Phylogenomic Branch Length Estimation using Quartets

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ISMB/ECCB

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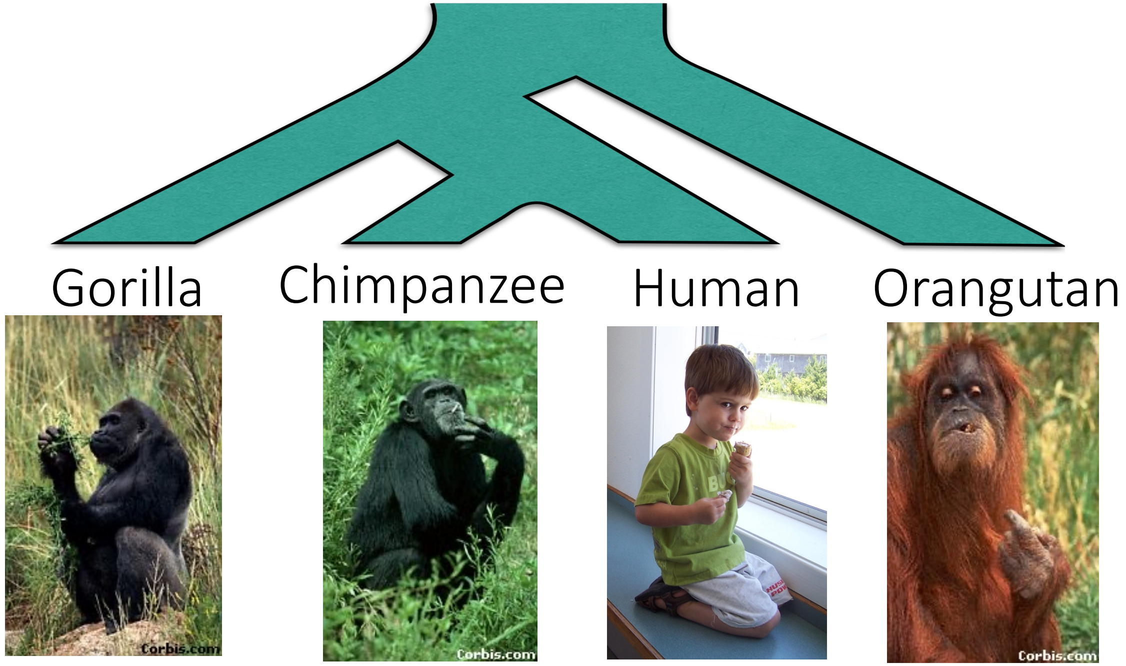
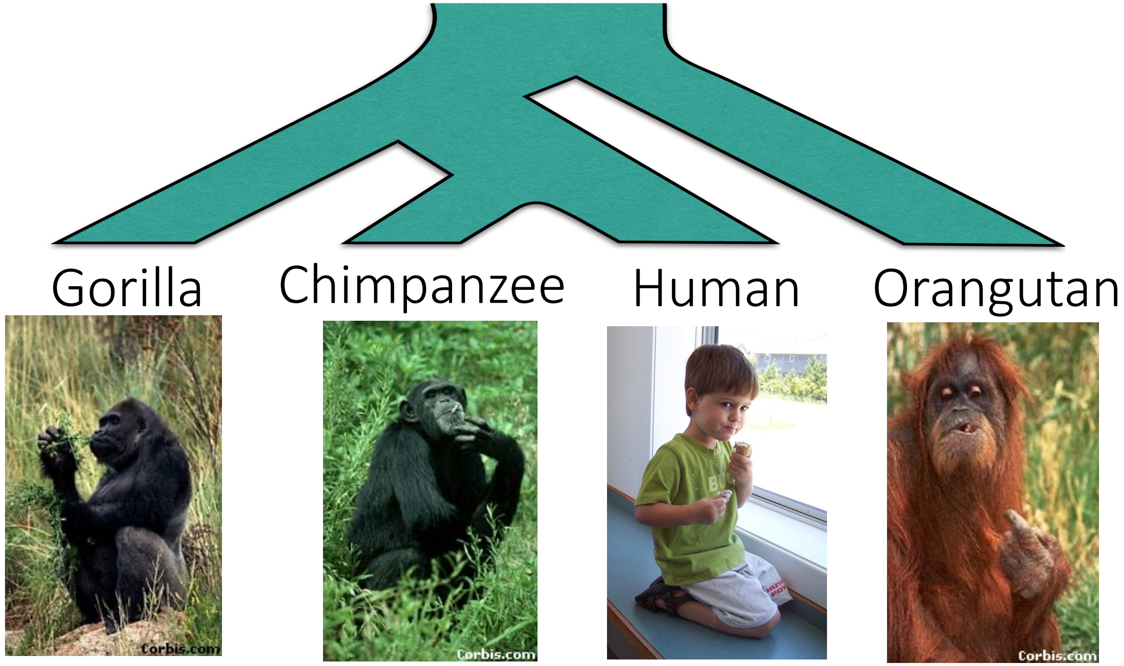
Phylogenomics and gene tree discordance



Gorilla Chimpanzee Human Orangutan

Species tree

Phylogenomics and gene tree discordance



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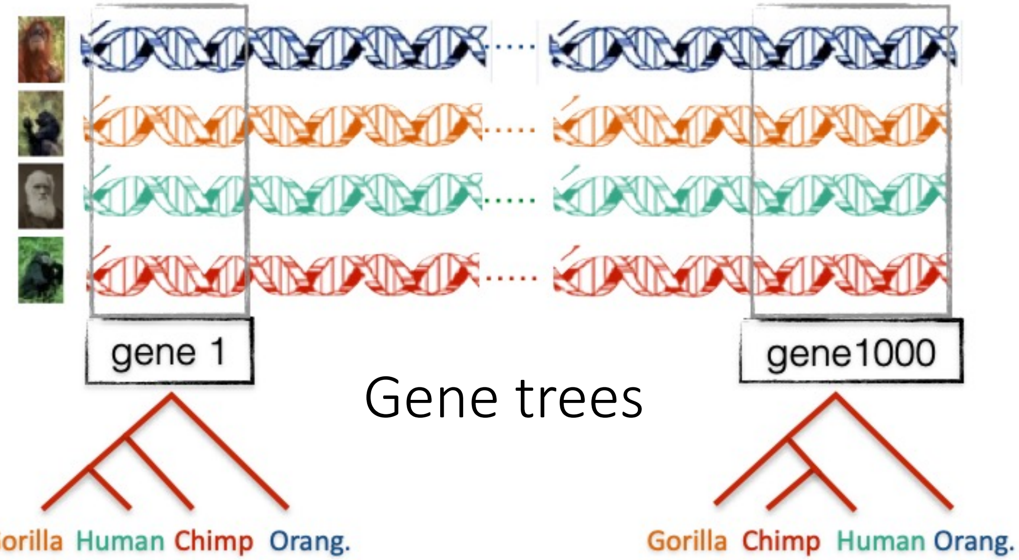
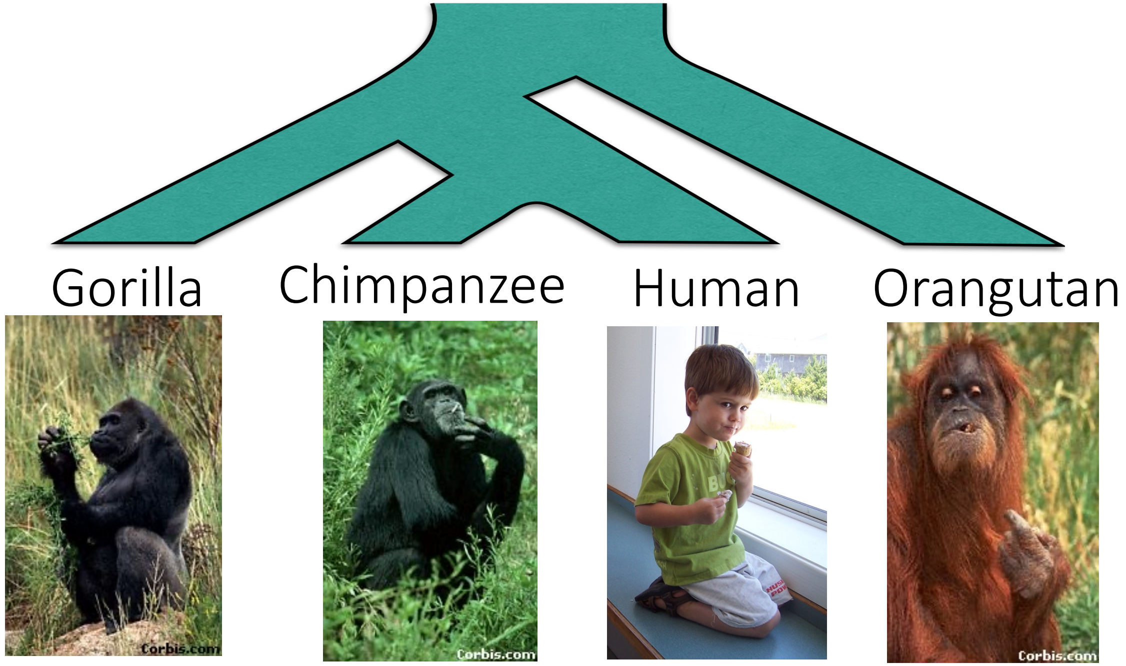
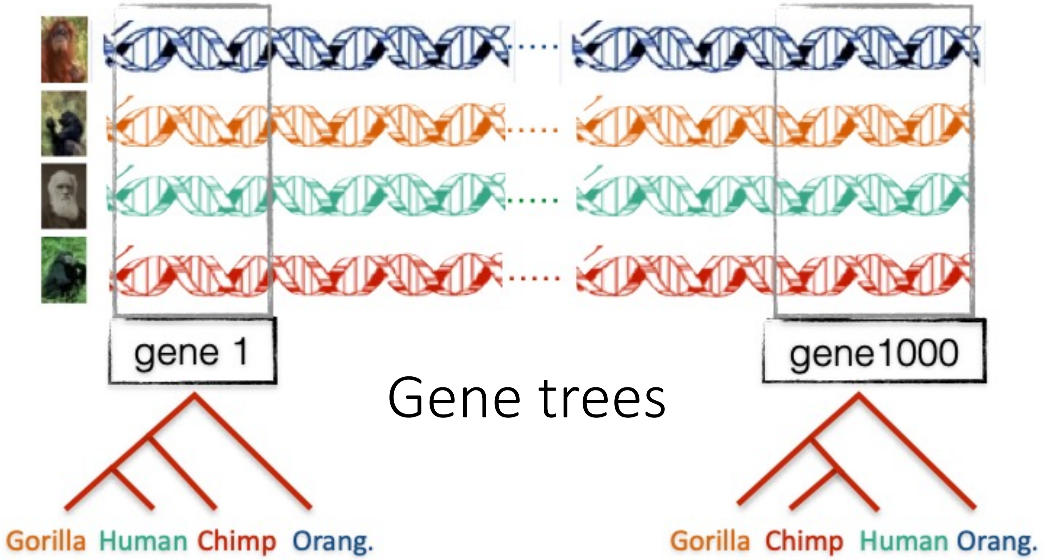


Gene trees

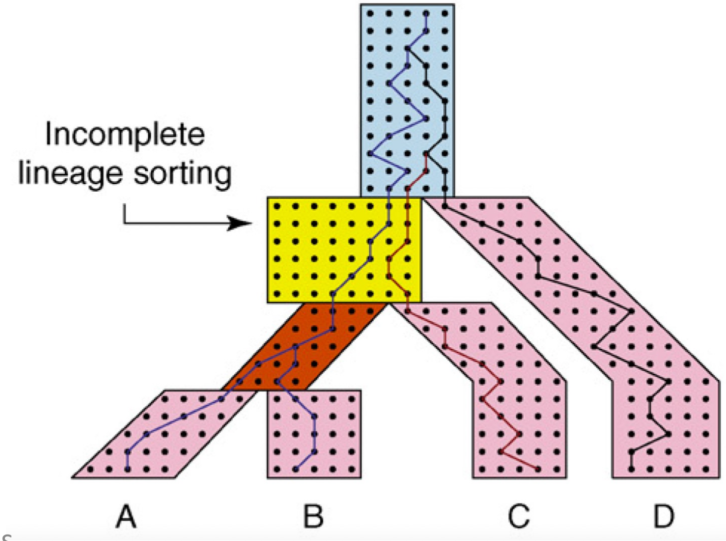
Phylogenomics and gene tree discordance



Species tree



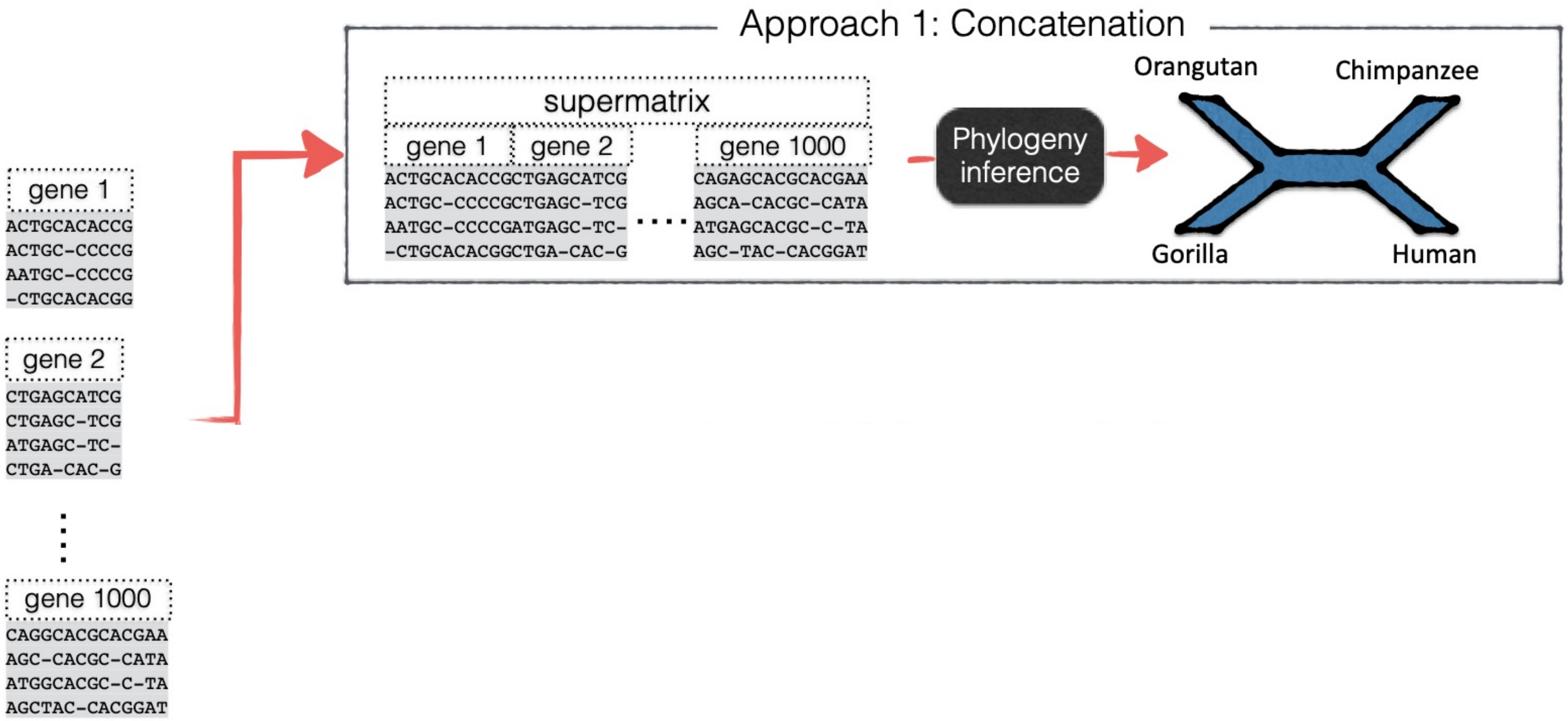
Gene trees



- Incomplete lineage sorting (ILS) is a major cause of gene tree discordance.
- ILS can be modeled by the multi-species coalescent (MSC) model.

Image Credit: Degnan and Rosenberg, 2009, Trends in Ecology and Evolution

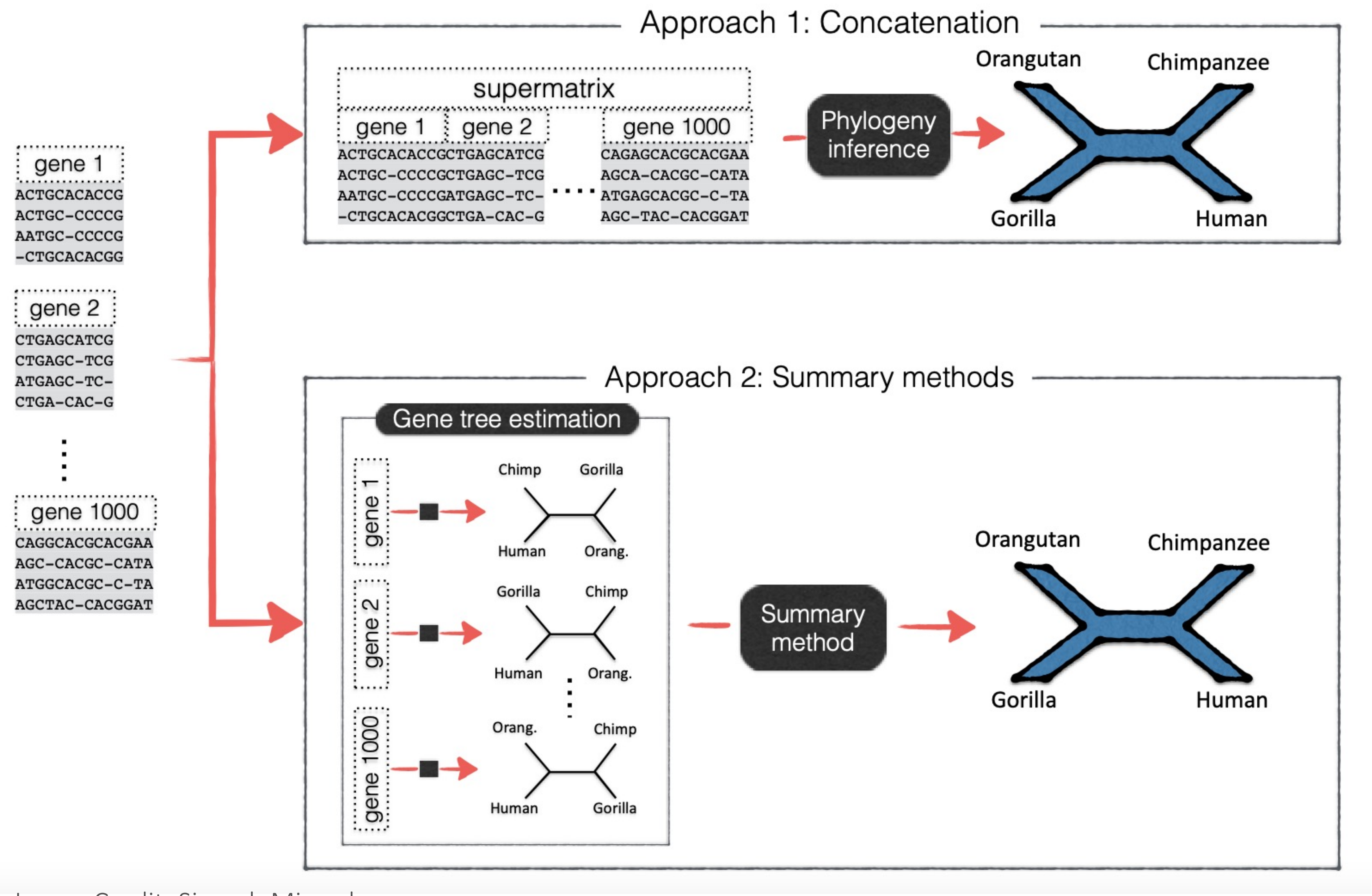
Species tree and branch length estimation



Maximum Likelihood, e.g.
RAxML [Stamatakis, 2014]
FastTree [Price et al, 2010]

Image Credit: Siavash Mirarab

Species tree and branch length estimation



Maximum Likelihood, e.g.
RAxML [Stamatakis, 2014]
FastTree [Price et al, 2010]

ASTRAL [Mirarab et al, 2014]
MP-EST [Liu et al, 2010]
...

