \) and the proof of tightness requires bounds for \( f \) depending on

\(^2\)For sequences \((a_N)_{N=1,2,\ldots}\) and \((b_N)_{N=1,2,\ldots}\) we write \( a_N \sim b_N \) iff \( a_N/b_N \to 1 \).
the time interval $h$, using that loss times for one of the $f$ oldest families in $(t - h, t]$ and $(t, t + h]$ are independent.

To obtain the form for the infinitesimal variance, it is essential to bound jumps between times 0 and $t$ of $\mathcal{L}^N$ for small $t$, uniformly in $N$; see Figure 3 for an illustration. Our proof is based on auxiliary calculations made in Sections 4.3 and 1.4. Note that changes in $\mathcal{L}^N$ come from two sources. First, between 0 and $t$, additional tree length is gained by tree growth ($\tilde{A}^N_{0,t}$ in the figure). The random variable $\tilde{A}^N_{0,t}$ equals the tree-length of a Kingman N-coalescent gained by time $t$ and for large $N$, we see from Lemma 4.10 that $\lim_{N \to \infty} \mathbb{V}[\tilde{A}^N_{0,t}] \overset{t \sim 0}{\sim} \frac{2}{3} t$. Second, a part of the tree at time $t$ breaks off ($\tilde{B}^N_{0,t}$ in the figure). This part is determined by the number $S^N_t$ of ancestors at time 0 of the population at time $t$. Additionally, note that the number of ancestors at time $t$ of the population of size $N$ converges in distribution to some random variable $S_t$ with $S_t \overset{t \sim 0}{\sim} \lfloor \frac{2}{3} t \rfloor$; see Lemma 4.6. Denoting by $B_K$ the difference of the compensated tree length of a coalescent with infinitely many lineages and the compensated length of the tree spanned by a subset of $K$ lineages, using some regularity, we can then show that $\mathbb{V}[B^N_{0,t}] \overset{N \to \infty}{\sim} \mathbb{V}[B^N_{0,t}] \overset{t \sim 0}{\sim} 4t \log^2 \frac{2}{3} t \overset{t \sim 0}{\sim} 4t \log t$ by Proposition 4.4. Combining the results for $\tilde{A}^N_{0,t}$ and $\tilde{B}^N_{0,t}$ we see that $\lim_{N \to \infty} \mathbb{V}[\mathcal{L}^N_t - \mathcal{L}^N_0] \overset{t \sim 0}{\sim} 4t \log t$.

**Remark 2.5** (Convergence of tree-valued processes). In [19], a topology $\tau$ on the space of trees is specified and it is proved that the sequence of tree-valued processes $\mathcal{T}^N$ converges in distribution to a tree-valued process $\mathcal{T}$, whose paths are a.s. continuous with respect to the topology $\tau$. One might be tempted to use convergence of $\mathcal{T}^N$ to $\mathcal{T}$ in order to show that $\mathcal{L}^N$ converges to some limit process $\mathcal{L}$ as well. Such an attempt would require that the function $\ell$ mapping finite trees to their (compensated) lengths is $\tau$-continuous. However, if $\ell$ would be $\tau$-continuous we would conclude that $\mathcal{L}$ has continuous paths, but $\mathcal{L}$ clearly makes jumps. Hence, $\ell$ is not continuous and convergence of $\mathcal{T}^N$ cannot be used to show convergence of $\mathcal{L}^N$.

**Remark 2.6** (Extension to $\Lambda$-coalescents). In the past decade, the so-called $\Lambda$-coalescents [24] have gained increasing interest (see e.g. [1] and references therein). Each of these coalescent processes arises as the large population limit of the genealogy of Cannings models and is uniquely determined by a finite measure $\Lambda$ on $[0; 1]$. The Kingman coalescent then arises for $\Lambda = \delta_0$. For $\Lambda \neq \delta_0$, the underlying Cannings models have unbounded variance and the $\Lambda$-coalescents admits the possibility of more than two lines merging at the same time. An interesting direction for further research is the investigation of potential limits of the tree-length process of the respective genealogies of Cannings-models. For this, recent results by [22], [12], [3] and [8] on moments and rescalings of $\Lambda$-coalescent trees, and by [2] on the speed of coming down from infinity (which extends Aldous’ result for the Kingman case, Lemma 4.6 below, to the $\Lambda$-case) will provide important ingredients.

**Remark 2.7** (Connection to empirical population genetics). Coalescent trees are of particular importance in empirical population genetics and in the analysis of sequence diversity data. In the infinite sites model, mutations leading to segregating sites fall on the genealogical tree at constant rate. As a consequence, the number of segregating sites is Poisson distributed with a parameter proportional to the tree length. As illustrated by Figure 2, the tree-length process makes jumps. Particularly large jumps occur when the most recent common ancestor of the total population changes. At such a time $F$, one of the two oldest families in the population dies out and a long external branch breaks off the genealogical tree (see also [27]). At time $F$—there are several segregating sites which are carried by all individuals which belong to the family which does not die out. Such segregating sites become fixed in the population when the MRCA of the population changes. In particular, fixation of segregating sites (also denoted by substitutions) come in bursts as time evolves, an observation already made by [31]. In addition, segregating sites which are present only in the oldest family which dies out at time $F$, are lost.

Observations concerned with the substitutions of segregating sites are special properties of the mutation-drift balance. This dynamic equilibrium is between the introduction of new segregating
sites due to mutation and loss of present ones due to genetic drift. Considered between times 0 and $t$, the introduction of new mutations in the population are due to mutation events falling on the part of the genealogical tree gained between times 0 and $t$ while the loss of existing mutations is due to some part of the genealogical tree at time 0 breaking off by time $t$. Most interestingly, the number of segregating sites in the total population, unlike many other processes in population genetics, is 'super-diffusive' in that it has infinite infinitesimal variance, as stated in Theorem 1.

3 Strong convergence of tree lengths

Proposition 2.1 and Theorem 1 establish convergence in distribution for the real-valued random variables $L_N^t$ ($t$ fixed) and the $\mathbb{D}$-valued random variables $L_N$. We extend these results by stronger notions of convergence, i.e. convergence in probability, almost sure convergence and convergence in $L^2$. We start with extensions for fixed times (Proposition 3.1) and then come to the extension involving the processes $L^N$ (Proposition 3.2). The proofs are given in Section 6.

3.1 Tree lengths at fixed times

For the extension of Proposition 2.1 fix $t \in \mathbb{R}$. An elegant way to encode a random coalescent tree $T := \mathcal{T}$ is in terms of (the completion of) a random metric on $\mathbb{N}$, as proposed by Evans [17]. To visualize this, consider a sequence of lineages indexed by $\mathbb{N}$, where lineage $i$ starts at time 0 in leaf $i$. Any pair of lineages coalesces independently at rate 1, and a random (ultra)metric $R$ is defined by

$$R(i, j) := 2 \cdot \text{time to the most recent common ancestor of leaves } i, j. \quad (3.1)$$

The completion of $(\mathbb{N}, R)$ is a.s. a compact ultra-metric space that represents the (uncountable set of) leaves of the coalescent tree.

There are two canonical ways to approach the compensated length of $T$ by a sequence of lengths of finite trees.

Figure 4: Kingman’s temporal coupling: In the tree $T$ coming down from infinitely many leaves, a tree with $N$ leaves can be embedded by considering the part of $T$ which is below the time at which $T$ comes down to $N$ lines. The resulting tree length is $\Lambda_N^1$. 

number of ancestral lines
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Figure 5: Kingman’s natural coupling: In the tree $T$ coming down from infinitely many leaves, a tree with $N$ leaves can be embedded by working down from the first $N$ leaves (obtained by sampling) from the infinite tree. The resulting tree length is $\Lambda^N$. In the natural coupling, $K^N_i$ is the number of lines in the small tree while the full tree has $i$ lines.

1. **From the root to the leaves:** Let $R_{(1)}, R_{(2)}, \ldots$ be a listing of the set $\{R(i,j) : i, j \in \mathbb{N}, i \neq j\}$ in decreasing order. The random variable

$$X_k := \frac{1}{2}(R_{(k-1)} - R_{(k)})$$

then gives the time the tree $T$ spends with $k$ lines “in parallel”, $k = 2, 3, \ldots$. We set

$$\Lambda^N_1 := \sum_{k=2}^{N} kX_k - 2 \log N, \quad N = 2, 3, \ldots$$

The random sequence $(\Lambda^N_1)_{N=2,3,\ldots}$ is called **temporal coupling** in [21]; see also Figure 4.

