Generalizing phylogenetics to infer patterns predicted by processes of diversification

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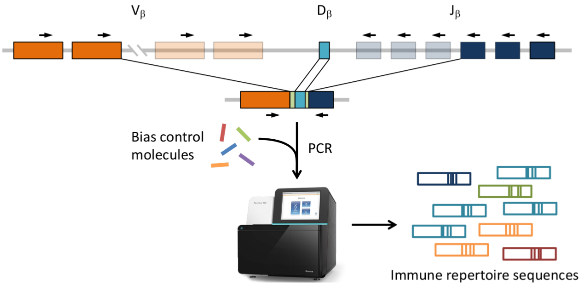

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Generalizing phylogenetics to infer patterns of shared evolutionary events

The Phyleticians

Postdocs

- Perry Wood, Jr
- *Brian Folt*
- *Jesse Grismer*

Graduate students

- Tashitso Anamza
- Matt Buehler
- Kerry Cobb
- Kyle David
- Saman Jahangiri
- Randy Klabacka
- Morgan Muell
- Tanner Myers
- Claire Tracy
- *Breanna Sipley*
- *Aundrea Westfall*

Undergraduate students

- Laura Lewis
- Mary Wells
- Hailey Whitaker
- Noah Yawn
- *Charlotte Benedict*
- *Eric Carbo*
- *Ryan Cook*
- *Andrew DeSana*
- *Miles Horne*
- *Jacob Landrum*
- *Nadia L'Bahy*
- *Jorge Lopez-Perez*
- *Holden Smith*
- *Virginia White*
- *Kayla Wilson*

- Phylogenetics is rapidly becoming the statistical foundation of biology

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- “Big data” present exciting possibilities and challenges

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- Phylogenetics is rapidly becoming the statistical foundation of biology
- "Big data" present exciting possibilities and challenges
- Many opportunities to develop new ways to study biology in light of phylogeny

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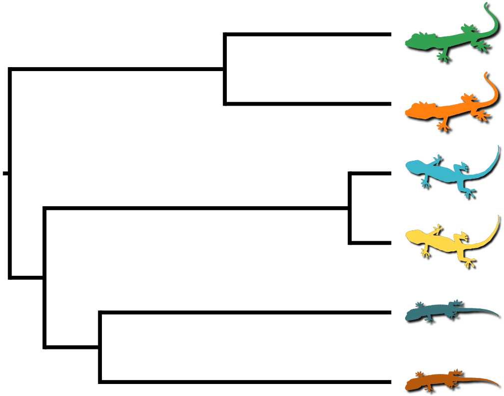

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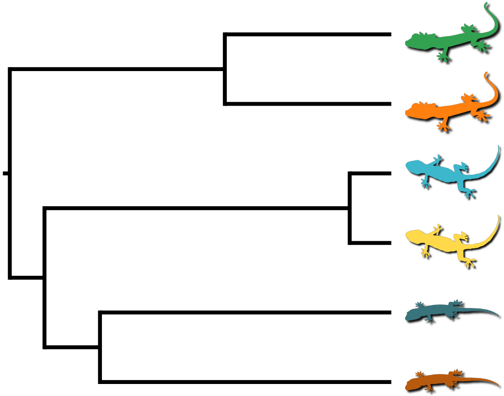
- **Assumption:** All processes of diversification affect each lineage independently



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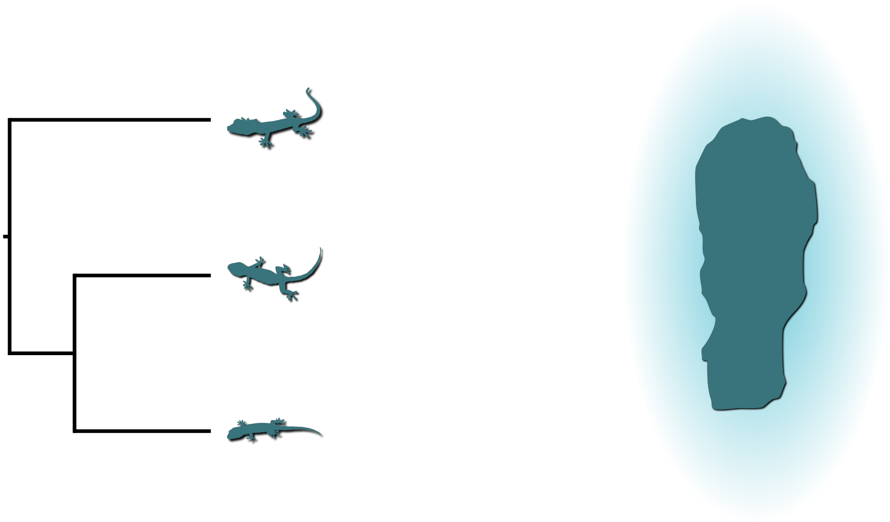
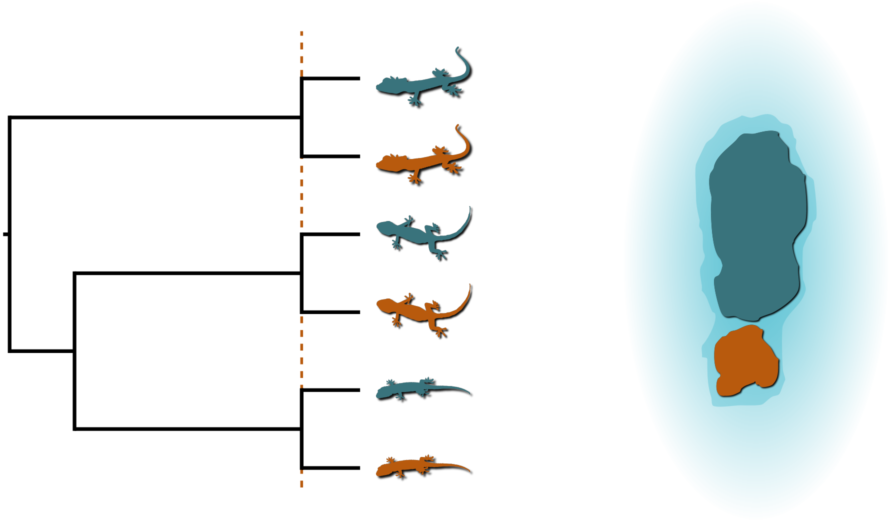
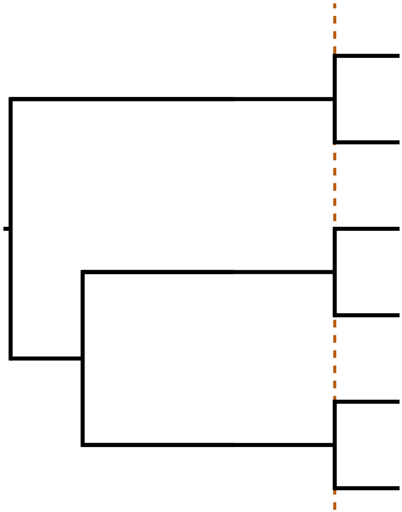




Biogeography

- Environmental changes that affect whole communities of species



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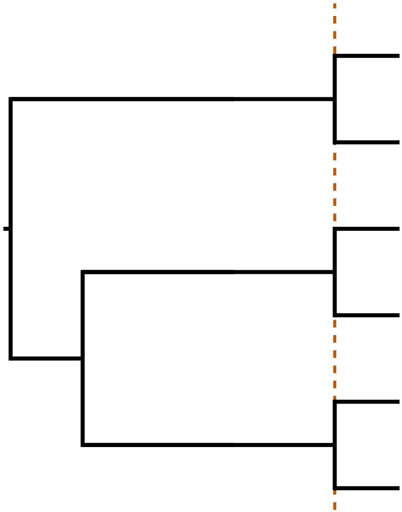
- Duplication of a chromosome segment harboring gene families



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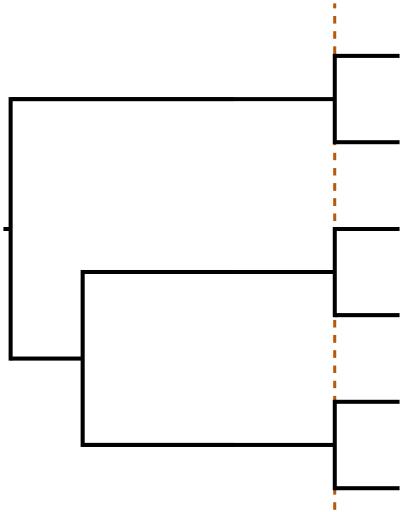
- Transmission at social gatherings



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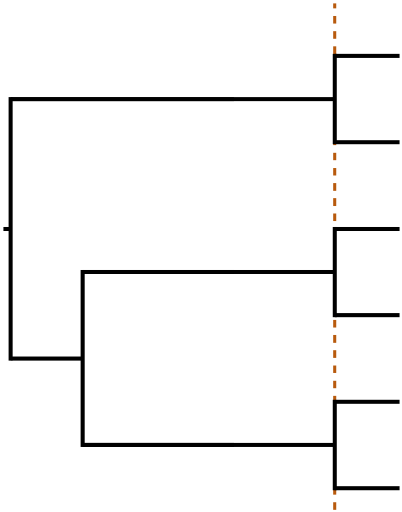
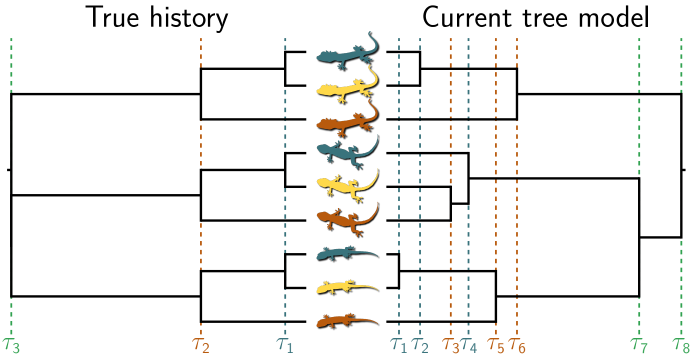


Why account for shared divergences?

J. R. Oaks et al. (2022). *PNAS* 119: e2121036119

Why account for shared divergences?

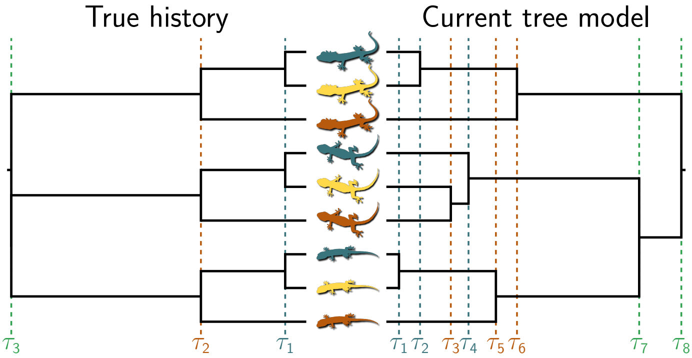
1. Improve inference



J. R. Oaks et al. (2022). *PNAS* 119: e2121036119

Why account for shared divergences?

