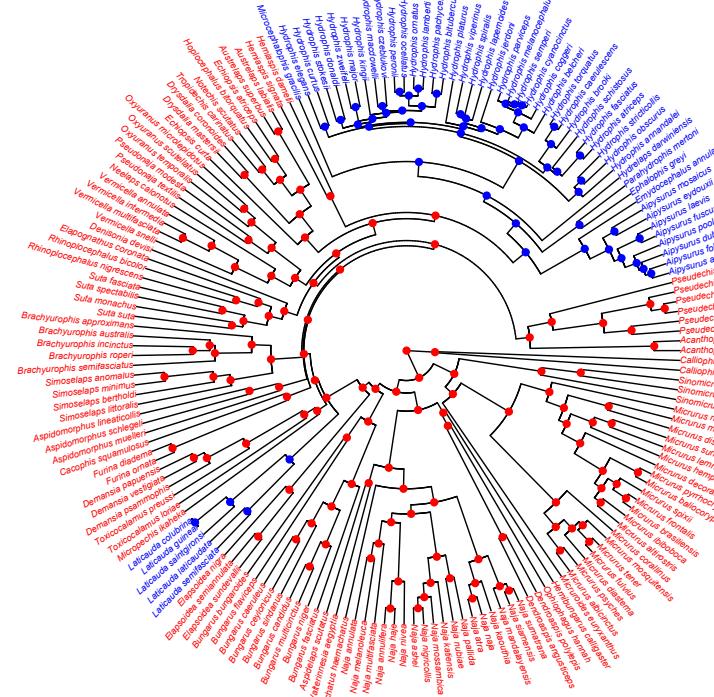


Methods for detecting trait-dependent diversification



Benedict King
Postdoc, Naturalis Biodiversity Center

Key innovations

- An important concept in evolutionary biology
- The definition of a key innovation has changed through time.
- Recent definitions have focused on increased diversification rates
- However this discounts some adaptations (such as the human brain) from being key innovations
- Convincing evidence for a key innovation should include both comparative evidence for increased diversification and a plausible mechanism

Box 1. Contrasting definitions of key innovation

Miller (1949): '... key adjustments in the morphological and physiological mechanism which are essential to the origin of new major groups'³.

Van Valen (1971): 'A key character, in the adaptive sense, is a structure or element of physiology that makes a taxon more or less committed to a way of life different from, or appreciably more efficient than, that of its ancestors'⁵.

Levinton (1988): 'key innovation is necessary, but not sufficient for a subsequent radiation'⁶.

Baum & Larson (1991): '... a trait that greatly modifies the selective regime of the lineage in which it evolves'¹⁵.

Rosenzweig & McCord (1991): 'A key adaptation is a change in the mathematical rule governing a trade-off constraint so that after the change, the trade-off is less severe'¹³.

Erwin (1992): '[K]ey innovations characterize particular clades and are both necessary and sufficient to explain diversification within the clade'³⁹

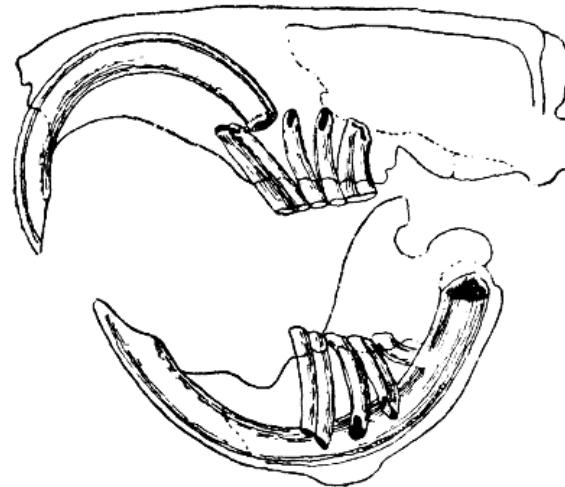
Heard & Hauser (1995): 'an evolutionary change in individual trait(s) that is causally linked to an increased diversification rate in the resulting clade (for which it is a synapomorphy)'⁹.

Types of key innovation

1. adaptations that allow invasion of a new adaptive zone
e.g. flight



2. adaptations that increase fitness
e.g. continuous incisor growth in rodents



3. adaptations that promote reproductive isolation
e.g. Pollinia in orchids



Sister clade contrasts

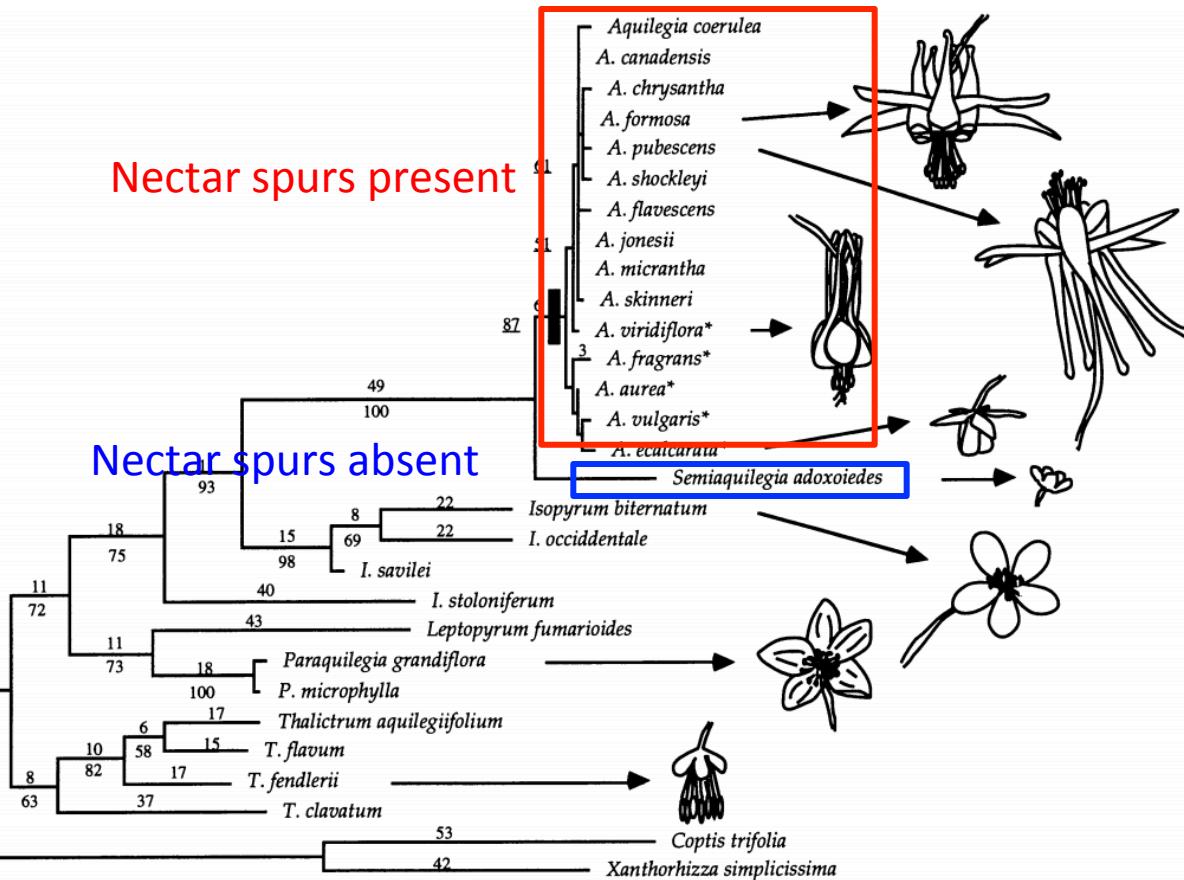
- Compare species richness of clades containing the trait of interest with their immediate sister groups
- Each clade is the same age as its sister group

Nectar spurs are a key innovation in flowering plants (Hodges 1997)



Nectar spurs present

Nectar spurs absent



Sister clade contrasts

- Comparing multiple groups with a trait to their sister groups
- Are groups with the trait more diverse compared to their sister groups than expected by chance?

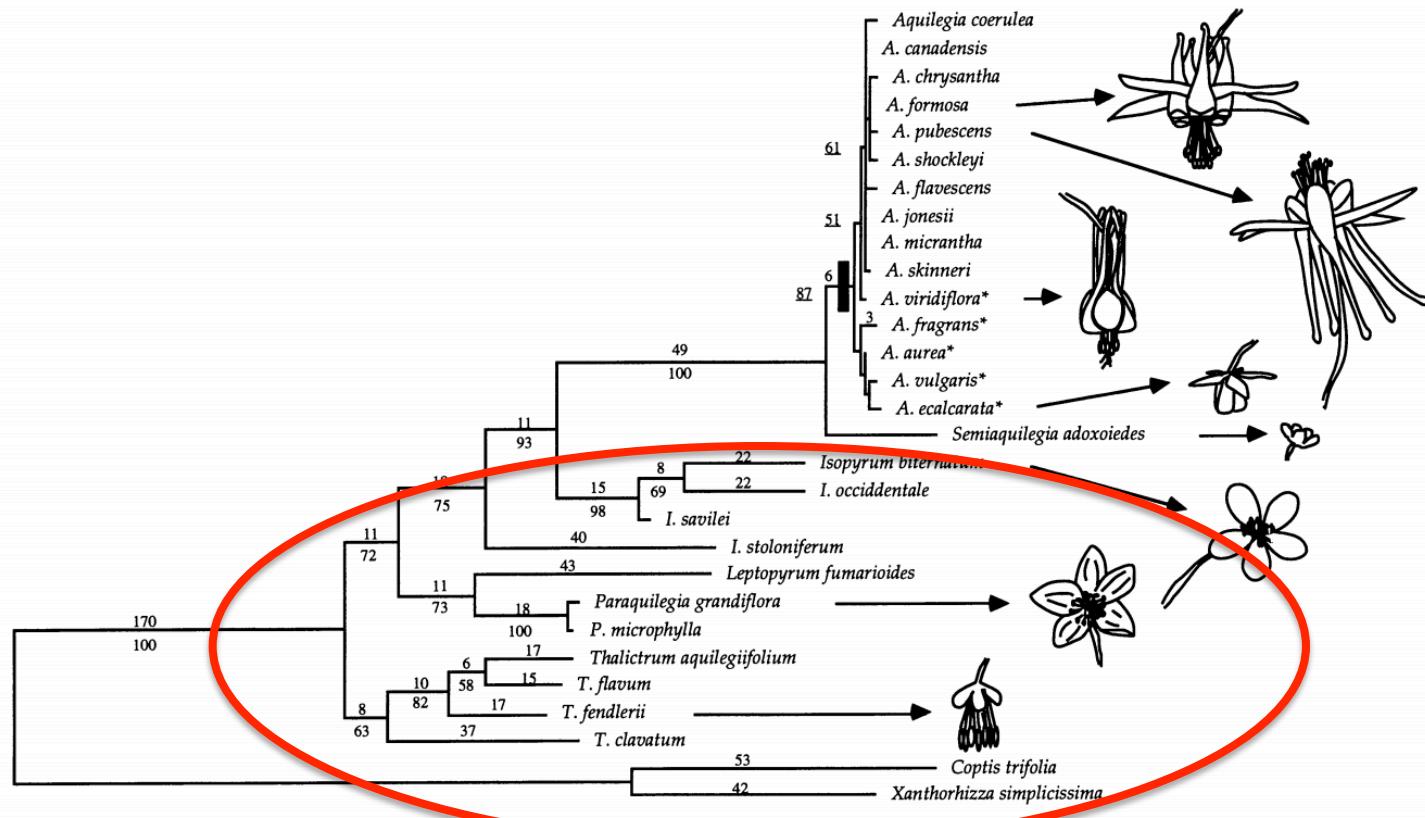
Table 2

NUMBER OF SPECIES IN GROUPS THAT HAVE INDEPENDENTLY EVOLVED FLORAL NECTAR SPURS AND THEIR INFERRRED SISTER GROUPS (see references)

Spurred taxa	Nonspurred sister taxa	No. of spurred spp.: nonspurred spp.	P	References
<i>Aquilegia</i>	<i>Semiaquilegia</i>	70:1	0.014	Hodges and Arnold 1995
<i>Delphinium, Aconitum</i>	<i>Nigella</i> or <i>Nigella, Actaea, Cimicfuga</i>	350:14 or 350:37	0.039 or 0.095	Hoot 1991, 1995 Johansson and Jansen 1993
<i>Fumariaceae</i>	<i>Hypericum</i>	450:15	0.032	Hoot and Crane 1995
<i>Tropaeolaceae</i>	<i>Akaniaceae, Bretschneideraceae</i>	88:2	0.022	Chase et al. 1993; Rodman et al. 1993
<i>Anchiectia, Corynostylis</i>	<i>Agatea</i>	12:1	0.083	Hodges, Ballard, Arnold, and Chase, unpublished data
<i>Noisettia, Viola</i>	Subset of <i>Hybanthus</i>	401:<150	?	Hodges, Ballard, Arnold, and Chase, unpublished data
<i>Lentibulariaceae</i>	<i>Byblidaceae</i>	245:2	0.008	Olmstead et al. 1993; Bremer et al. 1994
<i>Pelargonium</i>	<i>Geranium, Erodium,</i> <i>Monsonia, Sarcocaulon</i>	280:399	0.588	Price and Palmer 1993

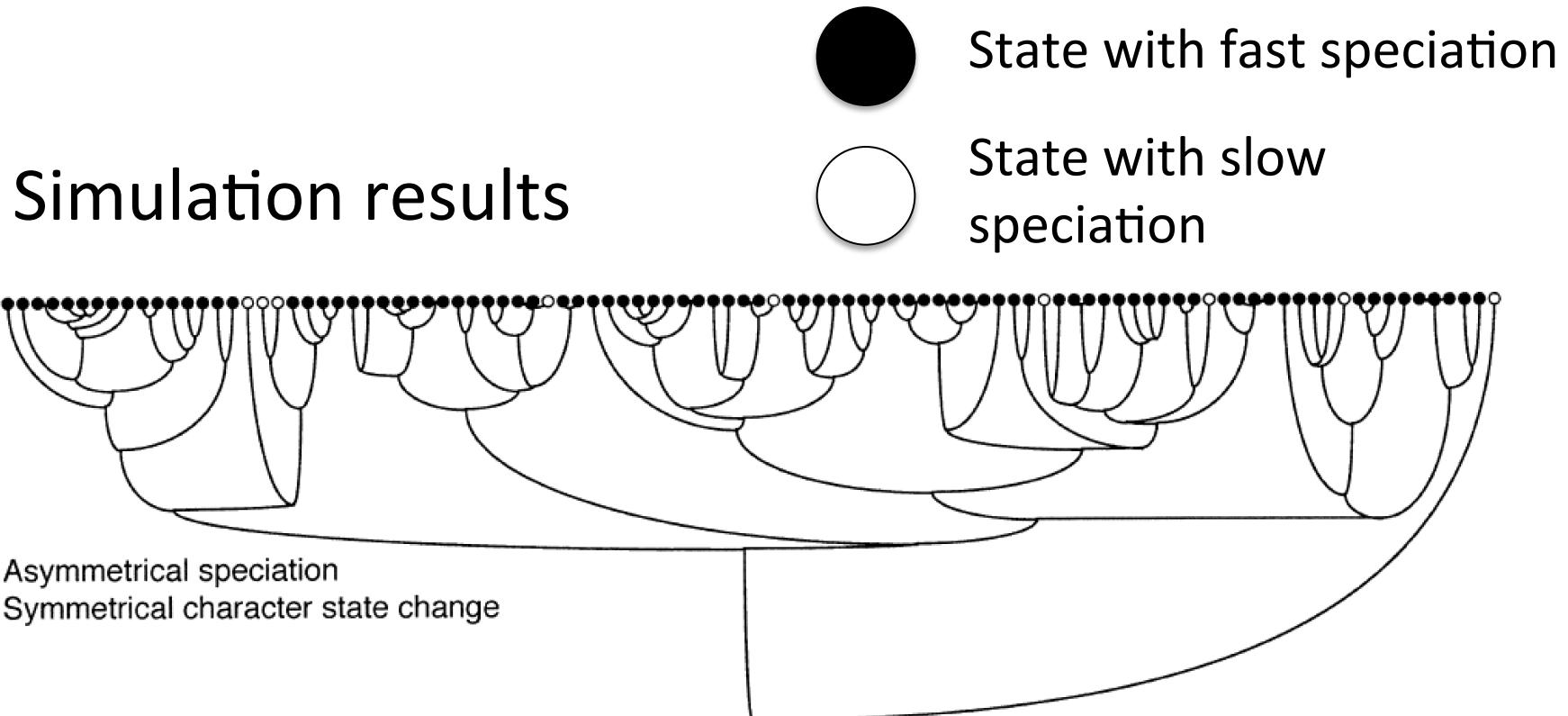
Problems with sister-clade constraints

- Cannot tell if the pattern is caused by different speciation or extinction
- Throws away a lot of information by only considering sister clades



