

Generalizing phylogenetics to infer patterns predicted by processes of diversification

Jamie Oaks

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- ▶ Brian Folt
- ▶ Jesse Grismer

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- ▶ Kyle David
- ▶ Saman Jahangiri
- ▶ Randy Klabacka
- ▶ Morgan Muell
- ▶ Tanner Myers
- ▶ Claire Tracy
- ▶ Branna Sipley
- ▶ Aundrea Westfall



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- ▶ 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

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- ▶ Phylogenetics is rapidly becoming the statistical foundation of biology



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- ▶ Phylogenetics is rapidly becoming the statistical foundation of biology
- ▶ “Big data” present exciting possibilities and challenges

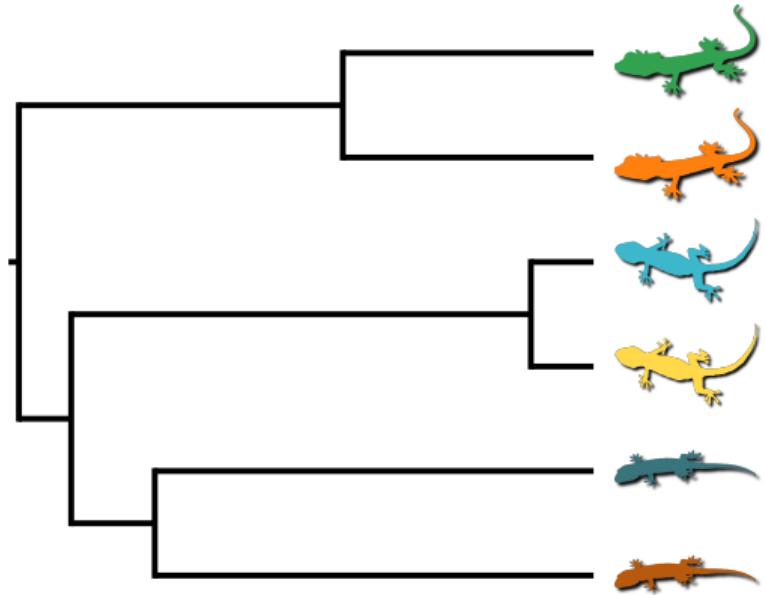


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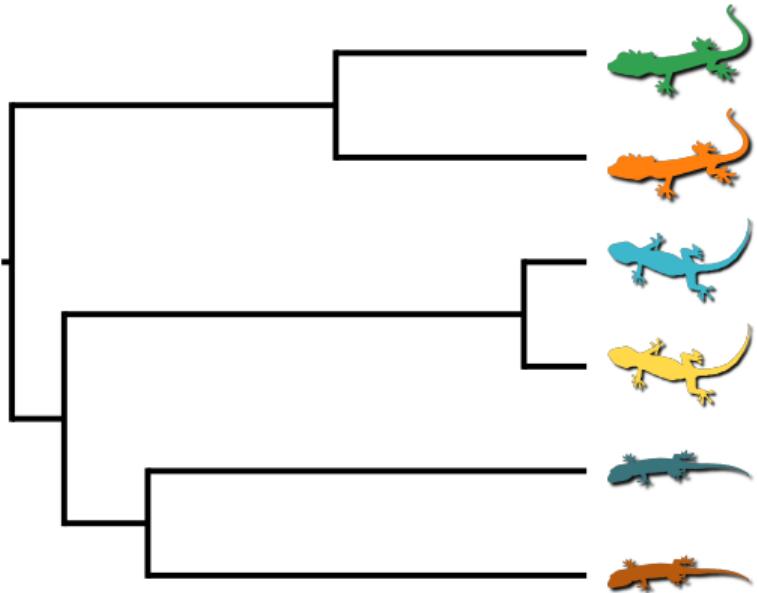
- ▶ Phylogenetics is rapidly becoming the statistical foundation of biology
- ▶ “Big data” present exciting possibilities and challenges
- ▶ Many opportunities to develop new ways to study biology in light of phylogeny

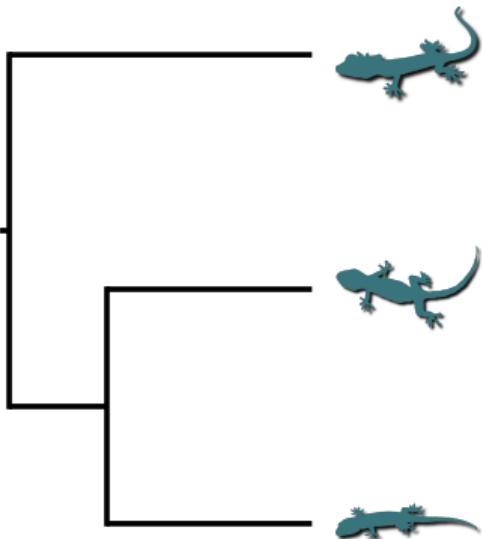


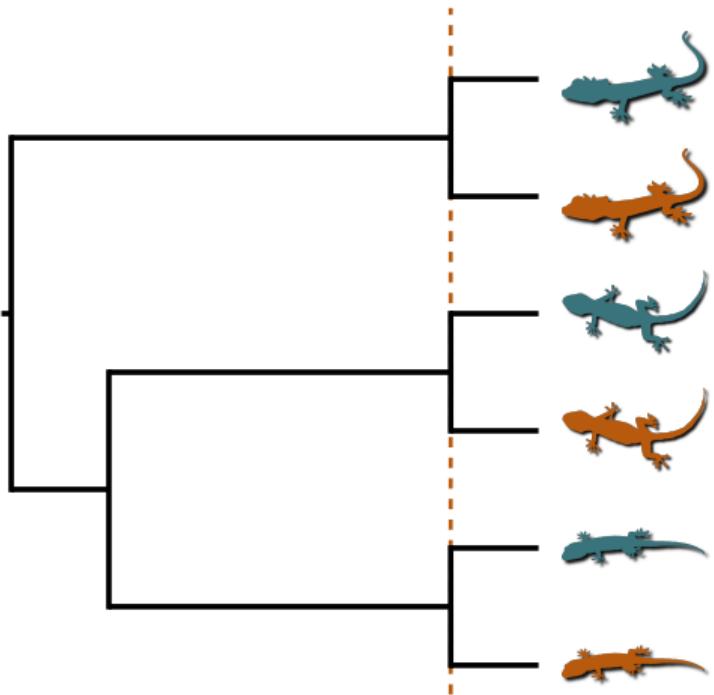
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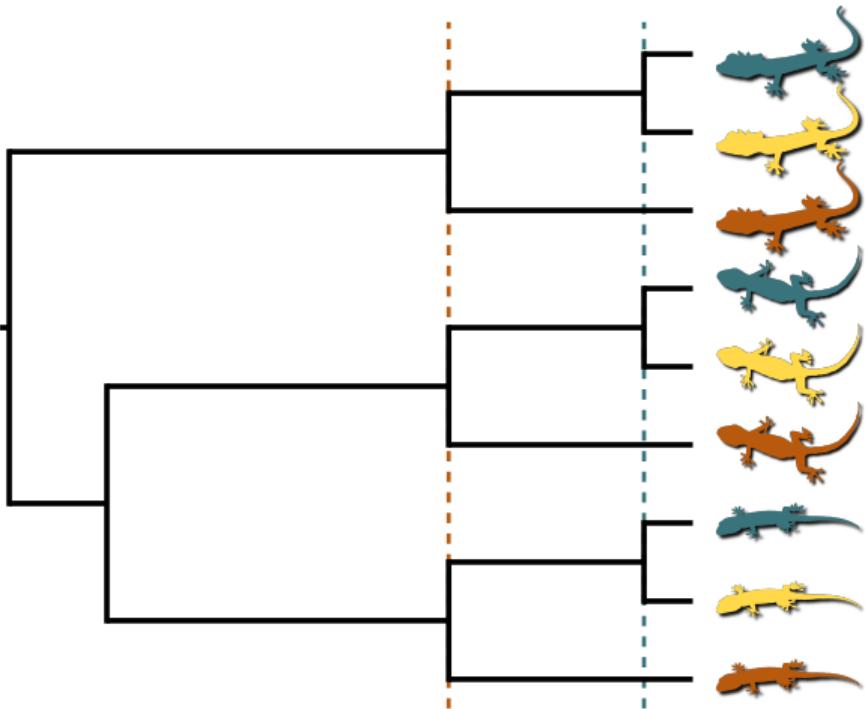


- ▶ **Assumption:** All processes of diversification affect each lineage independently



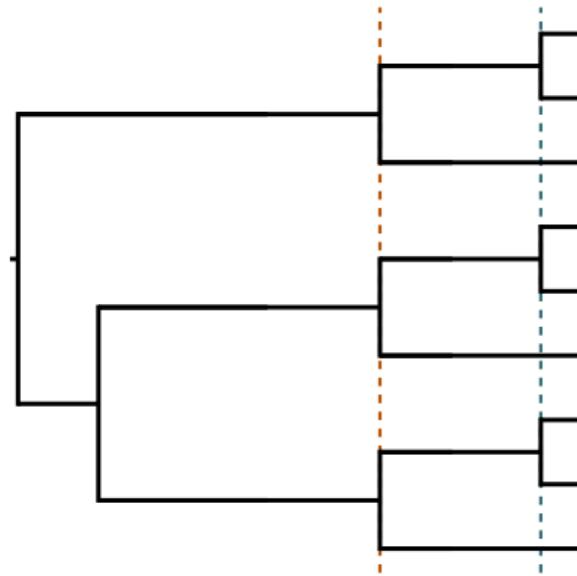






Biogeography

- ▶ Environmental changes that affect whole communities of species

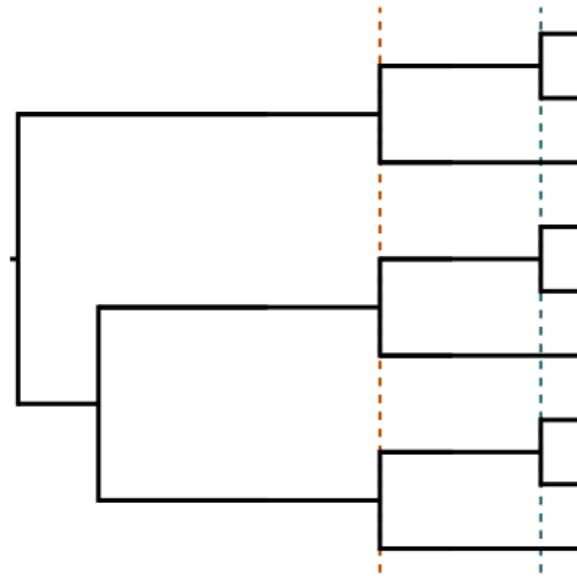


Biogeography

- ▶ Environmental changes that affect whole communities of species

Genome evolution

- ▶ Duplication of a chromosome segment harboring gene families



Biogeography

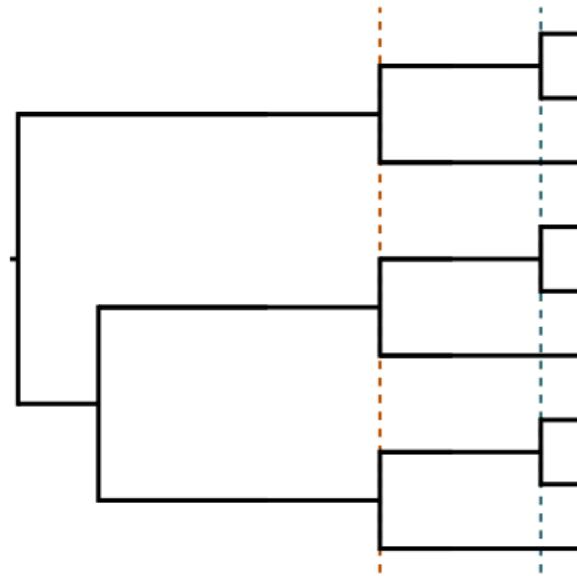
- ▶ Environmental changes that affect whole communities of species

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Epidemiology

- ▶ Transmission at social gatherings



Biogeography

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Genome evolution

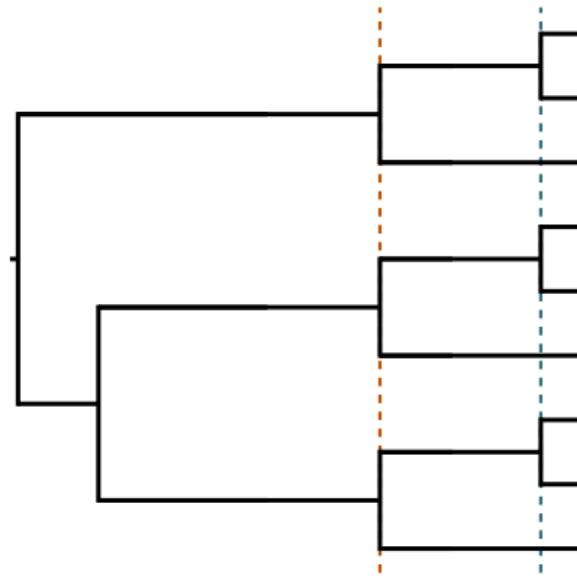
- ▶ Duplication of a chromosome segment harboring gene families

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Endosymbiont evolution (e.g., parasites, microbiome)

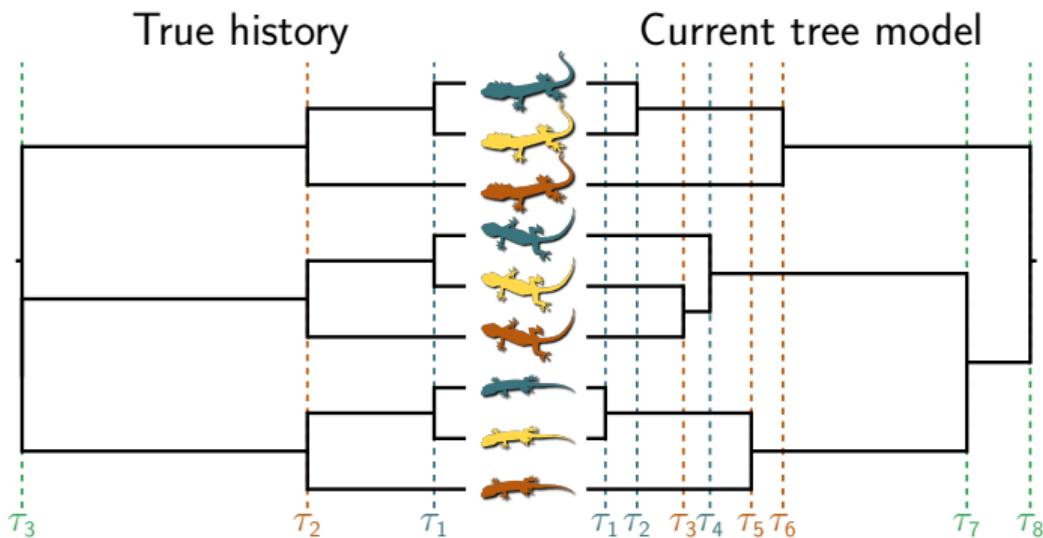
- ▶ Speciation of the host
- ▶ Co-colonization of new host species



Why account for shared divergences?

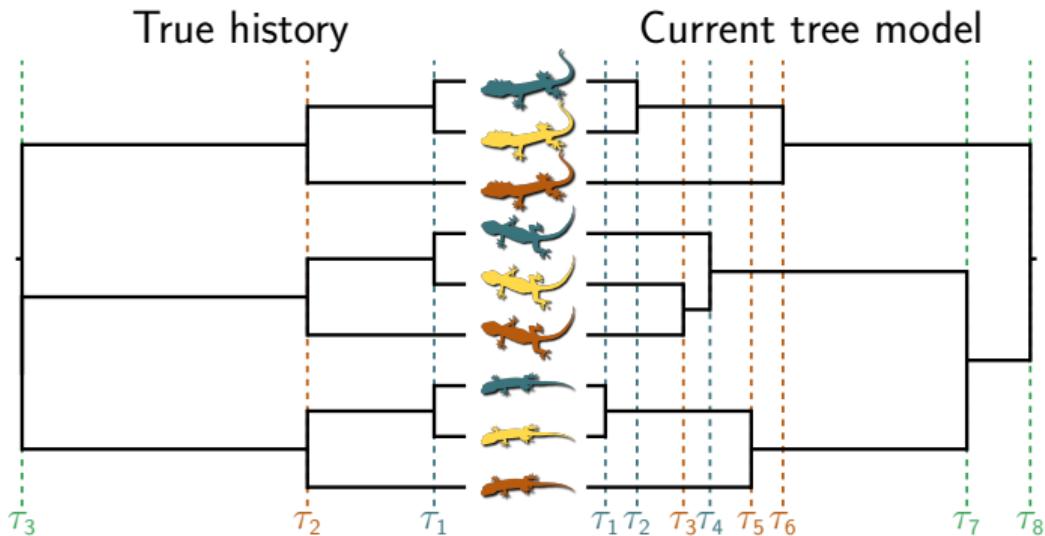
Why account for shared divergences?

1. Improve inference



Why account for shared divergences?

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



Biogeography

- ▶ Environmental changes that affect whole communities of species

Genome evolution

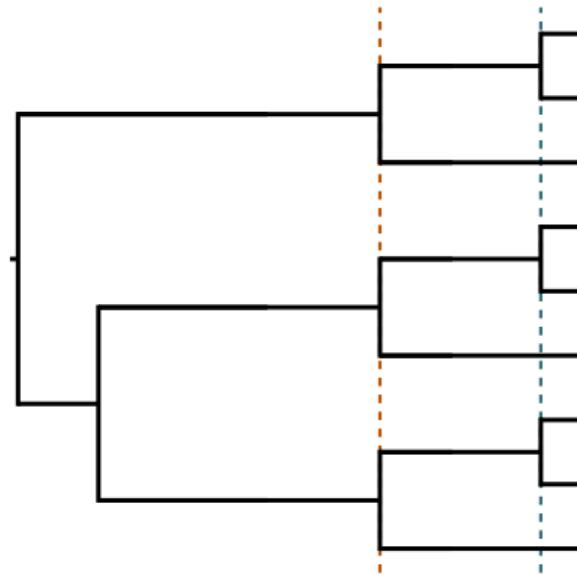
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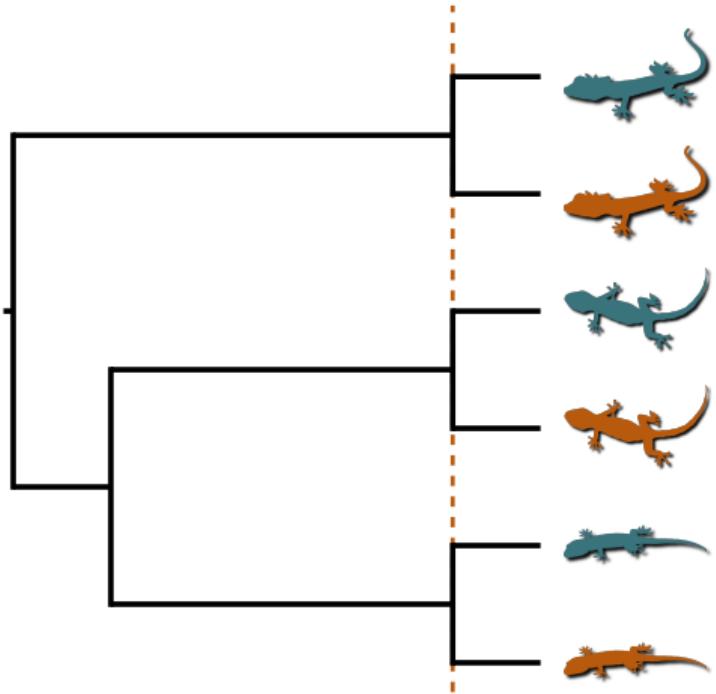
Approaches to the problem

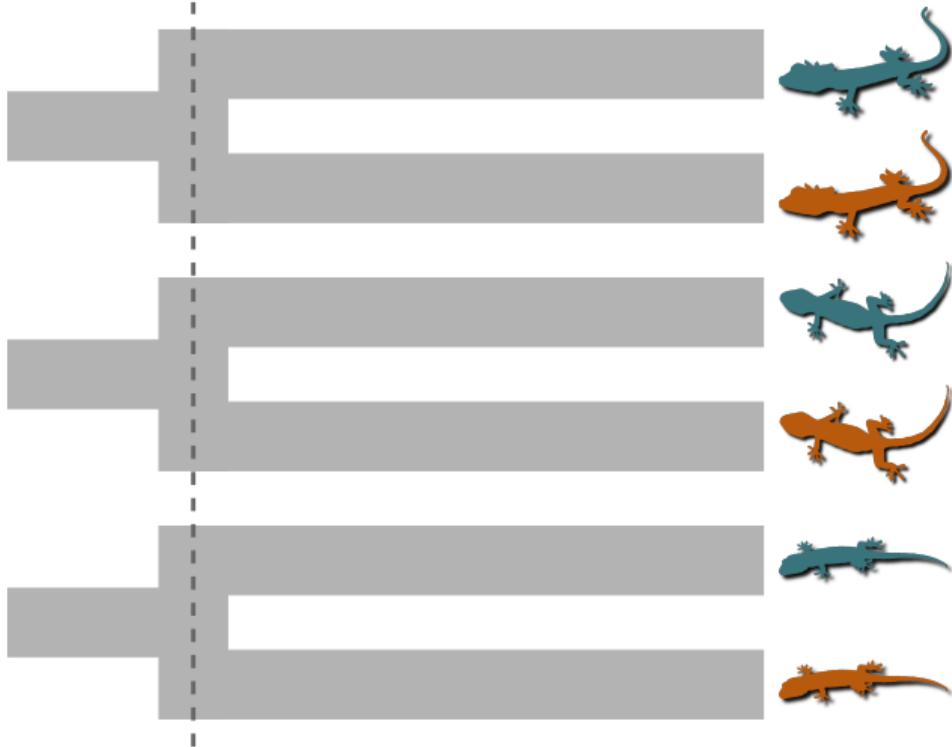
A pairwise approach (keep it “simple”)

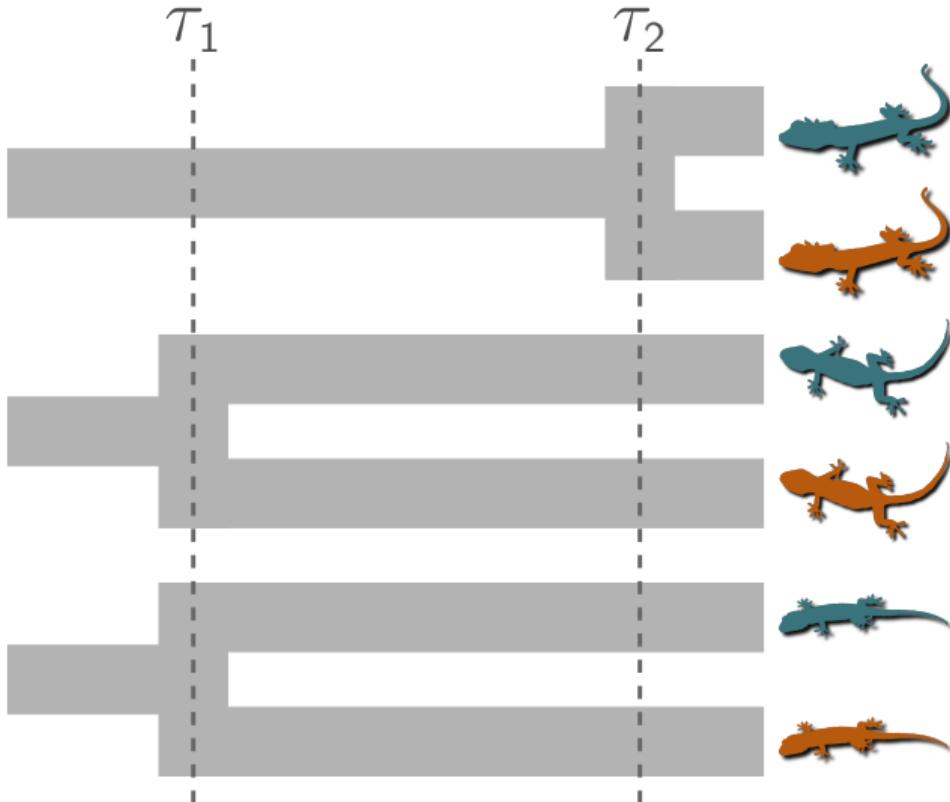
An aside for a related problem with population demography

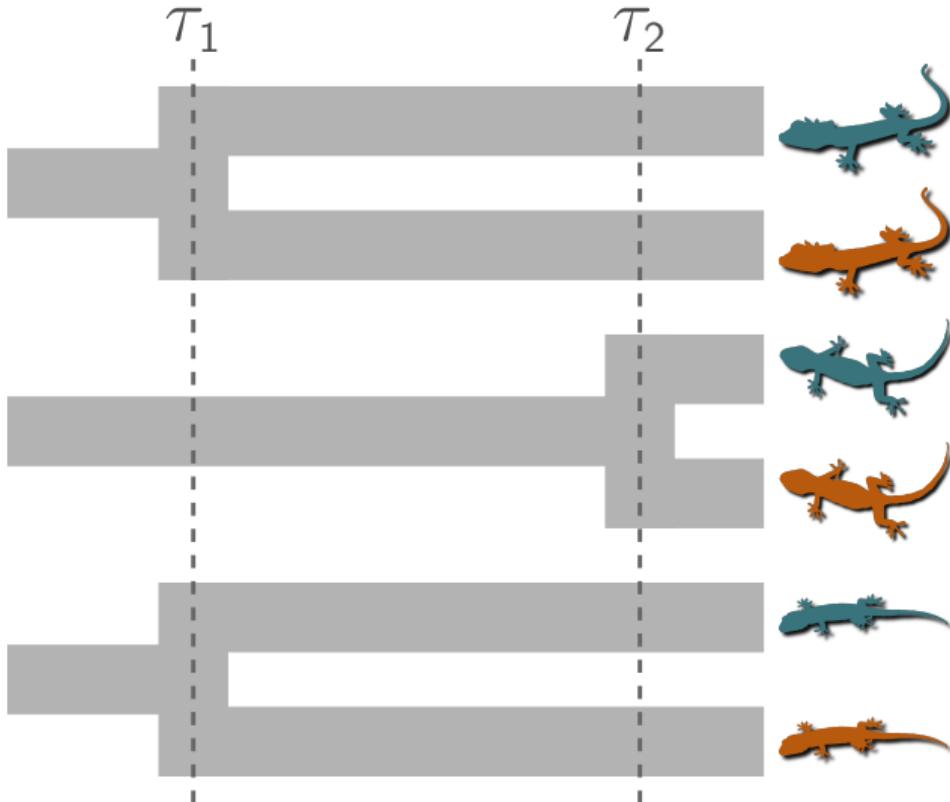
A fully phylogenetic approach

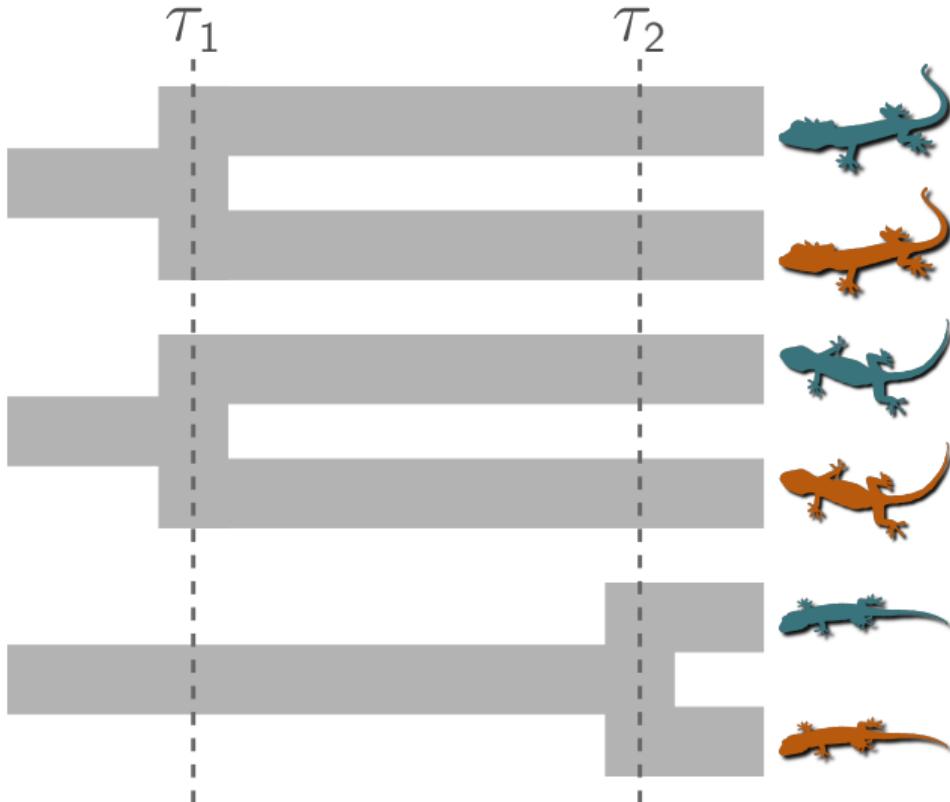
The next 5 years in the Phyletica Lab

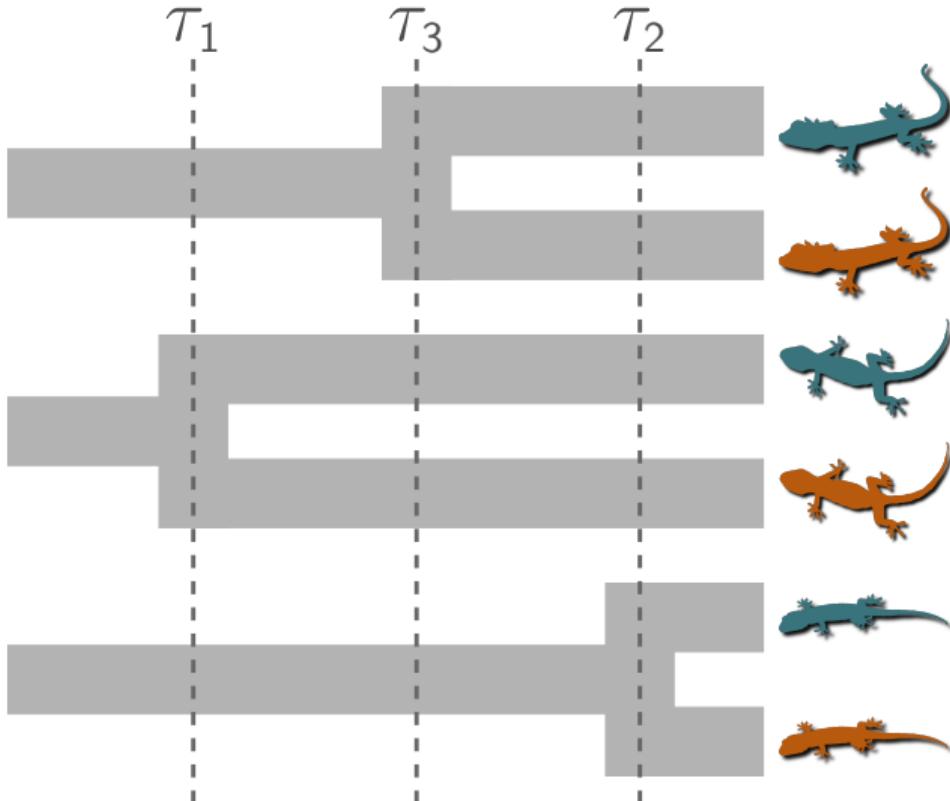


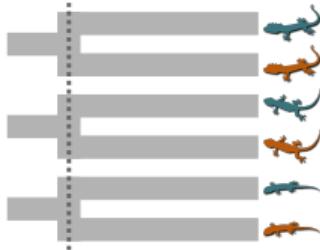
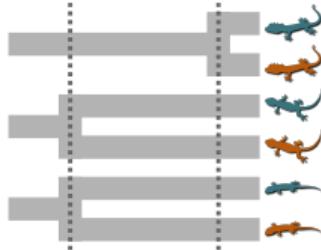
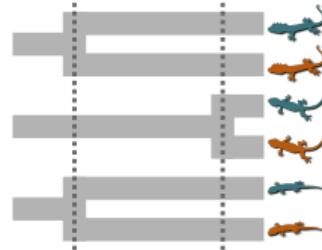
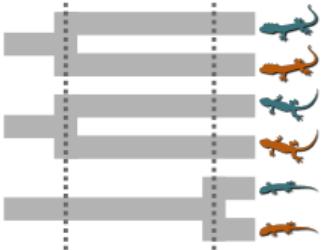
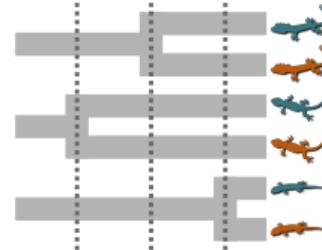
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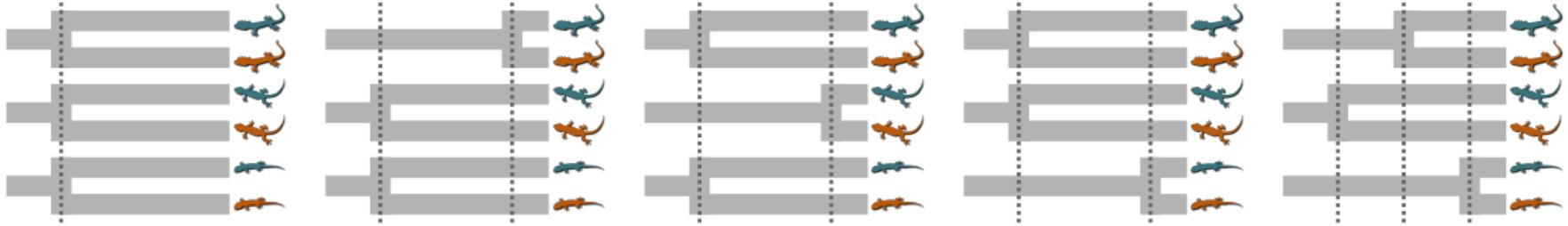