Image Credit: Siavash Mirarab

Species tree and branch length estimation

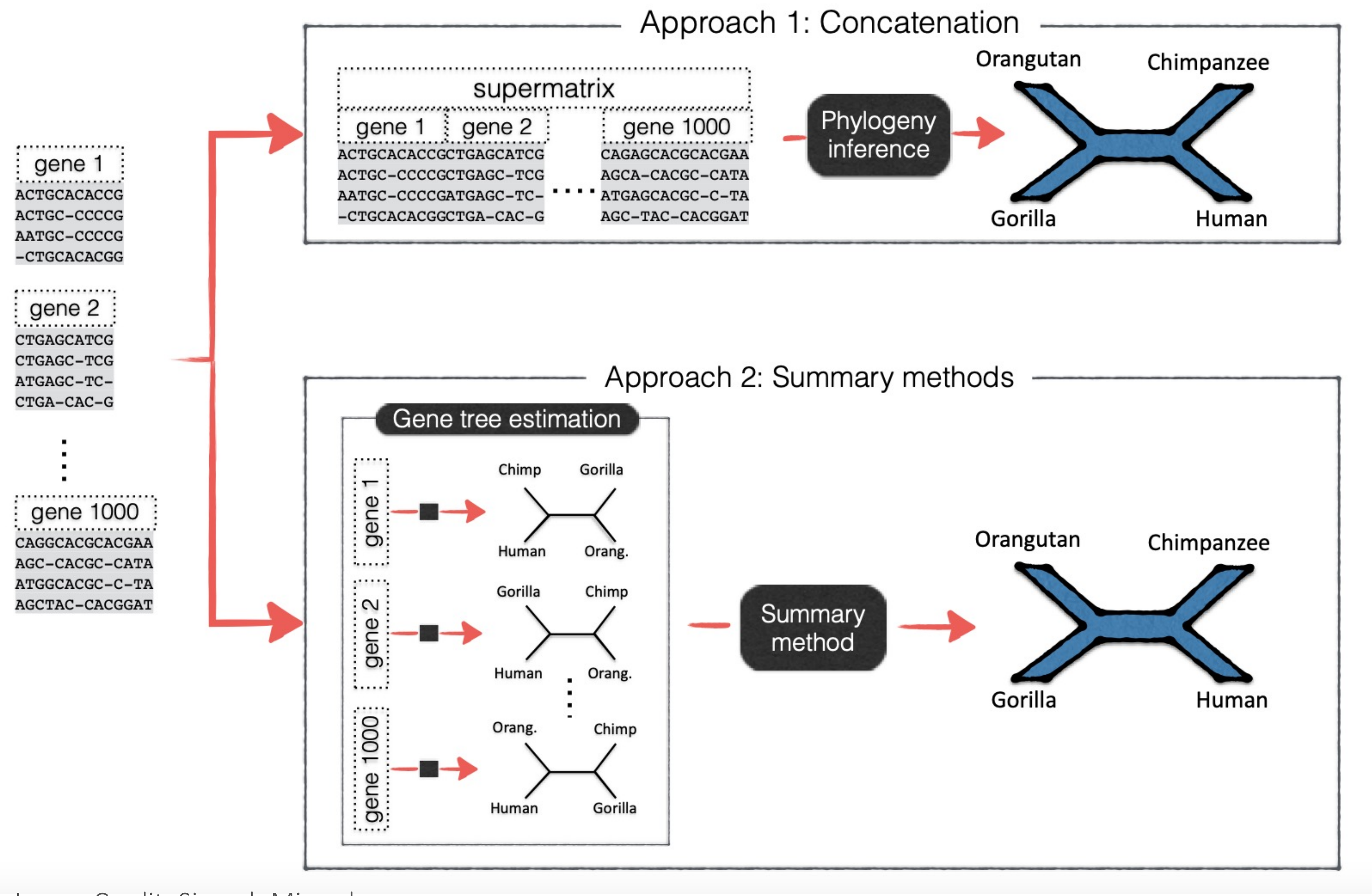


Image Credit: Siavash Mirarab

- Summary methods are more scalable and more accurate when ILS is high, but produce branch lengths in coalescent units (CU)

- CU branch lengths are not useful for most downstream analysis

- **Two-step approach**:

1. infer the topology with summary methods (e.g. ASTRAL, MP-EST)
2. infer branch lengths on that fixed topology with concatenation

Species tree and branch length estimation

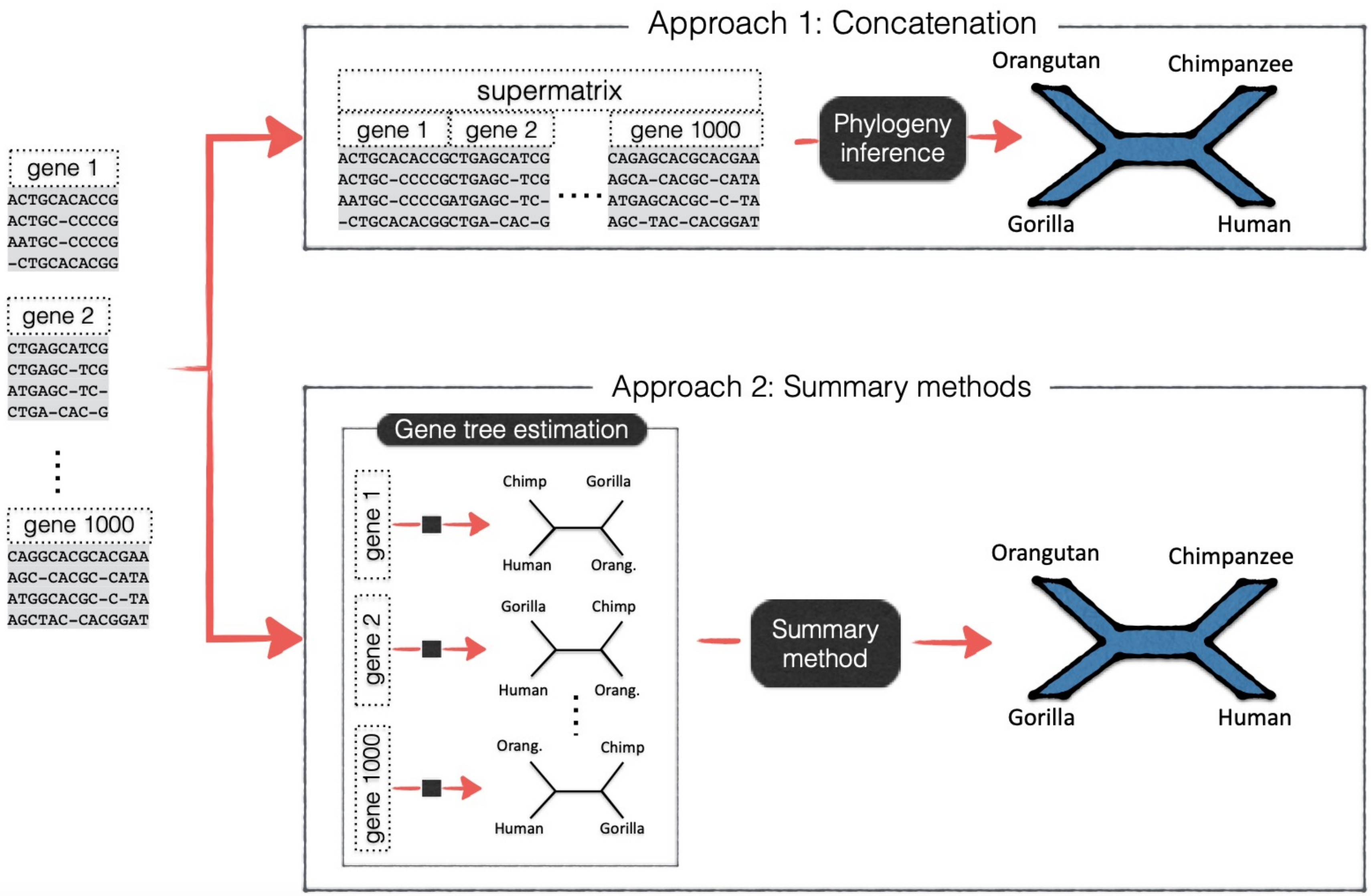


Image Credit: Siavash Mirarab

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- CU branch lengths are not useful for most downstream analysis

- **Two-step approach**:

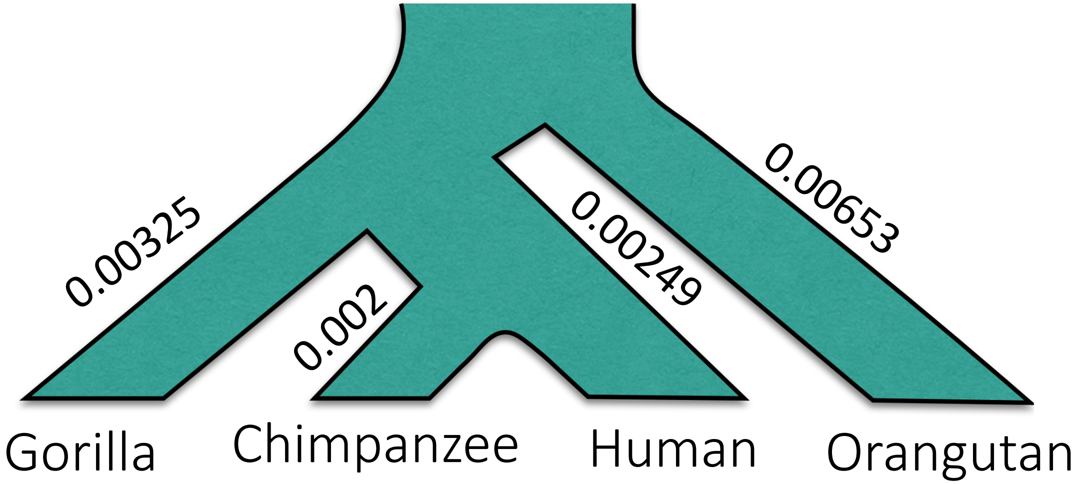
1. infer the topology with summary methods (e.g. ASTRAL, MP-EST)
2. infer branch lengths on that fixed topology with concatenation

ignores heterogeneity across the genome

Branch lengths are necessary for downstream analysis

- Most downstream analysis need branch lengths in the unit of the expected number of substitutions per sites (SU)

- Applications of SU branch lengths
  - Dating
  - Comparative genomics
  - Species delimitation
  - Detecting and characterizing selection
  - …



- CU branch lengths do not directly lead to SU branch lengths and are only inferable for internal branches

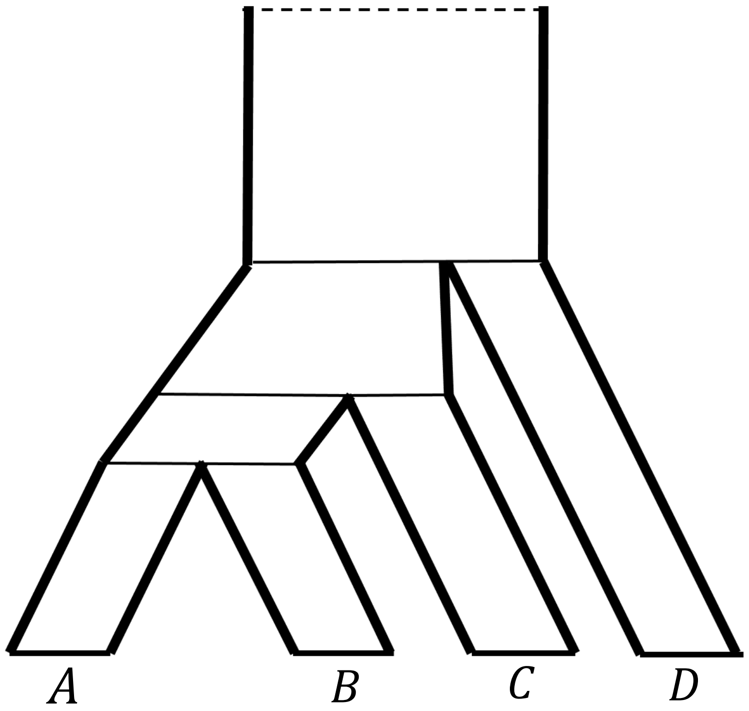
Our motivation

Can we design a branch length estimation method that…

- estimates branch lengths in substitution units (SU)
- addresses gene tree heterogeneity due to ILS and variation in mutation rates
- has strong theoretical foundation based on the MSC
- is scalable to large genome-wide datasets with hundreds to thousands of genes and species?

MSC+Substitution model

species tree S



MSC+Substitution model

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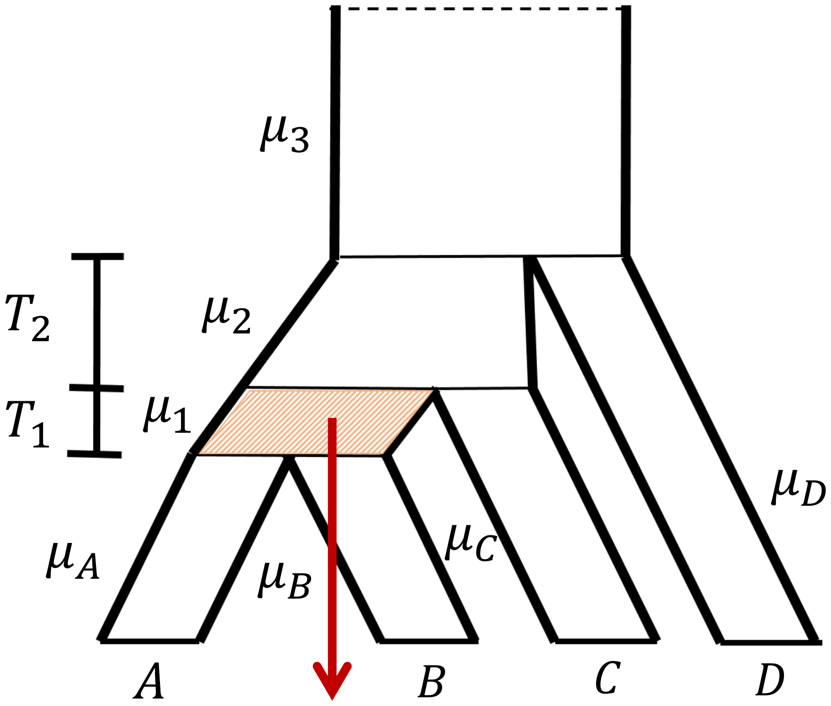
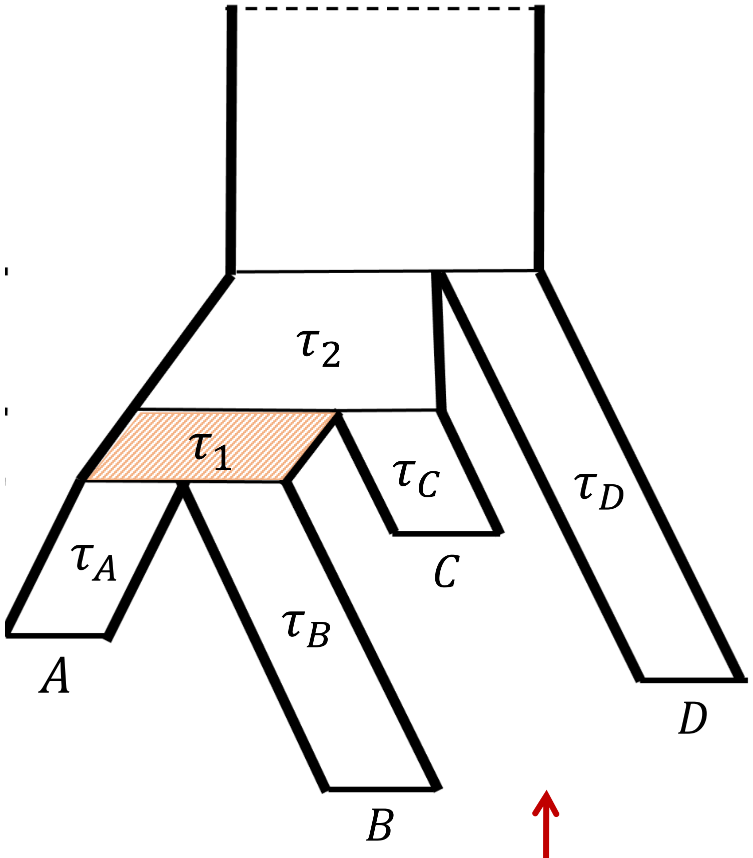


Parameters of branch 1:

μ_1	Substitution rate
T_1	Branch length in coalescent units (CU)
$\tau_1 = T_1.\mu_1$	Branch length in substitution units (SU)

MSC+Substitution model

S with SU branch lengths



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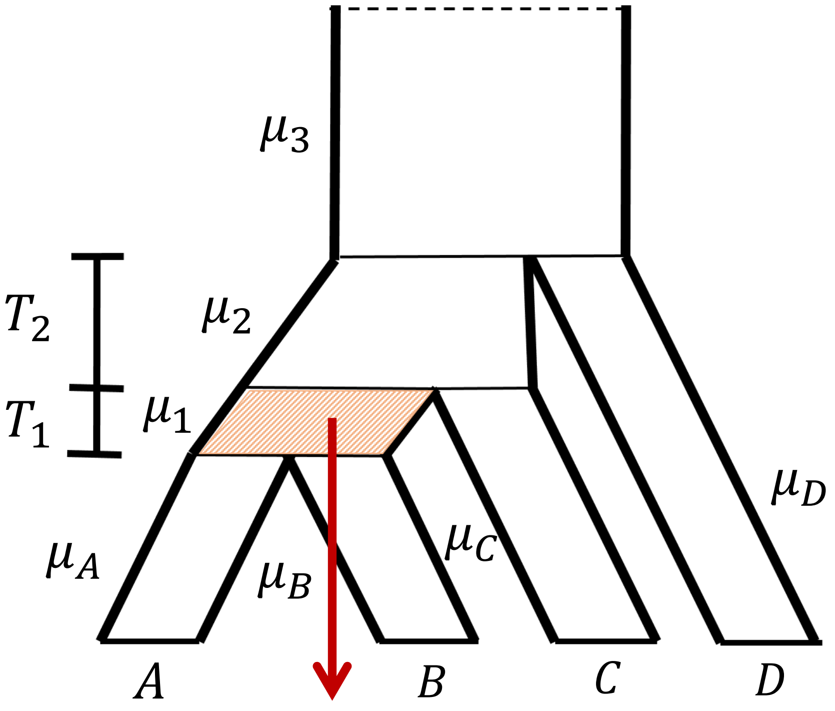

