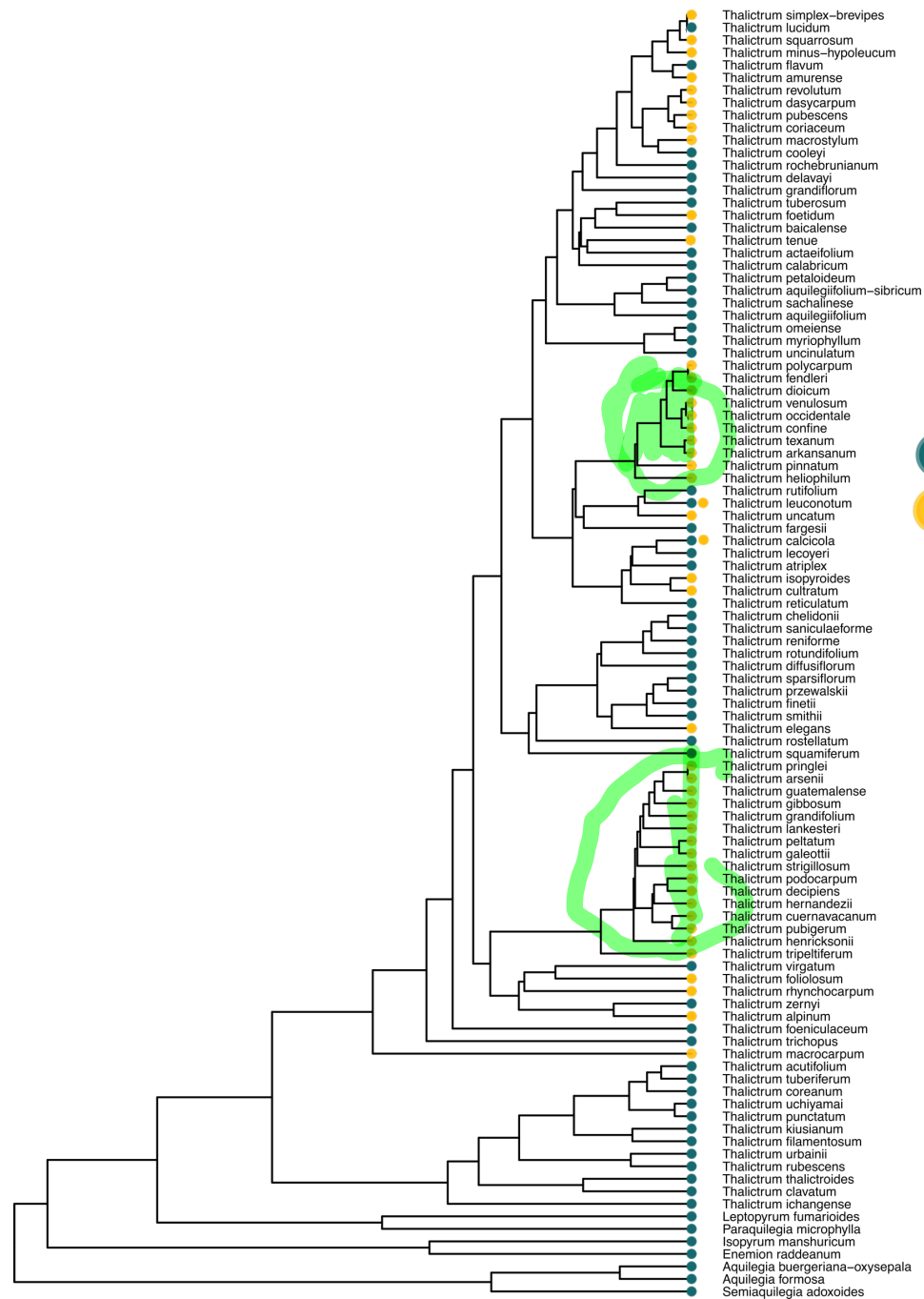


# Discrete trait models

Comparing models and correlating traits



● Insect  
● Wind

- Always plot your data!
- Check for nestedness of trait!
- Transitions are the effective sample size for these analyses

