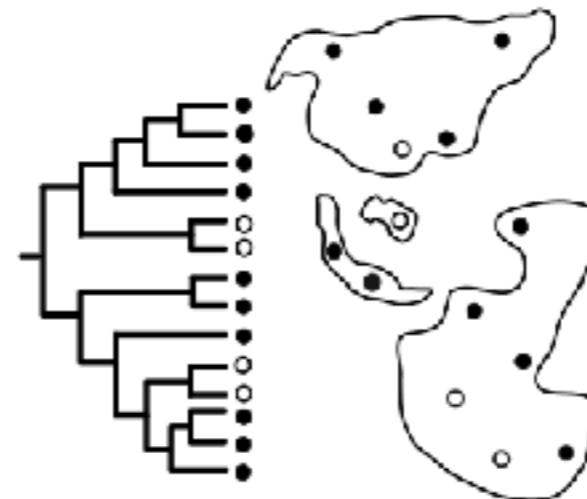


PHYLOGENETIC COMPARATIVE METHODS

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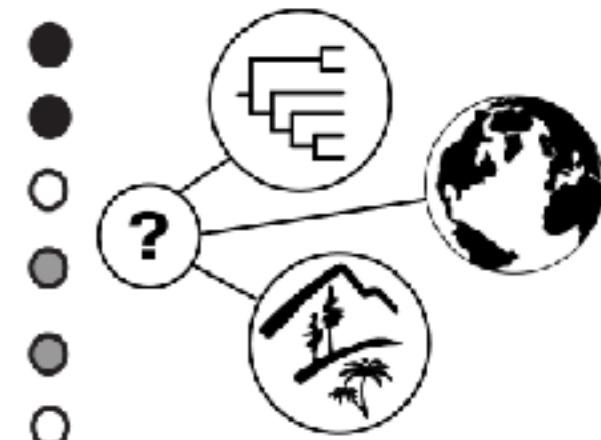
EXPLORATORY

How are features distributed across societies?



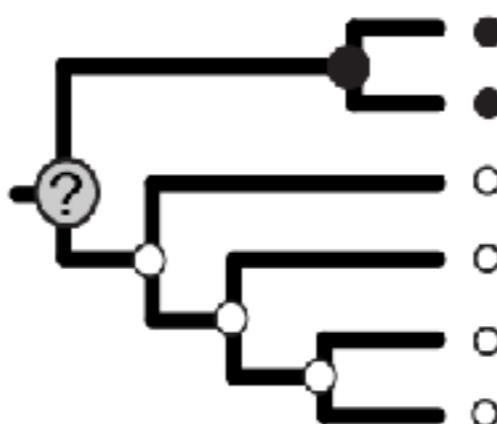
REGRESSION ANALYSIS

What predicts patterns of cultural diversity?



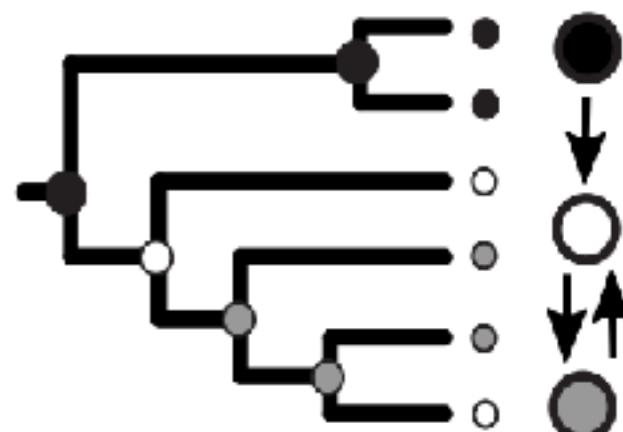
ANCESTRAL STATES

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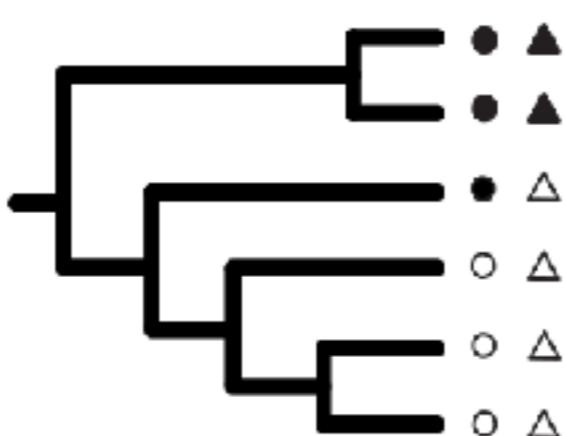
TRANSFORMATION

How do cultural features change form?



CORRELATED EVOLUTION

Do features change together?



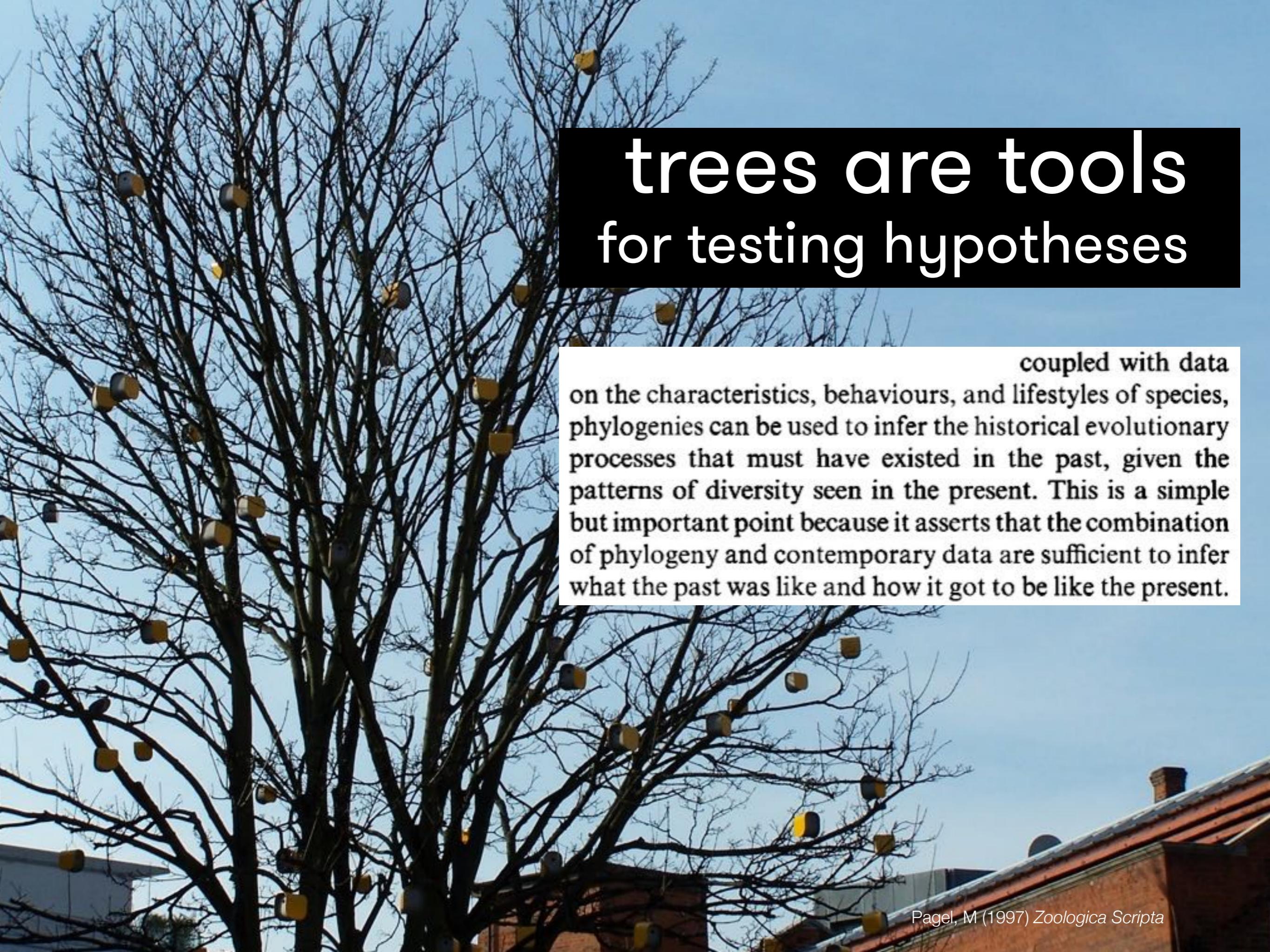
MODE AND TEMPO

How and when do features diversify?



design & diversity



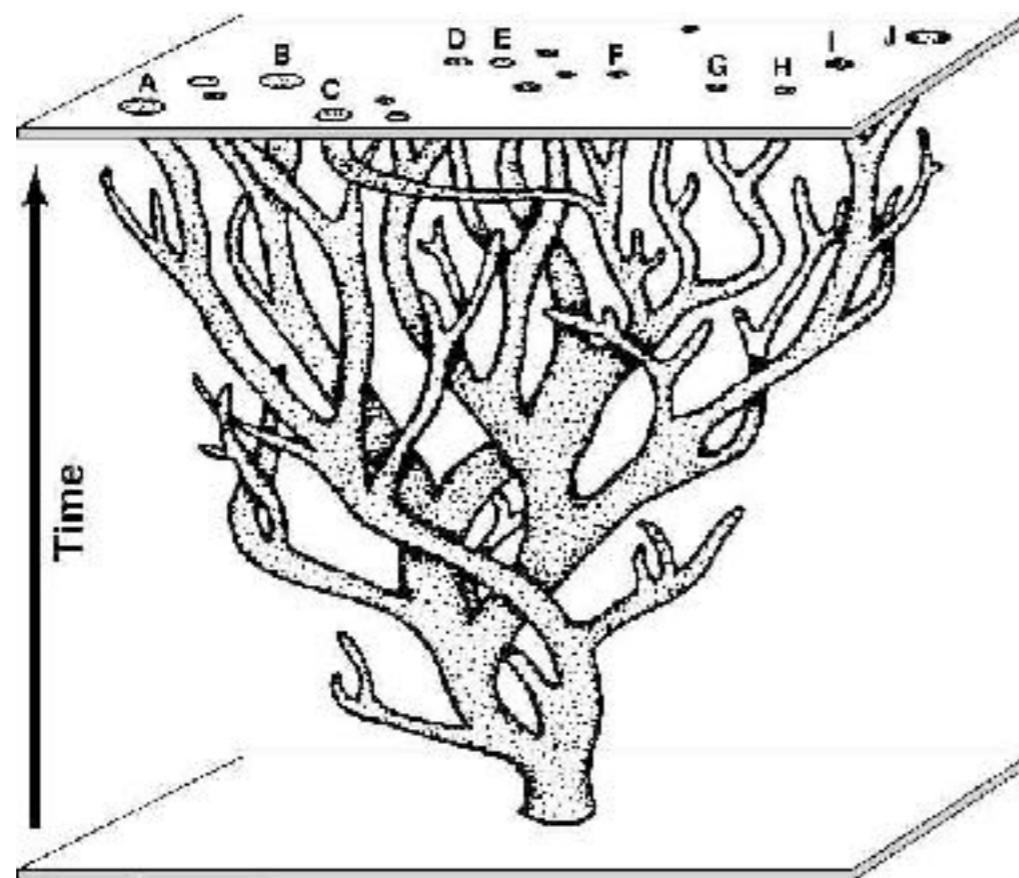


trees are tools for testing hypotheses

coupled with data on the characteristics, behaviours, and lifestyles of species, phylogenies can be used to infer the historical evolutionary processes that must have existed in the past, given the patterns of diversity seen in the present. This is a simple but important point because it asserts that the combination of phylogeny and contemporary data are sufficient to infer what the past was like and how it got to be like the present.

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.



Phylogenetic comparative methods

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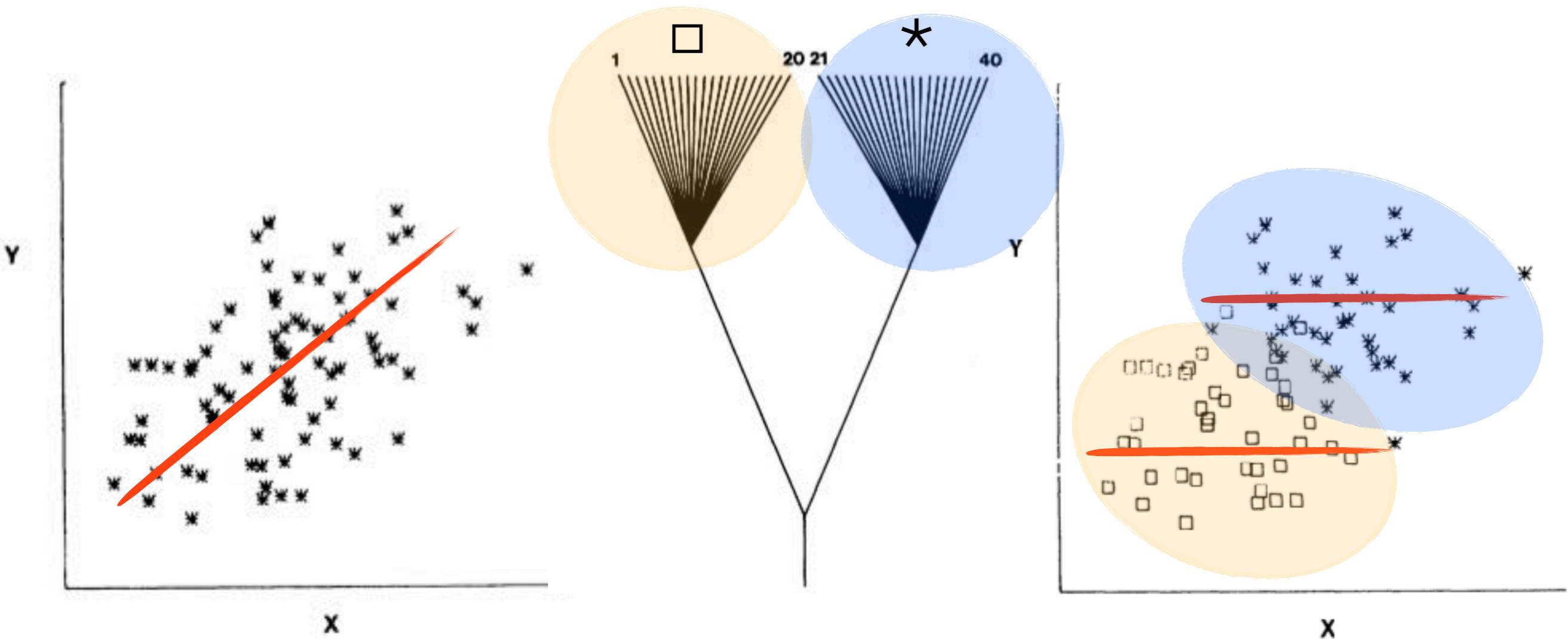
Let us explain diversity using phylogenetic history.

Originally developed for the study of adaptation by comparing
suites of traits across species.

Formalised by Felsenstein (1985) in a classic paper you should read.

Phylogenies and the comparative method

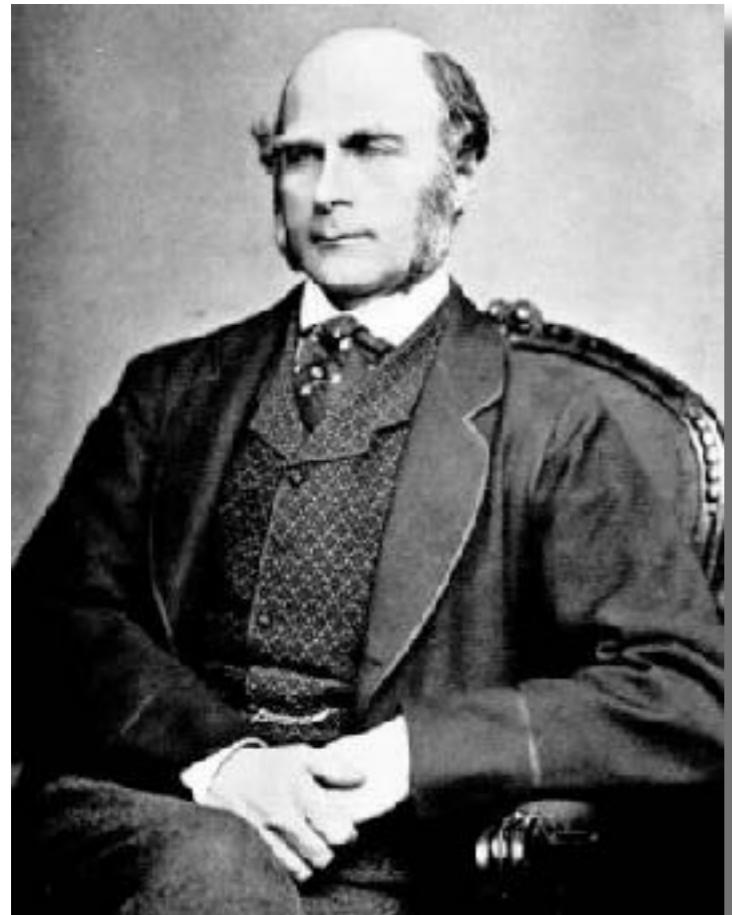
- **Species** data points might not be independent



Hierarchical structuring of evolutionary history

- “Species are part of a hierarchically structured phylogeny, and thus cannot be regarded for statistical purposes as if drawn independently from the same distribution.”
- Can’t just sample taxa because we simply push back the unknown effect of hierarchical structure.
- This “control for phylogeny” is not just important in studying correlated evolution
Important in ALL analyses of traits that have an evolutionary history INCLUDING linguistic and cultural features

Galton's Problem



It was extremely desirable for the sake of those who may wish to study the evidence for Dr. Tylor's conclusions, that full information should be given as to the degree in which the customs of the tribes and races which are compared together are independent. It might be, that some of the tribes had derived them from a common source, so that they were duplicate copies of the same original. Certainly, in such an investigation as this, each of the

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

Historical relatedness means that traits cannot be assumed to have arisen anew in each population: data points may not be independent of one another.

The Comparative Method in Anthropology¹

by Ruth Mace
and Mark Pagel

Cross-cultural comparison is a central tool for testing hypotheses regarding the co-evolution of the adaptiveness of a cultural environment. It has long been recognized that cultures are not independent but rather related by virtue of common ancestry. In order to address this issue, known as Cultural Phylogenetics, it is necessary to statistically remove confounding variables of "independent cultures." We propose a hypothesis of co-evolution of culture and environment to identify independent cultures or to compare them. In cross-cultural comparative studies, the identification of independent events of cultural change is a key task. If this principle is applied, it becomes apparent that closely related cultures that are geographically close together are likely to share many elements, making it difficult for testing cross-cultural hypotheses. A key task is to identify independent instances of cultural change and placing upon the cultural elements' arising or changing task.

RUTH MACE is a Royal Society Research Fellow at the Department of Anthropology, University College London, Gower St., London WC1E 6BT, England. She was born in 1961, and was educated at Oxford University [B.A., 1983; D.Phil., 1987] and has held research positions in the Centre for Environmental Technology of Imperial College [1987–89] and the School of Development Studies of the University of East Anglia [1989–91]. Her research interests are subsistence economics, pastoralism, human ecology, and conservation. She has published "Pastoralist Strategies for Survival in an Unpredictable Environment: A Model of Herd Composition" [*Agricultural Systems* 31:185–204], "Overgrazing Overstated" [*Nature* 349:280–91], "Nomadic Pastoralists Adopt Strategies That Maximise Long-term Household Survival" [*Behavioral Ecology and Sociobiology* 33:329–34], and "Transitions between Cultivation and Pastoralism in Sub-Saharan Africa" [*CA* 34:565–82].

MARK PAGEL directs a research unit on ecology and behaviour in the Department of Zoology of Oxford University. He was born in 1954 and educated at the University of Washington [B.A., 1976; Ph.D., 1980]. He has taught evolutionary theory and statistics at Harvard University [1990–92] as well as at Oxford. His publications include "Detecting Correlated Evolution on Phylogenies: A General Method for the Comparative Analysis of Discrete Characters" [*Proceedings of the Royal Society B* 255:37–45], "The

Adaptationist Wager," in *Phylogenetics and Ecology*, edited by P. Eggleton and D. Vane-Wright [London: Academic Press, in press], "The Evolution of Conspicuous Oestrous Advertisement in Old World Monkeys" [*Animal Behaviour* 47:1333–41], and, with P. H. Harvey, *The Comparative Method in Evolutionary Biology* [Oxford: Oxford University Press, 1991].

The present paper was submitted in final form 6 XII 93.

For well over a century, anthropologists have used infor-

The critical point of this essay is that the validity of comparative methods for anthropology depends upon correctly counting independent instances of cultural change. Independent instances of cultural change, in turn, cannot be identified without the construction of a phylogeny (or cladogram) showing the patterns of hierarchical descent of the cultures being studied.

issues that have recently been addressed using cross-cultural comparison as empirical evidence include questions concerning the co-evolution of rules of inheritance and marriage [Hartung 1982, 1985], pathogen risk and polygyny [Low 1988, 1990], incest taboos and exogamy [Durham 1991, Thornhill 1991], reproduction and social organization [Lesthaeghe 1989], and modes of subsistence and fertility [Campbell and Wood 1988, Bentley, Goldberg, and Jasienka 1993].

Most models of cultural evolution include the assumption that culture evolves by "descent with modification" [Cavalli-Sforza and Feldman 1981, Lumsden and Wilson 1981, Boyd and Richerson 1985, Durham 1991], probably from a single origin. Most models of cultural evolution also acknowledge the existence of bundles of characters that can be transmitted as independent units [i.e., even when other aspects of the culture are not passed on]; we shall call these "elements" of culture.

Perhaps the most common way of analysing comparative data is to correlate two or more elements across a group of cultures. However, Francis Galton realized as early as 1889 that cultures cannot be treated as independent for purposes of investigating cross-cultural trends.

1. This research was funded by the Royal Society (RM) the Science and Engineering Research Council, the National Environment Research Council, and the Biotechnology and Biological Sciences Research Council (MP).



Fertility and Mode of
Subsistence: A Phylogenetic
Analysis¹

Ritual human sacrifice promoted and sustained the evolution of stratified societies

Joseph Watts¹, Oliver Sheehan^{1,2}, Quentin D. Atkinson^{1,2}, Joseph Bulbulia³ & Russell D. Gray^{1,2,4,5}

DANIEL W. SELLEN AND RUTH MACE

From Bridewealth to Dowry?

A Bayesian Estimation of Ancestral States of Marriage Transfers in Indo-European Groups

Laura Fortunato, Clare Holden, and Ruth Mace
University College London

The sequential evolution of land tenure norms

Geoff Kushnick^{a,*}, Russell D. Gray^{b,c}, Fiona M. Jordan^{d,e}

A Phylogenetic Analysis of the Evolution of Austronesian Sibling Terminologies

FIONA M. JORDAN¹

Testing for Divergent Transmission Histories among Cultural Characters: A Study Using Bayesian Phylogenetic Methods and Iranian Tribal Textile Data

Luke J. Matthews^{1*}, Jamie J. Tehrani², Fiona M. Jordan³, Mark Collard^{4,5}, Charles L. Nunn¹

THE EVOLUTION OF HUMAN SEX RATIO AT BIRTH: A BIO-CULTURAL ANALYSIS

Ruth Mace and Fiona Jordan

Matrilocal residence is ancestral in Austronesian societies

Fiona M. Jordan^{1,2,*}, Russell D. Gray³, Simon J. Greenhill³ and Ruth Mace^{1,2}

Spread of cattle led to the loss of matrilineal descent in Africa: a coevolutionary analysis

Clare Janaki Holden* and Ruth Mace

Phylogenetic reconstruction of Bantu kinship challenges Main Sequence Theory of human social evolution

Christopher Opie^{a,1}, Susanne Shultz^b, Quentin D. Atkinson^c, Thomas Currie^d, and Ruth Mace^a

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. Gray³, Toshikazu Hasegawa¹ & Ruth Mace²

“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.”

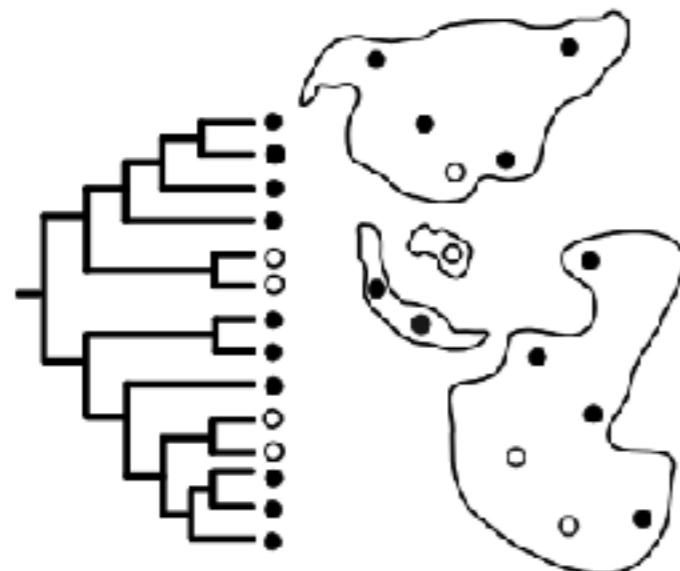
Franz Boas 1948



Comparative methods

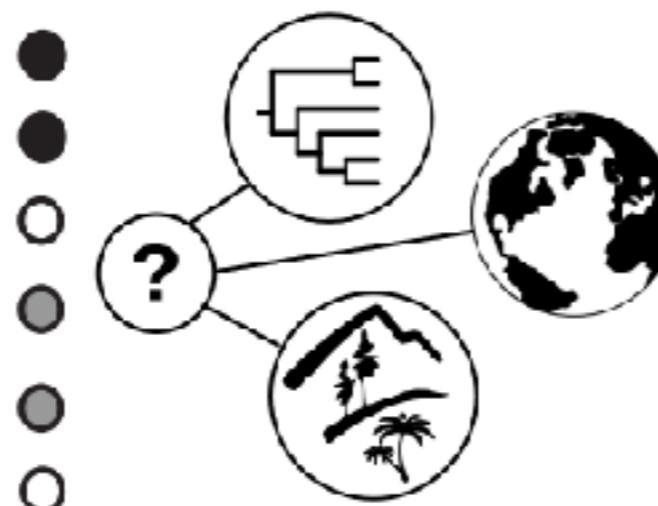
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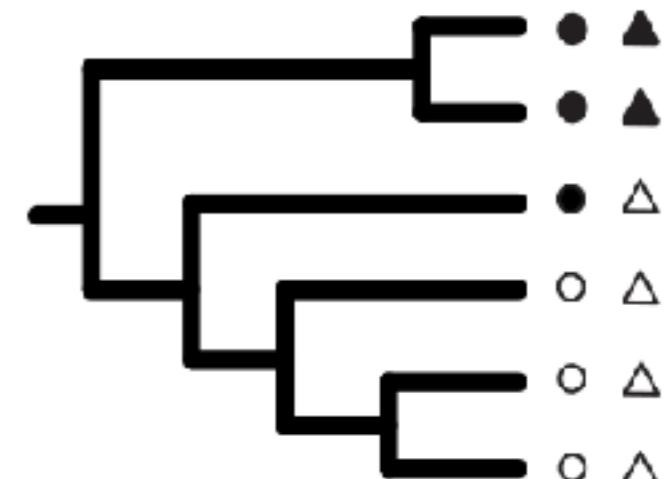
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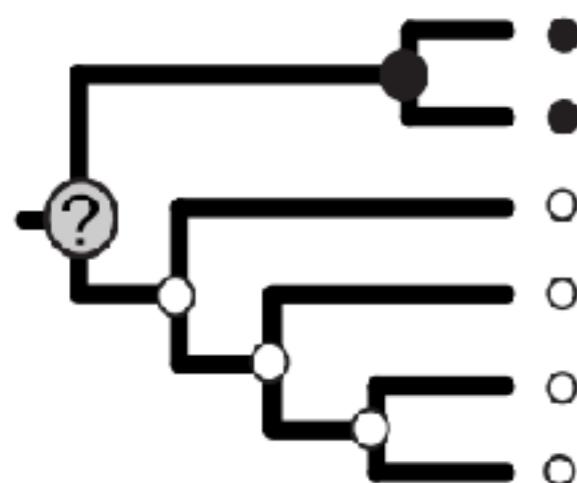
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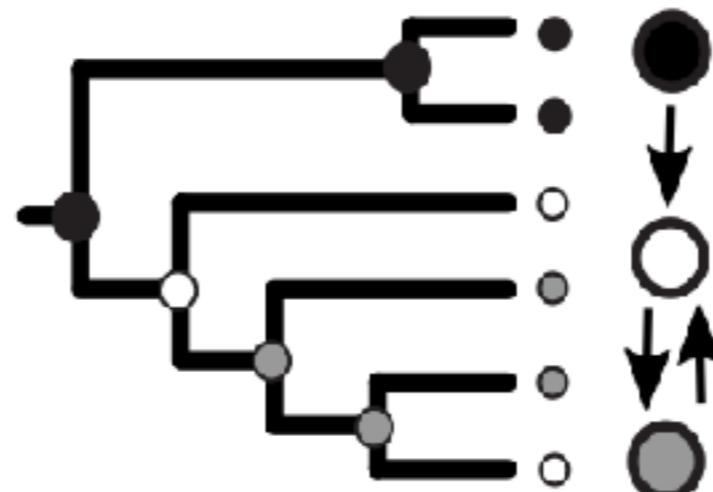
ANCESTRAL STATES

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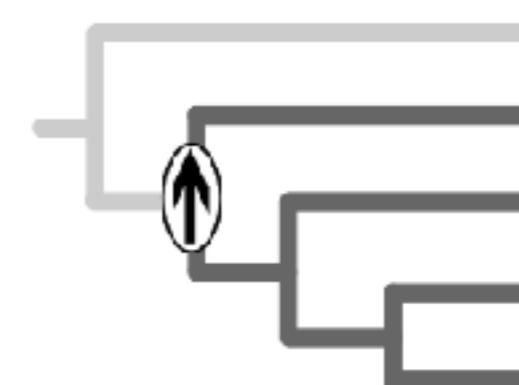
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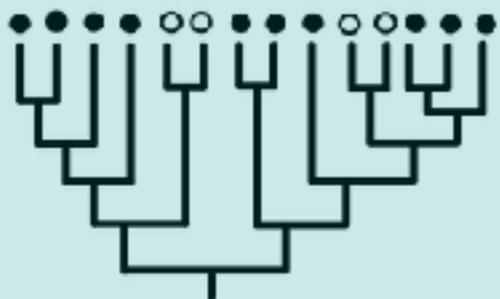
MODE AND TEMPO

How and when do features diversify?



Components of a comparative analysis

discrete
continuous



data

inference
method

trees
tip data

MP
ML
Bayesian

Markov

Brownian
stabilising
speciation

model

parameter
estimates

change
description

node values
transition rates

Modelling change on phylogenies

- Discrete and continuous characters change differently
Different model/assumptions required

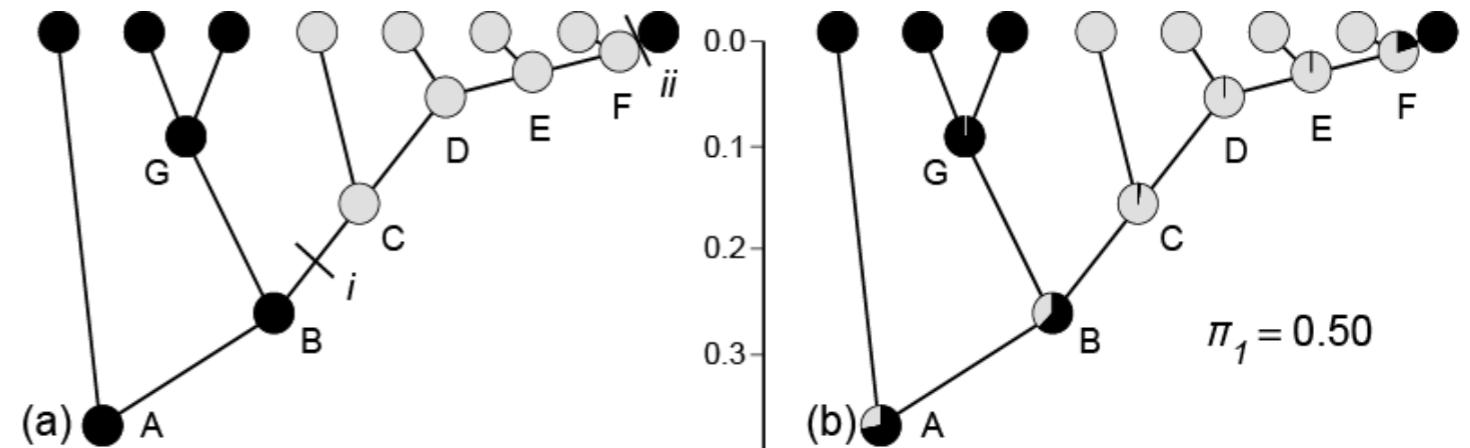
- Same types of inference methods as for tree-building

Parsimony

Maximum likelihood

Bayesian

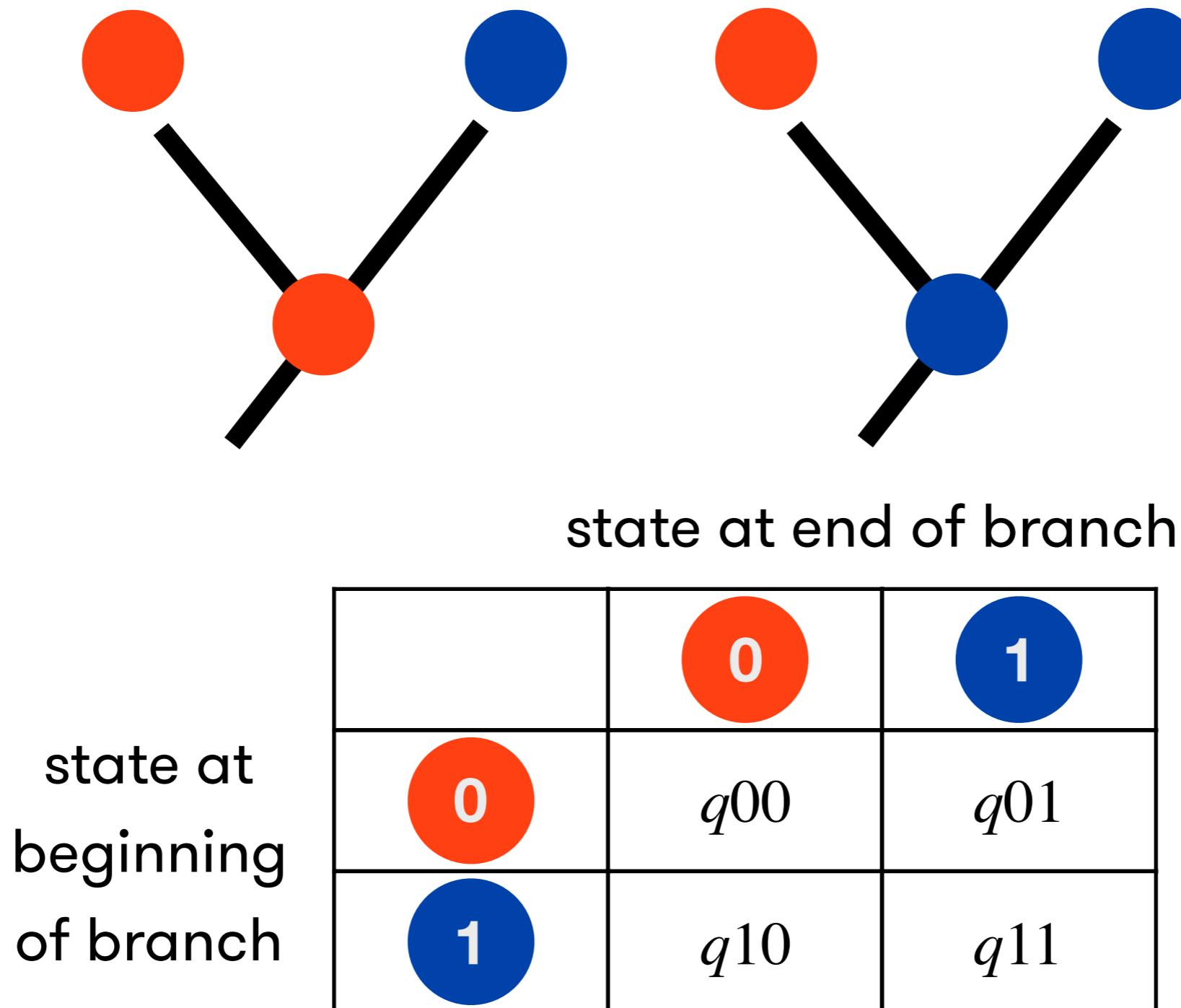
... and the same pros and cons.



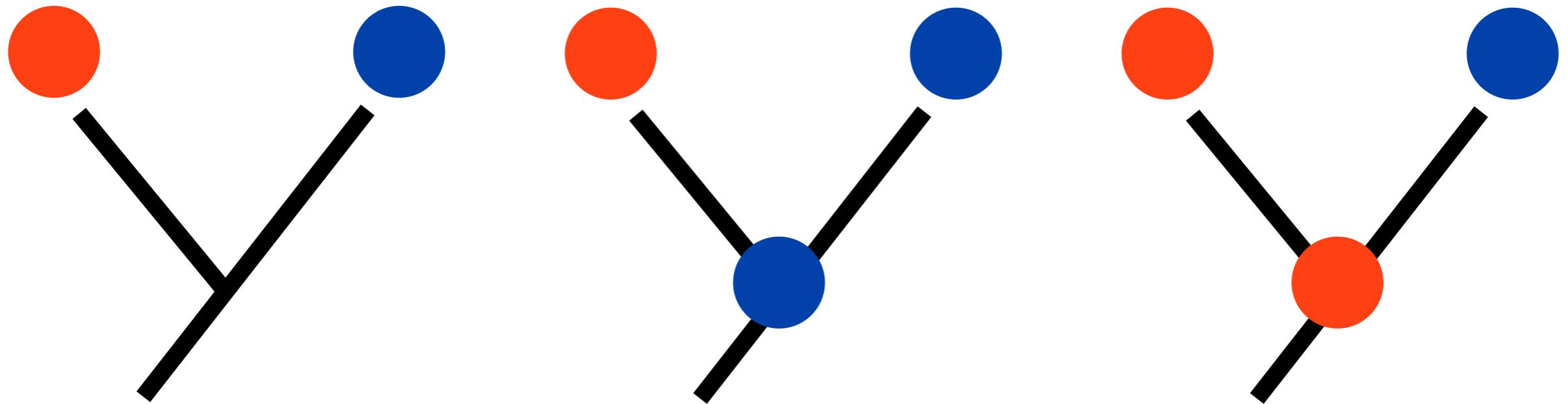
- PCMs implemented in a wide range of software packages

R, BayesTraits, Mesquite

Discrete data in a probabilistic framework

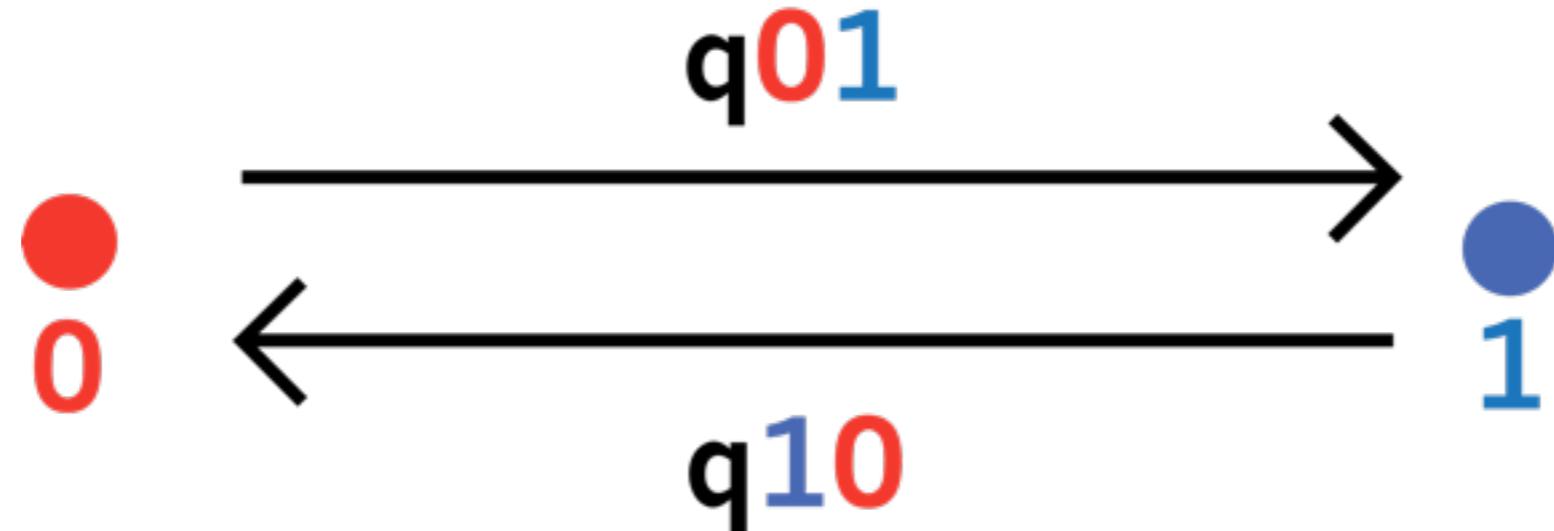


Discrete data in a probabilistic framework



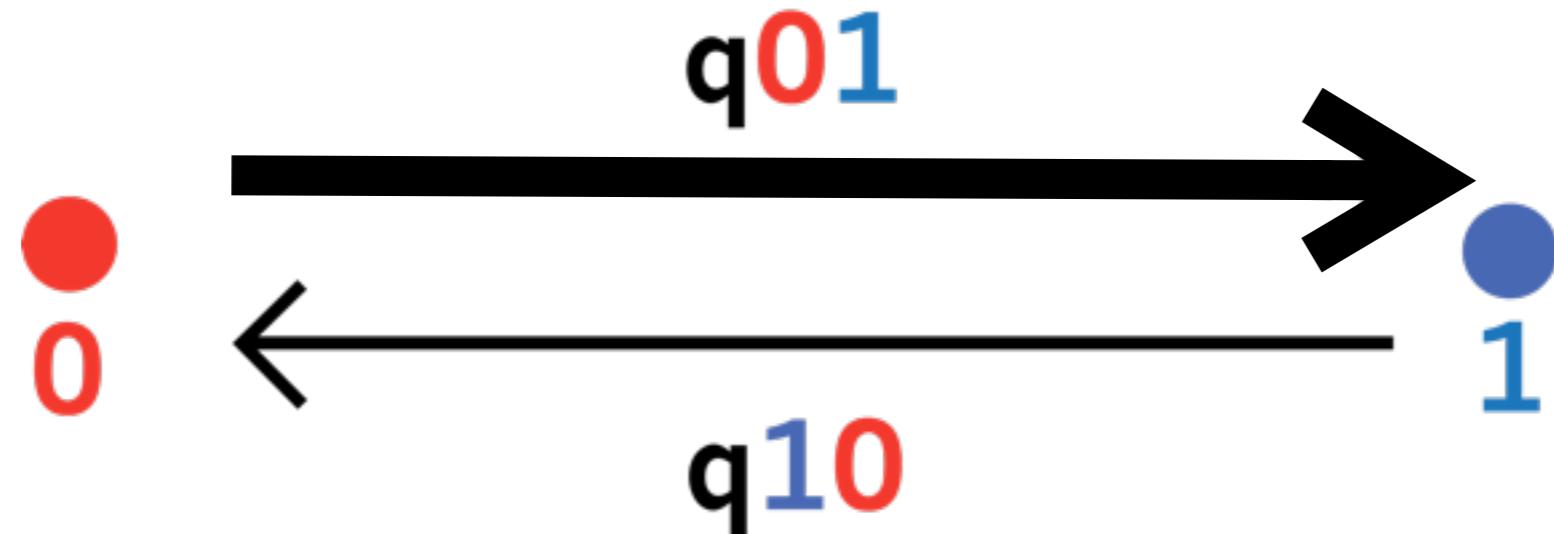
continuous-time Markov models

these specify a matrix $[Q]$ of transition probabilities
probability of change at each tiny increment along branch



transition-rate parameters

describe the probability of change from one state to another



Modelling discrete change on phylogenies

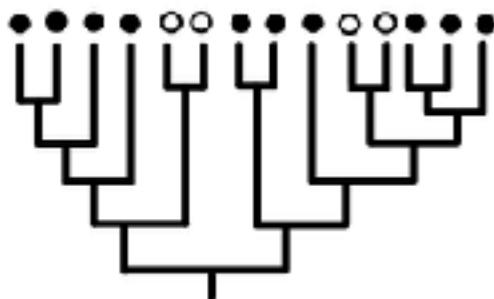
- The TREES are treated as fixed, like the DATA
- Very similar to estimating the evolution of a single character when inferring phylogenies
- More fine-grained investigation of the model of evolution.

