

ON THE HEIGHT AND LENGTH OF THE ANCESTRAL RE-COMBINATION GRAPH

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Abstract

The goal of this paper is to give formulas for the expectation and variance of the height and length of the ancestral recombination graph (ARG). The first formula is known, see e.g. [8], the others seem to be new. We obtain in particular (see Theorem 4.1 below) a very simple formula which expresses the expectation of the length of the ARG as a linear combination of the expectations of both the length of the coalescent tree, and the height of the ARG. Finally we study the speed at which the ARG comes down from infinity. *Keywords:* Wright–Fisher model, Coalescent, Recombination, Ancestral Recombination Graph.

2000 Mathematics Subject Classification: Primary 60J27

Secondary 60G51;92D10

1. Introduction and Preliminaries

Consider a sample of size n from a population of fixed size N . If the genealogy of the population is described by Canning’s model [2] (which generalizes the Wright–Fisher model) or by Moran’s model [9], and time is scaled by a factor $1/N$, then under very mild assumptions on the model, the genealogy of the above sample, looking backward in time, is described in the limit $N \rightarrow \infty$ by Kingman’s n -coalescent [7].

If we ignore the partitions (i.e. which genes coalesce at each coalescence event),

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Kingman's n -coalescent is a death process $\{X_t, t \geq 0\}$, where X_t is the number of lineages ancestral to the sample which are alive at time t , starting from $X_0 = n$, and ending at state 1 at the random time $\tau_1 = \inf\{t > 0, X_t = 1\}$, when the Most Recent Common Ancestor is found. Each death happens at a time when two lineages ancestral to the sample find a common ancestor. The waiting time T_k in state k is exponential with parameter $k(k-1)/2$, the various T_k 's being mutually independent. Clearly $\tau_1 = T_n + T_{n-1} + \dots + T_2$.

Let us now account for recombinations. At rate $\rho/2$ along each branch of Kingman's coalescent tree, a recombination takes place between an individual from the sample and an individual from outside the sample. Now X_t is a birth and death process, since at each recombination, the genome of an individual splits into two genomes of two different individuals. Kingman's coalescent tree is replaced by the Ancestral Recombination Graph, abbreviated ARG. The effect of recombination will be that the ancestral material to a specific DNA sequence comes from two DNA sequences in the parental generation, which again came from two different grandparents, etc. In the generation before a sequence was created by a recombination, there would have been one more sequence carrying ancestral material than after. If we focus on a single point on the sequence, it will be inherited from one parent only, thus the Wright-Fisher model with recombination reduces to the Wright-Fisher model without recombination for each point on the sequence, but different points on the sequence are correlated instances of the Wright-Fisher process without recombination. The tree relating the sequences in a single position is called the local tree of that position. Thus, the genealogy of the whole sequence can be seen as a collection of local trees, one for each position.

Births happen at rate $\rho X_t/2$, while deaths happen at rate $X_t(X_t-1)/2$. Because the death rate is a quadratic function of X_t , while the birth rate is linear, one easily shows that $\tau_1 = \inf\{t > 0, X_t = 1\}$ is finite a.s. We refer to [6], [4], [5] and [12] for more complete introductions and descriptions of Kingman's coalescent and the ARG.

Now we define the height of the ARG as $H = \tau_1 = \inf\{t, X_t = 1\}$ and the length of the ARG as $L = \int_0^{\tau_1} X_t dt$.

It does not seem possible to give formulas for the laws of H and L . In this paper we compute the first two moments of these r. v.'s. While the formula for the expectation of the height of the ARG (Theorem 2.1) is not new (see [12], and [8] where they

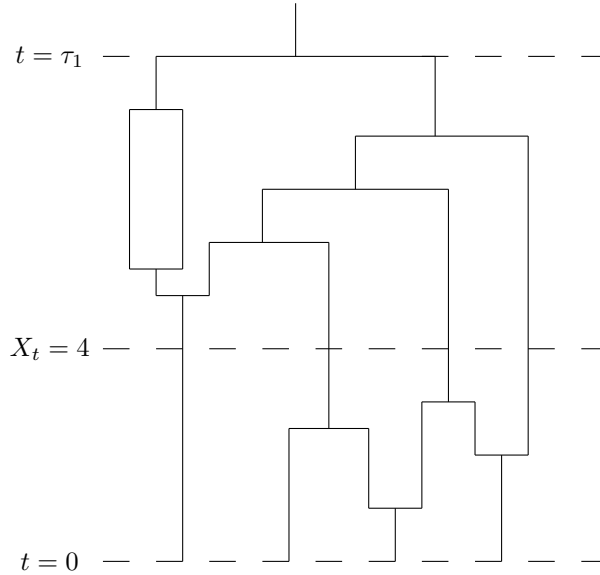


FIGURE 1: ARG

provided the analogue of Kingman’s coalescent for models with selection rather than recombination), we believe that our three other formulas are new. In particular, we obtain a very simple formula which expresses the expectation of the length of the ARG as a linear combination of that of Kingman’s coalescent, and of the expectation of the height of the ARG.

Let us make precise the fact that we do not specify any model for the splitting of the ancestral genome during a recombination event. Consequently we do not restrict the ARG to those branches which effectively contain genetic material ancestral to the sample. In other words, τ_1 is the time when the so-called Ultimate Ancestor (ancestor of all branches of the ARG) is found, which may very well differ from the MRCA of all the genetic material ancestral to the sample.

Note that a model formally identical to our ARG has been introduced by Krone and Neuhauser [8] under the name of *Ancestral selection graph*, abbreviated ASG, to model the genealogy of a population where some of the individuals possess a selective advantage. In this model an increase in the sample size while going backward in time corresponds to the fact that we do not know which branch we should follow, unless we

know whether the individual we are following backward in time possesses or not the selective advantage (this can be decided only when we follow the time forward, after having found the ultimate ancestor of the ASG). In the ASG, individuals follow one or the other branch depending upon whether they possess or not the selective advantage. In the ARG, a particular gene follows one or the other branch, depending upon whether it is located to the left or to the right of the recombination point. At any rate, our results apply as well to the ASG.

The first four sections of this paper give formulas for respectively the expectation and variance of the height of the ARG, the expectation and variance of the length of the ARG and we give formulas for the expectation and variance of the number of recombinations.

We write H_n (resp. L_n) for the height (resp. the length) of the ARG with n leaves.

It follows from the formulas below that the expectation of H_n remains bounded as $n \rightarrow \infty$. Consequently the ARG, like Kingman's coalescent, comes down from infinity, in the sense that we can define it with $X_0 = +\infty$, while $X_t < \infty$ for all $t > 0$. It is possible to describe the speed at which the ARG comes down from infinity, through a Law of Large Numbers (LLN) and a Central Limit Theorem (CLT). We show in section 8 that the ARG satisfies the same LLN and CLT as Kingman's coalescent. This indicates that asymptotically as $n \rightarrow \infty$, the number of recombination events, while X_t goes down from n to 1 is of order smaller than n . Nevertheless the number of recombination events which happen while X_t goes down from $+\infty$ is a.s. infinite. See more on this at the end of section 6.

In this paper, \mathbb{P}_ρ , \mathbb{E}_ρ and Var_ρ stand respectively for the probability, the expectation and the variance in the model where the recombination rate is $\rho/2$. The case $\rho = 0$ corresponds to Kingman's coalescent (no recombination).

