

# Phylogenetics

## Morphological Models & Model Adequacy

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June 09, 2022

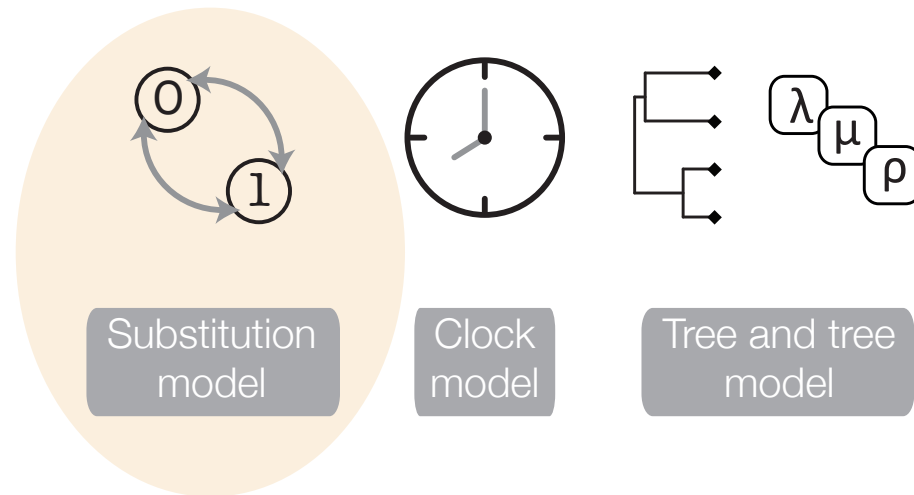
# Today's Objectives

Morphological substitution models used in Palaeobiology

How to choose what model to use

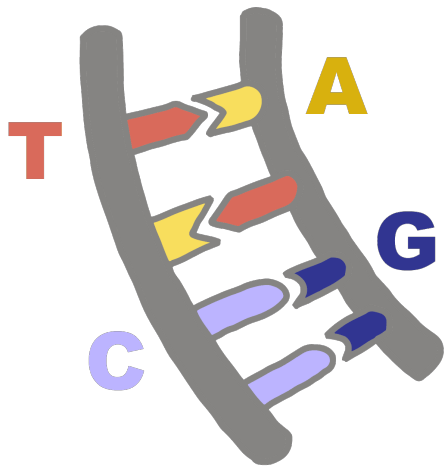
Exercise using model adequacy

# Phylogenetic Models



# Substitution models in Palaeobiology

- **Mk**: makes the same assumptions as the JC model. i.e. all transition probabilities are equal
- Only one model really used as morphological data is harder to generalise



Merychippus\_primus\_ORIG\_M\_primus

00001100000010010001001001021122000?001?0000011000100000

Merychippus\_sejunctus\_ORIG\_M\_nr\_sejunctus

000112000011301200010000020202211100002???00012001100000

Merychippus\_coloradense\_ORIG\_M\_coloradense

00?00200?10371?21003210020141130110?102???00212001121011

# Variations on the Mk model

- Discrete Gamma Model
- Variable Coding
- Multistate

# Variations on the Mk model

- Discrete Gamma Model : allows for rate variation across sites

# Variable Coding



|            | Lungs | jaws | Feathers | Gizzards | Fur |
|------------|-------|------|----------|----------|-----|
| Lamprey    | 0     | 0    | 0        | 0        | 0   |
| Sea bass   | 0     | 1    | 0        | 0        | 0   |
| Antelope   | 1     | 1    | 0        | 0        | 1   |
| Bald eagle | 1     | 1    | 1        | 1        | 0   |
| Alligator  | 1     | 1    | 0        | 1        | 0   |

- Causes ascertainment bias. Suggests that there is evolutionary distance between taxa than there is.
- Produces longer branches

