

Diversification: basics

The Rules of Macroevolutionary Modeling

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Beware the Sirens of Akaike



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- 3. Simple “old-school” tools often work much better (or are less likely to fail) than fancy new approaches**

The Rules of Macroevolutionary Modeling

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2. Develop healthy skepticism towards fancy “process-based” or “mechanistic” models
3. Simple “old-school” tools often work much better (or are less likely to fail) than fancy new approaches
- 4. Don’t believe any results that you can’t actually see**

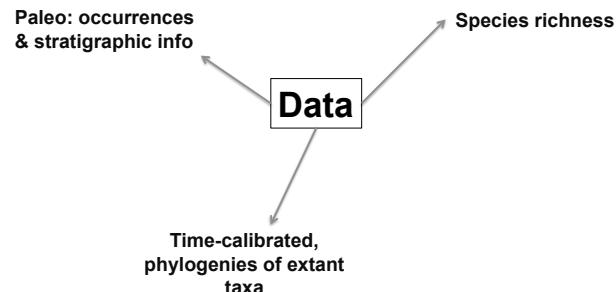
Simple tools to master

- Constant-rate birth-death process*
- Tree simulation*
- Gamma statistic*
- Tree balance statistics*
- Tip-based speciation estimates (equal splits)*
- Sister-clade comparisons*

Phylogenetic diversification: general questions

- Key questions:
- What is the rate of speciation? Rate of extinction?**
 - Why does species richness vary among groups?**
 - What controls diversity?**
 - How do traits etc affect species diversification?**

Taxonomy of *data* for diversification analyses

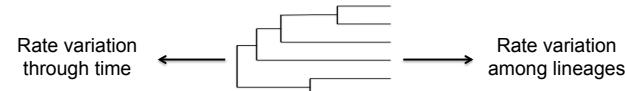


Terminology basics

Speciation
extinction
net diversification
relative extinction

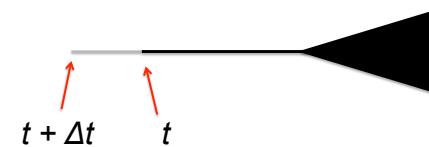
Waiting time
Reconstructed phylogeny
Pure-birth process (yule process)
Birth-death process

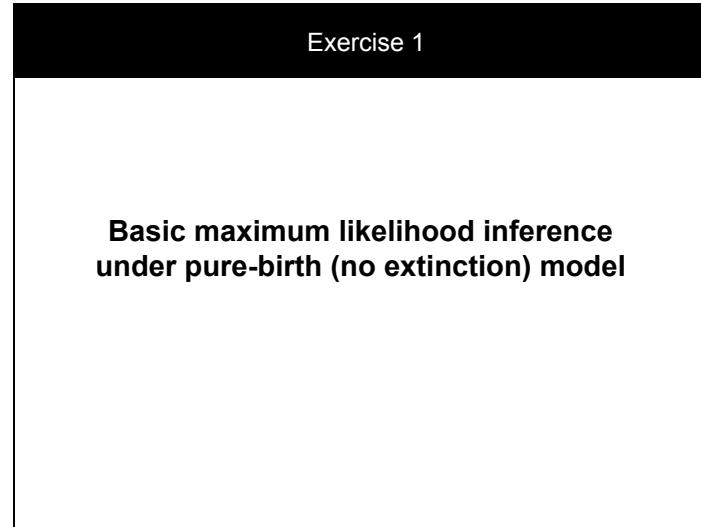
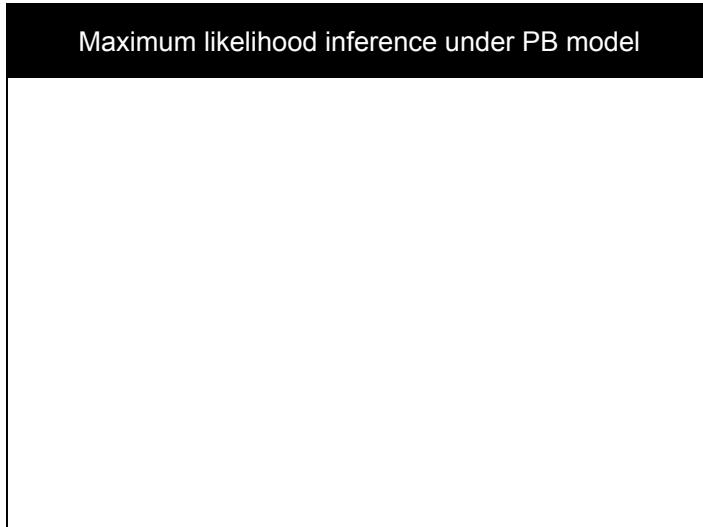
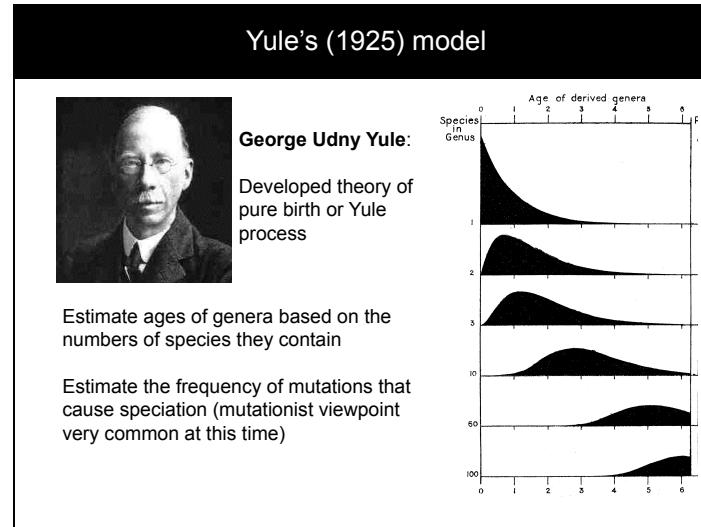
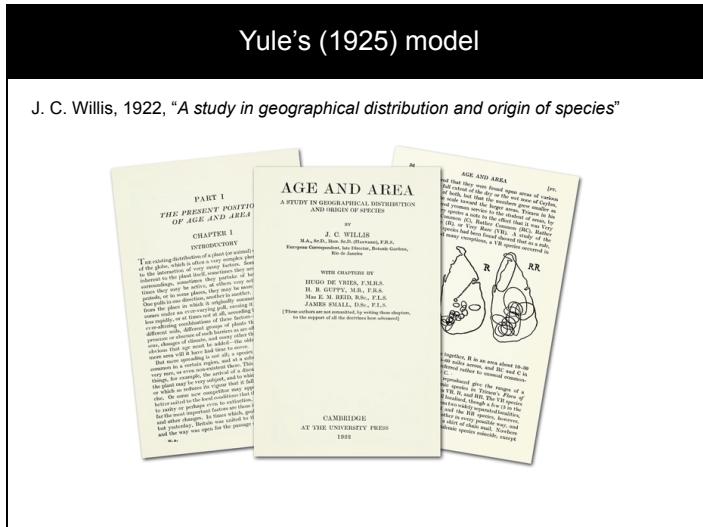
Conceptually: why are we doing these analyses?



