

# A selection of ongoing work

## Floral evolution

O'Meara\*, Stacey Smith\*, Armbruster,  
Harder, Hardy, Hileman, Hufford, Litt,  
Magallon, Stephen Smith, Stevens,  
Fenster, Diggle

## Flexible trait evolution

O'Meara and Banbury<sup>P</sup>

## Phylogeographic models

O'Meara, Jackson<sup>P</sup>, Morales-Garcia,  
Carstens

\* = equal lead authors

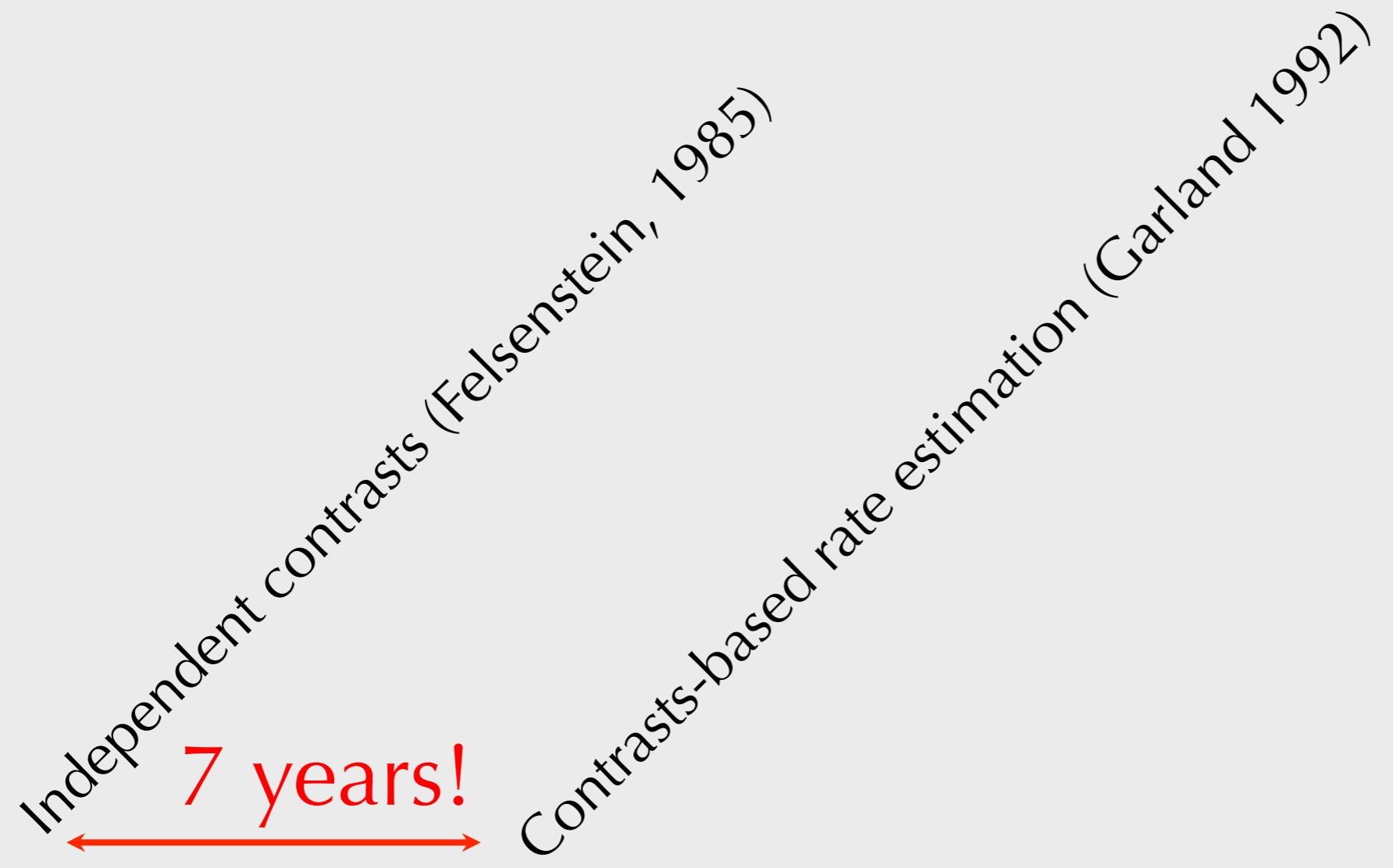
<sup>P</sup> = postdoc mentee

Independent contrasts (Felsenstein, 1985)

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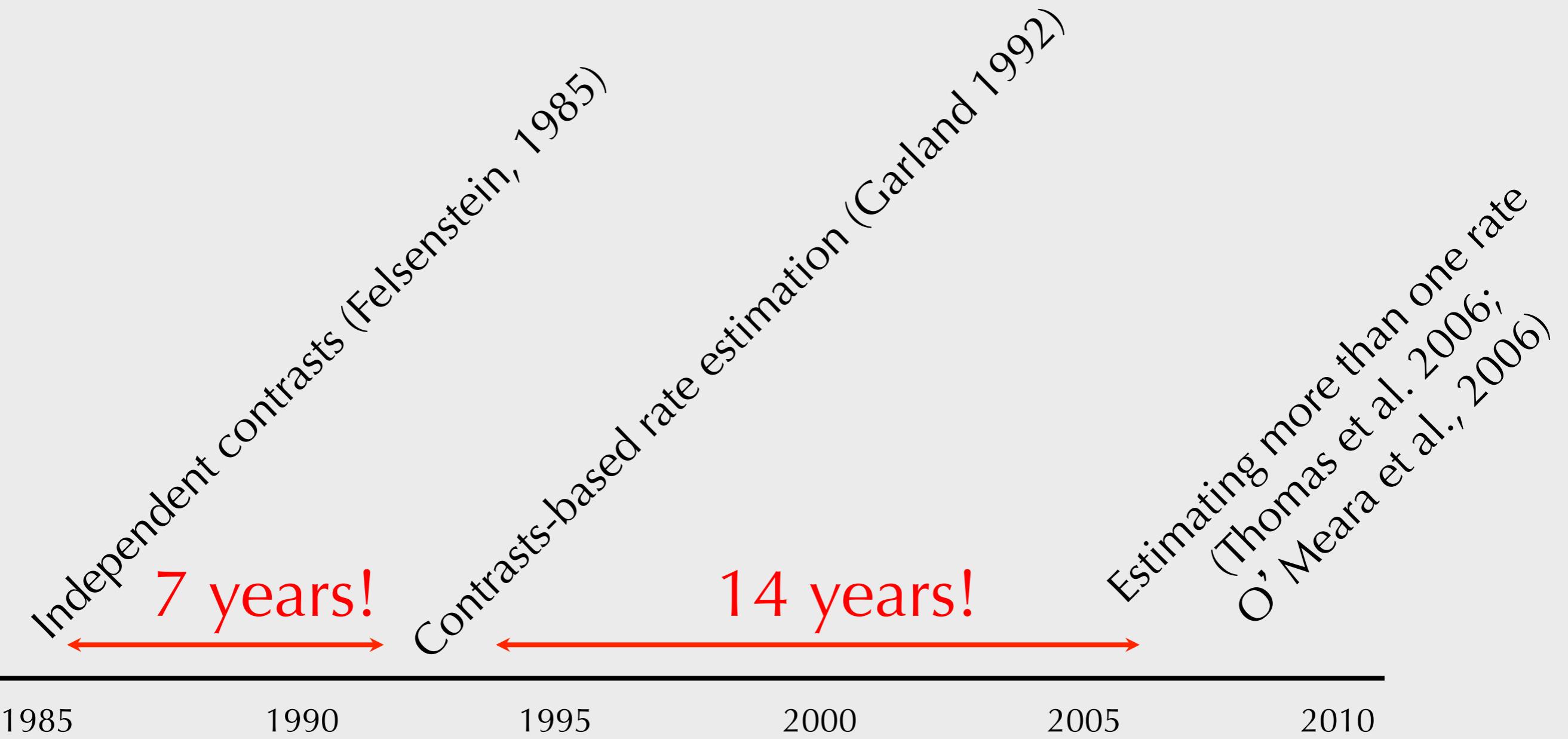
1985      1990      1995      2000      2005      2010

Progress in comparative methods



1985      1990      1995      2000      2005      2010

Progress in comparative methods



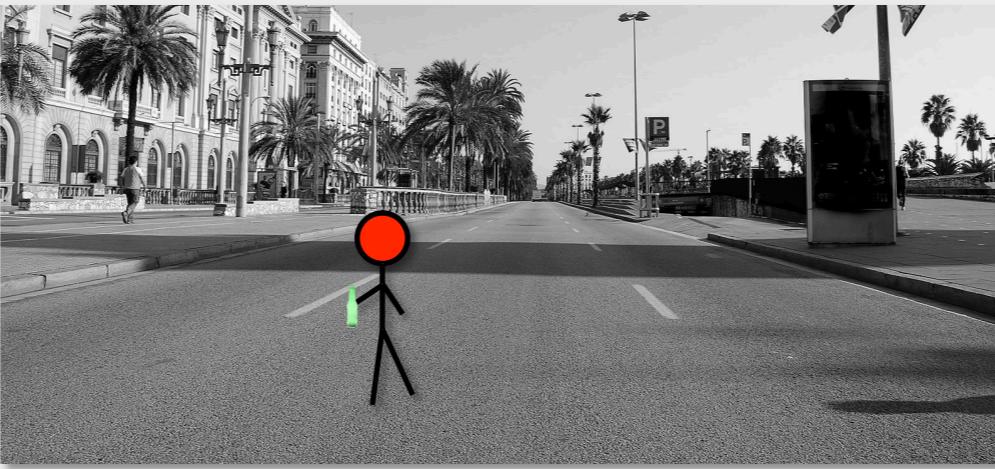
Progress in comparative methods

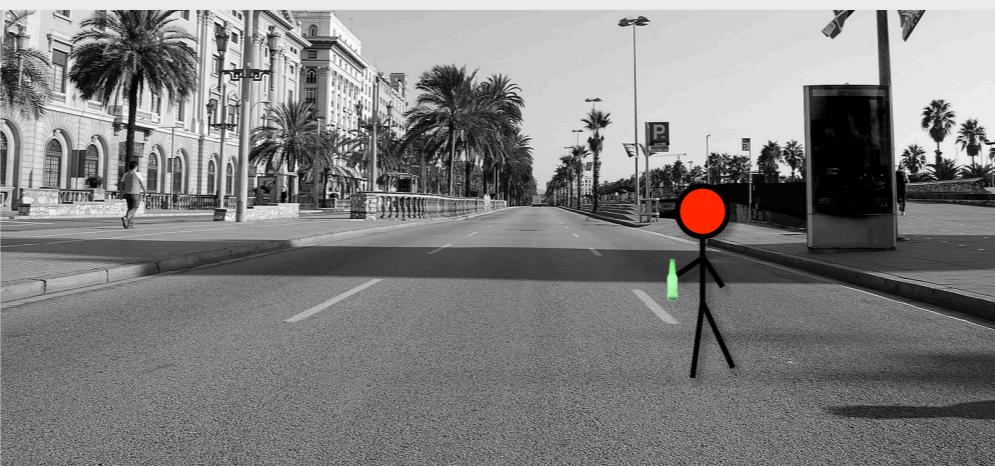
# Multivariate normal

$$f(x) = \frac{1}{\sqrt{2\pi} \sqrt{|\Sigma|}} \exp\left(-\frac{1}{2}(x - \mu)' \Sigma^{-1} (x - \mu)\right)$$

Model	Description	$\Sigma$	$\mu$
Classic Brownian motion	Single rate of change	Rate x shared time between every pair of species	State at root
Multiple rate Brownian motion	Multiple rates of change	Appropriate rate(s) x shared time between every pair of species	State at root
Multiple mean Ornstein-Uhlenbeck	Attraction to particular value(s), but constant attraction and wiggle	Transformation of rate x time matrix	Expected tip states given model
Multiple everything model	Multiple attractors, attraction, and wiggles	Transformation of rate x time matrix	Expected tip states given model















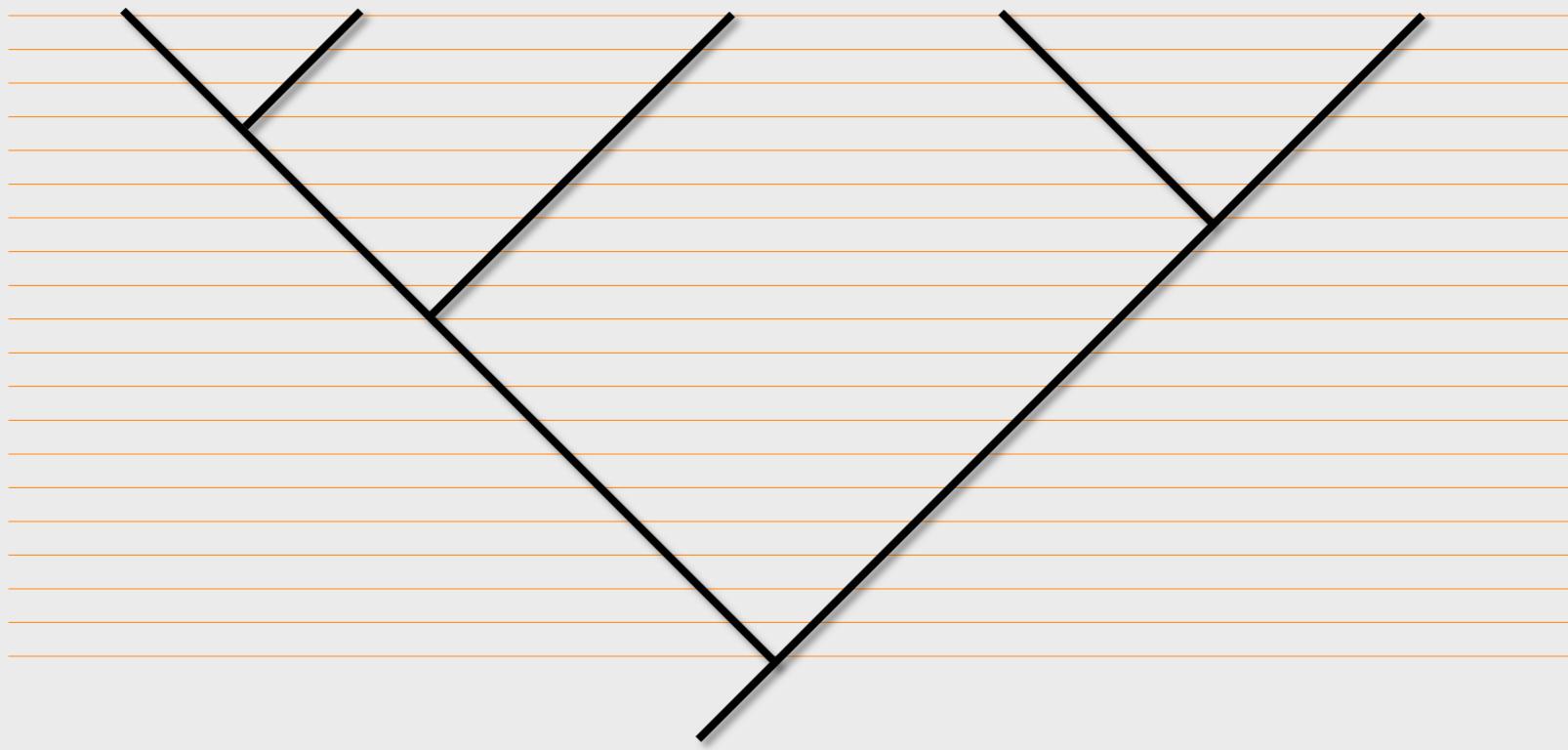
# Hard or impossible to analyze currently:

- Bounded evolution
- Character displacement
- Mimicry
- Effect of varying external parameter
- Mixture of processes

**Our goal:** Allow empiricists to build and use their own models for comparative data

**Our approach:** Approximate Bayesian computation

# Discrete time



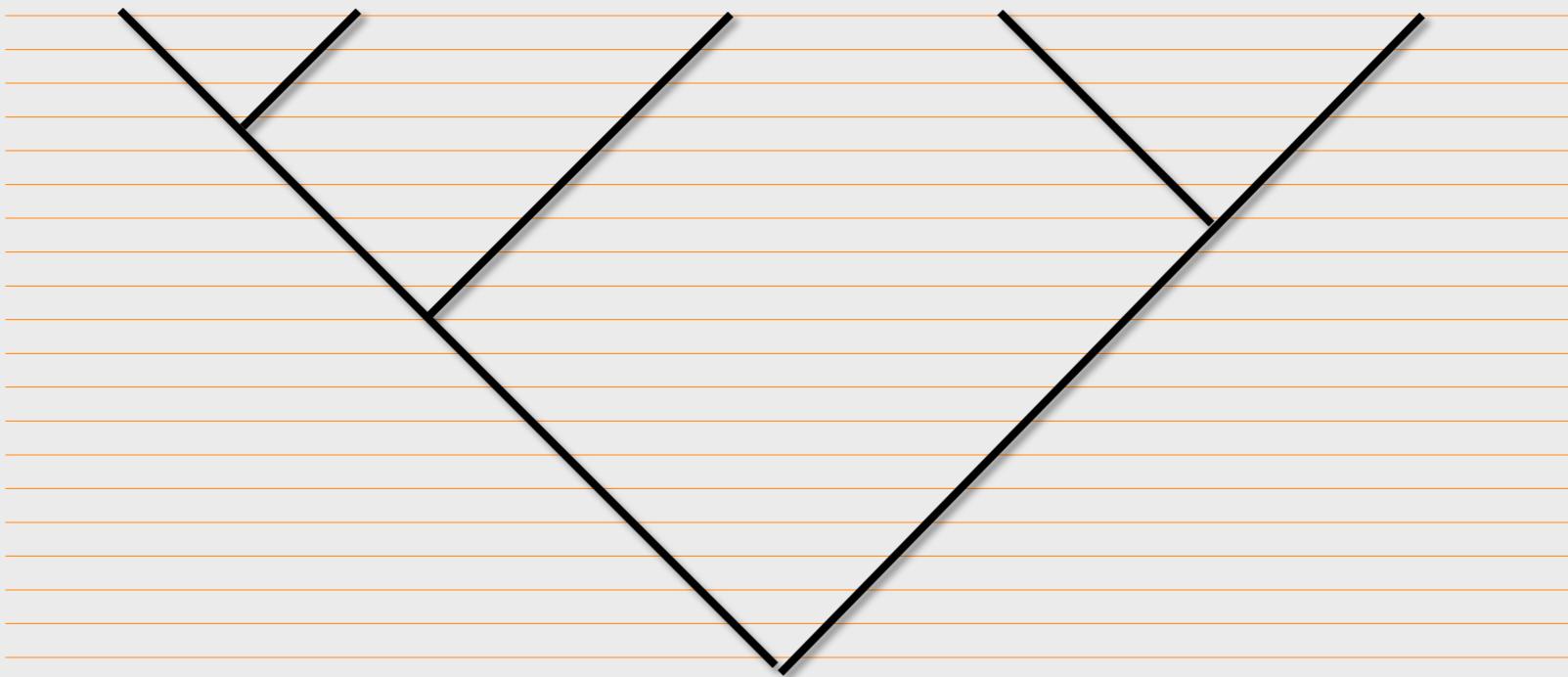
Continuous time is scary:

$$f(x) = \frac{1}{\sqrt{2\pi} \sqrt{|\Sigma|}} \exp\left(-\frac{1}{2}(x - \mu)' \Sigma^{-1} (x - \mu)\right)$$

Discrete time is not:

```
x(t+1) = x(t) + rnorm(n=1, mean=0, sd=0.4)
```

# Discrete time



```
taxa[[i]]$nextstates = taxa[[i]]$states  
+ intrinsicFn(...)  
+ extrinsicFn(...)
```

## Discrete time

`intrinsicFn()`

Model affecting evolution of a species independent of what the other species are doing

`extrinsicFn()`

Model affecting evolution of a species based on the traits of other species

## Discrete time

`intrinsicFn(model parameters, taxon state,  
time from present)`

model parameters	Brownian motion rate, OU mean, trait minimum values, etc.
taxon state	Current state of focal taxon
time from present	Allows time-dependent models: was a max size constraint lifted from mammals 65 MYA?

## Discrete time

`extrinsicFn(model parameters, taxon state,  
states of other taxa,  
time from present)`

states of  
other taxa

Allows non-independence of  
species: character displacement,  
mimicry, etc.



Binomial: for probability heads:

Actual string: HTTHHHHT

Proportion heads: 5/8

Result of last flip: T

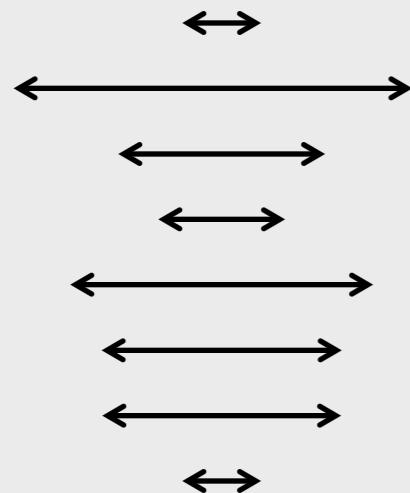
- Actual string:

HTTHHHHHT

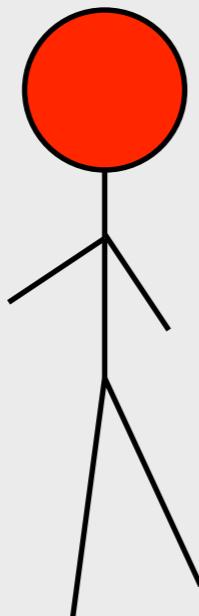
If  $(\text{observed} - \text{simulated}) == 0$   
Count as match

- Prop. heads:

5/8



If  $|\text{observed} - \text{simulated}| < \epsilon$   
Count as match



Sufficient summary statistics: contain all the info you need



Binomial: for probability heads:

Actual string: HTTHHHHT

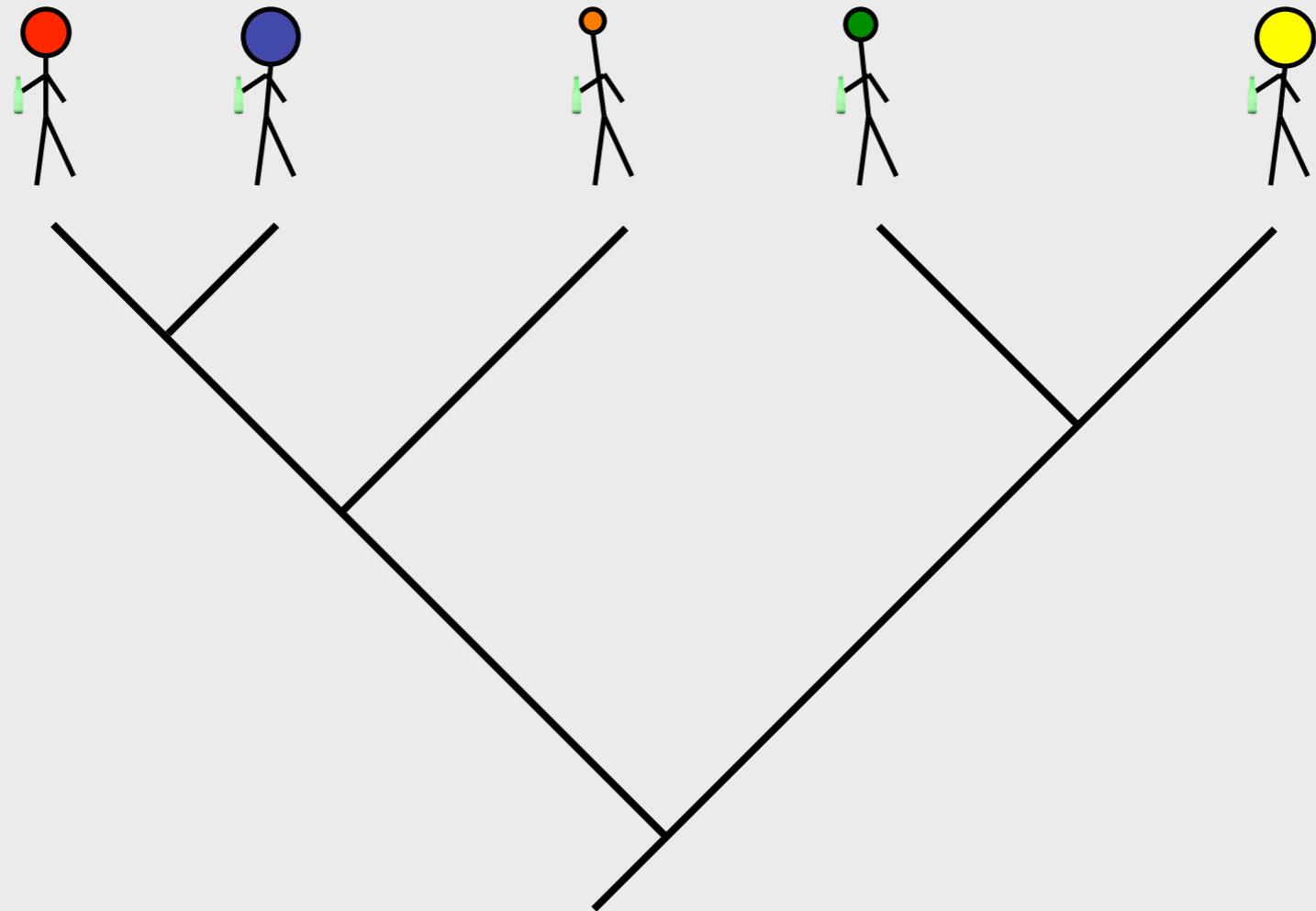
Proportion heads: 5/8

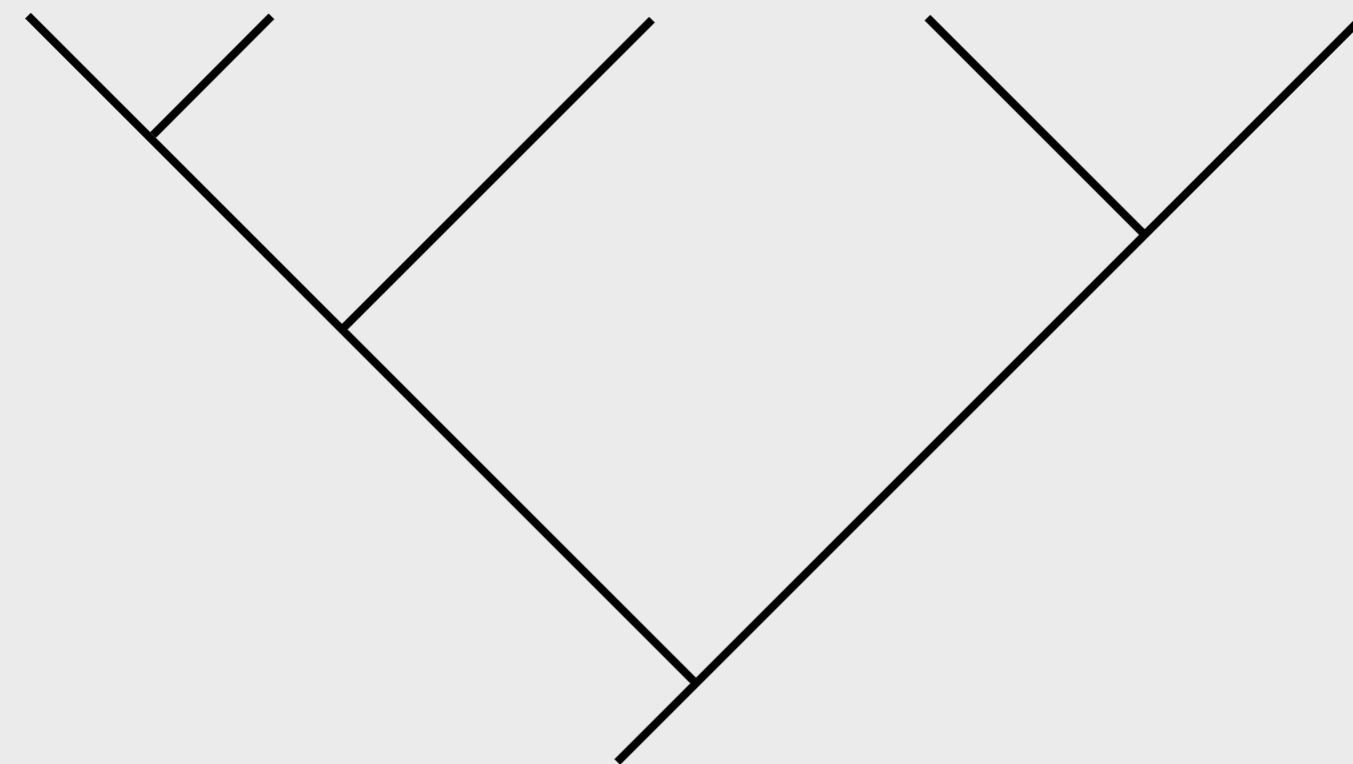
Result of last flip: T

# Sufficient summary statistics: contain all the info you need



But perhaps there are no sufficient summary statistics, or sufficiency is unknown.

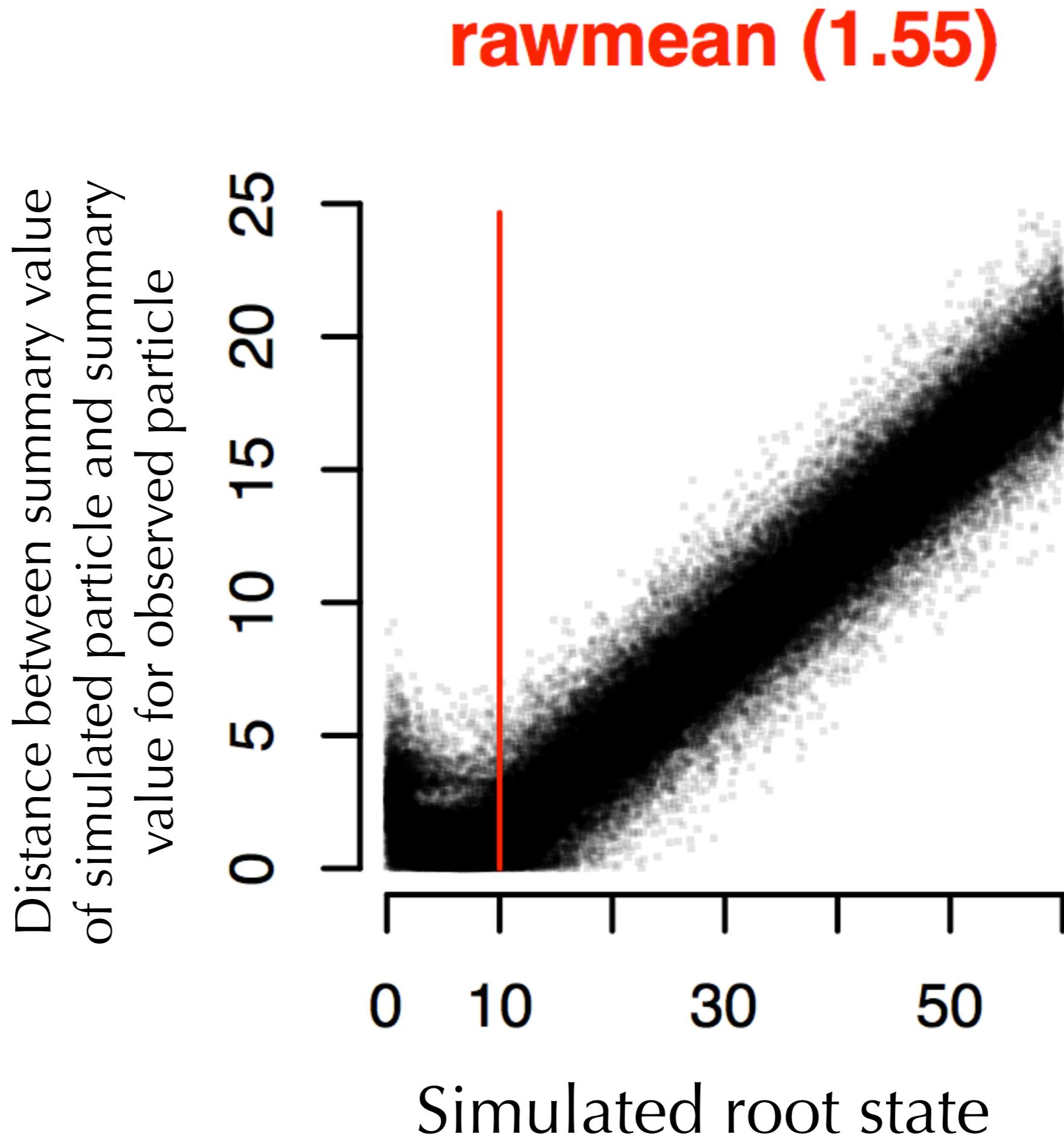




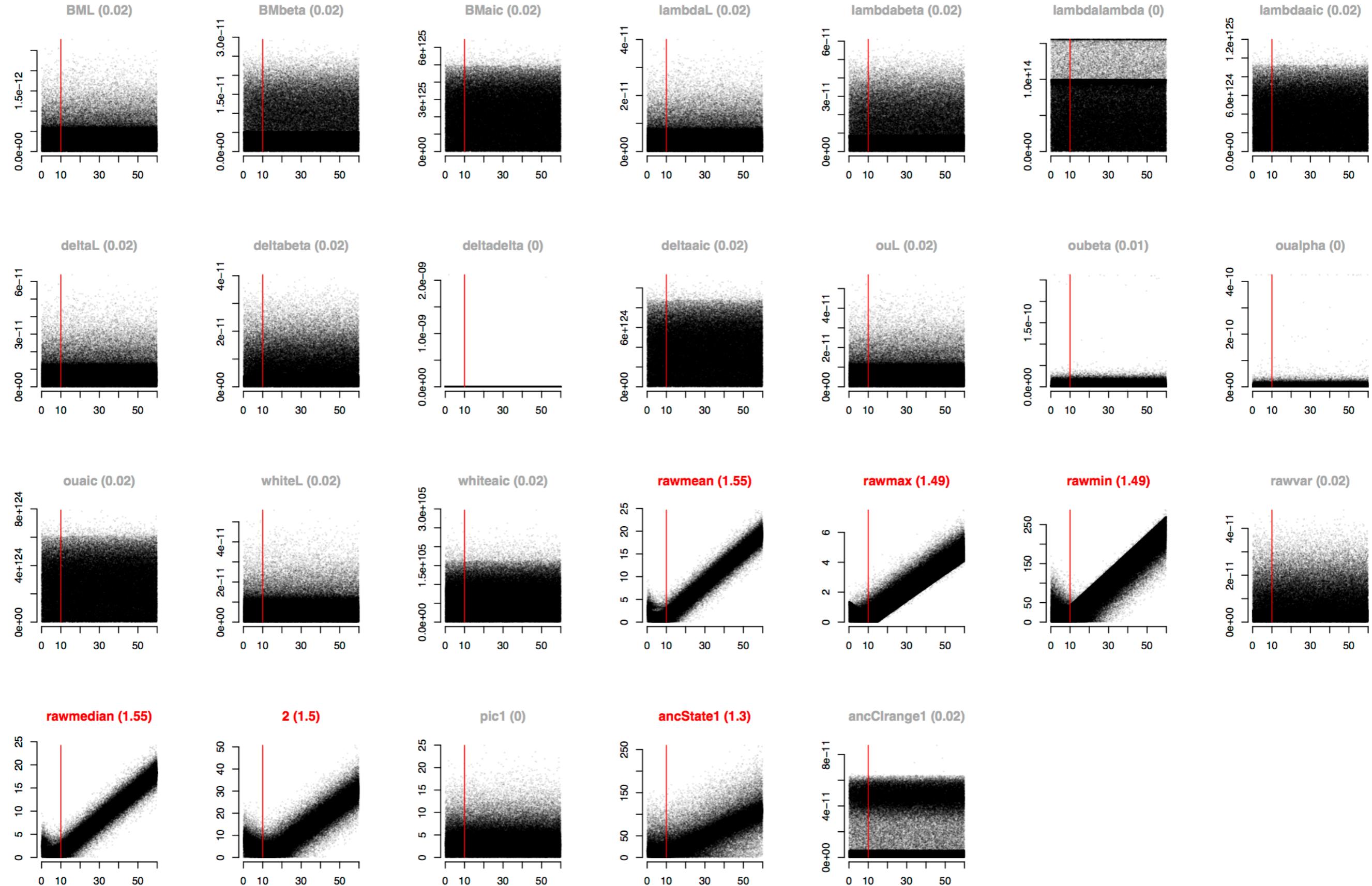
# Our approach: multiple summary stats

Model	Values used	Software
Brownian motion model	Rate, lnL, AIC	
Lambda model	Lambda, beta, lnL, AIC	
Delta model	Delta, beta, lnL, AIC	Geiger (Harmon et al., 2009)
Ornstein-Uhlenbeck	Alpha, beta, lnL, AIC	
White noise	lnL, AIC	
Trait raw values	Trait mean, median, max, min, variance	R
Tip values	All	
Contrasts	All	
Ancestral states	All	Ape (Paradis et al. 2004)
Width of ancestral state confidence interval	All	

