

The Depth of the Most Recent Common Ancestor of a Random Sample of Species

(joint with Mike Steel)

Michael Fuchs

Department of Mathematical Sciences
Chengchi University
Taipei, Taiwan



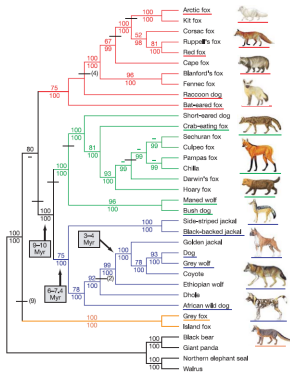
August 4th, 2025

What is a Phylogenetic Tree (PT)?

X ... a finite set.

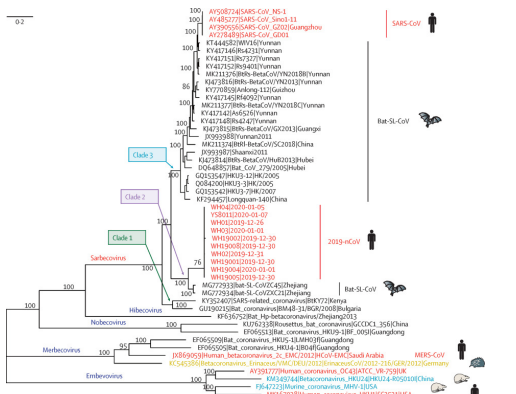
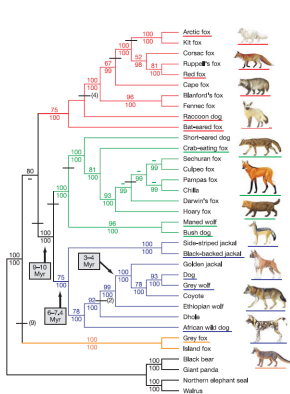
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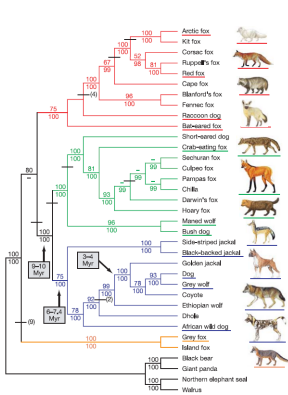
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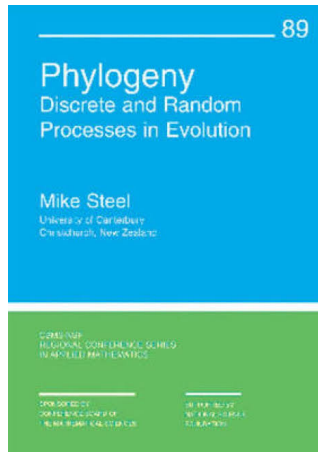
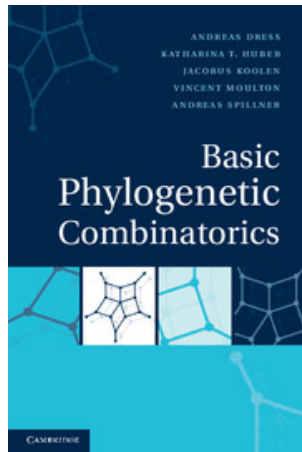
What is a Phylogenetic Tree (PT)?

$X \dots$ a finite set.



Phylogenetic tree: rooted, binary, non-plane tree with leaves labeled by X .

Phylogenetics



Yule-Harding Model

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Thus, higher probability is assigned to more “balanced” trees.

- Probability of t under Yule-Harding model:

$$\mathbb{P}(t) = \frac{2^{n-1}}{n! \prod_{r=3}^n (r-1)^{d_r(t)}},$$

where $d_r(t)$ is the number of nodes of r with r descendant leaves.

Sanderson's work

Definition

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Theorem (Sanderson; 1996)

Let k leaves be randomly sampled from a random PT of size n under the Yule-Harding model. Then, as $n \rightarrow \infty$,

$$\mathbb{P}(\text{MRCA} = \text{root}) \sim 1 - \frac{2}{k+1}.$$

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E.g. with $k = 40$, the probability equals $\approx 0.9512\dots$.

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→ This gives a **probability distribution on PTs** of size n .

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$$f(x) = \frac{\Gamma(2\beta + 2)}{\Gamma^2(\beta + 1)} x^\beta (1 - x)^\beta, \quad x \in [0, 1].$$

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Then,

$$\pi_{n,i} = \frac{1}{\pi_n(\beta)} \frac{\Gamma(\beta + i + 1)\Gamma(\beta + n - i + 1)}{i!(n - i)!}, \quad (1 \leq i \leq n - 1),$$

where $\pi_n(\beta)$ is a suitable constant.

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Note that the above expression makes also sense for $-2 < \beta \leq -1$.