Stochastic process #1: The “pure-birth” process

Derivation of the pure-birth process



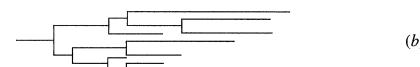


Birth-death process

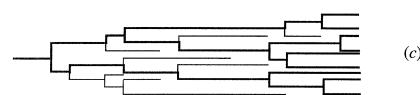
The Markov model for the pure birth process can easily be extended to the *birth-death* process.

Types of trees

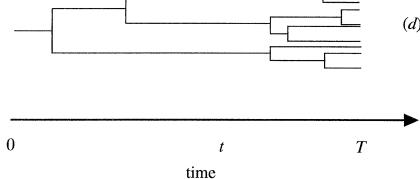
The *complete tree*
(extinct)



The *complete tree*
(extant)



The *reconstructed*
phylogenetic tree



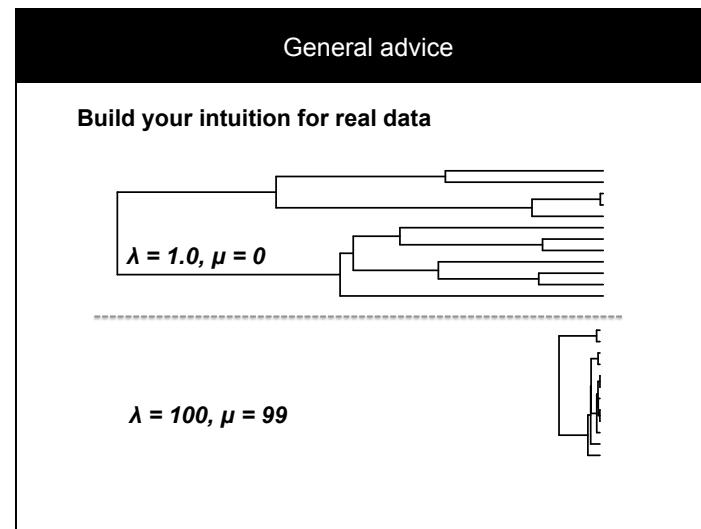
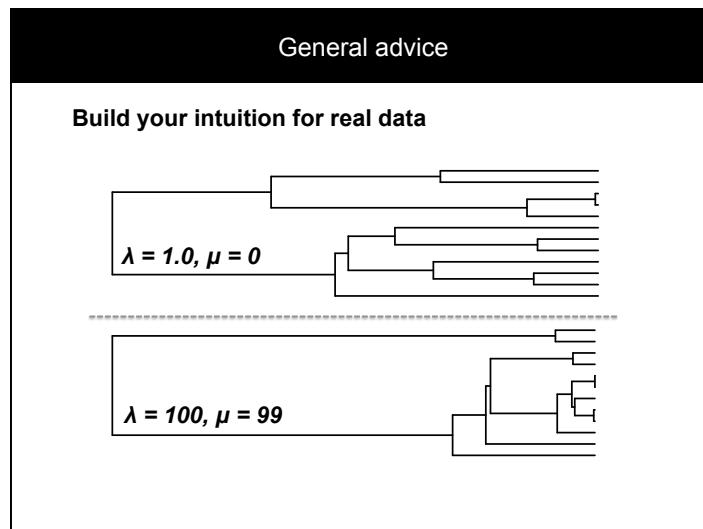
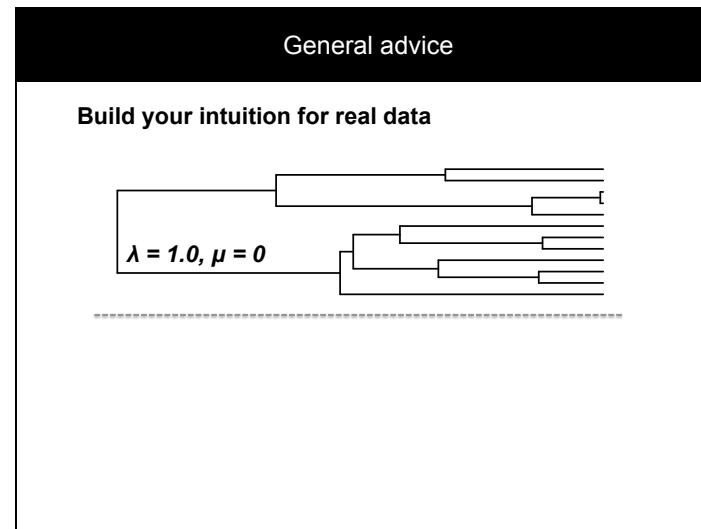
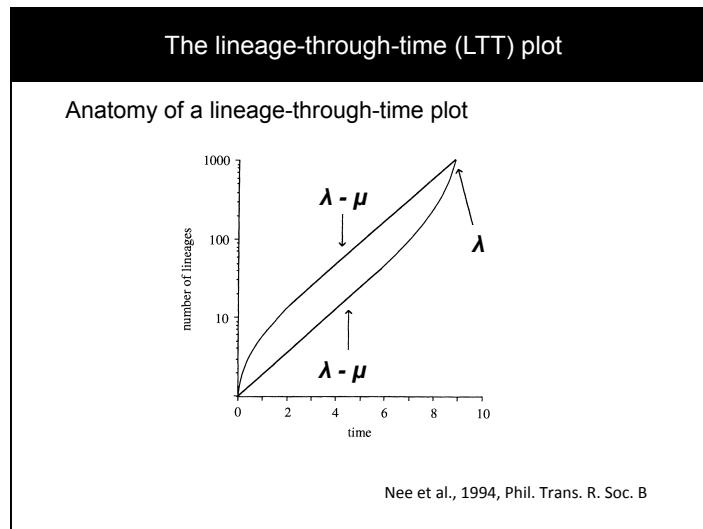
Likelihood of tree under *reconstructed* BD process

