## Codon substitution models

the instantaneous rate matrix, Q, is very big: 61 × 61

phenomenological codon models: just a few parameters are needed to cover the 3721 changes between codons!

	to codon below:							
From codon below:	TTT (Phe)	TTC (Phe)	TTA (Leu)	ΠG (Leu)	CTT (Leu)	CTC (Leu)	••••	GGG (Gly)
TTT (Phe)		$\kappa\pi_{\mathrm{TTC}}$	$\omega\pi_{ ext{TTA}}$	$\omega\pi_{\mathrm{TTG}}$	$\omega \kappa \pi_{ ext{TTT}}$	0	···▶	0
TTC (Phe)	$\kappa\pi_{ m TTT}$		$\omega\pi_{ ext{TTA}}$	$\omega\pi_{ ext{TTG}}$	0	$\omega \kappa \pi_{\mathrm{CTC}}$	•••	0
TTA (Leu)	$\omega\pi_{ ext{TTT}}$	$\omega\pi_{\mathrm{TTC}}$			0	0	•••	0
TTG (Leu)	$\omega\pi_{ ext{TTT}}$	$\omega\pi_{\mathrm{TTC}}$	$\kappa\pi_{ ext{TTA}}$		0	0	···▶	0
CTT (Leu)	$\omega\kappa\pi_{\mathrm{TTT}}$	0	0	0		$\kappa\pi_{\mathrm{CTC}}$	••••	0
CTC (Leu)	0	$\omega \kappa \pi_{\mathrm{TTC}}$	0	0	$\kappa\pi_{ m TTT}$		···▶	0
<u>:</u>	<u>:</u>	<u>:</u>	<u>:</u>	<u>:</u>	<u>:</u>	<b>.</b>	******	
GGG (Gly)	0	0	0	0	0	0	0	

<sup>\*</sup> This is equivalent to the codon model of Goldman and Yang (1994). Parameter  $\omega$  is the ratio  $d_N/d_S$ ,  $\kappa$  is the transition/transversion rate ratio, and  $\pi_i$  is the equilibrium frequency of the target codon (i).

## Illuminating the darkness in molecular evolution

