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Part 3. Biological applications

TOTAL INTERNAL AND EXTERNAL LENGTHS OF THE BOLTHAUSEN–SZNITMAN COALESCENT

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TOTAL INTERNAL AND EXTERNAL LENGTHS OF THE BOLTHAUSEN–SZNITMAN COALESCENT

By GÖTZ KERSTING, JUAN CARLOS PARDO and ARNO SIRI-JÉGOUSSE

Abstract

In this paper we study a weak law of large numbers for the total internal length of the Bolthausen–Sznitman coalescent, thereby obtaining the weak limit law of the centered and rescaled total external length; this extends results obtained in Dhersin and Möhle (2013). An application to population genetics dealing with the total number of mutations in the genealogical tree is also given.

Keywords: Coalescent process; Bolthausen–Sznitman coalescent; external branch; block counting process; recursive construction; Iksanov–Möhle coupling

2010 Mathematics Subject Classification: Primary 60J70; 60J80; 60J25; 60F05; 92D25

1. Introduction and main results

In population genetics, one way of explaining disparity in a sample is to observe how many genes appear only once. A gene carried by a single individual is the result of two possible events: either the gene comes from a mutation that appeared in an external branch of the genealogical tree, or the gene is of the ancestral type and mutations occurred in the rest of the sample (see Figure 1). We suppose that events of the second type occur much less frequently than events of the first type (this is indeed the case when the size of the sample is large). The total number of genes carried by a single individual is then closely related to the so-called total external length, which is the sum of all external branch lengths of the tree.

The Bolthausen–Sznitman coalescent (see, for instance, [6]) is a well-known example of an exchangeable coalescent with multiple collisions (see [19] and [20] for a proper definition of this type of coalescent). It was first introduced in physics in order to study spin glasses, but it has also been considered as a limiting genealogical model for evolving populations with selective killing at each generation (see, for instance, [7, 8]). Recently, Berestycki *et al.* [5] noted that this coalescent represents the genealogies of branching Brownian motion with absorption.

The Bolthausen–Sznitman coalescent $(\Pi_t,\ t \geq 0)$ is a continuous-time Markov chain with values in the set of partitions of $\mathbb{N}$, starting with an infinite number of blocks/individuals. In order to give a formal description of this coalescent, it is sufficient to give its jump rates. Let $n \in \mathbb{N}$; then the restriction $(\Pi_t^{(n)},\ t \geq 0)$ of $(\Pi_t,\ t \geq 0)$ to $[n] := \{1, \dots, n\}$ is a Markov chain with values in $\mathcal{P}_n$, the set of partitions of $[n]$, with the following dynamics: whenever $\Pi_t^{(n)}$ is a partition consisting of b blocks, any particular k of them merge into one block at rate

$$\lambda_{b,k} = \frac{(k-2)!\,(b-k)!}{(b-1)!},$$

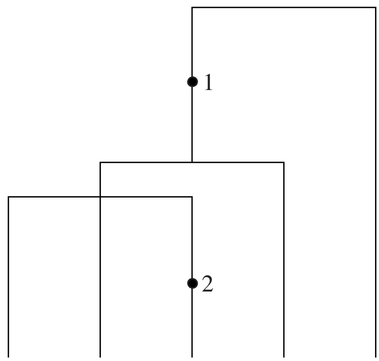

FIGURE 1: An example of a genealogical tree containing two mutations. Mutation 1 is in an internal branch and is shared by four individuals. Mutation 2 is in an external branch and is carried by one individual. Also, in this example an ancestral gene is carried by one individual.

so the next coalescence event occurs at total rate

$$\lambda_b = \sum_{k=2}^{b} \binom{b}{k} \lambda_{b,k} = b - 1. \tag{1}$$

Note that mergers of several blocks into a single block are possible, but multiple mergers do not occur simultaneously. Moreover, this coalescent process is exchangeable, i.e. its law does not change under the effect of a random permutation of the labels of its blocks.

One of our aims is to study the total external length of the Bolthausen–Sznitman coalescent. More precisely, we determine the asymptotic behaviour as $n \to \infty$ of the total external length $E^{(n)}$ of the Bolthausen–Sznitman coalescent restricted to $\mathcal{P}_n$, and relate $E^{(n)}$ to its total length $L^{(n)}$ (the sum of lengths of all external and internal branches). A first orientation can be gained from coalescents without proper frequencies, for which class Möhle [18] proved that, suitably scaled, the asymptotic distributions of $E^{(n)}$ and $L^{(n)}$ are equal. Now while the Bolthausen–Sznitman coalescent does not belong to this class, loosely speaking, it is located at the borderline. Also, it is known for the Bolthausen–Sznitman coalescent [12] that

$$\frac{(\log n)^2}{n} L^{(n)} - \log n - \log\log n \xrightarrow{\mathrm{D}} Z \quad \text{as } n \to \infty, \tag{2}$$

where '$\xrightarrow{\mathrm{D}}$' denotes convergence in distribution and Z is a strictly stable random variable with index 1, i.e. the characteristic exponent of Z satisfies

$$\Psi(\theta) := -\log \mathbb{E}[\mathrm{e}^{\mathrm{i}\theta Z}] = \tfrac{1}{2}\pi|\theta| - \mathrm{i}\theta \log|\theta|, \qquad \theta \in \mathbb{R}. \tag{3}$$

In their recent work, Dhersin and Möhle [10] showed that the ratio $E^{(n)}/L^{(n)}$ converges to 1 in probability. Thus, one might guess that $E^{(n)}$ satisfies the same asymptotic relation with the same scaling. A principal result of this paper is that this is almost true, but not entirely.

Consider $(\Pi_t^{(n)},\ t \geq 0)$. Denote by $U_k^{(n)}$ the size of the kth jump, i.e. the number of blocks that the Markov chain loses in the kth coalescence event. Denote by $X_k^{(n)}$ the number of blocks after k coalescence events. Observe that $X_0^{(n)} = n$ and $X_k^{(n)} = X_{k-1}^{(n)} - U_k^{(n)} = n - \sum_{i=1}^{k} U_i^{(n)}$.

