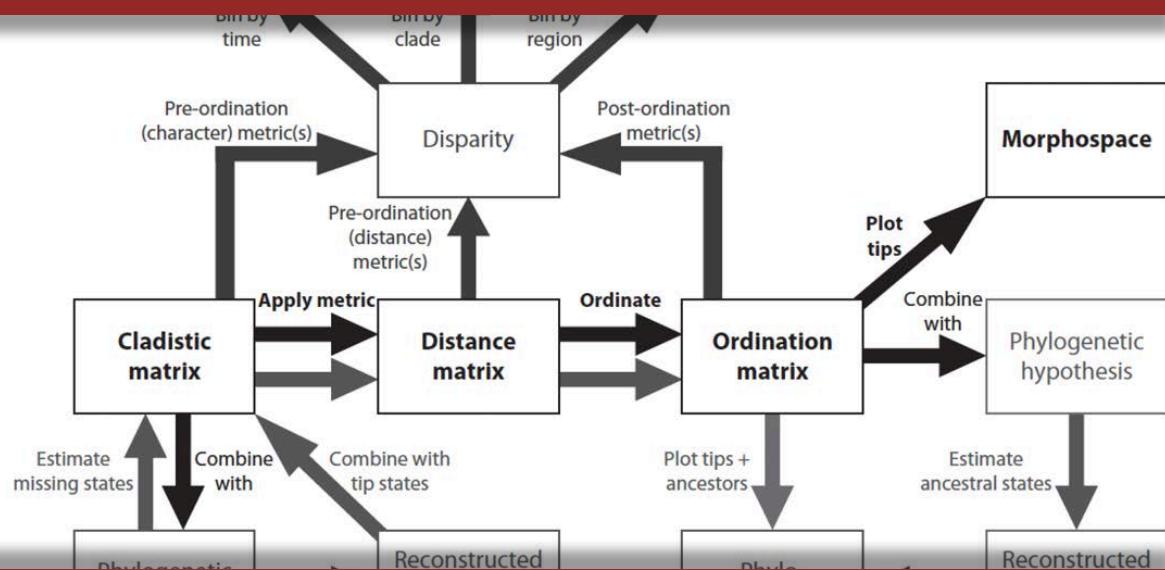
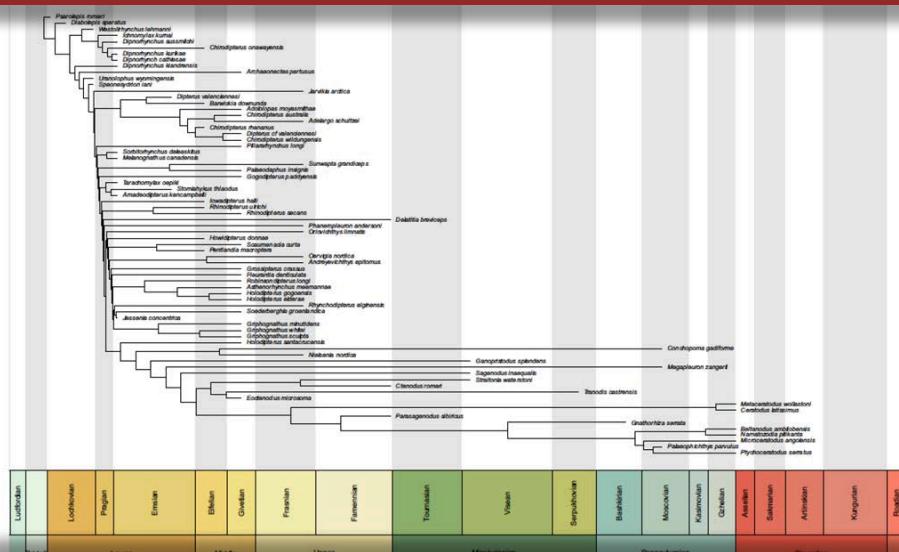


# Plotting phylogenies against stratigraphy and generating discrete character phylomorphospaces



Graeme T. Lloyd @GraemeTLloyd

# Shout outs



Dave  
Bapst



Mark  
Bell



Roger  
Benson



Steve  
Brusatte



Rich  
Fitzjohn



Dani  
Fraser



Matt  
Friedman



Thomas  
Guillerme



Melanie  
Hopkins



Matt  
Pennell



Liam  
Revell



Emma  
Sherratt



Steve  
Wang



Peter  
Smits



Australian Government

Australian Research Council



MACQUARIE  
University  
SYDNEY · AUSTRALIA

NERC  
SCIENCE OF THE  
ENVIRONMENT

# R packages

strap

Claddis

metatree

disperse

hypRspace

# R packages

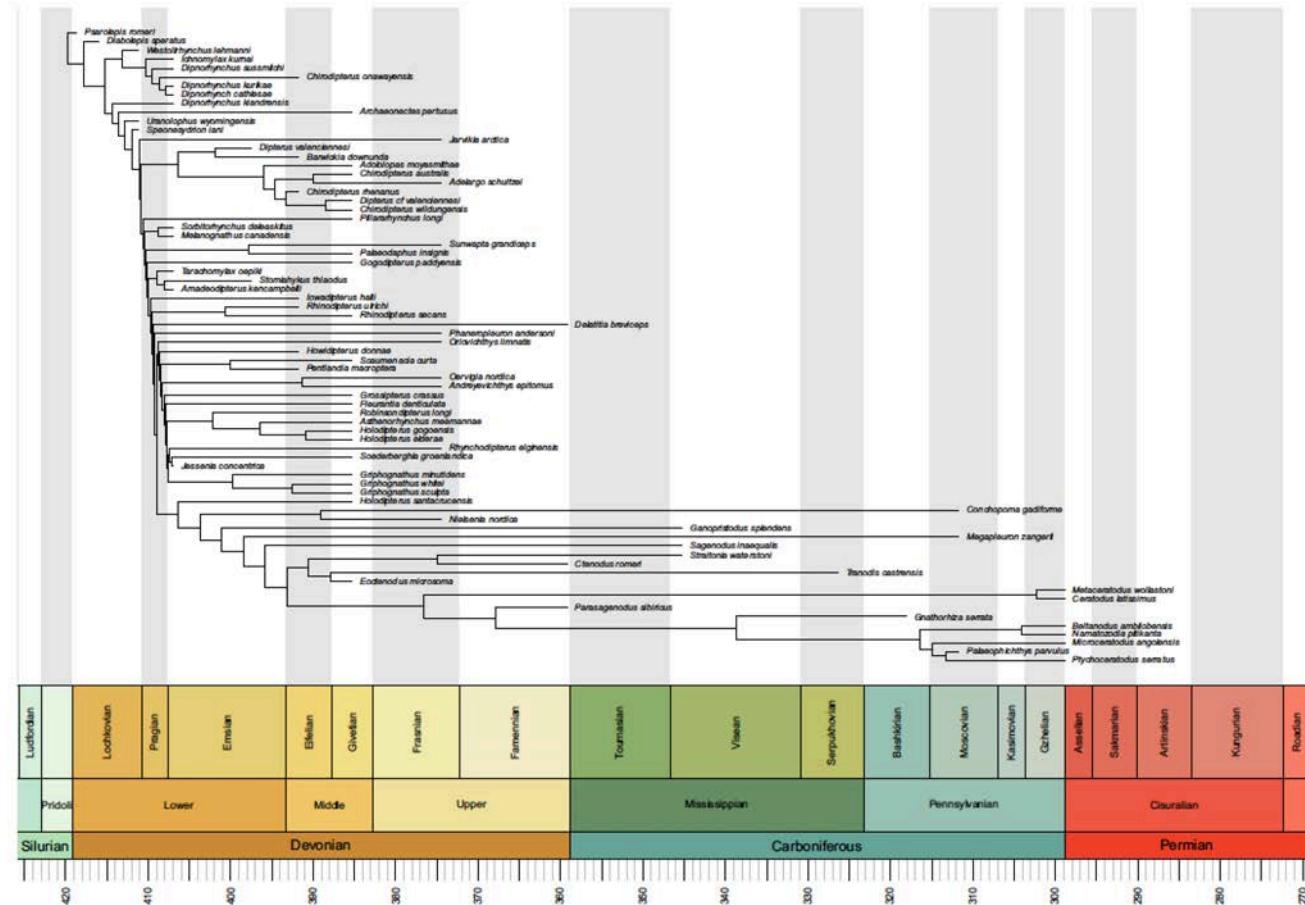
strap

Claddis

metatree

disperse

hypRspace



Bell et Lloyd 2015; *Palaeontology*, 58, 379-389

strap::geoscalePhylo()

# R packages

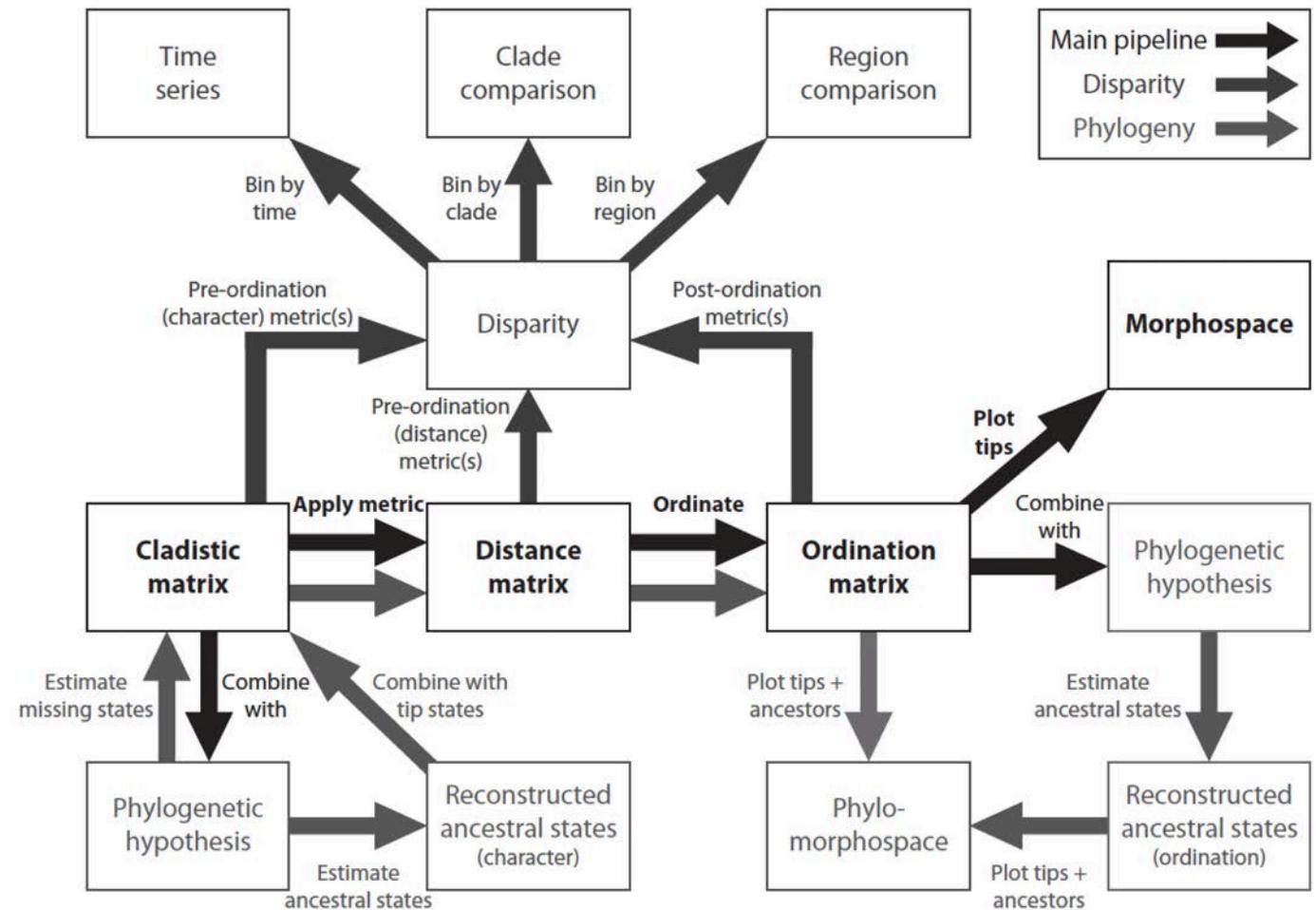
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Claddis

metatree

disperse

hypRspace



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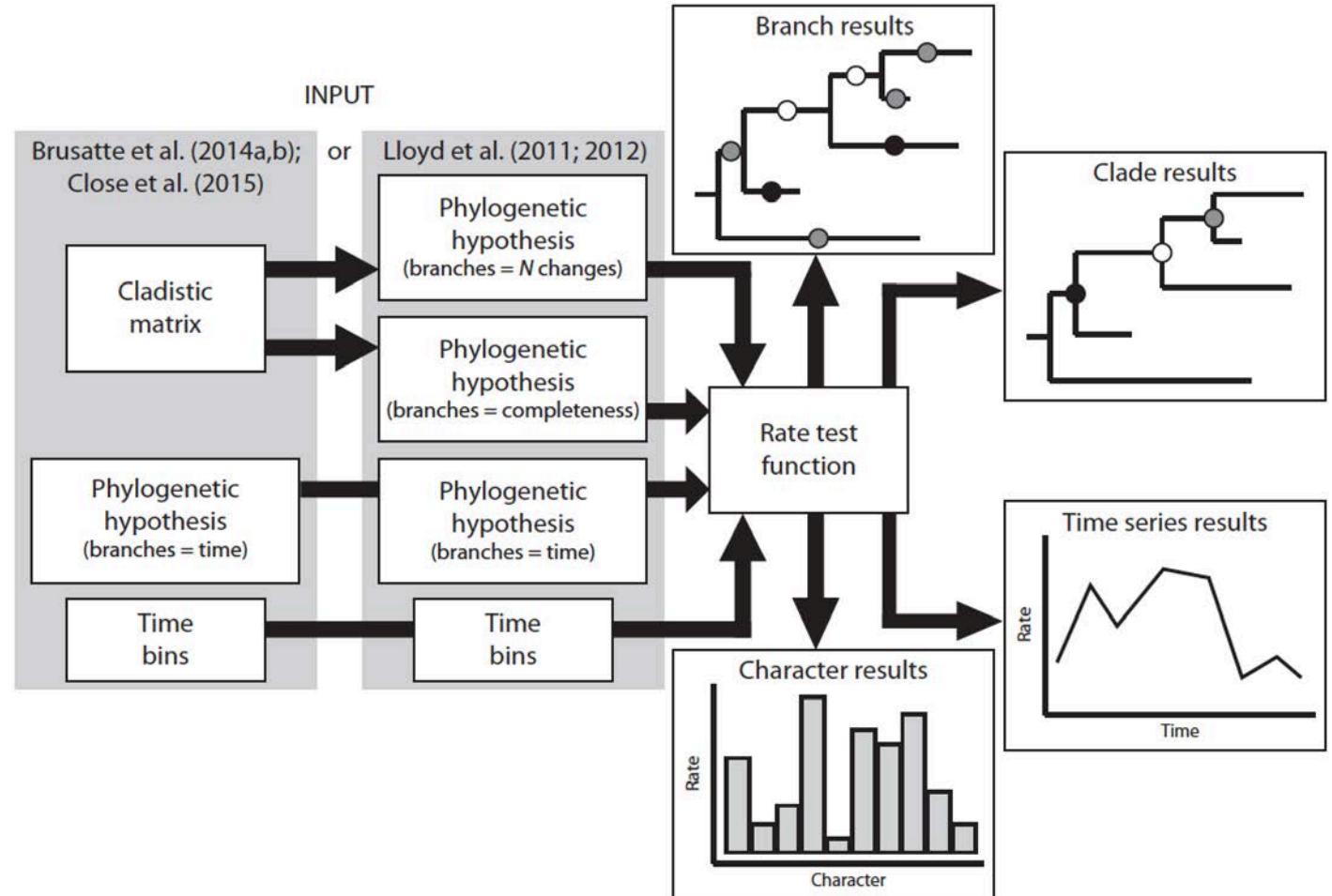
strap

Claddis

metatree

disperse

hypRspace



Lloyd 2016; *Biological Journal of the Linnean Society*, **118**, 131-151

Claddis::DiscreteCharacterRate()

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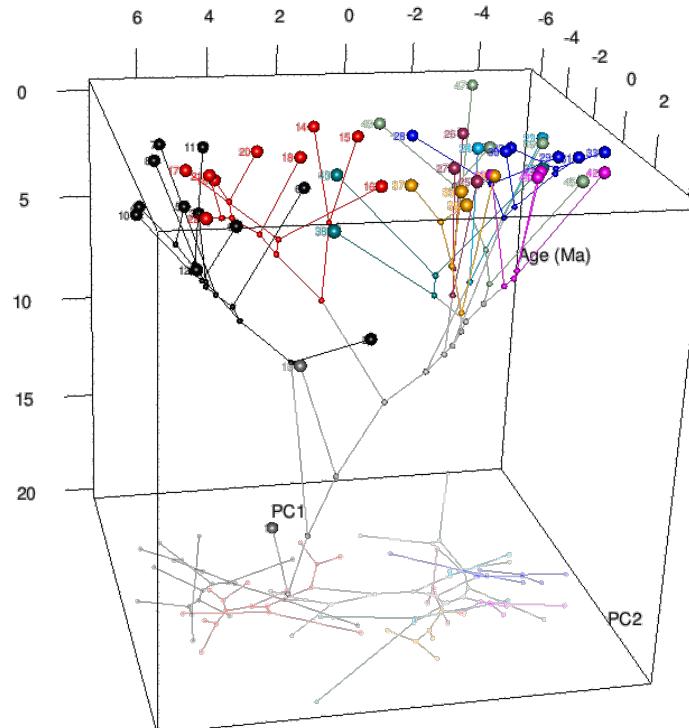
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Claddis

metatree

disperse

hypRspace



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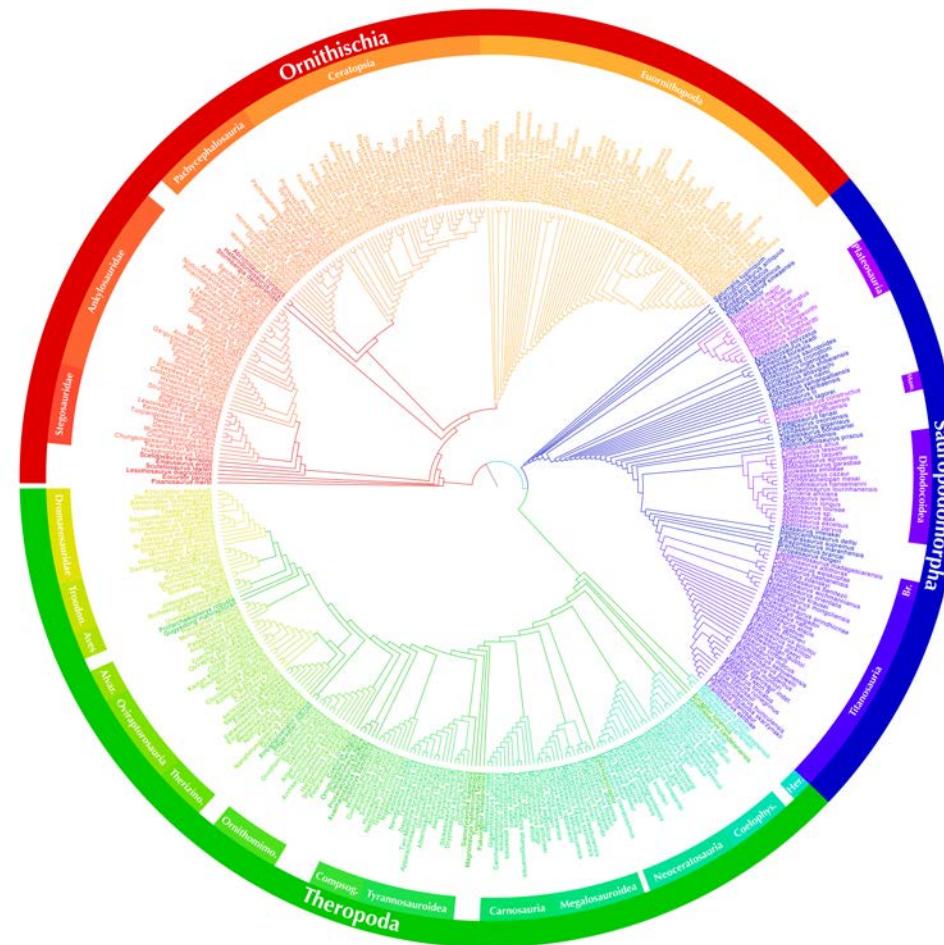
strap

claddis

metatree

disperse

hypRspace



Lloyd unpublished; Lloyd et al 2016; *Biology Letters*, 12, 20160609

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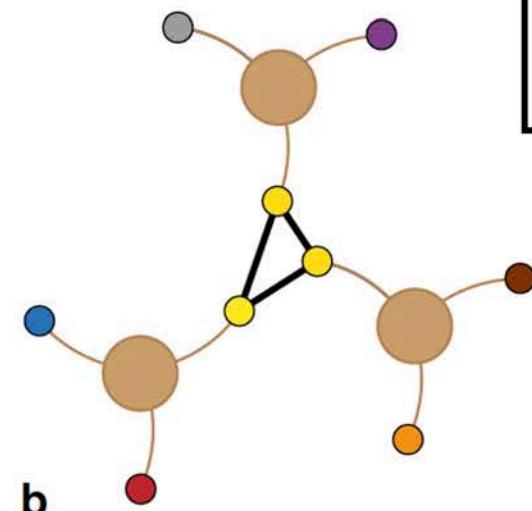
strap

Claddis

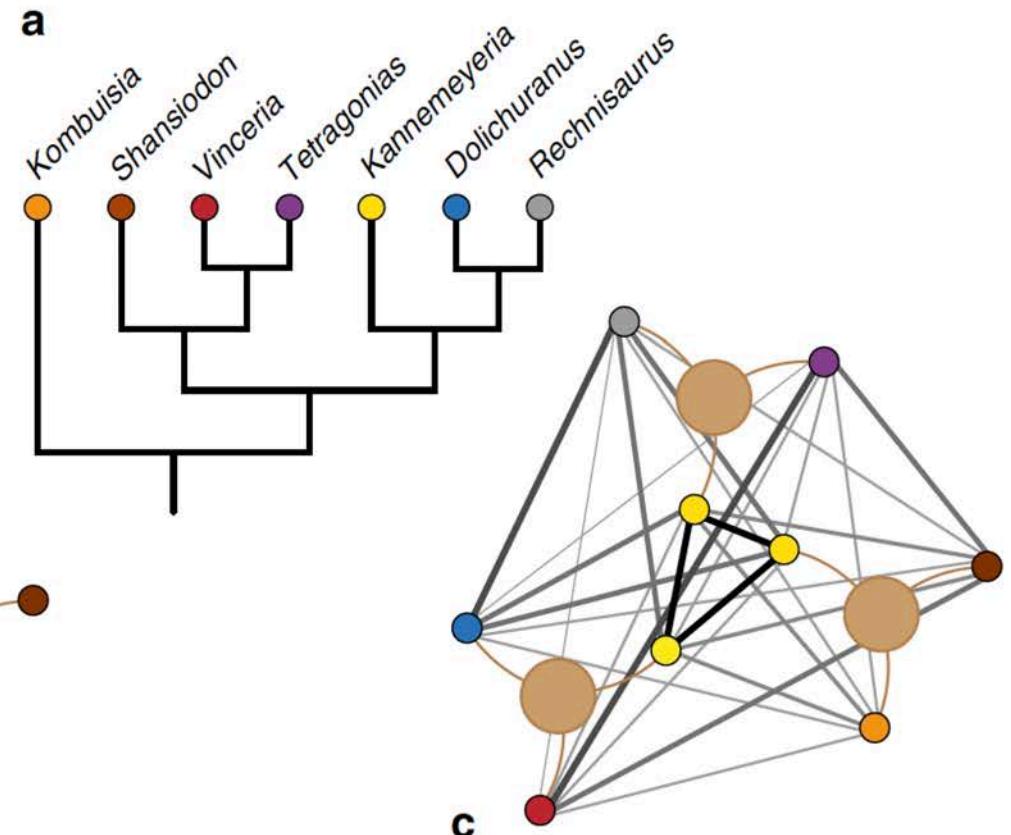
metatree

dispeRse

hypRspace



b



c

# R packages

strap

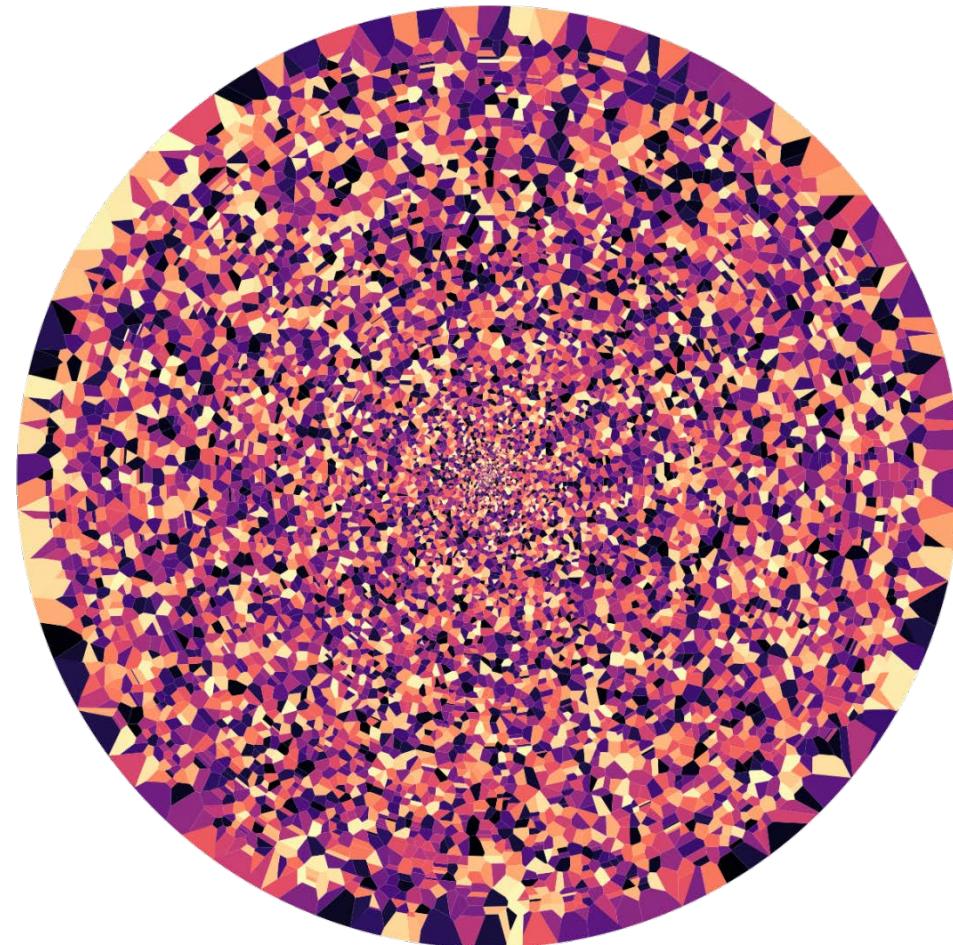
Claddis

metatree

disperse

**hypRspace**

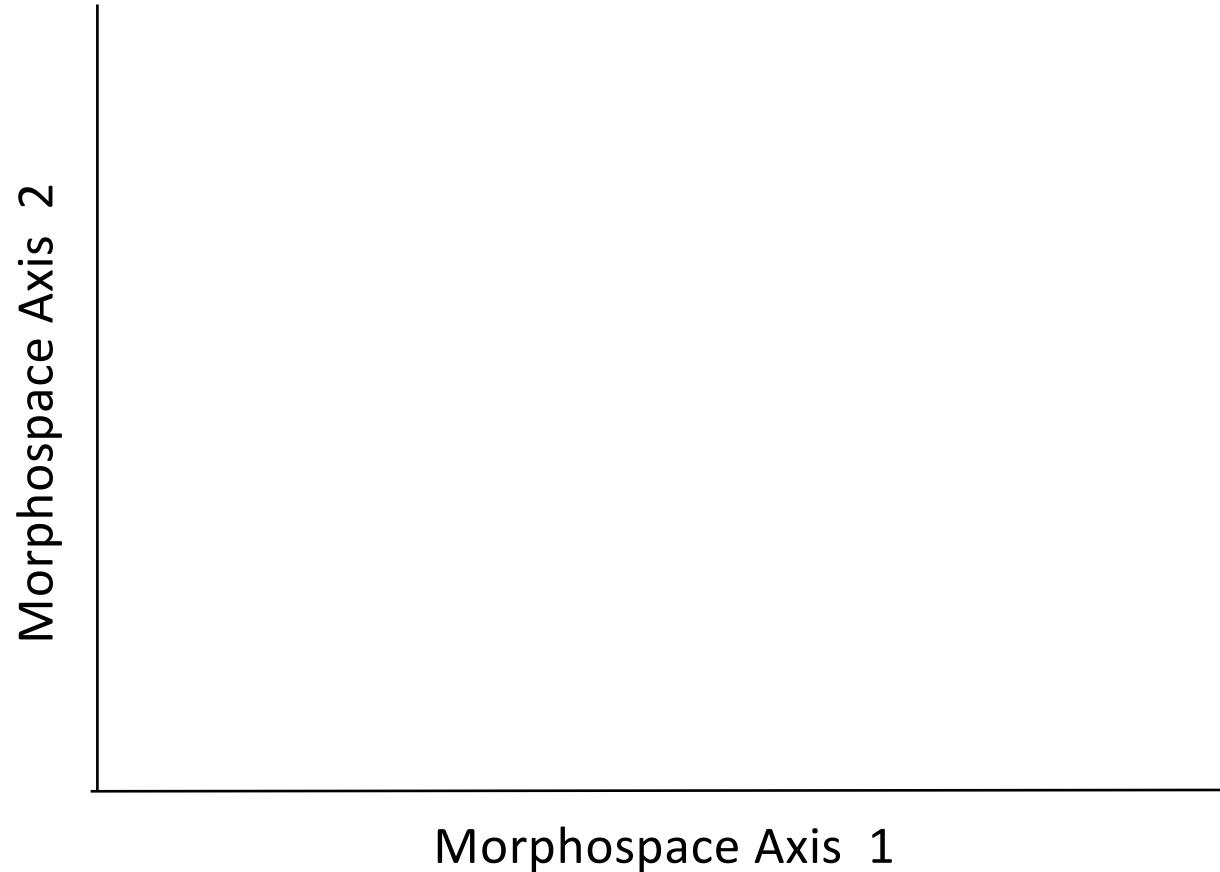
Lloyd unpublished



hypRspace::CircularVoronoi()

