

Data-Driven Approaches vs. Hypothesis testing

**Why do we care about
phylogeny?**

Discrete Character Correlations

Pagel's Method (1994)

b Binary correlation

	00	01	11	10
00	-	r_A	0	r_B
01	r_C	-	r_D	0
11	0	r_E	-	r_F
10	r_G	0	r_H	-

If we can reject all of:
 $r_B = r_D$, $r_E = r_G$, $r_A = r_H$, $r_C = r_F$

Then there is evidence that
traits are correlated

Why?

**“Phylogenies help us to identify
independent evolutionary events,
and it is independent events that
statistical tests rely on”**

Harvey and Pagel, 1991

**Phylogeny introduces statistical
non-independence**

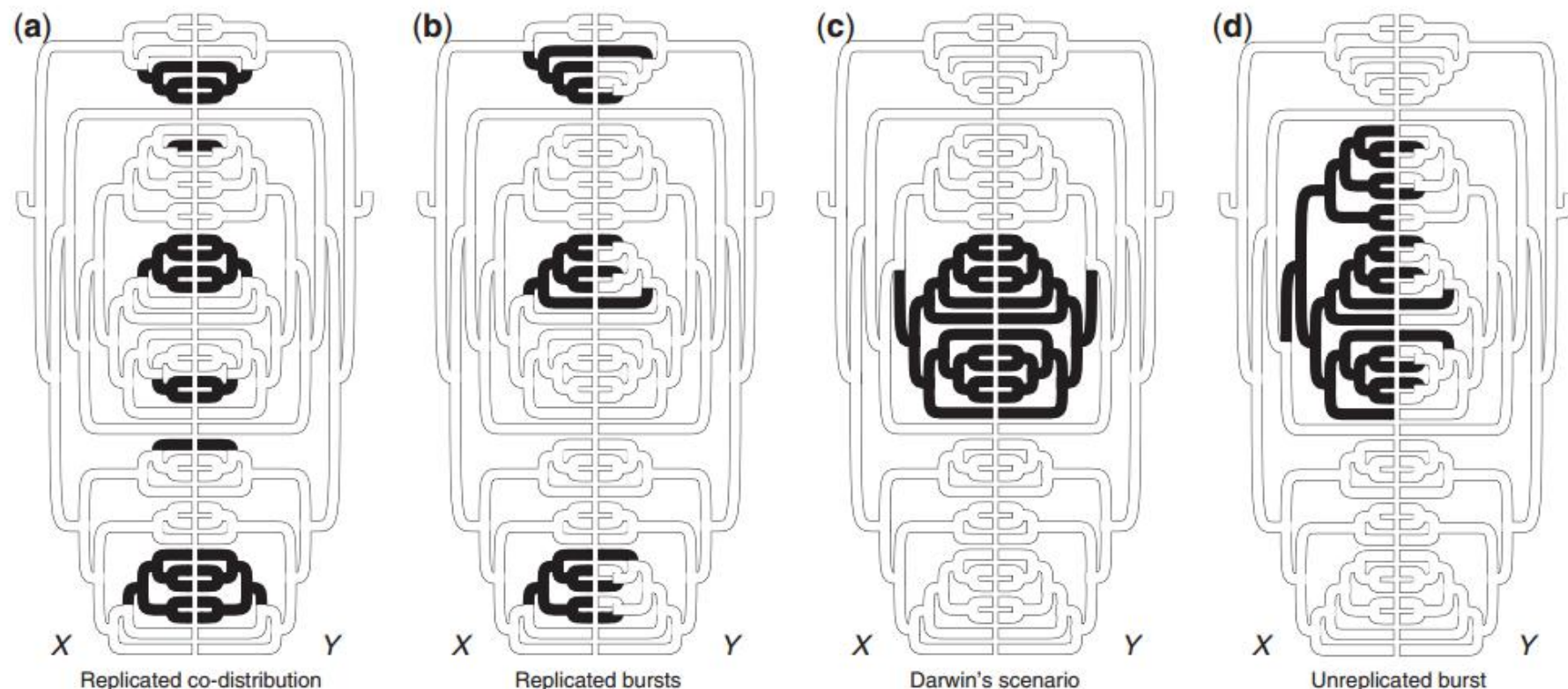
We may often falsely attribute to correlated variation structures which are common to whole groups of species, and which in truth are simply due to inheritance; for an ancient progenitor may have acquired through natural selection some one modification in structure, and, after thousands of generations, some other and independent modification; and these two modifications, having been transmitted to a whole group of descendants with diverse habits, would naturally be thought to be in some necessary manner correlated.

The Unsolved Challenge to Phylogenetic Correlation Tests for Categorical Characters

WAYNE P. MADDISON^{1,*} AND RICHARD G. FITZJOHN^{2,3}

¹*Departments of Zoology and Botany and Beaty Biodiversity Museum, University of British Columbia, 6270 University Boulevard, Vancouver, British Columbia, Canada V6T 1Z4;* ²*Departments of Zoology and Biodiversity Research Centre, University of British Columbia, 6270 University Boulevard, Vancouver, British Columbia, Canada V6T 1Z4 and* ³*Department of Biological Sciences, Macquarie University, Sydney NSW 2109, Australia*
*Correspondence to be sent to: Department of Zoology, University of British Columbia, 6270 University Boulevard, Vancouver, British Columbia, Canada V6T 1Z4; E-mail: wayne.maddison@ubc.ca.

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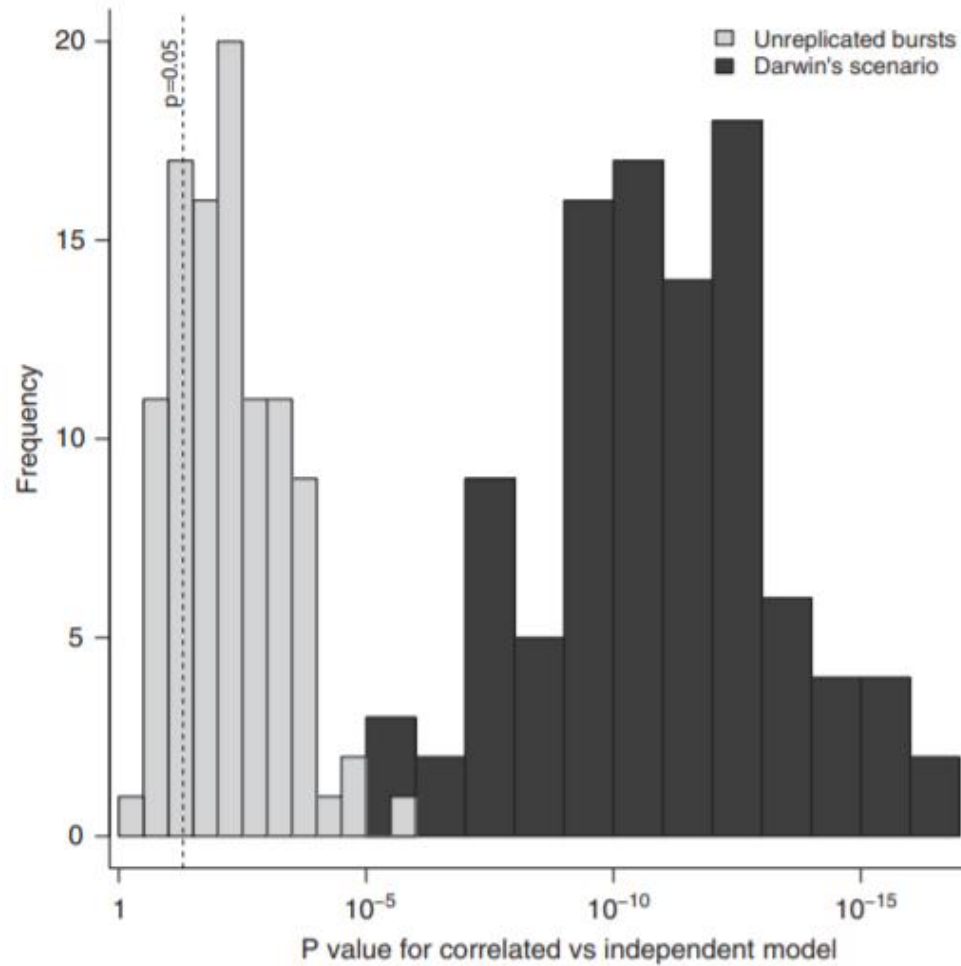
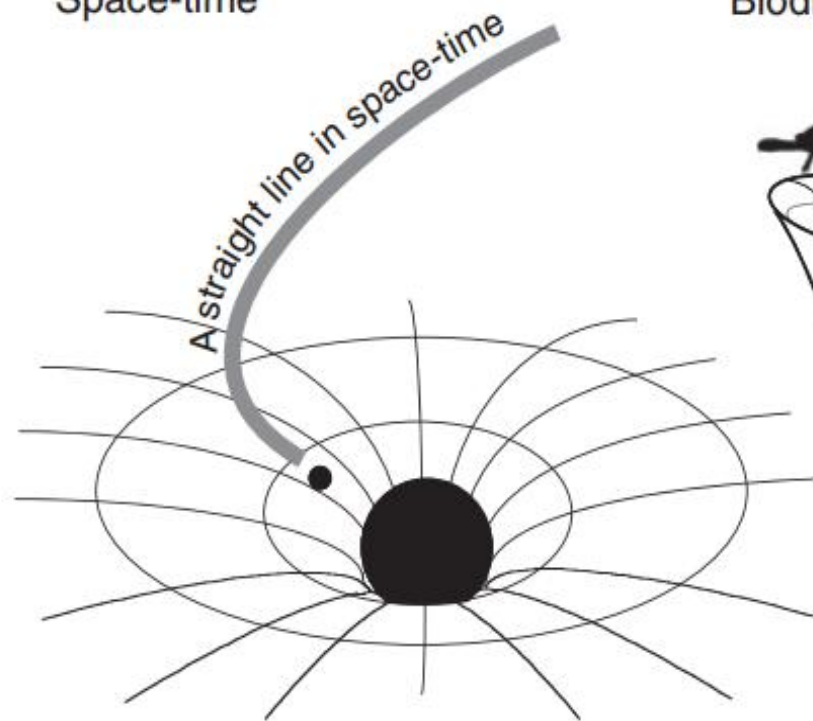


FIGURE 2. [Pagel's \(1994\)](#) test applied to 100 simulated cases like Fig. 1c (Darwin's scenario, dark grey) and like Fig. 1d (unreplicated bursts, light gray). Frequencies of log likelihood difference of correlated versus independent model $2(\ln(P(\text{data} | \text{correlated})) - \ln(P(\text{data} | \text{independent})))$. Vertical dashed line shows $P=0.05$.

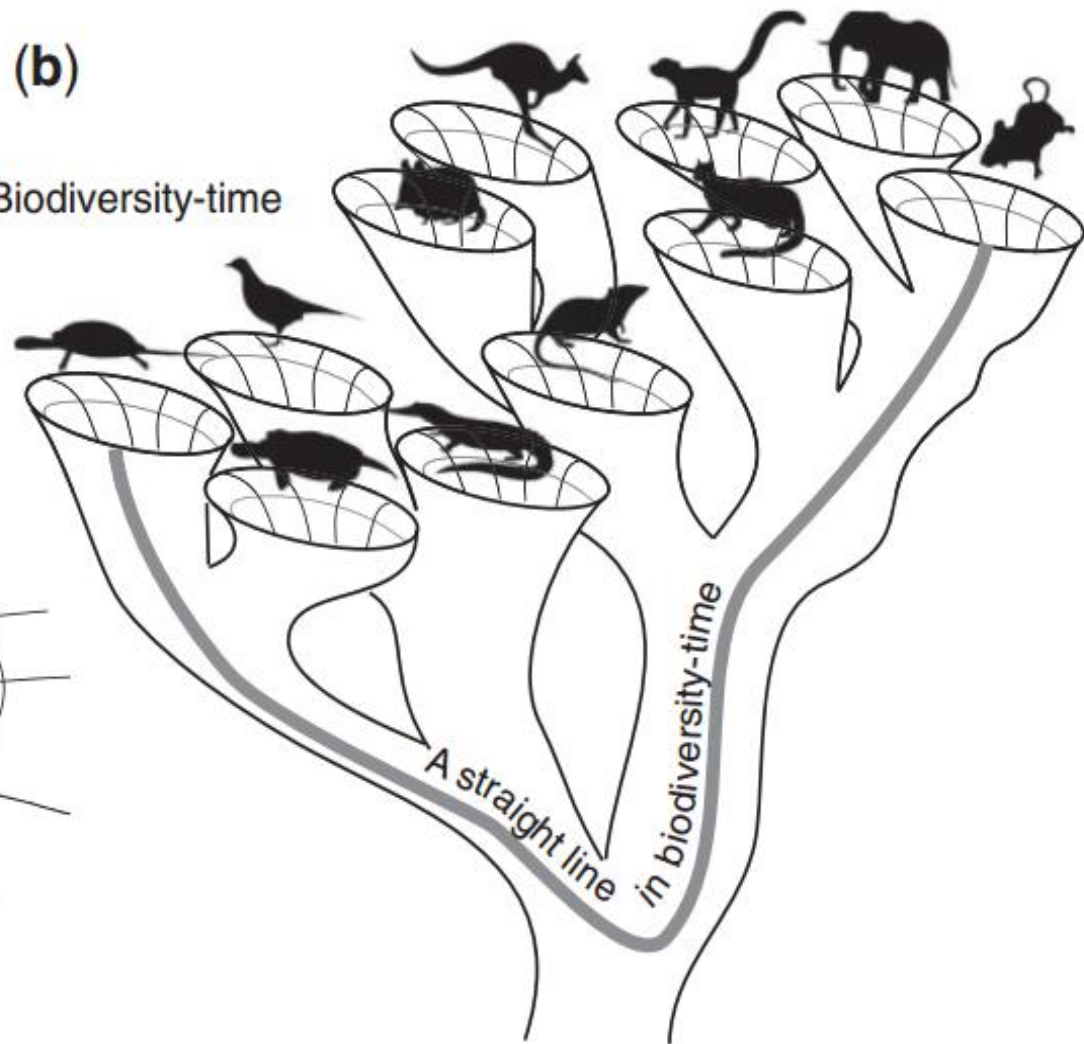
(a)

Space-time

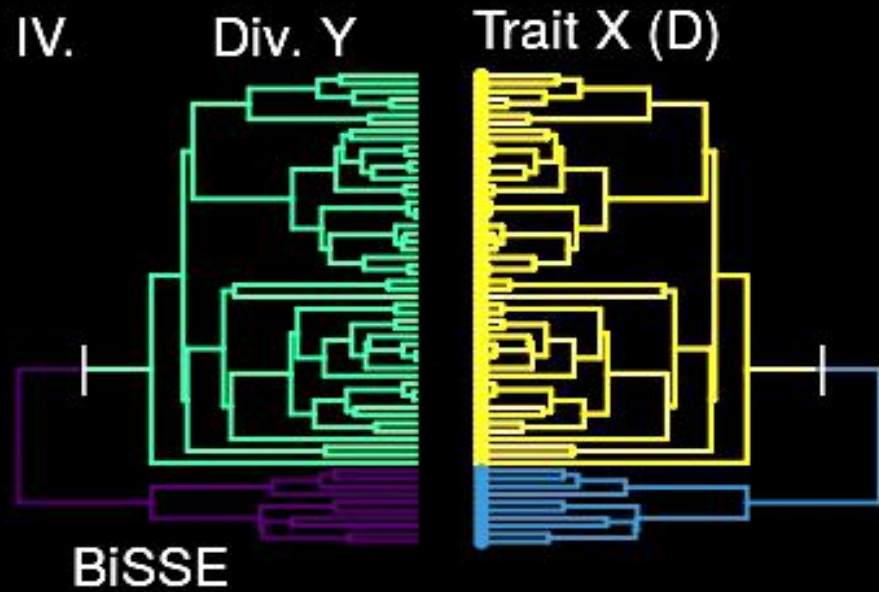
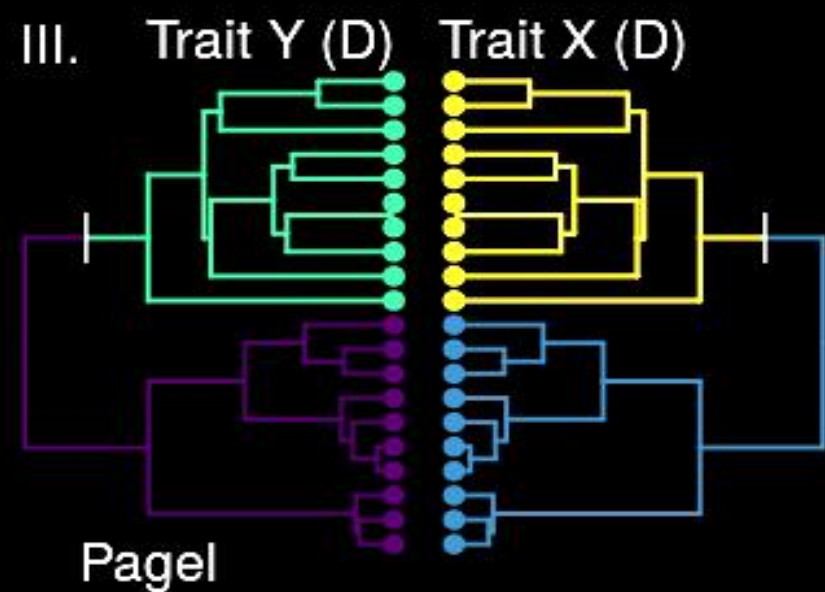
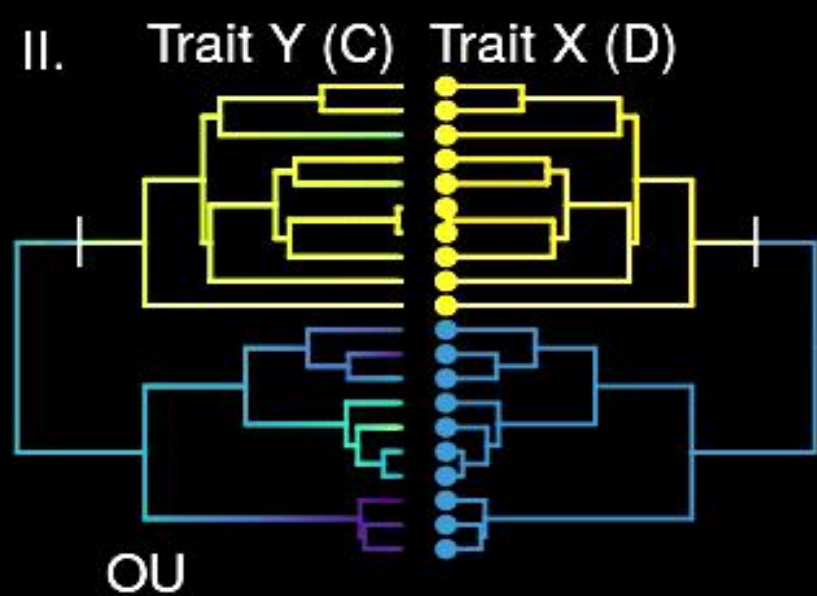
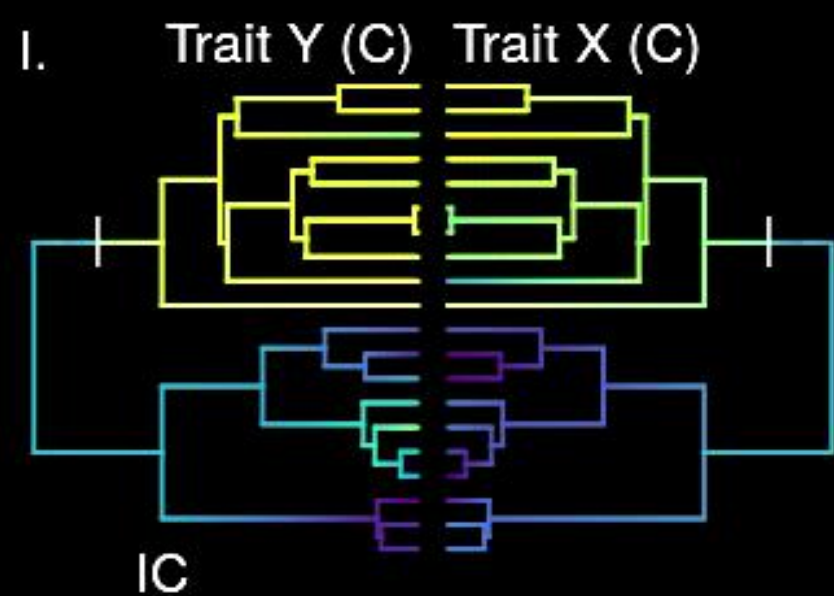