Since the merging blocks coalesce into one, there are $U_k^{(n)} + 1$ blocks involved in the kth coalescence event and, for $l < X_{k-1}^{(n)}$,

$$\mathbb{P}(U_k^{(n)} = l \mid X_{k-1}^{(n)} = b) = \binom{b}{l+1}\frac{\lambda_{b,l+1}}{\lambda_b} = \frac{b}{b-1}\frac{1}{l(l+1)}.$$

Let $\tau^{(n)}$ be the number of coalescence events, i.e. $\tau^{(n)} = \inf\{k,\ X_k^{(n)} = 1\}$. According to Iksanov and Möhle [15] (see also [13]), $\tau^{(n)}$ has the asymptotic behaviour

$$\frac{(\log n)^2}{n}\tau^{(n)} - \log n - \log\log n \xrightarrow{\mathrm{D}} Z \quad \text{as } n \to \infty, \tag{4}$$

where Z is as in (2).

The main result of this paper describes the behaviour of the total internal length $I^{(n)}$ as $n \to \infty$. To this end, introduce the random variable $Y_k^{(n)}$ representing the number of internal branches after k coalescence events. Thus, $Y_k^{(n)}$ is the number of remaining blocks which have already participated in a coalescence event. Note that at time 0 all branches are external, i.e. $Y_0^{(n)} = 0$. Let $(e_k,\ k \geq 1)$ be a sequence of independent and identically distributed standard exponential random variables, independent of $X_k^{(n)}$ and $Y_k^{(n)}$; so, from (1),

$$I^{(n)} \stackrel{\mathrm{D}}{=} \sum_{k=1}^{\tau^{(n)}-1} Y_k^{(n)} \frac{e_k}{X_k^{(n)} - 1}\,. \tag{5}$$

Our main result is the following weak law of large numbers for $I^{(n)}$. Here '$\xrightarrow{\mathbb{P}}$' denotes convergence in probability.

Theorem 1. *The total internal length $I^{(n)}$ of the Bolthausen–Sznitman coalescent satisfies*

$$\frac{(\log n)^2}{n} I^{(n)} \xrightarrow{\mathbb{P}} 1 \quad \text{as } n \to \infty.$$

Now noting that $L^{(n)} = I^{(n)} + E^{(n)}$, and using (2) and our main result, we deduce the asymptotic distribution of the total external length $E^{(n)}$.

Corollary 1. *The total external length $E^{(n)}$ of the Bolthausen–Sznitman coalescent satisfies*

$$\frac{(\log n)^2}{n} E^{(n)} - \log n - \log\log n \xrightarrow{\mathrm{D}} Z - 1 \quad \text{as } n \to \infty,$$

where the strictly stable random variable Z is as in (2).

Observe that the Bolthausen–Sznitman coalescent can be seen as a special case ($\alpha = 1$) of the so-called Beta$(2-\alpha, \alpha)$-coalescent (this class is defined for $0 < \alpha < 2$; see Section 3.1.4 of [2]). Möhle's work [18] shows that, for $0 < \alpha < 1$, the variable $E^{(n)}/n$ converges in law to a random variable defined in terms of a driftless subordinator that depends on α. For $1 < \alpha < 2$, we refer the reader to [9] where it is proved that $(E^{(n)} - cn^{2-\alpha})/n^{1/\alpha+1-\alpha}$ converges weakly to a stable random variable with index α, c being a constant that also depends on α (see also [3, 4, 11]). In Kingman's case ($\alpha \to 2$) a logarithmic correction appears and the limit law is normal (see [16]).

The remainder of the paper is structured as follows. In Section 2 we prove our main results using a coupling method which was introduced in [15] and which provides more information on the chain $X^{(n)} = (X_k^{(n)},\ k \geq 0)$. Finally, Section 4 is devoted to the asymptotic behaviour of the number of mutations appearing in external and internal branches of the Bolthausen–Sznitman coalescent. For analogous results concerning the allele frequency spectrum of a Bolthausen–Sznitman coalescent, we refer the reader to [1].

2. A coupling

In this section we use the coupling method introduced by Iksanov and Möhle [15] in order to study the number of jumps $\tau^{(n)}$.

Let $(V_i)_{i\geq 1}$ be a sequence of independent and identically distributed random variables with distribution

$$\mathbb{P}(V_1 = k) = \frac{1}{k(k+1)}, \qquad k \geq 1. \tag{6}$$

Note that $\mathbb{P}(V_1 \geq k) = 1/k$. Let $S_n = V_1 + \cdots + V_n$. It is well known, see, for instance, [14], that

$$\frac{S_n - n\log n}{n} \xrightarrow{\text{D}} Z \quad \text{as } n \to \infty, \tag{7}$$

where Z is the stable random variable appearing in (2). This convergence in distribution is directly extended to a convergence of processes. From Theorem 15.12 of [17], there is a Lévy process $L = (L(t),\ 0 \leq t \leq 1)$, unique in distribution, such that $L(1) \overset{\text{D}}{=} Z$. Note that, due to the logarithmic term in (7), the stable random variable Z is not strictly stable, which is reflected in the behaviour of L. This process is not scaled in the ordinary fashion, but

$$L_t \overset{\text{D}}{=} tL_1 - t\log t,$$

as follows from (3).

Lemma 1. *The sequence of processes* $(L_n(t),\ 0 \leq t \leq 1)$, $n = 1, 2, \ldots,$ *defined by*

$$L_n(t) = \frac{S_{\lfloor nt\rfloor} - \lfloor nt\rfloor \log n}{n},$$

converges as $n \to \infty$ *to* L *in the Skorokhod space* $\mathcal{D}[0, 1]$.

Proof. Using (7), apply Theorem 16.14 of [17] to the random walks $(S^n_k)_{k\geq 0} = (L_n(k/n))_{k\geq 0}$, $n = 1, 2, \ldots,$ with $m_n = n$.

