Critical threshold for ancestral reconstruction by maximum parsimony on general phylogenies *

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August 9, 2017

Abstract

We consider the problem of inferring an ancestral state from observations at the leaves of a tree, assuming the state evolves along the tree according to a two-state symmetric Markov process. We establish a general branching rate condition under which maximum parsimony, a common reconstruction method requiring only the knowledge of the tree, succeeds better than random guessing uniformly in the depth of the tree. We thereby generalize previous results of [GS10, ZSYL10]. Our results apply to both deterministic and i.i.d. edge weights.

*Keywords: Markov model on a tree, reconstruction problem, branching number, parsimony principle, application to phylogenetics.

†Department of Mathematics, UW–Madison. Work supported by NSF grants DMS-1248176, DMS-1149312 (CAREER) and DMS-1614242.

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1 Introduction

Ancestral reconstruction In biology, the inferred evolutionary history of organisms is depicted by a phylogenetic tree, that is, a rooted tree whose branchings indicate past speciation events with the leaves representing living species [Fel04]. The evolution of features, such as the nucleotide at a given position in the genome of a species, the presence or absence of a protein or the number of horns in a lizard, is commonly assumed to follow Markovian dynamics along the tree [Ste16]. That is, on each edge, the state of the feature changes according to a Markov process; at bifurcations, two independent copies of the feature evolve along the outgoing edges starting from the state at the branching point.

Here we consider the problem of inferring an ancestral state from observations of a feature at the leaves of a known phylogenetic tree. We refer to this problem, which has important applications in biology [Tho04, Lib07, Mos04, DMR11], as the ancestral reconstruction problem. Many rigorous results have been obtained in previous work; see, e.g., [KS66, BRZ95, Iof96, TS97, Mos98, EKPS00, Mos01, MP03, BCMR06, Sly09, GS10, ZSYL10, BST10, BVVW11, Sly11, FRa, FRb] for a partial list. Typically, one seeks an estimator of the root state which is strictly superior to random guessing—uniformly in the depth of the tree—under a uniform prior on the root [Mos01]. Whether such an estimator exists has been shown to depend on a trade-off between the mixing rate of the Markov process and the growth rate of the tree. In some cases, for instance in two-state symmetric Markov chains on binary trees [KS66, Iof96] as well as on more general trees [EKPS00], sharp thresholds have been established. We focus on that special case here.

The threshold of maximum parsimony Maximum parsimony is an ancestral reconstruction method with a long history in evolutionary biology. See e.g. [Fel04, Ste16]. Its underlying principle is simple and intuitive: it calls for assigning a state to each internal vertex in such a way as to minimize the total number of changes along the edges; the resulting state at the root (possibly not unique) is the desired reconstructed state. An advantage of maximum parsimony, which accounts partly for its use in practice, is that it only requires knowledge of the tree—not of the substitution probabilities along the edges. The latter can be difficult to estimate accurately from data. In fact maximum parsimony is equivalent to maximum likelihood under those circumstances [TS97]. Another root state estimator with that property is recursive majority, studied in [Mos98, Mos04].

From its very definition, one might expect maximum parsimony to perform well when the probabilities of substitution along the edges are “sufficiently small.”
This statement was confirmed rigorously for the two-state symmetric model on complete binary trees with constant mutation probability in [ZSYL10] (as first conjectured in [Ste89]). Below a critical probability, maximum parsimony does indeed beat random guessing. A related result was obtained in [GS10] under a common random tree model known as the Yule tree. Here we substantially generalize both of these results. We give a general condition on the branching rate under which maximum parsimony succeeds. Our condition is related to the branching number, which plays an important in many processes on trees. See e.g. [LP16].

**Definitions** In order to state our results formally, we begin with some definitions. Let $T = (V, E)$ be an infinite complete binary tree rooted at $\rho$. That is, all vertices of $T$ have exactly two children; in particular, $T$ has no leaf. Every edge $e \in E$ is assigned a weight $\theta_e \in [0, 1]$. If $e = (x, y)$ where $x$ is the parent of $y$, we also write $\theta_y = \theta_e$. We use the notation $x \leq y$ to indicate that $x$ is an ancestor of $y$ and we write $x < y$ for $x \leq y$ and $x \neq y$. We also let $s(x)$ be the sibling of $x \neq \rho$.

Under the Cavender-Farris (CF) model [Cav78, Far73] over $T$ and $\theta = (\theta_y)_{y \in V}$, also known as Neyman 2-state model [Ney71], we associate to each vertex $x \in V$ a state $\sigma_x \in \{0, 1\}$ as follows. The state at the root, $\sigma_\rho$, is picked uniformly at random in $\{0, 1\}$. Recursively, if $y$ has parent $x$, state $\sigma_y$ is equal to $\sigma_x$ with probability $\theta_y$, otherwise it is picked uniformly at random in $\{0, 1\}$. We let
\[
P_y = P_{T, \theta}[\sigma_x \neq \sigma_y] = \frac{1 - \theta_y}{2},
\]
be the probability of a substitution on edge $e = (x, y)$. Here $P_{T, \theta}$ stands for the probability operator under the CF model over $T$ and $\theta$. The CF model is equivalent to the Fortuin-Kastelyn random cluster representation of the ferromagnetic Ising model on $T$ with a free boundary. See e.g. [EKPS00] and references therein.

Informally, a root state estimator is a map returning a (possibly randomized) guess for the state of the root, based on the knowledge of the states on an observed cutset.

**Definition 1 (Cutset).** A cutset is a minimal, finite set of vertices $\pi \subseteq V$ such that all infinite self-avoiding paths starting at $\rho$ must visit $\pi$. We let $\mathcal{C}(T)$ be the collection of all cutsets of $T$. We denote by $T^\pi = (V^\pi, E^\pi)$ the finite tree obtained from $T$ after removing all descendants of the vertices in $\pi$.

As mentioned above, our focus in this work is on a root state estimator known in phylogenetics as maximum parsimony. The parsimony principle dictates that one
assigns to each vertex $x$ (ancestor to the observed cutset $\pi$) a state $\hat{\sigma}_x$ such that the overall number of changes along the edges of $T^{\pi}$, namely,

$$\sum_{(x,y) \in E^{\pi}} 1\{\hat{\sigma}_x \neq \hat{\sigma}_y\},$$

is minimized, where we let by default $\hat{\sigma}_z = \sigma_z$ for all $z \in \pi$. In case both 0 and 1 can be obtained in this way as root state, a uniformly random value in $\{0, 1\}$ is returned. We let $\text{RA}^{\pi}_{T, \theta}$ be the reconstruction accuracy of maximum parsimony, i.e. the probability that it correctly reconstructs the root state.

