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A Central Limit Theorem for punctuated equilibrium

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ABSTRACT

Current evolutionary biology models usually assume that a phenotype undergoes gradual change. This is in stark contrast to biological intuition, which indicates that change can also be punctuated—the phenotype can jump. Such a jump could especially occur at speciation, i.e., dramatic change occurs that drives the species apart. Here we derive a Central Limit Theorem for punctuated equilibrium. We show that, if adaptation is fast, for weak convergence to normality to hold, the variability in the occurrence of change has to disappear with time.

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1. Introduction

A long-standing debate in evolutionary biology is whether changes take place at times of speciation (punctuated equilibrium Eldredge and Gould^[28], Gould and Eldredge^[32] or gradually over time (phyletic gradualism, see references in Eldredge and Gould^[28]). Phyletic gradualism is in line with Darwin's original envisioning of evolution (Eldredge and Gould^[28]). On the other hand, the theory of punctuated equilibrium was an answer to what fossil data was indicating (Eldredge and Gould^[28], Gould and Eldredge^[31,32]). A complete unbroken fossil series was rarely observed, rather distinct forms separated by long periods of stability (Eldredge and Gould^[28]). Darwin saw “the fossil record more as an embarrassment than as an aid to his theory” (Eldredge and Gould^[28]) in the discussions with Falconer at the birth of the theory of evolution. Evolution with jumps was proposed under the name “quantum evolution” (Simpson^[50]) to the scientific community. However, only later (Eldredge and Gould^[28]) was punctuated equilibrium re-introduced into contemporary mainstream

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evolutionary theory. Mathematical modeling of punctuated evolution on phylogenetic trees seems to be still in its infancy (but see Bokma^[19,21,22], Mattila and Bokma^[37], Mooers and Schluter^[42], Mooers et al.^[43]). The main reason is that we do not seem to have sufficient understanding of the stochastic properties of these models. An attempt was made in this direction (Bartoszek^[10])—to derive the tips’ mean, variance, covariance and interspecies correlation for a branching Ornstein–Uhlenbeck (OU) process with jumps at speciation, alongside a way of quantitatively assessing the effect of both types of evolution. Very recently Bastide et al.^[15] considered the problem from a statistical point of view and proposed an Expectation–Maximization algorithm for a phylogenetic Brownian motion with jumps model and an OU with jumps in the drift function model. This work is very important to indicate as it includes estimation software for a punctuated equilibrium model, something not readily available earlier. Bitseki Penda et al.^[18] also recently looked into estimation procedures for bifurcating Markov chains.

Combining jumps with an OU process is attractive from a biological point of view. It is consistent with the original motivation behind punctuated equilibrium. At branching, dramatic events occur that drive species apart. But then stasis between these jumps does not mean that no change takes place, rather that during it “fluctuations of little or no accumulated consequence” occur (Gould and Eldredge^[32]). The OU process fits into this idea because if the adaptation rate is large enough, then the process reaches stationarity very quickly and oscillates around the optimal state. This then can be interpreted as stasis between the jumps—the small fluctuations. Mayr^[38] supports this sort of reasoning by hypothesizing that “The further removed in time a species from the original speciation event that originated it, the more its genotype will have become stabilized and the more it is likely to resist change.” It should perhaps be noted at this point, that a Reviewer pointed out that the modeling approach presented in this work is not the same as the “classical view of punctuated equilibrium”. One would expect the jump to take place in the direction of the optimum trait value. However, here at speciation the jump is allowed to take place in any direction, also away from the optimum. Then, after the jump, a relaxation period occurs and the trait is allowed to evolve back to the optimum. Such a view on the jumps is similar to e.g. Bokma’s^[19,21] modeling approach, however, there the Brownian motion (BM) process was considered so no optimum parameter was present. All the presented here results, concern the balance between the relaxation phenomena and the jumps’ magnitudes and chances of occurring. One way of maybe thinking about jumps going against the optimum, is that at the speciation event a short-lived (as afterwards evolution goes again in the direction of the previous optimum),

random environmental niche appeared that allowed part of the species' population to break-off and form a new species. However, to make this any more formal one would have to link it with models for the environment, fitness and trait dependent speciation, which is beyond the scope of this paper.

In this work we build up on previous results (Bartoszek^[10], Bartoszek and Sagitov^[12]) and study in detail the asymptotic behavior of the average of the tip values of a branching OU process, with jumps at speciation points, evolving on a pure birth tree. To the best of our knowledge the work here is one of the first to consider the effect of jumps on a branching OU process in a phylogenetic context (but also look at Bastide et al.^[15]). It is possible that some of the results could be special subcases of general results on branching Markov processes (e.g. Abraham and Delmas^[1], Bansaye et al.^[8], Cloez and Hairer^[24], Marguet^[36], Ren et al.^[46–48]). However, these studies use a very heavy functional analysis apparatus, which unlike the direct one here, could be difficult for the applied reader. Bansaye et al.^[8], Guyon^[33], Bitseki Penda et al.^[17]'s works are worth pointing out as they connect their results on bifurcating Markov processes with biological settings where branching phenomena are applicable, e.g., cell growth.

In the work here we can observe the (well known) competition between the tree's speciation and OU's adaptation (drift) rates, resulting in a phase transition when the latter is half the former (the same as in the no jumps case Adamczak and Miłoś^[2,3], Ané et al.^[4], Bartoszek and Sagitov^[12]). We show here that if variability in jump occurrences disappears with time or the model is in the critical regime (plus a bound assumption on the jumps' magnitude and chances of occurring), then the contemporary sample mean will be asymptotically normally distributed. Otherwise the weak limit can be characterized as a "normal distribution with a random variance". Such probabilistic characterizations are important as tools for punctuated phylogenetic models are starting to be developed (e.g., Bastide et al.^[15]). This is partially due to an uncertainty of what is estimable, especially whether the contribution of gradual and punctuated change may be disentangled (but Bokma^[22] indicates that they should be distinguishable). Large sample size distributional approximations will allow for choosing seeds for numerical maximum likelihood procedures and sanity checks if the results of numerical procedures make sense. For example in the one-dimensional OU case it is known that (for a Yule tree) the sample average is a consistent estimator of the long term mean and the sample variance of the OU process' stationary variance (Bartoszek and Sagitov^[12]). In the BM (Yule tree) case one can have a consistent estimator of the diffusion coefficient.^[13] Hence, from these sample statistics one can construct starting values for numerical estimation procedures (as e.g. mvSLOUCH does now^[14]).

Often a key ingredient in studying branching Markov processes is a “Many-to-One” formula—the law of the trait of an uniformly sampled individual in an “average” population (e.g. Marguet^[36]). The approach in this paper is that on the one hand we condition on the population size, n , but then to obtain the law (and its limit) of the contemporary population, we consider moments of uniformly sampled species and the covariance between a uniformly sampled pair of species.

The strategy to study the limit behavior is to first condition on a realization of the Yule tree and jump pattern (on which branches after speciation did the jump take place). This is, as conditional on the phylogeny and jump locations, the collection of the contemporary tips’ trait values will have a multivariate normal distribution, and hence their sample average will be normally distributed. We are able to represent (under the above conditioning) the variance of the sample average in terms of transformations of the number of speciation events on randomly selected lineage, time to coalescent of randomly selected pair of tips and the number of common speciation events for a randomly selected pair of tips. We consider the conditional (on the tree and jump pattern) expectation of these transformations and then look at the rate of decay to 0 of the variances of these conditional expectations. If this rate of decay is fast enough, then they will converge to a constant and the normality of an appropriately scaled average of tips species will be retained in the limit. Very briefly this rate of decay depends on how the product of the probability and variance of the jump behaves along the nodes of the tree. We do not necessarily assume (as previously by Bartoszek^[10]) that the jumps are homogeneous on the whole tree.

First, in [Section 2](#) we provide a series of formal definitions that introduce key random variables associated with the phylogeny that are necessary for this study. Afterwards, in [Section 3](#) we introduce the considered probabilistic model and the concepts from [Section 2](#) in a more intuitive manner. Then, in [Section 4](#) we present the main results. [Section 5](#) is devoted to a series of technical convergence lemmata that characterize the speed of decay of the effect of jumps on the variance and covariance of tip species. Finally, in [Section 6](#) we calculate the first two moments of a scaled sample average, introduce a particular random variable related to the model and put this together with the previous convergence lemmata to prove the Central Limit Theorems (CLTs) of this paper. It should be acknowledged at this point that in the original arXiv preprint of this paper the convergence to normality results were stated in an incomplete manner. In particular the limiting normality in the critical regime was not described correctly. The current characterization was noticed during the collaboration with Torkel Erhardsson^[11]

and more details on the previous mischaracterization can be found in [Remark 4.7](#).

2. Notation

We first introduce two separate labellings for the tip and internal nodes of the tree. Let the origin of the tree have label “0”. Next we label from “1” to “ $n - 1$ ” the internal nodes of the tree in their temporal order of appearance. The root is “1”, the node corresponding to the second speciation event is “2” and so on. We label the tips of the tree from “1” to “ n ” in an arbitrary fashion. This double usage of the numbers “1” to “ $n - 1$ ” does not generate any confusion as it will always be clear whether one refers to a tip or internal node.

Definition 2.1.

$$N_{\text{Tip}}(t) = \{\text{set of tip nodes at time } t\}$$

Definition 2.2.

$$U^{(n)} = \inf \{t \geq 0 : |N_{\text{Tip}}(t)| = n\},$$

where $|A|$ denotes the cardinality of set A .

Definition 2.3.

For $i \in N_{\text{Tip}}(U^{(n)})$,

$\Upsilon^{(i,n)}$: number of nodes on the path from the root
(internal node 1, including it) to tip node i

Definition 2.4.

For $i \in N_{\text{Tip}}(U^{(n)})$, define the finite sequence of length $\Upsilon^{(i,n)}$ as

$$I^{(i,n)} = \left(I_j^{(i,n)} : I_j^{(i,n)} \text{ is a node on the root to tip node } i \text{ path and} \right. \\ \left. I_j^{(i,n)} < I_k^{(i,n)} \text{ for } 1 \leq j < k \leq \Upsilon^{(i,n)} \right)_{j=1}^{\Upsilon^{(i,n)}}$$

Definition 2.5.

For $i \in N_{\text{Tip}}(U^{(n)})$ and $r \in \{1, \dots, n - 1\}$, let $\mathbf{1}_r^{(i,n)}$ be a binary random variable such that

$$\mathbf{1}_r^{(i,n)} = 1 \text{ iff } r \in I^{(i,n)},$$

where the \in should be understood in the natural way that there exists a position j in the sequence $I^{(i,n)}$ s.t. $I_j^{(i,n)} = r$.

Definition 2.6. For $i \in N_{\text{Tip}}(U^{(n)})$ and $r \in \{1, \dots, \Upsilon^{(i,n)}\}$, let $J_r^{(i,n)}$ be a binary random variable equaling 1 iff a jump (an event that will be discussed in more detail Section 3) took place just after the r -th speciation event in the sequence $I^{(i,n)}$.

Definition 2.7. For $i \in N_{\text{Tip}}(U^{(n)})$ and $r \in \{1, \dots, n-1\}$, let $Z_r^{(i,n)}$ be a binary random variable equaling 1 iff $\mathbf{1}_r^{(i,n)} = 1$ and $J_k^{(i,n)} = 1$, where $I_k^{(i,n)} = r$.

Definition 2.8. For $i, j \in N_{\text{Tip}}(U^{(n)})$,

$$I^{(i,j,n)} = I^{(i,n)} \cap I^{(j,n)},$$

where for two sequences $a = (a_j)$ and $b = (b_j)$ we define the operation

$$a \cap b = (a_j : a_j = b_j)$$

or in other words $a \cap b$ is the common prefix of sequences a and b .

Definition 2.9. For $i, j \in N_{\text{Tip}}(U^{(n)})$,

$$v^{(i,j,n)} = |I^{(i,j,n)}| - 1,$$

where for a finite sequence v , $|v|$ means its length.

Remark 2.10. We have the -1 in the above definition of $v^{(i,j,n)}$ as we are interested in counting the speciation events that could have a jump common to both lineages. As the jump occurs after a speciation event, the jumps connected to the coalescent node of tip nodes i and j cannot affect both of these tips (see Section 3.2).

Definition 2.11. For $i, j \in N_{\text{Tip}}(U^{(n)})$ and $r \in \{1, \dots, \max(I^{(i,j,n)}) - 1\}$, let $\mathbf{1}_r^{(i,j,n)}$ be a binary random variable such that

$$\mathbf{1}_r^{(i,j,n)} = 1 \text{ iff } r \in I^{(i,j,n)}.$$

For a sequence a , the operation $\max(a)$ chooses the maximum value present in the sequence.

Definition 2.12. For $i, j \in N_{\text{Tip}}(U^{(n)})$,

$$\tau^{(i,j,n)} = U^{(n)} - \inf \left\{ t \geq 0 : N_{\text{Tip}}(t) = \max(I^{(i,j,n)}) \right\}.$$

Definition 2.13. For $i, j \in N_{\text{Tip}}(U^{(n)})$ and $r \in \{1, \dots, v_{i,j}^{(n)}\}$, let $J_r^{(i,j,n)}$ be a binary random variable equaling 1 iff $J_r^{(i,n)} = 1$ and $J_r^{(j,n)} = 1$.

Definition 2.14. For $i, j \in N_{\text{Tip}}(U^{(n)})$ and $r \in \{1, \dots, n-1\}$, let $Z_r^{(i,j,n)}$ be a binary random variable equaling 1 iff $Z_r^{(i,n)} = 1$ and $Z_r^{(j,n)} = 1$.

Definition 2.15. Let R be uniformly distributed on $\{1, \dots, n\}$ and (R, K) be uniformly distributed on the set of ordered pairs drawn from $\{1, \dots, n\}$ (i.e., $\text{Prob}((R, K) = (r, k)) = \binom{n}{2}^{-1}$, for $1 \leq r < k \leq n$)

$$\begin{aligned}\tau^{(n)} &= \tau^{(R, K, n)}, \quad \Upsilon^{(n)} = \Upsilon^{(R, n)}, \quad v^{(n)} = v^{(R, K, n)}, \quad I^{(n)} = I^{(R, n)}, \\ \tilde{I}^{(n)} &= I^{(R, K, n)}, \quad \mathbf{1}_i = \mathbf{1}_i^{(R, n)}, \quad \tilde{\mathbf{1}}_i = \mathbf{1}_i^{(R, K, n)}, \quad J_i = J_i^{(R, n)}, \quad \tilde{J}_i = J_i^{(R, K, n)}, \\ Z_i &= Z_i^{(R, n)}, \quad \tilde{Z}_i = Z_i^{(R, K, n)}.\end{aligned}$$

Some of the variables defined in [Defn. 2.15](#) are illustrated in [Figures 1, 5](#) and further described in the captions. It might be also useful to refer to [Bartoszek^{\[10\]}](#), especially [Figure A.8](#), therein.

Remark 2.16. For the sequences $I^{(n)}, I^{(r, n)}, I^{(R, n)}, \tilde{I}^{(n)}, I^{(r, k, n)}, I^{(R, K, n)}$ the i -th element is naturally indicated as $I_i^{(n)}, I_i^{(r, n)}, I_i^{(R, n)}, \tilde{I}_i^{(n)}, I_i^{(r, k, n)}, I_i^{(R, K, n)}$ respectively.

Remark 2.17. We drop the n in the superscript for the random variables $\mathbf{1}_i, \tilde{\mathbf{1}}_i, J_i, \tilde{J}_i, Z_i$ and \tilde{Z}_i as their distribution will not depend on n (see [Lemma 3.1 Section 3](#)). In fact, in principle, there will be no need to distinguish between the version with and without the tilde. However, such a distinction will make it more clear to what one is referring to in the subsequent derivations in this work.

3. A model for punctuated stabilizing selection

3.1. Phenotype model

Stochastic differential equations (SDEs) are today the standard language to model continuous traits evolving on a phylogenetic tree. The general framework is that of a diffusion process

$$dX(t) = \mu(t, X(t))dt + \sigma_a dB_t. \quad (1)$$

The trait, $X(t) \in \mathbb{R}$, follows [Eq. \(1\)](#) along each branch of the tree (with possibly branch specific parameters). At speciation times this process divides into two processes evolving independently from that point. A work-horse of contemporary phylogenetic comparative methods (PCMs) is the OU process

$$dX(t) = -\alpha(X(t) - \theta)dt + \sigma_a dB_t, \quad (2)$$

where sometimes the parameters α, θ, σ_a are allowed to vary over the tree (see e.g. [Bartoszek et al.^{\[14\]}](#), [Beaulieu et al.^{\[16\]}](#), [Butler and King^{\[23\]}](#),

Hansen^[34], Mitov et al.^[40,41]). Without loss of generality, for the purpose of the results here, we could have taken $\theta=0$. However, we choose to retain the parameter for consistency with previous literature. In this work we keep all the parameters (α , θ , σ_a) identical over the whole tree.

The probabilistic properties (e.g. de Saporta and Yao^[7]) and statistical procedures (e.g., Azaïs et al.^[6]) for processes with jumps have of course been developed. In the phylogenetic context there have been a few attempts to go beyond the diffusion framework into Lévy process, including Laplace motion, (Bartoszek^[9], Duchen et al.^[26], Landis et al.^[35]) and jumps at speciation points (Bartoszek^[10], Bastide et al.^[15], Bokma^[20,21]). We follow in the spirit of the latter and consider that just after a branching point, with a probability p , independently on each daughter lineage, a jump can occur. It is worth underlining here a key difference of this model from the one considered by Bastide et al.^[15]. Here after speciation each daughter lineage may with probability p jump (independently of the other). In Bastide et al.^[15]'s model, in the OU case, the jump is not in the trait value but in the drift function, θ of Eq. (2). We assume that the jump random variable, added to the trait's value, is normally distributed with mean 0 and variance $\sigma_c^2 < \infty$. In other words, if at time t there is a speciation event, then just after it, independently for each daughter lineage, the trait process $X(t^+)$ will be

$$X(t^+) = (1 - Z)X(t^-) + Z(X(t^-) + \zeta), \quad (3)$$

where $X(t^{-/+})$ means the value of $X(t)$ respectively just before and after time t , Z is a binary random variable with probability p of being 1 (i.e., jump occurs) and $\zeta \sim \mathcal{N}(0, \sigma_c^2)$. The parameters p and σ_c^2 can, in particular, differ between speciation events. Taking $p=0$ or $\sigma_c^2=0$ we recover the YOU without jumps model and results (described by Bartoszek and Sagitov^[12]).