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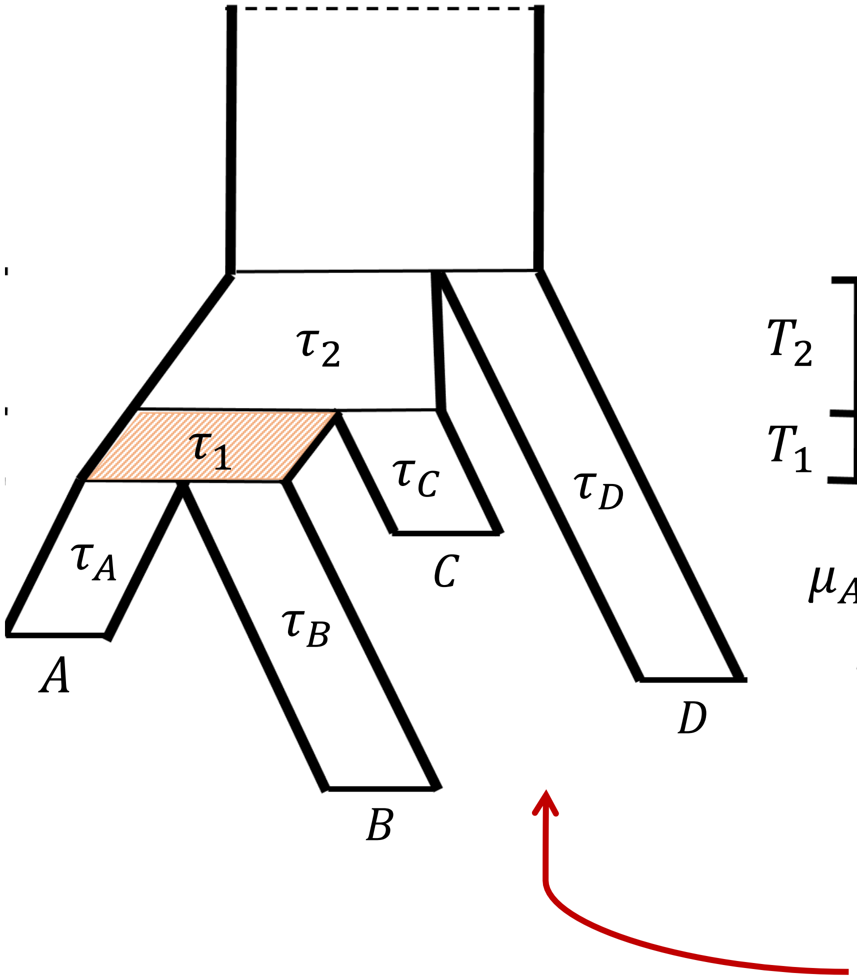
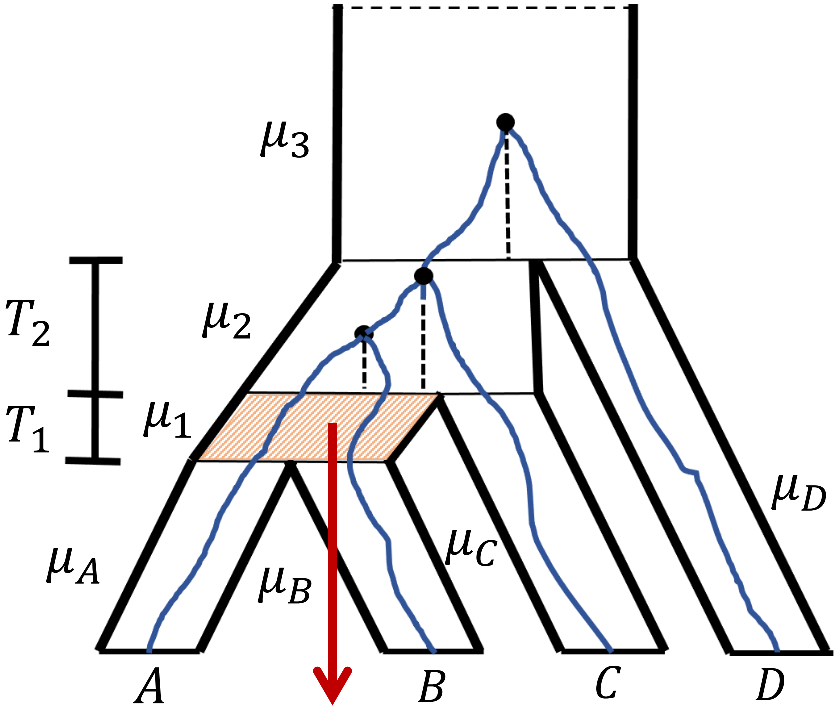


species tree S



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MSC+Substitution model

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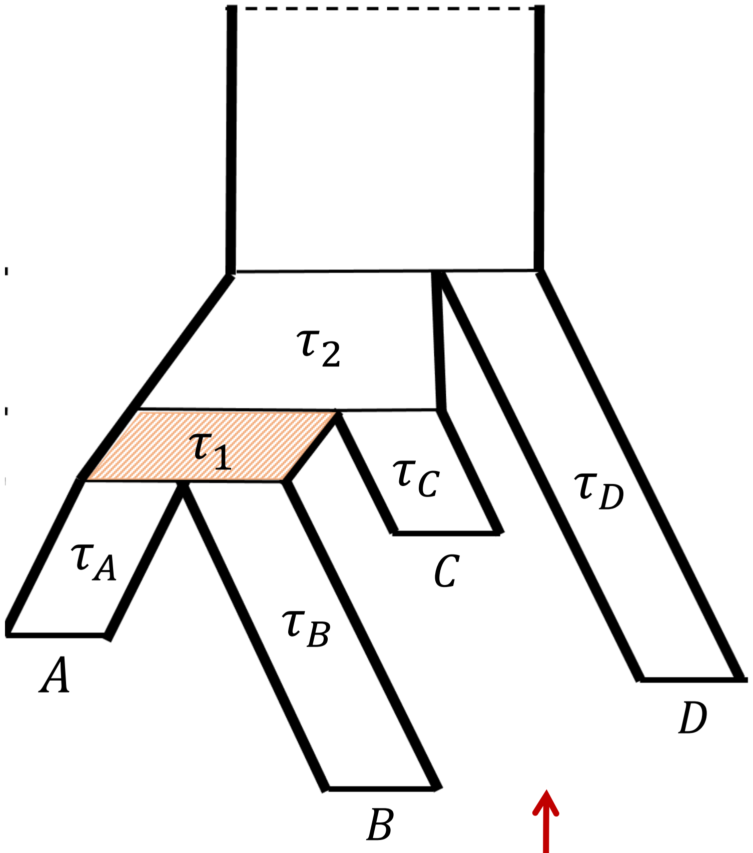
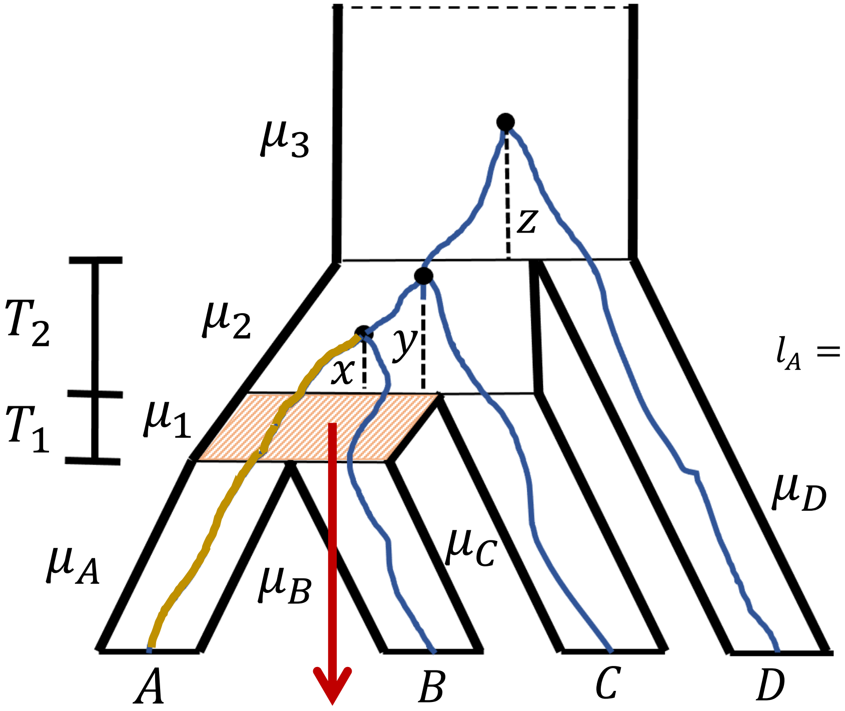
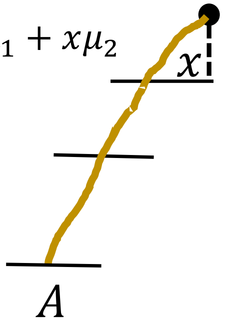


species tree S



$l_A = T_A\mu_A + T_1\mu_1 + x\mu_2$



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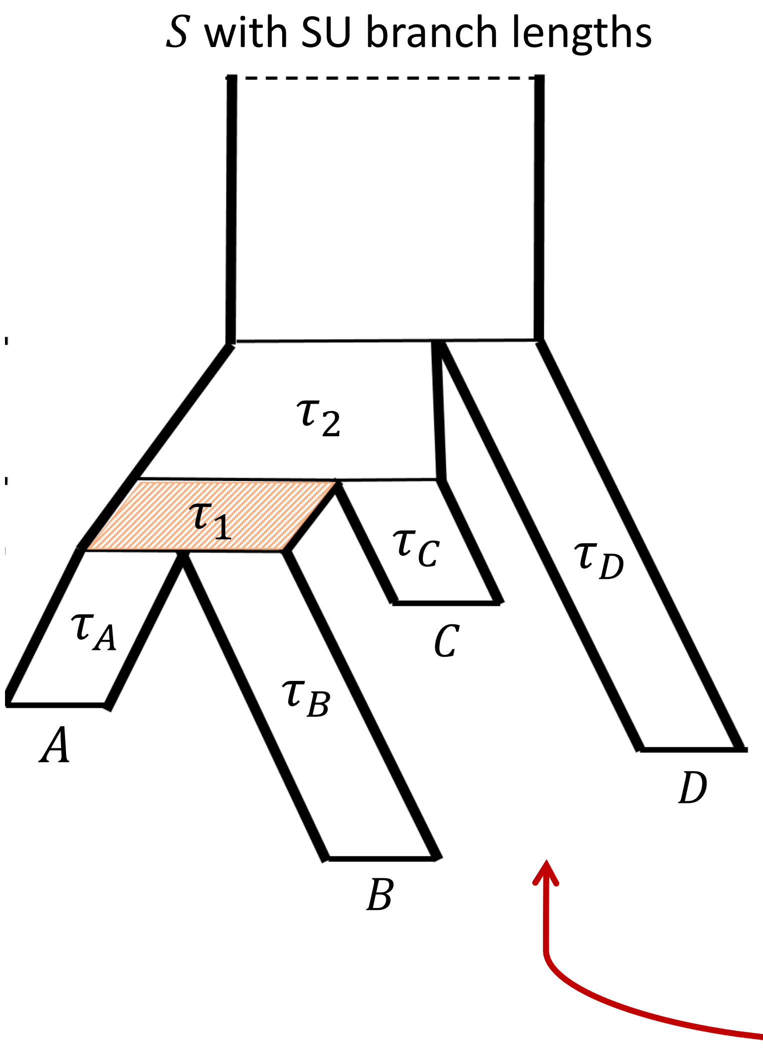
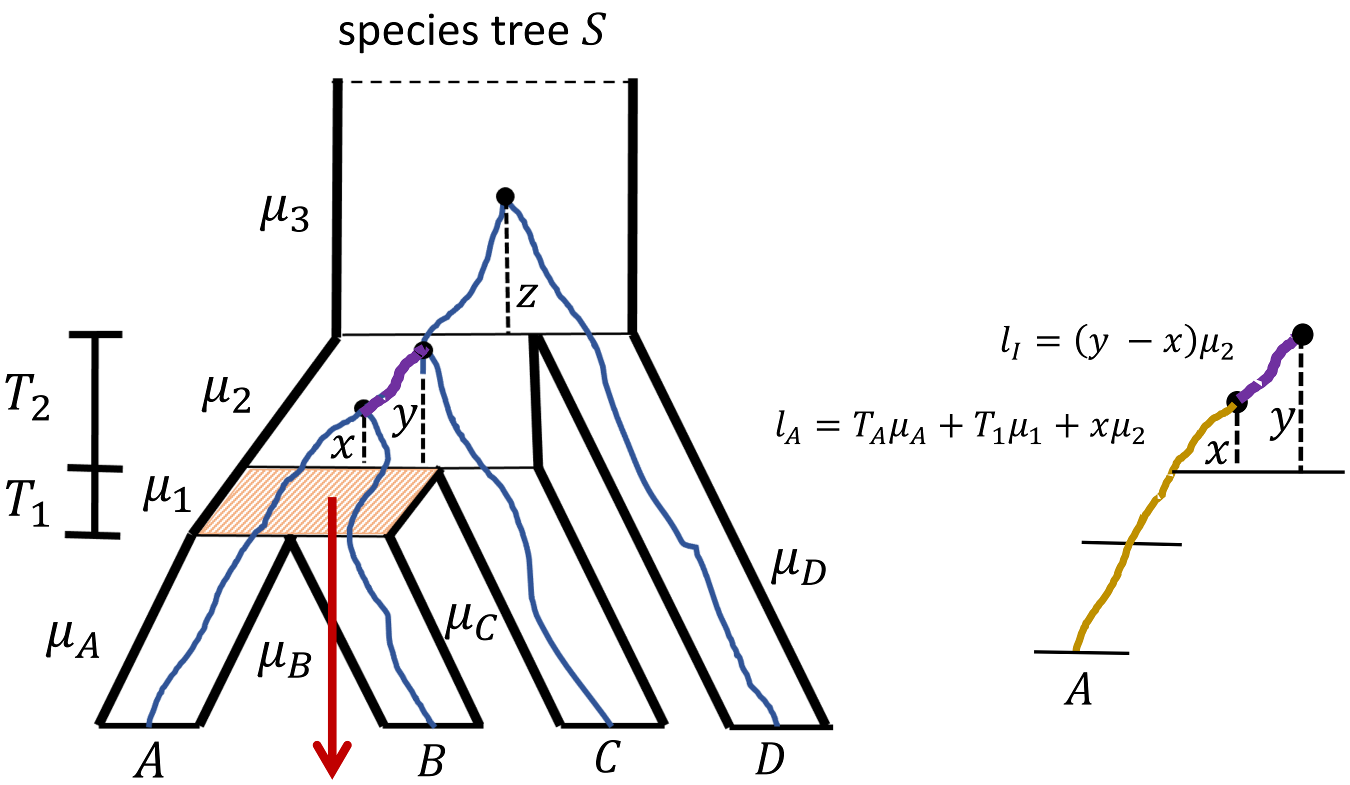
MSC+Substitution model





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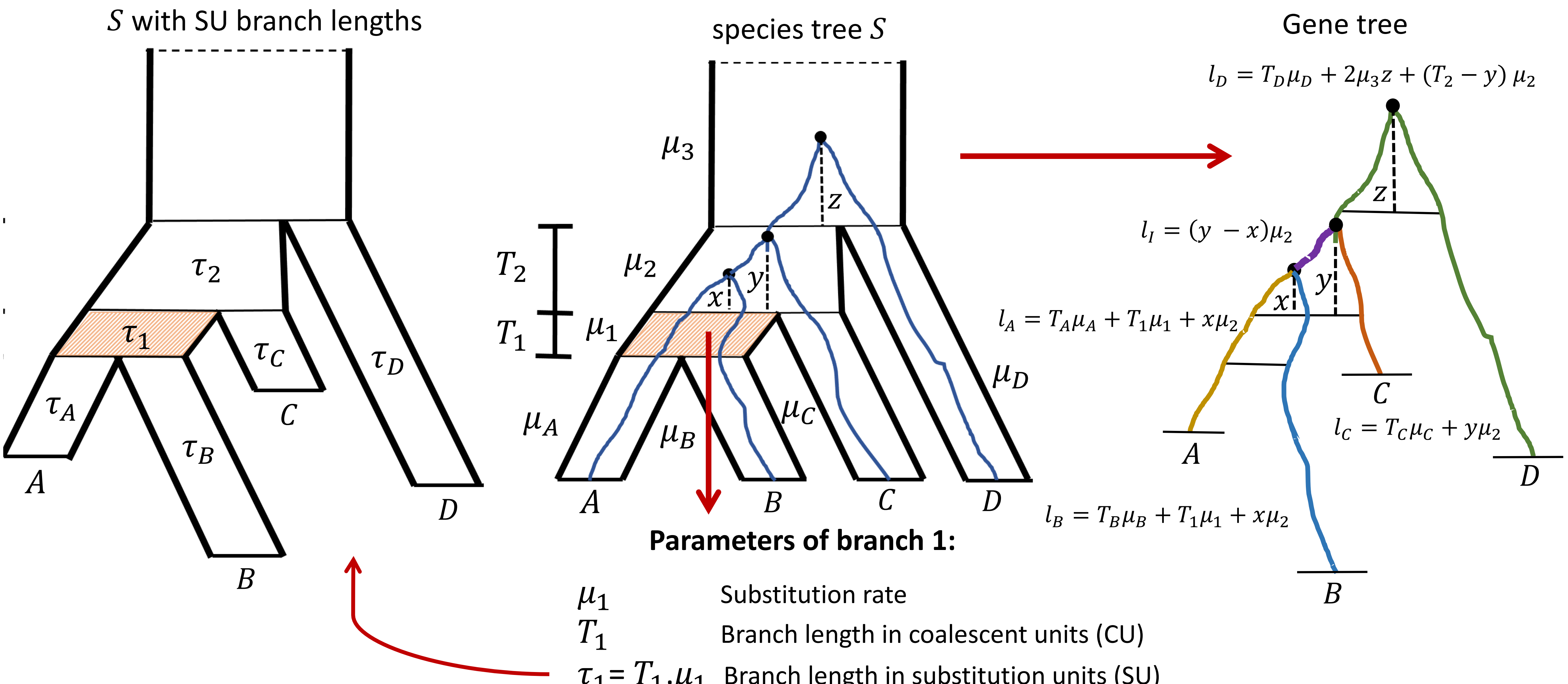

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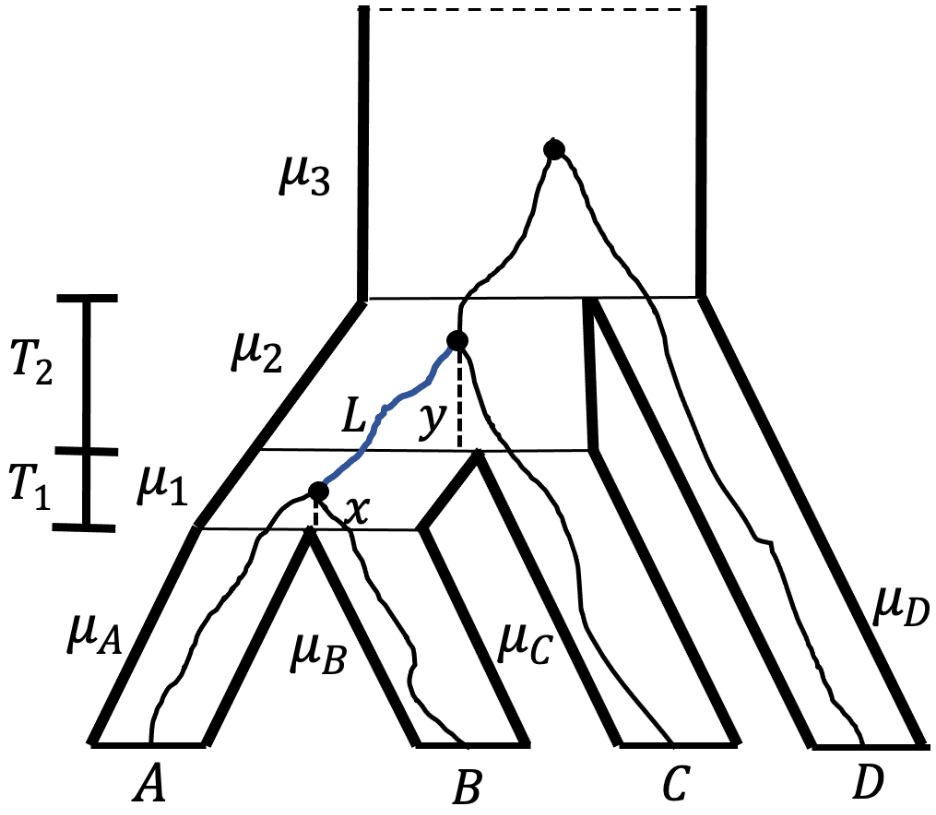
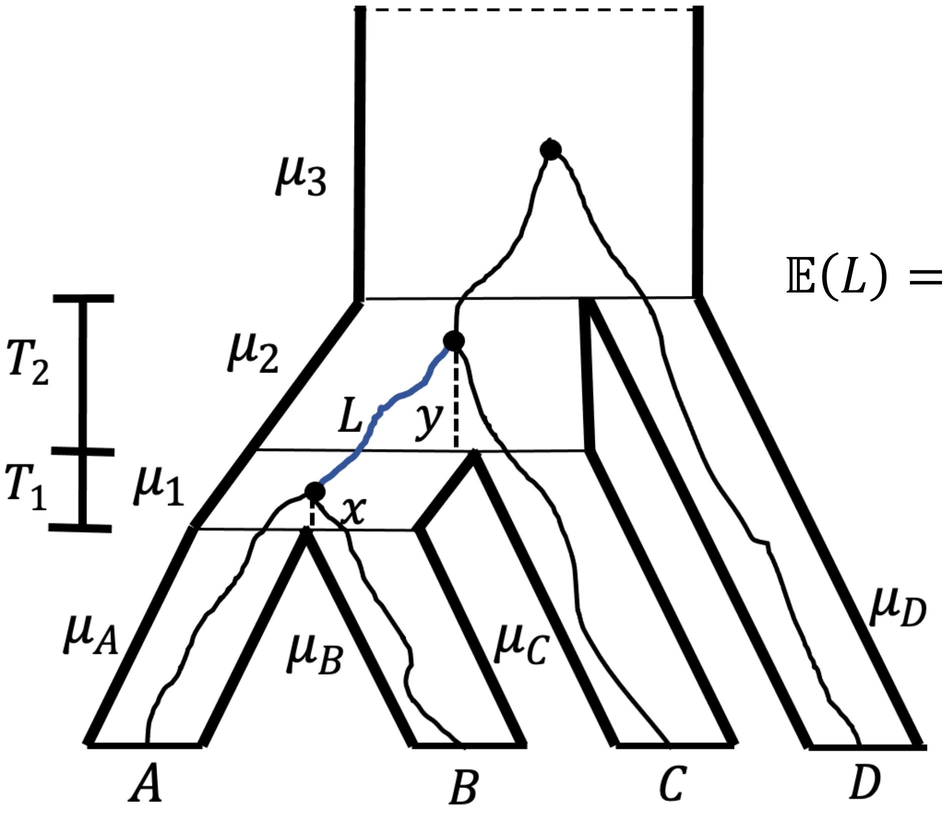
Expected quartet branch lengths under MSC



$$L = (T_1 - x)\mu_1 + y\mu_2$$

Expected quartet branch lengths under MSC



$$L = (T_1 - x)\mu_1 + y\mu_2$$

$$\mathbb{E}(L) = \int_0^{T_1}\int_0^{T_2} e^{-x}\, e^{-y}\big((T_1 - x)\mu_1 + y\mu_2\big)dydx$$