(b)

Biodiversity-time



Rare, singular events break
everything



Model Inadequacy and Mistaken Inferences of Trait-Dependent Speciation

DANIEL L. RABOSKY^{1,*} AND EMMA E. GOLDBERG²

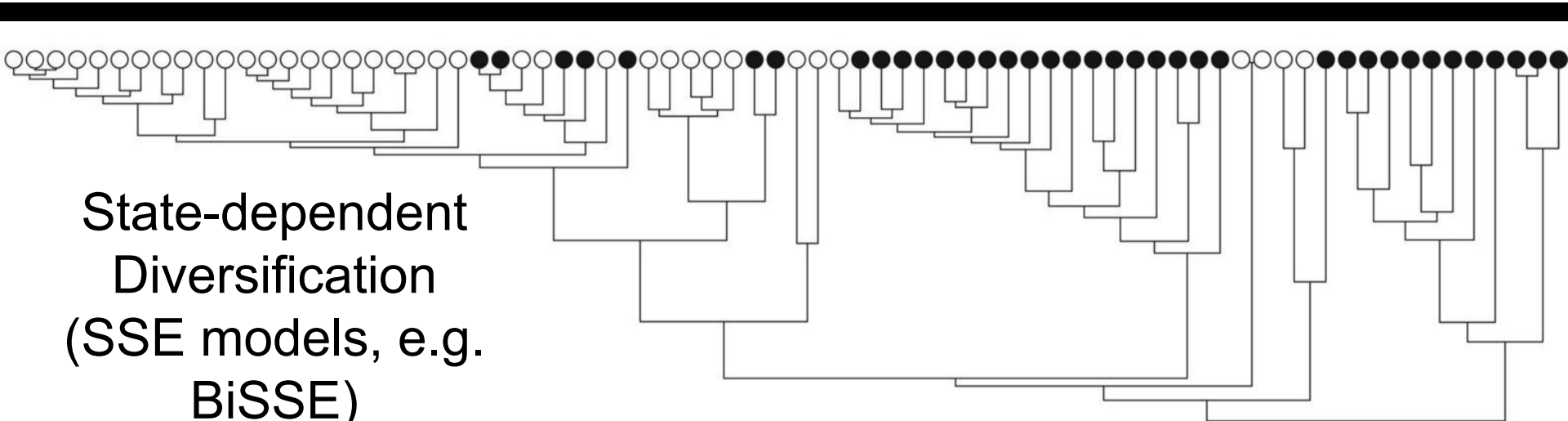
¹Museum of Zoology and Department of Ecology and Evolutionary Biology, University of Michigan, Ann Arbor, MI 48109; and ²Department of Ecology, Evolution, and Behavior, University of Minnesota, Saint Paul, MN 55108, USA

*Correspondence to be sent to: Museum of Zoology and Department of Ecology and Evolutionary Biology, University of Michigan, Ann Arbor, MI 48109 USA; E-mail: drabosky@umich.edu.

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Daniel L. Rabosky and Emma E. Goldberg contributed equally to this article.



**77% of 400 datasets showed a significant
association between speciation rate and
*taxon name length (!!!)***

The story of the boy who cried wolf is a popular mnemonic for understanding what we mean when we refer to the difference between true type I and type II errors, which can be extended to include comparisons between complex and overly simplistic models. When the boy first cried wolf, but there was no wolf, he was making a type I error—that is, falsely rejecting the null of a wolf-free meadow. When the townspeople later ignored him when there was actually a wolf, they were making a type II error. If the sheep were instead perishing in a snowstorm, and the only options for the boy are to yell “no wolf!” or “wolf!” it is not clear what the best behavior is—“no wolf” implies no change in sheep mortality rates from when they happily gambol in a sunny meadow, even though they have begun to perish, whereas “wolf” communicates the mortality increase even though it is the wrong mechanism. It is the same here when looking at a tree coming from an unknown, but complex empirical branching process and trying to compare a constant rate model (no wolf) against a state-dependent (wolf), age-dependent (bear), or density-dependent model (snowstorm).

ORIGINAL ARTICLE |  Full Access |

Hidden state models improve state-dependent diversification approaches, including biogeographical models

Daniel S. Caetano✉, Brian C. O'Meara, Jeremy M. Beaulieu

Constant rate diversification Vs. Trait-dependent diversification

Beaulieu and O'Meara (2016)

Constant rate diversification

Vs.

Trait-dependent diversification

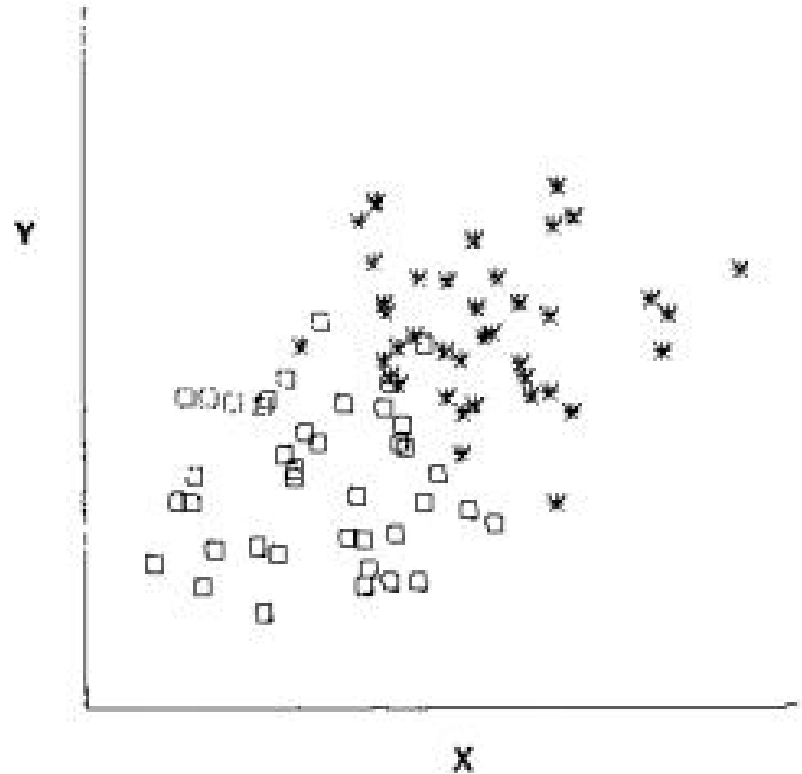
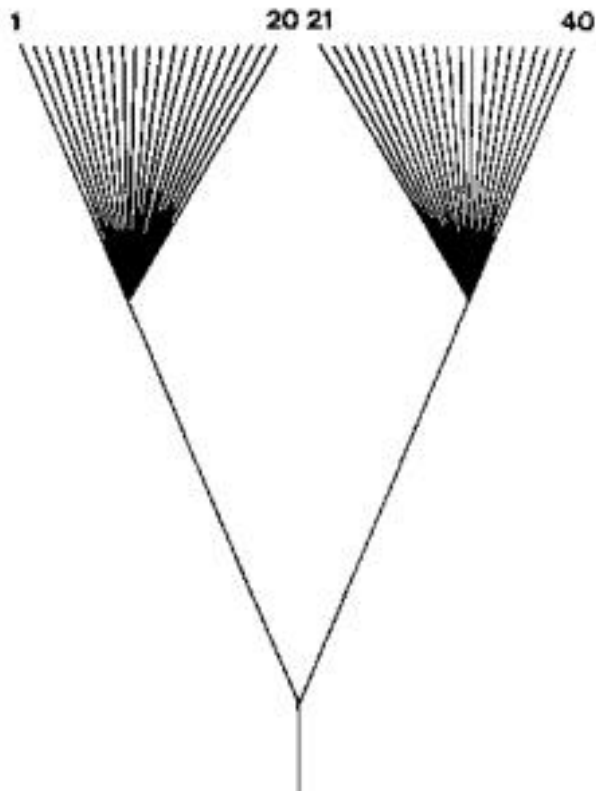
Vs.

**Variable diversification
independent of trait**

Beaulieu and O'Meara (2016)

Case Study I.

Let's revisit Felsenstein 1985...

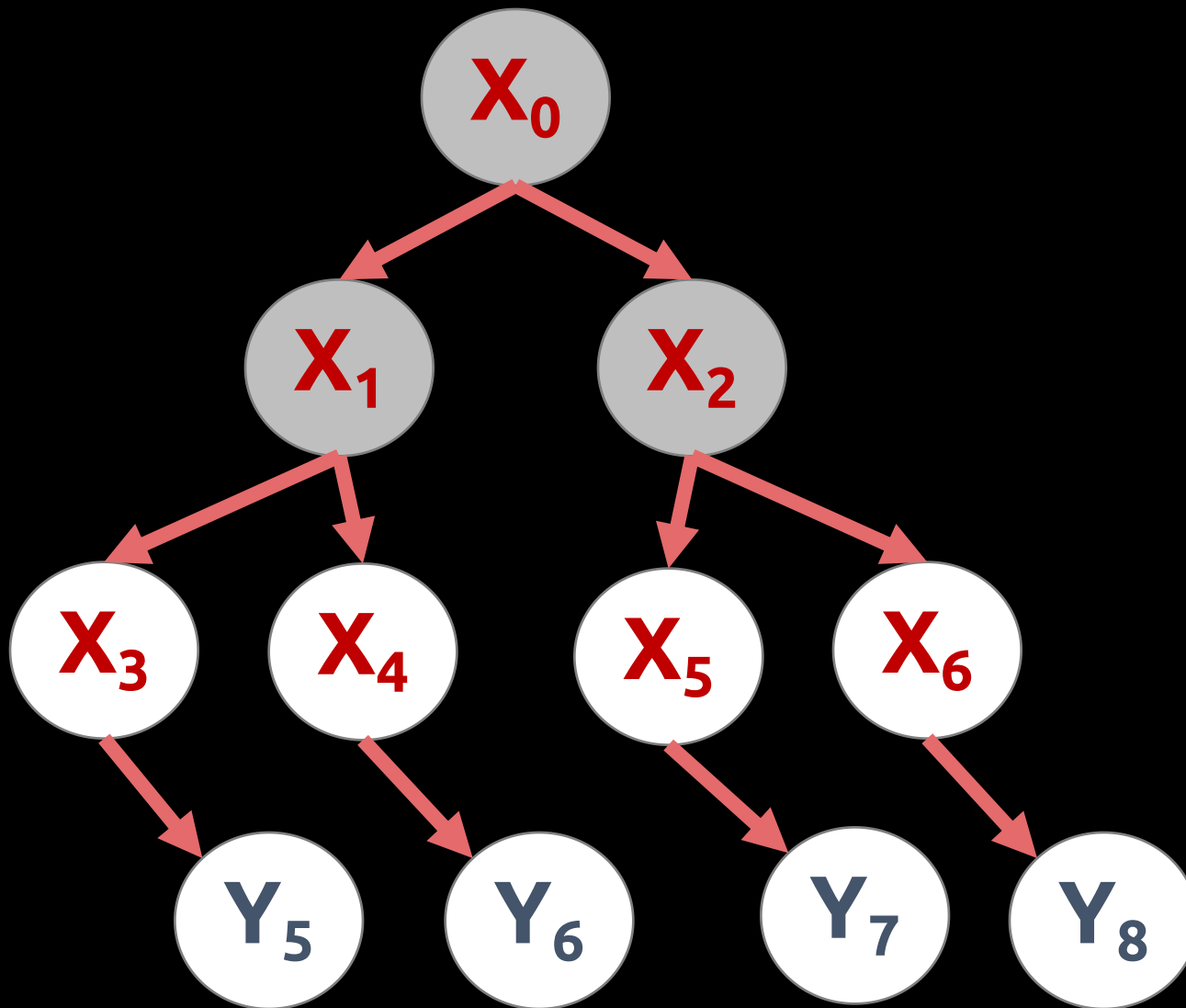


Why can't we do "regular" linear regression again?



**Non-independence
of species**

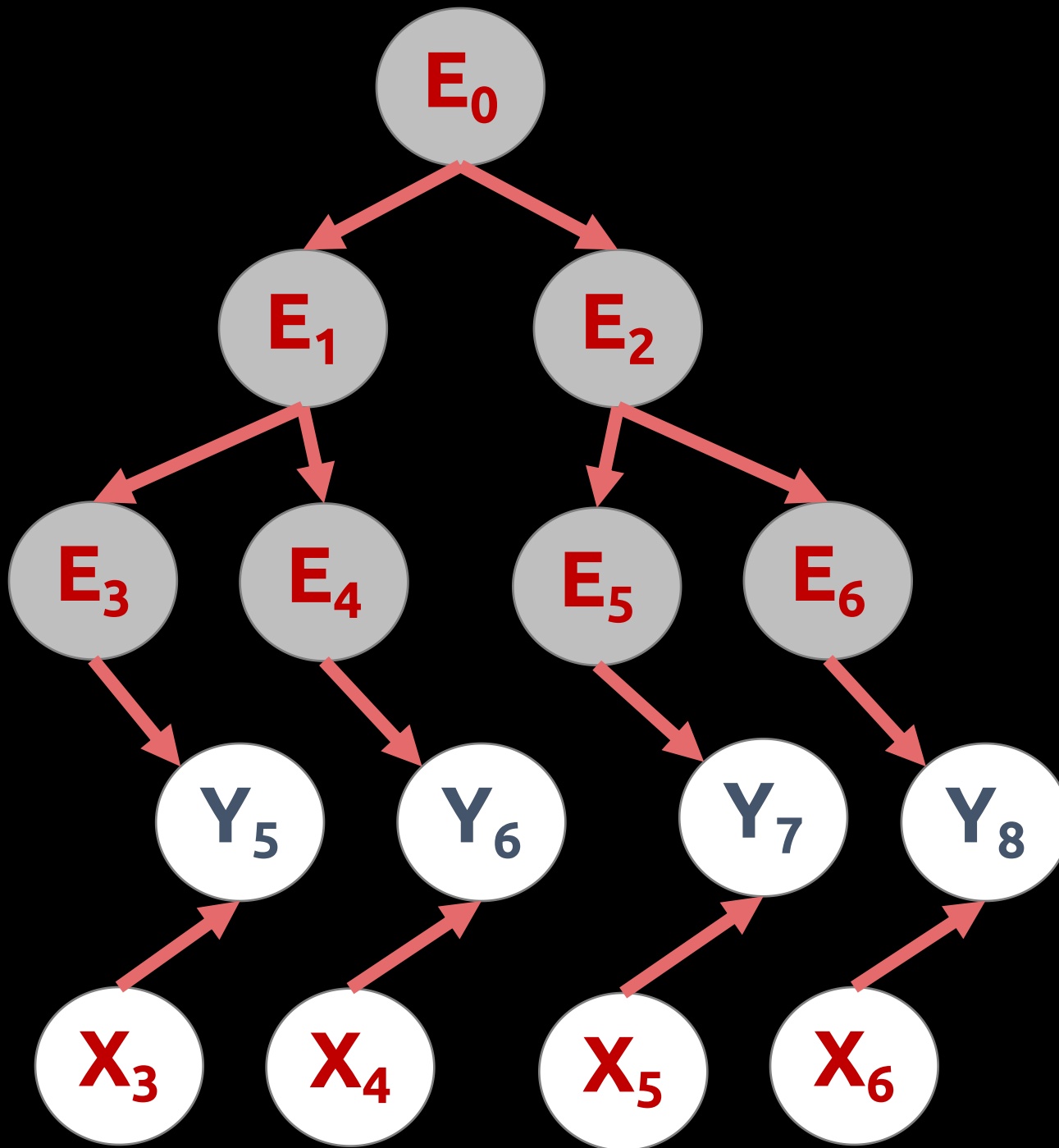
$$Y \sim X$$

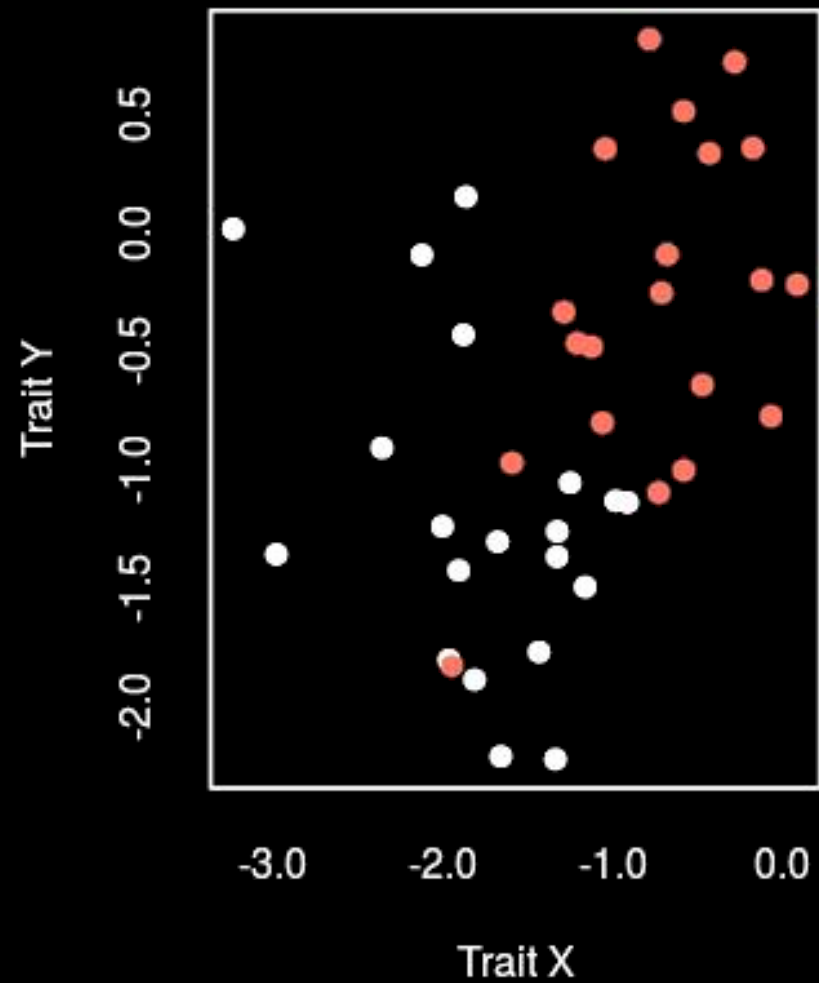
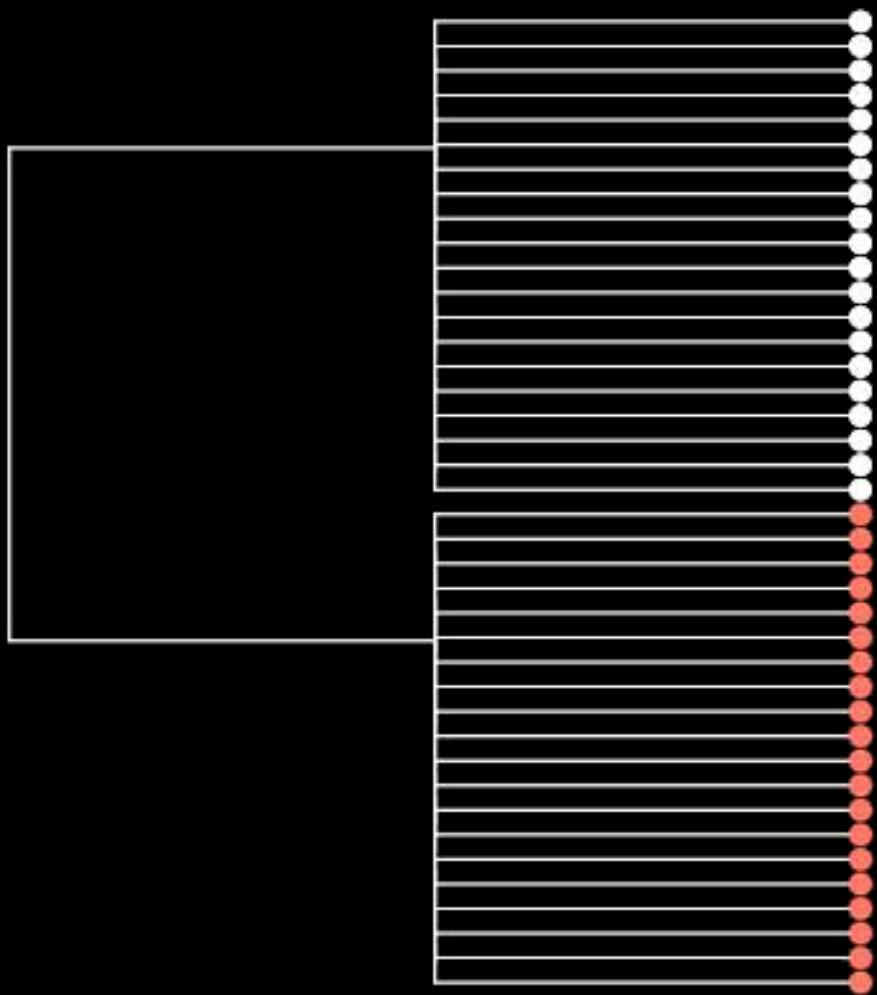