3.2. The branching phenotype

In this work we consider a fundamental model of phylogenetic tree growth — the conditioned on number of tip species pure birth process (Yule tree). We first make the notation from Section 2 more intuitive, illustrating it also in Figures 1 and 5 (see also Bartoszek^[10], Bartoszek and Sagitov^[12], Sagitov and Bartoszek^[49]). We consider a tree that has n tip species. Let $U^{(n)}$ be the tree height, $\tau^{(n)}$ the time from today (backwards) to the coalescent of a pair of randomly chosen tip species, $\tau_{ij}^{(n)}$ the time to coalescent of tips i, j , $\Upsilon^{(n)}$ the number of speciation events on a random lineage, $v^{(n)}$ the number of common speciation events for a random pair of tips minus one and $v_{ij}^{(n)}$ the number of common speciation events for tips i, j minus one.

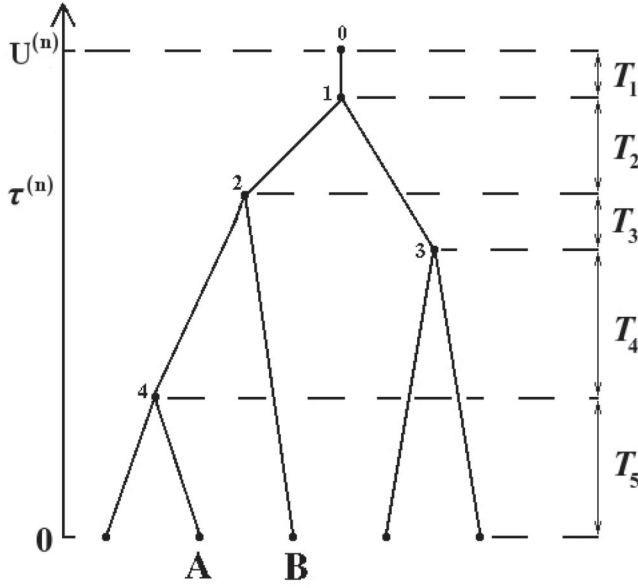


Figure 1. A pure-birth tree with the various time components marked on it. If we “randomly sample” node “A”, then $\Upsilon^{(n)} = 3$ and the indexes of the speciation events on this random lineage are $l_3^{(n)} = 4$, $l_2^{(n)} = 2$ and $l_1^{(n)} = 1$. Notice that $l_1^{(n)} = 1$ always. The between speciation times on this lineage are T_1 , T_2 , $T_3 + T_4$ and T_5 . If we “randomly sample” the pair of extant species “A” and “B”, then $v^{(n)} = 1$ and the two nodes coalesced at time $\tau^{(n)} = T_3 + T_4 + T_5$. The random index of their joint speciation event is $\tilde{l}_1 = 1$. See also Figure 5 and Bartoszek’s^[10] Figure A.8. for a more detailed discussion on relevant notation. The internal node labellings 0–4 are marked on the tree. The OUJ process evolves along the branches of the tree and we only observe the trait values at the n tips. For given tip, say “A” the value of the trait process will be denoted $X_A^{(n)}$. Of course here $n = 5$.

The jumps take place after the speciation event so any jump associated with the speciation event that split the two lineages, e.g., in Figure 1 speciation event 2 for the pair of lineages A and B, cannot be common to the the two lineages. Hence, in the caption Figure 1, we have $v_{AB}^{(n)} = 1$, see also Remark 2.10.

Furthermore, let $I^{(n)}$ be the sequence of nodes on a randomly chosen lineage and $J^{(n)}$ be a binary sequence indicating if a jump took place after each respective node in the $I^{(n)}$ sequence. Finally, let T_k be the time between speciation events k and $k + 1$, p_k and $\sigma_{c,k}^2$ be respectively the probability and variance of the jump just after the k -th speciation event on each daughter lineage. It is worth recalling that both daughter lineages may jump independently of each other. It is also worth reminding the reader that previously (Bartoszek^[10]) the jumps were homogeneous over the tree, in this manuscript we allow their properties to vary with the nodes of the tree.

The following simple, yet very powerful, lemma comes from the uniformity of the choice of pair to coalesce at the i -th speciation event in the backward description of the Yule process. The proof can be found in Bartoszek^[10] on p. 45 (by no means do I claim this well known result as my own).

Lemma 3.1. *Consider for a Yule tree the indicator random variables $\mathbf{1}_i$ that the i -th (counting from the root) speciation event lies on a randomly selected lineage and $\tilde{\mathbf{1}}_i$ that the i -th speciation event lies on the path from the origin to the most recent common ancestor of a randomly selected pair of tips. Then for all $i \in \{1, \dots, n-1\}$*

$$\mathbb{E}[\tilde{\mathbf{1}}_i] = \mathbb{E}[\mathbf{1}_i] = \text{Prob}(\mathbf{1}_i = 1) = \frac{2}{i+1}.$$

We called the model a conditioned one. By conditioning we consider stopping the tree growth just before the $n+1$ species occurs, or just before the n -th speciation event. Therefore, the tree's height $U^{(n)}$ is a random stopping time. The asymptotics considered in this work are when $n \rightarrow \infty$.

The key model parameter describing the tree component is λ , the birth rate. At the start, the process starts with a single particle and then splits with rate λ . Its descendants behave in the same manner. Without loss generality we take $\lambda = 1$, as this is equivalent to rescaling time.

In the context of phylogenetic methods this branching process has been intensively studied (e.g. Bartoszek and Sagitov^[12], Crawford and Suchard^[25], Edwards^[27], Gernhard^[29,30], Mulder and Crawford^[44], Sagitov and Bartoszek^[49], Steel and McKenzie^[53]), hence here we will just describe its key property. The time between speciation events k and $k+1$ is exponential with parameter k . This is immediate from the memoryless property of the process and the distribution of the minimum of k i.i.d. exponential random variables. From this we obtain some important properties of the process. Let $H_n = 1 + 1/2 + \dots + 1/n$ be the n -th harmonic number, $x > 0$ and then their expectations and Laplace transforms are (Bartoszek and Sagitov^[12], Sagitov and Bartoszek^[49])

$$\begin{aligned} \mathbb{E}[U^{(n)}] &= H_n, \\ \mathbb{E}[e^{-xU^{(n)}}] &= b_{n,x}, \\ \mathbb{E}[\tau^{(n)}] &= \frac{n+1}{n-1}H_n - \frac{2}{n-1}, \\ \mathbb{E}[e^{-x\tau^{(n)}}] &= \begin{cases} \frac{2-(n+1)(x+1)b_{n,x}}{(n-1)(x-1)} & x \neq 1, \\ \frac{2}{n-1}(H_n - 1) - \frac{1}{n+1} & x = 1, \end{cases} \end{aligned}$$

where

$$b_{n,x} = \frac{1}{x+1} \cdots \frac{n}{n+x} = \frac{\Gamma(n+1)\Gamma(x+1)}{\Gamma(n+x+1)} \sim \Gamma(x+1)n^{-x},$$

$\Gamma(\cdot)$ being the gamma function.

Now let \mathcal{Y}_n be the σ -algebra that contains information on the Yule tree and jump pattern. By this we mean that conditional on \mathcal{Y}_n we know exactly how the tree looks like (esp. the interspeciation times T_i) and we know at what parts of the tree (at which lineage(s) just after which speciation events) did jumps take place. The motivation behind such conditioning is that conditional on \mathcal{Y}_n the contemporary tips sample is a multivariate normal one. When one does not condition on \mathcal{Y}_n the normality does not hold—the randomness in the tree and presence/absence of jumps distorts normality.

Bartoszek^[10] previously studied the branching Ornstein–Uhlenbeck with jumps (OUj) model and it was shown (but, therein for constant p_k and $\sigma_{c,k}^2$ and therefore there was no need to condition on the jump pattern) that, conditional on the tree height and number of tip species the mean and variance of the trait value of tip species r (out of the n contemporary), $X_r^{(n)} \equiv X_r^{(n)}(U^{(n)})$ (see also Figure 1), are

$$\begin{aligned} \mathbb{E}[X_r^{(n)} | \mathcal{Y}_n] &= \theta + e^{-\alpha U^{(n)}}(X_0 - \theta) \\ \text{Var}[X_r^{(n)} | \mathcal{Y}_n] &= \frac{\sigma_a^2}{2\alpha} (1 - e^{-2\alpha U^{(n)}}) + \sum_{i=1}^{\Upsilon^{(r,n)}} \sigma_{c, I_i^{(r,n)}}^2 J_i^{(r,n)} e^{-2\alpha \left(T_n + \dots + T_{I_i^{(r,n)}+1} \right)}, \end{aligned} \quad (4)$$

$\Upsilon^{(r,n)}, I^{(r,n)}$ and $J^{(r,n)}$ are realizations of the random variables $\Upsilon^{(n)}, I^{(n)}$ and $J^{(n)}$ when lineage r is picked. A key difference that the phylogeny brings in, is that the tip measurements are correlated through the tree structure. One can easily show that conditional on \mathcal{Y}_n , the covariance between traits belonging to tip species r and k , $X_r^{(n)}$ and $X_k^{(n)}$ is

$$\begin{aligned} \text{Cov}[X_r^{(n)}, X_k^{(n)} | \mathcal{Y}_n] &= \frac{\sigma_a^2}{2\alpha} (e^{-2\alpha \tau^{(r,k,n)}} - e^{-2\alpha U^{(n)}}) \\ &\quad + \sum_{i=1}^{v^{(r,k,n)}} \sigma_{c, I_i^{(r,k,n)}}^2 J_i^{(r,k,n)} e^{-2\alpha \left(\tau^{(r,k,n)} + \dots + T_{I_i^{(r,k,n)}+1} \right)}, \end{aligned} \quad (5)$$

where $J^{(r,k,n)}, I^{(r,k,n)}$ correspond to the realization of random variables $J^{(n)}, I^{(n)}$, but reduced to the common part of lineages r and k , while $v^{(r,k,n)}, \tau^{(r,k,n)}$ correspond to realizations of $v^{(n)}, \tau^{(n)}$ when the pair (r, k) is picked. We will call, the considered model the Yule–Ornstein–Uhlenbeck with jumps (YOUj) process.

Remark 3.2. Keeping the parameter θ constant on the tree is not as simplifying as it might seem. Varying θ models have been considered since the introduction of the OU process to phylogenetic methods (Hansen^[34]). However, it can very often happen that the θ parameter is constant over whole clades, as these species share a common optimum due to some common discrete characteristic. Therefore, understanding the model's behavior with a constant θ is a crucial first step. Furthermore, if constant θ clades are apart far enough one could think of them as independent samples and attempt to construct a test (based on normality of the species' averages) if jumps have a significant effect (compare Thms. 4.1 and 4.6). For this one would have to make the very difficult to biologically justify assumption of constant model parameters between clades. Though, one can imagine special situations where the levels of θ are connected to a discrete characteristic common to many clades, e.g., fresh water or seawater. On the other hand CLTs and other asymptotical results for changing model parameters and different levels of θ are an exciting future research direction.

Remark 3.3. It should be noted that the phylogeny could be introduced using a formal branching process approach and the offspring's' generating function (e.g. Ch. III.3, Athreya and Ney^[5]). Then, the branching trait model can be described (jointly with the tree) as a “Markov process in the space of integer-valued measures on \mathbb{R} ” (Adamczak and Miłoś^[3]). However, in this work here we do not use any of the machinery from that direction and so we refrain from defining the setup in that language so as to avoid adding yet another layer of notation. On the other hand, the way of defining the model used here is constructive—in the sense that it can be directly coded in a simulation procedure.

3.3. Martingale formulation

Our main aim is to study the asymptotic behavior of the sample average and it actually turns out to be easier to work with scaled trait values, for each $r \in \{1, \dots, n\}$, $Y_r^{(n)} = (X_r^{(n)} - \theta) / \sqrt{\sigma_a^2 / 2\alpha}$. Denoting $\delta = (X_0 - \theta) / \sqrt{\sigma_a^2 / 2\alpha}$ we have

$$\mathbb{E}[Y^{(n)}] = \delta b_{n,\alpha}. \quad (6)$$

The initial condition of course will be $Y_0 = \delta$.

Remark 3.4. We remark, that here it becomes evident that the specific value of θ , will not play any role in obtaining the presented here results. What only matters is the initial displacement from θ , but even this will not

contribute in any way to the rate of convergence, only as a scaling constant for the expectation of \bar{Y}_n (see Proof of Thm. 4.1).

Just as was done by Bartoszek and Sagitov^[12] we may construct a martingale related to the average

$$\bar{Y}_n = \frac{1}{n} \sum_{i=1}^n Y_i^{(n)}.$$

It is worth pointing out that \bar{Y}_n is observed just before the n -th speciation event. An alternative formulation would be to observe it just after the $(n-1)$ -st speciation event. Then (cf. Lemma 10 of Bartoszek and Sagitov^[12]), we define

$$H_n := (n+1)e^{(\alpha-1)U^{(n)}} \bar{Y}_n, \quad n \geq 0.$$

This is a martingale with respect to \mathcal{F}_n , the σ -algebra containing information on the Yule n -tree and the phenotype's evolution, i.e., $\mathcal{F}_n = \sigma(\mathcal{Y}_n, Y_1, \dots, Y_n)$.

4. Asymptotic regimes — main results

Branching Ornstein–Uhlenbeck models commonly have three asymptotic regimes (Adamczak and Miłoś^[2,3], Ané et al.^[4], Bartoszek^[10], Bartoszek and Sagitov^[12], Ren et al.^[46,47]). The dependency between the adaptation rate α and branching rate $\lambda=1$ governs in which regime the process is. If $\alpha > 1/2$, then the contemporary sample is similar to an i.i.d. sample, in the critical case, $\alpha = 1/2$, we can, after appropriate rescaling, still recover the “near” i.i.d. behavior and if $0 < \alpha < 1/2$, then the process has “long memory” (“local correlations dominate over the OU’s ergodic properties”, Adamczak and Miłoś^[2,3]). In the context considered here by “near” and “similar” to i.i.d. we mean that the resulting CLTs resemble those of an i.i.d. sample. For example the limit distribution of the normalized sample average in the $\alpha > 0.5$ YOU regime [Thm. 1 in 12] is $\mathcal{N}(0, (2\alpha+1)/(2\alpha-1))$ and taking $\alpha \rightarrow \infty$ we obtain the classical $\mathcal{N}(0, 1)$ limit (as intuition could suggest with instantaneous adaptation). In the YOUj setup the same three asymptotic regimes can be observed, even though Adamczak and Miłoś^[2,3], Ren et al.^[46,47] assume that the tree is observed at a given time point, t , with n_t being random. In what follows here, the constant C may change between (in)equalities. It may in particular depend on α . We illustrate the below Theorems in Figure 2.

We consider the process $\bar{Y}_n = (\bar{X}_n - \theta)/\sqrt{\sigma_a^2/2\alpha}$ which is the normalized sample mean of the YOUj process with $\bar{Y}_0 = \delta$. The next two Theorems consider its, depending on α , asymptotic with n behavior.

Theorem 4.1. *Assume that the jump probabilities and jump variances are constant equaling p and $\sigma_c^2 < \infty$ respectively.*

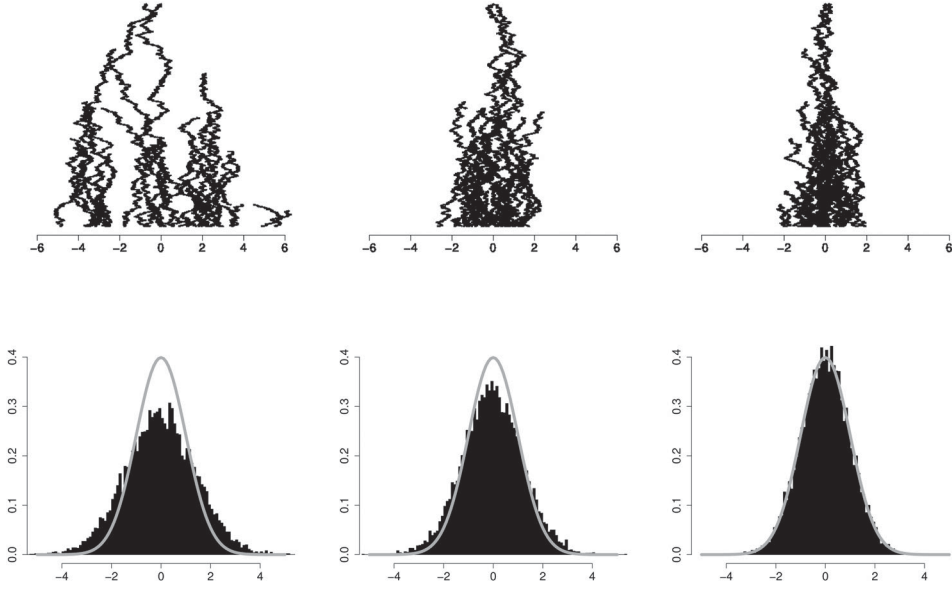


Figure 2. Left: $\alpha = 0.25$ center: $\alpha = 0.5$ and right: $\alpha = 1$. Top row: examples of simulated YOUNG process trajectories, bottom row: histograms of sample averages, left: scaled by $n^{0.25} \sqrt{5\Gamma(3/2)/2}$, center: scaled by $\sqrt{n \ln^{-1} n/2}$, right: scaled by $\sqrt{n/3}$. In all three cases, $p = 0.5$, $\sigma_c^2 = 1$, $\sigma_a^2 = 1$, $X_0 = \theta = 0$. The phylogenetic trees are pure birth trees with $\lambda = 1$ conditioned on number of tips, $n = 30$ for the trajectory plots and $n = 200$ for the histograms. The histograms are based on 10000 simulated trees. The sample mean and variances of the scaled data in the histograms are left: $(-0.015, 2.037)$, center: $(-0.033, 1.481)$ and right: $(0.004, 1.008)$. The gray curve painted on the histograms is the standard normal distribution. The phylogenies are simulated by the TreeSim R package (Stadler^[51,52]) and simulations of phenotypic evolution and trajectory plots are done by functions of the, available on CRAN, mvSLOUCH R package. We can see that as α decreases the sample variance is further away from the asymptotical 1 (after scaling) and the histogram from normality (though when $\alpha = 0.25$ we should not expect normality). This is as with smaller α convergence is slower.