The reconstructed evolutionary process

SEAN NEE, ROBERT M. MAY AND PAUL H. HARVEY
A.F.R.C. Unit of Ecology and Behaviour, Department of Zoology, University of Oxford, South Parks Road, Oxford OX1 3PS, U.K.

Phil. Trans. R. Soc. B. 1994

Shapes of phylogenetic trees under simple models



Exercise 2

Phylogenetic tree simulation and lineage-through-time plots

Exercise 3

How well can we infer speciation & extinction under constant-rate birth-death process?

Exercise 3, part i

Basic maximum likelihood inference on simulated trees

First: simulate a tree under birth-death model:

```
simulateTree(....)
```

Then: fit constant-rate birth-death process:

```
fitCRBD(....)
```

Exercise 3, part ii

How well can we infer speciation & extinction under constant-rate birth-death process?

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How well can we infer speciation & extinction under constant-rate birth-death process?

Now: simulate 1000 phylogenies of 100 taxa each. Randomly sample a lambda parameter from (0, 5), and a relative extinction parameter from (0, 0.95).

```
lambda <- runif(1, min=0, max = 5)  
samples a single random number from the interval (0, 5)
```

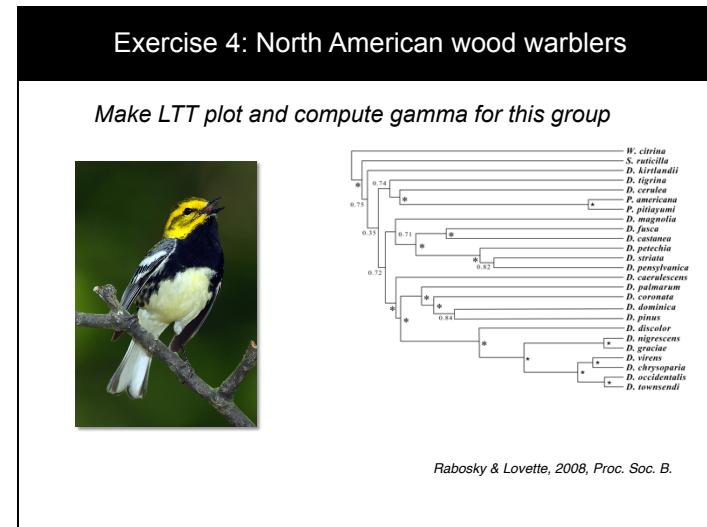
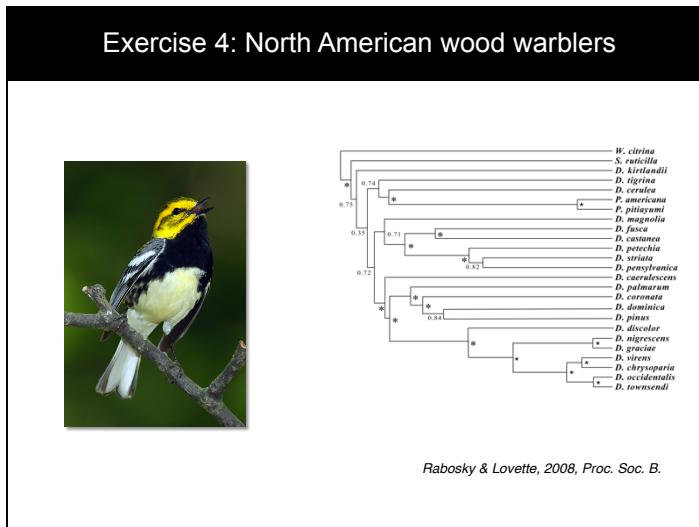
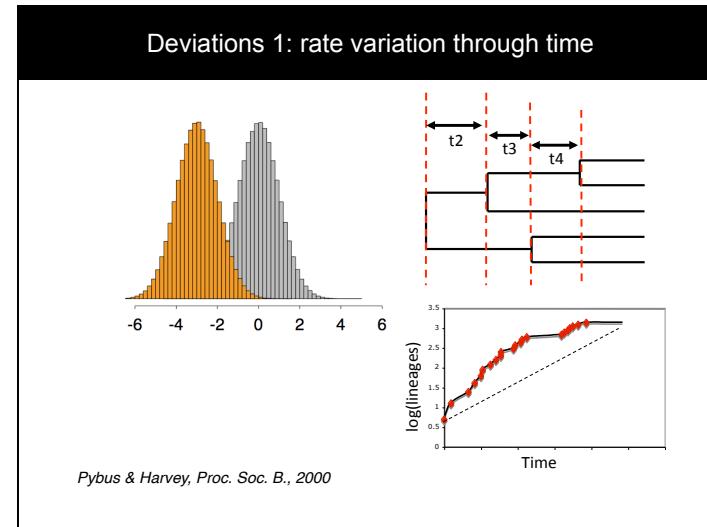
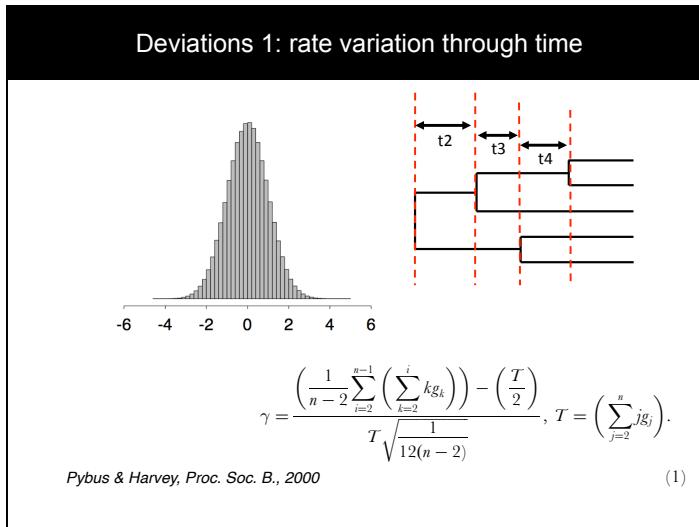
Estimate lambda and mu from each simulation. **Which parameter can you estimate with greater accuracy???**