↑

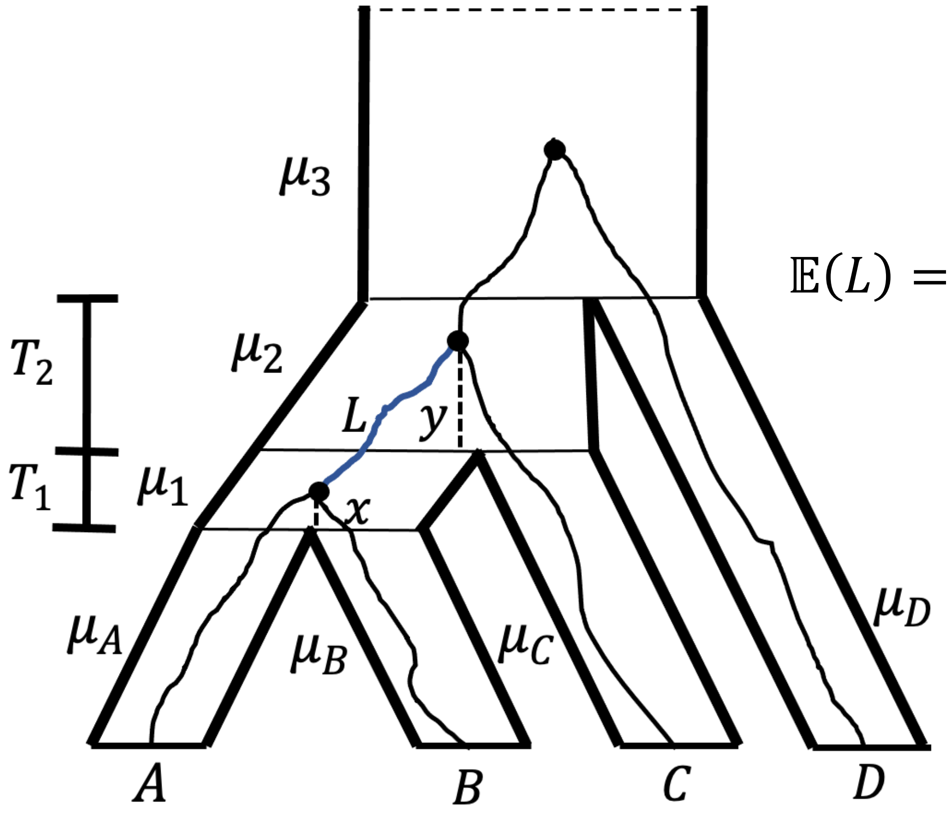
$k = 2$ lineages not coalescing in an interval with length x

- Under MSC, waiting times before coalescent events are exponential random variables with rate $\lambda = \binom{k}{2}$ where k is the number of lineages entering an interval

↓

$$f_X(x) = \binom{k}{2} e^{-\binom{k}{2}x}$$

Expected quartet branch lengths under MSC



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What about other patterns of coalescence?

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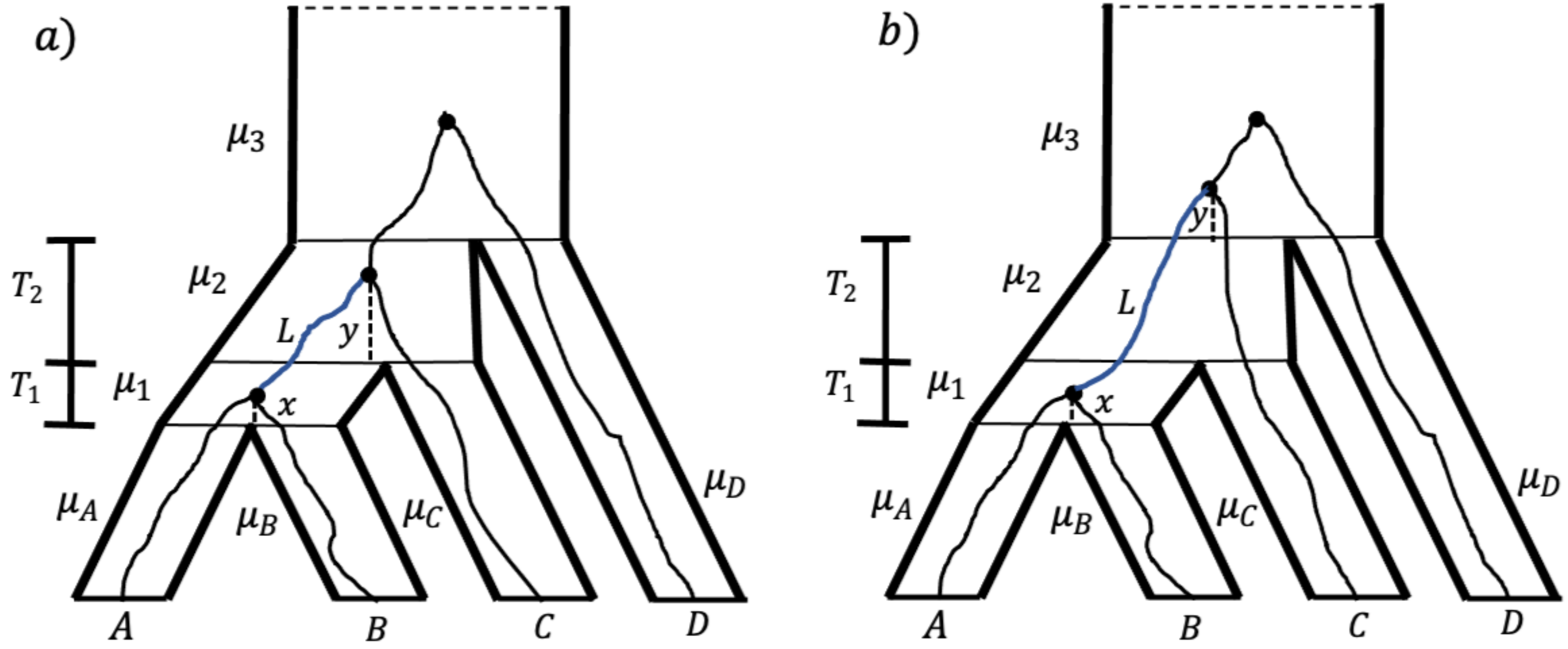
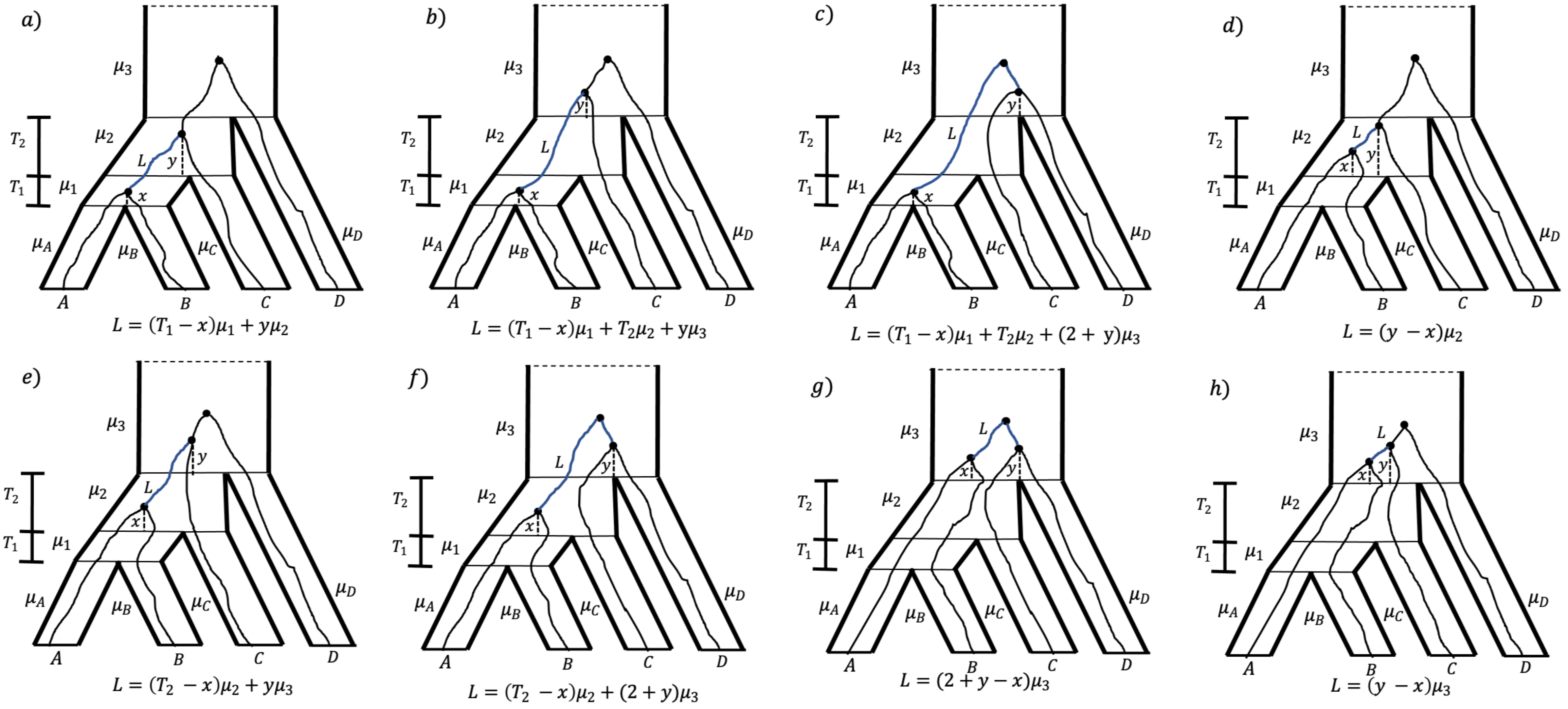


$$L = (T_1 - x)\mu_1 + y\mu_2$$

$$L = (T_1 - x)\mu_1 + T_2\mu_2 + y\mu_3$$

different patterns → different expected lengths

Scenarios for gene tree matching the unbalanced species tree



$L = (T_1 - x)\mu_1 + y\mu_2$

$L = (T_1 - x)\mu_1 + T_2\mu_2 + y\mu_3$

$L = (T_1 - x)\mu_1 + T_2\mu_2 + (2 + y)\mu_3$

$L = (y - x)\mu_2$

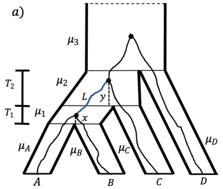
$L = (T_2 - x)\mu_2 + y\mu_3$

$L = (T_2 - x)\mu_2 + (2 + y)\mu_3$

$L = (2 + y - x)\mu_3$

$L = (y - x)\mu_3$

Expected quartet branch lengths under MSC

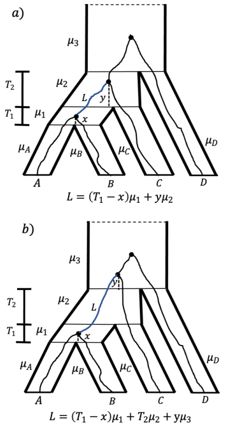


$L = (T_1 - x)\mu_1 + y\mu_2$

$$L_I = (\int_0^{T_1}\int_0^{T_2} e^{-x}\, e^{-y}\big((T_1 - x)\mu_1 + y\mu_2\big)dydx$$

scenario (a)

Expected quartet branch lengths under MSC



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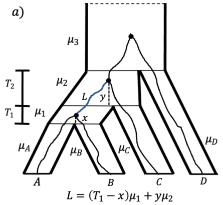
scenario (a)

$$+2e^{-T_2} \int_0^{T_1} \int_0^{\infty} e^{-x}\, e^{-3y}\big((T_1 - x)\mu_1 + T_2\mu_2 + y\mu_3\big)dydx$$

scenario (b)

Expected quartet branch lengths under MSC



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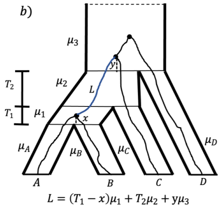
scenario (a)



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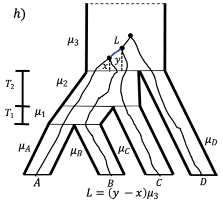
scenario (b)

$$\vdots$$



$$+4e^{-T_1} e^{-3T_2} \int_0^{\infty} \int_x^{\infty} e^{-6x}\, e^{-3(y-x)} (y - x)\mu_3 dydx) \,/ (1 - \frac{2}{3} e^{-T_1})$$

scenario (h)

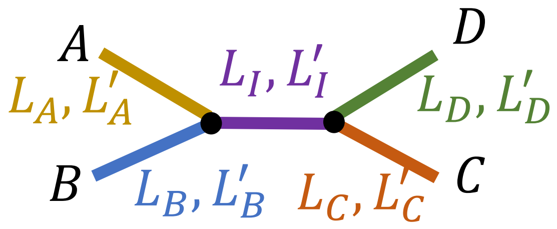
Expected value of internal branch length conditioned on gene tree matching the species tree

$$= \boxed{\frac{(e^{-3T_2} + 3e^{-T_2} - 6e^{T_1 - T_2})(\mu_2 - \mu_3) + 6(1 - e^{T_1} + T_1 e^{T_1})\mu_1}{2(3e^{T_1} - 2)} + \mu_2}$$

How do we infer the species tree parameters?

- We derive expected values for all branches (internal and terminal), for both matching and non-matching gene trees.

- The parameters of the species tree can be estimated from these 10 equations.



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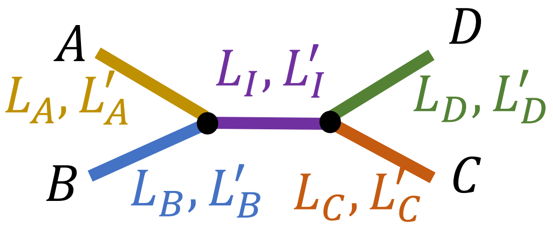


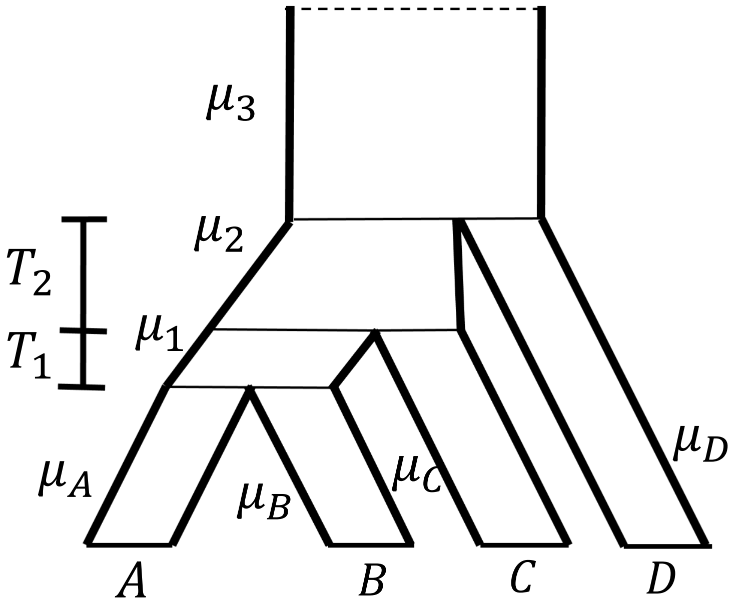
- **Challenge**: Solving these systems of equations directly can cause numerical instabilities and may not produce optimal solutions.

- We use simplifications that give analytical formulas for every branch of a quartet tree.

Simplifications (example)

Expected lengths for internal branch

$$\begin{cases} L_I = \dfrac{(e^{-3T_2} + 3e^{-T_2} - 6e^{T_1-T_2})(\mu_2 - \mu_3) + 6(1\ - e^{T_1} + T_1 e^{T_1})\mu_1}{2(3e^{T_1} - 2)} + \mu_2 \\ L_I' = \mu_2 + \frac{1}{2}(\mu_2 - \mu_3)\ (e^{-3T_2} - e^{-T_2}) \end{cases}$$



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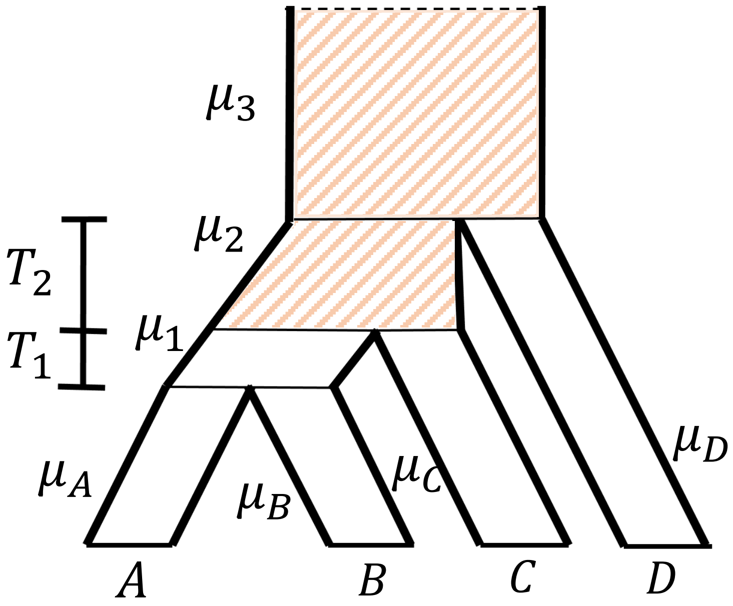
Local clock assumption: $\mu_2 = \mu_3$

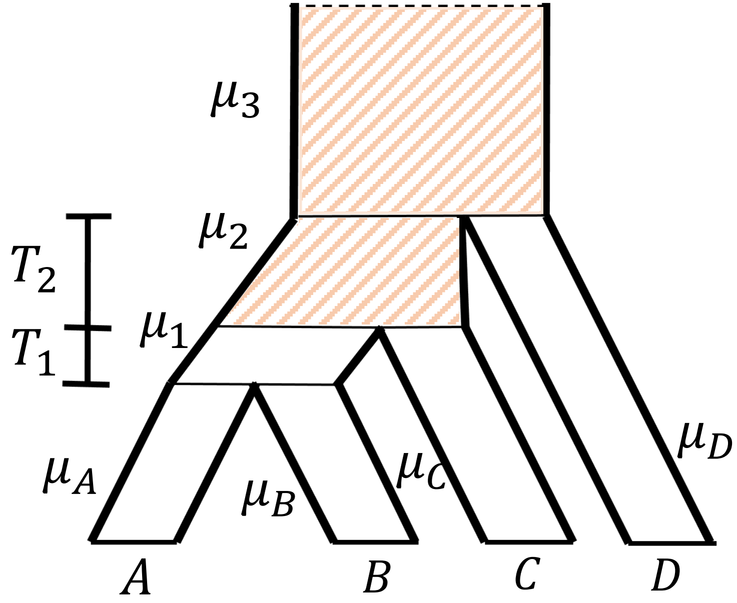


Simplifications (example)