2. **Across lineages:** For $N = 2, 3, \ldots$, consider the finite subtree

$T^N$ encoded by $\left( \{1, \ldots, N\}, R\big|_{\{1,\ldots,N\}^2} \right)$, \quad $N = 1, 2, \ldots$.

Define

$$\Lambda^N_2 := \tilde{\ell}(T^N) - 2 \log N, \quad N = 2, 3, \ldots$$

This random sequence is called **natural coupling** in [21]; see also Figure 5.

**Proposition 3.1.** There is a random variable $\Lambda = \Lambda(R)$ such that $\frac{1}{2}\Lambda$ is Gumbel distributed,

$$\Lambda^N_1 \xrightarrow{N \to \infty} \Lambda$$

almost surely and in $L^2$ and

$$\Lambda^N_2 \xrightarrow{N \to \infty} \Lambda$$

in $L^2$. 

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3.2 The evolution of tree lengths

For the extension of Theorem 1 we briefly review the lookdown construction of [11]; see also [28] for a detailed description and Figure 6 for an illustration.

Consider the set of vertices \( V := \mathbb{R} \times \mathbb{N} \). A vertex \((t, i)\) is referred to as the individual at time \( t \) at level \( i \). The source of randomness in the lookdown construction is a family of rate one Poisson processes \( (P_{i,j})_{1 \leq i < j} \). At times \( t \in P_{i,j} \), the individual at level \( j \) looks down to level \( i \). As the illustration in Figure 6 shows, at a lookdown event in \( P_{i,j} \), all individuals at levels \( k \geq j \) are pushed one level up, and a new line of ascent is born at level \( j \). Note that the individual at level \( k \) is pushed to level \( k + 1 \) at rate \((\frac{1}{2})^k\).

We define the partition \( G \) of \( \mathbb{R} \times \{2, 3, \ldots\} \) into lines of ascent as follows. Every \( s_0 \in P_{i,j} \) gives rise to a partition element \( G \) of the form

\[
\left( [s_0, s_1) \times \{j\} \cup ([s_1, s_2) \times \{j+1\}) \cup ([s_2, s_3) \times \{j+2\}) \cup \ldots \right.
\]

with \( s_{k+1} > s_k \) for all \( k = 0, 1, 2, \ldots \). Here, \( s_{k+1} \) is the smallest element in \([s_k, \infty) \cap \bigcup_{1 \leq i' < j' \leq k+1} P_{i',j'}\). We say that \( G \) is born by \((s_0, i)\) and pushed one level up at times \( s_1, s_2, \ldots \). If \((s_0, i) \in G'\), we say that \( G \) descends from \( G' \). Since the individual at level \( k \) is pushed up by one at rate \((\frac{1}{2})^k\) and hence, for \( G \) as above, \( \lim_{k \to \infty} s_k \) is finite.

For \( s \leq t, i \leq j \) let \( G, G' \in \mathcal{G} \) be such that \((s, i) \in G', (t, j) \in G\). We say that \((s, i)\) is ancestor of \((t, j)\) if either \( G = G' \) or there are \( G_1, \ldots, G_n \) such that \( G \) descends from \( G_n \), \( G_k \) descends from \( G_{k-1} \), \( k = 2, \ldots, n \) and \( G_1 \) descends from \( G' \). In this case, we define \( A_s(t, j) := i \). In addition, for \( t \in \mathbb{R} \), define the random metric \( R_t^{ld} \) (compare with (3.1)) on \( \mathbb{N} \) by

\[
R_t^{ld}(i, j) = 2 \cdot \inf\{t - s: A_s(t, i) = A_s(t, j)\}.
\]

We define the random trees

\[
T_t^{ld,N} := \left( \{1, \ldots, N\}, R_t^{ld}|_{\{1, \ldots, N\}} \right), \quad N = 2, 3, \ldots
\]

and

\[
\mathcal{L}_t^{ld,N} := \bar{t}(T_t^{ld,N}) - 2 \log N.
\]

Recall the complete Skorokhod metric \( d_{Sk} \) on \( \mathcal{D} \) from [16] Section 3.5. We are now ready to state a result extending Theorem 1 to convergence in probability, proved in Section 6.
**Proposition 3.2.** There is a process $L^{ld}$, having the same distribution as $L$ from Theorem 1, such that

$$d_{Sk}(L^{N,ld}, L^{ld}) \xrightarrow{N \to \infty} 0$$

in probability.

### 4 Auxiliary results on Kingman's coalescent and the Moran model

In this section we collect some facts on Kingman's coalescent (Subsections 4.1–4.5) and the Moran model (Subsection 4.6) which will be required for the proof of Theorem 1.

For the Kingman coalescent, we take the tree $T$ as introduced in Section 3. Recall the subtrees $T_{N, N = 2, 3, ...}$ as defined in (3.3) and the inter-coalescence times $X_2, X_3, ...$ from (3.2). Recall that $X_k$ is exponentially distributed with parameter $(k^2)$.

#### 4.1 The Markov Chain $K^N$

We define

$$K^N_i := \text{number of lines in } T^N \text{ while } T \text{ has } i \text{ lines} \quad (4.1)$$

and $K^N := (K^N_i)_{i=1,2,...}$; see also Figure 3. Note that

$$\Lambda_2^N = \sum_{i=2}^{\infty} K^N_i X_i - 2 \log N. \quad (4.2)$$

The connection between the trees $T^N$ and $T$ has been described e.g. by [28], [26] and [15, Section 4.4]. Lemma 4.8 of [15] states that $K^N$ builds a Markov chain with one- and two-dimensional distributions

$$P[K^N_i = k] = \frac{(N-1) \binom{i}{k}}{N+1}, \quad i \geq 1, 1 \leq k \leq N \quad (4.3)$$

$$P[K^N_j = \ell | K^N_i = k] = \frac{(N-\ell) \binom{i+k-1}{j}}{(N+i-1)} \quad 1 \leq i \leq j, 1 \leq k \leq \ell \leq N. \quad (4.4)$$

We will need some moment properties of this Markov chain. We leave out the straightforward details of the proof.

**Lemma 4.1.** For $i \geq 1$,

$$E[i - K^N_i] = \frac{i(i-1)}{N+i-1}, \quad (4.5)$$

and for $1 \leq i \leq j$

$$E[(i - K^N_i)(j - K^N_j)] = \frac{i(i-1)j(j-1)}{(N+i-1)(N+j-1)} + \frac{i(i-1)N(N-1)}{(N+j-1)(N+i-1)(N+i-2)}. \quad (4.6)$$

#### 4.2 The length of an external branch

We will recall several facts of the length of a randomly chosen external branch in an $N$-coalescent $T^N$. In this setting we take the inter-coalescence times $X^N_2, ..., X^N_N$ such that $X^N_i$ is exponentially distributed with rate $\binom{i}{2}$, $i = 2, ..., N$. We denote by $J^N$ the length of a randomly chosen external
branch. The results we describe in this section are collected from [18], [13], [6] and [8] and stated here for completeness.

We define

\[ F^N := f \quad \text{iff} \quad J^N = \sum_{k=f+1}^{N} X_k, \]

i.e. \( F^N \) denotes the number of lines extant in the N-coalescent at the time at which the external branch connects to the tree. We give a basic fact about \( F^N \) and properties of \( J^N \).

