PHYLOGENETIC
COMPARATIVE METHODS

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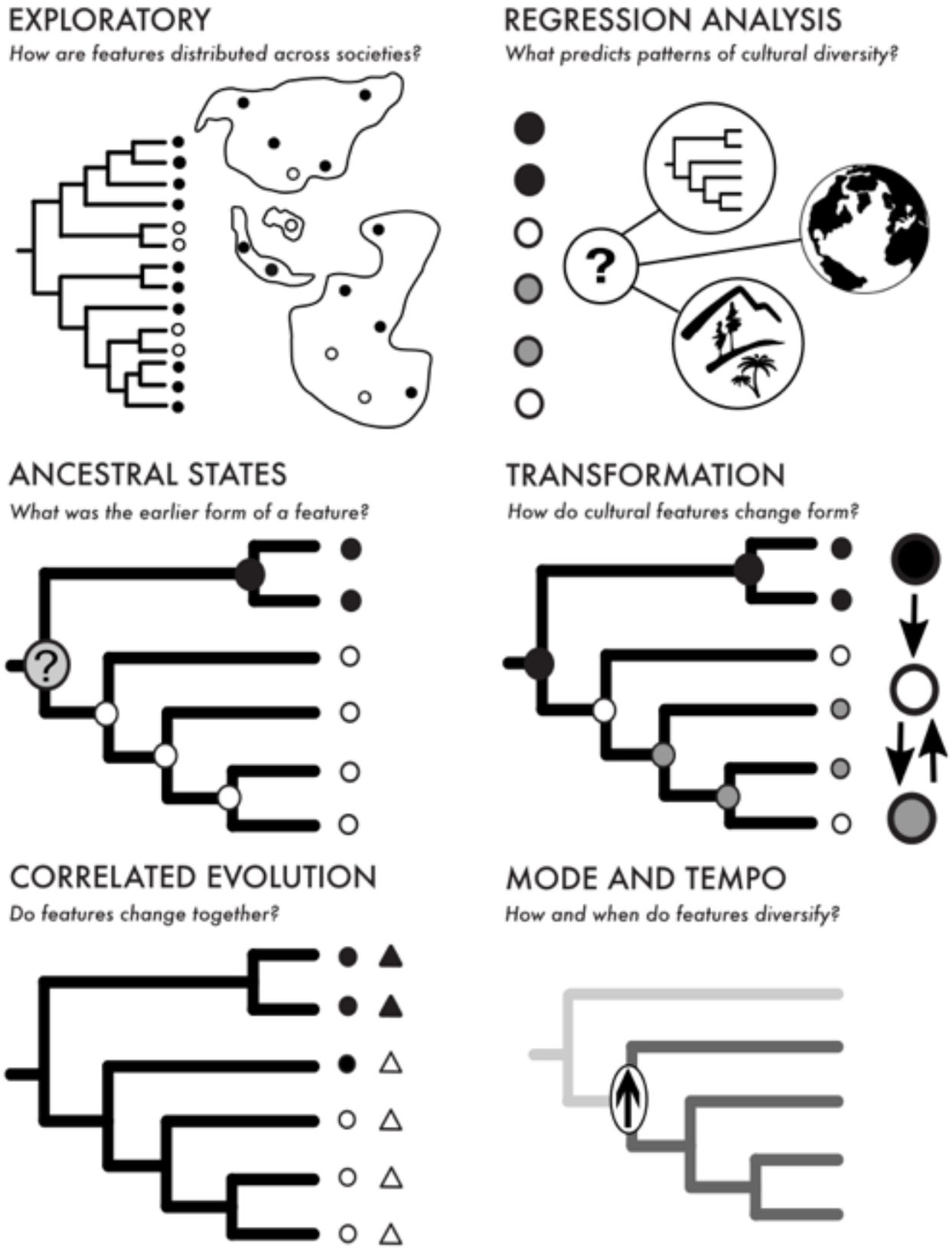
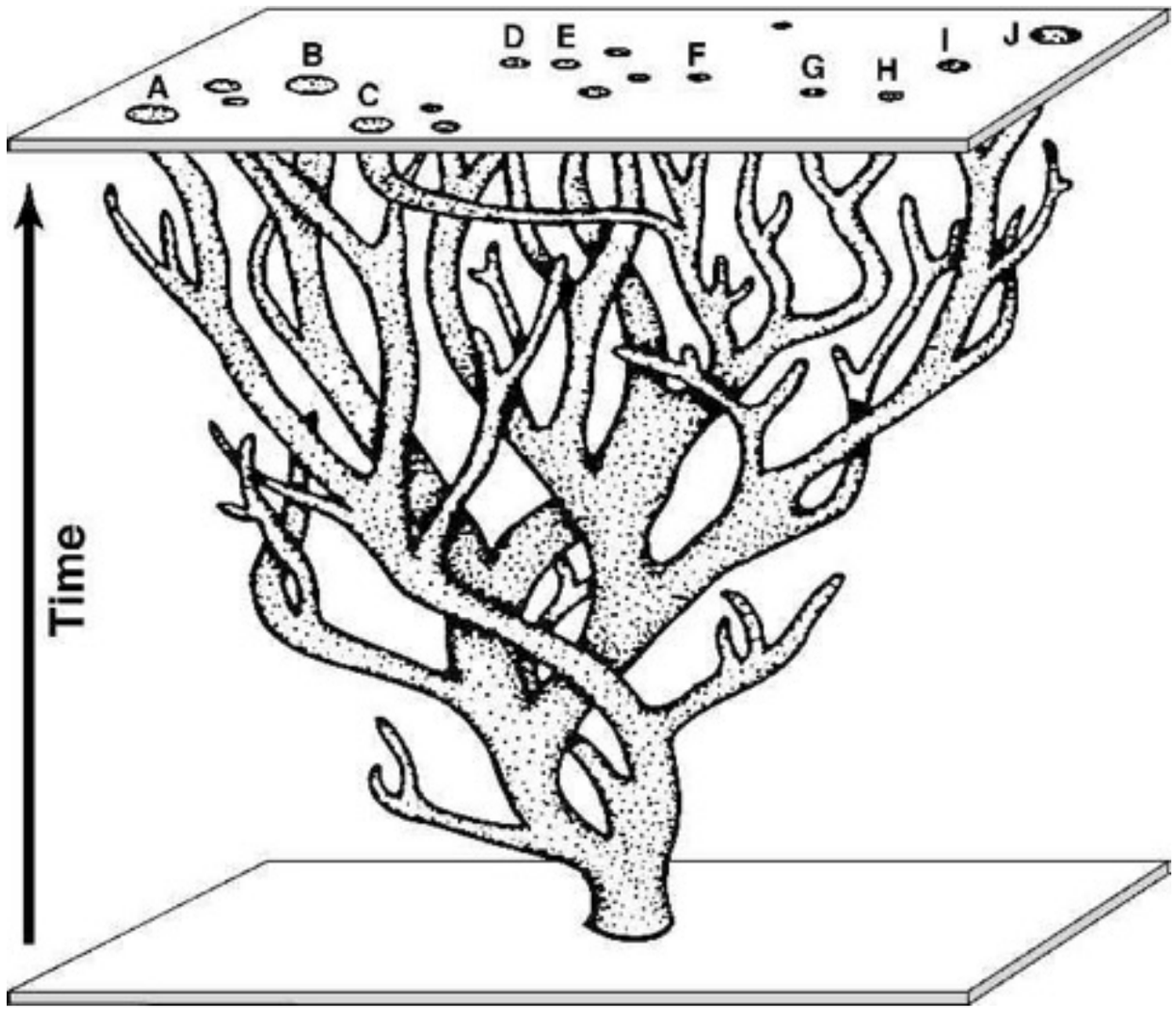


Phylogenetic comparative methods

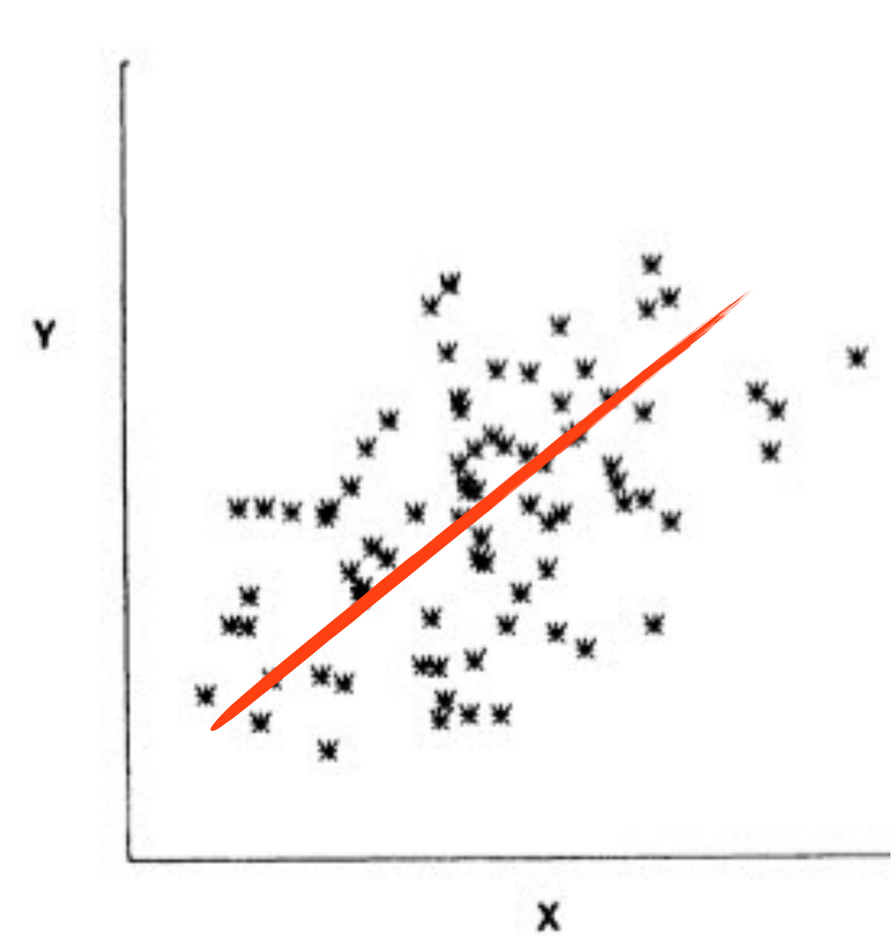
A suite of computational and statistical tools, for investigating hypotheses about the evolution of a set of traits, against the background of their evolutionary relationships.

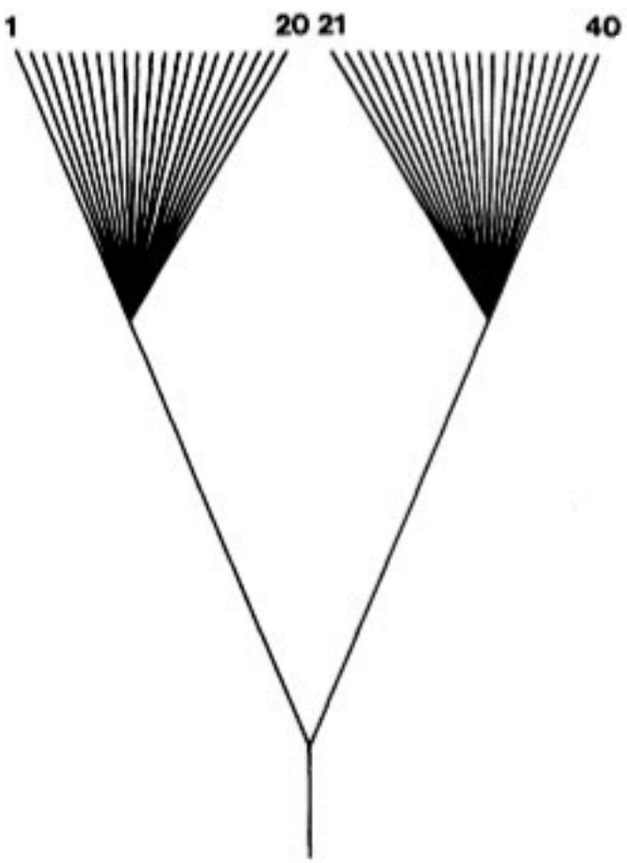


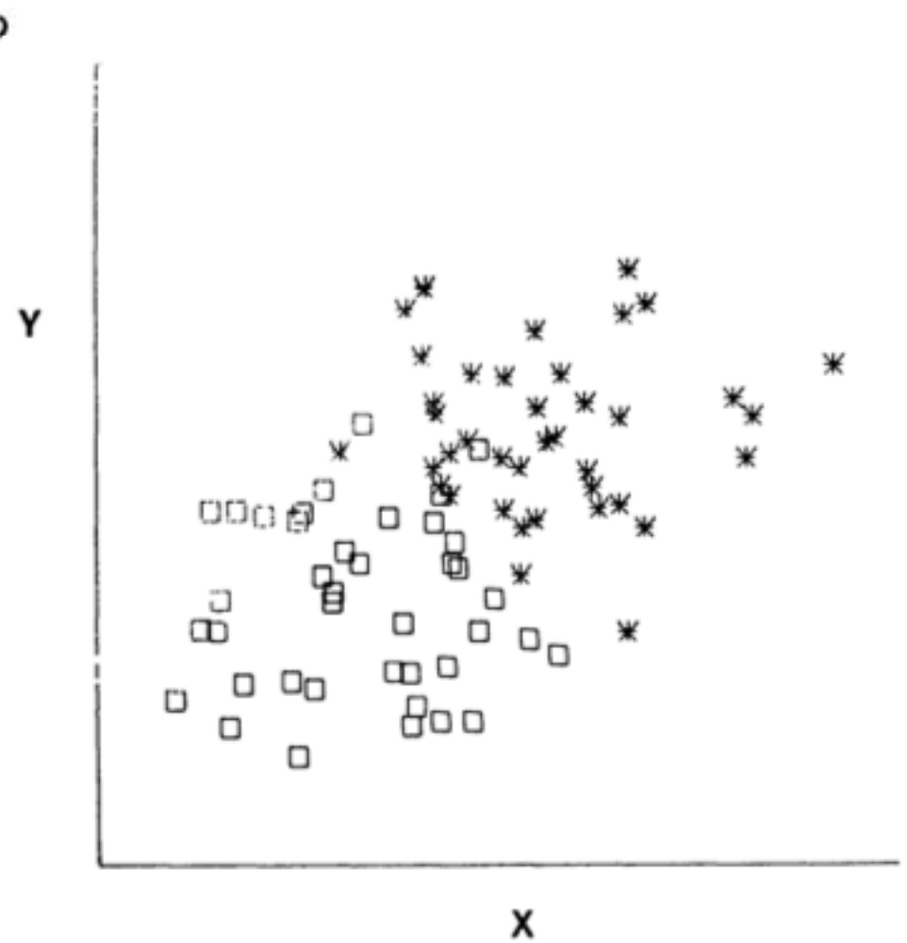
Ord & Martins 2009 / Felsenstein 1985

Phylogenies and the comparative method

- Historical relationships mean that data points might not be independent



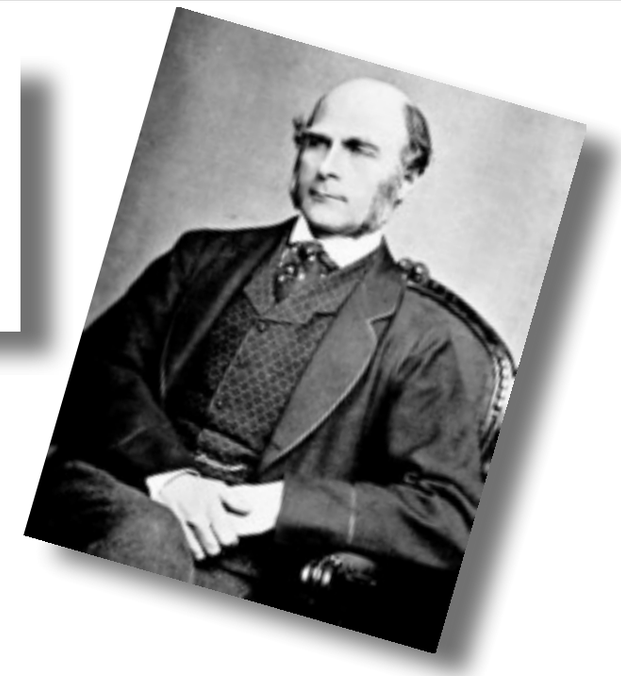


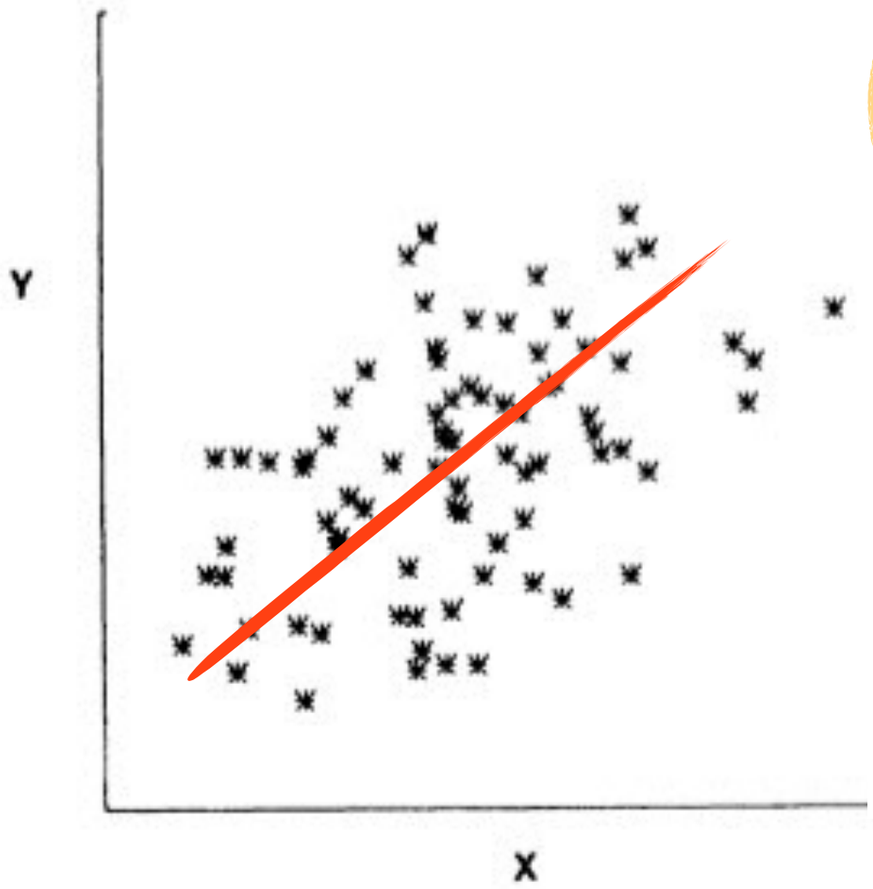


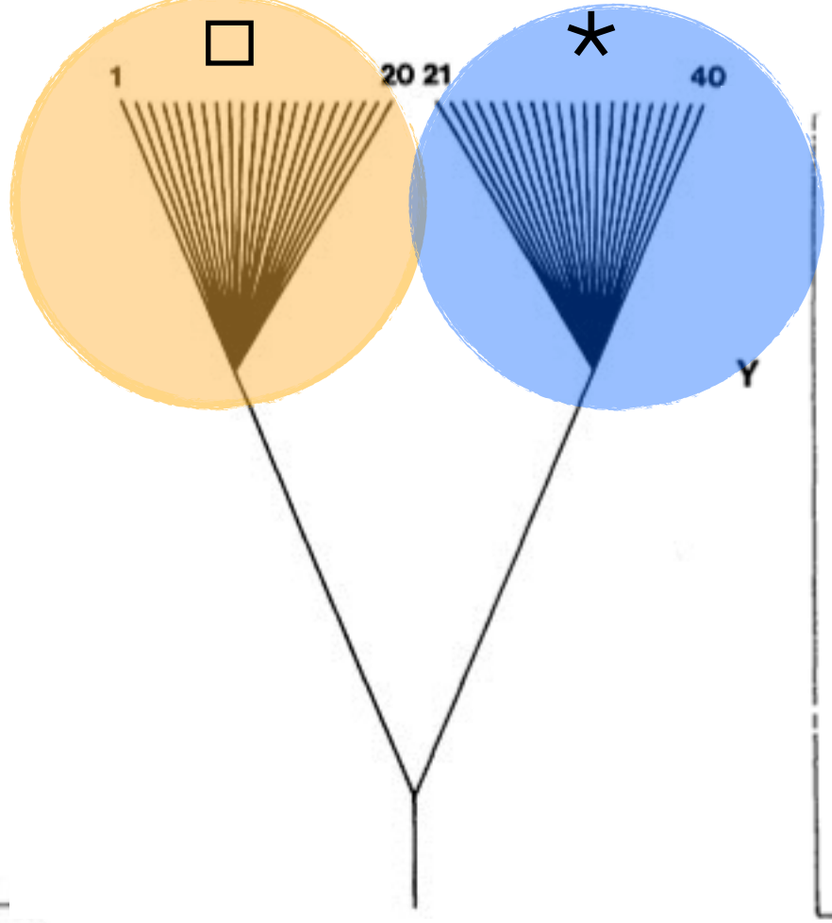
Felsenstein 1985 / Galton 1889 in response to Tylor

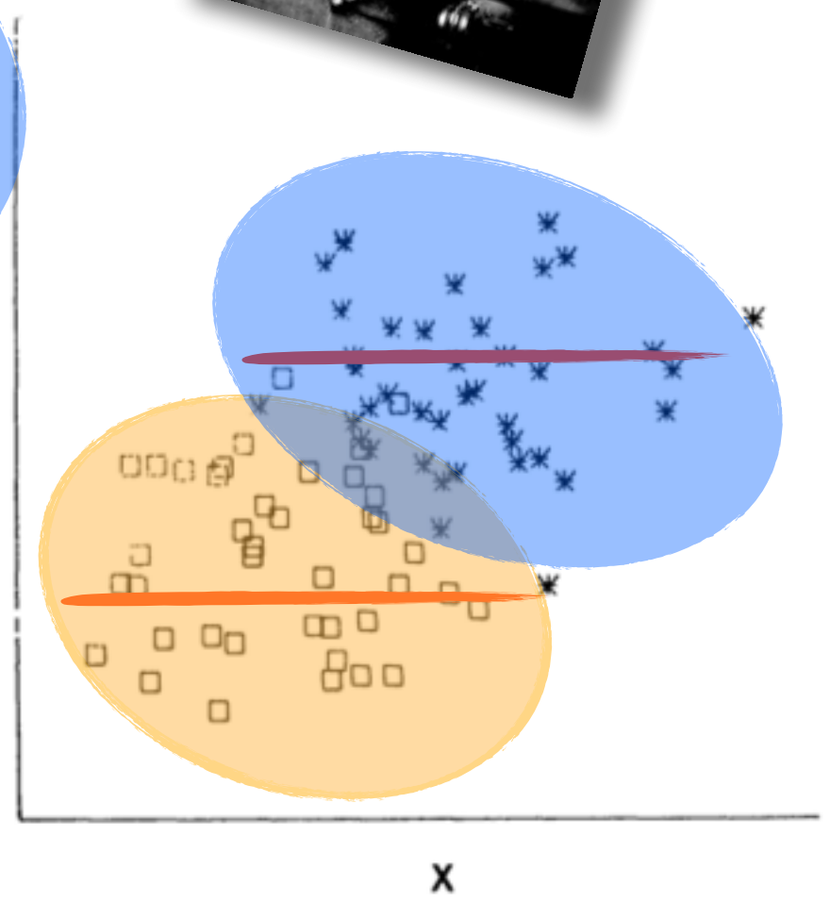
Phylogenies and the comparative method

to permanent settlement. The difficulty raised by Mr. Galton that some of the concurrences might result from transmission from a common source, so that a single character might be counted several times from its mere duplicates, is a difficulty ever present in such investigations, as for instance in the Malay region, where







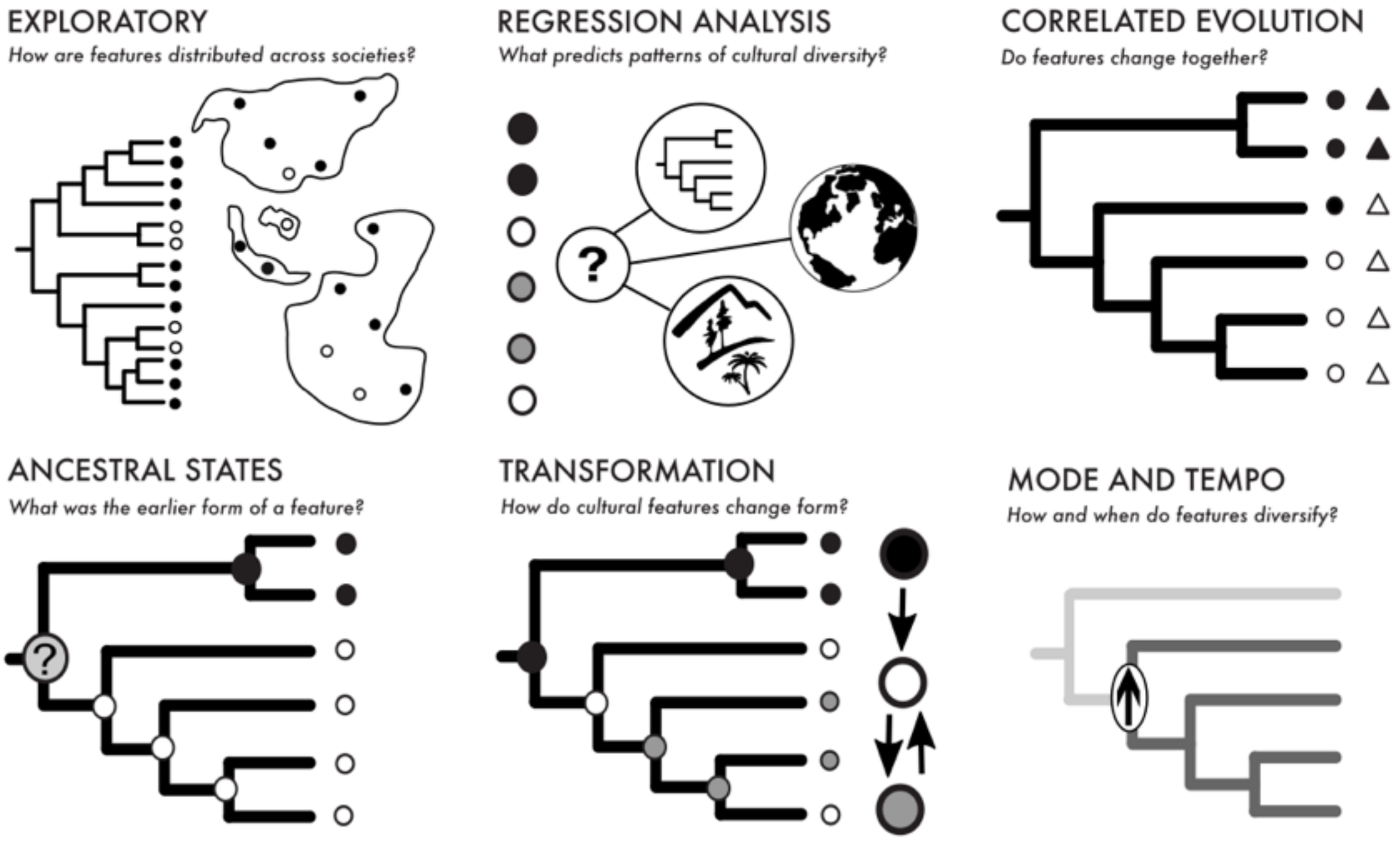


Felsenstein 1985 / Galton 1889 in response to Tylor

“the largest and most important aspects of culture leave no trace in the soil; language, social organization, religion - in short, everything that is not material - vanishes with the life of each generation.”