Ancestral state inference

Specifying and testing a model of discrete character evolution

Components of a comparative analysis

discrete
continuous



data

**inference
method**

Markov

Brownian
stabilising
speciation

model

**parameter
estimates**

trees
tip data

MP
ML
Bayesian

change
description

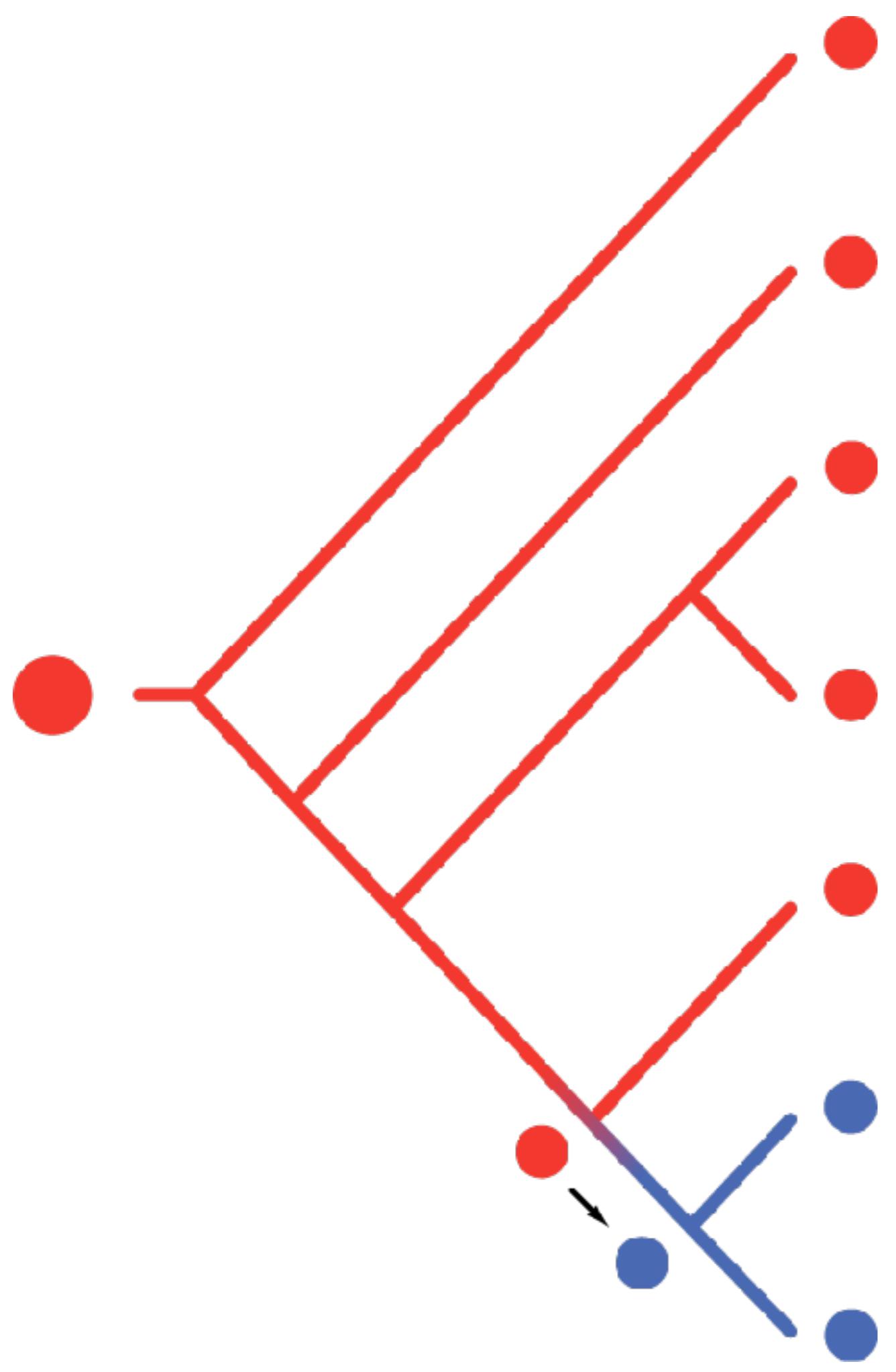
node values
transition rates

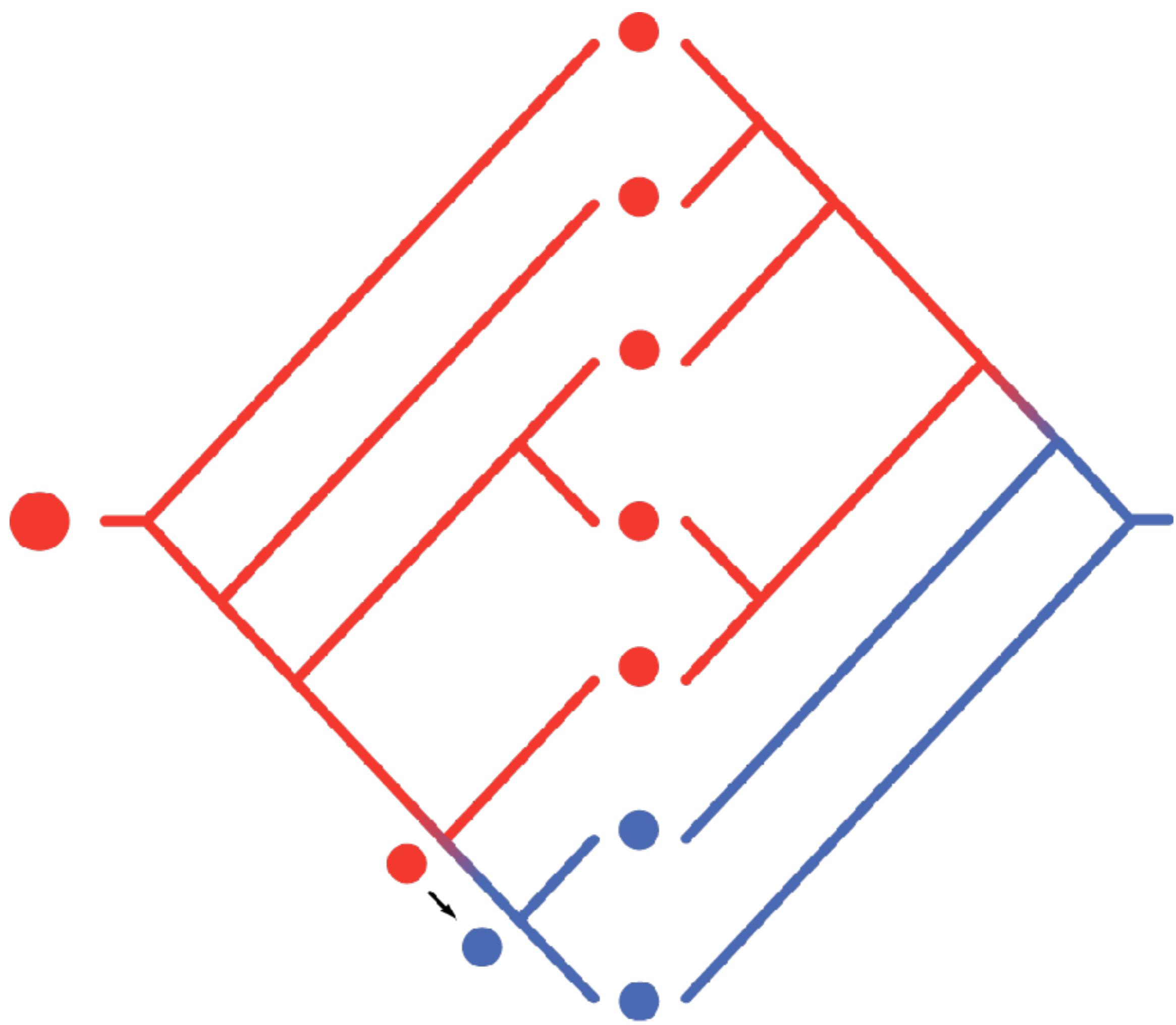
BAYESIAN MCMC

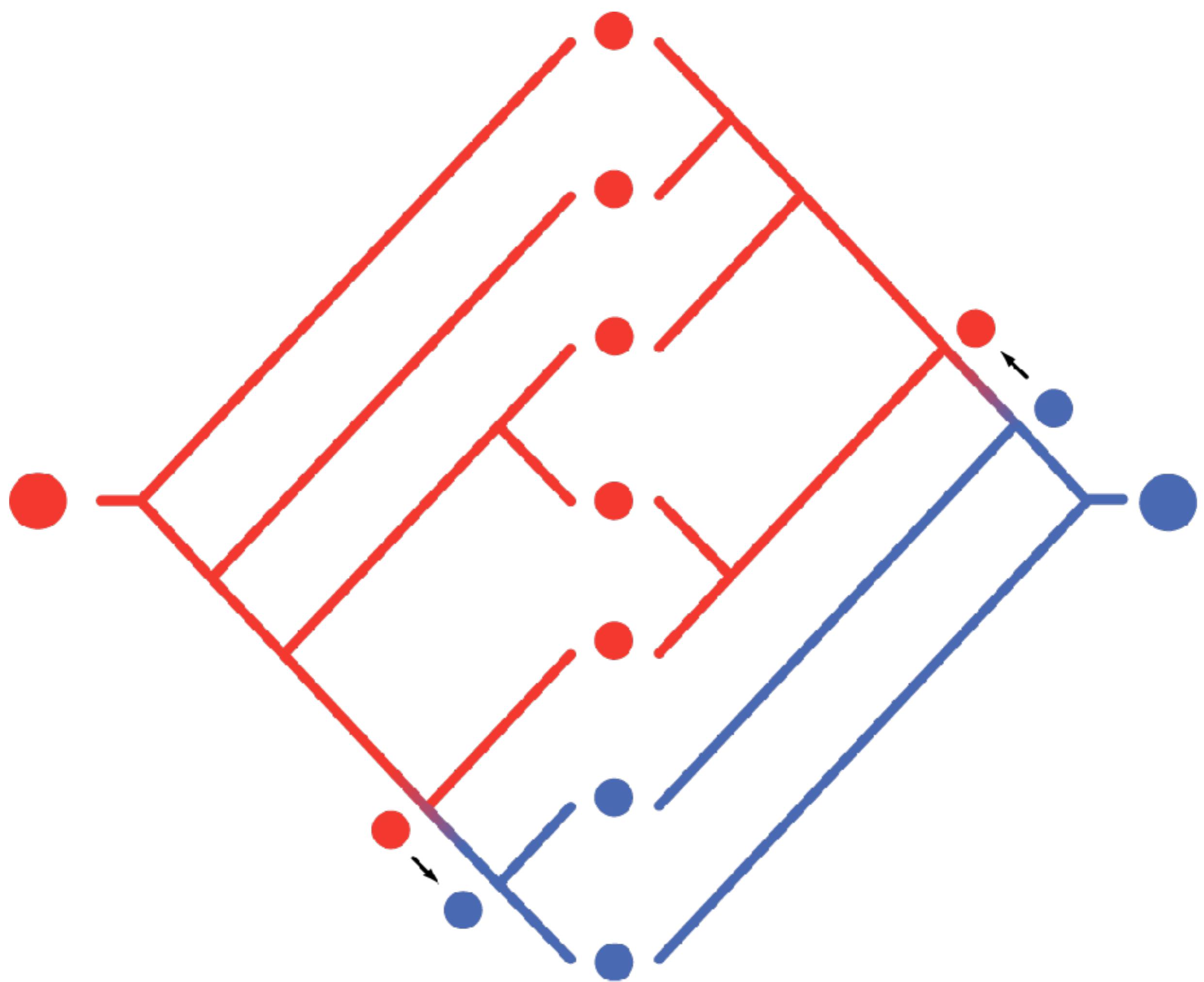


Phylogeny affects our estimates of ancestral states





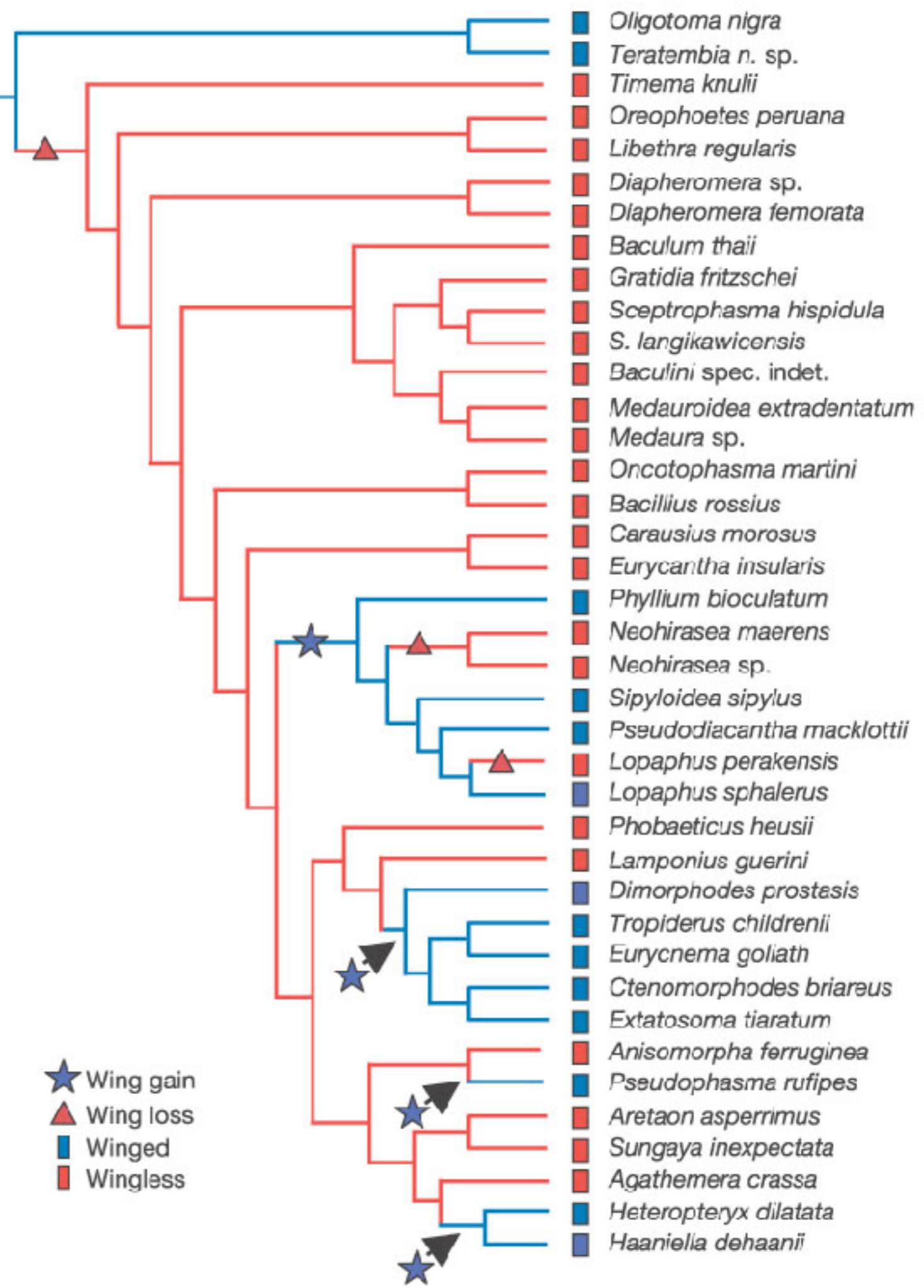




Ancestral states

What kinds of questions?

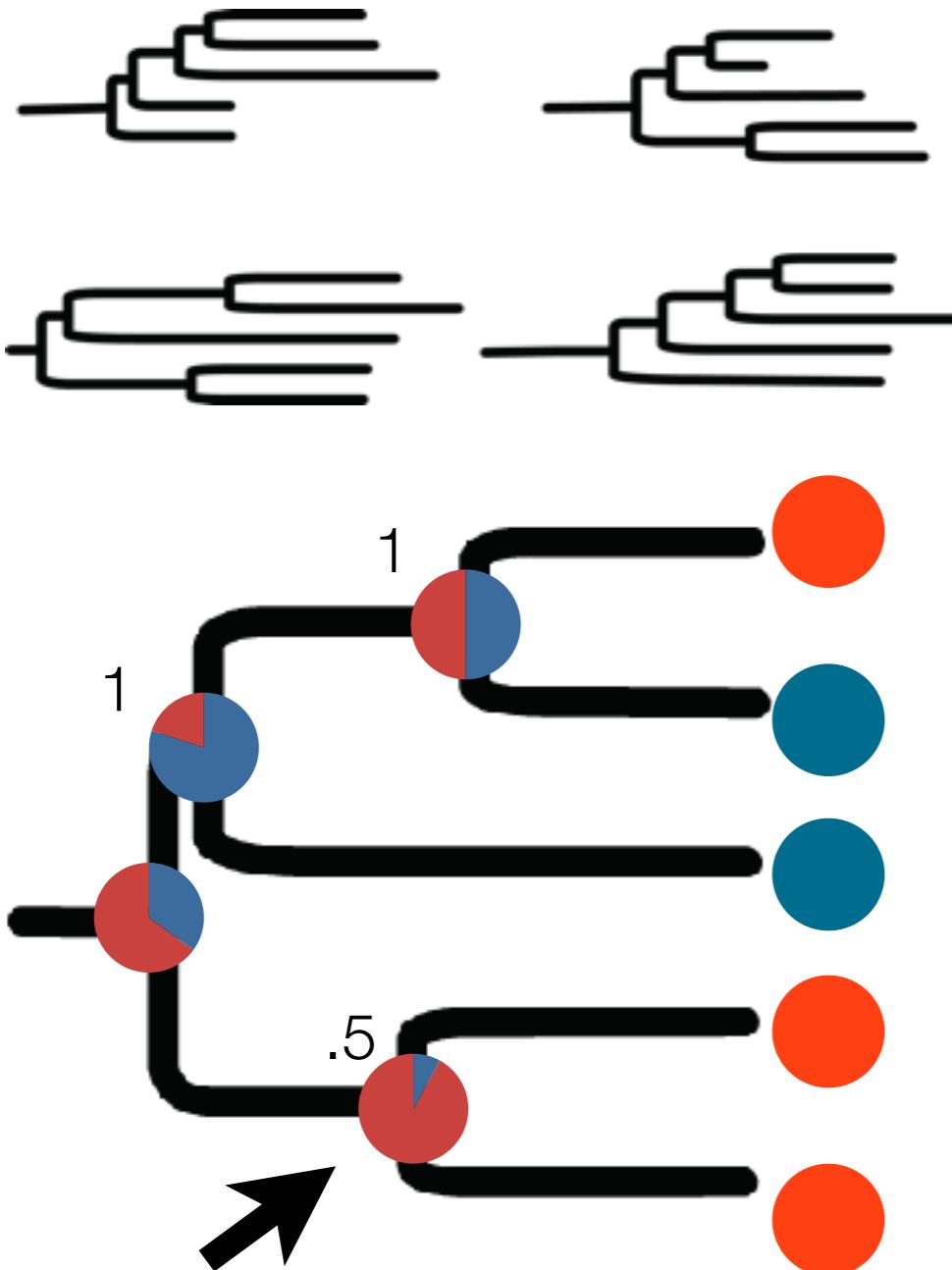
- What is the earlier form of a trait?
- What form of the trait do we see at a specific node?
- How certain are we in our estimates of node values?
- Given some independent evidence about ancestral forms, how much do we prefer one hypothesis over another?
- Does altering the ancestral states affect our 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 $\text{pr}(\text{red}) = .5 \times .9 = .45$

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



matrilocal





patrilocal





neolocal

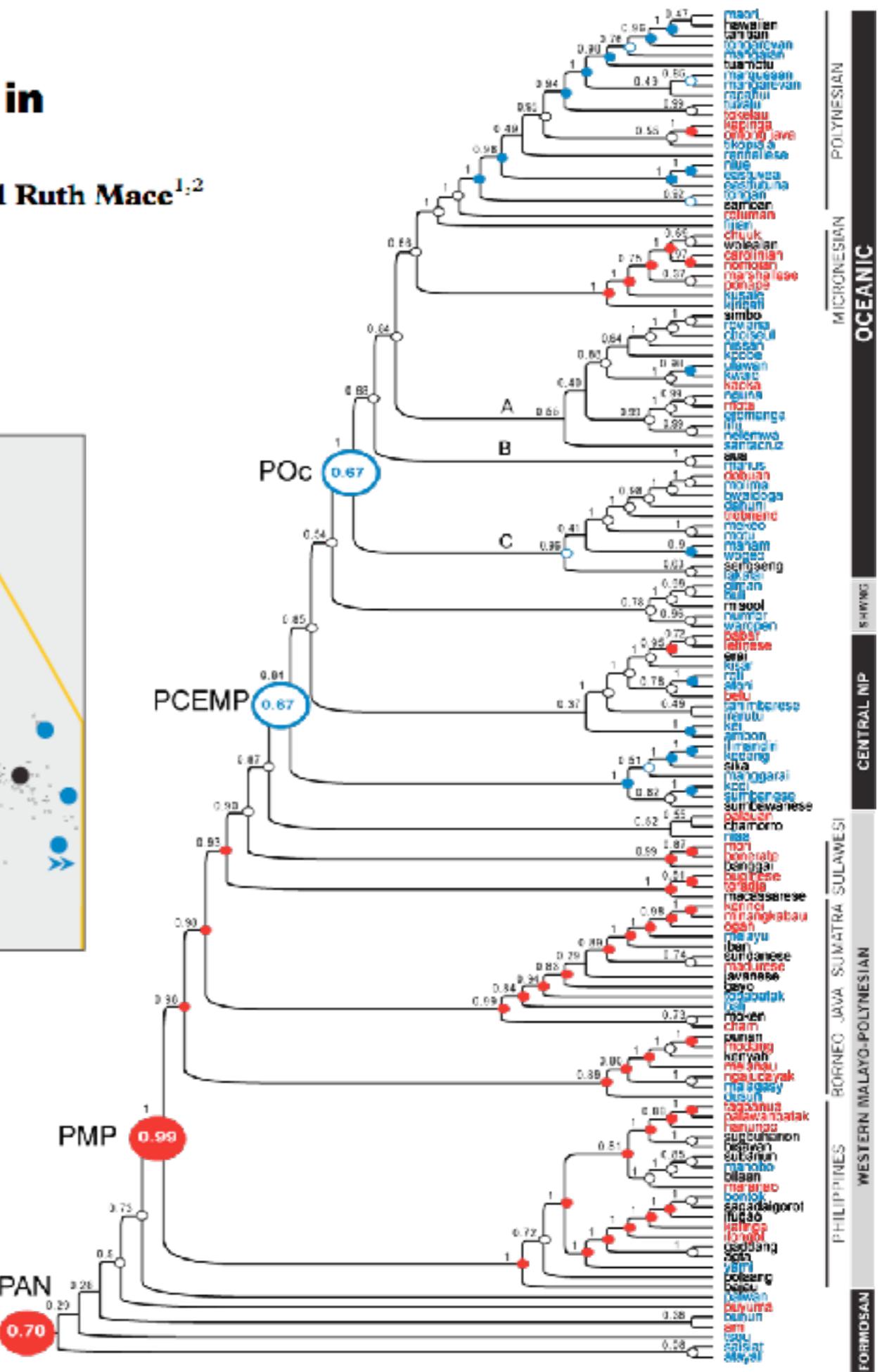
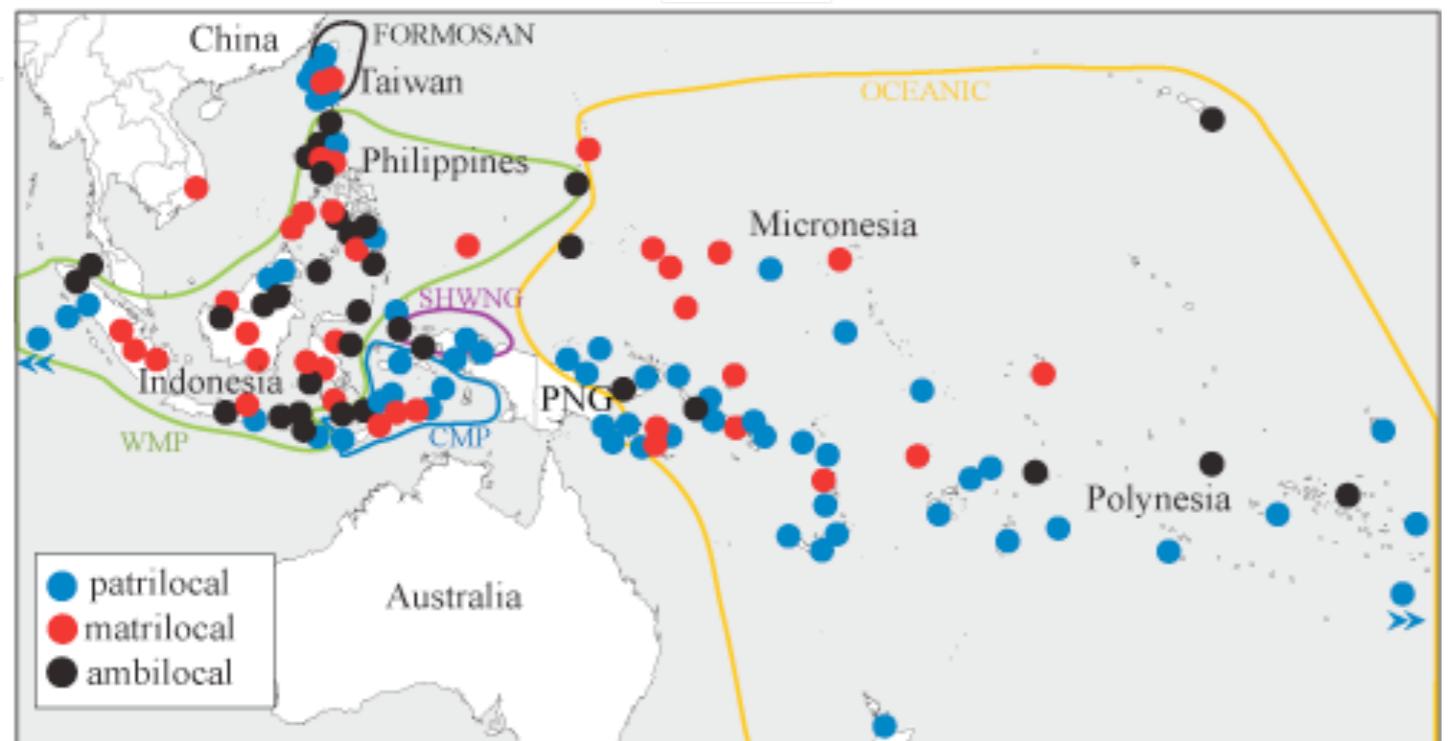
Inferring ancestral residence

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

Matrilocal residence is ancestral in Austronesian societies

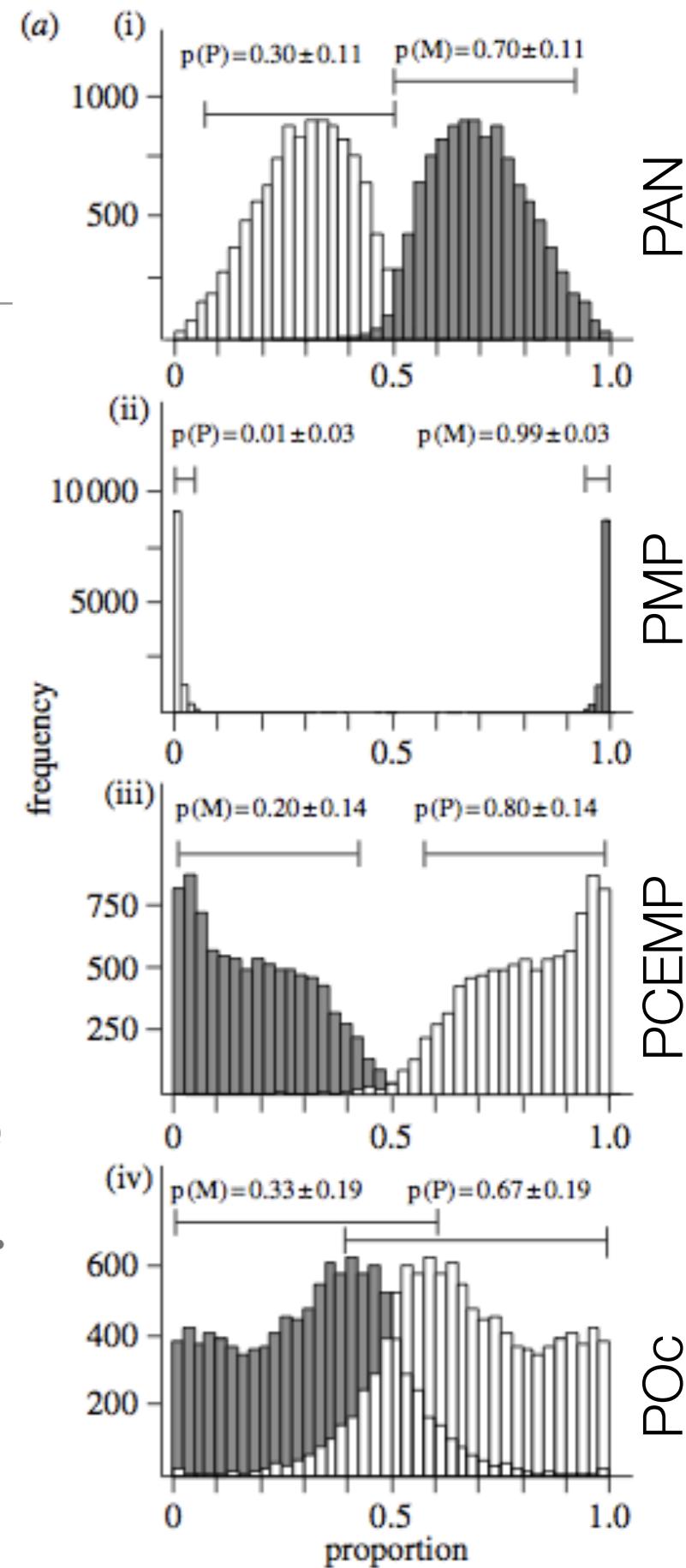
Fiona M. Jordan^{1,2,*}, Russell D. Gray³, Simon J. Greenhill³ and Ruth Mace^{1,2}



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.



Inferring ancestral residence

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- We inferred a node's state by multiplying:
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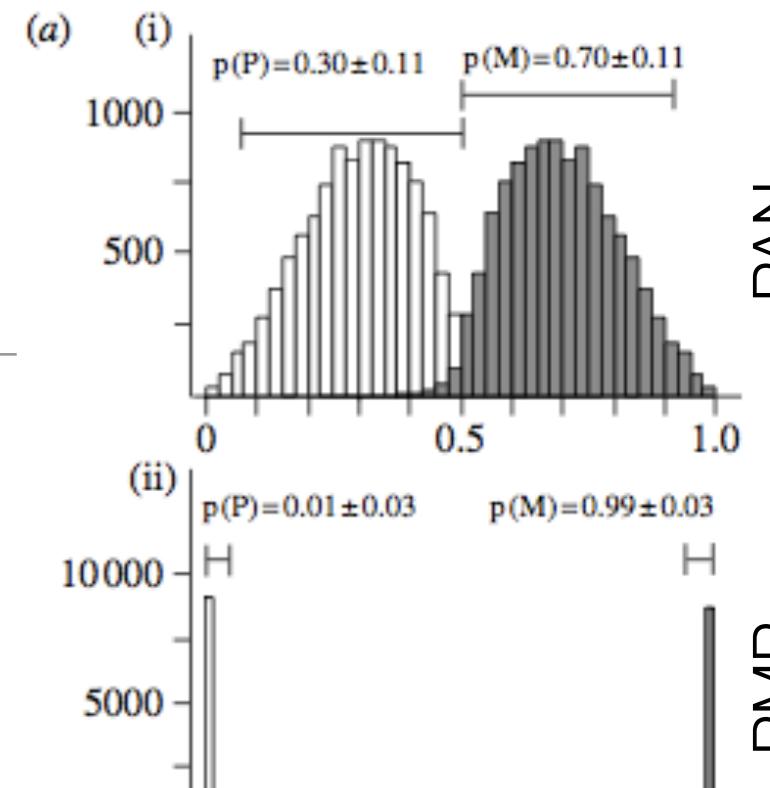
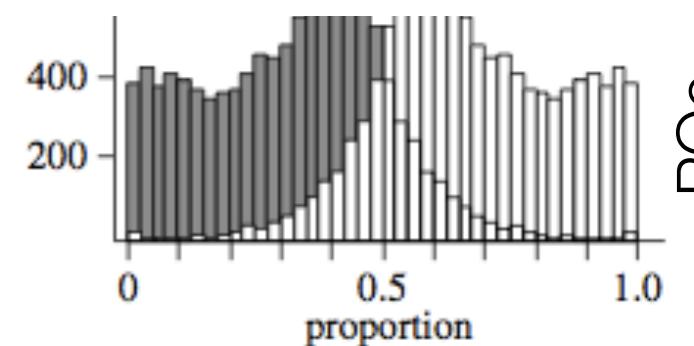


Table 1. Comparing model support with the Bayes factor. (Bayes factors were calculated as follows: $BF = 2(\ln L_hA - \ln L_hB)$, where $\ln L_hx$ is the marginal likelihood (i.e. the harmonic mean of the post-convergence $\ln L_h$ likelihoods, allowing us to compare the posterior distributions). BF 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	$\ln L_h$	model B	$\ln L_h$	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

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



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



data on traits
across populations

language phylogenies
as population history



data on traits
across populations

language phylogenies
as population history

a model of
how traits evolve
(and ancestral states)



data on traits
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equal probability of change

data on traits
across populations

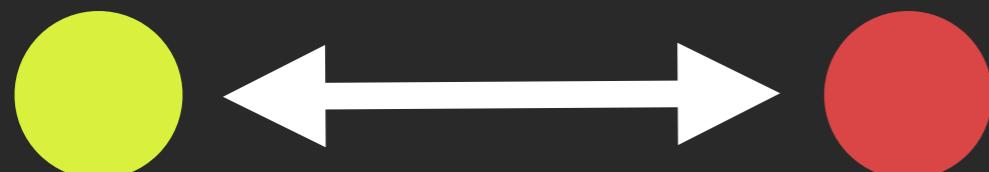
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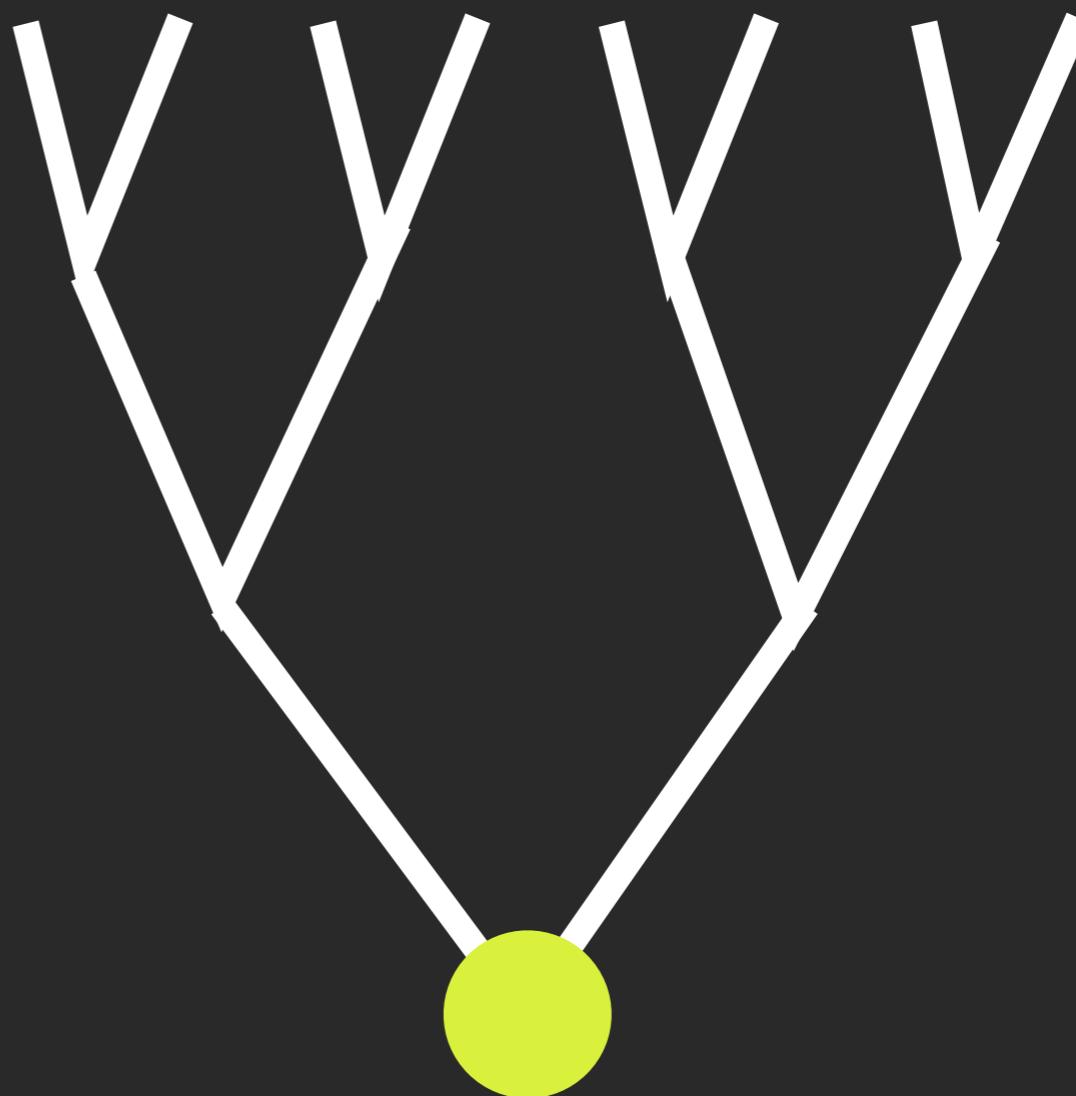
equal probability of change

actual data



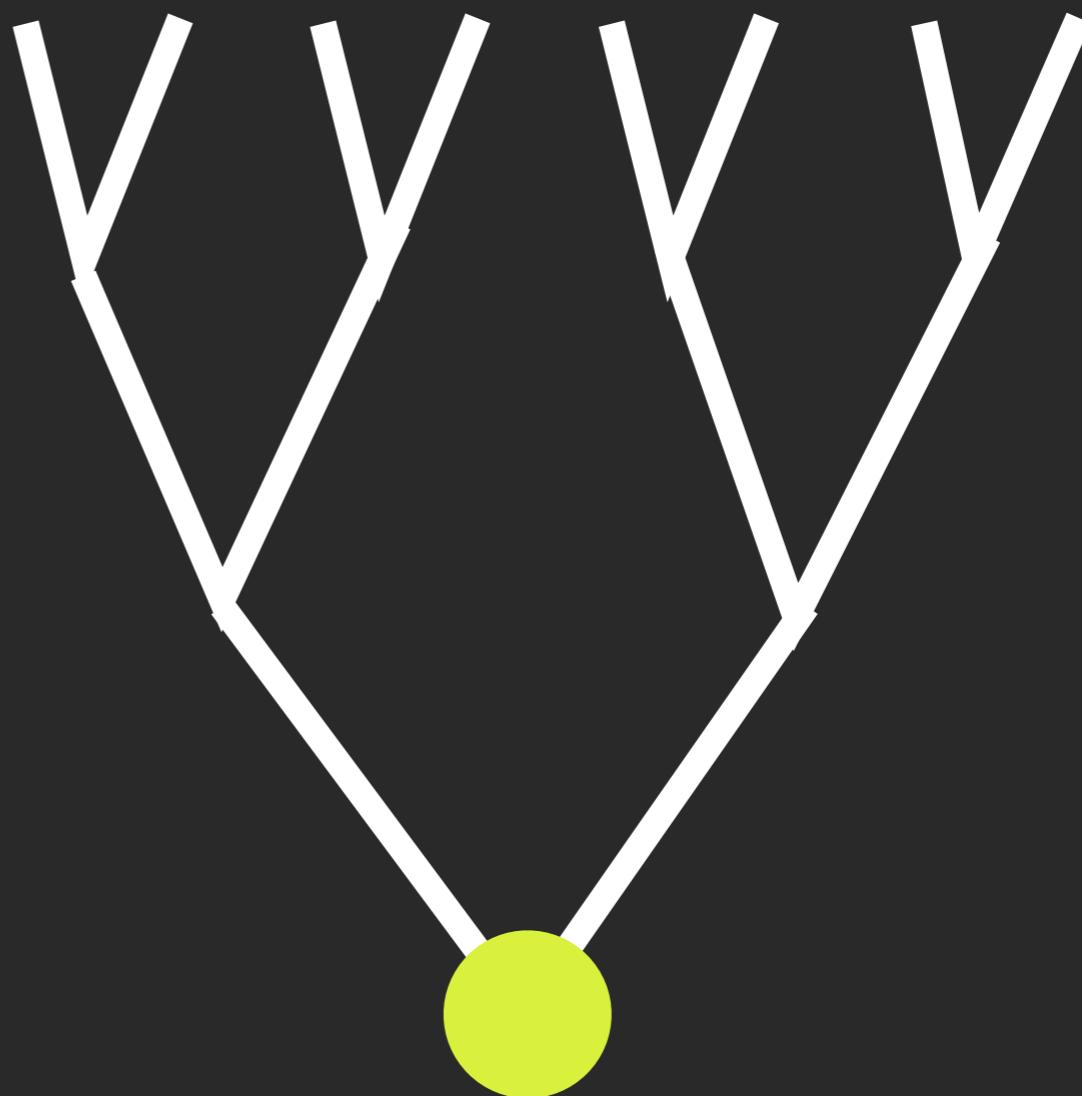
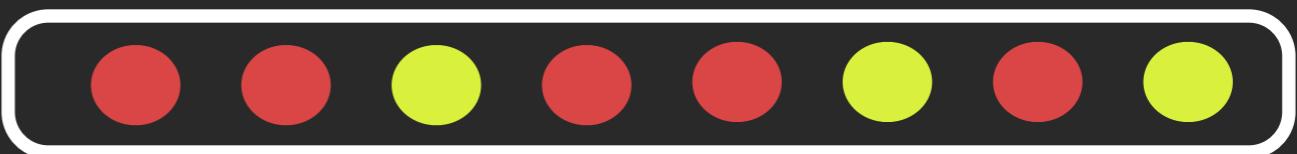
simulate evolution from all possible starting states

actual data



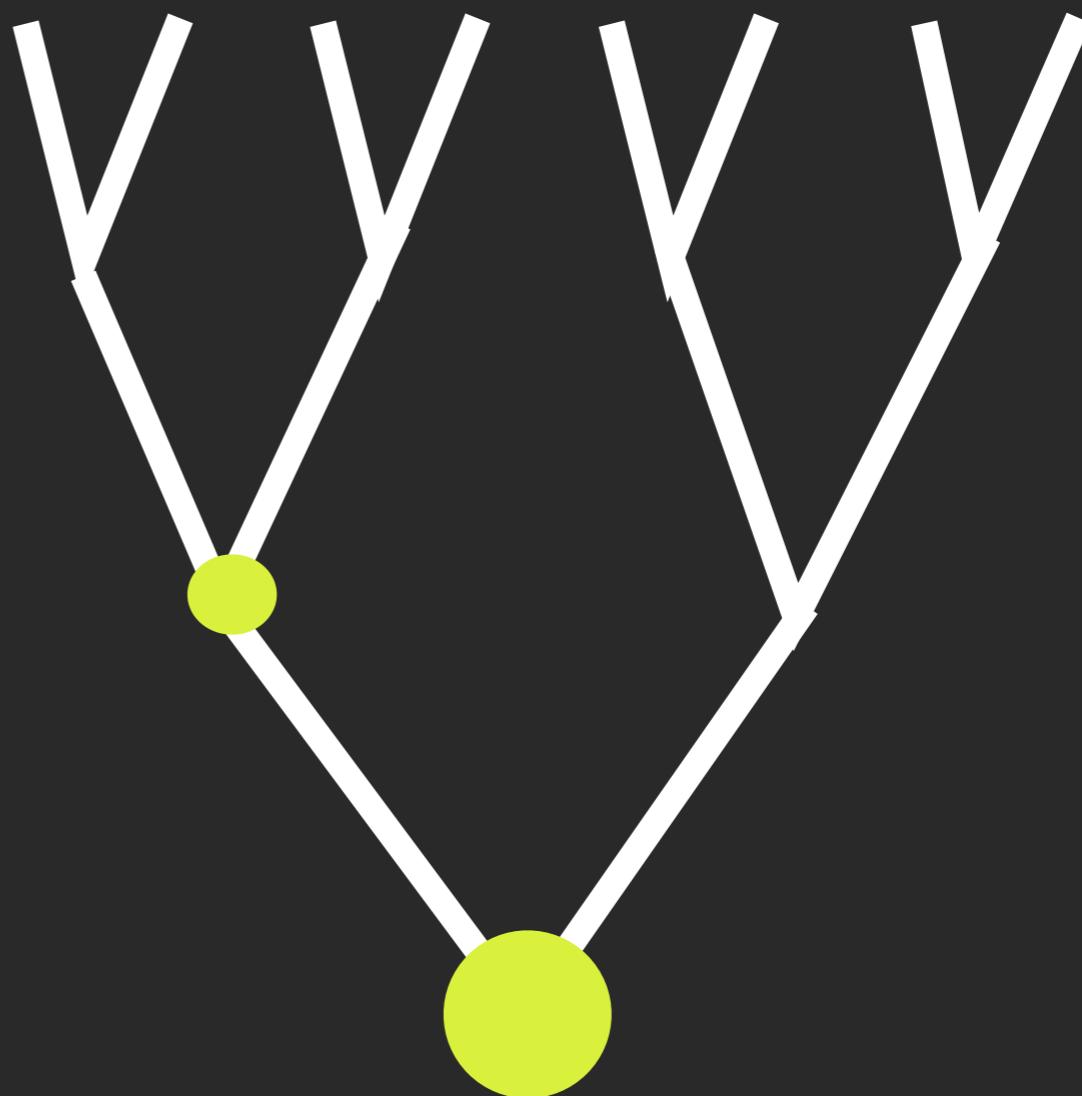
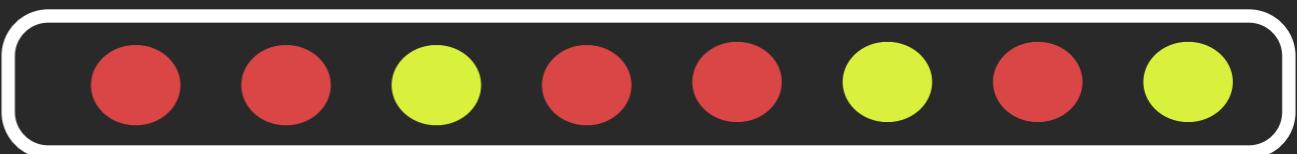
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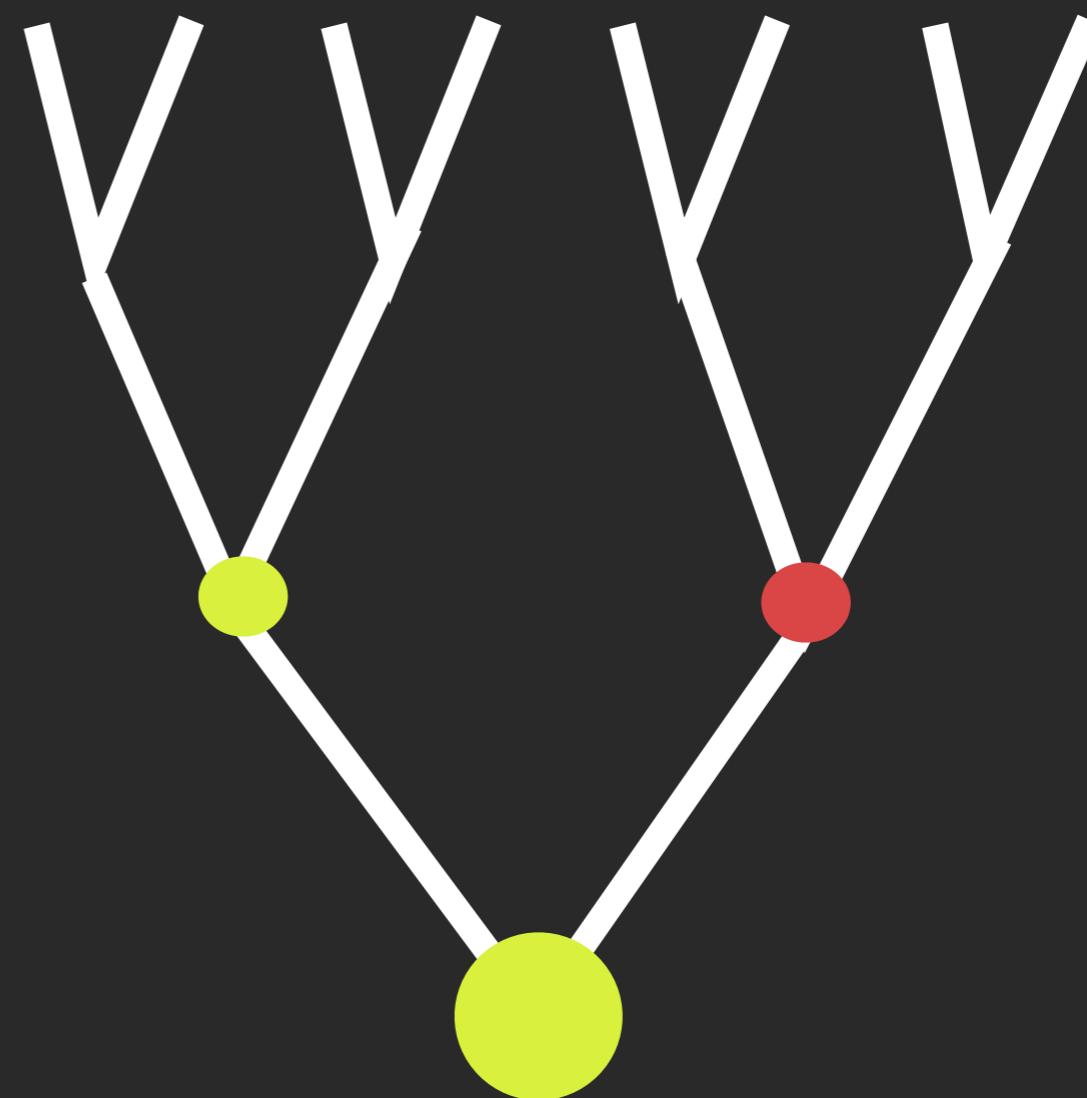
simulation one

