

# The comparative biogeography of Philippine geckos challenges predictions from a paradigm of climate-driven vicariant diversification across an island archipelago

Jamie R. Oaks<sup>1</sup> Cameron D. Siler<sup>2</sup> Rafe M. Brown<sup>3</sup>

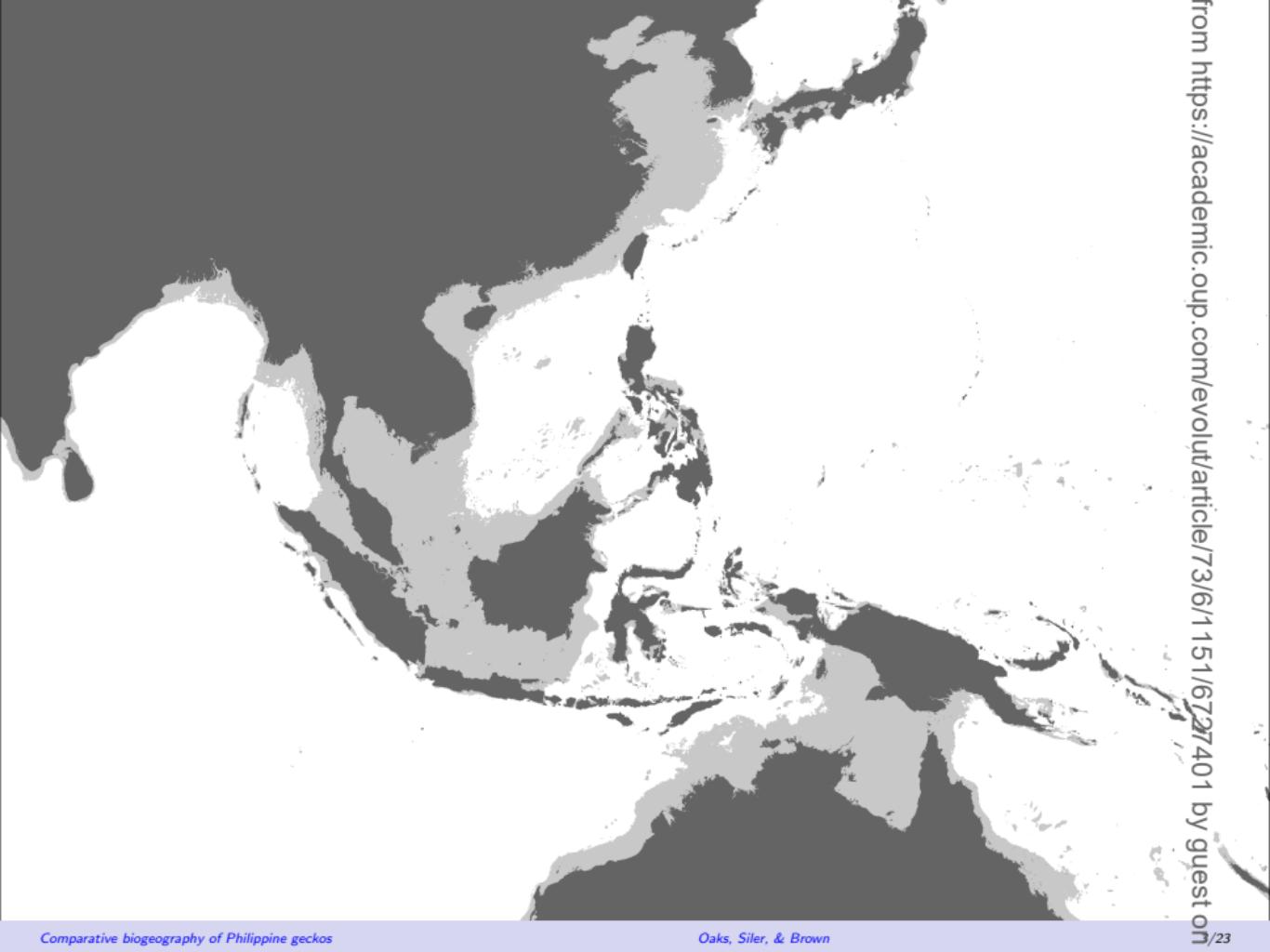
<sup>1</sup>Department of Biological Sciences & Museum of Natural History, Auburn University,  
Auburn, Alabama 36849, USA

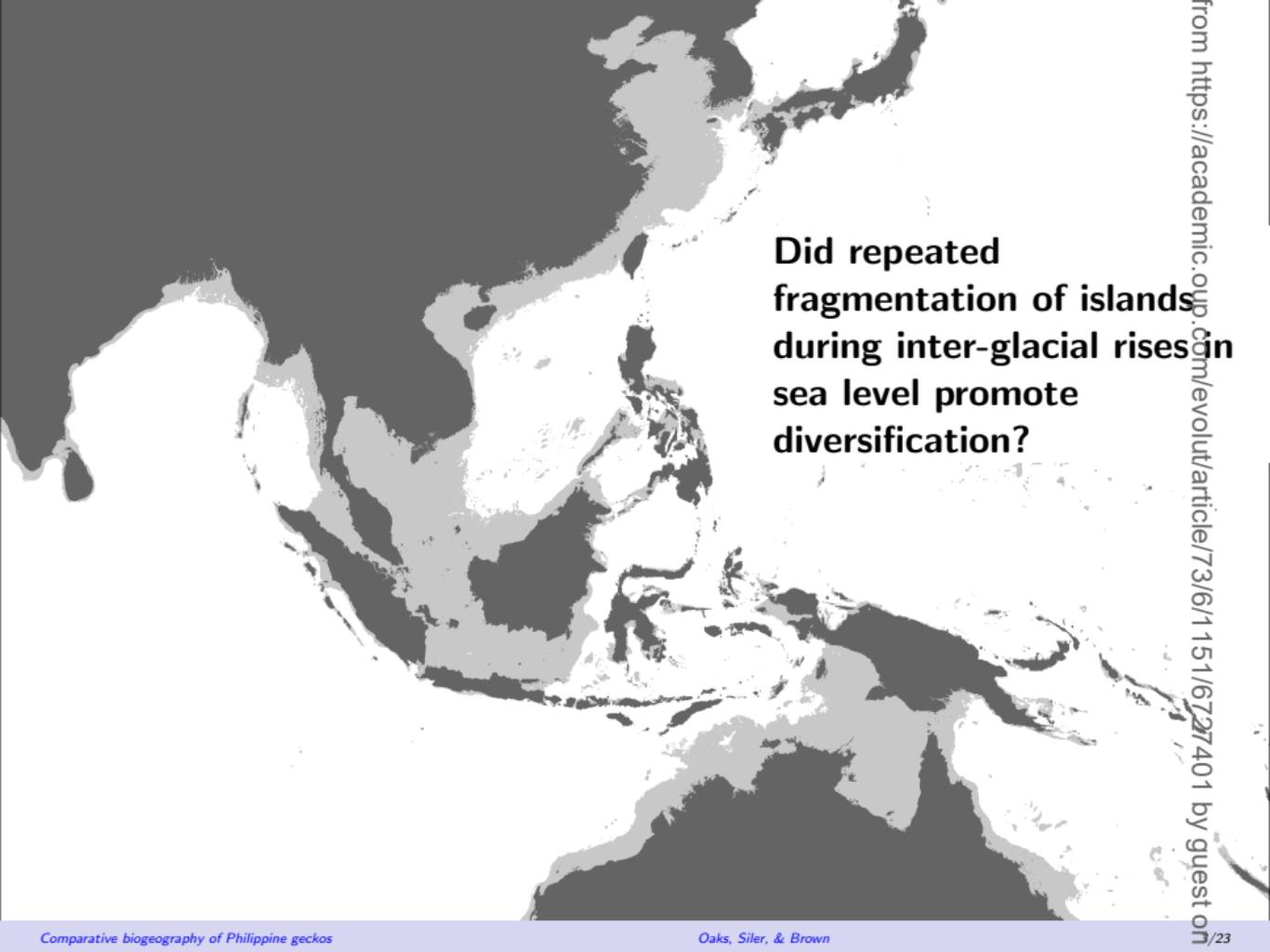
<sup>2</sup>Sam Noble Oklahoma Museum of Natural History and Department of Biology, University of  
Oklahoma, Norman, Oklahoma 73072-7029

<sup>3</sup>Biodiversity Institute and Department of Ecology and Evolutionary Biology, University of  
Kansas, Lawrence, Kansas 66045, USA

May 3, 2019

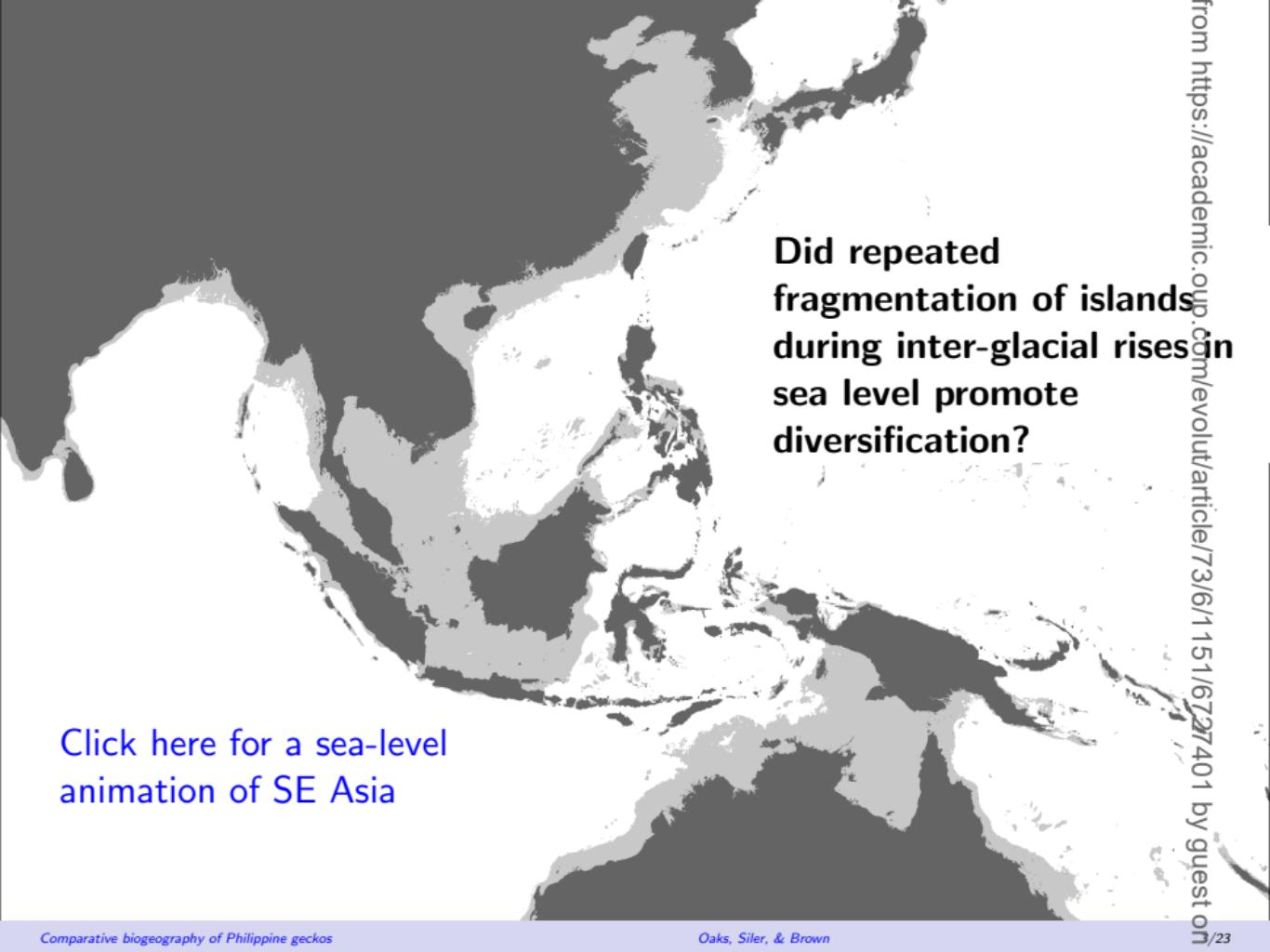






A grayscale map of Southeast Asia, specifically focusing on the Philippines and surrounding islands. The map uses different shades of gray to represent land areas, with darker shades indicating larger landmasses like the Philippines and Indonesia, and lighter shades for smaller, more isolated island groups. This visual representation illustrates the concept of island fragmentation mentioned in the text.