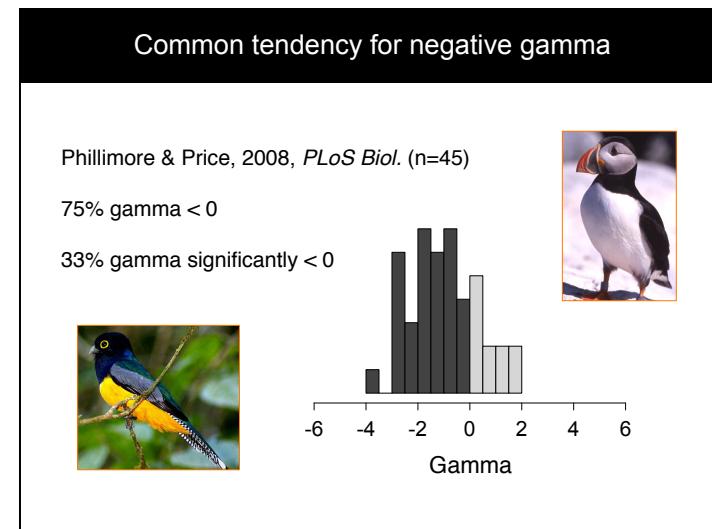
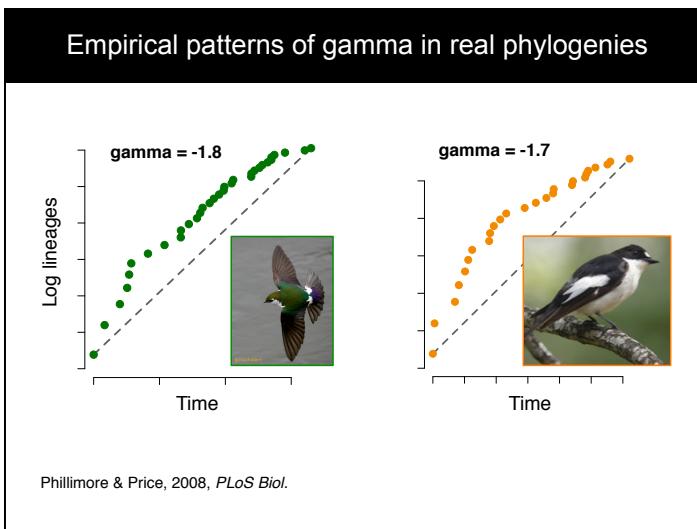
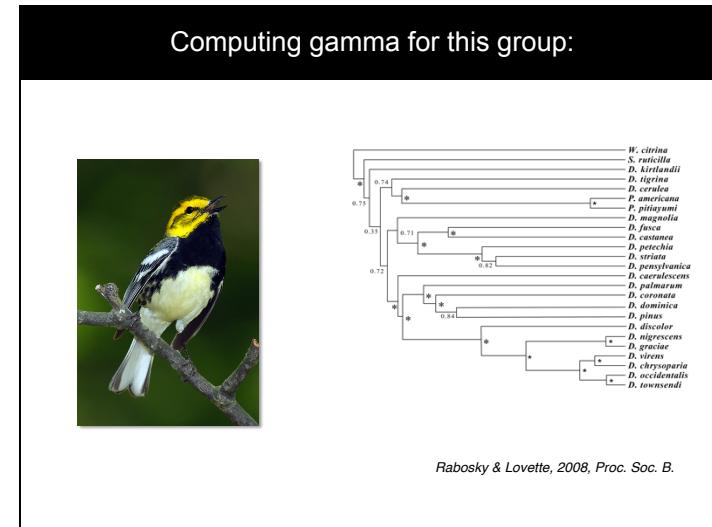
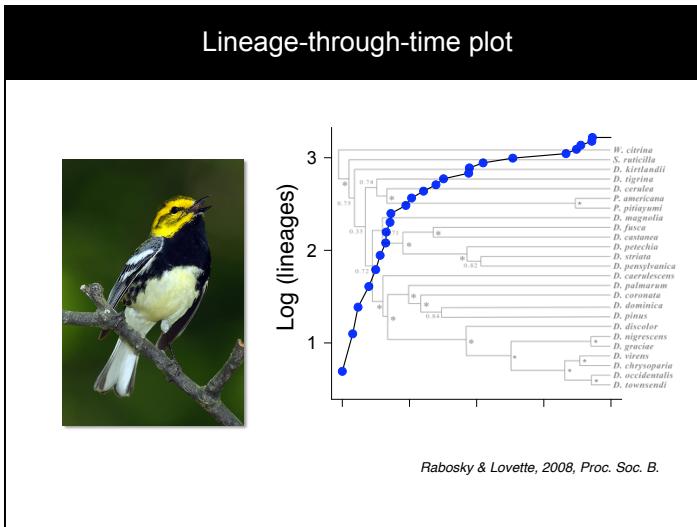
Assumptions of the simple BD model

- (1) Diversification rates do not vary through time
- (2) Diversification rates do not vary among lineages

Variation in rates through time

How does rate variation through time affect LTT plot?



