



# Impossibility of Consistent Distance Estimation from Sequence Lengths Under the TKF91 Model

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## Abstract

We consider the problem of distance estimation under the TKF91 model of sequence evolution by insertions, deletions and substitutions on a phylogeny. In an asymptotic regime where the expected sequence lengths tend to infinity, we show that no consistent distance estimation is possible from sequence lengths alone. More formally, we establish that the distributions of pairs of sequence lengths at different distances cannot be distinguished with probability going to one.

## 1 Introduction

Phylogeny estimation consists in the inference of an evolutionary tree from extant species data, commonly molecular sequences (e.g. DNA, amino acid). A large body of theoretical work exists on the statistical properties of standard reconstruction methods (Steel 2016; Warnow 2017). Typically in such analyses, one assumes that sequences have evolved on a fixed rooted tree, from a common ancestor sequence to the leaf sequences, according to some Markovian stochastic process. Often these processes model site substitutions exclusively, with the underlying assumption being that the data have been properly aligned in a pre-processing step. In contrast, relatively little theoretical work has focused on models of insertions and deletions (indels) together with substitutions, in spite of the fact that such models have been around for some time (Thorne et al. 1991, 1992). See e.g. (Thatte 2006; Daskalakis and Roch 2013; Allman et al. 2015; Fan and Roch 2020).

One extra piece of information available under indel models is the length of the sequence, which itself evolves according to a Markov process on the tree. The notable work of Thatte (2006) shows that leaf sequence lengths *alone* are in fact enough to

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reconstruct phylogenies, through a distance-based approach. More specifically, it is shown in (Thatté 2006, (27)) that under the TKF91 model (Thorne et al. 1991) the expectation of the sequence length  $N_v$  at a leaf  $v$  conditioned on the sequence length  $N_u$  at another leaf  $u$  separated from  $v$  by an amount of time  $t_{uv}$  is

$$\mathcal{N}_v(t) = \bar{L} + (N_u - \bar{L}) e^{-\mu t_{uv}(1-\lambda/\mu)} \quad (1)$$

where  $\bar{L} = \frac{\lambda/\mu}{1-\lambda/\mu}$  is the expected length at stationarity, where  $\lambda < \mu$  are the rates of insertion and deletion, respectively (full details on the TKF91 model are provided in Sect. 2). Hence, we see from (1) that the full distribution of sequence lengths suffices to recover  $\lambda/\mu$  and all  $\mu t_{uv}$ 's.

The tree topology can then be recovered using standard results about the metric properties of phylogenies (Steel 2016). That is, the tree is identifiable from the sequence lengths under the TKF91 model in the sense that two distinct tree topologies  $T_1 \neq T_2$  necessarily produce distinct joint distributions of sequence lengths at the leaves.

It is also suggested in Thatté (2006)—without a full rigorous proof—that the scheme above could be used to reconstruct phylogenies from a single sample of sequence lengths at the leaves in the limit where  $\lambda \nearrow \mu$ . The latter asymptotics ensure that the expected sequence length at stationarity  $\bar{L}$  diverges and serves as a proxy for the amount of data growing to infinity. However, we show that no consistent distance estimator exists in this limit. Formally we establish that the distributions of pairs of sequence lengths at different distances cannot be distinguished with probability going to 1 as  $\lambda \nearrow \mu$ . Hence, while the tree is identifiable from the distribution of the sequence lengths at the leaves, one sample of the sequence lengths alone cannot be used in a distance-based approach of the type described above to reconstruct the tree consistently as  $\lambda \nearrow \mu$ . On the technical side our proof follows by noting that, under the TKF91 model, the sequence length is (morally) a sum of independent random variables with finite variances, to which we apply a central limit theorem. One complication is to obtain a limit theorem that is uniform in the parameter  $\lambda/\mu$ . We expect that our techniques will be useful to analyze other bioinformatics methods under indel processes, for instance methods based on  $k$ -mer statistics [see e.g. (Yang and Zhang 2008; Haubold 2013)]. Further intuition on our results is provided in Sect. 3.

**Organization** The rest of the paper is organized as follows. The TKF91 model is reviewed in Sect. 2. Our main result, together with a proof sketch, is stated in Sect. 3. Details of the proof are provided in Sect. 4.

## 2 Basic Definitions

In this section, we recall the TKF91 sequence evolution model (Thorne et al. 1991). To simplify the presentation, we restrict ourselves to a two-state version of the model, as we will only require the underlying sequence-length process.

**Definition 1** (TKF91 model: two-state version) Consider the following Markov process  $\mathcal{I} = \{\mathcal{I}_t\}_{t \geq 0}$  on the space  $\mathcal{S}$  of binary digit sequences together with an **immortal**

link “•”, that is,

$$\mathcal{S} := \text{“•”} \otimes \bigcup_{M \geq 1} \{0, 1\}^M,$$

where the notation above indicates that all sequences begin with the immortal link. Positions of a sequence, except for that of the immortal link, are called **sites or mortal links**. Let  $(\nu, \lambda, \mu) \in (0, \infty)^3$  and  $(\pi_0, \pi_1) \in [0, 1]^2$  with  $\pi_0 + \pi_1 = 1$  be given parameters. The continuous-time dynamics are as follows: If the current state is the sequence  $\vec{x} \in \mathcal{S}$ , then the following events occur independently:

- *Substitution* Each site is substituted independently at rate  $\nu > 0$ . When a substitution occurs, the corresponding digit is replaced by 0 and 1 with probabilities  $\pi_0$  and  $\pi_1$ , respectively.
- *Deletion* Each site is removed independently at rate  $\mu$ .
- *Insertion* Each site, as well as the immortal link, gives birth to a new digit independently at rate  $\lambda$ . When a birth occurs, the new site is added immediately to the right of its parent site. The newborn site has digit 0 and 1 with probabilities  $\pi_0$  and  $\pi_1$ , respectively.