**Proposition 4.2 (External branches).** For \( f = 1, \ldots, N - 1 \),

\[
P[F^N < f] = \frac{f(f - 1)}{N(N-1)} \quad \text{i.e.} \quad P[F^N = f] = \frac{2f}{N(N-1)}
\]

The first two moments of \( J^N \) are given by

\[
\mathbb{E}[J^N] = \frac{2}{N}, \quad \mathbb{V}[J^N] = \frac{8 \sum_{k=1}^{N} \frac{1}{k} - 12 + 4}{N(N-1)}.
\]

**Proof.** We obtain the distribution of \( F^N \) as follows: With probability \( \begin{pmatrix} N-1 \\ 2 \end{pmatrix} \) the randomly chosen external branch is not involved in the first coalescence event (bringing the number of lines from \( N \) down to \( N - 1 \)). Iterating this argument, we immediately see that the probability that the randomly chosen line did not take part in the first \( N - f + 1 \) coalescence events is

\[
P[F^N < f] = \left( \frac{N-1}{2} \right) \cdot \left( \frac{N-2}{2} \right) \cdots \left( \frac{f}{2} \right) = \left( \frac{f}{2} \right) = \frac{f(f - 1)}{N(N-1)}.
\]

To compute moments of \( J^N \), we use the representation

\[ J^N = \sum_{k=F^N+1}^{N} X^N_k. \]

Recalling that \( X^N_2, \ldots, X^N_N \) are independent of the tree topology, and \( F^N \) is measurable with respect to the tree topology, we get that \( F^N, X^N_2, \ldots, X^N_N \) are independent. The first two moments of \( J^N \) are now obtained by

\[
\mathbb{E}[J^N] = \mathbb{E}[\mathbb{E}[J^N|F^N]] = \mathbb{E} \left[ \frac{2}{F^N} - \frac{2}{N} \right] = \left( 2 \sum_{f=1}^{N-1} \frac{f}{\binom{N}{2}} \right) \frac{1}{f} - \frac{2}{N} = \frac{2}{N},
\]
which also implies that \( \mathbb{E}[\frac{2}{M}] = \frac{4}{N} \) and
\[
\mathbb{V}[J^N] = \mathbb{E}[\mathbb{V}[J^N|F^N]] + \mathbb{V}[\mathbb{E}[J^N|F^N]] = \mathbb{E}\left[ \sum_{k=F^N+1}^{N} \frac{1}{(k^2)} \right] + \mathbb{V}\left[ \frac{2}{F^N} \right]
\]
\[
= \sum_{f=1}^{N} \sum_{k=f+1}^{N} \frac{2f}{N(N-1)} \left( \frac{1}{(k^2)} \right) + 4 \sum_{f=1}^{N} \frac{2f}{N(N-1)} \left( \frac{1}{f^2} \right) - \frac{16}{N^2}
\]
\[
= \frac{1}{N^2} \sum_{k=2}^{N} \sum_{f=1}^{k-1} \frac{1}{(k^2)} + 4 \sum_{f=1}^{N} \frac{1}{f^2} - \frac{16}{N^2}
\]
\[
= \frac{4}{N^2} + \frac{8}{N(N-1)} \left( \sum_{f=1}^{N-1} 1 \right) - \frac{16}{N^2}
\]
\[
= \frac{8 \sum_{k=1}^{N} \frac{1}{k} - 12 + \frac{8}{N}}{N(N-1)}.
\]

\[\square\]

### 4.3 Subtrees of coalescents and their lengths

The aim of this section is to analyze the difference of the tree lengths of \( \mathcal{T} \) and of \( \mathcal{T}^N \). Since this difference is infinite, we have to carry out a limiting procedure, compensating by the mean. Recall that the inter-coalescence times \( X_2, X_3, \ldots \) are independent of the tree topology of \( \mathcal{T} \) in general and of \( K_2^N, K_3^N, \ldots \) in particular. We study the random variable
\[
B_N := \sum_{i=2}^{\infty} \left( (i - K_i^N)X_i - \mathbb{E}[i - K_i^N] \cdot \mathbb{E}[X_i] \right)
\]
which is the compensated difference of the tree lengths of \( \mathcal{T} \) and \( \mathcal{T}^N \).

**Remark 4.3.** Let us first make sure that the infinite sum in the definition of \( B_N \) exists and has expectation zero. To see this, we fix \( M \in \{2, 3, \ldots\} \) and consider the sequences \( (B_{N,M})_{M=2,3,\ldots} \) where \( B_{N,M} \) is defined as \( B_N \) but with the sum ranging from \( i = 2 \) to \( i = M \). For \( M < M' \), by Lemma 4.1 and using that \( \mathbb{E}[X_iX_j] \leq 2 \cdot \mathbb{E}[X_i] \cdot \mathbb{E}[X_j] \) for all \( i, j = 2, 3, \ldots \)
\[
\mathbb{E}[B_{N,M'} - B_{N,M}]^2
\]
\[
= \mathbb{E}\left[ \left( \sum_{i=M+1}^{M'} \left( (i - K_i^N)X_i - \frac{2}{N+i-1} \right) \right)^2 \right]
\]
\[
\leq 8 \sum_{i=M+1}^{M'} \sum_{j=M+1}^{M'} \mathbb{E}\left[ \left( \frac{i - K_i^N}{i(i-1)} - \frac{1}{N+i-1} \right) \left( \frac{j - K_j^N}{j(j-1)} - \frac{1}{N+j-1} \right) \right]
\]
\[
\leq 8 \sum_{i=M+1}^{M'} \sum_{j=M+1}^{M'} \frac{1}{(i-1)^2} \leq 8 \sum_{i=M+1}^{M'} \frac{1}{(i-1)^2}
\]
\[
= \mathcal{O}\left( \frac{1}{M} \right)
\]
as \( M \to \infty \).

Hence, the sequence \( (B_{N,M})_{M=2,3,\ldots} \) is Cauchy in \( L^2 \) and thus converges in \( L^2 \) to the limit variable \( B_N \) defined in (4.7). Furthermore we obtain that \( \mathbb{E}[B_N] = 0 \) by continuity of the linear functional \( \mathbb{E} \) on \( L^2 \).

**Proposition 4.4** (Variance of the difference in length of an infinite and a finite coalescent in the natural coupling).
\[
\mathbb{E}[B_N^2] \sim \frac{8 \log N}{N}.
\]
Proof. First,

\[ E[X_i X_j] = E[X_i] \cdot E[X_j] \cdot (1 + \delta_{ij}) \]

In order to obtain (4.8), by a straightforward calculation using Lemma 4.1,

\[
\mathbb{E}[B_N^2] = 8 \sum_{j=3}^{\infty} \sum_{i=2}^{j-1} \frac{N(N-1)}{j(j-1)(N+j-1)(N+i-1)(N+i-2)} \\
+ \sum_{i=2}^{\infty} \left( \frac{8 \cdot N(N-1)}{i(i-1)(N+i-1)^2(N+i-2)} + \frac{4}{(N+i-1)^2} \right)
\]

(4.9)

It is clear that the expression in the last line tends to 0 as \( C/N \), for some \( C > 0 \), as \( N \to \infty \). For the expression in the next to last line, we obtain

\[
8 \sum_{j=3}^{\infty} \frac{N(N-1)}{j(j-1)(N+j-1)(N+j-2)} = 8 \sum_{j=3}^{\infty} \frac{(N-1)(j-2)}{j(j-1)(N+j-1)(N+j-2)}
\]

\[
N \to \infty \quad 8 \sum_{j=1}^{\infty} \frac{N}{j(N+j)^2} \quad \sim \quad 8 \sum_{j=1}^{\infty} \frac{1}{j(N+j)} \quad \sim \quad 8 \sum_{j=1}^{\infty} \frac{1}{j} \quad \sim \quad 8 \log N
\]

which proves the Proposition. \( \square \)

4.4 Numbers of ancestors near the tree top

Let \( u > 0 \). Define \( S_u^N \) to be the (random) number of ancestors at time \( -u \) in \( T^N \) and \( S_u \) the number of ancestors by time \( -u \) in \( T \), where \( T^N \) and \( T \) are defined as in Section 3. We give results on convergence of \( S_u^N \) as \( N \to \infty \) (Lemma 4.5) and on convergence of \( S_u \) as \( u \to 0 \) (Lemma 4.6).

Lemma 4.5. For \( u > 0 \),

\[ S_u^N \xrightarrow{N \to \infty} S_u \]

almost surely and in \( L^p \) for all \( p > 0 \).