**Main result: deterministic weights** In our main result, we give conditions under which the reconstruction accuracy of maximum parsimony is uniformly bounded away from $1/2$.

**Theorem 1** (Reconstruction accuracy of parsimony: deterministic weights). Let $T = (V, E)$ be an infinite complete binary tree with edge weights $\theta = (\theta_z)_{z \in V}$ satisfying

$$\inf_{z \in V} \theta_z > 0,$$  \hspace{1cm} (1)

and

$$\sup \left\{ \kappa > 0 : \inf_{\pi \in \mathcal{E}(T)} \sum_{x \in \pi} \prod_{\rho \neq z \leq x} \kappa^{-1} \theta_z > 0 \right\} > \frac{3}{2}. \hspace{1cm} (2)$$

Then the reconstruction accuracy of maximum parsimony on $T$ is bounded away from $1/2$, that is,

$$\inf_{\pi \in \mathcal{E}(T)} \text{RA}^{\pi}_{T, \theta} > \frac{1}{2}.$$

Although $T$ is an infinite complete binary tree, since we allow arbitrary cutsets, our results in fact apply implicitly to general finite trees. Condition (2) is closely related to the *branching number*, a generalized notion of branching rate which plays a key role in the analysis of many stochastic processes on trees and tree-like graphs. See e.g. [Per99, LP16] for a survey; see also [Lyo89, Lyo90]. The following example provides some intuition in a special case.

**Example 1** (Fixed edge weights). As a simple illustration, observe that, when all weights are equal to $\theta_* \in (0, 1]$, the supremum in (2) is attained for $\kappa = 2\theta_*$. Indeed, the sum in (2) when $\kappa = 2\theta_*$ simplifies to

$$\sum_{x \in \pi} \prod_{\rho \neq z \leq x} (2\theta_*)^{-1} \theta_z = \sum_{x \in \pi} \prod_{\rho \neq z \leq x} \frac{1}{2} = 1 > 0$$
for any cutset \( \pi \), where the equality can be proved by induction on the graph distance from the root to the furthest vertex in \( \pi \). On the other hand, letting \( \pi_n \) be the cutset of all vertices at graph distance \( n \) from \( \rho \), for any \( \varepsilon > 0 \) it holds that

\[
\sum_{x \in \pi_n} \prod_{\rho \neq z \leq x} (2 + \varepsilon)^{-1}\theta_z = (2 + \varepsilon)^{-n} \cdot 2^n \to 0,
\]
as \( n \to +\infty \). Hence, in this case, condition (2) reduces to \( 2\theta_* > 3/2 \), that is, \( \theta_* > 3/4 \). In terms of substitution probability, this is \( p_* = \frac{1-\theta_*}{2} < 1/8 \).

The argument in the example above leads to the following corollary.

**Corollary 1** (All substitution probabilities below the threshold). Let the substitution probabilities \( (p_z)_{z \in V} \) satisfy \( p_z \in [0, p_*] \) for all \( z \in V \), for some \( p_* < 1/8 \). Then the reconstruction accuracy of maximum parsimony on \( T \) is bounded away from 1/2.

In general, Theorem 1 cannot be improved in the following sense. It was shown in [ZSYL10, Theorem 4.1] that when \( p_z = p_* > 1/8 \), that is, \( \theta_z = 1 - 2p_z = \theta_* < 3/4 \) for all \( z \) then

\[
\inf_n RA_{T,\theta}^{\pi_n} = \frac{1}{2},
\]
where \( \pi_n \) is defined in Example 1. On the other hand, it is not known whether the reconstruction accuracy necessarily converges to 1/2 if (2) is not satisfied. We leave this as an open problem.

Zhang et al. [ZSYL10] also established the special case of Theorem 1 when \( p_z = p_* < 1/8 \) for all \( z \) and \( \pi = \pi_n \). Their proof proceeds through a careful analysis of the limit of a recurrence for \( RA_{T,\theta}^{\pi_n} \) first derived in [Ste89]. Our more general result follows from a softer argument which relies on the instability of a fixed point of this recurrence corresponding to asymptotic reconstruction accuracy 1/2. A more detailed proof sketch is given in Section 2 following some preliminaries. We note that our proof method may be of more general interest, e.g., to extend the results beyond the two-state case where the higher dimensionality of the system may complicate significantly the derivation of an explicit limit even when edge weights are constant.

**Main result: i.i.d. weights** We also obtain a related result in the case of edge weights that are i.i.d. No lower bound on the weights is needed in this case (and, hence, it does not immediately follow from Theorem 1).
Theorem 2 (Reconstruction accuracy of parsimony: i.i.d. weights). Let $\mathcal{T} = (\mathcal{V}, \mathcal{E})$ be an infinite complete binary tree with edge weights $\theta = (\theta_z)_{z \in \mathcal{V}}$ drawn i.i.d. from a distribution $\Theta$ over $(0, 1]$. Let $\mu$ be the mean of $\Theta$ and assume that $\mu > 3/4$. Then, for any $\delta > 0$, there is $\varepsilon > 0$ such that

$$\inf_{\pi \in \mathcal{C}(\mathcal{T})} RA_{\mathcal{T}, \theta}^\pi > \frac{1}{2}(1 + \varepsilon),$$

with probability at least $1 - \delta$.

The previous theorem covers in particular the case of the pure birth process, or Yule tree, which is a popular random model of phylogenetic trees. See e.g. [SS03, Ste16]. In that case, $\theta_z = e^{-2T_z}$, where $T_z$ is an exponential with rate $\lambda$. To derive the corresponding threshold, we note that

$$\mu = \mathbb{E}[\theta_z] = \int_0^{\infty} e^{-2t} \lambda e^{-\lambda t} \, dt = \frac{\lambda}{\lambda + 2}.$$

Then

$$\mu > \frac{3}{4} \iff \lambda > 6,$$

which is consistent with the results of [GS10].