This indel process is time-reversible with respect to the measure  $\Pi$  given by

$$\Pi(\vec{x}) = \left(1 - \frac{\lambda}{\mu}\right) \left(\frac{\lambda}{\mu}\right)^M \prod_{i=1}^M \pi_{x_i}$$

for each  $\vec{x} = (x_1, x_2, \dots, x_M) \in \{0, 1\}^M$  where  $M \geq 1$ , and  $\Pi(\text{“•”}) = \left(1 - \frac{\lambda}{\mu}\right)$ . We assume further that  $\lambda < \mu$ . In that case,  $\Pi$  is the stationary distribution of  $\mathcal{I}$ .

We will be concerned with the underlying sequence-length process.

**Definition 2** (Sequence length) The **length** of a sequence  $\vec{x} \in \mathcal{S}$  is defined as the number of sites and is denoted by  $|\vec{x}|$ . Therefore, if  $\vec{x} = (\bullet, x_1, \dots, x_M)$ , then  $|\vec{x}| = M$ .

Under  $\Pi$ , the sequence-length process  $|\mathcal{I}|$  is stationary and is geometrically distributed. Specifically the stationary distribution of the length process  $|\mathcal{I}|$  is

$$\gamma_M^{(\lambda)} := \left(1 - \frac{\lambda}{\mu}\right) \left(\frac{\lambda}{\mu}\right)^M, \quad M \in \mathbb{Z}_+. \tag{2}$$

We are interested in this process on a rooted tree  $T$ . Denote the index set by  $\Gamma_T$ . The root vertex  $\rho$  is assigned a state  $\mathcal{I}_\rho \in \mathcal{S}$ , drawn from stationary distribution on  $\mathcal{S}$ . This state is then evolved down the tree according to the following recursive process. Moving away from the root, along each edge  $e = (u, v) \in E$ , conditionally on the state  $\mathcal{I}_u$ , we run the indel process for a time  $\ell_{(u,v)}$ . Denote by  $\mathcal{I}_t$  the resulting state at  $t \in e$ . Then the full process is denoted by  $\{\mathcal{I}_t\}_{t \in \Gamma_T}$ . In particular, the set of leaf states is  $\mathcal{I}_{\partial T} = \{\mathcal{I}_v : v \in \partial T\}$ .

**Setting** Throughout this paper, we let  $\mathbb{P}_{\vec{x}}$  be the probability measure when the root state is  $\vec{x}$ . If the root state is chosen according to a distribution  $\nu$ , then we denote the

probability measure by  $\mathbb{P}_v$ . We also denote by  $\mathbb{P}_M$  the conditional probability measure for the event that the root state has length  $M$ .

For our purposes, it will suffice to focus on the space  $\mathcal{T}_2$  of star trees with two leaves that have the same finite distance  $h \in (0, \infty)$  from the root and are labeled as  $\{1, 2\}$ . This distance  $h$  is the height of the tree. The indel process on a tree  $T \in \mathcal{T}_2$  reduces to a pair of indel processes  $(\mathcal{I}_t^1, \mathcal{I}_t^2)_{t \geq 0}$  that are independent upon conditioning on the root state  $\mathcal{I}_\rho = \mathcal{I}_0^1 = \mathcal{I}_0^2$ . We always assume the root state is chosen according to the equilibrium distribution  $\Pi$ . So the distribution of  $(\mathcal{I}_0^1, \mathcal{I}_0^2) \in \mathcal{S} \times \mathcal{S}$  is

$$\widehat{v}_0(\vec{x}, \vec{y}) = \begin{cases} \Pi(\vec{x}) & \text{if } \vec{x} = \vec{y}, \\ 0 & \text{otherwise.} \end{cases}$$

### 3 Main Result

Our main theorem is an impossibility result: the distributions of pairs of sequence lengths at different distances cannot be distinguished with probability going to 1 as  $\lambda \nearrow \mu$ . Following (Thattai 2006), we consider the asymptotic regime where  $\lambda \nearrow \mu$ , which implies that the expected sequence length at stationarity tends to  $+\infty$ . Recall that the total variation distance between two probability measures  $\tau_1$  and  $\tau_2$  on a countable measure space  $E$  is

$$\|\tau_1 - \tau_2\|_{TV} = \sup_{A \subseteq E} |\tau_1(A) - \tau_2(A)|. \tag{3}$$

**Theorem 1** (*Impossibility of distance estimation from sequence lengths*) *Let  $T^1$  and  $T^2$  be two trees in  $\mathcal{T}_2$  with heights  $h_1 > h_2 > 0$ , respectively. For  $i \in \{1, 2\}$ , we consider a TKF91 process on tree  $T^i$  and let  $\vec{N}^{(i)} = (N_1^{(i)}, N_2^{(i)}) \in \mathbb{Z}_+^2$  be the pair of sequence lengths at the leaves  $\partial T^i$ . Let*

$$\mathcal{L}_i = \mathbb{P}_\Pi(\vec{N}^{(i)} \in \cdot)$$

*be the distribution of  $\vec{N}^{(i)}$  under  $\mathbb{P}_\Pi$ . Then for any fixed deletion rate  $\mu \in (0, \infty)$ ,*

$$\limsup_{\lambda \nearrow \mu} \|\mathcal{L}_1 - \mathcal{L}_2\|_{TV} < 1. \tag{4}$$

From (3), we see that (4) implies that there is no test that can distinguish between  $\mathcal{L}_1$  and  $\mathcal{L}_2$  with probability going to 1 as  $\lambda \nearrow \mu$ .