# Compared to molecular data

|                                |     |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |
|--------------------------------|-----|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| <i>Bufo regularis</i>          | [ 1 | G | G | A | T | T | A | C | G | A | G | C | A | A | G | C | T | T | A | A | A | A | C | C | C | A | A | A | G | G | A | C | T | T | G | A | C | G | G | T | A | C | C | C | C | C | T | C | T | A | G | A | G | G | A | G | C | C | T | G | T | T | C | T | A | T | A | A | T | C | G | A | T | A | A | T | C | C |   |   |
| <i>Hyla cinerea</i>            | [ 1 | G | G | A | C | T | A | C | G | A | G | C | A | A | G | C | T | T | A | A | A | A | C | C | C | A | A | A | G | G | A | C | T | T | G | A | C | G | G | T | A | C | C | C | C | A | C | C | T | A | G | A | G | G | A | G | C | C | T | G | T | C | C | T | G | T | A | A | T | C | G | A | T | A | A | T | C | C |   |   |
| <i>Hyla versicolor</i>         | [ 1 | G | G | A | C | T | A | C | G | A | G | C | A | A | G | C | T | T | A | A | A | A | C | C | C | A | A | A | G | G | A | C | T | T | G | A | C | G | G | T | A | C | C | C | C | A | C | C | T | A | G | A | G | G | A | G | C | C | T | G | T | C | C | T | A | T | A | A | T | C | G | A | T | A | A | T | C | C |   |   |
| <i>Hyperolius viridiflavus</i> | [ 1 | A | A | A | C | T | A | C | A | A | G | C | G | A | G | C | T | T | A | A | A | A | C | T | T | A | A | A | G | G | A | C | T | T | G | A | C | G | G | T | G | C | C | C | C | T | A | C | C | T | A | G | A | G | G | A | G | C | C | T | G | T | T | C | T | A | T | A | A | T | C | G | A | T | A | A | T | C | C |   |
| <i>Leptodactylus mystaceus</i> | [ 1 | G | G | A | C | T | A | C | G | A | G | C | T | A | G | C | T | T | A | A | A | A | C | C | C | A | A | A | G | G | A | C | T | T | G | A | C | G | G | T | A | C | C | C | C | C | C | T | A | G | A | G | G | A | G | C | C | T | G | T | C | C | T | A | T | A | A | T | C | G | A | T | A | A | T | C | C |   |   |   |
| <i>Litoria gracilentia</i>     | [ 1 | G | G | A | C | T | A | C | G | A | G | C | A | A | G | C | T | T | A | A | A | A | C | C | C | A | A | A | G | G | A | C | T | T | G | A | C | G | G | T | A | C | C | C | C | A | C | C | T | A | G | A | G | G | A | G | C | C | T | G | T | C | C | T | A | T | A | A | T | C | G | A | T | A | A | T | C | C |   |   |
| <i>Phrynohyas venulosa</i>     | [ 1 | G | G | A | C | T | A | C | G | A | G | C | A | A | G | C | T | T | A | A | A | A | C | C | C | A | A | A | G | G | A | C | T | T | G | A | C | G | G | T | A | C | C | C | C | A | C | C | T | A | G | A | G | G | A | G | C | C | T | G | T | C | C | T | G | T | A | A | T | C | G | A | T | A | A | T | C | C |   |   |
| <i>Physalaemus cuvieri</i>     | [ 1 | G | G | A | C | T | A | C | G | A | G | C | A | A | G | C | T | T | A | A | A | A | C | C | C | A | A | A | G | G | A | C | T | T | G | A | C | G | G | T | A | C | C | C | C | A | C | C | T | A | G | A | G | G | A | G | C | C | T | G | T | C | C | T | A | T | A | A | T | C | G | A | T | A | A | T | C | C |   |   |
