

The patterns of codon usage between chordates and arthropods are different but co-evolving with mutational biases

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1 Abstract

2 Different frequencies amongst codons that encode the same amino acid (i.e. synonymous codons) have
3 been observed in multiple species. Studies focused on uncovering the forces that drive such codon
4 usage bias showed that a combined effect of mutational biases and translational selection works to
5 produce different frequencies of synonymous codons. However, only few have been able to measure
6 and distinguish between these forces that may leave similar traces on the coding regions. Here, we
7 have developed a codon model that allows the disentangling of mutation, selection on amino acids
8 and synonymous codons, and GC-biased gene conversion (gBGC) which we employed on an extensive
9 dataset of 415 chordates and 191 arthropods. We found that chordates need 15 more synonymous
10 codon categories than arthropods to explain the empirical codon frequencies, which suggests that the
11 extent of codon usage can vary greatly between animal phyla. Moreover, methylation at CpG sites
12 seems to partially explain these patterns of codon usage bias in chordates but not in arthropods. Our
13 findings also demonstrate that GC-rich codons are disfavoured in both phyla when mutations are GC-
14 biased, and the opposite is true when mutations are AT-biased. This indicates that selection on the
15 genomic coding regions might act primarily to stabilise its GC/AT content. Our study shows that
16 the degree of synonymous codon usage varies considerably among animals, but is likely governed by a
17 common underlying dynamic.

18 **Keywords:** synonymous codon usage; GC-biased gene conversion; translational selection; mutational
19 bias; evolution; chordates; arthropods; non-model organisms