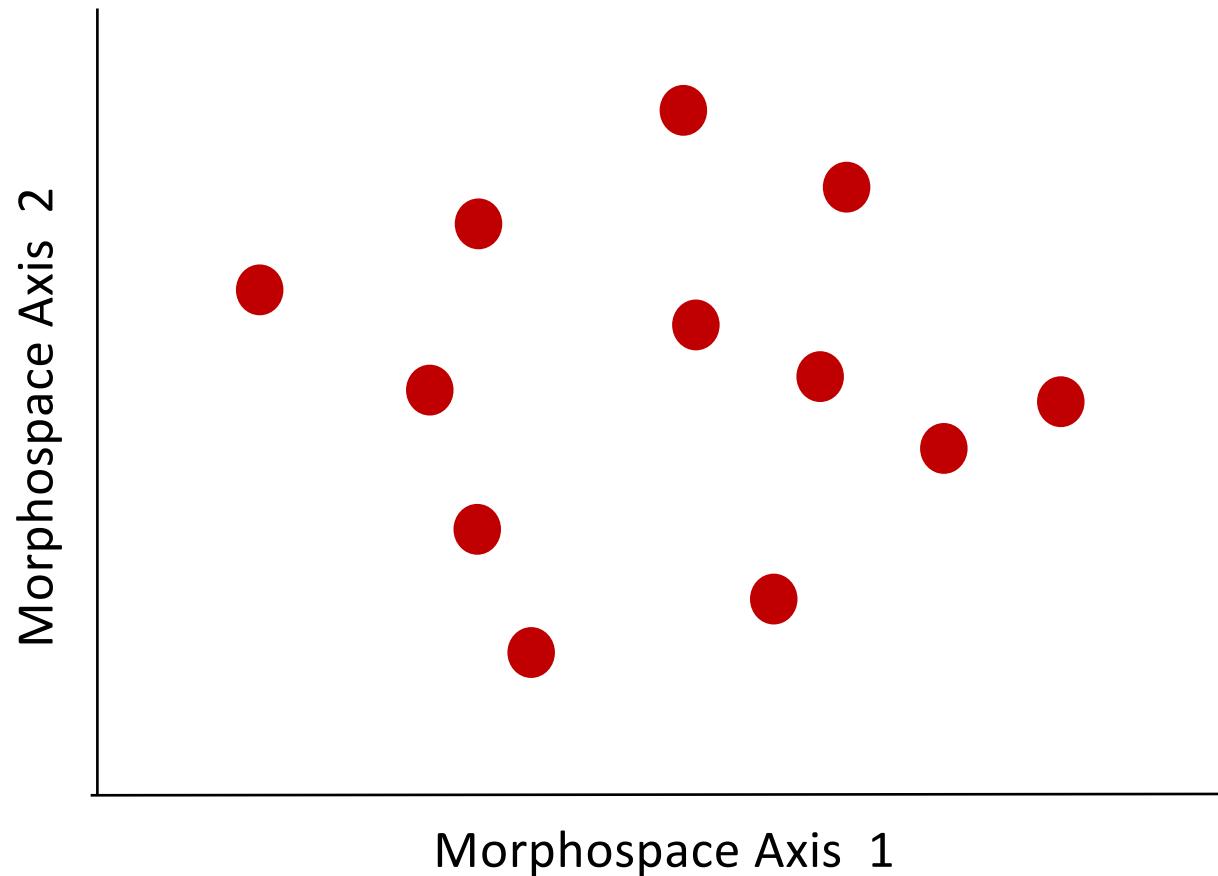
# The phylomorphospace

# The phylomorphospace



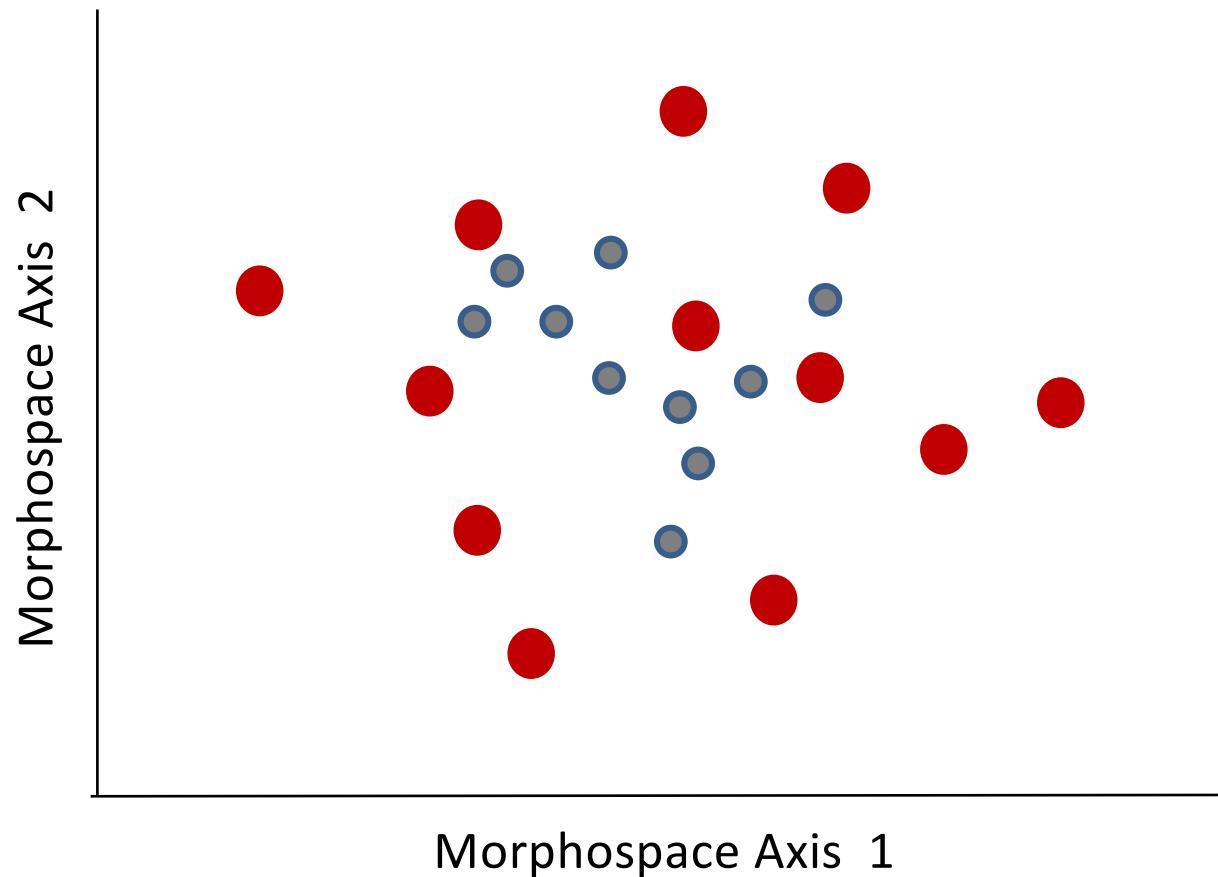
Sidlauskas 2008, *Evolution*, **62**, 3135-3156

# The phylomorphospace

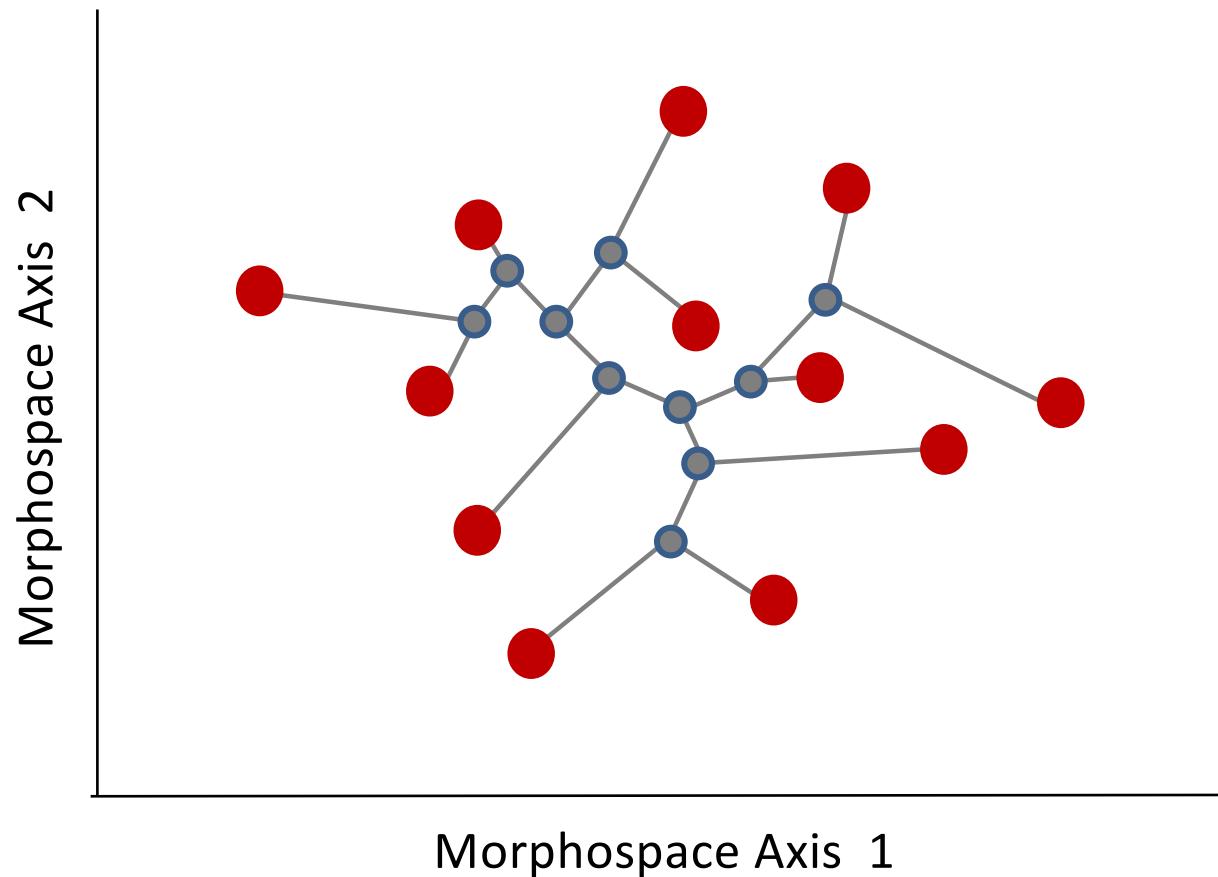


Sidlauskas 2008, *Evolution*, **62**, 3135-3156

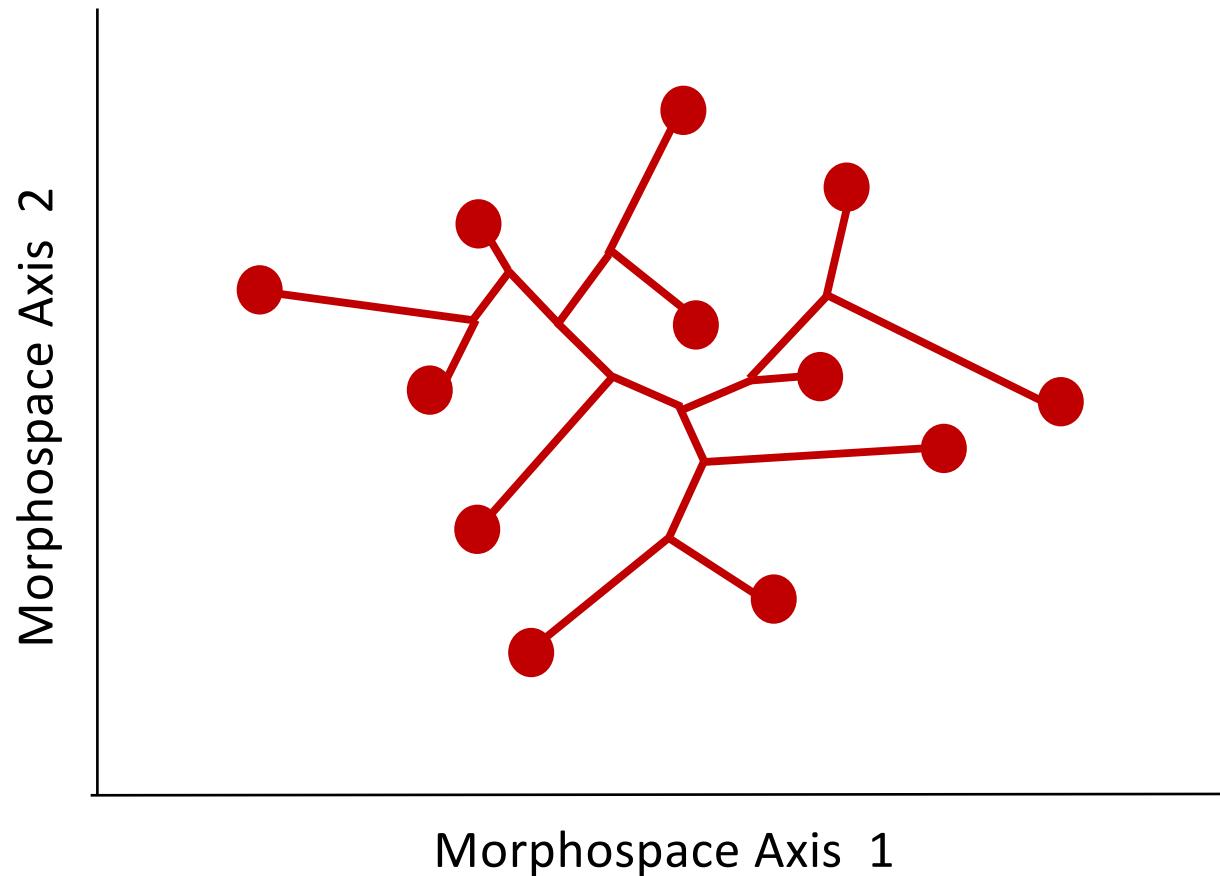
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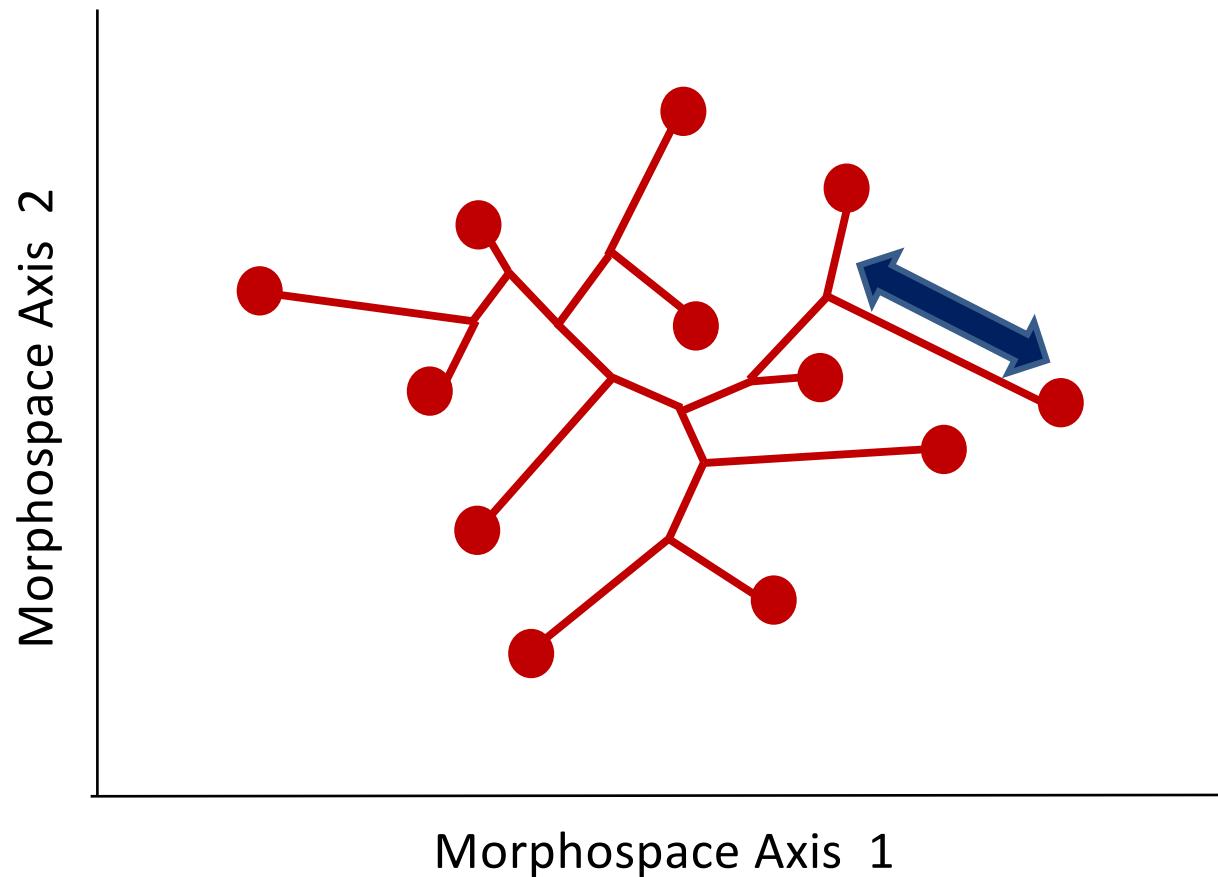


# The phylomorphospace



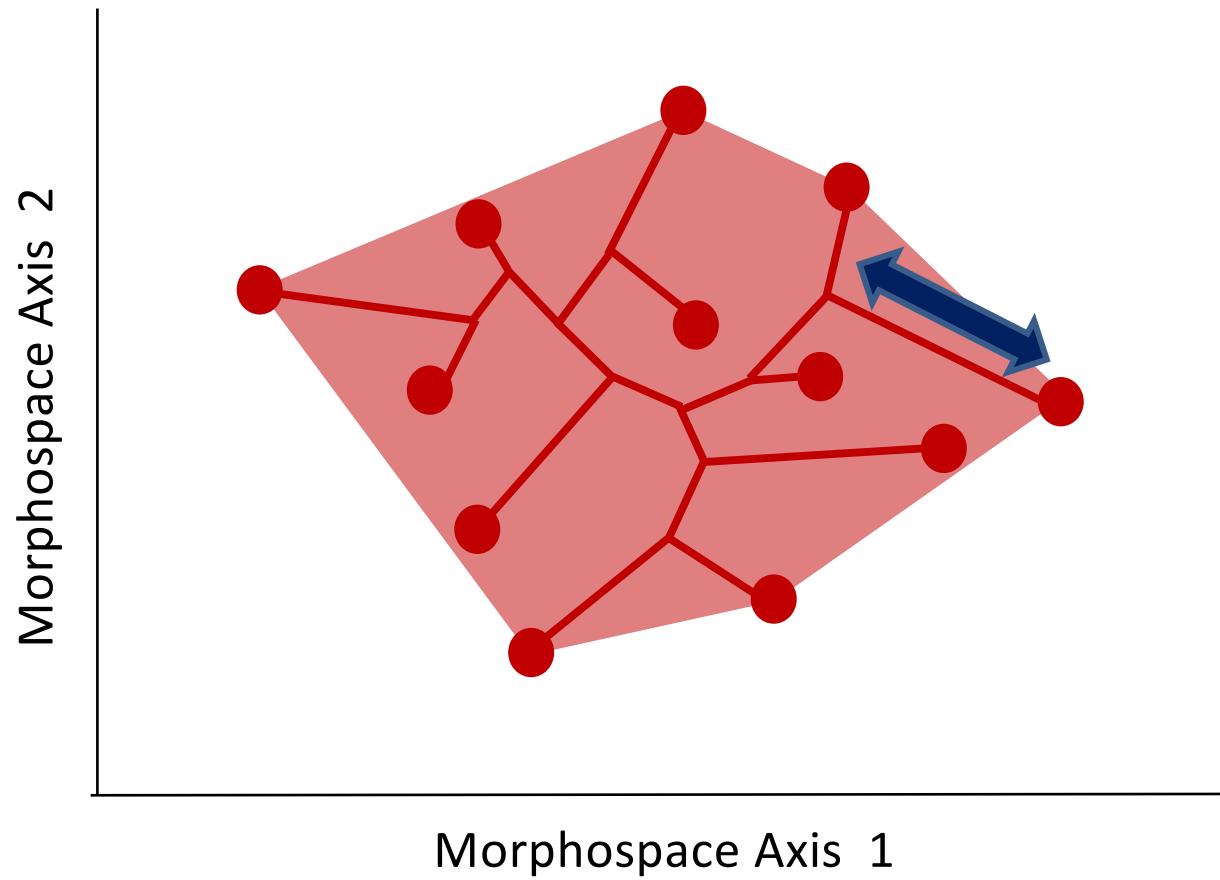
Sidlauskas 2008, *Evolution*, 62, 3135-3156

# The phylomorphospace



Sidlauskas 2008, *Evolution*, 62, 3135-3156

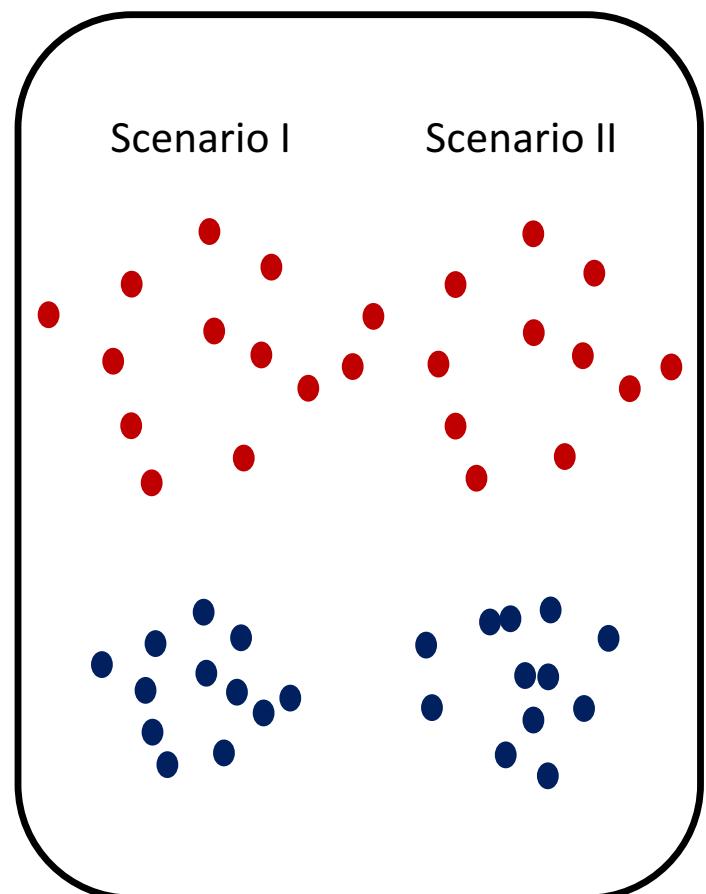
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Sidlauskas 2008, *Evolution*, 62, 3135-3156

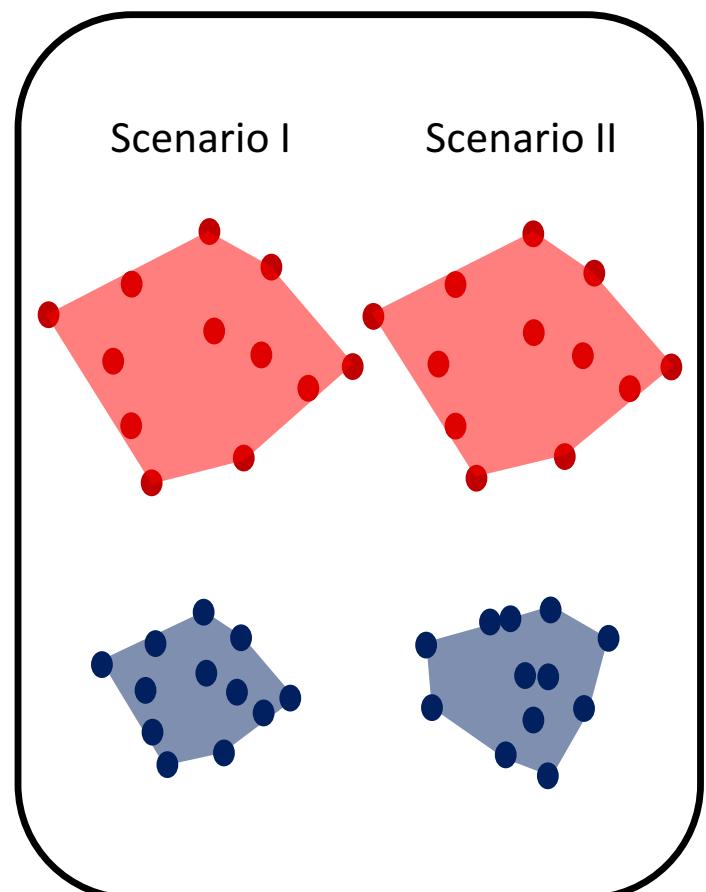
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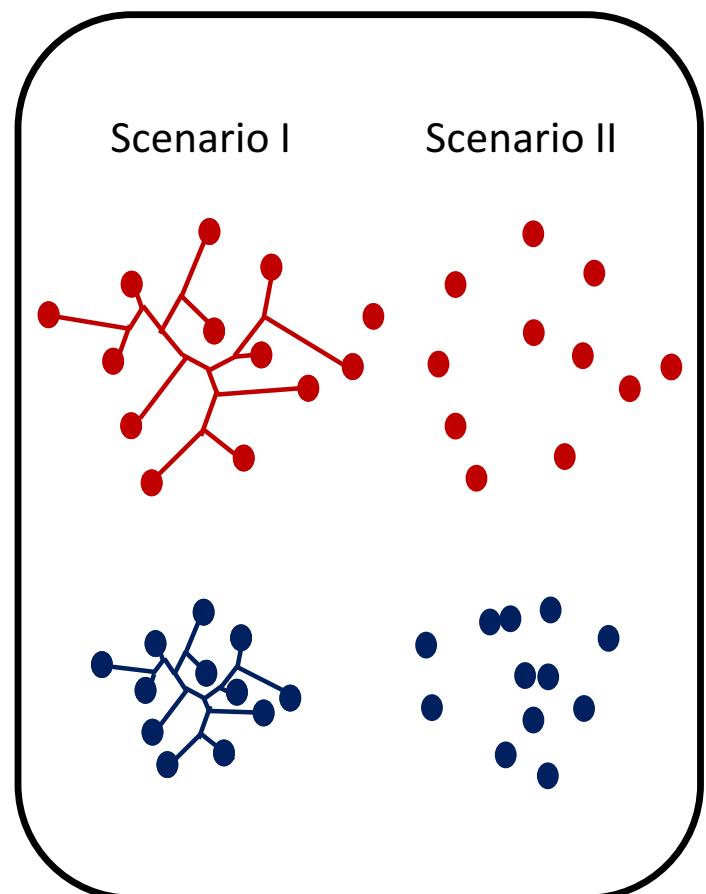
Sidlauskas 2008, *Evolution*, **62**, 3135-3156

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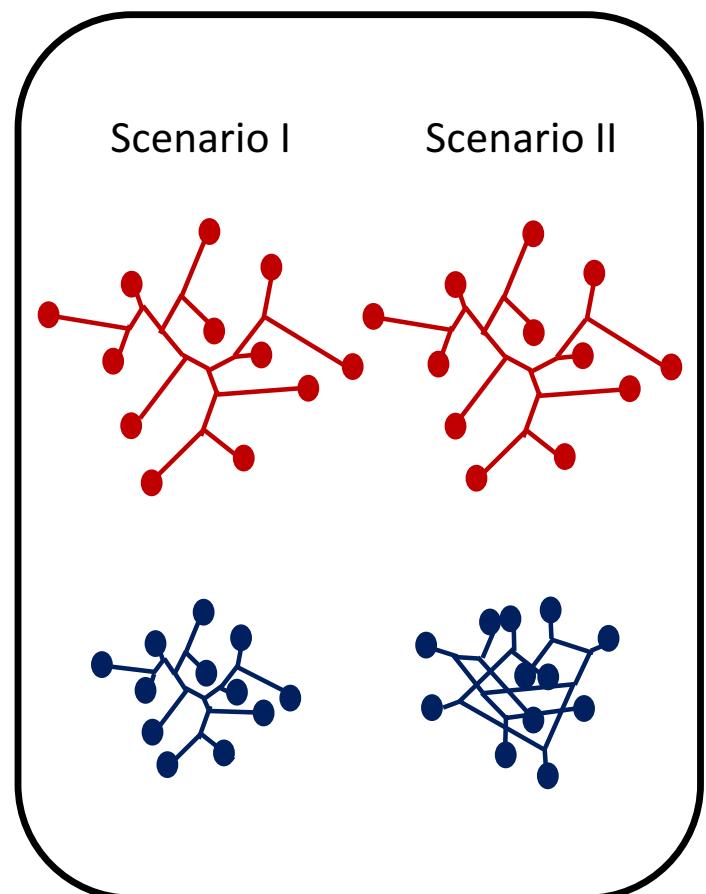
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# The phylomorphospace



