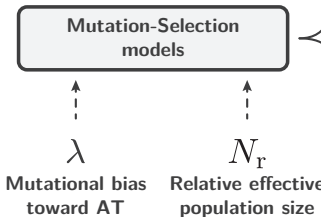
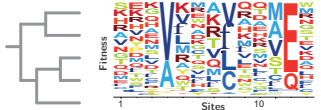


Species tree **Amino-acid site-specific fitness profiles**



Simulations

$\langle 2N_e P_{\text{fix}} \rangle$ is the mean scaled fixation probability of non-synonymous mutations.

$\langle 2N_e P_{\text{fix}}(x \rightarrow y) \rangle$ is between pairs of amino acids.

$\langle 2N_e P_{\text{fix}}(\text{GC} \rightarrow \text{AT}) \rangle$ is from strong to weak nucleotides.

$\langle 2N_e P_{\text{fix}}(\text{AT} \rightarrow \text{GC}) \rangle$ is from weak to strong nucleotides.

ATG|GGA|TCC|ATG|CTA|CGA|TCG
 ATG|CGA|TCC|ATG|GTA|CGA|TCG
 ATG|CGA|TCG|AAG|CTT|CGA|TCC
 ATG|CGA|TAG|AAG|CTT|CGA|TCG
 ATG|CGA|TCG|ATC|CAT|CGA|TCG

Alignment of coding sequence

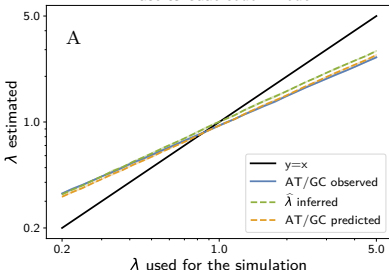
$\langle 2N_e P_{\text{fix}} \rangle$ **Mean-field estimation**

$\hat{\lambda}, \hat{\omega}_{x,y}$ **Mean-field model**

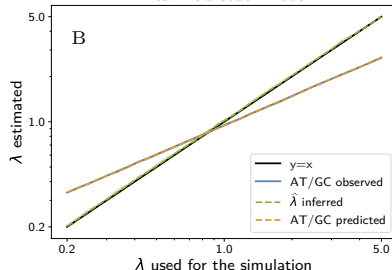
Inference of parameters with maximum likelihood estimators

$\hat{\lambda}, \hat{\omega}$ **Muse & Gaut model**

Muse & Gaut codon model



Mean-field codon model



General time-reversible (GTR) on third positions