2. Expectation of the height of ARG

Let us first recall that (also this result is not new, see e. g. [8] for a proof, we provide a proof since it is the model for some other proofs in this paper)

Theorem 2.1. *The expectation of the height of the ARG for a sample of n individuals*

is given by

$$\mathbb{E}_\rho(H_n) = 2 \left(1 - \frac{1}{n}\right) + 2 \sum_{k=1}^{n-1} \frac{1}{k(k+1)} \frac{e^\rho}{\rho^{k+1}} \int_0^\rho t^{k+1} \exp(-t) dt.$$

Note that the first term in this formula is well known to be $\mathbb{E}_0(H_n)$, the expectation of the height of Kingman's n -coalescent tree. The second term thus is the expectation of the additional height due to the recombinations.

Proof. Define $U_n = \mathbb{E}_\rho(H_n)$. Clearly $U_1 = 0$. Let us write a recursion formula for the U_n 's. The mean waiting time of X_t in state n is $\frac{2}{n(n+\rho-1)}$, the next state is $n+1$ with probability $\frac{\rho}{n+\rho-1}$, $n-1$ with probability $\frac{n-1}{n+\rho-1}$. Consequently, for $n \geq 2$,

$$U_n = \frac{2}{n(n+\rho-1)} + \frac{\rho}{n+\rho-1} U_{n+1} + \frac{n-1}{n+\rho-1} U_{n-1}.$$

If we define $W_n = U_n - U_{n-1}$, we obtain the following relation

$$\begin{aligned} W_n &= (n-2)! \left(2 \sum_{k=0}^{m-1} \frac{\rho^k}{(n+k)!} + \frac{\rho^m}{(n+m-2)!} W_{n+m} \right) \\ &= \frac{2(n-2)!}{\rho^n} \left(e^\rho - \sum_{k=0}^{n-1} \frac{\rho^k}{k!} \right) + \lim_{m \rightarrow \infty} \frac{(n-2)! \rho^m}{(n+m-2)!} W_{n+m}. \end{aligned}$$

On the other hand, we have

$$W_{n+m} = U_{n+m} - U_{n+m-1} = \mathbb{E}_\rho(H_{n+m}) - \mathbb{E}_\rho(H_{n+m-1}) := \mathbb{E}_\rho(T_{n+m})$$

where T_{n+m} is thought of as the time until the Birth and Death process started from $n+m$, reaches the value $n+m-1$. Let R_{n+m} be the number of recombinations which occur before the process reaches $n+m-1$, starting at state $n+m$. For $k \geq 1$ we have

$$\mathbb{P}_\rho(R_{n+m} = k) \leq a_k \left(\frac{\rho}{n+m-1} \right)^k$$

where a_k is the number of distinct sequences of $k-1$ recombinations and $k-1$ coalescences which respect the constraint that there are always at least n alive lineages. It is the ‘‘Catalan number’’ (see [11])

$$a_k = \frac{1}{k+1} \binom{2k}{k} \sim \frac{4^k}{k^{3/2} \sqrt{\pi}}. \quad (1)$$

Conditionally upon $R_{n+m} = k$, there are k births and $k+1$ deaths until the process reaches the value $n-1$. Bounding the expectation of the time between two consecutive

of those events we obtain

$$\mathbb{E}_\rho(T_{n+m} | R_{n+m} = k) \leq \frac{2(2k+1)}{(n+m)(n+m-1)}.$$

Moreover $\mathbb{P}_\rho(R_n = 0) \leq 1$. Finally, provided $n+m > 1+4\rho$,

$$\begin{aligned} \mathbb{E}_\rho(T_{n+m}) &= \sum_{k=0}^{\infty} \mathbb{E}_\rho(T_{n+m} | R_n = k) \mathbb{P}_\rho(R_{n+m} = k) \\ &\leq \frac{c}{(n+m)(n+m-1)} \sum_{k=0}^{\infty} \left(\frac{4\rho}{n+m-1} \right)^k \\ &\leq \frac{c'}{(n+m)(n+m-1)} \end{aligned}$$

It is now easy to deduce that $U_{n+1} - U_n = 2 \frac{(n-1)!}{\rho^{n+1}} \sum_{j=n+1}^{\infty} \frac{\rho^j}{j!}$ and consequently

$$U_n = \sum_{k=1}^{n-1} (U_{k+1} - U_k) = 2 \sum_{k=1}^{n-1} \frac{(k-1)!}{\rho^{k+1}} \sum_{j=k+1}^{\infty} \frac{\rho^j}{j!}$$

since $U_1 = 0$. We now deduce the following formula for $\mathbb{E}_\rho(H_n) = U_n$

$$\begin{aligned} \mathbb{E}_\rho(H_n) &= 2 \sum_{k=1}^{n-1} \sum_{j=0}^{\infty} \frac{(k-1)!}{(k+j+1)!} \rho^j \\ &= 2 \left(1 - \frac{1}{n} \right) + 2 \sum_{k=1}^{n-1} \frac{1}{k(k+1)} \frac{(k+1)!}{\rho^{k+1}} \sum_{\ell=k+2}^{\infty} \frac{\rho^\ell}{\ell!} \end{aligned} \quad (2)$$

and the result finally follows from the following identity, which is easily checked by successive integrations by parts

$$e^\rho \int_0^\rho t^{k+1} \exp(-t) dt = (k+1)! \left(e^\rho - \sum_{\ell=0}^{k+1} \frac{\rho^\ell}{\ell!} \right).$$

Corollary 2.1. *For small $\rho > 0$*

$$\mathbb{E}_\rho(H_n) = 2 \left(1 - \frac{1}{n} \right) + \frac{(n-1)(n+2)}{2n(n+1)} \rho + \frac{(n-1)(n^2+4n+6)}{9n(n+1)(n+2)} \rho^2 + O(\rho^3).$$

Corollary 2.2. *As $n \rightarrow \infty$*

$$\lim_{n \rightarrow \infty} \mathbb{E}_\rho(H_n) = \frac{2}{\rho} \int_0^1 \frac{e^{\rho x} - 1}{x} dx.$$

Proof.

$$\begin{aligned} \lim_{n \rightarrow \infty} \mathbb{E}_\rho(H_n) &= 2 \sum_{j=1}^{\infty} \sum_{k=1}^{\infty} \frac{\rho^j}{k(k+1) \cdots (k+j+1)} \\ &= \frac{2}{\rho} \sum_{j=1}^{\infty} \frac{\rho^j}{j \cdot j!} \\ &= \frac{2}{\rho} \int_0^\rho \frac{e^x - 1}{x} dx \end{aligned}$$

where the second equality follows from

$$\sum_{k=1}^{\infty} \frac{1}{k(k+1) \cdots (k+j)} = \frac{1}{j \cdot j!}, \quad \forall j \geq 1. \quad (3)$$

See the Appendix A for a proof.

3. Variance of the height of the ARG

Definition 3.1. For all $p, q \in \mathbb{N}$, we define the hypergeometric function ${}_pF_q$ as a mapping from $\mathbb{R}_+^p \times \mathbb{R}_+^q \times \mathbb{R}$ into \mathbb{R} as follows

$${}_pF_q([a_1, \dots, a_p], [b_1, \dots, b_q], z) = \sum_{r=0}^{\infty} \frac{(a_1)_r \cdots (a_p)_r}{(b_1)_r \cdots (b_q)_r} \frac{z^r}{r!},$$

where for all $a \in \mathbb{R}$ and $r \in \mathbb{N}$,

$$(a)_r = a(a+1) \cdots (a+r-1).$$

For more on this subject see [10].

Theorem 3.1. *The variance of the height of the ARG is given by*

$$\begin{aligned} \text{Var}_\rho(H_n) &= \sum_{p=2}^n 4 \frac{{}_3F_3([1, p, p+\rho-1], [p+\rho, p+1, p+1], \rho)}{(p+\rho-1)p^2(p-1)} \\ &\quad + \sum_{p=2}^n \sum_{k=1}^{\infty} \frac{4(p-2)! \rho^k}{(p+k-3)!(p+k+\rho-2)((p+k-1)^2-1)^2(p+k-1)^2} \\ &\quad \times \left(2(p+k-1) + \rho + \frac{(p+k+\rho-2)e^\rho}{\rho^{p+k}} \int_0^\rho t^{p+k} e^{-t} dt \right)^2. \end{aligned}$$

Proof. The proof of this result is deferred to the Appendix B.