Proof. With probability one, the completion of \( R \) from (3.1) is compact, so \( T \) comes down from infinity, i.e. with probability one there are at most finitely many lines left by time \( -u \). Since \( S_u^N \) is increasing with \( N \), the almost sure convergence follows. To see the \( L^p \)-convergence, note that all moments of the distribution of \( S_u \) exist; see e.g. [28, Section 5.4]. Since \( S_u^N \) is bounded by \( S_u \), the families \( (S_u^N)^p \) are uniformly integrable and convergence in \( L^p \) follows. \( \square \)

Lemma 4.6. For the number of ancestors \( S_u \)

\[ u \cdot S_u \xrightarrow{u \to 0} 2, \]

almost surely and in \( L^2 \). Moreover,

\[ \frac{S_u - 2/u}{\sqrt{2/(3u)}} \xrightarrow{u \to 0} N(0, 1). \]

(4.11)

In addition, for \( u, v \to 0 \), \( u \leq v \), \( u/v \to \Gamma \leq 1 \)

\[ \left( \frac{S_u - 2/u}{\sqrt{2/(3u)}}, \frac{S_v - 2/u}{\sqrt{2/(3u)}} \right) \Rightarrow N(0, C) \]

(4.12)
with the covariance matrix $C$ given by

$$C = \begin{pmatrix} 1 & \Gamma^{3/2} \\ \Gamma^{3/2} & 1 \end{pmatrix}. \quad (4.13)$$

**Remark 4.7.** As a consequence of the previous lemma, the finite dimensional distributions of \((S_{tu} - 2tu)/\sqrt{2/(3tu)}\) converge as $u \to 0$ to those of a Gaussian process \((A_t)_{t \geq 0}\) with covariance $\text{COV}[A_s, A_t] = (s/t)^{3/2}$ for $s \leq t$.

**Proof of Lemma 4.6.** The convergences (4.10) and (4.11) can be found on p. 27 in [1]. For further use below, we prove (4.11) in all detail. Define $T_n$ as the time it takes the coalescent to come down to $n$ lines, i.e.,

$$T_n := \sum_{i=n+1}^{\infty} X_i.$$ 

Note that

$$\mathbb{E}[T_n] = \sum_{i=n+1}^{\infty} \frac{2}{i(i-1)} = \frac{2}{n}, \quad \mathbb{V}[T_n] = \sum_{i=n+1}^{\infty} \frac{4}{i^2(i-1)^2} \overset{n \to \infty}{\sim} \frac{4}{3n^3}. \quad (4.14)$$

The central ingredients in the proof are the two facts

$$\mathbb{P}[S_n \leq n] = \mathbb{P}[T_n \leq u], \quad T_n - \frac{2u}{\sqrt{4/(3u^3)}} \overset{n \to \infty}{\longrightarrow} N(0, 1), \quad (4.15)$$

where the second assertion is a consequence of (4.14) and the central limit theorem. Hence we may define

$$a_u(x) := \left[\frac{2}{u} + x\sqrt{2/(3u)}\right], \quad (4.16)$$

and write

$$\mathbb{P}\left[\frac{S_u - 2u}{\sqrt{2/(3u)}} \leq x\right] = \mathbb{P}[S_u \leq a_u(x)]$$

$$= \mathbb{P}[T_{a_u(x)} \leq u]$$

$$= \mathbb{P}\left[\frac{T_{a_u(x)} - 2/a_u(x)}{\sqrt{4/(3a_u(x)^3)}} \leq \frac{u - 2/a_u(x)}{\sqrt{4/(3a_u(x)^3)}}\right]$$

$$\overset{u \to 0}{\sim} \mathbb{P}\left[\frac{T_{a_u(x)} - 2/a_u(x)}{\sqrt{4/(3a_u(x)^3)}} \leq x\right],$$

since

$$u - 2/a_u(x) \overset{u \to 0}{\sim} x\sqrt{w^3/6}, \quad \sqrt{4/3(a_u(x)^3)} \overset{u \to 0}{\sim} \sqrt{w^3/6}. \quad (4.17)$$

Now, (4.11) follows from (4.15). Since the event in (4.10) is measurable with respect to the terminal $\sigma$-algebra generated by the independent random variables $X_2, X_3, ...$, the convergence in (4.10) holds almost surely. The $L^2$-convergence follows from moment results for $S_u$ given e.g. in [28, Section 5.4].

Let us turn to the proof of (4.12). Since for $m \leq n$

$$\text{COV}[T_m, T_n] = \sum_{i=n+1}^{\infty} \mathbb{V}[X_i] \overset{n \to \infty}{\sim} \frac{4}{3n^3},$$
and using \( (4.14) \) it is an easy exercise to show that for \( m, n \to \infty, m/n \to \Gamma \leq 1, \)
\[
\left( \frac{T_n - 2/n}{\sqrt{4/(3n^3)}}, \frac{T_m - 2/m}{\sqrt{4/(3m^3)}} \right) \Rightarrow N(0, C)
\]
with the covariance matrix \( C \) given in \( (4.13) \). To see \( (4.12) \) from this, note that for \( m \leq n, u \leq v, \) an extension of \( (4.15) \) gives
\[
\mathbb{P}[T_n \leq u, T_m \leq v] = \mathbb{P}[S_u \leq n, S_v \leq m]
\]
and thus for \( x, y \in \mathbb{R}, \) and using \( (4.16) \),
\[
\mathbb{P}\left[ S_u - \frac{2}{u} \leq x, S_v - \frac{2}{v} \leq y \right] = \mathbb{P}[T_u(x) \leq u, T_v(y) \leq v] = \mathbb{P}\left[ \frac{T_u(x) - 2/a_u(x)}{\sqrt{4a_u(x)^{3/2}}} \leq \frac{u - 2/a_u(x)}{\sqrt{4a_u(x)^{3/2}}} \right. \frac{T_v(y) - 2/a_v(y)}{\sqrt{4a_v(y)^{3/2}}} \leq \frac{v - 2/a_v(y)}{\sqrt{4a_v(y)^{3/2}}}, \left. \right. u,v \to 0 \mathbb{P}\left[ \frac{T_u(x) - 2/a_u(x)}{\sqrt{4a_u(x)^{3/2}}} \leq x, \frac{T_v(y) - 2/a_v(y)}{\sqrt{4a_v(y)^{3/2}}} \leq y \right] \]
by \( (4.17) \) and thus, if \( u, v \to 0, u/v \to \Gamma \leq 1, \) \( (4.12) \) follows from \( (4.18) \) since \( a_v(x)/a_u(y) \to 0 \)
\( u/v. \)

### 4.5 The tree length near the tree top

We analyze now the contribution to the tree length that comes from a small time interval near
the tree top. To this purpose we define
\[
\Delta_u^N := \int_0^u (S_v^n - \mathbb{E}[S_v^n])dv, \quad \Delta_u := \int_0^u (S_V - \mathbb{E}[S_v])dv.
\]
Note that \( \Delta_u^N \) equals \( \hat{A}_{0,u}^N - \mathbb{E}[\hat{A}_{0,u}^N] \) from Figure 3 in distribution. Again, we give results on
convergence of \( \Delta_u^N \) as \( N \to \infty \) (Lemma 4.9) and of \( \Delta_u \) as \( u \to 0 \) (Lemma 4.10).

**Remark 4.8** (\( \Delta_u \) as an \( L^2 \)-limit). Since the integrand in the definition of \( \Delta_u \) is unbounded, we have to make sure that the random variable \( \Delta_u \) exists. Indeed, using Lemma 4.6 it is easy to check that \( \left( \int_{n=1}^u (S_v - \mathbb{E}[S_v])dv \right)_{u=1,2,...} \) is a Cauchy sequence in \( L^2 \), and we define \( \Delta_u \) as its \( L^2 \)-limit. In
particular, by continuity of \( \mathbb{E} \) on \( L^2 \) and Fubini’s Theorem we further obtain \( \mathbb{E}[\Delta_u] = \mathbb{E}[\Delta_u^N] = 0. \)

**Lemma 4.9.** For the random variables \( \Delta_u^N \) and \( \Delta_u, \)
\[
\Delta_u^N \xrightarrow{N \to \infty} \Delta_u \quad (4.20)
\]
in \( L^2 \).

