



Rate matrix  $Q$

$$P(b, c, d, u | a) = (e^{Qu})_{ad} (e^{Qu})_{db} (e^{Q(t-u)})_{dc} \frac{e^{-u}}{\int_0^t e^{-v} dv}$$

$$= \frac{1}{1 - e^{-t}} e^{-u} (e^{Qu})_{ad} (e^{Qu})_{db} (e^{Q(t-u)})_{dc}$$

$$P(b, c, d | a) = \int_0^t P(b, c, d, u | a) du$$

$$P(b, c | a) = \sum_d P(b, c, d | a)$$

Jules-Cartier rate matrix. Rate  $\mu$  for mutation.

$$e^{Qu} = \frac{1}{4} \cancel{I} + e^{-4\mu u} \left( \frac{1}{4} \begin{pmatrix} 3 & -1 & -1 & -1 \\ -1 & 3 & -1 & -1 \\ -1 & -1 & 3 & -1 \\ -1 & -1 & -1 & 3 \end{pmatrix} \right)$$

$$\frac{\mu}{4} = \frac{\theta}{3}, \text{ i.e. } \mu = \frac{4}{3} \theta$$

$$\begin{pmatrix} -\theta & \frac{\theta}{3} & \frac{\theta}{3} & \frac{\theta}{3} \end{pmatrix}$$

## Terms in the integral

$$e^{-u} \left( \frac{1}{4} + \alpha e^{-u\mu} \right) \left( \frac{1}{4} + \beta e^{-u\mu} \right) \left( \frac{1}{4} + \gamma e^{-(t-u)\mu} \right)$$

where

$$\alpha = \begin{cases} 3/4 & a=d \\ -1/4 & a \neq d \end{cases}$$

$$\beta = \begin{cases} 3/4 & b=d \\ -1/4 & b \neq d \end{cases}$$

$$\gamma = \begin{cases} 3/4 & c=d \\ -1/4 & c \neq d \end{cases}$$

$$= e^{-u} \left( \frac{1}{16} + \frac{1}{4} (\alpha + \beta) e^{-u\mu} + \alpha\beta e^{-2u\mu} \right) \left( \frac{1}{4} + \gamma e^{-(t-u)\mu} \right) =$$

$$\frac{1}{64} e^{-u} +$$

$$\frac{1}{16} \gamma e^{-u} e^{-(t-u)\mu} +$$

$$\frac{1}{16} (\alpha + \beta) e^{-u} e^{-u\mu} +$$

$$\frac{1}{4} (\alpha + \beta) \gamma e^{-u} e^{-u\mu} e^{-(t-u)\mu} +$$

$$\frac{1}{4} \alpha\beta e^{-u} e^{-2u\mu} +$$

$$\alpha\beta\gamma e^{-u} e^{-2u\mu} e^{-(t-u)\mu} =$$

$$\frac{1}{64} e^{-u} + \frac{1}{16} \gamma e^{-t\mu} e^{(\mu-1)u} + \frac{1}{16} (\alpha + \beta) e^{-(1+\mu)u} +$$

$$\frac{1}{4} (\alpha + \beta) \gamma e^{-t\mu} e^{-u} + \frac{1}{4} \alpha\beta e^{-(1+2\mu)u} + \alpha\beta\gamma e^{-t\mu} e^{-(1+\mu)u}$$



All integrals are of the form

$$I(\varepsilon) = \int_0^t e^{-\varepsilon u} du = \int_0^t e^{-\varepsilon u} du$$

$$= \left[ -\frac{1}{\varepsilon} e^{-\varepsilon u} \right]_0^t = \frac{1}{\varepsilon} (1 - e^{-\varepsilon t})$$

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$$\varepsilon=0 : I(t, \varepsilon) = t$$

$$P(b, c, d | a) = \frac{1}{64} I(1) + \frac{1}{16} \gamma e^{-t\mu} I(1-\mu) +$$

$$\frac{1}{16} (\alpha + \mu) I(1+\mu) + \frac{1}{4} (\alpha + \beta) \gamma e^{-t\mu} I(1) +$$

$$\frac{1}{4} \alpha \beta I(1+2\mu) + \alpha \beta \gamma e^{-t\mu} I(1+\mu)$$

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Computation: Give  $t, \mu$ . Fill array  $y^4$

for  $a$  in  $1:4$

$b$

$c$

$d$

$\alpha = \text{ifelse}(a=d, 3/4, -1/4)$

$\beta = d$

$\gamma = c$