Expected lengths for internal branch

$$L_I = \frac{(e^{-3T_2} + \cancel{3e^{-T_2} - 6e^{T_1-T_2})(\mu_2 - \mu_3}) + 6(1 - e^{T_1} + T_1 e^{T_1})\mu_1}{2(3e^{T_1} - 2)} + \mu_2$$

$$L_I' = \mu_2 + \frac{1}{2}\cancel{(\mu_2 - \mu_3)\,(e^{-3T_2} - e^{-T_2})}$$



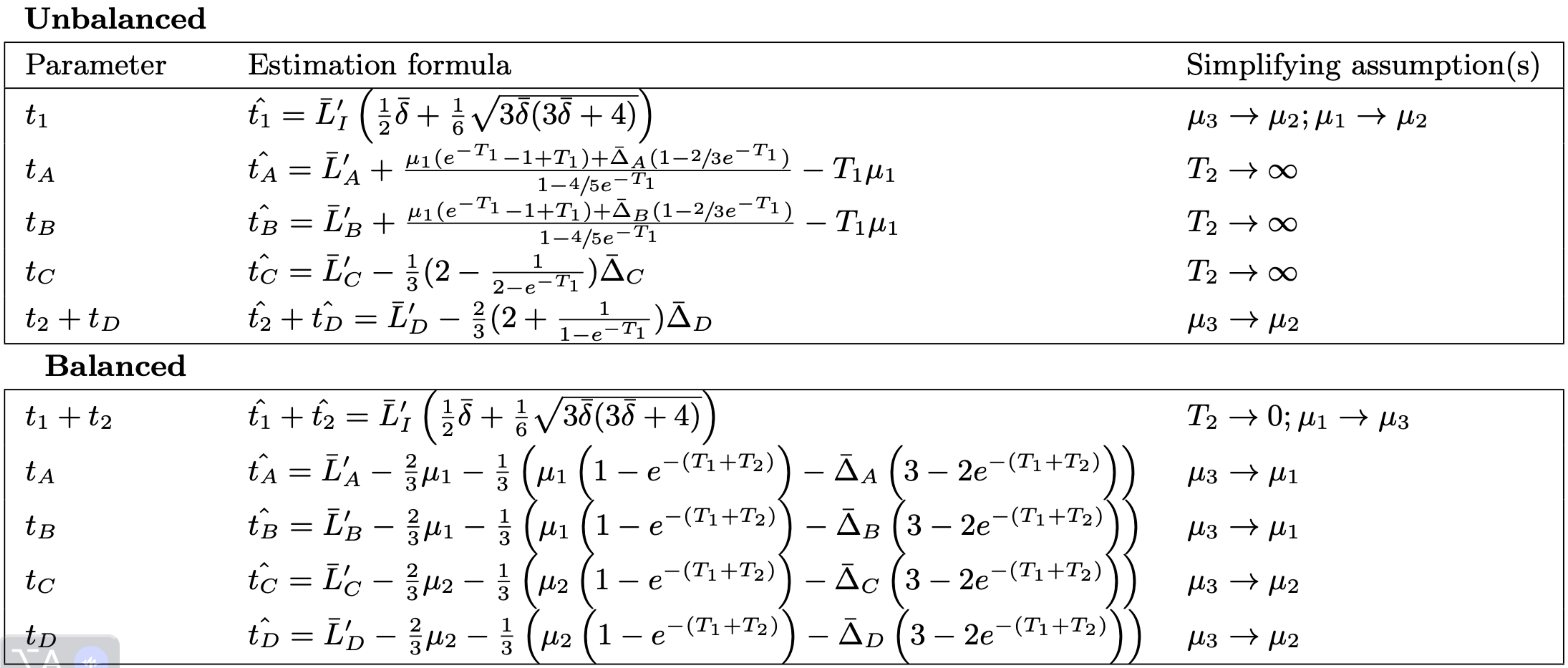
Local clock assumption: $\mu_2 = \mu_3$

Simplified formulas

$$\lim_{\mu_2 \to \mu_3} L_I = \frac{3\mu_1(e^{-T_1} - 1 + T_1)}{3 - 2e^{-T_1}} + \mu_2$$

$$\lim_{\mu_2 \to \mu_3} L_I' = \mu_2$$

Summary of SU branch length formulas



Unbalanced

Parameter	Estimation formula	Simplifying assumption(s)
t_1	$\hat{t_1} = \bar{L}'_I \left(\frac{1}{2}\bar{\delta} + \frac{1}{6}\sqrt{3\bar{\delta}(3\bar{\delta}+4)}\right)$	$\mu_3 \to \mu_2; \mu_1 \to \mu_2$
t_A	$\hat{t_A} = \bar{L}'_A + \frac{\mu_1(e^{-T_1}-1+T_1)+\bar{\Delta}_A(1-2/3e^{-T_1})}{1-4/5e^{-T_1}} - T_1\mu_1$	$T_2 \to \infty$
t_B	$\hat{t_B} = \bar{L}'_B + \frac{\mu_1(e^{-T_1}-1+T_1)+\bar{\Delta}_B(1-2/3e^{-T_1})}{1-4/5e^{-T_1}} - T_1\mu_1$	$T_2 \to \infty$
t_C	$\hat{t_C} = \bar{L}'_C - \frac{1}{3}(2 - \frac{1}{2-e^{-T_1}})\bar{\Delta}_C$	$T_2 \to \infty$
$t_2 + t_D$	$\hat{t_2} + \hat{t_D} = \bar{L}'_D - \frac{2}{3}(2 + \frac{1}{1-e^{-T_1}})\bar{\Delta}_D$	$\mu_3 \to \mu_2$

Balanced

$t_1 + t_2$	$\hat{t_1} + \hat{t_2} = \bar{L}'_I \left(\frac{1}{2}\bar{\delta} + \frac{1}{6}\sqrt{3\bar{\delta}(3\bar{\delta}+4)}\right)$	$T_2 \to 0; \mu_1 \to \mu_3$
t_A	$\hat{t_A} = \bar{L}'_A - \frac{2}{3}\mu_1 - \frac{1}{3}\left(\mu_1\left(1-e^{-(T_1+T_2)}\right) - \bar{\Delta}_A\left(3-2e^{-(T_1+T_2)}\right)\right)$	$\mu_3 \to \mu_1$
t_B	$\hat{t_B} = \bar{L}'_B - \frac{2}{3}\mu_1 - \frac{1}{3}\left(\mu_1\left(1-e^{-(T_1+T_2)}\right) - \bar{\Delta}_B\left(3-2e^{-(T_1+T_2)}\right)\right)$	$\mu_3 \to \mu_1$
t_C	$\hat{t_C} = \bar{L}'_C - \frac{2}{3}\mu_2 - \frac{1}{3}\left(\mu_2\left(1-e^{-(T_1+T_2)}\right) - \bar{\Delta}_C\left(3-2e^{-(T_1+T_2)}\right)\right)$	$\mu_3 \to \mu_2$
t_D	$\hat{t_D} = \bar{L}'_D - \frac{2}{3}\mu_2 - \frac{1}{3}\left(\mu_2\left(1-e^{-(T_1+T_2)}\right) - \bar{\Delta}_D\left(3-2e^{-(T_1+T_2)}\right)\right)$	$\mu_3 \to \mu_2$

CASTLES

Coalescent-**A**ware **S**pecies **T**ree **L**ength **E**stimation in **S**ubstitution-units

Input:

- Rooted species tree *topology* S
- A set of gene trees $\mathcal{G}$ with SU branch lengths

Output:

- Species tree S with SU branch lengths

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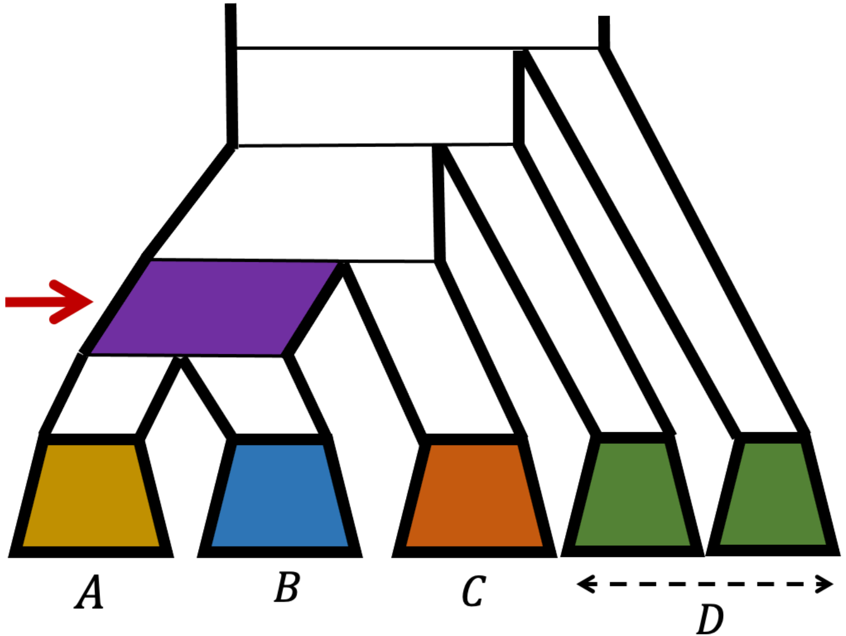

Quadripartition $AB|CD$

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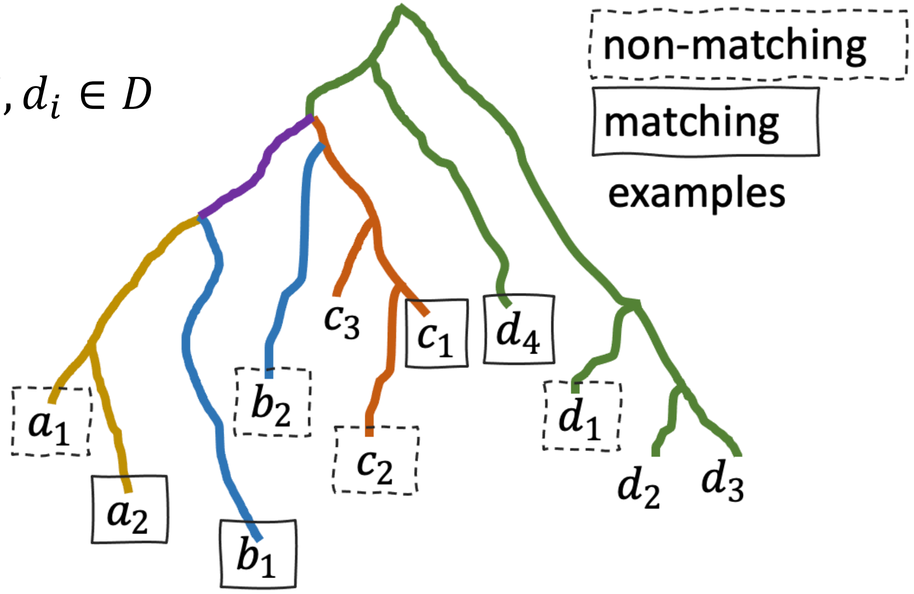
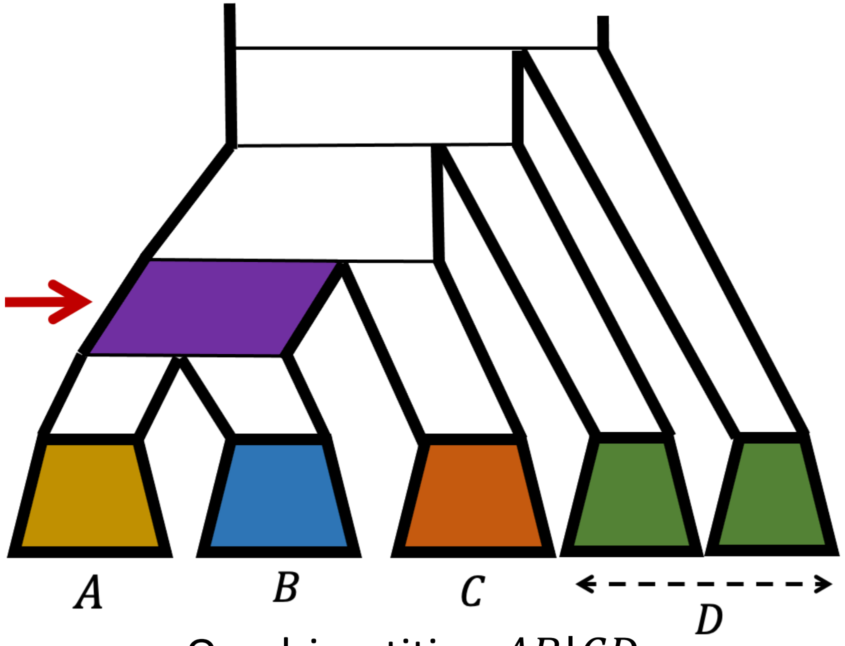
Quartets: $a_i \in A, b_i \in B, c_i \in C, d_i \in D$





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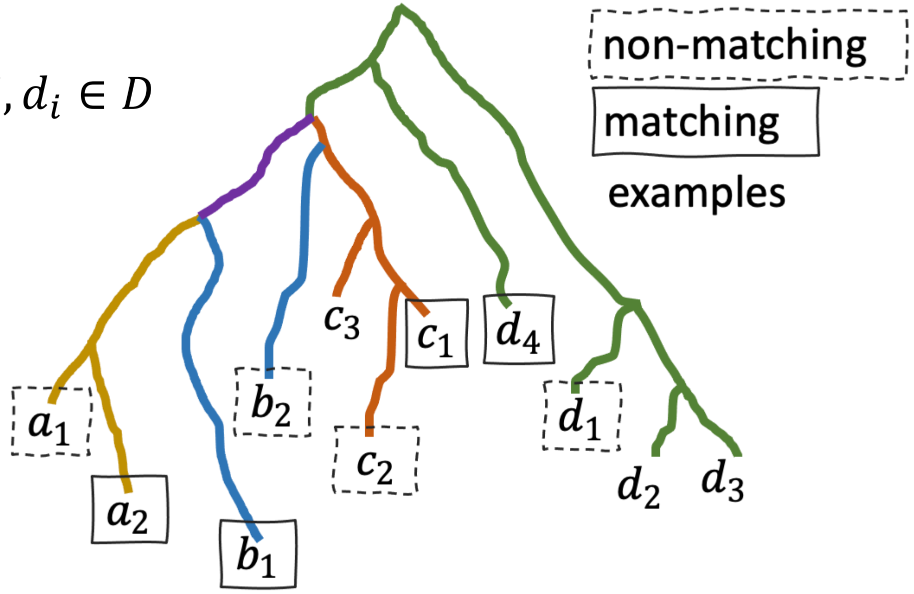
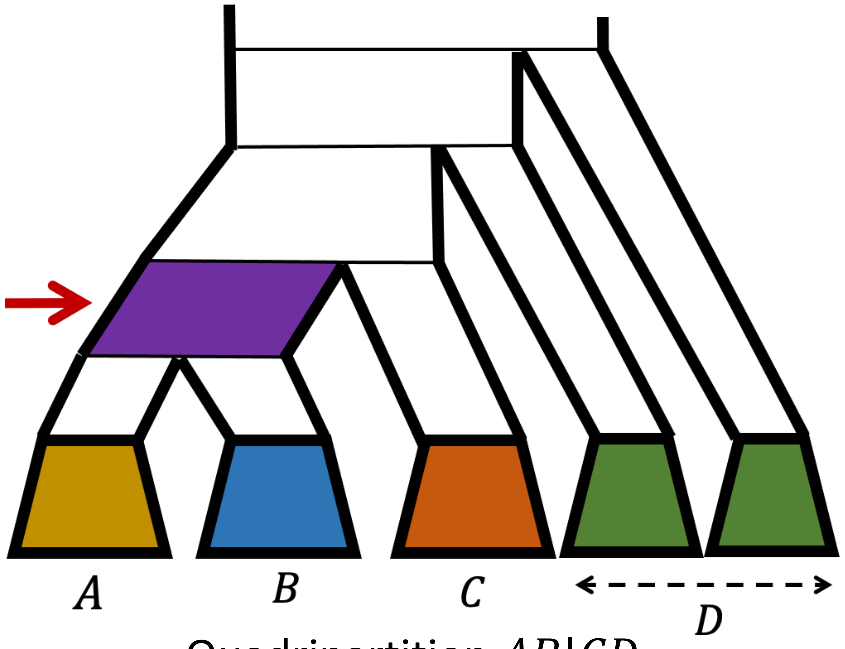
Quartets: $a_i \in A, b_i \in B, c_i \in C, d_i \in D$

- We average branch lengths over all quartets with an $O(n^2k)$ dynamic programming

n species, k genes

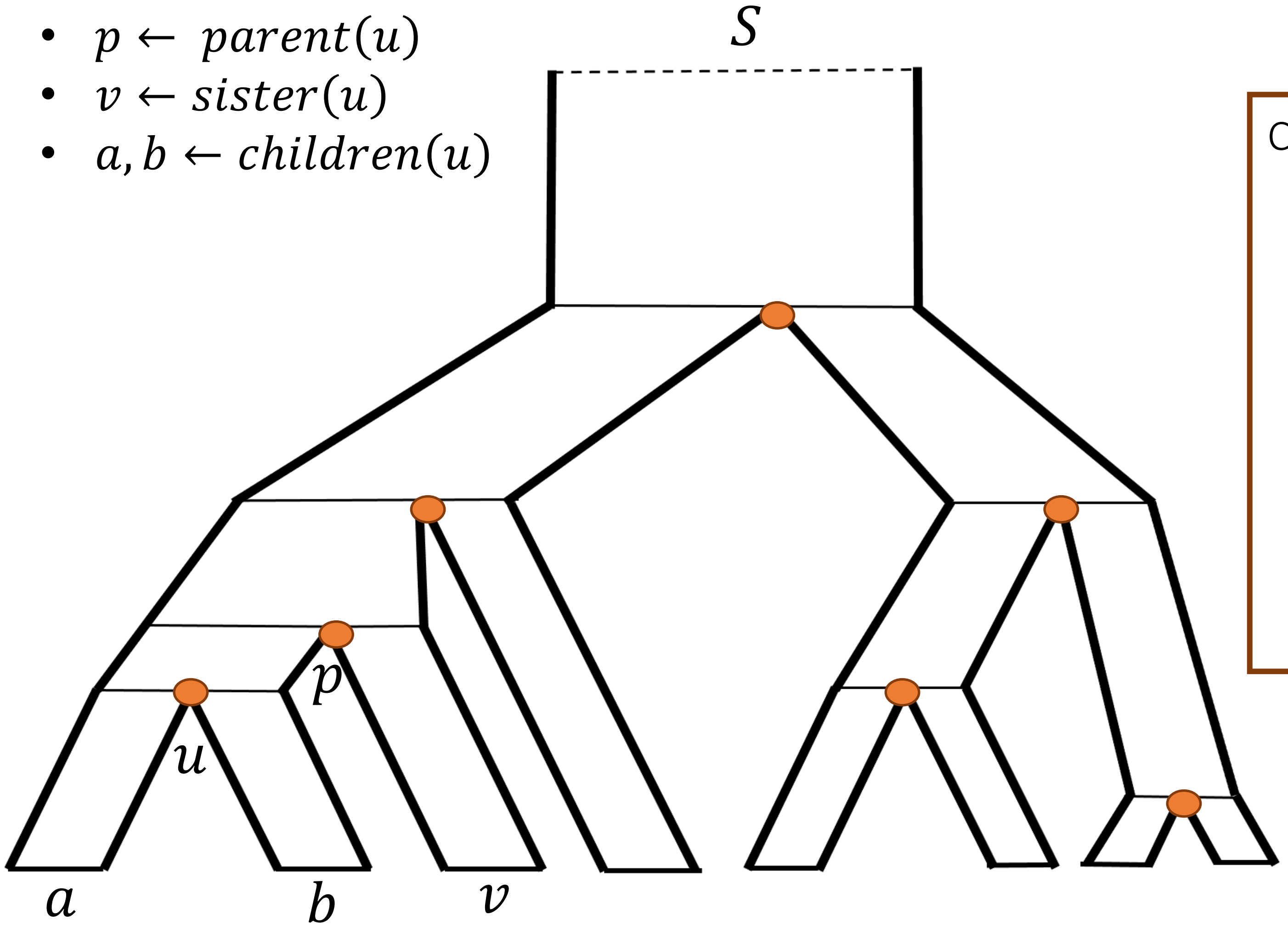




Quadripartition $AB|CD$

Large tree algorithm

- $p \leftarrow parent(u)$
- $v \leftarrow sister(u)$
- $a, b \leftarrow children(u)$



$O(n^2k)$ dynamic programming

Calculate $\overline{L_a}, \overline{L_b}, \overline{L_v}, \overline{L_p}, \overline{L'_a}, \overline{L'_b}, \overline{L'_v}, \overline{L'_p}$ for each branch