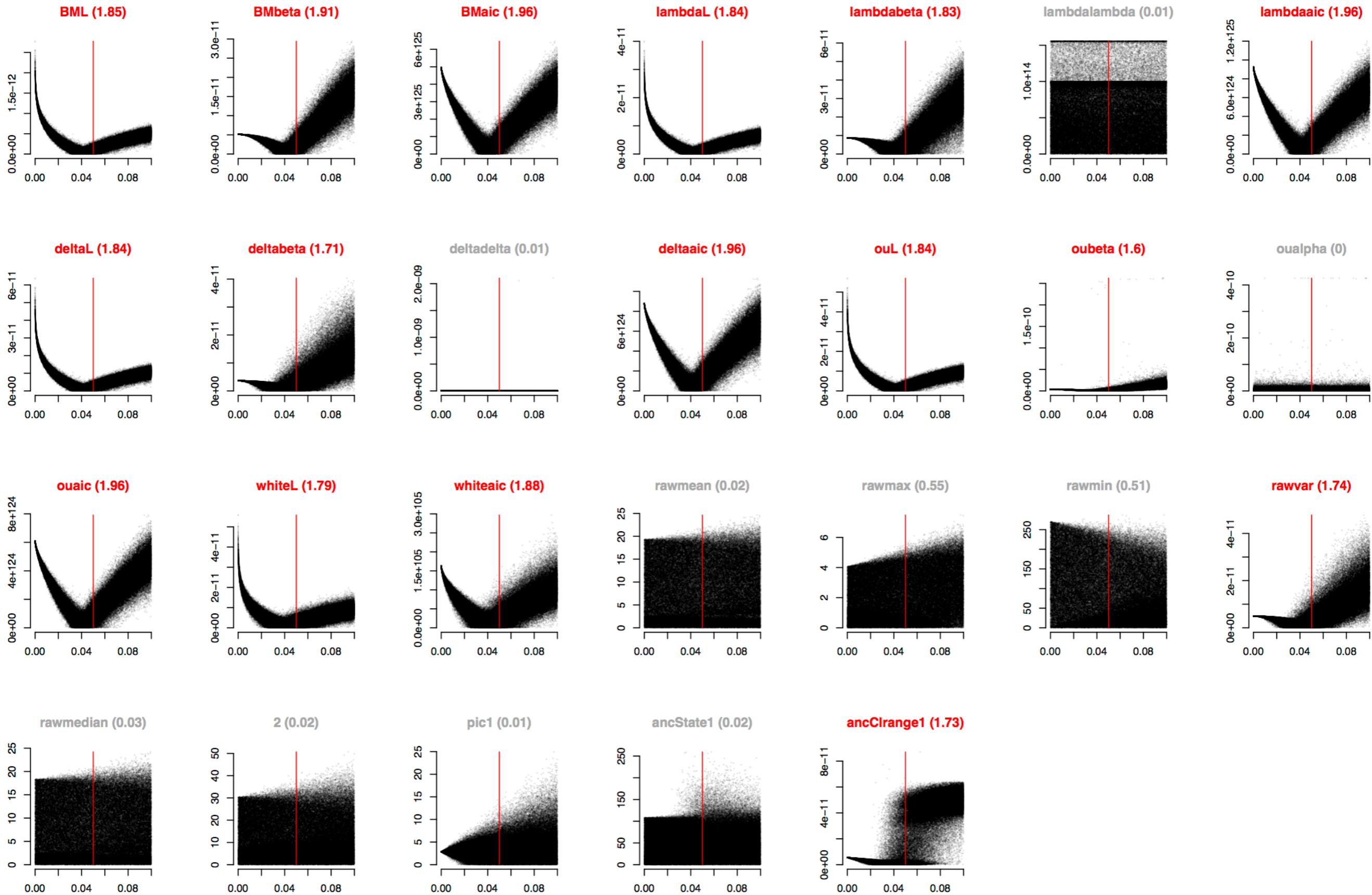
Root state



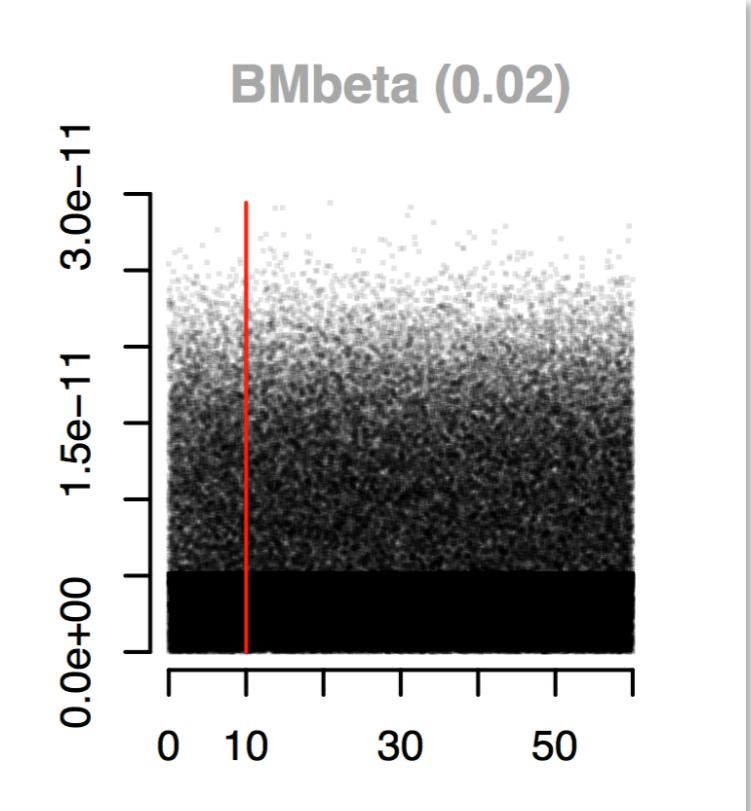
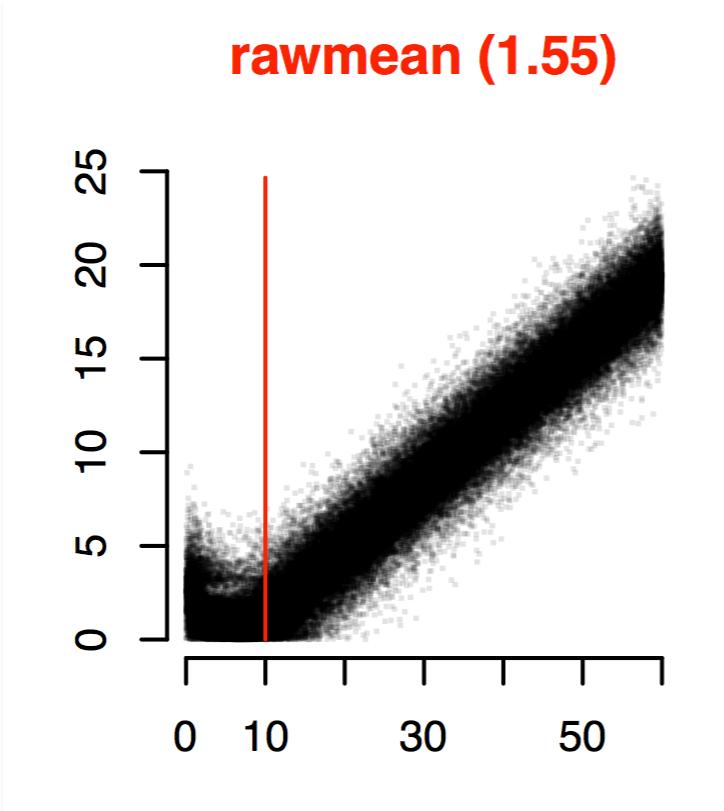
# Root state



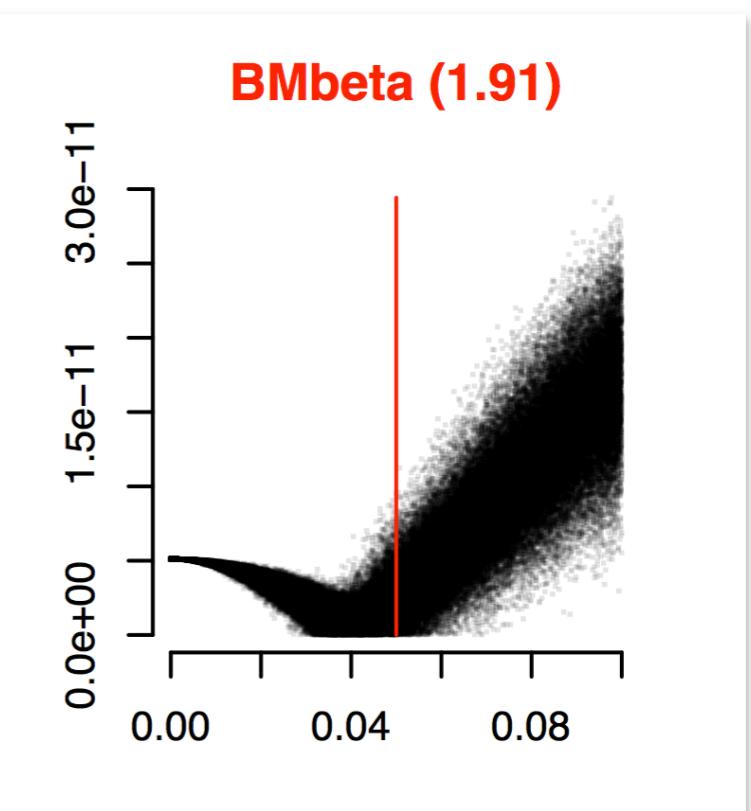
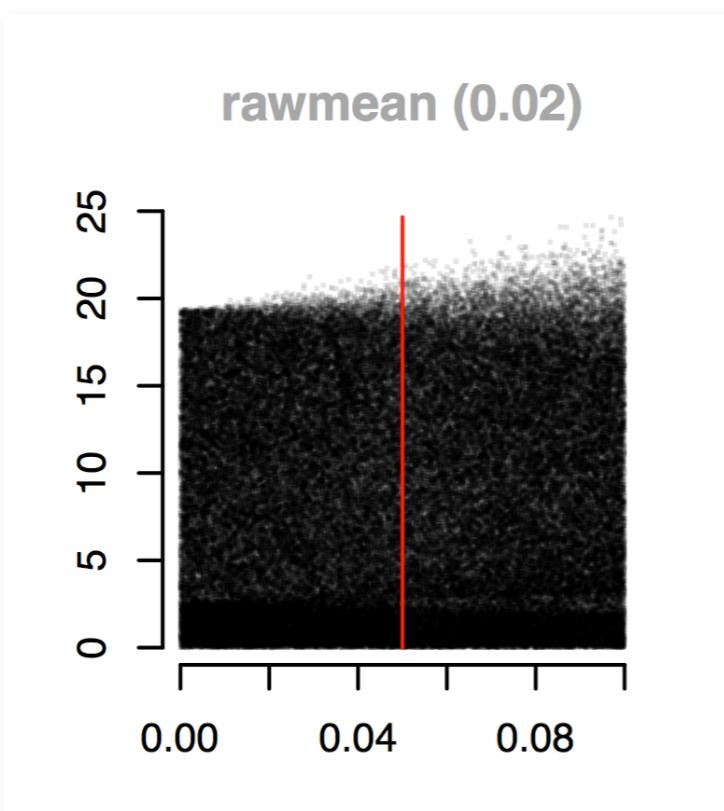
# Brownian rate



Root state



Brownian  
rate



# Bayes Rule

$$\text{Prob}(\text{parameter} \mid \text{data}) = \frac{\text{Prob}(\text{data} \mid \text{parameter}) \times \text{Prob}(\text{parameter})}{\text{normalizing term}}$$

# Bayes Rule

$\text{Prob}(\text{parameter} \mid \text{data}) =$

$\text{Prob}(\text{data} \mid \text{parameter}) \times$   
 $\text{Prob}(\text{parameter}) \div$   
normalizing term

Let  $p = 0.2$

Sim 1: HTTTTHTT  
Sim 2: TTHHTTTT  
Sim 3: TTHHHTHH  
Sim 4: TTTTTTTT  
Sim 5: TTTTTTTT  
Sim 6: THHTTTTH  
Sim 7: TTHHTTHT  
Sim 8: TTTTHHHT  
Sim 9: HTTHTTTT  
Sim 10: THHHTHTT

$P(\text{data}) \approx 1/10$

# Bayes Rule

$\text{Prob}(\text{parameter} \mid \text{data}) =$

$\text{Prob}(\text{data} \mid \text{parameter}) \times$   
**Prob(parameter)** ÷  
normalizing term

Sample  $p$   
from prior

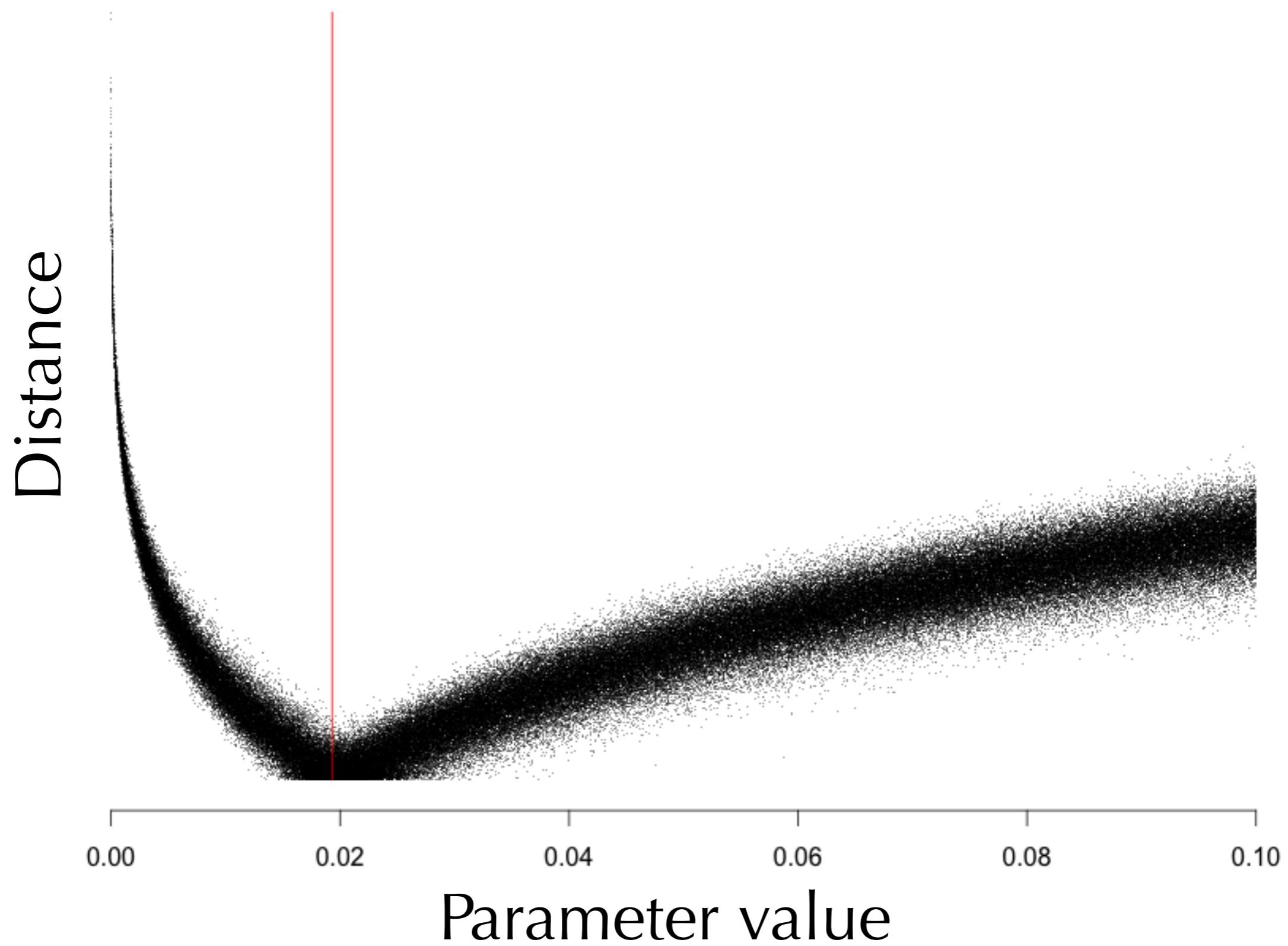
Let  $p = 0.2$

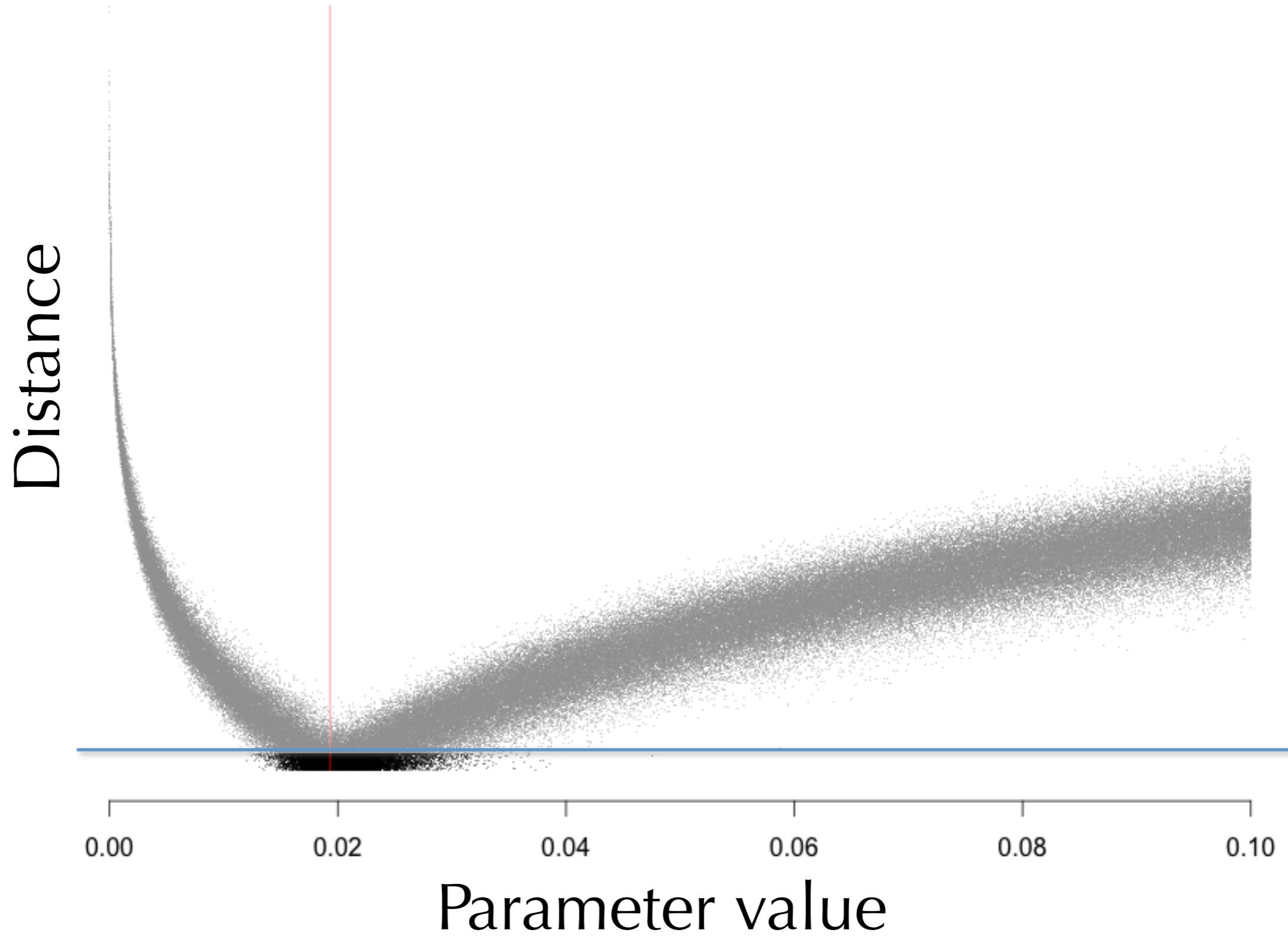
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Sim 3:	TTTHHTHH
Sim 4:	TTTTTTTT
Sim 5:	TTTTTTTT
Sim 6:	<b>THHTTTTH</b>
Sim 7:	TTHHTTHT
Sim 8:	TTTTHHHT
Sim 9:	HTTHHTTT
Sim 10:	THHHTHTT

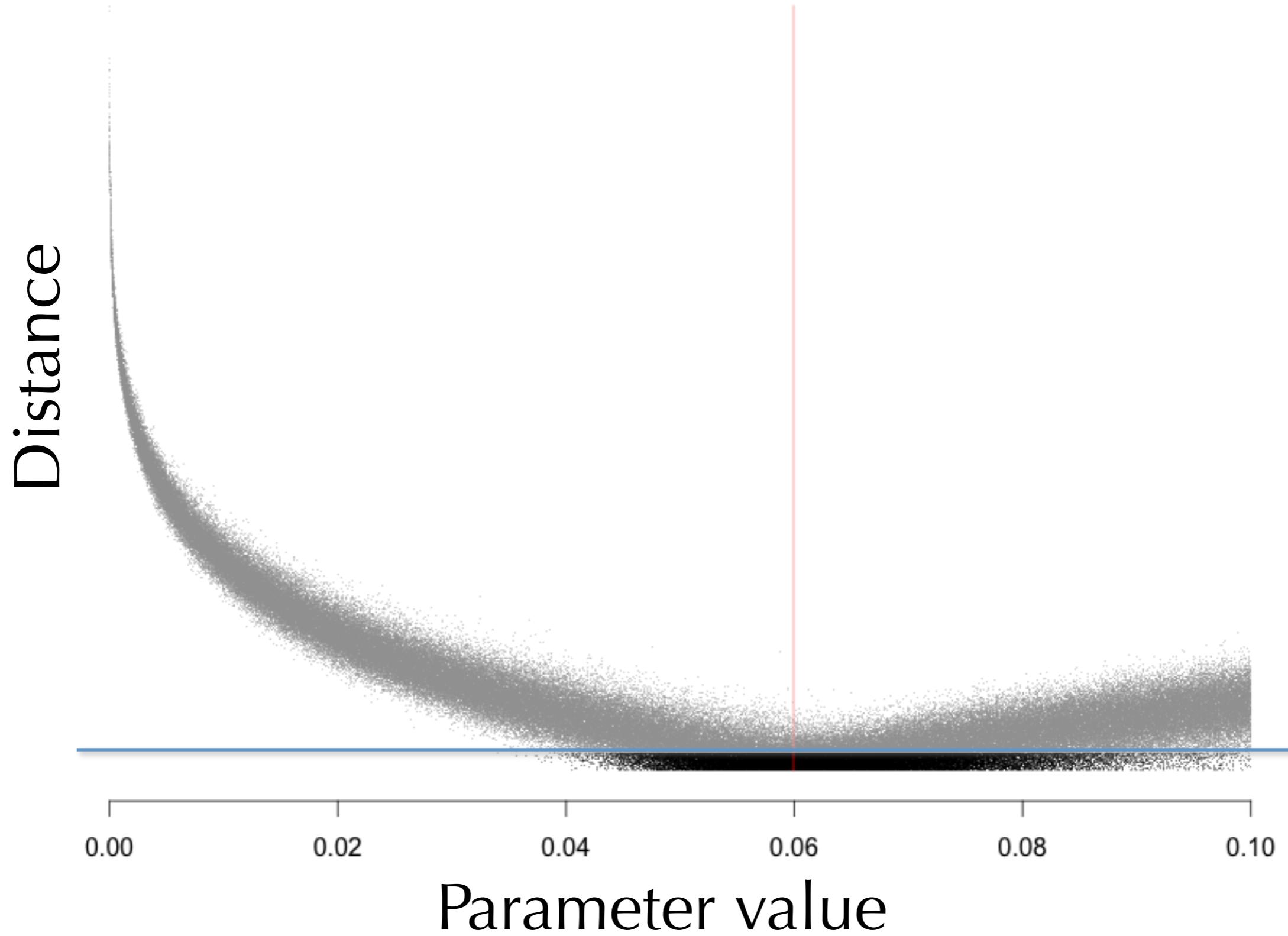
$P(\text{data}) \approx 1/10$

# Rejection

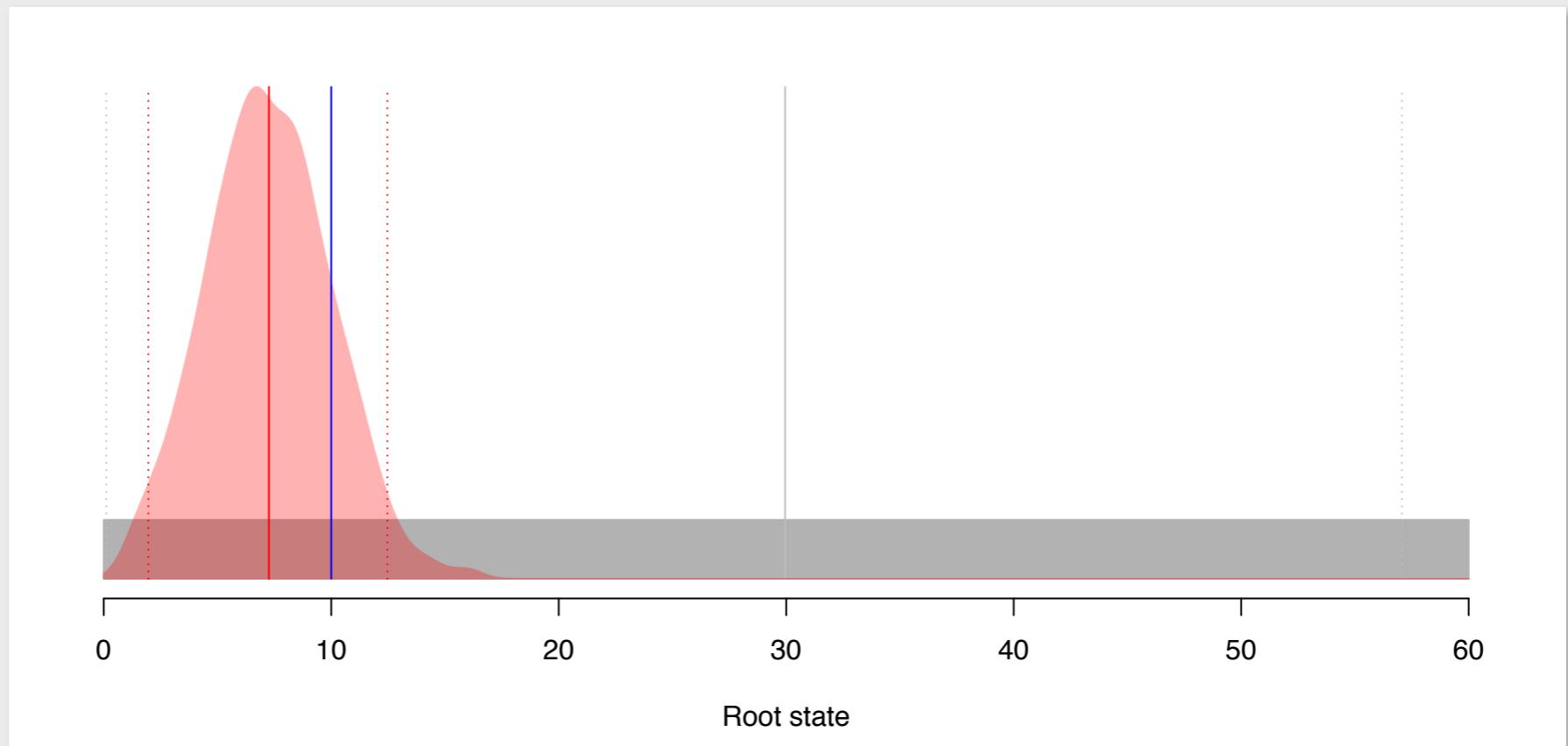
1. Sample parameters from prior distributions
2. Simulate data using those parameters
3. Summary(simulated data)
4. If  $|Summary(\text{observed data}) - Summary(\text{simulated data})| < \varepsilon$  , save that simulation
5. The distribution of parameters of saved simulations = posterior distribution of those parameters



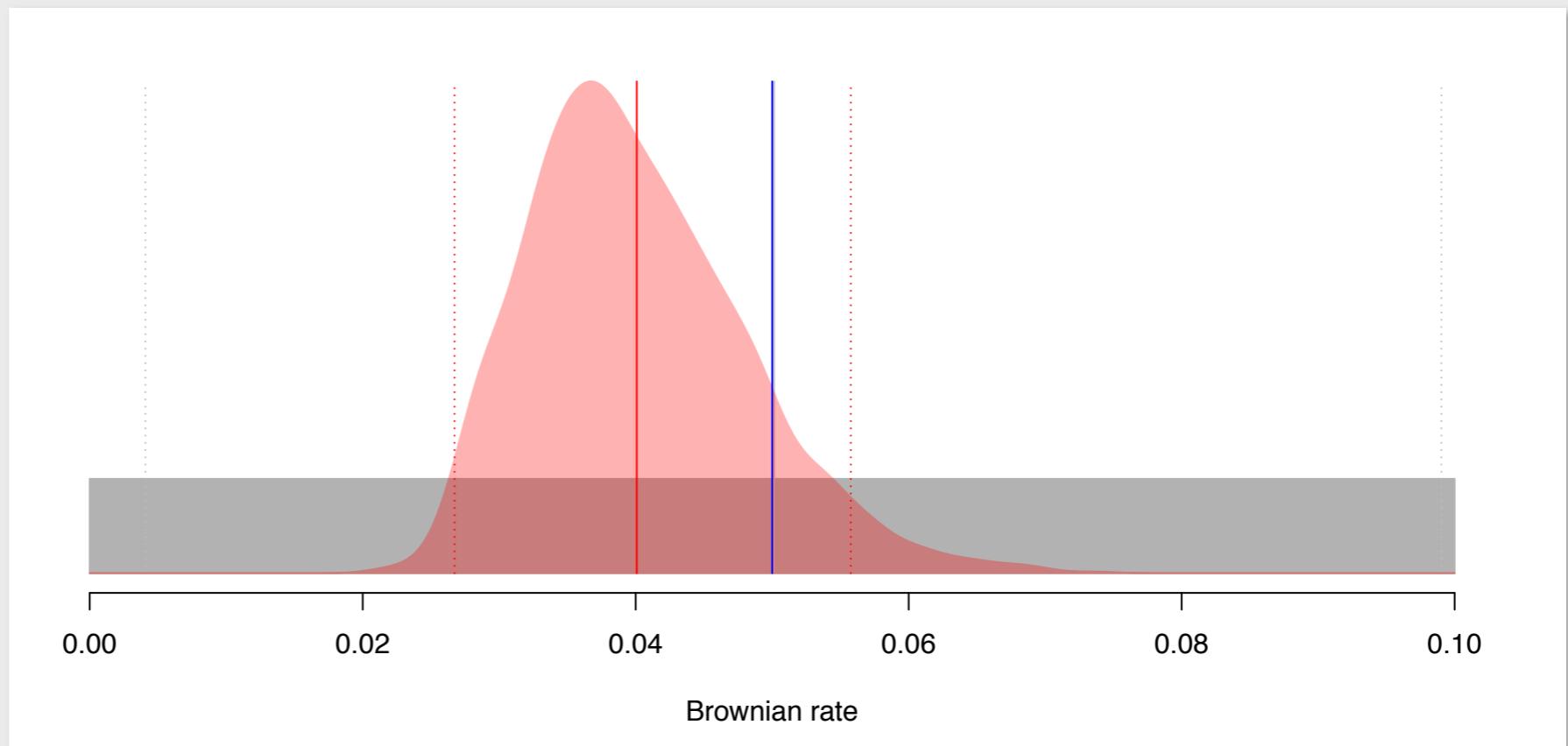




## Root state

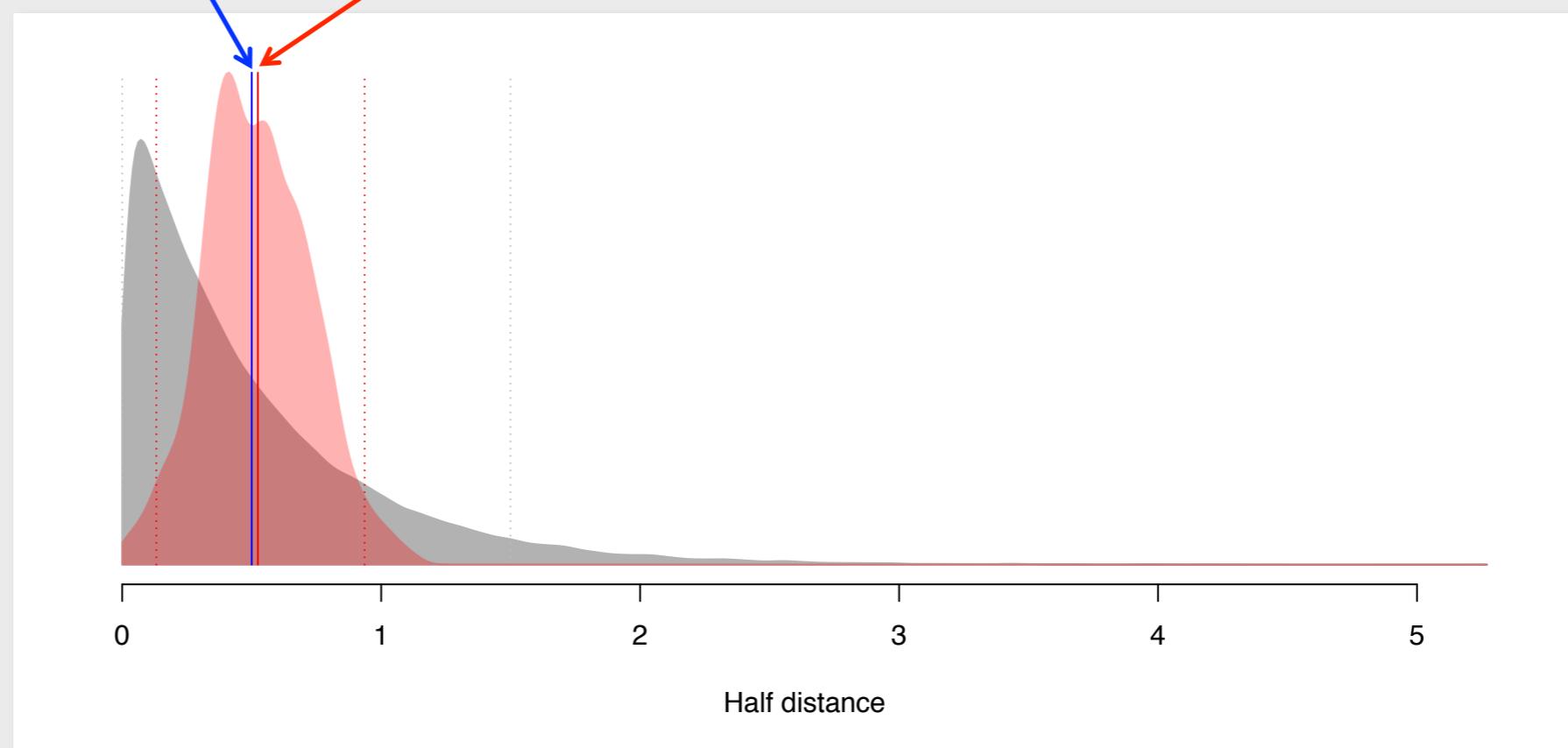


## Brownian rate



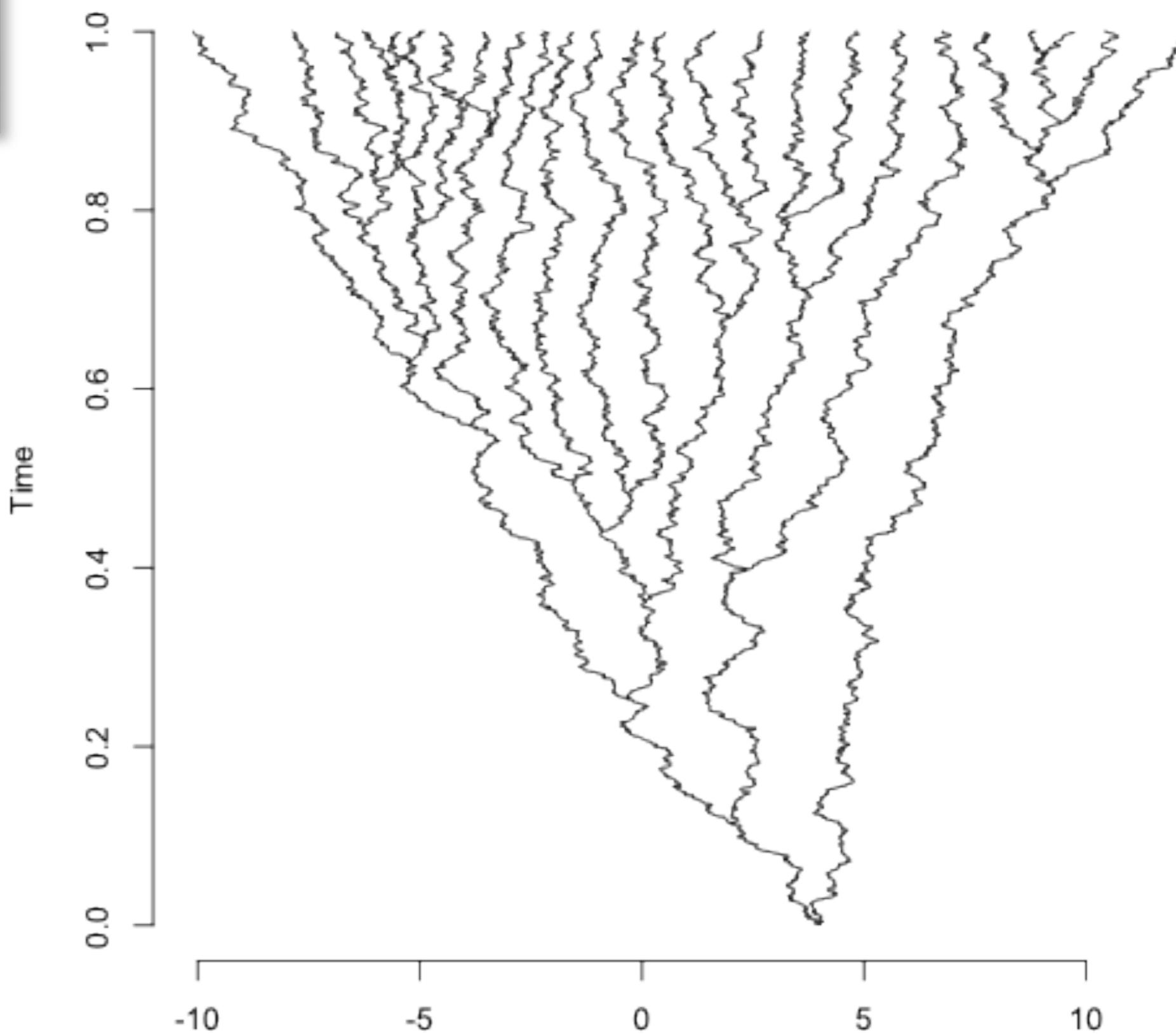
Character  
displacement  
(phenotypic distance  
at which repulsion is  
half the maximum  
repulsion)