1. Improve inference
2. **Provide a framework for studying processes of co-diversification**



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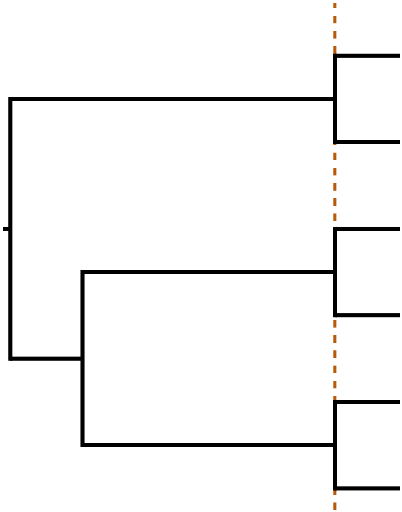

Approaches to the problem

A pairwise approach (keep it "simple")

A fully phylogenetic approach

Tashitso Anamza

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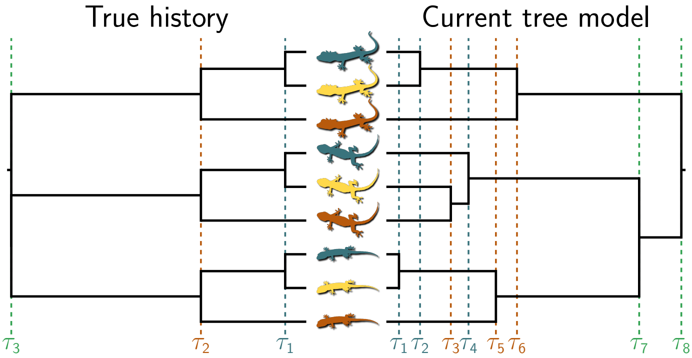
Dr. Perry Wood, Jr.

Challenges to accounting for shared divergences



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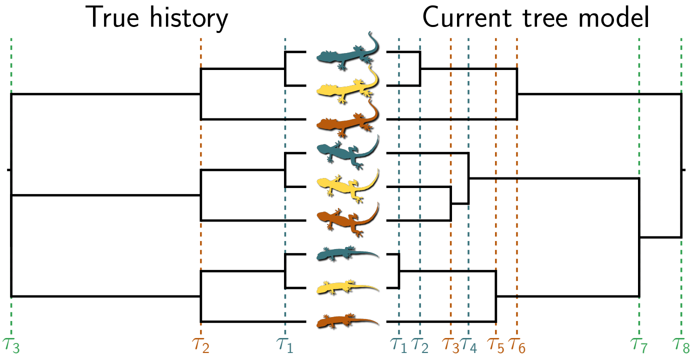
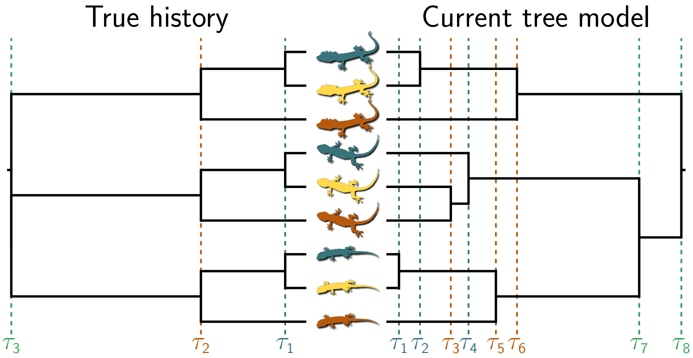
Challenges to accounting for shared divergences

1. Likelihood for genomic data is tricky



Challenges to accounting for shared divergences

1. Likelihood for genomic data is tricky
2. Lots of possible trees of different dimensions



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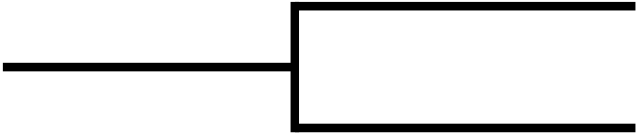


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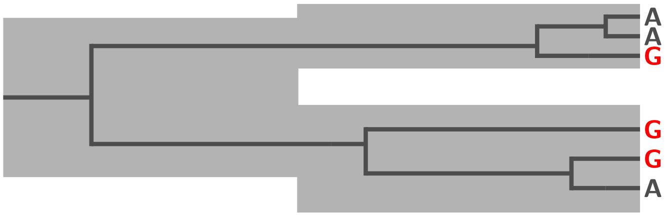
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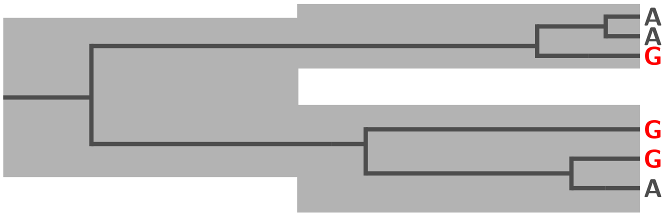
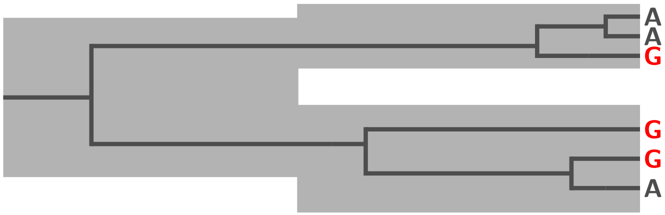


- Conditional on "population tree" (T), model "gene trees" (G) using coalescent



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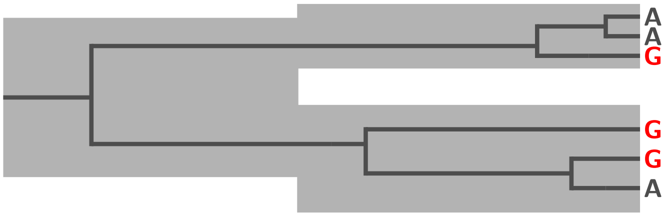

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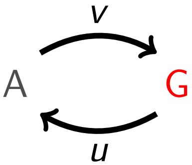

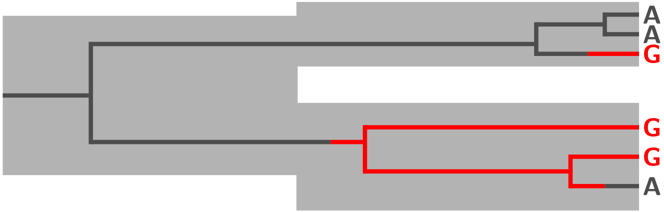

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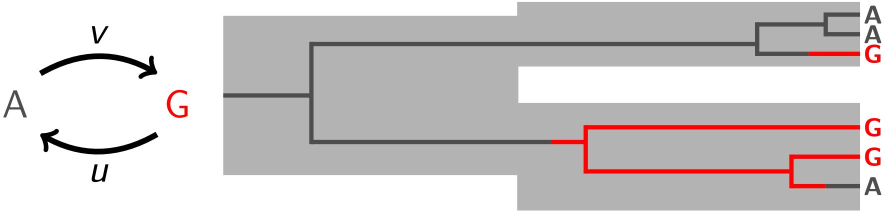

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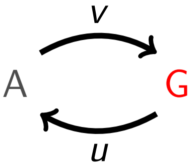

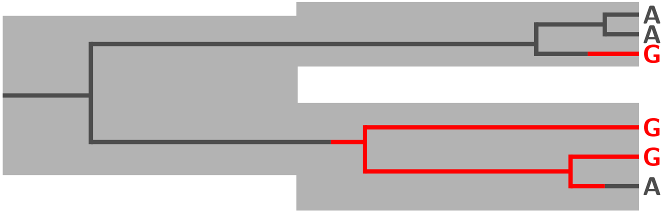

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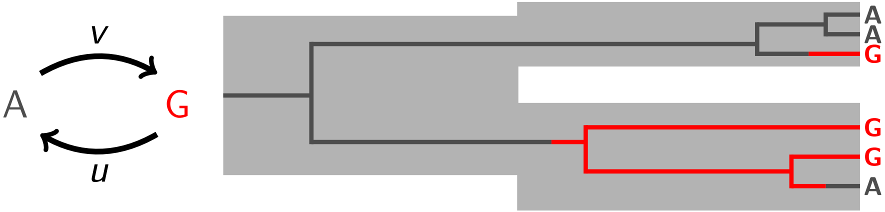
- Genetic characters provide information about G
- G informs T (population sizes, divergence times, and relationships)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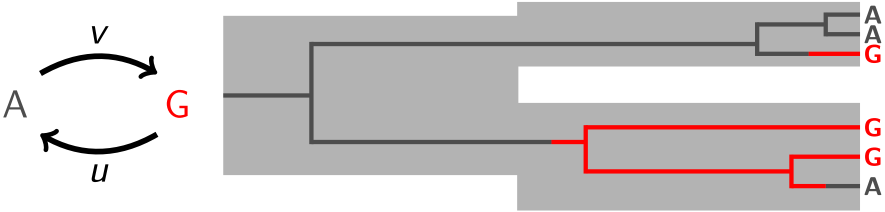
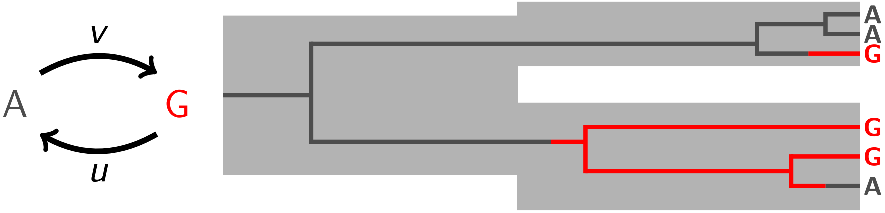
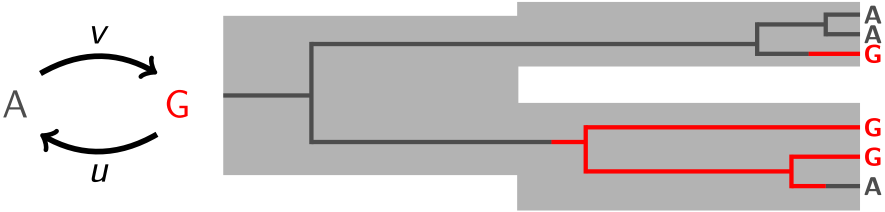


- “Standard” hierarchical approach



- “Standard” hierarchical approach
  - Calculate $p(\text{genetic data} \mid G) \times p(G \mid T)$