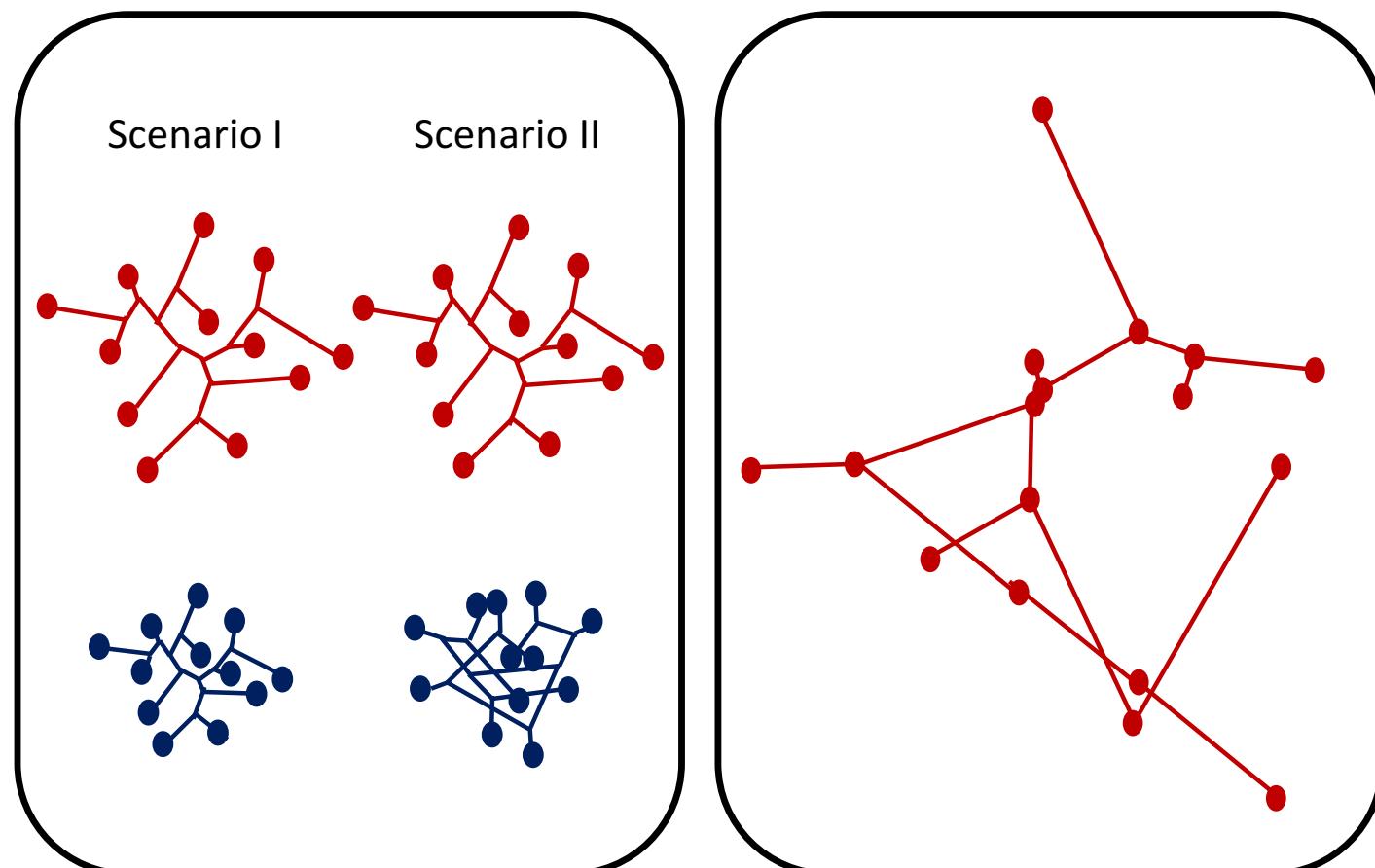
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# The phylomorphospace



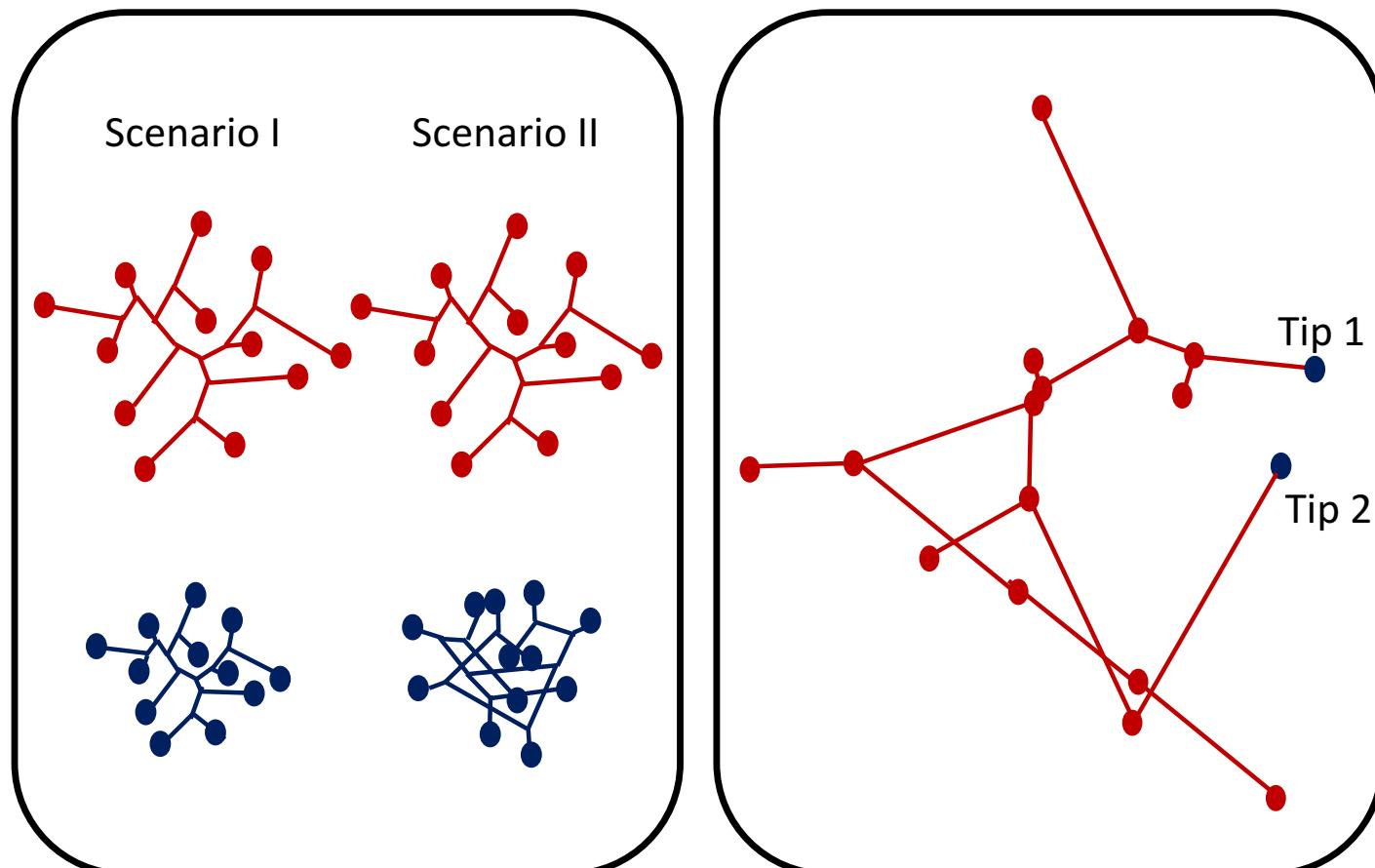
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# The phylomorphospace



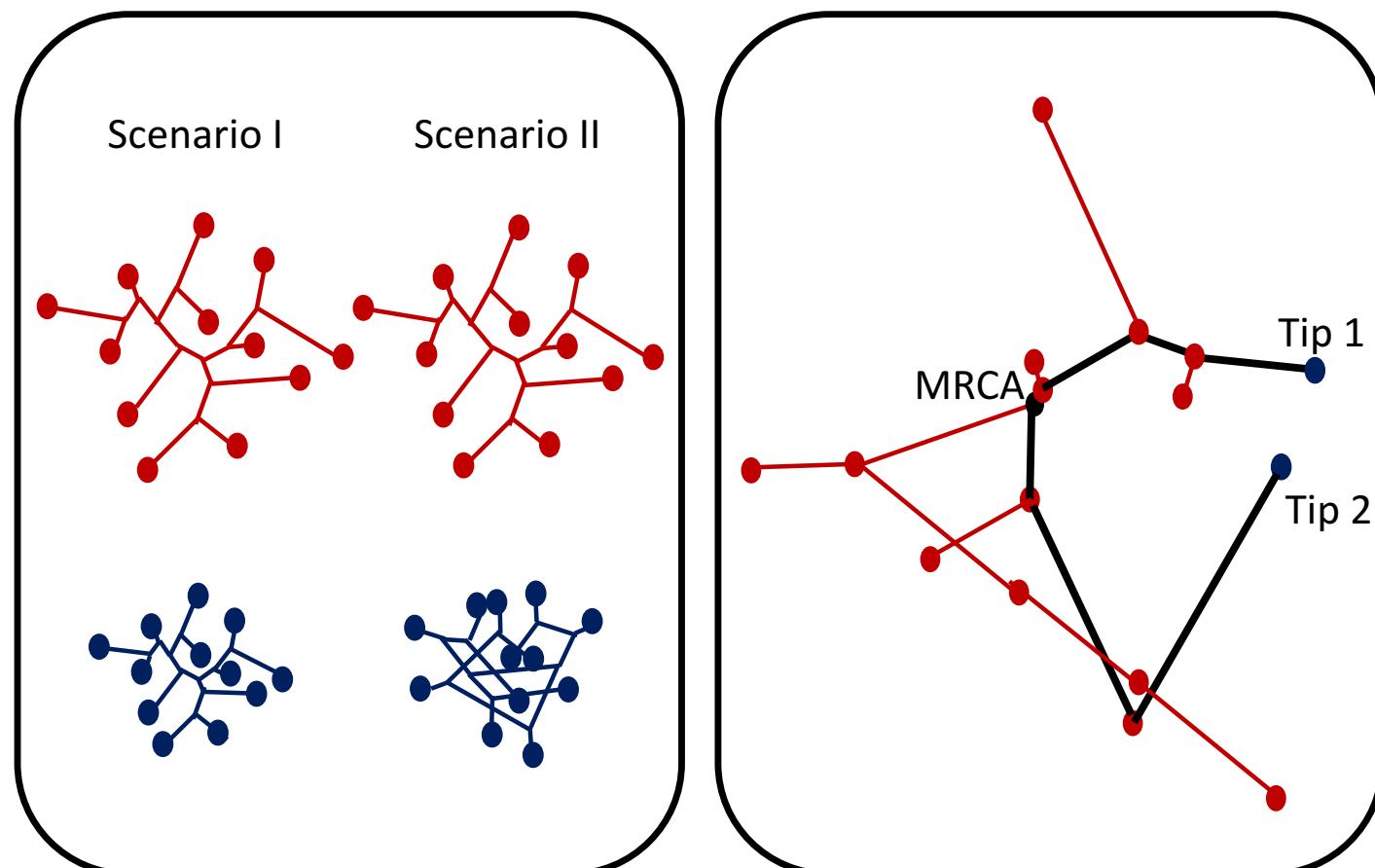
Sidlauskas 2008, *Evolution*, **62**, 3135-3156; Stayton 2015; *Evolution*, **69**, 2140-2153

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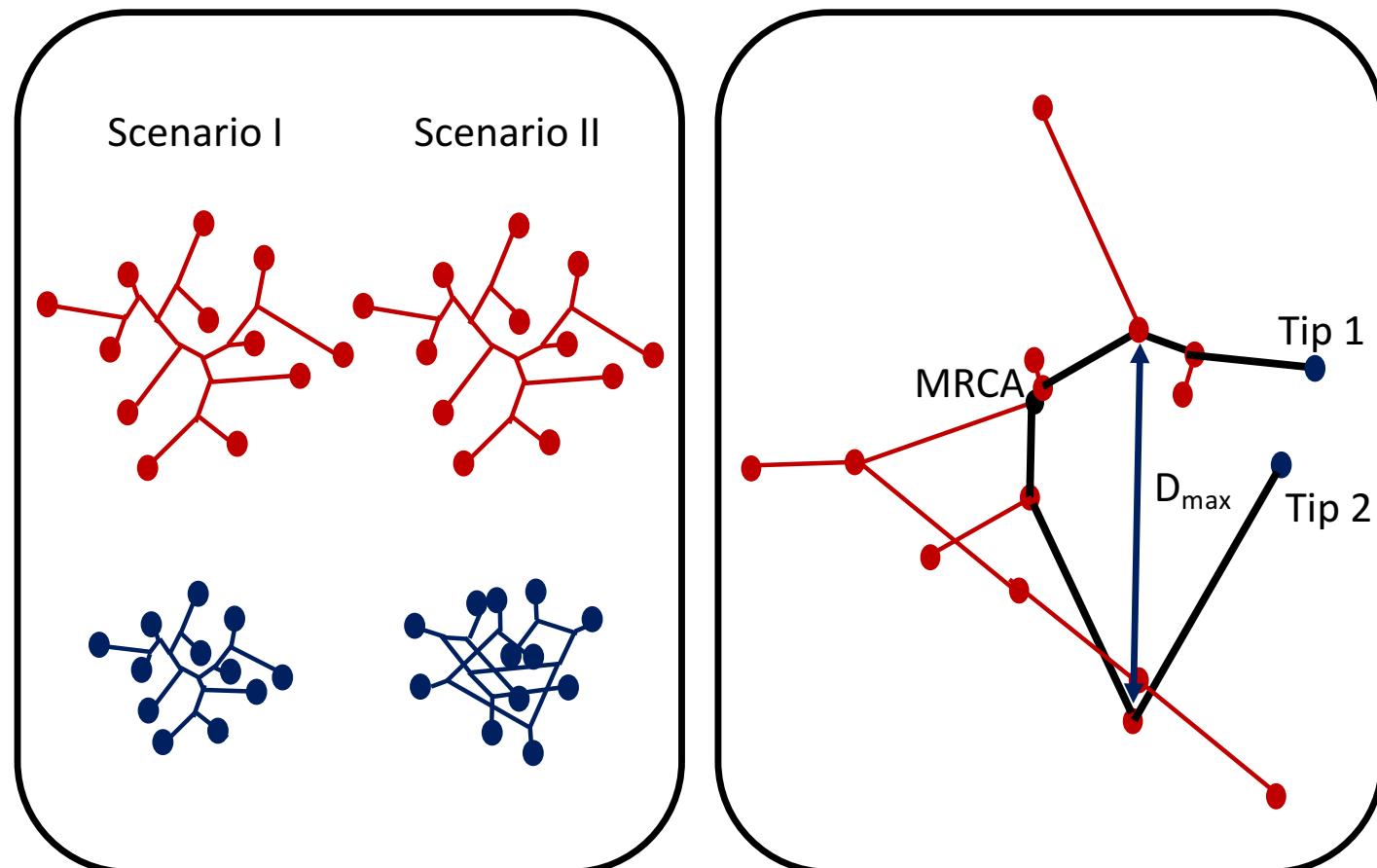
Sidlauskas 2008, *Evolution*, **62**, 3135-3156; Stayton 2015; *Evolution*, **69**, 2140-2153

# The phylomorphospace



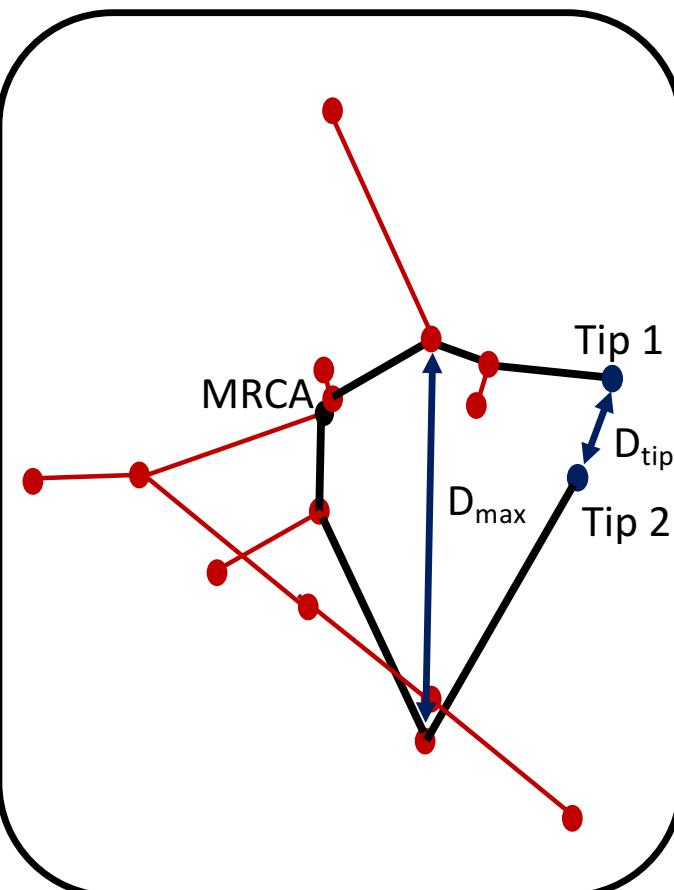
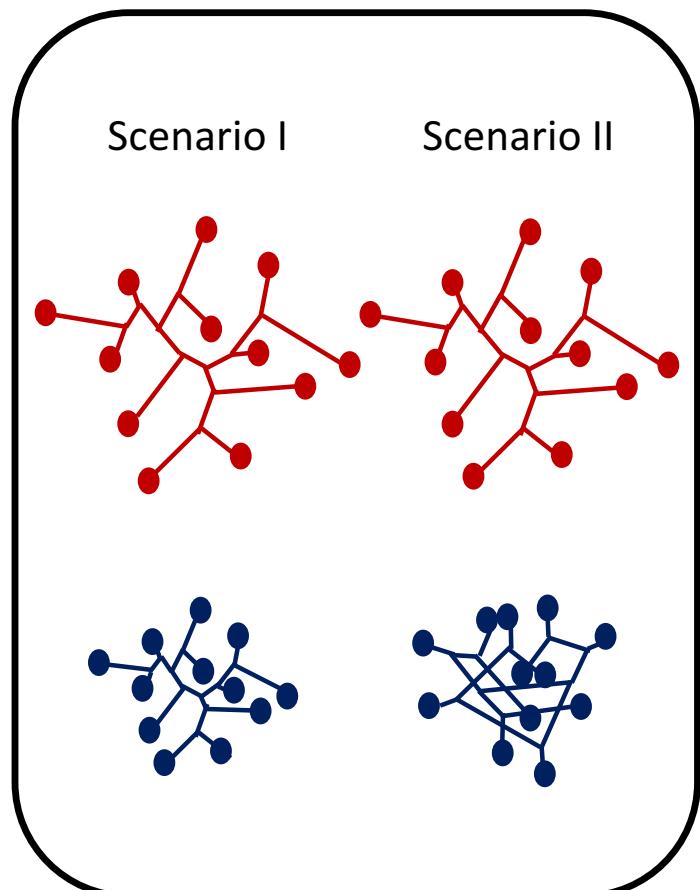
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# The phylomorphospace



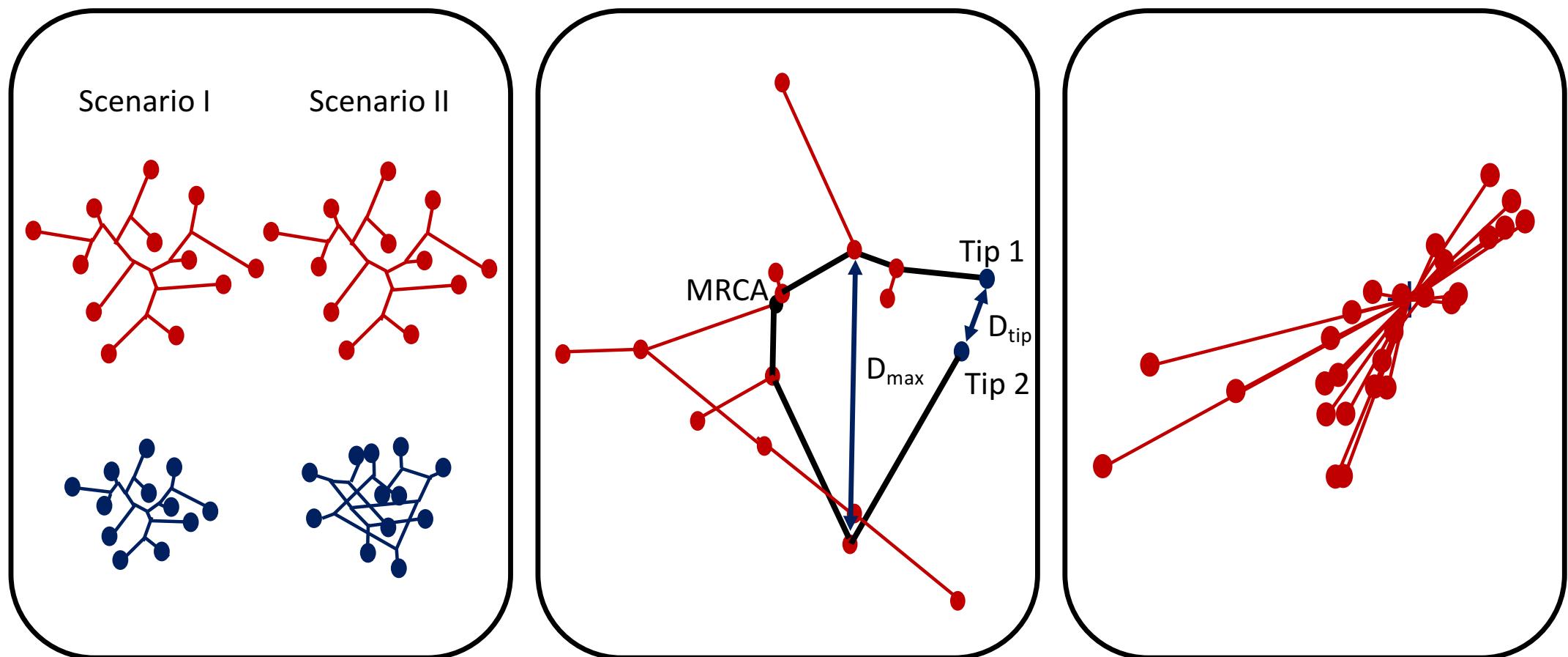
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# The phylomorphospace



Sidlauskas 2008, *Evolution*, **62**, 3135-3156; Stayton 2015; *Evolution*, **69**, 2140-2153

# The phylomorphospace



Sidlauskas 2008, *Evolution*, **62**, 3135-3156; Stayton 2015; *Evolution*, **69**, 2140-; Hopkins 2016; *Biol. J. Linn. Soc.*, **118**, 116-130