**Proof idea** We first give a heuristic argument that underlies our formal proof. Without loss of generality, assume that the deletion rate is  $\mu = 1$ . The stationary length  $M$  at the root is geometric with mean and standard deviation both of order  $1/(1 - \lambda)$ . So we can think of the root length as roughly  $M \approx C/(1 - \lambda)$  with significant probability. Ignoring the small effect of the immortal link and conditioning on  $M$ , the lengths at the leaves are sums of independent random variables, specifically

the progenies of the  $M$  mortal links of the root. Here the progeny of a site is its descendants including itself.

The mean and variance of these variables can be computed explicitly from continuous-time Markov chain theory (see (11) below; see also (Thatte 2006, (27), (31))). As  $\lambda \nearrow 1$ , the difference in expectation between heights  $h_1$  and  $h_2$  turns out to be

$$Me^{-(1-\lambda)h_1} - Me^{-(1-\lambda)h_2} \approx \frac{C}{1-\lambda} [-(1-\lambda)h_1 + (1-\lambda)h_2] \approx C(h_2 - h_1), \tag{5}$$

while the variance is of order

$$M \frac{e^{-(1-\lambda)h_i} (1 - e^{-(1-\lambda)h_i})}{1-\lambda} \approx \frac{C}{1-\lambda} \frac{(1-\lambda)h_i}{1-\lambda} \approx \frac{Ch_i}{1-\lambda}. \tag{6}$$

The key observation is that the variance (6) is  $\gg$  than the square of the expectation difference (5). Hence, by the central limit theorem, one can expect significant overlap between the length distributions under  $h_1$  and  $h_2$ , making them hard to distinguish even as  $\lambda \nearrow 1$ . We formalize this argument next.

We observe that (4) is equivalent to

$$\liminf_{\lambda \nearrow 1} \sum_{\vec{y} \in \mathbb{Z}_+^2} \mathbb{P}_\Pi(\vec{N}^{(1)} = \vec{y}) \wedge \mathbb{P}_\Pi(\vec{N}^{(2)} = \vec{y}) > 0. \tag{7}$$

Indeed the total variation distance between two probability measures  $\tau_1$  and  $\tau_2$  on a countable space  $E$  can also be written as

$$\|\tau_1 - \tau_2\|_{TV} = 1 - \sum_{\sigma \in E} \tau_1(\sigma) \wedge \tau_2(\sigma).$$

The rest of the proof is to establish (7). It involves a series of steps:

1. We first reduce the problem to a sum of independent random variables by conditioning on the root sequence length and ignoring the immortal link. In particular, we use the fact that there is a fairly uniform probability that  $M$  is in an interval of size  $1/(1-\lambda)$  around 1. And we remove the effect of the immortal link by conditioning on its having no descendant, an event of positive probability.
2. The central limit theorem (CLT) implies that there is a significant overlap between the two sums. More precisely, we need a local CLT [see e.g. (Durrett 2010)] to derive the sort of pointwise lower bound needed in (7). However, the bound we require must be uniform in  $\lambda$  and we did not find in the literature a result of quite this form. Instead, we use an argument based on the Berry-Esséen theorem [again see e.g. (Durrett 2010)]. We first establish overlap over  $\Omega(\sqrt{M})$  constant size intervals for the sum of the first  $M - 1$  mortal links, and then we use the final mortal link to match the probabilities on common point values under heights  $h_1$  and  $h_2$ .
3. Finally we bound the sum in (7).

### 4 Proof

In this section, we give the details of the proof of Theorem 1. We follow the steps described in the previous section.

**Step 1. Reducing the problem to a sum of independent random variables** We first show that  $\mathbb{P}_\Pi$  in (7) can be replaced by  $\mathbb{P}_M$  where  $M$  is of the order of the expected sequence length  $1/(1-\lambda)$  under  $\Pi$ . That is, we condition on the length of the ancestral sequence. After that, we further ignore the progenies of the immortal link so that each leave sequence consists of i.i.d. progenies of the  $M$  sites in the ancestral sequence. These two simplifications are achieved in (8) and (9), respectively.