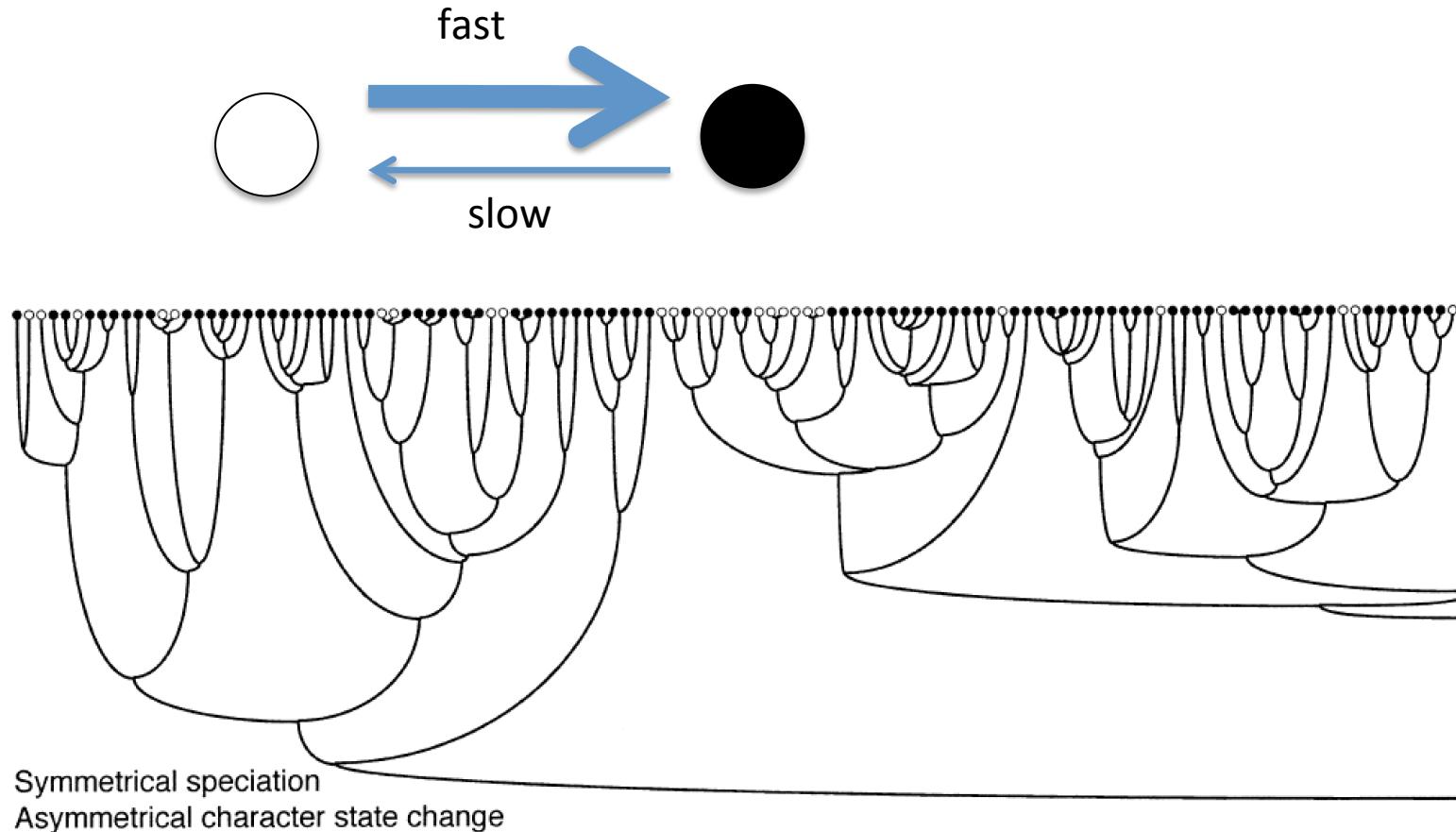
Problems with sister-clade constraints

An increased diversification rate for state 1 would produce a pattern in which state 0 is rare and state 1 is common



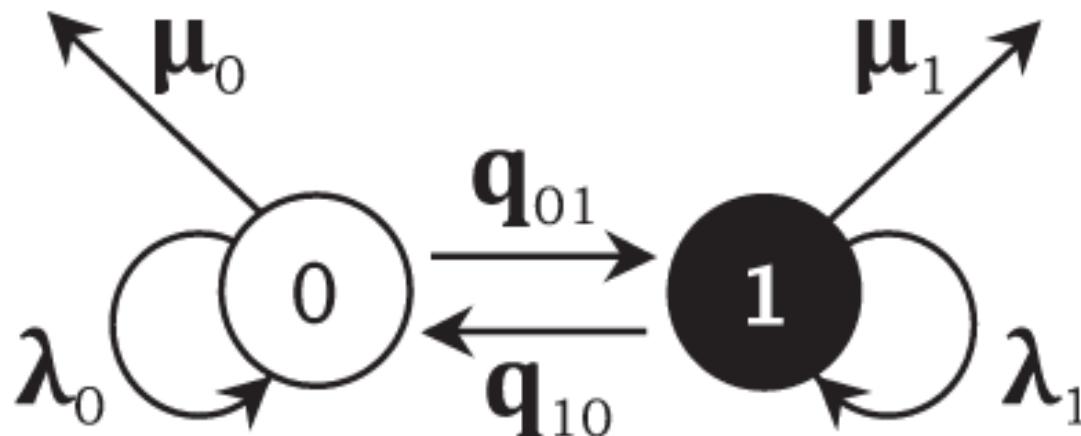
Problems with sister-clade constraints

The same pattern is produced by different transition rates between states



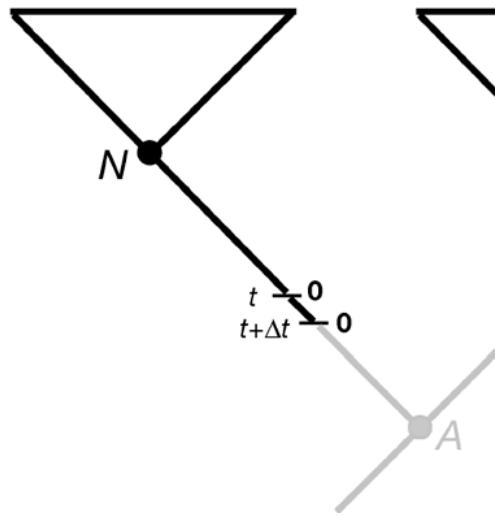
Binary state speciation and extinction (BiSSE)

- Avoids the confounding effects of diversification rate and character state changes. Can be used to study both
- Based on a model of evolution
- The model has two states (0 and 1)
- Each state has a speciation (λ_0, λ_1) and extinction parameter (μ_0, μ_1)
- There are also transitions between states

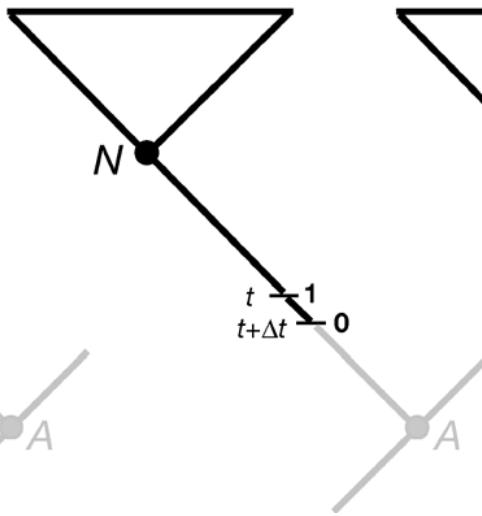


BiSSE likelihood search

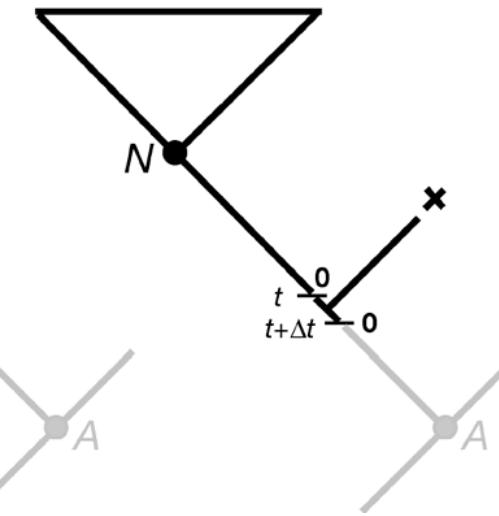
a) No state change,
No speciation



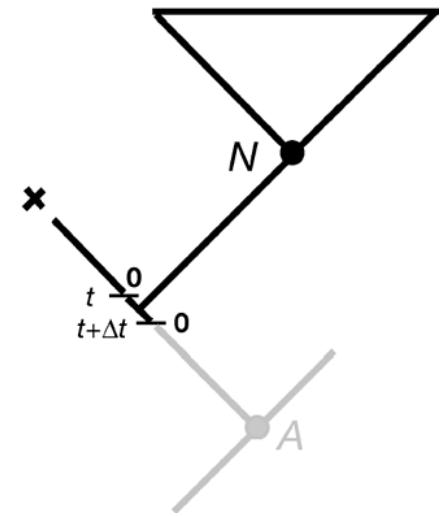
b) State change,
No speciation



c) No state change,
Speciation & Extinction



d) No state change,
Speciation & Extinction



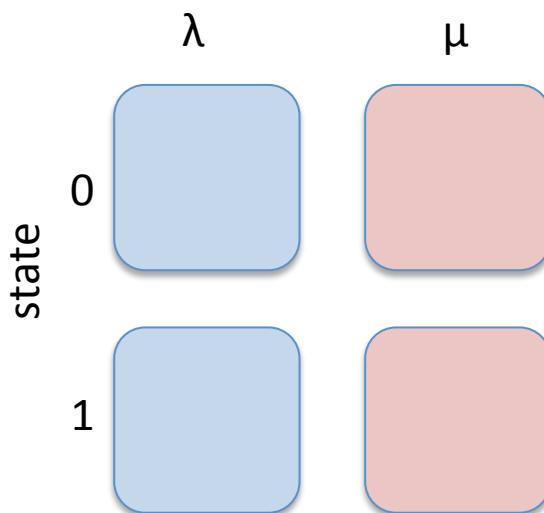
- The BiSSE algorithm calculates the probability of the tree and the traits for a range of parameter values
- The parameter values with the maximum likelihood are found
- The likelihood search can be inefficient and may not find the true maximum likelihood estimate

BiSSE model testing

- The 6 parameter model for BiSSE must be compared to simpler models
- For each model the maximum likelihood is calculated

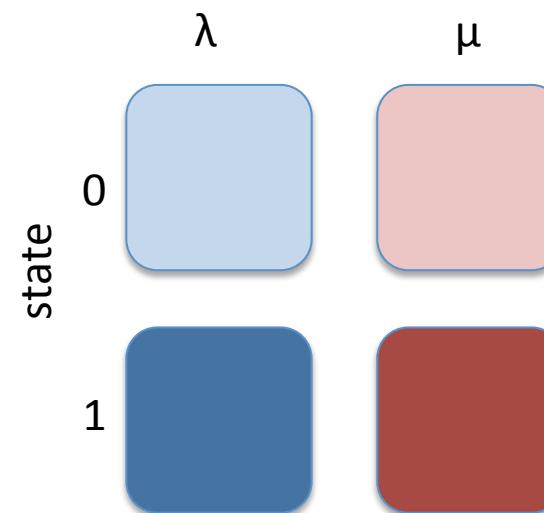
Trait independent
diversification

Diversification rate



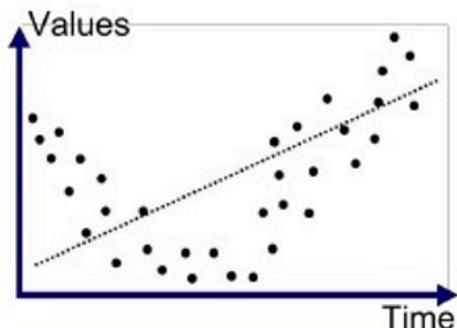
Trait dependent
diversification

Diversification rate

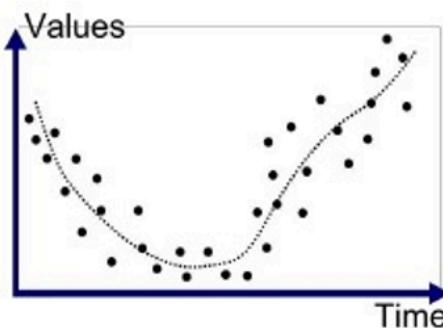


BiSSE model testing

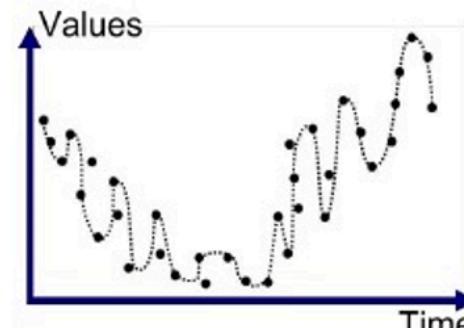
Find the best fit model without “overfitting”



Underfitted



Good Fit/Robust



Overfitted

Akaike information criterion (AIC) or likelihood ratio tests can be used to choose the model

$$\text{AIC} = 2 \times (\text{number of parameters}) - 2 \times \ln(\text{likelihood})$$

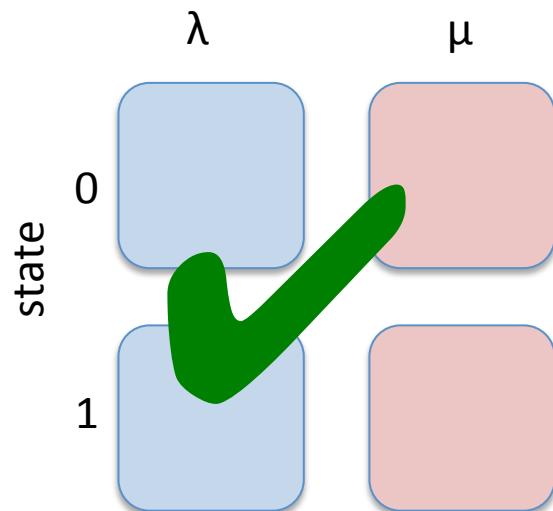
Penalty for number of parameters

Raw model fit

BiSSE model testing

Trait independent
diversification

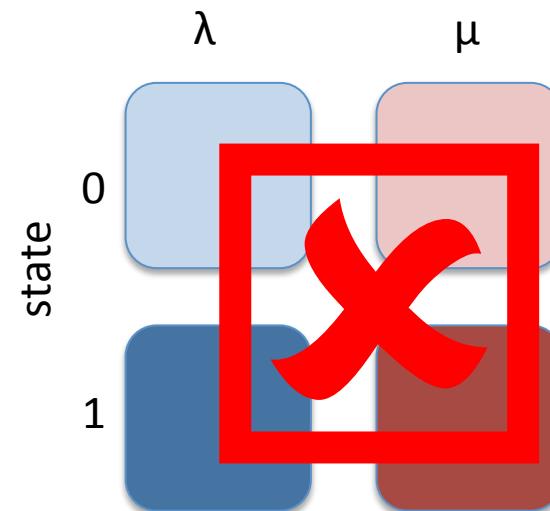
Diversification rate



Log likelihood -680.6

Trait dependent
diversification

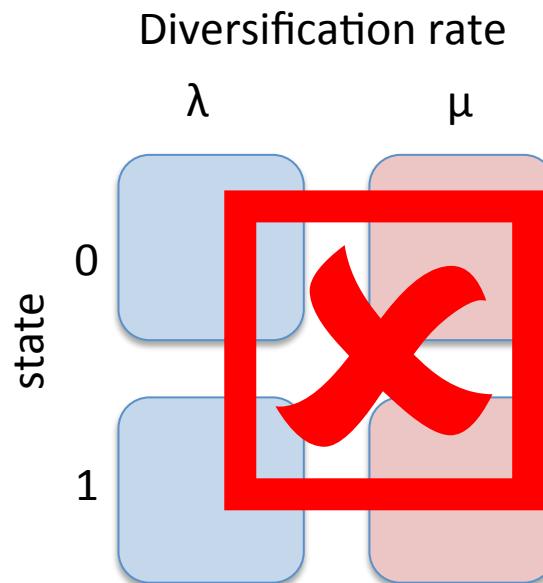
Diversification rate



Log likelihood -680.5

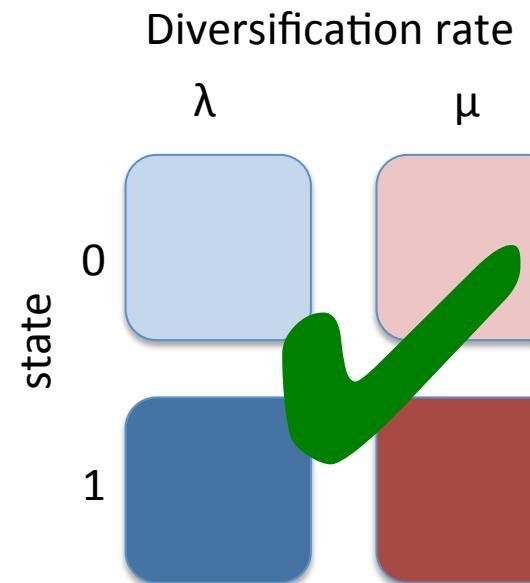
BiSSE model testing

Trait independent
diversification



Log likelihood -680.6

Trait dependent
diversification



Log likelihood -667.2

BiSSE method limitations

- Possibly another character with the same distribution is affecting the diversification rate
- This is less likely if there are many origins of the character