2 Preliminaries

Our proofs are based on a recurrence for the reconstruction accuracy. After reviewing this recurrence, we give a proof sketch of Theorem 1.

2.1 Fitch method

The maximum parsimony solution can be computed efficiently by dynamic programming, which in this context is referred to as the Fitch method.

Definition 2 (Fitch method [Fit71, Har73]). The Fitch method recursively constructs a set $\hat{S}_z$ of possible states for each vertex $z \in \mathcal{V}_\pi$, starting from $\pi$, as follows.

(a) If $z \in \pi$, then $\hat{S}_z^\pi = \{\sigma_z\}$. 

5
(b) If \( z \notin \pi \) and has children \( x \) and \( y \), then

\[
\hat{S}_z^\pi = \begin{cases} 
\hat{S}_x^\pi \cap \hat{S}_y^\pi, & \text{if } \hat{S}_x^\pi \cap \hat{S}_y^\pi \neq \emptyset \\
\hat{S}_x^\pi \cup \hat{S}_y^\pi, & \text{o.w.}
\end{cases}
\]

The method returns the maximum parsimony estimator \( \hat{\sigma}_\rho \) which is equal to the unique state in \( \hat{S}_\rho^\pi \) if \( |\hat{S}_\rho^\pi| = 1 \), and otherwise returns a uniformly random value in \( \{0, 1\} \).

What is described above is the bottom-up phase of the Fitch method. A top-down phase, which we will not require here, then assigns a state to each vertex in \( V^\pi \) consistent with a maximum parsimony solution. See e.g. [SS03]. Let \( \pi \) be an arbitrary cutset on \( T \) with states \( \sigma_u, u \in \pi \), and let \( \hat{S}_z, z \in V^\pi \), be the corresponding reconstructed sets under the Fitch method. We define

\[
\alpha_z^\pi = P_{T,\theta} \left[ \hat{S}_z^\pi = \{\sigma_z\} \right],
\]

\[
\beta_z^\pi = P_{T,\theta} \left[ \hat{S}_z^\pi = \{1 - \sigma_z\} \right].
\]

Under our randomization rule, the reconstruction accuracy of maximum parsimony is given by

\[
RA_{T,\theta}^\pi = P_{T,\theta} \left[ \hat{S}_\rho^\pi = \{\sigma_\rho\} \right] + \frac{1}{2} P_{T,\theta} \left[ \hat{S}_\rho^\pi = \{0, 1\} \right]
\]

\[
= \alpha_\rho^\pi + \frac{1}{2}(1 - \alpha_\rho^\pi - \beta_\rho^\pi)
\]

\[
= \frac{1}{2} + \frac{1}{2}(\alpha_\rho^\pi - \beta_\rho^\pi). \quad (3)
\]

2.2 Proof sketch

Fix \( \theta \) satisfying the assumptions of Theorem 1 and fix a cutset \( \pi \). To analyze \((\alpha_z^\pi, \beta_z^\pi)\), it is natural to take advantage of the recursive nature of \( T \) [Ste89, SS07, ZSYL10]. Let \( x \) and \( y \) be the children of \( z \). The event \( \hat{S}_z^\pi = \{\sigma_z\} \) occurs when either (a) \( \hat{S}_x^\pi = \{\sigma_z\} \) and \( \hat{S}_y^\pi = \{\sigma_z\} \), or (b) \( \hat{S}_x^\pi = \{\sigma_z\} \) and \( \hat{S}_y^\pi = \{0, 1\} \) or vice versa. By the Markov property of the CF model, the random variables \( \hat{S}_x^\pi \) and \( \hat{S}_y^\pi \), which are functions only of the states of \( \pi \) under \( x \) and \( y \) respectively, are conditionally independent given \( \sigma_z \). Hence, letting \( q_u = 1 - p_u \) for \( u = x, y \) and
taking into account the possibility of a mutation along the edges \((z, x)\) and \((z, y)\), it follows that

\[
\alpha_z^\pi = (q_x \alpha_x^\pi + p_x \beta_x^\pi)(q_y \alpha_y^\pi + p_y \beta_y^\pi) \\
+ (q_x \alpha_x^\pi + p_x \beta_x^\pi)(1 - \alpha_y^\pi - \beta_y^\pi) \\
+ (1 - \alpha_x^\pi - \beta_x^\pi)(q_y \alpha_y^\pi + p_y \beta_y^\pi),
\]

(4)

where the first and second lines on the r.h.s. correspond respectively to cases (a) and (b) above. Similarly,

\[
\beta_z^\pi = (p_x \alpha_x^\pi + q_x \beta_x^\pi)(p_y \alpha_y^\pi + q_y \beta_y^\pi) \\
+ (p_x \alpha_x^\pi + q_x \beta_x^\pi)(1 - \alpha_y^\pi - \beta_y^\pi) \\
+ (1 - \alpha_x^\pi - \beta_x^\pi)(p_y \alpha_y^\pi + q_y \beta_y^\pi).
\]

(5)

This recurrence was first derived in [Ste89, Lemma 7.20]. See also [Mad95].

In the case that \(p_u = p\) for all \(u\), a fixed point analysis was performed in [Ste89, Theorem 7.22]. It was found that, if \(p \geq 1/8\), there is a single fixed point \((1/3, 1/3)\) which corresponds informally to “having no information about the root.” While if \(p < 1/8\), there is an additional fixed point \((\alpha_p^\infty, \beta_p^\infty)\) with \(\alpha_p^\infty > \beta_p^\infty\). Convergence to \((1/3, 1/3)\) in the first case and \((\alpha_p^\infty, \beta_p^\infty)\) in the second case was established rigorously in [ZSYL10]. One step in [ZSYL10] involved the derivation of a new recurrence in terms of the quantities \(\alpha_n^\pi z - \beta_n^\pi z\) and \(1 - (\alpha_n^\pi z + \beta_n^\pi z)\), which facilitates the analysis of the limit in the fixed edge weight case.