Precisely, for any  $\lambda_* \in (0, 1)$  and  $0 < c_1 < 1 < c_2 < +\infty$ , using (2)

$$\begin{aligned}
 & \liminf_{\lambda \nearrow 1} \sum_{\vec{y} \in \mathbb{Z}_+^2} \mathbb{P}_\Pi(\vec{N}^{(1)} = \vec{y}) \wedge \mathbb{P}_\Pi(\vec{N}^{(2)} = \vec{y}) \\
 & \geq \inf_{\lambda \in (\lambda_*, 1)} \sum_{\vec{y} \in \mathbb{Z}_+^2} \mathbb{P}_\Pi(\vec{N}^{(1)} = \vec{y}) \wedge \mathbb{P}_\Pi(\vec{N}^{(2)} = \vec{y}) \\
 & = \inf_{\lambda \in (\lambda_*, 1)} \sum_{\vec{y} \in \mathbb{Z}_+^2} \left[ \sum_{M \in \mathbb{Z}_+} \gamma_M^{(\lambda)} \mathbb{P}_M(\vec{N}^{(1)} = \vec{y}) \right] \wedge \left[ \sum_{M \in \mathbb{Z}_+} \gamma_M^{(\lambda)} \mathbb{P}_M(\vec{N}^{(2)} = \vec{y}) \right] \\
 & = \inf_{\lambda \in (\lambda_*, 1)} \sum_{\vec{y} \in \mathbb{Z}_+^2} \sum_{M \in \mathbb{Z}_+} (1-\lambda)\lambda^M \left[ \mathbb{P}_M(\vec{N}^{(1)} = \vec{y}) \wedge \mathbb{P}_M(\vec{N}^{(2)} = \vec{y}) \right] \\
 & \geq \inf_{\lambda \in (\lambda_*, 1)} \sum_{M \in \left[ \frac{c_1}{1-\lambda}, \frac{c_2}{1-\lambda} \right]} (1-\lambda)\lambda^M \sum_{\vec{y} \in \mathbb{Z}_+^2} \mathbb{P}_M(\vec{N}^{(1)} = \vec{y}) \wedge \mathbb{P}_M(\vec{N}^{(2)} = \vec{y}) \\
 & \geq c_3 \inf_{\lambda \in (\lambda_*, 1)} \inf_{M \in \left[ \frac{c_1}{1-\lambda}, \frac{c_2}{1-\lambda} \right]} \sum_{\vec{y} \in \mathbb{Z}_+^2} \mathbb{P}_M(\vec{N}^{(1)} = \vec{y}) \wedge \mathbb{P}_M(\vec{N}^{(2)} = \vec{y}), \tag{8}
 \end{aligned}$$

where  $c_3 := \inf_{\lambda \in (\lambda_*, 1)} (1-\lambda) \sum_{M \in \left[ \frac{c_1}{1-\lambda}, \frac{c_2}{1-\lambda} \right]} \lambda^M$ . Note that  $c_3 \in (0, \infty)$  because the expression  $(1-\lambda) \sum_{M \in \left[ \frac{c_1}{1-\lambda}, \frac{c_2}{1-\lambda} \right]} \lambda^M$  is continuous in  $\lambda$  and tends to  $e^{-c_1} - e^{-c_2}$  as  $\lambda \rightarrow 1$ .

Let  $\mathcal{Z}_0$  be the event that the immortal link of the root sequence produces no mortal link in either leaf sequences. Let  $\mathbb{P}_{M, \bullet}$  be the probability conditioned on that event, and  $c_4$  be a lower bound on the probability of  $\mathcal{Z}_0$  uniform in  $\lambda \in (\lambda_*, 1)$ . Under  $\mathbb{P}_{M, \bullet}$ , the two components of  $\vec{N}^{(1)}$  are conditionally independent and each is a sum of  $M$  i.i.d. random variables corresponding to the progenies of mortal links. Hence, (8) is at least

$$\begin{aligned}
 c_4 c_3 \inf_{\lambda \in (\lambda_*, 1)} & \inf_{M \in \left[ \frac{c_1}{1-\lambda}, \frac{c_2}{1-\lambda} \right]} \sum_{\vec{y} \in \mathbb{Z}_+^2} \mathbb{P}_{M, \bullet}(\vec{N}^{(1)} = \vec{y}) \wedge \mathbb{P}_{M, \bullet}(\vec{N}^{(2)} = \vec{y}) \\
 & = c_4 c_3 \inf_{\lambda \in (\lambda_*, 1)} \inf_{M \in \left[ \frac{c_1}{1-\lambda}, \frac{c_2}{1-\lambda} \right]} \sum_{\vec{y} \in \mathbb{Z}_+^2} \left[ p_{M, y_1}^{(\lambda)}(h_1) p_{M, y_2}^{(\lambda)}(h_1) \right] \wedge \left[ p_{M, y_1}^{(\lambda)}(h_2) p_{M, y_2}^{(\lambda)}(h_2) \right],
 \end{aligned} \tag{9}$$

where we let  $p_{i,j}^{(\lambda)}(t) = \mathbb{P}_{i, \bullet}(|\mathcal{I}_t| = j)$  for  $i, j \in \mathbb{Z}_+$  be the transition probabilities of the length process *without* the immortal link.

The sum in (9) leads us to study the overlap between the probability distributions  $p_{M, \cdot}^{(\lambda)}(t) := \{p_{M,j}^{(\lambda)}(t)\}_{j \in \mathbb{Z}_+}$  for  $t = h_1, h_2$  and  $M \in \left[ \frac{c_1}{1-\lambda}, \frac{c_2}{1-\lambda} \right]$ . The central limit theorem is what we need. However, because of our need for a bound that is uniform in  $\lambda$ , we shall apply the Berry-Esséén theorem. Specifically, we apply the latter bound to the progenies of the first  $M - 1$  mortal links of the root sequence. The idea is to show that  $\Omega(\sqrt{M})$  summands in (9) have value  $\Omega(1/\sqrt{M})$ , for each of  $h_1$  and  $h_2$  separately, and then use the last mortal link to “match” all these values between  $h_1$  and  $h_2$ .