Special Cases

- $\beta = 0$: Yule-Harding model:

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- $\beta = -3/2$: Uniform or PDA model:

$$\pi_{n,i} = \frac{C_{i-1}C_{n-i-1}}{C_{n-1}}, \quad (1 \leq i \leq n-1),$$

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- $\beta = -1$: with H_n the harmonic numbers:

$$\pi_{n,i} = \frac{n}{2H_{n-1}} \cdot \frac{1}{i(n-i)}, \quad (1 \leq i \leq n-1).$$

This model seems to have the best match with “real” trees.

Extensions of Sanderson's Result (i)

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Theorem (F. & Steel; 2025+)

(i) For $\beta = -1$:

$$\mathbb{P}(D_{n,k} = 0) = \frac{H_{k-1}}{H_{n-1}},$$

where H_m denotes the m -th harmonic number.

(ii) For $\beta \neq -1$:

$$\mathbb{P}(D_{n,k} = 0) = 1 - \frac{2(\beta+1) \cdots (\beta+k)}{k! \binom{n}{k}} \times \frac{\binom{n+2\beta+1}{n-k} - \binom{n+\beta}{n-k}}{\binom{n+2\beta+1}{n} - 2\binom{n+\beta}{n}}.$$

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Thus, $\lim_{n \rightarrow \infty} \mathbb{P}(D_{n,k} = 0) = 0$ iff $-2 < \beta \leq -1$.

Extensions of Sanderson's Result (ii)

Corollary (F. & Steel; 2025+)

- (i) For $\beta > -1$: $\lim_{n \rightarrow \infty} \mathbb{P}(D_{n,k} = 0) = 1 - \frac{(\beta+2) \cdots (\beta+k)}{(2\beta+3) \cdots (2\beta+k+1)}.$
- (ii) For $\beta = -1$: $\lim_{n \rightarrow \infty} \mathbb{P}(D_{n,k} = 0) = \alpha$ if $k \sim n^\alpha.$
- (iii) For $-2 < \beta < -1$:

$$\lim_{n \rightarrow \infty} \mathbb{P}(D_{n,k} = 0) = \begin{cases} c^{-\beta-1}, & \text{if } k \sim cn; \\ 0, & \text{if } k = o(n). \end{cases}$$

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n	10	10^2	10^3	10^4	10^5	10^6
$\beta = 0$	8	29	38	39	39	39
$\beta = -1$	9	78	688	6131	54635	486930
$\beta = -3/2$	10	91	903	9026	90251	902501

Figure: Values of k such that $\mathbb{P}(D_{n,k} = 0) \geq 0.95$.

Limit Laws for $D_{n,k}$ (i)

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As $n \rightarrow \infty$,

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Proof. By induction on r ,

$$\mathbb{P}(D_{n,k} \geq r) = q(\beta, k)^r,$$

where one uses that with high probability no subtrees of the root is small.

Limit Laws for $D_{n,k}$ (ii)

Theorem (F. & Steel; 2025+)

(i) For $\beta = -1$,

$$\frac{H_{k-1} D_{n,k}}{\log n} \xrightarrow{d} \text{Exp}(1),$$

where $\text{Exp}(1)$ is the standard exponential distribution.

(ii) For $\beta = -3/2$,

$$\frac{D_{n,k}}{\sqrt{n}} \xrightarrow{d} D_k,$$

where D_k has the three-parameter Mittag-Leffler distribution $\text{ML}(1/2, 1/2, k-1)$.

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Both results are proved with the method of moments.

Sketch of Proof (i)

We have,

$$(D_{n,k}|I_n = j) \stackrel{d}{=} \begin{cases} D_{j,k} + 1, & \text{with probability } \binom{j}{k} / \binom{n}{k}; \\ D_{n-j,k} + 1, & \text{with probability } \binom{n-j}{k} / \binom{n}{k}; \\ 0, & \text{otherwise,} \end{cases}$$

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For $\beta = -3/2$, set

$$D^{[m]}(z) := \sum_{n \geq 1} C_{n-1} \binom{n}{k} \mathbb{E}(D_{n,k}^m) z^n.$$

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Then,

$$D^{[m]}(z) = \sum_{\ell=1}^m \binom{m}{\ell} D^{[m-\ell]}(z) ((1-4z)^{-1/2} - 1).$$

Sketch of Proof (ii)

Proposition

As $z \rightarrow 1/4$,

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Corollary

As $n \rightarrow \infty$,

$$\mathbb{E}(D_{n,k}^m) \sim \frac{m! C_{k-1} 4^{1-k} k! \sqrt{\pi}}{\Gamma(k + (m-1)/2)} n^{m/2}.$$

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Remark: The sequence

$$\frac{m! C_{k-1} 4^{1-k} k! \sqrt{\pi}}{\Gamma(k + (m-1)/2)}$$

is the (unique) moment sequence of $\text{ML}(1/2, 1/2, k-1)$.