**Proof.** We start with proving the intuitively obvious fact that \( S_v - S_v^N \) and \( S_w - S_w^N \) have nonnegative correlation. For \( w \leq v, \) we write
\[
\text{COV}[S_v - S_v^N, S_w - S_w^N] = \text{COV}[\mathbb{E}[S_v - S_v^N|S_v, S_w], \mathbb{E}[S_w - S_w^N|S_v, S_w]]
\]
\[
= \text{COV}[\frac{S_v(S_v - 1)}{N + S_v - 1}, \frac{S_w(S_w - 1)}{N + S_w - 1}] + \mathbb{E}\left[ \frac{S_v(S_v - 1)(N(N - 1))}{(N + S_w - 1)(N + S_v - 1)(N + S_v - 2)} \right].
\]
(4.21)
where we have used (4.3) for the first and (4.4) for the second term. The second term on the r.h.s. is nonnegative, and so is the first term, since $i \mapsto \frac{i(i-1)}{N+i-1}$ is increasing and $(S_v, S_w)$ are associated, i.e.

$$\text{COV}[f(S_v), g(S_w)] \geq 0$$

(4.22)

for all non-decreasing functions $f, g$. Indeed, to verify (4.22) it is enough to show this inequality for $f(S_v) = 1_{S_v \geq t}$ and $g(S_w) = 1_{S_w \geq k}$. This, however, is clear since

$$\text{COV}[1_{\{S_v \geq t\}}, 1_{\{S_w \geq k\}}] = \text{COV}[1_{\{S_v \geq t\}}, \mathbb{E}[1_{\{S_w \geq k\}} | S_w]] \geq 0$$

by the well-known fact that a single random variable (here $S_w$) is associated and both $1_{\{S_v \geq t\}}$ and $\mathbb{E}[1_{\{S_w \geq k\}} | S_w]$ are non-decreasing functions of $S_w$. So we have proved that

$$\text{COV}[S_v - S_v^N, S_w - S_w^N] \geq 0$$

(4.23)

for all $v, w \geq 0$.

Now we come to the proof of (4.20). By Fubini’s Theorem and (4.23),

$$\mathbb{E}[(\Delta^N_a - \Delta_a)^2] = 2 \int_0^u \int_0^v \mathbb{E}[(S^N_v - S_v - \mathbb{E}[S^N_v - S_v]) (S^N_w - S_w - \mathbb{E}[S^N_w - S_w])] \, dwdv$$

$$= 2 \int_0^u \int_0^v \text{COV}[S_v - S_v^N, S_w - S_w^N] \, dwdv$$

$$\leq 2 \int_0^\infty \int_0^v \text{COV}[S_v - S_v^N, S_w - S_w^N] \, dwdv = \mathbb{E}[(\Delta^N_a - \Delta_a)^2] \xrightarrow{N \to \infty} 0$$

by Proposition 4.4 since $(\Delta^N_a - \Delta_a)^2$ is distributed as $B^2_N$ in that Proposition. □

**Lemma 4.10.** For the random variables $\Delta_u$,

$$\mathbb{V}[\Delta_u] \xrightarrow{u \to 0} \frac{2}{3} u.$$  

(4.24)

**Proof.** By Lemma 4.6 we see that for $w \leq v$

$$\text{COV}[S_v, S_w] \xrightarrow{w \leq v \to 0} \sqrt{\frac{2}{3w} \frac{w^3}{3v^2}} = \frac{2}{3} \sqrt{\frac{w}{v^2}}.$$  

Hence, by Fubini’s Theorem,

$$\mathbb{V}[\Delta_u] = 2 \int_0^u \int_0^v \text{COV}[S_v, S_w] \, dwdv \xrightarrow{u \to 0} \frac{4}{3} \int_0^u \int_0^v \frac{w}{v^2} \, dwdv = \frac{2}{3} u.$$  

□

**Remark 4.11.** Note that $\Delta_u$ is an integral over approximately Gaussian random variables for small $u$. In addition, for $s \leq t$,

$$\text{COV}\left[\Delta_u / \sqrt{\frac{3}{2} su}, \Delta_t / \sqrt{\frac{3}{2} tu}\right] = \frac{3}{2u \sqrt{s} t} \int_0^s \int_0^t \text{COV}[S_v, S_w] \, dwdv$$

$$\xrightarrow{u \to 0} \frac{3}{2u \sqrt{s} t} \left(2 \int_0^s \int_0^v \frac{w}{v^2} \, dwdv + \frac{2}{3} \int_0^s \int_0^v \frac{w}{v} \, dwdv \int_0^v \frac{1}{v^2} \, dv\right)$$

$$= \sqrt{\frac{s}{t}} + \frac{1}{2} \left(\sqrt{\frac{s}{t}} - \sqrt{\frac{s^3}{t}}\right) = \frac{3}{2} \sqrt{\frac{s}{t}} - \frac{1}{2} \sqrt{\frac{s^3}{t}}.$$  

Hence, as an extension of (4.24), we see that the finite dimensional distributions of $(\Delta_t / \sqrt{\frac{3}{2} tu})_{t \geq 0}$ converge as $u \to 0$ to those of a centered Gaussian process $(A_t)_{t \geq 0}$ with covariance COV$[A_s, A_t] = \frac{3}{2} \sqrt{\frac{s}{t}} - \frac{1}{2} \sqrt{\frac{s^3}{t^2}}$ for $s \leq t$.  


4.6 The evolution of the $f$ oldest families in the Moran model

Consider the graphical representation of a Moran model given in Figure 1. For any time $t \in \mathbb{R}$ the tree $\mathcal{T}^N_t$ can be identified with a random subset of $(-\infty; t] \times \{1, \ldots, N\}$ which we continue to denote by $\mathcal{T}^N_t$. For any $t \in \mathbb{R}$ we define the inter-coalescence times

$$X^N_i(t) := \text{length of the time interval in which } \mathcal{T}^N_i \text{ has } i \text{ lines}$$

for $i = 2, \ldots, N$. We denote by $\mathcal{R}^N$ the rate $\binom{N}{2}$ Poisson process of all resampling events, viewed as a random subset of $\mathbb{R}$. For $f = 2, \ldots, N$ and $t \in \mathbb{R}$, consider the $f$ oldest families at time $t$, i.e. the $f$ subtrees of $\mathcal{T}^N_t$ (call them $F^N_t(1), \ldots, F^N_t(f)$) whose union is $\mathcal{R}^N \cap \left\{(t - \sum_{i=1}^{f+1} X^N_i; t] \times \{1, \ldots, N\}\right\}$. Let

$$\mathcal{D}^N,f := \left\{ t : X^N_f(t) \neq X^N_f(t^-) \right\} \subseteq \mathcal{R}^N,$$

i.e. $\mathcal{D}^N,f$ is the point process of times when one of the $f$ oldest families gets extinct. We set $Z^N,f = (Z^N,f(1), \ldots, Z^N,f(f))$, where

$$Z^N,f(i) := \text{size of the family } F^N_t(i),$$

i.e. the number of leaves in the tree $F^N_t(i)$. Note that $Z^N,f \in \mathcal{D}^{f+1}_t := \{(z_1, \ldots, z_f) : z_i \geq 1, z_1 + \ldots + z_f = N\}$. The following lemma is essential in the proof of Theorem 1.

**Lemma 4.12** (The $f$ oldest families in a Moran model). Fix $f \in \{2, \ldots, N\}$. Let $\mathcal{N} = \{\tau_n : n \in \mathbb{Z}\}$ with $... < \tau_0 < \tau_1 < ...$

1. The uniform distribution on $\mathcal{D}^{f+1}_{\tau}$ is the stationary distribution for the Markov chains $(Z^N,f)_{t \in \mathbb{R}}$ and $(Z^N,f)_{n \in \mathbb{Z}}$.

2. The events $\{\tau_n \in \mathcal{D}^N,f\}_{n \in \mathbb{Z}}$ are independent and $\mathbb{P}[\tau_n \in \mathcal{D}^N,f] = \left(\frac{f}{2}\right) / \binom{N}{2}$. In particular, $\mathcal{D}^N,f$ is a Poisson process with rate $\left(\frac{f}{2}\right)$.

**Proof.** Let $t \in \mathbb{R}$. Looking at the Moran genealogy during the time interval $[t - \sum_{i=1}^{f+1} X^N_i; t]$, one sees that the $f$ oldest families have been built up through a Pólya urn with $f$ ancestral balls. This already explains 1. for a fixed (non-random) $t$. The same arguments apply if $t$ is a resampling time. Hence, we have proved assertion 1.