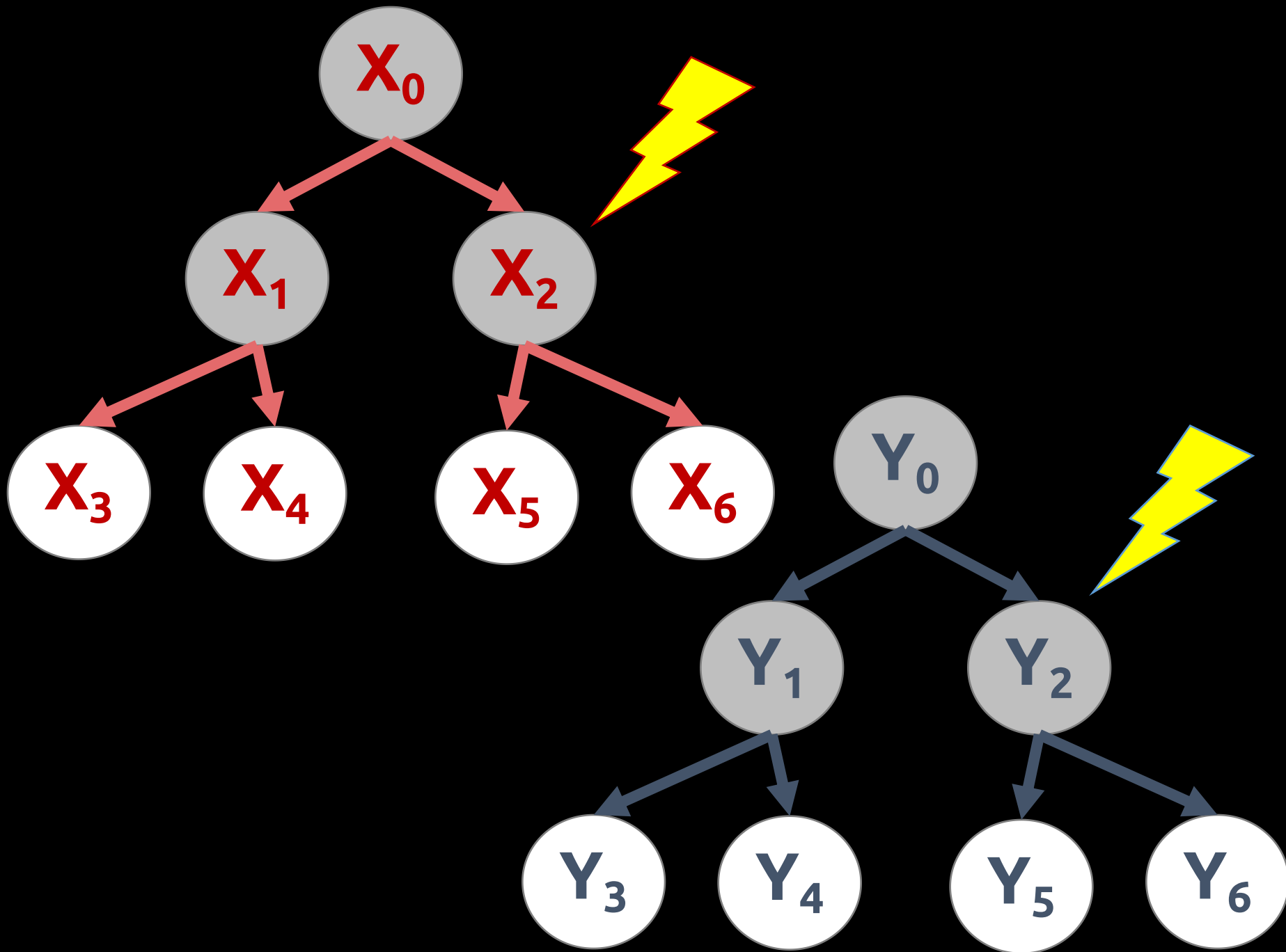
Why can't we do "regular" linear regression again?

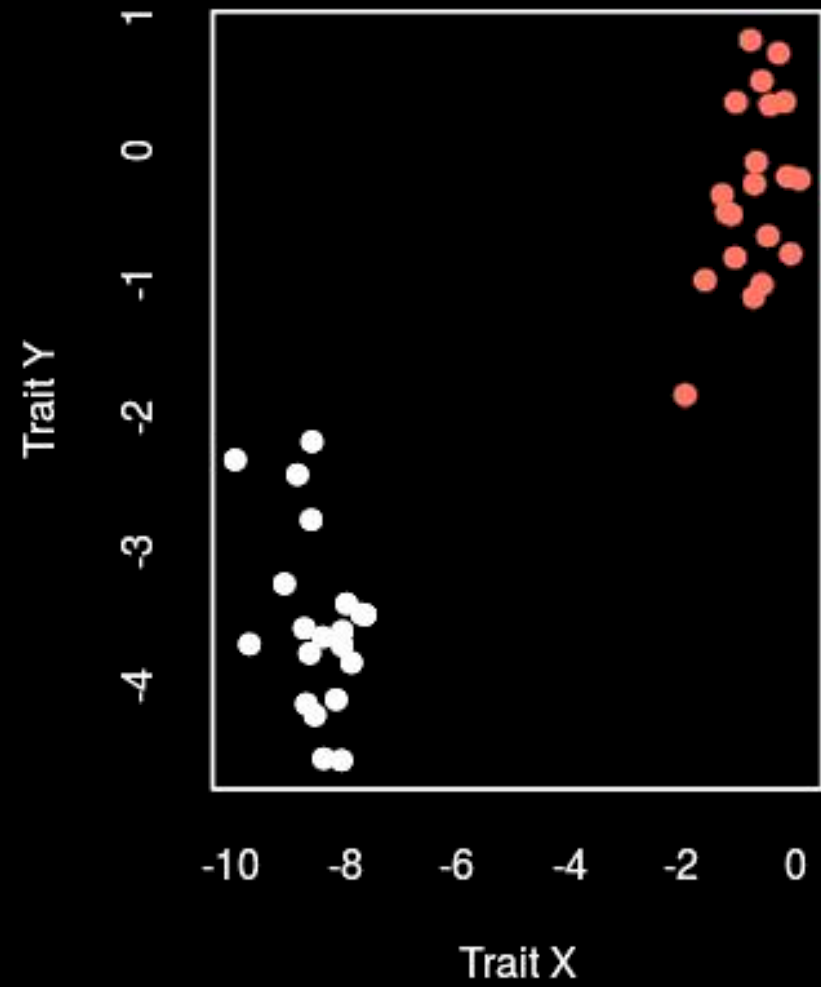
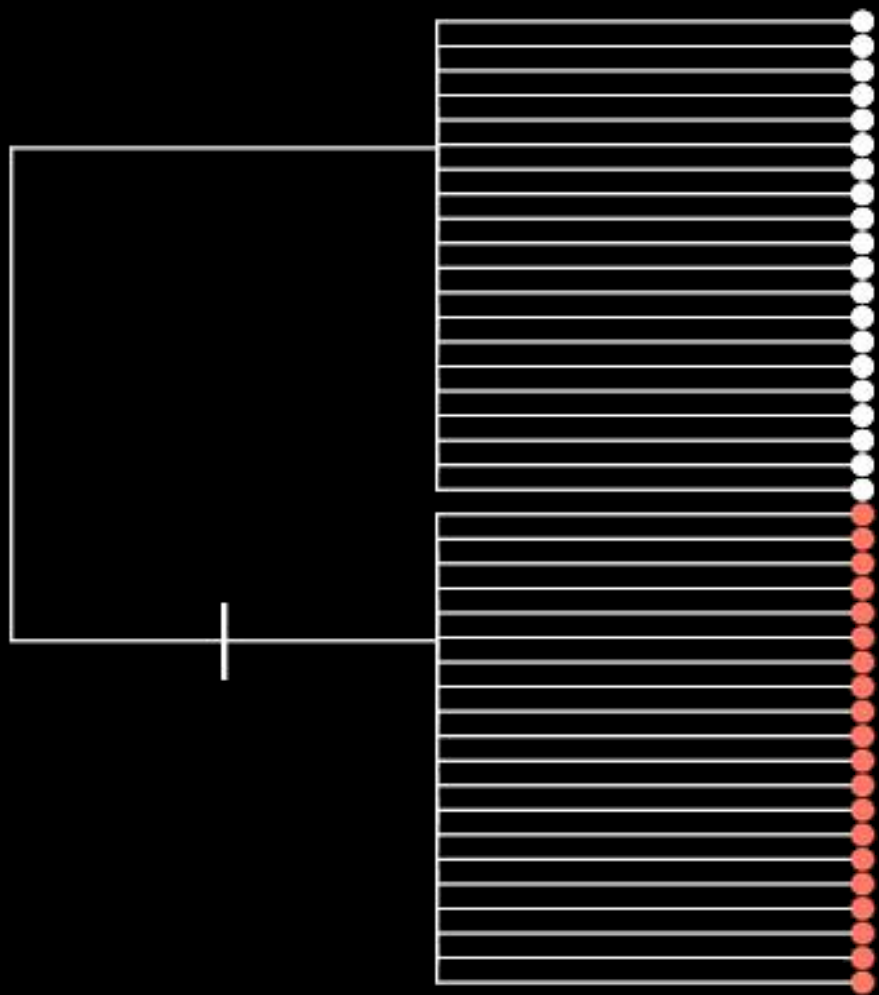
**Non-independence
of *residual error variation***

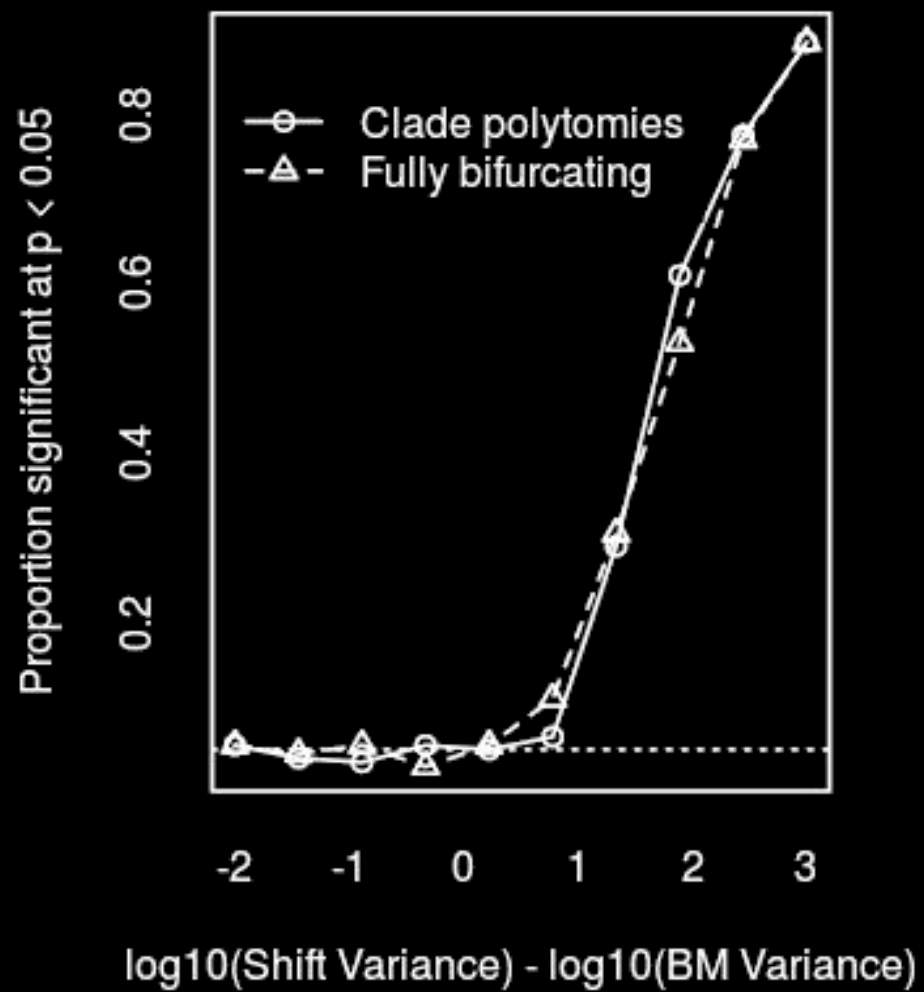
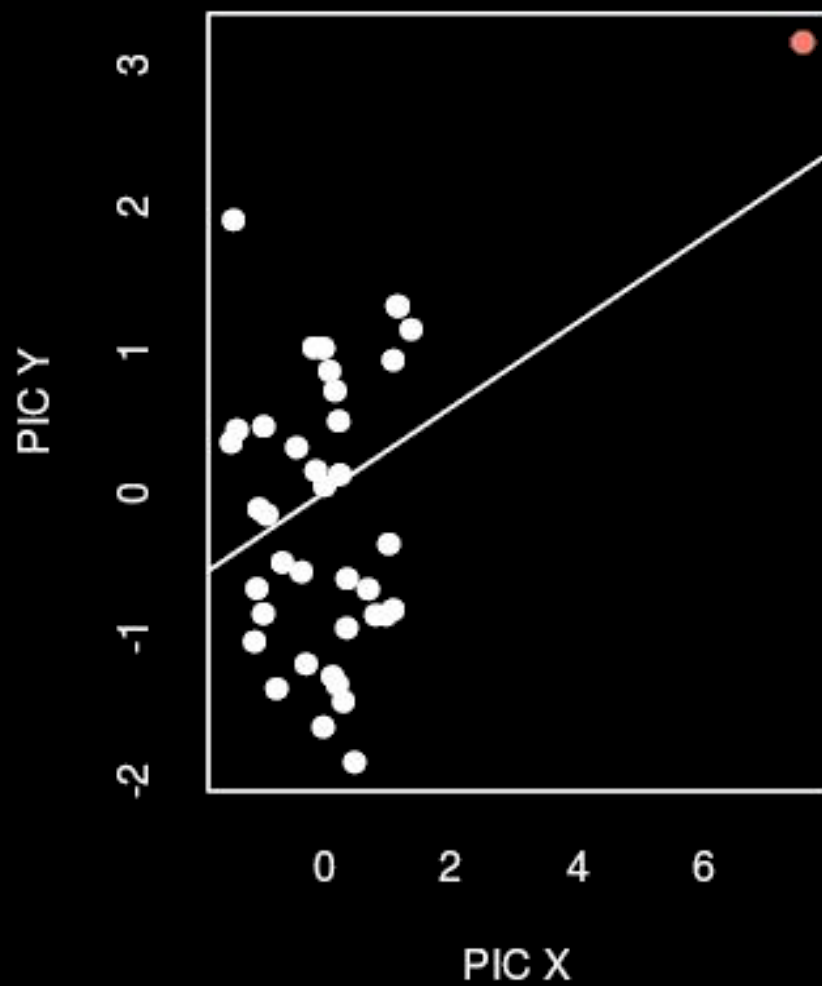
$$Y \sim X$$