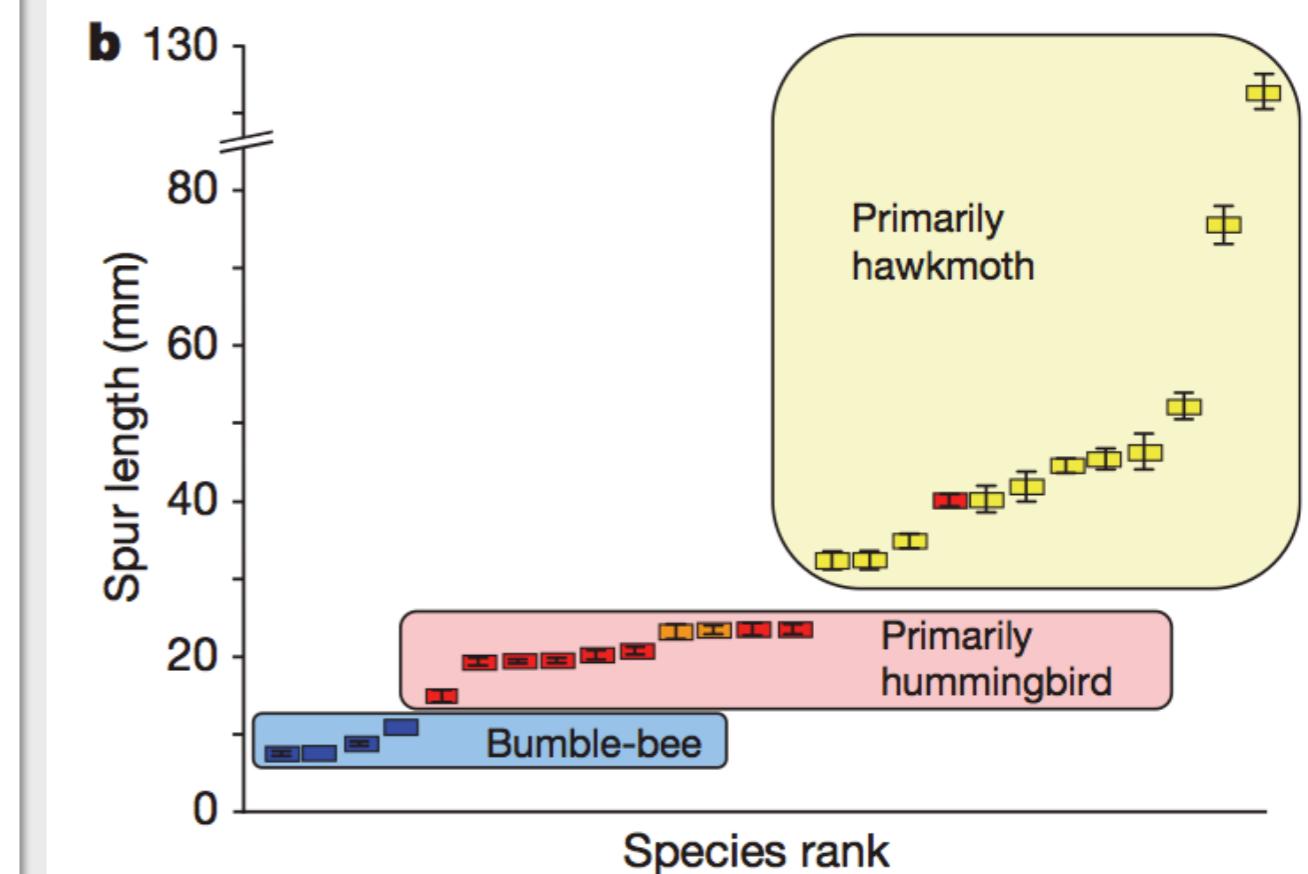
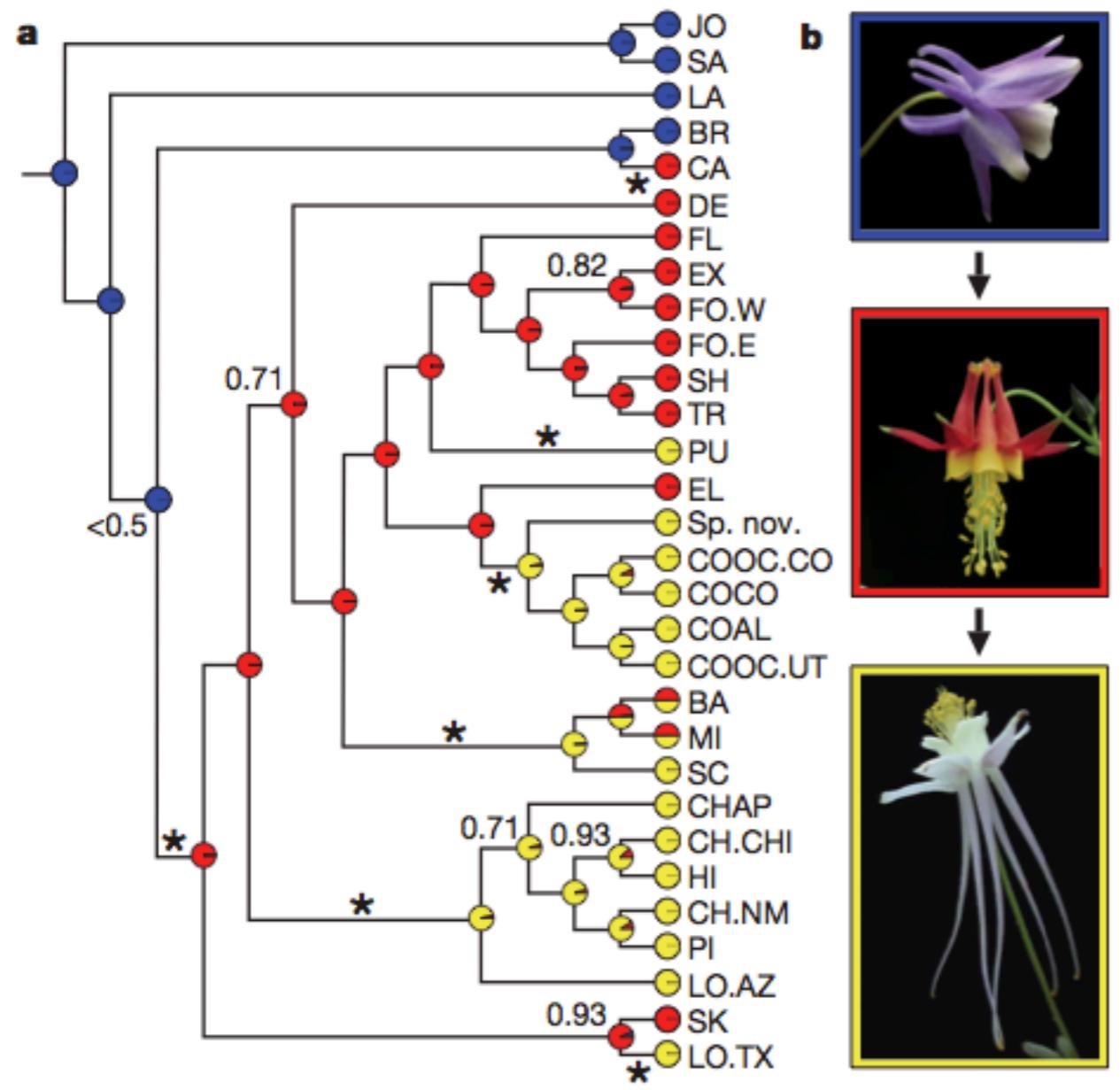
True  
value      Estimated  
value



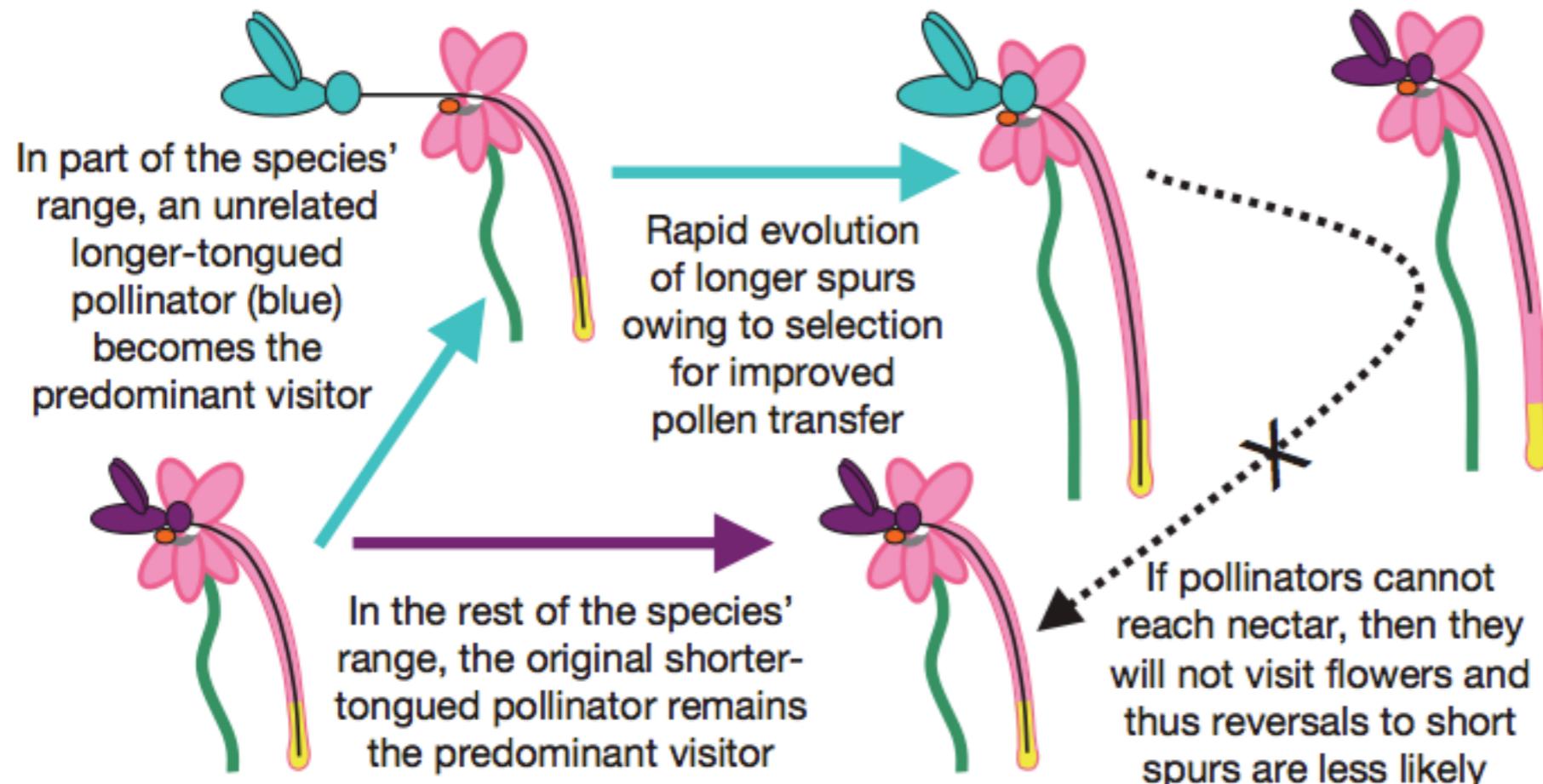


Ilanaré Sévi

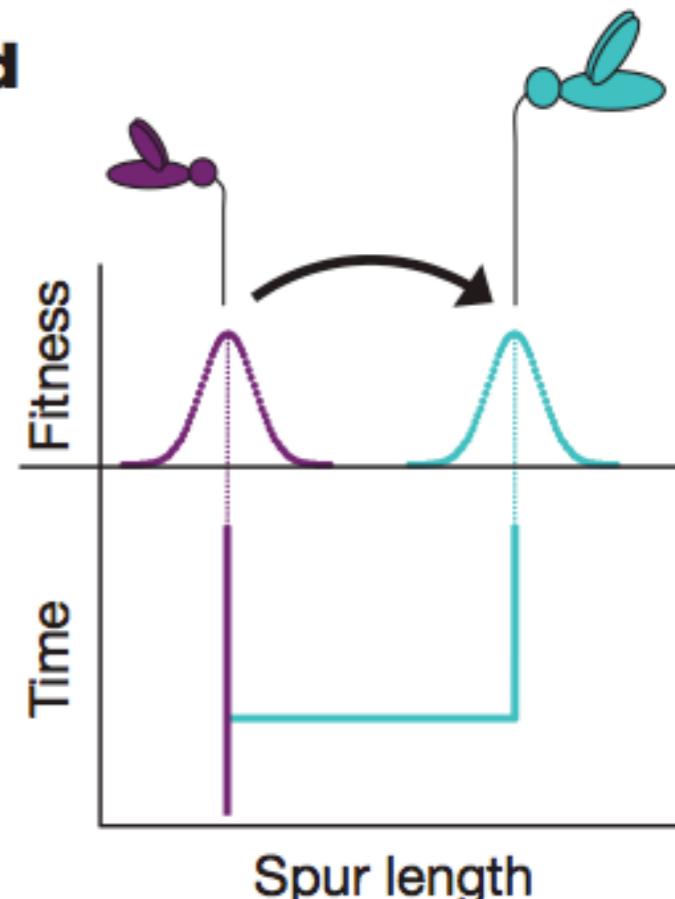




### c Pollinator shift



d



**Are there distinct peaks?**

Yes, best-fitting model had three OU peaks.

**Is evolution punctuated?**

Yes, a model with change only at speciation events fits better than a gradual one.

```
pollinatorShiftIntrinsic <-function(params, states, timefrompresent) {
  #params[1] is sd for normal process,
  #params[2] is sd for jump size of shift,
  #params[3] is mean of shift (mean of normal process is zero),
  #params[4] is per generation probability of shift
  background.process <- TRUE
  if (runif(1, 0, 1) < params[4]) {
    background.process<-FALSE
  }
  if (background.process) {
    newdisplacement <- rnorm(n=length(states),mean=0,sd=params[1])
    return(newdisplacement)
  }
  else {
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}
```

## Parameter

## Prior

Tree height

**Fixed** at 300,000 generations  
(~3MY for radiation, ~10 years/generation (Cooper et al. 2010) )

Root state

**Fixed** at minimum spur length (proxy for using outgroup info)

Background rate for length

**Exponential**, mean set to rough guess based on max difference between taxa

Variation in displacement with pollinator shift

**Fixed** at zero

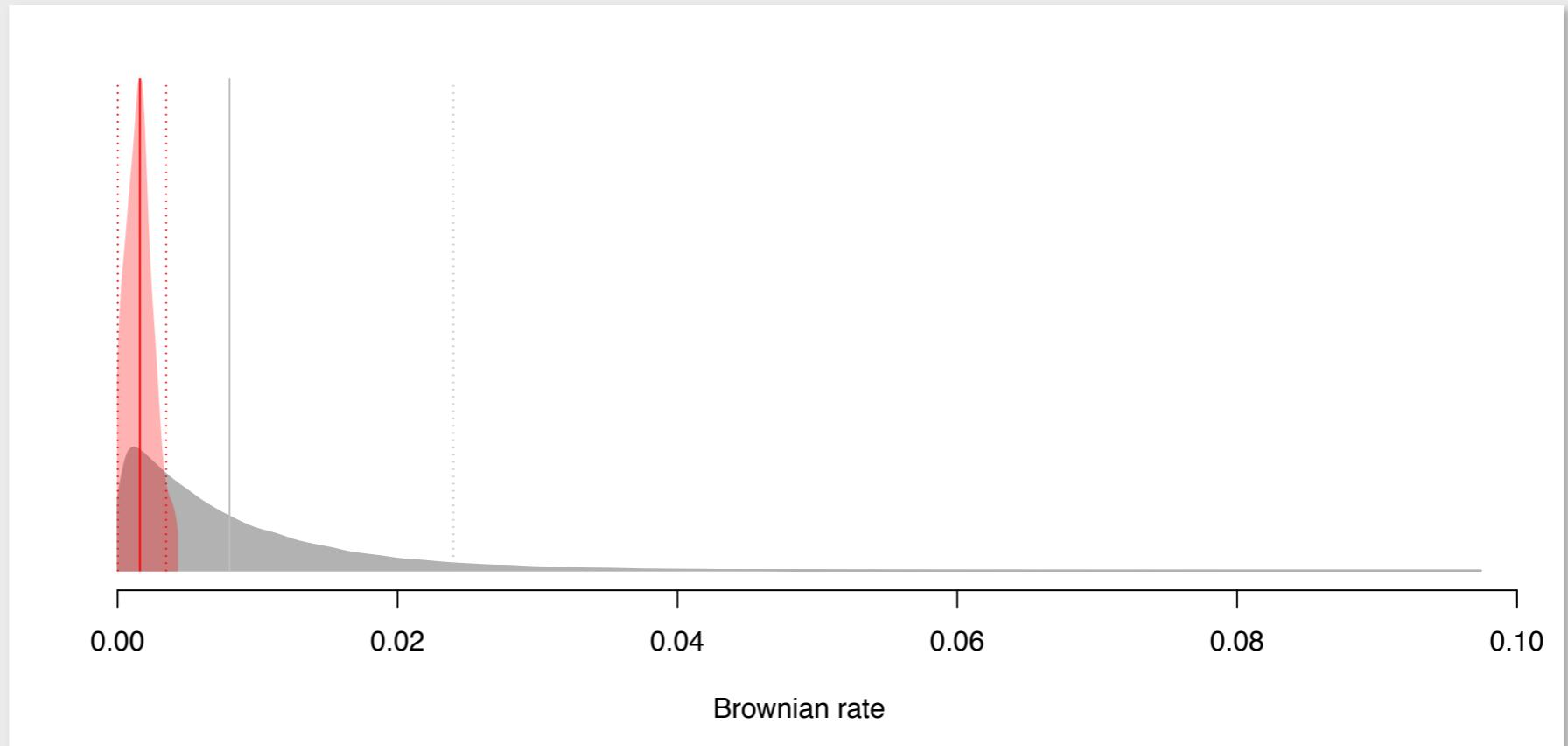
Mean displacement with pollinator shift

**Uniform**, bounds are +/- the biggest difference in trait values

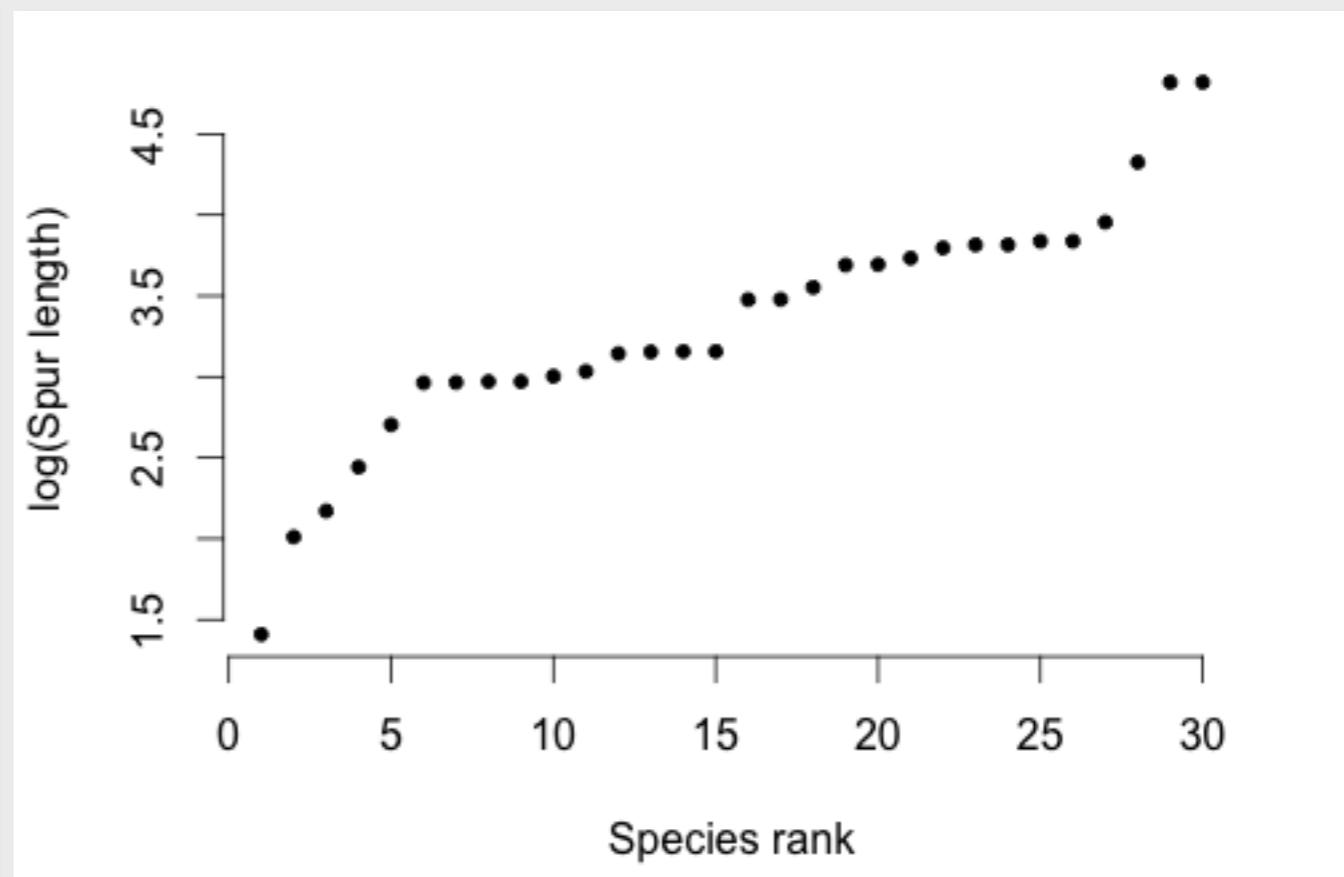
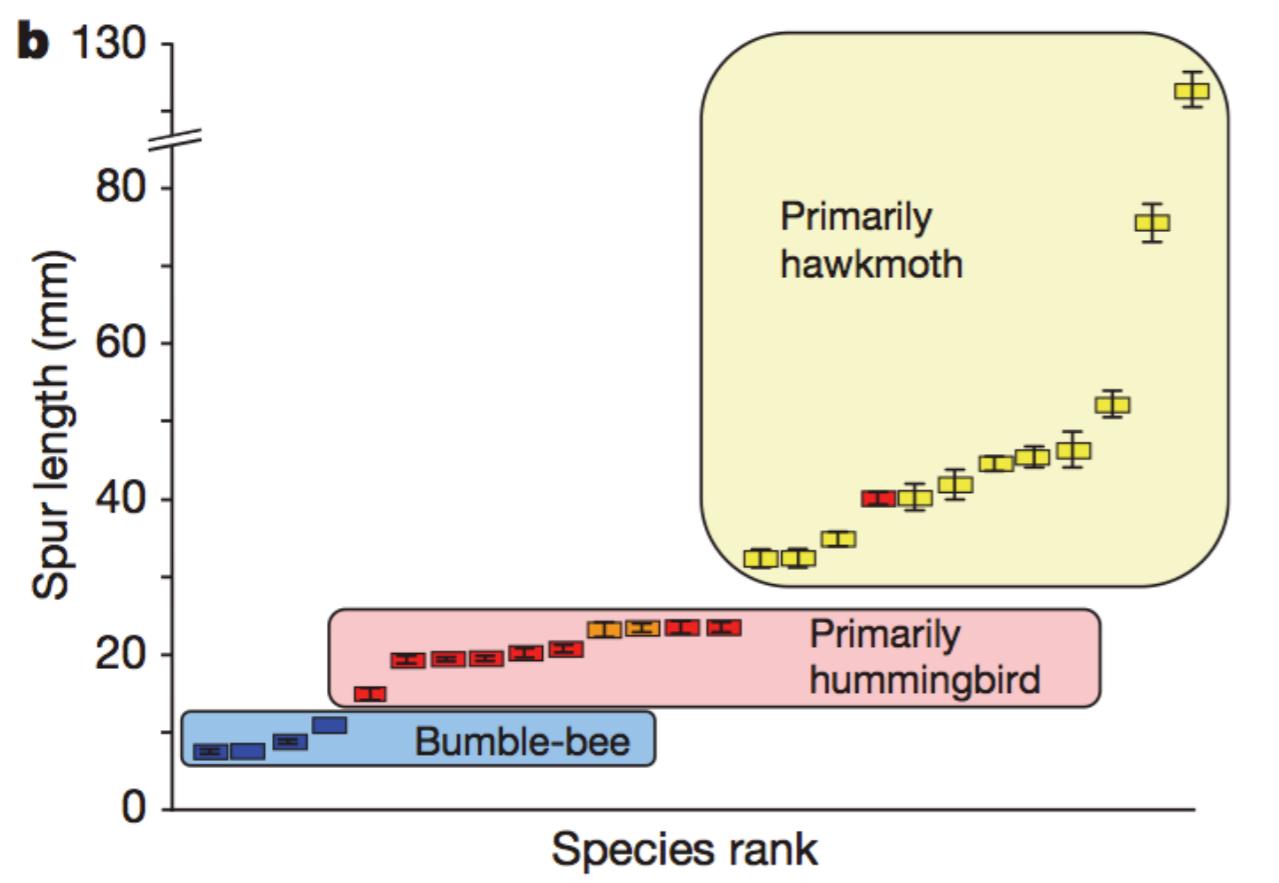
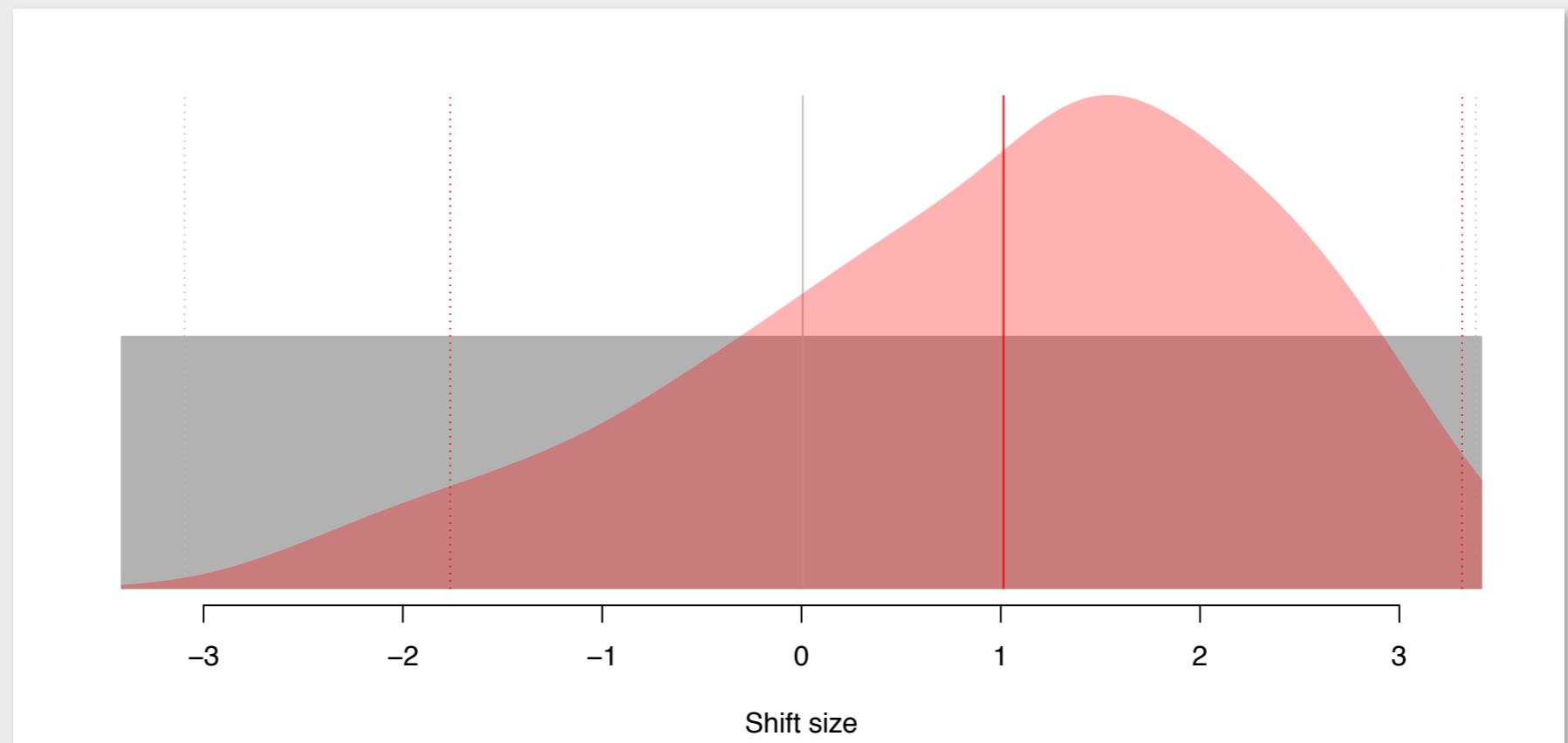
Frequency of pollinator shift