**Did repeated  
fragmentation of islands  
during inter-glacial rises in  
sea level promote  
diversification?**



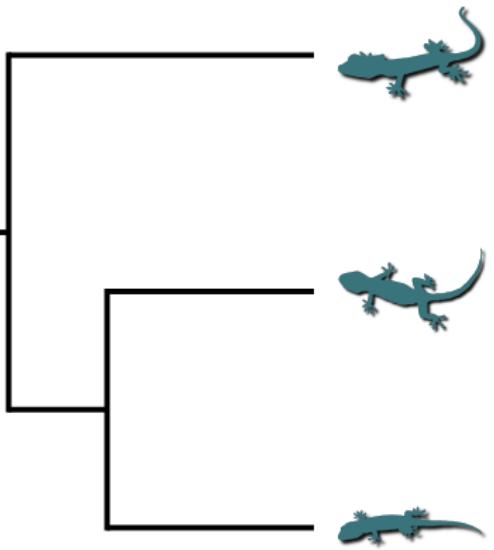
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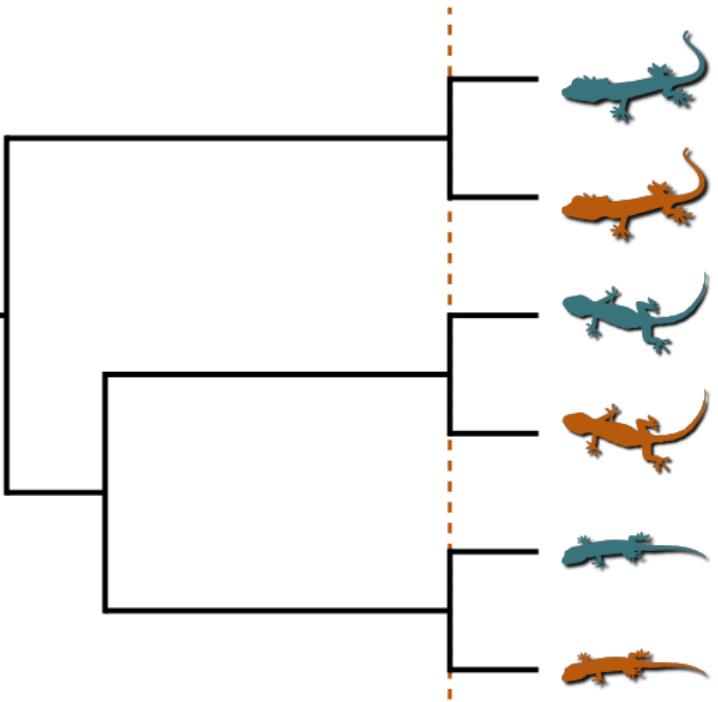
Click here for a sea-level  
animation of SE Asia

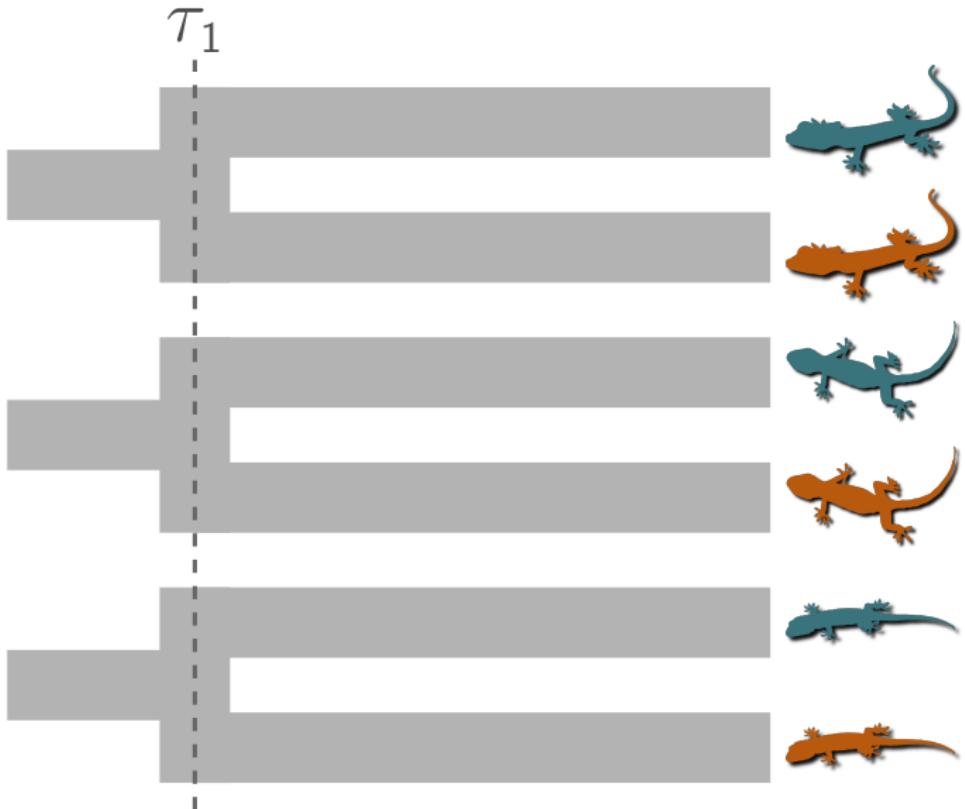
**“Species-pump” Hypothesis** Repeated climate-driven fragmentation of the Philippine Islands was a primary mechanism of speciation for terrestrial fauna

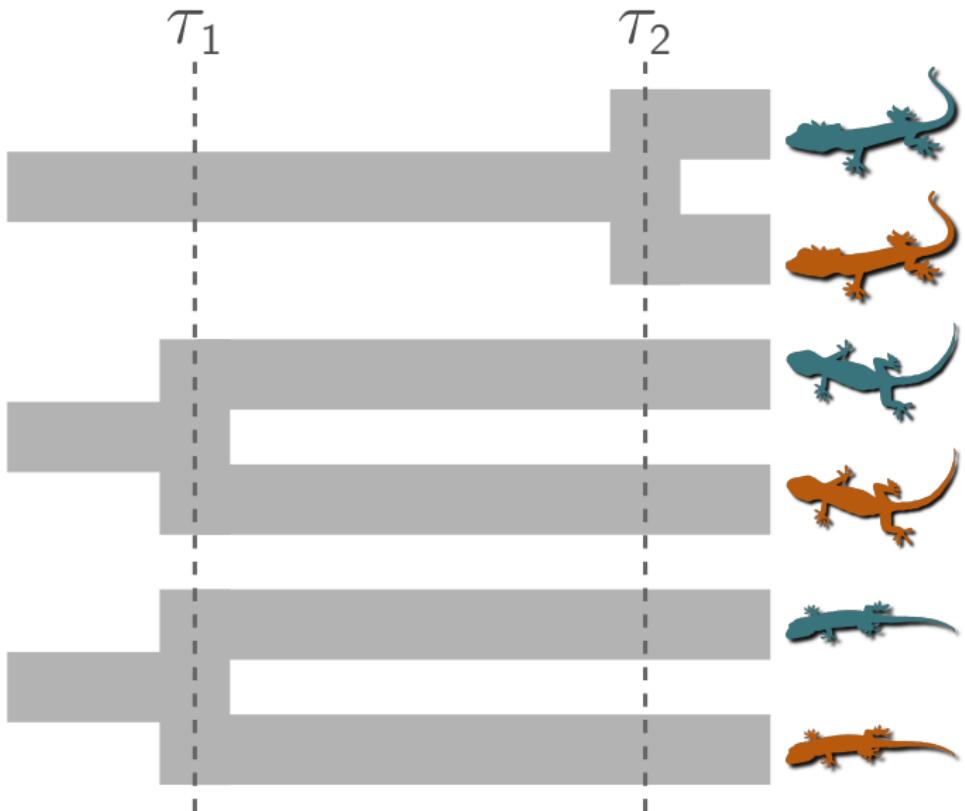
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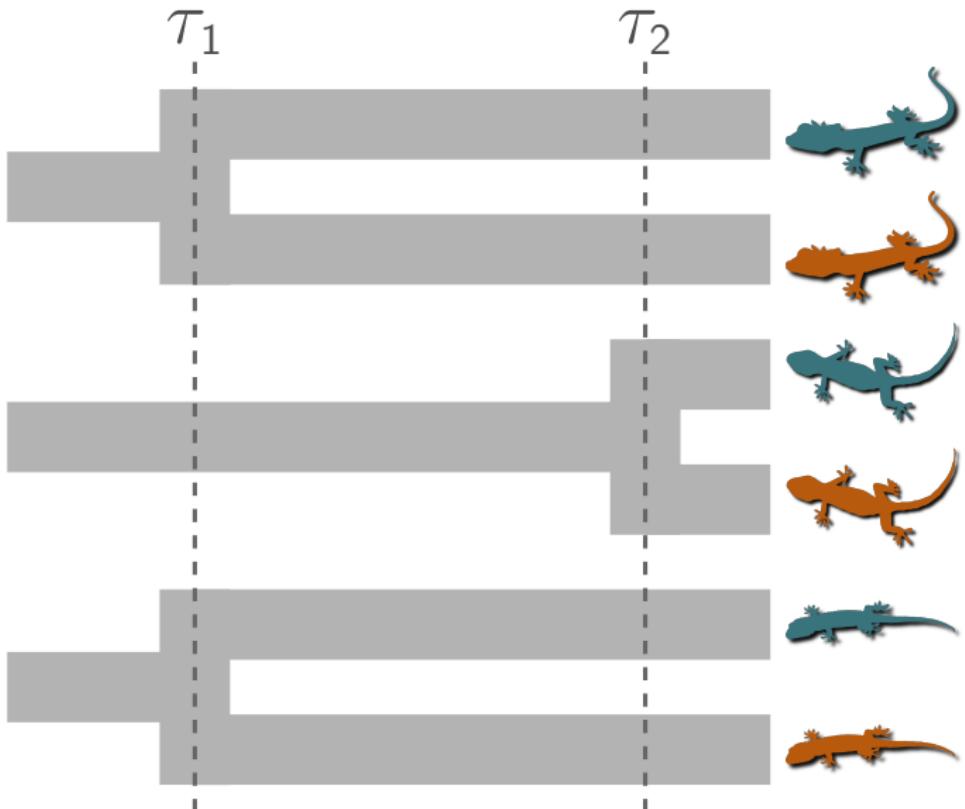
**Prediction** Taxa co-distributed across islands within the same Pleistocene aggregate island complex (PAIC) will have divergence times that tend to be clustered around times when sea levels fragmented the islands