Let us now consider the dynamics of the sizes of the $f$ oldest families $(Z^N,f)_{n \in \mathbb{Z}}$ in its equilibrium, the uniform distribution on $\mathcal{D}^{f+1}_t$. The Moran model is set up as follows: Each pair of balls is chosen at unit rate. As soon as a pair is chosen, one of the two balls (selected at random from the pair) is transferred into the box of the other ball. (If two balls from the same box are chosen, nothing changes.) For the transition of the Markov chain, we compute for $(z_1, \ldots, z_f) \in \mathcal{D}^{f+1}_t$

$$\mathbb{P}[Z^N,f_{\tau_{n+1}} = (z_1, \ldots, z_f), \tau_{n+1} \notin \mathcal{D}^{N,f}] = \sum_{i,j=1 \atop i \neq j}^{f} \mathbb{P}[Z^N,f_{\tau_n} = (z_1, \ldots, z_i + 1, \ldots, z_j - 1, \ldots, z_f)] \frac{1}{2} \frac{(z_i + 1)(z_j - 1)}{\binom{N}{2}}$$

$$+ \sum_{i=1}^{f} \mathbb{P}[Z^N,f_{\tau_n} = (z_1, \ldots, z_i, \ldots, z_f)] \frac{1}{2} \cdot \left( \binom{f}{2} - \sum_{i,j=1 \atop i \neq j}^{f} (z_i - 1) \right)$$

$$= \mathbb{P}[Z^N,f_{\tau_n} = (z_1, \ldots, z_f)] \cdot \frac{1}{2} \cdot \left( \binom{f}{2} - \sum_{i,j=1 \atop i \neq j}^{f} (z_i - 1) \right)$$

This calculation reveals two things: first, by summing over all possible $(z_1, \ldots, z_f)$ on both sides, we see that $\mathbb{P}[\tau_{n+1} \in \mathcal{D}] = \left(\frac{f}{2}\right) / \binom{N}{2}$. Secondly, we see that $Z^N,f_{\tau_{n+1}}$, given $\tau_{n+1} \in \mathcal{D}$, is again uniformly
5 Proof of Theorem \[1\]

We will prove Theorem 1 in three steps. For convergence of \(\mathcal{L}^N\) we need to show (see e.g. \[10\] Lemma 3.4.3)

(a) The sequence of processes \(\mathcal{L}^N\) is tight in \(\mathbb{D}\),

(b) The finite-dimensional distributions of the sequence \(\mathcal{L}^N\) converge.

The main work is to show tightness of \((\mathcal{L}^N)_{N \in \mathbb{N}}\) in \(\mathbb{D}\). For this, it is enough to show (see \[10\] Theorem 3.8.6 and Theorem 3.8.8]

\[
(\mathcal{L}^N_0)_{N \in \mathbb{N}} \text{ is tight in } \mathbb{R}
\]

and there exists \(\beta > 0\) and \(\theta > 1\) such that for all \(t \in \mathbb{R}\),

\[
\limsup_{N \to \infty} \mathbb{E}[1 \wedge |\mathcal{L}_t^N - \mathcal{L}_t^N|^\beta \wedge |\mathcal{L}_t^N - \mathcal{L}_{t-h}^N|^\beta] \lesssim h^\theta. \quad (5.1)
\]

Proposition 2.1 already shows that \(\frac{1}{2} \mathcal{L}^N_0\) converges to a Gumbel distributed random variable, which implies (5.1). Now, the main work is to show (5.2), which will be done in Step 1. In Step 2 we show convergence of finite-dimensional distributions. Step 3 then shows (2.2).

**Step 1** (Proof of (5.2)). Consider a Moran model of size \(N\). We will use the same notation as in Subsection 4.6. For any two time points \(t\) and \(t+h\), we put

\[
F_{(t,t+h)}^N = \min\{i = 2, \ldots, N : X_i^N(t) \neq X_i^N(t+h)\}.
\]

Note that \(\{F_{(t,t+h)}^N \geq f\}\) is the event that none of the \(f\) oldest families gets extinct during \((t;t+h]\).

Since the point process of losses of one of the \(f\) oldest families is Poisson with rate \(\binom{f}{2}\) by Lemma 4.12, we conclude that

\[
\mathbb{P}[F_{(t-h,t]}^N \wedge F_{(t,t+h)}^N < f] = (1 - e^{-\binom{f}{2}h})^2 \lesssim f^4 h^2 \wedge 1. \quad (5.3)
\]

Using this equation, we will now show (5.2) for \(\theta = \frac{10}{9}\) and \(\beta = 10\). We write

\[
\mathbb{E}[1 \wedge (\mathcal{L}_{t+h}^N - \mathcal{L}_t^N)^{10} \wedge (\mathcal{L}_t^N - \mathcal{L}_{t-h}^N)^{10}] \leq \mathbb{E}[1 \wedge (\mathcal{L}_{t+h}^N - \mathcal{L}_t^N)^{10} ; F_{(t,t+h)}^N \geq F_{(t-h,t)}^N] + \mathbb{E}[1 \wedge (\mathcal{L}_t^N - \mathcal{L}_{t-h}^N)^{10} ; F_{(t-h,t)}^N \geq F_{(t,t+h)}^N]. \quad (5.4)
\]

We will next bound the first term on the right hand; the bound for the second term is obtained in the same manner. We get

\[
\mathbb{E}[1 \wedge (\mathcal{L}_{t+h}^N - \mathcal{L}_t^N)^{10} ; F_{(t,t+h)}^N \geq F_{(t-h,t)}^N]
\leq \mathbb{P}[F_{(t-h,t)}^N \leq F_{(t,t+h)}^N \leq h^{-2/9}] + \mathbb{E}[(\mathcal{L}_{t+h}^N - \mathcal{L}_t^N)^{10} ; F_{(t,t+h)}^N \geq h^{-2/9}] \leq \mathbb{P}[F_{(t-h,t)}^N \vee F_{(t,t+h)}^N \leq h^{-2/9}]
+ \mathbb{E}\left[\left(\sum_{i=2}^{N} i \left(X_i^N(t+h) - \frac{1}{\beta}\right) - \sum_{i=2}^{N} i \left(X_i^N(t) - \frac{1}{\beta}\right)\right)^{10} ; F_{(t,t+h)}^N \geq h^{-2/9}\right] \leq h^{10/9} + \mathbb{E}\left[\left(\sum_{i=2}^{N} i \left(X_i^N(t+h) - \frac{1}{\beta}\right) - \sum_{i=2}^{N} i \left(X_i^N(t) - \frac{1}{\beta}\right)\right)^{10} \right].
\]

\footnote{For functions \(a, b : \mathbb{R}_+ \to \mathbb{R}_+\) we write \(a(h) \lesssim b(h)\) iff there is a \(C > 0\), independent of any other parameter, such that \(a(h) \leq C \cdot b(h)\) for all \(h > 0\).}
where the last inequality follows from (5.3) and the fact that \( X_i(t + h) = X_i(t) \) on \( \{ F^N_{(t,t+h)} \geq h^{-2/9} \} \) for all \( i < [h^{-2/9}] \) by definition of \( F^N_{(t,t+h)} \). It remains to bound the second term in the last line. For this, we define for \( n = 1, 2, ... \)

\[
a_n(h) := \sum_{i=\lfloor h^{-2/9} \rfloor}^{N} \mathbb{E} \left[ \left( i \left( X_i(t) - \frac{1}{2} \right) \right)^n \right]
\]

and observe that

\[
a_1(h) = 0, \quad a_n(h) \lesssim h^{2(n-1)/9},
\]

since the \( n \)th central moment of an exponentially distributed random variable with parameter \( \lambda \) is proportional to \( \lambda^{-n} \). In addition, we use that \((x-y)^n \leq (2x)^n + (2y)^n\) for even \( n \) and all \( x, y \in \mathbb{R} \), and independence of \( X_1^N(t), ..., X_n^N(t) \) as well as of \( X_1^N(t+h), ..., X_n^N(t+h) \) to obtain

\[
\begin{align*}
\mathbb{E} & \left[ \left( \sum_{i=\lfloor h^{-2/9} \rfloor}^{N} i \left( X_i(t+h) - \frac{1}{2} \right) \right)^{10} \right] \\
& \lesssim \mathbb{E} \left[ \left( \sum_{i=\lfloor h^{-2/9} \rfloor}^{N} i \left( X_i(t) - \frac{1}{2} \right) \right)^{10} \right] + \mathbb{E} \left[ \left( \sum_{i=\lfloor h^{-2/9} \rfloor}^{N} i \left( X_i(t) - \frac{1}{2} \right) \right)^{10} \right] \\
& \lesssim \sum_{k=1}^{10} \sum_{n_1 + ... + n_k = 10} a_{n_1}(h) \cdots a_{n_k}(h) \lesssim (a_2(h))^5 \lesssim h^{10/9}.
\end{align*}
\]

by (5.6). Plugging (5.7) and (5.5) into (5.4) shows that (5.2) holds with \( \beta = 10 \) and \( \theta = \frac{10}{9} \).