**Step 2a. Establishing a uniform bound for  $p_{M-1, \cdot}^{(\lambda)}(t)$**  Note that  $p_{M, \cdot}^{(\lambda)}(t)$  is the distribution of  $S_M(t) := \sum_{i=1}^M L_t^i$ , where  $\{L_t^i\}_{i \geq 1}$  are i.i.d. random variables having the distribution of the progeny length of a single mortal link at time  $t > 0$ .

Let the mean and the variance of  $L_t^i$  be

$$\beta := \beta(\lambda, t) := \mathbb{E}[L_t^i] \quad \text{and} \quad \sigma^2 := \sigma^2(\lambda, t) := \mathbb{E}|L_t^i - \beta|^2. \tag{10}$$

As is expected, the distribution  $p_{M, \cdot}^{(\lambda)}(t)$  is approximately Gaussian with mean  $\beta M$  and variance  $\sigma^2 M$ . We quantify this statement in the bound (12) below, after proving some moment bounds.

**Lemma 1** *Let  $\beta(\lambda, t)$  and  $\sigma(\lambda, t)$  be the mean and the standard deviation of  $L_t^i$  defined in (10) and consider the absolute third moment  $\rho(\lambda, t) := E|L_t^i - \beta|^3$ . For any  $t \in (0, \infty)$ ,*

$$\beta(\lambda, t) = e^{-(1-\lambda)t} \quad \text{and} \quad \sigma^2(\lambda, t) = \frac{1 + \lambda}{1 - \lambda} e^{-(1-\lambda)t} (1 - e^{-(1-\lambda)t}). \tag{11}$$

Furthermore,

$$0 < \inf_{\lambda \in [\lambda_*, 1)} \sigma(\lambda, t) < \sup_{\lambda \in [\lambda_*, 1)} \sigma(\lambda, t) < \infty \quad \text{and} \quad \sup_{\lambda \in [\lambda_*, 1)} \rho(\lambda, t) < \infty.$$

**Proof** For (11), see e.g. (Daskalakis and Roch 2013, (3), (4)).

Moreover, from (Thorne et al. 1991, (8)–(10)) or (Thatte 2006, (7)–(8)), the probability that a normal link has  $n$  descendants including itself is

$$\mathbb{P}(L_t^i = n) = \begin{cases} (1 - \eta(\lambda, t))(1 - \lambda\eta(\lambda, t))[\lambda\eta(\lambda, t)]^{n-1} & \text{for } n \geq 1 \\ \eta(\lambda, t) & \text{for } n = 0 \end{cases},$$

where  $\eta(\lambda, t) = \frac{1 - e^{-(1-\lambda)t}}{1 - \lambda e^{-(1-\lambda)t}}$ . It can be seen from L'Hospital's rule that  $\eta(\lambda, t)$  is continuous as a function of  $\lambda$  around 1 and that  $\eta(\lambda, t) = \frac{t}{1+t} + O(|1 - \lambda|)$  as  $\lambda \rightarrow 1$ . From this explicit formula for the probability mass function of  $L_t^i$ , which we note is a geometric sequence, it follows that all moments of  $L_t^i$  are bounded from above uniformly in  $\lambda \in [\lambda_*, 1)$ .

To show that the variance is bounded from below uniformly in  $\lambda \in [\lambda_*, 1)$ , we note (again using L'Hospital's rule) that  $\sigma^2(\lambda, t)$  is continuous in  $\lambda$  around 1, strictly positive and tends to  $2t$  as  $\lambda \rightarrow 1$ . Hence, the variance is bounded from below, uniformly in  $\lambda \in [\lambda_*, 1)$   $\square$

Let  $F_M^{(\lambda)}(t)$  be the cumulative distribution function (CDF) of the probability distribution  $p_{M,\cdot}^{(\lambda)}(t)$ . That is,

$$F_M^{(\lambda)}(t)(x) = \sum_{j:j \leq x} p_{M,j}^{(\lambda)}(t) = \mathbb{P}(S_M(t) \leq x).$$

**Lemma 2** [Uniform bound for  $p_{M-1,\cdot}^{(\lambda)}(t)$ ] For each  $t > 0$ , there exists a constant  $C > 0$  such that

$$\sup_{\lambda \in [\lambda_*, 1)} \sup_{x \in \mathbb{R}} \left| F_M^{(\lambda)}(t) \left( M\beta(\lambda, t) + x \sigma(\lambda, t) \sqrt{M} \right) - \mathcal{N}(x) \right| \leq \frac{C}{\sqrt{M}}, \tag{12}$$

for all  $M \in \mathbb{Z}_+$ , where  $\mathcal{N}$  is the CDF of the standard normal distribution.

