Goal: Describe substitutions over time τ. Say V_t is a random variable that models the state of a system over a discrete alphabet Σ with $|\Sigma| = d$.
Find $P^{\tau}_{a,b} = P(V_t + \tau = b | V_t = a)$.
Let $\pi_a = P(V_t = a)$ a background or equilibrium distribution.

Typical assumptions:

- Continuous-time Markov chain, i.e. at each point in time the probability of the next state only depends on the current state but not on the past states
- Stationary: $P_{a,b}$ does not depend on t
- Time reversibility: $\pi_a P^{\tau}_{a,b} = \pi_b P^{\tau}_{b,a}$ for any $\tau > 0$

A model with such assumptions is called *general time-reversible substitution model* (GTRM).

Parameters

Rate matrix $Q \in \mathbb{R}^{d \times d}$ and *equilibrium* $\pi \in [0,1]^d$ with $Q_{i,i} = -\sum_{j \neq i} Q_{i,j}$, $\pi_i Q_{i,j} = \pi_j Q_{j,i}$ and $\sum_i \pi_i = 1$.

Then $P^{\tau} = expm(\tau Q)$.

Jukes-Cantor

$\pi_a = \frac{1}{d}$
$Q_{i,i} = -\frac{d-1}{d}\mu$
$Q_{i,j} = \frac{\mu}{d}$

Then
$P^{\tau}_{i,i} = \frac{1}{d} + \frac{d-1}{d}\exp(-\mu\tau)$
$P^{\tau}_{i,j} = \frac{1}{d} - \frac{1}{d}\exp(-\mu\tau)$

Normalized (1 expected change per unit time) for $\mu = \frac{d}{d-1}$.