Franz Boas 1948

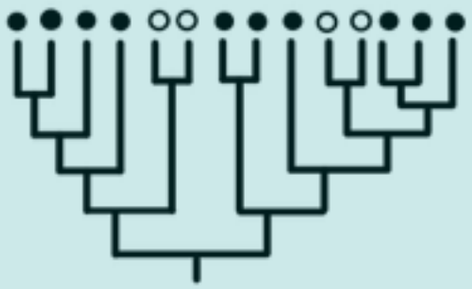
Comparative methods



Gray et al 2007 / Jordan 2013 / Nunn 2011 / Kirby et al 2016

Components of a comparative analysis

discrete
continuous



data

inference method

trees
tip data

MP
ML
Bayesian

Markov

Brownian
stabilising
speciational

model

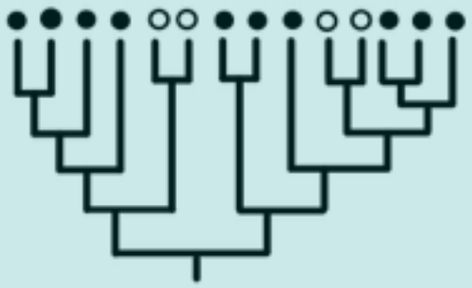
parameter estimates

change description

node values
transition rates

Components of a comparative analysis

discrete
continuous



data

inference method

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Modelling change on phylogenies

- Discrete and continuous characters change differently

  Different model/assumptions required

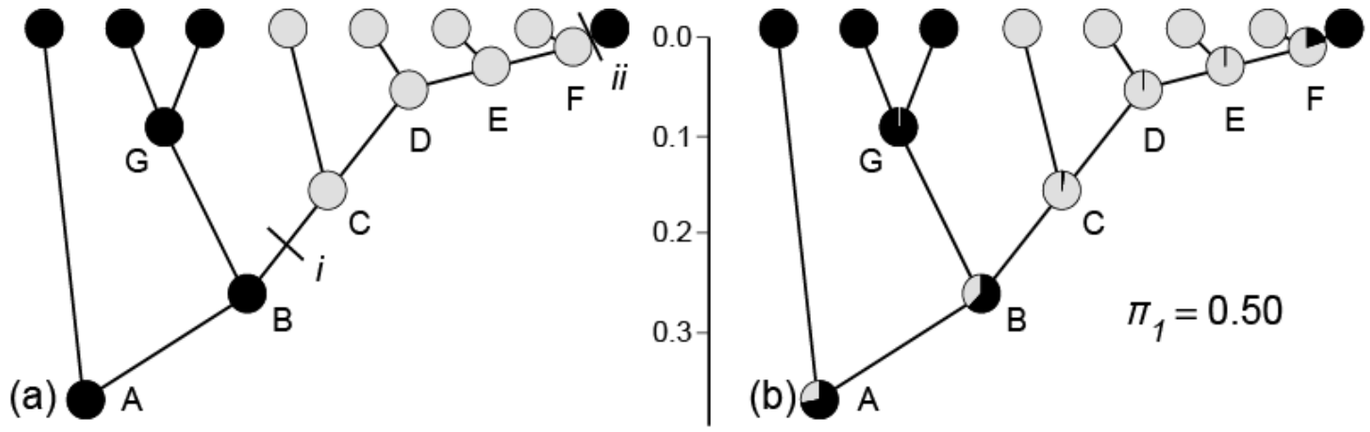
- Same types of inference methods as for tree-building

  Parsimony

  Maximum likelihood

  Bayesian

  ... and the same pros and cons.



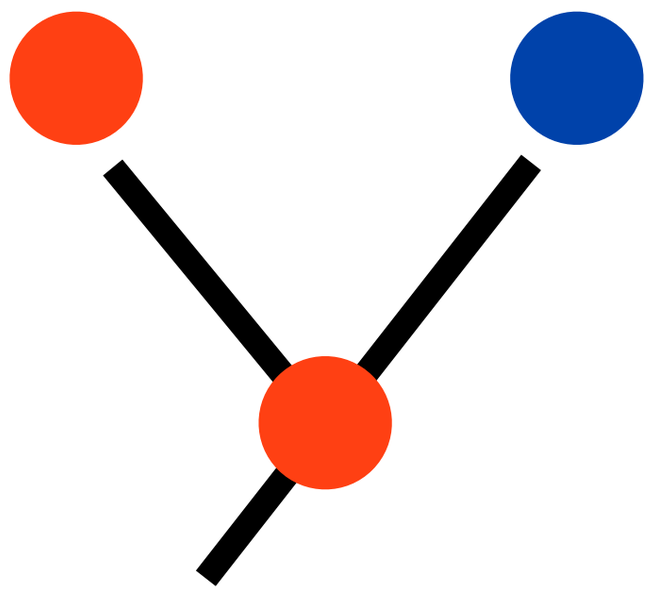
- PCMs implemented in a wide range of software packages

  R, BayesTraits, Mesquite

Ord & Martins 2010 / Nunn 2011

Models of change for discrete data

Discrete data in a probabilistic framework

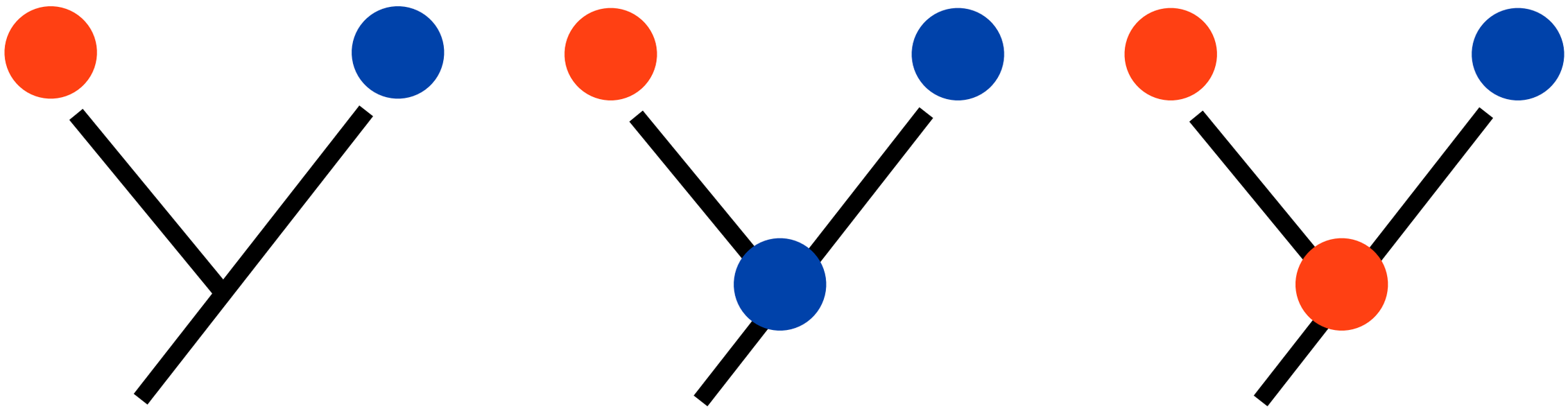


state at end of branch

state at beginning of branch	0	1
0	$q00$	$q01$
1	$q10$	$q11$

Pagel 1994

Discrete data in a probabilistic framework

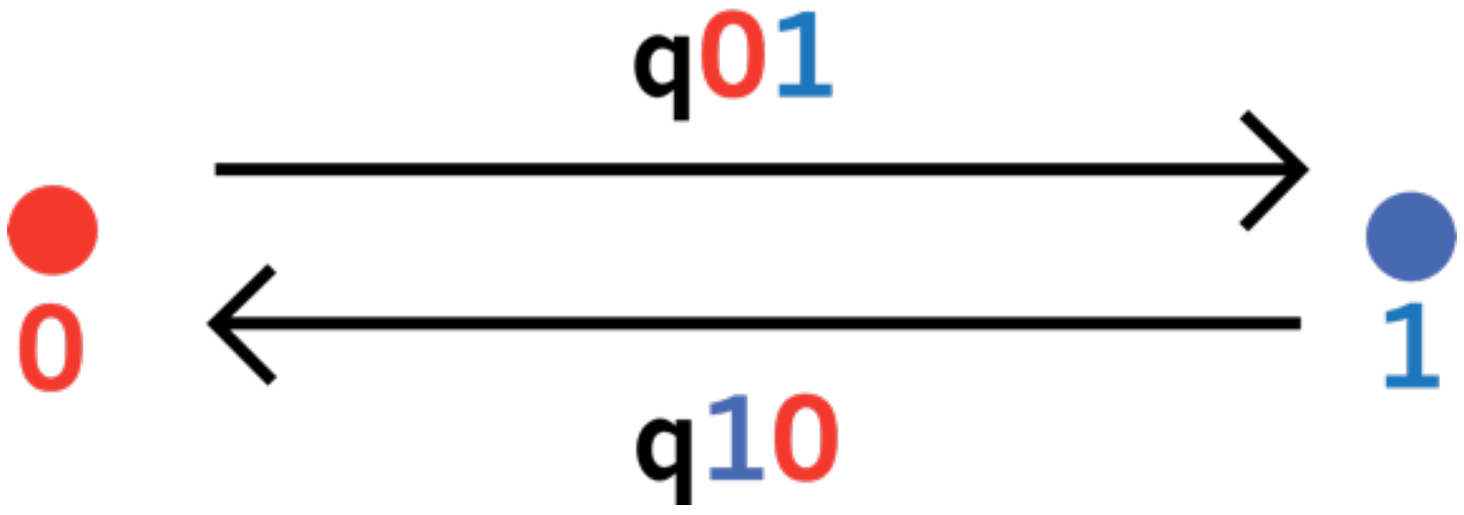


continuous-time Markov models

these specify a matrix [Q] of transition probabilities

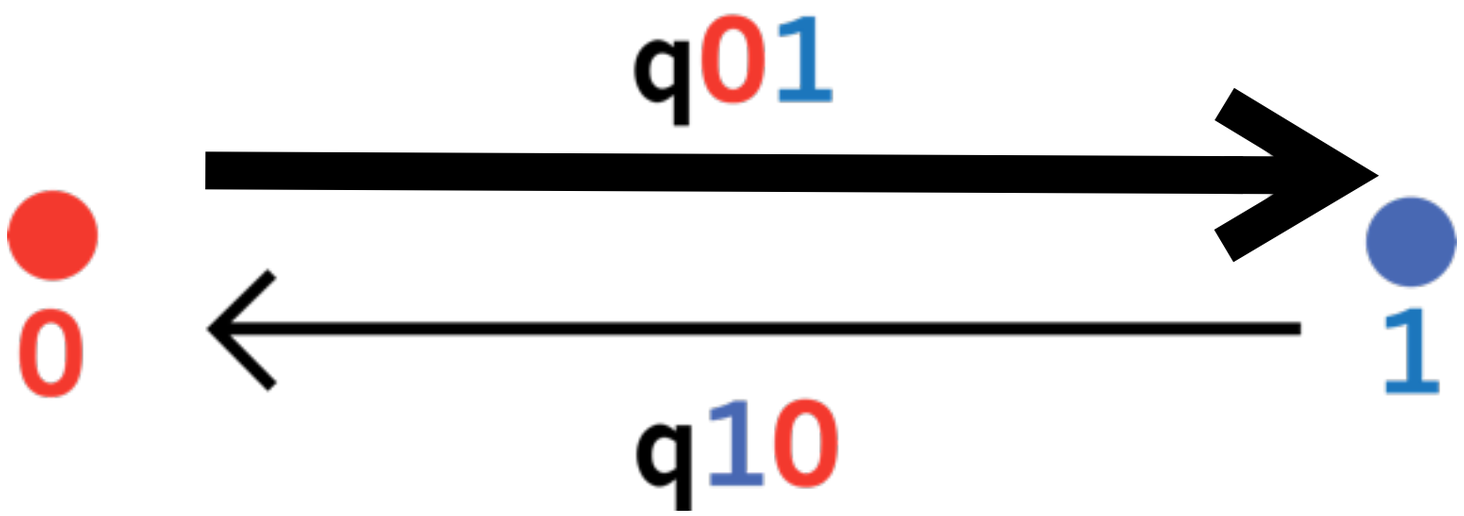
probability of change at each tiny increment along branch

Pagel 1994



transition-rate parameters

describe the probability of change from one state to another



Pagel 1999 *Systematic Biology* / Pagel & Meade 2004 *American Naturalist*

Modelling discrete change on phylogenies

- The TREES are treated as fixed, like the DATA

- Very similar to estimating the evolution of a single character when inferring phylogenies

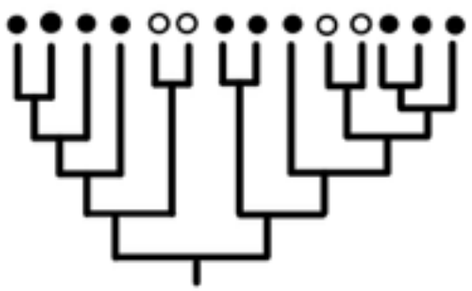
- More fine-grained investigation of the model of evolution.

Ancestral state inference

Specifying and testing a model of discrete character evolution

Components of a comparative analysis

discrete
continuous



Markov

Brownian
stabilising
speciational

data

inference
method

model

parameter
estimates

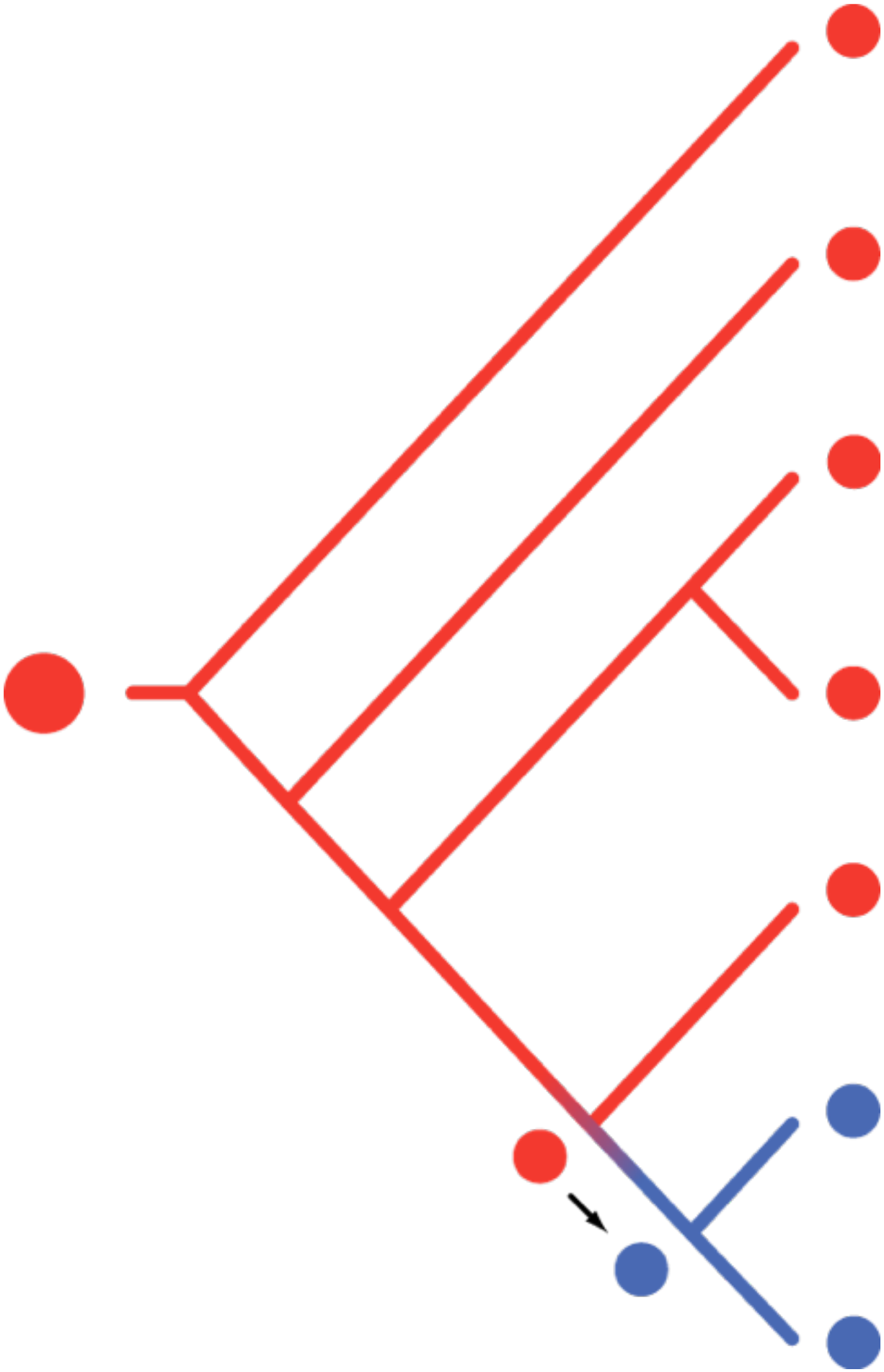
trees
tip data

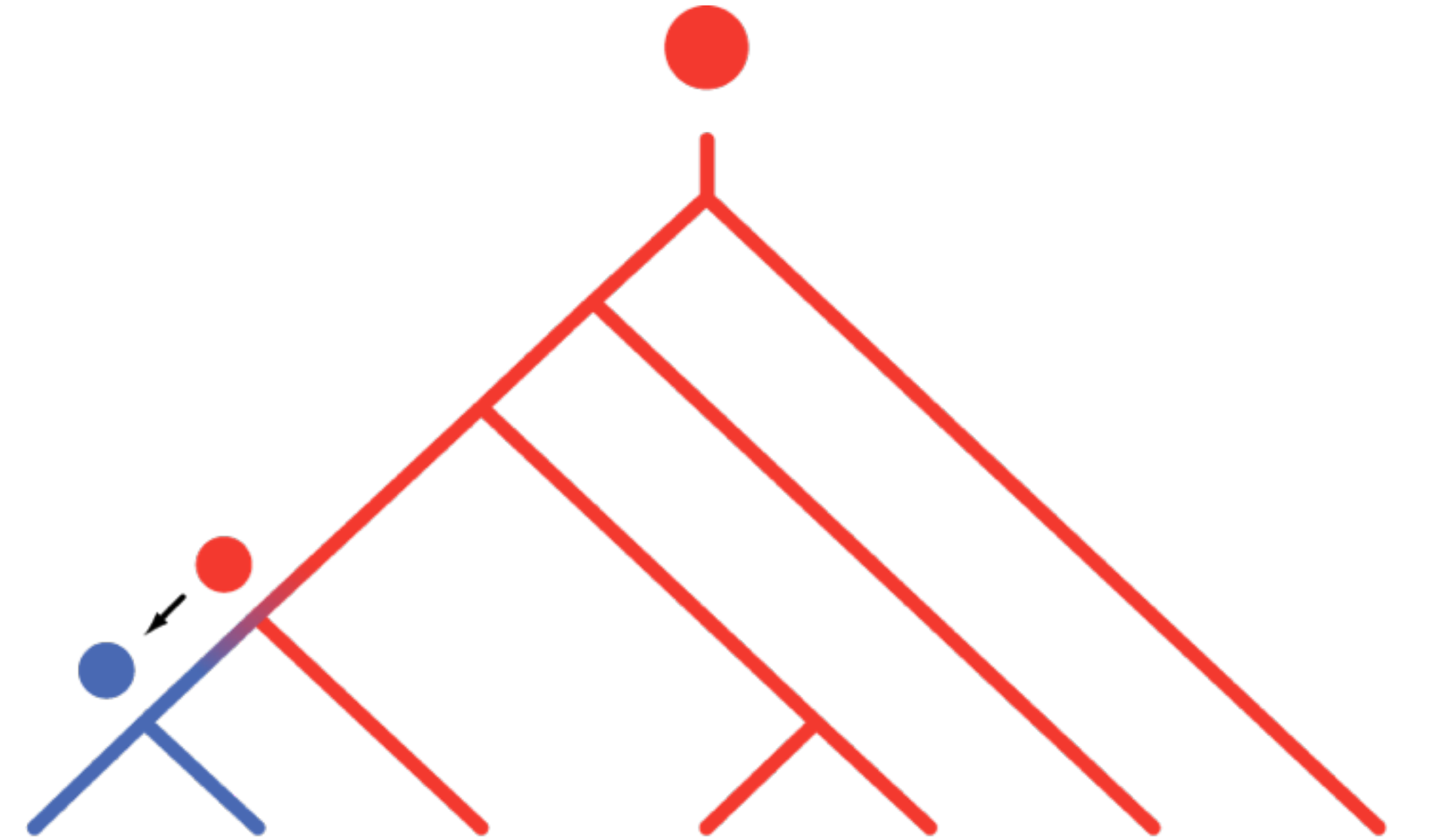
MP
ML
Bayesian

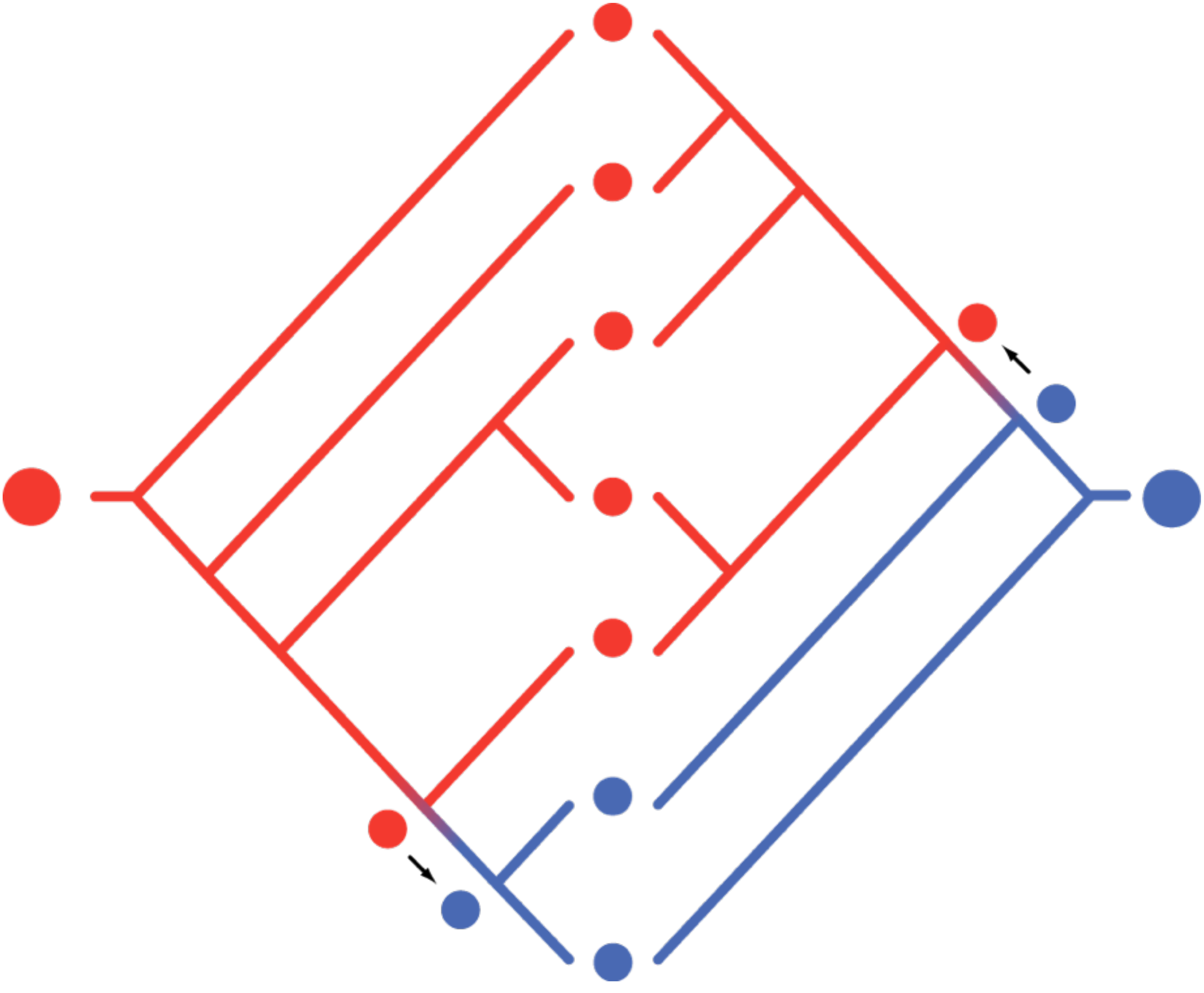
change
description

node values
transition rates

Phylogeny
affects our estimates of ancestral states







Ancestral states

What kinds of questions?

- What is the earlier form of a trait?

- What form of the trait do we see at a specific node?

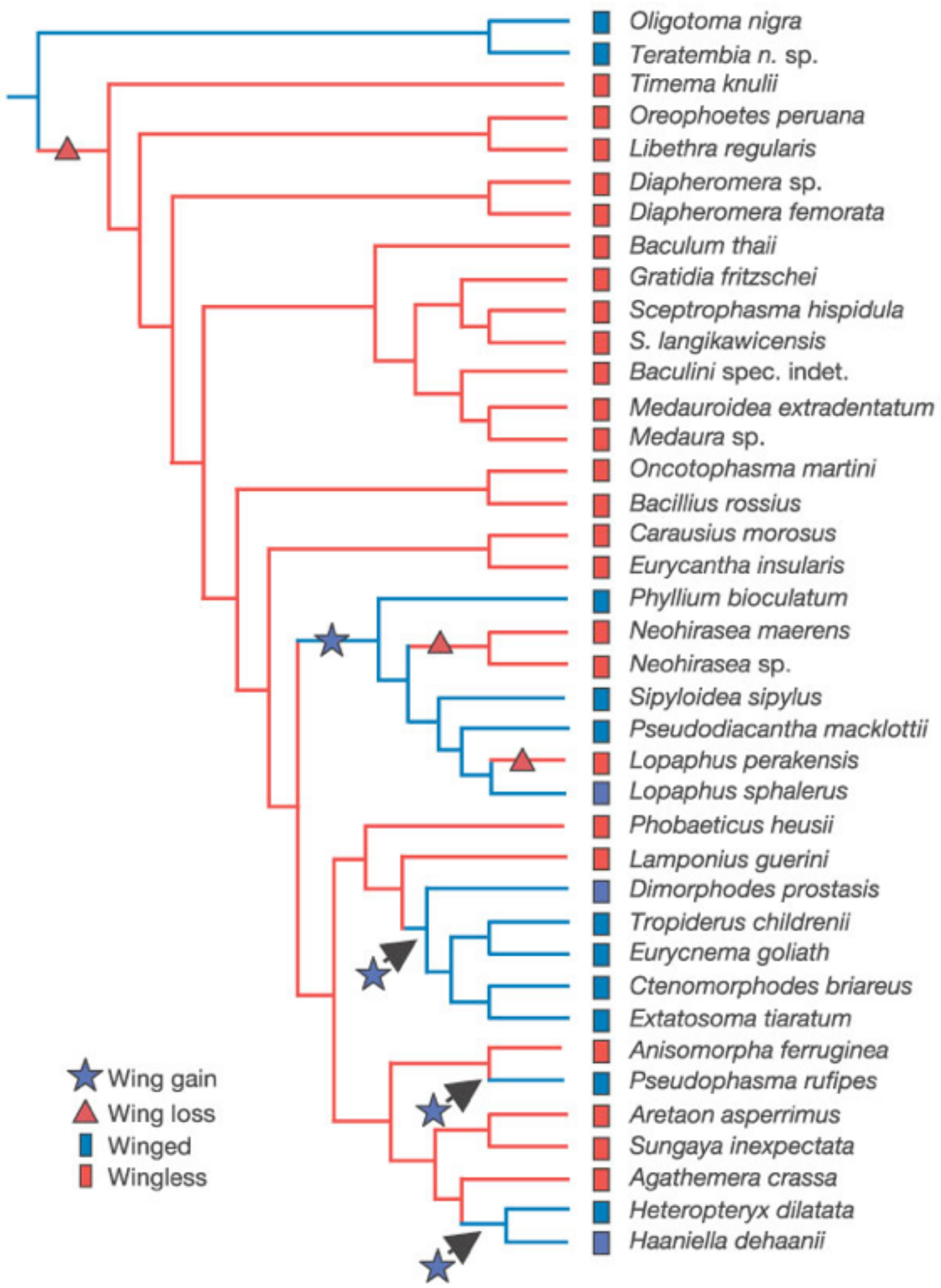
- How certain are we in our estimates of node values?

- Given some independent evidence about ancestral forms, how much do we prefer one hypothesis over another?