Sketch of Proof (iii)

For $\beta = -1$, all moments of $D_{n,k}$ satisfy the recurrence

$$a_n = \frac{1}{H_{n-1}} \sum_{j=1}^{n-1} \frac{a_j}{n-j} + b_n.$$

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Proposition

Let $t \in \mathbb{N}$ and $s \in \mathbb{Z}$.

- (i) If $b_n = O(n^t \log^s n)$, then $a_n = O(n^t \log^{s+1} n)$.
- (ii) If $b_n = cn^t \log^s n$, then $a_n \sim cn^t \log^{s+1} n / H_t$.

Sketch of the Proof (iv)

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$$A_{n,k}^{[m]} = \frac{1}{H_{n-1}} \sum_{j=1}^{n-1} \frac{A_{j,k}^{[m]}}{n-j} + \frac{1}{H_{n-1}} \sum_{\ell=0}^{m-1} \binom{m}{\ell} \sum_{j=1}^{n-1} \frac{A_{j,k}^{[\ell]}}{n-j}.$$

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Thus,

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E.g., for $m=1$:

$$b_n = \frac{1}{H_{n-1}} \sum_{j=1}^{n-1} \frac{(j-1)_{(k-1)}}{n-j} = (n-1)_{(k-1)} \left(1 - \frac{H_{k-1}}{H_{n-1}}\right)$$

and thus,

$$\mathbb{E}(D_{n,k}) \sim \log n / H_{k-1}.$$

Sketch of Proof (v)

Using “moment pumping”, one obtains the following.

Proposition

Set

$$A_{n,k}^{[m]} := (n-1)_{(k-1)} \mathbb{E}(D_{n,k}^m).$$

Then, as $n \rightarrow \infty$,

$$A_{n,k}^{[m]} \sim \frac{m!}{H_{k-1}^m} n^{k-1} \log^m n.$$

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Thus, as $n \rightarrow \infty$,

$$\mathbb{E}(D_{n,k}^m) \sim \frac{m!}{H_{k-1}^m} \log^m n$$

which implies the claimed limit law.

A Conjecture

Conjecture

For $-2 < \beta < -1$,

$$\frac{D_{n,k}}{n^{-\beta-1}} \xrightarrow{d} D_k,$$

where D_k is uniquely characterized by the moment sequence

$$c_m = m! \prod_{j=1}^m e(\beta, k, j)$$

and

$$e(\beta, k, m) := \frac{\Gamma((- \beta - 1)m + \beta + k + 1)}{\Gamma((- \beta - 1)m + 2\beta + k + 2)} - \frac{\Gamma(\beta + 2)}{\Gamma(2\beta + 3)}.$$

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Remark: Relatively little is known so far for the range $-2 < \beta < -1$.

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where I_n is the size of the left subtree.

Let $p = \lambda/n$.

Random Sample of Species (ii)

Theorem (F. & Steel; 2025+)

(i) For $\beta > -1$,

$$\mathbb{P}(D_n = 0) \sim \frac{1 - 2\Gamma(2\beta + 2) \int_0^1 e^{-\lambda x} x^\beta (1-x)^\beta dx / \Gamma(\beta + 1)^2 + e^{-\lambda}}{1 - e^{-\lambda}}.$$

(ii) For $\beta = -1$,

$$\mathbb{P}(D_n = 0) \sim \frac{E_1(\lambda) + \log \lambda + \gamma - e^{-\lambda}(\text{Ei}(\lambda) - \lambda - \gamma)}{(1 - e^{-\lambda})H_{n-1}}.$$

(iii) For $-2 < \beta < -1$,

$$\mathbb{P}(D_n = 0) \sim \frac{cn^{\beta+1}}{\Gamma(\beta + 1)(1 - e^{-\lambda})}.$$

Random Sample of Species (iii)

Corollary (F. & Steel; 2025+)

(i) For $\beta > -1$,

$$\frac{1 - 2\Gamma(2\beta + 2) \int_0^1 e^{-\lambda x} x^\beta (1-x)^\beta dx / \Gamma(\beta + 1)^2 + e^{-\lambda}}{1 - e^{-\lambda}} \sim 1 - \frac{2\Gamma(2\beta + 2)}{\lambda^{\beta+1} \Gamma(\beta + 1)}.$$

(ii) For $\beta = -1$,

$$\frac{E_1(\lambda) + \log \lambda + \gamma - e^{-\lambda}(\text{Ei}(\lambda) - \lambda - \gamma)}{(1 - e^{-\lambda})H_{n-1}} \sim \frac{\log \lambda}{H_{n-1}}.$$

(iii) For $-2 < \beta < -1$,

$$\frac{cn^{\beta+1}}{\Gamma(\beta + 1)(1 - e^{-\lambda})} \sim \left(\frac{\lambda}{n}\right)^{-\beta-1}.$$

Reference



M. Fuchs and M. Steel. Predicting the depth of the most recent common ancestor of a random sample of k species: the impact of phylogenetic tree shape, J. Math. Biol., in press.

Reference



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Thanks for the attention!