- (I) If $0.5 < \alpha$ and $0 < p < 1$, then the conditional variance of the scaled sample mean $\sigma_n^2 := n \text{Var}[\bar{Y}_n | \mathcal{Y}_n]$ converges in \mathbb{P} to a finite mean and variance random variable σ_∞^2 . The scaled sample mean, $\sqrt{n} \bar{Y}_n$ converges weakly to random variable whose characteristic function can be expressed in terms of the Laplace transform of σ_∞^2

$$\forall x \in \mathbb{R} \quad \lim_{n \rightarrow \infty} \phi_{\sqrt{n} \bar{Y}_n}(x) = \mathcal{L}(\sigma_\infty^2)(x^2/2).$$

- (II) If $0.5 = \alpha$, then $\sqrt{(n/\ln n)} \bar{Y}_n$ is asymptotically normally distributed with mean 0 and variance $2 + 4p\sigma_c^2/\sigma_a^2$. In particular the conditional variance of the scaled sample mean $\sigma_n^2 := n \ln^{-1} n \text{Var}[\bar{Y}_n | \mathcal{Y}_n]$ converges in L^2 (and hence in \mathbb{P}) to the constant $2 + 4p\sigma_c^2/\sigma_a^2$.
- (III) If $0 < \alpha < 0.5$, then $n^\alpha \bar{Y}_n$ converges almost surely and in L^2 to a random variable $Y_{\alpha,\delta}$ with finite first two moments.

Remark 4.2. For the a.s. and L^2 convergence to hold in Part 3, it suffices that the sequence of jump variances is bounded. Of course, the first two moments will differ if the jump variance is not constant.

Remark 4.3. After this remark we will define the concept of a sequence converging to 0 with density 1. Should the reader find it easier, they may forget that the sequence converges with density 1, but think of the sequence simply converging to 0. The condition of convergence with density 1 is a technicality that through ergodic theory allows us to slightly weaken the assumptions of the theorem that gives a normal limit.

Definition 4.4. A subset $E \subset \mathbb{N}$ of positive integers is said to have density 0 (e.g., Petersen^[45]) if

$$\lim_{n \rightarrow \infty} \frac{1}{n} \sum_{k=0}^{n-1} \chi_E(k) = 0,$$

where $\chi_E(\cdot)$ is the indicator function of the set E .

Definition 4.5. A sequence a_n converges to 0 with density 1 if there exists a subset $E \subset \mathcal{N}$ of density 0 such that

$$\lim_{n \rightarrow \infty, n \notin E} a_n = 0.$$

Theorem 4.6. Assume that the sequence $\{\sigma_{c,k}^4 p_k\}$ is bounded. Then, depending on α the process \bar{Y}_n has the following asymptotic with n behavior.

- (I) If $0.5 < \alpha$, $\sigma_{c,k}^4 p_k(1 - p_k)$ goes to 0 with density 1 and the sequences $\{\sigma_{c,k}^2\}, \{p_k\}$ are such that the sequences of expectations

$$\begin{aligned} \mathbb{E} \left[\sum_{k=1}^{\gamma^{(n)}} \sigma_{c, I_k^{(n)}}^2 J_k e^{-2\alpha \left(T_n + \dots + T_{I_k^{(n)}+1}^{(n)} \right)} \right] &\rightarrow \sigma_Y^2 \\ n \mathbb{E} \left[\sum_{k=1}^{v^{(n)}} \sigma_{c, \tilde{I}_k^{(n)}}^2 \tilde{J}_k e^{-2\alpha \left(\tau^{(n)} + \dots + T_{\tilde{I}_k^{(n)}+1}^{(n)} \right)} \right] &\rightarrow \sigma_v^2 \end{aligned}$$

converge, then the process $\sqrt{n} \bar{Y}_n$ is asymptotically normally distributed with mean 0 and variance $(2\alpha + 1)/(2\alpha - 1) + (\sigma_Y^2 + \sigma_v^2)/(\sigma_a^2/(2\alpha))$.

- (II) If $0.5 = \alpha$, and the sequences $\{\sigma_{c,k}^2\}, \{p_k\}$ are such that the sequence of expectations

$$(n \ln^{-1} n) \mathbb{E} \left[\sum_{k=1}^{v^{(n)}} \sigma_{c, \tilde{I}_k^{(n)}}^2 \tilde{J}_k e^{-\left(\tau^{(n)} + \dots + T_{\tilde{I}_k^{(n)}+1}^{(n)} \right)} \right] \rightarrow \sigma_v^2$$

converges, then $\sqrt{(n/\ln n)} \bar{Y}_n$ is asymptotically normally distributed with mean 0 and variance $2 + \sigma_v^2/\sigma_a^2$.

It is worth pointing out that [Thm. 4.6](#) covers the extreme cases $p = 0$ and $p = 1$. The convergence conditions on the expectations look rather daunting, however they will simplify very compactly if $\sigma_{c,k}^2$ and p_k are constant or $\sigma_{c,k}^4 p_k \rightarrow 0$ (with density 1). These we discuss after the proof of the theorem, when we also mention why the assumptions on these expectations are necessary.

Remark 4.7. In the original arXiv preprint of this paper it was stated that convergence to normality in the $\alpha \geq 0.5$ regimes will only take place if $\sigma_{c,k}^4 p_k$ is bounded and goes to 0 with density 1. Normality in the $\alpha = 0.5$ and $p_k = 1$ regimes was noticed thanks to the collaboration with Torkel Erhardsson^[11] and then, the results and proofs in this manuscript were adjusted.

Remark 4.8. The assumption $\sigma_{c,k}^4 p_k (1 - p_k) \rightarrow 0$ with density 1 is an essential one for the limit to be a normal distribution, when $\alpha > 0.5$. This is visible from the proof of Lemma 5.5. In fact, this is the key difference that the jumps bring in—if their magnitude or their uncertainty in occurrence is too large, then they will disrupt the weak convergence.

One possible way of achieving the above condition is to keep $\sigma_{c,k}^2$ constant and allow $p_k \rightarrow 0$, the chance of jumping becomes smaller relative to the number of species. Alternatively, $\sigma_{c,k}^2 \rightarrow 0$, which could mean that with more and more species—smaller and smaller jumps occur at speciation. Actually, one could intuitively think of this as biologically more realistic. We are in the Yule, no extinction, case so with time there will be more and more species (species here can be understood, if it helps intuition as non-mixing, for some reason, populations). If they all live in some spatially confined area, then as the number of species grows there could be more and more competition. If one considers a trait that is related to what is competed for, then smaller and smaller differences in phenotype could drive the species apart. Specialization occurs and tinier and tinier niches are filled. This reasoning of course further assumes that the number of individuals grows with the number of species. Furthermore, under the considered YOUj model the long time mean, θ , is the same for all species, so even though there is an initial displacement (into a different niche) with time the trait will try to revert to its optimum. Hence, the above is not aiming for making any authoritative biological statements, nor provide an interpretation of the whole YOUj model. Rather, it has as its goal of giving some intuition on jump variance decreasing to 0 with time/number of species.

Remark 4.9. In [Thm. 4.6](#) we do not consider the “fast branching/slow adaptation”, $0 < \alpha < 0.5$ regime. By assuming $\sigma_{c,k}^4 p_k \rightarrow 0$ with density 1, it

is possible to make the influence of the jumps disappear asymptotically, just like in the $\alpha \geq 0.5$ case, see Example 6.6. However, no further insights, than those in Thm. 4.1 will be readily available, similarly as Bartoszek and Sagitov^[12] note for the YOU without jumps model. This is as the used here methods, do not seem to easily extend to the $0 < \alpha < 0.5$ situation, beyond what is presented in this manuscript.

5. A series of technical lemmata

We will now prove a series of technical lemmata describing the asymptotics of driving components of the considered YOUj process. For two sequences a_n, b_n the notation $a_n \lesssim b_n$ will mean that $a_n/b_n \rightarrow C \neq 0$ with n and $a_n \leq (1 + o(1))b_n$. Notice that always when $a_n \lesssim b_n$ is used a defined or undefined constant C is present within b_n . The key property is that the asymptotic behavior with n does not change after the \lesssim sign. The general approach to proving these lemmata is related to that in the proof of Bartoszek and Sagitov's^[12] Lemma 11. What changes here is that we need to take into account the effects of the jumps [which were not considered in 12]. However, we noticed that there is an error in the proof of Bartoszek and Sagitov's^[12] Lemma 11. Hence, below for the convenience of the reader, we do not only cite the lemma but also provide the whole corrected proof. In Remark 5.2, following the proof, we briefly point the problem in the original wrong proof and explain why it does not influence the rest of Bartoszek and Sagitov's^[12] results.

Lemma 5.1. (*Lemma 11 of Bartoszek and Sagitov^[12]*)

$$\text{Var} \left[\mathbb{E} \left[e^{-2\alpha\tau^{(n)}} | \mathcal{Y}_n \right] \right] = \begin{cases} O(n^{-4\alpha}) & 0 < \alpha < 0.75, \\ O(n^{-3} \ln n) & \alpha = 0.75, \\ O(n^{-3}) & 0.75 < \alpha. \end{cases} \quad (7)$$

Proof. For a given realization of the Yule n -tree we denote by $\tau_1^{(n)}$ and $\tau_2^{(n)}$ two versions of $\tau^{(n)}$ that are independent conditional on \mathcal{Y}_n . In other words $\tau_1^{(n)}$ and $\tau_2^{(n)}$ correspond to two independent choices of pairs of tips out of n available. Conditional on \mathcal{Y}_n all heights in the tree are known—the randomness is only in the choice out of the $\binom{n}{2}$ pairs or equivalently sampling out of the set of $n - 1$ coalescent heights. We have,

$$\mathbb{E} \left[\left(\mathbb{E} \left[e^{-2\alpha\tau^{(n)}} | \mathcal{Y}_n \right] \right)^2 \right] = \mathbb{E} \left[\mathbb{E} \left[e^{-2\alpha(\tau_1^{(n)} + \tau_2^{(n)})} | \mathcal{Y}_n \right] \right] = \mathbb{E} \left[e^{-2\alpha(\tau_1^{(n)} + \tau_2^{(n)})} \right].$$

Let $\pi_{n,k}$ be the probability that two randomly chosen tips coalesced at the k -th speciation event. We know that (cf. Stadler^[51]'s proof of her Theorem

4.1, using m for our n or Bartoszek and Sagitov's^[12] Lemma 1 for a more general statement)

$$\pi_{n,k} = 2 \frac{n+1}{n-1} \frac{1}{(k+1)(k+2)}.$$

Writing

$$f_\alpha(k, n) := \frac{k+1}{\alpha+k+1} \cdots \frac{n}{\alpha+n} = \frac{\Gamma(n+1)\Gamma(\alpha+k+1)}{\Gamma(k+1)\Gamma(\alpha+n+1)}$$

and as the times between speciation events are independent and exponentially distributed we obtain

$$\begin{aligned} \mathbb{E} \left[\left(\mathbb{E} \left[e^{-2\alpha\tau^{(n)}} | \mathcal{Y}_n \right] \right)^2 \right] &= \sum_{k=1}^{n-1} f_{4\alpha}(k, n) \pi_{n,k}^2 \\ &\quad + 2 \sum_{k_1=1}^{n-1} \sum_{k_2=k_1+1}^{n-1} f_{2\alpha}(k_1, k_2) f_{4\alpha}(k_2, n) \pi_{n,k_1} \pi_{n,k_2}. \end{aligned}$$

On the other hand,

$$\left(\mathbb{E} \left[e^{-2\alpha\tau^{(n)}} \right] \right)^2 = \left(\sum_{k_1=1}^{n-1} f_{2\alpha}(k_1, n) \pi_{n,k_1} \right) \left(\sum_{k_2=1}^{n-1} f_{2\alpha}(k_2, n) \pi_{n,k_2} \right).$$

Taking the difference between the last two expressions we find

$$\begin{aligned} \text{Var} \left[\mathbb{E} \left[e^{-2\alpha\tau^{(n)}} | \mathcal{Y}_n \right] \right] &= \sum_k \left(f_{4\alpha}(k, n) - f_{2\alpha}(k, n)^2 \right) \pi_{n,k}^2 \\ &\quad + 2 \sum_{k_1=1}^{n-1} \sum_{k_2=k_1+1}^{n-1} f_{2\alpha}(k_1, k_2) \left(f_{4\alpha}(k_2, n) - f_{2\alpha}(k_2, n)^2 \right) \pi_{n,k_1} \pi_{n,k_2}. \end{aligned}$$

Noticing that we are dealing with a telescoping sum and hence using the relation

$$a_1 \cdots a_n - b_1 \cdots b_n = \sum_{i=1}^n b_1 \cdots b_{i-1} (a_i - b_i) a_{i+1} \cdots a_n \quad (8)$$

we see that it suffices to study the asymptotics of,

$$\sum_{k=1}^{n-1} A_{n,k} \pi_{n,k}^2 \quad \text{and} \quad \sum_{k_1=1}^{n-1} \sum_{k_2=k_1+1}^{n-1} f_{2\alpha}(k_1, k_2) A_{n,k_2} \pi_{n,k_1} \pi_{n,k_2},$$

where

$$A_{n,k} := \sum_{j=k+1}^n f_{2\alpha}(k, j)^2 \left(\frac{4\alpha^2}{j(j+4\alpha)} \right) f_{4\alpha}(j, n).$$

To consider these two asymptotic relations we observe that for large n

$$A_{n,k} \leq 4\alpha^2 \frac{b_{n,4\alpha}}{b_{k,2\alpha}^2} \sum_{j=k+1}^n \frac{b_{j,2\alpha}^2}{b_{j,4\alpha} j(4\alpha+j)} \leq C \frac{b_{n,4\alpha}}{b_{k,2\alpha}^2} \sum_{j=k+1}^n j^{-2} \leq C \frac{b_{n,4\alpha}}{b_{k,2\alpha}^2} k^{-1}.$$

Now since $\pi_{n,k} = \frac{2(n+1)}{(n-1)(k+2)(k+1)}$, it follows

$$\begin{aligned} \sum_{k=1}^{n-1} A_{n,k} \pi_{n,k}^2 &\leq C b_{n,4\alpha} \sum_{k=1}^{n-1} \frac{1}{k^5 b_{k,2\alpha}^2} \leq C n^{-4\alpha} \sum_{k=1}^n k^{4\alpha-5} \\ &\leq C \begin{cases} n^{-4\alpha} & 0 < \alpha < 1 \\ n^{-4} \ln n & \alpha = 1 \\ n^{-4} & 1 < \alpha \end{cases} \end{aligned}$$

and

$$\begin{aligned} \sum_{k_1=1}^{n-1} \sum_{k_2=k_1+1}^{n-1} f_{2\alpha}(k_1, k_2) A_{n,k_2} \pi_{n,k_1} \pi_{n,k_2} &\leq C b_{n,4\alpha} \sum_{k_1=1}^{n-1} \sum_{k_2=k_1+1}^{n-1} \frac{1}{b_{k_1,2\alpha} b_{k_2,2\alpha}} \frac{1}{k_1^2 k_2^3} \\ &\leq C n^{-4\alpha} \sum_{k_1=1}^{n-1} k_1^{2\alpha-2} \sum_{k_2=k_1+1}^{n-1} k_2^{2\alpha-3} \leq C \begin{cases} n^{-4\alpha} \sum_{k_1=1}^{n-1} k_1^{4\alpha-4} & 0 < \alpha < 1 \\ n^{-4} \sum_{k_2=2}^n k_2^{-1} \sum_{k_1=1}^{k_2} 1 & \alpha = 1 \\ n^{-4\alpha} \sum_{k_2=2}^n k_2^{4\alpha-4} & 1 < \alpha \end{cases} \\ &\leq C \begin{cases} n^{-4\alpha} & 0 < \alpha < 0.75 \\ n^{-3} \ln n & \alpha = 0.75 \\ n^{-3} & 0.75 < \alpha < 1 \\ n^{-4} \sum_{k_2=2}^n 1 & \alpha = 1 \\ n^{-3} & 1 < \alpha \end{cases} \leq C \begin{cases} n^{-4\alpha} & 0 < \alpha < 0.75 \\ n^{-3} \ln n & \alpha = 0.75 \\ n^{-3} & 0.75 < \alpha < 1 \\ n^{-3} & \alpha = 1 \\ n^{-3} & 1 < \alpha. \end{cases} \end{aligned}$$

Summarizing

$$\sum_{k_1=1}^{n-1} \sum_{k_2=k_1+1}^{n-1} f_{2\alpha}(k_1, k_2) A_{n,k_2} \pi_{n,k_1} \pi_{n,k_2} \leq C \begin{cases} n^{-4\alpha} & 0 < \alpha < 0.75 \\ n^{-3} \ln n & \alpha = 0.75 \\ n^{-3} & 0.75 < \alpha < 1. \end{cases}$$

Remark 5.2. Bartoszek and Sagitov^[12] wrongly stated in their Lemma 11 that $\text{Var}\left[\mathbb{E}\left[e^{-2\alpha\tau^{(n)}}|\mathcal{Y}_n\right]\right] = O(n^{-3})$ for all $\alpha > 0$. From the above we can see that this holds only for $\alpha > 3/4$. This does not however change Bartoszek and Sagitov's^[12] main results. If one inspects the proof of Theorem 1 therein, then one can see that for $\alpha > 0.5$ it is required that

$\text{Var}\left[\mathbb{E}\left[e^{-2\alpha\tau^{(n)}}|\mathcal{Y}_n\right]\right] = O(n^{-(2+\epsilon)})$, where $\epsilon > 0$. This by [Lemma 5.1](#) holds. Bartoszek and Sagitov's^[12] Thm. 2 does not depend on the rate of convergence, only that $n^2\text{Var}\left[\mathbb{E}\left[e^{-2\alpha\tau^{(n)}}|\mathcal{Y}_n\right]\right] \rightarrow 0$ with n . This remains true, just with a different rate.