Going back to general trees, as our starting point we further modify the recurrence of [ZSYL10]. For all \(z \in V\), we define

\[
d_z^\pi = \alpha_z^\pi - \beta_z^\pi, \tag{6}
\]

\[
u_z^\pi = 3(\alpha_z^\pi + \beta_z^\pi) - 2. \tag{7}
\]

We show in Proposition 1 below that \((d_z^\pi, u_z^\pi)\) satisfies the following recurrence

\[
d_z^\pi = \left(\frac{4 - u_y^\pi}{6}\right) \theta_x d_x^\pi + \left(\frac{4 - u_x^\pi}{6}\right) \theta_y d_y^\pi, \tag{8}
\]

\[
u_z^\pi = \frac{3}{2} \theta_x \theta_y d_x^\pi d_y^\pi - \frac{1}{2} u_x^\pi u_y^\pi, \tag{9}
\]

for \(z \in V^\pi - \pi\) with children \(x, y\), as well as the inequalities \(0 \leq d_z^\pi \leq 1\) and \(-1/2 \leq u_z^\pi \leq 1\) for all \(z \in V^\pi\) and the boundary conditions \(d_x^\pi = u_x^\pi = 1\) for
all $z \in \pi$. Our choice of parametrization is motivated in part by the fact that the “no information” fixed point is now at $(0, 0)$ and that $|d^\pi_z|, |u^\pi_z| \leq 1$. At a high level we show that, under the branching rate condition (2), the fixed point $(0, 0)$ is “unstable” and that $d^\pi_z$ in particular stays bounded away from 0. That in terms implies a lower bound on the reconstruction accuracy as, by (3), we have

$$RA^\pi_{T, \theta} = \frac{1}{2} + \frac{1}{2}d^\pi.$$

The link between stability and the weighted branching rate in (2) is easily seen from (8). First, when all weights are equal to $\theta^*_{x}$ and $\pi = \pi_n$, we get by symmetry that close to $(0, 0)$ to the first order

$$d^\pi_z \approx \frac{4}{3}\theta^*_x d^\pi_x.$$

Hence, in that case, the solution can be expected to grow when $\frac{4}{3}\theta^*_x > 1$, corresponding to the condition derived in Example 1. More generally, we use (8) to relate the $d$-value at the root to the $d$-values on a cutset (see Lemma 1). To deal with the nonlinear nature of (8) and (9), we control the $u$-values thanks to the quadratic form of (9) which implies a quick decay towards 0 (see Lemma 3).

2.3 Recurrence

Before proceeding to the proof of our main results, we first establish a basic recurrence which follows from the work of [ZSYL10]. We give a short proof for completeness.

Proposition 1 (Recurrence and basic properties). The following hold:

- [Boundary conditions] For all $z \in \pi$,
  
  $$d^\pi_z = 1,$$
  $$u^\pi_z = 1.$$  

- [Recurrence] For all $z \in \mathcal{V}^\pi - \pi$, if $x, y$ are the children of $z$,
  
  $$d^\pi_z = \left(\frac{4 - u^\pi_y}{6}\right) \theta_x d^\pi_x + \left(\frac{4 - u^\pi_x}{6}\right) \theta_y d^\pi_y,$$
  $$u^\pi_z = \frac{3}{2} \theta_x \theta_y d^\pi_x d^\pi_y - \frac{1}{2}u^\pi_x u^\pi_y.$$  

8
For all $z \in \mathcal{V}_\pi$,  

\begin{align*}
0 &\leq d^\pi_z \leq 1, \\
-\frac{1}{2} &\leq u^\pi_z \leq 1.
\end{align*}

**Proof.** We start with the boundary conditions. By Definition 2(a) and the definitions of $\alpha^\pi_z$ and $\beta^\pi_z$, we have for all $z \in \pi$  

\begin{align*}
\alpha^\pi_z &= \mathbb{P}_{T,\theta} [\hat{S}^\pi_z = \{\sigma_z\}] = 1, \\
\beta^\pi_z &= \mathbb{P}_{T,\theta} [\hat{S}^\pi_z = \{1 - \sigma_z\}] = 0.
\end{align*}

So $u^\pi_z = 3(\alpha^\pi_z + \beta^\pi_z) - 2 = 1$ and $d^\pi_z = \alpha^\pi_z - \beta^\pi_z = 1$, which proves (11) and (10).

Let $z \in \mathcal{V}_\pi - \pi$ with children $x, y$. We define $\Sigma_z = \alpha^\pi_z + \beta^\pi_z$ and $\Delta_z = \alpha^\pi_z - \beta^\pi_z$.

By the definitions of $p_x$ and $q_x$, note that  

\begin{align*}
q_x\alpha^\pi_x + p_x\beta^\pi_x &= \left(\frac{1 + \theta_x}{2}\right)\alpha^\pi_x + \left(\frac{1 - \theta_x}{2}\right)\beta^\pi_x = \frac{1}{2}\Sigma_x + \frac{1}{2}\theta_x\Delta_x, \\
and, \text{ similarly,} \\
p_x\alpha^\pi_x + q_x\beta^\pi_x &= \frac{1}{2}\Sigma_x - \frac{1}{2}\theta_x\Delta_x.
\end{align*}

Hence, by (4) and (5),  

$$\alpha^\pi_z = \frac{1}{4}(\Sigma_x + \theta_x\Delta_x)(\Sigma_y + \theta_y\Delta_y) + \frac{1}{2}(\Sigma_x + \theta_x\Delta_x)(1 - \Sigma_y) + \frac{1}{2}(1 - \Sigma_x)(\Sigma_y + \theta_y\Delta_y),$$

and  

$$\beta^\pi_z = \frac{1}{4}(\Sigma_x - \theta_x\Delta_x)(\Sigma_y - \theta_y\Delta_y) + \frac{1}{2}(\Sigma_x - \theta_x\Delta_x)(1 - \Sigma_y) + \frac{1}{2}(1 - \Sigma_x)(\Sigma_y\theta_y\Delta_y).$$

Adding up the above two equations, we get  

\begin{align*}
\Sigma_z &= \frac{1}{2}\Sigma_x\Sigma_y + \frac{1}{2}\theta_x\theta_y\Delta_x\Delta_y + \Sigma_x(1 - \Sigma_y) + (1 - \Sigma_x)\Sigma_y \\
&= \Sigma_x + \Sigma_y - \frac{3}{2}\Sigma_x\Sigma_y + \frac{1}{2}\theta_x\theta_y\Delta_x\Delta_y. \\
\Delta_z &= \frac{1}{2}\theta_x\Delta_x\Sigma_y + \frac{1}{2}\theta_y\Delta_y\Sigma_x + \theta_x\Delta_x(1 - \Sigma_y) + \theta_y\Delta_y(1 - \Sigma_x) \\
&= \left(1 - \frac{1}{2}\Sigma_y\right)\theta_x\Delta_x + \left(1 - \frac{1}{2}\Sigma_x\right)\theta_y\Delta_y.
\end{align*}
which after plugging in (6) and (7) gives (12). Moreover, multiplying (16) by 3 and using that by (7) it holds that $3\Sigma_u = u_π^π + 2$, we obtain

$$u_π^π + 2 = (u_π^π + 2) + (u_π^π + 2) - \frac{1}{2}(u_π^π + 2)(u_π^y + 2) + \frac{3}{2}\theta_x\theta_yd_π^πd_y^π.$$  

After rearranging, this produces (13).