**Exponential**, mean set to rough guess based on observed distribution (7 shifts over entire tree)

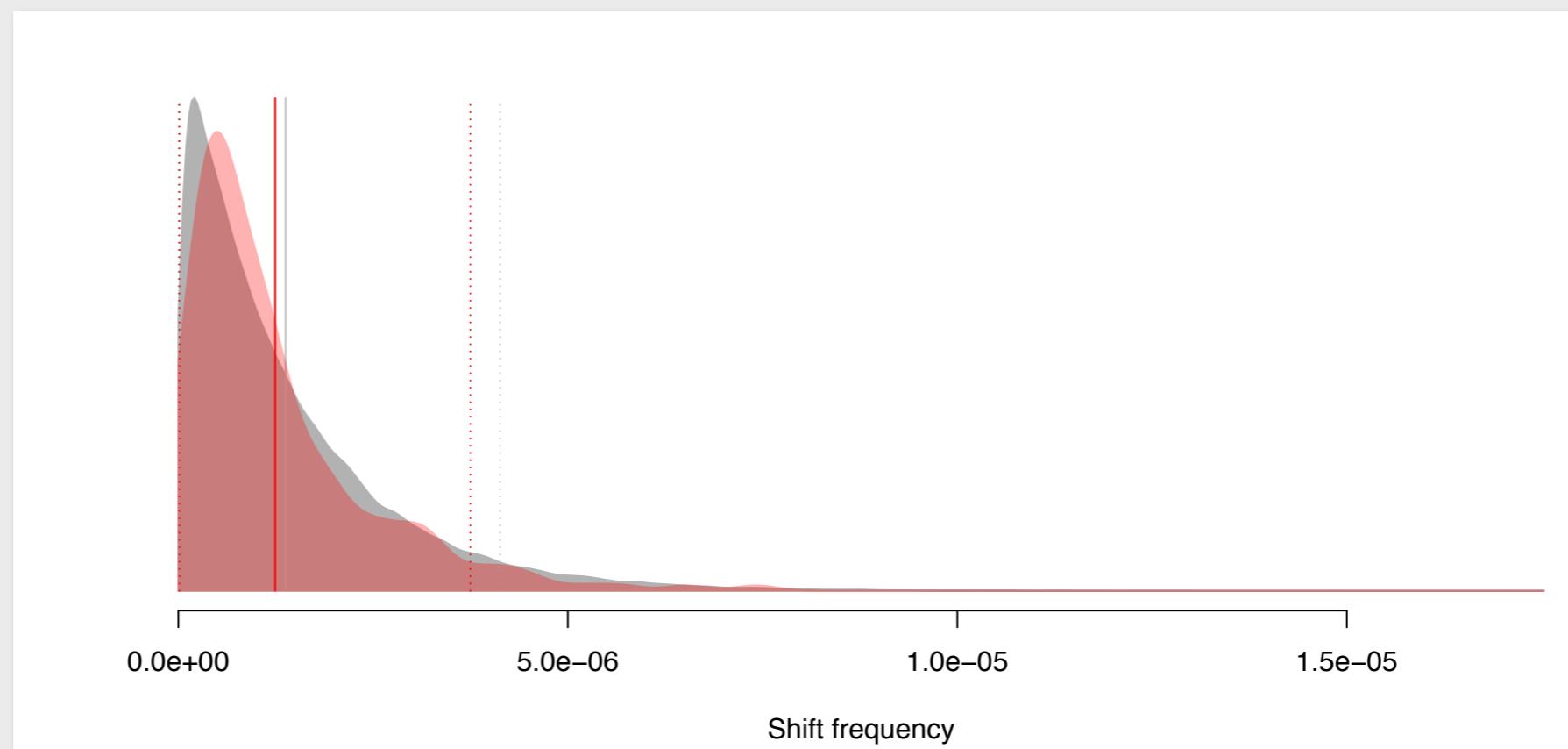
# Brownian rate for background



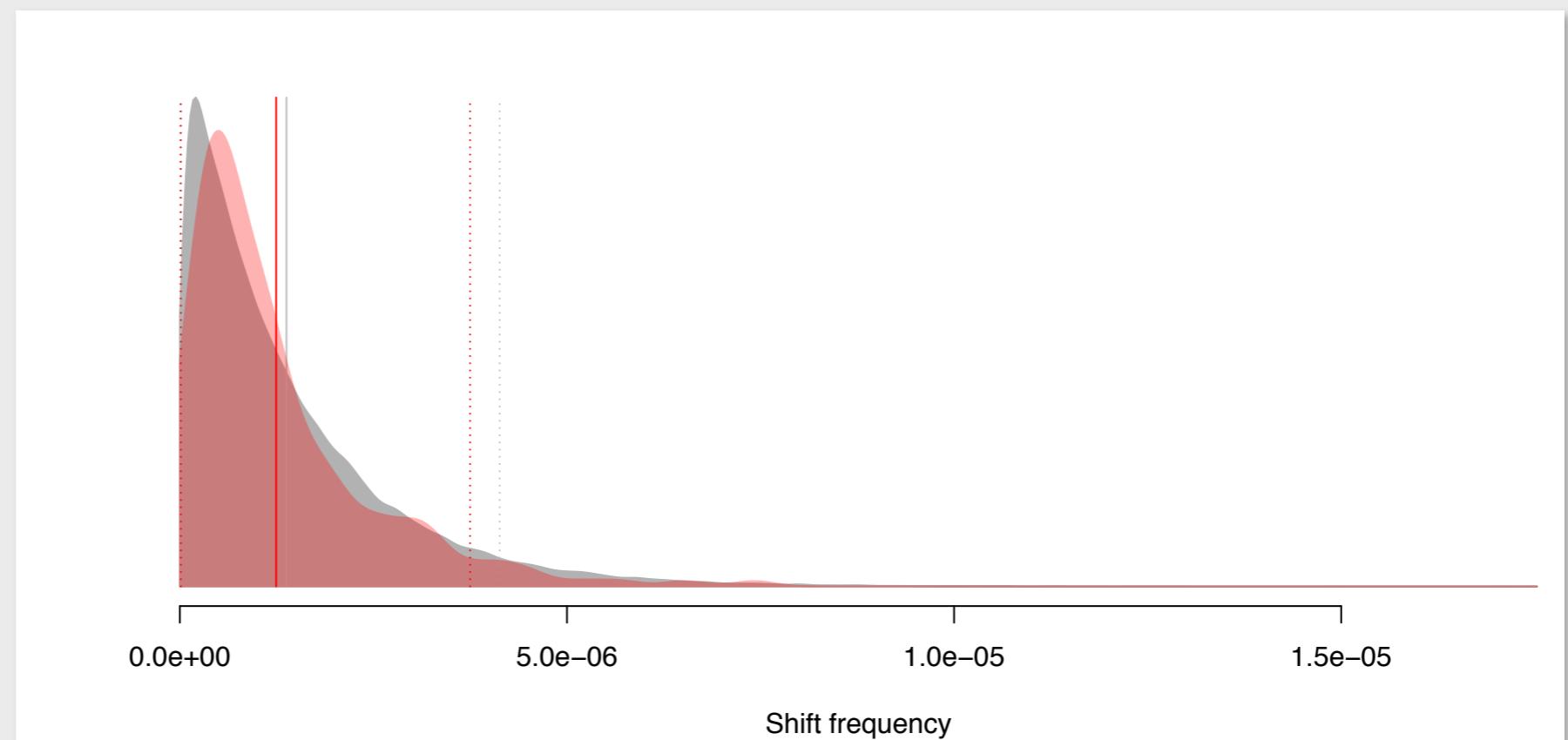
# Nectar spur change at pollinator shift



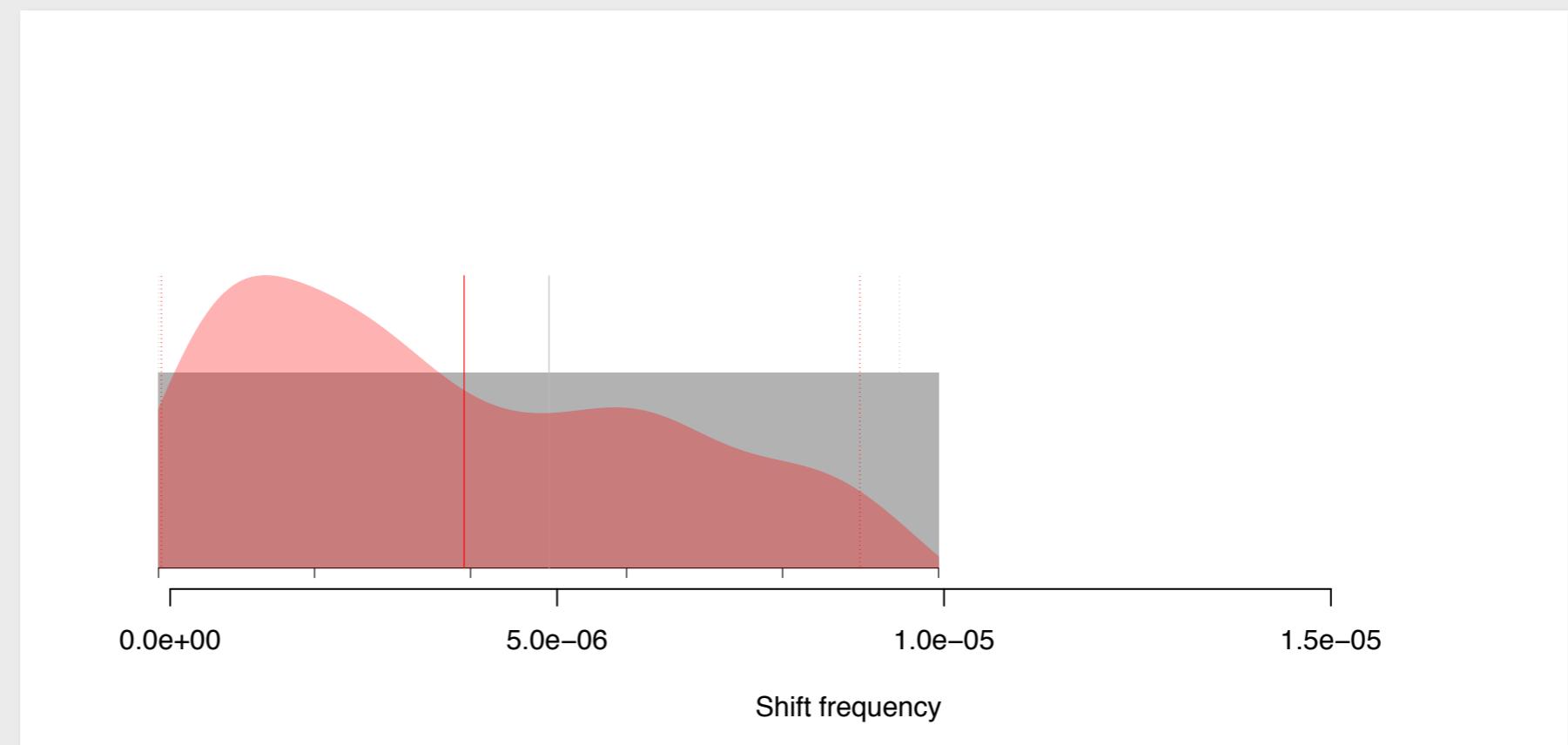
Frequency  
of pollinator  
shift (per  
generation)



Frequency  
of pollinator  
shift  
(exponential  
prior)



Frequency  
of pollinator  
shift  
(uniform  
prior)



# Advantages

- Bayesian
- Flexible: make your own model
- Somewhat robust to user ~~laziness~~ efficient behavior
- Gets faster as computers get faster

# Disadvantages

- Bayesian
- Far slower than closed form solutions where they are available
- No checking for model feasibility (i.e., inferring a trend on an ultrametric tree)
- More still to discover

# A selection of ongoing work

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## Flexible trait evolution

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## Phylogeographic models

O'Meara, Jackson<sup>P</sup>, Morales-Garcia,  
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<sup>P</sup> = postdoc mentee

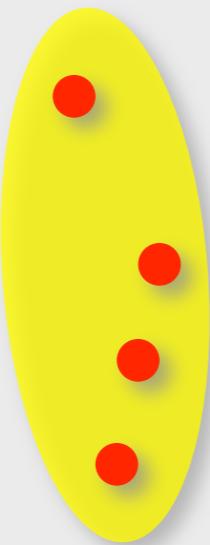
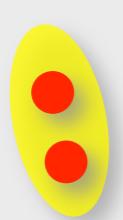


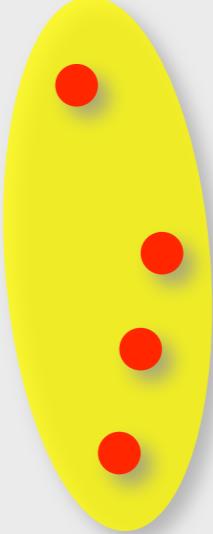




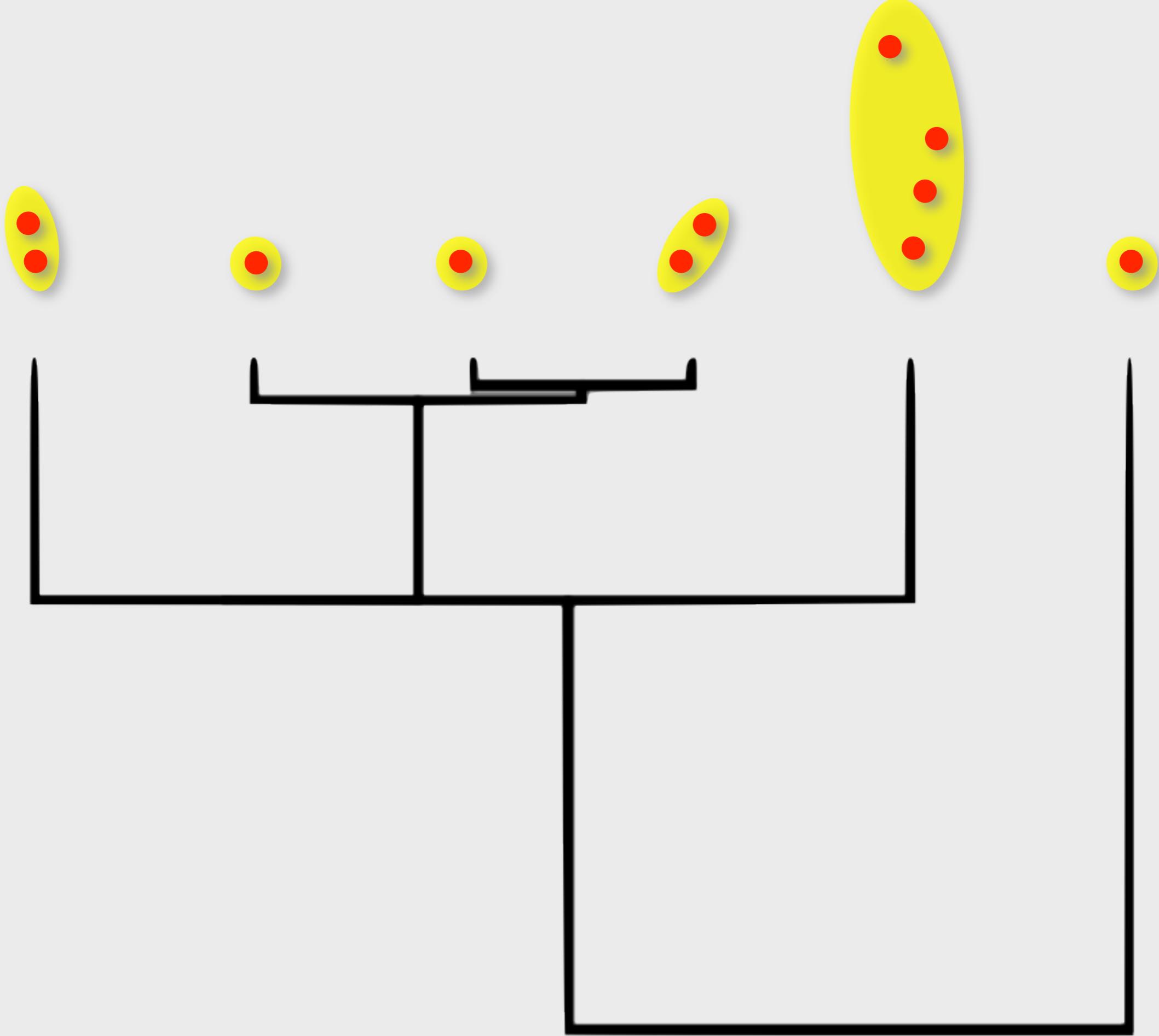


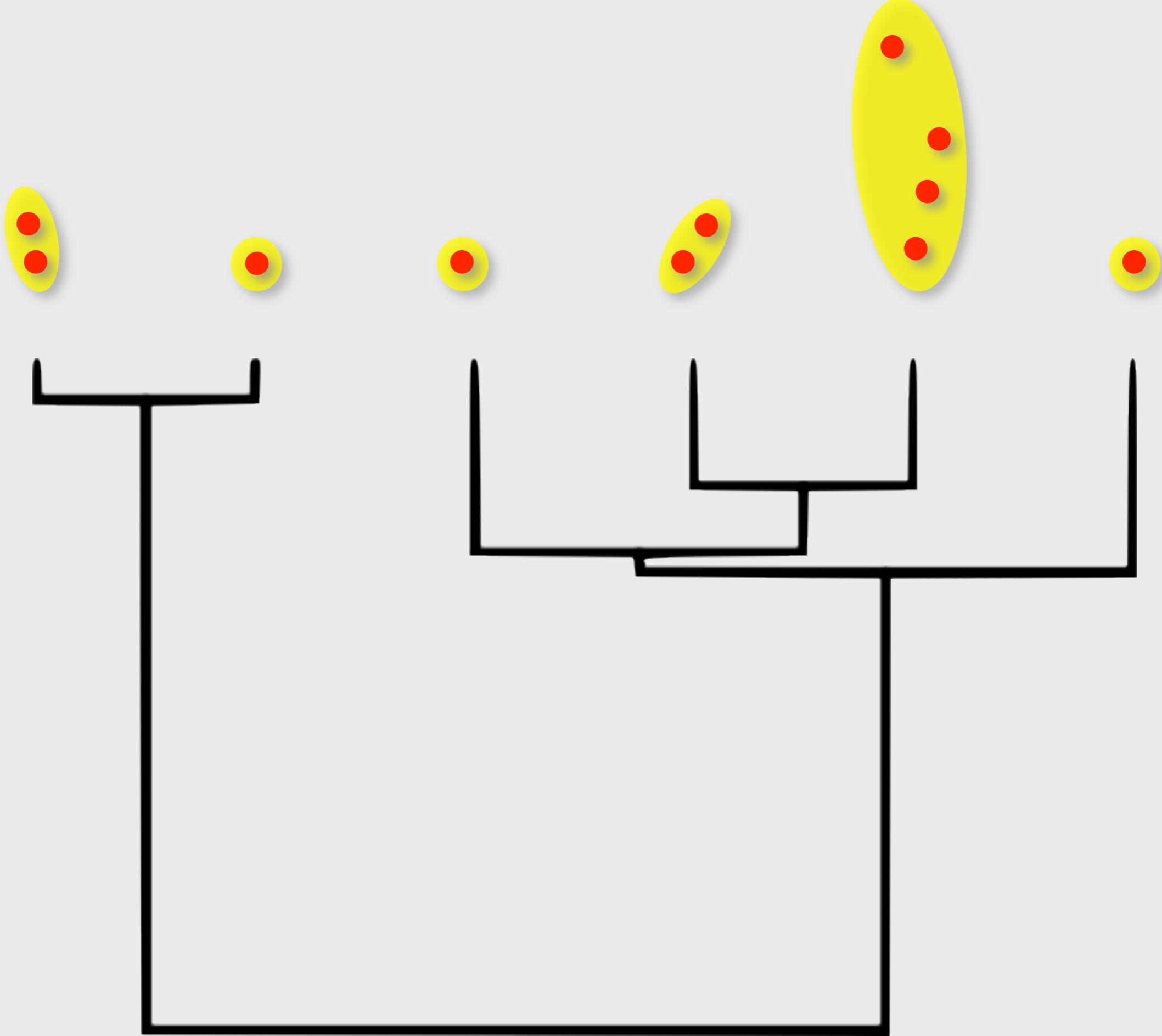


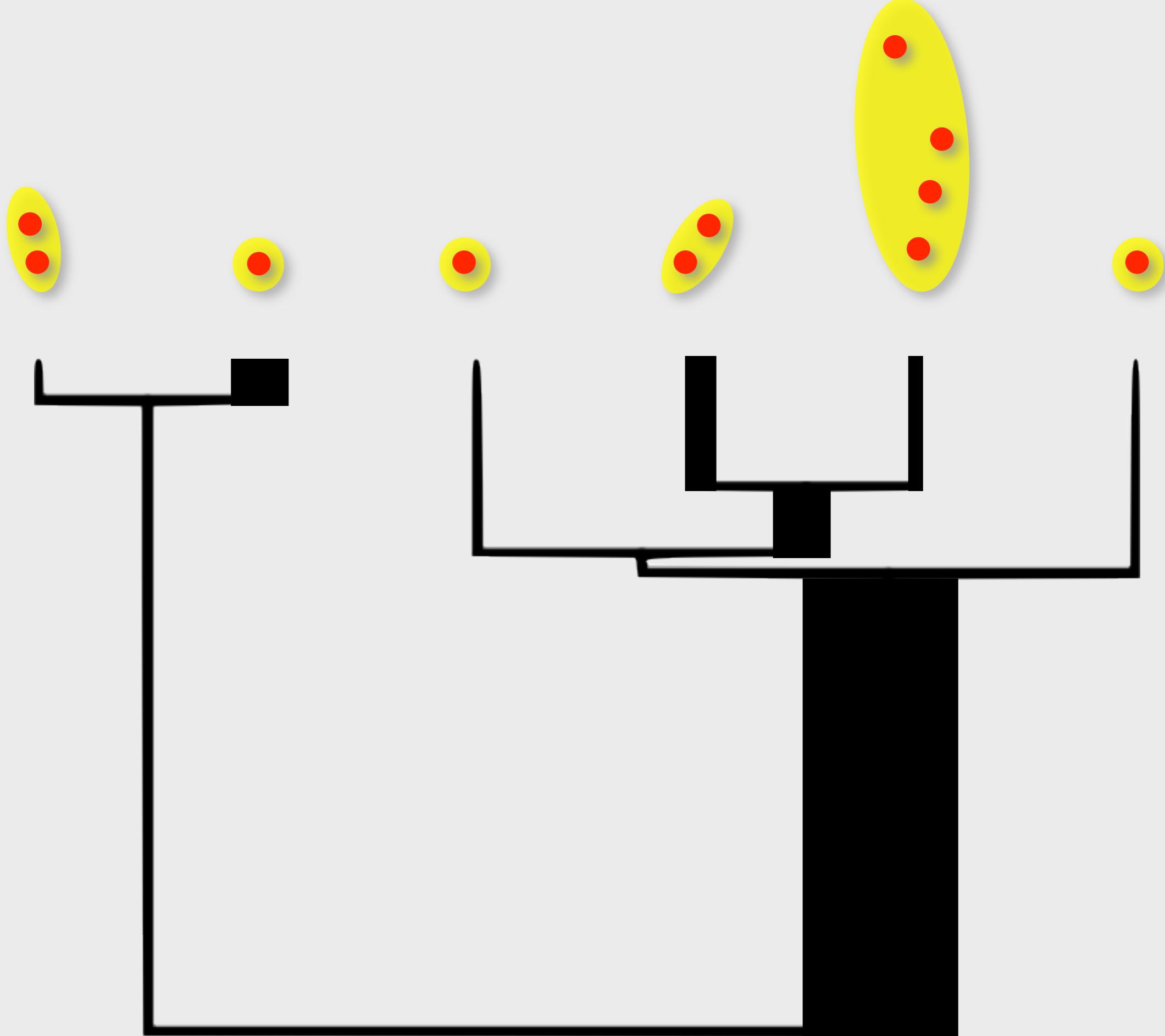


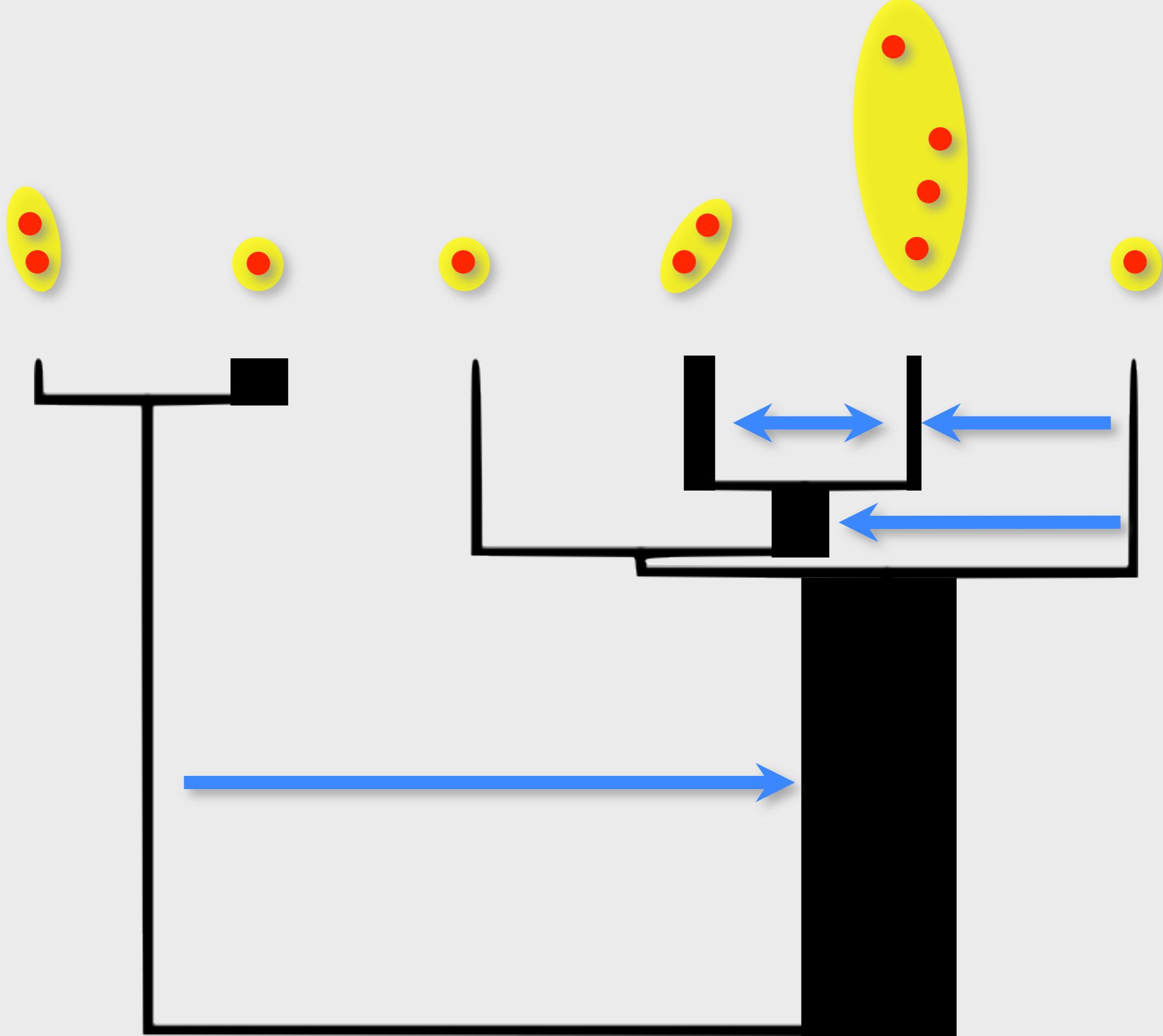


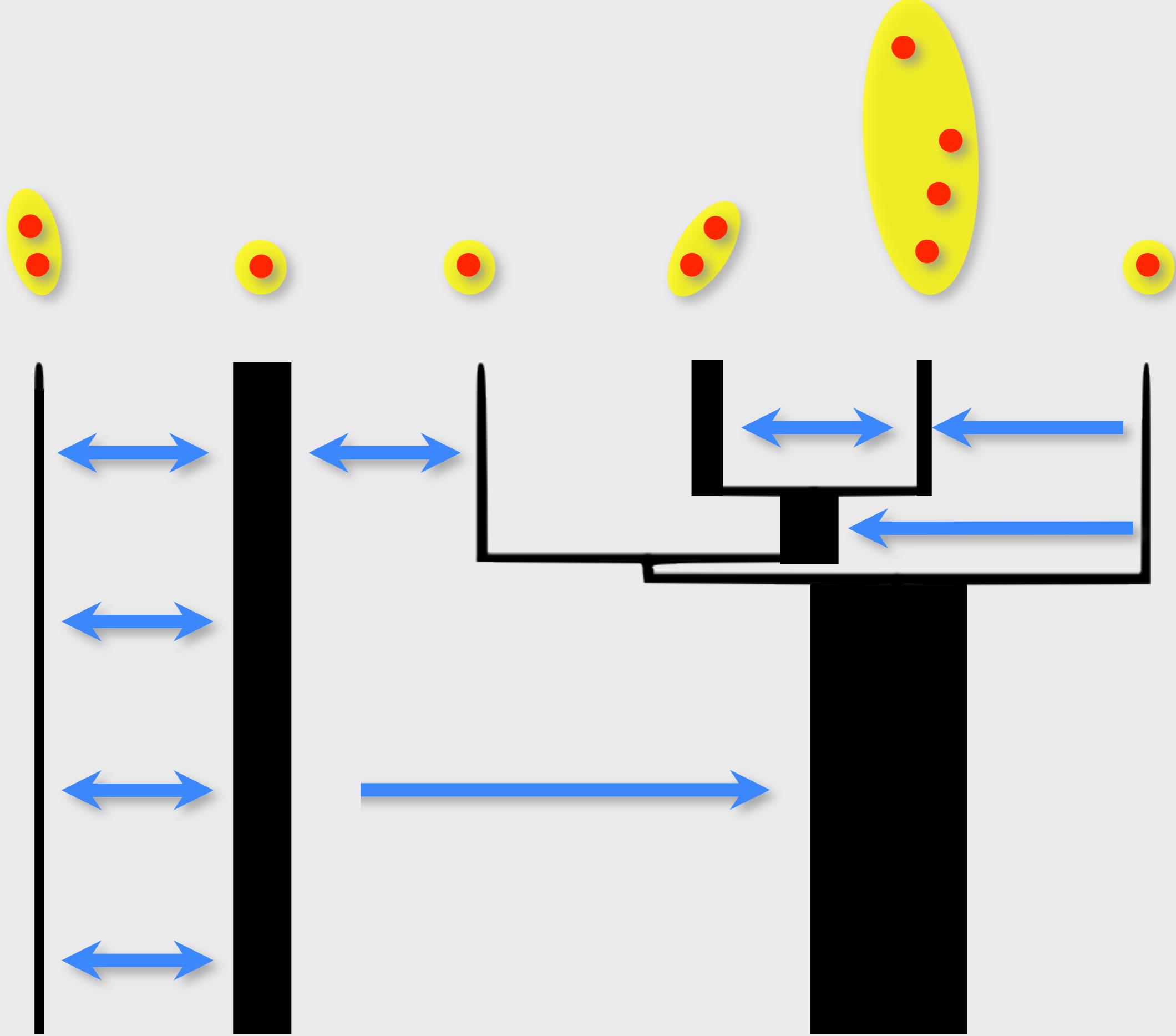


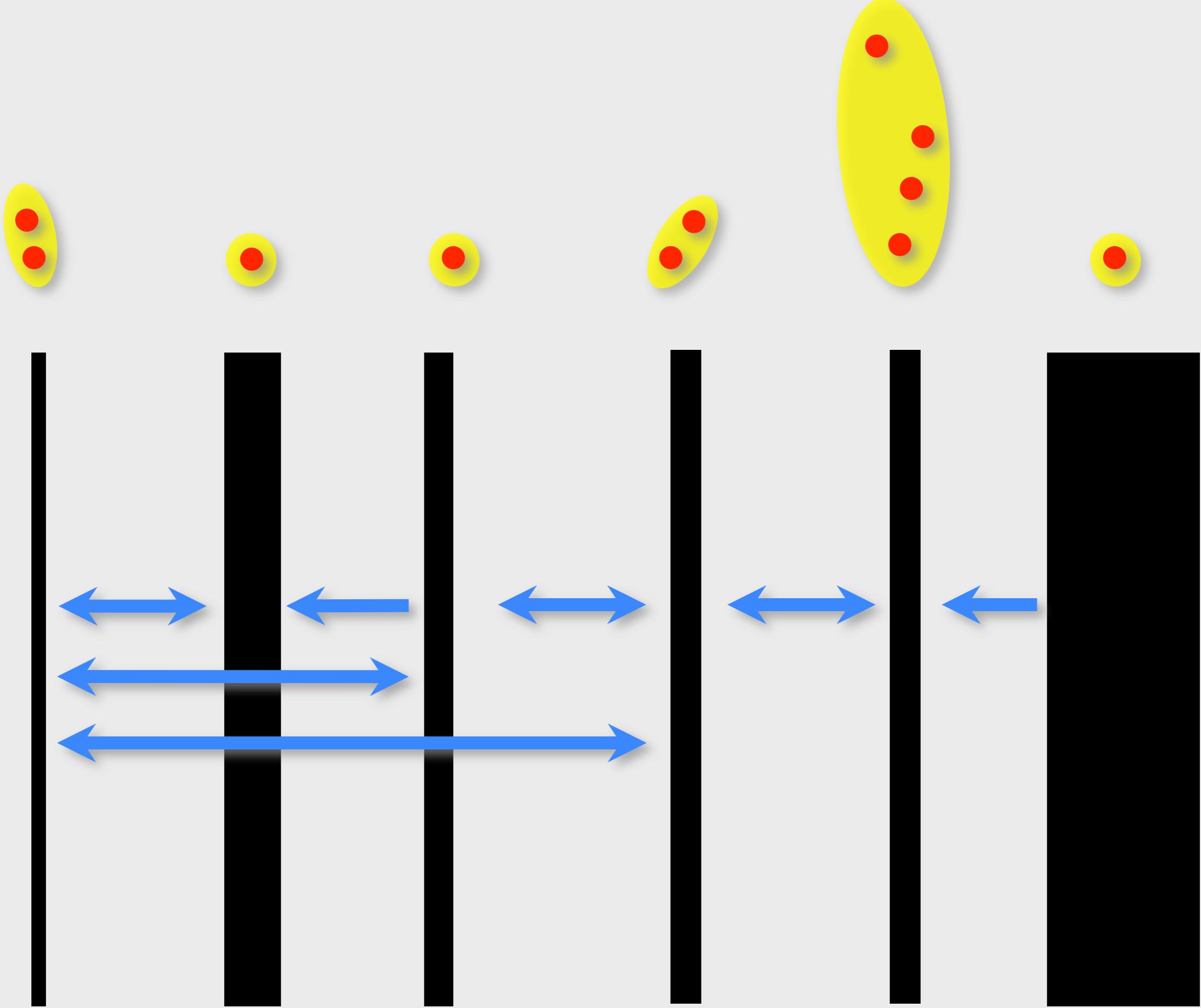




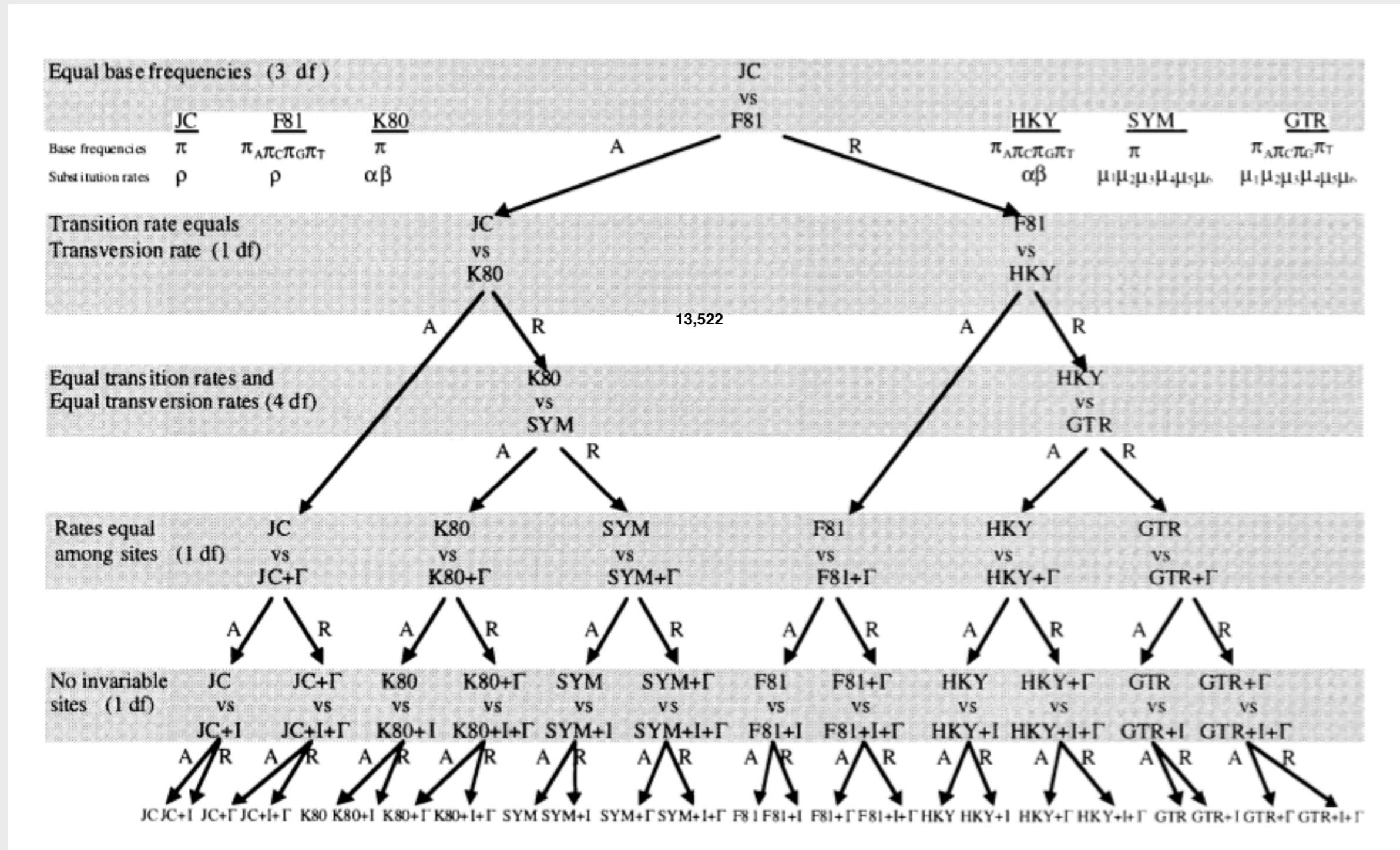








# 13,522 citations of first ModelTest paper (Posada and Crandall 1998) alone



<b>Question</b>	<b>Specified hypothesis method</b>	<b>Try all method</b>
DNA model	PAML	ModelTest
AA model	PAML	ProtTest
Continuous trait model	OUCH, Brownie (traits), OUWie	SURFACE, auteur
Diversification model	laser	Medusa
Phylogeographic	various ABC approaches	<b>phrapl</b>

# **phrapl**

## **phylogeographic inference using approximated likelihoods**

Input:

- gene topologies
- assignments of samples to populations

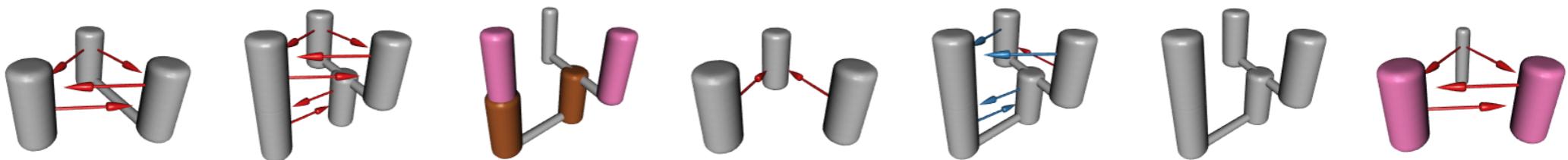
Jargon

- $N$  = number of populations
- $K$  = number of free parameters (as in AIC)

# Generate all possible models

Given  $N$  populations,  $\leq K$  free parameters

1



## Filter

(only tree models, no more than two migration rates, etc.)