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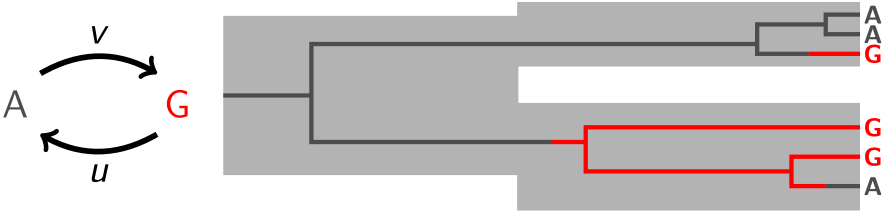

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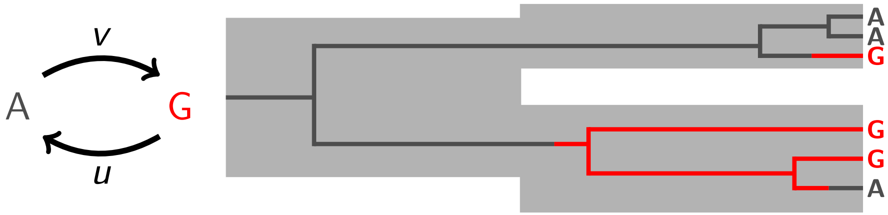
- But, G and T are highly correlated



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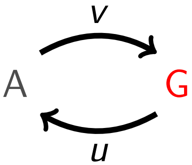

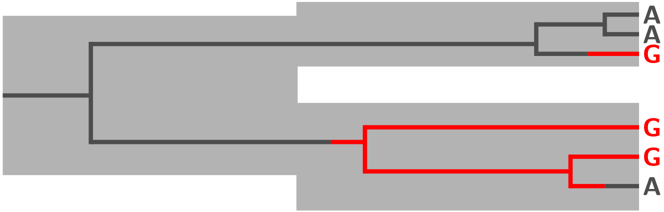

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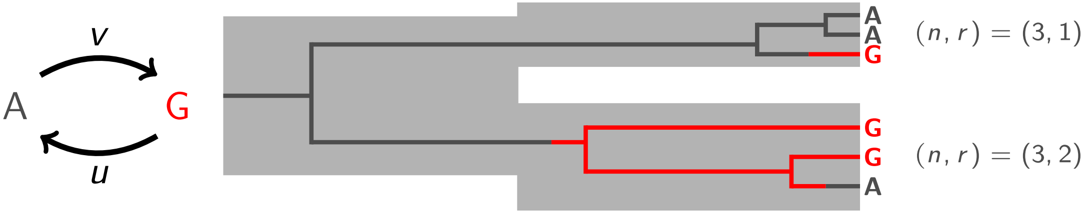
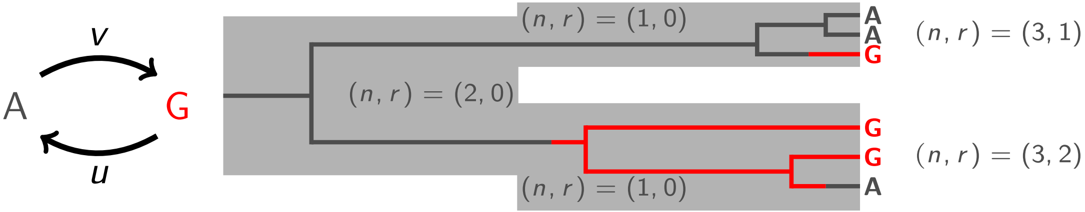
- But, G and T are highly correlated
- As the number of loci (gene trees) increases, MCMC falls apart
- Can we integrate G analytically?



[1] T. Schmelzer and L. N. Trefethen (2007). *Electronic Transactions on Numerical Analysis* 29: 1–18

[2] D. Bryant et al. (2012). *Molecular Biology and Evolution* 29: 1917–1932



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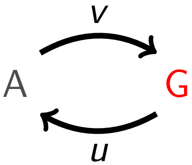

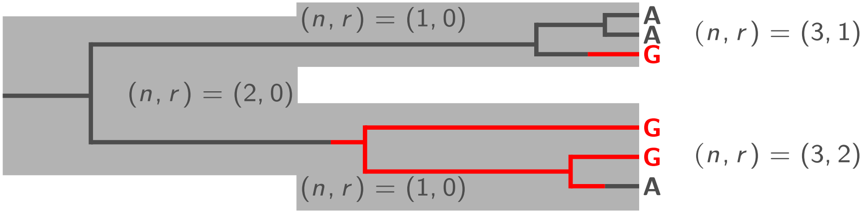

$Q =$

	(1, 0)	(1, 1)	(2, 0)	(2, 1)	⋯	**(n, n)**
(1, 0)	·	·	·	·		·
(1, 1)	·	·	·	·		·
(2, 0)	·	·	·	·		·
(2, 1)	·	·	·	·		·
⋮						
(n, n)	·	·	·	·		·

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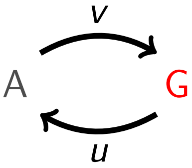

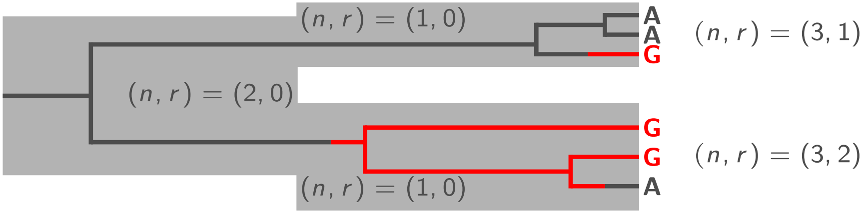

$$Q = \begin{array}{c|cccccc} & (1,0) & (1,1) & (2,0) & (2,1) & \cdots & (\mathbf{n},\mathbf{n}) \\ (1,0) & \cdot & \cdot & \cdot & \cdot & & \cdot \\ (1,1) & \cdot & \cdot & \cdot & \cdot & & \cdot \\ (2,0) & \cdot & \cdot & \cdot & \cdot & & \cdot \\ (2,1) & \cdot & \cdot & \cdot & \cdot & & \cdot \\ \vdots & & & & & & \\ (\mathbf{n},\mathbf{n}) & \cdot & \cdot & \cdot & \cdot & & \cdot \end{array}$$

$$\begin{aligned} Q_{(n,r);(n,r-1)} &= (n-r+1)v, && \text{mutation}, \\ Q_{(n,r);(n,r+1)} &= (r+1)u, && \text{mutation}, \\ Q_{(n,r);(n-1,r)} &= \frac{(n-1-r)n}{2N_e(u+v)}, && \text{coalescence}, \\ Q_{(n,r);(n-1,r-1)} &= \frac{(r-1)n}{2N_e(u+v)}, && \text{coalescence}, \\ Q_{(n,r);(n,r)} &= -\frac{(n-1)n}{2N_e(u+v)} - (n-r)v - ru. && \end{aligned}$$

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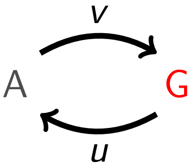

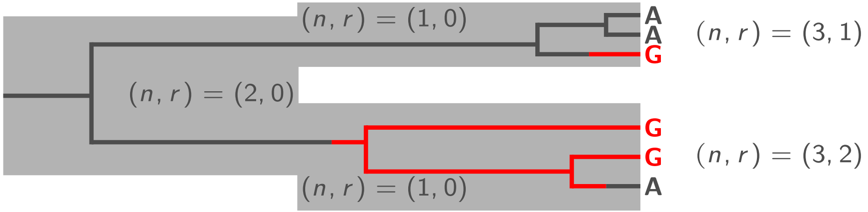

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- e^{Qt} to keep track of all conditional probabilites along each branch (Carathéodory-Fejér method[1])

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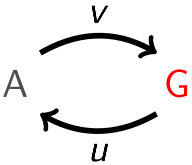

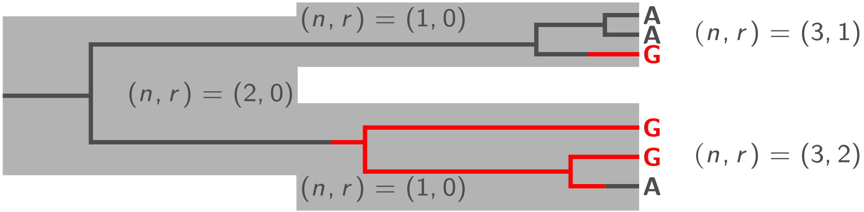

$$
Q = \begin{array}{c|cccccc}
 & (1,0) & (1,1) & (2,0) & (2,1) & \cdots & (\mathbf{n},\mathbf{n}) \\
\hline
(1,0) & \cdot & \cdot & \cdot & \cdot & & \cdot \\
(1,1) & \cdot & \cdot & \cdot & \cdot & & \cdot \\
(2,0) & \cdot & \cdot & \cdot & \cdot & & \cdot \\
(2,1) & \cdot & \cdot & \cdot & \cdot & & \cdot \\
\vdots & & & & & & \\
(\mathbf{n},\mathbf{n}) & \cdot & \cdot & \cdot & \cdot & & \cdot
\end{array}
$$

$$
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\end{aligned}
$$

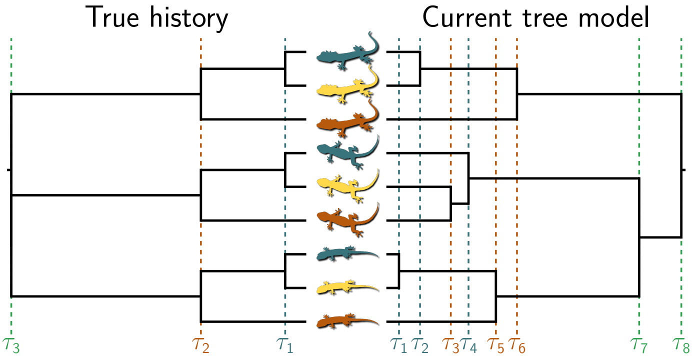
- e^{Qt} to keep track of all conditional probabilites along each branch (Carathéodory-Fejér method[1])
- At root, get likelihood of population tree integrated over all possible gene trees and mutational histories[2]

[1] T. Schmelzer and L. N. Trefethen (2007). *Electronic Transactions on Numerical Analysis* 29: 1–18