| <i>Ptychadena anchietae</i>    | [ 1 | G | G | A | T | T | A | C | G | A | G | C | A | A | G | C | T | T | A | A | A | A | T | C | C | A | A | A | G | G | A | C | T | T | G | A | C | G | G | T | G | T | C | C | C | C | A | T | C | T | A | G | A | G | G | A | G | C | C | T | G | C | C | T | A | T | A | A | T | C | G | A | T | T | A | T | C | C |   |   |
| <i>Rana rugosa</i>             | [ 1 | G | G | A | C | T | A | C | A | A | G | C | A | C | G | C | T | T | A | A | A | A | C | C | C | A | A | A | G | G | A | T | T | T | G | A | C | G | G | T | G | T | C | C | C | C | A | C | C | T | A | G | A | G | G | A | G | C | C | T | G | T | T | C | T | G | T | A | A | T | C | G | A | T | A | A | T | C | C |   |
| <i>Rana temporaria</i>         | [ 1 | G | G | A | T | T | A | C | G | A | G | C | A | T | G | C | T | T | A | A | A | A | C | C | C | A | A | A | G | G | A | T | T | T | G | A | C | G | G | T | G | T | C | C | C | C | A | C | T | A | G | A | G | G | A | G | C | C | T | G | T | T | C | T | A | T | A | A | T | C | G | A | T | G | A | T | C | C |   |   |
| <i>Rhacophorus arboreus</i>    | [ 1 | G | G | A | C | T | A | C | G | A | G | C | C | A | G | C | T | T | A | A | A | A | C | C | C | A | A | A | G | G | A | C | T | T | G | A | C | G | G | T | G | A | T | C | C | C | C | A | A | C | T | A | G | A | G | G | A | G | C | C | T | G | T | T | C | T | A | T | A | A | T | C | G | A | T | G | A | T | C | C |
| <i>Rhacophorus maximus</i>     | [ 1 | G | G | A | C | T | A | C | G | A | G | C | C | A | G | C | T | T | A | A | A | A | C | C | C | A | A | A | G | G | A | C | T | T | G | A | C | G | G | T | G | A | T | C | C | C | C | G | A | C | T | A | G | A | G | G | A | G | C | C | T | G | T | T | C | T | A | T | A | A | T | C | G | A | T | G | A | T | C | C |
| <i>Rhacophorus omeimontis</i>  | [ 1 | G | G | A | C | T | A | C | G | A | G | C | C | A | G | C | T | T | A | A | A | A | C | C | C | A | A | A | G | G | A | C | T | T | G | A | C | G | G | T | A | C | C | C | C | C | C | T | A | G | A | G | G | A | G | C | C | T | G | T | T | C | T | T | A | A | T | C | G | A | T | A | A | T | C | C |   |   |   |   |
| <i>Schismaderma carens</i>     | [ 1 | G | G | A | C | T | A | C | G | A | G | C | C | A | G | C | T | T | A | A | A | A | C | C | C | A | A | A | G | G | A | C | T | T | G | A | C | G | G | T | A | C | C | C | C | C | C | T | A | G | A | G | G | A | G | C | C | T | G | T | T | C | T | T | A | A | T | C | G | A | T | A | A | T | C | C |   |   |   |   |
| <i>Smilisca baudinii</i>       | [ 1 | G | G | A | C | T | A | C | G | A | G | C | A | A | G | C | T | T | A | A | A | A | C | C | C | A | A | A | G | G | A | C | T | T | G | A | C | G | G | T | A | C | C | C | C | A | C | C | T | A | G | A | G | G | A | G | C | C | T | G | T | C | C | T | G | T | A | A | T | C | G | A | T | A | A | T | C | C |   |   |
| <i>Strongylopus fasciatus</i>  | [ 1 | G | G | A | T | T | A | C | G | A | G | C | T | A | G | C | T | T | A | A | A | A | C | T | C | A | A | A | G | G | A | C | T | T | G | A | C | G | G | T | G | T | C | C | C | C | A | C | C | T | A | G | A | G | G | A | G | C | C | T | G | T | T | C | T | A | T | A | A | T | C | G | A | C | T | C | T | C | C |   |