actual data



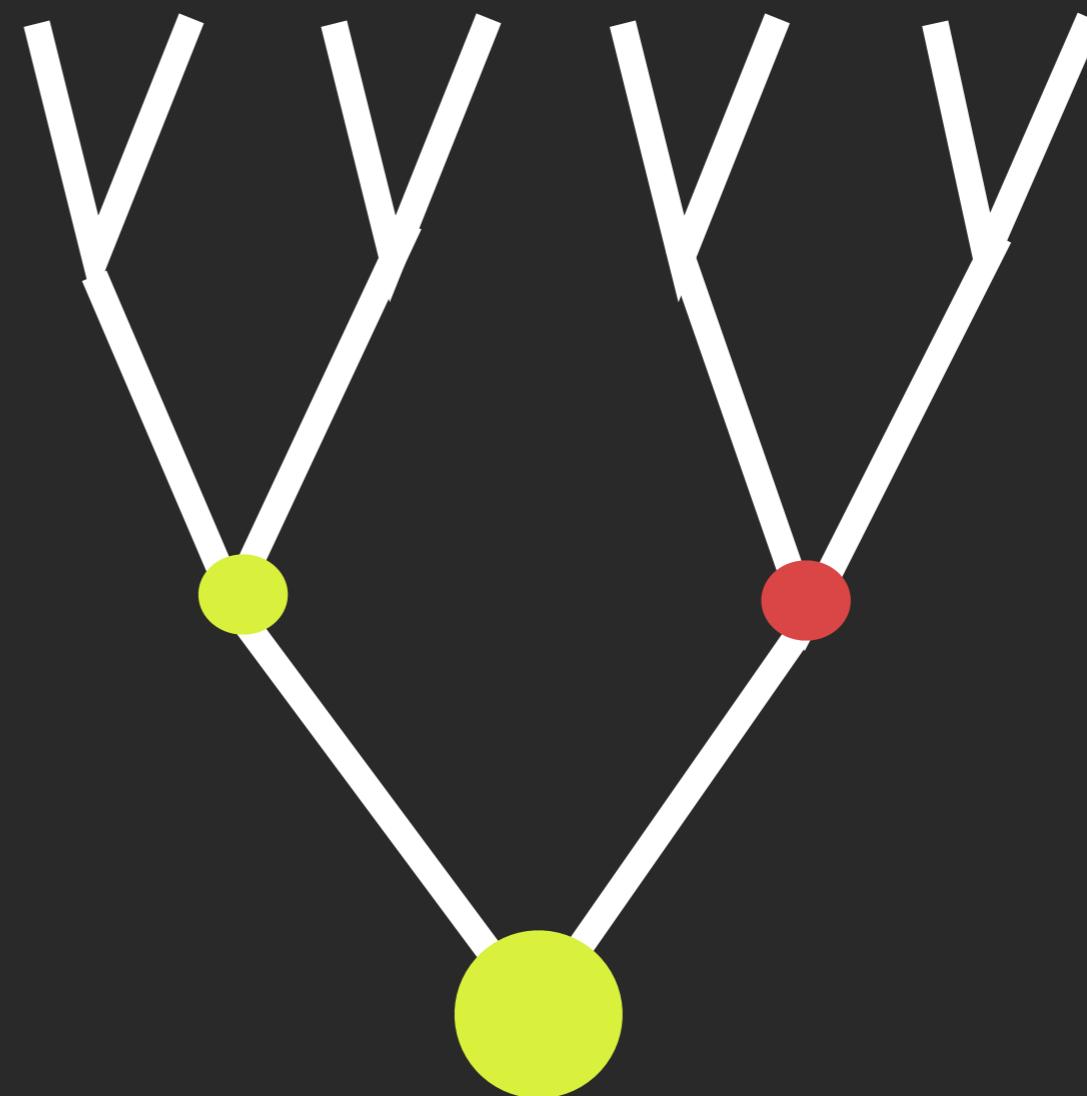
simulation one

actual data



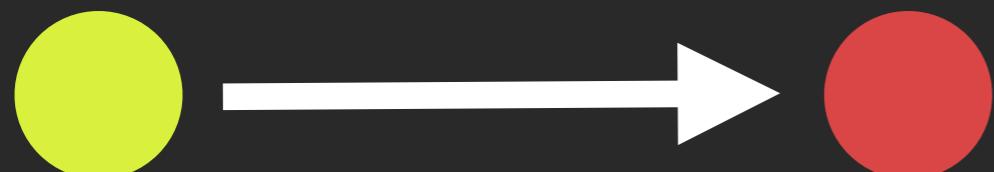
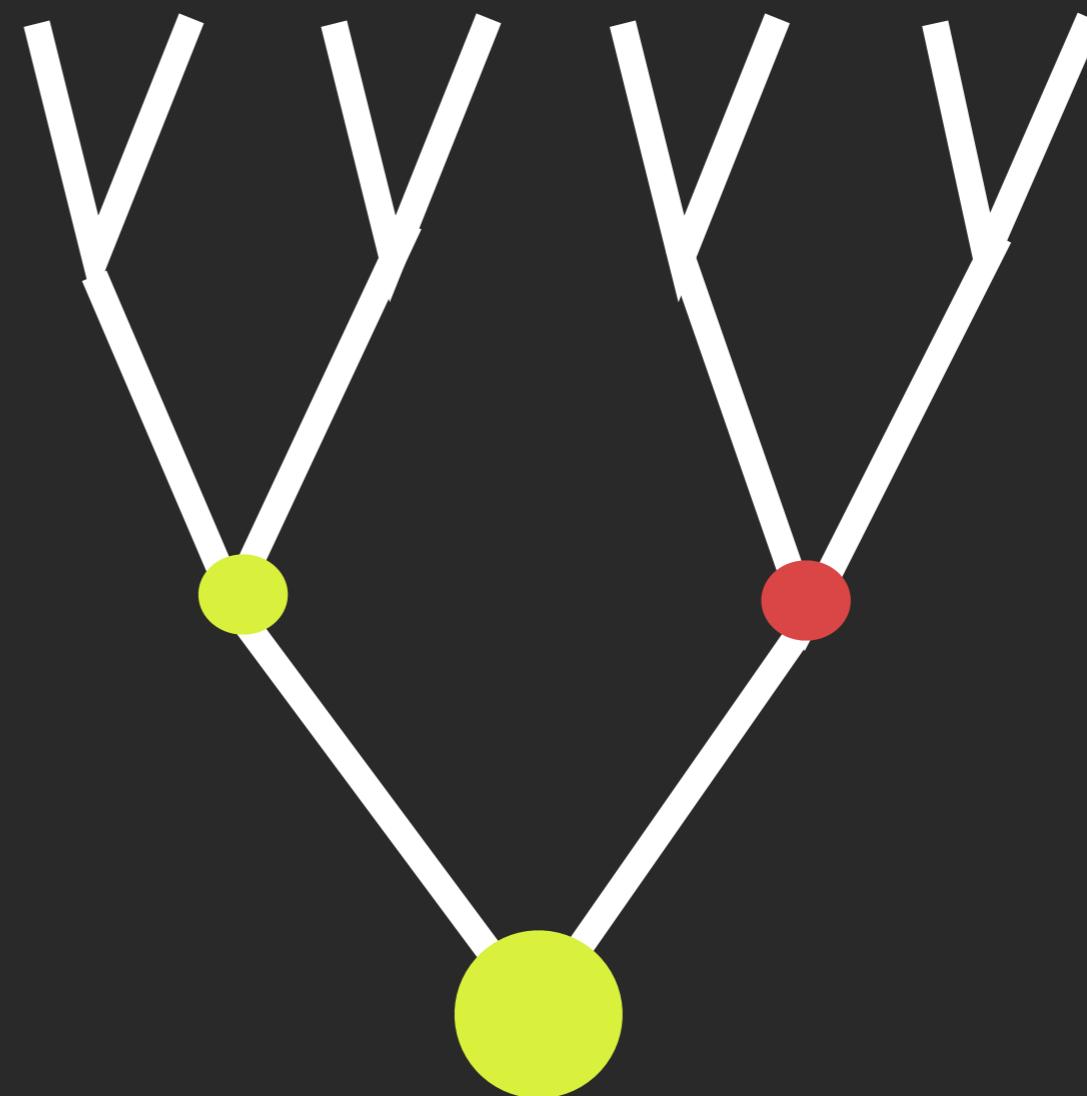
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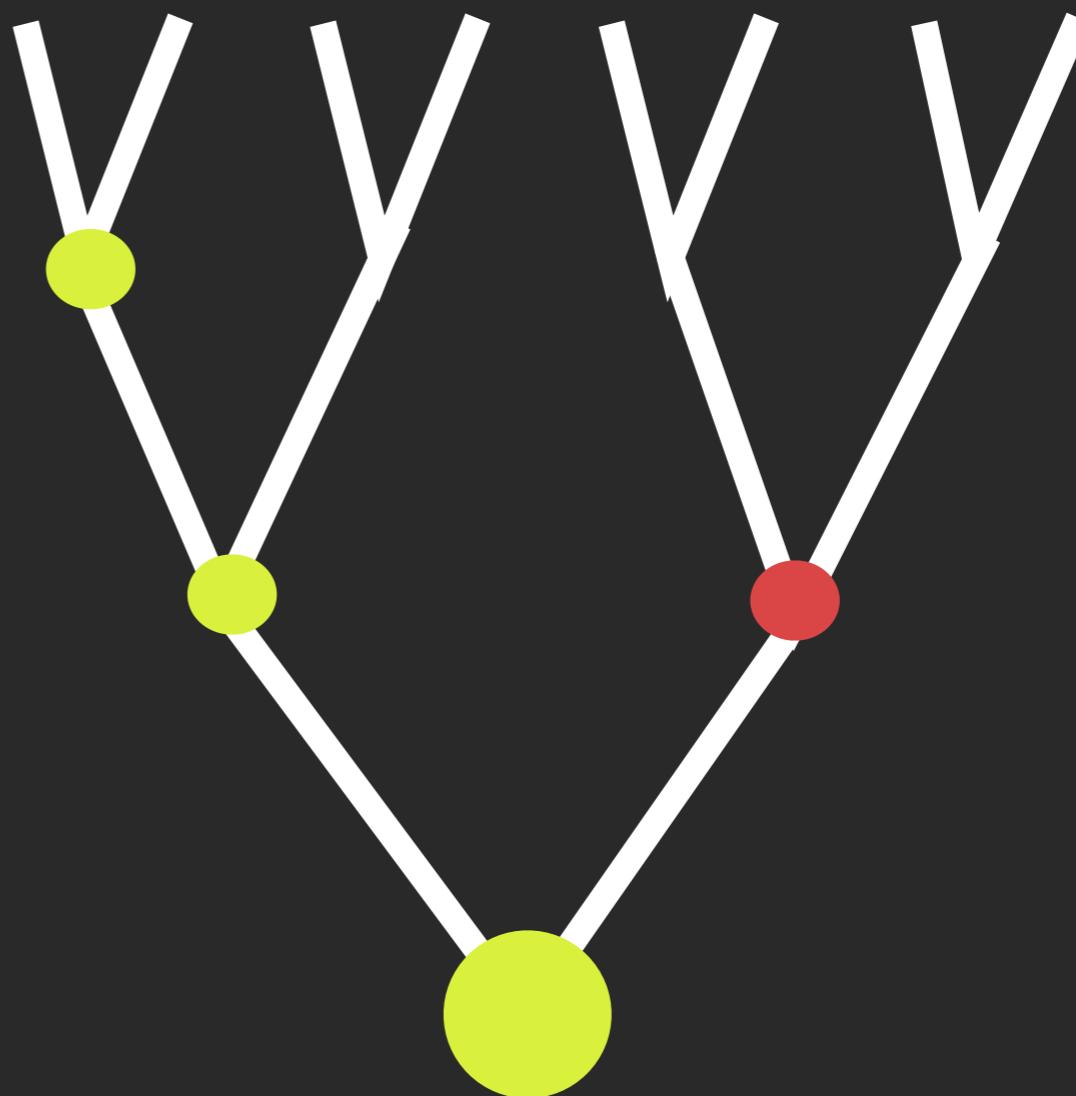
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actual data



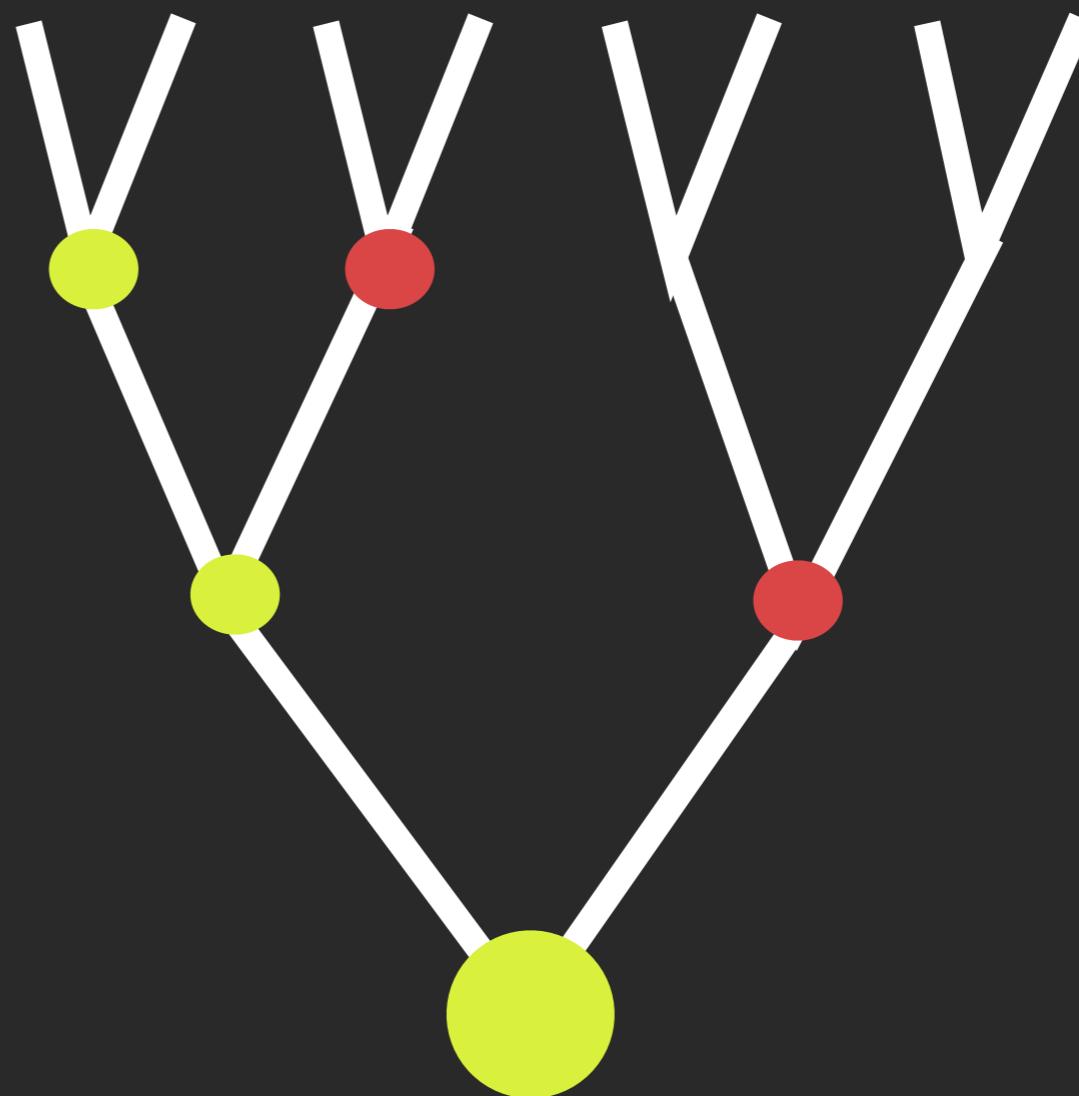
simulation one

actual data



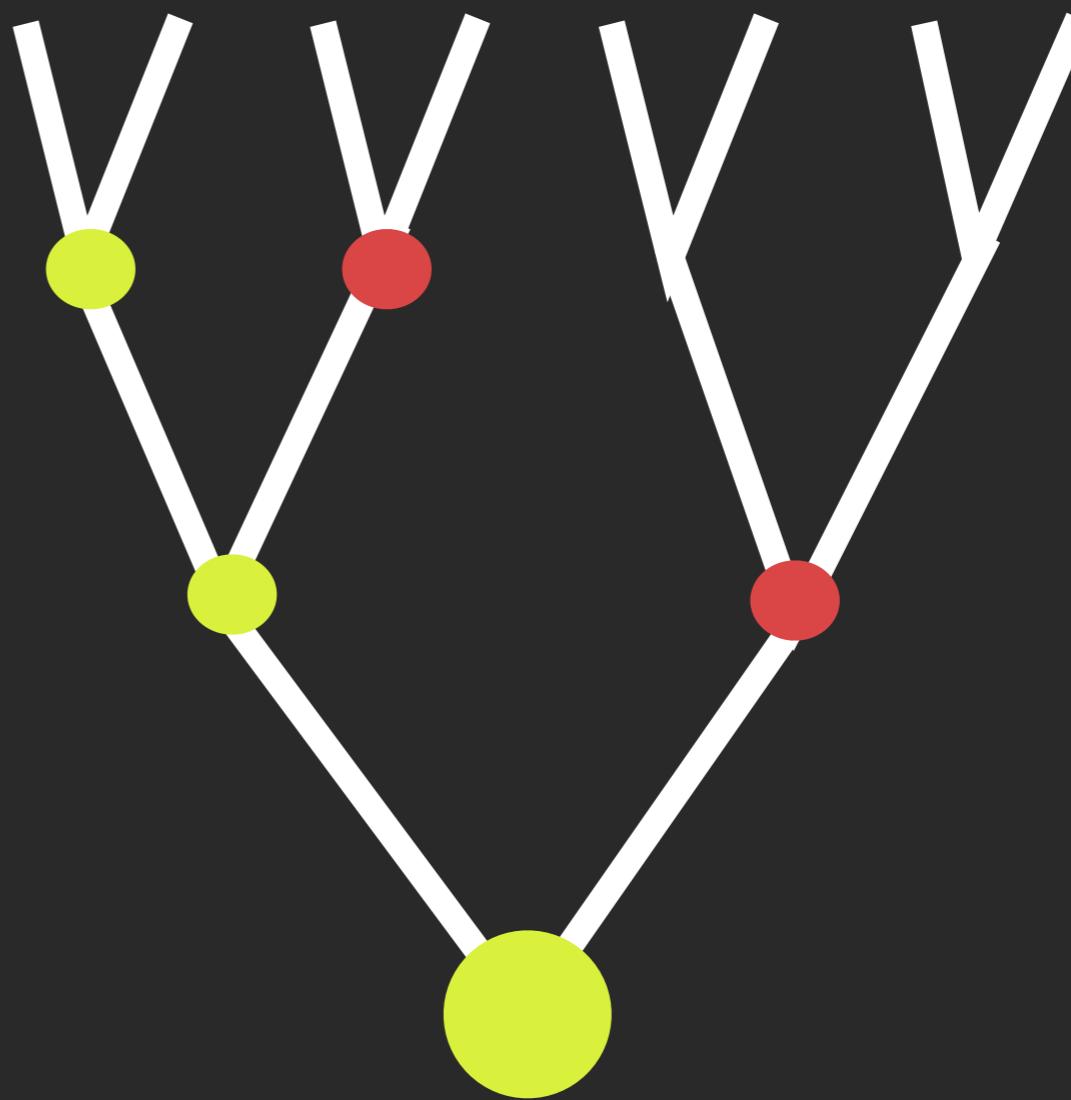
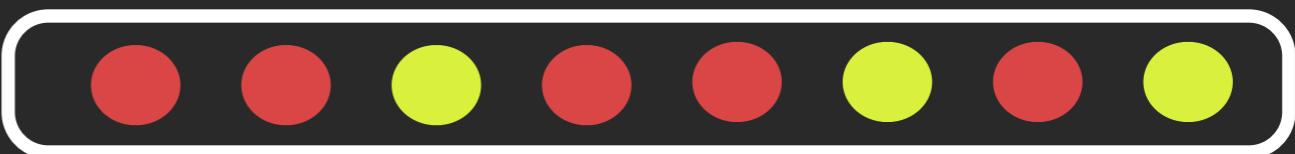
simulation one

actual data



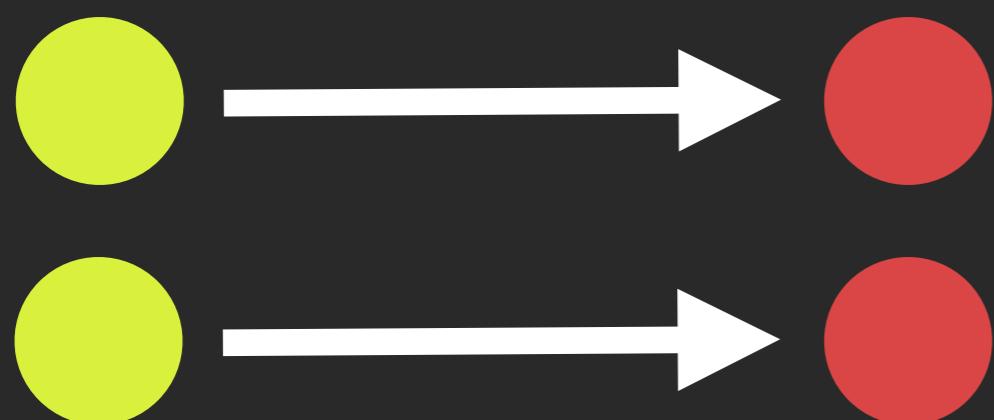
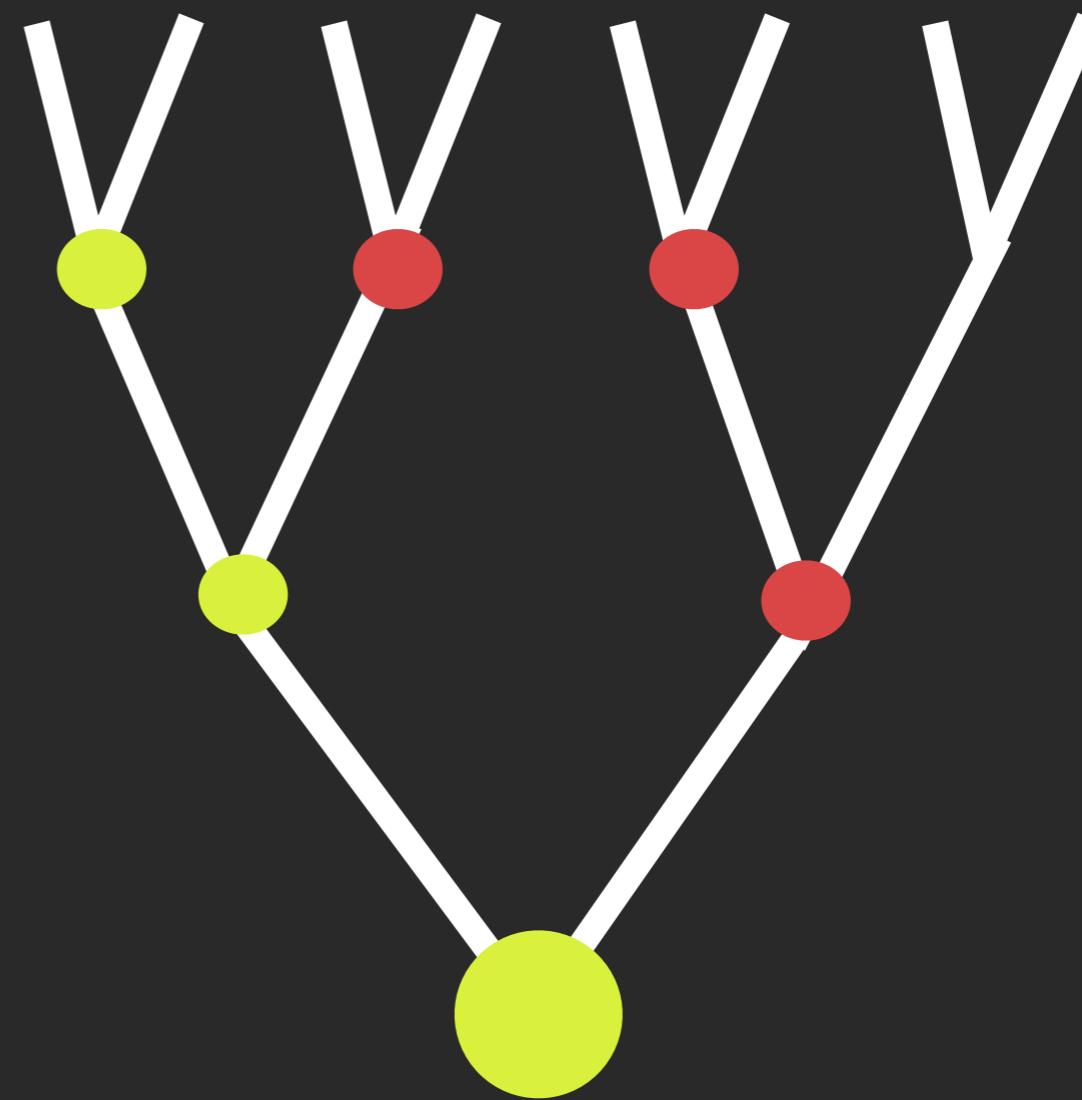
simulation one

actual data



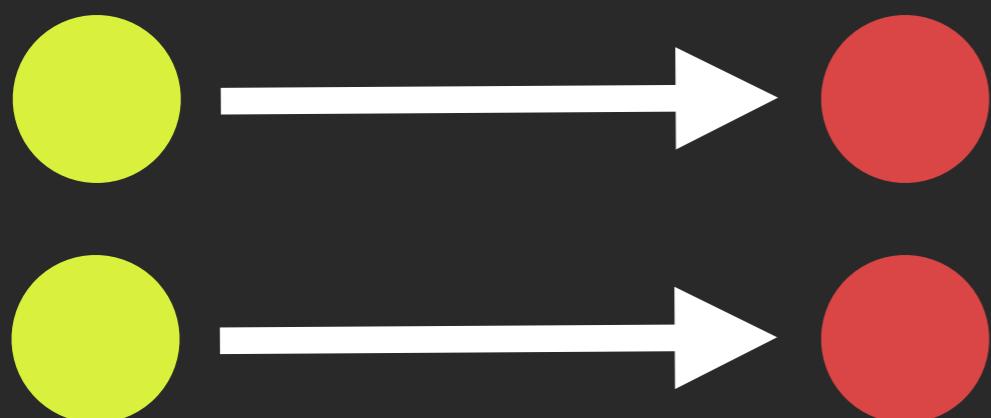
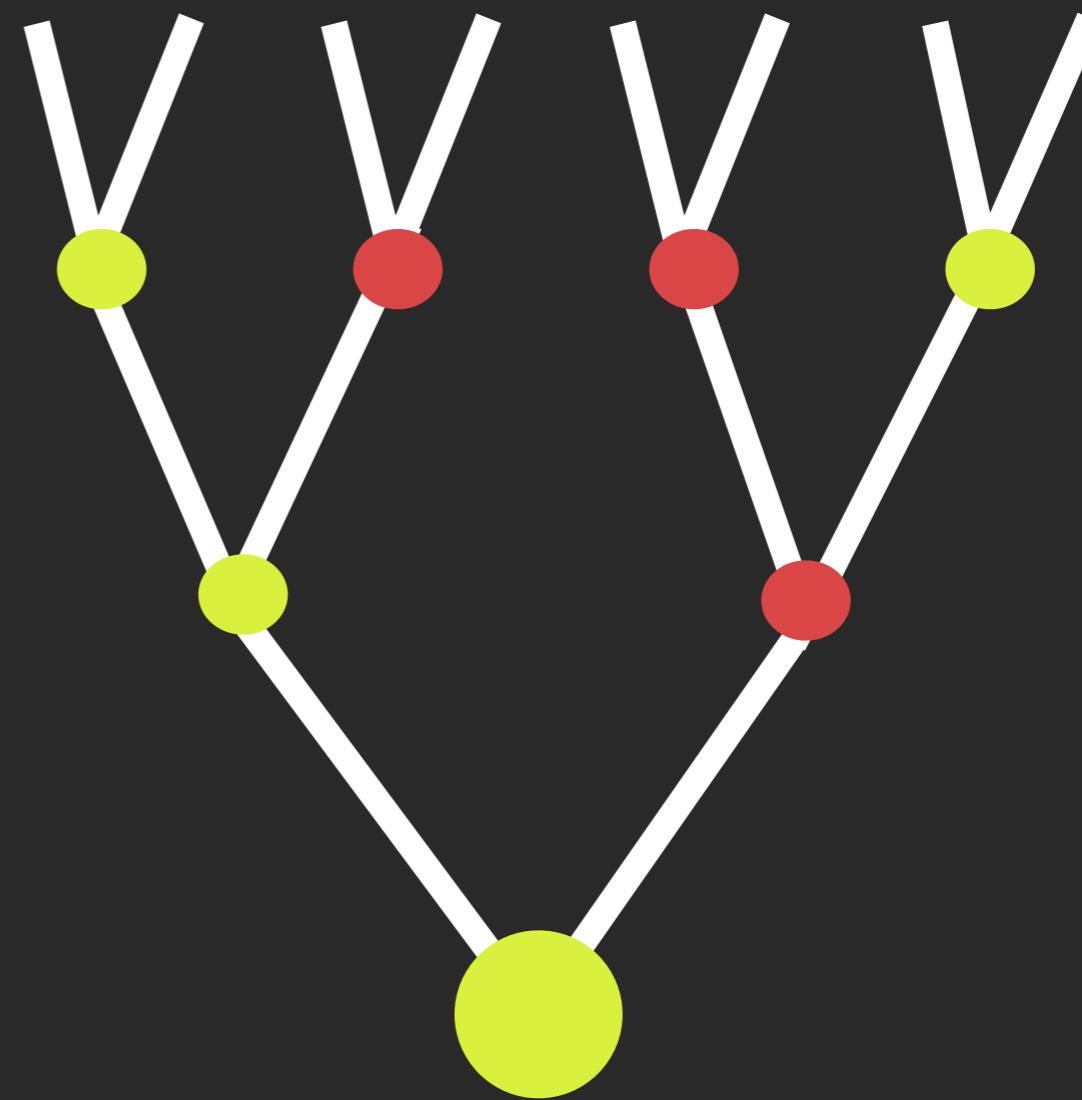
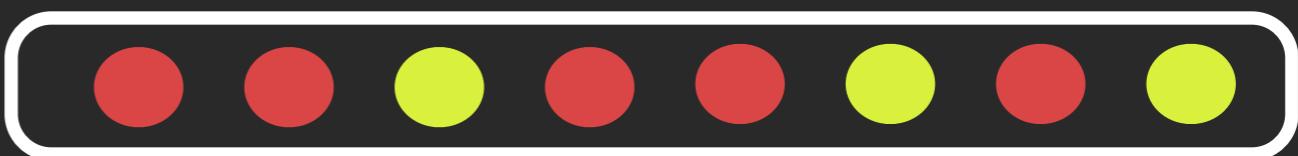
simulation one

actual data



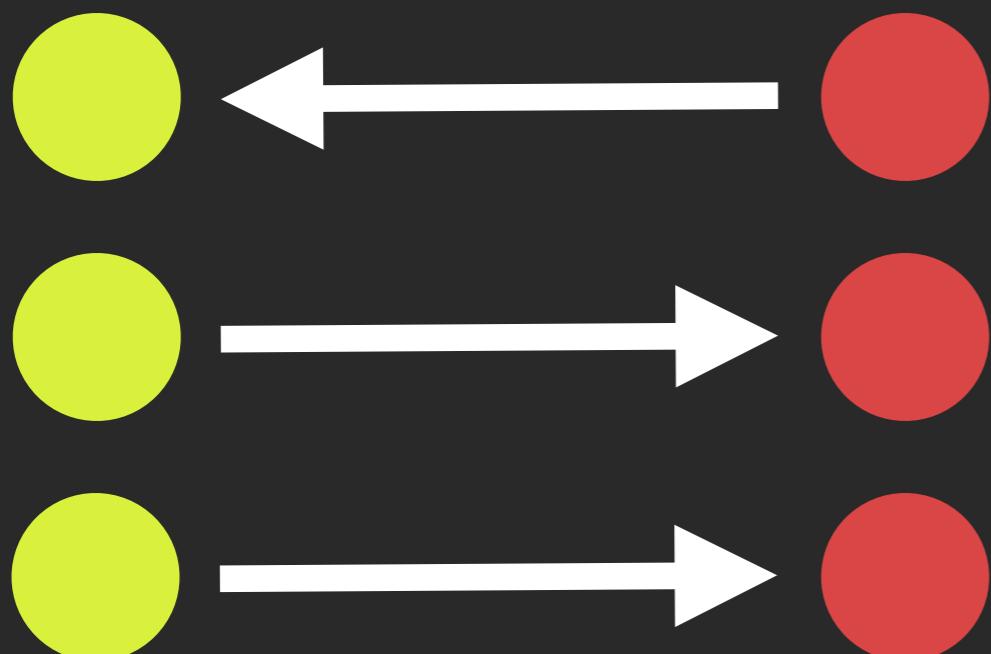
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actual data

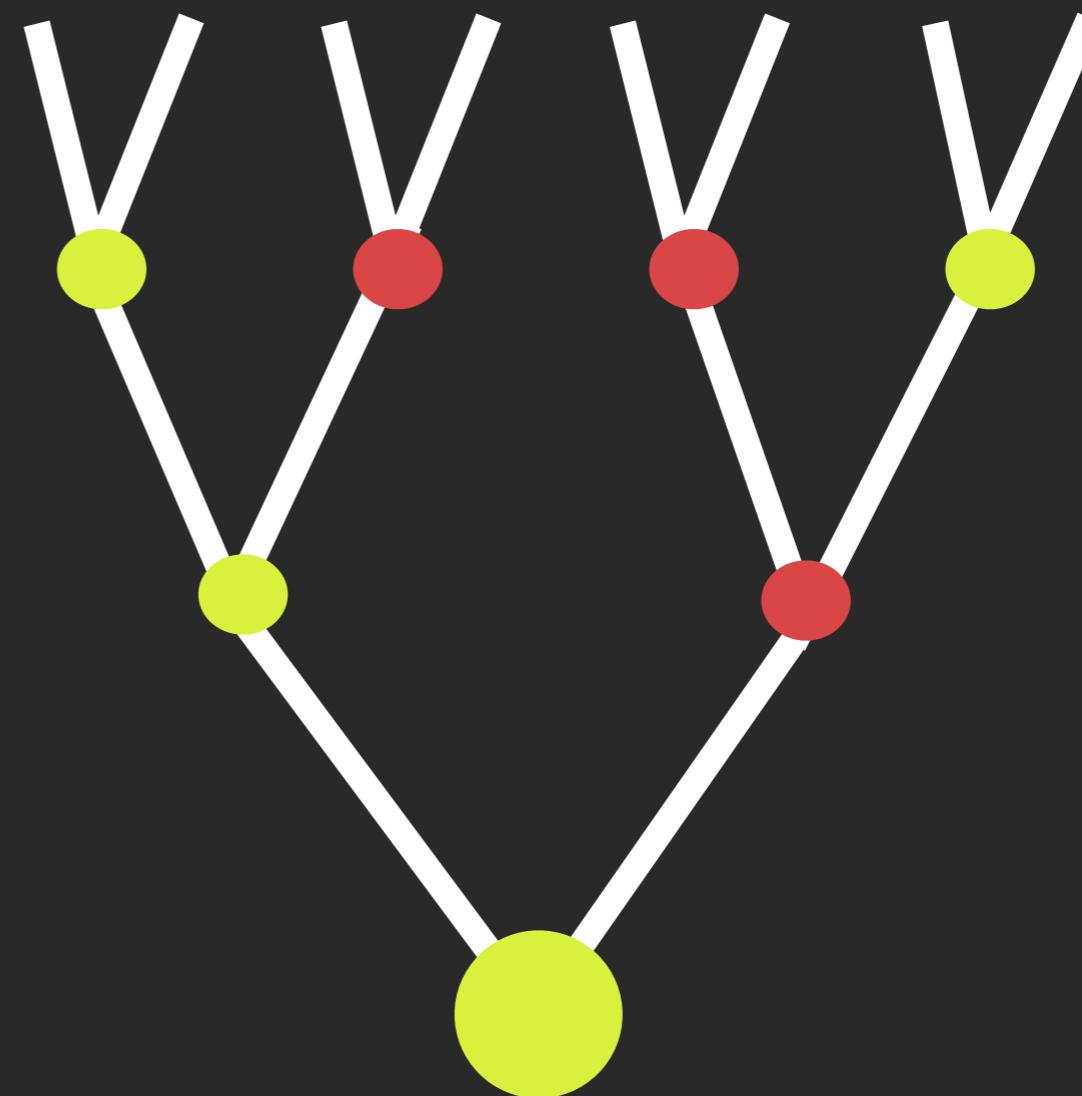


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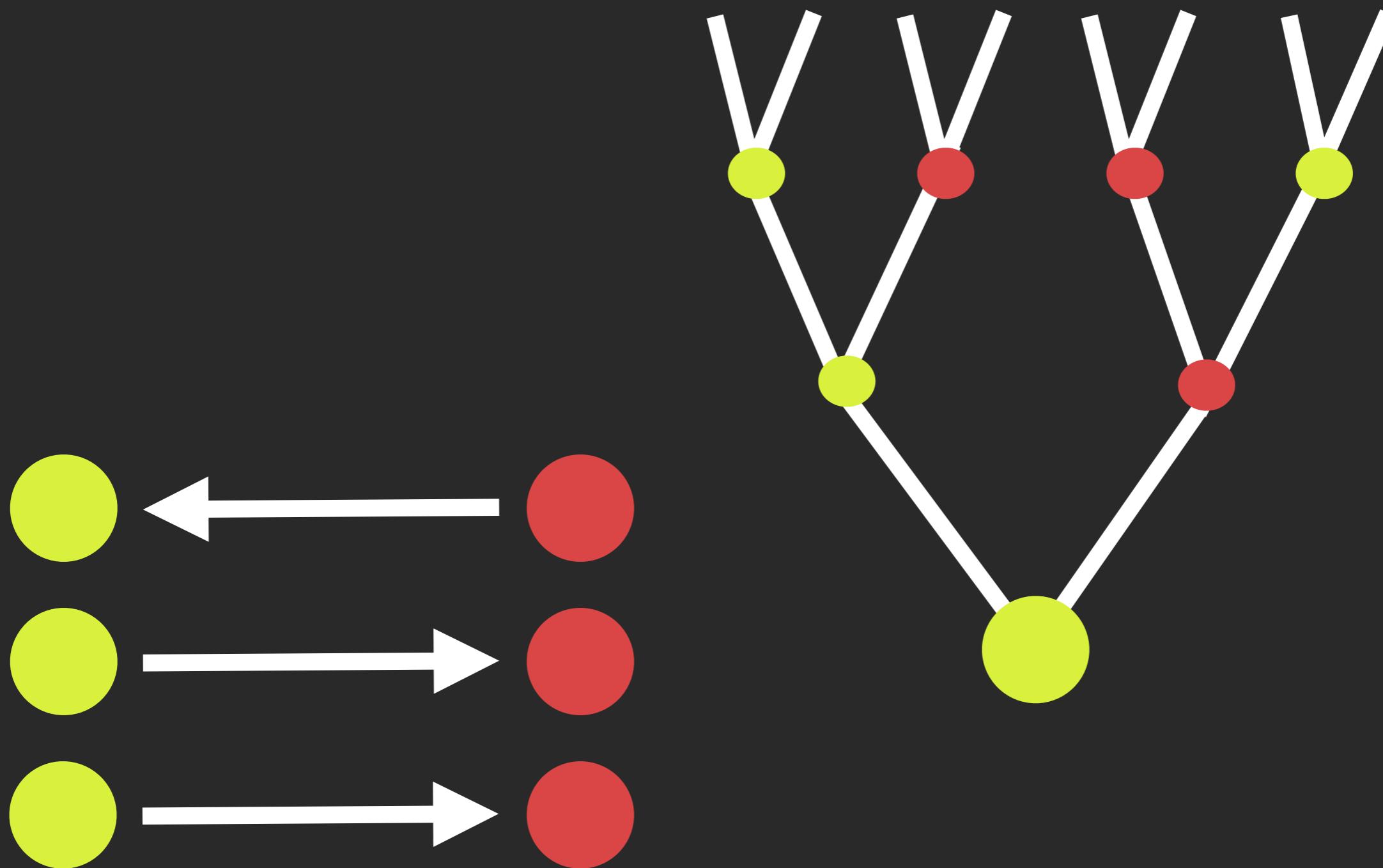
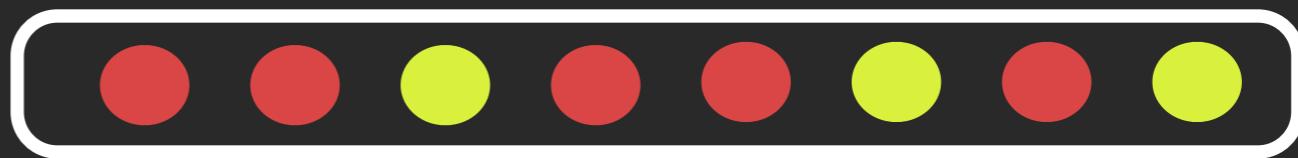
actual data