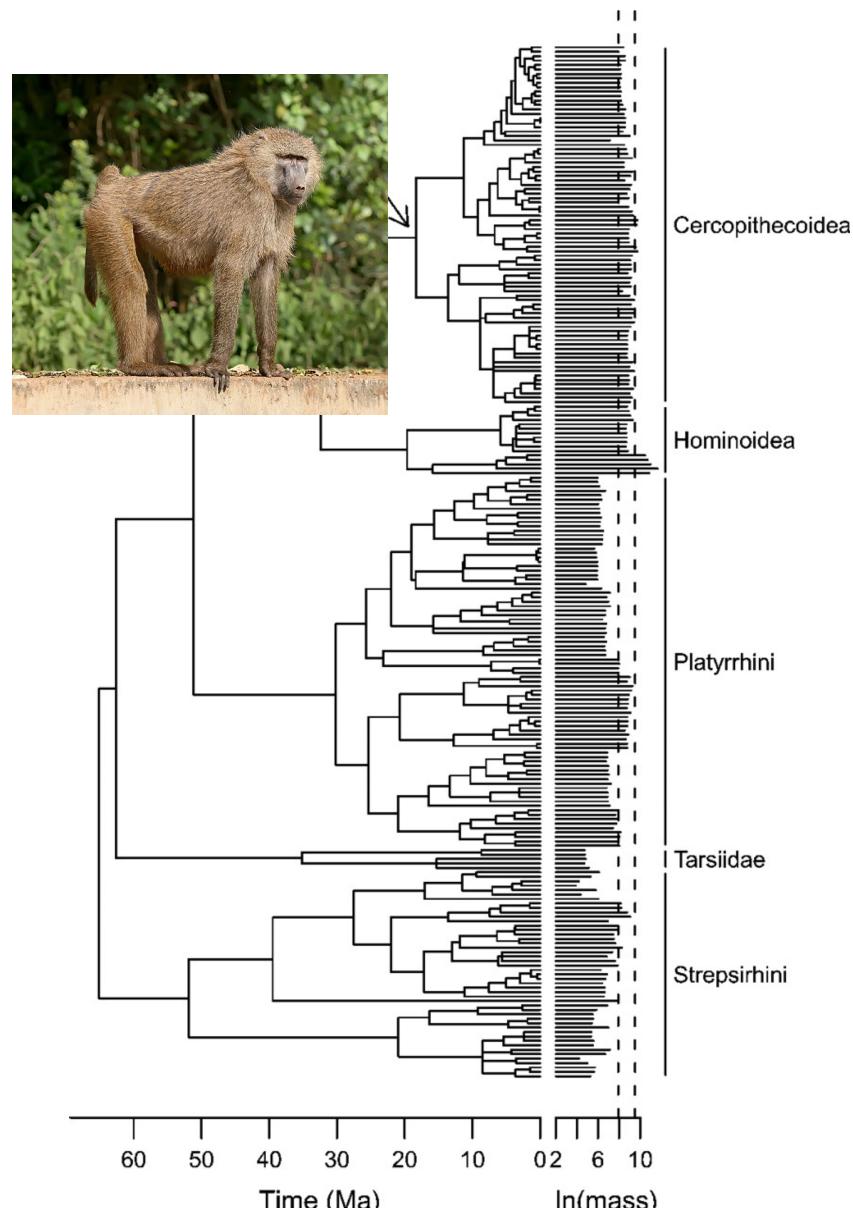
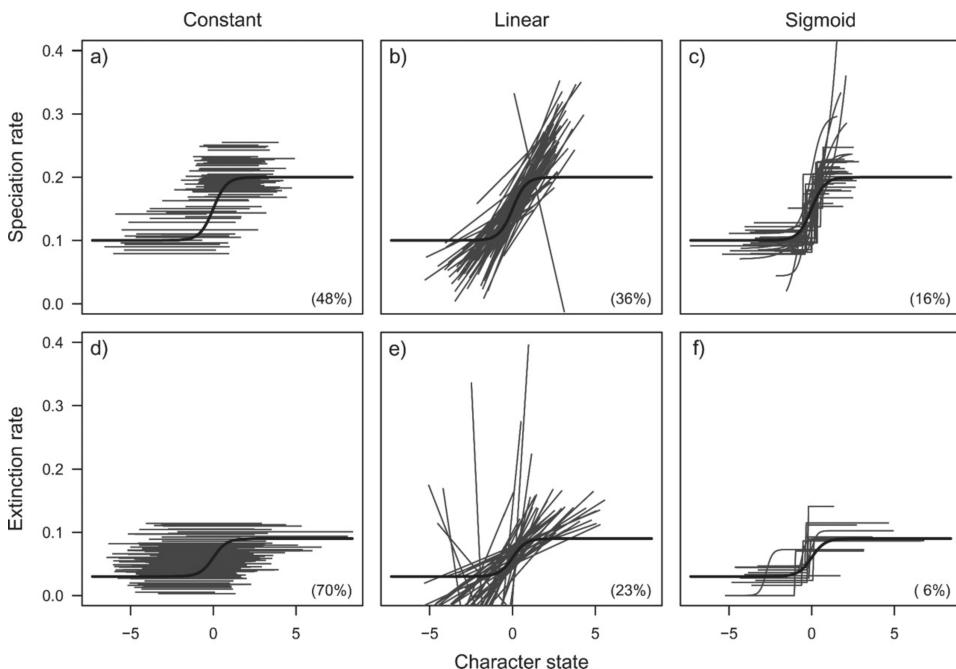
Ditrysia - 98% of butterfly and moth species.

Major synapomorphies include the separation of the tracts for egg-laying and mating and a reorganisation of the renal system

Which trait is responsible for diversification?

BiSSE extensions

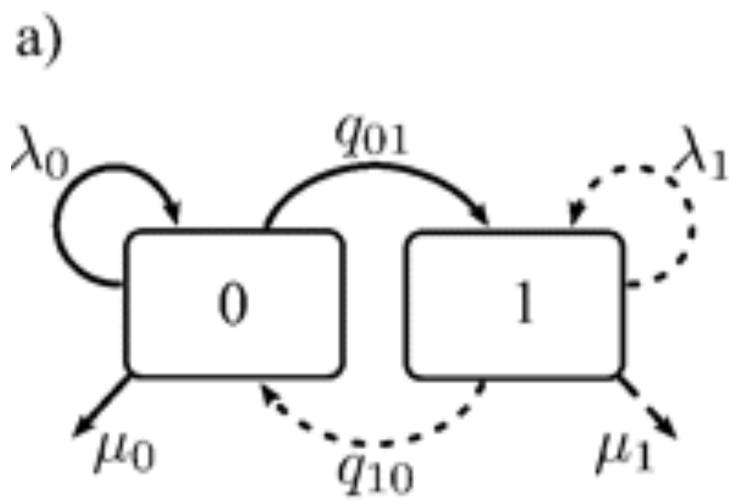
- QuaSSE – continuous characters
- Can be used to test the effect of body size on diversification rates



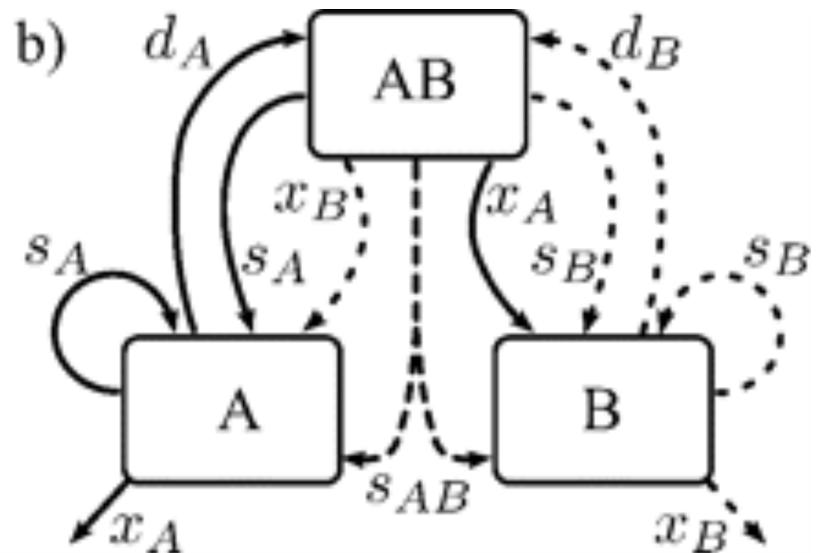
Fitzjohn 2010

BiSSE extensions

GeoSSE – geographic regions



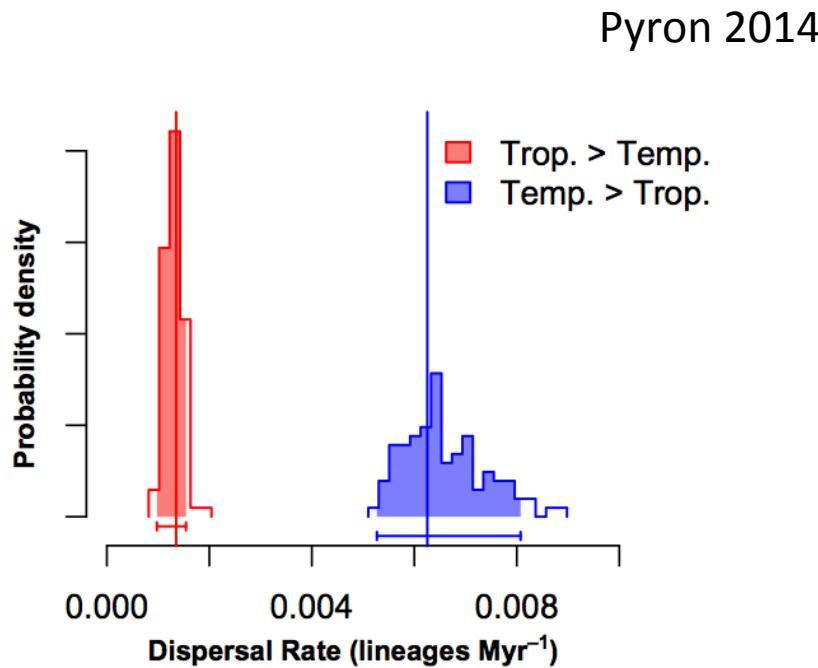
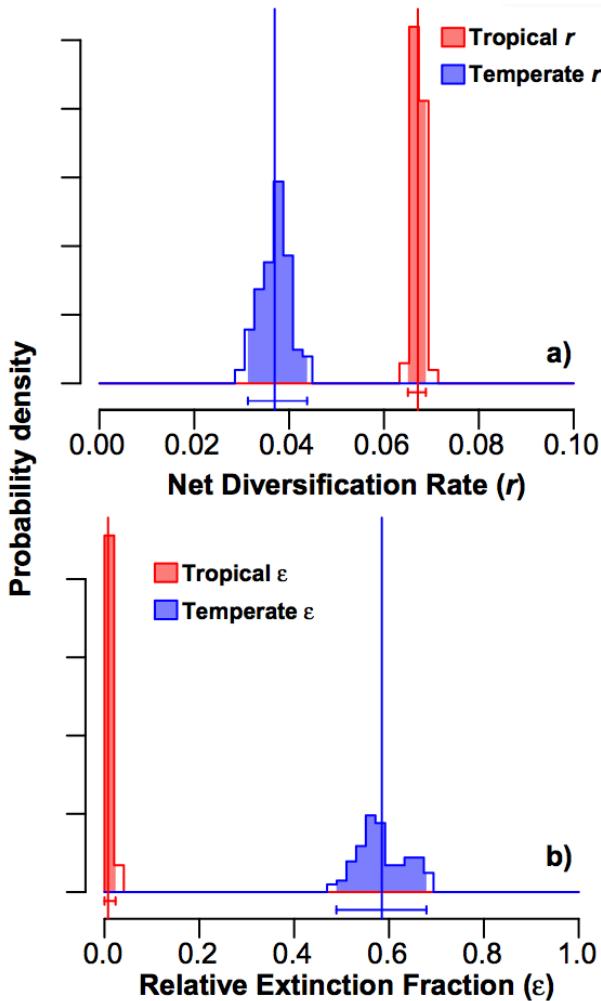
BiSSE



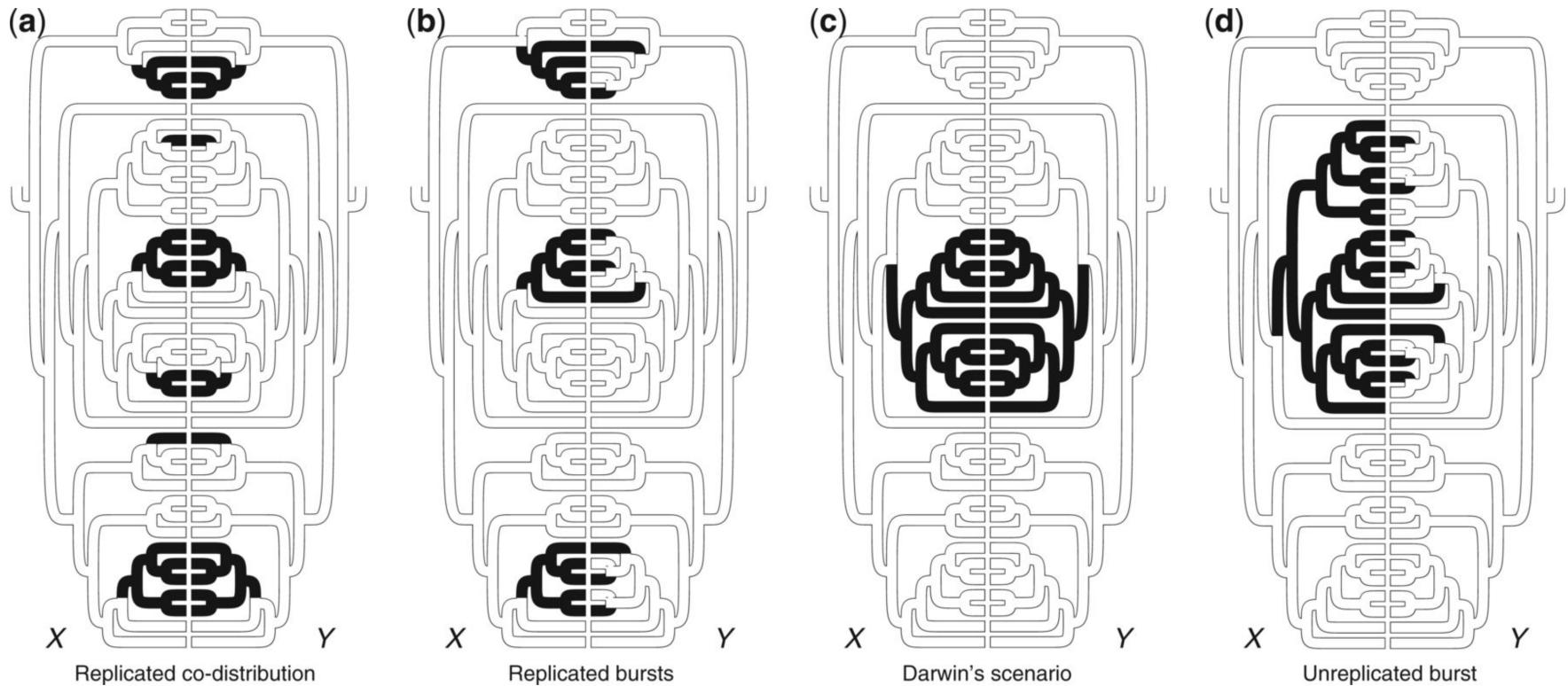
GeoSSE – includes an additional state AB (present in both regions), and additional speciation parameter (a species in AB splits into two, one in A and one in B)