m_1  m_2  m_3  m_4  m_5 

m_1 m_2 m_3 m_4 m_5 

We want to infer the model and divergence times given genetic data

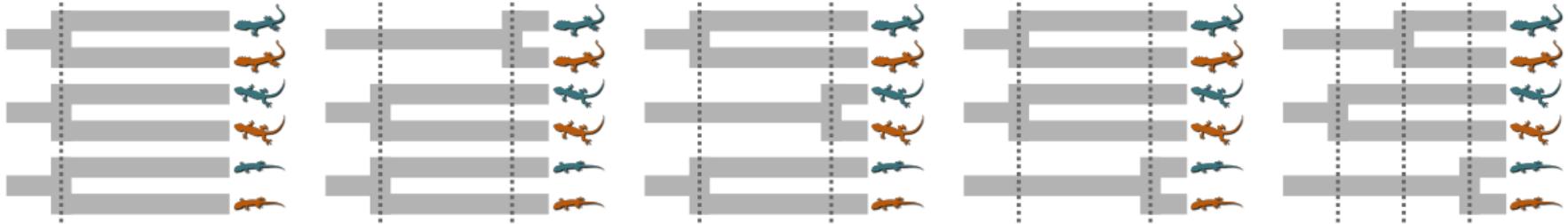
$p(m_1 | \mathbf{D})$

$p(m_2 | \mathbf{D})$

$p(m_3 | \mathbf{D})$

$p(m_4 | \mathbf{D})$

$p(m_5 | \mathbf{D})$



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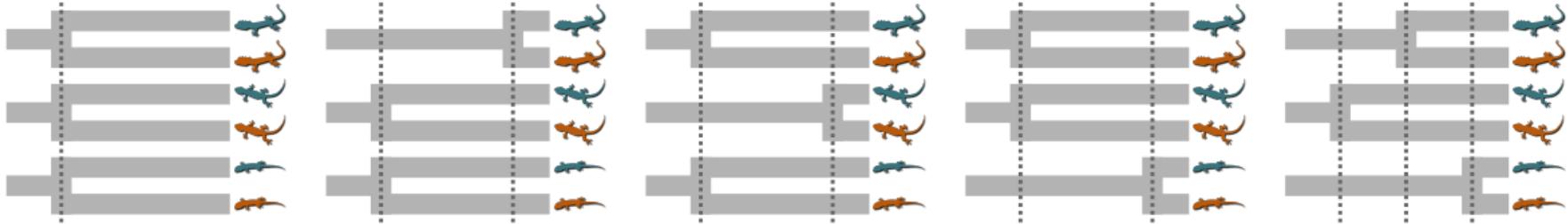
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We want to infer the model and divergence times given genetic data

$$p(m_i | \mathbf{D}) \propto p(\mathbf{D} | m_i)p(m_i)$$

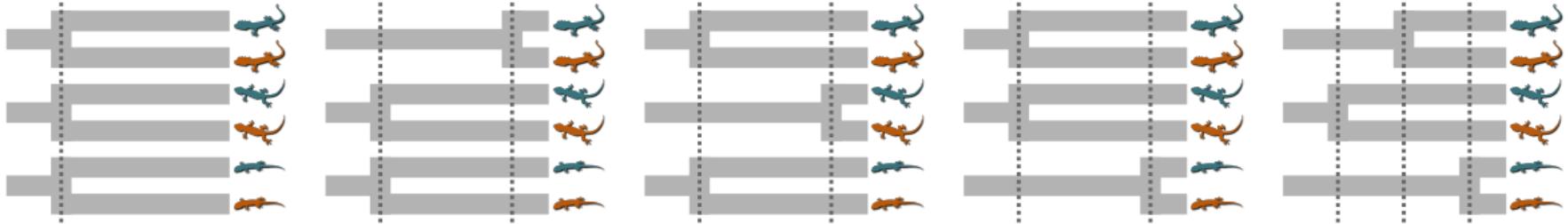
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$$p(m_i | \mathbf{D}) \propto p(\mathbf{D} | m_i) p(m_i)$$

$$p(\mathbf{D} | m_i) = \int_{\theta} p(\mathbf{D} | \theta, m_i) p(\theta | m_i) d\theta$$

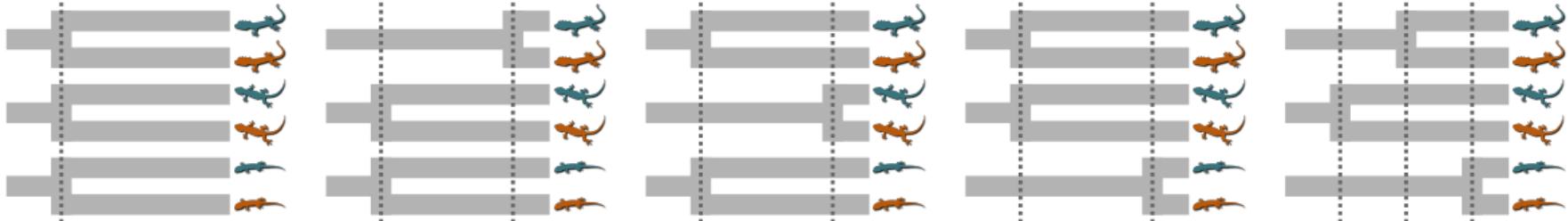
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- ▶ Divergence times
- ▶ Substitution parameters
- ▶ Gene trees
- ▶ Demographic parameters

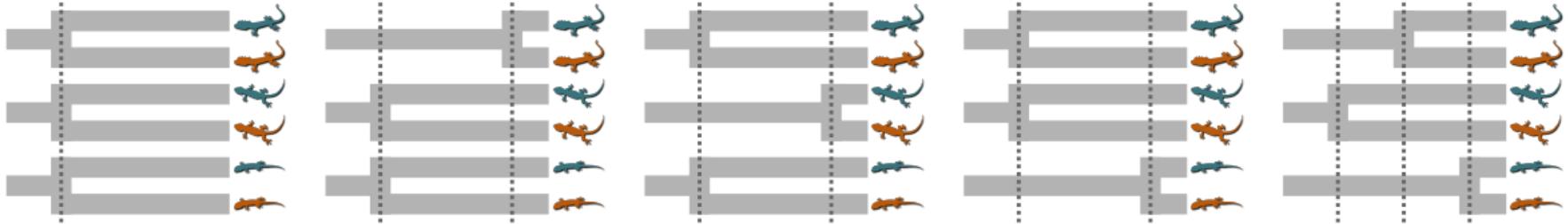
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We want to infer the model and divergence times given genetic data

Challenges:

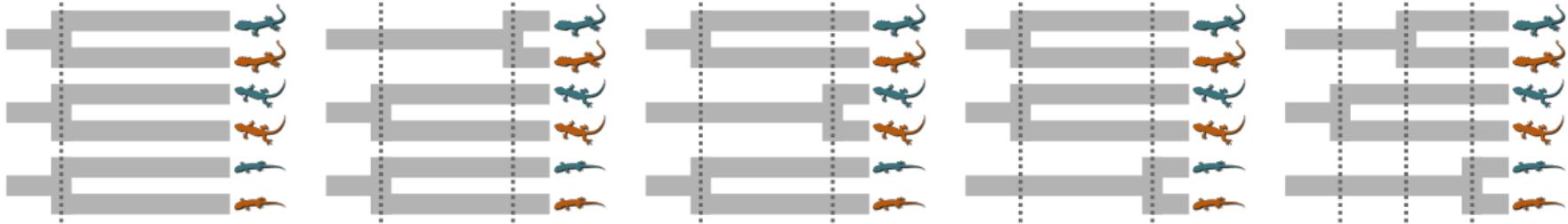
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We want to infer the model and divergence times given genetic data

Challenges:

1. Likelihood is tractable, but gene trees are difficult

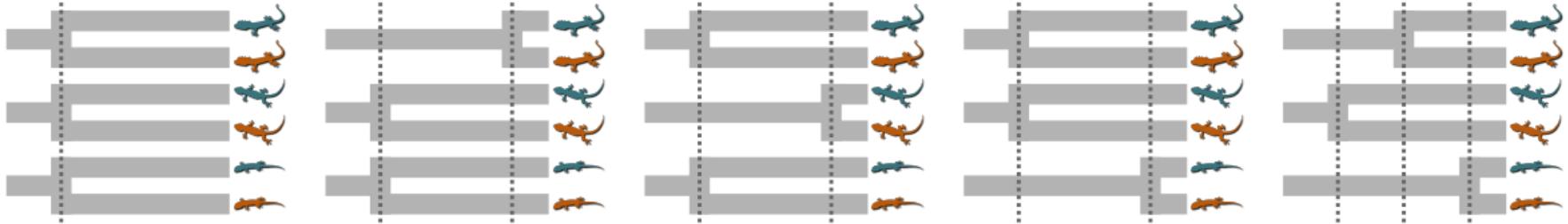
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Challenges:

1. Likelihood is tractable, but gene trees are difficult
2. Sampling over all possible models

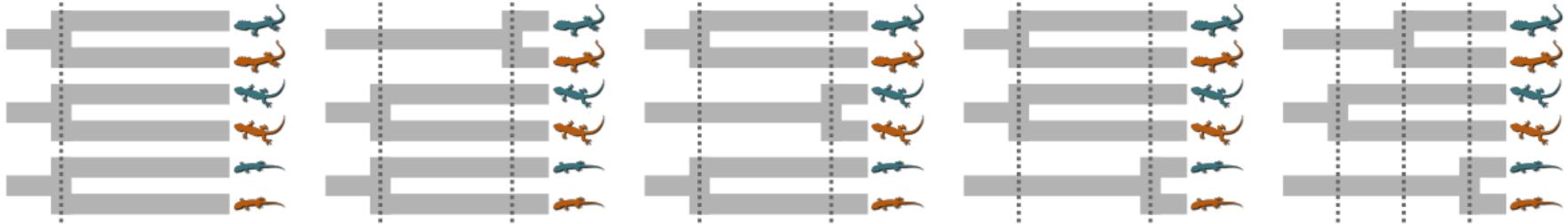
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Challenges:

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 - 3 taxa = 5 models

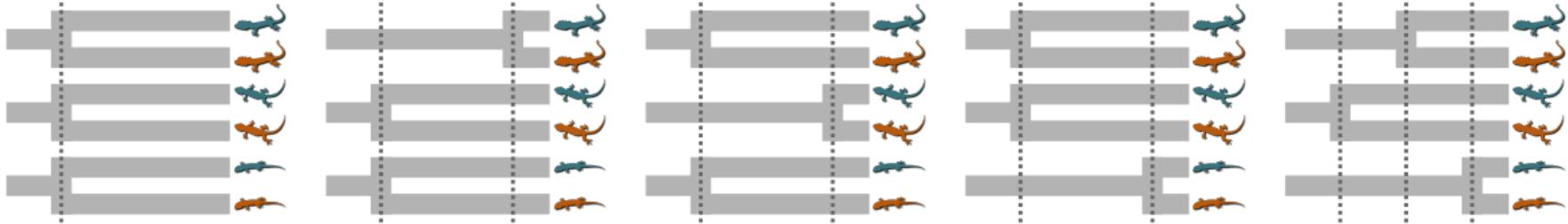
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We want to infer the model and divergence times given genetic data

Challenges:

1. Likelihood is tractable, but gene trees are difficult
2. Sampling over all possible models
 - ▶ 3 taxa = 5 models
 - ▶ 10 taxa = 115,975 models

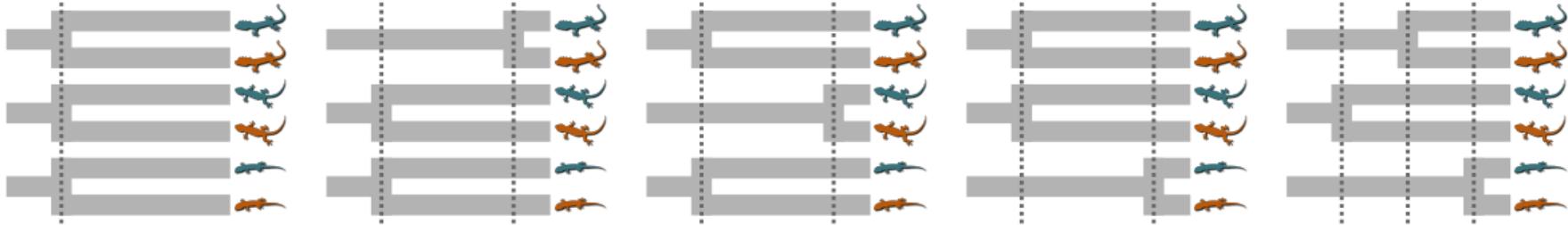
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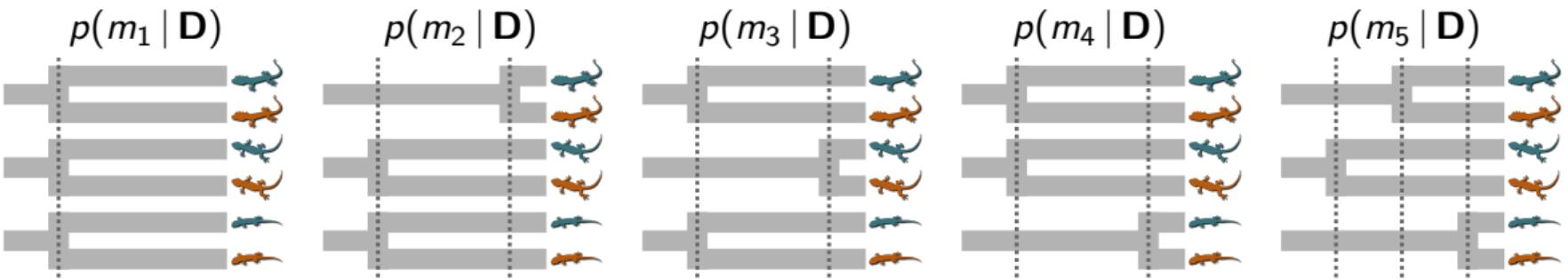
$p(m_5 | \mathbf{D})$



We want to infer the model and divergence times given genetic data

Challenges:

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2. Sampling over all possible models
 - ▶ 3 taxa = 5 models
 - ▶ 10 taxa = 115,975 models
 - ▶ 20 taxa = 51,724,158,235,372 models!!



We want to infer the model and divergence times given genetic data

Challenges:

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2. Sampling over all possible models
 - ▶ 3 taxa = 5 models
 - ▶ 10 taxa = 115,975 models
 - ▶ 20 taxa = 51,724,158,235,372 models!!

Approximate Bayesian computation (ABC) methods do not perform well for this model-choice problem

Ecoevolvity

Estimating evolutionary coevality

J. R. Oaks (2019). *Systematic Biology* 68: 371–395

- ▶ Goal: Fast, full-likelihood Bayesian method to infer patterns of co-diversification from genome-scale data

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

² R. M. Neal (2000). *Journal of Computational and Graphical Statistics* 9: 249–265

Ecoevolvity

Estimating evolutionary coevality

J. R. Oaks (2019). *Systematic Biology* 68: 371–395

- ▶ Analytically integrate over gene trees and mutational histories¹
- ▶ Dirichlet-process prior across divergence models
- ▶ Gibbs sampling² to numerically sample models

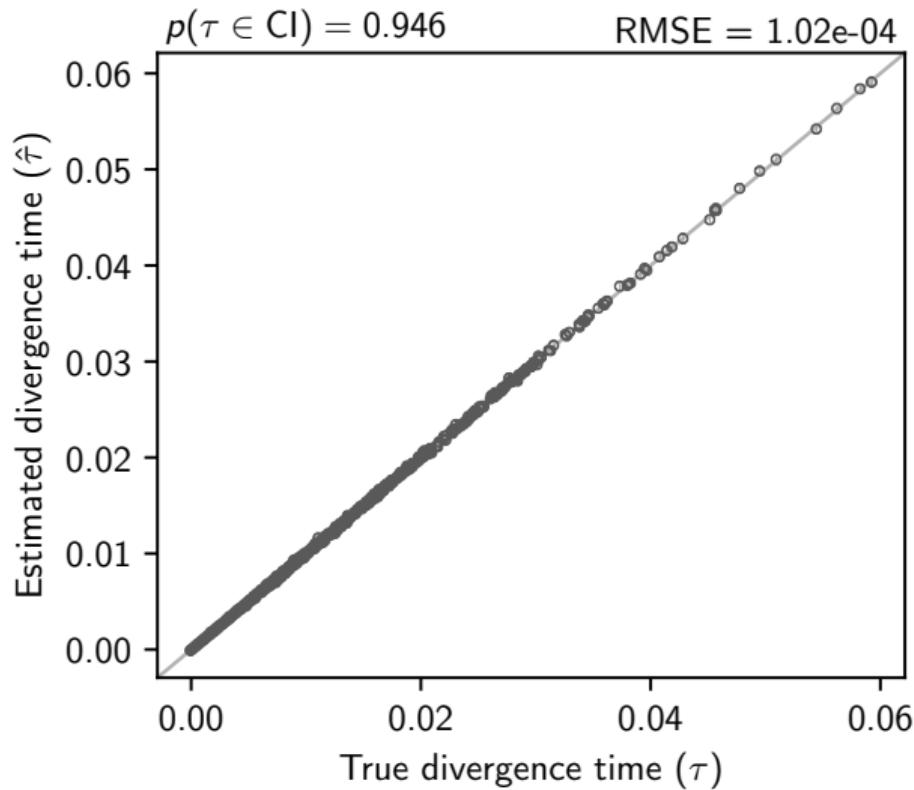
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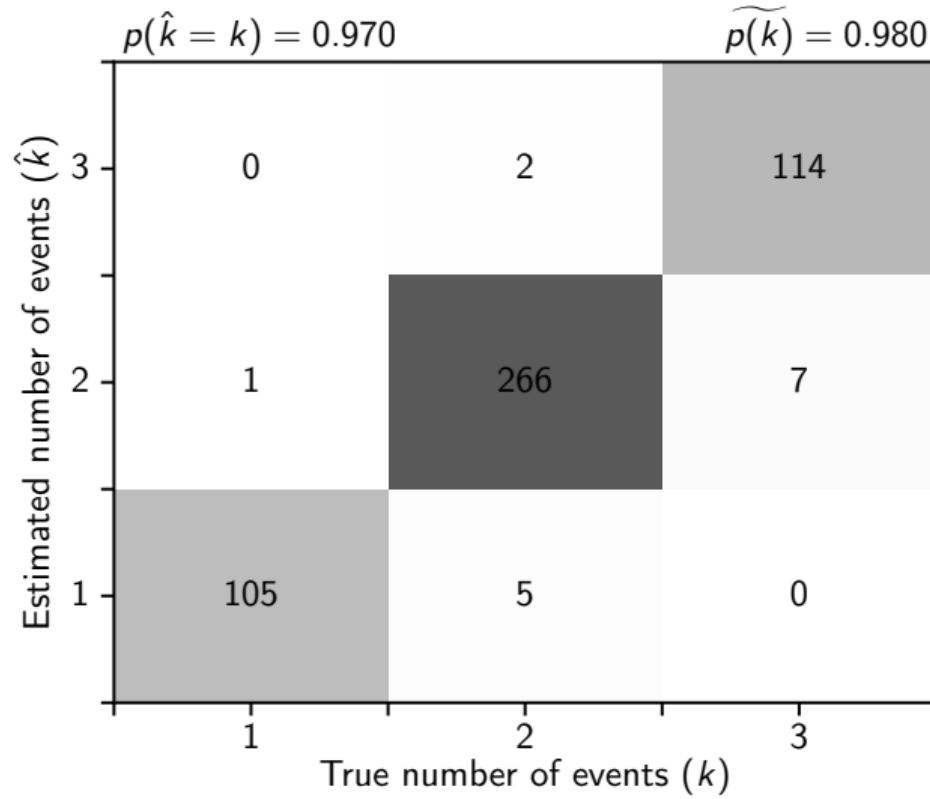
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Does it work?

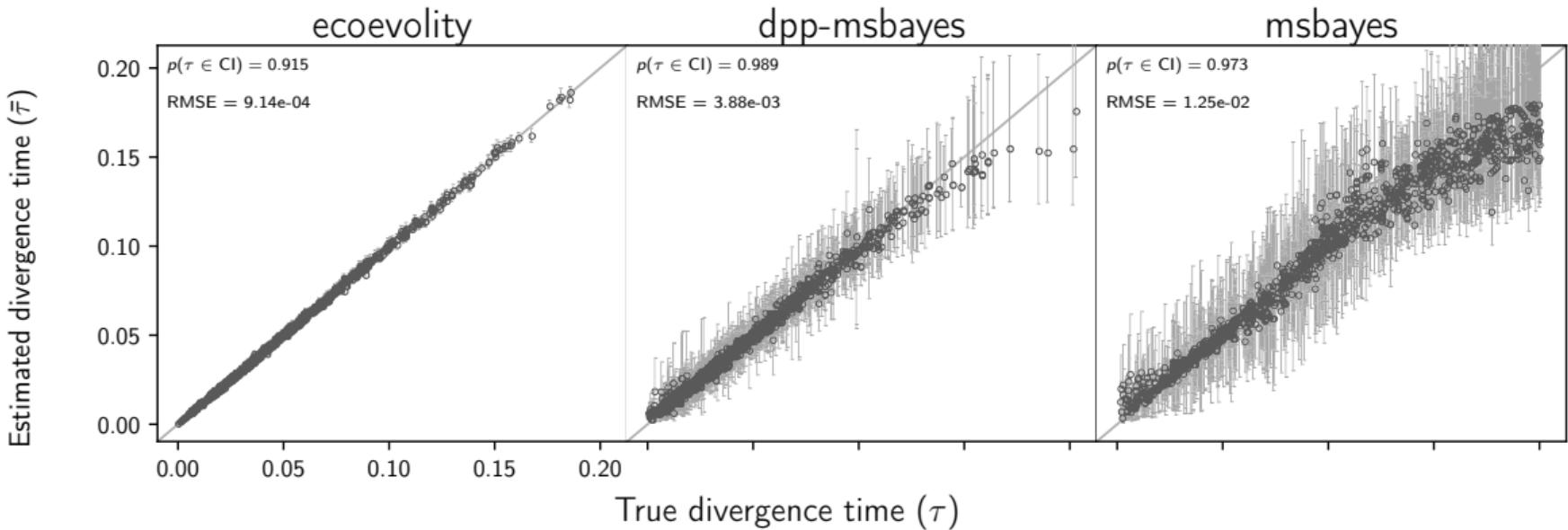
Simulation results



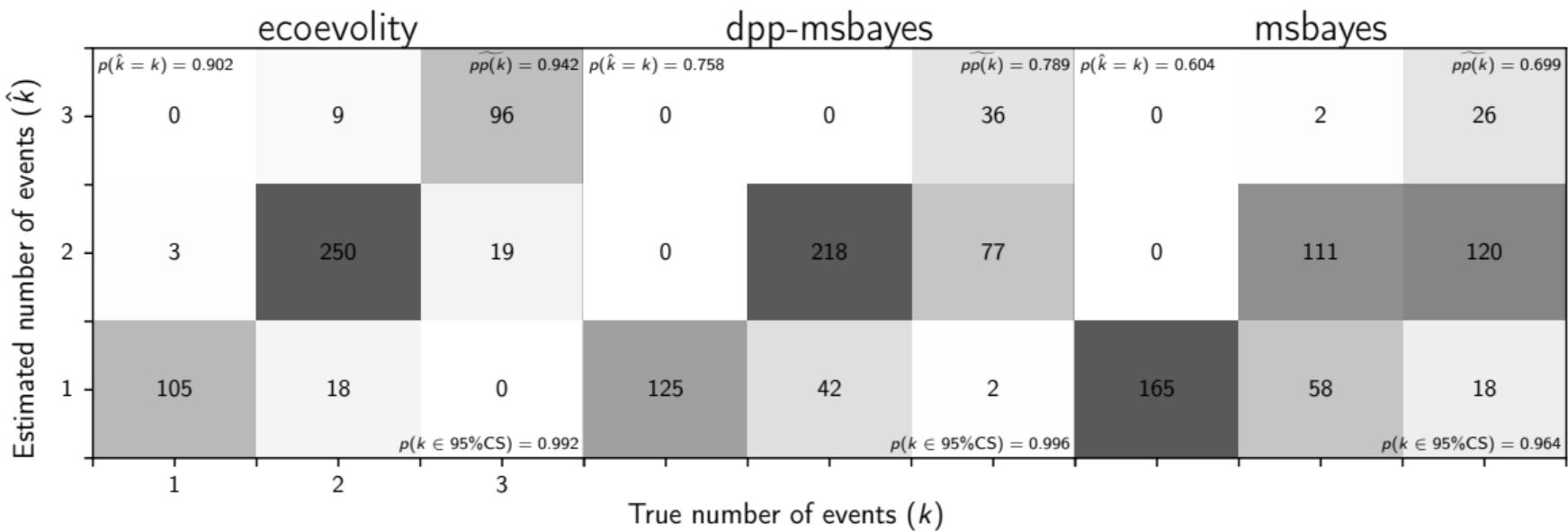
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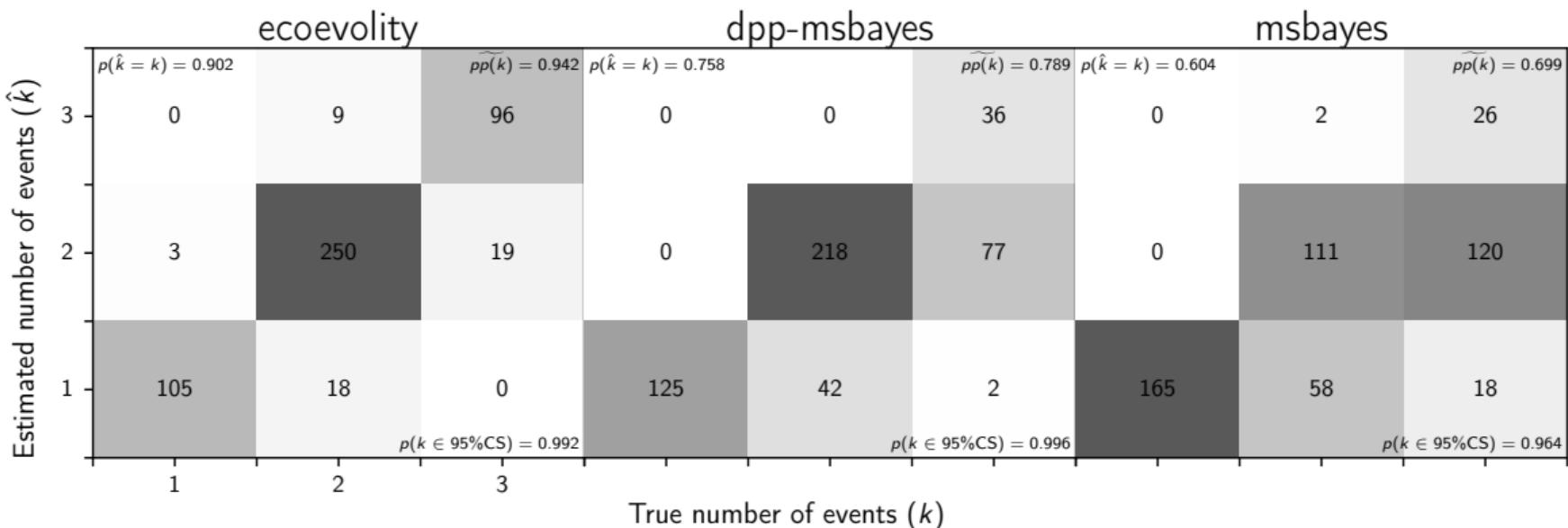
“Bake-off” results



"Bake-off" results



“Bake-off” results



Average run time:

33.4 minutes

4.4 days



Scan for sea-level animation

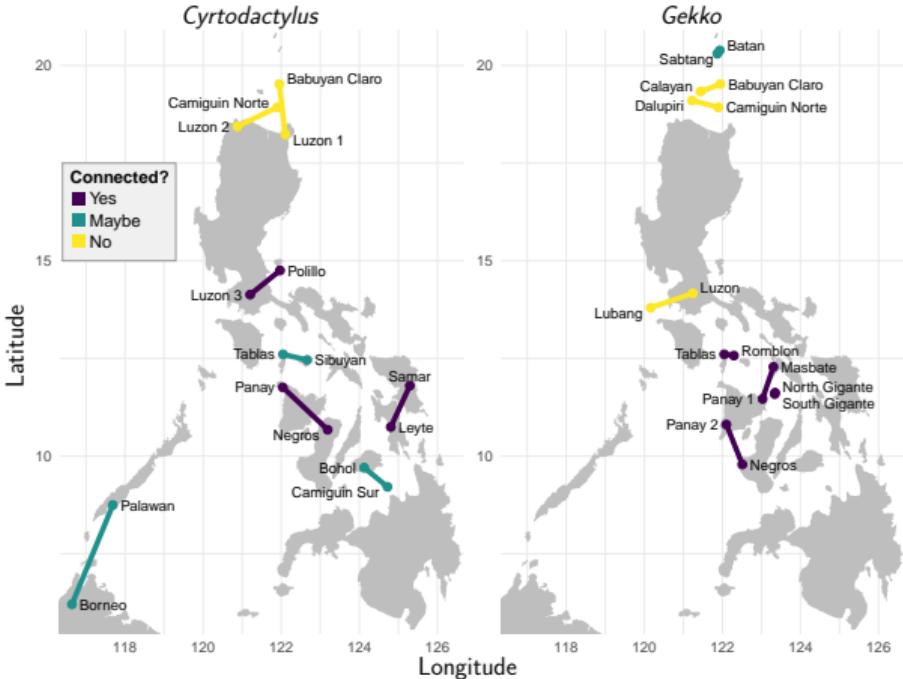


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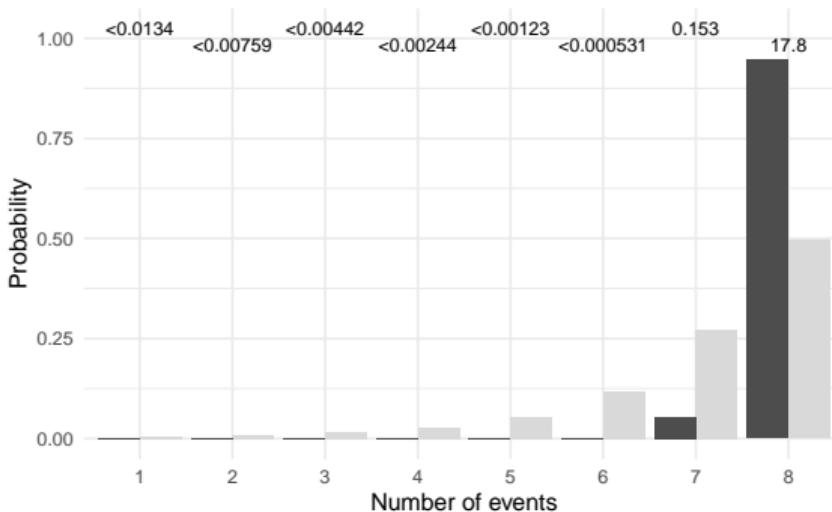
Scan for sea-level animation

**Did fragmentation of islands
promote diversification?**

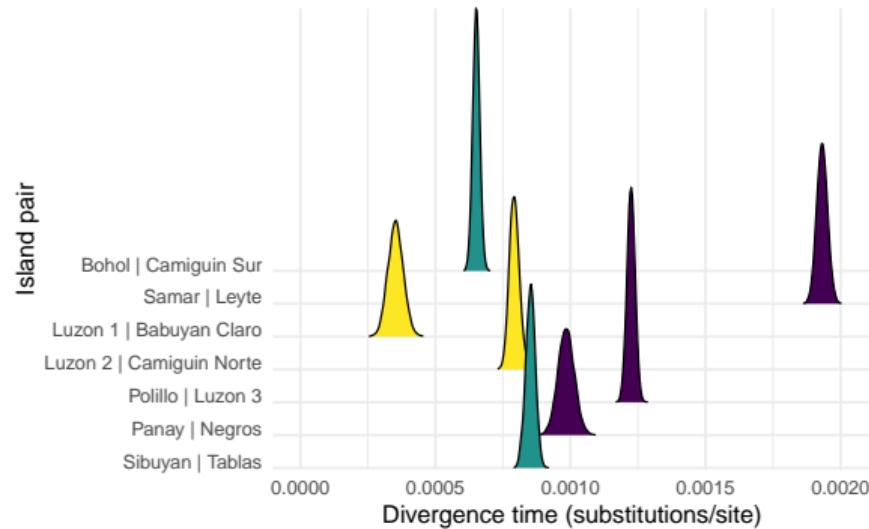
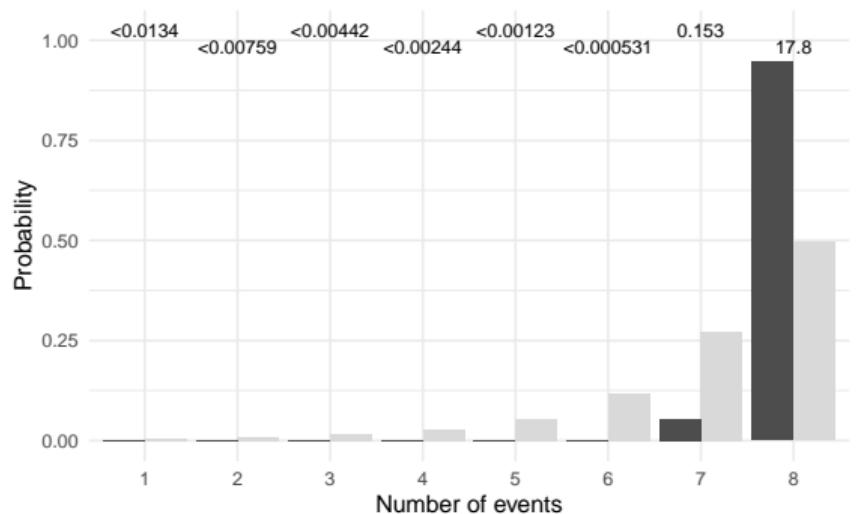


- ▶ Sampled 2–5 individuals from 8 pairs of populations for both *Cyrtodactylus* and *Gekko*
- ▶ Collected short DNA sequences (RADseq) from across genome of each individual

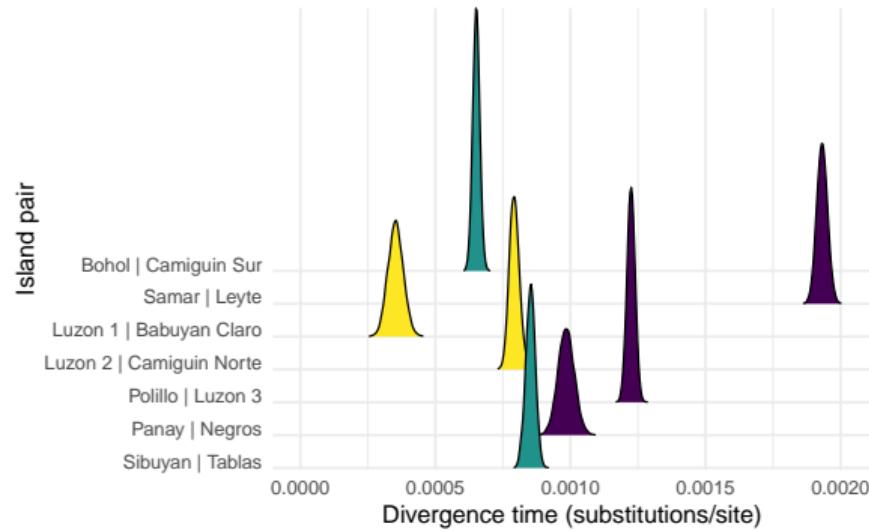
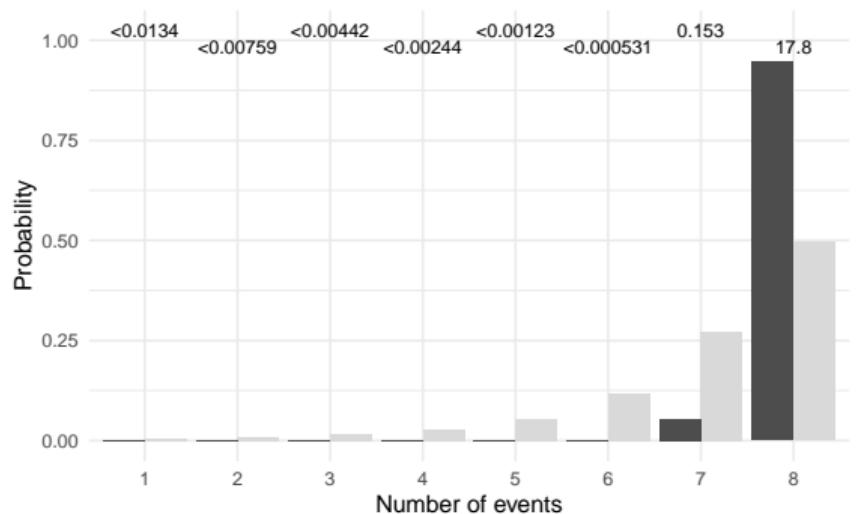
Results: *Cyrtodactylus*



Results: *Cyrtodactylus*



Results: *Cyrtodactylus*



Strong support for independent divergences

Take-home points

- ▶ Support against the climate-driven “species-pump” hypothesis

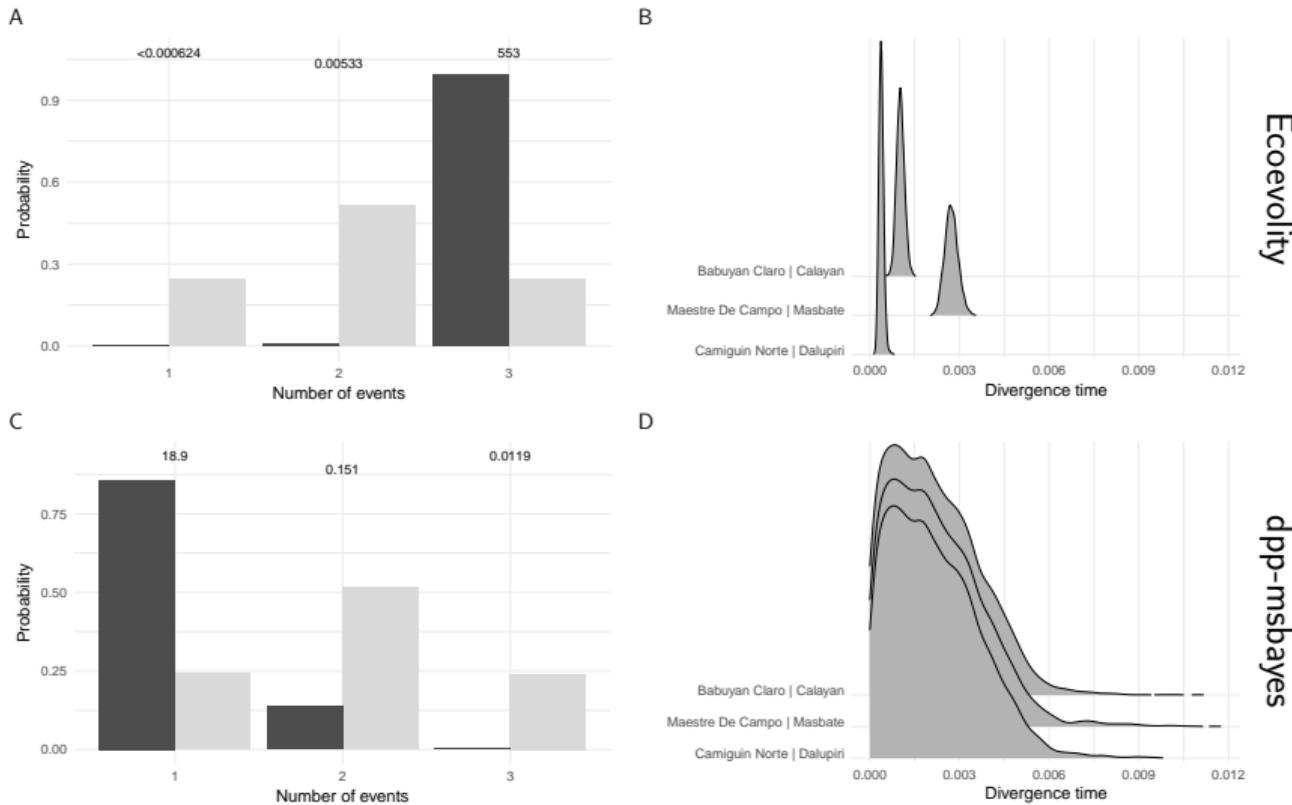
Take-home points

- ▶ Support against the climate-driven “species-pump” hypothesis
- ▶ Habitat heterogeneity and rare over-water dispersal via rafting on vegetation are likely more important

Take-home points

- ▶ Support against the climate-driven “species-pump” hypothesis
- ▶ Habitat heterogeneity and rare over-water dispersal via rafting on vegetation are likely more important
- ▶ Full-likelihood, Bayesian approach is faster and more accurate than ABC

ABC vs ecoevolity results



Why so different?



J. R. Oaks et al. (2019). *Systematic Biology* 68: 681–697



Interactive coin-flipping demo

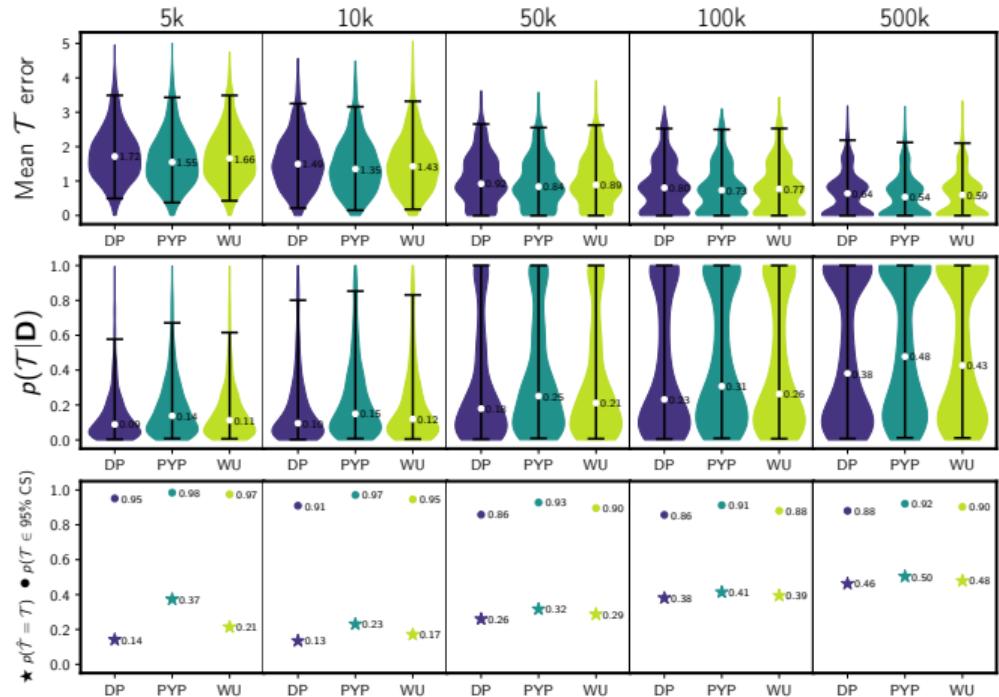
tl;dr:

Averaging likelihood with respect to “diffuse” priors creates a strong penalty against divergence-time parameters

Better priors than the Dirichlet process?



Better priors than the Dirichlet process?



Developed and tested 2 additional priors over models

Pitman-Yor process performs better

What about smaller data sets?

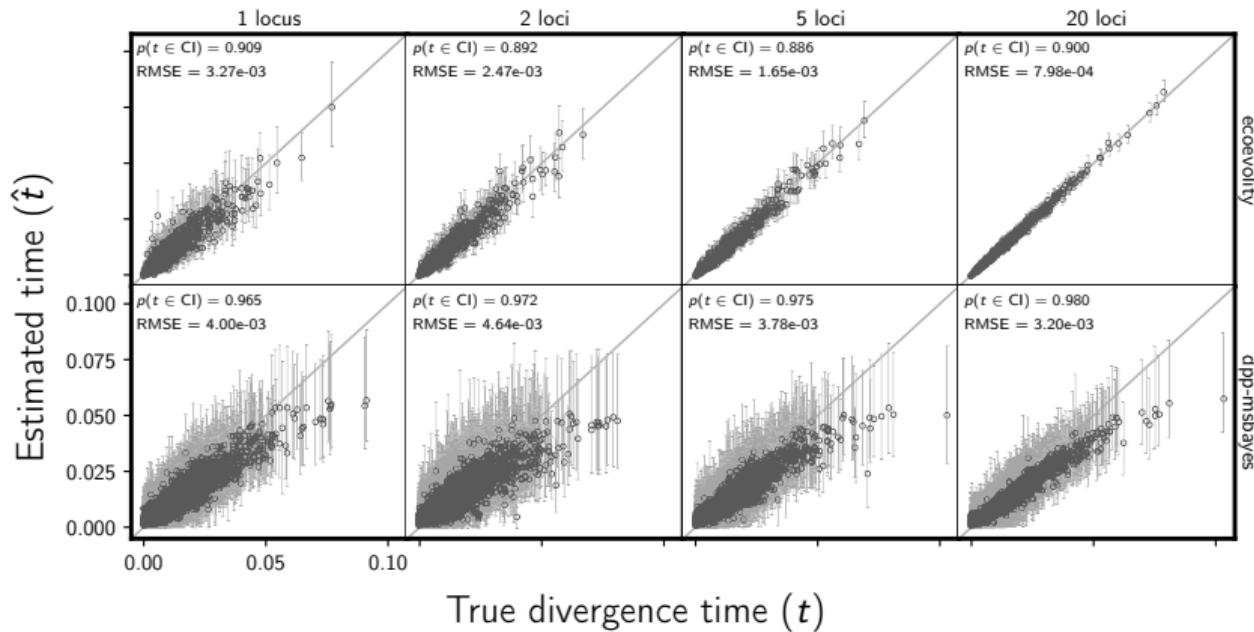


What about smaller data sets?



Full-likelihood Bayesian approach performs better than ABC

Many “legacy” data sets can be re-evaluated



Open science: everything is available...

Software:

- ▶ Ecoevolity:
phyletica.org/ecoevolity

Open-Science Notebooks:

- ▶ Gecko RADseq:
github.com/phyletica/gekgo
- ▶ Simulation analyses:
github.com/phyletica/ecoevolity-experiments
github.com/phyletica/ecoevolity-model-prior
github.com/phyletica/codiv-sanger-bake-off



phyletica.org/codiv-sanger-bake-off

Approaches to the problem

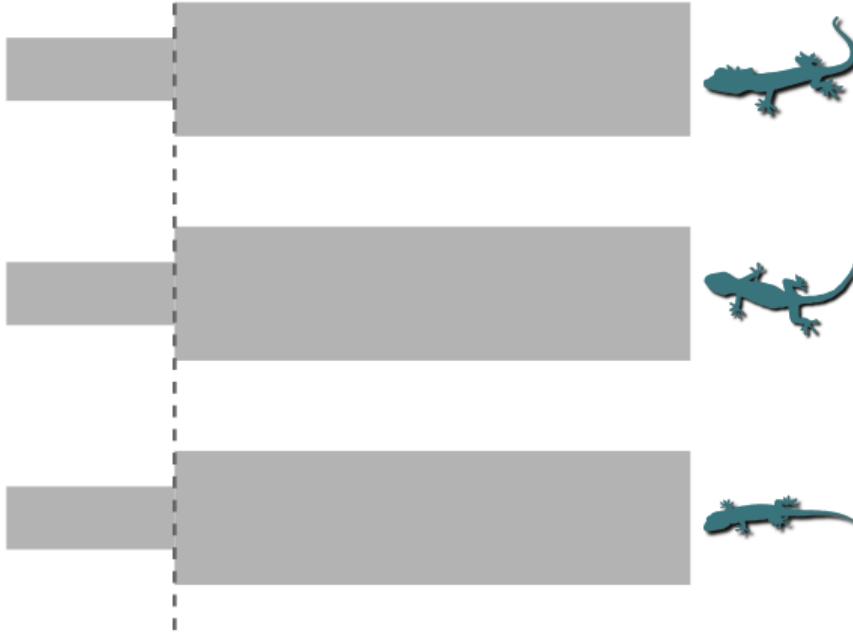
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The next 5 years in the Phyletica Lab

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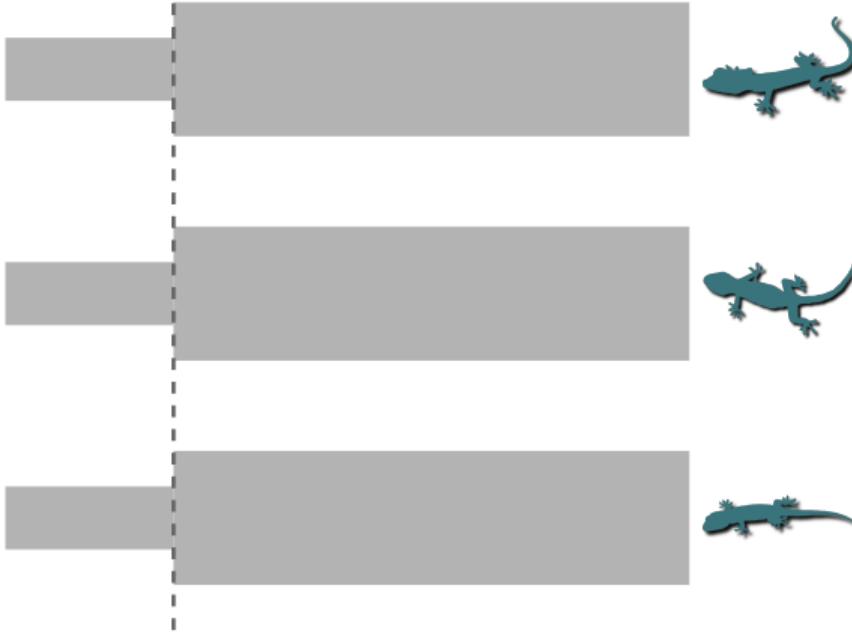
- ▶ Recent interest in testing shared demographic changes

¹ Y. L. Chan, D. Schanzenbach, and M. J. Hickerson (2014). *Molecular Biology and Evolution* 31: 2501–2515

² A. T. Xue and M. J. Hickerson (2015). *Molecular Ecology* 24: 6223–6240

³ A. T. Xue and M. J. Hickerson (2017). *Molecular Ecology Resources* 17: e212–e224

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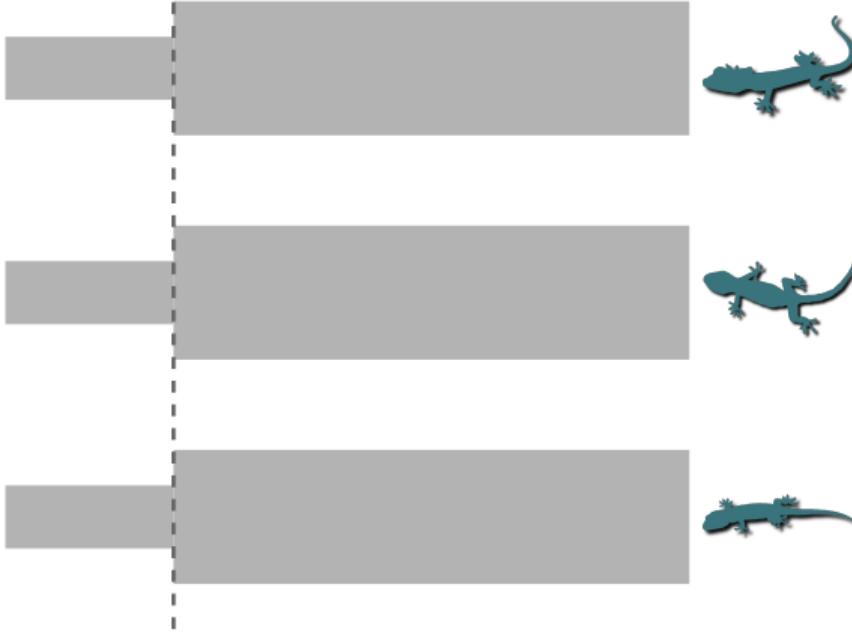
- ▶ Recent interest in testing shared demographic changes
- ▶ Several nice ABC approaches^{1,2,3}
 - ▶ Inferred simultaneous expansion of 5 Alaskan populations of sticklebacks (posterior probability = 0.99)²

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τ_1



- ▶ Recent interest in testing shared demographic changes
- ▶ Several nice ABC approaches^{1,2,3}
 - ▶ Inferred simultaneous expansion of 5 Alaskan populations of sticklebacks (posterior probability = 0.99)²
 - ▶ It's a tricky inference problem
 - ▶ Change in population size can become unidentifiable in 3 ways

¹ Y. L. Chan, D. Schanzenbach, and M. J. Hickerson (2014). *Molecular Biology and Evolution* 31: 2501–2515

² A. T. Xue and M. J. Hickerson (2015). *Molecular Ecology* 24: 6223–6240

³ A. T. Xue and M. J. Hickerson (2017). *Molecular Ecology Resources* 17: e212–e224

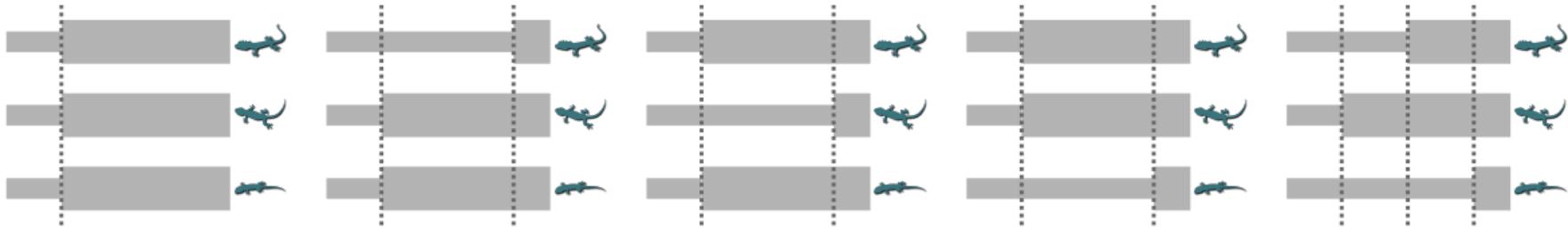
$$p(m_1 | \mathbf{D})$$

$$p(m_2 | \mathbf{D})$$

$$p(m_3 | \mathbf{D})$$

$$p(m_4 | \mathbf{D})$$

$$p(m_5 | \mathbf{D})$$



Given genomic data, can we infer the correct model and the timing of the demographic events?

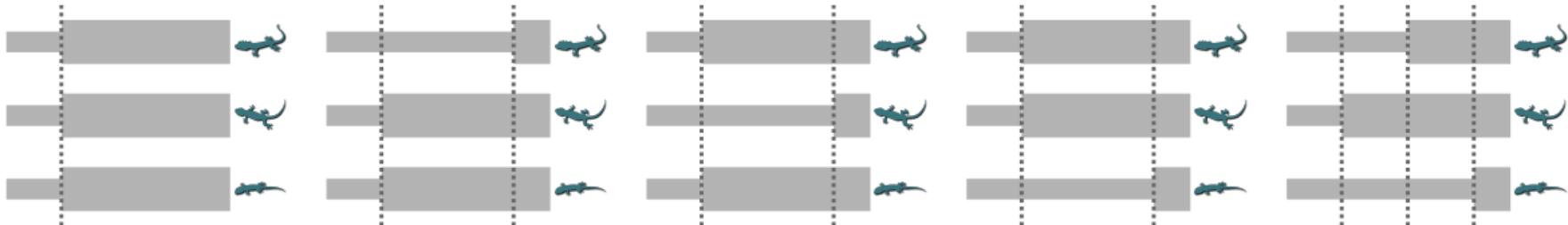
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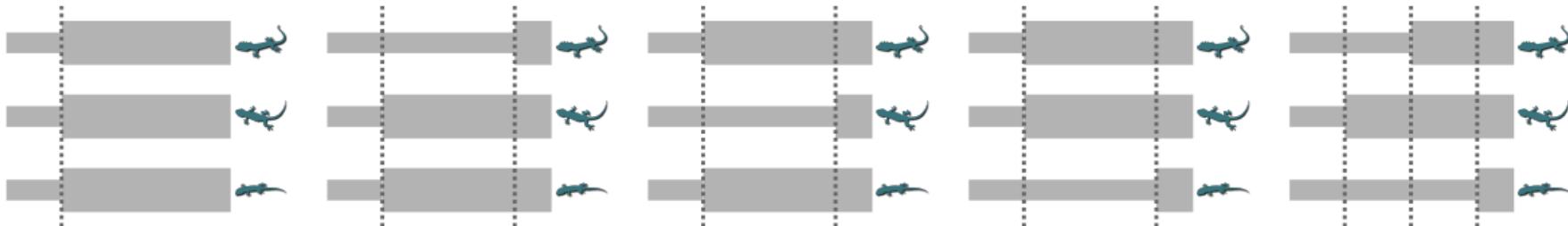
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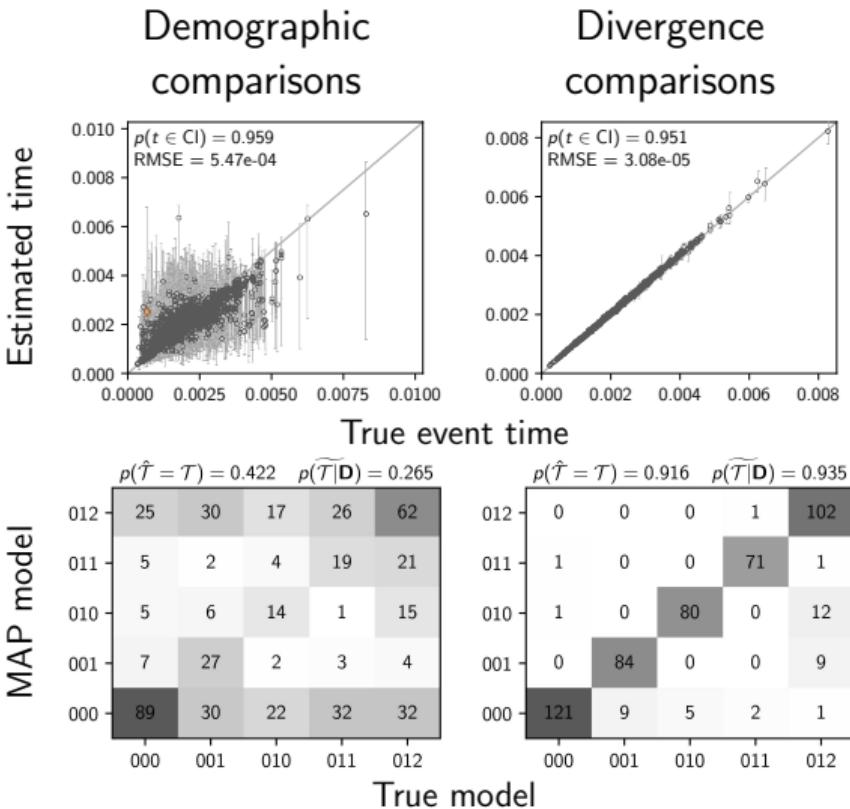


Given genomic data, can we infer the correct model and the timing of the demographic events?