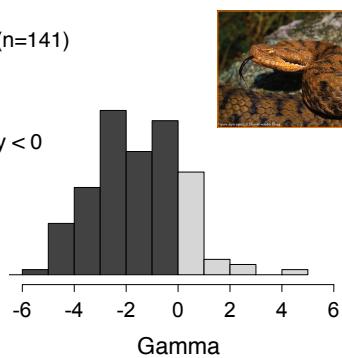


Common tendency for negative gamma

McPeek, 2008, *Am Nat* (n=141)

80% gamma < 0

50% gamma significantly < 0



Exercise 4, part B

Simulate slowdowns in rate of speciation through time and compute gamma statistic

Some factors that bias *rate-through-time* analyses

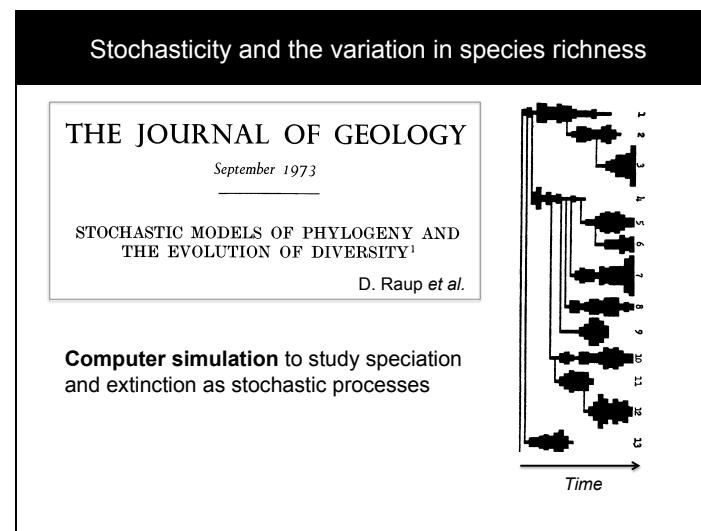
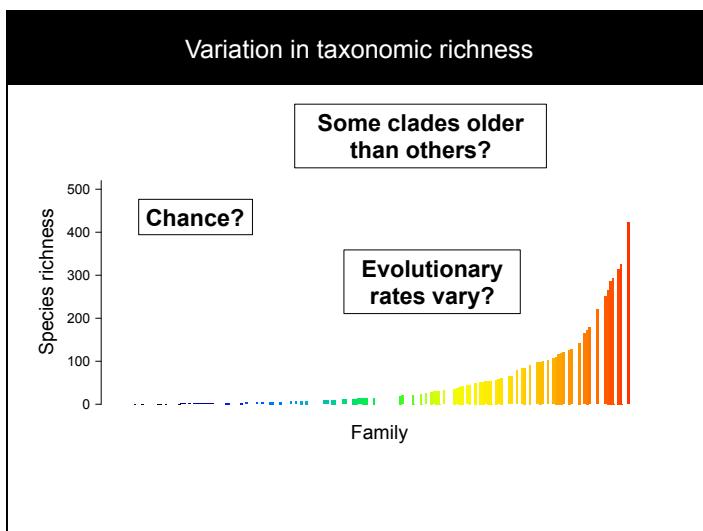
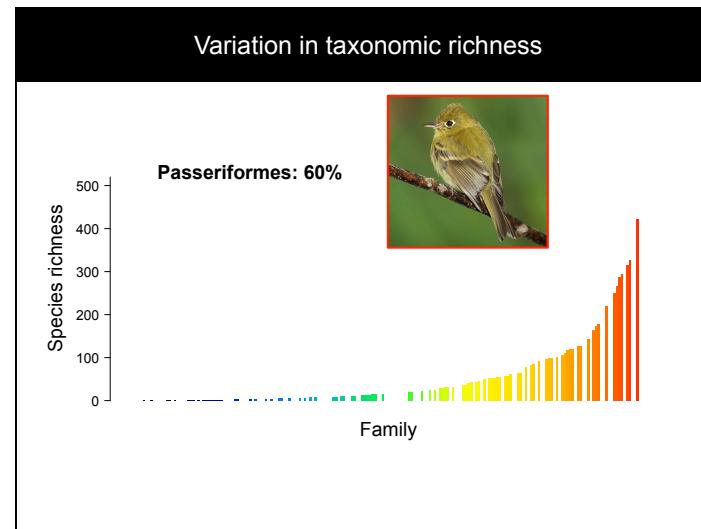
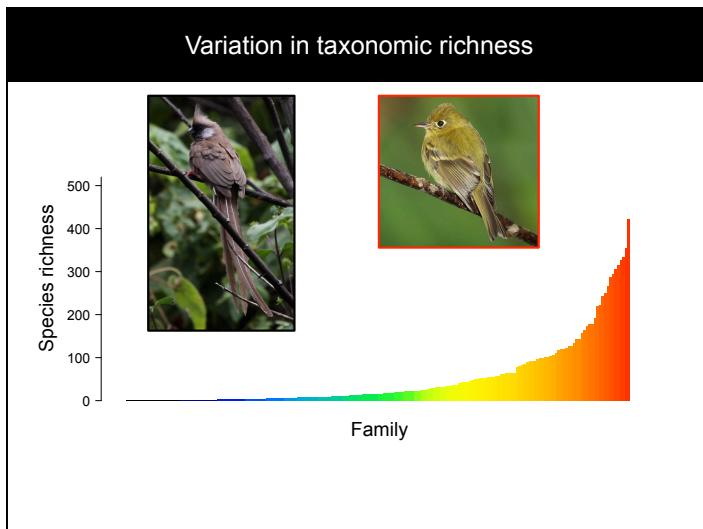
Incomplete taxon sampling

Phylogenetically non-random taxon sampling

Artifacts of tree construction

Not going to discuss these....