We introduce further notation. For a stochastic process $(Z_n,\ n \geq 0)$ and a function $c(n) > 0$, write $Z_n = O_p(c(n))$ as $n \to \infty$ if $Z_n/c(n)$ is stochastically bounded as $n \to \infty$, i.e. if $\lim_{x\to\infty} \limsup_{n\to\infty} \mathbb{P}(|Z_n| > xc(n)) = 0$. We also write $Z_n = o_p(c(n))$ as $n \to \infty$ if $Z_n/c(n) \to 0$ in probability.

From Lemma 1 we deduce that

$$\sup_{1\leq k\leq n} |S_k - k\log n| = O_p(n). \tag{8}$$

Now recursively define $(\rho(k))_{k\geq 0}$, a sequence of stopping times such that $\rho(0) = 0$ and

$$\rho(k+1) = \inf\left\{i > \rho(k),\ V_i + \sum_{j=1}^{k} V_{\rho(j)} < n\right\},$$

with the convention $\inf\{\varnothing\} = \infty$. Thus, the sequence $(\rho(k))_{k\geq 1}$ is the collection of indices of the random variables V_i such that their sum does not exceed $n - 1$. It was proved in [15] that

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$\tau^{(n)}$ and $\sup\{k,\ \rho(k) < \infty\}$ are equal in law, and that the terms of the block-counting Markov chain of the Bolthausen–Sznitman coalescent can be represented as $X_0^{(n)} = n$ and

$$X_k^{(n)} \overset{\text{D}}{=} n - \sum_{i=1}^{k} V_{\rho(i)}.$$

Next, define

$$\sigma^{(n)} = \inf\{k,\ \rho(k) > k\},$$

the first time that the random walk meets or exceeds n, and

$$\theta_\gamma^{(n)} = \tau^{(n)} - \frac{n}{(\log n)^{1+\gamma}}, \qquad \gamma \in (0, \infty], \tag{9}$$

with the convention $\theta_\infty^{(n)} = \tau^{(n)}$. Our first result allows us to consider the random walk instead of the process of disappearing blocks until time $\theta_\gamma^{(n)}$.

Proposition 1. *Let* $0 < \gamma < \gamma' \le \infty$. *Then, as* $n \to \infty$,

$$\mathbb{P}(\theta_\gamma^{(n)} < \sigma^{(n)}) \to 1 \quad \textit{and} \quad \frac{(\log n)^\gamma}{n} X^{(n)}_{\theta_\gamma^{(n)}} \xrightarrow{\mathbb{P}} 1, \tag{10}$$

and

$$\sup_{1 \le k \le \theta_\gamma^{(n)}} \left| \frac{X_k^{(n)}}{\theta_{\gamma'}^{(n)} - k} - \log n \right| = o_p(\log n) \quad \textit{for sufficiently large } n. \tag{11}$$

To prove this proposition, we first prove a similar result for the family of stopping times

$$\eta_{c,\gamma}^{(n)} = \inf\left\{k,\ X_k^{(n)} < \frac{cn}{(\log n)^\gamma}\right\},$$

where c is a positive constant, and then note that, for $0 < \varepsilon < 1$,

$$\mathbb{P}(\eta_{1-\varepsilon,\gamma}^{(n)} \le \theta_\gamma^{(n)} \le \eta_{1+\varepsilon,\gamma}^{(n)}) \to 1 \quad \text{as } n \to \infty.$$

The proof of Proposition 1 then relies on the following lemma.

Lemma 2. *Let* $0 < \gamma < \infty$. *Then, as* $n \to \infty$,

$$\mathbb{P}(\eta_{c,\gamma}^{(n)} < \sigma^{(n)}) \to 1 \quad \textit{and} \quad \frac{(\log n)^\gamma}{cn} X^{(n)}_{\eta_{c,\gamma}^{(n)}} \xrightarrow{\mathbb{P}} 1,$$

and

$$\sup_{1 \le k \le \eta_{c,\gamma}^{(n)}} \left| \frac{X_k^{(n)}}{\tau^{(n)} - k} - \log n \right| = o_p(\log n) \quad \textit{for sufficiently large } n.$$

Proof. Our proof proceeds in two steps: first we prove the relations (at (13), (15), and (17) below) for $\gamma < 1$, and then extend them to $X^{(n)}$ started not from 0 but from $\eta_{c,\gamma}^{(n)}$ for some $\gamma < 1$, say $\gamma = \frac{1}{2}$. Iterating this argument leads to a proof for $\gamma \le \frac{1}{2}p$, with induction on p.

Step 1. Let $\gamma < 1$. Observe from (6) that, for any $0 < \varepsilon < 1$,

$$\mathbb{P}\left(V_k < \frac{n}{(\log n)^{1-\varepsilon}} \text{ for all } k \le \frac{2n}{\log n}\right) \ge \left(1 - \frac{(\log n)^{1-\varepsilon}}{n}\right)^{2n/\log n} \to 1 \quad \text{as } n \to \infty.$$

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Now, since $\mathbb{P}(\tau^{(n)} \le 2n/\log n) \to 1$ as $n \to \infty$ (this follows from (4)), we obtain

$$\sup_{1\le k\le \tau^{(n)}} V_k = O_p\Big(\frac{n}{(\log n)^{1-\varepsilon}}\Big). \tag{12}$$

For simplicity, write $\eta^{(n)}$ in place of $\eta^{(n)}_{c,\gamma}$. Then, from our definitions, it follows that

$$\begin{aligned}\mathbb{P}(\sigma^{(n)} \le \eta^{(n)}) &= \mathbb{P}(V_k \ge X^{(n)}_{k-1} \text{ for some } k \le \eta^{(n)}) \\ &\le \mathbb{P}\Big(V_k \ge \frac{cn}{(\log n)^\gamma} \text{ for some } k \le \tau^{(n)}\Big) \\ &= \mathbb{P}\Big(\sup_{1\le k\le \tau^{(n)}} V_k \ge \frac{cn}{(\log n)^\gamma}\Big),\end{aligned}$$

so, by taking $\varepsilon \in (0, 1-\gamma)$ in (12), it follows that

$$\mathbb{P}(\sigma^{(n)} \le \eta^{(n)}) \to 0 \quad \text{as } n \to \infty. \tag{13}$$