[2] D. Bryant et al. (2012). *Molecular Biology and Evolution* 29: 1917–1932

Challenges to accounting for shared divergences

1. Likelihood for genomic data is tricky
2. Lots of possible trees of different dimensions

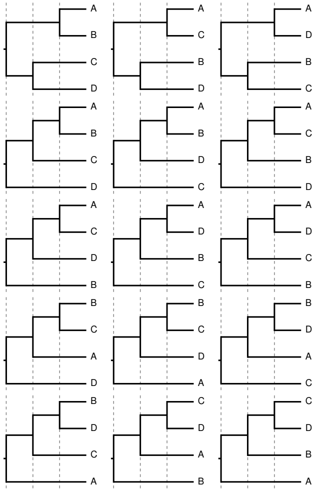


J. R. Oaks et al. (2022). *PNAS* 119: e2121036119

Generalizing tree space

Generalizing tree space

$n_{\mathcal{T}} = 3$



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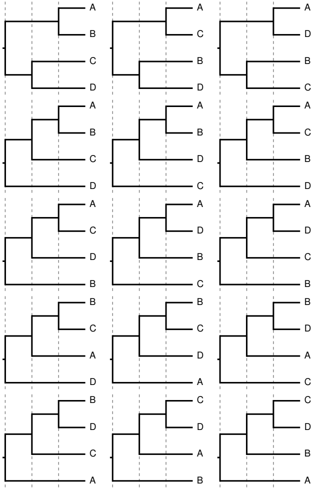
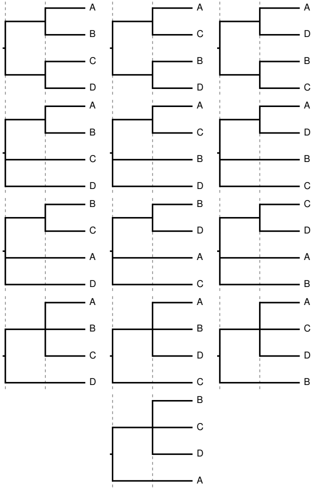
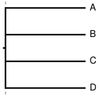


$n_{\mathcal{T}} = 2$



$n_{\mathcal{T}} = 1$



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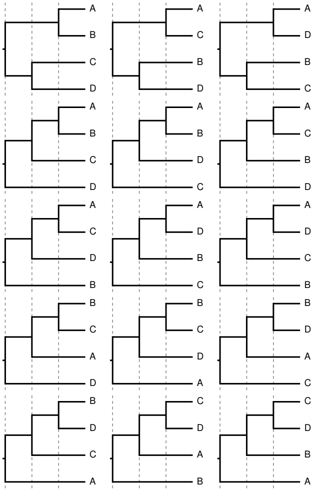
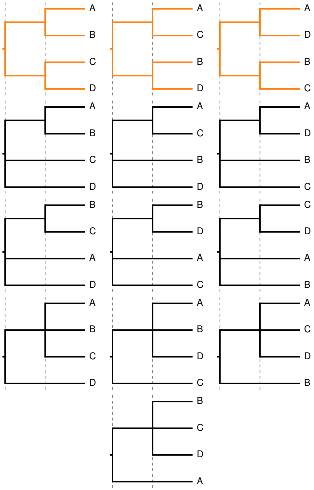


$n_{\mathcal{T}} = 2$



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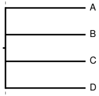
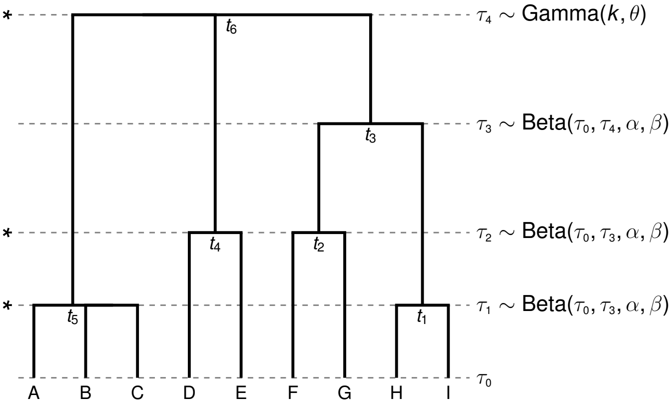


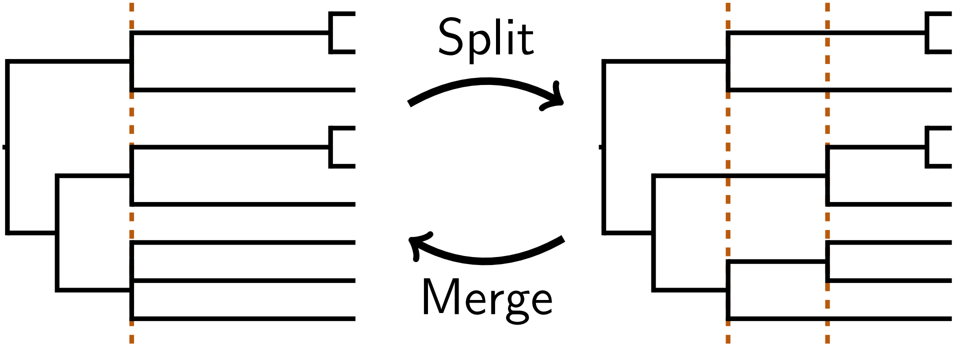
Generalized tree distribution

- All topologies equally probable
- Parametric distribution on age of root
- Beta distributions on other divergence times



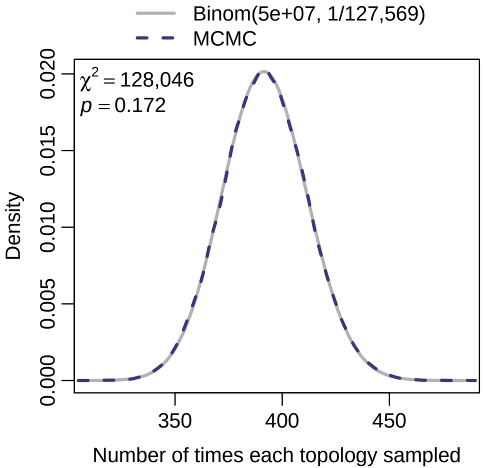
J. R. Oaks et al. (2022). *PNAS* 119: e2121036119

Inferring trees with shared divergences



Reversible-jump MCMC

Validating rjMCMC with 7-leaf tree



The rjMCMC algorithms sample the expected generalized tree distribution

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PhycoEval
Phylogenetic coevality
J. R. Oaks et al. (2022). *PNAS* 119: e2121036119

Ecoevolity
Estimating evolutionary coevality
J. R. Oaks (2019). *Systematic Biology* 68: 371–395

- **Tree model**
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- **Tree model**
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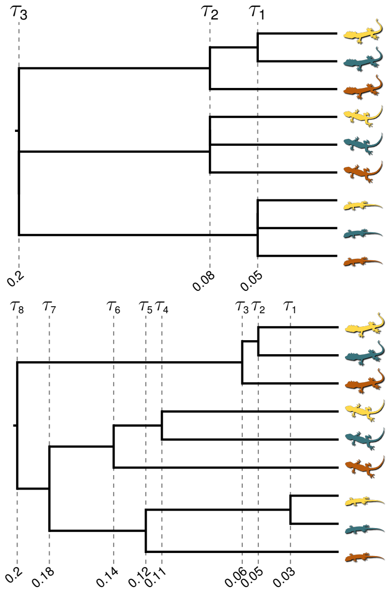
- *Goal: Co-estimation of phylogeny and shared divergences from genomic data*

[1] D. Bryant et al. (2012). *Molecular Biology and Evolution* 29: 1917–1932

Does it work?

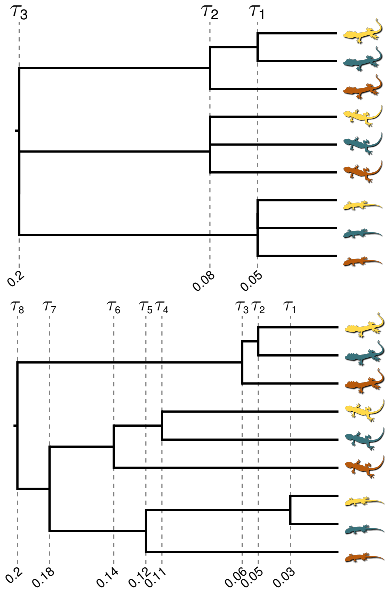
Methods: Simulations

- Simulated 100 data sets with 50,000 base pairs



Methods: Simulations

- Simulated 100 data sets with 50,000 base pairs
- Analyzed each data set with:
  - M_G = Generalized tree model
  - M_{IB} = Independent-bifurcating tree model



Methods: Simulations

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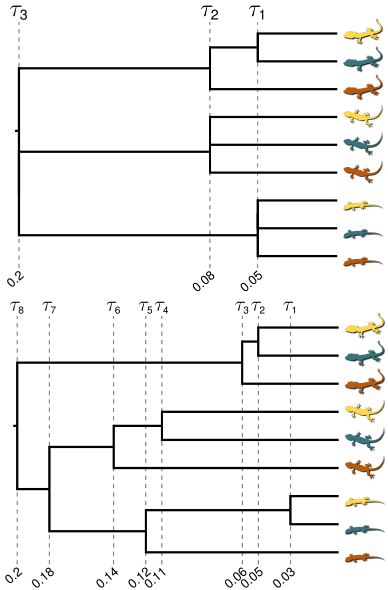
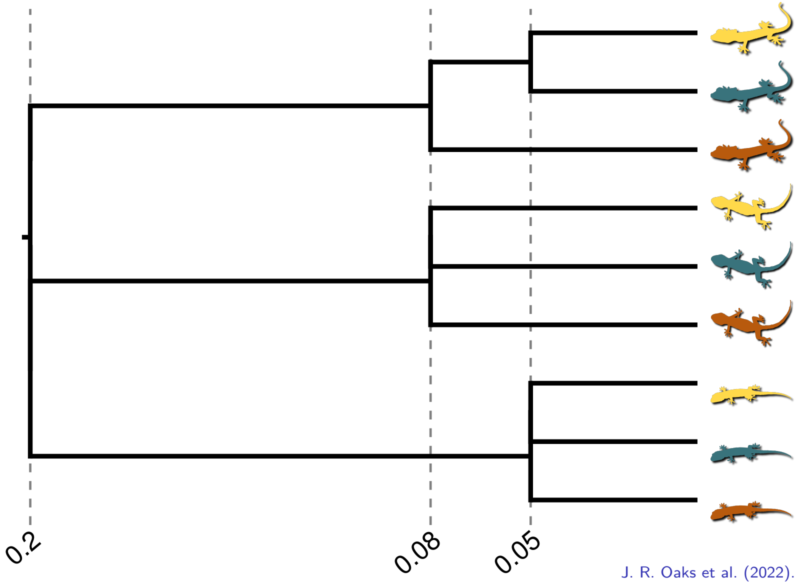
- Simulated 100 data sets where topology and div times randomly drawn from M_G and M_{IB}