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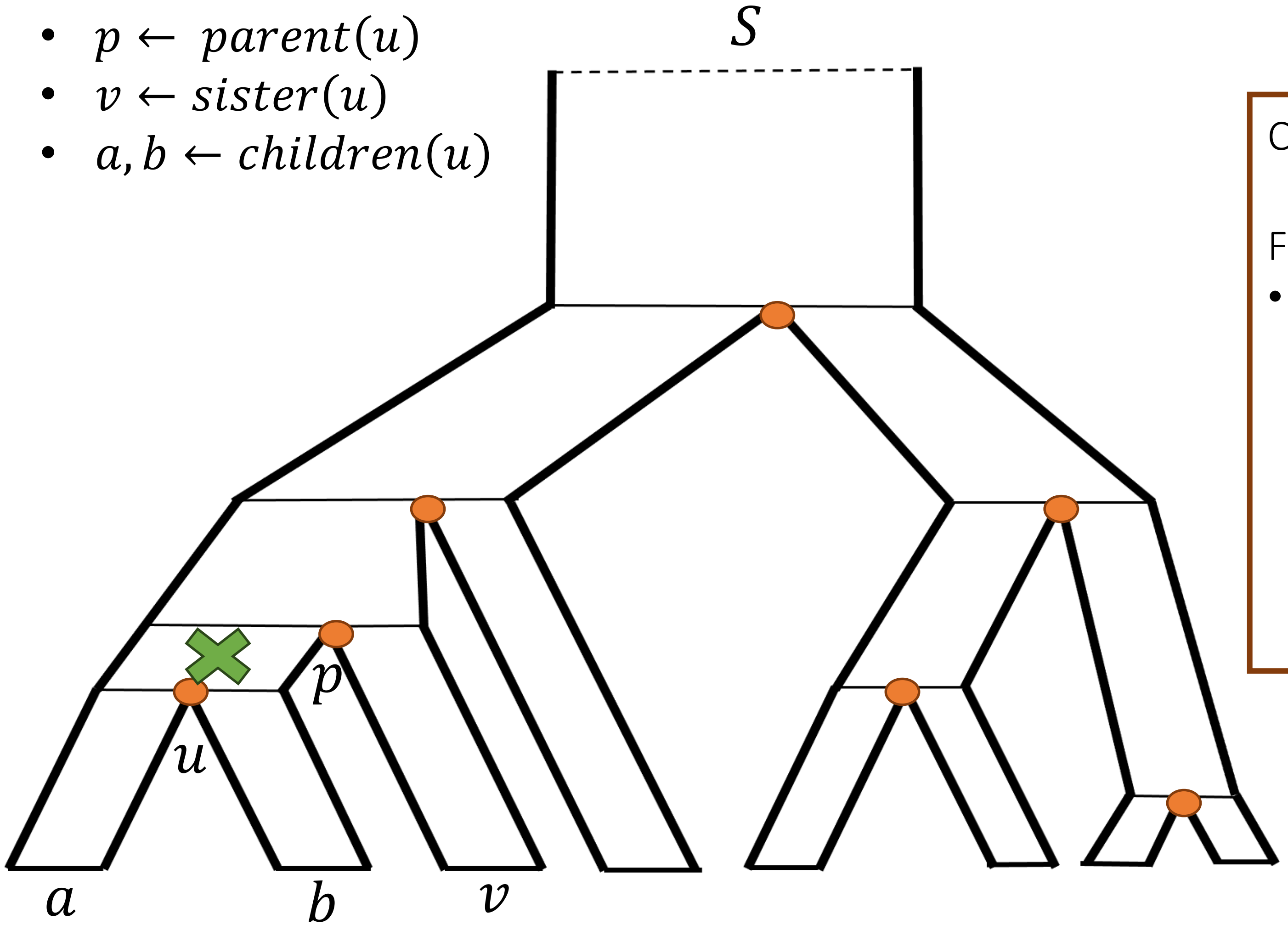