On the event $\{\sigma^{(n)} > \eta^{(n)}\}$, it is clear that

$$\sup_{1\le k\le \eta^{(n)}} \bigg|\frac{X^{(n)}_k}{X^{(n)}_{k-1}} - 1\bigg| = \sup_{1\le k\le \eta^{(n)}} \frac{V_k}{X^{(n)}_{k-1}} \le \frac{(\log n)^\gamma}{cn} \sup_{1\le k\le \tau^{(n)}} V_k\,.$$

Hence, we conclude from (12) and (13) that

$$\sup_{1\le k\le \eta^{(n)}} \bigg|\frac{X^{(n)}_k}{X^{(n)}_{k-1}} - 1\bigg| = o_p(1). \tag{14}$$

In particular, since $X^{(n)}_{\eta^{(n)}} \le cn/(\log n)^\gamma \le X^{(n)}_{\eta^{(n)}-1}$,

$$\frac{(\log n)^\gamma}{cn} X^{(n)}_{\eta^{(n)}} \xrightarrow{\mathbb{P}} 1 \quad \text{as } n \to \infty. \tag{15}$$

Next, note that

$$X^{(n)}_k - (\tau^{(n)} - k)\log n = X^{(n)}_k - n + k\log\Big(\frac{2n}{\log n}\Big) + (n - \tau^{(n)}\log n) + k\log\Big(\frac{\log n}{2}\Big),$$

while, from (4), it is clear that

$$\frac{(\log n)^2}{n}\tau^{(n)} = \log n + O_p(\log\log n).$$

Then, on the event $\{\eta^{(n)} < \sigma^{(n)},\ \eta^{(n)} < 2n/\log n\}$, it follows from (8) that

$$\begin{aligned}\sup_{1\le k\le \eta^{(n)}} |X^{(n)}_k - (\tau^{(n)} - k)\log n| &\le \sup_{1\le k\le 2n/\log n} \bigg|S_k - k\log\Big(\frac{2n}{\log n}\Big)\bigg| + O_p\Big(\frac{n\log\log n}{\log n}\Big) \\ &= O_p\Big(\frac{n\log\log n}{\log n}\Big).\end{aligned}$$

Finally, (15) and the strong Markov property for $\tilde X^{(n)}_k = X^{(n)}_{k+\eta^{(n)}}$ yield

$$\tau^{(n)} - \eta^{(n)} = \tau^{(\tilde X^{(n)}_0)} = \frac{X^{(n)}_{\eta^{(n)}}}{\log X^{(n)}_{\eta^{(n)}}}(1 + o_p(1)) = \frac{cn}{(\log n)^{1+\gamma}}(1 + o_p(1)). \tag{16}$$

Then, putting all the pieces together, we obtain

$$\sup_{1\le k\le \eta^{(n)}}\left|\frac{X_k^{(n)}}{\tau^{(n)}-k}-\log n\right| \le \frac{\sup_{1\le k\le \eta^{(n)}}|X_k^{(n)}-(\tau^{(n)}-k)\log n|}{\tau^{(n)}-\eta^{(n)}}$$
$$= O_p((\log n)^{\gamma}\log\log n),$$

and, since $\gamma < 1$,

$$\sup_{1\le k\le \eta^{(n)}}\left|\frac{X_k^{(n)}}{\tau^{(n)}-k}-\log n\right| = o_p(\log n). \tag{17}$$

Step 2. We now prove (13)–(17) for any $\gamma > 0$ by showing that the lemma holds for $\gamma \le \frac{1}{2}p$ for any $p \in \mathbb{N}$, using induction on p. Step 1 established this claim for $p = 1$.

Suppose that the asymptotics in (13)–(17) hold for $\gamma \le \frac{1}{2}p$. For simplicity, write $\hat{\eta}^{(n)} = \eta^{(n)}_{c,p/2}$. The idea is to use the strong Markov property at the stopping time $\hat{\eta}^{(n)}$ and apply the above results for $\gamma < 1$ to the Markov chain $\hat{X}_k^{(n)} = X^{(n)}_{k+\hat{\eta}^{(n)}}$ started at $\hat{n} = X^{(n)}_{\hat{\eta}^{(n)}}$ (instead of $n = X_0^{(n)}$). Define the family of stopping times

$$\zeta^{(n)} = \inf\left\{k,\ X_k^{(n)} < \frac{\hat{n}}{(\log \hat{n})^{2/3}}\right\}.$$

Observe that $\zeta^{(n)} = \hat{\eta}^{(n)} + \eta^{(\hat{n})}_{1,2/3}$. Hence, using the strong Markov property at the stopping time $\hat{\eta}^{(n)}$ and the behaviour in (15), with $\gamma = \frac{2}{3}$, we obtain

$$\frac{(\log X^{(n)}_{\hat{\eta}^{(n)}})^{2/3}}{X^{(n)}_{\hat{\eta}^{(n)}}} X^{(n)}_{\zeta^{(n)}} \xrightarrow{\mathbb{P}} 1 \quad \text{as } n\to\infty.$$

Then, from this asymptotic behaviour and the induction hypothesis taken in (15),

$$\frac{(\log n)^{2/3+p/2}}{cn} X^{(n)}_{\zeta^{(n)}} \xrightarrow{\mathbb{P}} 1 \quad \text{as } n\to\infty.$$