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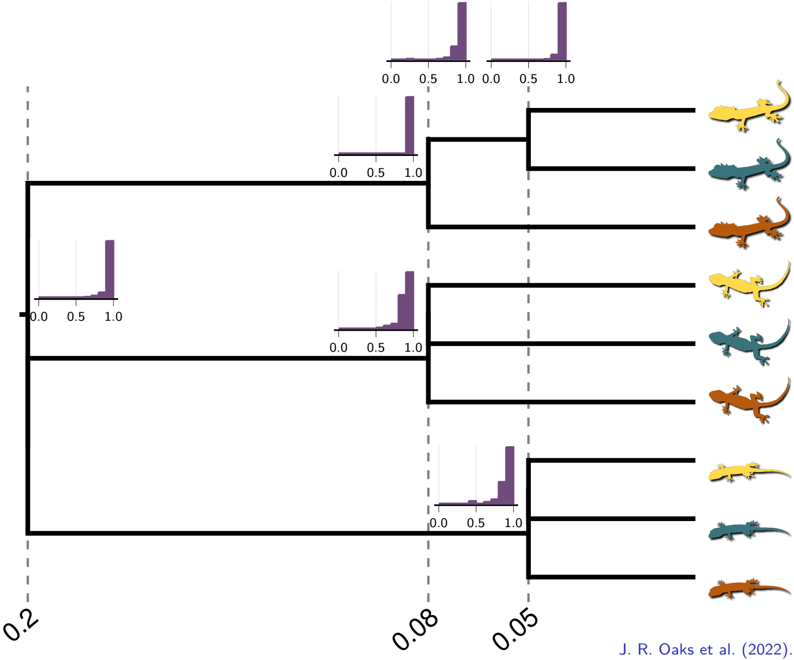
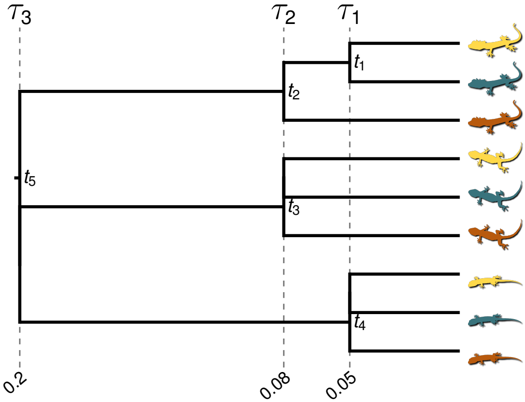
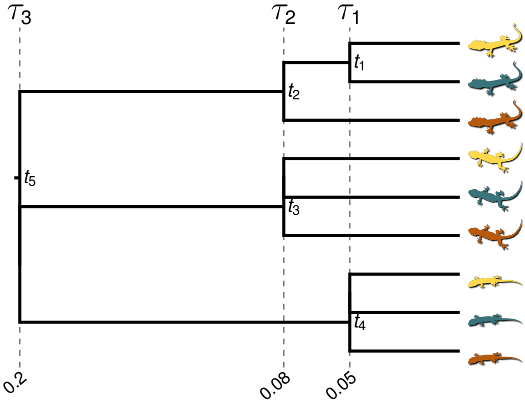
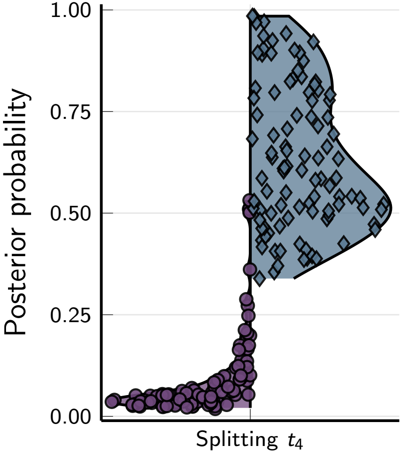


J. R. Oaks et al. (2022). *PNAS* 119: e2121036119


τ_3
τ_2
τ_1
t_1
t_2
t_3
t_4
t_5
0.2
0.08
0.05

M_G = Generalized model M_{IB} = Independent-bifurcating model





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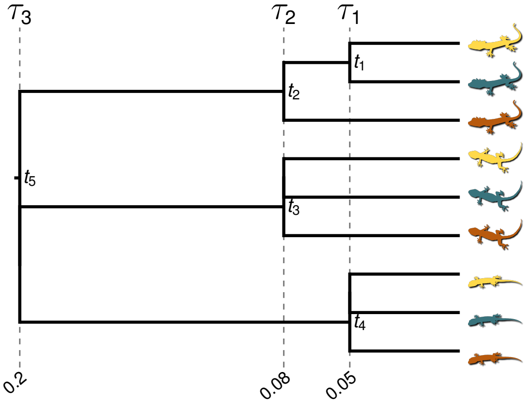

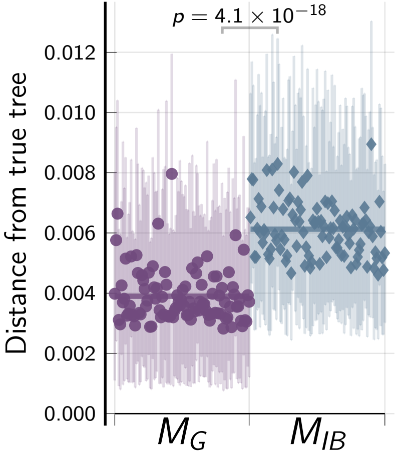

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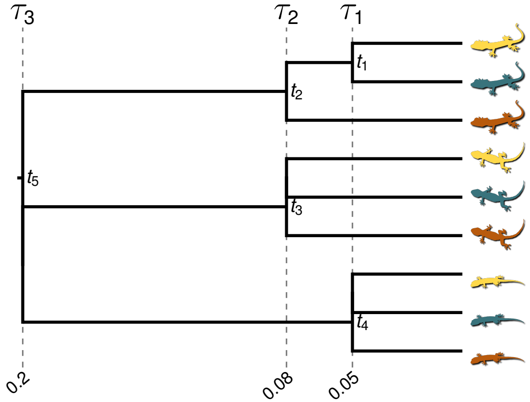

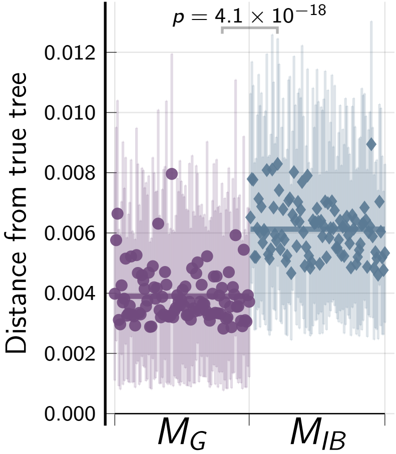

M_G significantly better at inferring trees with shared divergences

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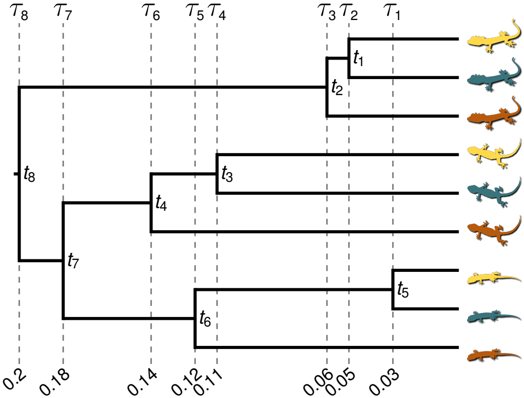

J. R. Oaks et al. (2022). *PNAS* 119: e2121036119

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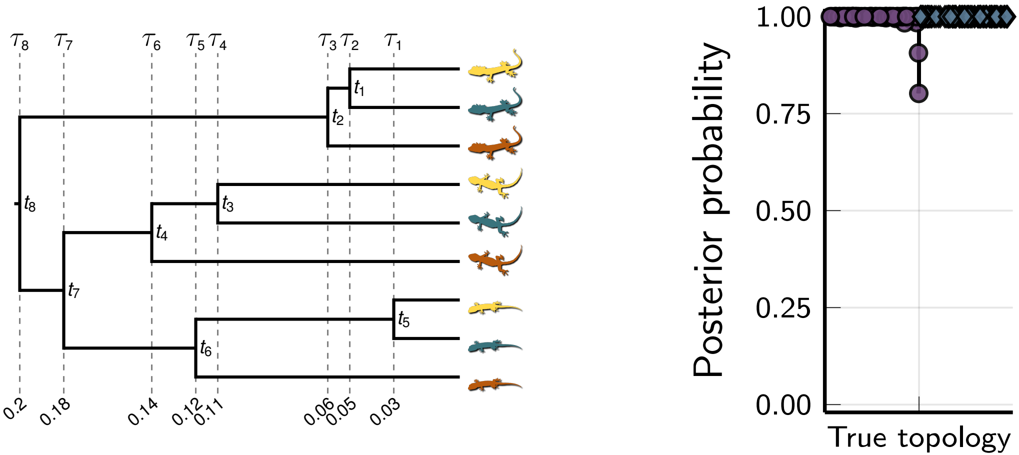

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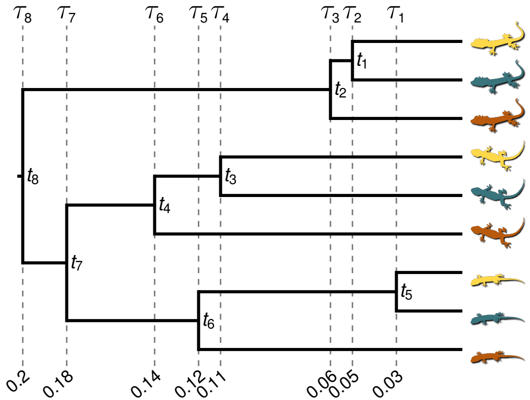

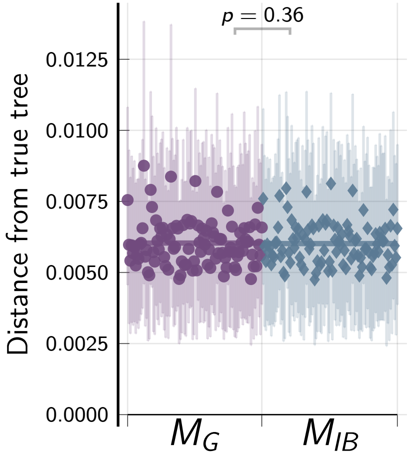

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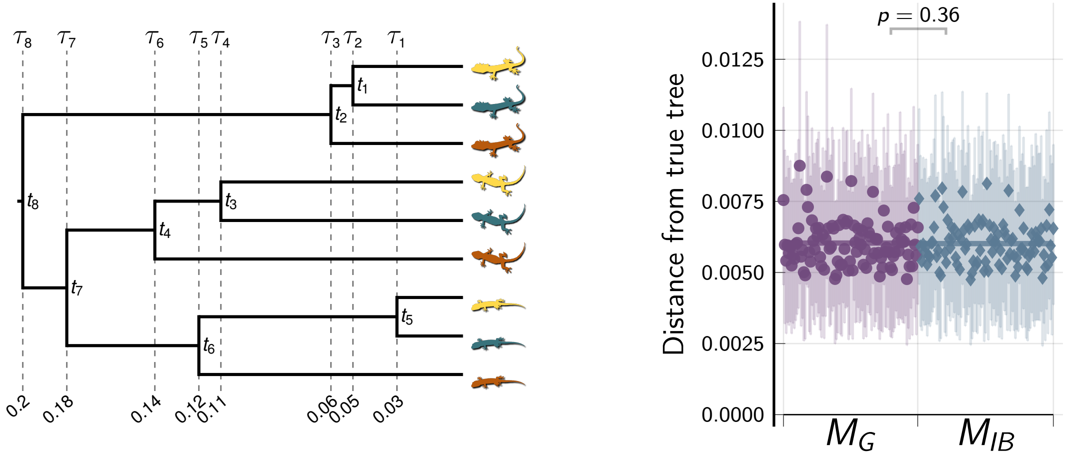