Let $\mathbf{I}^{(n)}$ be the sequence of speciation events on a random lineage and (J_i) be the jump pattern (binary sequence 1 jump took place, 0 did not take place just after speciation event i) on a randomly selected lineage.

Lemma 5.3. *For random variables $(\Upsilon^{(n)}, \mathbf{I}^{(n)}, (J_i)_{i=1}^{\Upsilon^{(n)}})$ derived from the same random lineage and a fixed jump probability p we have*

$$\text{Var}\left[\mathbb{E}\left[\sum_{i=1}^{\Upsilon^{(n)}} J_i e^{-2\alpha(T_n + \dots + T_{\mathbf{I}_i^{(n)}+1})}|\mathcal{Y}_n\right]\right] \lesssim pC \begin{cases} n^{-4\alpha} & 0 < \alpha < 0.25 \\ n^{-1} \ln n & \alpha = 0.25 \\ n^{-1} & 0.25 < \alpha. \end{cases} \quad (9)$$

Proof. We introduce the random variables

$$\Psi^{*(n)} := \sum_{i=1}^{\Upsilon^{(n)}} J_i e^{-2\alpha(T_n + \dots + T_{\mathbf{I}_i^{(n)}+1})}$$

and

$$\phi_i^* := Z_i e^{-2\alpha(T_n + \dots + T_{i+1})} \mathbb{E}[\mathbf{1}_i|\mathcal{Y}_n],$$

where Z_i is the binary random variable if a jump took place at the i -th speciation event of the tree for our considered random lineage. Obviously

$$\mathbb{E}[\Psi^{*(n)}|\mathcal{Y}_n] = \sum_{i=1}^{n-1} \phi_i^*.$$

Immediately (for $i < j$)

$$\begin{aligned} \mathbb{E}[\phi_i^*] &= \frac{2p}{i+1} \frac{b_{n,2\alpha}}{b_{i,2\alpha}}, \\ \mathbb{E}[\phi_i^* \phi_j^*] &= \frac{4p^2}{(i+1)(j+1)} \frac{b_{n,4\alpha}}{b_{j,4\alpha}} \frac{b_{j,2\alpha}}{b_{i,2\alpha}}, \\ \mathbb{E}[\phi_i^{*2}] &= p \frac{b_{n,4\alpha}}{b_{i,4\alpha}} \mathbb{E}[(\mathbb{E}[\mathbf{1}_i|\mathcal{Y}_n])^2]. \end{aligned}$$

We illustrate the random objects defined above in [Figure 5](#). The term $\mathbb{E}[(\mathbb{E}[\mathbf{1}_i|\mathcal{Y}_n])^2]$ can be expressed as $\mathbb{E}[\mathbf{1}_i^{(1)} \mathbf{1}_i^{(2)}]$ (same as with $\mathbb{E}\left[\left(\mathbb{E}\left[e^{-2\alpha\tau^{(n)}}|\mathcal{Y}_n\right]\right)^2\right]$ in [Lemma 5.1](#)), where $\mathbf{1}_i^{(1)}$ and $\mathbf{1}_i^{(2)}$ are two copies of

$\mathbf{1}_i$ that are independent given \mathcal{Y}_n , i.e., for a given tree we sample two lineages and ask if the i -th speciation event is on both of them. This will occur if these lineages coalesced at a speciation event $k \geq i$. Therefore,

$$\begin{aligned} \mathbb{E}[\mathbf{1}_i^{(1)} \mathbf{1}_i^{(2)}] &= \frac{2}{i+1} \sum_{k=i+1}^{n-1} \pi_{k,n} + \pi_{i,n} = \frac{n+1}{n-1} \frac{2}{i+1} \left(\sum_{k=i+1}^{n-1} \frac{2}{(k+1)(k+2)} + \frac{1}{i+2} \right) \\ &= \frac{n+1}{n-1} \frac{2}{i+1} \left(\frac{2}{i+2} - \frac{2}{n+1} + \frac{1}{i+2} \right) = \frac{n+1}{n-1} \frac{6}{(i+1)(i+2)} - \frac{2}{n-1} \frac{2}{i+1}. \end{aligned}$$

Together with the above

$$\mathbb{E}[\phi_i^{*2}] = p \frac{b_{n,4\alpha}}{b_{i,4\alpha}} \left(\frac{n+1}{n-1} \frac{6}{(i+1)(i+2)} - \frac{1}{n-1} \frac{4}{i+1} \right).$$

Now

$$\begin{aligned} \text{Var} \left[\sum_{i=1}^{n-1} \phi_i^* \right] &= \sum_{i=1}^{n-1} \left(\mathbb{E}[\phi_i^{*2}] - (\mathbb{E}[\phi_i^*])^2 \right) + 2 \sum_{i=1}^{n-1} \sum_{j=i+1}^{n-1} \left(\mathbb{E}[\phi_i^* \phi_j^*] - \mathbb{E}[\phi_i^*] \mathbb{E}[\phi_j^*] \right) \\ &= \sum_{i=1}^{n-1} \left(p \frac{b_{n,4\alpha}}{b_{i,4\alpha}} \left(\frac{n+1}{n-1} \frac{6}{(i+1)(i+2)} - \frac{1}{n-1} \frac{4}{i+1} \right) - \frac{4p^2}{(i+1)^2} \left(\frac{b_{n,2\alpha}}{b_{i,2\alpha}} \right)^2 \right) \\ &\quad + 2 \sum_{i=1}^{n-1} \sum_{j=i+1}^{n-1} \left(\frac{4p^2}{(i+1)(j+1)} \frac{b_{n,4\alpha}}{b_{j,4\alpha}} \frac{b_{j,2\alpha}}{b_{i,2\alpha}} - \frac{4p^2}{(i+1)(j+1)} \frac{b_{n,2\alpha}}{b_{i,2\alpha}} \frac{b_{n,2\alpha}}{b_{j,2\alpha}} \right) \\ &\leq 2p \sum_{i=1}^{n-1} \frac{1}{(i+1)^2} \left(3 \frac{b_{n,4\alpha}}{b_{i,4\alpha}} - 2p \left(\frac{b_{n,2\alpha}}{b_{i,2\alpha}} \right)^2 \right) \quad \textcircled{I} \\ &\quad + 4p(n-1)^{-1} \sum_{i=1}^{n-1} \frac{b_{n,4\alpha}}{b_{i,4\alpha}} \left(\frac{3}{(i+1)^2} - \frac{1}{i+1} \right) \quad \textcircled{II} \\ &\quad + 8p^2 \sum_{i=1}^{n-1} \sum_{j=i+1}^{n-1} \left(\frac{1}{(i+1)(j+1)} \frac{b_{j,2\alpha}}{b_{i,2\alpha}} \left(\frac{b_{n,4\alpha}}{b_{j,4\alpha}} - \left(\frac{b_{n,2\alpha}}{b_{j,2\alpha}} \right)^2 \right) \right). \quad \textcircled{III} \end{aligned} \tag{10}$$

We notice that we are dealing with a telescoping sum, we take advantage of Eq. (8) again and consider the three parts in turn.

①

$$\begin{aligned} &\sum_{i=1}^{n-1} \frac{1}{(i+1)^2} \left(3 \frac{b_{n,4\alpha}}{b_{i,4\alpha}} - 2p \left(\frac{b_{n,2\alpha}}{b_{i,2\alpha}} \right)^2 \right) \\ &= \sum_{i=1}^{n-1} \frac{1}{(i+1)^2} \left(\left(\frac{b_{n-1,2\alpha}}{b_{i,2\alpha}} \right)^2 \left(\frac{3n}{n+4\alpha} - \frac{2pn^2}{(n+2\alpha)^2} \right) \right. \\ &\quad \left. + 3 \sum_{k=i+1}^{n-1} \left(\frac{b_{k-1,2\alpha}}{b_{i,2\alpha}} \right)^2 \left(\frac{k}{k+4\alpha} - \frac{k^2}{(k+2\alpha)^2} \right) \frac{b_{n,4\alpha}}{b_{k,4\alpha}} \right) \end{aligned}$$

$$\begin{aligned}
&= \sum_{i=1}^{n-1} \frac{1}{(i+1)^2} \left(\left(\frac{b_{n-1,2\alpha}}{b_{i,2\alpha}} \right)^2 \frac{n^2}{(n+2\alpha)^2} \frac{(3-2p)n + (3-2p)4\alpha + n^{-1}12\alpha^2}{n+4\alpha} \right. \\
&\quad \left. + 3 \sum_{k=i+1}^{n-1} \left(\frac{b_{k-1,2\alpha}}{b_{i,2\alpha}} \right)^2 \frac{k^2}{(k+2\alpha)^2} \frac{4\alpha^2}{k(k+4\alpha)} \frac{b_{n,4\alpha}}{b_{k,4\alpha}} \right) \\
&\leq C \left((3-2p)n^{-4\alpha} \sum_{i=1}^n i^{4\alpha-2} + 12\alpha^2 n^{-4\alpha} \sum_{i=1}^n i^{4\alpha-3} \right) \\
&\sim C \begin{cases} n^{-4\alpha} & 0 < \alpha < 0.25 \\ n^{-1} \ln n & \alpha = 0.25 \\ n^{-1} & 0.25 < \alpha. \end{cases}
\end{aligned}$$

II

$$\begin{aligned}
n^{-1} \sum_{i=1}^{n-1} \frac{b_{n,4\alpha}}{b_{i,4\alpha}} \left(\frac{3}{(i+1)^2} - \frac{1}{i+1} \right) &\sim C \left(3n^{-4\alpha-1} \sum_{i=1}^n i^{4\alpha-2} - n^{-4\alpha-1} \sum_{i=1}^n i^{4\alpha-1} \right) \\
&\sim -Cn^{-1}
\end{aligned}$$

III

$$\begin{aligned}
&\sum_{i=1}^{n-1} \sum_{j=i+1}^{n-1} \left(\frac{1}{(i+1)(j+1)} \frac{b_{j,2\alpha}}{b_{i,2\alpha}} \left(\frac{b_{n,4\alpha}}{b_{j,4\alpha}} - \left(\frac{b_{n,2\alpha}}{b_{j,2\alpha}} \right)^2 \right) \right) \\
&= \sum_{i=1}^{n-1} \sum_{j=i+1}^{n-1} \frac{1}{(i+1)(j+1)} f_{2\alpha}(i,j) A_{n,j} \\
&\leq Cn^{-4\alpha} \sum_{i=1}^n \sum_{j=i+1}^n i^{-1+2\alpha} j^{-2+2\alpha} \leq C \begin{cases} n^{-4\alpha} & 0 < \alpha < 0.25 \\ n^{-1} \ln n & \alpha = 0.25 \\ n^{-1} & 0.25 < \alpha. \end{cases} \tag{11}
\end{aligned}$$

Putting these together we obtain

$$\text{Var} \left[\sum_{i=1}^{n-1} \phi_i^* \right] \leq pC \begin{cases} n^{-4\alpha} & 0 < \alpha < 0.25 \\ n^{-1} \ln n & \alpha = 0.25 \\ n^{-1} & 0.25 < \alpha. \end{cases}$$

On the other hand the variance is bounded from below by III. Its asymptotic behavior is tight as the calculations there are accurate up to a constant (independent of p). This is further illustrated by graphs in [Figure 3](#). \square

Corollary 5.4. *Let p_k and $\sigma_{c,k}^2$ be respectively the jump probability and variance at the k -th speciation event, such that the sequence $\sigma_{c,k}^4 p_k$ is bounded. We have*

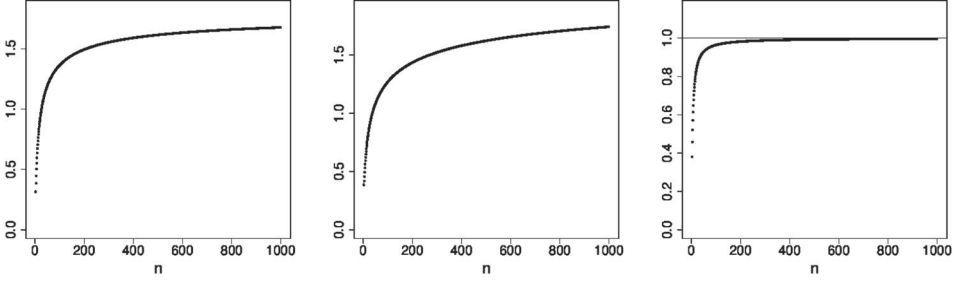


Figure 3. Numerical evaluation of scaled Eq. (10) for different values of α . The scaling for left: $\alpha = 0.1$ equals $n^{-4\alpha}$, center: $\alpha = 0.25$ equals $n^{-1} \log n$ and right $\alpha = 1$ equals $(2p(3-2p)/(4\alpha-1) - 4p/(4\alpha) + 32p^2\alpha^2(1/(8\alpha^2) + 1/(2\alpha(2\alpha-1)) - 1/(4\alpha^2)^{-1} - 1/((2\alpha-1)(4\alpha-1))))n^{-1}$. In all cases, $p=0.5$. The value of the leading constant comes from a careful treatment of the summation in Lemma 5.3. The sums are approximated by definite integrals and the leading constant resulting from the integration is remembered (in the panel on the right).

$$n \ln^{-1} n \text{Var} \left[\sum_{i=1}^{n-1} \sigma_{c,i}^2 \phi_i^* \right] \rightarrow 0 \text{ for } \alpha = 0.25,$$

$$n \text{Var} \left[\sum_{i=1}^{n-1} \sigma_{c,i}^2 \phi_i^* \right] \rightarrow 0 \text{ for } 0.25 < \alpha.$$

iff $\sigma_{c,k}^4 p_k \rightarrow 0$ with density 1.

Proof. We consider the case, $\alpha > 0.25$. Notice that in the proof of Lemma 5.3 $\text{Var} \left[\sum_{i=1}^{n-1} \phi_i^* \right] \leq p n^{-4\alpha} \sum_{i=1}^{n-1} i^{4\alpha-2}$. If the jump probability and variance are not constant, but as in the Corollary, then

$$\text{Var} \left[\sum_{i=1}^{n-1} \sigma_{c,i}^2 \phi_i^* \right] \leq n^{-4\alpha} \left(\sum_{i=1}^{n-1} p_i \sigma_{c,i}^4 i^{4\alpha-2} + \sum_{i=1}^{n-1} p_i \sigma_{c,i}^2 i^{4\alpha-2} \right).$$

Notice that if $p_i \sigma_{c,i}^4 \rightarrow 0$ with density 1, then so will $p_i \sigma_{c,i}^2$.

The Corollary is a consequence of a more general ergodic property, similar to Petersen's^[45] Lemma 6.2 (p. 65). Namely take $u > 0$ and if a bounded sequence $a_i \rightarrow 0$ with density 1, then

$$n^{-u} \sum_{i=1}^{n-1} a_i i^{u-1} \rightarrow 0.$$

To show this say the sequence a_i is bounded by A , let $E \subset \mathbb{N}$ be the set of natural numbers such that $a_i \rightarrow 0$ if $i \in E^c$ and define $E_n = E \cup \{1, \dots, n\}$. Then

$$n^{-u} \sum_{i=1}^{n-1} a_i i^{u-1} = n^{-u} \sum_{\substack{i=1 \\ i \in E_{n-1}}}^{n-1} a_i i^{u-1} + n^{-u} \sum_{\substack{i=1 \\ i \notin E_{n-1}}}^{n-1} a_i i^{u-1}.$$

Denoting by $|E_i|$ the cardinality of a set E_i , the former sum is bounded above by $A \frac{|E_{n-1}|}{n}$, which, by assumption, tends to 0 as $n \rightarrow \infty$. For the latter sum, given $\epsilon > 0$, if we choose N_1 such that $|a_n| < \epsilon/2$ for all $n > N_1$ and N_2 such that $(N_1/n)^u < \epsilon/(2A)$ for all $n > N_2$, then for all $n > N = \max\{N_1, N_2\}$, one has that

$$n^{-u} \sum_{\substack{i=1 \\ i \notin E_{n-1}}}^{n-1} a_i i^{u-1} = n^{-u} \sum_{\substack{i=1 \\ i \notin E_{n-1}}}^{N_1} a_i i^{u-1} + n^{-u} \sum_{\substack{i=N_1+1 \\ i \notin E_{n-1}}}^{n-1} a_i i^{u-1},$$

and now one has that the former sum is bounded above by $An^{-u}N_1N_1^{u-1} < \epsilon/2$ and the latter by $n^{-u}n^{u-1}(n - N_1)(\epsilon/2) < \epsilon/2$. This proves the result.

On the other hand if a_i does not go to 0 with density 1, then $\limsup_n n^{-u} \sum_{i=1}^{n-1} a_i i^{u-1} > 0$.