Outline

A. Rare singular events break everything

I. Felsenstein's worst-case scenario

II. Models of adaptation

III. Discrete character correlations

B. We need to think about causation better

Two approaches

Hypothesis testing

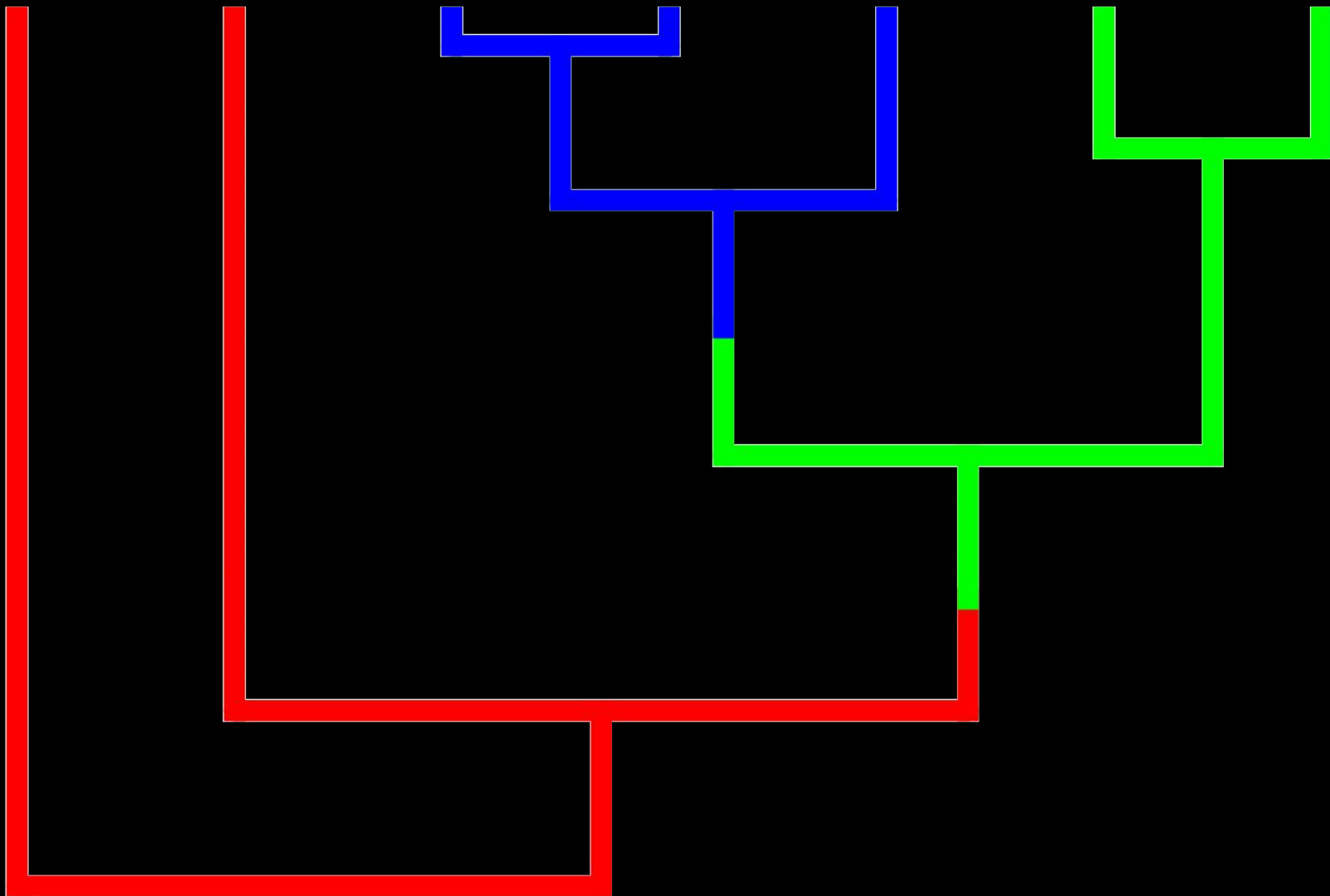
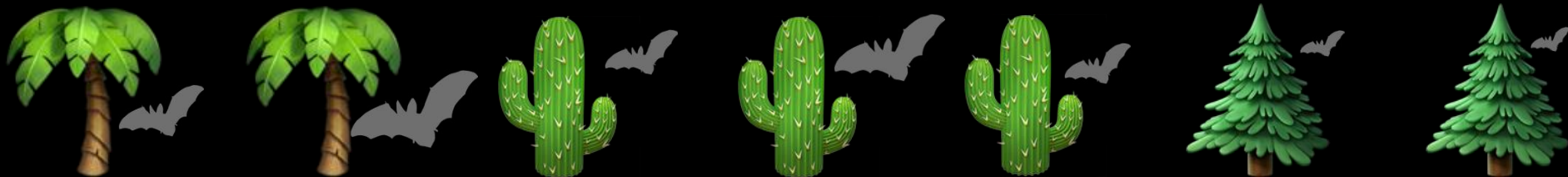
Tests biological predictors

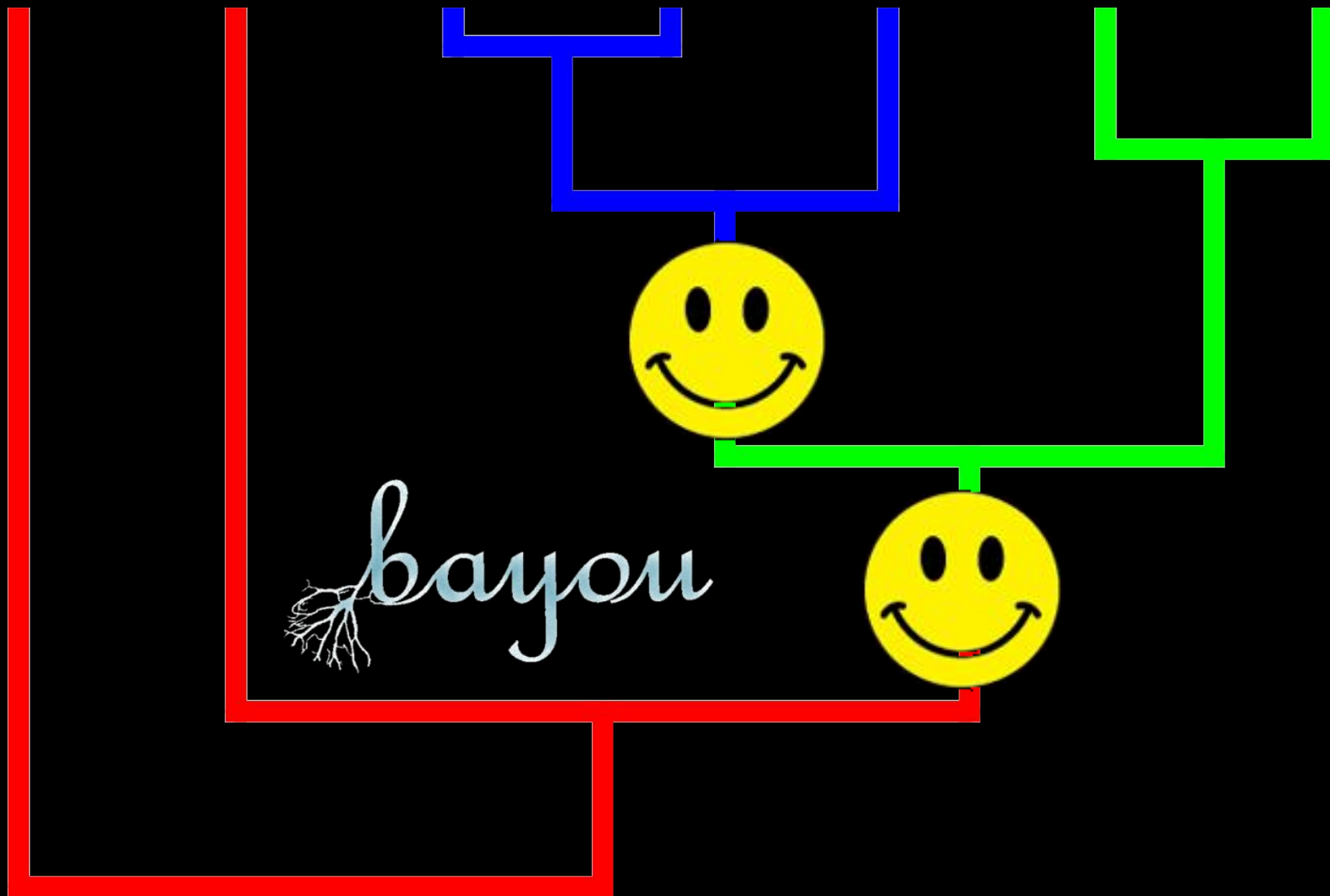
Best model may be still be bad

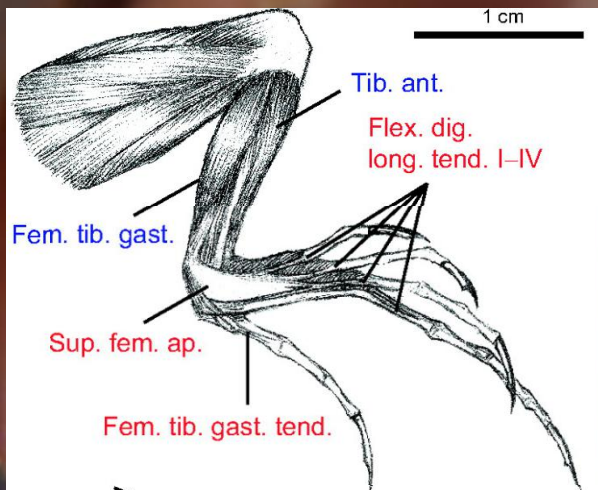
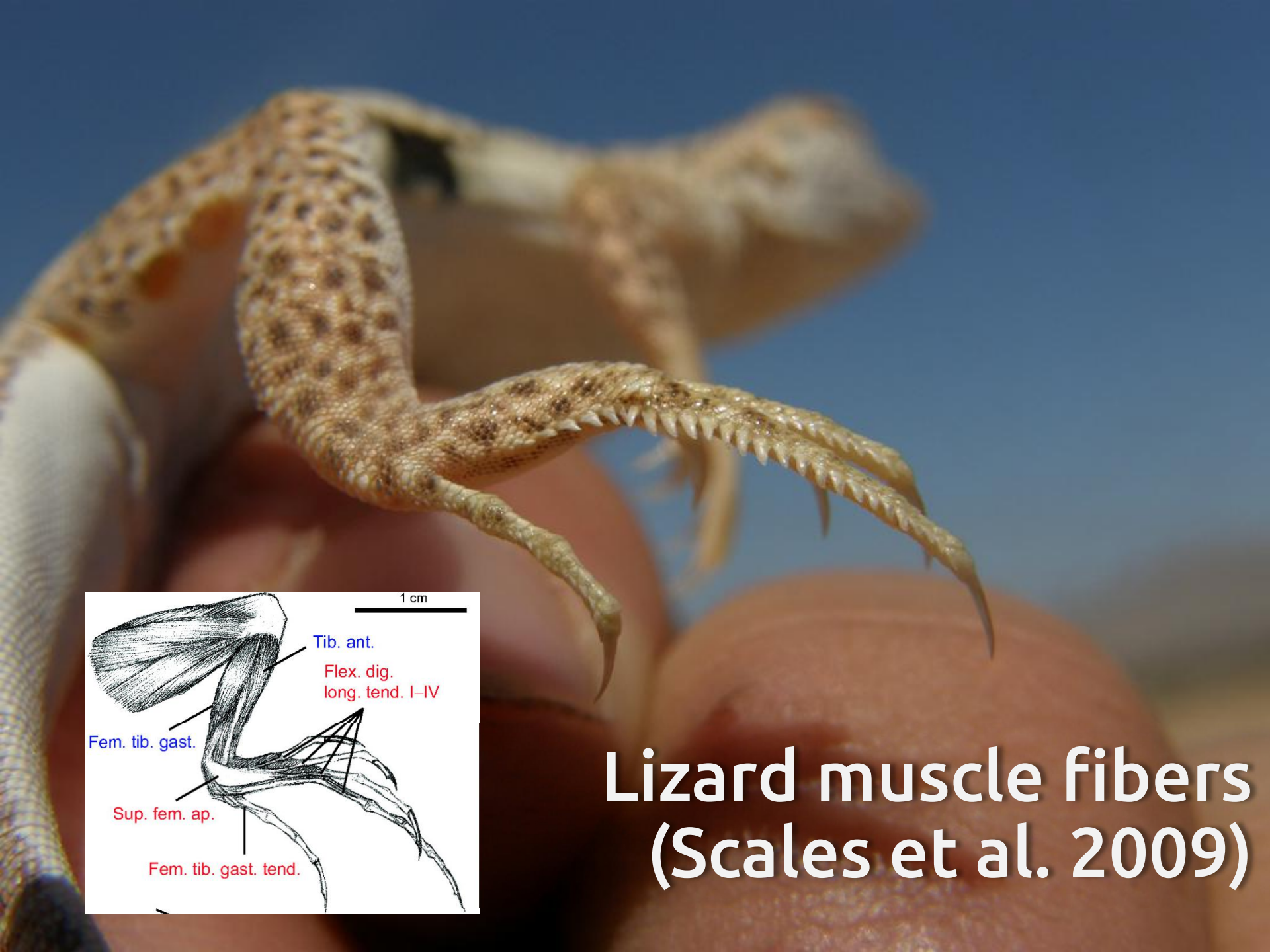
Phylogenetic natural history

Descriptive:
“stuff happens”

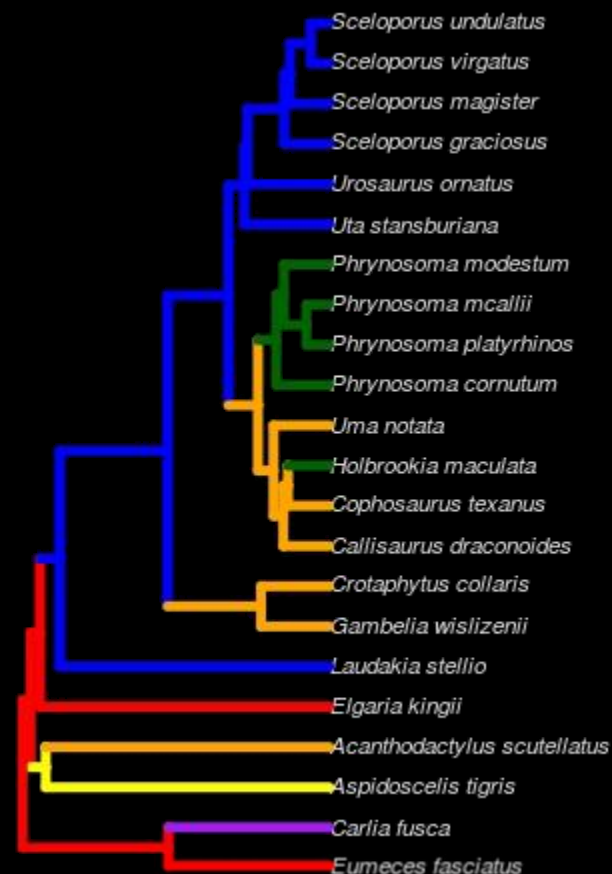
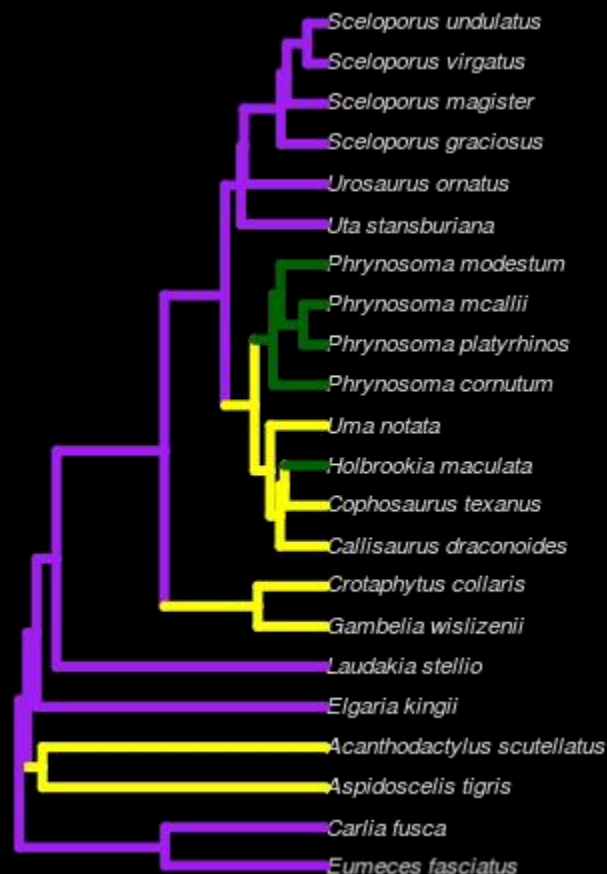
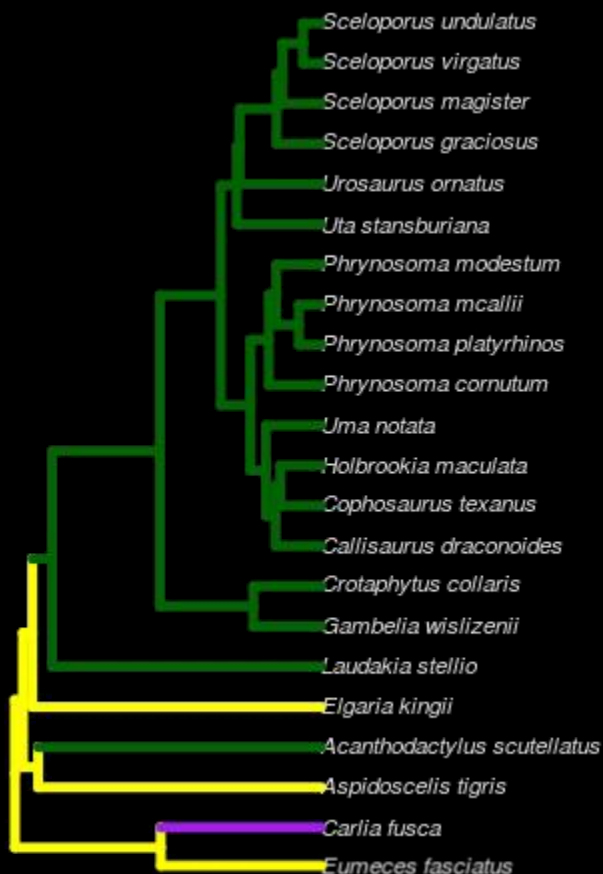
Finds major events





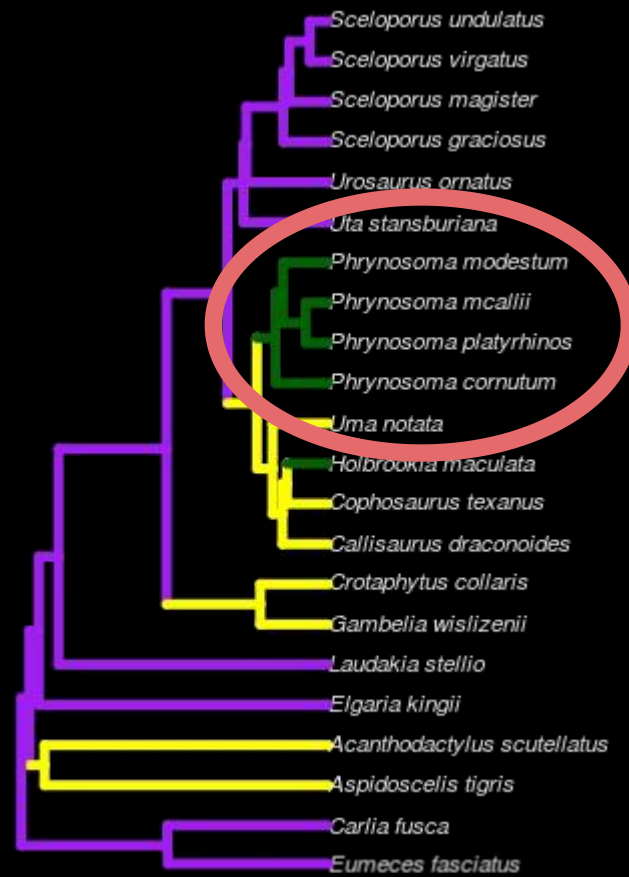


Lizard muscle fibers
(Scales et al. 2009)