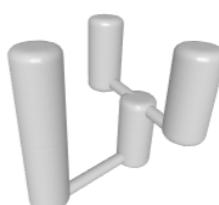
2



## Analyze

(find best, find AIC for all)

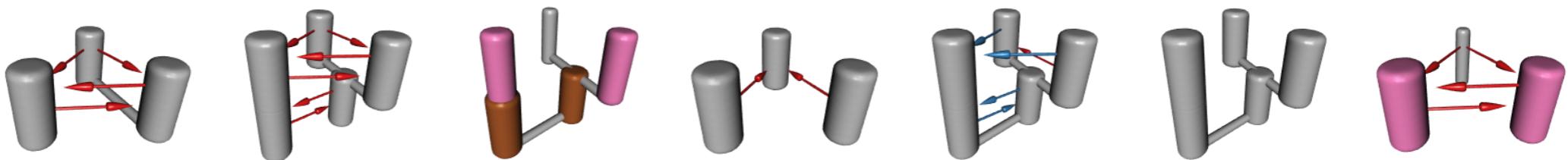
3



# Generate all possible models

Given  $N$  populations,  $\leq K$  free parameters

1



## Filter

(only tree models, no more than two migration rates, etc.)

2



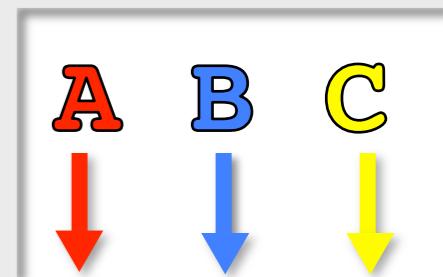
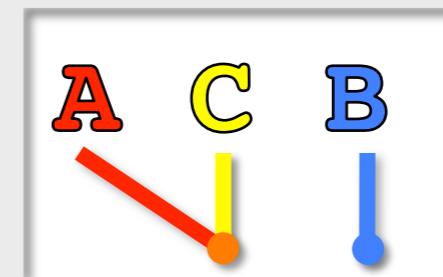
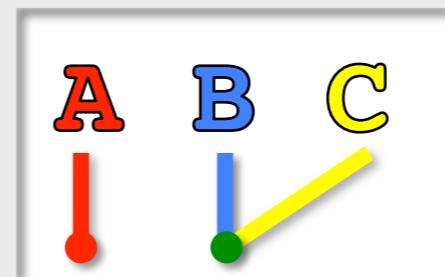
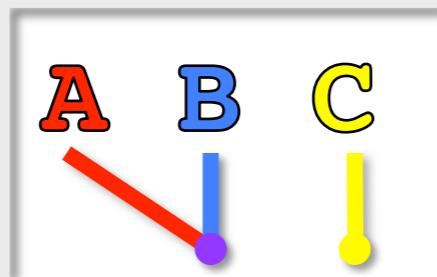
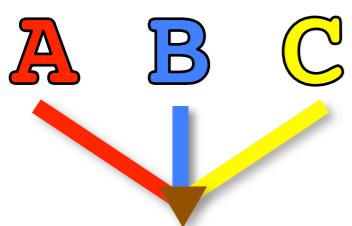
## Analyze

(find best, find AIC for all)

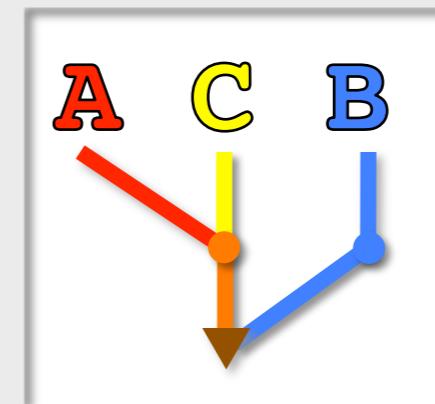
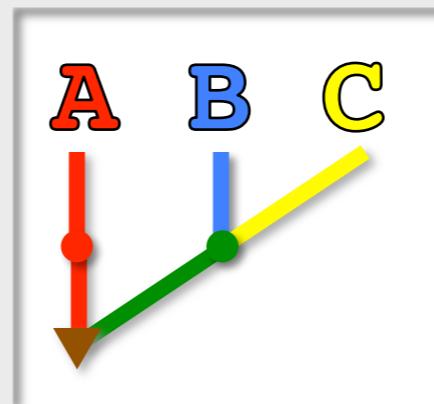
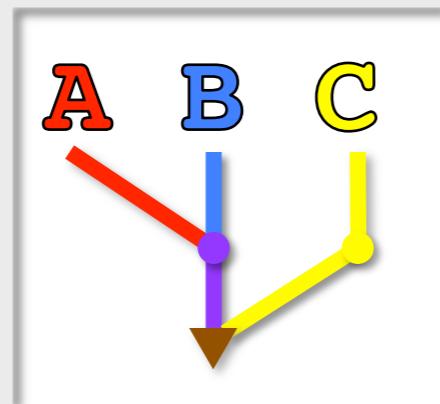
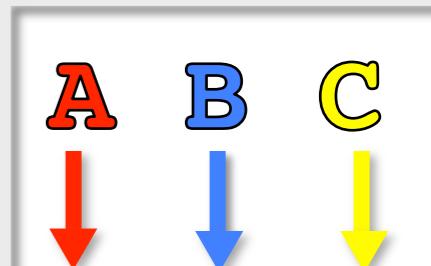
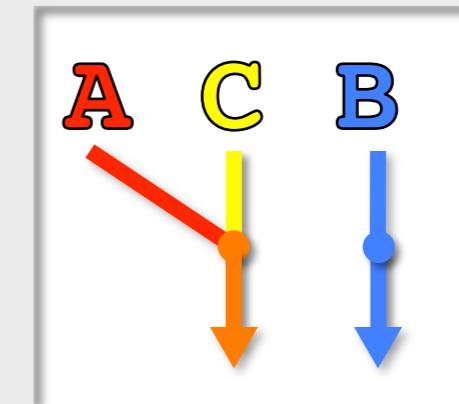
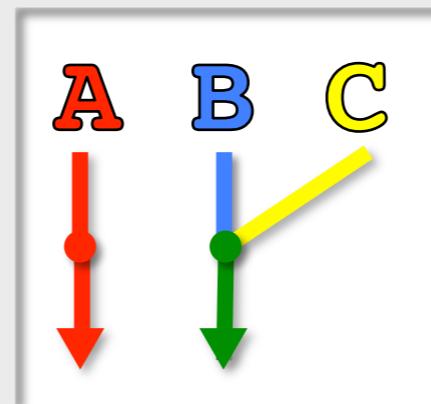
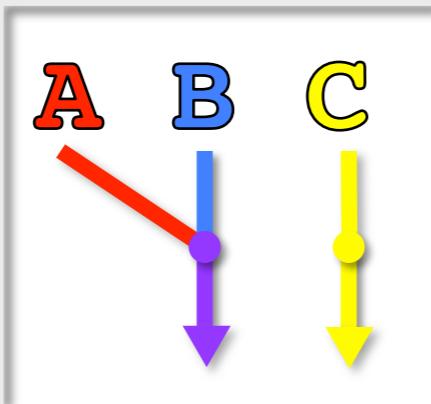
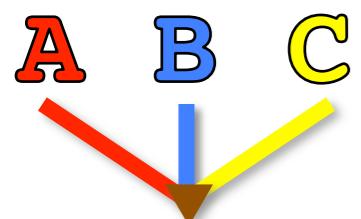
3



# Coalescence of populations

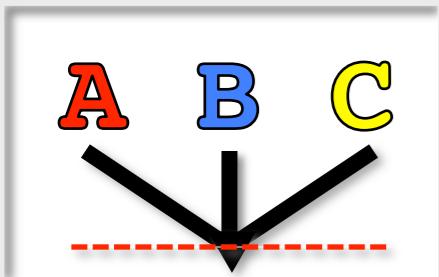


# Coalescence of populations

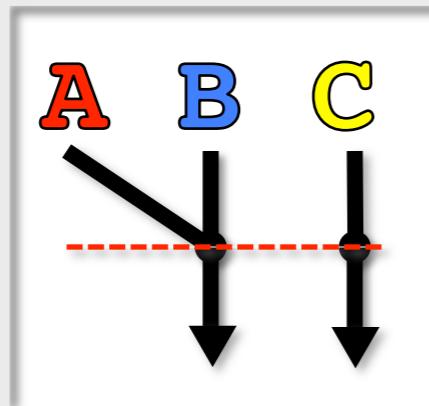


# Coalescence of populations

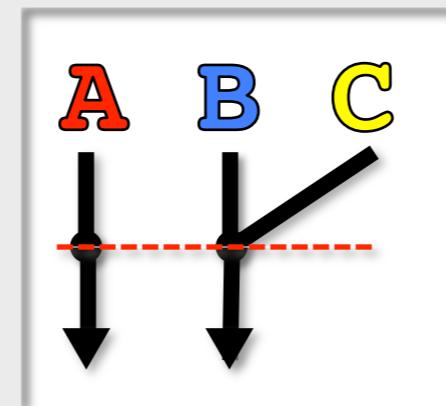
K=1



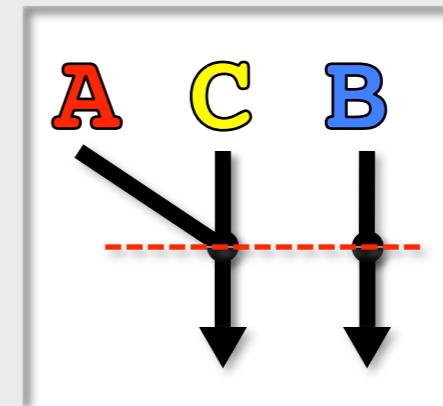
K=1



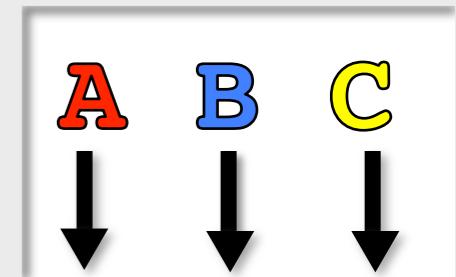
K=1



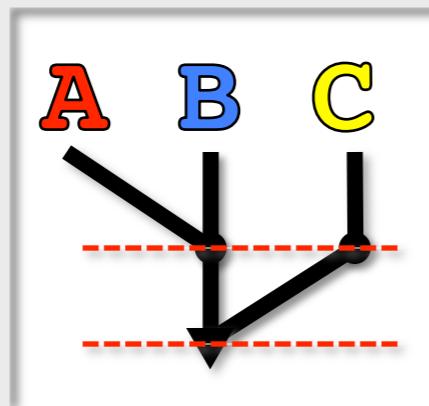
K=1



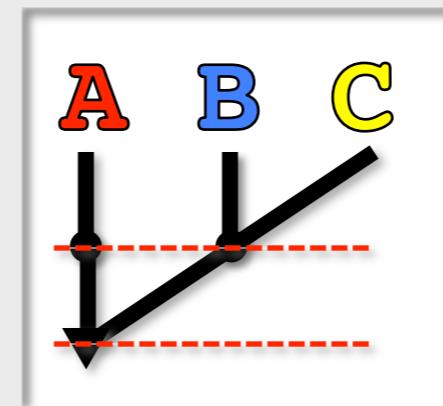
K=0



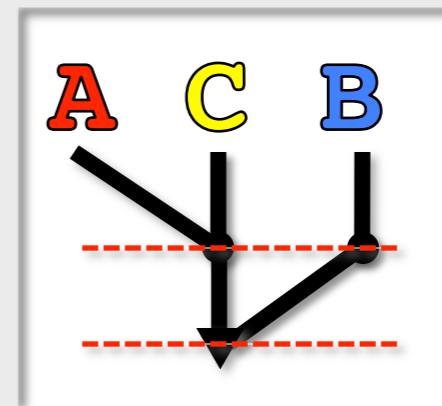
K=2



K=2



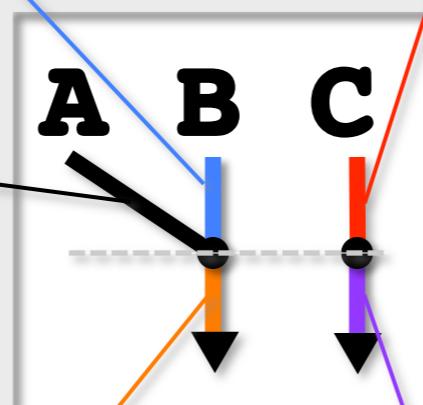
K=2



B: Same or  
different as A

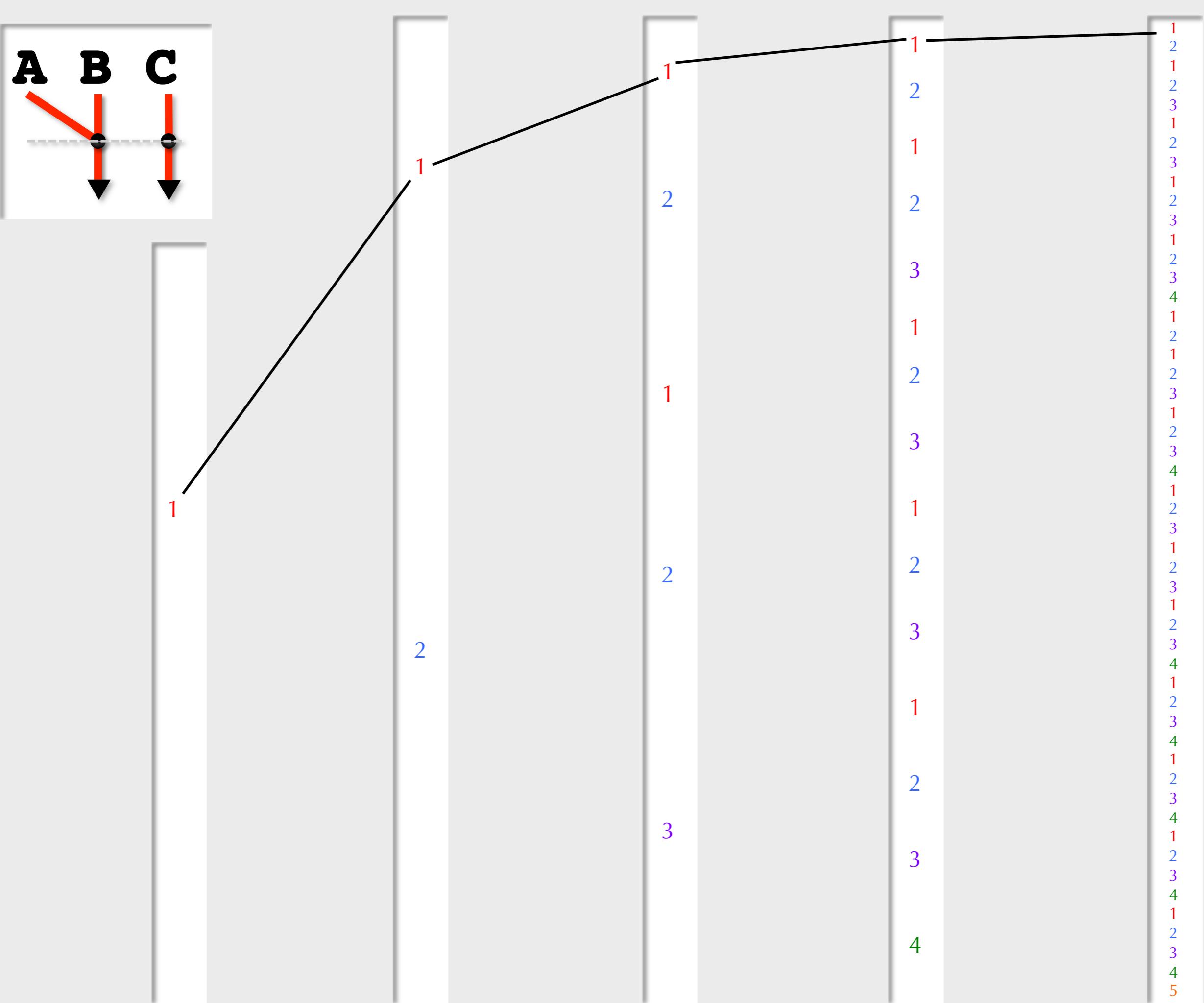
A:  $N_1$

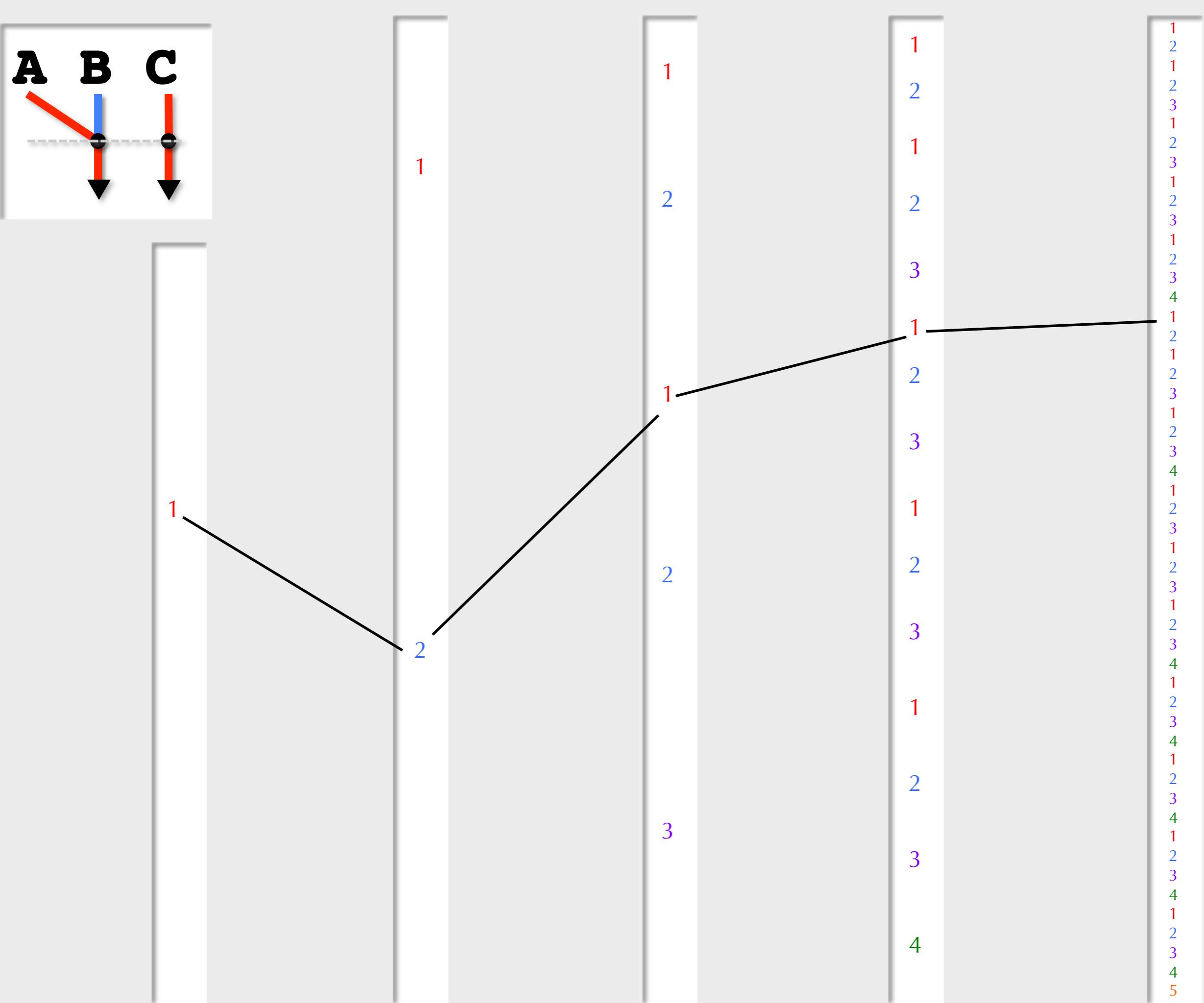
AB: Same or  
different as A  
and/or B

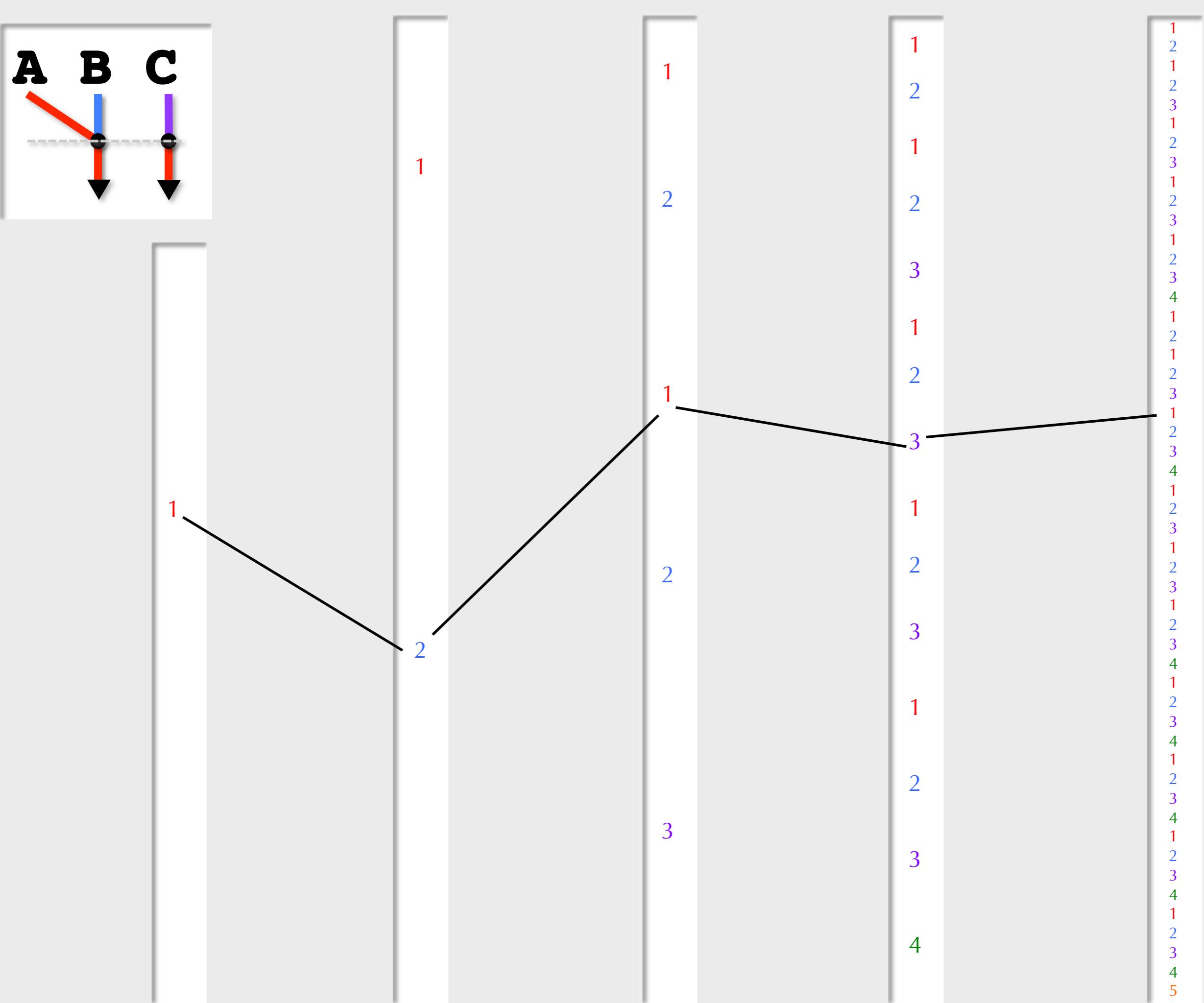


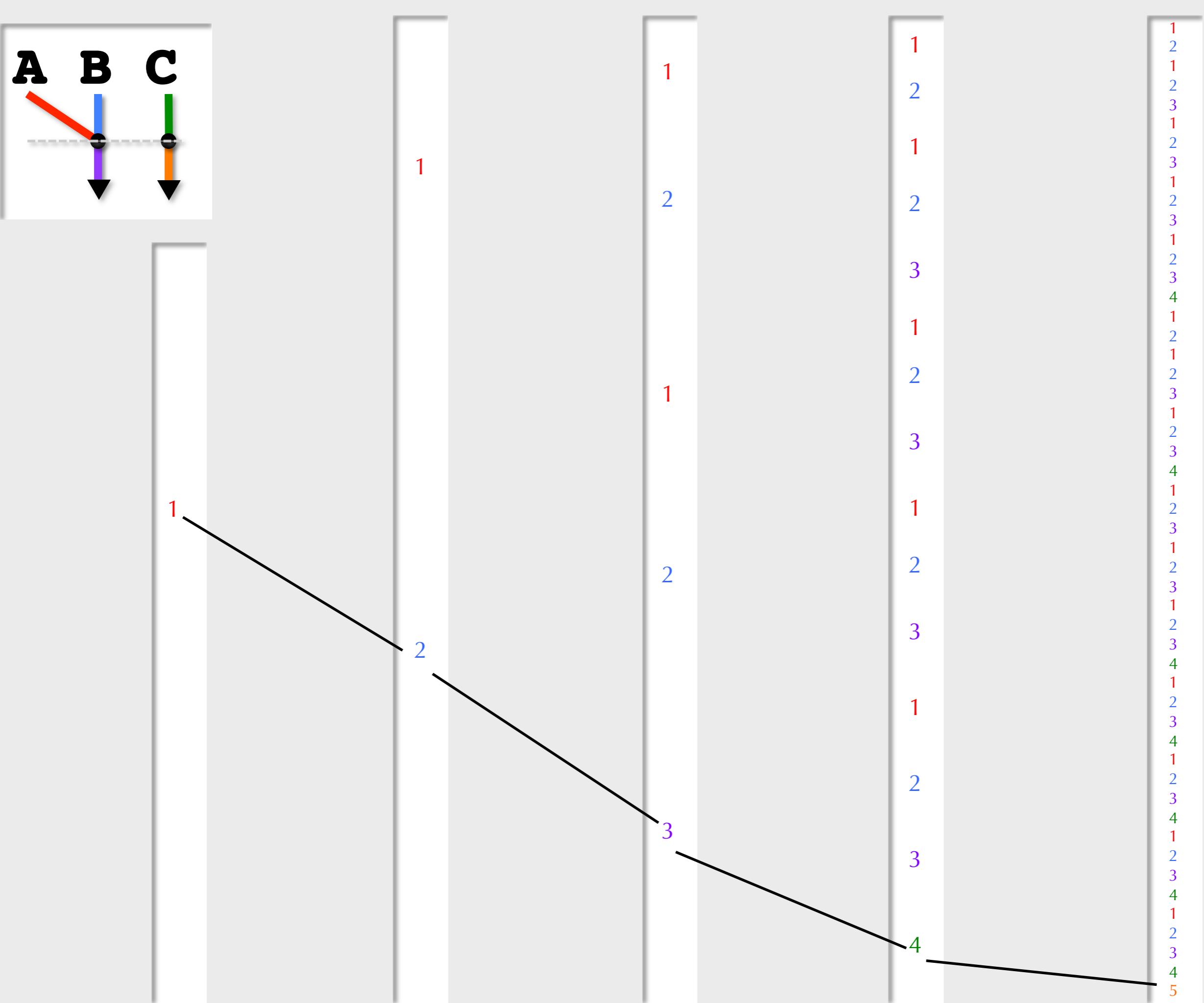
C1: Same or  
different as A  
and/or B and/or AB

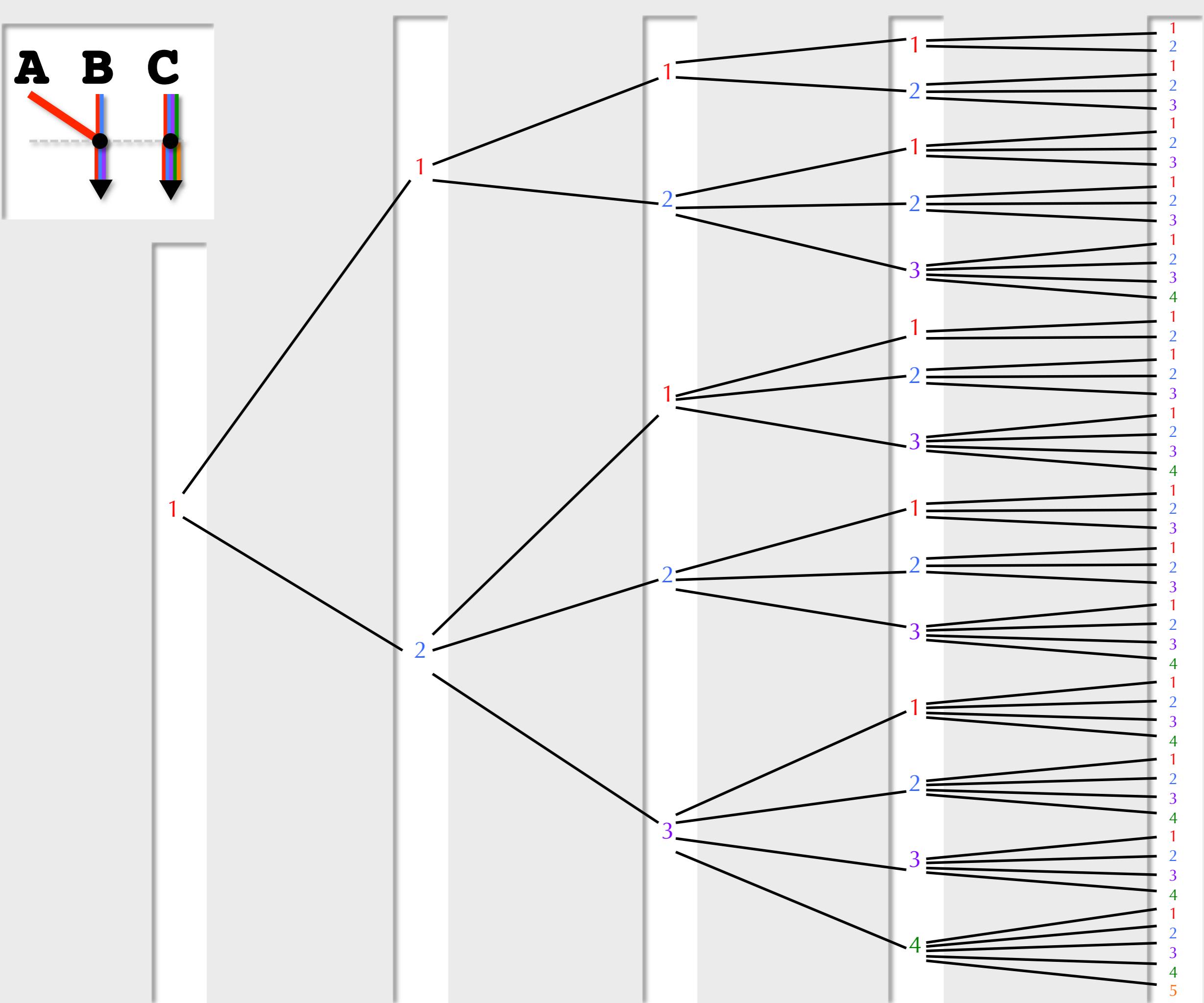
C2: Same or  
different as A and/or  
B and/or AB and/or  
C1

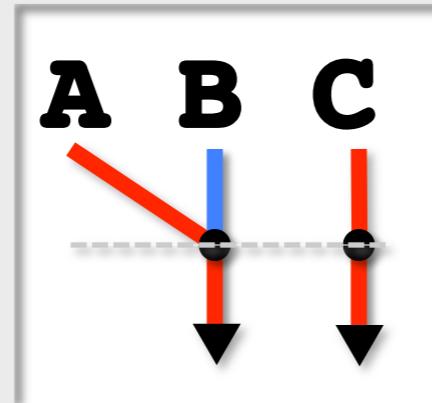




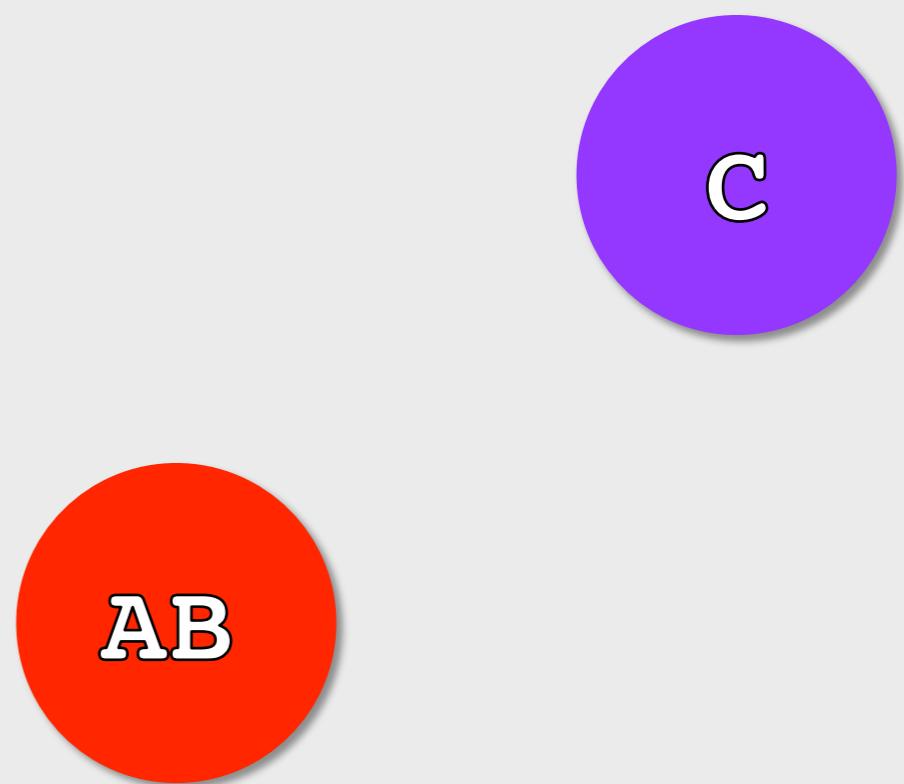
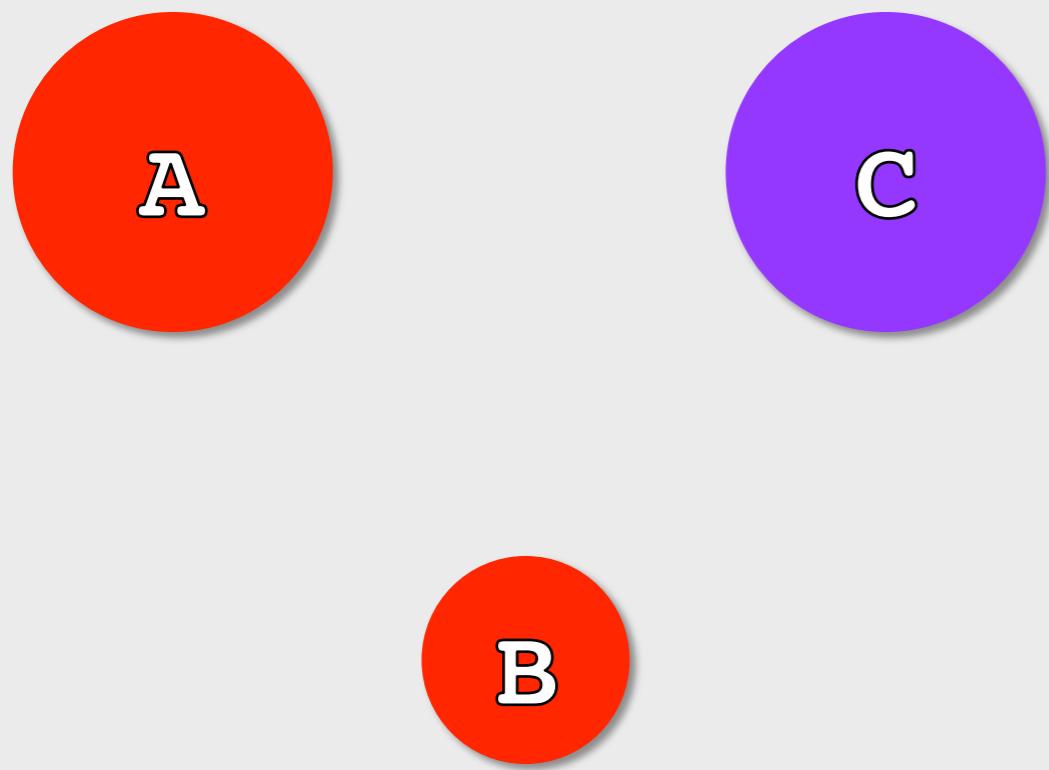
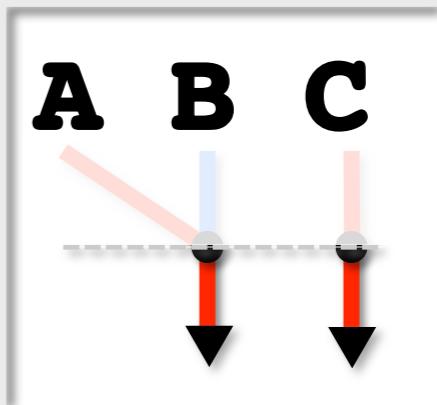
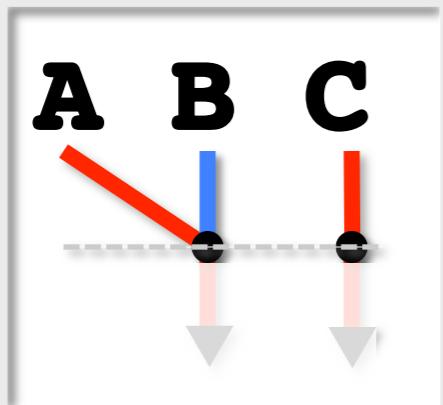