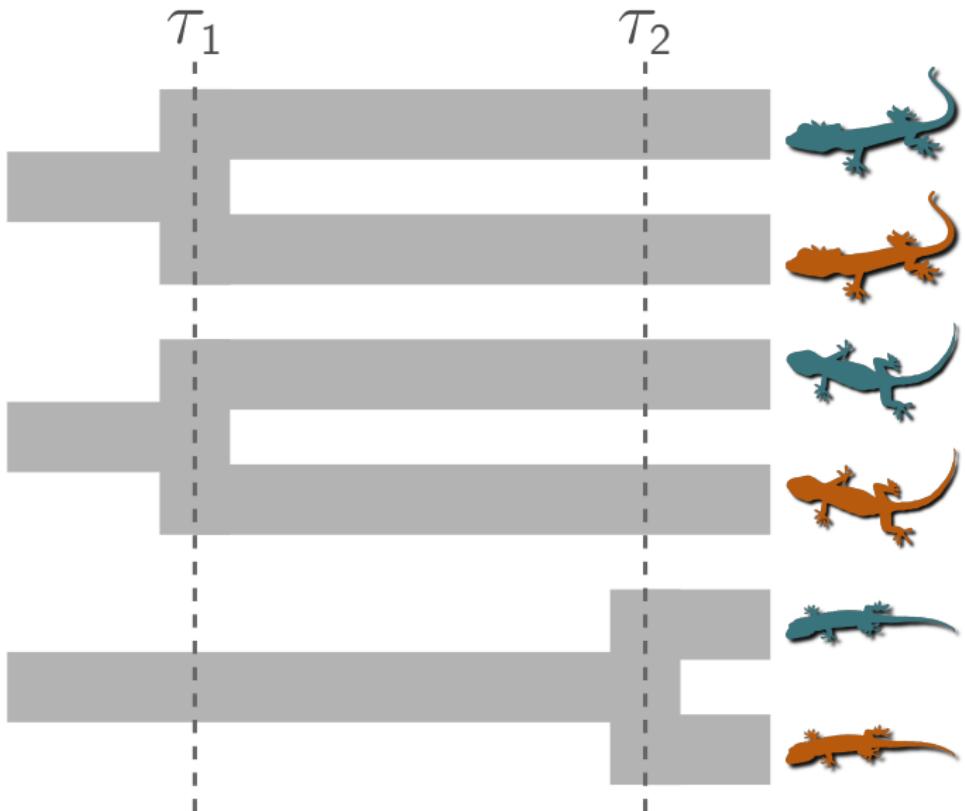


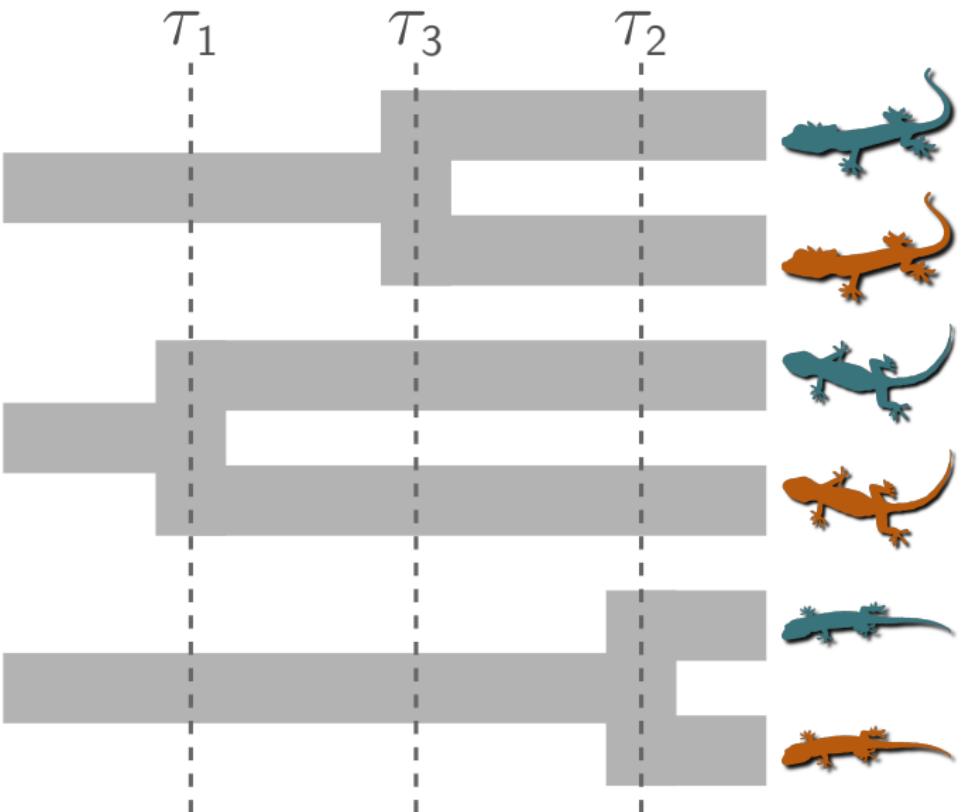












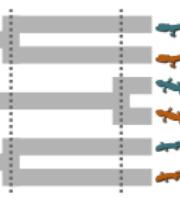
$m_5$



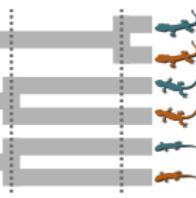
$m_4$



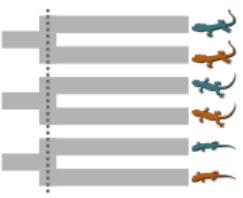
$m_3$

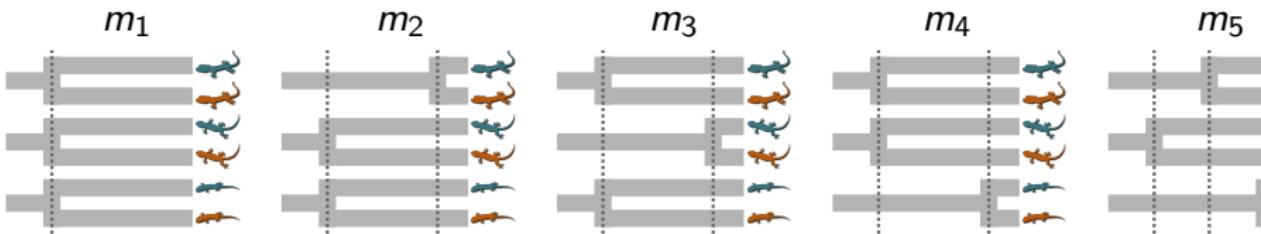


$m_2$



$m_1$





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

## Previous tests of “species-pump”

- ▶ Oaks et al. (2013)<sup>1</sup> collected mitochondrial DNA sequences from 22 pairs of populations (including bats, shrews, skinks, geckos, snakes, and frogs)

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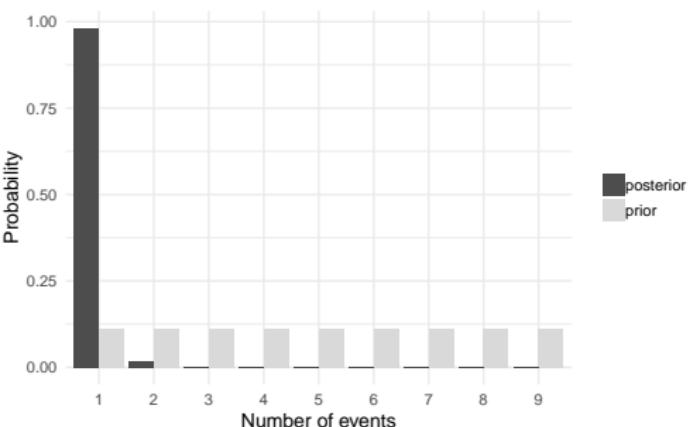
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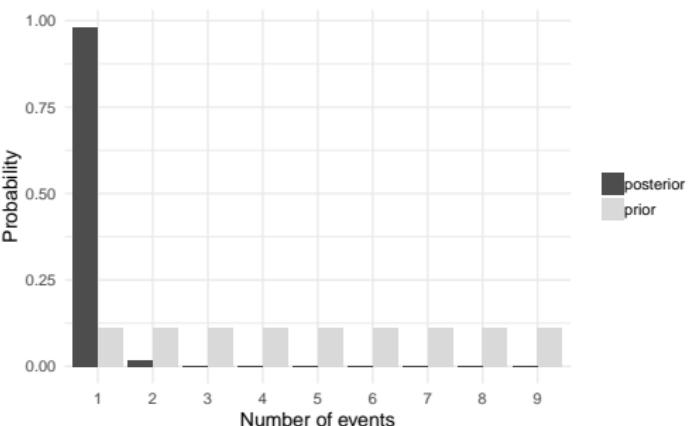
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  - ▶ But, method was very sensitive to prior assumptions and often biased toward estimating co-divergences



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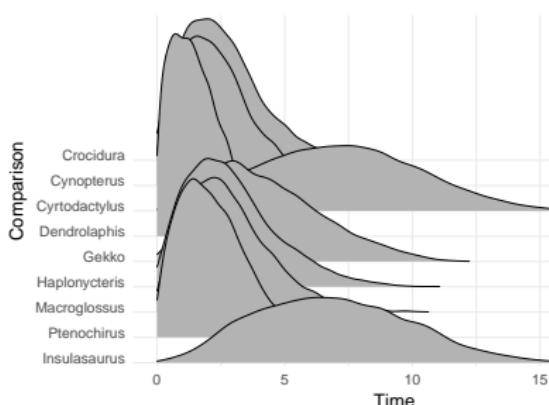
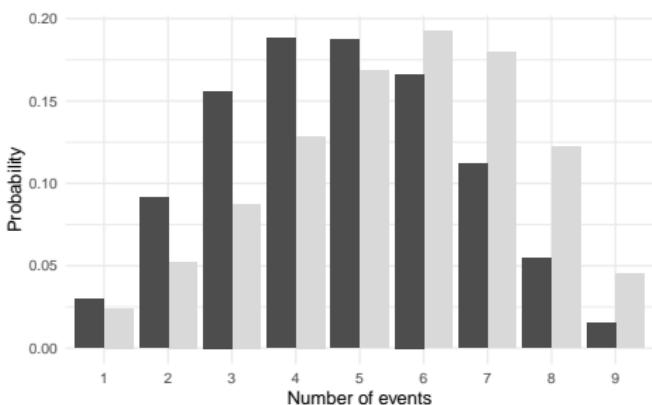
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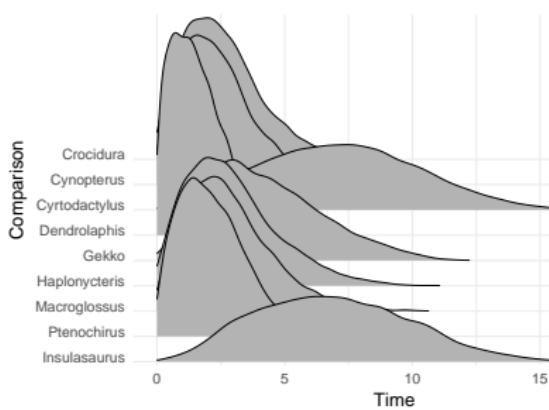
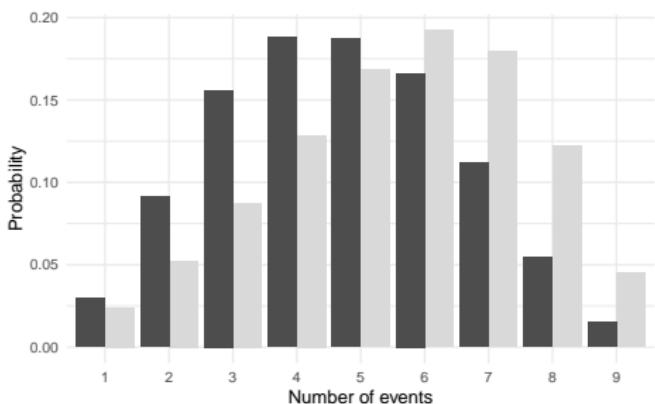
- ▶ Oaks (2014)<sup>1</sup> reanalyzed the data from Oaks et al. (2013)<sup>2</sup> with a modified ABC method dpp-msbayes
  - ▶ New method was less biased, but little information in summary statistics to inform divergence times