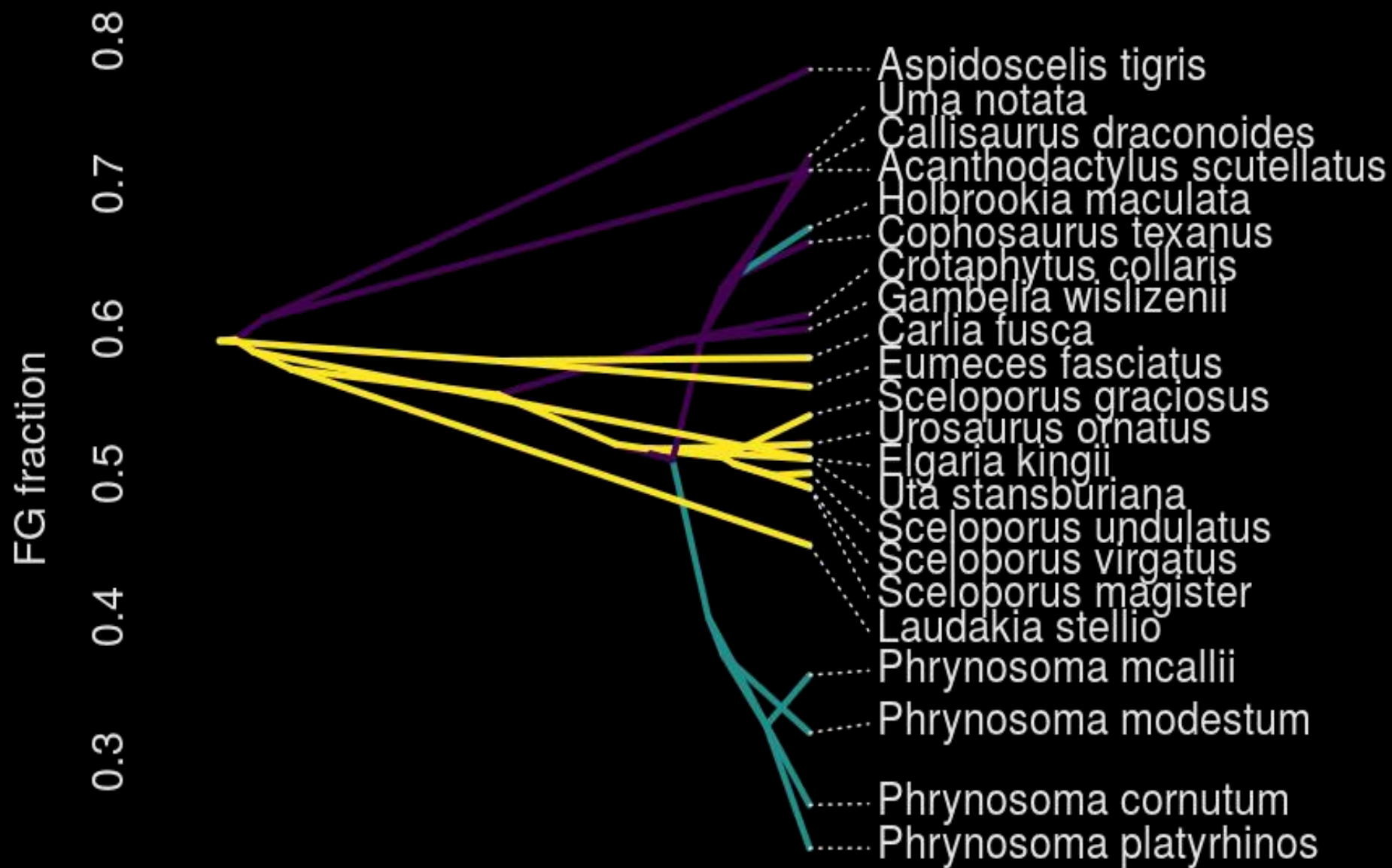


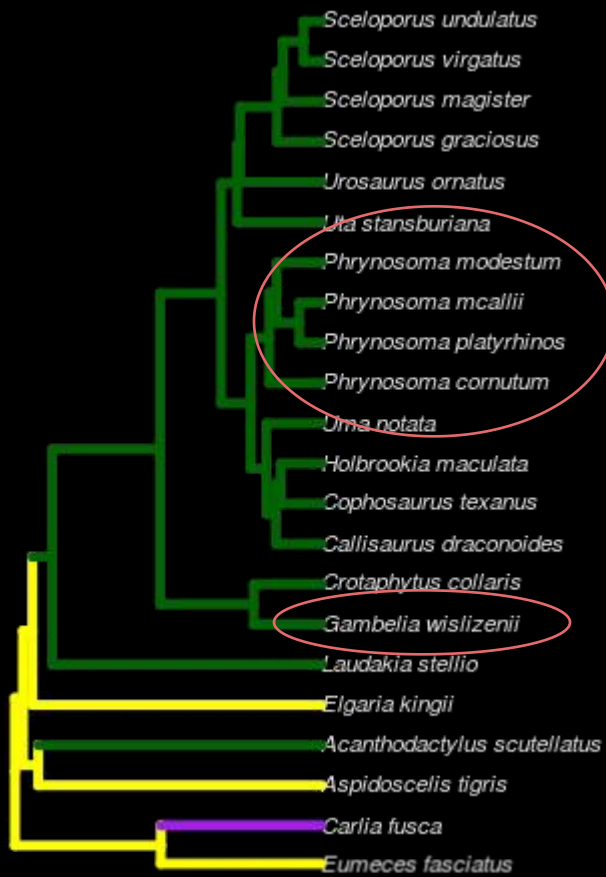
Origin Mode
(PE)(FM)

FM & PE



Predator Escape (PE)





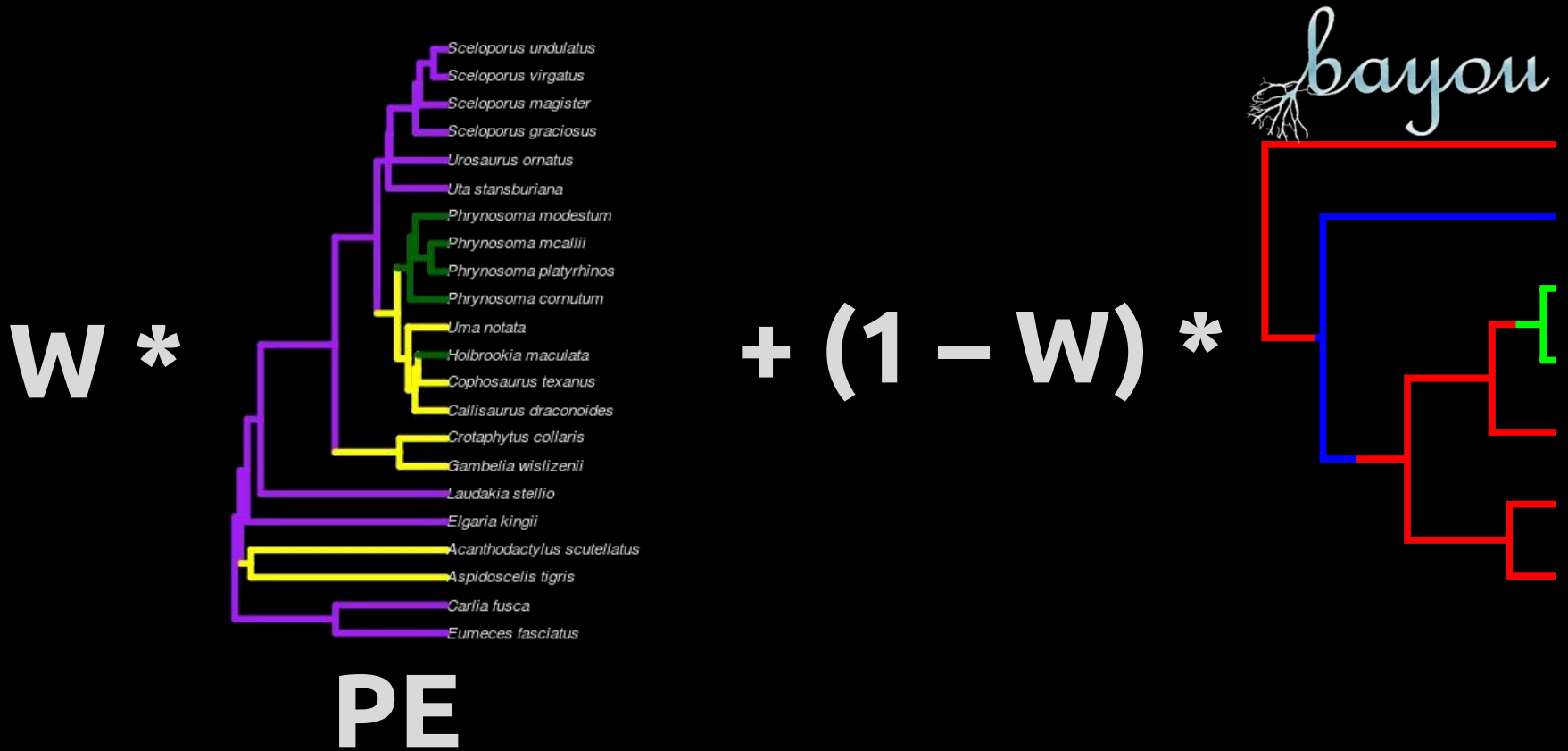
**Foraging Mode
(FM)**



Vs.



Combine approaches

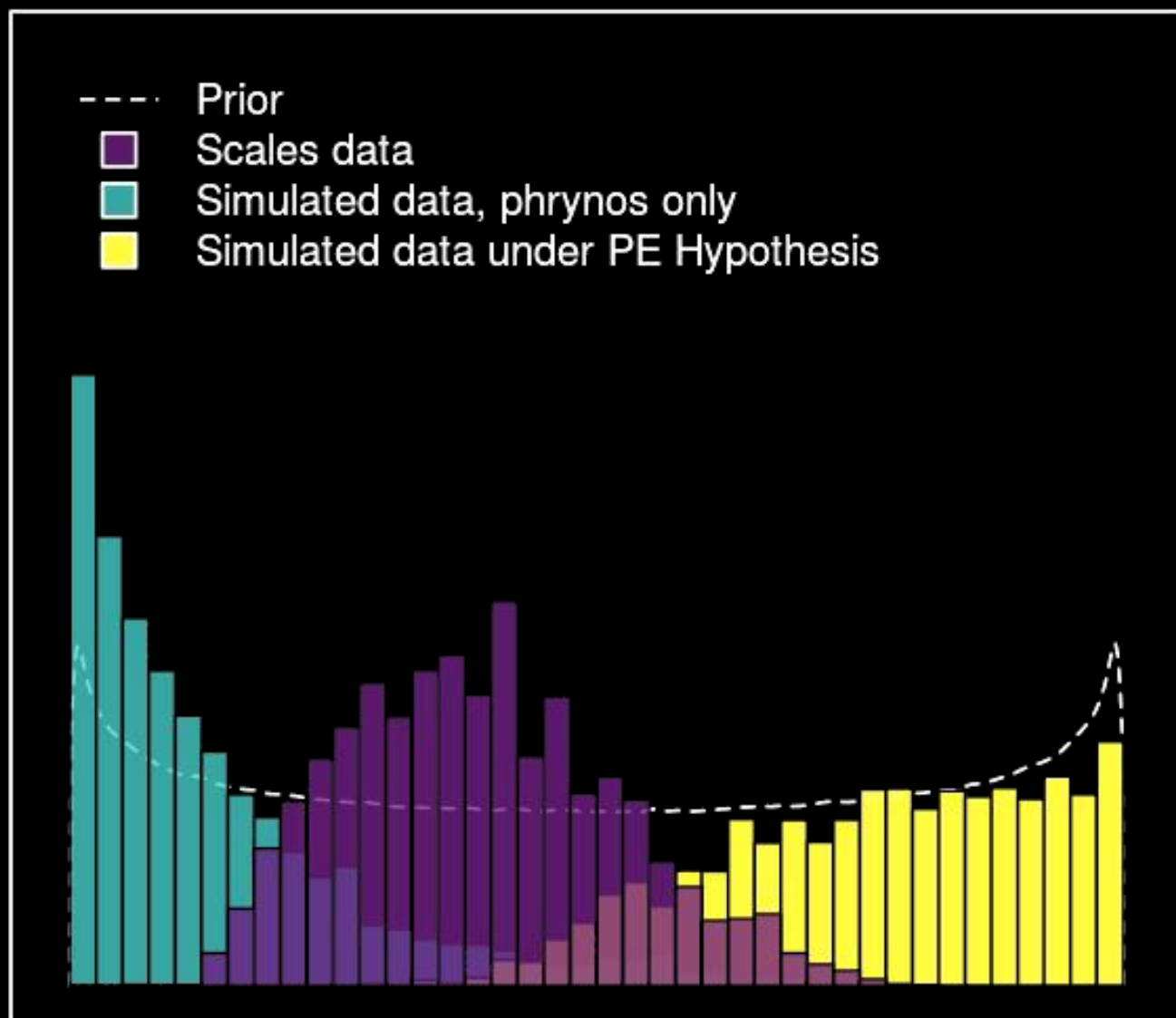


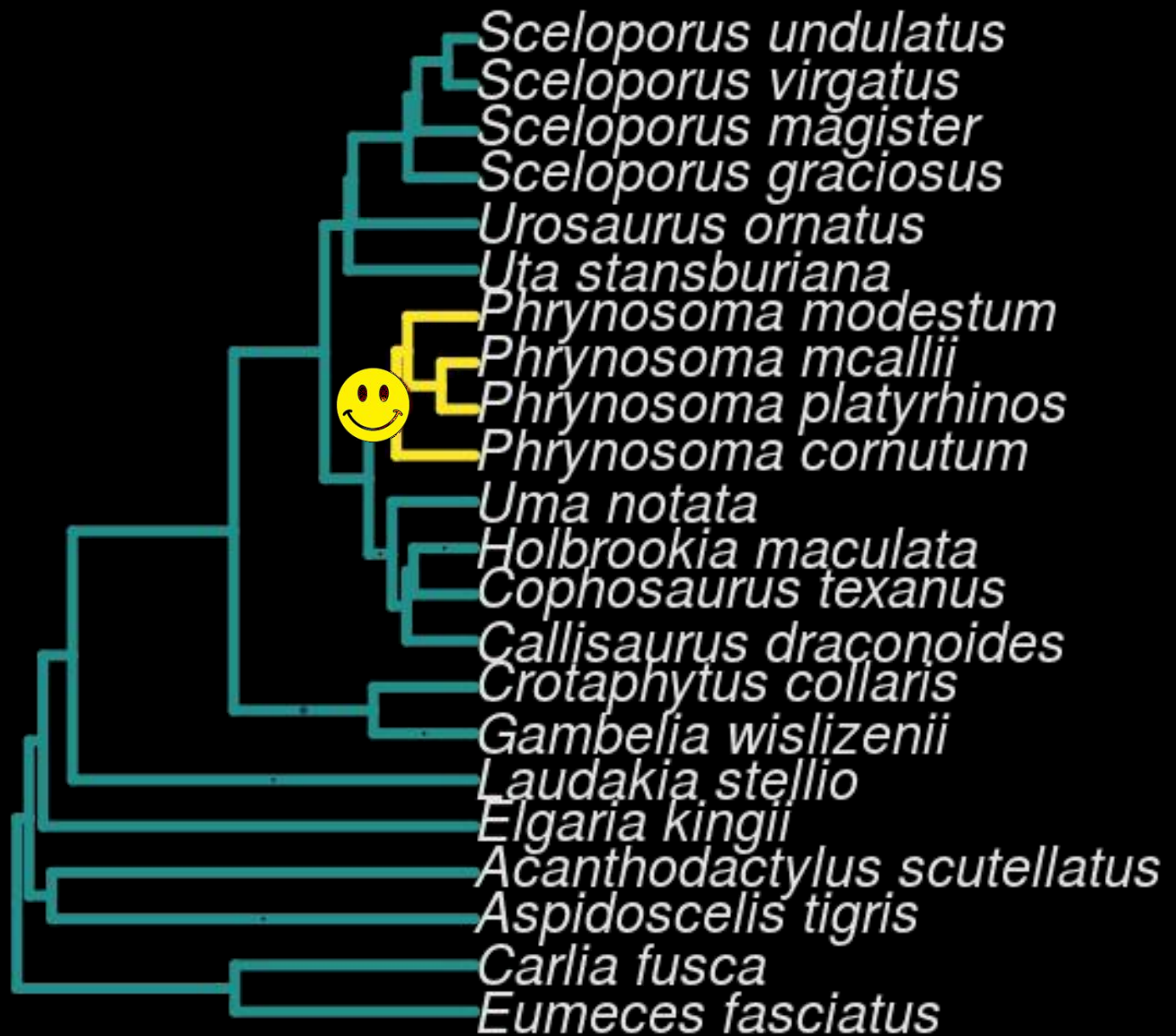
Density

- Prior
- Scales data
- Simulated data, phrynos only
- Simulated data under PE Hypothesis