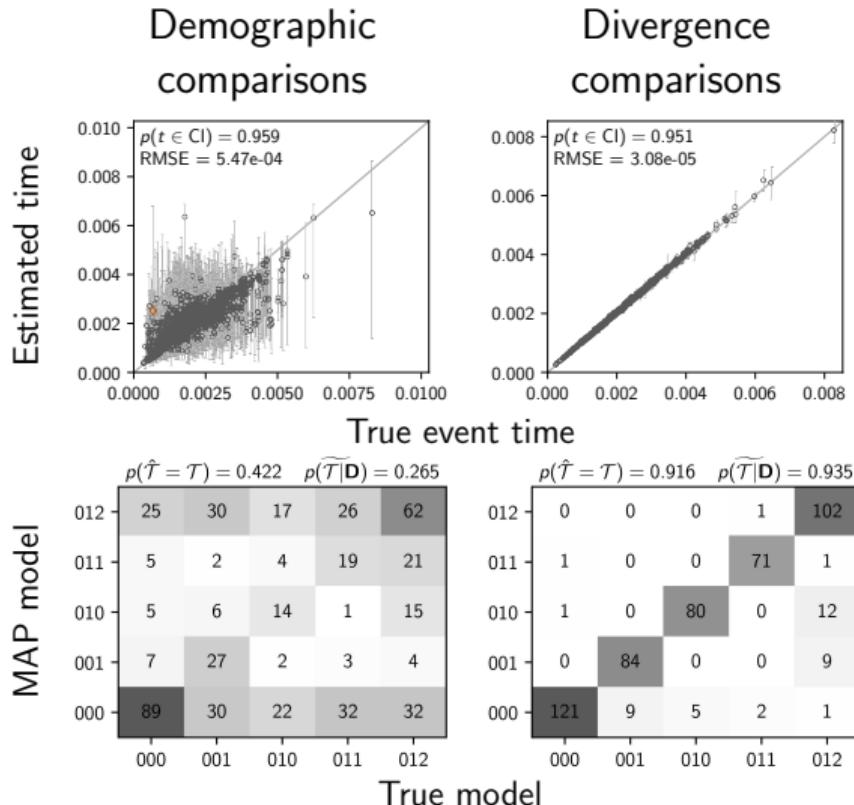
- ▶ Implemented full-likelihood Bayesian approach in ecoevolity
- ▶ Assessed performance with simulations
- ▶ Applied to stickleback genomic data

Simulation results

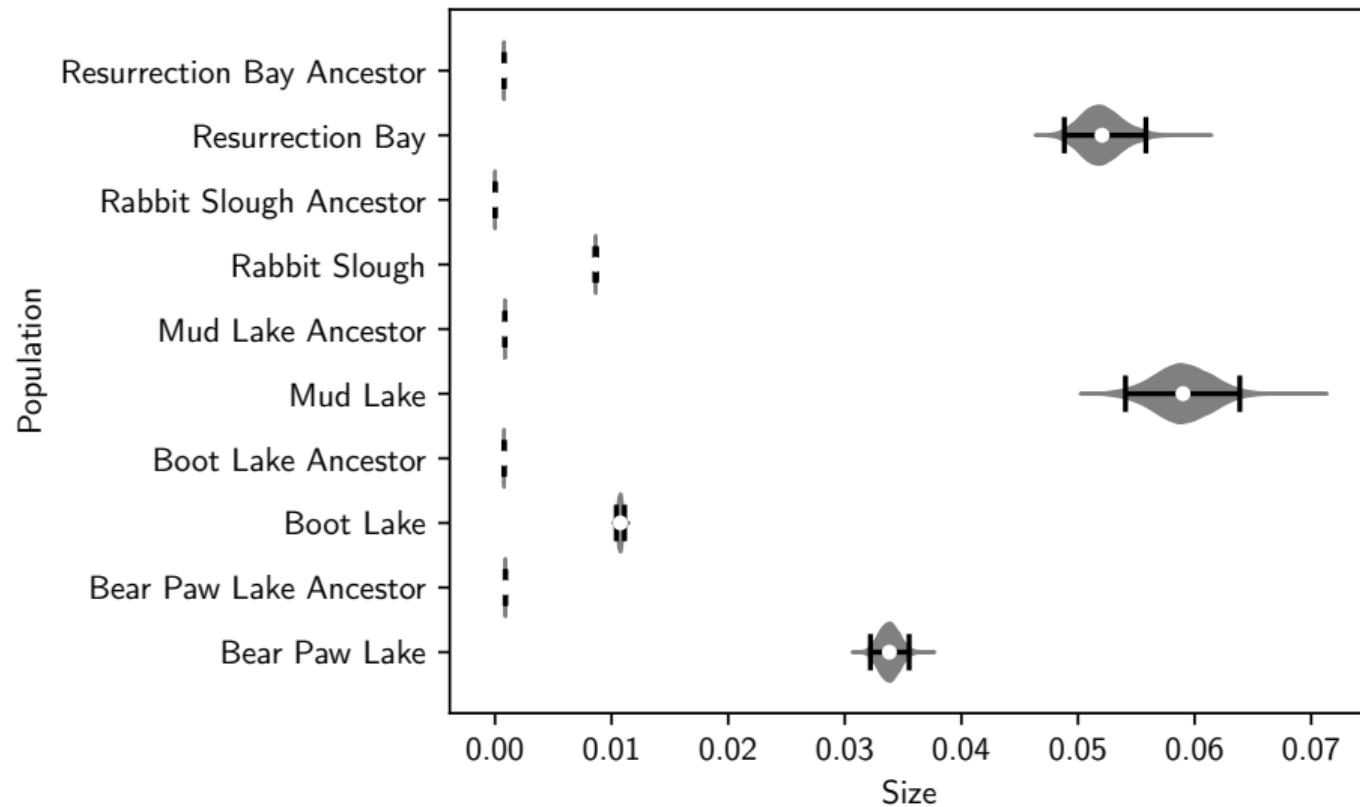


Simulation results

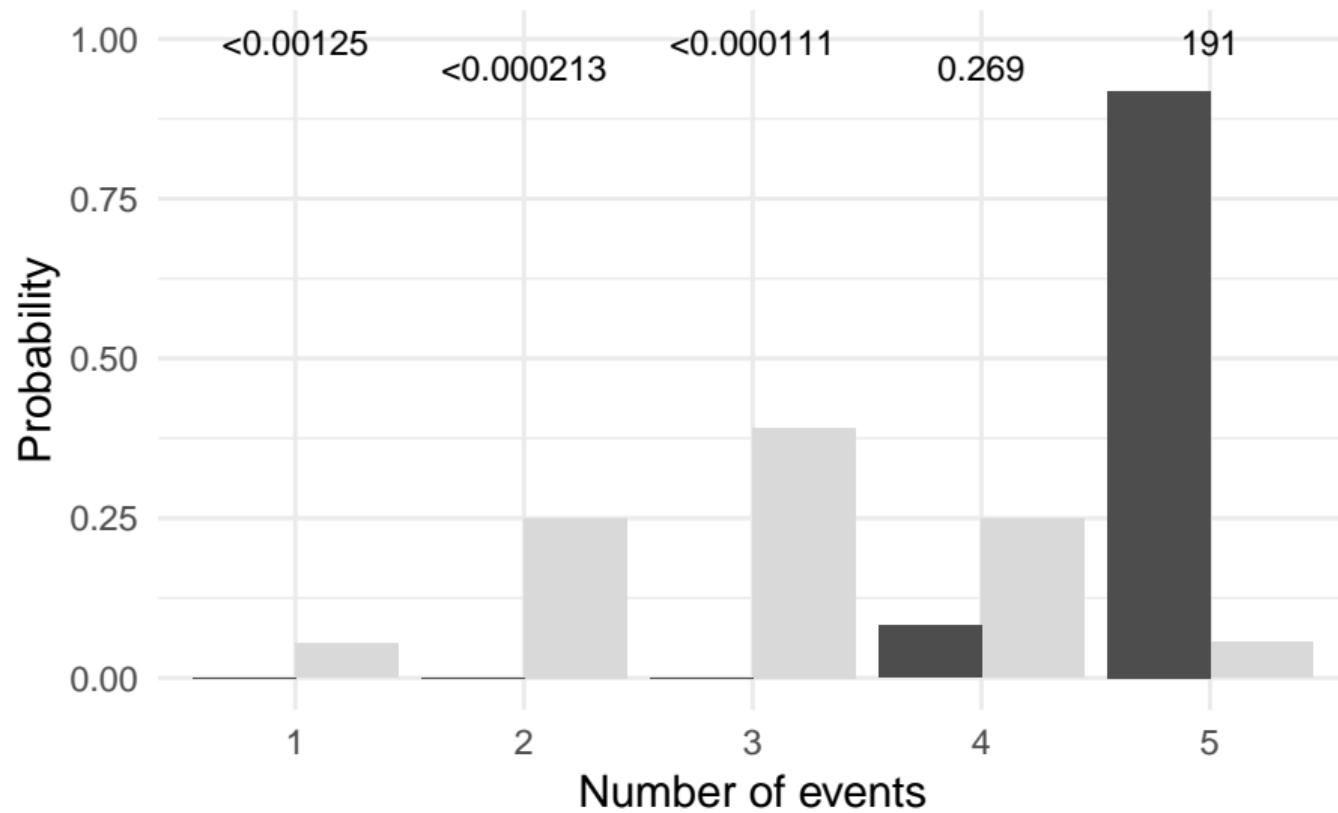
Simulations confirm theoretical expectations that changes in population size are difficult to estimate



Stickleback results



Stickleback results



Open science: everything is available...

Software:

- ▶ Ecoevolity: phyletica.org/ecoevolity

Open-Science Notebooks:

github.com/phyletica/ecoevolity-demog-experiments

Approaches to the problem

A pairwise approach (keep it “simple”)

An aside for a related problem with population demography

A fully phylogenetic approach

The next 5 years in the Phyletica Lab



Biogeography

- ▶ Environmental changes that affect whole communities of species

Genome evolution

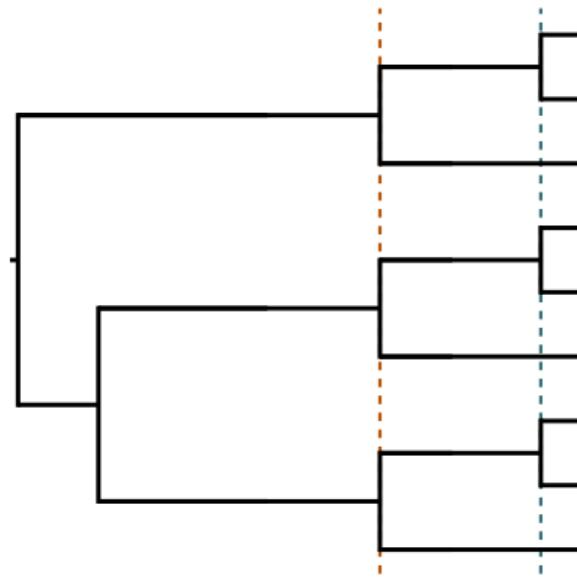
- ▶ Duplication of a chromosome segment harboring gene families

Epidemiology

- ▶ Transmission at social gatherings

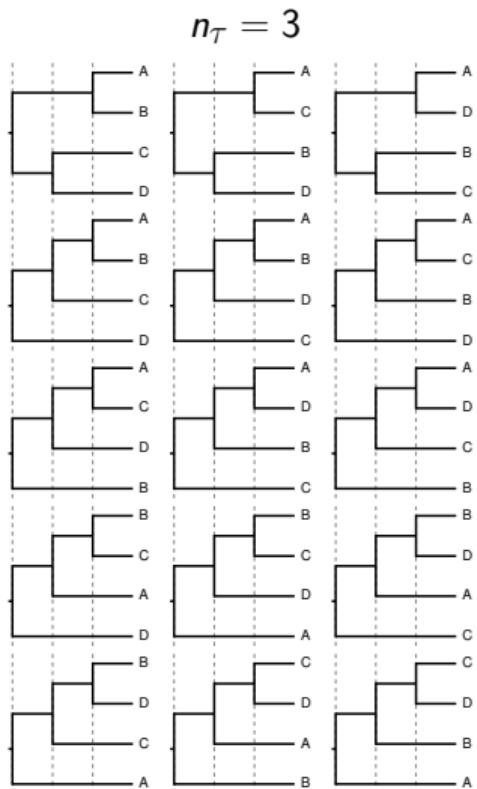
Endosymbiont evolution (e.g., parasites, microbiome)

- ▶ Speciation of the host
- ▶ Co-colonization of new host species



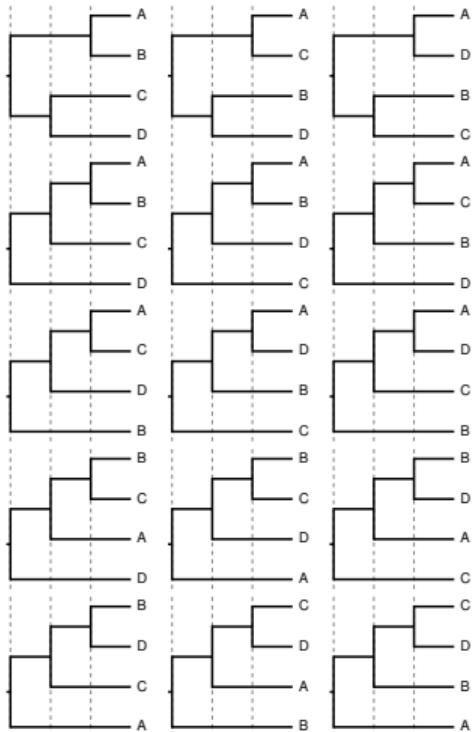
Generalizing tree space

Generalizing tree space

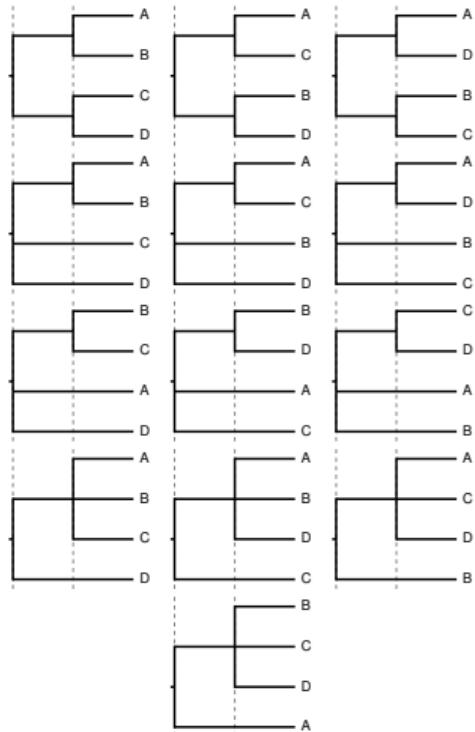


Generalizing tree space

$$n_T = 3$$



$$n_T = 2$$

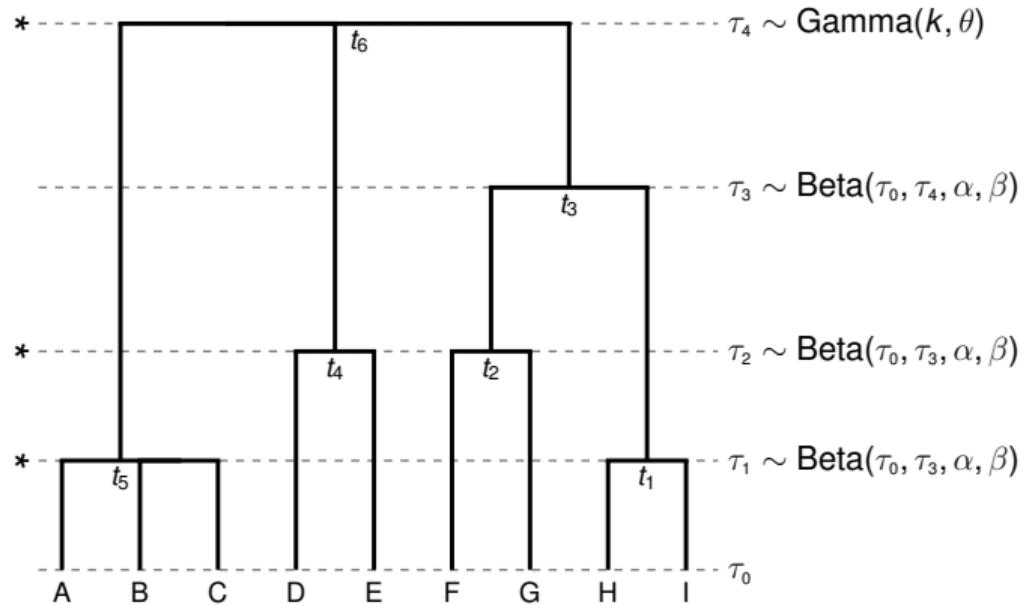


$$n_T = 1$$

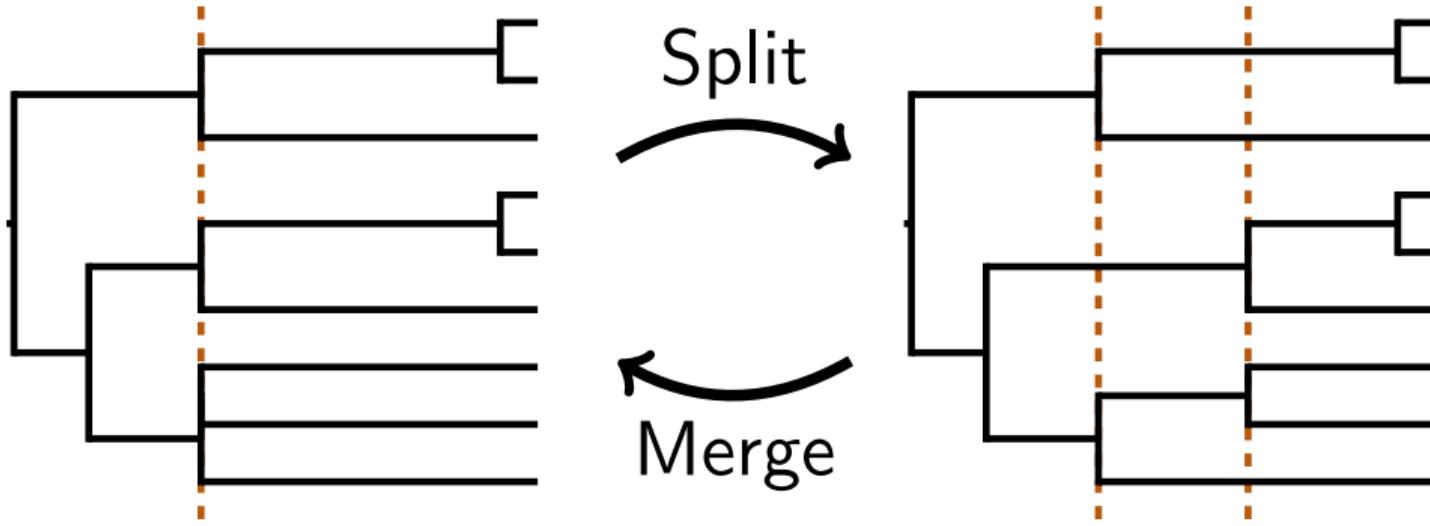


Generalized tree distribution

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

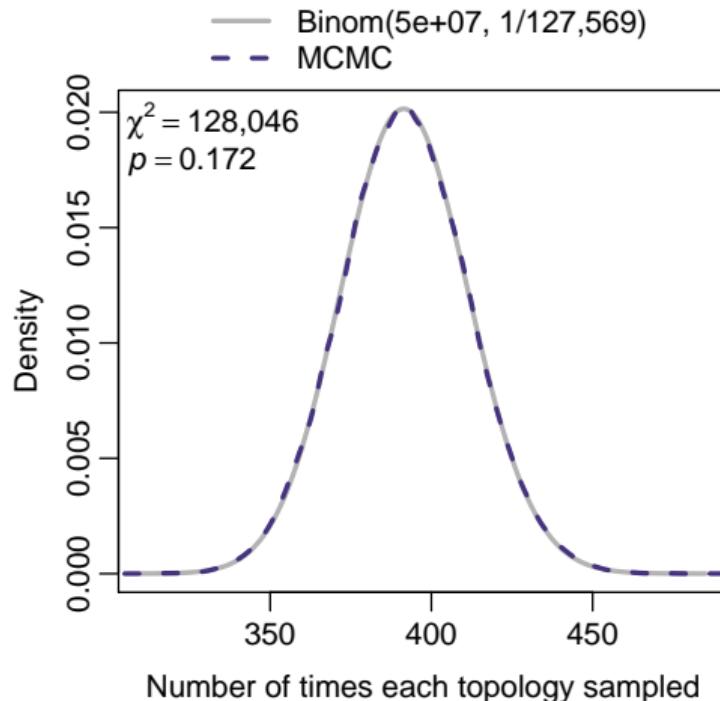


Inferring trees with shared divergences



Reversible-jump MCMC

Validating rjMCMC with 7-leaf tree



The rjMCMC algorithms sample the expected generalized tree distribution

PhycoEval

Phylogenetic coevality

J. R. Oaks and P. L. Wood, Jr. (2021). *bioRxiv*

Ecoevolity

Estimating evolutionary coevality

J. R. Oaks (2019). *Systematic Biology* 68: 371–395

► Tree model

- rjMCMC sampling of generalized tree distribution

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

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- ▶ **Tree model**
 - ▶ rjMCMC sampling of generalized tree distribution
- ▶ **Likelihood model**
 - ▶ CTMC model of characters evolving along genealogies
 - ▶ Infer species trees by analytically integrate over genealogies¹

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PhycoEval

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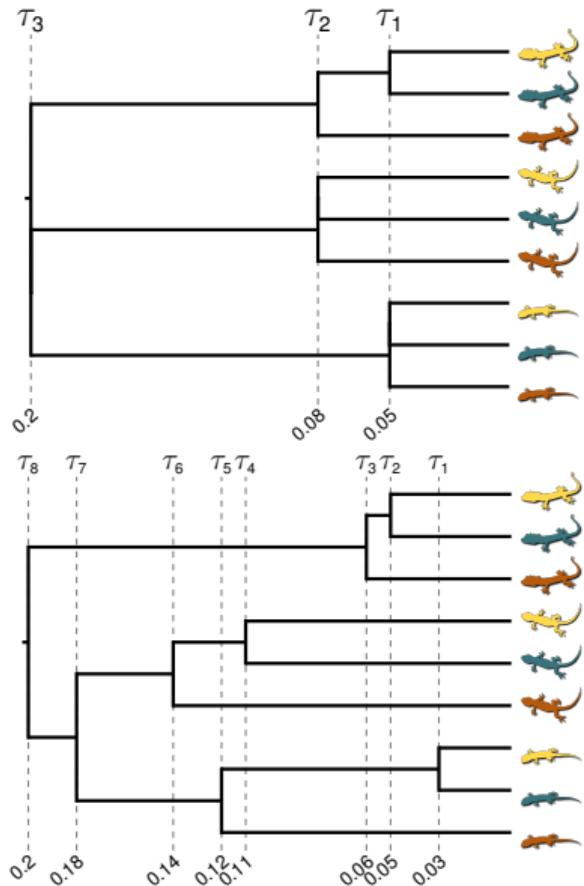
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 - ▶ Infer species trees by analytically integrate over genealogies¹
- ▶ *Goal: Co-estimation of phylogeny and shared divergences from genomic data*

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

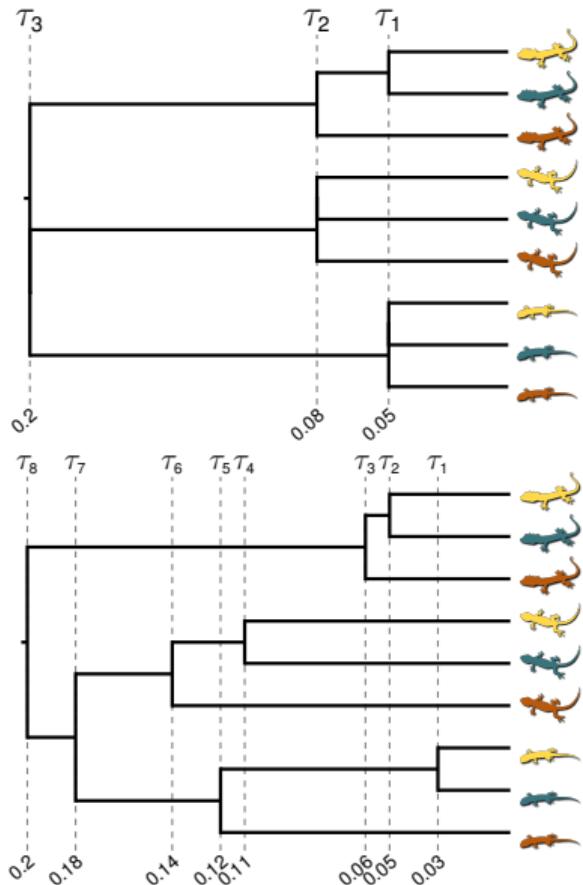
Methods: Simulations

- ▶ Simulated 100 data sets with 50,000 characters



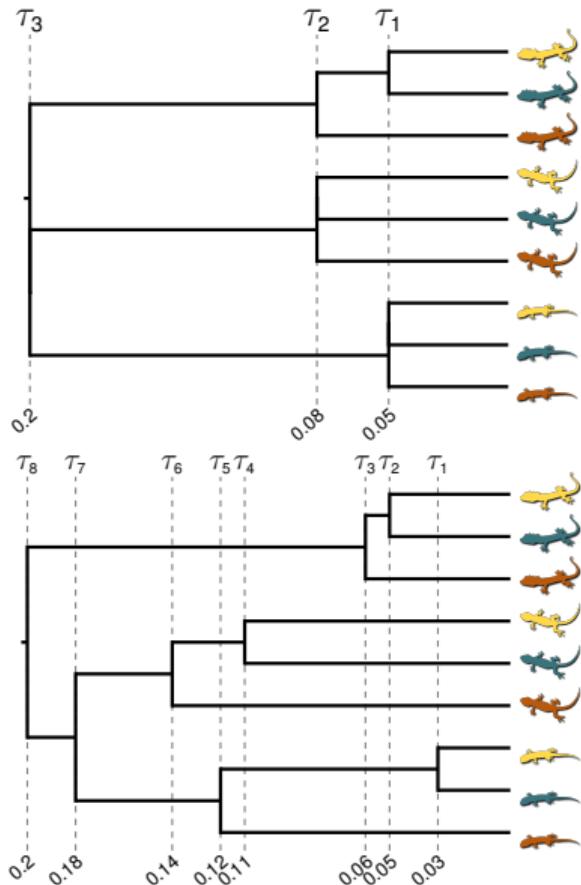
Methods: Simulations

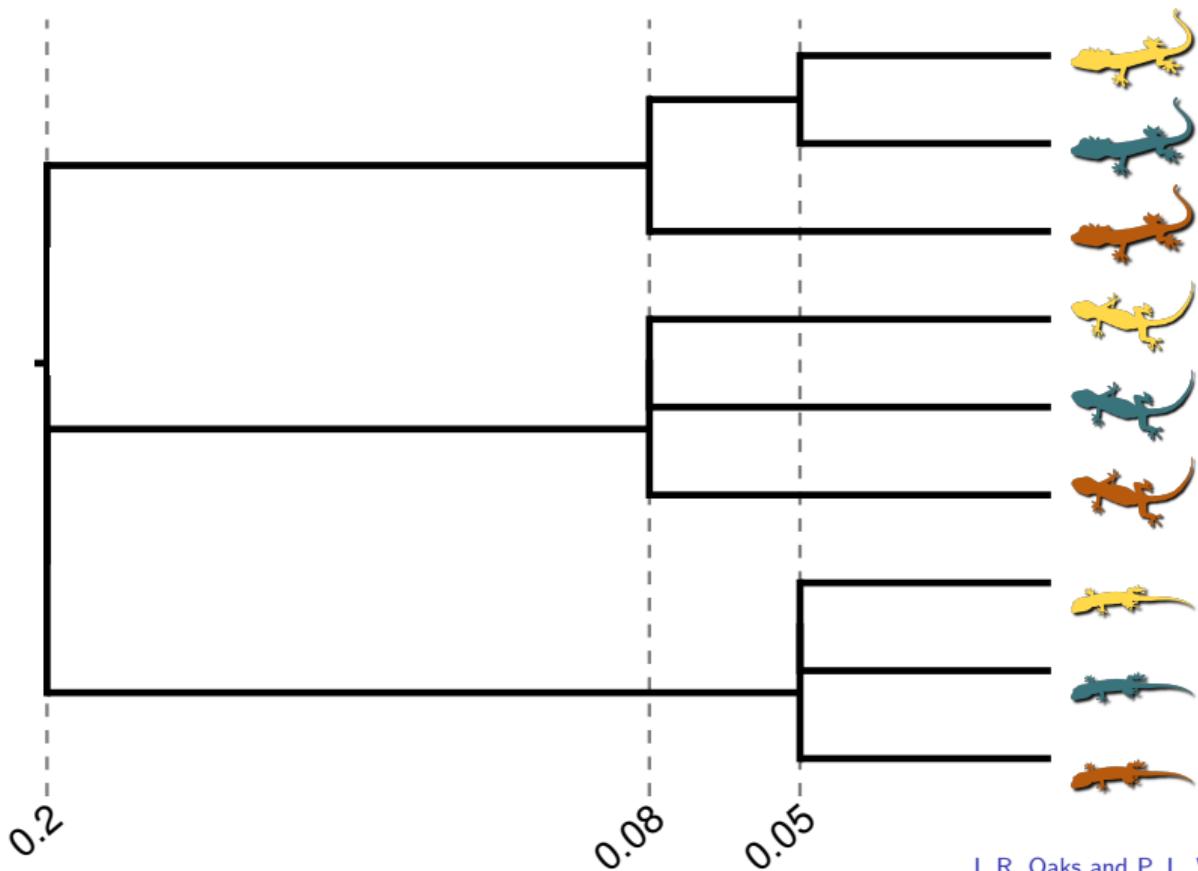
- ▶ Simulated 100 data sets with 50,000 characters
- ▶ Analyzed each data set with:
 - ▶ M_G = Generalized tree model
 - ▶ M_{IB} = Independent-bifurcating tree model