# Discrete character (phylo)morphospace challenges

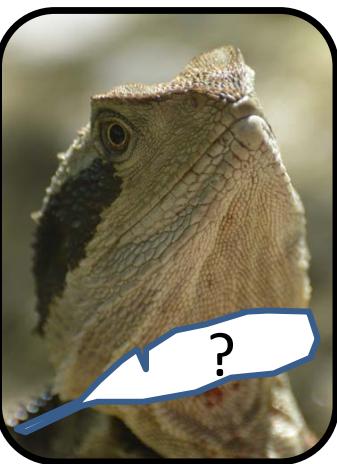
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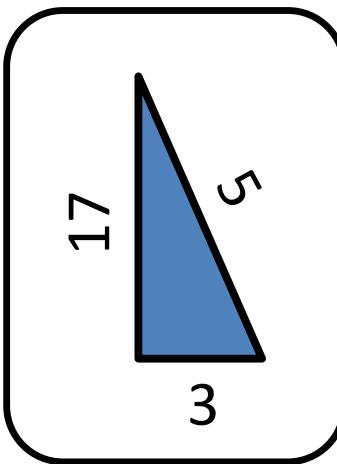
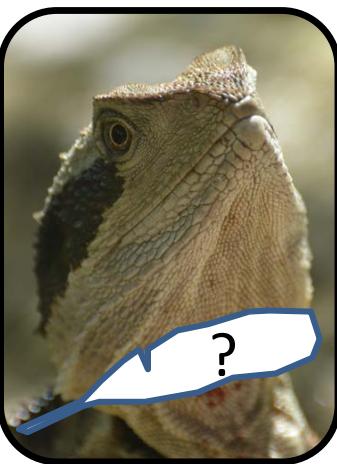
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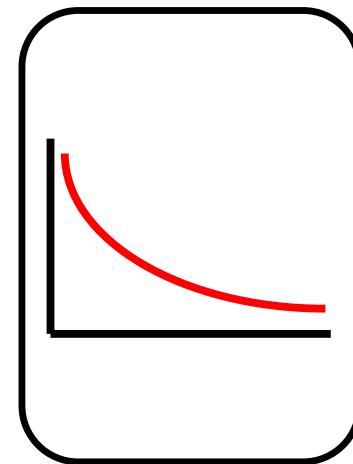
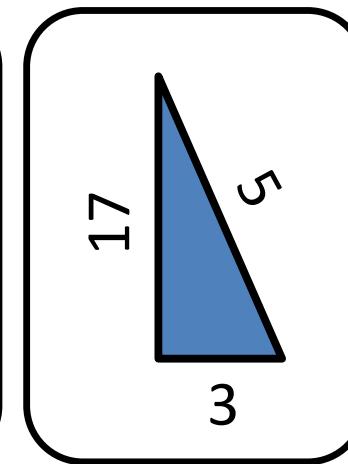
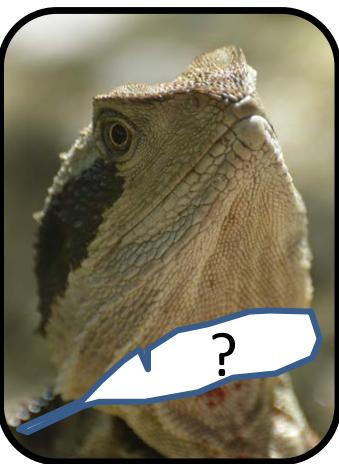
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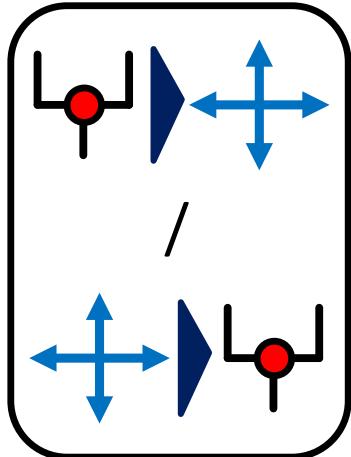
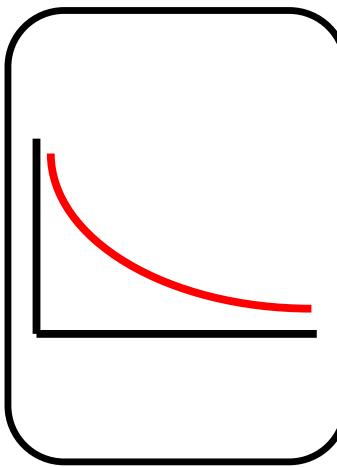
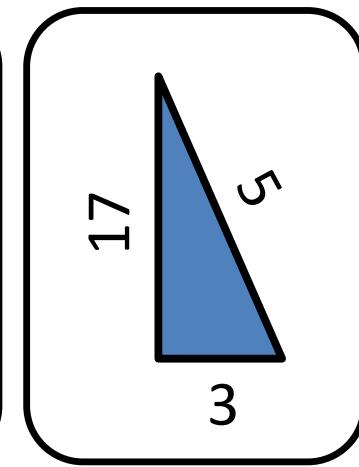
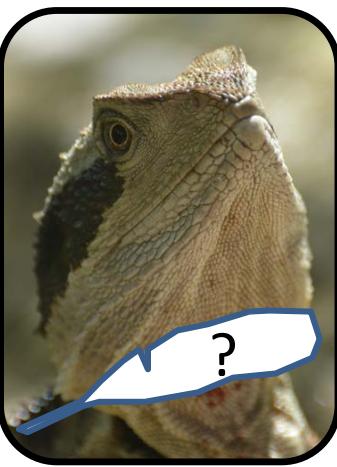
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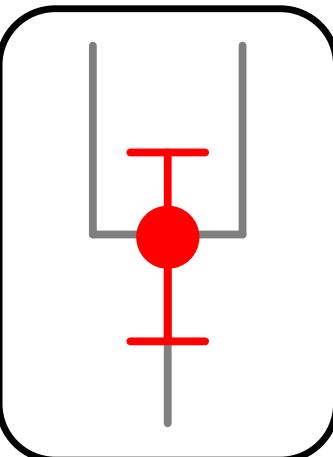
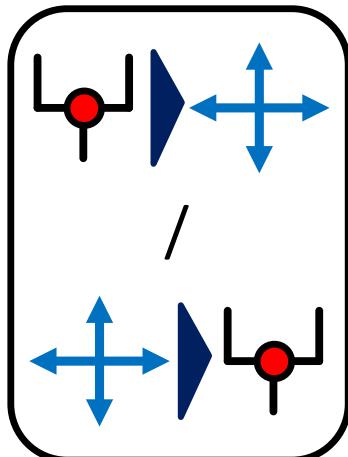
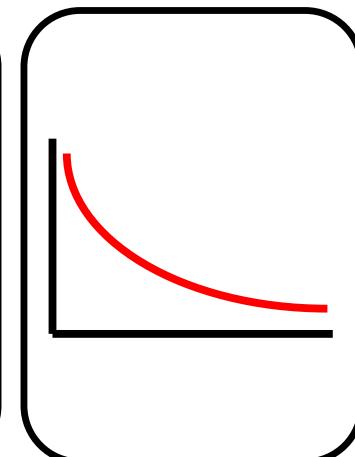
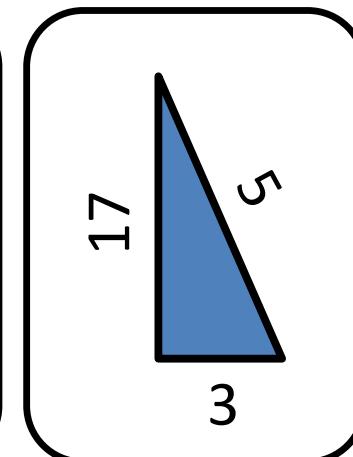
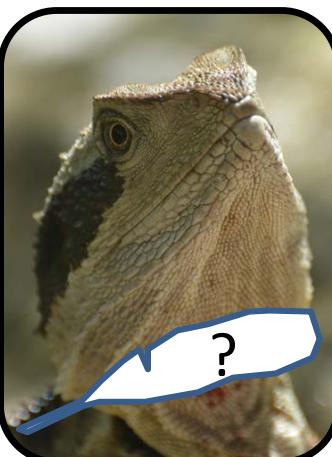
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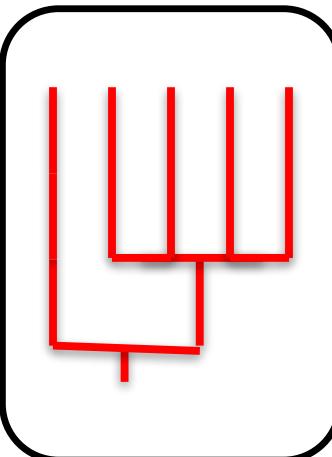
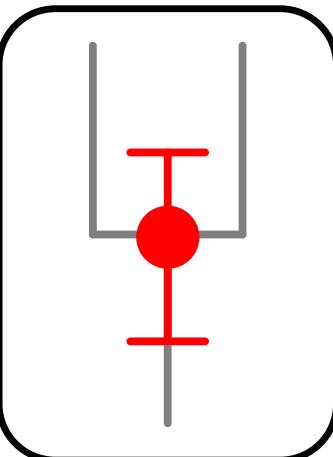
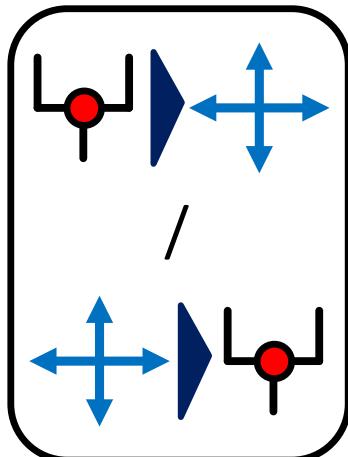
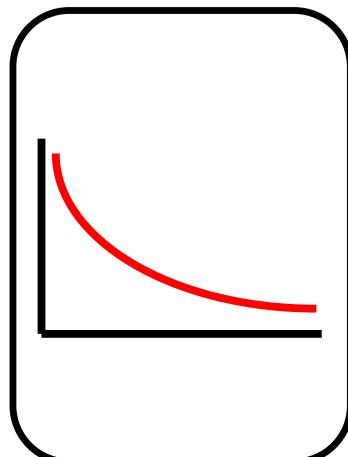
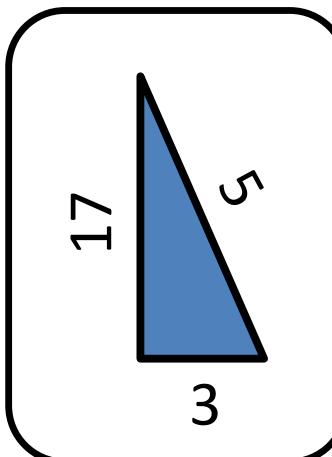
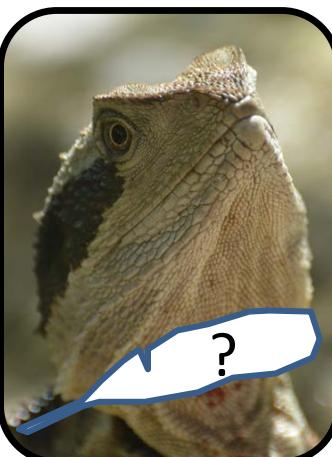
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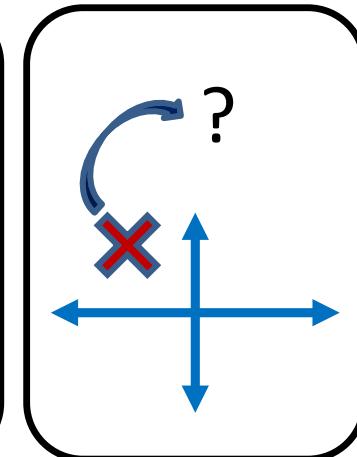
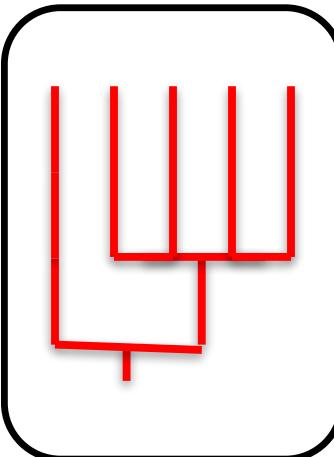
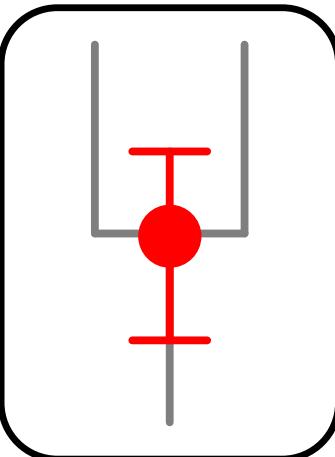
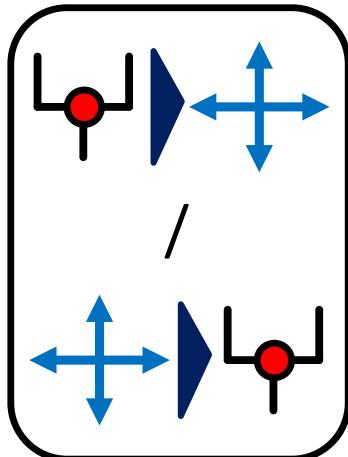
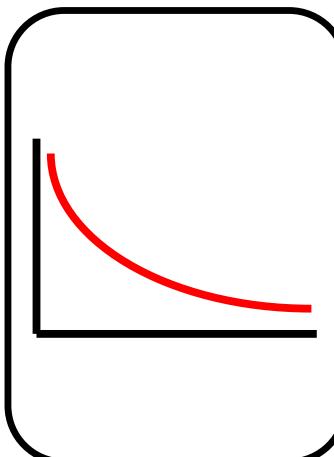
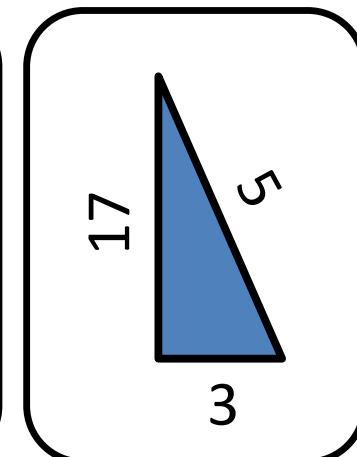
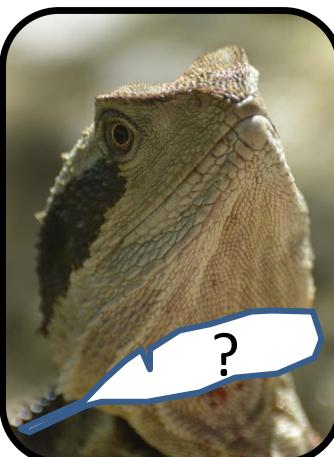
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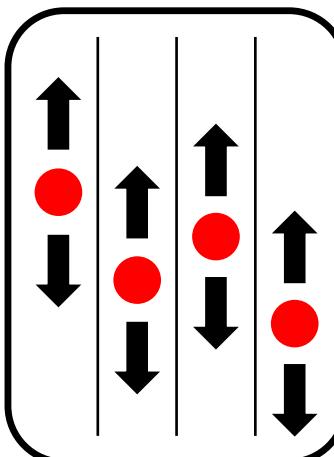
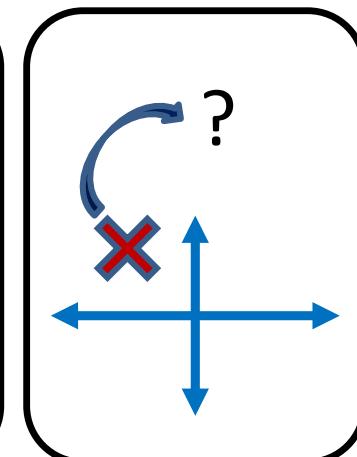
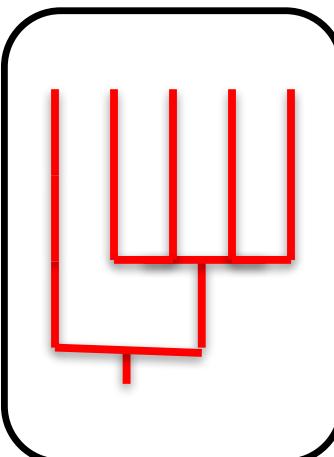
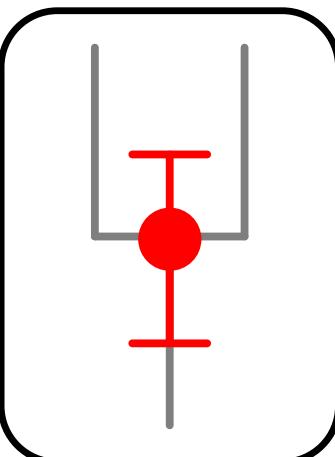
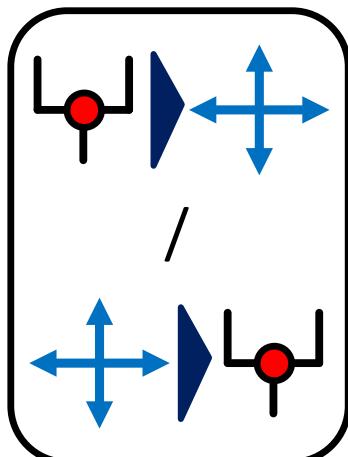
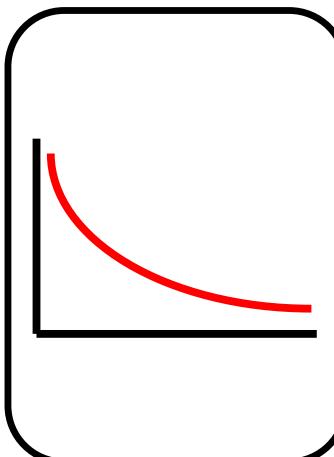
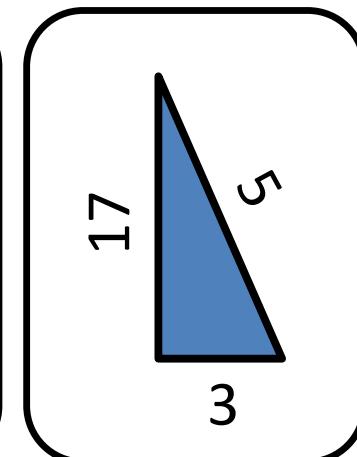
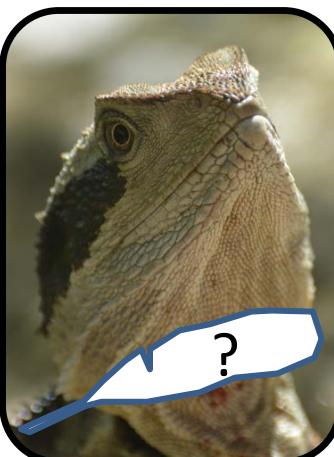
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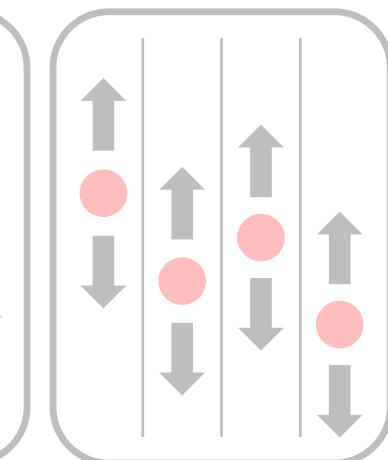
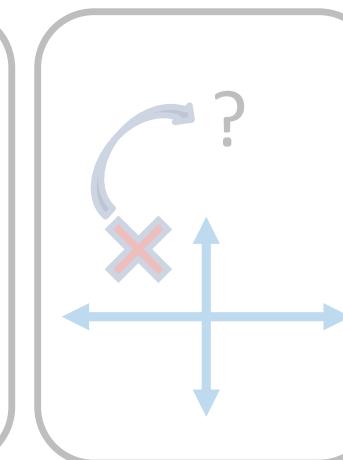
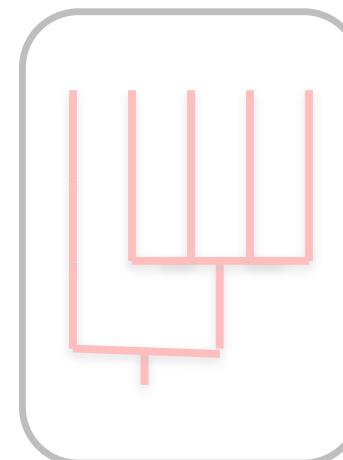
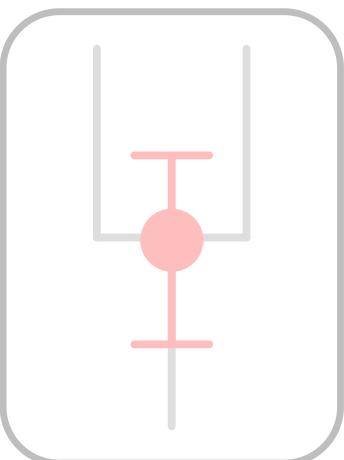
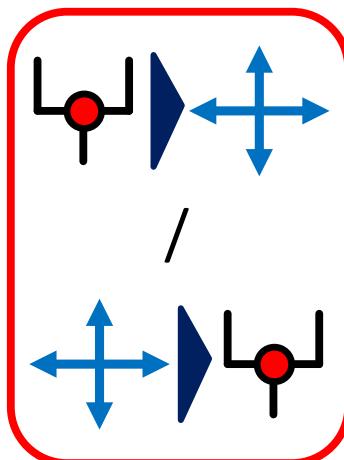
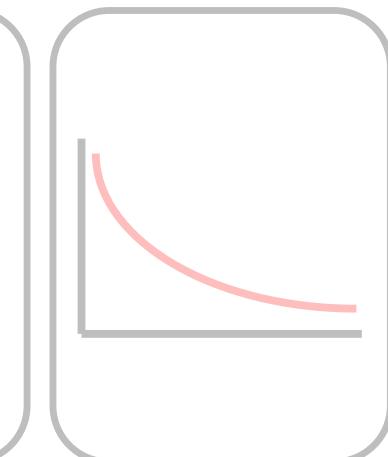
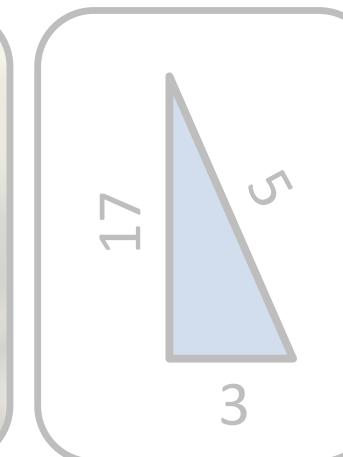
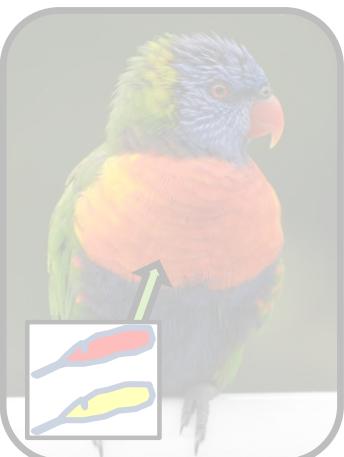
# Discrete character (phylo)morphospace challenges



# Discrete character (phylo)morphospace challenges



# Discrete character (phylo)morphospace challenges



# Two routes to a phylomorphospace

# Two routes to a phylomorphospace

## **Post-ordination ASE**

Hopkins and Smith 2015, *PNAS*

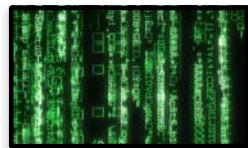
Wright 2017, *Sci. Reports*

# Two routes to a phylomorphospace

## Post-ordination ASE

Hopkins and Smith 2015, *PNAS*

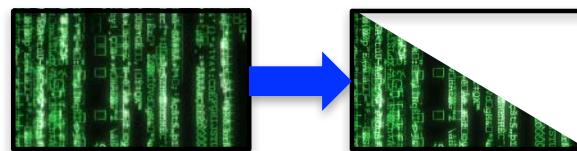
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# Two routes to a phylomorphospace

## Post-ordination ASE

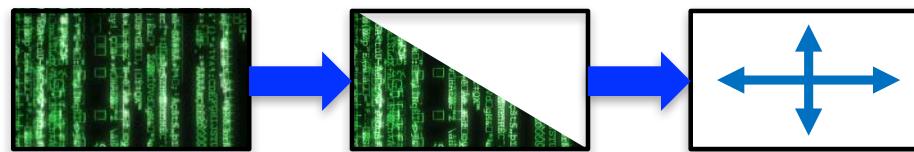
Hopkins and Smith 2015, *PNAS*  
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# Two routes to a phylomorphospace

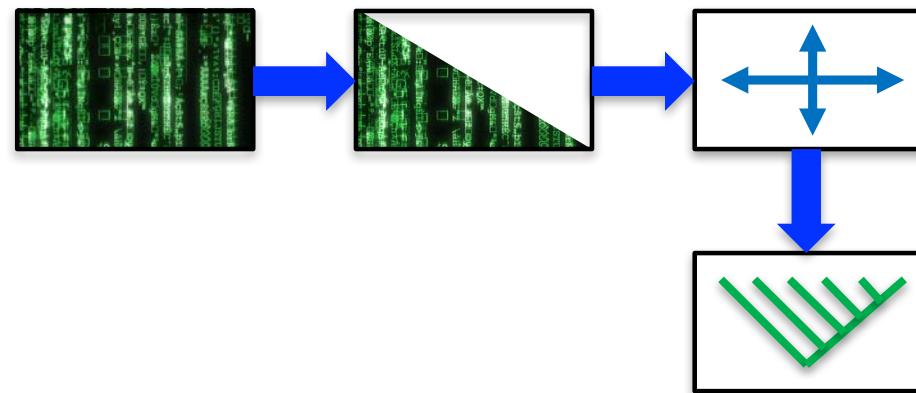
## Post-ordination ASE

Hopkins and Smith 2015, *PNAS*  
Wright 2017, *Sci. Reports*



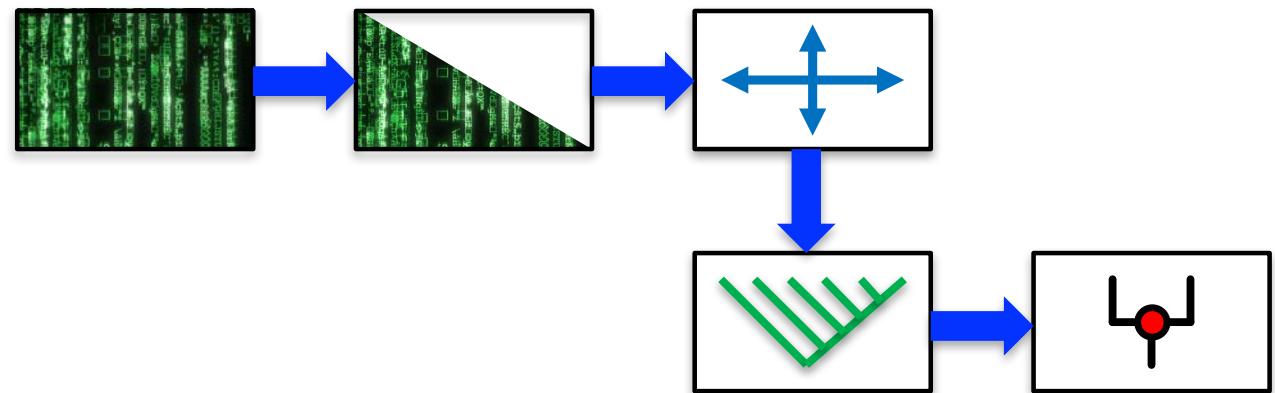
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Wright 2017, *Sci. Reports*



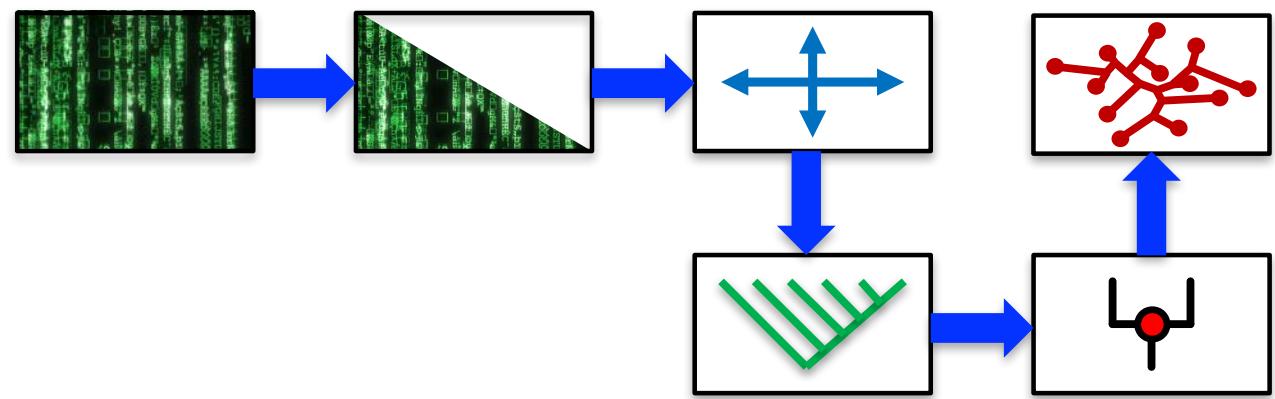
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Wright 2017, *Sci. Reports*



# Two routes to a phylomorphospace

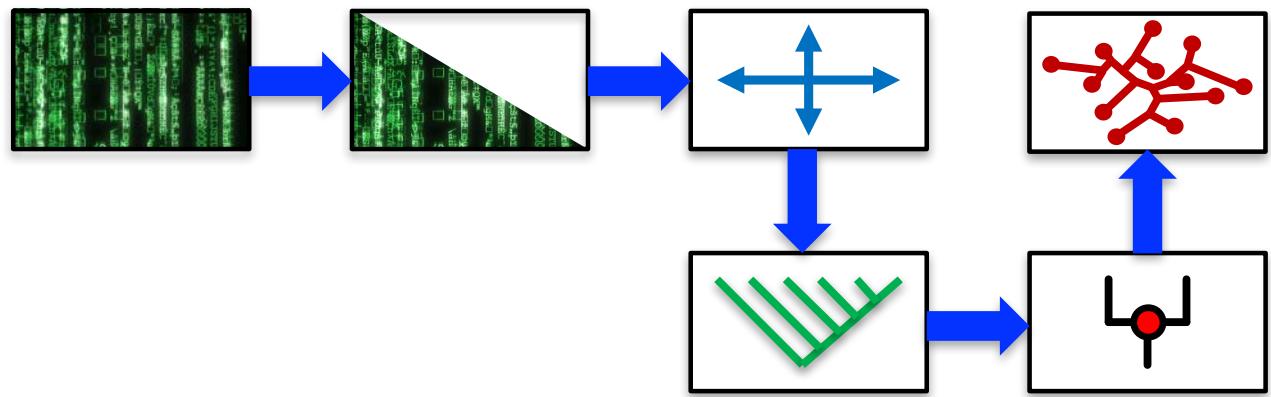
**Post-ordination ASE**  
Hopkins and Smith 2015, *PNAS*  
Wright 2017, *Sci. Reports*



# Two routes to a phylomorphospace

## Post-ordination ASE

Hopkins and Smith 2015, *PNAS*  
Wright 2017, *Sci. Reports*



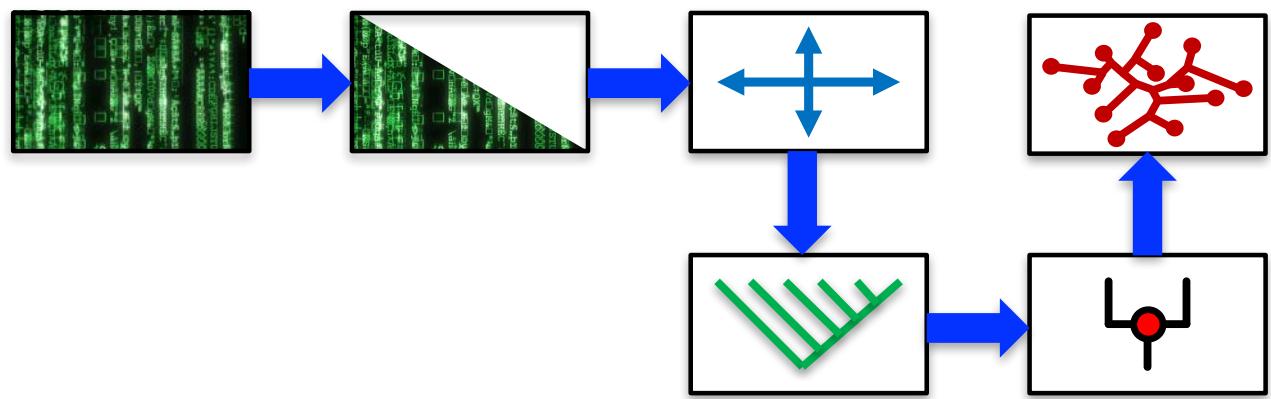
## Pre-ordination ASE

Brusatte et al 2011, *Paleobiology*  
Butler et al 2011, *Evolution*

# Two routes to a phylomorphospace

## Post-ordination ASE

Hopkins and Smith 2015, *PNAS*  
Wright 2017, *Sci. Reports*



## Pre-ordination ASE

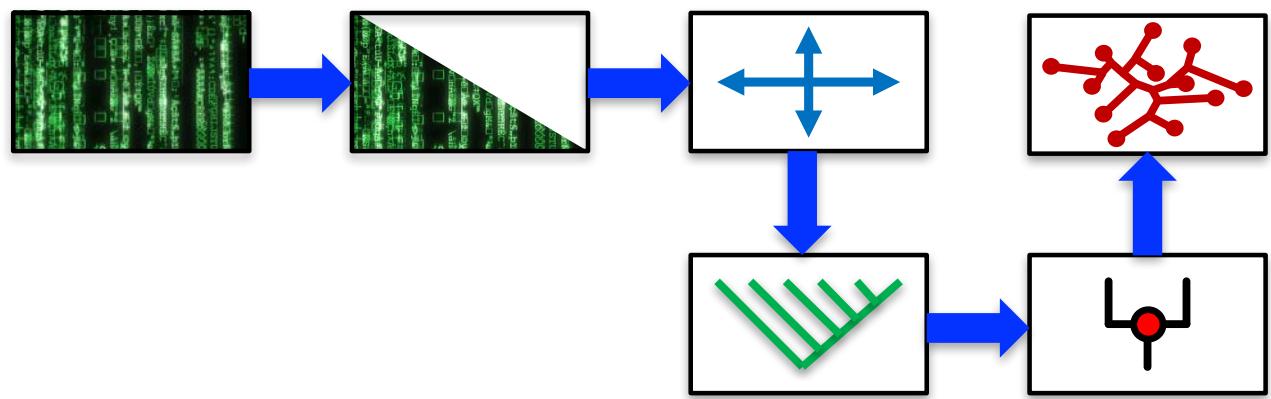
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# Two routes to a phylomorphospace