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For $u$ ∈ post order traversal of internal nodes of $S$:
    • if $p$ is not root:
        • $t_{p\to u}$ ← internal branch equation
```

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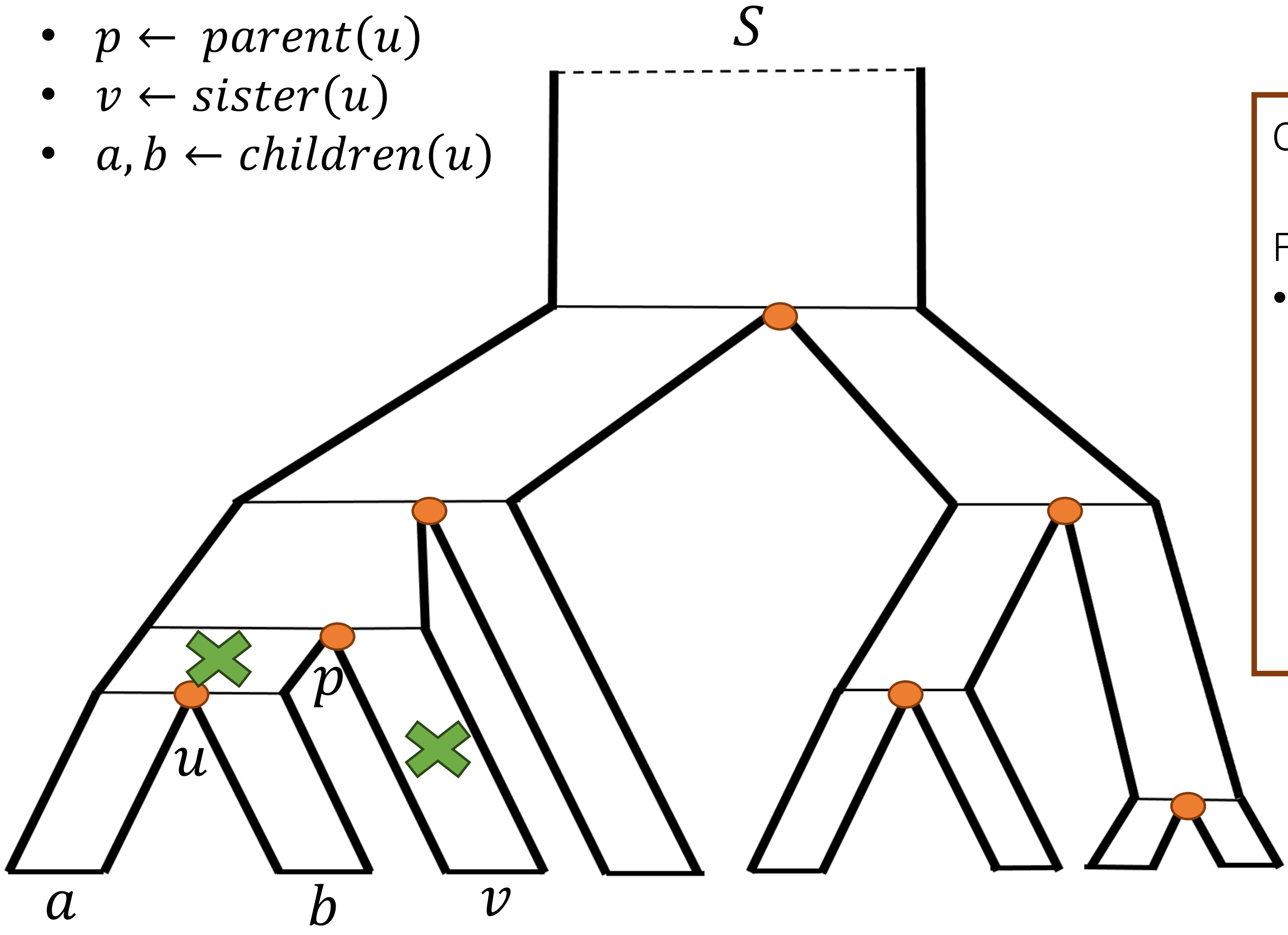

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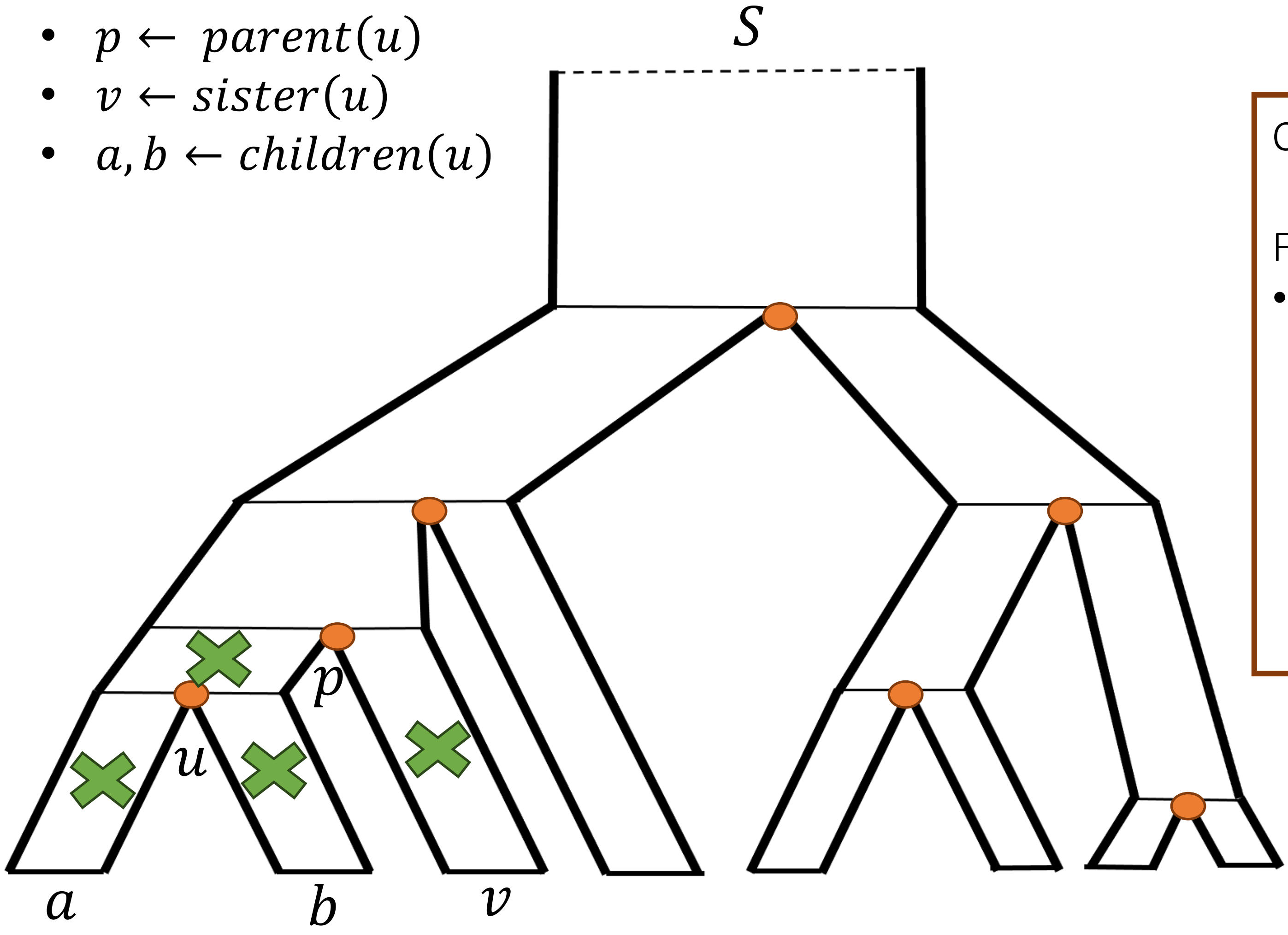

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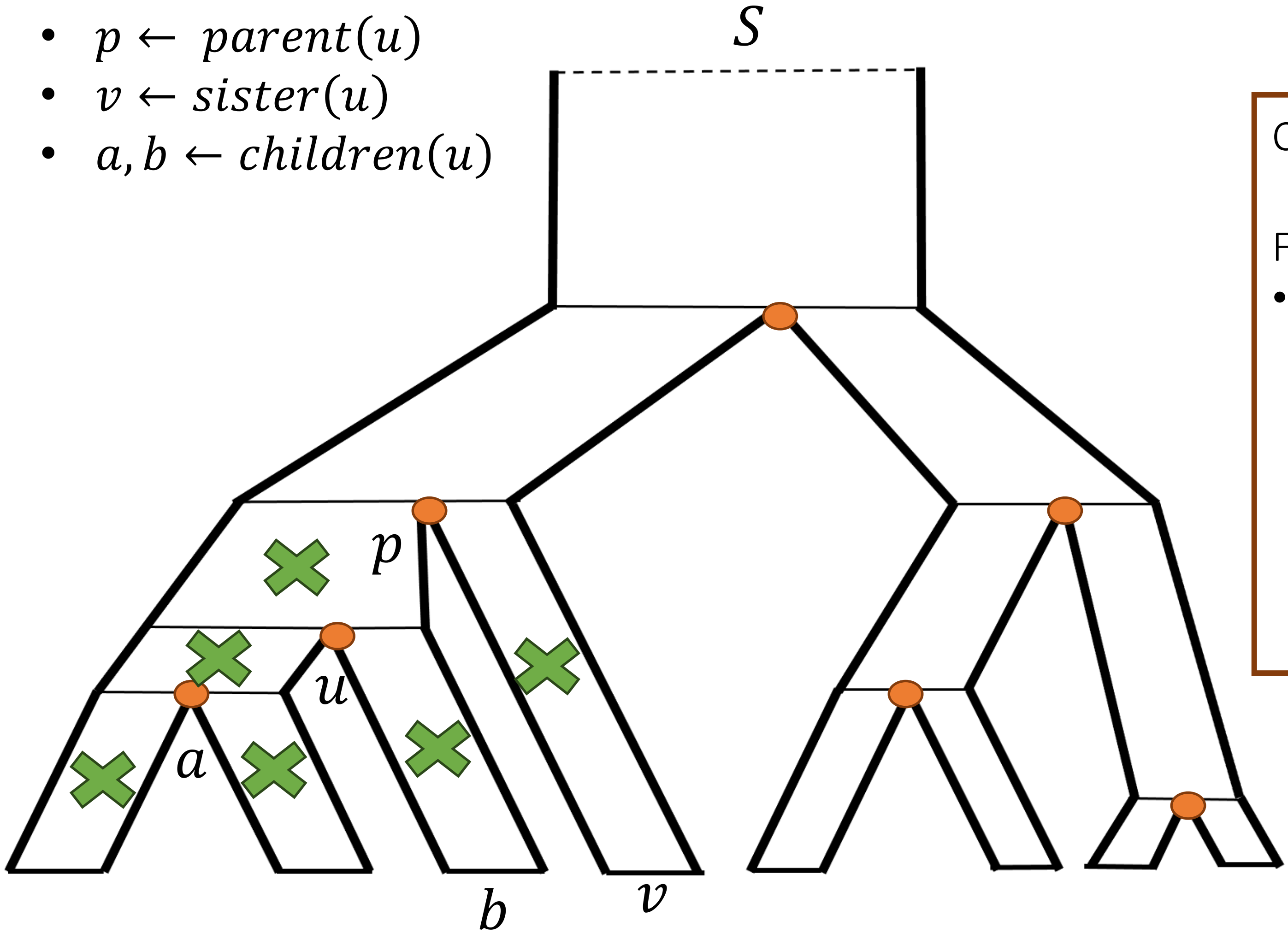

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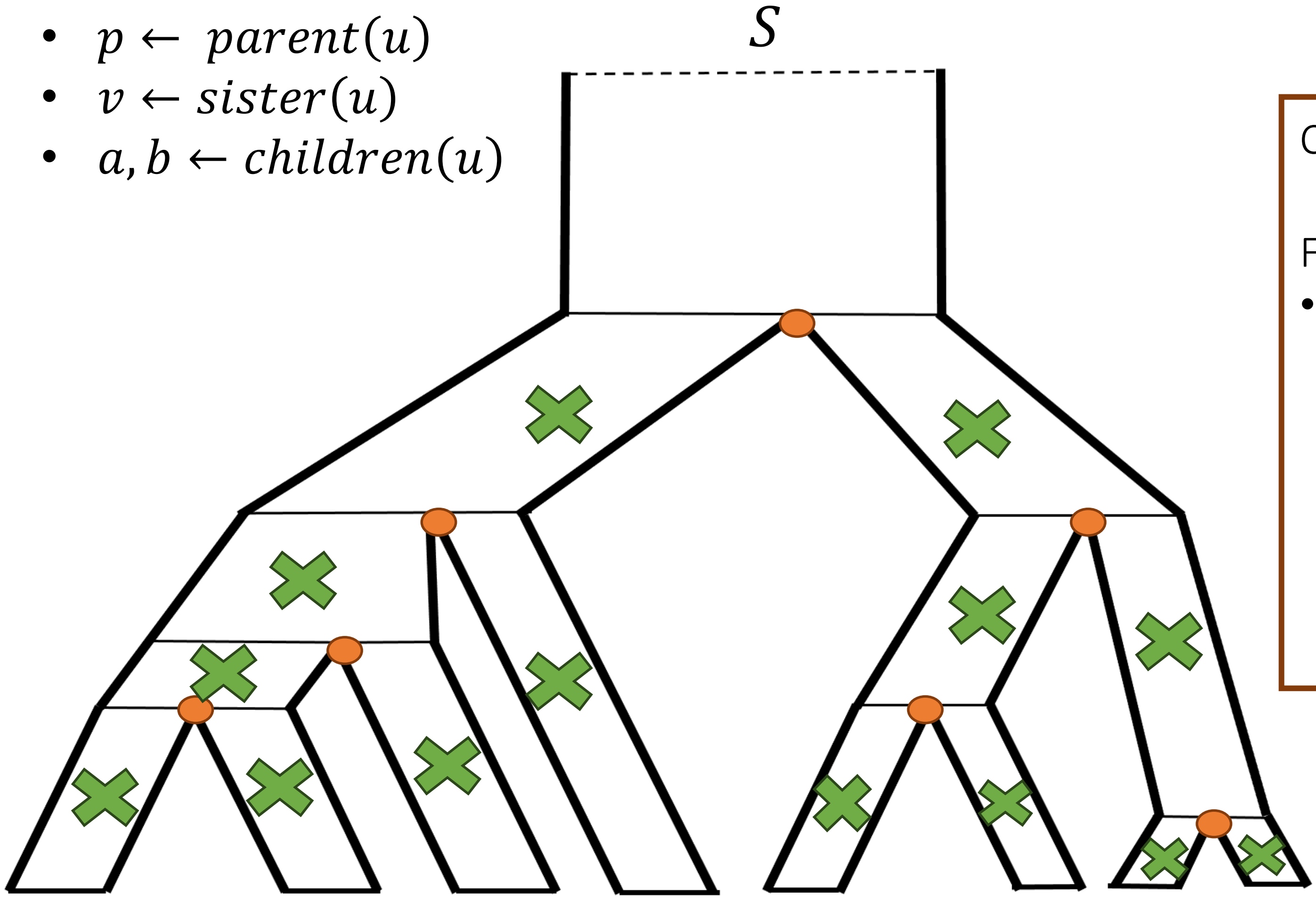

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```

Total runtime: $O(n^2k)$

in practice: ~**50s** on 100-taxon tree with 1000 genes

Summary of results so far

- We derived expected branch lengths for matching/non-matching gene trees for an unbalanced/balanced quartet species tree under MSC+Substitution model.

- We presented simplifications that lead to analytical formulas for each branch in the species tree.

- We introduced CASTLES that uses these formulas to estimate branch lengths on a species tree in $O(n^2k)$.

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How well does it work in practice?

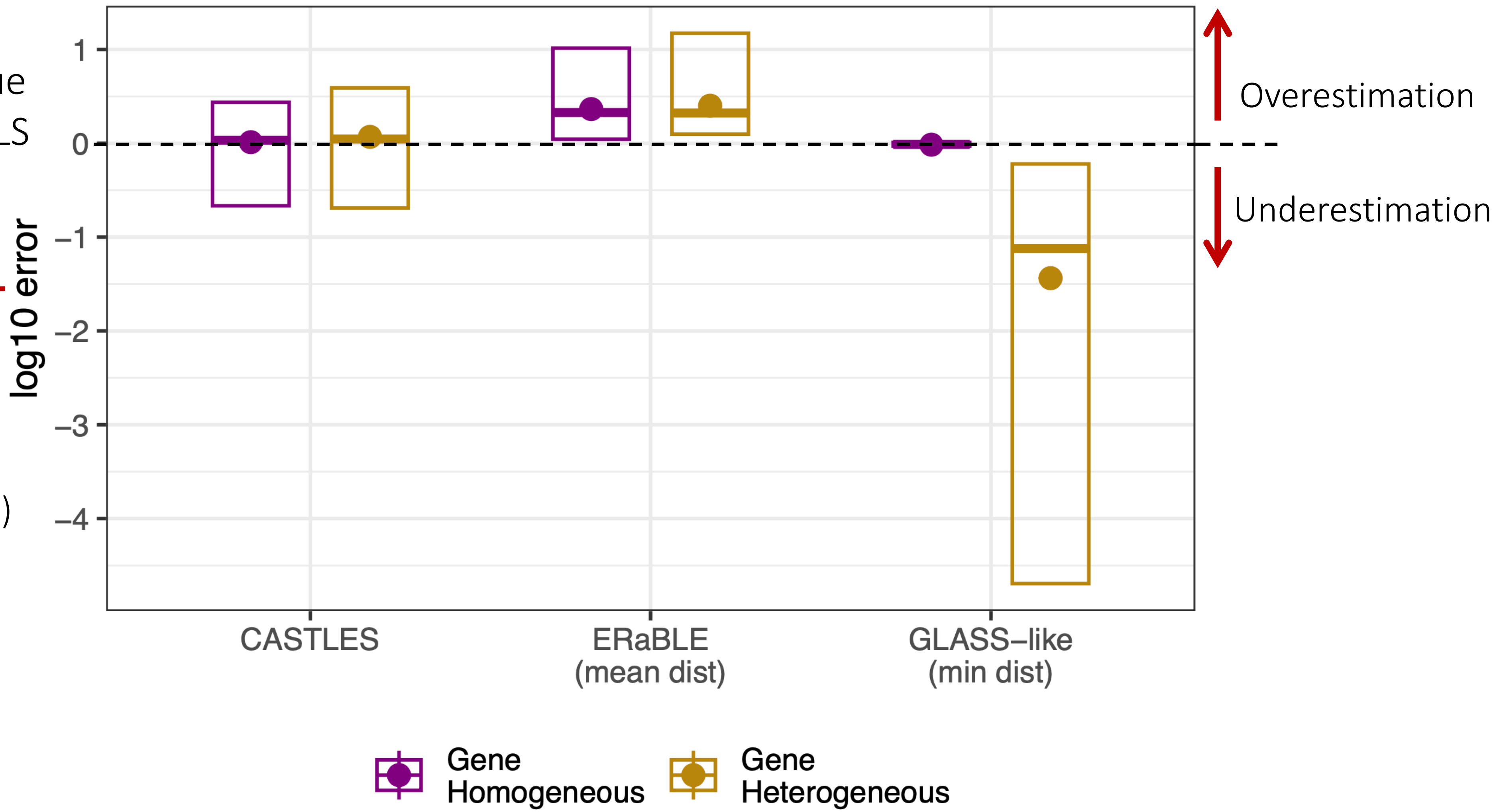
Experimental study

- Modified SimPhy [Mallo et al., 2016] to generate species trees with SU lengths
- Estimating branch lengths on the *true* species tree topology
- Three ILS simulated datasets and a mammalian biological dataset
- Evaluating using bias, absolute error, RMSE, and log error
- **Methods**: Concatenation with RAxML [Stamatakis, 2014], FastME [Lefort et al, 2015] with minimum and average distance matrices and ERaBLE [Binet et al., 2016]

CASTLES is robust to rate heterogeneity across genes

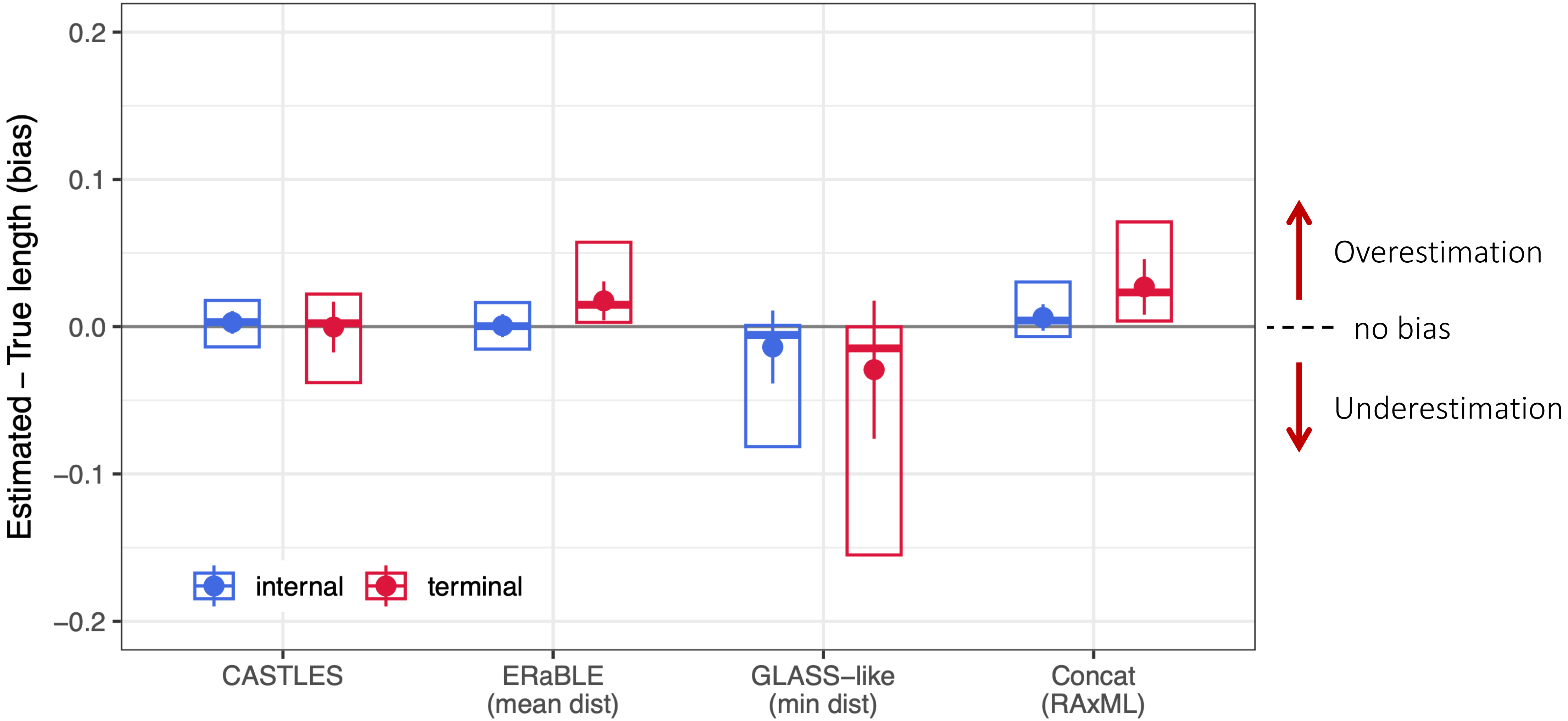
- Quartet ILS simulated dataset with 10,000 true gene trees, moderate ILS

log10 (est. length / true length)



CASTLES is less biased than other methods

- 100-taxon ILS simulated dataset with 1000 genes, moderate ILS, 200bp sequence length [Zhang et al (2018)]



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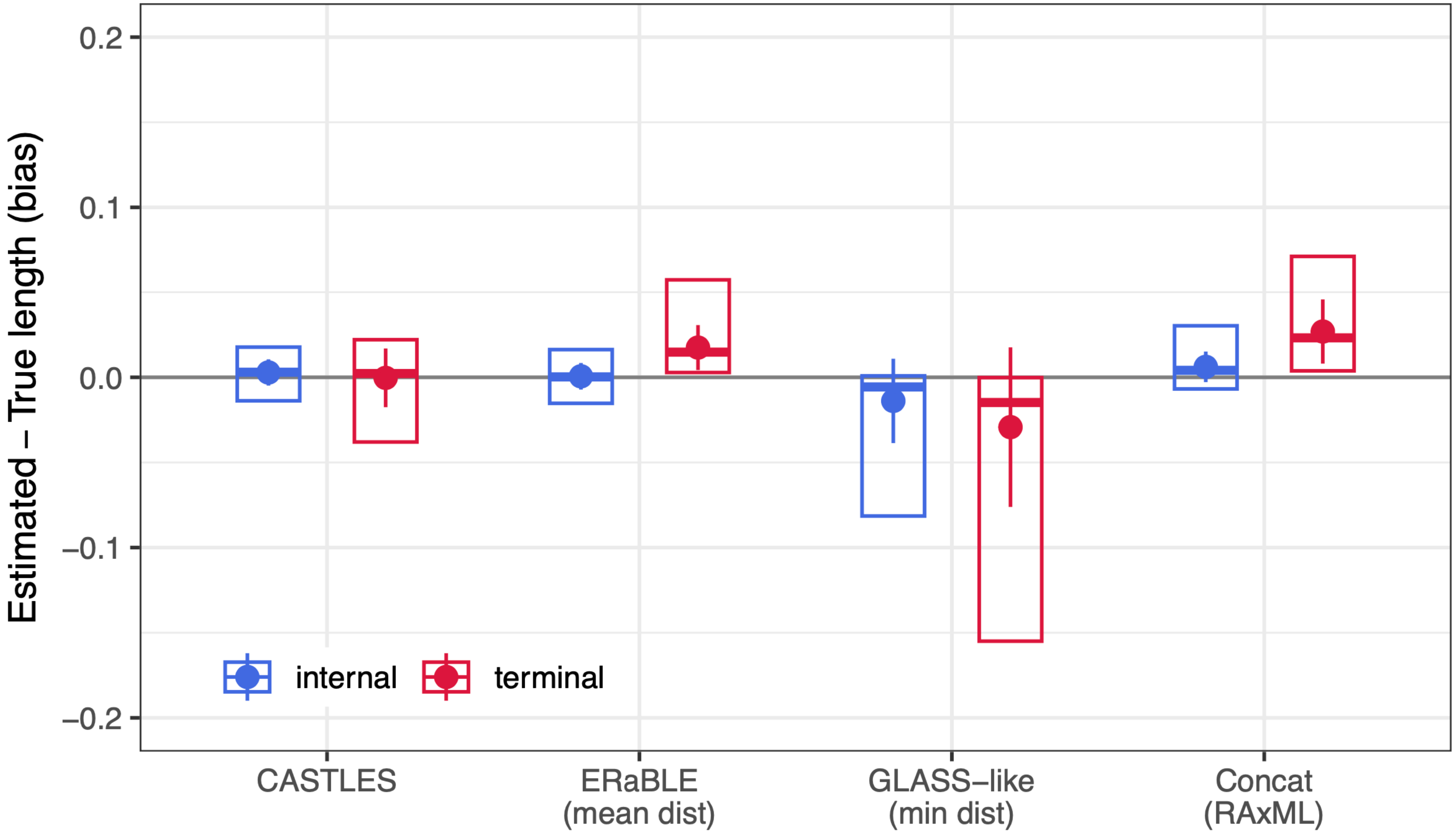
Bias is higher for **terminal** branches.



Overestimation

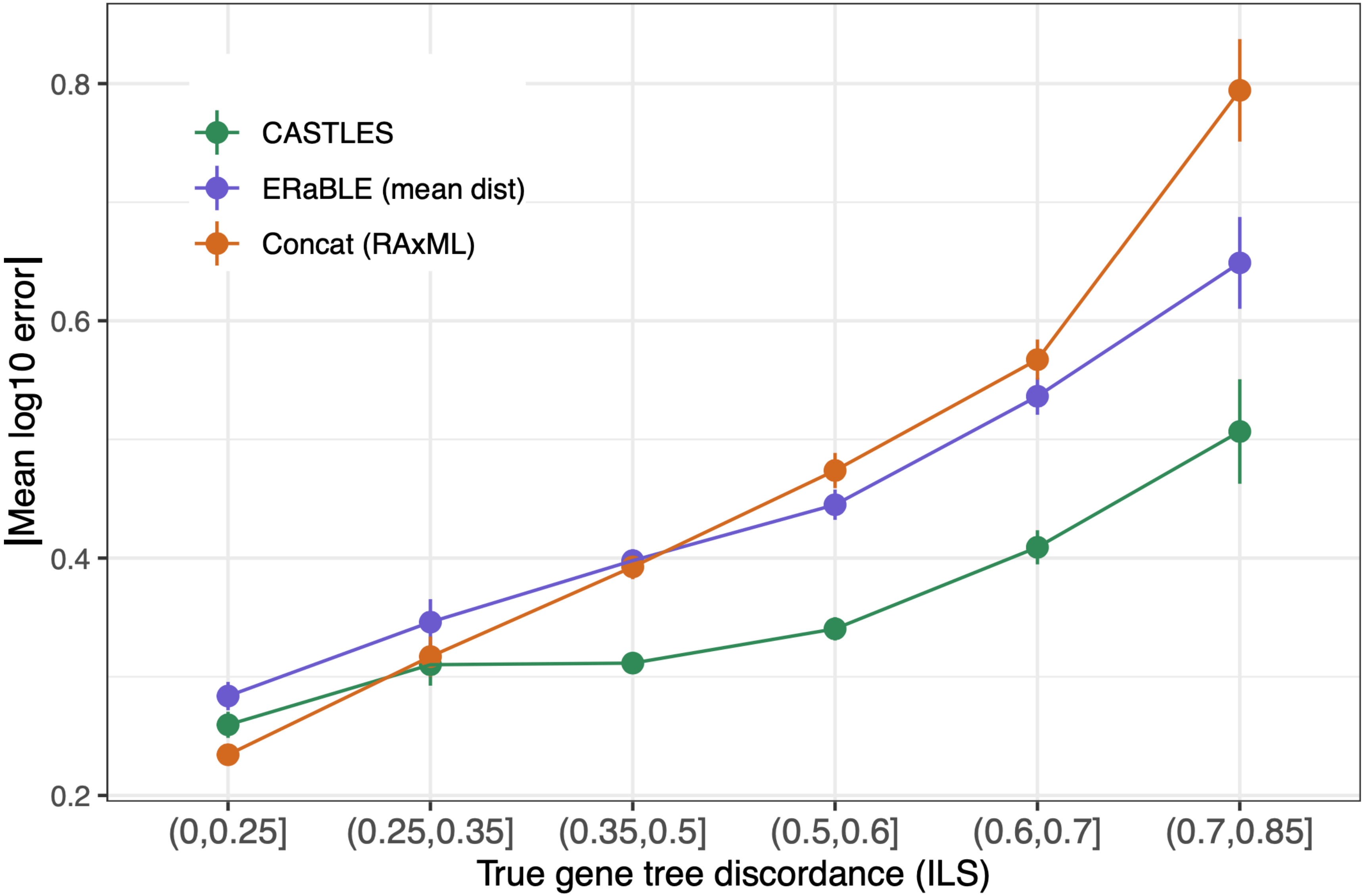
no bias

Underestimation

CASTLES's advantage increases with ILS

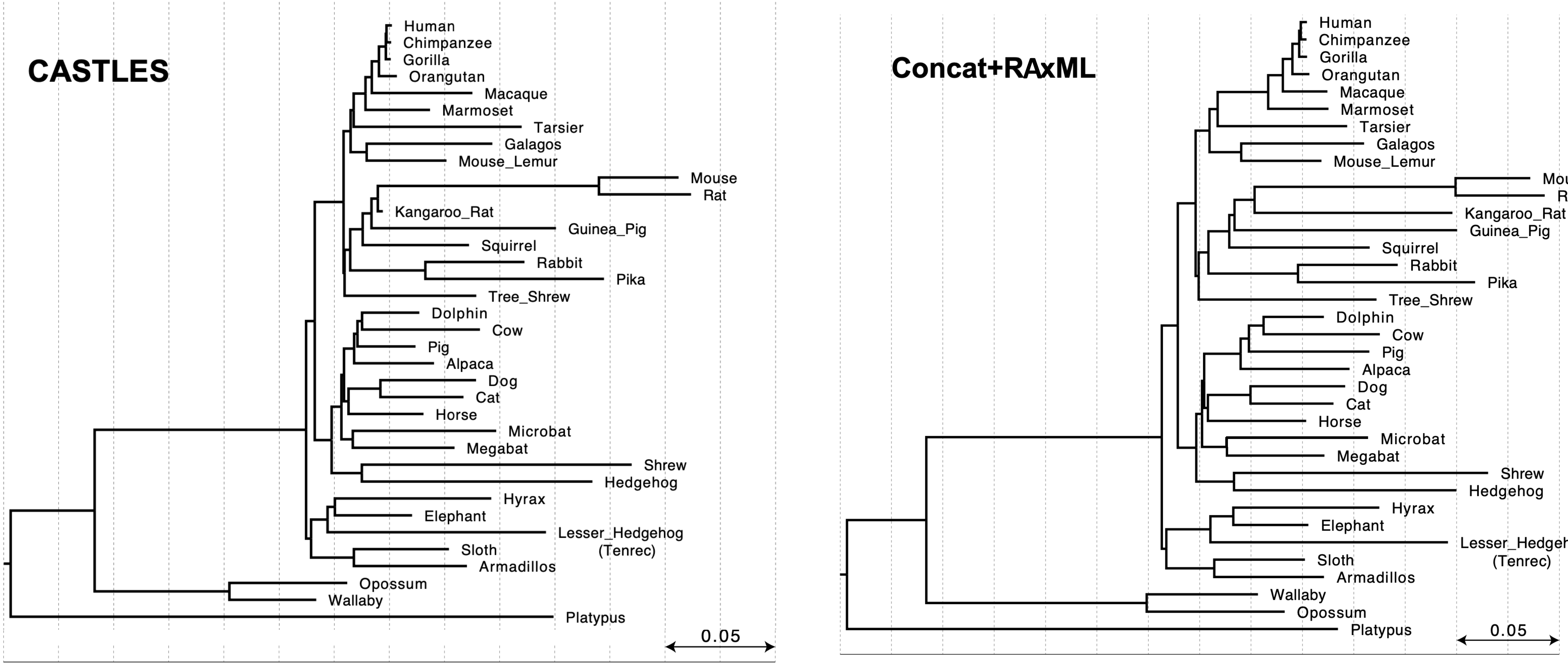