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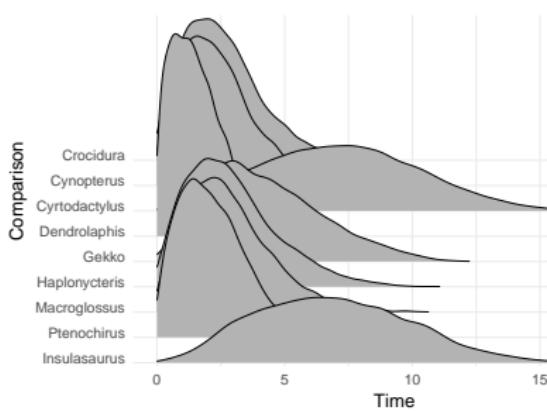
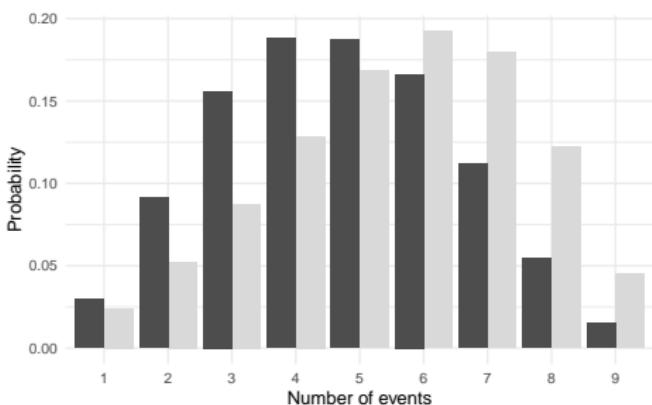


What now? We need **more data** and/or an **improved method** that better utilizes the information in those data.

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What now? We need **more data** and/or an **improved method** that better utilizes the information in those data. **Our goal is to do both.**

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# *Cyrtodactylus* (Gekkonidae)

- ▶ 265+ species across Asia
- ▶ 10+ species across Philippines
- ▶ Nocturnal, scansorial lizards that eat terrestrial invertebrates
- ▶ Specialized bent toes for climbing

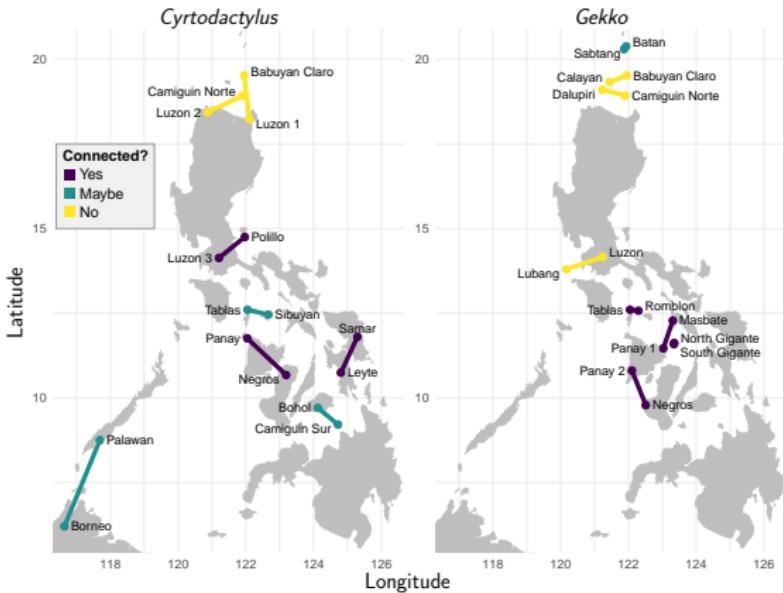


## *Gekko* (Gekkonidae)

- ▶ 60+ species across Southeast Asia
- ▶ 14+ species across Philippines
- ▶ Nocturnal, scansorial lizards that eat terrestrial invertebrates
- ▶ Subdigital lamellae for climbing



# Methods



- ▶ Sampled individuals from 8 pairs of populations for both *Cyrtodactylus* and *Gekko*
  - ▶ Sampled 2–5 individuals per population
- ▶ Collected genome-wide DNA sequence data from each individual
  - ▶ Restriction-site-associated DNA sequencing (RADseq)

Analyzed RADseq data with full-likelihood Bayesian comparative phylogeographic method:

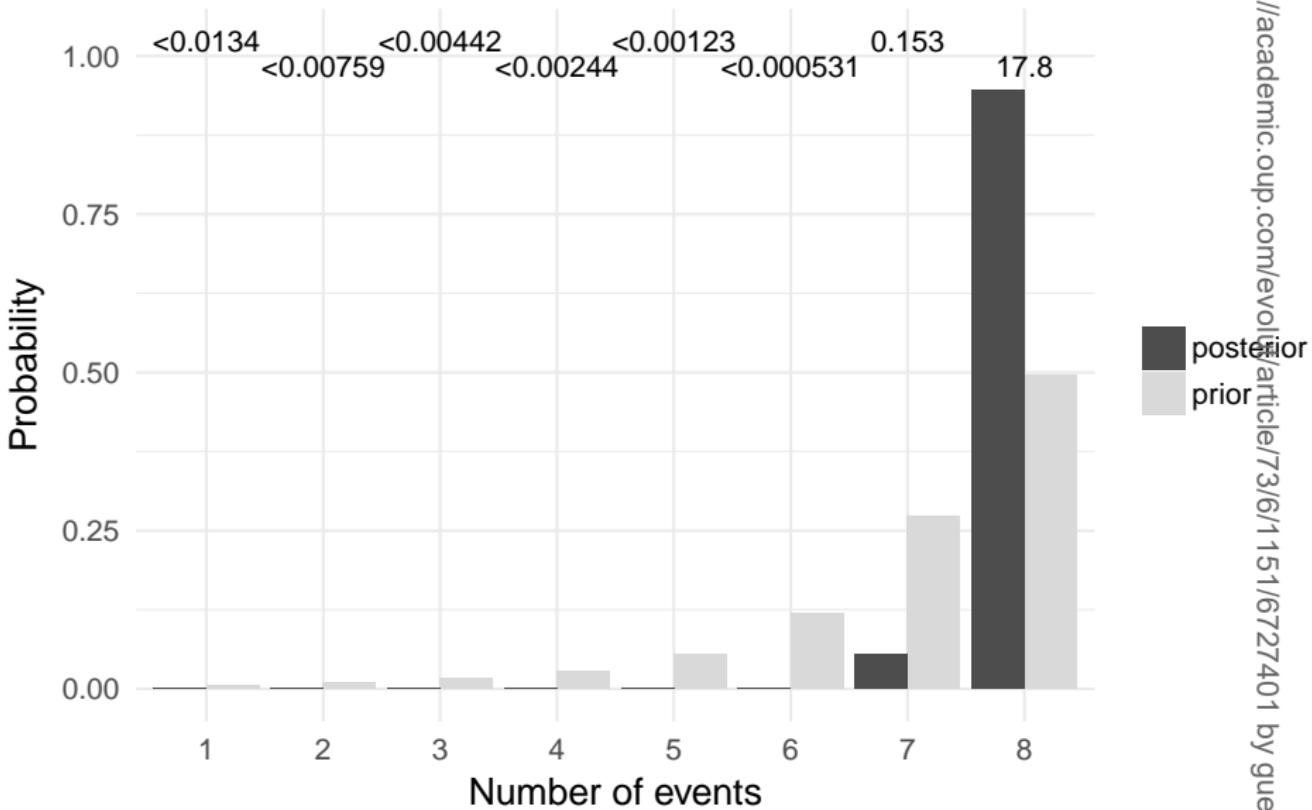
## Ecoevolity: Estimating evolutionary coevality

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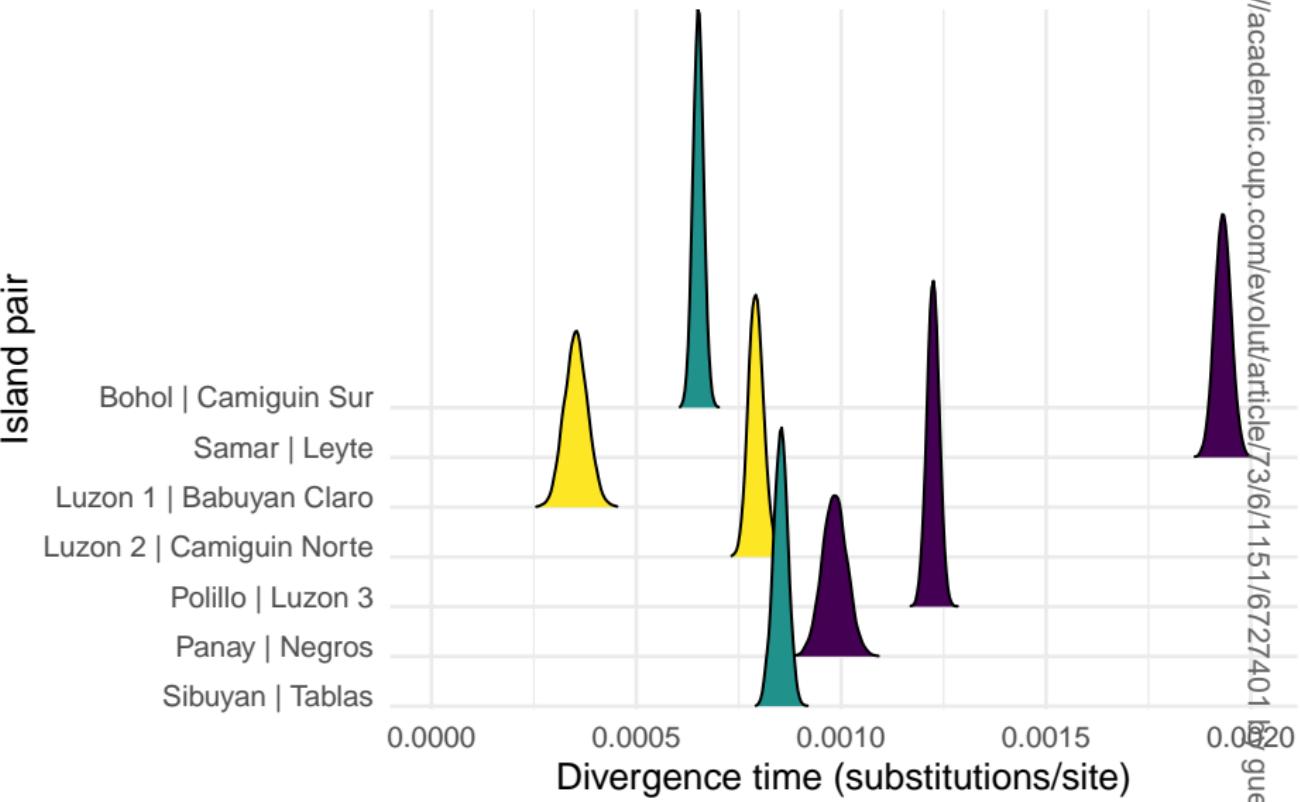
## Ecoevolity: Estimating evolutionary coevolutivity