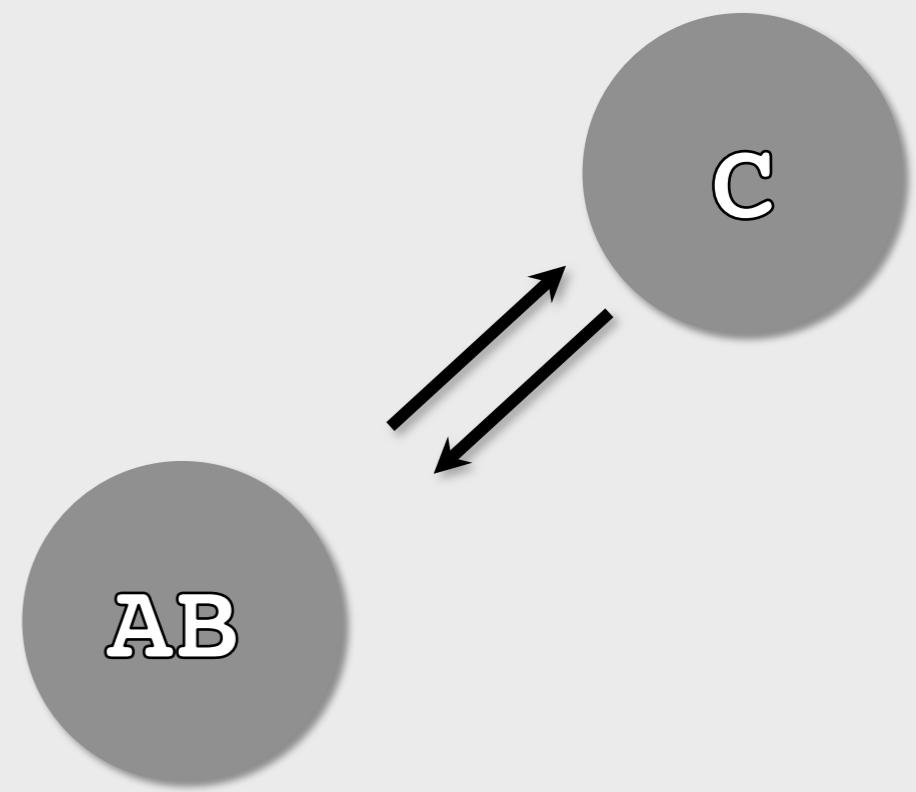
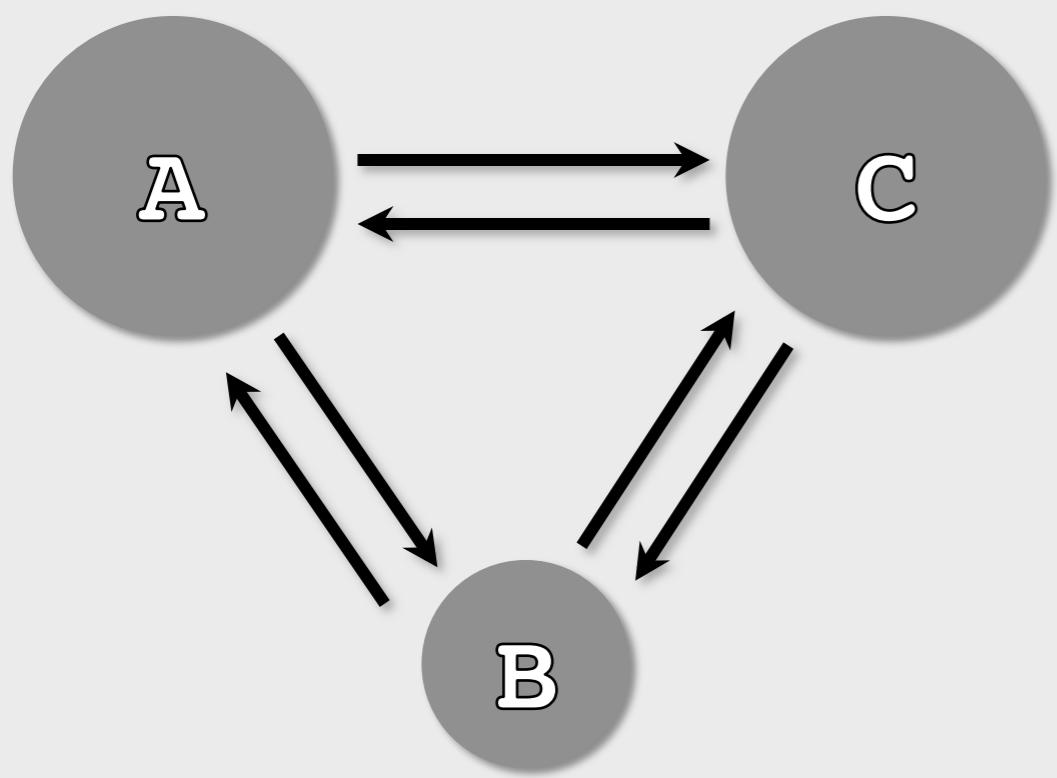
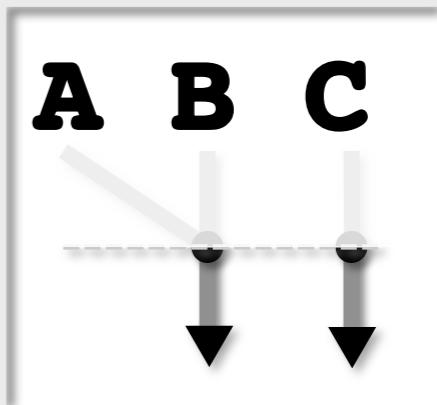
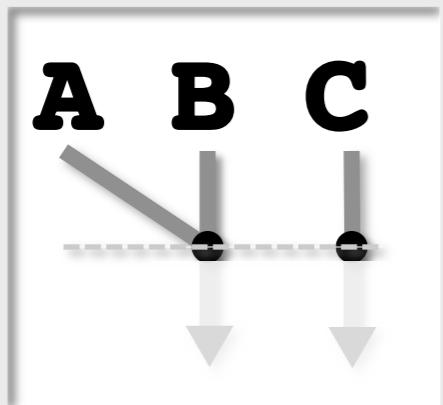


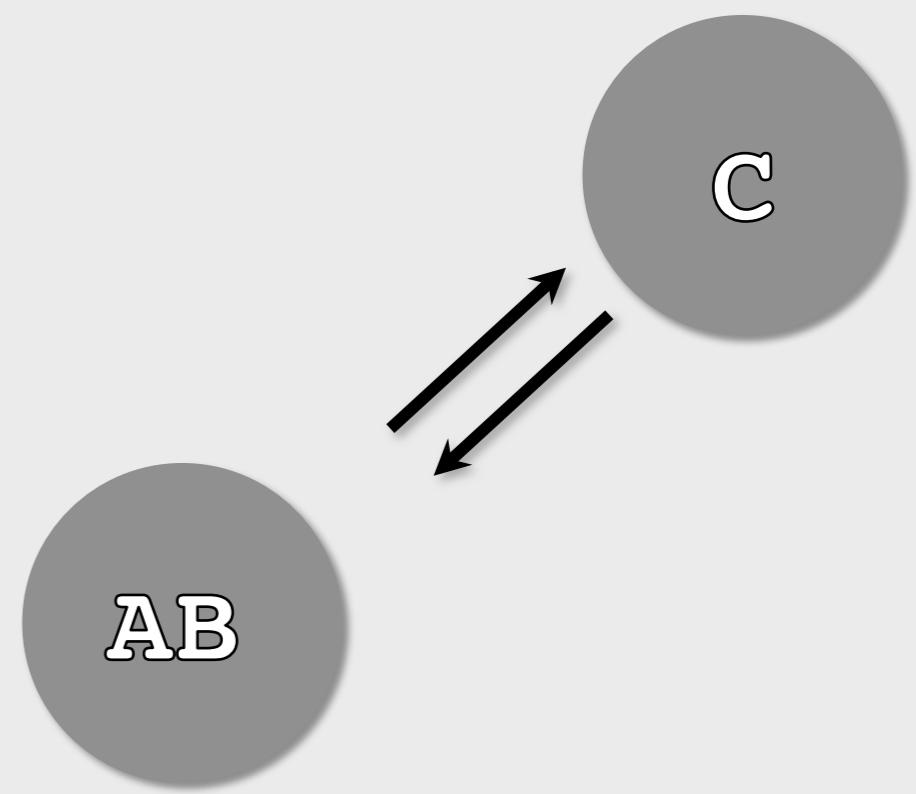
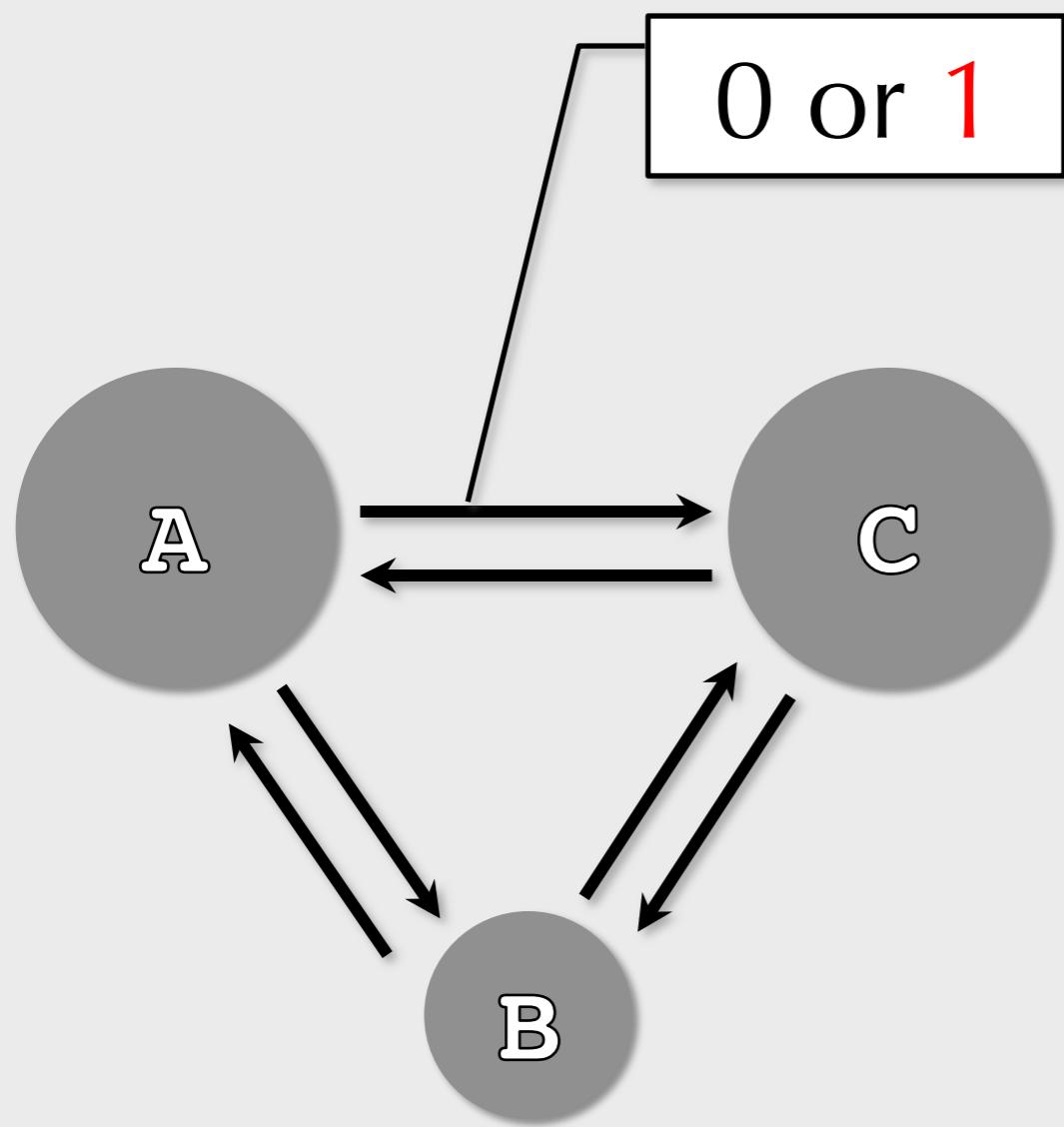
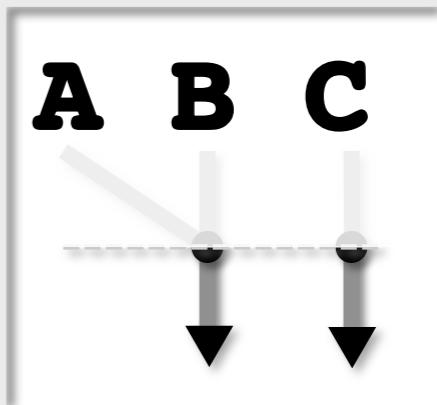
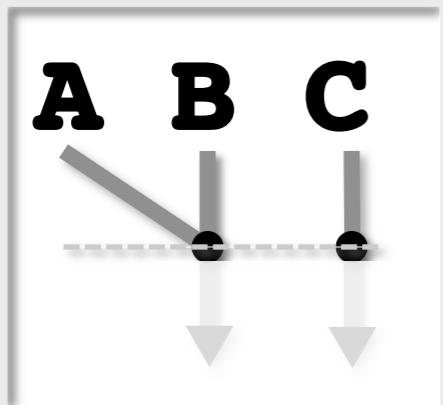


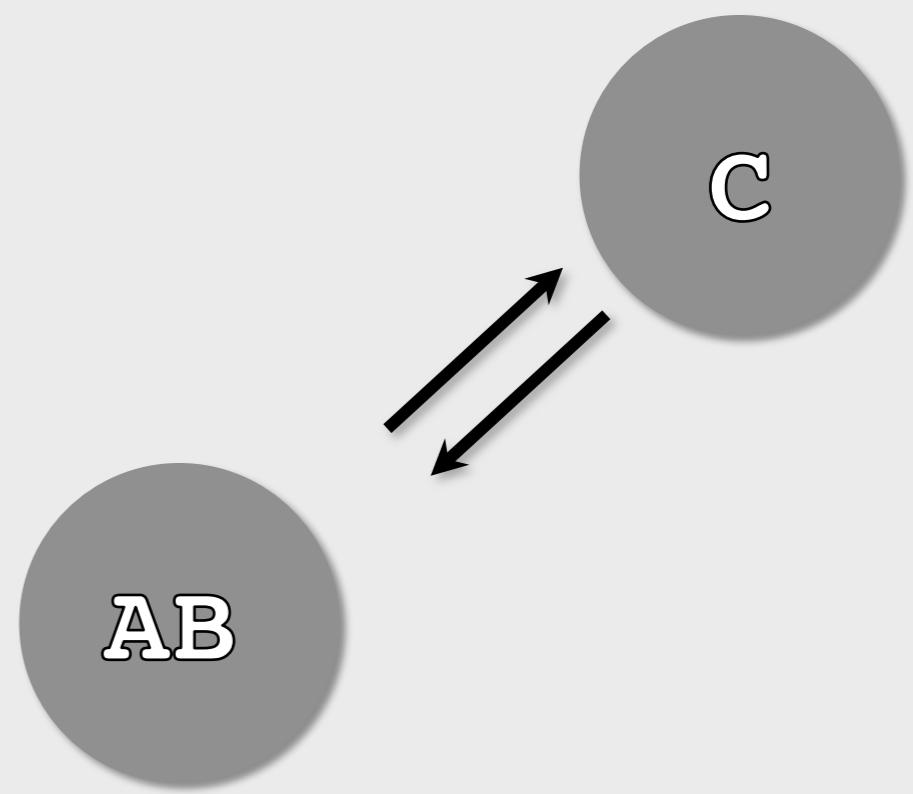
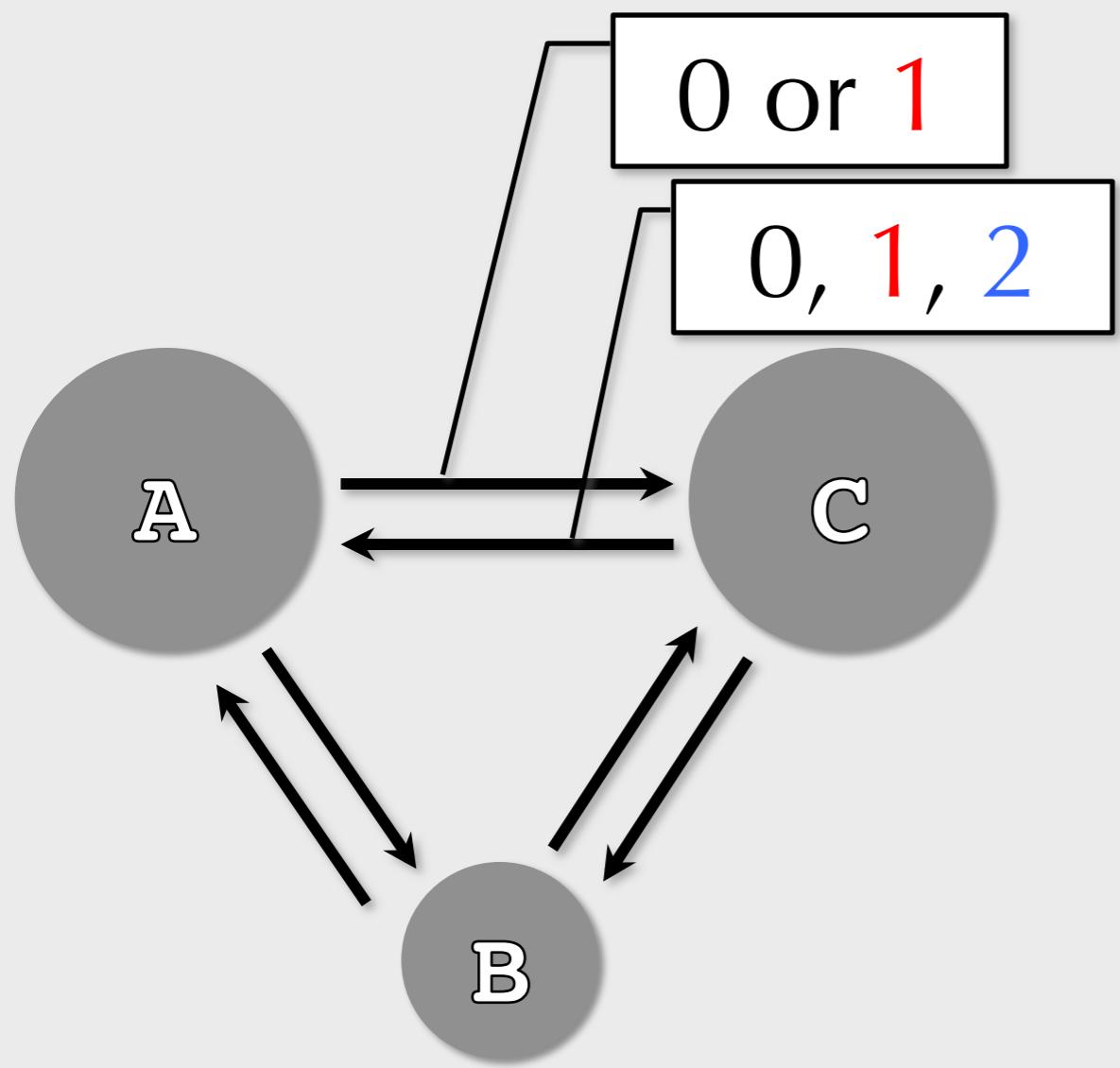
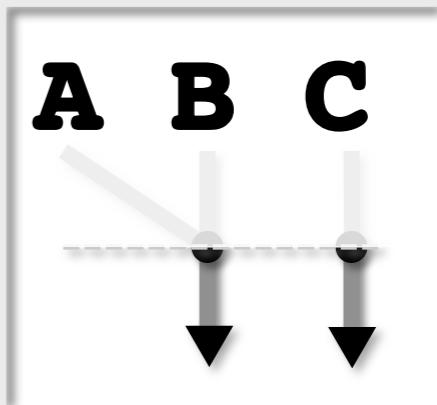
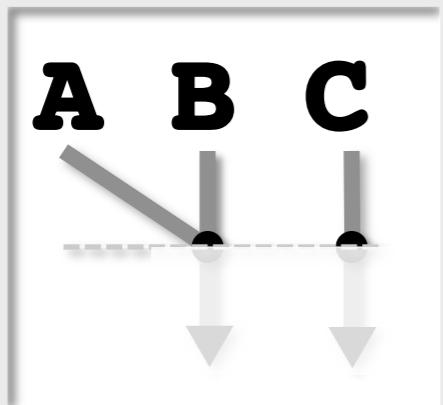


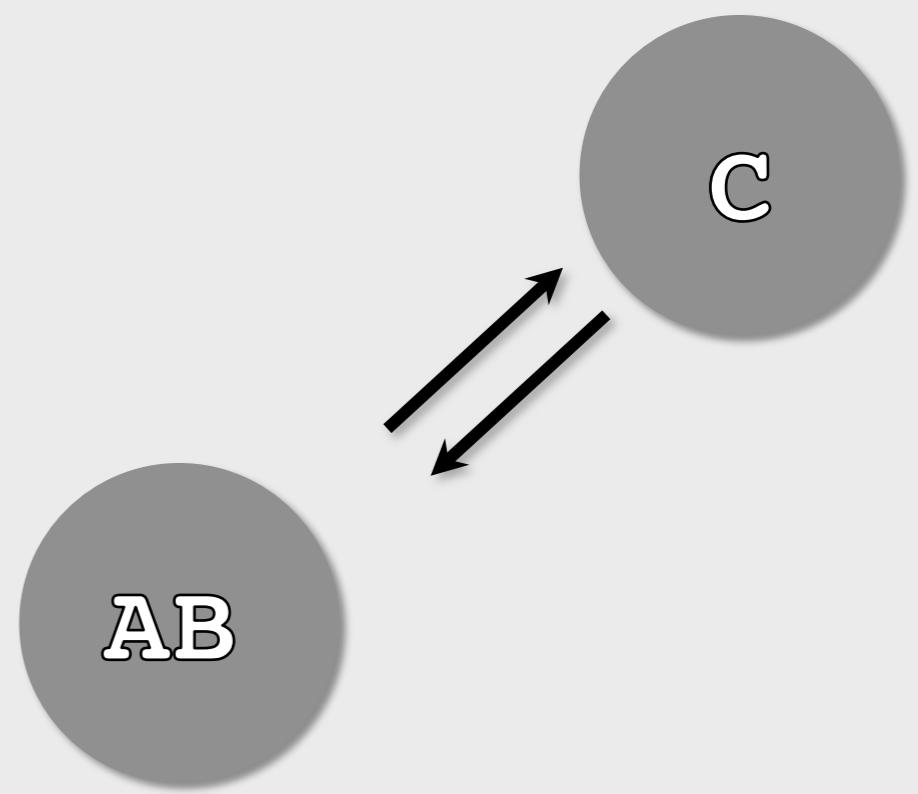
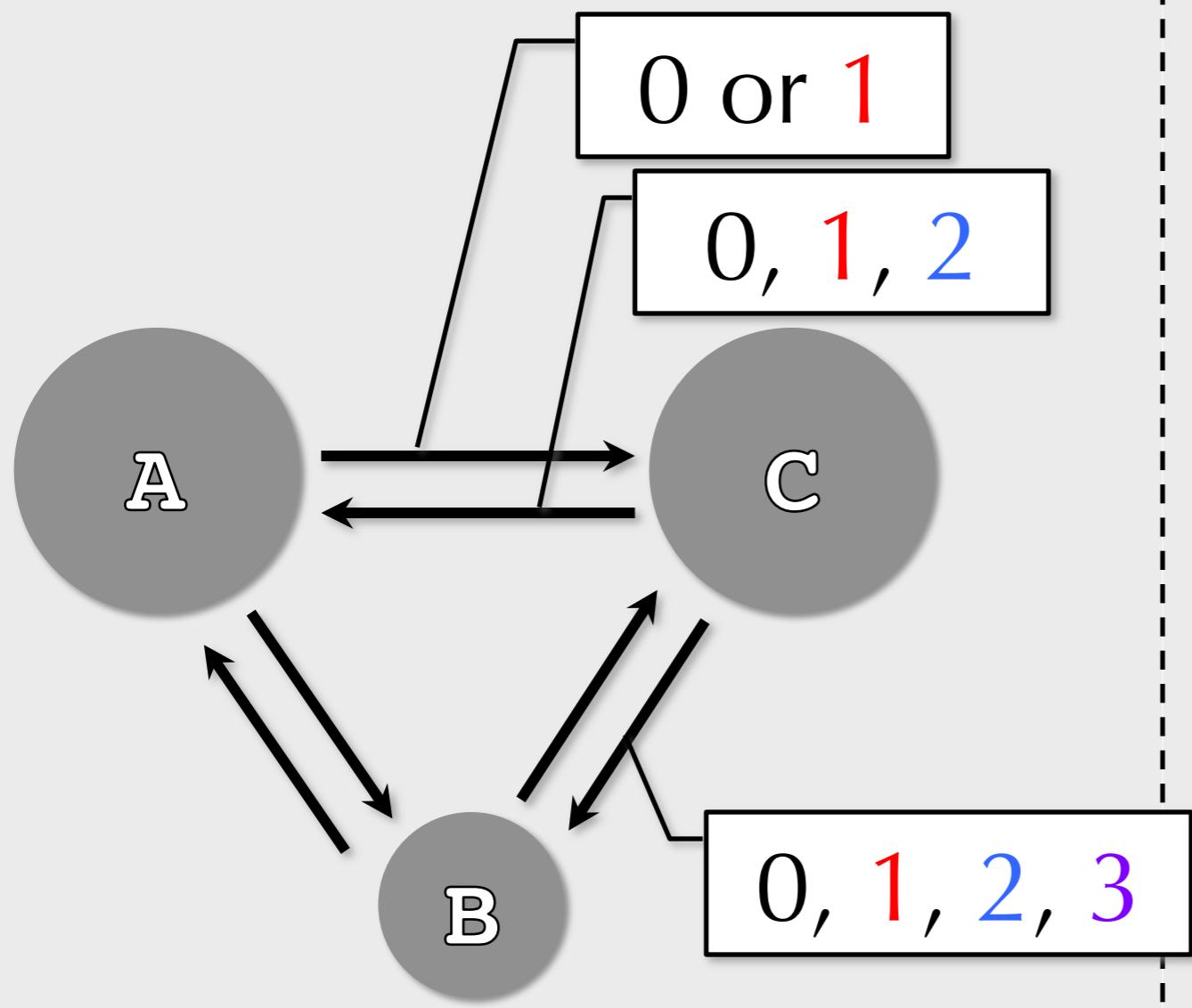
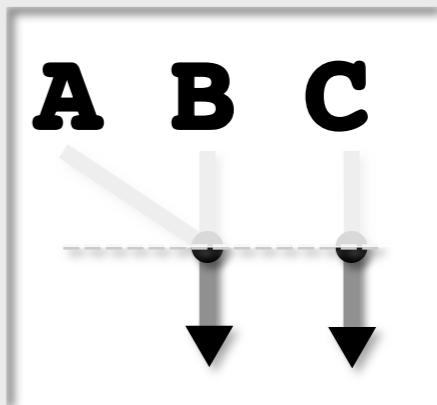
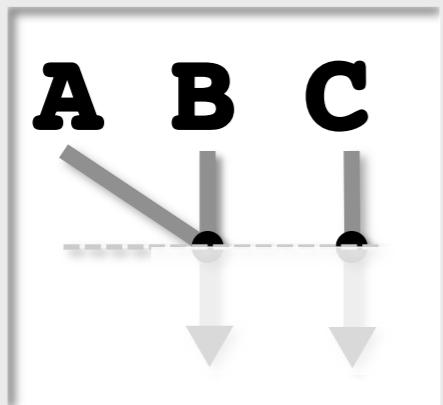
1 collapse parameter  
2 population size parameters

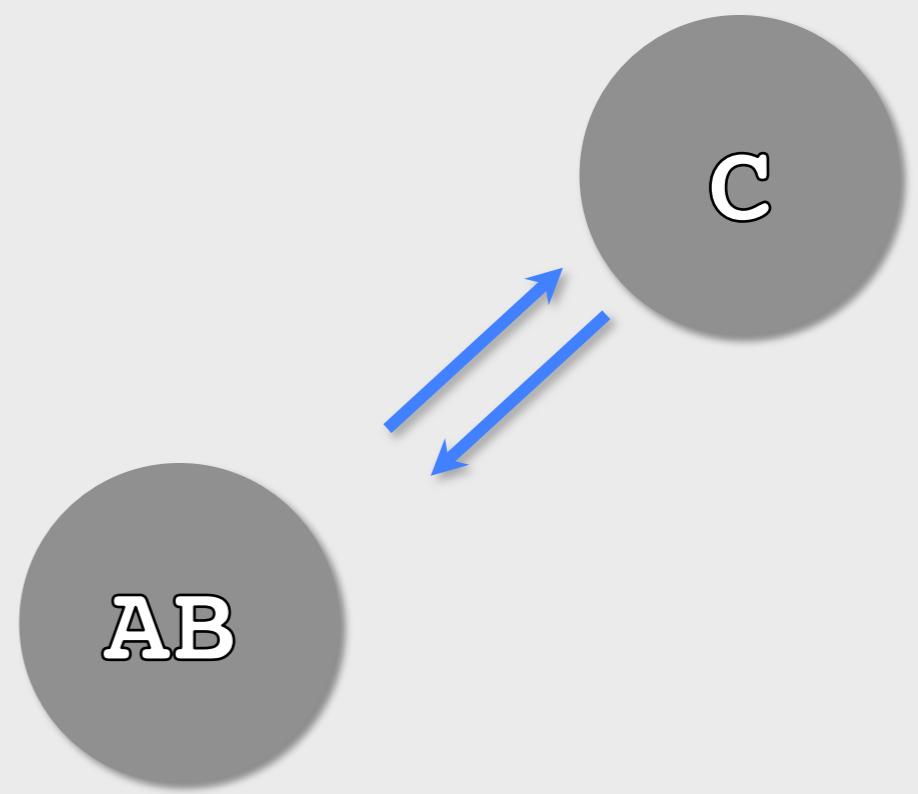
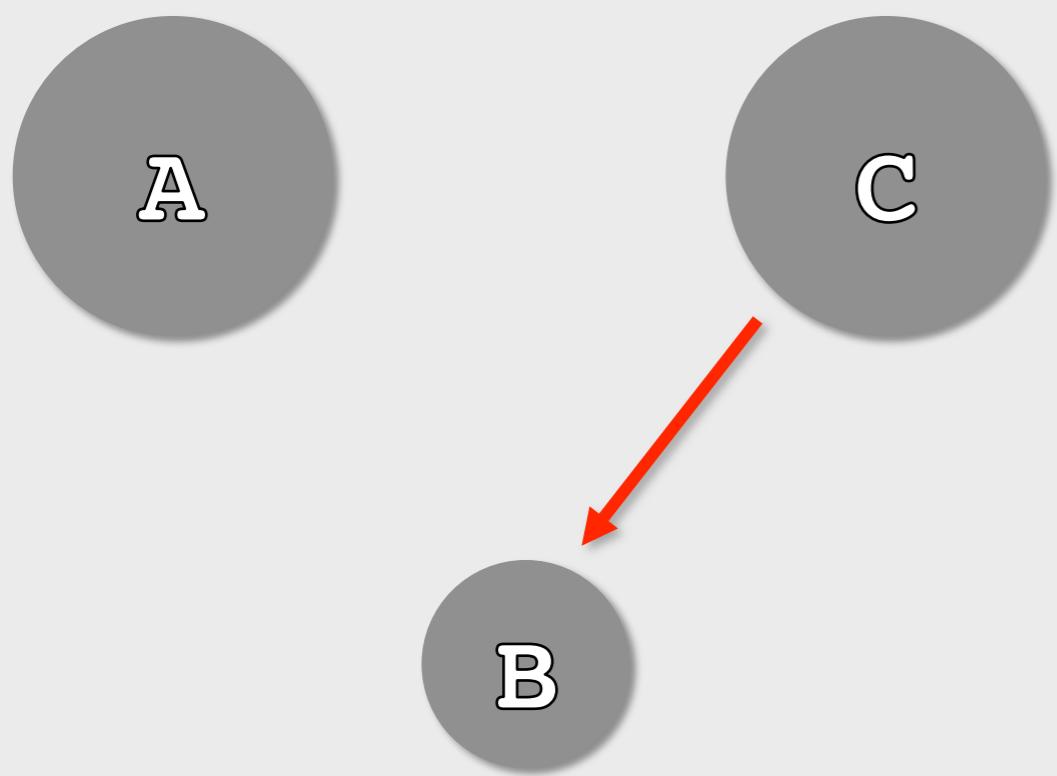
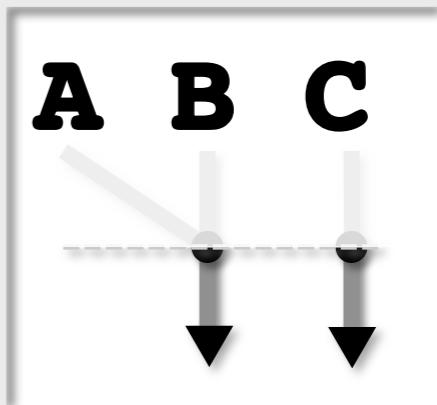
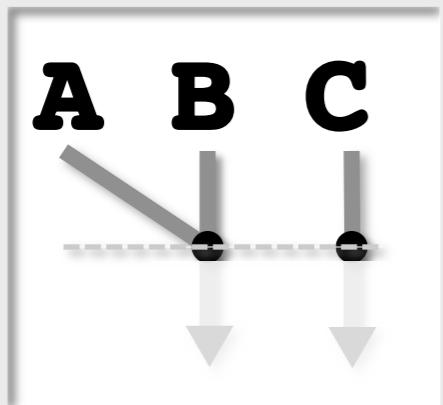