Note that it can be shown that $\text{Var}_\rho(H_n) \leq c(\rho) < \infty$ for all $n \geq 2$, where $c(\rho) = \frac{2}{45} \pi^4 (e^\rho + 4e^{2\rho}(e^\rho - 1))$.

4. Expectation of the length of the ARG

We now state and prove a very simple formula for the expectation of the length of the ARG.

Theorem 4.1. *The expectation of the length of the ARG is given by*

$$\mathbb{E}_\rho(L_n) = \mathbb{E}_0(L_n) + \rho \mathbb{E}_\rho(H_n).$$

Proof. The proof of this Theorem is given in the Appendix C.

Recalling that (in case $\rho = 0$, the ARG reduces to Kingman's coalescent)

$$\mathbb{E}_0(L_n) = 2 \left(1 + \cdots + \frac{1}{n-1} \right),$$

we deduce from the last Theorem

Corollary 4.1. *For large n ,*

$$\lim_{n \rightarrow \infty} \mathbb{E}_\rho(L_n) \sim 2 \ln(n) + \frac{2}{\rho} \int_0^\rho \frac{e^x - 1}{x} dx.$$

We note that the additional length produced by the recombinations is bounded in mean, as $n \rightarrow \infty$.

5. Variance of the length of the ARG

Theorem 5.1. *The variance of the length of the ARG is given by*

$$\text{Var}_\rho(L_n) = \sum_{p=2}^n \left[4 \frac{{}_2F_2([1, p + \rho - 1], [p + \rho, p], \rho)}{(p + \rho - 1)(p - 1)} + \sum_{k=1}^{\infty} \frac{(p - 2)! \rho^{k-1}}{(p + k - 3)!} B_{p+k-1} \right]$$

where

$$B_n = \frac{4\rho}{n^2(n-1)^2(n+\rho-1)} \left(2n-1 + \frac{2n\rho + \rho^2}{n+1} + \frac{(n+\rho-1)e^\rho}{(n+1)\rho^n} \int_0^\rho t^{n+1} e^{-t} dt \right)^2.$$

Proof. The proof of this Theorem is postponed to Appendix D.

It can be shown that $\text{Var}_\rho(L_n) \leq c'(\rho)$ for all $n \geq 2$, where $c'(\rho) \leq \frac{2}{3} \pi^2 e^\rho (4e^\rho + 1)$.

6. Expectation of the number of recombinations

We denote again by R_n the number of recombinations which happen before the process $\{X_t, t \geq 0\}$ reaches the value $n - 1$, while starting from $X_0 = n$.

Theorem 6.1. *The expectation of R_n is given by*

$$\mathbb{E}_\rho(R_n) = \rho \int_0^1 s^{n-2} e^{\rho(1-s)} ds.$$

Proof. The proof of this Theorem is given in the Appendix E.

Theorem 6.2. *Let $R(n)$ denote the total number of recombination events in the sample of size n before X_t reaches the value 1. We have the identity*

$$\mathbb{E}_\rho(L_n) = \frac{2}{\rho} \mathbb{E}_\rho(R(n)).$$

Proof. Starting from the identity (2), we have

$$\begin{aligned} \mathbb{E}_\rho(H_n) &= 2 \sum_{k=1}^{n-1} \frac{(k-1)!}{\rho^{k+1}} \sum_{j=k+1}^{\infty} \frac{\rho^j}{j!} \\ &= \frac{2}{\rho^2} \sum_{k=1}^{n-1} \frac{(k-1)!}{\rho^{k-1}} \sum_{j=k}^{\infty} \frac{\rho^j}{j!} - \sum_{k=1}^{n-1} \frac{2}{k\rho} \\ &= \frac{2}{\rho^2} \sum_{k=1}^{n-1} \mathbb{E}_\rho(R_{k+1}) - \frac{1}{\rho} \mathbb{E}_0(L_n) \\ &= \frac{2}{\rho^2} \mathbb{E}_\rho(R(n)) - \frac{1}{\rho} \mathbb{E}_0(L_n). \end{aligned}$$

The result now follows from Theorem 4.1.

Remark 1. Note that

$$\frac{\rho}{n-1} < \mathbb{E}_\rho(R_n) < \frac{\rho e^\rho}{n-1}.$$

This is consistent with

$$\frac{\rho}{n+\rho-1} = \mathbb{P}_\rho(R_n \geq 1) \leq \mathbb{E}_\rho(R_n).$$

Since the R_n 's are mutually independent and $\sum_n \mathbb{P}_\rho(R_n \geq 1) = +\infty$, it follows from the Borel–Cantelli Lemma that a.s. infinitely many recombination events occur while the ARG comes down from infinity.

On the other hand, the expectation of the total number of recombination events which occur while X_t goes down from n to 1 equals

$$\sum_{k=2}^n \mathbb{E}_\rho(R_k) = \rho \int_0^1 \frac{1-s^{n-1}}{1-s} e^{\rho(1-s)} ds.$$

This grows, up to a multiplicative constant, like $\rho \ln(n-1)$ while the number of coalescence events grows like n .

7. Variance of the number of recombinations

Theorem 7.1. *The variance of the number of recombinations is given by*

$$\text{Var}_\rho(R_n) = \frac{\rho(n-2)}{(n-2)!} \sum_{i=0}^{\infty} \frac{(n+i-1)!}{\rho^{n-i-3}} \prod_{k=0}^i \frac{1}{(n+k+\rho-1)^2 - \rho(n-1)}.$$

Proof. See the Appendix F for a proof.

8. The speed at which the ARG comes down from infinity

We have

$$\begin{aligned} \mathbb{E}_\rho(H_n) &= 2 \sum_{k=1}^{n-1} \sum_{j=0}^{\infty} \frac{(k-1)!}{(k+j+1)!} \rho^j \\ &= 2 \sum_{k=1}^{n-1} \frac{1}{k(k+1)} \sum_{j=0}^{\infty} \frac{\rho^j}{(k+2) \cdots (k+j+1)} \\ &\leq 2 \sum_{k=1}^{n-1} \frac{1}{k(k+1)} \sum_{j=0}^{\infty} \frac{\rho^j}{j!} \\ &= 2e^\rho \left(1 - \frac{1}{n}\right). \end{aligned}$$

So for fixed ρ , $\mathbb{E}_\rho(H_n) \leq 2e^\rho$ for all $n \geq 2$. Consequently $H_\infty = \lim_{n \rightarrow \infty} H_n$ is finite a.s. We can then clearly define the population size $\{X_t, 0 < t \leq \tau_1\}$, where again $\tau_1 = \inf\{t, X_t = 1\}$, in such a way that $X_0 = +\infty$, while $X_t < \infty$ for all $t > 0$. Here as in the Introduction, X_t is a birth and death process, with birth rate $\rho X_t/2$ and death rate $X_t(X_t - 1)/2$. Indeed, if we let $\{X_t^n, 0 < t \leq \tau_1\}$ denote the same process satisfying the initial condition $X_0^n = n$, then one can show that $X_{\cdot \wedge \tau_1} = \lim_{n \rightarrow \infty} X_{\cdot \wedge \tau_1}^n$ exists, where the limit is a weak limit for the Skorohod topology of $D_E[0, +\infty)$, with $E = \{0, 1, 2, \dots\} \cup \{+\infty\}$, following the arguments in [3].