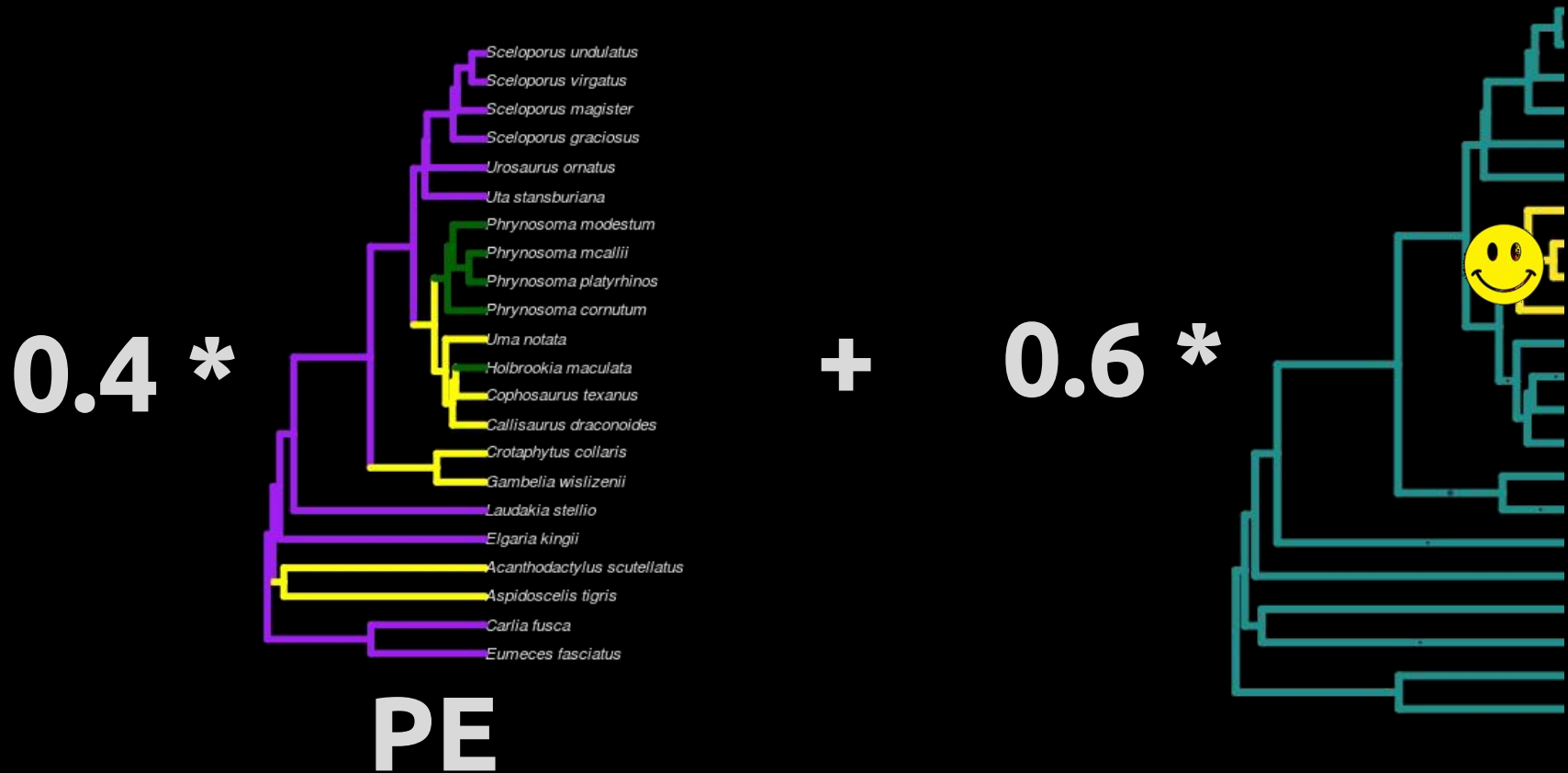
0.0 0.2 0.4 0.6 0.8 1.0

Weight to PE Hypothesis





Combine approaches



**Predator escape is a good
predictor of muscle fibers in
lizards!**

**...and horned lizards
are weird**

Outline

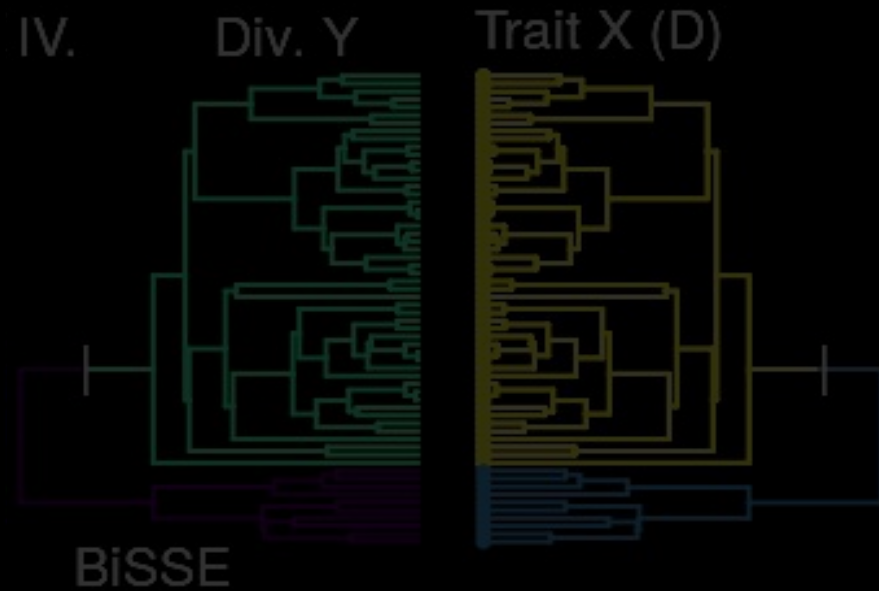
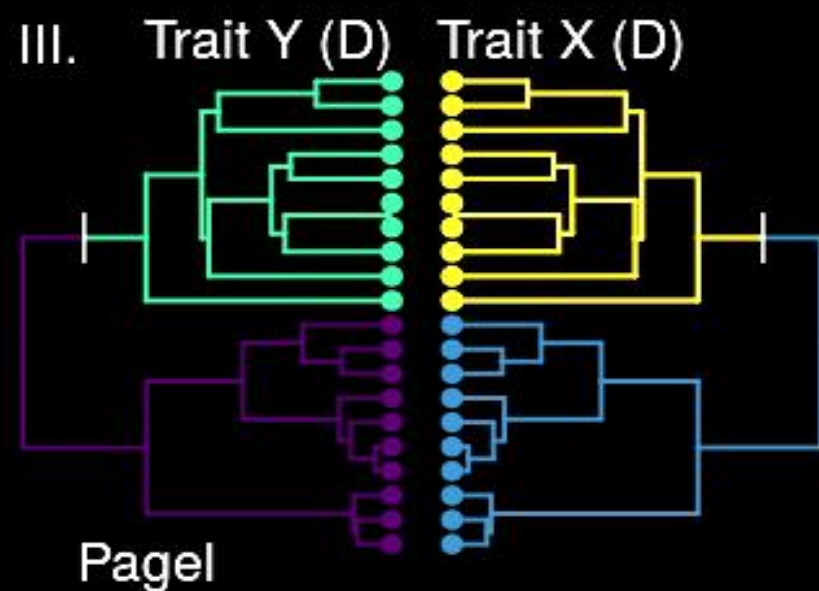
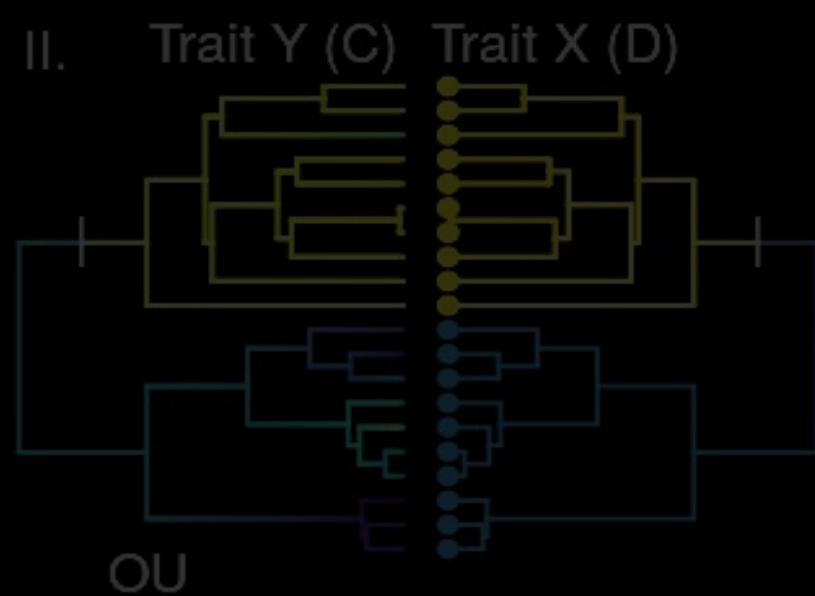
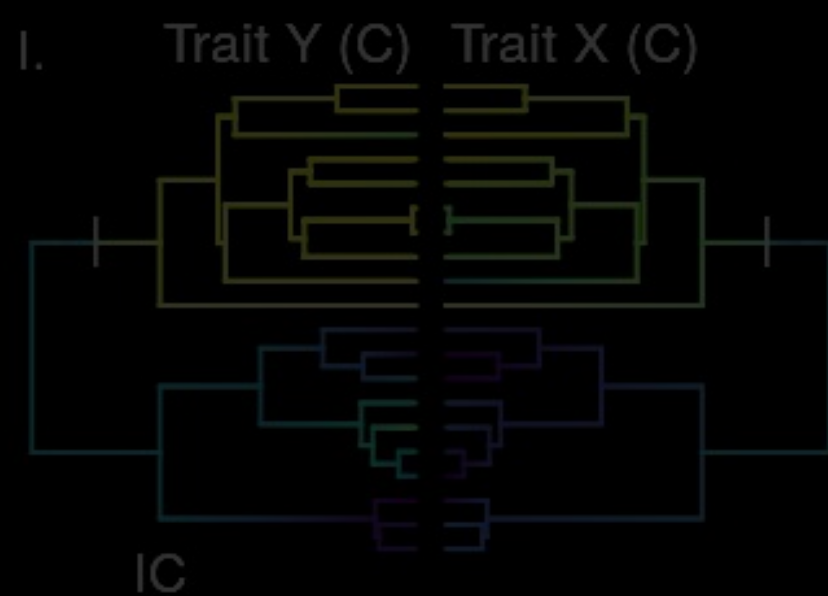
A. Rare singular events break everything

I. Felsenstein's worst-case scenario

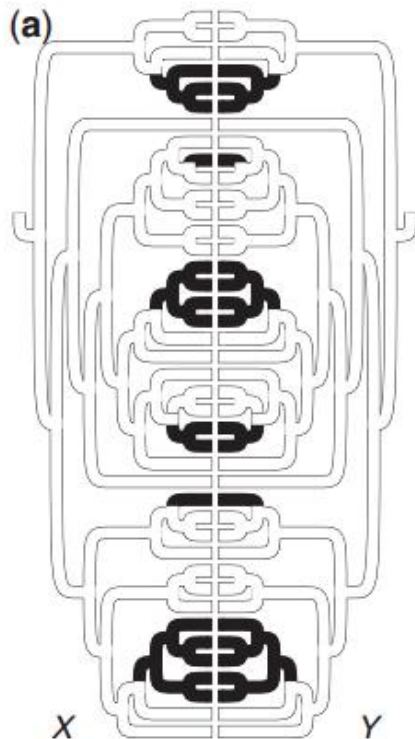
II. Models of adaptation

III. Discrete character correlations

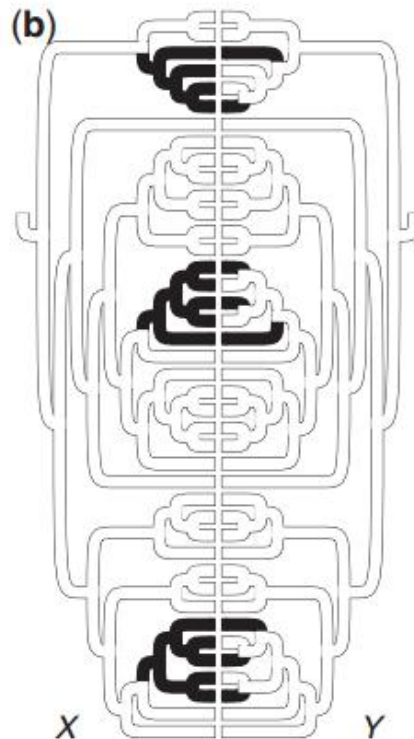
B. We need to think about causation better



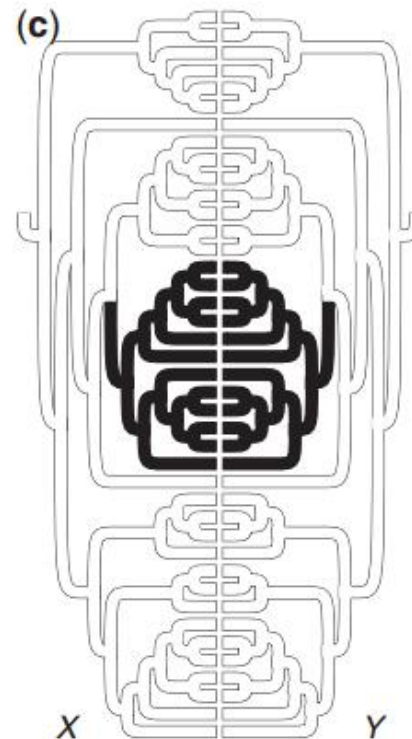
All the above cases reduce to Darwin's scenario



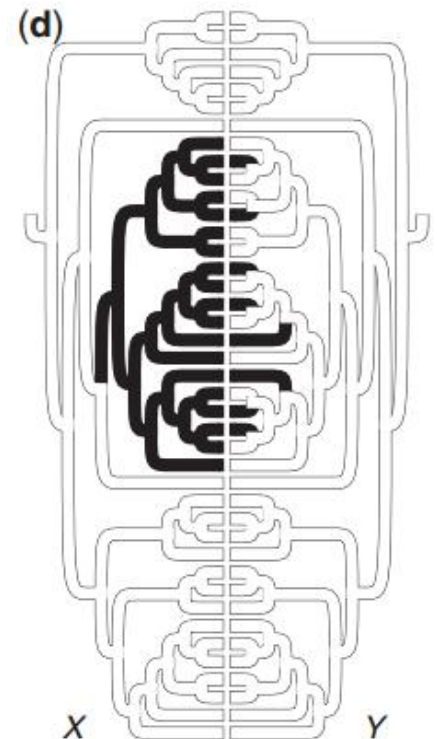
Replicated co-distribution



Replicated bursts



Darwin's scenario

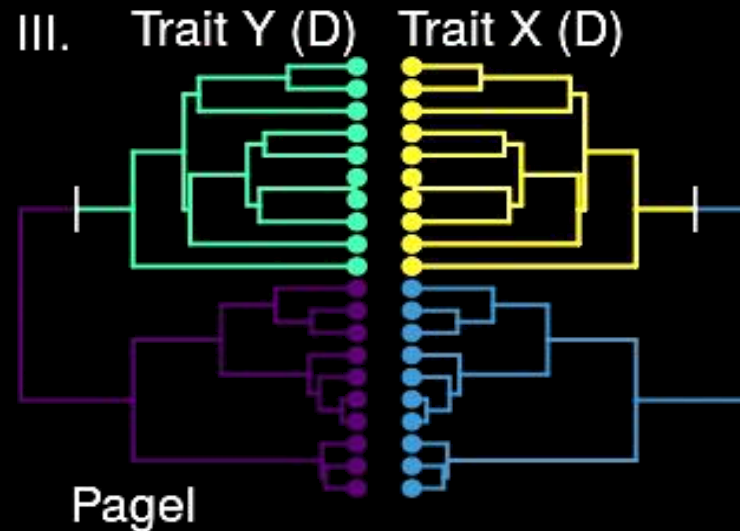


Unreplicated burst



**"Replaying the tape
of evolution"**

We can reduce “Darwin’s Scenario” to:



$P(1 \text{ event on branch } i)$

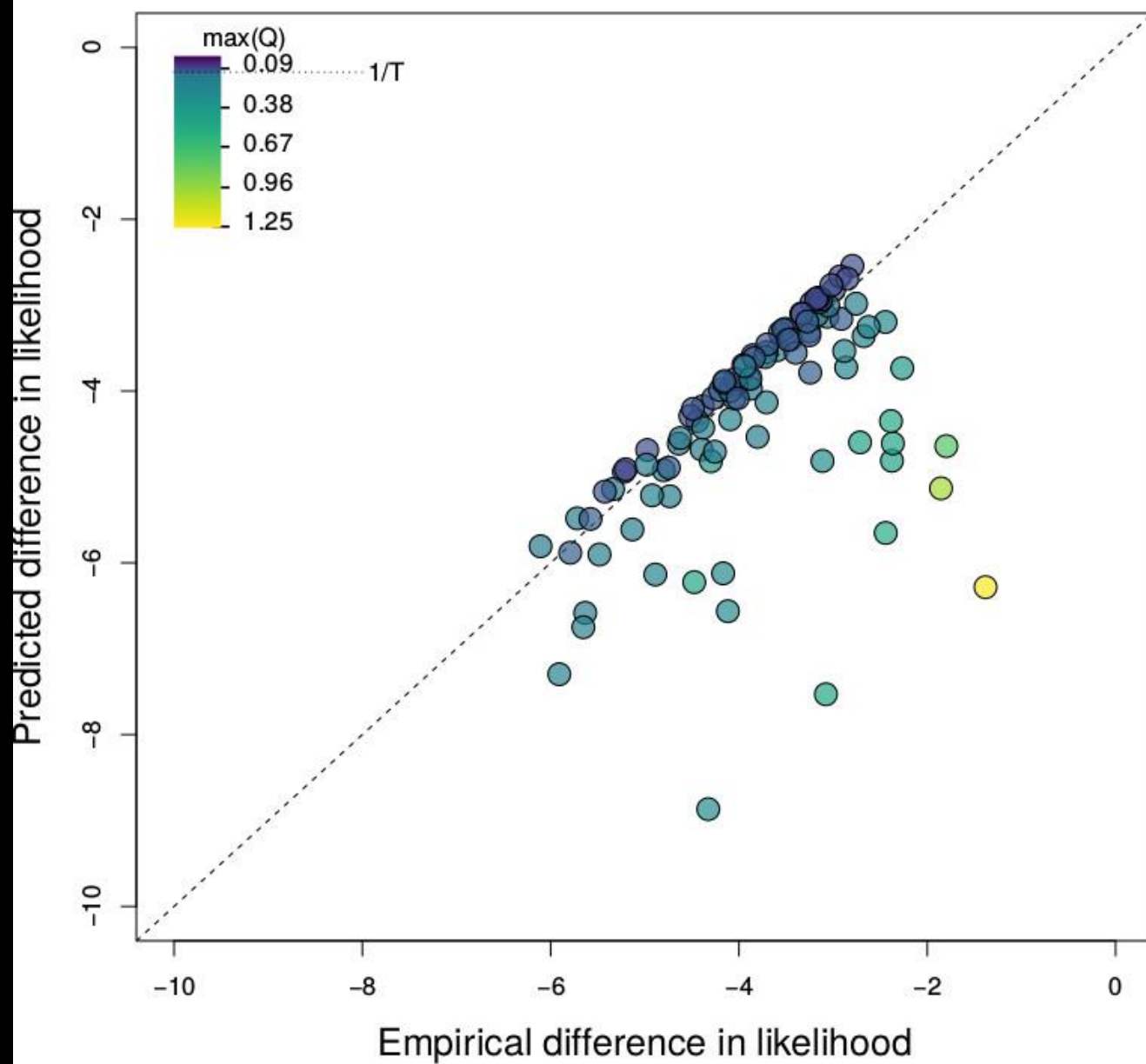
vs.

$P(2 \text{ events on branch } i)$

Length of Branch i

Total Branch Length of Tree

$$\left(\frac{\text{Length of Branch i}}{\text{Total Branch Length of Tree}} \right)^2$$



If traits were selected randomly,
this would be OK,
but ascertainment bias....

Conclusions

All comparative methods break with rare, singular events

We need to allow for background shifts and “phylogenetic natural history” models

“Darwin’s Scenario” is a boundary condition – gives hope

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A. Rare singular events break everything

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Old fights reborn...

*Journal of
Ecology* 1995,
83, 535–536

FORUM

Why ecologists need to be phylogenetically challenged

PAUL H. HARVEY, ANDREW F. READ* and SEAN NEE

*Department of Zoology, University of Oxford, South Parks Road, Oxford OX1 3PS and *Institute of Cell, Animal and Population Biology, University of Edinburgh, West Mains Road, Edinburgh EH9 3JT, UK*

Riddled with errors

We now progress through some other errors in the article.