**Step 2** (Convergence of finite-dimensional distributions). Fix \( t_1 < ... < t_n \). We will show that \( (\mathcal{L}_{t_1}^N, ..., \mathcal{L}_{t_n}^N) \) converges weakly for \( N \to \infty \). The strategy is to define a probability space on which all \( \mathcal{L}_{t_i}^N, i = 1, ..., n, N = 2, 3, ... \), are defined.

Consider a coalescent, started with infinitely many lines which are numbered by \( 1, 2, ..., n \), for some time \( t_0 - t_n - 1 \). Denote the number of the ancestors at time \( t_0 - t_n - 1 \) by \( S_{t_0} \). Number the lines going back from these by \( 1_{n-1}, ..., (S_{t_0})_{n-1} \) and augment them by lines numbered \( (S_{t_0}+1)_{n-1}, (S_{t_0}+2)_{n-1}, ... \). Let these infinitely many lines coalesce for some time \( t_0 - t_{n-2} \), number the \( S_{t_0-1} \) ancestors at time \( t_0 - t_{n-2} - 1 \) by \( 1_{n-2}, ..., (S_{t_0-1})_{n-2} \) and augment their lines by lines numbered \( (S_{t_0-1}+1)_{n-2}, (S_{t_0-1}+2)_{n-2}, ... \).... In this way we get iteratively \( n \) genealogies for an infinite population back from times \( t_1, ..., t_n \). Considering the compensated tree lengths of lines numbered \( 1, ..., N_i \) gives the compensated tree length of a population of size \( N \) at time \( t_i, i = 1, ..., n \). Moreover, as shown in Proposition 3.1 these tree lengths converge in \( L^2 \) as \( N \to \infty \) for each \( i = 1, ..., n \). Since \( L^2 \)-convergence implies convergence in probability, which, in turn, implies weak convergence, we are done.

**Step 3** (Decomposition of \( \mathcal{L}_{t_1}^N - \mathcal{L}_{t_0}^N \) and proof of (2.2)). Recall the graphical representation of a Moran model from Figure 1. Using the random set \( \mathcal{F}^N_t \subseteq (\mathcal{X}^N_t - 2 \log N)_{t \in \mathbb{R}} \) (recall Subsection 4.2) we have the representation \( (\mathcal{L}_{t_1}^N)_{t \in \mathbb{R}} \equiv (\lambda^N(\mathcal{F}^N_t) - 2 \log N)_{t \in \mathbb{R}} \) where \( \lambda^N \) is Lebesgue measure on \( \mathbb{R} \times \{1, ..., N\} \). We set

\[
\begin{align*}
A_{0,t}^N & := \lambda^N(\mathcal{F}^N_t \setminus \mathcal{F}_0^N), \quad A_{0,t}^N := \mathbb{E}[A_{0,t}^N], \\
B_{0,t}^N & := \lambda^N(\mathcal{F}^N_T \setminus \mathcal{F}_0^N), \quad B_{0,t}^N := \mathbb{E}[B_{0,t}^N],
\end{align*}
\]

compare also with Figure 3. Note that \( \mathbb{E} \lambda^N(\mathcal{F}^N_t \setminus \mathcal{F}_0^N) = \mathbb{E} \lambda^N(\mathcal{F}^N_T \setminus \mathcal{F}_0^N) \) due to stationarity, and thus

\[
\mathcal{L}_{t_1}^N - \mathcal{L}_{t_0}^N \equiv A_{0,t}^N - B_{0,t}^N.
\]
For the infinitesimal variance, we find by the convergence of finite dimensional distributions and (5.9) that
\[ \mathbb{E}[(L_t - L_0)^2] = \lim_{N \to \infty} \mathbb{E}[(L^N_t - L^N_0)^2] = \lim_{N \to \infty} \mathbb{E}[(\Delta^N_t - B^N_{0,t})^2]. \quad (5.10) \]

From (5.8) and (4.19) we conclude that \( A^N_{0,t} \overset{d}{=} \Delta^N_t \), again see Figure 3. We have, using the \( L^2 \)-convergence from Lemma 4.9 and Lemma 4.10
\[ \lim_{N \to \infty} \mathbb{V}[A^N_{0,t}] = \lim_{N \to \infty} \mathbb{V}[\Delta^N_t] = \mathbb{V}[\Delta_t] \overset{t \to 0}{\sim} \frac{2}{3} t. \quad (5.11) \]

For the variance of \( B^N_{0,t} \), note that \( B^N_{0,t} \overset{d}{=} B_N - B_{S_N^t} \), where \( B_N \) and \( S_N^t \) are as in Sections 4.3 and 4.4, with \( T := \mathcal{T}_0 \) and \( S^N_t \) independent. We thus have for fixed \( t \) and \( N \to \infty \), because of Proposition 4.4,
\[ \mathbb{V}[B^N_{0,t}] = \mathbb{V}[B_N - B_{S^t_N}] \overset{N \to \infty}{\sim} \mathbb{V}[B_{S^t_N}] \overset{N \to \infty}{\sim} \mathbb{V}[B_{S^t}]. \quad (5.12) \]

Since \( t \cdot S_t \to 2 \) almost surely as \( t \to 0 \) (see Lemma 4.6), we conclude from (5.12) and Proposition 4.4, (4.8), that
\[ \lim_{N \to \infty} \mathbb{V}[B^N_{0,t}] = \mathbb{V}[B_{S_t}] \overset{t \to 0}{\sim} \mathbb{V}[B_{S^t}] \overset{t \to 0}{\sim} 4t |\log t|. \quad (5.13) \]

Finally, combining (5.10), (5.11) and (5.13), and noting that \( \mathbb{C} \mathbb{O} \mathbb{V}[A^N_{0,t}, B^N_{0,t}] \overset{t \to 0}{\lesssim} t \sqrt{\frac{2}{3} |\log t|} \) by the Cauchy-Schwartz inequality, we arrive at
\[ \mathbb{E}[(L_t - L_0)^2] \overset{t \to 0}{\sim} 4t |\log t|. \]

This completes the proof of Theorem 1.

6 Proofs of strong convergence results

In this section we prove Propositions 3.1 and 3.2

6.1 Proof of Proposition 3.1

From Proposition 2.1 we know that \( \Lambda^N_t \) converges weakly as \( N \to \infty \) to a random variable \( \Lambda \) such that \( \frac{1}{\sqrt{N}} \Lambda \) is Gumbel distributed. Since \( \Lambda^N_t \) is a sum of independent random variables, Kolmogorov’s three series criterion shows that the convergence holds almost surely as well. Moreover, since the norms converge in (3.4), the convergence also holds in \( L^2 \).