The speed at which the ARG comes down from infinity is described by the following result, which contains both a law of large numbers and a central limit Theorem.

Theorem 8.1. *For all $\rho \geq 0$, as $t \rightarrow 0$,*

$$\frac{t X_t}{2} \rightarrow 1 \quad \mathbb{P}_\rho \text{ a.s.} \quad (4)$$

and moreover under \mathbb{P}_ρ ,

$$\sqrt{\frac{6}{t}} \left(\frac{t X_t}{2} - 1 \right) \Rightarrow \mathcal{N}(0, 1). \quad (5)$$

This Theorem says in a sense that X_t is asymptotically $\mathcal{N}(2/t, 2/3t)$ as $t \rightarrow 0$. This result does not depend upon ρ . It is the same for $\rho > 0$ and $\rho = 0$. This means that the number R_n of recombinations which happen before X_t reaches 1, starting with $X_t = n$, is of order smaller than n , as was already pointed out at the end of section 6.1. Denote again by T_n the time taken by the process X_t to reach the value $n - 1$, starting with $X_t = n$, and define

$$V_n = \sum_{k=n+1}^{\infty} T_k,$$

which is the time taken by the process X_t to reach the value n , starting from $X_0 = +\infty$.

Clearly

$$\sum_{n=1}^{\infty} n \mathbb{I}_{\{V_n \leq t < V_{n-1}\}} \leq X_t \leq \sum_{n=1}^{\infty} (n + R_n) \mathbb{I}_{\{V_n \leq t < V_{n-1}\}}.$$

Theorem 8.1 follows from

Proposition 8.1. *For all $\rho \geq 0$, as $n \rightarrow \infty$,*

$$\frac{n V_n}{2} \rightarrow 1 \quad \mathbb{P}_\rho \text{ a.s.} \quad (6)$$

and moreover under \mathbb{P}_ρ ,

$$\sqrt{3n} \left(\frac{n V_n}{2} - 1 \right) \Rightarrow \mathcal{N}(0, 1), \quad (7)$$

which in turn follows from

Proposition 8.2. *For all $\rho > 0$,*

$$\mathbb{E}_\rho(|V_n - \mathbb{E}_\rho(V_n)|^4) \leq \frac{c(\rho)}{n^6}; \quad (8)$$

$$\mathbb{E}_\rho(V_n) = \frac{2}{n} + O\left(\frac{1}{n^2}\right); \quad (9)$$

$$n^3 \text{Var}_\rho(V_n) \rightarrow \frac{4}{3}. \quad (10)$$

Note that the only difference in the statements of Proposition 8.2 between the cases $\rho > 0$ and $\rho = 0$ is that in case $\rho = 0$ (9) reads $\mathbb{E}_0(V_n) = 2/n$.

Aldous [1] states Theorem 8.1 in the case $\rho = 0$ (no recombination). The proof of the three above statements, in reversed order, will be the object of the next three subsections.

8.1. Proof of Proposition 8.2

Proof of (8) Recall that

$$\mathbb{P}_\rho(R_n = k) \leq a_k \left(\frac{\rho}{n-1}\right)^k,$$

where a_k is the Catalan number given by (1). So

$$\begin{aligned} \mathbb{E}_\rho(|V_n - \mathbb{E}_\rho(V_n)|^4) &= \mathbb{E}_\rho \left(\sum_{k=n+1}^{\infty} |T_n - \mathbb{E}_\rho(T_n)|^4 \right) \\ &\quad + 6\mathbb{E}_\rho \left(\sum_{n < k < l} |T_k - \mathbb{E}_\rho(T_k)|^2 |T_l - \mathbb{E}_\rho(T_l)|^2 \right) \\ &= \sum_{k=n+1}^{\infty} \mathbb{E}_\rho(|T_n - \mathbb{E}_\rho(T_n)|^4) \\ &\quad + 6 \sum_{n < k < l} \mathbb{E}_\rho(|T_k - \mathbb{E}_\rho(T_k)|^2) \mathbb{E}_\rho(|T_l - \mathbb{E}_\rho(T_l)|^2). \end{aligned}$$

So we have to estimate both $\mathbb{E}_\rho(|T_k - \mathbb{E}_\rho(T_k)|^4)$ and $\mathbb{E}_\rho(|T_k - \mathbb{E}_\rho(T_k)|^2)$. It is not hard to prove that

$$\mathbb{E}_\rho(T_k^2 | R_k = m) \leq \frac{2^3(2m+1)^2}{(k+1)^2 k^2}.$$

Hence

$$\mathbb{E}_\rho(|T_k - \mathbb{E}_\rho(T_k)|^2) \leq \mathbb{E}_\rho(T_k^2) \leq \frac{2^3}{(k+1)^2 k^2} \left(1 + \frac{c'\rho}{k}\right).$$

By a similar argument

$$\mathbb{E}_\rho(|T_k - \mathbb{E}_\rho(T_k)|^4) \leq \mathbb{E}_\rho(T_k^4) \leq \sum_{l=1}^{\infty} \mathbb{E}_\rho(T_k^4 | R_k = l) a_l \left(\frac{\rho}{k}\right)^l + \frac{2^5}{k^4(k+1)^4},$$

and standard arguments lead to

$$\mathbb{E}_\rho(T_k^4 | R_k = m) \leq \frac{2^5(2m+1)^4}{k^4(k+1)^4}.$$

Now we have

$$\mathbb{E}_\rho(|T_k - \mathbb{E}_\rho(T_k)|^4) \leq \frac{2^5}{k^4(k+1)^4} \left(1 + \sum_{l=1}^{\infty} (2l+1)^4 \left(\frac{4\rho}{k} \right)^l \right).$$

It is easy to show that for $k > 8\rho$

$$\sum_{l=1}^{\infty} (l+1)^4 \left(\frac{4\rho}{k} \right)^l \leq 32 \frac{4\rho}{k}. \quad (11)$$

Hence

$$\mathbb{E}_\rho(|T_k - \mathbb{E}_\rho(T_k)|^4) \leq \frac{2^5}{k^4(k+1)^4} \left(1 + 32 \frac{4\rho}{k} \right). \quad (12)$$

Now by combining (11)-(12) we obtain

$$\begin{aligned} \mathbb{E}_\rho(|V_n - \mathbb{E}_\rho(V_n)|^4) &\leq \sum_{k=n+1}^{\infty} \frac{2^5}{k^4(k+1)^4} \left(1 + \frac{c''\rho}{k} \right) \\ &\quad + 6 \sum_{n < k < l} \frac{2^3}{k^2(k+1)^2} \left(1 + \frac{c'\rho}{k} \right) \frac{2^3}{l^2(l+1)^2} \left(1 + \frac{c'''\rho}{l} \right) \\ &\leq 2(1+c''\rho) \sum_{k=n+1}^{\infty} \frac{2^4}{k^4(k+1)^4} + \sum_{n \leq k < l} \frac{3 \times 2^7 (1+c'\rho)(1+c'''\rho)}{k^2(k+1)^2 l^2(l+1)^2} \\ &\leq \frac{2^5(1+c''\rho)}{7(n-1)^7} + \frac{2^7(1+c'\rho)(1+c'''\rho)}{3(n-1)^6}. \end{aligned}$$

Proof of (9) Since $T_n = H_n - H_{n-1}$, we deduce from Theorem 2.1

$$\mathbb{E}_\rho(T_n) = 2 \sum_{j=0}^{\infty} \frac{(n-2)!}{(n+j)!} \rho^j.$$

Then

$$\mathbb{E}_\rho(V_n) = \frac{2}{n} + 2 \sum_{k=n+1}^{\infty} \sum_{j=1}^{\infty} \frac{(k-2)!}{(k+j)!} \rho^j = \frac{2}{n} + O\left(\frac{1}{n^2}\right).$$