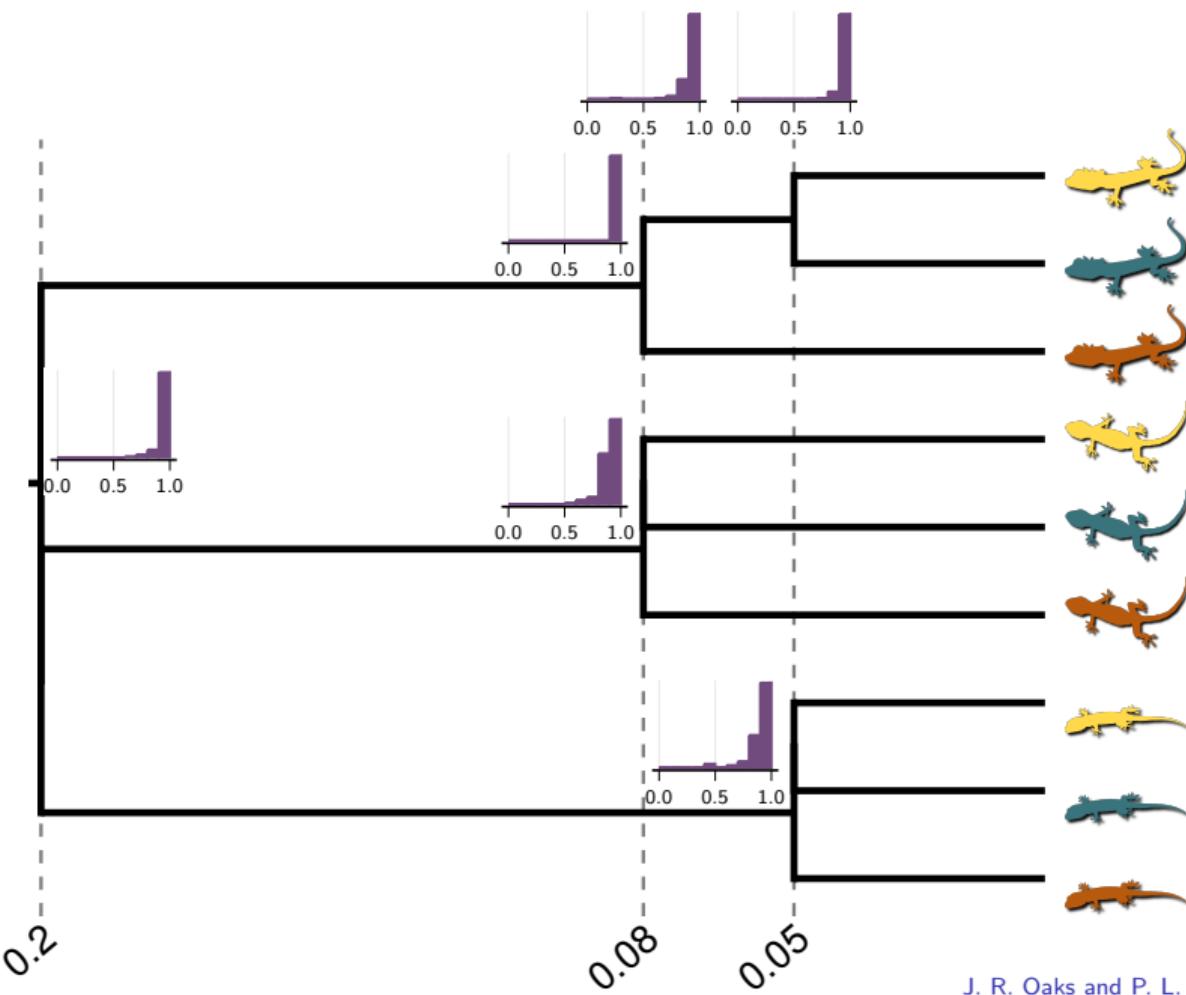


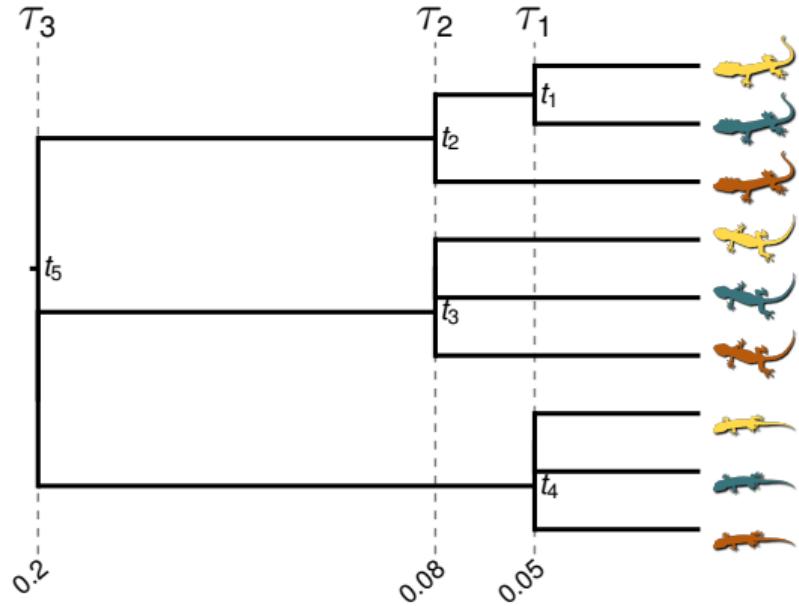
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 - ▶ M_{IB} = Independent-bifurcating tree model
- ▶ Simulated 100 data sets where topology and div times randomly drawn from M_G and M_{IB}



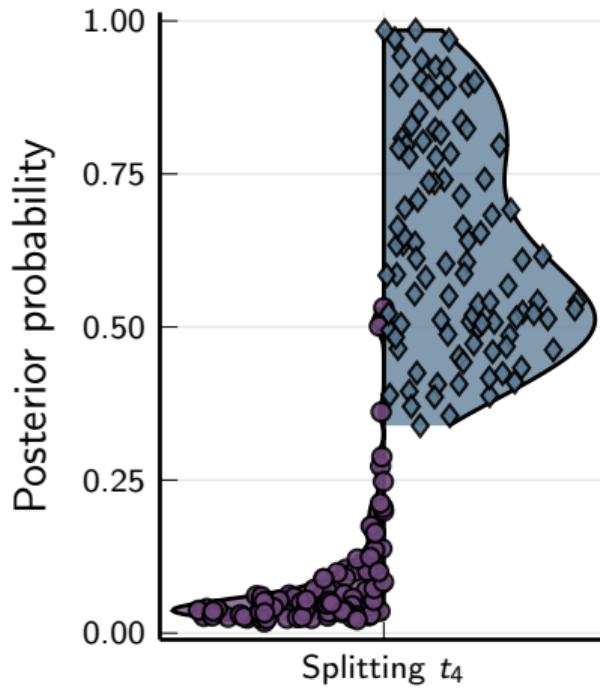
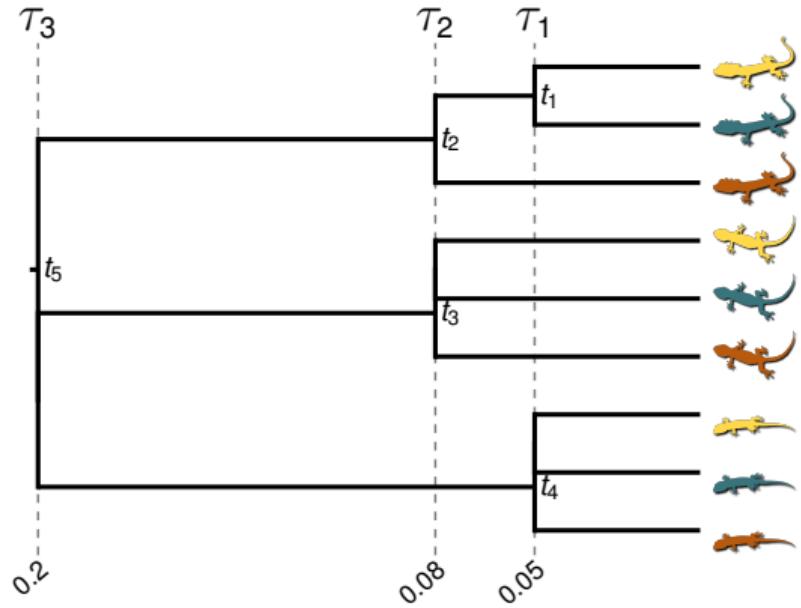






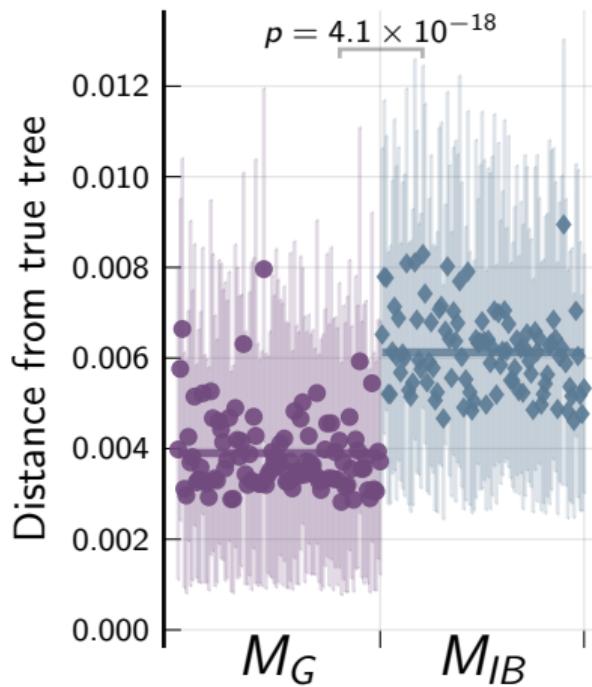
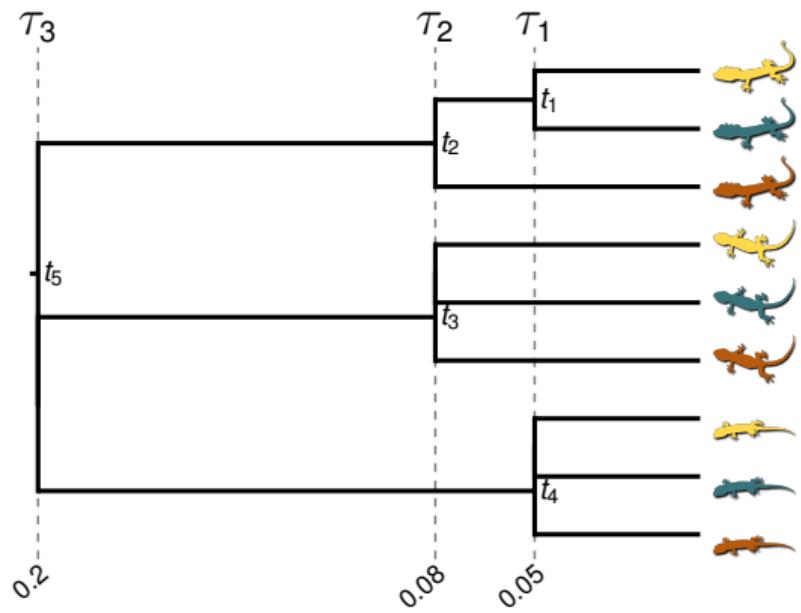
● M_G = Generalized model

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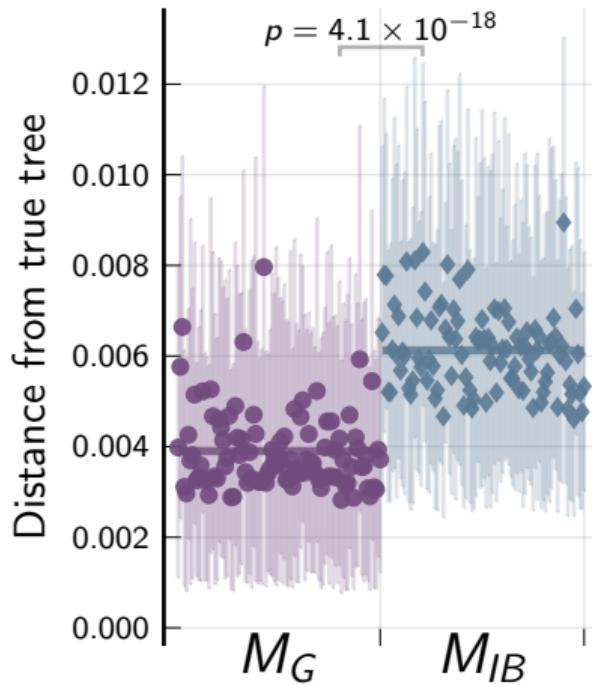
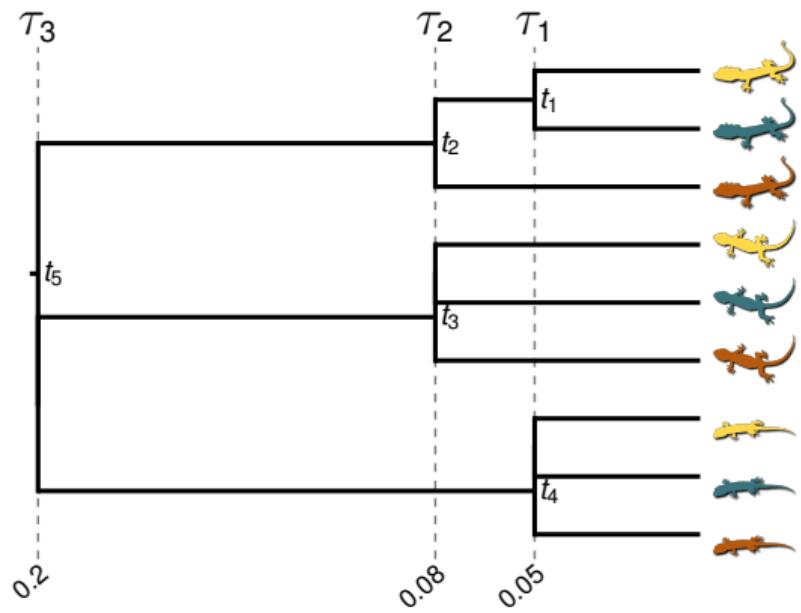
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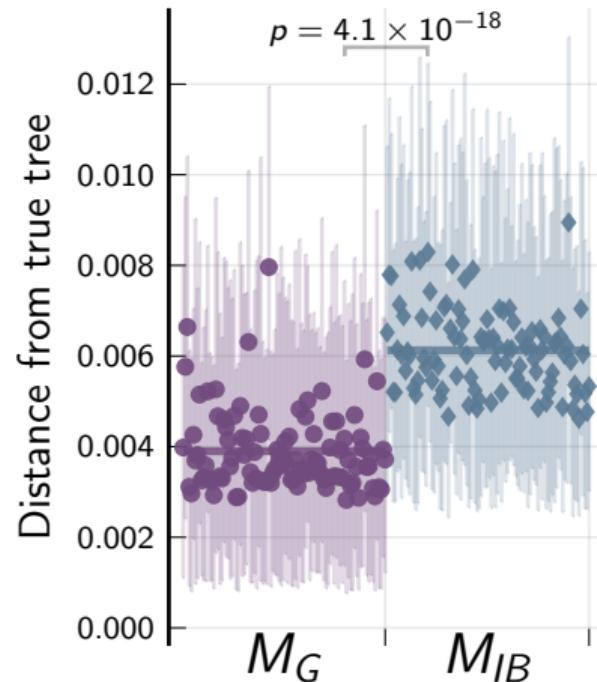
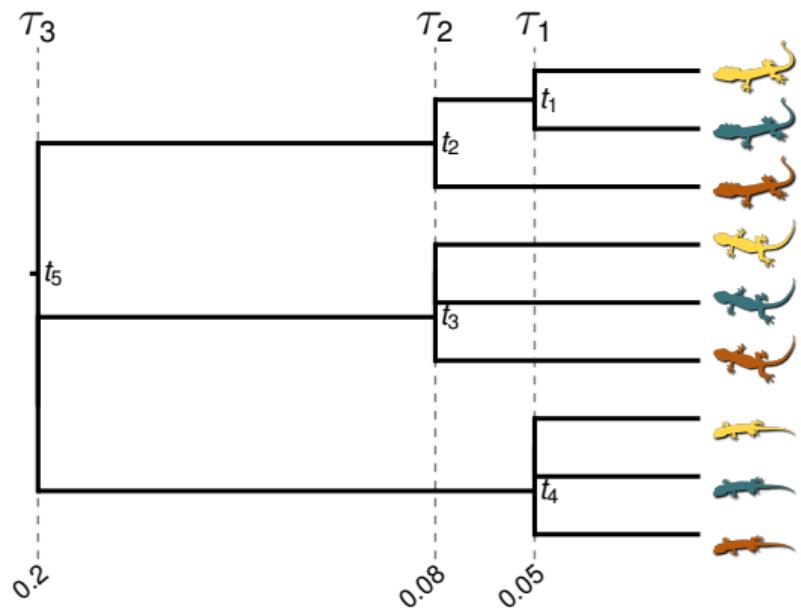
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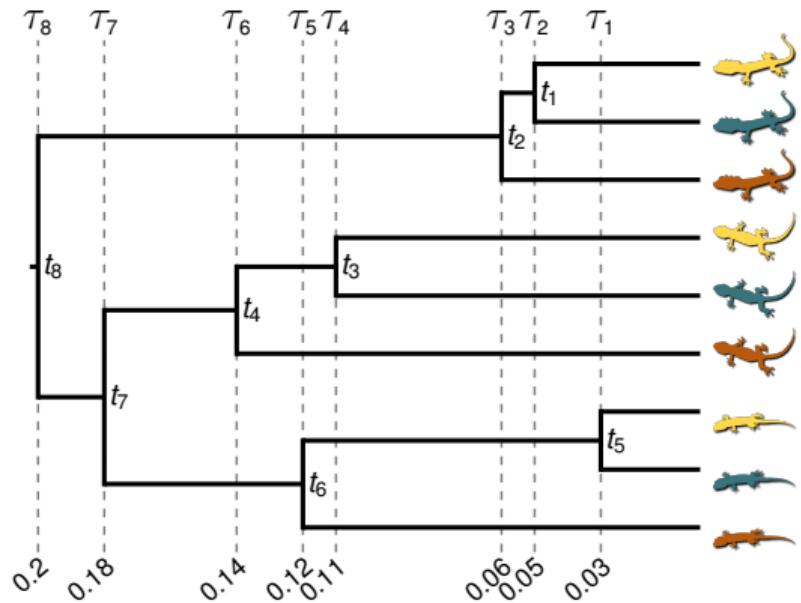
◆ M_{IB} = Independent-bifurcating model



M_G significantly better at inferring trees with shared divergences

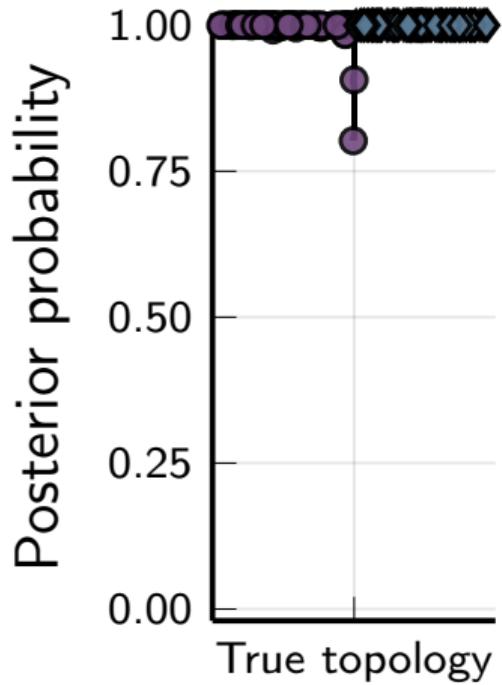
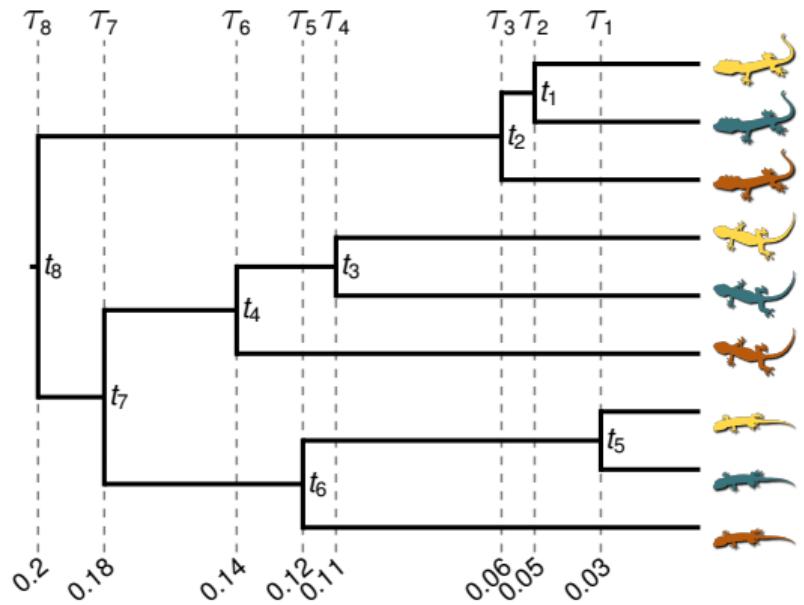
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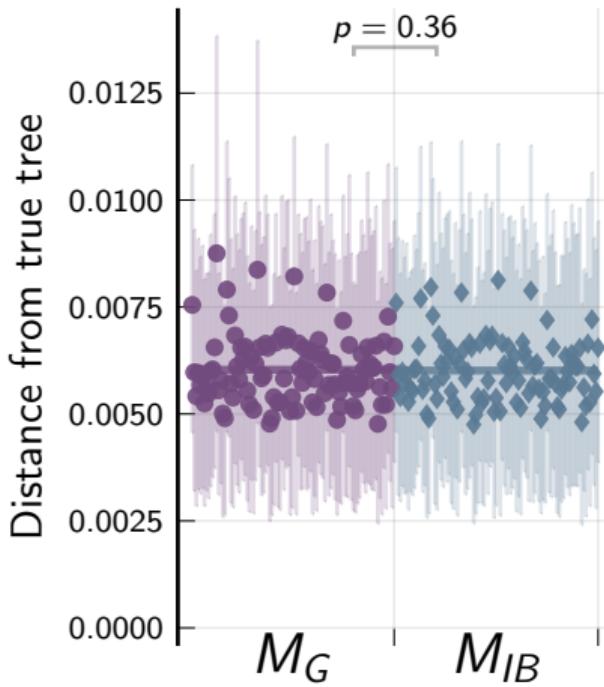
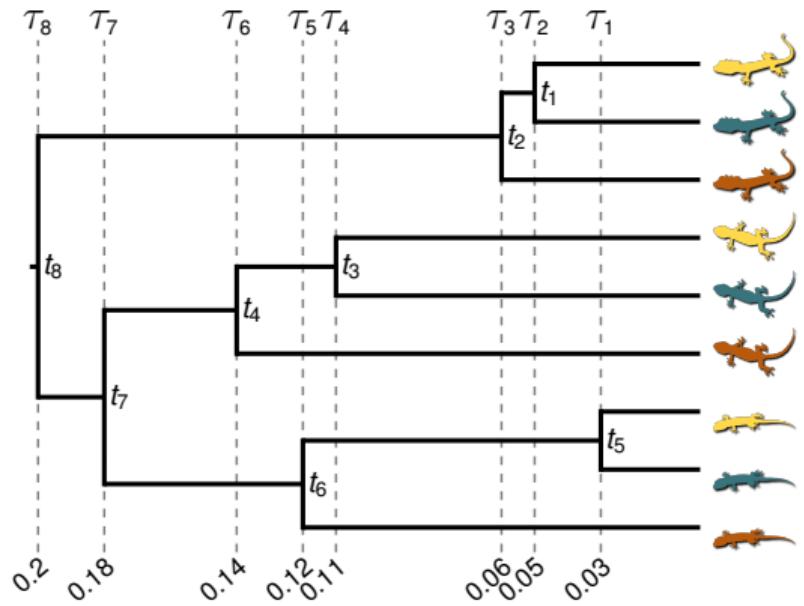
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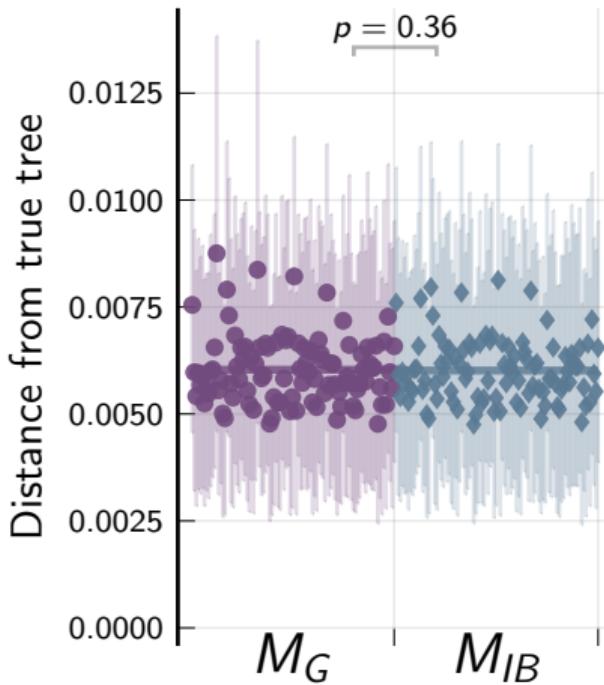
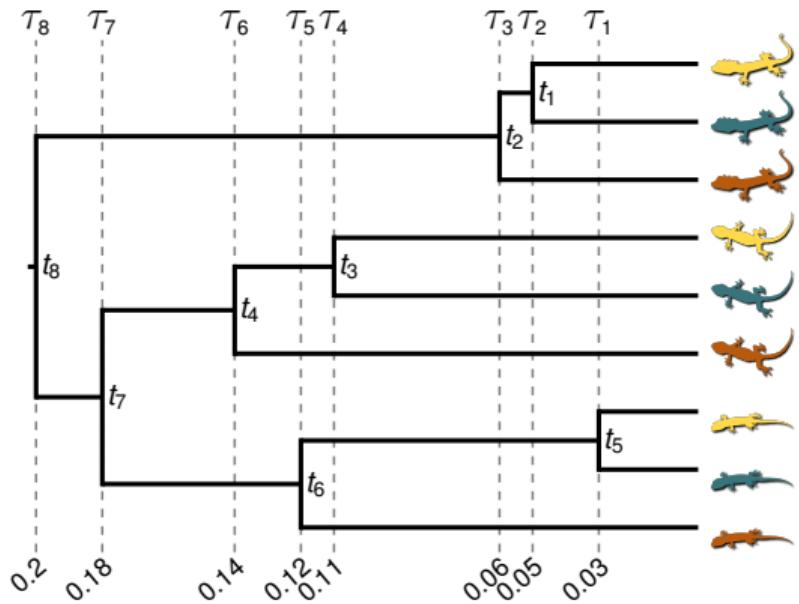
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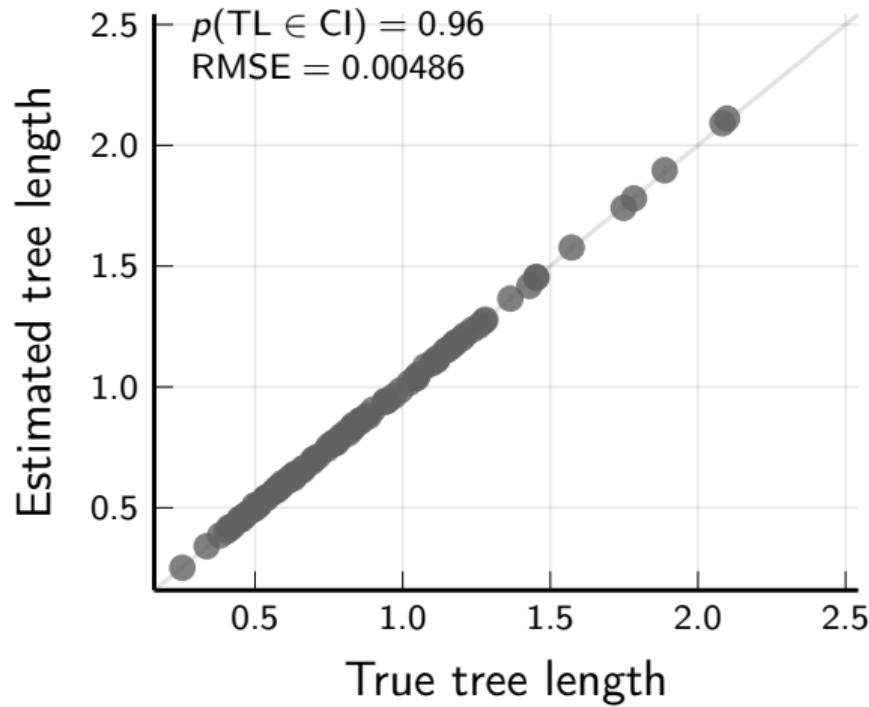
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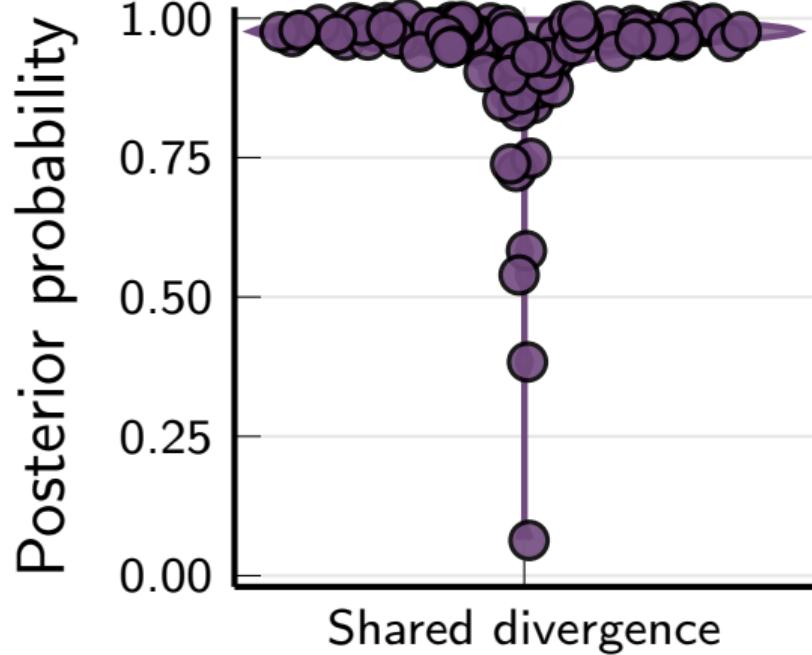
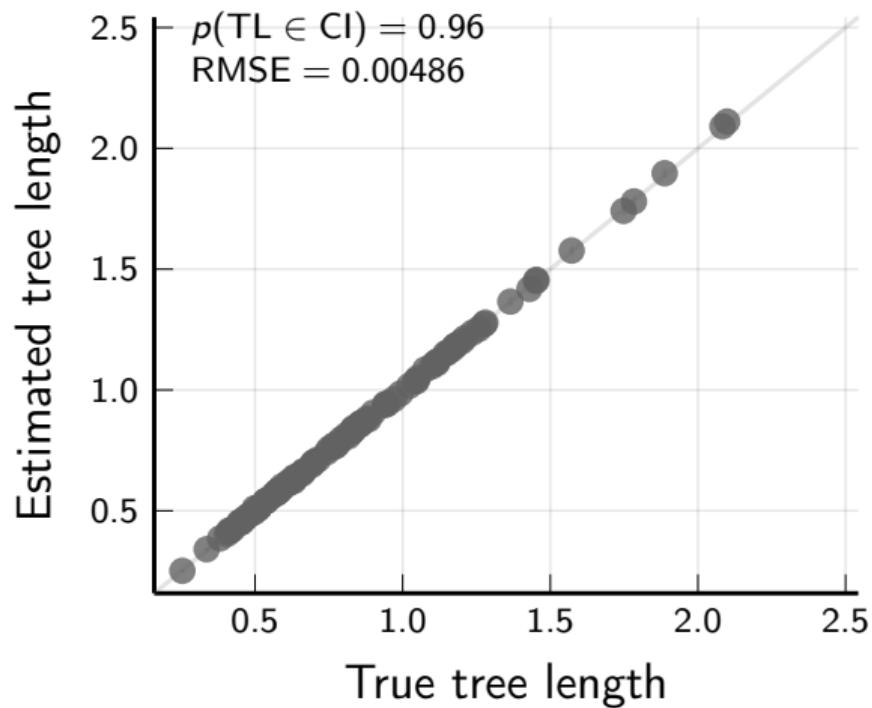