simulation one

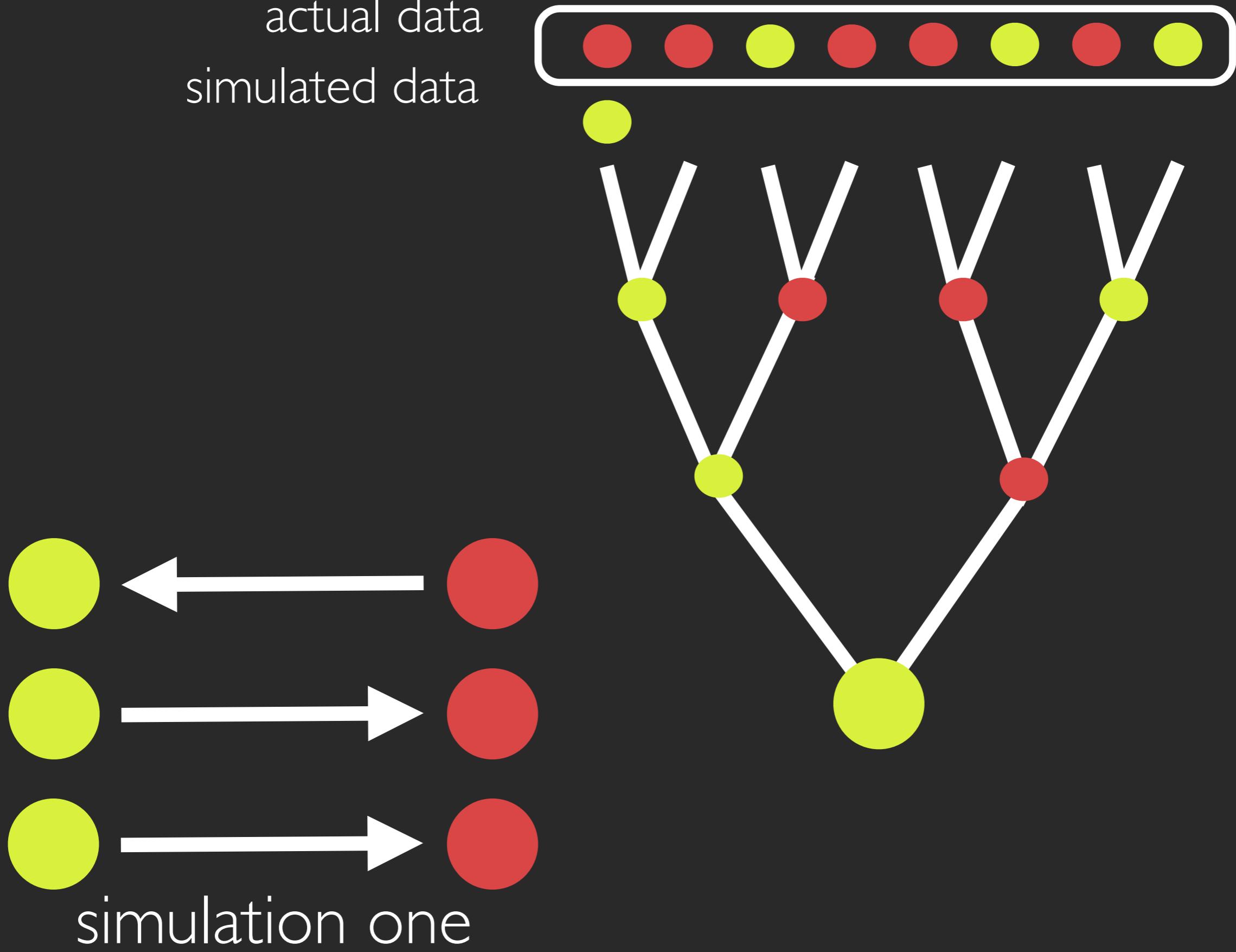


actual data
simulated data

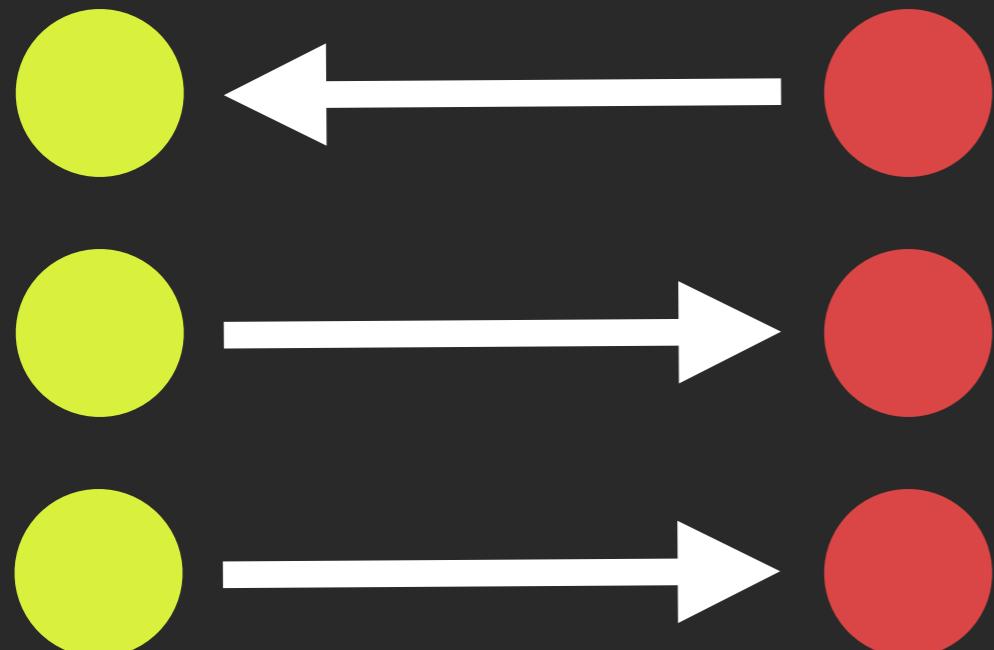


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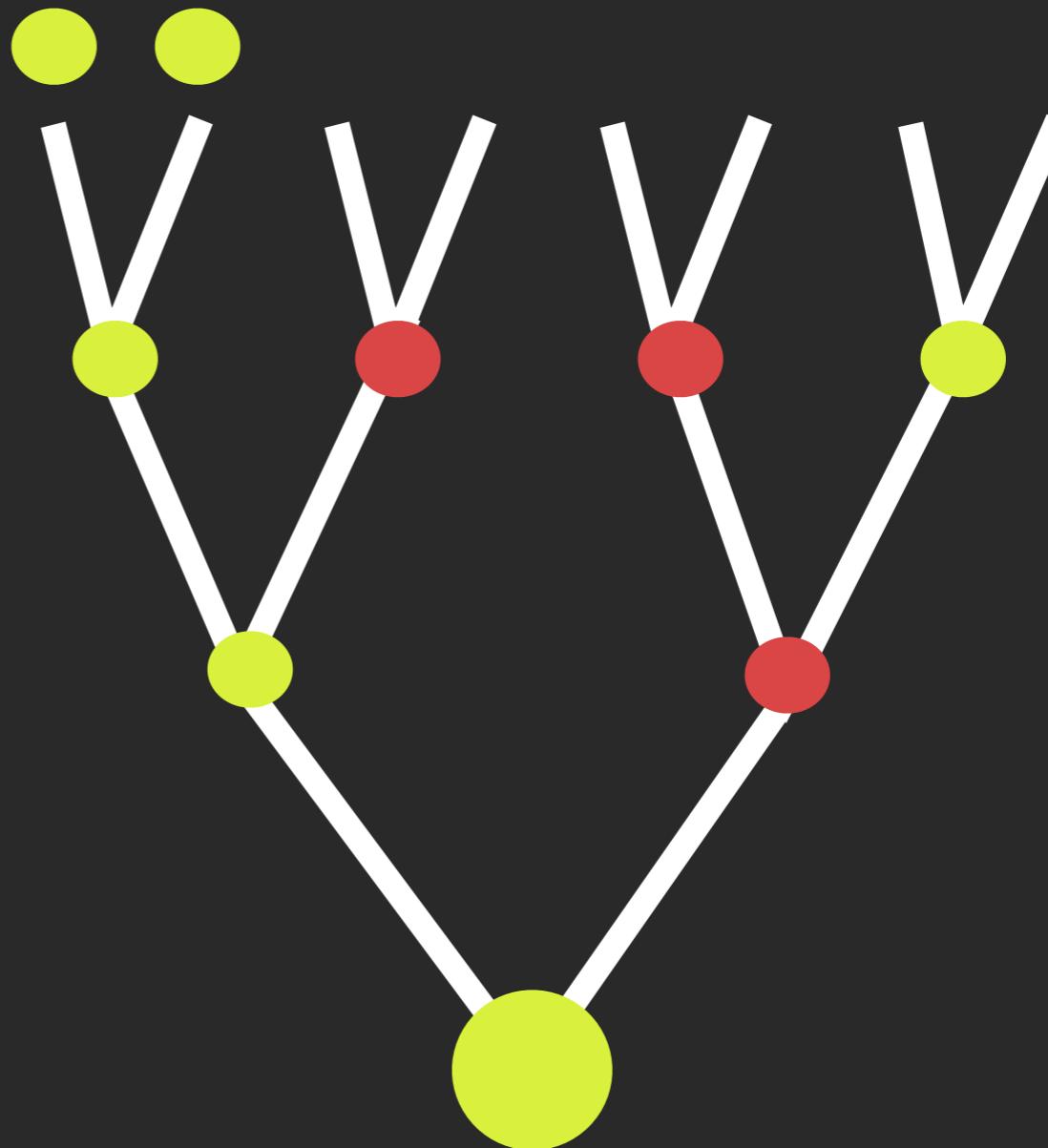
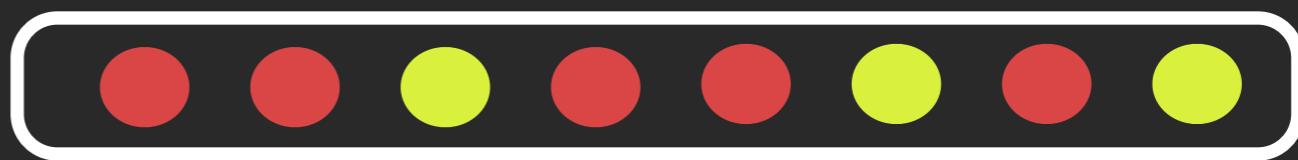
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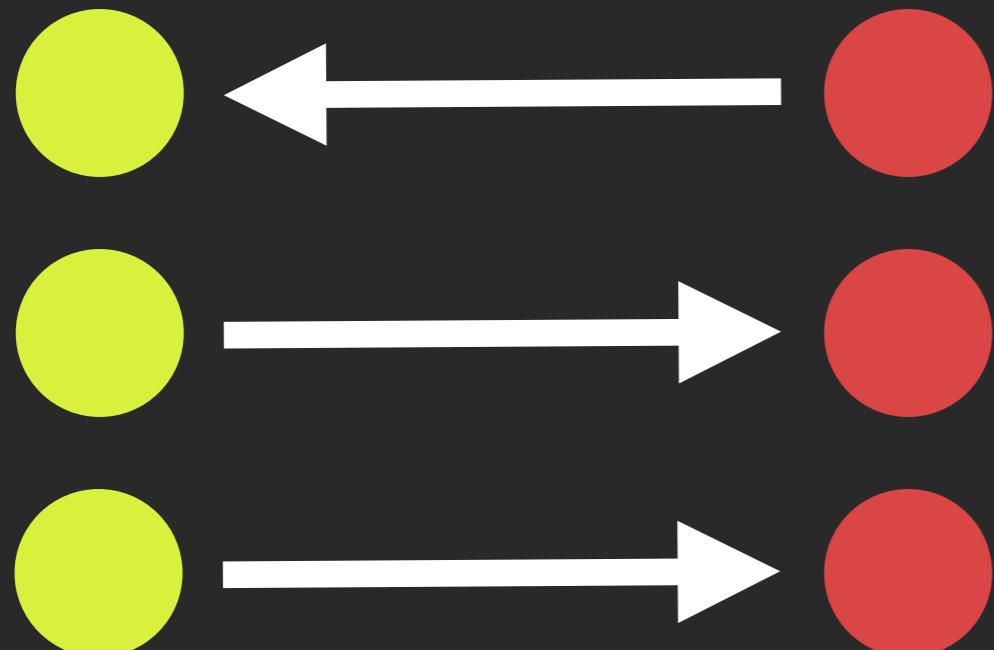
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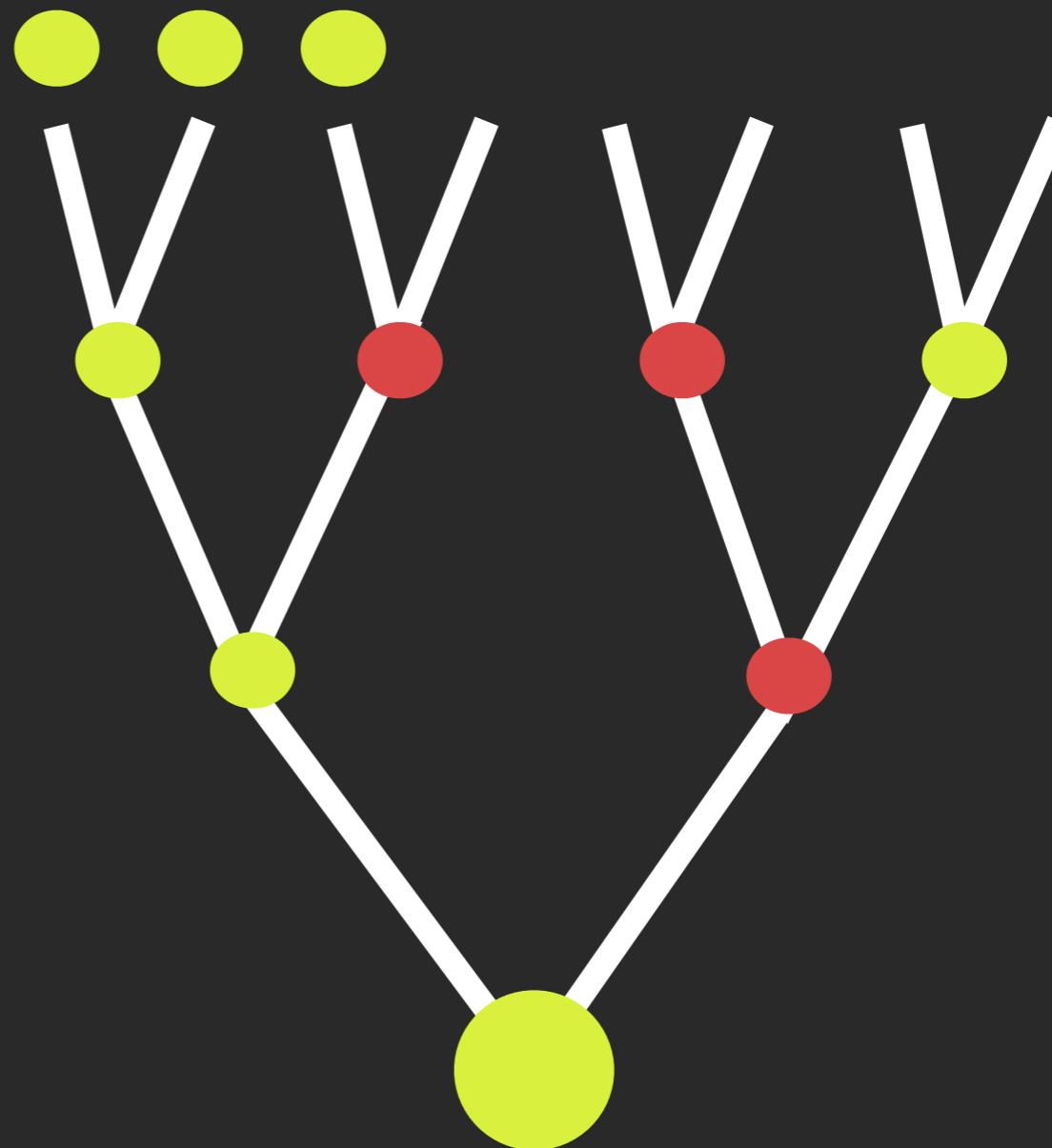
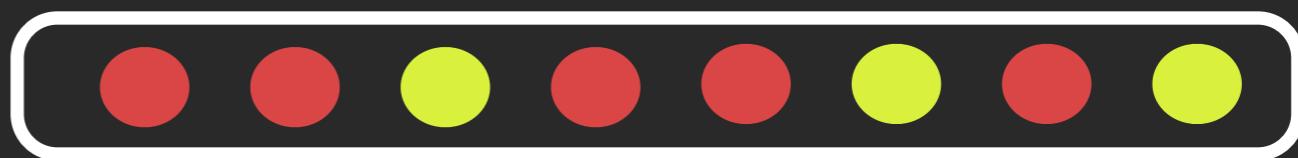
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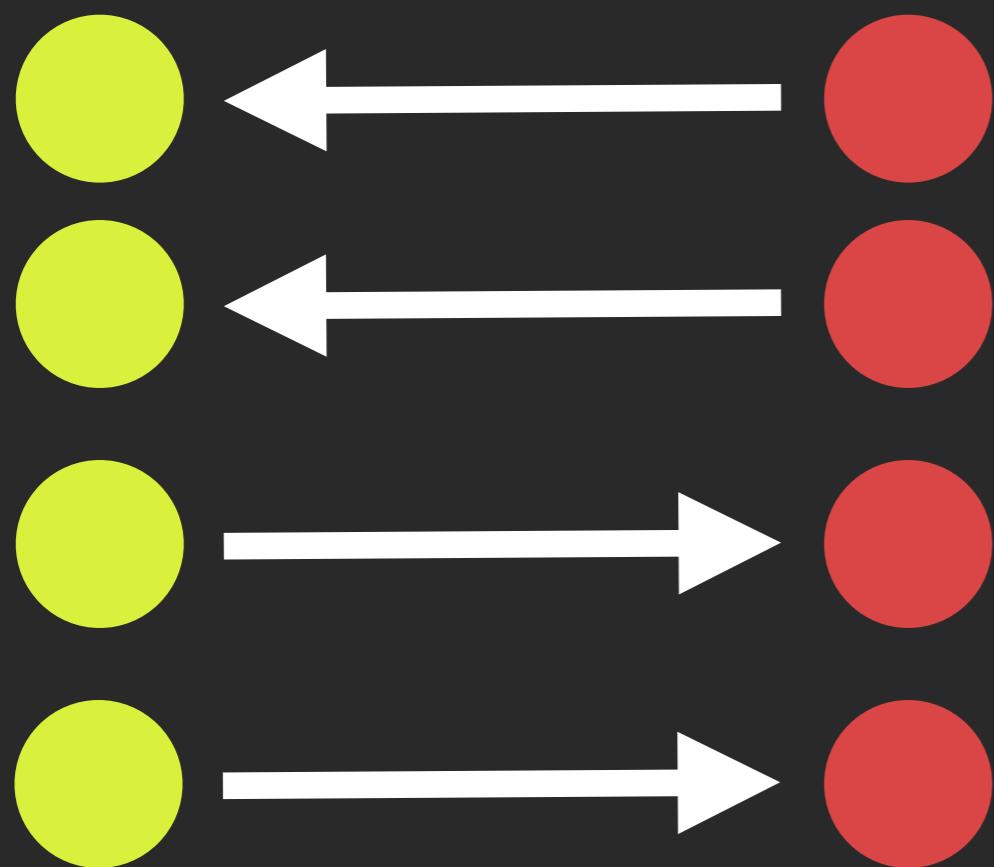
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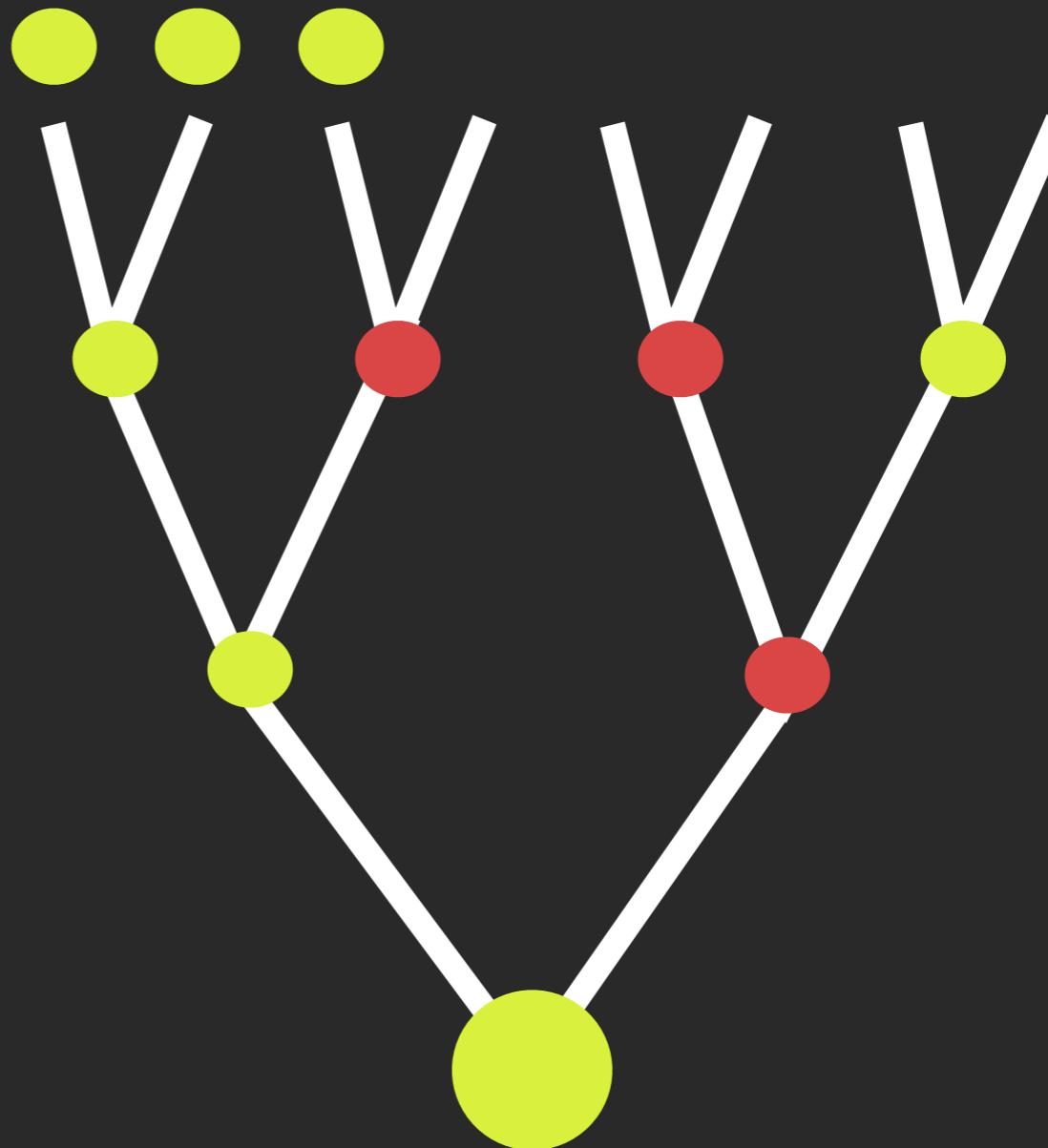
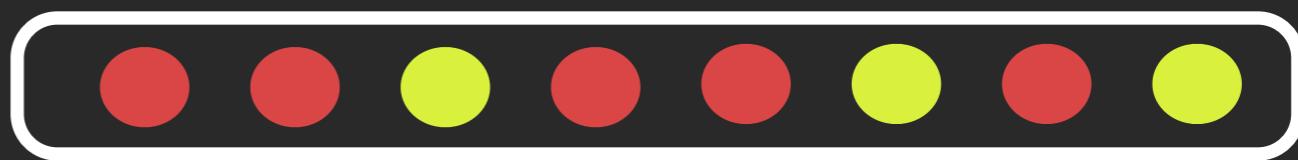
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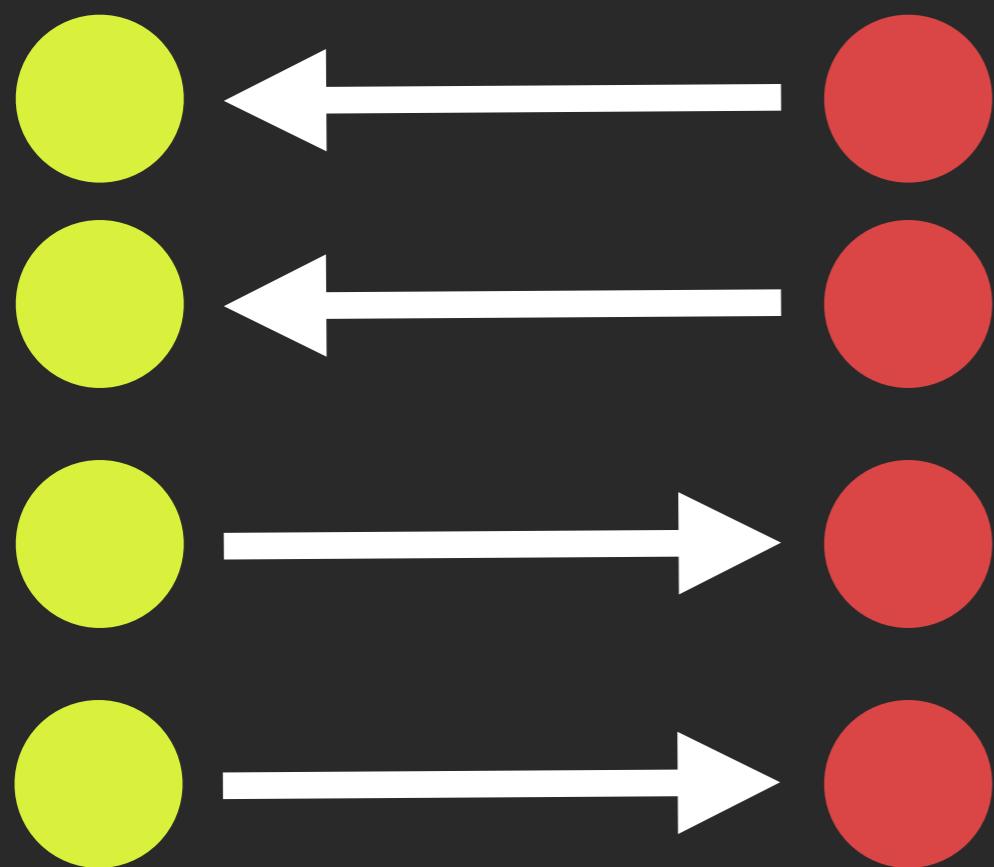
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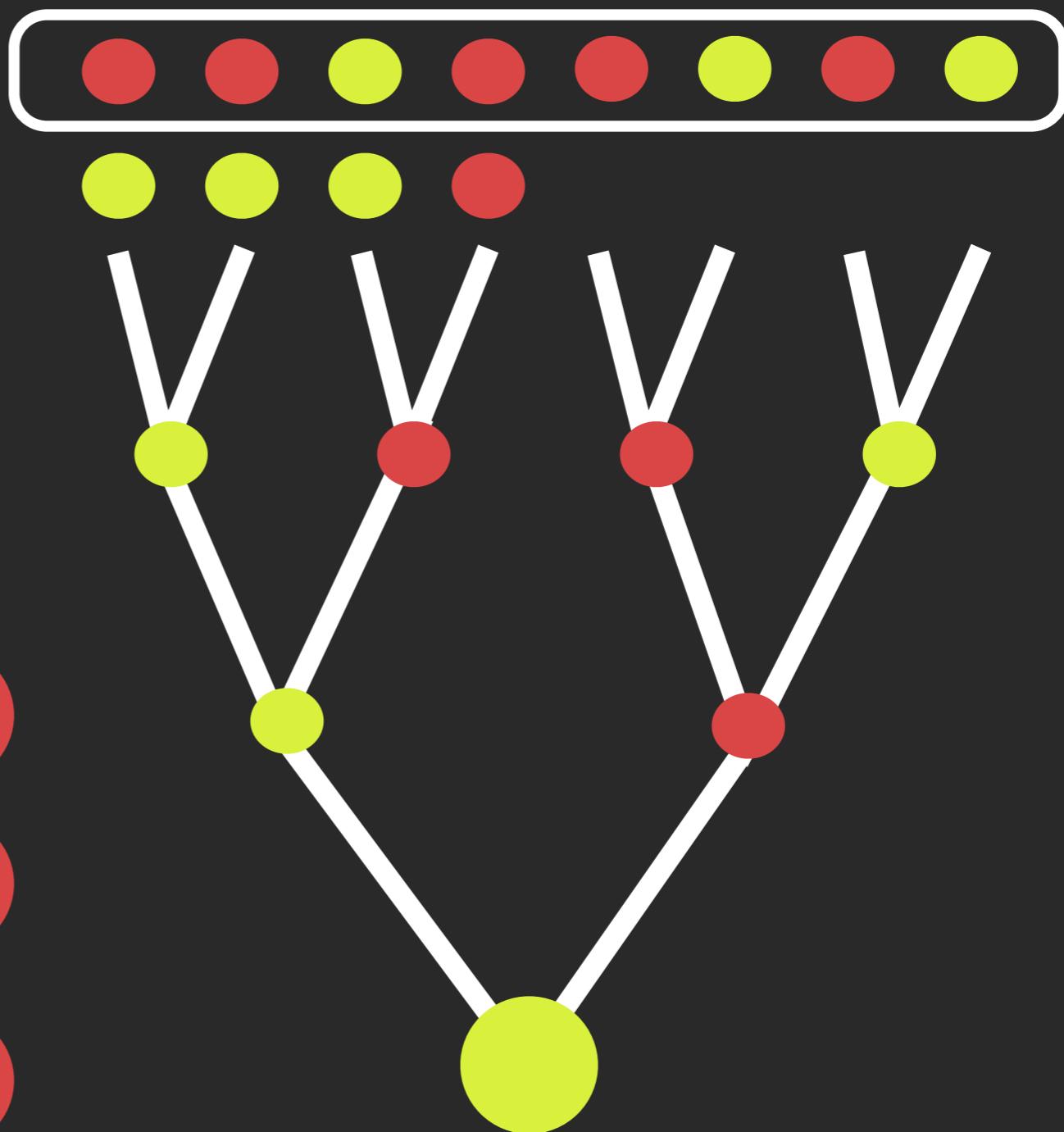
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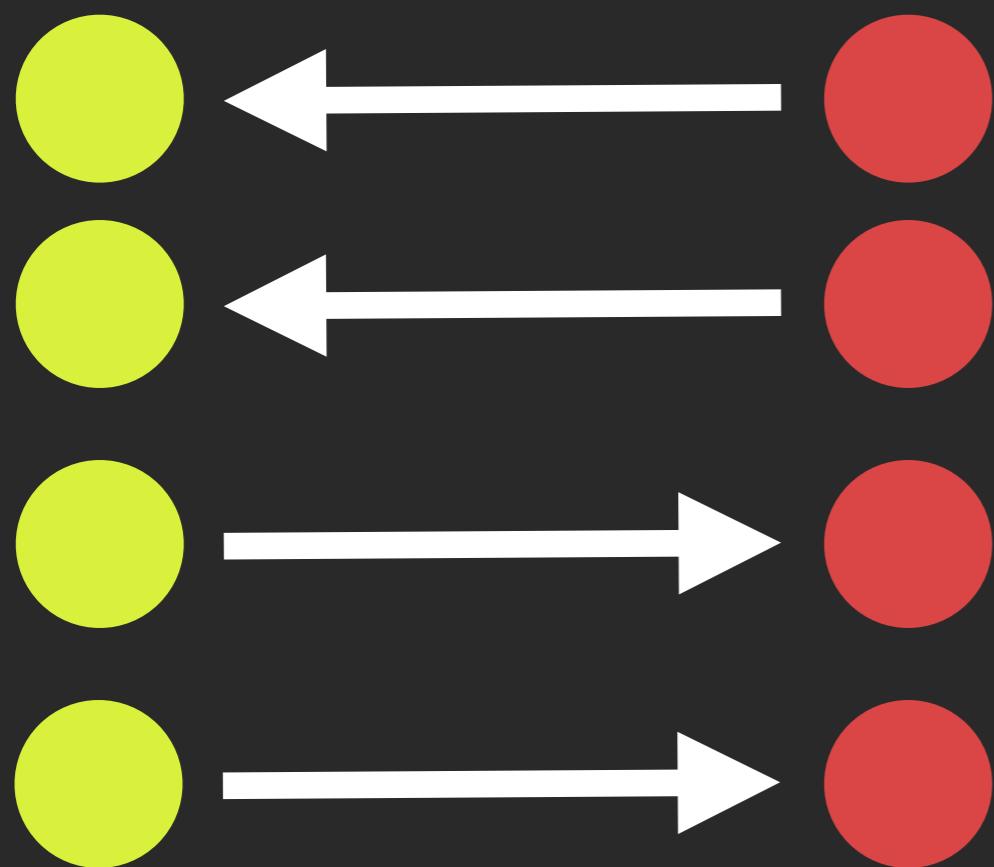
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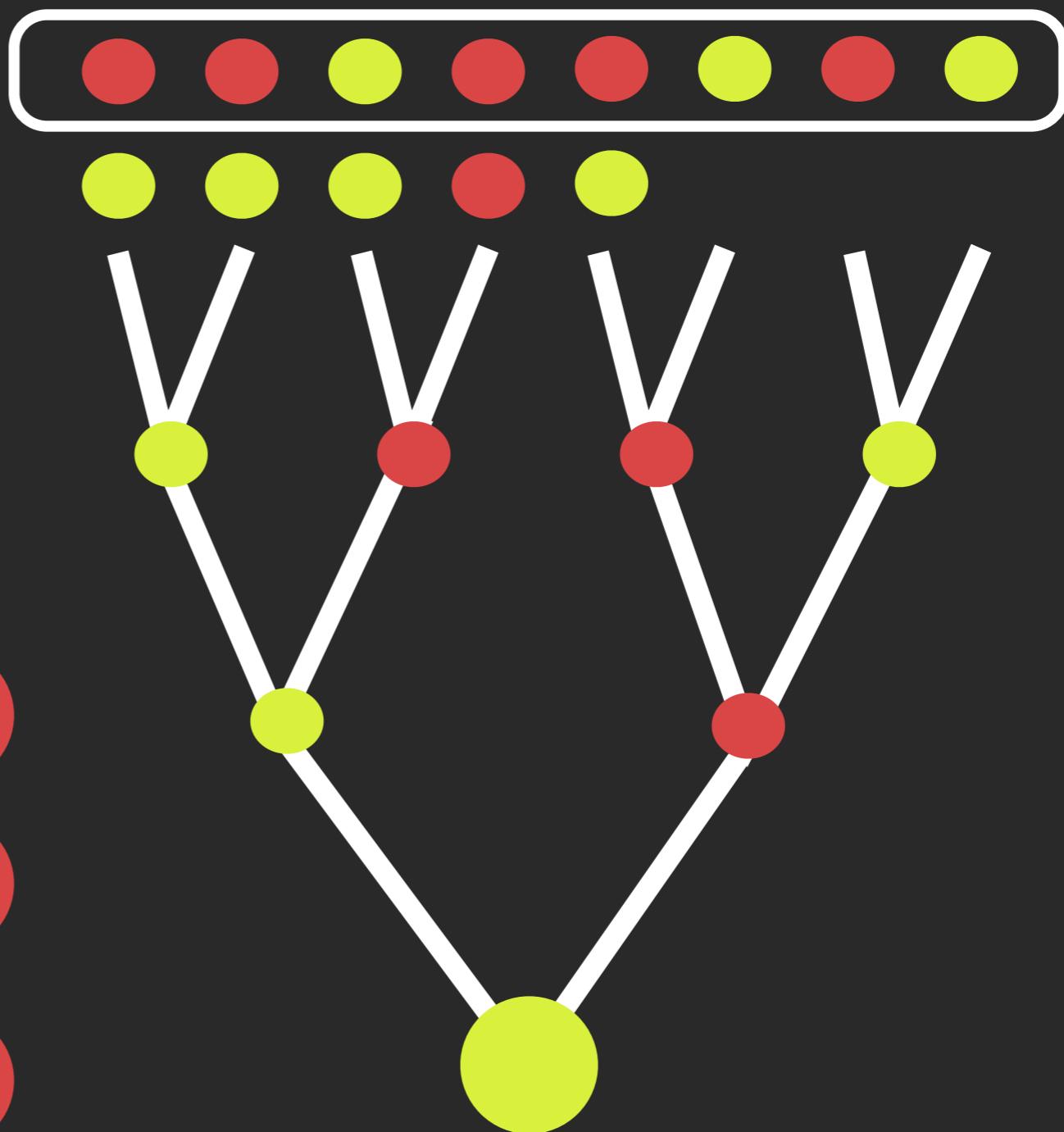
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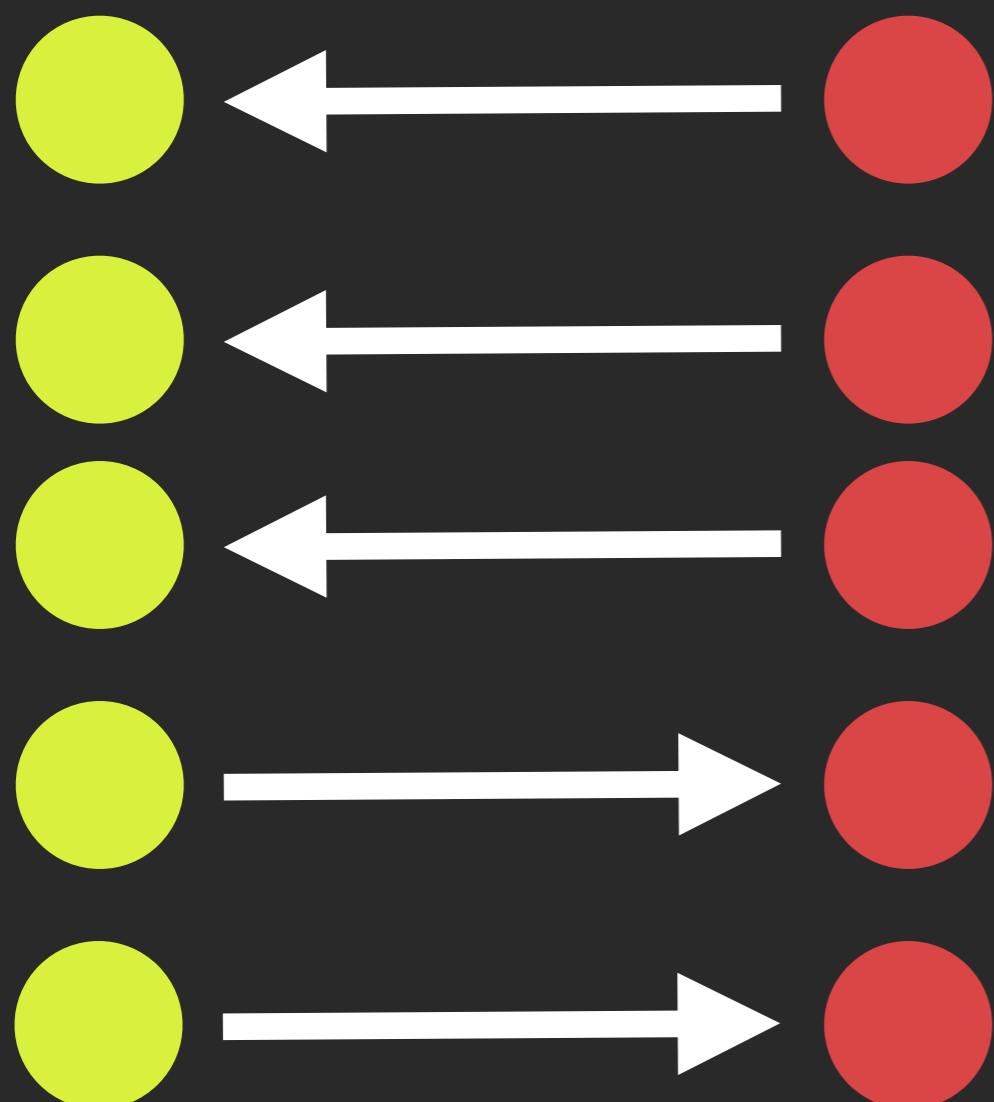
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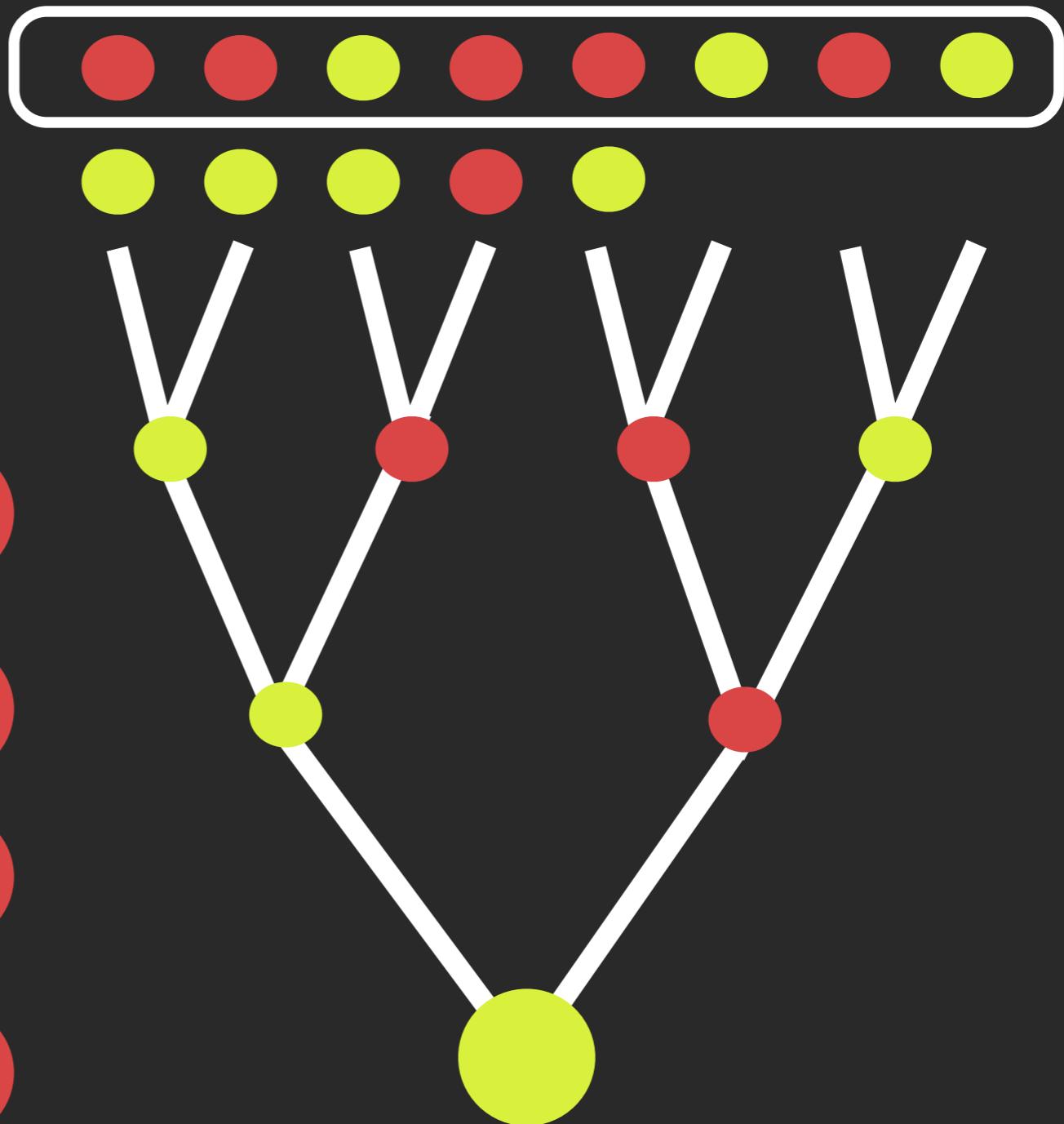
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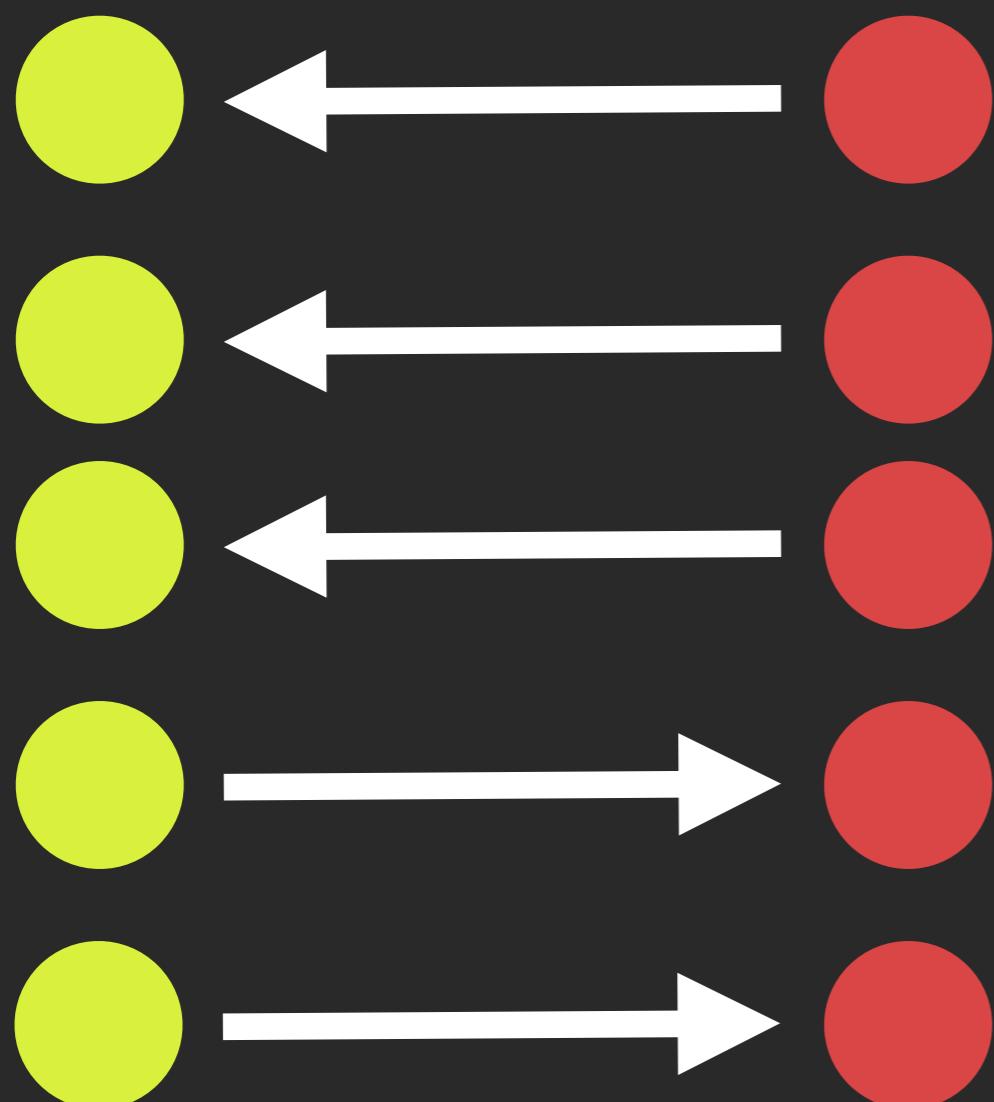
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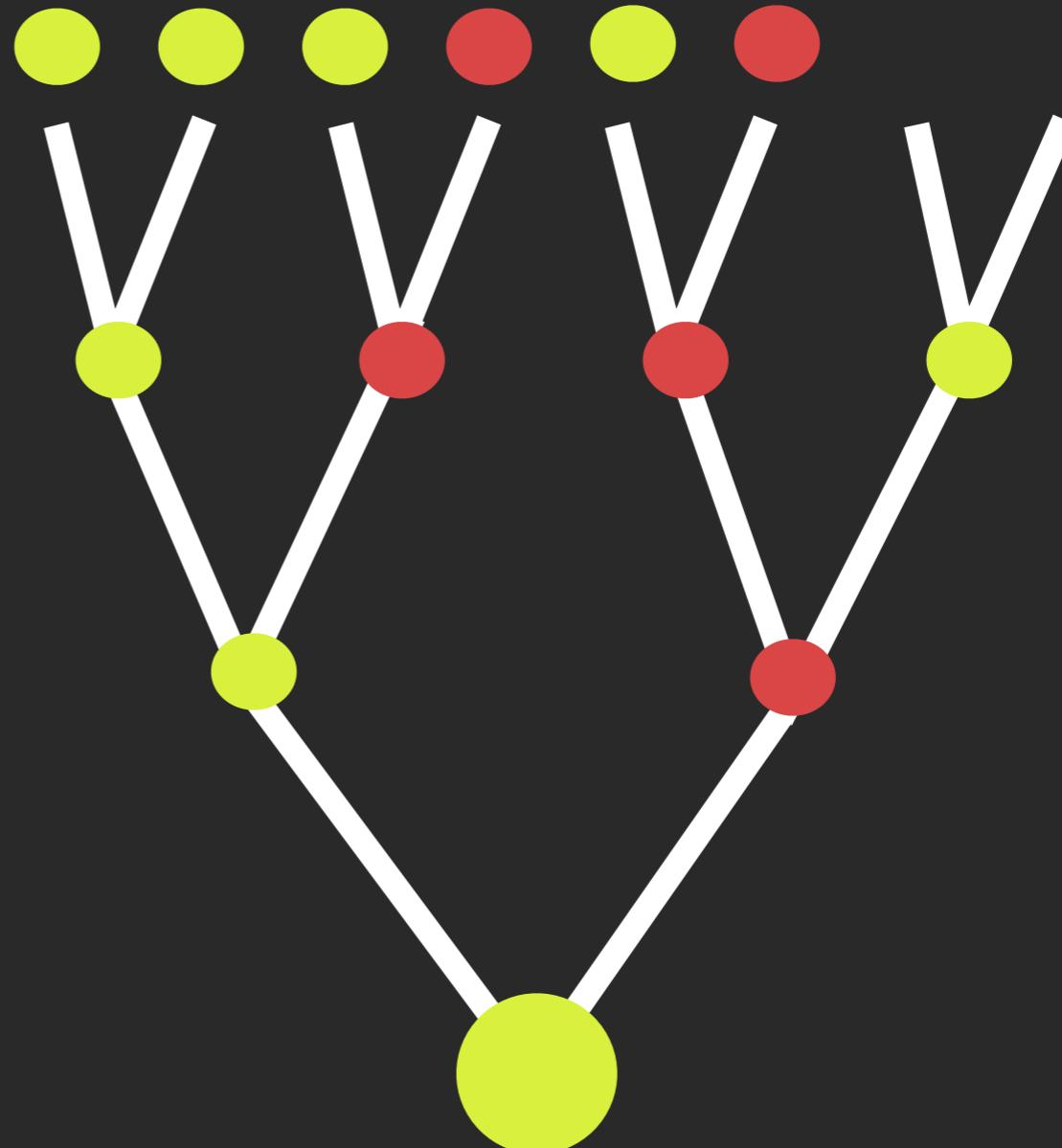
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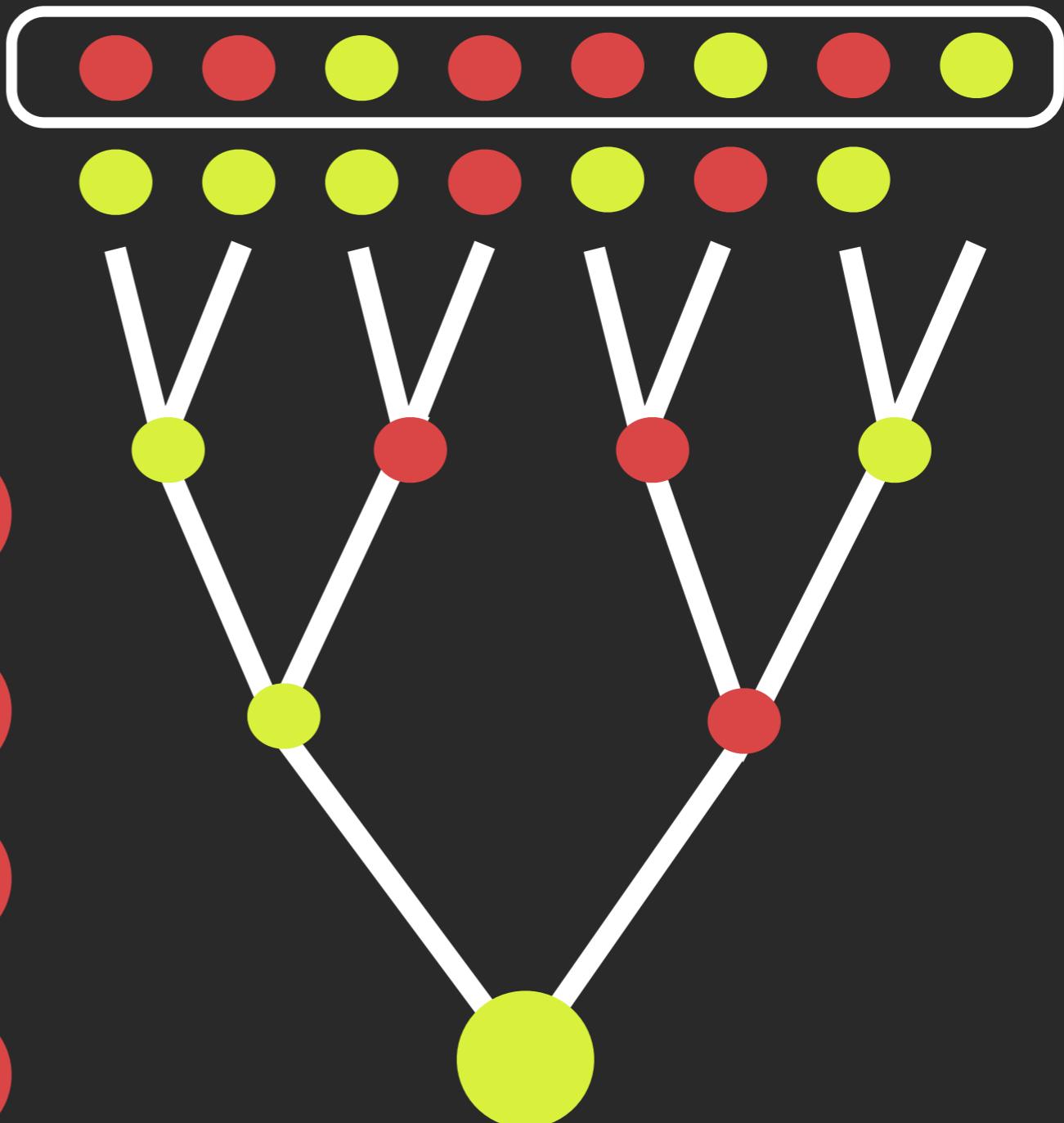
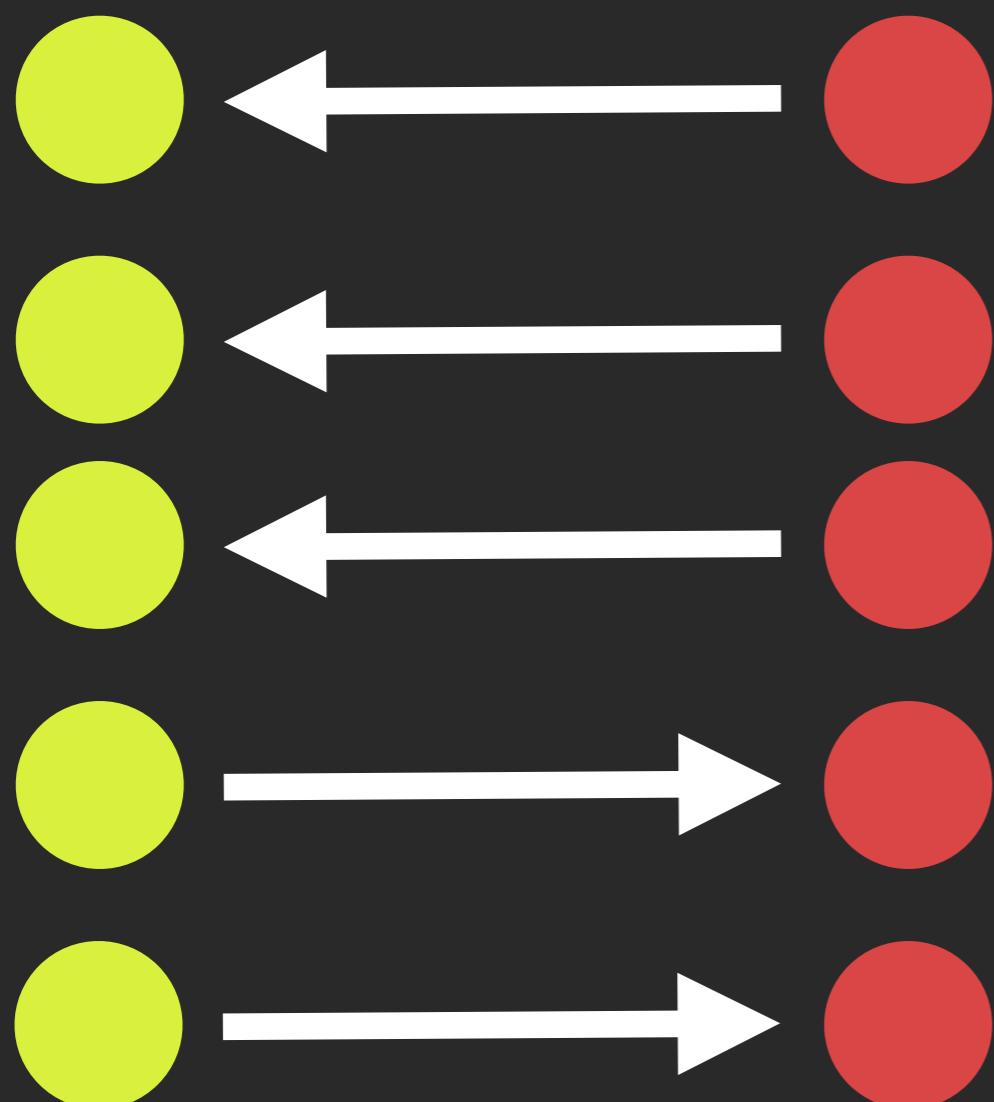
actual data
simulated data