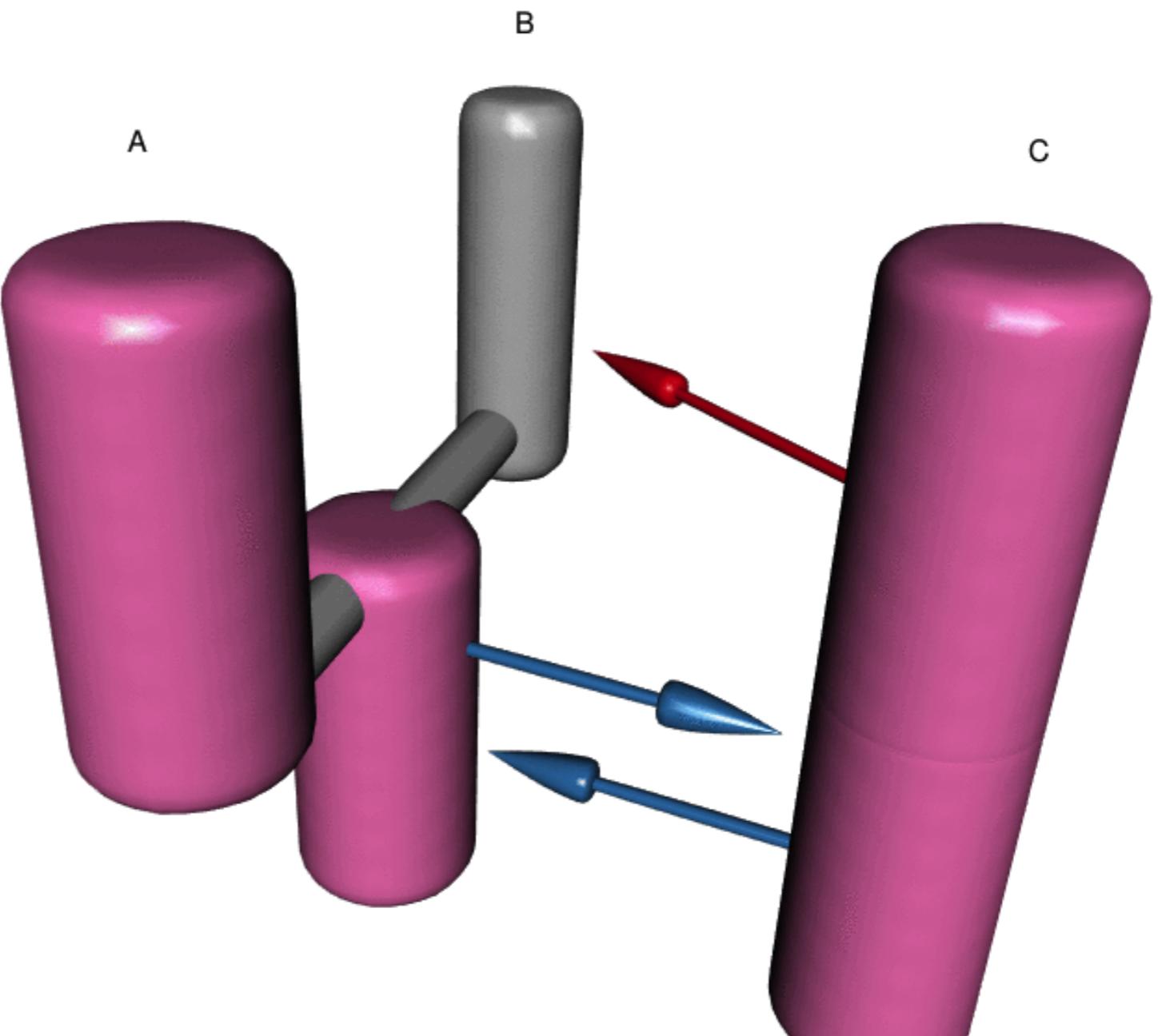
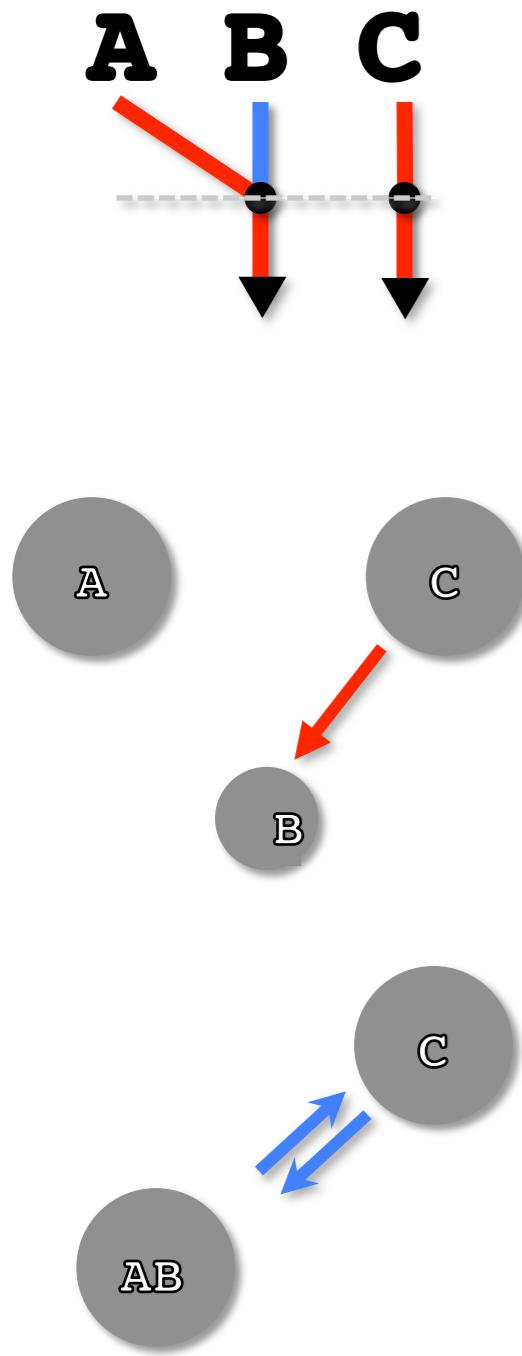


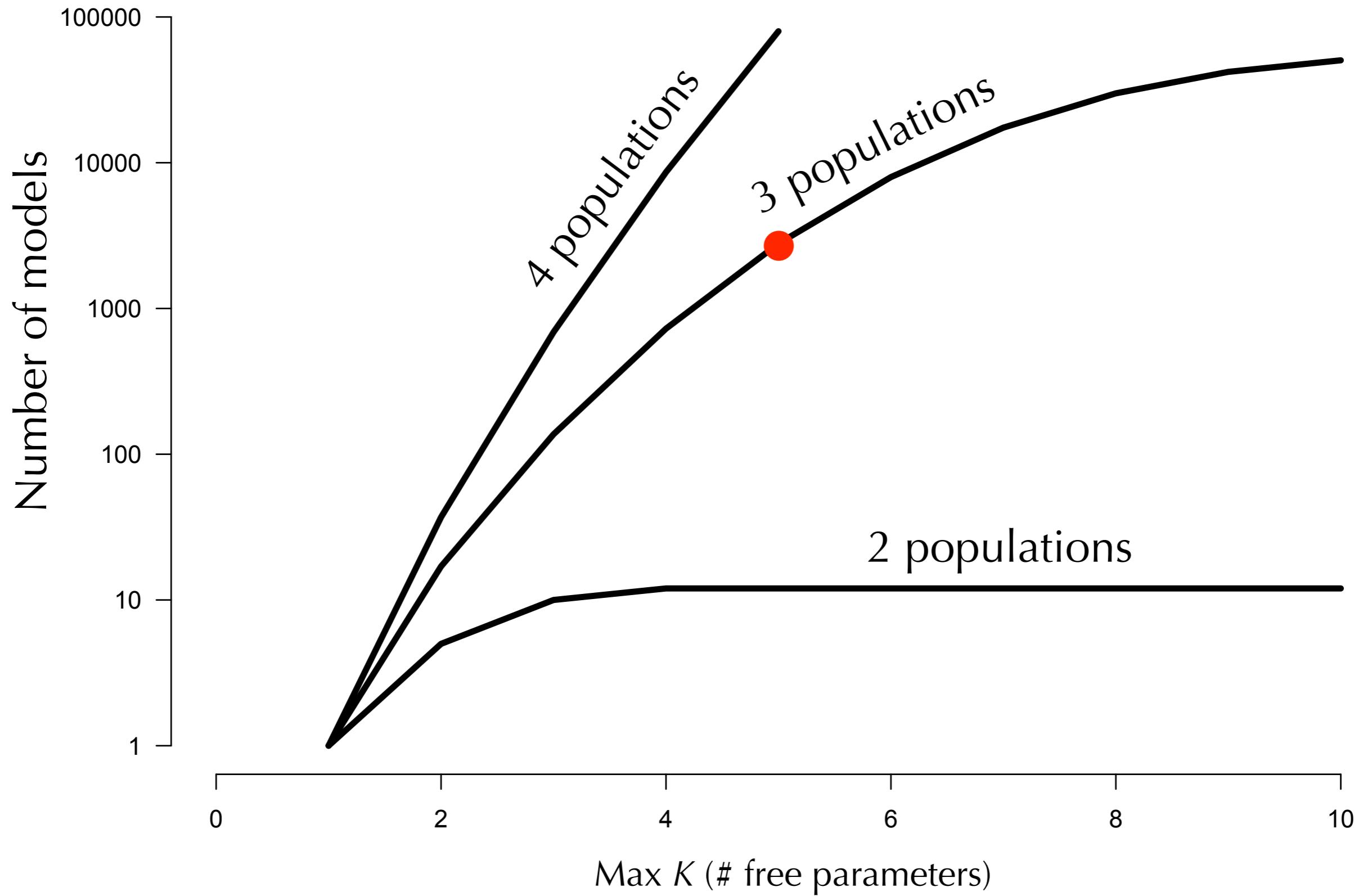


1 collapse parameter

2 population size parameters

2 migration parameters

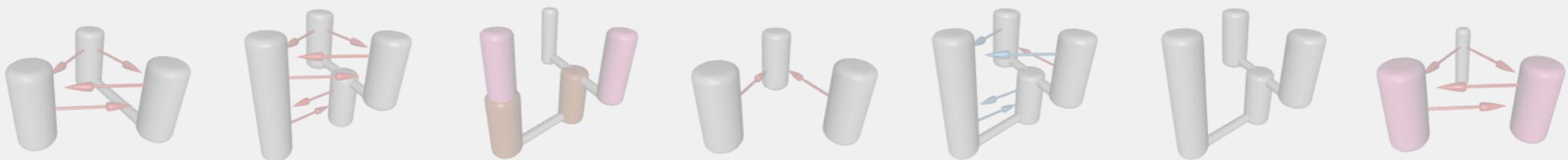




# Generate all possible models

Given  $N$  populations,  $\leq K$  free parameters

1



## Filter

(only tree models, no more than two migration rates, etc.)

2



## Analyze

(find best, find AIC for all)

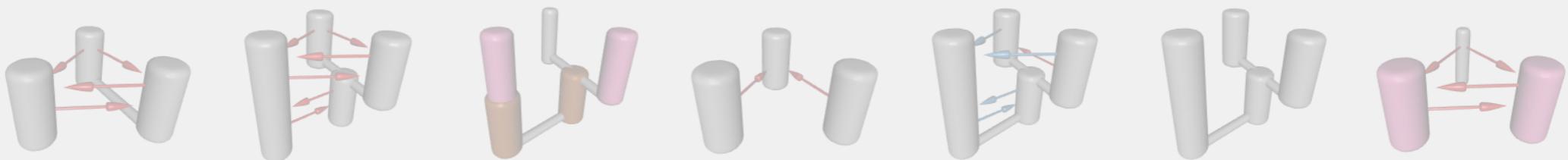
3



# Generate all possible models

Given  $N$  populations,  $\leq K$  free parameters

1



## Filter

(only tree models, no more than two migration rates, etc.)

2

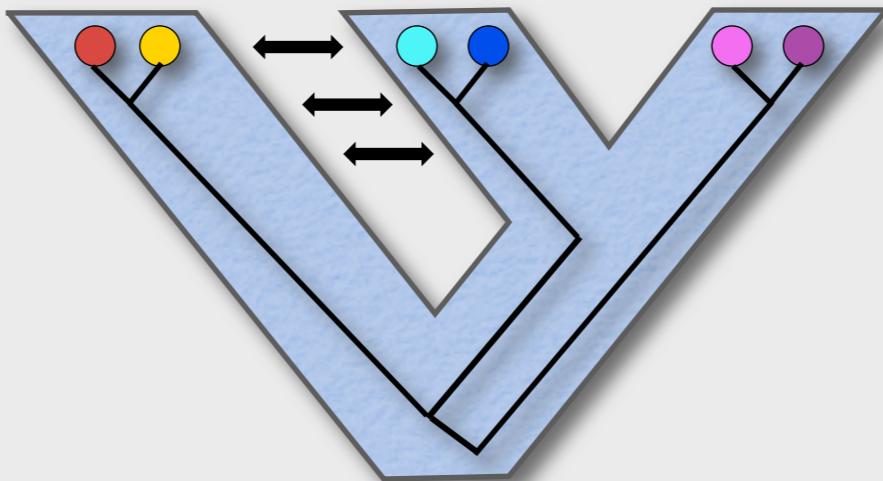


## Analyze

(find best, find AIC for all)

3

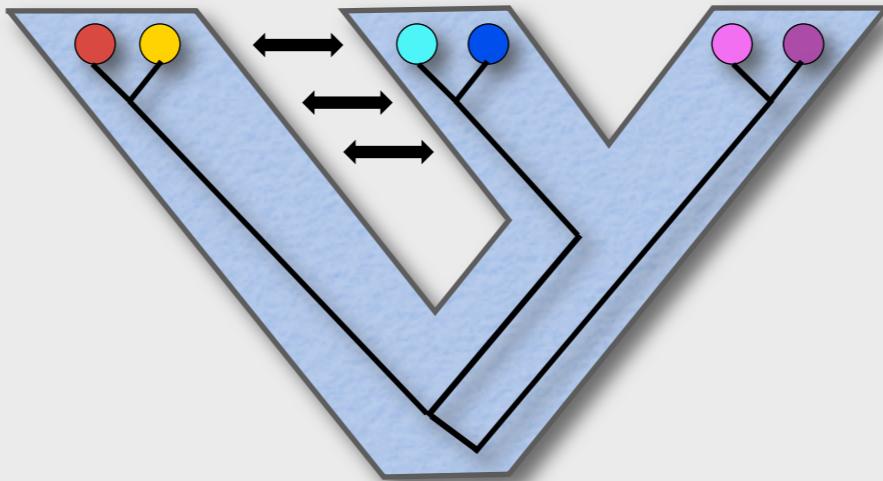




Exact likelihood:  $P(\text{gene tree} \mid \text{population history})$

COAL (Degnan and Salter 2005), STEM (Kubatko et al. 2009), BPP (Yang and Rannala 2010), IM (Nielsen and Wakely 2001), etc.

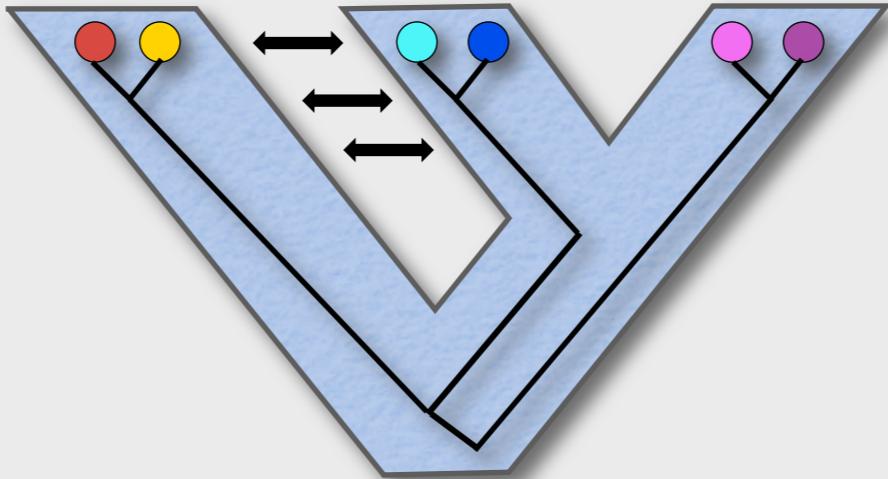
Issue: Not all models (currently) have analytical solutions, and it's always simpler to simulate (think of selection). But if it does work, can use it.



# Approximate Bayesian Computation

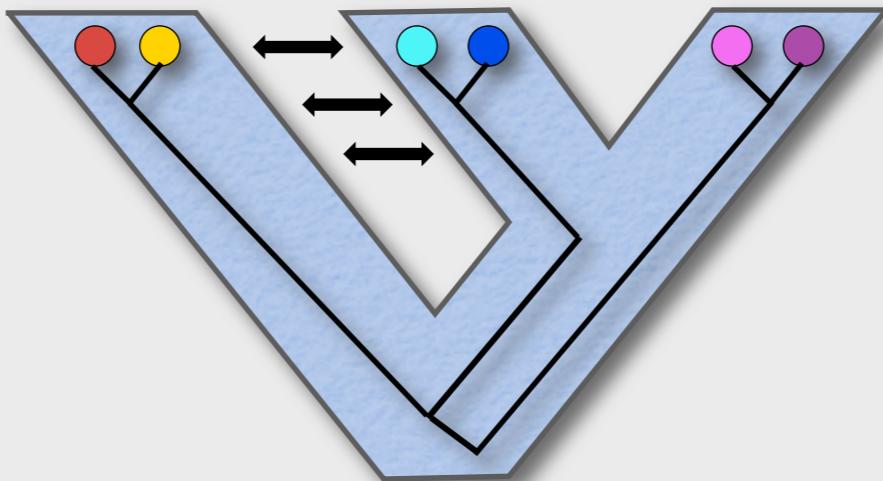
Carmago et al. 2012, DIYABC (Cornuet et al. 2010), PopABC (Lopes et al. 2009)

```
for (many reps) {  
    sample parameters (or models) from prior  
    simulate dataset using these parameters  
    if (|(summary(dataset) - summary(observed)| < ε)){  
        count as match, save these parameters  
    }  
}  
  
plot(saved parameters) #or other way to summarize
```



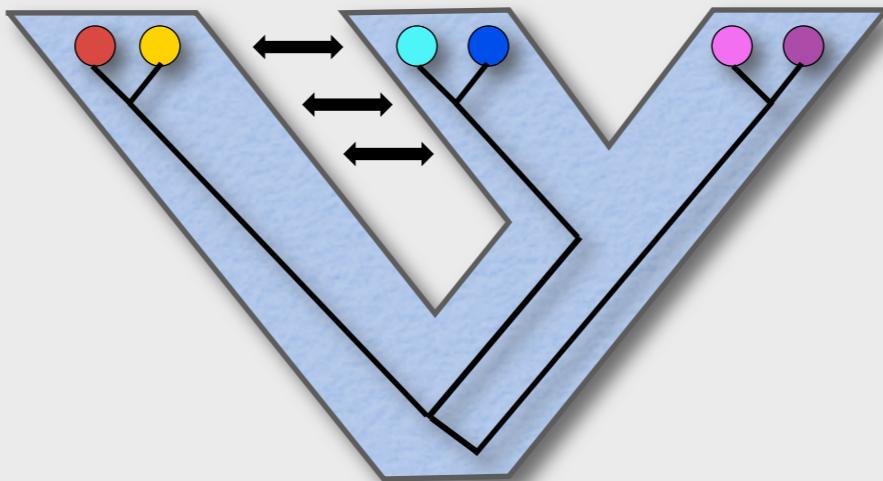
## Approximate Likelihood

Estimate probability of data  
counting exact matches



## Approximate Likelihood

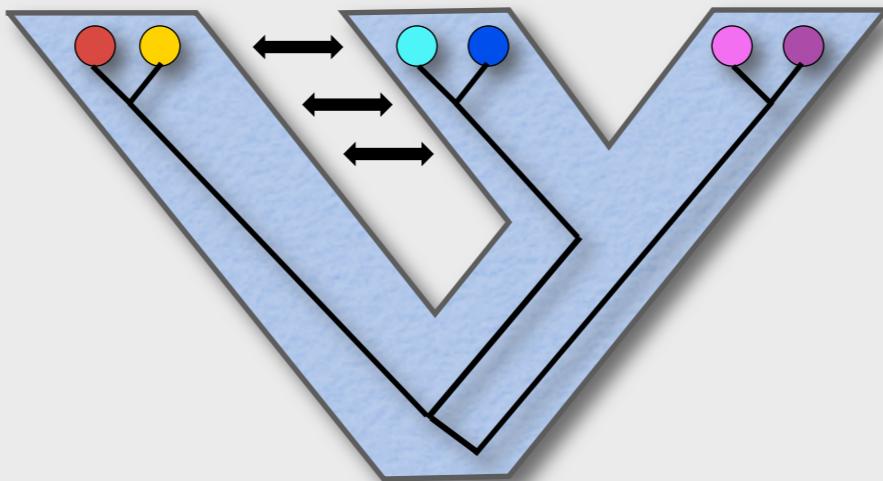
```
for (many reps) {  
    sample parameters (or models) from prior  
    simulate dataset using these parameters  
    if (|(summary(dataset) - summary(observed)| < ε)){  
        count as match, save these parameters  
    }  
}  
  
plot(saved parameters) #or other way to summarize
```



## Approximate Likelihood

```
sample parameters (or models) from prior guesses
for (many reps) {
    sample parameters (or models) from prior
    simulate dataset using these parameters
    if (|(summary(dataset) - summary(observed)| < ε) {
        count as match, save these parameters
    }
}

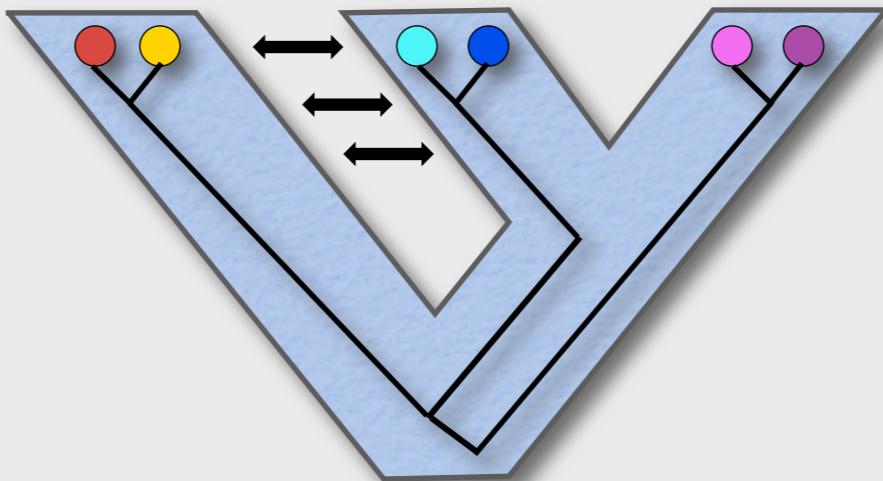
plot(saved parameters) #or other way to summarize
```



## Approximate Likelihood

```
sample parameters (or models) from prior guesses
for (many reps) {
    sample parameters (or models) from prior
    simulate dataset using these parameters
    if ( topology(dataset) == topology(observed) ) {
        count as match, save these parameters
    }
}

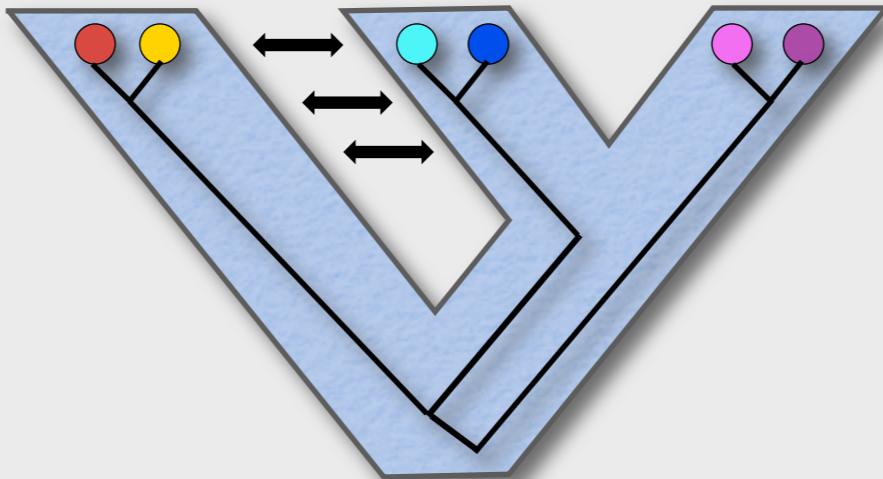
plot(saved parameters) #or other way to summarize
```



## Approximate Likelihood

```
sample parameters (or models) from prior guesses
for (many reps) {
    sample parameters (or models) from prior
    simulate dataset using these parameters
    if ( topology(dataset) == topology(observed) ) {
        count as match, save these parameters
    }
}

plot(saved parameters) #or other way to summarize
```



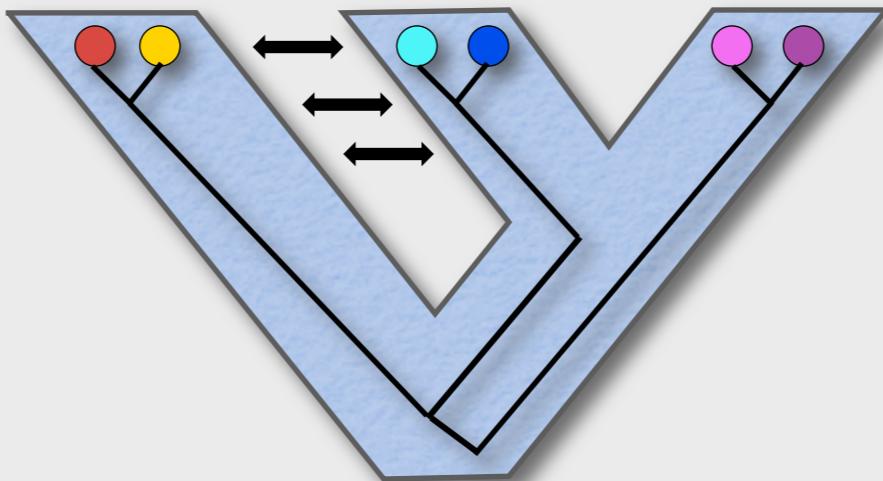
## Approximate Likelihood

```

sample parameters (or models) from prior guesses
for (many reps) {
    sample parameters (or models) from prior
    simulate dataset using these parameters
    if ( topology(dataset) == topology(observed) ) {
        count as match, save these parameters
    }
}

```

$\text{Likelihood} \equiv \text{prob}(\text{topology}(\text{observed}) \mid \text{parameters})$



## Approximate Likelihood

```

sample parameters (or models) from prior guesses
for (many reps) {
    sample parameters (or models) from prior
    simulate dataset using these parameters
    if ( topology(dataset) == topology(observed) ) {
        count as match, save these parameters
    }
}

```

$\text{Likelihood} = \text{prob}(\text{topology}(\text{observed}) \mid \text{parameters}) \approx \#\text{matches} / \#\text{reps}$

## **Approximate Bayesian Computation**

Summary stats as functions of the data

Simulation

Approximate match

Priors

Integration

## **Approximate Likelihood**

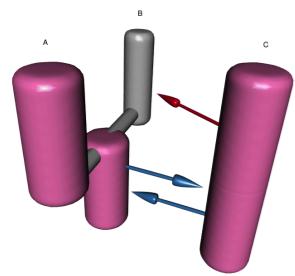
Topologies (= the data)

Simulation

Exact match

Starting values, but optimize

Maximum

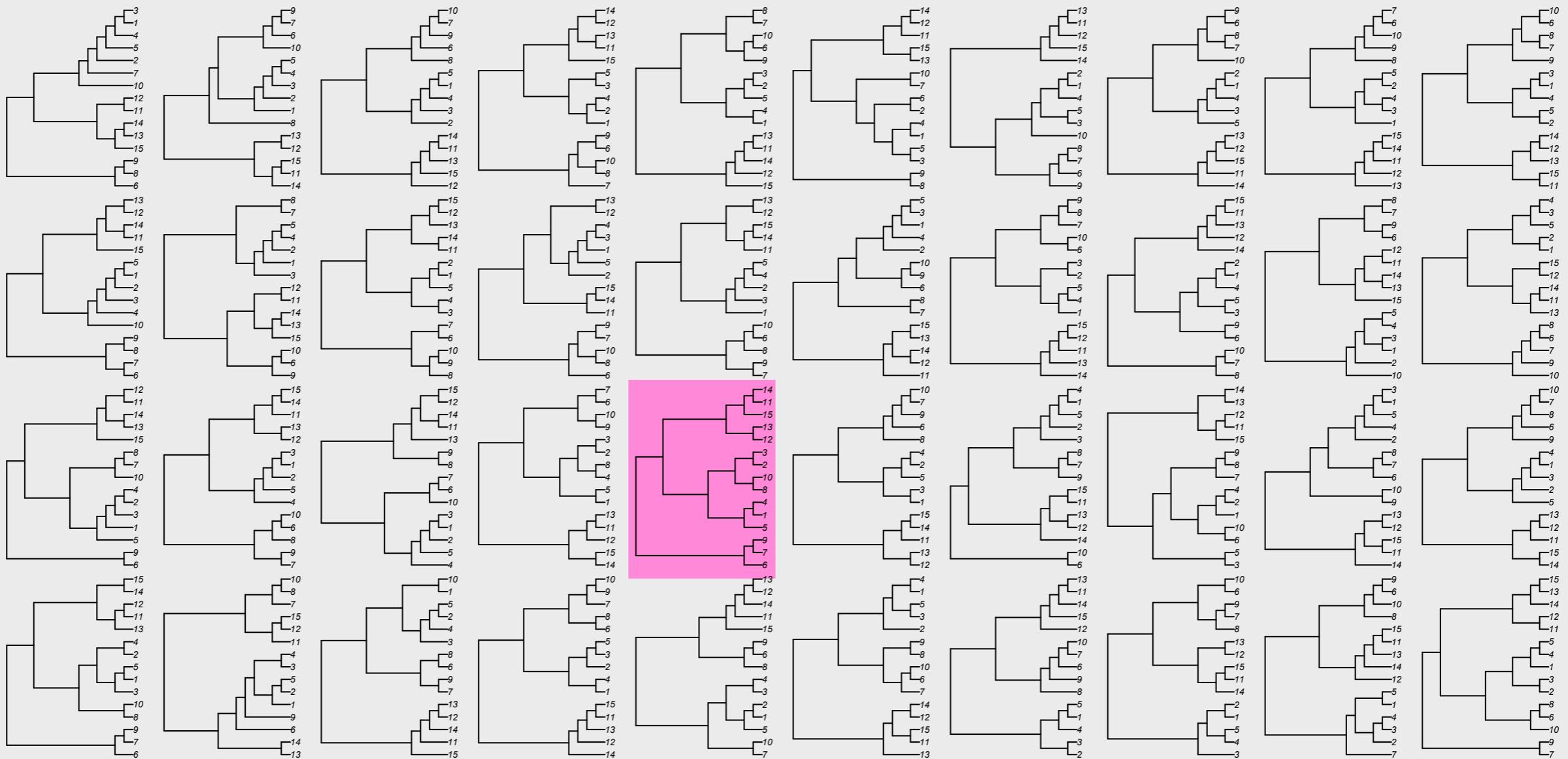


Collapse 1	Pop size 1	Pop size 2	Migration 1	Migration 2
4	1	3	0.2	0.6

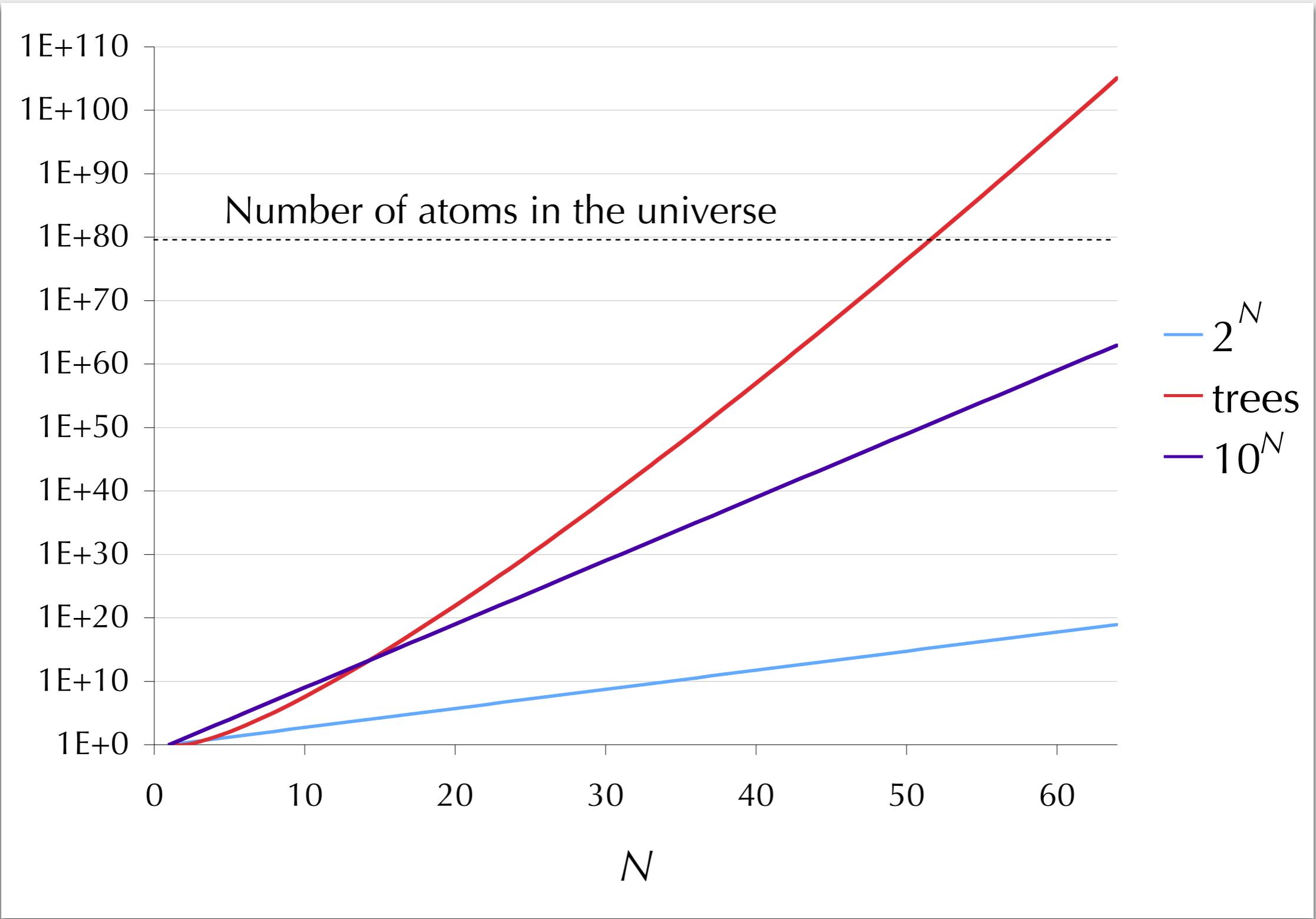
Generate 100,000 trees, three populations, five samples per population (~5 sec):

```
ms 15 100000 -T -I 3 5 5 5 -n 1 1.0 -n 2 3.0 -n 3 3.0 -ma x 0.0 0.0 0.2 x 0.0 0.0 0.0 x
      -ej 4.0 3 1 -en 4.0 1 3.0 -en 4.0 2 3.0 -em 4.0 1 2 0.6 -em 4.0 2 1 0.6
```

ms (Hudson 2002)