Variation in rates among lineages



Exercise 5: how much stochastic variation in richness?

Exercise: Chance

Simulate trees:

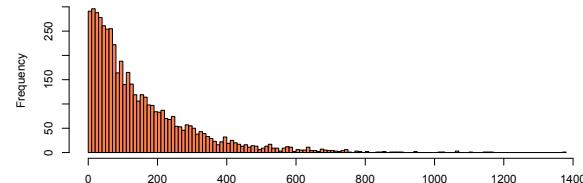
```
Function simulateTree
lambda = 0.2
mu = 0
max.t = 25
```

Exercise 5: how much stochastic variation in richness?

Exercise: Chance

Lots of variation: this is a very noisy process!

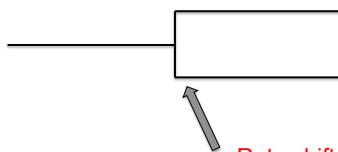
Distribution of richness is geometric



Exercise 5b: consequences of rate variation

Consider a pair of sister clades with ancestral $r = 0.1$ lineages * my⁻¹. One member of the clade undergoes a doubling of rates to 0.2 lineages * my⁻¹.

How does this doubling affect the difference in diversity between these clades?



Rate shift happens here:

Slowinski & Guyer 1989

Vol. 134, No. 6

The American Naturalist

December 1989

TESTING THE STOCHASTICITY OF PATTERNS OF ORGANISMAL DIVERSITY: AN IMPROVED NULL MODEL

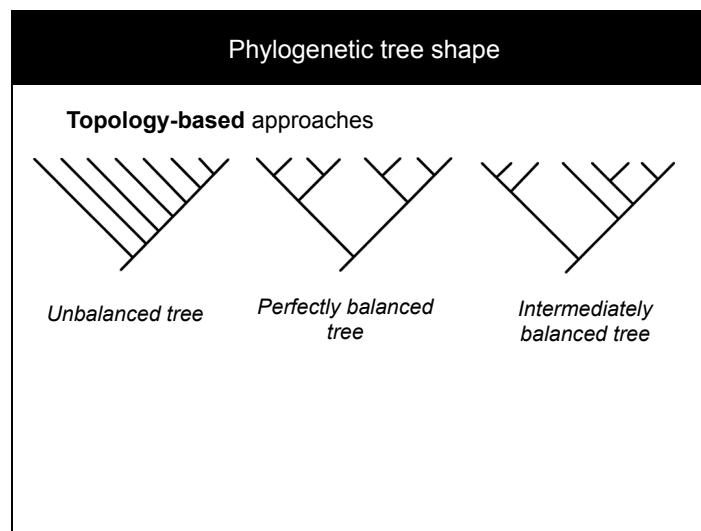
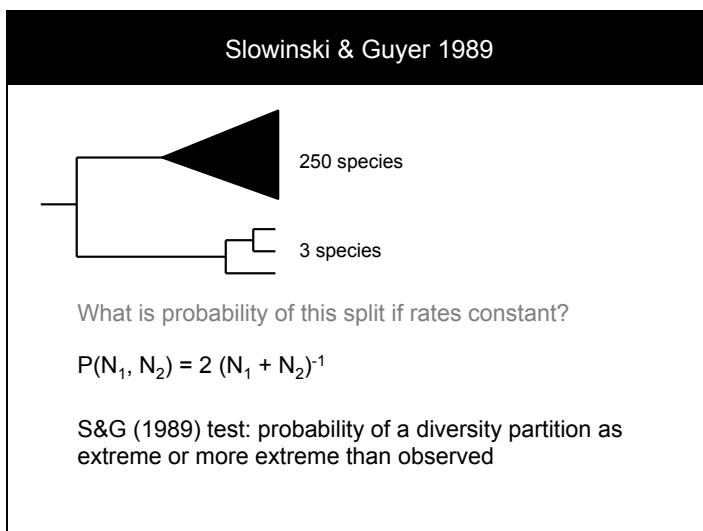
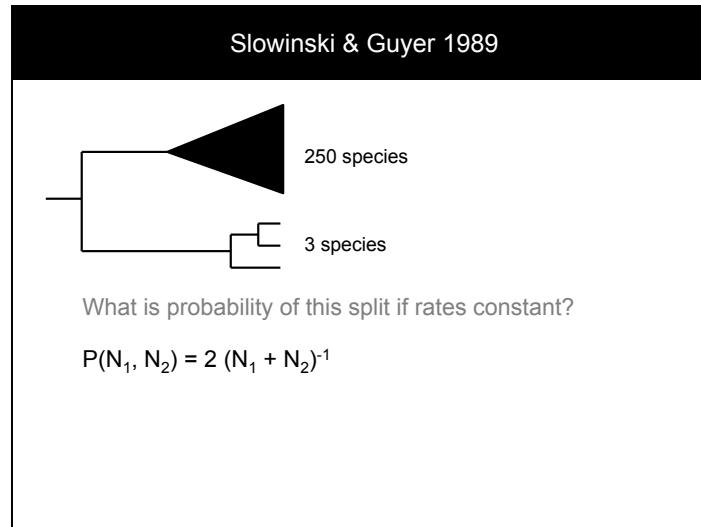
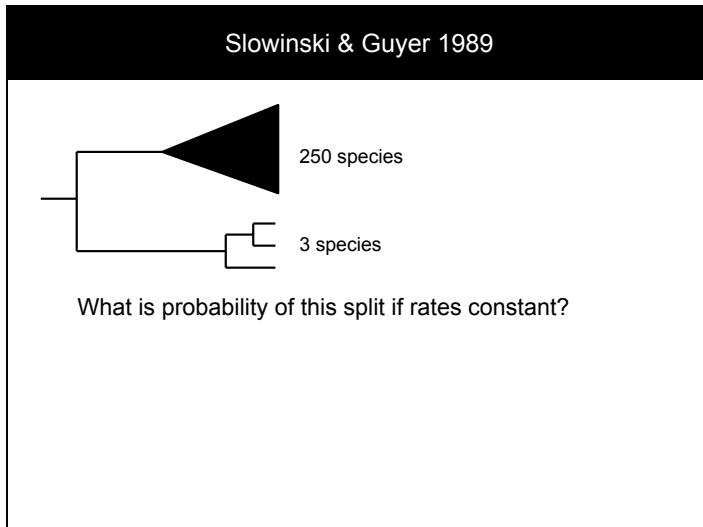
JOSEPH B. SLOWINSKI AND CRAIG GUYER