Because $\alpha_π^π$ and $\beta_π^π$ are probabilities and further $\alpha_π^π + \beta_π^π \leq 1$, we have that

$$d_π^π \leq 1,$$

$$u_π^π \leq 1,$$

for all $z$. Moreover, (10), (12) and (18) imply that $d_π^π \geq 0$ for all $z$ by induction. That, together with (11), (13), and (18), in turn implies that $u_π^π \geq -1/2$ for all $z$, by induction.

\section{Deterministic weights}

Before proceeding with the proof of Theorem 1, we first prove some lemmas.

\subsection{Controlling $d$- and $u$-values}

In the first lemma, we express the $d$-value at the root as a function of the $d$- and $u$-values above an arbitrary cutset.

\textbf{Lemma 1 (Controlling the root with a cutset).} For any cutset $\pi'$ in $T_\pi$, it holds that

$$d_π^π = \sum_{x \in \pi'} d_{\pi^x} \prod_{\rho \neq z \leq x} \left\{ \frac{4 - u_{s(z)}^π}{6} \right\} \theta_z,$$

where recall that $s(z)$ is the sibling of $z$.

\textbf{Proof.} The result follows by recursively applying (12) from the root down to $\pi'$.

We implicitly use the fact that, by definition, a cutset is minimal. \hfill \Box

Our second lemma shows that $d$-values cannot grow too fast down the tree. This fact will be useful to proving the next key lemma. We will need the lower bound

$$\theta_\ast = \inf_{z \in V_\pi} \theta_z > 0,$$

on the $\theta$-values. For $v, w \in V_\pi$, we let $\gamma(v, w)$ be the graph distance between $v$ and $w$ in $T_\pi$. 

10
Lemma 2 (Growth of $d$-values). Fix any $v \in V^\pi$. Then, for all $\varepsilon' > 0$,

$$d_v^\pi \leq \varepsilon' \quad \implies \quad d_w^\pi \leq \varepsilon' \left( \frac{2}{\theta_*} \right)^\gamma(v,w).$$

for all descendants $w$ of $v$ in $V^\pi$.

**Proof.** Let $z \in V^\pi$, not on $\pi$, have children $x$ and $y$. Recall recursion (12)

$$d_z^\pi = \left( \frac{4 - u_y^\pi}{6} \right) \theta_x d_x^\pi + \left( \frac{4 - u_x^\pi}{6} \right) \theta_y d_y^\pi.$$

(Note that, in the case where $z$ is the parent of a vertex on the cutset $\pi$, $z$ itself cannot be on the cutset by minimality and therefore both its children are in $V^\pi$.) By the bounds (14) and (15), we have $u_x^\pi, u_y^\pi \leq 1$ and $d_x^\pi, d_y^\pi \geq 0$, which implies that both terms on the r.h.s. above are non-negative. Hence, using $\theta_x \geq \theta_*$, we obtain

$$d_z^\pi \geq \frac{1}{2} \theta_* d_x^\pi. \quad (20)$$

In particular, $d_z^\pi \leq \varepsilon'$ implies that $d_x^\pi \leq \frac{\varepsilon'}{\theta_*} d_x^\pi$. Applying (20) recursively gives the claim. This includes the case where $w$ in the statement of the lemma is on the cutset $\pi$. \qed

Our final lemma gives us control over $u$-values at the root of a subtree where $d$-values are uniformly small.

Lemma 3 (Controlling $u$ when $d$ is small). Fix any $0 < \phi' \leq 1/9$ and $v \in V^\pi$. Then there exists $\varepsilon' > 0$ depending only on $\theta_*$ and $\phi'$ such that

$$d_v^\pi \leq \varepsilon' \frac{2}{\theta_*} \implies |u_v^\pi| \leq 4\phi'.$$

**Proof.** We use Lemma 2 and recurrence (9), namely,

$$u_z^\pi = \frac{3}{2} \theta_x \theta_y d_x^\pi d_y^\pi - \frac{1}{2} u_x^\pi u_y^\pi,$$

where recall that $z \in V^\pi$, not on $\pi$, has children $x$ and $y$.

First, we need some constants. Let $H$ be the smallest non-negative integer such that

$$\left( \frac{1}{2} \right)^{-1 + 2^H} \leq \phi'.$$ \quad (21)
Define $\varepsilon' > 0$ to be the largest positive real such that

$$\frac{3}{2} \left[ \varepsilon' \left( \frac{2}{\theta_*} \right)^{H+1} \right]^2 \leq \phi',$$

and

$$\varepsilon' \left( \frac{2}{\theta_*} \right)^{H+1} \leq 0.99.$$  

The rest of the proof proceeds in two steps. We first derive a simplified recurrence for the $u$-values and then solve it.