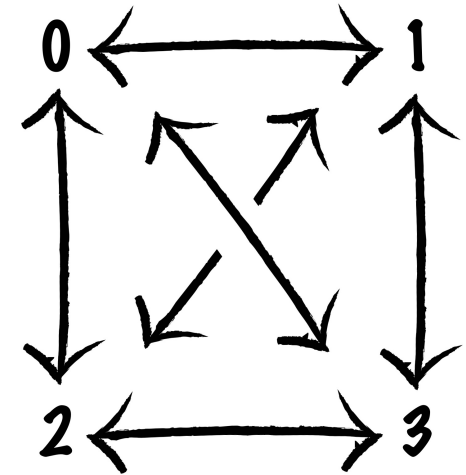
Sequence the whole gene. Not every character will be informative



# Multistate

- Create different Q matrices for characters traits with different number of states.

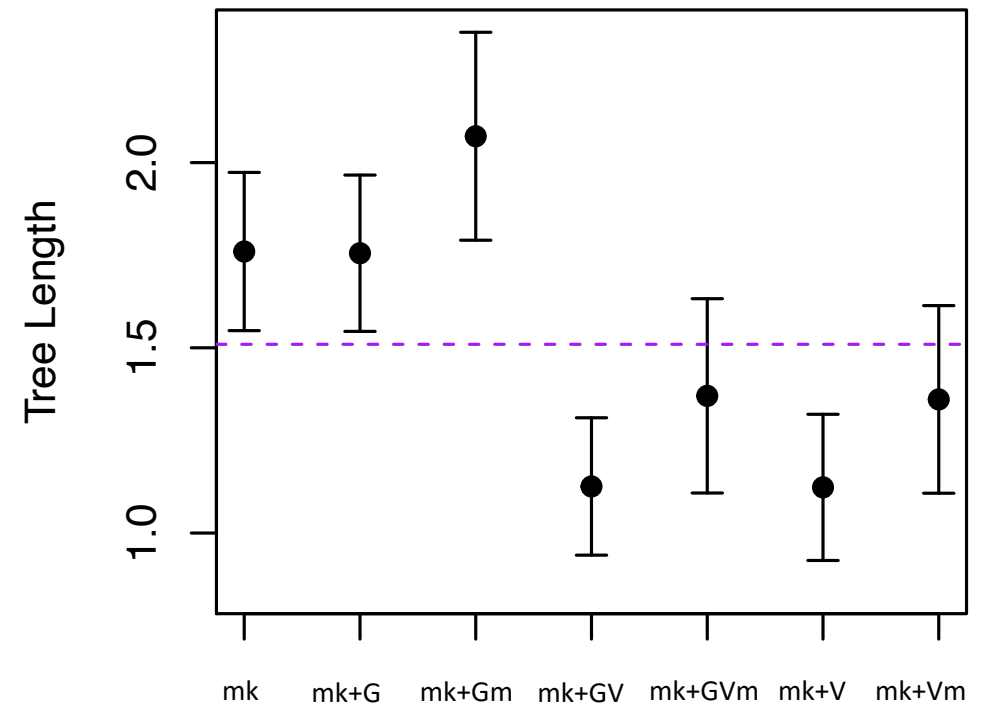
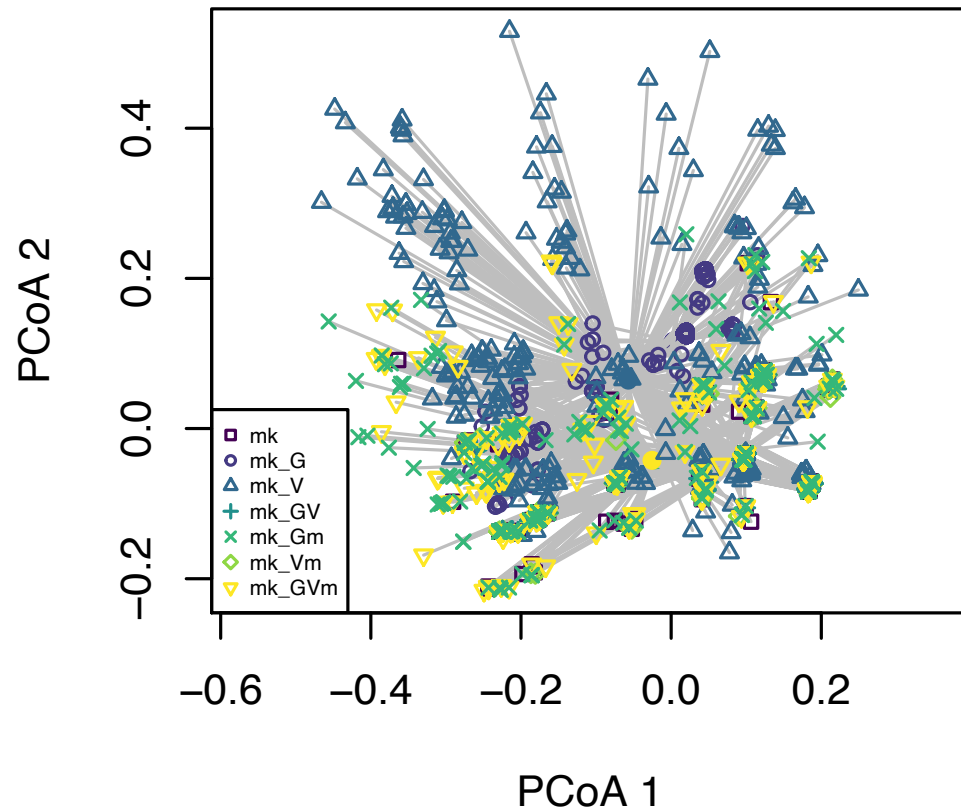
|        | A | B | C |
|--------|---|---|---|
| taxa 1 | 0 | 0 | 1 |
| taxa 2 | 1 | 1 | 1 |
| taxa 3 | 0 | 2 | 0 |