Proof of (10) Since $H_n = T_n + H_{n-1}$, H_{n-1} and T_n are independent,

$$\begin{aligned} \text{Var}_\rho(T_n) &= \sum_{k=1}^{\infty} \frac{4(n-2)! \rho^{k-1}}{(n+\rho+k-2)(n+k-1)^2(n+k-2)!} \\ &\quad + \sum_{k=1}^{\infty} \frac{(n-2)! \rho^k}{(n+k-3)!(n+k+\rho-2)} \left(\sum_{j=0}^{\infty} \frac{2(n+k-3)!(2n+2k+j-2)}{(n+k+j)!} \rho^j \right)^2. \end{aligned}$$

It is easy to show that

$$\sum_{l=n+1}^{\infty} \left[\sum_{k=1}^{\infty} \frac{4(l-2)!\rho^{k-1}}{(l+\rho+k-2)(l+k-1)^2(l+k-2)!} \right] = \sum_{l=n}^{\infty} \frac{4}{(l+\rho)(l+1)^2 l} + O\left(\frac{1}{n^4}\right)$$

and also

$$\sum_{l=n+1}^{\infty} \sum_{k=1}^{\infty} \frac{(l-2)!\rho^k}{(l+k-3)!(l+k+\rho-2)} \left[\sum_{j=0}^{\infty} \frac{2(l+k-3)!(2l+2k+j-2)}{(l+k+j)!} \rho^j \right]^2 = O\left(\frac{1}{n^4}\right).$$

Hence

$$\text{Var}_{\rho}(V_n) = \sum_{l=n}^{\infty} \frac{4}{(l+\rho)(l+1)^2 l} + O\left(\frac{1}{n^4}\right).$$

But

$$\frac{1}{3(n+\rho)^3} = \int_{n+1}^{\infty} \frac{dx}{(x+\rho)^4} \leq \sum_{l=n}^{\infty} \frac{1}{(l+\rho)(l+1)^2 l} \leq \int_{n-1}^{\infty} \frac{dx}{x^4} = \frac{1}{3(n-1)^3},$$

and the result follows.

8.2. Proof of Proposition 8.1

The relation (6) follows easily from (8), (9) and the Borel–Cantelli lemma. We now prove (7). It suffices to prove that the sequence

$$Z_n = \frac{\sqrt{3n^3}}{2}(V_n - \mathbb{E}_{\rho}(V_n))$$

converges in law to $\mathcal{N}(0, 1)$.

Let ϕ_n be the characteristic function of the r.v. Z_n , $c_n = \sqrt{3n^3}/2$ and $\bar{T}_k = T_k - \mathbb{E}_{\rho}(T_k)$. For every $t \in \mathbb{R}$, the characteristic function of \bar{T}_k satisfies

$$\Psi_{\bar{T}_k} = 1 - t^2 \frac{c_n^2}{2} \text{Var}_{\rho}(\bar{T}_k) - \frac{ic_n^3 t^3}{6} (\mathbb{E}_{\rho}[(\bar{T}_k)^3] + \delta_k(t))$$

where for all $k \geq 1$, $\delta_k(t) \rightarrow 0$ as $t \rightarrow 0$, and $|\delta_k(t)| \leq 2\mathbb{E}_\rho(|\bar{T}_k|^3), \forall t \in \mathbb{R}$. We have

$$\begin{aligned}
\phi_n(t) &= \mathbb{E}_\rho \left[e^{itc_n \sum_{k=n+1}^{\infty} \bar{T}_k} \right] \\
&= \prod_{k=n+1}^{\infty} \mathbb{E}_\rho \left[e^{itc_n \bar{T}_k} \right] \\
&= \exp \left(\sum_{k=n+1}^{\infty} \log \left(1 - t^2 \frac{c_n^2}{2} \text{Var}_\rho(\bar{T}_k) - \frac{ic_n^3 t^3}{6} (\mathbb{E}_\rho[(\bar{T}_n)^3] + \delta_k(t)) \right) \right) \\
&= \exp \left(\sum_{k=n+1}^{\infty} \left(-t^2 \frac{c_n^2}{2} \text{Var}_\rho(\bar{T}_k) - \frac{ic_n^3 t^3}{6} (\mathbb{E}_\rho[(\bar{T}_n)^3] + \delta_k(t)) \right) \right) \\
&= \exp \left(-t^2 \frac{c_n^2}{2} \text{Var}_\rho(V_n) - \sum_{k=n+1}^{\infty} \frac{ic_n^3 t^3}{6} (\mathbb{E}_\rho[(\bar{T}_n)^3] + \delta_k(t)) \right) \\
&= \exp \left(-t^2 \frac{3n^3}{8} \text{Var}_\rho(V_n) + O\left(\frac{1}{n^{3/2}}\right) \right) \\
&\rightarrow \exp(-t^2/2).
\end{aligned}$$

The fourth identity follows from

$$\mathbb{E}_\rho(|\bar{T}_n|^3) = \mathbb{E}_\rho(|T_k - \mathbb{E}_\rho(T_k)|^3) \leq (\mathbb{E}_\rho(|T_k - \mathbb{E}_\rho(T_k)|^4))^{3/4} = \frac{c}{k^6} (1 + O(1/k)).$$

8.3. Proof of Theorem 8.1

The idea is to use the relations $I_t \leq X_t \leq J_t$, where

$$I_t = \sum_{n=1}^{\infty} n \mathbb{I}_{\{V_n \leq t < V_{n-1}\}}, \quad J_t = \sum_{n=1}^{\infty} (n + R_n) \mathbb{I}_{\{V_n \leq t < V_{n-1}\}}.$$

We first show

Lemma 8.1. *As $t \rightarrow 0$,*

$$\sqrt{t}(J_t - I_t) \rightarrow 0 \quad \mathbb{P}_\rho \text{ a.s.}$$

Proof. We note that for all $\varepsilon > 0$,

$$\{\limsup_{t \rightarrow 0} \sqrt{t}(J_t - I_t) > \varepsilon\} \subset \limsup_n A_n,$$

where

$$A_n = \{\sqrt{V_{n-1}} R_n > \varepsilon\}.$$

But

$$\begin{aligned} \mathbb{P}_\rho(A_n) &\leq \mathbb{P}_\rho(V_{n-1} > \varepsilon^2 n^{-1/4}) + \mathbb{P}_\rho(R_n > n^{1/8}) \\ &\leq \frac{\sqrt{n}}{\varepsilon^4} \mathbb{E}_\rho(V_{n-1}^2) + n^{-1/4} \mathbb{E}_\rho(R_n) \\ &\leq c(\varepsilon, \rho) n^{-3/2} + \rho e^\rho n^{-9/8}. \end{aligned}$$

Consequently $\sum_n \mathbb{P}_\rho(A_n) < \infty$. The result follows.

It now remains to prove Theorem 8.1 with X_t replaced by I_t , i.e. we only have to verify that as $t \rightarrow 0$,

$$\frac{t I_t}{2} \rightarrow 1 \quad \mathbb{P}_\rho \text{ a.s.} \quad (13)$$

and moreover

$$\sqrt{\frac{6}{t}} \left(\frac{t I_t}{2} - 1 \right) \Rightarrow \mathcal{N}(0, 1) \text{ under } \mathbb{P}_\rho. \quad (14)$$

Let us first prove (13). We have

$$\left\{ \limsup_{t \rightarrow 0} \left| \frac{t I_t}{2} - 1 \right| > \varepsilon \right\} \subset \limsup_n B_n,$$

where

$$B_n = \left\{ \sup_{V_n \leq t < V_{n-1}} \left| \frac{tn}{2} - 1 \right| > \varepsilon \right\}.$$

Consequently

$$B_n \subset \left\{ \left| \frac{nV_n}{2} - 1 \right| > \varepsilon \right\} \cup \left\{ \left| \frac{(n-1)V_{n-1}}{2} - 1 \right| > \varepsilon/2 \right\} \cup \{V_{n-1} > \varepsilon\}.$$

It follows from (6) that $\mathbb{P}_\rho(\limsup_n B_n) = 0$ provided $\varepsilon > 0$. Hence (13) is established.