1. **Simplified recurrence.** Assume that $d_{v_0}^\pi \leq \varepsilon' \frac{2}{\theta_*}$. Let $w$ be a descendant of $v$ with graph distance $\gamma(v, w) \leq H$. Then, by Lemma 2,

$$d_{w}^\pi \leq \varepsilon' \left( \frac{2}{\theta_*} \right)^{H+1} < 1,$$

where the last inequality follows from (23) and where we used that $\theta_* \leq 1 < 2$, since $\theta_*$ is a probability. This shows, in particular, that all descendants of $v$ in $\mathcal{V}$ within graph distance $H$ are in fact strictly above $\pi$, because $d$-values are 1 on the cutset $\pi$. Moreover, by the recurrence (13) and the inequality (22), for any descendant $w_0$ of $v$ with children $w_1, w_2$ in $\mathcal{V}^\pi$ that are within graph distance $H$ of $v$, we have

$$\|u_{w_0}^\pi\| \leq \frac{3}{2} \theta_{w_1} \theta_{w_2} d_{w_1}^\pi d_{w_2}^\pi \|u_{w_1}^\pi\| \|u_{w_2}^\pi\| \leq \phi' + \frac{1}{2} \|u_{w_1}^\pi\| \|u_{w_2}^\pi\|,$$

where we used that $\theta_* \leq 1$, since $\theta_*$ is a probability. Define

$$U_h = \sup \{ |u_w^\pi| : w \in \mathcal{V}^\pi, v \leq w \text{ and } \gamma(v, w) = h \},$$

and $U_0 = |u_v^\pi|$. By the remark above, the set in the previous display is non-empty for all $h = 0, \ldots, H - 1$. Taking a supremum on both sides of (24) gives the recurrence

$$U_h \leq \phi' + \frac{1}{2} U_{h+1}^2,$$

where $0 \leq h \leq H - 1$. 

12
2. **Solution.** We show by induction on $h$ (backwards from $H - 1$) that

$$U_h \leq 3\phi' + \left(\frac{1}{2}\right)^{-1+2^{H-h}}. \tag{26}$$

For the base of the induction $h = H - 1$, we have indeed that

$$U_{H-1} \leq \phi' + \frac{1}{2} \leq 3\phi' + \left(\frac{1}{2}\right)^{-1+2^{H-(H-1)}},$$

where we used (25) and the fact that $u$-values are $\leq 1$ in absolute value. Assume the induction claim (26) holds for all $h' + 1 \leq h \leq H - 1$. We show it then holds for $h = h'$. Indeed, by (25) again,

$$U_{h'} \leq \phi' + \frac{1}{2} U_{h'+1}^2 \leq \phi' + \frac{1}{2} \left[3\phi' + \left(\frac{1}{2}\right)^{-1+2^{H-(h'+1)}}\right]^2 \leq \phi' \left[1 + \frac{9\phi'}{2} + 3 \left(\frac{1}{2}\right)^{-1+2^{H-(H-1)}}\right] + \left(\frac{1}{2}\right)^2 \left[2^{-1+2^{H-(h'+1)}}\right] + 1 \leq \phi' \left[\frac{5}{2} + \frac{9\phi'}{2}\right] + \left(\frac{1}{2}\right)^{-1+2^{H-h'}}.$$

Because by assumption $\phi' \leq 1/9$, the square bracket above is $\leq 3$. That concludes the induction.

By our choice of $H$ in (21), that implies

$$|u_0^\pi| = U_0 \leq 3\phi' + \left(\frac{1}{2}\right)^{-1+2^{H}} \leq 4\phi',$$

which establishes the claim. $\square$

### 3.2 Proof of main theorem

**Proof of Theorem 1.** We now prove our main theorem. Fix $\pi \in C(\mathcal{T})$ and assume that

$$\inf_{z \in V} \theta_z > 0,$$
and
\[
\sup \left\{ \kappa > 0 : \inf_{\pi \in \mathcal{C}(T)} \sum_{x \in \pi} \prod_{\rho \neq z \leq x} \kappa^{-1} \theta_z > 0 \right\} > \frac{3}{2}.
\]

Then, there is a \( \kappa > \frac{3}{2} \) (which, for reasons that will become clear, we take close enough to \( \frac{3}{2} \)) such that the sum above is greater than a positive constant (which we take smaller than 1). Formally, there is \( 0 < \phi' \leq 1/9 \) and \( 0 < \zeta < 1 \) such that
\[
\sum_{x \in \pi'} \prod_{\rho \neq z \leq x} \left\{ \frac{2}{3} (1 - \phi') \right\} \theta_z \geq \zeta,
\]
for all cutsets \( \pi' \in \mathcal{C}(T) \). For this value of \( \phi' \), let \( \varepsilon' \) be as in Lemma 3 and define
\[
\varepsilon = \varepsilon' \zeta < \varepsilon'.
\]

The proof proceeds by contradiction. Assume that \( d_{\pi} \leq \varepsilon \).

Let \( \pi' \) be the cutset of those nodes closest to the root where the d-values first cross above \( \varepsilon' \), i.e., formally
\[
\pi' = \{ x \in V^\pi : d_x^\pi > \varepsilon' \text{ and } d_z^\pi \leq \varepsilon', \ \forall z \leq x \}.
\]

Such a cutset (which is necessarily minimal) exists because \( d_v^\pi = 1 \) for all \( v \in \pi \) and \( \varepsilon' > \varepsilon \). By Lemma 2, for all \( z \) on or above \( \pi' \), i.e. such that \( z \leq x \) for some \( x \in \pi' \), we have
\[
d_z^\pi \leq \varepsilon' \frac{2}{\theta_s} \text{ and } d_{s(z)}^\pi \leq \varepsilon' \frac{2}{\theta_s},
\]
since the immediate parent of \( z \) (and \( s(z) \)) has d-value \( \leq \varepsilon' \) by definition of \( \pi' \). By Lemma 3, we then have
\[
|u_z^\pi| \leq 4\phi' \text{ and } |u_{s(z)}^\pi| \leq 4\phi'.
\]

By Lemma 1, (27) and (29), summing over \( \pi' \)
\[
d_\rho^\pi = \sum_{x \in \pi'} d_x^\pi \prod_{\rho \neq z \leq x} \left\{ \frac{4 - u_{s(z)}^\pi}{6} \right\} \theta_z
\]
\[
> \sum_{x \in \pi'} \varepsilon' \prod_{\rho \neq z \leq x} \left\{ \frac{2}{3} (1 - \phi') \right\} \theta_z
\]
\[
\geq \varepsilon' \zeta
\]
\[
= \varepsilon,
\]
which contradicts (28). That concludes the proof. \( \square \)
4 I.i.d. weights

In this section, we prove our main in the i.i.d. weight case. Because there is no lower bound on the weights, Theorem 1 cannot be applied directly to this case. In particular, the absence of a lower bound makes controlling the \(u\)-values more challenging. Here we identify a subtree of \(T\) where \(u\)-values are well-behaved.