simulation one

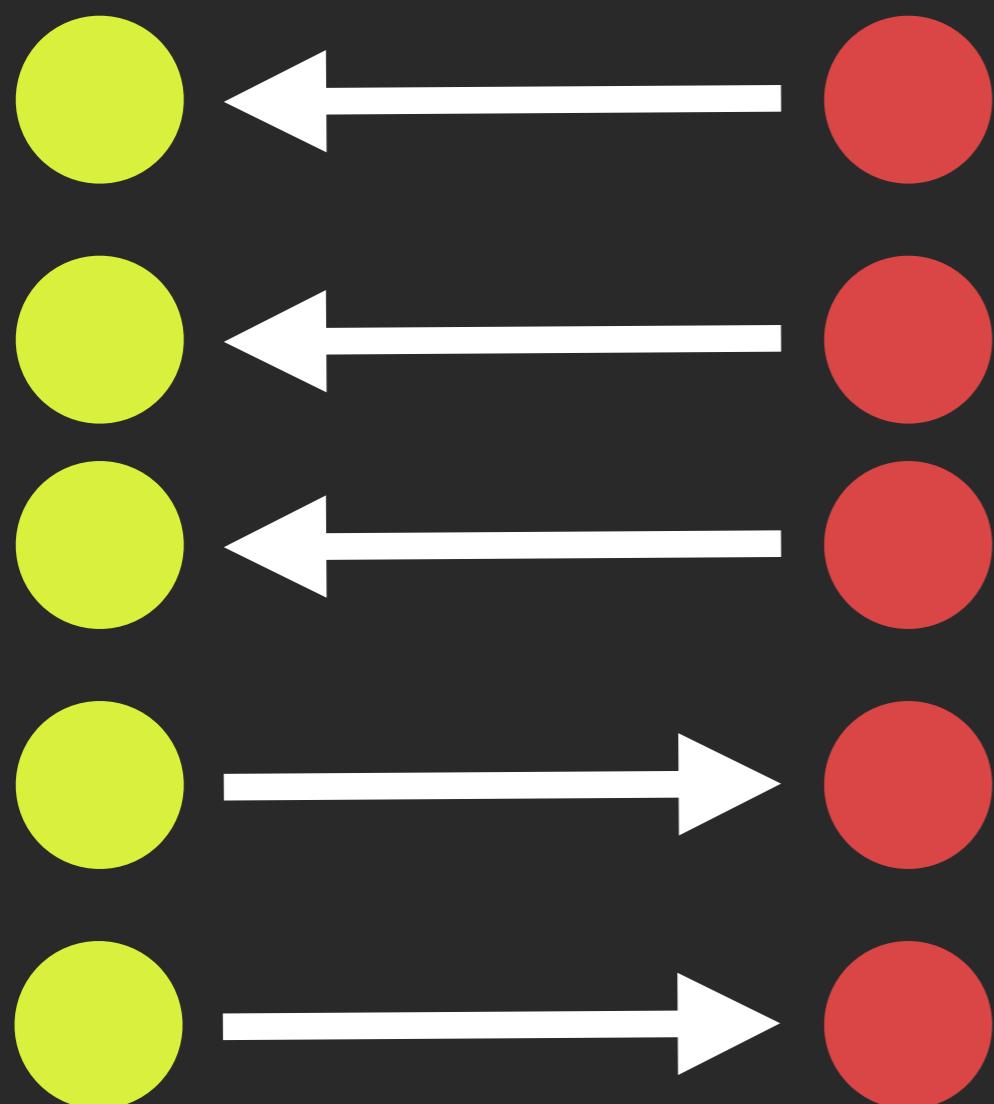


actual data
simulated data

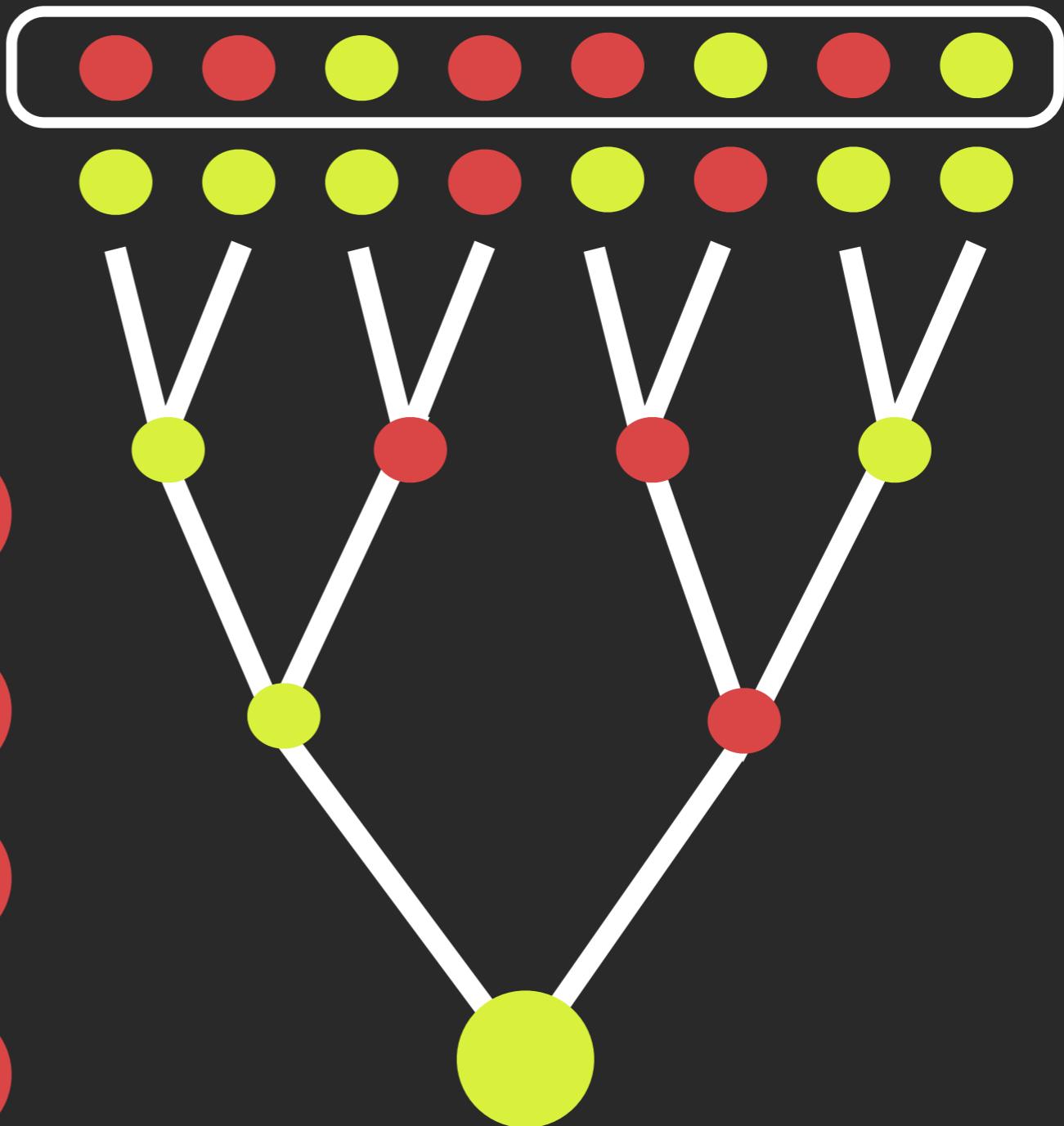


simulation one

actual data
simulated data

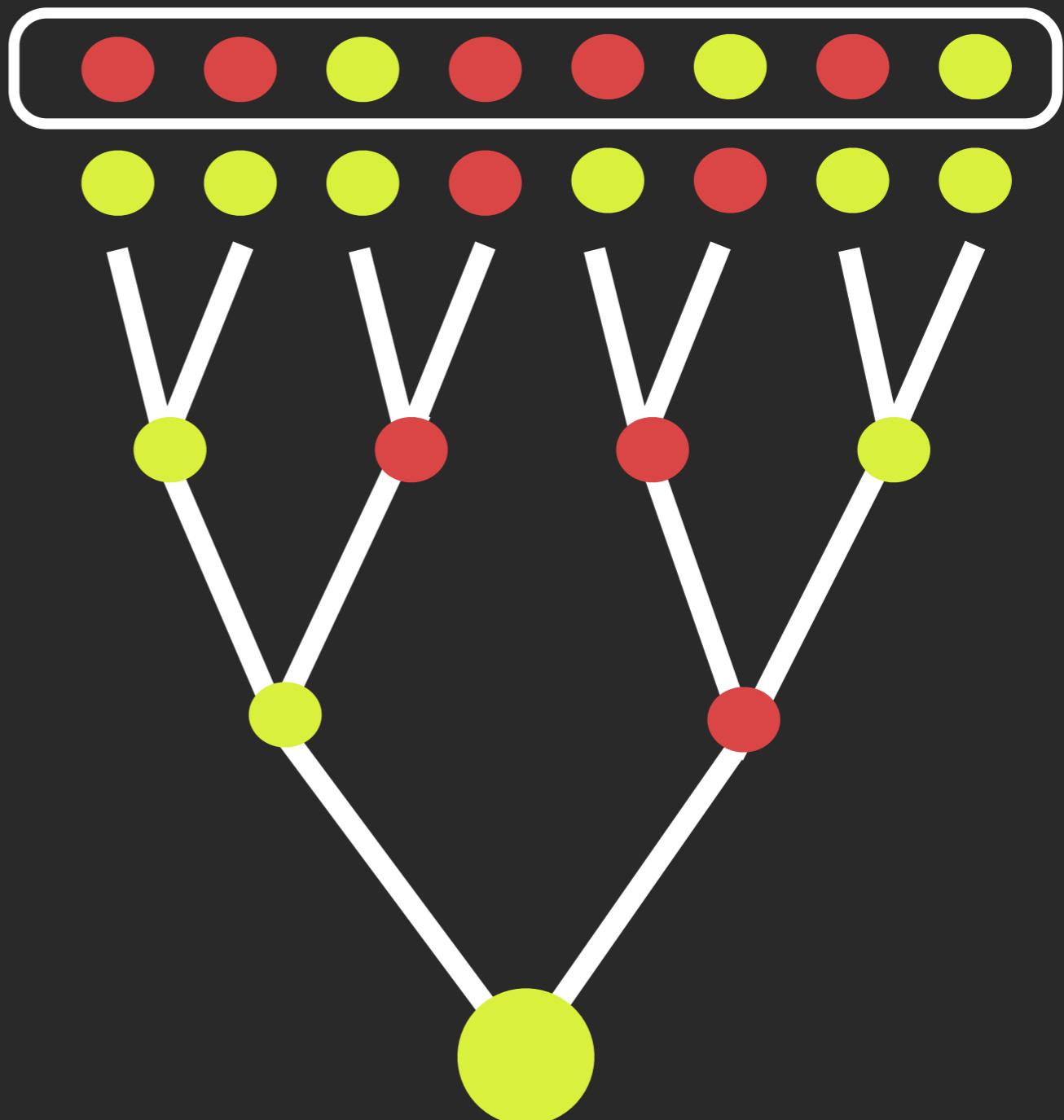


simulation one



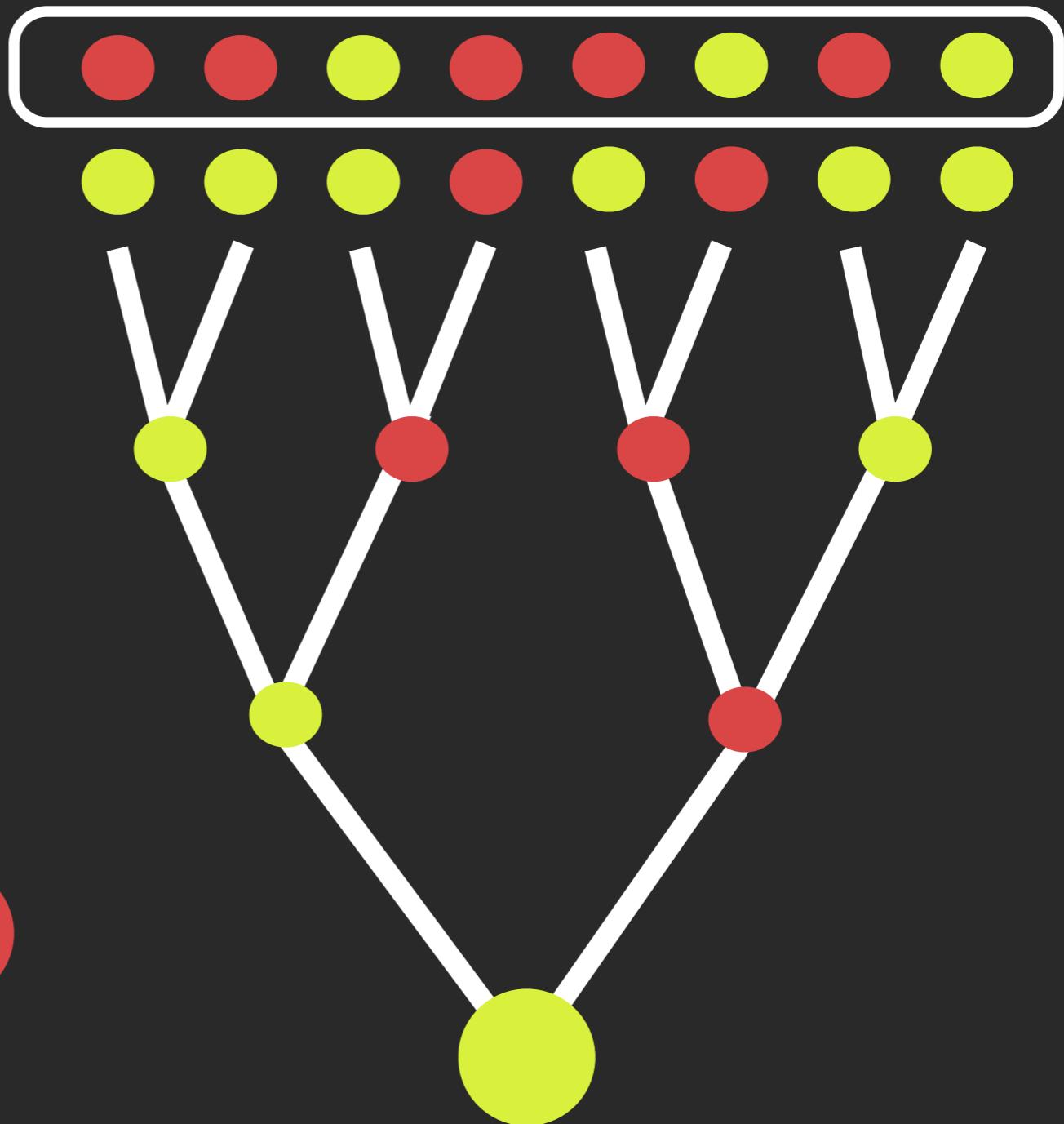
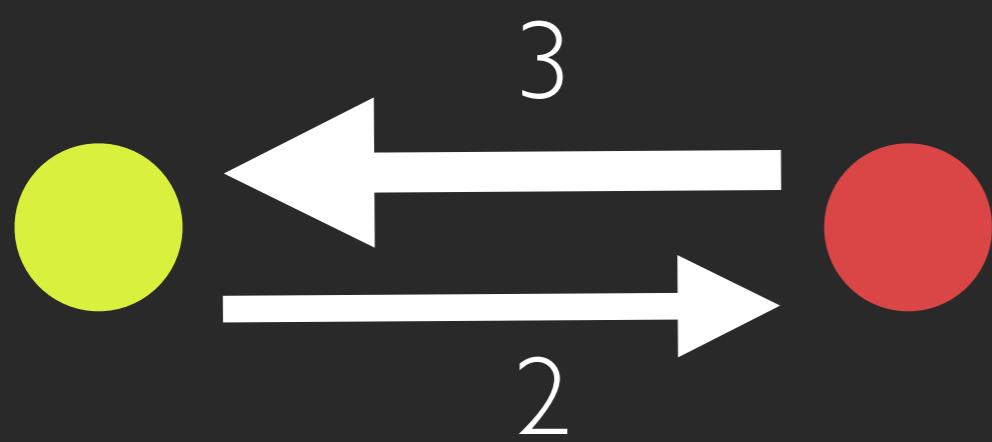
actual data

simulated data

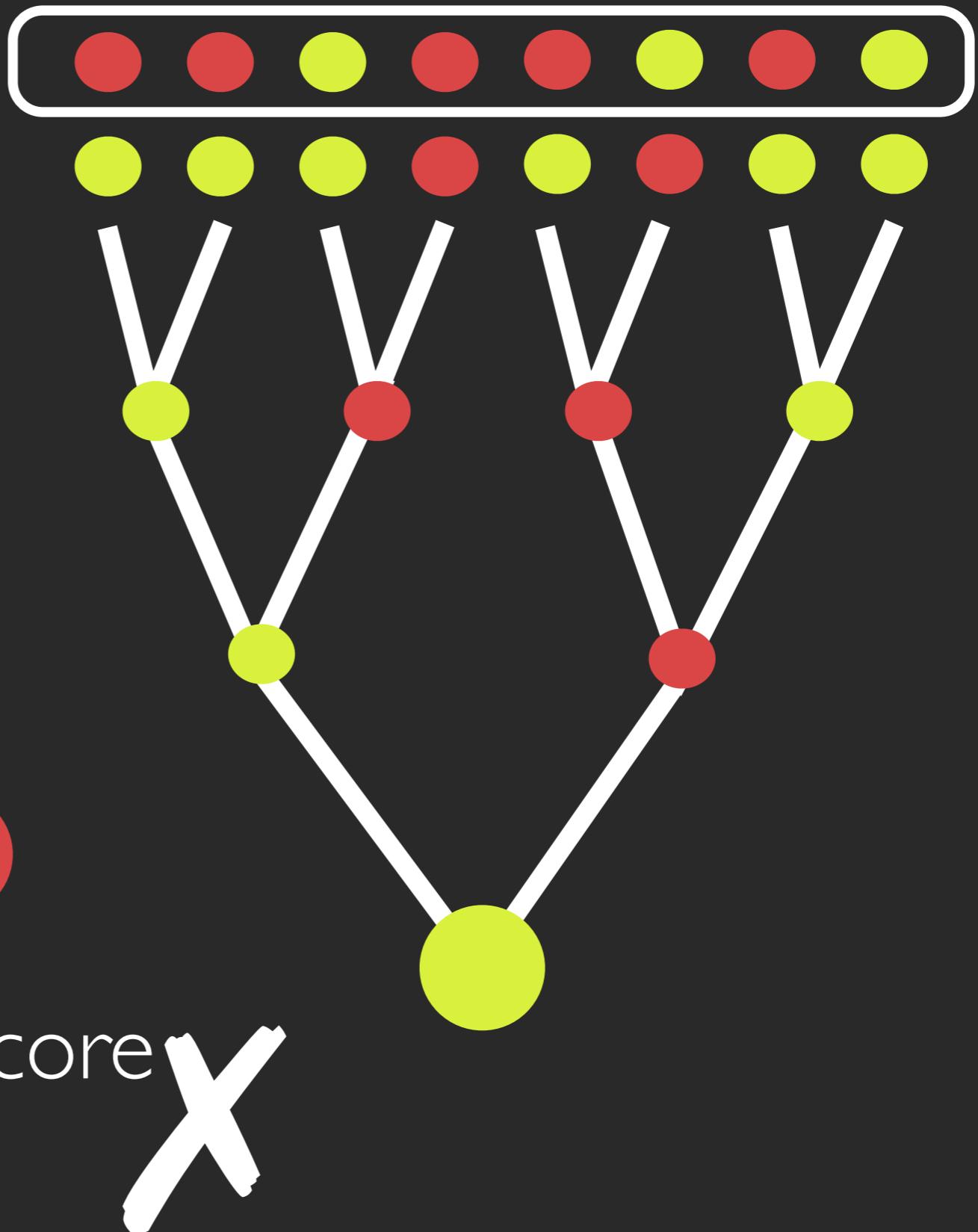


simulation one

actual data
simulated data

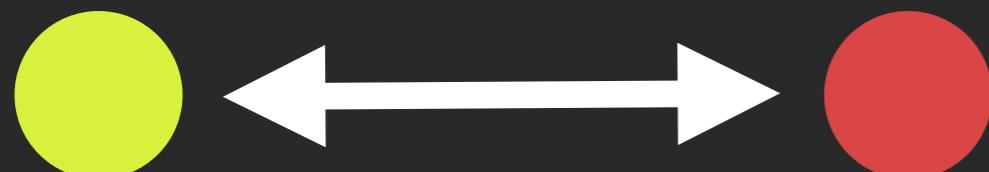
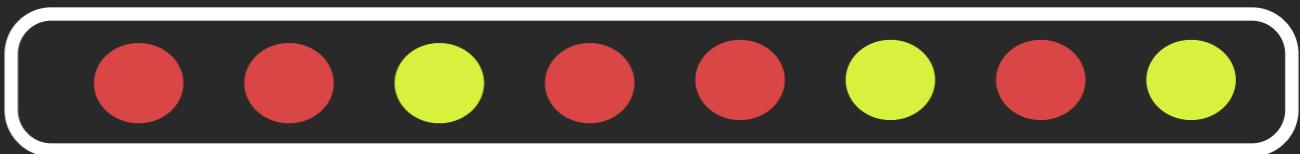


actual data
simulated data



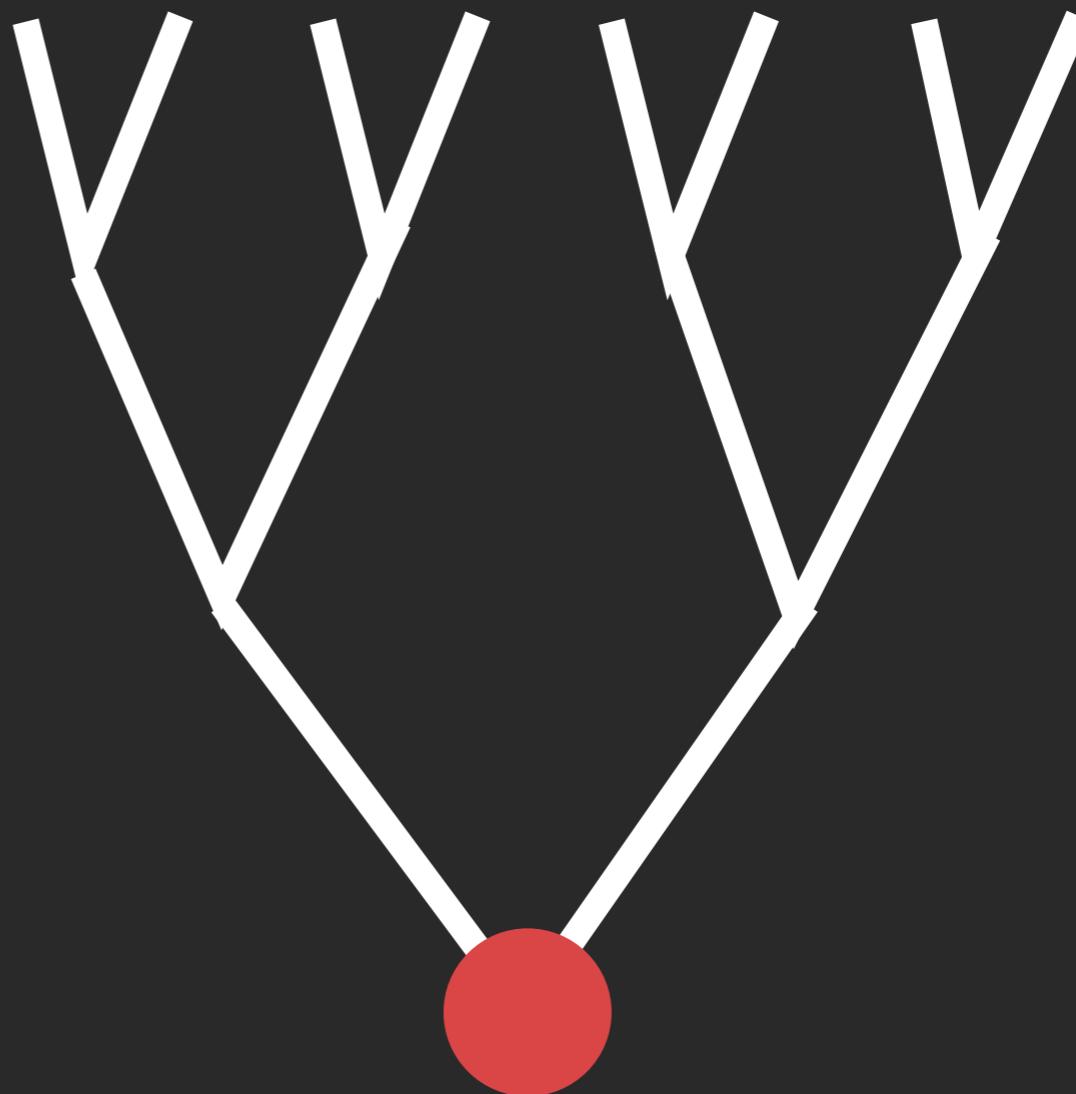
simulation one

actual data



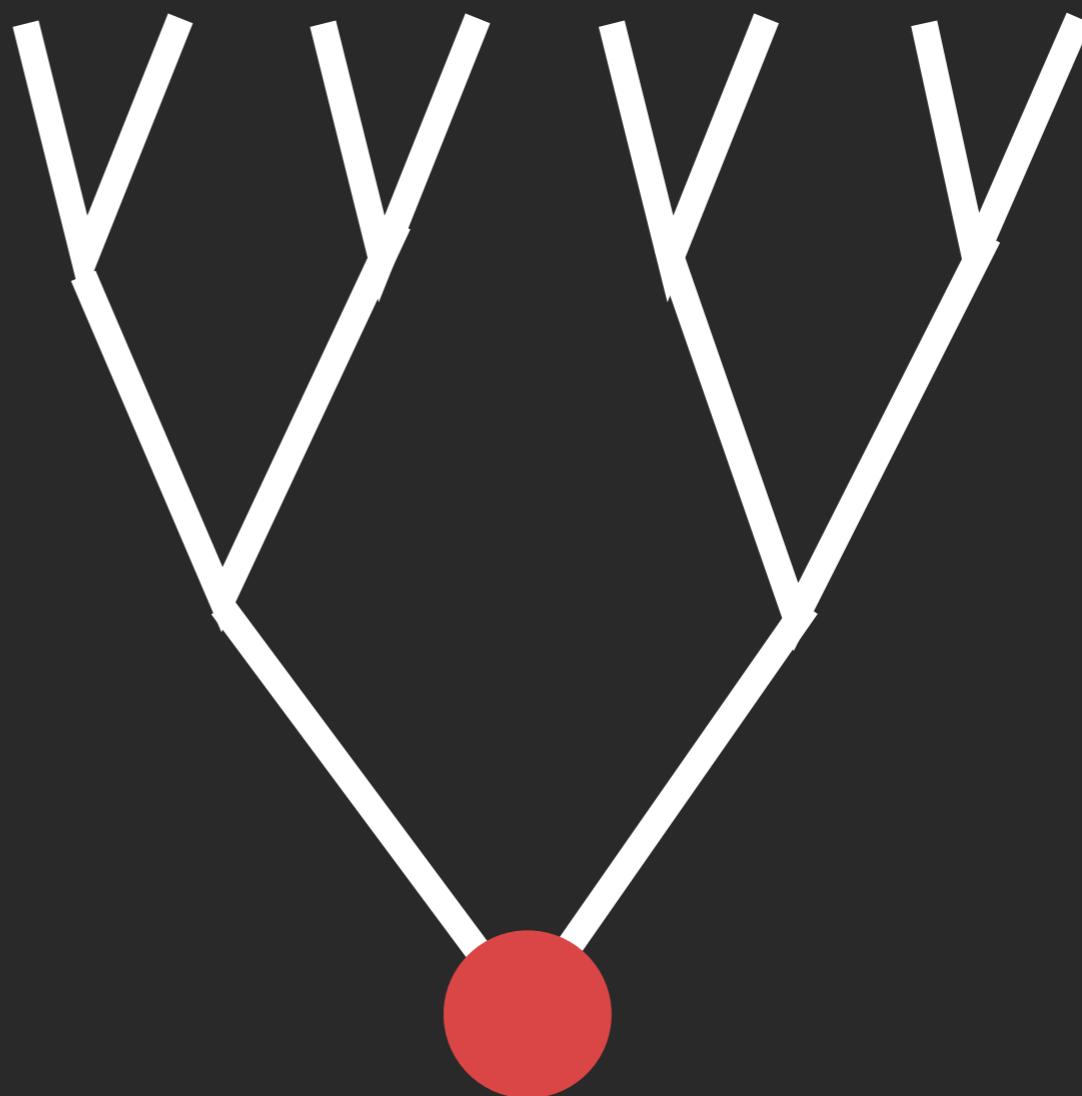
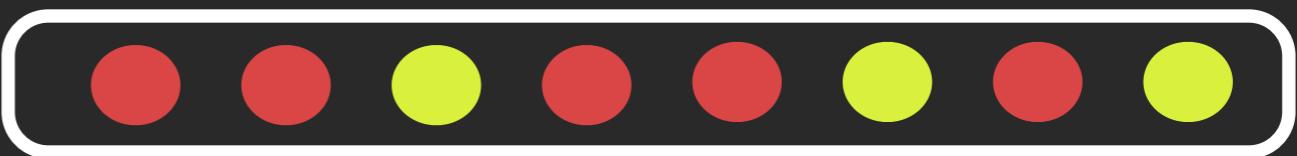
simulate evolution from all possible starting states

actual data



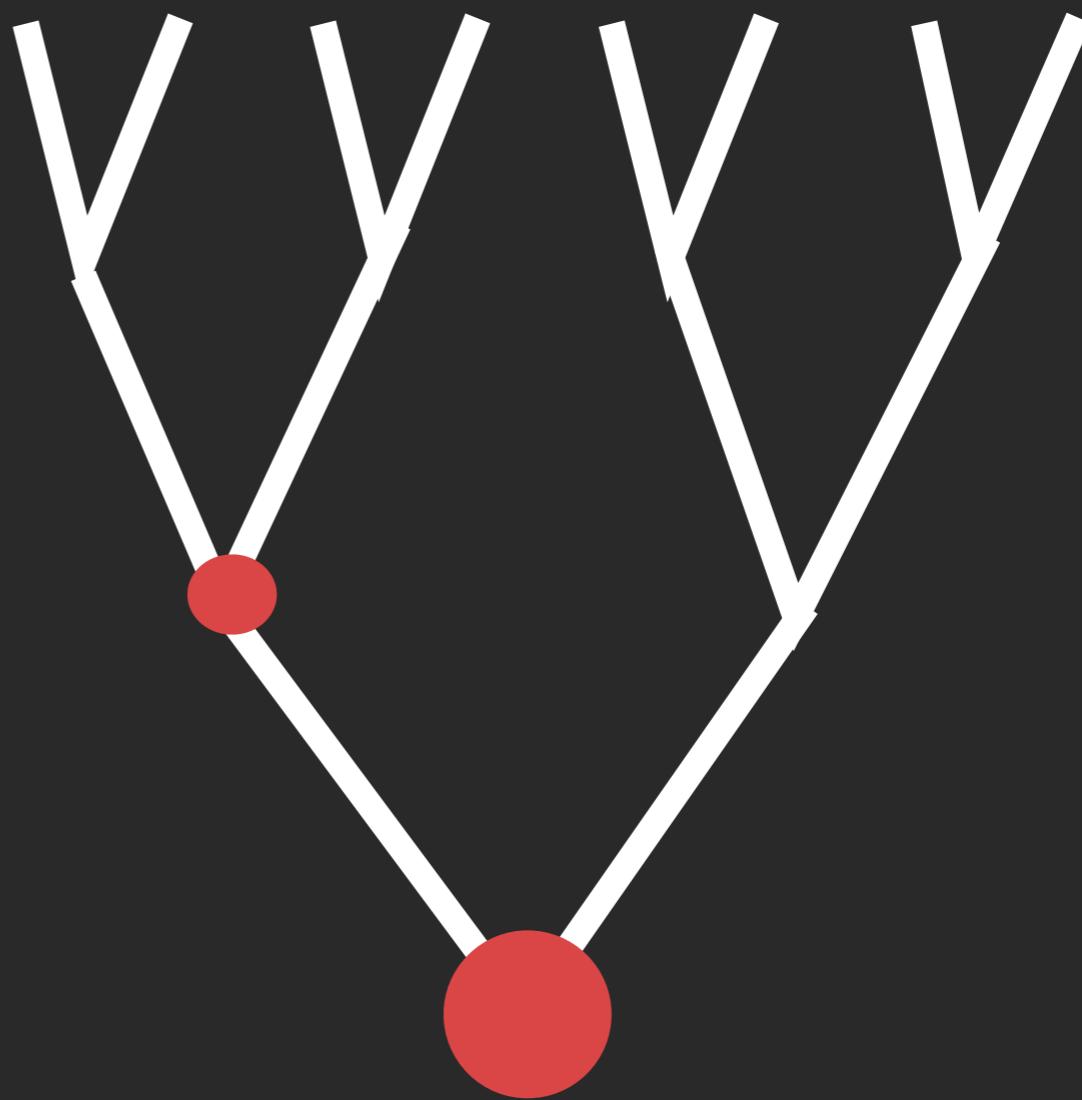
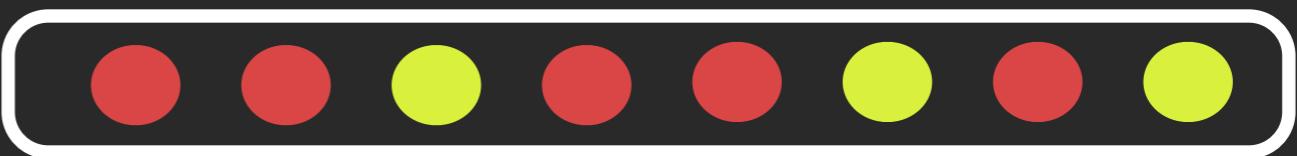
simulate evolution from all possible starting states

actual data



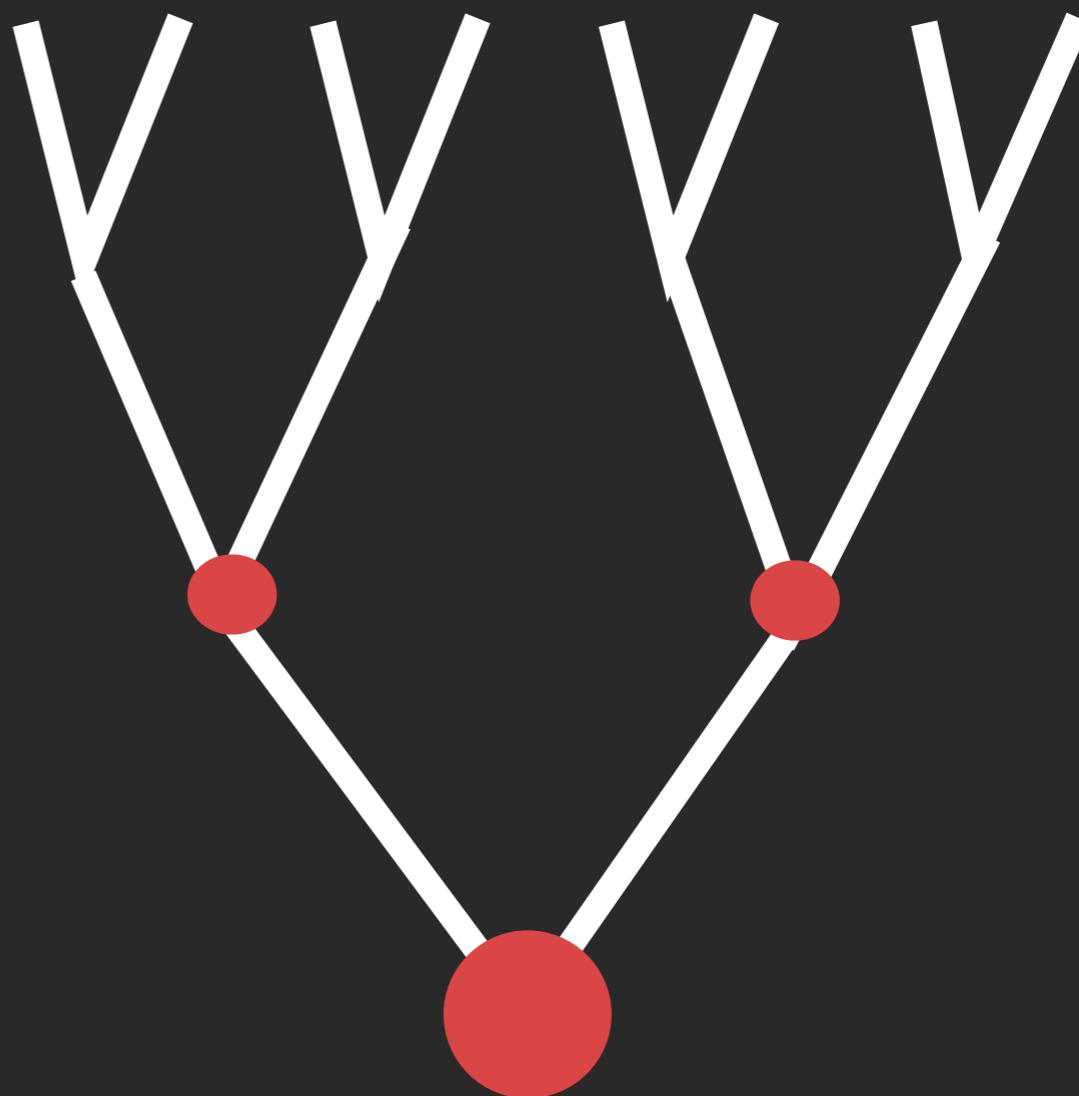
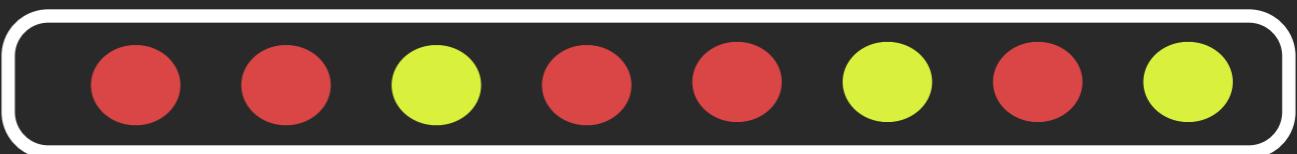
simulation two

actual data



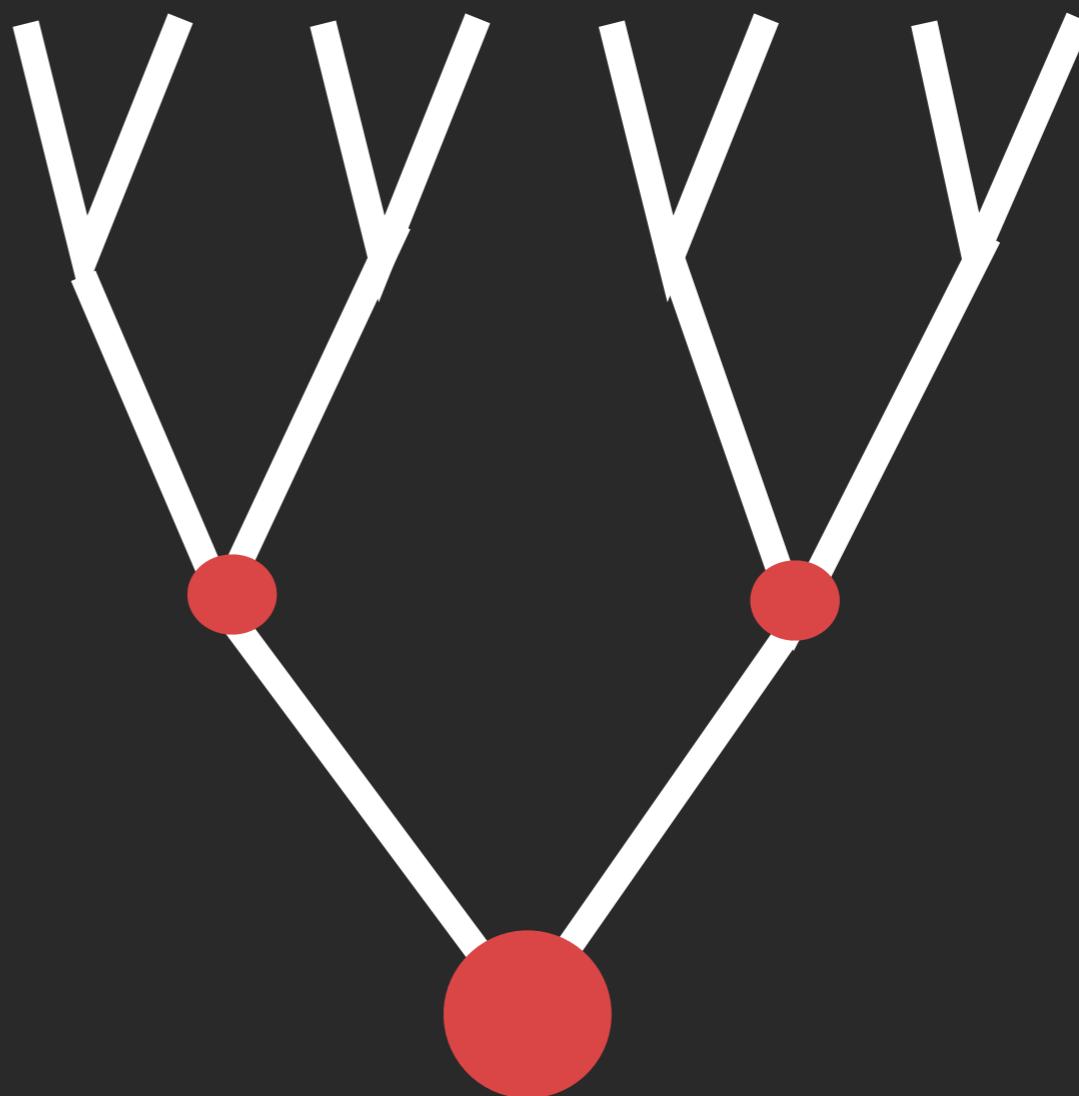
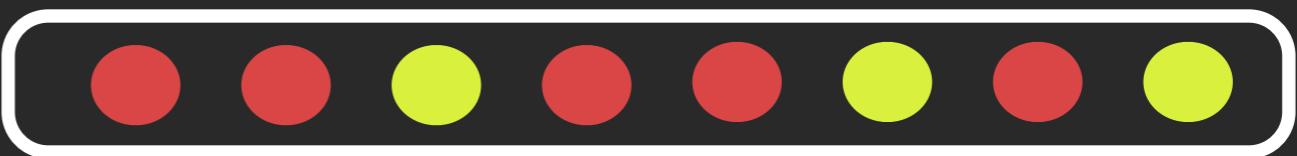
simulation two