# Continuous-Time Markov Chains (CTMC)

$$\{X(t), t \geq 0\}$$

Stochastic models that follow change in time with an associated **probability**

$X(t)$  = phenotype (trait) value at time  $t$

$t$  = millions of years or expected number of substitutions

# Discrete models of evolution

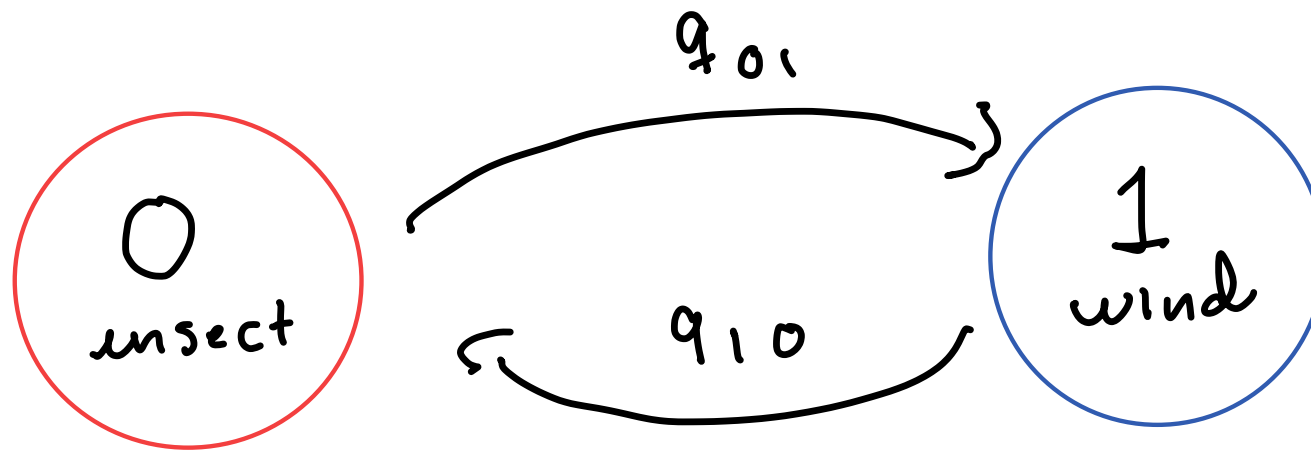
$X(t)$  = phenotype (trait) value at time  $t$

$X(t)$  = Insect (0), Wind (1)

We use conditional probabilities. For example:

$$P(X(t) = 1 | X(0) = 0)$$

# Drawing the FULL model



$$Q = \begin{matrix} & \begin{matrix} \text{from} \\ \downarrow \\ 0 \\ 1 \end{matrix} & \begin{matrix} \text{to} \rightarrow \\ 0 & 1 \end{matrix} \\ \begin{pmatrix} -q_{01} & q_{01} \\ q_{10} & -q_{10} \end{pmatrix} \end{matrix}$$

full-model

$$\begin{pmatrix} 0 & 1 \\ 2 & 0 \end{pmatrix}$$

$f, M \in \mathbb{R}$   
model

$q_{01}$  is parameter 1

$q_{10}$  is parameter 2

Estimation : Full model

$$q_{01}^{\text{MLE}} = 0.05$$

Change per lineage per 1 my  
(Events)

$$E / L / 1 \text{ my}$$

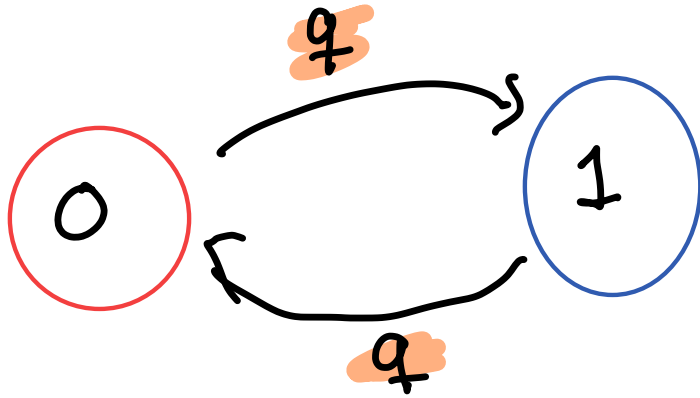
$$q_{10}^{\text{MLE}} = 0.13$$

Estimates MLE = Maximum Likelihood Estimate

$$\log \text{Like} : -47.78$$

logarithm  
(natural) of the likelihood

# Drawing a Reduced model



$$Q = \begin{pmatrix} -q & q \\ q & -q \end{pmatrix}$$

Null hypothesis  
there is no  
difference between  
rates  
(a.k.a rates are equal)