The existence of such a subtree is established with a coupling to a percolation process, where open edges roughly indicate that weights are uniformly bounded in a properly defined neighborhood.

**Proof of Theorem 2.** First, we need the following percolation result. To each edge \(e = (x, y)\) of \(T\), where \(x\) is the parent of \(y\), we assign an independent random weight \(\tilde{\theta}_y\) drawn from a distribution \(\tilde{\Theta}\) over \((0, 1]\). We also pick an independent indicator variable \(\tilde{J}_y\), which is 1 with probability \(\tilde{q} \in [0, 1]\) and 0 otherwise. Let \(\tilde{T} = (\tilde{V}, \tilde{E})\) be the subtree of \(T\) whose vertices \(x\) satisfy \(\prod_{\rho \neq z \leq x} \tilde{J}_z = 1\). We let \(\mathcal{N}_{\text{ext}}\) be the event of non-extinction, i.e., the event that \(\tilde{T}\) is infinite. The following result can be proved along the lines of Proposition 3.2, Proposition 5.1 and Corollary 5.2 in [Per99]. See also [Lyo89, Lyo90].

**Lemma 4** (Branching condition: random edge weights on open cluster). Fix \(\tilde{q} \in [0, 1]\) and assume that \(\tilde{\Theta}\) has mean \(\tilde{\mu} \in (0, 1)\). Then, conditioned on \(\mathcal{N}_{\text{ext}}\), almost surely

\[
\sup \left\{ \kappa > 0 : \inf_{\pi \in \mathcal{P}(\tilde{T})} \sum_{x \in \pi} \prod_{\rho \neq z \leq x} \kappa^{-1} \tilde{\theta}_z > 0 \right\} = 2\tilde{q}\tilde{\mu}. \tag{30}
\]

By standard branching process arguments [AN72], the extinction probability \(\tilde{\varphi}\) satisfies

\[
\tilde{\varphi} = \tilde{q}^2 \tilde{\varphi}^2 + 2(1 - \tilde{q})q\tilde{\varphi} + (1 - \tilde{q})^2,
\]

i.e.,

\[
\mathbb{P}[\mathcal{N}_{\text{ext}}] = \left( \frac{1 - \tilde{q}}{\tilde{q}} \right)^2. \tag{31}
\]

As discussed briefly above, we use a coupling argument. In order to describe the coupling, we first need to define some constants (not depending on \(\theta\)). Recall that \(\mu\) is the mean of the edge weight distribution \(\Theta\) and that \(\delta\) is the desired failure probability. Let \(q \in (0, 1)\) be close enough to 1 that

\[
\left( \frac{1 - q}{q} \right)^2 \leq \frac{\delta}{3}, \tag{32}
\]

15
and

$$2q\mu > 3/2.$$  

Let then $0 < \phi' \leq 1/9$ be such that

$$2q\mu > \frac{3}{2(1-\phi')}.$$  \hspace{1cm} (33)  

Let $H$ be the smallest non-negative integer such that

$$\left(\frac{1}{2}\right)^{-1+2^H} \leq \phi'.$$

Because $\mathbb{P}_{\theta \sim \Theta}[\theta \leq \theta_*] \to 0$ as $\theta_* \to 0$, we can take $\theta_* \in (0, 1)$ small enough that

$$\tau = \mathbb{P}[\theta \leq \theta_*],$$

satisfies

$$(1 - \tau)^{2^{H+1}} > q,$$ \hspace{1cm} (34)  

and

$$1 - (1 - \tau)^{2^{H+2}} \leq \frac{\delta}{3}.$$ \hspace{1cm} (35)  

We are now ready to define the coupled process $(\tilde{T}, \tilde{\theta})$. We use the following notation: Ber($\psi$) is a Bernoulli random variable with success probability $\psi$ and $Z|A$ is the random variable $Z$ conditioned on the event $A$. For each $z$, we generate $\theta_z$ as

$$\theta_z = (1 - I_z)\theta_{z,0} + I_z\theta_{z,1},$$

where $I_z \sim \text{Ber}(\mathbb{P}[\theta_z > \theta_*])$, $\theta_{z,0} \sim \theta_z\{\theta_z \leq \theta_*\}$, and $\theta_{z,1} \sim \theta_z\{\theta_z > \theta_*\}$ are independent. For $z \in \mathcal{V}$, let $\mathcal{D}_h(z)$ be the descendants of $z$ lying exactly $h$ levels below it, i.e.,

$$\mathcal{D}_h(z) = \{w \in \mathcal{V} : z \leq w \text{ and } \gamma(z, w) = h\}.$$  

Define

$$\tilde{J}_z = \prod_{w \in \mathcal{D}_{H+1}(z)} I_w,$$  

and

$$\tilde{\theta}_z = \theta_{z,1}.$$
Note that by construction the random variables \( \tilde{J}_z \sim \text{Ber}((1 - \tau)^{2H+1}) \) and \( \tilde{\theta}_z \sim \theta_z | \{ \theta_z > \theta_* \}, \) \( z \in \mathcal{V}, \) are independent. Let \( \tilde{T} \) be defined as in Lemma 4, let
\[
\tilde{q} = (1 - \tau)^{2H+1}
\]
and let \( \tilde{\mu} \) be the mean of \( \Theta \) conditioned on being larger than \( \theta_* \). By (31), (32), and (34)
\[
\mathbb{P}[\mathcal{N}_{\text{ext}}] \leq \frac{\delta}{3}.
\]

We first apply Lemma 4 to \((\tilde{T}, \tilde{\theta})\) to obtain a branching rate condition similar to (27), which was used in the proof of Theorem 1 to control \( d \) at the root.