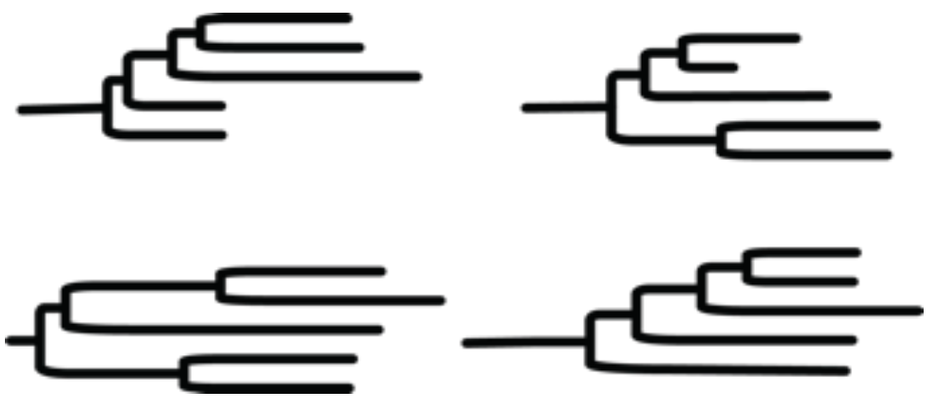
- Does altering the ancestral states affect our model of evolution?
  If so, for better or worse?

Loss and recovery of wings in stick insects

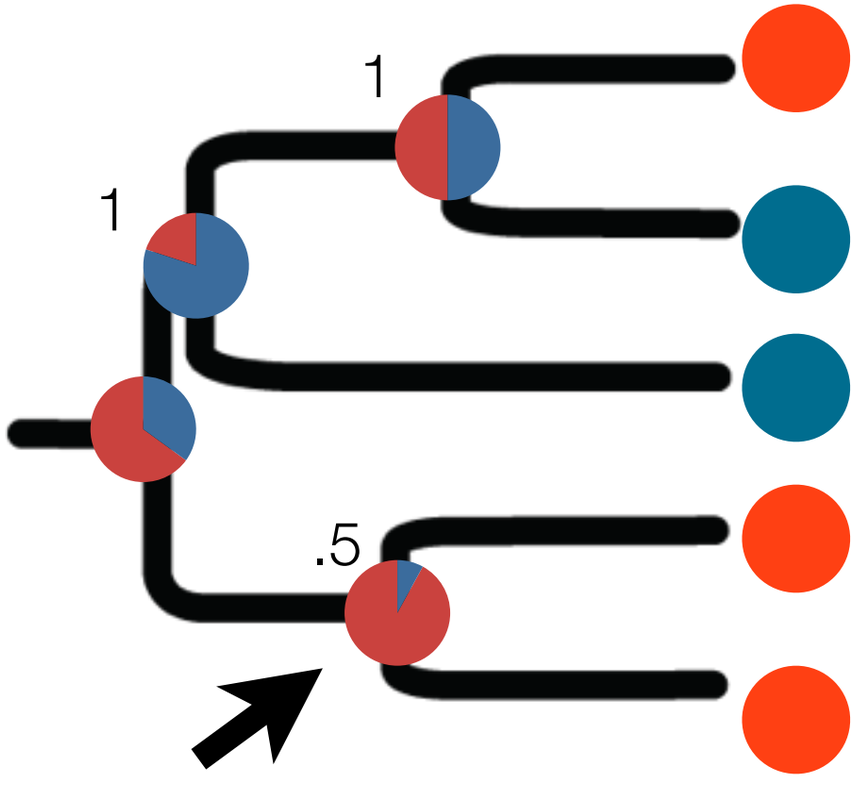
Michael F. Whiting*, Sven Bradler† & Taylor Maxwell‡



Ancestral states are always *estimates* (ASE)



1. posterior distribution of trees to account for “phylogenetic uncertainty”



2. map trait data onto tree at tips

3. estimate ancestral state at nodes to get “character uncertainty”: represented by probability of each ancestral state

4. condition each ASE on that node’s posterior probability on the tree. e.g. the arrowed node has pr(●) = .5 × .9 = .45

Steps
in ancestral state inference

- REQUIREMENTS: Trait data, tree(s), question, method

- IMPLEMENTATION: Mesquite, BayesTraits, APE, geiger … [R]

- Designate which nodes are to be inferred: (root? all? some?)
  - Incorporate any independent evidence on prehistory using a “fossilisation” procedure to fix a state at a node.
  - Incorporate any independent evidence on process (different models of change)

- Examine the distributions of obtained node values

- Test how robust the ASE is under different models of evolution using LRT / BF tests

postmarital residence

Inferring ancestral residence
What did we do?

- Used independently-derived lexical phylogenies of AN languages
  Matched ethnographic descriptions to linguistic groups

- Data on residence was coded as ONE TRAIT with TWO STATES
  Societies could have mixed strategies e.g. MP = ambilocal

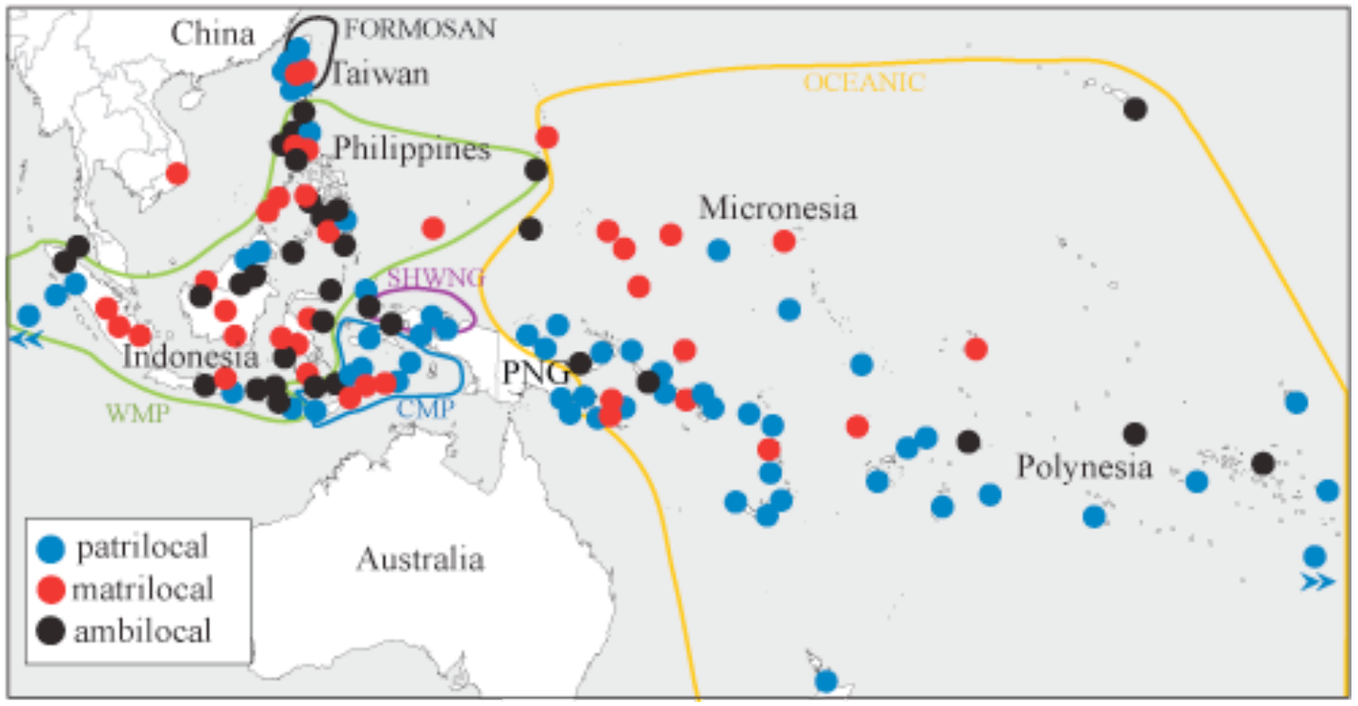
- Used Multistate in BayesTraits to infer ancestral states and the parameters of the most likely model of evolution
  Tested our hypotheses over a posterior sample of 1000 trees
  Used reversible-jump MCMC procedure to help find the best model of evolution
  "Fossilised" early nodes to each possible state to test for early matrilocal

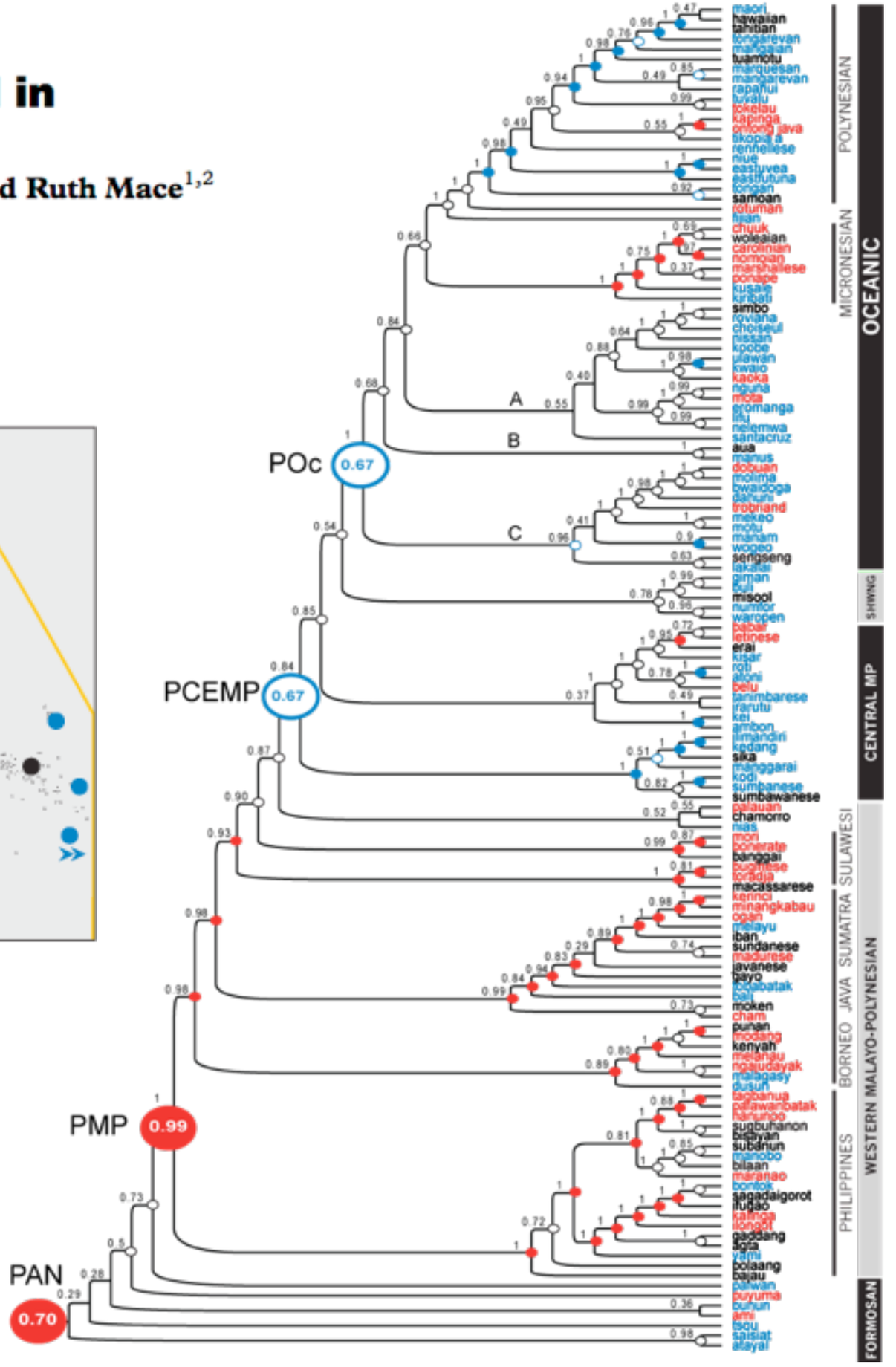
- Compared the Lh of each "version of history" using the BF test

Jordan *et al* 2009 *Proceedings B*

Matrilocal residence is ancestral in Austronesian societies

Fiona M. Jordan[1,2,*], Russell D. Gray[3], Simon J. Greenhill[3] and Ruth Mace[1,2]





Jordan et al 2009 *Proceedings B*

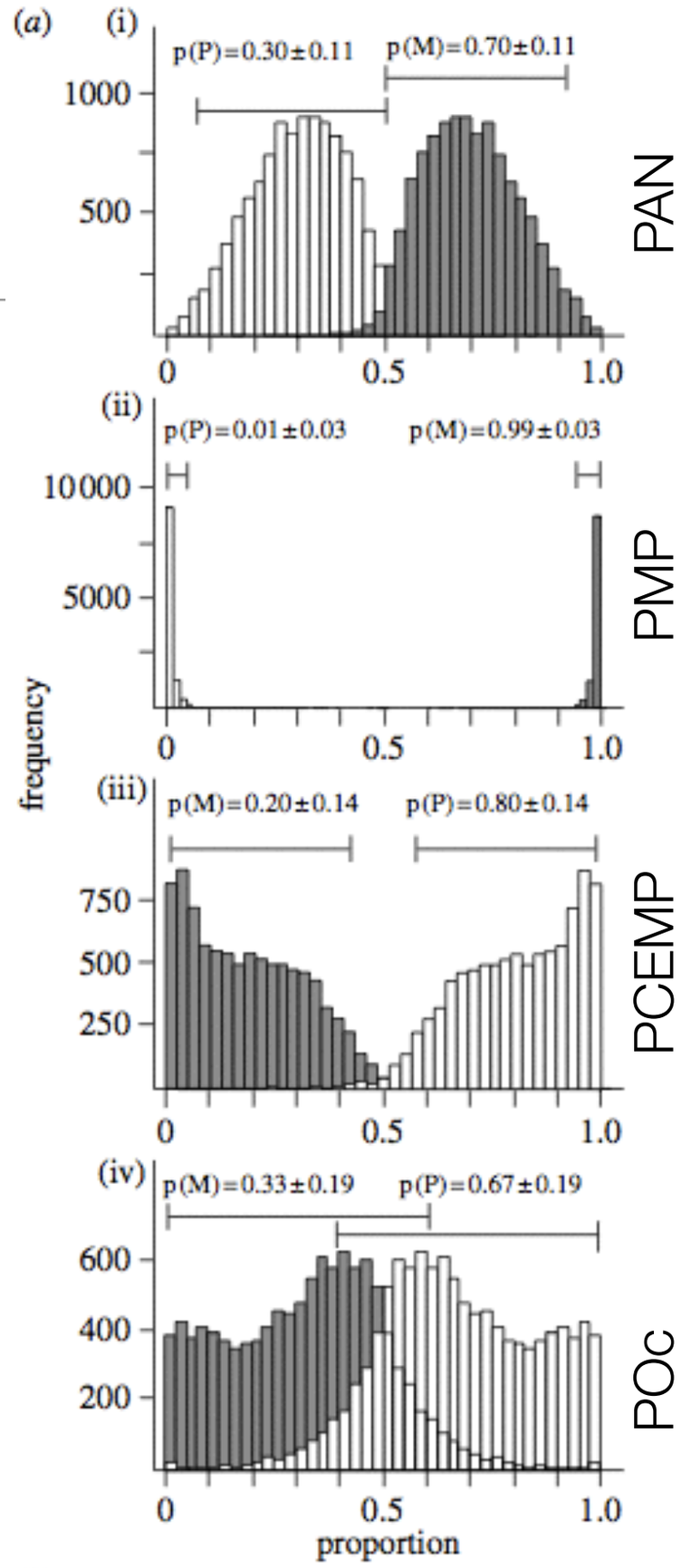
Inferring ancestral residence

What did we do?

- We inferred a node's state by multiplying:
  - our character certainty about the state (e.g. .95 patrilocal)
  - our phylogenetic certainty that the node existed i.e. the posterior probability

- We used "fossilisation" procedures to test the robustness of our inferences about residence.

- We compared one- and two- parameter models and found evidence for unequal rates of change.



Jordan *et al* 2009 *Proceedings B*

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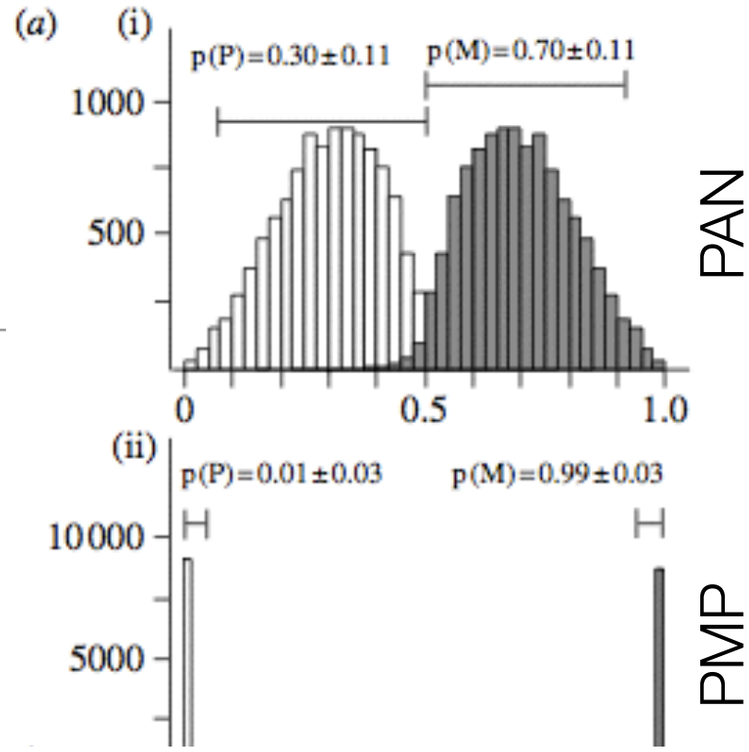
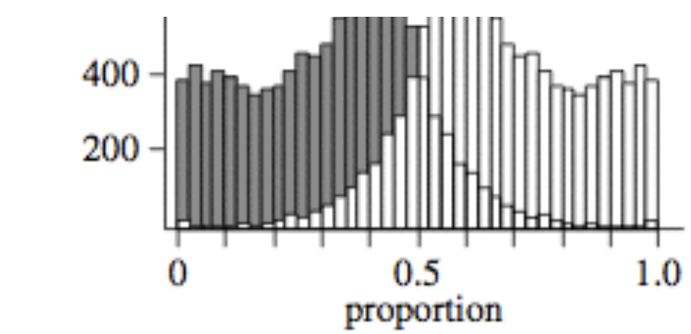


Table 1. Comparing model support with the Bayes factor. (Bayes factors were calculated as follows: BF = 2(ln LhA − ln LhB), where ln Lhx is the marginal likelihood (i.e. the harmonic mean of the post-convergence ln likelihoods, allowing us to compare the posterior distributions). BF values indicate evidence in favour of model A: 0–2, barely worth mentioning; 2–6, positive; 6–10, strong; above 10, very strong/decisive (Kass & Raftery 1995). Negative values favour model B. m, matrilocal; p, patrilocal.)

model A	ln Lh	model B	ln Lh	BF	verbal description
PAN-m	−61.36	PAN-p	−62.49	2.26	positive evidence for matrilocality
PMP-m	−60.80	PMP-p	−64.99	8.38	strong evidence for matrilocality
POC-m	−62.79	POC-p	−61.50	−2.58	positive evidence for patrilocality
equal rates	−63.12	default	−59.61	−7.03	strong evidence for unequal rates of character change

PCEMP

- We compared one- and two- parameter models and found evidence for unequal rates of change.



Jordan *et al* 2009 *Proceedings B*

Modelling evolutionary change

Modelling change
What kinds of questions?

- How do traits change their state?
- Do traits change sequentially/stepwise, or are all changes possible?
- Are some types of changes more likely than others?
- Do gains and losses happen at equal rates?
- Which model of change is preferred when we compare hypotheses?
- How do models of change compare across different groups of taxa?

Steps
in modelling evolutionary change

- REQUIREMENTS: Trait data, tree(s), question, method

- IMPLEMENTATION: Mesquite, BayesTraits, R packages

- PROCESS:

  First infer an unrestricted model of evolution

  Specify any restrictions or conditions

  Compare models using LRT or Bayes Factors

  ... Compare dynamics across groups of taxa (e.g. language families)

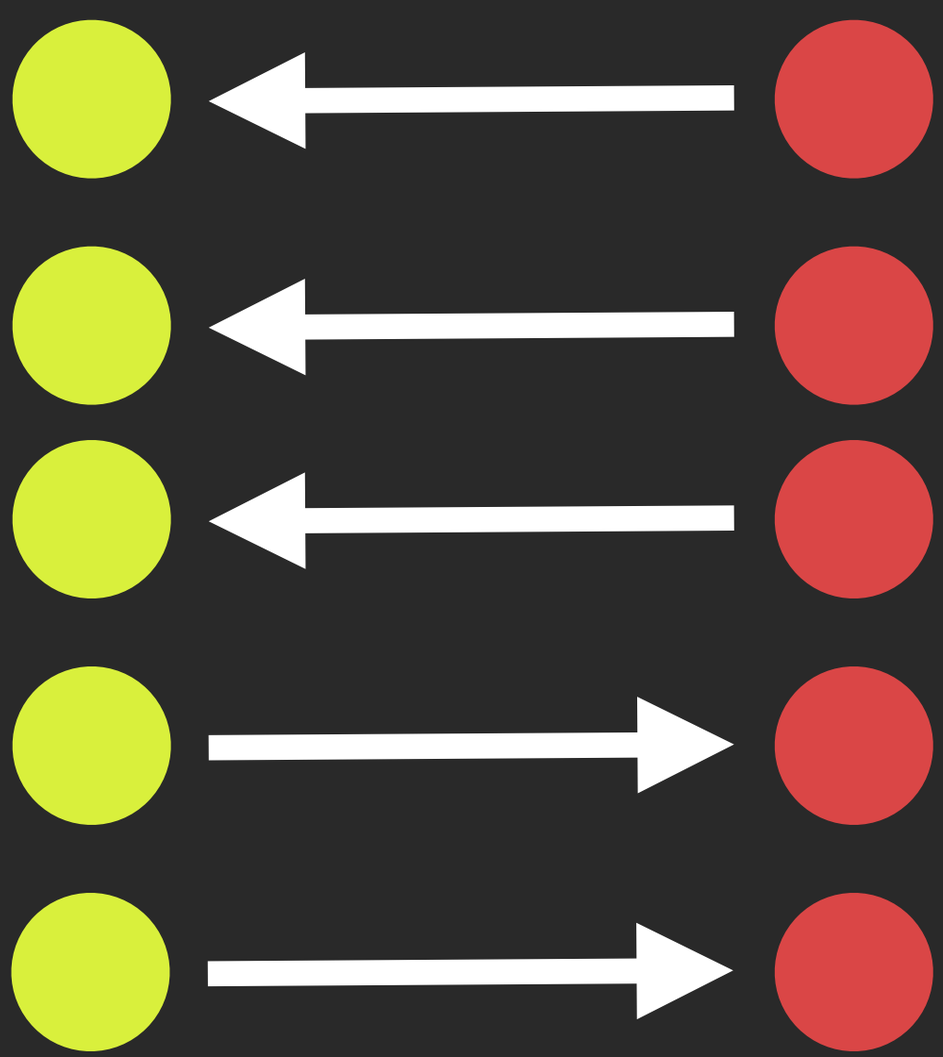
data on traits
across populations

language phylogenies
as population history

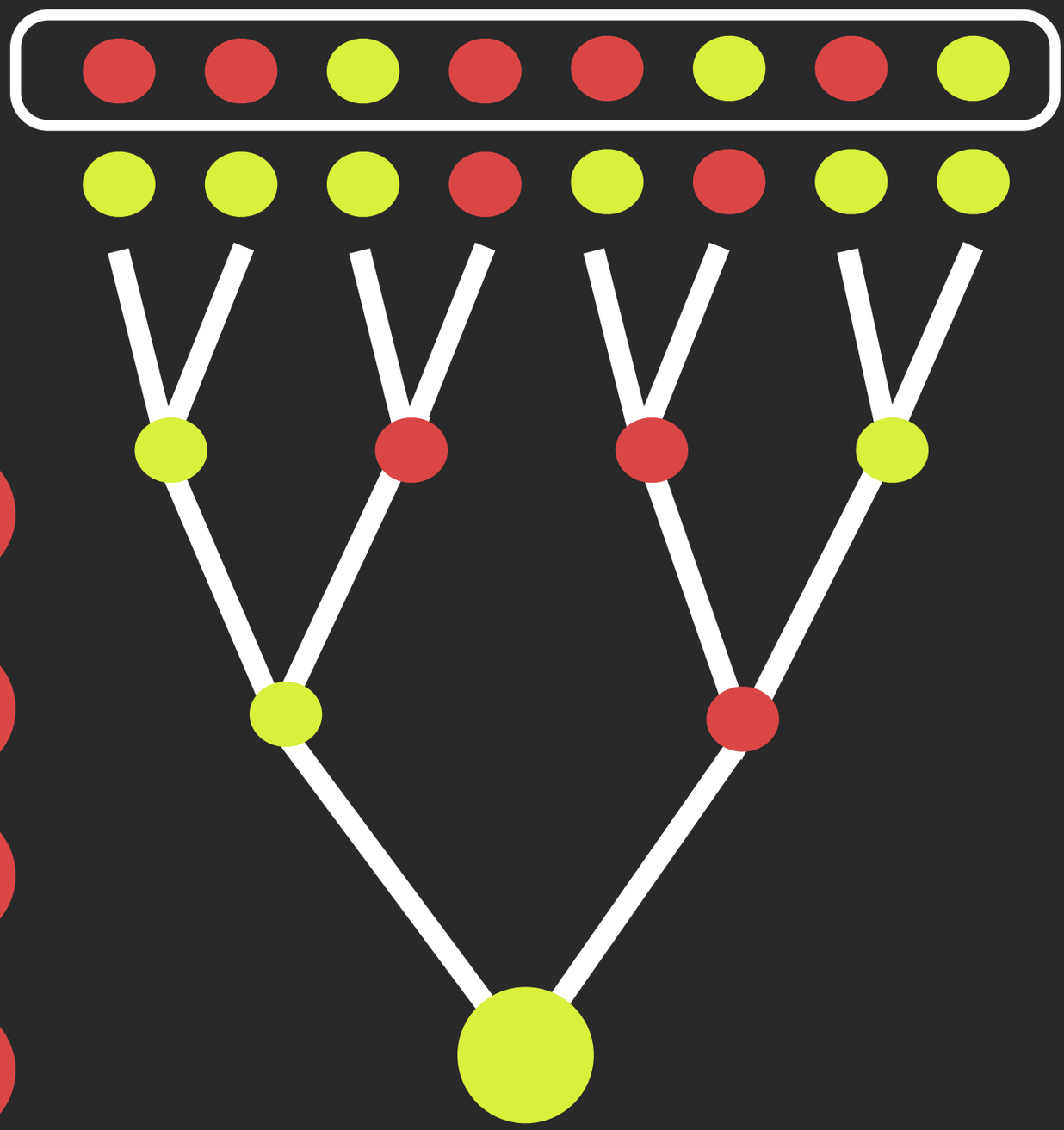
a model of
how traits evolve
(and ancestral states)