Goldberg 2011

GeoSSE to test the causes of latitudinal diversity gradients in squamate reptiles



Problems with BiSSE – phylogenetic pseudoreplication

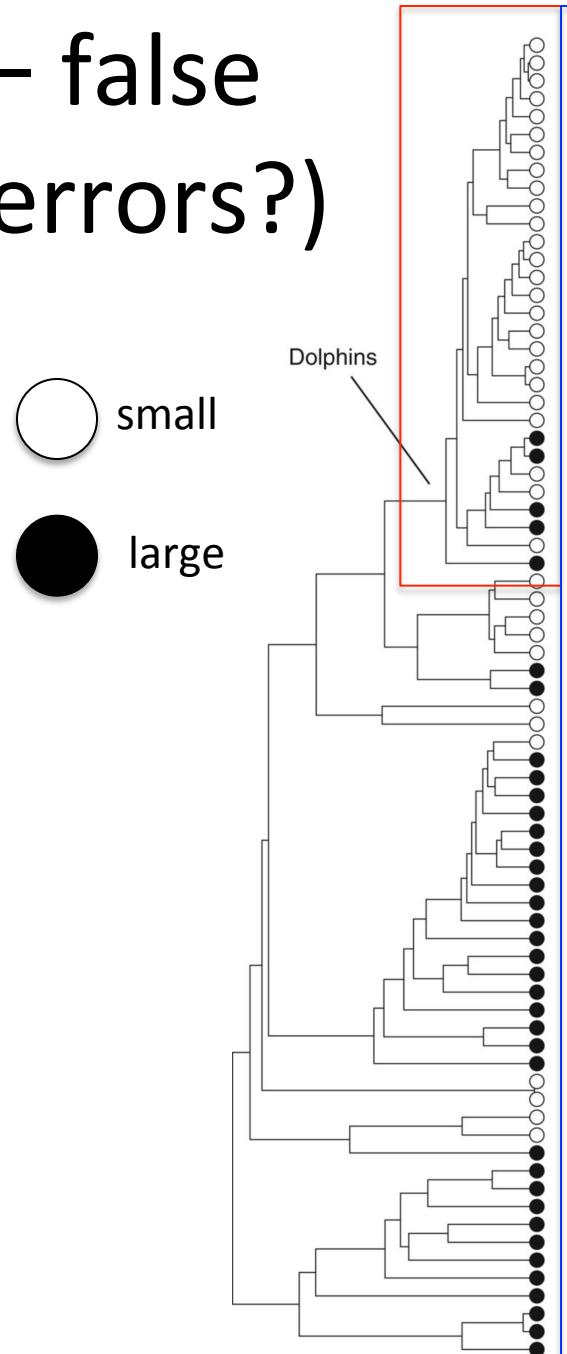


Maddison and Fitzjohn 2015

A and B show good evidence for a correlation between traits. C and D do not

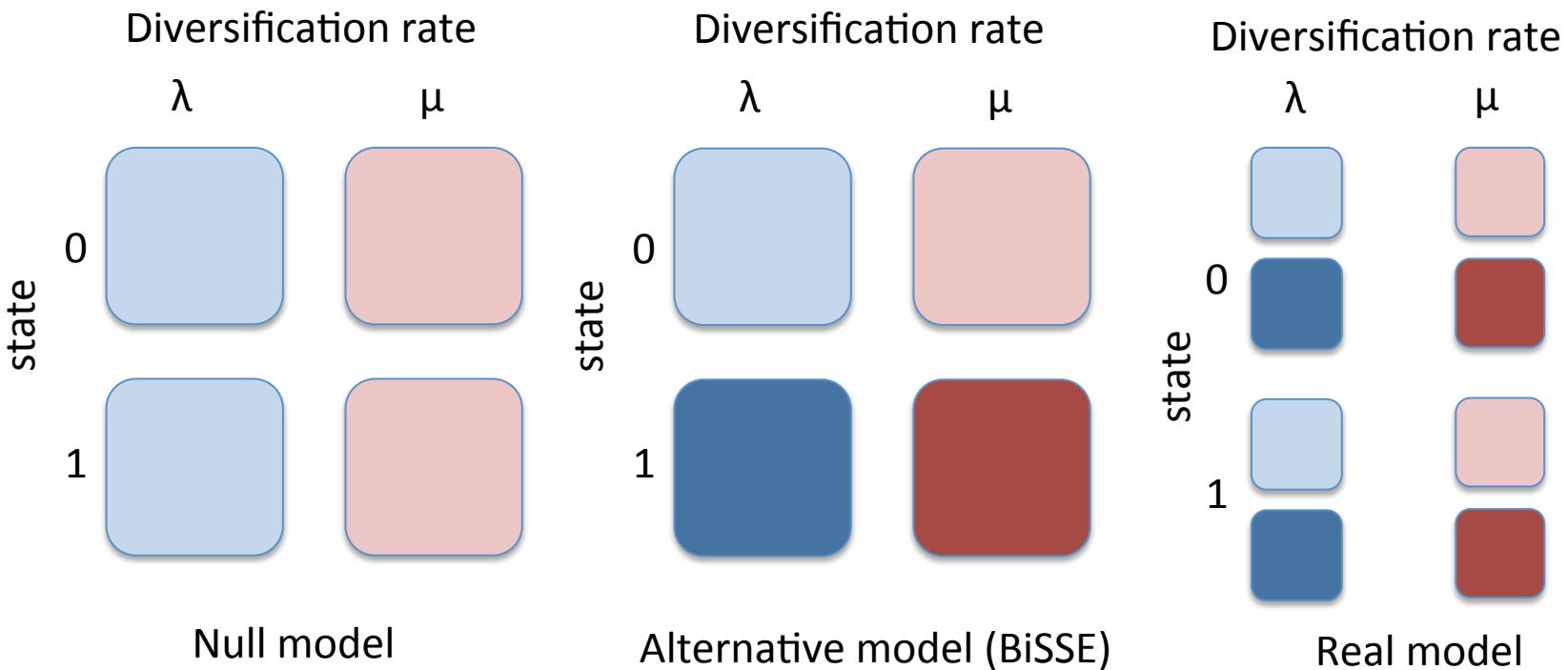
Problems with BiSSE – false positive results (type I errors?)

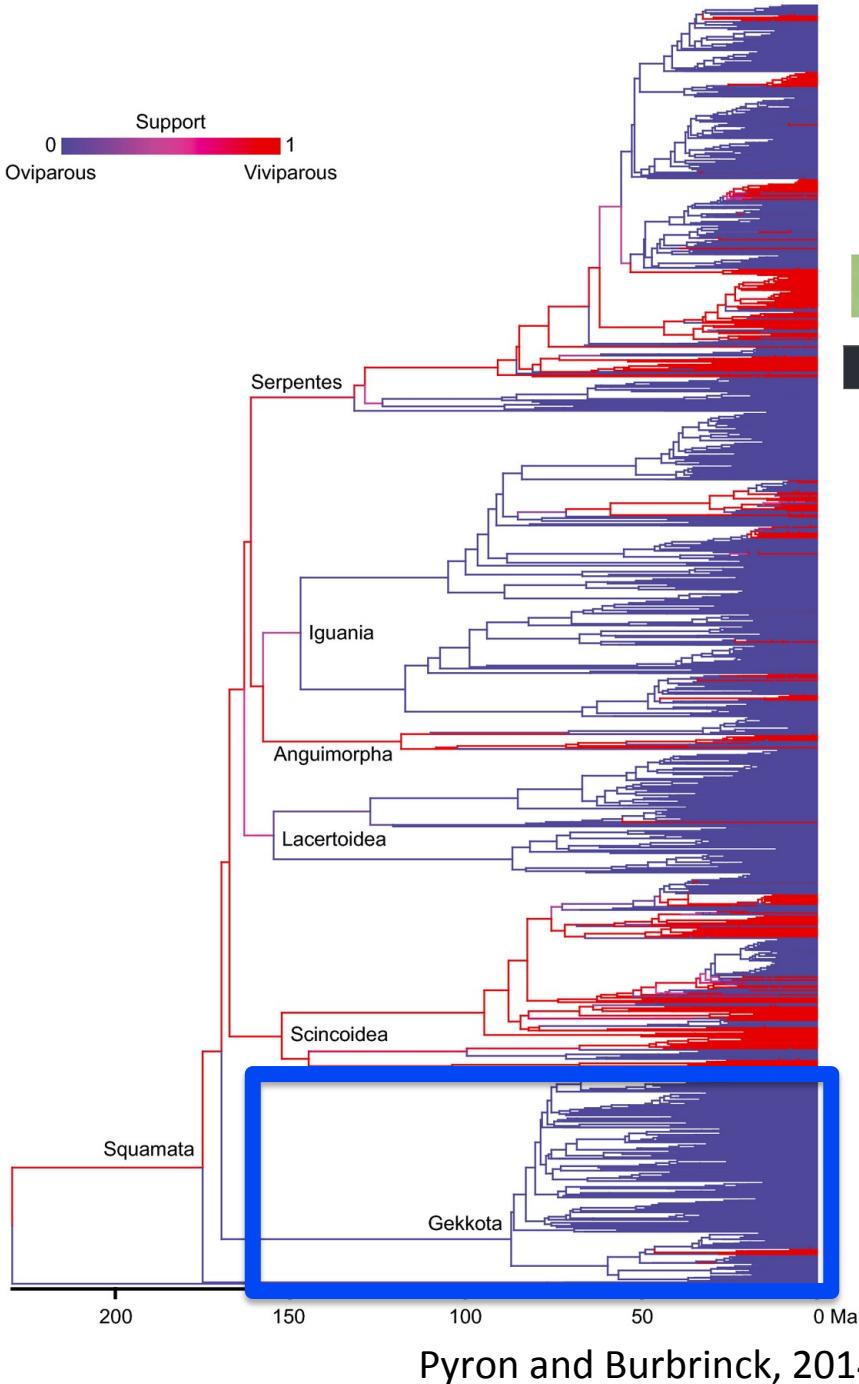
- According to BiSSE, small body size promotes diversification in dolphins
- Simulate neutral characters i.e. with no correlation with speciation rates
- Run BiSSE
- 77% of analyses returned a positive association
- Particularly problematic when there are low numbers of transitions between character states
- However, false positives **still occur at when there are many transitions**



Problems with BiSSE – false positive results

- These are *not* type I errors. A type I error is when the null model is correct but the alternative model is supported
- In BiSSE the null model is constant diversification
- The problem with BiSSE is that it *only* allows diversification rates to vary with the traits. But life is rarely so simple
- This is **model inadequacy**





Unusual ancestral state reconstructions

ECOLOGY LETTERS

Ecology Letters, (2014) 17: 13–21

doi: 10.1111/ele.12168

LETTER

Early origin of viviparity and multiple reversions to oviparity in squamate reptiles

- Using BiSSE, strong support for viviparity as the ancestral state for lizards, with egg –laying evolving multiple times
- Result is counter to knowledge of biology
- Strong support at the root of the tree is counter-intuitive because there are three successive egg-laying outgroups