$$q = q_{01} = q_{10}$$

reduced-model

$$\begin{pmatrix} 0 & 1 \\ 1 & 0 \end{pmatrix}$$


$$q^{\text{MLE}} = 0.05 \quad \text{E/L/My}$$

$$\log \text{like} = -49.08$$



# Comparing nested models

- Likelihood Ratio Test

- Null hypothesis:  $H_0: q_{01} = q_{10}$   Reject  
of  
Fail to reject

- Test statistic:  $LRT = -2 \times \log\left(\frac{\text{Likelihood (Reduced model)}}{\text{Likelihood (Full model)}}\right)$

- $LTR \sim \chi^2$  with degrees of freedom  $k = \text{\#parameters full model} - \text{\#parameters reduced model}$

$$LRT = -2 \log \left( \frac{\text{likelihood (Reduced model)}}{\text{likelihood (Full model)}} \right)$$

$$\log \left( \frac{a}{b} \right) = \log(a) - \log(b)$$

$$LRT = -2 \left( \log \text{lik (Reduced)} - \log \text{lik (Full)} \right)$$

$$= -2 \left( -49.00 - (-47.7) \right)$$

$$= -2 \left( -1.30 \right)$$

$$\boxed{LRT = 2.78}$$

test statistic

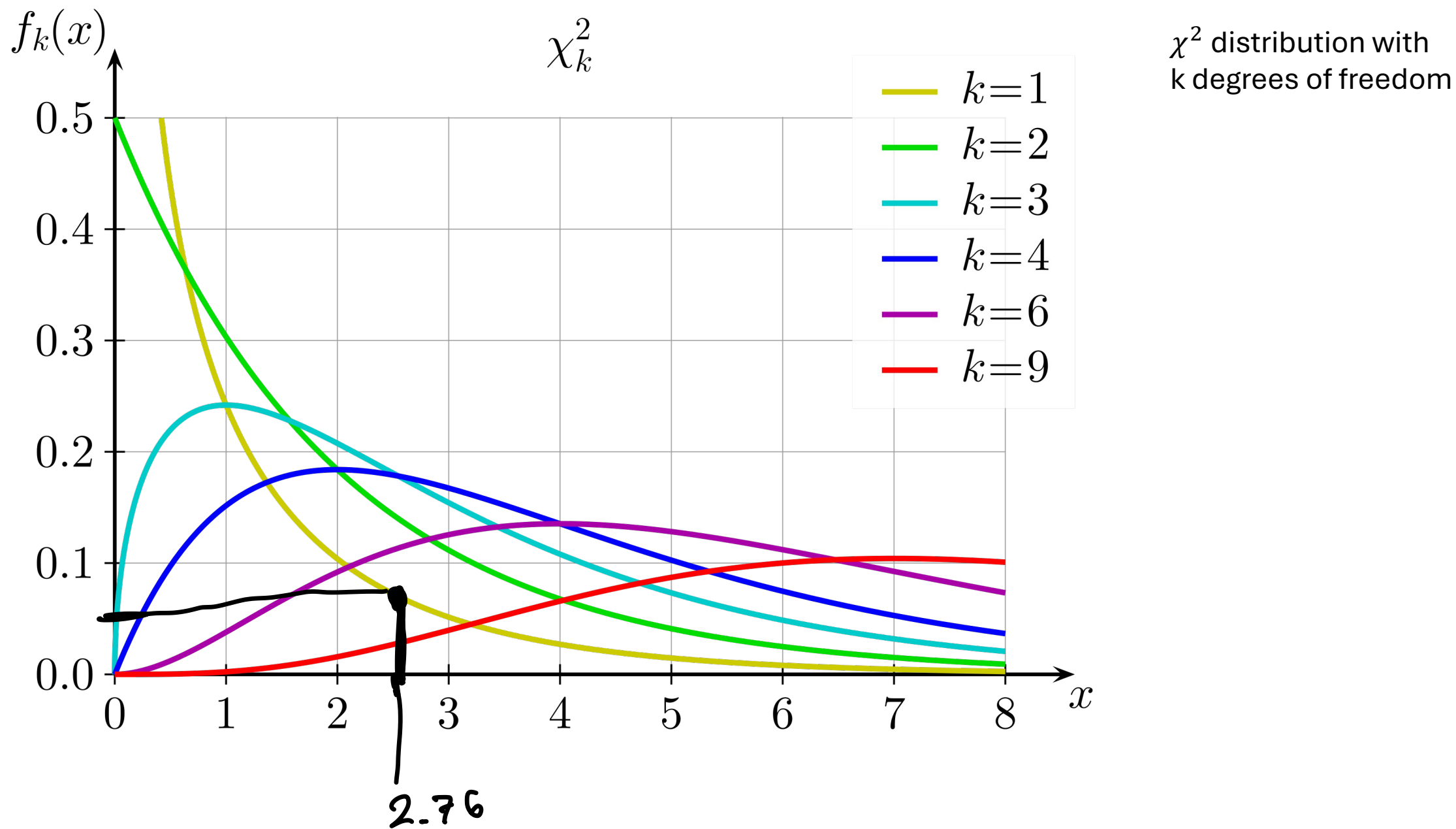
~ Probability  $\chi^2$

degrees of freedom

$$k = (2 - 1) = 1$$