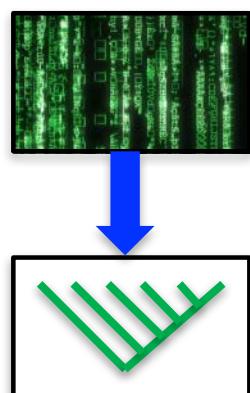
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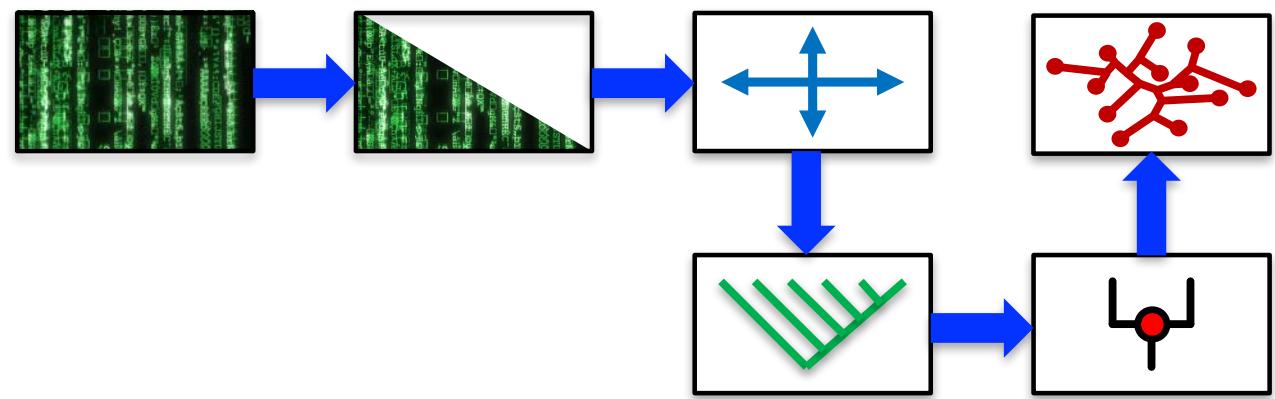
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Butler et al 2011, *Evolution*



# Two routes to a phylomorphospace

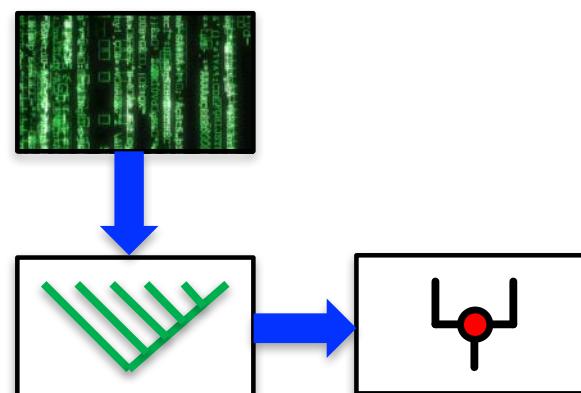
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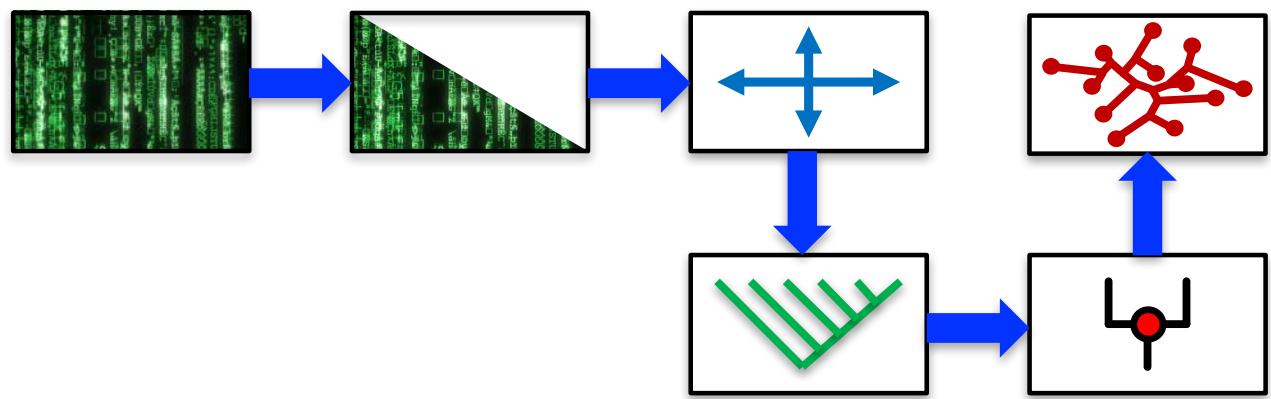
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# Two routes to a phylomorphospace

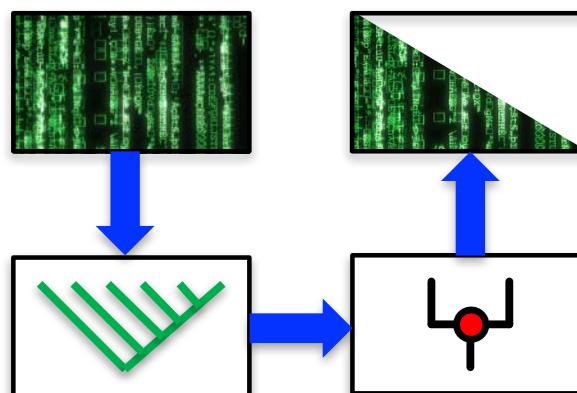
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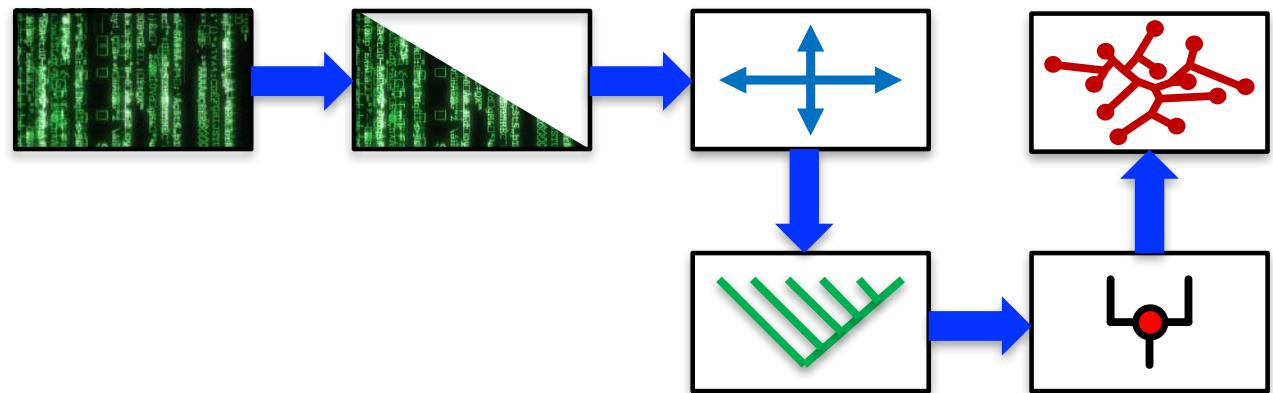
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# Two routes to a phylomorphospace

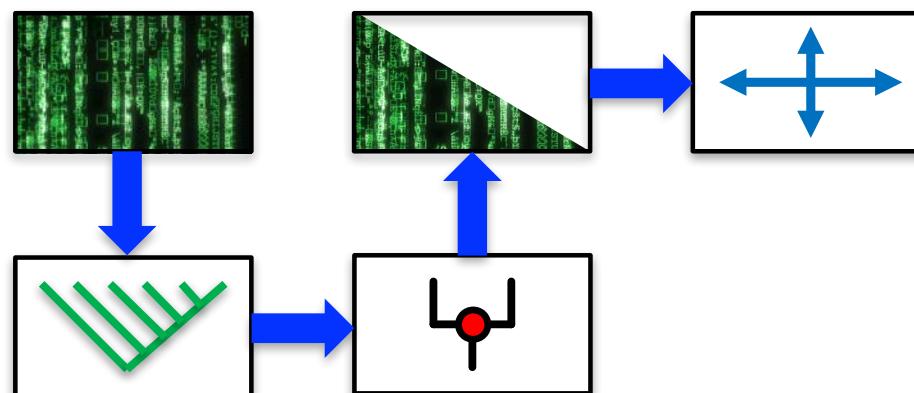
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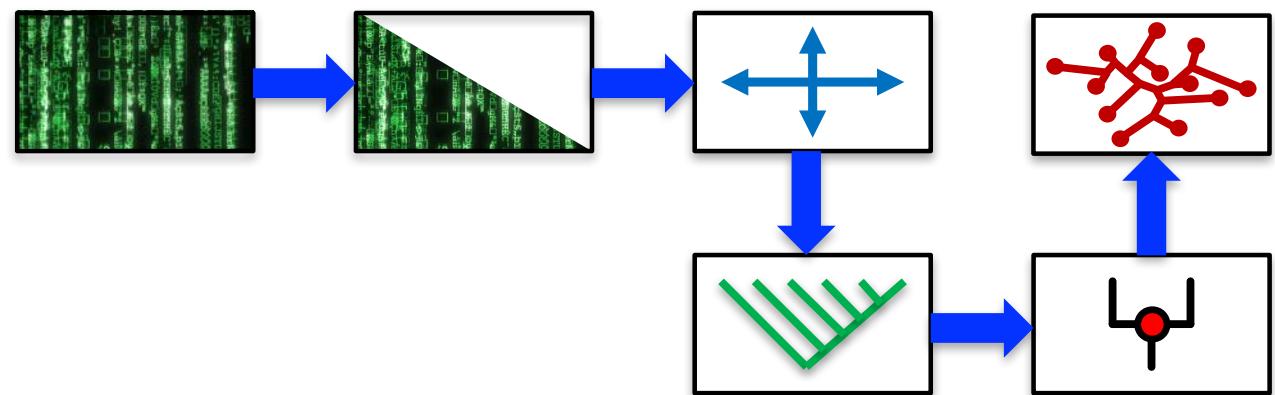
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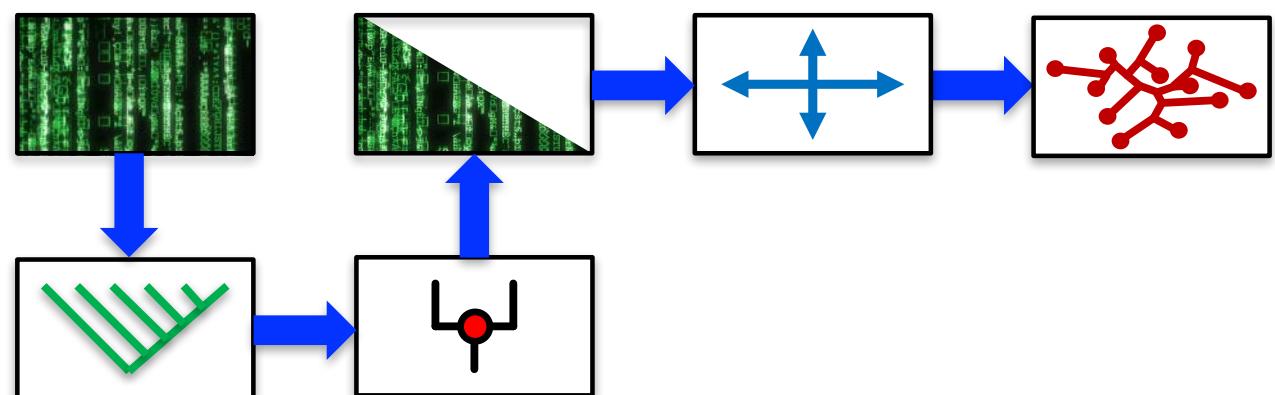
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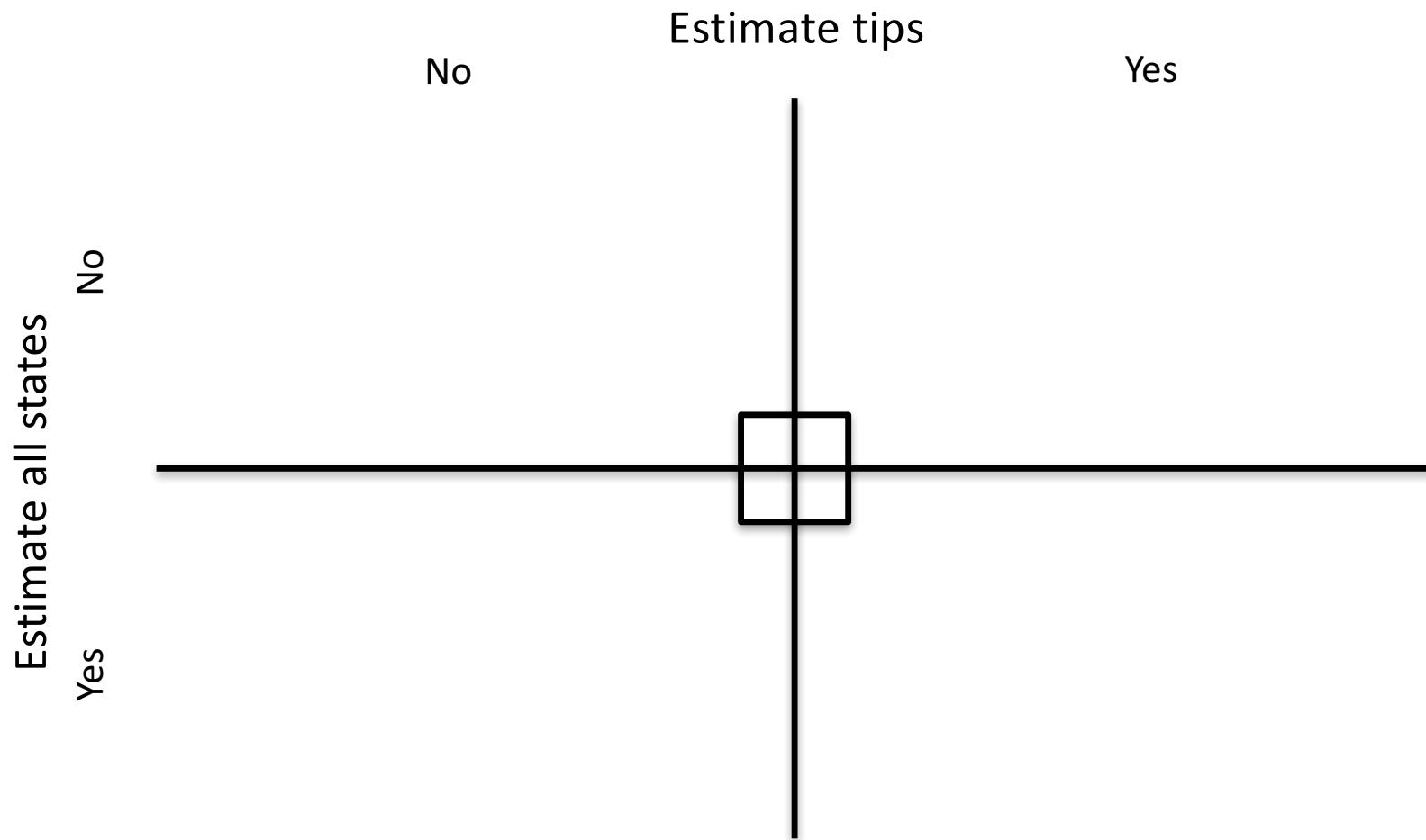
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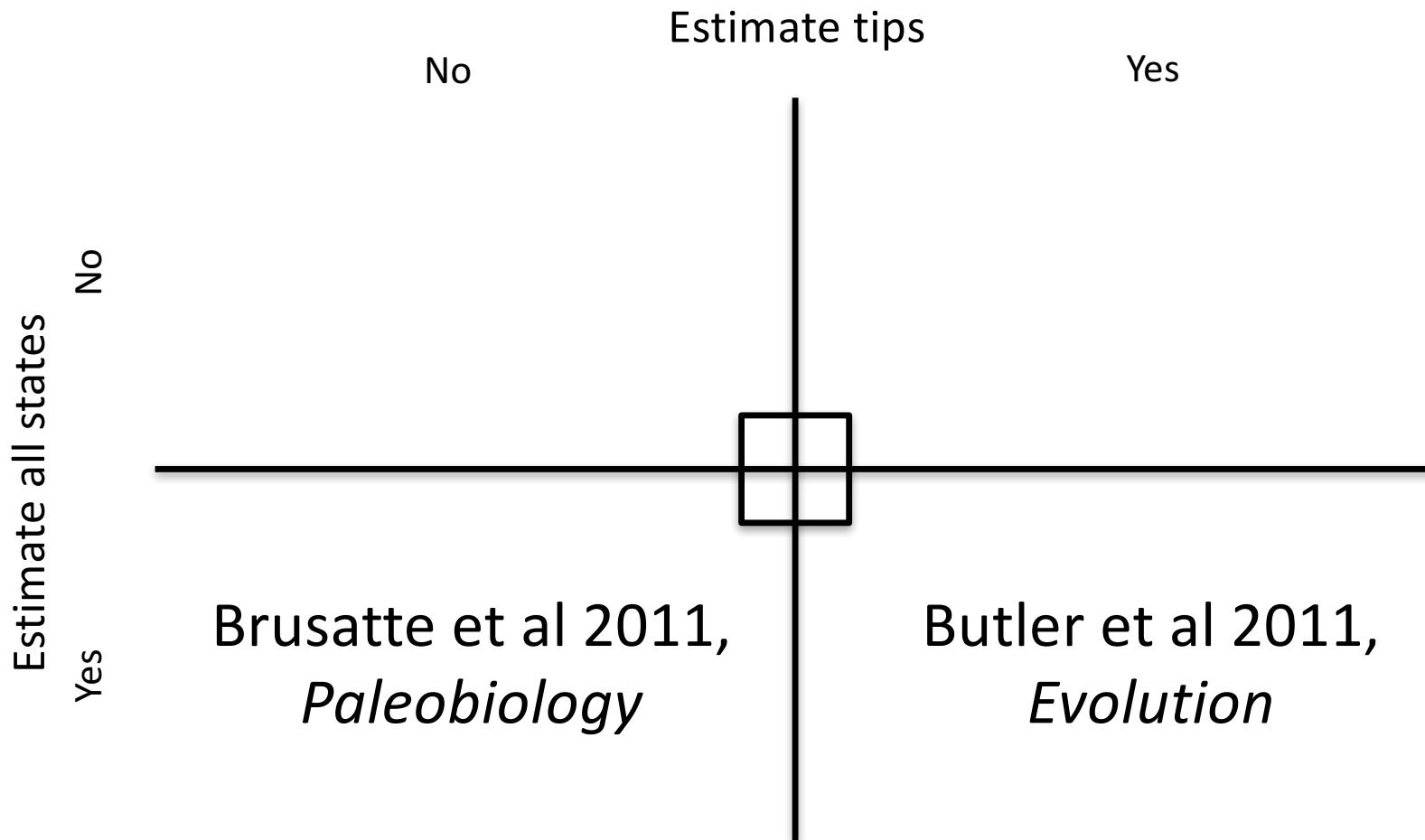


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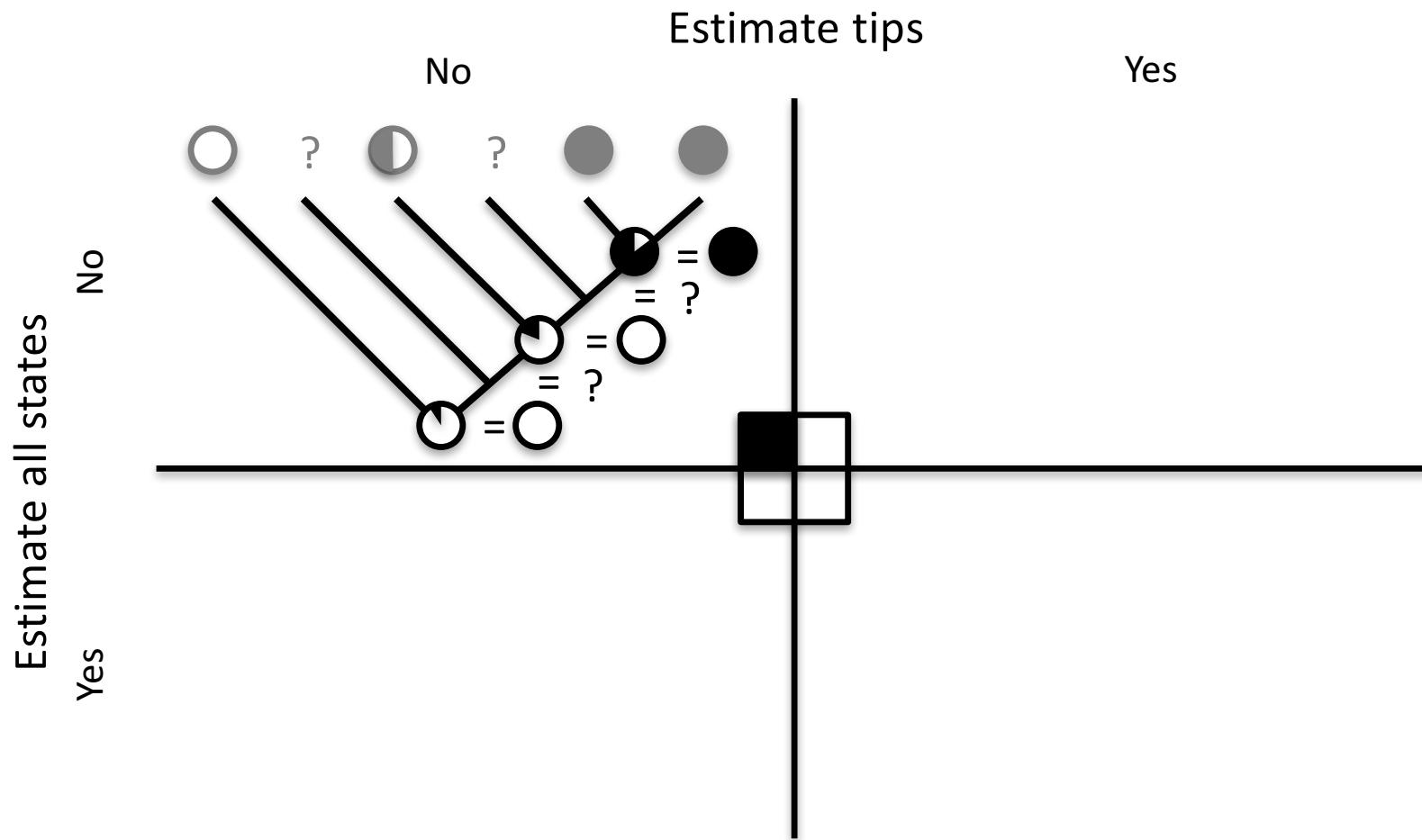
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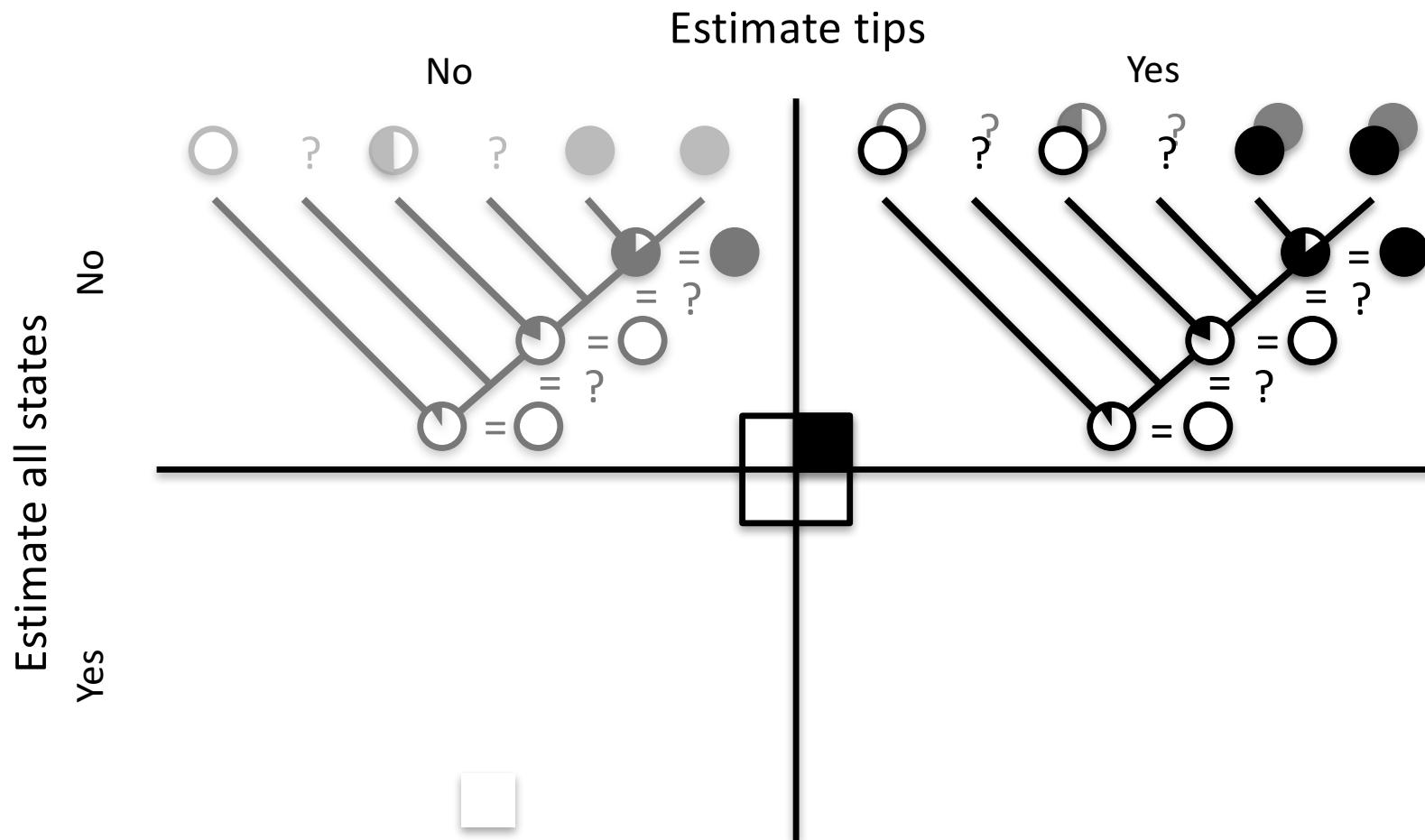
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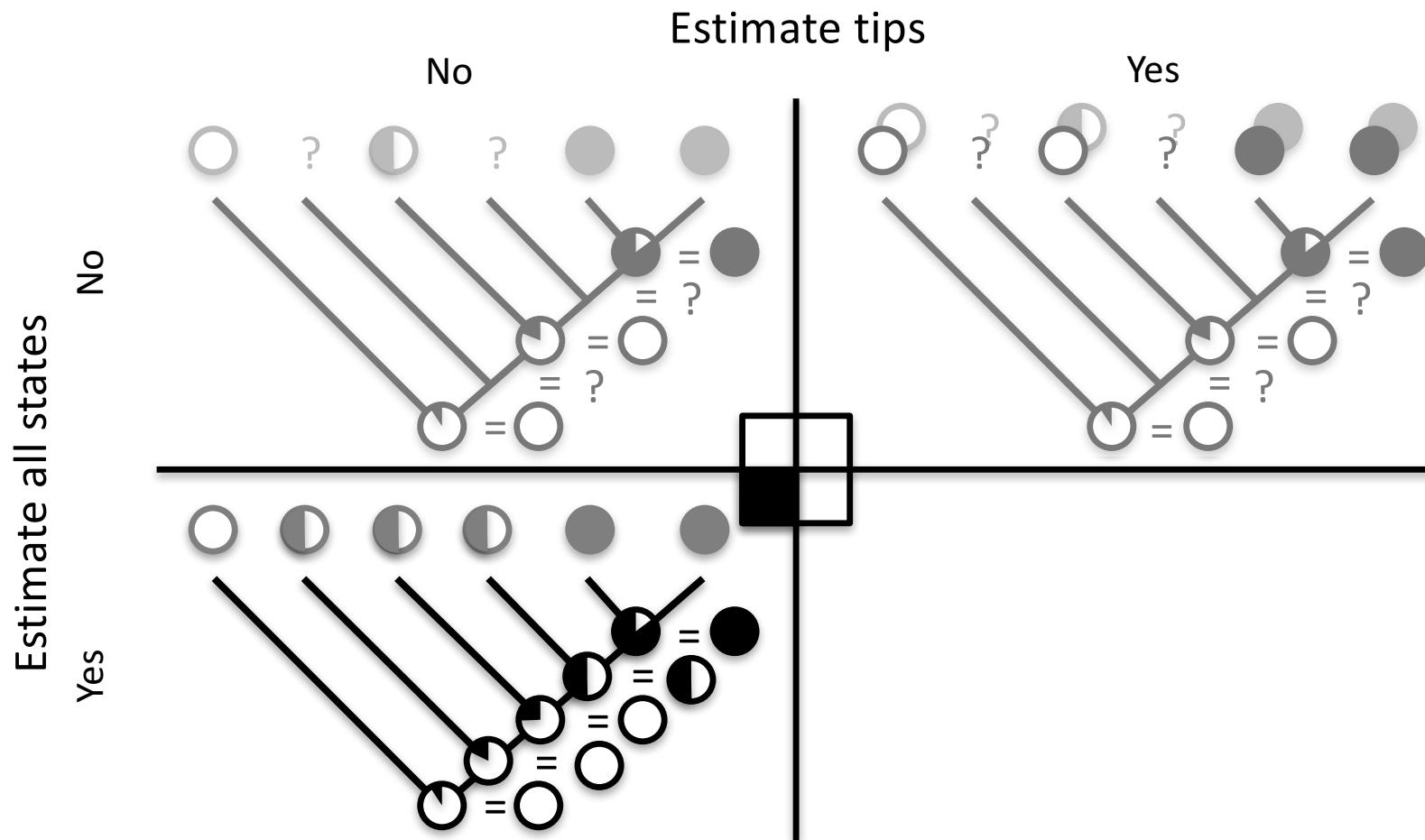
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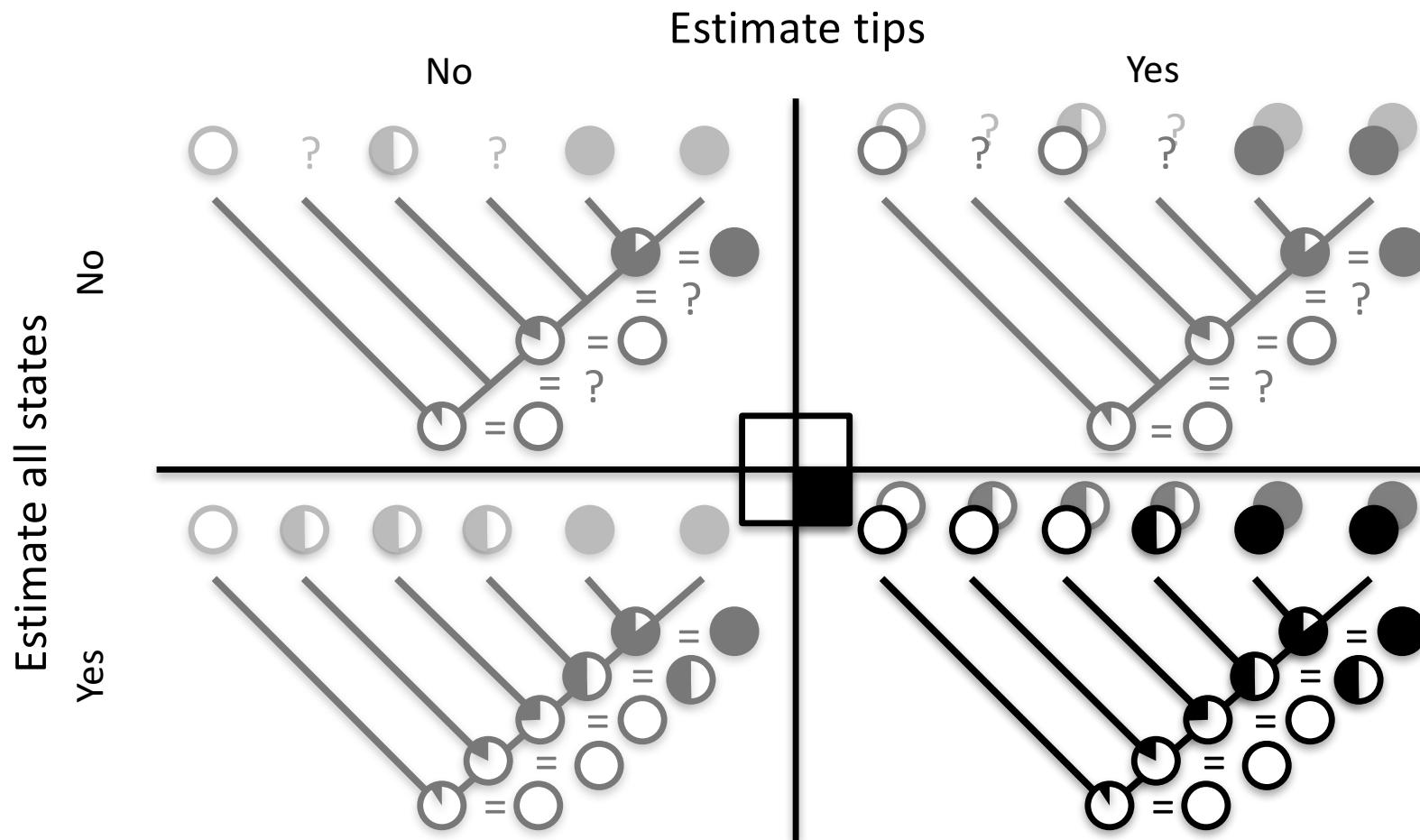
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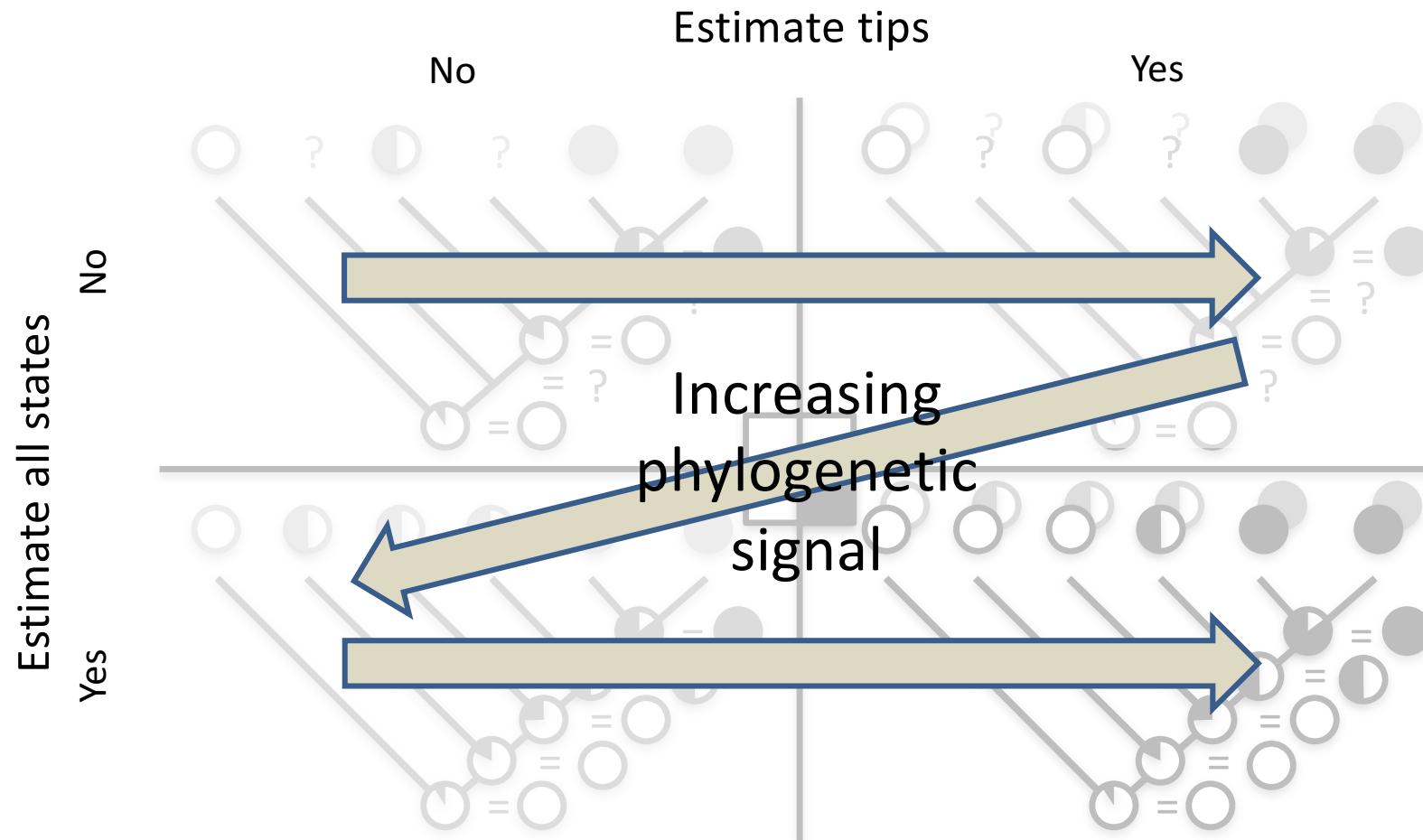
# Four pre-ordination flavours