actual data



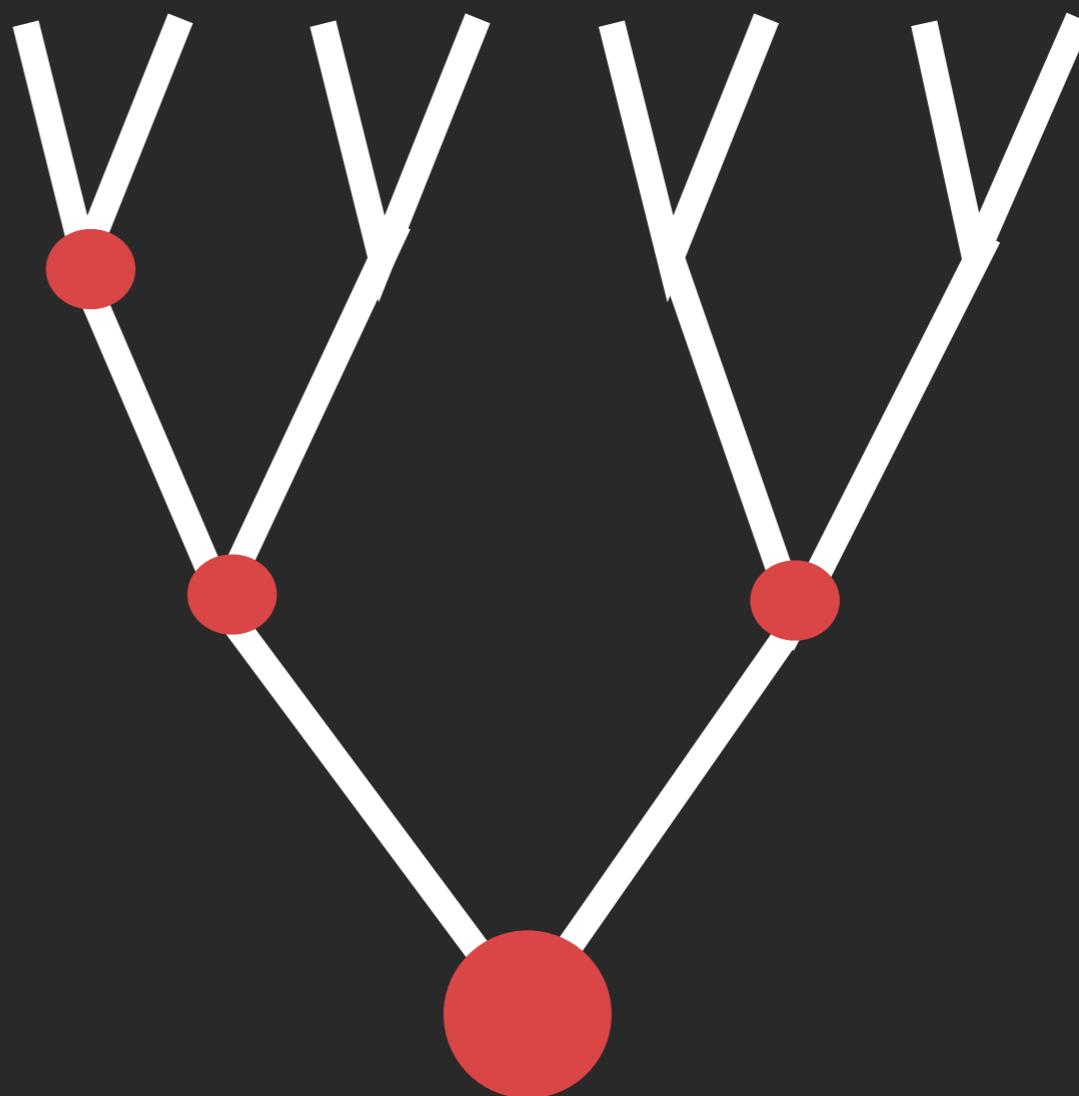
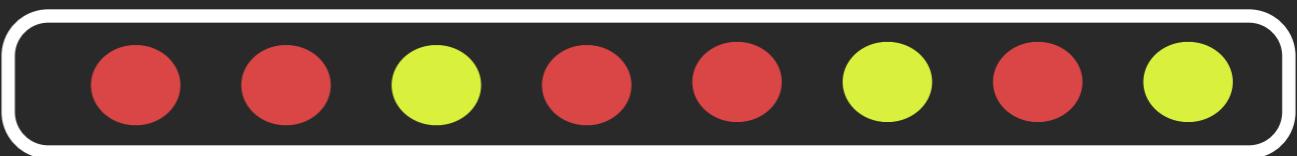
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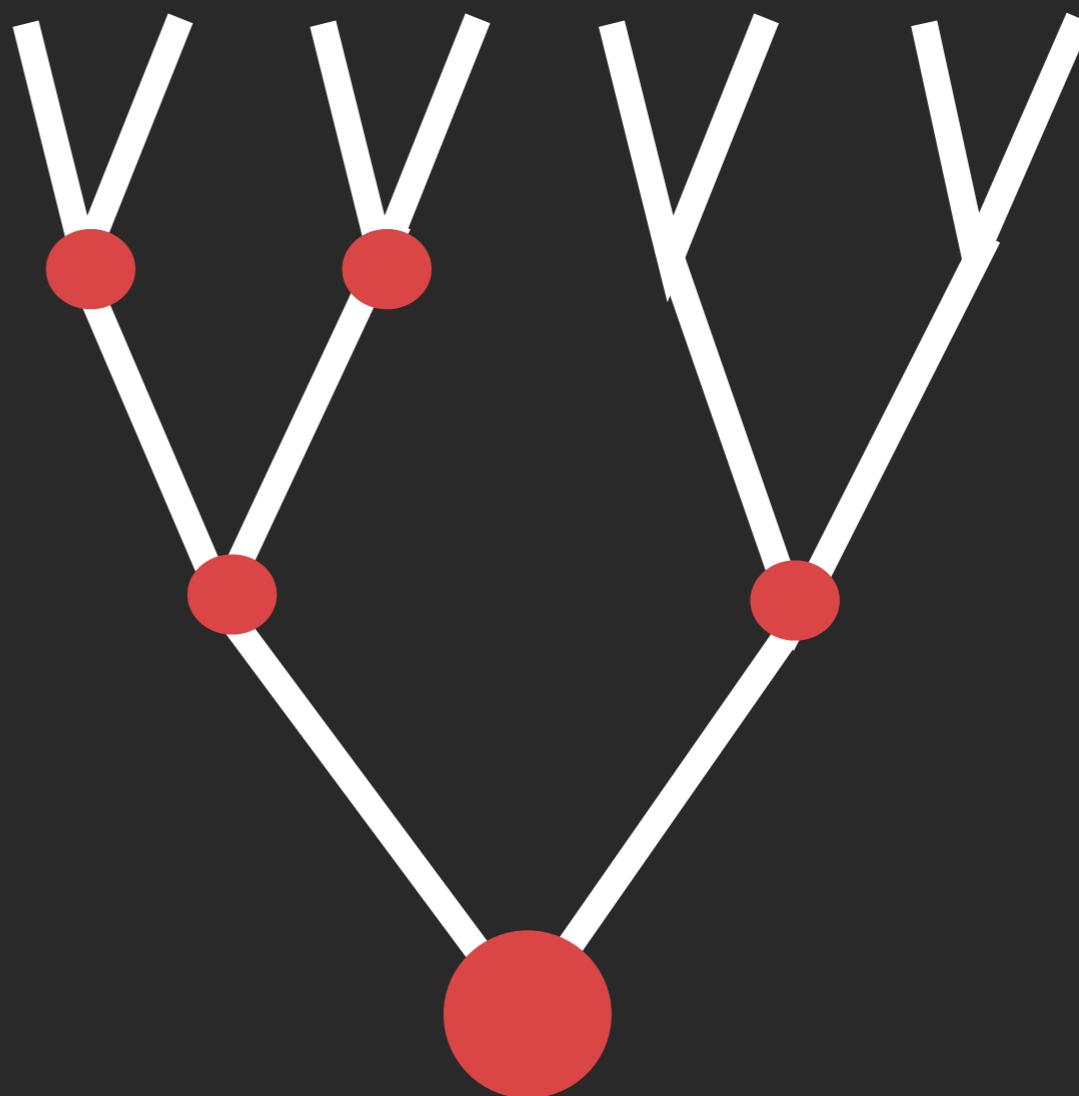
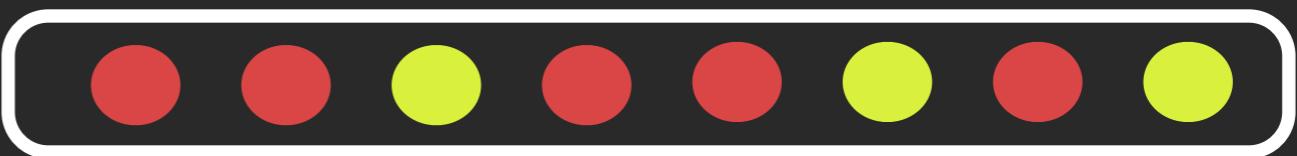
simulation two

actual data



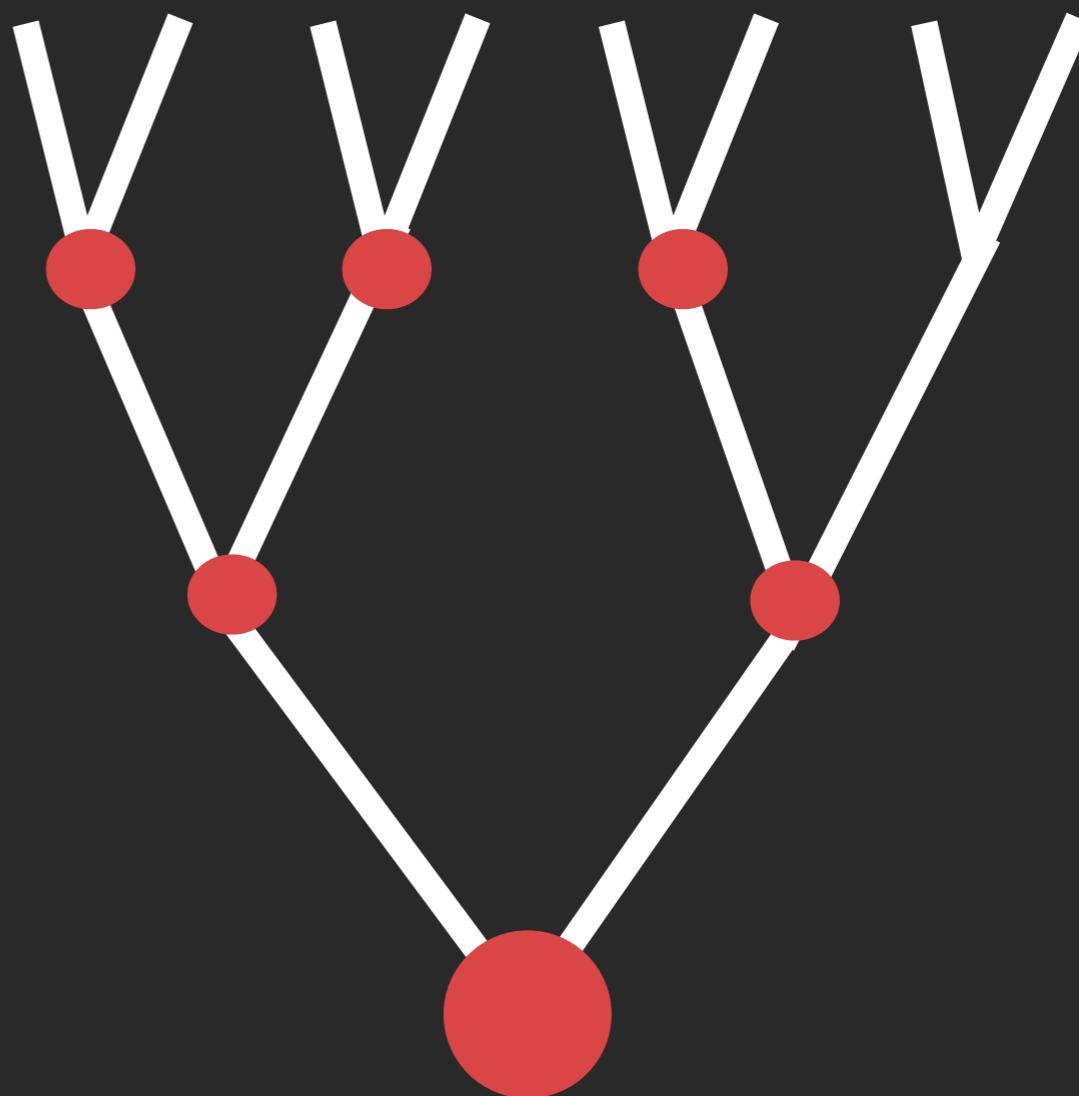
simulation two

actual data



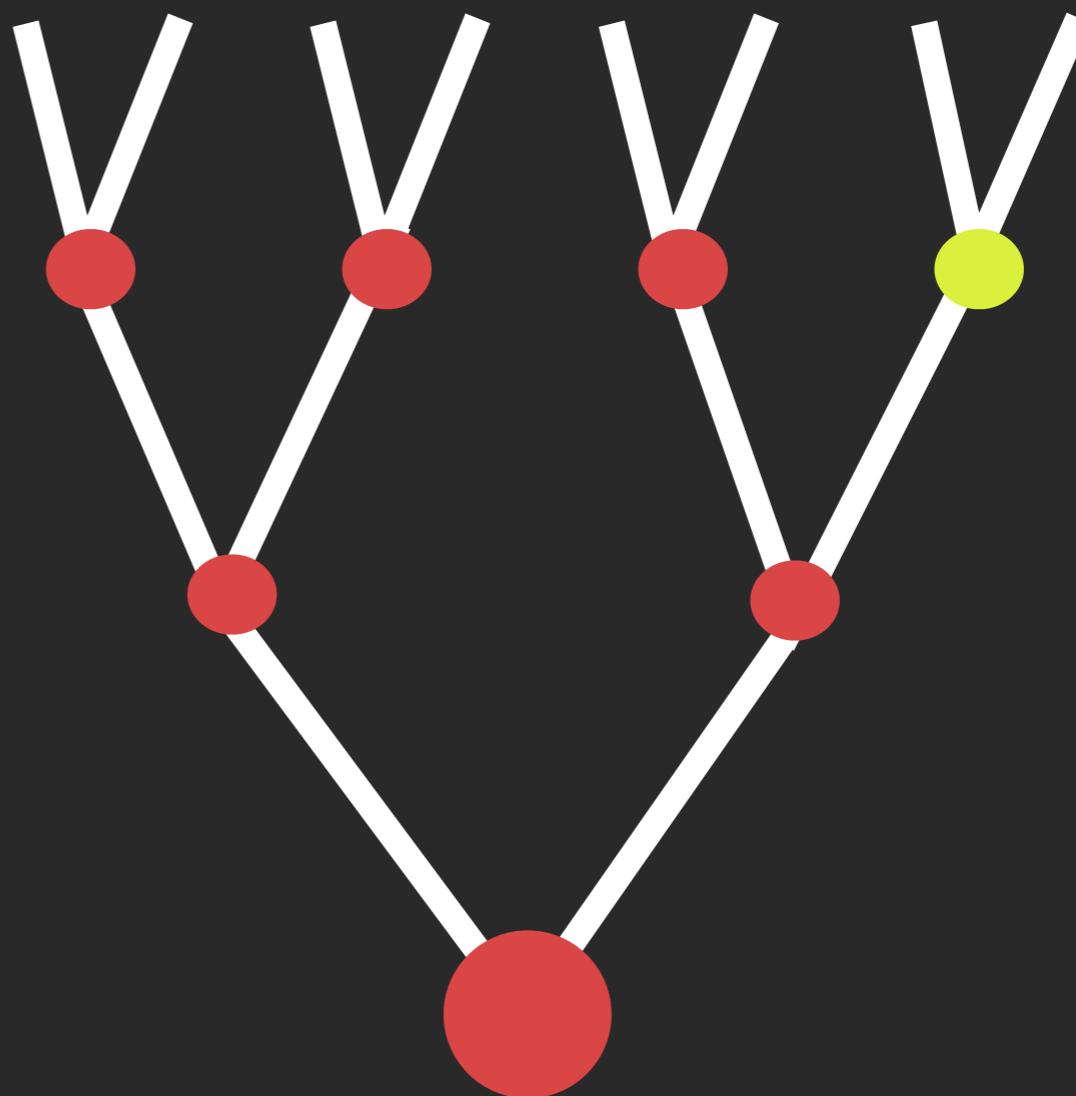
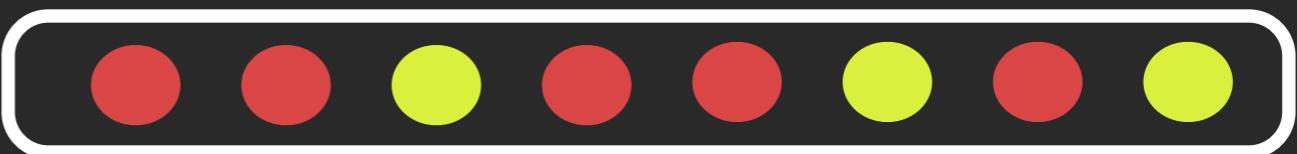
simulation two

actual data



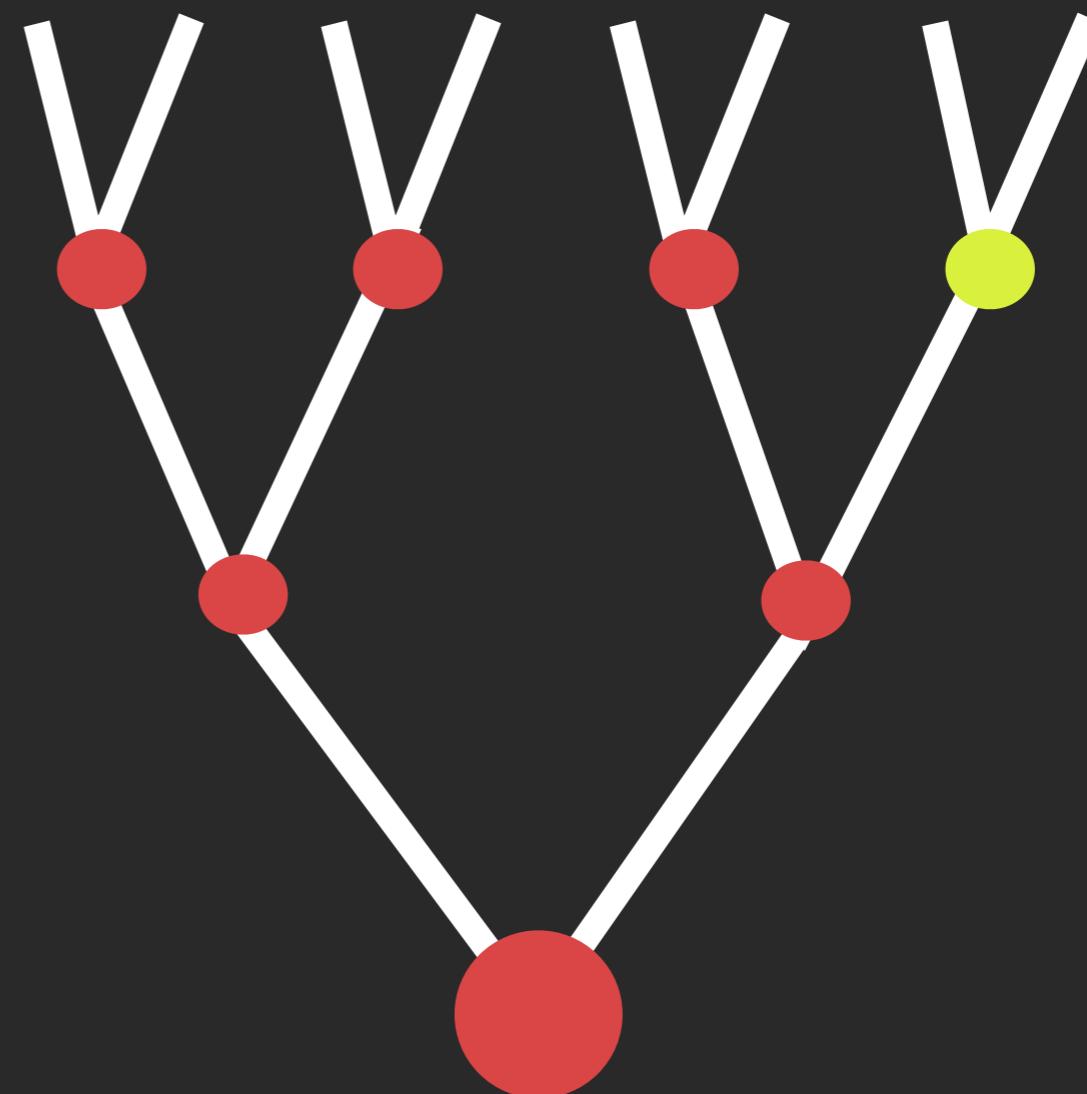
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actual data



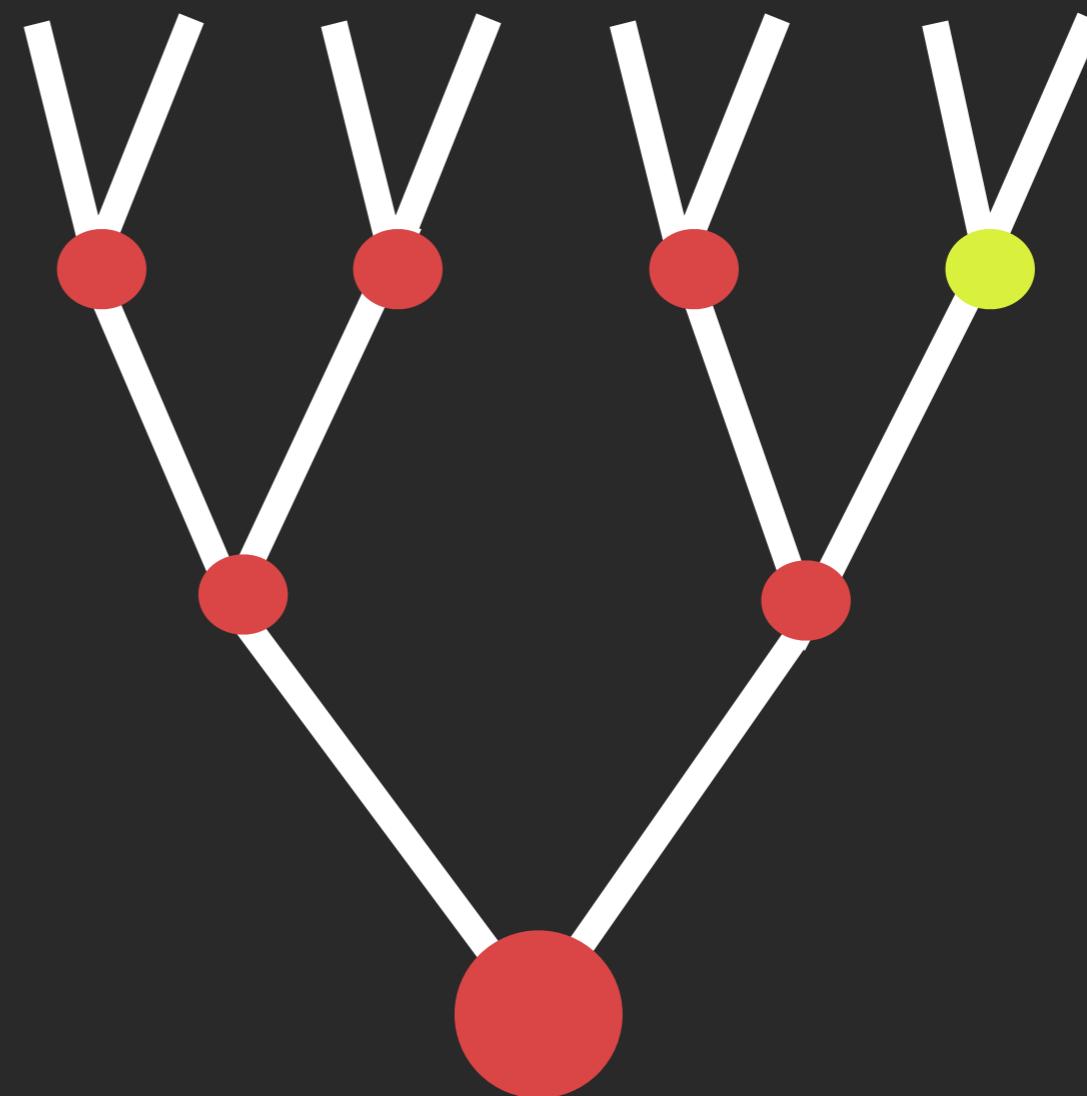
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actual data



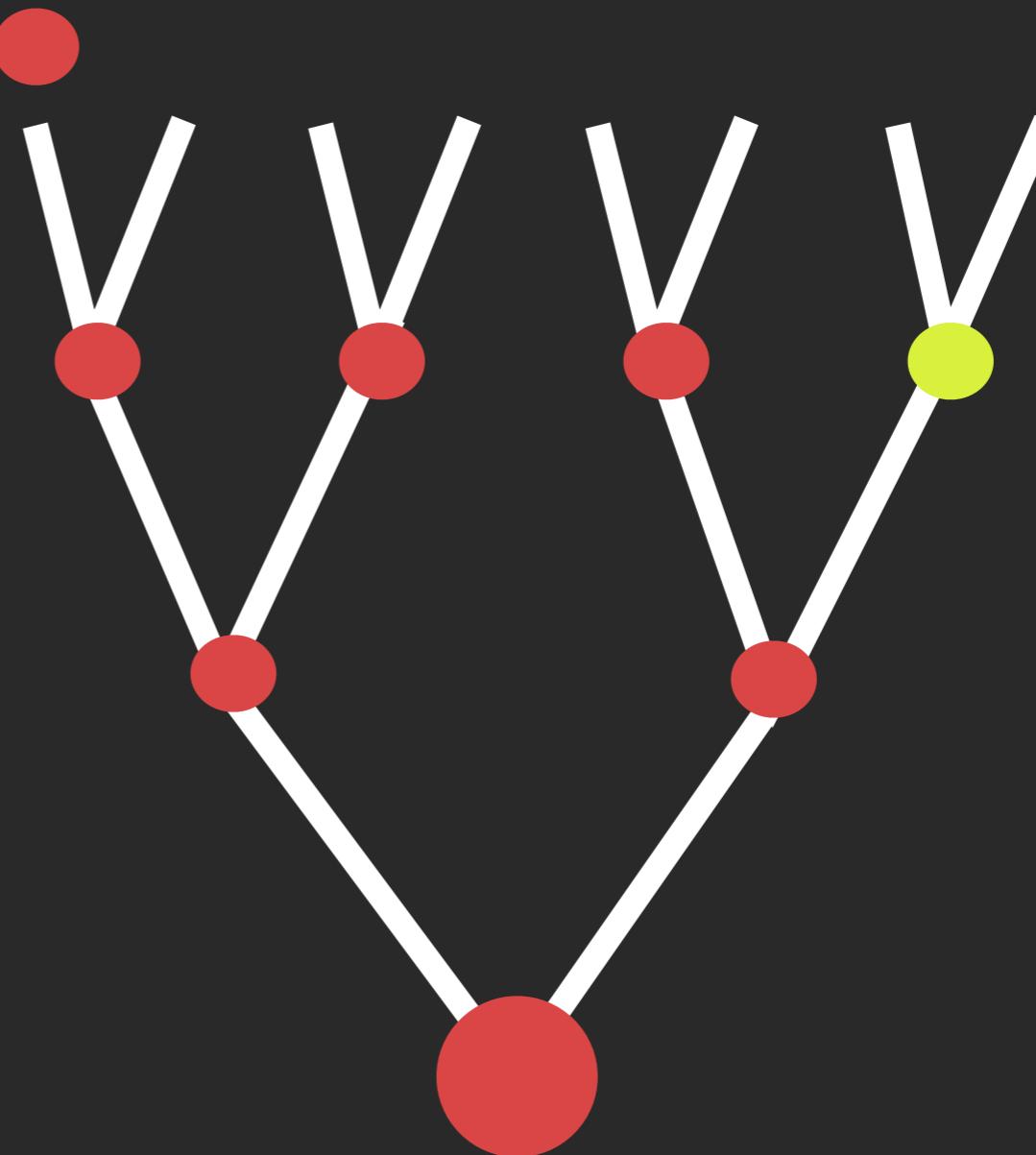
simulation two

actual data
simulated data



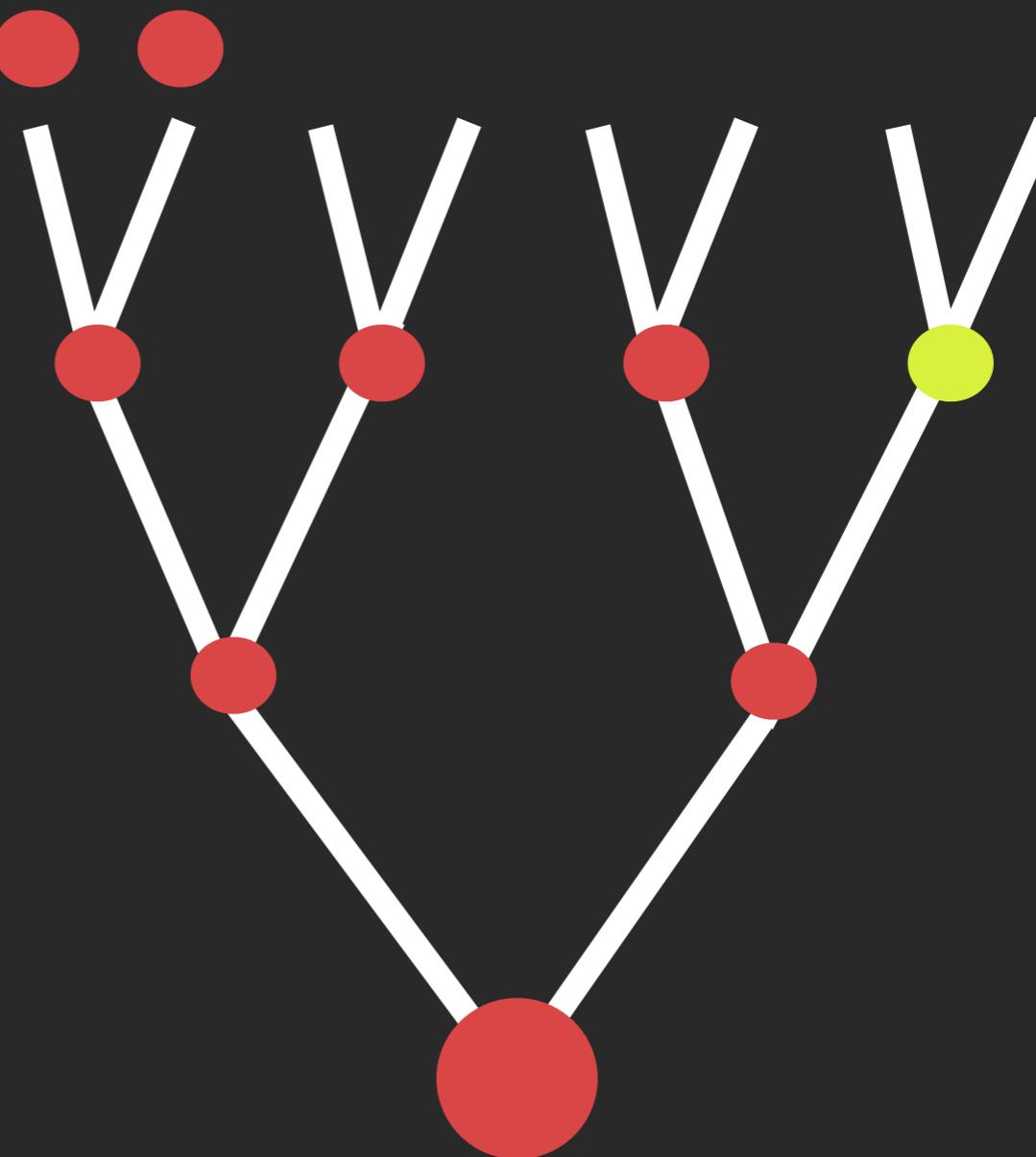
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actual data
simulated data



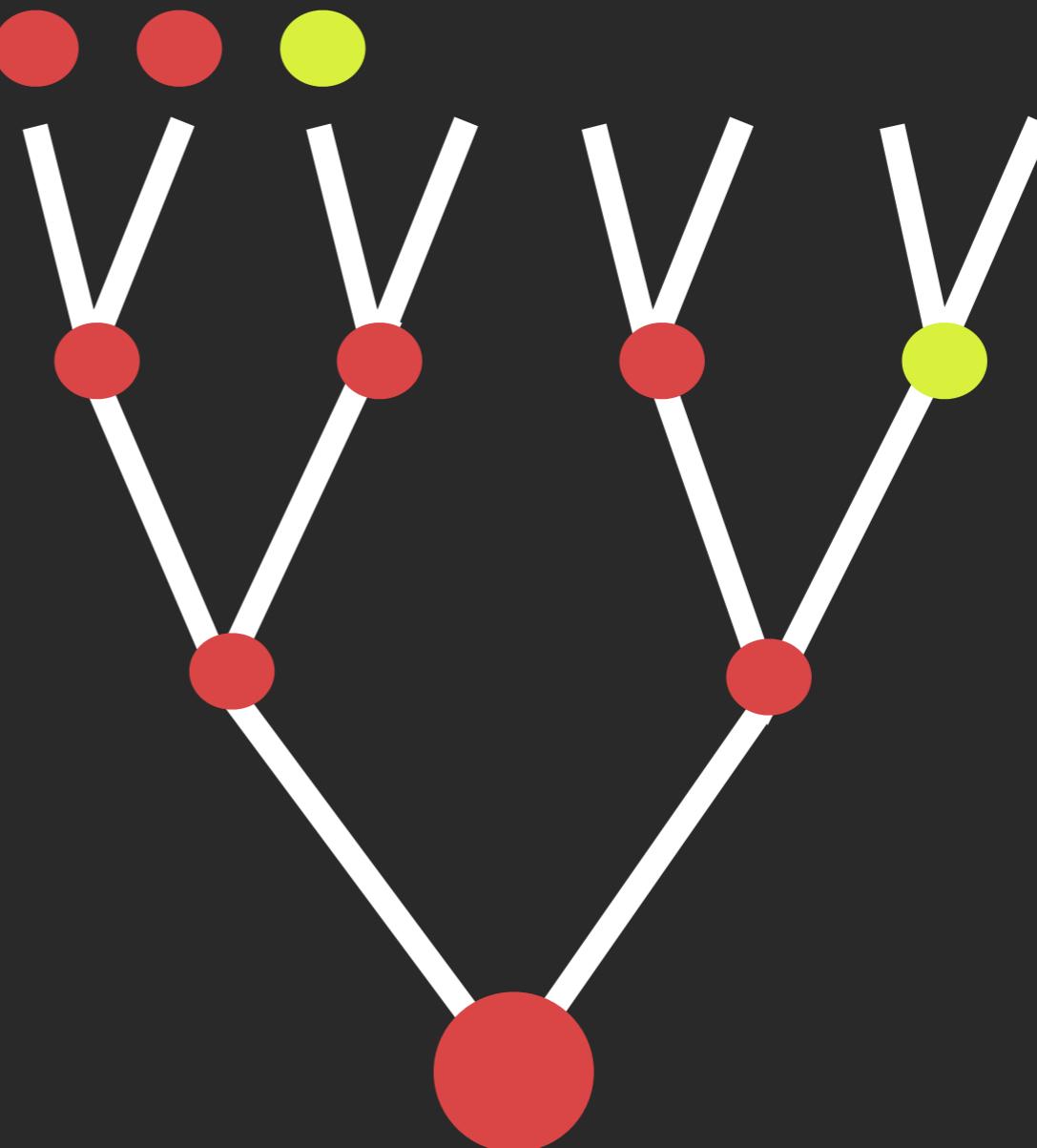
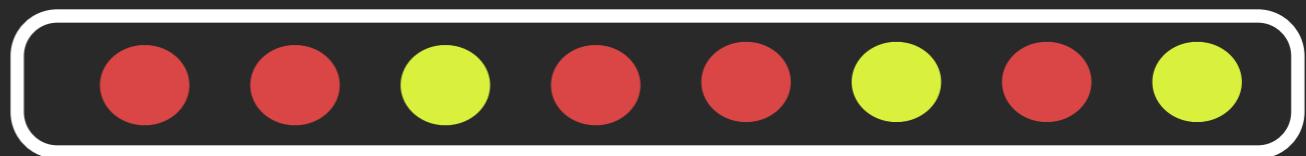
simulation two

actual data
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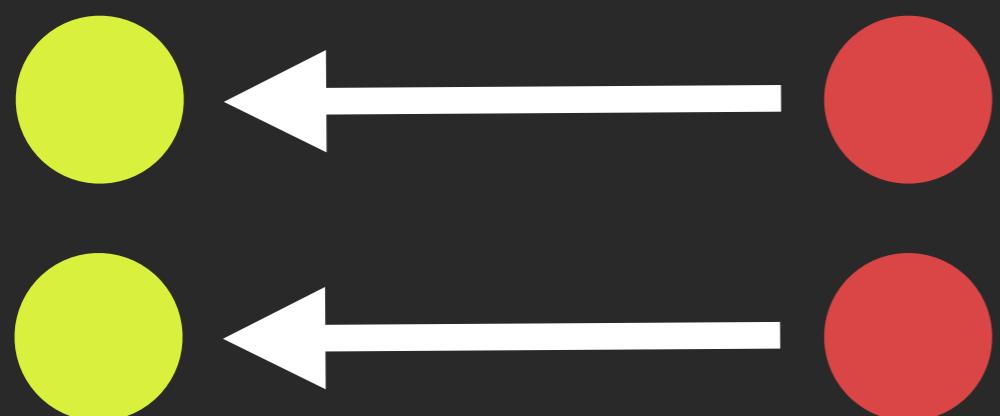
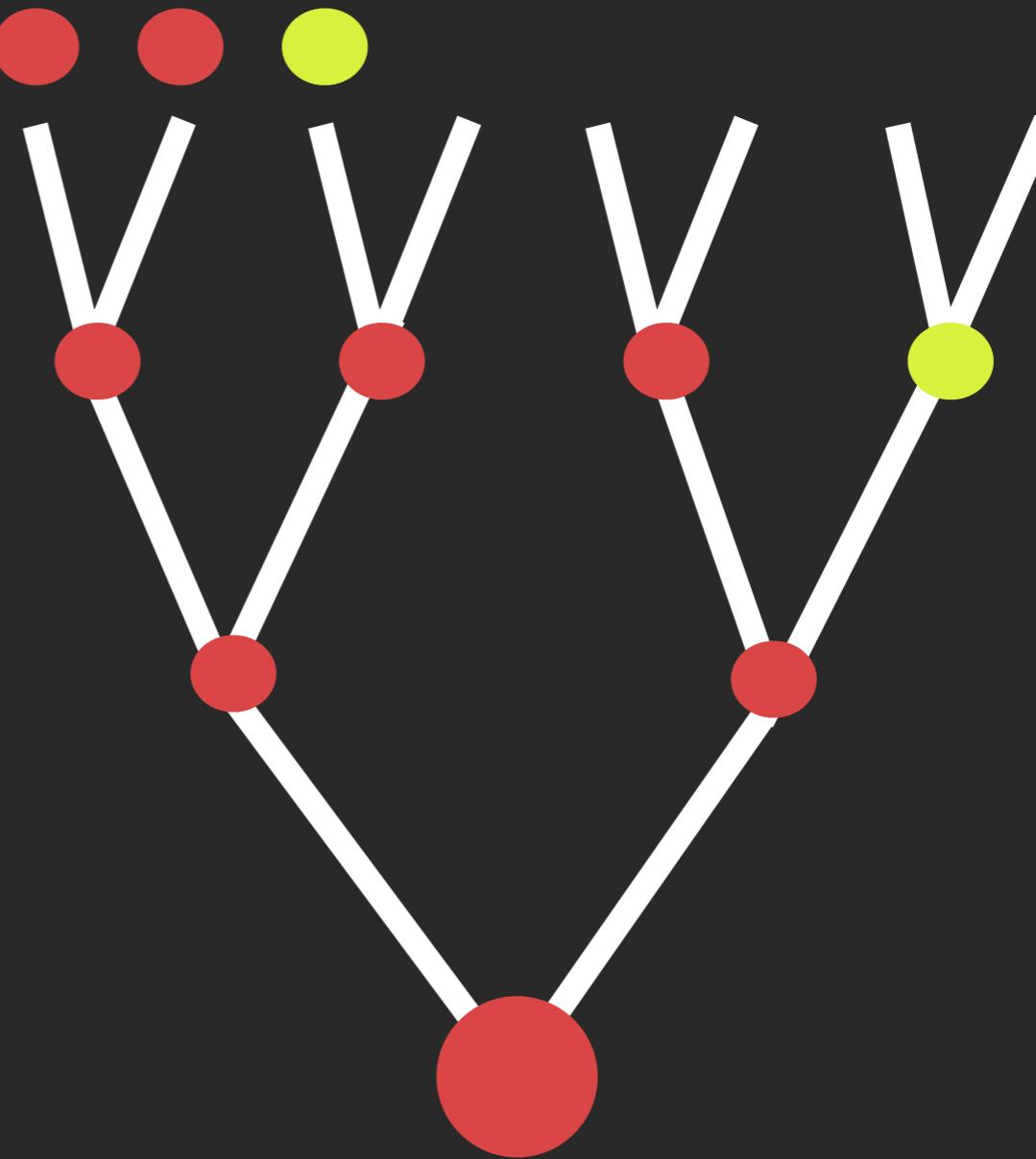
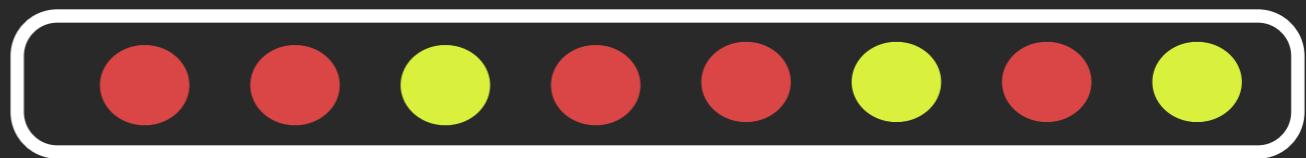
simulation two

actual data
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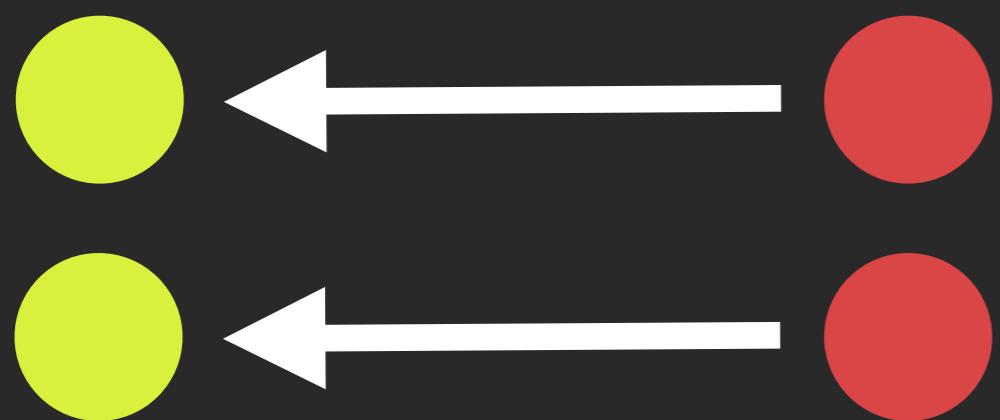
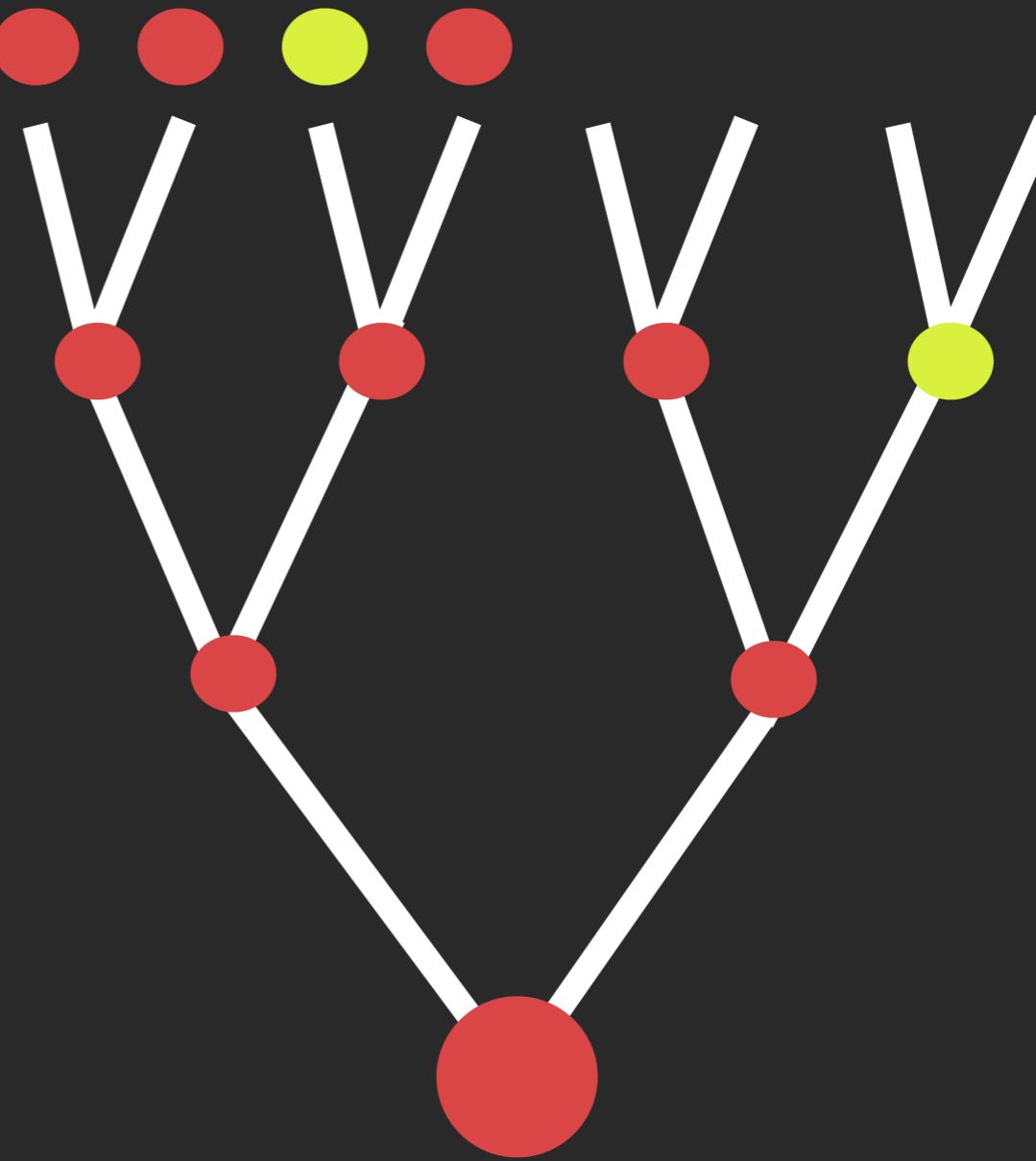
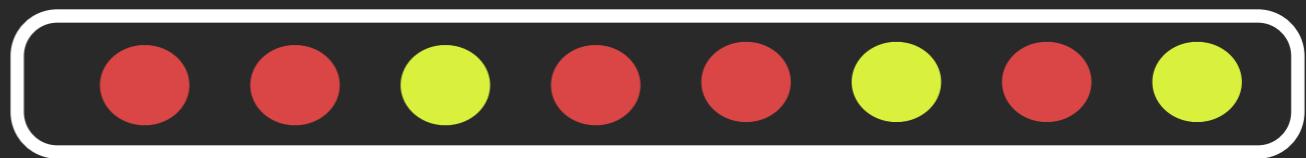
simulation two