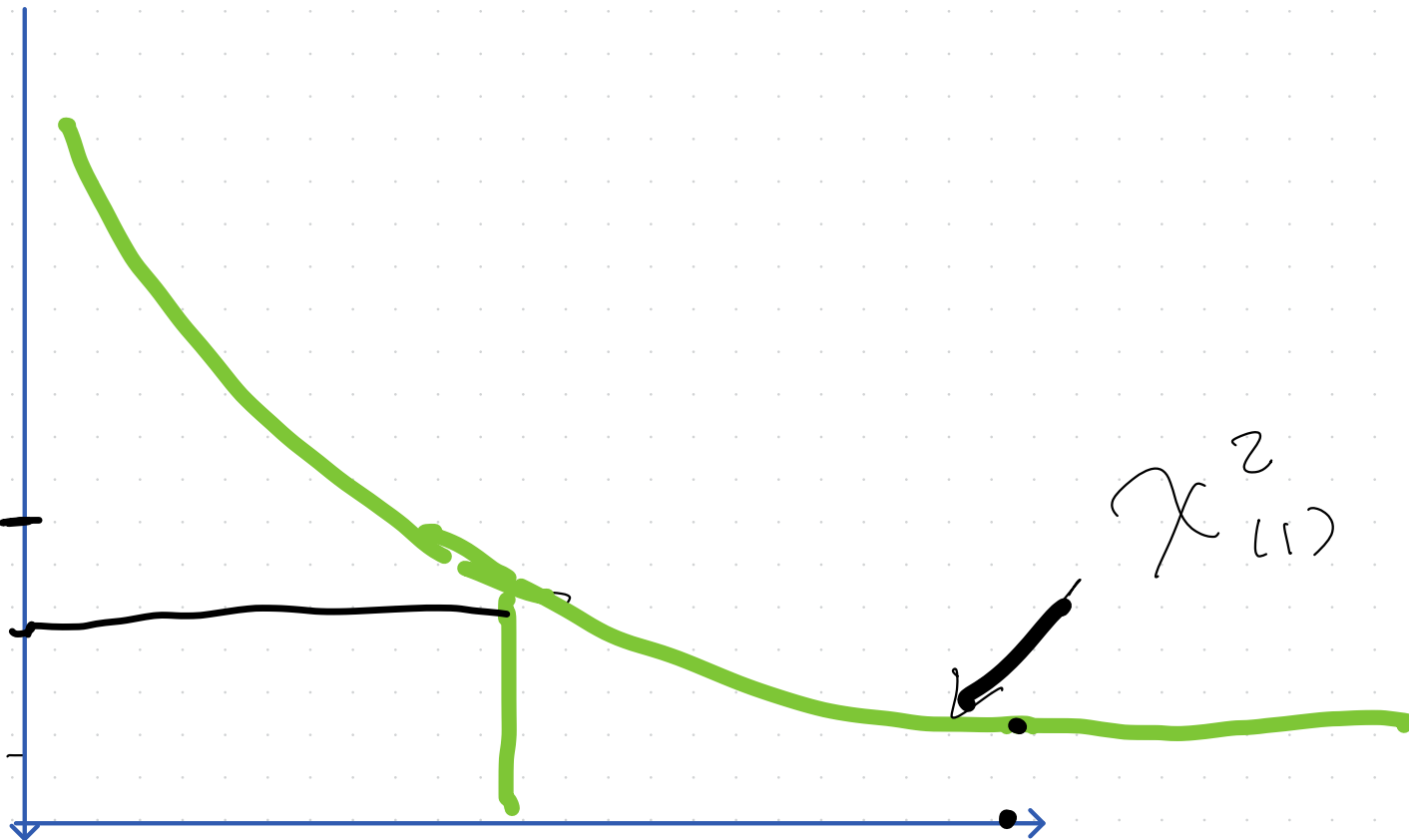
parameters full

parameters reduced



Probability

0.1  
0.05



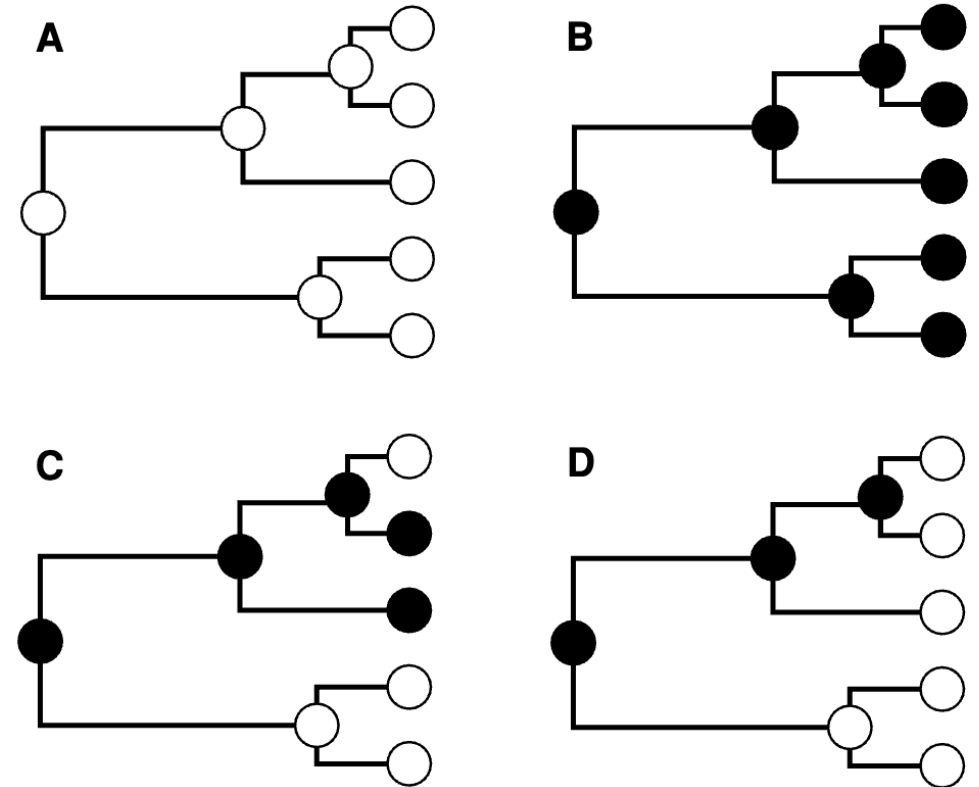
$\chi^2_{(1)}$

LTR = 2.76

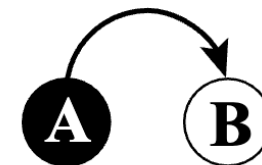
Test statistic value

# Biologically what are we testing?

Dollo's law of irreversibility: An organism never returns exactly to a former state, even if it finds itself placed in conditions of existence identical to those which it has previously lived (Louis Dollo (1893))