# Variations on the Mk model

- Discrete Gamma Model
- Variable Coding
- Multistate

# Effects different models have on the inference



(Mulvey et al in prep.)

# How to choose a model

$$P(\text{parameters} \mid \text{data}, \text{model}) =$$

Posterior

Likelihood

Priors

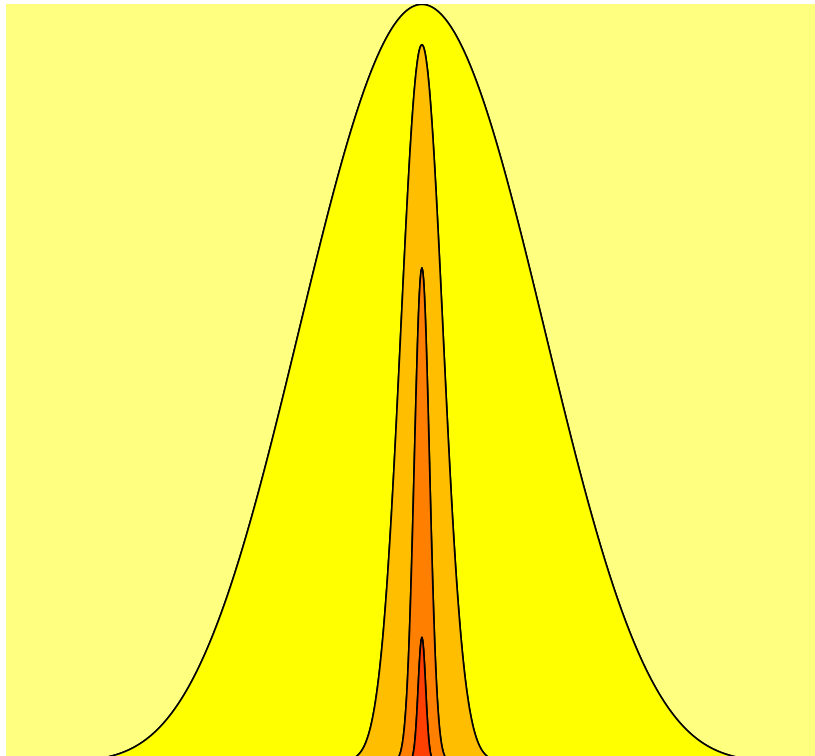
$$P(\text{data} \mid \text{parameters}, \text{model}) P(\text{parameters} \mid \text{model})$$

---

$$P(\text{data} \mid \text{model})$$

Marginal  
probability

# Model selection: Stepping Stone



- Estimates the marginal likelihood by estimating the area under nested curves. Using smaller and smaller curves until you get down to the size of the marginal likelihood curve
- Simulated data sets show this approach seems to always choose the most complex model

# Model selection vs. Model adequacy

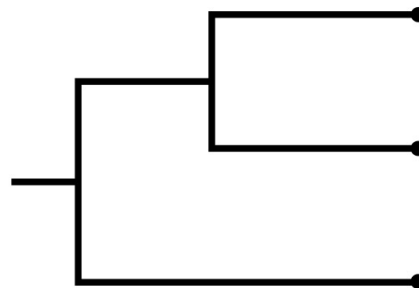
Take a bunch of  
different models and  
test which is the *best*

Gives the **relative** fit

0102  
0110  
2001



?