- ▶ Used simulations to assess how well ecoevolity works given the gekkonid RADseq data sets

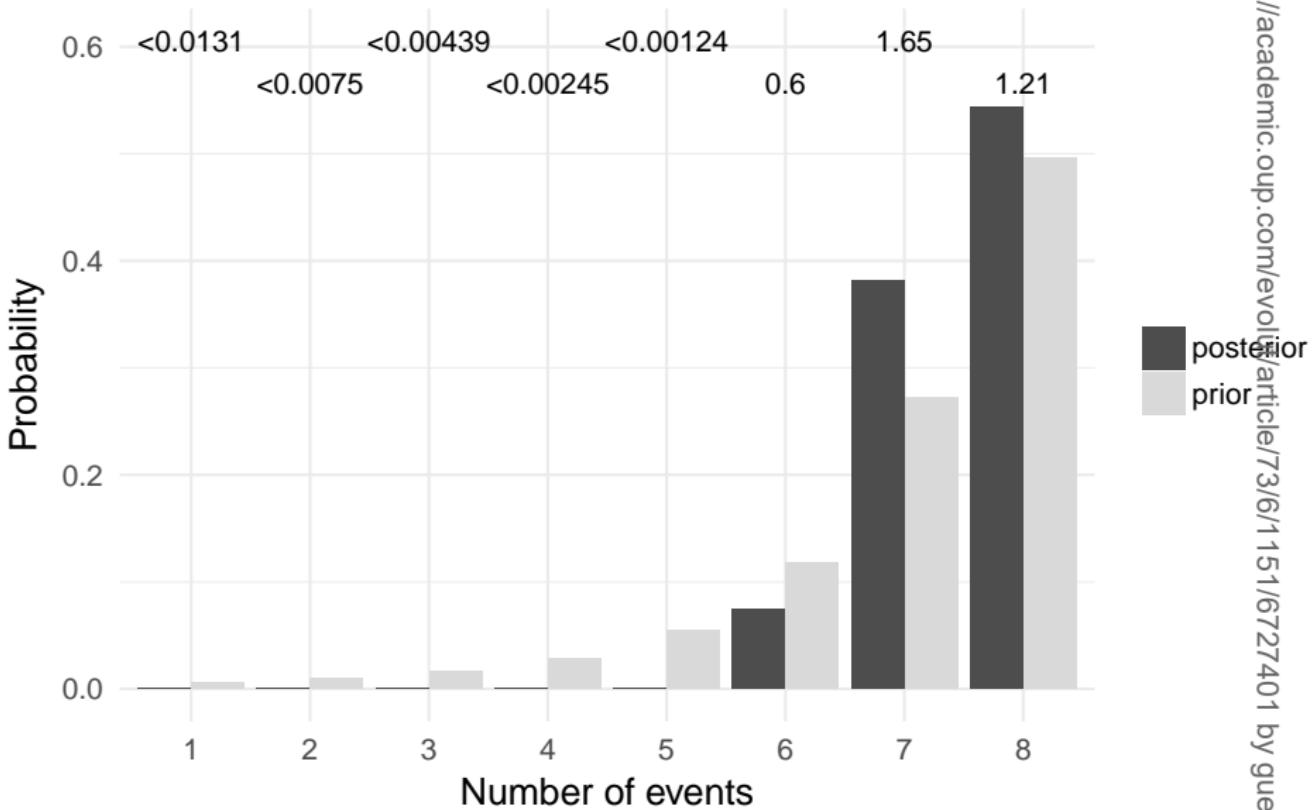
## Results: *Cyrtodactylus* (Figure 2)



# Results: *Cyrtodactylus* (Figure 3)

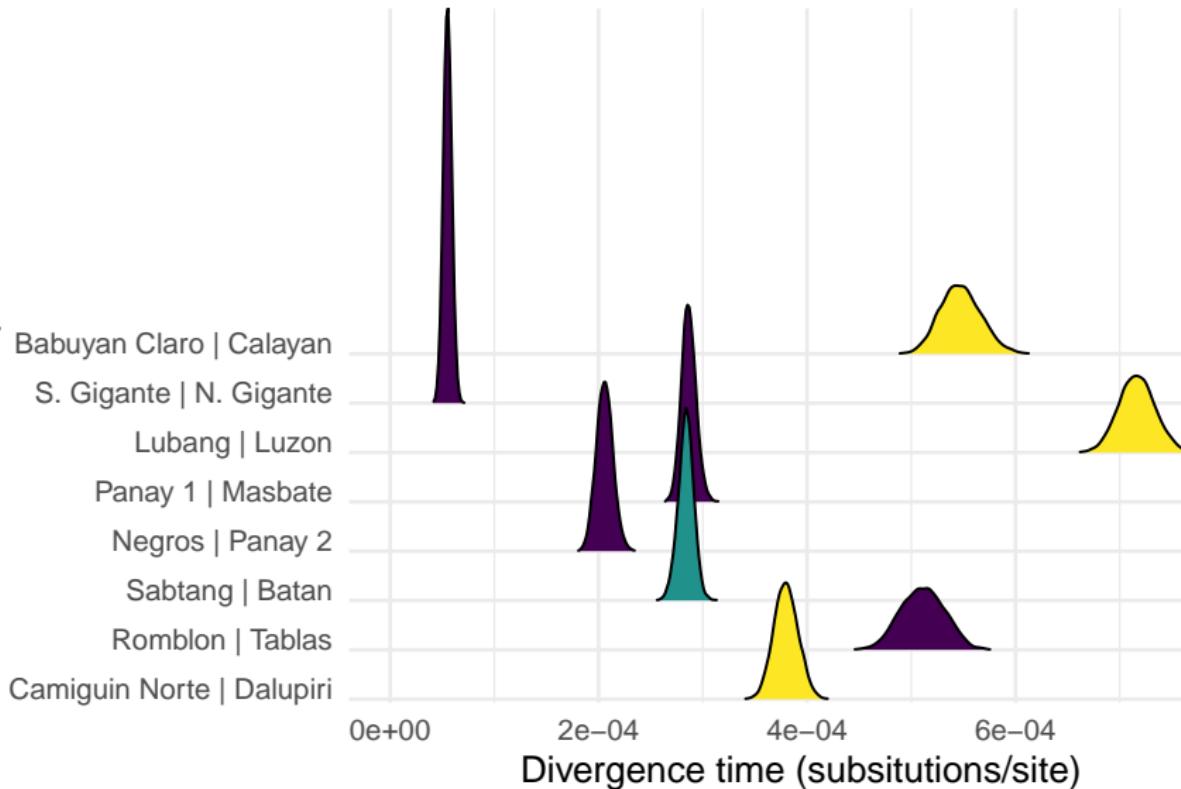


## Results: Gekko (Figure 4)



## Results: Gekko (Figure 5)

Island pair



## Key findings

- ▶ Strong support that all 8 pairs of *Cyrtodactylus* populations diverged independently

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- ▶ Strong support that all 8 pairs of *Cyrtodactylus* populations diverged independently
- ▶ Weak support that all 8 pairs of *Gekko* populations diverged independently
- ▶ Simulation results suggest ecoevolvity can accurately estimate the timing and number of divergences given the gekkonid RADseq data

## Caveats

- ▶ Too few island pairs to rule out climate-driven vicariant speciation
- ▶ Differences in divergence times could be due to variation in fragmentation times among island pairs
- ▶ Differences in divergence could also be due to variation in mutation rates

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- ▶ Too few island pairs to rule out climate-driven vicariant speciation
- ▶ Differences in divergence times could be due to variation in fragmentation times among island pairs
- ▶ Differences in divergence could also be due to variation in mutation rates
  
- ▶ Seems safe to conclude that the “species-pump” is not the rule for gekkonids, but maybe the exception

## Take home points

- ▶ Support against the “species-pump” hypothesis

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- ▶ Results suggest repeated cycles of climate-driven island fragmentation were not an important mechanism of speciation for gekkonid lizards in the Philippines

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- ▶ Support against the “species-pump” hypothesis
- ▶ Results suggest repeated cycles of climate-driven island fragmentation were not an important mechanism of speciation for gekkonid lizards in the Philippines
- ▶ Rare over-water dispersal via rafting on vegetation is likely an important mechanism responsible for the distribution of gekkonid lizards in the Philippines

# Everything is on GitHub...

Software:

- ▶ Ecoevolity: <https://github.com/phyletica/ecoevolity>

Open-Science Notebook:

- ▶ Gecko RADseq: <https://github.com/phyletica/gekgo>

# Acknowledgments

## Ideas and feedback:

- ▶ Phyletica Lab (the Phyleticians)
- ▶ Constructive feedback from Editor-in-Chief Mohamed Noor, Associate Editor David Weisrock, and four anonymous reviewers greatly improved this work

## Lab work:

- ▶ Patrick Monnahan and John Kelly for their help with the MSG libraries

## Computation:

- ▶ Alabama Supercomputer Authority
- ▶ Auburn University Hopper Cluster

## Funding:



## Photo credits:

- ▶ Rafe Brown and Cam Siler
- ▶ PhyloPic!