- *Only after variation correlated with phylogeny has been extracted, is residual 'corrected' variation analysed and later PC gives priority to phylogeny over ecology as a correlate of trait variation.* Wrong. Most recent comparative methods, such as contrast analyses, merely partition the variance so that degrees of freedom are biologically meaningful. Over a decade ago, some authors, particu-

Simpson's paradox

Male recovery rate

Drug: 60% (18/30)

No drug: 70% (7/10)

Female recovery rate

Drug: 20% (2/10)

No Drug: 30% (9/30)

Combined

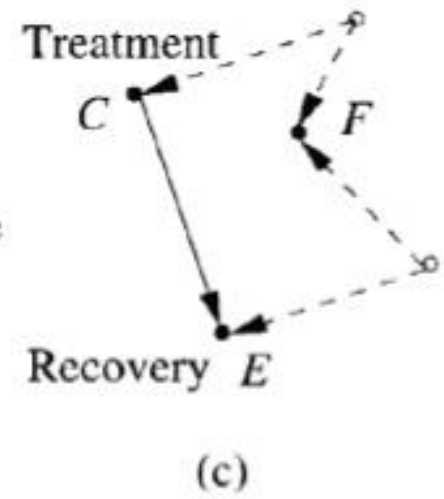
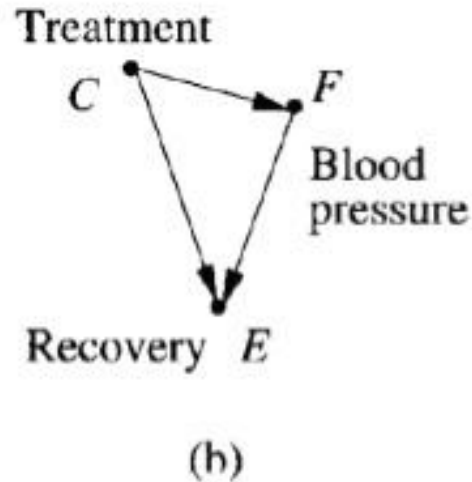
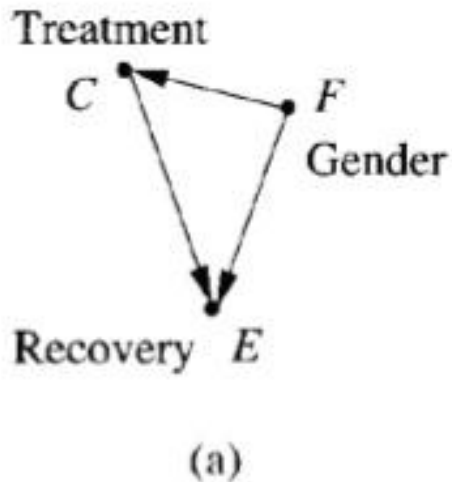
recovery rate:

Drug: 50% (20/40)

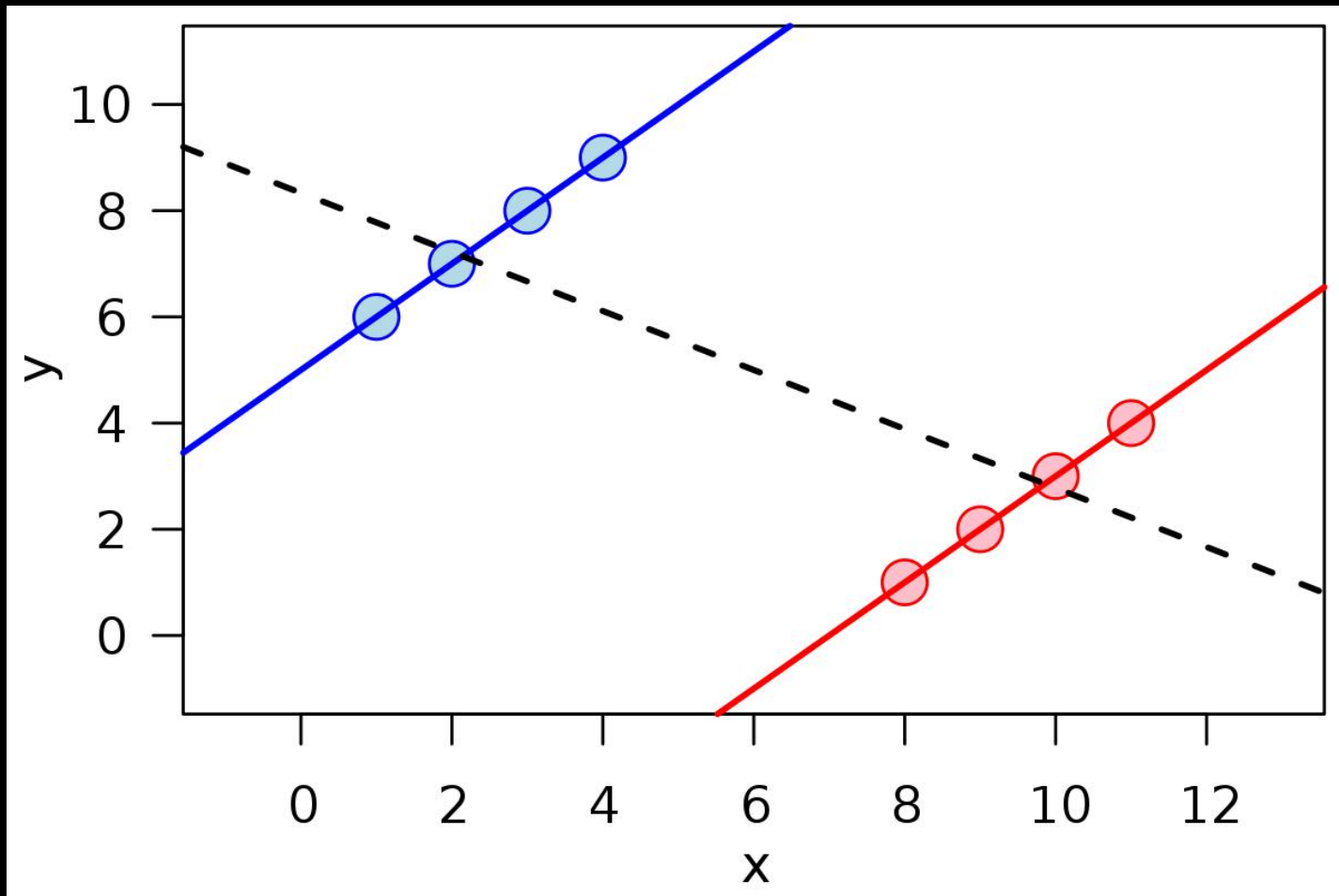
No drug: 40% (16/40)

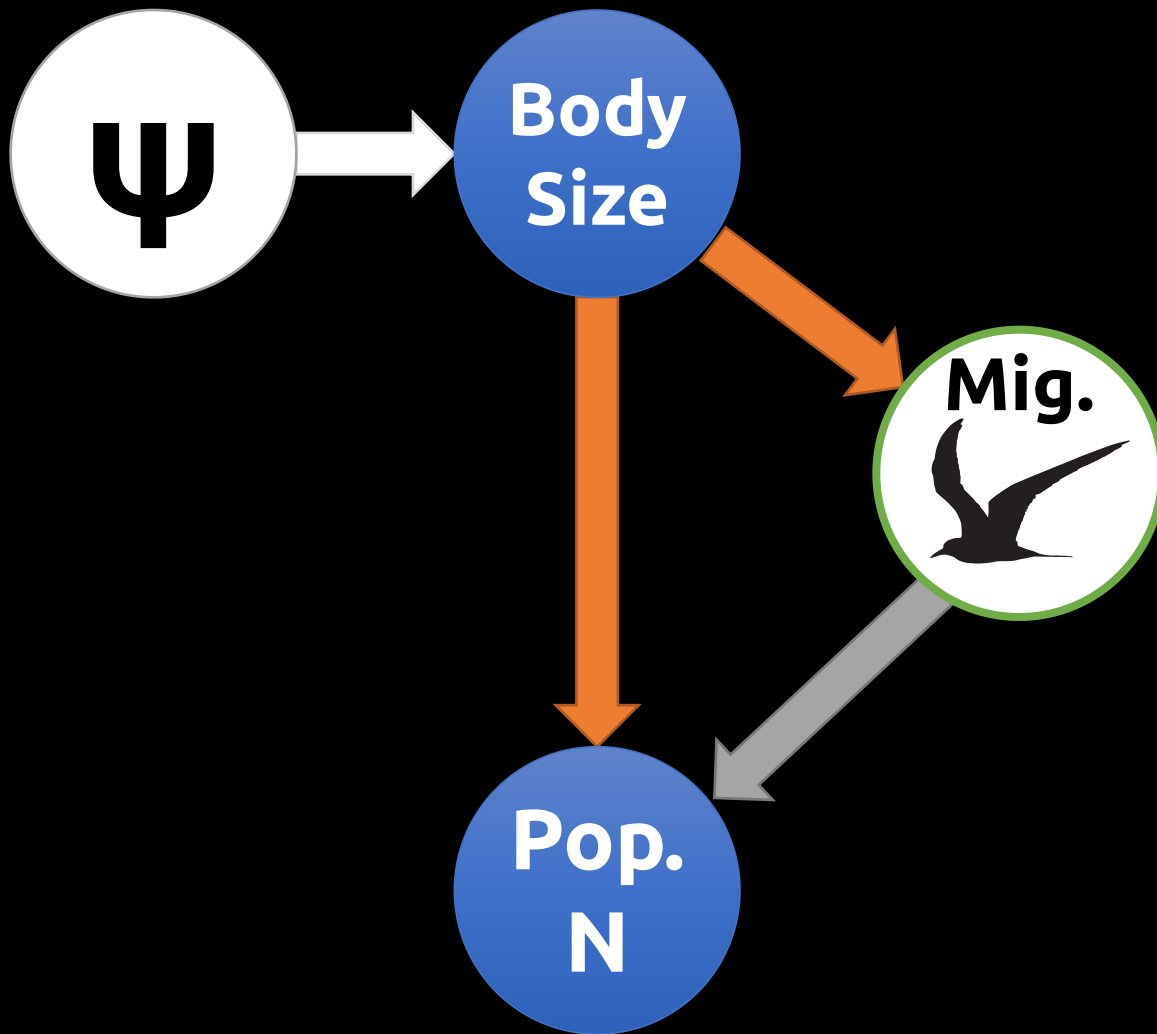
Causal interpretations

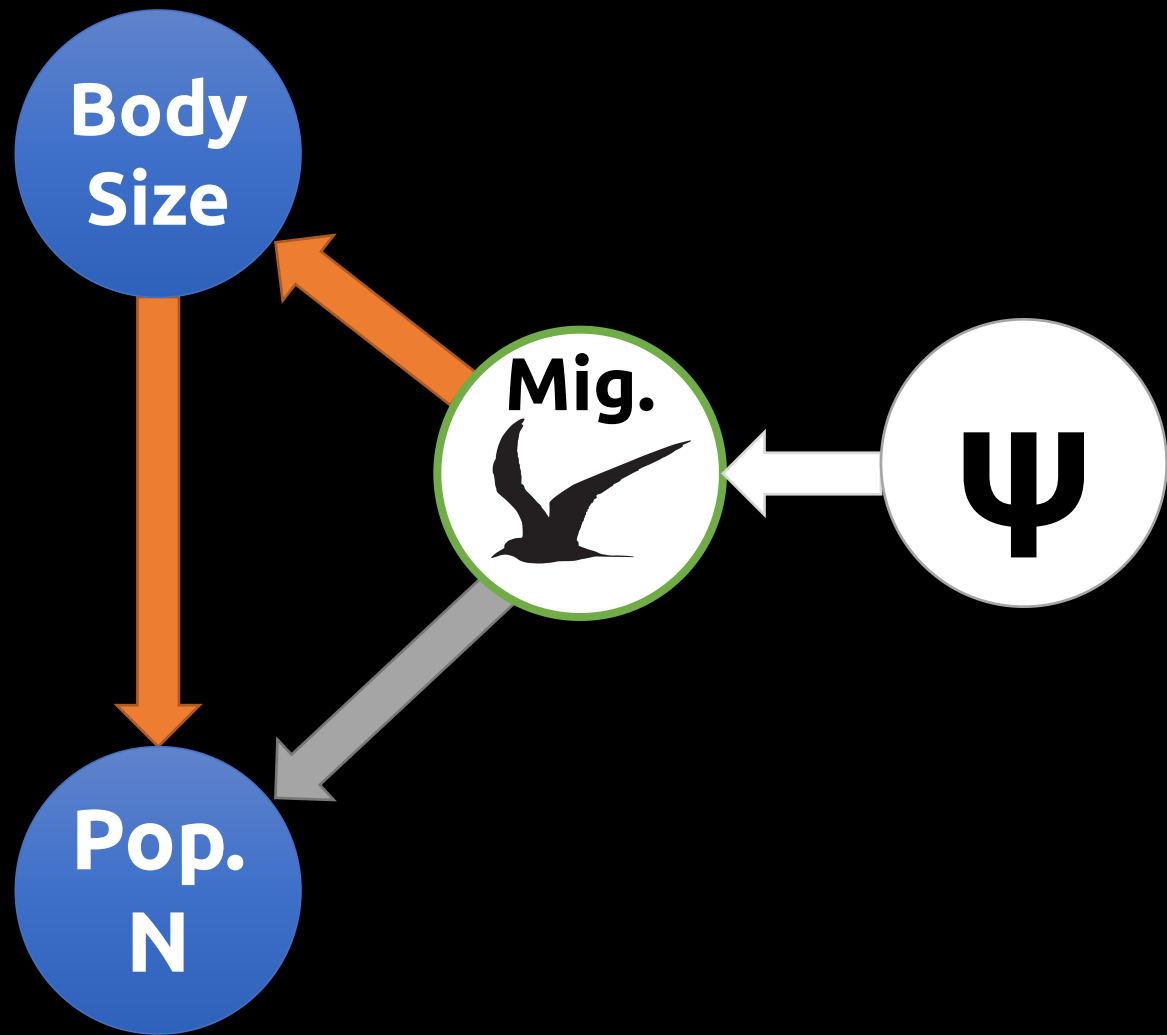
Three causal models capable of generating the data Model (a) dictates use of the **gender-specific tables**, whereas (b) and (c) dictate use of the **combined table**.

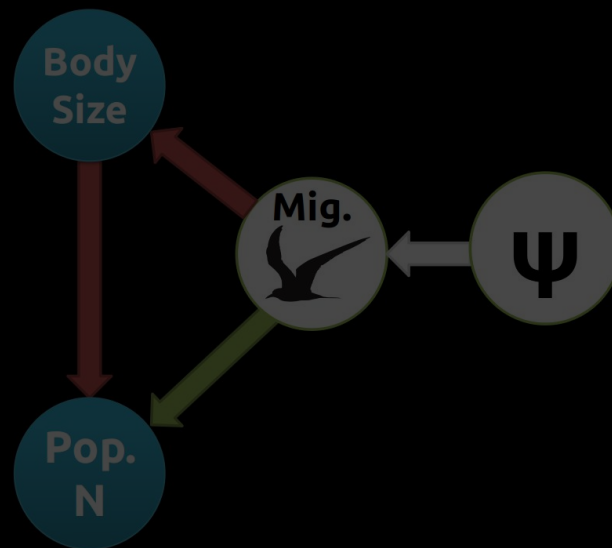
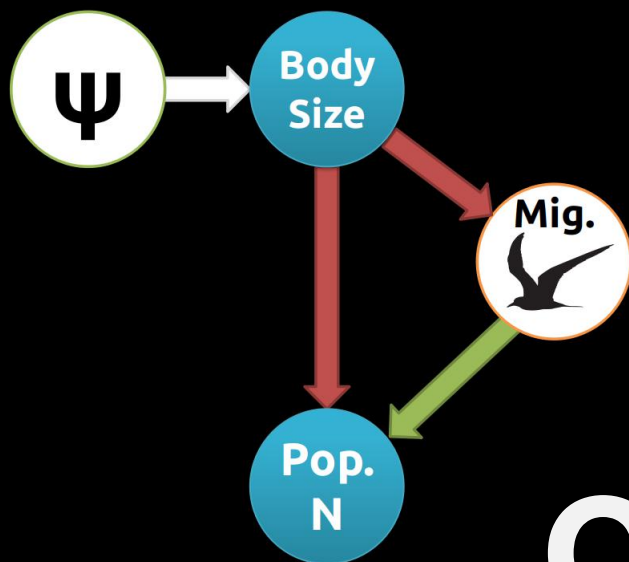


Simpson's paradox

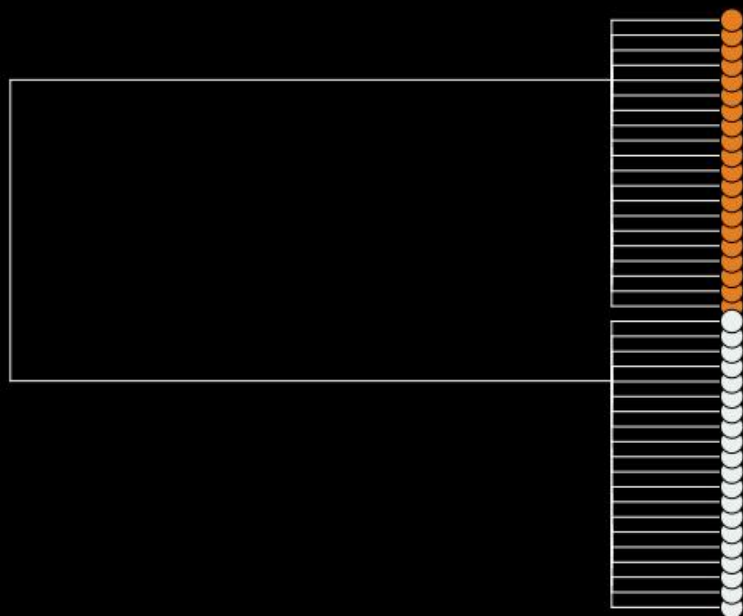




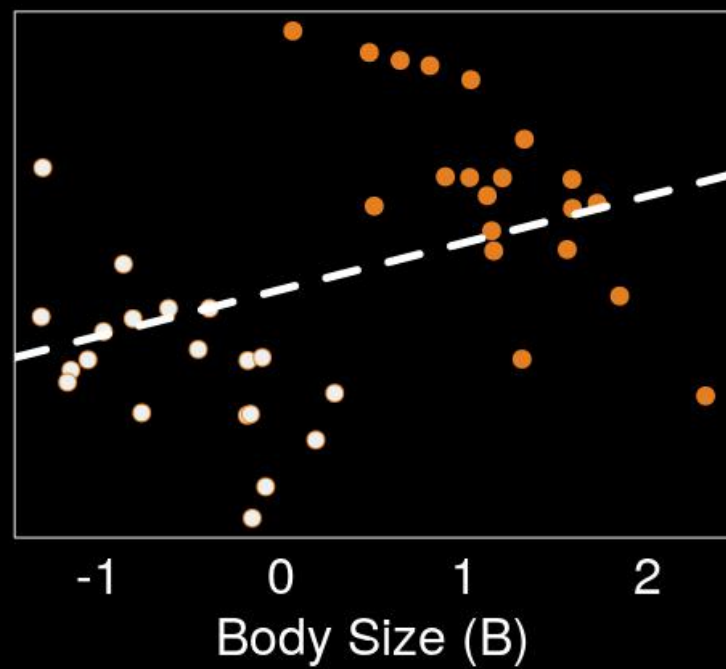


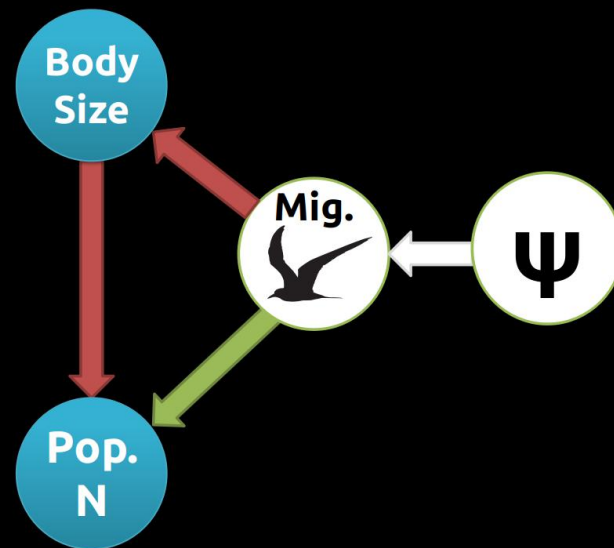
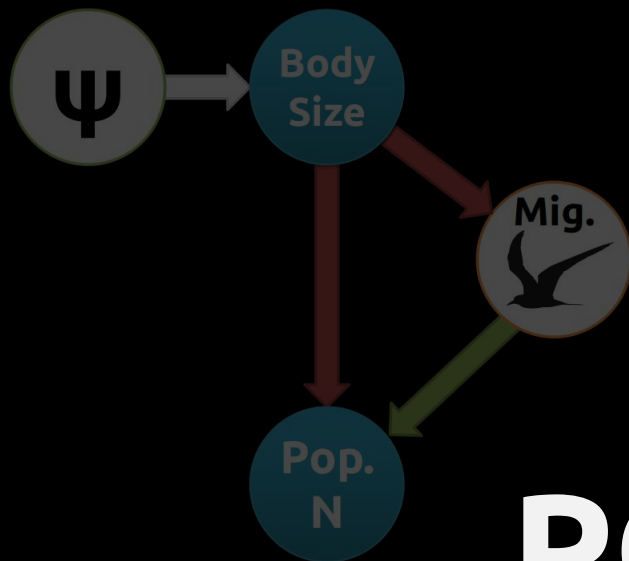