actual data

simulated data

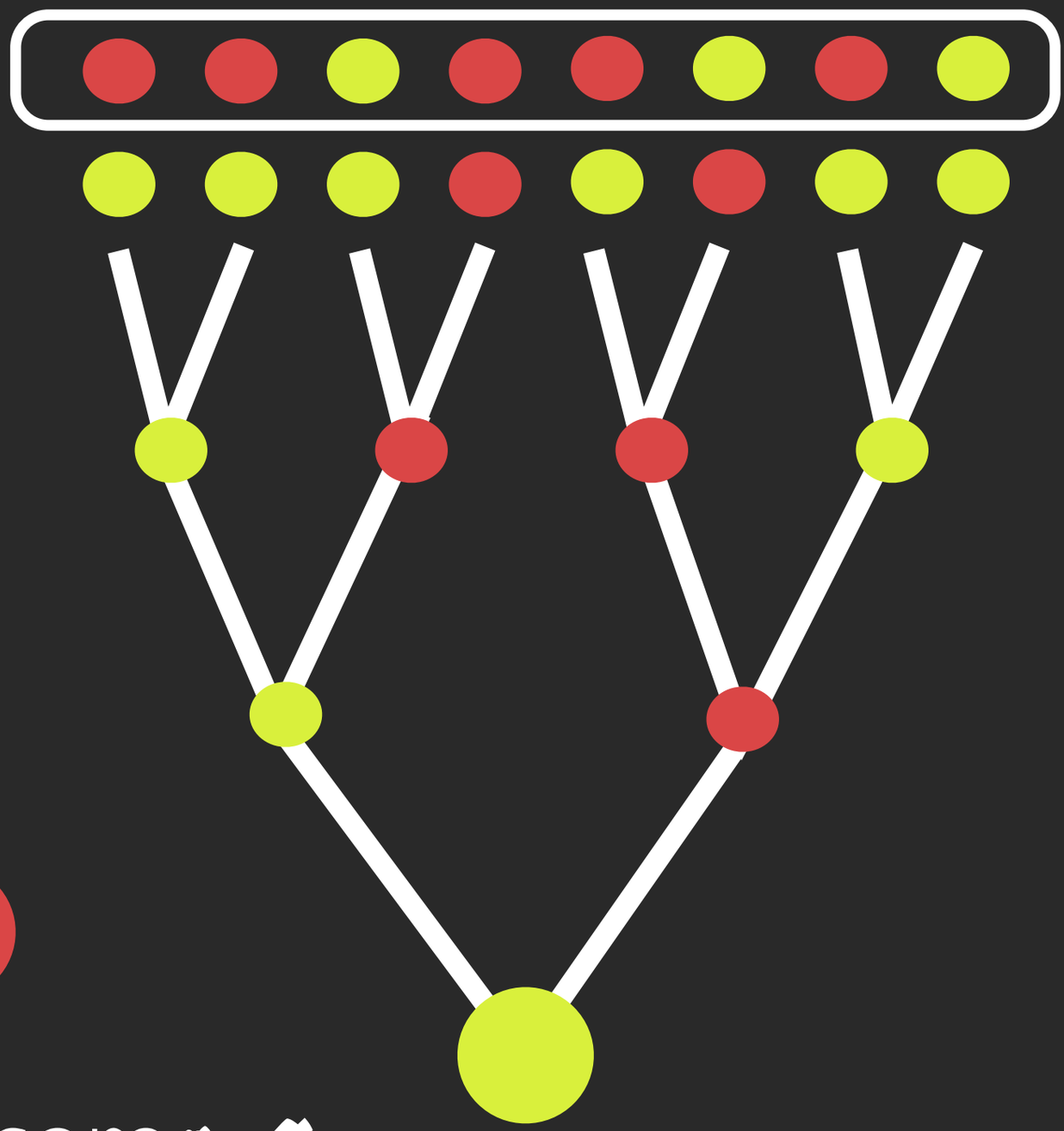


simulation one



actual data

simulated data



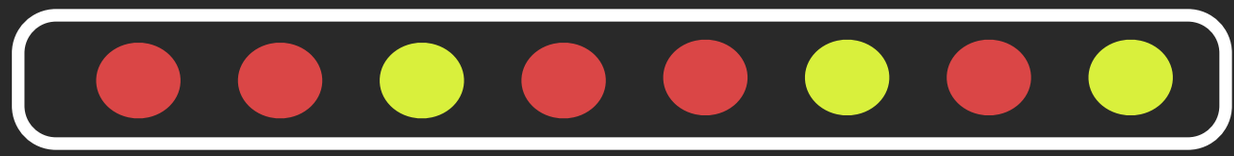
3

2

model likelihood score

simulation one

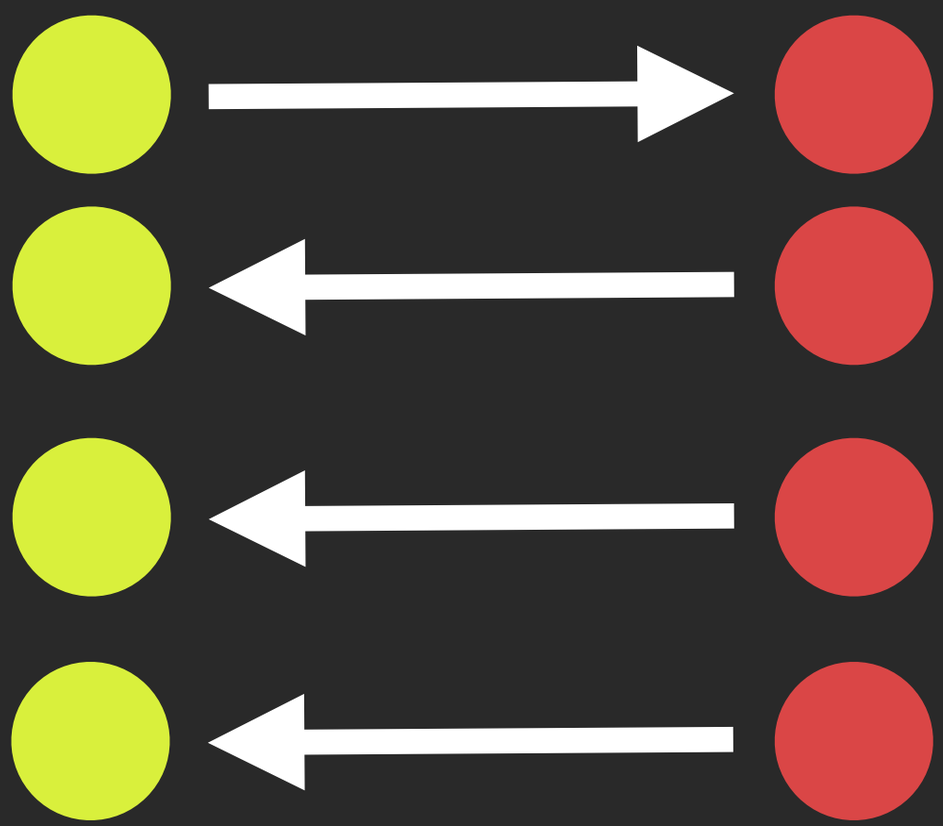
actual data



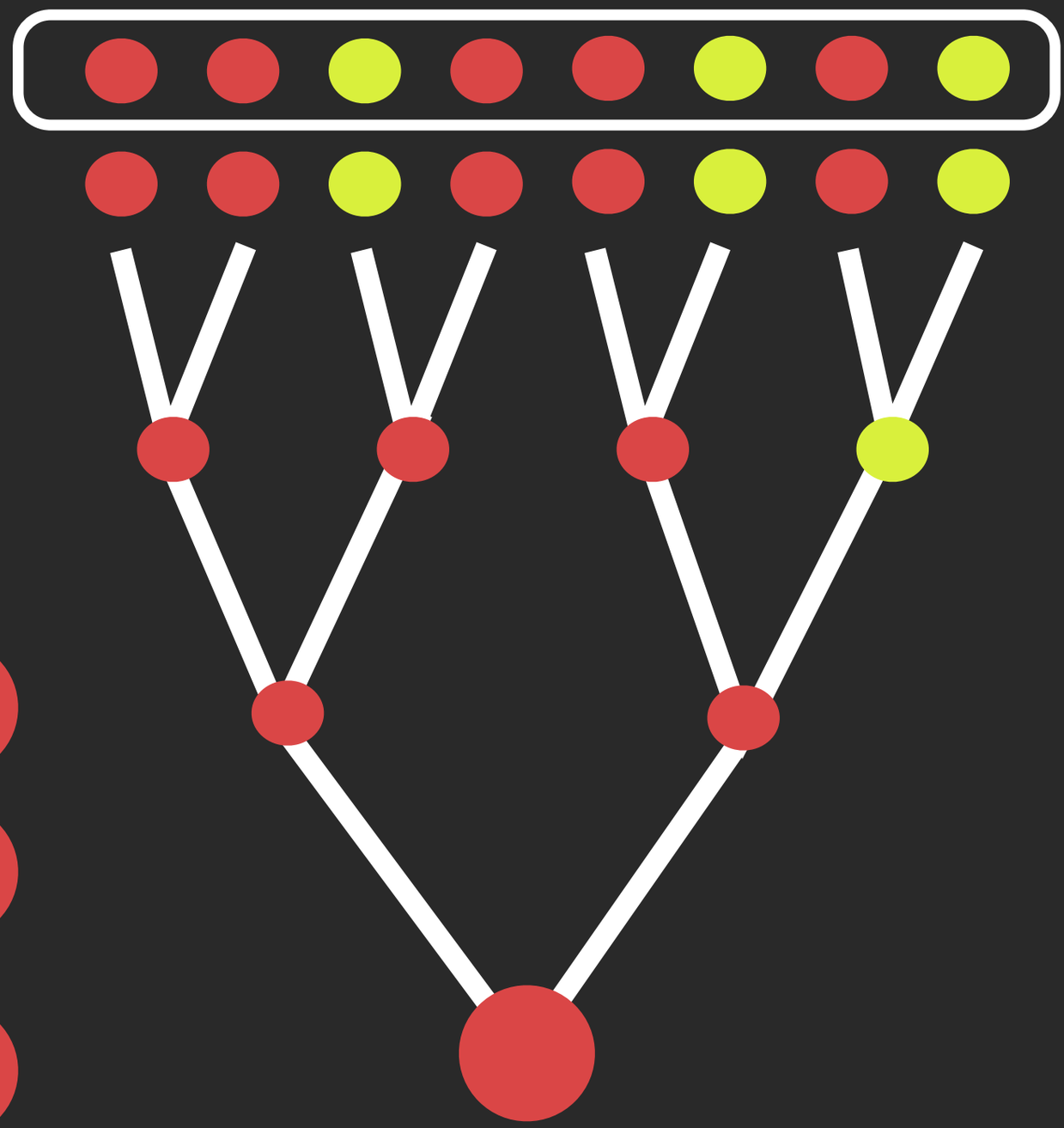
simulate evolution from all possible starting states

actual data

simulated data

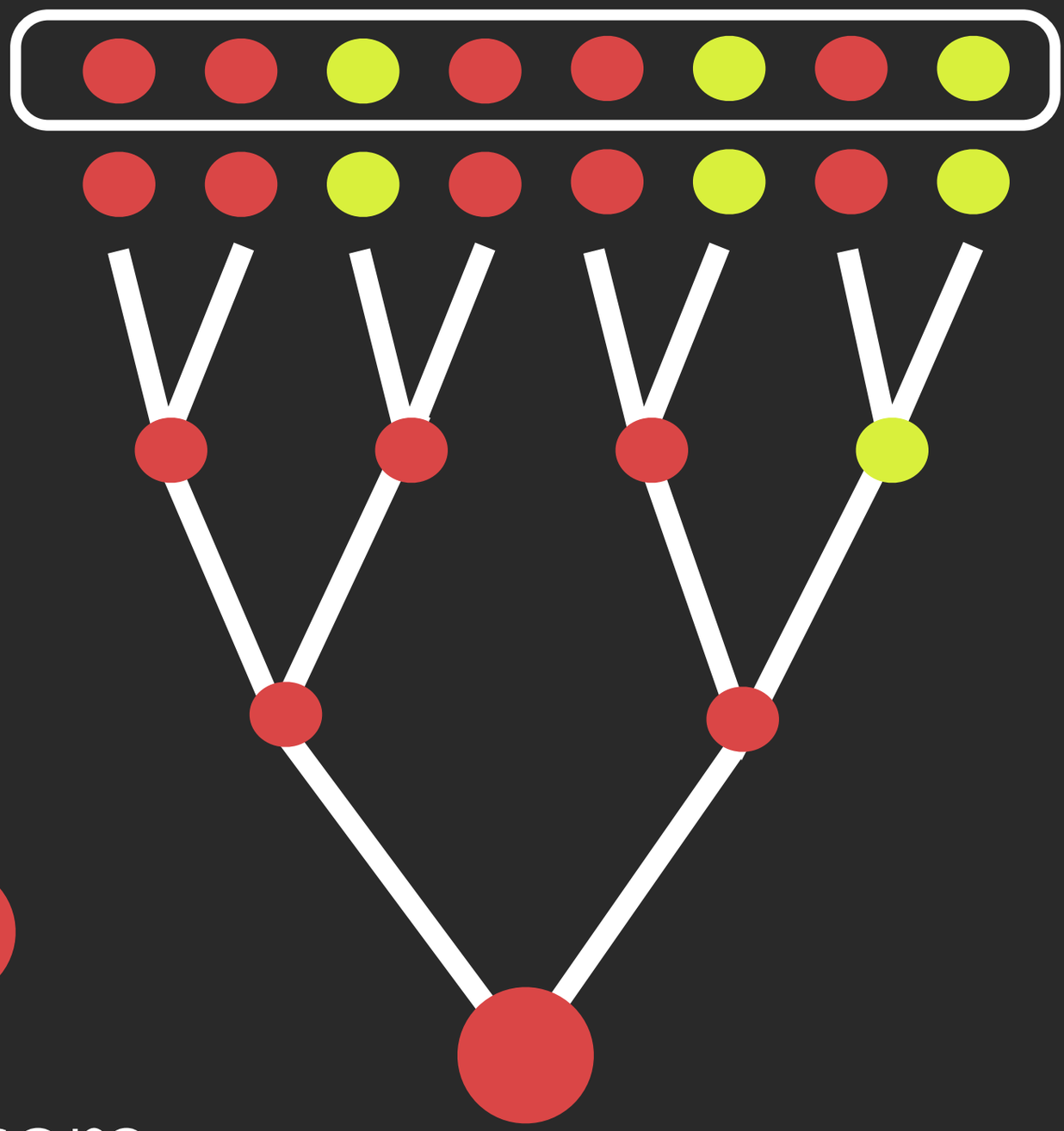


simulation two



actual data

simulated data



3

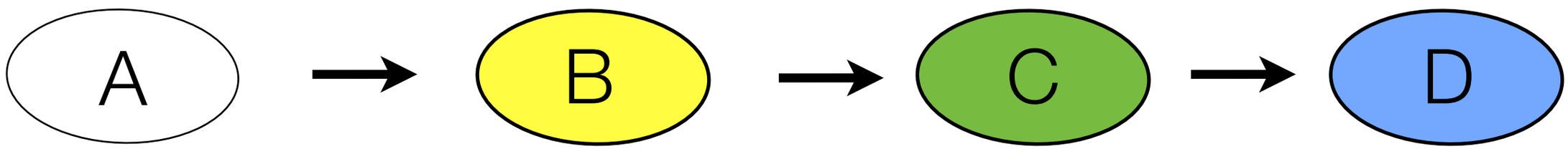
model likelihood score

simulation two

we combine KNOWN data & phylogenies
and INFER the best models & ancestral states

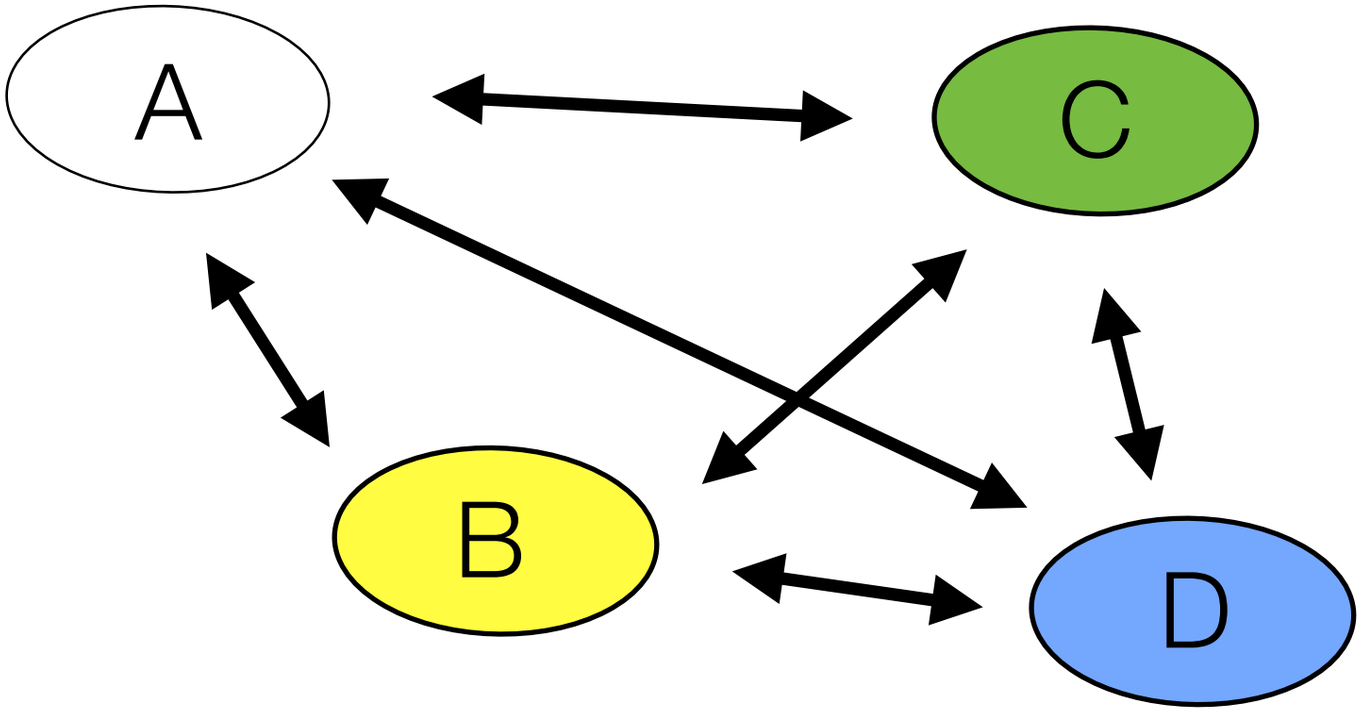
How do characters evolve?

- ORDERED CHANGE
  Sequential model



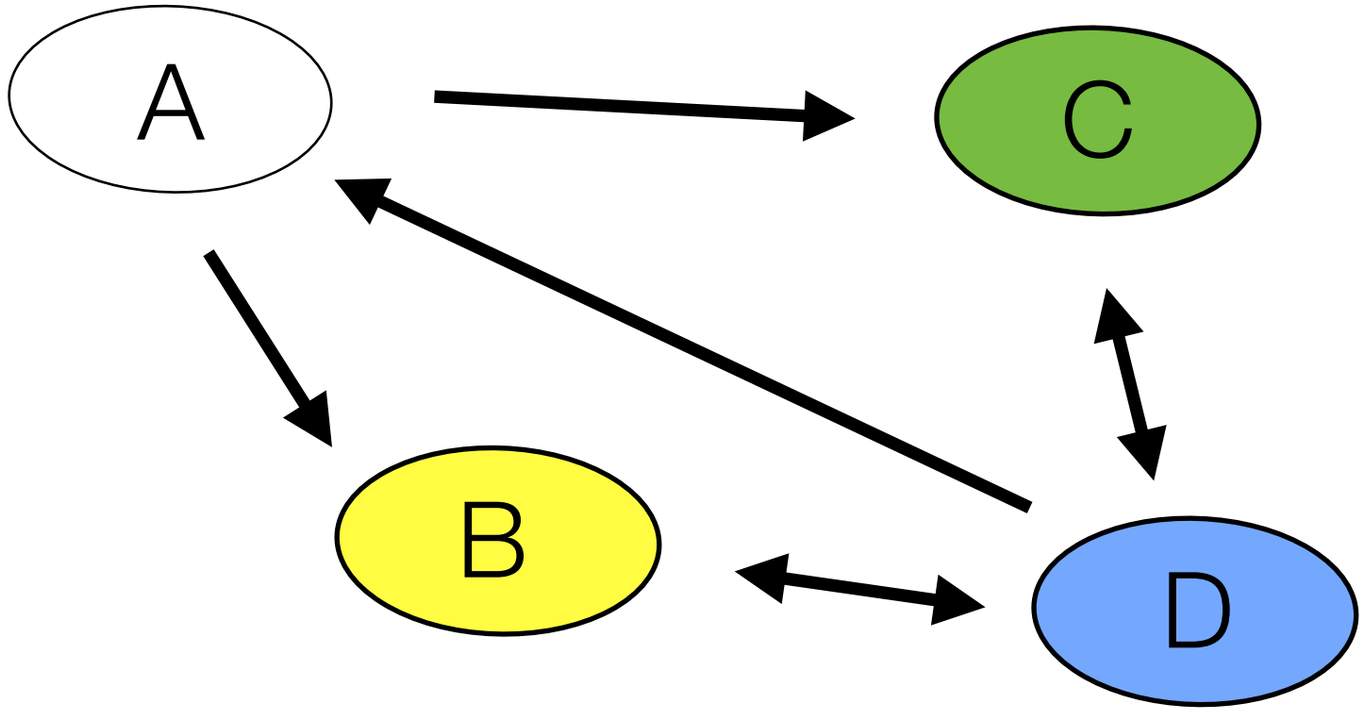
How do characters evolve?

- UNORDERED CHANGE
  all changes are possible



How do characters evolve?

- RESTRICTED CHANGE
  some changes are possible, and/or
  some changes are weighted



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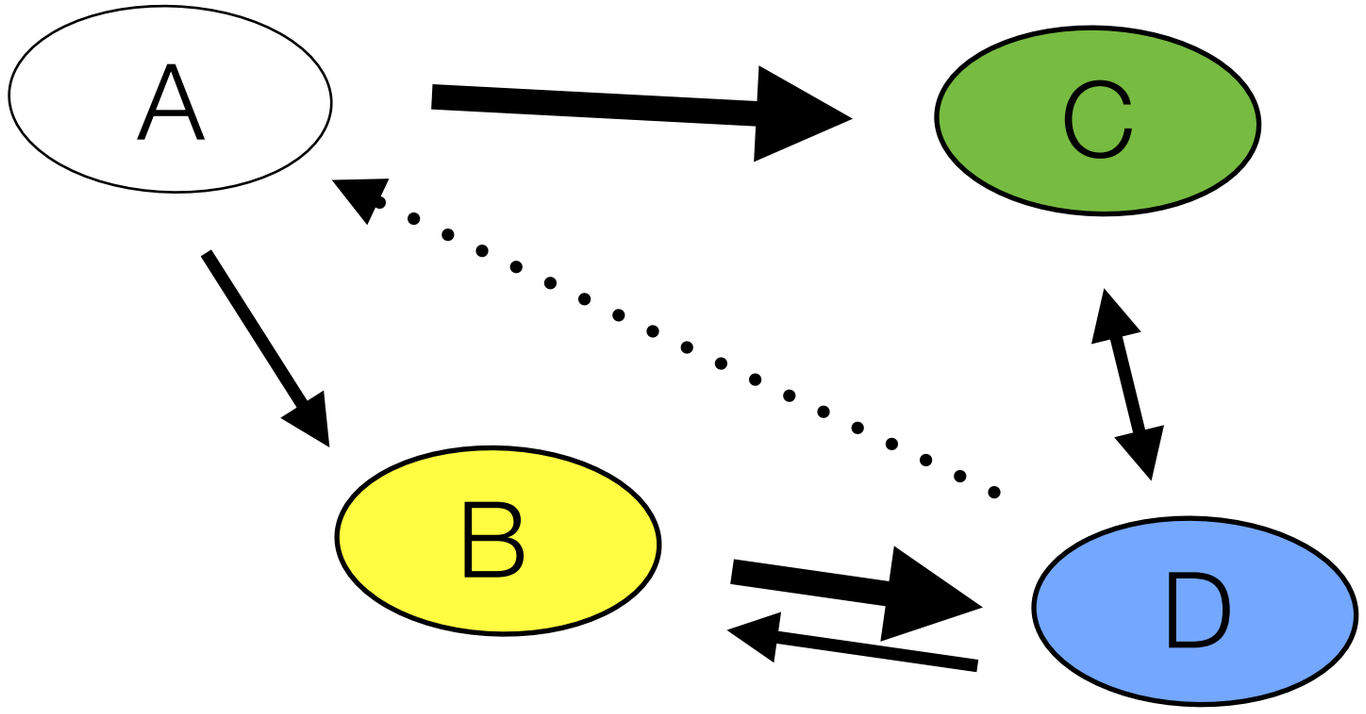


LAND TENURE

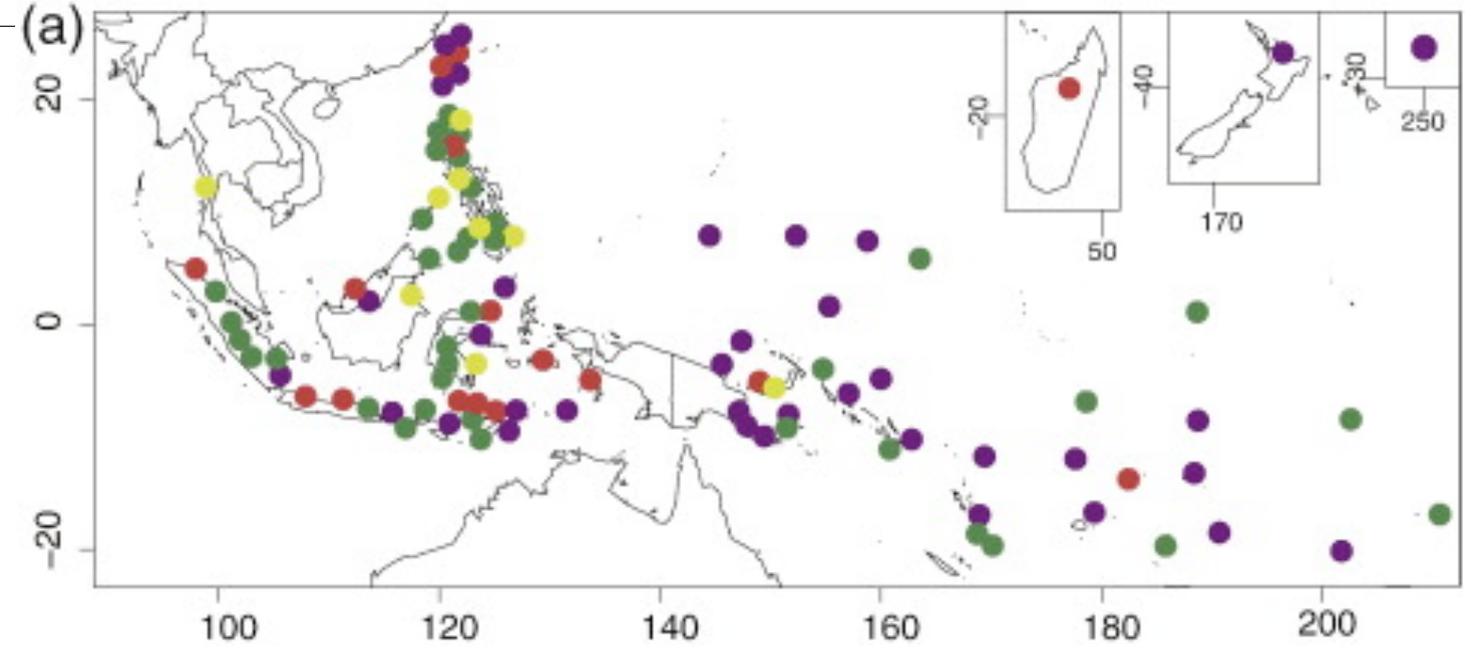
Are there generalised trajectories of cultural change?
If so, what is the pattern of land tenure evolution?

What can we infer about ancestral landownership in Austronesian societies?

Which norms have historical signal?