**Proof** Since  $\beta(\lambda, t), \sigma^2(\lambda, t), \rho(\lambda, t) \in (0, \infty)$ , the Berry-Esséen theorem [as stated e.g. in Durrett (2010)] applies and asserts that

$$\sup_{x \in \mathbb{R}} \left| \mathbb{P} \left( \frac{S_{M-1} - (M-1)\beta(\lambda, t)}{\sigma(\lambda, t)\sqrt{M-1}} \leq x \right) - \mathcal{N}(x) \right| \leq \frac{3\rho(\lambda, t)}{\sigma^3(\lambda, t)\sqrt{M-1}} \tag{13}$$

for all  $\lambda \in [0, 1)$ . By Lemma 1, for each  $t > 0$ , the right-hand side is bounded from above uniformly for  $\lambda \in [\lambda_*, 1)$ .  $\square$

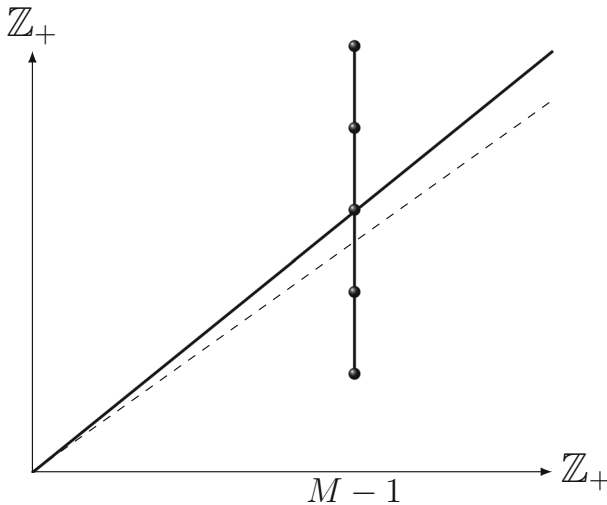
**Step 2b. Controlling the overlap of  $p_{M-1,\cdot}^{(\lambda)}(h_1)$  and  $p_{M-1,\cdot}^{(\lambda)}(h_2)$  in (9)** To quantify the overlap between  $p_{M-1,\cdot}^{(\lambda)}(h_1)$  and  $p_{M-1,\cdot}^{(\lambda)}(h_2)$ , we first compare their expectations. For simplicity, we write  $\beta_i := \beta(\lambda, h_i), \sigma_i := \sigma(\lambda, h_i)$  and  $\rho_i := \rho(\lambda, h_i)$  for  $i = 1, 2$ , where these functions are defined in Lemma 1. From the formula of  $\beta$  in (11), we have

$$|\beta_1 - \beta_2| \leq (1 - \lambda)(h_1 - h_2)$$

and so, for  $M \in \left[ \frac{c_1}{1-\lambda}, \frac{c_2}{1-\lambda} \right]$ , the means of  $S_{M-1}$  for  $h_1$  and  $h_2$  are close in the sense that

$$|\beta_1(M-1) - \beta_2(M-1)| \leq c_6 \tag{14}$$





**Fig. 1** The solid straight line  $j = \beta_1 M$  has slope  $\beta_1$  and the dotted line  $j = \beta_2 M$  has slope  $\beta_2$  where  $\beta_i = \beta(\lambda, h_i)$  for  $i = 1, 2$ . The vertical line has length  $2\sigma_1 \sqrt{M-1}$  where  $\sigma_1 = \sigma(\lambda, h_1)$  and represents the union of sub-intervals  $\bigcup_{r \in \Lambda_K^M} \mathcal{J}_r^M(K)$ . Lemma 3 says that for each  $M \in \left[ \frac{c_1}{1-\lambda}, \frac{c_2}{1-\lambda} \right]$ , both probability measures  $p_{M-1, \cdot}^{(\lambda)}(h_1)$  and  $p_{M-1, \cdot}^{(\lambda)}(h_2)$  have mass at least  $c_8/\sqrt{M-1}$  on  $\mathcal{J}_r^M(K)$ , uniformly for all  $r \in \Lambda_K^M$  and  $\lambda \in [\lambda_*, 1)$

for some  $c_6 > 0$  not depending on  $\lambda$ .

Now consider first the interval with length roughly twice the standard deviation of  $p_{M-1, \cdot}^{(\lambda)}(h_1)$  and centered at around its means  $\beta(\lambda, h_1)(M-1)$ , then consider an equi-partition of this interval into roughly  $\frac{2\sqrt{M-1}}{K}$  many pieces of constant length  $\sigma_1 K$ , where  $K > 0$  is an arbitrary constant. Precisely, we consider the sub-intervals

$$\mathcal{J}_r^M(K) := (\beta_1(M-1) + r\sigma_1 K, \beta_1(M-1) + (r+1)\sigma_1 K) \tag{15}$$

for  $r \in \Lambda_K^M$ , where

$$\Lambda_K^M := \left\{ -\left\lfloor \frac{\sqrt{M-1}}{K} \right\rfloor, \dots, -1, 0, 1, \dots, \left\lfloor \frac{\sqrt{M-1}}{K} \right\rfloor - 1 \right\} \tag{16}$$

and  $\lfloor x \rfloor$  denotes the largest integer smaller than or equal to  $x$ .

Lemma 3 says that there exist positive constants  $K = c_7$  large enough and  $c_8$  small enough, depending on  $c_6$  but not on  $\lambda \in (\lambda_*, 1)$ , such that each of these intervals contains mass at least  $\frac{c_8}{\sqrt{M-1}}$  under both probability distributions  $p_{M-1, \cdot}^{(\lambda)}(h_1)$  and  $p_{M-1, \cdot}^{(\lambda)}(h_2)$ . See Fig. 1. Write  $p_{M-1, A}^{(\lambda)}(t) = \sum_{j \in A} p_{M-1, j}^{(\lambda)}(t)$  for simplicity.