# Questions?

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[phyletica.org](http://phyletica.org)



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Figure 6

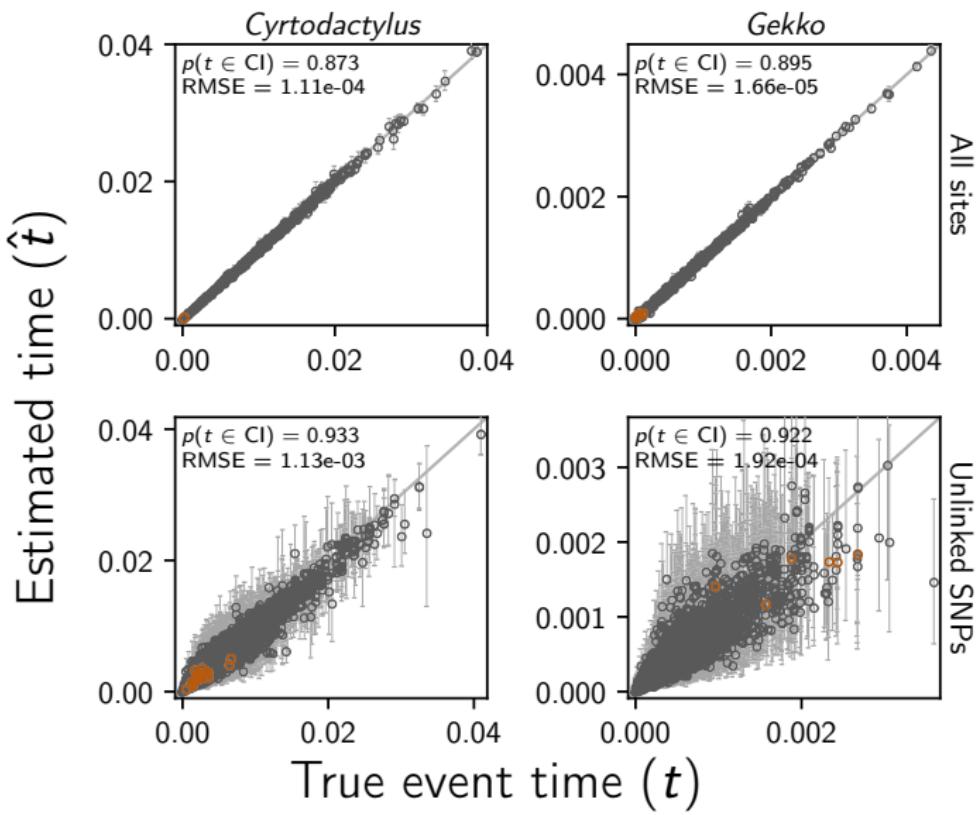
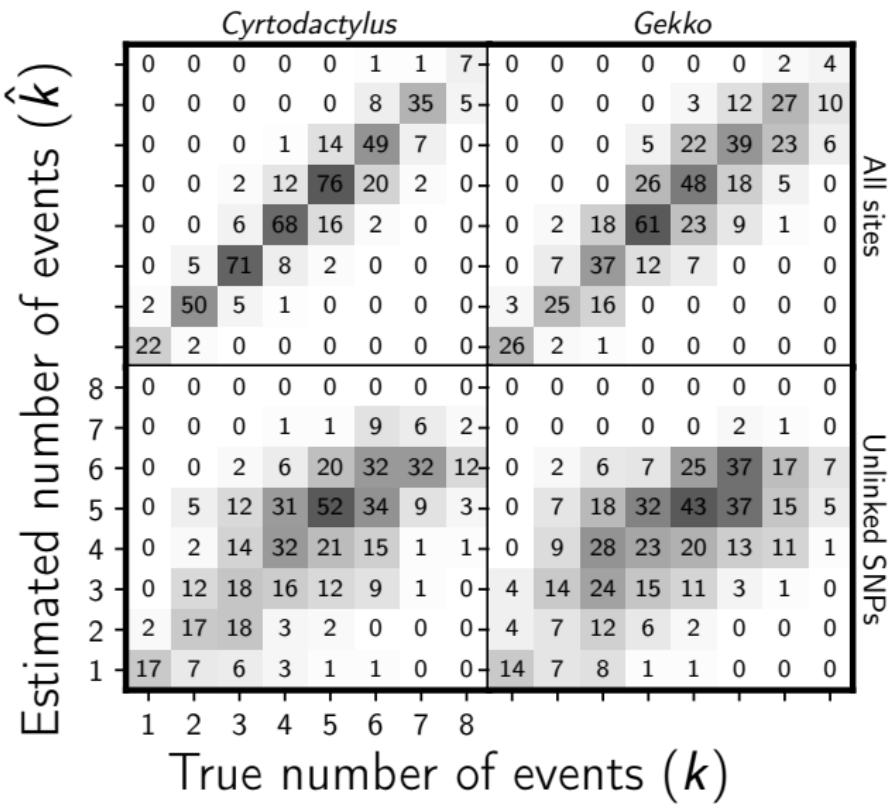
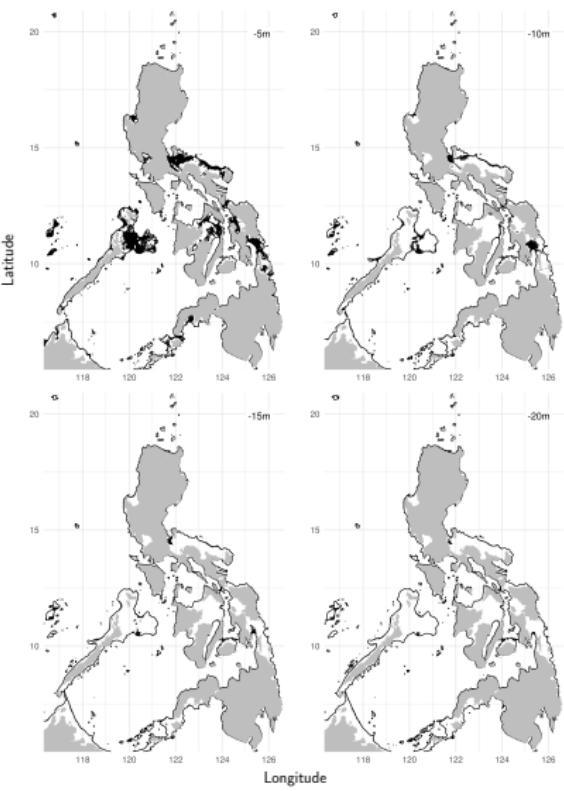


Figure 7



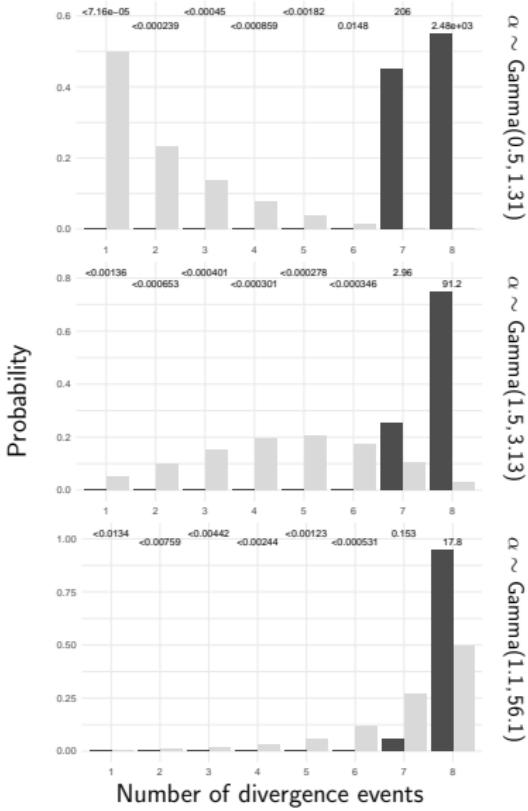
# Figure S1



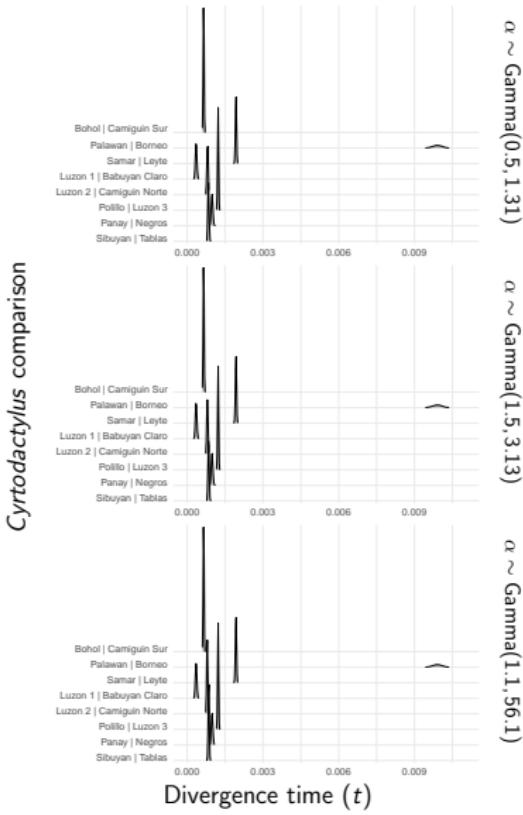
## Figure S2

[Click here for a sea-level animation of SE Asia](#)

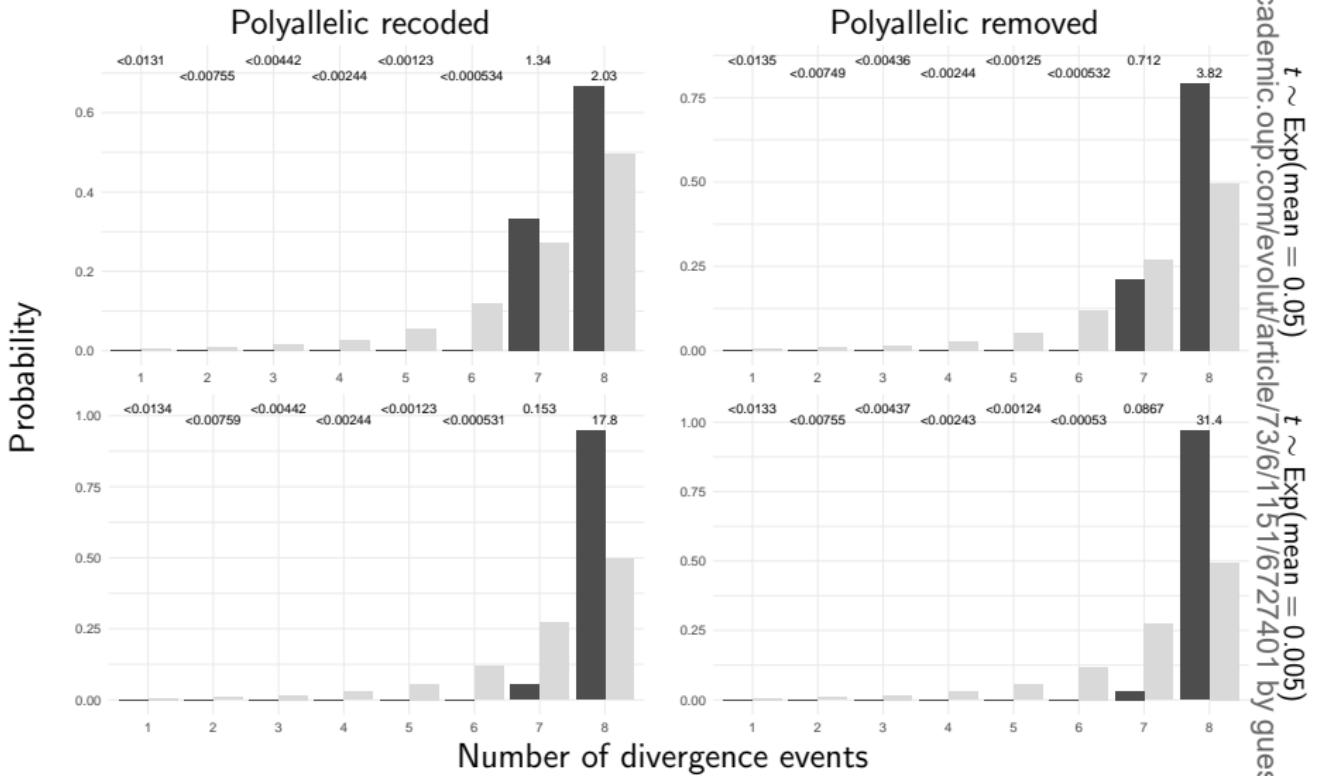
# Figure S3



# Figure S4



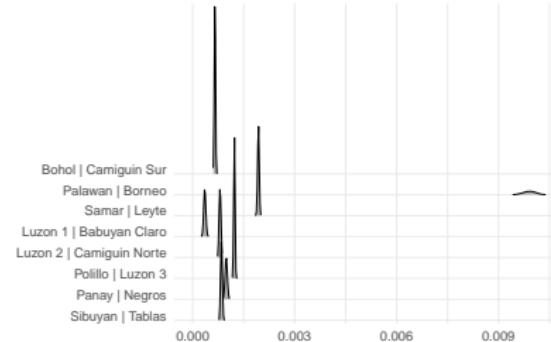
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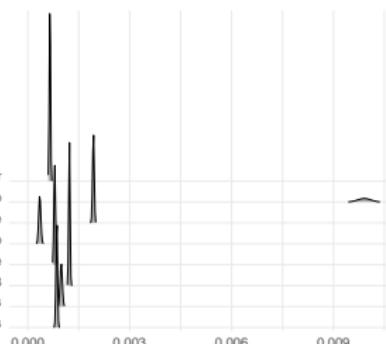
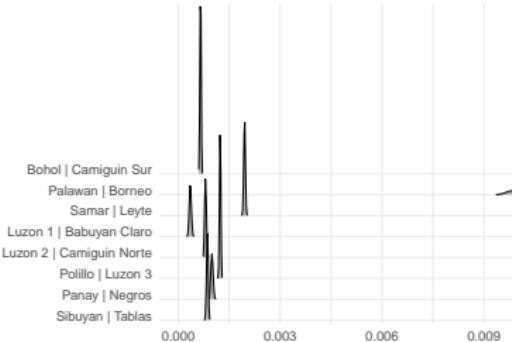
# Figure S6

