Quantifying selection on coding sequences

1.) selectively constrained:

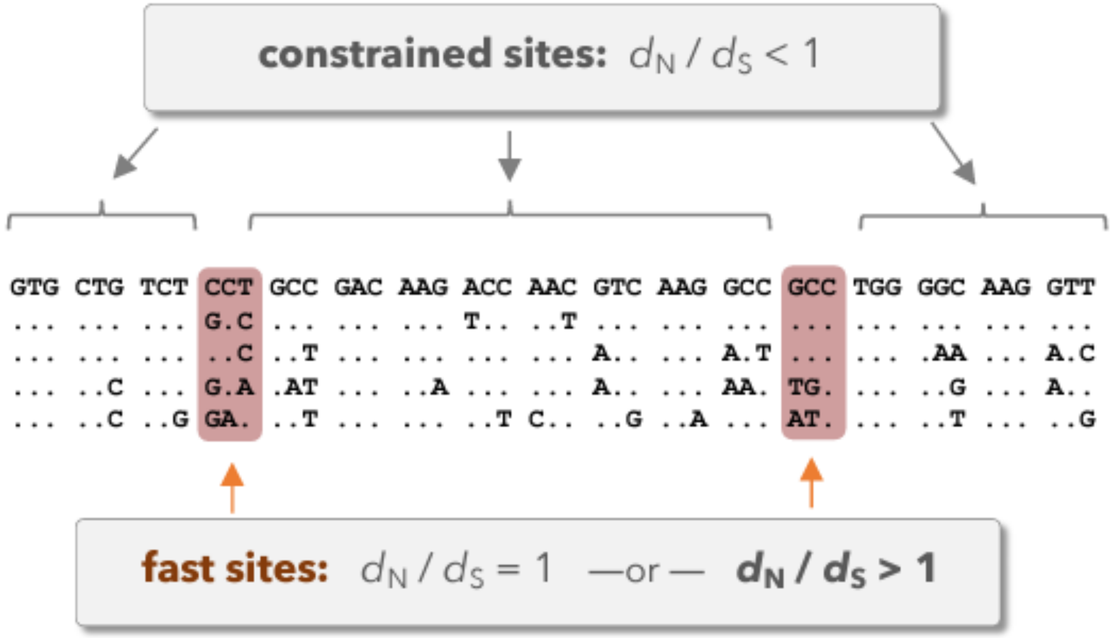
$d_N / d_S < 1$

2.) strictly neutral:

$d_N / d_S = 1$

3.) adaptive evolution:

$d_N / d_S > 1$



Credit: Joe Bielawski

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)**	**TTG (Leu)**	**CTT (Leu)**	**CTC (Leu)**	⋯▸	**GGG (Gly)**
TTT (Phe)	——	$\kappa\pi_{TTC}$	$\omega\pi_{TTA}$	$\omega\pi_{TTG}$	$\omega\kappa\pi_{TTT}$	0	⋯▸	0
TTC (Phe)	$\kappa\pi_{TTT}$	——	$\omega\pi_{TTA}$	$\omega\pi_{TTG}$	0	$\omega\kappa\pi_{CTC}$	⋯▸	0
TTA (Leu)	$\omega\pi_{TTT}$	$\omega\pi_{TTC}$	——		0	0	⋯▸	0
TTG (Leu)	$\omega\pi_{TTT}$	$\omega\pi_{TTC}$	$\kappa\pi_{TTA}$	——	0	0	⋯▸	0
CTT (Leu)	$\omega\kappa\pi_{TTT}$	0	0	0	——	$\kappa\pi_{CTC}$	⋯▸	0
CTC (Leu)	0	$\omega\kappa\pi_{TTC}$	0	0	$\kappa\pi_{TTT}$	——	⋯▸	0
⋮	⋮	⋮	⋮	⋮	⋮	⋮	⋱	
GGG (Gly)	0	0	0	0	0	0	0	——

* This is equivalent to the codon model of Goldman and Yang (1994). Parameter ω is the ratio d_N/d_S, κ is the transition/transversion rate ratio, and π_i is the equilibrium frequency of the target codon (i).