M_G performs as well as true model when divergences are independent

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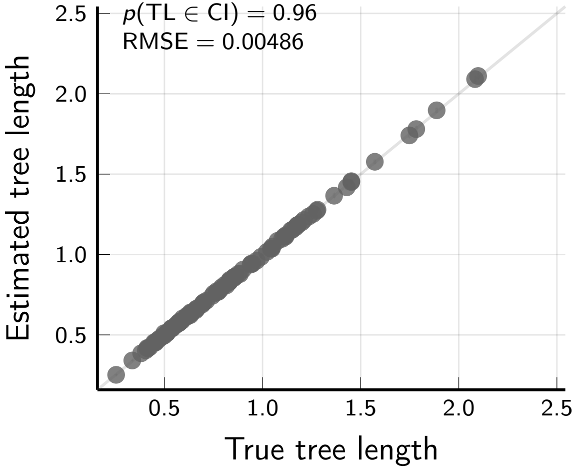
Results: random M_G trees



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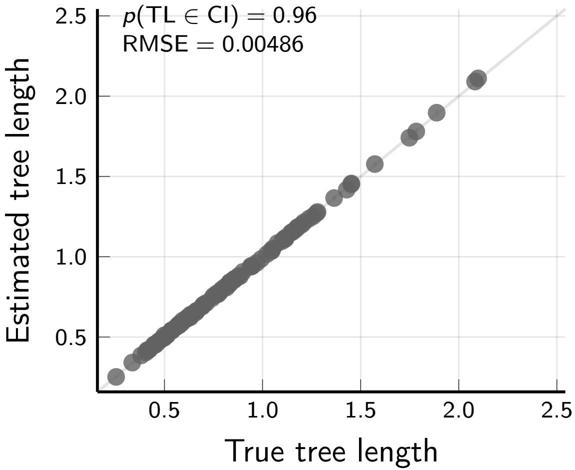

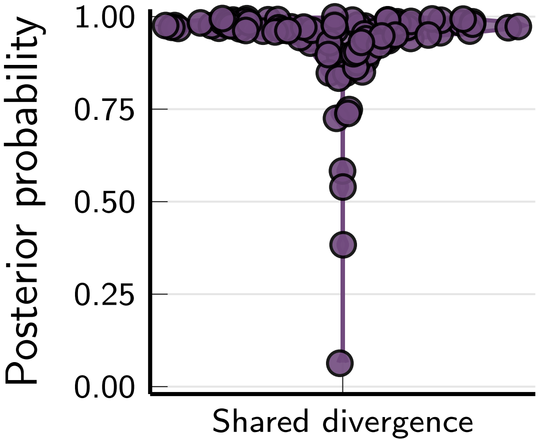

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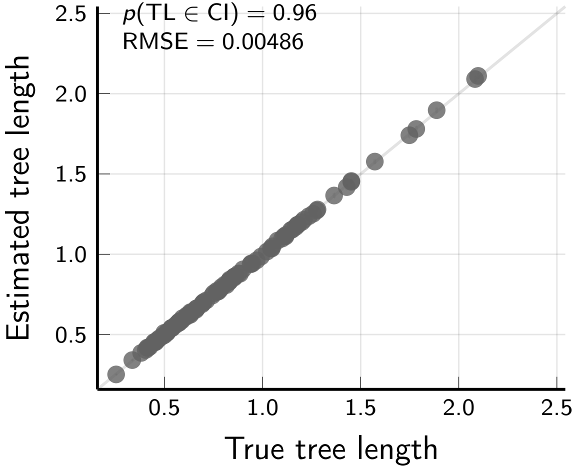

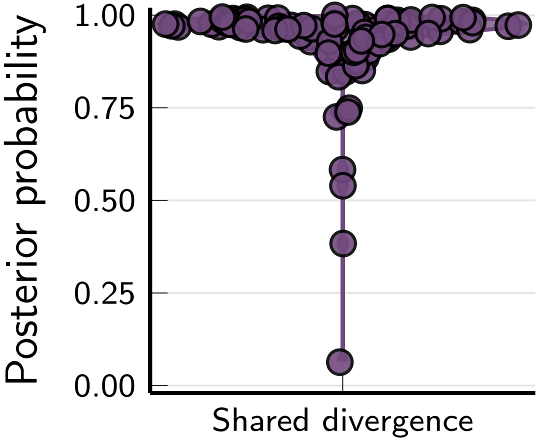

M_G performs well with data simulated on random trees with shared divergences

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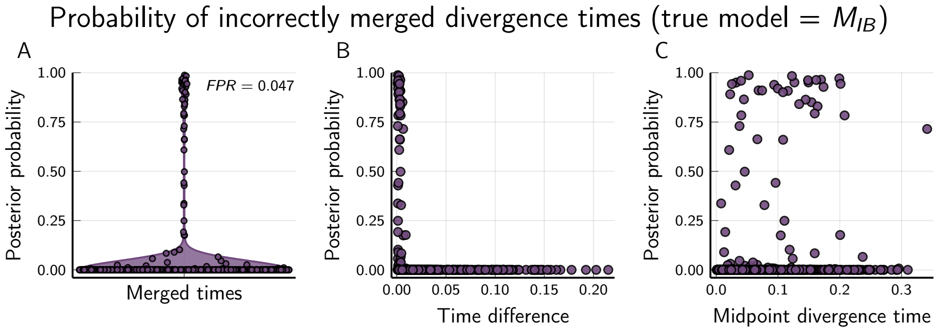
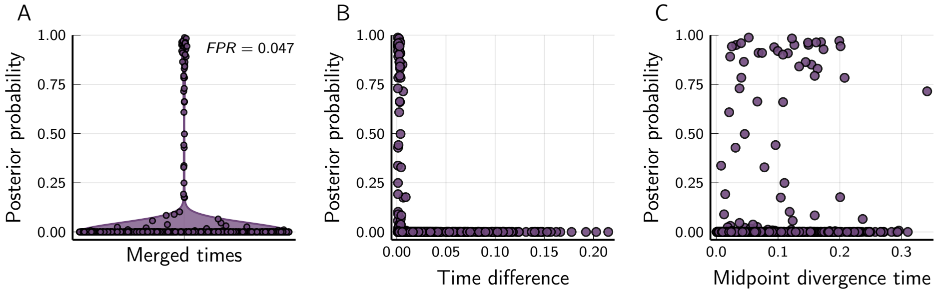
Results: random M_{IB} trees

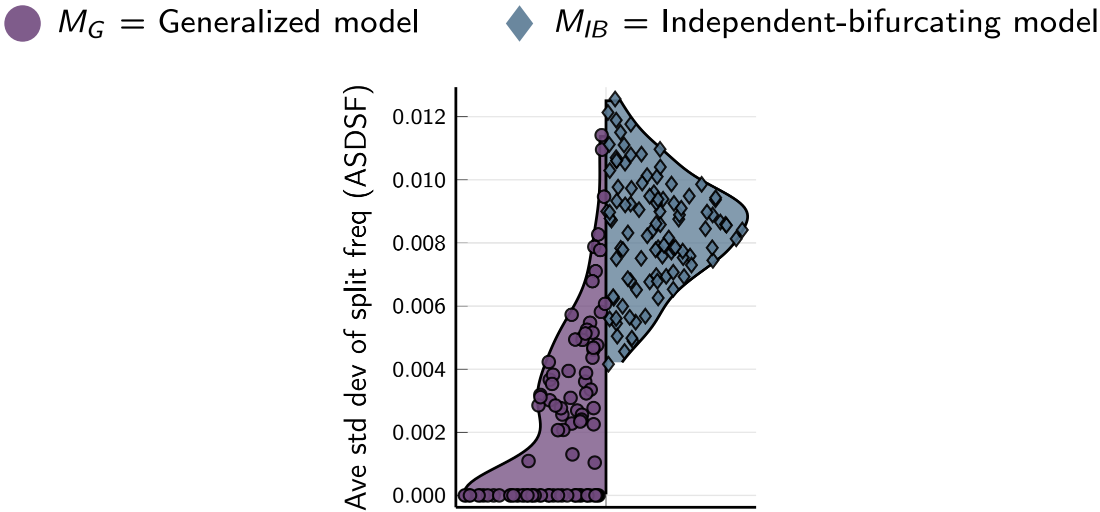


Results: random M_{IB} trees

Probability of incorrectly merged divergence times (true model = M_{IB})