Cytochrome *c* comparison

Polyallellic recoded

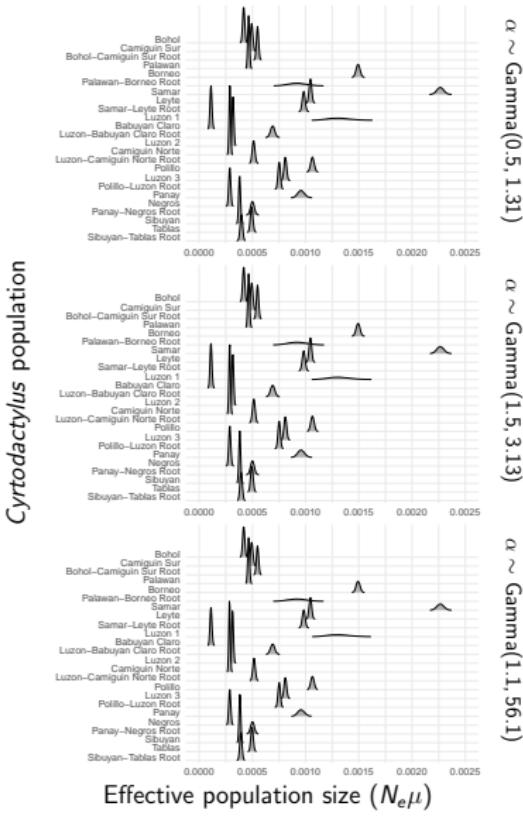


Polyallellic removed



Divergence time ( $t$ )

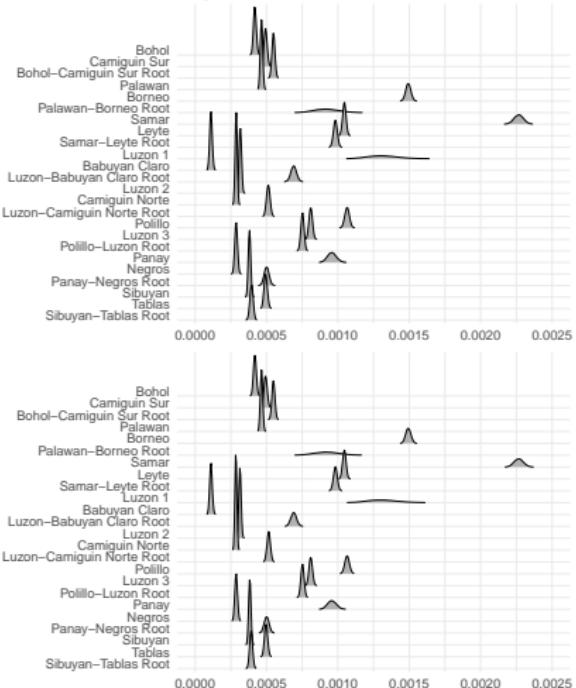
Figure S7



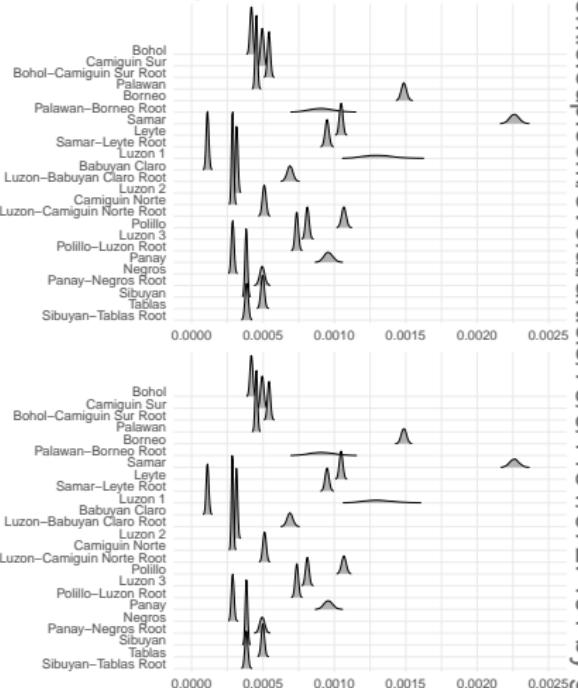
# Figure S8

Cyrtodactylus comparison

## Polyallelic recoded

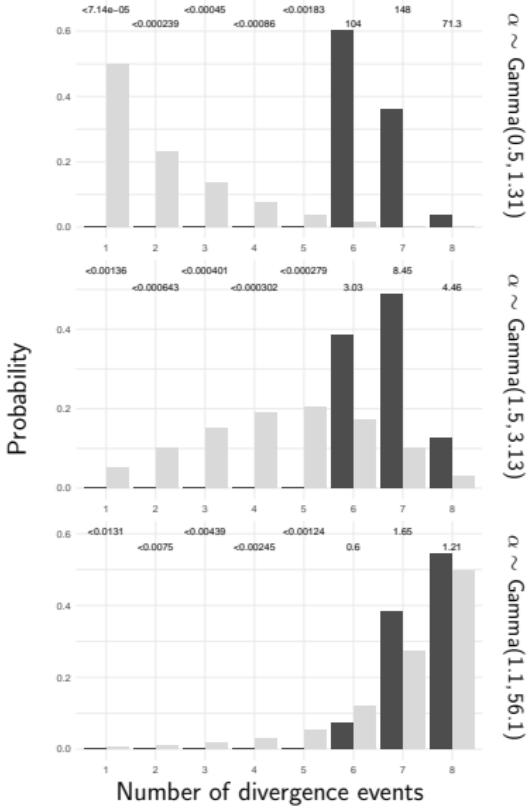


## Polyallelic removed

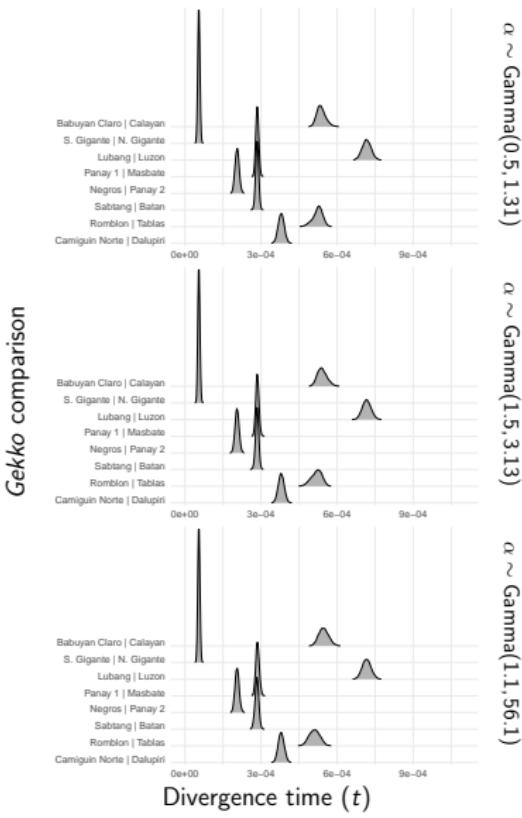


Effective population size ( $N_e\mu$ )