Next, we will show that
\[ \Lambda^N_t - \Lambda^N_0 \overset{N \to \infty}{\to} 0 \]
in \( L^2 \). Together with the \( L^2 \)-convergence of \( \Lambda^N_t \) this gives (3.5). We compute directly, recalling
Proposition 6.1. Let \( \Lambda^1_N = \Lambda^2_N \) in the third equality and Lemma 4.1.

\[
\mathbb{E}[(\Lambda^1_N - \Lambda^2_N)^2] = \mathbb{E}\left[\left(\sum_{i=2}^{\infty} K_i^N X_i - \sum_{i=2}^{N} iX_i\right)^2\right] = \mathbb{E}\left[\left(\sum_{i=2}^{\infty} K_i^N X_i\right)^2\right] + \mathbb{E}\left[\left(\sum_{i=2}^{N} iX_i\right)^2\right] - 2\mathbb{E}\left[\sum_{i=2}^{\infty} \sum_{j=2}^{N} K_i^N jX_i X_j\right]
\]

\[
= 2\left(\mathbb{E}\left[\left(\sum_{i=2}^{N} iX_i\right)^2\right] - \sum_{i=2}^{N} \sum_{j=2}^{N} \frac{ijN}{N+i-1} \mathbb{E}[X_i X_j]\right)
\]

\[
= 2\left(\mathbb{E}\left[\left(\sum_{i=2}^{N} iX_i\right)^2\right] - \sum_{i=2}^{N} \sum_{j=2}^{N} \frac{ijN}{N+i-1} \frac{4}{i(i-1)j(j-1)} (1 + \delta_{ij})\right)
\]

\[
= 8\sum_{i=1}^{N-1} \frac{1}{i^2} \left(1 - \frac{N}{N+i}\right) + 8\sum_{i=1}^{N-1} \frac{1}{i} \left(\sum_{j=1}^{N-1} \frac{1}{j}\right) - 8\sum_{j=1}^{N-1} \frac{1}{j} \sum_{i=1}^{N-1} \left(\frac{1}{i} - \frac{1}{N+i}\right)
\]

\[
= 8\sum_{i=1}^{N-1} \frac{1}{i(N+i)} = 8\sum_{i=1}^{N-1} \left(\frac{1}{i} - \frac{1}{N+i}\right) \mathbb{E}\left[\begin{array}{c}
\frac{1}{i} - \frac{1}{N+i}
\end{array}\right] \sim 8\log N \frac{N}{N} \rightarrow_\infty 0.
\]

6.2 Proof of Proposition 3.2

We recall [10] Lemma A2.1:

Proposition 6.1. Let \( (X^n)_{n=1,2,...} \) be a sequence of processes with sample paths in \( \mathbb{D} \), defined on the same probability space. Suppose that \( (X^n)_{n=1,2,...} \) is relatively compact in \( \mathbb{D} \) (in the sense of convergence in distribution) and that for a dense set \( H \subseteq \mathbb{R} \), \( (X^n)_{n=1,2,...} \) converges in probability in \( \mathbb{R} \) for each \( t \in H \). Then, there is a process \( X \) such that \( d_{Sk}(X^n, X) \rightarrow_\infty 0 \) in probability.

We use this Proposition for \( (\mathcal{L}^{ld,N})_{N=2,3,...} \). First, \( \mathcal{L}^{ld,N} \subseteq \mathcal{L}^N \) with \( \mathcal{L}^N \) as in Theorem [1]. Hence, as Theorem 1 shows, \( (\mathcal{L}^{ld,N})_{N=2,3,...} \) converges weakly. In particular, the sequence is relatively compact in \( \mathbb{D} \).

For all \( t \in \mathbb{R} \), we have that \( \mathcal{F}^{ld,N} \mathcal{F}^N \) with \( \mathcal{F}^N \) from [3,3]. Consequently, \( \mathcal{L}^{ld,N} \mathcal{L}^N \mathcal{L}^{ld,N} \mathcal{L}^N \rightarrow_\infty 0 \) in \( L^2 \). Since the \( L^2 \)-convergence implies convergence in probability we have proved Proposition 3.2.

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References

[1] D. Aldous. Deterministic and stochastic models for coalescence (aggregation and coagulation): a review of the mean-field theory for probabilists. Bernoulli 5(1):3–48, 1999.
[2] J. Berestycki, N. Berestycki, and V. Limic. The A-coalescent speed of coming down from infinity. *Ann. Probab.* 38(1):207–233, 2010.

[3] J. Berestycki, N. Berestycki, and J. Schweinsberg. Small-time behavior of beta coalescents. *Ann. Inst. H. Poincar Probab. Statist.* 44(2):214–238, 2008.

[4] N. Berestycki. Recent progress in coalescent theory. *Ensaio Matematicos* 16:1–193, 2009.

[5] M. G. Blum and O. François. Minimal clade size and external branch length under the neutral coalescent. *Adv. Appl. Probab.* 37:647–662, 2005.

[6] A. Caliebe, R. Neininger, M. Krawczak, and U. Rösler. On the length distribution of external branches in coalescence trees: genetic diversity within species. *Theo. Popul. Biol.* 72(2):245–252, 2007.

[7] D.A. Dawson. Measure-valued Markov processes. In P.L. Hennequin, editor, *École d’Été de Probabilités de Saint-Flour XXI–1991*, volume 1541 of *Lecture Notes in Mathematics*, pages 1–260, Berlin, 1993. Springer.

[8] J.-F. Delmas, J.-S. Dhersin, and A. Siri-Jegousse. Asymptotic results on the length of coalescent trees. *Ann. Appl. Prob.* 18(3):997–1025, 2008.

[9] J.-F. Delmas, J.-S. Dhersin, and A. Siri-Jegousse. On the two oldest families for the Wright-Fisher process. *Electron. J. Probab.* to appear, 2010.

[10] P. Donnelly and T.G. Kurtz. A countable representation of the Fleming Viot measure-valued diffusion. *Ann. Probab.* 24(2):698–742, 1996.

[11] P. Donnelly and T.G. Kurtz. Particle representations for measure-valued population models. *Ann. Probab.* 27(1):166–205, 1999.

[12] M. Drmota, A. Iksanov, M. Möhle, and U. Rösler. Asymptotic results concerning the total branch length of the Bolthausen–Sznitman coalescent. *Stochastic. Process. Appl.* 117(10):1404–1421, 2007.

[13] R. Durrett. *Probability Models for DNA Sequence Evolution*. Springer, second edition, 2008.

[14] A. Etheridge. *An introduction to superprocesses*. American Mathematical Society, 2001.

[15] A. Etheridge, P. Pfaffelhuber, and A. Wakolbinger. An approximate sampling formula under genetic hitchhiking. *Ann. Appl. Probab.* 15:685–729, 2006.

[16] S.N. Ethier and T. Kurtz. *Markov Processes. Characterization and Convergence*. John Wiley, New York, 1986.

[17] S. Evans. Kingman’s coalescent as a random metric space. In *Stochastic Models: Proceedings of the International Conference on Stochastic Models in Honor of Professor Donald A. Dawson, Ottawa, Canada, June 10-13, 1998* (L.G Gorostiza and B.G. Ivanoff eds.), Canad. Math. Soc., 2000.

[18] Y.-X. Fu and W.-H. Li. Statistical tests of neutrality of mutations. *Genetics* 133:693–709, 1993.

[19] A. Greven, P. Pfaffelhuber, and A. Winter. Tree-valued resampling dynamics. Martingale problems and applications. *Submitted*, 2010.

[20] J. F. C. Kingman. The coalescent. *Stochastic Process. Appl.* 13(3):235–248, 1982.

[21] J. F. C. Kingman. On the genealogy of large populations. *J. Appl. Probab.* 19A:27–43, 1982.
[22] M. Möhle. On the number of segregating sites for populations with large family sizes. *Adv. Appl. Probab.* 38:750–767, 2006.

[23] P. Pfaffelhuber and A. Wakolbinger. The process of most recent common ancestors in an evolving coalescent. *Stochastic Process. Appl.* 116:1836–1859, 2006.

[24] J. Pitman. Coalescents with multiple collisions. *Ann. Prob.* 27(4):1870–1902, 1999.

[25] E. M. Rauch and Y. Bar-Yam. Theory predicts the uneven distribution of genetic diversity within species. *Nature* 431:449–452, 2004.

[26] I. W. Saunders, S. Tavaré, and G. A. Watterson. On the genealogy of nested subsamples from a haploid population. *Adv. Appl. Probab.* 16:471–491, 1984.

[27] F. Tajima. Relationship between DNA polymorphism and fixation time. *Genetics* 125:447–454, 1990.

[28] S. Tavaré. Line-of-descent and genealogical processes and their applications in population genetics models. *Theor. Pop. Biol.* 26:119–164, 1984.

[29] S. Tavaré. *Ancestral Inference in Population Genetics, in: Lectures on Probability and Statistics 1188, in: Lecture Notes in Mathematics, vol. 1837.* Springer, 2004.

[30] J. Wakeley. *Coalescent Theory: An Introduction.* Roberts & Company, 2008.

[31] G.A. Watterson. Mutant substitutions at linked nucleotide sites. *Adv. Appl. Prob.* 14:166–205, 1982.

[32] C. Wiuf and J. Hein. Recombination as a point process along sequences. *Theo. Pop. Biol.* 55:248–259, 1999.