- 30-taxon ILS simulated dataset with 500 genes [Mai et al (2017)]
- Average 0.38 GTEE

|log10 (est. length / true length)|



CASTLES produces shorter branches than concatenation on mammalian dataset

- 37-taxon mammalian biological dataset with 424 genes [Song et al (2012)], ASTRAL species tree



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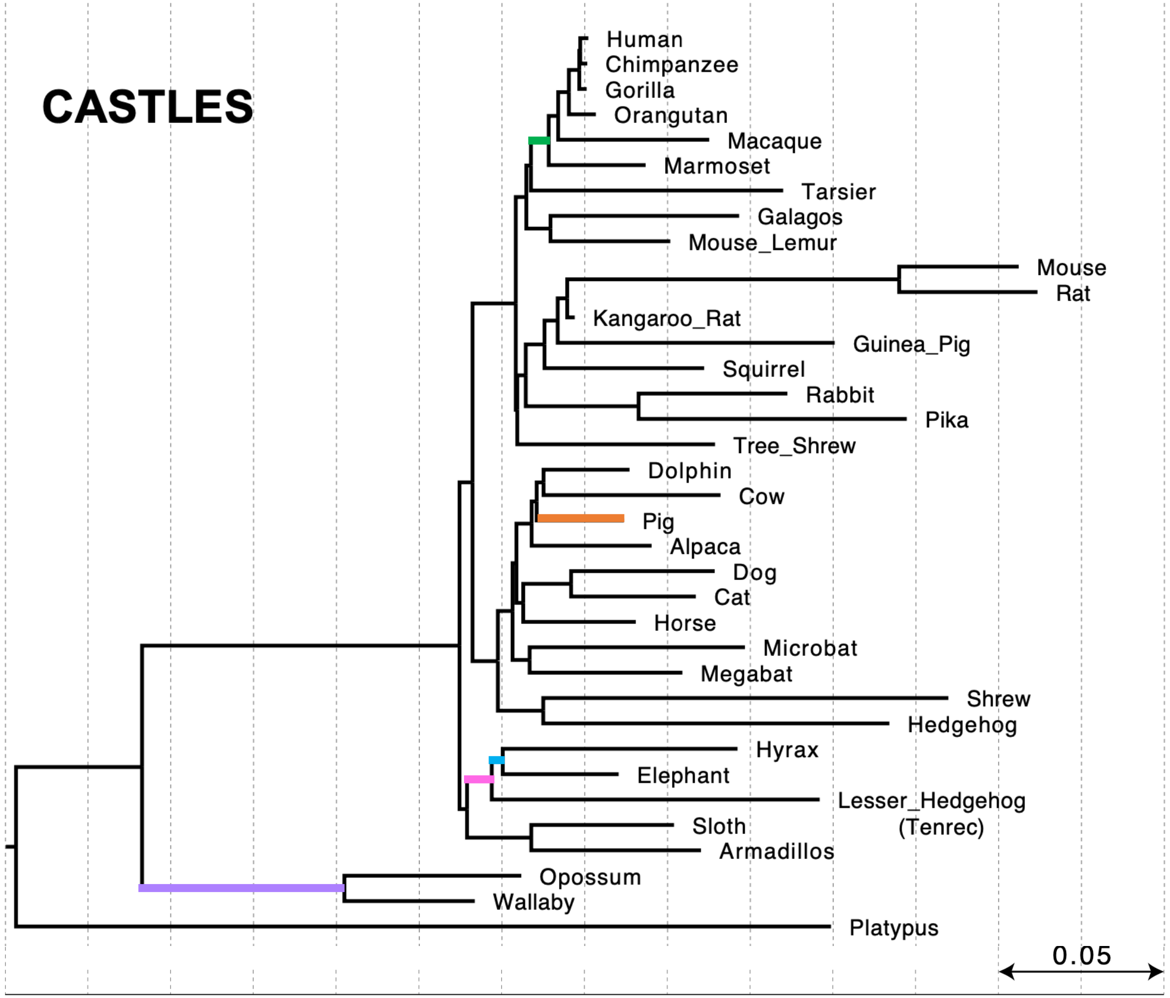

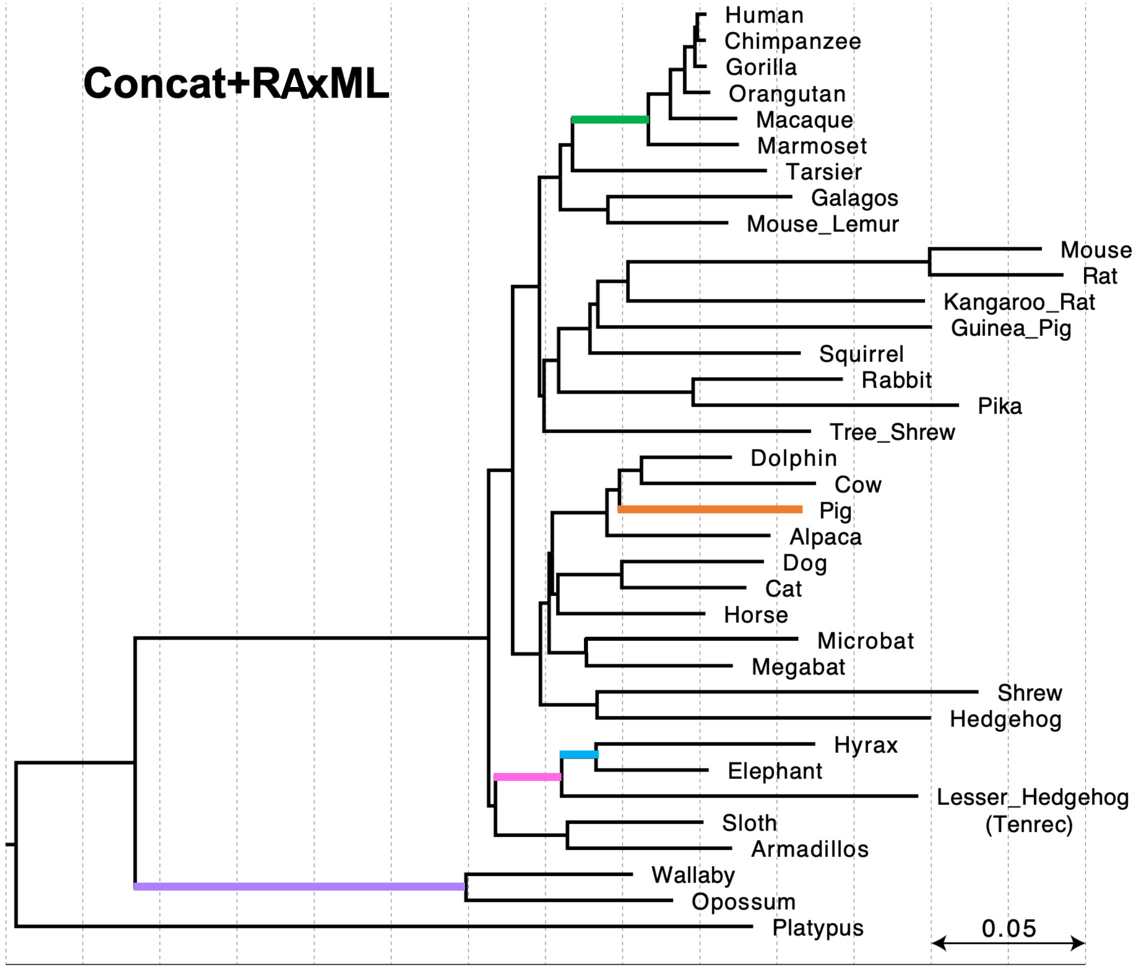

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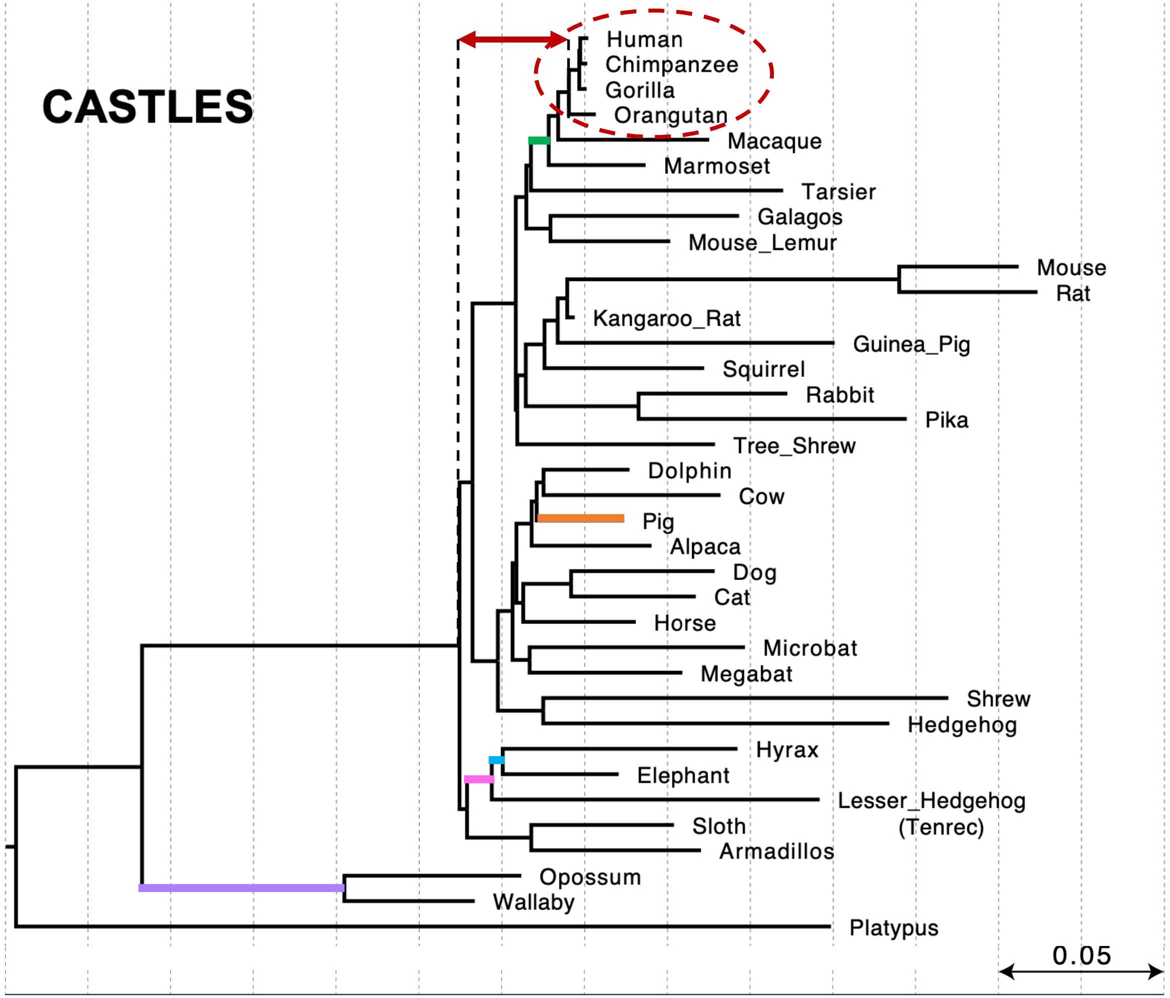

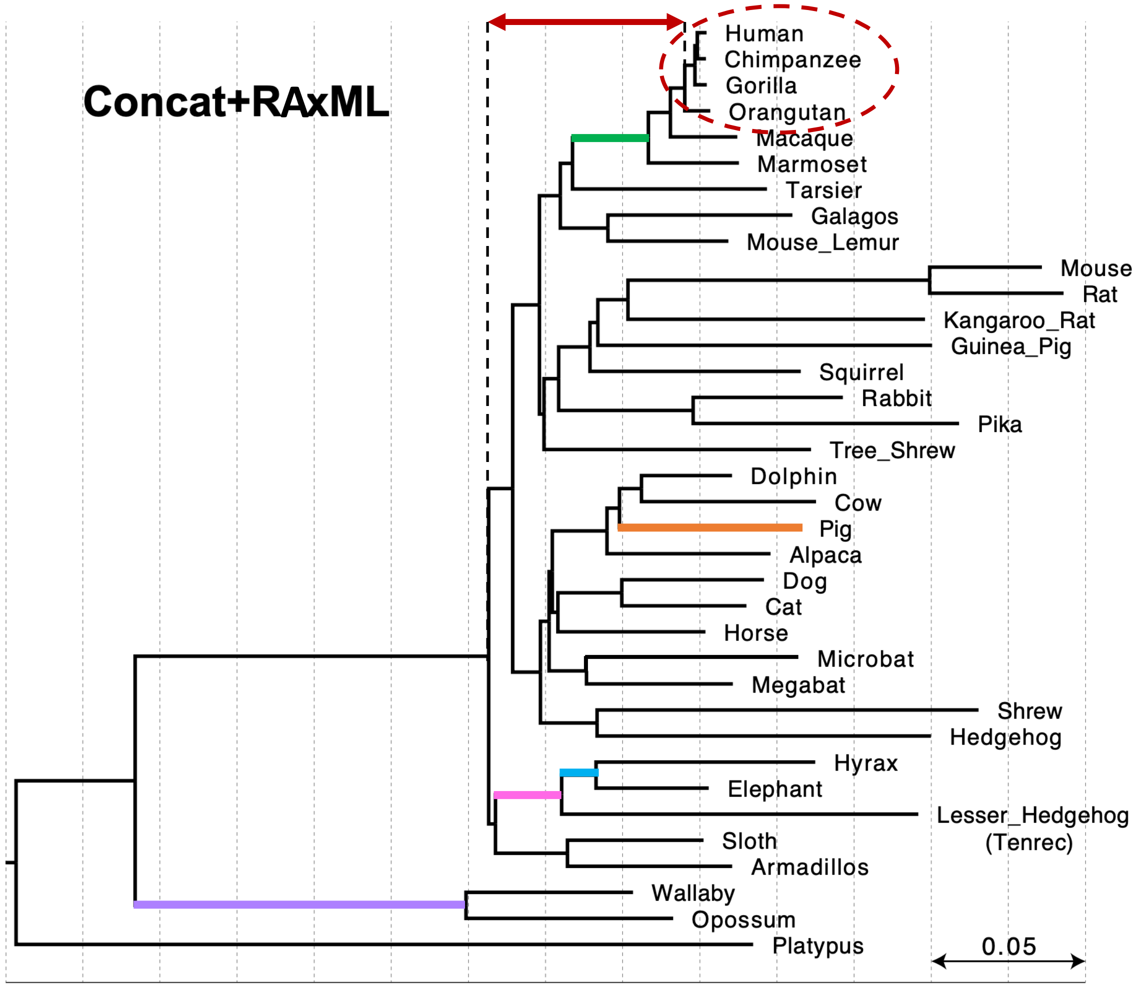

Summary & Future Directions

Summary

- CASTLES is a scalable method for estimating branch lengths of a species tree given gene tree branch lengths
- CASTLES addresses gene tree heterogeneity due to ILS, and naturally occurring variations in mutation rates
- CASTLES produces more accurate and less biased branch lengths than prior methods in many model conditions

Future Directions

- Addressing other sources of gene tree discordance, such as gene duplication and loss and horizontal gene transfer
- Evaluating CASTLES on datasets with model misspecification, missing data, etc
- Are SU lengths identifiable under MSC+Substitution model, and is CASTLES statistically consistent?

Acknowledgements

Thank you!

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Siavash Mirarab

Paper is available at:
https://doi.org/10.1093/bioinformatics/btad221

CASTLES is available on Github:
https://github.com/ytabatabaee/CASTLES

UC San Diego

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UNIVERSITY OF CALIFORNIA

COMPUTER SCIENCE

Funding:

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NIH
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Computing Resources:
UIUC Campus Cluster

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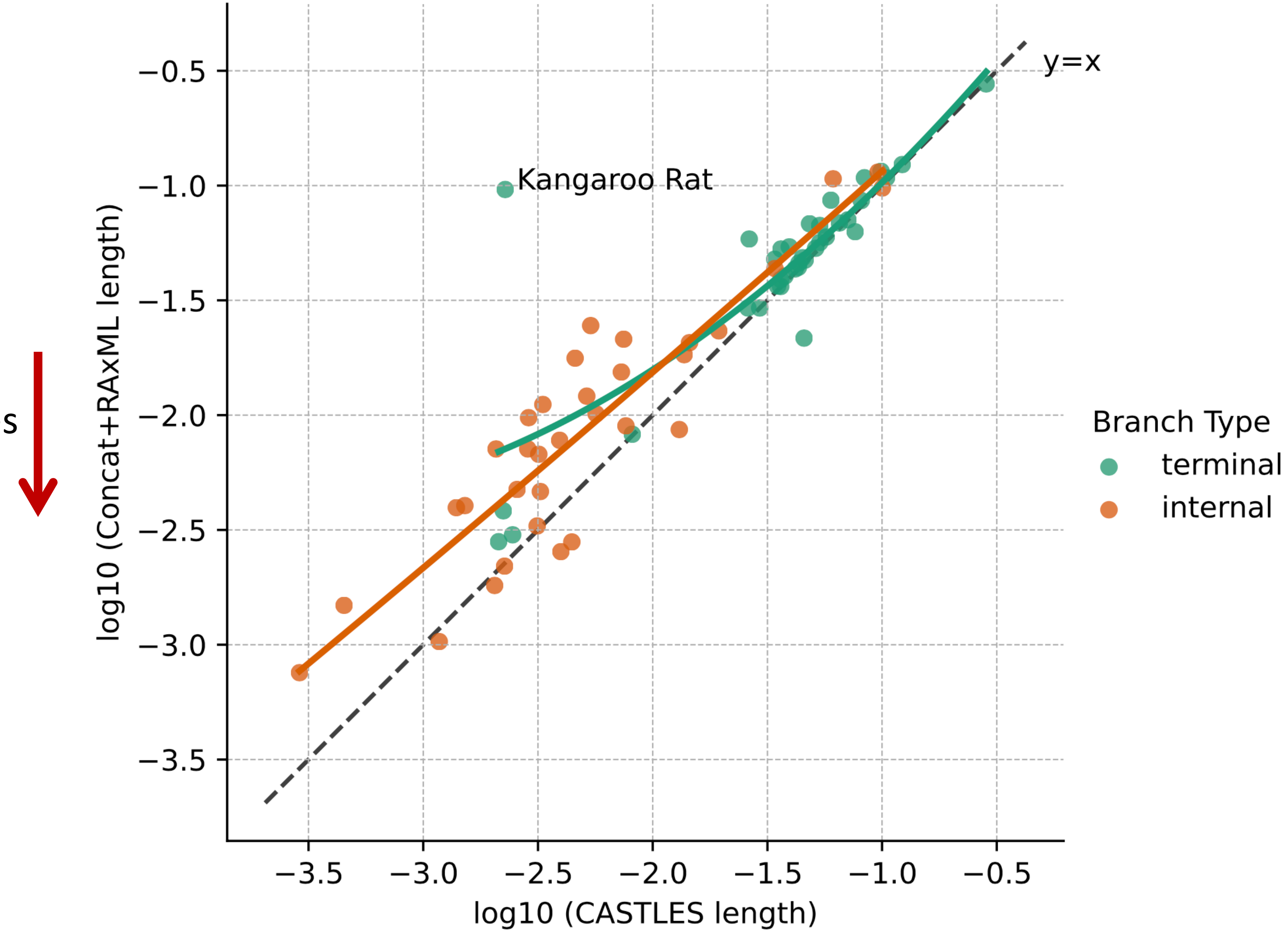
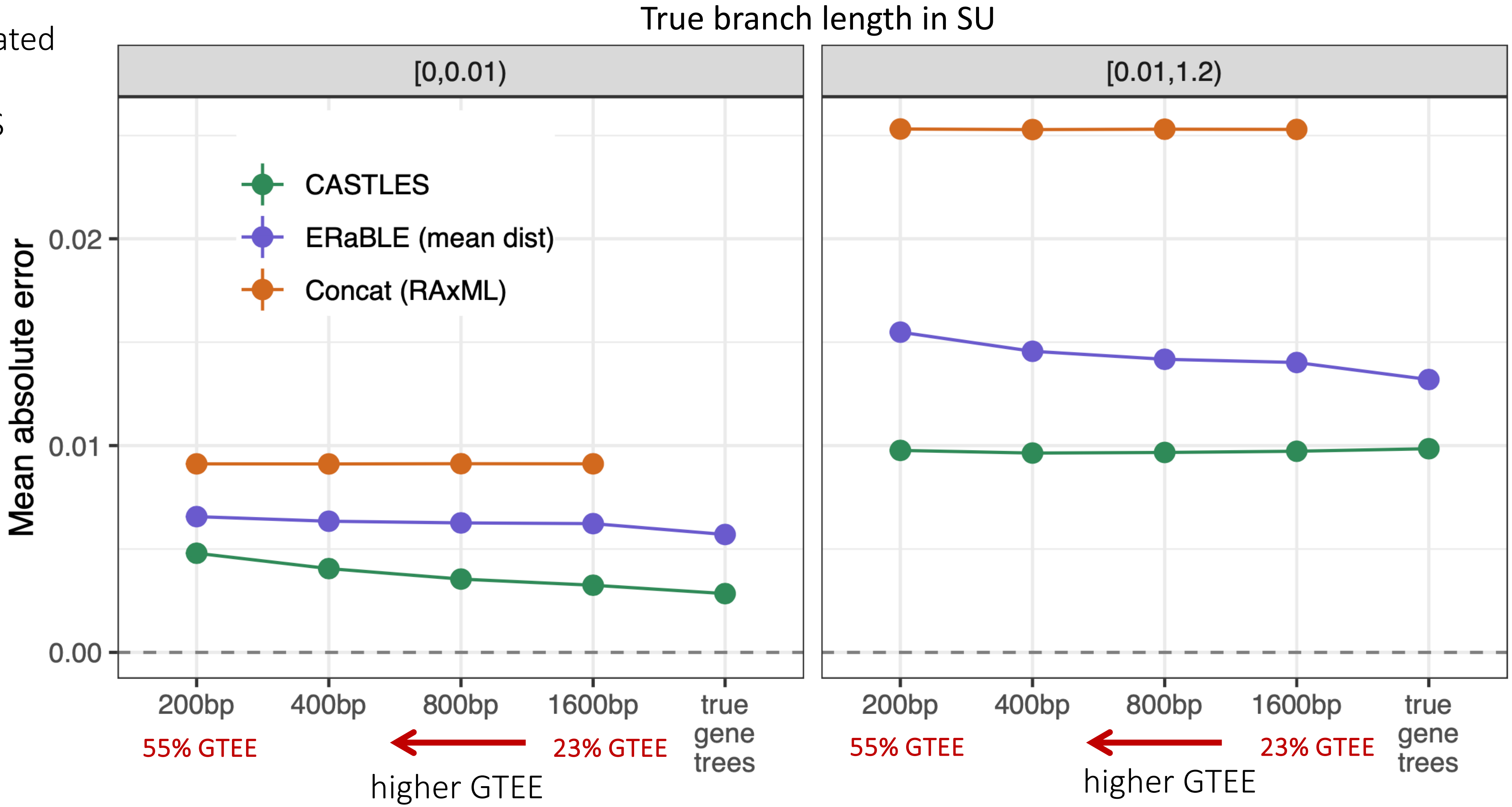
Shorter branches



Phylogenetic signal has relatively small impact on branch length accuracy

- 100-taxon ILS simulated dataset with 1000 genes, moderate ILS [Zhang et al (2018)]


True branch length in SU
[0,0.01)
[0.01,1.2)
CASTLES
ERaBLE (mean dist)
Concat (RAxML)
Mean absolute error
200bp
400bp
800bp
1600bp
true gene trees
55% GTEE
23% GTEE
higher GTEE
200bp
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