When $\alpha = 0.25$ we obtain the Corollary using the same ergodic argumentation for

$$\ln^{-1} n \left(\sum_{i=1}^{n-1} p_i \sigma_{c,i}^4 i^{-1} + \sum_{i=1}^{n-1} p_i \sigma_{c,i}^2 i^{-1} \right).$$

□

Let $\tilde{I}^{(n)}$ be the sequence of speciation events on the lineage from the origin of the tree to the most recent common ancestor of a pair of randomly selected tips and (\tilde{J}_i) be the jump pattern (binary sequence 1 jump took place, 0 did not take place just after speciation event i) on the lineage from the origin of the tree to the most recent common ancestor of a pair of randomly selected tips.

Lemma 5.5. *For random variables $(v^{(n)}, \tilde{I}^{(n)}, (\tilde{J}_i)_{i=1}^{v^{(n)}})$ derived from the same random pair of lineages and a fixed jump probability $0 < p < 1$*

$$\begin{aligned} \text{Var} \left[\mathbb{E} \left[\sum_{i=1}^{v^{(n)}} \tilde{J}_i e^{-2\alpha \left(\tau^{(n)} + \dots + T_{\tilde{I}_i^{(n)}+1} \right)} \middle| \mathcal{Y}_n \right] \right] \\ \leq p(1-p)C \begin{cases} n^{-4\alpha} & 0 < \alpha < 0.5, \\ n^{-2} \ln n & \alpha = 0.5, \\ n^{-2} & 0.5 < \alpha. \end{cases} \end{aligned} \quad (12)$$

Proof. We introduce the notation

$$\Psi^{(n)} := \sum_{i=1}^{v^{(n)}} \tilde{J}_i e^{-2\alpha \left(\tau^{(n)} + \dots + T_{\tilde{I}_i^{(n)}+1} \right)}$$

and by definition we have

$$\text{Var} \left[\mathbb{E} \left[\sum_{i=1}^{v^{(n)}} \tilde{J}_i e^{-2\alpha \left(\tau^{(n)} + \dots + T_{\tilde{I}_i}^{(n)} \right)} \middle| \mathcal{Y}_n \right] \right] = \mathbb{E} \left[\left(\mathbb{E}[\Psi^{(n)} | \mathcal{Y}_n] \right)^2 \right] - \left(\mathbb{E}[\Psi^{(n)}] \right)^2.$$

We introduce the random variable

$$\phi_i = \tilde{Z}_i \tilde{\mathbf{1}}_i e^{-2\alpha(T_n + \dots + T_{i+1})},$$

where \tilde{Z}_i is the binary random variable if a jump took place just after the i -th speciation event of the tree for our considered lineage and obviously (for $i_1 < i_2$)

$$\begin{aligned} \mathbb{E}[\phi_i] &= \frac{2p}{i+1} b_{n,2\alpha}/b_{i,2\alpha}, \\ \mathbb{E}[\phi_i^2] &= \frac{2p}{i+1} b_{n,4\alpha}/b_{i,4\alpha}, \\ \mathbb{E}[\phi_{i_1} \phi_{i_2}] &= \frac{4p^2}{(i_1+1)(i_2+1)} \frac{b_{n,4\alpha}}{b_{i_2,4\alpha}} \frac{b_{i_2,2\alpha}}{b_{i_1,2\alpha}}. \end{aligned}$$

We illustrate the random objects defined above in [Figure 5](#). We can write similarly (but not exactly the same) as for $\Psi^{*(n)}$

$$\Psi^{(n)} = \sum_{i=1}^{k-1} \phi_i.$$

As usual (just as for $\tau_1^{(n)}, \tau_2^{(n)}$ in [Lemma 5.1](#)) let $(\tau_1^{(n)}, v_1^{(n)}, \Psi_1^{(n)})$ and $(\tau_2^{(n)}, v_2^{(n)}, \Psi_2^{(n)})$ be two conditionally on \mathcal{Y}_n independent copies of $(\tau^{(n)}, v^{(n)}, \Psi^{(n)})$ and now

$$\begin{aligned} \mathbb{E} \left[\left(\mathbb{E}[\Psi^{(n)} | \mathcal{Y}_n] \right)^2 \right] &= \mathbb{E} \left[\mathbb{E}[\Psi_1^{(n)} | \mathcal{Y}_n] \mathbb{E}[\Psi_2^{(n)} | \mathcal{Y}_n] \right] \\ &= \mathbb{E} \left[\mathbb{E}[\Psi_1^{(n)} \Psi_2^{(n)} | \mathcal{Y}_n] \right] = \mathbb{E}[\Psi_1^{(n)} \Psi_2^{(n)}]. \end{aligned}$$

Writing out a product of two sums, for $k_1 < k_2$, as

$$\begin{aligned} \left(\sum_{i_1=1}^{k_1-1} a_{i_1} \right) \left(\sum_{i_2=1}^{k_2-1} a_{i_2} \right) &= \left(\sum_{i=1}^{k_1-1} a_i \right)^2 + \left(\sum_{i_1=1}^{k_1-1} a_{i_1} \right) \left(\sum_{i_2=k_1}^{k_2-1} a_{i_2} \right) \\ &= \left(\sum_{i=1}^{k_1-1} a_i^2 \right) + 2 \left(\sum_{i_1=1}^{k_1-1} \sum_{i_2=i_1+1}^{k_1-1} a_{i_1} a_{i_2} \right) \\ &\quad + \left(\sum_{i_1=1}^{k_1-1} a_{i_1} \right) \left(\sum_{i_2=k_1}^{k_2-1} a_{i_2} \right) \end{aligned}$$

and using the law of total probability to condition on the speciation event at which the two nodes coalesced, we have

$$\begin{aligned}
 \text{Var}[\mathbb{E}[\Psi^{(n)}|\mathcal{Y}_n]] &= \mathbb{E}[\Psi_1^{(n)}\Psi_2^{(n)}] - (\mathbb{E}[\Psi^{(n)}])^2 \\
 &\quad \textcircled{\text{I}} \quad \textcircled{\text{II}} \\
 &= \sum_{k=1}^{n-1} \pi_{k,n}^2 \left(\sum_{i=1}^{k-1} (\mathbb{E}[\phi_i^2] - \mathbb{E}[\phi_i]^2) + 2 \sum_{i_1=1}^{k-1} \sum_{i_2=i_1+1}^{k-1} (\mathbb{E}[\phi_{i_1}\phi_{i_2}] - \mathbb{E}[\phi_{i_1}]\mathbb{E}[\phi_{i_2}]) \right) \\
 &\quad + 2 \sum_{k_1=1}^{n-1} \sum_{k_2=k_1+1}^{n-1} \pi_{k_1,n} \pi_{k_2,n} \left(\sum_{i=1}^{k_1-1} (\mathbb{E}[\phi_i^2] - \mathbb{E}[\phi_i]^2) \quad \textcircled{\text{III}} \right. \\
 &\quad \left. + 2 \sum_{i_1=1}^{k_1-1} \sum_{i_2=i_1+1}^{k_1-1} (\mathbb{E}[\phi_{i_1}\phi_{i_2}] - \mathbb{E}[\phi_{i_1}]\mathbb{E}[\phi_{i_2}]) + \sum_{i_1=1}^{k_1-1} \sum_{i_2=k_1}^{k_2-1} (\mathbb{E}[\phi_{i_1}\phi_{i_2}] - \mathbb{E}[\phi_{i_1}]\mathbb{E}[\phi_{i_2}]) \right). \\
 &\quad \textcircled{\text{IV}} \quad \textcircled{\text{V}}
 \end{aligned} \tag{13}$$

To aid intuition, we point out that cases I and II correspond to the case when the two pairs of tips coalesce at the same node k while cases III–V when at different nodes, $k_1 < k_2$. We first observe

$$\begin{aligned}
 \mathbb{E}[\phi_i^2] - \mathbb{E}[\phi_i]^2 &= \frac{2p}{i+1} \left(\frac{b_{n,4\alpha}}{b_{i,4\alpha}} - \frac{2p}{i+1} \left(\frac{b_{n,2\alpha}}{b_{i,2\alpha}} \right)^2 \right) \\
 &= \frac{2p}{i+1} \left(\frac{(i+1)^2}{(i+1+2\alpha)^2} \frac{(i+1) + (4\alpha-1) + (i+1)^{-1}4\alpha(\alpha-1)}{(i+1+4\alpha)} \frac{b_{n,4\alpha}}{b_{i+4\alpha}} \right. \\
 &\quad \left. + 4\alpha^2 \frac{b_{n,4\alpha}}{b_{i,2\alpha}^2} \sum_{j=i+2}^{n-1} \frac{b_{j,2\alpha}^2}{b_{j,4\alpha} j(j+4\alpha)} \frac{1}{j(j+4\alpha)} + \left(\frac{b_{n,2\alpha}}{b_{i,2\alpha}} \right)^2 \frac{n(1-2p) + 4\alpha(1-2p) + n^{-1}4\alpha^2}{n+4\alpha} \right)
 \end{aligned}$$

and

$$\begin{aligned}
 \mathbb{E}[\phi_{i_1}\phi_{i_2}] - \mathbb{E}[\phi_{i_1}]\mathbb{E}[\phi_{i_2}] &= \frac{4p^2}{(i_1+1)(i_2+1)} \left(\frac{b_{n,4\alpha}}{b_{i_2,4\alpha}} \frac{b_{i_2,2\alpha}}{b_{i_1,2\alpha}} - \left(\frac{b_{n,2\alpha}}{b_{i_1,2\alpha}} \right) \left(\frac{b_{n,2\alpha}}{b_{i_2,2\alpha}} \right) \right) \\
 &= \frac{4p^2}{(i_1+1)(i_2+1)} \frac{b_{n,4\alpha} b_{i_2,2\alpha}}{b_{i_1,2\alpha} b_{i_2,2\alpha}^2} \left(\sum_{j=i_2+1}^n \frac{b_{j,2\alpha}^2}{b_{j,4\alpha} j(j+4\alpha)} \frac{4\alpha^2}{j(j+4\alpha)} \right).
 \end{aligned} \tag{14}$$

Using the above, we consider each of the five components in this sum separately.

Ⓘ

$$\begin{aligned}
& \sum_{k=1}^{n-1} \pi_{k,n}^2 \sum_{i=1}^{k-1} \left(\mathbb{E}[\phi_i^2] - \mathbb{E}[\phi_i]^2 \right) \\
& \leq p C n^{-4\alpha} \sum_{i=1}^n \left(i^{4\alpha-1} + (4\alpha-1)i^{4\alpha-2} + 4\alpha(\alpha-1)i^{4\alpha-3} + 4\alpha^2 i^{4\alpha-2} \right. \\
& \quad \left. + (1-2p)i^{4\alpha-1} \right) \sum_{k=i+1}^n k^{-4} \\
& \leq p C \begin{cases} n^{-4\alpha} & 0 < \alpha < 0.75 \\ n^{-3} \ln n & \alpha = 0.75 \\ n^{-3} & 0.75 < \alpha \end{cases}
\end{aligned}$$

Ⓜ

$$\begin{aligned}
& \sum_{k=1}^{n-1} \pi_{k,n}^2 \sum_{i_1=1}^{k-1} \sum_{i_2=i_1+1}^{k-1} \left(\mathbb{E}[\phi_{i_1} \phi_{i_2}] - \mathbb{E}[\phi_{i_1}] \mathbb{E}[\phi_{i_2}] \right) \\
& \leq p^2 C n^{-4\alpha} \sum_{k=1}^n k^{-4} \sum_{i_1=1}^k i_1^{2\alpha-1} \sum_{i_2=i_1+1}^k i_2^{2\alpha-2} \\
& \leq C p^2 \begin{cases} n^{-4\alpha} \sum_{i_1=1}^n i_1^{4\alpha-2} \sum_{k=i_1+1}^n k^{-4} & 0 < \alpha < 0.5 \\ n^{-2} \sum_{k=1}^n k^{-4} \sum_{i_2=2}^k 1 & \alpha = 0.5 \\ n^{-4\alpha} \sum_{i_1=1}^n i_1^{4\alpha-2} \sum_{k=i_1+1}^n k^{-4} & 0.5 < \alpha \end{cases} \leq C p^2 \begin{cases} n^{-4\alpha} & 0 < \alpha < 1 \\ n^{-4} \ln n & \alpha = 1 \\ n^{-4} & 1 < \alpha \end{cases}
\end{aligned}$$

Ⓝ

$$\begin{aligned}
& \sum_{k_1=1}^{n-1} \sum_{k_2=k_1+1}^{n-1} \pi_{k_1,n} \pi_{k_2,n} \sum_{i=1}^{k_1-1} \left(\mathbb{E}[\phi_i^2] - \mathbb{E}[\phi_i]^2 \right) \\
& \leq p C n^{-4\alpha} \sum_{i=1}^n \left(i^{4\alpha-1} + (4\alpha-1)i^{4\alpha-2} + 4\alpha(\alpha-1)i^{4\alpha-3} + 4\alpha^2 i^{4\alpha-2} \right. \\
& \quad \left. + (1-2p)i^{4\alpha-1} \right) \sum_{k_1=i+1}^n k_1^{-3} \\
& \leq p(1-p) C \begin{cases} n^{-4\alpha} & 0 < \alpha < 0.5 \\ n^{-2} \ln n & \alpha = 0.5 \\ n^{-2} & 0.5 < \alpha \end{cases}
\end{aligned}$$

(IV)

$$\begin{aligned}
& \sum_{k_1=1}^{n-1} \sum_{k_2=k_1+1}^{n-1} \pi_{k_1, n} \pi_{k_2, n} \sum_{i_1=1}^{k_1-1} \sum_{i_2=i_1+1}^{k_1-1} (\mathbb{E}[\phi_{i_1} \phi_{i_2}] - \mathbb{E}[\phi_{i_1}] \mathbb{E}[\phi_{i_2}]) \\
& \leq p^2 C n^{-4\alpha} \sum_{k_1=1}^n \sum_{k_2=k_1+1}^n k_1^{-2} k_2^{-2} \sum_{i_1=1}^{k_1} \sum_{i_2=i_1+1}^{k_1} (i_1^{2\alpha-1} i_2^{2\alpha-2}) \\
& \leq p^2 C \begin{cases} n^{-4\alpha} & 0 < \alpha < 0.75 \\ n^{-3} \ln n & \alpha = 0.75 \\ n^{-3} & 0.75 < \alpha \end{cases}
\end{aligned}$$

(V)

$$\begin{aligned}
& \sum_{k_1=1}^{n-1} \sum_{k_2=k_1+1}^{n-1} \pi_{k_1, n} \pi_{k_2, n} \sum_{i_1=1}^{k_1-1} \sum_{i_2=k_1}^{k_2-1} (\mathbb{E}[\phi_{i_1} \phi_{i_2}] - \mathbb{E}[\phi_{i_1}] \mathbb{E}[\phi_{i_2}]) \\
& \leq p^2 C n^{-4\alpha} \sum_{k_1=1}^n \sum_{k_2=k_1+1}^n k_1^{-2} k_2^{-2} \sum_{i_1=1}^{k_1} \sum_{i_2=k_1}^{k_2} (i_1^{2\alpha-1} i_2^{2\alpha-2}) \\
& \leq p^2 C n^{-4\alpha} \begin{cases} \sum_{i_1=1}^n i_1^{2\alpha-1} \sum_{k_1=i_1+1}^n k_1^{-2} \left(\sum_{i_2=k_1}^n i_2^{2\alpha-2} \sum_{k_2=i_2+1}^n k_2^{-2} \right) & \alpha \notin \{0.5, 1\} \\ \sum_{k_1=1}^n k_1^{-1} \left(\sum_{k_2=k_1+1}^n k_2^{-2} H_{k_2} \right) & \alpha = 0.5 \\ \frac{1}{2} \sum_{1 \leq k_1 < k_2}^n k_2^{-1} & \alpha = 1 \end{cases} \\
& \leq p^2 C \begin{cases} n^{-2} & \alpha = 0.5 \\ n^{-4\alpha} \sum_{i_1=1}^n i_1^{2\alpha-1} \sum_{k_1=i_1+1}^n k_1^{-2\alpha-4} & \alpha \in (0, 1) \setminus \{0.5\} \\ n^{-3} & \alpha = 1 \\ n^{-4\alpha} \sum_{i_1=1}^n i_1^{2\alpha-1} \sum_{k_1=i_1+1}^n k_1^{2\alpha-4} & 1 < \alpha \end{cases} \\
& \leq p^2 C \begin{cases} n^{-4\alpha} & 0 < \alpha \leq 0.75 \\ n^{-3} \ln n & \alpha = 0.75 \\ n^{-3} & 0.75 \leq \alpha. \end{cases}
\end{aligned}$$

Putting I-V together we obtain

$$\text{Var}[\mathbb{E}[\Psi^{(n)} | \mathcal{Y}_n]] \leq p(1-p)C \begin{cases} n^{-4\alpha} & 0 < \alpha < 0.5 \\ n^{-2} \ln n & \alpha = 0.5 \\ n^{-2} & 0.5 < \alpha. \end{cases}$$

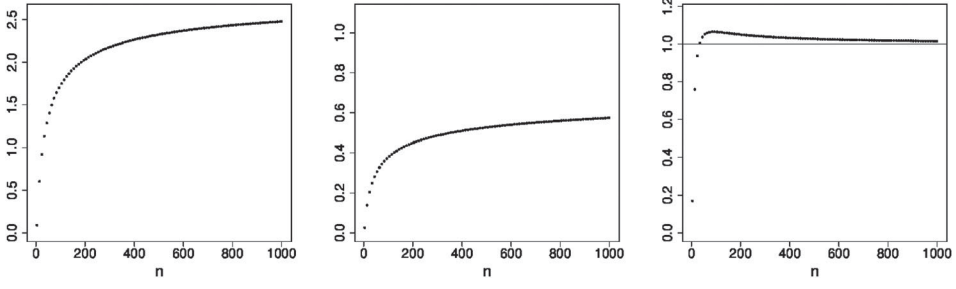


Figure 4. Numerical evaluation of scaled Eq. (13) for different values of α . The scaling for left: $\alpha = 0.35$ equals $n^{-4\alpha}$, center: $\alpha = 0.5$ equals $16p(1-p)n^{-2}\log n$ and right $\alpha = 1$ equals $(32p(1-p)/((4\alpha-2)(4\alpha-1)(4\alpha)))n^{-2}$. In all cases, $p=0.5$. The value of the leading constant comes from a careful treatment of the summation in Lemma 5.5, component III. The sums (center and right panel) are approximated by definite integrals and the leading constant resulting from the integration is remembered. In the $\alpha = 0.5$ case the convergence is very slow.