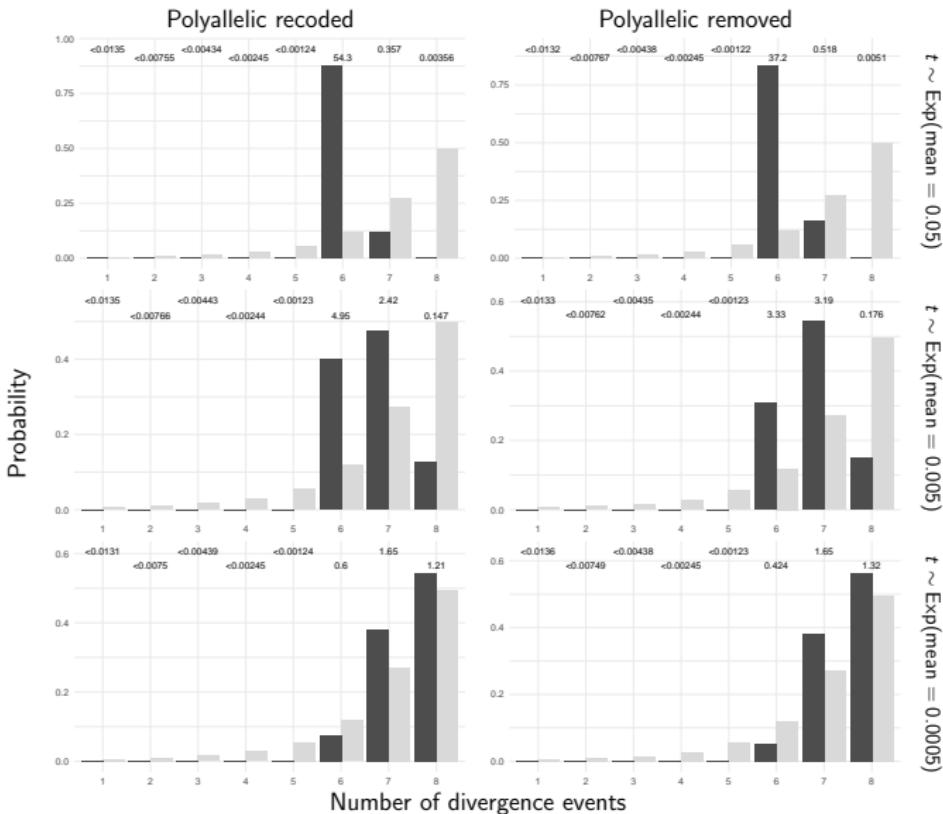
# Figure S9



# Figure S10



# Figure S11



# Figure S12

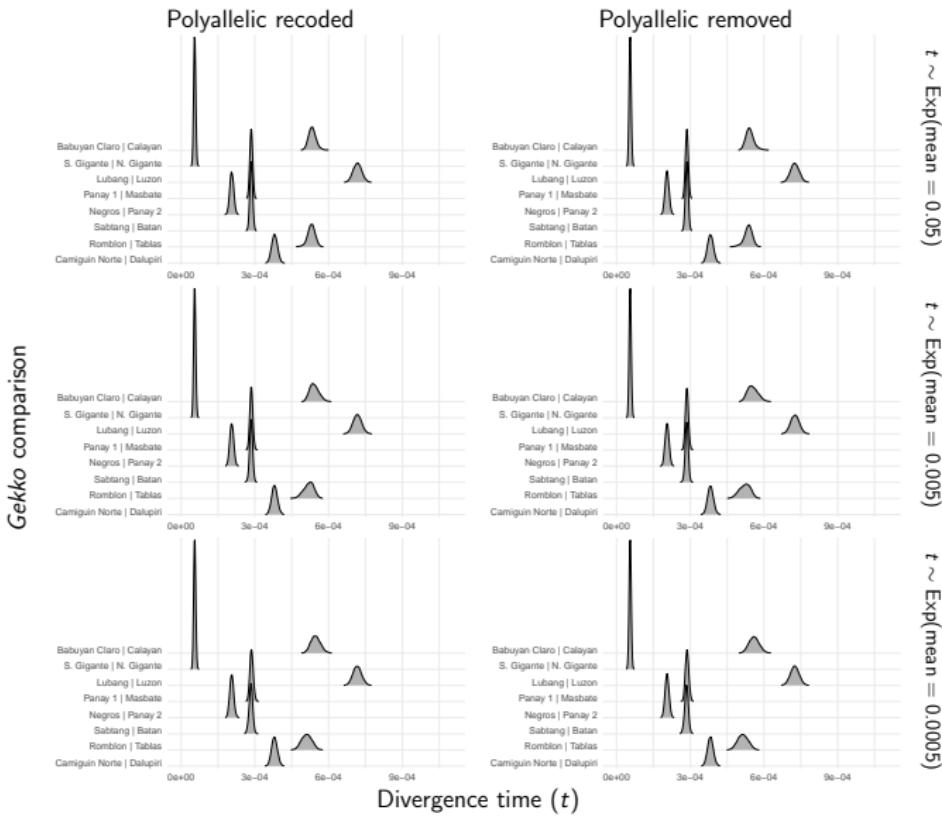


Figure S13

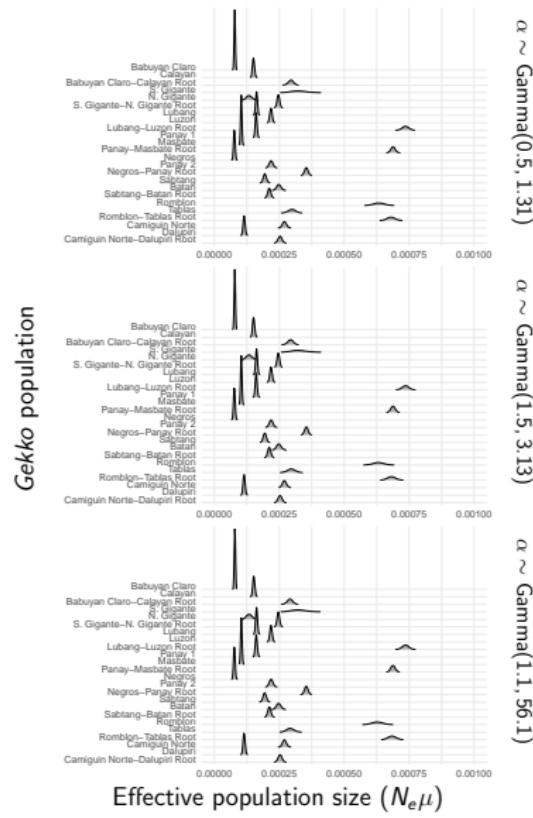


Figure S14

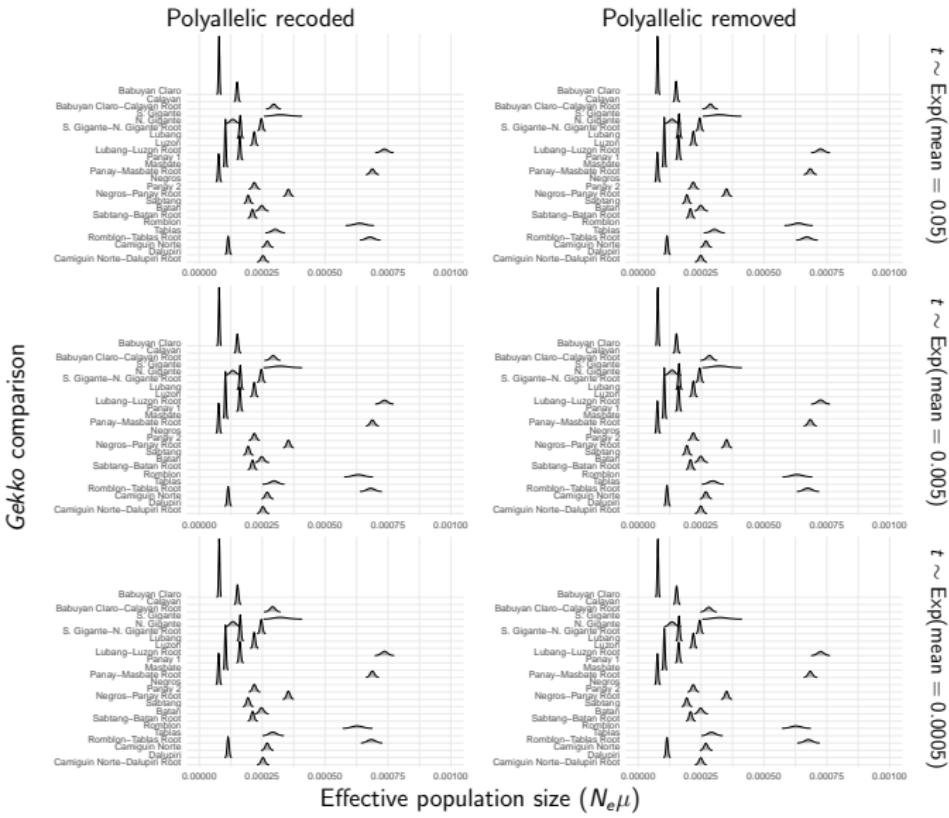


Figure S15

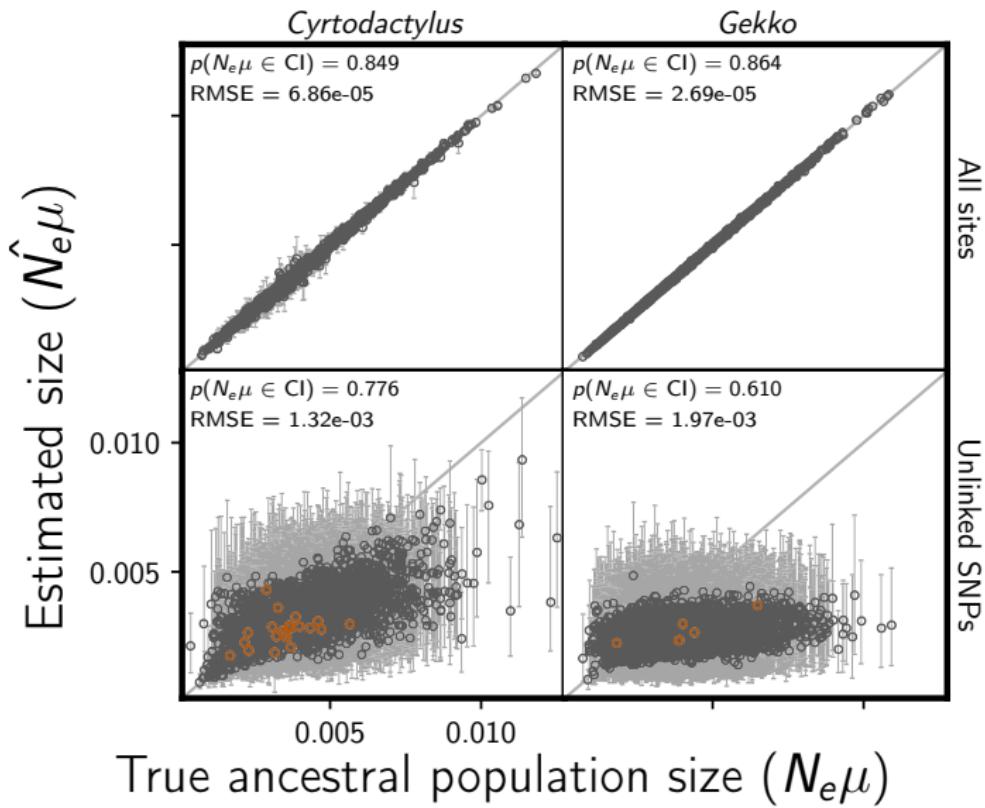
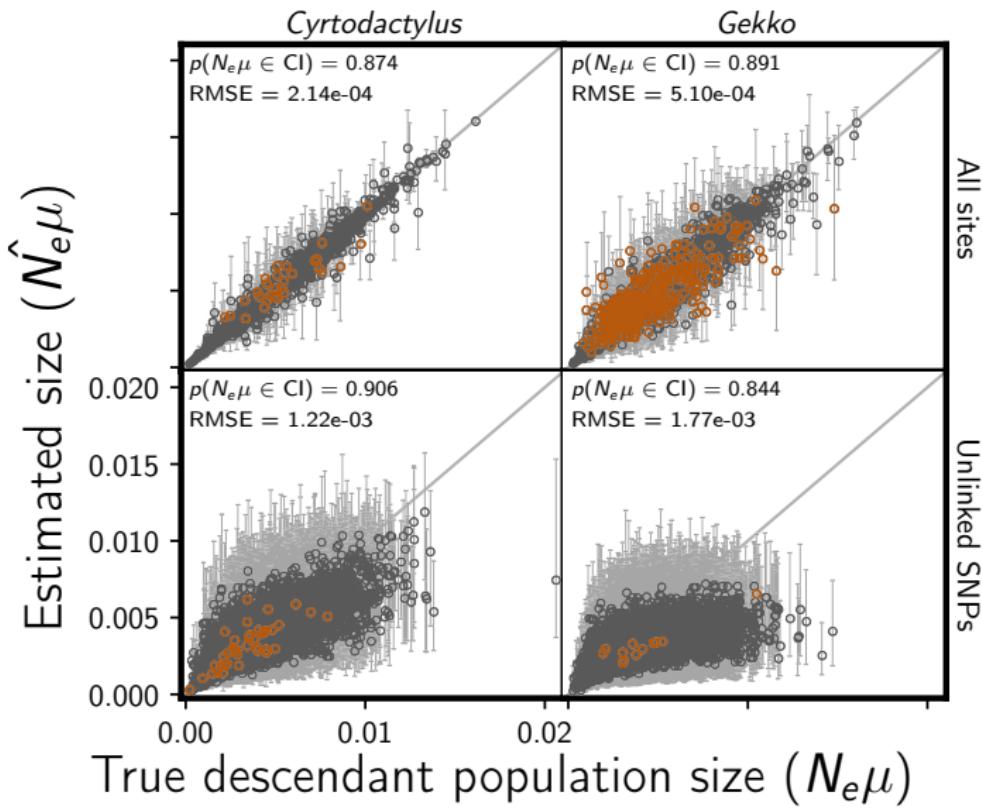


Figure S16



# Figure S17