M_G has low false positive rate



Generalizing tree space improves MCMC convergence and mixing

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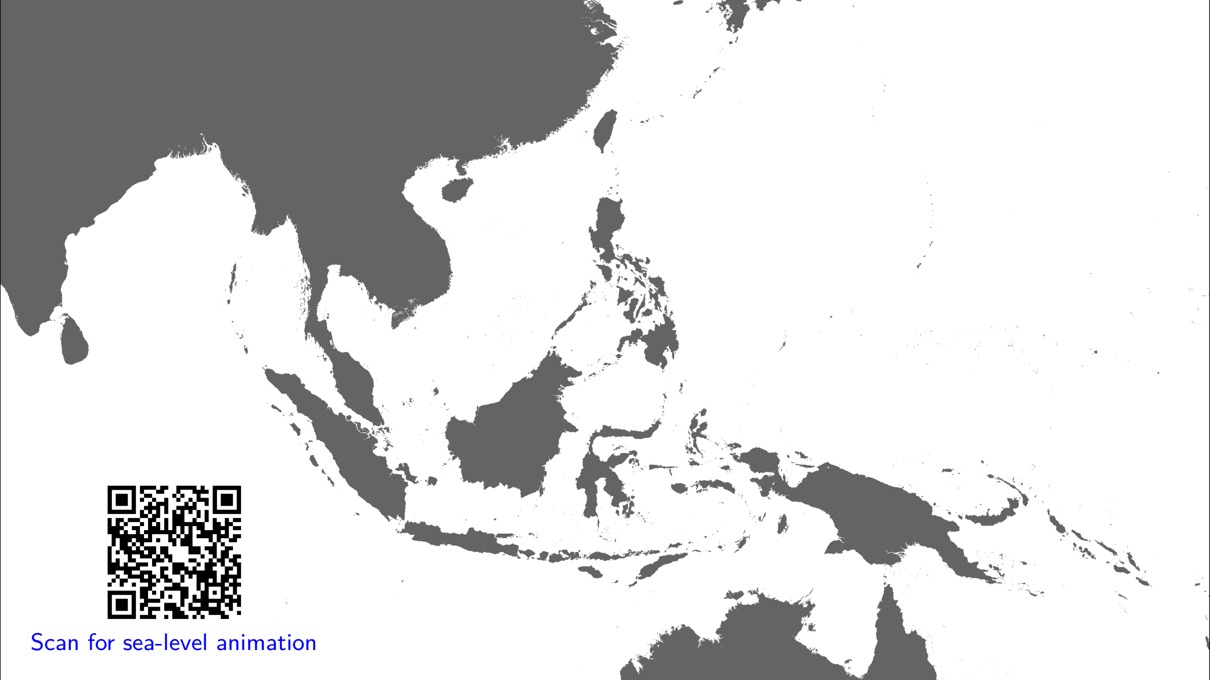
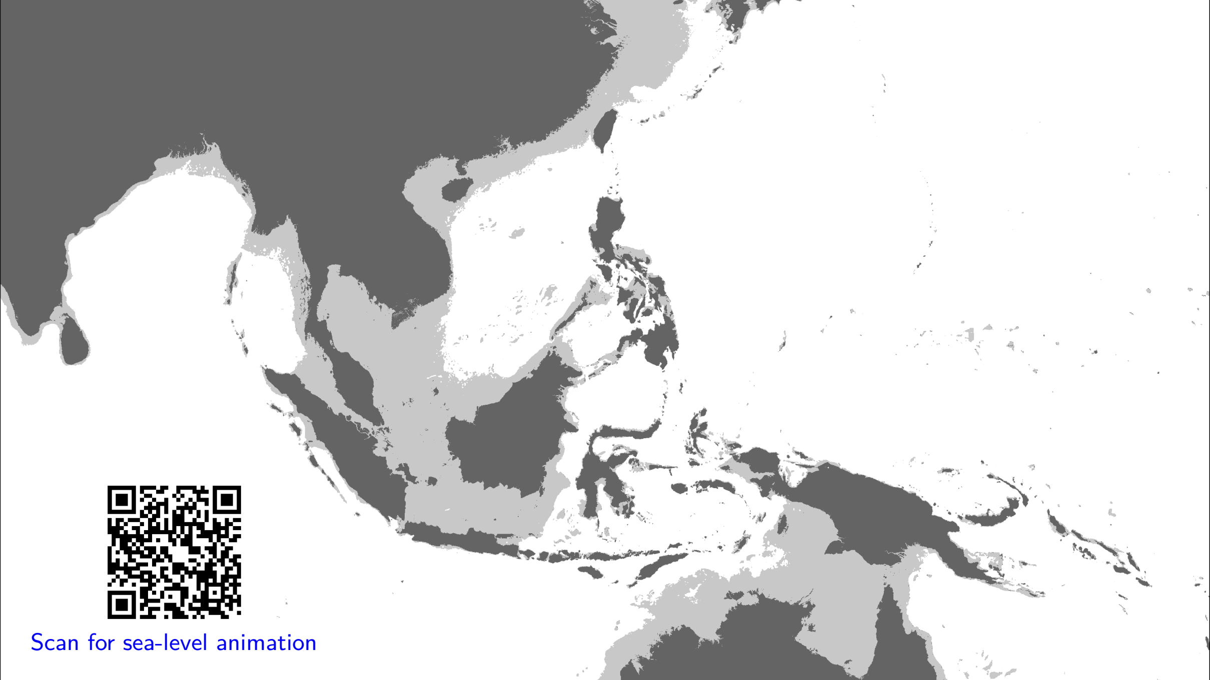


Scan for sea-level animation



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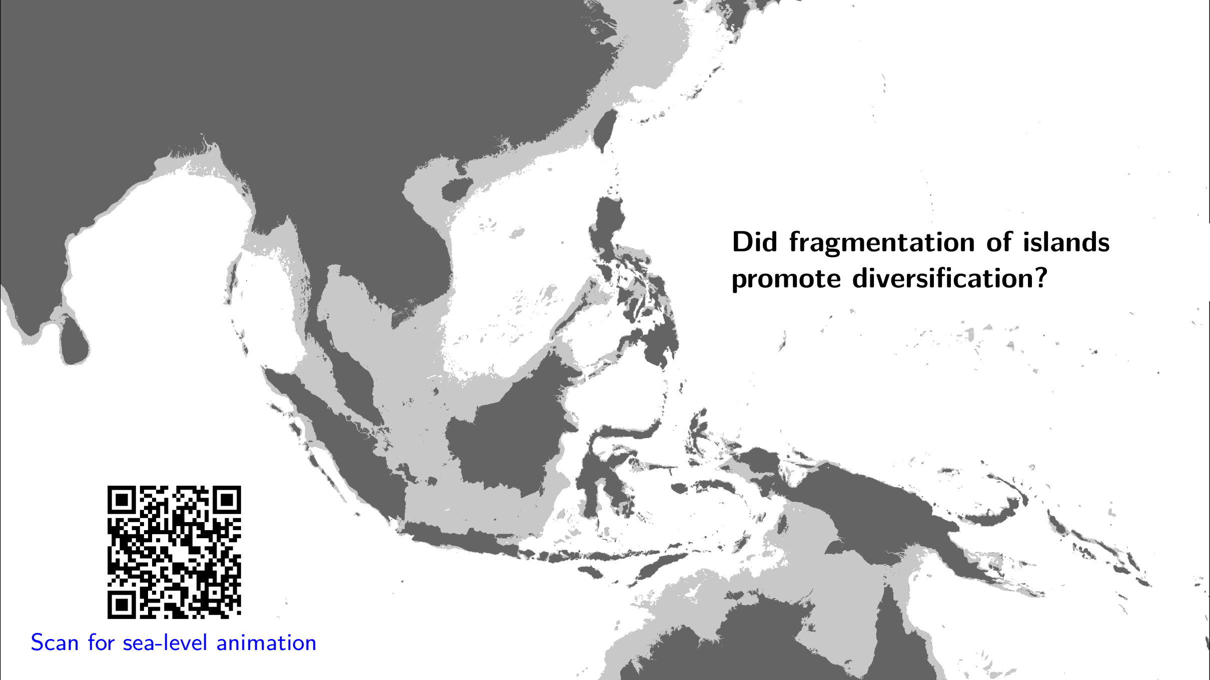

Did fragmentation of islands promote diversification?

Scan for sea-level animation

Cyrtodactylus

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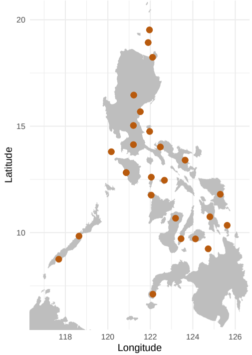
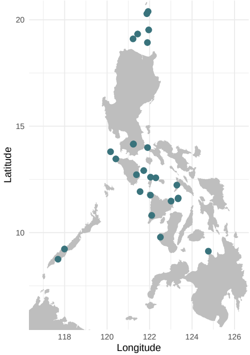


Gekko



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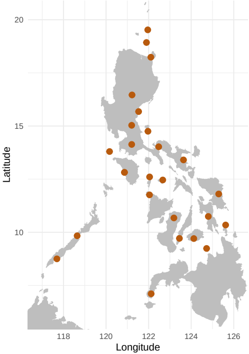
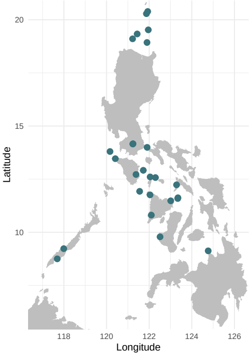


1702 loci
155,887 sites

Gekko



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1033 loci
94,813 sites

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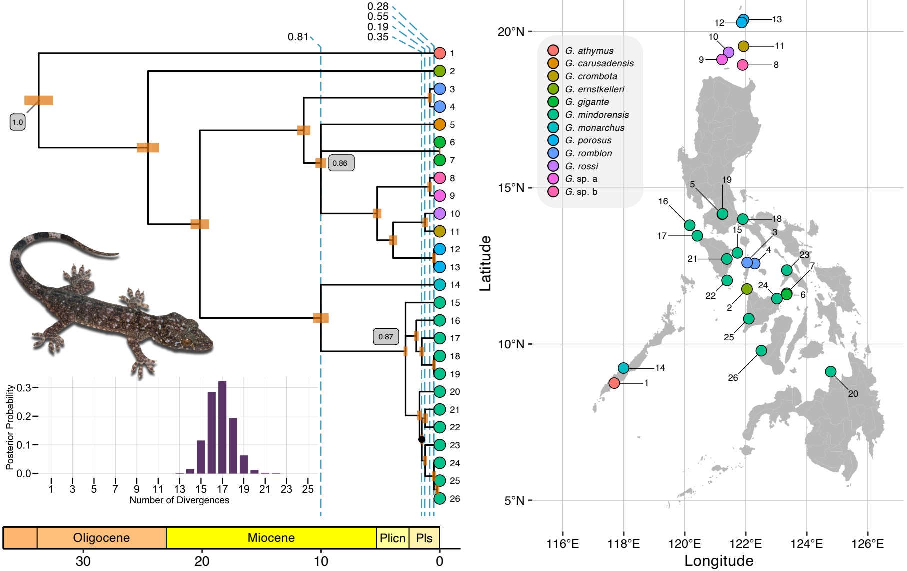
Gekko



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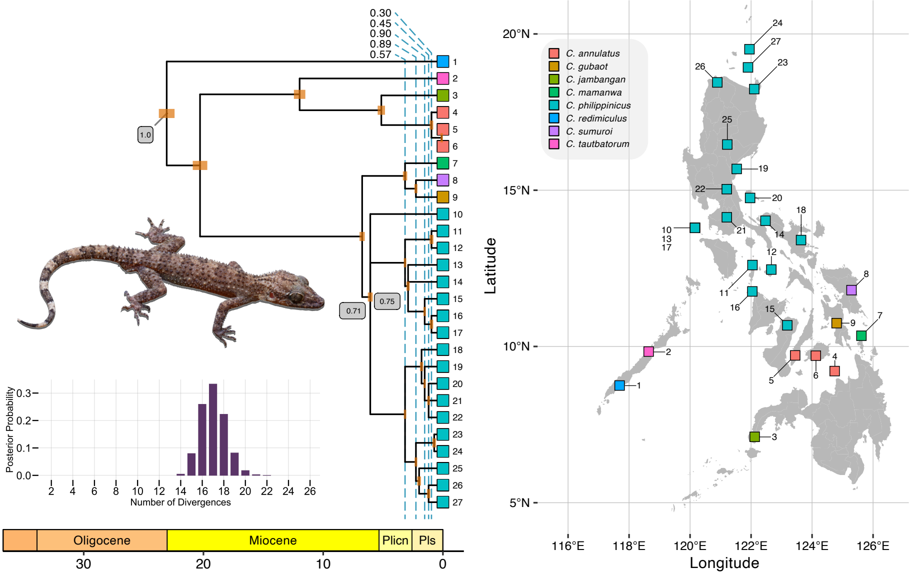

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Take-home points

- We can accurately infer phylogenies with shared divergences

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- Generalizing tree space avoids spurious support incorrect relationships and improves MCMC mixing
- Among Philippine gekkonids, we found support for shared divergences predicted by sea-level changes

Open science: everything is available. . .