**Lemma 5 (Towards controlling \( d \) at the root).** There is a deterministic (i.e., not depending on \( \theta \)) \( 0 < \zeta < 1 \) such that, on the event of non-extinction, with probability at least \( 1 - \delta/3 \)
\[
\inf_{\pi' \in \mathcal{E}(\tilde{T})} \sum_{x \in \pi'} \prod_{\rho \neq z \leq x} \left\{ \frac{2}{3}(1 - \phi') \right\} \tilde{\theta}_z \geq \zeta.
\]

**Proof.** On the event of non-extinction, we have almost surely that
\[
\sup \left\{ \kappa > 0 : \inf_{\pi \in \mathcal{E}(\tilde{T})} \sum_{x \in \pi} \prod_{\rho \neq z \leq x} \kappa^{-1} \tilde{\theta}_z > 0 \right\} = 2q\tilde{\mu} > 2q\mu > \frac{3}{2(1 - \phi')},
\]
where we used the fact that \( \tilde{\mu} > \mu \) as well as (33) and (34). In particular,
\[
\inf_{\pi' \in \mathcal{E}(\tilde{T})} \sum_{x \in \pi'} \prod_{\rho \neq z \leq x} \left\{ \frac{2}{3}(1 - \phi') \right\} \tilde{\theta}_z > 0.
\]
We can then choose a deterministic (i.e., not depending on \( \theta \)) \( 0 < \zeta < 1 \) such that, on the event of non-extinction, with probability at least \( 1 - \delta/3 \)
\[
\inf_{\pi' \in \mathcal{E}(\tilde{T})} \sum_{x \in \pi'} \prod_{\rho \neq z \leq x} \left\{ \frac{2}{3}(1 - \phi') \right\} \tilde{\theta}_z \geq \zeta.
\]
That establishes the lemma. \( \Box \)

The purpose of the coupling is to show that the argument used in Lemma 3 to control the \( u \)-values can be applied to the vertices in \( \tilde{T} \). This is stated in the next
lemma. For the choice of $\phi'$, $H$ and $\theta_*$ above, let $\varepsilon'$ be chosen as in the proof of Lemma 3, i.e., the largest positive real such that

$$\frac{3}{2} \left[ \varepsilon' \left( \frac{2}{\theta_*} \right)^{H+1} \right]^2 \leq \phi',$$

and

$$\varepsilon' \left( \frac{2}{\theta_*} \right)^{H+1} \leq 0.99.$$

**Lemma 6** (Controlling $u$ on $\tilde{T}$). For all $z \in V \cap \tilde{V}$

$$d_\pi^z \leq \varepsilon' \frac{2}{\theta_*} \implies |u_\pi^z| \leq 4\phi' \quad \text{and} \quad d_{s(z)}^\pi \leq \varepsilon' \frac{2}{\theta_*} \implies |u_{s(z)}^\pi| \leq 4\phi'. \quad (38)$$

**Proof.** We make two observations:

1. Observe that for any $z \in V \cap \tilde{V}$ it must be that

   $$\theta_w > \theta_*, \quad \forall w \in \bigcup_{h \leq H+1} D_h(z).$$

   Indeed, note that the unique $v$ such that $v \leq z$ and $\gamma(v, z) = h$ satisfies $v \in \tilde{T}$ and $D_{H+1-h}(z) \subseteq D_{H+1}(v)$.

2. As a result, repeating the proof of Lemma 3, it follows that for all $z \in V \cap \tilde{V}$

   $$d_\pi^z \leq \varepsilon' \frac{2}{\theta_*} \implies |u_\pi^z| \leq 4\phi' \quad \text{and} \quad d_{s(z)}^\pi \leq \varepsilon' \frac{2}{\theta_*} \implies |u_{s(z)}^\pi| \leq 4\phi',$$

   where we used the fact that the parent of $z$ is in $\tilde{T}$ and therefore has all its descendants within $H + 1$ level with $\theta$-values above $\theta_*$. The latter in turn implies that $s(z)$ itself has all its descendants within $H$ level with $\theta$-values above $\theta_*$. That concludes the proof of the lemma.

The rest of the proof of Theorem 2 is similar to that of Theorem 1, except that we restrict the argument to $\tilde{T}$. Define

$$\varepsilon = \varepsilon' \zeta < \varepsilon'.$$
Let $\mathcal{H}$ be the event that $\theta_w > \theta_*$ for all $w$ such that $\gamma(\rho, w) \leq H$. By (35), $\mathbb{P}[\mathcal{H}] \geq 1 - \delta/3$. Condition on $\mathcal{H}$, $\mathcal{N}_{\text{ext}}$ and (37), which jointly occur with probability at least $1 - \delta$. Assume by contradiction that

$$d^\pi_\rho \leq \varepsilon,$$  

(39)

and let

$$\pi' = \{x \in \mathcal{V}^\pi : d^\pi_x > \varepsilon' \text{ and } d^\pi_z \leq \varepsilon', \ \forall z \leq x\}.$$  

By Lemma 2, for all $z \in \mathcal{V} \cap \tilde{T}$ such that $z \leq x$ for some $x \in \pi'$, we have

$$d^\pi_x \leq \varepsilon' \frac{2}{\theta_*} \quad \text{and} \quad d^\pi_{s(z)} \leq \varepsilon' \frac{2}{\theta_*},$$

since the immediate parent of $z$ (and $s(z)$) has $d$-value $\leq \varepsilon'$ by definition of $\pi'$ and $\theta$-values on $\tilde{T}$ are above $\theta_*$. By (38), we then have

$$|u^\pi_z| \leq 4\phi' \quad \text{and} \quad |u^\pi_{s(z)}| \leq 4\phi',$$  

(40)

for all $z \in \mathcal{V} \cap \tilde{T}$ such that $z \leq x$ for some $x \in \pi'$. By Lemma 1, (37) and (40),

$$d^\pi_\rho = \sum_{x \in \pi'} d^\pi_x \prod_{\rho \neq z \leq x} \left\{ \frac{4 - u^\pi_{s(z)}}{6} \right\} \theta_z$$

$$\geq \sum_{x \in \pi' \cap \tilde{T}} d^\pi_x \prod_{\rho \neq z \leq x} \left\{ \frac{4 - u^\pi_{s(z)}}{6} \right\} \tilde{\theta}_z$$

$$> \sum_{x \in \pi'} \varepsilon' \prod_{\rho \neq z \leq x} \left\{ \frac{2}{3} (1 - \phi') \right\} \tilde{\theta}_z$$

$$\geq \varepsilon' \zeta$$

$$= \varepsilon,$$

where, on the second line, we used again the fact that $\theta$-values on $\tilde{T}$ are above $\theta_*$ as well as the fact that all terms in the sum are non-negative by the general bounds on the $d$- and $u$-values. This contradicts (39) and concludes the proof. \qed
Acknowledgments

We thank Mike Steel for helpful discussions.

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