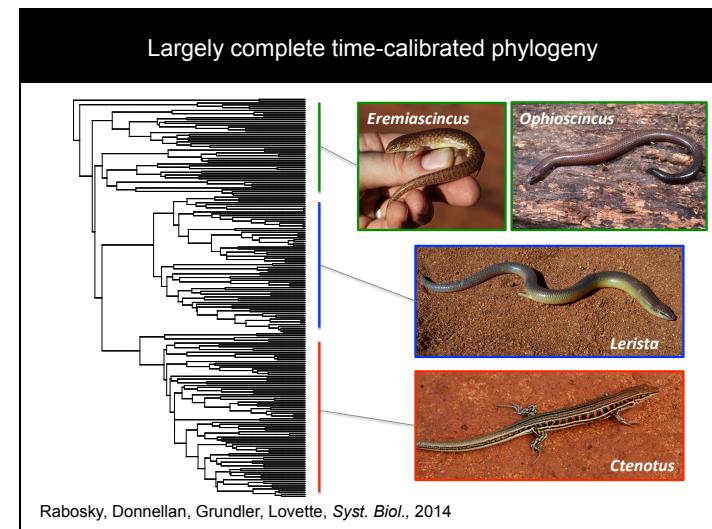
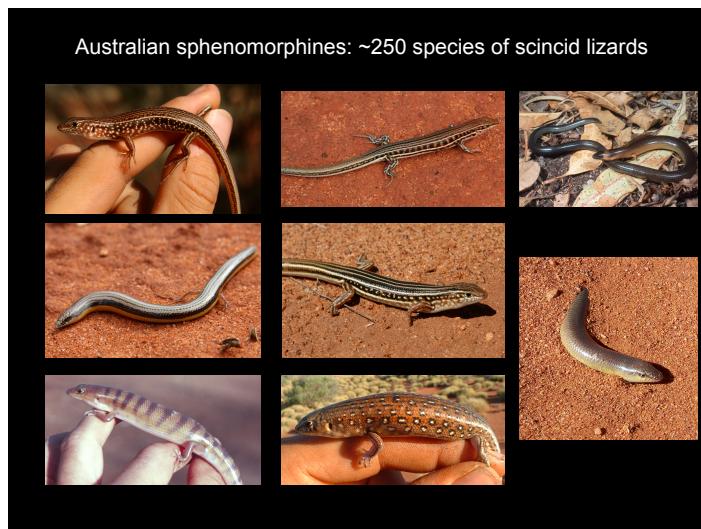
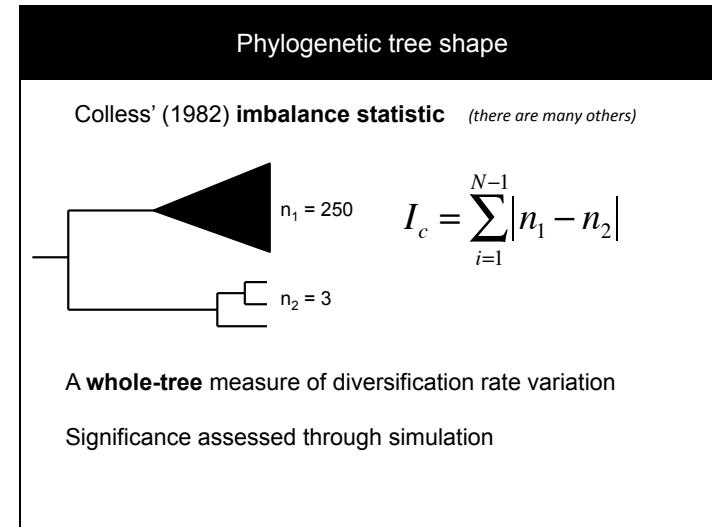
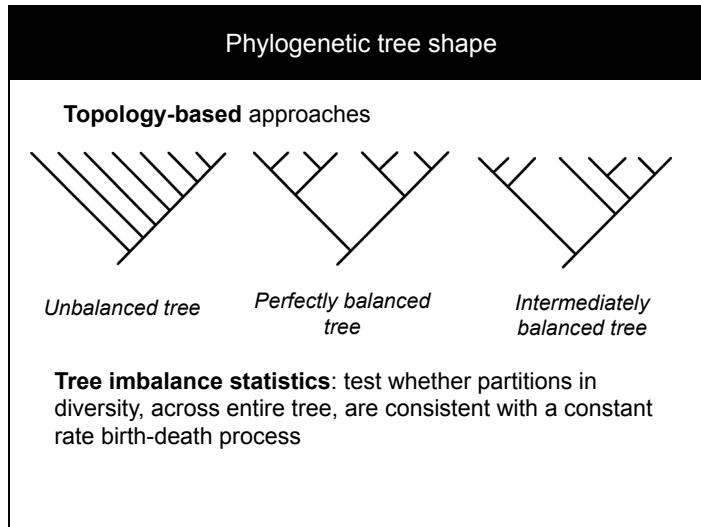
P.O. Box 249118, Department of Biology, University of Miami, Coral Gables, Florida 33124;