Geoff Kushnick @ ANU
Russell Gray @ MPI-SHH

(a)



Main form of land tenure
- no ownership
- group ownership
- kin-group ownership
- individual ownership

Nomadic (no ownership) — *Pastoral* (group held land) — *Agricultural* (patrilineal kin group ownership) — *Agricultural* (individual ownership)

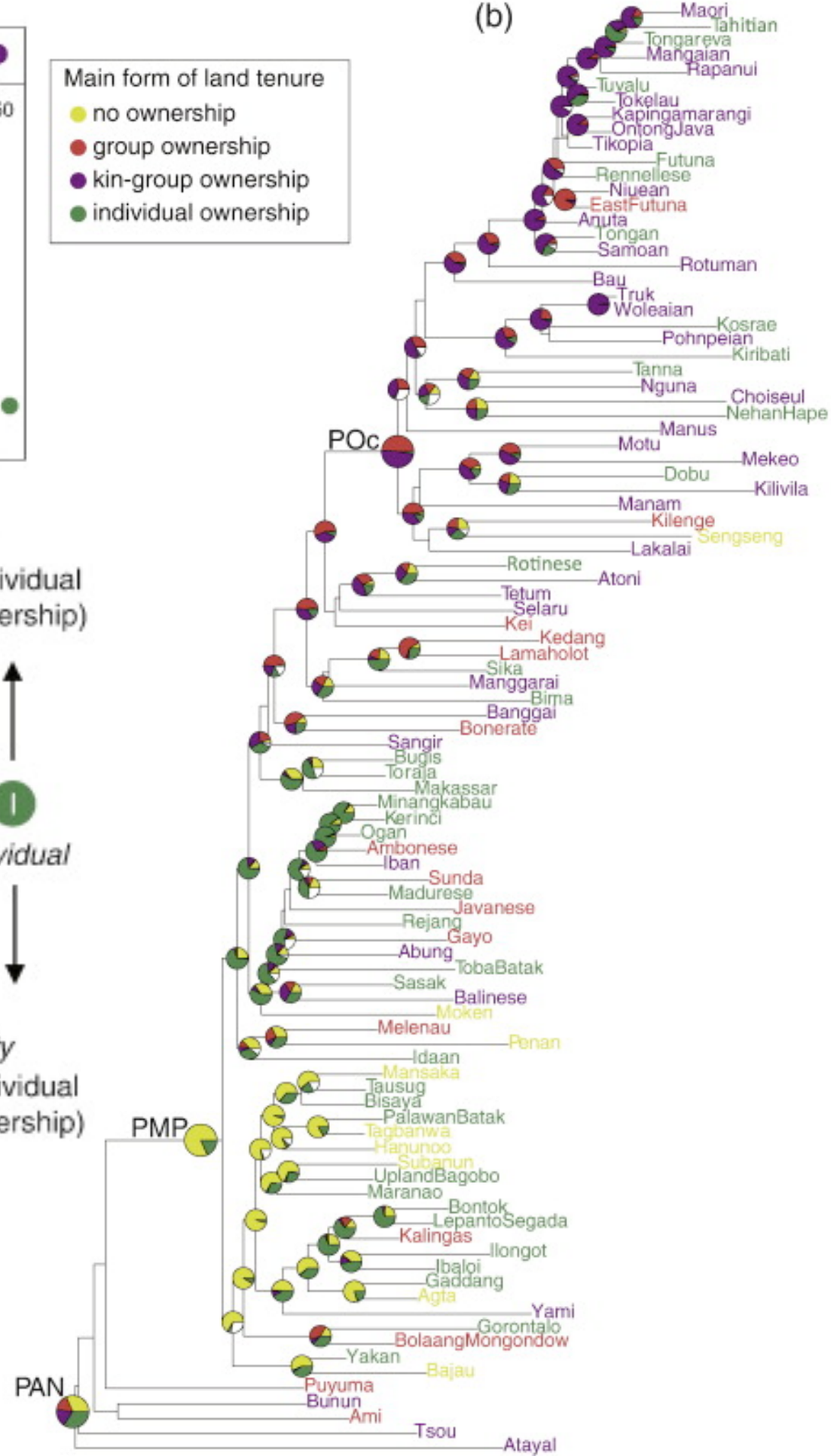
N — *None* → *Commons* (common property)

G — *Group* → *Reciprocal Access* (communal property) | *Territoriality* (local group ownership)

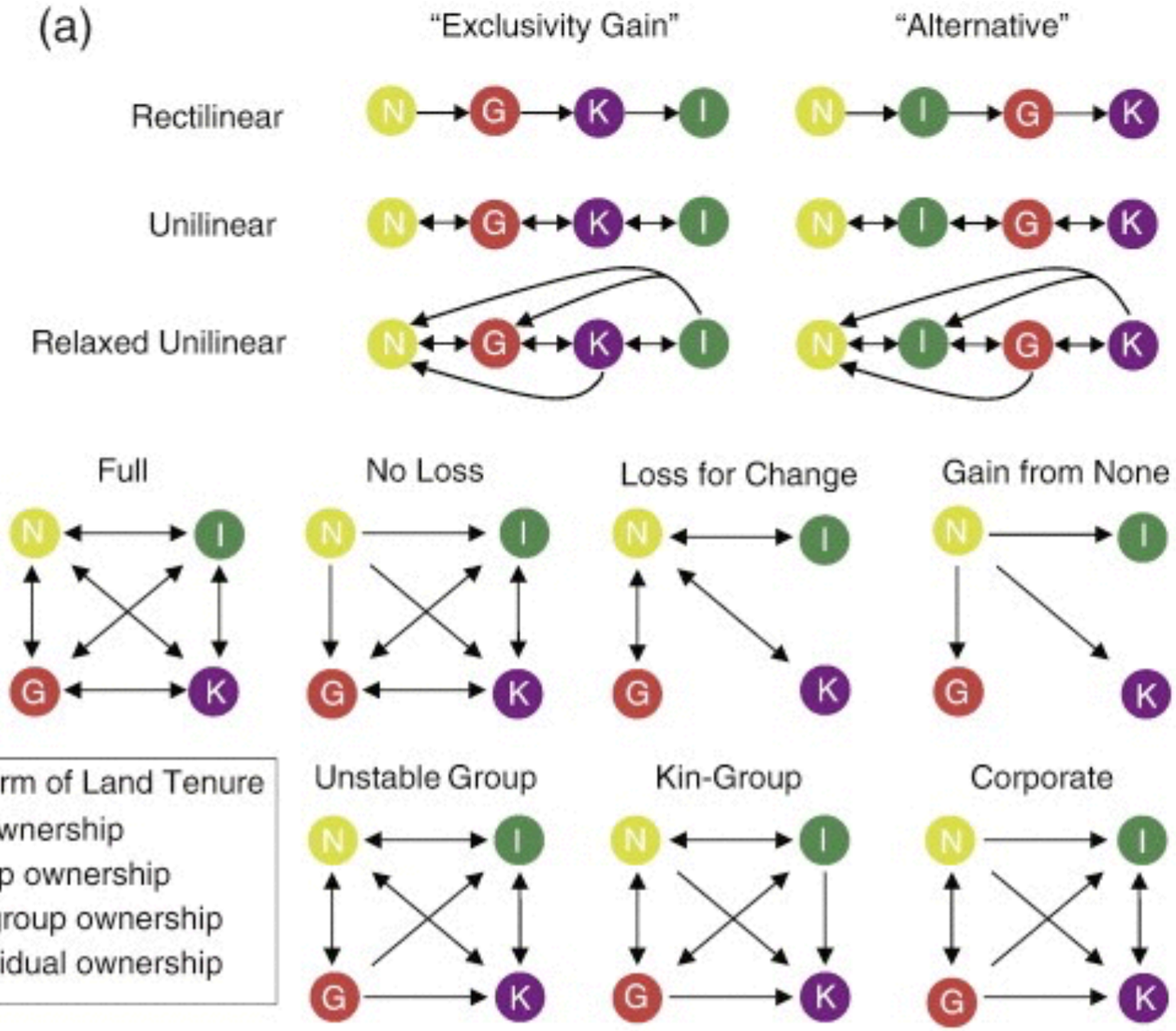
K — *Kin* → *Private Property* (kin group ownership)

I — *Individual* → *Private Property* (individual ownership)

(b)



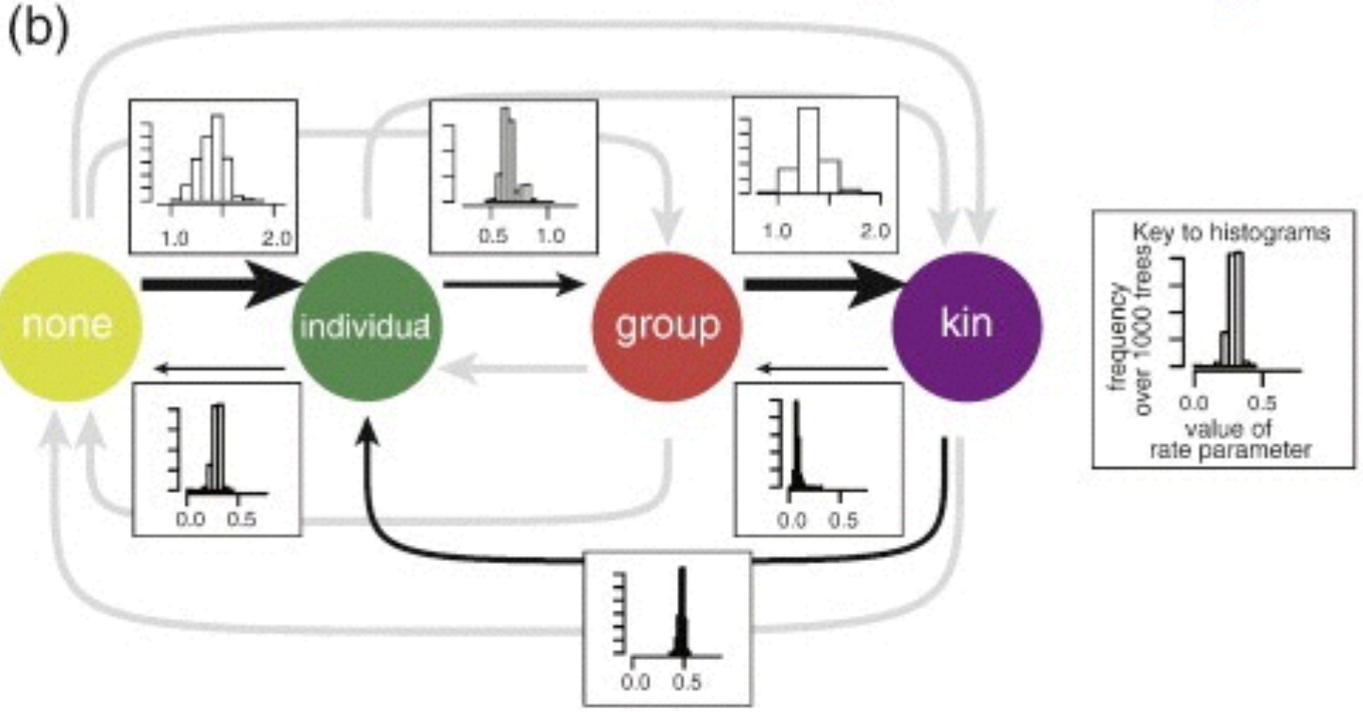
(a)

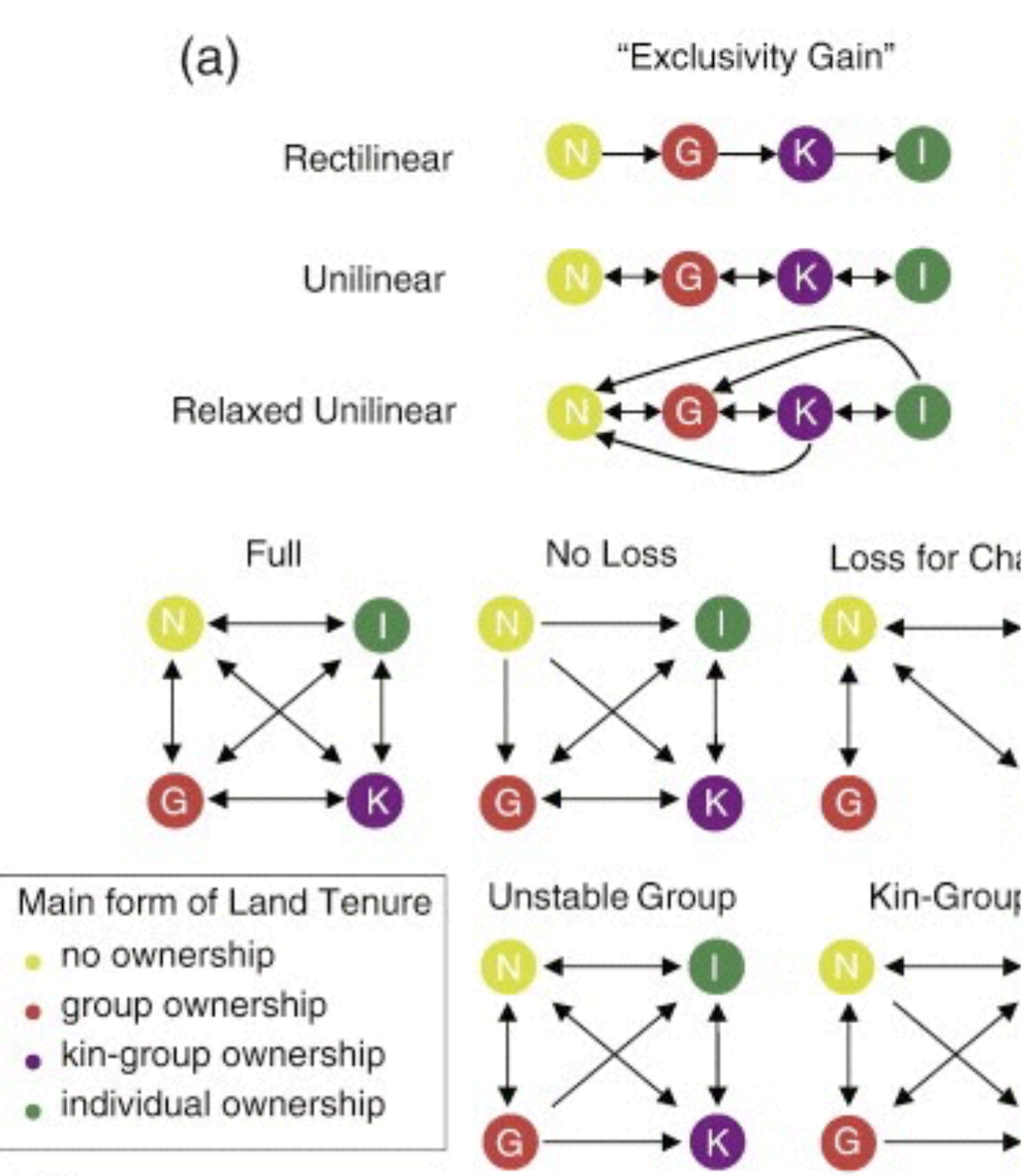


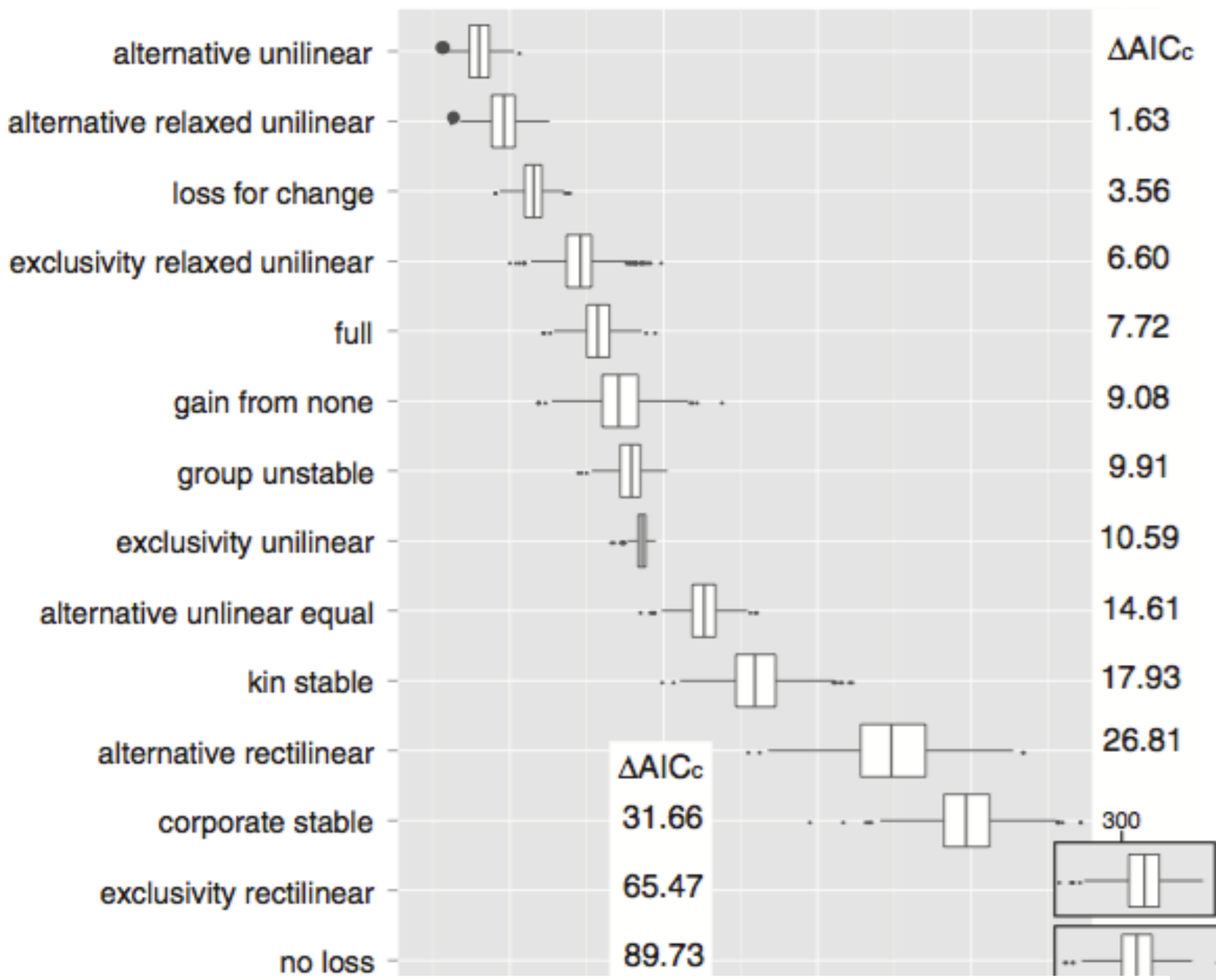
Main form of Land Tenure

- no ownership
- group ownership
- kin-group ownership
- individual ownership

(b)







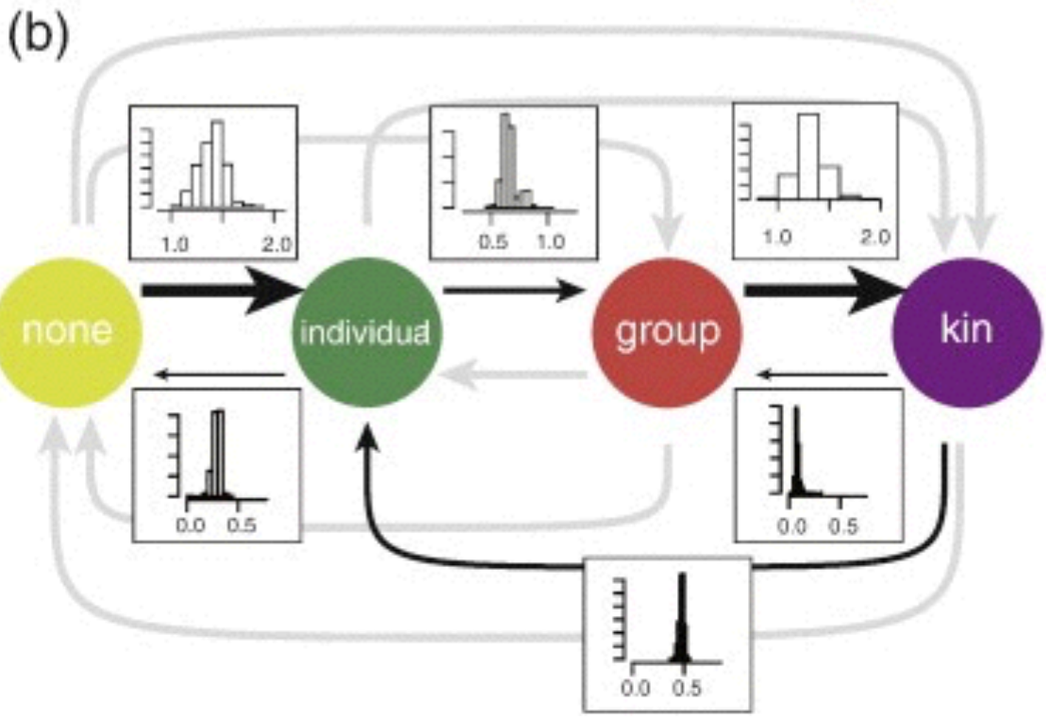


Table 1
Phylogenetic signal of each of the main type of land tenure norms (n = 97).

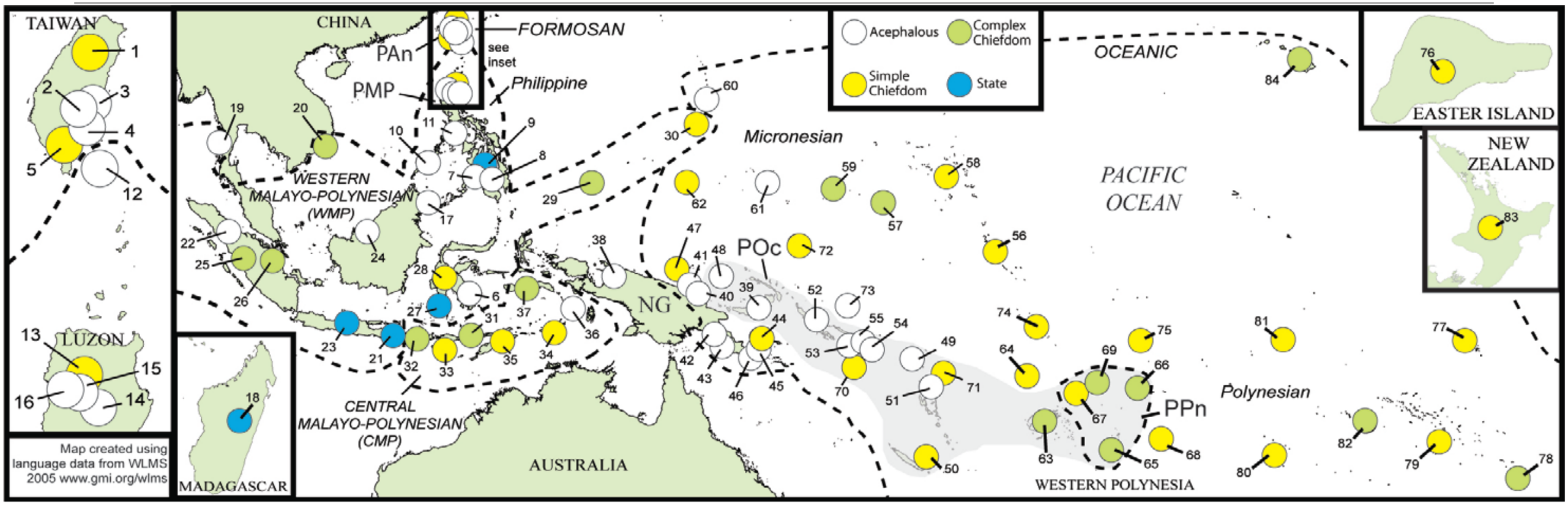
Land Tenure	D-Statistic[1]		Phylogenetic Signal?
	Median[2]	Range	
None	0.30	−0.09–0.64	Moderate
Individual	1.19***	0.98–1.34	Significant absence
Group	0.87*	0.62–1.09	Significant absence
Kin-Group	0.17***	−0.04–0.29	Significant and strong

[1] D and *p*-values estimated from all 1,000 trees in the posterior.
[2] * 95% $p < 0.05$; *** all $p < 0.005$.

Rise and fall of political complexity in island South-East Asia and the Pacific

Thomas E. Currie[1,2], Simon J. Greenhill[3,4], Russell D. Gray[3], Toshikazu Hasegawa[1] & Ruth Mace[2]

Currie et al. 2010 *Nature*



Type of society	n	description
Acephalous	35	Small independent local communities (i.e. villages), no official positions of political leadership
Simple Chiefdom	28	Official political leader (chief) ruling over a collection of villages
Complex Chiefdom	16	Two levels of political leadership beyond the local community (often other official positions e.g. high priest)
State	5	Three or more supra-local decision-making levels, many political and bureaucratic offices

Evolution of political complexity
What did they do?