Let us finally prove (14). For all $t > 0$, let

$$\tau(t) = \inf\{0 < s \leq t, I_s = I_t\}.$$

It follows readily from (7) that The relation

$$\sqrt{3I_t} \left(\frac{\tau(t)I_t}{2} - 1 \right) \Rightarrow \mathcal{N}(0, 1).$$

Combining with (13), we deduce that

$$\sqrt{\frac{6}{t}} \left(\frac{\tau(t)I_t}{2} - 1 \right) \Rightarrow \mathcal{N}(0, 1).$$

(14) will follow if we prove that

$$\frac{t - \tau(t)}{\sqrt{t}} I_t \rightarrow 0 \quad \text{in probability, as } t \rightarrow 0,$$

which from (13) is equivalent to

$$t^{-3/2}(t - \tau(t)) \rightarrow 0 \quad \text{in probability, as } t \rightarrow 0.$$

This is a consequence of

$$V_n^{-3/2} T_n \rightarrow 0 \quad \text{in probability, as } n \rightarrow \infty.$$

Since $nS_n \rightarrow 2$ a.s. as $n \rightarrow \infty$, it suffices to show that $n^{3/2}T_n$ tends to 0 in probability.

But $\mathbb{E}_\rho(T_n) \leq c/n^2$. The result follows.

Appendix A. Proof of (3)

We define

$$C_j := \sum_{k=1}^{\infty} \frac{1}{k(k+1)\dots(k+j)}.$$

It is easy to show that $C_j - C_{j+1} = C_j - \frac{1}{(j+1)!} + jC_{j+1}$, so

$$C_{j+1} = \frac{1}{(j+1)(j+1)!}, \forall j \geq 0.$$

On the other hand,

$$\sum_{j=1}^{\infty} \frac{\rho^{j-1}}{j!} = \frac{e^\rho - 1}{\rho} \quad \text{hence} \quad \sum_{j=1}^{\infty} \frac{\rho^j}{j \cdot j!} = \int_0^\rho \frac{e^x - 1}{x} dx.$$

Appendix B. Proof of Theorem 3.1

$$H_n = S_n + H_{n-1} \mathbb{I}_{\{Coalescence\}} + H_{n+1} \mathbb{I}_{\{Recombination\}}$$

where S_n is the time until the first jump, starting with n individuals. It is easy to show that S_n is independent of $H_{n-1} \mathbb{I}_{\{Coalescence\}} + H_{n+1} \mathbb{I}_{\{Recombination\}}$, hence

$$\text{Var}_\rho(H_n) = \text{Var}_\rho(S_n) + \text{Var}_\rho(H_{n-1} \mathbb{I}_{\{Coalescence\}} + H_{n+1} \mathbb{I}_{\{Recombination\}}).$$

Since moreover H_{n-1} and the event $\{Coalescence\}$ are independent, as well as H_{n+1} and the event $\{Recombination\}$,

$$\begin{aligned} \text{Var}_\rho(H_n) - \text{Var}_\rho(H_{n-1}) &= \frac{4}{(n+\rho-1)n^2(n-1)} + \frac{\rho}{n-1}(\text{Var}_\rho(H_{n+1}) - \text{Var}_\rho(H_n)) \\ &\quad + \frac{\rho}{n+\rho-1}(\mathbb{E}_\rho(H_{n+1}) - \mathbb{E}_\rho(H_{n-1}))^2. \end{aligned}$$

But we have

$$\mathbb{E}_\rho(H_{n+1}) - \mathbb{E}_\rho(H_{n-1}) = \sum_{j=0}^{\infty} \frac{2(n-2)!(2n+j)}{(n+j+1)!} \rho^j.$$

If we now define $Y_n := \text{Var}_\rho(H_n) - \text{Var}_\rho(H_{n-1})$, we have

$$Y_n = \frac{4}{(n+\rho-1)n^2(n-1)} + \frac{\rho}{n-1}Y_{n+1} + \frac{\rho}{n+\rho-1} \left(\sum_{j=0}^{\infty} \frac{2(n-2)!(2n+j)}{(n+j+1)!} \rho^j \right)^2.$$

Hence

$$Y_n = \frac{4}{(n+\rho-1)n^2(n-1)} + \frac{\rho}{n-1}Y_{n+1} + A_n$$

where

$$A_n = \frac{\rho}{n+\rho-1} \left(\sum_{j=0}^{\infty} \frac{2(n-2)!(2n+j)}{(n+j+1)!} \rho^j \right)^2.$$

It is easy to deduce the following recursion formula for Y_n

$$\begin{aligned} Y_n &= \sum_{k=1}^m \frac{4(n-2)!\rho^{k-1}}{(n+\rho+k-2)(n+k-1)^2(n+k-2)!} \\ &\quad + \sum_{k=1}^m \frac{(n-2)!\rho^{k-1}}{(n+k-3)!} A_{n+k-1} + \frac{(n-2)!\rho^m}{(n+m-2)!} Y_{n+m}. \end{aligned}$$

But we have

$$A_n = \frac{4\rho}{n+\rho-1} \left(\sum_{j=0}^{\infty} \frac{2n}{(n-1)n \cdots (n+j+1)} \rho^j + \sum_{j=0}^{\infty} \frac{j}{(n-1)n \cdots (n+j+1)} \rho^j \right)^2 \quad (15)$$

and easily we obtain

$$\begin{aligned}
& \sum_{j=0}^{\infty} \frac{\rho^j}{n(n+1)\cdots(n+j+1)} \\
&= \frac{1}{n(n+1)} + \frac{1}{n(n+1)} \left[\frac{\rho}{n+2} + \frac{\rho^2}{(n+2)(n+3)} + \frac{\rho^3}{(n+2)(n+3)(n+4)} + \cdots \right] \\
&= \frac{1}{n(n+1)} + \frac{1}{n(n+1)} \frac{e^\rho}{\rho^{n+1}} \sum_{j=0}^{\infty} (-1)^j \frac{\rho^{n+j+2}}{j!(n+j+2)} \\
&= \frac{1}{n(n+1)} + \frac{1}{n(n+1)} \frac{e^\rho}{\rho^{n+1}} \int_0^\rho t^{n+1} \exp(-t) dt.
\end{aligned}$$

The second identity follows from

$$\frac{1}{(n+2)(n+3)\cdots(n+j+1)} = \frac{a_2}{n+2} + \frac{a_3}{n+3} + \cdots + \frac{a_{j+1}}{n+j+1},$$

where the coefficients are given by $a_l = \frac{(-1)^l}{(l-2)!(j-l+1)!}$.