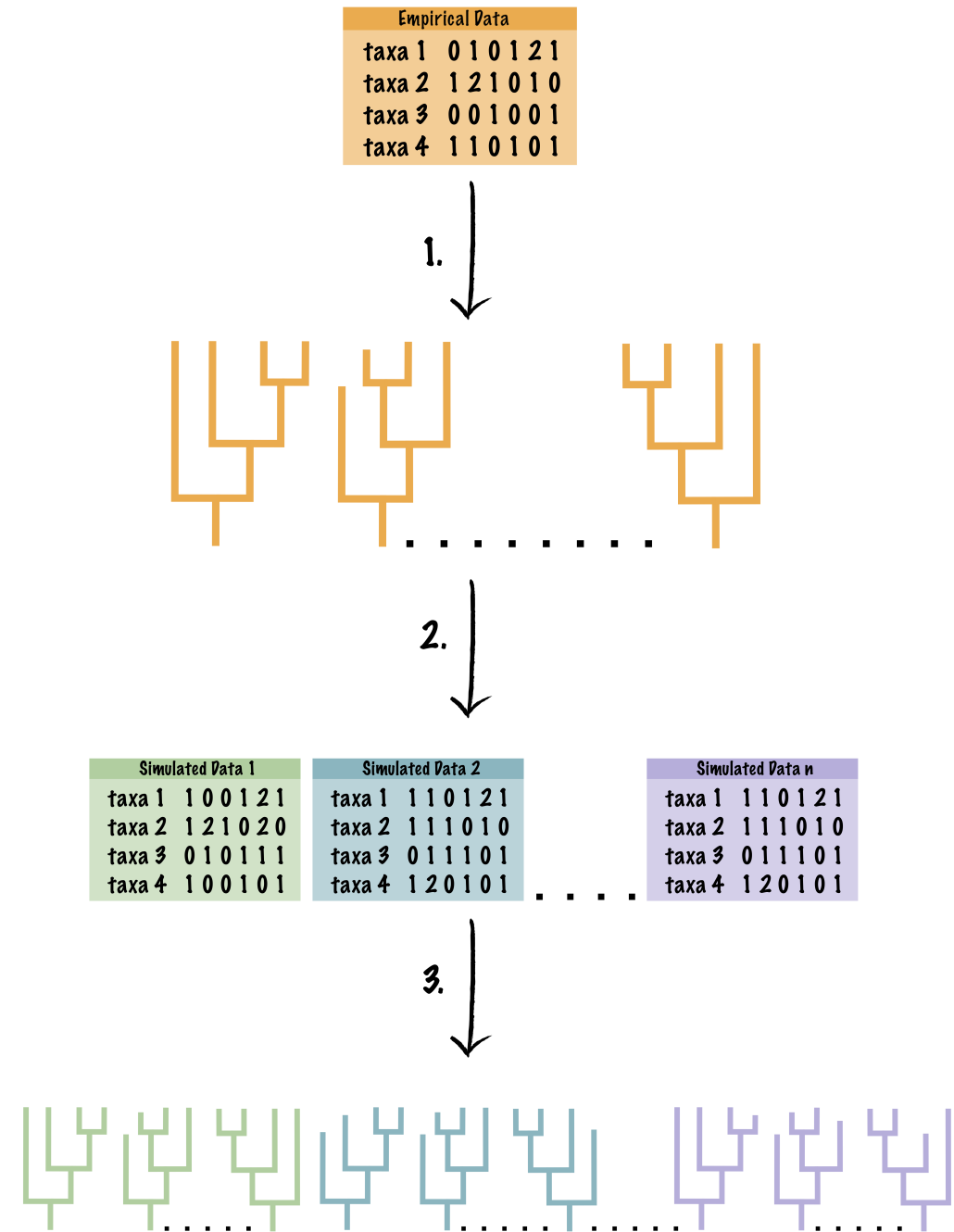


Assess whether a  
model is capturing the  
evolutionary dynamics  
that generated the  
data

Gives the **absolute** fit

# Model Adequacy

1. Carry out inference under the chosen model, while sampling parameters from the posterior
2. Simulate new data sets using the parameters from step 1
3. Carry out the same inference as in step 1 using the new simulated data sets



(Mulvey et al in prep.)

# How can you compare different models using model adequacy?

## 1. Inference based

**Tree length** : Sum of all the branches

**Robinson Foulds**: the distance between phylogenetic trees

## 2. Mixed Inference

**Consistency Index** : measure of how well an individual character fits on a phylogenetic tree

**Retention Index** : measure of how well an individual character fits on a phylogenetic tree



# Exercise 7