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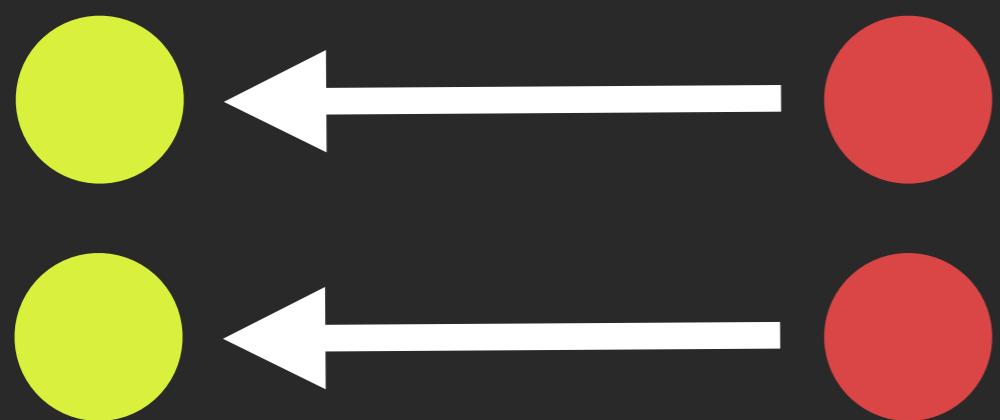
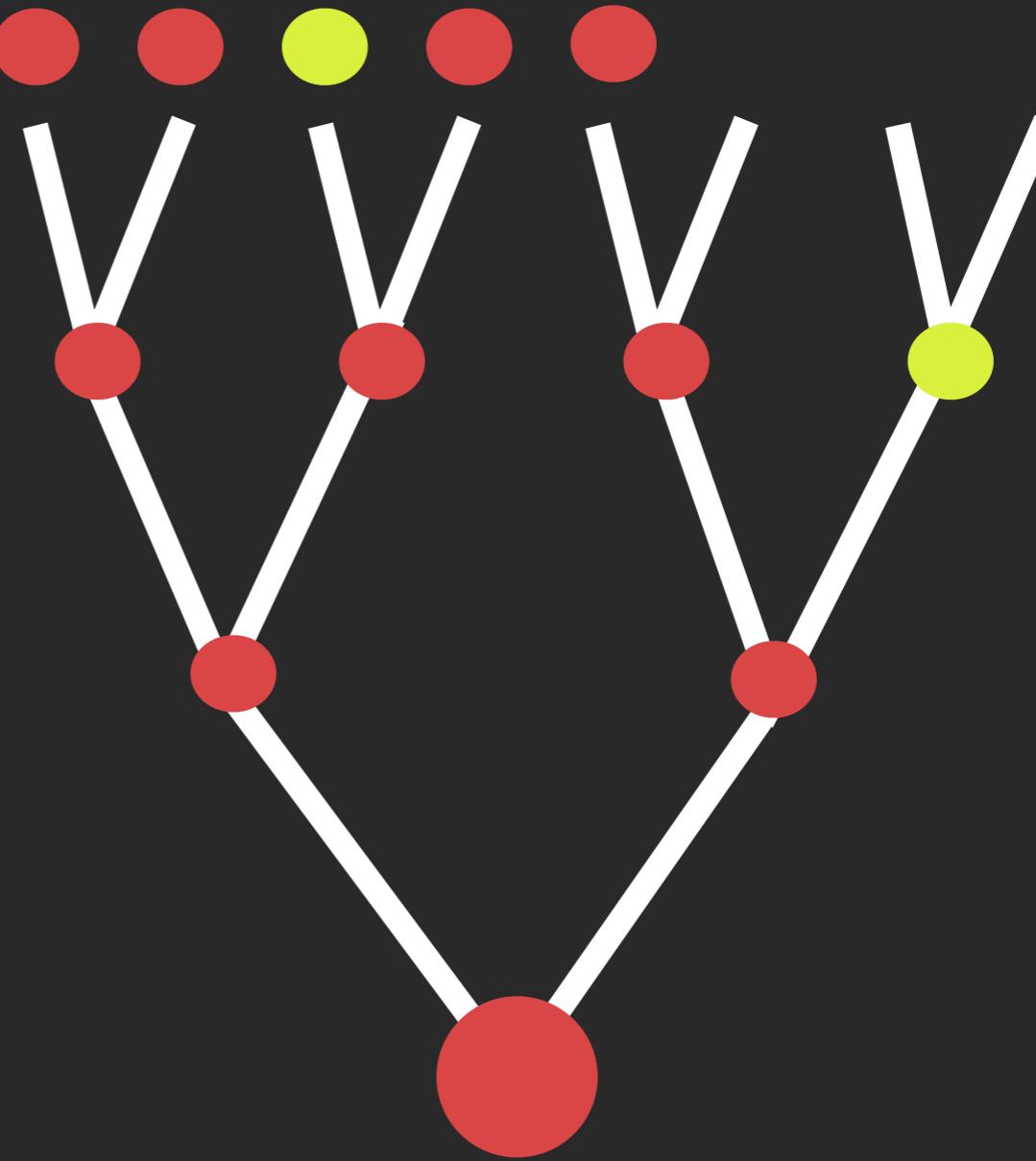
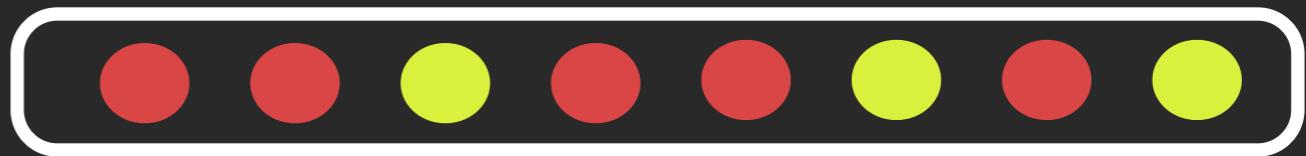
simulation two

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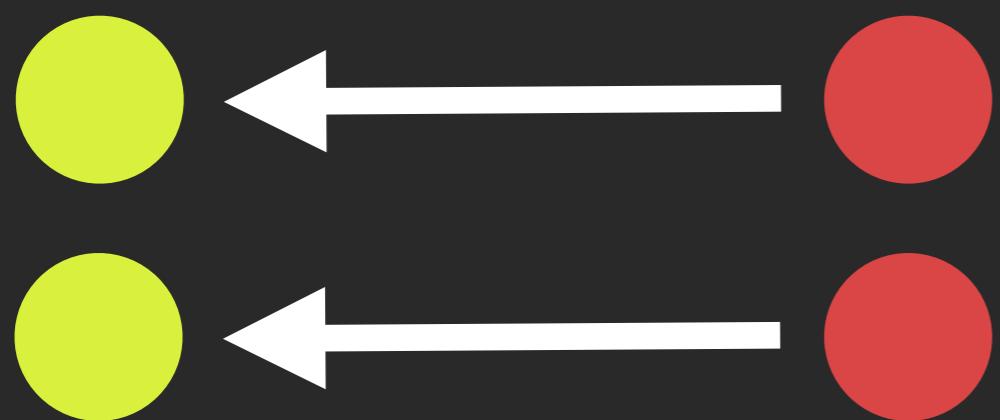
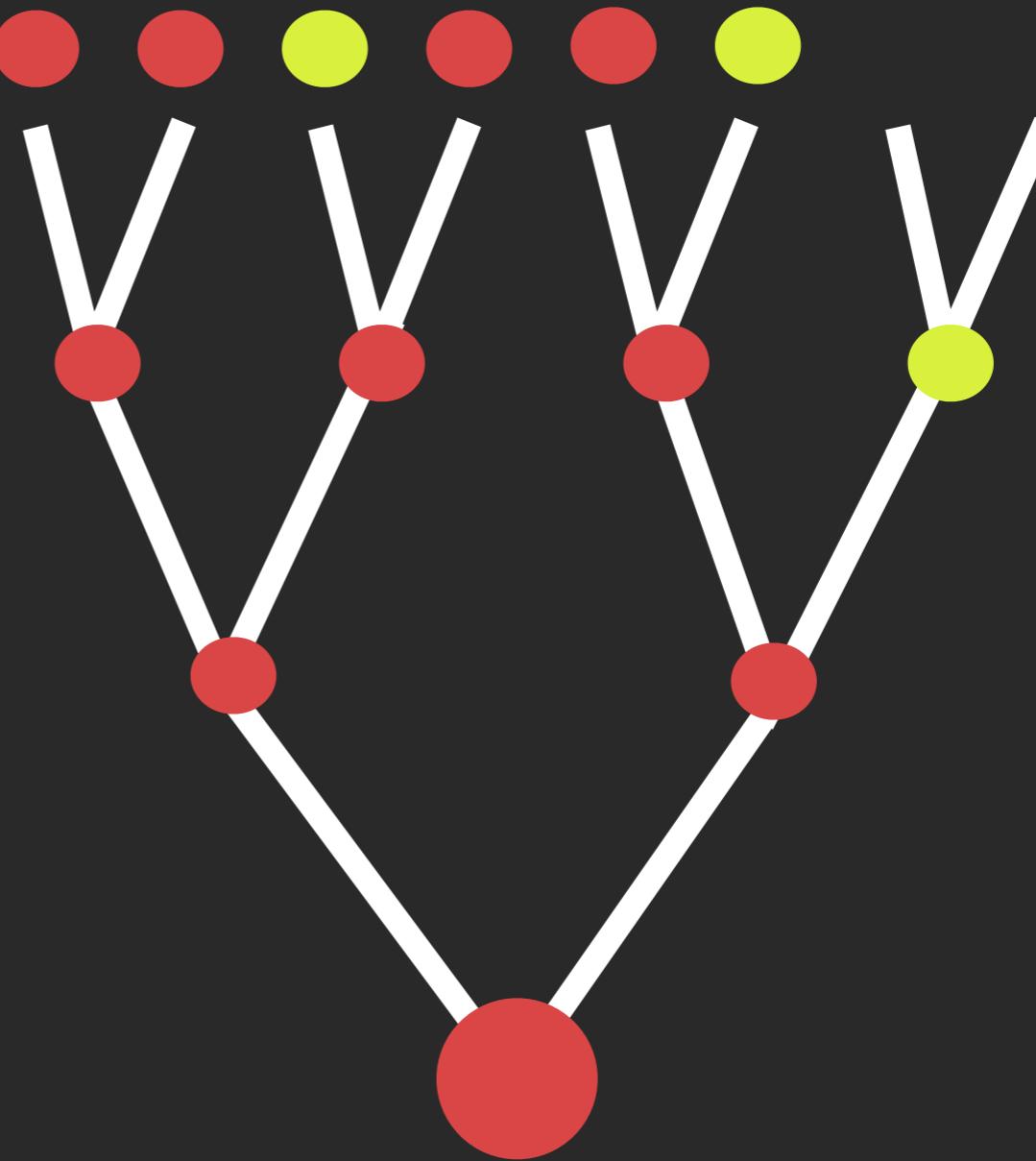
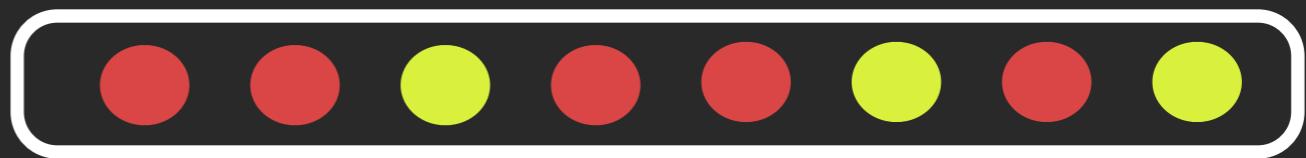
simulation two

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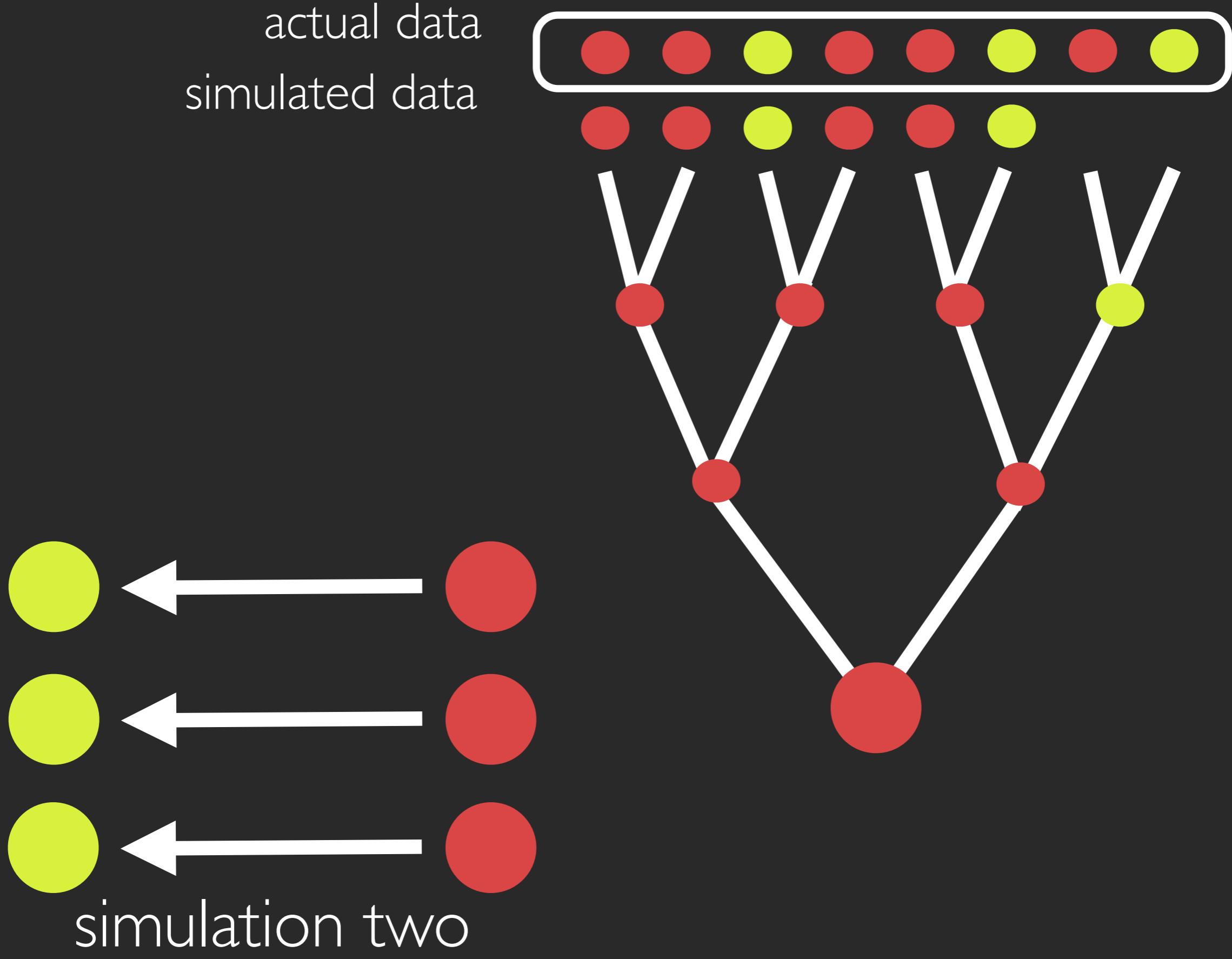
simulation two

actual data
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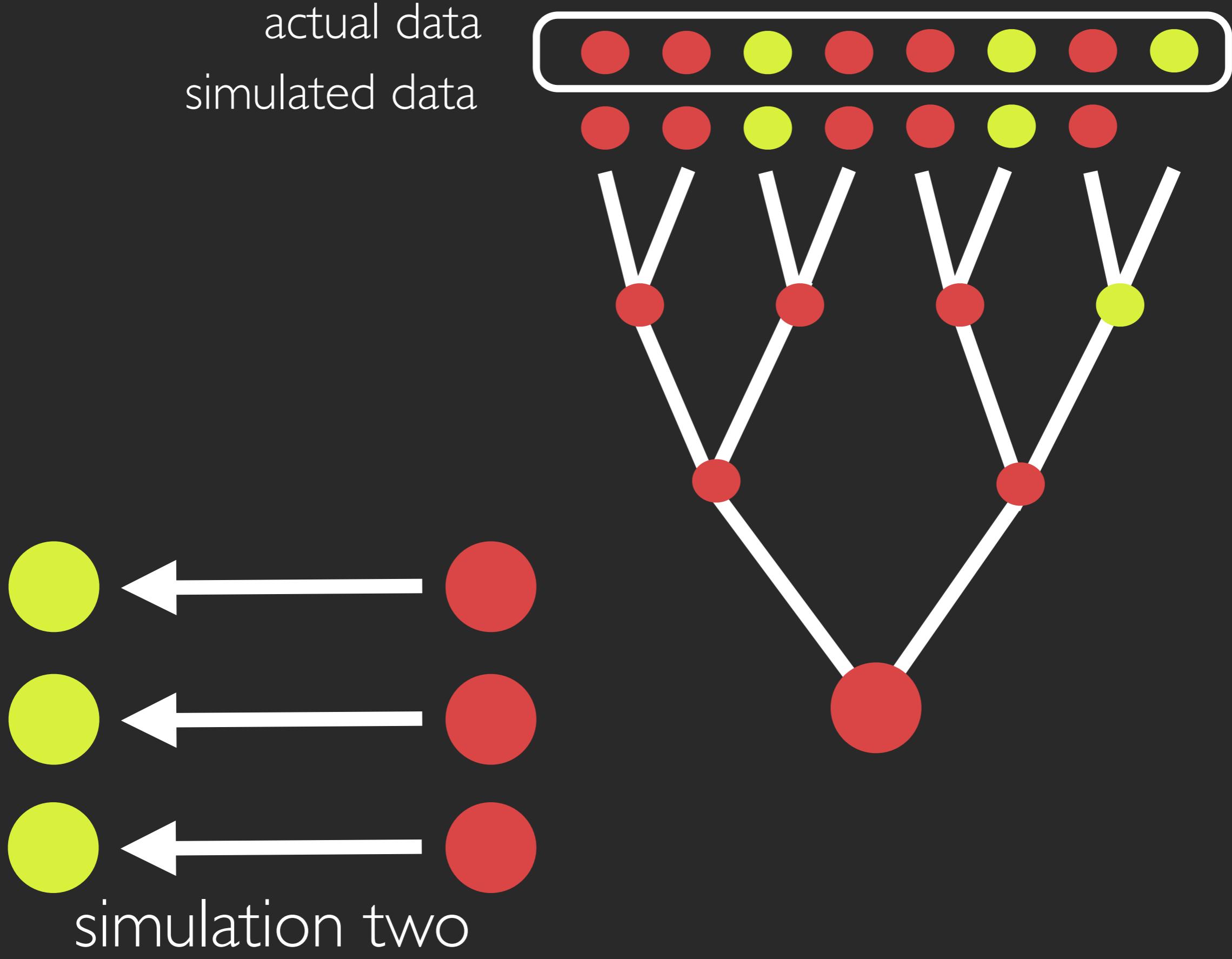


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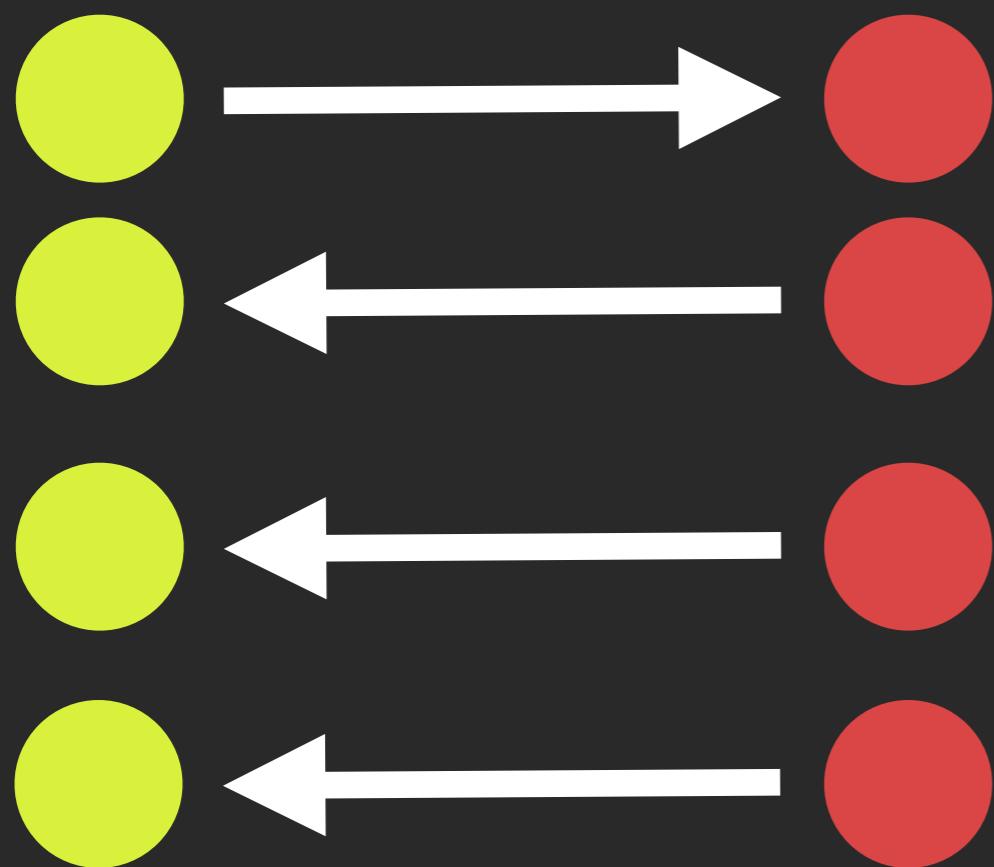
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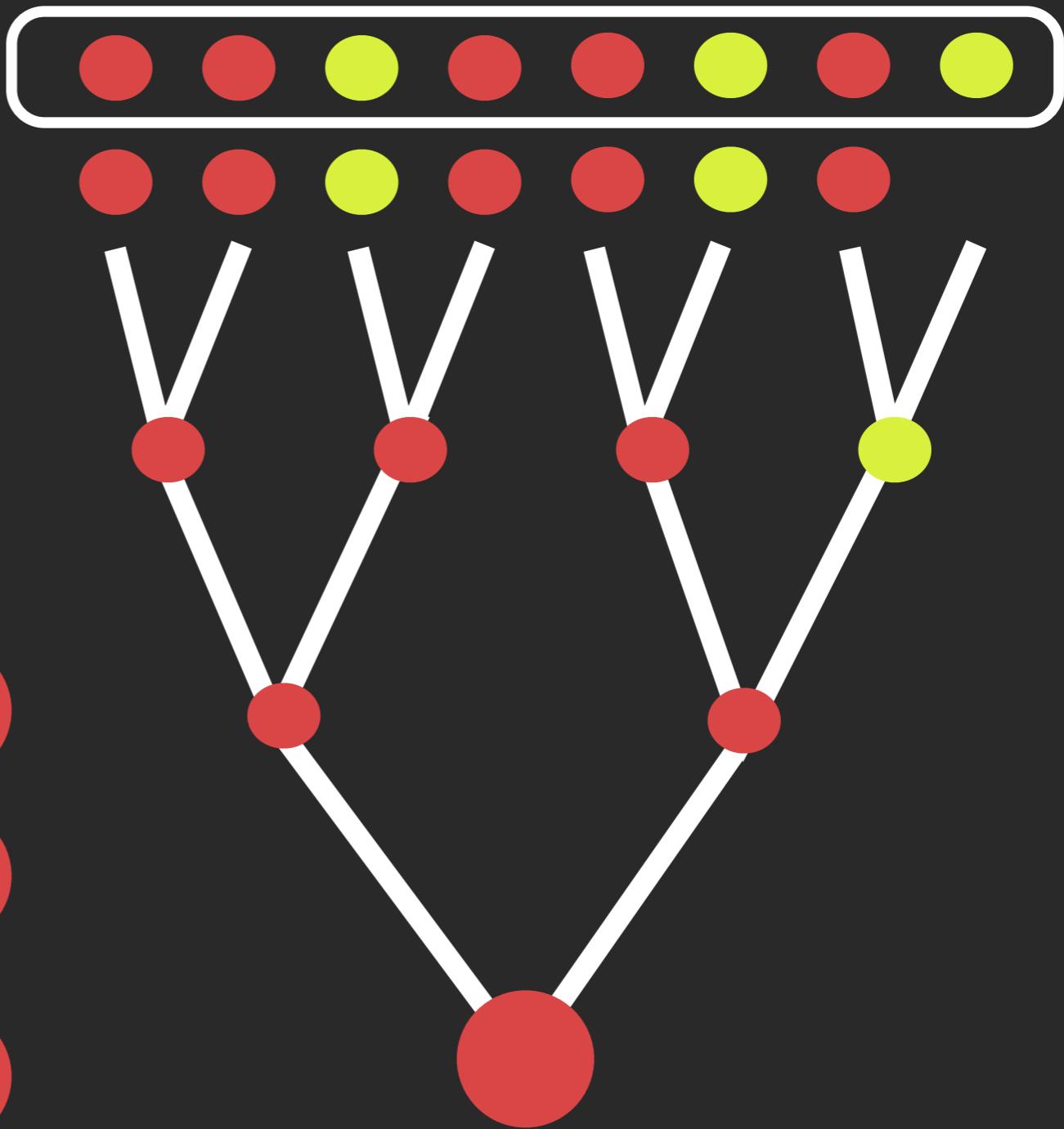
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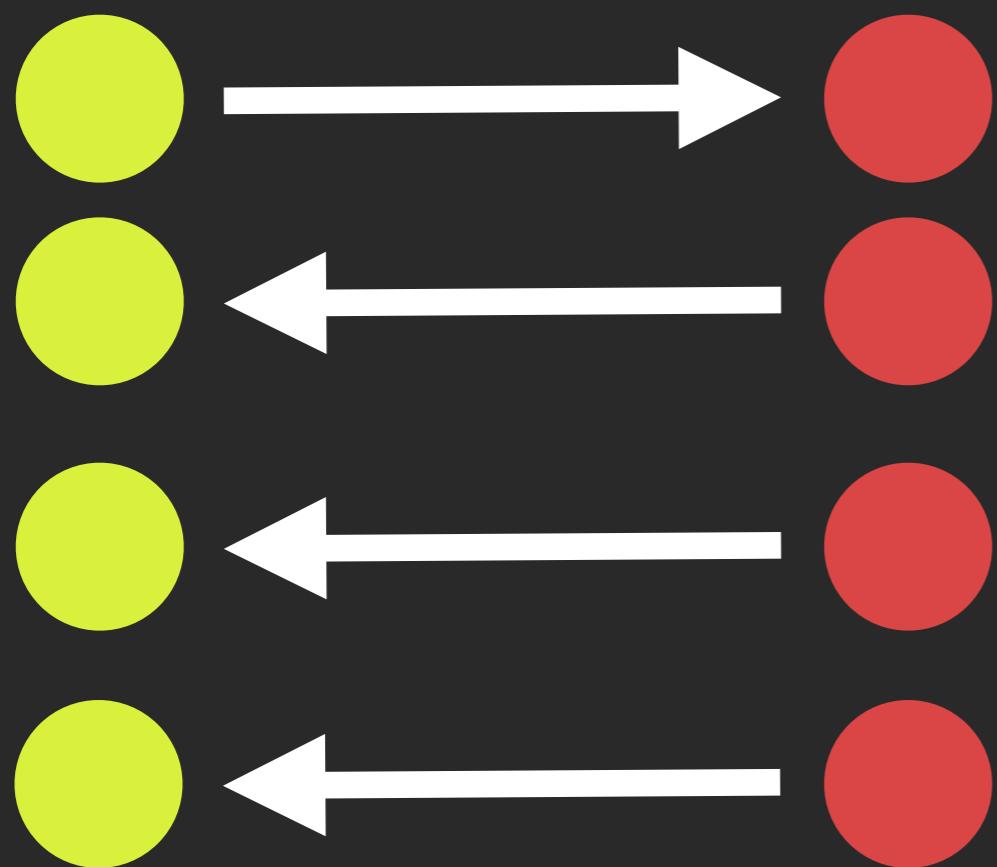
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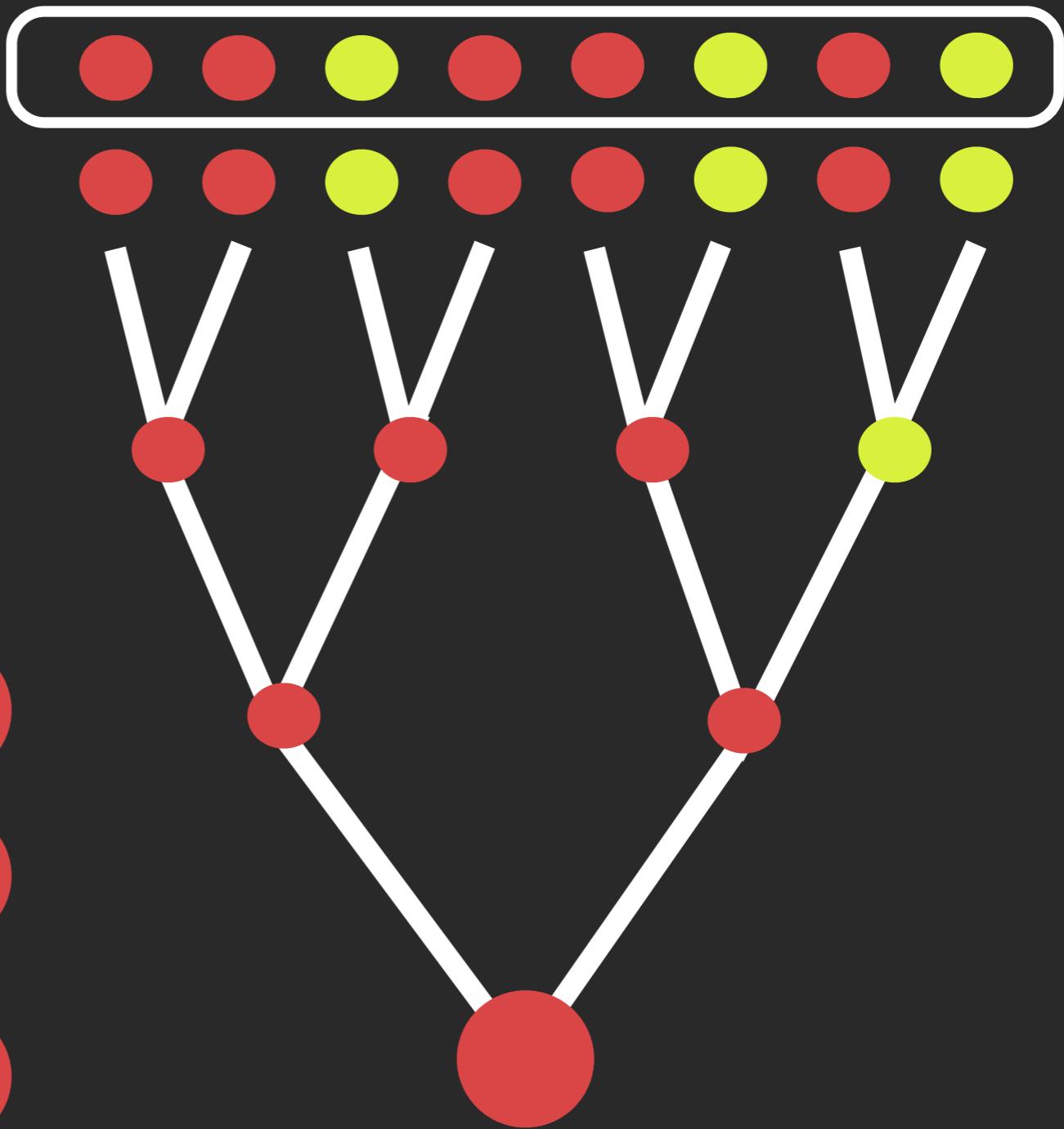
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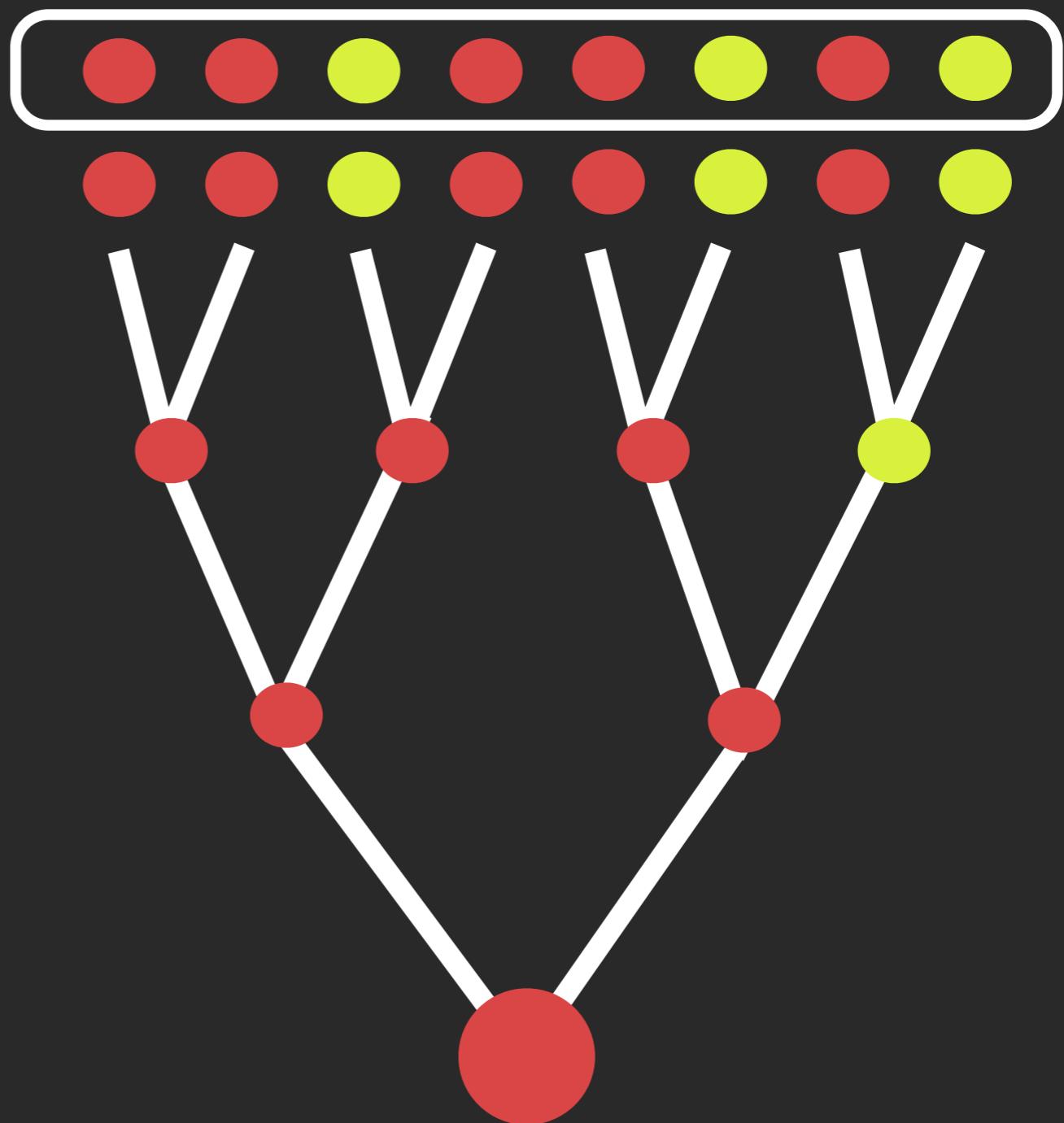
actual data
simulated data



simulation two

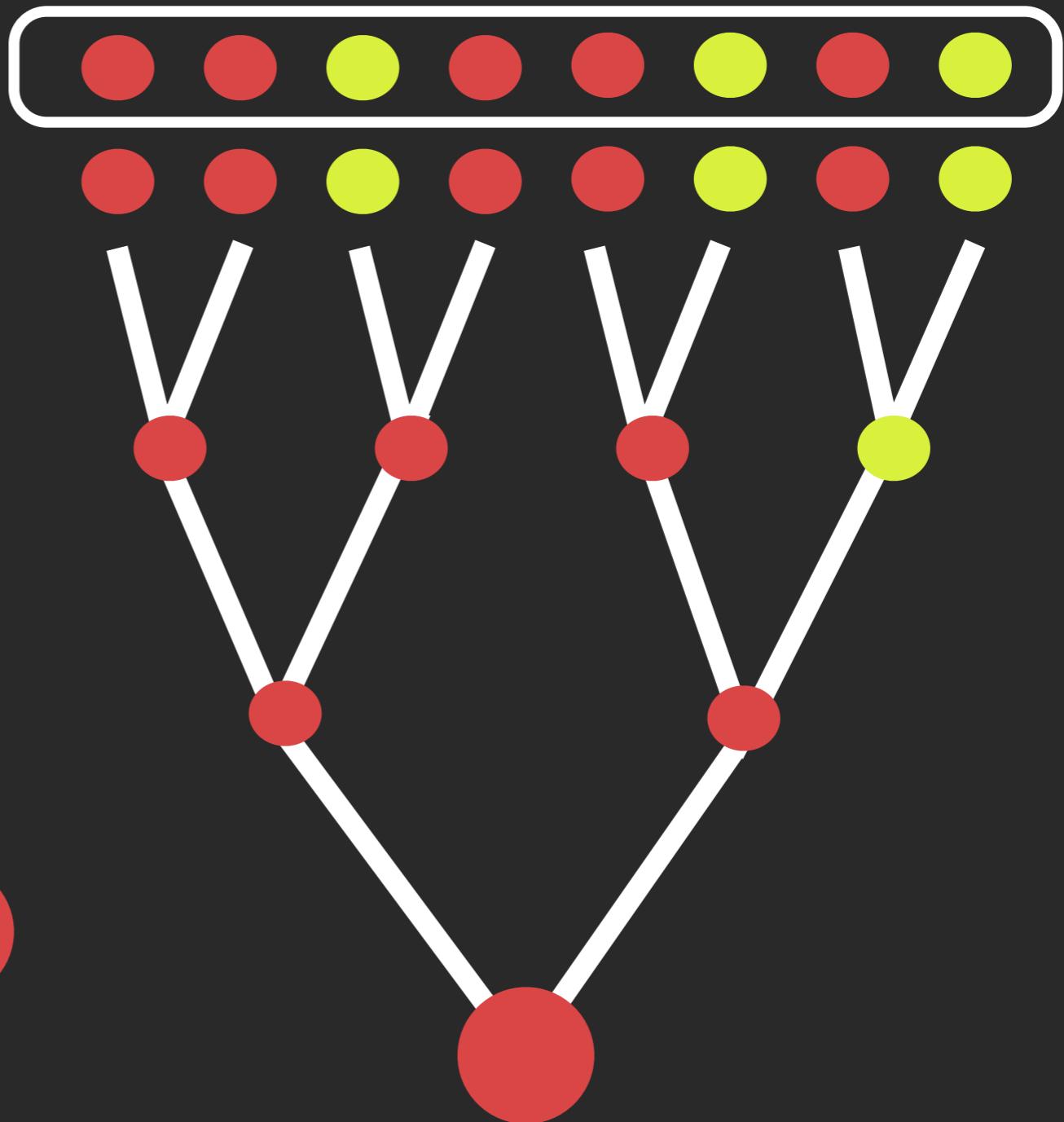
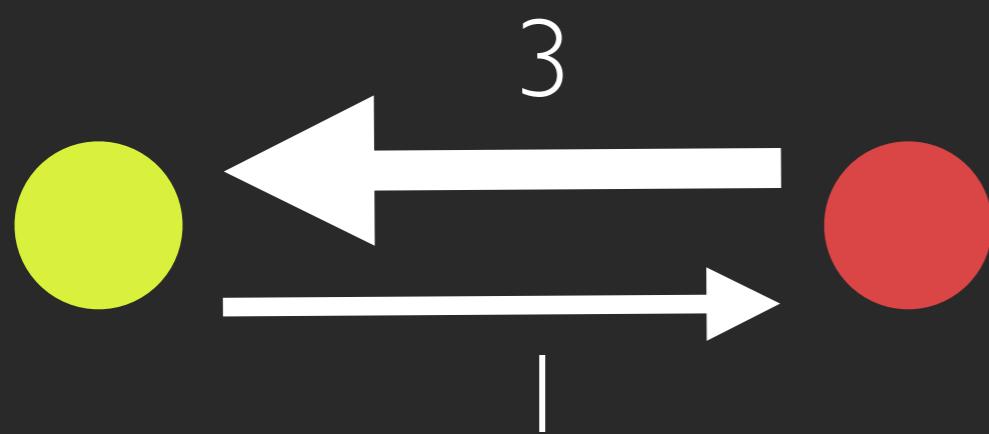


actual data
simulated data



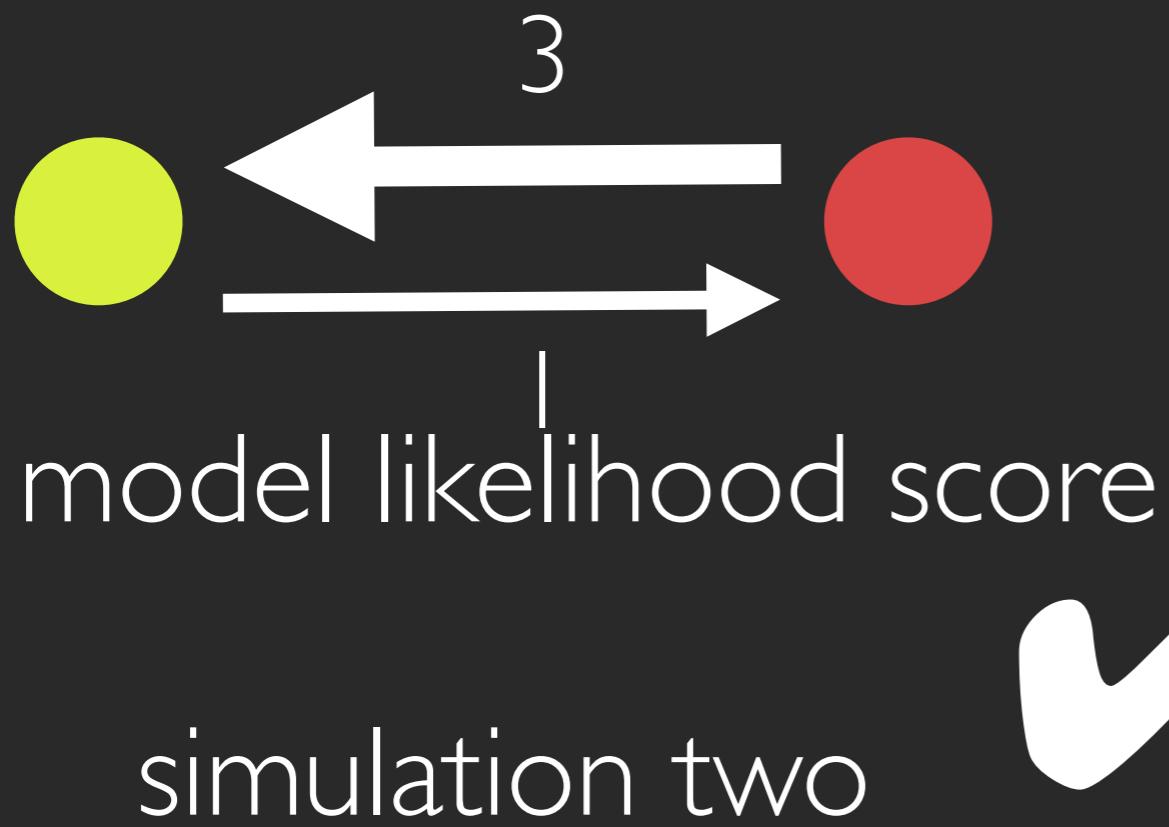
simulation two

actual data
simulated data



simulation two

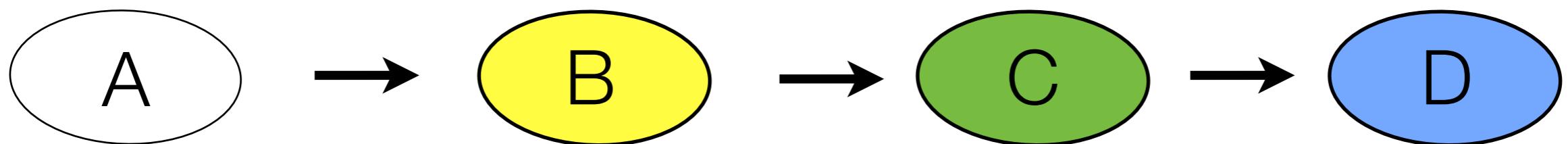
actual data
simulated data



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

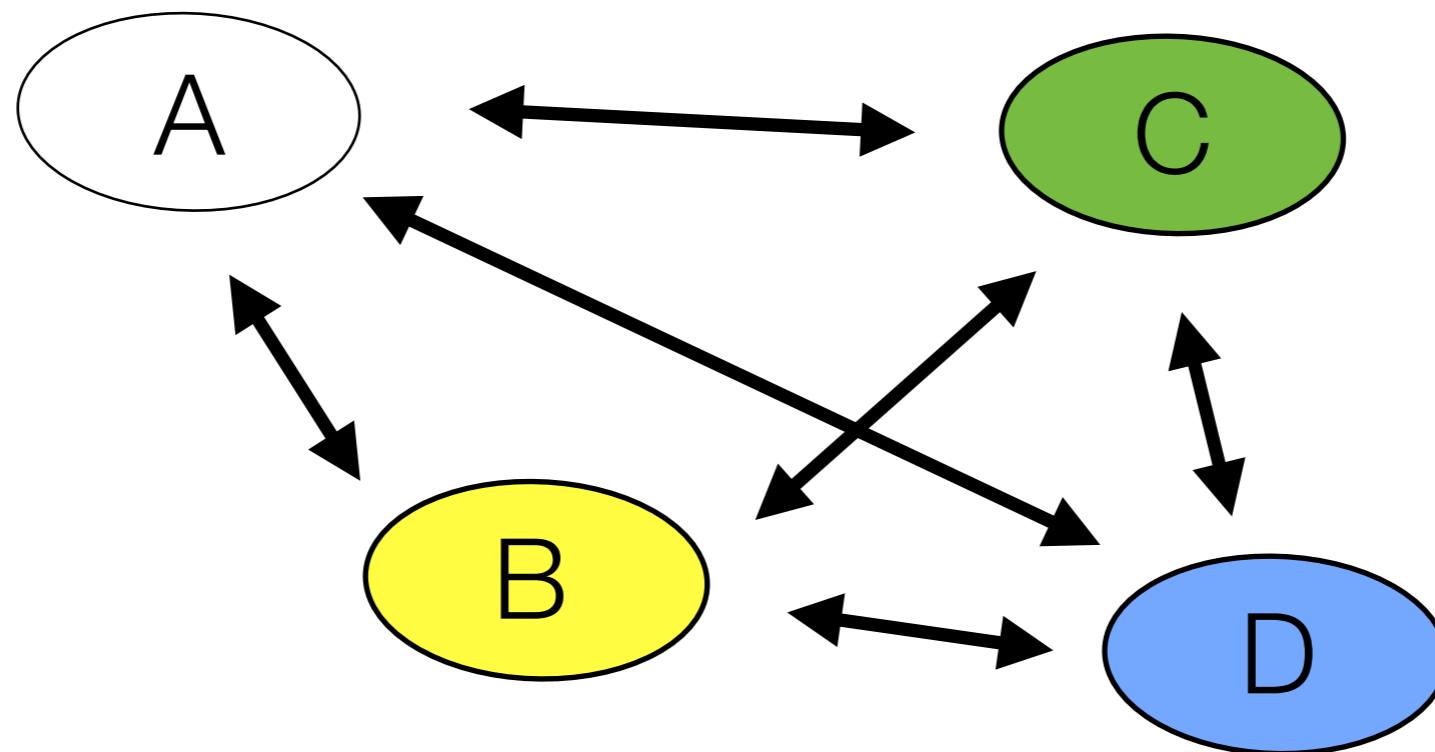
How do characters evolve?