Unusual ancestral state reconstructions

ECOLOGY LETTERS

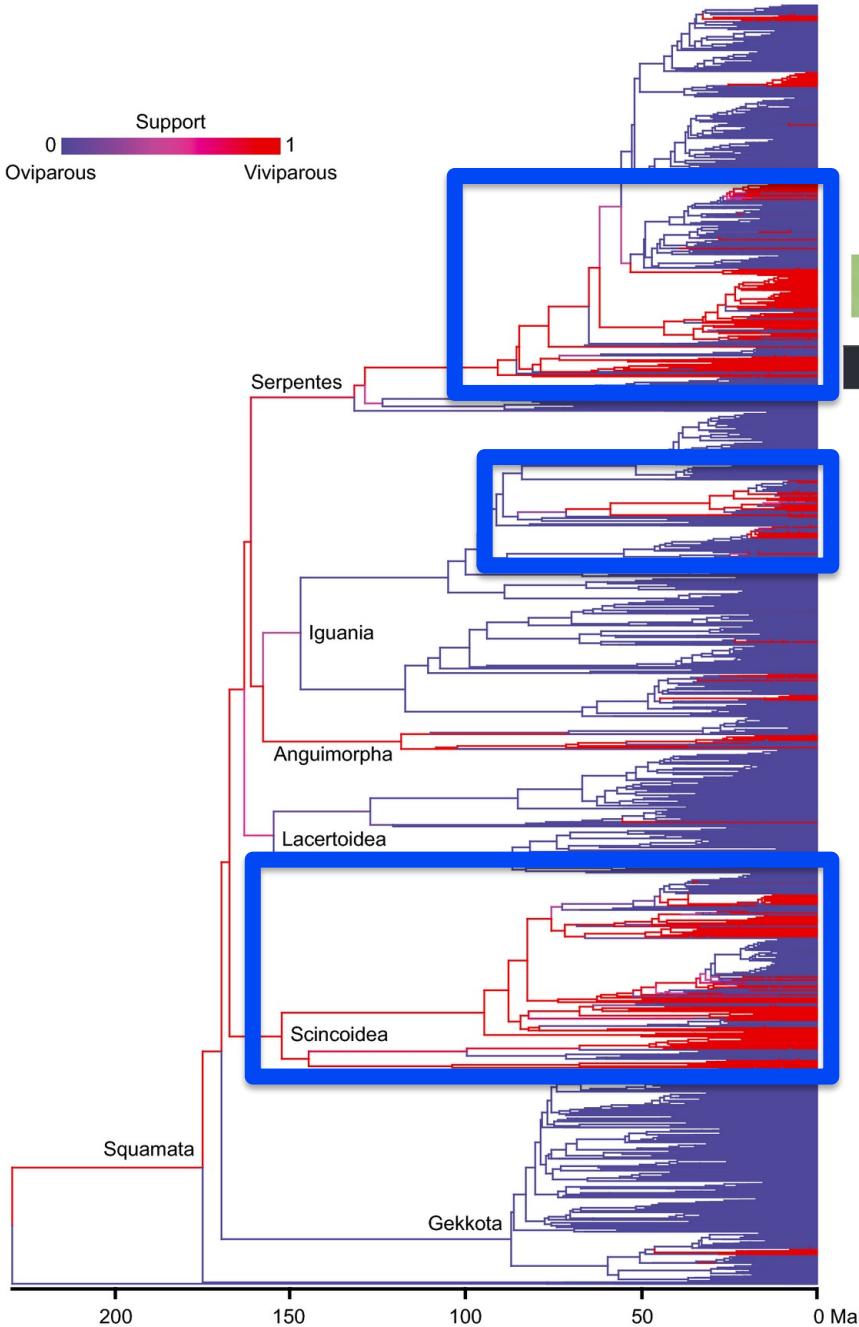
Ecology Letters, (2014) 17: 13–21

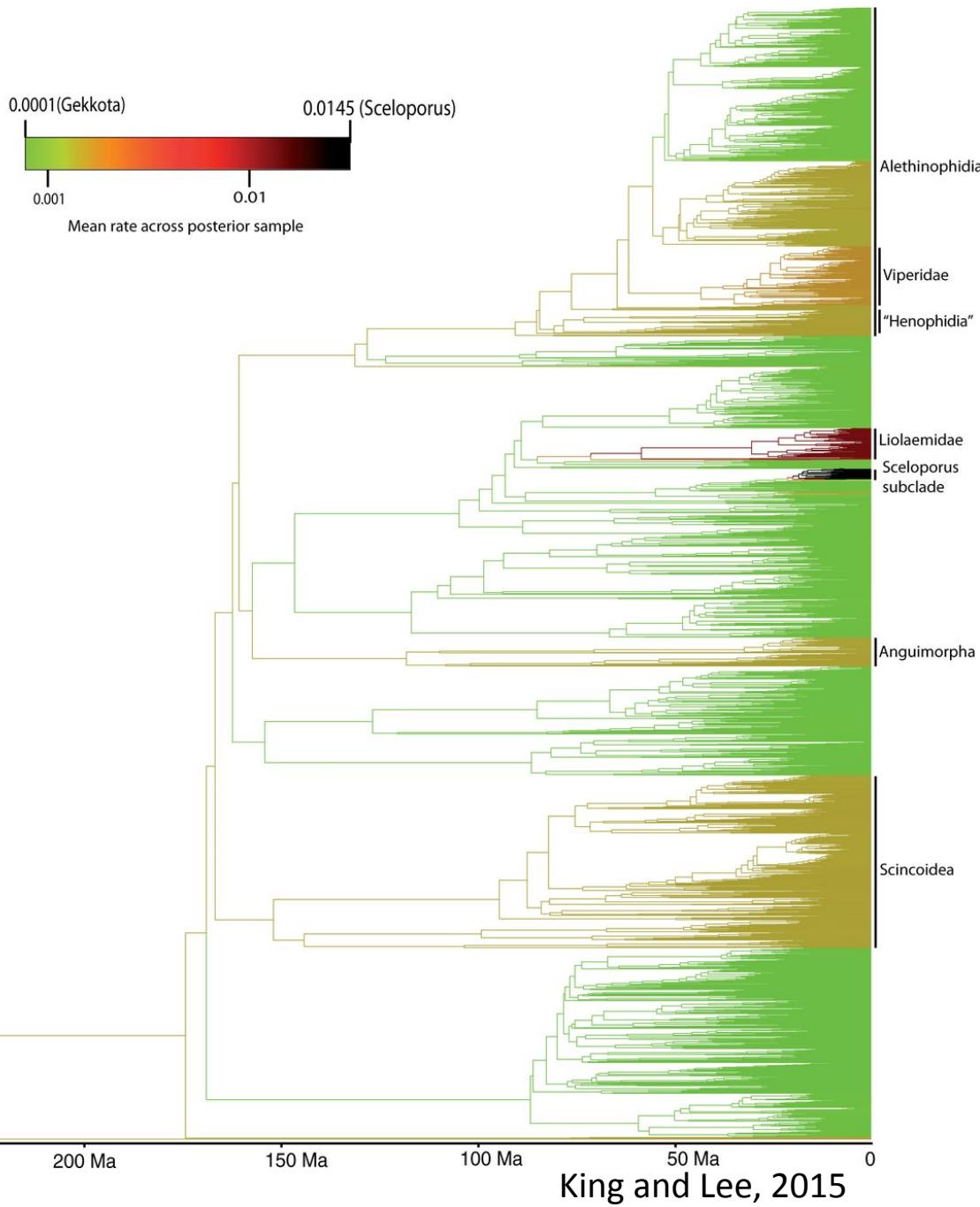
doi: 10.1111/ele.12168

LETTER

Early origin of viviparity and multiple reversions to oviparity in squamate reptiles

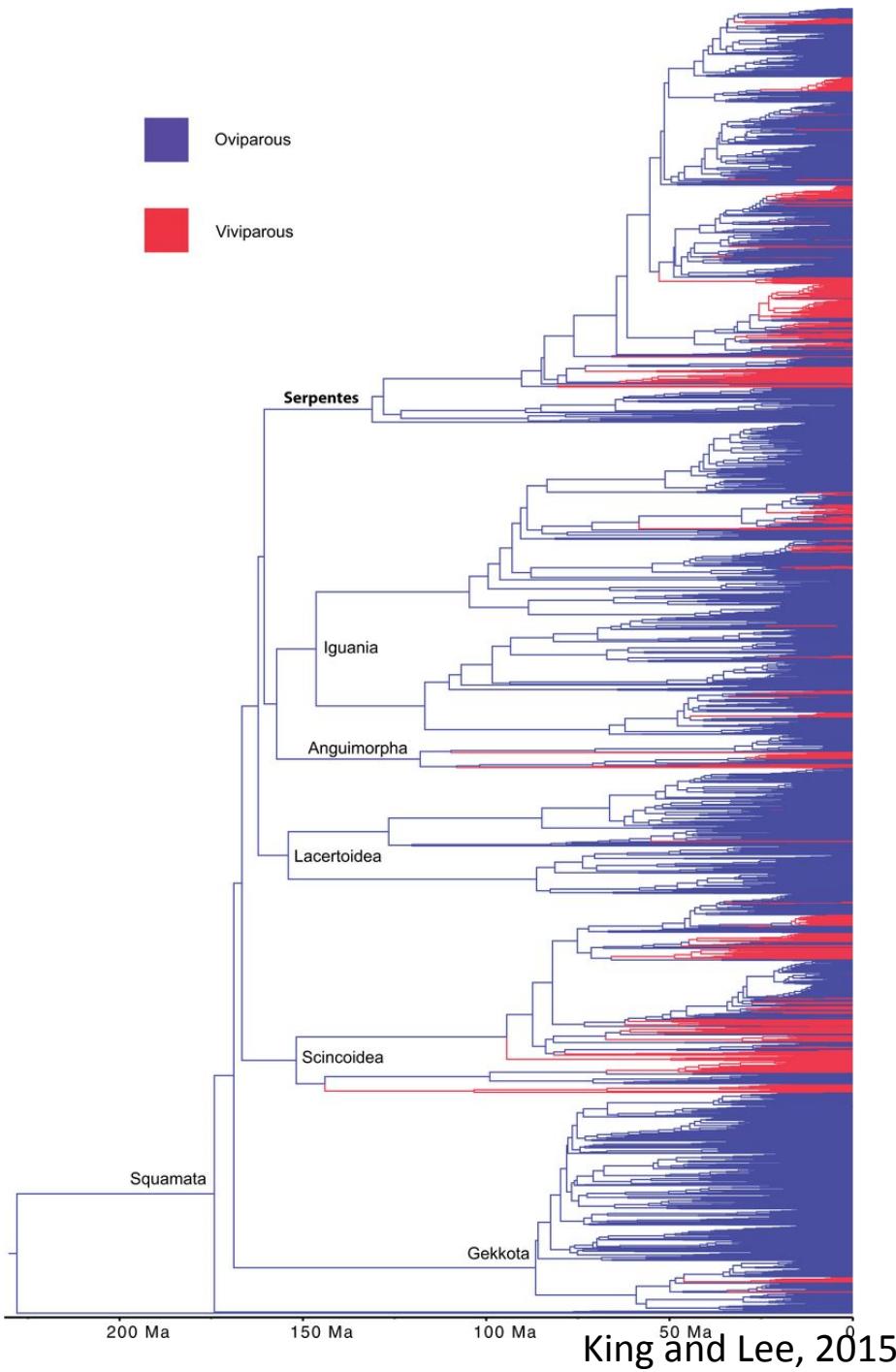
- Most changes occur in particular parts of the phylogeny
- BiSSE (and models in general) assume a single rate of evolution across the tree





“Random local clock” methods allow different rates in parts of the tree

- Most changes occur in particular parts of the phylogeny
- BiSSE (and models in general) assume a single rate of evolution across the tree

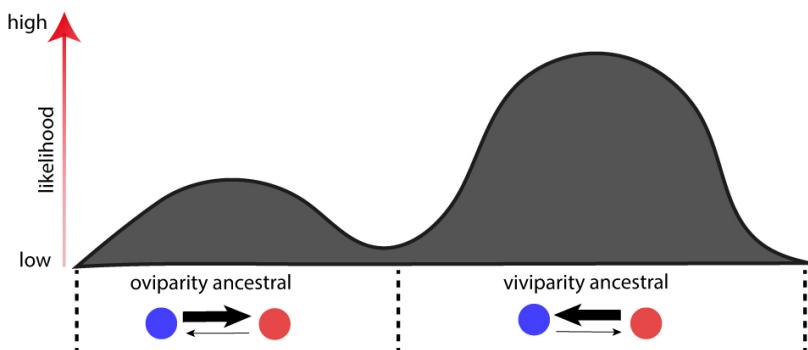


“Random local clock” methods allow different rates in parts of the tree

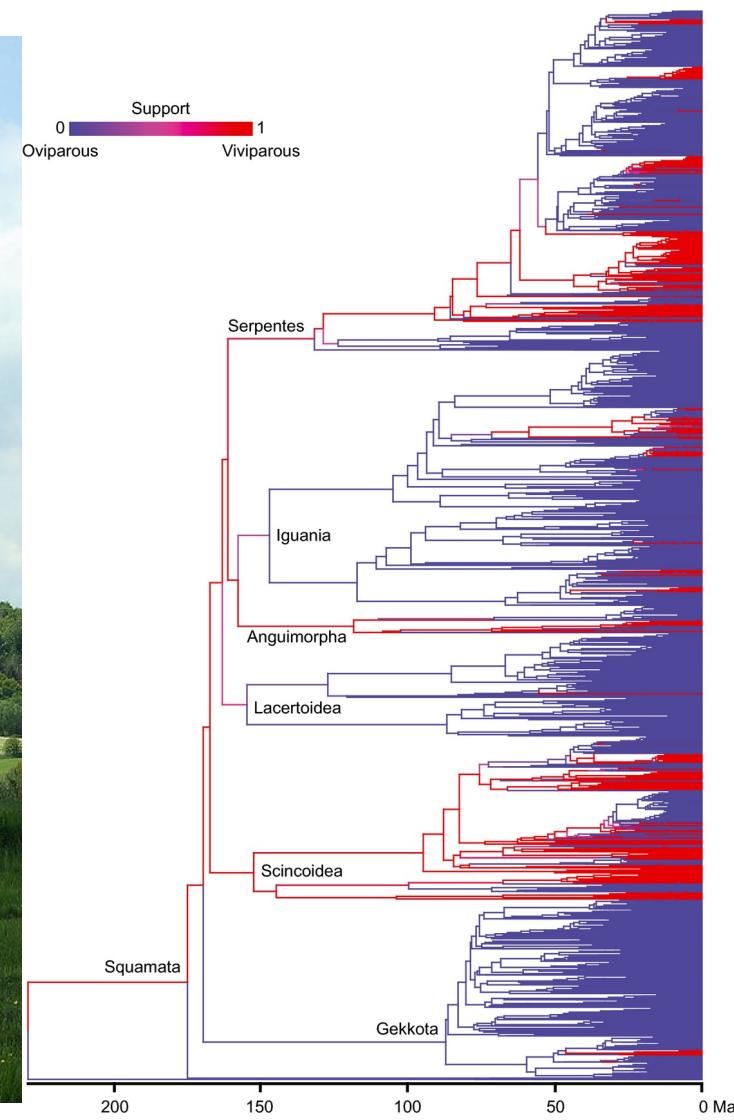
- Produce strong support for oviparity as the ancestral state, in total contrast to models that do not incorporate rate heterogeneity

The likelihood landscape

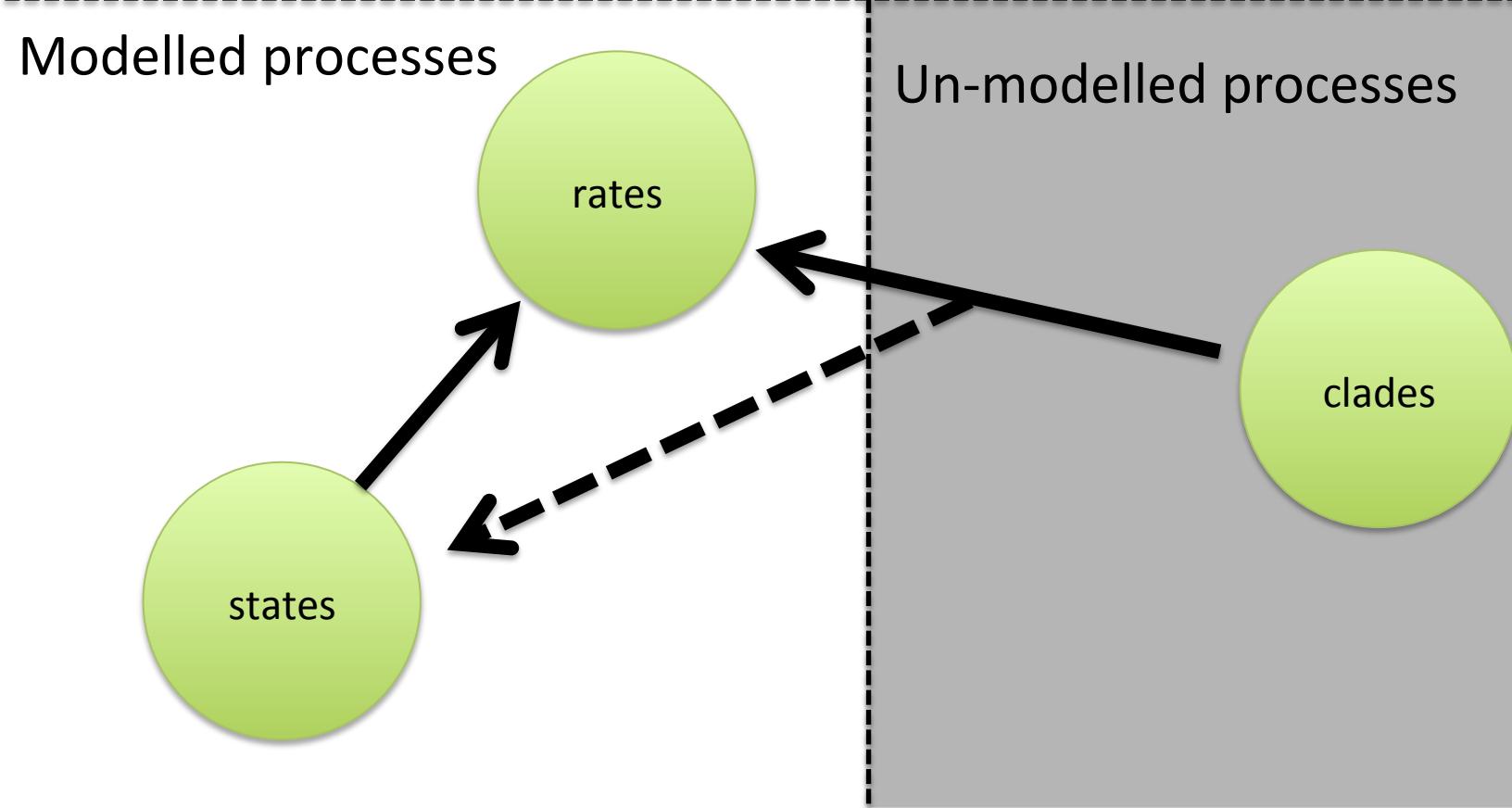
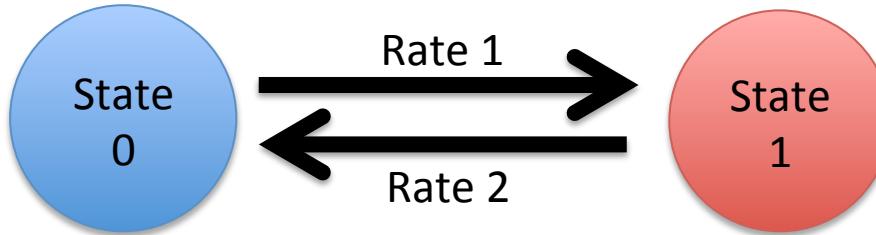
- Viviparity as the ancestral state has a higher likelihood peak
- However, we have restricted ourselves to a region of the likelihood landscape in which rates are the same across the whole tree



