Evolutionary Modes

Positive Selection (Diversifying)	dS < dN or $\omega := dN/dS > 1$
Negative Selection	dS > dN or $\omega < 1$
Neutral Evolution	dS ≃ dN or $\omega ≃ 1$

Codon-substitution models

- In 1994, first tractable mechanistic evolutionary models for codon sequences were proposed by **Muse and Gaut** (MG94), and, independently, by **Goldman and Yang** (GY94) [in the same issue of MBE, back to back]

- Markov models of codon substitution provide a powerful framework for **estimating substitution rates** from coding sequence data, as they

  - *encode our mechanistic understanding of the evolutionary process,*

  - *enable one to compute the phylogenetic likelihood,*

  - *permit hypothesis testing or Bayesian inference,*

  - *systematically account for confounding processes (unequal base frequencies, nucleotide substitution biases, etc.),*

  - *afford many opportunities for extension and refinement (still happening today).*

A likelihood approach for comparing synonymous and nonsynonymous nucleotide substitution rates, with application to the chloroplast genome
S. V. Muse and B. S. Gaut
Mol Biol Evol 11 715-724 (1994)

A codon-based model of nucleotide substitution for protein-coding DNA sequences.
N. Goldman and Z. Yang
Mol Biol Evol 11 725--736 (1994)