The first term in the right of (15) can be written as

$$\frac{2n}{n-1} \sum_{j=0}^{\infty} \frac{\rho^j}{n(n+1)\cdots(n+j+1)} = \frac{2}{n^2-1} \left(1 + \frac{e^\rho}{\rho^{n+1}} \int_0^\rho t^{n+1} e^{-t} dt \right),$$

and also

$$\sum_{j=0}^{\infty} \frac{\rho^j}{(n-1)n\cdots(n+j+1)} = \frac{2}{n(n^2-1)} \left(1 + \frac{e^\rho}{\rho^{n+1}} \int_0^\rho t^{n+1} e^{-t} dt \right).$$

Differentiating with respect to ρ and multiplying by ρ , we deduce

$$\sum_{j=0}^{\infty} \frac{j\rho^j}{(n-1)n\cdots(n+j+1)} = \frac{\rho}{n(n^2-1)} \left(1 + \frac{(\rho-n-1)e^\rho}{\rho^{n+2}} \int_0^\rho t^{n+1} e^{-t} dt \right).$$

So we have the following identity

$$A_n = \frac{4\rho}{(n+\rho-1)(n^2-1)^2 n^2} \left(2n + \rho + \frac{(n+\rho-1)e^\rho}{\rho^{n+1}} \int_0^\rho t^{n+1} e^{-t} dt \right)^2 \quad (16)$$

from which we deduce that

$$A_n \leq \frac{16\rho}{n^2(n-1)^2(n+\rho-1)} \left(\sum_{j=0}^{\infty} \frac{\rho^j}{j!} \right)^2 \leq 16\rho e^{2\rho}.$$

Hence $\sum_{k=0}^{\infty} \frac{A_{k+2}\rho^k}{k!}$ converges for all ρ .

Now, by letting m tend to ∞ , we have the following

$$Y_n = \sum_{k=1}^{\infty} \frac{4(n-2)! \rho^{k-1}}{(n+\rho+k-2)(n+k-1)^2(n+k-2)!} \\ + \sum_{k=1}^{\infty} \frac{(n-2)! \rho^{k-1}}{(n+k-3)!} A_{n+k-1} + \lim_{m \rightarrow \infty} \frac{(n-2)! \rho^m}{(n+m-2)!} Y_{n+m}.$$

It is easy to check that

$$\sum_{k=1}^{\infty} \frac{4(n-2)! \rho^{k-1}}{(n+\rho+k-2)(n+k-1)^2(n+k-2)!} \\ = 4 \frac{{}_3F_3([1, n, n+\rho-1], [n+\rho, n+1, n+1], \rho)}{(n+\rho-1)n^2(n-1)}.$$

We need to show that

$$\lim_{m \rightarrow \infty} \frac{(n-2)! \rho^m}{(n+m-2)!} Y_{n+m} = 0.$$

With the notation introduced in section 2, we have that $H_{n+m} = T_{n+m} + H_{n+m-1}$, and from the strong Markov property, T_{n+m} and H_{n+m-1} are independent, consequently

$$\text{Var}_{\rho}(H_{n+m}) - \text{Var}_{\rho}(H_{n+m-1}) = \text{Var}_{\rho}(T_{n+m}) \leq \mathbb{E}_{\rho}(T_{n+m}^2).$$

By an argument similar to that in the proof of Theorem 2.1, one can show that

$$\mathbb{E}_{\rho}(T_{n+m}^2) \leq \frac{c'}{(n+m)^2(n+m-1)^2}. \quad (17)$$

Consequently

$$\lim_{m \rightarrow \infty} \frac{(n-2)! \rho^m}{(n+m-2)!} (\text{Var}_{\rho}(H_{n+m}) - \text{Var}_{\rho}(H_{n+m-1})) = 0.$$

The Theorem follows.

Appendix C. Proof of Theorem 4.1

Let $Q_n = \mathbb{E}_{\rho}(L_n)$. The following recursion formula for Q_n follows by considering the possible states after the first transition

$$Q_n = \frac{2}{n+\rho-1} + \frac{\rho}{n+\rho-1} Q_{n+1} + \frac{n-1}{n+\rho-1} Q_{n-1}.$$

It is easy to show that $F_n := \mathbb{E}_0(L_n) + \rho \mathbb{E}_{\rho}(H_n)$ satisfies the same recursion. So we have

$$(n-1)(Q_n - Q_{n-1}) = 2 + \rho(Q_{n+1} - Q_n).$$

If we define $M_n = Q_n - Q_{n-1}$, we obtain the following relation

$$M_n = 2 \sum_{k=1}^m \frac{\rho^{k-1}}{(n-1)n \cdots (n+k-2)} + \frac{\rho^m}{(n-1)n \cdots (n+m-2)} M_{n+m}.$$

Hence

$$M_n = 2 \sum_{k=1}^{\infty} \frac{\rho^{k-1}}{(n-1)n \cdots (n+k-2)} + \lim_{m \rightarrow \infty} \frac{\rho^m}{(n-1)n \cdots (n+m-2)} M_{n+m}.$$

On the other hand, we have

$$M_{n+m} = Q_{n+m} - Q_{n+m-1} = \mathbb{E}_\rho(L_{n+m}) - \mathbb{E}_\rho(L_{n+m-1}) := \mathbb{E}_\rho(L'_{n+m}).$$

Again by conditioning upon the value of R_{n+m} , we can show that

$$\mathbb{E}_\rho(L'_{n+m}) \leq \frac{c'}{(n+m)(n+m-1)}.$$

It is now easy to deduce that

$$\lim_{m \rightarrow \infty} \frac{\rho^m (n-2)!}{(n+m-2)!} M_{n+m} = 0, \quad \forall \rho \geq 0.$$

We can easily obtain the following relation

$$\begin{aligned} F_n &= 2 \sum_{k=1}^{\infty} \frac{\rho^{k-1}}{(n-1)n \cdots (n+k-2)} \\ &\quad + \lim_{m \rightarrow \infty} \frac{\rho^m}{(n-1)n \cdots (n+m-2)} (\mathbb{E}_0(L_{n+m}) - \mathbb{E}_0(L_{n+m-1})) \\ &\quad + \lim_{m \rightarrow \infty} \frac{\rho^{m+1}}{(n-1)n \cdots (n+m-2)} (\mathbb{E}_\rho(H_{n+m}) - \mathbb{E}_\rho(H_{n+m-1})). \end{aligned}$$

Again the two limits on the right vanish. The result follows.

Appendix D. Proof of Theorem 5.1

We have for $n \geq 2$, with the same notation as in section 3,

$$L_n = nS_n + L_{n-1} \mathbb{I}_{\{\text{Coalescence}\}} + L_{n+1} \mathbb{I}_{\{\text{Recombination}\}}.$$

It is easy to show that S_n is independent of $L_{n-1} \mathbb{I}_{\{\text{Coalescence}\}} + L_{n+1} \mathbb{I}_{\{\text{Recombination}\}}$,

hence

$$\begin{aligned} \text{Var}_\rho(L_n) - \text{Var}_\rho(L_{n-1}) &= \frac{4}{(n+\rho-1)(n-1)} + \frac{\rho}{n-1} [\text{Var}_\rho(L_{n+1}) - \text{Var}_\rho(L_n)] \\ &\quad + \frac{\rho}{n+\rho-1} [\mathbb{E}_\rho(L_{n+1}) - \mathbb{E}_\rho(L_{n-1})]^2. \end{aligned}$$

But we have

$$\mathbb{E}_\rho(L_{n+1}) - \mathbb{E}_\rho(L_{n-1}) = \frac{4n-2}{n(n-1)} + \sum_{j=1}^{\infty} \frac{2(n-2)!(2n+j-1)}{(n+j)!} \rho^j.$$

Define $D_n := \text{Var}_\rho(L_n) - \text{Var}_\rho(L_{n-1})$, hence

$$D_n = \frac{4}{(n+\rho-1)(n-1)} + \frac{\rho}{n-1} Z_{n+1} + B_n,$$

where

$$B_n = \frac{\rho}{n+\rho-1} \left(\frac{4n-2}{n(n-1)} + \sum_{j=1}^{\infty} \frac{2(n-2)!(2n+j-1)}{(n+j)!} \rho^j \right)^2.$$

Then

$$D_n = \sum_{k=1}^m \frac{4(n-2)! \rho^{k-1}}{(n+\rho+k-2)(n+k-2)!} + \sum_{k=1}^m \frac{(n-2)! \rho^{k-1}}{(n+k-3)!} B_{n+k-1} + \frac{(n-2)! \rho^m}{(n+m-2)!} Z_{n+m}.$$

Similarly to the proof of (16) we have

$$B_n = \frac{4\rho}{n^2(n-1)^2(n+\rho-1)} \left(2n-1 + \frac{2n\rho+\rho^2}{n+1} + \frac{(n+\rho-1)e^\rho}{(n+1)\rho^n} \int_0^\rho t^{n+1} e^{-t} dt \right)^2. \quad (18)$$

It is easy to show that $\sum_{k=1}^{\infty} \frac{B_{k+2}\rho^k}{k!}$ converges for all ρ .