The variance is bounded from below by III and as these derivations are correct up to a constant (independent of p) the variance behaves as above. This is further illustrated by graphs in Figure 4. \square

Remark 5.6. In Lemma 5.5 we assumed that $0 < p < 1$. The case of $p = 0$ is trivial, as then for all i , $\tilde{J}_i = 0$ and hence the variance will be 0. The case $p = 1$ is more interesting. It means that there will be a jump on each lineage after each speciation event. This however implies that the variability due to the uncertainty, if a jump did or did not take place, disappears. Hence, a faster rate of convergence will be present in component III. It will be $n^{-4\alpha}$ for $0 < \alpha < 0.75$, $n^{-3}\log n$ for $\alpha = 0.75$ and n^{-3} for $\alpha > 0.75$, i.e., same as in components I, IV and V.

The proof of the next Corollary, 5.7, is exactly the same as of Corollary 5.4.

Corollary 5.7. Let p_k and $\sigma_{c,k}^2$ be respectively the jump probability and variance at the n -th speciation event, such that the sequence $\sigma_{c,k}^4 p_k(1-p_k)$ is bounded. We have

$$n^2 \ln^{-1} n \text{Var} \left[\sum_{i=1}^{n-1} \sigma_{c,i}^2 \phi_i \right] \rightarrow 0 \text{ for } \alpha = 0.5,$$

$$n^2 \text{Var} \left[\sum_{i=1}^{n-1} \sigma_{c,i}^2 \phi_i \right] \rightarrow 0 \text{ for } 0.5 < \alpha.$$

iff $\sigma_{c,k}^4 p_k(1-p_k) \rightarrow 0$ with density 1.

Lemma 5.8. For random variables $U^{(n)}, \Psi^{(n)}$ and a fixed jump probability p

$$\text{Cov}\left[e^{-2\alpha U^{(n)}}, \mathbb{E}[\Psi^{(n)} | \mathcal{Y}_n]\right] \leq pC \begin{cases} n^{-4\alpha} & \alpha < 0.5 \\ n^{-2} \ln n & \alpha = 0.5 \\ n^{-(2\alpha+1)} & 0.5 < \alpha \end{cases}. \quad (15)$$

Proof. We introduce the random variable

$$\bar{\phi}_i = \tilde{Z}_i \tilde{\mathbf{1}}_i e^{-4\alpha(T_n + \dots + T_{i+1})} - 2\alpha(T_i + \dots + T_1)$$

and obviously

$$\mathbb{E}[\bar{\phi}_i] = \frac{2p}{i+1} (b_{n,4\alpha}/b_{i,4\alpha}) b_{i,2\alpha}.$$

Writing out

$$\begin{aligned} \text{Cov}\left[e^{-2\alpha U^{(n)}}, \mathbb{E}[\Psi^{(n)} | \mathcal{Y}_n]\right] &= \mathbb{E}\left[e^{-2\alpha U^{(n)}} \Psi^{(n)}\right] - (\mathbb{E}[e^{-2\alpha U^{(n)}}]) (\mathbb{E}[\Psi^{(n)}]) \\ &= \sum_{k=1}^{n-1} \pi_{k,n} \left(\sum_{i=1}^{k-1} (\mathbb{E}[\bar{\phi}_i] - b_{n,2\alpha} \mathbb{E}[\phi_i]) \right) \\ &= \sum_{k=1}^{n-1} \pi_{k,n} \left(\sum_{i=1}^{k-1} \frac{2p}{i+1} \left(\frac{b_{n,4\alpha} b_{i,2\alpha}}{b_{i,4\alpha}} - \frac{b_{n,2\alpha}^2}{b_{i,2\alpha}} \right) \right) \\ &= \sum_{k=1}^{n-1} \pi_{k,n} \left(\sum_{i=1}^{k-1} \frac{2p}{i+1} b_{i,2\alpha} \left(\frac{b_{n,4\alpha}}{b_{i,4\alpha}} - \left(\frac{b_{n,2\alpha}}{b_{i,2\alpha}} \right)^2 \right) \right) \\ &= \text{see Eq. (11)} \\ &= 2pb_{n,4\alpha} \sum_{k=1}^{n-1} \pi_{k,n} \left(\sum_{i=1}^{k-1} \frac{1}{i+1} \frac{1}{b_{i,2\alpha}} \sum_{j=i+1}^n \frac{b_{j,2\alpha}^2}{b_{j,4\alpha}} \frac{4\alpha^2}{j(j+4\alpha)} \right) \\ &\leq Cpn^{-4\alpha} \sum_{i=1}^n i^{2\alpha-1} \sum_{k=i+1}^{n-1} k^{-2} \\ &\leq Cpn^{-4\alpha} \sum_{i=1}^n i^{2\alpha-2} \leq pC \begin{cases} n^{-4\alpha} & \alpha < 0.5 \\ n^{-2} \ln n & \alpha = 0.5 \\ n^{-2\alpha-1} & 0.5 < \alpha \end{cases}. \end{aligned} \quad (16)$$

Lemma 5.9. For random variables $\tau^{(n)}, \Psi^{(n)}$ and a fixed jump probability p

$$\text{Cov}\left[\mathbb{E}\left[e^{-2\alpha \tau^{(n)}} | \mathcal{Y}_n\right], \mathbb{E}[\Psi^{(n)} | \mathcal{Y}_n]\right] \geq 0 \quad (17)$$

Proof. We introduce the random variable for $i < k$

$$\phi_{k,i} = \tilde{Z}_i \tilde{\mathbf{1}}_i e^{-4\alpha(T_n + \dots + T_{k+1})} - 2\alpha(T_k + \dots + T_i)$$

and obviously

$$\phi_{k,i} = \frac{2p}{i+1} \frac{b_{n,4\alpha}}{b_{k,4\alpha}} \frac{b_{k,2\alpha}}{b_{i,2\alpha}}.$$

As in the proofs of previous lemmata we denote by $\tau_1^{(n)}$ and $\Psi_2^{(n)}$ realizations of $\tau^{(n)}$ and $\Psi^{(n)}$ that are conditionally independent given \mathcal{Y}_n . In other words, given a particular Yule tree $\tau_1^{(n)}$ and $\Psi_2^{(n)}$ will correspond to two independent choices of pairs of tip species. In the below derivations k_1 will correspond to the node where the random pair, connected to $\tau_1^{(n)}$, coalesced and k_2 will correspond to the node where the random pair $\Psi_2^{(n)}$ coalesced. Notice that the conditional expectation of $e^{-2\alpha\tau^{(n)}}$ given that the coalescent took place at node k_1 is $b_{n,2\alpha}/b_{k_1,2\alpha}$. Writing out

$$\begin{aligned} & \text{Cov} \left[\mathbb{E} \left[e^{-2\alpha\tau^{(n)}} | \mathcal{Y}_n \right], \mathbb{E} [\Psi^{(n)} | \mathcal{Y}_n] \right] \\ &= \mathbb{E} \left[e^{-2\alpha\tau_1^{(n)}} \Psi_2^{(n)} \right] - (\mathbb{E} [e^{-2\alpha\tau^{(n)}}]) (\mathbb{E} [\Psi^{(n)}]) \\ &= \sum_{k=1}^{n-1} \pi_{k,n}^2 \left(\sum_{i=1}^{k-1} \left(\mathbb{E} [\phi_{k,i}] - \frac{b_{n,2\alpha}}{b_{k,2\alpha}} \mathbb{E} [\phi_i] \right) \right) \quad \textcircled{I} \\ &+ \sum_{k_1=2}^n \sum_{k_2=1}^{k_1-1} \pi_{k_1,n} \pi_{k_2,n} \left(\sum_{i=1}^{k_2-1} \left(\mathbb{E} [\phi_{k_1,i}] - \frac{b_{n,2\alpha}}{b_{k_1,2\alpha}} \mathbb{E} [\phi_i] \right) \right) \quad \textcircled{II} \\ &+ \sum_{k_1=1}^{n-1} \sum_{k_2=k_1+1}^n \pi_{k_1,n} \pi_{k_2,n} \left(\sum_{i=1}^{k_1} \left(\mathbb{E} [\phi_{k_1,i}] - \frac{b_{n,2\alpha}}{b_{k_1,2\alpha}} \mathbb{E} [\phi_i] \right) \right) \quad \textcircled{III} \\ &+ \sum_{k_1=1}^{n-1} \sum_{k_2=k_1+1}^n \pi_{k_1,n} \pi_{k_2,n} \left(\sum_{i=k_1+1}^{k_2-1} \left(\mathbb{E} [\phi_{i,k_1}] - \frac{b_{n,2\alpha}}{b_{k_1,2\alpha}} \mathbb{E} [\phi_i] \right) \right) \quad \textcircled{IV} \\ &= \sum_{k=1}^{n-1} \pi_{k,n}^2 \left(\sum_{i=1}^{k-1} \frac{2p}{i+1} \left(\frac{b_{n,4\alpha}}{b_{k,4\alpha}} \frac{b_{k,2\alpha}}{b_{i,2\alpha}} - \frac{b_{n,2\alpha}}{b_{k,2\alpha}} \frac{b_{n,2\alpha}}{b_{i,2\alpha}} \right) \right) \\ &+ \sum_{k_1=2}^n \sum_{k_2=1}^{k_1-1} \pi_{k_1,n} \pi_{k_2,n} \left(\sum_{i=1}^{k_2-1} \frac{2p}{i+1} \left(\frac{b_{n,4\alpha}}{b_{k_1,4\alpha}} \frac{b_{k_1,2\alpha}}{b_{i,2\alpha}} - \frac{b_{n,2\alpha}}{b_{k_1,2\alpha}} \frac{b_{n,2\alpha}}{b_{i,2\alpha}} \right) \right) \\ &+ \sum_{k_1=1}^{n-1} \sum_{k_2=k_1+1}^n \pi_{k_1,n} \pi_{k_2,n} \left(\sum_{i=1}^{k_1} \frac{2p}{i+1} \left(\frac{b_{n,4\alpha}}{b_{k_1,4\alpha}} \frac{b_{k_1,2\alpha}}{b_{i,2\alpha}} - \frac{b_{n,2\alpha}}{b_{k_1,2\alpha}} \frac{b_{n,2\alpha}}{b_{i,2\alpha}} \right) \right) \\ &+ \sum_{k_1=1}^{n-1} \sum_{k_2=k_1+1}^n \pi_{k_1,n} \pi_{k_2,n} \left(\sum_{i=k_1+1}^{k_2-1} \frac{2p}{i+1} \left(\frac{b_{n,4\alpha}}{b_{i,4\alpha}} \frac{b_{i,2\alpha}}{b_{k_1,2\alpha}} - \frac{b_{n,2\alpha}}{b_{k_1,2\alpha}} \frac{b_{n,2\alpha}}{b_{i,2\alpha}} \right) \right). \end{aligned}$$

We may recognize that, after bounding $(i+1)^{-1}$ from below by appropriately k^{-1} , $(k_1+1)^{-1}$ or k_2^{-1} , under the sums over i we will have a

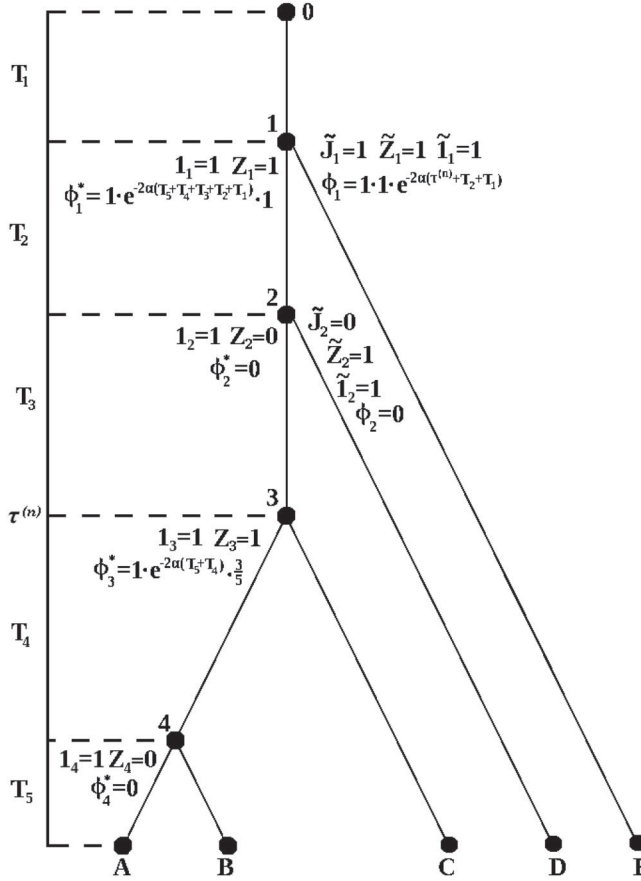


Figure 5. Illustration of the key random variables used in Lemmata 5.3, 5.5 and defined in Section 2. We “randomly sample” (out of the five) the lineage leading to tip A and the pair of tips (A,C) out of $\binom{5}{2}$ possible. As jumps take place just *after* speciation events there is no associated jump at the third speciation event for the (A,C) pair. We have $E[1_3|\mathcal{Y}_n] = 0.6$ as it would be one for three (A,B, or C) randomly sampled lineages out of the five possible. One should remember that for an OU process, $X(\cdot)$, for $s < t$ one has $E[X(t)|X(s)] = e^{-\alpha(t-s)}X(s) + (1 - e^{-\alpha(t-s)})\theta$, hence all contributions of the jumps to the variance and covariance are modified by $e^{-2\alpha t}$, where t is the distance from the jump to the tip. Intuitively writing, the variable $\Psi^{*(n)}$ will then be (for $\sigma_{c,k}^2 = 1$) the contribution of the jumps to the variance of the randomly sampled lineage, while $\Psi^{(n)}$ will then be (for $\sigma_{c,k}^2 \equiv 1$) the contribution of the jumps to the variance of the randomly sampled lineage.

difference corresponding to a telescoping sum, i.e., Eq. (8). This implies that the whole covariance must be positive. Notice the similarity to the sums present in Eqs. (11) and (16).

We also give intuition how all the individual sums arose. Component 5 corresponds to the case where both randomly sampled pairs coalesce at the same node. Component 5 corresponds to the situation where the random pair of tips associated with $\tau^{(n)}$ coalesced later (further away from the origin of the

tree), than the random pair associated with $v^{(n)}$. Components 5 and 5 correspond to the opposite situation. In particular component 5 is when the “ i ” node on the path from the origin to node “ $v^{(n)}$ ” is earlier than or at the same node as the coalescent associated with $\tau^{(n)}$ and component 5 when later. \square

Remark 5.10. Notice that the proof of Lemma 5.9 can easily be continued, in the same fashion as the proofs of Lemmata 5.1–5.8 to find the rate of the decay to 0 of $\text{Cov}\left[\mathbb{E}\left[e^{-2\alpha\tau^{(n)}}|\mathcal{Y}_n\right], \mathbb{E}\left[\Psi^{(n)}|\mathcal{Y}_n\right]\right]$. However, in order not to further lengthen the technicalities we remain at showing the sign of the covariance, as we require only this property.