OLS

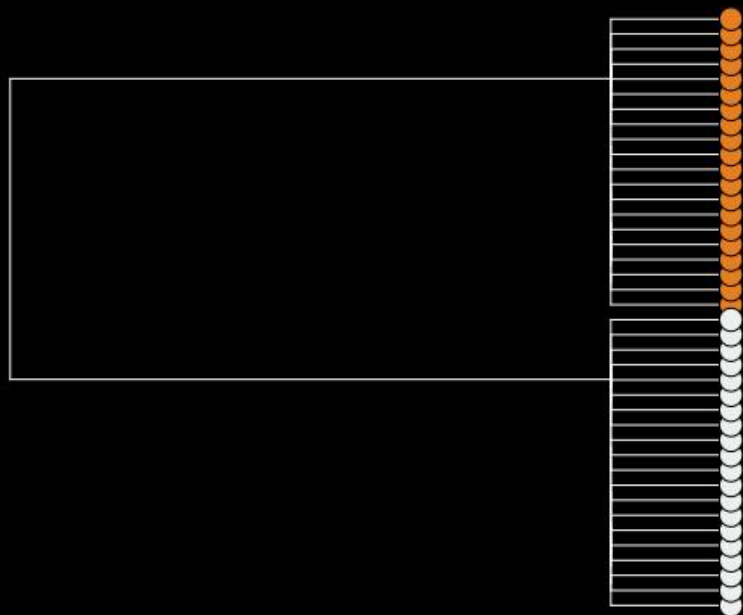


Species Abundance (N)

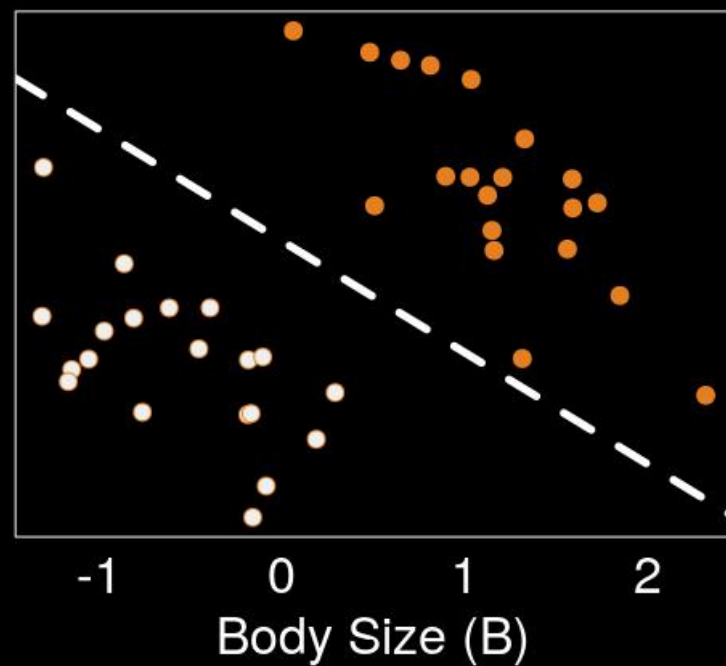




PGLS

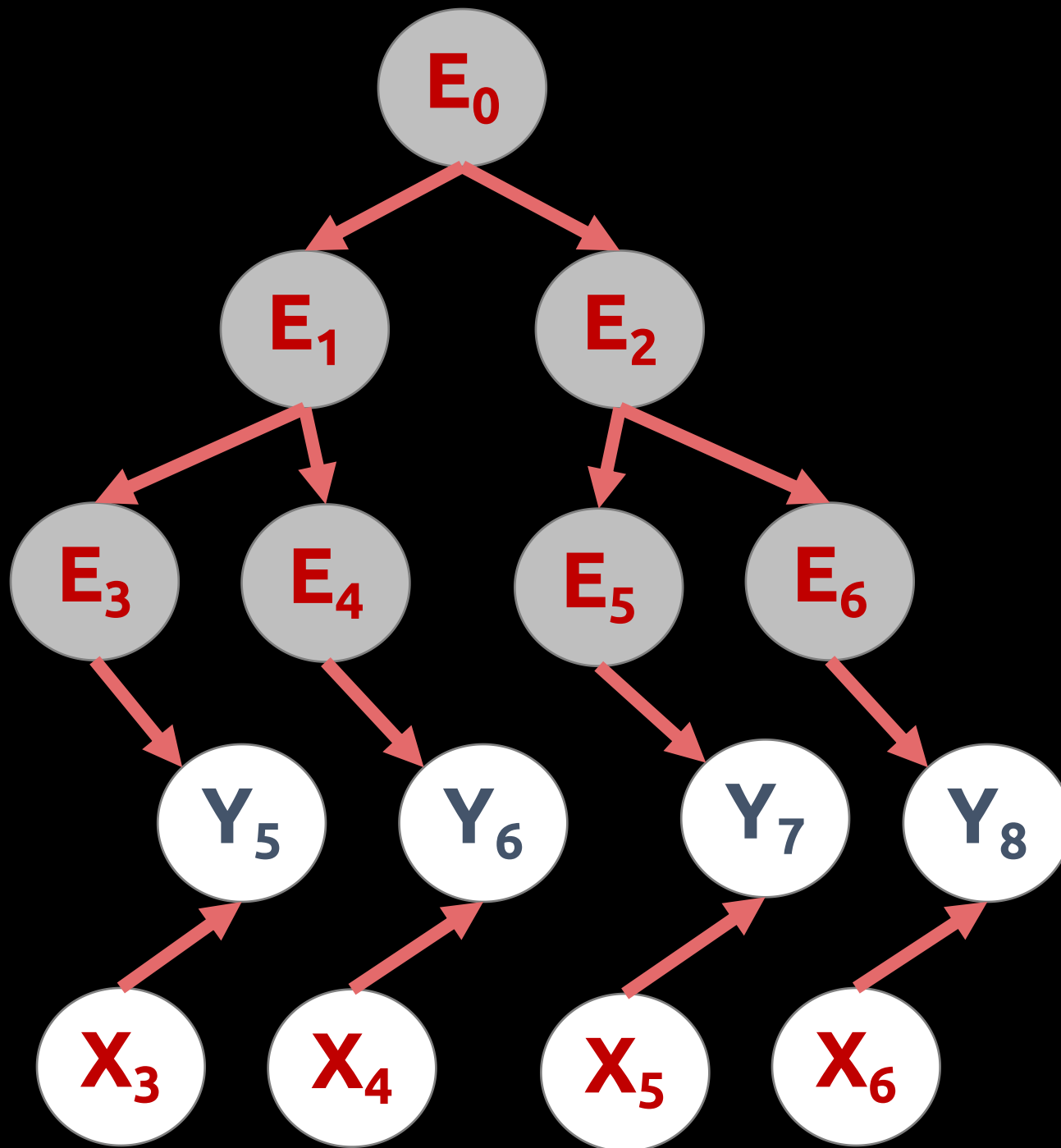


Species Abundance (N)



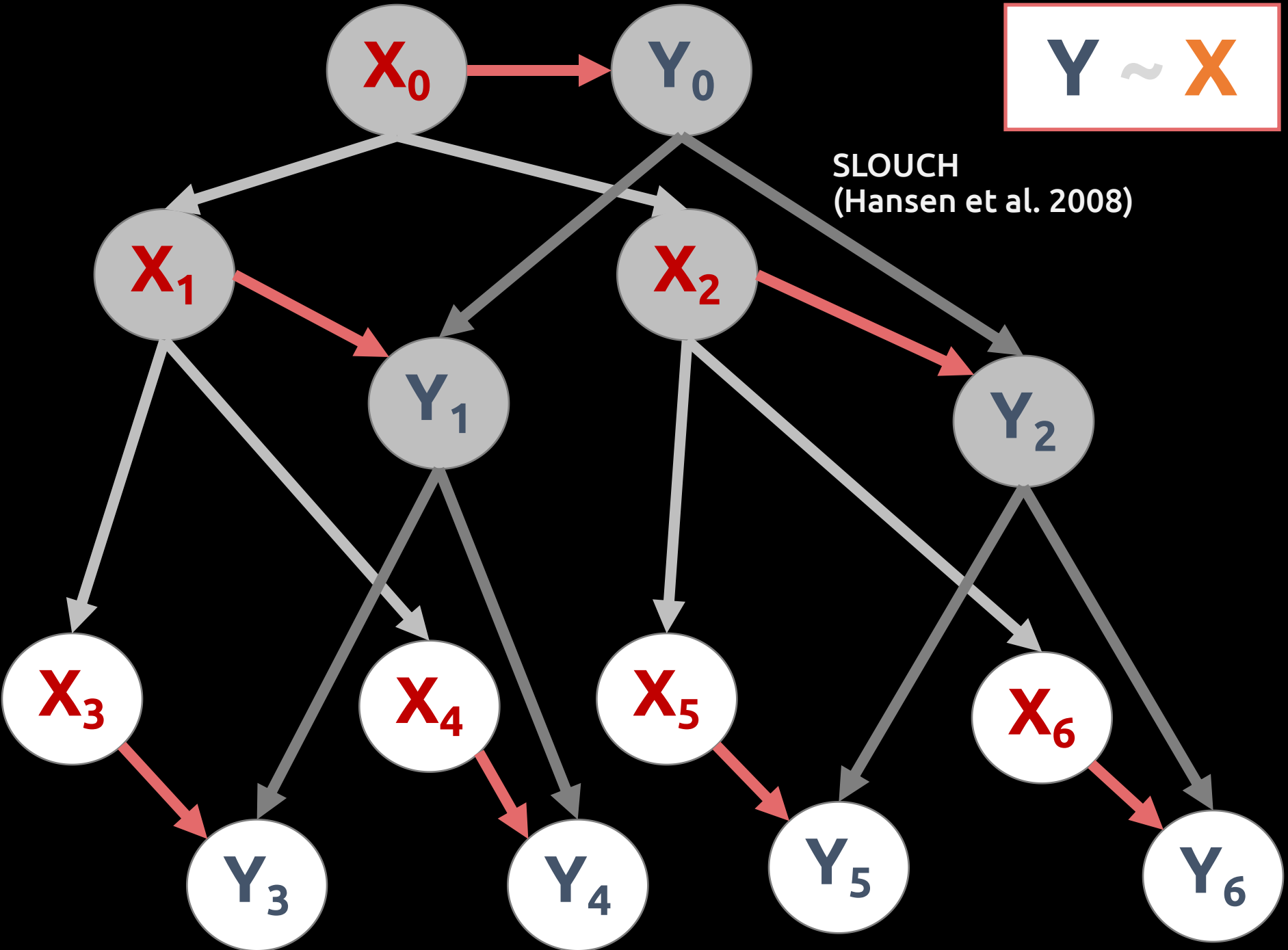
Phylogenies are causal graphs

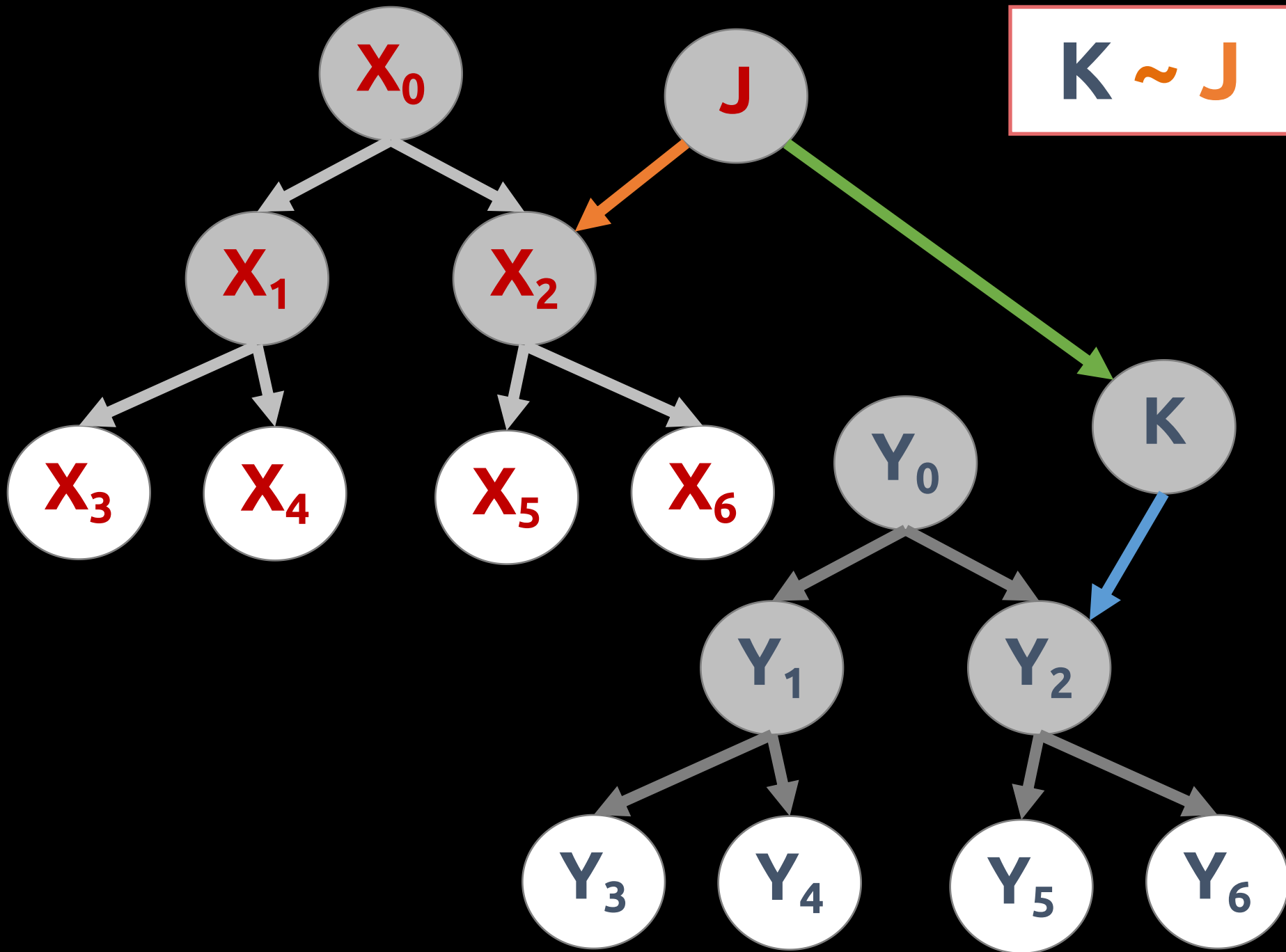
$$Y \sim X$$



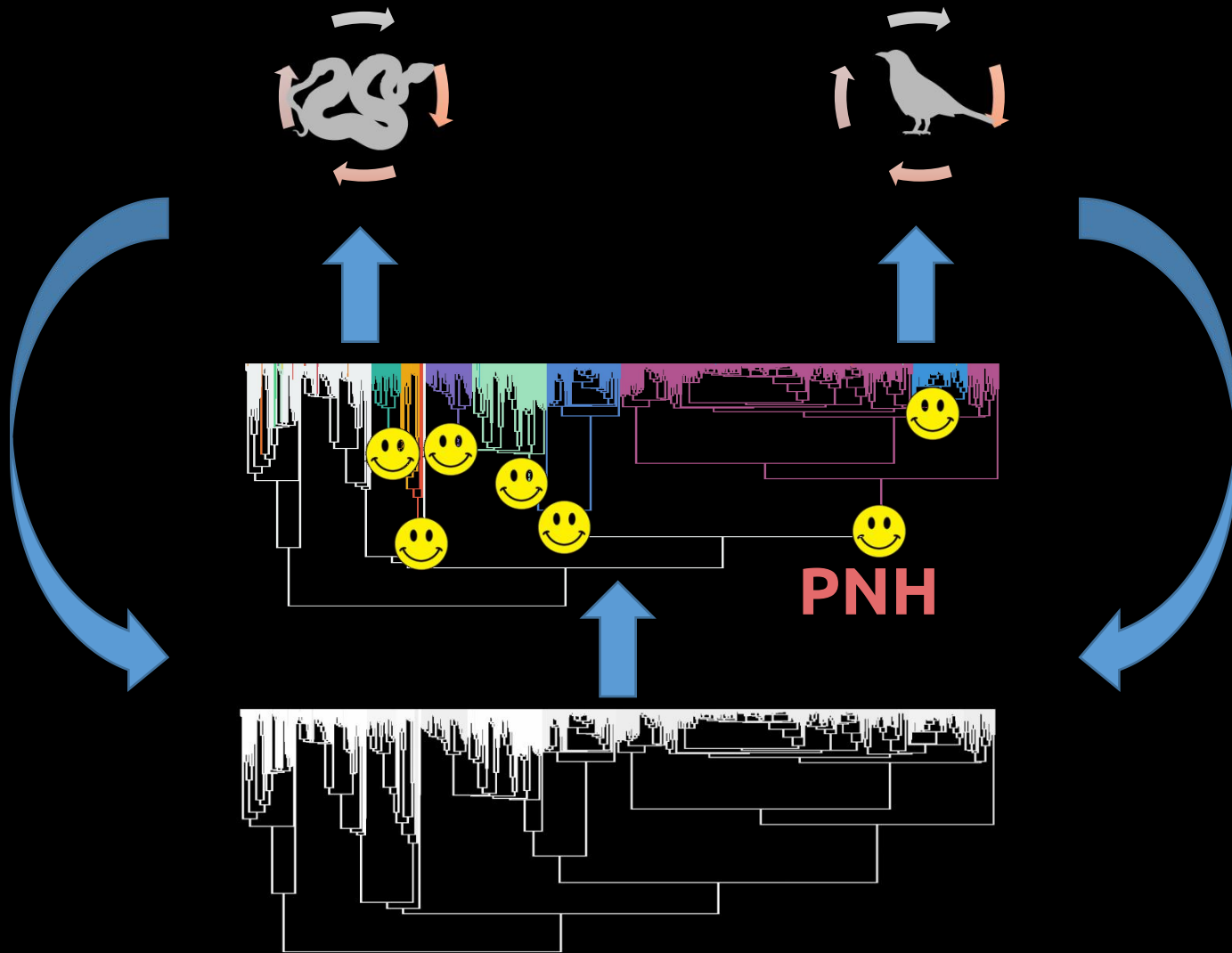
$Y \sim X$

SLOUCH
(Hansen et al. 2008)





A Micro to Macroevolutionary Research program



**"No statistical procedure can substitute
for thinking about alternative evolutionary
scenarios and their plausibility"**
- Westoby et al. 1996