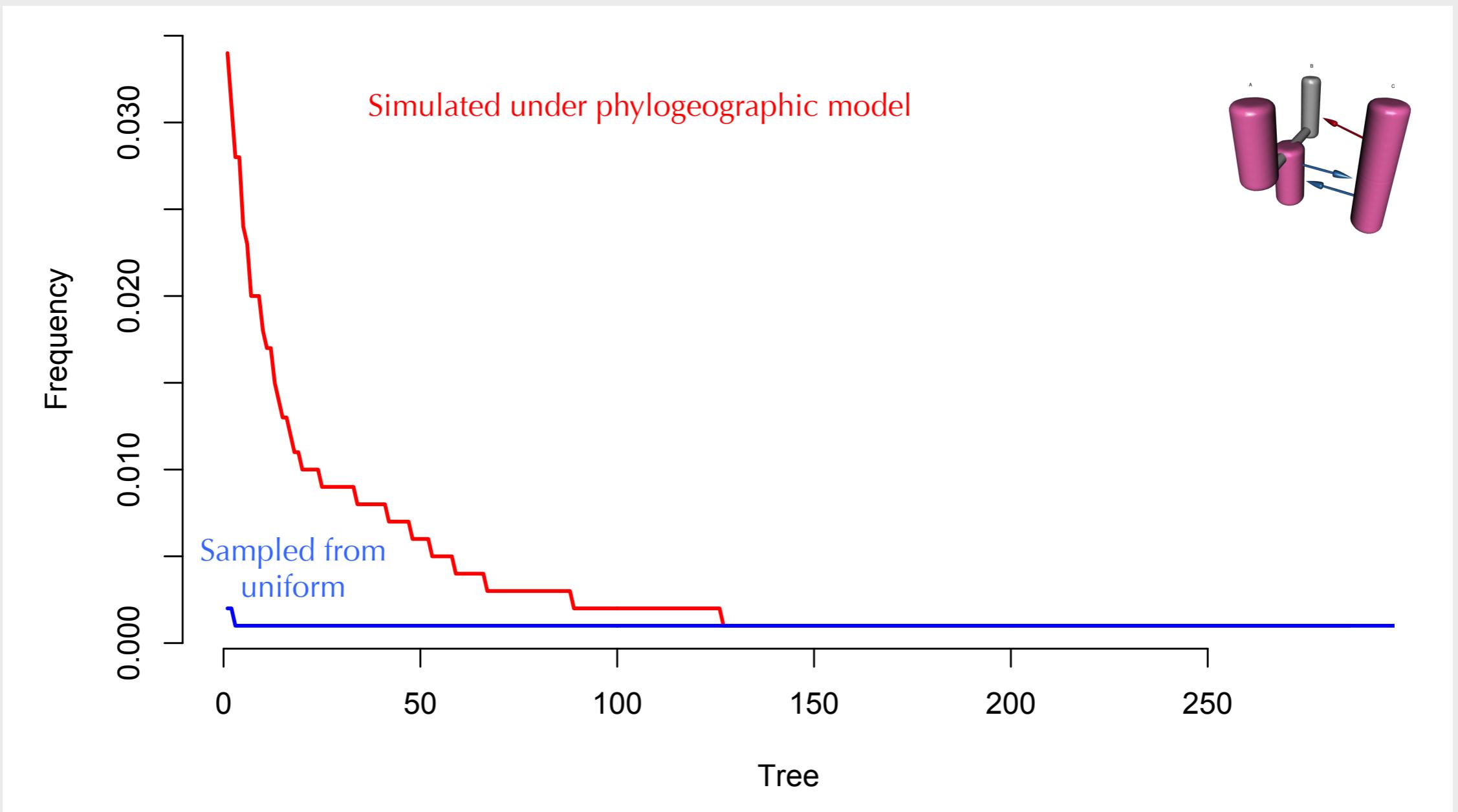


# A dumb idea?



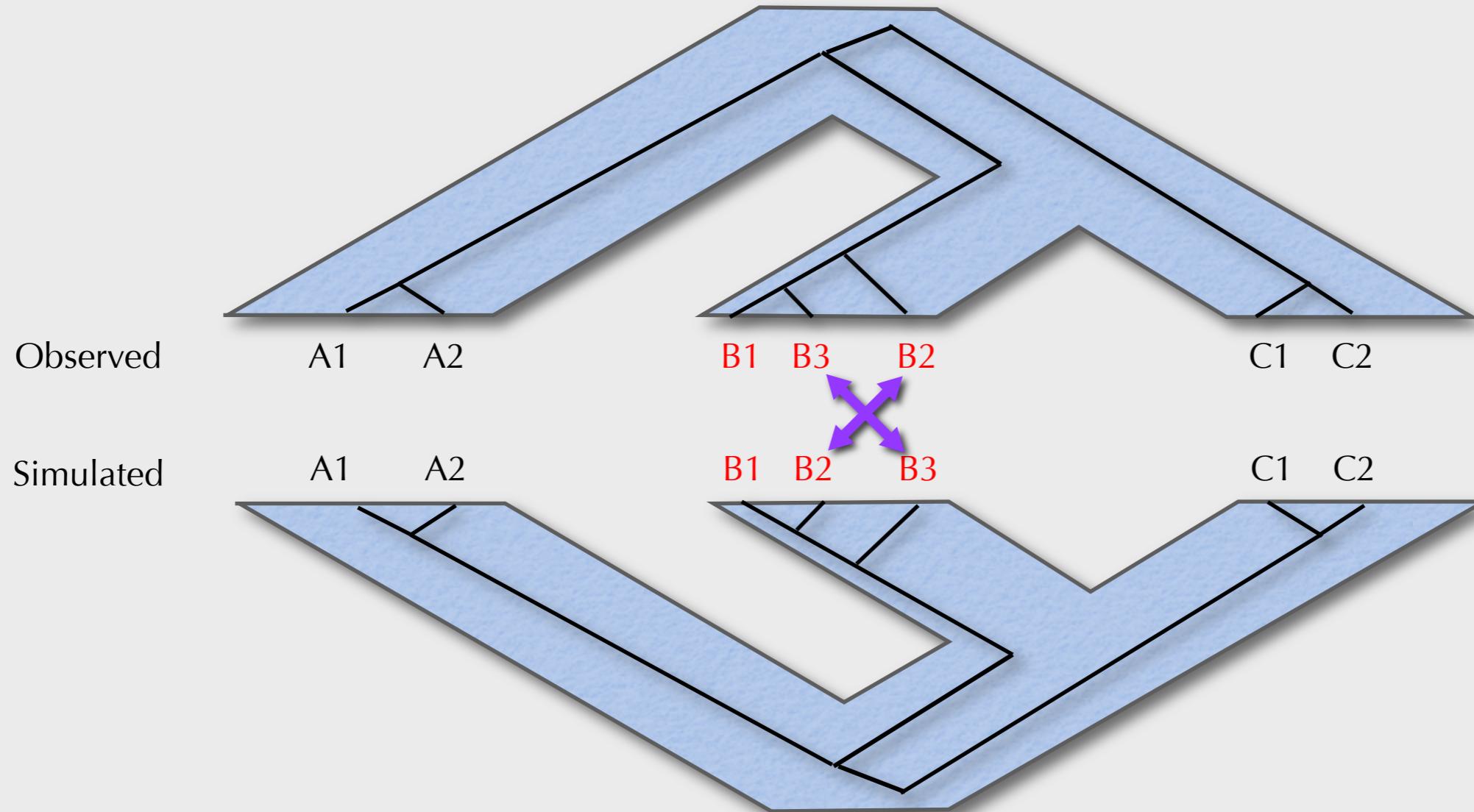
# A dumb idea?

Tree probabilities not uniform (some trees *much* more likely than others)



# A dumb idea?

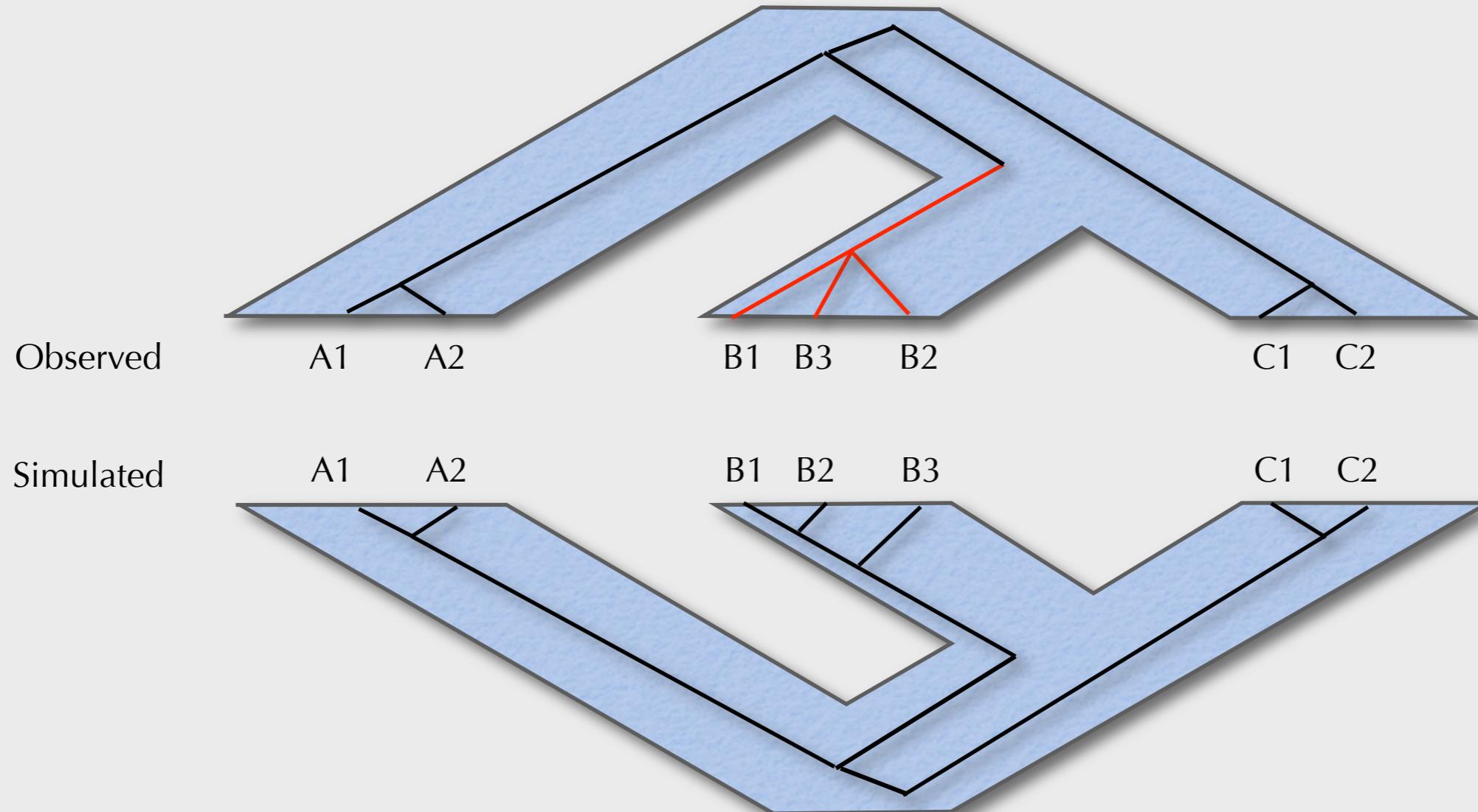
## Clever idea 1: Sample labels within populations arbitrary



Match based on all possible labeling, then correct for this  
i.e., three possible permutations, so if there is a match divide by 3 to get probability

# A dumb idea?

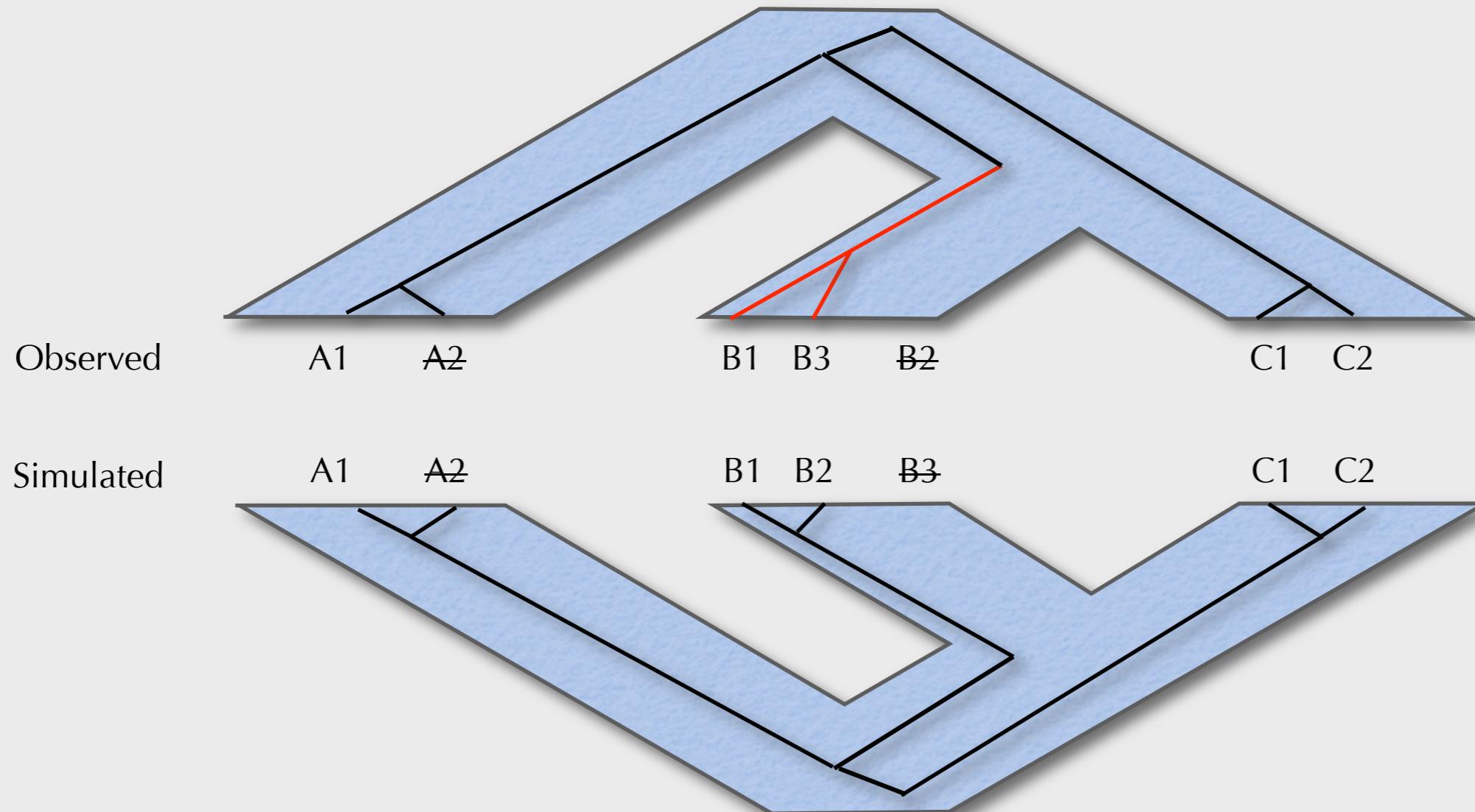
## Clever idea 2: Polytomies are soft in gene trees (optional)



Match based on all possible resolutions, then correct for this

# A dumb idea?

## Clever idea 3: Subsample



Reduce the gene tree size (speed gain, precision loss)

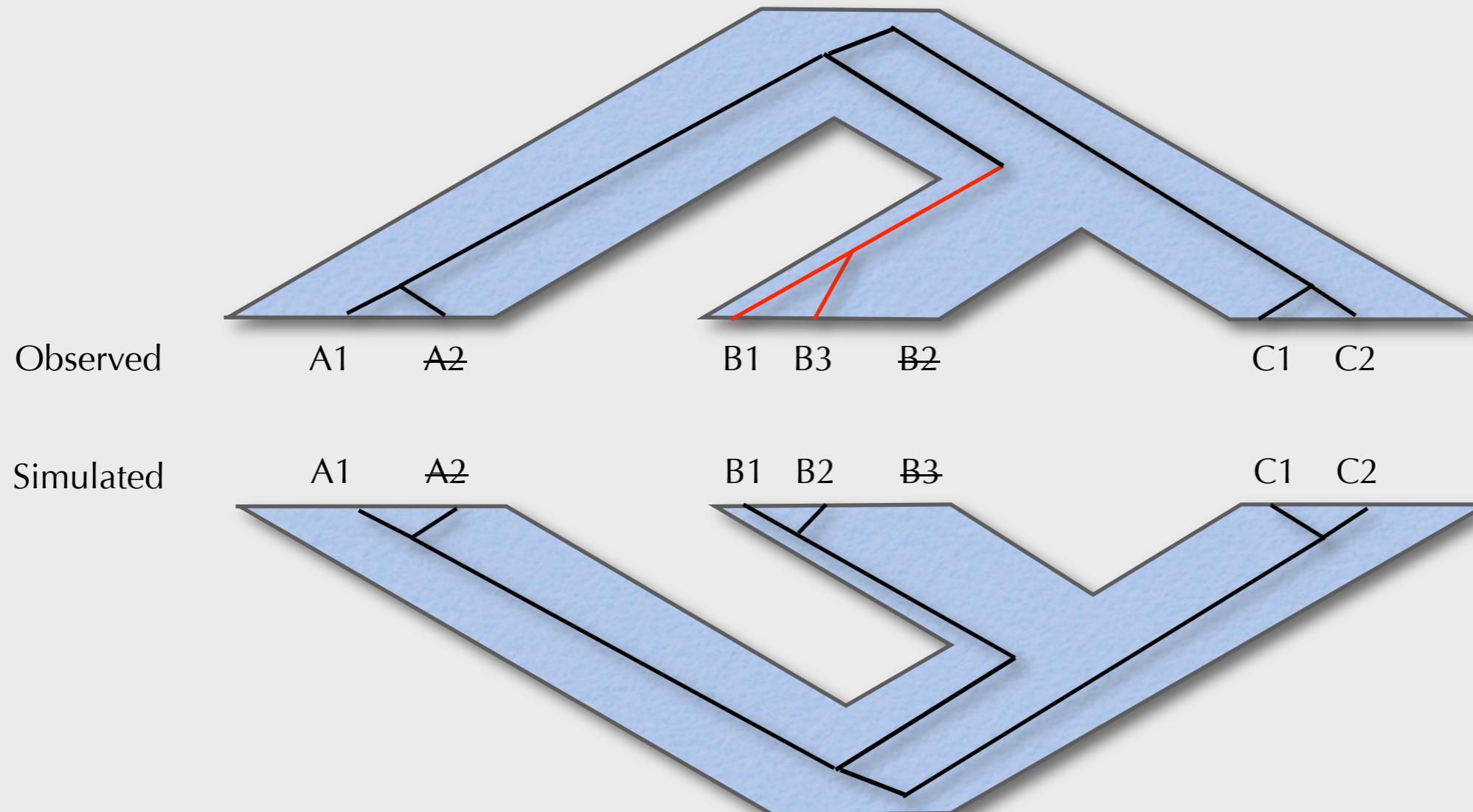
A dumb idea?

Clever idea 4: Do many empirical loci, some are the same

The run time should increase linearly or better with number of gene trees.

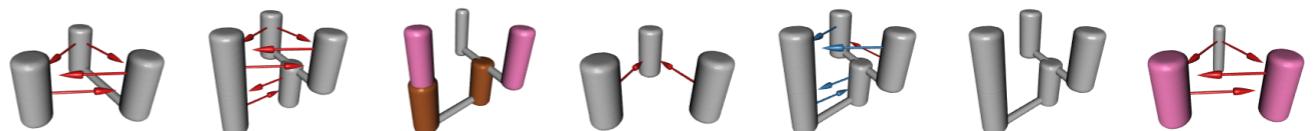
# A dumb idea?

## Clever idea 5: Your suggestion.....

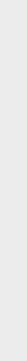


Grows (quickly) with  
number of populations

Generate all possible models



Filter

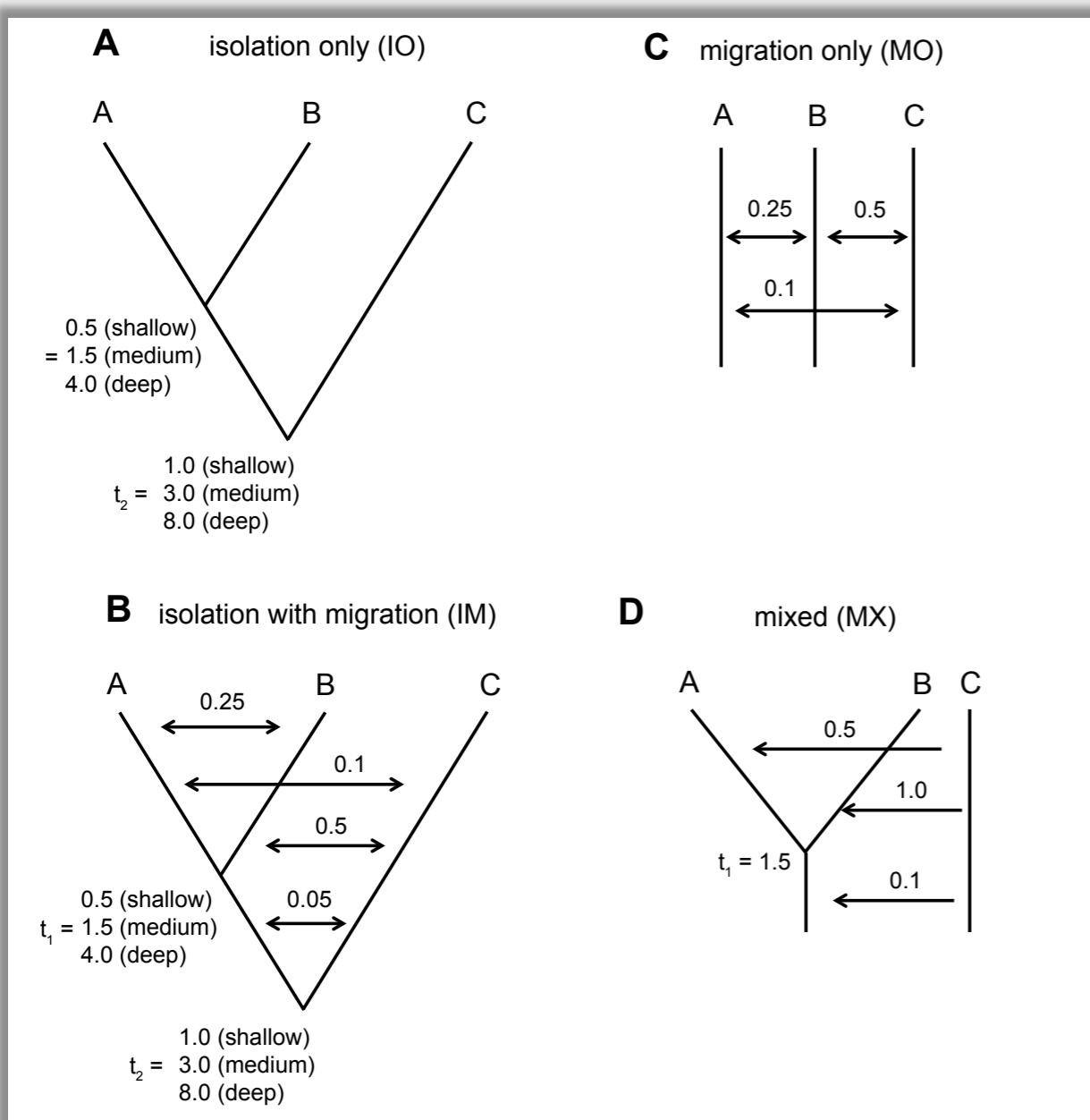


Analyze



Grows quickly with  
number of samples per  
population, but only  
linearly with number  
of genes

# True model



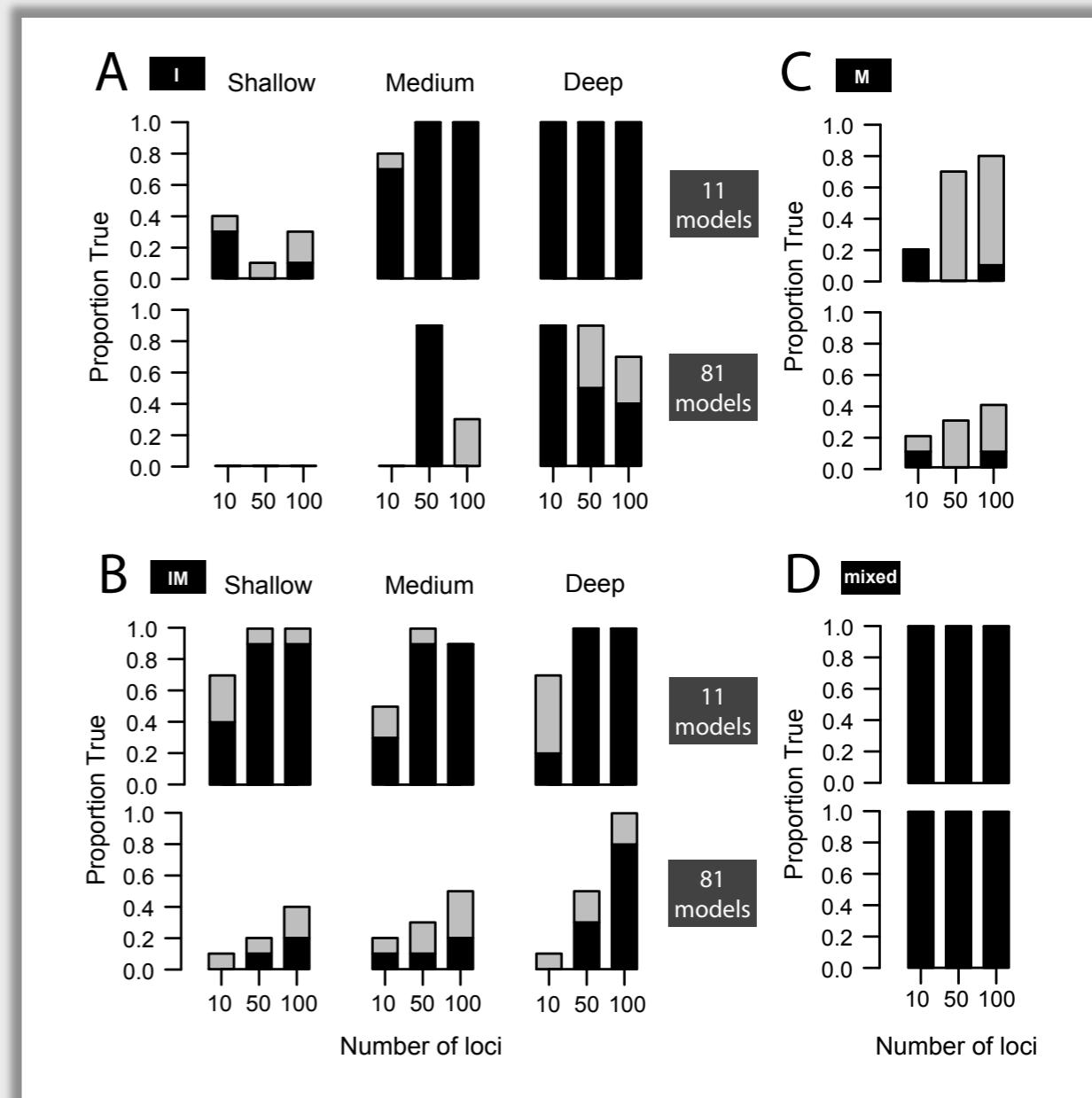
Simulate DNA

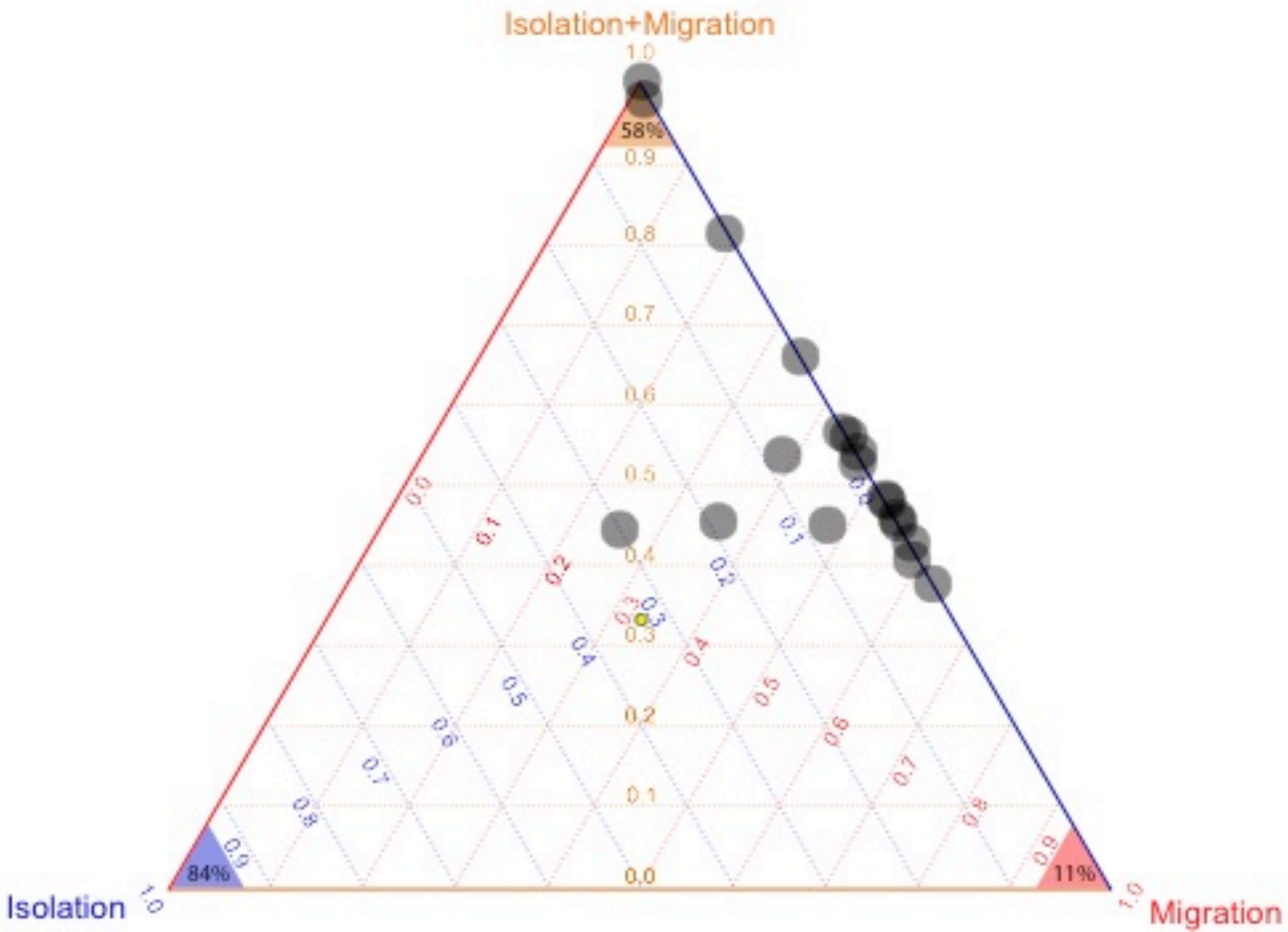
Simulate gene trees

Infer gene trees

Run PHRAPL

# Inferred model





# Summary

- Way to create many models
- Evaluate many models
- Prior free, but complementary with other approaches
- Should scale better than linearly with gene number (due to multiple identical histories)

# Conclusion

- Addressed questions about how species move through landscapes, what limits rates of evolution, predictability of evolution, competition between organisms, and more
- Creation of methods and open software to deal with rate heterogeneity for discrete characters, more flexible ways of dealing with continuous characters, simulating millions of species, examining correlations, and much more
- Taught hundreds of students to think critically and to understand science as a process
- Mentored 4 students and 10 postdocs
- 28 grant proposals (including 16 full and 5 preproposals to NSF), \$1.4M in external funds
- Service in improving representation of women in science, Darwin Day outreach, numerous workshops, hackathons, and conferences

End



akaike weight



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Akaike weights are can be used in model averaging. They represent the relative likelihood of a model. To calculate them, for each model first calculate the relative likelihood of the model, which is just  $\exp(-0.5 * \Delta AIC)$  score for that model).

[Model Selection Using the Akaike Information Criterion \(AIC ...](#)  
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Akaike weights are can be used in model averaging. They represent the relative likelihood of a model. To calculate them, for each model first calculate the relative likelihood of the model, which is just  $\exp(-0.5 * \Delta AIC)$  score for that model).

[Akaike information criterion - Wikipedia, the free encyclopedia](#)

[en.wikipedia.org/wiki/Akaike\\_information\\_criterion](http://en.wikipedia.org/wiki/Akaike_information_criterion) ▾ Wikipedia ▾

The Akaike information criterion (AIC) is a measure of the relative quality of a ... (3 ) take a weighted average of the first two models, with weights 1 and 0.368, ...

[Bayesian information criterion - Hirotugu Akaike - Deviance information criterion](#)

[AICc Weight](#)

[warnercnr.colostate.edu/.../qaicc\\_weight.htm](http://warnercnr.colostate.edu/.../qaicc_weight.htm) ▾ Colorado State University ▾

The QAICc Weight (called an Akaike Weight by Burnham and Anderson 1998) of a model is  $\exp(-1/2 * \Delta QAICc)$  divided by the sum of this quantity for all ...

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## Elsevier agrees with criticism about the lack of gender diversity in a recent email campaign

We're sending an update and talking about programs and partnerships to support gender equality in the sciences

By Nicoline van der Linden | Posted on 14 February 2014

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This image was just used by Elsevier's Marketing Communications department in an email campaign to authors about our Communications Preference Center. It was accompanied by the caption "All 2013, 2012 and 2011 Nobel Prize winners published with Elsevier."

This email [campaign](#) has been highlighted on social media and blogs as an example of Elsevier perpetuating the negative stereotype that science is the province of white men.

That was certainly never our intention. With the wisdom of hindsight, we should have chosen a different image, or have included the several female winners prior to 2011 who have published with us. Unfortunately, we didn't.

Below we have highlighted what the image would have looked like if we had gone back to 2009. We agree it looks much better. And as an update to this campaign, we are sending this story through all of our journal-related [social media channels](#) so it will reach over 796,000 combined followers – more than 10 times as many people than the original email campaign.

We wanted to include even more women Nobel laureates, but we only have permission to use the ones in the photo. The original image does highlight a problem that concerns us all – the fact that science is not an even playing field – and we want that image to change.

In addition to updating this campaign, there are numerous other ways we are working with you to change this image.

Over the past seven years, the [Elsevier Foundation](#) has invested more than \$2 million in 35 grants to support programs that promote equality in science.



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## The Communications Guy Bet the Gender Equality Policy and Lost

Posted: 17/02/2014 12:01 GMT | Updated: 16/04/2014 10:59 BST

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My part of the Twitterverse is hopping this morning. First, the publisher Elsevier sent out a letter with a picture of a bunch of scientists, all of whom are white men. Pictures like that reinforce the stereotypes that keep young women away from science.

But as if that wasn't enough, a spokesman from Elsevier went onto Twitter and made a cringeworthy mess of it all. Communications consultants: Take note!

The short version of the story goes like this: Brian O'Meara (@omearabrian) received a letter from Elsevier, took a picture of it, and posted the following tweet.

ELSEVIER

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Let Elsevier help you complete the picture of reputable research in Life Sciences.



Brian O'Meara  
[@omearabrian](https://twitter.com/omearabrian)



Dear Elsevier: I think the missing piece from your ad includes women and minorities as reputable researchers

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