- ORDERED CHANGE
- Sequential model



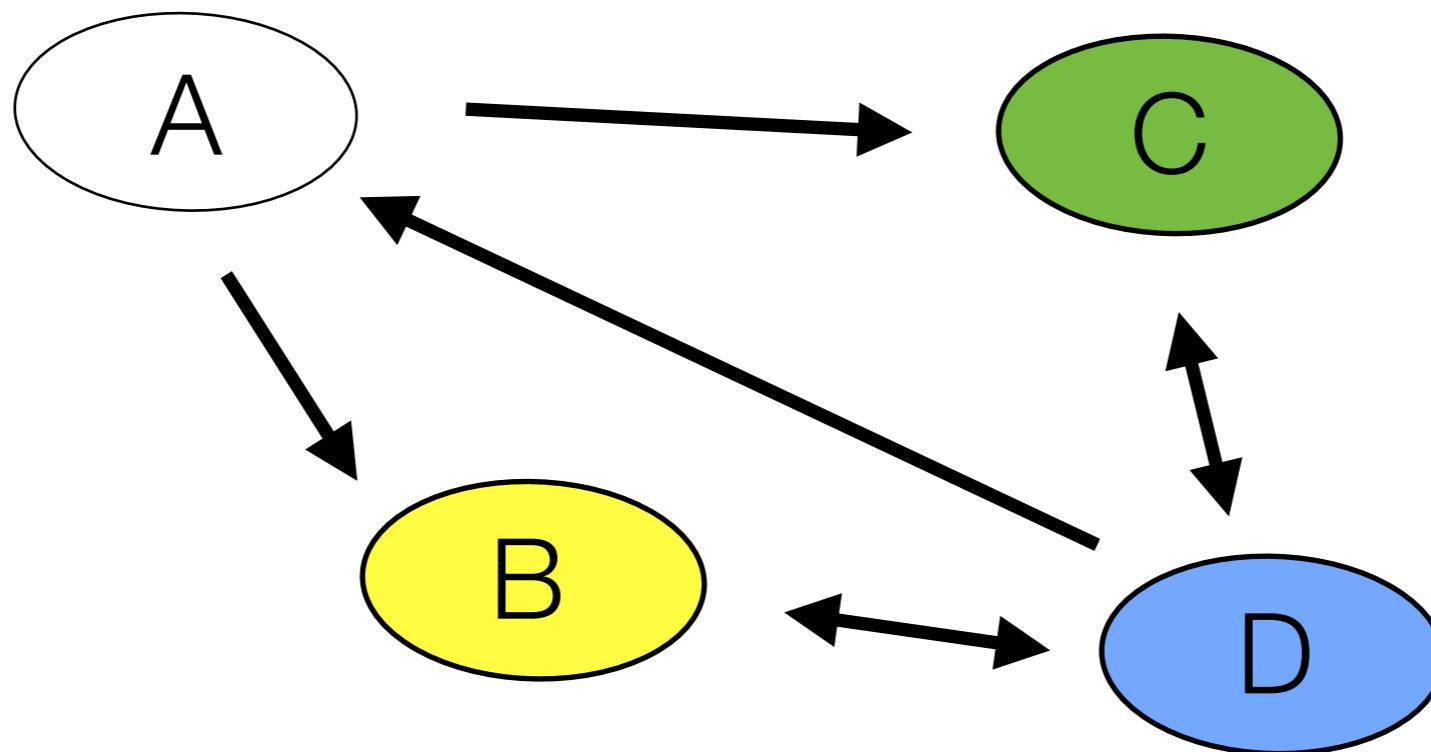
How do characters evolve?

- UNORDERED CHANGE
all changes are possible



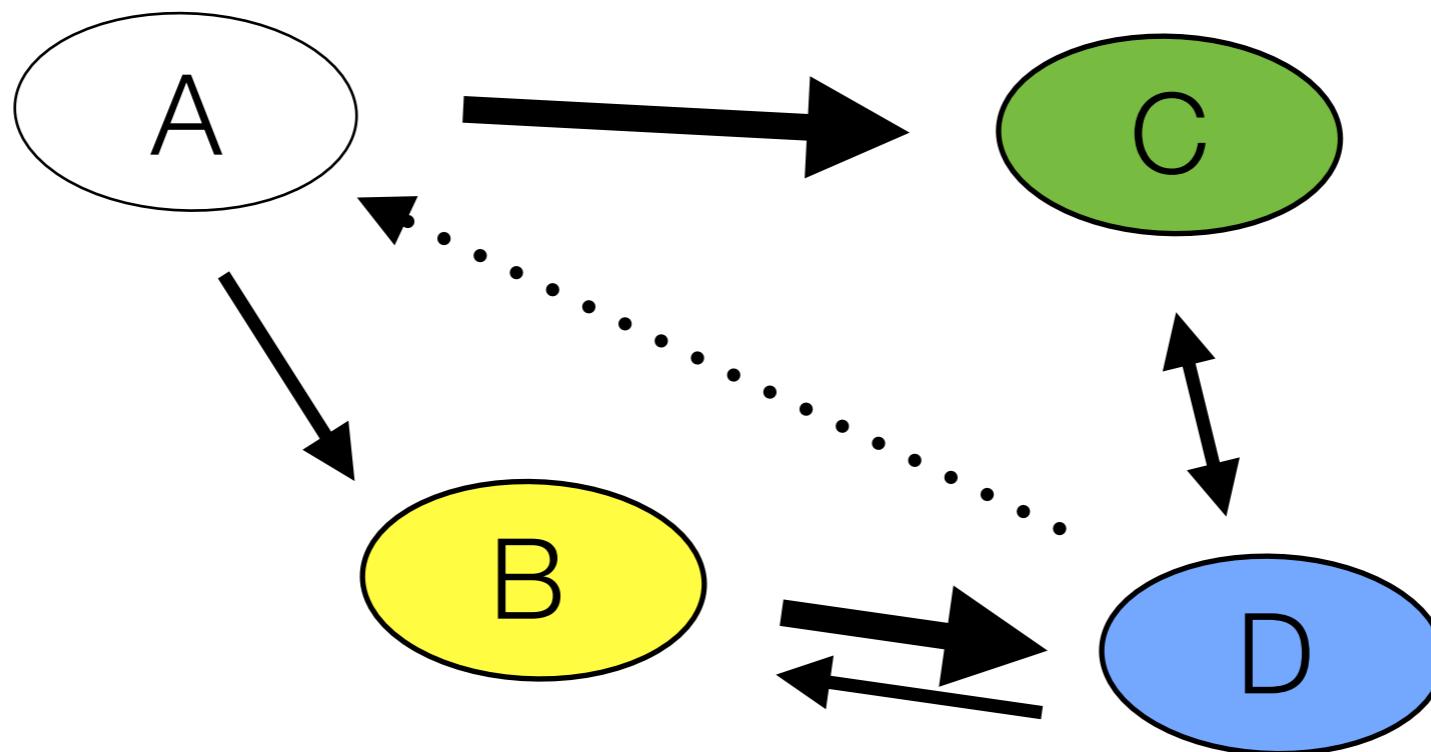
How do characters evolve?

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



How do characters evolve?

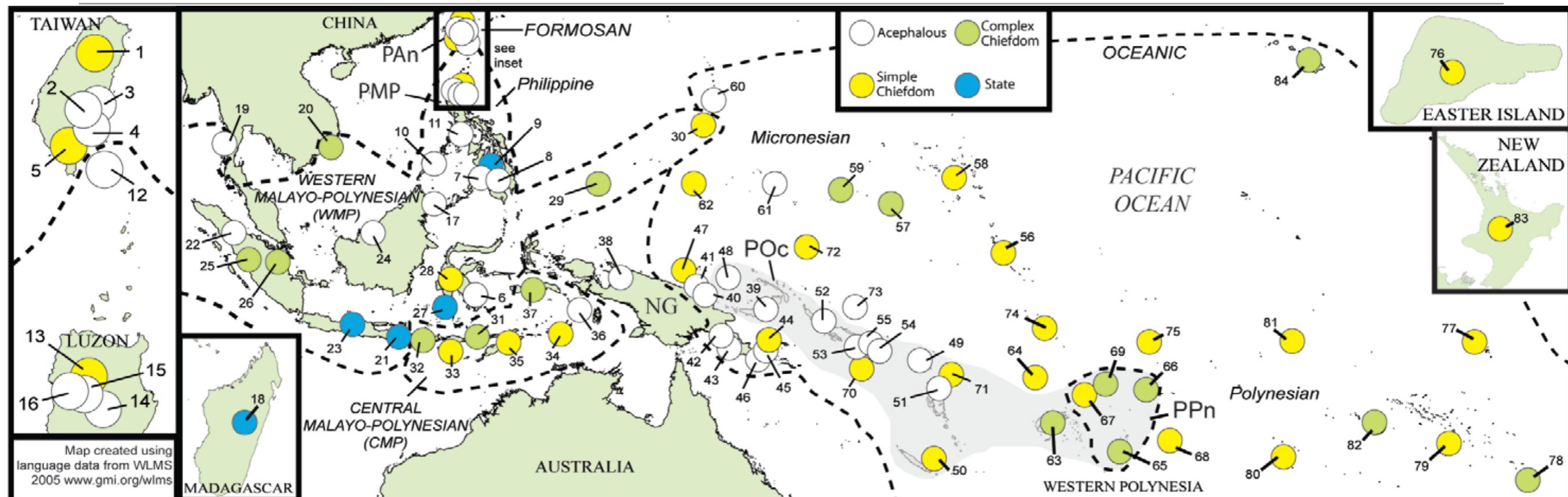
- RESTRICTED CHANGE
 - some changes are possible, and/or
 - some changes are weighted



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. Gray³, Toshikazu Hasegawa¹ & Ruth Mace²

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

Model testing

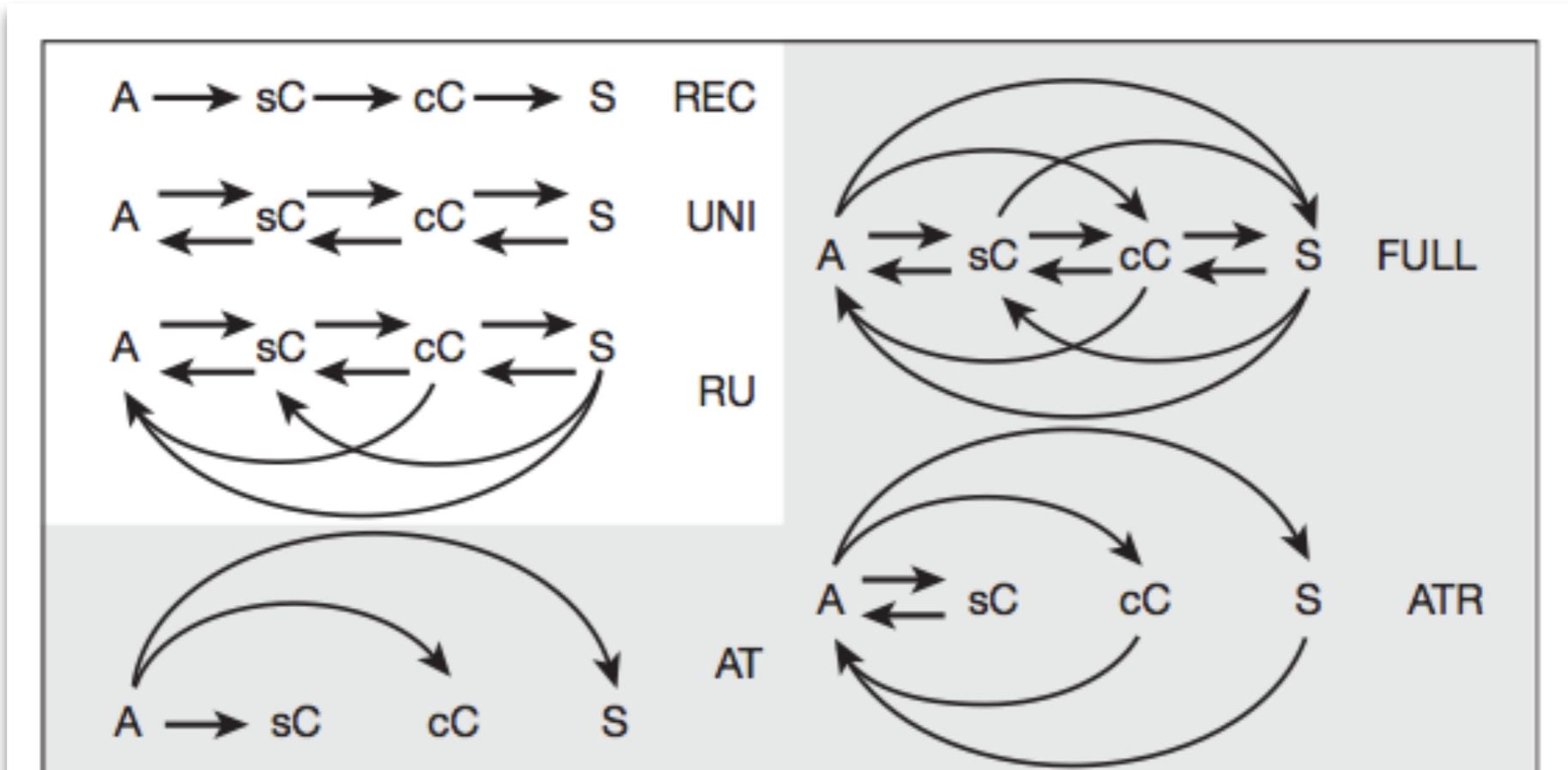


Figure 2 | Models of political evolution tested in this study. The three models on the white background (UNI, unilinear; RU, relaxed unilinear; REC, rectilinear) represent the idea that political evolution follows a sequence of incremental steps in the direction of increasing complexity, but differ as 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.

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?



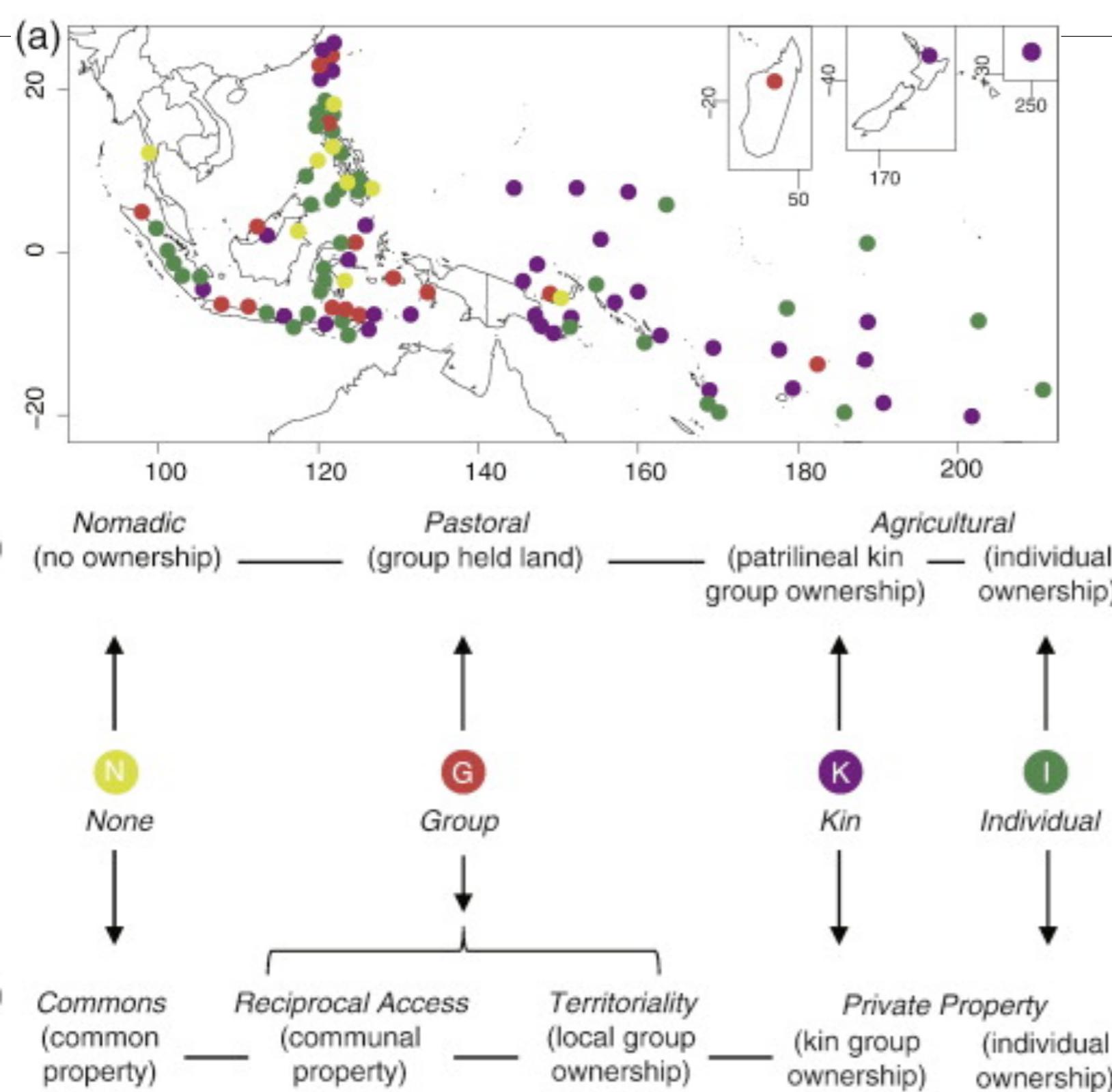
Geoff Kushnick @ ANU
Russell Gray @ MPI-SHH

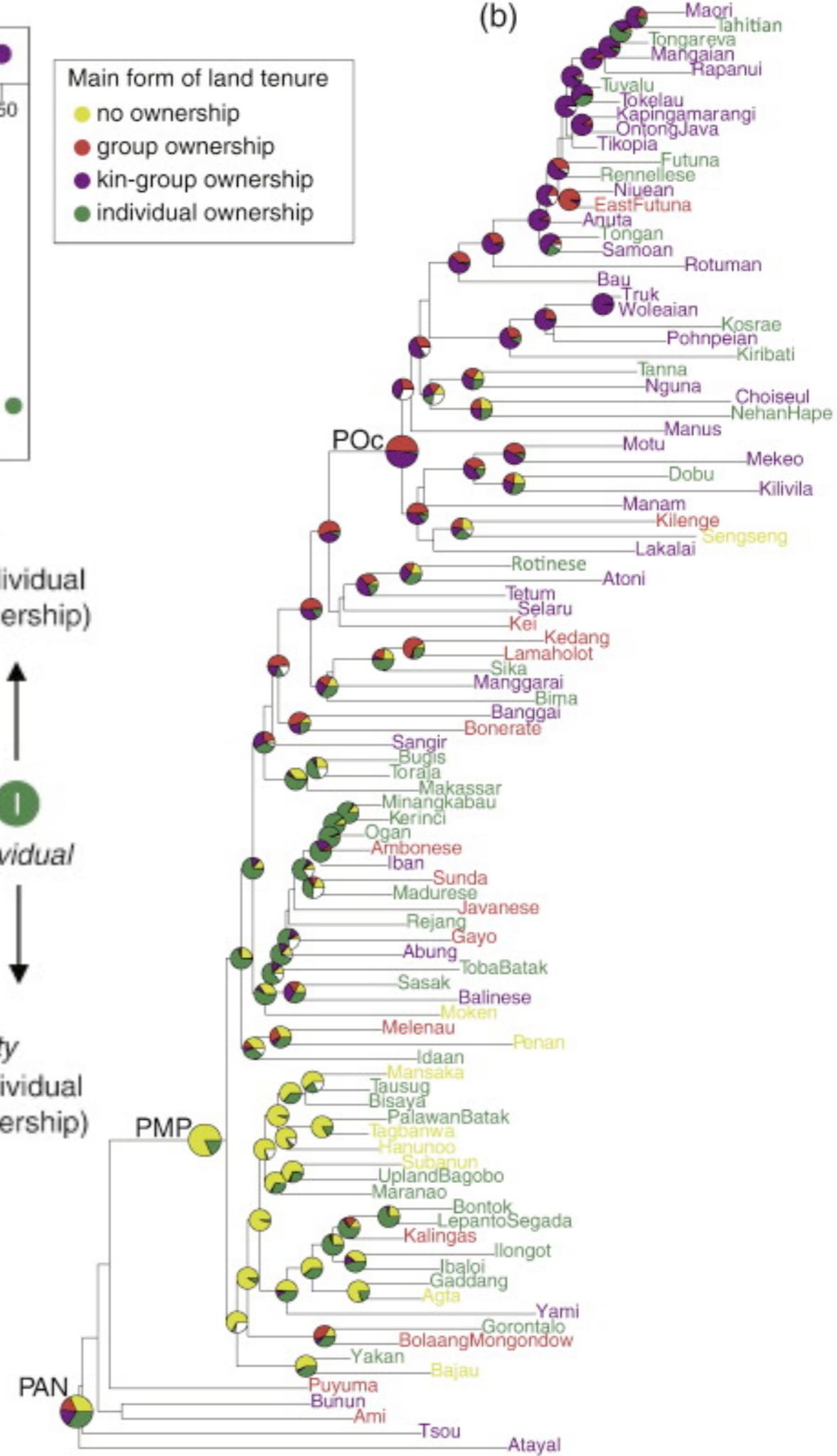
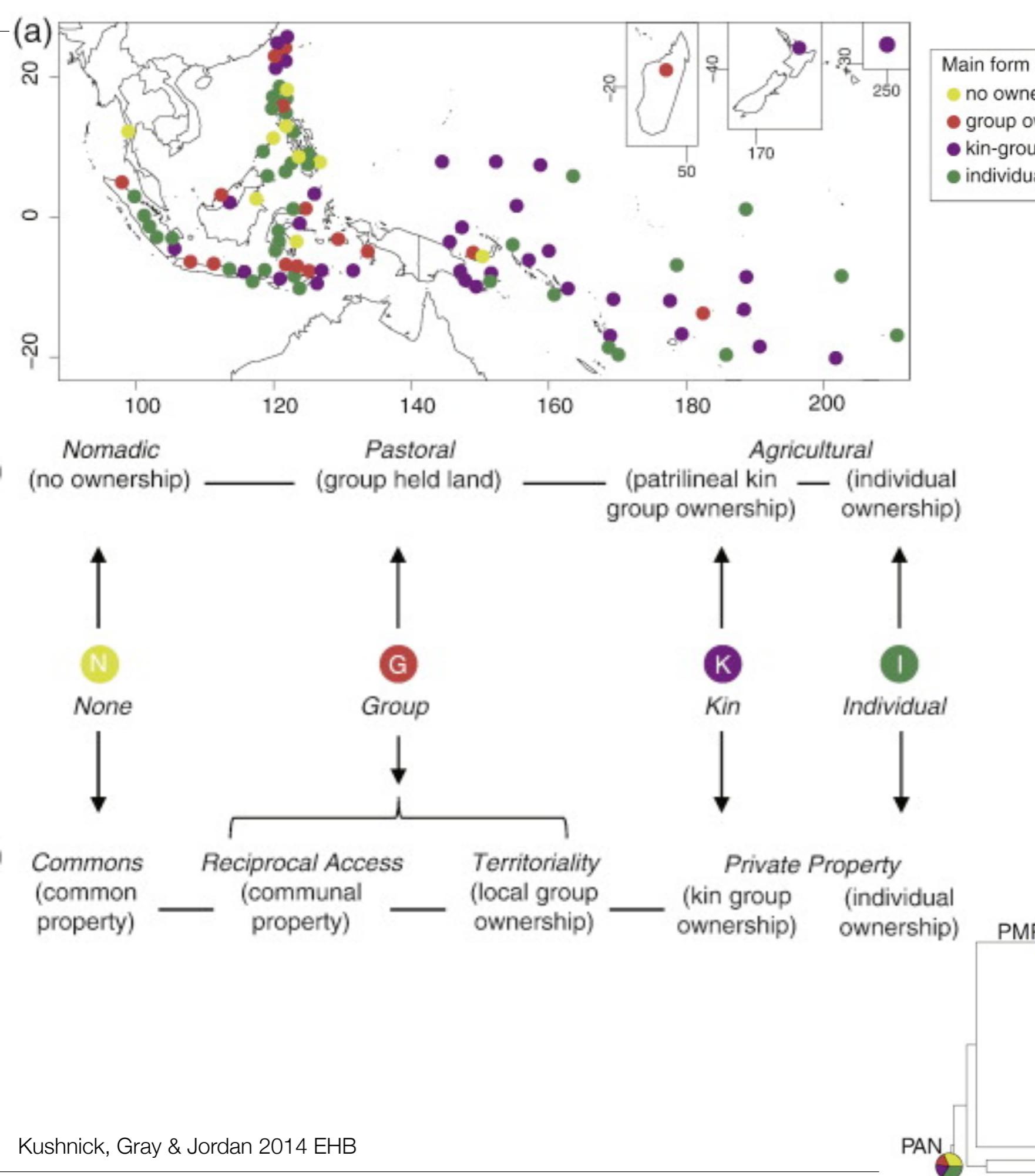
Evolution of land tenure in Austronesian

What did we do?

- Data on land tenure coded as ONE trait with FOUR states
 - Categorised a range of hypotheses as models where traits could change between these states:
- 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

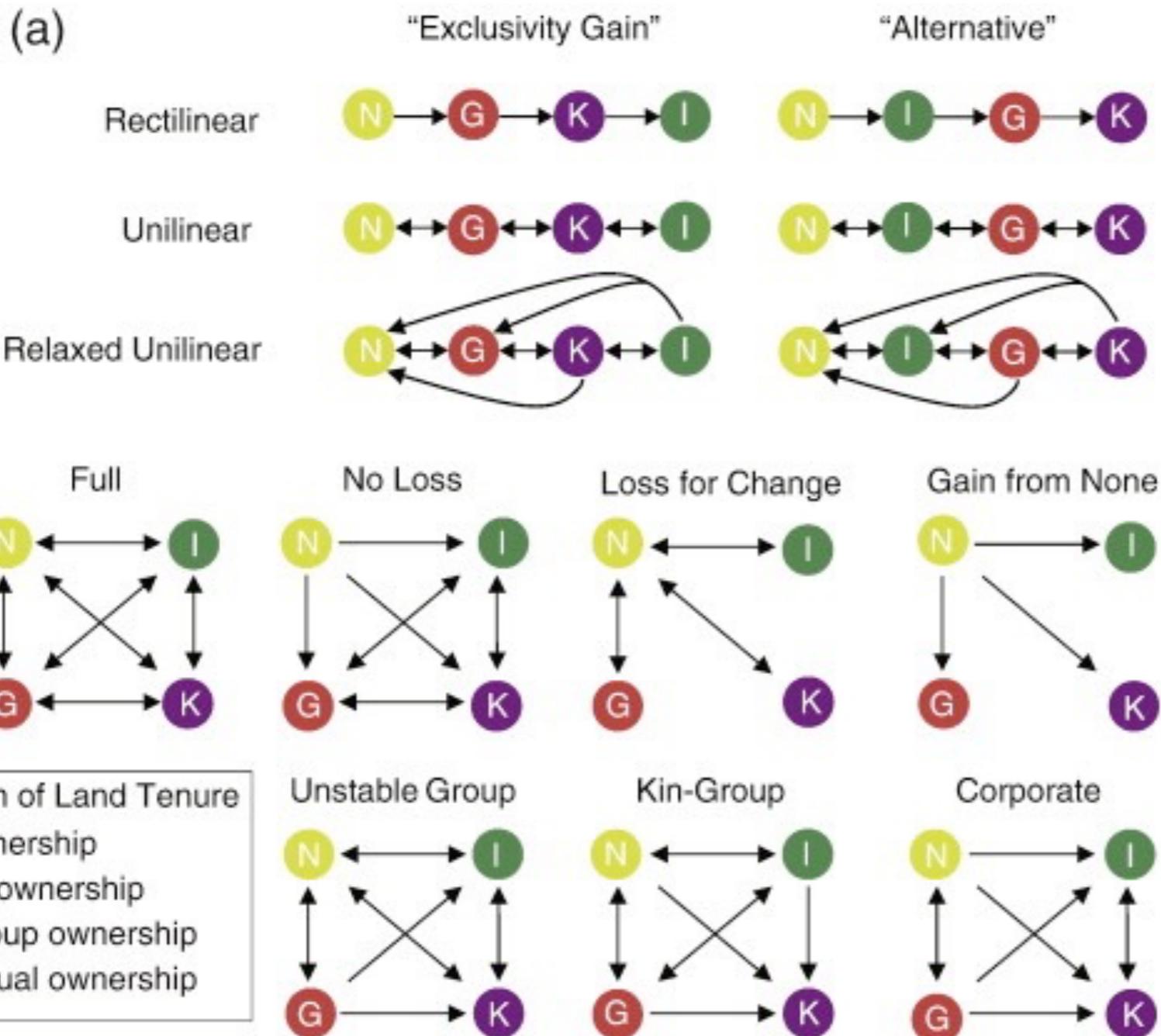






Evolution of land tenure

Inferring and testing models of change



Evolution of land tenure

Inferring and testing models of change

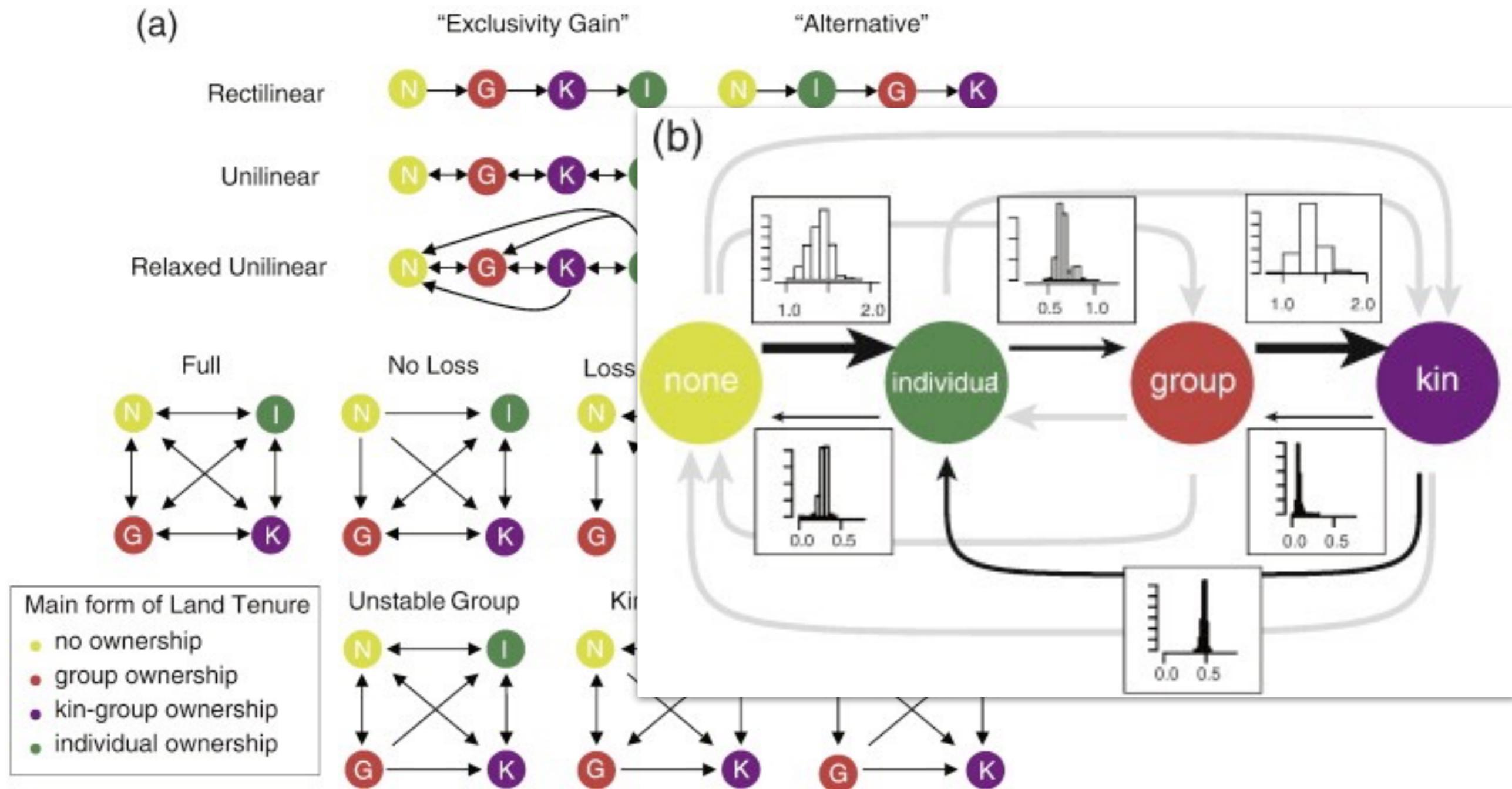
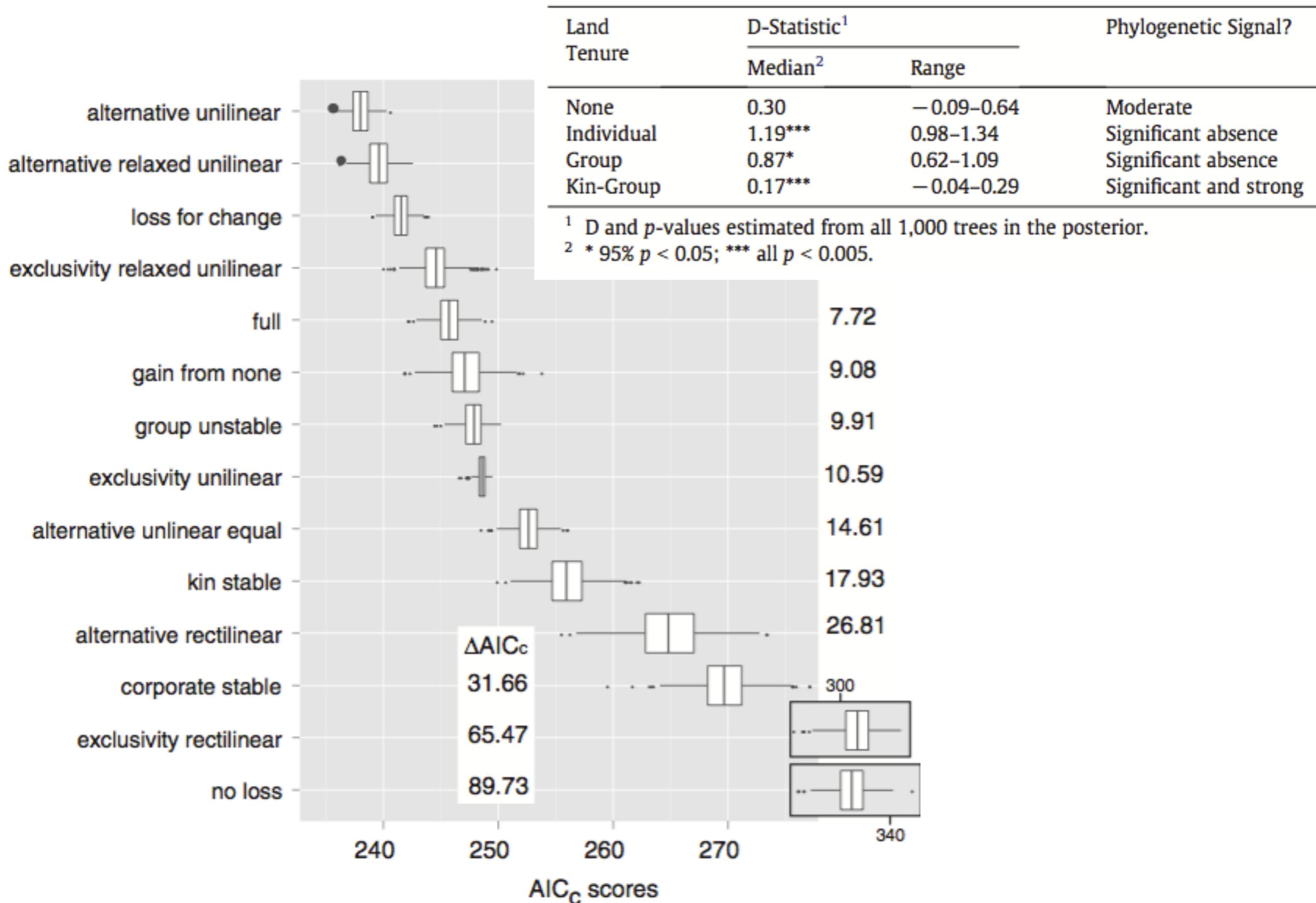


Table 1
Phylogenetic signal of each of the main type of land tenure norms ($n = 97$).





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

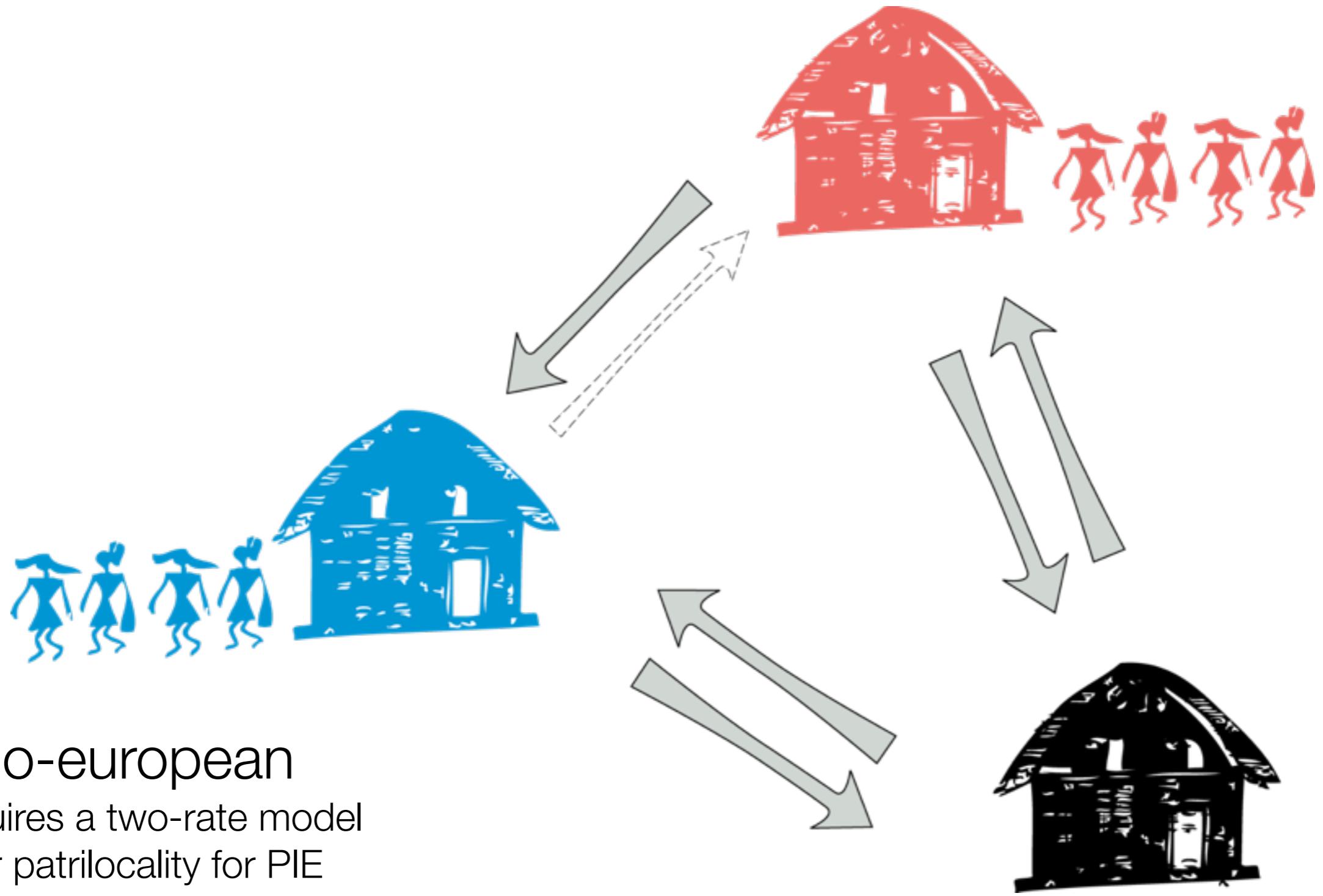
Laura Fortunato^{1,2,*†} and Fiona Jordan^{1,2,‡}



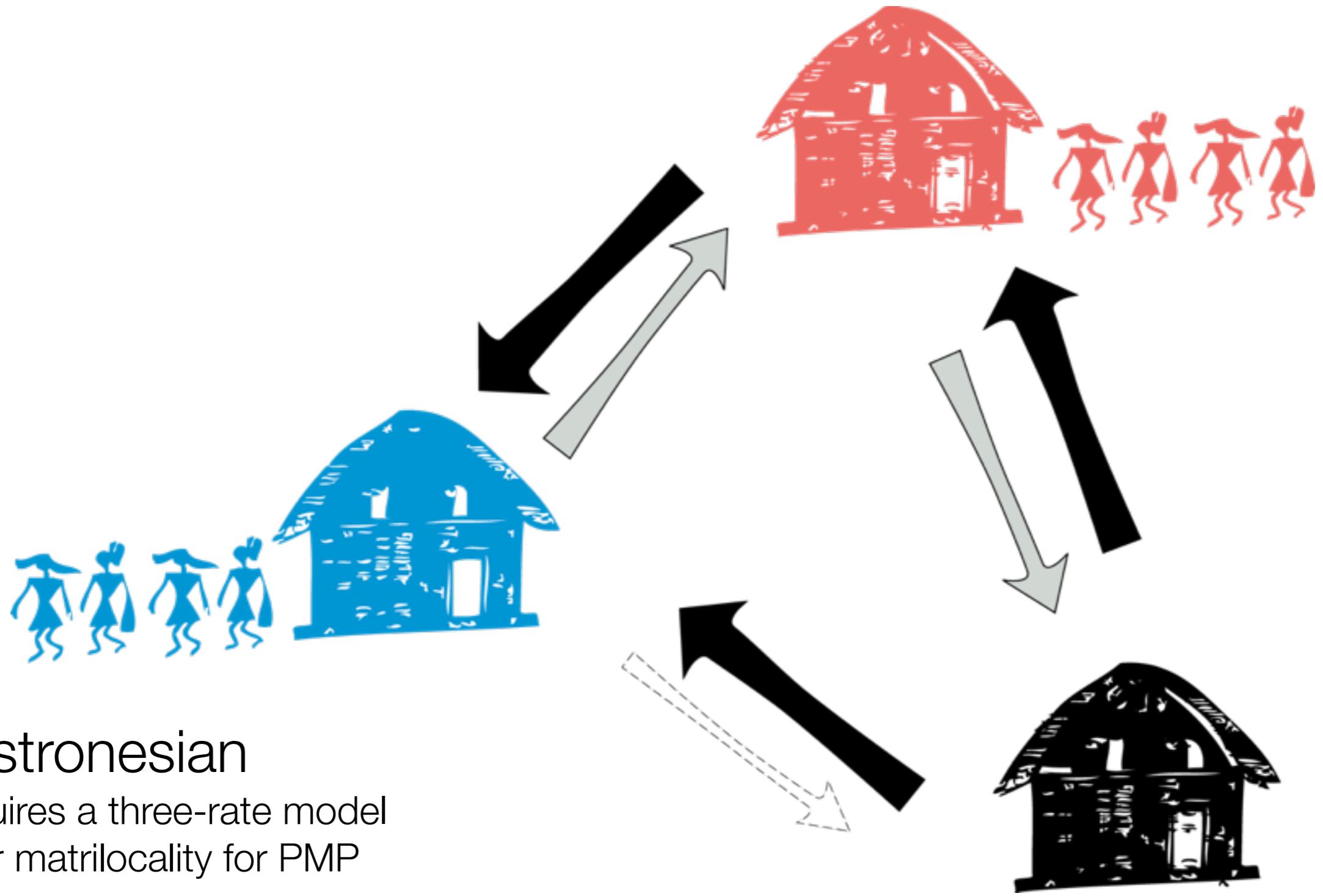
The evolution of marital residence

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



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
- 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 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 step forward in our ability to infer the general mechanisms of cultural evolutionary change, that is, the identification of lineage-specific processes within global domains.”*