M_G performs as well as true model when divergences are independent

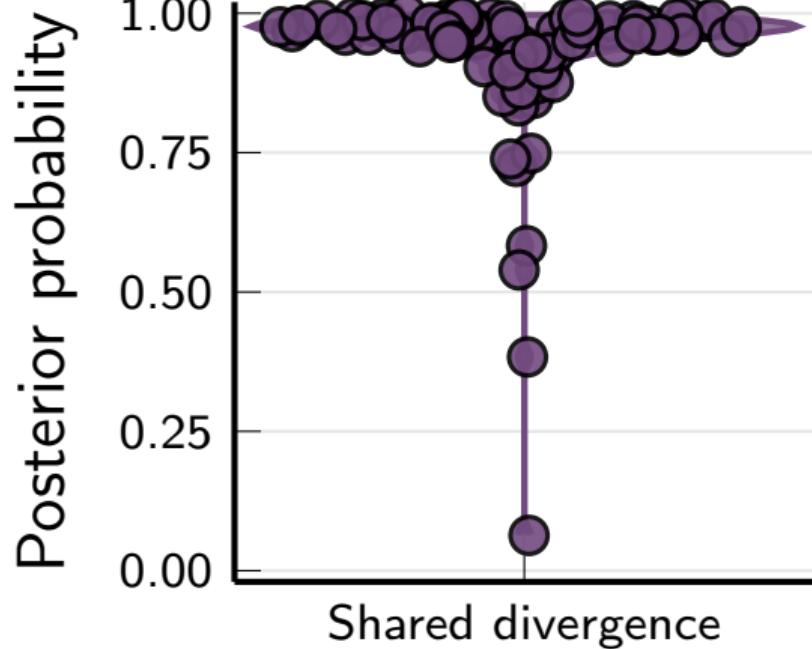
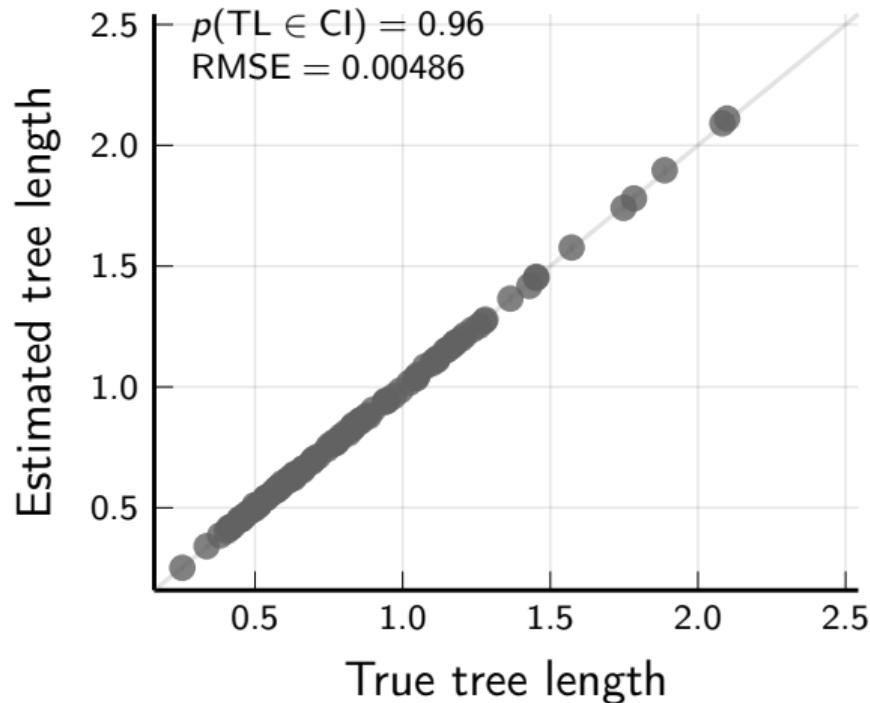
Results: random M_G trees



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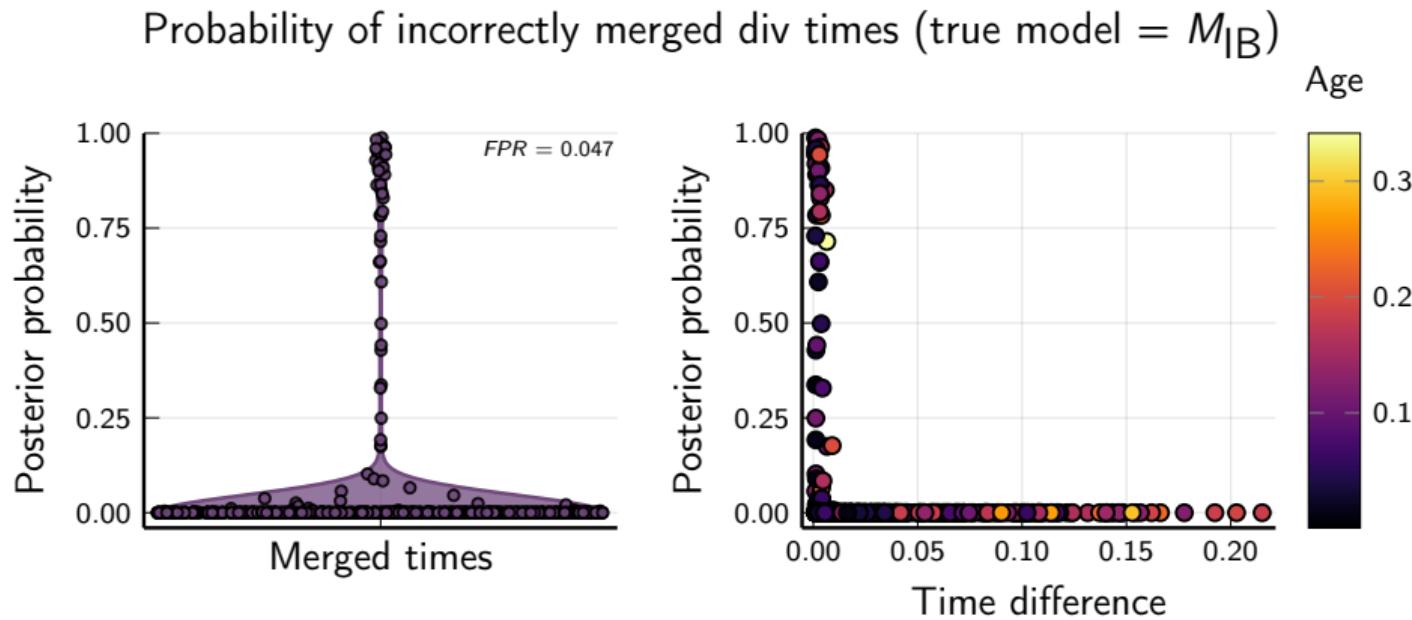


Results: random M_G trees

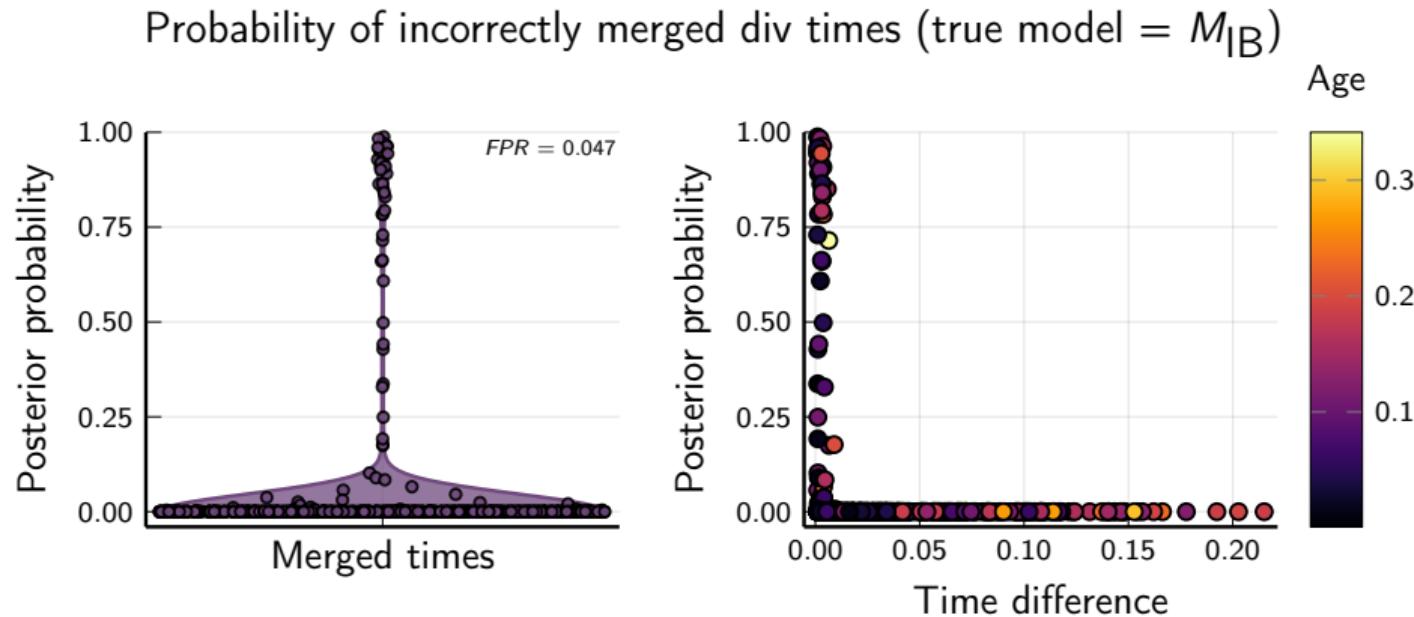


M_G performs well with data simulated on random trees with shared divergences

Results: random M_{IB} trees



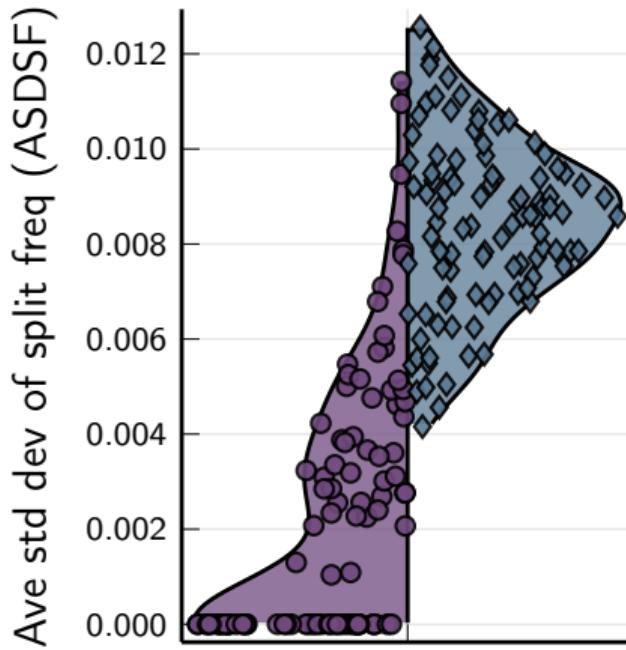
Results: random M_{IB} trees



M_G has low false positive rate

● M_G = Generalized model

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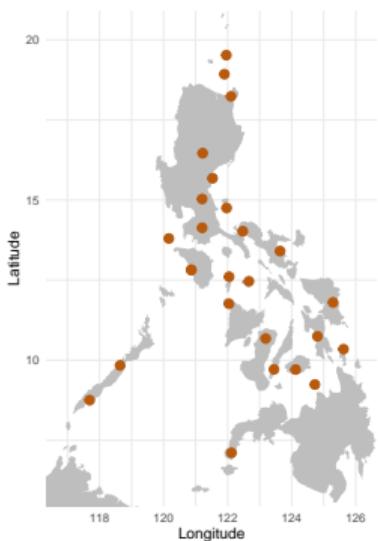
Generalizing tree space improves MCMC convergence and mixing



Scan for sea-level animation

**Did fragmentation of islands
promote diversification?**

Cyrtodactylus



©Rafe M. Brown

Gekko



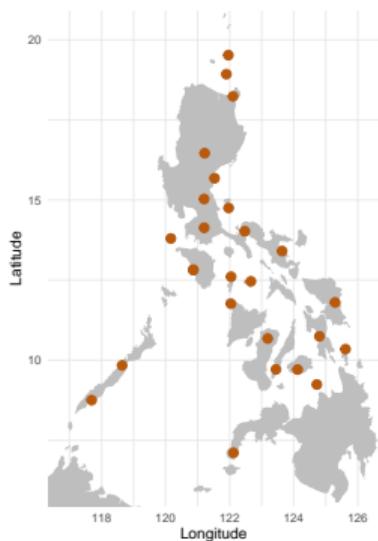
©Rafe M. Brown

Cyrtodactylus



©Rafe M. Brown

1702 loci
155,887 sites



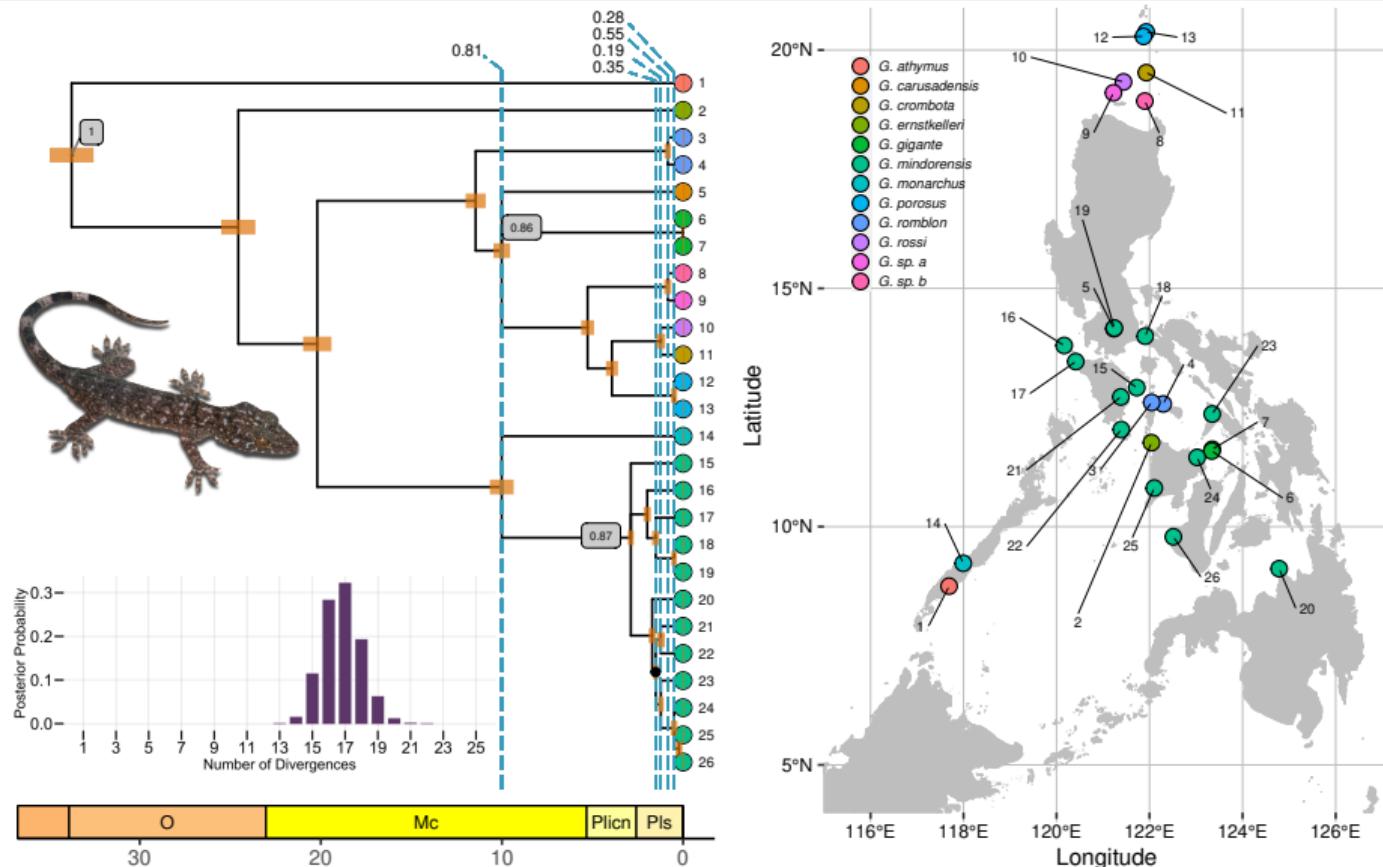
Gekko



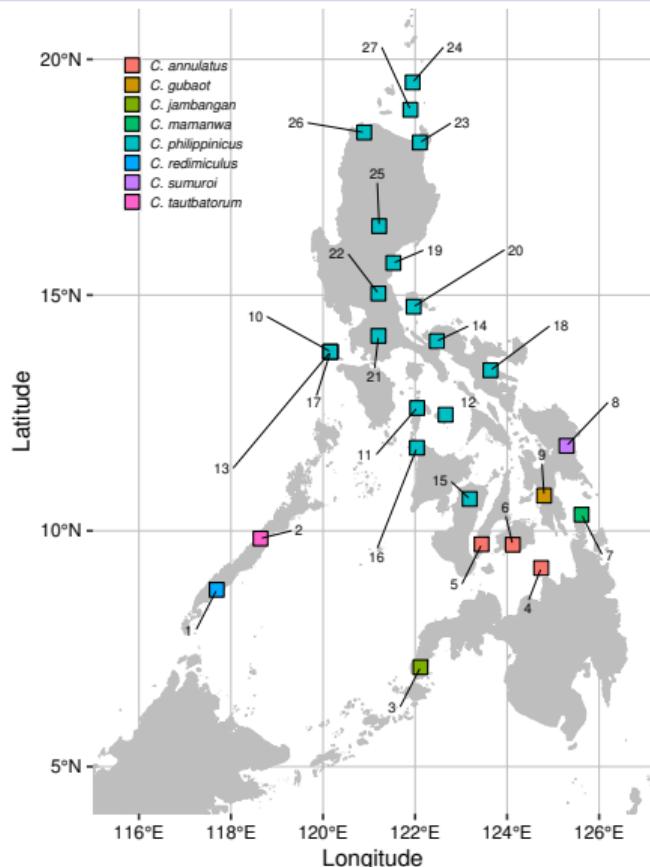
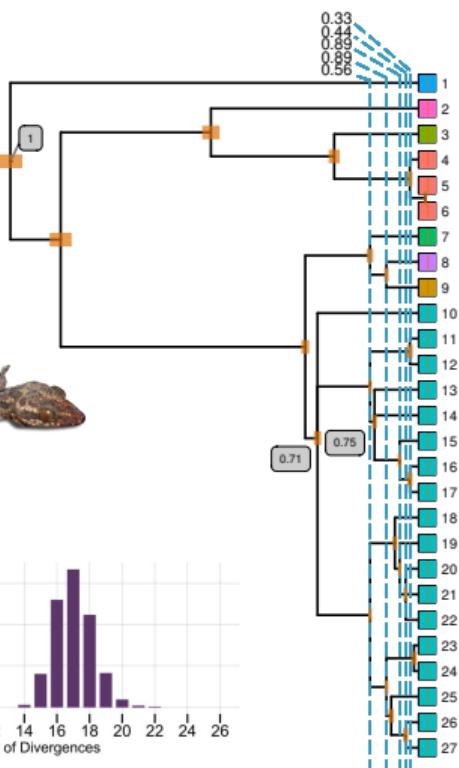
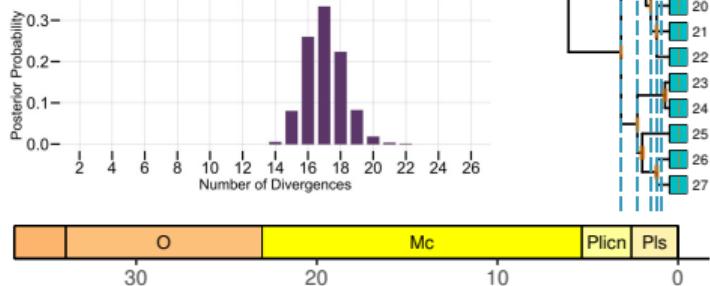
©Rafe M. Brown

1033 loci
94,813 sites

Gekko



Cyrtodactylus



Take-home points

- ▶ We can accurately infer phylogenies with shared divergences with moderately sized data sets

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- ▶ We can accurately infer phylogenies with shared divergences with moderately sized data sets
- ▶ Generalizing tree space avoids spurious support 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

Approaches to the problem

- A pairwise approach (keep it “simple”)
- An aside for a related problem with population demography
- A fully phylogenetic approach

The next 5 years in the Phyletica Lab

Looking forward

Phylogenetic theory/methods

- ▶ Develop process-based and trait-dependent distributions over the space of generalized trees

Empirical work

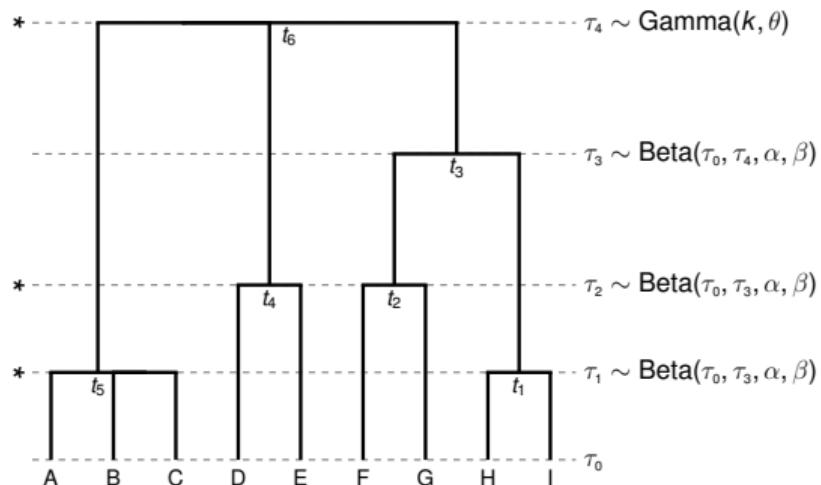
- ▶ Did the evolution of habitat preference affect the diversification of bent-toed geckos?
- ▶ Epidemiological dynamics of “super-spreading” events during the COVID-19 pandemic

Prison education

- ▶ Coding to learn evolution

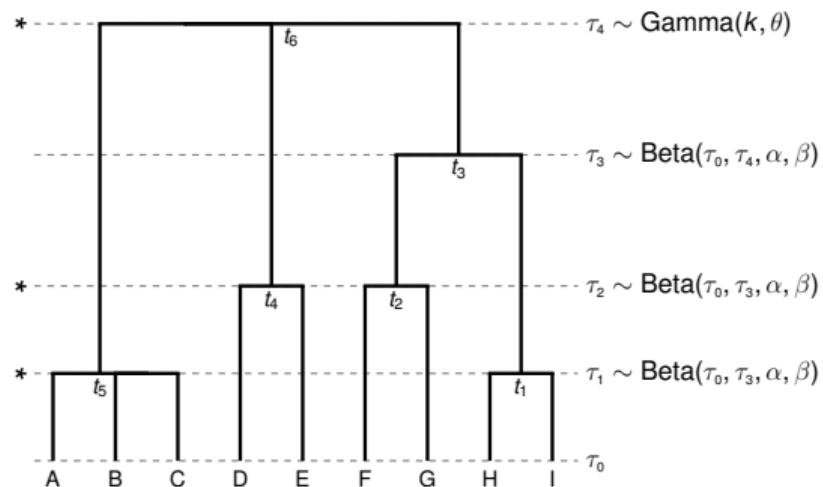
Generalized tree distribution

- ▶ Our current distribution over trees is motivated by mathematical convenience



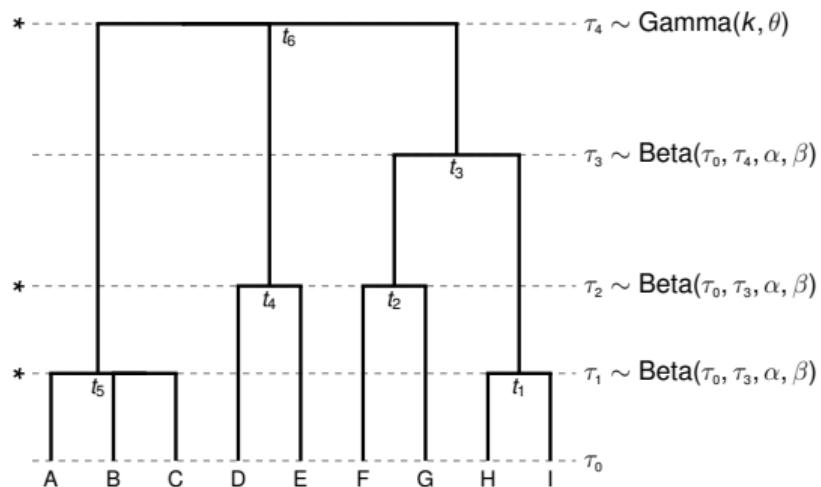
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Generalized tree distribution

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 - ▶ Goal: port M_G algorithms to RevBayes and develop generalized birth-death model

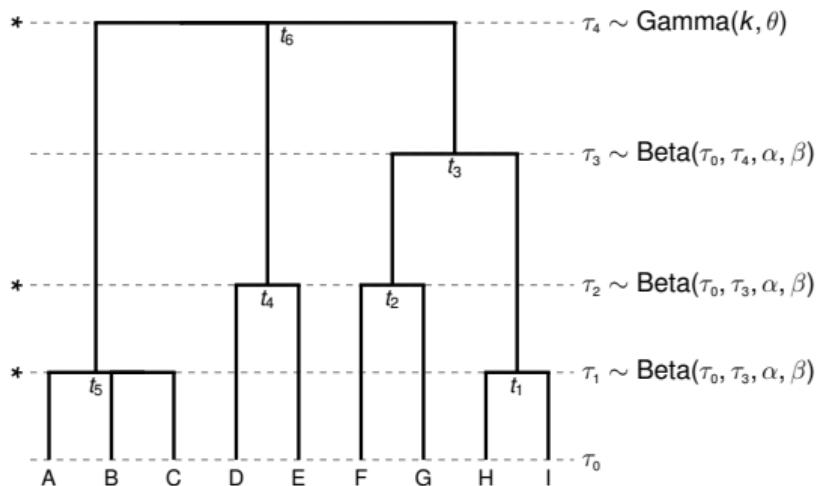


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Sebastian Höhna
LMU Munich

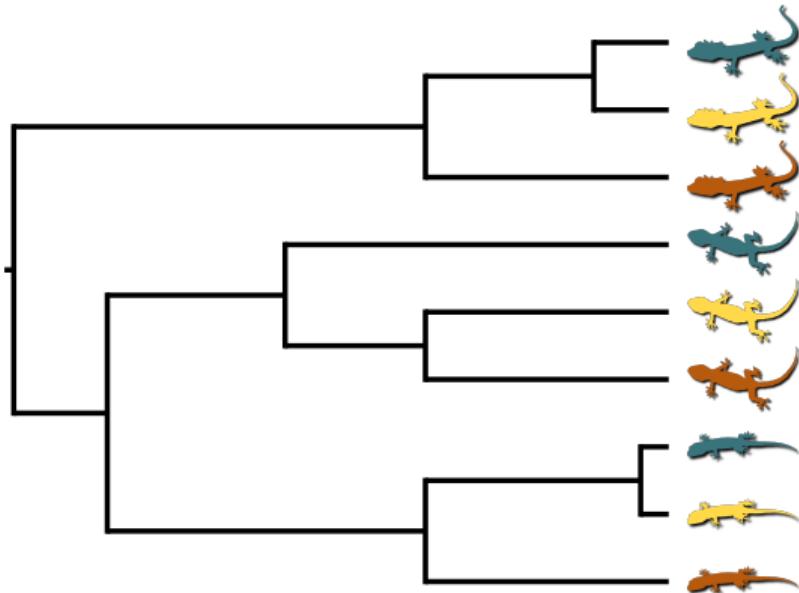


Generalizing the birth-death process

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Birth-death basics:

- ▶ Lineages speciate at rate λ
- ▶ Lineages go extinct at rate μ
- ▶ We sample extant lineages with probability ρ



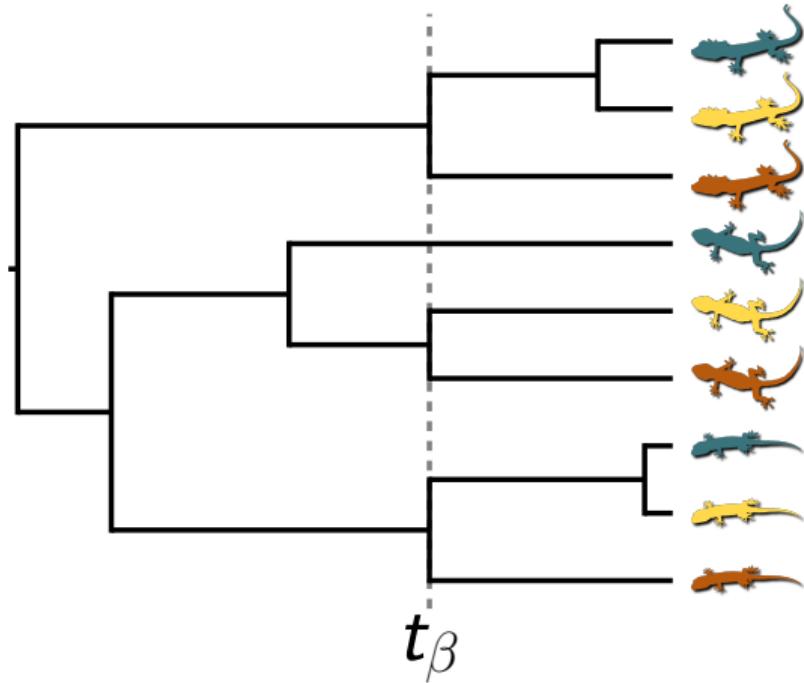
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“Birth-death-burst” (BDB) process:

- ▶ Include “burst events” that occur at rate λ_β
- ▶ Each lineage diverges with probability β



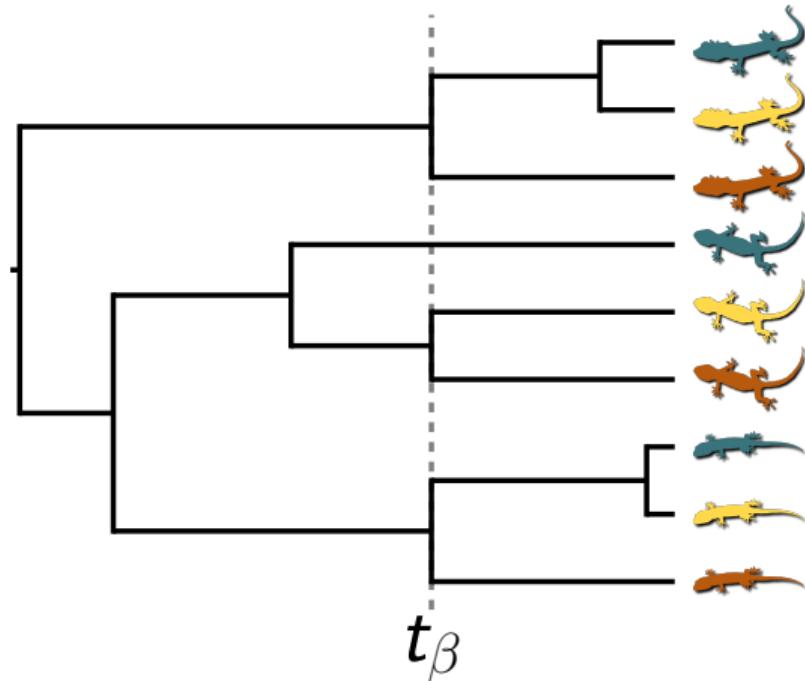
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- ▶ Allow λ , μ , λ_β , & β to vary depending on the traits of lineages across the tree



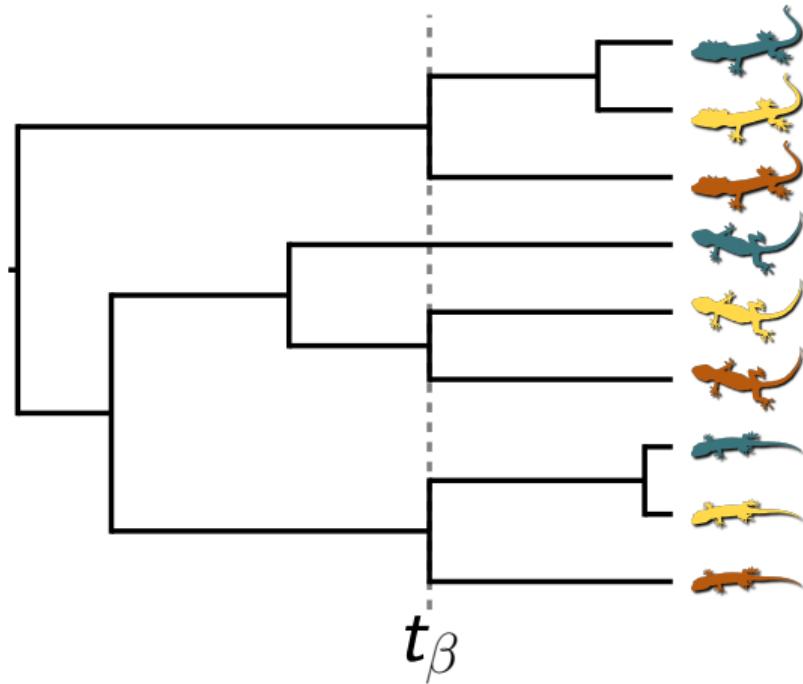
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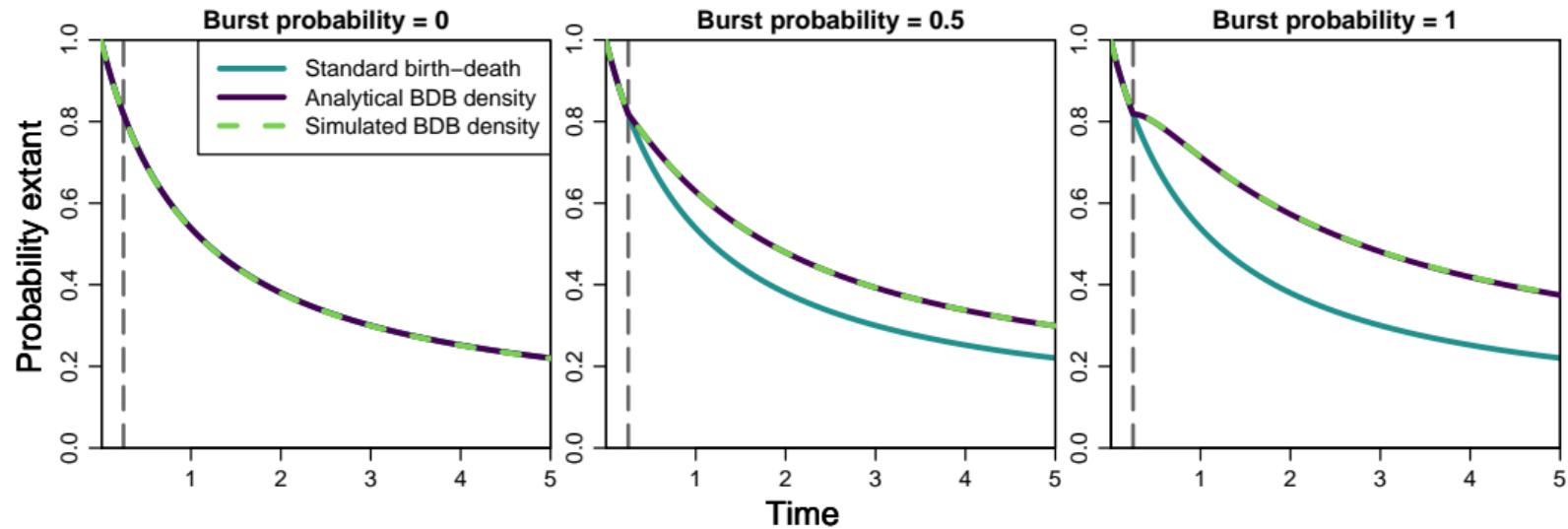
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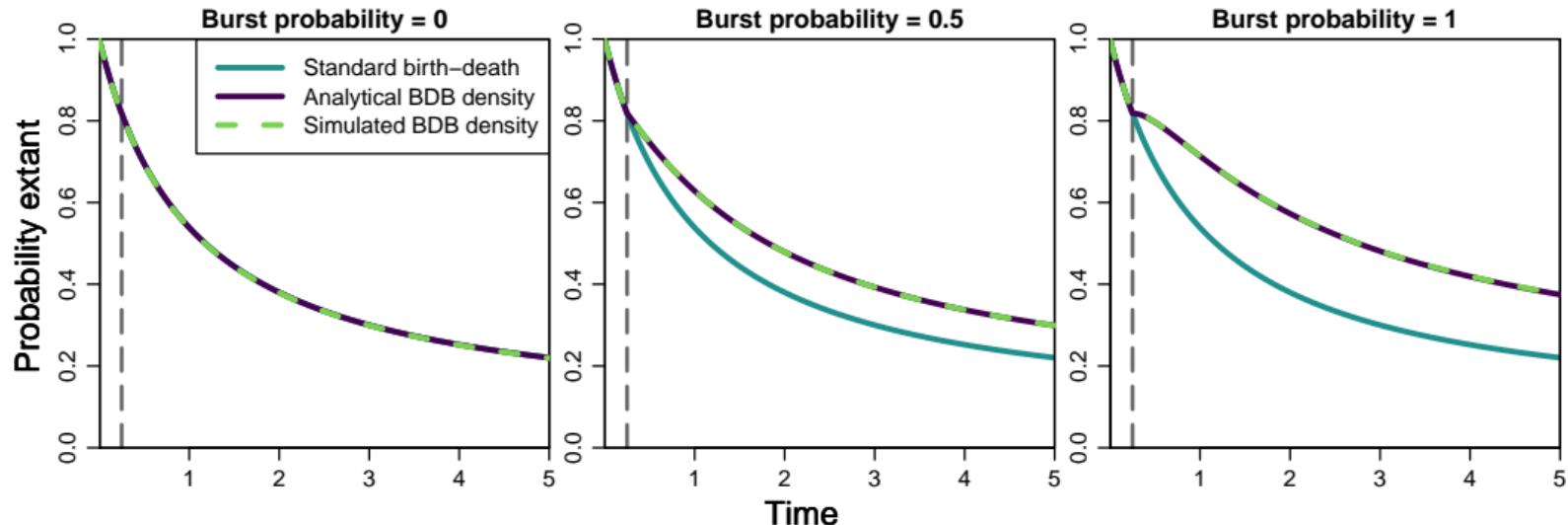
- ▶ Include “burst events” that occur at rate λ_β
- ▶ Each lineage diverges with probability β
- ▶ Allow λ , μ , λ_β , & β to vary depending on the traits of lineages across the tree
- ▶ Bayesian model-averaging to infer set of trait-dependent BDB models that best explain data



Birth-death-burst validation

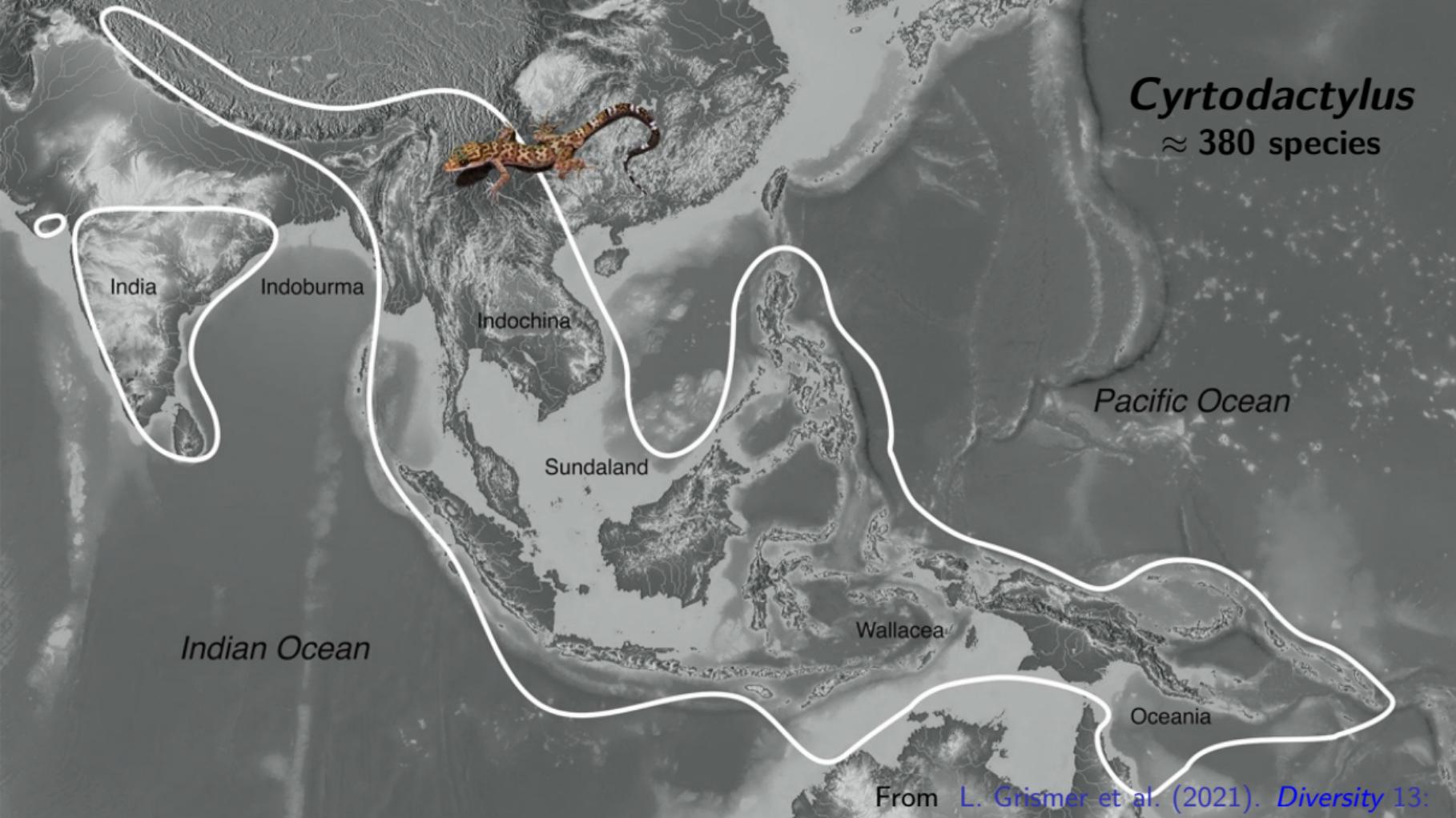


Birth-death-burst validation



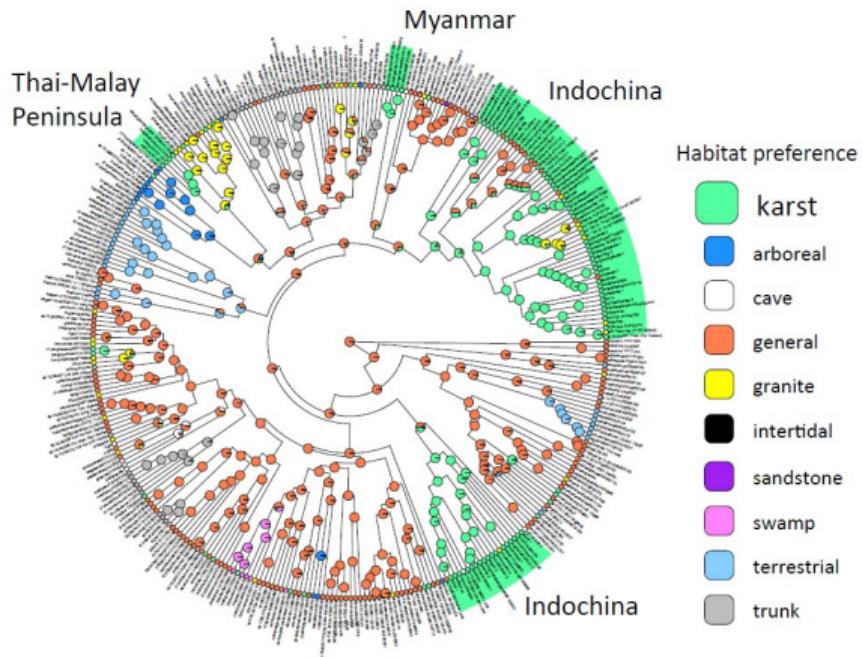
We have correctly derived the likelihood of trees under the BDB model

Cyrtodactylus
≈ 380 species



Karst endemism in *Cyrtodactylus*

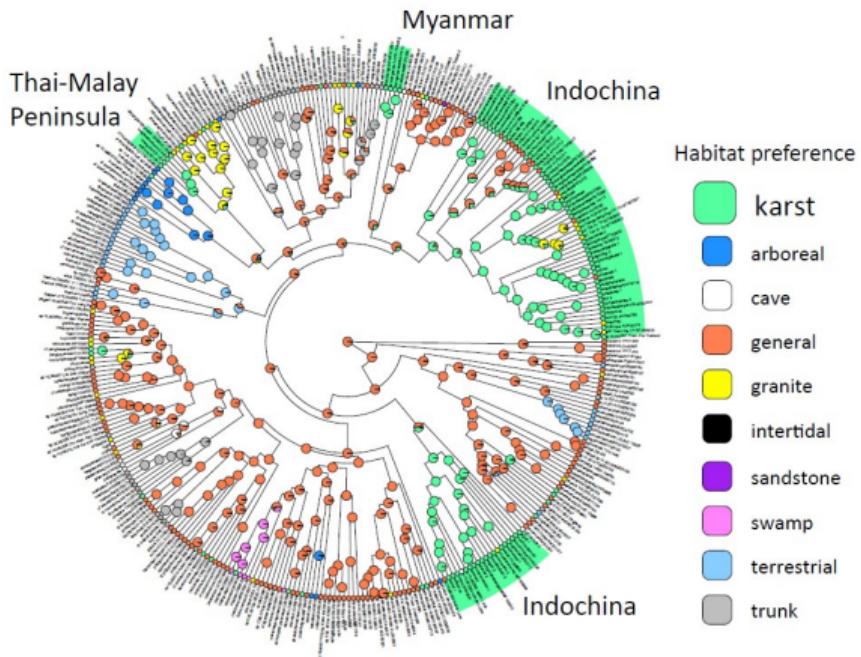
- ▶ *Cyrtodactylus* are ecologically diverse, ranging from generalists to microhabitat specialists



L. Grismer et al. (2021). *Diversity* 13:

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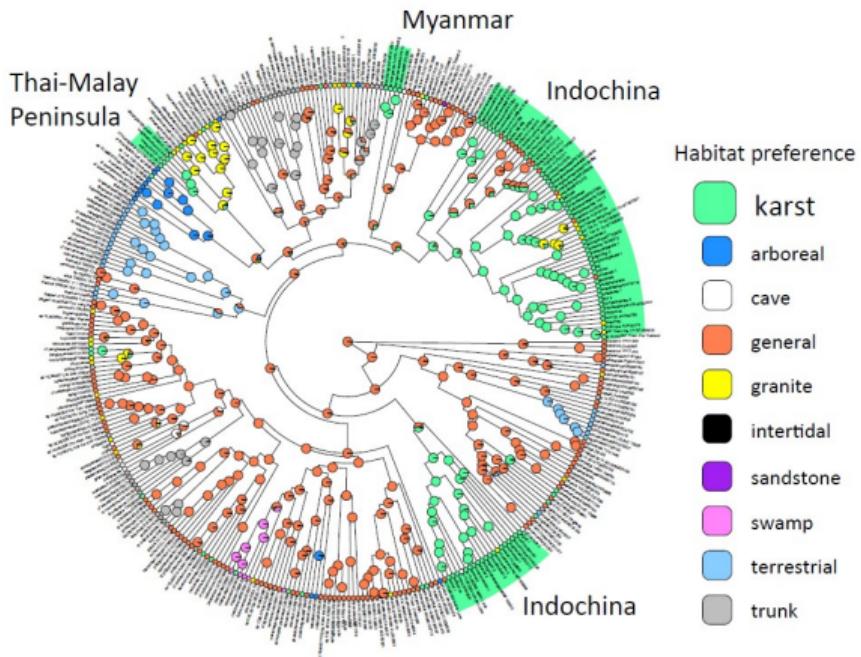
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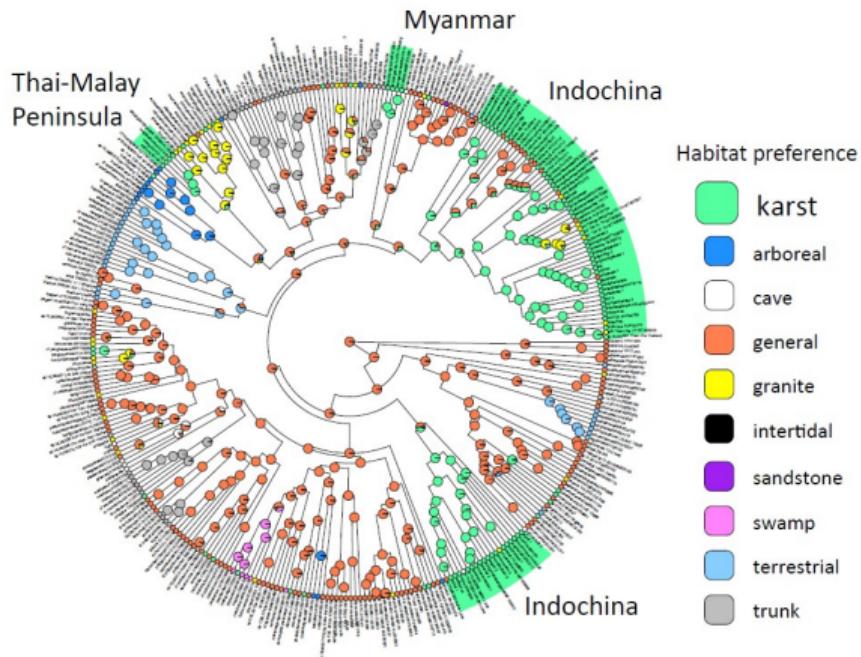
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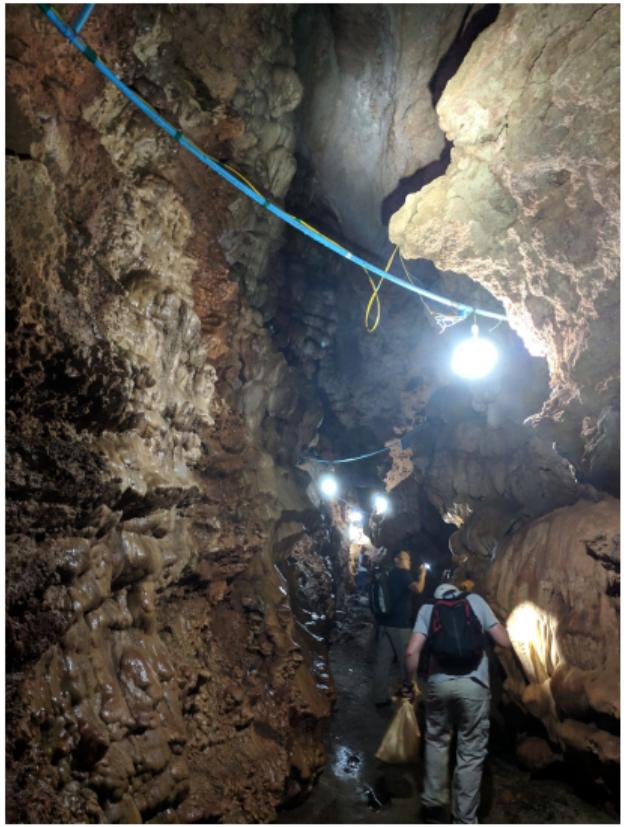
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- ▶ Comprise 25% of species despite tiny fraction of landscape being karst
- ▶ Karst-specific species show remarkable levels of micro-endemism



L. Grismer et al. (2021). *Diversity* 13:





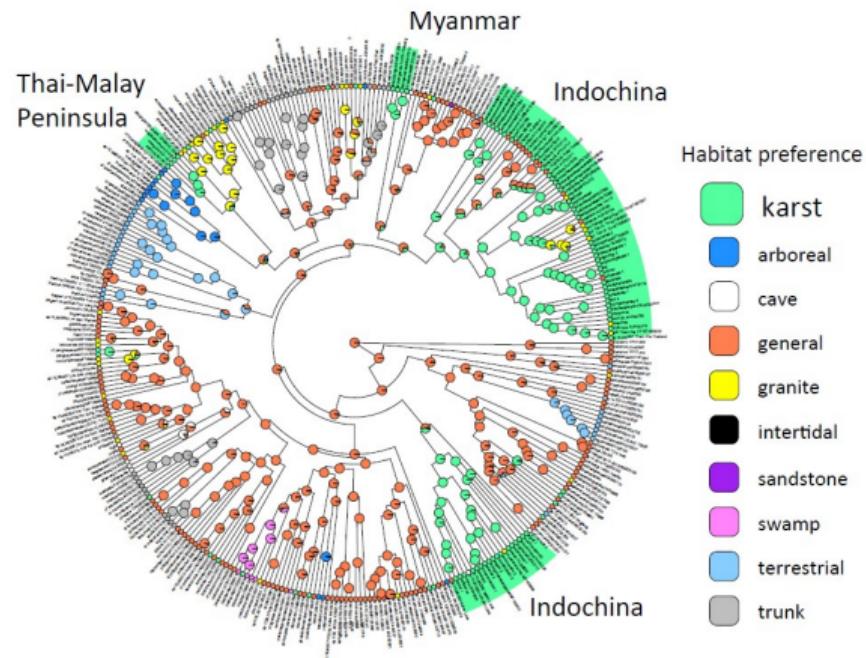




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Why high levels of diversity and endemism on karst?

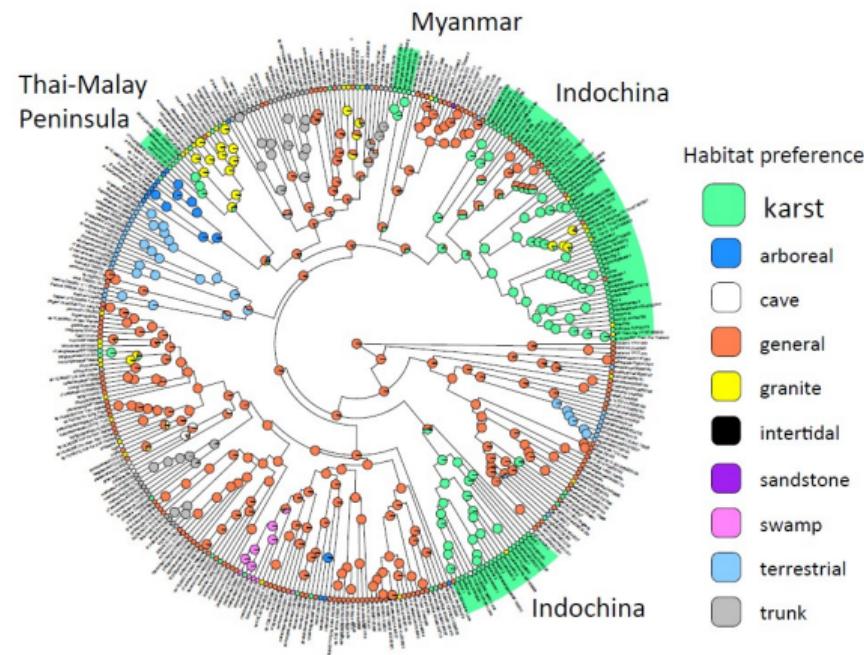
- ▶ “Rapid” fragmentation of karst habitat caused by the uplift and subsequent erosion of limestone sediment over the last 30my



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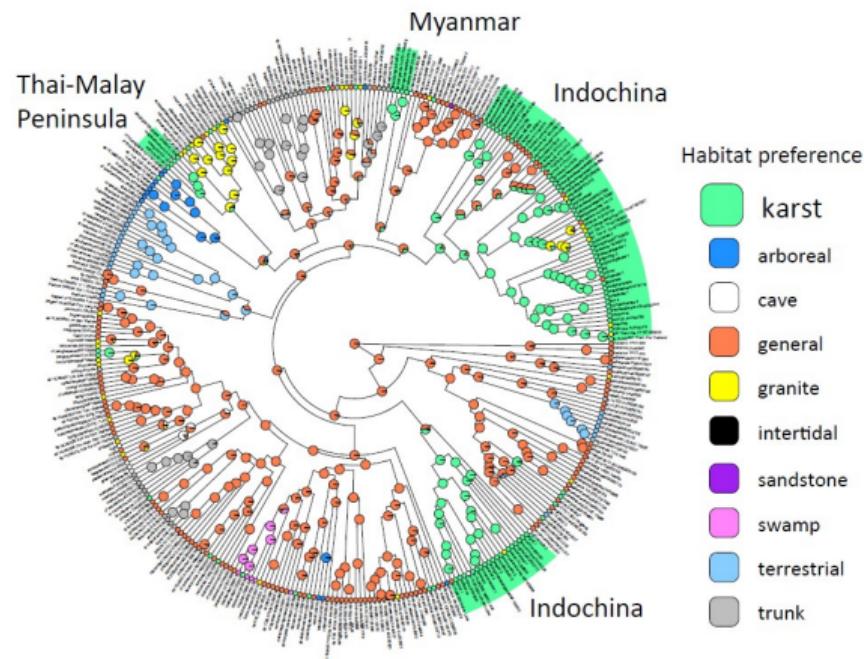
- ▶ “Rapid” fragmentation of karst habitat caused by the uplift and subsequent erosion of limestone sediment over the last 30my
- ▶ E.g., Major river systems carved through and isolated limestone karst formations (Ayeyarwady, Chiang Mai, Mekong, Red, and Salween)



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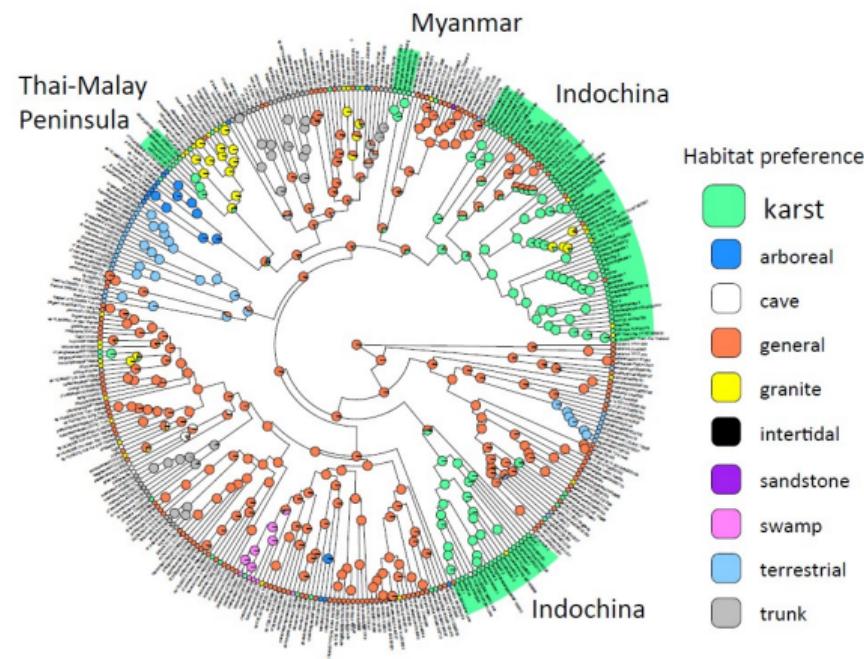
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L. Grismer et al. (2021). *Diversity* 13:

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- ▶ **Prediction:** Increased rate of ***shared divergences*** in karst-adapted lineages

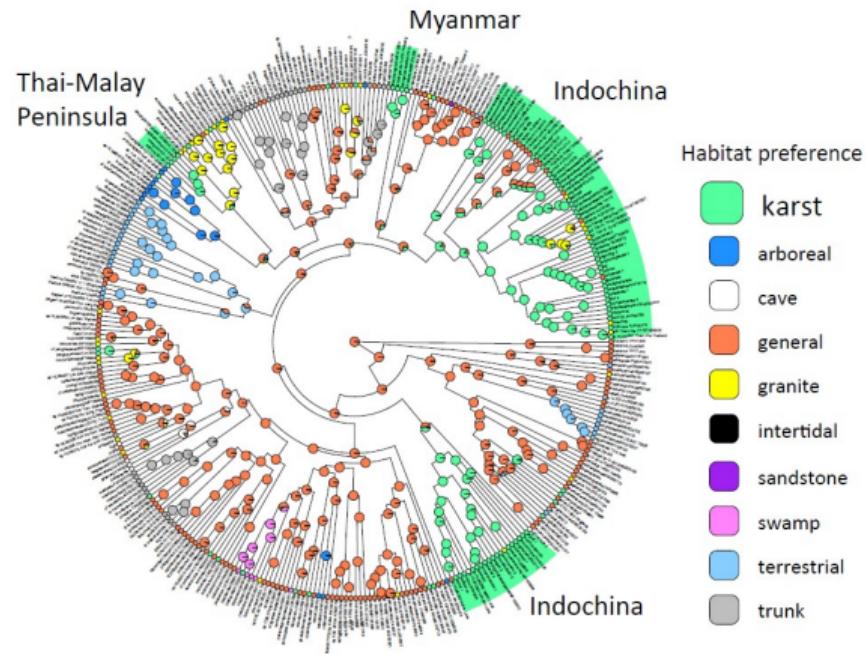


L. Grismer et al. (2021). *Diversity* 13:

Why high levels of diversity and endemism on karst?