From this relation, (15), and

$$\frac{(\log n)^{\gamma}}{cn} X^{(n)}_{\eta^{(n)}} < 1 \le \frac{(\log n)^{\gamma}}{cn} X^{(n)}_{\eta^{(n)}-1},$$

we obtain, for $p/2 < \gamma \le (p+1)/2$,

$$\mathbb{P}(\hat{\eta}^{(n)} < \eta^{(n)} \le \zeta^{(n)}) \to 1 \quad \text{as } n\to\infty. \tag{18}$$

Now, on the event $\{\sigma^{(n)} > \hat{\eta}^{(n)}\}$, using the strong Markov property at $\hat{\eta}^{(n)}$ and (13) with the initial state $X^{(n)}_{\hat{\eta}^{(n)}}$, we obtain

$$\mathbb{P}(\sigma^{(n)} \le \zeta^{(n)} \mid \sigma^{(n)} > \hat{\eta}^{(n)}) \to 0 \quad \text{as } n\to\infty.$$

The induction hypothesis gives $\mathbb{P}(\sigma^{(n)} > \hat{\eta}^{(n)}) \to 1$ as $n\to\infty$. Together, these two facts give

$$\mathbb{P}(\sigma^{(n)} > \eta^{(n)}) \to 1 \quad \text{as } n\to\infty \text{ for } \gamma \in (p/2, (p+1)/2].$$

From (14) and again the strong Markov property at $\hat{\eta}^{(n)}$, we obtain

$$\sup_{\hat{\eta}^{(n)} \le k \le \zeta^{(n)}} \left| \frac{X_k^{(n)}}{X_{k-1}^{(n)}} - 1 \right| = o_p(1).$$

From the above relation, (18), and the induction hypothesis, we have

$$\sup_{1 \le k \le \eta^{(n)}} \left| \frac{X_k^{(n)}}{X_{k-1}^{(n)}} - 1 \right| = o_p(1)$$

for $\gamma \in (p/2, (p+1)/2]$. Again, the strong Markov property and the above behaviour imply that, for all $\gamma \in (p/2, (p+1)/2]$,

$$\tau^{(n)} - \eta^{(n)} = \frac{cn}{(\log n)^{1+\gamma}}(1 + o_p(1)).$$

From (17) and the strong Markov property, we deduce that

$$\sup_{\hat{\eta}^{(n)} \le k \le \zeta^{(n)}} \left| \frac{X_k^{(n)}}{\tau^{(n)} - k} - \log X_{\hat{\eta}^{(n)}}^{(n)} \right| = o_p\Big(\log X_{\hat{\eta}^{(n)}}^{(n)}\Big).$$

We know from the induction hypothesis that $\log X_{\hat{\eta}^{(n)}}^{(n)} \sim \log n$ for $n \to \infty$. We now use the induction hypothesis again and (18) to conclude that

$$\sup_{1 \le k \le \eta^{(n)}} \left| \frac{X_k^{(n)}}{\tau^{(n)} - k} - \log n \right| = o_p(\log n)$$

for all $\gamma \in (p/2, (p+1)/2]$. Hence, the induction is complete and the asymptotic behaviour in (13)–(17) holds for any $\gamma > 0$.

Proof of Proposition 1. First recall the definition of $\theta_\gamma^{(n)}$ in (9), and define $\eta_-^{(n)} = \eta_{1-\varepsilon,\gamma}^{(n)}$ and $\eta_+^{(n)} = \eta_{1+\varepsilon,\gamma}^{(n)}$. From (16), it is clear that

$$\mathbb{P}(\eta_+^{(n)} \le \theta_\gamma^{(n)} \le \eta_-^{(n)}) \to 1 \quad \text{as } n \to \infty,$$

while (13) implies that

$$\mathbb{P}(\sigma^{(n)} > \eta_-^{(n)}) \to 1 \quad \text{as } n \to \infty.$$

Thus, the first asymptotic relation in (10) holds. Then noting also that

$$\mathbb{P}(X_{\eta_-^{(n)}}^{(n)} \le X_{\theta_\gamma^{(n)}}^{(n)} \le X_{\eta_+^{(n)}}^{(n)}) \to 1 \quad \text{as } n \to \infty,$$

the second asymptotic relation in (10) follows from (15). Equation (17) implies that

$$\sup_{1 \le k \le \theta_\gamma^{(n)}} \left| \frac{X_k^{(n)}}{\tau^{(n)} - k} - \log n \right| = o_p(\log n),$$

which gives (11) for $\gamma' = \infty$. Also,

$$\sup_{1 \le k \le \theta_\gamma^{(n)}} \left| \frac{\theta_{\gamma'}^{(n)} - k}{\tau^{(n)} - k} - 1 \right| = \sup_{1 \le k \le \theta_\gamma^{(n)}} \left| \frac{\tau^{(n)} - \theta_{\gamma'}^{(n)}}{\tau^{(n)} - k} \right| \le \frac{\tau^{(n)} - \theta_{\gamma'}^{(n)}}{\tau^{(n)} - \theta_\gamma^{(n)}} = \frac{(\log n)^\gamma}{(\log n)^{\gamma'}}(1 + o_p(1)).$$

This gives (11) generally, and completes the proof.

3. Proof of Theorem 1

First define

$$\tilde{I}^{(n)} = \sum_{k=1}^{\tau^{(n)}-1} \frac{Y_k^{(n)}}{X_k^{(n)}}; \tag{19}$$

this is obtained from (5) on replacing the exponential random variable e_k by its mean and approximating the denominator. Similarly, define

$$\hat{I}^{(n)} = \sum_{k=1}^{\tau^{(n)}-1} \frac{\mathbb{E}[Y_k^{(n)} \mid X^{(n)}]}{X_k^{(n)}};$$