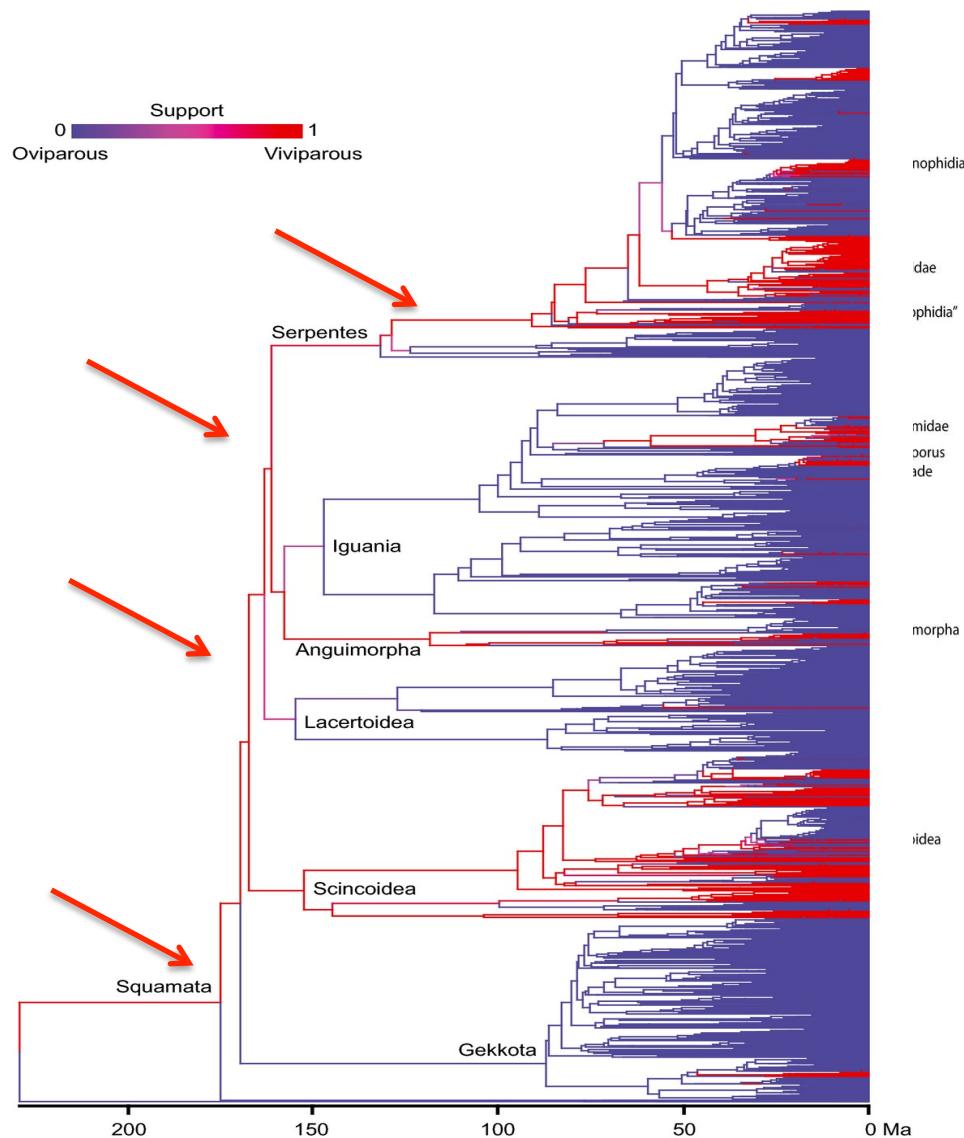
If you never leave the Netherlands, this might look like a mountain



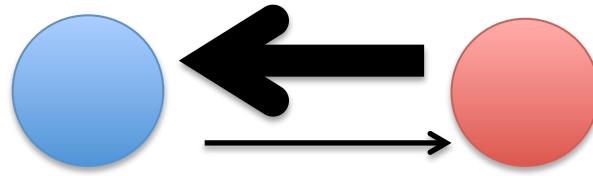
Processes that are not included in the model can lead to “parameter hijacking”



Parameter hijacking



1. Generate rate heterogeneity



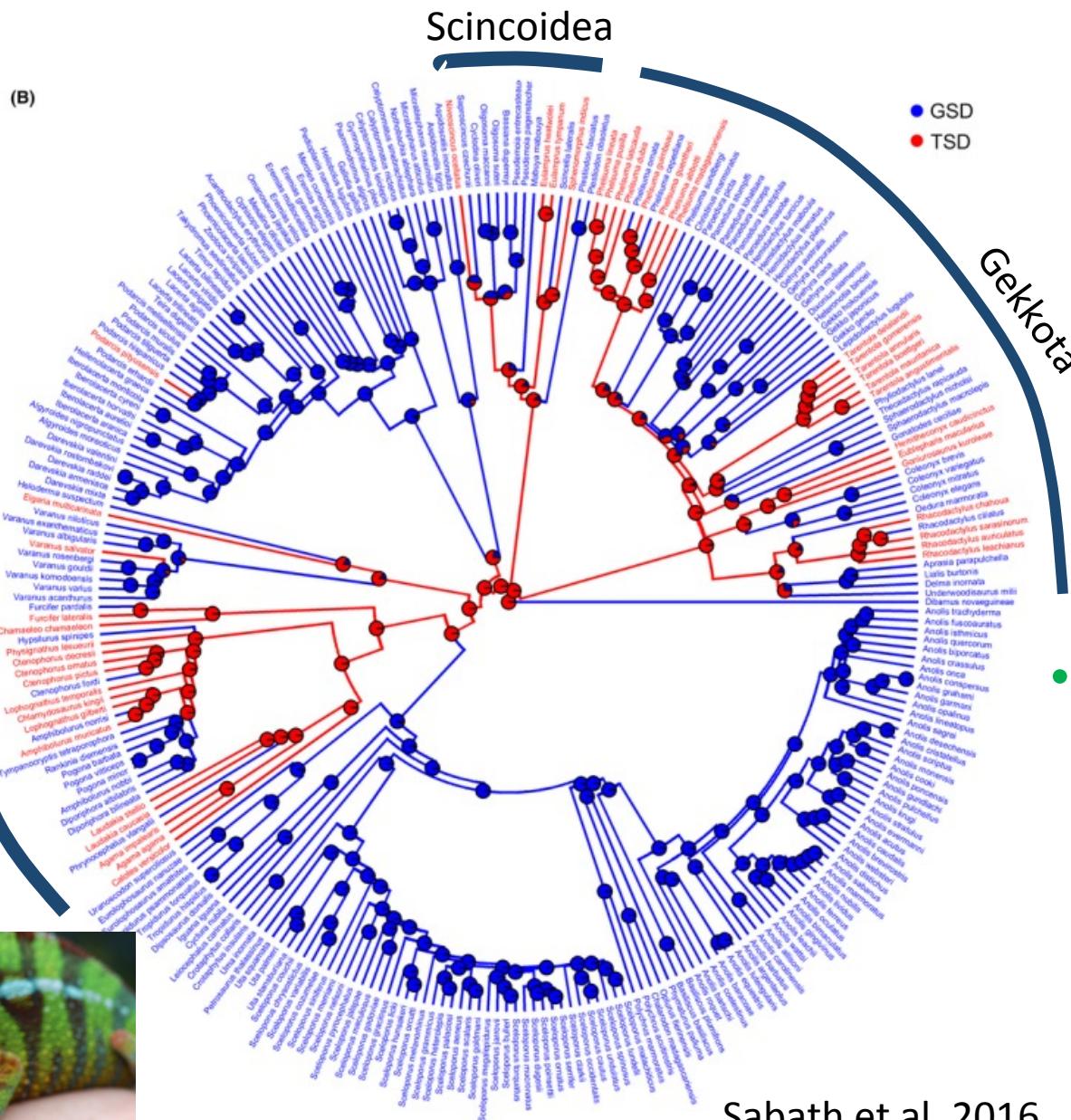
3. Place state with rapid rate in the clades with rapid rates

4. Bias in rates is so high that an ancestral state of the state with the rapid rate is strongly supported

RESULTS:

- **THE ANCESTRAL STATE RECONSTRUCTION IS A MEANINGLESS ARTIFACT**
- **INCORRECT ESTIMATION OF TRANSITION RATE ASYMMETRY I.E. HIGH RATE OF REVERSALS**

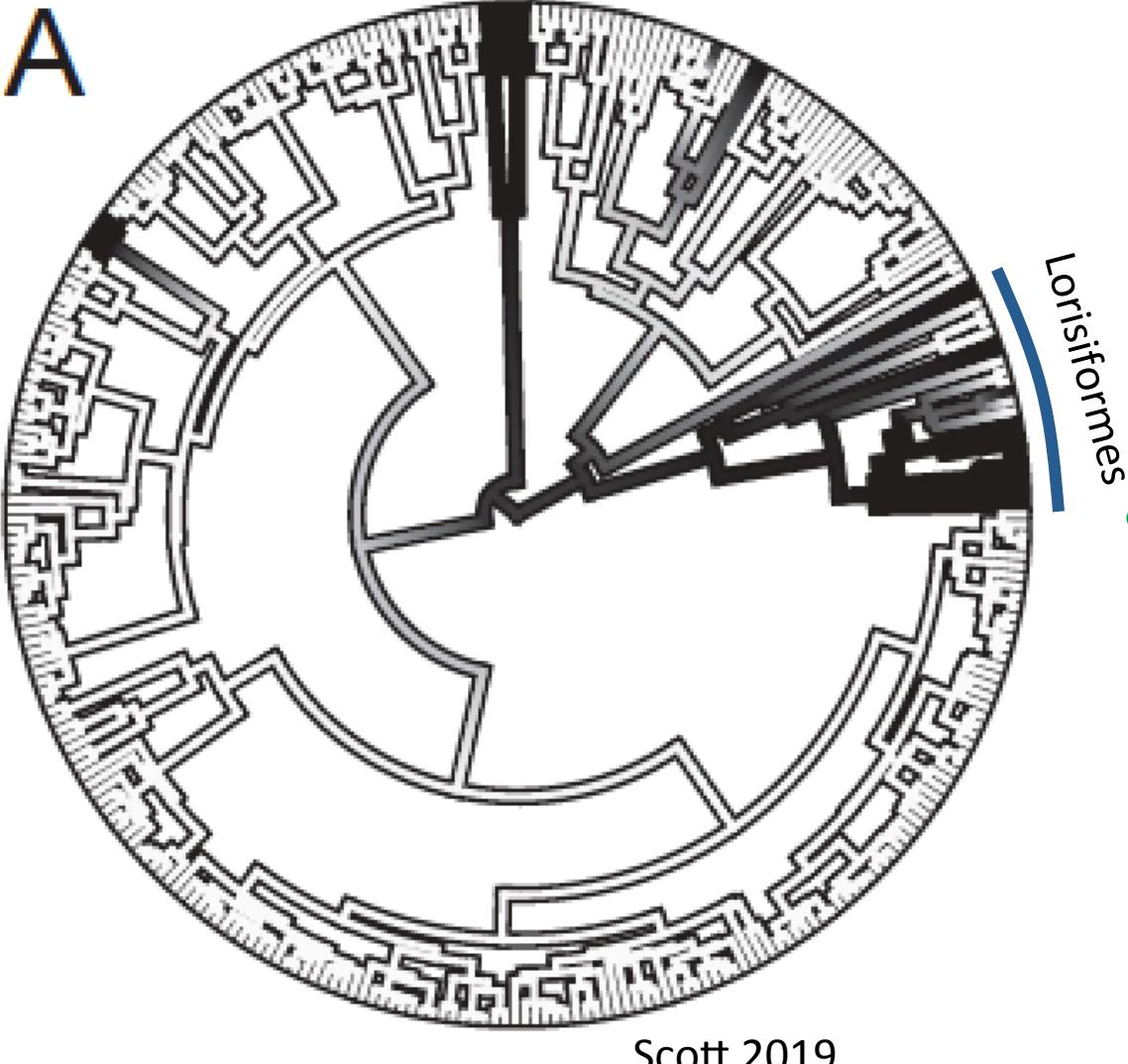
A common problem?



- Is temperature-dependent sex determination the ancestral state for reptiles?

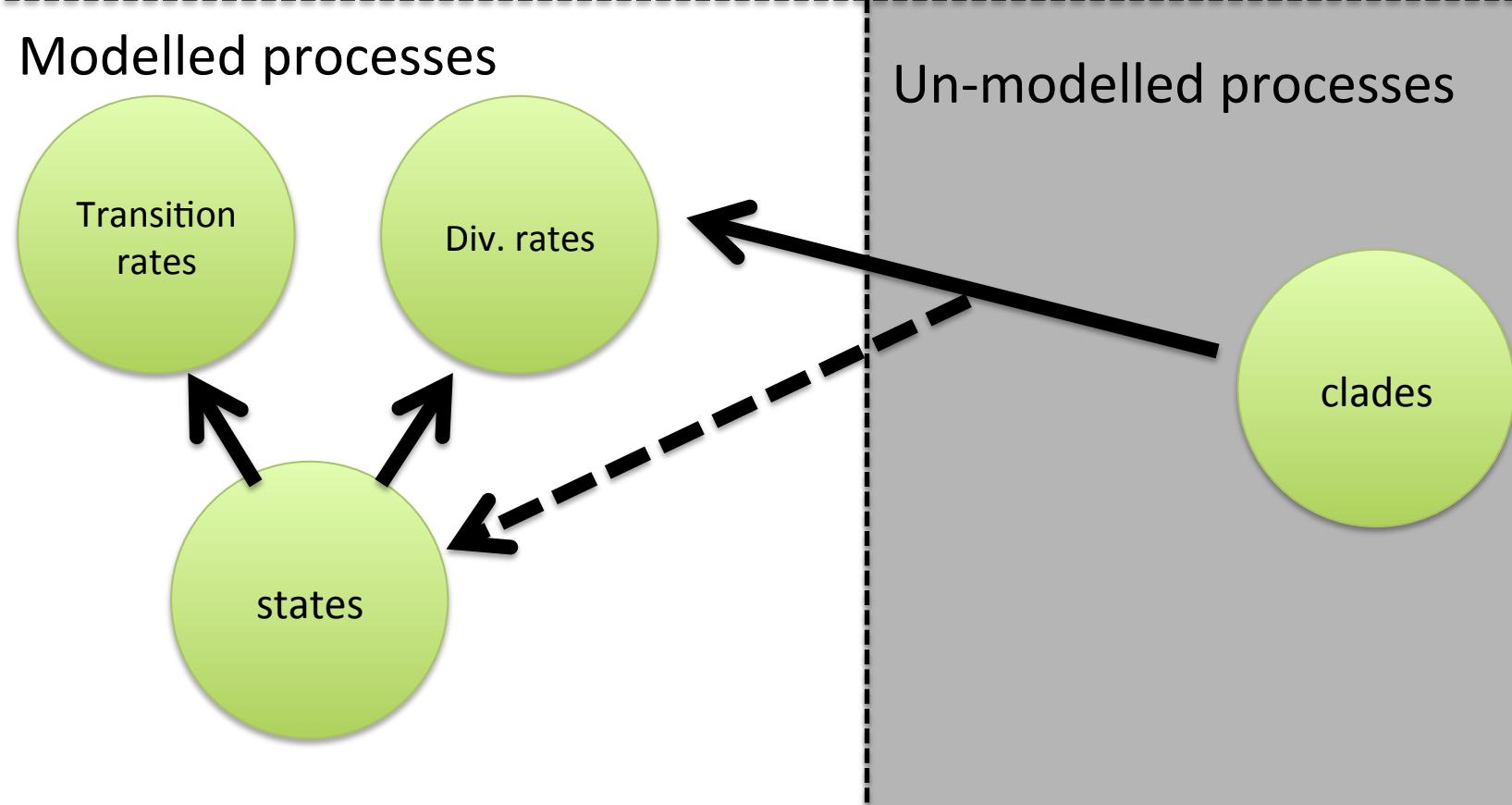
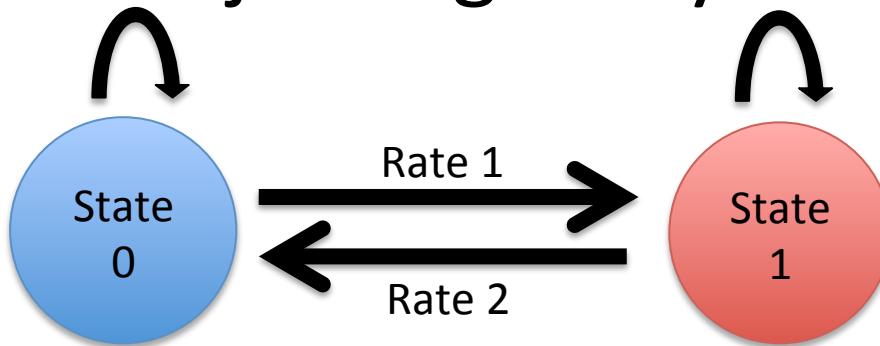
A common problem?