Plan:

- ▶ Access to tissue samples of 368 of the 380 *Cyrtodactylus* species

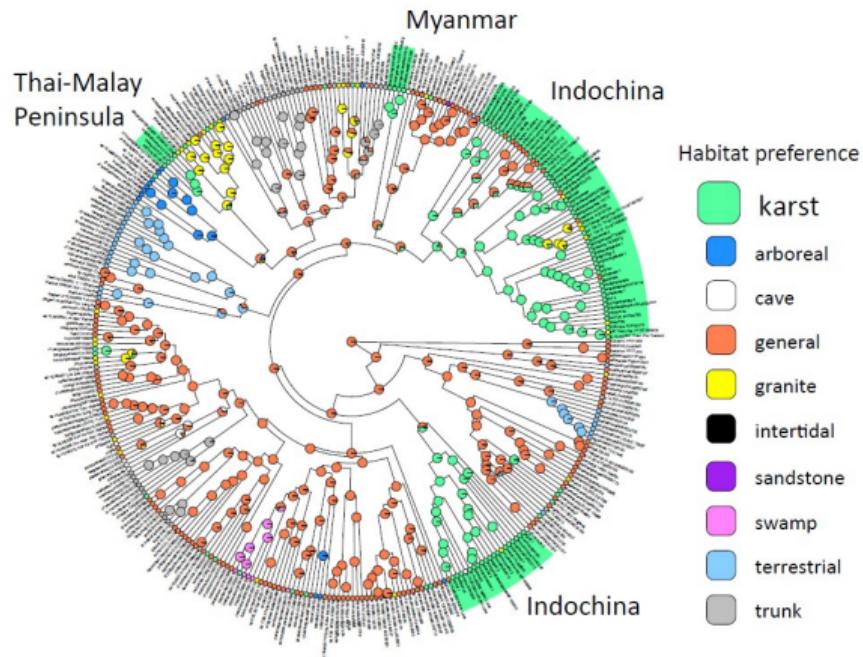


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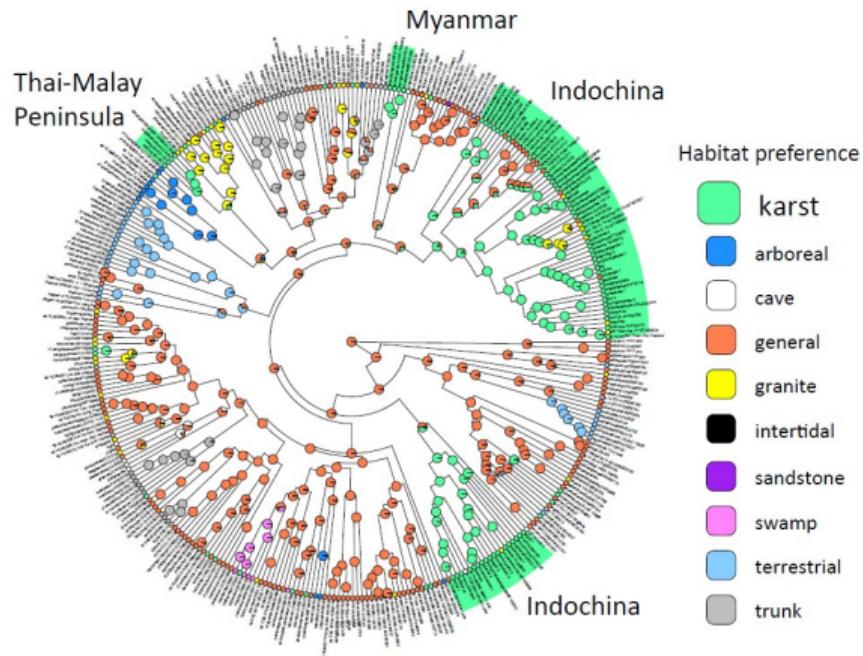


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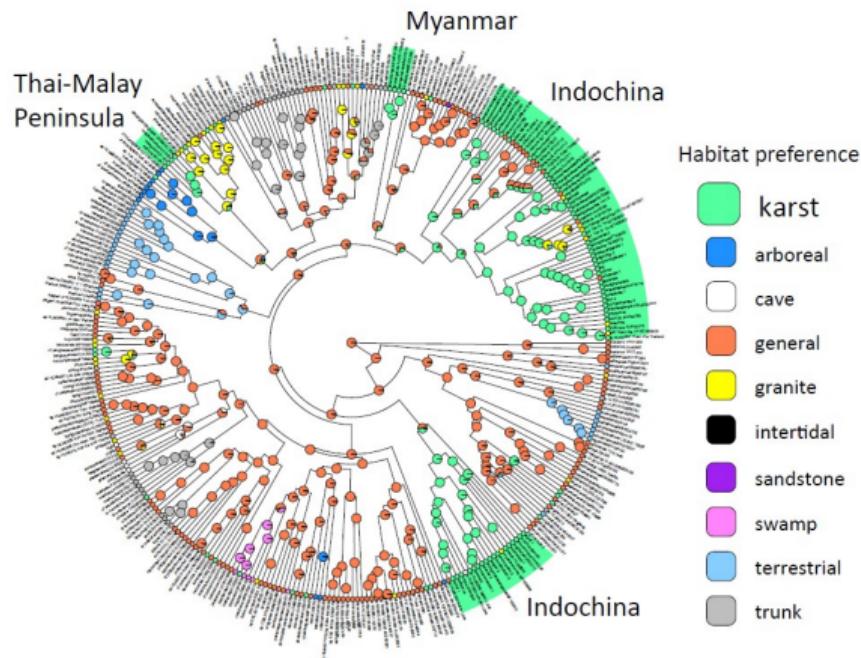


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- ▶ Approximate posterior probability that
karst-specific lineages have higher rate of
shared divergences (λ_β)

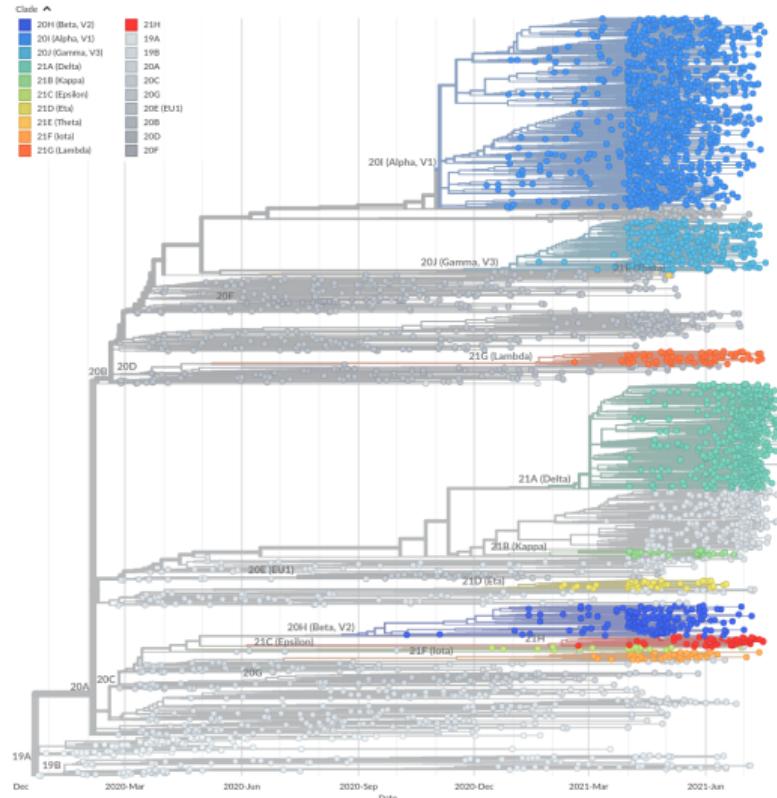


L. Grismer et al. (2021). *Diversity* 13:

Epidemiological dynamics of COVID-19 pandemic

Questions:

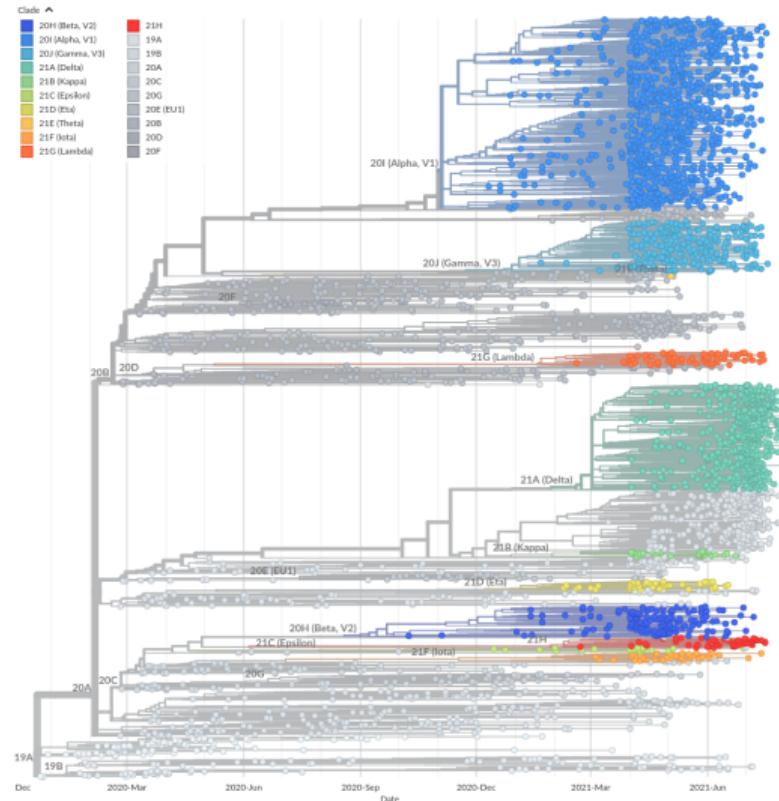
- ▶ What is the relative contribution of social gatherings to the spread of SARS-CoV-2?



Epidemiological dynamics of COVID-19 pandemic

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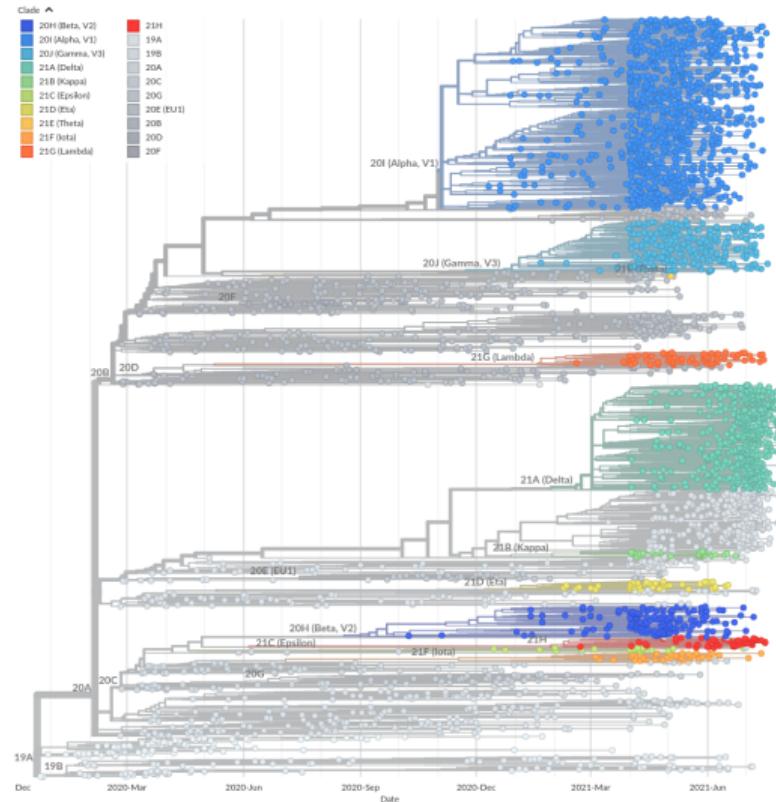
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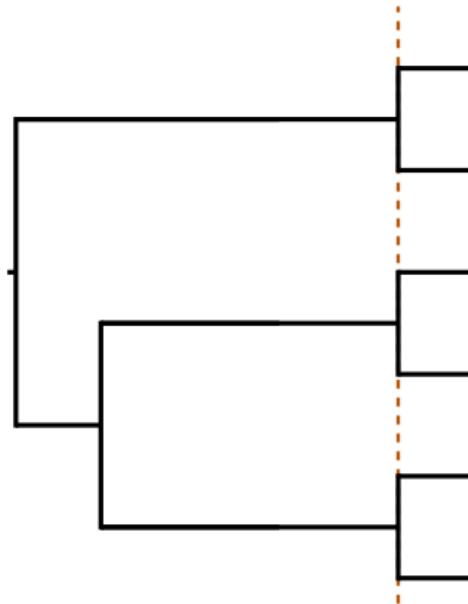
- ▶ What is the relative contribution of social gatherings to the spread of SARS-CoV-2?
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 - ▶ Does this increase during holidays?



Divergence patterns predicted by gatherings

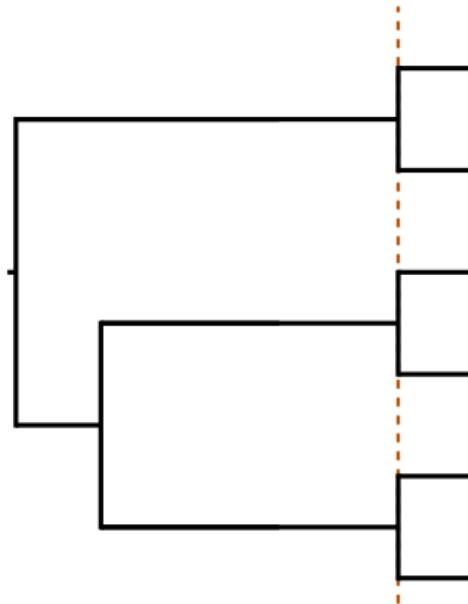
Divergence patterns predicted by gatherings

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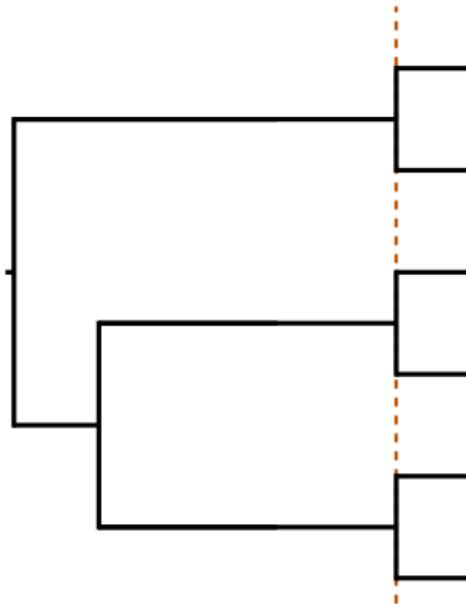
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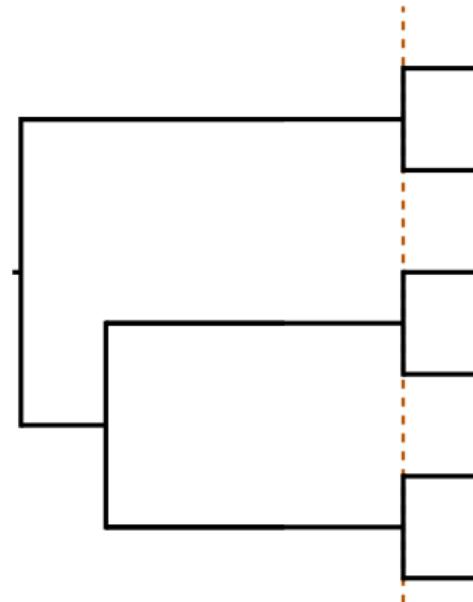


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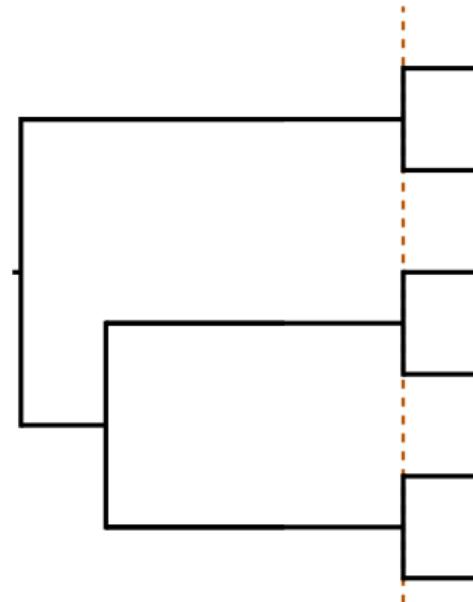


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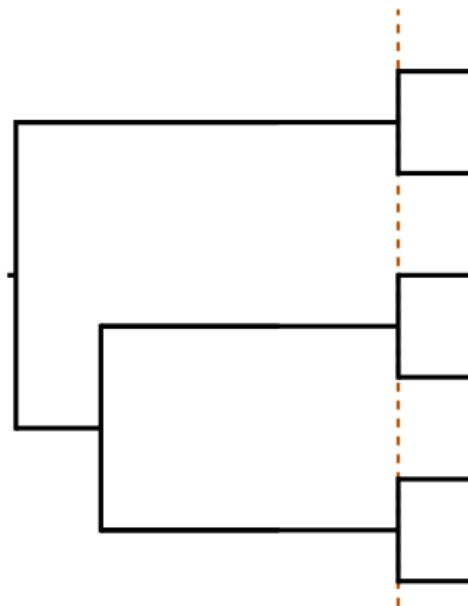


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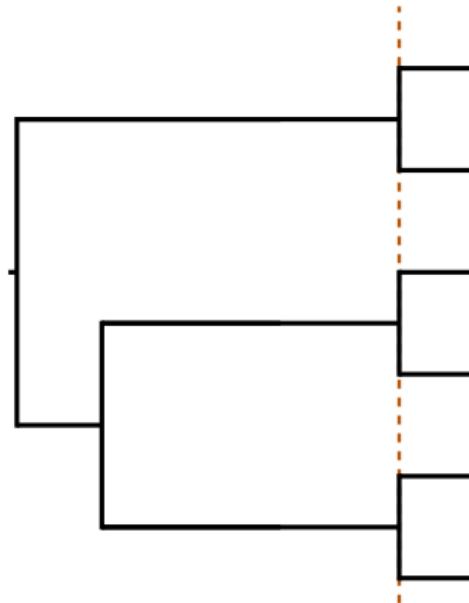


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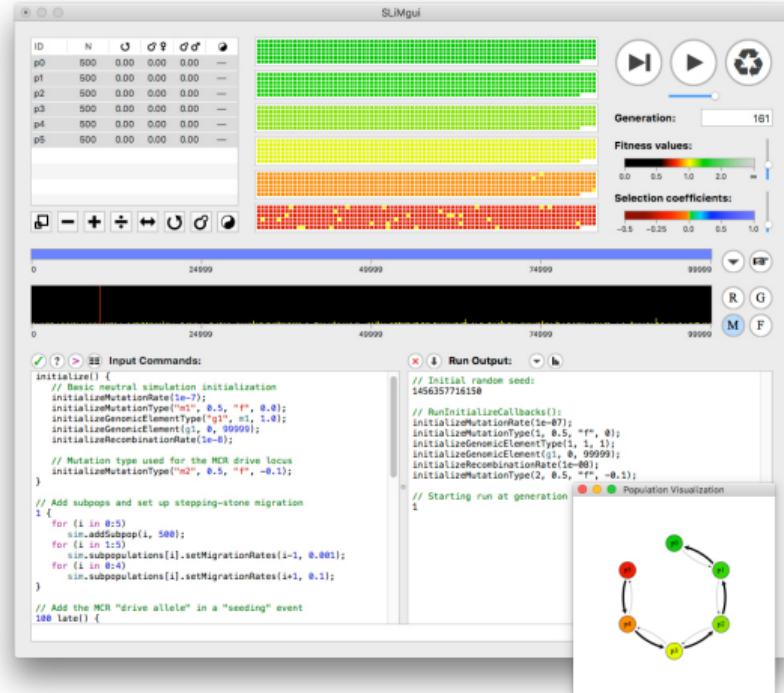
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- ▶ Summarize λ_β over time to quantify the effect of holidays



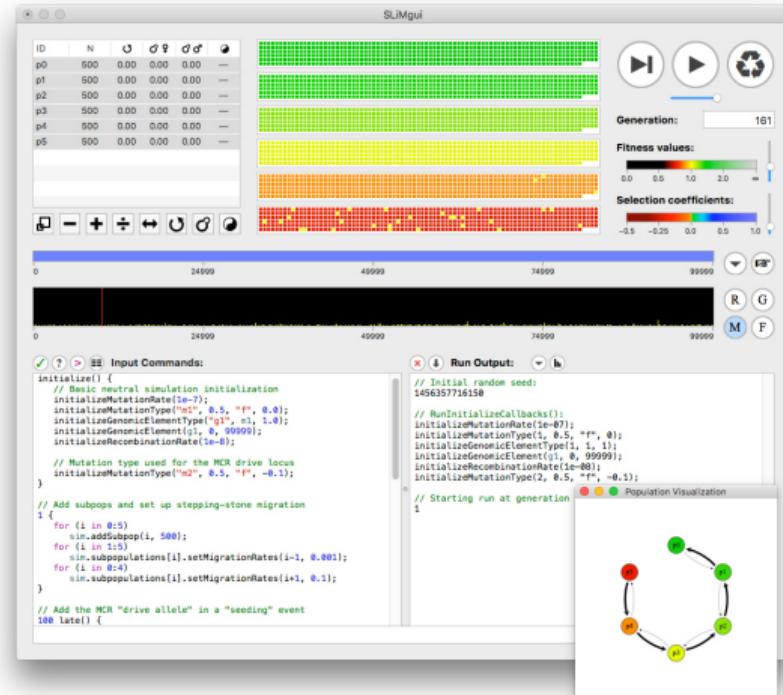
Prison Ed: Coding to learn evolution

- ▶ Develop coding-to-learn evolution course
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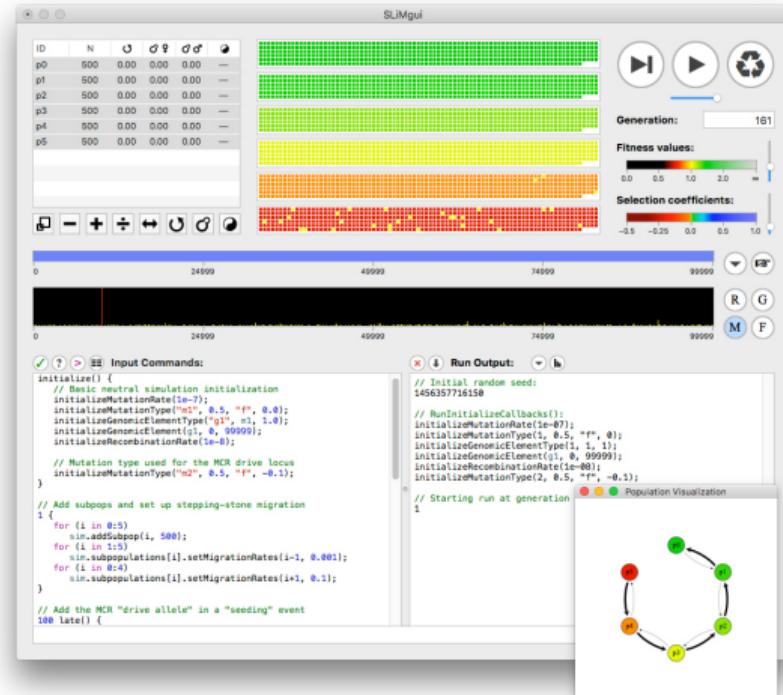
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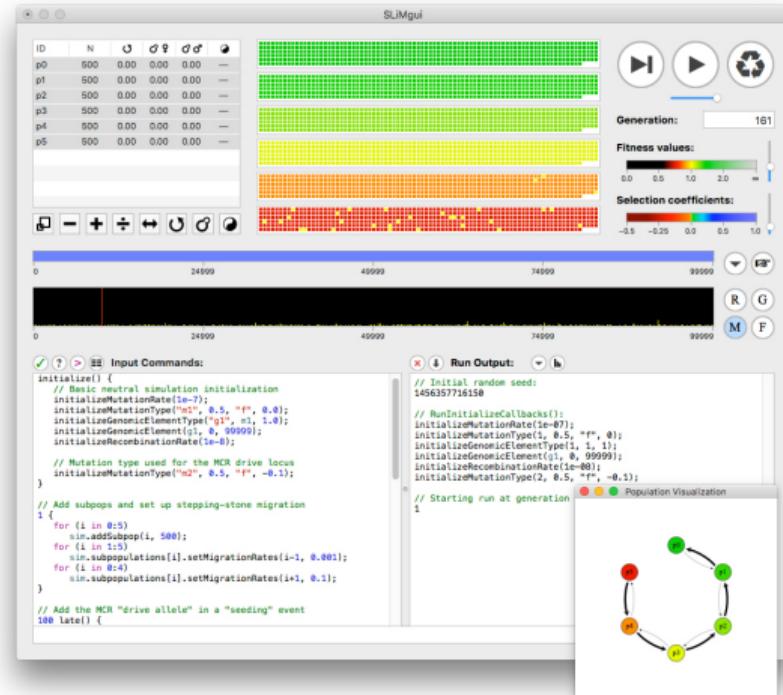
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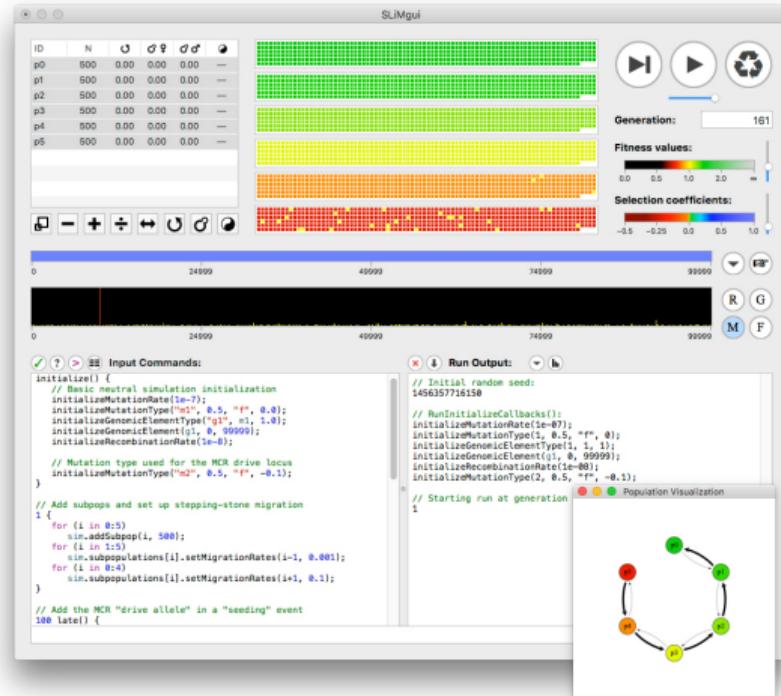
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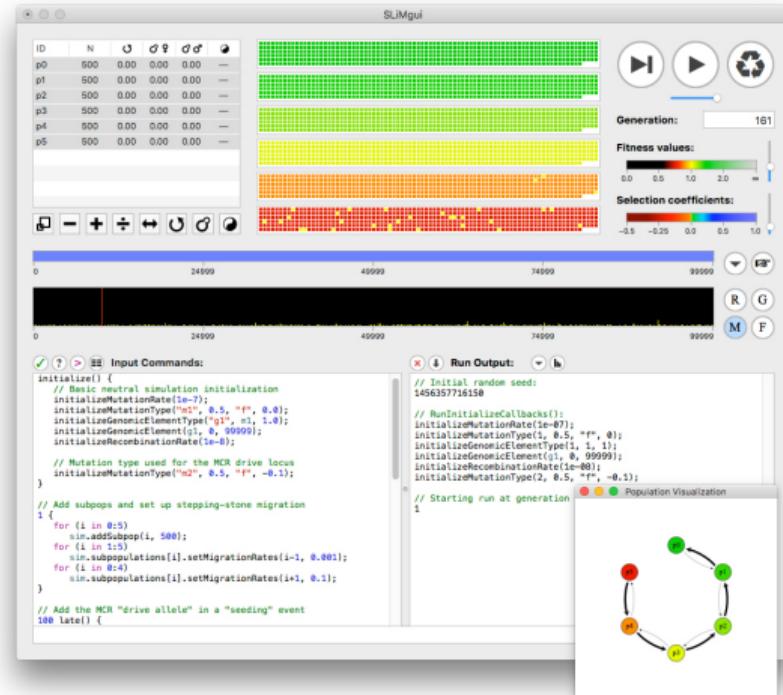
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- ▶ Students co-author paper



Acknowledgments

- ▶ Phyletica Lab (the Phyleticians)
- ▶ AU DBS
- ▶ Mark Holder
- ▶ Rafe Brown
- ▶ Cam Siler
- ▶ Lee Grismer

Computation:

- ▶ Alabama Supercomputer Authority
- ▶ Auburn University Hopper Cluster

Funding:



Photo credits:

- ▶ Rafe Brown
- ▶ Perry Wood, Jr.
- ▶ PhyloPic

Acknowledgments



Questions?

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phyletica.org



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