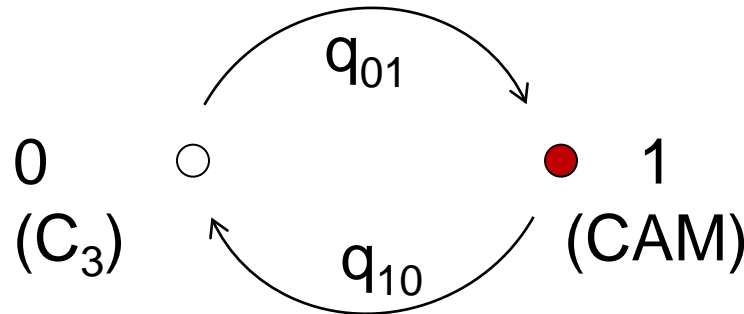


Markov Process for 1 discrete trait

Basic case: a single trait Y , only 2 states: 0, 1.

Markov process: needs

- transition rates q_{01} (gain) and q_{10} (loss)
- probability of each state at the root: π_0, π_1



Similar to evolutionary models for DNA, but only a single 'column' of data.

1. Maximum Likelihood: estimate rates

Choose gain (q_{01}) and loss (q_{10}) rates so as to **maximize the likelihood**:

$P(\text{tip data} \mid \text{rates } q_{01} \ q_{10}, \text{ prior frequency at root})$

Possible **prior frequencies** at the root:

➤ equal: $\pi_0 = \pi_1 = 0.5$

➤ equilibrium: $\pi_0 = q_{10} / (q_{10} + q_{01})$, $\pi_1 = q_{01} / (q_{10} + q_{01})$

Possible constraints on rates:

➤ none

➤ equal: $q_{01} = q_{10}$

➤ fixed value for gain rate. Ex: $q_{01} = 0.1$

2. Maximum Likelihood: ancestral states

Conditioned on the estimated rates, estimate ancestral states using the posterior probabilities:

$P(0 \text{ at node } j \mid \text{tip data, rates } q_{01}, q_{10}, \text{ prior } \pi_0, \pi_1 \text{ at root})$

$P(1 \text{ at node } j \mid \text{tip data, rates } q_{01}, q_{10}, \text{ prior } \pi_0, \pi_1 \text{ at root})$

and plot these as a pie chart.

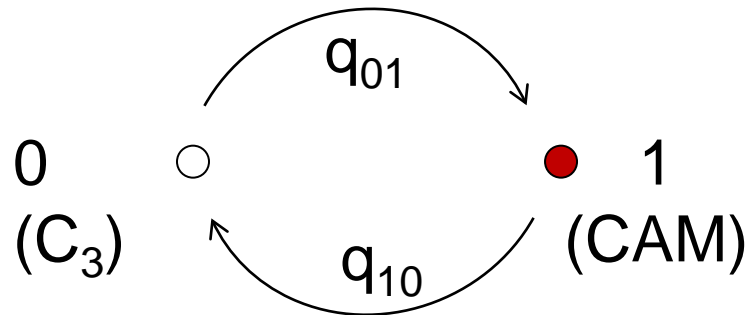
Choices made in Silvera et al.

In Silvera et al. and Mesquite:

“Mk1” = Markov, k-state trait, 1 parameter: $q_{01} = q_{10}$

“Asymmetric Mk” = Markov, 2-state trait, 2 parameters

“bias” = q_{01}/q_{10} . Used the constraint $\text{bias} < 1$ i.e. $q_{01} < q_{10}$



Choices made in Silvera et al.

Continuous data analysis:

“Correlated divergence analysis was performed by constructing a 0-intercept linear regression between divergence in trait 1 ($\delta^{13}\text{C}$) and divergence in trait 2 (epiphytism) [...]. We used **divergence width instead of independent contrasts** as a measure of absolute trait radiation because the SD (divergence width) can be used when polytomies are present in the phylogeny)”

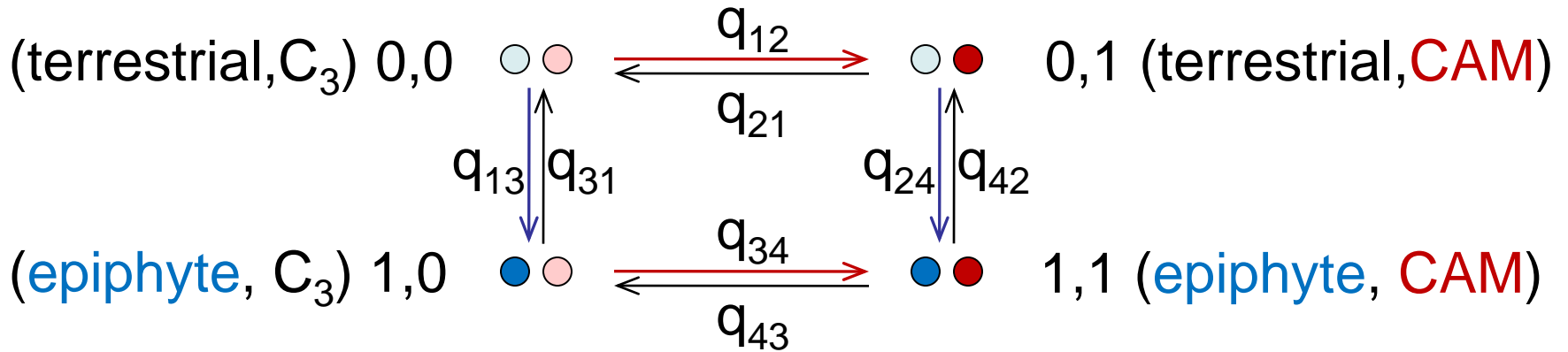
“divergence width” = SD across daughter nodes compared to their parent (Phylocom). For resolved nodes:
divergence ~ absolute value of non-standardized contrast.

Markov Process for 2 discrete traits

Basic case: traits X and Y , 2 states each : 0,1.

Markov process: needs

- transition rates q 's
- probability of each state at the root: π 's



Maximum Likelihood

Same as with 1 trait: get rates (q values) that **maximize the likelihood**:

$P(\text{tip data} \mid \text{rates } q\text{'s, prior frequency at root})$

Possible **prior frequencies** at the root:

➤ equal: $\pi_{00} = \pi_{10} = \pi_{01} = \pi_{11} = 0.25$

➤ equilibrium: $\pi = \text{some function } f(q\text{'s})$

➤ For better accuracy or numeric stability: Fix small value for “first gain” rates. Ex: $q_{12} = q_{13} = 0.1$

Testing correlation with ML

➤ Independent evolution for the 2 traits: parallel arrows have equal rates:

$$q_{12} = q_{34}, \quad q_{21} = q_{43}, \quad q_{13} = q_{24}, \quad q_{31} = q_{42}$$

If any of these equalities does not hold, then correlated evolution.

➤ Likelihood Ratio Test for correlation:

$l_0 = \log L(\text{tip data} \mid \text{independence equalities enforced})$

$l_1 = \log L(\text{tip data} \mid \text{independence equalities NOT enforced})$

Compare $2^*(l_1 - l_0)$ to a chi-square distribution.