this comes from (19) on replacing the random variable $Y_k^{(n)}$ by its conditional expectation. This new formulation is of interest because much as in [9] we can determine $\hat{I}^{(n)}$ recursively as follows. Let $Z_k^{(n)}$ be the number of external branches after k jumps, $k \geq 1$, and take the conditional expectation of each $Z_k^{(n)}$ with respect to $X^{(n)}$ and $Z_{k-1}^{(n)}$. Observe that $Z_{k-1}^{(n)} - Z_k^{(n)}$ is the number of external branches which contribute to the kth coalescence event. Then, conditional on $X^{(n)}$ and $Z_0^{(n)}, \dots, Z_{k-1}^{(n)}$, this random variable is distributed as a hypergeometric random variable with parameters $X_{k-1}^{(n)}$, $Z_{k-1}^{(n)}$ and $1 + U_k^{(n)}$. Recall that $U_k^{(n)} = X_{k-1}^{(n)} - X_k^{(n)}$ denotes the size of the kth jump of the block counting process. It is then clear that

$$\mathbb{E}[Z_k^{(n)} \mid X^{(n)}, Z_{k-1}^{(n)}] = Z_{k-1}^{(n)} - (1 + U_k^{(n)}) \frac{Z_{k-1}^{(n)}}{X_{k-1}^{(n)}} = Z_{k-1}^{(n)} \frac{X_k^{(n)} - 1}{X_{k-1}^{(n)}},$$

$$\mathbb{E}[Z_k^{(n)} \mid X^{(n)}] = \mathbb{E}[Z_{k-1}^{(n)} \mid X^{(n)}] \frac{X_k^{(n)} - 1}{X_{k-1}^{(n)}},$$

and

$$\frac{\mathbb{E}[Z_k^{(n)} \mid X^{(n)}]}{X_k^{(n)}} = \prod_{i=1}^{k} \left(1 - \frac{1}{X_i^{(n)}}\right).$$

Finally, since $Y_k^{(n)} = X_k^{(n)} - Z_k^{(n)}$, it follows that

$$\hat{I}^{(n)} = \sum_{k=1}^{\tau^{(n)}-1} \left(1 - \prod_{i=1}^{k} \left(1 - \frac{1}{X_i^{(n)}}\right)\right). \tag{20}$$

This last expression helps us to understand the asymptotic behaviour of the total internal branch via the following lemma for the asymptotic behaviour of $\hat{I}^{(n)}$.

Lemma 3. *As $n \to \infty$,*

$$\frac{(\log n)^2}{n} \hat{I}^{(n)} \to 1 \quad \textit{in probability.}$$

Proof. Let $0 < \varepsilon < 1$, and take $\theta_\gamma^{(n)}$ as in (9); also, let $\theta_-^{(n)} = \lfloor \theta_{1-\varepsilon}^{(n)} \rfloor$ and $\theta_+^{(n)} = \lfloor \theta_{1+\varepsilon}^{(n)} \rfloor$. Consider $\hat{I}^{(n)}$ as given in (20), but rewrite it as $\hat{I}^{(n)} = \hat{I}_1^{(n)} + \hat{I}_2^{(n)}$, where

$$\hat{I}_1^{(n)} = \sum_{k=1}^{\theta_+^{(n)}-1} \left(1 - \prod_{i=1}^{k} \left(1 - \frac{1}{X_i^{(n)}}\right)\right) \quad \text{and} \quad \hat{I}_2^{(n)} = \sum_{k=\theta_+^{(n)}}^{\tau^{(n)}-1} \left(1 - \prod_{i=1}^{k} \left(1 - \frac{1}{X_i^{(n)}}\right)\right).$$

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Note that

$$\hat{I}_2^{(n)} \le \tau^{(n)} - \theta_+^{(n)} \le \frac{n}{(\log n)^{2+\varepsilon}} + 1,$$

implying that

$$\frac{(\log n)^2}{n} \hat{I}_2^{(n)} \to 0 \quad \text{almost surely as } n \to \infty.$$

Hence, it is enough to prove the lemma for $\hat{I}_1^{(n)}$. To this end, start by noting that

$$\sum_{i=1}^{k} \frac{1}{X_i^{(n)}} - \sum_{j=2}^{k} \sum_{i=1}^{j-1} \frac{1}{X_i^{(n)} X_j^{(n)}} \le 1 - \prod_{i=1}^{k} \Bigl(1 - \frac{1}{X_i^{(n)}}\Bigr) \le \sum_{i=1}^{k} \frac{1}{X_i^{(n)}}$$

(this can be viewed as two Bonferroni inequalities for independent events with entrance probabilities $1/X_i^{(n)}$). On the one hand,

$$\sum_{k=1}^{\theta_+^{(n)}-1} \sum_{i=1}^{k} \frac{1}{X_i^{(n)}} = \sum_{i=1}^{\theta_+^{(n)}-1} \frac{\theta_+^{(n)} - i}{X_i^{(n)}},$$

so

$$\sum_{i=1}^{\theta_-^{(n)}-1} \frac{\theta_+^{(n)} - i}{X_i^{(n)}} \le \sum_{k=1}^{\theta_+^{(n)}-1} \sum_{i=1}^{k} \frac{1}{X_i^{(n)}} \le \sum_{i=1}^{\theta_+^{(n)}-1} \frac{\tau^{(n)} - i}{X_i^{(n)}}.$$

Applying (11) to these two inequalities yields

$$\frac{1}{\log n} (\theta_-^{(n)} - 1)(1 + o_p(1)) \le \sum_{k=1}^{\theta_+^{(n)}-1} \sum_{i=1}^{k} \frac{1}{X_i^{(n)}} \le \frac{1}{\log n} (\theta_+^{(n)} - 1)(1 + o_p(1)).$$

From the two limit relations

$$\frac{\theta_-^{(n)} \log n}{n} \xrightarrow{\mathbb{P}} 1 \quad \text{and} \quad \frac{\theta_+^{(n)} \log n}{n} \xrightarrow{\mathbb{P}} 1 \quad \text{as } n \to \infty,$$

it follows that

$$\sum_{k=1}^{\theta_+^{(n)}-1} \sum_{i=1}^{k} \frac{1}{X_i^{(n)}} = \frac{n}{(\log n)^2} (1 + o_p(1)).$$