# Four pre-ordination flavours



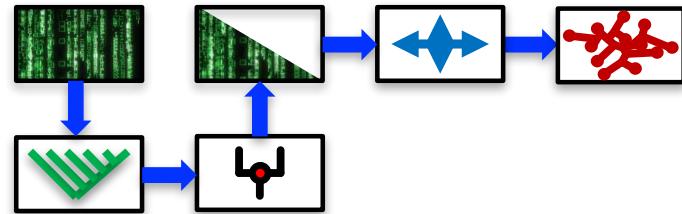
# Four pre-ordination flavours



# Phylomorphospace comparison

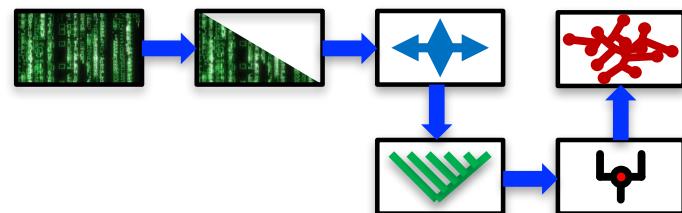
# Phylomorphospace comparison

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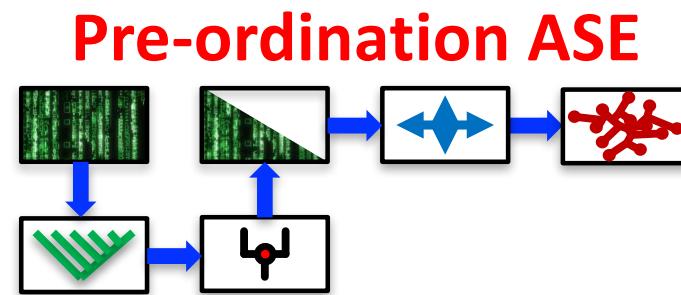


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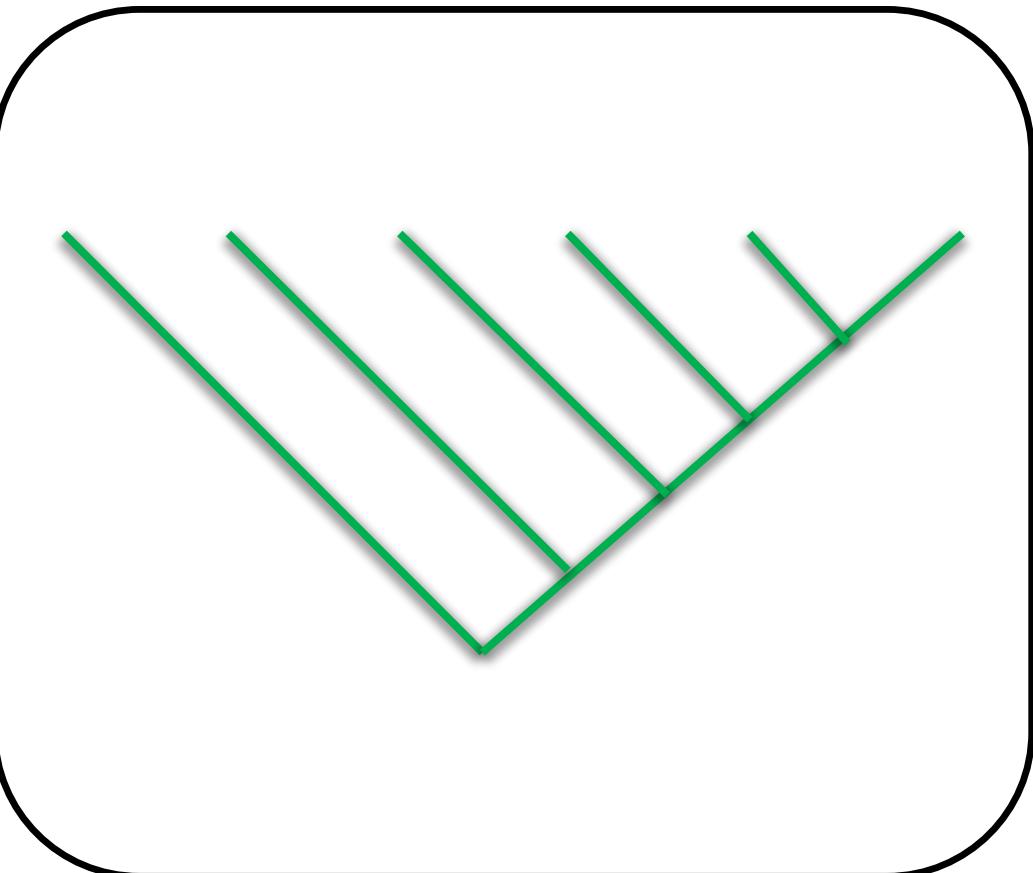
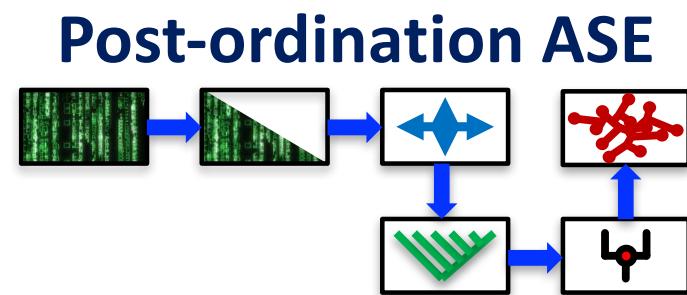
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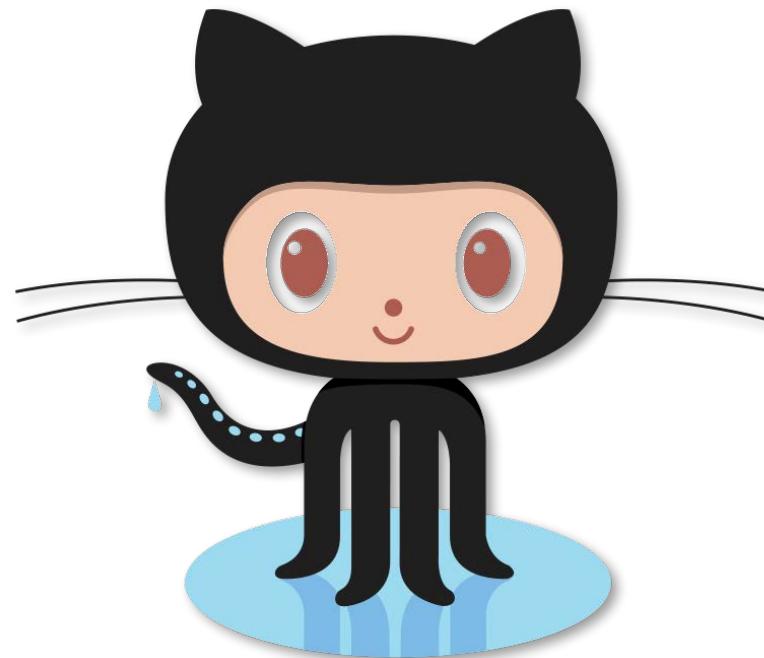
# Phylomorphospace comparison



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# Phylomorphospace comparison



[github.com/graemetlloyd/Claddis](https://github.com/graemetlloyd/Claddis)

Lloyd 2016; *Biological Journal of the Linnean Society*, **118**, 131-151

# Phylomorphospace comparison

# Phylomorphospace comparison

Current Biology 24, 2386–2392, October 20, 2014 ©2014 Elsevier Ltd All rights reserved. <http://dx.doi.org/10.1016/j.cub.2014.08.094>

**Report**

## Gradual Assembly of Avian Body Plan Culminated in Rapid Rates of Evolution across the Dinosaur-Bird Transition

Stephen L. Brusatte,<sup>1,2</sup>\* Graeme T. Lloyd,<sup>2</sup> Steve C. Wang,<sup>3</sup> and Mark A. Norell<sup>4</sup>

<sup>1</sup>School of GeoSciences, University of Edinburgh, Edinburgh EH9 3JW, UK  
<sup>2</sup>Department of Earth Sciences, University of Oxford, Oxford OX1 3AN, UK  
<sup>3</sup>Department of Mathematics and Statistics, Swarthmore College, Swarthmore, PA 19081, USA  
<sup>4</sup>Division of Paleontology, American Museum of Natural History, New York, NY 10024, USA

**Summary**

The evolution of birds from theropod dinosaurs was one of the great evolutionary transitions in the history of life [1–22]. The macroevolutionary tempo and mode of this transition is poorly studied, which is surprising because it may offer key insights into the general principles of evolution, particularly where the origins of evolutionary novelties and new ecological opportunities are associated with unusually elevated “bursts” of evolution [23,24]. We present a comprehensive phylogeny placing birds within the context of theropod evolution and quantify rates of morphological evolution across the avian-bird transition. Our results show that the assembly of the avian body plan was gradually assembled, birds experienced an early burst of rapid anatomical evolution, and then the assembly continued at a relatively constant rate across the dinosaur-bird transition. Birds are indistinguishable from their closest relatives in morphospace. Our results demonstrate that the origin of birds was a complex process; birds are a composite of many clades of theropods that evolved, and there was no great jump between nonbirds and birds in morphospace, but once the avian body plan was gradually assembled, birds experienced an early burst of rapid anatomical evolution. This suggests that high rates of morphological evolution were associated with the assembly of a common feature of macroevolution, as first hypothesized by G.G. Simpson more than 60 years ago [25].

**Results**

The fossil record provides unique insight into major evolutionary transitions: the origins of entirely new body plans and behaviors. In one of the greatest transitions in the history of life, bipedal carnivorous theropod dinosaurs evolved feathers and wings, became the most successful body plan on Earth, and gave rise to birds. The dinosaur-bird transition is captured by a rich fossil record that has expanded tremendously in recent years—including thousands of feathered dinosaur specimens from northern China. Over the past two decades it has provided an unparalleled opportunity to study a major morphological, behavioral, and paleobiological transformation in deep time. In particular, the dinosaur-bird transition can provide key insight into major questions in contemporary evolutionary biology, particularly whether the origins of evolutionary novelties or new ecological opportunities are

associated with unusually elevated “bursts” of evolution [23,24]. This hypothesis was first articulated by George Gaylord Simpson in the 1940s [25] and has been the subject of intense debate ever since.

**Phylogenetic Analysis**

Birds are members of the theropod dinosaur subgroup Coelurosauria, a diverse clade that includes tyrannosauroids and dromaeosaurids, among others [7–14]. Our comprehensive, new phylogeny includes a large number of taxa that include nearly all Mesozoic coelurosaurs that are known from well-preserved and diagnostic fossils available for study. It is the latest iteration of the Theropod Working Group (TWIG) project, a 20-year program centered at the American Museum of Natural History. The TWIG phylogeny is the largest phylogeny available, with data sets of comprehensive phylogeny based on personal study of specimens. Previous TWIG analyses have focused extensively on the most derived paravian coelurosaurans (feathered birds as avians) and their very closest relatives, such as dromaeosaurids and troodontids [8,9]. Here, for the first time, we incorporate a broad range of more basal (nonparavian) coelurosaurs into a TWIG analysis. Our data set includes 150 coelurosaurs scored for 863 characters, approximately twice the size of previous TWIG data sets (Table S1). Our phylogenetic analysis places birds within the broader framework of theropod evolution (Figure 1; see also Figures S1 and S2). Tyrannosauroids are the most basal major coelurosaurian clade; therizinosaurids and avialans are sister to all other coelurosaurs, and paravians exclusive of more basal coelurosaurs; therizinosaurid and ornithopodosaurs are not sister taxa and, for the first time, a TWIG analysis recovers a polytomy between avialans, dromaeosaurids, and troodontids, meaning that the immediate relatives of birds cannot be determined with confidence. The clade containing troodontids and Anchisaurus comprises a clade of basal troodontids, not avians, as recently proposed [14]. The iconic *Archaeopteryx* is positioned as the basal-most avian taxon, a “traditional” placement that is in agreement with most previous studies [8–10], not as a closer relative of ornithopodosaurs, as was found in a recent series of analyses [11,12].

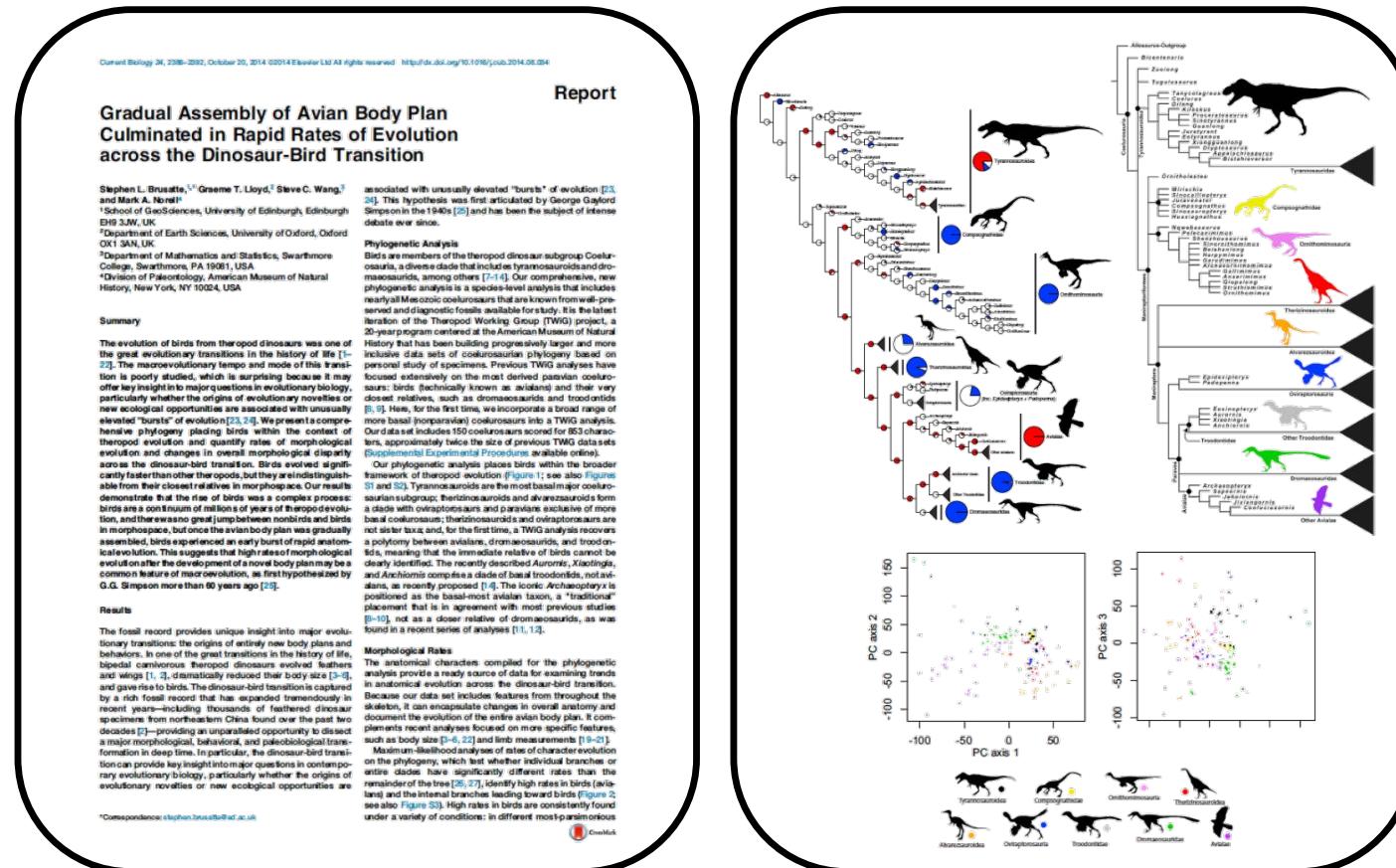
**Morphological Rates**

The avian characters compiled for the phylogenetic analysis provide a ready source of data for examining trends in anatomical evolution across the dinosaur-bird transition. Because our data set includes features from throughout the skeleton, it can encapsulate changes in overall anatomy and specific traits. To examine trends in the entire data set, it complements recent analyses focused on more specific features, such as body size [16–22] and limb measurements [19–21]. Maximum likelihood analyses of rates of character evolution on the phylogeny, which test whether individual branches exhibit distinct patterns of differentiation from the rest of the tree [26,27], identify high rates in birds (avians) and the internal branches leading toward birds (Figure 2; see also Figure S3). High rates in birds are consistently found under a variety of conditions: in different most-parsimonious

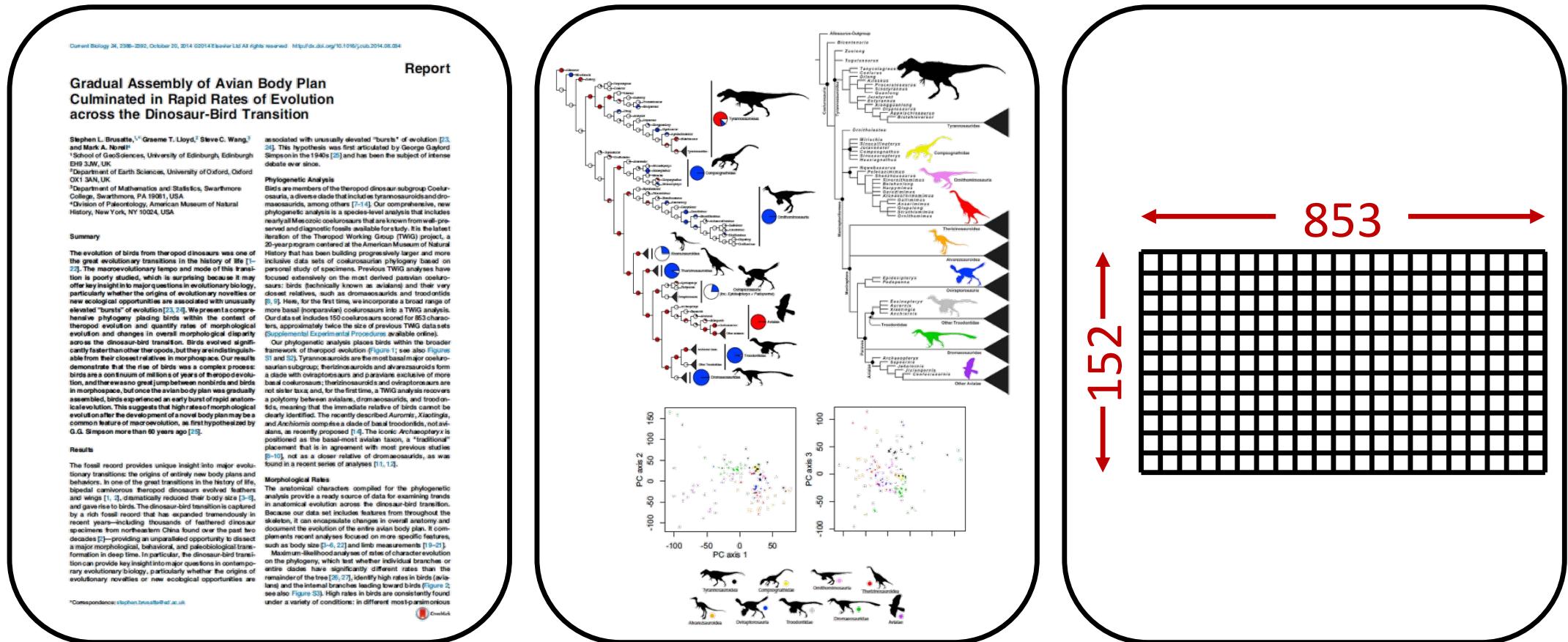
\*Correspondence: [sstephen.brusatte@ed.ac.uk](mailto:sstephen.brusatte@ed.ac.uk)

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http://dx.doi.org/10.1016/j.cub.2014.08.094