- Data on political complexity coded as ONE trait with FOUR states

  Defined their hypotheses as models where traits could change between:

- Used Multistate in BayesTraits to infer the parameters of the most likely model of evolution (and ASE)

  Tested hypotheses over a posterior sample of 1000 trees

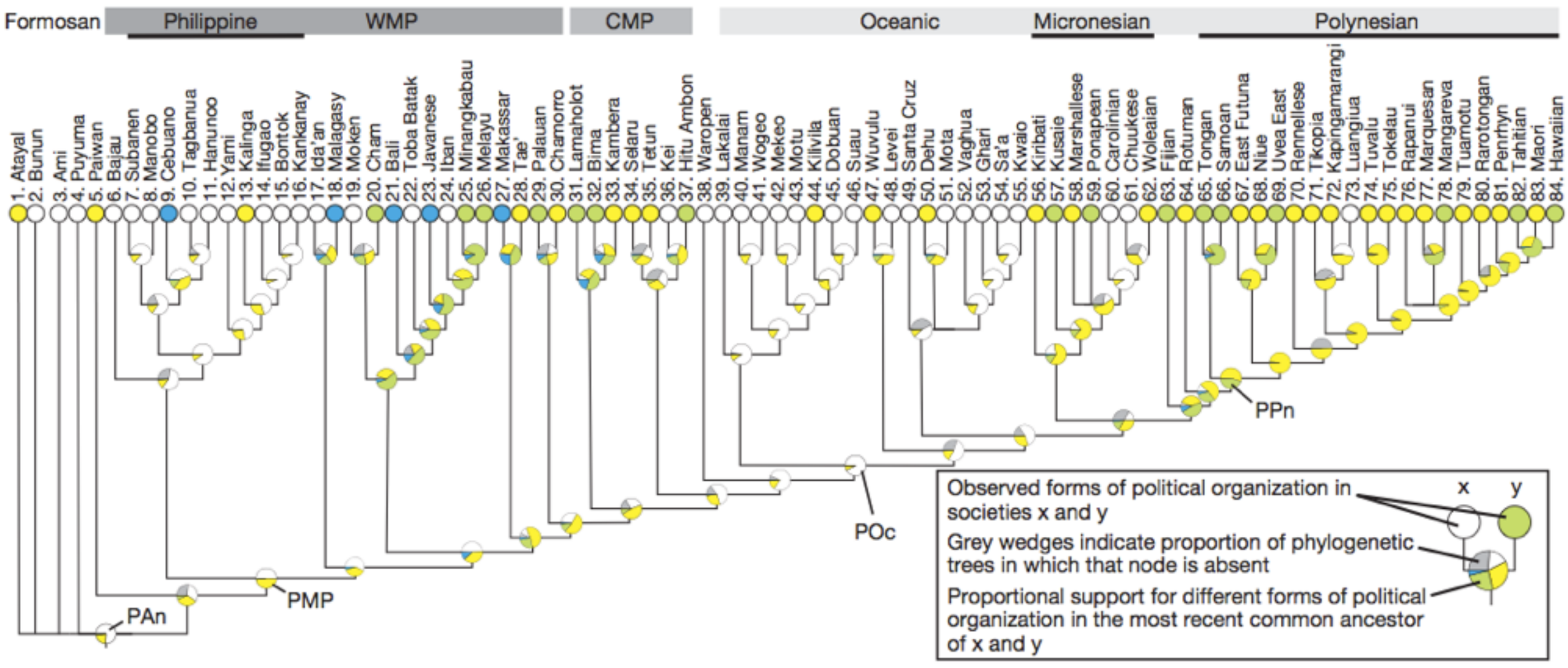
  Used reversible-jump MCMC procedure to help find the best model of evolution

- Compared sequential models to assess which was best supported

Currie *et al* 2010 *Nature*

Evolution of political complexity
Ancestral state estimates

Acephalous | **Simple Chiefdom** | **Complex Chiefdom** | **State**



Currie et al. 2010 *Nature*

Evolution of political complexity

Model testing

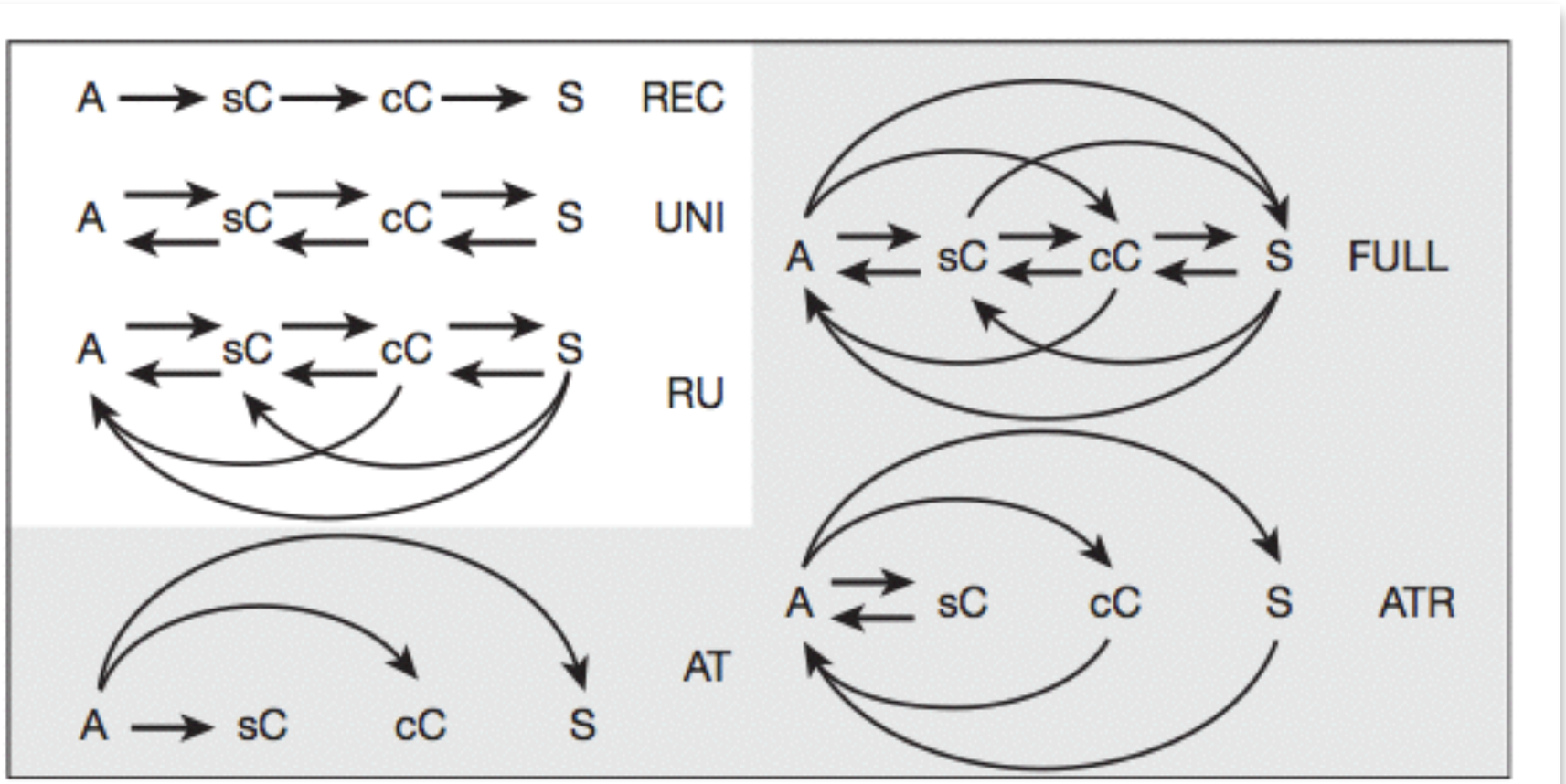
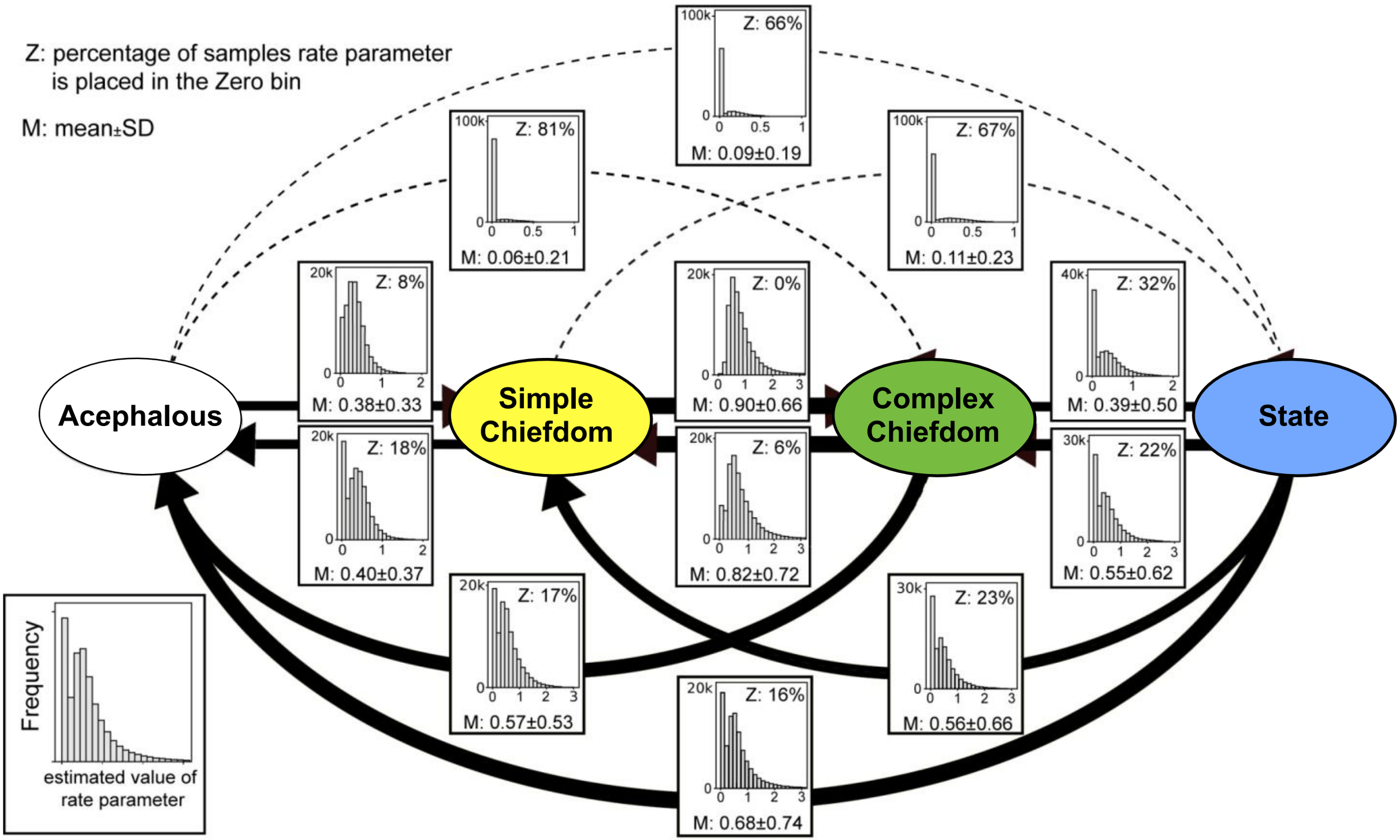


Figure 2 | Models of political evolution tested in this study. The three models on the white background (UNI, unilinear; RU, relaxed unilinear; REC, rectilinear) represent the idea that political evolution follows a sequence of incremental steps in the direction of increasing complexity, but differ as to whether and how decreases can occur. The three models on the grey background (AT, alternative trajectories; ATR, alternative trajectories (reversible); FULL) allow non-sequential increases in political complexity. Forms of political organization: A, acephalous society; sC, simple chiefdom; cC, complex chiefdom; S, state.

Currie et al. 2010 *Nature*

Currie et al. 2010 *Nature*



Posterior distribution of rate parameter

Currie et al. 2010 *Nature*

Evolution of political complexity
What did they conclude?

- A “unilinear” model of stepwise change was the best supported, but a “rectilinear” model was also well-supported.
  In these societies, political complexity only accrues stepwise, but then can “collapse” to less complex forms.

- “*This potential distinction between the patterns of change for increasing and decreasing complexity may be due to it being easier to break up forms of political organization than to develop practices and institutions that enable units to be joined together in a stable manner*”

Currie et al. 2010 *Nature*

Your place or mine? A phylogenetic comparative analysis of marital residence in Indo-European and Austronesian societies

Laura Fortunato[1,2,*,†] and Fiona Jordan[1,2,‡]

Fortunato & Jordan 2010 *Phil Trans Roy Soc London*

The evolution of marital residence

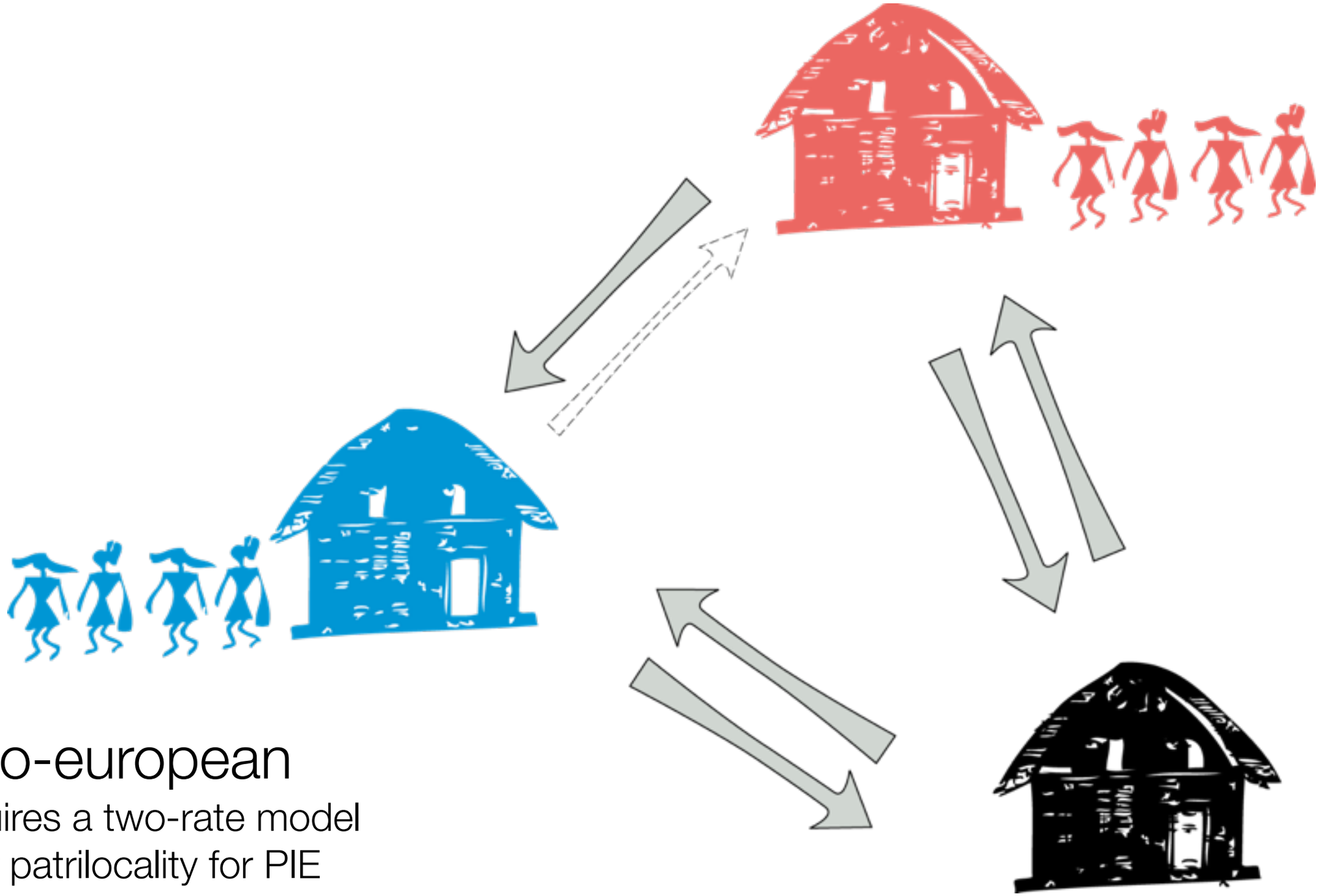
What did we do?

- Used independently-derived lexical phylogenies of AN and IE
  Matched ethnographic descriptions to linguistic groups

- Data on residence was coded as ONE TRAIT with THREE STATES
  Matrilocal, patrilocal, neolocal
  We allowed for mixed strategies e.g. MP = ambilocal and main/alternative forms

- Used Multistate in BayesTraits to infer ancestral states and the parameters of the most likely model of evolution
  Tested our hypotheses over a posterior sample of 1000 trees
  Used reversible-jump MCMC procedure to help find the best model of evolution
  “Fossilised” early nodes to each possible state to test robustness

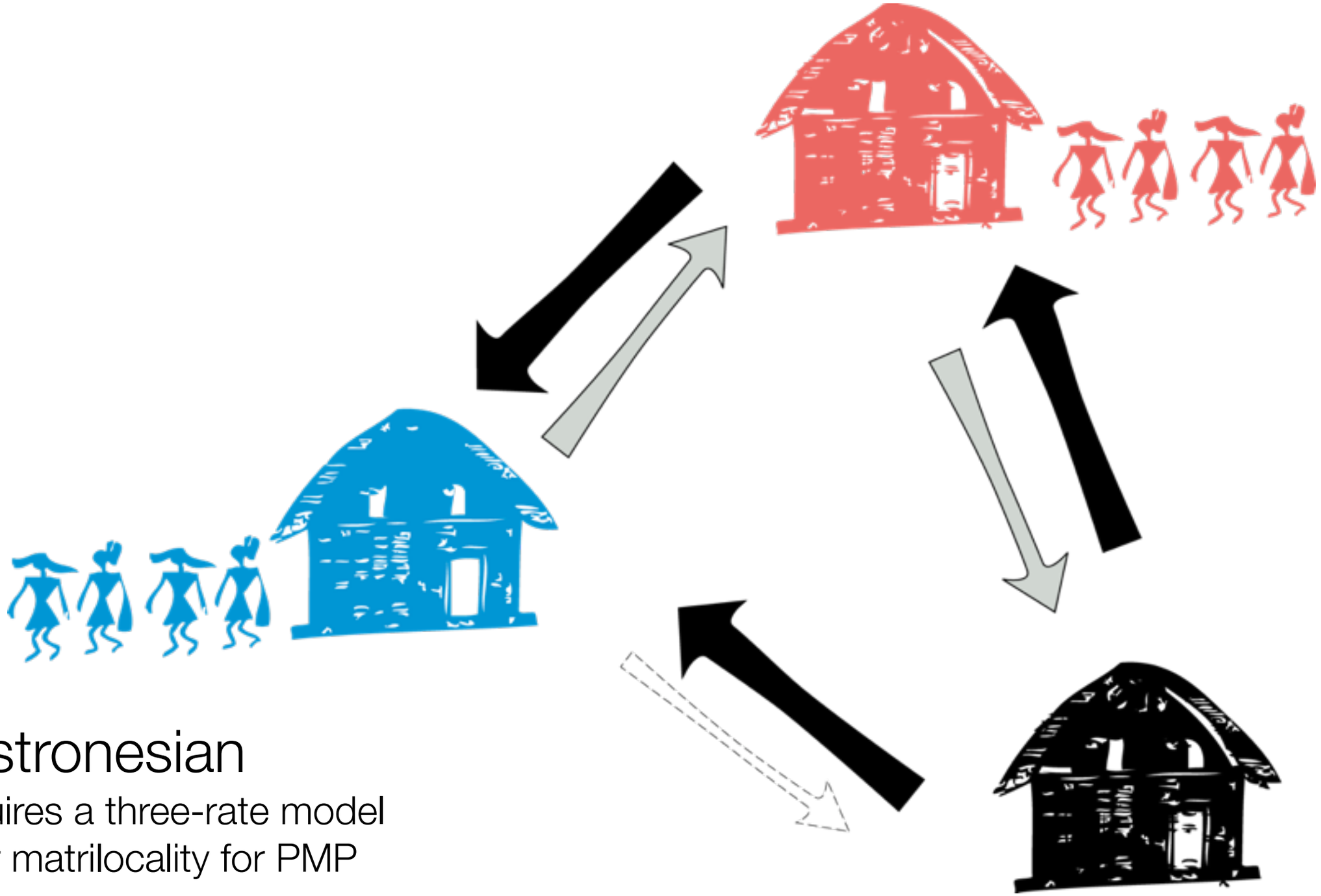
Fortunato & Jordan 2011 *Phil Trans Roy Soc*



indo-european

requires a two-rate model

infer patrilocality for PIE



austronesian

requires a three-rate model

infer matrilocality for PMP

The evolution of marital residence
What did we conclude?

- Commonalities in process:
  Unstable matrilocality
  Rare loss of patrilocality once gained

- Differences in pattern and process:
  Require different number of rates of trait change (IE = 2, AN = 3)
  Different starting points

- Coding procedure can affect robustness
  For AN, including neolocality and considering prevailing/alternative forms means
  that PAN is less securely inferred to be matrilocal (though PMP still robust).

- *"Asking the same questions in different ethnographic regions heralds a useful*

Fortunato & Jordan 2011 *Phil Trans Roy Soc*

Correlated change and coevolution

Correlated change and coevolution

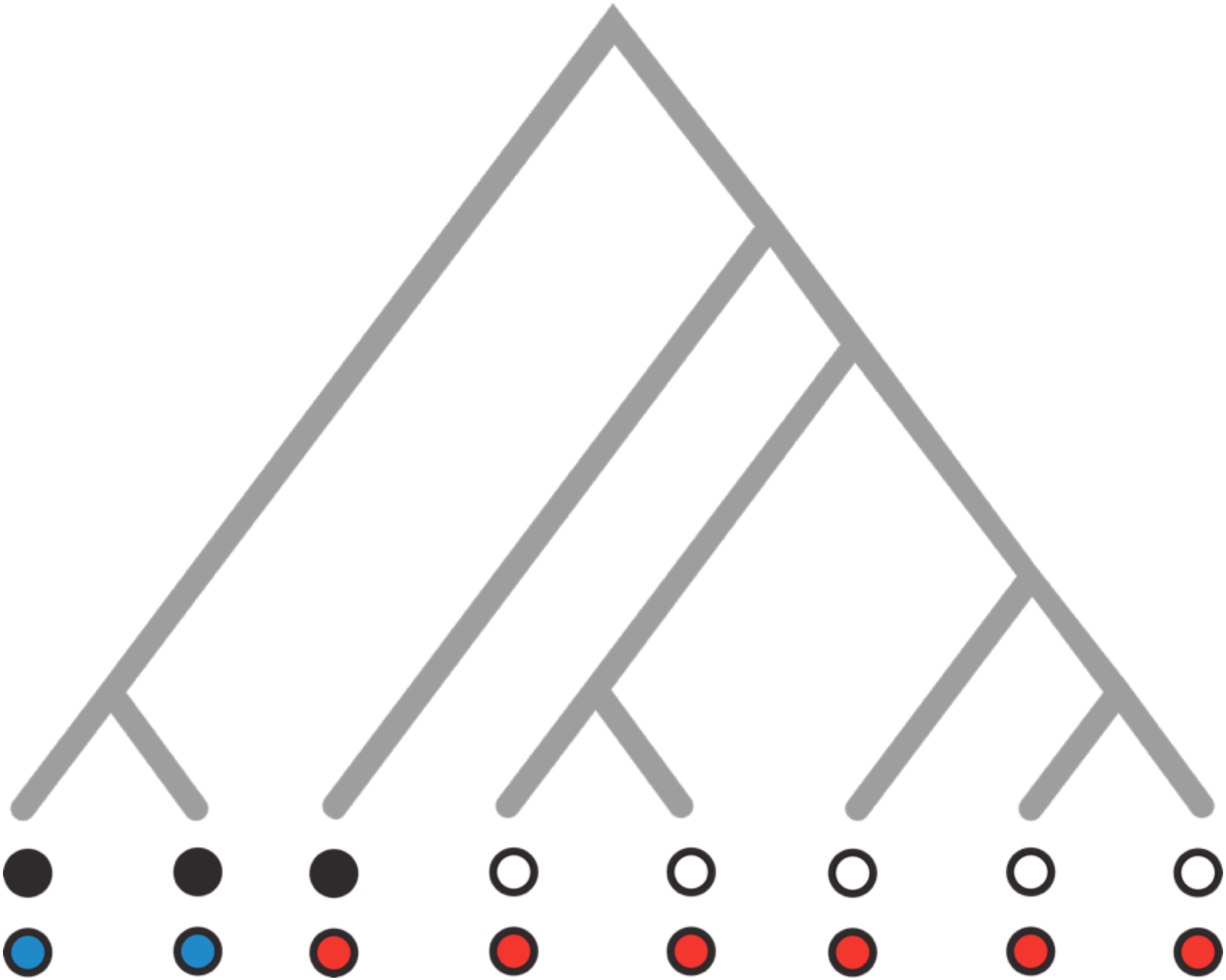
- Why are evolving traits correlated?

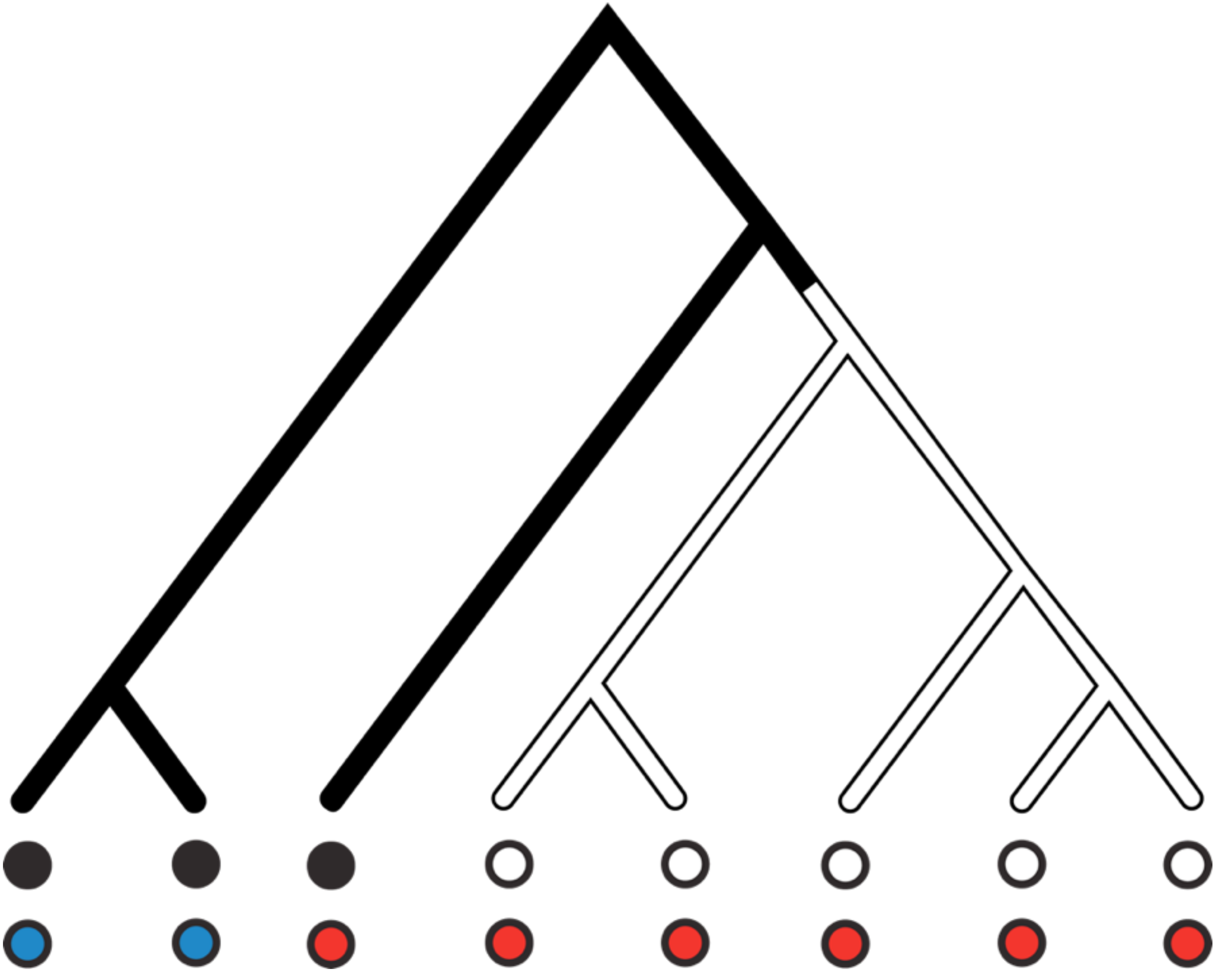
    1. The "correlation" imposed by the phylogeny (Galton's Problem)
    2. Repeated instances of changing together = *correlated change*
        Could be due to a third variable
        Or the characters being part of a suite of dependent characters
    3. Repeated instances of changing together
        that is due to one character influencing another = *coevolution*

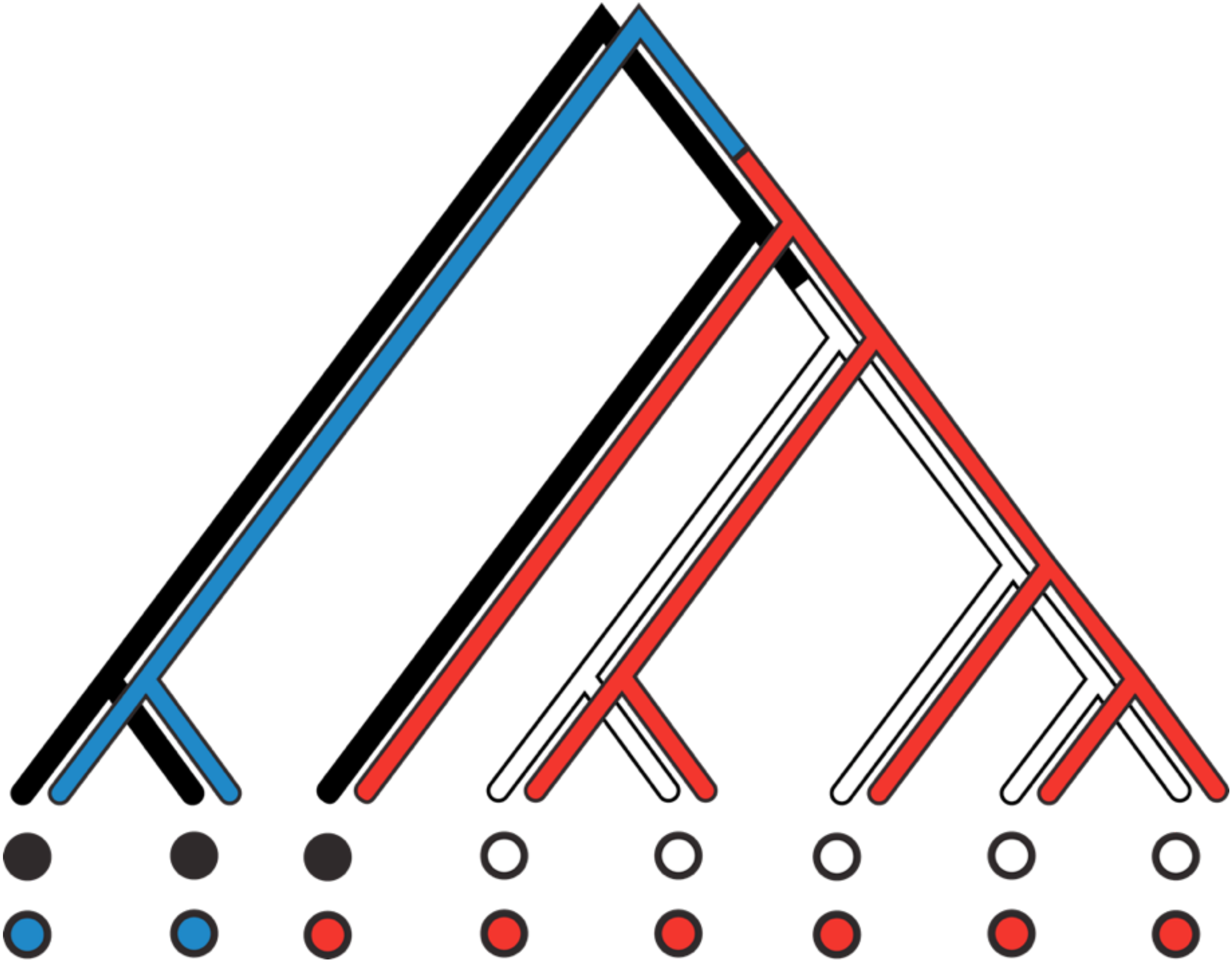
- Comparative methods originally proposed as a way to assess the cross-species evidence for adaptation, along with:
    - experimental manipulations
    - observational studies
    - optimality modelling