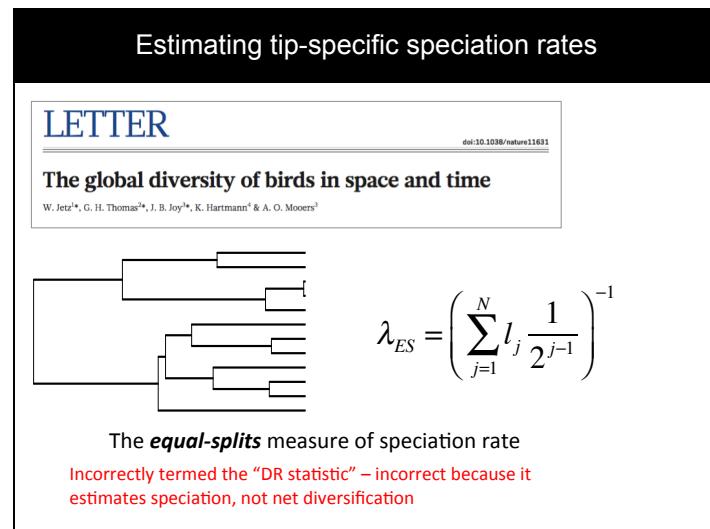
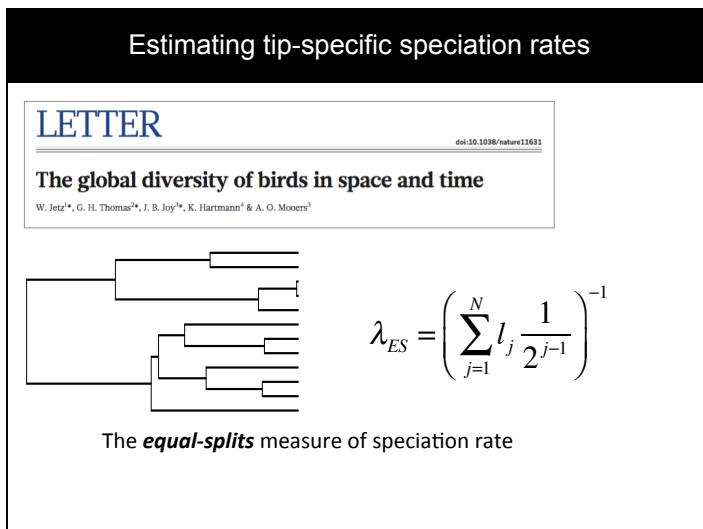
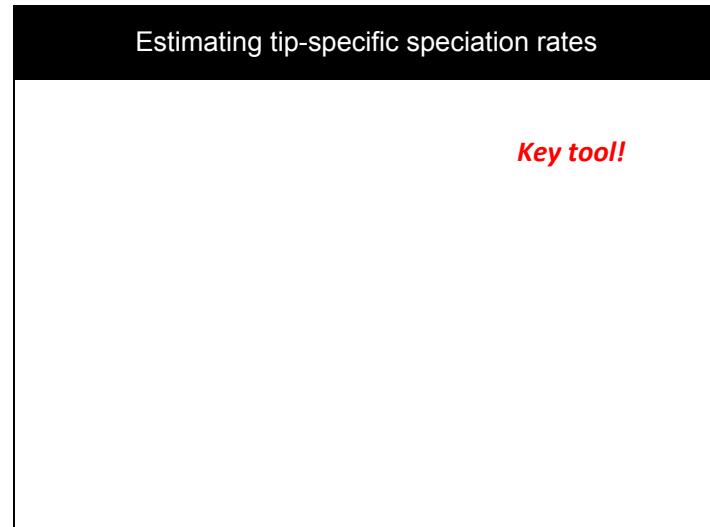
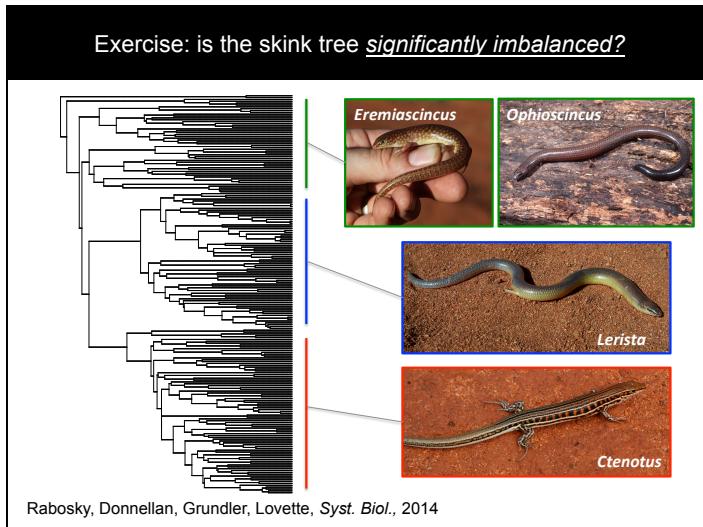
Department of Zoology and Wildlife Science, Auburn University, Auburn, Alabama 36849

Submitted May 22, 1988; Revised October 24, 1988; Accepted February 1, 1989

“... the debate about stochasticity versus determinism in the evolution of diversity has not been adequately resolved because a quantitative method based purely on the topology of phylogeny has not been employed”







Exercise 6: computing tip rates with ES metric