# Phylomorphospace comparison



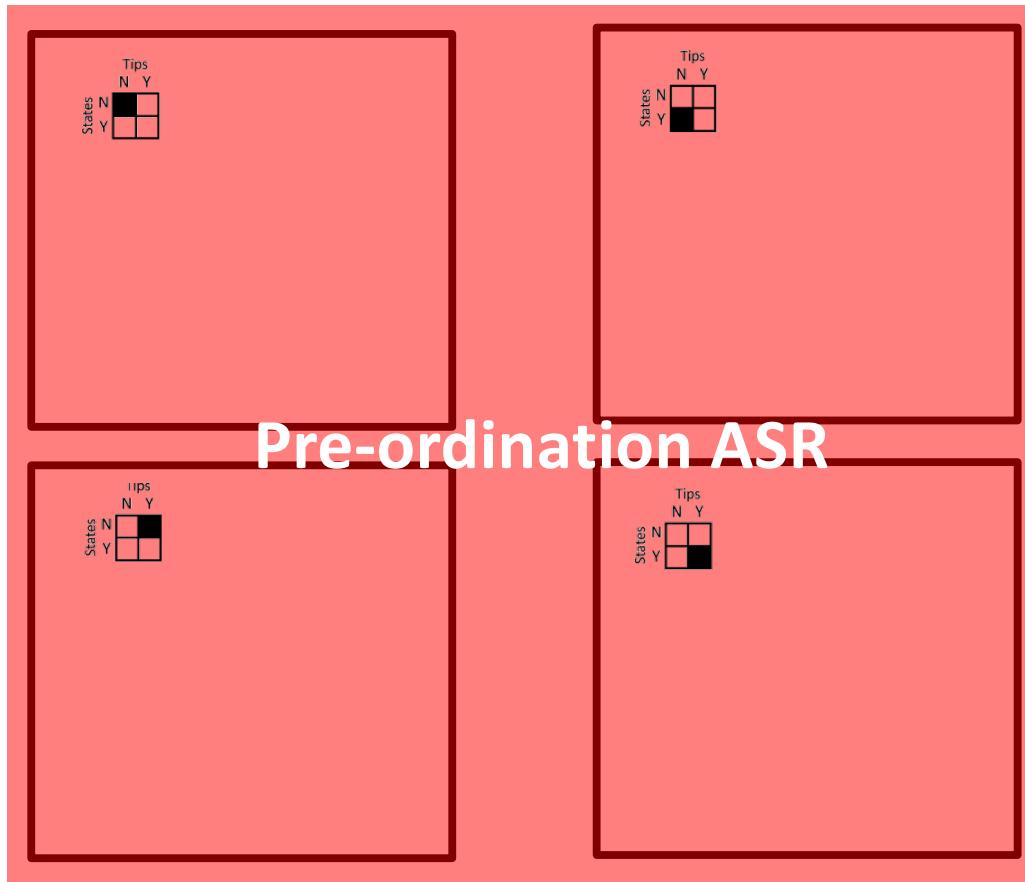
# Phylomorphospace comparison



# Phylomorphospace comparison

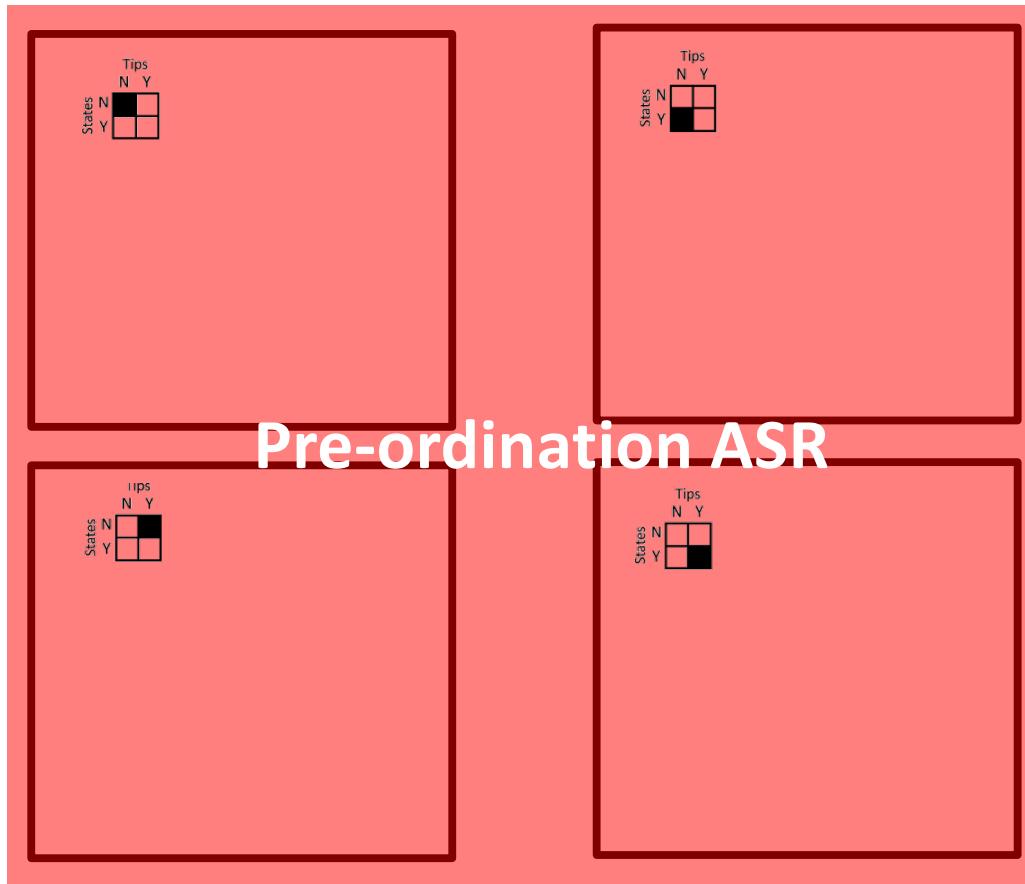
Lloyd 2018; *Palaeontology*, **61**, 637-645

# Phylomorphospace comparison

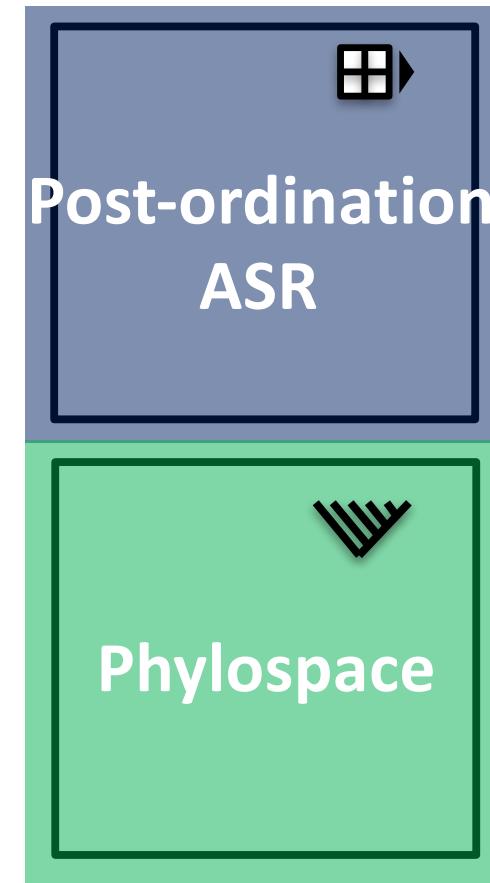
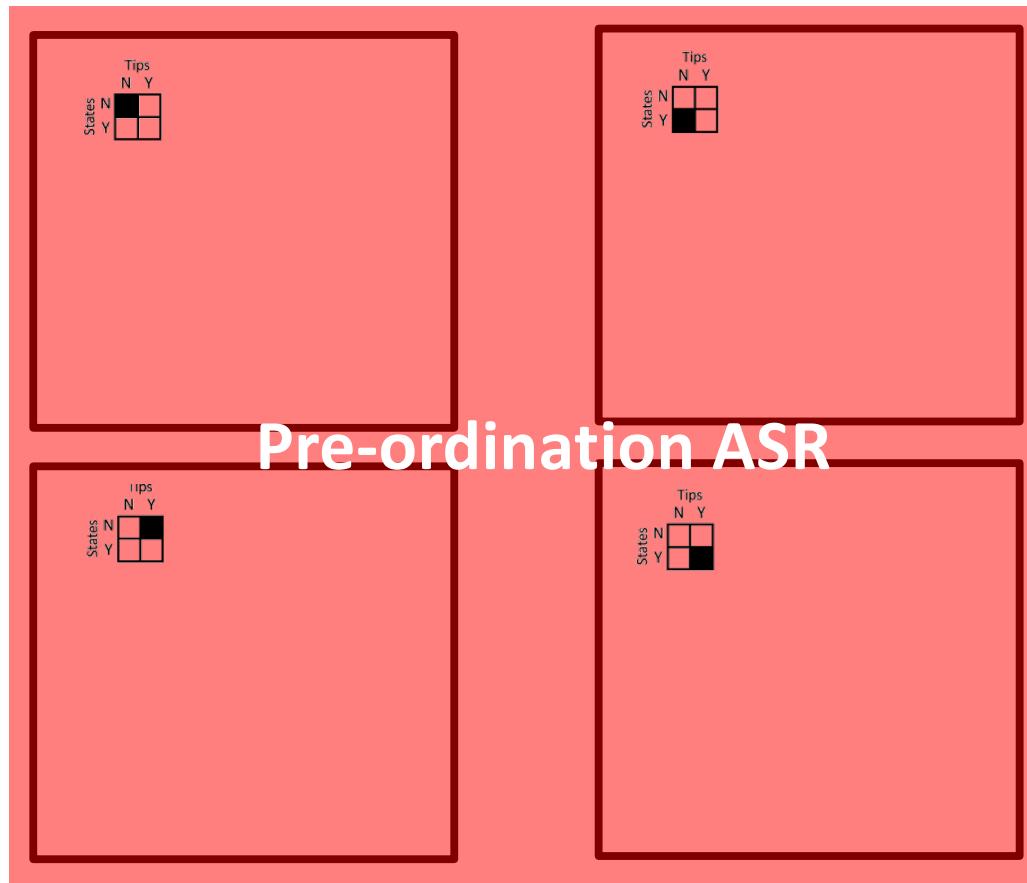


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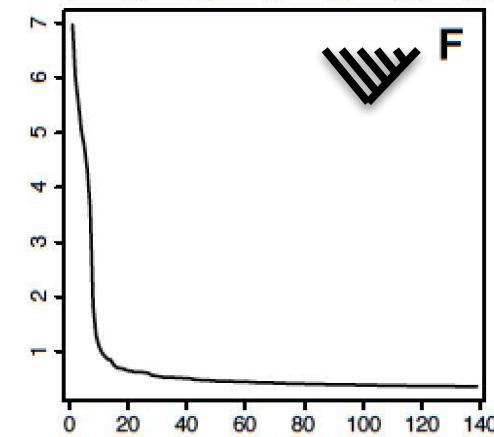
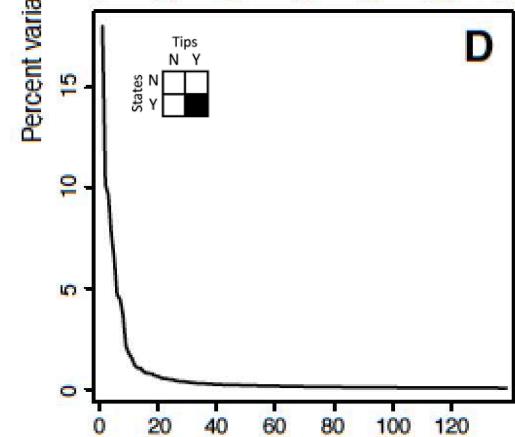
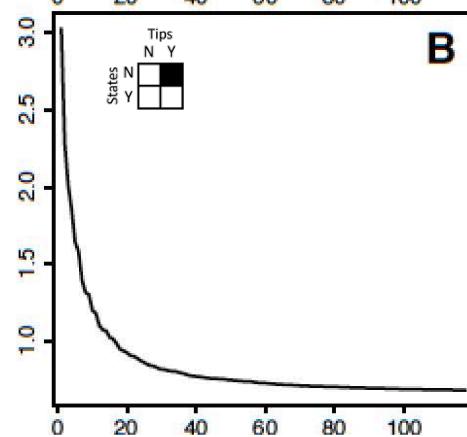
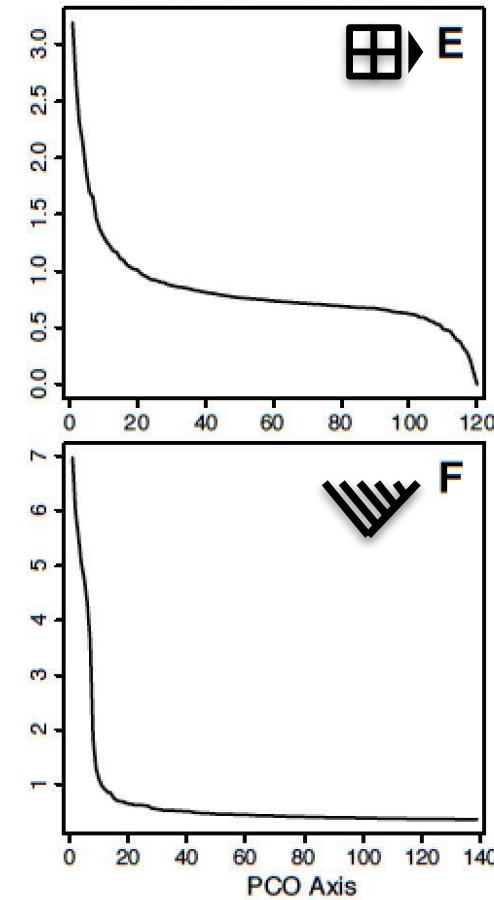
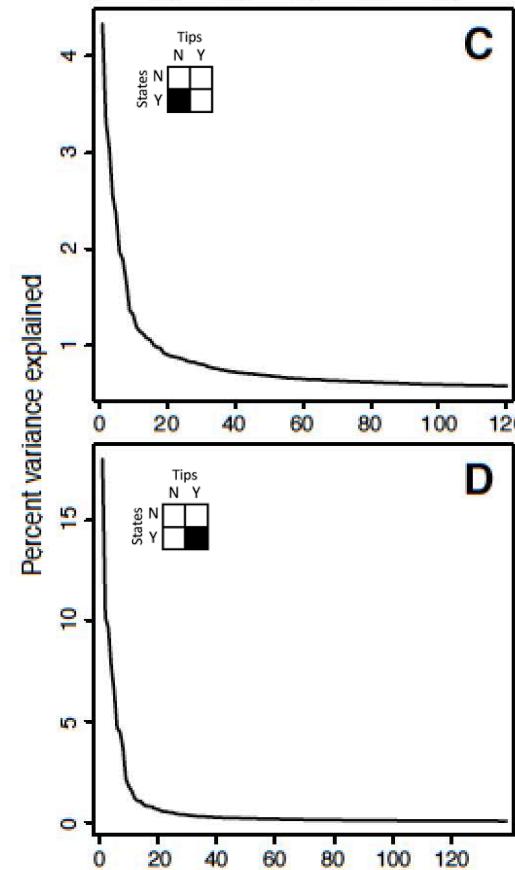
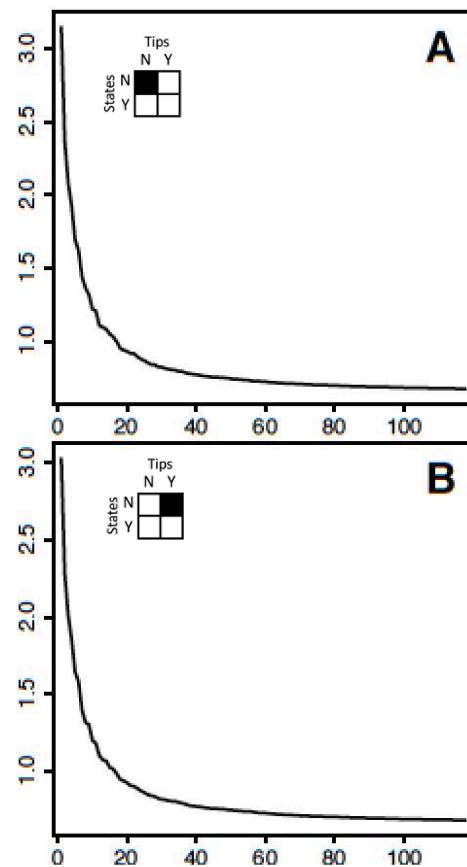
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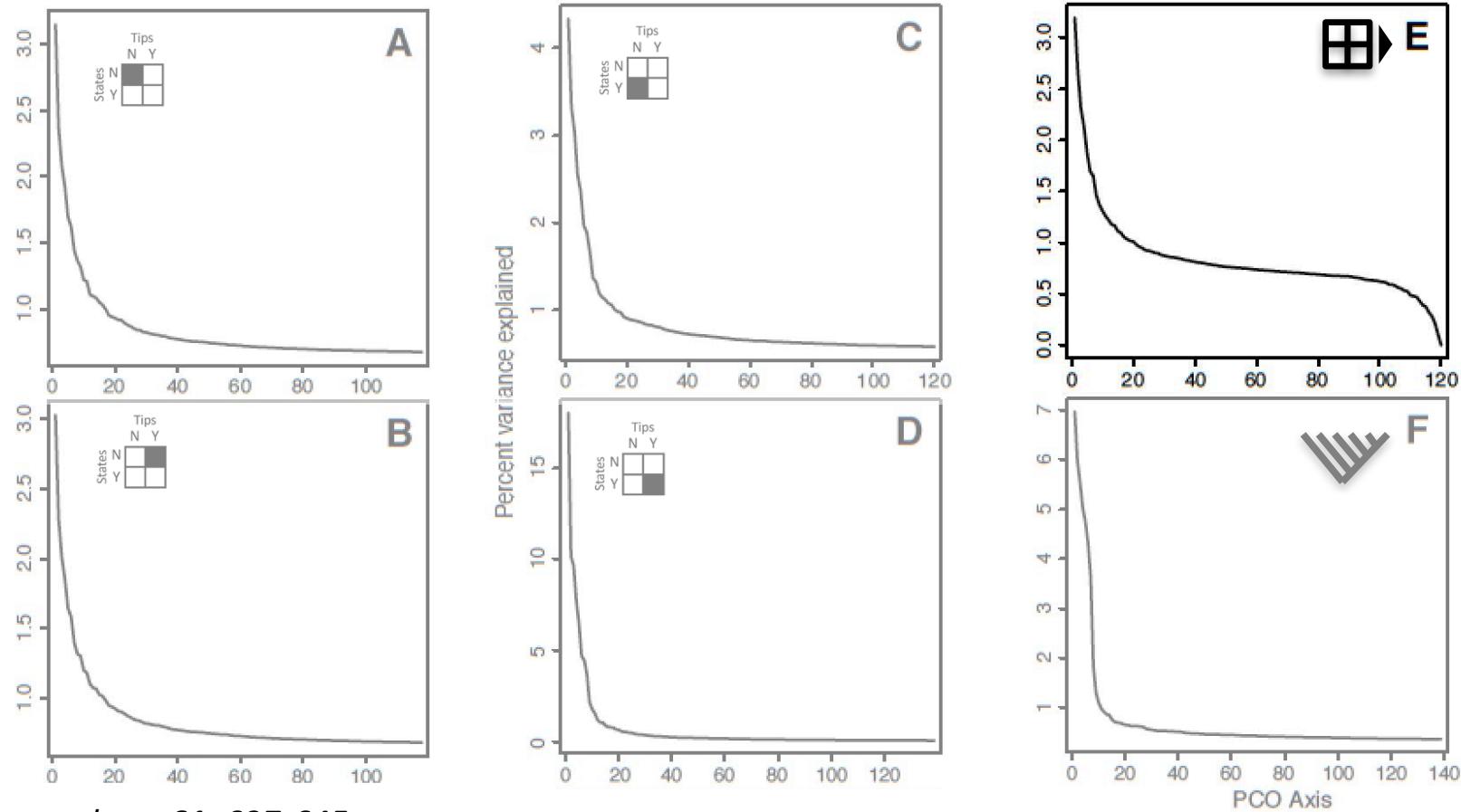
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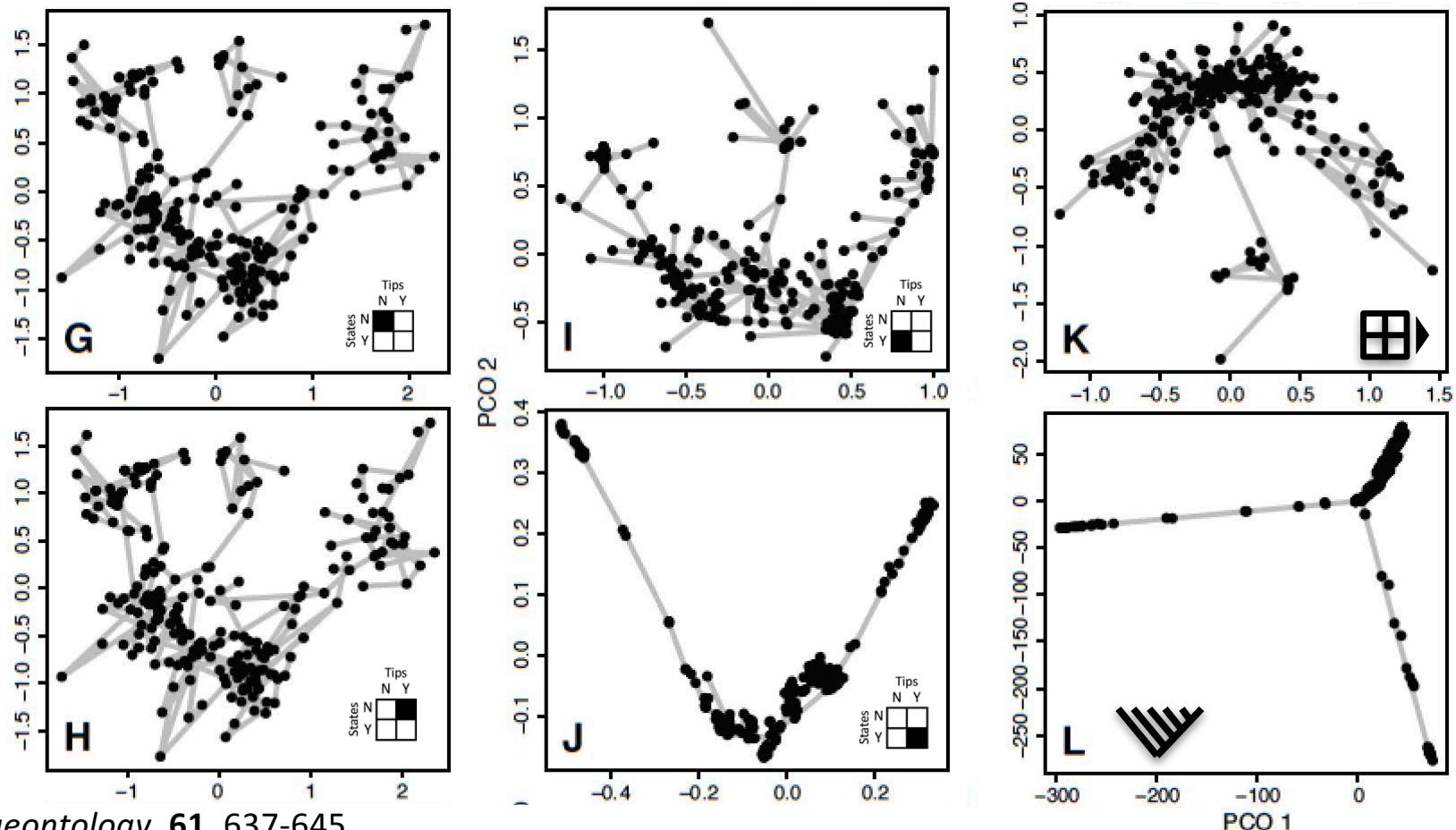
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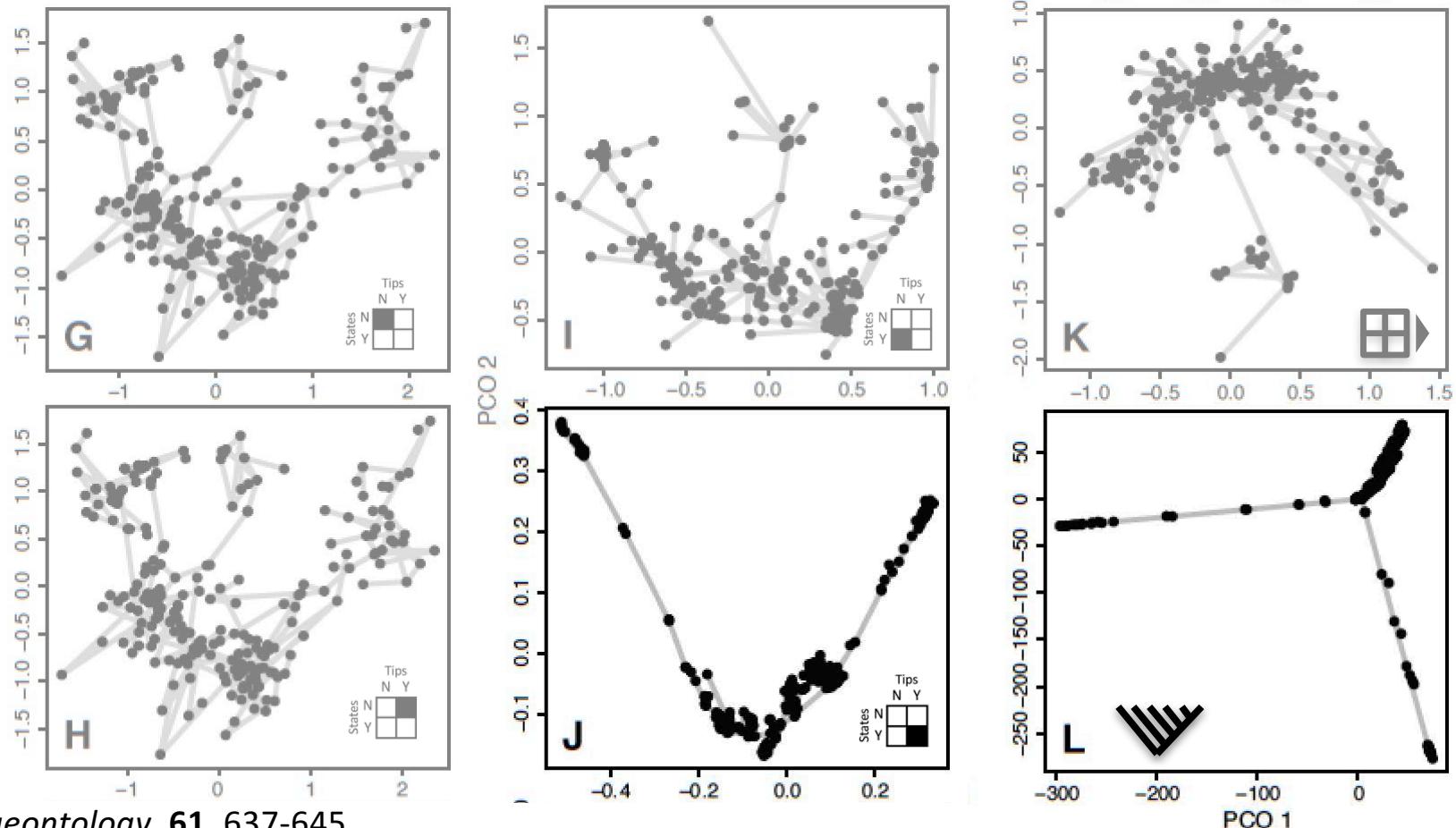
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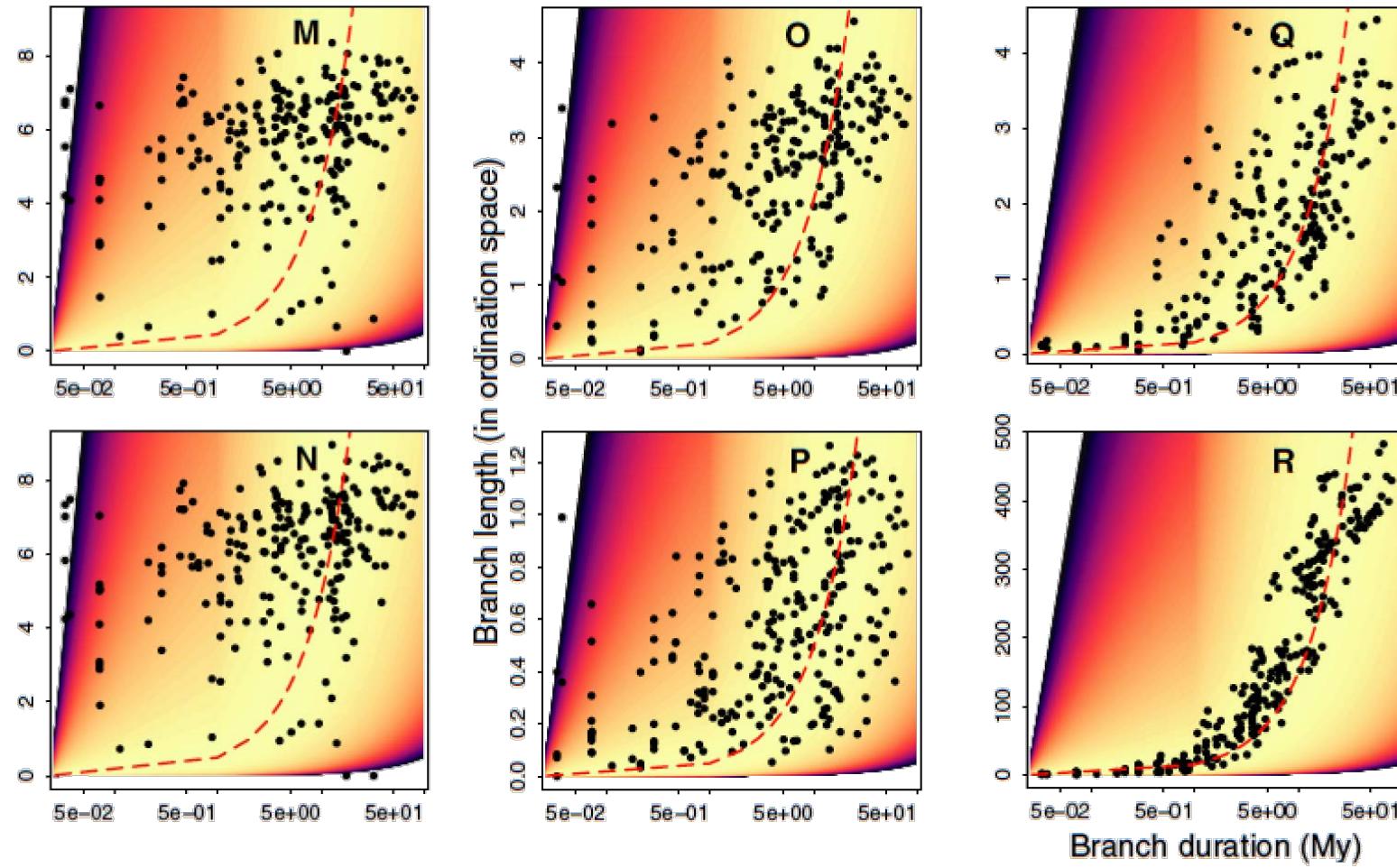
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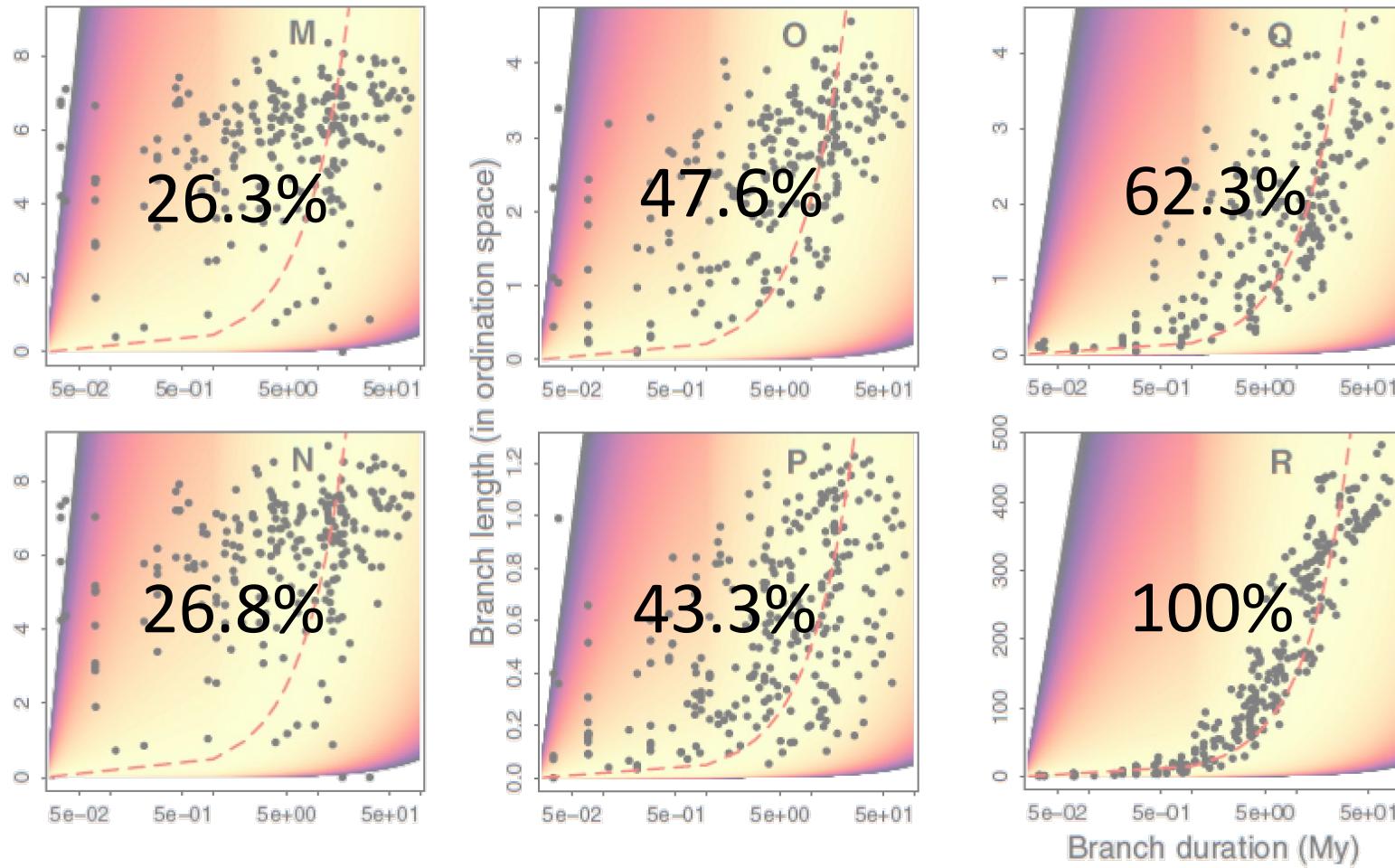
# Phylomorphospaces