**Lemma 3** *There exist positive constants  $c_7, c_8$  such that  $c_7 \inf_{\lambda \in [\lambda_*, 1)} \sigma_1 > 1$  and, with  $\mathcal{J}_r = \mathcal{J}_r^M(c_7)$  and  $\Lambda^M = \Lambda_{c_7}^M$ ,*

$$P_{M-1, \mathcal{J}_r}^{(\lambda)}(h_1) \wedge P_{M-1, \mathcal{J}_r}^{(\lambda)}(h_2) \geq \frac{c_8}{\sqrt{M-1}}$$

for all  $r \in \Lambda^M$ ,  $M \in \left[ \frac{c_1}{1-\lambda}, \frac{c_2}{1-\lambda} \right]$  and  $\lambda \in [\lambda_*, 1)$ .

**Proof** The Berry-Esséen theorem (13) implies that

$$\sup_{r \in \Lambda_K^M} \left| P_{M-1, \mathcal{J}_r}^{(\lambda)}(h_1) - \int_{\mathcal{J}_r} \frac{1}{\sqrt{2\pi}} e^{-\frac{x^2}{2}} dx \right| \leq \frac{6\rho_1}{\sigma_1^3 \sqrt{M-1}} \tag{17}$$

for all  $\lambda \in [\lambda_*, 1)$ ,  $M \geq 2$  and  $K > 0$ , where  $\mathcal{J}_r = \mathcal{J}_r^M(K)$  is defined in (15),  $\Lambda_K^M$  is defined in (16), and

$$\tilde{\mathcal{J}}_r := \frac{\mathcal{J}_r - (M-1)\beta_1}{\sigma_1 \sqrt{M-1}} = \left( \frac{rK}{\sqrt{M-1}}, \frac{(r+1)K}{\sqrt{M-1}} \right).$$

Then  $\{\tilde{\mathcal{J}}_r\}_{r \in \Lambda^M}$  is roughly an equi-partition of the interval  $(-1, 1)$  into  $\frac{2\sqrt{M-1}}{K}$  sub-intervals of length  $\frac{K}{\sqrt{M-1}}$ . Furthermore, since  $\tilde{\mathcal{J}}_r \subset [-1, 1]$  for all  $r \in \Lambda_K^M$ ,

$$\int_{\tilde{\mathcal{J}}_r} \frac{1}{\sqrt{2\pi}} e^{-\frac{x^2}{2}} dx \geq \frac{K}{\sqrt{M-1}} \frac{e^{-1/2}}{\sqrt{2\pi}}.$$

From (17), there exists an absolute constant  $C$  large enough such that when  $K = C \sup_{\lambda \in (\lambda_*, 1)} \frac{\rho_1}{\sigma_1^3}$ , we have

$$\inf_{r \in \Lambda_K^M} P_{M-1, \mathcal{J}_r}^{(\lambda)}(h_1) \geq \frac{c}{\sqrt{M-1}}$$

for some constant  $c > 0$  that depends neither on  $M \in \left[ \frac{c_1}{1-\lambda}, \frac{c_2}{1-\lambda} \right]$  nor  $\lambda \in [\lambda_*, 1)$ . Therefore, we let  $c_7 := C \sup_{\lambda \in (\lambda_*, 1)} \frac{\rho_1}{\sigma_1^3}$  and take  $K = c_7$ .

We now repeat the above argument for  $h_2$ , using (14). Similarly to (17), inequality (13) implies that

$$\sup_{r \in \Lambda^M} \left| P_{M-1, \mathcal{J}_r}^{(\lambda)}(h_2) - \int_{\mathcal{E}_r} \frac{1}{\sqrt{2\pi}} e^{-\frac{x^2}{2}} dx \right| \leq \frac{6\rho_2}{\sigma_2^3 \sqrt{M-1}}$$

for all  $\lambda \in [\lambda_*, 1)$  and  $M \geq 2$ , where  $\mathcal{J}_r = \mathcal{J}_r^M(c_7)$  is defined in (15) using  $h_1$ , and

$$\mathcal{E}_r := \frac{\mathcal{J}_r - (M-1)\beta_2}{\sigma_2 \sqrt{M-1}} = \frac{(\beta_1 - \beta_2)\sqrt{M-1}}{\sigma_2} + \frac{\sigma_1}{\sigma_2} \left( \frac{rc_7}{\sqrt{M-1}}, \frac{(r+1)c_7}{\sqrt{M-1}} \right).$$

and we denote  $a + bI = \{a + bx : x \in I\}$  for any interval  $I$  and  $a, b \in \mathbb{R}$ .

By (14),  $\mathcal{E}_r \subset [-A, A]$  for all  $r \in \Lambda^M$  and  $M \geq 2$ , where  $A := c_6 + \sup_{\lambda \in (\lambda_*, 1)} \frac{\sigma_1}{\sigma_2} \in (0, \infty)$ . Hence, as before, we have

$$\inf_{r \in \Lambda^M} p_{M-1, \mathcal{J}_r}^{(\lambda)}(h_2) \geq \frac{c'}{\sqrt{M-1}}$$

for some constant  $c' > 0$  that depends neither on  $M \in \left[\frac{c_1}{1-\lambda}, \frac{c_2}{1-\lambda}\right]$  nor  $\lambda \in [\lambda_*, 1)$ , even though  $\mathcal{J}_r$  is constructed using  $h_1$ .