On the other hand, by inverting the sums we obtain

$$\sum_{k=1}^{\theta_+^{(n)}-1} \sum_{j=2}^{k} \sum_{i=1}^{j-1} \frac{1}{X_i^{(n)} X_j^{(n)}} = \sum_{j=2}^{\theta_+^{(n)}-1} \sum_{k=j}^{\theta_+^{(n)}-1} \sum_{i=1}^{j-1} \frac{1}{X_i^{(n)} X_j^{(n)}} = \sum_{j=2}^{\theta_+^{(n)}-1} \frac{\theta_+^{(n)} - j}{X_j^{(n)}} \sum_{i=1}^{j-1} \frac{1}{X_i^{(n)}}.$$

Using (11) again, we obtain

$$\sum_{k=1}^{\theta_+^{(n)}-1} \sum_{j=2}^{k} \sum_{i=1}^{j-1} \frac{1}{X_i^{(n)} X_j^{(n)}} \le \sum_{j=2}^{\theta_+^{(n)}-1} \frac{\tau^{(n)} - j}{X_j^{(n)}} \sum_{i=1}^{j-1} \frac{1}{X_i^{(n)}} \le \frac{1 + o_p(1)}{\log n} \sum_{j=1}^{\theta_+^{(n)}-1} \sum_{i=1}^{j} \frac{1}{X_i^{(n)}},$$

so, finally,

$$\sum_{k=1}^{\theta_+^{(n)}-1} \sum_{j=2}^{k} \sum_{i=1}^{j-1} \frac{1}{X_i^{(n)} X_j^{(n)}} \le \frac{n}{(\log n)^3}(1+o_p(1)).$$

Putting all these pieces together gives

$$\frac{(\log n)^2}{n} \hat{I}_1^{(n)} \xrightarrow{\mathbb{P}} 1 \quad \text{as } n \to \infty,$$

which proves the lemma.

In order to prove Theorem 1, it remains only to control our approximations. This is done via the next two lemmas.

Lemma 4. *As $n \to \infty$, $I^{(n)} - \tilde{I}^{(n)} = O_P(\sqrt{n})$.*

Proof. Recall that $X^{(n)}$ denotes the Markov chain $(X_k^{(n)},\ k \ge 0)$. A simple computation gives

$$I^{(n)} - \tilde{I}^{(n)} = \sum_{k=1}^{\tau^{(n)}-1} Y_k^{(n)} \frac{e_k - 1}{X_k^{(n)}} + \sum_{k=1}^{\tau^{(n)}-1} Y_k^{(n)} \frac{e_k}{X_k^{(n)}(X_k^{(n)}-1)}.$$

Conditional on $X^{(n)}$ and $Y^{(n)}$, the random variables $Y_k^{(n)}(e_k - 1)/X_k^{(n)}$ are independent with zero mean. This implies, when coupled with the fact that $Y_k^{(n)} \le X_k^{(n)}$ almost surely that

$$\mathbb{E}\biggl[\biggl(\sum_{k=1}^{\tau^{(n)}-1} Y_k^{(n)} \frac{e_k - 1}{X_k^{(n)}}\biggr)^2 \biggm| X^{(n)}, Y^{(n)}\biggr] = \sum_{k=1}^{\tau^{(n)}-1} \biggl(\frac{Y_k^{(n)}}{X_k^{(n)}}\biggr)^2 \le \tau^{(n)} \le n.$$

Chebychev's inequality now implies that

$$\sum_{k=1}^{\tau^{(n)}-1} Y_k^{(n)} \frac{e_k - 1}{X_k^{(n)}} = O_P(\sqrt{n}).$$

Again using $Y_k^{(n)} \le X_k^{(n)}$ almost surely, we obtain

$$\mathbb{E}\biggl[\sum_{k=1}^{\tau^{(n)}-1} Y_k^{(n)} \frac{e_k}{X_k^{(n)}(X_k^{(n)}-1)}\biggr] \le \mathbb{E}\biggl[\sum_{k=1}^{\tau^{(n)}-1} \frac{e_k}{X_k^{(n)}-1}\biggr] \le \sum_{k=2}^{n-1} \frac{1}{k-1}.$$

This fact and Markov's inequality complete the proof of the lemma.

Lemma 5. *As $n \to \infty$, $\tilde{I}^{(n)} - \hat{I}^{(n)} = O_P(\sqrt{n})$.*

Proof. We proceed much as in [9]. Recall that $Z_k^{(n)}$ is the number of external branches after k coalescing events. Since $Y_k^{(n)} = X_k^{(n)} - Z_k^{(n)}$,

$$\tilde{I}^{(n)} - \hat{I}^{(n)} = -\sum_{k=1}^{\tau^{(n)}-1} \frac{Z_k^{(n)} - \mathbb{E}[Z_k^{(n)} \mid X^{(n)}]}{X_k^{(n)}}.$$

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Recall also that, given $X^{(n)}$ and $Z_{k-1}^{(n)}$, $Z_k^{(n)} - Z_{k-1}^{(n)}$ has a conditional hypergeometric distribution. Therefore,

$$Z_k^{(n)} = Z_{k-1}^{(n)} - (U_k^{(n)} + 1)\frac{Z_{k-1}^{(n)}}{X_{k-1}^{(n)}} - H_k^{(n)} = Z_{k-1}^{(n)}\frac{X_k^{(n)} - 1}{X_{k-1}^{(n)}} - H_k^{(n)},$$

where $H_k^{(n)}$ denotes a random variable with conditional hypergeometric distribution with parameters $X_{k-1}^{(n)}$, $Z_{k-1}^{(n)}$, and $1 + U_k^{(n)}$ as above, centered at its (conditional) expectation. Setting

$$D_k^{(n)} = Z_k^{(n)} - \mathbb{E}[Z_k^{(n)} \mid X^{(n)}],$$

it follows that

$$D_k^{(n)} = D_{k-1}^{(n)}\frac{X_k^{(n)} - 1}{X_{k-1}^{(n)}} - H_k^{(n)}.$$

Because $D_0^{(n)} = 0$, iterating this linear recursion leads to

$$\frac{D_k^{(n)}}{X_k^{(n)}} = -\sum_{j=1}^{k}\frac{H_j^{(n)}}{X_j^{(n)}}\prod_{i=j+1}^{k}\biggl(1 - \frac{1}{X_i^{(n)}}\biggr),$$