Uniform diversification,
unequal transition rates

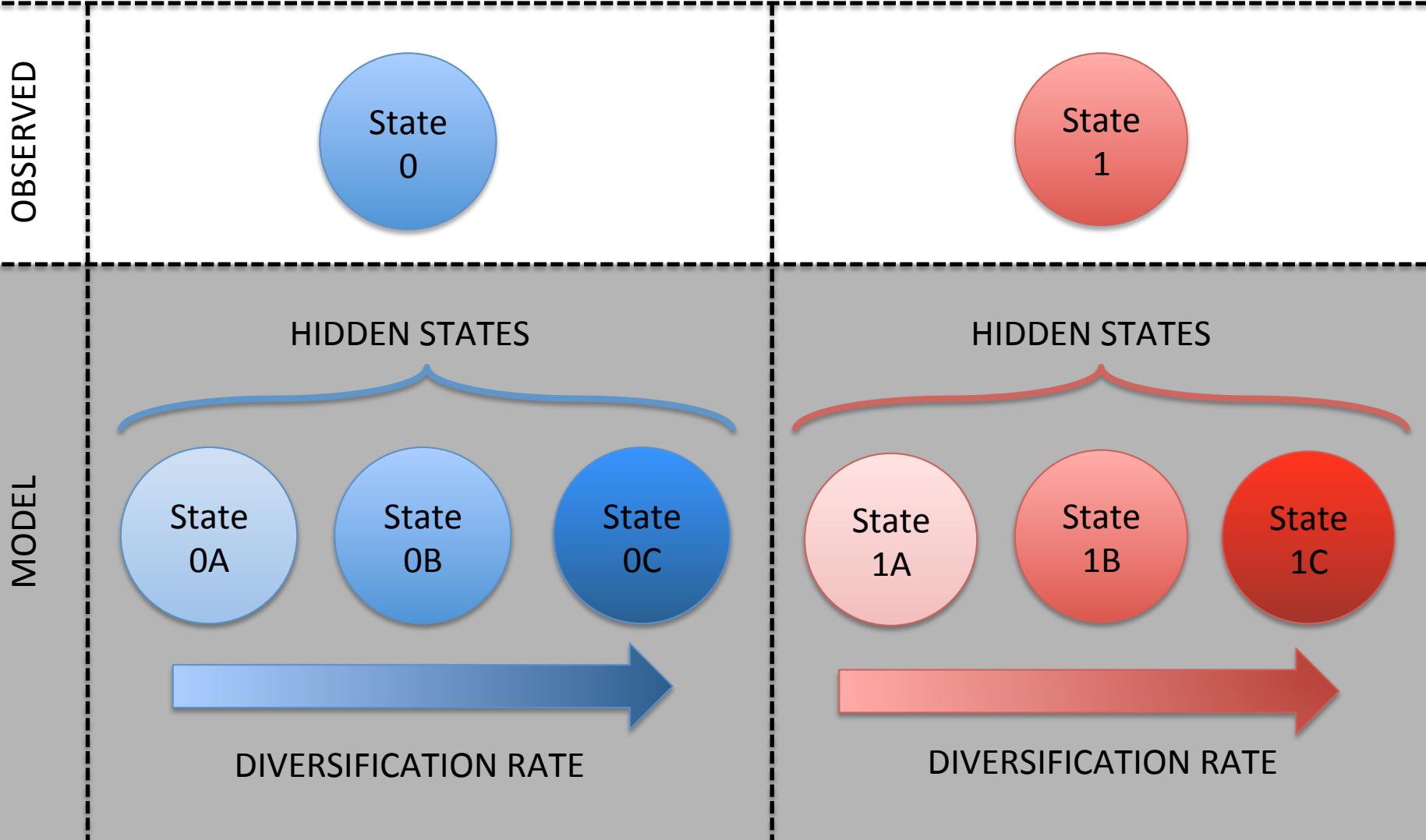


- Is insectivory (rather than herbivory) the ancestral state for primates?

“Parameter hijacking” may affect BiSSE

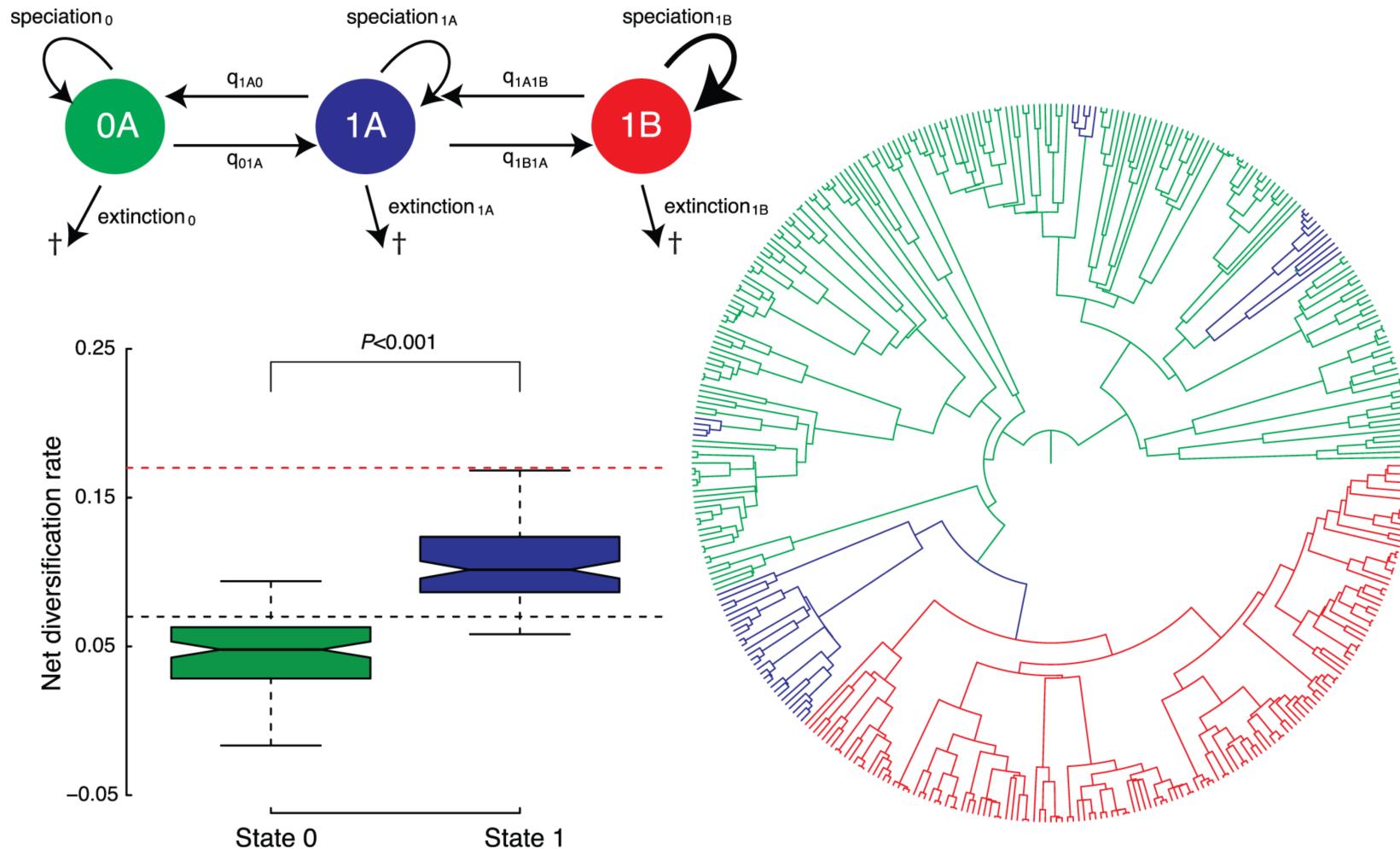


Hidden state models can improve model adequacy



HiSSE – hidden state speciation and extinction

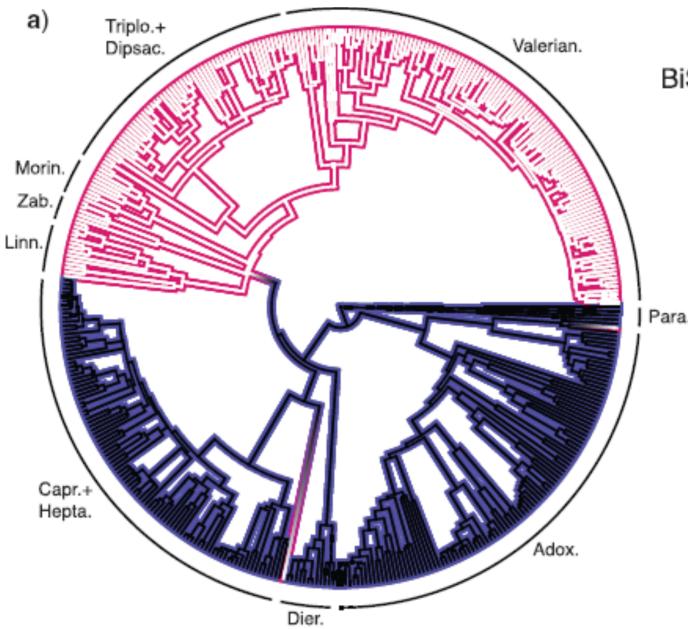
- Incorporates the possibility of unobserved processes affecting diversification



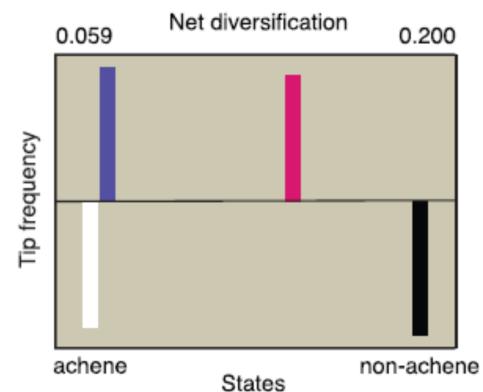
HiSSE example - Do achene fruits promote diversification



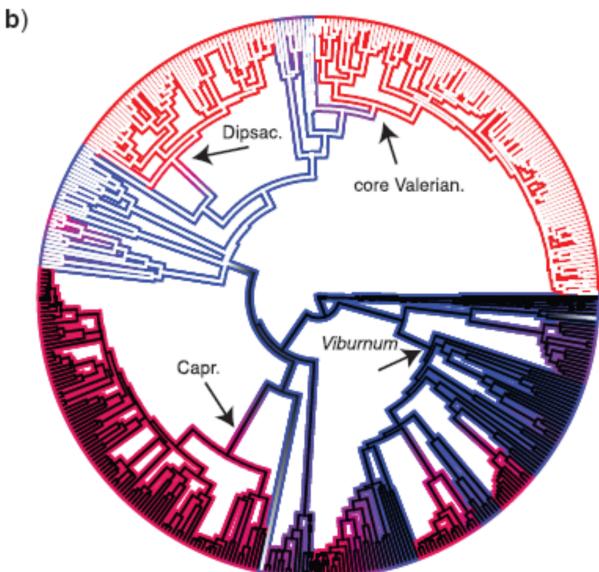
BiSSE suggests
achene fruits
promote
diversification



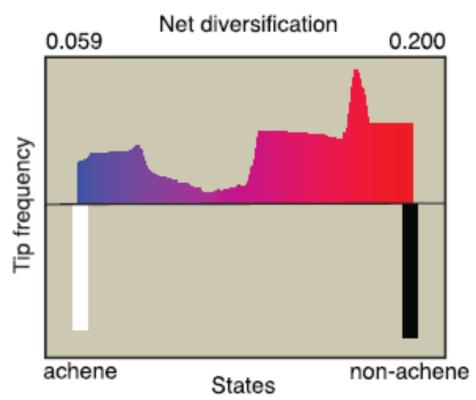
BiSSE



HiSSE reveals a
complex
pattern of
diversification
rates

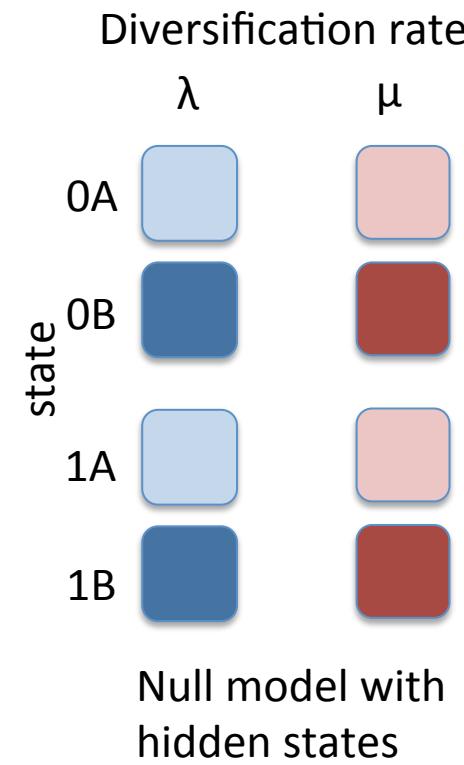
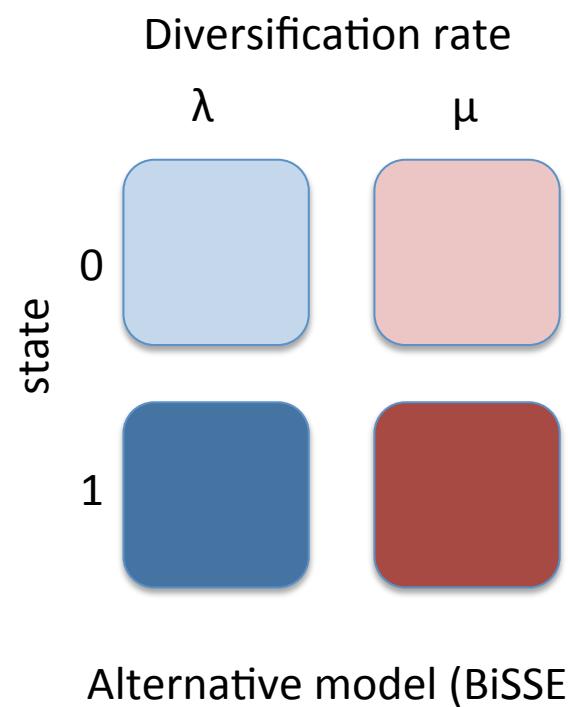
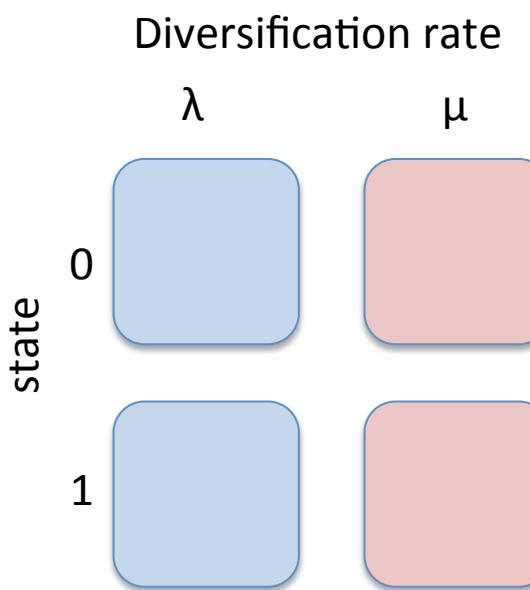