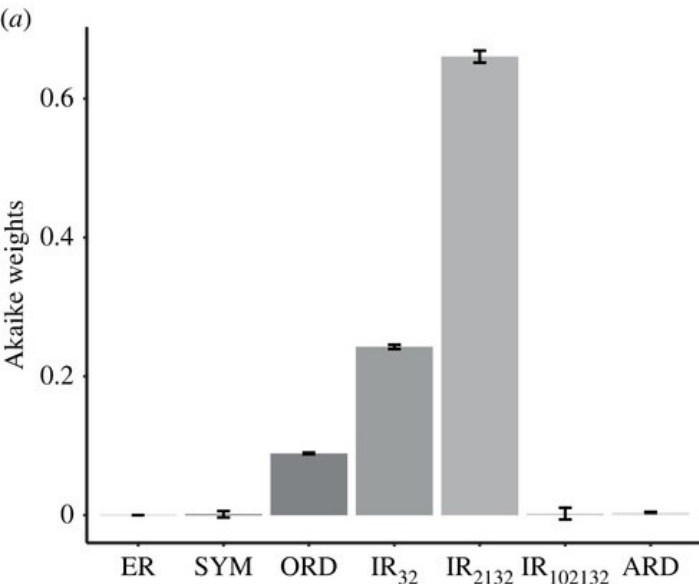


Goldberg and Igić. 2008

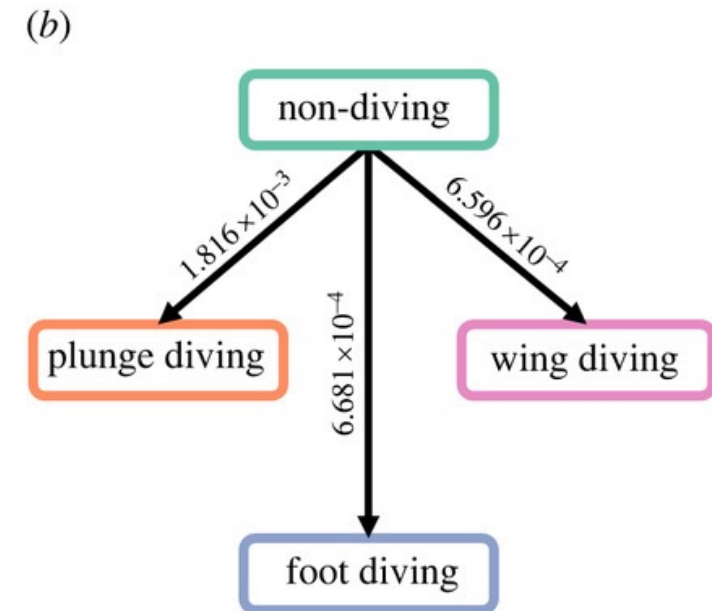
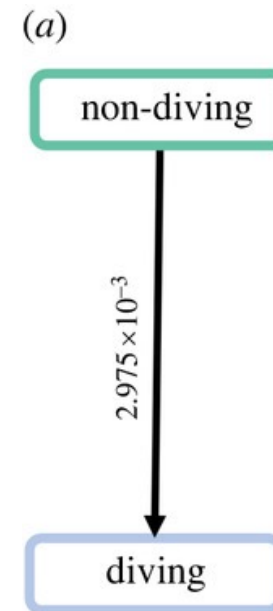
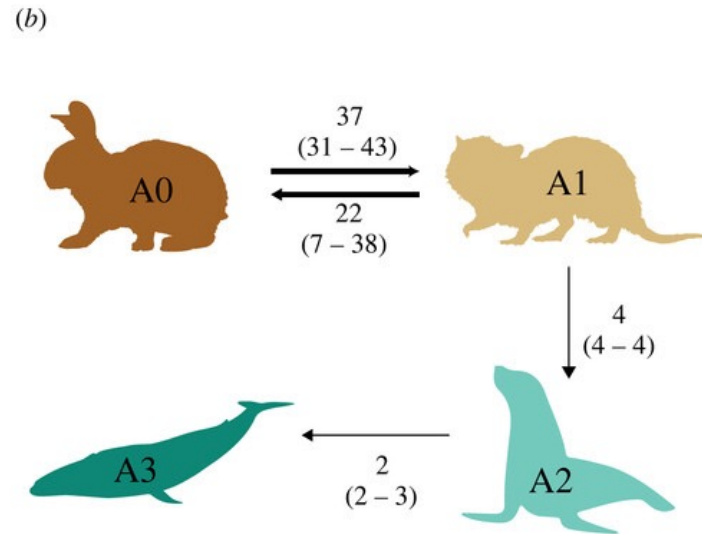


# Biologically what are we testing?

Dollo's law of irreversibility: An organism never returns exactly to a former state, even if it finds itself placed in conditions of existence identical to those which it has previously lived (Louis Dollo (1893))



Secondary adaptation to aquatic environments (Farina and Silvestro, 2023)



Waterbirds diving  
Tyler and Younger, 2022