The proof is complete by taking  $c_8 = \min\{c, c'\}$ . □

**Step 2c. Matching  $p_{M, \cdot}^{(\lambda)}(h_1)$  and  $p_{M, \cdot}^{(\lambda)}(h_2)$  by the last mortal link** Lemma 3 establishes overlap of  $p_{M-1, \cdot}^{(\lambda)}(h_1)$  and  $p_{M-1, \cdot}^{(\lambda)}(h_2)$  over constant size intervals. The next lemma uses the final mortal link to establish overlap of  $p_{M, \cdot}^{(\lambda)}(h_1)$  and  $p_{M, \cdot}^{(\lambda)}(h_2)$  over specific values.

**Lemma 4** *There exists a positive constant  $c_9$  such that*

$$\inf_{j_{r+1}^* \in \mathcal{J}_{r+1} \cap \mathbb{Z}_+} p_{M, j_{r+1}^*}^{(\lambda)}(h_1) \wedge p_{M, j_{r+1}^*}^{(\lambda)}(h_2) > \frac{c_8 c_9}{\sigma_1^* c_7 \sqrt{M-1}}.$$

for all  $r \in \Lambda^M$ ,  $M \in \left[\frac{c_1}{1-\lambda}, \frac{c_2}{1-\lambda}\right]$  and  $\lambda \in [\lambda_*, 1)$ , where  $\sigma_1^* := \sup_{\lambda \in (\lambda_*, 1)} \sigma_1$ .

**Proof** By Lemma 3,  $\mathcal{J}_r$  contains at least one integer, say  $j_r^{(1)}$ , with mass at least  $\frac{c_8}{\sigma_1^* c_7 \sqrt{M-1}}$  under the probability measure  $p_{M-1, \cdot}^{(\lambda)}(h_1)$ . This is because (i)  $\mathcal{J}_r$  is non-empty since  $c_7 \inf_{\lambda \in [\lambda_*, 1)} \sigma_1 > 1$  by Lemma 3, and (ii) there are at most  $\lceil c_7 \sigma_1^* \rceil$  many integers in  $\mathcal{J}_r$ .

Similarly, there exists  $j_r^{(2)}$  with mass at least  $\frac{c_8}{\sigma_1^* c_7 \sqrt{M-1}}$  under  $p_{M-1, \cdot}^{(\lambda)}(h_2)$ . Hence,

$$p_{M-1, j_r^{(1)}}^{(\lambda)}(h_1) \wedge p_{M-1, j_r^{(2)}}^{(\lambda)}(h_2) \geq \frac{c_8}{\sigma_1^* c_7 \sqrt{M-1}}.$$

Let  $j_{r+1}^*$  be an arbitrary integer in  $\mathcal{J}_{r+1}$ . The progeny of the  $M$ -th mortal link has a probability at each integer in  $[0, 2\sigma_1^* c_7]$  bounded from below by a positive constant  $\tilde{c}$  uniformly for all such integers and all  $\lambda \in [0, 1)$ . It follows that

$$\begin{aligned} p_{M, j_{r+1}^*}^{(\lambda)}(h_1) &= \sum_{k=0}^{j_{r+1}^*} p_{M-1, k}^{(\lambda)}(h_1) p_{1, j_{r+1}^* - k}^{(\lambda)}(h_1) > p_{M-1, j_r^{(1)}}^{(\lambda)}(h_1) p_{1, j_{r+1}^* - j_r^{(1)}}^{(\lambda)}(h_1) \\ &\geq \frac{c_8 \tilde{c}}{\sigma_1^* c_7 \sqrt{M-1}} \end{aligned}$$

and similar for  $h_2$ . The proof is complete. □

**Step 3. Putting everything together** Lemma 4 implies the sum in (9) is at least a positive constant, uniformly in  $M \in \left[ \frac{c_1}{1-\lambda}, \frac{c_2}{1-\lambda} \right]$  and  $\lambda \in (\lambda_*, 1)$ , because that sum is

$$\begin{aligned}
 & \sum_{\vec{y} \in \mathbb{Z}_+^2} \left[ p_{M,y_1}^{(\lambda)}(h_1) p_{M,y_2}^{(\lambda)}(h_1) \right] \wedge \left[ p_{M,y_1}^{(\lambda)}(h_2) p_{M,y_2}^{(\lambda)}(h_2) \right] \\
 & \geq \sum_{y_1 \in \cup_{r \in \Lambda} M \mathcal{J}_{r+1} \cap \mathbb{Z}_+, y_2 \in \cup_{r \in \Lambda} M \mathcal{J}_{r+1} \cap \mathbb{Z}_+} \left[ p_{M,y_1}^{(\lambda)}(h_1) \wedge p_{M,y_1}^{(\lambda)}(h_2) \right] \\
 & \quad \cdot \left[ p_{M,y_2}^{(\lambda)}(h_1) \wedge p_{M,y_2}^{(\lambda)}(h_2) \right] \\
 & \geq \left( \frac{c_8 c_9}{\sigma_1^* c_7 \sqrt{M-1}} \right)^2 \left| \{y_1 \in \cup_{r \in \Lambda} M \mathcal{J}_{r+1} \cap \mathbb{Z}_+, y_2 \in \cup_{r \in \Lambda} M \mathcal{J}_{r+1} \cap \mathbb{Z}_+\} \right| \\
 & \geq \left( \frac{c_8 c_9}{\sigma_1^* c_7} \right)^2.
 \end{aligned}$$

The proof of (7) and hence that of Theorem 1 are complete.

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