HiSSE



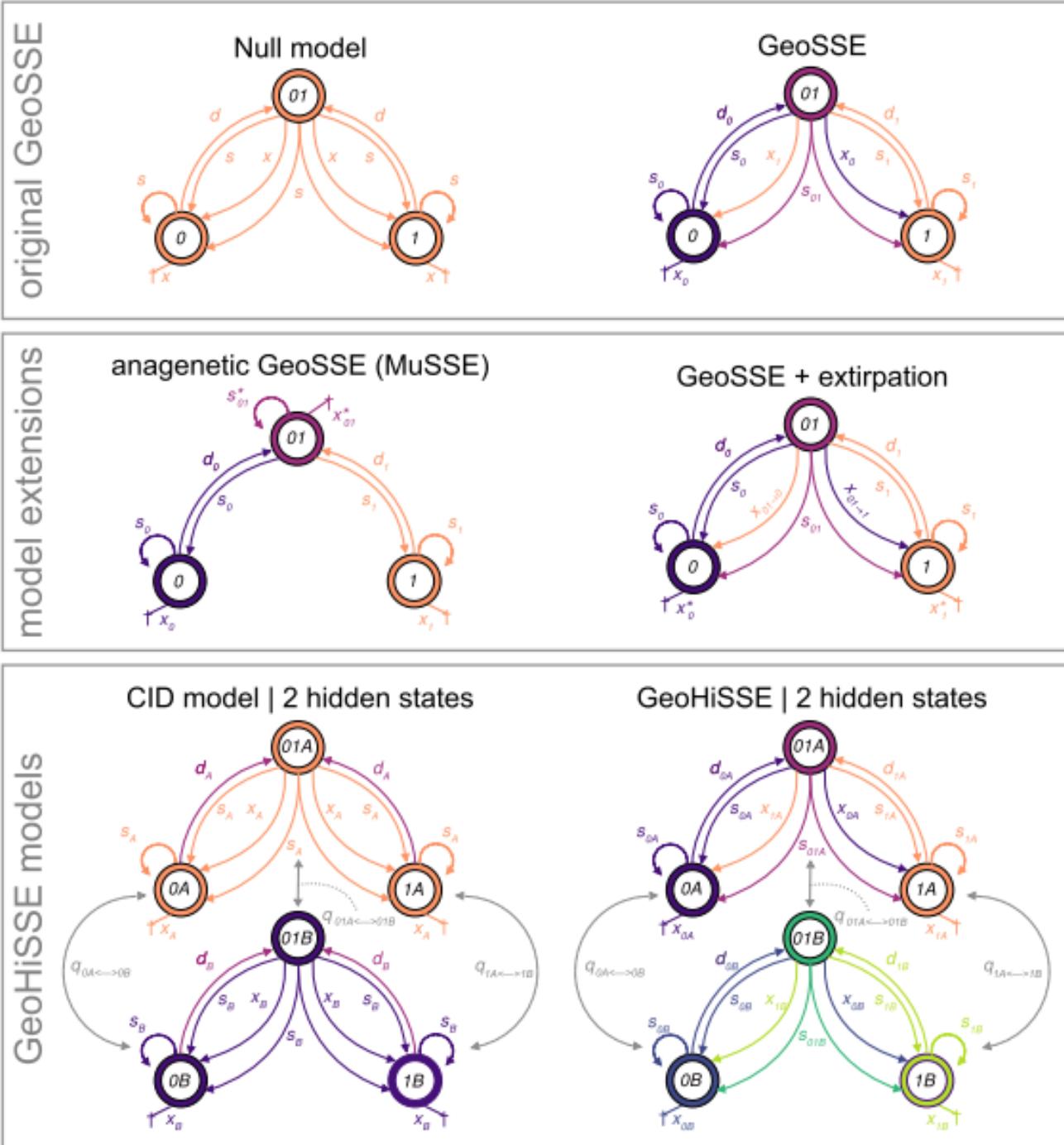
Hidden state models can be used to construct appropriate null models for BiSSE

- BiSSE might be supported over a null model without state dependent diversification simply because it contains at least **some** diversification rate heterogeneity
- A better comparison is to a model which contains the same amount of diversification rate heterogeneity, but where this is **not linked to the traits**



GeoHiSSE

- An extension of GeoSSE with hidden states

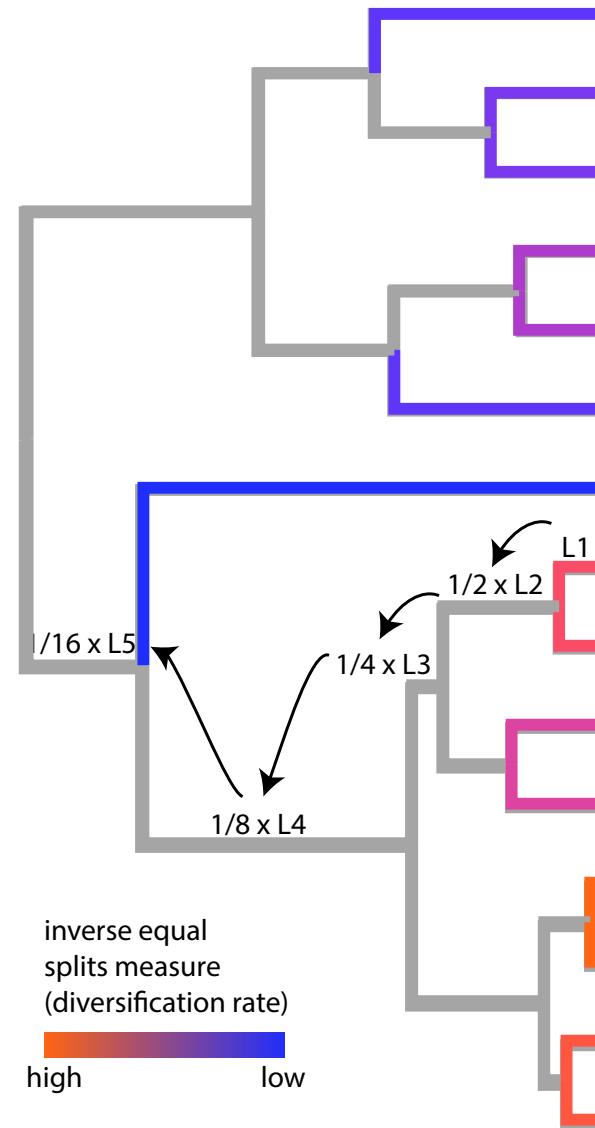


Non-parametric and semiparametric methods

- HiSSE is still susceptible to phylogenetic pseudoreplication
- Non-parametric methods have been developed to be used as additional tests
- These methods **calculate diversification rates without considering character states, then look for correlations**

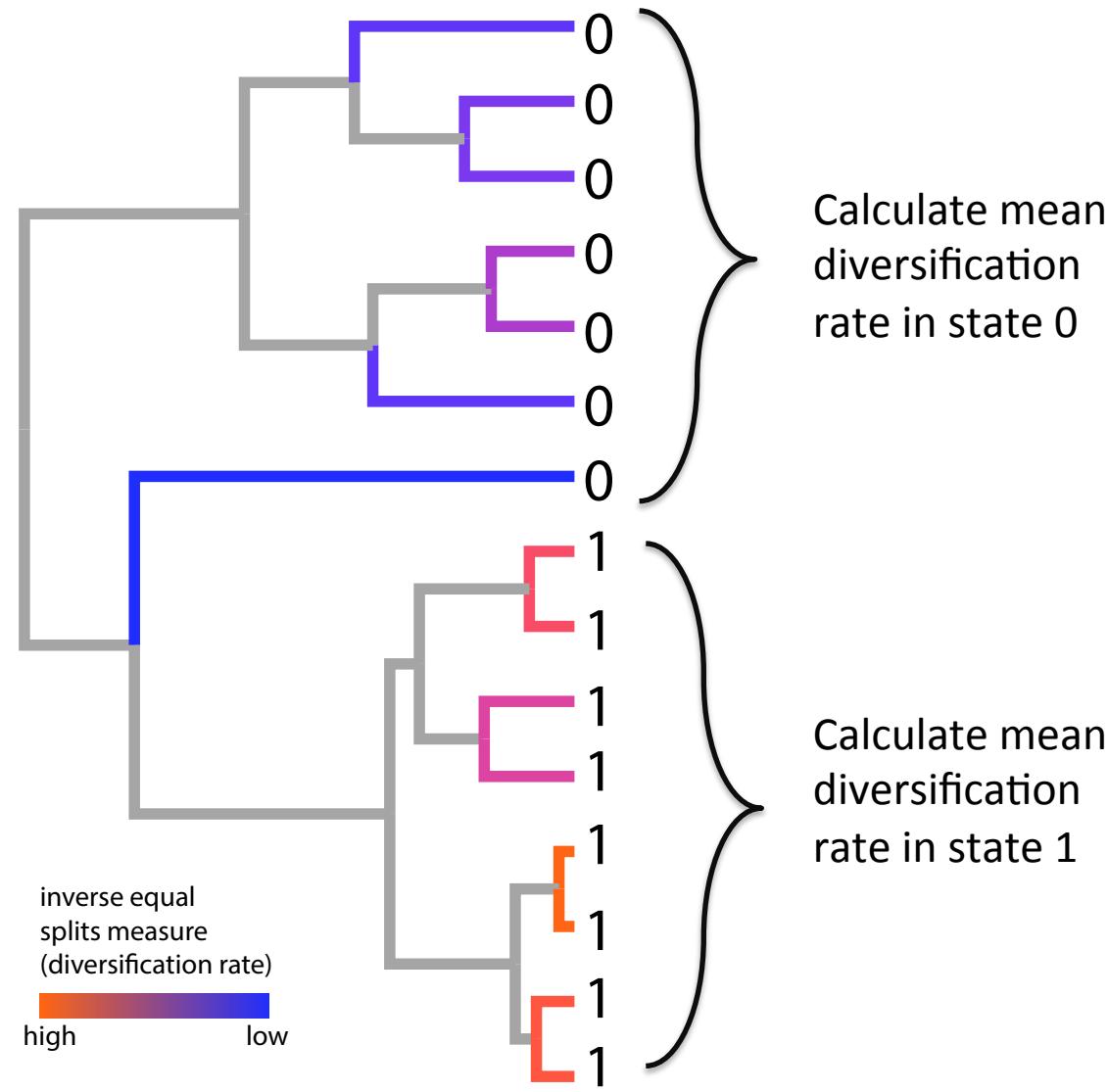
FiSSE – a nonparametric method

- First calculates diversification rates without considering the characters
- Inverse equal splits measure is a simple estimate of diversification rate



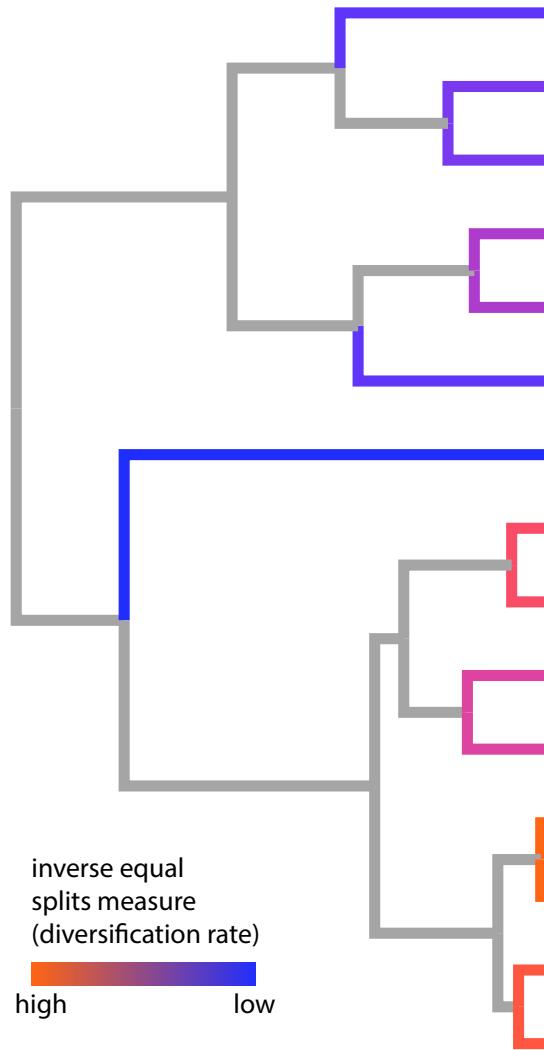
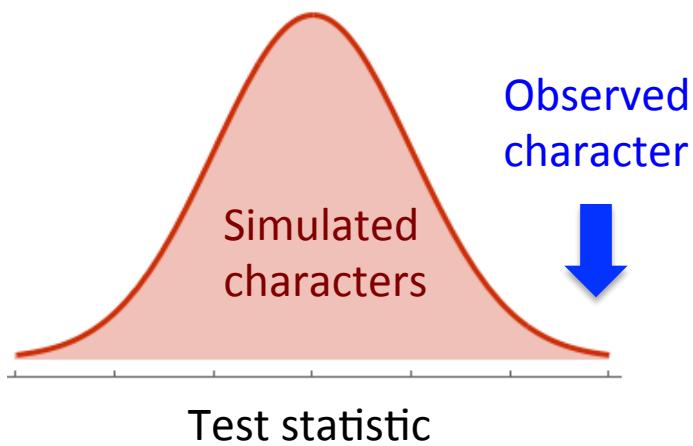
FiSSE – a nonparametric method

- Calculates mean diversification rate of state 0 and state 1
- The difference in mean is the test statistic



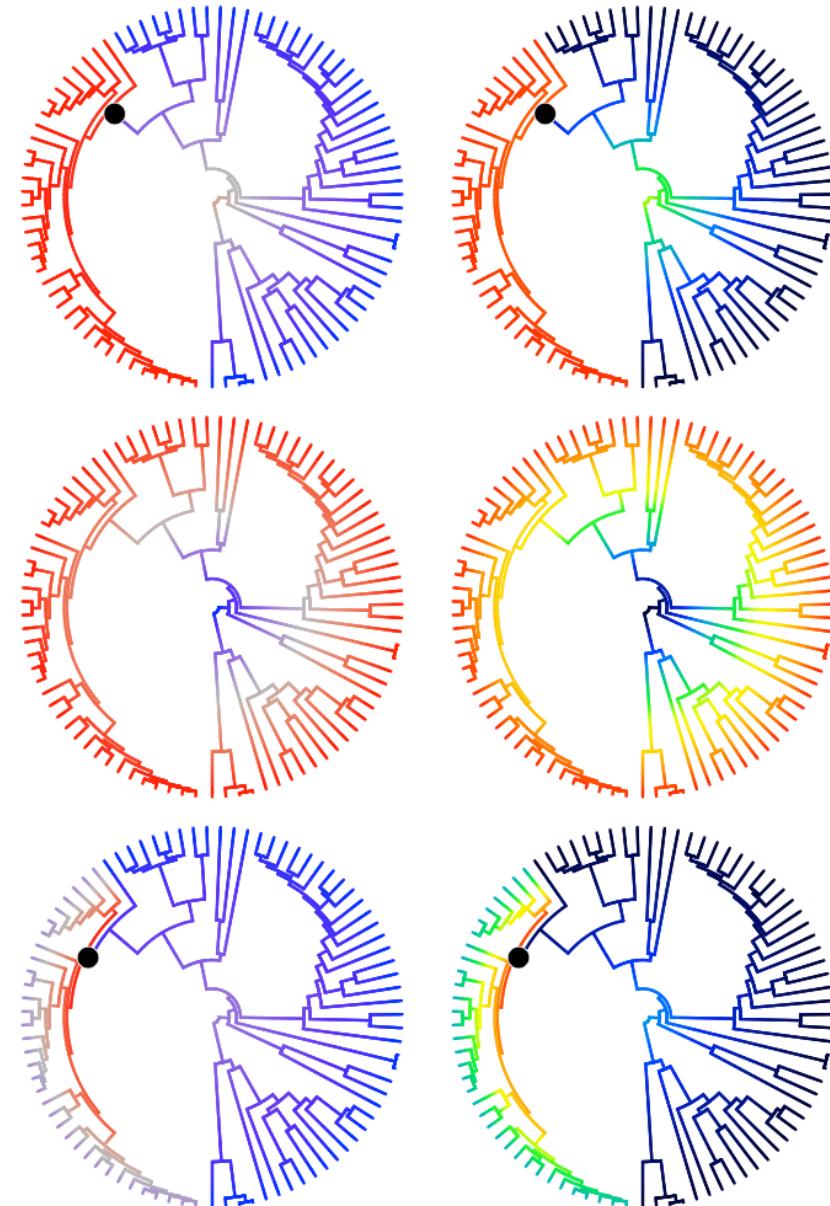
FiSSE – a nonparametric method

- Simulate random characters on the same tree
- Calculate the same test statistic for each of these



STRAPP – a semi-parametric method

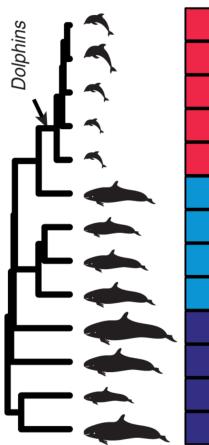
- First diversification rates are estimated without considering characters, using a program called BAMM
- BAMM splits the tree into a number of discrete blocks, each with a diversification rate “regime”
- BAMM produces a set of trees with assigned rate regimes
- If a particular rate regime appears in most of this sample, then it has strong support



Semi-parametric methods

- Randomly sample a BAMM rate regime configuration from the posterior sample
- Then calculate the correlation coefficient between diversification rate and character states
- Reshuffle the diversification rate regimes and calculate the correlation coefficient again
- Calculate how often the correlation for the random reshuffled data is greater than the true data – this proportion is the p value.

a) Permuting 1st sample from BAMM posterior rate distribution



Semi-parametric methods

- Always require several transitions
- For example if there is only one change in diversification rate and only one character change, even if they are perfectly correlated, the p value will be ~0.5
- Found to have lower false positive rates than BiSSE
- FiSSE and STRAPP both have low statistical power

Summary