so $\tilde{I}^{(n)} - \hat{I}^{(n)}$ equals

$$\sum_{k=1}^{\tau^{(n)}-1}\sum_{j=1}^{k}\frac{H_j^{(n)}}{X_j^{(n)}}\prod_{i=j+1}^{k}\biggl(1 - \frac{1}{X_i^{(n)}}\biggr) = \sum_{j=1}^{\tau^{(n)}-1}\frac{H_j^{(n)}}{X_j^{(n)}}\sum_{k=j}^{\tau^{(n)}-1}\prod_{i=j+1}^{k}\biggl(1 - \frac{1}{X_i^{(n)}}\biggr).$$

Now, given $X^{(n)}$ and $Z_0^{(n)}, \dots, Z_{k-1}^{(n)}$, $H_k^{(n)}$ has a centered hypergeometric distribution with zero mean and finite variance, and $H_j^{(n)}$ is a function of $X^{(n)}$, $Z_0^{(n)}, \dots, Z_{k-1}^{(n)}$ for $j < k$. Consequently, the $H_k^{(n)}$ are uncorrelated. Also, from the formula for the variance of a hypergeometric distribution,

$$\mathbb{E}[(H_j^{(n)})^2 \mid X^{(n)}, Z_{j-1}^{(n)}] \le (U_j^{(n)} + 1)\frac{Z_{j-1}^{(n)}}{X_{j-1}^{(n)}}.$$

Then, since $Z_{j-1}^{(n)} \le X_{j-1}^{(n)}$ almost surely, $\mathbb{E}[(H_j^{(n)})^2 \mid X^{(n)}] \le U_j^{(n)} + 1$. Gathering all these facts now gives

$$\mathbb{E}[(\hat{I}^{(n)} - \tilde{I}^{(n)})^2 \mid X^{(n)}] \le \sum_{j=1}^{\tau^{(n)}-1}\frac{U_j^{(n)} + 1}{(X_j^{(n)})^2}\biggl(\sum_{k=j}^{\tau^{(n)}-1}\prod_{i=j+1}^{k}\biggl(1 - \frac{1}{X_i^{(n)}}\biggr)\biggr)^2.$$

The product can be estimated by 1, so

$$\mathbb{E}[(\hat{I}^{(n)} - \tilde{I}^{(n)})^2 \mid X^{(n)}] \le \sum_{j=1}^{\tau^{(n)}-1}\frac{U_j^{(n)} + 1}{(X_j^{(n)})^2}(\tau^{(n)} - j)^2 \le \sum_{j=1}^{\tau^{(n)}-1}(U_j^{(n)} + 1) \le n + \tau_n \le 2n,$$

where the second inequality follows from the fact that $\tau^{(n)} - j \le X_j^{(n)}$. Applying Chebychev's inequality now completes the proof of both the lemma and Theorem 1.

4. Application to population genetics

Suppose that mutations occur along genealogical trees according to a Poisson process with parameter $\mu > 0$. Write $M^{(n)}$ for the total number of mutations in the Bolthausen–Sznitman n-coalescent. The Poisson representation implies that, conditional on $L^{(n)}$, $M^{(n)}$ is distributed as a Poisson random variable with parameter $\mu L^{(n)}$. Each mutation is called either external or internal according to the type of branch where it appears; denote their numbers by $M_{\mathrm{E}}^{(n)}$ and $M_{\mathrm{I}}^{(n)}$, respectively, so $M^{(n)} = M_{\mathrm{E}}^{(n)} + M_{\mathrm{I}}^{(n)}$.

Proposition 2. *As $n \to \infty$,*

$$\frac{(\log n)^2}{n} M_{\mathrm{I}}^{(n)} \to \mu \quad \textit{in probability}$$

and

$$\frac{(\log n)^2}{n} M_{\mathrm{E}}^{(n)} - \mu \log n - \mu \log\log n \to \mu(Z-1) \quad \textit{in distribution.}$$

Proof. Let $N = (N_t,\ t \ge 0)$ be a Poisson process with parameter μ. Note first that $M_{\mathrm{I}}^{(n)}$ has the same distribution as $N_{I^{(n)}}$. This implies that

$$\mathbb{E}[M_{\mathrm{I}}^{(n)}] = \mathbb{E}[\mathbb{E}[M_{\mathrm{I}}^{(n)} \mid I^{(n)}]] = \mu \mathbb{E}[I^{(n)}].$$

Theorem 1 implies that $I^{(n)} \to \infty$ almost surely, so it follows that $N_{I^{(n)}}/I^{(n)} \to \mu$ in probability, and

$$\frac{M_{\mathrm{I}}^{(n)}}{\mathbb{E}[M_{\mathrm{I}}^{(n)}]} \overset{\mathrm{D}}{=} \frac{N_{I^{(n)}}}{\mu I^{(n)}} \frac{I^{(n)}}{\mathbb{E}[I^{(n)}]} \xrightarrow{\mathbb{P}} 1 \quad \text{as } n \to \infty,$$

again by appeal to Theorem 1. Therefore, the first part of the proposition follows from $\mathbb{E}[M_{\mathrm{I}}^{(n)}] = \mu \mathbb{E}[I^{(n)}] \sim \mu n/(\log n)^2$ for $n \to \infty$.

To prove the second part, we only need to observe that $M^{(n)} = M_{\mathrm{I}}^{(n)} + M_{\mathrm{E}}^{(n)}$ satisfies (see Corollary 6.2 of [12])

$$\frac{(\log n)^2}{n} M^{(n)} - \mu \log n - \mu \log\log n \to \mu Z \quad \text{in distribution, as } n \to \infty.$$

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