It is not hard to show that

$$\sum_{k=1}^{\infty} \frac{4(n-2)! \rho^{k-1}}{(n+\rho+k-2)(n+k-2)!} = 4 \frac{{}_2F_2([1, n+\rho-1], [n+\rho, n], \rho)}{(n-1)(n+\rho-1)}.$$

Similarly as in section 3, $L_{n+m} = X_{n+m} + L_{n+m-1}$, where

$$X_{n+m} \leq (n+m+R_{n+m})T_{n+m}$$

with again X_{n+m} and L_{n+m-1} independent, so that

$$\begin{aligned} \text{Var}_\rho(L_{n+m}) - \text{Var}_\rho(L_{n+m-1}) &= \text{Var}_\rho(X_{n+m}) \\ &\leq 2(n+m)^2 \mathbb{E}_\rho(T_{n+m}^2) + 2\mathbb{E}_\rho(R_{n+m}^2 T_{n+m}^2). \end{aligned}$$

We deduce from (17) that for m large enough, say $(m+n \geq 8\rho)$

$$(n+m)^2 \mathbb{E}_\rho(T_{n+m}^2) \leq \frac{c_1}{(n+m-1)^2},$$

and also

$$\begin{aligned}\mathbb{E}_\rho(R_{n+m}^2 T_{n+m}^2) &= \sum_{k=1}^{\infty} k^2 \mathbb{E}_\rho(T_{n+m}^2 | R_{n+m} = k) \mathbb{P}_\rho(R_{n+m} = k) \\ &\leq \frac{c_2}{(n+m)(n+m-1)} \sum_{k=1}^{\infty} (k+1)^2 \left(\frac{4\rho}{n+m-1} \right)^k \\ &\leq \frac{c'_2}{(n+m)(n+m-1)}.\end{aligned}$$

Consequently for all $\rho \geq 0$, as $m \rightarrow \infty$,

$$\frac{(n-2)! \rho^m}{(n+m-2)!} D_{n+m} \rightarrow 0.$$

Therefore we obtain the following relation

$$\text{Var}_\rho(L_n) - \text{Var}_\rho(L_{n-1}) = 4 \frac{{}_2F_2([1, n+\rho-1], [n+\rho, n], \rho)}{(n+\rho-1)(n-1)} + \sum_{k=1}^{\infty} \frac{(n-2)! \rho^{k-1}}{(n+k-3)!} B_{n+k-1}.$$

The Theorem follows.

Appendix E. Proof of Theorem 6.1

We can obtain the following relation for R_n

$$R_n = \xi_n(1 + R'_n + R'_{n+1}), \quad (19)$$

noting that (ξ_n, R'_n, R'_{n+1}) is a sequence of independent random variables, ξ_n is a Bernoulli($\frac{\rho}{n+\rho-1}$) random variable and R'_n (resp. R'_{n+1}) is a copy of R_n (resp. of R_{n+1}). So we have

$$\mathbb{E}_\rho(R_n) = \frac{\rho}{n+\rho-1} (1 + \mathbb{E}_\rho(R_n) + \mathbb{E}_\rho(R_{n+1})).$$

We can easily deduce the following relation from the above recursion formula

$$\mathbb{E}_\rho(R_n) = \sum_{k=1}^m \frac{(n-2)! \rho^k}{(n+k-2)!} + \frac{(n-2)! \rho^m}{(n+m-2)!} \mathbb{E}_\rho(R_{n+m}).$$

On one hand, we have

$$\lim_{m \rightarrow \infty} \frac{(n-2)! \rho^m}{(n+m-2)!} \mathbb{E}_\rho(R_{n+m}) = 0,$$

because

$$\mathbb{E}_\rho(R_{n+m}) = \sum_{k=1}^{\infty} k \mathbb{P}_\rho(R_{n+m} = k) \leq \sum_{k=1}^{\infty} k a_k \left(\frac{\rho}{n+m-1} \right)^k \leq \frac{4\rho}{n+m-1-4\rho}$$

for $n + m - 1 \geq 8\rho$, where again a_k is the Catalan number. On the other hand it is easy to show that

$$\sum_{k=1}^{\infty} \frac{(n-2)! \rho^k}{(n+k-2)!} = \frac{e^\rho}{\rho^{n-2}} (\Gamma(n-1) - \Gamma(n-1, \rho))$$

where $\Gamma(a, x)$ is the incomplete gamma function defined as

$$\Gamma(a, x) = \int_x^{\infty} t^{a-1} e^{-t} dt.$$

Hence for all ρ we obtain

$$\begin{aligned} \mathbb{E}_\rho(R_n) &= \frac{e^\rho}{\rho^{n-2}} (\Gamma(n-1) - \Gamma(n-1, \rho)) \\ &= \frac{e^\rho}{\rho^{n-2}} \int_0^\rho t^{n-2} e^{-t} dt \\ &= \rho \int_0^1 s^{n-2} e^{\rho(1-s)} ds. \end{aligned}$$

The Theorem follows.

Appendix F. Proof of Theorem 7.1

From the recursion formula (19) we deduce the following formula for the variance of R_n

$$\begin{aligned} \text{Var}_\rho(R_n) &= \sum_{i=0}^m \Pi_{k=0}^i \frac{\rho(n+k-1)}{(n+k+\rho-1)^2 - \rho(n-1)} \\ &\quad + \Pi_{k=0}^m \frac{\rho(n+k-1)}{(n+k+\rho-1)^2 - \rho(n-1)} \text{Var}_\rho(R_{n+m}). \end{aligned}$$

We have

$$\mathbb{E}_\rho(R_{n+m}^2) = \sum_{k=1}^{\infty} k^2 \left(\frac{4\rho}{n+m-1} \right) \leq \sum_{k=1}^{\infty} k^2 a_k \left(\frac{4\rho}{n+m-1} \right) \leq \frac{4(n+m-1)\rho}{(n+m-1-4\rho)^2}. \quad (20)$$

for $8\rho \leq n + m - 1$. From this we deduce

$$\text{Var}_\rho(R_{n+m}) \leq \frac{4(n+m-1)\rho}{(n+m-1-4\rho)^2}.$$

We can easily show that $\lim_{m \rightarrow \infty} \Pi_{k=0}^m \frac{\rho(n+k-1)}{(n+k+\rho-1)^2 - \rho(n-1)} \text{Var}_\rho(R_{n+m}) = 0$. Hence

$$\text{Var}_\rho(R_n) = \sum_{i=0}^{\infty} \Pi_{k=0}^i \frac{\rho(n+k-1)}{(n+k+\rho-1)^2 - \rho(n-1)}.$$

The result follows after some algebraic simplifications. It is easy to show that

$$\text{Var}_\rho(R_n) = \frac{\rho(n-1)}{(n-1)^2 + \rho(n-1) + \rho^2} + O\left(\frac{1}{n^2}\right).$$

Acknowledgements

This work was partially supported by the ANR MAEV under contract ANR-06-BLAN-0113.

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