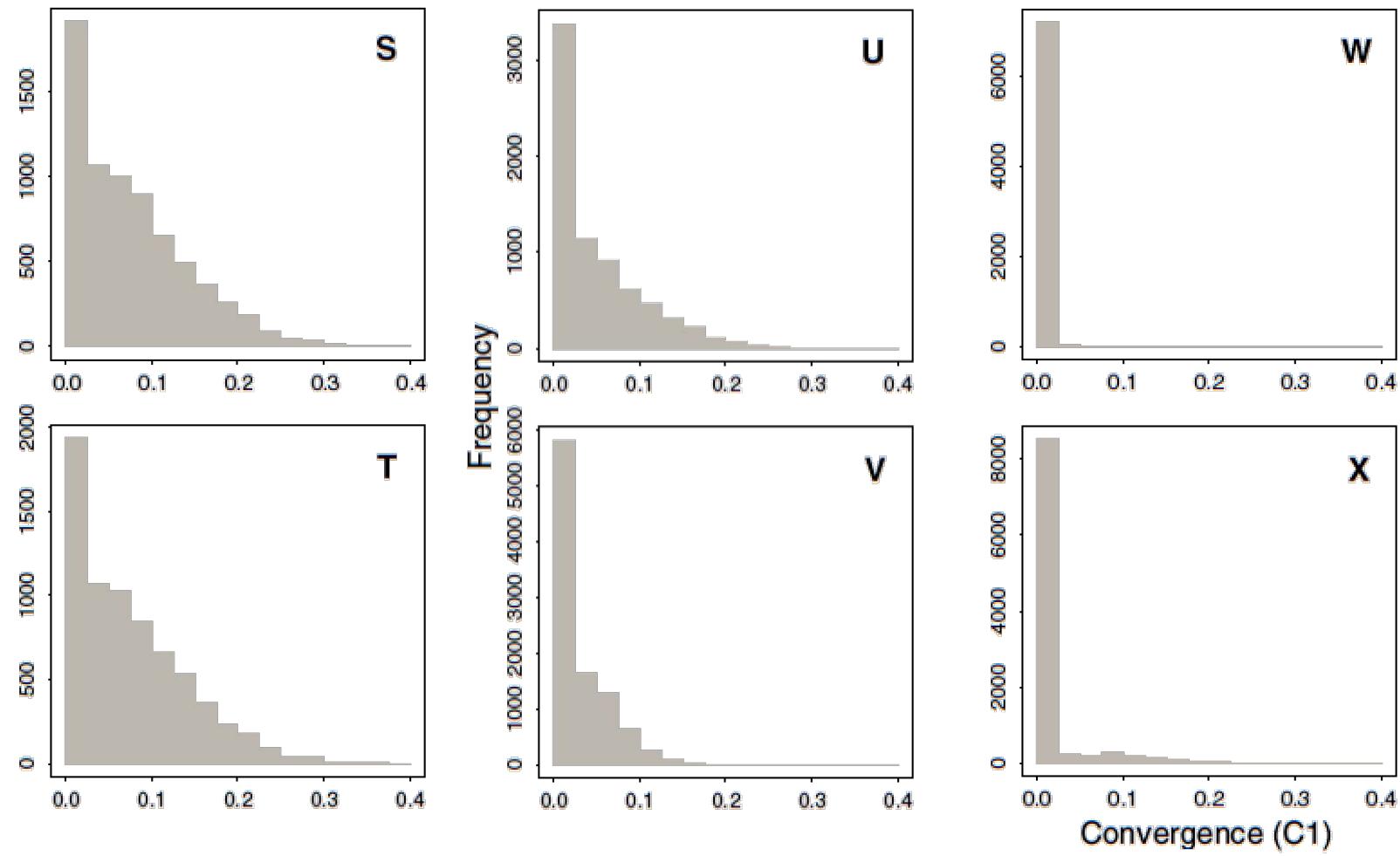
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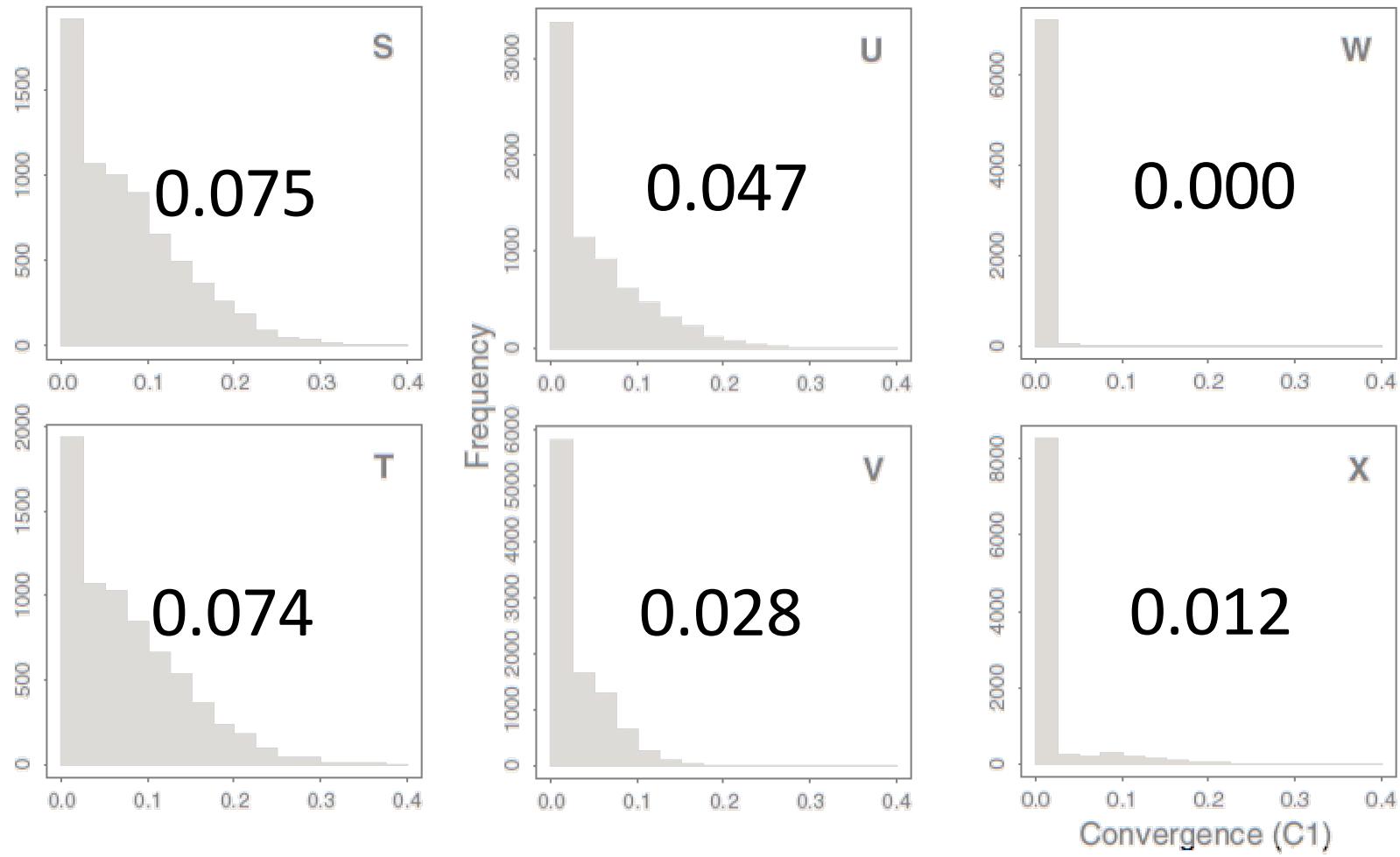
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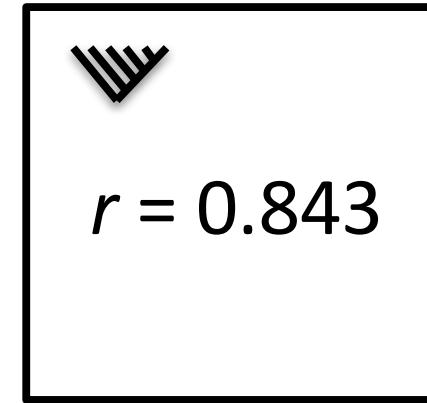
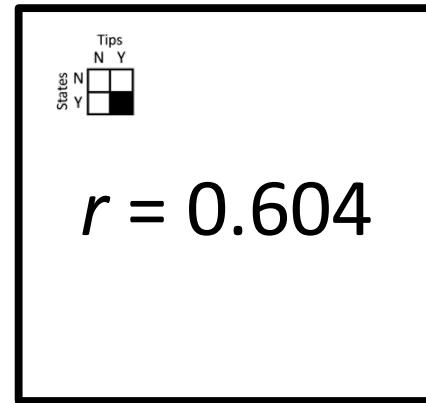
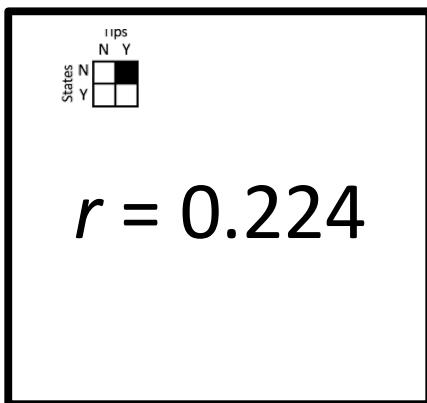
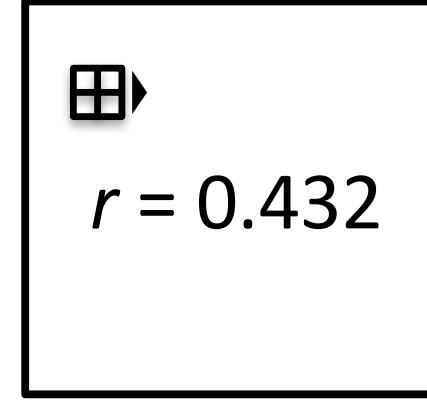
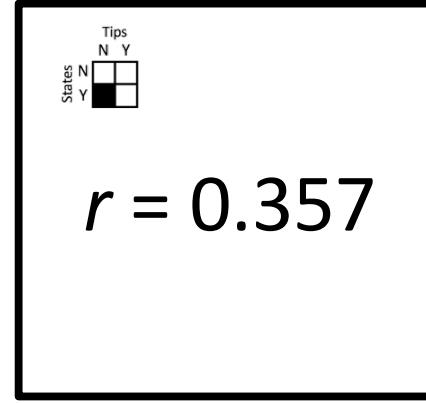
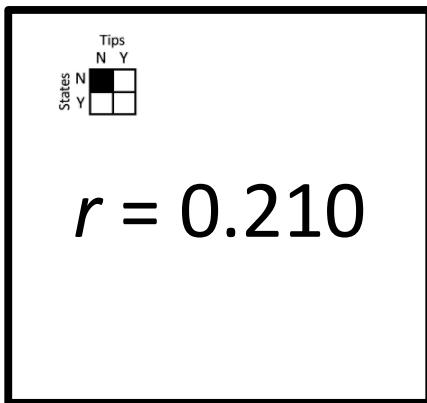
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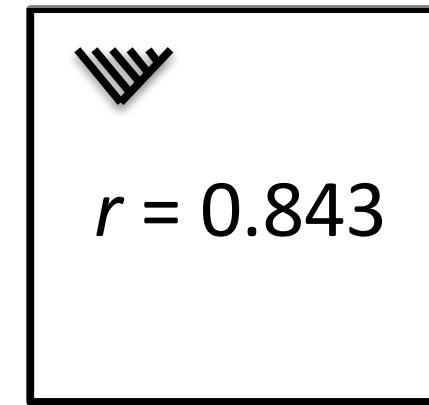
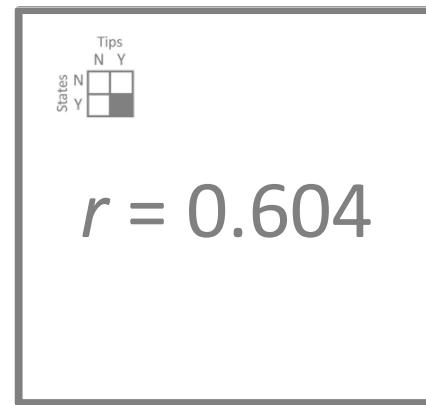
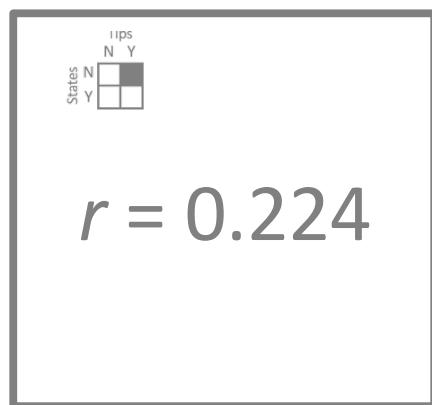
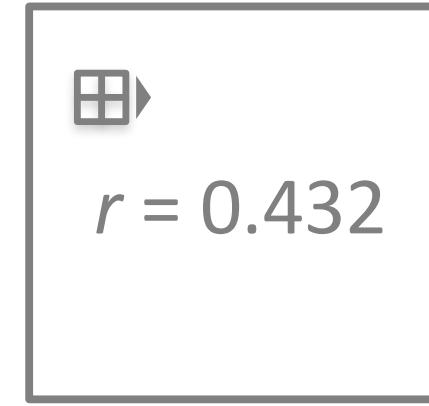
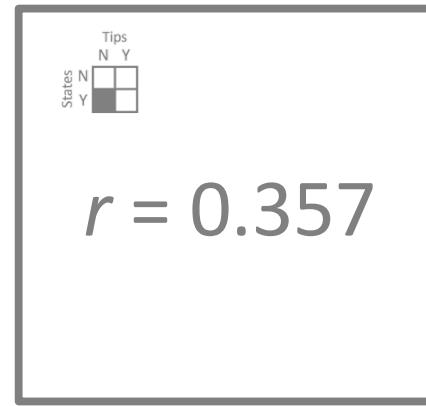
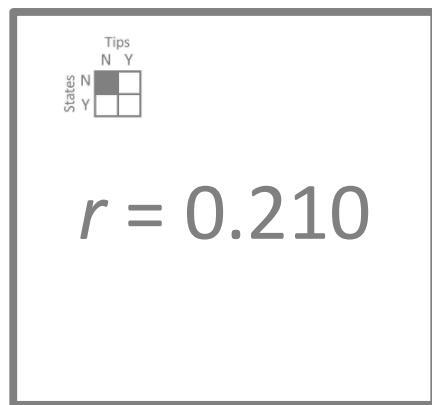
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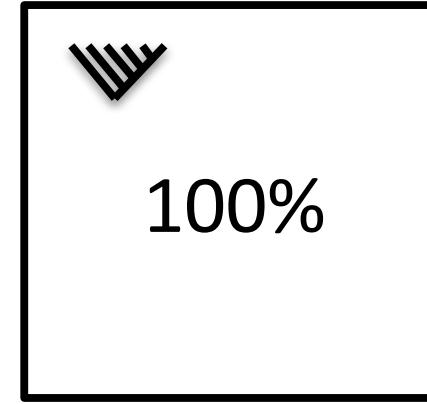
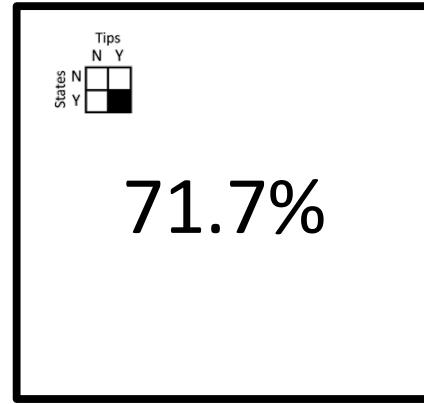
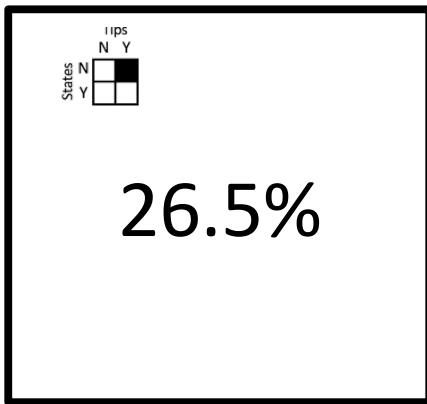
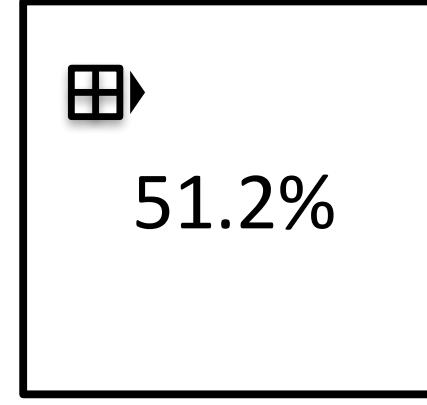
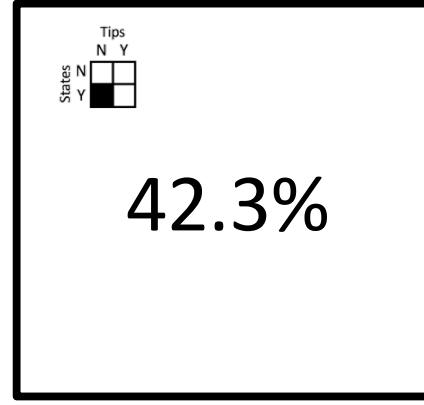
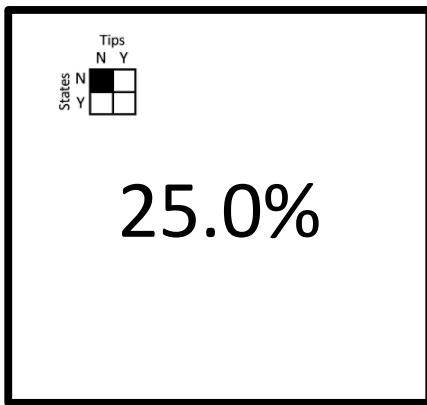
# Correlation with phylogenetic distance



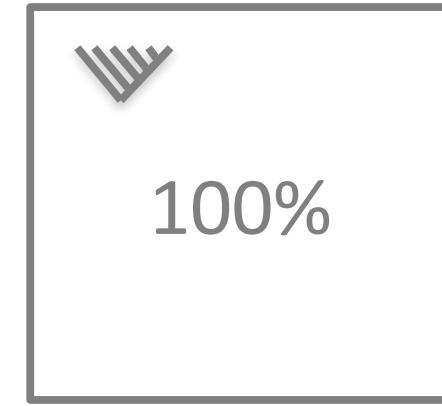
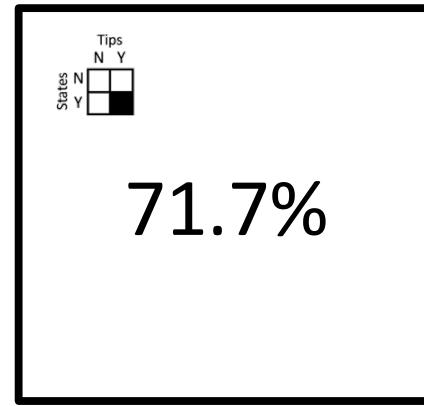
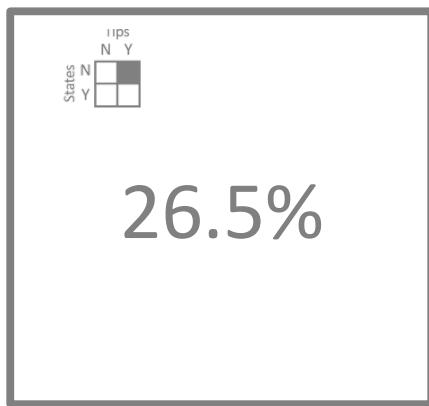
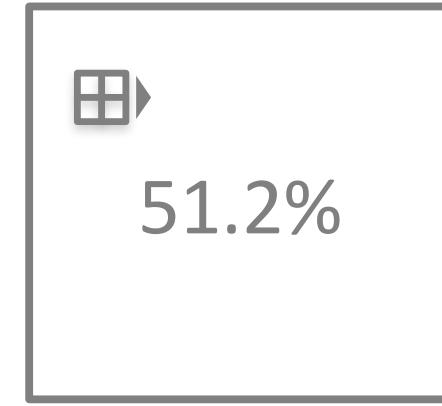
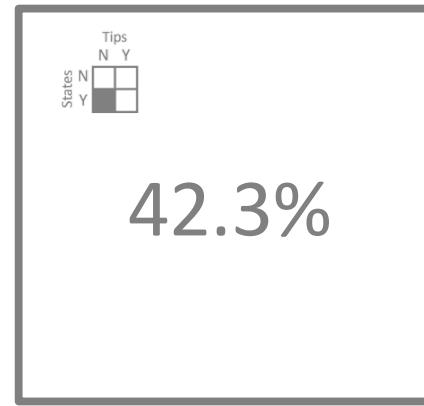
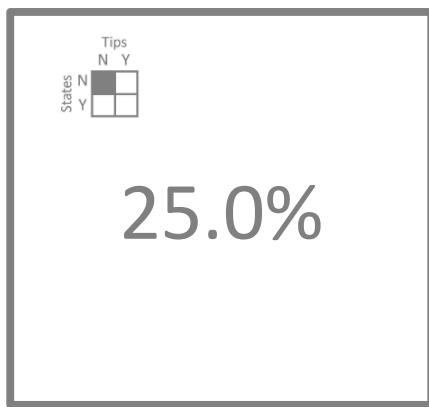
# Correlation with phylogenetic distance



# Percent phylogenetic signal



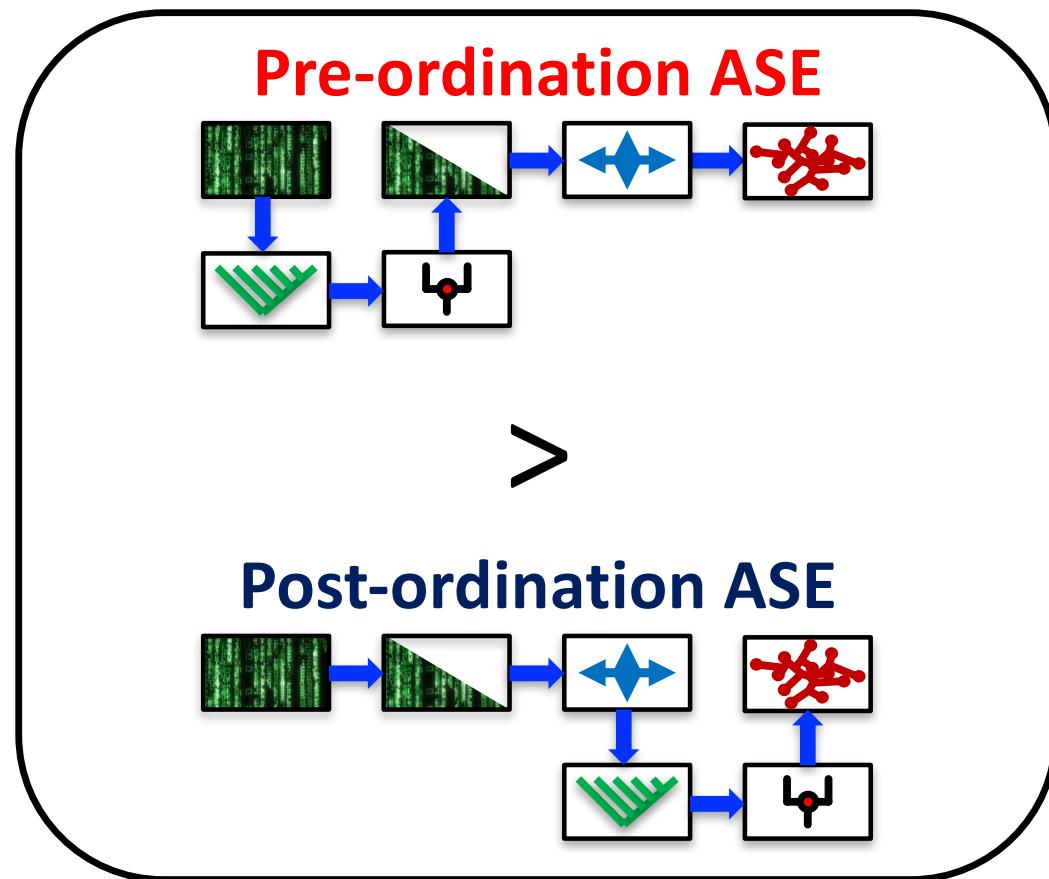
# Percent phylogenetic signal



# Phylomorphospace conclusions

Lloyd 2018; *Palaeontology*, **61**, 637-645

# Phylomorphospace conclusions



Lloyd 2018; *Palaeontology*, 61, 637-645

# Phylomorphospace conclusions