6. Proof of the Central Limit Theorems 4.1 and 4.6

To avoid unnecessary notation it will be always assumed that under a given summation sign the random variables $\left(\Upsilon^{(n)}, \mathbf{I}^{(n)}, (J_i)_{i=1}^{\Upsilon^{(n)}}\right)$ are derived from the same random lineage and also $\left(v^{(n)}, \tilde{\mathbf{I}}^{(n)}, (\tilde{J}_i)_{i=1}^{v^{(n)}}\right)$ are derived from the same random pair of lineages

Lemma 6.1. *Conditional on \mathcal{Y}_n the first two moments of the scaled sample average are*

$$\begin{aligned} \mathbb{E}[\bar{Y}_n|\mathcal{Y}_n] &= \delta e^{-\alpha U^{(n)}} \\ \mathbb{E}[\bar{Y}_n^2|\mathcal{Y}_n] &= n^{-1} - (1 - \delta^2)e^{-2\alpha U^{(n)}} + (1 - n^{-1})\mathbb{E}\left[e^{-2\alpha\tau^{(n)}}|\mathcal{Y}_n\right] \\ &\quad + n^{-1}(\sigma_a^2/(2\alpha))^{-1}\mathbb{E}\left[\sum_{k=1}^{\Upsilon^{(n)}} \sigma_{c, \mathbf{I}_k^{(n)}}^2 J_k e^{-2\alpha\left(T_n + \dots + T_{\mathbf{I}_k^{(n)}+1}\right)} \middle| \mathcal{Y}_n\right] \\ &\quad + (1 - n^{-1})(\sigma_a^2/(2\alpha))^{-1}\mathbb{E}\left[\sum_{k=1}^{v^{(n)}} \sigma_{c, \tilde{\mathbf{I}}_k^{(n)}}^2 \tilde{J}_k e^{-2\alpha\left(\tau^{(n)} + \dots + T_{\tilde{\mathbf{I}}_k^{(n)}+1}\right)} \middle| \mathcal{Y}_n\right], \\ \text{Var}[\bar{Y}_n|\mathcal{Y}_n] &= n^{-1} - e^{-2\alpha U^{(n)}} + (1 - n^{-1})\mathbb{E}\left[e^{-2\alpha\tau^{(n)}}|\mathcal{Y}_n\right] \\ &\quad + n^{-1}(\sigma_a^2/(2\alpha))^{-1}\mathbb{E}\left[\sum_{k=1}^{\Upsilon^{(n)}} \sigma_{c, \mathbf{I}_k^{(n)}}^2 J_k e^{-2\alpha\left(T_n + \dots + T_{\mathbf{I}_k^{(n)}+1}\right)} \middle| \mathcal{Y}_n\right] \\ &\quad + (1 - n^{-1})(\sigma_a^2/(2\alpha))^{-1}\mathbb{E}\left[\sum_{k=1}^{v^{(n)}} \sigma_{c, \tilde{\mathbf{I}}_k^{(n)}}^2 \tilde{J}_k e^{-2\alpha\left(\tau^{(n)} + \dots + T_{\tilde{\mathbf{I}}_k^{(n)}+1}\right)} \middle| \mathcal{Y}_n\right]. \end{aligned}$$

Proof. The first equality is immediate. The variance follows from

$$\begin{aligned}
& \text{Var}[Y_1 + \dots + Y_n | \mathcal{Y}_n] \\
&= n(1 - e^{-2\alpha U^{(n)}}) + (\sigma_a^2/(2\alpha))^{-1} \sum_{i=1}^n \sum_{k=1}^{\Upsilon^{(i,n)}} \sigma_{c, I_k^{(i,n)}}^2 J_k^{(i,n)} e^{-2\alpha(T_n + \dots + T_{I_k^{(i,n)}}^{(i,n)})} \\
&\quad + 2 \sum_{i=1}^n \sum_{j=i+1}^n \left(e^{-2\alpha \tau^{(i,j,n)}} - e^{-2\alpha U^{(n)}} \right) \\
&\quad + (\sigma_a^2/(2\alpha))^{-1} \sum_{k=1}^{v^{(i,j,n)}} \sigma_{c, I_k^{(i,j,n)}}^2 J_k^{(i,j,n)} e^{-2\alpha(\tau^{(i,j,n)} + \dots + T_{I_k^{(i,j,n)}}^{(i,j,n)})} \\
&= n - n^2 e^{-2\alpha U^{(n)}} + n(n-1) \mathbb{E} \left[e^{-2\alpha \tau^{(n)}} | \mathcal{Y}_n \right] \\
&\quad + n(\sigma_a^2/(2\alpha))^{-1} \mathbb{E} \left[\sum_{k=1}^{\Upsilon^{(n)}} \sigma_{c, I_k^{(n)}}^2 J_k e^{-2\alpha(T_n + \dots + T_{I_k^{(n)}}^{(n)})} \middle| \mathcal{Y}_n \right] \\
&\quad + n(n-1)(\sigma_a^2/(2\alpha))^{-1} \mathbb{E} \left[\sum_{k=1}^{v^{(n)}} \sigma_{c, \tilde{I}_k^{(n)}}^2 \tilde{J}_k e^{-2\alpha(\tau^{(n)} + \dots + T_{I_k^{(n)}}^{(n)})} \middle| \mathcal{Y}_n \right].
\end{aligned}$$

This immediately entails the second moment. \square

Before stating the next lemma we remind the reader of a key, for this manuscript, result presented in Bartoszek's^[10] Appendix A.2 (top of second column, p. 55) in the case of p constant

$$\mathbb{E}[\Psi^{(n)}] = p \begin{cases} \frac{1}{\alpha} \left(\frac{2-(2\alpha+1)(2\alpha n-2\alpha+2)b_{n,2\alpha}}{(n-1)(2\alpha-1)} \right) & \alpha \neq 0.5 \\ \frac{4}{n-1} \left(H_n - \frac{5n-1}{2(n+1)} \right) & \alpha = 0.5 \end{cases}. \quad (18)$$

Lemma 6.2. *Assume that the jump probability is constant, equaling $0 < p < 1$, at every speciation event. Let*

$$a_n(\alpha) = \begin{cases} n^{2\alpha} & 0 < \alpha < 0.5, \\ n \ln^{-1} n & 0.5 = \alpha, \\ n & 0.5 < \alpha \end{cases}$$

and then for all $\alpha > 0$ and n greater than some $n(\alpha)$

$$W_n := a_n(\alpha) \mathbb{E}[\Psi^{(n)} | \mathcal{Y}_n],$$

converges a.s. and in L^1 to a random variable W_∞ with expectation

$$\mathbb{E}[W_\infty] = \begin{cases} \frac{2p(2\alpha+1)\Gamma(2\alpha+1)}{(1-2\alpha)} & 0 < \alpha < 0.5, \\ 4p & 0.5 = \alpha, \\ 2p/(\alpha(2\alpha-1)) & 0.5 < \alpha. \end{cases}$$

In particular for $\alpha = 0.5$ (and also $p = 1$, see Remark 6.3) W_∞ is a constant and the convergence is a.s. and L^2 .

Proof. for $\alpha > 0.5$ We know that $E[W_n] < C_E$ for some constant C_E , as $E[W_n] \rightarrow 2p/(\alpha(2\alpha - 1))$ by Eq. (20). Furthermore, by Lemma 5.5 $\text{Var}[W_n] < C_V$, for some constant C_V . Looking in detail, one can see from Eq. (20), that $E[W_n]$ will (from n large enough) converge monotonically to its limit. It will be decreasing with n for $\alpha > 1$ and increasing for $0.5 < \alpha \leq 1$. If one considers the asymptotic behavior, then the leading term will be $4p/(\alpha(2\alpha - 1))(1 + 1/(n - 1))(1 - \alpha\Gamma(2\alpha + 2)n^{-2\alpha+1})$. Direct calculations show that for $\alpha > 1$ it will be decreasing, as it behaves as $4p/(\alpha(2\alpha - 1))(1 + 1/(n - 1))$, for $\alpha = 1$ it will be increasing as it behaves as $4p(1 - 5n^{-1})$, while for $0.5 < \alpha < 1$ it will be increasing as it behaves as $4p/(\alpha(2\alpha - 1))(1 - \alpha\Gamma(2\alpha + 2)n^{-2\alpha+1})$.

Therefore, if one studies the proof of the downcrossing inequality and submartingale convergence theorem (e.g. Thm. 1.71, Cor. 1.72, p. 44, Medvedevyev^[39]) one will notice that only the monotonicity (which in the classical submartingale convergence theorem is a consequence of the sequence being a submartingale) and boundedness of the expectations of the sequence of positive random variables are required for the almost sure convergence. All of the above is met in our case for W_n .

Hence, by the above $W_n \rightarrow W_\infty$ a.s. for some random variable W_∞ and as all expectations are finite, and the variance is uniformly bounded we have $E[W_\infty] < \infty$. This entails $E[W_n] \rightarrow E[W_\infty] = 2p/(\alpha(2\alpha - 1))$. Also we have uniform integrability of $\{W_n\}$ and hence L^1 convergence.

Proof for $\alpha = 0.5$ By Lemma 5.5 we know that $\text{Var}[E[W_n|\mathcal{Y}_n]]$ behaves as $n^{-2} \ln n$. Therefore, $\text{Var}[W_n] = a_n^2(0.5) \cdot \text{Var}[E[W_n|\mathcal{Y}_n]] \sim C(n^2 \ln^{-2} n)(n^{-2} \ln n) = C \ln^{-1} n \rightarrow 0$. Therefore, W_n converges a.s. and in L^2 to a constant $W_\infty = 4p$.

Proof for $0 < \alpha < 0.5$ is the same as the proof for $\alpha > 0.5$, except that now the leading terms in the asymptotic behavior of $E[W_n]$ will be $p(2\alpha\Gamma(2\alpha + 2) + 2n^{2\alpha-1})/(\alpha(1 - 2\alpha))$. This causes the sequence of expectations to be increasing (from n large enough) and we may argue similar as when $\alpha > 0.5$. From Eq. (20) we obtain $E[W_n] \rightarrow 2p(2\alpha + 1)\Gamma(2\alpha + 1)/(1 - 2\alpha)$ and $\text{Var}[W_n]$ is bounded by a constant by Lemma 5.5. \square

Remark 6.3. If $p = 0$, we are in the trivial case of no jumps. When $p = 1$, in $\alpha > 0.5$ regime we will have W_n converging a.s. and in L^2 to a constant, denoted above as $E[W_\infty]$, by the same argument that takes place for $\alpha = 0.5$, i.e., as the rate of decay to 0 of $\text{Var}[E[W_n|\mathcal{Y}_n]]$ is faster than n^{-2} . In

the $\alpha < 0.5$ regime the argumentation presented above holds for $p = 1$ and no convergence to a constant can be deduced, as [Lemma 5.5](#) does not provide a different rate of decay of $\text{Var}[\mathbb{E}[W_n | \mathcal{Y}_n]]$.

Remark 6.4. It is worth noticing that W_n has a very interesting recursive structure. Denote by $\Psi_{ij}^{(n+1)}$ the value that $\Psi^{(n+1)}$ would take if the randomly chosen pair of species would be tips i and j and by $\Psi_i^{*(n)}$ the value that $\Psi^{*(n)}$ would take if tip i is sampled.

$$\begin{aligned} W_{n+1} &= (n+1) \frac{2}{(n+1)n} \sum_{i=1}^n \sum_{j=i+1}^{n+1} \Psi_{ij}^{(n+1)} \\ &= e^{-2\alpha T_{n+1}} \left(\frac{n-1}{n} W_n + \frac{2}{n} \sum_{i=1}^n \xi_i \sum_{k=1}^{Y^{(i,n)}} J_k^{(i,n)} e^{-2\alpha (T_n + \dots + T_{I_k^{(i,n)}+1})} \right. \\ &\quad \left. + \frac{2}{n} \sum_{i=1}^n \xi_i \sum_{j \neq i}^n \sum_{k=1}^{v^{(i,j,n)}} J_k^{(i,j,n)} e^{-2\alpha (\tau^{(i,j,n)} + \dots + T_{I_k^{(i,j,n)}+1})} \right) \\ &= e^{-2\alpha T_{n+1}} \left(\frac{n-1}{n} W_n + \frac{2}{n} \sum_{i=1}^n \xi_i \Psi_i^{*(n)} + \frac{2}{n} \sum_{i=1}^n \xi_i \sum_{j \neq i}^n \Psi_{ij}^{(n)} \right), \end{aligned}$$

where ξ_i is a binary random variable indicating whether it is the i -th lineage that split (see [Figure 6](#)). It is worth emphasizing that the sum defining W_{n+1} splits according to whether one picks both members of the pair of species splitting in the last speciation event or only one of them.

Obviously the distribution of the vector (ξ_1, \dots, ξ_n) is uniform on the n -element set $\{(1, 0, \dots, 0), \dots, (0, \dots, 0, 1)\}$. In particular note

$$\begin{aligned} \mathbb{E}[W_{n+1} | \mathcal{Y}_n] &= \frac{n+1}{n+1+2\alpha} \left(\frac{n-1}{n} W_n + \frac{2}{n^2} \mathbb{E} \left[\sum_{i=1}^n \Psi_i^{*(n)} | \mathcal{Y}_n \right] + \frac{2}{n^2} \mathbb{E} \left[\sum_{i=1}^n \sum_{j \neq i}^n \Psi_{ij}^{(n)} | \mathcal{Y}_n \right] \right) \\ &= \frac{n+1}{n+1+2\alpha} \left(\frac{n-1}{n} W_n + \frac{2}{n} \mathbb{E} [\Psi^{*(n)} | \mathcal{Y}_n] + \frac{2n(n-1)}{n^2} \mathbb{E} [\Psi^{(n)} | \mathcal{Y}_n] \right) \\ &= \frac{n+1}{n+1+2\alpha} \left(\frac{n-1}{n} W_n + \frac{2}{n} \mathbb{E} [\Psi^{*(n)} | \mathcal{Y}_n] + \frac{2(n-1)}{n^2} W_n \right) \\ &= \frac{n+1}{n+1+2\alpha} \left(\frac{(n-1)(n+2)}{n^2} W_n + \frac{2}{n} \mathbb{E} [\Psi^{*(n)} | \mathcal{Y}_n] \right) \\ &= \frac{(n-1)(n+1)(n+2)}{n^2(n+1+2\alpha)} W_n + \frac{2(n+1)}{n(n+1+2\alpha)} \mathbb{E} [\Psi^{*(n)} | \mathcal{Y}_n]. \end{aligned}$$

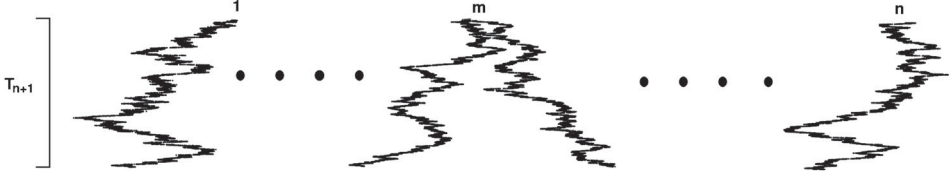


Figure 6. The situation of the process between the n -th and $n+1$ -st split. Node m split so $\xi_m = 1$ and $\xi_i = 0$ for $i \neq m$. The time between the splits is $T_{n+1} \sim \exp(n+1)$.

Furthermore, W_n shows resemblance to a martingale as the coefficient $\frac{(n-1)(n+1)(n+2)}{n^2(n+1+2\alpha)}$ converges to 1 monotonically, depending on α from above or below, while $\frac{2(n+1)}{n(n+1+2\alpha)} \mathbb{E} \left[\Psi^{*(n)} | \mathcal{Y}_n \right] \xrightarrow{\mathbb{P}, L^2} 0$.

Proof of Theorem 4.1, Part 1, $\alpha > 0.5$

We will show convergence in probability of the conditional mean and variance

$$\begin{aligned} \mu_n &:= \sqrt{n} \mathbb{E}[\bar{Y}_n | \mathcal{Y}_n] \xrightarrow{\mathbb{P}} 0 \quad n \rightarrow \infty \\ \sigma_n^2 &:= n \text{Var}[\bar{Y}_n | \mathcal{Y}_n] \xrightarrow{\mathbb{P}} \sigma_\infty^2 \quad n \rightarrow \infty, \end{aligned}$$

for a finite mean and variance random variable σ_∞^2 . Then, due to the conditional normality of \bar{Y}_n this will give the convergence of characteristic functions and the desired weak convergence, i.e.,

$$\mathbb{E}[e^{ix\sqrt{n}\bar{Y}_n}] = \mathbb{E}[e^{i\mu_n x - \sigma_n^2 x^2/2}] \rightarrow \mathbb{E}[e^{-\sigma_\infty^2 x^2/2}].$$

Using [Lemma 6.1](#) and that the Laplace transform of the average coalescent time [[Lemma 3](#) in 12] is

$$\mathbb{E}[e^{-2\alpha\tau_{ij}^{(n)}}] = \frac{2 - (n+1)(2\alpha+1)b_{n,2\alpha}}{(n-1)(2\alpha-1)} = \frac{2}{2\alpha-1}n^{-1} + O(n^{-2\alpha}) \quad (19)$$

we can calculate

$$\begin{aligned} \mathbb{E}[\mu_n] &= \delta \mathbb{E}[e^{-\alpha U^{(n)}}] = \delta b_{n,\alpha} = O(n^{-\alpha}), \\ \text{Var}[\mu_n] &= n \left(\mathbb{E}[\mu_n^2] - (\mathbb{E}[\mu_n])^2 \right) = \delta^2 n \left(\mathbb{E}[e^{-2\alpha U^{(n)}}] - (\mathbb{E}[e^{-\alpha U^{(n)}}])^2 \right) \\ &= \delta^2 n \left(b_{n,2\alpha} - b_{n,\alpha}^2 \right) \\ &= \delta^2 \alpha n b_{n,2\alpha} \sum_{j=1}^n \frac{b_{j,\alpha}^2}{b_{j,2\alpha} j(j+2\alpha)} = O(n^{-2\alpha+1}). \end{aligned}$$

Therefore we have $\mu_n \rightarrow 0$ in L^2 and hence in \mathbb{P} .

Remembering that $\sigma_{c,k}^2$ was assumed constant, equaling σ_c^2 , [Lemma 6.1](#) states that

$$\begin{aligned}\sigma_n^2 &= 1 - ne^{-2\alpha U^{(n)}} + n(1 - n^{-1})\mathbb{E}\left[e^{-2\alpha\tau^{(n)}}|\mathcal{Y}_n\right] \\ &\quad + (\sigma_a^2/(2\alpha))^{-1}\sigma_c^2\mathbb{E}\left[\Psi^{*(n)}|\mathcal{Y}_n\right] + n(1 - n^{-1})(\sigma_a^2/(2\alpha))^{-1}\sigma_c^2\mathbb{E}\left[\Psi^{(n)}|\mathcal{Y}_n\right]\end{aligned}$$

Remembering that p_k was assumed constant, equaling p , we know that

1. $n\mathbb{E}\left[e^{-2\alpha\tau^{(n)}}\right] \rightarrow 2/(2\alpha - 1)$ (Eq. (4) in Lemma 3, Bartoszek and Sagitov^[12]),
2. $n^2\text{Var}\left[\mathbb{E}\left[e^{-2\alpha\tau^{(n)}}|\mathcal{Y}_n\right]\right] \rightarrow 0$ (Lemma 5.1),
3. $\mathbb{E}\left[\Psi^{*(n)}\right] \rightarrow 2p/(2\alpha)$ (Appendix A.2, p. 54 just above Figure A.8., Bartoszek^[10]),
4. $4\cdot\text{Var}\left[\mathbb{E}\left[\Psi^{*(n)}|\mathcal{Y}_n\right]\right] \rightarrow 0$ (Lemma 5.3),
5. $5\cdot n\mathbb{E}\left[\Psi^{(n)}|\mathcal{Y}_n\right] \xrightarrow{\mathbb{P}} W_\infty$ (Lemmata 5.5, 6.2).

Hence, we have $n\mathbb{E}\left[e^{-2\alpha\tau^{(n)}}|\mathcal{Y}_n\right] \xrightarrow{\mathbb{P}, L^2} 2/(2\alpha - 1)$ and $\mathbb{E}\left[\Psi^{*(n)}|\mathcal{Y}_n\right] \xrightarrow{\mathbb{P}, L^2} 2p/(2\alpha)$.