Software:

- Phycoeval: github.com/phyletica/ecoevolity
  (release coming soon)

Open-Science Notebooks:

- Phycoeval analyses: github.com/phyletica/phycoeval-experiments
- Gecko RADseq: github.com/phyletica/gekgo

Moving forward: Theory/methods

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- Develop process-based and trait-dependent distributions over the space of generalized trees
  - "Birth-death-burst" model

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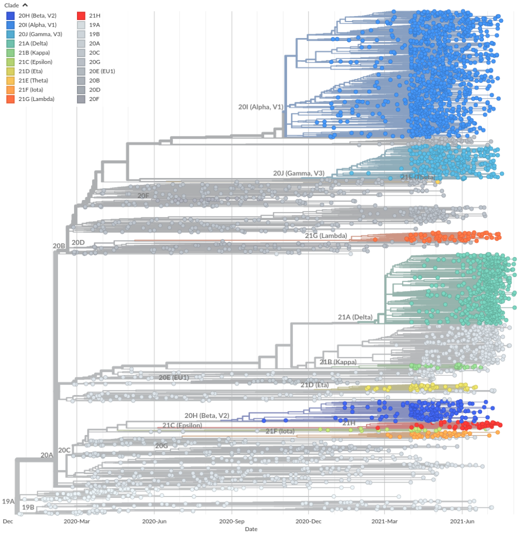
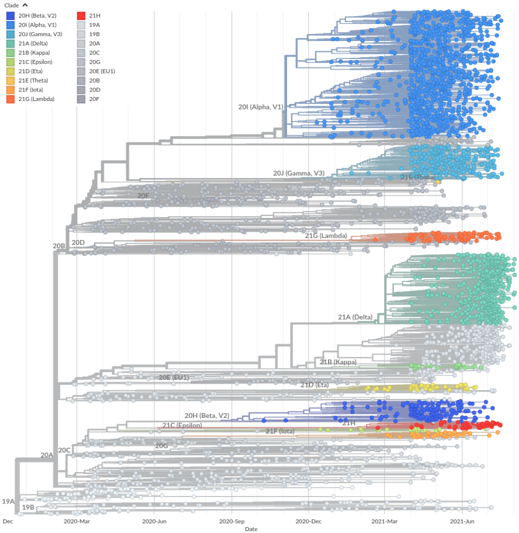


nextstrain.org J. Hadfield et al. (2018). *Bioinformatics* 34: 4121–4123

Moving forward: Theory/methods

- Develop process-based and trait-dependent distributions over the space of generalized trees
  - "Birth-death-burst" model
- Extend generalized tree distribution to trees that are not ultrametric
- Couple generalized tree distribution with other phylogenetic likelihood models



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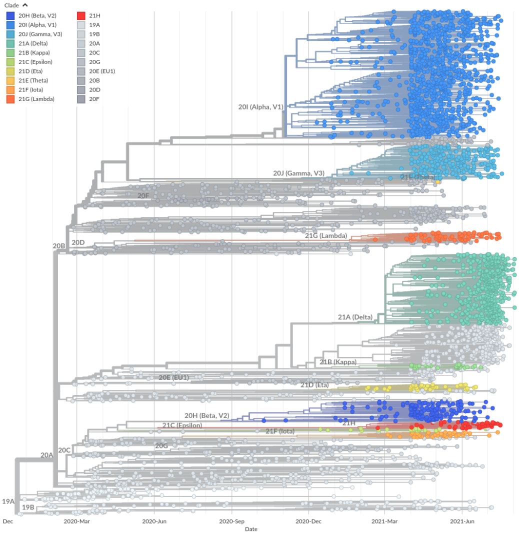
Moving forward: Applications



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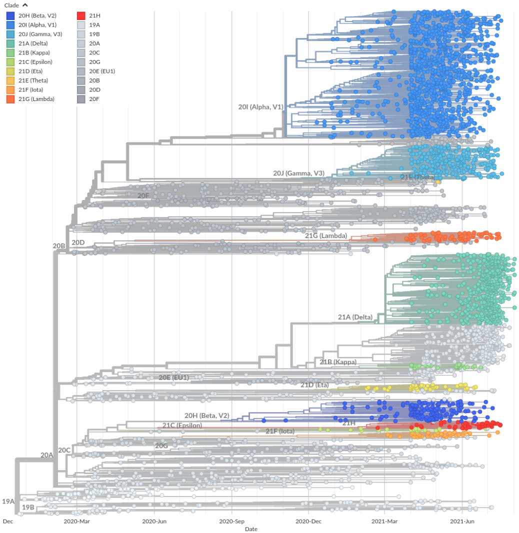
Moving forward: Applications

Epidemiological dynamics of “super-spreading” events during the COVID-19 pandemic



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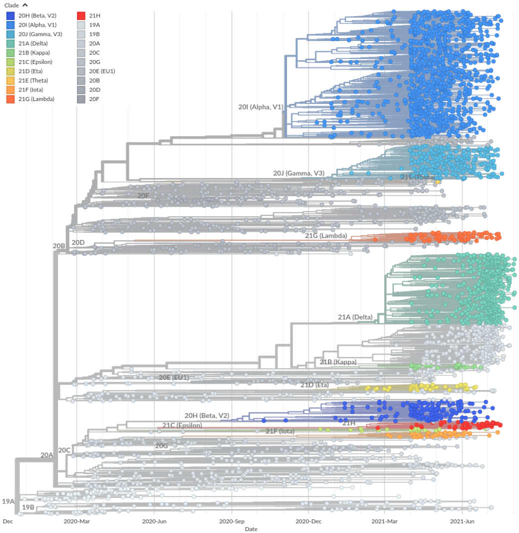

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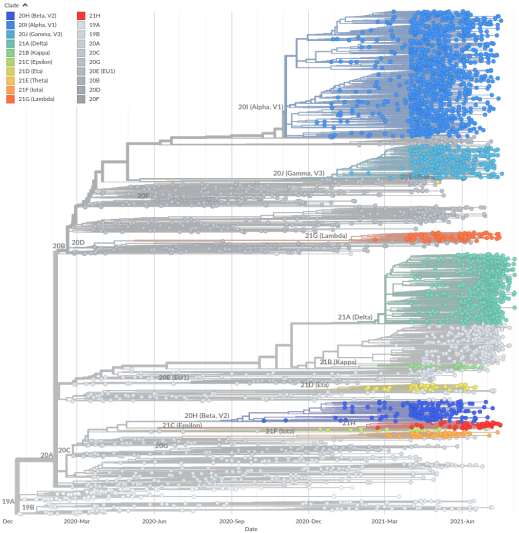

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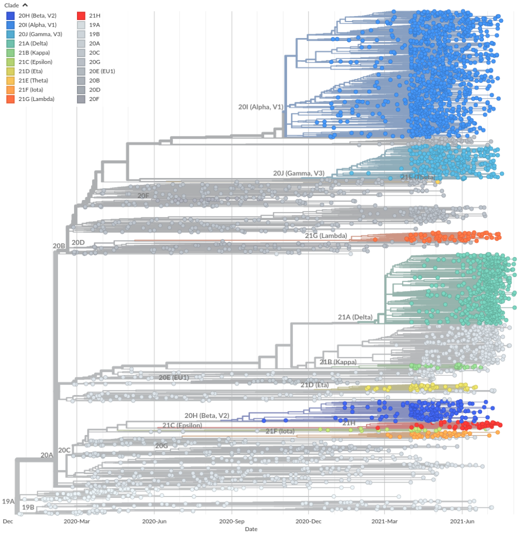
Moving forward: Applications

Epidemiological dynamics of “super-spreading” events during the COVID-19 pandemic

- Spread at social gatherings creates shared and multifurcating divergences in the viral “transmission tree”
- Estimate rate of shared divergences as proxy for spread via social gatherings
- Test if this varies over time, among regions, and among variants of SARS-CoV-2



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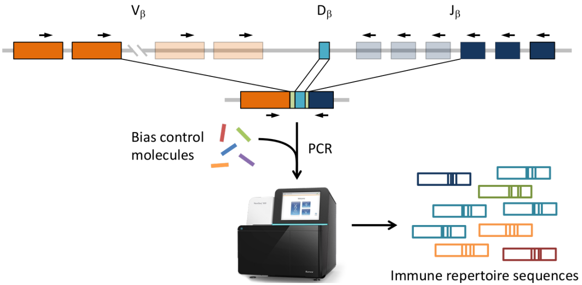

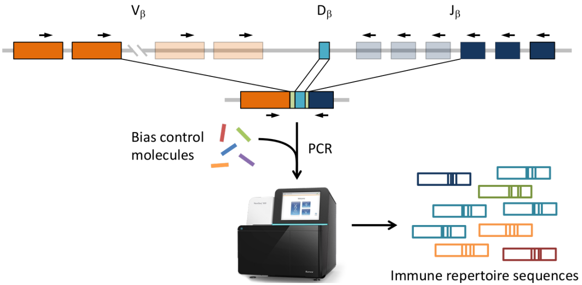

V_β
D_β
J_β
Bias control molecules
PCR
Immune repertoire sequences

Stats & Algorithms

- Our team is very cross-functional
  - We solve statistical and computational challenges for many stakeholders across Adaptive

Erin Calfee
Computational Biologist I

Travers Ching
Sr Computational Biologist

Amy Ko
Computational Biologist II

Jamie Oaks
Sr Manager, Computational Bi...

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Remote (WFH)

Intern, Computational Biology
Remote (WFH)

Intern, Computational Biology, Antigen Map
Remote (WFH)

Intern, Computational Biology (CRI)
Remote (WFH)

Intern, Computational Biology, Stats and Algorithms
Remote (WFH)

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