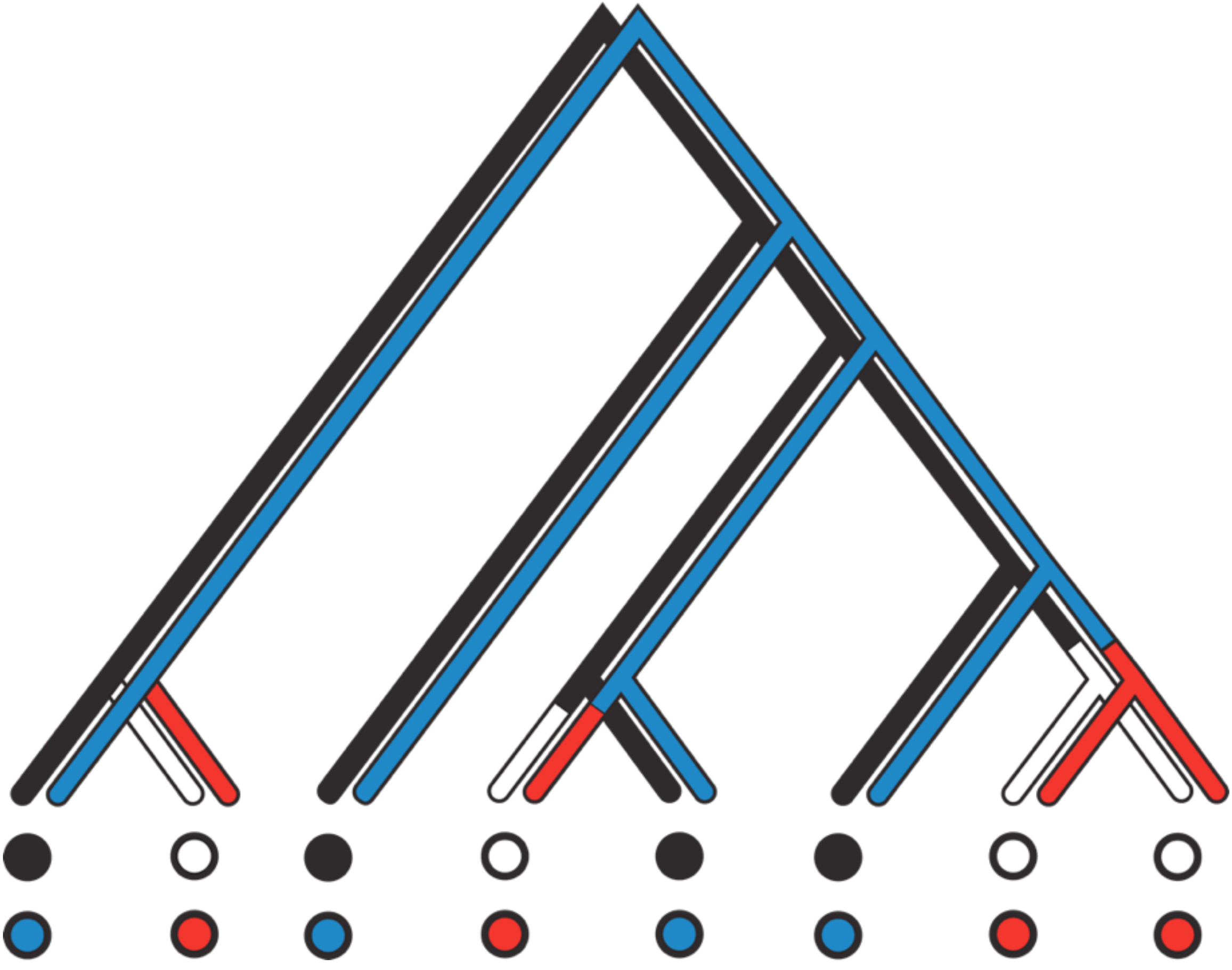
Krebs & Davies 1992

a b c d e f g h









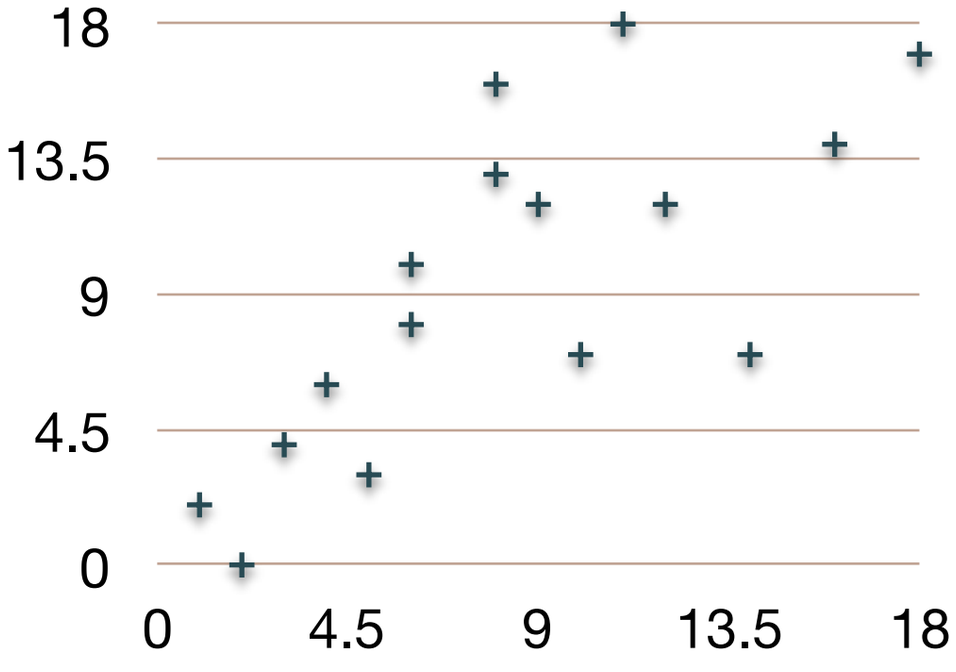
Correlated change between discrete characters

Standard correlation/regressions are for continuous characters

Assess the degree to which a unit of change in X predicts a unit of change in Y.

Discrete characters have traditionally been tested for correlation using contingency tables and chi-square tests

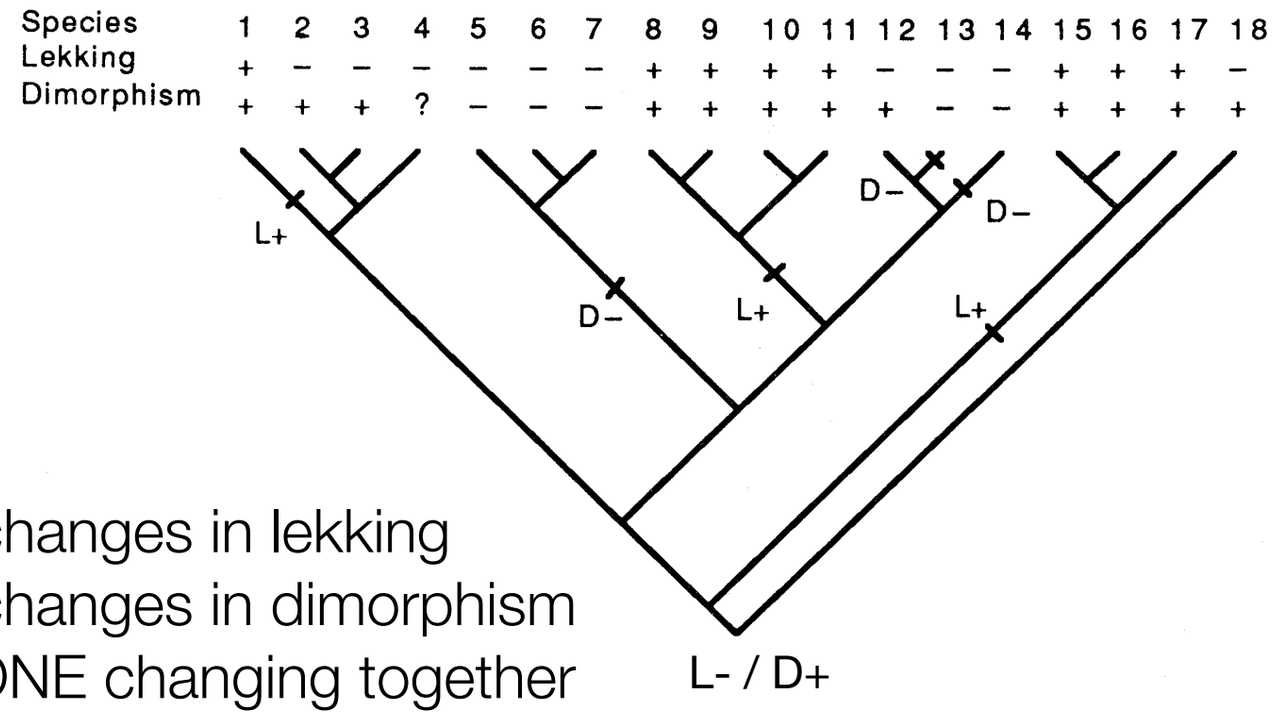
BUT Galton's Problem!



	post	pre
OV	15	4
VO	2	26

Co-occurences of evolutionary events not co-occurences of traits

- Ridley's method (1983)
- Concentrated changes (Maddison 1990)
- Pagel's method (1994)



3 changes in lekking
3 changes in dimorphism
NONE changing together

L- / D+

Table 4.4 Lekking and sexual dimorphism in size and plumage in birds. Each data point represents a single species. The associations between lekking and size and plumage dimorphism are both significant at $P<0.001$ in this comparison with species counted as independent points. (After Höglund 1989).

Mating system	Sexual size dimorphism		Plumage dimorphism	
	Present	Absent	Present	Absent
Lekking	69	18	55	33
Non-lekking	13	13	8	18

Ord & Martins 2010 / Nunn 2011

Discrete
A model-based method for correlated change

- Allows for tests of directionality when used in conjunction with ancestral state inference

- Takes TWO binary-coded traits that have TWO states each

	Trait1	Trait2
L1	0	0
L2	1	1
L3	1	0
L4	0	1

- We infer the Lh of two models

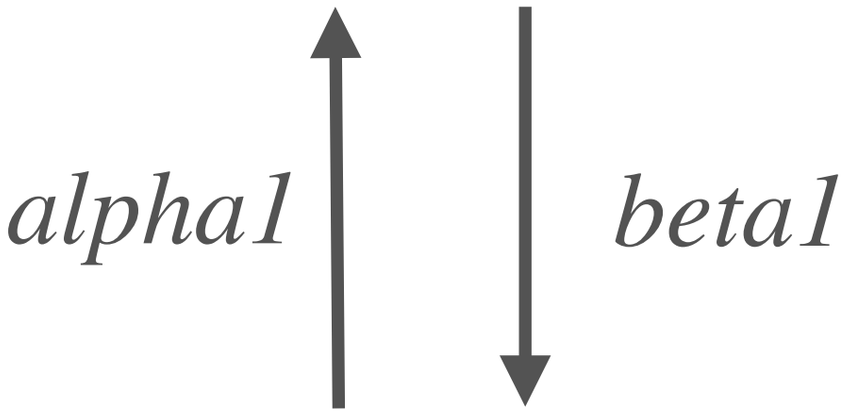
INDEPENDENT:

the traits change their state independent of the other trait and states
i.e. changes in trait A are not affected by changes in trait B

DEPENDENT:

Pagel 1994 / Pagel & Meade 2004

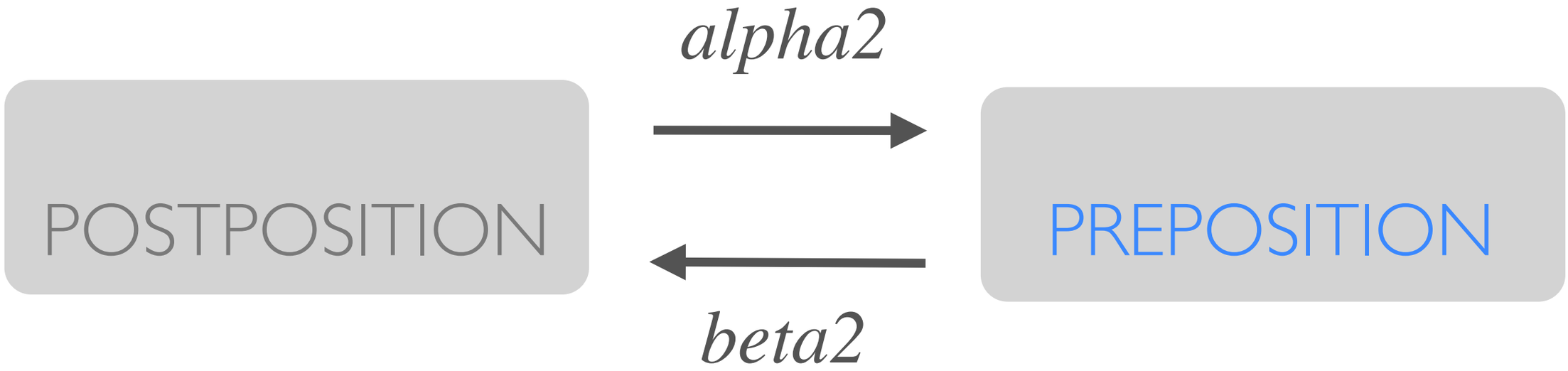
OV



VO

	Trait1	Trait2
L1	0	0
L2	1	1
L3	1	0
L4	0	1

independent model



	Trait1	Trait2
L1	0	0
L2	1	1
L3	1	0
L4	0	1

independent model

OV
POSTPOSITION

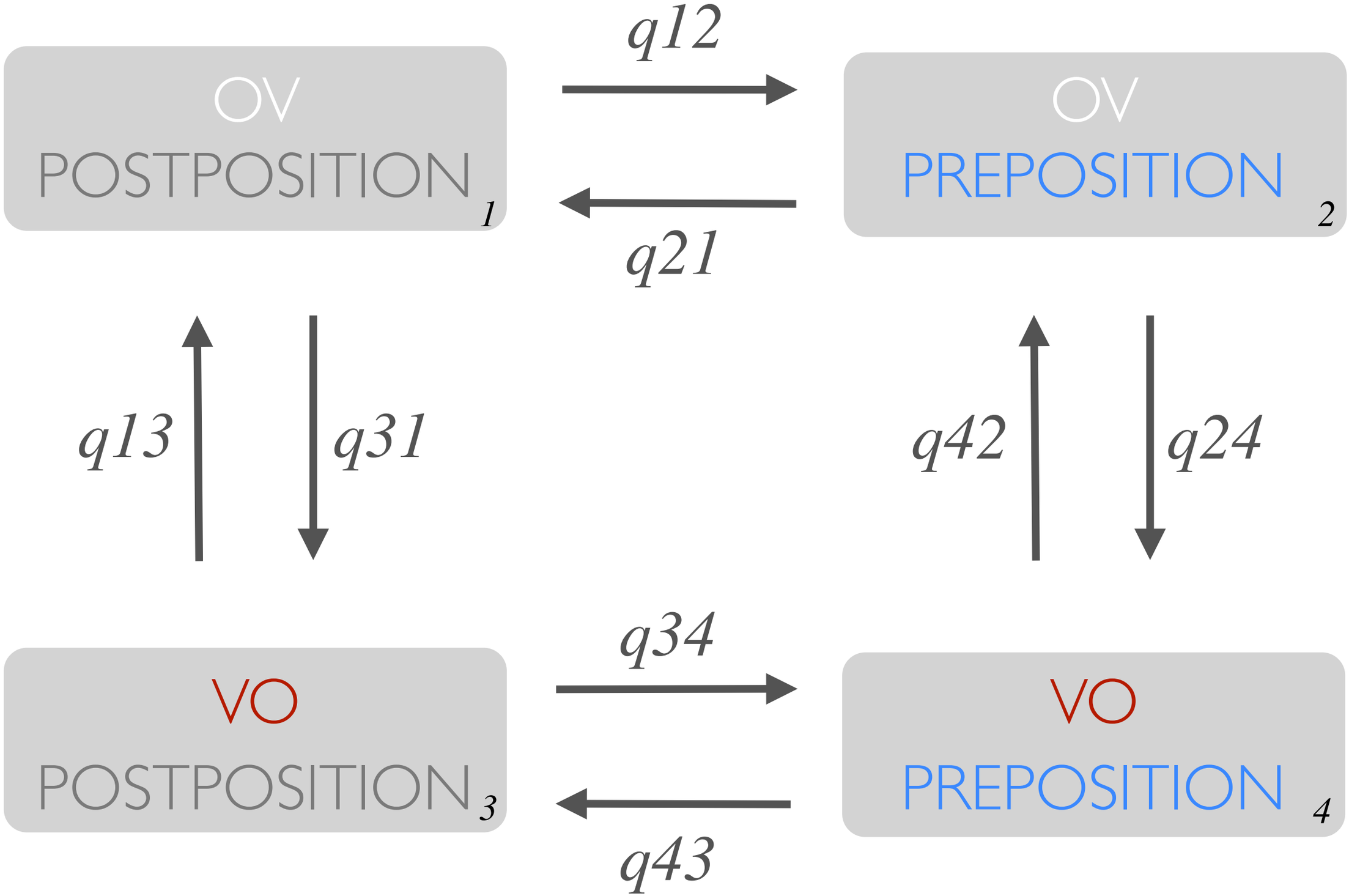
OV
PREPOSITION

	post	pre
OV	15	4
VO	2	26

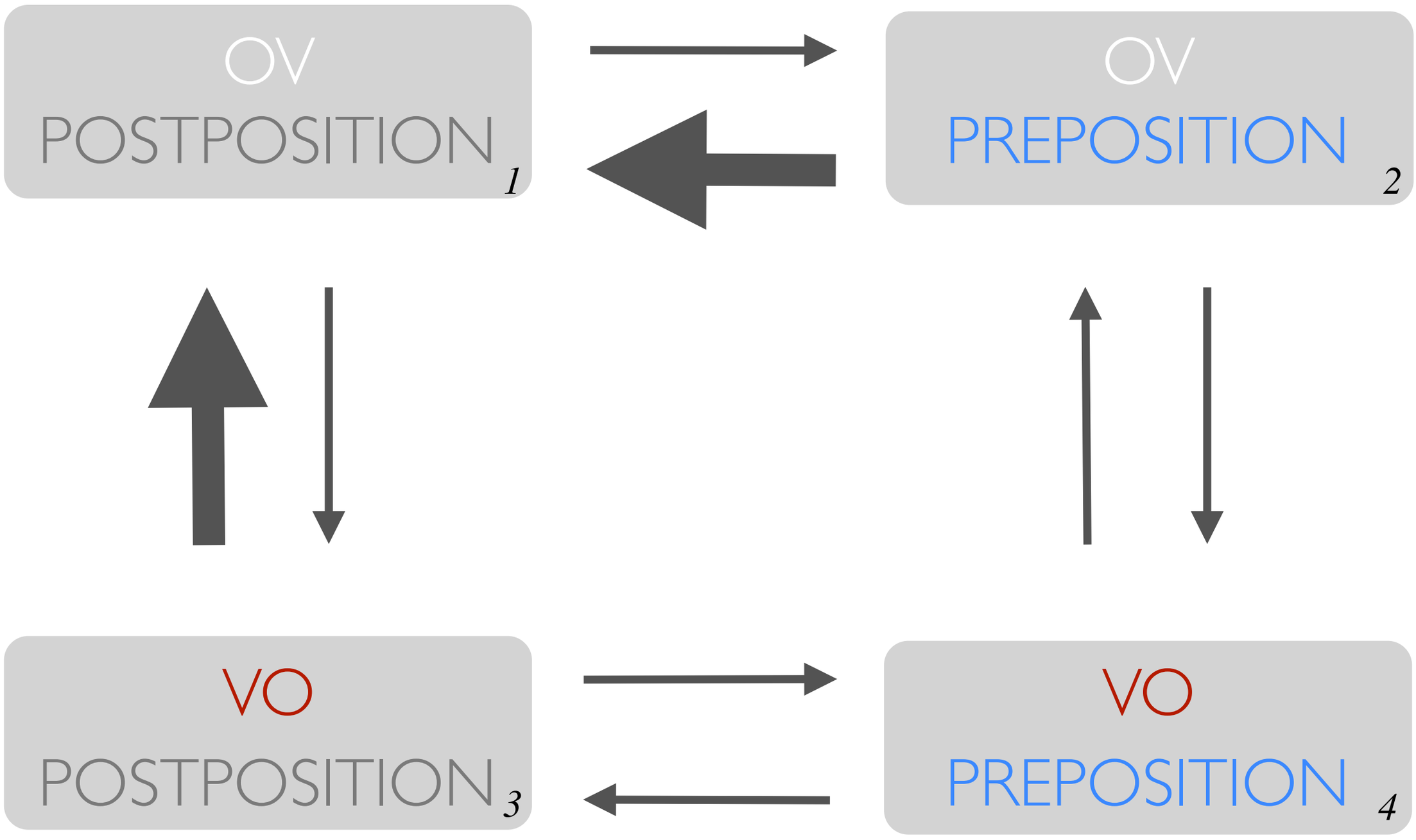
VO
POSTPOSITION

VO
PREPOSITION

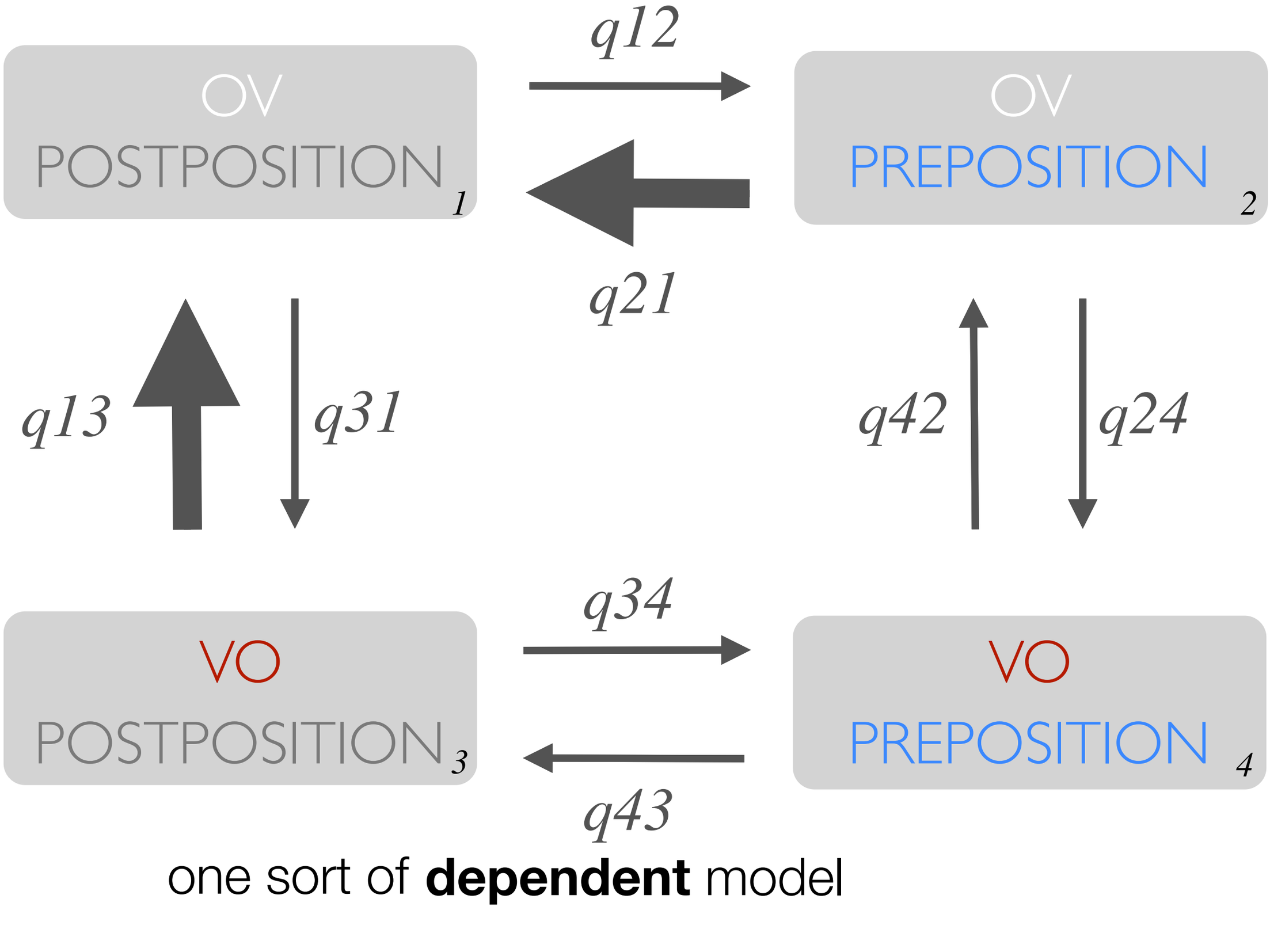
dependent model



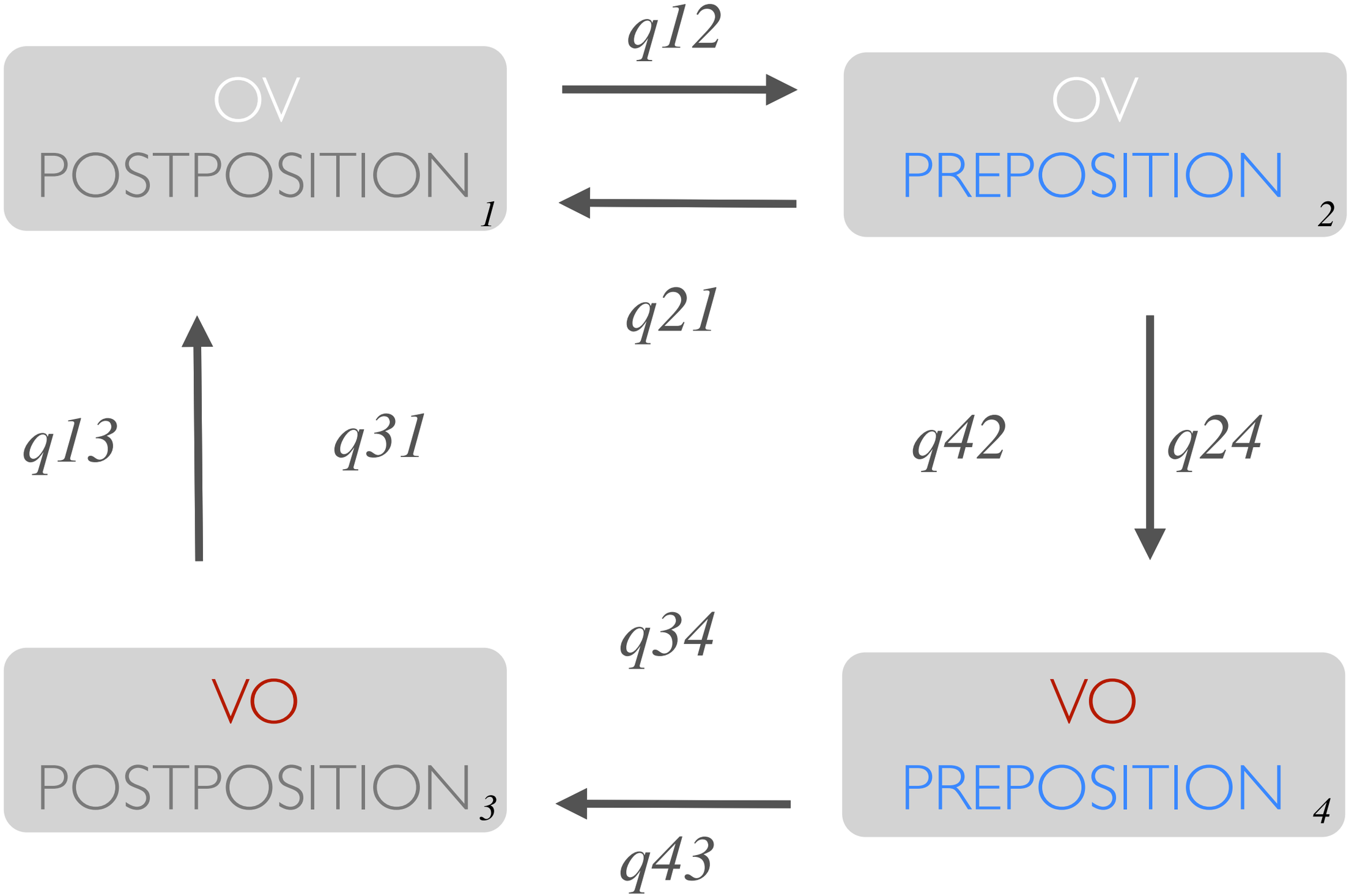
(in)dependent model



one sort of **dependent** model



one sort of **dependent** model



another sort of **dependent** model

Discrete in a Bayesian MCMC framework

- Bayesian approach allows us to incorporate uncertainty:

  Phylogenetic uncertainty: by using a posterior distribution of trees

  Character uncertainty: by incorporating probabilistic models of evolution

  Model uncertainty: gives us distributions of the rate parameters

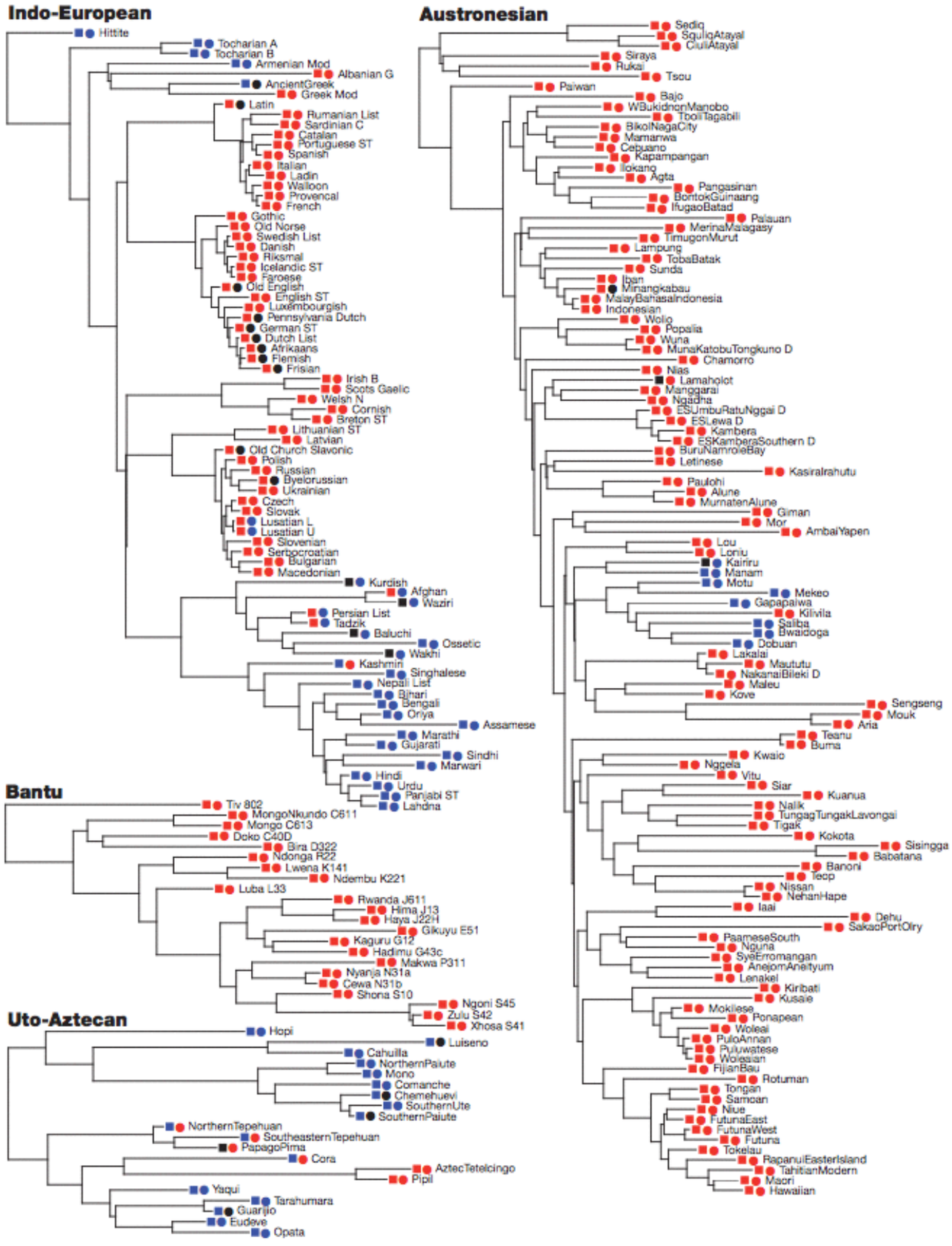
- **PROCEDURE**: Run both dependent and independent models

  If dependent model has higher likelihood, then prefer over independent.

  - Examine dynamics of change in dependent model, incorporating ancestral state estimates if known.
  - Compare dynamics of models across lineages/families.
  - Test the robustness of the model with fossilisation or model-specification.
  - Decide to what extent uncertainty impacts your confidence in the inferences.

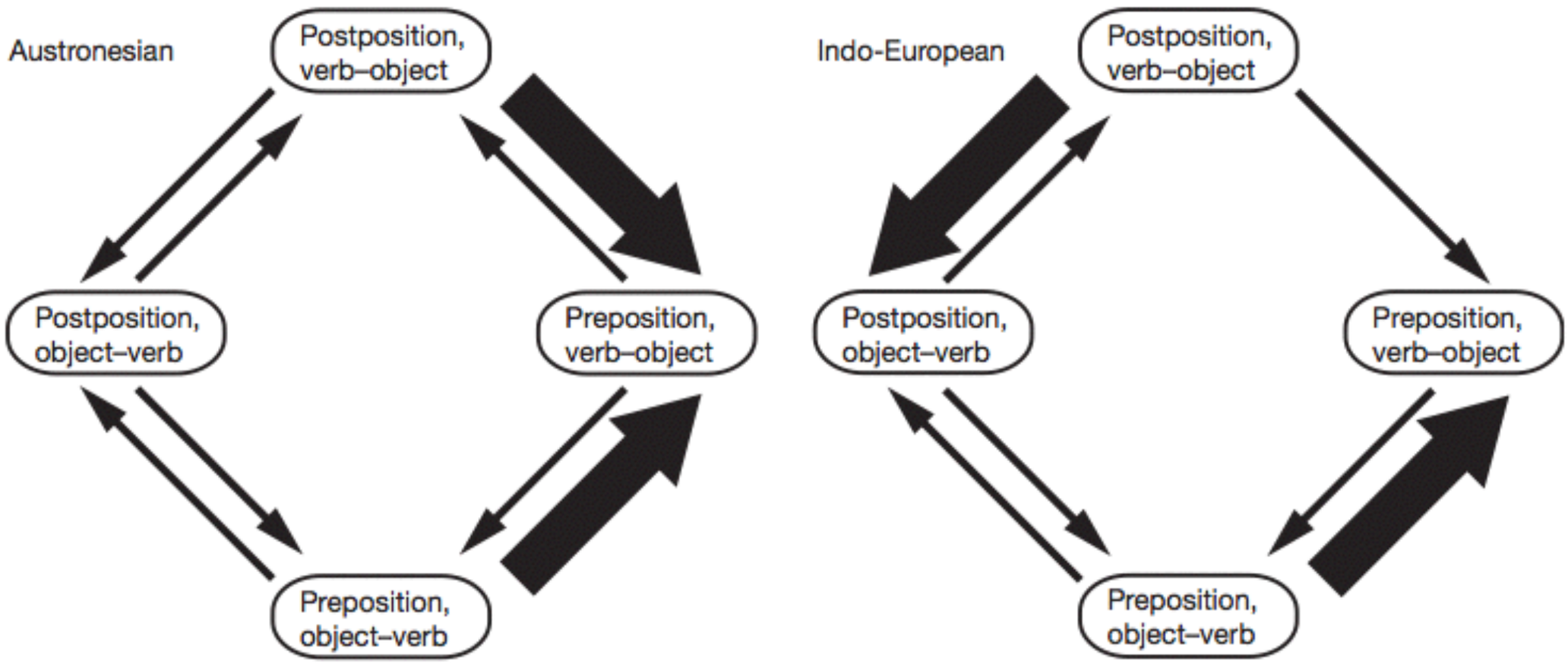
Word-order across language families

postposition
preposition
object-verb
verb-object



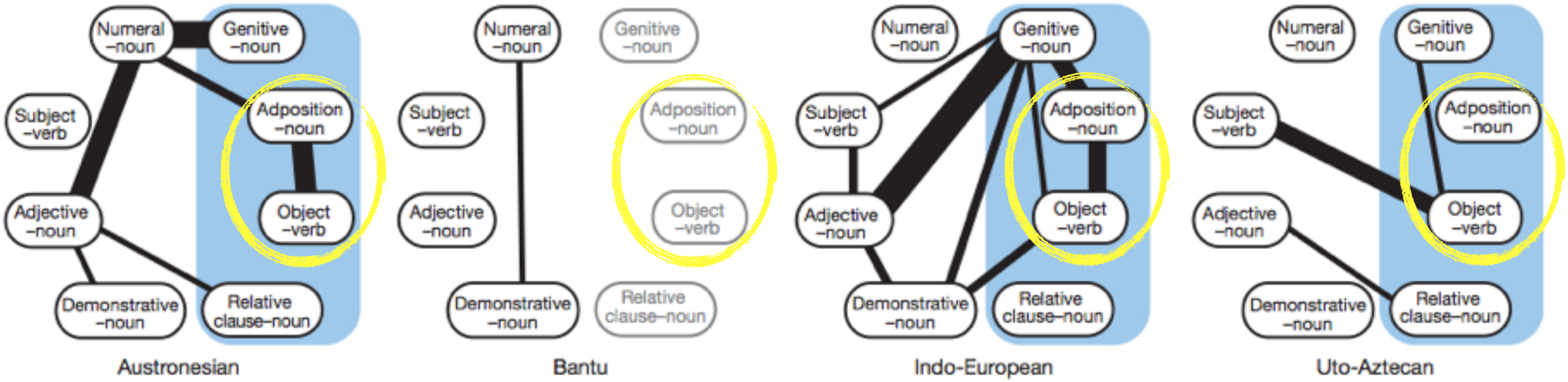
Dunn *et al* 2011 *Nature*

Word-order
across language families



Dunn *et al* 2011 *Nature*

Word-order
across language families



Evolved structure of language shows lineage-specific trends in word-order universals

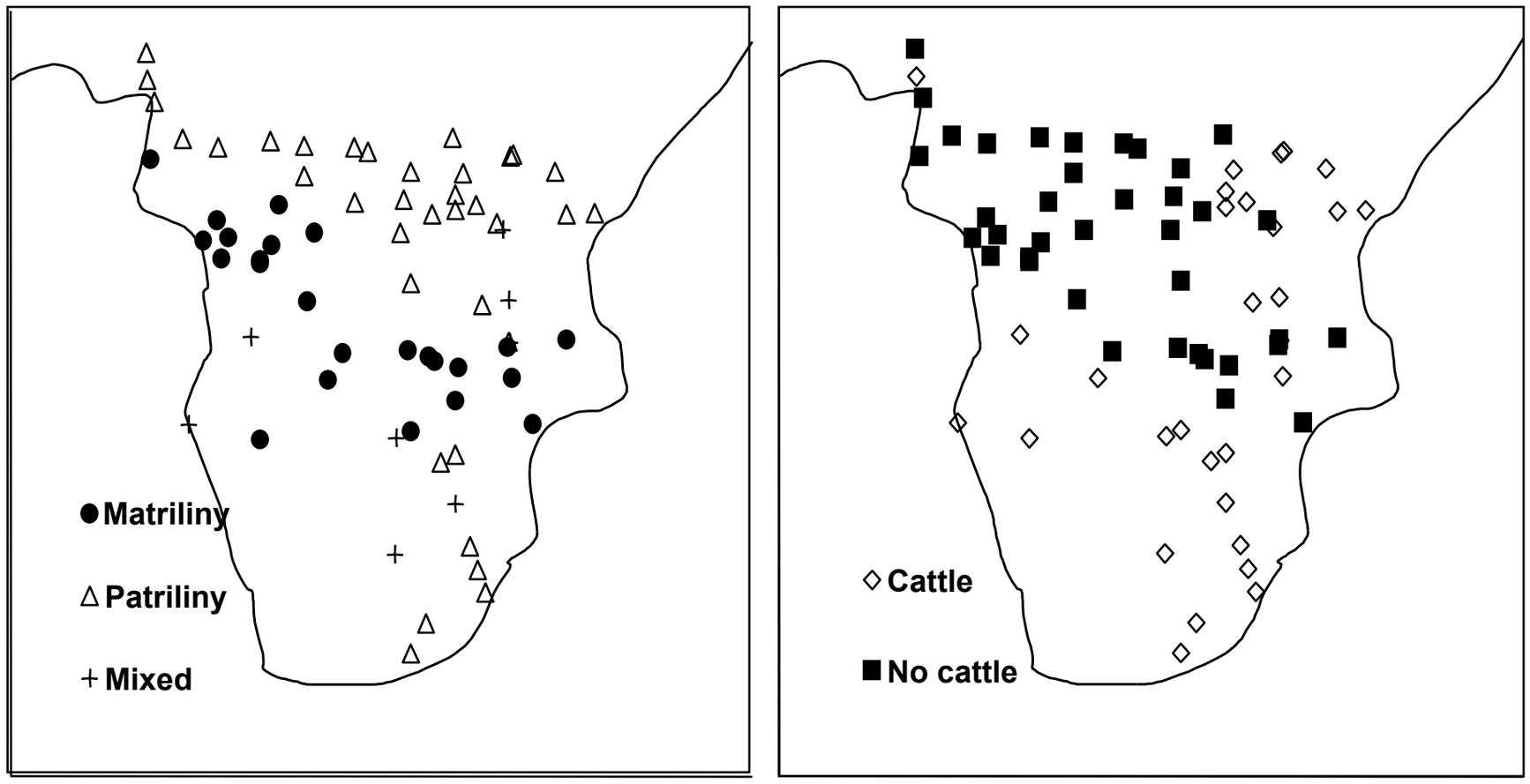
Michael Dunn[1,2], Simon J. Greenhill[3,4], Stephen C. Levinson[1,2] & Russell D. Gray[3]

Language families: previously a problem for sampling approaches, now crucial resources

Dunn *et al* 2011 *Nature*

Coevolutionary test
Bantu descent and mode of subsistence

Is patriliny (descent following a male lineage) associated with the acquisition of heritable resources that individual men can monopolise?



“The cow is the enemy of matriliny”

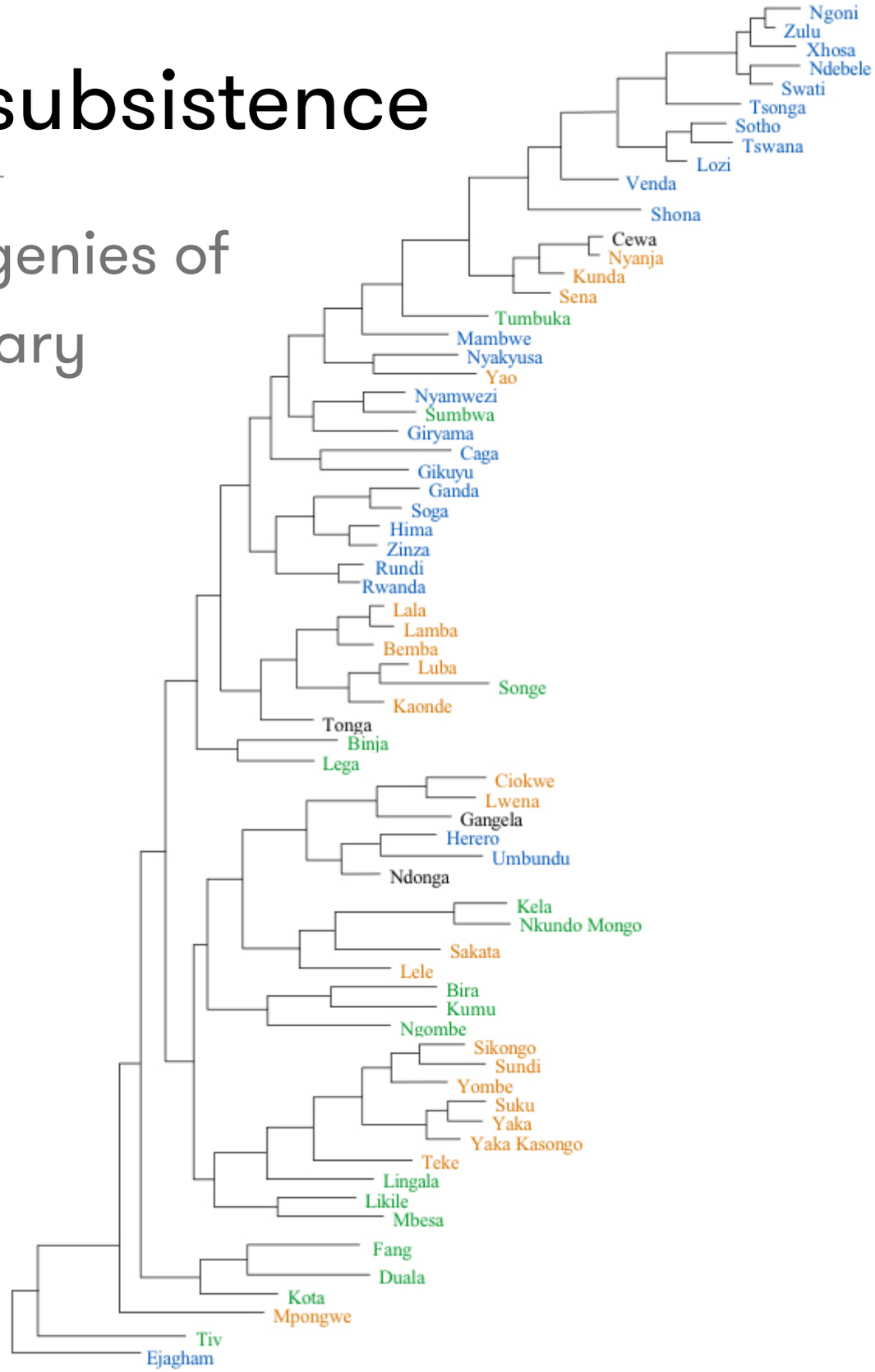
Holden & Mace 2003

Bantu descent and mode of subsistence

- Independently-derived lexical phylogenies of cognate-coded Bantu basic vocabulary (n=68)

- Coded ethnographic data

	cattle	no cattle
patrilineal	25	18
matrilineal	5	20



Holden & Mace 2003

Bantu descent and mode of subsistence

Matrilineal descent
Cattle present

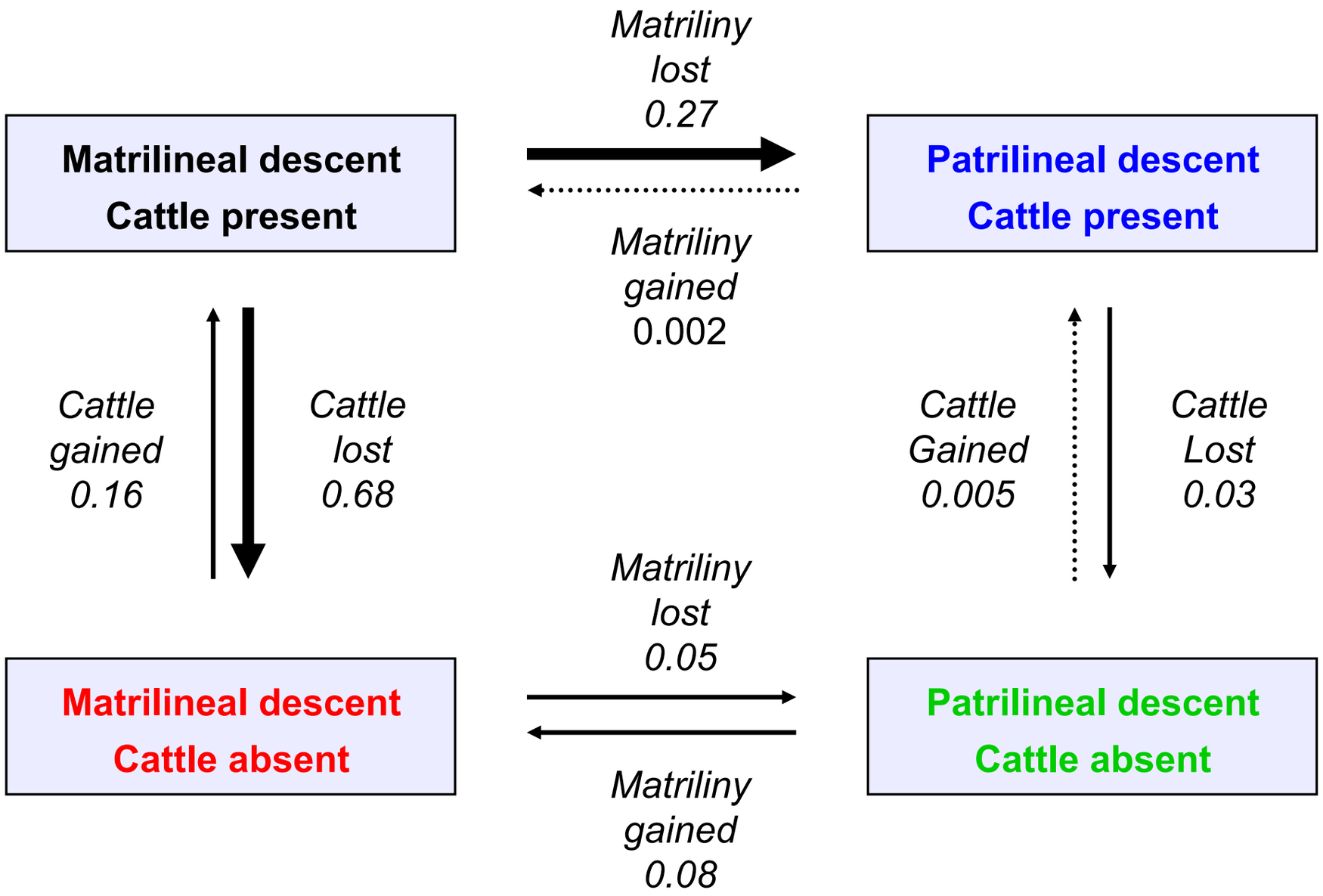
Patrilineal descent
Cattle present

Matrilineal descent
Cattle absent

Patrilineal descent
Cattle absent

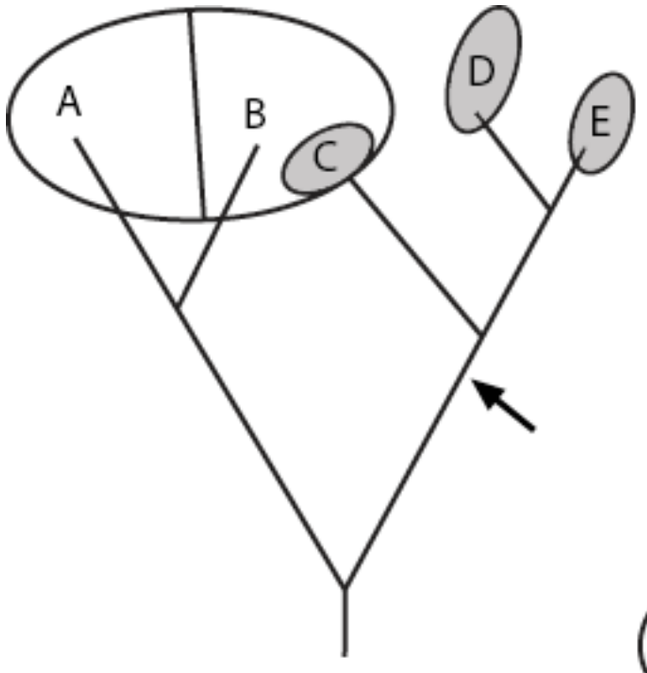
L_I= -62.52 L_D= -56.80 LR=5.72, *p*=0.02

Bantu descent and mode of subsistence

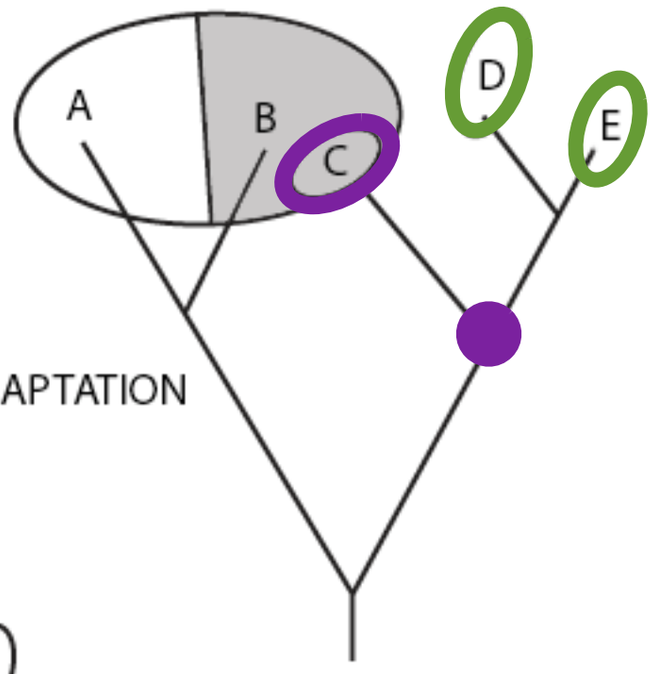


L_I= -62.52 L_D= -56.80 LR=5.72, p=0.02

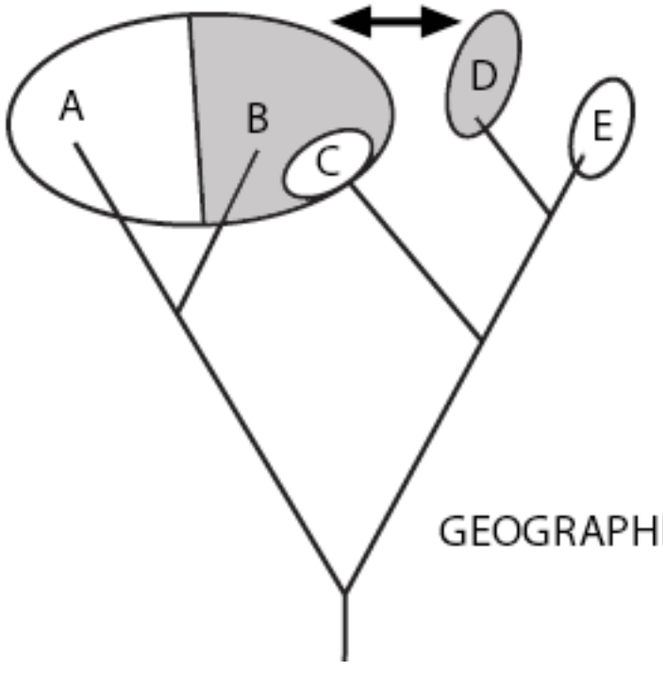
Phylogeny and geography



PHYLOGENETIC INHERITANCE



ECOLOGICAL ADAPTATION



GEOGRAPHICAL DIFFUSION

geographic and phylogenetic nearest neighbours

Guglielmino et al 1995 PNAS / Mace & Jordan 2011 *Phil. Trans Roy Soc London B*

Mace & Jordan 2011 *Phil. Trans Roy Soc London B.*

Mace & Jordan 2011 *Phil. Trans Roy Soc London B.*