Putting these individual components together we obtain

$$\sigma_n^2 \xrightarrow{\mathbb{P}} 1 + \frac{2}{2\alpha - 1} + \frac{2p\sigma_c^2}{\sigma_a^2} + \frac{\sigma_c^2 W_\infty}{\sigma_a^2/(2\alpha)} =: \sigma_\infty^2.$$

By Lemma 6.2

$$\mathbb{E}\left[\sigma_\infty^2\right] = 1 + \frac{2}{2\alpha - 1} + \frac{2p\sigma_c^2}{\sigma_a^2} + \frac{4p\sigma_c^2}{(2\alpha - 1)\sigma_a^2}.$$

Proof of Part 2, $\alpha = 0.5$

We again show convergence in probability of the conditional mean and variance

$$\begin{aligned}\mu_n &:= \sqrt{(n \ln^{-1} n)}\mathbb{E}\left[\bar{Y}_n|\mathcal{Y}_n\right] \xrightarrow{\mathbb{P}} 0 \quad n \rightarrow \infty \\ \sigma_n^2 &:= (n \ln^{-1} n)\text{Var}\left[\bar{Y}_n|\mathcal{Y}_n\right] \xrightarrow{\mathbb{P}} 2 + 4p\sigma_c^2/\sigma_a^2 \quad n \rightarrow \infty.\end{aligned}$$

As all the steps are the same as in Part 1 we just explicitly write the key part concerning

$$\begin{aligned}\sigma_n^2 &= (\ln^{-1} n)(1 - ne^{-U^{(n)}}) + (n \ln^{-1} n)(1 - n^{-1})\mathbb{E}\left[e^{-\tau^{(n)}}|\mathcal{Y}_n\right] \\ &\quad + (\sigma_c^2/\sigma_a^2)(\ln^{-1} n)\mathbb{E}\left[\Psi^{*(n)}|\mathcal{Y}_n\right] + (n \ln^{-1} n)(1 - n^{-1})(\sigma_c^2/\sigma_a^2)\mathbb{E}\left[\Psi^{(n)}|\mathcal{Y}_n\right]\end{aligned}$$

As before $p_k \equiv p$ and we know that

1. $(n \ln^{-1} n)\mathbb{E}\left[e^{-\tau^{(n)}}\right] \rightarrow 2$ (Eq. (4) in Lemma 3, Bartoszek and Sagitov^[12]),
2. $(n^2 \ln^{-2} n)\text{Var}\left[e^{-\tau^{(n)}}|\mathcal{Y}_n\right] \rightarrow 0$ (Lemma 5.1),

3. $(\ln^{-1}n)E[\Psi^{*(n)}] \rightarrow 0$ (Appendix A.2, p. 54 just above Figure A.8., Bartoszek^[10]),
4. $(\ln^{-2}n)\text{Var}\left[E[\Psi^{*(n)}|\mathcal{Y}_n]\right] \rightarrow 0$ (Lemma 5.3),
5. $(n \ln^{-1}n)E[\Psi^{(n)}] \rightarrow 4p$ (Eq. 20), $(n^2 \ln^{-2}n)\text{Var}[E[\Psi^{(n)}|\mathcal{Y}_n]] \rightarrow 0$ (Lemma 5.5).

Putting these individual components together we obtain the L^2 convergence and hence

$$\sigma_n^2 \xrightarrow{\mathbb{P}} 2 + 4p\sigma_c^2/\sigma_a^2.$$

Proof of Part 3, $0 < \alpha < 0.5$

We notice that the martingale (with respect to \mathcal{F}_n) $H_n = (n+1)e^{(\alpha-1)U^{(n)}}\bar{Y}_n$ has uniformly bounded second moments. Namely by Lemma 6.1, a modification of Lemma 5.8, Cauchy-Schwarz, bounding $E[(\Psi^{*(n)})^2]$ by a constant and remembering that in this case σ_c^2 is constant

$$\begin{aligned} E[H_n^2] &= (n+1)^2 E\left[e^{2(\alpha-1)U^{(n)}} E[\bar{Y}_n^2|\mathcal{Y}_n]\right] \\ &\leq Cn^2 \left(n^{-1} E[e^{-2(1-\alpha)U^{(n)}}] + E[e^{-2(1-\alpha)U^{(n)}-2\alpha\tau^{(n)}}] \right. \\ &\quad \left. + n^{-1} (\sigma_a^2/(2\alpha))^{-1} E[e^{-2(1-\alpha)U^{(n)}} \Psi^{*(n)}] \right. \\ &\quad \left. + (\sigma_a^2/(2\alpha))^{-1} E[e^{-2(1-\alpha)U^{(n)}} \Psi^{(n)}] \right) \\ &\leq Cn^2 (n^{-1}n^{-2(1-\alpha)} + n^{-2(1-\alpha)}n^{-2\alpha} + n^{-1}n^{-2(1-\alpha)} + n^{-2}) \\ &\leq C(n^{-1+2\alpha} + 1 + n^{-1+2\alpha} + 1) \rightarrow C < \infty. \end{aligned}$$

To deal with $E[e^{-2(1-\alpha)U^{(n)}} \Psi^{(n)}]$ one slightly modifies the proof of Lemma 5.8. Namely instead of considering the random variable $\bar{\phi}_i$, consider

$$\tilde{Z}_i \tilde{\mathbf{I}}_i \exp(-(2(T_n + \dots + T_{i+1}) + 2(1-\alpha)(T_i + \dots + T_1)))$$

and then doing similar calculations one will obtain a decay of order n^{-2} . It is also worth pointing out that using Bartoszek and Sagitov's^[12] Lemma 3 for a more detailed consideration of $E[e^{-2(1-\alpha)U^{(n)}-2\alpha\tau^{(n)}}]$, would not result in a different rate of decay, than what Cauchy-Schwarz provides, i.e., n^{-2} . Hence, $\sup_n E[H_n^2] < \infty$ and by the martingale convergence theorem, $H_n \rightarrow H_\infty$ a.s. and in L^2 . We obtain $n^\alpha \bar{Y}_n \rightarrow V^{(\alpha-1)} H_\infty$ a.s. and in L^2 , where $V^{(x)}$ is the a.s. and L^2 limit of $V_n^{(x)} = b_{n,x}^{-1} e^{-xU^{(n)}}$ (cf. Lemma 9 of Bartoszek and Sagitov^[12]). Notice that for the convergence to hold in the $0 < \alpha < 0.5$ regime, it is not required that $\sigma_{c,k}^2$ is constant, only bounded. We may also obtain directly the first two moments of $n^\alpha \bar{Y}_n$ (however, for these formulae to hold, $\sigma_{c,k}^2$ has to be constant)

$$\begin{aligned}
n^\alpha \mathbb{E}[\bar{Y}_n] &= \delta n^\alpha b_{n,\alpha} \rightarrow \delta \Gamma(1 + \alpha) \\
n^{2\alpha} \mathbb{E}[\bar{Y}_n^2] &= n^{2\alpha-1} - (1 - \delta^2) n^{2\alpha} b_{n,2\alpha} + n^{2\alpha} (1 - n^{-1}) \mathbb{E}[e^{-2\alpha\tau^{(n)}}] \\
&\quad + n^{2\alpha-1} \sigma_c^2 (\sigma_a^2 / (2\alpha))^{-1} \mathbb{E}[\Psi^{*(n)}] + n^{2\alpha} \sigma_c^2 (\sigma_a^2 / (2\alpha))^{-1} \mathbb{E}[\Psi^{(n)}] \\
&\rightarrow -(1 - \delta^2) \Gamma(2\alpha + 1) + \frac{1 + 2\alpha}{1 - 2\alpha} \Gamma(1 + 2\alpha) \left(1 + 2p\sigma_c^2 (\sigma_a^2 / (2\alpha))^{-1}\right).
\end{aligned}$$

Proof of [Theorem 4.6](#), Part 1, $\alpha > 0.5$

From the proof of Part 1, [Theorem 4.1](#) we know that $\mu_n \rightarrow 0$ in probability. Then, by the assumptions of the theorem on the expectations

$$\begin{aligned}
\mathbb{E}[\sigma_n^2] &= n(n^{-1} - \mathbb{E}[e^{-2\alpha U^{(n)}}]) + (1 - n^{-1}) \mathbb{E}[e^{-2\alpha\tau^{(n)}}] \\
&\quad + n^{-1} (\sigma_a^2 / (2\alpha))^{-1} \mathbb{E} \left[\sum_{k=1}^{Y^{(n)}} \sigma_{c, I_k^{(n)}}^2 J_k e^{-2\alpha \left(T_n + \dots + T_{I_k^{(n)}+1} \right)} \right] \\
&\quad + (1 - n^{-1}) (\sigma_a^2 / (2\alpha))^{-1} \mathbb{E} \left[\sum_{k=1}^{v^{(n)}} \sigma_{c, \tilde{I}_k^{(n)}}^2 \tilde{J}_k e^{-2\alpha \left(\tau^{(n)} + \dots + T_{\tilde{I}_k^{(n)}+1} \right)} \right] \Bigg) \\
&\rightarrow \frac{2\alpha + 1}{2\alpha - 1} + (\sigma_Y^2 + \sigma_v^2) / (\sigma_a^2 / (2\alpha)).
\end{aligned}$$

Furthermore, [Lemma 5.3](#) (the sequence $\sigma_{c,k}^4 p_k$ is bounded by assumption) and [Corollary 5.7](#) ($\sigma_{c,k}^4 p_k (1 - p_k) \rightarrow 0$ with density 1 by assumption) imply

$$\begin{aligned}
\text{Var}[\sigma_n^2] &= n^2 \text{Var}[\text{Var}[\bar{Y}_n | \mathcal{Y}_n]] = n^{-2} \text{Var}[\text{Var}[Y_1 + \dots + Y_n | \mathcal{Y}_n]] \\
&\leq C(n^2 \text{Var}[e^{-2\alpha U^{(n)}}] + (n - 1)^2 \text{Var}[\mathbb{E}[e^{-2\alpha\tau^{(n)}} | \mathcal{Y}_n]]) \\
&\quad + (\sigma_a^2 / (2\alpha))^{-2} \text{Var} \left[\mathbb{E} \left[\sum_{k=1}^{Y^{(n)}} \sigma_{c, I_k^{(n)}}^2 J_k e^{-2\alpha \left(T_n + \dots + T_{I_k^{(n)}+1} \right)} \middle| \mathcal{Y}_n \right] \right] \\
&\quad + (n - 1)^2 (\sigma_a^2 / (2\alpha))^{-2} \text{Var} \left[\mathbb{E} \left[\sum_{k=1}^{v^{(n)}} \sigma_{c, \tilde{I}_k^{(n)}}^2 \tilde{J}_k e^{-2\alpha \left(\tau^{(n)} + \dots + T_{\tilde{I}_k^{(n)}+1} \right)} \middle| \mathcal{Y}_n \right] \right] \Bigg) \\
&\rightarrow 0.
\end{aligned}$$

Therefore we obtain that $\sigma_n^2 \rightarrow (2\alpha + 1)/(2\alpha - 1) + (\sigma_Y^2 + \sigma_v^2) / (\sigma_a^2 / (2\alpha))$ in probability and by convergence of characteristic functions

$$\mathbb{E}[e^{ix\sqrt{n} \cdot \bar{Y}_n}] = \mathbb{E}[e^{i\mu_n x - \sigma_n^2 x^2 / 2}] \rightarrow \mathbb{E}\left[e^{-\left((2\alpha+1)/(2\alpha-1) + (\sigma_Y^2 + \sigma_v^2) / (\sigma_a^2 / (2\alpha))\right) x^2 / 2}\right]$$

we obtain the asymptotic normality. Notice that on the other hand using the Cauchy–Schwarz inequality, Lemmata 5.8 and 5.9 we obtain

$$\begin{aligned} \text{Var}[\sigma_n^2] &\geq n^2 \text{Var}[e^{-2\alpha U^{(n)}}] \\ &+ (n-1)^2 (\sigma_a^2 / (2\alpha))^{-2} \text{Var} \left[\mathbb{E} \left[\sum_{k=1}^{v^{(n)}} \sigma_{c, \tilde{I}_k}^2 \tilde{J}_k e^{-2\alpha (\tau^{(n)} + \dots + T_{\tilde{I}_k^{(n)}+1})} \middle| \mathcal{Y}_n \right] \right] + b_n(\alpha), \end{aligned}$$

where $b_n(\alpha)$ is some sequence decaying to 0 with a rate depending on α . Assume now that $p_k(1-p_k)\sigma_{c,k}^4$ does not converge 0 with density 1. Then, by [Corollary 5.7](#) we will have

$$\limsup_{n \rightarrow \infty} \text{Var} \left[\mathbb{E} \left[\sum_{k=1}^{v^{(n)}} \sigma_{c, \tilde{I}_k}^2 \tilde{J}_k e^{-2\alpha (\tau^{(n)} + \dots + T_{\tilde{I}_k^{(n)}+1})} \middle| \mathcal{Y}_n \right] \right] > 0$$

implying $\limsup_{n \rightarrow \infty} \text{Var}[\sigma_n^2] > 0$ and hence, the convergence of the characteristic functions as above does not hold. Therefore, the convergence $p_k(1-p_k)\sigma_{c,k}^4 \rightarrow 0$ with density 1 is a necessary assumption for the asymptotic normality.

Proof of Part 2, $\alpha = 0.5$ This is proved in the same way as Part 1. Due to the boundedness of $\sigma_{c,k}^4 p_k$ (implying $\sigma_{c,k}^2 p_k$ is bounded)

$$(\ln^{-1} n) \mathbb{E} \left[\sum_{k=1}^{\Upsilon^{(n)}} \sigma_{c, I_k}^2 J_k e^{-\left(T_n + \dots + T_{I_k^{(n)}+1}\right)} \right] \rightarrow 0$$

and as before

$$(\ln^{-2} n) \text{Var} \left[\mathbb{E} \left[\sum_{k=1}^{\Upsilon^{(n)}} \sigma_{c, I_k}^2 J_k e^{-\left(T_n + \dots + T_{I_k^{(n)}+1}\right)} \middle| \mathcal{Y}_n \right] \right] \rightarrow 0.$$

Then, due to the assumption on the expectation we have that $\sigma_n^2 \rightarrow 2 + \sigma_v^2 / \sigma_a^2$ as due to the boundedness of $\sigma_{c,k}^4 p_k$ by [Lemma 5.5](#)

$$(n^2 \ln^{-2} n) \text{Var} \left[\mathbb{E} \left[\sum_{k=1}^{v^{(n)}} \sigma_{c, \tilde{I}_k}^2 \tilde{J}_k e^{-\left(\tau^{(n)} + \dots + T_{\tilde{I}_k^{(n)}+1}\right)} \middle| \mathcal{Y}_n \right] \right] \rightarrow 0.$$

Remark 6.5. The boundedness assumption for $\sigma_{c,k}^4 p_k$ ($\alpha \geq 0.5$), together with the convergence to 0 with density 1 of $\sigma_{c,k}^4 p_k(1-p_k)$ (for $\alpha > 0.5$) allows for controlling $\text{Var}[\sigma_n^2] \rightarrow 0$. The boundedness assumption would still allow for showing that $\mathbb{E}[\sigma_n^2]$ is bounded but would not suffice for convergence. For example, consider $p_k \equiv 1$ constant and $\sigma_{c,k}^2 = 1$ for k odd and 2 for k even. Then, for $\alpha > 0.5$ we would have in probability

$$\liminf_{n \rightarrow \infty} \sigma_n^2 = 1 + \frac{2}{2\alpha - 1} + \frac{2}{\sigma_a^2} + \frac{4}{(2\alpha - 1)\sigma_a^2} \quad \text{and}$$

$$\limsup_{n \rightarrow \infty} \sigma_n^2 = 1 + \frac{2}{2\alpha - 1} + \frac{4}{\sigma_a^2} + \frac{8}{(2\alpha - 1)\sigma_a^2}.$$

It does seem that for $\alpha > 0.5$ the assumption that $\sigma_{c,k}^4 p_k$ is bounded could be relaxed. However, it would essentially require that one explicitly assumes that the sequences $\{\sigma_{c,k}^2\}, \{p_k\}$ are such that the sequences of the variances of the conditional expectations converge to 0 (as was needed for the sequences of the expectations).

Example 6.6. Assume that $\sigma_{c,k}^4 p_k \rightarrow 0$ with density 1. Then, by the same ergodic argument as in Corollary 5.4 and following the steps in the proof of Thm. 4.6 we obtain that for $\alpha > 0.5$ we have

$$\mathbb{E} \left[\sum_{k=1}^{\Upsilon^{(n)}} \sigma_{c, I_k^{(n)}}^2 J_k e^{-2\alpha \left(T_n + \dots + T_{I_k^{(n)}+1} \right)} \right] \rightarrow 0$$

$$n \mathbb{E} \left[\sum_{k=1}^{v^{(n)}} \sigma_{c, \tilde{I}_k^{(n)}}^2 \tilde{J}_k e^{-2\alpha \left(\tau^{(n)} + \dots + T_{\tilde{I}_k^{(n)}+1} \right)} \right] \rightarrow 0$$

resulting in $\sigma_n^2 \xrightarrow{\mathbb{P}} (2\alpha + 1)/(2\alpha - 1)$ and for $\alpha = 0.5$ we have also

$$(n \ln^{-1} n) \mathbb{E} \left[\sum_{k=1}^{v^{(n)}} \sigma_{c, \tilde{I}_k^{(n)}}^2 \tilde{J}_k e^{-\left(\tau^{(n)} + \dots + T_{\tilde{I}_k^{(n)}+1} \right)} \right] \rightarrow 0$$

resulting in $\sigma_n^2 \xrightarrow{\mathbb{P}} 2$. Hence, to recover^[12]s CLTs one needs the stronger assumption of $\sigma_{c,k}^4 p_k \rightarrow 0$ with density 1.

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